Research Article

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Primary production by phytoplankton in the territorial seas of the Republic of Korea

An Suk Lim[1] **and Hae Jin Jeong**[2,3,*]

[1]*Division of Life Science, Gyeongsang National University, Jinju 52828, Korea*
[2]*School of Earth and Environmental Sciences, College of Natural Sciences, Seoul National University, Seoul 08826, Korea*
[3]*Research Institute of Oceanography, Seoul National University, Seoul 08826, Korea*

The primary production (PP) by phytoplankton in marine ecosystems is essential for carbon cycling and fueling food webs. Hence, estimating the PP in the territorial sea of each country is a necessary step to achieving carbon neutrality. To estimate the PP in the territorial sea of the Republic of Korea from 2005 to 2021, we analyzed various physiochemical parameters, such as sea surface temperature (SST), Secchi depth, and concentrations of chlorophyll-*a* and nutrients in the seas of five regions, including the East Sea, West Sea, western South Sea, eastern South Sea, and the waters off Jeju Island. During the 17-year study period, the SST tended to increase, while the nutrient concentrations declined, except in the Jeju area. Overall, the PP did not show a specific temporal trend, but daily PP in the western South Sea was the highest among the five regions. Moreover, the maximum PP in the Korean territorial waters (76,450 km^2) was estimated at 11,227 Gg C y^{-1}, which accounts for 0.03% of the global PP. The results may give insights into a better understanding of the PP, further resource utilization, and environmental sustainability in the studied region.

Keywords: carbon cycle; light utilization; photosynthetic assimilation; phytoplankton; primary productivity

INTRODUCTION

Oceans are one of the largest storages of carbon dioxide (CO_2) on the planet and play a major role in the global carbon cycle by absorbing approximately 30% of atmospheric CO_2 each year (Raven and Falkowski 1999). Although both pelagic and benthic communities of primary producers are responsible for primary production (PP) in the ocean, approximately half of the global annual net PP is produced by marine phytoplankton (Field et al. 1998, Spector and Edward 2020, Luo et al. 2021). This primary source of energy supports the entire marine biomass through food webs (Turner 2004, Eom et al. 2021, Jeong et al. 2021, Lee et al. 2021, Ok et al. 2021). Thus, it is crucial to accurately assess the geographical and temporal variability in phytoplankton production to better understand the global carbon dynamics and trophic energy flow.

Coastal waters support a high PP of approximately 10–30% of the global ocean production (Muller-Karger et al. 2005, Salgado-Hernanz et al. 2022). Moreover, physical and biological processes in coastal waters play an important role in carbon transport to deep oceans (Cai 2011). Therefore, estimating and comprehending PP in coastal waters is crucial for improving our understanding of the marine carbon cycle.

However, PP by marine phytoplankton is influenced by various physiochemical factors that are directly related to phytoplankton physiology, such as light, turbidity, water

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***Corresponding Author**
E-mail: hjjeong@snu.ac.kr
Tel: +82-2-880-6746, Fax: +82-2-874-9695

temperature, salinity, and nutrients (Valiela 1984, Cloern 1987). Due to the difficulty in acquiring all of these variables, the estimation of marine PP is challenging. Several methods, including the measurement of oxygen production using light and dark bottle incubation (Nielsen 1975), have been used to determine the PP. Moreover, photosynthetic carbon assimilation in water samples can be measured using radioactive or stable isotopes (e.g., ^{14}C and ^{13}C) (Yoo and Shin 1995, Park 1996, Kwak et al. 2013*a*, 2013*b*). More recently, active fluorescence techniques, such as pulse-amplitude-modulated fluorometry and fast repetition rate fluorometry, have been applied to estimate photosynthetic parameters and / or PP (Falkowski et al. 2004, Smyth et al. 2004, Ko et al. 2019). As an indirect method, some algorithms developed using satellite images have been used to provide a global estimation of PP (Eppley et al. 1985, Yoon et al. 2012).

Over the last 10 years, long-term monitoring programs have been developed, and many scientists have monitored various environmental parameters in a bid to evaluate the quality of coastal waters. Therefore, in the present study, the PP in the Korean coastal waters was estimated using environmental parameters such as light intensity, chlorophyll-*a* (Chl-*a*) concentration, and Secchi depth (SeD) from 2005 to 2021. The photosynthetic assimilation rate and light utilization efficiency were obtained from the literature for each season to calculate the primary productivity of marine phytoplankton. The temporal PP in each area was then estimated by combining environmental and physiological parameters. The results have implications for understanding PP trends and coastal water management.

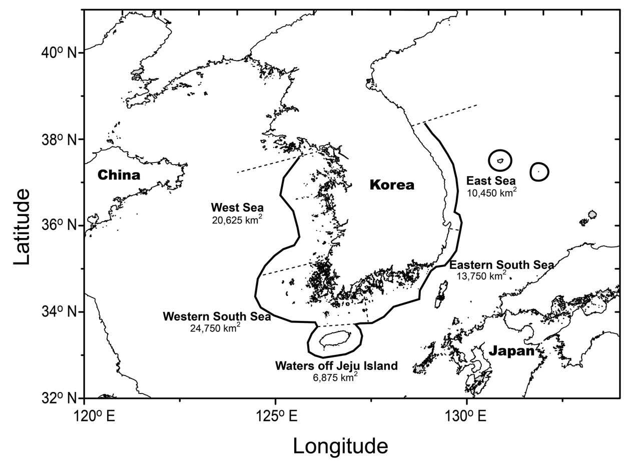

Fig. 1. A map showing the study area. The bold solid line indicates the terrestrial waters and, the area of the terrestrial waters was divided into five regions where the dotted lines were indicated. The area of each region indicated the numbers under each region's name.

MATERIALS AND METHODS

The dataset

Data were obtained from the National Fisheries Research and Development Institute (NFRDI, https://www.nifs.go.kr/femo/data_obs.femo) and the Korea Marine Environment Management Cooperation (KOEM, https://www.meis.go.kr/mei/observe/port.do). A total of 376 sampling stations (231 from NFRDI and 145 from KOEM) were located near or along the coastline of the Korean Peninsula (Fig. 1). The dataset of each station included sea surface temperature (SST), SeD, dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), and Chl-*a* concentrations in the surface and bottom waters. The concentrations (μM) of DIN and DIP were converted from those in μg L^{-1} with conversion factors of 14 for DIN and 31 for DIP. Data from sites with a salinity of less than 30 were excluded because these sampling sites had extremely high nutrient concentrations (e.g., >200 μM DIN) and were highly likely to have been influenced by artificial effects. The total number of data points was 21,540 from 2005 to 2021 (2011–2019 from NFRDI and 2005–2021 from KOEM). The data included samples from every other month (NFRDI) or from February, May, August, and November (KOEM) (Supplementary Table S1). Only data on both Chl-*a* and SeD that were available simultaneously were included in the PP calculation. The area of the territorial waters of Korea was obtained from the Korea Hydrographic and Oceanographic Agency (KHOA, https://www.meis.go.kr/map/oemsBaseMap.do) (Fig. 1).

Estimation of PP

The daily PP was calculated from the photosynthesis-irradiance parameters, calculated depth profiles of photosynthetic active radiation (PAR), and the Chl-*a* concentration. To estimate the PP of phytoplankton in a water column for a day, the hourly primary productivity at each water depth was integrated from the sea surface (Z_o) to the euphotic depth (Z_{eu}) for the day length. It was assumed that no photoinhibition occurred. Therefore,

$$PP_{day} = \int_{Z_0}^{Z_{eu}} B \times P_m^B \left[1 - \exp\left(-\alpha^B \times I_z / P_m^B\right)\right] \times D_{irr}$$

, where PP_{day} is depth-integrated PP (mg C m^{-2} d^{-1}), B is the

Chl-*a* concentration (mg Chl-*a* m^{-3}) at each depth, P_m^B is the maximum Chl-*a* normalized photosynthetic rate (mg C mg Chl-a^{-1} h^{-1}), α^B is the photosynthetic efficiency (mg C mg Chl-a^{-1} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$), I_z is the irradiance (μmol photons m^{-2} s^{-1}) at each depth, and D_{irr} is the day length (h).

As a physiological response of phytoplankton to light, the maximum Chl-*a* normalized photosynthetic rate (P_m^B), known as the assimilation number or the activity coefficient of chlorophyll, is the maximum primary productivity under optimal light conditions. Photosynthetic efficiency (α^B) is controlled by the counteracting effects of light limitation and depends on the capability of the cell to gather incident light (Côté and Platt 1983). The photosynthetic parameters P_m^B and α^B were obtained from the literature, which measured each parameter using a short-term ^{14}C experiment within the Korean coastal waters. The mean values for each parameter were categorized according to season and region (Table 1, Supplementary Table S2). The Chl-*a* concentration at each depth of each sampling station was calculated using the linear equations that were obtained by plotting the concentrations of Chl-*a* at the surface and bottom against the two depths. We considered the bottom depth to be 1 m above the reported water depth of each sampling station. It is possible that Chl-*a* exhibits a non-linear decrease from the surface to the bottom or a subsurface chlorophyll maximum layer exists. However, data on the vertical profiles of the Chl-*a* are scare. Therefore, it was assumed that the concentration of Chl-*a* decreased linearly from the surface to the bottom waters.

The irradiance (μmol photons m^{-2} s^{-1}) was converted from the total solar radiation (MJ m^{-2} d^{-1}) obtained from the Korea Meteorological Administration (KMA). The monthly average values were applied for the conversion. In the present study, irradiance is considered at wavelengths between 400 and 700 nm (PAR, *I*), which consists of 44% of solar radiation (Moon 1940, Morel and Smith 1974, Shim 2003) (Supplementary Table S1). The irradiance at a given depth in the water column (I_z) was estimated using the following equation:

$$I_z = I_0 \times e^{-k^*z}$$

, where I_z is the irradiance at each depth (μmol photons m^{-2} s^{-1}), I_0 is the irradiance at the surface (μmol photons m^{-2} s^{-1}), k is the attenuation coefficient, and z is the depth (m). To estimate k, SeD was used, and k was converted using the relationship $k = 1.44$ / SeD (Holmes 1970). The euphotic depth (Z_{eu}) was calculated as the depth at which PAR is 1% of the surface PAR and is given by 4.6 / k (Morel and Berthon 1989). Given the relationship with SeD, Z_{eu} was then given by $Z_{eu} = 3.2 \times$ SeD. When the water column depth at the station was shallower than the calculated value of Z_{eu}, the water depth was considered as the euphotic zone depth. The average day length (h) in the sampling month was obtained from the KMA and applied to the equation to calculate the PP_{day}.

Statistical analyses

The photosynthetic parameters in each season in each group of regions were analyzed using a one-way analysis of variance (ANOVA). Prior to analysis, the normality and homogeneity of the data were tested using Kolmogorov–Smirnov and Levene's median tests, respectively. If the data did not satisfy the assumption of homogeneity, Welch's one-way ANOVA was performed. If the data did not fit the Kolmogorov–Smirnov and Leven's tests, the Kruskal-Wallis H test was conducted. Moreover, the photosynthetic parameters between the two groups of regions were analyzed using the t-test or Mann-Whitney U

Table 1. The photosynthetic parameters used in this study

Region	Season	P_m^B	α^B	Reference
East Sea, eastern South Sea and waters off Jeju island	Winter	1.42 (1.44)	0.020 (0.016)	Park (1996), Yoshikawa and Furuya (2008), Ko (2014), Kwon et al. (2015)
	Spring	3.11 (2.17)	0.051 (0.039)	
	Summer	3.91 (3.13)	0.025 (0.016)	
	Autumn	5.73 (3.94)	0.034 (0.018)	
West Sea and western South Sea	Winter	4.34 (2.50)	0.155 (0.200)	Kang et al. (1992), Yoo and Shin (1995), Chung (1996), Son et al. (2005), Park and Kim (2010), Ko (2014)
	Spring	7.50 (5.49)	0.141 (0.140)	
	Summer	5.84 (2.85)	0.054 (0.035)	
	Autumn	7.34 (6.41)	0.168 (0.247)	

P_m^B, maximum Chl-*a* normalized photosynthetic rate, mg C mg Chl-a^{-1} h^{-1}; α^B, photosynthetic efficiency, mg C mg Chl-a^{-1} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$. The numbers in parentheses are standard deviations. Winter includes data from January, February, and December. Spring includes data from March, April, and May. Summer includes data from June, July, and August. Autumn includes data from September, October, and November.

test. Linear regression analyses were performed to determine whether there was a long-term trend in the change in SST and nutrient concentration. All statistical analyses were performed using SPSS ver. 27.0 (IBM-SPSS Corp., Armonk, NY, USA). The significance criterion was set at $p < 0.05$.

RESULTS

Photosynthetic parameters

Overall, the maximum photosynthetic rate (P_m^B) and photosynthetic efficiency (α^B) values in the East Sea, eastern South Sea, and waters off Jeju Island were significantly lower than those in the West Sea and western South Sea (t-test, $t_{101} = 2.732$, $p = 0.004$ for P_m^B and Mann-Whitney U = 1,863.5, $p = 0.000$ for α^B). In the East Sea, eastern South Sea, and waters off Jeju Island, the highest mean P_m^B (mg C mg Chl-a^{-1} h^{-1}) was 5.73 in autumn, while the lowest rate was 1.42 in winter (Table 1). The mean P_m^B (mg C mg Chl-a^{-1} h^{-1}) differed significantly depending on the season (ANOVA, $F_{3, 41} = 3.736$, $p = 0.018$). Moreover, the mean α^B (mg C mg Chl-a^{-1} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$) was the highest in spring (0.051), but the lowest in winter (0.020) in these regions (Table 1). Unlike photosynthetic rates, the α^B in one season was not significantly different from that in the other seasons (Welch's ANOVA, $F_{3,15.6} = 2.536$, $p = 0.94$).

In the West and western South Seas, the highest mean photosynthetic rate was 7.50 mg C mg Chl-a^{-1} h^{-1} in

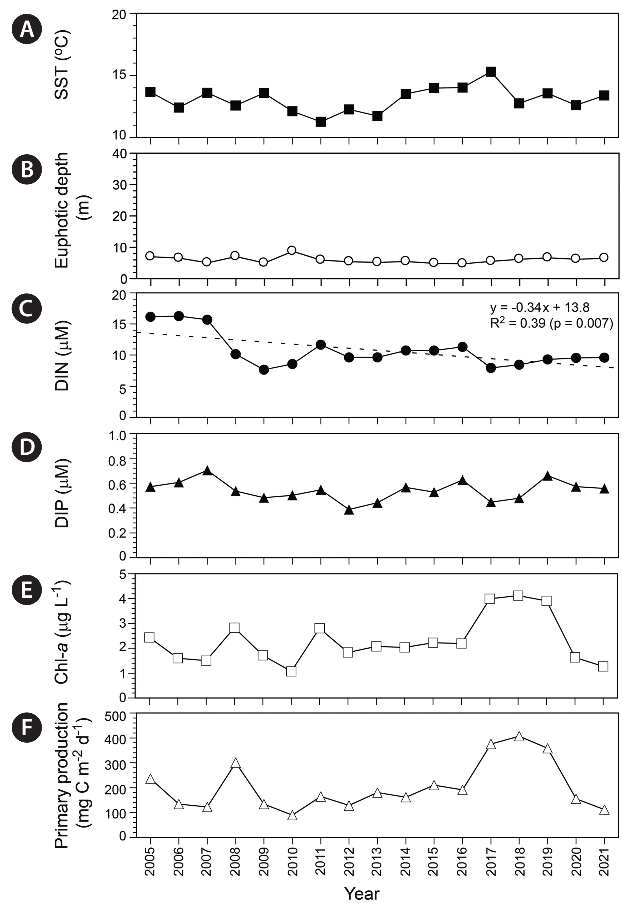

Fig. 2. Long-term trends in annual mean of sea surface temperature (SST) (A), euphotic depth (B), dissolved inorganic nitrogen (DIN) concentration (C), dissolved inorganic phosphorus (DIP) concentration (D), chlorophyll-*a* (Chl-*a*) concentration (E), and primary production (F) in the West Sea. Regression lines were shown with statistical significance.

Table 2. Physiochemical environmental conditions and the primary production (PP) in the West Sea

Year	SST (°C)	Euphotic depth (m)	DIN (μM)	DIP (μM)	Chl-*a* (μg L^{-1})	PP (mg C m^{-2} d^{-1})
2005	2.4–25.8 (13.7 ± 7.3)	2.6–19.8 (7.0 ± 3.7)	0.7–31.3 (16.2 ± 7.5)	0.19–1.39 (0.57 ± 0.3)	0.5–9.3 (2.4 ± 1.9)	33–807 (236 ± 214)
2006	2.5–25.7 (12.4 ± 7.3)	1.6–13.1 (6.6 ± 3.1)	1.1–36.9 (16.3 ± 10.4)	0.10–1.32 (0.61 ± 0.3)	0.2–16.7 (1.6 ± 2.7)	10–1,244 (134 ± 203)
2007	4.7–22.9 (13.6 ± 6.4)	0.6–12.5 (5.1 ± 3.2)	1.3–27.9 (15.7 ± 7.0)	0.08–1.06 (0.70 ± 0.2)	0.4–3.1 (1.5 ± 0.6)	19–279 (122 ± 71)
2008	2.4–26.1 (12.6 ± 7.1)	2.6–14.4 (7.1 ± 3.4)	0.4–33.2 (10.2 ± 7.9)	0.13–0.87 (0.53 ± 0.2)	0.2–14.9 (2.8 ± 2.9)	32–1,237 (300 ± 308)
2009	4.2–24.3 (13.6 ± 6.9)	1.6–11.5 (5.0 ± 2.7)	0.3–15.9 (7.7 ± 5.0)	0.10–0.97 (0.48 ± 0.3)	0.0–8.4 (1.7 ± 1.6)	3–477 (134 ± 127)
2010	2.8–26.9 (12.1 ± 7.2)	1.6–20.2 (8.7 ± 5.5)	0.9–19.6 (8.6 ± 5.5)	0.03–0.87 (0.50 ± 0.3)	0.1–2.6 (1.1 ± 0.8)	4–248 (89 ± 69)
2011	1.4–20.7 (11.3 ± 6.9)	1.0–11.2 (5.9 ± 3.3)	3.1–16.5 (11.7 ± 3.5)	0.12–0.87 (0.55 ± 0.2)	0.7–9.2 (2.8 ± 2.3)	39–468 (164 ± 98)
2012	0.7–29.6 (12.3 ± 8.4)	0.6–19.8 (5.4 ± 3.8)	0.2–35.0 (9.6 ± 7.4)	0.00–0.97 (0.39 ± 0.3)	0.0–37.2 (1.8 ± 3.6)	2–1,231 (128 ± 191)
2013	1.2–28.0 (11.7 ± 7.3)	0.3–24.0 (5.2 ± 3.8)	0.2–25.7 (9.6 ± 5.8)	0.00–1.29 (0.44 ± 0.3)	0.0–16.7 (2.1 ± 2.9)	2–1,723 (180 ± 264)
2014	1.4–25.9 (13.5 ± 7.4)	0.3–17.6 (5.5 ± 3.5)	0.7–40.0 (10.7 ± 7.4)	0.00–1.61 (0.57 ± 0.3)	0.2–28.2 (2.0 ± 2.8)	3–1,355 (161 ± 198)
2015	1.8–29.1 (14.0 ± 7.7)	0.3–19.8 (4.9 ± 3.0)	0.7–39.3 (10.7 ± 7.7)	0.00–1.61 (0.53 ± 0.4)	0.1–18.8 (2.2 ± 3.1)	4–2,039 (211 ± 332)
2016	2.4–30.2 (14.0 ± 7.7)	0.3–19.8 (4.8 ± 3.2)	0.7–48.6 (11.3 ± 8.0)	0.00–1.94 (0.62 ± 0.4)	0.1–13.1 (2.2 ± 2.3)	2–1,048 (191 ± 224)
2017	1.9–31.1 (15.3 ± 8.5)	0.3–25.6 (5.5 ± 3.7)	0.1–50.7 (7.9 ± 8.0)	0.00–1.61 (0.45 ± 0.4)	0.4–21.5 (4.0 ± 3.7)	28–2,322 (376 ± 372)
2018	-0.9–30.7 (12.8 ± 8.7)	0.3–26.2 (6.2 ± 3.5)	0.7–50.7 (8.5 ± 8.1)	0.00–2.26 (0.48 ± 0.4)	0.0–25.5 (4.1 ± 4.6)	3–3,118 (407 ± 571)
2019	2.1–28.1 (13.6 ± 7.7)	1.0–24.0 (6.7 ± 3.3)	0.3–37.1 (9.3 ± 7.4)	0.00–14.84 (0.66 ± 0.9)	0.4–20.7 (3.9 ± 3.6)	26–1,777 (358 ± 361)
2020	5.4–22.3 (12.6 ± 5.3)	1.6–22.4 (6.2 ± 4.4)	0.4–15.3 (9.6 ± 3.5)	0.04–0.88 (0.57 ± 0.2)	0.6–3.6 (1.6 ± 0.8)	49–436 (155 ± 117)
2021	3.3–25.4 (13.4 ± 7.2)	3.2–22.4 (6.5 ± 3.7)	0.3–17.3 (9.6 ± 4.8)	0.01–1.13 (0.56 ± 0.3)	0.3–4.0 (1.3 ± 0.6)	28–311 (111 ± 61)

SST, sea surface temperature; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; Chl-*a*, chlorophyll-*a*.
The numbers in parenthesis are mean ± standard deviation.

spring, whereas the lowest rate was 4.34 mg C mg Chl-*a*$^{-1}$ h^{-1} in winter (Table 1). The highest mean α^B was 0.168 in autumn, while the lowest α^B was 0.054 in summer (Table 1). The $P_m{}^B$ and α^B in one season were not significantly different from those in the other seasons (Kruskal-Wallis, H_3 = 1.858, p = 0.602 for $P_m{}^B$ and H_3 = 2.647, p = 0.449 for α^B).

Environmental parameters and calculated PP

From 2005 to 2021, in the West Sea of Korea, the annual mean SST fluctuated slightly from 11.3 to 15.3°C (Fig. 2A). The highest surface temperature was observed in 2017, whereas the lowest was observed in 2018 (Table 2). The calculated annual mean euphotic depth (Z_{eu}) ranged from 4.8 to 8.7 m (Fig. 2B); the deepest Z_{eu} was 26.2 m (Table 2). The annual mean DIN concentration in the surface waters significantly decreased from 2005 to 2021 (p = 0.007), whereas there was no distinct trend in the DIP concentration (Fig. 2C & D). The annual mean Chl-*a* concentration at the surface water fluctuated between 1.1 and 2.8 μg L^{-1} from 2005 to 2016 but maintained in high concentration (3.9–4.1 μg L^{-1}) in 2017–2019, and then decreased as low as 1.3 μg L^{-1} in 2021 (Fig. 2E). The calculated mean PP showed a similar pattern to that of the Chl-*a* concentration, ranging from 89 mg C m^{-2} d^{-1} in 2010 to 407 mg C m^{-2} d^{-1} in 2018 (Fig. 2F).

In the western South Sea of Korea, the annual mean SST from 2005 to 2021 fluctuated slightly from 14.9 to 17.8°C (Fig. 3A). The minimum and maximum SST were -0.2 and 32.0°C in 2018 (Table 3). The annual mean Z_{eu} ranged from 3.2 to 5.6 m (Fig. 3B) and the greatest Z_{eu}

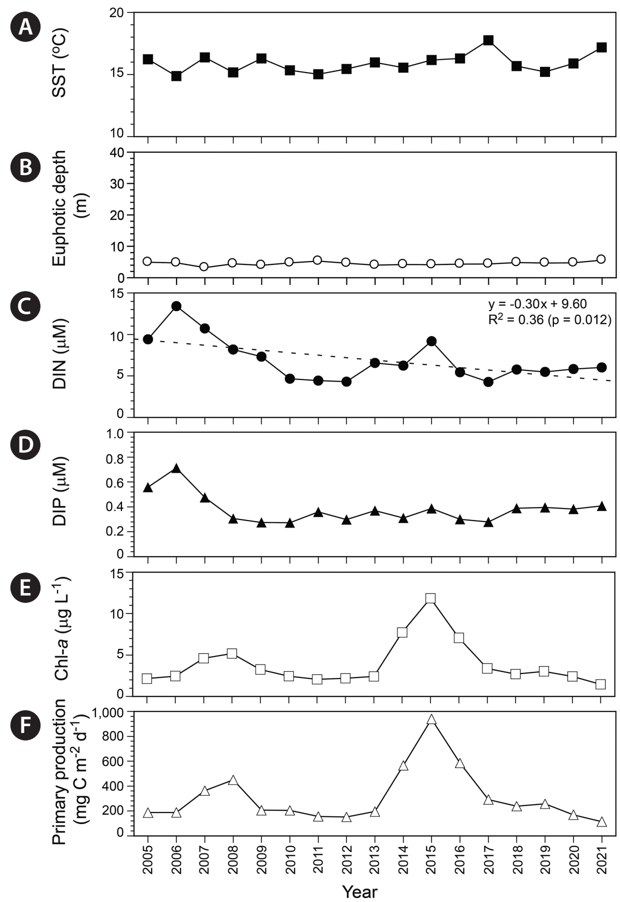

Fig. 3. Long-term trends in annual mean of sea surface temperature (SST) (A), euphotic depth (B), dissolved inorganic nitrogen (DIN) concentration (C), dissolved inorganic phosphorus (DIP) concentration (D), chlorophyll-*a* (Chl-*a*) concentration (E), and primary production (F) in the western South Sea. Regression lines were shown with statistical significance.

Table 3. Physiochemical environmental conditions and the primary production (PP) in the western South Sea

Year	SST (°C)	Euphotic depth (m)	DIN (μM)	DIP (μM)	Chl-*a* (μg L^{-1})	PP (mg C m^{-2} d^{-1})
2005	2.4–28.5 (16.2 ± 6.4)	0.3–14.0 (4.9 ± 3.0)	1.1–31.3 (9.4 ± 5.4)	0.07–2.43 (0.56 ± 0.4)	0.2–8.8 (2.2 ± 1.6)	3–779 (186 ± 157)
2006	2.7–27.7 (14.9 ± 6.4)	0.3–10.2 (4.7 ± 2.4)	1.9–41.1 (13.4 ± 7.2)	0.06–5.84 (0.71 ± 0.6)	0.0–36.2 (2.5 ± 3.9)	1–1,675 (188 ± 206)
2007	6.1–28.5 (16.4 ± 6.2)	0.3–12.8 (3.2 ± 2.4)	1.5–47.8 (10.7 ± 8.5)	0.00–3.87 (0.48 ± 0.6)	0.0–23.7 (4.6 ± 3.6)	0–1,358 (363 ± 315)
2008	2.8–29.0 (15.2 ± 6.7)	0.6–13.6 (4.4 ± 2.9)	1.5–28.0 (8.2 ± 4.6)	0.00–2.16 (0.31 ± 0.4)	1.1–24.0 (5.2 ± 4.1)	42–1,842 (450 ± 388)
2009	4.9–28.6 (16.3 ± 5.9)	0.3–16.0 (4.0 ± 3.0)	0.0–18.4 (7.3 ± 4.3)	0.00–0.81 (0.28 ± 0.2)	0.1–24.9 (3.3 ± 3.6)	1–1,394 (205 ± 193)
2010	2.9–29.3 (15.3 ± 6.7)	0.3–16.0 (4.7 ± 2.8)	0.1–12.9 (4.7 ± 3.8)	0.00–0.68 (0.27 ± 0.2)	0.1–8.0 (2.5 ± 1.6)	14–633 (205 ± 151)
2011	2.0–27.3 (15.0 ± 6.7)	0.6–14.4 (5.3 ± 2.8)	0.0–25.8 (4.4 ± 4.3)	0.00–1.29 (0.36 ± 0.3)	0.2–12.5 (2.1 ± 2.1)	16–864 (156 ± 139)
2012	2.3–30.0 (15.4 ± 8.1)	0.3–24.0 (4.6 ± 2.7)	0.0–22.1 (4.3 ± 4.2)	0.00–0.97 (0.30 ± 0.2)	0.2–14.3 (2.2 ± 1.9)	4–1,032 (152 ± 142)
2013	2.4–31.8 (16.0 ± 7.5)	0.3–29.6 (4.0 ± 2.6)	0.0–22.1 (6.6 ± 4.7)	0.00–1.40 (0.37 ± 0.3)	0.3–17.3 (2.4 ± 2.1)	6–1,180 (195 ± 176)
2014	3.4–26.9 (15.5 ± 6.2)	0.6–13.5 (4.2 ± 2.2)	0.2–35.7 (6.2 ± 4.5)	0.00–0.97 (0.31 ± 0.2)	0.1–88.2 (7.7 ± 11.4)	5–5,410 (566 ± 768)
2015	3.6–31.1 (16.2 ± 7.1)	0.3–17.5 (4.2 ± 2.2)	0.3–38.6 (9.2 ± 6.7)	0.00–0.97 (0.39 ± 0.2)	0.2–167.1 (11.9 ± 17.3)	2–11,805 (940 ± 1,280)
2016	1.6–31.8 (16.3 ± 7.7)	0.3–26.9 (4.3 ± 3.5)	0.5–27.9 (5.4 ± 4.6)	0.00–1.94 (0.30 ± 0.3)	0.1–72.9 (7.1 ± 10.1)	2–5,287 (585 ± 843)
2017	4.2–30.0 (17.8 ± 7.6)	0.3–14.0 (4.4 ± 2.3)	0.0–20.7 (4.3 ± 3.8)	0.00–1.61 (0.28 ± 0.3)	0.0–62.9 (3.4 ± 4.5)	1–5,456 (292 ± 369)
2018	-0.2–32.0 (15.7 ± 8.1)	1.3–14.4 (4.8 ± 2.2)	0.0–23.6 (5.8 ± 4.5)	0.00–1.29 (0.39 ± 0.3)	0.1–23.5 (2.7 ± 3.0)	7–2,320 (239 ± 276)
2019	2.9–30.7 (15.2 ± 6.9)	0.3–15.4 (4.7 ± 2.5)	0.1–27.1 (5.5 ± 4.0)	0.00–1.42 (0.39 ± 0.2)	0.1–15.5 (3.0 ± 2.9)	8–1,519 (257 ± 265)
2020	5.9–25.7 (15.9 ± 5.1)	0.3–15.0 (4.7 ± 3.2)	0.4–12.6 (5.8 ± 2.9)	0.01–0.72 (0.38 ± 0.2)	0.1–17.9 (2.4 ± 3.3)	10–1,178 (169 ± 202)
2021	5.4–29.6 (17.2 ± 6.9)	1.0–16.0 (5.6 ± 3.7)	0.3–16.4 (6.0 ± 3.8)	0.00–1.02 (0.41 ± 0.2)	0.1–7.4 (1.5 ± 1.3)	6–561 (114 ± 98)

SST, sea surface temperature; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; Chl-*a*, chlorophyll-*a*.
The numbers in parenthesis are mean ± standard deviation.

among the sites was 29.6 m in 2013 (Table 3). The annual mean DIN concentration in this region slightly decreased during the 17-year period (p = 0.012), whereas the annual mean DIP concentration showed no distinct trend (Fig. 3C & D). The minimum and maximum mean concentrations for DIN and DIP were 4.3 and 13.4 µM and 0.27 and 0.71 µM, respectively. An annual mean Chl-*a* concentration lower than 5.2 µg L^{-1} was maintained from 2005 to 2013, but largely increased to 11.9 µg L^{-1} in 2015 and then decreased to 1.5 µg L^{-1} in 2021 (Fig. 3E). The mean PP trend in the western South Sea was similar to that of Chl-*a*. The PP ranged from 114 mg C m^{-2} d^{-1} in 2021 to 940 mg C m^{-2} d^{-1} in 2015 (Fig. 3F).

In the eastern South Sea of Korea, the annual mean SST increased slightly from 2005 to 2021, ranging from 15.2 to 19.2°C (p = 0.045) (Fig. 4A). The minimum SST was 3.3°C in 2018, but the maximum SST was 31.6°C in 2013 (Table 4). The annual mean Z_{eu} was between 10.7 m in 2008 and 15.0 m in 2012 (Fig. 4B) and the maximum Z_{eu} was 64.0 m in 2012 (Table 4). The annual mean concentrations of DIN and DIP decreased slightly during 2005–2021 (p = 0.001 for DIN and p = 0.003 for DIP) (Fig. 4C & D). The minimum and maximum mean DIN concentrations were 3.5 µM in 2021 and 7.0 µM in 2007, respectively, while those of DIP were 0.28 µM in 2021 and 0.56 µM in 2007, respectively (Fig. 4). The annual mean Chl-*a* concentration fluctuated from 2005 to 2021, ranging from 2.0 µg L^{-1} in 2021 to 4.3 µg L^{-1} in 2015 (Fig. 4E). Similarly, the PP in the Korea Strait fluctuated between 69 mg C m^{-2} d^{-1} in 2021 and 183 mg C m^{-2} d^{-1} in 2015 (Fig. 4F).

In the East Sea of Korea, the annual mean SST gradu-

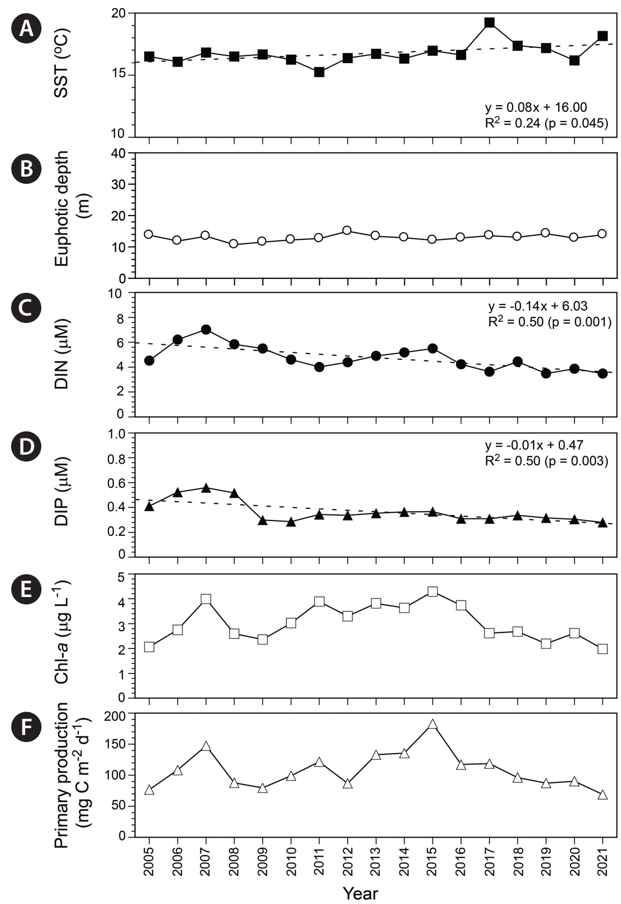

Fig. 4. Long-term trends in annual mean of sea surface temperature (SST) (A), euphotic depth (B), dissolved inorganic nitrogen (DIN) concentration (C), dissolved inorganic phosphorus (DIP) concentration (D), chlorophyll-*a* (Chl-*a*) concentration (E), and primary production (F) in the eastern South Sea. Regression lines were shown with statistical significance.

Table 4. Physiochemical environmental conditions and the primary production (PP) in the eastern South Sea

Year	SST (°C)	Euphotic depth (m)	DIN (µM)	DIP (µM)	Chl-*a* (µg L^{-1})	PP (mg C m^{-2} d^{-1})
2005	5.3–29.8 (16.5 ± 5.2)	3.2–38.4 (13.7 ± 6.6)	0.6–19.4 (4.5 ± 3.5)	0.00–1.64 (0.41 ± 0.3)	0.0–14.1 (2.1 ± 1.9)	1–419 (77 ± 79)
2006	5.4–31.3 (16.1 ± 5.4)	3.2–35.2 (11.9 ± 5.7)	0.0–22.9 (6.2 ± 4.7)	0.00–2.29 (0.52 ± 0.5)	0.1–15.6 (2.7 ± 2.9)	4–722 (108 ± 138)
2007	6.5–25.8 (16.8 ± 4.7)	3.2–38.4 (13.4 ± 6.3)	0.7–32.0 (7.0 ± 5.3)	0.01–2.00 (0.56 ± 0.4)	0.1–79.9 (4.0 ± 6.4)	3–2,811 (148 ± 235)
2008	5.0–29.3 (16.5 ± 5.2)	0.0–34.3 (10.7 ± 6.2)	0.5–18.0 (5.8 ± 4.1)	0.00–1.95 (0.52 ± 0.4)	0.2–12.9 (2.6 ± 2.4)	4–477 (88 ± 89)
2009	5.7–27.0 (16.7 ± 5.1)	3.2–30.4 (11.5 ± 5.1)	0.3–15.9 (5.5 ± 3.5)	0.01–1.26 (0.30 ± 0.2)	0.1–13.9 (2.4 ± 2.3)	1–697 (80 ± 107)
2010	5.1–28.1(16.3 ± 5.3)	1.6–35.2 (12.2 ± 6.0)	0.1–18.9 (4.6 ± 3.6)	0.00–1.12 (0.29 ± 0.2)	0.1–24.4 (3.0 ± 2.9)	1–954 (99 ± 110)
2011	3.5–26.6 (15.2 ± 5.6)	3.2–44.0 (12.7 ± 5.8)	0.0–34.3 (4.0 ± 4.2)	0.00–1.61 (0.34 ± 0.3)	0.0–57.7 (3.9 ± 5.0)	1–1,880 (122 ± 154)
2012	3.8–29.5 (16.4 ± 6.9)	2.2–64.0 (15.0 ± 8.4)	0.0–52.1 (4.4 ± 4.9)	0.00–3.87 (0.34 ± 0.4)	0.0–235.1 (3.3 ± 10.5)	0–3,709 (87 ± 175)
2013	4.9–31.6 (16.7 ± 6.0)	1.5–44.8 (13.4 ± 7.1)	0.0–33.6 (4.9 ± 4.8)	0.00–2.90 (0.35 ± 0.4)	0.0–205.7 (3.8 ± 8.3)	2–7,017 (133 ± 296)
2014	5.5–27.7 (16.3 ± 5.2)	1.5–51.2 (12.9 ± 6.7)	0.0–52.1 (5.2 ± 5.1)	0.00–1.61 (0.36 ± 0.3)	0.0–32.9 (3.6 ± 4.3)	1–1,371 (136 ± 186)
2015	5.4–31.4 (17.0 ± 6.0)	2.6–48.0 (12.1 ± 6.3)	0.0–37.1 (5.5 ± 5.2)	0.00–1.54 (0.37 ± 0.3)	0.1–50.6 (4.3 ± 5.9)	1–3,894 (183 ± 394)
2016	4.1–30.0 (16.6 ± 6.3)	0.6–43.0 (12.8 ± 6.7)	0.3–27.9 (4.2 ± 3.9)	0.00–1.61 (0.31 ± 0.3)	0.1–84.5 (3.7 ± 6.4)	2–2,216 (117 ± 169)
2017	5.6–29.6 (19.2 ± 6.4)	2.0–51.2 (13.6 ± 6.7)	0.0–24.3 (3.6 ± 3.5)	0.00–1.61 (0.31 ± 0.3)	0.1–18.3 (2.6 ± 2.5)	1–835 (119 ± 120)
2018	3.3–30.9 (17.4 ± 7.0)	2.6–54.4 (13.1 ± 7.0)	0.0–35.0 (4.4 ± 4.2)	0.00–1.94 (0.34 ± 0.3)	0.0–52.2 (2.7 ± 3.2)	0–841 (96 ± 104)
2019	6.2–30.3 (17.2 ± 5.8)	2.0–58.0 (14.2 ± 7.0)	0.0–17.9 (3.5 ± 3.3)	0.00–1.94 (0.32 ± 0.3)	0.2–22.3 (2.2 ± 2.0)	6–1,217 (87 ± 106)
2020	8.5–26.7 (16.2 ± 3.7)	3.2–41.0 (12.8 ± 6.1)	0.1–17.2 (3.9 ± 3.2)	0.00–1.24 (0.31 ± 0.2)	0.3–9.7 (2.6 ± 1.8)	4–336 (91 ± 72)
2021	7.7–30.0 (18.1 ± 6.1)	3.0–41.6 (13.9 ± 6.3)	0.2–17.2 (3.5 ± 3.3)	0.00–1.12 (0.28 ± 0.2)	0.1–6.4 (2.0 ± 1.3)	4–255 (69 ± 54)

SST, sea surface temperature; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; Chl-*a*, chlorophyll-*a*.
The numbers in parenthesis are mean ± standard deviation.

ally increased from 14.2 to 17.5°C during the study period ($p < 0.001$) (Fig. 5A). The minimum and maximum SST were 2.3°C in 2011 and 29.3°C in 2018, respectively (Table 5). The annual mean Z_{eu} was between 23.0 and 31.7 m in 2020 and 2015, respectively (Fig. 5B), and the maximum Z_{eu} was 73.6 m in 2016 (Table 5). The annual mean concentrations of DIN and DIP decreased slightly during the study period ($p = 0.002$ for both DIN and DIP) (Fig. 5C & D). The maximum and minimum mean DIN concentrations were 7.4 µM in 2006 and 2.4 µM in 2017, respectively (Fig. 5C). Meanwhile, the maximum and minimum mean DIP concentrations were 0.36 µM in 2005 and 0.17 µM in 2015, respectively (Fig. 5D). The annual mean Chl-*a* concentrations were maintained between 0.5 and 2.2 µg L^{-1} observed in 2015 and 2020, respectively (Fig. 5E). The PP in the East Sea also changed in the range of 17 and 78 mg C m^{-2} d^{-1}, and the minimum and maximum values were obtained in 2015 and 2020, respectively (Fig. 5F).

In the waters off Jeju Island, the annual mean SST showed no significant change during the study period, ranging from 18.2 to 20.1°C (Fig. 6A). The minimum and maximum SST were 8.5°C in 2015 and 31.1°C in 2018, respectively (Table 6). The annual mean Z_{eu} fluctuated until 2015, reaching the shallowest at 17.1 m, but increased in recent years. The deepest annual mean Z_{eu} was 52.0 m in 2017 (Fig. 6B). The annual mean concentrations of DIN and DIP tended to increase, except in recent years. The maximum and minimum annual mean DIN were 12.9 µM in 2015 and 3.1 µM in 2020, respectively (Fig. 6C). Meanwhile, the maximum and minimum DIP concentrations were 0.59 µM in 2012 and 0.16 µM in 2007, respectively

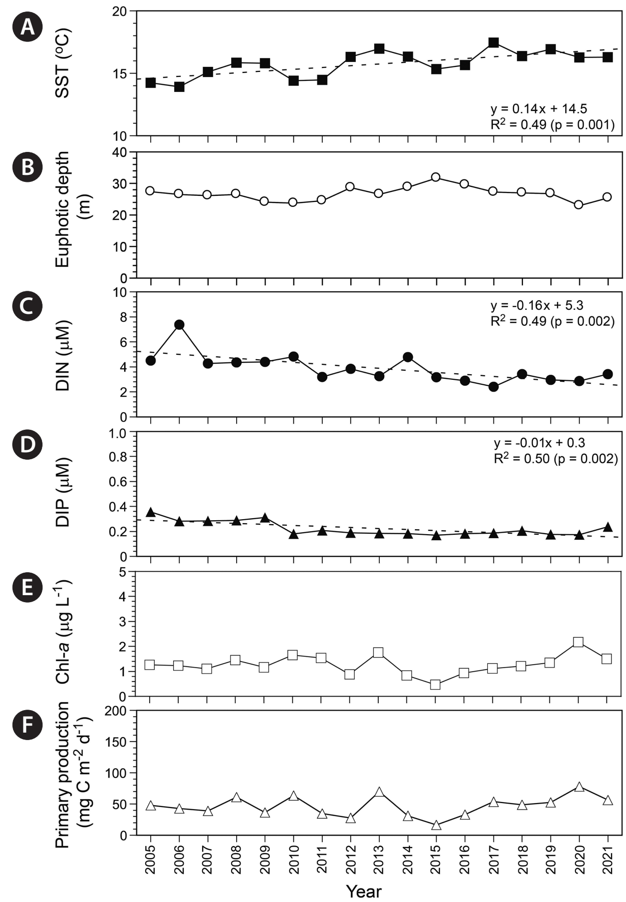

Fig. 5. Long-term trends in annual mean of sea surface temperature (SST) (A), euphotic depth (B), dissolved inorganic nitrogen (DIN) concentration (C), dissolved inorganic phosphorus (DIP) concentration (D), chlorophyll-*a* (Chl-*a*) concentration (E), and primary production (F) in the East Sea. Regression lines were shown with statistical significance.

Table 5. Physiochemical environmental conditions and the primary production (PP) in the East Sea

Year	SST (°C)	Euphotic depth (m)	DIN (µM)	DIP (µM)	Chl-*a* (µg L^{-1})	PP (mg C m^{-2} d^{-1})
2005	4.2–25.6 (14.2 ± 5.8)	8.0–48.0 (27.4 ± 8.4)	0.6–20.8 (4.5 ± 3.1)	0.03–1.77 (0.36 ± 0.3)	0.1–7.5 (1.3 ± 1.2)	1–439 (48 ± 55)
2006	3.5–27.7 (13.9 ± 6.1)	8.0–49.0 (26.5 ± 7.3)	0.4–33.8 (7.4 ± 4.6)	0.01–1.06 (0.28 ± 0.2)	0.1–4.4 (1.2 ± 0.6)	1–201 (43 ± 31)
2007	7.4–22.5 (15.1 ± 3.3)	8.0–48.0 (26.1 ± 6.9)	0.4–15.8 (4.3 ± 2.4)	0.00–0.94 (0.28 ± 0.2)	0.0–7.8 (1.1 ± 1.2)	1–390 (39 ± 53)
2008	8.0–26.2 (15.8 ± 5.1)	8.0–51.2 (26.5 ± 8.7)	0.5–15.4 (4.4 ± 3.1)	0.02–0.74 (0.29 ± 0.2)	0.0–8.6 (1.4 ± 1.4)	2–377 (61 ± 81)
2009	6.1–25.9 (15.8 ± 4.9)	8.0–48.0 (24.1 ± 7.5)	0.2–14.6 (4.4 ± 3.5)	0.01–1.30 (0.31 ± 0.2)	0.0–3.4 (1.2 ± 0.6)	0–155 (37 ± 33)
2010	3.4–24.2 (14.4 ± 5.3)	4.8–44.8 (23.7 ± 8.0)	0.4–10.0 (4.8 ± 2.8)	0.00–0.61 (0.18 ± 0.2)	0.5–18.3 (1.7 ± 1.6)	5–692 (64 ± 68)
2011	2.3–25.1 (14.5 ± 5.9)	3.2–57.6 (24.5 ± 9.0)	0.3–11.9 (3.2 ± 2.3)	0.00–0.62 (0.21 ± 0.2)	0.2–6.9 (1.5 ± 1.4)	5–115 (35 ± 25)
2012	6.9–28.1 (16.3 ± 6.1)	9.6–57.6 (28.7 ± 9.6)	0.2–11.4 (3.8 ± 2.9)	0.00–0.65 (0.19 ± 0.2)	0.0–4.5 (0.9 ± 0.6)	1–146 (28 ± 26)
2013	5.8–28.4 (17.0 ± 5.9)	1.6–54.4 (26.6 ± 7.8)	0.1–15.9 (3.3 ± 2.8)	0.00–0.65 (0.18 ± 0.2)	0.0–32.4 (1.8 ± 4.3)	1–1,391 (70 ± 184)
2014	4.7–24.6 (16.3 ± 4.9)	6.4–54.4 (28.8 ± 8.3)	0.0–22.1 (4.8 ± 5.3)	0.00–0.97 (0.18 ± 0.2)	0.0–18.8 (0.8 ± 1.3)	1–532 (31 ± 51)
2015	5.1–26.8 (15.3 ± 5.9)	9.6–51.2 (31.7 ± 8.7)	0.0–10.6 (3.2 ± 2.9)	0.00–0.65 (0.17 ± 0.2)	0.0–2.7 (0.5 ± 0.5)	1–159 (17 ± 22)
2016	4.7–28.5 (15.7 ± 5.5)	7.0–73.6 (29.6 ± 9.4)	0.0–23.6 (2.9 ± 2.9)	0.00–0.65 (0.18 ± 0.2)	0.0–5.0 (0.9 ± 0.9)	2–266 (33 ± 39)
2017	7.9–28.6 (17.5 ± 5.5)	6.4–56.0 (27.3 ± 9.5)	0.0–10.5 (2.4 ± 2.4)	0.00–0.65 (0.19 ± 0.2)	0.0–7.8 (1.1 ± 1.2)	0–431 (54 ± 71)
2018	2.7–29.3 (16.4 ± 6.2)	6.5–57.6 (27.0 ± 9.3)	0.0–13.6 (3.4 ± 3.4)	0.00–0.97 (0.20 ± 0.3)	0.0–18.1 (1.2 ± 1.3)	0–790 (49 ± 62)
2019	5.2–27.3 (16.9 ± 5.2)	7.0–57.6 (26.8 ± 9.1)	0.0–10.7 (3.0 ± 2.6)	0.00–0.73 (0.18 ± 0.2)	0.0–16.1 (1.3 ± 1.5)	3–1,076 (53 ± 79)
2020	10.8–24.2 (16.3 ± 3.8)	6.0–49.0 (23.0 ± 8.3)	0.1–8.7 (2.9 ± 2.6)	0.00–0.55 (0.17 ± 0.2)	0.4–8.8 (2.2 ± 1.6)	8–336 (78 ± 70)
2021	6.4–27.8 (16.3 ± 5.9)	6.4–57.6 (25.4 ± 8.5)	0.3–11.0 (3.4 ± 2.9)	0.00–0.58 (0.24 ± 0.2)	0.2–5.3 (1.5 ± 1.1)	6–243 (57 ± 54)

SST, sea surface temperature; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; Chl-*a*, chlorophyll-*a*.
The numbers in parenthesis are mean ± standard deviation.

(Fig. 6D). The annual mean Chl-*a* concentration ranged from 0.6 μg L^{-1} in 2019 to 1.9 μg L^{-1} in 2015 (Fig. 6E). Similar to Chl-*a* concentration, the PP fluctuated between 24 and 68 mg C m^{-2} d^{-1} in 2009 and 2015, respectively (Fig. 6F).

The annual total PP in the territorial waters (TPP, 76,450 km^2) (Fig. 1) was calculated by multiplying 365 days and the area of each region by the daily depth integrated mean PP and then summing the PP in each region. The TPP fluctuated between 2,981 Gg C y^{-1} in 2012 and 7,278 Gg C y^{-1} in 2014, but increased to 11,227 Gg C y^{-1} in 2015, and then decreased to 2,542 Gg C y^{-1} in 2021 (Fig. 7A). In 2015, when the TPP was the greatest among the studied years, the annual PP in the western South Sea accounted for the greatest, followed by the West Sea (Fig. 7B). The annual PPs in the western South Sea and West Sea were 343,024 and 76,834 kg C km^{-2} y^{-1}, respectively (Fig. 7C). The annual PP in the East Sea in 2015 was the lowest (1% of the TPP and 6,072 kg C km^{-2} y^{-1}) among the five regions of the territorial waters (Fig. 7B & C).

DISCUSSION

The photosynthetic rate and efficiency are essential parameters to evaluate the photosynthetic performance of the phytoplankton community and to analyze primary productivity. In our results, the photosynthetic rates in a season in the East Sea, the eastern South Sea, and the waters off Jeju Island were significantly different from those in the other seasons (p = 0.018), in agreement with

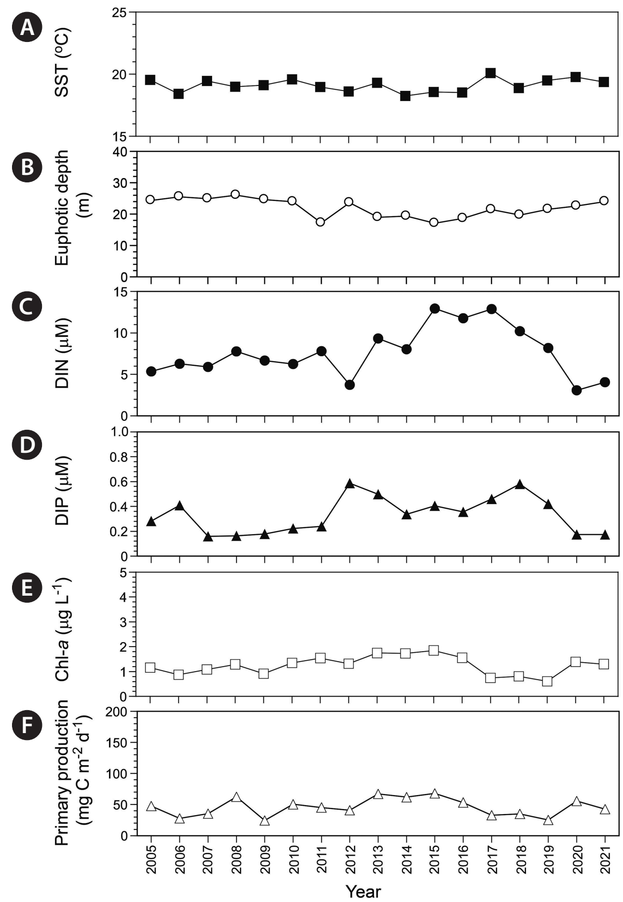

Fig. 6. Long-term trends in annual mean of sea surface temperature (SST) (A), euphotic depth (B), dissolved inorganic nitrogen (DIN) concentration (C), dissolved inorganic phosphorus (DIP) concentration (D), chlorophyll-*a* (Chl-*a*) concentration (E), and primary production (F) in the waters off Jeju Island. Regression lines were shown with statistical significance.

Table 6. Physiochemical environmental conditions and the primary production (PP) in the waters off Jeju Island

Year	SST (°C)	Euphotic depth (m)	DIN (μM)	DIP (μM)	Chl-*a* (μg L^{-1})	PP (mg C m^{-2} d^{-1})
2005	14.1–26.7 (19.5 ± 4.3)	14.0–44.8 (24.3 ± 6.8)	1.3–12.1 (5.3 ± 1.9)	0.00–0.85 (0.28 ± 0.2)	0.2–4.0 (1.2 ± 0.8)	4–232 (48 ± 53)
2006	13.2–28.7 (18.4 ± 4.6)	14.0–46.0 (25.5 ± 7.6)	1.7–25.1 (6.3 ± 3.2)	0.00–1.35 (0.41 ± 0.4)	0.0–3.4 (0.9 ± 0.6)	2–165 (28 ± 27)
2007	14.6–28.2 (19.4 ± 4.4)	14.0–46.0 (24.9 ± 7.7)	0.9–16.1 (5.9 ± 3.3)	0.00–0.40 (0.16 ± 0.1)	0.3–5.0 (1.1 ± 0.7)	9–172 (35 ± 26)
2008	13.8–27.4 (19.0 ± 4.4)	14.0–45.7 (26.0 ± 7.8)	0.6–30.1 (7.8 ± 5.3)	0.03–0.39 (0.16 ± 0.1)	0.3–5.5 (1.3 ± 1.1)	12–245 (63 ± 66)
2009	14.2–26.9 (19.1 ± 4.1)	14.0–44.8 (24.6 ± 7.0)	0.8–12.6 (6.7 ± 3.5)	0.02–0.46 (0.18 ± 0.1)	0.3–2.8 (0.9 ± 0.6)	5–81 (24 ± 16)
2010	13.8–28.6 (19.6 ± 5.0)	14.0–43.0 (23.9 ± 7.2)	1.9–14.4 (6.2 ± 2.9)	0.05–0.44 (0.22 ± 0.1)	0.6–3.4 (1.3 ± 0.6)	8–147 (50 ± 34)
2011	13.1–25.8 (19.0 ± 4.2)	1.6–44.8 (17.2 ± 8.5)	0.7–30.0 (7.8 ± 6.2)	0.00–0.97 (0.24 ± 0.2)	0.0–6.5 (1.5 ± 1.0)	7–315 (45 ± 41)
2012	12.7–27.8 (18.6 ± 3.7)	9.0–40.0 (23.6 ± 6.4)	0.0–9.8 (3.7 ± 2.2)	0.00–9.68 (0.59 ± 1.4)	0.4–4.7 (1.3 ± 1.0)	7–142 (41 ± 35)
2013	12.6–29.9 (19.3 ± 4.7)	5.0–48.0 (19.0 ± 7.8)	0.3–121.4 (9.3 ± 15.0)	0.00–4.19 (0.50 ± 0.7)	0.2–11.6 (1.7 ± 1.5)	8–581 (67 ± 77)
2014	11.8–26.8 (18.2 ± 3.3)	4.4–50.0 (19.4 ± 7.7)	0.7–122.9 (8.0 ± 12.8)	0.00–5.16 (0.34 ± 0.5)	0.0–5.1 (1.7 ± 1.1)	2–235 (62 ± 53)
2015	8.5–27.3 (18.6 ± 4.2)	0.3–35.2 (17.1 ± 6.4)	0.4–113.6 (12.9 ± 17.9)	0.00–5.81 (0.40 ± 0.7)	0.2–5.1 (1.9 ± 1.1)	1–223 (68 ± 57)
2016	13.2–28.4 (18.5 ± 3.7)	7.0–46.0 (18.6 ± 7.1)	1.2–85.7 (11.8 ± 13.9)	0.00–3.23 (0.36 ± 0.5)	0.0–3.7 (1.6 ± 0.8)	2–136 (53 ± 40)
2017	13.7–29.3 (20.1 ± 4.7)	8.4–52.0 (21.4 ± 8.2)	0.1–121.4 (12.9 ± 20.6)	0.00–3.55 (0.46 ± 0.6)	0.0–3.1 (0.7 ± 0.7)	0–183 (33 ± 34)
2018	12.9–31.1 (18.9 ± 4.2)	7.0–39.4 (19.7 ± 6.2)	0.1–81.4 (10.2 ± 14.8)	0.00–6.13 (0.58 ± 0.9)	0.0–5.7 (0.8 ± 0.8)	1–256 (35 ± 41)
2019	11.3–28.5 (19.5 ± 4.5)	7.0–46.0 (21.5 ± 6.9)	0.1–65.0 (8.2 ± 12.5)	0.00–3.87 (0.42 ± 0.7)	0.0–2.4 (0.6 ± 0.5)	1–104 (25 ± 25)
2020	14.5–29.4 (19.8 ± 4.6)	9.6–42.0 (22.6 ± 6.9)	0.3–14.0 (3.1 ± 2.5)	0.00–0.48 (0.17 ± 0.2)	0.1–7.7 (1.4 ± 1.3)	2–369 (56 ± 65)
2021	14.8–26.8 (19.4 ± 3.7)	10.0–41.6 (24.0 ± 7.1)	0.3–19.5 (4.1 ± 2.8)	0.00–0.45 (0.17 ± 0.1)	0.1–9.2 (1.3 ± 1.4)	2–211 (43 ± 43)

SST, sea surface temperature; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; Chl-*a*, chlorophyll-*a*.
The numbers in parenthesis are mean ± standard deviation.

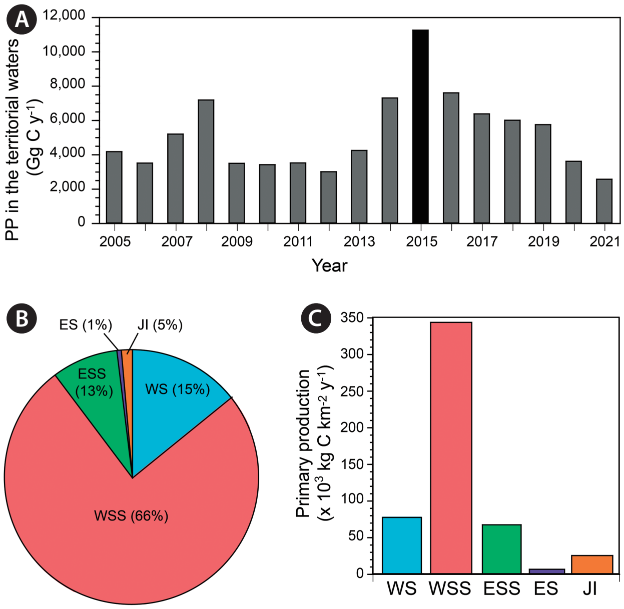

Fig. 7. Trend of annual primary production (PP) in the terrestrial waters (A), the percentage (B) and the amount (C) of PP of each region in 2015. The black bar in (A) indicates the year showing the highest PP during the study period. WS, West Sea; WSS, western South Sea; ESS, eastern South Sea; ES, East Sea; JI, waters off Jeju Island.

the fact that the photosynthetic rate is affected by water temperature and / or nutrient concentration (Park and Kim 2010). Moreover, the photosynthetic rates in the East Sea, eastern South Sea, and waters off Jeju Island were significantly lower than those in the West Sea and western South Sea ($p = 0.004$). Therefore, the results showed that different photosynthetic rates according to environmental conditions should be applied to the models or algorithms developed for estimating PP. Estimation of photosynthetic parameters based on the ecological environment should also be continued to accurately measure PP. The seasonal mean values of the photosynthetic rates ranged from 1.42 to 7.50 mg C mg Chl-a^{-1} h^{-1} in the Korean coastal waters, showing similar ranges to the values in the various marine environments ranging from 0.4 to 10 mg C mg Chl-a^{-1} h^{-1} (Eppley 1972). In particular, the values in the present study considerably overlapped the photosynthetic rates of phytoplankton in upwelling regions when water temperatures were between 17–25°C and ranged from 5 to 10 mg C Chl-a^{-1} h^{-1} (Eppley 1972).

The photosynthetic efficiencies of the phytoplankton communities from the West Sea and western South Seas were significantly higher than those of the East Sea, eastern South Sea, and waters off Jeju Island ($p = 0.000$). This means that the phytoplankton communities in the West and western South Seas likely assimilated carbon more efficiently through photosynthesis under the same light conditions. According to Côté and Platt (1983), photosynthetic efficiency is correlated with community structure, such as species composition, cell size, and species diversity. The disparate phytoplankton communities derived from the different environmental conditions between regions may result in differences in photosynthetic efficiency.

The annual mean SSTs in the eastern South Sea and East Sea significantly increased during the 17-year study period (Figs 4 & 5). Although the increase in the annual mean temperatures in other regions was not significant in the present study, there was a tendency to increase the SST in the Korean coastal waters, which is in agreement with previous studies (Han and Lee 2020, Lee and Park 2020).

The calculated euphotic depths did not exhibit any particular temporal pattern. However, it was clearly shown that the euphotic depths in the West and western South Seas were shallower than those in the eastern South Sea, East Sea, and waters off Jeju Island. This is not only because the average water depth in the West Sea and western South Sea of Korea (mostly less than 30 m, http://www.meis.go.kr) is shallower than that in the eastern South Sea and / or East Sea, but also because there are several large rivers in the western part of Korea. Moreover, the coastlines of the West Sea and western South Sea of Korea are characterized by a complicated coastline consisting of numerous islands, extensive tidal flats, and relatively strong tides (Kang et al. 2009). Strong tidal currents and mixing over shallow bathymetry may increase turbidity (Park et al. 1998) and cause shallow euphotic depths in the West and western South Seas of Korea.

The concentrations of DIN in the Korean coastal waters were significantly decreased, except in the Jeju area, indicating a reduction in nutrient concentrations in the coastal waters of the Korean Peninsula (Figs 2–6). Moreover, DIP concentrations in the eastern South Sea and East Sea decreased significantly. These decreases in nutrients in the Korean coastal waters have been reported in many studies (Kim et al. 2013, Ministry of Oceans and Fisheries and Korea Marine Environment Management Corporation 2022). Several processes, such as input from rivers, submarine groundwater discharge, and topographic environmental changes, may contribute to the dynamics of nutrient concentrations in Korean coastal waters (Hwang et al. 2005, Kim et al. 2013). For example, the reduction of nutrients in river discharge is partially responsible for decreasing nutrients in Korean coastal waters (Kim et al. 2013). Massive civil constructions, such as tidal power plants or sea dikes, are also suggested as possible reasons for the reduction of nutrients by decreasing nutrient input from sediments due to the decrease in tidal mixing (Kim et al. 2013).

Unlike other regions, the nutrient concentrations in the waters off Jeju Island tended to increase, except in recent years (Fig. 6). Several researchers have studied the quality and eutrophication of coastal waters off Jeju Island, and some nutrient sources have been suggested as possible reasons for the high concentration of nutrients. For example, there are concentrated inland aquacultures on Jeju Island, accounting for more than 50% of Korea in 2021 (KOSIS 2022), and thus the discharge of aquaculture effluent water has effects on the nutrient concentration in the coastal area of Jeju (Koh et al. 2013, Oh et al. 2021). Nutrient concentrations in the coastal area of Jeju are influenced by the submarine groundwater discharge (Hwang et al. 2005). Moreover, the excrement of migrating birds may be partially responsible for the high concentration of organic matter in the local coastal waters in Jeju (Kim and Kim 2017).

The trend in the Chl-*a* concentration differed across

Table 7. Comparison of the primary production (PP) in each region

Region	Year	Month	PP (mg C m^{-2} d^{-1})	Method	Reference
West Sea	1989	3, 5, 6, 8, 10	37–708	^{14}C	Kang et al. (1992)
	1990	2, 3, 5, 7, 8, 10	37–1,104	^{14}C	Kang et al. (1992)
	1992	1, 4, 8, 10	45–2,523	^{14}C	Lee and Choi (2000)
	1994	7	1,324	^{14}C	Yoo and Shin (1995)
	1995	1, 10	28–2,698	^{14}C	Yoo and Shin (1995), Choi et al. (1997)
	1996	3, 8	1,382–1,888	^{14}C	Choi et al. (1997)
	2004	4	94	^{13}C	Lee et al. (2006)
	2006	4	100–700	^{14}C	Yoo et al. (2018)
	2008	10	226–521	^{14}C	Park and Kim (2010)
	2016	8	67–456	^{13}C	Jang et al. (2018)
	2018	2, 4, 8, 10	68–487	^{13}C	Jang et al. (2021)
	2005–2021	All	2–3,118	Calculated	This study
Western South Sea	1992	9	620	^{14}C	Choi et al. (1995)
	2004	3	51–67	^{13}C	Kim et al. (2016)
	2009	2, 5, 7, 8, 11	9–8,927	^{13}C	Lee et al. (2011), Min et al. (2011, 2012)
	1992–1998	5, 9	554–734	^{14}C	Son et al. (2005)
	2011–2012	7–12	17–1,052	Numerical model	Jeong and Cho (2018)
	2005–2021	All	0.4–11,805	Calculated	This study
Eastern South Sea	1985	10	700–2,740	^{14}C	Shim and Park (1986)
	1992	4, 7, 10, 12	317–3,539	^{14}C	Yeo et al. (1996)
	1994	10–12	72–656	Calculated	Jeong et al. (2009)
	1995	All	32–1,527	^{14}C, calculated	Han et al. (1998), Jeong et al. (2009)
	1996	1–4	151–917	Calculated	Jeong et al. (2009)
	2013–2014	All	160–2,880	^{14}C	Kim et al. (2019)
	2005–2021	All	0.4–3,894	Calculated	This study
East Sea	1984	4, 5, 10	204–637	Calculated	Shim et al. (1985)
	1986	10	750–2,040	^{14}C	Chung et al. (1989)
	1988	5	284–4,574	^{14}C	Shim et al. (1992)
	1989	7	444–3,605	^{14}C	Shim et al. (1992)
	1990	4, 8	310–3,909	^{14}C	Park et al. (1991), Shim et al. (1992)
	2006	4	159–777	^{14}C	Hyun et al. (2009)
	2008	6, 8, 10	280–2,410	^{13}C	Kwak et al. (2013*a*)
	2009	5	490–940	^{13}C	Kwak et al. (2013*a*)
	2010	5, 11	550–1,074	^{13}C	Kwak et al. (2013*b*)
	2011	6	1,026	^{13}C	Kwak et al. (2013*b*)
	2012	10	181	^{13}C	Lee et al. (2017)
	2015	5	442	^{13}C	Lee et al. (2017)
	2016	4	378–986	^{13}C	Kang et al. (2020)
	2003–2012	All	447–1,263	MODIS-derived	Joo et al. (2014)
	2005–2021	All	0.03–1,391	Calculated	This study
Waters off Jeju Island	1989	4, 11	517–1,727	^{14}C	Chung and Yang (1991)
	1990	3	314	^{14}C	Chung and Yang (1991)
	1991	9, 11	25–145	^{14}C	Lee et al. (1993)
	1992	1, 3, 5, 6	4–805	^{14}C	Lee et al. (1993)
	2005–2021	All	0.2–581	Calculated	This study

regions. However, abnormally high Chl-*a* concentrations were observed from 2014 to 2016 in the western South Sea of Korea (Fig. 3). Heavy phytoplankton blooms frequently occur in the western South Sea of Korea. During 2014–2015, there also were massive algal bloom events caused by *Margalefidinium* (previously known as *Cochlodinium*) (Jeong et al. 2017, National Institute of Fisheries Science 2020). Even if the data for 2014–2016 were not included, the overall concentrations of Chl-*a* (1.5–5.2 μg L^{-1}) (Fig. 3) were greater than those in the East Sea and waters of Jeju Island, of which the maximum values were 2.2 and 1.9 μg L^{-1}, respectively (Figs 5 & 6). The relatively higher nutrient concentrations and photosynthetic abilities, as described above, in the western South Sea than in the East Sea may be partially responsible for the high Chl-*a* concentration range.

The trends and magnitudes of the PP differed in each region. Among the five regions, the PP in the western South Sea was the highest, reaching a maximum value of 940 mg C m^{-2} d^{-1} (Fig. 3, Supplementary Fig. S1). Even if the exceptionally high PP in 2014–2016 was excluded, the PP in the western South Sea exceeded 150 mg C m^{-2} d^{-1} on average. The high range of Chl-*a* concentrations may be a reason for the high PP in this region. The second largest region in the PP was the West Sea, although its Chl-*a* concentration range was similar to that of the eastern South Sea. Overall, the nutrient concentrations in the West Sea were higher than those in the eastern South Sea, and these eutrophic environments may have led to the high photosynthetic rate and efficiency values in the region. Thus, the physiological characteristics of the plankton communities, such as high photosynthetic ability, may be responsible for the high PP in the West Sea and are fundamental to evaluating PP.

The ranges of PP in the West Sea and western and eastern South Seas in the present study were similar to previously reported PP values in the same areas (Table 7). However, the PP derived from this study in the East Sea (1,391 mg C m^{-2} d^{-1}) was approximately one-third of the previously reported highest PP values in 1988 (4,574 mg C m^{-2} d^{-1}) but was similar to the values reported in the same years as the study period. In the waters off Jeju Island, the maximum PP in this study was one-third of that in 1989 (Table 7). However, recent values of PP in the waters off Jeju Island were not available; it could not be said that the PP was reduced compared to the past.

Based on the daily production from our results, the maximum annual PP was 343 g C m^{-2} y^{-1} in the western South Sea in 2015 (Table 3, Fig. 7C), indicating that it is one of the most productive marine environments compared to other regions. Previously, PP in various environments, including upwelling waters, continental shelves, and oceanic waters, was reported to be between 55 and 350 g C m^{-2} y^{-1}, except for a few abnormal values of 521 and 858 g C m^{-2} y^{-1} in the Mediterranean Sea (Eppley et al. 1985, Kwak et al. 2013*b*, Tiselius et al. 2016, Salgado-Hernanz et al. 2022). Therefore, the western South Sea of Korea may have a considerable effect on the carbon cycle in the Korean coastal waters and further studies should focus more on the western South Sea of Korea. Moreover, as a global aspect, the maximum annual TPP in the Korean territorial waters (11,227 Gg C y^{-1} = 0.011 Pg C y^{-1}) (Fig. 7A) accounted for approximately 0.03% of the global PP (42.5 Pg C y^{-1}) (Gregg et al. 2003), suggesting that they play an essential role in the global carbon cycle.

In the present study, PP was calculated with the assumption that the concentration of Chl-*a* linearly decreased from the surface to the bottom waters owing to a lack of data on the vertical profile of Chl-*a*. If the Chl-*a* concentrations exponentially decreased with increasing water depths, the PP calculated in the present study might have been overestimated. On the other hand, if a subsurface chlorophyll maximum layer existed, the calculated PP might have been underestimated. Acquisition of data on Chl-*a* at several depths may increase the accuracy of PP estimation.

In the Korean coastal regions, red tide events seem to have considerable effects on PP. Moreover, coastal marine environments, such as nutrients and water temperature, have changed in the study area, and thus potentially change PP in the future. Recent studies have revealed that increased SST and decreased nitrate concentrations decrease global PP (Gregg et al. 2003, Gregg and Rousseaux 2019). Therefore, the PP should be monitored to better understand how ongoing climate change affects the same and for further resource utilization and environmental sustainability.

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CONFLICTS OF INTEREST

The authors declare that they have no potential conflicts of interest.

SUPPLEMENTARY MATERIALS

Supplementary Table S1. Dataset used for the analysis in the present study (https://www.e-algae.org).

Supplementary Table S2. Photosynthetic parameters used in the present study (https://www.e-algae.org).

Supplementary Fig. S1. Long-term trend of primary production in each region (https://www.e-algae.org).

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