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

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ABSTRACT

A long-term study on a benthic community was conducted in two different localities, one in semi-enclosed bay of Jinhae (n = 10, south coast) and the other in open sea area of Samcheok (n = 10, east coast), Korea, respectively. 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 the 3 years, encompassing 12 consecutive seasons, in 2013–2016. Among the 22 environmental variables measured, organic matter, dissolved oxygen, mean grain size, and water depth showed clear differences between two study areas. 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 in the 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. Principle component analysis further identified major environmental factors, i.e., sediment properties in Jinhae and water quality parameters in Samcheok community, respectively. 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 nearshore habitats showed distinct community differences, in time and space, that were influenced by site-dependent environmental conditions.

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 (Foshtomi et al., 2015; Iskaros and El-Otify, 2003). Thus, monitoring macrozoobenthos contributes to the understanding of relationships between biotic and abiotic components in the dynamic marine ecosystem (Guest et al., 2016; Hagberg and Tunberg, 2000; Yasuhara et al., 2007).

Many studies have reported a significant association between macrozoobenthic composition and the properties of sediments

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(Gray et al., 2002; Olsgard et al., 2003; Thorson, 1950), water temperature (Rosa and Bemvenuti, 2006), dissolved oxygen (DO) (Middelburg and Levin, 2009), and, in particular, water depth (Kröncke et al., 2003; Paterson and Lambshead, 1995; Rex, 1981). Significant variation in the structure of macrozoobenthos occurs across seasons, and is primarily associated with temperature and other 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 examined the mechanisms that cause an increase or decrease in biological diversity in the dynamic marine ecosystem. The effects of environmental variables on macrozoobenthos would vary depending on habitat conditions, such as geomorphological feature, type and/or degree of anthropogenic pressures etc. Few studies have addressed 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 parameters 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 in 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 seemingly have the most severe effect on shallow, semi-enclosed bays with poor water exchange (Newton et al., 2014; Read and Fernandes, 2003). 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) (Dufrene and Legendre, 1997; 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 changes, and anthropogenic effects (Liu et al., 2017; Valença and Santos, 2012); thus, it represents a powerful tool of site-specific ecosystem responses in dynamic coastal environments.

Here, we conducted a comparative investigation of a semi-enclosed bay and an open coastal area in Korea during the study period of 3 years, encompassing 12 consecutive seasons, where we compared spatiotemporal patterns of macrozoobenthos at both the community and species levels. Specifically, 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.

2. Materials and methods

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. 1A & Table S1). 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. 1B & Table S1), 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 stations (11–24 m, mean = 18 m) (Fig. 1A & Table S1). 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).

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 October 2013 to July 2016 (Table S1). 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 m^2. 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, and 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 seawater on the sea bottom were monitored using a multi-probe (YSI 556 MPS) that measured pH, salinity, DO, and temperature.

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 the CA, DA was performed to extract significant discriminant functions and to identify the major environmental variables

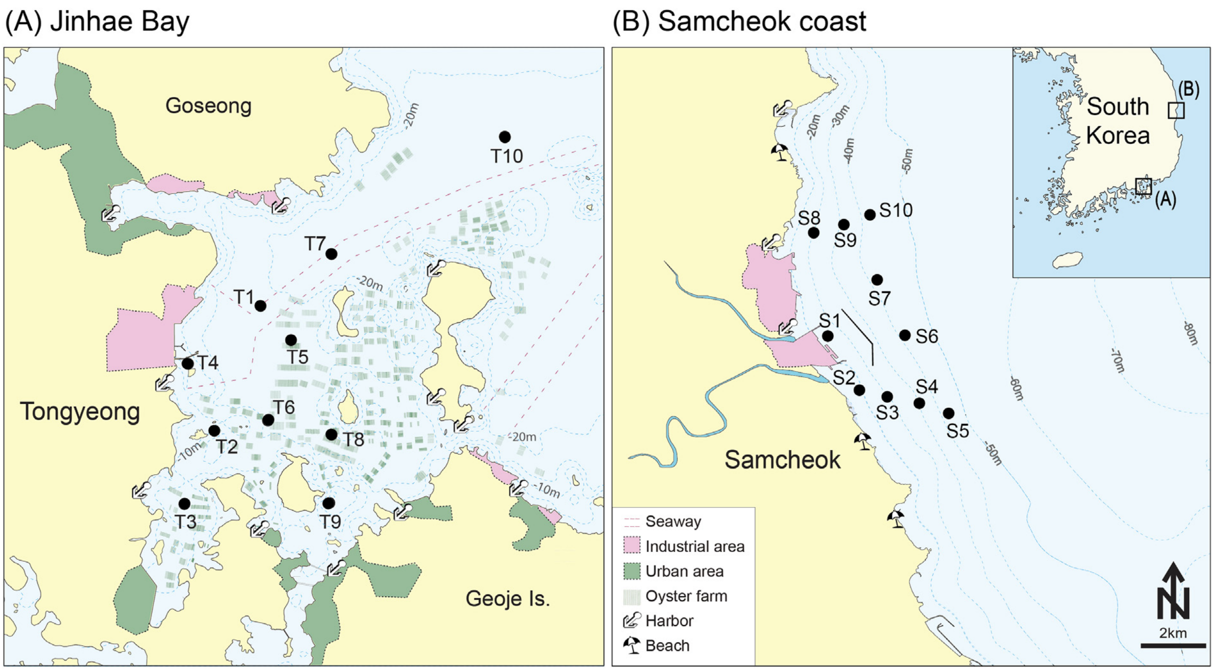

Fig. 1. Maps showing the sampling stations in (A) Jinhae Bay (T1–T10) and (B) Samcheok coastal area (S1–S10), Korea. Major land-use and selected marine activities are given.

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 (Dufrene and Legendre, 1997). The IndVal index was calculated by the Eq (1):

$$\mathrm{IndVal}_{ij} = \mathrm{A}_{ij} \times \mathrm{B}_{ij} \times 100 \quad (1)$$

where, A_{ij} represents specificity (i.e., the proportion of individuals of species *i* that were in group *j*) and B_{ij} represents fidelity (i.e., the proportion of stations in group *j* that contained species *i*). The value of this index was maximum (max = 100%) when all specimens of a species were found in a single group of samples and when the species occurred in all samples of that group. For each species, the largest value was used to express its indicator value. The indicator value was calculated by the Eq (2):

$$\mathrm{IndVal}_{i} = \max[\mathrm{IndVal}_{ij}] \quad (2)$$

The index was maximum (max = 1) when the individuals of species *i* were observed at all sites belonging to a single group. The analysis was performed using the freely downloaded software RStudio version 1.0.153 (www.rstudio.com).

3. Results

3.1. Spatiotemporal variation in environmental conditions

Environmental variables were measured in situ or in the laboratory, depending on the parameters during the 3-year study period. Table 1 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 1). The bottom DOs tended to decrease noticeably during summer to levels even lower than that of hypoxia (<2 mg O_2 L^{-1}) at some northern stations of the study region. Fairly high nutrient concentrations were measured in all seasons. The mean concentration of NO_3-N and SiO_2-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 2).

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 NO_3-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) were considerably different to those in Jinhae Bay (Table 2), 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.

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 study period, especially in Jinhae

Table 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)
Water depth (m)	11.0	24.0	18.0 (±3.9)	18.0 (±3.9)	18.0 (±3.9)	18.0 (±3.9)	18.0 (±3.9)	15.0	52.0	36.7 (±12.6)	36.7 (±12.6)	36.7 (±12.6)	36.7 (±12.6)	36.7 (±12.6)
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})	0.0	2.6	0.8 (±0.5)	0.6 (±0.4)	0.6 (±0.5)	0.8 (±0.4)	1.2 (±0.6)	0.0	2.5	0.6 (±0.7)	0.2 (±0.2)	0.3 (±0.2)	0.7 (±0.6)	1.3 (±0.7)
SPM (mg L^{-1})	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 (μmol L^{-1})	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)

[a] nd: not detected.

Bay (Fig. 2A). The density and species diversity (viz., number of species) of the macrozoobenthic communities in Jinhae Bay varied greatly with time, whereas Samcheok community showed a consistent number of species over seasons and years (Fig. 2B). 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 occurred in Jinhae Bay, which decreased to about one third in number during the summer and fall of 2014. The polychaete *Lumbrineris longifolia* was the only consistent dominant species that was common at both sites over the all seasons and years.

CA was performed to delineate the station groups with similar macrozoobenthos species composition, producing three representative groups (TG1, TG2, and TG3) among 10 stations in Jinhae Bay (ANOSIM: $R = 0.957$, $p < 0.005$, Fig. 3). 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). *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. 2, Table 2). After the defaunation during summer hypoxia, the most dominant species in TG2 assemblage was *P. patiens*, occurring at 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. 2 & Table 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

Table 2
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})			
1st	*L. longifolia* (473)	*P. patiens* (693)	*T. fragilis* (383)
2nd	*Corophium* sp. (174)	*C. capitata* (533)	*P. patiens* (97)
3rd	*N. minor* (47)	*L. longifolia* (484)	*Tharyx* 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
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})			
1st	*S. bombyx* (7446)	*M. johnstoni* (2632)	*E. analis* (240)
2nd	*C. teres* (633)	*L. longifolia* (1135)	*P. kefersteini* (143)
3rd	*E. analis* (501)	*S. bombyx* (933)	Gammaridea 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

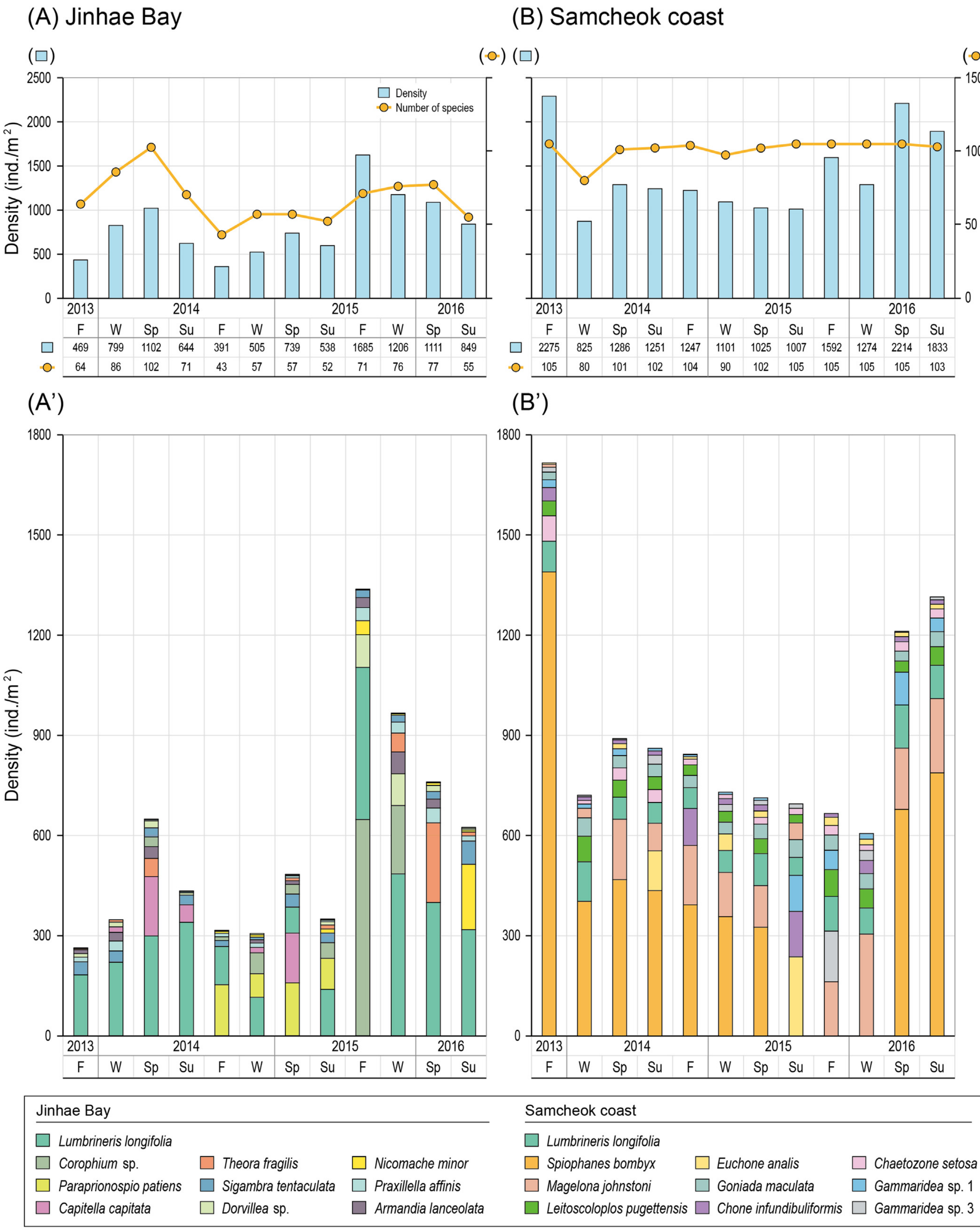

Fig. 2. Total species abundance (given as mean density), total number of species, and density of the top 10 dominant species in (A) Jinhae Bay and (B) Samcheok coastal area, during the 3-year study period (from fall 2013 to summer 2016); 12 consecutive seasons.

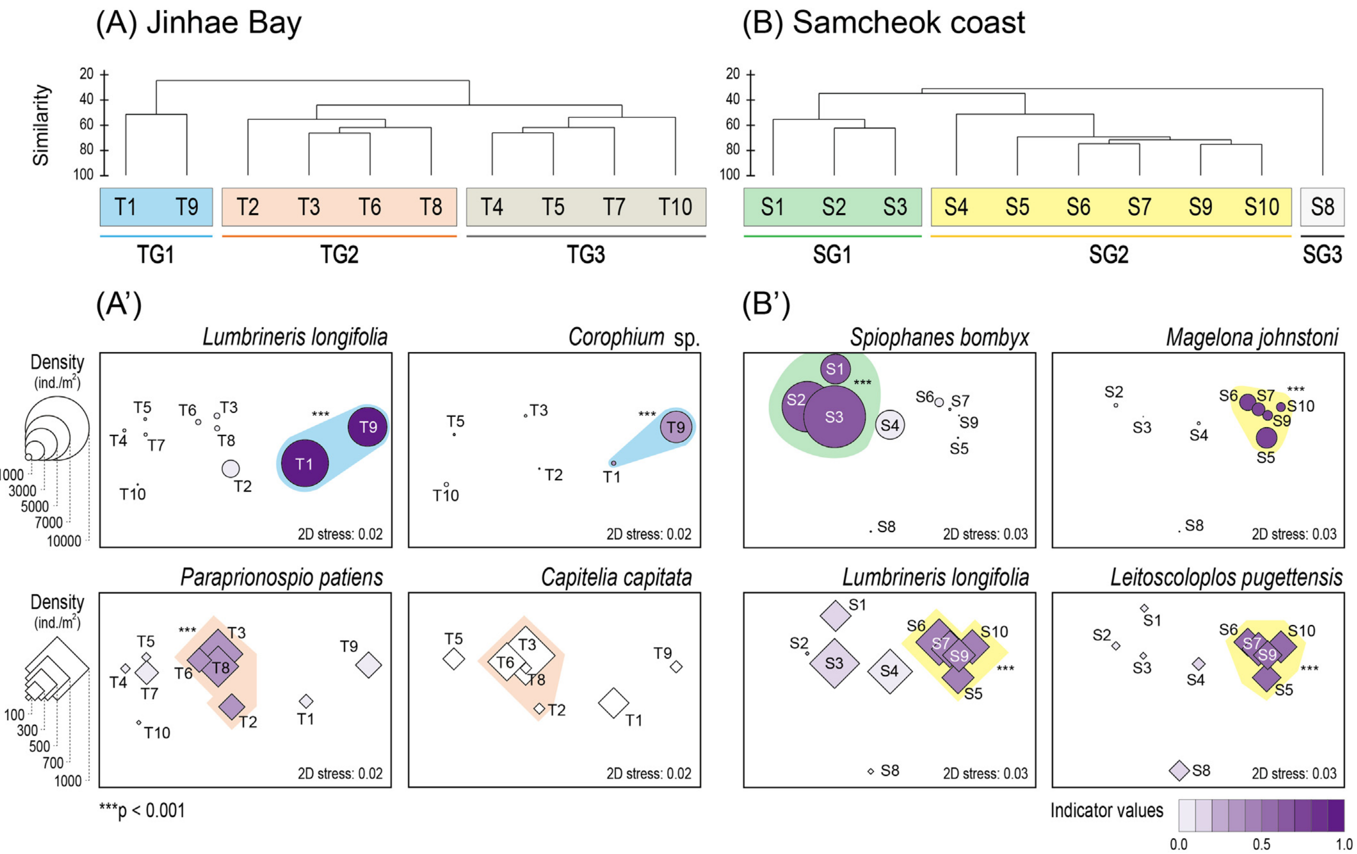

Fig. 3. Illustration of the macrozoobenthic community groups in the two study areas of (A) Jinhae Bay (TG1–TG3) and (B) Samcheok coastal area (SG1–SG3), based on cluster analysis and non-metric multidimensional scaling (NMDS). NMDS provides information on the top four dominant species, including density and indicator values.

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, and SG3) by CA (ANOSIM: $R = 0.971$, $p < 0.005$, Fig. 3). The SG1 assemblage included S1, S2, and S3, which were located relatively close to the land; namely, the shallow subtidal stations (water depth range = 15–20 m). This group was characterized by the greatest abundance of 2470 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 *E. 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 water depth range of 45–52 m. This group was characterized by the highest number of species, with a mean density of 1020 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. 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 water depth) noticeably differed between Jinhae Bay and Samcheok coastal area. Fig. 4 shows the dominant species associated with the four environmental factors. The ranges of all species (blue shaded in Fig. 4) 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 water 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; water depth range, 16–20 m), but over half of the species in Samcheok occurred in coarser sediment and deeper water (Mz, 3.7–6; water 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. S3). 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*, *L. longifolia*, and *Praxillella affinis* occurred in a relatively wide range of organic matter and Mz.

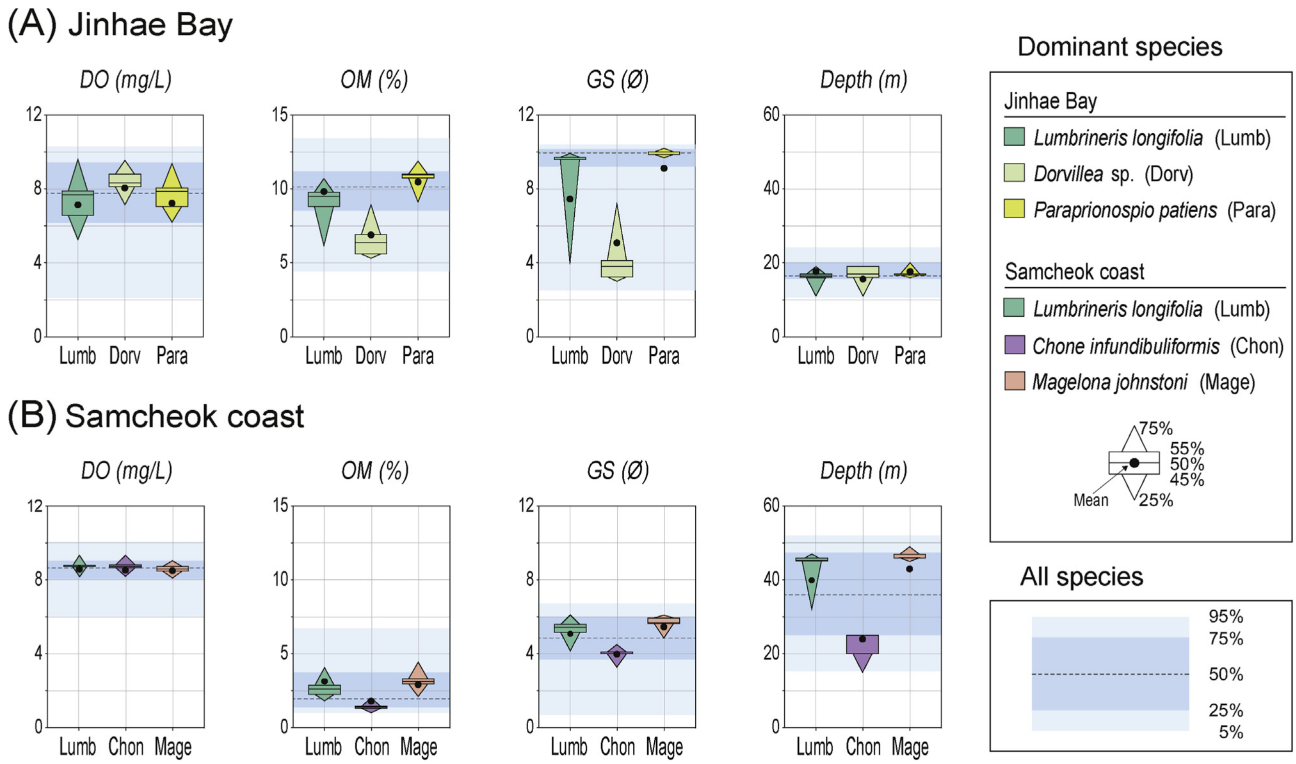

Fig. 4. Box-and-whisker plots (minimum, 25%, median, 75%, and maximum) for the three selected species each in the two study areas of (A) Jinhae Bay (Lumb, *Lumbrineris longifolia*; Dorv, *Dorvillea* sp.; Para, *Paraprionospio patiens*) and (B) Samcheok coastal area (Lumb, *Lumbrineris longifolia*; Chon, *Chone infundibuliformis*; Mage, *Magelona johnstoni*), with respect to parameters of species abundance (density), diversity index (*H′*), dissolved oxygen (DO), organic matter (OM), mean grain size (Mz), and water depth.

4. Discussion

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. 5).

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 the southern parts of Jinhae Bay during the summer. It seemed to be the

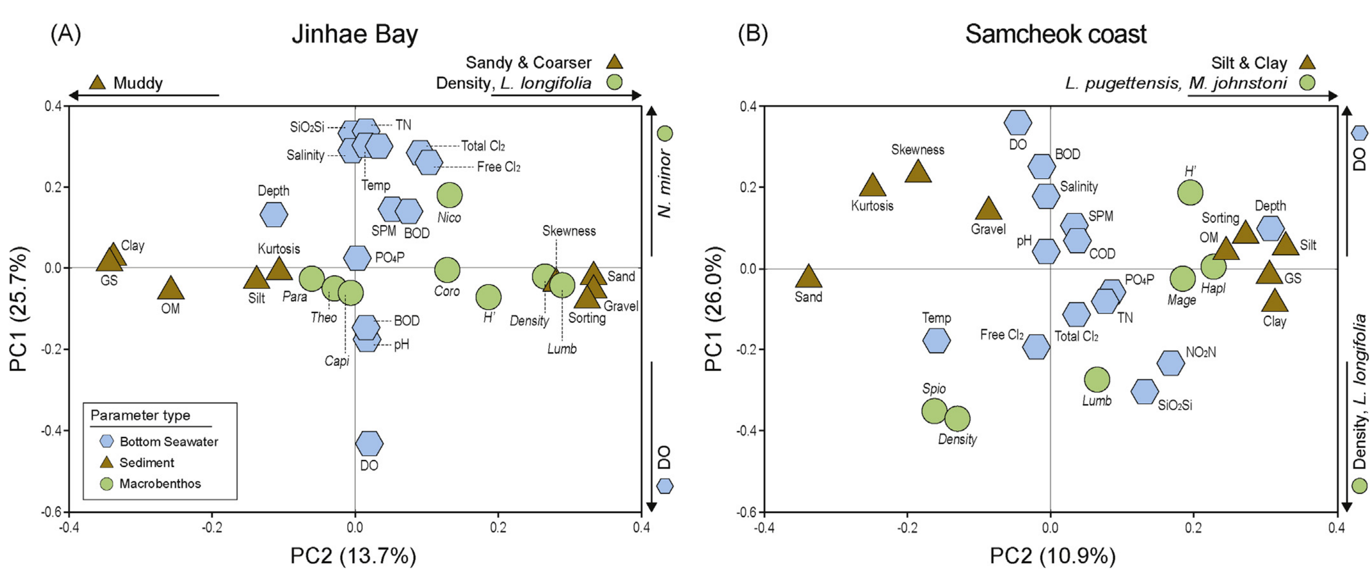

Fig. 5. Principal component analysis of macrobenthos (including total species abundance, *H′* index, and density of dominant species) and 22 environmental variables, including parameters of water quality (refer to all the raw data in App. 1 of the Supplementary Materials) and sediment properties (refer to all the raw data in App. 2 of the Supplementary Materials), for (A) Jinhae Bay and (B) Samcheok coastal area.

result of the combined effects of natural (restricted circulation) and anthropogenic (a large oyster farming area) induced processes (Lim et al., 2006). Meantime, changes to species composition, and even the elimination of macrozoobenthos, are evidenced in the southern parts of Jinhae Bay, namely in the hypoxic stations. Not surprisingly, 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). Also, threshold effects at community level have been well documented with respect to oxygen deficiency (Diaz and Rosenberg, 1995; Levin and Gage, 1998; Nilsson and Rosenberg, 1994). The complete loss of macrozoobenthos in hypoxic or anoxic areas evidenced in the present study was consistent with the previous studies, elsewhere (Middelburg and Levin, 2009). 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 seemed to be assocaited with total density, *H'*, and the density of the dominant species (*L. longifolia*) in Jinhae Bay.

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 (Tables S2 and S3, Fig. S4). The DAs formulated the discriminant functions (DFs) for Jinhae and Samcheok, respectively, using Eq (3) and Eq (4).

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

$$\text{DF-Samcheok} = a \cdot \text{Free } Cl_2 + b \cdot \text{Gravel} + c \cdot \text{Water depth} \quad (4)$$

where, a–e should be replaced by the standardized canonical discriminant coefficients presented in Tables S2 and S3. 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).

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 S2). Fig. S4 (A) 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 water 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 (Tables S2 and S3).

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 levels (Fig. 2 & Fig. S1). 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.

Capitella 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 (Fig. 4) 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. S2). In any case, the less contaminated Samcheok environment showed a relatively stable community structure in time and space, in which assemblage groups were primarily discriminated by geophysical factors, such as %-gravel and water 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).

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). 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 & Table S4). 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 would have information on the species composition in the given area, and vice versa. 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 *L. longifolia* and *C. infundibuliformis* 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 the future biomonitoring in the two contrasting marine environments.

5. Conclusions

The present study provided a comprehensive understanding of the spatio-seasonal variations of macrozoobenthos associated with the key environmental factors in the two different marine localities (viz., semi-enclosed bay versus open sea coastal area). The degree of association between the spatio-seasonal distributions of macrozoobenthos and environmental parameters varied greatly at both the species and community levels. The abundance of the dominant species peaked in certain season(s), and then suddenly decreased or, even, disappeared entirely for long periods of time. The macrofaunal assemblages were clustered into three groups in both study areas, with the traits of the groups varying with a wide range of environmental and macrozoobenthic characteristics. Such variations to the benthic community structure were explained by a few selected environmental factors that were identified from the PCA and DA. Furthermore, a wide range of environmental gradients could be predicted by the presence of certain indicator species having different habitat preferences and/or tolerances for specific environmental conditions. In conclusion, the two contrasting nearshore habitats were fairly well explained by the long-term changes (seasonal to annual) in macrozoobenthos at both the species and community levels in response to varying and dynamic environmental conditions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.envpol.2018.05.098.

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