

REPORT

# Brown algae as winners: Divergent resilience to high light under acidified conditions shapes macroalgal communities around a carbon dioxide vent

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## Abstract

To investigate the effects of ocean acidification (OA) on macroalgae, we conducted in situ surveys along a natural CO<sub>2</sub> vent gradient in Shikine Island, Japan, together with complementary laboratory culture experiments. The in-situ surveys revealed that near the CO<sub>2</sub> vent (where pH dropped by 0.37), macroalgal diversity and species-richness were less than half those at the reference sites under ambient pH conditions. Nevertheless, the rates of CO<sub>2</sub> assimilation of several common macroalgae increased from the reference site to the areas near the CO<sub>2</sub> vent. This enhancement coincided with decreased photosynthetic CO<sub>2</sub> affinity, reflecting that the acidified area down-regulated CO<sub>2</sub>-concentrating mechanisms in the algae. Measured photosystem II activity revealed that macroalgae at reference sites had lower electron transport rate and light utilization efficiency. The laboratory culture experiments, in which the dominant species (*Gelidium elegans* and *Dictyopteria undulata*), were cross-exposed to ambient and elevated CO<sub>2</sub> conditions, further demonstrated that the stress near the CO<sub>2</sub> vent significantly exacerbated photoinhibition under high light stress. Our results demonstrate that reduced pH and high sunlight act synergistically to impair macroalgal photosynthesis through exacerbated photoinhibition. This effect was more pronounced in red algae (e.g., *G. elegans*) than in brown algae (e.g., *D. undulata*). These different physiological responses provide a mechanistic explanation for an observed community shift, from red algal dominance in ambient pCO<sub>2</sub> areas to brown algal dominance near the vent. Our findings imply that future OA, when combined with high-light stress, may selectively disadvantage high-light-sensitive species, thereby altering macroalgal community structure in coastal waters.

Progressive ocean acidification (OA) is known to affect many marine organisms and ecological processes (Gao et al. 2020). The scientific literature shows that OA may result in positive, negative, and neutral effects on macroalgae (Ji and Gao 2020). Although there are a number of works focused on the effects of OA on different macroalgal species based on controlled experiments, little has been documented on the effects of in situ macroalgae (Porzio et al. 2011; Agostini et al. 2018; Xu et al. 2019; Hall-Spencer and Harvey 2019). While laboratory-controlled experiments advance the understanding of mechanisms in algae with respect to species-specific

responses, such as photoinhibition dynamics, CO<sub>2</sub> concentrating mechanisms (CCMs), and energy allocation, these findings do not reveal ecosystem-level responses, including shifts in species composition, biodiversity loss, and alterations in ecosystem function (Pörtner et al. 2019). This is due to the complex and variable interactions between acidification and other environmental drivers, and to regional physical, chemical, and biological conditions that can alter OA impacts (Riebesell and Gattuso 2015). It is now well established that the effects of OA are modulated by co-occurring factors such as light, nutrients, and temperature, which are believed to alter algal community structures to varying degrees (Baggini et al. 2014; Hofmann et al. 2014; Celis-Plá et al. 2015). While previous multi-driver studies on organisms such as *Chlamydomonas* have demonstrated that both the identity and number of

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environmental stressors can strongly influence algal growth, photosynthetic performance, and adaptive responses under ocean change scenarios (Brennan and Collins 2015; Brennan et al. 2017), conducting similarly controlled multi-factor experiments with larger and physiologically more complex macroalgae remains logistically challenging. Moreover, in the natural environment, OA does not act in isolation; it occurs concurrently with warming and deoxygenation, which jointly influence primary productivity in regionally variable ways (see the review by Gao et al. 2019 and literature therein). Therefore, it is pivotal to conduct in-situ investigations and examine the combined effects of multiple drivers (Boyd et al. 2018). Toward this, CO<sub>2</sub> vents have been used as a window to look into future OA ecological impacts (Hall-Spencer et al. 2008).

Submarine CO<sub>2</sub> vents have been used to examine ecological effects of OA on marine benthic organisms (Hall-Spencer et al. 2008; Agostini et al. 2018). Elevated CO<sub>2</sub> concentrations in the seawater close to the vents significantly reduces the abundance of most macroalgae and simplifies their community structures. At Shikine island calcified coralline algae are especially vulnerable to OA (Peña et al. 2021). Although non-calcifying algae are less sensitive to the stress associated with the elevated pCO<sub>2</sub>, their diversity is also reduced near the vents (Agostini et al. 2018; Connell et al. 2018). An investigation near a CO<sub>2</sub> vent at Ischia, Italy, demonstrated that non-calcified macroalgae also declined along a pH gradient in addition to OA-sensitive calcifying algae (Porzio et al. 2011). It appears that species shifts toward the CO<sub>2</sub> vents along the pH gradients are related to different physiological responses of benthic algae to OA as well as their tolerance of low pH through life cycles (Ji and Gao 2020).

Changes in photosynthetic performances can directly and/or indirectly affect growth and survival of algae. A number of studies have shown that CO<sub>2</sub> enrichment and the associated pH drop affect photosynthetic performances of many macroalgae in different ways (as the review by Ji and Gao 2020 and literatures therein; Carlot et al. 2026). Elevated pCO<sub>2</sub> up to 1500 μatm stimulated growth in *Pyropia yezoensis* (Gao et al. 1991), *Ulva* spp. (Gordillo et al. 2001; Xu and Gao 2012; Huan et al. 2016), and *Gracilaria* spp. (Gao et al. 1993; Zou and Gao 2009). Laboratory CO<sub>2</sub> enrichment experiments have shown that increased seawater pCO<sub>2</sub> (achieved by bubbling with CO<sub>2</sub>) can enhance cyclic electron transfer in a red macroalga (Zhang et al. 2021) and stimulate photorespiration in a green macroalga (Xu and Gao 2012). These photosynthetic pathways are known to play essential roles for algae to cope with photo-stress under high light. The red alga *Jania rubens* inhabiting areas near CO<sub>2</sub> vents exhibited lower photosynthetic efficiency and up to 40% lower growth rates compared to conspecifics from ambient pH areas (Porzio et al. 2018, 2020). In contrast, the brown alga *Sargassum vulgare* can adapt to low pH, showing high levels of photochemical activity and carboxylation, thereby becoming dominant in acidified zones (Porzio et al. 2017). It is likely that

photoprotective processes, including cyclic electron transfer, photorespiration and non-photochemical quenching (NPQ), are modulated by OA under sunlight, so that their survivals at the CO<sub>2</sub> vents are controlled interactively by high solar radiation and the acidic stress. Therefore, we hypothesized that macroalgae distributed along gradients in OA have different sensitivities to photoinhibition under saturating or excessive light, and that this differential response, rather than OA alone, may explain the observed shifts in community composition. Specifically, we predicted that species with limited photoprotective capacity (e.g., red algae) would be more vulnerable to high-light stress under acidified conditions, favoring the dominance of more tolerant groups (e.g., brown algae).

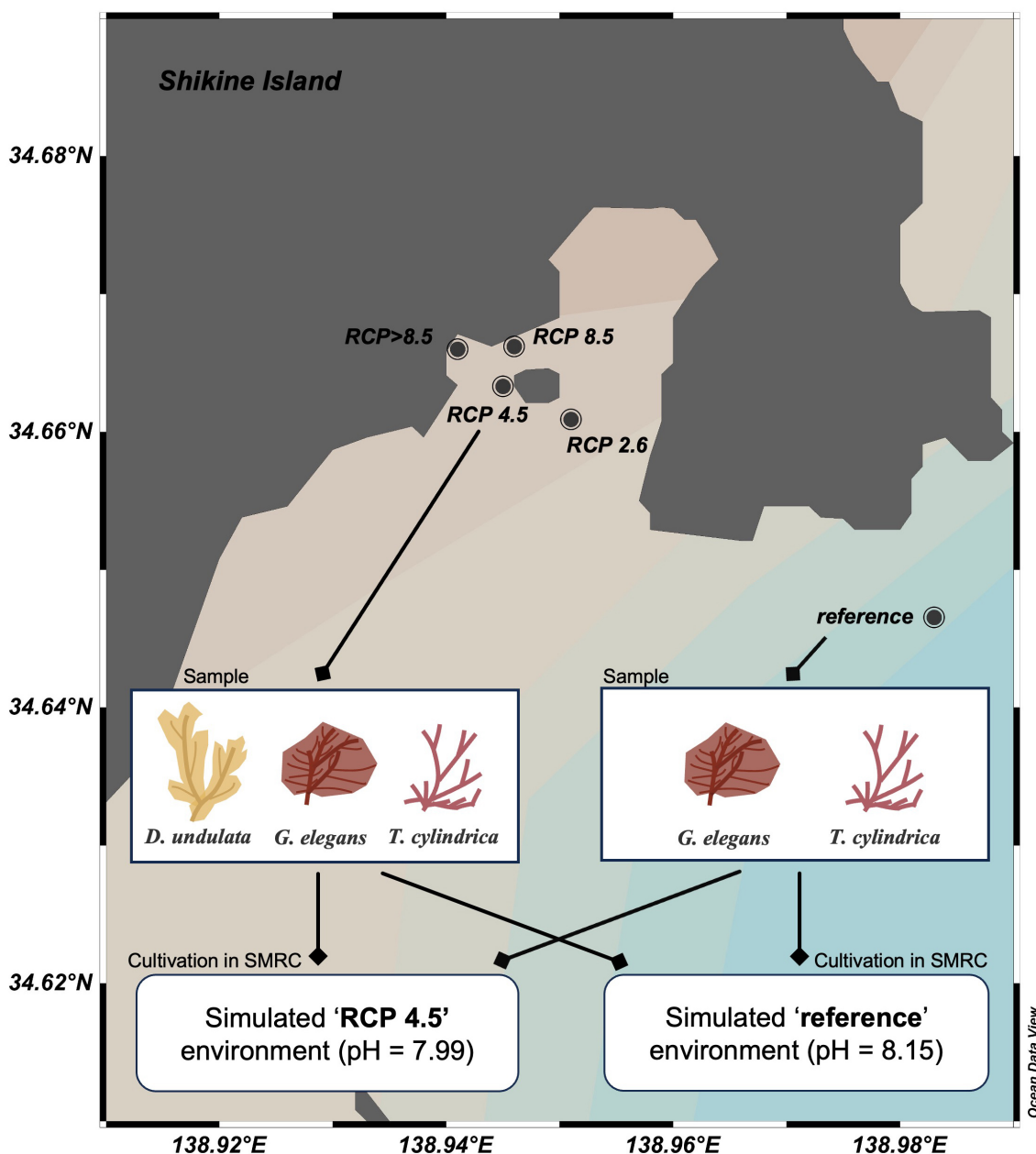
## Materials and methods

### Study area, carbonate chemistry, and solar irradiance

Samples of macroalgae from different sites were collected using a RV Tsukuba II at Shikine island on the Izu archipelago in Japan (34°19'12"N, 139°12'11"E) during June, where several CO<sub>2</sub> vents in shallow waters have been recorded (Agostini et al. 2015). We chose five sites of different seawater pCO<sub>2</sub> ranging from 300 to 1200 μatm. These sites were denoted as “reference” (pH<sub>T</sub> = 8.15, pCO<sub>2</sub> = 360 μatm), “RCP 2.6” (pH<sub>T</sub> = 8.09, pCO<sub>2</sub> = 433 μatm), “RCP 4.5” (pH<sub>T</sub> = 7.99, pCO<sub>2</sub> = 571 μatm), “RCP 8.5” (pH<sub>T</sub> = 7.94, pCO<sub>2</sub> = 661 μatm) and “RCP > 8.5” (pH<sub>T</sub> = 7.73, pCO<sub>2</sub> = 1170 μatm) (Fig. 1), according to Intergovernmental Panel on Climate Change Representation Concentration Pathway (RCP) scenarios (IPCC 2013; Harvey et al. 2021).

The carbonate chemistry parameters of seawater from these sites were assessed by measuring in-situ pH, temperature and salinity by using a YSI sensor (YSI Pro Plus). Seawater samples for total alkalinity and nutrients were collected by SCUBA divers at the sites close to the bottom and stored in high density polyethylene bottles. Total alkalinity was measured by titration (785 DMP Titrino, Metrohm) with HCl at 0.1 mol L<sup>-1</sup>, and calculated from the Gran function between pH 4.2 and 3.0. The titrations were cross-validated using a working standard (SD ± 9 μmol kg<sup>-1</sup>) against certified reference material purchased from the A.G. Dickson laboratory (No. 284-77336). Values of other carbonate chemistry parameters, for example, total dissolved inorganic carbon concentration were calculated with CO2SYS (Pierrot et al. 2006) according to the measured values of total alkalinity, pH, and other factors. Nutrient concentrations, including dissolved inorganic nitrogen (as the sum of nitrate [NO<sub>3</sub><sup>-</sup>], nitrite [NO<sub>2</sub><sup>-</sup>], and ammonium [NH<sub>4</sub><sup>+</sup>]), and dissolved inorganic phosphorus were measured in duplicate via a continuous flow analyzer (Seal QuAAtro).

The underwater photosynthetically active radiation (PAR) was continuously recorded by three independent sensors (DEFI2-L, JFE Advantech Co., Ltd.), which were placed at ~ 10 cm (~ 7–10 m below the sea surface) above the bottom of the sites at “reference,” “RCP 4.5,” and “RCP 8.5,” sites,



**Fig. 1.** Study area off the volcanic island of Shikine in Japan, and a macroalgal culture set-up at Shimoda Marine Research Center. Macroalgae were collected from rocky substrata at depths of 8–10 m at five sites along a gradient of increasing mean seawater pCO<sub>2</sub>: 360 (reference site), 433 (Representation Concentration Pathway [RCP] 2.6), 571 (RCP 4.5), 661 (RCP 8.5), and 1170 (RCP > 8.5)  $\mu\text{atm}$ .

respectively. The daytime average PAR was calculated as the mean PAR during daylight hours (approximately 06:00 to 18:00 local time), and the full-day average PAR was calculated as follows: the mean PAR over the diel 24-h cycle.

#### Algae collection and experimental design

A total of 13 species of macroalgae were collected from five different sites by SCUBA divers and taken to the laboratory in Shimoda Marine Research Center, Tsukuba University, in a flow-through seawater tank within 2 h of collection. Following

rinsing, the collected algae were cultured in five different 30 × 50 cm tanks with flow-through seawater. The seawater temperature (referred to the in situ temperature) was ~ 23°C and the room light intensity was ~ 100  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . The rapid light curves of 13 different species and photosynthesis vs. CO<sub>2</sub> curves (photosynthesis vs. CO<sub>2</sub> curves) of four different species were measured by using chlorophyll fluorescence and gas exchange (detailed as below) within 24 h.

Subsequently, we did a culture experiment using three representative algae to investigate the effects of OA on

macroalgae. The two fleshy algae, *G. elegans* and *Dictyopteris undulata*, were dominant species at the “reference” and “RCP 4.5” sites, and a calcified alga, *Tricleocarpa cylindrica*, was also included. Thalli of *G. elegans* and *T. cylindrica* were collected from both “reference” and “RCP 4.5” sites, whereas the *D. undulata* was only collected from “RCP 4.5.” A shift experiment was employed to assess the physiological adaptation of these macroalgae to  $p\text{CO}_2/\text{pH}$  gradient. In the shift experiment, macroalgae from each location were cross-cultured at both their native (“reference”/“RCP. 4.5”) and the contrasting site (“RCP 4.5”/“reference”). Fresh macroalgal thalli weighted  $\sim 1$  g weight (Fresh Weight) for each alga were placed into two different tanks and cultured for 7 d. During the culture, each tank contained  $\sim 30$  L seawater, where the pH was maintained at  $\sim 7.9$  (high  $\text{CO}_2$ ) and 8.1 (ambient  $\text{CO}_2$ ) by regularly adding saturated  $\text{CO}_2$  seawater and natural seawater every 3–4 h, and the seawater was renewed every 2 d. According to the in situ seawater temperature and the monthly average full-day average light intensity, the seawater temperature and the light intensity during culture experiment were set as  $23^\circ\text{C}$  and  $\sim 70 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , respectively. To characterize OA-induced photophysiological changes, the macroalgal thalli were exposed to incident sunlight at the end of the culture period. The exposure to an average daytime PAR intensity of  $\sim 300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  was aimed to examining their susceptibility to photoinhibition. These measurements resulted in a total of 10 sets of data (Fig. 1).

### Measurements of chlorophyll fluorescence and photosynthetic gas exchanges

A dual-wavelength pulse-amplitude modulated fluorescence monitoring system (Dual-PAM-100, Walz) was applied to measure photosynthetic performance as described by Klughammer and Schreiber (Klughammer and Schreiber 1994, 2008). The minimal fluorescence ( $F_o$ ) for 20 min dark-adapted thalli was induced by a pulsed red measuring light of low irradiance ( $\sim 8 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ), and the maximum fluorescence ( $F_m$ ) was measured during a 0.8 s saturating flash ( $\sim 5000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). The steady-state fluorescence ( $F$ ) was recorded periodically under actinic light of  $200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ . The 0.8 s saturating flash was applied to obtain the maximum fluorescence ( $F_m'$ ) under the steady actinic light. The effective quantum yield of photosystem II (PSII) (YII), the electron transport rate (ETR) of PSII, and the NPQ of PSII were assessed as follows:

$$\text{YII} = (F_m' - F) / F_m'$$

$$\text{ETR} = \text{YII} \times \text{PAR}$$

$$\text{NPQ} = (F_m - F_m') / F_m'$$

For the measurements of rapid light curves, the sampled thalli were illuminated for 20 s with 11 incremental steps of increasing

actinic light. A saturation flash was applied following each light to generate corresponding  $F$  and  $F_m'$  values. Relative electron transport rates (rETRs) were calculated as follows:

$$\text{rETR} = ((F_m' - F) / F_m') \times \text{PAR}$$

Photosynthetic light harvesting efficiency ( $\alpha$ ) and  $\text{rETR}_{\text{max}}$  were obtained by fitting the rETR and PAR data to the following function:

$$\text{rETR} = \text{rETR}_{\text{max}} \times \tanh\left(\frac{\alpha \times \text{PAR}}{\text{rETR}_{\text{max}}}\right)$$

and the apparent saturating light intensity ( $E_k$ ) was calculated as follows:

$$E_k = \frac{\text{rETR}_{\text{max}}}{\alpha}$$

The damage and recovery processes of the photosynthetic apparatus were obtained by periodically measuring the YII during the high light exposure according to Heraud and Beardall (2000) and Zhang et al. (2024). The damage ( $k$ ,  $\text{min}^{-1}$ ) and repair ( $r$ ,  $\text{min}^{-1}$ ) rates were estimated using the Kok as follows:

$$\frac{Y_n}{Y_o} = \frac{r}{k+r} + \frac{k}{k+r} \times e^{-(k+r)/t}$$

where  $Y_n$  and  $Y_o$  are YII at time  $t_n$  and  $t_o$ , respectively.

A GFS-3000 gas exchange system (Walz) was employed to measure net photosynthetic  $\text{CO}_2$  uptake by the algae. During the measurements, six incremental external aerial  $\text{CO}_2$  concentrations, 60, 200, 500, 800, 1500, and 2000  $\mu\text{atm}$ , were pumped into the chamber with a flow rate of  $500 \mu\text{mol min}^{-1}$ . The relative air humidity and the temperature were 80% and  $23^\circ\text{C}$ , respectively, and the actinic light was  $\sim 200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ . The  $\text{CO}_2$  assimilation rates ( $P_n$ ,  $\mu\text{mol CO}_2 \text{ g}^{-1} \text{FW h}^{-1}$ ) were calculated according to von Caemmerer and Farquhar (Von Caemmerer and Farquhar 1981) as follows:

$$P_n = \Delta C \times F \times 60 \times \frac{273}{(273 + T) \times 22.4 \times \text{FW}}$$

where  $\Delta C$  represents the difference in  $\text{CO}_2$  concentrations of influx and efflux to and from the chamber ( $\mu\text{atm}$ ),  $F$  the gas flow rate ( $\text{L min}^{-1}$ ) with conversions based on the molar volume of gas at standard atmospheric pressure ( $22.4 \text{ L mol}^{-1}$ ),  $T$  the temperature inside the chamber ( $^\circ\text{C}$ ) and FW the fresh weight of algal thalli (g). The maximal photosynthetic rate  $V_{\text{max}}$  ( $\mu\text{mol CO}_2 \text{ g}^{-1} \text{FW h}^{-1}$ ) and the half-saturation constant ( $k_{0.5}$ ,  $\mu\text{atm}$ ) were obtained by fitting  $P_n$  at various  $\text{CO}_2$  concentrations with the Michaelis–Menten formula.

## Statistical analyses

Statistical analyses were performed using SPSS 21.0 (SPSS Inc.). Prior to all statistical analyses, homogeneity of variance was tested using Levene's test. One-way ANOVA was applied to evaluate differences among experimental treatments, with treatment conditions considered as fixed factors. When significant differences were detected, Tukey's multiple comparison test was conducted for post hoc analysis. Independent-samples *t*-tests were used for comparisons between two groups where appropriate. Differences were considered statistically significant at  $p < 0.05$ .

## Results

### Water chemistry and solar irradiance

The  $\text{pH}_T$  ranged from 7.73 to 8.15 in the selected five sites with the temperature ranging from 23.8°C to 24.5°C, the salinity ranged from 32.5 to 33.6, and the total alkalinity remained unaltered, with an average value  $\sim 2270 \mu\text{mol L}^{-1}$ . Accordingly, the calculated total dissolved inorganic carbon concentration and  $p\text{CO}_2$  ranged from 2118.3 to 1900  $\mu\text{mol L}^{-1}$  and 26.2 to 8.2  $\mu\text{mol L}^{-1}$  ( $\sim 1000\text{--}300 \mu\text{atm}$  for  $p\text{CO}_2$ ), respectively. Concentrations of dissolved inorganic nitrogen and dissolved inorganic phosphorus remained stable and ranged from 2.68 to 3.08  $\mu\text{mol L}^{-1}$  and 0.21 to 0.25  $\mu\text{mol L}^{-1}$ , respectively (Supporting Information Table S1).

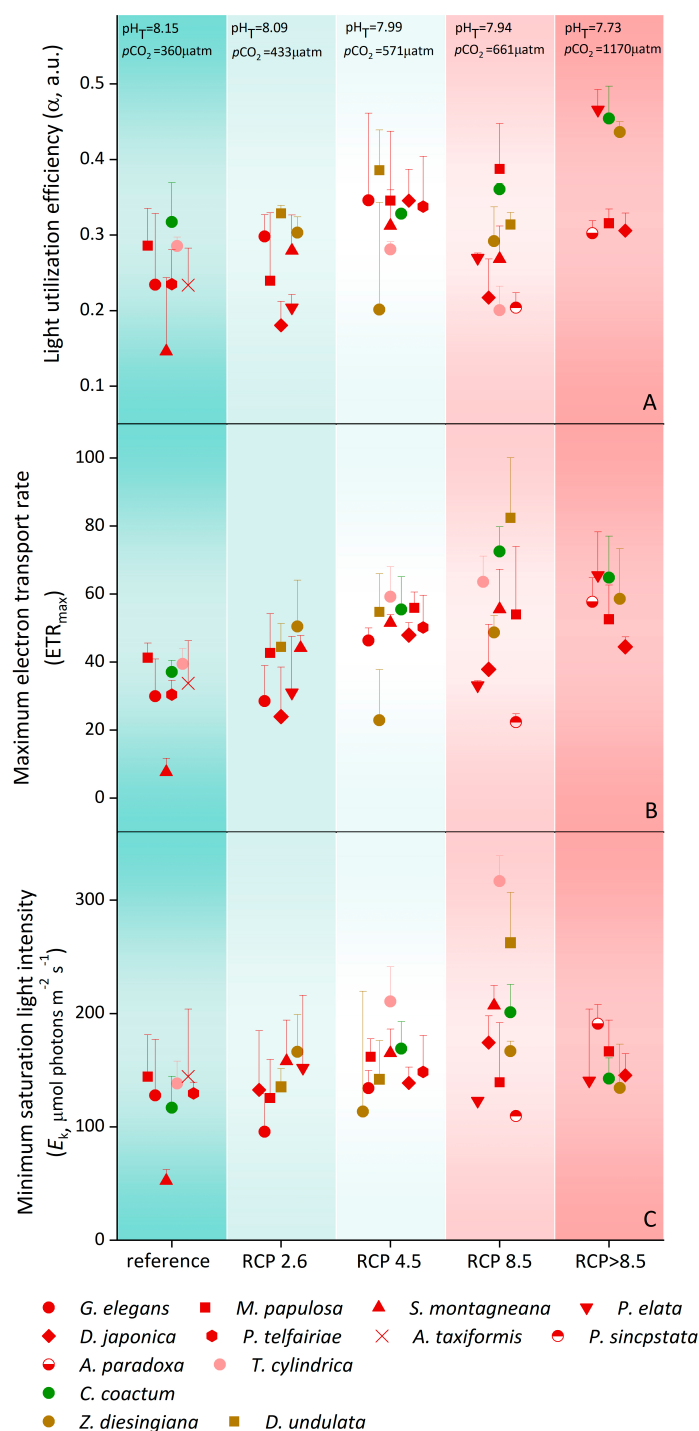
The continuously recorded PAR was similar at "reference," "RCP 4.5," and "RCP 8.5" sites, with the daytime and full-day average PAR were  $\sim 300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  and  $\sim 70 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , respectively (Supporting Information Fig. S1).

### Photochemical efficiency of the macroalgae

A total of 13 species from five sites (Supporting Information Table S2), including 10 species of Rhodophyta, 1 species of Chlorophyta, and 2 species of Phaeophyta, were used to measure the rapid light curves. As shown in Fig. 2 and Supporting Information Tables S3 and S4, both the light utilization efficiency ( $\alpha$ ) and the maximum electron transport rate ( $\text{ETR}_{\text{max}}$ ) increased with increased  $p\text{CO}_2$  or decrease of pH, leading to a lower minimum saturation light intensity ( $E_k$ ). However, the dominant species, *G. elegans* (red alga), grown in low pH water decreased its relative  $\text{ETR}_{\text{max}}$  from  $\sim 95$  arbitrary units at "reference" to  $\sim 60$  at "RCP 4.5," resulting in a 17% decrease of  $E_k$ . In contrast, the other dominant species, *D. undulata* (brown alga), distributed in the high  $\text{CO}_2$  area, increased its  $\text{ETR}_{\text{max}}$  and  $E_k$  from  $\sim 226$  a.u. and  $\sim 74 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  at "RCP 2.6" to  $\sim 261$  a.u. and  $\sim 83 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  at "RCP 4.5," respectively.

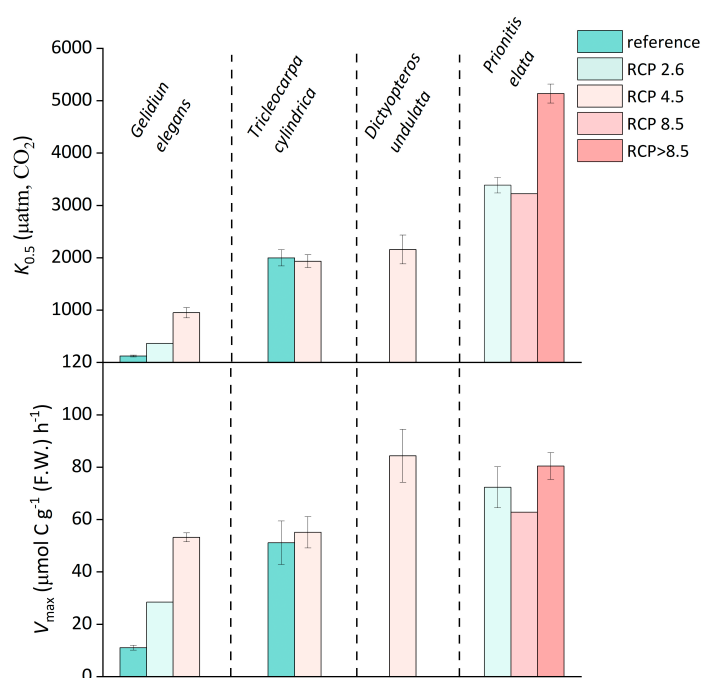
### Photosynthesis vs. $\text{CO}_2$ curves

The relationships of photosynthetic  $\text{CO}_2$  fixation rates with changed levels of  $\text{CO}_2$  (Fig. 3; Supporting Information Table S5) varied among the species, *G. elegans* (Rhodophyta, from the low  $\text{CO}_2$  sites), *T. cylindrica* (Rhodophyta, a calcified species), *Prionitis elata* (Rhodophyta, a common species in high  $\text{CO}_2$  areas) and *D. undulata* (Phaeophyta, the dominant



**Fig. 2.** Photosynthetic performance of macroalgae at five  $\text{pH}_T/p\text{CO}_2$  levels. (a) Light use efficiency ( $\alpha$ ), (b) maximum electron transport rate ( $\text{ETR}_{\text{max}}$ ), (c) minimum saturation light intensity ( $E_k$ ). Each data point is the mean  $\pm$  SD ( $n$  ranged from 2 to 3). Symbol colors represent red, brown and green species, respectively.

species in the high  $\text{CO}_2$  sites). With increased  $p\text{CO}_2$  toward the vents, the half-saturation constant ( $K_{0.5}$ ) for  $\text{CO}_2$ -dependent photosynthesis increased in both *G. elegans* and

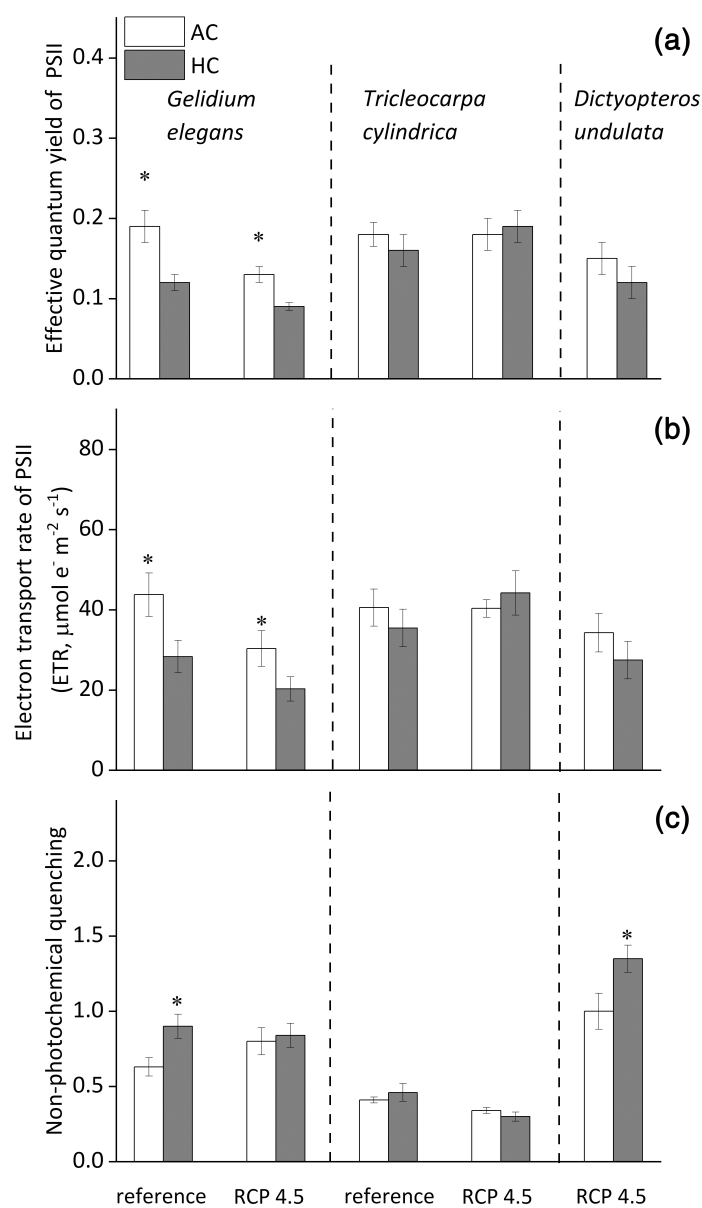


**Fig. 3.** Variation in carbon fixation rate in *Gelidium elegans*, *Tricleocarpa cylindrica*, *Dictyopteros undulata*, and *Prionitis elata* collected from sites along a gradient of increasing mean seawater  $p\text{CO}_2$ .  $K_{0.5}$  is the half-saturation constant, representing the  $\text{CO}_2$  concentration that results in half of  $V_{\text{max}}$ ;  $V_{\text{max}}$  is the maximum  $\text{CO}_2$  saturated photosynthetic carbon fixation rates. Each data point is the mean  $\pm$  SD ( $n$  ranged from 2 to 3).

*P. elata*, but not in *T. cylindrica*. The maximal photosynthetic rate ( $V_{\text{max}}$ ) in *G. elegans* increased with increased  $p\text{CO}_2$ , rising from  $11 \pm 0.9$  to  $53.2 \pm 1.7 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ FW h}^{-1}$ . In contrast, no significant changes were observed in *P. elata* or *T. cylindrica*, with  $V_{\text{max}}$  changing from  $51.1 \pm 8.3$  to  $55.1 \pm 6 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ FW h}^{-1}$  and from  $72.3 \pm 7.8$  to  $80.4 \pm 5.1 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ FW h}^{-1}$ , respectively. The dominant species from low to high  $\text{CO}_2$  sites increased the  $K_{0.5}$  and  $V_{\text{max}}$  in *G. elegans* and *D. undulata*.

### Photosynthetic performance of macroalgae shifted to opposing $p\text{CO}_2$ levels

Based on the result from shifting the cultures indoors (Figs. 1, 4), the thalli of *G. elegans* collected from the low  $\text{CO}_2$  sites ("reference") had significantly higher values of the effective quantum yield of PSII (YII) and ETR of PSII compared to those collected from the high  $\text{CO}_2$  sea area (RCP 4.5) (Fig. 4a,b). However, the NPQ showed no significant difference (Fig. 4c). For the calcified alga *T. cylindrica*, no significant changes were observed in YII, rETR, and NPQ between thalli collected from the low and high  $\text{CO}_2$  sites (Fig. 4). Nevertheless, the results showed that the high  $\text{CO}_2$  treatment decreased the YII and ETR, and increased the NPQ in *G. elegans*, but resulted in an insignificant change in *T. cylindrica*. For



**Fig. 4.** Effective quantum yield of photosystem II (PSII) (a), the photosynthetic electron transport rate of PSII (b) and the non-photochemical quenching (c) of the macroalgae exposed to high light ( $\sim 300 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ). *Gelidium elegans* and *Tricleocarpa cylindrica* were collected from "reference" ( $p\text{CO}_2 = 360 \mu\text{atm}$ ) and Representation Concentration Pathway (RCP) 4.5 ( $p\text{CO}_2 = 571 \mu\text{atm}$ ), *Dictyopteros undulata* was only collected from RCP 4.5 ( $p\text{CO}_2 = 571 \mu\text{atm}$ ). The open and gray bars represent ambient  $\text{CO}_2$  (AC,  $\text{pH} = 8.1$ ) and high  $\text{CO}_2$  (HC,  $\text{pH} = 7.9$ ) aquarium treatments, respectively. Each data point is the mean  $\pm$  SD ( $n = 3$ ). The symbol "\*" indicates significant differences between the treatments,  $p < 0.05$ .

*D. undulata* thalli collected from the high  $\text{CO}_2$  site, those cultured at ambient  $\text{CO}_2$  showed a decrease of NPQ (Fig. 4c).

The damage and recovery processes of the photosynthetic apparatus of the macroalgae exposed to high light, associated with the decreased YII and increased NPQ as shown above,

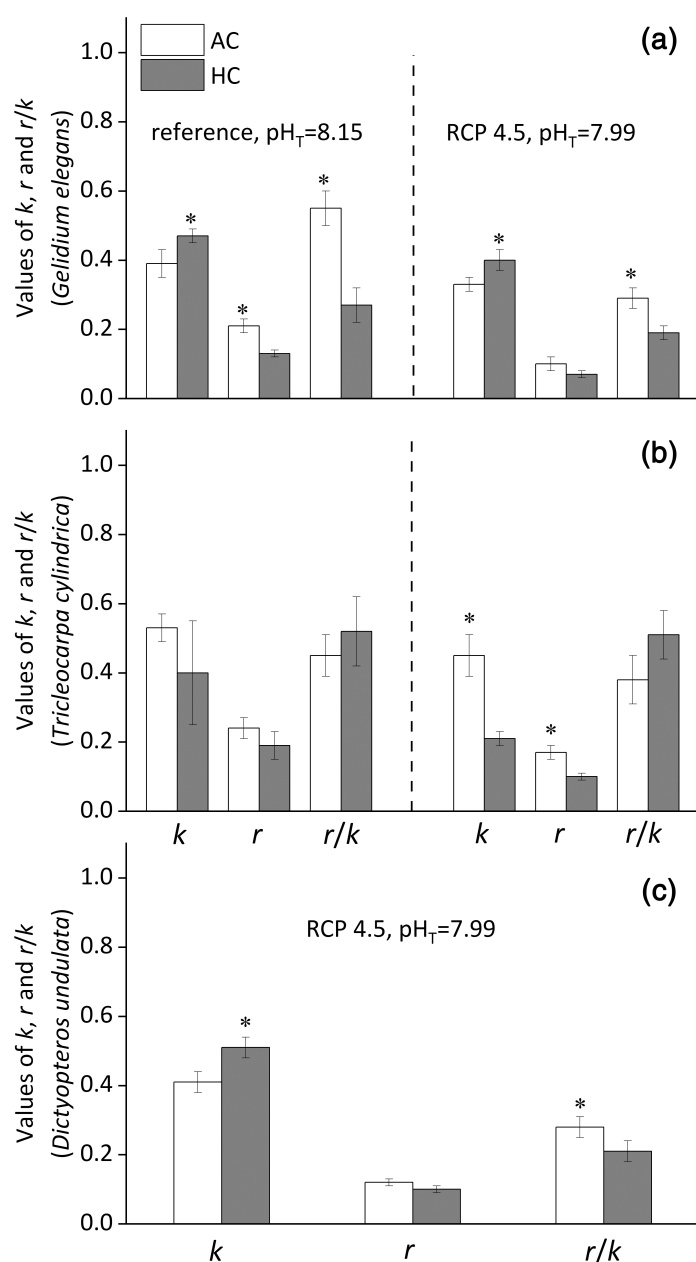
indicate that the high CO<sub>2</sub> grown thalli of *G. elegans* showed a higher damage rate and a lower recovery rate, characterized by an increase of  $k$  and a decrease of  $r$ , leading to a further decrease in the  $r/k$  ratio (Fig. 5a). In *T. cylindrica*, both  $r$  and  $k$  decreased in the thalli collected from “RCP 4.5” grown under the high CO<sub>2</sub> conditions (Fig. 5b). Similar to *G. elegans*, the high CO<sub>2</sub>-grown *D. undulata* had a higher value of  $k$  and a lower value of  $r/k$  ratio (Fig. 5c). A 30-min dark treatment following the high light exposure revealed a recovery from the photoinhibition, with an average YII value increased from  $\sim 0.1$  to  $\sim 0.4$  ( $t$ -test,  $p = 0.438$  and  $p = 0.527$  for ambient and high CO<sub>2</sub> treatments, respectively). To a lesser extent, the YII in *G. elegans* increased from  $\sim 0.1$ – $0.2$  to  $\sim 0.2$ – $0.3$  ( $t$ -test,  $p < 0.05$  in both ambient and high CO<sub>2</sub> treatments).

## Discussion

Growth and photosynthesis of some macroalgae in their adult or juvenile stages can be enhanced by elevated  $p\text{CO}_2$  (Ji and Gao 2020). However, results obtained from shallow CO<sub>2</sub> vents show that increased  $p\text{CO}_2$ , as windows for future OA, decreased the abundance and diversity of macroalgae in Japan, reflecting the same findings from the Mediterranean (Porzio et al. 2011; Agostini et al. 2018; Wada et al. 2025). In the present study, macroalgal species grown at high CO<sub>2</sub> downregulated their CCMs (Fig. 3) and suffered more from photoinhibition (Figs. 4, 5) under incident levels of solar radiation. This response is consistent with a reduction in CCM activity inferred from  $\delta^{13}\text{C}$  values (Wada et al. 2025). Since laboratory tests on many macroalgae used their adult thalli grown under low light, synergistic impacts of pH drop and high light as shown in this work explained the knowledge gap between laboratory-controlled experiments and field in-situ CO<sub>2</sub> observations.

Although elevated  $p\text{CO}_2$  near a vent increased photosynthetic activity in 13 species of macroalgae, as indicated by the enhanced electron transport ( $\text{ETR}_{\text{max}}$ ) and light utilization efficiency ( $\alpha$ ) (Fig. 2), this apparent benefit may be offset by concurrent physiological costs. OA-enhanced photorespiration (Xu and Gao 2012) and increased mitochondrial respiration (Ji and Gao 2020) likely exacerbate respiratory carbon loss, while the reduced photochemical saturation light intensity ( $E_k$ ) suggests that algae acclimated to high CO<sub>2</sub> become more susceptible to high-light stress during midday (Powles 1984; Aro et al. 1993; Häder et al. 1998; Vass and Aro 2008). The exacerbated PSII damage under combined high CO<sub>2</sub> and high light (Fig. 5) further confirms that acidification reduces macroalgal tolerance to solar radiation.

While earlier studies at CO<sub>2</sub> vents have documented reduced macroalgal diversity and shifts in community structure (Porzio et al. 2011; Agostini et al. 2018; Harvey et al. 2021), the underlying physiological mechanisms driving these patterns have remained largely unresolved. Superficially, our observation that macroalgae near the vent exhibited



**Fig. 5.** The damage rate to PSII ( $k$ ), the repair rate to PSII ( $r$ ) and the ratio of  $r$  to  $k$  in macroalgae exposed to high light ( $\sim 300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). (a) *Gelidium elegans* and (b) *Tricleocarpa cylindrica* were collected from “reference” ( $p\text{CO}_2 = 360 \mu\text{atm}$ ) and Representation Concentration Pathway (RCP) 4.5 ( $p\text{CO}_2 = 571 \mu\text{atm}$ ). (c) *Dictyopteros undulata* was only collected from RCP 4.5 ( $p\text{CO}_2 = 571 \mu\text{atm}$ ). The open and gray bars represent ambient CO<sub>2</sub> (AC, pH<sub>T</sub> = 8.1) and high CO<sub>2</sub> (HC, pH<sub>T</sub> = 7.9) treatments, respectively. Each data point is the mean  $\pm$  SD ( $n = 3$ ). The symbol “\*” indicates significant differences between treatments,  $p < 0.05$  ( $t$ -test).

higher  $\text{ETR}_{\text{max}}$  than those at the reference site appears to be contrastingly different from that by Porzio et al. (2018, 2020). While this discrepancy likely reflects species-specific responses, as well as differences in environmental conditions

(e.g., depth and light regime), previous studies have shown that macroalgae grown under high CO<sub>2</sub> had elevated photorespiration, which enhances electron flow even under zero dissolved inorganic carbon conditions (Xu and Gao 2012). Therefore, faster ETRs can be expected in macroalgae acclimated to high CO<sub>2</sub> and light, due to the combined effects of photorespiratory and carboxylation processes. These contrasting patterns underscore that OA acts as a selective filter rather than uniformly enhancing photosynthesis. Critically, our data reveal that this apparent contradiction is resolved by examining photoinhibition dynamics: OA exacerbates photoinhibition under high light, and this effect is significantly more pronounced in red algae than in brown algae. This differential sensitivity provides a mechanistic explanation for the observed community shifts toward brown algal dominance near the vent.

Specifically, the decrease in net photosynthetic rates ( $V_{max}$ ) and increase in half-saturation constants ( $K_{0.5}$ ) for CO<sub>2</sub>-dependent photosynthesis in *G. elegans*, *D. undulata*, and *P. elata* under OA conditions (Fig. 3; Supporting Information Table S5) indicate a decreased affinity for inorganic carbon, a physiological signature of CCM downregulation (Giordano et al. 2005; Cornwall et al. 2017). This interpretation is further supported by parallel  $\delta^{13}C$  analyses from the same vent system, which showed more negative values in macroalgae from high  $pCO_2$  zones, being consistent with a shift from active CCM-based HCO<sub>3</sub><sup>-</sup> uptake to passive CO<sub>2</sub> diffusion (Wada et al. 2025). While CCM down-regulation may confer energy savings under low light, it comes at a cost: under high-light conditions, the combination of reduced CCM activity and acidic stress exacerbates photoinhibition, leading to greater PSII damage and impaired repair (Fig. 5). Brown algae, with their greater capacity for NPQ (Fig. 4c), are better able to dissipate excess energy and mitigate this damage. This differential photoprotective capacity offers a physiological explanation for the observed replacement of red algae by brown algae in acidified, shallow waters. Conclusively, macroalgae can benefit from the increased CO<sub>2</sub> availability under low light but be harmed under high light due to enhanced photoinhibition and photodamages (Figs. 3, 4) (Crawley et al. 2010; Hopkinson et al. 2011; Xu and Gao 2012).

Results from the shifting tests, in which the macroalgal species were transplanted between the CO<sub>2</sub> vent sites and the distant reference sites (Figs. 4, 5) further confirmed that OA increases the sensitivity of representative macroalgae to high light. This was evidenced by decreases in the effective quantum yield of PSII and ETR of PSII, as well as an increased NPQ. Non-photochemical quenching is known to dissipate excessively absorbed light energy (Adams III and Demmig-Adams 1994; Ruban 2016), which involves xanthophyll cycles (Young and Frank 1996; Lohr and Wilhelm 1999), that are known to be absent in red macroalgae (Falkowski and Raven 1997). The red macroalga, *G. elegans*, exhibited higher levels of damage with less capability for repair under the

combination of high light and high CO<sub>2</sub> (Fig. 5). Brown algae are known to possess xanthophyll cycle pigments, along with rapid formation and slow epoxidation of zeaxanthin (García-Mendoza and Colombo-Pallotta 2007; Nan et al. 2022), so that they have a high capacity to dissipate excess energy and protect them from photoinhibition, thus allowing them to dominate near CO<sub>2</sub> vents (Fig. 4c).

In conclusion, our study demonstrates that: (1) along a natural pH/ $pCO_2$  gradient at Shikine island, increased  $pCO_2$  was associated with reduced macroalgal diversity and a shift from red to brown algal dominance; (2) elevated  $pCO_2$  exacerbates photoinhibition under high light, with red algae (*G. elegans*) suffering greater PSII damage and impaired recovery compared to brown algae (*D. undulata*); and (3) this differential photoinhibition sensitivity is linked to photoprotective capacity, brown algae possess greater NPQ, enabling them to dissipate excess energy more effectively under combined acidification and high-light stress. Together, these findings reveal that the ecological impacts of OA on macroalgal communities are mediated by interactive effects with light stress, and that photophysiological traits, particularly photoprotective capacity, may serve as predictors of species vulnerability under future ocean conditions. Brown algae, with their superior resilience, are likely to emerge as “winners” in shallow, acidified coastal waters where high light and low pH co-occur.

### Authors Contributions

Di Zhang: conceptualization, investigation, funding acquisition, writing – original draft preparation, writing – review and editing. Shigeki Wada: investigation, writing – review and editing. Jason Hall-Spencer: writing – review and editing. Kunshan Gao: conceptualization, funding acquisition, writing – review and editing. All authors contributed to the article and approved the submitted version.

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### Conflicts of Interest

None declared.

## Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article.

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