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ARTICLE

Influence of Region-Specific Marine Environments on Phytoplankton and Bacterial Communities in the Korean Coastal Waters in Winter 2021

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Abstract

We assessed the influence of the distinct characteristics of the three seas surrounding the Korean coast (the Yellow Sea, YS; the South Sea, SS; and the East Sea, ES) on the phytoplankton and bacterial communities by conducting field surveys at 23 stations in February 2021. The average water temperature (WT) of the ES and the SS (9.5 ± 2.4℃) was significantly higher compared to that of the YS (4 ± 1.3℃), on account of the Tsushima Warm Current and their relatively deep depth. Additionally, the unique tidal range of the YS, combined with its low WT, led to the highest dissolved oxygen concentration (YS: 11 ± 1.2 mg L^{-1}. SS: 10 ± 1.3 mg L^{-1}. ES: 9 ± 1.0 mg L^{-1}). This difference was related to regional Chl. *a* concentrations and the dominance of diatoms. Particularly, due to freshwater input, the diatom *Thalassiosira rotula* proliferated significantly at St. Y2, while strong tides in the YS led to the sub-dominance of benthic diatom *Paralia sulcata*. In addition, we found a relatively higher number of endemic species (13 species) in intermediate SS region than in other regions (YS: 6 species with strong mixing condition and ES: 3 species with low seed population). Moreover, there were differences in the number of shared species depending on proximity of each region (YS-SS: 10; SS-ES: 4; YS-ES: 2 species). The dominant diatoms, *Eucampia zodiacus* and *Chaetoceros pseudocurvisetus*, in the SS exhibited a negative correlation with the concentrations of nutrients in PCA analysis, suggesting that nutrients supplied by water mixing were being utilized for their growth. Despite high nutrient levels, the biomass was low in the deep ES region, averaging Chl. $a < 0.3$ μg L^{-1} with *Cryptomonas* spp. dominating instead of diatoms, indicating a lower presence of the seed population of diatoms in this region. Bacterial communities were dominated by the genus *Polaribacter* within the order Flavobacteriales and the genus *Sulfitobacter* within the order Rhodobacterales, showing their association with WT and dominant species of phytoplankton. Additionally, the dominance of specific bacterial species associated with predominant phytoplankton resulted in a decrease in bacterial diversity. These findings suggest that the region-specific oceanographic factors, such as water depth, tidal range, and ocean currents of Korean coastal waters, during winter have a significant impact on the micro-ecosystem, including phytoplankton and bacterial communities.

Keywords Regional differences · Winter environmental characteristics · Ocean current · Phytoplankton · Bacteria

1 Introduction

Coastal ecosystems within bays and estuaries are significantly influenced and shaped by major land–ocean interactions (Paerl et al. 1990; Cloern 2001; Lee et al. 2018). In these regions, the increase in pollutants, such as domestic sewage and industrial waste, has been exacerbated by population growth and industrial development, leading to heightened concerns regarding water quality and the frequency of phytoplankton blooms that affect human health and marine ecosystems adversely (Mallin et al. 1991; Hung et al. 2004;

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Baek et al. 2015; Lu et al. 2018). Temperate coastal areas, recognized as global hotspots for marine productivity, are crucial for supporting significant fisheries yields and providing essential nutrients to approximately 40% of the global human population (Boyd et al. 2007). Positioned in a temperate zone, the Korean Peninsula is subject to pronounced seasonality driven by seasonal monsoons (Kim et al. 2014), where frequent occurrences of phytoplankton blooms, including harmful algal blooms, often lead to substantial economic losses (Lim et al. 2021; Lee and Kim 2008).

In the temperate coastal regions of the Northern Hemisphere, the dry winter season is marked by strong winds from the north and northwest, coupled with minimal precipitation. Conversely, the summer season features winds from the south and southeast, which bring substantial rainfall. This distinct seasonal pattern has a profound influence on nutrient dynamics and phytoplankton population dynamics in coastal waters (Baek et al. 2009; Baek et al. 2019; Yoon et al. 2024). During winter, windstorms promote significant water mixing, enhancing nutrient loading throughout the water column (Baek et al. 2020). This nutrient accumulation persists in the euphotic layer, driven by reduced uptake of phytoplankton nutrients due to diminished light levels and shorter photoperiods. Such availability of nutrients is a critical factor in determining the patterns and processes of phytoplankton blooms in these waters (Kim et al. 2019), thereby affecting the population dynamics and distribution patterns of phytoplankton along the coast.

Marine bacteria are fundamental to marine ecosystems, as they regulate nutrient cycles, synthesize vitamins, and decompose pollutants (Buchan et al. 2014; Park et al. 2015; Seymour et al. 2017). Their interaction with phytoplankton is crucial for cycling nutrients, enhancing microbial diversity, and maintaining stability of the ecosystem. Bacteria aid phytoplankton growth by absorbing and transforming available nutrients into forms accessible to phytoplankton, and also contribute to the recycling of nutrients through the synthesis and breakdown of organic compounds (Buchan et al. 2014; Teeling et al. 2016). This interaction also affects the proliferation and decline of phytoplankton populations, influencing the structure and diversity of microbial plankton communities significantly. For example, in mesocosm studies, the addition of nitrogen and phosphate can trigger phytoplankton blooms, subsequently increasing bacterial abundance (Park et al. 2020).

The Korean Peninsula is bordered by the Yellow Sea to the west, the South Sea (connected to the East China Sea) to the south, and the East Sea (Sea of Japan) to the east (Fig. 1). These Korean coastal waters (KCWs) are significantly influenced by ocean currents, particularly the Jeju Warm Current (JWC) and the Tsushima Warm Current (TWC), both of which are branches of the Kuroshio Current and are characterized by high salinity (Lie and Cho 2016). The JWC and TWC notably affect the characteristics of water mass in the southern part of Korea, especially during the autumn and winter seasons. The East Sea, a large marginal sea positioned between the Eurasian continent and Japan, with an average depth of 1800 m, interacts with the TWC from the Kuroshio Warm Current and the North Korean Cold Current (NKCC) from the colder Liman Current. This dynamic results in the formation of a distinct subpolar front around 38–40°N, where the warm water mass from the East Korea Warm Current (EKWC) meets the cold water mass from the NKCC (Isoda and Saitoh 1993; Mitchell et al. 2005; Chang et al. 2004; Lee et al. 2009). To the west, the Yellow Sea, a shallow semi-enclosed marginal sea with a depth of approximately 200 m, lies along the western coast of the Korean Peninsula and is bordered by Korea and China (Lie and Cho 2016). This region is renowned for its high productivity and is a vital area for the production of marine fisheries (Chang et al. 2014; Jin and Tang 1996).

Seasonal monsoons, especially during winter, influence coastal waters significantly by lowering water temperatures and enhancing vertical mixing (Baek et al. 2020). While the nutrient supply from land is typically reduced in winter due to lower rainfall, the increased vertical mixing during this period promotes the transfer of nutrients from the bottom layer to the surface, thereby boosting overall concentrations of nutrients (Lee et al. 2018; Baek et al. 2019). It is thought that these variations in environmental factors among the Yellow Sea, South Sea, and East Sea drive shifts in the composition of phytoplankton and bacterial communities. Despite this general awareness, current knowledge on the interactions between phytoplankton and bacteria in the coastal waters of the Korean Peninsula remains sparse. This study aims to assess how specific environmental factors in coastal waters across various regions of the Korean Peninsula, particularly during the winter of 2021, affected phytoplankton and bacterial communities, with the objective of gathering foundational data.

2 Materials and Methods

2.1 Field Sampling

Field sampling was conducted at eight stations in the Yellow Sea (Y1–Y8), eight stations in the South Sea (S1–S8), and seven stations in the East Sea (E1–E7) along the Korean coastal waters (KCWs) in February 2021 (Fig. 1). In situ measurements of water quality parameters, including temperature, salinity, pH, and dissolved oxygen (DO), were performed at the surface water using YSI EXO2 Sonde probes (Yellow Springs, USA). Samples of surface water were collected with a bucket at all stations. For chlorophyll

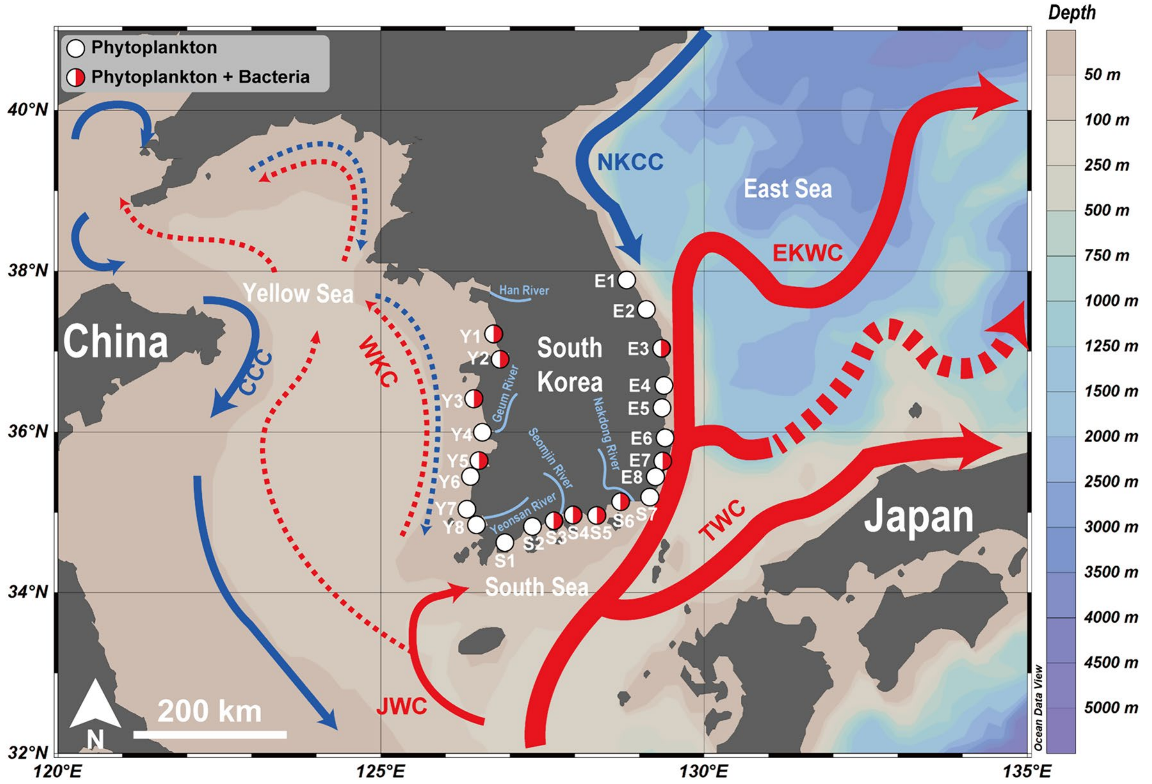


Fig. 1 Map of study area with sampling stations (white circles: sampling only phytoplankton, red semicircles: sampling both phytoplankton and bacteria) and the ocean currents (red arrows: warm currents, blue arrows: cold currents), including Tsushima warm current (TWC), Jeju warm current (JWC), East Korean warm current (EKWC), West Korean current (WKC), China cold current (CCC), North Korean cold current (NKCC)

a (Chl. *a*) measurements, the collected 300 mL of surface water was filtered immediately through a 47 mm diameter GF/F filter with a pore size of 0.7 μm (Whatman, U.K.), and processed on-site. The filtrates were transferred to acid-cleaned 15-mL conical tubes (SPL Life Sciences, Korea), and $HgCl_2$ was added to a final concentration of 0.1% to inhibit biological activity. Both filters and filtrates were stored at − 20 °C in the dark until laboratory analysis. For the analyses of bacterial community, 300 mL of surface water was passed through polycarbonate membrane filters (pore size: 0.22 μm, filter diameter: 47 mm; Millipore, USA), and these filters were similarly stored at − 20 °C in the dark. Phytoplankton samples, consisting of 500 mL of surface water, were preserved immediately in polyethylene bottles with Lugol's solution at a final concentration of 3% and stored at room temperature in the dark until analysis (Sournia 1978).

2.2 Chl. *a* and Nutrients

For laboratory analysis of field samples, the concentration of Chl. *a* (μg L^{-1}) was determined using a Turner 10-AU Fluorometer (Turner BioSystems, USA). Prior to analysis, the filtered material was extracted with 90% acetone and stored in dark and cold (4 °C) conditions for 24 h. The concentrations of dissolved inorganic nutrients (ammonium, nitrate + nitrite, phosphate, and silicate) were measured using a flow injection auto-analyzer Quattro 39 (Seal Analytical, U.K.), calibrated using Reference Materials for Nutrients in Seawater (RMNS; KANSO Technos Co., Ltd., Japan).

2.3 Phytoplankton Community

To count and identify phytoplankton, each Lugol's-fixed sample (500 mL) was concentrated to approximately 50 mL by decanting the supernatant and storing it at room temperature. These sub-samples were allowed to settle for 10 min, after which 100 to 400 μL was transferred into a Sedgewick-Rafter Chamber. Phytoplankton cells were identified and counted using light microscopy at magnifications of 200 × or 400 ×.

2.4 Bacterial Community

Species- and genus-level identification was performed for morphologically distinct species. For genetic analysis of the bacterial community, the filters were cut into pieces prior to extraction of genomic DNA (gDNA) using the DNeasy Plant Mini Kit (Qiagen, USA). The extracted gDNA was quantified using Quant-IT PicoGreen (Invitrogen, USA). A sequencing library was prepared using the Illumina Metagenomic Sequencing Library protocols to amplify the V3 and V4 hypervariable regions of the bacterial 16S ribosomal RNA (rRNA) gene. The input gDNA (2 ng) was PCR-amplified using $5\times$reaction buffer, 1 mM of dNTP mix, and 500 nM each of the universal Illumina tagged forward and reverse PCR primers (Herlemann et al. 2011) (341F: 5′-TCGTCGGCAGCGTC -AGATGTGTATAAGAGACAG-CCTACGGGNGGCWGCAG-3′; 805R: 5′-GTCTCGTGGGCTCGG-AGATGTGTATAAGAGACAG-GACTACHVGGGTATCTAATCC-3′. The underlined sequences indicate the target region primer), and Herculase II fusion DNA polymerase (Agilent Technologies, USA). The first PCR protocol took 3 min at 95 °C for heat activation; 25 cycles of 30 s at 95 °C, 30 s at 55 °C, and 30 s at 72 °C; and a 5 min final extension at 72 °C. The first PCR product was purified using AMPure beads (Agencourt Bioscience, USA). Following purification, 2 μL of this product was amplified for final library construction containing the index using NexteraXT Indexed Primer. The protocol for the second PCR was the same as for the first PCR; however, there were 10 (rather than 25) amplification cycles. The PCR product was purified using AMPure beads, and was quantified using qPCR in accordance with the qPCR Quantification Protocol Guide (KAPA Library Quantification kits for Illumina Sequencing platforms). Quality was assessed using the TapeStation D1000 ScreenTape (Agilent Technologies, Germany). Paired-end sequencing (2×300 bp) was performed by Macrogen using the MiSeq™ platform (Illumina, USA). Sequencing adaptors and barcodes were removed using Cutadapt (Martin 2011). To correct errors in amplicon sequencing, the reads were filtered based on quality scores and trimmed using the DADA2 package version 1.18.0 (Callahan et al. 2016) in R software version 4.0.3. Forward and reverse reads were truncated at 250 bp and 200 bp, respectively, and then filtered to remove any reads with an expected error rate of two or more. After the merging of paired-end reads and the correction of sequencing errors, PCR chimera sequences were removed using the consensus method of DADA2 to infer amplicon sequence variants (ASVs). Each ASV was aligned with the most similar organism in the NCBI_16S Reference Database using algorithms such as BLAST. QIIME (v1.9.0) was employed for downstream ASV analysis. All ASVs associated with Archaea, mitochondria, or chloroplasts were excluded from the dataset. Alpha diversity metrics, such as the Shannon Index and Gini-Simpson Index, were calculated to assess species complexity within individual samples.

2.5 Statistical Analysis

Variations in phytoplankton abundance, environmental factors, and nutrient concentrations across KCWs including the Yellow Sea, South Sea, and East Sea did not consistently meet the assumptions regarding normality and equality of variances required for one-way analysis of variance (ANOVA). Therefore, the non-parametric Kruskal–Wallis test was applied, followed by the Mann–Whitney U test for post hoc pairwise comparisons, with a Bonferroni correction set at $p = 0.017$ (equivalent to $p < 0.05/3$), using SPSS version 25 (Chicago, USA). To investigate the correlation coefficients between environmental factors (temperature, salinity, DO, pH, Chl. *a*) and nutrient concentrations (nitrite + nitrate, ammonium, phosphate, silicate) in these waters, a non-parametric Spearman correlation analysis was conducted using the 'PerformanceAnalytics' package in R version 4.2.1. Additionally, principal component analysis (PCA) was applied to explore the associations among predominant phytoplankton (maximum composition > 40%), bacteria (maximum composition > 20%), environmental factors, and nutrient concentrations, and also performed in R to identify the variables exerting the most significant influences at different stations in KCWs.

3 Results

3.1 Environmental Factors

During the winter, surface water temperatures ranged from 2.1 °C (St. Y1) to 12.4 °C (St. E8), showing significant regional variations (Fig. 2a). Water temperatures in the Yellow Sea (St. Y1 − Y7) were consistently lower than those at the southeastern sites of the Korean peninsula (Kruskal–Wallis test; $p < 0.05$) (Fig. 2b). Surface salinity was notably lower at St. Y1 (30.8, near the Inchon Domestic Port) and St. Y2 (29.6, near the Anseong Stream), and higher at St. E2 (35.1) (Fig. 2c). Overall, salinity levels in the Yellow Sea were generally lower than those in the South Sea and East Sea (Kruskal–Wallis test; $p < 0.05$; Fig. 2d). The pH of surface water varied from 8.09 (St. Y1) to 8.55 (St. E5) (Fig. 2e), with surface pH values in the Yellow Sea slightly lower than those in the East Sea (Kruskal–Wallis test; $p < 0.05$; Fig. 2f). Dissolved oxygen (DO) concentrations

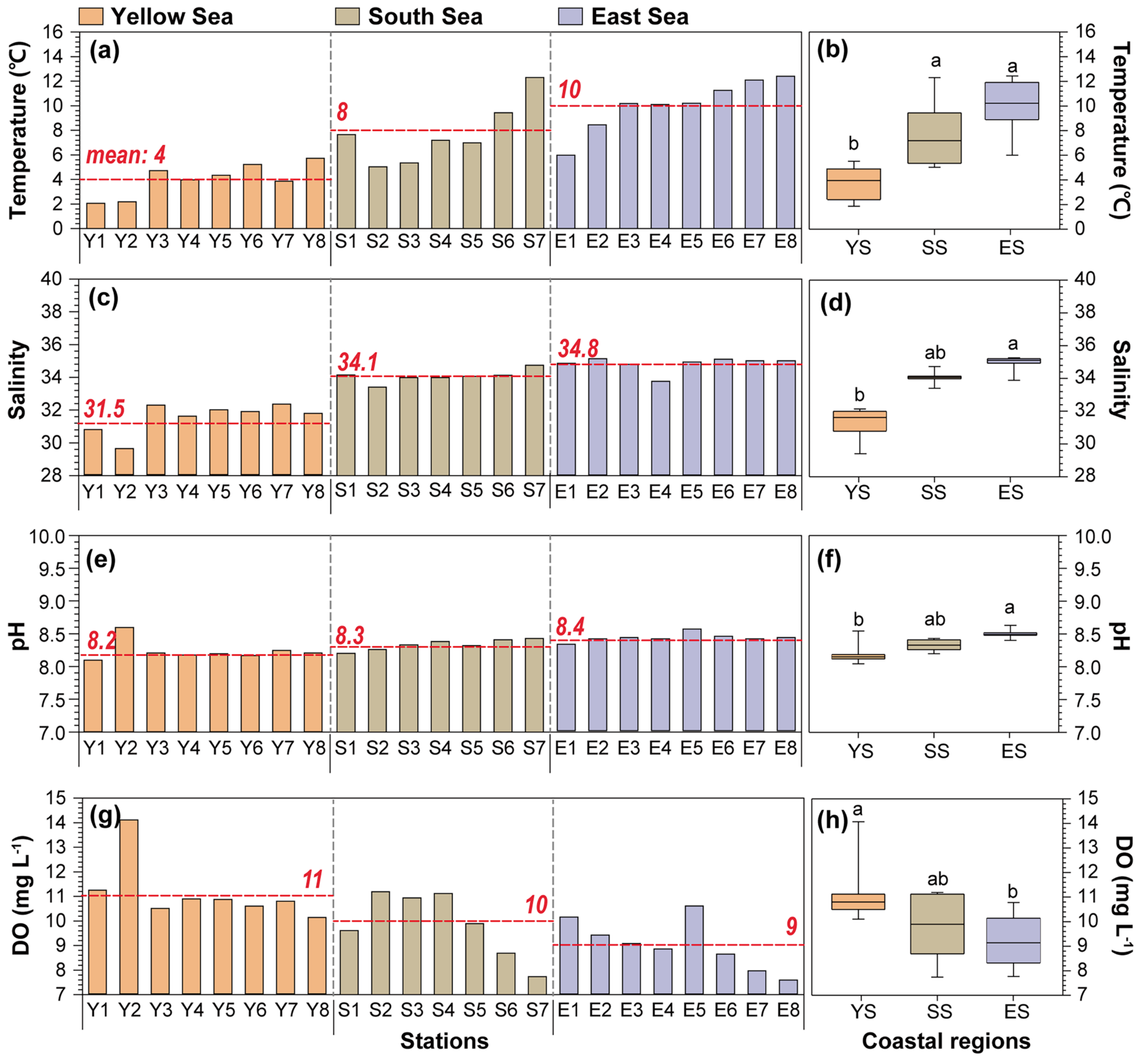


Fig. 2 Values of environmental factors at each stations (left) and boxplots (right) in the three Korean coastal regions (Yellow Sea; YS, South Sea; YS, and East Sea; ES), including temperature (**a** and **b**), salinity (**c** and **d**), pH (**e** and **f**), dissolved oxygen (DO; **g** and **h**). The red dashed line indicates the means, and letters denote significant differences (p < 0.05; Kruskal-Wallis test)

ranged from 7.5 mg L^{-1} (St. E8) to 14.08 mg L^{-1} (St. Y2) (Fig. 2g), with significant differences observed, particularly with lower DO levels in the East Sea compared to the Yellow Sea (Kruskal–Wallis test; $p < 0.05$; Fig. 2h). In summary, water temperature, salinity, and pH levels were generally higher in the East Sea compared to the Yellow Sea, while the DO levels were higher in the Yellow Sea.

Figure 3 illustrates the concentrations of dissolved inorganic nutrients in surface water across various sites. Silicate concentrations ranged from 0.8 μM (St. S3) to 20.3 μM (St. E3) (Fig. 3a). The mean concentration of silicate in the East Sea was significantly higher at 15.0 ± 4.5 μM compared to the South Sea, where it averaged 5.6 ± 4.0 μM ($p < 0.05$; Fig. 3b). The highest concentration of nitrate + nitrite was observed at St. Y8 (23.2 μM), and the lowest at St. S3 (0.8 μM) (Fig. 3c). The mean concentration of nitrate + nitrite in the Yellow Sea was 15.7 ± 6.6 μM, surpassing values in the East Sea and South Sea (Kruskal–Wallis test; $p < 0.05$; Fig. 3d) significantly. Ammonium concentrations were notably higher in the Yellow Sea compared to those in the East Sea and

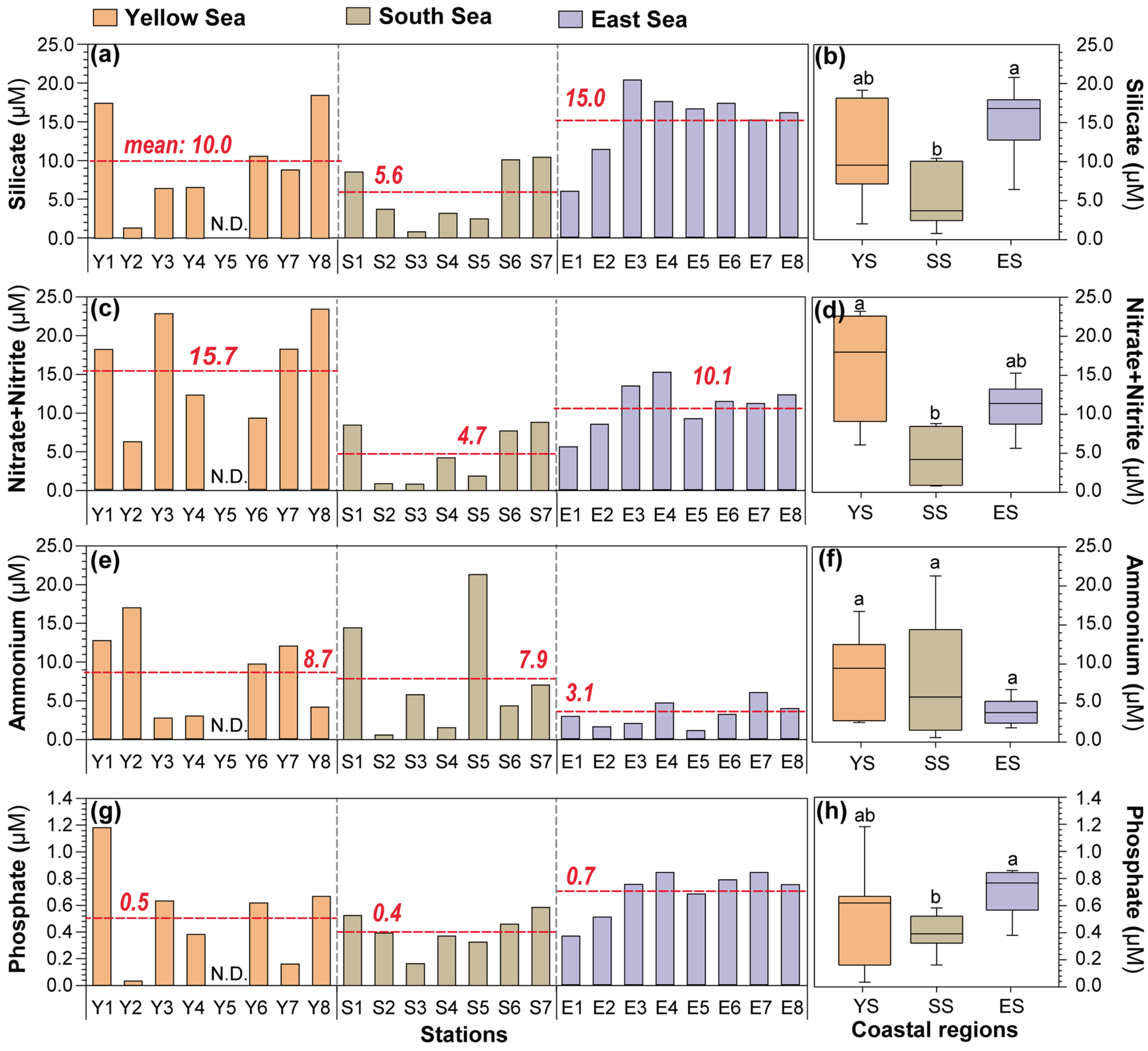


Fig. 3 Concentrations of nutrient at each stations (left) and box-plots (right) in the three Korean coastal regions (Yellow Sea; YS, South Sea; SS, and East Sea; ES), including silicate (**a** and **b**), nitrate+nitrite (**c** and **d**), ammonium (**e** and **f**), and phosphate (**g** and **h**). The red dashed line indicates the means, and letters denote significant differences ($p < 0.05$; Kruskal-Wallis test)

South Sea ($p < 0.05$; Figs. 3e and f). Phosphate concentrations ranged from 0.03 μM (St. Y2) to 0.8 μM (St. E4), with significant differences noted, particularly with higher levels in the East Sea compared to the South Sea ($p < 0.05$; Figs. 3g and 3h).

3.2 Biological Factors and Phytoplankton Community

Figure 4a shows the spatial variations in concentrations of Chl. *a* at each station and the differences among geographical regions. The highest concentration of Chl. *a* was recorded in the Yellow Sea (3.7 μg L^{-1} at St. Y2), with an average concentration of 1.2 μg L^{-1}. In contrast, most stations in the East Sea reported Chl. *a* concentrations below 0.3 μg L^{-1} (Fig. 4a). The mean concentration in the Yellow Sea was significantly higher compared to that in the East Sea (Kruskal-Wallis test; $p < 0.05$; Fig. 4b). The average phytoplankton abundance was significantly higher in the South Sea (0.9 × 10^{5} cells L^{-1}) compared to the East Sea (0.2 × 10^{5} cells L^{-1}), while notably high abundance at St. Y2 (5.6 × 10^{5} cells L^{-1}) in the Yellow Sea (average: 1.0 × 10^{5} cells L^{-1}) (Fig. 4c and d).

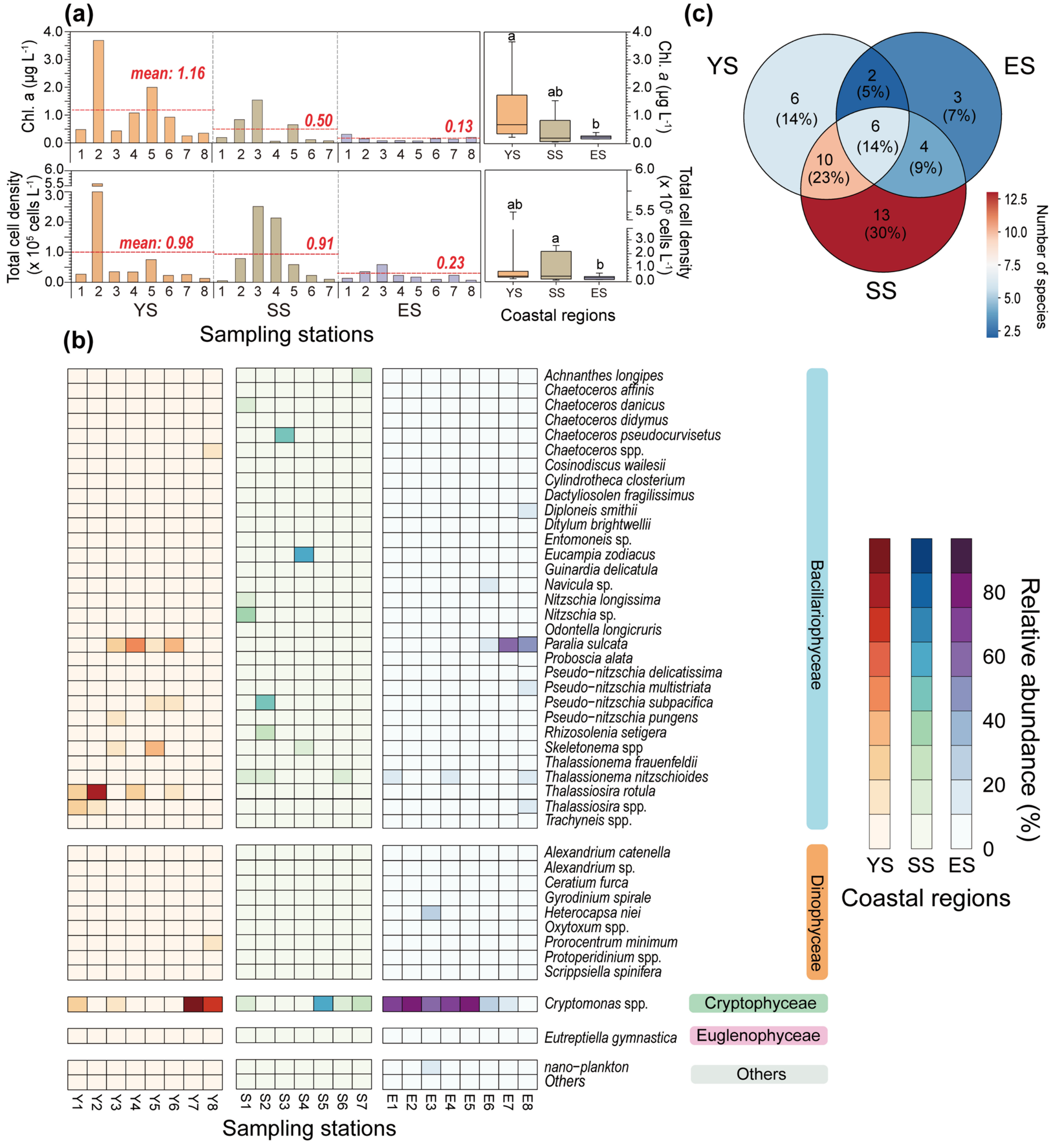


Fig. 4 Concentrations of chlorophyll a and total phytoplankton abundance (**a**), and relative abundance of phytoplankton community (**b**), and venn diagram for species numbers appearance phytoplankton species (**c**) in the three Korean coastal regions (Yellow Sea; YS, South Sea; SS, and East Sea; ES)

Common diatom species across the Yellow Sea, South Sea, and East Sea included *Cylindrotheca closterium*, *Nitzschia longissima*, *Thalassionema nitzschioides*, and *Thalassiosira* spp. (Fig. 4b). *Thalassiosira rotula* was particularly dominant in the Yellow Sea, peaking at high densities at St. Y2 (4.4×10^5 cells L^{-1}, 79%). *Chaetoceros pseudocurvisetus* and *Eucampia zodiacus* maintained high densities at St. S3 (1.1×10^5 cells L^{-1}, 46%) and St. S4 (1.2×10^5 cells L^{-1}, 55%), respectively. *Paralia sulcata* exhibited high relative compositions at St. E7 and E8 (mean 56%). The dinoflagellate *Prorocentrum minimum* and *Heterocapsa niei* showed high relative compositions at St. Y8 (17%) and St. E3 (23%), respectively. *Cryptomonas* spp. had a high composition of over 55% at St. Y7, Y8 of Yellow Sea, St. S5 of the South Sea, and St. E1–E5 of the East Sea.

A total of 33 phytoplankton species were identified in the South Sea, 24 species in the Yellow Sea, and 15 species in the East Sea (Fig. 4c). Notably, 13 species were unique to the South Sea, accounting for 30% of the total phytoplankton community. The Yellow Sea and East Sea hosted 6 and 3 unique species, making up 14% and 7% of their respective total communities. Six species were common across all samples, constituting 14% of the entire community.

3.3 Bacterial Community

In the analyses of bacterial community, Alphaproteobacteria were found to be the dominant class with 37 ± 10%, followed by Flavobacteriia at 25 ± 12% (Fig. 5a). At the order level, Rhodobacterales accounted for 31 ± 9% and Flavobacteriales for 26 ± 12% of the community composition (Fig. 5b). Notably, at Station Y2, Rhodobacterales and Flavobacteriales constituted 99% of the community, while at Station S4, including Verrucomicrobiales, three bacterial orders accounted for 96% of the community. Within the order Rhodobacterales, the genus *Sulfitobacter* comprised 16 ± 12% in the Yellow Sea, 12 ± 6% in the South Sea, and 2 ± 9% in the East Sea, peaking at 34% at Station Y2. Similarly, the genus *Polaribacter*, within the order Flavobacteriales, represented 13 ± 17% in the Yellow Sea, 10 ± 10% in the South Sea, and 6 ± 2% in the East Sea, with a dominance of 43% at Station Y2 (Fig. 5c). At Station S4, the genus *Oceaniferula* within the order Verrucomicrobiaceae dominated uniquely, comprising 57% of the community.

Diversity indices of bacterial community were also calculated, with the Shannon Index being 5.6 ± 1.6 for the Yellow Sea, 5.1 ± 1.1 for the South Sea, and 6.2 ± 1.1 for the East Sea. The Gini-Simpson Index was 0.92 ± 0.09 for the Yellow Sea, 0.88 ± 0.12 for the South Sea, and 0.95 ± 0.03 for the East Sea (Table 1). The lowest diversity within bacterial communities was observed at Station Y2 and Station S4, both recording an ASV of 88, a Shannon Index of 2.9, and a Gini-Simpson Index of 0.8.

3.4 Relationship between Abiotic and Biotic Parameters

The levels of DO exhibited significant negative correlations with water temperature (-0.87; $p < 0.001$) and salinity ($r = -0.75$, $p < 0.001$), while DO showed a positive correlation with Chl. *a* ($r = 0.76$, $p < 0.001$) (Fig. 6). In addition, Chl. a showed a positive correlation with concentration of ammonium ($r = 0.43$, $p < 0.05$) and negative correlations with phosphate ($r = -0.55$, $p < 0.01$) and silicate ($r = -0.54$, $p < 0.01$) concentrations. There was no correlation between salinity and nutrients including nitrate + nitrite, phosphate, and silicate.

According to our PCA results, both diatoms *C. pseudocurvisetus* and *E. zodiacus* showed a negative correlation with nutrients, such as nitrate + nitrite, silicate, and phosphate (Fig. 7). Another diatom *T. rotula* exhibited a positive correlation with bacterial genus *Polaribacter* and *Sulfitobacter*. In addition, the diatom *P. sulcata* showed a positive correlation with nutrients and a negative correlation with bacterial genus *Oceaniferula*.

From a broader perspective beyond the sampling stations, we used satellite image data to investigate sea surface temperature (SST), ocean currents, and Chl. a during the field survey (Fig. 8). Consistent with our findings, the SST was the highest in the East Sea, followed by the South Sea, and then the Yellow Sea. Conversely, Chl. a concentrations were the highest in the Yellow Sea, followed by the South Sea, and then the East Sea. Additionally, a front between the North Korean Cold Current (NKCC) and the East Korean Warm Current (EKWC) was observed near 37° N in the East Sea.

4 Discussion

During the winter survey, the water temperature in the Yellow Sea was notably lower compared to temperatures in the South Sea and East Sea. The shallow depth and significant tidal range of the Yellow Sea play a major role in amplifying the cooling effect of low atmospheric temperatures during winter. In contrast, the South Sea and East Sea are influenced by ocean currents, particularly the Jeju Warm Current (JWC) and the Tsushima Warm Current (TWC) (Fig. 1), both branches of the Kuroshio Current characterized by high temperatures and salinity (Kim and Yoon 1999; Lie and Cho 2016). In our observations, we found higher water temperatures along the East Sea coast, influenced by the East Korea Warm Current (EKWC). Interestingly, there was a significant temperature difference of around 5 °C between E1 and E3 despite the relatively short geographical distance. This difference is confirmed in satellite imagery data, where the North Korean Cold Current (NKCC) interacts with the East Korean Warm Current near 37° N, resulting in the formation of a distinct subpolar front around 36–38°N (Fig. 8). Isoda and Saitoh (1993) and Mitchell et al. (2005) also demonstrated that a subpolar front exists between the warm water mass of the EKWC and the cold water mass from the NKCC, which is similar to our findings.

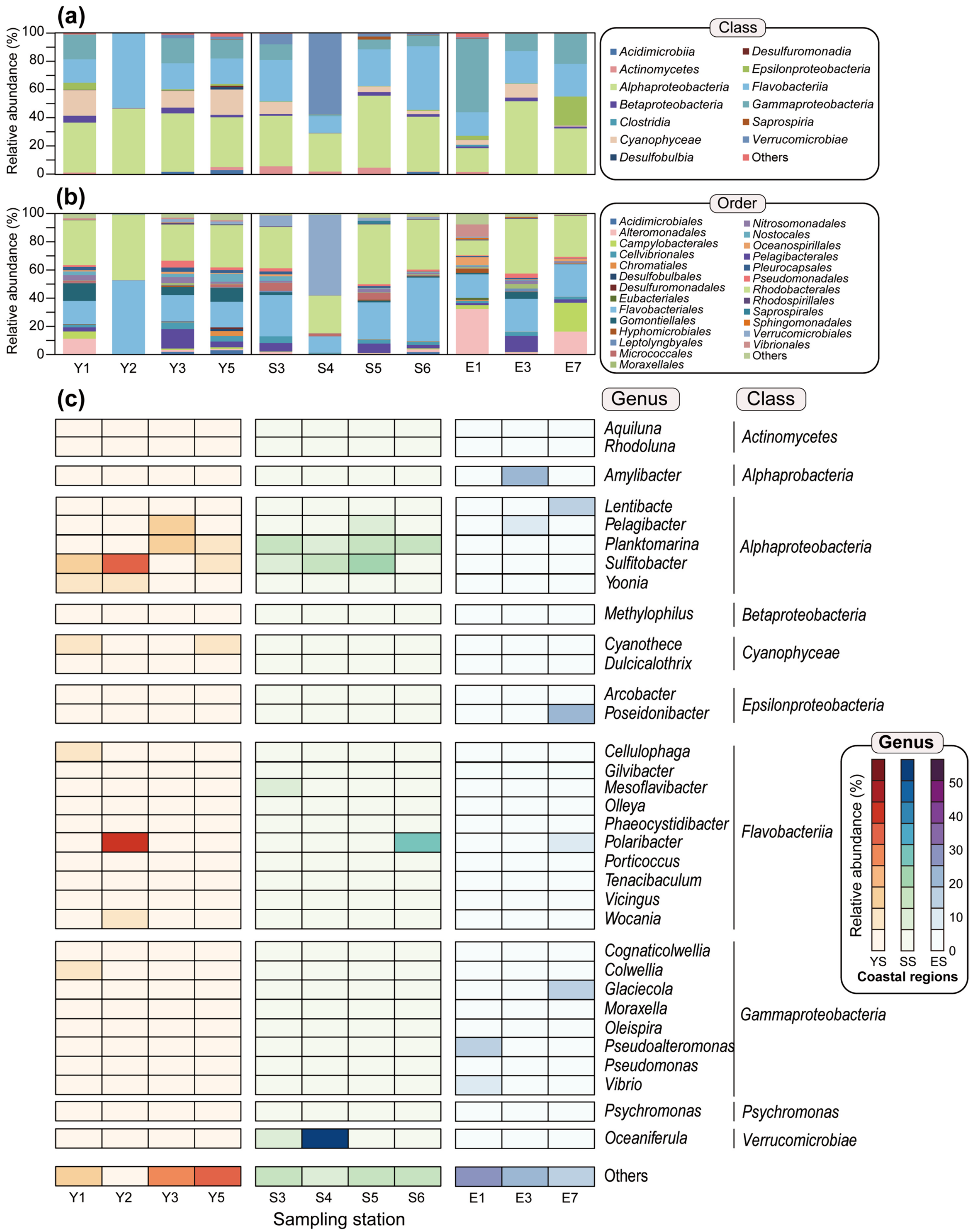


Fig. 5 Relative abundance of the bacterial community at each station by class (**a**), order (**b**), and genus (**c**) level at 11 stations

Table 1 Values of number of amplicon sequence variants (ASVs), Shannon index, and Gini-Simpson index in bacterial communities at different stations in the three Korean coastal waters (YS = Yellow Sea, SS = South Sea, ES = East Sea)

Regions	Stations	ASVs	Shannon index	Gini-Simpson index
YS	Y1	384	6.0	1.0
	Y2	88	2.9	0.8
	Y3	381	6.6	1.0
	Y5	580	7.1	1.0
SS	S3	210	5.7	1.0
	S4	213	3.2	0.7
	S5	296	5.6	0.9
	S6	436	5.8	0.9
ES	E1	581	7.7	1.0
	E3	307	6.0	1.0
	E7	285	5.0	0.9

On the other hand, the Yellow Sea was characterized by high concentrations (11 ± 1.2 mg L^{-1}) of dissolved oxygen (DO) along with low temperatures, compared to the South Sea (10 ± 1.3 mg L^{-1}) and the East Sea (9 ± 1.0 mg L^{-1}). In addition, DO levels have a strong negative correlation with water temperature ($r = -0.87$; $p < 0.001$) and salinity ($r = -0.75$, $p < 0.001$), while DO showed a positive correlation with Chl. *a* ($r = 0.76$; $p < 0.001$) (Fig. 6), indicating their close relationship in the Yellow Sea. Together with these findings, abiotic factors including water temperature and DO, influenced by geographical characteristics, such as currents, water depth, and tides, particularly affect water temperature and DO levels in winter, with phytoplankton further influencing DO. Conversely, these characteristics of the region-specific coastal environment have a significant impact on the changes of phytoplankton and bacteria communities, as described below.

In temperate waters, including Korea, winter experiences low rainfall, while summer sees high rainfall (Baek et al. 2015, 2019; Lee et al. 2018), leading to higher salinity in winter and lower salinity in summer, especially in the coastal areas of the Yellow Sea and South Sea, influenced by the inflow of water from major rivers, such as Han River, Geum River, Yeongsan River, Seomjin River, and Nakdong River (Figs. 1 and 2). According to Ocean Predictability Experiment for Marine environment (OPEM) by Yoon et al. 2022, there were clear differences in salinity among the regions, with the lowest salinity observed in the Yellow Sea compared to the East Sea and South Sea during summer. Similarly, in the present study, salinity in the Yellow Sea was found to be significantly lower even in winter compared to the other two regions ($p < 0.05$), particularly at St. Y2, which is related to the influx of freshwater from the Anseong Stream. The shallow depth of the Yellow Sea amplifies the impact of freshwater influx, and this influx of terrestrial runoff is possibly related to the high concentrations of nutrients and Chl. *a*. On the other hand, both the South Sea, being influenced by the JWC, and the East Sea, being influenced by the EKWC originating from the Kuroshio Warm Current, had relatively high salinity and temperature levels. Nutrient concentrations in the South Sea were lower compared to the East Sea, which has little river influence (Chang et al. 2004; Kim and Yoon 2010), except for ammonium ($p < 0.01$). Interestingly, the South Sea has maintained a relatively high Chl. *a* level, while the East Sea has extremely low Chl. *a* ($p < 0.001$). The imbalance in nutrient and Chl. *a* concentrations in the two regions appears to be related to consumption by phytoplankton growth, while the high ammonium levels in the South Sea may be evidence of regeneration from the dead phytoplankton. Despite the high nutrient concentrations in the East Sea, the very low Chl. *a* concentrations observed in the East Sea through field survey data (mean: 0.13 μg L^{-1}) and satellite imagery data indicate minimal phytoplankton consumption (Fig. 8). Based on the field data we collected and satellite imagery data, we hypothesized that the shallow depths of the Yellow Sea region would play a significant role in supplying resting diatom spores from sediment through winter mixing, thereby contributing to the seed population in the euphotic layer. Diatom resting spores have thick siliceous frustules with diverse ornamentations, and they can germinate under favorable conditions even in the winter season (Ishii et al. 2011; Montresor et al. 2013). The deeper oceanic waters in the East Sea result in a less efficient supply of sediment-derived seeds to the upper euphotic layer, leading to the maintenance of high nutrient levels associated with low density of phytoplankton population in winter.

It is well known that large diurnal differences in tidal range in coastal waters of the Yellow Sea have resulted in rapid water mixing and relatively short residence times, leading to the dominance of diatoms throughout all seasons (Estrada and Berdalet 1997; Oh and Koh 1995). During winter, the South Sea also experiences high nutrient concentrations due to the influence of vertical mixing, leading to a dominance of diatoms (Jang et al. 2013; Baek et al. 2015; Lee et al. 2018). However, during summer when surface nutrients are depleted by stratification, blooms of harmful dinoflagellates tend to occur using their manner of vertical behavior (Baek et al. 2019; Lim et al. 2021, 2022). Additionally, the East Sea has a lower phytoplankton biomass compared to the Yellow Sea and the South Sea due to the various influences described above (Yoon et al. 2022; Jang et al. 2023). Six endemic species were identified in the Yellow Sea (YS), thirteen endemic species in the South Sea (SS), and three endemic species in the East Sea (ES). The YS has fewer endemic species possibly due to

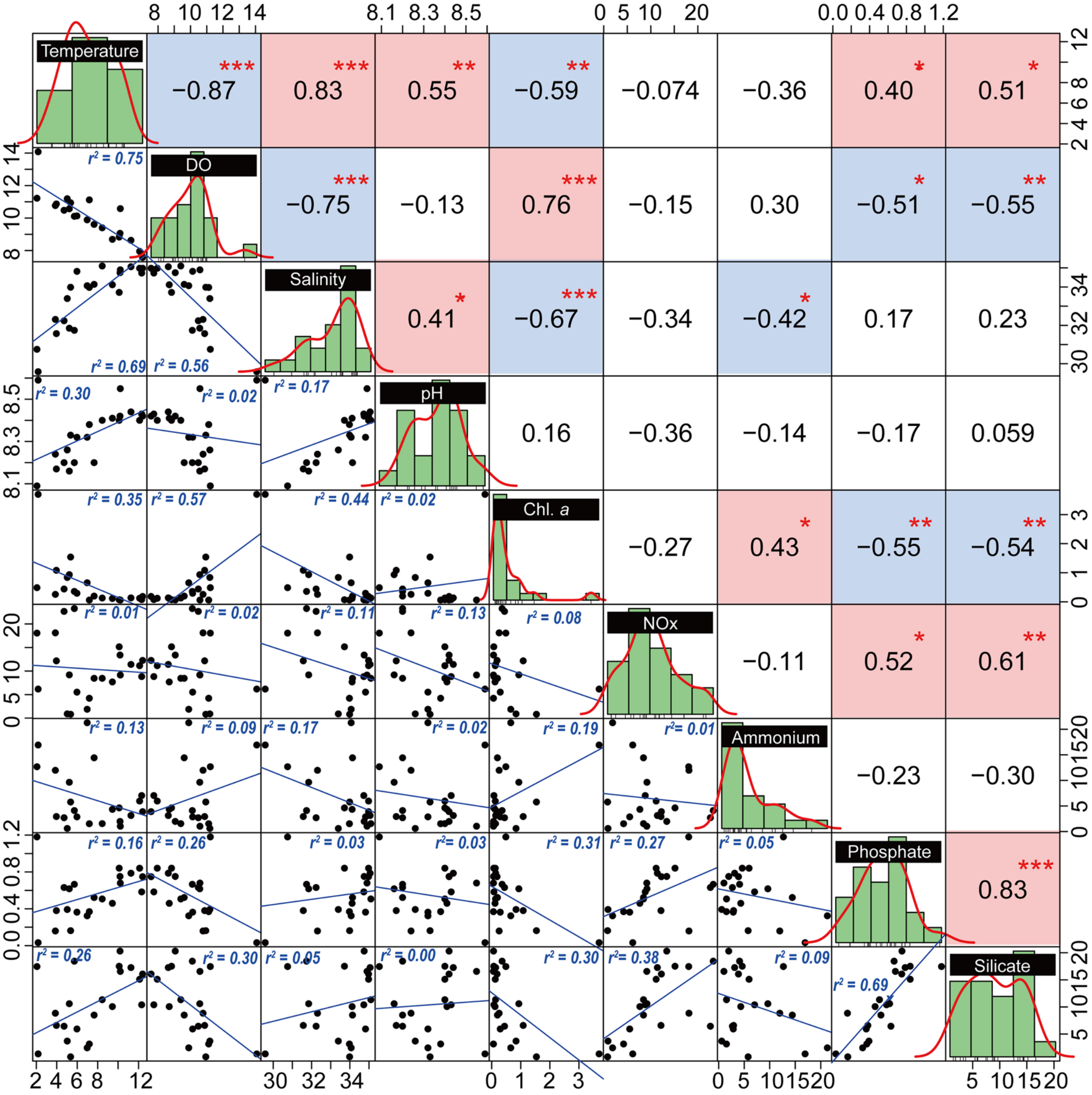
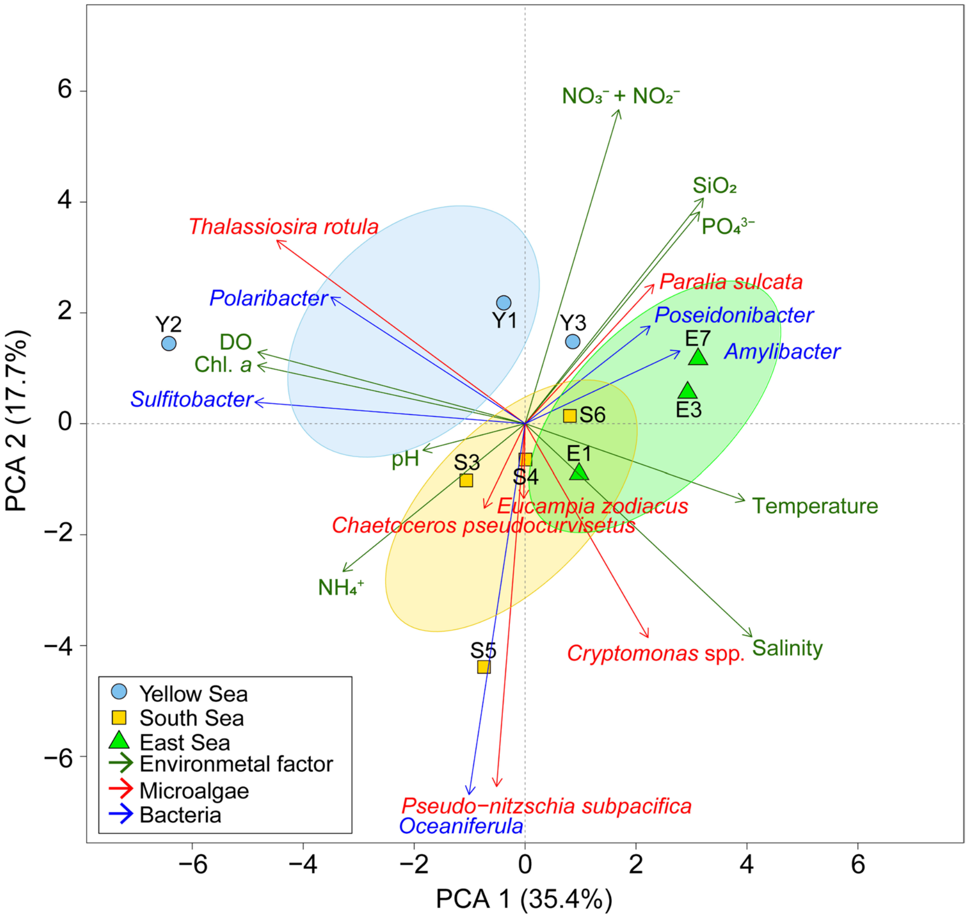


Fig. 6 Correlation analysis for non-parametric Spearman correlation coefficients (upper layer) and linear regression (lower layer) among environmental factors in the entire coastal regions

significant environmental changes. The ES also has a low number of endemic species, which can be attributed to a reduced seed population. In contrast, the SS supports the highest number of endemic species, presumably due to moderate environmental changes and an adequate supply of seed populations. Interestingly, the number of shared species between adjacent regions, YS-SS and SS-ES, was 10 species and 4 species, respectively, which is relatively higher than the number of shared species between non-adjacent regions, YS-ES, which was 2 species. Only six species, representing 14%, were commonly found in the three geographical regions. These findings suggest that environmental characteristics influence the communities of phytoplankton in these regions.

Phytoplankton communities can change over time in response to biological, physical, and chemical environmental factors. It is well known that the genus *Chaetoceros* is a cosmopolitan species and sometimes forms dense blooms in coastal waters (Malviya et al. 2016), making a significant contribution to phytoplankton communities worldwide (Suzuki and Takahashi 1995). According to Kuwata and Tkahashi (1990), *Chaetoceros pseudocurvisetus* is well adapted to the warm conditions of temperate waters. On the other hand, *C. pseudocurvisetus* isolated from cold water environments can survive even in a wide temperature range between 10 and 30 °C (Suzuski and Takahashi 1995; Vrana et al. 2023). In the present study, diatoms *C. pseudocurvisetus* at St. S3 and

Fig. 7 Principal component analysis of stations in the Yellow Sea (blue circles), South Sea (orange squares), and East Sea (green triangles), showing the relationships of environmental factors (green arrows) with microalgae species (red arrows) and bacteria (blue arrows)



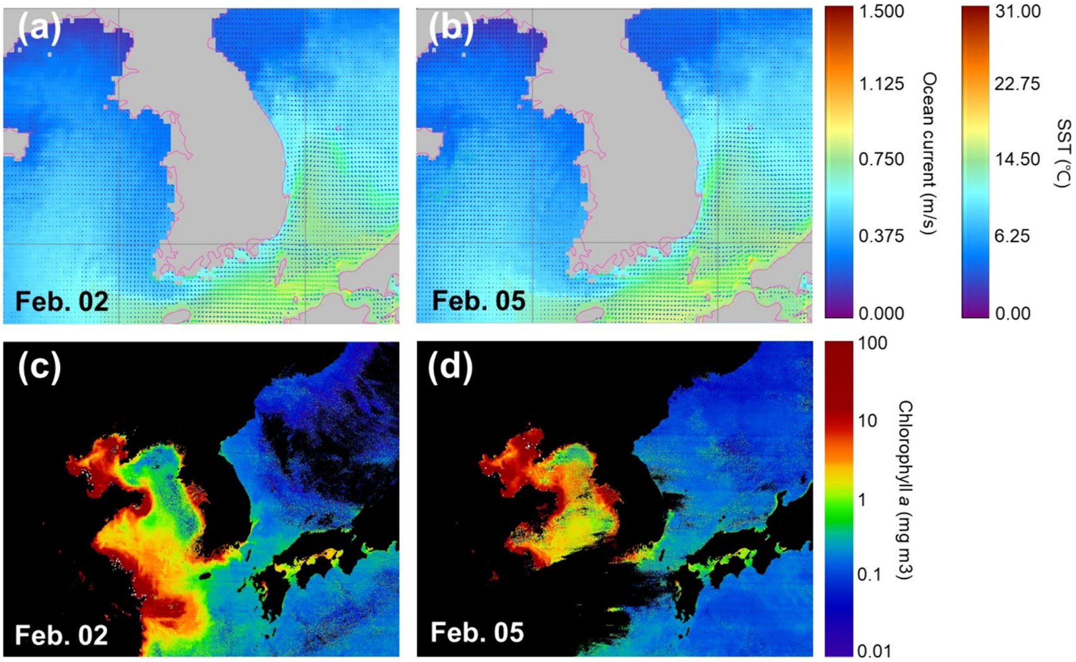


Fig. 8 Satellite image data provided by Japan Aerospace Exploration Agency (JAXA) at the time of the field survey. The data includes sea surface temperature (℃), ocean currents (**a** and **b**), and Chlorophyll *a* (**c** and **d**)

Eucampia zodiacus at St. S4 were dominant, influenced by the relatively low salinity of the estuarine areas and low temperature. Baek et al. (2015, 2019) demonstrated that blooms of *C. pseudocurvisetus* and *E. zodiacus* had occurred in winter and spring in the South Sea, and that they can grow favorably even in low temperatures. *E. zodiacus* is distributed globally and sometimes forms dense blooms in Tokyo Bay (Yoshida et al. 2011), Harimanada (Nishikawa et al. 2007), the Ariake Sea (Ito et al. 2013), and the Bay of Fundy in Canada (Martin et al. 2007). In particular, *E. zodiacus* has a strong tendency to grow under conditions of high nutrients and low water temperatures (Nishikawa et al. 2007; Baek et al. 2015). Based on the PCA analysis, abundance of both diatoms *C. pseudocurvisetus* and *E. zodiacus* showed a negative correlation with nutrients, such as nitrate + nitrite, silicate, and phosphate, suggesting that these nutrients were consumed during their population growth. Therefore, our findings imply that these physiological characteristics of diatoms, *C. pseudocurvisetus* and *E. zodiacus*, serve as an advantage over other phytoplankton species under low temperatures and high nutrient levels associated with winter, resulting in their dominance.

Diatom *Thalassiosira rotula* is known to grow particularly well in low-temperature environments during winter in temperate regions (Sin et al. 2015; Mönnich et al. 2020). In the present study, *T. rotula* was observed at most stations in the Yellow Sea, notably reaching a peak of 4.40×10^5 cells L^{-1} (79%) at St. Y2. As mentioned, significantly low temperature (2 °C) and low salinity (29.5) were observed this area. In addition, concentrations of nutrients, such as silicate, nitrate + nitrite, and phosphate, remained at approximately one-tenth of those at neighboring stations Y1 and Y3. In addition, no correlation was observed between abundance of *T. rotula* and nutrient levels in PCA analysis. According to Sin et al. (2015), the peak of *T. rotula* during winter is attributed to the high nutrient input following the low salinity after freshwater discharge. Therefore, these findings suggest that *T. rotula* may utilize nutrients for its growth. This capability allows it to potentially become a dominant species in the Yellow Sea during winter, where the influence of freshwater inflow is relatively significant.

The diatom *Paralia sulcata*, known as a benthic species, exhibits planktonic behavior occasionally in regions with active water mixing and sediment resuspension, which can be particularly active in the whole water mixing periods of winter compared to other seasons (Chen et al. 2014). Indeed, *P. sulcata* is abundant in modern coastal and shallow marine areas of the Yellow Sea when significant differences in tidal currents occur (Tanimura et al. 2002; Chen et al. 2014). Similarly, in the present study, a high abundance of *P. sulcata* was observed at St. Y3, Y4, Y5, and Y6 in the Yellow Sea and at St. E7 and E8 in the East Sea. According to the results of our PCA, there was a positive correlation with nutrients and the target *P. sulcata*, implying that the benthic diatom thrives in high-nutrient environments formed by water mixing. In particular, *P. sulcata* forms chains, and these chains are robust and resistant to breakage, implying that they can adapt to regions with water mixing and sediment resuspension related to high tidal currents. Therefore, due to these characteristics, *P. sulcata* has an advantage over other algal species in the turbid conditions of resuspension regions and can adapt flexibly to high nutrients through sediment resuspension.

Marshall and Lacouture (1986) reported seasonal fluctuations in the biomass of *Cryptomonas* spp. in the Lower Chesapeake Bay, with higher biomass in the summer and fall and lower biomass in the winter. In addition, *Cryptomonas* spp. are characterized by opportunistic dominance in nutrient-limited conditions in environments with relatively few competitors (Klaveness 1989; Baek et al. 2019; Baek et al. 2023). In the present study, *Cryptomonas* spp. tended to be relatively dominant in environments with low concentrations of Chl. *A* averaging 0.3 μg L^{-1} or less, and fewer competing diatoms, which was similar to the results observed in the East Sea, as reported by Baek et al. (2023). Therefore, these results imply that *Cryptomonas* spp. are well adapted to low water temperature conditions, and the absence of diatoms along the Korean coasts in winter is favorable for the growth of *Cryptomonas* spp. Population, particularly in the East Sea.

Bacteria and phytoplankton contribute to carbon cycling and biodiversity within marine ecosystems through their interactions (Buchan et al. 2014). Microalgae and bacteria are partners that interact closely, with species-specific bacterial communities comprising phytoplankton (Caruso 2020; Seymour et al. 2017). In marine microalgae, the bacterial classes Alphaproteobacteria and Flavobacteria are generally known to be major members of the phycosphere, a particle-associated bacterial community (Teeling et al. 2016; Grossart et al. 2005). In this study, the high composition of both bacterial classes in the coastal waters of Korea in winter, at over 60%, indicates a close relationship with phytoplankton. Another interesting finding in our study was the decrease in bacterial community diversity with phytoplankton dominance. At St. Y2 in the Yellow Sea, when the diatom *T. rotula* dominated at 79%, bacterial diversity was found to be the lowest with the genus *Polaribacter* and *Sulfitobacter* comprising 77% of the total bacterial community. The genus *Polaribacter*, belonging to the order Flavobacteriales, has been reported to exhibit a positive response to algal blooms in polar regions, possibly due to its capability to utilize algal exudates (Williams et al. 2013). Another dominant bacterium, the genus *Sulfitobacter*, from the order Rhodobacterales, is known to rapidly utilize dissolved organic matter (DOM; especially organic sulfide) released by diatoms for growth and has been reported to enhance diatom growth. Indeed, Mönnich et al. (2020) reported *Sulfitobacter* as a major constituent of the bacterial community associated with *T. rotula*. Thus, the high biomass of the diatom *T. rotula* in the low-temperature environment at St. Y2 possibly led to the dominance of these two bacteria. Similar to previous reports (Baek et al. 2015), the diatom *E. zodiacus* was dominant at the S4 station, heavily influenced by the Seomjin River estuary, and the brackish emergent groups such as bacteria Verrucomicrobiae (Freitas et al. 2012) were dominant, resulting in low biological diversity. Except for the stations where specific phytoplankton species was dominant, the bacterial biodiversity in the three seas showed no significant differences (Table 1). Consequently, our findings suggest that low water temperatures in winter and the dominance of certain phytoplankton may alter bacterial communities, leading to reduced diversity of the bacterial communities.

5 Summaries and Conclusion

Our field data highlighted the significant influence of different marine environments on phytoplankton and bacterial communities in the Korean coastal waters of the Yellow Sea, South Sea, and East Sea in winter 2021. The differences of oceanographic characteristics, such as water depth, tidal range, and ocean currents, in these three regions led to significant differences in environmental factors including water temperature, salinity, and nutrient levels. The strong tidal mixing in the shallow Yellow Sea caused low water temperature and high nutrient levels, resulting in dominance of diatoms including *Thalassiosira rotula* and *Paralia sulcata*. Conversely, the weak vertical mixing of the East Sea due to its great depth and warm currents led to low phytoplankton biomass, with dominance of *Cryptomonas* spp. instead of diatoms, indicating low seed populations of diatoms. The South Sea, an intermediate environment between the other two seas with tidal mixing and nutrient supply, was dominated by diatoms, such as *Chaetoceros pseudocurvisetus* and *Eucampia zodiacus*. In addition, we found that the dominance of specific phytoplankton species was correlated to the dominance of specific bacteria and decrease of bacterial biodiversity; for example, there is a high biomass of *T. rotula* and bacteria *Polaribacter* and *Sulfitobacter* with significantly low biodiversity. These findings underscore the complex interactions between environmental factors, phytoplankton communities, and bacterial populations in KCWs during winter. Overall, these region-specific characteristics of coastal environments in KCWs play an important role in determining the dynamics of phytoplankton and bacteria population in winter.

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Data Availability The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper. Seung Ho Baek is an editor of Ocean Science Journal.

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