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# Physiological acclimation of the green tidal alga *Ulva prolifera* to a fast-changing environment

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ABSTRACT

To aid early warning and prevent the outbreak of green tides in the Yellow Sea, both the growth and photosynthetic performance of *Ulva prolifera* were studied after culture in different temperatures (18, 22, and 26 °C) and light intensities (44, 160, and 280 μmol $m^{-2}·s^{-1}$). Furthermore, their instantaneous net photosynthetic performance (INPP) was studied to determine the resulting environmental acclimation. The relative growth rates of *U. prolifera* significantly decreased in response to increasing temperature, while they increased with increasing light intensity. Culture at higher light intensities significantly increased INPP, while higher temperatures decreased the INPP. Culture at lower temperatures lowered INPP, while increased growth temperature increased the effect. These results suggest that high temperatures during the cold season inhibited *U. prolifera* growth. However, low temperatures during the warm season increase biomass and may cause a large-scale green tide. These results help to understand the correlation between *U. prolifera* blooms and extreme weather.

## 1. Introduction

Green tides as a consequence of the proliferation of green algae such as *Ulva* and *Chaetomorpha* have been reported worldwide. Considerable blooms of green macroalgae have already happened in Europe (Denmark, Netherlands, France, and England), Asia (China, Japan, and Korea), North America, and Australia (Choi et al., 2010; Kim et al., 2011). Since 2007, *Ulva* blooms have consecutively occurred along the coastal areas of the Yellow Sea. In June 2008, the world's largest green-tide with an affected area of about 600 $km^2$ occurred along the coast of the Yellow Sea near Qingdao in China, severely threatening the 2008 Olympic Games sailing regatta (China Ocean News, 2008; Liu et al., 2010), causing considerable economic loss for the local government (Liu et al., 2009). The enormous biomass of green algae was suggested to destruct marine ecosystems and destroy ecological service functions, since it promotes oxygen depletion of both the water column and the benthic environment (Lomstein et al., 2006). Furthermore, green algae can negatively impact coastal ecosystems via rapid expansion and via interfering with coastal nitrogen and carbon cycles (Lomstein et al., 2006; Nelson et al., 2008). Therefore, increasing focus has been directed to green tide research with particular attention on its blooming mechanisms. According to previous records, no signs were observed prior to the sudden bloom (Liu et al., 2010; Zhang et al., 2014).

Numerous researchers have tried to explain the *Ulva* bloom. According to previous studies, *Ulva* microscopic propagules were widespread throughout the southern Yellow Sea, and *Porphyra* aquaculture rafts contributed to the attachment of *Ulva* spores (Huo et al., 2014; Zhang et al., 2016). Moreover, different species of *Ulva* showed varied competitive advantages, such as *Ulva prolifera* showed higher nutrient uptake (eg. with an N uptake rate of 33.9 μmol $g^{-1}$ DW·$h^{-1}$ and P uptake rate of 11.1 μmol $g^{-1}$ DW·$h^{-1}$), growth (eg. *U. prolifera* with a growth rate of 37%·$d^{-1}$) and diverse reproductive system than non-bloom forming *Ulva* species (Huo et al., 2013; Liu et al., 2013; Fan et al., 2014; Gao et al., 2017a,b). Especially the distinctive growth and reproductive strategies of *Ulva* spp., including enlarging tubular diameter, formation of new branches, release of zoids, and polarized growth, result in a high growth rate during green-tide formation (Ye et al., 2008; Zhang et al., 2016). These findings indicated *Ulva* as bloom-forming genus.

The influence of ecological factors on the growth and proliferation of *U. prolifera* have also been studied (Dan et al., 2002; Luo et al., 2012; Zhang et al., 2013; Gao et al., 2017a). Seaweeds enhance biomass via photosynthesis; however, excessive light intensity affects both photosynthesis and growth (Copertino et al., 2006; Gao et al., 2016). The level of nutrients including combined nitrogen, phosphorus, and dissolved inorganic carbon influences the photosynthesis, growth, and nutrient contents of macroalgae (Xu et al., 2014; Sjøtun et al., 2015; Ueno et al., 2017). Damaging nitrogen could increase the

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**Table 1**
Treatments of different light intensity and temperature.

| Treatment | 44 μmol $m^{-2}·s^{-1}$ (LL) | 160 μmol $m^{-2}·s^{-1}$ (ML) | 280 μmol $m^{-2}·s^{-1}$ (HL) |
|---|---|---|---|
| 18 °C (LL) | LL-LT | ML-LT | HL-LT |
| 22 °C (ML) | LL-MT | ML-MT | HL-MT |
| 26 °C (HL) | LL-HT | ML-HT | HL-HT |

photoprotective capacity of *Ulva* and sufficient nutrients dissolved in the Yellow Sea ensured the rapid growth of *Ulva* species (Zhang et al., 2013). In addition, Dan et al. (2002) reported the suitable salinity range for the release of reproductive cells of *U. prolifera* of about 13.2–45.3, with a light intensity above 16 μmol $m^{-2}·s^{-1}$. Furthermore, salinity levels of 20 and 35 have been suggested as helpful for the growth of *Ulva* spores (Sousa et al., 2007). Moreover, the photosynthesis and growth showed differences in response to different temperatures, $CO_2$ and pH levels (Xu and Gao, 2012; Li et al., 2016; Gao et al., 2017b).

In response to an increasing frequency of climatic fluctuations and extreme weather events, tolerance and adaptive performance of seaweeds to variable environmental factors have received more attention. Over the past 40 years, the temperature of the oceans increased with a rate of 0.1 °C per decade (IPCC, 2013). Since seaweeds showed a different tolerance to temperature, both abundance and distribution of seaweeds changed apparently after acclimation to environmental changes (Gallon et al., 2014; Sjøtun et al., 2015; Piñeiro-Corbeira et al., 2016). More recently, the correlation between the occurrence and distribution of seaweeds with temperature and varying salinity were reported (Sjøtun et al., 2015). Although the oceanic temperature follows an increasing trend in the long-term, temperature fluctuations have always been observed. A further study suggested that global warming enhances the frequency of extreme weather (Sun et al., 2016). When extreme weather occurs, environmental factors such as light intensity, transparency, and temperature change considerably during a short time, which raises new challenges for seaweed survival, even leading to succession and bloom of several species.

Previous studies have demonstrated the advantageous physiological characteristic of *Ulva*, particularly in response to climate changes (Xu and Gao, 2012; Cui et al., 2015; Sun et al., 2016; Gao et al., 2017b). However, no clear evidence was presented to date to explain the blooming mechanisms and the relationship between *Ulva* bloom and extreme weather. We therefore hypothesized that photosynthetic performances of *Ulva* serve to address the environmental variation. To test this hypothesis, we chose the dominate bloom species *U. prolifera* for this study and investigated its growth and photosynthetic performance when cultured at different light intensities and temperatures. For the first time, we exposed the experimental algae under instantaneous light intensities and temperature conditions to study their instantaneous photosynthetic performance. The results of this study will be helpful to understand the *Ulva* blooming mechanisms with relation to physiological acclimation. Particularly, the relationship between algae bloom and a fast-changing environment has been investigated, which will benefit the early warning and thus, the prevention of green tides.

## 2. Materials and methods

### 2.1. Sample collection and preparation of the Ulva materials

In May 2011, about 50 g thalli of *Ulva* at the vegetative state and at a length of about 7 cm were collected from the Lianyungang sea area (119.38 E, 34.58 N), Jiangsu province, China. The temperature and salinity at the sampling site were 22 °C and 28, respectively. Algae were cleaned of debris and epiphytes, gently rinsed using sterile seawater, and transported to the laboratory in a cool box at about 5 °C. Molecular methods were adopted to identify *Ulva prolifera* (Zhang et al., 2016). The healthy thalli of *U. prolifera* were cultured in tanks at 20 °C, 12:12 L:D photoperiod, and 100 μmol $m^{-2}$ $s^{-1}$ light intensity for two days prior to the experiments (Jiangnan, Ningbo, China). The natural seawater enrichment medium was obtained from sterile natural seawater under addition of 60 μM $NaNO_3$ and 8 μM $KH_2PO_4$ and gentle bubbling with filtered air.

### 2.2. Experimental design

Three light intensities (44, 160, and 280 μmol $m^{-2}$ $s^{-1}$) and three temperatures (18, 22 and 26 °C) were set via GXZ-300C intelligent llumination incubators (Jiangnan, Ningbo, China). Therefore, a total of nine growing/instantaneous conditions were used (see Table 1). Healthy thalli were cultured in 500 ml conical flasks in filtered natural seawater (salinity 30, enriched with 60 μM $NO_3^-$ and 8 μM $PO_4^{3-}$) at a stocking density of 0.02 g $L^{-1}$, and three triplicates were conducted per treatment. The photoperiod was set to 12:12 light:dark. The seawater medium was vigorously aerated and exchanged every two days; fresh weight was measured to evaluate the growth rate. After one week, the net photosynthetic rates (NPR) of *U. prolifera* were measured in the acclimation conditions and also after a sudden transfer to all conditions (i.e., 81 treatments were performed).

### 2.3. Measurement of growth

The fresh weight was obtained during the experiment and was used to calculate the growth rate of seaweeds according to the following formula: $RGR = 100*(lnW_2-lnW_1)/(T_2-T1)$, where *RGR* represents the relative growth rate (%·$day^{-1}$), $W_1$ and $W_2$ represent the fresh weight at days $T_1$ and $T_2$, respectively.

### 2.4. Measurement of net photosynthetic rate

A Clark-type oxygen electrode (YSI Model 5300, USA) was used to measure the net photosynthetic rates of *U. prolifera* in response to different conditions. The thalli were cut into segments with a length of about 1 cm, and then restored under growth conditions for 1 h (Zhou et al., 2016). After that, about 0.05 g of fresh weight thalli of every condition was introduced into a photosynthetic chamber containing 8 mL seawater. The photosynthetic rate was measured using normal seawater, the time for measurement was less than 6 min, and the $O_2$ concentration in seawater medium exceeded less than 10% at the end of measurement. The treatments under different light and temperature conditions were randomly distributed among the $O_2$ measurements.

### 2.5. Statistical analysis

All data analyses were conducted using the software Origin 9.0 and are displayed as mean ± standard deviation. A normal distribution (Shapiro-Wilk, $p > 0.05$) of the data under every treatment was conformed and the variances were equal (Levene's test, $p > 0.05$). Two-way or three-way ANOVA (Tukey's post-hoc test) were used to test for differences using the SPSS 17.0. $P < 0.05$ was considered to be significant.

## 3. Results

The effects of light and temperature on the growth of *U. prolifera* are

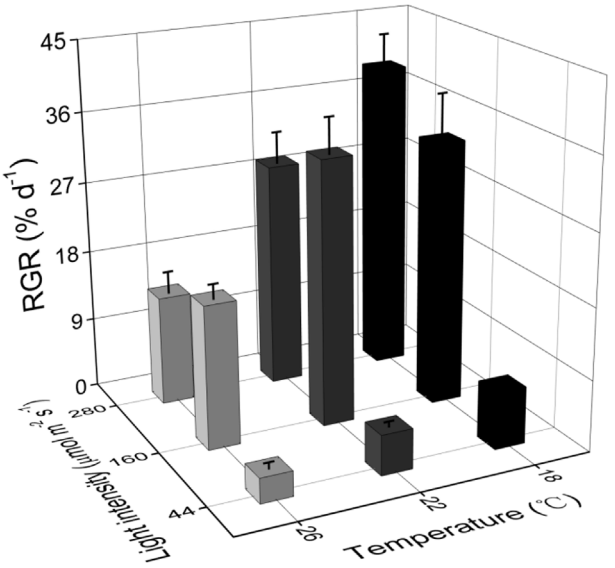


**Fig. 1.** Relative growth rate (RGR) of *U. prolifera* growing at different temperature and light intensity conditions in 1 week. n = 3 per treatment of light and temperature combination.

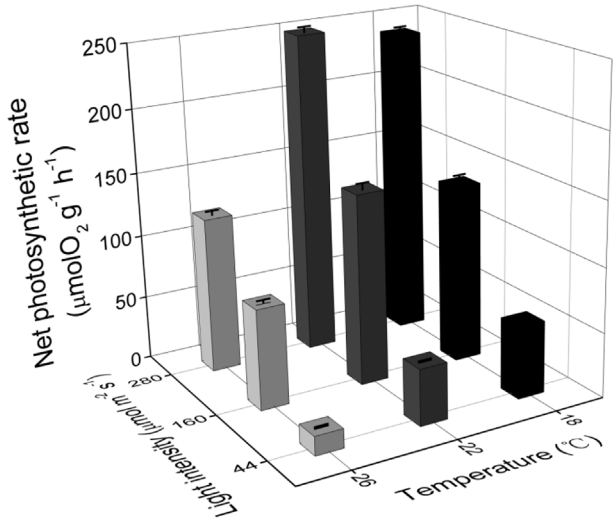


**Fig. 2.** Net photosynthetic rates of *U. prolifera* growing at different temperature and light intensity conditions after 1 week. n = 3 per treatment of light and temperature combination.

**Table 2**
Two-way analysis of variance for the effects of light and temperature on RGR and net photosynthetic rates (Photo). Temperature*light means the interactive effect of temperature and light, df means degree of freedom, F means the value of F statistic, and Sig. means p-value.

| Source | SGR | | | Photo | | |
|---|---|---|---|---|---|---|
| | df | F | Sig. | df | F | Sig. |
| Temperature | 2 | 51.76 | < 0.001 | 2 | 162.696 | < 0.001 |
| Light | 2 | 150.837 | < 0.001 | 2 | 599.543 | < 0.001 |
| Temperature*Light | 4 | 9.944 | < 0.001 | 4 | 20.747 | < 0.001 |
| Error | 18 | | | 18 | | |

shown in Fig. 1. Two-way ANOVA showed that light and temperature had an interactive effect, and both light and temperature exerted a main effect on the RGR of *U. prolifera* (see Table 2). A *post hoc* Tukey HSD comparison ($P = 0.05$) showed that RGR decreased with increasing temperature at all conditions during the experiment, *U. prolifera* showed an RGR of 3.15–39.31%·$d^{-1}$ and the highest RGR was observed at 18 °C and 280 μmol $m^{-2}$·$s^{-1}$. The RGR at the lowest light intensity (44 μmol $m^{-2}$·$s^{-1}$) was significantly lower than that at higher light intensities (160 and 280 μmol $m^{-2}$·$s^{-1}$) ($p < 0.05$); however, no significant difference was found between algae at 160 μmol $m^{-2}$·$s^{-1}$ and at 280 μmol $m^{-2}$·$s^{-1}$ ($p > 0.05$).

Results showed an interactive effect between light and temperature, and both light and temperature exerted a main effect on net photosynthetic performance of *U. prolifera* (Table 2 and Fig. 2). *Post hoc* Tukey HSD comparison ($P = 0.05$) demonstrated that the NPR increased with increasing light intensity and temperature. High NPR values of 43.64–250.00 μmol$O_2$·$g^{-1}$·$h^{-1}$ were observed at a temperature range from 18 to 22 °C, which was significant higher than the NPR of 14.76–121.50 μmol$O_2$·$g^{-1}$·$h^{-1}$ obtained at 26 °C ($p < 0.05$). The lowest NPR of 14.76 μmol$O_2$·$g^{-1}$·$h^{-1}$ was obtained at 26 °C and 44 μmol $m^{-2}$·$s^{-1}$, while the highest NPR of 250.00 μmol$O_2$·$g^{-1}$·$h^{-1}$ was obtained at 22 °C and 280 μmol $m^{-2}$·$s^{-1}$.

These results showed that NPR were significantly influenced by both growth light and temperature ($p < 0.05$) (Table 3). *U. prolifera* cultured at higher light intensities showed significantly higher instantaneous NPR, whereas culture at higher temperatures resulted in significantly lower instantaneous NPR ($p < 0.05$). NPR at the low light intensity of 44–160 μmol $m^{-2}$·$s^{-1}$ showed no significant differences

**Table 3**
Instantaneously net photosynthetic performances (NPR) of *U. prolifera* growing at different conditions. n = 3 per treatment of light and temperature combination. Data showed as values + SD.

| Measurement temperature (°C) | Growth light intensity (μmol·$m^{-2}$ $s^{-1}$) | Growth temperature (°C) | NPR (μmol$O_2$·$g^{-1}$·$h^{-1}$) |
|---|---|---|---|
| | 44 | 18 | 52.16 ± 6.95 |
| | 44 | 22 | 38.72 ± 5.75 |
| | 44 | 26 | 39.68 ± 6.87 |
| | 160 | 18 | 38.84 ± 11.36 |
| | 160 | 22 | 52.68 ± 15.57 |
| | 160 | 26 | 24.48 ± 2.2 |
| | 280 | 18 | 28.12 ± 10.98 |
| | 280 | 22 | 22.86 ± 10.78 |
| | 280 | 26 | 35.58 ± 4.5 |
| 22 | 44 | 18 | 139.08 ± 15.71 |
| | 44 | 22 | 116.68 ± 18.25 |
| | 44 | 26 | 112.44 ± 20.45 |
| | 160 | 18 | 138.88 ± 12.44 |
| | 160 | 22 | 162.42 ± 28.68 |
| | 160 | 26 | 69.64 ± 14.49 |
| | 280 | 18 | 145.08 ± 5.3 |
| | 280 | 22 | 105.84 ± 9.84 |
| | 280 | 26 | 119.4 ± 2.55 |
| 26 | 44 | 18 | 200.56 ± 20.82 |
| | 44 | 22 | 158.28 ± 17.92 |
| | 44 | 26 | 158 ± 32.43 |
| | 160 | 18 | 211.88 ± 24.78 |
| | 160 | 22 | 237.6 ± 29.46 |
| | 160 | 26 | 96.76 ± 13.95 |
| | 280 | 18 | 239.76 ± 8.71 |
| | 280 | 22 | 160.74 ± 0.93 |
| | 280 | 26 | 165 ± 19.52 |

($p > 0.05$), but was significantly higher than that at the high light intensity of 280 μmol $m^{-2}$·$s^{-1}$ ($p < 0.05$). Net photosynthetic performances were significantly influenced by temperature and indeed, *U. prolifera* at the lower temperature showed higher net photosynthetic performances ($p < 0.05$).

Three-way ANOVA showed that both growth light and temperature exerted a main effect on NPR of *U. prolifera* (Table 4). *U. prolifera* cultured at different temperatures showed significantly different photosynthetic performances in response to instantaneous temperatures (Fig. 3). Photosynthetic performances of *U. prolifera* cultured at a low temperature of 18 °C were significantly influenced by instantaneous

**Table 4**
Three-way analysis of variance for the effects of growth light, growth temperature and measurement temperature on net photosynthetic rates (NPR). df means degree of freedom, F means the value of F statistic, and Sig. means p-value.

| Source | | | NPR | | |
|---|---|---|---|---|---|
| Growth temperature (°C) | Growth light ($\mu mol \cdot m^{-2} s^{-1}$) | Measurement temperature (°C) | df | F | Sig. |
| 18 | 44 | 18 | 2 | 4.382 | 0.067 |
| | | 22 | 2 | 5.115 | 0.051 |
| | | 26 | 2 | 7.7 | 0.022 |
| | 160 | 18 | 2 | 0.26 | 0.779 |
| | | 22 | 2 | 6.481 | 0.032 |
| | | 26 | 2 | 10.295 | 0.011 |
| | 280 | 18 | 2 | 3.259 | 0.11 |
| | | 22 | 2 | 15.386 | 0.004 |
| | | 26 | 2 | 7.794 | 0.021 |
| 22 | 44 | 18 | 2 | 5.601 | 0.042 |
| | | 22 | 2 | 1.436 | 0.309 |
| | | 26 | 2 | 229.783 | < 0.001 |
| | 160 | 18 | 2 | 52.034 | < 0.001 |
| | | 22 | 2 | 1.688 | 0.262 |
| | | 26 | 2 | 94.683 | < 0.001 |
| | 280 | 18 | 2 | 90.075 | < 0.001 |
| | | 22 | 2 | 2.525 | 0.16 |
| | | 26 | 2 | 26.622 | 0.001 |
| 26 | 44 | 18 | 2 | 0.286 | 0.761 |
| | | 22 | 2 | 4.681 | 0.06 |
| | | 26 | 2 | 7.64 | 0.022 |
| | 160 | 18 | 2 | 3.088 | 0.12 |
| | | 22 | 2 | 20.15 | 0.002 |
| | | 26 | 2 | 38.864 | < 0.001 |
| | 280 | 18 | 2 | 1.879 | 0.232 |
| | | 22 | 2 | 15.896 | 0.004 |
| | | 26 | 2 | 71.79 | < 0.001 |

temperatures ($p < 0.05$). *U. prolifera* cultured at mid and high temperatures showed significantly higher instantaneously photosynthetic performances at temperatures between 18 and 22 °C than at a high temperature of 26 °C.

## 4. Discussion

Environmental acclimation of growth can be used to explain boh the wide distribution and bloom of opportunistic macroalgae. In previous studies, algal growth rates have been reported to be regulated by environmental factors such as nutrient level, irradiance, and temperature, while salinity significantly influenced the distribution (Taylor et al., 2001; Lideman et al., 2012; Kim et al., 2016). Given the relatively stable salinity conditions during different years and seasons and the decades of eutrophication of the Yellow Sea, both salinity and nutrient levels were regarded as basic rather than inducing factors of algae outbreak (Paerl, 1997; Wu et al., 2015, 2017). In contrast, the seasonal variation of day-night light period and temperature should be concerned. Indeed, due to global warming, extreme weather rapidly and more frequency induces changes of irradiance and temperature (Sun et al., 2016). Thus, studies about the influence of light intensity and temperature on the adaptive and acclimate performance of algae have attracted increasing attention. This study focused on the bloom stage of a green tide. Prior to the experiment, the field environmental conditions during the bloom stage were evaluated. According to a field survey, the field temperatures increased from 10.45 °C to 27.49 °C (Wu et al., 2015). However, the light intensity of the sea surface ranged below 30 $\mu mol\ m^{-2} s^{-1}$ on rainy days, between 30 and 300 $\mu mol\ m^{-2} s^{-1}$ on cloudy days, and generally above 300 $\mu mol\ m^{-2} s^{-1}$ on sunny days; the maximal light intensity was approximately 2000 $\mu mol\ m^{-2} s^{-1}$ (Cui et al., 2015). In the present study, the growth pattern of *U. prolifera* agreed with previous studies (Wu et al., 2000; Xu et al., 2014; Cui et al., 2015). However, different experimental designs or different adaptive abilities of algae at the sampling sites might strongly influence the resulting growth patterns.

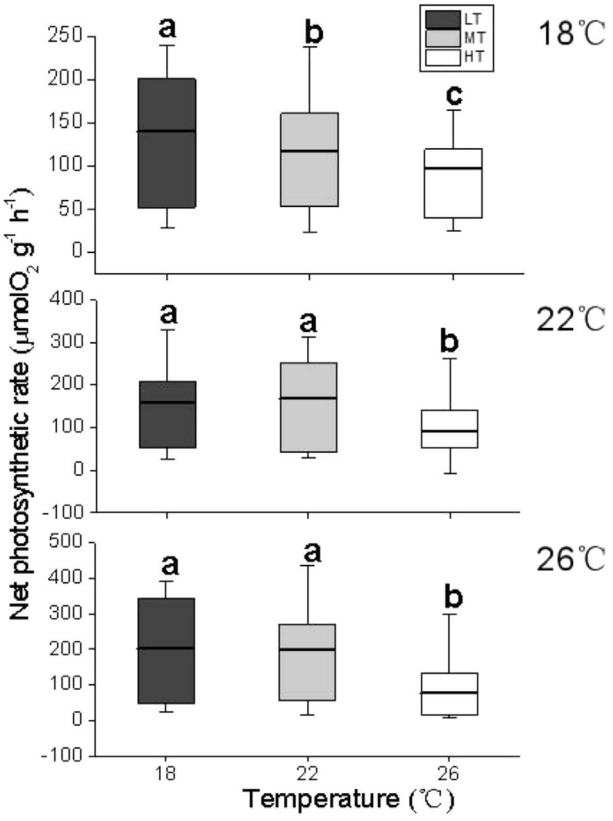


**Fig. 3.** Net photosynthetic performances of *U. prolifera* at different measurement conditions. Boxplots are displayed as is standard, the boxes as the ends of the lower and upper quartiles, whiskers extending to highest and lowest values that are within 1 interquartile range (IQR) of lower/upper quartile. n = 3 per treatment of light and temperature combination. (LT, MT, HT indicate different measurement temperatures of 18, 22 and 26 °C, respectively).

Algae collected from different sampling sites showed different growth performances in a new environment, which has been suggested to be the result of long-time environmental acclimation. At optimal light or temperature, algae growth increased with acclimation time, while it decreased under sub- and supra-optimal conditions (Eggert and Wiencke, 2000; Lideman et al., 2012). The same phenomenon was observed in a previous study by Novaczek et al. (1990). However, in the present study, after culture at low light and temperature conditions, *U. prolifera* showed lower photosynthetic rates when exposed to sudden higher light levels and temperature. While higher photosynthetic rates were observed in response to sudden lower temperature and light, after *U. prolifera* had been cultured at high levels of temperature and light. These findings show that specific physiological performance does not correspond to the light/temperature growth pattern and a similar phenomenon was demonstrated in a previous study on Antarctic algae (Eggert and Wiencke, 2000). Thus, to explain the observed phenomenon, the total metabolism including photosynthesis and respiration acclimation should be considered.

The involvement in photosynthesis of efficient $CO_2$ concentrating mechanisms (CCMs) of macroalgae has been reported before (Kremer

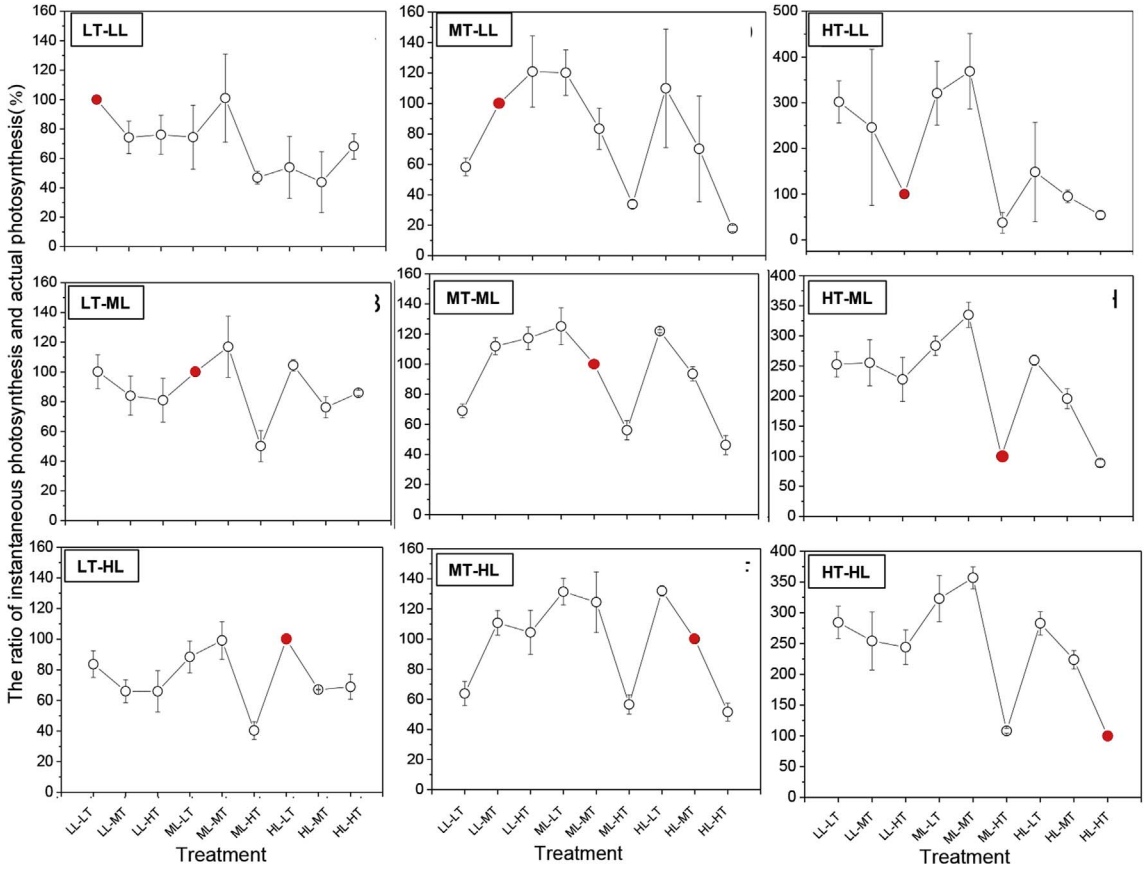


**Fig. 4.** Photosynthesis ratios of *U. prolifera* at different measurement conditions to at growth condition. The red dot represent net photosynthetic rate under growth conditions. n = 3 per treatment of light and temperature combination. (LT, MT, HT indicate different measurement temperatures of 18, 22 and 26 °C, respectively; LL, ML and HL indicate light intensities of 44, 160 and 280 μmol $m^{-2}$·$s^{-1}$, respectively). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and Küppers, 1977; Roberts et al., 2007; Xu et al., 2012; Gao et al., 2016). The mechanisms have been suggested as biological advantages to enhance the capacity of carbon fixation, biomass accumulation, and environmental acclimation via photosynthesis of alga (Liu et al., 2013). Thus, both distribution and growth of *U. prolifera* were observed on *Pyropia* rafts and rocks in winter under low daytime irradiance (Liu et al., 2010; Zhang et al., 2014). In addition, a living *U. prolifera* thallus was found under a shading condition caused by thick mats in summer, where the upper-most layers of algae were exposed to high solar radiation. The above acclimation was a result of light acclimation after growth at different light conditions. However, how a sudden change of light levels influenced the net photosynthetic performance of *U. prolifera* was not obvious in most cases in the present study.

In contrast, *U. prolifera* cultured at different temperatures showed significantly different photosynthetic performances to sudden temperatures changes (Fig. 4). With increasing growth temperatures, the net photosynthetic performances of algae at other instantaneous conditions decreased. These findings indicate that temperature acclimation significantly influenced instantaneous net photosynthetic performances of algae. To explain this phenomenon, mechanisms of changeable temperatures influencing photosynthesis should be considered. After long-term exposure to low temperatures, the concentrations of both photosystem II reaction centers and light-harvesting pigments decreased (Machalek et al., 1996; Ueno et al., 2017). Furthermore, higher levels of photosynthetic enzymes or iso-enzymes were synthesized (Mann, 1991; Scherner et al., 2016). While supra-optimal temperature led to structural changes of photosynthetic proteins, even causing denaturation, photosystem II was inhibited, resulting in decreased photosynthesis (Fork et al., 1979; Sendall et al., 2015).

In our experiment, the net photosynthetic rate was obtained via $O_2$ release; thus, temperature acclimation of respiration had to be considered. A previous study showed that respiration increased three-to six times when temperature increased from 0 °C to 10 °C; however, photosynthesis increased two-to three times, which indicated high temperature sensitivity of respiration. Changes of respiratory enzyme concentration were observed, while no evidence for changes of temperature optima of respiration were found under temperature acclimation (Wiencke et al., 1993). Accordingly, respiration was more temperature sensitive than photosynthesis. Thus, net photosynthetic performance was a meaningful metric to evaluate the temperature tolerance of algae, which has previously been suggested by Kübler et al. (1991).

Generally, our data suggests that high temperatures would inhibit the growth of *U. prolifera* during the cold season, resulting in a decrease of biomass, which would be meaningful for the prediction of the initial biomass of green tide algae. In contrast, the sudden appearance of cold weather during the warm season would lead to a sudden increase of *U. prolifera* biomass, thus potentially causing a large-scale green tide. In future, the frequency of extreme weather can be expected to enhance due to global warming; consequently, the boom of harmful algae, such as *U. prolifera*, will also increase. Accordingly, the floating patches of *Ulva* originating from the Pyropia yezoensis farms in Southern Yellow Sea then travelled northward towards Shandong Province, driven by prevailing winds and currents (Keesing et al., 2011). The samples collected from Lianyungang area also come from the origin, indicating the results of the study can explain the green tide phenomenon in Yellow Sea. However, more research should be conducted to further predict the bloom of *U. prolifera*.

## Acknowledgments

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