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Response of coralline algae *Porolithon onkodes* to elevated seawater temperature and reduced pH

Xinming Lei[1, 2], Lei Jiang[1, 2], Yuyang Zhang[1, 2], Guowei Zhou[1, 3], Jiansheng Lian[1, 2], Hui Huang[1, 2, 3]*

[1] CAS Key Laboratory of Tropical Marine Bio-resources and Ecology, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou 510301, China

[2] Innovation Academy of South China Sea Ecology and Environmental Engineering, Chinese Academy of Sciences, Guangzhou 510301, China

[3] CAS Tropical Marine Biological Research Station in Hainan, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Sanya 572000, China

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Abstract

Coralline algae (CA), a type of primary calcifying producer presented in coastal ecosystems, are considered one of the highly sensitive organisms to marine environmental change. However, experimental studies on coralline algae responses to elevated seawater temperature and reduced pH have documented either contradictory or opposite results. In this study, we analysed the growth and physiological responses of coralline algae *Porolithon onkodes* to the elevated temperature (30.8°C) and reduced pH (7.8). The aim of this analysis was to observe the direct and combined effects, while elucidating the growth and photosynthesis in this response. It was demonstrated that the algae thallus growth rate and photosynthesis under elevated temperature were depressed by 21.5% and 14.9% respectively. High $p\mathrm{CO}_2$ enhanced the growth and photosynthesis of the thallus at ambient temperature, while they were deceased when both temperature and $p\mathrm{CO}_2$ were elevated. CA is among the most sensitive organisms to ocean acidification (OA) because of their precipitate high Mg-calcite. We hypothesize that coralline algae could increase their calcification rate in order to counteract the effects of moderate acidification, but offset by the effect of elevated temperature. Accordingly, our results also support the conclusion that global warming (GW) is a stronger threat to algal performance than OA. Our findings are also proposed that coralline algae may be more resilient under OA than GW.

Key words: crustose coralline algae, response, elevated temperature, reduced pH, effects

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1 Introduction

It has been predicted that sea surface temperature will increase by (2.73±0.72)°C and pH will decline by 0.33±0.003 units in the ocean surface by the end of the 21st century due to the increasing human-induced changes, such as the rising atmospheric CO_2 (Bopp et al., 2013). An increasing number of studies predict that seawater acidification and warming will be the two main threats affecting marine species by the end of the century (Kroeker et al., 2013). Consequently, ocean acidification (OA) and global warming (GW) had received much scientific attention owing to significant influences on calcifying organisms (Riebesell et al., 2000; Anthony et al., 2008; Hofmann et al., 2010; Kroeker et al., 2013; Vásquez-Elizondo and Enríquez, 2016; Legrand et al., 2017).

CA is an important functional group in the marine ecosystem, playing as primary producers (Littler, 1973; Chisholm, 2003) and a key role in the reef framework development (Perry and Hepbum, 2008). They also provide habitats for a large variety of organisms (Foster, 2001; Steller et al., 2003; Nelson, 2009), and crustose coralline algae (CCA) serve as a settlement substrate for the coral larvae (Heyward and Negri, 1999; Perry and Hepbum, 2008). CA are also known to be among the most vulnerable species to ocean acidification (McCoy and Kamenos, 2015), due to their highly soluble Mg-calcite skeleton (Morse et al., 2006; Nash et al., 2015). CA species, especially *Porolithon onkodes*, can have dolomite infilling cell spaces which enhance their stability (Nash et al., 2015). Given the ecological significance of CA, the adverse impact of global change on this population will make a large variety of ecosystem processes in an unpredictable situation (Hoegh-Guldberg et al., 2007; Diaz-Pulido et al., 2012; Johnson and Carpenter, 2012).

Numerous studies concerning the responses of CA to OA and GW have yielded contradictory results. Some studies have reported that OA decreases calcification and photosynthesis rates (Anthony et al., 2008; Semesi et al., 2009; Gao and Zheng, 2010; Martin et al., 2013) and growth (Hofmann et al., 2012; Ragazzola et al., 2012), while others have not observed a clear effect of OA on algal metabolism (Martin and Gattuso, 2009; Egilsdottir et al.,

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*Corresponding author, E-mail: huanghui@scsio.ac.cn

2013; Noisette et al., 2013; Comeau et al., 2014). Investigations of the effects of thermal stress resulted in either no effect (Martin and Gattuso, 2009; Martin et al., 2013; Comeau et al., 2014) or significant decreases in photosynthesis and calcification (Anthony et al., 2008). Several authors have also concluded that thermal stress deteriorated the adverse effect of OA on CA calcification (Martin and Gattuso, 2009; Martin et al., 2013). These contradictory findings have been interpreted as consequences of coralline sensitivity to global environmental change.

Although results from the interaction of different stressors on CA become more and more, information on single or combined effects of increased temperature and acidification could improve our understanding on their current and near future responses to climate change. According to these contradictory findings above, we experimentally investigated the growth and photosynthesis responses of CA *P. onkodes* to reduced pH and elevated temperature by analyzing the direct and combined effects of OA and thermal stress. The aim of this research was to evaluate the actual interactive effects of a two-month moderate OA and ET on physiological aspects of *P. onkodes*, and whether there is a trade-off between the interactive effects of thermal and $p\mathrm{CO}_2$.

2 Materials and methods

2.1 *Species collection*

The CCA species, *P. onkodes* were collected with a hammer and a chisel as experimental organisms by SCUBA diving at a depth of 3–4 m within the coral community of Luhuitou fringing reef (18°13′N, 109°28′E) (Fig. 1a), Hainan Island in May 2016. The species grew in the intertidal zone of the reef with a red-pink color, and being the predominant encrusting species on tropical reefs (Nash et al., 2015). The characters of this species are: growing on rock and encrusting to slightly warty with flat uniporate conceptacles, and its tetrasporangial conceptacle often flush with thallus surface (Fig. 1b). Also, this species is one of the dominant species in this fringing reef (Lei et al., 2018).

When fragments of live *P. onkodes* were collected underwater carefully, they were put in a clear plastic sealing bag with seawater meanwhile. After that, the organisms were transported to the aquaria in the laboratory within half an hour. The aquaria were kept in ambient pH (~8.0) and *in situ* temperature (29°C) conditions with open-flow seawater. The illumination stayed on a 12 h: 12 h light-dark cycle and the irradiance was about 200 μmol photons $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$, to ensure the light condition of each tank the same as the sampling location. Prior to the experiment, approximately 1–2 cm^2 chips of the *P. onkodes* were cleaned off epiphytes and acclimated for at least one week in order to mitigate the stress experienced by the species during sampling and transport. All the preparations were completed in CAS Tropical Marine Biological Research Station in the Hainan Island.

2.2 *Experimental set-up*

All the experimental treatments were maintained in flow-through aquaria. Every experiment was performed in 70-L tanks supplied with open-flow sand-filtered seawater. The average flow rate in the experimental tanks was 0.7 L/min with a turnover rate of about 100 min.

After an initial pre-acclimation period, organisms (five fragments in each tank) were exposed for 60 d to four treatments. At the beginning of the experiment, samples were randomly distributed in the tanks. Each of the CCA experimental treatment was placed in independent tanks. Two replicate tanks were assigned to each treatment. The elevated temperature and reduced pH were designed according to projected conditions in the northern South China Sea by the 2100s (Gattuso et al., 2015). The four experimental treatments were as the following:

(1) Control treatment (Control): 29.0°C at sampling time (mean seawater temperature from May to September of the Luhuitou fringing reef) and ambient pH (~8.0);

(2) Elevated temperature treatment (ET): 31°C (thermal anomaly of 2°C above the long-term summer mean temperature (Li et al., 2012; Zhang et al., 2013; Jiang et al., 2018)) and ambient pH (~8.0);

(3) Low pH treatment (OA): control temperature 29.0°C and pH 7.8;

(4) Interaction treatment (ETOA): 31°C and pH 7.8 (Gattuso et al., 2015).

Seawater within the tanks was well mixed using submerged pumps (600 L/h), and water salinity and pH were measured daily with a Thermo Orion 5-star meter (Thermo Scientific, USA). The pH probe was calibrated at the beginning of the experiment using Tris-HCl buffers. Solenoid valves delivered bubbled CO_2 to the tanks for pH control. Seawater pH and temperature were monitored every 15 min with an aquarium controlling system at a precision of 0.1°C units for temperature and 0.05 units for pH (Weipro, China). Seawater temperature was controlled using commercial aquaria heaters (Weipro, China) located in the header tanks and the temperature was recorded continuously with a Hobo logger at 30-min intervals.

Full-spectrum fluorescent bulbs (Giesemann, Germany) were

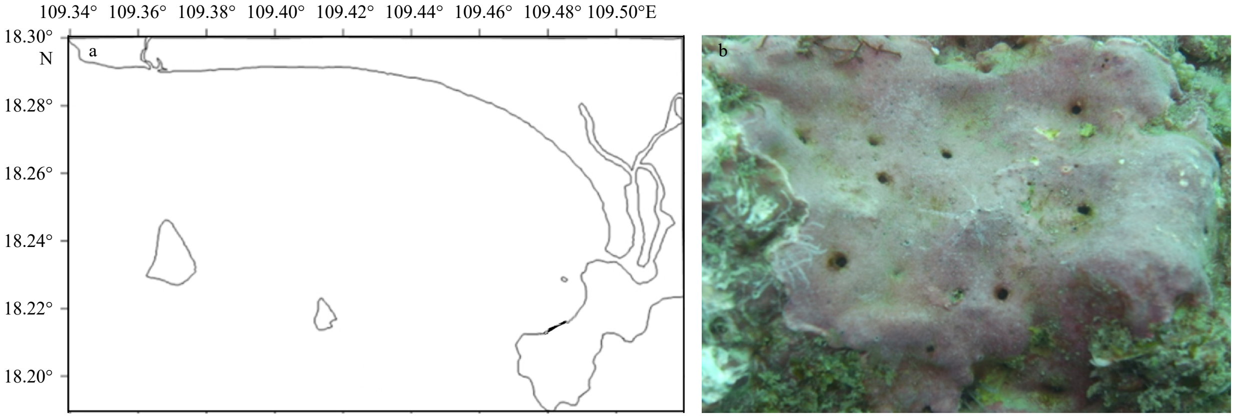

Fig. 1. Sampling site and image of the experimental species *Porolithon onkodes* in its natural habitat.

utilized to provide illumination on a 12 h:12 h light-dark cycle (from 6:30 am to 18:30 pm). The irradiance was determined by a 4-π light quantum probe (Li-cor Biosciences). Irradiance was adjusted to 200 μmol photons m^{-2} s^{-1} at the bottom of each tank according to the light condition at the 3–4 m depth, and experimental tanks were cleaned to prevent epiphyte growing and seawater samples were collected for seawater carbonate chemistry analyses every 4 d (Jiang et al., 2018). Total alkalinity was measured with an automatic titrator (AS-ALK2, Apollo, USA). Carbonate parameters were calculated based on the measured temperature, salinity, pH, and alkalinity using CO2SYS. The different seawater parameters for each treatment were shown in Table 1.

Table 1. Seawater parameter for each treatment (mean±SD)

Treatment	Temperature/°C	pH	TA/μmol·kg^{-1}	DIC/μmol·kg^{-1}	pCO$_2$/μatm	Ω_{Arag}
Control	29.0±0.3	8.05±0.04	2 300±14	2 016±24	479±50	3.38±0.24
ET	30.8±0.4	8.04±0.05	2 297±18	1 984±25	457±38	3.72±0.19
OA	29.1±0.3	7.80±0.03	2 284±25	2 138±20	1 012±80	1.97±0.15
ETOA	30.8±0.3	7.81±0.04	2 273±28	2 122±25	1 044±114	2.04±0.18

Note: Carbonate chemistry parameters, dissolved inorganic carbon (DIC), the partial pressure of carbon dioxide (pCO2) and aragonite saturation (ΩArag), were calculated from the measured temperature, pH (total scale), salinity, and total alkalinity (TA). 1 atm=1.01×10^5 Pa.

The maximum photochemical efficiency (F_v/F_m) was determined to evaluate the photosynthetic fitness of *P. onkodes*, using a diving PAM (Walz, Germany) with five segments from each tank on the beginning and end of the experiment. F_v/F_m can detect changes in photosynthetic efficiency under environmental stresses (Blake and Maggs, 2003; Burdett et al., 2014; Bach et al., 2017). Results are expressed relative to the control values (n=5 replicates per treatment). The buoyant-weighing method was explored to detect the calcification rate of the CA segments within each treatment following similar methodologies used in previous studies (Davies, 1989; Form and Riebesell, 2012).

2.3 *Data analyses*

Data was checked firstly for normality and homogeneity of variances by Kolmogorov-Smirnov test and Levene's test. Before the two-way ANOVA analyzing, three-way partly nested ANOVA was used to test the effects of temperature and pH on photochemical efficiency and growth rate, with temperature and pH as fixed effects and tank as a random factor nested within temperature and pH. Tank effects were removed from the model when insignificant at P>0.05 which were true for all analyses and tanks were pooled in subsequent analyses with specimens as independent replicates (Quinn and Keough, 2002). Tukey HSD posthot tests were applied for the identification of significant differences among the treatments. Statistical calculations were performed using SPSS software (IBM Inc.)

3 Results

The average growth rate (±standard deviation) of *P. onkodes* in control, ET, OA, and ETOA treatment was: (1.079±0.477)×10^{-3} g/d, (0.847±0.268)×10^{-3} g/d, (1.198±0.712)×10^{-3} g/d and (0.770±0.421)×10^{-3} g/d, respectively (Fig. 1). According to the statistics results, there were no significant effects on algae growth in each experimental treatment, neither single nor combined parameter (two-way ANOVA, P>0.05; Table 2). Compared to the control treatment, however, the average growth rate decreased 21.50% and 28.64% under ET and ETOA treatments respectively (Fig. 2).

F_v/F_m was significantly affected by the effect of increased temperature (P<0.001) and decreased pH (P=0.001) treatments respectively, but there are no significant effects in the interaction of temperature and pH (P=0.418) (Table 2), suggesting a positive interaction. Compared to the control treatment, both ET and ETOA treatments reduecd the F_v/F_m by 14.91% and 8.24% respectively, but it was comparable to the control treatment when both temperature and pCO$_2$ were elevated (Fig. 3), suggesting a complex interaction.

4 Discussion

In this experimental study, although there were no significant effects on algae growth in each treatment according to the statistics results, the numerical manifestation of ET, OA, and ETOA changed indeed comparing to the control treatment. Moreover, the average growth rate and photosynthesis level remained always higher under OA treatment than the control. However, when increased temperatures (31°C) were combined with decreased pH (7.8), the CCA species *P. onkodes* seemed to be less affected than when temperature stressor was applied independently. Indeed, decreased pH appeared to diminish the negative effects induced by increased temperature, especially relative to F_v/F_m, since at ETOA treatment *P. onkodes* displayed higher performance than the ET treatment. These findings indicated that the temperature-induced negative effect was restricted under decreased pH in the CCA species of *P. onkodes*. This finding highlights the view that GW is a stronger threat to algal performance than OA (Nash et al., 2016; Vásquez-Elizondo and Enríquez, 2016).

It was reported that calcifying macroalgae could result in increased photosynthesis, growth and carbonate deposition, if the elevating temperature within their tolerance ranges (Glynn, 1996; Martin and Hall-Spencer, 2017). In our investigation, the negative effect of increased temperature on *P. onkodes* can be attributed to exceeding the tolerance thresholds. Indeed, it has been

Table 2. Statistical results of two-way ANOVA examining the effects of temperature (T) and pH on the growth rate and photochemical efficiency (F_v/F_m) of *Porolithon onkodes*

Source of variation	Growth rate				F_v/F_m			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
T	1	5.445×10^{-7}	2.214	0.156	1	0.051	68.233	<0.001
pH	1	2.207×10^{-9}	0.009	0.926	1	0.013	17.261	0.001
T×pH	1	4.801×10^{-8}	0.195	0.664	1	0.001	0.69	0.418
Error	16	2.459×10^{-7}			16	0.001		

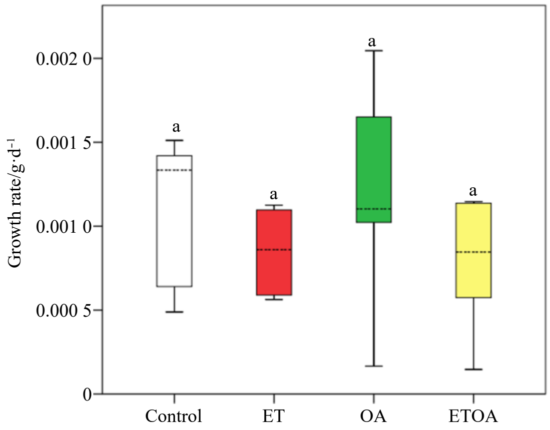

Fig. 2. The growth rate of *Porolithon onkodes* under the four different experimental treatments. The boxes represent the 25th and 75th percentiles. The horizontal dashed line is the median value, and the whiskers are minimum and maximum values. Letters indicate significant differences relative to control organisms (Tukey HSD, P>0.05).

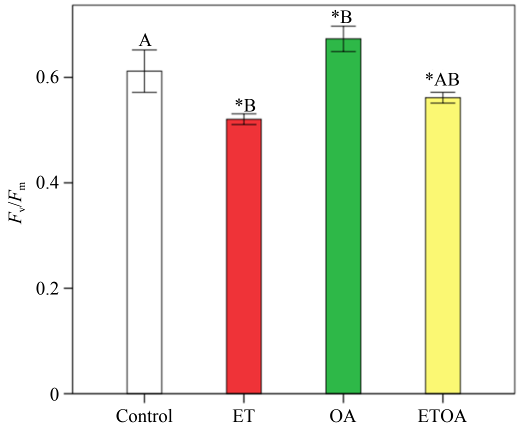

Fig. 3. The mean values of maximum photochemical efficiency (F_v/F_m) after 60 d under the experimental treatments. Error bars represent standard errors. Asterisks and letters indicate significant differences relative to control organisms (Tukey HSD, P>0.05).

observed that if beyond the tolerance temperature ranges, it could induce an excess in the levels of reactive oxygen species, subsequently affecting their carbon fixation, photorespiration, photosynthesis and development (Kim and Portis, 2004; Müller et al., 2012; Moenne et al., 2016; Pospíšil, 2016). Also, similar to the previous studies (Anthony et al., 2008; Vásquez-Elizondo and Enríquez, 2016) that photosynthesis (F_v/F_m) decreased under the increased seawater temperature, we observed a decline of 14.91% in ET treatments. Other investigations of the effects of thermal stress resulted in either no effect (Martin and Gattuso, 2009; Martin et al., 2013; Comeau et al., 2014) or not evidenced negative effects on photosynthesis (Noisette et al., 2013; Scherner et al., 2016). Hence, our results support the views that CCA photosynthesis performance under elevated seawater temperature showed a species-specific feature in CA, consistent with the previous studies (Vásquez-Elizondo and Enríquez, 2016; Muñoz et al., 2018).

CA has been thought to one of the groups of species most vulnerable to ocean acidification due to the solubility of their high magnesium-calcite skeletons (Diaz-Pulido et al., 2012). Different with the previous estimates of decreasing in CCA calcification and photosynthesis (Anthony et al., 2008; Semesi et al., 2009; Gao and Zheng, 2010; Martin et al., 2013), growth (Hofmann et al., 2012; Ragazzola et al., 2012), our results demonstrated that growth rate and photosynthesis of *P. onkodes* enhanced during the OA treatments. Other investigations had got similar results in some CCA species as well (Scherner et al., 2016; Martin and Hall-Spencer, 2017; Muñoz et al., 2018). Published research also suggested that photosynthesis enhancement in different macroalgae subject to OA, probably more related to CO_2 availability rather than pH reducing itself (Martin and Hall-Spencer, 2017). Calcification process is energy-demanding very much, and photosynthesis provides the energy required to support the formation of carbonate skeletons. Indeed, a higher concentration of CO_2 diffused in seawater may provide a greater substrate for CCA carbon fixation, photosynthesis, and growth (Martin and Hall-Spencer, 2017). And also, the physiological response of CA to near-future ocean acidification is species-specific (Noisette et al., 2013).

In the response to the combined effects of ET and OA treatments, our results demonstrated that the negative effects of increased temperature were softened by reduced pH. Accordingly, our results did not support the notion that CCA species were affected greater by the OA under ET conditions (Anthony et al., 2008; Diaz-Pulido et al., 2012). Similarly, experimental research found that photosynthetic O_2 exchanging increased in *Hydrolithon* sp. accompanied by the pH decreased (Semesi et al., 2009). Vásquez-Elizondo and Enríquez (2016) also found that the direct impact of reduced pH on algal calcification was smaller than the impact caused by elevated temperature. Other interesting observations revealed either increased environmental temperatures reduced the impact of lower pH in calcification rates (Noisette et al., 2013) or showed a higher level of calcification during the highest sea surface temperature season (Martin and Gattuso, 2009). Nevertheless, our experimental results suggested that OA diminishes the negative effects of ET in *P. onkodes*, it may be an interspecific feature that cannot be applied to all CCA species.

5 Conclusions

We observed that the interactions between OA and ET posed a significant challenge for coralline algal populations in the future, and support the conclusion that elevated temperature was a stronger threat to CCA species than OA, and also suggested that any potential adaptation or acclimatization by CCA to pCO_2 may be offset by thermal stress. The species-specific responses were considered an important limitation for the understanding of the impacts of GW and OA on reef-forming communities. Considering the ecological significance of CA for coastal ecosystems, the effective tools and long-term experiments should be implemented to understand the processes directly affected by every environmental threat. Moreover, predictions of survival thresholds for reef builders, such as CCA, under climate change must take account of acidification–warming interactions in the integrated biological and biogeochemical response, for that will compromise the contribution of CA to reef carbon budgets, coral larva recruitment and the maintenance of reef biodiversity.

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