

Enhancement of photosynthetic carbon assimilation efficiency of phytoplankton assemblage in the future coastal ocean

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Abstract

A mesocosm experiment was conducted to evaluate the effects of future climate conditions on photosynthesis and productivity of coastal phytoplankton. Natural phytoplankton assemblages were incubated in field mesocosms under the ambient condition (present condition: ca. 400 ppmv CO₂ and ambient temp.), and two future climate conditions (acidification condition: ca. 900 ppmv CO₂ and ambient temp.; greenhouse condition: ca. 900 ppmv CO₂ and 3 °C warmer than ambient). Photosynthetic parameters of steady-state light responses curves (LCs; measured by PAM fluorometer) and photosynthesis–irradiance curves (P–I curves; estimated by in situ incorporation of ¹⁴C) were compared to three conditions during the experiment period. Under acidification, electron transport efficiency (α_{LC}) and photosynthetic ¹⁴C assimilation efficiency (α) were 10 % higher than those of the present condition, but maximum rates of relative electron transport (rETR_{m,LC}) and photosynthetic ¹⁴C assimilation (P_{max}^B) were lower than the present condition by about 19 % and 7 %, respectively. In addition, rETR_{m,LC} and α_{LC} were not significantly different between and greenhouse conditions, but P_{max}^B and α of greenhouse conditions were higher than those of the present condition by about 9 % and 30 %, respectively. In particular, the greenhouse condition has drastically higher P_{max}^B and α than the present condition more than 60 % during the post-bloom period. According to these results, two future ocean conditions have major positive effects on the photosynthesis in terms of energy utilization efficiency for organic carbon fixation through the inorganic carbon assimilation. Despite phytoplankton taking an advantage on photosynthesis, primary production of phytoplankton was not stimulated by future conditions. In particular, biomass of phytoplankton was depressed under both acidification and greenhouse conditions after the the pre-bloom period, and more research is required to suggest that some factors such as grazing activity could be important for regulating phytoplankton bloom in the future ocean.

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1 Introduction

The ocean has been recognized as an anthropogenic CO₂ reservoir since the Industrial Revolution. Recently there has been increased attention to the acidification in the ocean, which is considered to be a critical problem. Ocean acidification increases $p\text{CO}_2$ and bicarbonate ion (HCO_3^-) and decreases of pH and carbonate ion (CO_3^{2-}) in the seawater. These changes of carbon chemistry cause the physiological changes of phytoplankton to future climate conditions affecting photosynthesis and respiration caused by the increase in CO₂ and HCO_3^- . Generally, phytoplankton groups require active inorganic carbon uptake mechanisms for photosynthesis (carbon concentrating mechanisms; CCMs) to overcome CO₂ limited conditions because of their poor CO₂ affinity of RuBisCO (Beardall and Raven, 2004; Raven, 2010). Phytoplankton physiology is positively affected by elevated CO₂ along with CO₂ affinity changes and downregulation of CCMs (Giordano et al., 2005; Hopkinson et al., 2011; Sobrino et al., 2008; Rost et al., 2003) On the contrary to some microalgae, which are already and permanently adjusted to limited CO₂ environments phytoplankton are not affected by oceanic CO₂ increase with active CCMs (Beardall and Raven 2004; Giordano et al., 2005). So far, many physiological results that evaluate the response of high CO₂ conditions on phytoplankton groups are yet to be disputed.

Physiological changes can cause the shift of growth and primary production of phytoplankton with direct increases of inorganic carbon source for photosynthesis (Schippers et al., 2004; Riebesell, 2004). Phytoplankton has the advantage of lower light energy requirements to synthesize organic carbon under high CO₂ conditions (Chen and Gao, 2004); therefore, more organic compounds are produced with less light energy. Energy consumption is optimized with energy savings due to downregulation of CCMs; furthermore, this surplus energy could be used for growth (Sobrino et al., 2008). Previous mesocosm studies have shown that cell growth and primary production are promoted by the enhanced dissolved inorganic carbon assimilation rate (Kim et al., 2006; Riebesell et al., 2007), and these results show that downregulation of CCMs could positively

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influence increases of biomass and primary production of natural phytoplankton assemblages.

One of the accompanied problems caused by increasing atmospheric CO₂ is ocean warming. The increased temperature range is about 2–5 °C within this century based on IPCC A2 Scenario (IPCC 2007). Numerous in situ mesocosm studies evaluated oceanic changes with atmospheric CO₂ changes, but they are less focused on the combined effects of temperature. Temperature has a profound influence on the physiology and ecology of marine organisms and the community structure responses (Feng et al., 2009; Lewandowska and Sommer, 2010; Sommer and Lewandowska, 2010). Photosynthesis and respiration related metabolisms are also accelerated with increased temperature based on Q₁₀ values under light saturated productive areas (Sommer and Lengfellner 2008). High temperature causes an increased photosynthetic rate, and temperature has more significance on the photosynthesis than on high CO₂ (Hare et al., 2007). Additionally, community structure and species composition are strongly affected by temperature increasing with an enhancement of top-down regulation across all trophic levels, and small size of phytoplankton is more abundant under the high temperature conditions (Hare et al., 2007; Kim et al., 2010; Lewandowska and Sommer, 2010).

Many experiments were conducted under well-controlled laboratory conditions to assess phytoplankton physiology in responses to future oceanic CO₂ and temperature changes, but in situ mesocosm experiment results are still deficient. Therefore, mesocosms are imperative to evaluating well-established hypotheses and to the responses to the future climatic environment entirely with organisms to ecosystem with specialized experimental setup (Kim et al., 2008; Riebesell et al., 2008, 2011). In this study, we conducted a mesocosm experiment in the coastal waters of Korea to evaluate how future oceanic CO₂ and temperature changes could affect phytoplankton performance and production. The aims of this study were (i) to investigate alteration in photosynthetic characteristics based on both methods of chlorophyll *a* fluorescence and radioactive carbon (¹⁴C) isotope incubation, and (ii) to examine change in primary production and

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biomass under present (ambient CO₂), acidification (high CO₂) and greenhouse (high CO₂/temperature) conditions.

2 Materials and methods

2.1 Mesocosm experimental setup

5 A mesocosm experiment was conducted at the South Sea of Korea (Jangmok Bay, Geoje Island; 34.6° N, 128.5° E) from 21 November–11 December 2008. The mesocosm facility that was used for this experiment consisted of nine enclosures to manipulate CO₂ concentration and temperature (Kim et al., 2008, 2010). To set up the present and future ocean conditions, we simulated three experimental conditions based on IPCC A2 Scenarios (IPCC 2007): ambient CO₂ and temperature (present: ca. 400 ppmv CO₂ and ambient temperature), a CO₂ only enriched (acidification: ca. 900 ppmv CO₂ and ambient temperature) and increased both CO₂ and temperature (greenhouse: ca. 900 ppmv CO₂ and 3°C warmer than ambient temperature) conditions. 1.5 tons of natural seawater was transported into each mesocosm bag, and initial Chl *a* concentration of seawater was ca. 1 µg L⁻¹. CO₂ oversaturated seawater was slowly diluted with natural seawater using a peristaltic pump to initiate high CO₂ condition at the beginning of experiment. Target concentration of CO₂ gases flowed into the headspace of mesocosm bags for the entire experimental period. A high heat conduction rate tube was fixed in the mesocosm bags at 1.5–2 m water depth to create the increased temperature treatment, and heated water was circulated within a tube that was coiled around the inside of the mesocosm system. For the initial experiment, nutrients were added to the initial development of a phytoplankton bloom (nitrate: ca. 41 µmol kg⁻¹, phosphate: ca. 2.5 µmol kg⁻¹ and silicate: ca. 40 µmol kg⁻¹). More information on the experimental conditions, including CO₂ concentration and pH, were provided in other series studies (Kim et al., 2010, 2011b).

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2.2 Biomass (chlorophyll *a*)

The concentration of Chl *a* was determined fluorometrically using a Turner 10-AU fluorometer (Turner Designs Inc., Sunnyvale, CA, USA) by filtering known volumes of seawater through GF/F filters (Whatman, Maidstone, UK). Chl *a* was extracted with 90 % acetone for 24 h in the dark (Holm-Hansen and Riemann, 1978).

2.3 Chl *a* fluorescence measurement

Seawater samples were collected 7–8 times during day (06:00–19:00 KST) under various irradiance conditions ($0\text{--}1200\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$), and the effective quantum yield of PSII (Φ_{PSII}) of the natural phytoplankton community was measured using an in vivo Chl *a* fluorometer (Phyto-PAM, Walz, Germany). The effective quantum yield of PSII was calculated as $\Phi_{\text{PSII}} = \Delta F / F'_m = (F'_m - F) / F'_m$, where F and F'_m represent the steady-state fluorescence and maximum fluorescence measured in the light, respectively. All Φ_{PSII} were obtained by saturation pulse after exposure to different intensities of actinic light (light intensities were determined by in situ irradiance at sampling time). These results represented the apparent efficiency of open PSII reaction centers at each sampling time. The relative electron transport rate (rETR) was calculated as $\text{rETR} = \Phi_{\text{PSII}} \times \text{irradiance}$. The absorption factor and relative fraction of PSII were not applied to the ETR calculation to avoid ambiguous problems (Ryan et al., 2009). Steady-state light response curves (LCs) were constructed as rETR-E curves, and these curves were fitted to a model with the photoinhibition parameter of Platt et al. (1980) to distinguish the efficiency of the PSII reaction centers depending on future environmental conditions (Kim et al., 2011a). Maximum relative electron transport rate ($\text{rETR}_{\text{m,LC}}$), electron transport efficiency (α_{LC}), and light saturation intensity of the LCs ($E_{\text{k,LC}}$) were obtained by curve fitting to a model with a photoinhibition parameter (Platt et al., 1980). All fluorescence measurements were carried out at days 1, 5, 9, 15, and 19.

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2.4 Gross photosynthesis

Seawater samples were collected at 10:00 a.m. for gross photosynthesis measurement by ^{14}C inoculation experiment. An 80 mL aliquot of seawater from each mesocosm bag was carried in a cell culture flask (Corning Inc., NY, USA) and $0.5\ \mu\text{Ci}$ of $\text{NaH}^{14}\text{CO}_3$ was injected to initiate the incubation experiment. The incubation bottles were wrapped in dark and neutral density screening of eight different light transmissions to provide various intensities of light (0, 6, 13, 17, 30, 43, 67, and 100 %) in the middle of the day. After 3-h incubation, seawater was filtered with a glass membrane filter (GF/F), and the filter paper was placed in a 20 mL plastic scintillation vial (PerkinElmer, Waltham, MA, USA). Acid fuming with 1 mL of 0.5 N HCl was conducted for 1 day under dark condition, and then 10 mL of UltimaGoldTM (PerkinElmer) scintillation cocktail was added to the scintillation vial. Radioactivity of synthesized particulate carbon was measured with a liquid scintillation counter (Tri-Carb 2100 TR, Packard Instruments Co., Downers Grove, IL, USA), and carbon uptake was calculated using an equation derived from Strickland and Parsons (1972). The results are shown as photosynthesis irradiance (P-I) curves, and fitted to a model with the photoinhibition parameter of Platt et al. (1980). Photosynthetic parameters such as biomass (Chl *a*)-specific maximum photosynthetic ^{14}C assimilation rate (P_{max}^B), photosynthetic ^{14}C assimilation efficiency (α), and irradiance at the onset of light saturation (E_k) were obtained from the curve fitting. P-I curves were obtained at days 0, 4, 8, 12, 16, and 21 from all mesocosm bags.

2.5 Gross community production

Primary production was calculated using photosynthetic parameters and Chl *a* concentration with time series incident light data, which was considered to water column light attenuation. Production data expressed as gross community production (GCP; Taylor, 1999). In situ daily irradiance was measured using a LI-1400 data logger with a LI-COR 2π PAR sensor (LI-190 and LI-192, LI-COR Inc., Lincoln, NE, USA). The quantum sensors were positioned at the atmosphere and at 1 m water depth outside of

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the mesocosm bags, and five HOBO Pendant Temperature/Light data loggers (Onset Computer Corp., Bourne, MA, USA) were fixed randomly at a 1 m water depth inside and outside enclosures to check the inside light intensity. As a result, differences in light intensity were negligible between the inside and outside of the mesocosm bags (Kim et al., 2010).

2.6 Statistical analysis

Analysis of variance (ANOVA) was used to determine the effects of increased CO₂ and CO₂/temperature on the photosynthetic parameters from the LCs and P-I curves. All datasets met assumptions of normality and homogeneity of variance. When the ANOVA identified a significant difference ($p < 0.05$), Tukey's HSD post hoc comparison was used. These analyses were performed using SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

3 Results

3.1 Biomass (Chl *a* concentration)

The mesocosm experiment was divided into three periods in terms of biomass and nutrients levels (pre-bloom period: days 0–5, bloom period: days 6–14 and post-bloom period: days 15–21) (Fig. 1). Biomass increased slowly during the pre-bloom period with no significant differences between the experimental conditions. The Chl *a* concentration reached monotonously about 5 µg Chl *a* L⁻¹ at the end of this period. Then biomass increased exponentially showing slightly higher content of Chl *a* under the acidification condition than under the present condition until day 13; however, the highest biomass reached 35 µg Chl *a* L⁻¹ under the present condition at the end of the exponential growth period (day 14). Since then inorganic nutrients were depleted in all mesocosms and biomass declined which characterized the post-bloom period under the present and acidification conditions. Contrastively, biomass came to an almost

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stagnant phase with a maximum $14.8 \mu\text{g Chl } a \text{ L}^{-1}$ after day 12 under the greenhouse condition (Fig. 1).

3.2 Chl *a* fluorescence parameters

The effective quantum yield (Φ_{PSII}) showed a typical diurnal pattern and it was intimately linked to the daily irradiance fluctuation (Fig. 2, left column). The Φ_{PSII} was 0.6–0.7 under low irradiances (i.e. at dawn and dusk) and decreased with increasing the field light intensity. rETR was not largely affected by experimental conditions at day 1, however it decreased slightly in high light intensity under acidification compared with present and greenhouse after day 5 (Fig. 2, right column). Among the Chl *a* fluorescence parameters (rETR_{m,LC}, α_{LC} , $E_{\text{k,LC}}$) of steady-state light response curves (LCs), rETR_{m,LC} had no significant difference between the experimental conditions during the pre-bloom period (Table 1). On days 9 and 15, rETR_{m,LC} value under the acidification condition was lower compared to other conditions, and it lowered significantly from those of the present condition at day 9 ($p < 0.05$) and greenhouse condition at day 15 ($p < 0.05$). The highest rETR_{m,LC} was observed at day 19 during the post-bloom period ($130.5\text{--}167.1 \mu\text{mol e}^{-} \text{ m}^{-2} \text{ s}^{-1}$). Other parameters (α_{LC} , $E_{\text{k,LC}}$) showed no significant difference between experimental conditions over the experiment period except for α_{LC} at day 1. The highest α_{LC} occurred on day 15 when Chl *a* reached a peak in the present and acidification conditions ($0.86\text{--}0.95 \mu\text{mol e}^{-} (\mu\text{mol photons})^{-1}$). Nevertheless, relatively small changes of Chl *a* fluorescence parameters occurred over the experiment conditions, overall tendency of rETR_{m,LC} and $E_{\text{k,LC}}$ in acidification condition was lower than other conditions except for day 1.

3.3 Photosynthetic ^{14}C assimilation parameters

At the initial day of experiment, the photosynthetic performance of phytoplankton community showed no significantly different between the present and treatment conditions (Fig. 3; Table 2). The $P_{\text{max}}^{\text{B}}$ during the bloom period (days 8 and 12) were higher than

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that of the pre-bloom period (ca. 30 %) and post-bloom period (ca. 50 %). This parameter showed significantly lower value under the acidification condition at day 4 ($p < 0.05$), but there was no difference in P_{\max}^B between present and acidification conditions after day 4 ($p > 0.05$). During the post-bloom period, P_{\max}^B was significantly higher under the greenhouse condition than under present conditions at day 16 ($p < 0.05$) and acidification conditions at days 16 and 21 ($p < 0.05$). No significant difference was found in α between the experimental conditions during the pre-bloom and bloom period (Table 2). But during the post-bloom period, significantly higher α values were found under greenhouse condition than under acidification condition ($p < 0.05$). The E_k ranged from 96–189 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ during the entire experimental period, but no significant differences were found between the present and experimental treatments for E_k except for day 4 ($p > 0.05$).

3.4 Daily/cumulative gross community production (GCP)

The GCP of phytoplankton initially ranged from 4.9–8.0 $\mu\text{mol CL}^{-1} \text{d}^{-1}$, then GCP increased slowly to 22.0 $\mu\text{mol CL}^{-1} \text{d}^{-1}$ during the pre-bloom period, showing no differences in GCP between experimental conditions (Fig. 4a). During the bloom period, GCPs increased rapidly at all conditions to ca. 5 fold higher values than those at day 5, and a peak reached at day 14 when the highest Chl *a* appeared, simultaneously. The highest value of GCP was 138 and 136 $\mu\text{mol CL}^{-1} \text{d}^{-1}$ under the present and acidification conditions, respectively. The GCPs decreased after peak to ca. 54 $\mu\text{mol CL}^{-1} \text{d}^{-1}$ during the post-bloom period. Cumulative GCP increased exponentially until day 14 (mean value: 599.0 $\mu\text{mol CL}^{-1}$; during the pre-bloom and bloom periods), and then it increased linearly (Fig. 4b). Total cumulative GCP was higher under the present ($1070 \pm 322.7 \mu\text{mol CL}^{-1}$) than under the acidification and greenhouse conditions (991 ± 64.2 and $959 \pm 32.5 \mu\text{mol CL}^{-1}$, respectively), but no significant differences were observed between the experimental conditions.

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4 Discussion

4.1 Physiological implications

Our mesocosm experiments elucidated the photo-physiological aspects based on actual response of PSII photochemistry and photosynthesis of phytoplankton, which could differ in timing of blooms and community structure in the future coastal ocean. The key physiological findings of this study are that phytoplankton could assimilate more inorganic carbon for photosynthesis with less light energy under acidification and greenhouse conditions compared to the present, and this finding could be interpreted from the steady-state light response curves and photosynthesis–irradiance curves (Figs. 2 and 3; Tables 1 and 2). Primary evidence leading to this hypothesis are (i) lower $rETR_{m,LC}$ under acidification than present without decrease in P_{max}^B and (ii) higher P_{max}^B and α under greenhouse than present without changing of $rETR_{m,LC}$ and α_{LC} . These results indicate that phytoplankton required less light energy without depressed photosynthetic activity under acidification condition, and maximizes photosynthetic carbon assimilation efficiency using same light energy under greenhouse condition. In other words, phytoplankton benefit largely from high CO_2 and temperature conditions on the energy utilization efficiency for synthesizing organic product.

PSII photochemical efficiency and photosynthesis were clearly affected by CO_2 concentration in some previous laboratory experiments, and these results represent that high photosynthesis of phytoplankton was observed under high CO_2 condition with altered PSII photochemical efficiency (Sobrino et al., 2008; Wu et al., 2010). These authors also hypothesized that surplus energy obtained by downregulation of CCMs can be used for cell growth with enhanced photosynthesis. There are no evidences to prove this hypothesis from our mesocosm experiments because photosynthesis is not highly increased in future conditions. We assume that light harvesting and photosynthetic carbon assimilation efficiencies could change under high CO_2 conditions (acidification and greenhouse), because downregulation of CCMs is linked to light requirement and

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carbon assimilation processes indirectly. Only 50 % of photosynthetic energy is generally allocated to growth, and 20 % of the energy is consumed by active pathway of carbon uptake with CCMs operation (Raven, 1991; Riebesell, 2004), however, less light energy is required for operating CCMs under high CO₂ conditions with depression of carbonic anhydrase activity (Hopkinson et al., 2010). Surplus energy saved from less CCMs operation could activate downregulation of the light-harvesting system due to the low light energy requirement; therefore, it takes advantage of photosynthesis and cell growth with efficient light energy utilization. These physiological responses could affect succession of coastal phytoplankton assemblage, because some species are put in an advantageous position in terms of energetic balance for growth (e.g. *Skeletonema costatum*: Kim et al., 2006; *Synechococcus* sp.: Fu et al., 2007; *Thalassiosira pseudonana*: Sobrino et al., 2008; *Phaeodactylum tricornutum*: Wu et al., 2010).

In addition, significantly improved photosynthetic performance (especially P_{max}^B and α during the post-bloom period) was observed under the greenhouse condition with changeless PSII photochemical properties (Fig. 2; Table. 1). Generally, temperature could influence the fluidity of the membrane and electron transport system (Falkowski and Raven 2007), and then the high temperature positively affects potential efficiency of PSII (Lassen et al., 2010). Temperature also has an effect on the regulation of CCM capacity due to the solubility of CO₂ and O₂ (Baker and Oxborough, 2004; Giordano et al., 2005). A high portion of O₂ in comparison to CO₂ could lead to the reduction of photosynthesis caused by competition between O₂ and CO₂ at the RuBisCO (Krause-Jensen et al., 1996). Enhanced primary production could be induced by high solubility of CO₂ and low solubility of O₂ under warming ocean (Krause-Jensen et al., 1996). Photosynthesis also could be promoted by high temperature included in the optimal temperature range (Claquin et al., 2008). Initial day of ambient temperature was ca. 14.1 °C, and it dropped down to ca. 11.7 °C at last day of experiment (Kim et al., 2010; see Fig. S1). Greenhouse condition showed the temperature range from ca. 16.5 to 14.1 °C as time goes on, and this temperature range belongs to the optimal temperature of many phytoplankton species. Therefore, we expect the decreasing PSII

efficiency under acidification to be offset by increasing temperature with recovery of PSII efficiency.

4.2 Ecological implications

Although prediction of primary production is highlighted in a high CO₂ ocean, the estimation of pelagic primary production under future climate conditions using a mesocosm experiment is rare (Delille et al., 2005; Egge et al., 2009). From the PeECEIII study, primary production, which was estimated by ¹⁴C bottle incubations for 24 h (NCP), had no dramatic change under doubled CO₂ concentration. Our results of photosynthesis and production calculated from the 3-h (relatively short-term) ¹⁴C incorporation experiment (GCP; Williams et al., 2002) are also not largely affected by acidification conditions. In addition, two previous shipboard experiments showed different results in primary production (Tortell et al., 2002; Gao et al., 2012). Equatorial Pacific phytoplankton community did not change, but productivity of phytoplankton in East and South China Sea decreased under high CO₂ conditions. Likewise, many outdoors experiments showed different primary production results under high CO₂ conditions, and those could be caused by unknown parameters, which necessitate future study.

Cumulative gross production also rapidly increased during the bloom period, and then the increasing rate was retarded after the phytoplankton bloom (Fig. 4b). In contrast PeECEIII study showed stationary phase of the GCP after the peak of phytoplankton biomass (Chl *a*) (Egge et al., 2009). The major factors affecting these differences are expected to be species composition and experimental environment. Species diversity was noticeably higher in our experiment because it was conducted in temperate coastal waters during the phytoplankton bloom period. *Skeletonema costatum*, *Chaetoceros* spp. and *Eucampyrococcus zodiacus* were dominant species within the diatom group, and 8 species included three dominant species consisting of more than 90% of diatom abundance. In particular, growth of *S. costatum* was strongly stimulated by high CO₂, and this species occupied most dominant species under acidification and greenhouse during the bloom period. After biomass peak (day 14), *Akashiwo sanguinea*,

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Nematodinium aratum and *Prorocentrum dentatum* were dominant species in dinoflagellate, and 6 species including three dominant species composed over 90 % of abundance of dinoflagellate. These bloom forming species largely independent of experiments (Egge et al., 2009; Kim et al., 2010). For these reasons, the phytoplankton communities are not able to generalize their changes in response to ocean acidification.

Biomass (Chl *a* concentration) changes were linked to photosynthesis and primary production direct. From the previous study, biomass changes did not occur in the diatom-dominate coastal phytoplankton community even when they were physiologically acclimated to high CO₂ condition (Tortell et al., 2000). In addition, small differences in Chl *a* concentration under the acidification condition were reported in previous research (Riebesell et al., 2007; Feng et al., 2009). From our data biomass also did not increased in acidification and greenhouse conditions, despite its positive affects towards photophysiology of phytoplankton under those conditions. If surplus energy was provided by downregulation of CCMs under high CO₂ condition, then phytoplankton biomass could be increased with this energy. However, there was no biomass increase associated with acidification over the experiment period. It seems biomass was not associated with physiological changes and production. Lewandowska and Sommer (2010) found remarkably lower phytoplankton biomass under warming conditions. These tendencies also apply to our results in greenhouse condition. Decline of biomass growth was observed under the greenhouse condition (Fig. 1a), even though photosynthesis and community production were not negatively affected by temperature. We suggest that one of the important factors which are regulate phytoplankton bloom in the future ocean environment is top-down control by grazers – top-down regulation enhanced by active grazers such as zooplankton under high temperature condition (Lewandowska and Sommer, 2010). Grazing activity also was significantly enhanced by heterotrophic dinoflagellate under acidification and greenhouse conditions (Kim et al., 2010); therefore, phytoplankton biomass will increase rapidly if grazer's activities decrease in acidified coastal waters.

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5 Summary

Our mesocosm study offers information about photosynthesis, primary production and total biomass changes. To our knowledge, this study suggests the first photophysiological interpretation, where the light utilization efficiency is accelerated under high CO₂ world regardless of temperature increase through the mesocosm experiment. The main objective of this study was to investigate the physiological and ecological affects in the phytoplankton community under future climate conditions. The phytoplankton community could take advantage of inorganic carbon assimilation with regulation of light utilization, but these changes were not largely reflected in ecological responses such as primary production and growth. Nevertheless, if these positive physiological changes do not affect primary production, species succession could occur with an advantage towards species with enhanced efficiency of light utilization in a high CO₂ world.

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Table 1. Photosynthetic parameters from steady-state light response curves (LCs) of the phytoplankton community during the experimental period. Different letters indicate a significant difference based on Tukey's multiple comparison ($p < 0.05$).

Day	$rETR_{m,LC}$ Maximum relative electron transport rate ($\mu\text{mol e}^{-1} \text{m}^{-2} \text{s}^{-1}$)			α_{LC} Electron transport efficiency ($\mu\text{mol e}^{-1} (\mu\text{mol photons})^{-1}$)			$E_{k,LC}$ Light-saturation coefficient of LCs ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)		
	Present	Acidification	Greenhouse	Present	Acidification	Greenhouse	Present	Acidification	Greenhouse
Day 1	118.3 ± 38.8	104.7 ± 19.0	110.8 ± 20.7	0.54 ± 0.08 ^a	0.64 ± 0.06 ^{ab}	0.74 ± 0.01 ^b	218.2 ± 67.4	163.4 ± 15.8	149.3 ± 26.7
Day 5	120.2 ± 6.6	101.8 ± 7.6	116.5 ± 19.6	0.54 ± 0.15	0.55 ± 0.01	0.65 ± 0.18	237.7 ± 75.6	185.5 ± 16.7	230.4 ± 120.1
Day 9	133.2 ± 27.6 ^a	97.8 ± 11.3 ^b	107.5 ± 3.8 ^{ab}	0.69 ± 0.20	0.80 ± 0.04	0.63 ± 0.24	215.1 ± 118.6	121.8 ± 9.1	195.8 ± 100.7
Day 15	96.3 ± 6.1 ^{ab}	77.5 ± 12.6 ^a	107.9 ± 12.8 ^b	0.86 ± 0.10	0.95 ± 0.03	0.88 ± 0.07	112.1 ± 5.7	79.39 ± 15.1	124.1 ± 21.8
Day 19	162.3 ± 14.8	130.5 ± 15.2	167.1 ± 16.9	0.67 ± 0.05	0.66 ± 0.04	0.72 ± 0.03	224.3 ± 32.8	200.7 ± 25.1	231.9 ± 17.9

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Table 2. Photosynthetic parameters from photosynthesis–irradiance (P–I) curves of the phytoplankton community obtained by the ^{14}C incubation experiment. Different letters indicate a significant difference based on Tukey's multiple comparison ($p < 0.05$).

Day	P_{\max}^{β} Chl <i>a</i> -specific maximum gross photosynthesis rate $\mu\text{mol C (mg Chl-}a\text{)}^{-1} \text{h}^{-1}$			α Photosynthetic efficiency $\mu\text{mol C mg}^{-1} \text{Chl-}a \text{ h}^{-1} (\mu\text{mol photons m}^{-2} \text{s}^{-1})^{-1}$			E_k Irradiance at the onset of light saturation $\mu\text{mol photons m}^{-2} \text{s}^{-1}$		
	Present	Acidification	Greenhouse	Present	Acidification	Greenhouse	Present	Acidification	Greenhouse
Day 0	571.8 ± 48.3	570.6 ± 98.8	489.5 ± 62.7	3.84 ± 0.34	5.38 ± 0.89	5.43 ± 2.21	149.0 ± 7.9	106.1 ± 7.7	100.2 ± 42.1
Day 4	604.8 ± 34.4 ^a	508.2 ± 42.3 ^b	630.0 ± 21.9 ^a	3.70 ± 0.51	4.12 ± 0.53	3.59 ± 0.34	164.3 ± 15.6 ^a	123.9 ± 7.5 ^{ab}	176.4 ± 12.9 ^b
Day 8	731.4 ± 29.6	767.4 ± 35.2	876.8 ± 111.1	4.31 ± 0.35	4.66 ± 0.43	5.73 ± 1.47	170.2 ± 7.4	165.4 ± 13.5	156.9 ± 28.0
Day 12	730.8 ± 108.4	566.1 ± 91.6	678.1 ± 46.3	4.25 ± 0.61	4.29 ± 0.25	4.77 ± 0.36	171.8 ± 3.2	129.9 ± 21.8	142.2 ± 5.3
Day 16	301.1 ± 60.1 ^a	296.4 ± 30.7 ^a	445.5 ± 34.8 ^b	1.61 ± 0.44 ^a	1.70 ± 0.36 ^a	2.96 ± 0.44 ^b	189.0 ± 20.1	177.6 ± 26.2	151.6 ± 12.9
Day 21	347.4 ± 32.0 ^{ab}	345.2 ± 56.8 ^a	484.0 ± 98.1 ^b	3.19 ± 0.41 ^{ab}	2.85 ± 0.80 ^a	4.68 ± 0.78 ^b	109.3 ± 5.9	124.4 ± 18.5	102.3 ± 14.6

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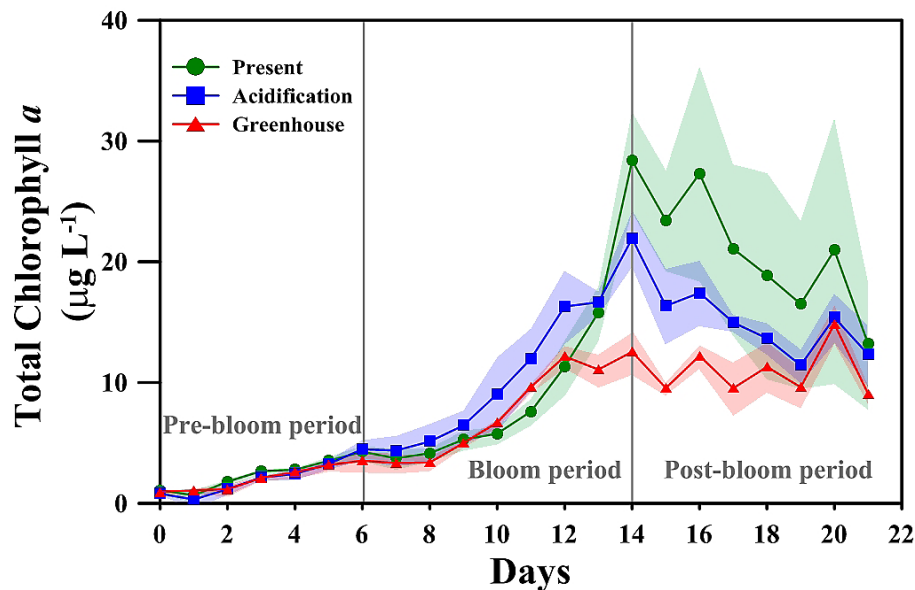


Fig. 1. Chl *a* concentration during the experimental period under the present (green), acidification (blue), and greenhouse (red) treatment conditions. Colored shading represents the standard deviation from the mean (colored symbols and lines) of the replicate enclosures ($n = 3$).

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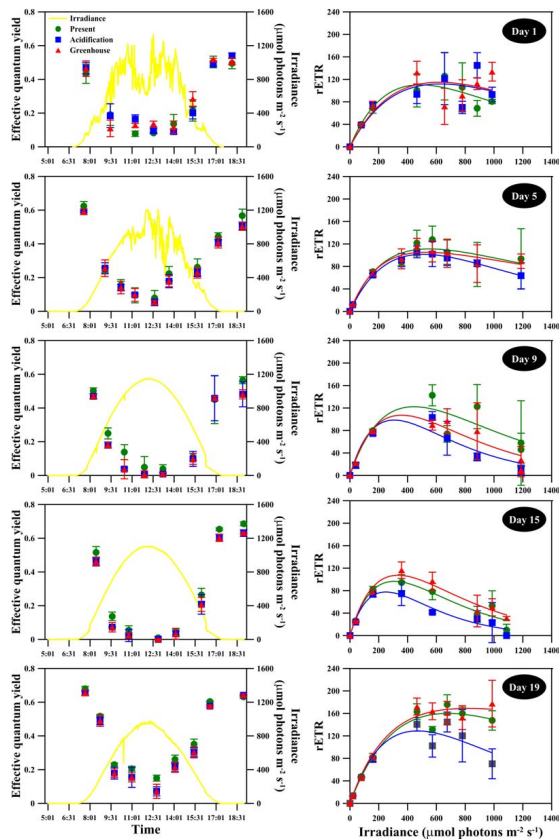


Fig. 2. Decrease and recovery of effective quantum yield of PSII (left column), and steady-state light response curves (LCs; right column) of the phytoplankton community during the experimental period under the present (green), acidification (blue), and greenhouse (red) treatment conditions. Error bars represent the standard deviation from the mean of replicate enclosures ($n = 3$).

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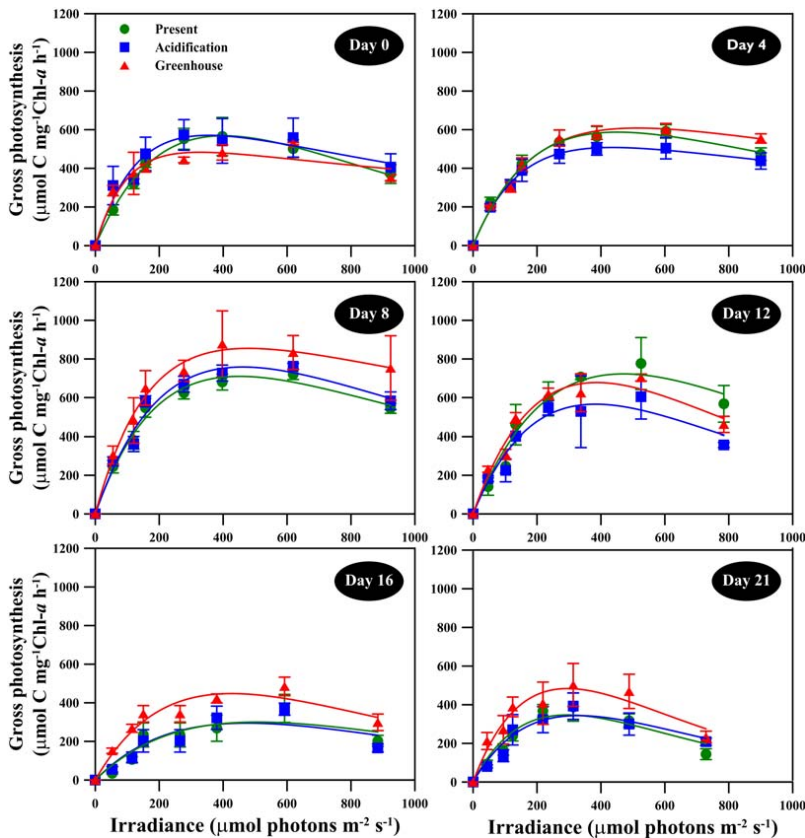


Fig. 3. Photosynthesis–irradiance (P–I) curves obtained by in situ incorporation of ^{14}C during the experimental period in the present (green), acidification (blue), and greenhouse (red) treatment conditions. Error bars represent the standard deviation from the mean of replicate determinations ($n = 3$).

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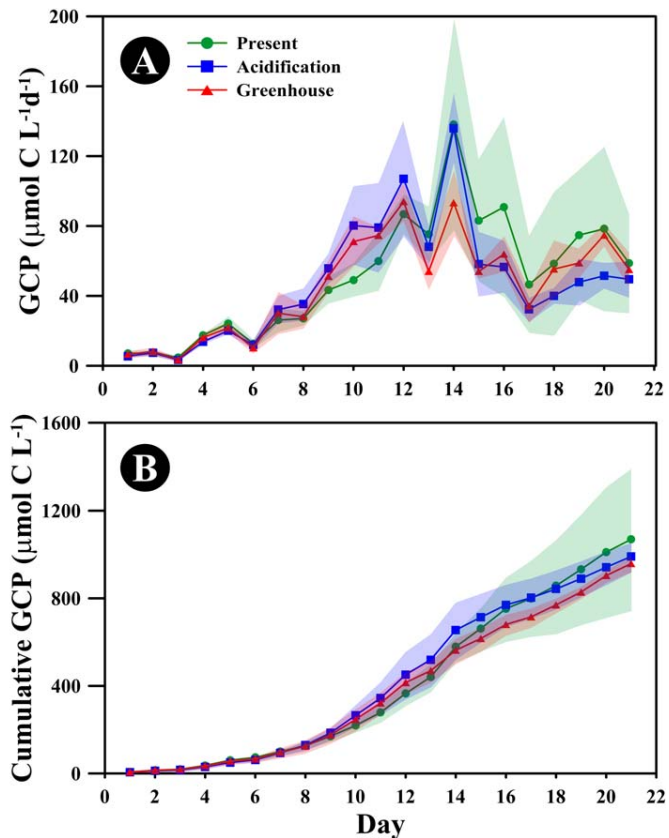


Fig. 4. Gross community production (GCP) **(A)**, and cumulative GCP **(B)** based on carbon assimilation rate, in situ irradiance profiles, and chlorophyll *a* concentration during the experimental period in the present (green), acidification (blue), and greenhouse (red) treatment conditions. Colored shading represents the standard deviation from the mean (colored symbols and lines) of replicate enclosures ($n = 3$).