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이학박사 학위논문

**Community structures and responses
of benthic diatoms and macrozoobenthos
to the various harsh environments**

다양한 극한 환경에서의
저서규조류 및 대형저서동물
군집구조 및 반응에 대한 연구

2021년 2월

서울대학교 대학원
지구환경과학부
배 한 나

**Community structures and responses
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to the various harsh environments**

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이 논문을 이학박사 학위논문으로 제출함

2021년 2월

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ABSTRACT

More than half of the Earth's surface is covered with extreme marine environments. Such environments offer unique opportunities for investigating the responses and adaptations of benthic organisms to stressful life conditions. The community structure of benthic diatoms and macrozoobenthos was investigated in various extreme environments to answer the following questions: 1) will the diversity be constant across increasing environmental gradients? 2) which species would be tolerable in such environments? and 3) what would be the adaptation process(es) of benthos? Target organisms were benthic diatoms and macrozoobenthos, which contribute to the marine ecosystem as both prey and consumers, carbon pumps and uptakers, among other processes. We investigated the characteristics of benthos in hypersaline area, under hypoxic condition, organic enrichment conditions, and glacier retreat area to establish whether the benthic communities show the environmental-specific responses. First, the benthic diatom community in solar salterns (artificial structures) was investigated to advance our understanding of how extremely high salinity impacts the community structure of diatoms. Living diatoms were observed at 24–205 psu (practical salinity unit), which is a considerably extreme condition. However, no diatoms were detected at 324 psu. Fewer species exhibited tolerance at higher salinities (100–200 psu). Consequently, the species diversity of diatom assemblages declined with increasing salinity stress. Importantly, aquafarms use and disturb the marine environment directly. Hypoxic events caused by the aquaculture industry could induce the complete loss of macrozoobenthos. After hypoxic environments recovered, opportunistic species temporarily increased. In addition, the habitats of the Yellow and Bohai seas are being altered by development and the discharge of land-derived pollutants, due to urbanization and industrialization. The spatial distribution patterns of diatom assemblages appeared to be correlated with the degree of terrestrial matter input. Analysis of sediment core samples to elucidate the past environment showed that contaminants of land origin caused fluctuations in diatom assemblages. The potential of using benthic diatoms as “indicator assemblages” to monitor the effects of glacial retreat effects on the polar benthic ecosystem has also been highlighted. This study provided new insights into the responses and changes of the marine ecosystem in sensitive polar regions under the current regime of global warming. Overall, benthic organisms exhibited tolerance thresholds or preference for specific environmental conditions. Marine habitats altered to extreme environments; however, few tolerant species were

detected that could endure severe environments. Consequently, species diversity tends to decrease when environmental factors reach extreme values. The present study provides insights into how we could predict and prepare for dynamic changes to the marine ecosystem under growing human impacts.

Keywords: Benthic diatom, macrozoobenthos, extreme environments, hypersaline, hypoxia, land-derived pollutants, glacier retreat

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TABLE OF CONTENTS

ABSTRACT	I–II
TABLE OF CONTENTS	III–VI
LIST OF ABBREVIATIONS	VII
LIST OF TABLES	VIII–X
LIST OF FIGURES	XI–XVII

CHAPTER 1. Introduction..... 1–10

1.1. Backgrounds	2
1.2. Objectives	8

CHAPTER 2. Shift in benthic diatom community structure and salinity thresholds in a hypersaline environment of solar saltern, Korea 12–53

2.1. Introduction	13
2.2. Materials and Methods	15
2.2.1. Study area	15
2.2.2. Sampling and laboratory analyses	17
2.2.3. Data analyses	22
2.3. Results	24
2.3.1. Environmental variables	24
2.3.2. Distributions in benthic diatom assemblages	26
2.3.3. Cluster analysis	36
2.4. Discussion	38
2.4.1. Distribution of diatom along the environmental gradient	38
2.4.2. Environmental factors controlling diatoms	41
2.4.3. Indicator species for salinity gradient	50
2.5. Summary	53

CHAPTER 3. Spatiotemporal variations in macrofaunal assemblages linked to site-specific environmental factors in two contrasting nearshore habitats

..... 55–91

3.1. Introduction	56
3.2. Materials and Methods	59
3.2.1. Study area	59
3.2.2. Sampling and laboratory analyses	62
3.2.3. Data analyses	65
3.3. Results	66
3.3.1. Spatiotemporal variation in environmental conditions	66
3.3.2. Spatiotemporal patterns in macrofaunal assemblages	70
3.3.3. Environment-macrofauna relationship	75
3.4. Discussion	78
3.4.1. Key factors influencing the occurrence and distribution of macrofauna	78
3.4.2. Variation in species composition	85
3.4.3. Indicator species	89
3.5. Summary	91

CHAPTER 4. Distribution and historical records of diatom assemblages in surface and sediment cores from the Yellow and Bohai seas under anthropogenic pressure..... 93–123

4.1. Introduction	94
4.2. Materials and Methods	97
4.2.1. Study area and laboratory analyses	97
4.2.2. Data analyses	102
4.3. Results	103
4.3.1. Environmental settings	103
4.3.2. Diatom assemblages inhabited on surface sediment	106
4.3.3. Diatom assemblages observed in sediment core	109

4.3.4. Cluster analysis	111
4.4. Discussion	114
4.4.1. Diatom monitoring in genus level versus species level	114
4.4.2. Diatoms reflecting present environments	115
4.4.3. Diatoms reflecting historical records of environment	119
4.5. Summary	123
CHAPTER 5. Shift in polar benthic community structure in a fast-retreating glacial area of the West Antarctica	125–171
5.1. Introduction	126
5.2. Materials and Methods	128
5.2.1. Study area	128
5.2.2. Sampling and laboratory analyses	130
5.2.3. Data analyses	140
5.3. Results	142
5.3.1. Environments	142
5.3.2. Assemblages of benthic diatoms	144
5.3.3. Distribution characteristics of benthic diatoms	148
5.4. Discussion	159
5.4.1. Impact of glacial retreat on the benthic ecosystem	159
5.4.2. Indicator species	162
5.4.3. Role of benthic diatoms on shift in polar community	165
5.5. Summary	171
CHAPTER 6. Conclusions.....	173–184
6.1. Summary	174
6.2. Environmental implications and Limitations	181
6.3. Future research directions	184

BIBLIOGRAPHY	185-194
ABSTRACT (IN KOREAN)	196-197

LIST OF ABBREVIATIONS

ANOSIM	Analysis of similarities
APs	Alkylphenols
CA	Cluster analysis
DA	Discriminant analysis
DO	Dissolved oxygen
EA-IRMS	Elemental analyzer-isotope ratio mass spectrometer
IndVal	Indicator value
LM	Light microscope
MC	Mud content
NMDS	Non-metric multidimensional scaling
PAHs	Polycyclic aromatic hydrocarbons
PCA	Principle component analysis
PERMANOVA	Permutational multivariate analysis of variance
POM	Particulate organic matter
SIMPER	Similarity percentages
SOs	Styrene oligomers
TN	Total nitrogen
TOC	Total organic carbon

LIST OF TABLES

Table 2.1.	19
Information of sampling areas and environmental data at 13 stations in the two salterns.	
Table 2.2.	25
Data on the environmental variables and diatom assemblages measured in the samples from the two saltern sites.	
Table 2.3.	27
List of benthic diatoms found in the two salterns, given in descending order of relative abundance (%) to total.	
Table 2.4.	35
Diversity indices of benthic diatom communities at 13 stations in the two salterns; <i>S</i> , number of species; <i>d</i> , species richness; <i>J'</i> , Pielou's evenness; <i>H'</i> , Shannon wiener diversity; $1-\lambda$, Simpson diversity	
Table 2.5.	39
Results of BIOENV analysis showing the strongest correlation for environmental variables that best matched the relative abundance and species composition of diatoms.	
Table 2.6.	44
Result of PERMANOVA showing the significance of variables across study area and salinity in species diversity and composition of benthic diatoms in the two salterns.	
Table 2.7.	47
Result of IndVal analysis listing the indicator diatom species by salinity group.	
Table 2.8.	48
Mini-review on the salinity thresholds reported for various marine organisms in the hypersaline environments	
Table 3.1.	61
Data on the environmental variables, such as water quality and sediment properties, measured in the samples collected from Jinhae Bay and Samcheok coastal areas, over three years (2013–2015); values given for all years combined and for each season.	
Table 3.2.	64
Sampling location (latitude and longitude), depth, and bottom sediment type in Jinhae Bay and Samcheok coastal area.	
Table 3.3.	68
Data on the macrofaunal assemblages and environmental variables identified and/or measured in the samples from Jinhae Bay; values given for three groups (TG1–TG3) identified from the cluster analysis.	

Table 3.4.	69
Data on the macrofaunal assemblages and environmental variables identified and/or measured in the samples from Samcheok coastal area; values given for three groups (SG1–SG3) identified from the cluster analysis.	
Table 3.5.	81
Discriminant analysis of environmental variables among the three groups in Jinhae Bay.	
Table 3.6.	82
Discriminant analysis of environmental variables among the three groups in Samcheok coastal area.	
Table 3.7.	90
IndVal analysis listing the indicator species in the groups delineated for Jinhae Bay and Samcheok coastal area.	
Table 4.1.	98
Information of sampling area with 18 samples in Yellow and Bohai seas.	
Table 4.2.	104
Data on the abiotic and biotic variables measured in the bottom water and surface sediment samples from the Yellow and Bohai seas. Dominant diatom taxa were given with relative abundances.	
Table 4.3.	105
Data on the abiotic and biotic variables measured in the bottom water and sediment core samples from the Yellow and Bohai seas. Dominant diatom taxa were given with relative abundances.	
Table 4.4.	107
Diversity indices of benthic diatom communities of 18 samples in the Yellow and Bohai seas; S , number of species; d , species richness; J' , Pielou's evenness; H' , Shannon wiener diversity; $1-\lambda$, Simpson diversity. The diversity indices were calculated based on species level of diatom data.	
Table 4.5.	116
Results of BIOENV analysis showing the strongest correlation for environmental variables that best match for diatom composition at genus and species level on the surface sediment in the Yellow and Bohai seas.	
Table 4.6.	120
Results of BIOENV analysis showing the strongest correlation for environmental variables that best match for diatom composition at genus and species level from the sediment core in the Yellow and Bohai seas.	
Table 5.1.	141
Summary of statistics with specific purposes, data description, and software.	
Table 5.2.	143

Data on the environmental variables measured at six intertidal locations (B1–B5 & B6 as a reference site), Marian Cove, Antarctica.

Table 5.3. **145**

Relative abundance (300 counts per sample) of benthic diatoms found at six intertidal locations (B1–B5 & B6 as a reference site), Marian Cove, Antarctica, data given by type substrates of rock (film and mat forms), macroalgae, and limpet shell.

Table 5.4. **147**

Relative abundance (300 counts per sample) of benthic diatoms on rocks at six intertidal locations (B1–B5 & B6 as a reference site), Marian Cove, Antarctica, in 2019.

Table 5.5. **151**

Relative abundance (300 counts per sample) of benthic diatoms in subtidal sediments from four locations (M1–M4; at two depths of 10 and 30 m), Marian Cove, Antarctica.

Table 5.6. **155**

Ecological type of benthic diatoms, by habitat preference, for those found at the intertidal and subtidal locations, Marian Cove, Antarctica. Bibliographic information of references presented in Supplementary reference.

Table 5.7. **161**

Diversity indices of benthic diatom communities at the intertidal and subtidal locations of Marian Cove, Antarctica, by substrate type; d , species richness; J' , Pielou's evenness; H' , Shannon wiener diversity.

Table 5.8. **164**

IndVal analysis listing the indicator epilithic diatom species by clustered groups delineated for Marian Cove, Antarctica. Given groups representing geographical setting, such as A: inner intertidal locations; B: outer intertidal locations; C: inner subtidal locations; D: outer subtidal locations.

Table 6.1. **180**

Summary of benthos from extreme environments

LIST OF FIGURES

Figure 1.1.	3
Illustration showing the benthic community in extreme environments under the human impacts.	
Figure 1.2.	4
Importance of benthos in extreme environments in terms of structure and function	
Figure 1.3.	7
Overview of study efforts on anthropogenic stresses to benthic ecosystem. Limitation of previous study also given.	
Figure 1.4.	9
Research questions of the study in terms of benthic community responses under extreme environments such as hypersaline areas, hypoxia, organic enrichment, and glacier retreat.	
Figure 1.5.	10
Frame of the present study with respect to scale of disturbance	
Figure 2.1.	16
Map showing the study area with an overview of the two salterns. (a) Site A located in Muan and Site B located in Sinan. Salinity increased from A1 to A5 (Site A) and from B1 to B6 (Site B). AR and BR located in the adjacent natural tidal flats refer to the reference stations. (b) Photographic information for the five habitat types (tidal flats, seawater reservoirs, small ditches, large ditches, and salt plates) of the Muan and Sinan salterns.	
Figure 2.2.	20
Light micrographs of dominant diatoms in two salterns, salinity (psu) of the station where each species was most abundant given in parenthesis. (a) <i>Cyclotella littoralis</i> (31); (b) <i>Paralia sulcata</i> (31); (c) <i>Navicula salinarum</i> (24); (d) <i>Navicula</i> sp. 1 (174); (e) <i>Nitzschia</i> cf. <i>sigma</i> (37); (f) <i>Navicula gregaria</i> (24); (g) <i>Navicula</i> cf. <i>erifuga</i> (31); (h) <i>Navicula</i> sp. 4 (165); (i) <i>Navicula</i> cf. <i>arenaria</i> (65); (j) <i>Nitzschia scalpelliformis</i> (74); (k) <i>Seminavis</i> sp. 4 (36); (l) <i>Amphora</i> cf. <i>boliviana</i> (174); (m) <i>Rhopaldia rumrichiae</i> (32); (n) <i>Navicula pavillardii</i> (24); (o) <i>Achnanthes</i> sp. 1 (205).	
Figure 2.3.	21
Site view in the saltern and tidal flat	
Figure 2.4.	37

Overview of benthic diatom communities under a wide range of salinities in the two salterns of sites A and B. (A) Number of occurred species and diversity indices along the salinity gradients in the two salterns. No diatom was detected at station A5. (B) Cluster analysis based on the relative abundance of diatom species with four categorized groups by specific range of salinities; brackish, seawater and hypersaline conditions. (C) Relative abundance of the top six dominant diatoms species (>5% of total abundance) belonging to each group are given.

Figure 2.5. 40

Boxplots for occurrence (viz., presence or absence) of the seven selected species (*Napa*, *Navicula* cf. *pavillardii*; *Cyli*, *Cyclotella litoralis*; *Naar*, *Navicula* cf. *arenaria*; *Nav4*, *Navicula* sp. 4; *Nisc*, *Nitzschia scalpelliformis*; *Ach1*, *Achnanthes* sp. 1; *Nav1*, *Navicula* sp. 1) with respect to salinity, mud content (MC), pH, and total nitrogen (TN) based on dataset II (site B). The benthic diatom species with a >1% of relative abundance was presented. The blue shading represents the occurrence ranges of all species in the study area. Seven species were arranged in ascending order of median values in their occurrences with respect to salinity gradient.

Figure 2.6. 42

Relationship between benthic diatoms and environmental parameters based on dataset II (site B). (A) Principal component analysis of 7 selected species (*Napa*, *Navicula* cf. *pavillardii*; *Cyli*, *Cyclotella litoralis*; *Naar*, *Navicula* cf. *arenaria*; *Nav4*, *Navicula* sp. 4; *Nisc*, *Nitzschia scalpelliformis*; *Ach1*, *Achnanthes* sp. 1; *Nav1*, *Navicula* sp. 1) and environmental variables. (B) Correlation analysis between salinity and benthic diatom community structure, in terms of species numbers and diversity, scatterplot shown for two categorized ranges of salinity, viz., <100 psu and >100 psu, for a comparison.

Figure 2.7. 52

Overview of salinity settings and schematic diagrams in benthic community structure at solar saltern environment in aspect of diversity, species composition (relative abundance of 4 indicator species and others illustrated), and euryhaline distributions of 4 selected species. Four selected indicator species include *Navicula* cf. *pavillardii*, *Cyclotella litoralis*, *Nitzschia scalpelliformis*, and *Achnanthes* sp. 1.

Figure 3.1. 60

Maps showing the sampling stations in (A) Jinhae Bay (T1–T10) and (B) Samcheok coastal area (S1–S10), Korea. Major land-use and selected marine activities are given.

Figure 3.2. 63

Site and field survey views in Samcheok Coast.

Figure 3.3. 71

Total species abundance (as mean density), total number of species, and density of the top 10 dominant species in (A) Jinhae Bay and (B) Samcheok coastal area, during the 3-year study period (from fall 2013 to summer 2016); 12 consecutive seasons.

Figure 3.4. 72

Illustration of the macrozoobenthic community groups in the two study areas of (A) Jinhae Bay (TG1–TG3) and (B) Samcheok coastal area (SG1–SG3), based on cluster analysis and non-metric multidimensional scaling (NMDS). NMDS provides information on the top four dominant species, including density and indicator values.

Figure 3.5. 76

Box-and-whisker plots (minimum, 25%, median, 75%, and maximum) for the three selected species each in the two study areas of (A) Jinhae Bay (Lumb, *Lumbrineris longifolia*; Dorv, *Dorvillea* sp.; Para, *Paraprionospio patiens*) and (B) Samcheok coastal area (Chon, *Chone infundibuliformis*; Mage, *Magelona johnstoni*; Euch, *Euchone analis*), with respect to parameters of species abundance (density), diversity index (H'), dissolved oxygen (DO), organic matter (OM), mean grain size (Mz), and depth.

Figure 3.6. 77

Box-and-whisker plots (minimum, 25%, median, 75%, maximum) for 20 dominant species with respect to organic matter, dissolved oxygen, and grain size in study area (Jinhae Bay and Samcheok coastal). The species are abbreviated as four-letter codes; Nico, *Nicomache minor*; Dorv, *Dorvillea* sp.; Arma, *Armandia lanceolata*; Para, *Paraprionospio patiens*; Capi, *Capitella capitata*; Theo, *Theora fragilis*; Coro, *Corophium* sp.; Siga, *Sigambra tentaculata*; Lumb, *Lumbrineris longifolia*; Prax, *Praxillella affinis*; Spio, *Spiophanes bombyx*; Chon, *Chone teres*; Euch, *Euchone analis*; Gam1, *Gammaridea* 1; Gam3, *Gammaridea* 3; Goni, *Goniada maculate*; Leit, *Leitoscoloplos pugettensis*; Mage, *Magelona johnstoni*; Chae, *Chaetozone setosa*.

Figure 3.7. 79

Principal component analysis of macrobenthos (including total species abundance, H' index, and density of dominant species) and 22 environmental variables, including parameters of water quality (refer to all the raw data in App. 1 of the Supplementary Materials) and sediment property (refer to all the raw data in App. 2 of the Supplementary Materials), for (A) Jinhae Bay and (B) Samcheok coastal area.

Figure 3.8.	83
Ordination of assemblage groups in the two-factor discriminant space, in (A) Jinhae Bay (TG1-TG3) and Samcheok coastal area (SG1-SG3). Vectors indicating the relative orientation of the environmental variables also given; determined from the correlation coefficients between the discriminant functions (DF1-DF2) and the environmental variables (gravel, mean grain size (Mz), organic matter (OM), dissolved oxygen (DO), and depth for Jinhae Bay; free Cl ₂ , gravel, and depth for Samcheok coastal area).	
Figure 3.9.	87
Spatiotemporal distribution of dominant species in Jinhae Bay.	
Figure 3.10.	88
Spatiotemporal distribution of dominant species in Samcheok coastal area.	
Figure 4.1.	99
Map showing the study area and stations and its surrounding environmental condition. (a) Stations located on Yellow and Bohai seas, in South Korea and East China. The city boundaries (white line) and rivers (blue line) were also given on the map. (b) Photographic information for each station with general information of environmental condition. (c) Sampling information.	
Figure 4.2.	100
Light micrographs of benthic diatoms in Yellow and Bohai seas. (a) <i>Gyrosigma</i> sp. 2; (b) <i>Paralia sulcata</i> ; (c) <i>Cyclotella</i> cf. <i>stylorum</i> ; (d) <i>Diploneis littoralis</i> ; (e) <i>Navicula flagellifera</i> ; (f) <i>Navicula</i> cf. <i>flagellifera</i> ; (g) <i>Navicula</i> sp. 14; (h) <i>Navicula</i> sp. 32; (i) <i>Biremis ambigua</i> ; (j) <i>Amphora</i> cf. <i>holsatica</i> ; (k) <i>Diploneis</i> cf. <i>littoralis</i>	
Figure 4.3.	101
Site and field survey view in the tidal flat of Yellow Sea.	
Figure 4.4.	108
Species diversity (H'), species evenness, relative abundance of diatoms on surface sediment (dataset I) with top 10 dominant taxa at (a) genus level and (b) species level, across 9 stations.	
Figure 4.5.	110
Species diversity (H'), species evenness, relative abundance of diatoms from sediment core samples (dataset II) with top 10 dominant taxa at (a) genus level and (b) species level, across 9 stations.	
Figure 4.6.	112
Illustration of the benthic diatom groups on the surface sediment in Yellow and Bohai seas at (a) genus level and (b) species level, based on cluster analysis and non-metric multidimensional scaling.	
Figure 4.7.	113
Illustration of the benthic diatom groups from sediment core in Yellow and Bohai seas at (a) genus level and (b) species level, based on cluster analysis and non-metric multidimensional scaling.	

- Figure 4.8.** 117
Principal component analysis (PCA) of abiotic parameters and biotic parameters (diatoms, other biotic parameters including meiofauna and macrofauna) based on dataset I at (a) genus level and (b) species level.
- Figure 4.9.** 118
Non-metric multidimensional scaling (NMDS) based on relative abundance of diatoms provides information on the concentrations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Indicator species were identified for two groups: high and low concentrations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.
- Figure 4.10** 121
Principal component analysis (PCA) of abiotic parameters and biotic parameters (diatoms, other biotic parameters including meiofauna and macrofauna) based on dataset I at (a) genus level and (b) species level.
- Figure 4.10.** 122
Non-metric multidimensional scaling (NMDS) based on relative abundance of diatoms provides information on the concentrations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.
- Figure 5.1.** 127
Overview of the study area, sampling locations, and benthic diatom community data; (a) Overview of glacier retreat in Marian Cove, West Antarctica, since 1989. Stations in the inner part of the cove are presented (B1, B2, M1, and M2). (b) Map showing sampling locations (intertidal zone: B1–B6; subtidal zone: M1–M4 at 10 and 30 m) surveyed in 2018–2019, with a summary of benthic community data; specifically, the number of species, relative abundance by salinity (marine, euryhaline, and freshwater), life-form (chain and solitary), and various substrates (cobble-mat, cobble-film, macroalgae, limpet shell, and sediment). Ecological type of diatom species in relation to salinity is provided in Table S8. The base map was obtained from Google Earth (<https://earth.google.com/web>) and Global USGS Visualization Viewer (<https://glovis.usgs.gov>).
- Figure 5.2.** 129
Map showing (a) the study area, (b) sampling locations (n = 10) with site views (B1–B6) and observed algal biomass. (c–d) sampling design was presented including information of substrate. The base maps were created in Adobe Illustrator CS6 based on the map of Google Earth (<https://earth.google.com/web/>).
- Figure 5.3.** 132
Light micrographs of centric diatoms in Marian Cove, Antarctica. (a–c) *Actinocyclus* sp. 1; (d–h) *Melosira* sp. 1 (scale bar = 10 μm).
- Figure 5.4.** 133
Light micrographs of centric diatoms in Marian Cove, Antarctica. (a) *Paralia* sp. 1; (b–g) *Cocconeis pinnata*; (h) *Cocconeis pinnata* var. *matsii*; (i–j) *Cocconeis melchiroides* (scale bar = 10 μm).

Figure 5.5. 134

Light micrographs of pennate diatoms in Marian Cove, Antarctica. (a–b) *Achnanthes* sp. 3; (c–f) *Achnanthes brevipes* var. *intermedia*; (g–h) *Brandinia mosimanniae*; (i–j) *Fragilaria striatula*; (k) *Halamphora* sp. 1; (l–m) *Navicula* sp. 5 (scale bar = 10 μm).

Figure 5.6. 135

Light micrographs of pennate diatoms in Marian Cove, Antarctica. (a) *Fragilariopsis curta*; (b) *Fragilaria islandica* var. *adeliae*; (c–e) *Tabulariopsis* cf. *australis*; (f–i) *Navicula* cf. *perminuta*; (j) *Navicula* cf. *directa*; (k) *Nitzschia* sp. 1; (l) *Pinnularia australomicrostauron*; (m) *Planothidium delicatulum*; (n) *Synedropsis recta*; (o–p) *Navicula glaciei*; (q–r) *Pteroncola carlinii*; (s–u) *Pseudogomphonema kamtschaticum* (scale bar = 10 μm).

Figure 5.7. 136

Scanning electron micrographs of benthic diatoms in Marian Cove, Antarctica. (a) *Melosira* sp. 1; (b) *Cocconeis pinnata*; (c–d) *Achnanthes brevipes* var. *intermedia*; (e) *Navicula* sp. 5; (f) *Halamphora* sp. 1 (scale bar = 10 μm).

Figure 5.8. 137

Scanning electron micrographs of benthic diatoms in Marian Cove, Antarctica. (a–b) *Brandinia mosimanniae*; (c–d) *Tabulariopsis* cf. *australis*; (e–f) *Fragilaria islandica* var. *adeliae* (scale bar = 10 μm).

Figure 5.9. 138

Scanning electron micrographs of benthic diatoms in Marian Cove, Antarctica. (a) *Fragilaria* cf. *striatula*; (b) *Licmophora gracilis*; (c) *Navicula* cf. *perminuta*; (d–e) *Navicula glaciei*; (f) *Pseudogomphonema kamtschaticum* (scale bar in a–b, and d–e = 10 μm , and in c = 2 μm).

Figure 5.10. 139

Field survey and laboratory analysis view in Marian Cove and King Sejong Station, Antarctica.

Figure 5.11. 149

Community structure of benthic diatoms in Marian Cove, West Antarctica; (a) Cluster analysis results showing the four groups of diatom assemblages. (b) The top three dominant species in the corresponding locations with site/substrate view and LM and SEM images.

Figure 5.12. 150

Four indicator species of each environment in Marian Cove, and the correlation between species and distance from the glacier; (a) Diagram of the study area with indicator diatom species (SEM images) along the cove and nMDS ordination plot based on relative abundance. (b) Correlation between top five dominant species in each intertidal and subtidal zone (Ncp, *Navicula* cf. *perminuta*; Fs, *Fragilaria striatula*; A3, *Achnanthes* sp. 3; N1, *Navicula glaciei*; Pk, *Pseudogomphonema kamtschaticum*; Nad, *Navicula directa*; Copi, *Cocconeis pinnata*) and distance from the glacier (Dis). *p*-values are given as numbers.

- Figure 5.13.** 158
Illustration of the groups of benthic diatom assemblages in Marian Cove, Antarctica, based on the NMDS (non-metric multidimensional scaling); five indicator species presented with corresponding indicator values and relative abundances (300 counts per sample).
- Figure 5.14.** 166
Mini-review on the ecological responses of marine benthic organisms affected by glacier retreat in Antarctica. Benthic community structure characterized in inner cove compared to outer cove in terms of % changes. % changes in diversity, abundance, and biomass of marine benthos between the inner (< 2.5 km to glacier) and outer (> 2.5 km) region; + indicates greater value in the inner region compared to outer one. Target marine organisms include diatoms, meiofauna, macroalgae, and a diversity of macrofauna.
- Figure 5.15.** 167
A schematic overview of the polar benthic community shift in an Antarctic cove under glacier retreat. This study and previous studies were simultaneously analyzed and incorporated to delineate a simplified feature with three stages: (1) early colonized community, (2) rapidly developed community, and (3) diversified and enriched community along with distance from the glacier.
- Figure 6.1.** 177
Response of benthic diatoms to extreme condition. Research summary and key findings of the present study are also provided.
- Figure 6.2.** 178
Research summary and key findings of the present study. Brown shaded background represents the diversity of benthic diatoms. Purple shaded background represents the diversity of macrozoobenthos.
- Figure 6.3.** 179
Research summary and key findings in the present study. Yellow to red gradient bar indicate gradients of each environmental variables. Gray-shaded backgrounds represent diversity of benthos. Indicator species also given.

CHAPTER 1.

INTRODUCTION

1.1. Backgrounds

Rothschild and Mancinelli published an article “life in extreme environments” in *Nature* in 2001. The first sentence of this article states that normal is passé, extreme is chic. Organisms inhabiting extreme environments have attracted the attention of both scientists and the public. Extreme environments are considered to have environmental parameters that permanently have values close to the lower or upper thresholds for life (CAREX 2011). Representative examples of extreme environments in nature include hydrothermal vents, soda lakes, volcanoes, and every planet beyond the earth.

In recent years, human activities have severe effects on marine ecosystems, with the level of impact increasing with our rapid population growth. Anthropogenic pressures threaten marine habitats globally (Halpern et al. 2008). Marine ecosystems are being significantly damaged and destroyed by human activities (Fig. 1.1.) (Waycott et al. 2009), with extreme marine environments being no exception. Reclamation, aquaculture, and pollution are directly affecting marine ecosystems. Such changes to habitats also generate new extreme conditions (i.e., hypersaline, hypoxic, polluted). In addition, climate change at a global scale is severely impacting marine ecosystems, inducing sea level rise, ocean acidification, and glacier retreat.

Consequently, many researchers have focused on investigating organisms inhabiting extreme environments. Over the last century, the boundary conditions under which life can thrive have been pushed in every possible direction, encompassing hypersaline and hypoxic environments, as well as high concentrations of toxic components. Yet, organisms continue to evolve to occupy all available environmental niches. Furthermore, organisms living in extreme environments have provided new insights into the process of succession, the origin of life, and the possibility of life existing on other planets (Fig. 1.2.) (Merino et al. 2019).

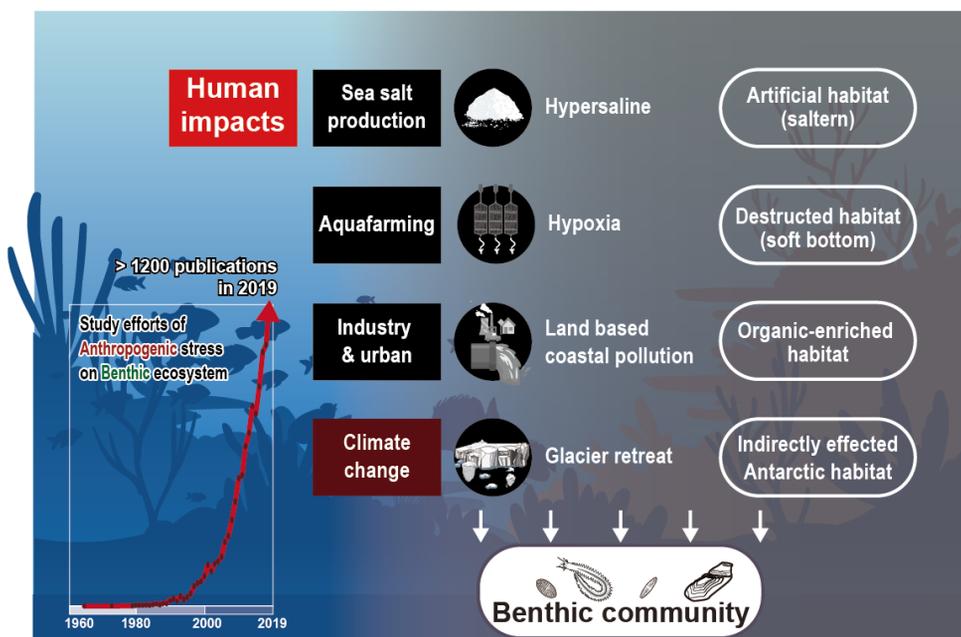


Figure 1.1. Illustration showing the benthic community in extreme environments under the human impacts.

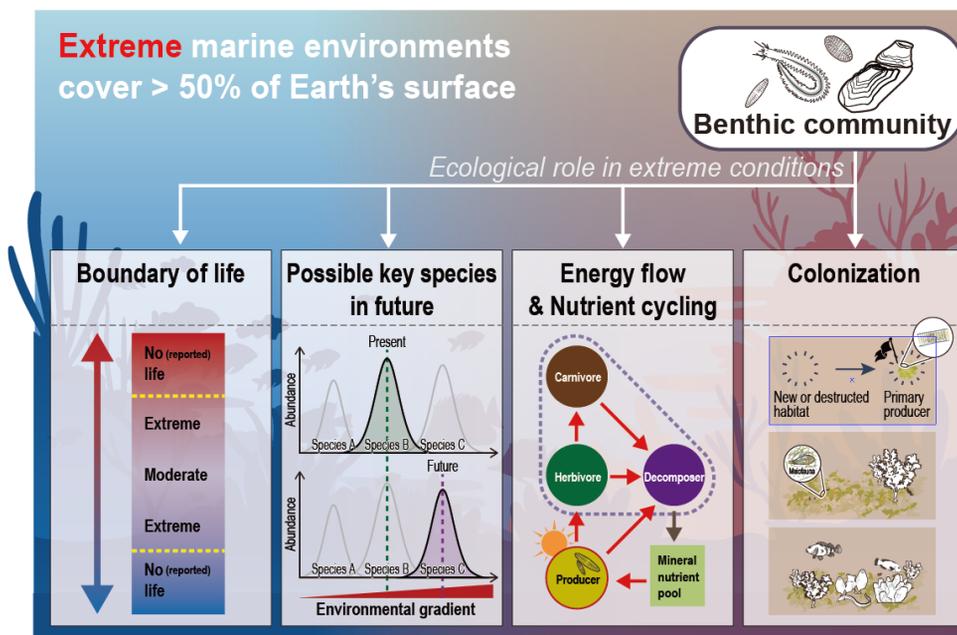


Figure 1.2.
Importance of benthos in extreme environments.

Diatoms are single-celled microscopic algae that are abundant in nearly all aquatic habitats, including extreme environments (Sabater 2009). Diatoms play key ecological roles in marine ecosystems, as major primary producers and prey for diverse heterotrophs. They also contribute to exportation of organic carbon from the surface water to the deep ocean (Treguer et al. 2018). Diatoms respond to various environmental and biological factors (i.e., salinity, dissolved oxygen, nutrient availability, grazing) by shifting their community structure and life forms (Sabater 2009). Macrozoobenthos encompass major taxonomic groups that largely contribute to various ecological processes, including nutrient cycling, carbon uptake, and oxygen consumption (Gray 1997; Glud 2008). Macrozoobenthos account for about 10–30 % of total community respiration in coastal sediments (Herman et al. 1999; Wijsman et al. 1999).

Aquatic species are often described depending on their salinity preferences and tolerances, especially in habitats with large fluctuations, such as estuaries, tidal pools, and salterns. Any change to ambient salinity has the potential to impact the ability of marine organisms to carry out vital biological processes and their ability to survive and thrive. Thus, salinity represents the most critical environmental factor in the marine ecosystem, including related environmental variables and aquatic communities. In particular, the dynamics of aquatic organisms in extreme hypersaline environments could help advance our understanding of how salinity impacts marine life.

Aquaculture is an important industry worldwide in socioeconomic aspects, but it is also a key anthropogenic factor contributing to water-column eutrophication and hypoxia. Macrozoobenthos could be seriously affected under extreme “hypoxic” conditions. Hypoxia means low oxygen conditions ($<2.0 \text{ mg L}^{-1}$), with hypoxic effects (deficiency) being well documented on marine organisms (Nilsson and Rosenberg 1994, Diaz and Rosenberg 1995, Levin and Gage 1998). Hypoxia has direct/indirect effects on the survival of organisms (Gray et al. 2002). Thus, it is important to monitor how aquatic communities fluctuate before and after hypoxia, from species to community levels.

Industrialization and urbanization generate anthropogenic pressure on the

marine environment, with mixed effects being detected from land-derived pollutants, especially in tidal flats. Pollutant emissions from organic matter of terrestrial origin are increasing, which could directly impact marine ecosystems. Terrestrial nitrogen pollutants cause major changes to the community composition of primary producers that form the basis of marine ecosystems (Kim et al. 2011). There are also reports that terrestrial nitrogen loads cause changes to chlorophyll concentrations (Lawrence et al. 2004b).

In recent decades, changes to marine ecosystems caused by global warming have received increasing attention. Adverse impacts on coastal and marine ecosystems due to such drastic changes to the climate are being repeatedly documented, particularly in vulnerable polar regions. Glacier retreat is a major long-standing global issue; however, the ecological impacts of such retreats on marine organisms remain unanswered. Kang et al. (2003) showed that benthic microalgae provide an important food source for planktonic and benthic herbivores when other food sources are scarce. However, despite their ecological importance in Antarctic coastal waters, benthic microalgae have received limited attention, especially in the intertidal zone. In addition, studies remain limited on shifts to primary producers in newly exposed benthic habitats.

Natural extreme environments already cover a significant portion of the natural ecosystem. However, in recent years, a number of marine environments have been rapidly and severely converted to extreme conditions due to human activities. Consequently, efforts to investigate anthropogenic stressors to benthic ecosystems have sharply increased since the 1990s (Fig.1.3).

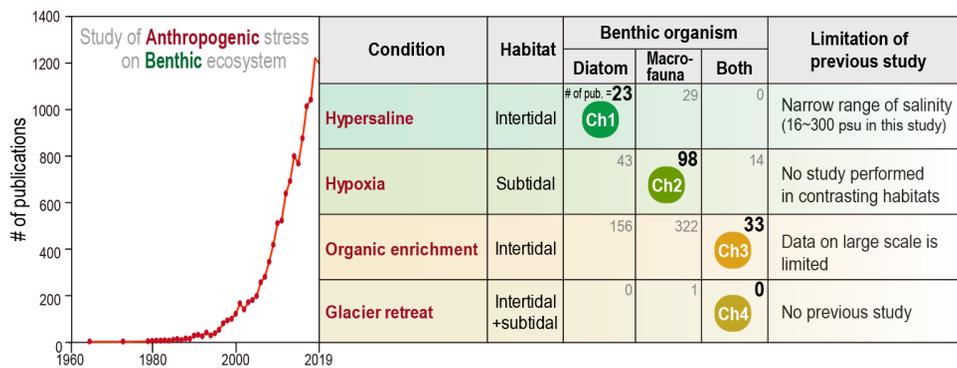


Figure 1.3.

Overview of study efforts on anthropogenic stresses to benthic ecosystem. Limitations of previous studies are also presented.

1.2. Objectives

The benthic community is more directly impacted by the extreme environments, and it reflects the surrounding environment intact. The community structure of benthic diatom and macrozoobenthos were investigated in various extreme environments to answer the following questions (Fig. 1.4.): 1) will the diversity be constant across increasing environmental gradient? 2) Which species would be tolerable in such environments? 3) what would be the adaptation process of benthos? Benthic community structures inhabiting various intertidal and subtidal habitats was examined to extreme environments through chapters 2 to 5 (Figure 1.5).

1. Chapter 2

Shift in benthic diatom community structure and salinity thresholds in a hypersaline environment of solar saltern, Korea

2. Chapter 3

Spatiotemporal variations in macrofaunal assemblages linked to site-specific environmental factors in two contrasting nearshore habitats

3. Chapter 4

Distribution and historical records of diatom assemblages in surface and sediment cores from the Yellow and Bohai seas under anthropogenic pressure

4. Chapter 5

Shift in polar benthic community structure in a fast retreating glacial area of Marian Cove, West Antarctica

Finally, Chapter 6 includes a summary of the thesis, environmental implications and limitations, and future research directions.

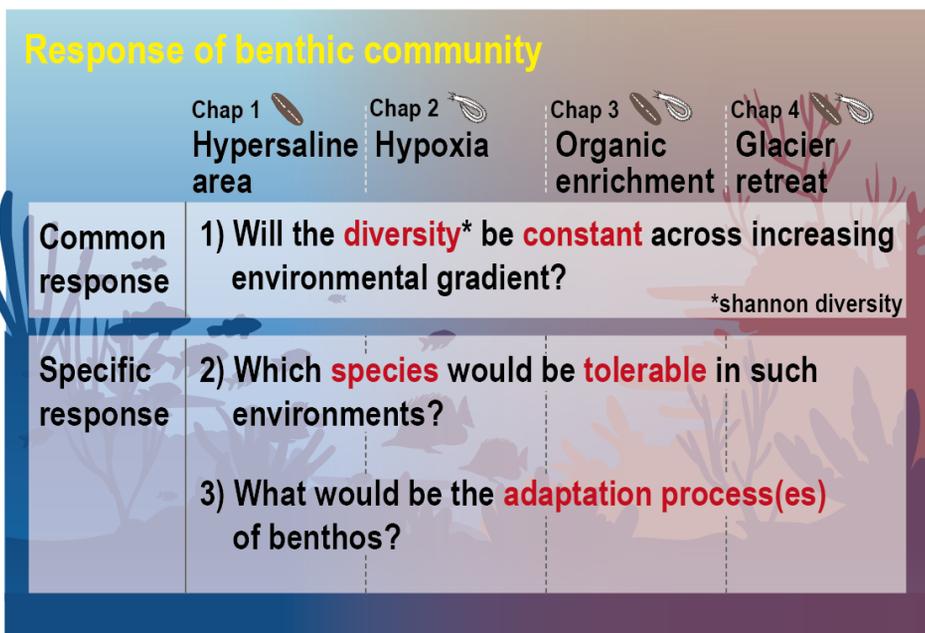


Figure 1.4.

Research questions of the study in terms of benthic community responses under extreme environments such as hypersaline areas, hypoxia, organic enrichment, and glacier retreat.

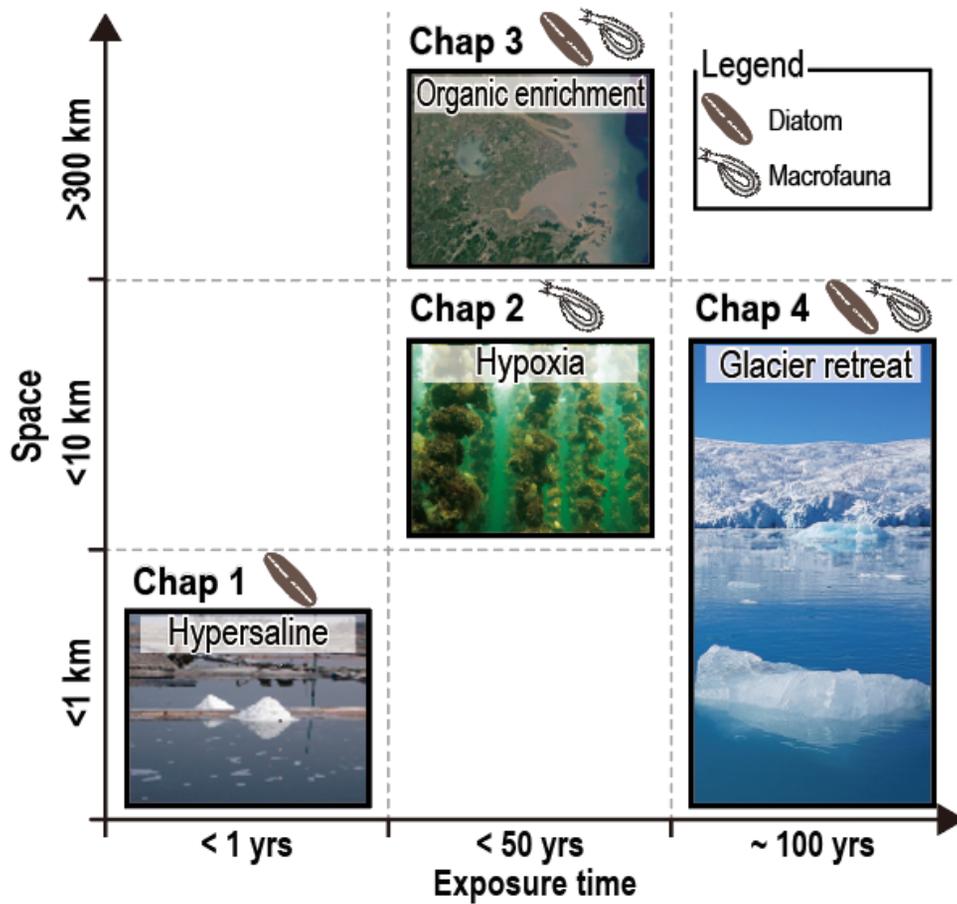


Figure 1.5.
Frame of the present study with respect to scale of disturbance.

CHAPTER 2.

Shift in benthic diatom community structure and salinity thresholds in a hypersaline environment of solar saltern, Korea

This chapter has been published in *Algae*

Bae, H., Park, J., Ahn, H., Khim, J.S. Shift in benthic diatom community structure and salinity thresholds in a hypersaline environment of solar saltern, Korea

2.1. Introduction

Salinity is one of the most significant environmental factors impacting the structure of aquatic communities (Lercari and Defeo 2006, Lozupone and Knight 2007, Choi et al. 2010). A substantial portion of the planet is of saline water, including marine environments (30–40 psu), hot springs (> 10.5 psu), and soda lakes (Merino et al. 2019). In particular, the extreme conditions of hypersaline environments serve as good models towards enhancing our understanding of both early stages of life on Earth and possibility of extraterrestrial life (Merino et al. 2019).

Microbial communities are predominated in such hypersaline environments; consequently, their ecology has attracted extensive scientific interests. Pedrós-Alió et al. (2000) reported that bacterivory and chlorophyll-*a* concentrations were maximal at salinity of ~ 100 psu and bacterivory disappeared above ~ 250 psu. Park et al. (2009) subsequently isolated two extremely halophilic flagellates from salt pools in Korea that had a salinity of > 300 psu.

Many studies have investigated aquatic microorganisms inhabiting high-saline environments; yet, numerous questions remain on ecology of benthic diatoms. Diatoms are crucial primary producers and important food sources for many aquatic lives in marine environments (Park et al. 2014). They are also one of the most diverse groups of extremophiles, being documented in almost every aquatic environment. Such ubiquity of diatoms is primarily attributable to their capability of producing bio-silica cell walls (Round et al. 1990). Diatom assemblages also exhibit high resistance to various other environmental stresses, such as pH (Dickman et al. 1984), temperature (Krebs et al. 1987), and UV (De Tommasi et al. 2018). Thus, their tolerance to poly-extreme environments means that they are anticipated to adapt to prospective environmental changes.

The earliest studies of diatoms in hypersaline environments mainly focused on describing new taxa (John 1991) and implementing culture-based experiments (Clavero et al. 2000, Yamamoto et al. 2017). Later, some studies have examined the structure of diatom communities in hypersaline environments, including tidal lagoon

(De Lomas et al. 2005) and lake and stream (Taukulis and John 2006). However, these studies are limited to examine specific salinity ranges and generally lacked in evidence of living diatoms in the given environments. Of note, simple detection and measurements of chloroplasts do not provide exact measures of diatom biomass. Furthermore, even the detection of frustules in samples does not mean that the diatom species were actually live, as their frustules tend to remain for up to several ten years (Sawai 2001).

While the diatom assemblages of various hypersaline environments have been explored, the solar salterns have been overlooked. Salterns are typically installed in coastal areas for salt production, which create a wide variety of artificial saline environments with increasing salt concentration from natural seawater to salt ponds. Thus, seawater is the initial source of sea salts in the salterns. As seawater evaporates in a series of salt ponds, saltern provides artificial salinity gradient (from brackish to > 300 psu), within a short walking distance (< 1 km). Although the densely developed biofilms of benthic diatoms are often found in solar salterns, the spatiotemporal dynamics linked to their survivals remain in question.

The present study aimed to investigate salterns to delineate the dynamics of benthic diatoms along the salinity gradient, particularly encompassing high salinity, up to > 300 psu. The specific objectives were to (1) understand the structure of benthic diatom assemblages at saltern environments across a wide range of salinity; (2) address the preference and/or tolerance of diatom species to different levels of salinity; and (3) identify indicator species for specific salinity ranges for use as ecosystem response predictors for hypersaline environments.

2.2. Materials and Methods

2.2.1. Study area

Salt production in solar salterns is based on consecutive concentrations of NaCl, along a series of shallow ponds where most water evaporates. In the final process, pure salt crystallizes out of the saturated brine solution. Therefore, the salinity of seawater in a saltern increases stepwise toward the end of the series of ponds.

The present study includes two datasets for investigation of the Korean saltern diatoms in 2005 (dataset I) and 2020 (dataset II). The first target saltern was surveyed at Muan (site A; n = 6) and the second survey was carried out at Sinan (site B; n = 7) (Fig. 2.1). Of note, it is unfortunate in that the access to Muan saltern was denied in 2020, thus temporal aspect could not be examined at present. The studied area is a major region for producing sea salt productions in Korea and the nearby marine environment generally represents the typical tidal flat system in the west coast of Korea. A considerable area of the former natural tidal flats has been reclaimed along the west coast to create artificial salterns as well as agricultural lands. The area of salterns in Muan and Sinan collectively reaches ~ 27 km² as of 2017.

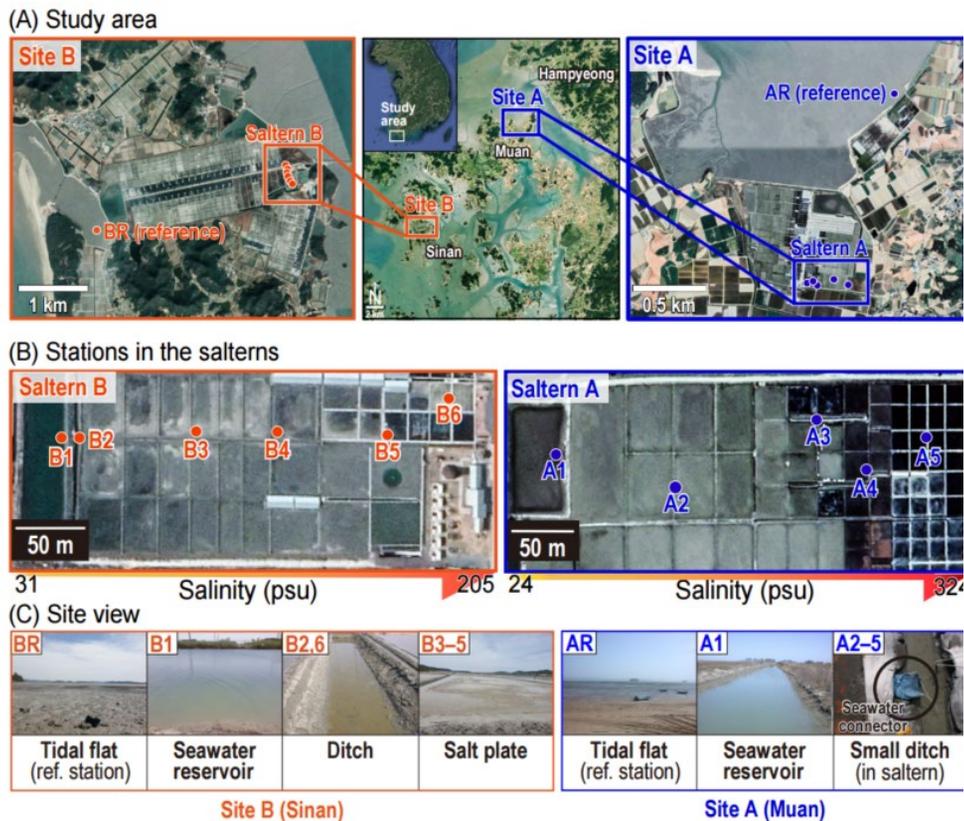


Figure 2.1.

Map showing the study area with an overview of the two salterns. (a) Site A located in Muan and Site B located in Sinan. Salinity increased from A1 to A5 (Site A) and from B1 to B6 (Site B). AR and BR located in the adjacent natural tidal flats refer to the reference stations. (b) Photographic information for the five habitat types (tidal flats, seawater reservoirs, small ditches, large ditches, and salt plates) of the Muan and Sinan salterns.

2.2.2. Sampling and laboratory analyses

A total of thirteen stations from two salterns were surveyed in Muan (site A) and Sinan (site B) in the present study (Fig. 2.1). The sampling was designed to encompass a wide range of salinity up to the highest measurable salinity of 324 psu (at site A). Of note, samples were collected from the adjacent tidal flats, viz., outside of the salterns which were considered to be the reference sites as well as the potential sources of diatoms to the salterns (Fig. 2.1A). For the details on each sampling point, refer to the notes provided in Table 2.1.

In brief, a saltern in Muan containing 61 salt pans with a wide salinity range of 32-324 psu was first investigated in 2005 (Fig. 2.1B). Samples were collected from five stations (A1–A5) including seawater reservoir and ditches in a saltern and one from outside tidal flat (AR). The top 0.5 cm of surface sediment was collected for the analysis of diatom assemblages. Light microscope (BX53; Olympus, Tokyo, Japan) and scanning electron microscope (MIRA3; Tescan, Seoul, Korea) were used to obtain photographic documentation of diatoms and/or to perform species identification. Diatoms were identified to the species level when possible. Microscopic photographs of the dominant species found in this study were presented in Fig. 2.2.

In 2020, the other saltern in Sinan, with 38 salt pans and salinity range of 31–205 psu, has been investigated (Fig. 2.1B). Six stations (B1–B6) encompassing seawater reservoir, ditches, and salt ponds were surveyed. Samples were also collected from the nearby tidal flat (BR) as reference site (Fig. 2.3). The environmental parameters potentially impacting diatom assemblages were extensively examined at this time to better understand the environmental conditions linked to the benthic diatom community structure. In this regard, more elaborated sampling efforts are given to measure and analyze several environmental parameters in situ and in the laboratory.

First, surface sediments (< 3 cm) were sampled to analyze general sediment properties such as water content, mud content (MC), and total organic content. In addition, sediment chlorophylls were measured as a proxy for the biomass of benthic

diatoms. Second, stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were measured for sediment, particulate organic matter, and diatoms. Stable isotopes were measured using an Elemental Analyzer–Isotope Ratio Mass Spectrometer (EA-IRMS; Elementar, GmbH, Hanau, Germany). Third, seawater parameters were measured in situ using multi-parameter water quality probe (YSI-Professional Plus; Ohio, OH, USA). They included temperature ($^{\circ}\text{C}$), dissolved oxygen (DO ; mg L^{-1}), salinity (psu), and pH. The concentrations of nutrients including total nitrogen (TN; mg L^{-1}), $\text{PO}_4\text{-P}$ (mg L^{-1}), and SiO_2 (mg L^{-1}) from filtered seawaters were also measured, using an auto nutrient analyzer (QuAatro39; Seal Analytical, Norderstedt, Germany), in the laboratory.

Table 2.1. Information of sampling areas and environmental data at 13 stations in the two salterns.

	ID	Salinity	Latitude	Longitude	Type	TN (mg L ⁻¹)	PO₄-P (mg L ⁻¹)	SiO₂ (mg L ⁻¹)	Note
Dataset I (2005)	AR	24	35° 8'2.28"N	126°19'32.56"E	Tidal flat		Not available		Under freshwater influence from small creek; reference
	A1	32	35° 7'19.79"N	126°19'17.34"E	Saltern				Seawater reservoir
	A2	36	35° 7'19.10"N	126°19'15.33"E	Saltern				Small ditch: microalgal patch was observed
	A3	74	35° 7'18.21"N	126°19'9.63"E	Saltern				Small ditch between salt plate
	A4	174	35° 7'18.69"N	126°19'7.25"E	Saltern				Small ditch between salt plate
	A5	324	35° 7'18.86"N	126°19'6.18"E	Saltern				Small ditch between salt plate
Dataset II (2020)	BR	35	34°59'15.70"N	126° 8'41.98"E	Tidal flat	2.60	0.02	^a n.d.	Muddy sand tidal flat; reference
	B1	31	34°59'36.96"N	126°10'21.92"E	Saltern	3.05	0.02	n.d.	Seawater reservoir
	B2	37	34°59'37.25"N	126°10'21.99"E	Saltern	1.95	0.02	n.d.	Large ditch
	B3	47	34°59'39.72"N	126°10'21.19"E	Saltern	5.65	0.02	0.04	Salt plate: microalgal patch was observed
	B4	65	34°59'41.47"N	126°10'20.84"E	Saltern	6.05	0.02	0.04	Salt plate: microalgal patch was observed
	B5	165	34°59'43.89"N	126°10'20.25"E	Saltern	7.45	0.02	0.13	Salt plate: sediment on PVC mat
	B6	205	34°59'45.06"N	126°10'18.83"E	Saltern	23.80	0.03	0.24	Small ditch between salt plate: thick patch

^a not detected

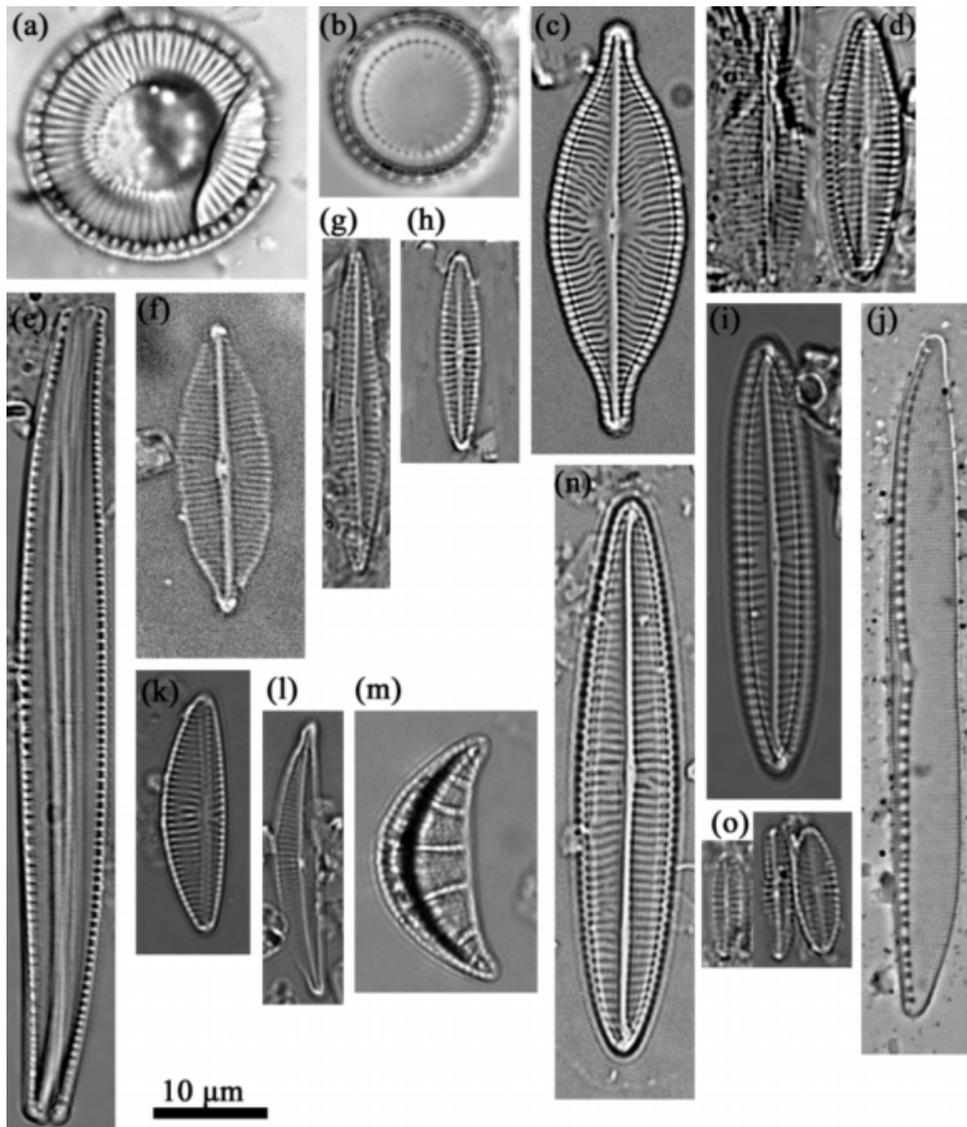


Figure 2.2.

Light micrographs of dominant diatoms in two salterns. Salinity (psu) of the station where each species was most abundant was given in parenthesis. (a) *Cyclotella littoralis* (31); (b) *Paralia sulcata* (31); (c) *Navicula salinarum* (24); (d) *Navicula* sp. 1 (174); (e) *Nitzschia* cf. *sigma* (37); (f) *Navicula gregaria* (24); (g) *Navicula* cf. *erifuga* (31); (h) *Navicula* sp. 4 (165); (i) *Navicula* cf. *arenaria* (65); (j) *Nitzschia scalpelliformis* (74); (k) *Seminavis* sp. 4 (36); (l) *Amphora* cf. *boliviana* (174); (m) *Rhopaldia rumrichiae* (32); (n) *Navicula pavillardii* (24); (o) *Achnanthes* sp. 1 (205).



Figure 2.3.
Site view in the saltern and tidal flat

2.2.3. Data analyses

The relative abundance of each taxon was calculated through counting diatom valves (ca. 500 valves per station for site A and ca. 300 per station for site B) under the light microscope. Cluster analysis (CA) and non-metric multidimensional scaling were then carried out on the resulting matrix. Species with less than 1% of total abundance to diatom assemblages in the two salterns were excluded from the analyses. Bray-Curtis similarity coefficients were calculated, and the data were subjected to group average sorting. Abundance was fourth root-transformed to balance it across the recorded taxa for measures of similarity. The analysis of similarities (ANOSIM) test was performed to confirm that these groups differed significantly. Similarity percentages (SIMPER) analysis was performed to identify the taxa responsible for differences between groups. Biota-environment (BIOENV) procedure was used to determine the factors determining the structure of diatom assemblages.

Permutational multivariate analysis of variance (PERMANOVA) was performed to assess the significance of variables across sites and salinities, in terms of species diversity and composition of benthic diatoms. PRIMER 6 statistical software was used to perform all analyses (Clarke and Gorley 2006).

Indicator value (IndVal) analysis (Dufrêne and Legendre 1997) was performed to identify indicator diatom species for specific ranges in the salinity groups: brackish (< 30 psu), saline (30–40 psu), hypersaline I (40–80 psu), and hypersaline II (> 100 psu).

The IndVal index was calculated using Eq. (1):

$$\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100 \quad (1)$$

where A_{ij} is specificity (i.e., proportion of individuals of species i in class j) and B_{ij} is fidelity (i.e., proportion of sites in class j that included species i). The maximum value (max = 100%) provided by the IndVal procedure indicates a perfect indicator when all specimens of a species are found in a single group of samples and

when the species occurs in all samples of that group. For each species, the highest value was considered as the indicator value. The indicator value was calculated as follows, using Eq. (2):

$$\text{IndVal}_i = \max [\text{IndVal}_{ij}] \quad (2)$$

The index was maximal (max = 1) when individuals of species *i* were detected at all sites belonging to a single group. IndVal analysis, principal component analysis (PCA), and a Pearson correlation analysis were performed using R Studio version 1.0.153 software (<http://www.rstudio.com>).

2.3. Results

2.3.1. Environmental settings

Fourteen environmental parameters for general qualities of seawater and sediments were measured in the study area (Table 2.2). The reference station of AR surveyed in 2005 showed the lowest salinity (24 psu), which is lower than the typical salinity range of the Yellow Sea (30–33 psu). This is because of a freshwater influence from a small upper creek in site A. Another reference station of BR surveyed in 2020 had relatively high salinity (~34 psu), similar to the normal seawater salinity. Salinity showed a clear gradient from the seawater reservoir to the end of the saltern at both surveyed salterns of site A (24–324 psu) and B (31–205 psu) (Table 2.2, Fig. 2.1). Of note, MC (%) in BR differed from those in the other sampling stations (B1-B6) situated within the saltern. Presumably finer sediments are more easily resuspended and transferred to the reservoir during the seawater intake (Fig. 2.1C).

DO was lower when salinity was higher. At a series of salt ponds with high salinity range of 165–205 psu, hypoxic conditions ($1.26\text{--}2.20\text{ mg O}_2\text{ L}^{-1}$) were evidenced. As seawater evaporated and concentrated along the series of ponds, nutrient concentrations tended to increase (except $\text{NO}_2\text{-N}$). It should be also noteworthy that sediment chlorophylls tended to keep increasing towards higher salinities, indicating potential contribution of bacterial biomass (or production) in addition to the benthic diatoms at the saltern. In anyhow, environmental data measured in the present study broadly supported dynamic abiotic conditions at hypersaline environments (Table 2.2).

Table 2.2. Data on the environmental variables and diatom assemblages measured in the samples from the two saltern sites.

	Site A						Site B						Mean±SD	
	AR	A1	A2	A3	A4	A5	BR	B1	B2	B3	B4	B5		B6
Salinity	24	32	36	74	174	324	35	31	37	47	65	165	205	
Seawater qualities														
Temperature (°C)							21.40	26.50	24.00	25.62	22.76	26.46	25.37	24.59±1.94
DO (mg L ⁻¹)							7.05	6.50	6.10	5.00	5.23	2.20	1.26	4.76±2.20
pH							6.47	6.87	7.30	6.80	7.24	6.01	6.18	6.70±0.50
NH ₄ -N (mg L ⁻¹)							0.08	0.09	0.07	0.14	0.15	0.17	0.46	0.17±0.14
NO ₂ -N (mg L ⁻¹)							0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02±0.01
NO ₃ -N (mg L ⁻¹)							0.03	0.03	0.02	0.03	0.03	0.04	0.08	0.04±0.02
TN (mg L ⁻¹)				not available			2.60	3.05	1.95	5.65	6.05	7.45	23.80	7.22±7.59
PO ₄ -P (mg L ⁻¹)							0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.02±0.01
SiO ₂ (mg L ⁻¹)							n.d. ^a	n.d.	n.d.	0.04	0.04	0.13	0.24	0.11±0.10
Sediment properties														
Water contents (%)							33.97	32.94	36.41	34.18	31.03	32.05	39.34	34.27±2.82
Mud contents (%)							65.48	99.20	98.57	99.41	99.38	96.37	95.01	93.35±12.40
Total organic content (%)							0.37	0.87	0.63	0.69	0.70	1.11	2.76	1.02±0.80
Chl- <i>a</i> (mg m ⁻²)							28.10	0.71	2.19	4.20	7.77	16.67	39.72	14.19±14.82
Diatom assemblages														
Number of species	61	64	34	24	33	0	89	62	45	34	37	28	24	169 ^b
Dominant species														
1 st <i>Nitzschia scalpelliformis</i>	0	0.2	6	66.8	16.4	0	0.1	0.4	2.8	39.1	30.1	3.9	1.3	12.9±20.6
2 nd <i>Navicula cf. arenaria</i>	0.4	6.8	7.2	0.4	0.2	0	7.7	27.0	30.1	33.7	39.4	1.3	0.2	11.9±14.9
3 rd <i>Achnanthes</i> sp. 1	0	0	0	0	0	0	2.3	1.4	0.7	0.2	0.1	49.4	73.2	9.8±23.4
4 th <i>Navicula gregaria</i>	54.4	0.4	1	0.2	28.8	0	0.7	0.7	0	0	0.1	0	0	6.6±16.4
5 th <i>Navicula</i> sp. 4	0.8	4.6	9.6	0.2	5.2	0	5.9	7.0	1.0	3.2	2.1	25.4	13.1	6.0±7.0

^a n.d.: not detected, ^b total number of species

2.3.2. Distribution of benthic diatom assemblages

A total of 169 diatom taxa were identified across the 13 sampling stations in the present study. Viability of diatom assemblages was also confirmed with observation of live diatom cells. A total of 104 species were documented (mean = 43) at site A, and 132 species (mean = 45) at site B. List of all diatom species found and identified in the two salterns with relative abundance data is provided in Table 2.3.

Species diversity (H') and evenness decreased with increase of salinity (Fig. 2.2a, Table 2.4). The highest number of diatom species was recorded at BR (89 species), and the lowest species diversity was observed at stations A3 and B6 (both 24 species). No diatoms were found at station A5, at which salinity was recorded highest (324 psu). Decreasing species evenness indicated that few species dominated the hypersaline environments. Diatom assemblages in water with higher salinity had the larger disparity in abundance within each species. For example, *Nitzschia scalpelliformis* had 66.8% of total abundance at station A3, while *Achnanthes* sp. 1 had 73.2% abundance at station B6.

N. scalpelliformis was the most dominant species, representing 13.9% of all counted individuals. The next most dominant diatom species were *Navicula* cf. *arenaria* (12.9%), *Achnanthes* sp. 1 (10.6%), *Navicula gregaria* (7.19%), and *Navicula* sp. 4 (6.52%) in order. In general, diatom assemblages varied considerably with respect to site- and station- (primarily salinity) specific distributions. As a site-specific example, *Achnanthes* sp. 1 was the most abundant species at site B (fourth most abundant species in the total study area); however, no individuals were found at site A. Regarding the salinity gradient, *Achnanthes* sp. 1 showed the lowest abundance at a salinity of < 65 psu; however, its abundance sharply increased in the last part of the series of ponds (> 165 psu) at site B.

Table 2.3. List of benthic diatoms found in the two salterns, given in descending order of relative abundance (%) to total.

Species	Total (%)	Site A							Site B						Sub-total	
		AR	A1	A2	A3	A4	A5	Sub-total	BR	B1	B2	B3	B4	B5		B6
<i>Nitzschia scalpelliformis</i>	13.9	-	0.20	6.00	66.8	16.4	-	17.8	0.11	0.44	2.78	39.1	3.11	3.89	1.33	11.1
<i>Navicula cf. arenaria</i>	12.9	0.40	6.80	7.20	0.40	0.20	-	3.00	7.67	27.0	3.11	33.7	39.4	1.33	0.22	19.9
<i>Achnanthes</i> sp. 1	10.6	-	-	-	-	-	-	0.00	2.33	1.44	0.67	0.22	0.11	49.4	73.2	18.2
<i>Navicula gregaria</i>	7.19	54.4	0.40	1.00	0.20	28.	-	16.9	0.67	0.67			0.11			0.20
<i>Navicula</i> sp. 4	6.52	0.80	4.60	9.60	0.20	5.20	-	4.08	5.89	7.00	1.00	3.22	2.11	25.4	13.1	8.25
<i>Paralia sulcata</i>	4.38	8.00	3.40	0.80	0.80	3.60	-	3.32	19.6	6.78	2.56	1.11	4.56	0.22	1.11	5.13
<i>Seminavis</i> sp. 4	4.32	-	0.40	40.8	4.60	1.00	-	9.36	0.89		2.44	0.56	0.89	0.22		0.71
<i>Navicula cf. erifuga</i>	2.53	-	-	0.40	-	0.80	-	0.24	1.89	10.2	6.00	1.78	4.44	4.56	0.22	4.16
<i>Amphora cf. boliviana</i>	2.24	0.20	-	3.80	4.80	16.8	-	5.12	0.33	-	0.11	-	0.33	0.33	0.11	0.17
<i>Nitzschia cf. sigma</i>	2.19	-	0.40	-	2.40	-	-	0.56	0.11	-	21.2	2.11	-	-	-	3.35
<i>Tryblionella cf. aerophila</i>	1.88	0.20	17.2	-	-	4.20	-	4.32	0.89	0.11	-	-	-	-	-	0.14
<i>Navicula</i> sp. 1	1.85	-	-	2.60	3.20	11.0	-	3.36	0.33	-	-		-	3.00	2.00	0.76
<i>Cyclotella litoralis</i>	1.68	0.20	1.80	1.60	0.20	0.40	-	0.84	3.56	3.89	3.22	0.67	2.22	1.11	1.33	2.29
<i>Navicula cf. spartinetensis</i>	1.32	-	-	-	-	-	-	0.00	2.78	3.44	2.44	1.22	4.78	0.44	0.67	2.25
<i>Navicula cf. flantica</i>	1.26	1.20	-	-	-	-	-	0.24	0.67	11.3	0.44	0.44	0.67	0.33	-	1.98
<i>Navicula cf. pavillardii</i>	1.16	6.80	-	0.20	-	0.20	-	1.44	1.78	0.67	3.00	0.44	0.78	-	-	0.95
<i>Rhopalodia rumrichiae</i>	1.05	-	9.80	-	1.40		-	2.24	-	-	-	1.33	-	-	-	0.19
<i>Rhopalodia</i> sp. 3	1.01	-	0.60	-	7.40	0.80	-	1.76	-	-	0.78	1.56	1.00	-	-	0.48
<i>Nitzschia hungarica</i>	0.95	1.00	10.4	-	-	-	-	2.28	-	-	-	-	-	-	-	0.00
<i>Nitzschia sigma</i>	0.75	-	2.00	0.20	0.40	0.40	-	0.60	0.22	1.33	2.78	0.33	0.56	0.78	-	0.86
<i>Navicula cf. salinarum</i>	0.75	4.60	0.40	2.00	0.60	1.40	-	1.80	-	-	-	-	-	-	-	0.00
<i>Thalassionema nitzschioides</i>	0.74	0.80	0.20	-	-	0.60	-	0.32	4.44	1.00	1.11	-	0.56	0.11	-	1.03

Table 2.3. (Continued)

Species	Total (%)	Site A							Site B							
		AR	A1	A2	A3	A4	A5	Sub-total	BR	B1	B2	B3	B4	B5	B6	Sub-total
<i>Rhopalodia</i> sp. 1	0.70	-	-	6.00	2.40	-	-	1.68	-	-	-	-	-	-	-	0.00
<i>Entomoneis alata</i>	0.66	0.20	-	1.20	-	-	-	0.28	1.11	1.44	3.44	0.33	0.22	-	-	0.94
<i>Nitzschia</i> sp. 9	0.64	-	-	-	-	-	-	0.00	6.78	0.22	0.33	0.11	-	-	0.22	1.10
<i>Navicula</i> sp. 12	0.53	-	1.20	1.80	-	1.60	-	0.92	-	0.89	0.11	0.11	0.11	0.11	0.44	0.25
<i>Tryblionella acuminata</i>	0.52	0.40	5.80	-	-	-	-	1.24	-	-	-	-	-	-	-	0.00
<i>Mastogloia pumila</i>	0.52	-	3.20	2.00	0.60	0.40	-	1.24	-	-	-	-	-	-	-	0.00
<i>Nitzschia</i> sp. 6	0.49	-	-	-	-	-	-	0.00	-	-	5.56	0.33	-	-	-	0.84
<i>Navicula</i> cf. <i>microcari</i>	0.48	0.80	2.00	2.80	0.20	-	-	1.16	-	-	-	-	-	-	-	0.00
<i>Amphora acutiuscula</i>	0.39	1.00	-	0.80	-	-	-	0.36	2.33	0.11	-	-	-	0.44	-	0.41
<i>Navicula</i> cf. <i>microdigitoradiata</i>	0.37	-	-	-	-	-	-	0.00	-	1.22	-	1.67	1.56	-	-	0.63
<i>Seminavis</i> sp. 2	0.35	-	-	-	-	-	-	0.00	0.33	-	0.56	2.67	-	0.22	0.44	0.60
<i>Actinoptychus senarius</i>	0.35	0.40	0.20	1.40	0.20	0.40	-	0.52	1.33	-	-	-	0.22	-	-	0.22
<i>Navicula</i> sp. 6	0.34	1.00	0.20	2.00	-	-	-	0.64	0.22	0.33	0.22	-	0.11	-	-	0.13
<i>Navicula</i> sp. 16	0.33	0.20	-	-	-	0.20	-	0.08	-	-	-	2.33	1.22	-	-	0.51
<i>Rhopalodia</i> sp. 2	0.32	-	2.60	0.40	-	-	-	0.60	-	0.11	0.44	0.33	-	-	-	0.13
<i>Nitzschia</i> cf. <i>scalpelliformis</i>	0.32	-	-	-	-	-	-	0.00	0.44	2.67	0.67	-	-	-	-	0.54
<i>Navicula</i> cf. <i>salinicola</i>	0.31	-	0.80	0.20	0.20	-	-	0.24	1.22	1.00	-	-	0.33	-	-	0.37
<i>Thalassiosira minima</i>	0.30	-	1.80	-	-	-	-	0.36	1.78	-	-	-	-	-	-	0.25
<i>Navicula salinicola</i>	0.30	0.40	1.20	-	-	0.20	-	0.36	-	0.22	0.22	-	0.11	0.56	0.67	0.25
<i>Amphora</i> sp. 2	0.29	0.20	0.80	0.20	-	1.00	-	0.44	0.44	0.89	-	-	-	-	-	0.19
<i>Navicula mediocostata</i>	0.28	0.60	0.40	2.00	-	0.20	-	0.64	-	-	-	-	0.11	-	-	0.02

Table 2.3. (Continued)

Species	Total (%)	Site A							Site B							
		AR	A1	A2	A3	A4	A5	Sub-total	BR	B1	B2	B3	B4	B5	B6	Sub-total
<i>Cyclotella choctawhatcheeana</i>	0.26	0.20	-	-	-	0.40	-	0.12	2.00	-	0.11	-	0.22	0.22	-	0.37
<i>Nitzschia compressa</i>	0.24		0.80	1.00	-	-	-	0.36	-	-	0.44	0.56	-	-	0.11	0.16
<i>Nitzschia</i> sp. 1	0.24	0.60	0.40	-	-	-	-	0.20	-	0.11	-	-	-	1.67	0.11	0.27
<i>Nitzschia pararostrata</i>	0.22	-	-	-	-	-	-	0.00	2.22	0.44	-	-	-	-	-	0.38
<i>Cocconeis scutellum</i>	0.22	-	0.20	0.20	-	-	-	0.08	0.67	1.56	-	-	-	-	-	0.32
<i>Gyrosigma obliquum</i>	0.21	-	-	-	-	-	-	0.00	0.89	-	1.33	0.33	-	-	-	0.37
<i>Navicula</i> cf. <i>abscondita</i>	0.20	1.00	1.40	-	-	-	-	0.48	-	-	-	-	-	-	-	0.00
<i>Tryblionella granulata</i>	0.20	0.40	1.40	-	-	-	-	0.36	0.33	0.22	-	-	-	-	-	0.08
<i>Rhaphoneis rhomboides</i>	0.19	0.40	-	-	-	0.60	-	0.20	1.11	-	-	-	0.22	-	-	0.19
<i>Gyrosigma procerum</i>	0.19	0.60	0.40	-	-	0.20	-	0.24	0.11	0.89	-	-	0.11	-	-	0.16
<i>Navicula groschopfii</i>	0.19	0.20	0.40	-	-	-	-	0.12	1.44	0.11	-	-	0.11	-	-	0.24
<i>Navicula</i> sp. 3	0.18	0.40	0.40	-	0.40	0.20	-	0.28	0.22	0.33	-	-	-	0.22	-	0.11
<i>Navicula</i> sp. 13	0.18	-	-	0.20	0.40	-	-	0.12	-	-	-	1.44	0.11	-	-	0.22
<i>Amphora</i> sp. 4	0.18	-	1.00	-	-	-	-	0.20	0.22	0.89	-	-	-	-	-	0.16
<i>Diploneis</i> sp. 1	0.18	-	-	-	-	-	-	0.00	0.33	0.33	0.33	-	-	-	1.11	0.30
<i>Giffenia cocconeiformis</i>	0.17	-	0.60	0.20	-	-	-	0.16	0.67	0.33	0.11	-	0.11	-	-	0.17
<i>Navicula</i> sp. 7	0.17	1.60	0.20	-	-	-	-	0.36	0.22	-	-	-	-	-	-	0.03
<i>Nitzschia guineensis</i>	0.17	-	-	-	-	-	-	0.00	0.44	0.78	0.78	-	-	-	-	0.29
<i>Navicula</i> sp. 17	0.17	-	-	-	-	-	-	0.00	-	0.11	0.22	-	1.56	-	0.11	0.29
<i>Nitzschia</i> sp. 4	0.17	-	-	-	-	-	-	0.00	-	-	-	-	-	-	2.00	0.29
<i>Amphora</i> sp. 3	0.16	0.20	1.20	0.40	-	-	-	0.36	0.11	-	-	-	-	-	-	0.02
<i>Thalassiosira</i> cf. <i>tenera</i>	0.16	-	-	-	-	-	-	0.00	1.89	-	-	-	-	-	-	0.27

Table 2.3. (Continued)

Species	Total (%)	Site A							Site B							
		AR	A1	A2	A3	A4	A5	Sub-total	BR	B1	B2	B3	B4	B5	B6	Sub-total
<i>Amphora</i> sp. 1	0.15	-	0.40	-	-	-	-	0.08	0.44	-	-	-	-	0.44	0.56	0.21
<i>Rhopalodia gibba</i>	0.15	-	-	-	1.80	-	-	0.36	-	-	-	-	-	-	-	0.00
<i>Nitzschia constricta</i>	0.15	-	-	-	-	-	-	0.00	-	-	-	-	0.11	1.33	0.33	0.25
<i>Amphora richardiana</i>	0.15	1.00	0.20	-	-	-	-	0.24	0.44	-	-	-	-	-	0.11	0.08
<i>Amphora</i> sp. 5	0.14	-	1.40	-	-	-	-	0.28	-	-	0.22	-	-	-	-	0.03
<i>Actinocyclus normanii</i>	0.13	0.60	-	-	-	-	-	0.12	1.00	-	-	-	-	-	-	0.14
<i>Gyrosigma fasciola</i>	0.13	-	0.60	-	-	-	-	0.12	-	0.78	0.22	-	-	-	-	0.14
<i>Navicula phylleptosoma</i>	0.13	1.00	0.60	-	-	-	-	0.32	-	-	-	-	-	-	-	0.00
<i>Achnanthes brevipes</i>	0.13	-	1.00	-	-	0.60	-	0.32	-	-	-	-	-	-	-	0.00
<i>Parlibellus</i> sp. 2	0.13	0.20	1.40	-	-	-	-	0.32	-	-	-	-	-	-	-	0.00
<i>Nitzschia lanceolata</i>	0.13	-	-	-	-	-	-	0.00	0.67	0.11	-	-	-	0.56	0.22	0.22
<i>Nitzschia</i> sp. 5	0.12	-	0.40	-	-	-	-	0.08	0.44	0.11	0.44	-	-	-	-	0.14
<i>Pleurosigma delicatulum</i>	0.12	-	0.40	-	-	-	-	0.08	0.33	-	0.67	-	-	-	-	0.14
<i>Tryblioptychus cocconeiformis</i>	0.11	0.60	-	-	-	-	-	0.12	0.78	-	-	-	-	-	-	0.11
<i>Climaconeis mabikii</i>	0.10	-	-	-	-	-	-	0.00	0.78	0.44	-	-	-	-	-	0.17
<i>Nitzschia coarctata</i>	0.10	-	-	-	-	-	-	0.00	0.56	0.67	-	-	-	-	-	0.17
<i>Nitzschia</i> cf. <i>erifuga</i>	0.10	-	-	-	-	-	-	0.00	-	-	-	-	-	1.22	-	0.17
<i>Navicula tripuncata</i>	0.10	0.40	-	-	-	0.80	-	0.24	-	-	-	-	-	-	-	0.00
<i>Entomoneis</i> sp. 1	0.09	-	-	-	-	-	-	0.00	-	-	1.11	-	-	-	-	0.16
<i>Staurophora salina</i>	0.09	1.00	-	-	-	-	-	0.20	-	-	0.11	-	-	-	-	0.02
<i>Thalassiosira eccentrica</i>	0.08	0.20	0.40	-	-	0.40	-	0.20	-	-	-	-	-	-	-	0.00
<i>Surirella</i> cf. <i>brebissonii</i>	0.08	0.20	0.80	-	-	-	-	0.20	-	-	-	-	-	-	-	0.00

Table 2.3. (Continued)

Species	Total (%)	Site A							Site B							
		AR	A1	A2	A3	A4	A5	Sub-total	BR	B1	B2	B3	B4	B5	B6	Sub-total
<i>Diploneis</i> cf. <i>smithii</i>	0.08	-	-	-	-	-	-	0.00	0.56	0.44	-	-	-	-	-	0.14
<i>Nitzschia</i> <i>epithemioides</i>	0.08	-	-	-	-	-	-	0.00	-	-	-	-	-	0.78	0.22	0.14
<i>Delphineis</i> <i>surirella</i>	0.08	0.20	-	-	-	-	-	0.04	0.78	-	-	-	-	-	-	0.11
<i>Frustulia</i> <i>vulgaris</i> var. <i>elliptica</i>	0.08	0.20	-	0.20	-	-	-	0.08	0.56	-	-	-	-	-	-	0.08
<i>Navicula</i> sp. 8	0.07	-	-	-	-	-	-	0.00	-	0.89	-	-	-	-	-	0.13
<i>Navicula</i> sp. 11	0.07	-	-	-	-	-	-	0.00	-	0.89	-	-	-	-	-	0.13
<i>Navicula</i> sp. 9	0.07	-	-	-	-	-	-	0.00	0.22	0.67	-	-	-	-	-	0.13
<i>Coscinodiscus</i> <i>decrescens</i>	0.07	-	-	-	-	-	-	0.00	0.67	0.11	-	-	0.11	-	-	0.13
<i>Amphora</i> sp. 7	0.07	-	-	-	-	-	-	0.00	0.44	-	-	0.33	0.11	-	-	0.13
<i>Navicula</i> cf. <i>cinta</i>	0.07	-	-	0.20	-	-	-	0.04	-	-	-	0.33	0.33	-	-	0.10
<i>Cocconeis</i> <i>placentula</i> var. <i>euglypta</i>	0.07	-	0.20	-	-	-	-	0.04	0.11	0.56	-	-	-	-	-	0.10
<i>Nitzschia</i> <i>lorenziana</i>	0.07	-	0.40	-	-	-	-	0.08	-	0.11	0.33	-	-	-	-	0.06
<i>Nitzschia</i> <i>frustulum</i>	0.07	0.20	0.60	-	-	-	-	0.16	-	-	-	-	-	-	-	0.00
<i>Rhopalodia</i> cf. <i>musculus</i>	0.07	-	0.60	-	0.20	-	-	0.16	-	-	-	-	-	-	-	0.00
<i>Navicula</i> <i>mannii</i>	0.07	-	0.80	-	-	-	-	0.16	-	-	-	-	-	-	-	0.00
<i>Navicula</i> sp. 5	0.06	-	-	-	-	-	-	0.00	-	0.78	-	-	-	-	-	0.11
<i>Nitzschia</i> <i>laevis</i>	0.06	-	-	-	-	-	-	0.00	0.78	-	-	-	-	-	-	0.11
<i>Nitzschia</i> sp. 8	0.06	-	-	-	-	-	-	0.00	0.78	-	-	-	-	-	-	0.11
<i>Pinnularia</i> <i>quadratarea</i>	0.06	-	-	-	-	-	-	0.00	-	-	-	-	-	0.78	-	0.11
<i>Seminavis</i> sp. 1	0.06	-	-	-	-	-	-	0.00	-	0.22	0.56	-	-	-	-	0.11
<i>Navicula</i> <i>gemmifera</i>	0.06	-	0.40	-	-	-	-	0.08	-	-	0.33	-	-	-	-	0.05

Table 2.3. (Continued)

Species	Total (%)	Site A							Site B							
		AR	A1	A2	A3	A4	A5	Sub-total	BR	B1	B2	B3	B4	B5	B6	Sub-total
<i>Diploneis</i> sp. 2	0.06	-	-	0.40	-	0.20	-	0.12	-	0.11	-	-	-	-	-	0.02
<i>Seminavis</i> sp. 3	0.06	-	-	-	-	-	-	0.00	-	-	0.11	0.56	-	-	-	0.10
<i>Parlibellus</i> sp. 1	0.05	0.20	-	-	0.20	-	-	0.08	0.22	-	-	-	-	-	-	0.03
<i>Berkeleya rutilans</i>	0.05	0.60	-	-	-	-	-	0.12	-	-	-	-	-	-	-	0.00
<i>Parlibellus</i> sp. 4	0.05	0.60	-	-	-	-	-	0.12	-	-	-	-	-	-	-	0.00
<i>Navicula</i> sp. 14	0.05	-	-	-	-	0.60	-	0.12	-	-	-	-	-	-	-	0.00
<i>Nitzschia</i> sp. 7	0.05	-	0.60	-	-	-	-	0.12	-	-	-	-	-	-	-	0.00
<i>Haslea</i> sp. 1	0.05	-	-	-	-	-	-	0.00	0.11	0.44	-	-	-	-	-	0.08
<i>Nitzschia distans</i>	0.05	-	-	-	-	-	-	0.00	0.56	-	-	-	-	-	-	0.08
<i>Cymatosira belgica</i>	0.05	-	-	-	-	-	-	0.00	0.56	-	-	-	-	-	-	0.08
<i>Amphora</i> sp. 6	0.04	-	-	-	-	-	-	0.00	0.22	0.22	-	-	-	-	-	0.06
<i>Navicula arenaria</i> var. <i>rostellata</i>	0.04	-	-	-	-	-	-	0.00	0.44	-	-	-	-	-	-	0.06
<i>Stephanocyclus</i> sp. 1	0.04	-	-	-	-	-	-	0.00	0.44	-	-	-	-	-	-	0.06
<i>Navicula</i> sp. 15	0.04	-	-	-	-	-	-	0.00	0.22	-	-	0.22	-	-	-	0.06
<i>Planothidium</i> sp. 1	0.04	-	0.20	-	-	-	-	0.04	0.11	0.11	-	-	-	-	-	0.03
<i>Cymatotheca weissflogii</i>	0.04	0.20	-	-	-	-	-	0.04	0.22	-	-	-	-	-	-	0.03
<i>Nitzschia</i> cf. <i>miserabilis</i>	0.03	0.40	-	-	-	-	-	0.08	-	-	-	-	-	-	-	0.00
<i>Odontella longicuris</i>	0.03	0.40	-	-	-	-	-	0.08	-	-	-	-	-	-	-	0.00
<i>Parlibellus</i> sp. 3	0.03	0.40	-	-	-	-	-	0.08	-	-	-	-	-	-	-	0.00
<i>Nitzschia</i> cf. <i>lanceolata</i>	0.03	0.20	0.20	-	-	-	-	0.08	-	-	-	-	-	-	-	0.00
<i>Delphineis</i> cf. <i>surirella</i>	0.03	-	0.40	-	-	-	-	0.08	-	-	-	-	-	-	-	0.00
<i>Tryblionella hyalina</i>	0.03	-	-	-	-	-	-	0.00	-	0.11	-	-	0.22	-	-	0.05

Table 2.3. (Continued)

Species	Total (%)	Site A							Site B							
		AR	A1	A2	A3	A4	A5	Sub-total	BR	B1	B2	B3	B4	B5	B6	Sub-total
<i>Plagiogrammopsis vanheurckii</i>	0.03	-	-	-	-	-	-	0.00	0.33	-	-	-	-	-	-	0.05
<i>Actinoptychus splendens</i>	0.03	-	-	-	-	-	-	0.00	0.33	-	-	-	-	-	-	0.05
<i>Parlibellus crucicula</i>	0.03	-	-	-	-	-	-	0.00	0.33	-	-	-	-	-	-	0.05
<i>Fogedia koreana</i>	0.03	-	-	-	-	-	-	0.00	0.33	-	-	-	-	-	-	0.05
<i>Thalassiosira</i> sp. 1	0.03	-	-	-	-	-	-	0.00	0.33	-	-	-	-	-	-	0.05
<i>Gomphonema</i> sp. 1	0.03	-	-	-	-	-	-	0.00	0.11	-	-	0.22	-	-	-	0.05
<i>Planothidium hauckianum</i>	0.03	0.20	-	-	-	-	-	0.04	0.11	-	-	-	-	-	-	0.02
<i>Navicula perrhombus</i>	0.03	-	0.20	-	-	-	-	0.04	0.11	-	-	-	-	-	-	0.02
<i>Nitzschia nana</i>	0.03	-	0.20	-	-	-	-	0.04	-	-	-	0.11	-	-	-	0.02
<i>Amphora holsaticoides</i>	0.03	-	0.20	-	-	-	-	0.04	-	-	0.11	-	-	-	-	0.02
<i>Nitzschia</i> sp. 3	0.02	-	-	-	-	-	-	0.00	-	0.22	-	-	-	-	-	0.03
<i>Nitzschia crasterium</i>	0.02	-	-	-	-	-	-	0.00	-	0.22	-	-	-	-	-	0.03
<i>Navicula</i> cf. <i>kepesii</i>	0.02	-	-	-	-	-	-	0.00	-	0.22	-	-	-	-	-	0.03
<i>Mastogloia exigua</i>	0.02	-	-	-	-	-	-	0.00	0.22	-	-	-	-	-	-	0.03
<i>Thalassiosira nordenskiöldii</i>	0.02	-	-	-	-	-	-	0.00	0.22	-	-	-	-	-	-	0.03
<i>Diploneis stroemii</i>	0.02	-	-	-	-	-	-	0.00	0.22	-	-	-	-	-	-	0.03
<i>Cocconeis costata</i>	0.02	-	-	-	-	-	-	0.00	0.22	-	-	-	-	-	-	0.03
<i>Delphineis</i> sp. 1	0.02	-	-	-	-	-	-	0.00	0.22	-	-	-	-	-	-	0.03
<i>Nitzschia aerophila</i>	0.02	-	-	-	-	-	-	0.00	-	-	-	-	-	0.22	-	0.03
<i>Navicula</i> cf. <i>phylleptosoma</i>	0.02	-	-	-	-	-	-	0.00	-	-	-	0.22	-	-	-	0.03
<i>Biremis ambigua</i>	0.02	0.20	-	-	-	-	-	0.04	-	-	-	-	-	-	-	0.00
<i>Hyalosira</i> sp. 1	0.02	0.20	-	-	-	-	-	0.04	-	-	-	-	-	-	-	0.00

Table 2.3. (Continued)

Species	Total (%)	Site A							Site B							
		AR	A1	A2	A3	A4	A5	Sub-total	BR	B1	B2	B3	B4	B5	B6	Sub-total
<i>Navicula microcari</i>	0.02	0.20	-	-	-	-	-	0.04	-	-	-	-	-	-	-	0.00
<i>Navicula</i> sp. 10	0.02	0.20	-	-	-	-	-	0.04	-	-	-	-	-	-	-	0.00
<i>Navicula</i> sp. 2	0.02	0.20	-	-	-	-	-	0.04	-	-	-	-	-	-	-	0.00
<i>Trachyneis aspera</i>	0.02	0.20	-	-	-	-	-	0.04	-	-	-	-	-	-	-	0.00
<i>Tryblionella punctata</i>	0.02	0.20	-	-	-	-	-	0.04	-	-	-	-	-	-	-	0.00
<i>Tryblioptichus</i> sp. 1	0.02	0.20	-	-	-	-	-	0.04	-	-	-	-	-	-	-	0.00
<i>Diploneis smithii</i>	0.02	-	-	-	-	0.20	-	0.04	-	-	-	-	-	-	-	0.00
<i>Amphora</i> cf. <i>richardiana</i>	0.02	-	-	0.20	-	-	-	0.04	-	-	-	-	-	-	-	0.00
<i>Hipodonta linearis</i>	0.02	-	0.20	-	-	-	-	0.04	-	-	-	-	-	-	-	0.00
<i>Cocconeis</i> sp. 1	0.01	-	-	-	-	-	-	0.00	-	0.11	-	-	-	-	-	0.02
<i>Nitzschia</i> sp. 2	0.01	-	-	-	-	-	-	0.00	-	0.11	-	-	-	-	-	0.02
<i>Diploneis aestuarii</i>	0.01	-	-	-	-	-	-	0.00	0.11	-	-	-	-	-	-	0.02
<i>Nitzschia tryblionella</i>	0.01	-	-	-	-	-	-	0.00	0.11	-	-	-	-	-	-	0.02
<i>Navicula pavillardii</i>	0.01	-	-	-	-	-	-	0.00	0.11	-	-	-	-	-	-	0.02
<i>Thalassiosira</i> cf. <i>leptopus</i>	0.01	-	-	-	-	-	-	0.00	0.11	-	-	-	-	-	-	0.02
<i>Navicula arenaria</i>	0.01	-	-	-	-	-	-	0.00	-	-	0.11	-	-	-	-	0.02
<i>Navicula flagellifera</i>	0.01	-	-	-	-	-	-	0.00	-	-	0.11	-	-	-	-	0.02

Table 2.4. Diversity indices of benthic diatom communities at 13 stations in the two salterns; S, number of species; d, species richness; J' , Pielou's evenness; H' , Shannon wiener diversity; $1-\lambda$, Simpson diversity.

Site	Station	Salinity	S	d	J'	H'	$1-\lambda$
A	AR	24	61	13.0	0.54	2.21	0.70
	A1	32	64	13.7	0.79	3.30	0.94
	A2	36	34	7.17	0.68	2.38	0.81
	A3	74	24	4.99	0.46	1.46	0.55
	A4	174	33	6.95	0.66	2.31	0.85
	A5	324	-	n.a.	n.a.	n.a.	n.a.
B	BR	35	89	19.1	0.79	3.57	0.95
	B1	31	62	13.3	0.71	2.92	0.90
	B2	37	45	9.55	0.68	2.57	0.86
	B3	47	33	6.95	0.55	1.92	0.74
	B4	65	37	7.82	0.54	1.94	0.75
	B5	165	28	5.86	0.52	1.73	0.69
	B6	205	24	4.99	0.36	1.14	0.45

S, number of species; d, species richness; J' , Pielou's evenness; H' , Shannon wiener diversity; $1-\lambda$, Simpson diversity; n.a., not available.

2.3.2. Cluster analysis

CA was used to delineate station groups with similar species compositions of diatoms (Fig. 2.4b). Four representative groups (groups A1, A2, B1, and B2) were detected across the 13 stations of the two sites (ANOSIM: $R = 0.77$, $p < 0.05$). These clusters showed clear differences between sites and further by salinity in each station.

First, stations of AR and A1 having salinity of < 35 psu at site A were separated into one representative group, group A1, with 42.4 % similarity. The species that contributed most to dissimilarities with other groups was *Paralia sulcata* (5.63%). Group A2 encompassed three stations (A2–A4), which were characterized by a hypersaline environment (> 74 psu, mean salinity = 191 psu) at site A. This group showed a noticeable peak in relative abundance for certain dominant species, *N. scalpelliformis* (29.7%). SIMPER analysis showed that this species was the most potent contributor to the dissimilarity of group A2 to other groups.

Group B1 encompassed five stations (BR and B1–B4) with salinity of < 70 psu. *N. cf. arenaria*, *N. scalpelliformis*, and *P. sulcata* dominated the group. Interestingly, *N. cf. arenaria* and *N. scalpelliformis* were more abundant at higher salinities, whereas the abundance of *P. sulcata* declined with increasing salinity. The dissimilarity of group B2 to other groups was mainly caused by *N. cf. arenaria* (9.71%). Finally, group B2 encompassed stations B5 and B6, with salinities of > 70 psu. This group was characterized by the lowest species diversity and evenness. The species that contributed most to the dissimilarities with other groups were *Achnanthes* sp. 1 (15.6%) and *Navicula* sp. 4 (11.2%), respectively.

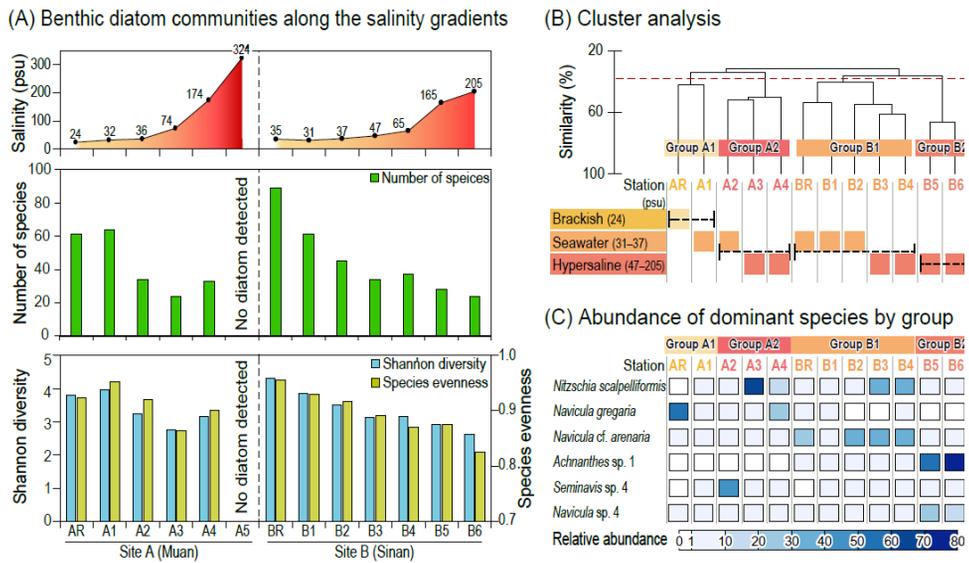


Figure 2.4.

Overview of benthic diatom communities under a wide range of salinities in the two salterns of sites A and B. (A) Number of occurred species and diversity indices along the salinity gradients in the two salterns. No diatom was detected at station A5. (B) Cluster analysis based on the relative abundance of diatom species with four categorized groups by specific range of salinities; brackish, seawater and hypersaline conditions. (C) Relative abundance of the top six dominant diatoms species ($> 5\%$ of total abundance) belonging to each group are given.

2.4. DISCUSSION

2.4.1. Distribution of diatoms along the environmental gradients

BIOENV analysis showed that salinity was the best matched single factor for the species composition and diversity (Table 2.5). Species composition had the strongest correlation with salinity, MC, pH, and TN. Species diversity showed the strongest correlation with salinity and MC. The dominant species were associated with the four environmental factors, i.e., salinity, MC, pH, and TN, identified by BIOENV analysis (Fig. 2.5). Overall, the ranges of all species in occurrence across salinity, MC, pH, and TN reflected their parameter-specific distribution preferences in the study area. For example, half of the species occurred from normal seawater to the moderately hypersaline environments (36–65 psu). However, most dominant species occurred across a wider range of salinity, even at salinities > 100 and 200 psu, though at relatively low frequencies. The most dominant species were assumed to have wide salinity tolerance ranges; in contrast, *Navicula cf. pavillardii* was primarily detected in seawater salinity ranges.

Interestingly, diatoms occupied distinct ranges in relation to MC. While most of the dominant species (except *N. cf. pavillardii*) occurred in a very narrow range of MC (95.0–99.4%), half of all species occurred over a much wider range of MC (65.5–99.2%). This phenomenon may be attributable to large differences in the MC between the reference station (BR, 65.5%) and stations in saltern (B1–B6, 95.0–99.4%). Compared to the saltern, the reference station was characterized by low MC and higher species numbers. It should be noted, however, that various species detected in the reference station would have been filtered out in the drawing process of seawater the salterns. pH and TN had negligible impacts on the distributions of dominant diatom species. However, *Navicula* sp. 1 and *Achnanthes* sp. 1 appeared to preferentially occupy environments with relatively low pH and high nutrients.

Table 2.5. Results of BIOENV analysis showing the strongest correlation for environmental variables that best matched the relative abundance and species composition of diatoms.

Species composition			Species diversity		
# of variables	Variables	Correlation	# of variables	Variables	Correlation
4	Salinity, TN, MC, pH	0.80	2	Salinity, MC	0.68
4	Salinity, PO ₄ , MC, pH	0.80	3	Salinity, TN, MC	0.61
4	Salinity, TOC, MC, pH	0.79	1	MC	0.61

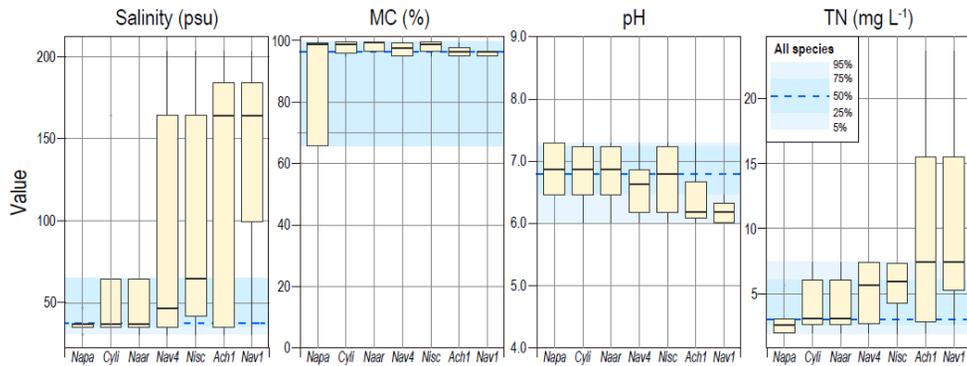


Figure 2.5.

Boxplots for occurrence (viz., presence or absence) of the seven selected species (*Napa*, *Navicula* cf. *pavillardii*; *Cyli*, *Cyclotella litoralis*; *Naar*, *Navicula* cf. *arenaria*; *Nav4*, *Navicula* sp. 4; *Nisc*, *Nitzschia scalpelliformis*; *Ach1*, *Achnanthes* sp. 1; *Nav1*, *Navicula* sp. 1) with respect to salinity, mud content (MC), pH, and total nitrogen (TN) based on dataset II (site B). The benthic diatom species with a > 1% of relative abundance was presented. The blue shading represents the occurrence ranges of all species in the study area. Seven species were arranged in ascending order of median values in their occurrences with respect to salinity gradient.

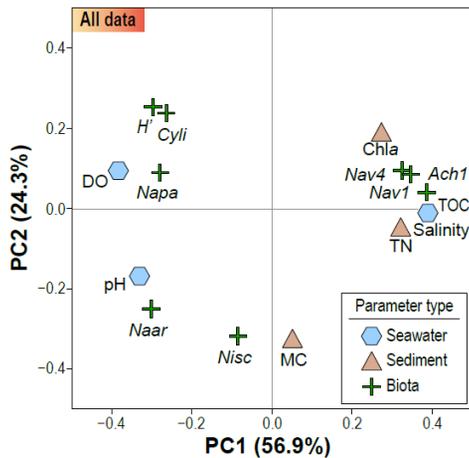
2.4.2. Environmental factors controlling saltern diatoms

To elucidate the relationship between various environmental parameters and diatoms, BIOENV and PCA were performed on dataset II (site B). PCA of diatom assemblages and environmental variables confirmed the key factors influencing the occurrence and distributions of benthic diatoms in the saltern (Fig. 2.6A). PCA generated two major components that collectively accounted for 81.2% of total variance.

The first axis was mainly explained by salinity, TN, and DO (explaining 56.9% of total variance), which are all related to the serial evaporation in the process of salt production. The most noticeable seawater parameter was salinity which seemed to directly influence species diversity of saltern diatoms. At the same time, salinity was found to be a key factor determining the distributions of selected taxa, as indicated by elevated occurrence of certain halophile species across specific range of salinity. At extreme salinity condition (station A5: 324 psu), the entire loss of diatoms was evidenced. Overall, a stepwise decrease in species diversity with increasing salinity (Fig. 2.2A) and occurrence of dominant species in relation to the salinity gradient (Fig.2.3) clearly explained the key role of “salinity” in dynamics of saltern diatoms.

The second axis (PC2) could be explained by sediment properties, primarily mud content. Most sediments in the saltern were composed of fine-grained particles; however, relatively low MC in sediment was the main feature of the tidal flat at site B (reference station of BR). Coarse sediment particles settle quickly during the irrigation of seawater, accordingly sediment inside the saltern tended to consist of fine muds. Such environments would favor for the dominance of epipelagic diatoms over epipsammic ones.

(A) Principal component analysis



(B) Correlation analysis

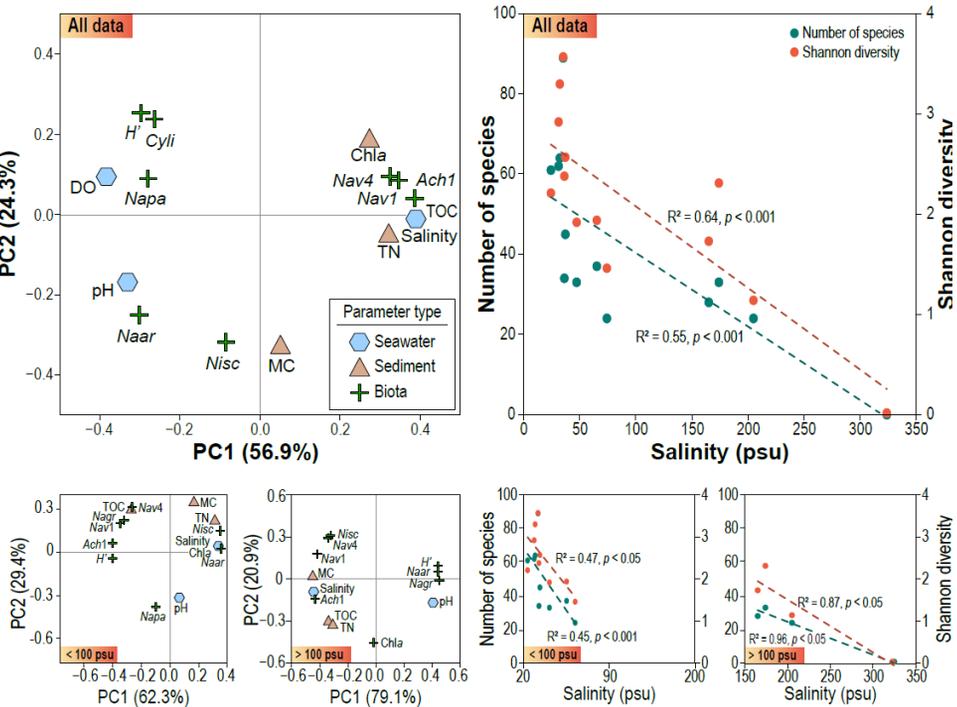


Figure 2.6.

Relationship between benthic diatoms and environmental parameters based on dataset II (site B). (A) Principal component analysis of 7 selected species (*Napa*, *Navicula* cf. *pavillardii*; *Cyli*, *Cyclotella litoralis*; *Naar*, *Navicula* cf. *arenaria*; *Nav4*, *Navicula* sp. 4; *Nisc*, *Nitzschia scalpelliformis*; *Ach1*, *Achnanthes* sp. 1; *Nav1*, *Navicula* sp. 1) and environmental variables. (B) Correlation analysis between salinity and benthic diatom community structure, in terms of species numbers and diversity, scatterplot shown for two categorized ranges of salinity, viz., < 100 psu and > 100 psu, for a comparison.

PERMANOVA showed that the composition of diatom species varied with both salinity and the reference stations as the initial source of diatom species to the saltern (Table 2.6). First, the number of diatom species significantly differed between the two sites ($df = 1$, Pseudo- $F = 4.45$, $p < 0.001$) and across the salinity range ($df = 3$, Pseudo- $F = 2.96$, $p < 0.001$). Second, the composition of diatom species significantly differed between the two sites ($df = 1$, Pseudo- $F = 4.57$, $p < 0.001$), across the salinity range ($df = 3$, Pseudo- $F = 3.21$, $p < 0.001$) and between site and salinity ($df = 2$, Pseudo- $F = 2.65$, $p < 0.001$). Thus, the composition of diatom species surviving under high salinity conditions might vary depending on the composition of diatom assemblages initially introduced to the salterns.

A significant linear relationship was detected between salinity and species diversity in the two salterns (Fig. 2.5). A simple linear regression between salinity and species numbers (or diversity) indicates a theoretical threshold of ~300 psu. Interestingly, however, the number of species and diversity index seemed to more rapidly decrease in the lower salinities (< 100 psu) compared to those in the higher salinities (> 150 psu). This phenomenon might reflect increasing salinity tolerance towards hypersaline environments, which should be further worthy to examine in aspect of biological mechanism. The complexity of community structure and functioning of microorganisms decays with increasing salinity stress (Pedrós-Alió et al. 2000). Of note, some previous studies demonstrated that high salinity has direct / indirect effects on the survival of diatoms (Clavero et al. 2000, Yamamoto et al. 2017).

Further, in order to investigate the salinity thresholds on marine lives, a mini-review was provided (Table 2.7). Both in situ and laboratory culture data are included. The diverse marine taxa were found to inhabit various hypersaline environments, encompassing solar saltern, dryland, and saline lake. The salinity thresholds greatly varied by the reported taxa, with maximum 360 psu from saline lake for a copepod species, *Celtocamptus retrogressus* (Anufrieva 2014). For diatoms, *Amphiprora paludosa* and *Amphora* sp. were reported from the maximum salinity of 213 psu from a solar saltern in Long Island, Bahamas (Davis 1978).

Table 2.6. Result of PERMANOVA showing the significance of variables across study area and salinity in species diversity and composition of benthic diatoms in the two salterns

Target	Term	df	Pseudo-F	p-value
Species diversity	Study area	1	4.45	0.001
	Salinity	3	2.96	0.001
	Study area × salinity	2	2.41	0.003
	Res	19	-	-
Species composition	Study area	1	4.57	0.001
	Salinity	3	3.21	0.001
	Study area × salinity	2	2.65	0.001
	Res	19	-	-

PERMANOVA, permutational multivariate analysis of variance.

Unidentified diatoms were also reported at 200 psu from a microbial food web study that conducted in two salterns on the Mediterranean coast of the Iberian Peninsula (Pedros-Alio et al. 2000). It should be noted that viability of diatom cells has not been evidenced in the above two literatures. Whilst, we observed 3 live benthic diatoms under light microscope, at salinity of 205 psu in Sinan (station B6); *Amphora* sp., *Navicula* sp. 1, and *N. scalpelliformis*. In fact, a total of 24 benthic diatom species, including above three live diatoms, were identified at the very station, which strongly supported the high diversity of benthic diatoms in Korean solar saltern, compared to others. We listed 9 species, which showed > 1% of relative abundance to total (except for *Amphora* sp.), in the mini-review table at present (Table 2.6).

the two sites ($df = 1$, Pseudo- $F = 4.45$, $p < 0.001$) and across the salinity range ($df = 3$, Pseudo- $F = 2.96$, $p < 0.001$). Second, the composition of diatom species significantly differed between the two sites ($df = 1$, Pseudo- $F = 4.57$, $p < 0.001$), across the salinity range ($df = 3$, Pseudo- $F = 3.21$, $p < 0.001$) and between site and salinity ($df = 2$, Pseudo- $F = 2.65$, $p < 0.001$). Thus, the composition of diatom species surviving under high salinity conditions might vary depending on the composition of diatom assemblages initially introduced to the salterns.

A significant linear relationship was detected between salinity and species diversity in the two salterns (Fig. 2.5). A simple linear regression between salinity and species numbers (or diversity) indicates a theoretical threshold of ~300 psu. Interestingly, however, the number of species and diversity index seemed to more rapidly decrease in the lower salinities (< 100 psu) compared to those in the higher salinities (> 150 psu). This phenomenon might reflect increasing salinity tolerance towards hypersaline environments (Fig. 2.6), which should be further worthy to examine in aspect of biological mechanism. The complexity of community structure and functioning of microorganisms decays with increasing salinity stress (Pedrós-Alió et al. 2000). Of note, some previous studies demonstrated that high salinity has direct/indirect effects on the survival of diatoms (Clavero et al. 2000, Yamamoto et al. 2017).

Further, in order to investigate the salinity thresholds on marine lives, a mini-review was provided (Table 2.6). Both in situ and laboratory culture data are included. The diverse marine taxa were found to inhabit various hypersaline environments, encompassing solar saltern, dryland, and saline lake. The salinity thresholds greatly varied by the reported taxa, with maximum 360 psu from saline lake for a copepod species, *Celtocamptus retrogressus* (Anufriieva 2014). For diatoms, *Amphiprora paludosa* and *Amphora* sp. were reported from the maximum salinity of 213 psu from a solar saltern in Long Island, Bahamas (Davis 1978). Unidentified diatoms were also reported at 200 psu from a microbial food web study that conducted in two salterns on the Mediterranean coast of the Iberian Peninsula (Pedros-Alio et al. 2000). It should be noted that viability of diatom cells has not been evidenced in the above two literatures. Whilst, we observed 3 live benthic diatoms under light microscope, at salinity of 205 psu in Sinan (station B6); *Amphora* sp., *Navicula* sp. 1, and *N. scalpelliformis*. In fact, a total of 24 benthic diatom species, including above three live diatoms, were identified at the very station, which strongly supported the high diversity of benthic diatoms in Korean solar saltern, compared to others. We listed 9 species, which showed > 1% of relative abundance to total (except for *Amphora* sp.), in the mini-review table at present (Table 2.7).

Table 2.7. Result of IndVal analysis listing the indicator diatom species by salinity group

Indicator species	Group			
	Brackish (< 30 psu)	Seawater (30–40 psu)	Hypersaline I (40–80 psu)	Hypersaline II (> 100 psu)
<i>Navicula gregaria</i>	0.84	0.01	0.00	0.05
<i>Navicula cf. pavillardii</i>	0.81*	0.11	0.03	0.00
<i>Navicula cf. salinarum</i>	0.80*	0.03	0.01	0.03
<i>Entomoneis alata</i>	0.11	0.63	0.07	0.00
<i>Cyclotella litoralis</i>	0.04	0.56**	0.21	0.19
<i>Rhopalodia sp. 3</i>	0.00	0.03	0.86*	0.02
<i>Nitzschia scalpelliformis</i>	0.00	0.04	0.83*	0.13
<i>Navicula cf. arenaria</i>	0.01	0.38	0.59	0.01
<i>Navicula sp. 1</i>	0.00	0.06	0.05	0.75
<i>Amphora cf. boliviana</i>	0.02	0.06	0.13	0.68
<i>Achnanthes sp. 1</i>	0.00	0.01	0.00	0.65*
<i>Navicula sp. 4</i>	0.04	0.25	0.08	0.64*

* $p < 0.05$, ** $p < 0.01$.

Table 2.8. Mini-review on the salinity thresholds reported for various marine organisms in the hypersaline environments

Taxa	Species	Threshold (psu)	Study area	Reference
Bacteria	Chromatiaceae	120	Saltern	Sorensen et al. (2004)
	(Bacterioivory, unidentified)	250	Saltern	Pedros-Alio et al. (2000)
Diatom	<i>Navicula arenaria</i>	45	Laboratory (culture)	Admiraal (1976)
	<i>Nitzschia sigma</i>	45	Laboratory (culture)	Admiraal (1976)
	<i>Amphora coffeaeformis</i> var. <i>perpusilla</i>	125	Laboratory (culture)	Clavero et al. (2000)
	(Diatom, unidentified)	200	Saltern	Pedros-Alio et al. (2000)
	<i>Navicula</i> sp. 1 ^a	205	Saltern	This study ^b
	<i>Nitzschia scalpelliformis</i> ^a	205	Saltern	This study
	<i>Amphora</i> sp. ^a	205	Saltern	This study
	<i>Achnanthes</i> sp. 1	205	Saltern	This study
	<i>Cyclotella litoralis</i>	205	Saltern	This study
	<i>Diploneis</i> sp.	205	Saltern	This study
	<i>Navicula</i> sp. 4	205	Saltern	This study
	<i>Nitzschia</i> sp. 4	205	Saltern	This study
	<i>Paralia sulcata</i>	205	Saltern	This study
	<i>Amphiprora paludosa</i>	213	Saltern	Davis (1978)
<i>Amphora</i> sp.	213	Saltern	Davis (1978)	
Seagrass	<i>Posidonia oceanica</i>	40	Coast & Laboratory	Sanchez-Lizaso et al. (2008)
Meiofauna				
Copepoda	<i>Calamoecia saline</i>	110	Dryland	Pinder et al. (2002)
	<i>Calamoecia trilobata</i>	240	Dryland	Pinder et al. (2002)
	<i>Meridiocyclops platypus</i>	240	Saline lake	Williams and Kokkinn (1988)
	<i>Cletocamptus retrogressus</i>	360	Saline lake	Anufrieva (2014)
Ostracoda	<i>Mytilocypris henricae</i>	45	Laboratory (culture)	Martens (1983)
	<i>Diacypris whitei</i>	147	Dryland	Pinder et al. (2002)
	<i>Reticypris</i> sp.	240	Dryland	Pinder et al. (2002)

Table 2.8. (Continued)

Taxa	Species	Threshold (psu)	Study area	Reference
Macrofauna				
Arthropoda	<i>Penaeus vannamei</i>	45	Laboratory (culture)	Briggs et al. (2004)
Polychaeta	<i>Manayunkia</i> sp.	49	Dryland	Pinder et al. (2002)
Mollusca	<i>Coxiella glabra</i>	127	Dryland	Pinder et al. (2002)

^aLive diatom observed under light microscope.

^bSpecies with > 1% of relative abundance to total (except for *Amphora* sp.)

2.4.3. Indicator species at hypersaline environments

Salinity was the most critical environmental factor that governed the occurrence and distributions of diatom species at A and B sites (Table 2.2). The sampling stations of the salterns in the present study had distinctive salinity gradients, and were grouped as: brackish (< 30 psu), seawater (30–40 psu), hypersaline I (40–100 psu), and hypersaline II (> 100 psu). IndVal identified indicator species corresponding to the four groups along the salinity gradient (Fig. 2.7).

Seven indicator species were identified for each salinity range group (IndVal > 0.5, $p < 0.05$) (Table 2.6). *N. cf. pavillardii* (IndVal = 0.81) and *Navicula cf. salinarum* (IndVal = 0.80) were the indicator species of the Brackish group. *N. cf. pavillardii* was present at the reference station in site A (AR), whereas few frustules were detected from the inside of the saltern. *Navicula pavillardii* is a cosmopolitan species that is closely related to *N. cf. pavillardii* in terms of taxonomic and ecological features. The species inhabit the sandy sediments of marine coasts (Witkowski et al. 2000) and has also been reported to frequently occur in brackish areas (Costa-Böddeker et al. 2017). *Cyclotella litoralis* (IndVal = 0.56) was identified as a seawater indicator species. It dominates the tidal flats of Sinan, where the present study sites were located (Lee 2013). It is also often recorded as a member of marine planktons along with *Cyclotella meneghiniana* and *Cyclotella striata*.

Rhopalodia sp. 3 (IndVal = 0.86) and *N. scalpelliformis* (IndVal = 0.83) were identified as indicator species for the hypersaline I (40–100 psu) group. *Rhopalodia* sp. 3 had a high indicator value, due to its strong preference for the higher salinities, despite representing only 1.01% of total abundance. In comparison, the relative abundance of *N. scalpelliformis* was 66.8% and 34.6% in the hypersaline I group of sites A and B, respectively. The relatively low dominance ratio found at site B was attributable to *N. cf. arenaria* dominating the hypersaline I group at site B, with 36.6% relative abundance. *N. cf. arenaria* had an indicator value of 0.59, dominating both the hypersaline environment and seawater, with 28.6% relative abundance (Table 2.6). Altogether, there seemed to be a highly salt tolerant species which are able to endure seawater to hypersaline environments, rather than occupying specific

hypersaline environments. In comparison, *Rhopalodia* sp. 3 and *N. scalpelliformis* preferentially inhabited hypersaline environments, or were the stronger competitors in the given environment.

Finally, *Achnanthes* sp. 1 (IndVal = 0.65) and *Navicula* sp. 4 (IndVal = 0.64) were identified as the indicator species of the hypersaline II (> 100 psu) group. *Achnanthes* sp. 1 dominated station B6 (73.2%), but was not identified as a significant indicator species because species of this genus were not detected in site A. Thus, *Achnanthes* sp. 1 could not have been supplied by the tidal flat in site A (AR), as the initial species pool. *Navicula* sp. 4 dominated environments with salinity of > 100 psu in sites A and B (except station A5 where no diatoms were observed).

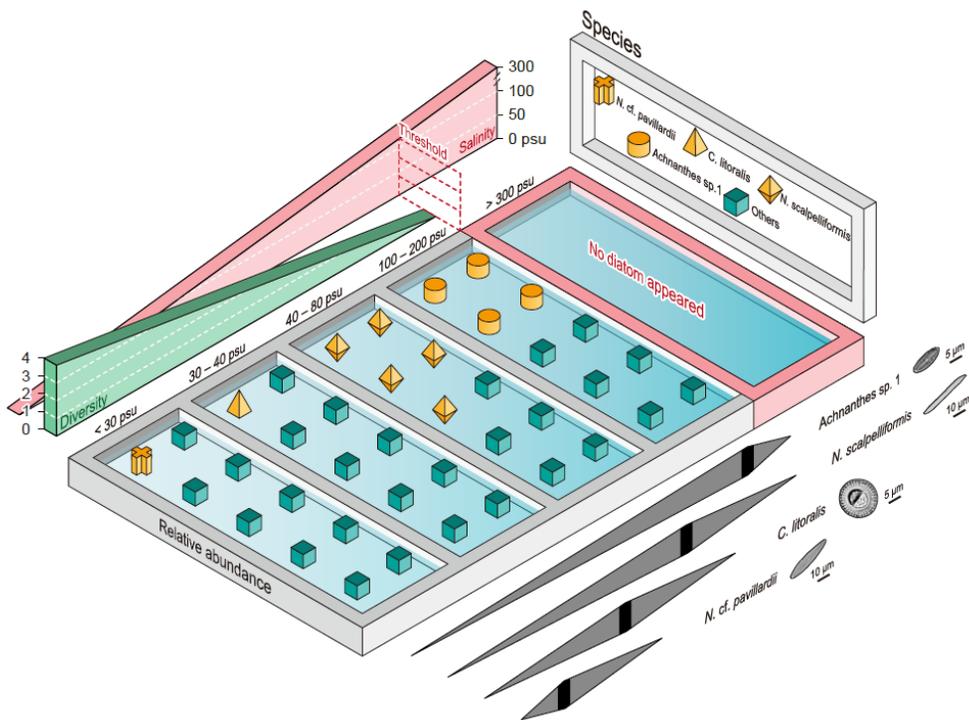


Figure 2.7.

Overview of salinity settings and schematic diagrams in benthic community structure at solar saltern environment in aspect of diversity, species composition (relative abundance of 4 indicator species and others illustrated), and euryhaline distributions of 4 selected species. Four selected indicator species include *Navicula cf. pavillardii*, *Cyclotella littoralis*, *Nitzschia scalpelliformis*, and *Achnanthes sp. 1*.

2.5. Summary

The dynamics of benthic diatoms in the hypersaline environment are investigated to advance our understanding how salinity impacts marine life. A total of 169 diatom species were identified and number of species and their composition varied greatly across sites and stations. First, not surprisingly, diatom assemblages at natural tidal flats showed relatively high diversity and abundance compared to those at salterns. The diatom assemblages at salterns generally showed salinity dependent distributions with distinct spatial changes in the dominant taxa. BIOENV and principal component analysis confirmed that salinity, mud content, and total nitrogen were key factors influencing the occurrence and/or distributions of diatoms. Of note, some dominant species, e.g., *Nitzschia scalpelliformis* and *Achnanthes* sp. 1, showed salinity tolerance, otherwise say salt preference. Number of diatom species at salinity of > 100 psu reduced over half and no diatoms were found at maximum salinity. A simple regression indicated a salinity threshold of 205 psu for survival of saltern diatoms. Finally, the indicator species were identified along the salinity gradient at salterns as well as natural tidal flats. Overall, high species numbers, varying taxa composition, and euryhaline distributions of marine diatoms at salterns collectively reflected a dynamic hypersaline ecosystem. The present study would provide backgrounds for biodiversity monitoring of important microalgal producers in some unique hypersaline environment, and elsewhere.

CHAPTER 3.

Spatiotemporal variations in macrofaunal assemblages linked to site-specific environmental factors in two contrasting nearshore habitats

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3.1. Introduction

Benthic organisms play a key role in marine ecosystem dynamics; for example, macrozoobenthos are reliable indicators of varying environmental conditions (Ryu et al. 2016). Macrozoobenthos are relatively sedentary and reflect the ecological conditions of subtidal habitats, exhibiting clear responses to the pollution gradients of various contaminants (Ryu et al. 2011, Yoon et al. 2017). Thus, macrozoobenthos is considered as a key component for determining ecological quality, particularly in shallow water systems. Macrozoobenthic responses to anthropogenic environmental changes are relatively tolerant in time and space (Iskaros and El-Otify 2013, Foshtomi et al. 2015). Thus, monitoring macrozoobenthos contributes to the understanding of relationships between biotic and abiotic components in the dynamic marine ecosystem (Hagberg and Tunberg 2000, Gray et al. 2002, Olsgard et al. 2003b, Yasuhara et al. 2007, Guest et al. 2016)

Many studies have reported a significant association between macrozoobenthic composition and the properties of sediments (Thorson 1950, Gray et al. 2002, Olsgard et al. 2003a), water temperature (Rosa and Bemvenuti 2006a, Rosa and Bemvenuti 2006b), dissolved oxygen (DO) (Middelburg and Levin 2009), and, in particular, water depth (Kröncke et al. 2003). Significant variation in the structure of macrozoobenthos occurs across seasons, and is primarily associated with temperature and other associated variables (Mahoney and Livingston 1982, Susan et al. 2014) or the introduction of species (Essink and Kleef 1993). Although many studies have focused on associations, few have explained the mechanisms that cause an increase or decrease in biological diversity in the dynamic marine ecosystem. The effects of environmental variables on macrozoobenthos tend to be diverse depending on habitat conditions, such as geomorphological feature, degree of anthropogenic pressures etc. Few studies have reported the temporal association of biotic and abiotic parameters in contrasting habitats through seasonal monitoring. Uncertainty in ecosystem responses due to the combined and mixed effects of varying environmental factors remains an open question, particularly when predicting long-term changes in the structure of macrozoobenthic assemblages.

Furthermore, most bays and coastal areas are subject to environmental deterioration caused by a high degree of land use and other human activities, which influence sediment and water quality, leading to changes to the ecosystem (Bae et al. 2017, Kim et al. 2017). The Jinhae Bay is a semi-enclosed habitat that is vulnerable to anthropogenic stresses and hypoxia. Long-term anthropogenic pressures caused by urbanization, land-driven coastal pollution, or oyster farming tend to have the most severe effect on shallow, semi-enclosed bays with poor water exchange (Read and Fernandes 2003, Newton et al. 2014). In comparison, the Samcheok coast is a nearshore open sea area, with relatively smaller anthropogenic stresses than those in Jinhae Bay. The Samcheok coast is considered to be a relatively lesser contaminated region, but there is shipping activity near the coast, representing one potential environmental stressor (Lee et al. 2011). Thus, it is important to track long-term changes in benthic populations that might lead to significant ecosystem threats in a given environment.

Various statistical tools have been proposed and applied to interpret the relationship between the environment and macrozoobenthos; for instance, several studies have applied useful statistical methods, such as indicator value analysis (IndVal) (Hermand et al. 2008, Noh et al. 2017), principal component analysis (Anderson and Willis 2003), and discriminant analysis (DA) (Ryu et al. 2011). IndVal is often used to identify representative species and groups as indicators of habitat preference, environmental change, and anthropogenic effects (Valença and Santos 2012, Liu et al. 2017); thus, it represents a powerful tool of site-specific ecosystem responses in dynamic coastal environments.

Here, we conduct a comparative investigation of a semi-enclosed bay and an open coastal area in Korea during a study period of 3 years encompassing 12 consecutive seasons. Specifically, we compared patterns of macrozoobenthos at both the community level and species level in the two contrasting habitats over the same study period with the same environmental parameters. We aimed to: 1) investigate how macrozoobenthos communities (viz., species composition and abundance) were associated with 22 target variables, in the two contrasting habitats, 2) analyze how

dominant species responded to highly heterogenic environments, and 3) identify indicator species under the prevailing environmental conditions of each habitat using various statistics. We hypothesized that certain environmental conditions could be predicted by the presence of certain indicator species across seasons and years in the macrozoobenthos community.

3.2. Materials and Methods

3.2.1. Study area

In the present study, two contrasting habitats were selected for the long-term monitoring of macrozoobenthos in two subtidal regions. First, Jinhae Bay, which is located on the south coast of Korea, is a shallow semi-enclosed bay that has monitoring stations at 11–24 m water depth (Fig. 3.1A and Table 3.1). This area has long been associated with severe coastal pollution, and is a representative hot-spot for pollution in Korea. Anthropogenic pressures include neighboring industries and populated cities, shipyards, commercial fishing, and oyster farming. In particular, the harvesting of oysters occurs year-round at a large scale with > 500 ha of aquaculture area. A sewage treatment plant, which is situated in the innermost part of Jinhae Bay, discharges up to 200 tons of sewage per day.

Second, Samcheok coastal area is located on the east coast of Korea (Fig. 3.1B and Table 3.1), of which coastline is directly exposed to the open ocean. The water depth at the monitoring stations of the Samcheok coastal area (15–52 m, mean = 37 m) was relatively deeper than those in Jinhae locations (11–24 m, mean = 18 m) (Fig. 3.1A and Table 3.1). Although shipping activity and tourist visiting could be potential anthropogenic sources in this region, geographical features and oceanographic conditions might have weakened sedimentary pollution in a given area (Lee et al. 2011).

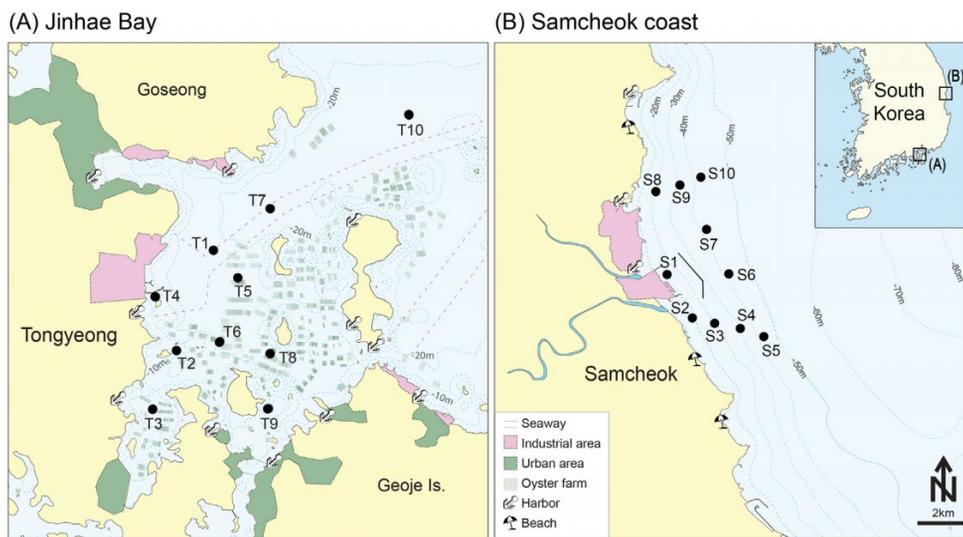


Figure 3.1.

Maps showing the sampling stations in (A) Jinhae Bay (T1–T10) and (B) Samcheok coastal area (S1–S10), Korea. Major land-use and selected marine activities are given.

Table 3.1. Data on the environmental variables, such as water quality and sediment properties, measured in the samples collected from Jinhae Bay and Samcheok coastal areas, over three years (2013-2015); values given for all years combined and for each season.

	Jinhae Bay								Samcheok coast					
	All (3 years total)			Season (mean ± sd)				All (3 years total)			Season (mean ± sd)			
	min.	max.	mean (± sd)	Fall	Winter	Spring	Summer	min.	max.	mean (± sd)	Fall	Winter	Spring	Summer
Bottom water														
Temperature (°C)	5.7	23.3	14.4 (± 5.1)	18.1 (± 2.1)	8.0 (± 1.5)	11.8 (± 1.7)	19.8 (± 1.6)	3.4	20.0	9.7 (± 3.8)	12.9 (± 3.7)	10.6 (± 0.9)	6.3 (± 2.7)	9.1 (± 3.7)
Depth (m)	11.0	24.0	24.0 (± 3.8)	18.0 (± 3.9)	18.0 (± 3.9)	18.0 (± 3.9)	18.0 (± 3.9)	15.0	52.0	36.7 (± 12.6)	36.3 (± 13.2)	36.3 (± 13.2)	36.3 (± 13.2)	36.3 (± 13.2)
Salinity (psu)	30.9	37.0	33.0 (± 1.3)	32.2 (± 0.4)	32.6 (± 0.3)	32.5 (± 0.4)	34.7 (± 1.6)	31.8	54.1	34.5 (± 2.1)	33.9 (± 0.8)	33.8 (± 0.2)	34.8 (± 3.7)	35.5 (± 1.6)
pH	7.3	11.1	8.1 (± 0.4)	8.1 (± 0.6)	8.3 (± 0.3)	8.0 (± 0.3)	8.0 (± 0.2)	7.0	9.3	8.1 (± 0.4)	8.1 (± 0.2)	8.4 (± 0.2)	7.9 (± 0.5)	7.9 (± 0.5)
DO (mg L ⁻¹)	0.6	11.6	7.5 (± 2.5)	7.1 (± 0.7)	10.0 (± 0.6)	8.4 (± 1.1)	4.3 (± 2.2)	5.6	10.8	8.4 (± 1.2)	6.7 (± 0.7)	8.5 (± 0.2)	8.8 (± 0.3)	9.7 (± 0.6)
COD (mg L ⁻¹)	0.3	3.3	1.4 (± 0.7)	1.8 (± 0.7)	1.3 (± 0.6)	1.2 (± 0.7)	1.0 (± 0.5)	<0.1	3.2	0.9 (± 0.8)	0.6 (± 0.4)	1.6 (± 1.2)	0.8 (± 0.6)	0.7 (± 0.4)
BOD (mg L ⁻¹)	-0.6	2.6	0.8 (± 0.5)	0.6 (± 0.4)	0.6 (± 0.5)	0.8 (± 0.4)	1.2 (± 0.6)	-0.3	2.5	0.6 (± 0.7)	0.2 (± 0.2)	0.3 (± 0.2)	0.7 (± 0.6)	1.3 (± 0.7)
SPM	0.5	24.2	4.9 (± 3.7)	2.9 (± 2.1)	4.0 (± 4.1)	5.6 (± 3.4)	7.1 (± 3.3)	0.4	24.7	4.6 (± 3.8)	4.0 (± 3.6)	3.7 (± 4.4)	4.4 (± 2.4)	6.4 (± 4.2)
TN	4.3	21.7	10.7 (± 3.7)	10.3 (± 3.7)	8.7 (± 1.7)	9.7 (± 3.1)	14.2 (± 3.4)	2.3	24.4	11.4 (± 4.1)	12.1 (± 3.8)	8.1 (± 1.3)	14.5 (± 5.5)	10.8 (± 1.4)
NO ₃ -N (μmol L ⁻¹)	nd ^a	14.2	2.8 (± 3.1)	2.3 (± 1.3)	1.7 (± 1.3)	2.1 (± 1.2)	5.2 (± 5.1)	nd	22.3	8.2 (± 4.6)	10.8 (± 5.2)	7.1 (± 1.4)	10.0 (± 4.8)	4.9 (± 3.2)
PO ₄ -P (μmol L ⁻¹)	nd	5.5	0.6 (± 0.7)	0.6 (± 0.2)	0.9 (± 1.1)	0.3 (± 0.1)	0.6 (± 0.6)	nd	5.2	0.8 (± 0.6)	0.8 (± 0.4)	0.6 (± 0.2)	1.1 (± 0.5)	0.6 (± 0.9)
SiO ₂ -Si (μmol L ⁻¹)	0.4	50.4	10.1 (± 9.0)	9.8 (± 10.8)	6.1 (± 5.1)	6.4 (± 3.0)	18.3 (± 9.0)	0.4	58.7	9.2 (± 6.8)	12.7 (± 10.9)	9.1 (± 1.8)	10.9 (± 5.0)	4.2 (± 2.3)
Free Cl ₂ (mg L ⁻¹)	nd	0.14	0.02 (± 0.02)	0.02 (± 0.01)	0.02 (± 0.01)	0.02 (± 0.01)	0.03 (± 0.04)	nd	0.07	0.01 (± 0.01)	0.02 (± 0.01)	0.01 (± 0.02)	0.01 (± 0.01)	0.01 (± 0.02)
Total Cl ₂ (mg L ⁻¹)	nd	0.17	0.03 (± 0.03)	0.03 (± 0.02)	0.03 (± 0.02)	0.03 (± 0.01)	0.04 (± 0.04)	nd	0.12	0.02 (± 0.02)	0.03 (± 0.01)	0.03 (± 0.03)	0.02 (± 0.01)	0.02 (± 0.02)
Sediment														
Gravel (%)	0.0	36.7	4.3 (± 8.9)	4.8 (± 10.5)	4.8 (± 9.4)	3.3 (± 7.6)	4.3 (± 8.9)	0.0	17.7	0.5 (± 2.0)	0.5 (± 2.4)	0.3 (± 1.3)	0.7 (± 2.6)	0.4 (± 1.6)
Sand (%)	0.0	63.0	9.1 (± 18.1)	8.9 (± 17.8)	9.5 (± 18.9)	8.1 (± 16.0)	9.1 (± 18.1)	0.6	94.6	58.9 (± 25.0)	62.5 (± 26.6)	53.1 (± 26.3)	58.5 (± 24.5)	61.7 (± 22.7)
Silt (%)	1.8	42.3	16.0 (± 6.4)	14.5 (± 4.5)	15.7 (± 7.7)	16.7 (± 6.4)	17.0 (± 6.5)	0.5	53.4	23.4 (± 17.9)	20.4 (± 17.5)	25.0 (± 18.9)	24.4 (± 18.2)	23.6 (± 17.6)
Clay (%)	12.8	90.2	70.6 (± 24.0)	71.7 (± 24.7)	69.9 (± 25.5)	71.9 (± 22.1)	68.8 (± 24.5)	3.7	54.1	17.2 (± 9.0)	16.6 (± 10.8)	21.6 (± 9.9)	16.4 (± 7.8)	14.3 (± 5.7)
Mean grain size (Ø)	1.8	10.6	8.7 (± 2.6)	8.8 (± 2.7)	8.6 (± 2.7)	8.9 (± 2.3)	8.5 (± 2.8)	0.6	8.4	4.7 (± 1.6)	4.5 (± 1.8)	5.3 (± 1.5)	4.6 (± 1.6)	4.4 (± 1.4)
Sorting (Ø)	0.0	5.3	2.3 (± 1.2)	2.4 (± 1.3)	2.4 (± 1.3)	2.4 (± 1.2)	2.3 (± 1.2)	1.7	3.6	2.6 (± 0.5)	2.5 (± 0.5)	2.9 (± 0.5)	2.6 (± 0.5)	2.5 (± 0.5)
Skewness	-2.5	1.4	-0.5 (± 0.6)	-0.5 (± 0.7)	-0.5 (± 0.7)	-0.6 (± 0.6)	-0.5 (± 0.6)	-0.2	3.8	1.0 (± 0.8)	0.9 (± 0.7)	1.0 (± 0.7)	1.0 (± 0.8)	1.0 (± 0.9)
Kurtosis	0.6	11.2	2.1 (± 1.9)	2.4 (± 2.2)	2.2 (± 2.3)	2.1 (± 1.7)	2.1 (± 1.9)	0.5	16.9	3.3 (± 3.1)	3.1 (± 2.2)	2.8 (± 2.9)	3.5 (± 3.3)	3.6 (± 3.8)
Organic matter (%)	4.2	16.7	9.9 (± 2.6)	9.7 (± 2.5)	10.2 (± 2.6)	10.1 (± 2.7)	9.9 (± 2.6)	0.9	11.3	2.9 (± 2.0)	2.5 (± 2.2)	3.4 (± 2.4)	3.1 (± 1.8)	2.7 (± 1.4)

^and: not detected

3.2.2. Sampling and laboratory analyses

Sampling was conducted in Jinhae Bay (n = 10; T1–T10) and Samcheok coastal area (n = 10; S1–S10) from 2013 to 2015 (Table 3.2). Subtidal sediment samples were collected over 12 consecutive seasons during the 3-year period to analyze macrofaunal assemblages and sedimentary parameters. In brief, during each sampling event, two samples were collected using a van Veen grab, covering a surface area of 0.1 m². Sediment samples from van Veen grab were sieved on site using a 1-mm mesh size. Pooled samples were used to identify species, with all individuals being counted. Surface sediments (< 3 cm) were subsampled from a grab sample to analyze sediment parameters, such as grain size (including % gravel, % sand, % silt, % clay, sorting, skewness, kurtosis) and organic content. Grain size was analyzed by the dry sieve and pipette method (Konert and Vandenberghe 1997), given as mean grain size (Mz). Organic content was determined by burning sediment to ashes at 550 °C for 4-h (Heiri et al. 2001) to obtain weight loss after combustion. In addition, environmental variables of sea water on the sea bottom were monitored using a multi-probe (YSI 556 MPS; Ohio, OH, USA) that measured pH, salinity, DO, and temperature. Photographs of field survey are presented in Fig. 3.2.

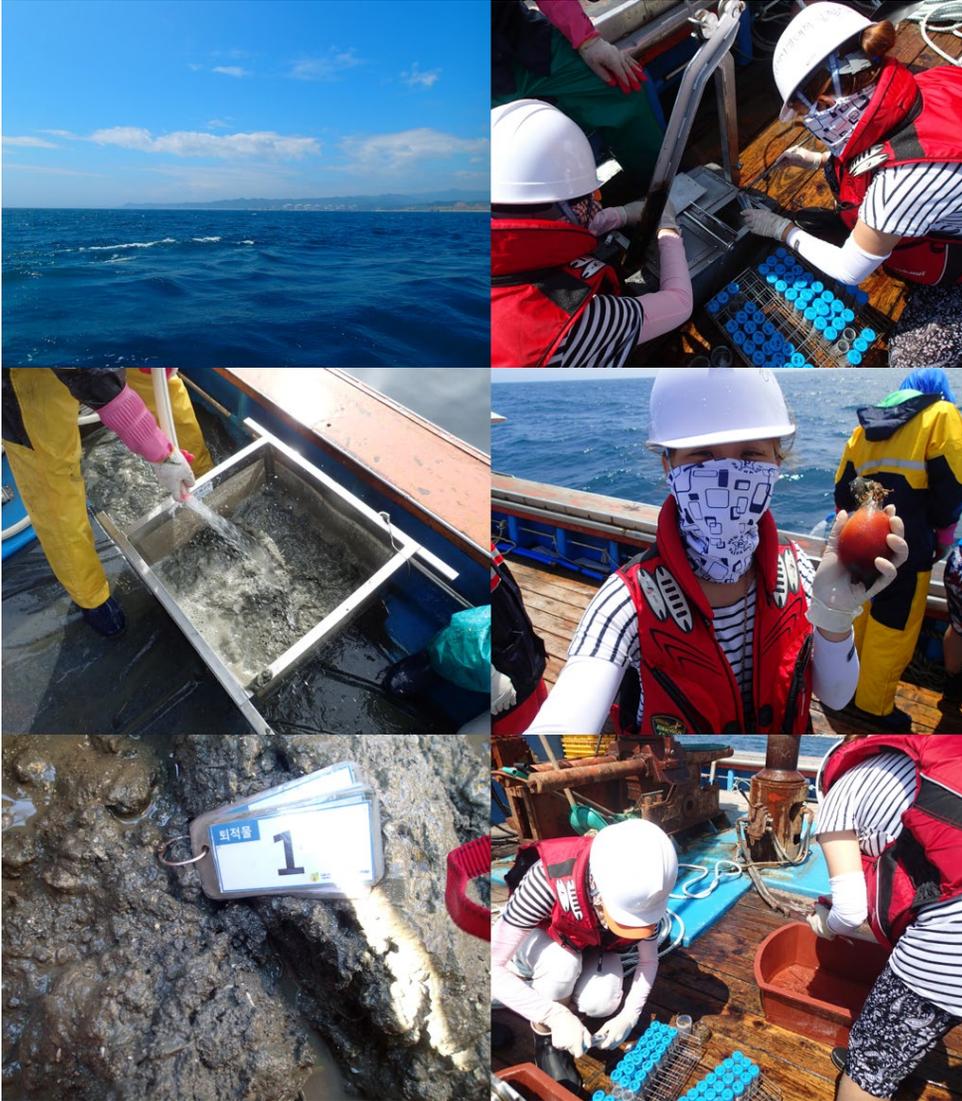


Figure 3.2.
Site and field survey views in Samcheok Coast

Table 3.2. Sampling location (latitude and longitude), depth, and bottom sediment type in Jinhae Bay and Samcheok coastal area.

Study area	Location	Latitude (°)	Longitude (°)	Depth (m)	Bottom sediment type^a
Jinhae Bay	T1	34.961	128.457	11	Sandy mud
	T2	34.927	128.442	16	Slightly sandy mud
	T3	34.906	128.432	14	Mud
	T4	34.945	128.433	20	Mud
	T5	34.952	128.468	20	Mud
	T6	34.930	128.460	17	Mud
	T7	34.976	128.481	23	Mud
	T8	34.926	128.481	16	Mud
	T9	34.907	128.481	19	Muddy sand
	T10	35.008	128.540	24	Slightly sandy mud
Sam-cheok coast	S1	37.171	129.355	20	Slightly muddy sand
	S2	37.160	129.362	15	Slightly muddy sand
	S3	37.158	129.370	25	Muddy sand
	S4	37.156	129.378	36	Sandy mud
	S5	37.153	129.388	52	Sandy mud
	S6	37.171	129.374	46	Sandy mud
	S7	37.183	129.371	45	Slightly muddy sand
	S8	37.196	129.350	32	Sandy mud
	S9	37.183	129.359	47	Sandy mud
	S10	37.203	129.369	49	Muddy sand

^aThe classification was followed to Flemming, 2000

3.2.3. Data analyses

Cluster analysis (CA) was carried out with PRIMER 6 statistical software (PRIMER-E Ltd., Plymouth, UK). The original data matrix was reduced by eliminating species that contributed < 1% of total abundance. Bray-Curtis similarity coefficients were calculated and the data were subjected to group average sorting. Abundance was fourth root-transformed to balance it across the recorded taxa in the measure of similarity (Clarke and Warwick 2001). Non-metric multidimensional scaling (NMDS) was also used to place sampling stations in two-dimensional space based on the same similarity matrix used for CA with information of the dominant species. The analysis of similarities (ANOSIM) test was performed to confirm that these groups differed significantly. After identifying the groups by using CA, DA was performed to extract significant discriminant functions and to identify the major environmental variables that discriminated the groups. Principle component analysis (PCA) was performed to describe the overall correlations cross all the components of environmental variables and macrozoobenthos assemblages. Subsequently, IndVal was performed to detect indicator species within each group by CA (Dufrêne and Legendre 1997).

3.3. Results

3.3.1. Spatiotemporal variation in environmental conditions

Environmental variables were measured in situ or in the laboratory, depending on the parameters during 3-year study period. Table 3.3 summarizes data on environmental variables including general water quality (temperature, salinity, and pH etc.) and sediment properties (grain size, sorting, and organic matter etc.). Environmental parameters varied significantly in time and space, clearly reflecting the two contrasting habitats of Jinhae Bay and Samcheok coast over the seasons and years.

In Jinhae Bay, the bottom water temperature and the concentrations of bottom DOs showed clear seasonal variation (Table 3.3). The bottom DOs tended to decrease noticeably during summer to levels even lower than that of hypoxia ($< 2 \text{ mg O}_2 \text{ L}^{-1}$) at some northern stations of the study region. Fairly high nutrient concentrations were measured in all seasons. The mean concentration of $\text{NO}_3\text{-N}$ and $\text{SiO}_2\text{-Si}$ was lowest in winter, on average, indicating an oligotrophic environment during the cold season. Over the 3-year survey period, sediment properties showed a highly distinctive spatial pattern. For example, most sediment samples collected from Jinhae Bay had low gravel and sand content, respectively, and high clay content (mean = 70.6%). Interestingly, sediment parameters measured in T1 and T9 had noticeably different properties to the other stations. These two stations had, by far, the highest compositions of gravel and sand (mean = 18.7% and 39.6%) and the lowest percentage of clay (mean = 28.7%) compared to the other stations (see Table 3.4).

In Samcheok coastal area, the bottom water temperature showed distinct seasonal variation, with a slightly lower range of temperature compared to that in Jinhae Bay. The mean bottom water temperature was lowest in spring and highest in fall. The concentrations of bottom DO varied less compared to those in Jinhae Bay. Concentrations of $\text{NO}_3\text{-N}$ were relatively high in Samcheok coastal area compared to Jinhae Bay year-round, except for summer. Sediment properties in Samcheok coastal area (Table 3.4) were considerably different to those in Jinhae Bay (Table

3.4), with mainly sand of low organic matter, in general. Spatial variation in sediment properties was also found; for example, S1–3 and S8 had the greater proportion of sand compared to other stations. In comparison, S1–3 and S8 had relatively small silt content than that in other stations.

Table 3.3 Data on the macrofaunal assemblages and environmental variables identified and/or measured in the samples from Jinhae Bay; values given for three groups (TG1–TG3) identified from the cluster analysis.

	TG1	TG2	TG3
Stations	T1, T9	T2, T3, T6, T8	T4, T5, T7, T10
Macrobenthos			
Mean density (ind./m ²)	3132	435	126
Number of species	199	110	79
Dominant species (ind./m ²)			
1 st	<i>L. longifolia</i> (473)	<i>P. patiens</i> (693)	<i>T. fragilis</i> (383)
2 nd	<i>Corophium</i> sp. (174)	<i>C. capitata</i> (533)	<i>P. patiens</i> (97)
3 rd	<i>N. minor</i> (47)	<i>L. longifolia</i> (484)	<i>Tharyx</i> sp. (58)
Bottom water			
Temperature (°C)	14.9	14.6	14.1
Salinity (psu)	32.9	33.0	33.1
pH	8.2	8.1	8.1
DO (mg L ⁻¹)	8.2	7.64	6.9
COD (mg L ⁻¹)	1.4	1.4	1.2
BOD (mg L ⁻¹)	0.9	0.9	0.7
SPM (mg L ⁻¹)	5.2	4.9	4.7
TN (μmol L ⁻¹)	10.4	10.8	10.8
NO ₃ -N (μmol L ⁻¹)	2.4	2.6	3.2
PO ₄ -P (μmol L ⁻¹)	0.6	0.5	0.7
SiO ₂ -Si (μmol L ⁻¹)	8.3	8.7	12.5
Free Cl ₂ (mg L ⁻¹)	0.03	0.02	0.02
Total Cl ₂ (mg L ⁻¹)	0.04	0.03	0.03
Sediment			
Gravel (%)	18.7	1.0	0.5
Sand (%)	39.6	1.6	1.3
Silt (%)	13.1	19.9	13.6
Clay (%)	28.7	77.5	84.6
Mean grain size (Ø)	4.1	9.7	10.0
Sorting (Ø)	4.4	2.0	1.7
Skewness	0.3	-0.8	-0.7
Kurtosis	1.5	2.4	2.2
Organic matter (%)	6.4	10.9	10.6

Table 3.4. Data on the macrofaunal assemblages and environmental variables identified and/or measured in the samples from Samcheok coastal area; values given for three groups (SG1–SG3) identified from the cluster analysis.

	SG1	SG2	SG3
Stations	S1, S2, S3	S4, S5, S6, S7, S9, S10	S8
Macrobenthos			
Mean density (ind./m ²)	2470	1020	667
Number of species	139	175	98
Dominant species (ind./m ²)			
1 st	<i>S. bombyx</i> (7446)	<i>M. johnstoni</i> (2632)	<i>E. analis</i> (240)
2 nd	<i>C. teres</i> (633)	<i>L. longifolia</i> (1135)	<i>P. kefersteini</i> (143)
3 rd	<i>E. analis</i> (501)	<i>S. bombyx</i> (933)	<i>Gammaridea</i> sp. 6 (86)
Bottom water			
Temperature (°C)	12.4	8.2	10.5
Salinity (psu)	34.3	34.7	34.4
pH	8.1	8.0	8.1
DO (mg L ⁻¹)	8.6	8.4	8.4
COD (mg L ⁻¹)	0.9	0.9	1.2
BOD (mg L ⁻¹)	0.6	0.6	0.7
SPM (mg L ⁻¹)	4.3	4.9	4.2
TN (μmol L ⁻¹)	10.2	11.9	12.0
NO ₃ -N (μmol L ⁻¹)	5.7	9.6	7.2
PO ₄ -P (μmol L ⁻¹)	0.5	0.8	1.1
SiO ₂ -Si (μmol L ⁻¹)	7.5	10.2	8.1
Free Cl ₂ (mg L ⁻¹)	0.01	0.01	0.01
Total Cl ₂ (mg L ⁻¹)	0.02	0.02	0.02
Sediment			
Gravel (%)	0.0	0.0	4.8
Sand (%)	79.0	45.6	77.2
Silt (%)	8.8	33.1	8.9
Clay (%)	12.0	21.2	9.1
Mean grain size (Ø)	4.0	5.6	1.8
Sorting (Ø)	2.3	2.8	2.5
Skewness	1.2	0.8	1.4
Kurtosis	4.3	2.2	6.7
Organic matter (%)	1.7	3.8	2.3

3.3.2. Spatiotemporal patterns in macrofaunal assemblages

There was considerable temporal variability in the macrofauna assemblage with respect to both seasonal and annual changes in the study areas over the 3-year period, especially in Jinhae Bay (Fig. 3.3A). The density and species diversity of the macrozoobenthic communities in Jinhae Bay varied greatly with time, whereas Samcheok had a consistent number of species over seasons and years (Fig. 3.3B). Interestingly, in Jinhae Bay, the maximum and minimum values for abundance were recorded in fall, with the highest density in 2015 and the lowest density in 2014. In the spring of 2014, the largest number of species was found in Jinhae Bay, which decreased to about one third the number in the summer and fall of 2014. The polychaete *Lumbrineris longifolia* was the only consistent dominant species that was common at both sites over all the seasons and years.

CA was performed to delineate the station groups with similar macrozoobenthos species composition, producing three representative groups (TG1, TG2, TG3) among 10 stations in Jinhae Bay (ANOSIM: $R = 0.957$, $p = 0.002$, see Fig. 3.4). First, T1 and T9, which had corresponding sediment properties that were distinct to all other stations, were grouped together (TG1 assemblage). TG1 assemblage was characterized by the great abundance and the highest number of species per station (mean = 36.75 ± 12.31), with *L. longifolia* as a dominant species (Fig. 3.4). *L. longifolia* had the highest abundance from the fall of 2015 to the following winter. At T9 station, the density of *Corophium* sp. sharply increased in the fall of 2015, while the density of *Nicomache minor* suddenly increased in the summer of 2016. TG2 assemblage encompassed four stations (T2, T3, T6, and T8) that were situated close to the oyster farming area. In general, TG2 assemblage had moderate abundance, with a mean density of 435 ind. m⁻², as well as moderate species diversity (mean = 9.71 ± 8.17). Interestingly, some of the dominant species in TG2 assemblage, such as *Paraprionospio patiens* and *Capitella capitata*, exhibited distinct seasonal peaks (Fig. 3.3, Table 3.4). After the defaunation during summer hypoxia, the most dominant species in TG2 assemblage was *P. patiens*, occurring at



Figure 3.3.

Total species abundance (as mean density), total number of species, and density of the top 10 dominant species in (A) Jinhae Bay and (B) Samcheok coastal area, during the 3-year study period (from fall 2013 to summer 2016); 12 consecutive seasons.

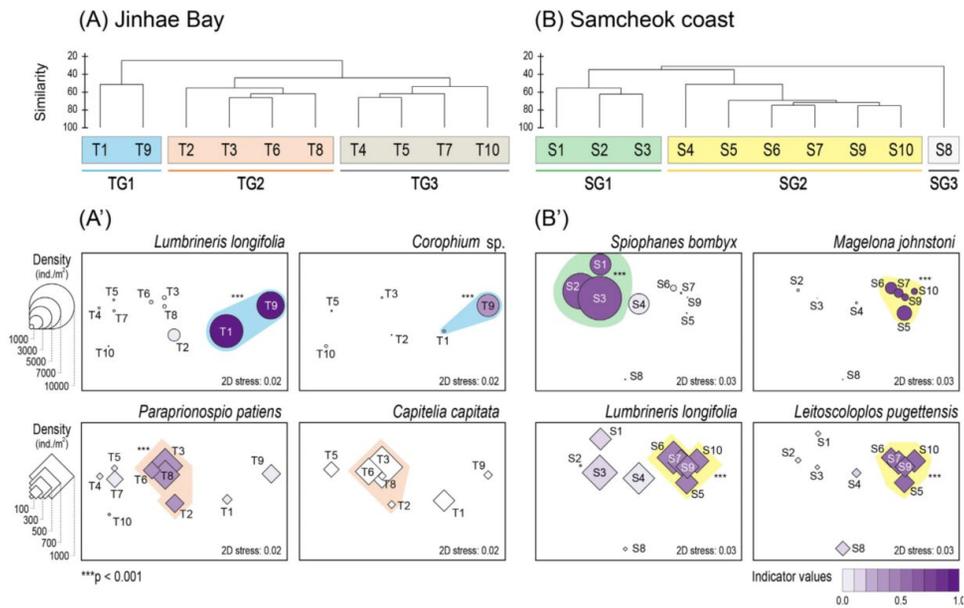


Figure 3.4.

Illustration of the macrozoobenthic community groups in the two study areas of (A) Jinhae Bay (TG1–TG3) and (B) Samcheok coastal area (SG1–SG3), based on cluster analysis and non-metric multidimensional scaling (NMDS). NMDS provides information on the top four dominant species, including density and indicator values.

high densities from the fall of 2014 to the summer of 2015. *C. capitata* peaked every spring, except for the spring of 2016. *Theora fragilis* was observed instead of *C. capitata* in the spring of 2016. In comparison, *L. longifolia* only occurred at high density in the summer of 2016.

Finally, T4, T5, T7, and T10 stations, which were primarily located in the northern part of Jinhae Bay, belonged to the TG3 assemblage. This assemblage was characterized by the lowest abundance, with a mean density of 126 ind. m⁻², and the lowest number of species (mean = 5.87±4.44). However, the TG3 assemblage also showed noticeable peaks in density for certain dominant species, such as *T. fragilis* and *P. patiens* (Fig. 3.2, Table 3.2). The most dominant species in the TG3 assemblage, *T. fragilis*, was dominant from the winter of early 2016 to the following spring. *P. patiens* dominated the assemblage in the fall of 2014 after the summer hypoxia. This species was also observed in the winter of early 2014, and peaked in the spring of 2015.

In Samcheok coastal area, the highest density was recorded in the fall of 2013, while the lowest density was found in the winter of early 2014, when the number of species was also at its lowest. Except for the winter of early 2014, the number of species in Samcheok coastal area remained fairly constant over years and seasons. The most commonly occurring species was the polychete *Spiophanes bombyx*, which was consistently and abundantly found throughout the study period, except from the summer of 2015 to the winter of early 2016. *Euchone analis* exhibited relatively constant seasonal patterns, peaking every summer, except for 2016. In general, the Samcheok coastal area showed less dynamic structure compared to Jinhae Bay in terms of the number of species.

The Samcheok coastal area was also divided into three distinct station groups (SG1, SG2, SG3) by CA (ANOSIM: R = 971, *p* = 0.001, Fig. 3.3). The SG1 assemblage included S1, S2, and S3, which were located relatively close to the land; namely, the shallow subtidal stations (depth range = 15–20 m). This group was characterized by the greatest abundance of 2,470 ind. m⁻². The most dominant

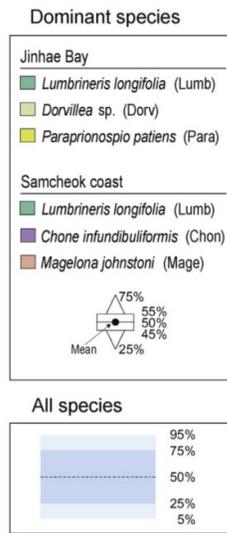
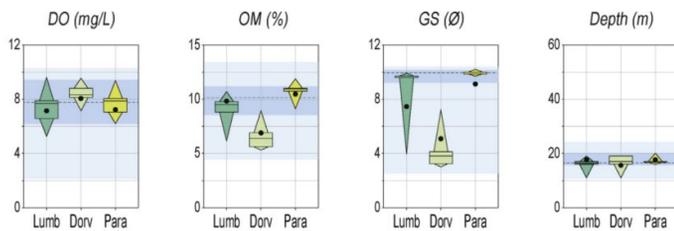
species *S. bombyx* occurred in high density with irregular seasonal variations over the entire study period. However, the density of *S. bombyx* sharply decreased from the summer of 2015 to the winter of early 2016. The abundance of *Euchone analis* was high in the summer, except 2016. *L. longifolia* was consistently observed at station S3. SG2 assemblage contained six stations (S4, S5, S6, S7, S9, and S10) that were located deeper offshore, at a depth range of 45–52 m. This group was characterized by the highest number of species, with a mean density of 1,020 ind. m⁻². *Magelona johnstoni* was the most dominant species in the SG2 assemblage, exhibiting irregular temporal variation. *L. longifolia* was steadily present over the entire study period. The SG3 assemblage only contained S8, and had the smallest abundance, with a mean density of 667 ind. m⁻² and the lowest number of species. The abundance of *E. analis* peaked in the summer of 2015.

3.3.3. Environment-macrofauna relationship

Out of the observed spatial variations in water quality parameters and bottom sediment properties, four environmental variables (namely organic matter, DO, Mz, and depth) noticeably differed between Jinhae Bay and Samcheok coastal area. Figure 3.5 shows the dominant species associated with the four environmental factors. The ranges of all species (blue shaded in Fig. 3.5) was distinct between two areas. For example, over half of the macrozoobenthos in Jinhae Bay occurred in an organic matter range of 8.5% to 11.3%, while over half of the macrozoobenthos in Samcheok coast occurred at a much lower organic matter (1.4–2.8%). Mz and depth showed similar distinctions, for example, half of the species in Jinhae Bay occurred in fine sediment and at shallow depths (Mz, 9.2–10.1; depth range, 16–20 m), but over half of the species in Samcheok occurred in coarser sediment and deeper water (Mz, 3.7–6; depth, 25–47 m). However, some species, such as *Dorvillea* sp. in Jinhae Bay and *Chone infundibuliformis* in Samcheok coast, showed distinct patterns.

Nicomache minor, *Dorvillea* sp., and *Armandia lanceoloata* mainly occurred in specific environments that were characterized by relatively low organic matter content (Fig. 3.6). In comparison, *P. patiens*, *C. capitata*, and *T. fragilis* were mainly found in the relatively narrow range of high organic matter content in sediments. However, *Corophium* sp., *Sigambra tentaculata*, *Lumbrineris longifolia*, and *Praxillella affinis* occurred in a relatively wide range of organic matter and Mz.

(A) Jinhae Bay



(B) Samcheok coast

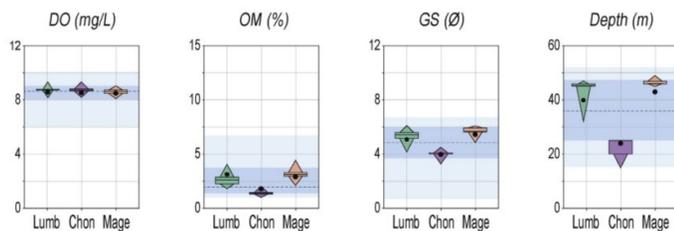


Figure 3.5.

Box-and-whisker plots (minimum, 25%, median, 75%, and maximum) for the three selected species each in the two study areas of (A) Jinhae Bay (Lumb, *Lumbrineris longifolia*; Dorv, *Dorvillea* sp.; Para, *Paraprionospio patiens*) and (B) Samcheok coastal area (Chon, *Chone infundibuliformis*; Mage, *Magelona johnstoni*; Euch, *Euchone analis*), with respect to parameters of species abundance (density), diversity index (H'), dissolved oxygen (DO), organic matter (OM), mean grain size (Mz), and depth.

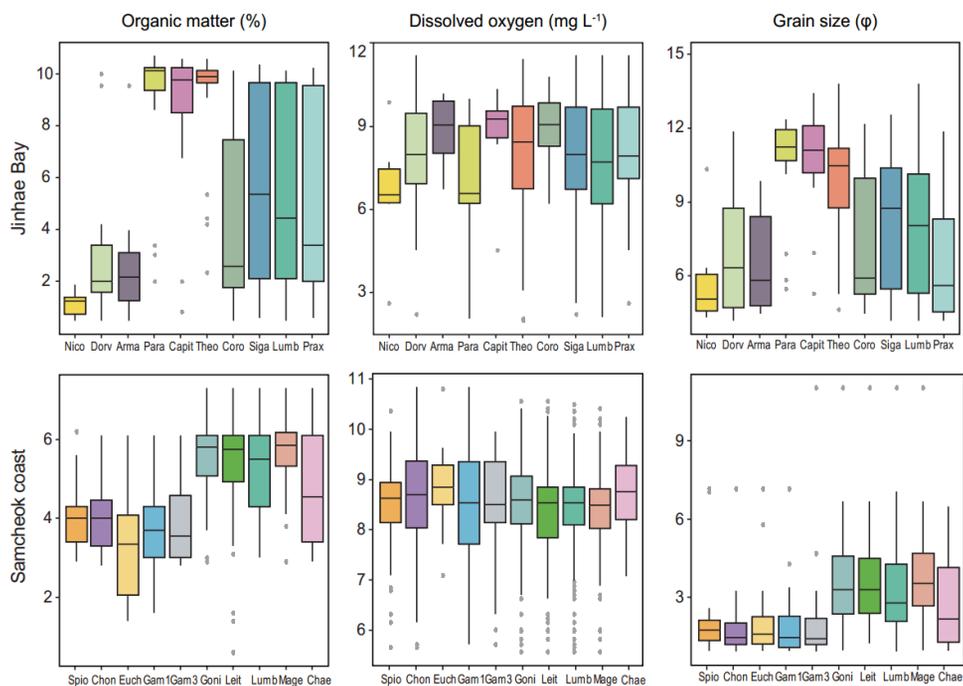


Figure 3.6.

Box-and-whisker plots (minimum, 25%, median, 75%, maximum) for 20 dominant species with respect to organic matter, dissolved oxygen, and grain size in study area (Jinhae Bay and Samcheok coast). The species are abbreviated as four-letter codes; Nico, *Nicomache minor*; Dorv, *Dorvillea* sp.; Arma, *Armandia lanceolata*; Para, *Paraprionospio patiens*; Capi, *Capitella capitata*; Theo, *Theora fragilis*; Coro, *Corophium* sp.; Siga, *Sigambra tentaculata*; Lumb, *Lumbrineris longifolia*; Prax, *Praxillella affinis*; Spio, *Spiophanes bombyx*; Chon, *Chone teres*; Euch, *Euchone analis*; Gam1, *Gammaridea* 1; Gam3, *Gammaridea* 3; Goni, *Goniada maculate*; Leit, *Leitoscoloplos pugettensis*; Mage, *Magelona johnstoni*; Chae, *Chaetozone setosa*.

3.4. Discussion

3.4.1. Key factors influencing the occurrence and distribution of macrofauna

PCA confirmed that macrofauna assemblages were correlated with specific environmental variables, including water quality indices and/or sediment properties (Fig. 3.6).

In Jinhae Bay, the first axis (PC1) was mainly explained by water quality parameters, indicating seasonal effects. One of the most noticeable water quality parameters was found to be bottom DO, which could be potentially fatal to macrozoobenthic communities. At the extreme range in conditions, hypoxia occurred in some of the southern parts of Jinhae Bay during the summer. It seemed to be the result of the combined effects of natural (restricted circulation) and anthropogenic (a large oyster farming area) induced processes (Lim et al. 2006). Thus, changes to species composition, and even the elimination of macrozoobenthos, were observed in the southern parts of Jinhae Bay, which was the hypoxic area. Changes to species composition, including species extinction, might occur more frequently in heavily contaminated coastal areas (Yoon et al. 2017). Hypoxia has direct/indirect effects on the survival of organisms (Gray et al. 2002, Middelburg and Levin 2009). Threshold effects at community levels have been well documented with respect to oxygen deficiency (Nilsson and Rosenberg 1994, Diaz and Rosenberg 1995, Levin and Gage 1998), and previous studies have reported the complete loss of macrozoobenthos in hypoxic or anoxic areas (Middelburg and Levin 2009), which was supported by our study. The second axis (PC2) may be explained by sediment properties, including Mz and organic matter. While most sediments in Jinhae Bay sediments were composed of fine-grained particles, high gravel/sand content and extremely poorly sorted sediment were the main features of TG 1. The exceptional conditions were positively correlated with total density, H' , and the density of the dominant species (*L. longifolia*) in Jinhae Bay.

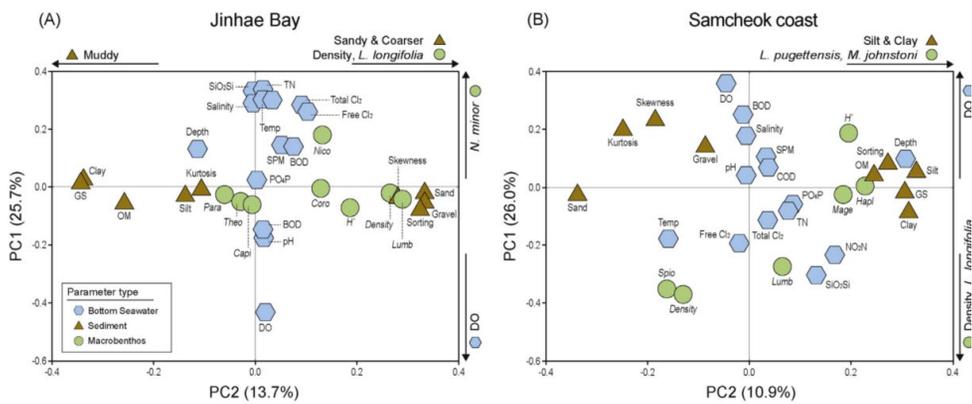


Figure 3.7.

Principal component analysis of macrobenthos (including total species abundance, H' index, and density of dominant species) and 22 environmental variables, including parameters of water quality (refer to all the raw data in App. 1 of the Supplementary Materials) and sediment property (refer to all the raw data in App. 2 of the Supplementary Materials), for (A) Jinhae Bay and (B) Samcheok coastal area.

In Samcheok coastal area, the first axis (PC1) was mainly explained by water quality, similar to Jinhae Bay. However, the parameter-wise association was differed to that of Jinhae Bay. DO, BOD, and salinity were negatively correlated with the density of *Spiophanes bombyx*, *L. longifolia*, total density, and species diversity. The second axis (PC2) was mainly explained by sediment properties and water depth. Sand content was positively correlated with a sandy tube-dwelling polychaete, *S. bombyx* (dominant species of SG1 assemblage) and total density. This result supported the close association between sediment properties and macrofaunal assemblages. Previous studies noted the sand-favoring characteristics of *S. bombyx* (Holtmann et al. 1996). Samcheok coastal area is an open sea habitat with a sandy environment, and is generally characterized by relatively moderate to low organic matter content. Unlike Jinhae Bay where excessive organic matter used to aggravate poor conditions, such as hypoxia, moderate organic matter content is positively associated with some macrozoobenthos in low organic matter environments (Weston 1990), such as Samcheok coastal area.

Furthermore, DA was used to determine which environmental variables best explained the differences among the groups determined by CA (Table 3.5, 3.6, Fig. 3.7). The DAs formulated the discriminant functions (DFs) for Jinhae and Samcheok, respectively, using Eq (3) and Eq (4).

$$\text{DF-Jinhae} = a \cdot \text{Gravel} + b \cdot \text{Mz} + c \cdot \text{Organic matter} + d \cdot \text{Depth} + e \cdot \text{DO} \quad \text{Eq (3)}$$

$$\text{DF-Samcheok} = a \cdot \text{Free Cl}_2 + b \cdot \text{Gravel} + c \cdot \text{Depth} \quad \text{Eq (4)}$$

where, a–e should be replaced by the standardized canonical discriminant coefficients presented in Table 3.5 and 3.6. Standardized DF coefficients refer to the relative contribution of environmental variables in calculating the discriminant scores for each DF. Accordingly, the coefficients might be used as a measure of the relative importance of variables between groups (Weston 1988).

Table 3.5. Discriminant analysis of environmental variables among the three groups in Jinhae Bay.

Discriminant function (DF)		DF1	DF2	
Details				
<i>Relative percent of discriminating power</i>		96.1	3.9	
<i>Eigen Value</i>		24.975	1.011	
<i>Canonical correlation</i>		0.981	0.709	
<i>Test of significance</i>				
Chi-squared value		138.454	24.454	
Significance level		p<0.001	p<0.001	
Degree of freedom		10	4	
<i>Standardized canonical discriminant function coefficients</i>				
Gravel		0.756	0.105	
Mean grain size (Mz)		1.903	0.181	
Organic matter (OM)		0.711	-0.569	
Depth		0.836	0.974	
Dissolved oxygen (DO)		-1.666	-0.161	
<i>Total structure coefficient (correlations between DFs and variables)</i>				
Gravel		-0.402	0.224	
Mean grain size (Mz)		0.47	-0.378	
Organic matter (OM)		0.366	-0.441	
Depth		0.169	0.795	
Dissolved oxygen (DO)		-0.005	-0.12	
Classification matrix for 40 cases (10 locations × 4 seasons)				
Original group	Number of stations	Predicted groups (%-accuracy)		
		TG1	TG2	TG3
TG1	8	8 (100%)	0	0
TG2	16	0	16 (100%)	0
TG3	16	0	0	16 (100%)

Table 3.6. Discriminant analysis of environmental variables among the three groups in Samcheok coastal area.

Discriminant function (DF)				
Details	DF1	DF2		
<i>Relative percent of discriminating power</i>	86.8	13.2		
<i>Eigen Value</i>	40.879	6.197		
<i>Canonical correlation</i>	0.988	0.928		
<i>Test of significance</i>				
Chi-squared value	205.50	71.052		
	5			
Significance level	p<0.001	p<0.001		
	1			
Degree of freedom	6	2		
<i>Standardized canonical discriminant function coefficients</i>				
Free Cl ₂	-0.769	-0.105		
Gravel	1.175	-0.045		
Depth	-0.075	0.99		
<i>Total structure coefficient (correlations between DFs and variables)</i>				
Free Cl ₂	-0.141	-0.162		
Gravel	0.76	-0.043		
Depth	0.02	0.991		
Classification matrix for 40 cases (10 locations × 4 seasons)				
Original group	Number of stations	Predicted groups (%-accuracy)		
		SG1	SG2	SG3
SG1	12	12 (100%)	0	0
SG2	24	0	24 (100%)	0
SG3	4	0	0	4 (100%)

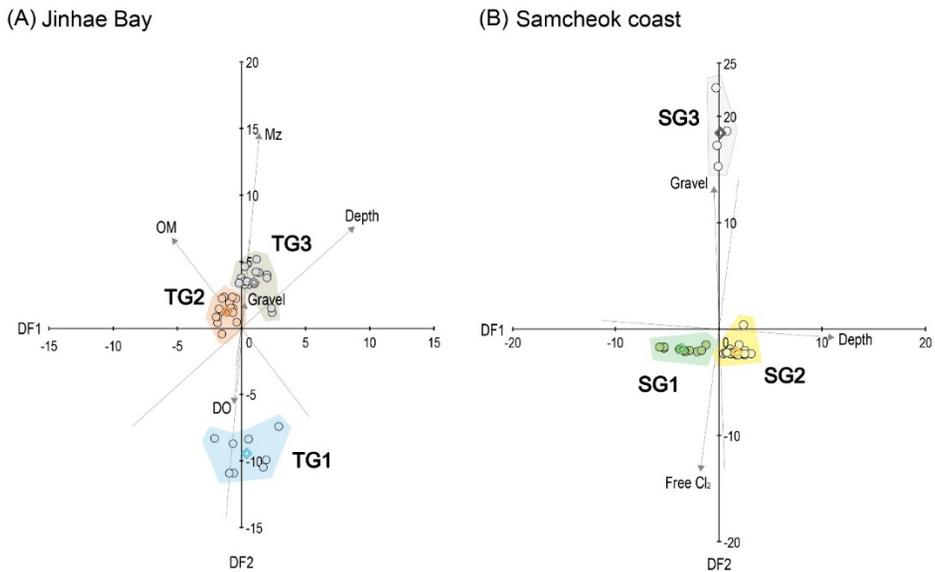


Figure 3.8

Ordination of assemblage groups in the two-factor discriminant space, in (A) Jinhae Bay (TG1-TG3) and Samcheok coastal area (SG1-SG3). Vectors indicating the relative orientation of the environmental variables also given; determined from the correlation coefficients between the discriminant functions (DF1-DF2) and the environmental variables (gravel, mean grain size (Mz), organic matter (OM), dissolved oxygen (DO), and depth for Jinhae Bay; free Cl₂, gravel, and depth for Samcheok coastal area).

The first DF had the strongest discriminating power in Jinhae Bay (96.1%). The standardized DF coefficients indicate that the environmental descriptors that best accounted for among-group variation were Mz and DO (Table 3.4). Figure 3.7A shows that the three groups were distributed along four gradients, the first of which was dominated by Mz (with TG2 and TG3 in coarse sediment and TG1 in fine sediment) and the second of which was dominated by DO, which showed the opposite correlation with Mz.

In Samcheok coastal area, gravel and free Cl_2 were identified as the most significant discriminating variables on DF1, followed by depth on DF2. The Pearson product-moment correlations between DFs and environmental variables (total structure coefficient) indicated the potential environmental factors that discriminate groups. Overall, the two DFs accurately predicted the faunal assemblage groups in both Jinhae Bay and Samcheok coastal area, based on the selected environmental variables in the corresponding areas. The functions represented a prediction accuracy of 100%, exactly matching the faunal assemblages in 40 cases (10 stations \times 4 seasons) in each of the study areas

3.4.2. Variation in species composition

Several features or patterns were identified in the species composition of the macrozoobenthos between the two contrasting habitats. First, seasonal fluctuations in species composition were clearly observed for the macrofaunal assemblage of Jinhae Bay. This seasonal variation was recorded at both species and community level (Fig. 3.2). The abundance of some dominant species sharply increased and then disappeared in the very next season, while some macrofauna were not observed at certain stations or during certain seasons.

C. capitata showed a clear seasonal pattern in abundance, peaking in spring at T3 and T6, but noticeably declined in the following season. The environment with an organic-enriched bottom together with reduced competitors might have allowed *C. capitata* numbers to increase explosively. Alternatively, the increased abundance of *C. capitata* in specific seasons might have been associated with its life cycle (Tsutsumi and Kikuchi 1984, Tsutsumi 1987). However, the abundance of *T. fragilis* increased in the spring of 2015, replacing *C. capitata*, as the dominant species. Perhaps, these two species are able to replace one another, as they have similar environmental preferences and are organic enrichment indicators. Interestingly, *T. fragilis* was present in more severe environments, such as sediment with extremely high organic matter and low concentrations of DO (Poore and Kudenov 1978).

Furthermore, different species dominated in the same season of different years, with a case in point being *C. capitata* and *T. fragilis* in Jinhae Bay. This phenomenon possibly arose due to the specific effect of environmental factors. For instance, the excessive inflow of organic matter or lower temperatures than average might have facilitated the dominance of opportunistic species in a given season of a given year. In addition, heterogeneity in the same habitat altered species compositions.

Seasonal changes to macrozoobenthos assemblage were only significant in Jinhae Bay, which is a typical semi-enclosed bay. In comparison, the lack of seasonal changes seemed to be a key characteristic of the Samcheok coastal community. The ranges of seasonal fluctuations or the timing of peaks and declines varied less across

the stations at the Samcheok coast compared to Jinhae Bay. Despite this, obvious seasonal patterns in the dominance of some macrozoobenthos occurred in the Samcheok assemblage (Fig. 3.8, 3.9). In any case, the less contaminated Samcheok environment show a relatively stable community structure in time and space, in which assemblage groups were primarily discriminated by geophysical factors, such as %-gravel and depth, rather than pollution indices. The negative effects on growth and/or reproduction of macrobenthos living in contaminated sediments have been reported earlier in the coastal areas of Korea, particularly in semi-enclosed industrial bays (Ryu et al. 2016).

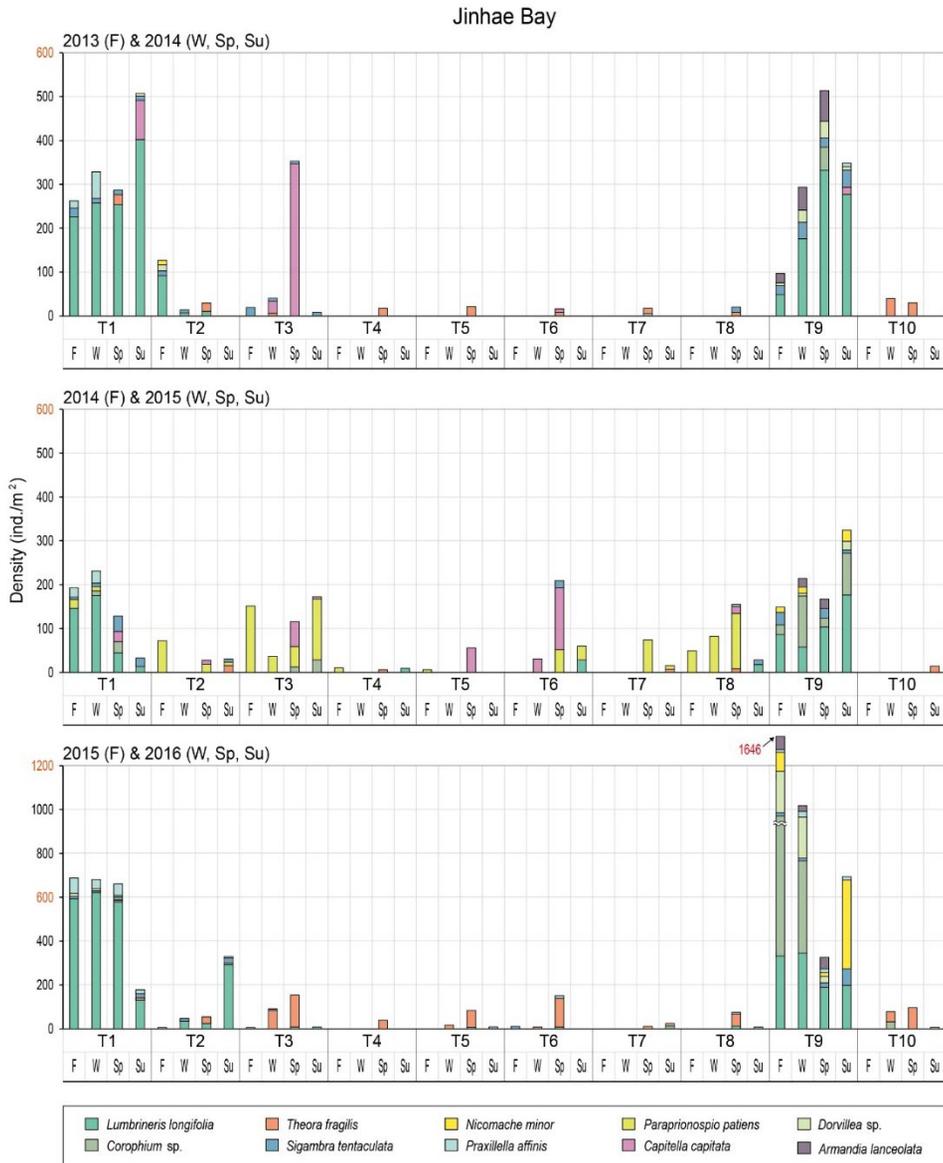


Figure 3.9.
Spatiotemporal distribution of dominant species in Jinhae Bay.

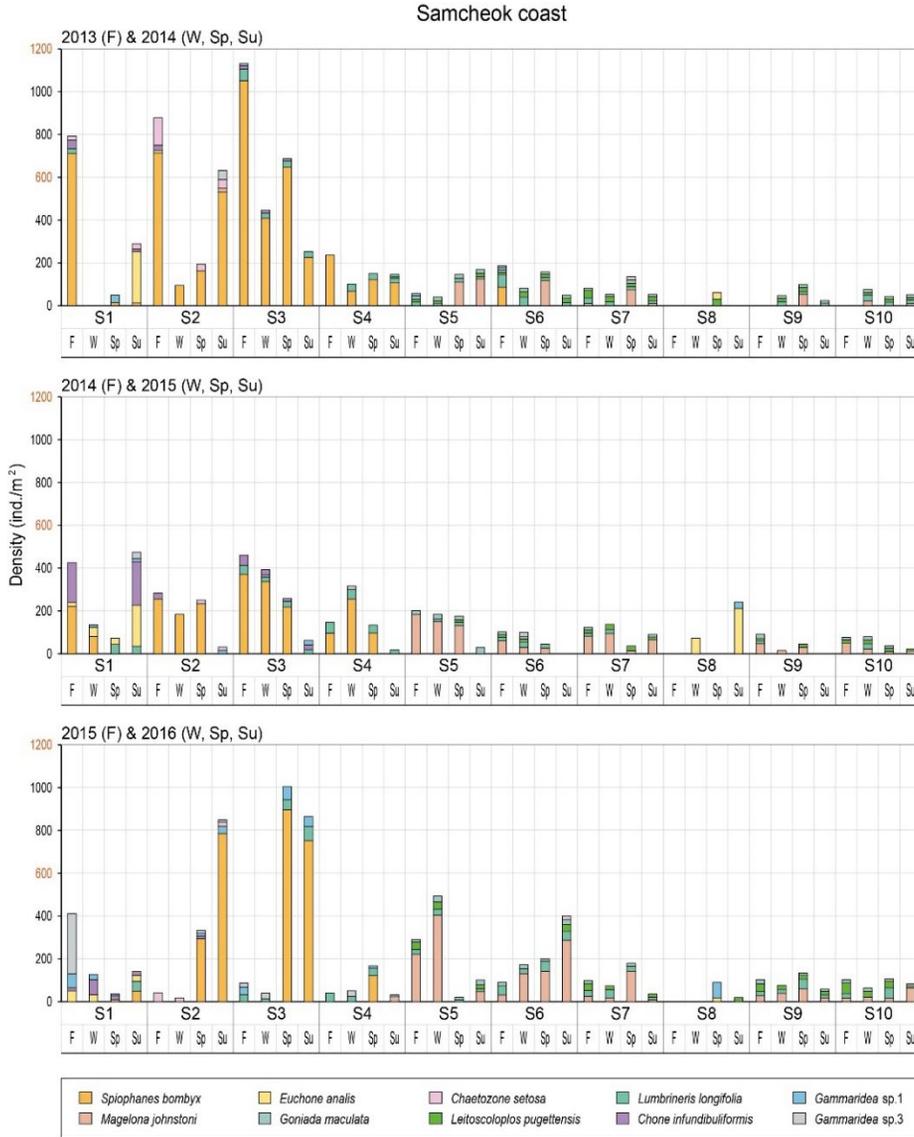


Figure 3.10
Spatiotemporal distribution of dominant species in Samcheok coastal area.

3.4.3 Indicator species

CA and NMDS are useful tools for analyzing the dynamic ecosystems observed in the two contrasting environments, by grouping assemblages that showed similar patterns (Fig. 3.3). Furthermore, IndVal identified a total of 26 indicator species ($p < 0.1$ in IndVal) that corresponded to the clustered groups in the two study areas (Fig. 3.3, Table 3.7). Indicator species also reflected specific environments. For instance, *L. longifolia* and *Dorvillea* sp. were indicator species of TG1 assemblages, which were characterized by relatively low organic matter and sandy bottoms. In comparison, *P. patiens* was an indicator species of TG2 assemblage, which was characterized by enriched organic matter and muddy bottoms.

Indicator species could be used to define a certain trait or characteristic of given habitats, by considering the distinctive environmental characteristics of each group, the indicator values of the species present in the groups, and the environmental preferences of the species. Thus, we could infer the environmental conditions of an unknown area, if we had information about the species composition in that area. Alternatively, we could infer the species composition of an unknown area, if we had sufficient information about the environmental conditions and indicator species in that area. Overall, the lack of overlapping in the indicator species was the two study areas, supporting the two contrasting macrofaunal assemblages. The two species, the polychaete *P. affinis* and the arthropod *Gammaridea* sp. 1 were identified as indicator species in Jinhae Bay (for TG1 assemblage) and Samcheok coastal area (for SG1 assemblage), respectively, and might represent potential sentinel species for biomonitoring the two contrasting marine environments.

Table 3.7. IndVal analysis listing the indicator species in the groups delineated for Jinhae Bay and Samcheok coastal area.

Jinhae Bay				Samcheok coast			
Indicator species	TG1	TG2	TG3	Indicator species	SG1	SG2	SG3
<i>Lumbrineris longifolia</i>	0.95	0.02	0.00	<i>Chone infundibuliformis</i>	0.93	0.00	0.00
<i>Dorvillea</i> sp.	0.90	0.00	-	<i>Nephtys polybranchia</i>	0.85	0.00	0.00
<i>Sigambra tentaculata</i>	0.78	0.16	0.01	<i>Spiophanes bombyx</i>	0.70	0.01	0.00
<i>Polydora</i> sp.	0.76	0.01	0.00	<i>Gammaridea</i> sp. 3	0.59	0.03	0.00
<i>Chone infundibuliformis</i>	0.71	0.01	-	<i>Gammaridea</i> sp. 4	0.56	0.01	0.03
<i>Praxillella affinis</i>	0.70	0.01	0.00	<i>Cumacea</i> sp.	0.55	0.01	0.09
<i>Gammaridea</i> sp. 1	0.58	0.02	0.00	<i>Gammaridea</i> sp. 1	0.48	0.02	0.11
<i>Armandia lanceolata</i>	0.54	-	-	<i>Gammaridea</i> sp. 5	0.47	0.01	0.16
<i>Corophium</i> sp.	0.49	-	0.00	<i>Magelona johnstoni</i>	0.01	0.82	0.00
<i>Paraprionospio patiens</i>	0.01	0.45	0.04	<i>Maldane cristata</i>	-	0.79	-
				<i>Goniada maculata</i>	0.17	0.73	0.01
				<i>Leitoscoloplos pugettensis</i>	0.01	0.61	0.25
				<i>Axinopsida subquadrata</i>	0.00	0.56	0.00
				<i>Lumbrineris longifolia</i>	0.27	0.56	0.00
				<i>Ophiuroidea</i> sp.	0.00	0.47	0.01
				<i>Euchone analis</i>	0.14	0.00	0.25

3.5. Summary

A long-term study on a benthic community was conducted in two different localities, in semi-enclosed bay of Jinhae and open sea area of Samcheok, Korea. We aimed to identify the spatiotemporal patterns of macrozoobenthos and the environmental variables influencing such patterns in the two contrasting habitats. The macrozoobenthos assemblages on the soft bottom of the subtidal zone were analyzed over 3 years encompassing 12 consecutive seasons. Accordingly, several ecological indices (such as the number of species, abundance, dominant species, and diversity index (H')) generally reflected site-specific benthic conditions. The macrofaunal community at Jinhae showed typical seasonal fluctuations, whereas the Samcheok community showed no significant change over time and space. Region- or site-dependent temporal variabilities of macrofaunal assemblages are depicted through cluster analysis (CA), indicating distinct temporal changes in the composition of dominant species. In particular, the abundance of some dominant species noticeably declined in certain seasons when several opportunistic species peaked. Such faunal succession might be explained by significant changes to specific environmental factors, such as bottom dissolved oxygen, grain size, and water depth. In addition, discriminant analysis confirmed the presence of several site-specific parameters for the faunal assemblage groups identified through CA. Finally, indicator value analysis identified species that were representative across stations and regions in accordance with their habitat preference and/or species tolerance. Overall, the two contrasting marine habitats showed distinct community differences, in time and space, that were influenced by site-dependent environmental conditions.

CHAPTER 4.

Distribution and historical records of diatom assemblages in surface and sediment cores from the Yellow and Bohai seas under anthropogenic pressure

This chapter has prepared to submitted

4.1. Introduction

Tidal flat is one of the most important coastal habitats, representing a key contributor to the maintenance of various marine ecosystems and services (Costanza et al. 1997, Barter 2002). These important habitats are increasingly threatened by human activities (Halpern et al. 2008), being primarily exposed to land-based stressors (Halpern et al. 2019). Rapid urbanization and industrialization have led to more terrestrial-origin pollutants ending up in the ocean via rivers (Galloway et al. 2008), and even the atmosphere; these pollutants can affect marine ecosystems, and evidence of their presence can be seen in the changing chemical composition of the oceans (Doney et al. 2007, Duce et al. 2008). Several previous studies have demonstrated that using fossil fuels, together with pollutants in runoff from agriculture and animal husbandry, can affect the marine environment (Doney et al. 2007, Kim et al. 2011). Terrestrial nitrogen pollutants, for example, can cause major changes in the community composition of the primary producers that form the basis of marine ecosystems (Kim et al. 2011). There are also reports that terrestrial nitrogen loads can lead to chlorophyll concentration changes (Lawrence et al. 2004a).

Half of the global population lives within 100 km of the coast, and this is also where most urbanization and industrialization are concentrated. In a marine ecosystem impact trend related to the recent rapid economic growth in East Asia, including areas such as Korea and China, emissions of terrestrial origin organic matter are increasing. The Yellow Sea (~10,486 km²) ecology contains some remarkable coastal habitats (Deppe 1999). Although regarded as a high ecological value area as it provides habitats for various marine organisms, it has been reported as suffering significant ecosystem damage from external artificial pressures.

Eastern China is adjacent to the area known as the 'Yellow and Bohai Seas', and supplies them with freshwater and terrestrial organic matter through rivers. This part of China is experiencing significantly increased urbanization, reporting average annual growth rates of 2.5% (Dong et al. 2018). Over 70% of the Chinese population

lives in its eastern regions, and development in this region has led to more terrestrial-origin pollutants reaching coastal areas (Zhang et al. 2017). Increasing human population and industrial activities have caused increases in the concentrations of polluting nitrogen species in particular (Galloway et al. 2008). In Korea, large-scale reclamation projects have been carried out in recent decades, due to societal demands, and large areas of natural tidal flats have been lost. Rapid industrialization and urbanization have caused pollution, and have resulted in increased threats to marine ecosystems. In response to this, a great deal of effort has gone into reducing marine pollution from these areas, in recent years (Lee et al. 2016, Lee et al. 2018).

Diatoms are taxa which are widespread across all coastal habitats (Round et al. 1990); they inhabit various substrates, in various habitats—including tidal flats, estuaries, soft / hard bottom subtidal areas, tidal pools, and so on—and flourish even in extreme environments, such as hypersaline, polluted, or acidic environments (DeNicola 2000, De Lomas et al. 2005). Thus, diatoms play a major role as marine primary producers, and as food sources present in many habitats. As diatom frustules (the siliceous exoskeleton) can be preserved for long periods of time (Sawai 2001), their presence, numbers and taxonomy can be monitored in terms of investigating present condition and historical dynamics (Round et al. 1990). Monitoring diatoms is one of most effective ways to investigate large areas, in terms of ecological assessment and the historical record.

As there are numerous such taxa, species-level diatom monitoring requires taxonomic expertise (Kelly et al. 1995). While some reports have assessed aquatic ecosystems using genus-level identification (Kelly et al. 1995, Chessman et al. 1999), Round (1991) cautioned that it would be dangerous to compare aquatic ecosystems based simply on genus-level comparisons, while results obtained from using higher-level taxonomic identification would be even more dubious. In contrast, Chen et al. (2016) reported that genus composition outperformed species composition in describing relationships between diatoms and selected environmental variables. These contrasting views indicate that performing ecological assessment using

diatoms identified at the genus level remains controversial.

The combined Yellow and Bohai seas are globally recognized marine habitats exhibiting high levels of diversity, however, strong human pressures, including the presence of land-derived contaminants, are threatening these valuable ecosystems. In order to investigate the wider habitat, diatom assemblages, which very commonly distributed in the past and present, were investigated. The objectives of the study described here were as follows:

- 1) To compare the efficiencies of benthic diatom species- and genus-level monitoring in tidal flats;
- 2) To monitor general diatomic compositions in the Yellow and Bohai Seas, for 2018; and,
- 3) To analyze sediment cores to evaluate the changes in the diatom communities inhabiting the Yellow and Bohai Seas over the past 100 years.

Diatom monitoring allows us to understand the past and present state of the ecosystem, and gives us the opportunity to suggest future trends.

4.2. Materials and Methods

4.2.1. Sampling and laboratory analyses

Sampling was conducted to examine two targets (Fig. 4.1, Table 4.1): (1) surface diatomic biota, representing the ecological condition current at the time of sampling (summer 2018); (2) sediment core biota (taken at three stations) representing historical conditions. Sediment samples were obtained from the Yellow and Bohai Seas, mainly from estuarine areas (except Station NT). Core samples were subsampled in the 0–5, 20–25, and 40–45 cm ranges, in order to analyze changes to sediment parameters and diatoms over time.

As for analysis of diatom assemblages, the top 0.5 cm of surface sediment was collected. Light microscope (BX53; Olympus, Tokyo, Japan) was used to obtain photographic documentation of diatoms as well as species identification. Diatoms were identified to the species level as possible. Light microscop h photographs of diatoms were presented in Figure 4.2

First, surface sediments (< 3 cm) were sampled to analyze general sediment properties such as water content, mud content, and total organic content. In addition, sediment chlorophylls were measured as for a proxy biomass for estimation of benthic diatoms. Second, stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in sediment were measured using an Elemental Analyzer-Isotope Ratio Mass Spectrometer (EA-IRMS; Elementar, GmbH, Hanau, Germany). Third, seawater parameters were measured in situ using multi-parameter water quality probe (YSI-Professional Plus; Ohio, OH, USA). They include temperature ($^{\circ}\text{C}$), dissolved oxygen (DO, mg L^{-1}), salinity (psu), and pH. Photographs of site and field survey vies are given in Figure 4.3.

Table 4.1. Information of sampling area with 18 samples in Yellow and Bohai seas.

	ID	Depth	Natio- nal	Latitude	Longitude	Type	Landuse	Tide range (m)	Remark
Dataset I present condition	DD	Surface	China	39°50'17.88"N	123°39'10.08"E	Estuary	Agriculture	4.0	A lot of fish ponds nearby
	DL	Surface	China	39°39'47.88"N	122°59'38.04"E	Estuary	Municipal	4.0	An area where three rivers join
	TS	Surface	China	39°25'50.88"N	119°16'48.00"E	Estuary	Agriculture	1.7	Some fish ponds nearby
	TJ	Surface	China	38°46'0.12"N	117°34'9.84"E	Estuary	Municipal	3.7	A dike nearby
	WF	Surface	China	37° 5'31.56"N	119°33'35.64"E	Estuary	Agriculture	1.8	Sandy area
	YT	Surface	China	37°34'31.08"N	121°17'47.76"E	Estuary	Municipal	1.7	Many ships nearby
	QD 1	Surface	China	36°15'39.24"N	120°19'33.24"E	Estuary	Municipal	4.8	Near the airport
	RZ	Surface	China	35°17'52.80"N	119°26'53.52"E	Estuary	Municipal	5.0	Some fish farm nearby
	NT	Surface	China	32°29'30.84"N	121°13'21.36"E	Coastal	Agriculture	5.4	
Dataset II historical condition	AS	0–5 cm	Korea	36°54'55.44"N	126°54'18.72"E	Estuary	Agriculture	9.6	
	AS	20–25 cm	Korea	36°54'55.44"N	126°54'18.72"E	Estuary	Agriculture		
	AS	40–45 cm	Korea	36°54'55.44"N	126°54'18.72"E	Estuary	Agriculture		
	YK	0–5 cm	China	40°25'30.00"N	122°17'3.84"E	Estuary	Agriculture	4.1	
	YK	20–25 cm	China	40°25'30.00"N	122°17'3.84"E	Estuary	Agriculture		Small confield nearby
	YK	40–45 cm	China	40°25'30.00"N	122°17'3.84"E	Estuary	Agriculture		
	QD 2	0–5 cm	China	36°14'7.08"N	120° 7'14.16"E	Estuary	Municipal	4.8	Between the river and estuary, under a bridge
	QD 2	20–25 cm	China	36°14'7.08"N	120° 7'14.16"E	Estuary	Municipal		
QD 2	40–45 cm	China	36°14'7.08"N	120° 7'14.16"E	Estuary	Municipal			

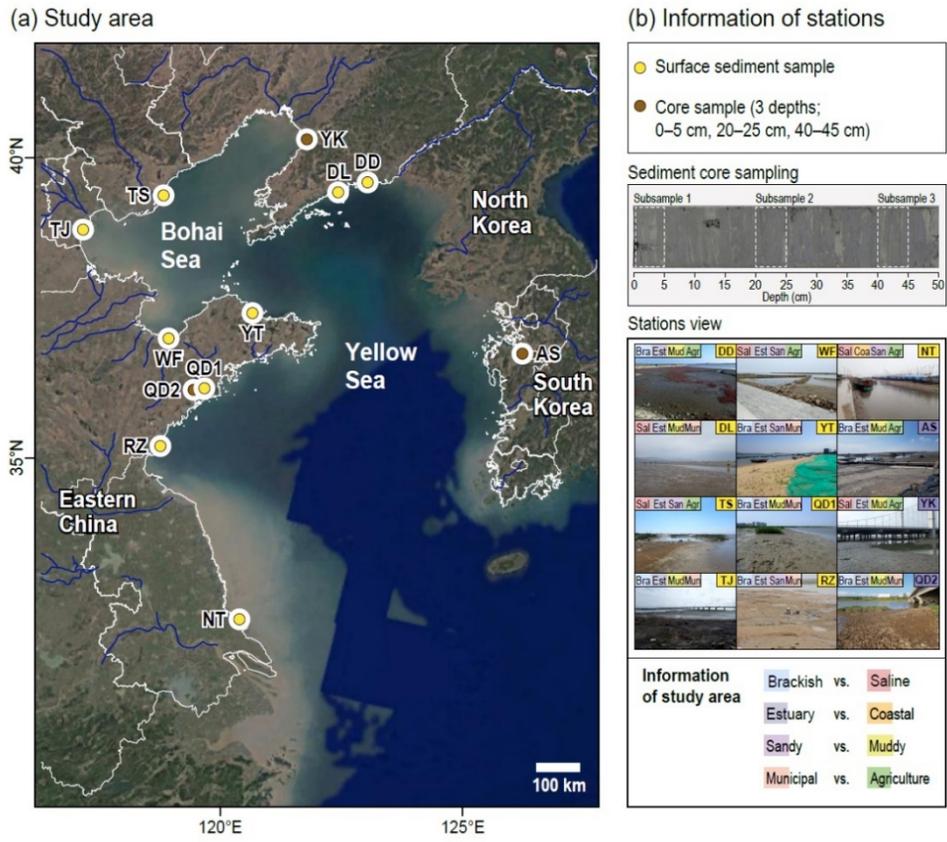


Figure 4.1.

Map showing the study area and stations and its surrounding environmental condition. (a) Stations located on Yellow and Bohai seas, in South Korea and East China. The city boundaries (white line) and rivers (blue line) were also given on the map. (b) Photographic information for each station with general information of environmental condition. (c) Sampling information.

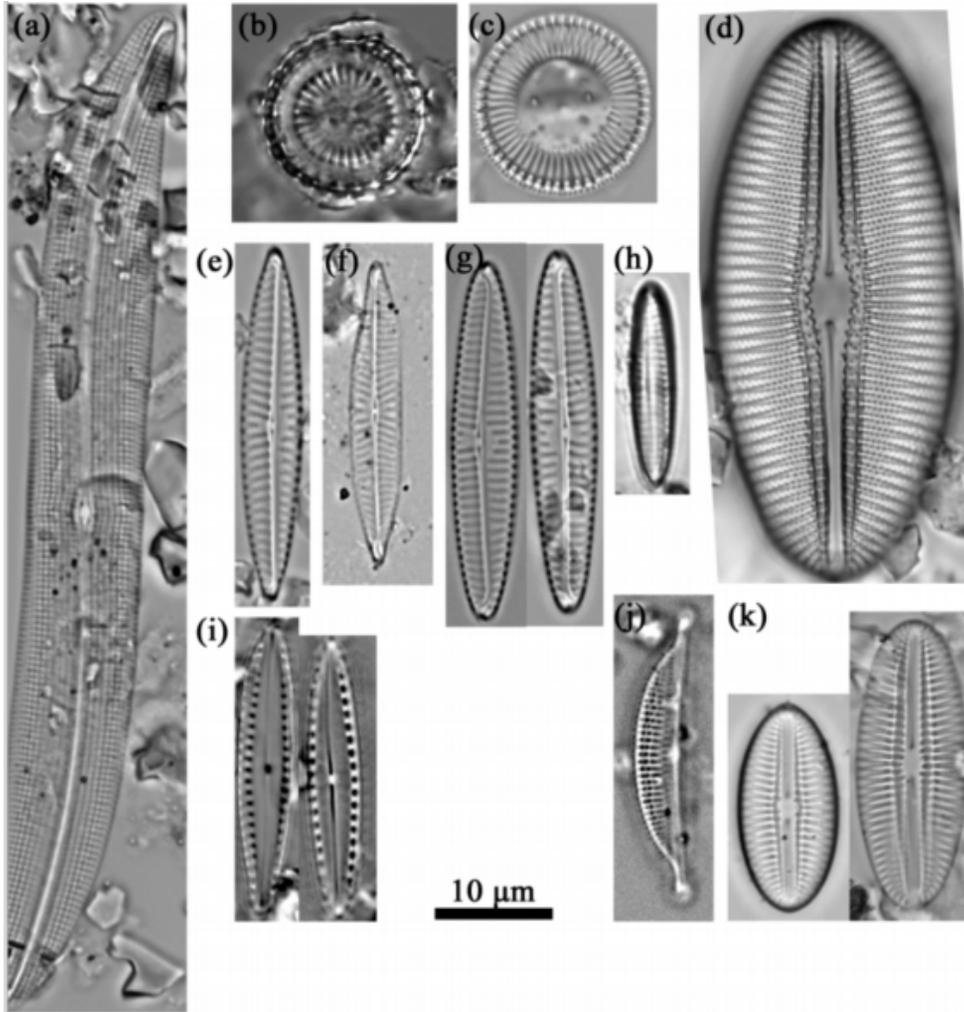


Figure 4.2.

Light micrographs of benthic diatoms in Yellow and Bohai seas. (a) *Gyrosigma* sp. 2; (b) *Paralia sulcata*; (c) *Cyclotella* cf. *stylum*; (d) *Diploneis littoralis*; (e) *Navicula flagellifera*; (f) *Navicula* cf. *flagellifera*; (g) *Navicula* sp. 14; (h) *Navicula* sp. 32; (i) *Biremis ambigua*; (j) *Amphora* cf. *holsatica*; (k) *Diploneis* cf. *littoralis*.



Figure 4.3
Photographs of site and field survey view in the tidal flat of Yellow Sea.

4.2.2. Data analyses

Cluster analysis (CA) and non-metric multidimensional scaling (NMDS) were carried out on the original data matrix. Species that contributed less than 1% of total abundance to diatom assemblages in the two salterns were excluded from the analyses. Bray-Curtis similarity coefficients were calculated, and the data were subjected to group average sorting. Abundance was fourth root-transformed to balance it across the recorded taxa for measures of similarity. The analysis of similarities (ANOSIM) test was performed to confirm that these groups differed significantly. Similarity percentages (SIMPER) analysis was performed to identify the taxa responsible for differences between groups. The BIOENV procedure was used to determine the factors regulating the structure of diatom assemblages.

Permutational multivariate analysis of variance (PERMANOVA) was performed to assess the significance of variables, including salinities and stations in terms of diatom diversity and composition. PRIMER 6 statistical software was used to perform all analyses (Clarke and Gorley 2006).

Indicator value (IndVal) analysis (Duf rene and Legendre 1997) was performed to identify indicator diatom species for specific ranges in the $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ groups (High versus low concentration of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$): The average value of $\delta^{15}\text{N}$ was 6.81, the average value of $\delta^{13}\text{C}$ was -20.91 in surface sediment. The average value of $\delta^{15}\text{N}$ in the sediment core was 7.40, and the average value of $\delta^{13}\text{C}$ was -22.01.

4.3. Results

4.3.1. Environmental settings

Surface sediments were analyzed for 16 environmental variables, with the data making up dataset I. Sediment cores, with subsamples at 0–5, 20–25, and 40–45 cm depth, were analyzed for ten variables, with the results gathered into dataset II, as shown in tables 4.2 and 4.3. Environmental data included bottom water and sediment properties.

Results for abiotic / biotic variables in the surface sediment and bottom water have been summarized in Table 4.2, and show distinctive spatial patterns (dataset I). The lowest salinity was observed at Station DD (9.9 practical salinity units (psu)), while Station NT showed the highest salinity, with hypersaline conditions (44.6 psu). Sediment grain sizes were evenly distributed, from mud to sand, for each station (Fig. 4.1 and Table 4.2). TN and TOC averaged 0.06% and 0.67% respectively, and showed a strong positive correlation with grain size ($r^2 = 0.86$ and 0.88 , respectively). $\delta^{15}\text{N}$ (3.8–8.5) and $\delta^{13}\text{C}$ (-23.0 to -17.78) concentrations were found to be distributed across a wide range at each station.

In sediment core samples (dataset II), 0–5 cm deep sediment generally showed similar mud content (83.76–98.96%). In stations YK and QD2, no significant differences were observed over depth, while the mud content at Station AS clearly decreased with increased depth, from 83.76% to 42.57%. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ concentrations showed small differences in sediment cores when compared to those detected in surface sediments.

Table 4.2. Data on the abiotic and biotic variables measured in the bottom water and surface sediment samples from the Yellow and Bohai seas. Dominant diatom taxa were given with relative abundances.

	DD	DL	TS	TJ	WF	YT	QD1	RZ	NT	Mean
Abiotic variables										
Bottom water properties										
pH	8.36	7.69	7.75	8.26	3.70	8.27	7.76	7.73	7.86	7.49
Tempertaure (°C)	25.00	26.20	28.40	29.30	29.00	25.80	31.70	31.30	29.40	28.46
DO (mg L ⁻¹)	6.62	6.09	8.37	8.80	21.78	9.80	3.83	4.88	7.93	8.68
Salinity (psu)	9.85	31.80	35.30	29.70	33.70	28.00	18.50	13.83	44.60	27.25
Sediment properties										
Grain size (ø)	5.04	6.29	3.52	5.65	3.69	1.83	6.46	2.70	2.47	4.18
Sorting (ø)	1.96	1.68	1.56	1.84	0.49	1.20	1.49	1.56	0.52	1.37
Gravel (%)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sand (%)	34.74	8.21	67.47	19.66	73.40	91.90	4.38	75.34	99.28	52.71
Silt (%)	55.91	74.68	30.38	67.14	26.06	7.56	79.37	23.41	0.72	40.58
Clay (%)	9.35	17.11	2.14	13.21	0.54	0.53	16.24	1.26	0.00	6.71
TN (%)	0.09	0.14	0.03	0.06	0.04	0.01	0.12	0.02	0.01	0.06
TOC (%)	0.96	1.53	0.43	0.82	0.20	0.06	1.83	0.11	0.08	0.67
C/N ratio	13.44	7.32	4.25	9.18	3.58	8.90	9.09	2.55	6.90	7.25
δ ¹⁵ N	7.94	8.49	7.72	8.19	6.22	3.78	8.17	6.35	5.55	6.93
δ ¹³ C	-23.01	-22.14	-21.79	-21.87	-17.78	-21.12	-22.89	-20.58	-19.13	-21.15
Biotic variables										
Chl- <i>a</i> (mg m ⁻²) ^a	25.71	17.31	17.31	14.62	60.00	3.03	17.82	17.48	6.05	3.57
Diatom										
Number of genus	36	36	21	21	23	14	24	33	12	70 ^b
Dominant genus										
1 st <i>Navicula</i>	27	21	30	32	16	10	23	35	40	26
2 nd <i>Diploneis</i>	3	2	1		4	75	1	9	9	13
3 rd <i>Nitzschia</i>	6	2	8	12	16	0	14	18	4	9
Number of species	72	69	49	43	49	28	51	75	28	228 ^b
Dominant species										
1 st <i>D. cf. littoralis</i>	2	0	1	0	0	61	0	0	0	22
2 nd <i>N. flagellifera</i>	15	0	3	30	3	0	1	1	0	9
3 rd <i>B. ambigua</i>	7	1	29	3	0	1	1	1	0	6
Meiofauna										
Nematoda	257	313	159	115	35	46	178	206	6	132
Copepoda	0	86	0	13	0	19	1	48	0	21
Total	257	503	159	133	35	74	181	273	6	145
Macrofauna (ind. m ⁻²)										
Total	74	96	85	209	0	55	63	173	97	97

^a biomass of microphytobenthos on surface sediment, ^b total number of taxa

Table 4.3. Data on the abiotic and biotic variables measured in the bottom water and sediment core samples from the Yellow and Bohai seas. Dominant diatom taxa were given with relative abundances.

	AS			YK			QD2			
Depth (cm)	0-5	20-25	40-45	0-5	20-25	40-45	0-5	20-25	40-45	Mean
Abiotic variables										
Bottom water properties										
pH	7.84			7.82			8			7.89
Tempertaure (°C)	29.45			27.9			27.4			28.25
DO (mg L ⁻¹)	4.2	n.a.		4.81	n.a.		7.09	n.a.		5.37
Salinity (psu)	24.9			38.5			18.64			27.35
Sediment properties										
Mud content (%)	83.76	76.18	42.57	98.96	98.22	99.09	86.08	91.06	96.23	85.79
TN (%)	0.07	0.05	0.00	0.11	0.10	0.11	0.04	0.05	0.06	0.07
TOC (%)	0.42	0.43	0.01	1.01	0.93	1.02	0.36	0.40	0.50	0.56
δ ¹⁵ N	7.95	7.63	n.d.	7.32	7.23	7.29	7.96	6.78	7.04	7.40
δ ¹³ C	-21.76	-22.98	-23.87	-21.85	-22.15	-22.11	-21.03	-21.37	-20.94	-22.01
Biotic variables										
Chl- <i>a</i> (mg m ⁻²) ^b	15.88	n.a.	n.a.	17.31	n.a.	n.a.	8.57	n.a.	n.a.	11.5
Diatom										
Number of genus	23	24	32	18	20	29	5	8	12	45 ^b
1 st <i>Navicula</i>	39	10	8	44	53	61	82	0	22	40
2 nd <i>Cyclotella</i>	7	9	4	2	5	8	2	20	30	10
3 rd <i>Coscinodiscus</i>	0	0	1	0	0	1	0	40	8	12
Number of species	40	53	71	42	45	55	16	8	15	105 ^c
1 st <i>Paralia sulcata</i>	74	78	116	3	16	6	0	1	7	38
2 nd <i>Navicula</i> sp. 32	24	0	0	42	71	0	2	0	0	34
3 rd <i>Navicula</i> sp. 28	46	7	0	0	13	4	0	0	0	18

^a not available, ^b biomass of microphytobenthos on surface sediment, ^c not detected, ^d total number of taxa,

4.3.2. Diatom assemblages inhabited on surface sediment

A total of 75 diatom genera, consisting of 287 species, as listed in Table 4.4, were observed across all sampling stations, including datasets I and II (diatoms from surface sediments and from cores).

70 diatom genera and 228 species were identified in the surface sediment samples in dataset I, across the nine sampling stations. Genus and species diversity trends were generally similar (Fig. 4.2 and Table 4.4), showing that the species appearing at each station were not concentrated in a specific genus.

Station assemblages averaged 24 genera and 51 species, with Station YT showing the lowest diversity (number of species = 28). *Navicula* was the predominant genus in the surface sediments, and was the most common genus across all stations, with a relative abundance of 10–40% (Table 4.2). *Diploneis* was the second dominant genus (except at YT where it was the most dominant), representing 4% of the relative abundance, and was found in all stations. Station YT showed significantly lower diversity than other stations, due to the predominance of *Diploneis*. *Diploneis* species included *D. cf. littoralis* and *stroemii*, which were among the top 10 dominant species. *D. cf. littoralis* was the most common species in surface sediment samples, accounting for 22% of the total; however, this species appeared in only three of the nine stations, showing a low frequency.

Table 4.4. Diversity indices of benthic diatom communities of 18 samples in the Yellow and Bohai seas; S, number of species; d, species richness; J' , Pielou's evenness; H' , Shannon wiener diversity; $1-\lambda$, Simpson diversity. The diversity indices were calculated based on species level of diatom data.

Dataset	ID	Depth (cm)	S	d	J'	H'	$1-\lambda$
Surface samples	DD	Surface	69.00	11.92	0.83	3.49	0.95
	DL	Surface	43.00	7.36	0.66	2.48	0.84
	TS	Surface	49.00	8.42	0.74	2.89	0.89
	TJ	Surface	28.00	4.73	0.49	1.62	0.60
	WF	Surface	49.00	8.42	0.82	3.20	0.93
	YT	Surface	28.00	4.73	0.72	2.40	0.87
	QD1	Surface	51.00	8.77	0.79	3.12	0.92
	RZ	Surface	72.00	12.45	0.86	3.68	0.96
	NT	Surface	75.00	12.97	0.82	3.55	0.95
Core samples	AS	0–5	42.00	7.19	0.83	3.11	0.94
	AS	20–25	45.00	7.71	0.78	2.97	0.91
	AS	40–45	55.00	9.47	0.86	3.46	0.96
	YK	0–5	40.00	6.84	0.77	2.85	0.90
	YK	20–25	53.00	9.12	0.77	3.07	0.90
	YK	40–45	71.00	12.27	0.68	2.90	0.83
	QD2	0–5	16.00	3.83	0.75	2.07	0.81
	QD2	20–25	8.00	2.34	0.84	1.75	0.81
	QD2	40–45	15.00	3.58	0.80	2.17	0.85

(a) Diatoms on surface sediment (genus level) (b) Diatoms on surface sediment (species level)

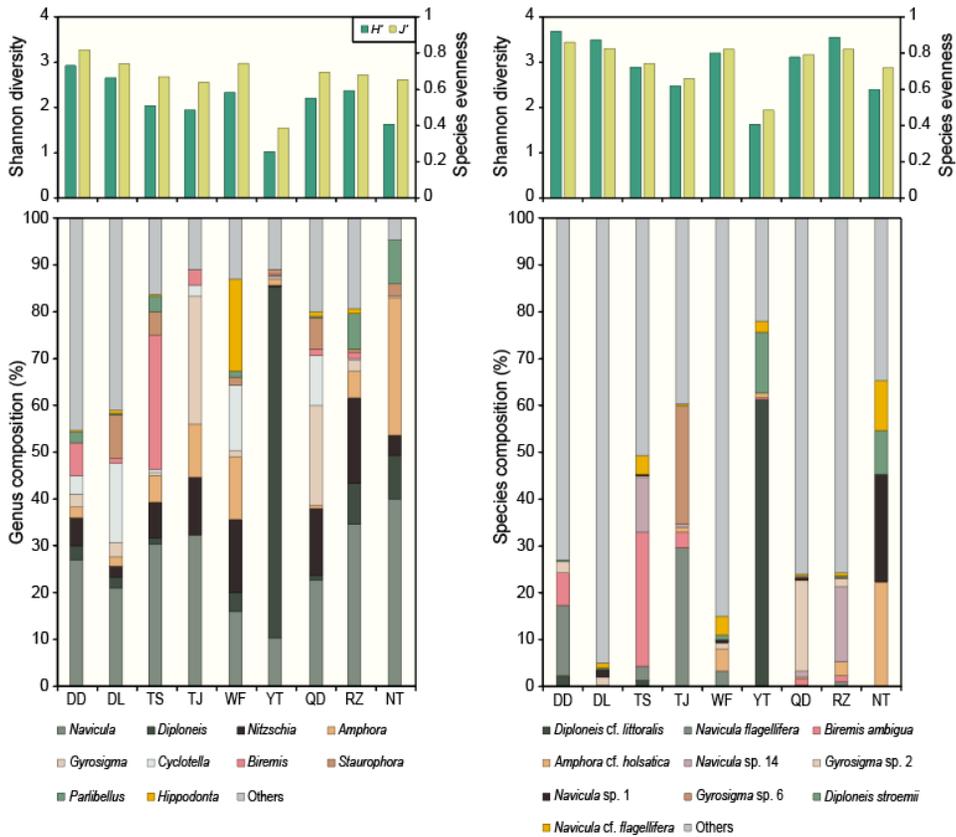


Figure 4.4

Species diversity, species evenness, relative abundance of diatoms on surface sediment (dataset I) with top 10 dominant taxa at (a) genus level and (b) species level, across 9 stations.

4.3.3. Diatom assemblages observed in sediment core

Inspection of dataset II (sediment core samples, involving 3 stations, with 0–5, 20–25, and 40–45 cm samples from each) revealed the presence of 45 diatom genera and 105 diatom species in the nine samples. Genus and species diversity exhibited dissimilar trends across the samples, as shown in Fig. 4.4. The lowest number of genera was observed in the 0–5 cm sample from core QD2, while the lowest species diversity was observed in the 20–25 cm sample from the same core. While *Navicula* was the most dominant genus overall (40% of total abundance), *Cyclotella* was the second most dominant genus, and the commonest in sediment core samples. *Coscinodiscus* was ranked third most dominant genus, with an average of 1% of relative abundance for all stations, with the exception of the 20–25 cm sample from Station QD2. *Paralia sulcata* was the most dominant species, representing 38% of all counted individuals, followed by *Navicula flagellifera* (9%), and *Biremis ambigua* (6%).

(a) Diatoms from sediment core (genus level) (b) Diatoms from sediment core (species level)

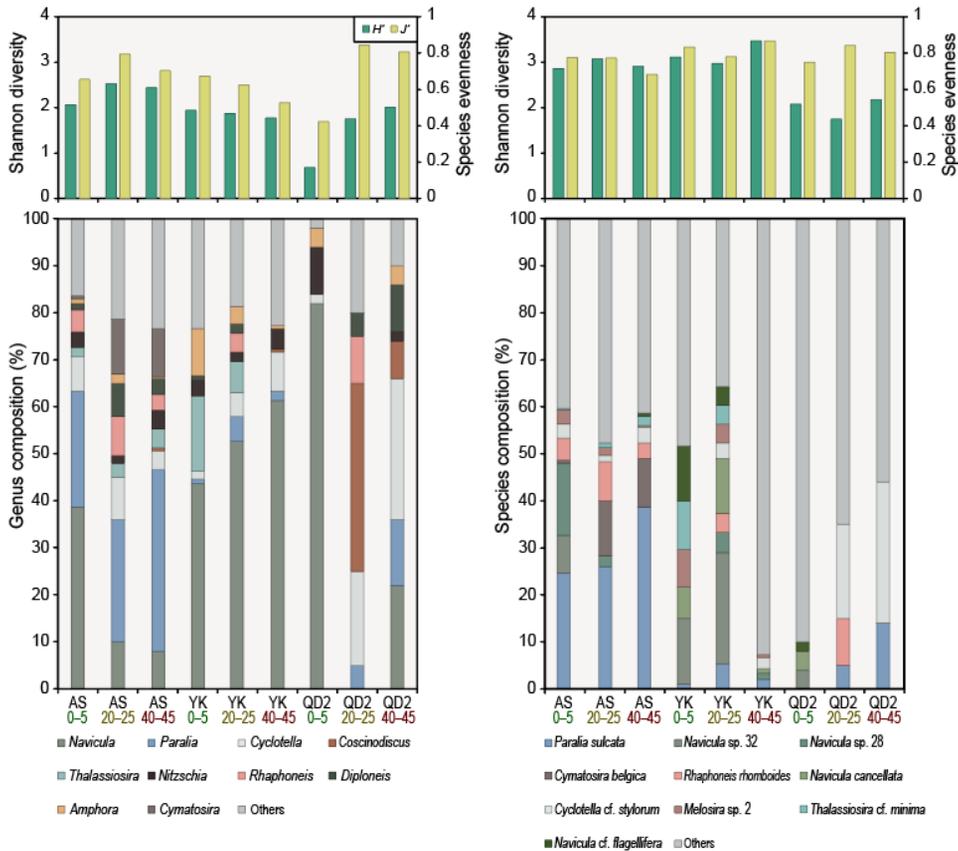


Figure 4.5.

Species diversity, species evenness, relative abundance of diatoms from sediment core samples (dataset II) with top 10 dominant taxa at (a) genus level and (b) species level, across 9 stations.

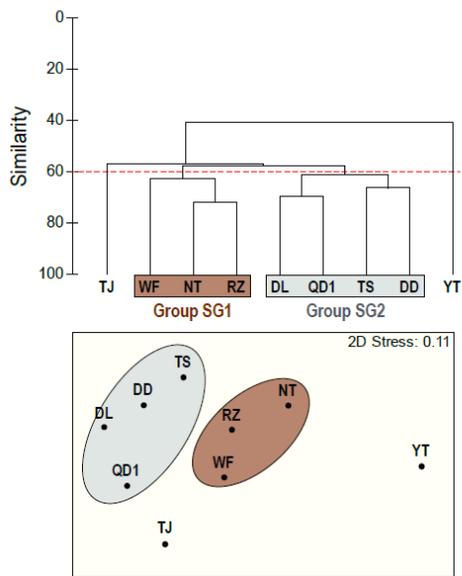
4.3.4. Cluster analysis

Cluster analysis (CA) was performed to delineate Yellow and Bohai Seas station groups with similar diatoms genus and species compositions (Figs 4.6 and 4.7). Surface sediment diatom assemblages were initially collected into two genus-level groups (ANOSIM: $R = 0.481$, $p < 0.029$). Diatom assemblages at species level were clustered into two groups as well (ANOSIM: $R = 0.691$, $p < 0.05$), however, the composition of the station clustering within each group was different (Fig. 4.6).

For genus-level groups, *Navicula* was found to have the highest abundance in both. The dissimilarity between the two groups was mainly explained by the second-most abundant genus, however, with *Amphora* coming second in Group SG1, and *Biremis* coming second in group SG2. SIMPER analysis confirmed that *Amphora* (9.37% of contribution) and *Biremis* (8.83%) were the significant contributors to the dissimilarity level between Group SG1 and Group SG2 (average dissimilarity = 42.4%). At species level, Group SS1 included stations TJ and DD, which had high relative abundances of *Navicula flagellifera* (22.33%). Five stations, including RZ, DL, QD1, TS, and WF, were clustered into Group SS2, which showed *Biremis ambigua* (6%) as its most dominant species.

In the sediment core samples, genus assemblages were divided into two distinct station groups—CG1 and CG2—using CA (ANOSIM: $R = 0.778$, $p < 0.01$, Fig. 1). Group CG1 encompassed samples from the three depths of Station AS, with 30% relative abundance of *Paralia*, the most dominant genus of the group. Group CG2 assemblages included Station YK, with its three different-depted samples predominated by *Navicula* (53%). Unlike the genus groups, the species assemblages were divided into three groups: Group CS1 was composed of the three Station AS samples, in a form similar to that of Group CG1. *Paralia sulcata* was the most dominant CS1 species, with 30% of the relative abundance. Station YK 0–5 cm and 20–25 cm samples were clustered into Group CS2. *Navicula* sp. 32 was the most dominant species (18.80%) in these sediment cores, followed by *Navicula cancellata* (9.17%), and *Navicula* cf. *flagellifera*. The third group, CS3, encompassed the 20–25 and 40–45 cm samples from Station QD2, which did not appear in the genus assemblages.

(a) Genus group on surface sediment



(b) Species group on surface sediment

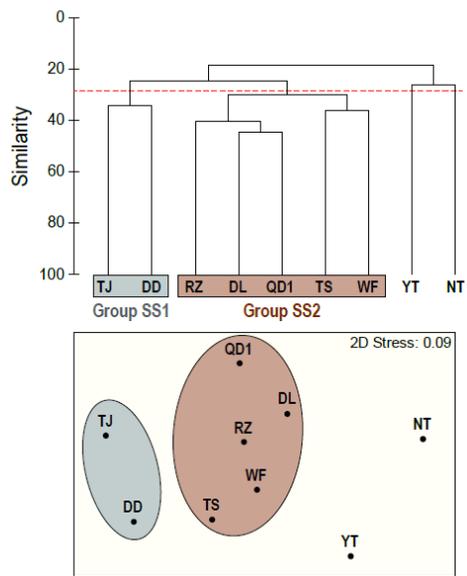
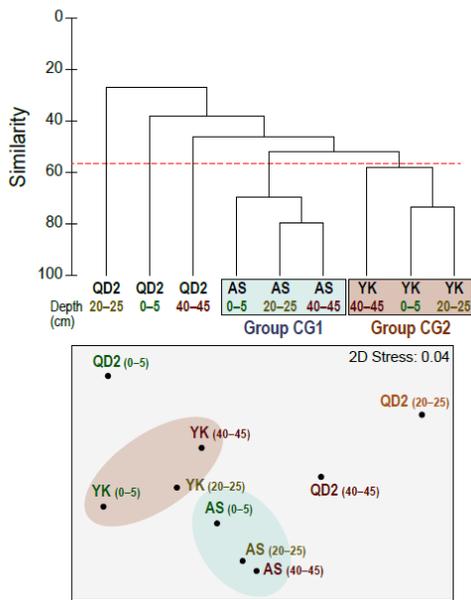


Figure 4.6

Illustration of the benthic diatom groups on the surface sediment in Yellow and Bohai seas at (a) genus level and (b) species level, based on cluster analysis and non-metric multidimensional scaling.

(a) Genus group from sediment core



(b) Species group from sediment core

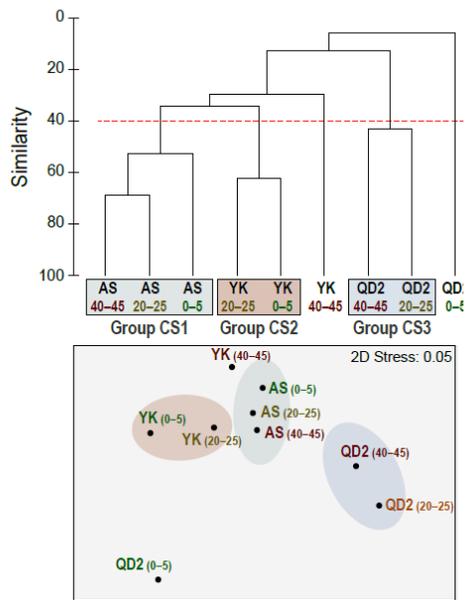


Figure 4.7

Illustration of the benthic diatom groups from sediment core in Yellow and Bohai seas at (a) genus level and (b) species level, based on cluster analysis and non-metric multidimensional scaling.

4.4. Discussion

4.4.1. Diatom monitoring in genus level versus species level

Monitoring diatoms is one of the most effective methods for assessing marine ecosystems. The technique has several advantages, including that diatoms are relatively simple to collect, show rapid and predictable responses to changes in habitat conditions, are taxonomically diverse, and so on. While the need for specialist taxonomic expertise can be a key limitation on using diatoms for biological monitoring due to the very large numbers of diatom species often involved (Kelly et al. 1995), some researchers have used simpler, genus-level surveys to assess aquatic environmental conditions (Wu 1999, Hill et al. 2000).

We found that, for the study area surface sediments, genus diversity reflected species diversity, in terms of general trends. When considering the most efficient use of time and effort, assemblage diversity can therefore be investigated satisfactorily using genus-level taxonomy. This survey format is particularly suitable if the purpose of the study is to compare diversity between regions, although it must be noted that diversity may be underestimated if there are several congeneric species. If the purpose of the investigation is to determine biodiversity for a specific region, a species-level investigation would be necessary to conduct an accurate assessment.

In the current study, three assemblages—the three depth samples from Station YK—showed similar compositions at the genus level, and were clustered into one group. However, CA performed at the species level showed that only two out of these three assemblages (0–5 and 20–25 cm depth samples) qualified to be clustered into one group (Group CS2). It seemed that community structure differences not apparent in genus-level examination were revealed when the samples were analyzed at the species level. Round (1991) warned that it would be 'dubious' to simply use genus-level identification for aquatic ecosystem surveys, and our results implied that, if only genus-level surveys and monitoring were performed, there was every possibility of overlooking subtle, environment-based changes in diatom assemblages.

4.4.2. Diatoms reflecting present environments

Diatoms living on the surface sediment can reflect the environment currently surrounding them. We performed a BIOENV analysis to identify the environmental factors affecting the diatoms on the surface sediment at the time of sampling; the results indicated that $\delta^{15}\text{N}$ was the best-matched single factor, in terms of explaining the diatomic genus and species composition in the Yellow and Bohai Seas at the time of sampling (Table 4.5). Genus composition had the strongest correlation with $\delta^{15}\text{N}$, while species composition had strong correlations with latitude, sorting, $\delta^{15}\text{N}$, Nematoda, and SOs.

We also conducted PCA analysis, to elucidate relationships between various abiotic/biotic variables and diatoms. PCA for dataset II identified two components which collectively accounted for 52.6% of the total variance. The first axis (PC1) generally indicated that diversities and / or abundances of marine organisms—including diatoms, meiofauna, and macrofauna—were related to carbon and nitrogen in the surface sediments, and to the bottom water salinity (Fig. 4.7). The second axis (PC2) indicated that PTSs, including PAHs, APs, and SOs seemed more related to abundances of bigger benthos (meiofauna and macrofauna) rather than to general diatom community structure characteristics, such as diversity or biomass. However, positive relationships with some diatomic genera (such as *Gyrosigma* and *Nitzschia*) and negative relationships with some diatom species (such as *Biremis ambigua*, *Navicula* sp. 14, and *D. cf. littoralis*) were revealed. When PCA results obtained for genus- and species-level analyses were compared, the relationships within the variables were similar at both levels.

Overall, the tidal flat diatom assemblages in the Yellow and Bohai Seas seemed to be greatly affected by the nearby rivers. PCA showed that multiple representative stressors affecting diatom assemblages—such as salinity (freshwater input) and chemical species and compounds of terrestrial origin ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and PTSs)—were found mainly in estuarine environments, with $\delta^{15}\text{N}$ in particular, showing strong correlations for diatom assemblages (Table 4.6). Figure 4.8 shows non-metric, multi-dimensional scaling (NMDS) for diatom abundance at the species level against $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ concentrations. The stations were grouped according to concentration, with the results showing that genus- and species-level outcomes differed, while overall, the diatom assemblages seemed to show similar trends of (dis)similarity with concentrations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Table 4.5. Results of BIOENV analysis showing the strongest correlation for environmental variables that best match for diatom composition at genus and species level on the surface sediment in the Yellow and Bohai seas.

Genus composition			Species composition		
# of variables	Variables	Correlation	# of variables	Variables	Correlation
1	$\delta^{15}\text{N}$	0.71	1	$\delta^{15}\text{N}$	0.45
2	Grain size, $\delta^{15}\text{N}$	0.67	2	Sorting, $\delta^{15}\text{N}$	0.48
3	Tide range, Grain size, $\delta^{15}\text{N}$	0.64	3	Latitude, $\delta^{15}\text{N}$, Sos	0.48
4	Tide range, TN, $\delta^{15}\text{N}$, Sos	0.51	4	Latitude, Sorting, $\delta^{15}\text{N}$, Sos	0.51
5	Grain size, $\delta^{15}\text{N}$, Chlorophyll a, Macrofauna, Sos	0.64	5	Latitude, Sorting, $\delta^{15}\text{N}$, Nematoda, Sos	0.52

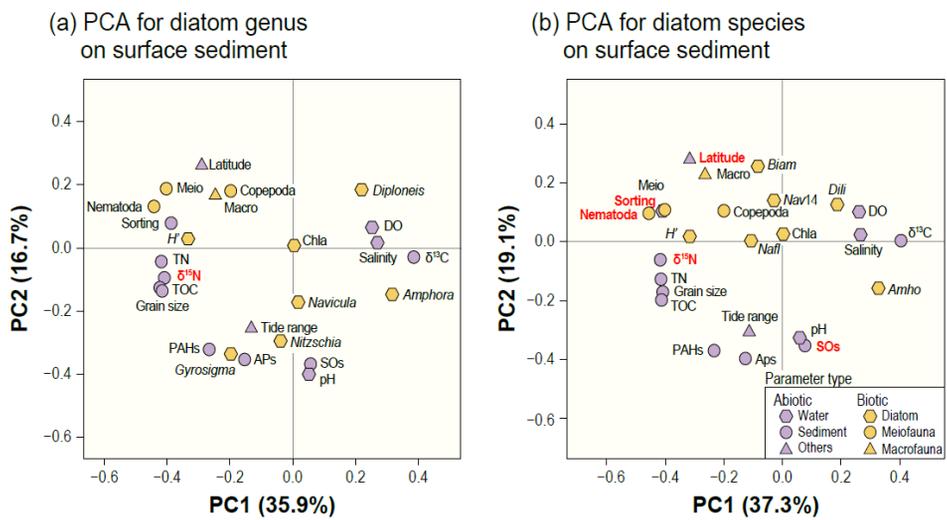


Figure 4.8

Principal component analysis (PCA) of abiotic parameters and biotic parameters (diatoms, other biotic parameters including meiofauna and macrofauna) based on dataset I at (a) genus level and (b) species level.

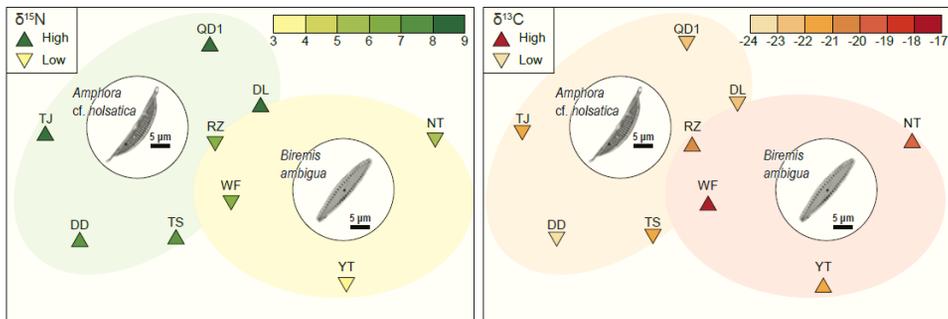


Figure 4.9

Non-metric multidimensional scaling (NMDS) based on relative abundance of diatoms provides information on the concentrations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Indicator species were identified for two groups: high and low concentrations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

4.4.3. Diatoms reflecting historical records of environment

Sediment core diatoms were not alive at the time of sampling. Their frustules represented historical records, showing which genera / species had inhabited the stations in the distant past. Over time, representatives of diatom genera with thin frustules may have disappeared, due to either frustule fracturing and dispersal, or by resuspension. Genera with sufficiently thick frustules may thus be more intensively preserved in deeper sediment layers, so that the observable species may be concentrated into a few, thick-frustuled genera. This phenomenon may have led to the difference between the genus and species level diversity in the sediment core sample diatom assemblages.

To identify the relationships between past environmental parameters and diatoms, BIOENV and PCA were conducted on dataset II, which consisted of frustule-based taxa from sediment core samples (Fig. 4.7 and Table 4.6). It was found that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ concentrations showed the strongest correlations with past diatom assemblages in the Yellow and Bohai Seas.

The NMDS analysis also showed that, diatom assemblage changes at the species level reflected $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ concentrations, especially in Station QD2. Past diatom assemblages had changed significantly over time, while $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ concentrations also showed distinct differences (Fig. 4.10), with the more recent (shallower sediment depth) $\delta^{15}\text{N}$ readings mostly found to be higher (enriched), with $\delta^{13}\text{C}$ lower (depleted). These $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ concentration trends may be indicating a marine origin for the modern sediment organic matter in the Yellow and Bohai Seas; further investigation is necessary to clarify whether this could have resulted from historic sea level rise.

Overall, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ concentrations were identified as being the most significant factors affecting diatom assemblages in the Yellow and Bohai Seas, and may be reflecting changes in the effect of land-derived influences over time.

Table 4.6. Results of BIOENV analysis showing the strongest correlation for environmental variables that best match for diatom composition at genus and species level from the sediment core in the Yellow and Bohai seas.

Genus composition			Species composition		
# of variables	Variables	Correlation	# of variables	Variables	Correlation
1	$\delta^{15}\text{N}$	0.25	1	$\delta^{15}\text{N}$	0.30
2	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$	0.37	2	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$	0.28
3	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$, TN	0.41	3	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$, TN	0.26
4	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$, TN, TOC	0.34	4	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$, TN, TOC	0.19
5	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$, TN, TOC, Mud content	0.25	5	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$, TN, TOC, Mud content	0.08

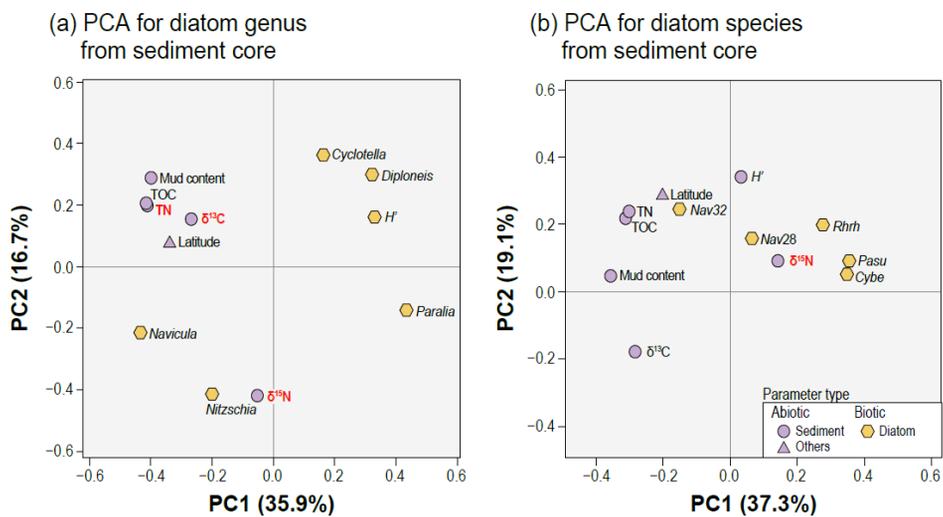


Figure 4.10
Principal component analysis (PCA) of abiotic parameters and biotic parameters (diatoms, other biotic parameters including meiofauna and macrofauna) based on dataset I at (a) genus level and (b) species level.

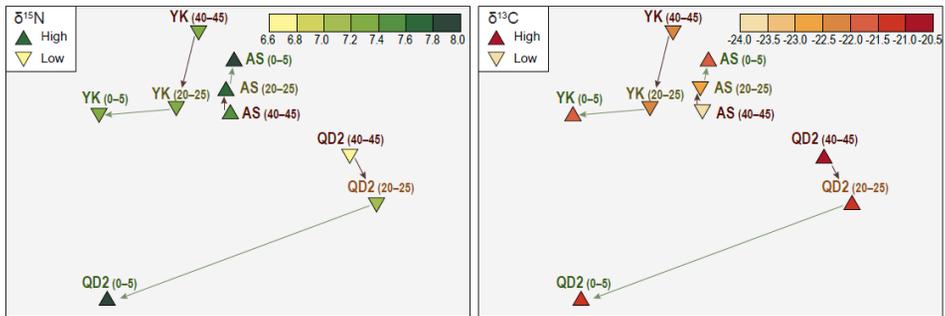


Figure 4.11

Non-metric multidimensional scaling (NMDS) based on relative abundance of diatoms provides information on the concentrations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

4.5. Summary

The very broad tidal flats common on the Yellow and Bohai Sea coasts are high value habitats, in terms of ecosystem services. The Yellow and Bohai Seas are experiencing high levels of anthropogenic impacts, stemming from the rapid regional industrialization and urbanization taking place in adjacent coastal areas. It is important to manage Yellow and Bohai Sea ecosystems that are being impacted by development and by land-derived pollutant discharges. Biological monitoring using diatoms can be a useful tool for investigating marine ecosystem health, especially on tidal flats. Investigating Yellow and Bohai seas diatom assemblages at the genus level can suggest general trends of diversity and distribution; however, monitoring at this level may result in subtle evolutions in diatom assemblages resulting from environmental changes, being overlooked. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ concentrations were found to be the most significant factors affecting diatom assemblages in the Yellow and Bohai Seas. It was generally found in more recent (shallower) samples, that $\delta^{15}\text{N}$ was enriched, while $\delta^{13}\text{C}$ was depleted.

CHAPTER 5.

Shift in polar benthic community structure in a fast-retreating glacial area of West Antarctica

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Shift in polar benthic community structure in a fast retreating glacial area of the West Antarctica.

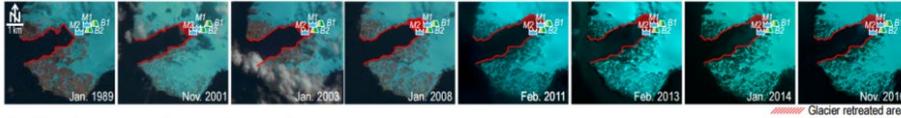
5.1. Introduction

The climate crisis is highlighted by the breaking of temperature records during the austral summer in the Antarctic continent especially in West Antarctica (Marshall et al., 2006), and the ecological impacts of these changes becoming increasingly serious (Clarke et al. 2007, Lee et al. 2017). Glacier retreat is reported to cause rapid and severe impacts on both plankton and benthos by melt-water and drifting ice (Peck et al. 2006). Glacier retreat together with ice-melt in the fjords of West Antarctica is also expected to affect benthic microflora, leading to blooms of seabed diatoms (Ahn et al. 2016). However, the ecological influence of glacier retreat on the spatial development and/or year-round variation of benthic diatoms remains largely unknown.

Diatoms are important primary producers in Antarctica (Clarke et al. 2007), and are used as biological indicators of the rapidly changing environment, such as global warming (Bopp et al. 2005, Hinder et al. 2012). Despite their ecological significance in the coastal waters of Antarctica, response of polar benthic diatoms to glacier retreat remains limited understanding. Given that shallow coastal waters in Antarctica will likely be impacted by anticipated glacial melting, it is necessary to obtain a sound ecological understanding of benthic diatoms.

Here, we examined changes to the polar benthic community structure of diatoms under current global warming in a recently retreated glacial area of Marian Cove, West Antarctica (Fig 5.1). In specific, we aimed to: 1) evaluate the overall diversity of benthic diatoms in intertidal and subtidal habitats, 2) characterize composition of species and their distribution characteristics with respect to the types of substrates that they inhabit, and 3) address early ecological responses of polar benthos and their adaptive strategies, by integrating the previous results (a mini-review) into the present findings. The results of the current study are expected to provide reference data on how the retreat of glaciers is affecting marine ecosystems in the rapidly changing and harsh environment of the polar region.

(a) Overview showing inner station and glacier retreat since 1989



(b) Study area and sampling station in 2018–2019

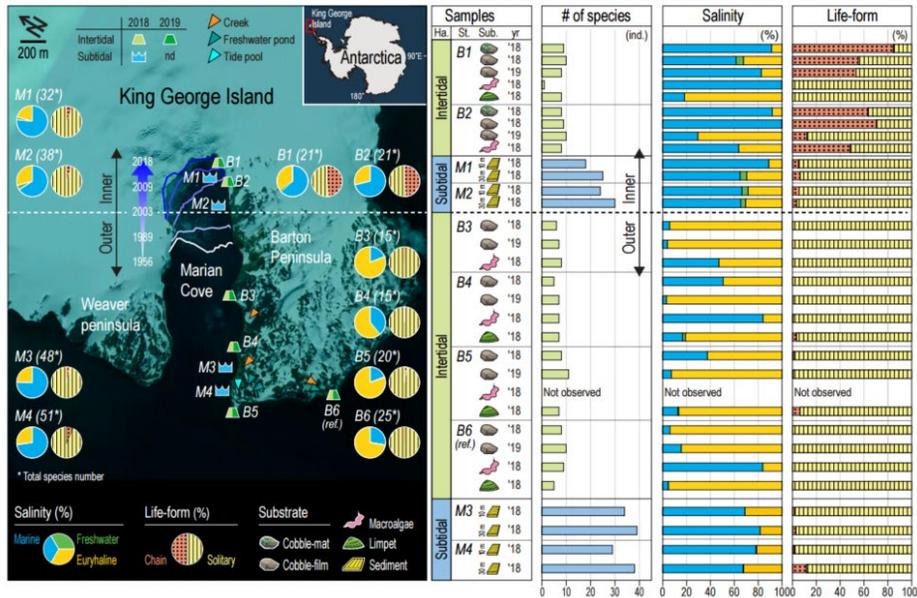


Figure 5.1.

Overview of the study area, sampling locations, and benthic diatom community data; (a) Overview of glacier retreat in Marian Cove, West Antarctica, since 1989. Stations in the inner part of the cove are presented (B1, B2, M1, and M2). (b) Map showing sampling locations (intertidal zone: B1–B6; subtidal zone: M1–M4 at 10 and 30 m) surveyed in 2018–2019, with a summary of benthic community data; specifically, the number of species, relative abundance by salinity (marine, euryhaline, and freshwater), life-form (chain and solitary), and various substrates (cobble-mat, cobble-film, macroalgae, limpet shell, and sediment). Ecological type of diatom species in relation to salinity is provided in Table S8. The base map was obtained from Google Earth (<https://earth.google.com/web>) and Global USGS Visualization Viewer (<https://glovis.usgs.gov>).

5.2. Materials and Methods

5.2.1. Study area

The South Shetland Islands encompass 11 mountainous islands situated ~160 km north of the Antarctic Peninsula. King George is the largest island of these islands. The study area is one of two large fjords on King George, located on the Barton Peninsula, West Antarctica (Fig. 5.2). Two tributary basins, Marian and Potter Cove, are situated on either side of Barton Peninsula. The present study focused on the marine benthic ecosystem of Marian Cove, which shows distinct environmental gradients caused by glacial melting during the austral summer (Ahn et al. 2004). As glacier retreated, the environment on the inner cove has become more deepened bay system, leading to provide relatively stable condition in physical stress such as wave, wind, current, and ice scouring compared to open shore (Cremer et al. 2003, Lim et al. 2013, Smale et al. 2008).

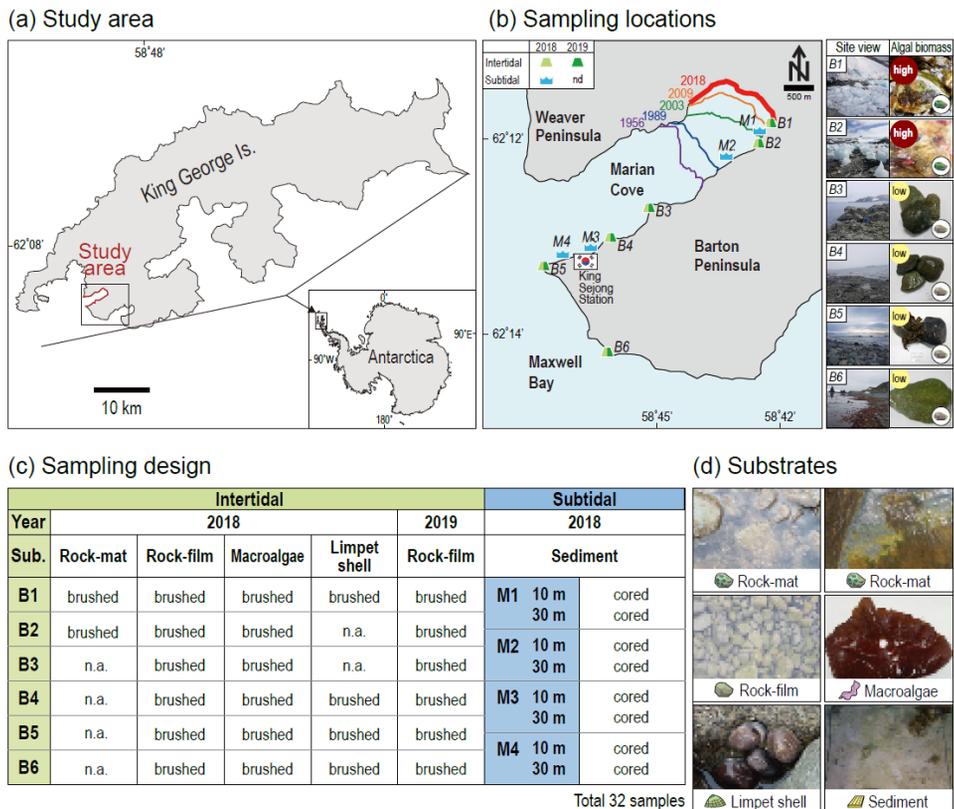


Figure 5.2.

Map showing (a) the study area, (b) sampling locations ($n = 10$) with site views (B1–B6) and observed algal biomass. (c–d) sampling design was presented including information of substrate. The base maps were created in Adobe Illustrator CS6 based on the map of Google Earth (<https://earth.google.com/web/>).

5.2.2. Sampling and laboratory analyses

Sampling was conducted at a total of 14 locations, encompassing intertidal locations ($n = 6$; B1–B6) and subtidal locations at two depths ($n = 8$; M1_{10m}–M4_{10m} and M1_{30m}–M4_{30m}) during the austral summer of 2018 and 2019 (Fig. 5.1). All of the intertidal and subtidal locations were surveyed simultaneously in 2018, and six locations (B1–B6) from the intertidal zone were surveyed again in 2019, with the specific aim of investigating year-round changes to the intertidal benthic community. Out of the intertidal locations, five (B1–B5) were situated along the coast of Marian Cove, while B6, a reference site, was located at the southern part of Barton Peninsula. Of note, B1 and B2 were situated in a recent glacier retreat zone, and were approximately 100 and 360 m distant from the glacier in Marian Cove, respectively, at the time of sampling in 2018.

Seawater properties were measured in situ using a multi-parameter water quality probe (YSI-Professional Plus; Ohio, OH, USA), and included temperature (°C), dissolved oxygen (DO, mg L⁻¹), salinity (psu), pH, and SiO₂ (µg L⁻¹). Total phosphorus (TP, µg L⁻¹) and nitrogen (TN, µg L⁻¹) were measured following standard methods (MOMAF, 2005). Waterborne particulate organic matter (POM) and diatom samples were lyophilized before stable isotope analysis. Concentrations of the stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in POM and diatom samples were measured using an Elemental Analyzer-Isotope Ratio Mass Spectrometer (EA-IRMS; Elementar, GmbH, Hanau, Germany). High purity carbon dioxide and nitrogen were used as reference gases, while helium and oxygen were used as carrier and combustion gases. Stable carbon and nitrogen isotopic compositions were expressed as ‰ delta notation (Eq. 1):

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} (\text{‰}) = [\text{R}_{\text{sam}}/\text{R}_{\text{ref}} - 1] \times 1000 \quad (1)$$

where, R_{sam} and R_{ref} are the compositions ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) of the sample and reference, respectively. Isotopic compositions were reported relative to

conventional reference materials; specifically, Vienna Peedee Belemnite (VPDB) for carbon, and atmospheric N₂ for nitrogen. IAEA-CH-3 and IAEA-N-2, which are international isotope standards, were used as reference materials to calculate the analytical error of carbon and nitrogen, respectively. Measurement precision was approximately 0.04‰ for δ¹³C and 0.2‰ for δ¹⁵N.

Diatom assemblages were collected from three different substrates in the intertidal zone ($n = 24$; viz., cobble, macroalgae, and *Nacella concinna* limpet shells) and one substrate type in the subtidal zone ($n = 8$; bottom sediment, < 1 mm). Of note, two different diatom forms were sampled on cobble surfaces; namely, thick carpet-like mat (cobble-mat) and thin biofilm (cobble-film) (Fig. 5.2). The only macrofaunal organism found in high numbers in the intertidal zone was the limpet *N. concinna*, the shell of which forms a habitat for diatoms. All the intertidal samples had been collected when the sites are exposed to the air during low tide.

Diatoms collected from intertidal zone were removed from the surface of substrates with a toothbrush. Sampling was conducted with three replicates of samples (cobbles, fronds of macroalgae and limpet shells). The top 1.0 cm of the surface sediment was collected from the subtidal zone by scuba divers. Three-hundred diatom valves per sample were identified and counted, in most cases, to calculate relative abundance. Of note, limited numbers of diatoms were attached to macroalgae at locations B1 and B5 (only 0–2 valves were observed). Diatoms were classified to the species level where possible. Concentrated solutions of HCl and H₂O₂ were used to remove calcium carbonate particles from sediment and organic material from cells, respectively. Permanent slides were made using Naphrax resin. A light microscope (BX53; Olympus, Tokyo, Japan) and scanning electron microscope (MIRA3; Tescan, Seoul, Korea) were used to obtain photographic documentation. Photographs of dominant diatoms are presented in Figures 5.3–5.9. Photographs of field view and laboratory analysis also given in Fig. 5.10.

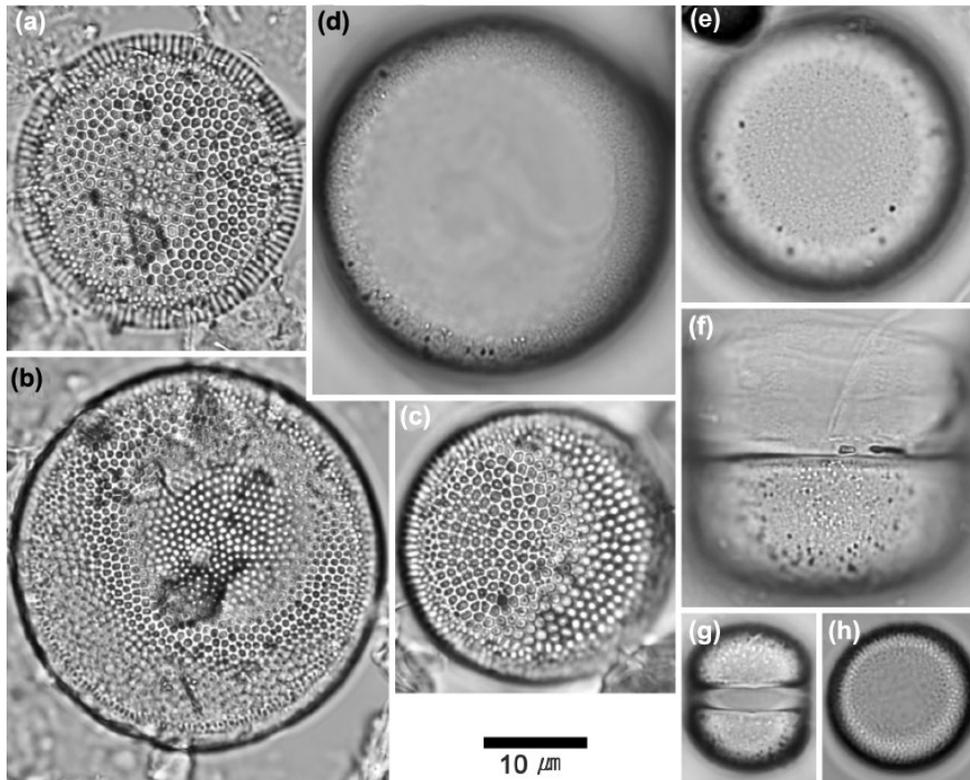


Figure 5.3. Light micrographs of centric diatoms in Marian Cove, West Antarctica. (a–c) *Actinocyclus* sp. 1; (d–h) *Melosira* sp. 1 (scale bar = 10 µm).

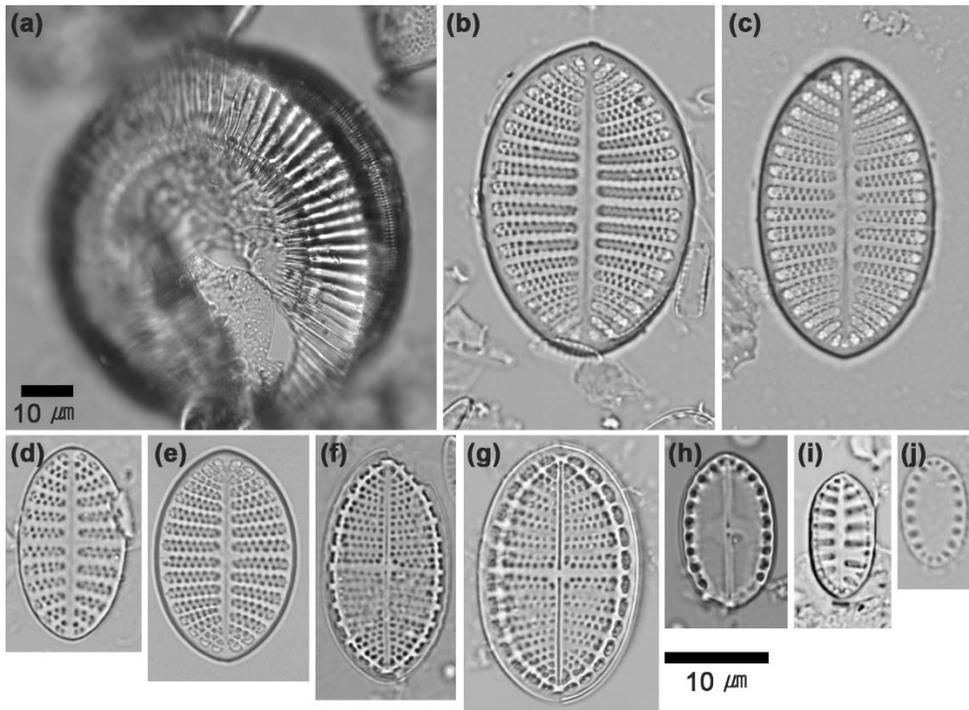


Figure 5.4.

Light micrographs of centric diatoms in Marian Cove, Antarctica. (a) *Paralia* sp. 1; (b–g) *Cocconeis pinnata*; (h) *Cocconeis pinnata* var. *matsii*; (i–j) *Cocconeis melchiroides* (scale bar = 10 μm).

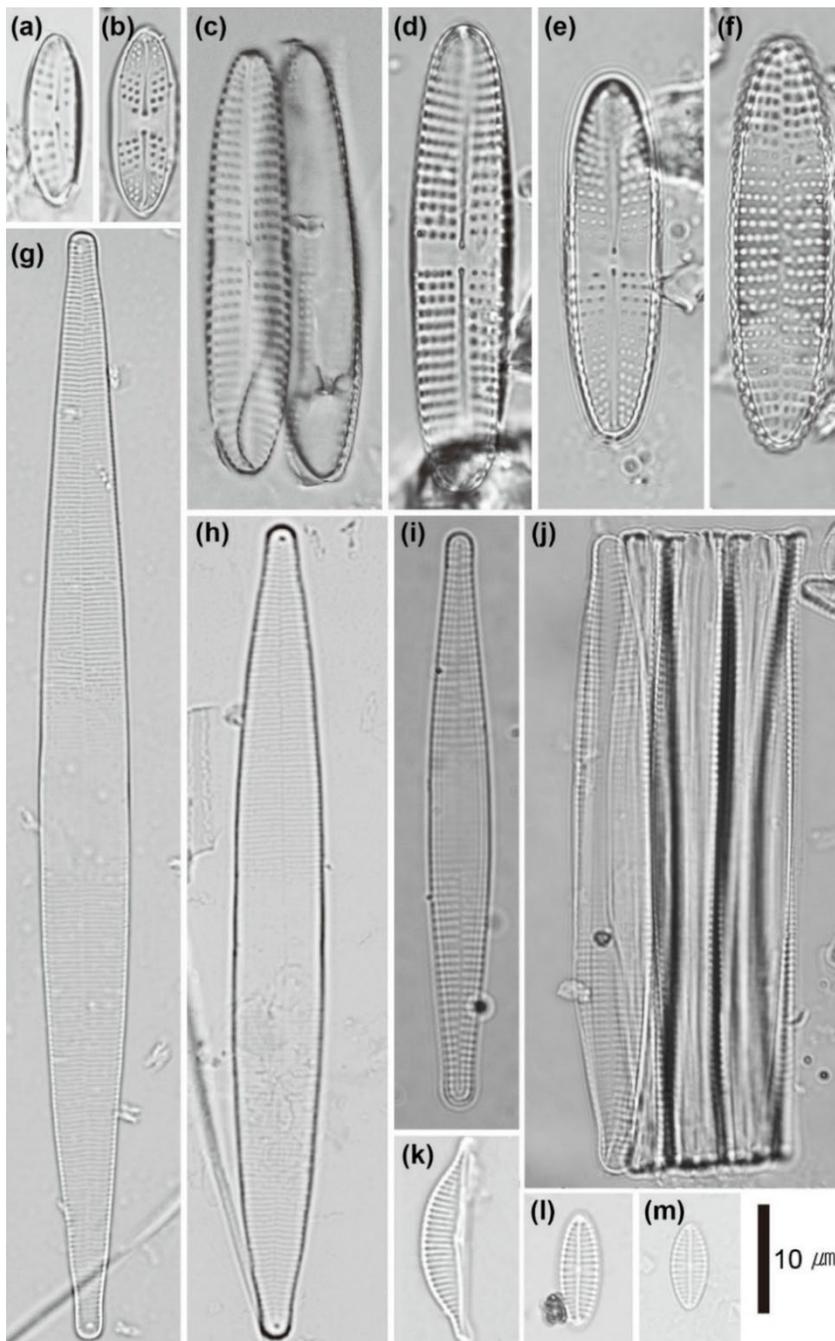


Figure 5.5. Light micrographs of pennate diatoms in Marian Cove, Antarctica. (a–b) *Achnanthes* sp. 3; (c–f) *Achnanthes brevipes* var. *intermedia*; (g–h) *Brandinia mosimanniae*; (i–j) *Fragilaria striatula*; (k) *Halamphora* sp. 1; (l–m) *Navicula* sp. 5 (scale bar = 10 μm).

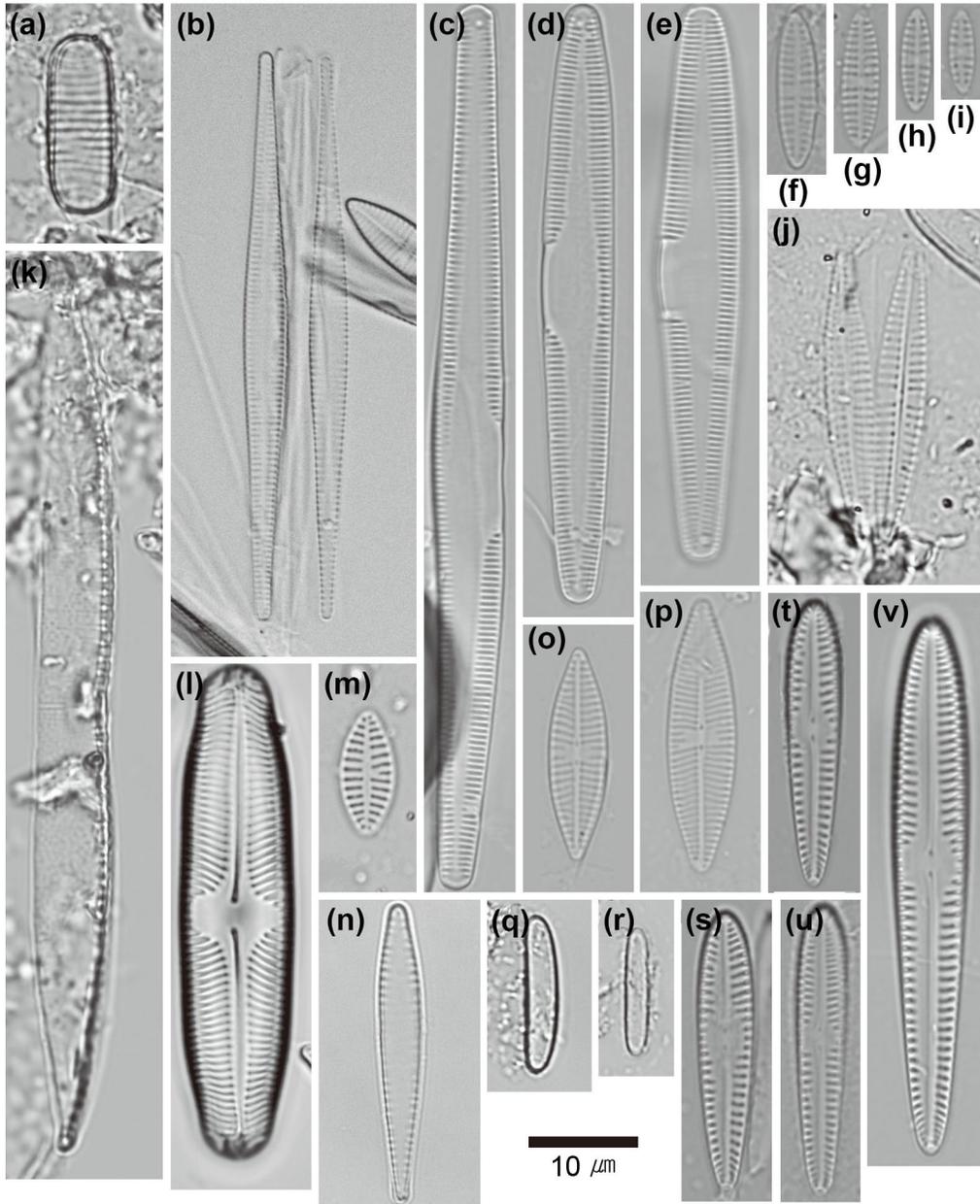


Figure 5.6.

Light micrographs of pennate diatoms in Marian Cove, Antarctica. (a) *Fragilariopsis curta*; (b) *Fragilaria islandica* var. *adeliae*; (c–e) *Tabulariopsis* cf. *australis*; (f–i) *Navicula* cf. *perminuta*; (j) *Navicula* cf. *directa*; (k) *Nitzschia* sp. 1; (l) *Pinnularia australomicrostauron*; (m) *Planothidium delicatulum*; (n) *Synedropsis recta*; (o–p) *Navicula glaciei*; (q–r) *Pteroncola carlinii*; (s–u) *Pseudogomphonema kamtschaticum* (scale bar = 10 μm).

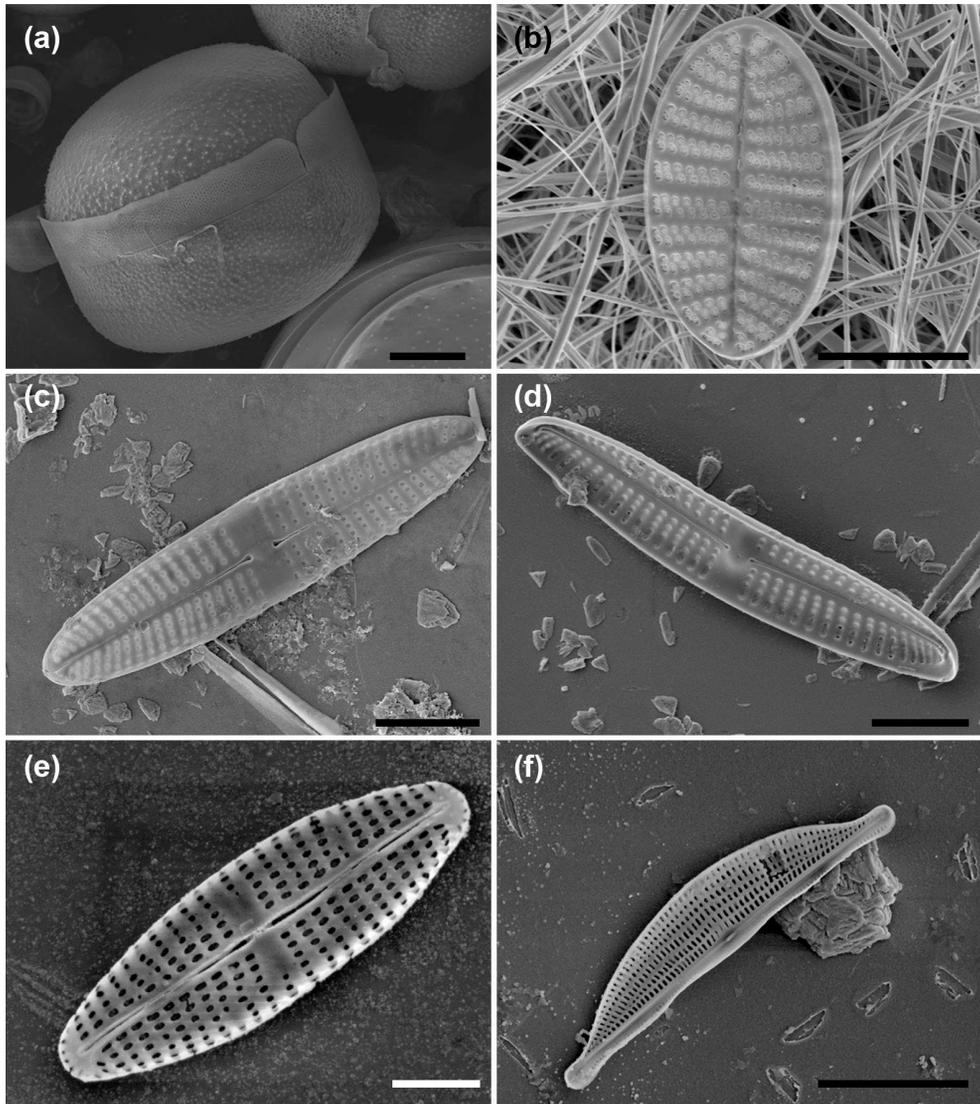


Figure 5.7.

Scanning electron micrographs of benthic diatoms in Marian Cove, Antarctica. (a) *Melosira* sp. 1; (b) *Cocconeis pinnata*; (c–d) *Achnanthes brevipes* var. *intermedia*; (e) *Navicula* sp. 5; (f) *Halamphora* sp. 1 (scale bar = 10 μ m).

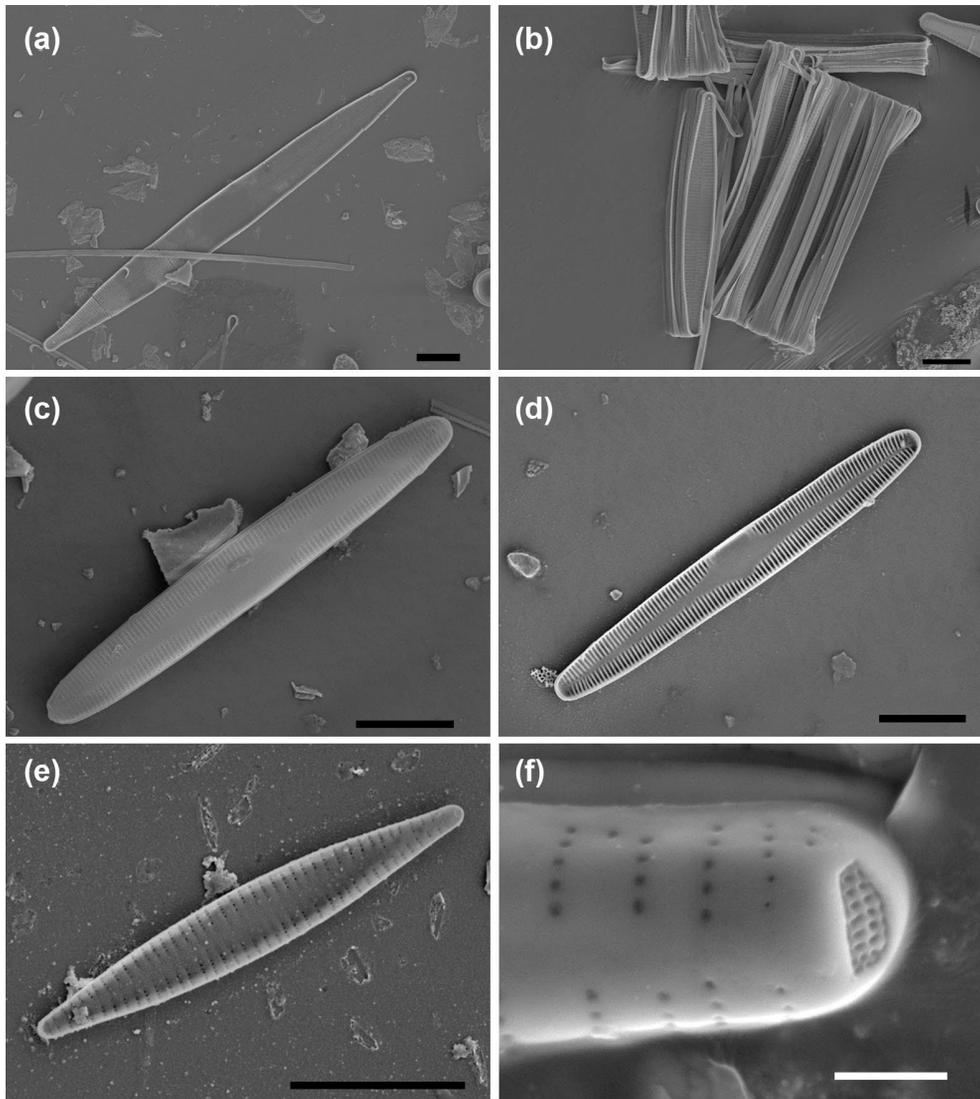


Figure 5.8.

Scanning electron micrographs of benthic diatoms in Marian Cove, Antarctica. (a–b) *Brandinia mosimanniae*; (c–d) *Tabulariopsis* cf. *australis*; (e–f) *Fragilaria islandica* var. *adeliae* (scale bar = 10 μm).

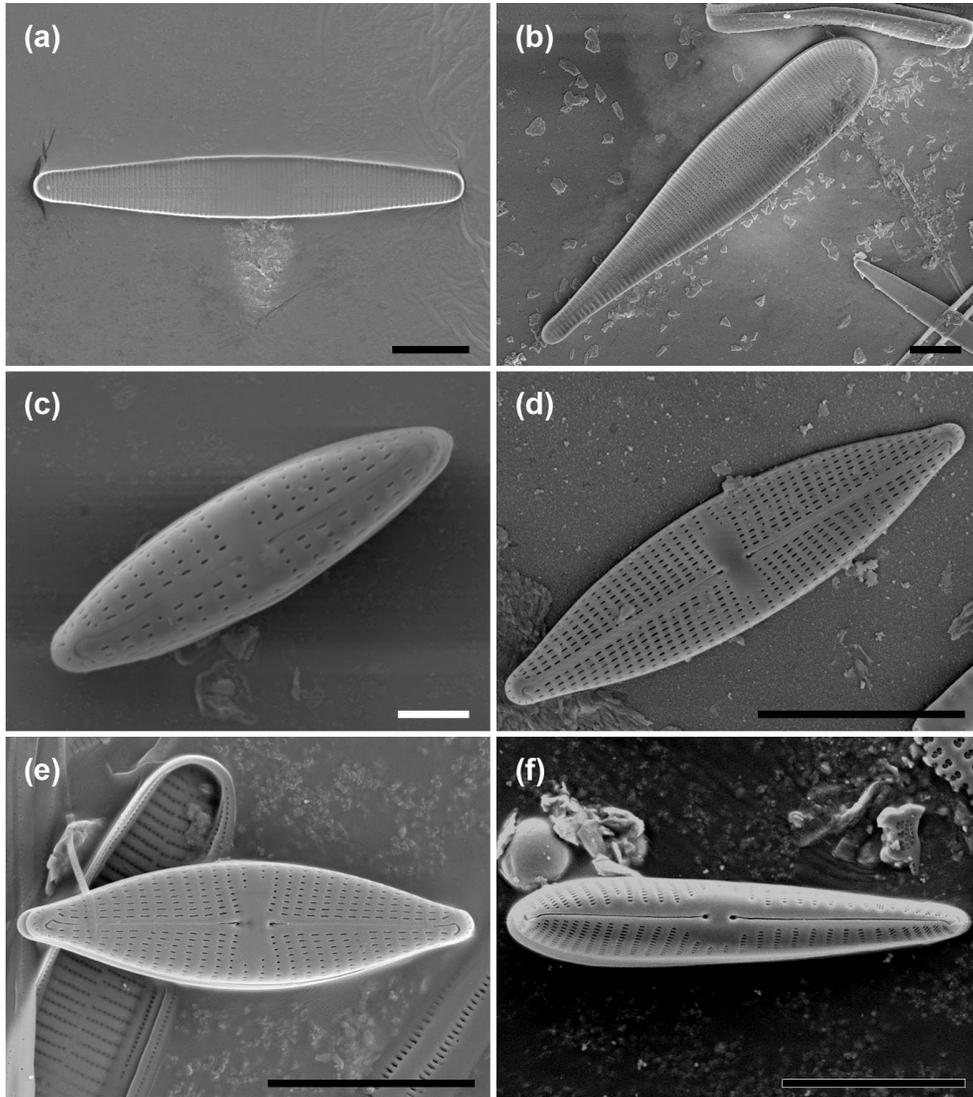


Figure 5.9.

Scanning electron micrographs of benthic diatoms in Marian Cove, Antarctica. (a) *Fragilaria* cf. *striatula*; (b) *Licmophora gracilis*; (c) *Navicula* cf. *perminuta*; (d–e) *Navicula glaciei*; (f) *Pseudogomphonema kamtschaticum* (scale bar in a–b, and d–e = 10 μm , and in c = 2 μm).



Figure 5.10. Field survey and laboratory analysis view in Marian Cove and King Sejong Station, Antarctica.

5.2.3. Data analysis

Data were analyzed statistically, as summarized in Table 5.1. Indicator value analysis (IndVal) was performed to identify indicator diatom species within each group following cluster analysis (Rimet et al. 2012). This was completed to identify indicator species that were linked to corresponding geographical features of habitats. Of note, among the types of intertidal substrates, epilithic diatoms are targeted. These diatoms would minimize bias due to substrate-dependent variation.

Table 5.1. Summary of statistics with specific purposes, data description, and software.

Method	Purpose	Remark	Software
Cluster analysis	Characterize diatom groups	Abundance data square root transformed	PRIMER 6
NMDS	Localize samples in two-dimensional space by site and by substrate	Abundance data square root transformed	PRIMER 6
ANOSIM	Confirm whether clustered groups differ significantly	-	PRIMER 6
SIMPER	Identify the species that contributed most to the dissimilarities within clustered groups	-	PRIMER 6
IndVal	Identify indicator diatom species within each group following cluster analysis	$\text{IndVal}_{ij} = A_{ij} \times B_{ij} = 100$ $\text{IndVal}_i = \max[\text{IndVal}_{ij}]$	R studio

A_{ij} : specificity (i.e., the proportion of individuals of species i that were in class j),

B_{ij} : fidelity (i.e., the proportion of sites in class j that included species i)

5.3. Results

5.3.1. Environments

The salinity of the study area showed no clear spatiotemporal variation and/or trends during the survey (Table 5.2). However, freshwater input to the cove was occasionally observed from the glacier and creeks at the time of sampling. To identify terrestrial influence on the cove, concentrations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the POM of seawater and benthic diatoms were measured along the cove (B2, B4–B6; insufficient samples were available for B1 and B3). The most enriched $\delta^{13}\text{C}$ concentrations of POM (-18.2‰) (size-fractionated at 20–100 μm reflecting microplankton size) and diatoms (-16.6‰) were detected in the inner cove (B2), near the glacier. Also, the $\delta^{13}\text{C}$ values of POM and diatoms tended to decrease with increasing distance from the glacier (-24.1 to -18.2‰ and -23.2 to -16.6‰ , respectively). The $\delta^{15}\text{N}$ values of POM and diatoms showed no clear spatial trend. The concentrations of total nitrogen did not vary across the locations (mean = $0.8 \mu\text{mol L}^{-1}$), but reference location B6 at the Narebski point, where large penguin colonies developed, showed the elevated TN ($1.8 \mu\text{mol L}^{-1}$).

Table 5.2. Data on the environmental variables measured at six intertidal locations (B1–B5 & B6 as a reference site), Marian Cove, West Antarctica.

Environmental Variables		2018						2019						Total		
		B1	B2	B3	B4	B5	B6	B1	B2	B3	B4	B5	B6	Mean	Min	Max
Temperature (°C)		1.1	2.1	1.3	1.5	1.9	2.8	1.3	1.8	6.1	5.1	2.3	2.7	2.4	1.1	6.1
DO (mg L ⁻¹)		15.1	14.3	12.3	11.7	13.5	15.6	16.2	13.6	12.2	11.2	12.5	17.1	14.2	11.7	17.1
Salinity (psu)		34.5	33.7	34.8	34.4	34.2	32.1	30.6	32.7	29.1	30.6	32.8	33.2	32.6	29.1	34.8
pH		8.22	8.45	8.18	8.26	8.26	8.52	8.30	8.15	7.94	7.84	7.89	8.43	8.32	7.84	8.52
Nutrients	SiO ₂ (µg L ⁻¹)	0.47	0.38	0.39	0.43	0.38	0.50	n.a. ^a	n.a.	n.a.	n.a.	n.a.	n.a.	0.42	0.38	0.50
	TP (µg L ⁻¹)	<0.01	0.1	<0.01	<0.01	<0.01	0.1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.1	<0.01	0.1
	TN (µg L ⁻¹)	0.51	0.78	0.53	0.61	0.52	1.84	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.8	0.5	1.8
δ ¹³ C (‰)	POM	n.a.	-18.1	n.a.	-20.3	-24.5	-24.9	n.a.	-18.2	n.a.	-18.4	-23.8	-24.1	-21.5	-24.9	-18.1
	Diatom	n.a.	-16.0	n.a.	-14.7	-17.9	-23.3	n.a.	-16.6	n.a.	-18.7	-23.8	-23.2	-19.2	-23.8	-14.7
δ ¹⁵ N (‰)	POM	n.a.	4.4	n.a.	4.9	5.0	5.4	n.a.	7.2	n.a.	10.7	3.5	4.9	6.0	3.5	10.7
	Diatom	n.a.	4.9	n.a.	6.3	5.5	7.4	n.a.	7.2	n.a.	6.3	7.2	7.5	6.4	4.9	7.5

^an.a.: not available

5.3.2. Assemblages of benthic diatoms

A total of 92 diatom taxa were recorded and identified from all surveyed locations during the study period (Table 5.3–5). In general, the community structure of benthic diatoms showed high spatial variation, but low temporal variation between 2018 and 2019 (Fig. 5.1b). Significant differences in the floral diversity were observed between inner and outer region, which was supported by the results of the stable isotopic analyses. In particular, the diversity of subtidal benthic diatoms almost doubled in the outer locations (M3–M4) compared to the inner locations (M1–M2). Benthic community structure between regions and/or locations lacked similarity, based on species compositions associated with ecological type and/or life-form (Rimet et al. 2012). For example, most diatoms were solitary, but chain-forming diatoms dominated in the inner intertidal zone of the Marine Cove, and had the most distinct distribution characteristics of polar benthic diatoms near the glacier.

Out of the 49 diatom taxa identified in the intertidal zone, *Navicula* cf. *perminuta* (53.5%) and *Fragilaria striatula* (14.4%) were the two predominant species. In comparison, chain-forming diatoms, such as *F. striatula*, *F. cf. striatula*, and *Fragilaria islandica* var. *adeliae*, dominated (48.0%) the inner intertidal locations (B1–B2).

Subtidal benthic diatoms included 82 taxa, which exhibited higher diversity compared to intertidal benthic diatoms, despite substrate type being limited to muddy bottoms. Dominant species were *N. cf. perminuta* (16.7%) and *Navicula glaciei* (15.9%). Of note, *N. cf. perminuta* appeared across all locations in Marian Cove. In comparison, the diatom, *N. glaciei*, dominated M1 and M2 (76.7% and 37.0%, respectively), and did not occur in the outer locations (M3–M4).

Table 5.3. Relative abundance (300 counts per sample) of benthic diatoms found at six intertidal locations (B1–B5 & B6 as a reference site), Marian Cove, Antarctica, data given by type substrates of rock (film and mat forms), macroalgae, and limpet shell.

Species	Total	Rock														Limpet shell				
		Film						Mat		Macroalgae						B1	B4	B5	B6	
		B1	B2	B3	B4	B5	B6	B1	B2	B1	B2	B3	B4	B5	B6					
<i>Navicula cf. perminuta</i>	2348	47	1	282	148	186	281	25	0	0	92	158	48	0	49	245	242	259	285	
<i>Fragilaria striatula</i>	756	160	201	0	0	0	0	252	0	0	143	0	0	0	0	0	0	0	0	0
<i>Pteroncola carlinii</i>	290	0	0	0	0	5	0	4	0	0	0	2	135	0	105	26	13	0	0	
<i>Pseudogomphonema kamtschaticum</i>	235	1	0	1	5	15	1	0	0	0	11	2	76	0	79	10	20	13	1	
<i>Navicula glaciei</i>	185	5	29	4	0	24	9	9	22	2	33	39	0	0	0	6	3	0	0	
<i>Achnanthes brevipes var. intermedia</i>	43	0	0	0	0	0	0	0	25	0	17	1	0	0	0	0	0	0	0	
<i>Fragilaria cf. striatula</i>	112	6	0	0	0	4	0	0	102	0	0	0	0	0	0	0	0	0	0	
<i>Fragilaria islandica var. adeliae</i>	104	0	0	0	0	0	0	2	88	0	2	0	0	0	0	0	0	12	0	
<i>Cocconeis pinnata var. matsii</i>	83	0	0	0	0	0	0	0	0	0	0	83	0	0	0	0	0	0	0	
<i>Achnanthes sp. 1</i>	63	0	0	0	0	63	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Achnanthes cf. bongrainii</i>	55	8	47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Parlibellus crucicula</i>	50	48	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	
<i>Licmophora antarctica</i>	48	0	1	5	0	0	0	0	33	0	1	0	0	0	8	0	0	0	0	
<i>Licmophora cf. gracilis</i>	37	0	0	0	0	0	0	0	0	0	0	0	0	0	30	7	0	0	0	
<i>Licmophora gracilis</i>	33	0	1	0	0	0	0	0	4	0	0	0	28	0	0	0	0	0	0	
<i>Pinnularia sp. 1</i>	25	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	
<i>Cocconeis pinnata</i>	23	0	0	0	15	0	0	0	0	0	0	0	8	0	0	0	0	0	0	
<i>Brandinia mosimanniae</i>	19	5	8	0	0	2	0	0	0	0	0	0	0	0	0	4	0	0	0	
<i>cf. Gomphonemopsis obscura</i>	18	0	0	4	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	
<i>Cocconeis melchioroides</i>	18	0	0	0	0	0	2	0	0	0	0	0	0	0	16	0	0	0	0	
<i>Tabulariopsis cf. australis</i>	17	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	
<i>Navicula sp. 5</i>	12	0	0	0	0	0	0	0	9	0	0	0	0	0	0	1	0	0	2	
<i>Paralia sp. 1</i>	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	

5.3. (continued)

Species	Total	Rock						Macroalgae						Limpet shell					
		Film						Mat		B1	B2	B3	B4	B5	B6	B1	B4	B5	B6
		B1	B2	B3	B4	B5	B6	B1	B2										
<i>Thalassiosira</i> sp. 3	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
<i>Cocconeis costata</i> var. <i>antarctica</i>	10	0	0	0	9	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontella litigosa</i>	10	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudogomphonema</i> sp. 1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0
<i>Melosira</i> sp. 1	9	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	7	0
<i>Navicula directa</i>	9	0	0	0	0	0	0	2	0	0	0	0	3	0	0	0	4	0	0
<i>Cyclotella</i> sp. 1	7	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	5	0
<i>Rhoicosphenia</i> sp. 2	4	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nitzschia</i> cf. <i>wilmotteana</i>	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
<i>Planothidium</i> cf. <i>delicatulum</i>	3	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Licmophora luxuriosa</i>	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
<i>Navicula</i> cf. <i>cancellata</i>	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
<i>Achnanthes</i> sp. 2	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Achnanthes</i> sp. 3	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
<i>Navicula</i> sp. 1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
<i>Nitzschia</i> cf. <i>homburgiensis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Planothidium</i> sp. 1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Cocconeis costata</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Cocconeis pottercovei</i>	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Navicula</i> sp. 3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Rhoicosphenia</i> sp. 1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Table 5.4. Relative abundance (300 counts per sample) of benthic diatoms on rocks at six intertidal locations (B1–B5 & B6 as a reference site), Marian Cove, Antarctica, in 2019

Species	Total	Station					
		B1	B2	B3	B4	B5	B6
<i>Navicula</i> cf. <i>perminuta</i>	1187	49	187	282	256	165	248
<i>Fragilaria striatula</i>	195	157	36	0	0	2	0
<i>Achnanthes brevipes</i> var. <i>intermedia</i>	166	3	11	3	34	113	2
<i>Navicula glaciei</i>	95	76	12	2	4	1	0
<i>Synedropsis recta</i>	41	1	19	9	2	7	3
<i>Pseudogomphonema kamtschaticum</i>	34	6	11	0	2	3	12
<i>Pteroncola carlinii</i>	21	0	0	0	0	3	18
<i>Planothidium</i> cf. <i>delicatulum</i>	18		13	2			3
<i>Brandinia mosimanniae</i>	12	5	5	0	0	2	0
<i>Cocconeis pinnata</i>	9	0	2	0	1	1	5
<i>Licmophora gracilis</i>	6	0	0	0	0	1	5
<i>Nitzschia pellucida</i>	6	0	4	1	0	0	1
<i>Nitzschia</i> sp. 1	3	0	0	0	0	0	3
<i>Fragilaria</i> cf. <i>striatula</i>	3	3	0	0	0	0	0
<i>Fragilariopsis curta</i>	2	0	0	0	0	2	0
<i>Synedropsis laevis</i>	1	0	0	1	0	0	0
<i>Cocconeis costata</i> var. <i>antarctica</i>	1	0	0	0	1	0	0

5.3.3. Distribution characteristics of benthic diatoms

Four benthic diatom groups were identified by cluster analysis (ANOSIM: $R = 0.83$, $p < 0.01$), and were separated in respect to: 1) water depth (intertidal and subtidal zones), 2) distance from the glacier, and 3) habitat substrate (Figs 5.11–13). For intertidal diatoms, inner and outer assemblages were separated as Group A and B, respectively. Two locations (B1–B2) in Group A belonged to the glacier retreat zone (< 1.5 km, ice-free area due to glacier retreat since the 1990s). The dominance of chain-forming diatom, *F. striatula*, was characteristic of Group A. Group B mainly encompassed outer intertidal locations (B3–B6), dominated by diatoms attached to limpet shells. The indicator species of Group B was *N. cf. perminuta* (69.2%), which is a commonly occurring species in Marian Cove (Fig. 5.11b). SIMPER analysis (cut-off 70%) confirmed that *N. cf. perminuta* contributed most to the Group B assemblage. Of note, each of the five predominant species from the intertidal and subtidal zones showed positive or negative correlations to distance from the glacier (Fig. 5.12b).

Subtidal diatom assemblages were also separated by geographical location. The genus *Navicula*, including *N. glaciei* and *N. cf. perminuta*, dominated the inner region (M1–M2), and belonged to Group C. *Cocconeis cf. pinnata* was the dominant species in Group D ($> 10\%$), which included the outer subtidal locations (M3–M4). When compared to the other groups, this species represented $< 2\%$ of the total relative composition of diatoms. Overall, the community structure of subtidal benthic diatoms had lower spatial variation compared to intertidal species. However, certain euryhaline species, such as *N. cf. perminuta* and *Achnanthes brevipes var. intermedia*, were consistently observed both in the inner and outer cove, regardless of water depth (Table 5.5). Significant positive correlations were obtained for some dominant species, such as *Pseudogomphonema kamtschaticum*, with other taxa ($p < 0.05$) both in the intertidal and subtidal zones, indicating spatial interactions among certain species (Fig. 5.12b).

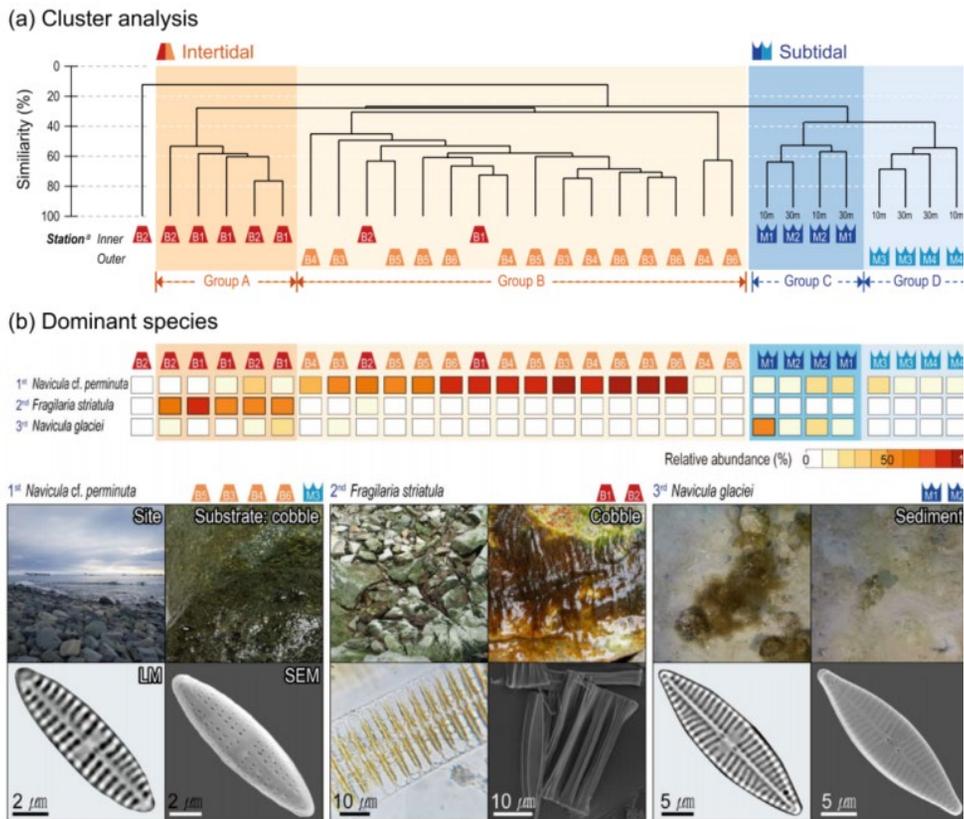


Figure 5.11. Community structure of benthic diatoms in Marian Cove, West Antarctica; (a) Cluster analysis results showing the four groups of diatom assemblages. (b) The top three dominant species in the corresponding locations with site/substrate view and LM and SEM images

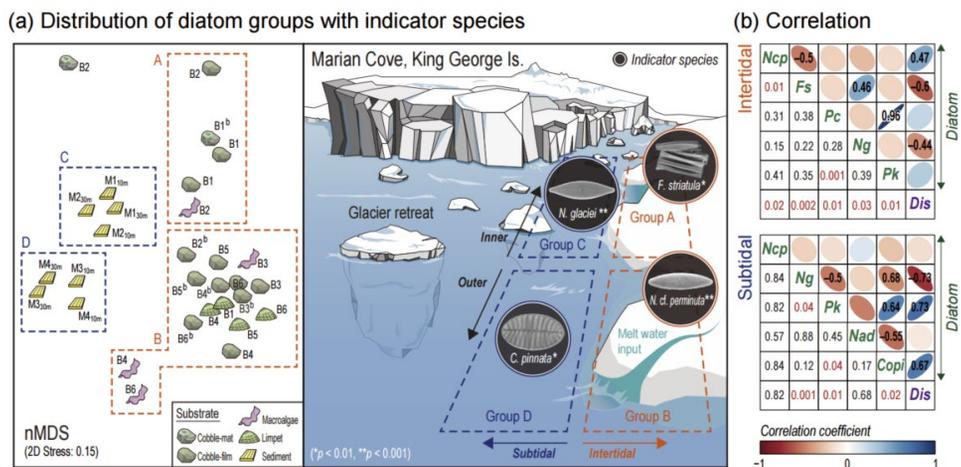


Figure 5.12.

Four indicator species of each environment in Marian Cove, and the correlation between species and distance from the glacier; (a) Diagram of the study area with indicator diatom species (SEM images) along the cove and nMDS ordination plot based on relative abundance. (b) Correlation between top five dominant species in each intertidal and subtidal zone (Ncp, *Navicula* cf. *perminuta*; Fs, *Fragilaria striatula*; A3, *Achnanthes* sp. 3; N1, *Navicula glaciei*; Pk, *Pseudogomphonema kamtschaticum*; Nad, *Navicula directa*; Copi, *Cocconeis pinnata*) and distance from the glacier (Dis). *p*-values are given as numbers.

Table 5.5. Relative abundance (300 counts per sample) of benthic diatoms in subtidal sediments from four locations (M1–M4; at two depths of 10 and 30 m), Marian Cove, Antarctica.

Species	Total	M1		M2		M3		M4	
		10 m	30 m						
<i>Navicula cf. perminuta</i>	400	29	75	60	46	77	32	40	41
<i>Navicula glaciei</i>	381	175	55	73	38	17	13	5	5
<i>Pseudogomphonema kamtschaticum</i>	202	11	4	18	11	37	30	71	20
<i>Navicula directa</i>	161	11	36	12	24	17	40	4	17
<i>Cocconeis pinnata</i>	145	6	3	14	0	11	5	51	55
<i>Achnanthes brevipes</i> var. <i>intermedia</i>	90	0	14	12	28	2	10	12	12
<i>Synedropsis recta</i>	74	0	0	0	0	25	26	12	11
<i>Cocconeis pottercovei</i>	69	1	0	2	4	13	10	31	8
<i>Fragilaria striatula</i>	66	15	19	16	6	5	2	2	1
<i>Nitzschia</i> sp. 1	58	1	7	0	2	34	13	1	0
<i>Navicula cf. cancellata</i>	53	21	2	7	10	3	3	2	5
<i>Planothidium cf. delicatulum</i>	43	5	0	9	17	3	1	1	7
<i>Cocconeis cf. scutellum</i>	42	0	0	0	0	2	6	7	27
<i>Cocconeis pinnata</i> var. <i>matsii</i>	35	0	0	0	0	4	8	23	0
<i>Fragilariopsis curta</i>	35	0	16	7	0	0	6	1	5
<i>Synedropsis laevis</i>	30	7	2	14	5	0	0	2	0
<i>Cocconeis costata</i> var. <i>antarctica</i>	28	0	5	3	20	0	0	0	0
<i>Pinnularia australomicrostauron</i>	25	0	0	0	25	0	0	0	0
<i>Pseudogomphonema</i> sp. 2	24	0	0	0	0	6	6	9	3
<i>Actinocyclus</i> sp. 1	23	0	0	0	0	2	9	2	10
<i>Paralia</i> sp. 1	23	0	0	0	1	0	4	2	16
<i>Nitzschia</i> sp. 3	20	1	0	16	0	0	2	0	1
<i>Thalassionema cf. nitzschiioides</i>	20	0	0	0	0	1	18	0	1
<i>Licmophora luxuriosa</i>	18	0	7	0	11	0	0	0	0

Table 5.5. (continued)

Species	Total	M1		M2		M3		M4	
		10 m	30 m						
<i>Nitzschia</i> cf. <i>homburgiensis</i>	18	0	4	11	2	0	0	1	0
<i>Haslea</i> sp. 1	17	0	14	3	0	0	0	0	0
<i>Navicula</i> sp. 2	17	0	0	0	0	8	5	0	4
<i>Pinnularia</i> sp. 2	15	0	6	0	8	0	0	0	1
<i>Synedra</i> cf. <i>kerguelensis</i>	13	0	0	0	13	0	0	0	0
<i>Pseudogomphonema</i> sp. 1	12	0	0	0	0	0	2	10	0
<i>Cyclotella</i> sp. 1	11	7	0	3	1	0	0	0	0
<i>Nitzschia</i> sp. 4	11	0	0	0	0	3	1	0	7
<i>Odontella litigosa</i>	11	0	0	0	0	0	1	0	10
<i>Tabularia tabulata</i>	11	0	0	0	0	2	1	0	8
<i>Thalassiosira</i> sp. 3	11	0	8	0	3	0	0	0	0
<i>Achnanthes</i> cf. <i>bongrainii</i>	9	5	2	0	0	2	0	0	0
<i>Cocconeis melchioroides</i>	9	0	0	0	0	0	8	0	1
<i>Navicula</i> sp. 4	9	0	0	0	0	4	5	0	0
<i>Fallacia marnierii</i>	8	0	0	0	0	3	3	0	2
<i>Nitzschia</i> cf. <i>gracilis</i>	8	0	0	5	3	0	0	0	0
<i>Thalassiosira</i> sp. 1	8	1	6	0	0	0	0	1	0
<i>Nitzschia</i> cf. <i>wilmotteana</i>	7	0	6	0	0	0	0	1	0
<i>Pleurosigma</i> cf. <i>obscurum</i>	7	0	0	0	0	4	3	0	0
<i>Amphora coffeaeformis</i>	6	0	0	4	0	0	0	1	1
<i>Cocconeis</i> cf. <i>imperatrix</i>	6	0	0	0	0	0	0	0	6
<i>Fragilariopsis separanda</i>	6	0	0	0	0	0	5	0	1
<i>Fragilariopsis</i> sp. 1	6	1	0	5	0	0	0	0	0
<i>Melosira</i> sp. 1	6	0	0	0	0	0	3	0	3
<i>Pteroncola carlinii</i>	6	0	0	0	3	0	0	3	0

Table 5.5. (continued)

Species	Total	M1		M2		M3		M4	
		10 m	30 m						
<i>Rhoicosphenia</i> sp. 1	6	0	1	0	5	0	0	0	0
<i>Cocconeis schuetti</i>	5	0	0	0	0	3	2	0	0
<i>Cocconeis</i> sp. 1	5	2	1	0	2	0	0	0	0
<i>Fragilaria</i> cf. <i>striatula</i>	5	0	0	1	1	1	1	0	1
<i>Fragilaria islandica</i> var. <i>adeliae</i>	5	0	0	0	0	1	0	0	4
<i>Pleurosigma</i> sp. 1	5	0	4	0	1	0	0	0	0
<i>Achnanthes</i> sp. 1	4	0	0	3	1	0	0	0	0
<i>Navicula</i> sp. 5	4	0	0	0	0	0	2	0	2
<i>Amphora marina</i>	4	0	0	0	0	0	2	0	2
<i>Thalassiosira</i> cf. <i>punctigera</i>	4	0	0	1	3	0	0	0	0
<i>Corethron</i> sp. 1	3	0	0	0	0	1	2	0	0
<i>Entomoneis</i> sp. 1	3	0	0	0	0	1	2	0	0
<i>Tabulariopsis</i> cf. <i>australis</i>	3	1	0	1	0	1	0	0	0
<i>Gyrosigma fasciola</i>	3	0	0	0	0	3	0	0	0
<i>Navicula</i> sp. 3	3	0	0	0	0	0	3	0	0
<i>Parlibellus crucicula</i>	3	0	0	0	0	0	2	1	0
<i>Achnanthes</i> sp. 3	2	0	0	0	0	1	0	1	0
<i>Amphora</i> cf. <i>proteus</i>	2	0	2	0	0	0	0	0	0
<i>Cocconeis imperatrix</i>	2	0	0	0	0	0	0	2	0
<i>Nitzschia</i> sp. 2	2	0	0	0	1	1	0	0	0
<i>Rhoicosphenia genuflexa</i>	2	0	0	0	0	2	0	0	0
<i>Thalassiosira</i> sp. 2	2	0	0	0	2	0	0	0	0
<i>Actinocyclus actinochilus</i>	1	0	0	0	0	0	1	0	0
<i>Actinocyclus curvatulus</i>	1	0	0	0	0	0	0	1	0
<i>Cocconeis californica</i>	1	0	0	0	0	0	1	0	0

Table 5.5. (continued)

Species	Total	M1		M2		M3		M4	
		10 m	30 m						
<i>Diploneis</i> sp. 1	1	0	0	0	1	0	0	0	0
<i>Entomoneis</i> sp. 2	1	0	0	0	1	0	0	0	0
<i>Eucampia antarctica</i>	1	0	0	0	0	0	0	0	1
<i>Halamphora</i> sp. 1	1	0	0	0	1	0	0	0	0
<i>Licmophora gracilis</i>	1	0	0	0	0	0	1	0	0
<i>Luticola</i> sp. 1	1	0	1	0	0	0	0	0	0
<i>Rhabdonema arcuatum</i>	1	0	0	0	0	0	0	0	1

Table 5.6. Ecological type of benthic diatoms, by habitat preference, for those found at the intertidal and subtidal locations, Marian Cove, Antarctica.

Species	Ecological type ^a			Reference
	m	eu	f	
<i>Achnanthes brevipes</i> var. <i>intermedia</i>	v	v	v	Cremer et al., 2003
<i>Achnanthes</i> sp. 1	v			Round et al., 1990; expert judge
<i>Achnanthes</i> sp. 2	v			Round et al., 1990; expert judge
<i>Achnanthes</i> sp. 3	v			Round et al., 1990; expert judge
<i>Achnanthes</i> sp. 4	v			Round et al., 1990; expert judge
<i>Actinocyclus actinochilus</i>	v			Cremer et al., 2003
<i>Actinocyclus curvatus</i>	v			Hasle and Syvertsen, 1996
<i>Actinocyclus</i> sp. 1	v			Round et al., 1990; expert judge
<i>Amphora</i> cf. <i>proteus</i>	v			Witkowski et al., 2000
<i>Amphora coffeaeformis</i>	v	v		Cremer et al., 2003
<i>Amphora marina</i>	v			Al-Handal and Wulff, 2008a
<i>Brandinia mosimanniae</i>	v			Fernandes et al., 2007
cf. <i>Gomphonemopsis obscura</i>	v			Witkowski et al., 2000
<i>Cocconeis californica</i>	v			Al-Handal and Wulff, 2008a
<i>Cocconeis</i> cf. <i>imperatrix</i>	v			Al-Handal and Wulff, 2008a
<i>Cocconeis</i> cf. <i>scutellum</i>	v	v		Al-Handal and Wulff, 2008a
<i>Cocconeis costata</i>	v			Al-Handal and Wulff, 2008a
<i>Cocconeis costata</i> var. <i>antarctica</i>	v			Al-Handal and Wulff, 2008a
<i>Cocconeis imperatrix</i>	v			Al-Handal and Wulff, 2008a
<i>Cocconeis melchioroides</i>	v			Al-Handal and Wulff, 2008b
<i>Cocconeis pinnata</i>	v			Al-Handal and Wulff, 2008a
<i>Cocconeis pinnata</i> var. <i>matsii</i>	v			Al-Handal et al., 2010
<i>Cocconeis pottercovei</i>	v			Al-Handal et al., 2010
<i>Cocconeis schuettii</i>	v			Al-Handal and Wulff, 2008a
<i>Cocconeis</i> sp. 1	v			Al-Handal and Wulff, 2008a
<i>Corethron</i> sp. 1	v			Round et al., 1990
<i>Cyclotella</i> sp. 1	v			Expert judge
<i>Diploneis</i> sp. 1	v			Expert judge
<i>Entomoneis</i> sp. 1	v			Expert judge
<i>Entomoneis</i> sp. 2	v			Expert judge
<i>Eucampia antarctica</i>	v			Al-Handal and Wulff, 2008a
<i>Fallacia marnierii</i>	v			Cremer et al., 2003
<i>Fragilaria</i> cf. <i>striatula</i>	v			Cremer et al., 2003
<i>Fragilaria islandica</i> var. <i>adeliae</i>	v			Cremer et al., 2003
<i>Tabulariopsis</i> cf. <i>australis</i>	v			Expert judge
<i>Fragilaria striatula</i>	v			Al-Handal and Wulff, 2008b
<i>Fragilariopsis curta</i>	v			Cremer et al., 2003
<i>Fragilariopsis separanda</i>	v			Cremer et al., 2003
<i>Fragilariopsis</i> sp. 1	v			Cremer et al., 2003
<i>Gyrosigma fasciola</i>	v	v		Al-Handal and Wulff, 2008a
<i>Halamphora</i> sp. 1	v			Cremer et al., 2003

Table 5.6. (Continued)

Species	Ecological type ^a			Reference
	m	eu	f	
<i>Haslea</i> sp. 1	v			Al-Handal and Wulff, 2008a
<i>Licmophora antarctica</i>	v			Fernandes et al., 2014
<i>Licmophora</i> cf. <i>gracilis</i>	v			Round et al., 1990
<i>Licmophora gracilis</i>	v			Cremer et al., 2003
<i>Licmophora luxuriosa</i>	v			Al-Handal and Wulff, 2008a
<i>Luticola</i> sp. 1			v	Al-Handal and Wulff, 2008a
<i>Melosira</i> sp. 1	v			Al-Handal and Wulff, 2008a
<i>Navicula</i> cf. <i>cancellata</i>	v			Expert judge
<i>Navicula</i> cf. <i>perminuta</i>	v	v	v	Expert judge
<i>Navicula directa</i>	v			Expert judge
<i>Navicula glaciei</i>	v			Whitaker and Richardson, 1980
<i>Navicula</i> sp. 1	v			Expert judge
<i>Navicula</i> sp. 2	v			Expert judge
<i>Navicula</i> sp. 3	v			Lange-Bertalot et al., 2017
<i>Navicula</i> sp. 4	v			Lange-Bertalot et al., 2017
<i>Navicula</i> sp. 5	v			Zindarova et al., 2016
<i>Nitzschia</i> cf. <i>gracilis</i>			v	Zindarova et al., 2016
<i>Nitzschia</i> cf. <i>homburgiensis</i>			v	Witkowski et al., 2000
<i>Nitzschia</i> cf. <i>wilmotteana</i>			v	Expert judge
<i>Nitzschia pellucida</i>	v			Witkowski et al., 2000
<i>Nitzschia</i> sp. 1	v			Expert judge
<i>Nitzschia</i> sp. 2	v			Al-Handal and Wulff, 2008a
<i>Nitzschia</i> sp. 3	v			Expert judge
<i>Nitzschia</i> sp. 4	v			Buczko et al., 2019
<i>Nitzschia</i> sp. 5	v			Expert judge
<i>Odontella litigosa</i>	v			Expert judge
<i>Paralia</i> sp. 1	v			Expert judge
<i>Parlibellus crucicula</i>	v		v	Al-Handal and Wulff, 2008a
<i>Pinnularia australomicrostauron</i>			v	Round et al., 1990; expert judge
<i>Pinnularia</i> sp. 1			v	Expert judge
<i>Pinnularia</i> sp. 2			v	Al-Handal and Wulff, 2008a
<i>Planothidium</i> cf. <i>delicatulum</i>		v	v	Expert judge
<i>Pleurosigma</i> cf. <i>obscurum</i>	v		v	Expert judge
<i>Pleurosigma</i> sp. 1	v			Expert judge
<i>Pseudogomphonema kamschaticum</i>	v			Almandoz et al., 2014
<i>Pseudogomphonema</i> sp. 1	v			Al-Handal and Wulff, 2008b
<i>Pseudogomphonema</i> sp. 2	v			Al-Handal and Wulff, 2008a
<i>Pteroncola carlinii</i>	v			Guiry and Guiry, 2020 (<i>AlgaeBase</i>)
<i>Rhabdonema arcuatum</i>	v		v	Expert judge
<i>Rhoicosphenia genuflexa</i>	v		v	Expert judge
<i>Rhoicosphenia</i> sp. 1	v			Flower et al., 1996
<i>Rhoicosphenia</i> sp. 2	v			Cremer et al., 2003
<i>Synedra</i> cf. <i>kerquelensis</i>	v			Cremer et al., 2003

Table 5.6. (Continued)

Species	Ecological type ^a			Reference
	m	eu	f	
<i>Synedropsis recta</i>	v			
<i>Synedropsis recta</i>			v	Cremer et al., 2003
<i>Tabularia tabulata</i>	v	v	v	Al-Handal and Wulff, 2008b
<i>Thalassionema</i> cf. <i>nitzschoides</i>	v			Al-Handal and Wulff, 2008a
<i>Thalassiosira</i> cf. <i>punctigera</i>	v			Hasle and Syvertsen, 1996
<i>Thalassiosira</i> sp. 1	v			Expert judge
<i>Thalassiosira</i> sp. 2	v			Expert judge
<i>Thalassiosira</i> sp. 3	v			Expert judge
Total (n = 92)	83	7	16	

^aEcological type classified into marine (m), euryhaline (eu), and freshwater (f)

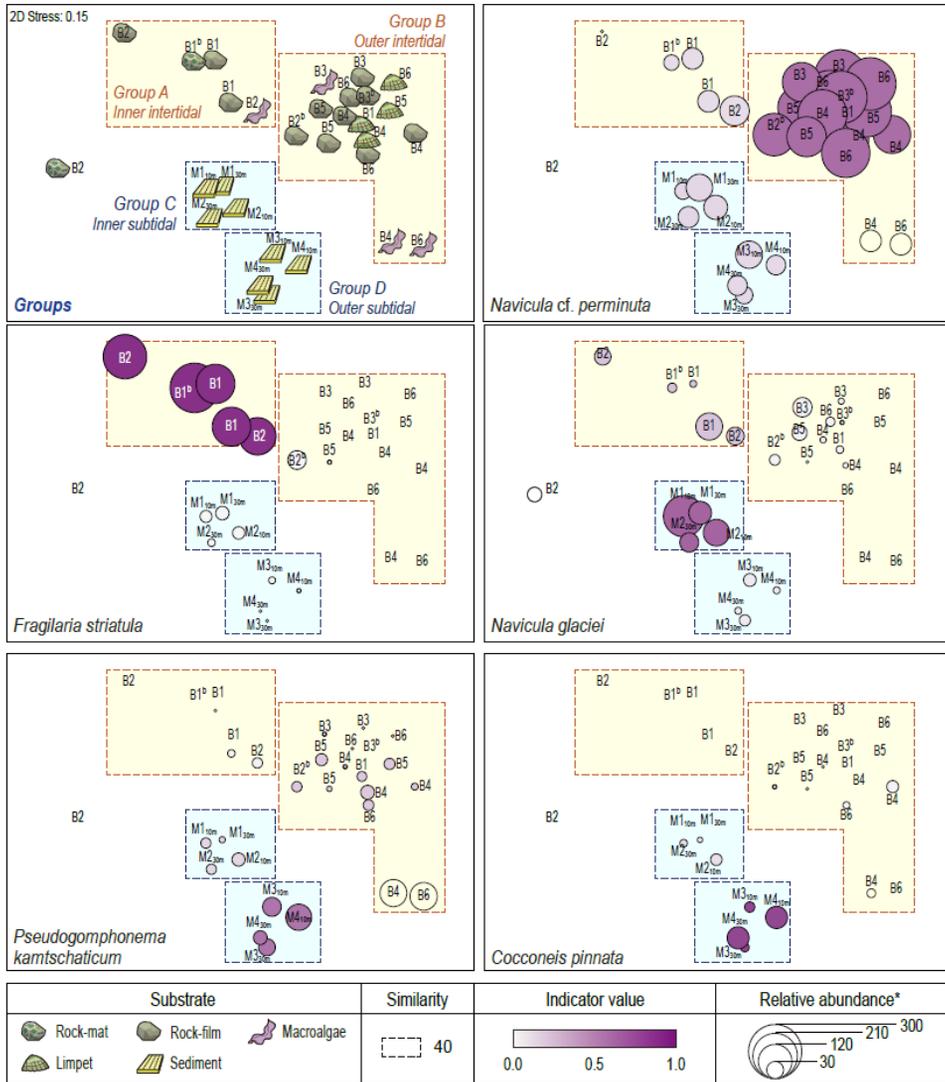


Figure 5.13.

Illustration of the groups of benthic diatom assemblages in Marian Cove, Antarctica, based on the NMSD (non-metric multidimensional scaling); five indicator species presented with corresponding indicator values and relative abundances (300 counts per sample).

5.4. Discussion

5.4.1. Impact of glacial retreat on the benthic ecosystem

Most enriched POM $\delta^{13}\text{C}$ concentrations in the inner cove location (B2) indicates a potential melt-water input near the glacier (Table 5.2). The $\delta^{13}\text{C}$ signature of diatoms showed a similar spatial concentration gradient along the cove, but was slightly more enriched than POM $\delta^{13}\text{C}$. This signature of freshwater influence has also been detected in other Antarctic regions. For example, the enriched $\delta^{13}\text{C}$ of POM and diatoms in Potter Cove was recently reported (Pasotti et al. 2015). In the enclosed environment beneath glaciers, $\delta^{13}\text{C}$ might be enriched due to increased HCO_3^- utilization and production of organic materials (Wing et al. 2012). The POM and diatom $\delta^{15}\text{N}$ concentrations showed the lack of parallel gradients over the study area. The POM $\delta^{15}\text{N}$, especially phytoplankton values, is affected by their nutrient sources. Snow melt-water input occasionally appears from the local creeks throughout the Marian Cove, and the melt-water is associated with the nutrient input as well. Thus, the POM and diatom $\delta^{15}\text{N}$ concentrations seemed to reflect the melt-water input throughout the cove.

The coastline of the inner locations (B1–B2; < 0.5 km to Marian Cove glacier) is covered by snow and ice during winter, and is exposed to the atmosphere during summer. The recent glacier retreats during the 2010s rendered the B1 location ice-free (Fig. 5.1a). In general, when ice cover melts, a rocky shore is revealed on which diatoms quickly emerge, ultimately attaining considerable biomass (Hedgpeth 1971). In our study area, a sea ice diatom *F. striatula* covered the inner intertidal rocky shore (B1–B2) like a thick carpet (Fig. 5.10b). This chain-forming species is likely a rapid colonizer in Marian Cove. Several species belonging to the genus *Fragilaria* have been previously reported as pioneering diatom taxa in ice-melting areas (Barnes and Conlan 2007) and estuary (Hudon and Bourget 1983). The inner cove environment seemed to stimulate the early aggregation of chain-forming diatoms, indicating the presence of adaptative community responses in glacier retreat zone.

N. cf. perminuta was the most abundant species at all locations. *N. cf.*

perminuta also dominated on limpet shells at all locations. Limpets are able to tolerate physical stress under rapid temperature change (Suda et al. 2015); thus, *N. cf. perminuta* might share and endure the conditions of limpets by settling on the top of shells. The diatoms on limpet shell might also be exposed to the harshest environments. However, the large abundance of limpets in the benthic environment of Marian Cove might represent the best alternative habitat when lacking in soft bottom sediment, on which they were rarely distributed. *N. cf. perminuta* is presented in various region of Antarctica including Marian Cove, South Bay, and Ross Sea (Ahn et al. 2016, Zidarova et al. 2020, Majewska et al. 2013). The species has also been reported to dominate across various substrates such as cobble (Domez and Maraslioglu 2016), most of macroalgae (Majewska et al. 2016), surface of animals (Kaleli et al. 2020), and artificial substrate (Zidarova et al. 2020), although it appeared less on macroalgae in this study area. Thereafter *N. cf. perminuta* is considered to be one of the best adapted species in Antarctica. The motility of limpets might also explain the broad occurrence of *N. cf. perminuta*; however, more information on its ecology is required (Schram et al. 2015).

The large numbers of euryhaline diatoms (including *N. cf. perminuta*) observed across all the locations indicated the presence of melt-water (freshwater) inputs around Marian Cove. However, the high numbers of marine species in subtidal locations (M1–M4) indicated low freshwater input in the deep waters of the cove (Fig. 5.1). Species diversity was much greater on the muddy bottoms of subtidal deep waters compared to intertidal substrates. Unlike the intertidal zone where few species dominated (*F. striatula* in inner cove (39.5%) and *N. cf. perminuta* in outer cove (68.5%)), sedimentary diatoms exhibited relatively high evenness (Table 5.7). Several diatoms belonging to the genera *Navicula* and *Cocconeis* were widespread subtidal species, occupying a distinct zone to intertidal habitats. Finally, relatively consistent proportions of subtidal diatom assemblages were recorded across all the surveyed locations. This phenomenon implies that thermohaline changes more prevailed by ice-melting and/or physical stress of ice-scouring in the intertidal areas than deep waters, supporting observations that shallow waters are relatively fragile to the effects of melting ice (Barnes and Conlan 2007).

Table 5.7. Diversity indices of benthic diatom communities at the intertidal and subtidal locations of Marian Cove, Antarctica, by substrate type; *d*, species richness; *J'*, Pielou's evenness; *H'*, Shannon wiener diversity.

Habitat (year)	Location	Type	<i>d</i>	<i>J'</i>	<i>H'</i>	
Intertidal (2018)	B1	Epilithic (mat)	1.4	0.3	0.7	
		Epilithic (film)	1.4	0.6	1.4	
		Epiphytic	0	-	0	
		Epizoic	1.2	0.4	0.8	
	B2	Epilithic (mat)	1.2	0.8	1.7	
		Epilithic (film)	1.2	0.5	1.0	
		Epiphytic	1.2	0.6	1.3	
	B3	Epilithic (film)	0.9	0.2	0.3	
		Epiphytic	1.2	0.6	1.2	
	B4	Epilithic (film)	0.7	0.6	1.0	
		Epiphytic	1.1	0.7	1.4	
		Epizoic	1.1	0.4	1.0	
	B5	Epilithic (film)	1.2	0.6	1.2	
		Epizoic	1.1	0.3	0.6	
	BR	Epilithic (film)	1.2	0.2	0.3	
Epiphytic		1.4	0.8	1.7		
Epizoic		0.7	0.2	0.2		
Intertidal (2019)	B1	Epilithic (film)	1.2	0.6	1.2	
	B2	Epilithic (film)	1.6	0.6	1.4	
	B3	Epilithic (film)	1.1	0.2	0.3	
	B4	Epilithic (film)	1.1	0.3	0.5	
	B5	Epilithic (film)	1.8	0.4	1.0	
	B6	Epilithic (film)	1.6	0.3	0.8	
Subtidal (2018)	M1	(10 m)*	Sediment	3.0	0.6	1.7
		(30 m)	Sediment	4.2	0.8	2.5
	M2	(10 m)	Sediment	4.0	0.8	2.6
		(30 m)	Sediment	5.1	0.8	2.9
	M3	(10 m)	Sediment	5.8	0.8	2.7
		(30 m)	Sediment	6.7	0.9	3.1
	M4	(10 m)	Sediment	4.9	0.7	2.5
		(30 m)	Sediment	6.7	0.8	3.0

5.4.2. Indicator species

Six indicator species were identified in Marian Cove ($p < 0.05$ in IndVal), with four species being representative of clusters A, B, C, and D, respectively (Fig. 5.11a, Table 5.8). Group A inhabited newly exposed ice-free areas, with dominance of *F. striatula*, being the indicator species. *F. striatula* has been reported as an indicator of cooler temperature with presence of floating sea ice throughout the austral summer (Cremer et al. 2003). In the meantime, results from the present study suggest that the species could also indicate the influence of broken pieces of floating sea ice which have drifted to the shore. *F. striatula* may have settled down on the intertidal zone after last sea ice melted, subsequently becoming a predominant indicator species as rapid colonizer to the newly exposed ice-free area. The indicator species of Group B was *N. cf. perminata*, which occupied the outer intertidal habitats. This species was able to withstand extreme conditions on hard substrate. The indicator species of Group C were Naviculoid diatoms such as *N. glaciei* (sea ice diatom) and *Navicula directa*, which occupied the inner subtidal sediment. *N. glaciei* seemed to be dominated through a similar process to the *F. striatula* in the intertidal zone. The dominated occurrence of *N. glaciei* and *F. striatula* found in the austral summer would reflect the presence of sea ice during the colder season followed by ice-melting at the time of sampling (Cremer et al. 2003). Of note, some earlier studies have reported the dominance of *N. glaciei* in the subtidal zone around the glacier retreating area (Ahn et al. 2016, Zidarova et al. 2020). Two epiphytic diatoms, *C. cf. pinnata* (Romero and Rivera, 1996) and *P. kamtschaticum* (Al-Handal and Wulff, 2008), were the indicator species of Group D. Although these diatoms inhabited sediment, the abundant epiphytic diatom reflected the available habitats for benthic diatoms in the deep waters of cove. The result was generally consistent with the previous studies that documented prevailed subtidal epiphytes on Antarctic macroalgae (Majewska et al. 2013, Majewska et al. 2016, Al-Handal and Wulff 2008). These abundant macroalgae colonized in the outer subtidal zone, which might represent the preferable habitat for those taxa.

The lack of overlapping indicator species across the groups supported clear distinct of benthic diatom assemblages among the groups. Overall, our analyses

revealed the presence of dynamic, sensitive, and distinct micro-benthic community that was responding to ice melting under the rapidly changing polar environment. In fjord-shaped coves, such as Marian Cove in the present study area, the sea ice of the inner part is the last to disappear. Interestingly, both indicator species of the inner part, viz. *F. striatula* and *N. glaciei*, were sea ice diatoms, which are released with melting ice during austral spring (Cremer et al. 2003, Kang et al. 1999). Considerable abundance of diatoms in the inner cove overlapped that of the sea ice diatom. Previous studies also reported that the sea ice diatoms are released into the water column after the sea ice has melted (Zidarova et al. 2020) and they may settle down on other substrates such as surface of macroalgae (Majewska et al. 2013). Thus, the high abundance of these species likely reflects a temperature cooling event in the area proximal to the glacier retreat region.

Table 5.8. IndVal analysis listing the indicator epilithic diatom species by clustered groups delineated for Marian Cove, Antarctica. Given groups representing geographical setting, such as A: inner intertidal locations; B: outer intertidal locations; C: inner subtidal locations; D: outer subtidal locations.

Indicator species	Group			
	A	B	C	D
<i>Fragilaria striatula</i>	0.91 ^{***}	0.00	0.07	0.01
<i>Navicula cf. perminuta</i>	0.12	0.59 ^{***}	0.15	0.14
<i>Navicula glaciei</i>	0.23	0.03	0.65 [*]	0.08
<i>Navicula directa</i>	0.00	0.00	0.51 [*]	0.47
<i>Cocconeis pinnata</i>	0.00	0.02	0.11	0.80 ^{**}
<i>Pseudogomphonema kamtschaticum</i>	0.03	0.21	0.16	0.57 [*]

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

5.4.3. Role of benthic diatoms on shift in polar community

Studies investigating the ecological responses of polar benthic organisms to glacier retreat remain limited. Our mini-review demonstrated that ecological responses vary depending on the target taxa present (Fig. 5.14). The diversity and abundance of macroalgae tends to be lower in inner cove (Quartino et al. 2013, Sahade et al. 2015). In comparison, the diversity and abundance of small organisms, such as meiofauna and diatoms, is higher in the inner cove. During our survey, we documented large benthic diatom blooms in the inner cove (Fig. 5.11b), with previous studies supporting this phenomenon (Ha et al. 2019, Cunningham and Leventer 1998). The elevated number of epibiotic diatom species in blooms occurring in the subtidal zone potentially indicate the presence of a mature benthic community that is less influenced by ice-melting events. The phenomenon of enriched massive chain-forming diatoms observed in the subtidal zone of Marian Cove were recently documented (Clarke et al. 2007). Of note, a higher diatom growth near the glacier at the initial phases of experiment using artificial substrates (macroalgae) was documented in Potter Cove, which is adjacent to Marian Cove (Campana et al. 2018).

To expand our focus on shift of polar benthic community structure, we conducted a mini-review and analyzed meta-data from literatures including the present study (Fig. 5.14). The result demonstrated that diversity and abundance of polar benthic organisms significantly vary with respect to ecological functioning groups. In other words, the functional diatom groups collectively contributed towards shifting the entire polar benthic community. The polar benthic community shift under the impacts of glacier retreat could be described in three stages. First, the new habitat exposed from retreating glacier and melting ice, then the diatoms melted out from sea ice during the warmer season. These diatoms formed a chain-like union of cells and quickly settled to the newly exposed substrates such as cobble and sediment. Life-forms and cell size are responses to various environmental condition (Smale et al. 2008). The diatoms appeared to have a strategy to survive the fast-evolving harsh environment, which involved energy-

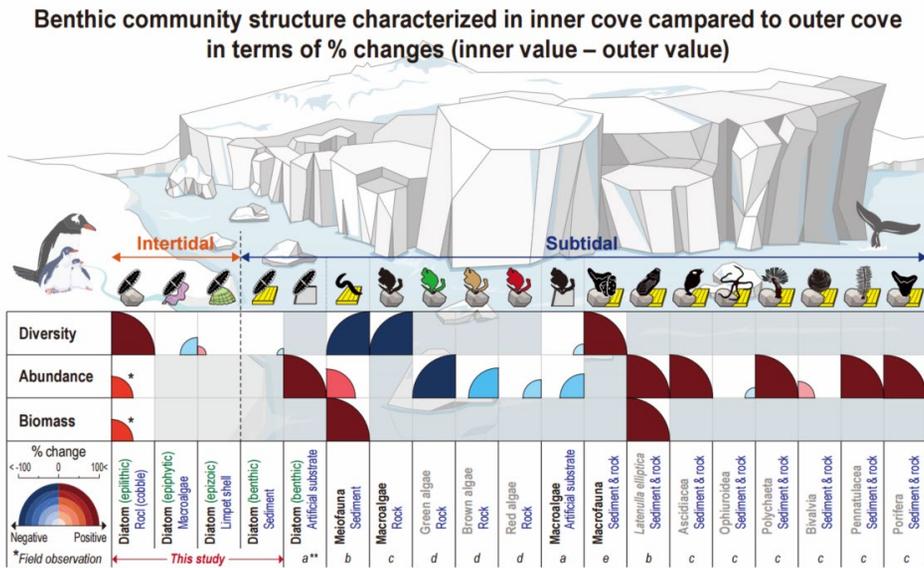


Figure 5.14.

Mini-review on the ecological responses of marine benthic organisms affected by glacier retreat in Antarctica (*this study and **five references). Benthic community structure characterized in inner cove compared to outer cove in terms of % changes. % changes in diversity, abundance, and biomass of marine benthos between the inner (< 2.5 km to glacier) and outer (> 2.5 km) region; + indicates greater value in the inner region compared to outer one. Target marine organisms include diatoms, meiofauna, macroalgae, and a diversity of macrofauna.

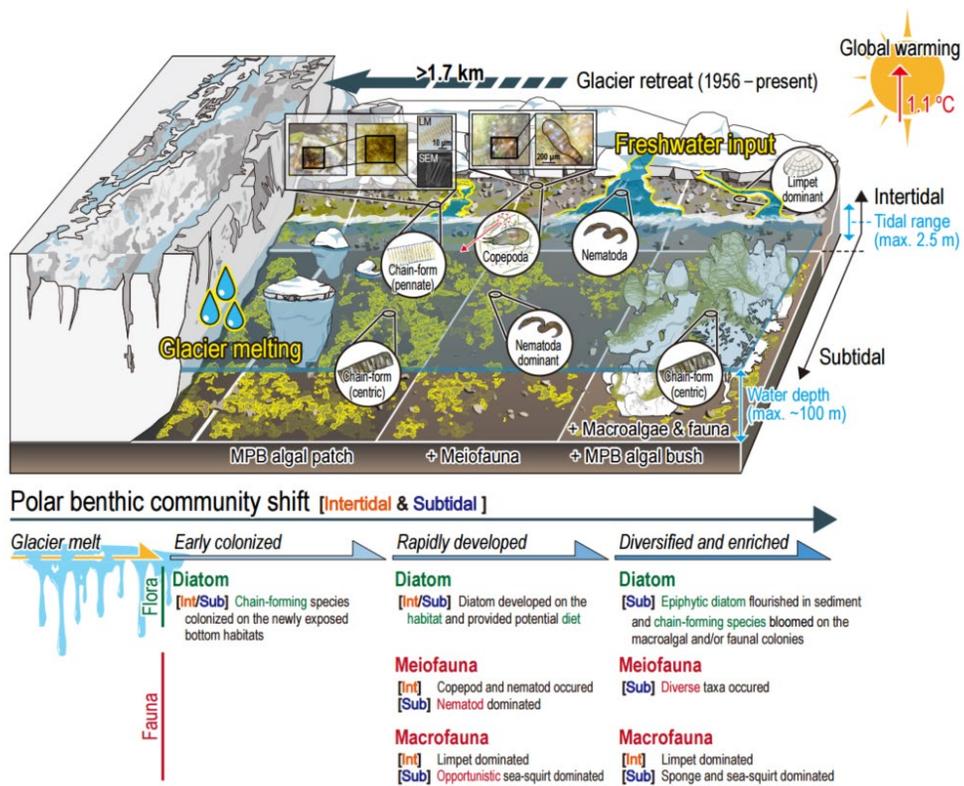


Figure 5.15.

A schematic overview of the polar benthic community shift in an Antarctic cove under glacier retreat. This study and previous studies were simultaneously analyzed and incorporated to delineate a simplified feature with three stages: (1) early colonized community, (2) rapidly developed community, and (3) diversified and enriched community along with distance from the glacier.

efficient chain clustering (Hoagland et al. 1993). Interestingly, sea ice pennate diatoms, such as *F. striatula*, dominated the intertidal zone, whereas centric diatoms, such as *Paralia* sp., dominated the subtidal zone.

Next, subsequently, microalgal dynamics would stabilize bottom habitats, providing refuge and potential diets to upper trophic organisms, such as meiofauna and/or macrofauna. A considerable number of copepods were observed that inhabited and ate the bushes of chain-form diatom, in the intertidal zone (Fig.5.15). Limpets were the dominant macrofauna in the intertidal zone of the Marian Cove. In the subtidal zone, both meiofauna and macrofauna communities were characterized by dominance of opportunistic taxa (nematode (Hoffmann et al. 2018) and opportunistic ascidian (Kim et al. 2020))

Finally, the diversified and enriched stage refers to the flourishing benthic communities through ecologically diverse diatom groups and abundant diatom (bloom) in the subtidal zone, and higher diversity of meiofauna and macrofauna (Fig. 5.15). Ecological status in the outer intertidal zone, say old habitat, also represented stable community structure with predominance of tolerant species, viz., small motile naviculoid diatoms, to harsh conditions such as salinity fluctuation, wave action, etc.

The diatom communities inhabiting the subtidal zone were divided into two types. First, the dominance of epiphytic diatoms (> 30%) was featured in the subtidal sediments. Second, the chain-form diatom lived on macroalgal and/or macrofaunal colonies in the form of bushes, of which observation was documented by Ahn et al., 2016. Macrofaunal communities in the outer cove represented the matured colonization of macrofauna and/or megafauna, with dominant species including clams, sponges, ascidians, and echinoderms (author observation). During this stage, extensive algal mats of chain-forming diatoms attached to fauna are evidenced, representing the most mature colonization of the benthic polar community (Ahn et al. 2016). Thus, polar benthic communities are developed through the support of the benthic diatom, a rapid colonizer (Campana et al. 2018, Wahl 1989), and promoted to diversified and enriched communities in the fast-

evolving, harsh polar environment.

The current study is novel in that it investigated both intertidal type habitats and subtidal deep waters simultaneously for polar benthic diatoms. Interestingly, benthic diatom assemblages exhibited diverse ecological responses (with respect to occurrence, distribution, and diversity) to the given environmental settings associated with glacier retreat. First, epilithic diatoms primarily consisted of chain-forming species, which dominated the intertidal cove. Second, epibiotic diatoms on limpets show constant species composition regardless of sampling position (in both inner and outer cove). Finally, the species diversity of epiphytic diatoms varied greatly across locations, but tended to increase in older habitats (viz., habitats that were exposed earlier), confirming the occurrence of micro-floral community shift. Overall, benthic diatoms seem to represent appropriate and promising indicator taxa for monitoring and/or predicting the status of the sensitive polar benthic community and associated long-term changes under the current climate change regime. pennate diatoms, such as *F. striatula*, dominated the intertidal zone, whereas centric diatoms, such as *Paralia* sp., dominated the subtidal zone.

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5.5. Summary

Glacier retreat is a major long-standing global issue; however, the ecological impacts of such retreats on marine organisms remain unanswered. Here, we examined changes to the polar benthic community structure of “diatoms” under current global warming in a recently retreated glacial area of Marian Cove, Antarctica. The environments and spatiotemporal assemblages of benthic diatoms surveyed in 2018–19 significantly varied between the intertidal (tidal height of 2.5 m) and subtidal zone (10 and 30 m). A distinct floral distribution along the cove (~4.5 km) was characterized by the adaptive strategy of species present, with chain-forming species predominating near the glacier. The predominant chain-forming diatoms, such as *Fragilaria striatula* and *Paralia* sp., are widely distributed in the innermost cove over years, indicating sensitive responses of benthic species to the fast-evolving polar environment. The site-specific and substrate-dependent distributions of certain indicator species (e.g., *F. striatula*, *Navicula glaciei*, *Cocconeis* cf. *pinnata*) generally reflected such shifts in the benthic community. Our review revealed that the inner glacier region reflected trophic association, featured with higher diversity, abundance, and biomass of benthic diatoms and macrofauna. Overall, the polar benthic community shift observed along the cove generally represented changing environmental conditions, (in)directly linked to ice-melting due to the recent glacier retreat.

CHAPTER 6.

CONCLUSIONS

6.1. Summary

The present study provided comprehensive insights on the distribution and dynamics of benthic communities inhabiting harsh environmental conditions (Figs 6.1–6.3). This study presented three research questions (Fig. 1.4). To answer these questions, I reported on the community structures and responses of benthos to various harsh environments in Chapter 2–5. Overall, species diversity (H') tends to decrease with increasing environmental extremes. This response was commonly detected across a variety of cases with extreme environments. However, the tolerant species occupying each environment differed. Representative species were presented for each condition in each chapter (Fig. 6.1). Representative harsh environments included hypersaline and hypoxic conditions and land-derived pollutant input and glacier retreat sites, all of which are associated with anthropogenic effects. To understand the responses of benthic organisms, various methods were implemented, including appropriate statistical techniques and identifying the indicator species of specific environments. The major findings of the present study are summarized below.

Chapter 2 provides a comprehensive insight on the dynamics of diatom assemblages in a harsh hypersaline environment. The benthic diatom assemblages in the two salterns were analyzed. The results showed that: 1) diatoms are able to survive salinity exceeding ~ 200 psu, but were not detected above 300 psu; 2) the species diversity of diatom assemblages decreased with increasing salinity stress; 3) mud content and nitrogen were significantly associated to the structure of diatom assemblages at salterns; 4) indicator species corresponded to specific ranges of salinity gradients in a site-specific manner; and 5) salterns provide a good model habitat for examining the dynamics of diatoms in hypersaline environments.

Chapter 3 presents a long-term study on a benthic community in a semi-enclosed bay (Jinhae, Korea) versus an open sea area (Samcheok, Korea). Macrozoobenthos assemblages inhabiting the soft bottom of the subtidal zone were investigated over a three-year period. The results showed that: 1) the abundance of dominant species peaked in certain season(s), and then suddenly decreased or, even, disappeared entirely for long periods of time; 2) the macrofaunal assemblages were

clustered with the traits of groups, which varied with a wide range of environmental and macrozoobenthic characteristics; 3) benthic community structure could be explained by a few selected environmental factors that were identified using PCA and DA; and 4) a wide range of environmental gradients could be predicted based on the presence of certain indicator species that had different habitat preferences and/or tolerances for specific environmental conditions.

In **Chapter 4**, diatoms were analyzed at the genus and species level in the Yellow and Bohai seas, which are impacted by human activities. Diatoms on the surface sediment and from the sediment core were used to elucidate past and present environmental conditions. The results showed that: 1) genus level data were representative of general trends to diatom diversity; 2) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were the most significant factors affecting diatom assemblages in studies seas; and 3) concentrations of $\delta^{15}\text{N}$ have become increasingly enriched over time (from past to present).

Chapter 5 examined changes to the structure of the polar benthic community of “diatoms” under current global warming in the recently retreated glacial area of Marian Cove, West Antarctica. The environments and spatiotemporal assemblages of benthic diatoms significantly varied between the intertidal and subtidal zone. The results showed that: 1) the distinct floral distribution along the cove was characterized by the adaptive strategy of species present; 2) predominant chain-forming diatoms became widely distributed in the innermost cove over several years, indicating the sensitive responses of benthic species to the fast-evolving polar environment; 3) the site-specific and substrate-dependent distributions of certain indicator species generally reflected shifts in the benthic community; and 4) a review of the published literature revealed that the inner glacier region reflected trophic associations, based on the documented higher diversity, abundance, and biomass of macrofauna and benthic diatoms (this study).

Overall, benthic organisms clearly have thresholds or preferences for specific environmental factors. Ecological responses of benthic organisms to extreme environments were surprisingly diverse, and depended on type of environmental

conditions (hypersaline, hypoxia, glacier retreat, and multiple anthropogenic pressures). Analysis of benthic communities inhabiting harsh anthropogenic environments showed that these benthic organisms adapted, declined, or disappeared from extreme environments. Specific taxa had the capacity to be abundant in response to the dynamics of extreme environments (i.e., hypoxic events in terms of seasonal changes and new habitat exposed from glacier retreat). Thus, anthropogenic pressure is diversifying and globalizing assemblages as it changes the marine ecosystem. Our data provide insights on how we can predict and prepare for dynamic changes to marine ecosystems under growing human impacts.

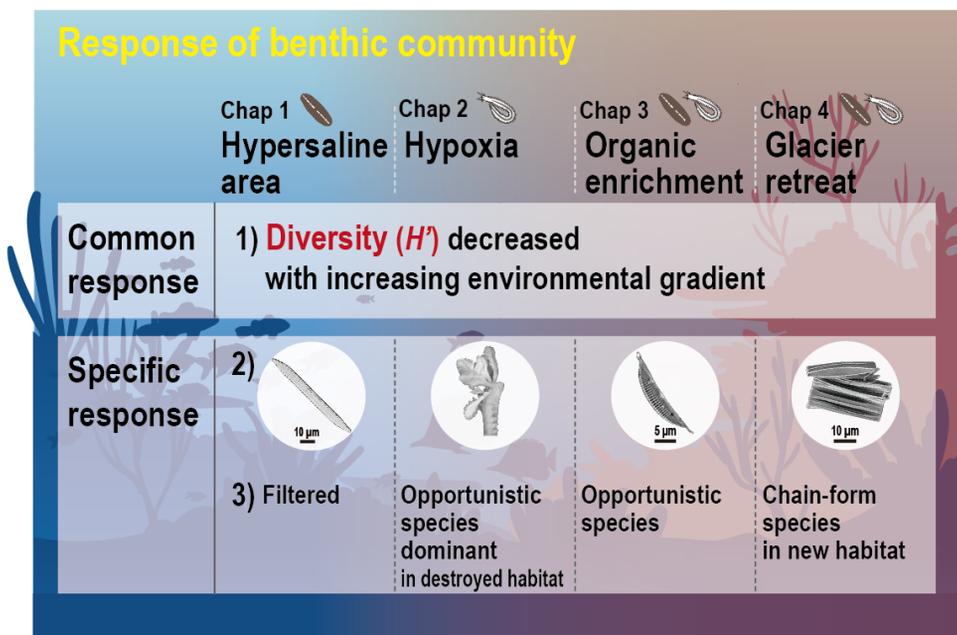


Figure 6.1. Response of benthic diatoms to extreme condition. Research summary and key findings of the present study are also provided.

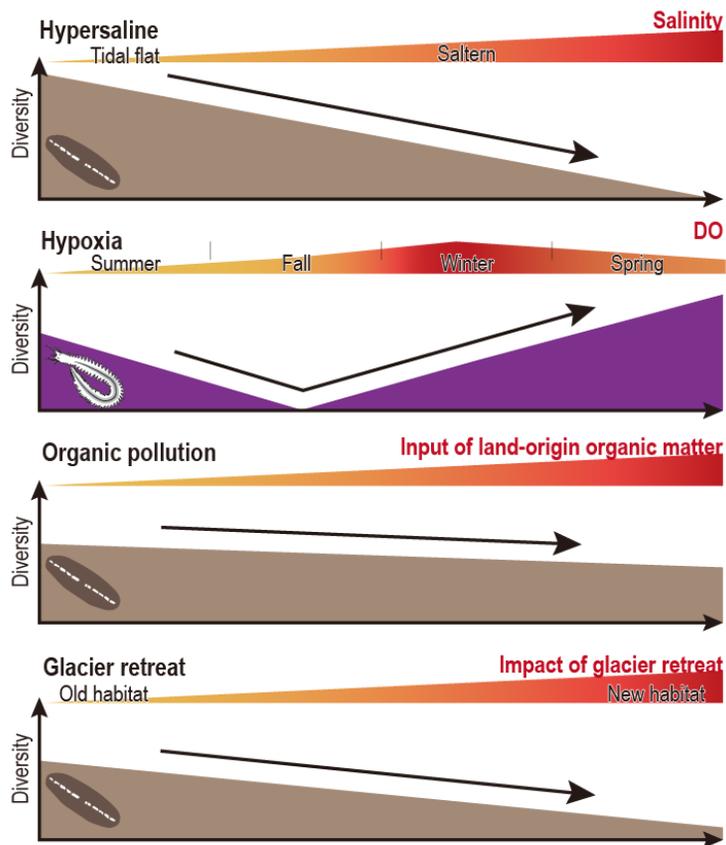


Figure 6.2.

Research summary and key findings of the present study. Brown shaded background represents the diversity of benthic diatoms. Purple shaded background represents the diversity of macrozoobenthos.

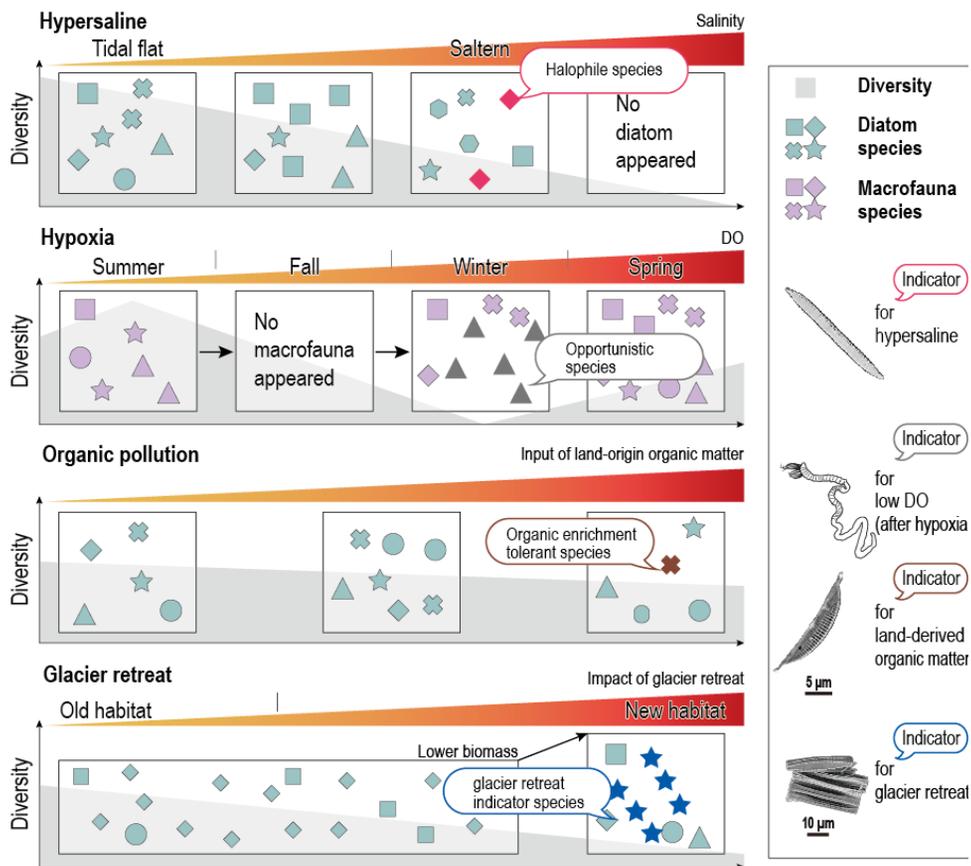


Figure 6.3.

Research summary and key findings of the present study. Yellow to red gradient bar indicates the gradients of each environmental variable. Gray-shaded background represents the diversity of benthos. Indicator species are also given.

Table 6.2. Summary of benthos from extreme environments

Ecosystem	Extreme parameters	Target Area	Stable/ unstable/ seasonal	Response (diversity(H'))			Adaptation	Threshold
				Diatom	Meiofauna	Macrofauna		
Hypersaline areas	High salinity	Saltern	Unstable/ Seasonal	Decrease	Unknown	Decrease	<i>Achnanthes</i> predominant; Nematoda abundant	Diatom: > 300 psu
Hypoxic environments	Very low oxygen	Subtidal under aquaculture	Temporary/ seasonal	Decrease ^{a,b} (More tolerant than macrofauna)	Decrease ^{a-c} (More tolerant than macrofauna)	Decrease/ Defaunation	Foraminifera and nematoda abundant; Macrofauna defaunation	Macrofauna: < 2.0 mg L ⁻¹
Organic polluted area	High concentration of organic pollutants	Intertidal under human impact	Unstable	Decrease	Decrease ^{c,d}	Decrease	Unknown	Unknown
Polar Region	Low temperature, low light intensity and unstable salinity, melt water.	Antarctic cove (glacier retreat area)	Seasonal	Increase	Increase ^e	Decrease ^f	Chain-form diatom dominant; Opportunistic meio/macrofauna dominant in glacier retreating area;	Unknown

^aRabalais et al., 2007, ^bDe Troch et al. 2013, ^cMurrell and Fleeger 1989, ^dWhitte and Zijlstra 1984, ^eHoffmann et al. 2018, ^fSahade, 2014
Green background: our own data, yellow background: reviewed data

6.2. Ecological implications and limitations

Benthic diatoms exhibit fast adaptation and survival under various extreme conditions. This study investigates structure of diatom communities in salterns, tidal flats, and Antarctic intertidal/subtidal zones. The presence of diatoms in these environments is of great ecological significance. Because they are the only or major primary producers and food sources in such environments. In Marian Cove, Antarctica, the epilithic diatom in the intertidal zone had an average primary production rate of 40.9 (unpublished data). At some intertidal regions microalgae (including diatoms) are major primary producers because macroalgae are lacking. Thus, benthic diatoms allow environments to become appropriate habitats for other benthic organisms.

Macrozoobenthos also drive distinctive changes to community structure under extreme environmental conditions, particularly before and after hypoxia occur in the semi-closed bays. Increased oxygen levels, after hypoxic conditions end, result in opportunistic species (mainly polychaetes) quickly colonizing once-devastated habitats, followed by the introduction of other common microbenthic animals, resulting in the final stabilization of the ecosystem. A combination of seasonal changes and anthropogenic pressure often facilitate dynamic changes in benthic community structure. Hypoxia, harmful algal blooms, and various aquatic pollutants are good examples of dynamic conditions associated with seasonal precipitation. The threshold tolerance of organisms for such environments remains unclear, due to the complex environmental factors being combined with the seasons (temperature) and anthropogenic effects. This issue could be addressed by identifying specific drivers through controlled laboratory experiments.

The responses of the benthic community, which are represented by the occurrence and diversity of benthic species, strongly reflect the gradient of environmental conditions. For example, the species diversity of benthic diatoms clearly decreased from marine to hypersaline conditions, with no diatoms being detected at ca. 300 psu. Macrozoobenthos diversity also tended to decrease with the prevalence of anoxia and hypoxia. No animal was observed in places with oxygen

concentrations below 2.0 mg L^{-1} . Rapid colonization by benthic diatoms in the newly exposed area following the glacier retreat in Antarctica was also documented. Many diatoms in this environment were considered to be pioneering species, while many typical dominant members of benthic diatom communities in the area also co-occurred. Interestingly, species diversity was higher in the new habitats, while old habitats, which were more distant from the glacier, had very low diversity, with a few competitive species dominating.

Organisms inhabiting extreme environments exhibit extreme adaptability. In other words, various extremophiles could be indicator species of their corresponding extreme environmental conditions. Thereafter the structure of the benthic community in a given area might reflect the extremity and/or characteristics of a given habitat. Prospective future evolution of the community could also be predicted based on past and present conditions. Thus, selecting appropriate taxonomic groups is important, as each taxon presents different adaptive capabilities to changing environments.

The various extreme environments examined in this thesis provide insights on the impacts of human activities. Some benthic communities were strongly impacted, while others were only indirectly affected. Diatoms inhabiting salterns under very strong human impact were evaluated in Chapter 2. These diatoms were not simply affected by human activities, but had become adapted to the artificial structure that functioned to produce salt. The influence of other environmental variables was minimized, and certain environmental factors (in this case, salinity) strongly controlled the structure of benthic diatom communities. Diatoms survived even in artificial hypersaline areas ($> 200 \text{ psu}$), where other living organisms could not live. In contrast, Antarctica is regarded as an extreme environment, even in the absence of human impact. However, accelerating glacier retreat has been widely reported due to recent rapid climate change. The current study demonstrated how diatoms in this region have settled and adapted to this fast-evolving environment. In this example, indirect changes to the environment were caused by a combination of human activities and natural changes (transition to Austral summer), resulting in a unique distribution of diatoms being detected.

Overall, the investigation of benthos under extreme conditions generated a useful and powerful dataset for monitoring global benthic ecosystems and understanding associated processes in environments subjected to great anthropogenic pressure, including climate change and marine pollution. Communities in extreme environments are highly vulnerable to such pressure, with more academic attention being required on this field of research.

6.3. Future research directions

Although the boundaries within which marine organisms can survive are expanding (Henger 2020, Merino et al. 2019), knowledge gaps remain about the environmental thresholds allowing organisms to survive. Actual ecosystems are impacted by single to multiple environmental factors, with mixed effects. Microorganisms that are able to tolerate extreme conditions are often polyextremophile (tolerance or preference for multiple factors combined). Ultimately, to improve our understanding of species inhabiting extreme environments, cell cultures, microcosm, and mesocosm experiments might be required.

The present study confirmed that benthic organisms could be abundant in extreme environments. One of the most important implications of organisms inhabiting extreme environments is that species or communities serve as indicators of specific environments. Through biomonitoring, the conditions of marine ecosystems could be assessed based on the tolerance and preference of indicators. In particular, diatoms might serve as powerful monitoring tools, effectively reflecting present environmental changes and past environmental conditions. The ecological monitoring of lakes and streams is already broadly based on freshwater diatoms. However, the use of marine diatoms as an ecological monitoring tool is not sufficiently developed, due to the lack of ecological data on marine diatoms. Thus, the database on marine benthos needs to be developed.

Finally, extreme environments could represent a very human-centered expression. For humans, an extreme environment may be the preferred environment for some taxa. Conversely, the “normal” environment for humans could be an extreme environment for other taxa. If the threshold for taxa or key species is clarified, it would be possible to establish the general boundaries of extreme environments for most of benthos. Through this better understanding, we could elucidate the general threshold at which the marine ecosystem suffers through human impact.

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ABSTRACT (IN KOREAN)

지구 표면의 절반 이상은 일부 생물만이 적응하여 살 수 있거나, 생물이 살지 못하는 극한 해양 환경으로 덮여있다. 극한 환경 내 서식 생물은 많은 연구자들의 관심을 받아왔다. 이들을 통해 생명의 기원에서부터 미래 환경 변화에 대한 생물의 반응 또는 적응을 예측할 수 있는 독특한 기회가 제공되기 때문이다. 본 연구에서는 다음 세 가지 질문에 답하기 위해 다양한 극한 환경에서 저서생물의 군집 구조를 조사하였다. 1) 일반적인 해양 환경과 극한 환경에서 생물다양성은 일정할 것인지? 2) 극한 환경에서 견딜 수 있는 종들은 무엇인지? 3) 저서생물은 극한 환경에서 어떠한 적응과정을 거치는지? 해양의 거의 모든 서식지에 존재하는 저서규조류와, 환경 변화의 누적 영향을 잘 반영하는 대형저서동물을 대상생물로 하였다. 해당 분류군들은 해양 생태계에서 주요 먹이원과 소비자, 그리고 탄소 펌프와 탄소 흡수자로서 중요한 기능을 한다. 먼저 고염 환경인 염전 내 저서 규조류 군집을 조사하였다. 염분 ~200 psu에서 살아있는 규조류가 출현하였으나, 300 psu에서는 규조류가 출현하지 않았다. 염분 스트레스가 증가함에 따라 규조류 군집의 종 다양성이 감소하였다. 극한 고염분 환경에서 생존할 가능한 종이 한정적이기에 종 다양성이 줄어든 것으로 보인다. 한편, 양식업은 바다를 직접적으로 이용하고 교란시키는데, 양식업이 야기한 빈산소 현상으로 저서환경이 황폐화되기도 한다. 흥미로운 점은 빈산소 환경이 회복되기 시작할 때 기회종이 폭발적인 밀도 증가를 나타낸다는 것이다. 다음으로, 도시화와 산업화로 인한 육상 기원의 유기물질이 황해 갯벌에 유입되며, 이들의 유입 정도에 따라 규조류 군집의 공간적 분포 패턴이 다르게 나타났다. 또한 과거 환경을 탐색하기 위한 퇴적물 코어 샘플을 분석한 결과, 과거에도 육상 기원의 오염물질이 규조류 군집에 큰 영향을 미치는 것으로 보였다. 마지막으로 빙하후퇴는 지구온난화와 함께 주목받고 있는 문제로, 본 연구에서는 빙하후퇴지역인 마리안 소만의 규조류 군집변화를 조사하였다. 빙하와 가까워 빙하후퇴의 영향을 강력하게 받는 소만 인쪽에서는 구조류의 높은 생물량과 함께 사슬형태의 모양을 형성하는 규조류 군집이 관찰되었다. 과거 문헌 리뷰 결과

규조류를 비롯하여 해조류, 대형저서동물 등 대부분의 남극 저서 군집은 빙하퇴각으로 인한 물리화학적 영향 등 변화하는 환경을 잘 반영하는 것으로 나타났다. 종합하자면, 저서생물은 종 별로 특정 환경 요인에 대한 임계값이나 선호도를 가지고 있음을 알 수 있다. 더불어 극한 환경을 견딜 수 있는 종들은 제한적이므로, 결과적으로 극한 환경에서는 종다양성이 감소하는 경향이 나타난다. 극한 환경이 회복 또는 복원되는 과정에서 기회주의적인 분류군이 해당 생태계에서 극우점하는 천이과정도 관찰되었다. 본 연구는 개발로 인한 환경 파괴와 기후변화 등으로 비롯된 해양 생태계의 급격한 변화를 대비하기 위한 통찰력을 제공한다.

주제어: 저서규조류, 대형저서동물, 극한 환경, 고염 환경, 빈산소 환경, 육상기원 오염물질, 빙하후퇴

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