



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

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Abstract. A mesocosm experiment was conducted to evaluate the influence of photosynthetic performance on the energetic balance of coastal phytoplankton, in relation to community production and autotrophic phytoplankton biomass in future coastal oceans. Natural phytoplankton assemblages were incubated in field mesocosms under ambient condition (control: ca. 400 μatm CO_2 and ambient temperature), and two sets of potential future ocean conditions (acidification: ca. 900 μatm CO_2 and ambient temperature; greenhouse: ca. 900 μatm CO_2 and 3 °C warmer). The photosynthetic performances were estimated by *in vivo* fluorometry (effective quantum yield (Φ_{PSII}), steady-state light response curves (LCs)) and *in situ* incorporation of ^{14}C (photosynthesis-irradiance curves). The Φ_{PSII} and $r\text{ETR}_{\text{m,LC}}$ (relative maximum electron transport rate) clearly reduced under acidification, in particular, when phytoplankton were exposed to high light levels. However, P_{max}^B (maximum photosynthetic rate) was the same in the ambient and acidification conditions. Thus, phytoplankton utilized less light under acidification condition, but could still assimilate a similar amount of carbon compared to the ambient condition. The P_{max}^B and α (photosynthetic efficiency) under greenhouse condition were significantly higher than those under ambient condition without any difference in Φ_{PSII} , $r\text{ETR}_{\text{m,LC}}$ and α_{LC} (electron transport efficiency) between the treatments. Therefore, phytoplankton utilized the same amount of light under greenhouse condition, but could assimilate more carbon than under ambient condition. As a result, Chl *a* normalized pri-

mary production was higher in greenhouse than in other conditions. Nevertheless, the community production did not change between the experimental treatments. The main reason for the lack of a change in primary production under future climate conditions is the control of autotrophic phytoplankton biomass by grazing. Consequently, acidification and greenhouse environments have a potential to increase growth and primary production of phytoplankton by enhancing inorganic carbon assimilation efficiency when top-down regulation is negligible.

1 Introduction

The ocean has been recognized as an anthropogenic CO_2 reservoir since the Industrial Revolution, but ocean acidification has only recently been considered to be a critical problem. Ocean acidification involves increases in $p\text{CO}_2$ and bicarbonate ion concentration (HCO_3^-) and decreases in pH and carbonate ion concentration (CO_3^{2-}) in seawater. Changes in carbon chemistry influence phytoplankton physiology, because photosynthesis and respiration are affected by increases in CO_2 and HCO_3^- concentrations. Generally, most phytoplankton require active inorganic carbon acquisition mechanisms for photosynthesis (carbon concentrating mechanisms; CCMs) to overcome CO_2 limitation and their poor CO_2 affinity of RuBisCO (Beardall and Raven, 2004; Raven, 2010). Thus, the photosynthesis of phytoplankton

could be positively affected by elevated CO₂ along with CO₂ affinity changes and downregulation of CCMs (Rost et al., 2003; Giordano et al., 2005; Sobrino et al., 2008; Hopkinson et al., 2011). On the contrary, some phytoplankton species that have already permanently adjusted to limited CO₂ environments, are not affected by oceanic CO₂ increases with active CCMs (Beardall and Raven, 2004; Giordano et al., 2005). Thus, physiological changes of phytoplankton might be complicated due to the various adaptation mechanisms under high CO₂ conditions, and they can heavily depend upon species-specific physiological characteristics of phytoplankton.

In response to ocean acidification, altered photosynthetic activities of different species can cause changes in cell growth and primary production, as well as in the community structure of the phytoplankton assemblage (Schippers et al., 2004; Riebesell, 2004). Some phytoplankton species have lower light-energy requirements to synthesize organic carbon under high CO₂ conditions (Chen and Gao, 2004), which can be an advantage allowing more organic compounds to be produced with less light energy. Energy consumption efficiency is also optimized for cell growth and division of phytoplankton under elevated CO₂ concentrations with energy savings due to the downregulation of CCMs (Sobrino et al., 2008). Previous mesocosm studies have shown that cell growth and primary production are promoted by an enhanced organic carbon assimilation rate alongside the community succession of phytoplankton (Riebesell et al., 2007). These results possibly suggest that the downregulation of CCMs could positively influence the biomass and primary production of natural phytoplankton assemblages. According to this perspective, photosynthesis, primary production and cell growth would be closely related to each other under high CO₂ conditions, but there is a lack of field mesocosm observations to corroborate this.

One of many problems caused by increasing atmospheric CO₂ is ocean warming. The temperature is expected to increase ca. 2–5 °C during this century based on the IPCC A2 Scenario (IPCC, 2007), and increased temperature has a profound influence on the physiology and ecology of phytoplankton and its community structure (Feng et al., 2009; Lewandowska and Sommer, 2010; Sommer and Lewandowska, 2010). Increased temperature also accelerates photosynthesis and respiration-related metabolic processes based on Q_{10} values in light-saturated productive areas (Sommer and Lengfellner, 2008). Previous studies suggest that increased temperature influences the production of phytoplankton more significantly than increased CO₂ (Hare et al., 2007; Feng et al., 2009). Additionally, community structure and species composition are strongly affected by increased temperature with altered and varied biophysical activities across all trophic levels (Hare et al., 2007; Rose et al., 2009; Lewandowska and Sommer, 2010). Although increased temperature can be an important factor to regulate the physiological response of phytoplankton in future envi-

ronmental conditions, pelagic mesocosm studies have rarely addressed the effects of temperature on photosynthesis and growth of the phytoplankton community, and numerous studies have focused only on the impact of elevated CO₂.

In this study, we focused on physiological changes and in turn ecological responses under future climate conditions. Photosynthetic adaptation, such as downregulation of CCMs, may alter ecological parameters such as changes of biomass, primary production and species composition in future environments. All of these changes could influence the energetic balance of entire metabolic processes with a positive response of photosynthesis. Most research on the energetic balance and energy flow process in response to future environments has relied on well-controlled laboratory conditions using single phytoplankton species (Fu et al., 2007; Sobrino et al., 2008, etc.). Because in situ mesocosm data are still scarce, it is hard to decide whether or not the results from single species studies can be applied at the ecosystem level. Mesocosms help evaluate well-established hypotheses and determine organismal to ecosystem level responses to future climatic environments (Kim et al., 2008; Riebesell et al., 2008). 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 photosynthetic activity of phytoplankton. The first aim of this study was to investigate the alteration of photosynthetic characteristics based on photosystem II chlorophyll *a* fluorescence (i.e., PSII photochemistry) and photosynthetic radioactive carbon incorporation (¹⁴C incubation). Also, we investigate the process by which photosynthetic carbon assimilation changes under future climate conditions alter the energetic balance of plankton communities. Thus, the second aim of this study was to examine the changes in primary production and phytoplankton biomass, which strongly correlate with photosynthetic activity in future climate conditions.

2 Materials and methods

2.1 Mesocosm experimental setup

A mesocosm experiment was conducted in the southern coastal waters of Korea (Jangmok Bay, Geoje Island; 34.6° N, 128.5° E), from 21 November to 11 December 2008. The mesocosm system consisted of a floating raft, *p*CO₂ concentration regulation units, seawater-mixing units, and mesocosm enclosures (Kim et al., 2008). The mesocosm facility consisted of nine polyethylene gas-tight enclosures. Three sets of experimental conditions were simulated in the initial phase of the experiment based on IPCC A2 Scenarios (IPCC, 2007): (1) ambient (control: ca. 400 μatm CO₂ and ambient temperature), (2) CO₂ only enriched (acidification: ca. 900 μatm CO₂ and ambient temperature), and (3) both increased CO₂ and temperature (greenhouse: ca. 900 μatm CO₂ and 3 °C warmer than ambient temperature)

(Fig. S-1A). About 1.6 tons of natural seawater was transferred into each mesocosm enclosure, and the initial Chl *a* concentration of seawater was ca. $1 \mu\text{g L}^{-1}$. CO_2 -saturated seawater was slowly diluted with natural seawater using a peristaltic pump to initiate the high CO_2 condition at the beginning of the experiment. The target concentration of CO_2 flowed into the headspace of the mesocosm bags for the entire duration of the experiment. A small fraction (ca. 0.5 L min^{-1}) of CO_2 also flowed into the seawater through the mixing unit for 20 min just before the daily seawater sampling. The bubbling time was sufficient to mix all the suspended and deposited material without causing bubbling effects on the living cells (Kim et al., 2008). This CO_2 gas regulation during the experimental period is not enough to maintain the initial conditions of $p\text{CO}_2$ because seawater carbon chemistry is very sensitive to biological activity. The CO_2 concentration was allowed to fluctuate due to biological activity during the experiment. The experiments were designed to interpret physiological responses of phytoplankton to future conditions, but not to specific CO_2 and temperature levels. To maintain the high temperature in the greenhouse condition, a heat exchange tube (PEX-A-PEX, Type-1216 (1/2")) was wrapped around the seawater-mixing unit at a water depth of 1.5–2.0 m. The heated freshwater circulated through the tubing with a flow rate of 25 L min^{-1} ; this was generated by a heating bath circulator (maximum heating capacity: 1 kW). This setup was enough to create seawater treatments 2–3 °C warmer than the ambient temperature regardless of natural temperature fluctuations during the whole experimental period (Fig. S-1C). Nutrients were added to each enclosure to create a phytoplankton bloom at the initial phase of the experiment (nitrate + nitrite: ca. $41 \mu\text{mol kg}^{-1}$, phosphate: ca. $2.5 \mu\text{mol kg}^{-1}$, and silicate: ca. $50 \mu\text{mol kg}^{-1}$; see Fig. S-2). Approximately 10 L of seawater was collected for daily sampling, and more than 1.3 tons of seawater remained in the mesocosm enclosures on the final day of the experiment. Further details of the experimental conditions, including the CO_2 concentration and pH, are provided in the Supplement, and in companion papers (Kim et al., 2010, 2011b).

2.2 Autotrophic phytoplankton biomass (Chl *a*)

The biomass (Chl *a*) of autotrophic phytoplankton 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

Seawater samples were collected 7–8 times during the day (06:00–19:00 local standard time-KST) under various irradiance conditions (0 – $1200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$). The ef-

fective quantum yield of PSII (Φ_{PSII}) was measured using an in vivo Chl *a* fluorometer (Phyto-PAM, Heinz Walz, Effeltrich, Germany). Measuring light pulses were generated by an array of light-emitting diodes (LED) with 4 different wavelengths, and a blue (470 nm) wavelength which was chosen to induce excitation of antenna pigments of autotrophic phytoplankton (Kim et al., 2013). Φ_{PSII} was obtained using a saturation pulse after exposure to different intensities of actinic light (light intensities were determined by in situ irradiance at sampling time), and 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. These results represent the apparent efficiency of open PSII reaction centers at each sampled time, after complete photoacclimation to ambient light intensities. The relative electron transfer 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. Steady-state light response curves (LCs) were constructed as rETR-I curves, which were fitted to a model with the photoinhibition parameter of Platt et al. (1980) to distinguish the efficiency of the PSII reaction centers as they would related to future environmental conditions. The photosynthetic parameters of Chl *a* fluorescence derived from LC fitting represented as the maximum relative electron transport rate (rETR_{m,LC}: maximum rETR capacity), electron transport efficiency (α_{LC} : efficiency quanta used in PSII electron transport), and the light saturation intensity of the LCs ($E_{\text{k,LC}}$: light level reaches saturation for rETR). All fluorescence measurements were carried out on days 1, 5, 9, 15, and 19 from all mesocosm enclosures.

2.4 Gross photosynthesis

Seawater samples were collected at 10:00 LT for gross photosynthesis measurements derived from ^{14}C incorporation. An 80 mL aliquot of seawater from each mesocosm enclosure was placed in a cell culture flask (Corning Inc., NY, USA), and $0.5 \mu\text{Ci}$ of $\text{NaH}^{14}\text{CO}_3$ was inoculated to initiate the incubation experiment. The incubation bottles were wrapped with dark and neutral density screens with 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 of incubation, the seawater was filtered through 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 undertaken for 1 day under dark conditions, and then 10 mL of UltimaGold™ (PerkinElmer) scintillation cocktail was added to the scintillation vial. The radioactivity of synthesized particulate carbon was measured with a liquid scintillation counter (Tri-Carb 2100 TR, Packard Instruments Co., Downers Grove, IL, USA), and the carbon uptake was calculated using an equation derived by 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 the 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 on days 0, 4, 8, 12, 16, and 21 from all mesocosm enclosures.

2.5 Gross community production (GCP)

Primary production was calculated using ^{14}C uptake photosynthetic parameters and Chl *a* concentration with the time series of incident light data. This is considered to represent water column light attenuation, and data were expressed as gross community production (GCP). 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 in the atmosphere and at 1 m water depth outside the mesocosm enclosures; and five HOBO Pendant Temperature/Light data loggers (Onset Computer Corp., Bourne, MA, USA) were installed randomly at a 1 m water depth inside and outside enclosures to examine the internal light intensity. GCP was expressed as volume-based, cumulative, and Chl *a* normalized GCP.

2.6 Statistical analysis

Analysis of variance (ANOVA) was used to identify the statistical difference between the treatments (ambient, acidification and greenhouse conditions), including P-I curves and LCs parameters. All datasets met the 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 Autotrophic phytoplankton biomass (Chl *a*)

The mesocosm experiment was divided into three periods in terms of autotrophic phytoplankton biomass and nutrient levels (pre-bloom period: days 0–5; bloom period: days 6–14; and post-bloom period: days 15–21) (Fig. 1). The phytoplankton biomass increased slowly during the pre-bloom period with no differences between the experimental conditions, and it reached about $5 \mu\text{g Chl } a \text{ L}^{-1}$ monotonously at the end of this period. When the biomass increased exponentially, it leads to slightly higher Chl *a* under the acidification condition than under the ambient condition until day 13. However, the highest phytoplankton biomass reached $35 \mu\text{g Chl } a \text{ L}^{-1}$ under the ambient condition at the end of the exponential growth period (day 14). Subsequently, inorganic

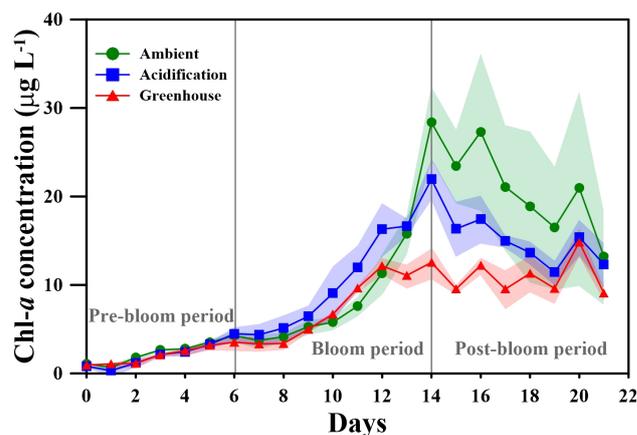


Fig. 1. Autotrophic phytoplankton biomass (Chl *a* concentration) during the experimental period under the ambient (green), acidification (blue), and greenhouse (red) treatment conditions. Colored shading represents the standard deviation from the mean (colored symbols and lines) of the replicate enclosures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

nutrients (nitrate + nitrite and phosphate) were depleted in all mesocosms (Fig. S2a, b), and the biomass also declined. This characterized a post-bloom period under the ambient and acidification conditions. In contrast, after 12 day incubation under greenhouse conditions, the autotrophic phytoplankton biomass (maximum = $14.8 \mu\text{g Chl } a \text{ L}^{-1}$) did not increase remarkably (Fig. 1).

3.2 Chl *a* fluorescence parameters

The effective quantum yield (Φ_{PSII}) showed a typical diurnal pattern that was intimately linked to the daily irradiance fluctuation (Fig. 2, left column). The Φ_{PSII} was 0.6–0.7 under low irradiances (at dawn and dusk) and decreased with increasing light intensity. The Φ_{PSII} was extremely low at 12:00 LT when the phytoplankton was exposed to high light intensity ($780\text{--}1188 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$), ranging from 0.0 to 0.2 over the overall experimental period. The general trend of Φ_{PSII} was slightly reduced in the acidification condition compared to the ambient and greenhouse conditions, but it is difficult to distinguish between the experimental conditions. Such trivial differences in Φ_{PSII} could lead to significant differences of rETR when phytoplankton is exposed to high light because total utilizable photon density is extremely high. Again, differences of Φ_{PSII} are more clearly distinguished in the rETR-I curves (LCs; steady-state light response curves), especially in the photoinhibition region. The pattern of LCs was not affected by experimental conditions on the first day of the experiment. After day 5, rETR decreased in high light levels (photoinhibition region) under the acidification rather than the ambient and greenhouse conditions (Fig. 2, right column). Among the LC parameters, $\text{rETR}_{\text{m,LC}}$ had no statistical difference between the experimental conditions during the pre-bloom period

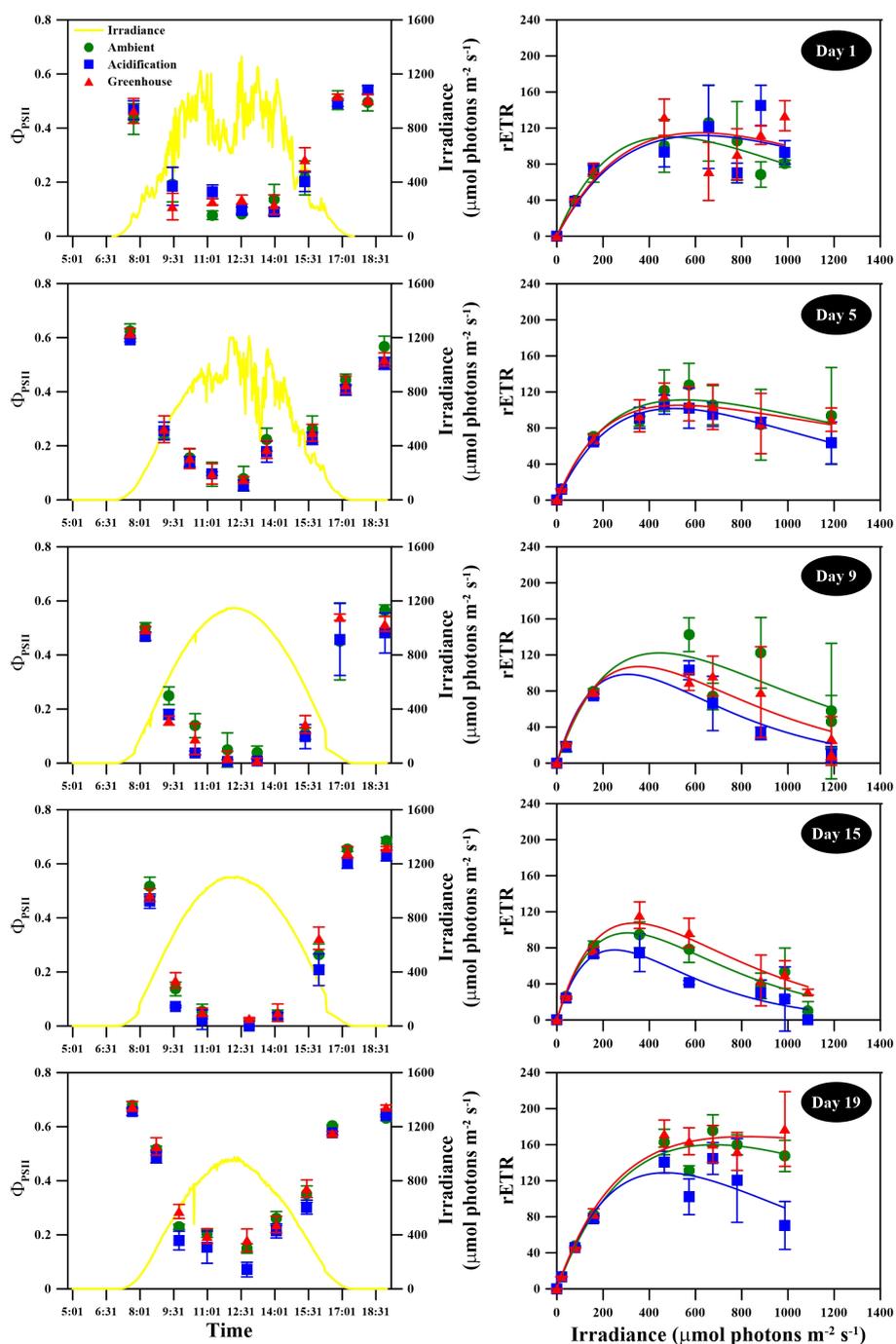


Fig. 2. Effective quantum yield of PSII (Φ_{PSII} , left column), and steady-state light response curves (rETR-I curves (LCs), right column) of the phytoplankton community during the experimental period under the ambient (green), acidification (blue), and greenhouse (red) treatment conditions. Error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

(Table 1). Otherwise, $rETR_{m,LC}$ values under the acidification condition were statistically lower compared to those in the other conditions on days 9 and 15, and these values were reduced compared to those of the ambient condition on day 9 and the greenhouse condition on day 15 ($p < 0.05$). The highest $rETR_{m,LC}$ was observed on day 19 during the

post-bloom period (130.5–167.1). Other parameters (α_{LC} and $E_{k,LC}$) showed no statistical difference between experimental conditions over the experimental period, except for α_{LC} on day 1. The highest α_{LC} occurred on day 15 when Chl *a* reached a peak in the ambient and acidification conditions (0.86–0.95). Nevertheless, relatively small changes in

Table 1. Photosynthetic parameters from steady-state light response curves (LCs) of 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 (a.u.)			α_{LC} Electron transport efficiency (a.u.)			$E_{k,LC}$ Light-saturation coefficient of LCs ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)		
	Ambient	Acidification	Greenhouse	Ambient	Acidification	Greenhouse	Ambient	Acidification	Greenhouse
Day 1	118.3 ± 38.8	104.6 ± 14.3	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	0.56 ± 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 ^{ab}	107.5 ± 3.7 ^{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 ± 0.09	0.95 ± 0.03	0.88 ± 0.07	112.1 ± 5.7	79.4 ± 15.1	124.1 ± 21.8
Day 19	162.3 ± 14.8	131.5 ± 15.1	167.1 ± 16.9	0.67 ± 0.05	0.66 ± 0.04	0.72 ± 0.03	224.3 ± 32.8	200.6 ± 25.1	231.9 ± 17.9

LC parameters occurred in the experimental conditions, and overall, rETR_{m,LC} and $E_{k,LC}$ in the acidification condition were clearly lower than in the other conditions except on day 1.

3.3 Photosynthetic ¹⁴C assimilation parameters

On the initial day of the experiment, the photosynthetic performance of the phytoplankton community showed no statistical difference between the ambient and future climate conditions (Fig. 3; Table 2). The P_{max}^B in the bloom period (days 8 and 12) was higher than that of the pre-bloom (ca. 30 %) and post-bloom (ca. 50 %) periods. This parameter showed a significantly lower value under the acidification condition on day 4 ($p < 0.05$), but there was no statistical difference in P_{max}^B between the ambient 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 the ambient condition on day 16 ($p < 0.05$) and under the acidification condition on days 16 and 21 ($p < 0.05$). No significant difference was found in α between the experimental conditions during the pre-bloom and bloom periods (Table 2). Statistically higher α values were found under the greenhouse condition compared to the acidification condition during the post-bloom period ($p < 0.05$). 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 ambient and future climate treatments for E_k , except on day 4 ($p > 0.05$).

3.4 Gross community production (GCP)

The gross community production (GCP) of autotrophic phytoplankton initially ranged from 4.9 to 8.0 $\mu\text{mol CL}^{-1} \text{d}^{-1}$, and then increased slowly to 22.0 $\mu\text{mol CL}^{-1} \text{d}^{-1}$ during the pre-bloom period, showing no differences between experimental conditions (Fig. 4a). During the bloom period, GCP increased rapidly in all conditions to values around 5 times higher than those on day 5, and reached a peak on day 14 when the highest Chl *a* occurred. The highest value of GCP was 138 and 136 $\mu\text{mol CL}^{-1} \text{d}^{-1}$ under the ambient and acidification conditions, respectively. The GCP de-

creased after the peak value to ca. 54 $\mu\text{mol CL}^{-1} \text{d}^{-1}$ during the post-bloom period. The 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 increased linearly (Fig. 4b). The total cumulative GCP was higher under the ambient (1069.5 ± 322.7 $\mu\text{mol CL}^{-1}$) than under the acidification and greenhouse conditions (991.3 ± 64.2 and 958.8 ± 32.5 $\mu\text{mol CL}^{-1}$, respectively), but remarkable differences were not observed between the experimental conditions. Although the daily and cumulative GCPs were not extensively affected by future climate conditions, the Chl *a* normalized GCP was more enhanced under greenhouse than under ambient and acidification conditions (Fig. 4c). Overall, the Chl *a* normalized GCP ranged from 1.6 to 10.6 $\mu\text{mol C } \mu\text{g}^{-1} \text{Chl } a \text{ d}^{-1}$ during the mesocosm experimental period, and it varied with the daily light intensity. The Chl *a* normalized GCP of the greenhouse treatment were higher than in the ambient and acidification conditions, especially during the blooming (days 7–10) and post-bloom periods (after day 14).

4 Discussion

4.1 Physiological implications

This mesocosm experiments elucidated the photo-physiological aspects based on actual responses of the PSII photochemistry. Also, the responses of photosynthesis of phytoplankton differed regarding the timing of blooms and community structure in future coastal ocean conditions. As far as we know, this is the first pelagic mesocosm study to evaluate the effects of future oceanic conditions on the physiological changes of phytoplankton through PAM (pulse-amplitude modulation) measurements. One previous field microcosm study focused on photo-physiological responses with a PAM fluorometer to evaluate the physiological effects of elevated CO₂ on a phytoplankton community (Gao et al., 2012). Our study first explored the energy balance changes from photosynthetic carbon assimilation to primary production and growth unlike previous studies.

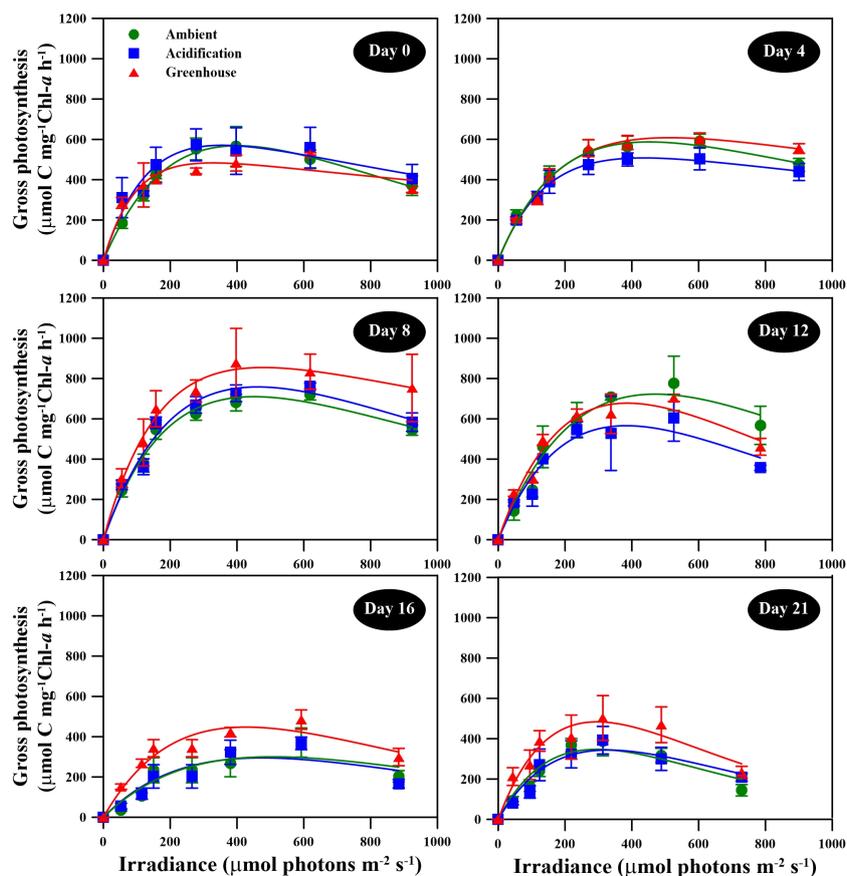


Fig. 3. Photosynthesis-irradiance (P-I) curves obtained by in situ incorporation of ¹⁴C during the experimental period in the ambient (green), acidification (blue), and greenhouse (red) treatment conditions. Error bars represent the standard deviation from the mean of replicate determinations (*n* =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

Table 2. Photosynthetic parameters from photosynthesis-irradiance (P-I) curves of the phytoplankton community obtained by the ¹⁴C uptake experiment. Different letters indicate a significant difference based on Tukey’s multiple comparison (*p* < 0.05).

Day	P_{max}^B Chl <i>a</i> -specific maximum gross photosynthesis rate ($\mu\text{mol C mg}^{-1} \text{ Chl } a \text{ h}^{-1}$)			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 ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)		
	Ambient	Acidification	Greenhouse	Ambient	Acidification	Greenhouse	Ambient	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	603.8 ± 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	478.0 ± 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

The key physiological finding of this study is that phytoplankton could assimilate inorganic carbon for photosynthesis more efficiently under acidification and greenhouse conditions compared to the ambient condition. This can be interpreted from the effective quantum yield (Φ_{PSII}) and steady-state response curves (LCs) (Fig. 2), the P-I curves (Fig. 3), and their photosynthetic parameters (Tables 1, 2). The primary evidences for this interpretation are (1) the lower Φ_{PSII} and $rETR_{m,LC}$ under the acidification condition

compared to the ambient condition without a decrease in ¹⁴C inorganic carbon incorporation, and (2) enhanced photosynthetic activity (e.g., increased P_{max}^B and α) under the greenhouse condition compared to the ambient condition without changes in the Φ_{PSII} and LC parameters. Phytoplankton utilize less light energy under the acidification condition but could assimilate a similar amount of carbon as in the ambient condition (from the 1st evidence). Also, they utilize the same light energy under the greenhouse condition, but

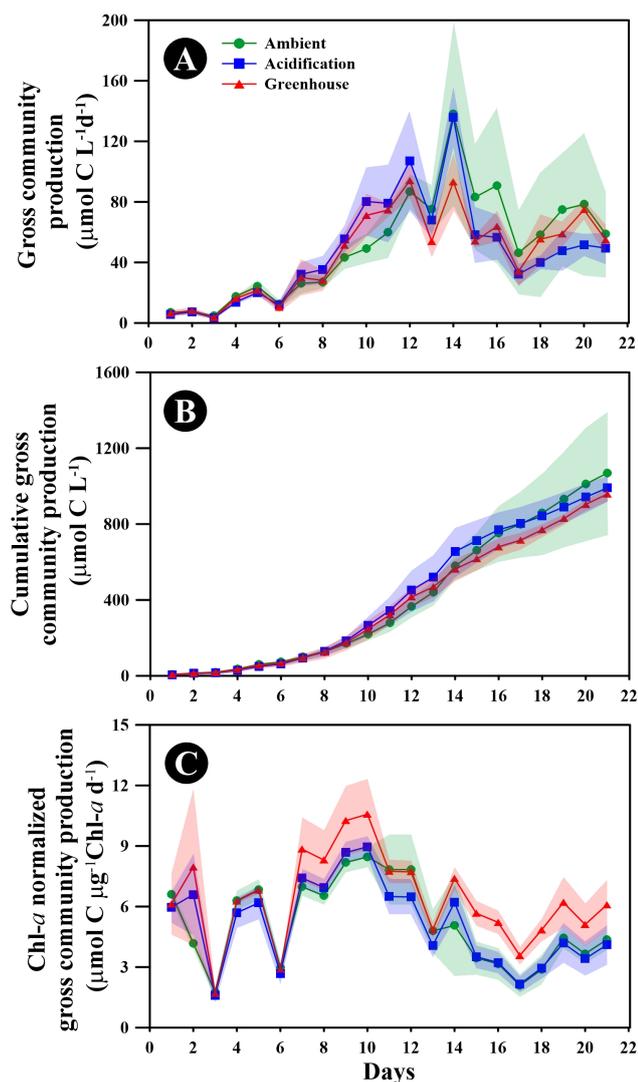


Fig. 4. Gross community production (GCP) (A), cumulative GCP (B), and Chl *a* normalized GCP (C) based on photosynthetic parameters, in situ irradiance profiles, and Chl *a* concentration during the experimental period in the ambient (green), acidification (blue), and greenhouse (red) treatment conditions.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

could assimilate more carbon than in the ambient condition (from the 2nd evidence). In this study, we avoid direct comparisons between LCs and P-I curves because several significant factors affect PSII photoinactivation and photochemistry (McCarthy et al., 2012). In particular, comparisons between LCs and P-I curves are not meaningful because the functional absorption section of PSII (σ_{PSII}) and the absorption factor are not considered in this study. Although σ_{PSII} is affected by environmental conditions such as CO_2 , temperature, irradiance, and community structure (MacKenzie et al., 2004, 2005), the LCs are an optimized tool to distinguish differences of Φ_{PSII} because it clearly reflects small changes

of Φ_{PSII} under different light conditions (Kim et al., 2011a). From the pattern of the LCs, rETR was obviously downregulated within a photoinhibition region under the acidification condition, also this tendency indirectly suggested that Φ_{PSII} was reduced significantly. However, the photoinhibition parameter from the LCs (β) did not show any statistical differences between treatments because the irradiance range of the region of photoinhibition was too narrow to estimate the photoinhibition parameter (Fig. S-5D). Consequently, the phytoplankton benefited the most from the acidification and greenhouse conditions with respect to light utilization efficiency for synthesizing organic products.

Previous laboratory studies showed similar results to our mesocosm experiment in respect of the energetic advantage of photosynthesis (Sobrinho et al., 2008; Wu et al., 2010). It was hypothesized that the surplus energy obtained from the downregulation of CCMs could be used for cell growth with improved photosynthetic activity. The downregulation of CCMs is indirectly linked to light requirements and carbon assimilation processes. Only 50% of the photosynthetic energy is generally allocated to growth, and 20% of the energy is consumed by the active pathway of carbon uptake with CCMs operation (Raven, 1991; Riebesell, 2004). However, less light energy is required for operating CCMs under high CO_2 conditions with depression of carbonic anhydrase activity (Hopkinson et al., 2010). The surplus energy saved from lower operation of the CCMs could activate the downregulation of a light-harvesting system due to the low light energy requirements. Thus, the phytoplankton takes advantage of photosynthesis and cell growth with efficient light energy utilization.

The greenhouse condition positively influences photosynthetic activity during the post-bloom period in this study. Carbon assimilation parameters were further increased (especially P_{max}^B and α) under the greenhouse condition with no change in PSII photochemical properties (Fig. 2; Table 1). The photosynthetic performance is accelerated by an optimized temperature condition (Claquin et al., 2008). The greenhouse condition showed a temperature range from 14.1 to 16.5 °C during the experimental period, and temperature under ambient and acidification conditions were ca. 2–3 °C colder than greenhouse conditions (Fig. S-1C). The temperature range for the greenhouse conditions is closer to optimal conditions for photosynthesis than ambient and acidification conditions, and is influence to photosynthetic performance positively to many phytoplankton species. Generally, temperature also has a positive influences on membrane fluidity and the electron transport system (Falkowski and Raven, 2007), and increased temperature positively affects the potential efficiency of PSII photochemistry within the optimized temperature range (Lassen et al., 2010). Temperature also has an influence on the regulation of CCM capacity due to the solubility of CO_2 and O_2 (Baker and Oxborough, 2004; Giordano et al., 2005). A higher portion of O_2 compared to CO_2 could lead to the reduction of photosynthesis caused

by competition between O₂ and CO₂ by RuBisCO, and enhanced photosynthesis could be induced by the high solubility of CO₂ and low solubility of O₂ in a warming ocean (Krause-Jensen et al., 1996). Therefore, we expect the decreasing PSII efficiency under acidification to be offset by the increasing temperature with the recovery of PSII efficiency.

Phytoplankton taxonomic groups and the succession of phytoplankton species could influence these physiological changes. A specific taxonomic group could be enhanced or inhibited by future climate conditions. In a North Atlantic study (shipboard continuous culture incubation system; Ecostat), the total Chl *a* under greenhouse treatment was higher than in ambient condition, and the dominant taxonomic group changed (Feng et al., 2009). In our mesocosm study, diatoms were the dominant taxonomic group during the overall experimental periods, and dinoflagellates increased somewhat in the post-bloom period (see Fig. S-3). More specifically, *Skeletonema costatum*, *Chaetoceros* spp., and *Eucampia zodiacus* were the dominant species within the diatom group, and the eight dominant species comprised more than 90 % of the diatom abundance (Kim et al., 2010). Also, *Akashiwo sanguinea*, *Nematodinium armatum*, and *Prorocentrum dentatum* were the dominant species among dinoflagellates, and the six dominant species were comprised over 90 % of the abundance of dinoflagellates (unpublished data). Some species benefited in terms of energetic balance for growth under acidified seawater from the previous laboratory and mesocosm studies (e.g., *Skeletonema costatum*: Kim et al., 2006; *Synechococcus* sp.: Fu et al., 2007; *Thalassiosira pseudonana*: Sobrino et al., 2008; *Phaeodactylum tricorutum*: Wu et al., 2010). In this mesocosm study, various species of diatoms and dinoflagellates responded differently to future climate conditions. For example, *Skeletonema costatum*, *Chaetoceros* spp. (positive to acidification condition), and *Eucampia zodiacus* (negative to acidification/greenhouse conditions) were largely affected by future climate conditions amongst the diatom group (Kim et al., 2010). In addition, *Gyrodinium* spp. (positive to acidification/greenhouse conditions), *Akashiwo sanguinea* (negative to acidification/greenhouse conditions) and *Nematodinium armatum* (positive to greenhouse) responded differently in the dinoflagellate group (unpublished data). However, physiological data could not be partitioned into specie-specific Chl *a* fluorescence and photosynthetic activities, because this study was investigated with community levels in response to future ocean conditions.

4.2 Ecological implications

Although the prediction of primary production has drawn considerable attention based on high CO₂ oceans, the estimation of pelagic primary production under future climate conditions using a field mesocosm experiment has been rare. In a comparable previous study (PeECEIII), primary production did not dramatically change under a doubled CO₂ concentra-

tion (Egge et al., 2009). In addition, two previous shipboard experiments showed contrary results in primary production (Tortell et al., 2002; Gao et al., 2012). An equatorial Pacific phytoplankton community did not change, but the productivity of phytoplankton in the East/South China Sea decreased under high CO₂ conditions. Daily and cumulative primary production results calculated from a short-term ¹⁴C incorporation experiment (GCP) showed only minor effect of future climate conditions (Fig. 5a, b). However, we expect that primary production will be promoted with photosynthetic improvements under future ocean conditions based on physiological results. Indeed, the contribution of Chl *a* to primary production (Chl *a* normalized primary production) was increased under the greenhouse condition (Fig. 4c). Nevertheless, primary production of the phytoplankton community was unchanged, which could have resulted from potential environmental factors such as grazing activity (detailed below).

Biomass (Chl *a* in this study) changes were directly linked to photosynthesis and primary production. In a previous study, biomass changes did not occur (Tortell et al., 2000), or small differences were observed (Riebesell et al., 2007; Feng et al., 2009) in the pelagic phytoplankton community, even when they were physiologically acclimated to high CO₂ condition. In our data, biomass also did not increase in acidification and greenhouse conditions, despite the positive effects on the photo-physiology of phytoplankton under those conditions. Moreover, biomass growth was not observed under the greenhouse condition, even though photosynthesis was positively affected by temperature (Fig. 1). Surplus energy was theoretically generated by the downregulation of CCMs under high CO₂ conditions, which might have further increased the phytoplankton biomass than with the energy in ambient condition. The optimal conditions for increases in biomass were the acidification and greenhouse conditions, but the biomass did not increase under these conditions over the experimental period. It seems that the biomass was not associated with physiological changes and production. This pattern represents the inconsistency between photosynthesis and primary production/biomass, which could be controlled by unexpected environmental factors. We suggest that one of the important factors is top-down regulation by grazers in mesocosm study, which will regulate phytoplankton blooms in the future ocean environment.

Grazing activity was significantly enhanced under acidification and greenhouse treatments after day 9 during the mesocosm experiment (Fig. S-4). The enhanced grazing rate was induced by heterotrophic dinoflagellate and microzooplankton under two sets of future conditions (Kim et al., 2010). Consequently, the abundance of grazers was increased, and positively affected by the two sets of future conditions, which also depressed the phytoplankton biomass blooms. Similarly to our study, Lewandowska and Sommer (2010) found remarkably lower phytoplankton biomass under warming conditions with enhanced top-down regulation induced by grazers such as zooplankton. Therefore,

primary production and cell biomass of phytoplankton may be promoted in acidified coastal waters when top-down regulation is negligible.

5 Summary

Our mesocosm study offers information about photosynthesis, primary production and total biomass changes. To knowledge, this mesocosm study is the first to suggest photo-physiological interpretation. The main objective of this study was to utilize photosynthetic performance as a means of evaluating physiological and ecological effects in the phytoplankton community under future climate conditions. The light utilization efficiency is accelerated for carbon assimilation through photosynthesis in a high CO₂ world regardless of increases in temperature. The phytoplankton community could take advantage of inorganic carbon assimilation with optimized light utilization under future climate conditions, but these changes were not largely reflected in primary production and autotrophic phytoplankton biomass. Again, positive physiological changes do not have a major effect on ecological responses under acidification and greenhouse conditions, because of the enhanced abundance of grazers and their grazing pressure. Future studies should consider various environmental factors for controlling phytoplankton dynamics by investigating phytoplankton communities in future ocean environments.

Supplementary material related to this article is available online at <http://www.biogeosciences.net/10/7525/2013/bg-10-7525-2013-supplement.pdf>.

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Data sets are available online at <http://mercury.chonnam.ac.kr/~ecoast/bbs/zboard.php?id=dataset>

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