Acutely Rising Temperature Reduces Photosynthetic Capacity of Phytoplankton Assemblages in Tropical Oceans: A Large-Scale Investigation

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Climate changes interacting with human activities are raising the temperature in global oceans. To explore physiological responses of in situ phytoplankton assemblages to increasing temperatures, we conducted a shipboard experiment in tropical regions of the eastern Indian Ocean, Java Sea, and southern South China Sea. Throughout the surveyed areas, phytoplankton biomass (Chl a) ranged from 0.09 to 0.86 µg L$^{-1}$ (median, 0.22 µg L$^{-1}$) in the surface and from 0.30 to 0.99 µg L$^{-1}$ (median, 0.50 µg L$^{-1}$) in maximal chlorophyll layer (DCM), respectively. Picophytoplankton that occupied 27–89% (79%) and 83–92% (88%) of total Chl a in the surface and DCM layers, ranged from 3.69 × 10$^4$ to 23.10 × 10$^4$ cells mL$^{-1}$ (3.69 × 10$^4$ cells mL$^{-1}$) and from 7.44 × 10$^4$ to 25.70 × 10$^4$ cells mL$^{-1}$ (12.60 × 10$^4$ cells mL$^{-1}$), respectively. Synechococcus took up 30–97% (78%) of pico-cells compositions in the surface layer, while, in the DCM layer, Prochlorococcus took up 42–98% (91%). Moreover, the maximal photochemical quantum yield ($F_V/F_M$) of photosystem II (PS II) and the rapid light curve (RLC)-derived light utilization efficiency ($\alpha$) were lower in the surface layer than that in the DCM layer, but the saturation irradiance ($E_k$) was higher. In particular, we found that acutely rising temperature decreased the $F_V/F_M$ and $\alpha$ in both the surface and the DCM layers but increased the absorption cross-section ($\sigma_{PSII}$) of PSII photochemistry. Our results clearly indicate that the presently rising temperature adversely affects the photophysiology of natural phytoplankton assemblages in tropical oceans.

Keywords: rising temperature, photosynthetic performance, phytoplankton assemblages, community structure, tropical oceans
INTRODUCTION

Marine phytoplankton, a group of single-cell organisms (Pachiappan et al., 2019), are the major primary producers in aquatic ecosystems. They contribute to about half of a global carbon fixation (Field et al., 1998) and are thus considered to play an important role in mitigating the effects caused by excessive atmospheric CO₂ by photosynthesis (Cavicchioli et al., 2019; Buesseler et al., 2020). The photosynthesis of phytoplankton is regulated by numerous environmental variables, such as solar UV radiation, temperature, and mixing, etc. (Gao et al., 2019; Jin et al., 2019), among which the temperature is a particularly important factor (Jin and Agustí, 2018). This is because the varying temperature can alter enzymes activities within cells, regulate their physiological metabolisms, and ultimately affect photosynthesis and growth (Gao et al., 2019). Rising temperature is often detected to enhance the activities of photosynthetic-involved enzymes of phytoplankton, like the Ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), thus leading to the promotion of photosynthetic oxygen production and carbon fixation (Li et al., 1984; Young et al., 2015). Such an increased temperature was also observed to compensate for the negative effects of other stressors like high light (Bouteflas et al., 2002) or UV-B radiation (Jin et al., 2019) upon photosynthesis. Therefore, the phytoplankton growth is often stimulated by increased temperature, such as for diatoms Chaetoceros tenuissimus and Synedra sp. (Jin and Agustí, 2018) or coccolithophore Emiliania huxleyi (Schlüter et al., 2014).

Owing to over-emissions of anthropogenic CO₂, global warming has accelerated since the industrial revolution (IPCC, 2013). In the global climate system, over 90% of the excess heat gained by the planet has been taken up by the oceans (von Schuckmann et al., 2020), enabling surface seawater temperature to rise up to 4°C by the end of this century (IPCC, 2013; Tokarska et al., 2020); the ocean-absorbed heat energy has been reported to penetrate even to 700 m (von Schuckmann et al., 2020). Meanwhile, the frequency and the intensity of marine heatwaves, the regional extreme warming in surface oceans (Hobday et al., 2016), have also increased in the global warming scenario (Oliver et al., 2018). The marine heat wave-induced increase of temperature has been recorded over 6°C in the South Island of the New Zealand during the austral hot summer of 2017/18, largely lowering the coverage of Durvillaea poha and varying local algal diversity (Thomsen et al., 2019). Such a temperature increase has also been detected to reduce nearly 50% of phytoplankton biomass and shift more than 50% of micro-cells to smaller ones (<5 µm) in the Pacific Northwest (Kosro et al., 2006; Kudela et al., 2006). On the other hand, the increasing temperature-activated diatoms blooms have also been observed for, e.g., Chaetoceros coarctatus in the south coast of the southern Australia during the austral summer 2013 (Roberts et al., 2019) and Pseudo-nitzschia australis along the western coast of the North America in April of 2015 (Gentemann et al., 2017; Trainer et al., 2020), as well as polar diatoms around the Antarctic region (Montie et al., 2020). To fully understand the underlying mechanisms, it is necessary to explore how phytoplankton physiologically responds to the increased temperature.

The Indian Ocean, Java Sea, and the southern South China Sea are geographically located in the center of the Indo-Pacific warm pool, the warm surface region of the world (Weller et al., 2016), wherein surface temperature generally maintains over 28°C throughout the year (De Decker, 2016). In the global warming scenario, these tropical regions, being no exception, are subjected to the increased temperature (De Decker, 2016; Weller et al., 2016), leading to a morphological shrink in cell size of phytoplankton (Mousings et al., 2014) and reduction in biomass (Roxy et al., 2016; Zhang et al., 2018). Using an ecological model study, Roxy et al. (2016) reported that the increased temperature had reduced over 20% phytoplankton biomass in the Indian Ocean from 1950 to 2012. With the shipboard experiments, Zhang et al. (2018) found that the increased temperature declined roughly 50% of surface biomass in the southern South China Sea in the summer period of 2017. To date, however, few studies on photosynthetic behaviors of natural phytoplankton assemblages in response to ocean warming have been conducted in these tropical regions. As ambient temperatures in these regions are high, close to or even over the optimal growth temperature of phytoplankton (Jin and Agustí, 2018), we, thus, hypothesized that further elevated temperature would be detrimental to phytoplankton in these regions. However, it is not practicable, although of significance, to launch a large-spatial and long-term incubation experiment to examine phytoplankton responses to rising temperature. Therefore, we investigated the photophysiological responses to acutely elevated temperature of phytoplankton assemblages from the surface or/and the maximal chlorophyll layer (DCM) of the eastern Indian Ocean, Java Sea, and southern South China Sea (Figure 1). Our results clarified how the increased temperature affects the photosynthetic performance of phytoplankton assemblages in the spatial and depth scales; it would be helpful for understanding the ecological effects of rising temperature in these tropical oceans.

MATERIALS AND METHODS

A Study Area and Sampling Protocol

During a cruise from September 21 to November 16, 2020, this experiment was conducted on board of R/V Shiyan 3 in the tropical oceans (i.e., eastern Indian Ocean, southern South China Sea, and Java Sea, and their connecting passages) (Figure 1). The seawater samples were collected from two depth layers: surface (~1-m depth) being taken with a clean pump system and that from the DCM layer being taken with an 8-L Niskin bottle mounted on an SBE 911 plus CTD (Sea-Bird Electronics, Inc., Bellevue, WA, USA). The DCM layer was determined, using a chlorophyll fluorometer equipped with CTD. To eliminate the effects of diel rhythm of phytoplankton photosynthetic activity (Xie et al., 2018), all the seawater samples were taken in the daytime (9 a.m. to 2 p.m.). During the cruise, the seawater temperature and salinity were measured with thermosalinographs (a shipboard CTD) and Sea-Bird CTD.

Experimental Design

To investigate the effects of acutely rising temperature upon the physiology of natural phytoplankton assemblages, the collected
seawater samples from the surface or/and the DCM layers of each station were used to measure photosynthetic performance, using a fast repetition rate fluorometer (FRRf, Chelsea Technologies Group, Ltd., West Molesey, UK) under four or five different temperatures. To improve the signal-to-noise ratio of chlorophyll fluorescence of phytoplankton assemblages, 2-L seawater was concentrated to 100 ml by gently filtering with a 0.45-µm pore-sized nitrocellulose membrane (25 mm, Millipore) within 10 min after being taken from in situ conditions. Then, the concentrated sample was quickly injected into a 10-mL chamber of FRRf that was encircled by a water jacket connected to a circulating thermostatted bath to maintain temperature and dark acclimated for 10 min, followed by measuring chlorophyll fluorescence with the FRRf at in situ temperature. After this, the temperature in a 10-mL chamber was acutely increased by 3°C and maintained for 10 min, and the fluorescence was measured again. The fluorescence of phytoplankton from the surface at each station was sequentially measured under in situ temperature, +3, +6, and +9°C, and that from the DCM layer was measured under in situ temperature, surface, +3, +6, and +9°C. After measuring the fluorescence for one step, we mixed the sample by turning on the mixing button of FRRf to eliminate the effect of light history signals in the sample by turning on the mixing button of FRRf to eliminate the influence of the blank (Cullen and Davis, 2003). We calculated the photochemical PSII quantum yields (Fv/Fm, Fq/Fm) in the dark- and light-regulated state (Genty et al., 1989) as:

\[
\frac{F_V}{F_M} = \frac{F_M - F_D}{F_M} \quad ; \quad \frac{F_q}{F_M} = \frac{F_M - F}{F_M}
\]

After this, we derived the photosynthetic parameters, including the light utilization efficiency (α) and saturation irradiance (Ek, µmol photons m\(^{-2}\) s\(^{-1}\)) from the rapid light curve (RLC) as follows (Webb et al., 1974; Silsbe and Kromkamp, 2012):

\[
\frac{F_q}{F_M} = \alpha \times E_K \times (1 - e^{-\frac{E}{E_K}}) \times E^{-1}
\]

where E denotes actinic light intensity (E, µmol photon m\(^{-2}\) s\(^{-1}\)).

**Chlorophylla Measurement**

To measure the size-fractioned Chlorophylla (Chla) concentration in the surface and the DCM layers, 1-L seawater was sequentially filtered through a 20-µm pore-sized nylon-net filter (25 mm, Millipore), a 3-µm pore-sized polycarbonate filter (25 mm, Millipore), and 0.7-µm pore-sized glass fiber filter (25 mm, Whatman GF/F). And, then, the filters were wrapped in aluminum foils, instantly stored at −20°C until laboratorial analysis. After returning to the laboratory, the refrigerated filters with phytoplankton cells were extracted overnight in magnesium carbonate-saturated 90% acetone (v/v) at 4°C; after centrifuging for 10 min at 3,500 rpm, the extraction was fluorescently measured with a Turner Designs 10 Fluorometer. Chla concentration was calculated, following Parsons et al. (1984). Total Chla concentration was obtained by summing all three size-fractioned Chla concentration.
Picophytoplankton Abundance Measurement

To measure picophytoplankton abundance, the seawater from the surface and DCM layers was pre-filtrated through a 20-µm pore-sized nylon-net filter, dispensed into triplicate 2-mL cryotubes and fixed with a final concentration of 0.5% glutaraldehyde (v/v). After shaken to make the samples being fully mixed, the cryotubes were kept in the dark for 20 min, and then were flash frozen and stored in liquid nitrogen until later analysis. Cell abundance of Prochlorococcus (Pro), Synechococcus (Syn), and pico-eukaryotes (Euk) was measured with an Accuri C6 flow cytometry (Becton-Dickinson, USA), excited with blue argon (488 nm) and red diode lasers (640 nm). The samples were run at a medium-flow rate and collected 40 µL for each measurement with the Accuri C6; and the data were then collected, saved, and analyzed with CellQUEST software.

Statistical Analysis

All the statistical analysis and figures were conducted, using R software (R Core Team, 2020), with packages of “ggOceanMaps” version 1.0.9 (Vihetakari, 2021), “ggplot2” (Wickham, 2016), “scatterpie” version 0.1.5 (Yu, 2020), and “rstatix” version 0.7.0 (Kassambara, 2021). To test the differences between the surface and DCM layers or among different geographical areas or temperature treatments, we firstly determined whether or not the measured parameters violate the normality and homogeneity of variance. If inviolate, the t-test or one-way repeated measures ANOVA was used; otherwise, the Wilcoxon test or the Friedman test was used. The post hoc tests for one-way repeated measures ANOVA and the Friedman test were pairwise paired t-test and the Wilcoxon signed-rank test, respectively. Linear regression was also applied to test the correlation of photochemical parameters to temperature. The significance level was set at 0.05.

RESULTS

During the investigated period, surface seawater temperature and salinity varied from 26.11 to 30.0°C (median, 29.10°C) and from 29.58 to 35.59 (median, 34.32) throughout the surveyed areas, respectively (Supplementary Figure 1). Depth of DCM shoaled from 100 to 35 m from the southern to northern parts of the eastern Indian Ocean, with the temperature increased from 23.28 to 29.30°C (median, 27.90°C); and the DCM depth was 59 m at the S2 station in the South China Sea, with the temperature of 25.80°C.
Surface phytoplankton biomass (Chla) ranged from 0.09 to 0.86 µg L$^{-1}$ throughout the surveyed areas, with a median of 0.22 µg L$^{-1}$ (Figure 2A). Chla concentration was higher in the northern part of the surveyed areas than that in the southern part (Wilcoxon test, $p < 0.001$). Chla in the DCM layer ranged from 0.29 to 0.99 µg L$^{-1}$ (median, 0.50 µg L$^{-1}$) (Figure 2B), being 1.5 to 6.0 times higher than the surface. Picophytoplankton cells (0.7–3 µm) took up 79% (median) of total Chla (range, 27% to 91%) in the surface layer and nano- and micro-cells took up 11 and 8%; while, in the DCM layer, pico-cells took up 88% (range, 80 to 92%), and nano- and micro-cells took up 8 and 4%, respectively. Coinciding with Chla, pico-cells density ranged from $3.20 \times 10^3$ to $2.31 \times 10^6$ cells mL$^{-1}$ (median, $3.69 \times 10^4$ cells mL$^{-1}$) in the surface (Figure 2C), being higher in the northern than the southern parts of the surveyed areas (Wilcoxon test, $p < 0.001$); while, in the DCM layer, their density ranged from $7.44 \times 10^4$ to $2.57 \times 10^6$ cells mL$^{-1}$ (median, $1.26 \times 10^5$ cells mL$^{-1}$) (Figure 2D). Finally, picophytoplankton compositions were dominated by *Synechococcus* (median, 79%; range, 22 to 98%) in the surface, but by *Prochlorococcus* (median, 91%; range, 42 to 98%) in the DCM layer (Figures 2C,D). The pico-eukaryotes contributed to <10% of pico-cells composition in both the surface and DCM layers.

To assess the general effect of acutely increased temperature on photophysiology of phytoplankton over the surveyed regions, the pooled F$_V$/F$_M$ and $\sigma_{PSII}$ were plotted against temperature. The F$_V$/F$_M$ decreased with increased temperature in both the surface and DCM layers (slope, $-0.009$, $p < 0.001$), with no significant difference between these two layers ($p = 0.97$) (Supplementary Figure 2); while the $\sigma_{PSII}$ increased in both the surface (slope, 0.105, $p < 0.001$) and DCM layers (slope, 0.041, $p = 0.03$) (Figure 3). The F$_V$/F$_M$ in the surface had a median value of 0.25 (range, 0.15 to 0.43), lower than that in the DCM layer (median, 0.29; range, 0.17 to 0.35) (t = 2.28, $p = 0.02$) (Figures 4A,B). The slope of F$_V$/F$_M$ against temperature, an indicator of the temperature-caused effect, ranged spatially from −0.018 to −0.001 (Figures 4C,D), with an insignificant difference between the surface and DCM layers. The $\sigma_{PSII}$ in the surface ranged from 3.00 to 7.07 nm$^2$ (median, 4.90 nm$^2$), lower than that in the DCM layer (range, 4.60 to 8.00; median, 6.04 nm$^2$) (Figures 4E,F). At the same time, the $\sigma_{PSII}$ in both the surface and the DCM, was higher in the southern than the northern parts of the surveyed areas (Wilcoxon test, $p < 0.05$), and the acutely increasing temperature-caused promotion (i.e., the slope) on $\sigma_{PSII}$ was higher in the surface than the DCM layer (Wilcoxon test, $p < 0.01$) (Figures 4G,H).

Acutely rising temperature also reduced the rapid light curve (RLC)-derived light utilization efficiency ($\alpha$) (slope, $-0.014$, $p < 0.001$) (Figure 5 and Supplementary Figure 2), with no significant difference between the surface and DCM layers (t = −0.98, $p = 0.33$, Figures 6C,D). Both the $\alpha$ (Figures 6A,B) and $E_K$ (Figures 6E,F) showed great variations throughout the surveyed areas.
FIGURE 4 | Spatial distributions of maximal PS II quantum yield ($A, B, F_{v}/F_{m}$) and dark-adapted absorption cross-section ($E, F, \sigma_{PSII}, \text{nm}^2$), as well as the rising temperature-induced effects (slope) on $F_{v}/F_{m}$ ($C, D$) and $\sigma_{PSII}$ ($G, H$) of phytoplankton assemblages in the surface ($A, C, E, G$) and DCM layers ($B, D, F, H$) throughout the surveyed areas. Bubble size indicates the corresponding value.
the surveyed areas. Moreover, the rising temperature-caused reduction did not occur in the RLC-derived saturation irradiance (E<sub>K</sub>) (Supplementary Figure 3). Finally, the higher α but lower E<sub>K</sub> prevailed in the DCM layer as compared with the surface layer, indicating the low-light acclimation of phytoplankton assemblages therein.

**DISCUSSION**

Model studies, together with field investigations, predicted that global warming would decrease marine primary production through dampening the nutrients up-transport from deep sea (Ruardij et al., 1997; Strom and Fredrickson, 2008; Roxy et al., 2016). In this study, we showed that the acutely increased temperature reduced the maximum photochemical efficiency (F<sub>v/F<sub>m</sub></sub>) and light utilization efficiency (α) of PSII of natural phytoplankton assemblages from both the surface and DCM layers in tropical oceans, thus providing physiological evidence for the adverse effect of rising temperature on the primary productivity. Moreover, we found both the F<sub>v/F<sub>m</sub></sub> and α<sub>PSII</sub> showed similar spatial variations throughout the surveyed regions, and the larger α<sub>PSII</sub>, the higher α, and the lower E<sub>K</sub> presented in the DCM than the surface layer, suggesting the low-light acclimation of phytoplankton assemblages (Jin et al., 2016; Xie et al., 2018).

Chl<sub>a</sub> biomass in the surface showed a markedly spatial variation, as well as pico-cells abundance (Figure 2). Generally, the growth and primary productivity of phytoplankton are regulated by macro- (e.g., nitrogen and phosphate) and/or micro-nutrients (e.g., dissolved iron) (Li et al., 2012a; Chinni et al., 2019; Sherman et al., 2020). In the surveyed areas, the surface N and the P levels were <1.0 and 0.10 µM (data not shown), with the N:P ratio being lower than 16, indicating a nitrogen limitation (Li et al., 2012a), especially in the southern Indian Ocean (Wilcoxon test, 0.05), where Chl<sub>a</sub> biomass and pico-cells abundance were lower. Such a biomass variation could also be attributed by the spatial changes of trace mental iron (Chinni et al., 2019; Twining et al., 2019) that is often believed to regulate phytoplankton growth and has been observed to covary with Chl<sub>a</sub> (Chinni et al., 2019; Sherman et al., 2020). On the other hand, the spatial variation in Chl<sub>a</sub> was less in the DCM layer; it could be explained by the high nutrients that may be enough to support the growth of phytoplankton. For phytoplankton compositions, pico- and nano-cells accounted for more than 90% of total Chl<sub>a</sub> in both the surface and DCM layers, consistent with previous results (e.g., Li et al., 2012a,b). Moreover, *Synechococcus* dominated in the surface layer but *Prochlorococcus* dominated in the DCM layer, as found in this study (Figures 2C,D) or in others (Wei et al., 2019a; Mitbavkar et al., 2020). Different light harvesting complexes between *Synechococcus* and *Prochlorococcus* (phycobilisomes vs. divinyl-Chl<sub>a</sub>/b antenna) and different cell sizes (ca. 0.9 µm vs. 0.6 µm) may make them adaptively prefer the light environments in surface and deep waters. Therefore, *Prochlorococcus* often has a lower light compensation point as compared with *Synechococcus* (Moore et al., 1995) and can more adaptively thrive and dominate in dim-deep waters. Moreover, the surface temperature in the surveyed areas was ~29°C over the thermal-inhibited temperature of 25°C for the growth of *Prochlorococcus* (Moore et al., 1995), probably attributing to its less abundance in the surface layer (Wei et al., 2019a; Mitbavkar et al., 2020).
In addition, weak fluorescence in surface waters often makes Prochlorococcus hardly distinguishable by flow cytometry (Olson et al., 1990), which may also attribute to the lower measured cell counts.

The Fv/Fm and α, the indicators of photosynthetic status of phytoplankton, generally decline under unfavorable growth condition, presumably because of the damage of the PSII reaction center (Ragni et al., 2008; Suggett et al., 2009; Trimborn et al., 2015). The temperature in the surveyed areas usually maintains over 28°C throughout the year (De Deckker, 2016), which is close to or even over the optimal growth temperature of phytoplankton (Jin and Agustí, 2018). Reduction of further elevated temperature in photosynthetic capacity is thus predictable, although phytoplankton in the surface layer may have adaptively tolerated high temperature as indicated by the insignificant effect of initially acute 3°C increase (Figures 3A, 5A). High temperature often makes cells generating excessive reactive oxygen species (ROS) (Anning et al., 2001; Deschaseaux et al., 2019) that is believed to unbalance the light absorption of photoautotrophs and utilization through inactivating the activities of photosynthetic enzymes, e.g., RubisCO, leading to a surplus accumulation of absorbed light energy, and, thus, the damage of photosynthetic apparatus and decrease of the Fv/Fm and α (Anning et al., 2001; Deschaseaux et al., 2019). Meanwhile, the absorption cross-section of PSII photochemistry (σPSII) increased with temperature in both the surface and DCM.
layers (Figures 3C, D). According to Suggett et al. (2009), many phytoplankton species can modulate the $\sigma_{\text{PSII}}$ to enable them to acclimate and adapt to varying light conditions; and the $\sigma_{\text{PSII}}$ can also be regulated by environmental variables, including temperature (Ni et al., 2017), cell size (Moore et al., 2005; Suggett et al., 2009), as well as nutrient status (Suggett et al., 2009). The increase of $\sigma_{\text{PSII}}$ with rising temperature can be explained by the “lake model” that assumes the energy absorbed by light-harvesting systems can transfer between photosynthetic units (Paillotin et al., 1983). If one functional PSII reaction center is inactivated or damaged due to, e.g., high temperature, its light-harvesting systems transfer the absorbed energy to neighboring active PS II, thus enlarging the $\sigma_{\text{PSII}}$. Although the long-term evolution may also enlarge the $\sigma_{\text{PSII}}$ to improve the light-absorbing ability to maintain photosynthesis (Suggett et al., 2009; Hughes et al., 2018b), major pigments of Synechococcus to constitute the light-harvesting complexes are phycobilisomes (Sliwińska-Wilczewska et al., 2020), while that of Prochlorococcus are divinyl derivatives Chla/b (Ralf and Repeta, 1992); such a pigment difference may vary their light-harvesting abilities, thus leading to the differential photosynthetic responses to the acutely increased temperature between the surface and DCM layers. Larger $\sigma_{\text{PSII}}$ prevailed in the southern part of the surveyed areas where phytoplankton may have adaptively improved its light-harvesting abilities to sustain growth (Zhu et al., 2017; Sherman et al., 2020), because of the low nutrient status therein (data not shown). The larger $\sigma_{\text{PSII}}$ has also been suggested to be attributed to light-adapted genotypic feature due to niche partition (Jin et al., 2016), evidenced by the higher $\sigma_{\text{PSII}}$ values of phytoplankton assemblages from deep waters.

In summary, we found that higher saturation irradiance ($E_{k}$), together with lower Chla biomass, prevailed in the Synechococcus-dominated surface layer of the surveyed areas but being opposite in the Prochlorococcus-dominated DCM layer; and lower $F_{V}/F_{M}$ and $\alpha$ occurred in the former than the latter layers. Furthermore, we found the acutely rising temperature decreased the photosynthetic capacity (i.e., $F_{V}/F_{M}$ and $\alpha$) of natural phytoplankton assemblages from the surface and DCM layers of the eastern Indian Ocean, Java Sea, and southern South China Sea. Our results complement others (Roxy et al., 2016) to demonstrate that the ongoing global warming may adversely affect primary productivity in tropical oceans.

**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 author/s.

**AUTHOR CONTRIBUTIONS**

GM conducted the shipboard sampling and physiological measurements. GM, JL, XS, and GL designed the experiments and analyzed the data. GM, XP, and JL performed the pico-cells count determination. LY collected the temperature and salinity data. GM, JL, XS, BL, XX, YT, and GL wrote, discussed, and edited the paper. All authors contributed to the article and approved the submitted version.

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**SUPPLEMENTARY MATERIAL**

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.710697/full#supplementary-material

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