



# Water Quality Improvement Shifts the Dominant Phytoplankton Group From Cryptophytes to Diatoms in a Coastal Ecosystem

Yoonja Kang<sup>1\*</sup>, Chang-Ho Moon<sup>2</sup>, Hyun-Jung Kim<sup>3</sup>, Yang Ho Yoon<sup>1</sup> and Chang-Keun Kang<sup>4</sup>

<sup>1</sup> Department of Ocean Integrated Science, Chonnam National University, Yeosu, South Korea, <sup>2</sup> Department of Oceanography, Pukyong National University, Busan, South Korea, <sup>3</sup> Marine Eco-Technology Institute, Busan, South Korea, <sup>4</sup> School of Earth Sciences and Environmental Engineering, Gwangju Institute of Science and Technology, Gwangju, South Korea

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### \*Correspondence:

Yoonja Kang  
yoonjakang@jnu.ac.kr

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We investigated long-term variations in the dominant phytoplankton groups with improvements in water quality over 11 years in the Yeongil Bay on the southeastern coast of Korea. River discharge declined during the study period but TN from river discharge remained stable, indicating the input of enriched nutrients to the bay was fairly consistent.  $\text{NH}_4^+$  levels decreased with a decrease in TN from the POSCO industrial complex. While the study region was characterized by the P-limited and deficient environment, cryptophytes dominated with the intensified P-limitations. The relative abundance of cryptophytes declined from 70% in 2010 to 10% in 2016, but that of diatoms increased from 70% in 2009 to 90% in 2016. Correlation analysis showed a positive correlation of cryptophytes with  $\text{NH}_4^+$  and a negative correlation with photic depth. Generalized additive models also exhibited an increase in diatom dominance and a decrease in cryptophyte dominance with an increase in water quality, indicating that a decrease in  $\text{NH}_4^+$  and increase in light favored the diatom growth but suppressed the cryptophyte growth. Thus, water quality improvements shift the dominant group in the coastal ecological niche from cryptophytes to diatoms.

**Keywords:** water quality, phytoplankton, Yeongil Bay, ammonium, photic depth, ecological niche

## INTRODUCTION

Coastal ecosystems in bays and estuaries experience strong land-ocean interactions (Spatharis et al., 2007; Wang et al., 2020). Excessive nutrients from river discharge induce hypoxia or eutrophication in coastal ecosystems, causing coastal acidification (Paerl et al., 1998; Cai et al., 2011) and the development of harmful algal blooms (Glibert et al., 2006; Heisler et al., 2008). Phytoplankton biomass (i.e., chlorophyll a) is often utilized as an indicator of water quality conditions because of its strong interaction with environmental conditions (Boyer et al., 2009; Sathicq et al., 2017), and phytoplankton photopigments identifying the functional phytoplankton groups can be applied to assess coastal eutrophication (Paerl et al., 2003). Long-term water quality management often reduces nutrient inputs into coastal ecosystems (Zhang et al., 2020) while nutrient reduction leads to a decrease in the formation of toxic phytoplankton blooms (Marshall et al., 2006; Zhong et al., 2019). Cyanobacteria abundance can sharply increase with the degree of impaired

water quality, whereas other phytoplankton groups such as diatoms and dinoflagellates perish (Marshall et al., 2006).

The ecological niche of phytoplankton is based on the nutrient strategies and functional differences among phytoplankton groups (Gobler et al., 2011; Alexander et al., 2015b). It is necessary to understand how the dominant group within a phytoplankton niche changes with variations in environmental conditions because it reveals the underlying mechanisms of phytoplankton bloom dynamics associated with group-specific or species-specific ecological and physiological features (Litchman et al., 2012; Brun et al., 2015). Functional group-specific or species-specific traits in resource partitioning and identification of the ecological and physiological traits of dominant phytoplankton have been investigated for various phytoplankton groups (Alexander et al., 2015a,b). Although cryptophytes are a cosmopolitan phytoplankton group found under a wide range of environmental conditions (Clay et al., 1999); previous studies on cryptophyte blooms have been confined to either the mixotrophic strategy or light conditions (Barone and Naselli-Flores, 2003; Adolf et al., 2008; Mendes et al., 2013; Johnson et al., 2018).

Most phytoplankton studies in Yeongil Bay are associated with the spatial and temporal distribution identified using morphological or pigment (e.g., chlorophyll *a*) characteristics (Kwak and Lee, 1977; Jo et al., 2000; Shim et al., 2013). Phytoplankton dynamics in the bay are largely influenced by P availability originating from Hyeongsan River (Shim et al., 2013) although most coastal bay ecosystems have seasonal-specific nutrient limitations due to seasonal variations in river discharge. Water quality in the bay mainly ascribes individual parameters such as dissolved inorganic nutrient levels and some physical parameters including DO and pH (Shim et al., 2013). Previously, the southern coastal estuarine ecosystem, Gwangyang Bay, the importance of nitrogen and suspended particulate matter (SPM) variations was suggested as the causal factors for the decline of phytoplankton biomass (Kang et al., 2020), emphasizing the role of  $\text{NH}_4^+$  and light on controlling phytoplankton biomass in an anthropogenically eutrophic estuary. However, the role of those parameters in Yeongil Bay phytoplankton dynamics has not been investigated. Particularly, cryptophytes and diatoms are the dominant phytoplankton groups, historically occupying the ecological niche in Yeongil Bay (Kang et al., 2019b). To the best of our knowledge, long-term variations in the major phytoplankton groups in response to water quality improvement have not been evaluated previously in Korean coastal waters. In this study, we assessed (1) which phytoplankton groups dominated the pelagic habitat in response to water quality improvement and (2) how the major phytoplankton groups were affected by environmental variables.

## MATERIALS AND METHODS

### Study Region

Yeongil Bay is a semi-enclosed shallow bay that interacts with both a river and the ocean. The bay is located at the southeastern tip of the Korean peninsula and is connected to the East Sea (Japan Sea). The geographical location of the bay characterizes

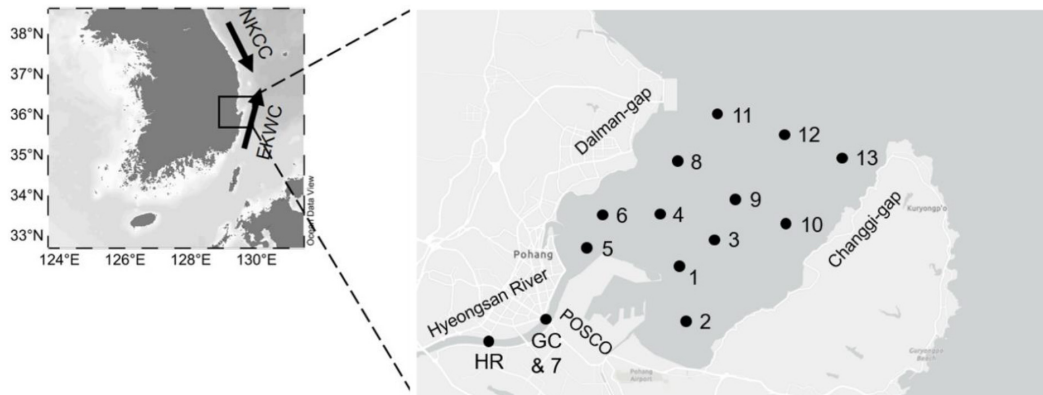
its unique features, which are fed by various bodies of water. Yeongil Bay is distinct in that the East Korea Warm Current (EKWC) intrudes into the surface of the bay from offshore, the North Korean Cold Current (NKCC), which propagates southward along the coast of the East Sea, appears on the southern coast of Korea, and the cold East Sea-proper water exists in the middle or bottom layer outside the bay (Lie, 1989). Once the water enters the bay, it circulates counterclockwise and flows out, bringing the diluted pollutants offshore (Choi, 1993). Pollutants from the Hyeongsan River sink and move toward the inner bay, which serves as a nutrient trap (Yoon et al., 2003). The freshwater input from the Hyeongsan River largely influences the spatial and temporal variations in water quality of the Yeongil Bay (Kim and Kim, 2004). The fast-growing population in the land area (Pohang city) surrounding the bay generates pollutants from industrial complexes, sewage, and livestock wastes that cause the coastal eutrophication, which is the excessive nutrient enrichment (Kim et al., 2001). The pollutant loads from industrial complexes or sewage decreased the water quality in the bay in the early 2000s (Yoon et al., 2002, 2003). In the 2010s, a water quality improvement action plan was applied to the coastal waters in Korea to mitigate coastal pollution (Nam and Han, 2011).

### Data Collection

Over 11 years from 2007 to 2017, field surveys were performed seasonally by the Marine Eco-Technology Institute at 13 stations for phytoplankton quantification in the winter (February), spring (May), summer (August), and fall (November) of each year (Figure 1). Seawater samples were collected in 1 L Nalgene polyethylene bottles using a Niskin water sampler (General Oceanics, Miami, FL, United States) from 1 m below the surface layer and 1 m above the bottom layer, and then preserved with Lugol's iodine solution at a final concentration of 1%, and then wrapped with aluminum foil to prevent the samples from degrading due to light exposure. Samples that were brought to a laboratory immediately after collection were settled for 48 h to allow the particles to settle to the bottom of the bottles, and the supernatant was carefully removed. The residue was transferred into 200 mL glass tubes and allowed to settle for another 48 h to form the final 10 mL samples for the microscopic observations. The final sample (1 mL) was mounted on a Sedgewick Rafter counting chamber to enumerate phytoplankton individuals at the species level through microscopy with a magnification of 100 $\times$  and 400 $\times$ . The final cell density was presented in cells/L.

Environmental data such as temperature, salinity, dissolved inorganic nitrogen (DIN; the sum of  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ , and  $\text{NH}_4^+$ ), dissolved inorganic phosphate (DIP;  $\text{PO}_4^{3-}$ ),  $\text{SiO}_2$ , and water quality index (WQI) were obtained from the Marine Environment Information System<sup>1</sup>. WQI was calculated based on standard measurement suggested by the Ministry of Oceans and Fisheries of Korea (see footnote 1). Ecosystem-specific water quality measurement was applied because region-specific characteristics exist. Chl *a* ( $\mu\text{g/L}$ ), DIN ( $\mu\text{g/L}$ ), DIP ( $\mu\text{g/L}$ ), DO saturation (%), and transparency (m) are utilized to calculate the

<sup>1</sup>www.meis.go.kr



**FIGURE 1** | Station maps showing the location of the Yeongil Bay on the southeastern coast of Korea. Black dots indicate the sample stations. HR and GC are locations where total nitrogen samples were collected. HR, Hyeongsan River; GC, Gumu Creek; POSCO, Pohang Iron and Steel Company; NKCC, North Korea Cold Current; EKWC, East Korea Warm Current. Phytoplankton samples were collected by the Marine Eco-Technology Institute and environmental data were obtained from the Marine Environmental Information System ([www.meis.go.kr](http://www.meis.go.kr)).

WQI. Standardized scores of each environmental variable were applied to calculate the WQI.

$$\begin{aligned} \text{WQI} = & 10 \times \text{Bottom DO saturation} \\ & + 6 \times \left[ \frac{\text{Chl a} + \text{Transparency}}{2} \right] \\ & + 4 \times \left[ \frac{\text{DIN} + \text{DIP}}{2} \right] \end{aligned}$$

Where DO is dissolved oxygen, chl a is chlorophyll a, DIN is dissolved inorganic nitrogen, and DIP is dissolved inorganic phosphorus.

River discharge data were acquired from the Water Resources Management Information System<sup>2</sup> and total nitrogen (TN) data from the Hyeongsan River and Gumu Creek near the Pohang Iron and Steel Company (POSCO) were obtained from the Water Environment Information System<sup>3</sup>.

## Data and Statistical Analyses

Nutrient data were analyzed after the DIN, DIP, and SiO<sub>2</sub> values in mg/L were converted to μM and the difference in TN between the Gumu Creek (GC) and Hyeongsan River (HR) was considered to obtain the TN from the POSCO (TN<sub>POSCO</sub> = TN<sub>GC</sub> − TN<sub>HR</sub>). Because a direct measure of TN from POSCO was not available and one end of GC was closed, we assumed that the difference between TN<sub>GC</sub> and TN<sub>HR</sub> can be representative of TN from POSCO. The mean annual variations in DIN, DIP, and SiO<sub>2</sub> were calculated to access the annual variation from 2007 to 2017. The proportion of NH<sub>4</sub><sup>+</sup> in DIN was calculated to investigate the variation in the NH<sub>4</sub><sup>+</sup> ratio over the 11-year period. Macronutrient limitations (i.e., Si-limitation, N-limitation, and P-limitation) were determined

based on the Redfield ratio (Tett et al., 1985): Si-limitation when Si:N < 1 and Si:P < 16, N-limitation when N:P < 16 and Si:N > 1, and P-limitation when N:P > 16 and Si:P > 16. Here, N denotes DIN.

Seasonal relative abundance represented the relative abundance of the identified phytoplankton groups, including cryptophytes, diatoms, dinoflagellates, euglenoids, green-algae, and silico-flagellates. Thereafter, the most abundant groups, which included cryptophytes, diatoms, and dinoflagellates, were further analyzed. The relative abundance of the three major phytoplankton groups was compared to assess the variation over the 11-year period. In addition, changes in the two most abundant groups, cryptophytes and diatoms, were compared with variations in environmental parameters such as WQI, proportion of NH<sub>4</sub><sup>+</sup> in DIN, and photic depth. The photic depth was calculated as 4.61/K<sub>d</sub> (Cloern, 1987), where K<sub>d</sub> is the light extinction coefficient, which was derived from Secchi depths (i.e., water transparency) using an equation applied to turbid waters, K<sub>d</sub> = 1.44/Z<sub>s</sub>, where Z<sub>s</sub> is the Secchi depth measured using a Secchi disk (Holmes, 1970). The equation, K<sub>d</sub> = 1.7/Z<sub>s</sub> was globally and locally applied to coastal waters (Poole and Atkins, 1929; Lee et al., 2017; Kang et al., 2020) but a modified coefficient, 1.44 was utilized for turbid waters (Holmes, 1970).

A correlation matrix was generated to investigate the relationship between the major phytoplankton groups, cryptophytes and diatoms, and environmental variables such as river discharge, photic depth, NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, PO<sub>4</sub><sup>3-</sup>, and SiO<sub>2</sub>. The correlation matrix visualized the correlations among the analytic parameters, correlation coefficients, and statistical significance (\**p* < 0.05, \*\**p* < 0.01, and \*\*\**p* < 0.001). Generalized additive models (GAMs) were performed using six main parameters (WQI, photic depth, NH<sub>4</sub><sup>+</sup>, the proportion of NH<sub>4</sub><sup>+</sup> in DIN, PO<sub>4</sub><sup>3-</sup>, and the N:P ratio) to investigate the variation in dominance between cryptophytes and diatoms in response to water quality improvement, light availability, and nutrient dynamics. Log-transformation was applied to phytoplankton abundance data prior to performing GAMs.

<sup>2</sup>[www.wamis.go.kr](http://www.wamis.go.kr)

<sup>3</sup>[water.nier.go.kr](http://water.nier.go.kr)

GAMs are non-parametric extensions of linear regression models with a linking function to predict the response of variables (dominance of cryptophytes and diatoms in this study) to a smoothed function of explanatory variables (the six parameters examined in this study), capturing the non-linearity between the responses and predictors (Kang et al., 2019a). The models were assembled as follows:  $\log(Y) \sim s(\text{WQI}) + s(\text{Photic depth}) + s(\text{NH}_4^+) + s(\text{NH}_4^+ \text{ ratio}) + s(\text{DIP}) + s(\text{N:P ratio})$ , where  $Y$  is representative of either diatom abundance or cryptophyte abundance and  $s$  is a smooth function of each parameter. Statistical analyses were performed in R version 3.6.2 (R Foundation for Statistical Computing, Vienna, Austria) using the “PerformanceAnalytics” package for the correlation matrix (Peterson et al., 2018) and “mgcv” package for GAMs (Wood and Wood, 2015). Plots were generated using the package “ggplot2” (Wickham, 2016).

## RESULTS

### River Discharge and Nutrient Dynamics

River discharge sharply declined from 92 m<sup>3</sup>/s in 2010 to 13 m<sup>3</sup>/s in 2017 after remaining stable for three 3 years from 2007 to 2009 (Figure 2A) while during the same period salinity increased from 33.3 to 33.7‰ in the surface layer and from 33.6 to 34.1‰ in the bottom layer (Figure 2B). The TN from the Hyeongsan River slightly decreased in the last 3 years but stayed consistent, and the TN from the POSCO declined sharply from 16.1 mg/L in 2010 to 4.1 mg/L in 2017, except a prompt increase in 2010 due to heavy rain (Figure 2C). Despite the dramatic decrease in river discharge, dissolved inorganic nutrients remained relatively stable (Figure 3). SiO<sub>2</sub> remained consistent for 9 years, after which the level at the bottom increased to 5.2 μM (Figure 3A), while the levels of other dissolved nutrients except for NH<sub>4</sub><sup>+</sup> were consistent (Figures 3B,D). NH<sub>4</sub><sup>+</sup> gradually declined to 0.34 μM in 2017 (Figure 3C).

### Long-Term Variations in the Major Phytoplankton Groups

Cryptophytes, diatoms, and dinoflagellates were the three major phytoplankton groups in the Yeongil Bay while the dominant species varied for the last 11 years (Supplementary Table 1). The long-term variations in these three groups showed that cryptophytes varied significantly but diatoms and dinoflagellates remained relatively stable in both the surface and bottom layers (Figure 4). Cryptophyte dominance declined sharply, from 90 to 10% over the 11-year period, whereas diatom dominance increased from 70 to 90% and dinoflagellate dominance slightly decreased from 30 to 10% during the same period (Figure 4).

The Redfield ratio, which was determined to be N:P:Si = 16:1:16, showed the macronutrient limitation in the bay. Silicate and nitrogen were not limited in most years (Figures 5A,B), whereas phosphate was limited during most periods except for 2007 and 2017 (Figure 5C). The P-limitation was more extreme on the surface layer where cryptophytes dominated, and the limitation was less intense in the bottom

where diatoms dominated; the limitation varied annually and was more severe when cryptophytes dominated (Figure 5C).

### Responses of Cryptophytes and Diatoms to Environmental Parameters

The correlations between the two major phytoplankton groups, cryptophytes and diatoms, and the studied environmental parameters were investigated (Figure 6). Cryptophytes were negatively correlated with photic depth (correlation coefficient = -0.87;  $p < 0.001$ ) whereas diatoms were not significantly related with the photic depth. Cryptophytes were positively correlated with NH<sub>4</sub><sup>+</sup> and PO<sub>4</sub><sup>3-</sup> (correlation coefficient = 0.45 and 0.42, respectively;  $p < 0.05$ ). Diatoms were positively correlated with PO<sub>4</sub><sup>3-</sup> but negatively correlated with NH<sub>4</sub><sup>+</sup>.

Generalized additive models showed variations in the dominance of cryptophytes and diatoms in response to environmental parameters, and cryptophytes and diatoms mostly exhibited opposing patterns (Figure 7). The dominance of cryptophytes increased as water quality worsened, but diatom dominance declined with an increase in the WQI (Figure 7A). An increase in light penetration (i.e., increase in photic depth) decreased cryptophyte dominance and favored diatom growth (Figure 7B). NH<sub>4</sub><sup>+</sup> favored cryptophyte growth whereas it suppressed diatom growth, but the growth did not change when NH<sub>4</sub><sup>+</sup> levels exceeded 4 μM (Figure 7C). In addition, diatoms resisted up to approximately 50% of NH<sub>4</sub><sup>+</sup> in DIN whereas cryptophytes benefited more from increased NH<sub>4</sub><sup>+</sup> in the DIN (Figure 7D). Cryptophytes positively responded to DIP levels and were resistant to P-limitation whereas the dominance of diatoms declined with both DIP and P-limitation (Figures 7E,F).

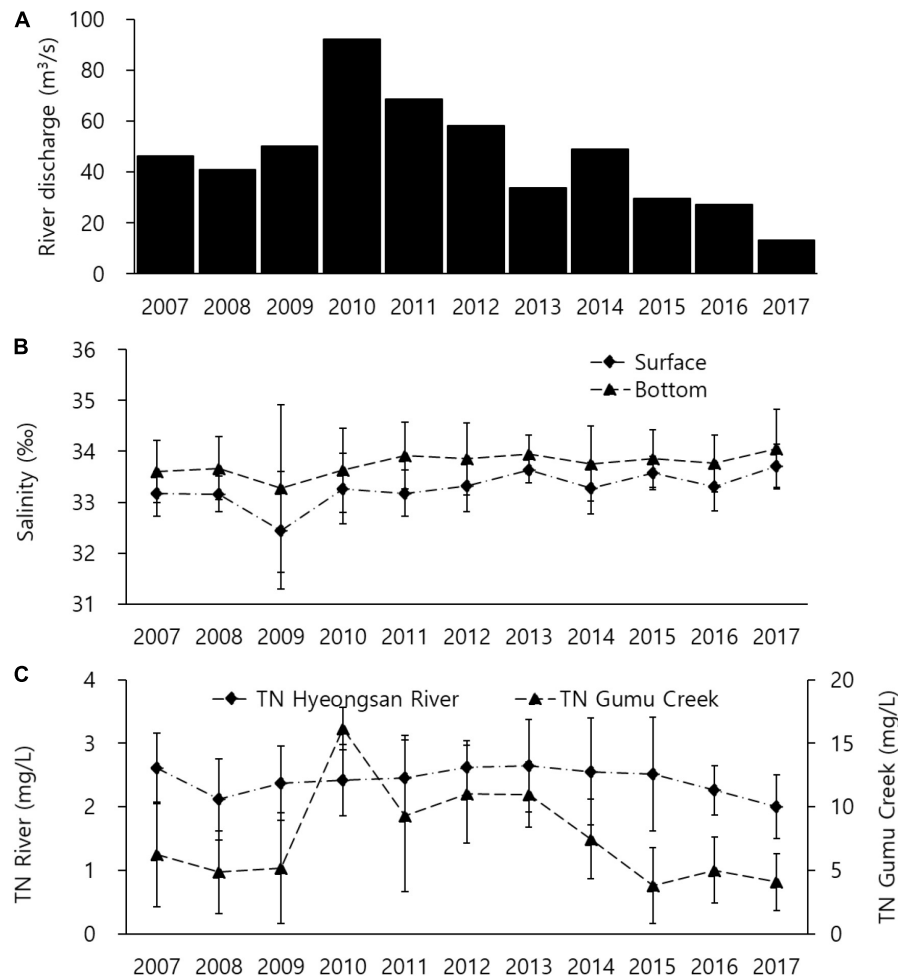
## DISCUSSION

Long-term phytoplankton dynamics in Yeongil Bay in response to environmental variations were investigated to assess the dominant groups, which are altered by water quality improvements. Although cryptophytes dominated in the surface layer and diatoms dominated in the bottom layer, cryptophyte abundance declined over the 11-year period and the diatom abundance relatively increased. An increase in photic depth and decrease in NH<sub>4</sub><sup>+</sup> indicating water quality improvement were strongly linked to a decrease in cryptophytes and increase in diatom dominance, while P-limitation and P-deficiency prevailed in this ecosystem. The GAMs depicted the variation in the cryptophyte and diatom dominances relative to environmental variations. Collectively, water quality improvement depressed the growth of cryptophytes but favored diatom dominance in the Yeongil Bay.

### Nutrient Dynamics in a P-Limited and P-Deficient Environment

River discharge usually affects nutrient levels (Baek et al., 2015), the level of suspended particulate matter (SPM) controlling light availability (Acharyya et al., 2012), and the residence time (Kang et al., 2020), which are all associated with phytoplankton blooms





**FIGURE 2** | Long-term variation in river discharge (A), salinity (B), and total nitrogen (TN) from the Hyeongsan River (HR) and Gummu Creek (C), where the Pohang Iron and Steel Company (POSCO) is located. This company is mainly responsible for the TN discharge from the Gummu Creek.

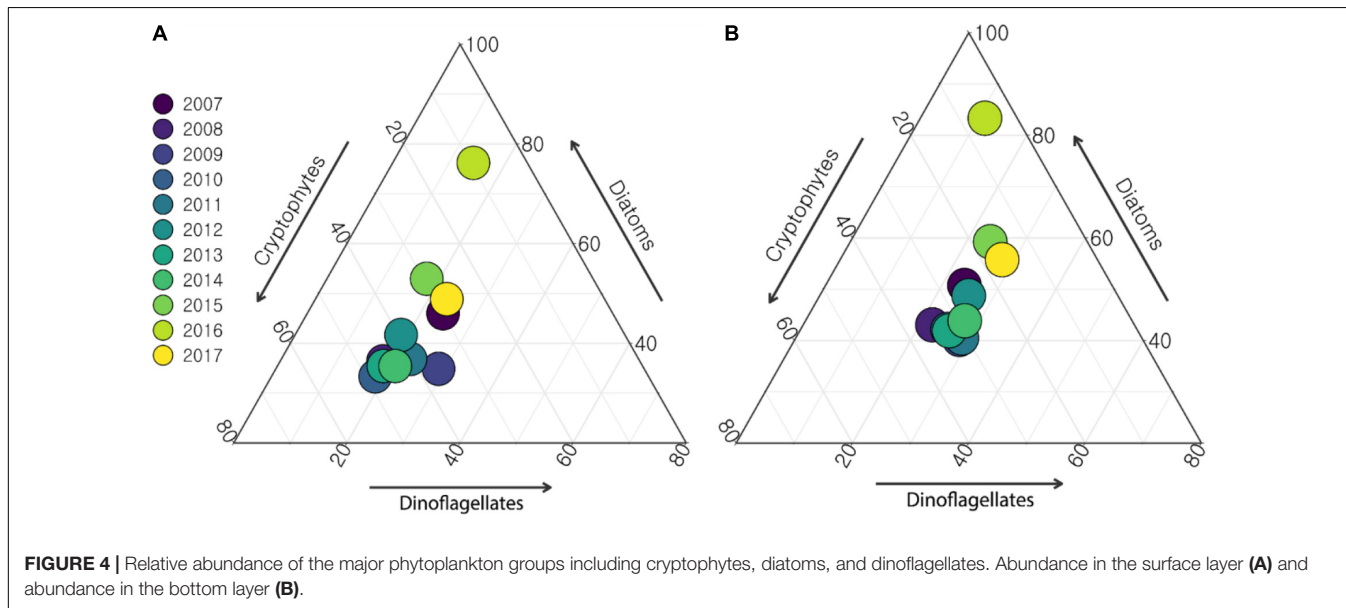
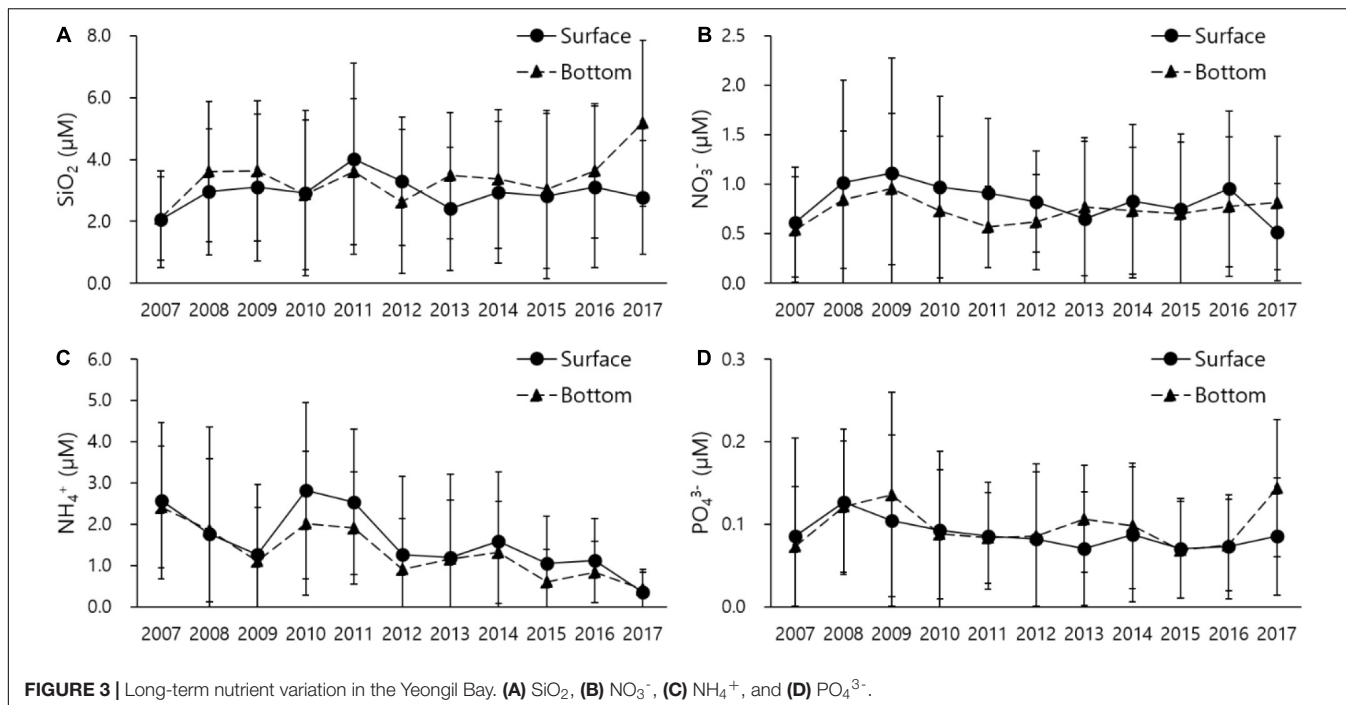
in coastal waters. A reduction in river discharge often causes the dominance of small phytoplankton because less nutrients are available (Kim et al., 2019); however, in this study, the nutrient levels were fairly consistent despite the reduced river discharge. Interestingly, salinity slightly increased and the change was more apparent in the bottom layer, implying that seawater intrusion from the East Sea was enhanced with the river discharge reduction. TN from POSCO, which gradually declined, drove a decrease in  $\text{NH}_4^+$  levels in Yeongil Bay, whereas the TN from the river was stable. This indicates that the amount of river discharge decreased but the concentration of dissolved inorganic nutrients was enriched, thereby inducing a stable input of nutrients *via* river discharge. The decadal increase in urban population and fertilizer usages and livestock near Yeongil Bay were potentially responsible for the remaining of enriched nutrient levels in the bay system.

Combined with the decline of  $\text{NH}_4^+$  over the 11-year period, P-limitation became less intense but P-deficiency, indicated by  $\text{DIP} < 0.2 \mu\text{M}$ , prevailed during the same period. DIN and  $\text{SiO}_2$  levels exceeded the lower limit (i.e.,  $\text{DIN} > 2 \mu\text{M}$ ,

$\text{SiO}_2 > 1 \mu\text{M}$ ). This suggests that phytoplankton in Yeongil Bay needed to resist P-limitation and is adapted to P-deficient environments. Given that the ample amount of  $\text{SiO}_2$  presented throughout the bay and that Si:N ratios far surpassed 1, diatom growth might not have been limited, and diatoms were able to outcompete dinoflagellates, meaning that the ecological niche was dominated by diatoms.

### Effects of Environmental Variables on the Dominance of Cryptophytes and Diatoms

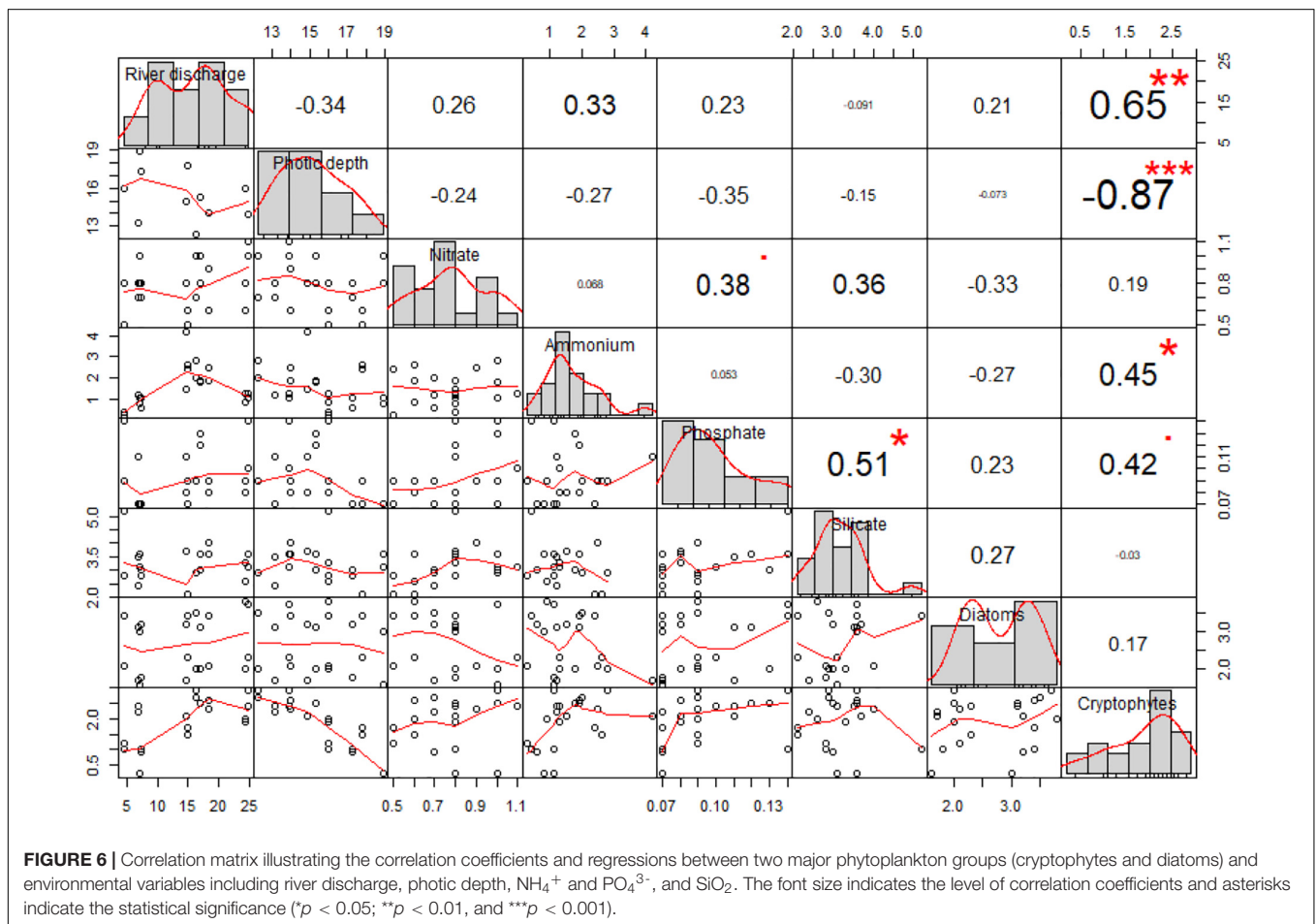
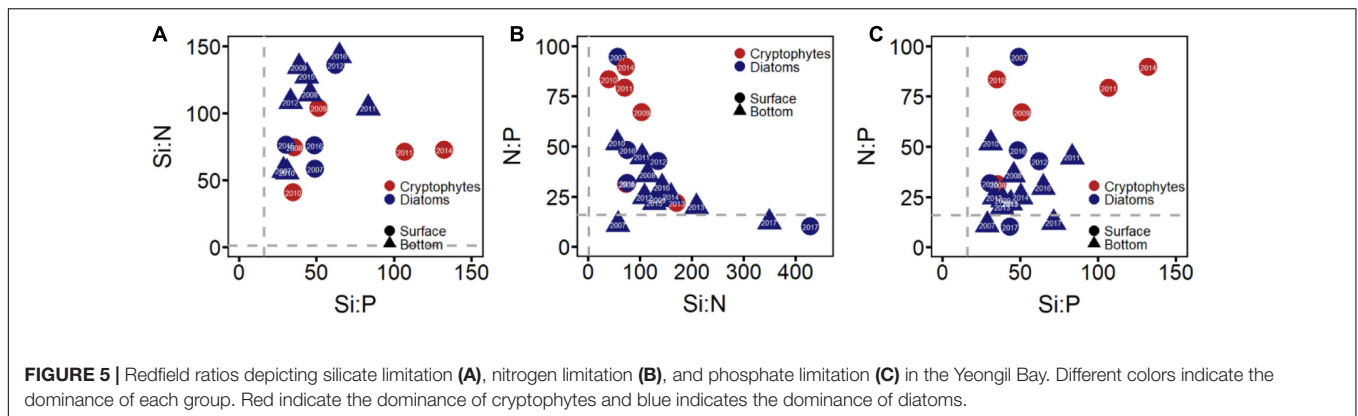
The decline in river discharge meant that less SPM was introduced to the Yeongil Bay ecosystem, thereby leading to more light penetration. Since 2010, river discharge has sharply declined, and photic depth has gradually increased. The photic depth had an inverse relationship with the cryptophyte abundance; as the depth increased, the abundance decreased (Supplementary Figure 1). Cryptophytes can tolerate a wide range of salinity from freshwater to saline water (Clay et al., 1999) and can adapt well to high turbidity and low light availability



(Barone and Naselli-Flores, 2003), conditions under which other phytoplankton (e.g., diatoms) are not usually able to experience optimal growth. Cryptophytes are opportunistic by proliferating under such conditions. Moreover, the photoprotective pigment which is enriched in cryptophytes also allows cryptophytes to thrive in surface water (Mendes et al., 2018).

Not only high turbidity but also high  $\text{NH}_4^+$  can favor the growth of cryptophytes, whereas high levels of  $\text{NH}_4^+$  suppress the growth of diatoms and dinoflagellates (Lomas and Glibert, 1999, 2000). In the Gwangyang Bay, which is located in the southern coastal waters of Korea, increases in  $\text{NH}_4^+$  and SPM

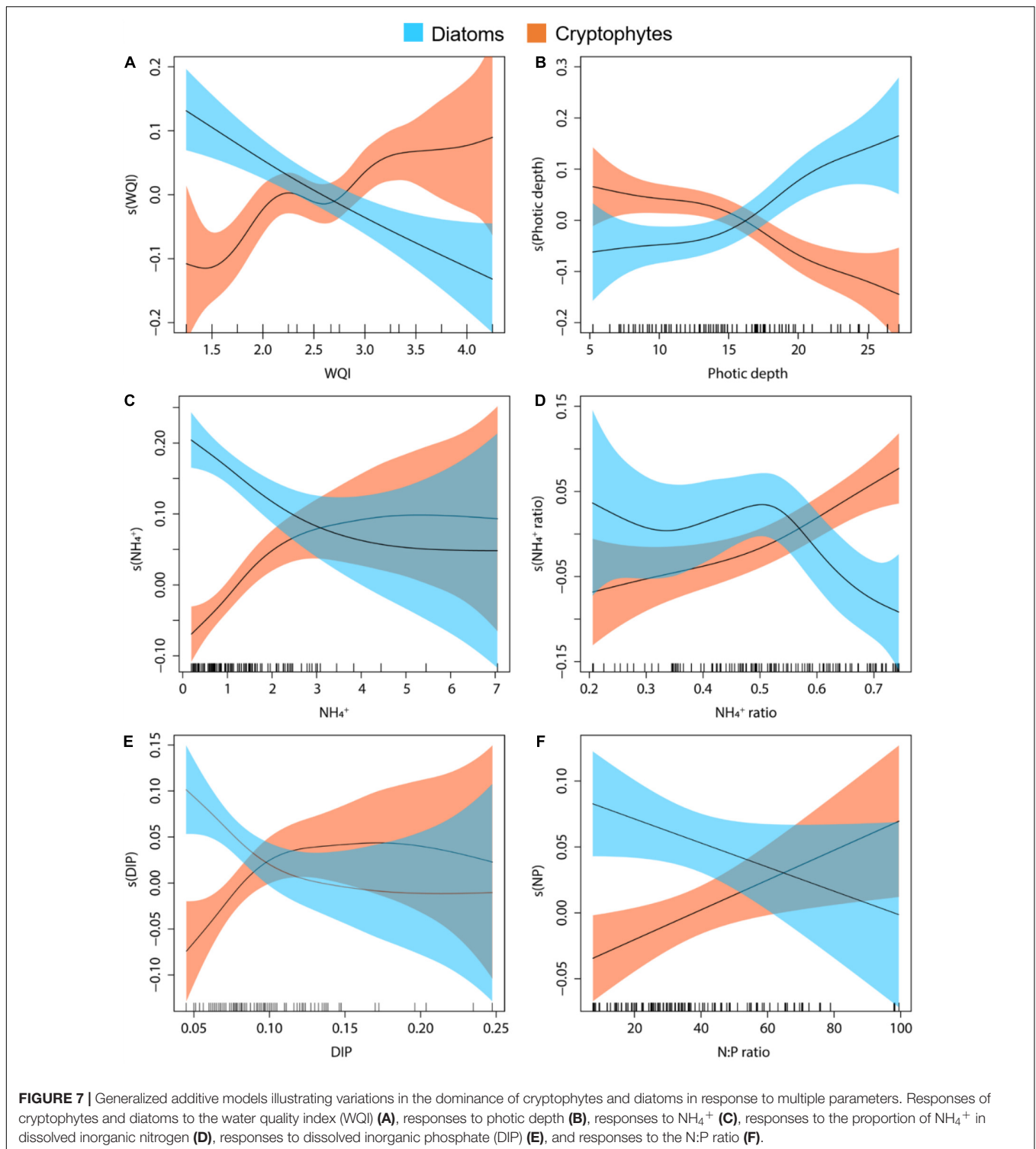
synergistically led to a decline in phytoplankton biomass (Kang et al., 2020), suggesting the dominance of small phytoplankton such as cryptophytes and picoplankton. The sharp decline in  $\text{NH}_4^+$  might favor the growth of diatoms, steering the diatom dominance in the Yeongil Bay. However, the GAM results showed that  $4 \mu\text{M}$  of  $\text{NH}_4^+$  was the upper limit of cryptophyte resistance. Consistent with our results, in the San Francisco Bay, suppression of phytoplankton growth also occurred when  $\text{NH}_4^+$  levels were above  $4 \mu\text{M}$  as it inhibited the uptake of nitrate in diatoms but favored the growth of smaller primary producers (Dugdale et al., 2007, 2012). Slower river discharge and



an increase in  $\text{NH}_4^+$  supported cryptophyte blooms in the Krka River estuary in the eastern Adriatic Sea (Šupraha et al., 2014).

Although the DIP levels were lower than  $0.2 \mu\text{M}$ , which is generally the lower limit for phytoplankton growth (Dortch and Whitedge, 1992), our results implied that the DIP levels were sufficient for phytoplankton growth, and particularly, high P-limitation triggered the cryptophyte dominance in the bay, whereas diatoms were favored by the weakened P-limitation. Consistent with this, Egge (1998) illustrated

that diatoms are not the best competitors compared to small phytoplankton (nano or picoplankton) when DIP levels are low, and transcriptomic and proteomic responses of diatoms showed that DIP limitation drives multiple biochemical pathways in diatoms, including the utilization of dissolved organic phosphate, changes in cellular P allocation, and the generation of more P transport (Dyhrman et al., 2012). In addition, cryptophytes acquire nutrients *via* a mixotrophic mode, switching from utilizing dissolved nutrients to feeding



on bacteria (Roberts and Laybourn-Parry, 1999; Yoo et al., 2017). This may be an alternative means of obtaining the required nutrients including N and P. Given that cryptophytes can tolerate harsher P-limited conditions, cryptophytes may express similar responses to diatoms; however, the transcriptomics or proteomics in response to P-limitation

should be investigated to assess the role of the physiology of cryptophytes in their blooms.

### Future Directions

A lack of hard exoskeleton structures and toxic metabolites enable cryptophytes to be nutritional food which contains high



highly unsaturated fatty acid (HUFA) concentrations (Brett and Muller-Navarra, 1997), promoting high zooplankton growth and reproduction (Sterner and Schulz, 1998). However, cryptophyte blooms cause red coloration of bivalve tissue when bivalves feed on cryptophytes, resulting in unfavorable fishery products for commercial needs (Pastoureaud et al., 2003). In the meantime, the dominance of diatoms can drive efficient food webs, which are fundamentally based on larger phytoplankton while red pigments of phytoplankton that degrade the bivalve quality would no longer cause economic losses in bivalve mariculture.

In this study, bottom-up effects (i.e., nutrient effects) were investigated using data regarding the long-term variations in the major phytoplankton groups and nutrient dynamics. However, the interactive role of the top-down and bottom-up effects on phytoplankton communities should be considered to assess the variations in phytoplankton communities as zooplankton grazing is another factor that controls phytoplankton gains and losses in marine ecosystems (Kang et al., 2015). In addition, an advanced model which combines the biogeochemical model and hydrodynamic models, such as the Regional Ocean Modeling System, are required to understand how blooms of different phytoplankton groups are associated with biogeochemical cycles and hydrodynamics in the ecosystem. Given that the size of small phytoplankton (nanoplankton or picoplankton) limits the observation of phytoplankton groups, other identification techniques such as flow cytometry, high performance liquid chromatography, and environmental DNA metabarcoding should be applied to estimate phytoplankton communities including small phytoplankton. Finally, physiological responses such as enzyme activity and pigment change or transcriptional responses for functional genes to acquire the opened ecological niche with water quality improvement should be studied to better understand the ecological and physiological characteristics of phytoplankton dynamics in ecosystems.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

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## AUTHOR CONTRIBUTIONS

YK: data acquisition and analysis and writing—original draft. H-JK: data analysis and reviewing. C-HM: supervision and funding acquisition. YY: reviewing and editing. C-KK: supervision and funding acquisition. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.710891/full#supplementary-material>

**Supplementary Figure 1** | Long-term variation in cryptophytes and diatoms in response to variation in water quality parameters. Variations in cryptophytes and diatoms with the water quality index (A,B), variations in cryptophytes and diatoms with the proportion of  $\text{NH}_4^+$  in the surface and bottom waters (C,D), and variations in cryptophytes and diatoms with the photic depth in the surface and bottom waters (E,F).

**Supplementary Table 1** | Long-term variation in dominant species for the last 11 years in Yeongil Bay. Parenthesis illustrates dominance in%.

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