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Impacts of ocean warming on a reef-building coralline alga *Amphiroa* cf. *fragilissima* under high irradiance

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Coralline algae, an important calcifying group, play vital roles in the primary productivity, reef frameworks construction, and carbon store. In this study, we investigated the responses of an articulated coralline alga *Amphiroa* cf. *fragilissima* to ocean warming under various light intensities. The relative growth rate significantly decreased under light or heat stress. When *A. cf. fragilissima* was exposed to high light intensity (120 μmol photons m^{-2} s^{-1}) at 32°C, the relative growth rate was lowest, which reduced by 87% compared with that of group A1 (60 μmol photons m^{-2} s^{-1}, 26°C). Meanwhile, a higher level of algal bleaching occurred when light intensity was 120 μmol photons m^{-2} s^{-1}. Similarly, Fv/Fm and Chl-*a* content were negatively affected by light and heat stress, but they were more affected by light. Furthermore, the mineralogical responses to temperature and light were investigated. The net calcification rate declined from 92.27 (60 μmol photons m^{-2} s^{-1}, 26°C) to 10.92 μmol $CaCO_3$ g^{-1} DW day^{-1} (120 μmol photons m^{-2} s^{-1}, 32°C). High temperature significantly decreased Ca content in live algal pigmented layer, whereas there were no significant differences in Ca content in the skeleton layer, implying that the pigmented layer could protect skeleton layer from mineral changes under ocean warming. The results revealed that *A. cf. fragilissima* was impaired by high light or thermal stress from various aspects, including growth, survival, photosynthesis, reproduction, and calcification. This study contributes to understand the effects of warming and light on coralline algae and provides a theoretical basis to protect the richness and diversity of calcified macroalgae.

KEYWORDS

coralline algae, *Amphiroa* cf. *fragilissima*, warming, irradiance, growth, calcification, mineralogical composition

Introduction

Annual global temperature has warmed 1.2°C between 1880 and 2020 (NASA/GISS). It is predicted that the global average air temperature will be warmer with an increase of 1.8°C–5.7°C by 2100 (IPCC, 2021). Such high increase in the temperature may bring serious negative threats on several marine calcifiers (Martone et al., 2010; Vásquez-Elizondo and Enríquez, 2016; Sully et al., 2019). Meanwhile, there are pieces of evidence that light availability is another important environmental factor affecting metabolic processes, such as growth, calcification, and photosynthesis of marine calcifiers (Suggett et al., 2013; Williams et al., 2018; Levy et al., 2020). The light intensity varied with depth, weather conditions, and turbidity. Generally, high irradiances and increased temperature occur together. Furthermore, there is a synergistic influence of light stress and heat stress on marine calcifiers (Downs et al., 2013; Rosic et al., 2020). Rosic et al. (2020) have reported that thermal stress under low light intensity induces higher levels of bleaching in coral *Acropora millepora*, which may eventually affect the diversity, abundance, and ecological functions of marine ecosystems. Therefore, there is an urgent need to investigate the responses of marine calcifiers to elevated temperature under various light intensities.

Coralline algae, a predominant calcifying group, are widespread in marine ecosystems from the intertidal zone to the deepest depths recorded for any attached autotroph (Steneck, 1986; Dean et al., 2015). They play important roles in the reef frameworks construction, carbon store, and sulfur cycle (Burdett et al., 2015; Van der Heijden and Kamenos, 2015; Jørgensbye and Halfar, 2017). Particular genera or species of coralline algae even form the massive algal ridges or rim on the high energy windward side. For example, the rhodolith beds were observed in Greeland, which could protect the inner reef and shoreline from wave energy (Jørgensbye and Halfar, 2017). Furthermore, certain species can induce the settlement of coral larvae and keep their surfaces free of opportunistic seaweeds and other epiphytes (Gomez-Lemos and Diaz-Pulido, 2017; Yang et al., 2020). Previous studies have revealed that the distribution, diversity, and ecosystem functions of coralline algae are affected by light availability, temperature, depth, and water motion (McCoy and Kamenos, 2015; Sañé et al., 2016; Sarkar, 2017). However, the study in which light variability modulates the physiological effects of warming on coralline algae has been limited (Comeau et al., 2013; Vásquez-Elizondo and Enríquez, 2016).

There have been 37 articles that investigate the physiological effects of ocean warming on coralline algae (Yang et al., 2021a). The studies have revealed that the algal physiological responses, especially calcification and photosynthesis, to warming are highly variable, including negative (Vásquez-Elizondo and Enríquez, 2016) or positive (Campbell et al., 2016), as well as no significant response (Tanaka et al., 2017; Cornwall et al., 2019). The different responses to increased temperature may be related to species-specific physiologies, geographic regions, treatment time, and algal life-history stages. Rendina et al. (2019) have revealed that calcification of *Corallina officinalis* is enhanced at 5 weeks but decreases at 7 weeks at high temperature, implying that a prolonged exposure to high temperature negatively affects the algal physiology. It is reported that the sensitivity of sporelings of *Porolithon onkodes* to warming is higher than that of adult thalli (Ordoñez et al., 2017; Tanaka et al., 2017). Unfortunately, among these studies, the comprehensive effects of irradiance availability and warming on coralline algae have rarely investigated (Comeau et al., 2013; Vásquez-Elizondo and Enríquez, 2016). Vásquez-Elizondo and Enríquez (2016) have reported that the light-induced photodamage is exacerbated under elevated temperature for *Neogoniolithon* sp., *Amphiroa tribulus*, and *Lithothamnion* sp. Furthermore, to our knowledge, there is currently very little information available on the mineralogical responses of coralline algae to warming under different light intensities.

The genus *Amphiroa* is important coralline algae in many shallow, near-shore exposed and tide-pool environments (Wai, 2018), which may experience different light intensities due to their distribution depth. They can fill the crevices in the reef structure and provide sand to the shore line *via* their calcified structures (Littler and Littler, 2013). Moreover, several species induce larval metamorphoses of *Haliotis asinina* (Williams et al., 2008). In our previous study, the impacts of temperatures on the growth and calcification rates of *A. cf. fragilissima* were investigated within 16 days. The results revealed that these physiological processes were significantly inhibited when the temperature was more than 32°C (Yang et al., 2021b). However, it is unknown about the photosynthesis and mineralogical responses when *A. cf. fragilissima* has prolonged exposure to warming under different light intensities. Here, we address two key questions. First, we investigated the physiological (growth, photosynthesis, chlorophyll, and calcification) and microstructure responses of *A. cf. fragilissima* to three different light intensities during heat stress. Second, we assessed and predicted the mineralogical changes at microscale under a combination of high temperature and light intensity treatments using scanning electron microscopy–energy-dispersive spectrometer (SEM-EDS) and X-ray diffraction (XRD).

Material and methods

Samples collecting and experimental design

Amphiroa cf. fragilissima was collected from coast of Sanya City (18°13′ N, 109°2′ E), Hainan Island in South China in December according to the method of Yang et al. (2021b). The temperature was approximately 26°C in December, whereas the mean monthly temperature was 22°C–30°C at this location (Jiang et al., 2017). The clean algal samples were placed into the filtered natural seawater collected from the sampling site to acclimate the experimental control conditions (60 µmol photons m^{-2} s^{-1}, 26°C, pH 8.05 ± 0.01, 35 psu, 12:12-h cycle from 8:00 to 20:00). The values of Fv/Fm were 0.58 ± 0.02, 0.55 ± 0.02, and 0.57 ± 001 at days 1, 4, and 7, respectively. After day 7, thalli were applied to the experimental manipulation.

The treatments included two temperature levels (ambient control, 26°C; and elevated, 32°C) and three light intensities (60, 80, and 120 µmol photons m^{-2} s^{-1}). In December, 26°C was the ambient temperature, whereas 32°C was 2°C higher than the mean monthly maximum temperature at the sampling site. There were six treatments in total, including A1 (26°C, 60 µmol photons m^{-2} s^{-1}), A2 (26°C, 80 µmol photons m^{-2} s^{-1}), A3 (26°C, 120 µmol photons m^{-2} s^{-1}), A4 (32°C, 60 µmol photons m^{-2} s^{-1}), A5 (32°C, 80 µmol photons m^{-2} s^{-1}), and A6 (32°C, 120 µmol photons m^{-2} s^{-1}). The elevated temperature was reached using one water heater (Aqua One, Glass Aquarium Heater, 100 W) per aquarium. There were three replicate tanks (12-L tank with 9 L of seawater) per treatment, with each tank containing approximately 20–25 g of wet thallus. There were 18 experimental tanks in total. All tanks and thallus were randomly allocated to treatments. During the experiment, all thallus were exposed to same conditions (pH, 8.05 ± 0.01; salinity, 35 psu) with 12:12-h (light:dark) cycle from 8:00 to 20:00 except temperature and irradiance. The filtered natural seawater was gently aerated with submerged pumps at 5 L min^{-1} in each tank and changed twice per week. The experiment ran for 4 weeks. The seawater salinity, pH value, and temperature of each tank were monitored daily with a calibrated handheld YSI meter (YSI, Yellow Springs, OH, USA). The values of salinity, pH, and temperature were listed in Figure S1.

The relative growth rate and photosynthetic efficiency

The relative growth rate (RGR, mg g^{-1} DW day^{-1}) was calculated by the following formula $RGR = \Delta W \times W_{T1}^{-1} \times \Delta T^{-1}$, where ΔW was the variation in wet weight (mg), W_{T1} was initial wet weight (g), and ΔT represented the culture time (28 days).

On day 28, a total of 15 branches of *A. cf. fragilissima* were haphazardly collected from each tank. Five branches were used for each measurement and subjected to dark for 30 min. The ratio of variable (F_v) to maximum (F_m) florescence (F_v/F_m), as an indicator of the maximum quantum efficiency of PSII, was measured by Hansatech FMS-2.

Pigment contents, phycocyanin, allophycocyanin, and phycoerythrin contents

Chlorophyll *a* (Chl-*a*) and carotenoids (Car) were calculated on day 28 (Lichtenthaler, 1987) and expressed as proportion of algal dry weight (mg g^{-1} DW).

Algal samples were subjected to freeze-thaw cycles and ultrasonic crushing on day 28. The contents of phycocyanin (PC), allophycocyanin (APC), and phycoerythrin (PE) were quantified spectrophotometrically in the supernatants at 565, 620, and 650 nm, respectively (Bermejo Roman et al., 2002), and expressed as proportion of algal dry weight (mg g^{-1} DW).

Net calcification rate and mineralogy analyses

The buoyant weighting technique was applied to calculate the net calcification rate ($\mu mol\ CaCO_3 g^{-1} DW\ day^{-1}$), by comparing the buoyant weights at the beginning and end of experiment (Peach et al., 2017). In addition, $CaCO_3$ content (tissue mineral content) was determined at the end of experiment. Briefly, thalli were collected, washed, freeze dried, and weighed on day 28 (W_1). Then, the samples were acidified with 5% HCl, lyophilized, and weighted (W_2). $CaCO_3$ content was calculated on the basis of the difference between W_1 and W_2 and expressed as the percent of algal dry weight.

Powder XRD and SEM-EDS were used to investigate the mineralogical responses of *A. cf. fragilissima* to conditional changes. Briefly, a portion of thalli were cleaned, freeze-dried, ground, and homogenized using a pestle and agate mortar. XRD measurements were performed in an angular range 2θ from 20° to 80° with a step scan of 0.02° using a Rigaku Ultima IV diffractometer with Cu Kα radiation. The tube conditions were 40 kV and 40 mA. Other algal samples were cleaned and dried using a critical point dryer (K850, Quorum technologies Ltd., Laughton, UK). After drying, the relative contents of elements were quantified using SEM (Regulus 8100, Hitachi, Japan)-EDS (Ultim Max 100, Oxford, UK). Meanwhile, the numbers of conceptacles per area on the algal surface were counted and expressed as conceptacles per square millimeter.

Statistical analyses

All statistical analyses were conducted using SPSS statistical software. Data were recorded as the mean ± standard deviation. Differences in the physiological parameters (i.e., RGR, pigment content, and net calcification rate) between different treatments were analyzed by one-way analysis of variance (ANOVA). The two-way ANOVA were performed to investigate the interaction effects between temperatures and light intensity on these physiological parameters in *A. cf. fragilissima*. When there were significant interactions, the Tukey *post hoc* test was used for multiple comparisons. $P< 0.05$ was considered statistically significant, whereas $P< 0.01$ was considered extremely statistically significant.

Results

Effects of increased temperature and light intensity on algal growth rate

The effects of temperature and light intensity on the photosynthesis and relative growth rate were investigated (Figure 1). As shown in Figure 1A, significant negative effects of increased light intensity or temperature on Fv/Fm were observed (F = 85.169, $P = 0.003$; F =31.427, $P = 0.003$, respectively; Table S1) although their interactive effects on Fv/Fm were not significant (F = 3.086, $P = 0.155$). When *A. cf. fragilissima* was exposed to high irradiance with 120 µmol photons m^{-2} s^{-1} (32°C, group A6), the value of Fv/Fm was lowest, which decreased by 56% compared with that of group A1 (26°C, 60 µmol photons m^{-2} s^{-1}). Similarly, heat stress and light stress had both significant negative effects on the relative growth rate in Figure 1B (F = 646.024, $P = 0.002$; F = 394.775, $P = 0.002$, respectively; Table S1). The relative growth rate declined by approximately 50% at 32°C compared with that of 26°C group when the light intensity was 60 µmol photons m^{-2} s^{-1}, although the thallus could grow at 32°C. The shift downward was more marked with the increasing light intensity (F = 1.517, $P = 0.323$; Table S1). When the light intensity was 120 µmol photons m^{-2} s^{-1}, *A. cf. fragilissima* exhibited the lowest growth rate, which decreased from 12.6 (group A1) to 3.7 mg g^{-1} DW day^{-1} (group A6).

Effects of increased seawater temperature and light on algal pigment contents

As shown in Figure 1C, Chl-*a* and carotenoid contents significantly decreased at 32°C (F = 62.818, $P = 0.016$; F =

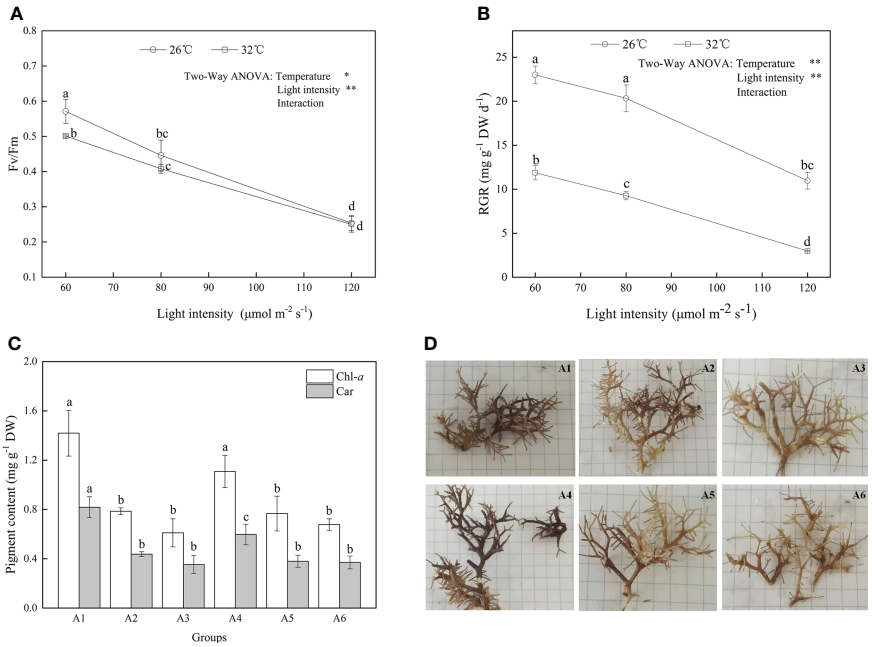

FIGURE 1
The **(A)** Fv/Fm, **(B)** relative growth rate, **(C)** pigment contents, and **(D)** morphological responses of *A cf. fragilissima* to increased temperature and light intensity (A1: 60 µmol photons m^{-2} s^{-1}, 26°C; A2: 80 µmol photons m^{-2} s^{-1}, 26°C; A3: 120 µmol photons m^{-2} s^{-1}, 26°C; A4: 60 µmol photons m^{-2} s^{-1}, 32°C; A5: 80 µmol photons m^{-2} s^{-1}, 32°C; and A6: 120 µmol photons m^{-2} s^{-1}, 32°C). Error bars correspond to the standard deviation with three independent replicates. ^{abcd}, Different letters implied significant differences ($P < 0.05$) for each parameter. *P < 0.05, **P < 0.01.

178.986, P = 0.006, respectively; Table 1). When light intensity increased from 60 to 80 µmol photons m^{-2} s^{-1}, the contents of Chl-*a* and carotenoid were inhibited (Tukey test, P = 0.007 and 0.002, respectively); However, no significant differences were observed in these parameters between groups of 80 and 120 µmol photons m^{-2} s^{-1} (Tukey test, P = 0.283 and 0.423, respectively). Figure 1D showed that the difference in algal morphology was unapparent under low light condition when temperature increased from 26°C to 32°C. However, algal color gradually became white with the increase of light intensity (i.e., bleaching), which was consistent with the variation of Chl-*a* content. The algal morphology was further investigated using SEM. As shown in Figure 2, the number of conceptacles distributed on the algal surface was highest when light intensity was 60 µmol photons m^{-2} s^{-1} (groups A1 and A4; Figure S2). The number of conceptacles gradually decreased with the enhancement of light intensity (F = 265.750, P <0.001; Table S1). Tukey test showed that there were no significant differences between groups of 80 and 120 µmol photons m^{-2} s^{-1} (P = 0.685; Table S1). The conceptacles were hardly observed when light intensity was 120 µmol photons m^{-2} s^{-1} (groups A3 and A6).

Figure 3 showed the contents of PE, PC, and APC among different treatments. Among these, APC content was highest, followed by PE, and PC in all treatments. APC content ranged from 1.93 to 12.70 mg g^{-1} DW. Heat stress significantly decreased APC content compared with 26°C groups (F = 55.503, P = 0.018; Table 1). Similarly, higher light intensity also inhibited APC accumulation (F = 194.722, P< 0.001, Table 1), resulting in a lowest value of 1.9 mg g^{-1} DW. As shown in Table 1, higher temperature and light intensity had both significant effects on PE content (F = 117.4834, P = 0.008; F = 75.488, P = 0.012, respectively); however, their interactive effects were not significant for PE content (P = 0.053; Table 1).

Effects of increased seawater temperature and light on algal calcification

As shown in Figure 4A, the tissue mineral content (i.e., $CaCO_3$ content) accounted for approximately 92% of thallus under different cultivation conditions. Furthermore, it did not exhibit a remarkable change in $CaCO_3$ content among treatments at the end of the experiment (P > 0.05). Figure 4B showed that there were obvious differences in the net calcification rate under heat stress or light stress (F = 14157.644, P < 0.001; F = 626.671, P < 0.001, respectively),

TABLE 1 Statistical analysis of Chl-*a*, Car, PC, APC, and PE of *A. cf. fragilissima* under different conditions.

Variations	Df	MS	F	*P*
Chl-a content (mg g^{-1} DW)				
Tem	1	0.036	62.818	0.016
Lig	2	1.043	71.158	0.007 (60 and 80 = 0.007; 60 and 120 = 0.003; 80 and 120 = 0.283)
Tem* Lig	2	0.057	1.701	0.292
Car content (mg g^{-1} DW)				
Tem	1	0.034	178.986	0.006
Lig	2	0.221	80.726	<0.001 (60 and 80 = 0.002; 60 and 120 = 0.001; 80 and 120 = 0.423)
Tem* Lig	2	0.022	4.009	0.111
PC content (mg g^{-1} DW)				
Tem	1	20.354	17.233	0.053
Lig	2	133.734	24.301	0.038 (60 and 80 = 0.011; 60 and 120 = 0.006; 80 and 120 = 0.659)
Tem* Lig	2	58.631	8.484	0.100
APC content (mg g^{-1} DW)				
Tem	1	56.728	55.503	0.018
Lig	2	96.934	194.722	<0.001 (60 and 80 = 0.005; 60 and 120 = <0.001; 80 and 120 = 0.009)
Tem* Lig	2	3.248	3.076	0.155
PE content (mg g^{-1} DW)				
Tem	1	11.478	117.4834	0.008
Lig	2	31.750	75.488	0.012 (60 and 80 = 0.004; 60 and 120 = <0.001; 80 and 120 = 0.008)
Tem* Lig	2	2.126	8.965	0.053

Df, degrees of freedom; MS, mean square; F, F-ratio; Tem, temperature; Lig, light intensity; 120, 120 µmol photons m^{-2} s^{-1}; 80, 80 µmol photons m^{-2} s^{-1}; 60, 60 µmol photons m^{-2} s^{-1}.
*for the interactive effects between light intensity and temperature.

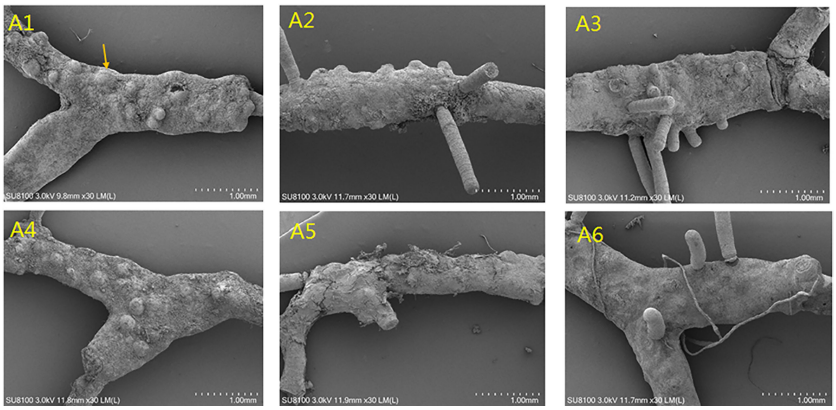

FIGURE 2
The effects of temperature and light intensity on algal surface by SEM (A1: 60 µmol photons m^{-2} s^{-1}, 26°C; A2: 80 µmol photons m^{-2} s^{-1}, 26°C; A3: 120 µmol photons m^{-2} s^{-1}, 26°C; A4: 60 µmol photons m^{-2} s^{-1}, 32°C; A5: 80 µmol photons m^{-2} s^{-1}, 32°C; and A6: 120 µmol photons m^{-2} s^{-1}, 32°C).

whereas the interaction effects between light and temperature were not significant on the net calcification rate (F = 2.472, P = 0.200; Table S1). Compared with 60 µmol photons m^{-2} s^{-1}, the net calcification rate did not significantly vary at 80 µmol photons m^{-2} s^{-1} (P = 0.203 and 0.095, respectively) but declined at 120 µmol photons m^{-2} s^{-1} (P = 0.003 and 0.002, respectively; Figure 4B). Furthermore, when seawater temperature was 32°C, the net calcification rate reached to the lowest value (10.92 $\mu mol\ CaCO_3 g^{-1} DW\ day^{-1}$; Figure 4B).

The mineral compositions were further investigated using XRD. Figure 5 showed a series of well-resolved diffraction peaks of the samples, including (104), (110), (113), (202), (018), and (116), which were in agreement with the power peaks obtained from the International Centre of Diffraction Data card (JCPDS card no. 05–0586.11). The result revealed that *A. cf. fragilissima* was mainly composed of carbonate calcite minerals. In addition, there was a higher calcite phase in group A1. However, there were no obvious differences in crystalline phase among groups.

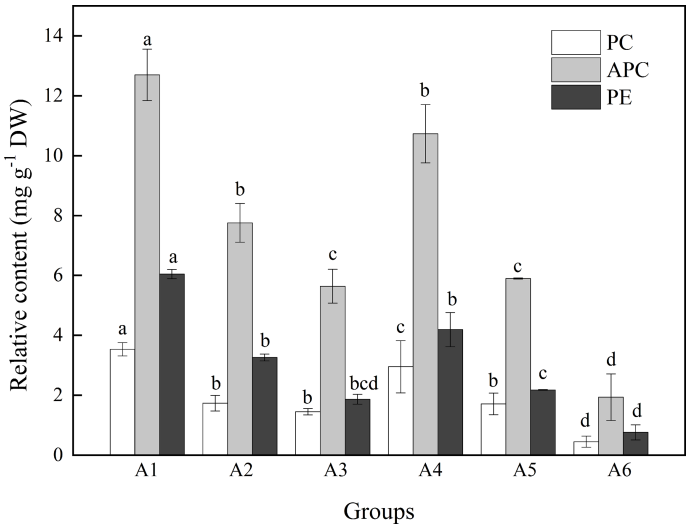

FIGURE 3
The contents (%) of PC, APC, and PE when *A. cf. fragilissima* was exposed to different conditions over 4 weeks (A1: 60 µmol photons m^{-2} s^{-1}, 26°C; A2: 80 µmol photons m^{-2} s^{-1}, 26°C; A3: 120 µmol photons m^{-2} s^{-1}, 26°C; A4: 60 µmol photons m^{-2} s^{-1}, 32°C; A5: 80 µmol photons m^{-2} s^{-1}, 32°C; and A6: 120 µmol photons m^{-2} s^{-1}, 32°C). Error bars correspond to the standard deviation with three independent replicates. ^{abcd}, Different letters implied significant differences ($P <$ 0.05) for each parameter.

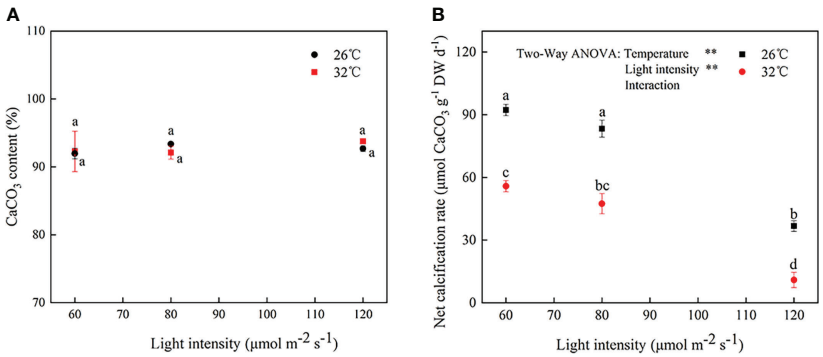

FIGURE 4
The **(A)** $CaCO_3$ content and **(B)** net calcification rate in *A cf. fragilissima* after 4-week cultivation period under different conditions. Error bars correspond to the standard deviation with three independent replicates. ^{abcd}, Different letters implied significant differences ($P < 0.05$) for each parameter. **P < 0.01.

SEM-EDS was applied to observe the algal morphology and elemental compositions. As shown in Figures 6 and 7, *A. cf. fragilissima* typically had calcite cell lining and cell infill. The mineral was mostly calcite in the form of $CaCO_3$. The top surface view showed that cell facets of a relatively regular geometry and epibionts (such as diatoms) attached on the algal surface (Figure 6A). As shown in Figure 6B, the elemental compositions included C, O, Na, Mg, Al, P, S, and Ca. Ca content of pink surficial crust (pigmented layer) on the original thalli varied between 10.52% and 21.24%, which was significantly influenced by temperature (F = 11.484, $P = 0.043$), but it was not affected by light intensity (F = 5.781, $P = 0.072$; Table 2). Similarly, the unpigmented skeleton layer of thallus was mostly consisted of Ca-calcite (Figure 7). The content of Ca ranged from 15.19% to 22.96%. By statistical analysis, the Ca content of the skeleton layer was not significantly affected by temperature and light intensity ($P = 0.268$ and 0.054, respectively). In addition, low levels of magnesium calcite were observed in all groups, which were not affected by temperature or light intensity.

Discussion

Coralline algae, marine calcifying macroalgae, are major contributors to primary productivity, $CaCO_3$ sediment, and

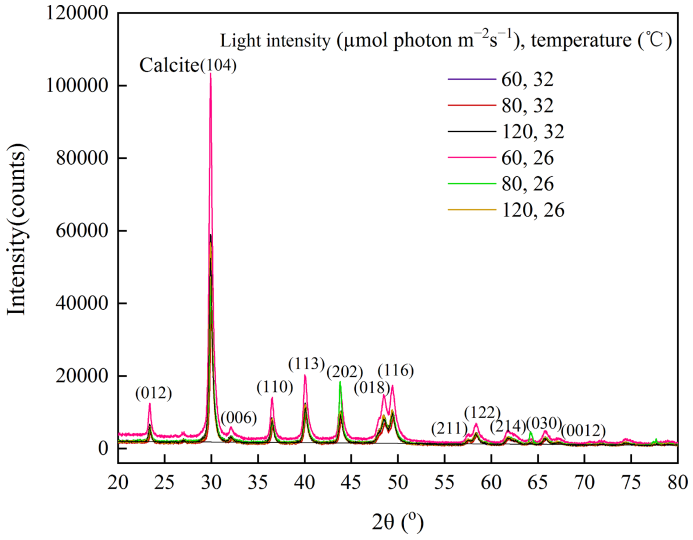

FIGURE 5
Mineral changes in *A. cf. fragilissima* exposed to different culture conditions using XRD.

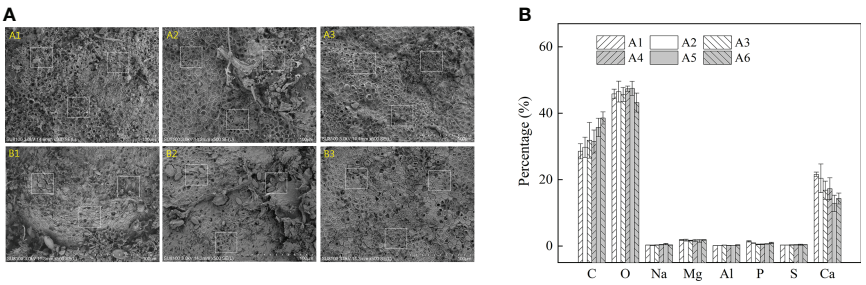

FIGURE 6
The **(A)** SEM pictures and **(B)** relative abundance (%) of main elements in the pink surficial crust/pigmented layer across temperature and light treatments for *A cf. fragilissima* (A1: 60 µmol photons m^{-2} s^{-1}, 26°C; A2: 80 µmol photons m^{-2} s^{-1}, 26°C; A3: 120 µmol photons m^{-2} s^{-1}, 26°C; A4: 60 µmol photons m^{-2} s^{-1}, 32°C; A5: 80 µmol photons m^{-2} s^{-1}, 32°C; and A6: 120 µmol photons m^{-2} s^{-1}, 32°C). Error bars correspond to the standard deviation with three independent replicates.

reef cementation (Nelson, 2009; Littler and Littler, 2013; Teichert et al., 2020). They are widely distributed from the tropics to polar latitudes and from intertidal zone to deeper water levels (Nelson, 2009; Schubert et al., 2020). Temperature and irradiance are considered as important factors that affect the algal physiology, growth, survival, abundance, and geographical distribution (Nejrup et al., 2013; Guy-Haim et al., 2016). For each algal species, generally, there is an optimal temperature and light range (Singh and Singh, 2015; Celis-Plá et al., 2020; Schmid et al., 2021). To date, the effects of temperature on coralline algae have been well investigated (Wilson et al., 2004; Diaz-Pulido et al., 2014; Ordoñez et al., 2017; Bach et al., 2017; Chan et al., 2020). However, the interaction effects between temperature and light on coralline algae remain unclear. Cornwall et al. (2022) have reported that coralline algae were more affected by light intensity compared with temperature. In our study, for *A. cf. fragilissima*, the optimal temperature and light intensity for calcification was 26°C–28°C (Yang et al., 2021b) and 60 µmol photons m^{-2} s^{-1}, respectively. Furthermore, *A. cf. fragilissima* was more susceptible to high light stress than heat stress within 32°C, which was in agreement with previous studies (Yoshioka et al., 2020; Cornwall et al., 2022). Interestingly, increased light intensity and temperature resulted in the decrease of conceptacle numbers and the increase of algal bleaching in our study. Prathep et al. (2018) have observed that *Halimeda* become whiter when exposed to more than 1,200 µmol photons m^{-2} s^{-1} for mid-day hours in the field, which may contribute to protect algae from light stress. Similar phenomenon was observed in another study, in which *C. officinalis* exhibited relatively high bleaching at light stress (Kim et al., 2013). *A. cf. fragilissima* is generally found under fleshy brown or green macroalgae, which can protect it from strong sunshine; thus, it

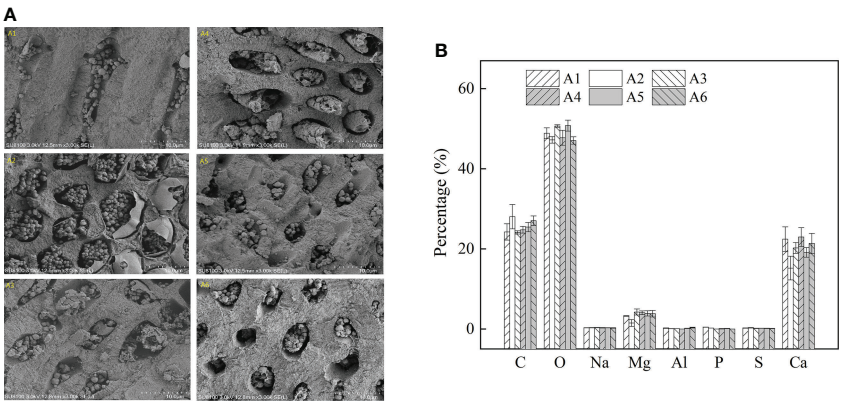

FIGURE 7
The **(A)** SEM pictures and **(B)** relative abundance (%) of main elements in the unpigmented skeletal layer under different temperature and light by SEM-EDS (A1: 60 µmol photons m^{-2} s^{-1}, 26°C; A2: 80 µmol photons m^{-2} s^{-1}, 26°C; A3: 120 µmol photons m^{-2} s^{-1}, 26°C; A4: 60 µmol photons m^{-2} s^{-1}, 32°C; A5: 80 µmol photons m^{-2} s^{-1}, 32°C; and A6: 120 µmol photons m^{-2} s^{-1}, 32°C). Error bars correspond to the standard deviation with three independent replicates.

TABLE 2 Statistical analysis of main elemental compositions under different conditions.

Variations	Df			MS			F			*P*		
	Tem	Lig	Tem* Lig	Tem	Lig	Tem* Lig	Tem	Lig	Tem* Lig	Tem	Lig	Tem* Lig
Pigmented layer												
Mg	1	2	2	0.042	0.017	0.125	1.433	0.119	3.600	0.317	0.890	0.094
Ca	1	2	2	164.798	55.540	21.455	11.484	5.781	2.171	0.043	0.072	0.195
O	1	2	2	0.005	15.242	9.386	$4.920e^{-4}$	4.807	2.149	0.984	0.057	0.198
Na	1	2	2	0.140	0.021	0.126	7.342	1.616	8.518	0.073	0.274	0.055
Al	1	2	2	0.003	0.088	$9.5e^{-4}$	1.038	32.274	0.260	0.383	0.005	0.779
C	1	2	2	163.282	53.781	8.045	14.544	4.468	1.806	0.032	0.065	0.243
Skeleton layer												
Mg	1	2	2	3.939	2.761	3.705	17.159	5.691	7.922	0.054	0.068	0.057
Ca	1	2	2	8.174	51.186	1.360	2.311	10.447	0.160	0.268	0.054	0.857
O	1	2	2	0.696	1.524	31.727	0.156	7.892	17.697	0.731	0.103	0.033
Na	1	2	2	0.009	1.389^{-5}	0.005	240.143	0.063	3.294	0.004	0.940	0.143
Al	1	2	2	0.001	0.033	0.139	0.510	15.430	45.165	0.549	0.035	0.019
C	1	2	2	41.678	112.469	117.44	40.090	11.524	10.022	0.024	0.071	0.087

Df, degrees of freedom; MS, mean square; F, F-ratio; Tem, temperature; Lig, light intensity.
*for the interactive effects between light intensity and temperature.

may be a low-light–adapted species. The enhancements in light or temperature that exceeded the physiological tolerance are likely to have strong influences for populations of *A. cf. fragilissima*.

The chlorophyll fluorescence parameter, Fv/Fm, is vital useful parameter to evaluate the eco-physiological responses to variations of environmental conditions. Huner et al. (2013) have reported that photoinhibition and photodamage occur when algae are exposed to high light intensity. Increasing temperature inhibited the net photosynthetic rate of *Porolithon cf. onkodes* (Page et al., 2021). In this study, Fv/Fm significantly decreased under thermal stress although the alga could survive within 4 weeks. The results combined with our previous data (Yang et al., 2021b), implying that *A. cf. fragilissima* could acclimate to thermal variation in short term by increasing antioxidant production; however, in the long-term exposure to environmental changes, this alga was seriously damaged and even bleached. In addition, Fv/Fm was significantly reduced at higher light intensity, revealing that the algal physiological responses to warming could be related to the degree of shade or sun stress experienced during their life history and depending on locality. Pigment is one of vital indicators of the stress conditions. In this study, *A. cf. fragilissima* exhibited a significant decrease in Chl-*a* content when light intensity was more than 80 µmol photons m^{-2} s^{-1}, which coincided with the variation of Fv/Fm. Perhaps, the light level with 80 µmol photons m^{-2} s^{-1} was higher than saturating irradiance in *A. cf. fragilissima*. Similar phenomenon was documented in the previous literatures (Fortes and Lüning, 1980; Esteban et al., 2015). Fortes and Lüning (1980) have revealed that pigment contents of *Saccharina latissima*, *Ulva lactuca*, *Porphyra umbilicalis*, and *Chondrus crispus* significantly vary when exposed to light stress ranging from 30 to 70 µmol photons m^{-2} s^{-1}. Similarly, Esteban et al. (2015) have reported that there are significant changes in Chl-*a* and PE levels when light intensities are between 30 and 60 µmol photons m^{-2} s^{-1}. Our study demonstrated that Fv/Fm is a suitable parameter to evaluate the algal acclimation to environment stress.

Calcification is an important physiological process for calcified algae. Several studies have shown that calcification is a light-stimulated metabolic process (EI Haïkali et al., 2004; Guy-Haim et al., 2016), which can be influenced by light (Teichert and Freiwald, 2014). For example, *Halimeda macroloba* exhibited a significant decrease in the calcification rate when exposed to high light level of 1,200 µmol photons m^{-2} s^{-1} or low light level of 50 µmol photons m^{-2} s^{-1} (Prathep et al., 2018). Decalcification was even observed when algae were exposed to darkness or heat stresses (Kim et al., 2013). However, Williams et al. (2018) have thought that calcification process is metabolically driven because *Clathromorphum compactum* can calcify in complete darkness for 2 months. In our study, high light intensity significantly suppressed the net calcification rate of *A. cf. fragilissima*. However, the relationship between calcification process and light needs further research. In addition, Cornwall et al. (2019) have assessed the effects of warming on coralline algal calcification based on previous reports. They have found that there is a net negative impact of

warming on algal calcification when temperature was 5.2°C higher than ambient condition. Similarly, in this present study, a negative impact was observed when temperature increased by 6°C. The data implied that *A. cf. fragilissima* could decrease the carbon fixation as a trade-off to living under light stress or heat stress.

The carbonate mineralogy of coralline algae is mainly composed of calcite, aragonite, and dolomite. Diaz-Pulido et al. (2014) have shown that ocean warming and acidification can induce the mineralogical changes, resulting in the enhancement of magnesium content and dolomite in *P. onkodes*, which may threat the structural integrity of reef ecosystems. However, mineralogical responses to high temperature and light intensity are unclear in coralline algae. Our study revealed that *A. cf. fragilissima* was mainly composed of carbonate calcite minerals, which was similar to the feature that documented previously in several coralline algae (Ries, 2010; Diaz-Pulido et al., 2014). In addition, increased temperature significantly decreased Ca content in algal pigmented layer; however, Ca content of the skeleton layer was not significantly affected by temperature and light intensity. Previous studies have suggested that the live, pigmented tissue layers have a vital role in modulating the mineralogical responses of coralline algae to environmental changes (Ries, 2006; Diaz-Pulido et al., 2014). Therefore, we speculated that the pigmented layer could limit mineralogical shifts of skeleton layer when exposed to short-term warming and cannot compensate for temperature influence.

Conclusions

This study showed that both high temperature and light intensity caused substantial changes in the physiological process of *A. cf. fragilissima* including major reductions in photosynthetic pigment, photosynthetic efficiency, conceptacle number, and growth. Furthermore, these physiological parameters were more strongly regulated by light. The lowest relative growth rate and algal bleaching were observed at light intensity of 120 μmol photons m^{-2} s^{-1}. Meanwhile, after 4 weeks of exposure to high temperature, net calcification rate and Ca content in the pigment layer were inhibited, indicating that warming and irradiance will not only affect the growth, reproduction, and photosynthesis but also likely affect the calcification process. Our data also indicate the live pigmented layer may protect skeleton layer from mineral changes under short-term warming.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

FY conceived and designed the experiments. FY preformed the experiments and wrote the paper. ZW analyzed the data. LL and FY revised the paper, and performed final approval. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.922478/full#supplementary-material

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