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Winter distribution of diatom assemblages along the coastline of R. O. Korea in 2010

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Abstract

Diatoms are a globally successful and eukaryotic photosynthetic organism with an ornamented silica external wall. The relationship between their valve morphology and habitat means that diatoms can be used as bioindicators to characterize the aquatic environment. To estimate the differential distribution and diversity of diatom assemblages along the coastal line, we collected phytoplankton samples from 114 coastal sites of waters of R. O. Korea. We applied the unweighted pair-group technique using the arithmetic averages clustering method to cluster the sampling sites, apart from those where the biota consisted of other groups, such as dinoflagellates, into four regions: the Yellow Sea, South Sea, southern East Sea, and northern East Sea. Indicator species analysis in each region led to the selection of tychoplanktonic, chain-forming, attached species to substrates and psychrophilic indicator diatoms, respectively, each of which represented a planktonic lifestyle associated with one of the four regions. This study shows the diatom assemblages to serve as bioindicators of Korean coastal water in winter, and the subsequent seasonal survey will provide a starting point for the improved understanding of Korean diatom-based ecoregions, in both time and space.

Key words: diatom assemblage, indicator species, life-form, Korean coastal waters, species diversity

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1 Introduction

Diatoms are a successful and ubiquitous phytoplankton group with various estimations from a low value of 1 800 species (Sournia et al., 1991) to a high value of 200 000 species (Mann and Droop, 1996), recent estimates range from 12 000 to 30 000 species (Guiry, 2012; Mann and Vanormelingen, 2013). They range in size between 10 μm and 200 μm and exist either as single cells or as chains of connected cells (Kooistra et al., 2007). These silica-depositing microalgae have been abundant for more than 180 million years (Falkowski et al., 2004); marine phytoplankton contribute ca. 50% of global primary production (Sommer et al., 2017) and there is a well-known biogeographic trend in marine phytoplankton body size (Barton et al., 2013). In particular, diatoms are the most abundant and diverse group of phytoplankton communities (Simon et al., 2009) and they contribute nearly 20% to the total primary production of the world ocean. In coastal waters and other nutrient-rich zones, their contribution reaches 75% (Falkowski, 2012).

Diatoms in coastal waters support the most productive fisheries, and in the open ocean, they sink rapidly from the surface to become food for deep-water organisms (Sarthou et al., 2005). Thus, diatoms are crucial contributors to the global carbon cycle and have even been considered as a potential solution for reducing atmospheric CO_2 levels (Denman, 2008). Given their ubiquitous nature, diatoms are logical subjects for researchers interested in global ecological trends such as climate change, as foreseen in the concept that “everything is everywhere, but the environment selects” (Finlay, 2002). Changes in diatom community diversity can be considered as indicative adaptation on occurring in response to selective pressures.

The Korean Peninsula is surrounded by the Yellow Sea (YS), the South Sea (SS; also known as coastal waters of R. O. Korea connected to the East China Sea), and the East Sea (ES, or the Sea of Japan), each with its distinguishing characteristics. The YS, located between Chinese mainland and the Korean Peninsula, is a shallow (generally <100 m), post-glacially submerged, epicontinental sea with one of the largest continental shelves in the world (Wang et al., 2003). The SS is subjected to Kuroshio currents and receives outflows from the Changjiang River which is among the world’s largest rivers (Ichikawa and Beardsley, 2002). Also bordering Japan and Russia, the ES is a typical, mid-latitude, marginal sea, approximately the size of the western Mediterranean and is somewhat unusual in exhibiting typical characteristics of both closed basins and oceans. Similarities to the former

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are due to its sill depths of <150 m, which limits seawater exchange with the North Pacific Ocean. The ES also contains oceanic deep basins (>3 000 m), large seasonal variations in sea surface temperatures (>15°C), and highly active biological processes, and exhibits a sub-Arctic polar front between its sub-polar and sub-tropical seas (Kim et al., 2001).

The history on diatom studies of Korea was well summarized by Lee (1996). He emphasized the importance of positive identification of species to correctly understand the aquatic ecosystem using diatoms. Since late 1990, the diatom studies have been mainly focused on taxonomy on specific genera (e.g., Lee et al., 2014a, 2014b; Park et al., 2016a, 2016b, 2017a) or identification of new and unrecorded species from Korea (e.g., Lee et al., 2012; Lee and Park, 2015; Park et al., 2017b; Jung and Park, 2019). These studies were sporadically performed from non-studied area to enhance the knowledge of species diversity of diatom in Korea. There was little attention to the broad approach to know the association of diatom from Korean waters. Recently, Kim et al. (2019) investigated the epilithic diatom communities throughout 512 sampling sites in Korean estuaries, and divided the coastal water based on the similarity of diatom communities between studying areas. However, there have been no extensive studies conducted in a short period of time to know the association of plankton diatom assemblage along the coastline of Korea.

Diatom communities tend to dominate in well-mixed coastal and upwelling regions, as well as along sea-ice edges where sufficient light, inorganic nitrogen, phosphorus, silicon, and trace elements are available to sustain their growth (Morel and Price, 2003). Therefore, the purpose of the present study is to investigate the diversity and distribution of diatom communities in the coastal areas of R. O. Korea through a winter survey of 114 sampling sites and to clarify each sea characteristic using analyses of the indicator value method and cluster analysis of the diatom community.

2 Materials and methods

2.1 *Study area and diatom sampling*

Diatom sampling was performed at 114 sites along the coast of R. O. Korea (Fig. 1, Table S1) during January and February 2010. We chose sites accessible from the coast for phytoplankton netting, and that were <40 km apart in order to achieve full coverage of Korean waters. One-liter water samples (sampling depth: 1 m under sea surface) were collected in clean polyethylene bottles for quantitative analysis, and phytoplankton samples were taken using a 20 μm mesh net (horizontal netting for 10 m) for qualitat-

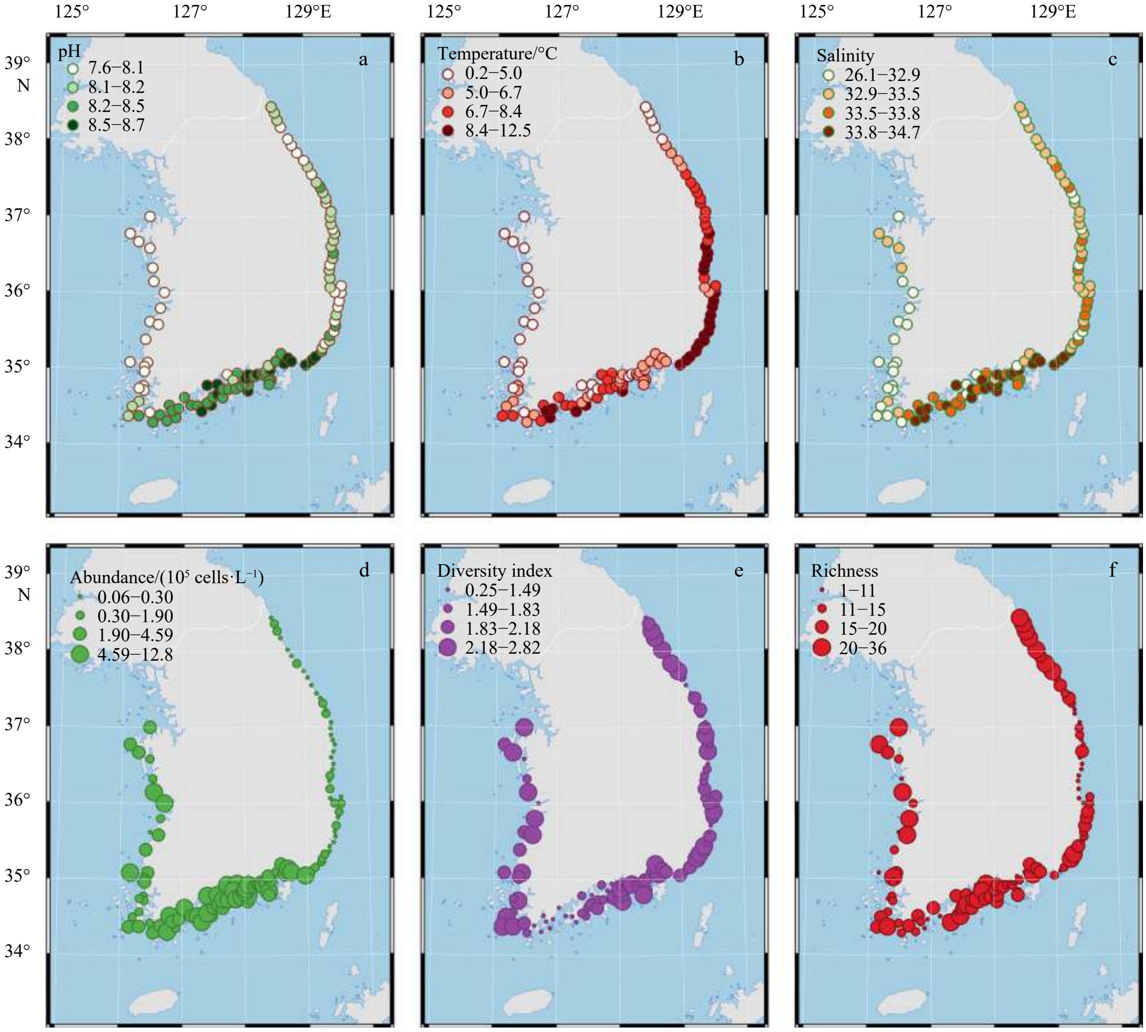

Fig. 1. Abiotic variables in study area: pH (a), water temperature (b), and salinity (c); biotic variables in study area: abundance (d), Shannon’s diversity index (e), and species richness (f).

ive analysis. Collected samples were immediately fixed with 5% Lugol's solution (Sigma, USA) and transported to the laboratory. Environmental data, including temperature, salinity, and pH were measured *in situ*, using a YSI-6600 portable meter (YSI, USA).

2.2 *Diatom assemblage analysis*

The Lugol's fixed water samples were settled for 1 d, and then the supernatant was removed to concentrate the inorganic and organic particles including phytoplankton communities at approximately 50 mL. The counting of total phytoplankton communities focused on diatoms in each concentrated sample under a light microscope (Axioskop 40, Zeiss, Germany) was continued until the minimum 600 cells per sample using a Sedgwick-Rafter counting chamber (Kim et al., 2016; Kang et al., 2021; Jung et al., 2021). To analyze the fine structure of diatom species, we cleaned the diatom sample. Briefly, cellular organic material in a diatom cell was removed using equal amounts of $KMnO_4$ and HCl in a 70°C water bath until the sample became clear, and then the acid was rinsed using distilled water in five time. Selected cleaned samples were mounted in a Pleurax (Cat. No.139-06682, Wako, Japan) and observed under the light microscope equipped with a CCD camera (AxioCamMRc5, Zeiss, German). In addition, we observed using a scanning electron microscope (SEM) (JSM7600F, Jeol, Tokyo, Japan) by cleaning sample (Jung and Park, 2019; Lim et al., 2012). For examination using the SEM, the rest of the cleaned samples were filtered onto a polycarbonate membrane (3.0-μm pore size; TSTP02500, Millipore, USA), which was then dried in air. The filtrated membranes were attached to an aluminum stub using carbon tape and then sputter-coated with gold. The SEM was operated at accelerating voltage of 5 kV using a 10 mm working distance. Diatom identification is based on the authoritative literatures such as Schmidt's Atlas der Diatomaceen-kunde (Schmidt, 1874–1959), Hustedt's Die Kieselalgen series (Hustedt, 1927–1966), (Round et al., 1990), and (Halse and Syvertsen, 1996). In particular, the highly diverse genera such as *Chaetoceros* and *Thalassiosira* are identified based on Lee et al. (2014a, 2014b) and (Park et al., 2016).

2.3 *Statistical analysis*

Species that contributed ⩾1% (relative abundance) of total diatomic assemblage of each sample were selected for numerical analysis resulting in 156 diatom taxa being used. Diatom assemblage diversity was calculated using the Shannon-Wiener diversity index. The absolute abundance of each species was transformed by its fourth root into normalizing skewed composition, data and pairwise distances between sampling sites were calculated using the Bray-Curtis similarity algorithm.

To identify spatial similarity between sampling sites, we performed eight hierarchical clustering methods based on the pairwise distance matrix. These were as follows: the single linkage method, the complete linkage method, the unweighted pair-group method using arithmetic averages (UPGMA), the weighted pair-group method using arithmetic averages, the unweighted pair-group method using centroids, the weighted pair-group method using centroids, and two variants of ward's minimum variance method (ward.D and ward.D2). The degrees of data distortion from the eight methods were then assessed based on cophenetic correlation coefficients (Sokal and Rohlf, 1962). Pairwise distances between sampling sites were calculated in the "vegan" package (Oksanen et al., 2013), and clustering was visualized using the "factoextra" package (Kassambara and Mundt, 2017), both in R (the R Project for Statistical Computing, supported by the R Foundation for Statistical Computing).

The indicator value method (IndVal) was applied to identify indicator species among the groups of sites using the "indicspecies" method in R (De Cáceres, 2013). The IndVal values ranged from zero for "not an indicator species" to one for "maximum indicator ability".

3 Results

3.1 *Species composition, variable characteristics, and diatom-based grouping of coastal waters of R. O. Korea*

Based on the cophenetic correlation coefficient values (r=0.73), the UPGMA clustering algorithm provided the best dissimilarity approximation compared with the other seven methods, and so we adopted the groupings achieved by this method to establish diatom-based regions. The UPGMA clustering, based on the Bray-Curtis similarity matrices, clustered the data into four major groups and three additional unique groups (Fig. 2). Group 1 consisted of 22 sites, mostly in the YS but including one in the SS (Site 64) and two in the ES (Sites 75 and 86). Group 2 included 51 sites located in the SS with four sites from the YS (Sites 3, 10, 12 and 13) also included. Group 3 included 25 sites in the SES, while Group 4 had 11 sites from the NES, as well as solitary site (Site 82) from the SES region. Three unique groups with one to two sites were separated from these four major groups: Unique Group 1 and Unique Group 2 included two sites each: Sites 47 and 48, and Sites 102 and 104, respectively, while Unique Group 3 included just Site 105**.**

Abiotic variability for water temperature, salinity, and pH, was relatively low in the YS, high in the SS, and moderate in the ES (Table 1, Figs 1a–c). Mean diatom abundance across the entire study area was $2.89{\times}10^5$ cells/L, with means in the YS, SS, SES and NES of $2.21{\times}10^5$ cells/L, $4.80{\times}10^5$ cells/L $0.24{\times}10^5$ cells/L, and $0.22{\times}10^5$ cells/L, respectively (Table 1, Fig. 1d). The changes in Shannon diversity were similar to the pattern of change of the richness, while the Simpson evenness followed the opposite trend (Table 1, Fig. 1e). Shannon diversity indices were variable (0.25–2.82) site-by-site with low values in the western SS**,** dominated by *Thalassiosira nordenskioeldii* (0.42–0.79 in Sites 25–30), and *Eucampia zodiacus* (0.42 at Site 31). Diatom richness was 7–36 with low values in the SES (7–9 at Sites 89–91, 93, 100 and 101) (Fig. 1f).

3.2 *Indicator species*

The indicator species for the four major regions were identified using calculated indicator values (p<0.05), and 7, 17, 6 and 7 indicator species were found for the four regions, respectively (Table 2, Fig. 3). Among the 37 indicator species, *Actinoptychus senarius* (Fig. 4i), *Cyclotella litoralis* (Fig. 4ii), *Melosira nummuloides* (Fig. 4iii), *Paralia sulcata* (Fig. 4iv), *Thalassiosira eccentrica* (Fig. 4v) and *Pleurosigma angulatum* (Fig. 4vi) were identified as being significant for the YS, while *Asterionellopsis glacialis* (Figs 4vii, viii), *Ch. affinis* (Fig. 4xii), *Ch. brevis* (Fig. 4xii), *Ch. constrictus* (Fig. 4xii), *Ch. contortus* (Fig. 4ix), *Ch. curvisetus* (Fig. 4x), *Ch. debilis* (Fig. 4xi), *Ch. laciniosus* (Fig. 4xiii), *Chaetoceros* spp. (Fig. 4xiii), *Detonula pumila* (Fig. 4xiii), *Skeletonema dohrnii-marinoii* complex (Fig. 4xiv), *Eucampia zodiacus* (Fig. 4xvii), *Pseudo-nitzschia pungens* (Fig. 4xviii), *Thalassionema curviseriata* (Fig. 4xv), *Thalassiosira curviseriata* (Fig. 4xv), and *T. nordenskioeldii* (Fig. 4xvi) were identified as being significant for the SS. *Achnanthes* spp. (Figs 4xix, xx), *Entomoneis paludosa* (Fig. 4xxiv), *Licmophora grandis* (Fig. 4xxi), *L. paradoxa* (Fig. 4xxii), *L. paradoxa* and *Odontella aurita* (Fig. 4xxiii) were identified as be-

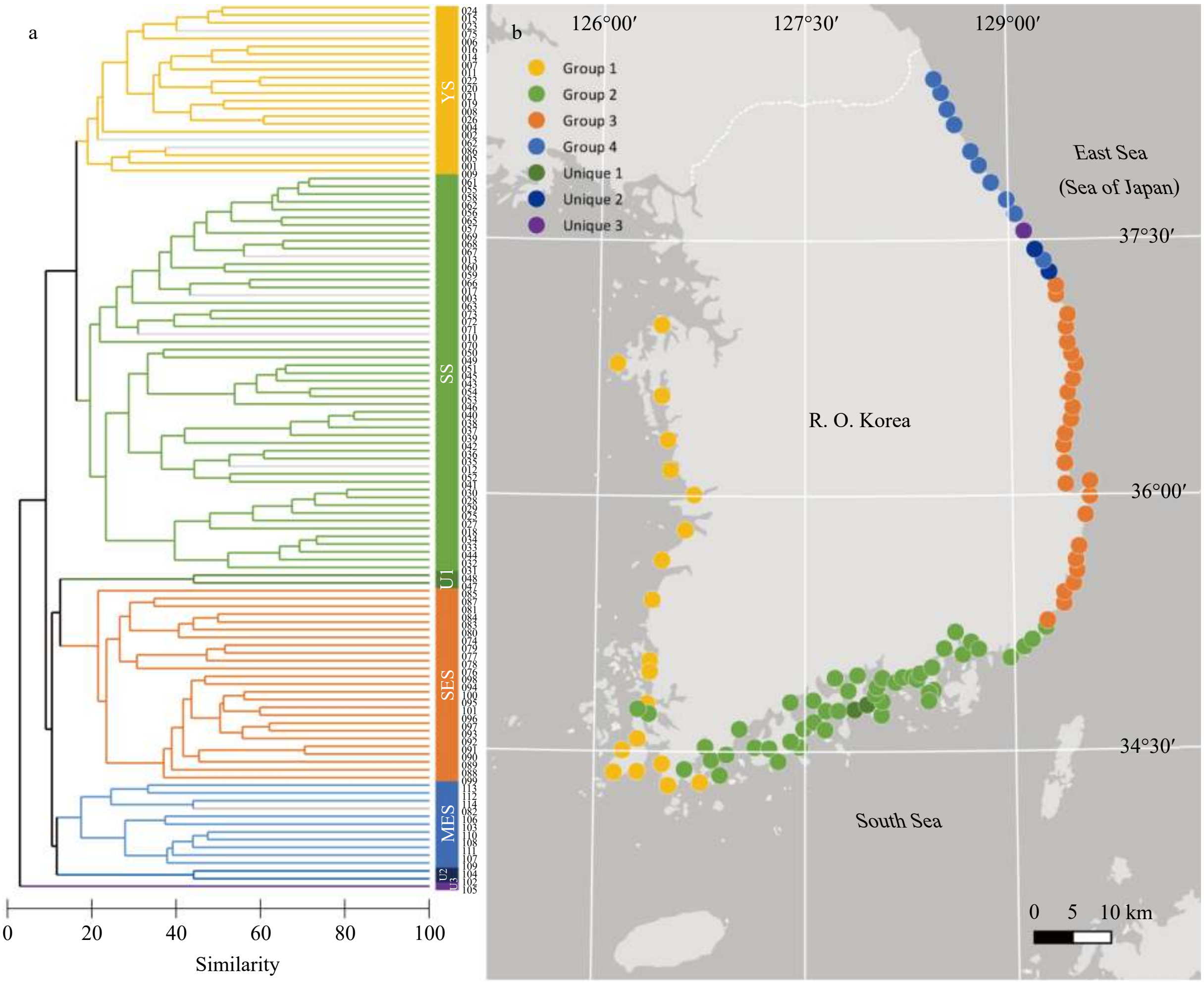

Fig. 2. Hierarchical cluster analysis (UPGMA) of diatom communities based on Bray-Curtis similarity (a), and biogeographic zonation in the Yellow Sea (YS), South Sea (SS), and East Sea (ES) along the coastline of R. O. Korea during winter (b). U represents Unique group.

Table 1. Means and ranges of abiotic variables including pH, water temperature, salinity and biotic variables including number of diatoms species, abundance, Shannon's diversity index, evenness, and species richness. Numbers in parentheses indicate the range between minimum and maximum. Groups 1–4 and Unique groups 1–3 were obtained from UPGMA hierarchical cluster analysis presented in Fig. 2

Group	Sea	Site No.	pH	WT/°C	Salinity	Species No.	Abundance/(10^5 cells·L^{-1})	Diversity	Evenness	Richness
Group 1	YS	22	8.03±0.18 (7.70–8.32)	4.75±2.73 (0.30–12.47)	32.26±1.20 (28.60–34.10)	98	2.21±1.45 (0.07–4.81)	1.92±0.50 (0.27–0.92)	0.73±0.15 (0.27–0.92)	16.88±5.37 (10–28)
Group 2	SS	51	8.41±0.25 (7.62–8.71)	6.39±2.44 (0.20–11.40)	33.67±0.94 (30.40–34.70)	111	4.80±3.05 (0.68–12.80)	1.69±0.59 (0.42–2.73)	0.68±0.22 (0.15–0.92)	16.27±5.07 (8–30)
Group 3	SES	25	8.19±0.09 (8.07–8.41)	9.36±1.53 (5.98–12.21)	33.02±1.50 (26.07–33.80)	77	0.24±0.10 (0.10–0.44)	1.87±0.42 (1.09–2.82)	0.75±0.14 (0.45–0.93)	12.32±4.13 (7–23)
Group 4	NES	11	8.15±0.09 (7.97–8.36)	5.41±1.87 (3.00–9.38)	33.18±0.56 (31.59–33.61)	90	0.22±0.13 (0.06–0.46)	2.15±0.51 (1.32–2.75)	0.76±0.15 (0.50–0.92)	23.18±6.06 (14–36)
Unique 1	SS	2	8.50 (8.48, 8.51)	8.15 (8.00, 8.30)	34.35 (34.20, 34.50)	25	5.40 (5.10, 5.69)	2.03 (1.80, 2.27)	0.75 (0.65, 0.86)	17.50 (16, 19)
Unique 2	NES	2	8.20 (9.19, 8.20)	7.55 (7.50, 7.59)	33.05 (32.58, 33.52)	21	0.24 (0.13–0.34)	0.80 (0.62, 0.98)	0.30 (0.22, 0.38)	14 (14, 14)
Unique 3	NES	1	8.04	7.39	33.23	18	0.16	0.25	0.08	18

Note: WT represents water temperature; YS, the Yellow Sea; SS, the South Sea; SES, the southern East Sea; NES, the northern East Sea.

ing significant for the SES, with *Ch. radicans* (Fig. 4xxv), *Corethron pennatum* (Fig. 4xxvi), *Coscinodiscus centralis* (Fig. 4xxvii), *L. ehrenbergii* (Fig. 4xxx), *Porosira glacialis* (Fig. 4xxiv), *Thalassiosira pacifica*. (Fig. 4xxviii) and *Thalassiosira pacifica* (Fig. 4xxviii) identified as being significant for the NES.

The three unique groups also had indicator species: *Amphora* spp., *Bacillaria paxillifera*, *Grammatophora marina*, *Lauderia annulata*, *L. flabellata*, *Navicula elegans*, and *Tabularia fasciculata* species, were identified for Unique Group 1 and *L. debilis* and *Licmophora* spp., representing Unique Group 2. An indic-

Table 2. Indicator values of diatom species in each group. The indicator species are listed systematically according to Medlin and Kaczmarska (2004)

Groups (Region)	Class	Order	Species	Statistic	*p* value
Group 1 (Yellow Sea)	Coscinodiscophyceae	Coscinodiscales	*Actinoptychus senarius*	0.434	0.024 3*
		Melosirales	*Melosira nummuloides*	0.516	0.003 0**
		Paraliales	*Paralia sulcata*	0.842	0.000 1***
	Mediophyceae	Thalassiosirales	*Cyclotella striata*	0.603	0.000 5***
			Thalassiosira eccentrica	0.481	0.008 1**
	Bacillariophyceae	Fragilariales	*Asteroplanus kariana*	0.614	0.001 7**
		Naviculales	*Pleurosigma angulatum*	0.462	0.011 1*
Group 2 (South Sea)	Mediophyceae	Chaetocerotales	*Chaetoceros affinis*	0.380	0.048 2*
			Chaetoceros brevis	0.413	0.023 3*
			Chaetoceros constrictus	0.613	0.000 1***
			Chaetoceros contortus	0.550	0.000 3***
			Chaetoceros curvisetus	0.490	0.002 7**
			Chaetoceros debilis	0.563	0.000 9***
			Chaetoceros laciniosus	0.538	0.000 1***
			Chaetoceros socialis	0.429	0.037 7*
			Chaetoceros spp.	0.479	0.009 4**
		Hemiaulales	*Eucampia zodiacus*	0.596	0.000 1***
		Thalassiosirales	*Detonula pumila*	0.520	0.001 1**
			Skeletonema dohrnii-marinoii	0.707	0.000 1***
			Thalassiosira curviseriata	0.657	0.000 1***
			Thalassiosira nordenskioeldii	0.745	0.000 1***
	Bacillariophyceae	Bacillariales	*Pseudo-nitzschia pungens*	0.450	0.008 3**
		Fragilariales	*Asterionellopsis glacialis*	0.660	0.000 1***
		Thalassionematales	*Thalassionema nitzschioides*	0.582	0.001 1**
Group 3 (southern East Sea)	Mediophyceae	Eupodiscales	*Odontella aurita*	0.463	0.015 7*
	Bacillariophyceae	Licmophorales	*Licmophora grandis*	0.732	0.000 1***
			Licmophora paradoxa	0.462	0.007 2**
		Mastogloiales	*Achnanthes* spp.	0.400	0.040 2*
		Naviculales	*Navicula* spp.	0.605	0.000 6***
		Surirellales	*Entomoneis paludosa*	0.460	0.013 5*
Group 4 (northern East Sea)	Coscinodiscophyceae	Corethrales	*Corethron pennatum*	0.521	0.011 7*
		Coscinodiscales	*Coscinodiscus centralis*	0.707	0.000 1***
	Mediophyceae	Chaetocerotales	*Chaetoceros radicans*	0.522	0.020 7*
		Thalassiosirales	*Porosira glacialis*	0.674	0.000 9***
			Thalassiosira pacifica	0.507	0.045 8*
	Bacillariophyceae	Licmophorales	*Licmophora ehrenbergii*	0.522	0.017 1*
		Rhabdonematales	*Rhabdonema* spp.	0.522	0.026 3*

Note: *** represents >0.001; **, >0.01; *, >0.1.

ator value was not calculated for Unique Group 3 as only one sample (Site 105) was included, but although an indicator was not calculated here, we noted that the nearby Site 105 was strongly dominated by *Ch. curvisetus*.

4 Discussion

4.1 *Abiotic variables and diatom-based regional grouping of Korean coastal waters*

The Korean coastal waters were able to be divided into four groups based on the diatom assemblage data by clustering analysis, and each group is geographically separated, namely YS, SS, SES, and NES. Overall, the data indicated that differences in the geographic, physical, and environmental factors affected diatom assemblages in each coastal area. In other words, this result implies that the diatom assemblages reflect the characteristics of Korean coastal waters, and can be used as a bioindicator for defining the eco-regions of Korean water based on the diatoms. We sampled during winter, and the water temperature did not exceed the 13°C seasonal average for Korean waters. Despite lower water temperature of the sampling sites, the diatom species were comprised to the common coastal species in temperate regions, except for northern part of the East Sea (Table S2). The diatom occurrences in Korean coastal waters seem to be influenced by the salinity and tidal current rather than the water temperature. For example, although the water temperatures in the YS were low (0.2–5.7°C), the diatom species found were comprised to the frequently occur year-round species such as *Actinoptychus senarius*, *Paralia sulcata* and *Cyclotella litoralis*. Although we did not analyze inorganic nutrients in the present study, previous studies reported that rivers supply inorganic nutrients to both coastal upwelling and tidal fronts in the YS and SS, and the nutrient concentrations are associated with increased diatom community abundance (Lim et al., 2012; Yeo and Kang, 1998). Warm currents from Tsushima (a branch of the Kuroshio warm currents) continuously flow into the SS which also experiences coastal up-

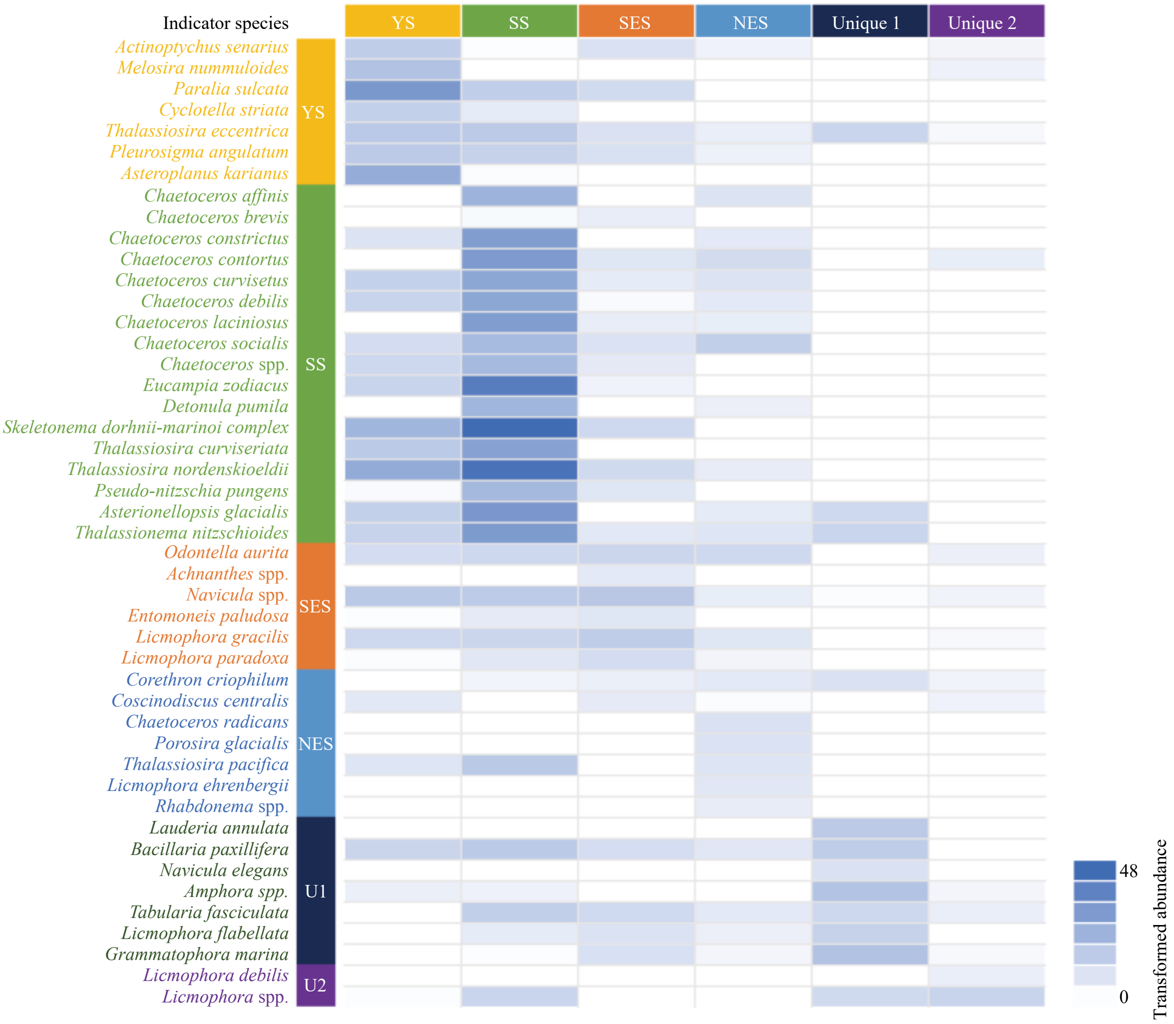

Fig. 3. Heatmap graph for indicator species in the Yellow Sea (YS), South Sea (SS), southern East Sea (SES), and northern East Sea (NES) regions. Colors for species denote the selected indicator species for each region: YS (yellow), SS (green), SES (orange), and NES (blue). Scale bar indicates the transformed abundance by its fourth root. U represents Unique group.

welling and front structures. Fronts in the YS and SS occur at the boundary between turbid coastal waters and stratified offshore waters leading to high levels of phytoplankton abundance and primary production (Choi, 1991; Seung et al., 1990). Jung et al. (2013) reported that in the YS and SS, inorganic nutrient concentrations (dissolved nitrogen, dissolved phosphorus, and dissolved silica) were three times higher than those measured for the ES, and such differences probably played a major role in increasing diatom abundance. The low diatom abundance for the ES, which has the characteristics of the open sea, may be related to a low inorganic nutrient flux caused by the area's deep water and lack of river mixing inputs (Kang et al., 2004; Kim et al., 2001; Yun et al., 2004). The patterns in these results with lower abundance in the ES reflected previous studies (e.g., Kang et al., 2004, 2005). Most diversity studies in marine ecosystems have focused on revealing the community composition, in relation to habitats, depth within the water column or biogeographical patterns (DeLong et al., 2006; Galand et al., 2009). In the present study, the diversity and evenness of diatom community in the NES, suggesting a comparatively high diversity (Table 1): this may be affected by mixing between cold and warm water currents. In the present study, diatom assemblage may be most influenced by current, such as *Porosira glacialis* and *Coscinodiscus centralis* known to be typical polar diatom (Villareal and Fryxell, 1983) and cosmopolitan (Halse and Syvertsen, 1996), respectively.

4.2 *Indicator species in diatom-based regional grouping of Korean waters*

We performed diatom indicator species analyses to identify the meaningful species from four diatom-based groups in the coastal waters of R. O. Korea. This analysis was used to identify diatom species that reflected the geographic and seasonal characteristics of each group. In the YS group, the indicator species included tychoplanktonic diatoms known to be typically benthic and brackish water species (Table 2). *Paralia sulcata, Actinoptychus senarius, Pleurosigma angulatum*, *Cyclotella litoralis,* and *Asteroplanus karianus* were selected as indicator species here. *Paralia sulcata* is an environmental indicator for vertically well-mixed water due to its tychoplanktonic nature (McQuoid and Nordberg, 2003); this species is typically found in regions with frequent upwelling, and its abundance is correlated with high nutrient concentrations (Abrantes, 1988). *Pleurosigma angulatum* is a typical epipelic intertidal diatom which overcomes its severe environment by undergoing periodic vertical migrations coincident with the tides and light (Happey-Wood and Jones, 1988). *Cyclotella litoralis* is a euryhaline diatom frequently found

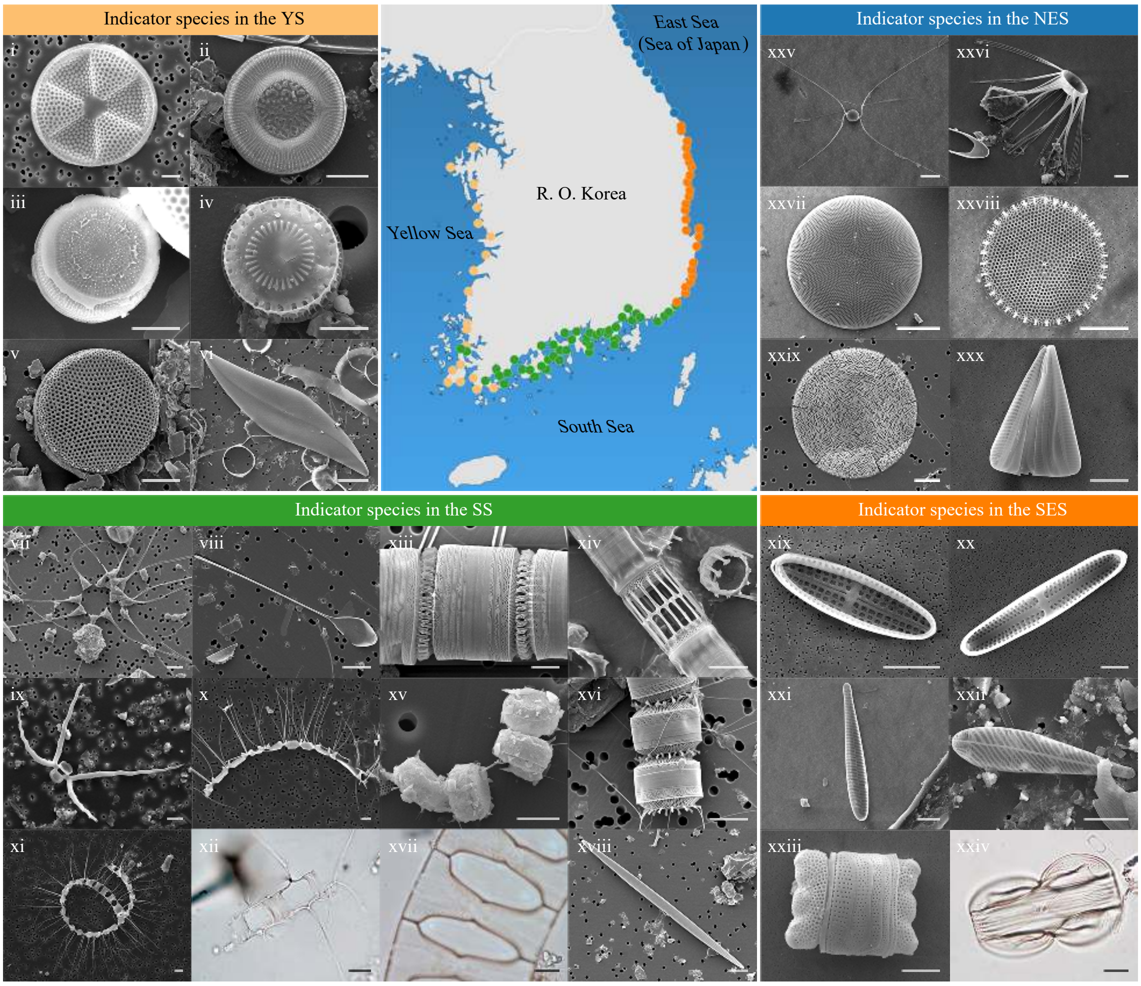

Fig. 4. Micrographs of representative indicator species for the four regions identified in this study: (i) *Actinoptychus senarius*, (ii) *Cyclotella litoralis*, (iii) *Melosira nummuloides*, (iv) *Paralia sulcata*, (v) *Thalassiosira eccentrica*, (vi) *Pleurosigma angulatum*, (vii, viii) *Asterionellopsis glacialis*, (ix) *Chaetoceros contortus*, (x) *Ch. curvisetus*, (xi) *Ch. debilis*, (xii) *Ch. constrictus*, (xiii) *Detonula pumila*, (xiv) *Skeletonema dohrnii-marinoii* complex, (xv) *T. curviseriata*, (xvi) *T. nordenskioeldii*, (xvii) *Eucampia zodiacus*, (xviii) *Pseudo-nitzschia pungens*, (xix, xx) *Achnanthes* spp., (xxi) *Licmophora grandis*, (xxii) *L. paradoxa*, (xxiii) *Odontella aurita*, (xxiv) *Entomoneis paludosa*, (xxv) *Ch. radicans*, (xxvi) *Corethron pennatum*, (xxvii) *Coscinodiscus centralis*, (xxviii) *T. pacifica*, (xxix) *Porosira glacialis*, (xxx) *L. ehrenbergii*. YS is the abbreviation of the Yellow Sea; SS, the South Sea; SES, the southern East Sea; NES, the northern East Sea.

in the estuaries of YS (Park et al., 2013), while *Asteroplanus karianus* can rapidly uptake nutrients and form very large blooms (Yamaguchi et al., 2014), and so nutrient inputs from sediments and rivers draining into YS provide a suitable habitat for this species. In summary, the characteristics of the YS indicator species have straightforward explanations including a liking for areas exhibiting well-established vertical mixing of the water column, freshwater inputs, and nutrient enrichment. The water column in winter is well-mixed vertically by tidal currents and winds in the YS; the NW monsoon cools the surface water and the water temperature vertical gradient becomes more uniform (Roelofs, 1984; Hobson and McQuoid, 1997; Gebühr et al., 2009). Vertical mixing in the water column provides nutrient enrichment from the sediment to the surface and gives benthic and tychoplanktonic diatoms a chance to access both nutrients and light. The Han River and Keum River (two of the five largest rivers in R. O. Korea) drain into the YS region providing additional nutrient enrichment (Koh and Khim, 2014; Wang et al., 2003).

The indicator species in the SS group were colony and chain-forming diatoms, such as *Asterionellopsis glacialis*, *Chaetoceros* spp. and *Eucampia zodiacus*, and Thalassiosirales such as *Detonula pumila*, *Skeletonema dohrnii-marinoii* complex, *Thalassiosira curviseriata,* and *T. nordenskioeldii*. The SS coastline of R. O. Korea is geologically a ria with many bays and islands, and is physically influenced by south-western, wind-driven currents, tidal currents, and the Tsushima Warm Current. These physical factors encourage the SS sediment re-suspension and the geologically complex coastline emphasizes tidal effects in bays (Bae and Kim, 2012). Several theories have been advanced to explain the success of chain-forming diatoms with the advantages of chain formation being reported as including beneficial responses to physical, chemical and biological constraints (Musielak et al., 2009; Peters et al., 2006; Bjærke et al., 2015). Recently, turbulence shear has been reported as enhancing nutrient uptake in chain-forming diatoms (Bergkvist et al., 2018), and although the type of turbulence in the SS was not studied, its physical and geological characteristics cause continuous turbulence, which may well be increasing the nutrient availability for chain-forming diatoms.

The ES has a coastal terrace with a simple, linear coastline, where diatom distribution is mainly affected by two major currents—the S-trending Liman Current, and the N-trending Tsushima Current. These currents meet and form the subpolar fronts and mesoscale eddies that influence phytoplankton community structure and distribution in this area (Choi et al., 2016). In our study, the ES diatom-based regions were divided into distinct southern and northern groups. In the SES, the indicator species were estuarine, stalk-forming diatoms, such as *L. grandis*, *L. paradoxa*, *Achnanthes* spp, and *Odontella aurita*. *Licmophora* is a diatom that is usually found submerged in rock pools throughout the littoral zone (Honeywill, 1998). Its species are known to survive on various substrates, including sediments, rocks, microalgae, vertebrates, and ice. The stalk attachment has to be strong to survive intertidal forces and wave action, as well as being pounded against rocks and macroalgae, although in sub-optimal conditions cells can easily become dislodged (Honeywill, 1998). In a recent study, *Licmophora* grew well and successfully formed colonies under experimental high light intensities and low turbulence, and their growth rate showed no relationship to nutrients (Ravizza and Hallegraeff, 2015). Currently, no clear explanation exists for the significant presence of attached diatoms such as *Licmophora* species, including *L. grandis* and *L. paradoxa*, in the water column. The occurrence of *Licmophora* species and *Odontella aurita* as indicator species in the SES might be related to the extensive presence of the massive macroalgae habitats which are preferred by attached diatoms (Jeong et al., 2014). It is also likely that the continuous effect of the Tsushima current may cause diatoms to become detached from substrates and suspended in the water column (Kooistra et al., 2009).

The selected indicator species in the NES included psychrophilic diatoms such as *Corethron pennatum*, *Coscinodiscus centralis, Porosira glacialis*, and *Thalassiosira pacifica*. *Coscinodiscus centralis* is a large, centric diatom known to be cosmopolitan (Halse and Syvertsen, 1996) even occurring in the Arctic region (Lovejoy et al., 2002; Duerksen et al., 2014). *Porosira glacialis* is a typical polar diatom (Villareal and Fryxell, 1983), while *Thalassiosira pacifica* has been reported from cold to tropical regions (Park et al., 2016a), although most frequently occurring in the Arctic (Joo et al., 2012). In the NES, the Liman Cold Current has a more undiluted impact, while cold water and warm water probably differ in their effects. In winter, the Liman Cold Current flows strongly southward, and the indicator species are those related to the temperature transitions associated with the Liman Cold Current (Yun et al., 2004). Specifically, our work indicated that the NES region was probably characterized by the action of the Liman Cold Current weakening the Tsushima Warm Current (Kim and Min, 2008) suggesting that this region’s diatom assemblage may be most influenced by current, rather than by geography.

5 Conclusions

We have investigated winter diatom distribution in coastal waters of R. O. Korea finding four major regions (the YS, SS, SES, and NES). The diatom assemblages can cluster the sampling stations into four major groups (the YS, SS, SES, and NES). The indicator species analysis for each group selected the diatoms that related to the environmental conditions: In the YS region, the selected indicator species were characterized as tychoplanktonic and euryhaline diatoms indicating that the region had uniform water column mixing with freshwater inputs. In the SS region, the dominance of chain-forming diatoms was considered to be a response to the turbulence caused by an uneven coastline and strong tidal flows, and by the Tsushima Warm Current. In the SES region, having stalk-forming diatoms such as *Licmophora* and *Achnanthes* as indicator species was thought to be associated with a simpler coastline with the strong Tsushima Warm Current limiting the distribution of planktonic species in this region. In the NES region, the Liman Cold Current was considered to be the main factor influencing diatom distribution as our analysis showed that cold-water species such as *Corethron pennatum* and *Porosira glacialis* were its indicator species. Although the detailed influences such as physical, chemical, and biological factors on diatom distribution was not investigated in this study, the diatom-based biogeographical groupings and their indicators species have reflected some factors that can influence the spatial distribution of diatoms in the coastal waters of R. O. Korea, in winter.

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Supplementary information:

Table. S1. Information of sampling sites in the presnet study.

Table. S2. Diatom species that contributed ⩾1% of the total diatomic assemblage in at least one sample.

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