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Interactive Effects of Elevated CO_2 Concentration and Light on the Picophytoplankton *Synechococcus*

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Synechococcus is a major contributor to the primary production in tropic and subtropical oceans worldwide. Responses of this picophytoplankton to changing light and CO_2 levels is of general concern to understand its ecophysiology in the context of ocean global changes. We grew *Synechococcus* sp. (WH7803), originally isolated from subtropic North Atlantic Ocean, under different PAR levels for about 15 generations and examined its growth, photochemical performance and the response of these parameters to elevated CO_2 (1,000 μatm). The specific growth rate increased from 6 μmol m^{-2} s^{-1} to reach a maximum (0.547 ± 0.026) at 25 μmol m^{-2} s^{-1}, and then became inhibited at PAR levels over 50 μmol m^{-2} s^{-1}, with light use efficiency (α) and photoinhibition coefficient (β) being 0.093 and 0.002, respectively. When the cells were grown at ambient and elevated CO_2 concentration (400 vs. 1,000 μatm), the high-CO_2 grown cells showed significantly enhanced rates of electron transport and quantum yield as well as significant increase in specific growth rate at the limiting and inhibiting PAR levels. While the electron transport rate significantly increased at the elevated CO_2 concentration under all tested light levels, the specific growth did not exhibit significant changes under the optimal growth light condition. Our results indicate that *Synechococcus* WH7803 grew faster under the ocean acidification (OA) treatment induced by CO_2 enrichment only under limiting and inhibiting light levels, indicating the interactive effects and implying that the picophytoplankton respond differentially at different depths while exposing changing light conditions.

Keywords: CO_2, growth, light, *Synechococcus*, WH7803

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INTRODUCTION

Synechococcus is a group of picoplanktonic cyanobacteria, along with *Prochlorococcus* constituting the most widespread and abundant group of marine pico-prokaryotic primary producers (Varkey et al., 2016; Kim et al., 2018). *Synechococcus* strains are distributed widely in both freshwater and oceanic environments, with stain-specific physiological traits under influences of nutrients, temperature and light (Partensky et al., 1999; Callieri et al., 2013; Flombaum et al., 2013; Kim et al., 2018). In marine environments, most species and/or strains of *Synechococcus* are found more abundantly in mesotrophic and moderately oligotrophic marine environments (Scanlan et al., 2009; Domínguez-Martín et al., 2016) in tropical to subtropical oceans from 40°S to 40°N,

contributing by about 16% of the global oceanic annual net primary production (Badger et al., 2006; Flombaum et al., 2013).

Among various strains of *Synechococcus*, WH7803 is featured with the presence of abundant phycoerythrin (PE), awarding it a distinguishable red appearance (Morris and Glover, 1981; Stockner and Antia, 1986). The absorption spectra of PE (450–600 nm) is similar to the spectra at the bottom of euphotic zone where the irradiance intensity is about 1% of the surface, suggesting this strain can be adapted to dim light levels (Fogg, 1986; Glover et al., 1986; Stockner and Antia, 1986; Piazena et al., 2002; Flombaum et al., 2013). However, vertical mixing processes in the oceans can episodically move *Synechococcus* cells to shallower layers where light levels are higher (Flombaum et al., 2013), possibly resulting in photoinhibition (Huner et al., 1998). Based on the light attenuation coefficient (K_d) in the clearest pelagic waters, the theoretical light intensity for WH7803 to survive was estimated to be about 23% of the surface intensity (Smith and Baker, 1981). However, laboratory studies revealed that the optimum light levels for its growth ranged from 25 to 200 μmol m^{-2} s^{-1} of PAR (Glover and Morris, 1981; Alberte et al., 1984; Barlow and Alberte, 1985; Campbell and Carpenter, 1986; Kana and Glibert, 1987). In spite of the reported wide range of PAR for optimal growth, little has been documented on its photophysiological performances under different PAR levels.

With progressive ocean climate changes, on the other hand, it has been predicted that the abundance of *Synechococcus* would increase by about 14%, with its distribution range extended to higher latitudes including the Bering Sea, Gulf of Alaska, and Southern Ocean (Flombaum et al., 2013). While increased levels of CO_2 and higher temperature were both suggested to influence *Synechococcus*, experimental tests on its responses to these drivers have been rarely examined (*Synechococcus* sp. CCMP1334 strain under pCO_2 of 750 ppmv at 24°C, pCO_2 380 ppmv at 24°C, and pCO_2 750 ppmv at 20°C, Fu et al., 2007; Lu et al., 2006). Growth of *Synechococcus* strains can be stimulated (Fu et al., 2007; *Synechococcus* sp. CCMP839 strain under pCO_2 of 800 ppmv, Lu et al., 2006) or unaffected (*Synechococcus elongatus* CCMP1379 strain under pCO_2 of 350, 600, 800 ppmv and *Synechococcus* sp. CCMP839 strain under pCO_2 of 350 and 600 ppmv, Lu et al., 2006) by elevated CO_2 concentrations, showing a strain-specific response when grown under constant light levels (40–45 μmol m^{-2} s^{-1} of PAR). It has been suggested that increased availability of CO_2 and the associated acidic stress can affect phytoplankton growth to different directions, leading to positive, neutral and negative effects under different light levels (Gao et al., 2012) due to carbon concentration mechanisms (CCMs) regulation and involved energetic changes. *Synechococcus* strains possess active CCMs, that can concentrate intracellular CO_2 up to about 1,000 times higher than that in seawater (Badger and Andrews, 1982). Therefore, we hypothesize that *Synechococcus* respond differently under different light levels to elevated CO_2 concentration projected to future ocean acidification (OA), and increasing CO_2 availability and different light levels would result in interactive effects on *Synechococcus* WH7803 strain, which was isolated from subtropical North Atlantic Ocean where anthropogenic CO_2 has been drastically increased with progressive OA (Bates and Johnson, 2020). In this work, we examined physiological performances of the strain WH7803 under various light levels and two CO_2 levels (ambient and elevated levels for the present and end of this century, which were about 400 or 1,000 μatm, respectively), and found that the elevated CO_2 concentration to 1,000 μatm did not affect its growth rate at the optimal growth light level but enhanced it at light-limiting and inhibiting levels.

MATERIALS AND METHODS

Synechococcus WH7803 strain, originally isolated from the North Atlantic Ocean (67.496°W, 33.748°N), was obtained from Professor Rui Zhang's lab at the College of Ocean and Earth, Xiamen University, Xiamen, China. The cells were maintained in A^+ medium in 100 mL Quartz tubes under 6 μmol m^{-2} s^{-1} light intensity with a light-dark period of 12:12 h at 23.5 ± 0.5°C in an illuminating incubator (HP1000G-D, Wuhan Ruihua Instrument and Equipment Co., Ltd., China). Before inoculation, the medium and quartz tubes were sterilized at 110°C for 30 min in an autoclave.

Light (PAR) intensity within the incubator was measured using Datalogging Radiometer Model PMA2100 (Solar Light Company, Inc., United States). Six PAR levels of 6, 13, 25, 38, 50, and 100 μmol m^{-2} s^{-1} were set to grow the *Synechococcus* cells by adjusting distance from the light source and/or covering with neutral filters. The cultures were aerated (30 ml min^{-1}) with filtered air (0.22 μm, PVDF Syringe Filter, AllPure, United States). There were three replicates of culture at each treatment (n = 3). Each culture under different light levels was run for 15 generations before measurements of the physiological and biochemical parameters, including specific growth rate, electron transport rate, effective quantum yield and pigments concentration. The initial cell concentration was set at about 500,000 cells mL^{-1}. The concentration of cells was monitored at 9:00 am every other day.

Then we set up experiments to test how the picophytoplankton respond to future OA under the elevated CO_2 level (1,000 ppmv) based on RCP8.5 senario using the current CO_2 level as control (Gattuso et al., 2010; Gao et al., 2012). CO_2 concentrations in the culture medium were initially set up at 400 (LC) or 1,000 (HC) μatm by using the CO_2 pre-equilibrated medium, which were aerated and prepared through a sterilized filter with outdoor air for LC and the air of 1,000 ppmv CO_2 (achieved by using a plant CO_2 chamber) for HC, respectively. After pre-equilibration, the pH of the medium was measured by a pH meter (Orion Star A211, Thermo Fisher Scientific, United States). In the cultures at LC and HC treatments (pH 8.1 vs. 7.8), the pH_{nbs} was significantly different at the early phase (4 days) with less difference at the end (day 10) of the cultures. The initial cell concentrations in the cultures under both CO_2 levels were 500,000 cells mL^{-1}.

Measurement of Specific Growth Rate

The cell concentration in the cultures was enumerated (each sample for at least 30 s) by a flow cytometer (CytoFLEX S, Beckman Coulter, Inc., United States) with a 488 nm emitter (PE and Chl *a* are both excited by this laser beam, with the

emitted wavelengths of 575 and 675 nm, respectively) (Givan, 2011). The tunnels of the auxiliary software CytExpert 2.0 (Beckman Coulter, Inc., United States) were FSC-A (forward scatter light for diameter), PI-A (690 nm for Chl *a*) and PAO-A (585 nm for PE). When phycoerythrin and chlorophyll *a* in *Synechococcus* cells become excited by 488 light, they emit the characteristic lights as mentioned above. By analyzing those emitted light signals through the software, a *Synechococcus* cell could be distinguished from other particles based on its species-specific emission wavelength characteristics. The specific growth rates were calculated using the following formula based on the enumerated cells (Iturriaga and Mitchell, 1986):

$$\mu = \frac{\ln N - \ln N_0}{\Delta t}$$

where N indicates the cell concentration at T time, N_0 the initial cell concentration at T_0, and Δt the duration (days, $T - T_0$). The non-linear fitting of the specific growth rates to growth light levels was performed using the following formula (Platt et al., 1980):

$$\mu = \mu_{\max}(1 - e^{-\frac{\alpha \times PAR}{\mu_{\max}}}) \times e^{-\frac{\beta \times PAR}{\mu_{\max}}}$$

where PAR is the growth light intensity. The μ_{max}, α and β indicate maximal growth rate, light use efficiency and growth photoinhibition coefficient, respectively.

Measurement of Electron Transport Rate and Effective Quantum Yield

Samples for the measurement of relative electron transport rate (*rETR*) were collected directly during the exponential growth phase, which had different concentrations of cells as well as the contents of intracellular chlorophyll. The ETR was measured by using a Multi-color Pulse Amplitude Modulated chlorophyll fluorometer (Multi-color PAM, Walz, Germany), setting measuring wavelength of actinic light at 625 nm (measuring mode Al white, with all samples showing the similar basic fluorescence levels). The range of light curve measurement was from 0 to 798 μmol m^{-2} s^{-1}, which included 13 irradiance steps and each irradiance step was about 10 s. The saturating light pulse (800 ms, 5,000 μmol photons m^{-2} s^{-1}) was applied for determination of ETR. The *rETR* was calculated as follows (Ralph and Gademann, 2005):

$$rETR = \Phi_{\mathrm{PSII}} \times PAR$$

where Φ_{PSII} represents the measured effective quantum yield of photosystem II, and PAR the measuring or assay light intensity. Φ_{PSII} was determined by setting actinic light level to the growth light level for each sample that had been grown under different light levels.

Measurement of Pigments Concentrations

A 10 mL of culture from each replicate culture was used for the extraction of Chl *a* and total carotenoids (CARs), and another 10 mL was used for the extraction of APC (allophycocyanin), PC (phycocyanin), and PE (phycoerythrin), respectively. For measurements of Chl *a* and CARs, cells were collected on 0.22 μm GF/F filter and then extracted in 5 mL of pure methanol for 24 h at 4°C in darkness before being centrifuged at 6,000 × *g* for 10 min. The supernatant was scanned for absorbance from 400 to 800 nm by using a spectrophotometer (model DU800 Beckman Coulter, United States). The concentrations of Chl *a* and CARs were determined according to Ritchie (2006) and Strickland and Parsons (1972).

Extractions of APC, PC, and PE were performed according to Lüder et al. (2001) as described by Zhang et al. (2013). Briefly, the collected cells were suspended in 10 mL phosphate buffer. The freezing (liquid nitrogen) and thawing (4°C) processes were repeated for at least four times for each extraction. Optical absorbances of the supernatant after centrifugation were scanned as mentioned above using the spectrophotometer. The concentrations of APC, PC, and PE were calculated according to Lüder et al. (2001).

Data Analysis

One-way ANOVA with post hoc multiple comparisons of Tukey was operated for distinguishing significant ($P < 0.05$) differences using SPSS (PASW 18.0, IBM, United States), since we need to compare more than two groups with the follow-up *post hoc* test for analysis of equality of multiple overall mean values. The significant levels (*p*-values) are given in the Supplementary Material. The fitting and charting were conducted by OriginPro 9.0.0 (64-bit) b45 (OriginLab Corp., United States). All data are presented as the means ± SD of three independent cultures.

RESULTS

The specific growth rate (μ) of *Synechococcus* WH7803 increased from 6 μmol m^{-2} s^{-1} to reach a maximum at 25 μmol m^{-2} s^{-1}, but thereafter declined with increased levels of PAR (**Figure 1**),

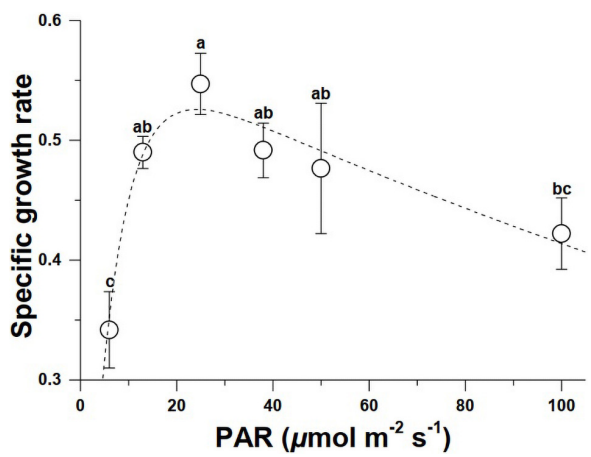

FIGURE 1 | The specific growth rates of *Synechococcus* WH7803 grown under various PAR levels (n = 3, triplicate cultures). Different letters above the data indicate significant difference ($p < 0.05$).

resulting in no significance in μ at between 6 and 100 μmol m^{-2} s^{-1} (**Supplementary Table 1**). The results derived from the non-linear fitting of μ revealed that the growth light use efficiency (α) and high light inhibiting coefficient (β) were 0.093 and 0.002, respectively.

The relative electron transport (*rETR*) during photochemical reactions of the cells grown under 6, 12, 25, and 38 μmol m^{-2} s^{-1} of PAR were nearly superimposed, however, the *rETR*s in the cells grown under 50 and 100 μmol m^{-2} s^{-1} significantly increased further with increased levels of PAR (**Figure 2A**). The maximal *rETR* in the cells grown at 100 μmol m^{-2} s^{-1} was nearly twice that grown at 38 μmol m^{-2} s^{-1} or lower PAR levels (**Figure 2A**). The effective quantum yield did not show significant changes (**Figure 2B**) (**Supplementary Table 2**).

When the cells were exposed to elevated CO_2 concentrations for about 10 days under 6 (limiting), 25 (optimal), and 100 (inhibiting) μmol m^{-2} s^{-1} of PAR, its specific growth rate significantly increased at the limiting and inhibiting growth light levels of 6 and 100 μmol m^{-2} s^{-1}, respectively (**Supplementary Table 3**). No significant change was observed between the two CO_2 levels under the optimal light level of 25 μmol m^{-2} s^{-1} (**Figure 3A**). The photosynthetic electron transport rate increased significantly with increased light levels, with higher

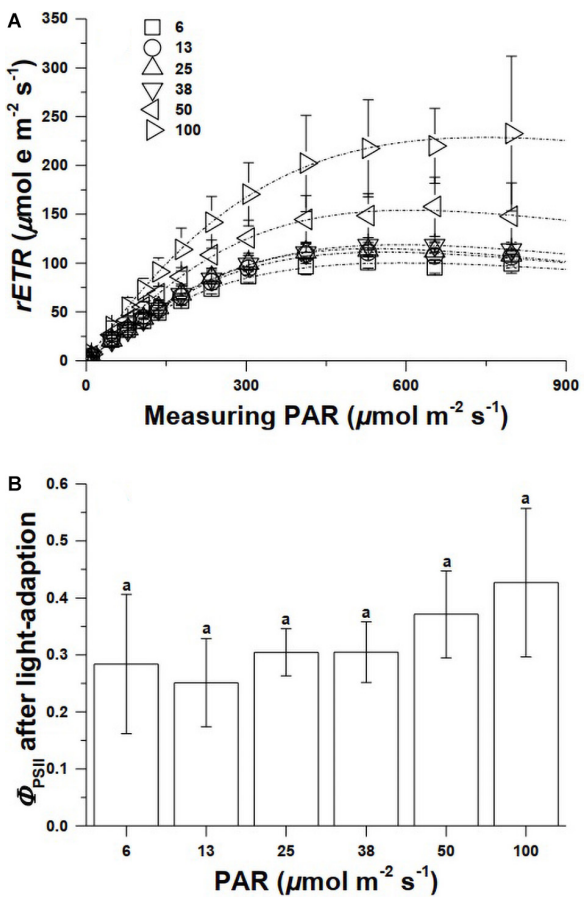

FIGURE 2 | The photosynthetic electron transport vs. light curves of *Synechococcus* WH7803 grown under different PAR levels **(A)**, and the effective quantum yield (Φ_{PSII}) of the cells adapted to growth light levels **(B)** (n = 3, triplicate cultures).

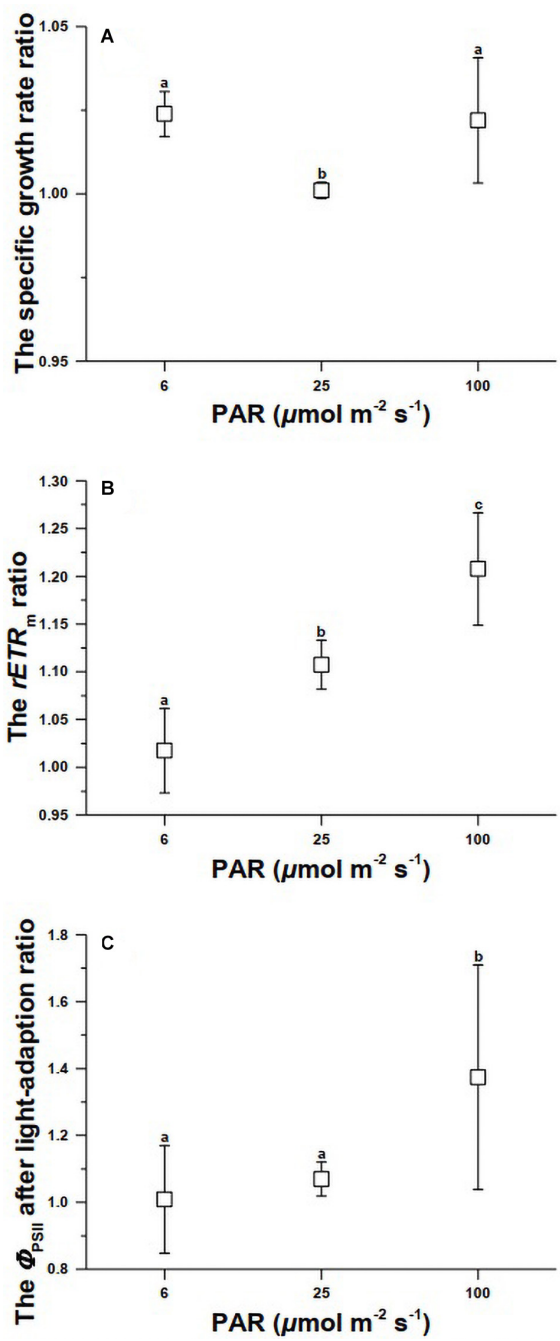

FIGURE 3 | The growth **(A)**, *rETR* **(B)**, and Φ_{PSII} **(C)** ratios of high- to low-CO_2-grown *Synechococcus* cells. Different letters above the data indicate significant difference at $P < 0.05$. The ratios of high CO_2-grown to ambient CO_2 grown cells were based on the data obtained under three levels of light and two levels of CO_2 (18 cultures with each treatment of three replicates). The absolute values for high CO_2-grown cells can be obtained using the ratio and the values in **Figures 1**, **2**.

values in the high CO_2-grown cells (**Figure 3B**) (**Supplementary Table 4**). While elevated CO_2 availability appeared to enhance the quantum yield at all test light levels, significant difference was only found at growth light of 100 μmol m^{-2} s^{-1} (**Figure 3C**), though the specific growth rate was enhanced in the high CO_2-grown cells at both limiting and inhibiting light levels (**Figure 3A**).

While contents of Chl *a* (0.013 ± 0.001 for LC and 0.021 ± 0.001 pg $cell^{-1}$ for HC), carotenoids (0.012 ± 0.002 for LC and 0.019 ± 0.001 pg $cell^{-1}$ for HC) and phycoerythrin (0.208 ± 0.079 for LC and 0.485 ± 0.030 pg $cell^{-1}$ for HC) showed significantly higher values at the optimal growth light of 25 μmol m^{-2} s^{-1}, no significant changes were found among the light levels for allophycocyanin and phycoerythrin (**Table 1**) (**Supplementary Table 5**). However, at any of the growth light levels, all types of photosynthetic pigments increased significantly at the elevated CO_2 level compared to the ambient level, by 58.76, 57.96, 82.10, 177.13, and 132.91%, respectively, for Chl *a*, carotenoids, allophycocyanin, phycocyanin, and phycoerythrin in the cells grown at the optimal light intensity (**Table 1**) (**Supplementary Table 5**).

DISCUSSION

Our results indicate that *Synechococcus* strain WH7803 accelerated its electron transport rate with increased growth light and CO_2 levels, and the elevated CO_2 to 1,000 μatm significantly enhanced its growth under limiting (6 μmol m^{-2} s^{-1}) and inhibiting (100 μmol m^{-2} s^{-1}) light levels, but did not bring about significant effect on it at the optimal light level of 25 μmol m^{-2} s^{-1}. Although the extent of the enhancement due to increased CO_2 availability at the low and high light levels was only by 2–2.5% per day (**Figure 3A**), the accumulative effects over longer periods can hardly be ignored considering the large proportion of *Synechococcus*'s contribution to marine primary productivity. Insignificant effects of elevated CO_2 on *Synechococcus* strains CCM 839 and 1334 were reported when they were grown at optimal light levels of about 40 μmol m^{-2} s^{-1} (Lu et al., 2006; Fu et al., 2007). Our finding first demonstrated the positive effects of elevated CO_2 on *Synechococcus* cells grown under limiting and inhibiting light levels and showed consistency with the previous reports (Lu et al., 2006; Fu et al., 2007) on the CO_2 effects at optimal light intensity.

In the present study, the specific growth rate of *Synechococcus* (WH7803) increased to reach a peak at 25 μmol m^{-2} s^{-1} but then gradually declined at higher light levels, showing a photoinhibition. Barlow and Alberte (1985) showed that *Synechococcus* WH7803 as well as clone WH8018 became light saturated for growth at light levels between 25 and 50 μmol m^{-2} s^{-1}, and was severely inhibited at 250 μmol m^{-2} s^{-1}. This is consistent with our growth vs. light curves (**Figure 1**). While Morris and Glover (1981) reported that growth of *Synechococcus* (WH7803) saturated at 45 μmol m^{-2} s^{-1}, Kana and Glibert (1987) reported that growth of the same strain was saturated at about 200 μmol m^{-2} s^{-1}. Since culture vessels of different materials and culture volumes may lead to different levels of light exposures to the cells within them, such difference in light levels for saturating its growth can be attributed to different transparency of light and to different volumes of culture, since large volume of cultures and the flasks made of polystyrene attenuate or block considerable amount of light. We have used 100 mL Quartz tubes, and the high transparency of the tubes with small volume of water provided higher light exposures to the cells, therefore leading to relatively lower saturating light level for growth (**Figure 1**) compared to other works aforementioned.

Photosynthetic electron transport increased with growth light levels till 100 μmol m^{-2} s^{-1} of PAR, with faster tempo at the elevated CO_2 level across all the growth light levels (**Figure 3B**). The faster electron drainage, which means faster energy supply for physiological processes, can be attributed to enhanced CO_2 assimilation processes and/or photorespiration (Gao et al., 2012). While increased light levels are known to enhance CCMs in phytoplankton species, but elevated CO_2 levels usually down-regulate CCMs (Giordano et al., 2005; Beardall and Raven, 2020), the enhanced electron transport and growth of *Synechococcus* strain WH7803 by elevated CO_2 could be attributed to enhancement of carboxylation under the elevated CO_2, which resulted in faster growth rate under growth limiting and inhibiting light levels (**Figure 3A**). The inhibited growth rate at 100 μmol m^{-2} s^{-1} (**Figure 1**) could be due to light stress, since the cells increased their electron transport with increasing growth light levels to result photoinhibition (**Figure 2**). The reason why growth at optimal growth light level was not enhanced by the elevated CO_2 could be attributed to balanced carbon loss and

TABLE 1 | The per cell concentrations of pigments (pg $cell^{-1}$) of *Synechococcus* WH7803 grown under different light and CO_2 levels (n = 3, triplicate cultures).

Pigments (pg $cell^{-1}$)	LC			HC		
	6 μ mol m^{-2} s^{-1}	25 μ mol m^{-2} s^{-1}	100 μ mol m^{-2} s^{-1}	6 μ mol m^{-2} s^{-1}	25 μ mol m^{-2} s^{-1}	100 μ mol m^{-2} s^{-1}
Chl *a*	0.005 ± 0.000^{aA}	0.013 ± 0.001^{bA}	0.007 ± 0.001^{aA}	0.006 ± 0.000^{aB}	0.021 ± 0.001^{bB}	0.039 ± 0.002^{cB}
CARs	0.004 ± 0.000^{aA}	0.012 ± 0.002^{bA}	0.009 ± 0.001^{cA}	0.006 ± 0.000^{aB}	0.019 ± 0.001^{bB}	0.035 ± 0.003^{cB}
APC	0.187 ± 0.006^{aA}	0.393 ± 0.175^{aA}	0.234 ± 0.033^{aA}	0.302 ± 0.015^{aB}	0.716 ± 0.050^{bB}	1.204 ± 0.193^{cB}
PC	0.079 ± 0.003^{aA}	0.105 ± 0.067^{aA}	0.097 ± 0.012^{aA}	0.127 ± 0.008^{aB}	0.292 ± 0.021^{bB}	0.460 ± 0.067^{cB}
PE	0.130 ± 0.004^{aA}	0.208 ± 0.079^{bA}	0.120 ± 0.017^{cA}	0.209 ± 0.013^{aB}	0.485 ± 0.030^{bB}	0.753 ± 0.120^{cB}

LC and HC indicate CO_2 partial pressures of 400 and 1,000 μatm, respectively. Different types of pigments are shown as Chl a, CARs (carotenoids), APC (allophycocyanin), PC (phycocyanin), and PE (phycoerythrin). Different letters above the data indicate significant difference, with the superscripted lowercases and uppercases representing that for light levels at the same CO_2 and for CO_2 levels at the same light level, respectively.

carboxylation, since the acidic stress associated with elevated CO_2 can stimulate respiratory carbon loss in phytoplankton (see the review by Gao and Campbell (2014) and literatures therein).

Synechococcus strains are known to operate active CCMs, though they lack extracellular carbonic anhydrase (Badger and Andrews, 1982; Price, 2011). Elevated CO_2 concentrations down-regulate the CCMs in microalgae and cyanobacteria, with depressed activity of carbonic anhydrase (Beardall and Raven, 2020). The down-regulated operation of CCMs in *Synechococcus* strain WH7803 could have saved energy (operation of CCMs requires energy expenditure), and the saved energy helps to enhance growth of *Synechococcus* strain WH7803 when light is limiting. That is, it is not the CO_2 fertilization effect that led to enhanced growth of the picophytoplankton under limited light condition. When CCMs become down-regulated, photorespiration or Rubisco-catalyzed oxygenation can speed up at high light levels due to decreased ratio of CO_2 to O_2 (Bailey et al., 2008). In the present work, when *Synechococcus* strain WH7803 was grown under inhibiting light level (100 μmol m^{-2} s^{-1}), its photorespiration might have been enhanced to result in negative effects on growth under the elevated CO_2. However, on the contrary, the increased CO_2 availability enhanced its growth significantly under the high light (**Figure 3A**). It has been shown that *Synechococcus* releases CO_2 by about 30% of the CCMs concentrated DIC while its CCMs operate (Badger et al., 1985), elevated CO_2 concentration in milieu might have counteracted the CO_2 release, therefore aiding the cells with enhancement of electron transport and quantum yield (**Figures 3B,C**) with stimulated growth (**Figure 3A**). More photosynthetic carbon fixation would demand more energy. In the present work, the picophytoplankton increased its photosynthetic pigments with increased levels of light and CO_2, which is consistent with that reported by Fu et al. (2007). Increased availability of CO_2 significantly increased the cells' light capturing capacity, as reflected in the increased photosynthetic pigments (**Table 1**). Under the high levels of light and CO_2, the cells of *Synechococcus* showed the highest increase in Chl. a content to ensure sufficient energy supply to support increased levels of carboxylation and photorespiration, which has been shown to increase under OA conditions (Gao et al., 2012).

In natural marine environments, phytoplankton cells are exposed to different light levels spatio-temporally. *Synechococcus* strains are usually distributed in the lower part of euphotic zone, being exposed relatively low light. However, during noon period or during periods of intensive mixing, the picophytoplankton cells may episodically exposed to high inhibiting light levels. Therefore, elevated CO_2 concentrations can positively and negatively affect its productivity at different depths or times during daytime. Consequently, the effects of OA on *Synechococcus* productivity could be strain-, depth-, and time-dependent, showing spatiotemporal differences in its response to progressive ocean acidification.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

KG and NB contributed to the designing and planning the experiments and writing the manuscript. NB performed the experiments. Both 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.2021.634189/full#supplementary-material

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

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