Marine Pollution Bulletin 194 (2023) 115377

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Baseline

# Spatial distribution of meiofaunal and macrofaunal assemblages in the tidal flats of the southern Korean coast in relation to natural and anthropogenic impacts

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ARTICLE INFO

*Keywords:*
South Sea
Meiofauna
Macrofauna
Spatial variation
Benthic ecology

ABSTRACT

We investigated the spatial variability of macrofaunal and meiofaunal assemblages in intertidal flats on the southern coast of Korea. Abiotic and biotic samples were collected at five stations. The species richness, density, and composition of the assemblages differed significantly among stations. Nematoda and Annelida were the most dominant meiofaunal and macrofaunal taxa, respectively, although taxon dominance differed among stations. Distance-based linear models showed that sediment-related variables and heavy metals were the main environmental factors determining the spatial variability of the assemblages. Macrofauna had only sediment-related variables and heavy metals as major environmental factors, but meiofauna were also influenced by other environmental factors such as sea surface temperature, dissolved oxygen-related variables, and salinity. This study can provide basic ecological data for understanding the spatial distribution of macro-meiofaunal assemblages and aid in the development of marine environmental management strategies on the western south coast of Korea.

Benthic organisms play important roles in marine ecosystem functioning, participating in processes such as mineralization, nutrient cycling, and decomposition (Wi et al., 2014; Schratzberger and Ingels, 2018). For example, the burrows created by various benthic organisms increase nutrient and oxygen supply in sediment, while increased oxygen availability stimulates aerobic microbial communities to promote the decomposition of organic matter (Middelburg and Meysman, 2007). Thus, an understanding of the distribution and variation of benthic organisms across habitats is needed to evaluate marine ecosystem structure and functioning.

Meiofaunal and macrofaunal assemblages, two major groups in the marine benthic ecosystem, have been examined in numerous environmental assessments (Magni et al., 2022). Macrofauna are widely considered to be useful indicators of biological responses to environmental disturbances (Whomersley et al., 2008; Valença and Santos, 2012). Characteristics of benthic macrofauna, such as their life cycles, feeding patterns, and life strategies (e.g., burrowing, predation, and commensalism) allow them to respond to a wide range of environmental changes (Simboura et al., 1995; Teixeira et al., 2009; Patrício et al., 2012). Moreover, macrofauna are relatively easy to taxonomically identify and have been considerably well-studied scientifically, compared to smaller benthic organisms (Patrício et al., 2012). Meiofauna have received less attention, although they are useful indicators of environmental change due to their ubiquitous variability, small sizes, high abundance, sedentary habits, and rapid generation times and metabolic rates (Kennedy and Jacoby, 1999; Patrício et al., 2012).

Meiofauna and macrofauna respond differently to physical and chemical environmental changes; macrofauna are more influenced by

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https://doi.org/10.1016/j.marpolbul.2023.115377
Received 13 June 2023; Received in revised form 1 August 2023; Accepted 2 August 2023
Available online 12 August 2023
0025-326X/

physical disturbances (i.e. storm, hypoxia) (Norkko et al., 2006; Machado et al., 2016), whereas meiofauna are more sensitive to chemical pollution such as heavy metals and persistent toxic substances (Somerfield et al., 1994; Moreno et al., 2008). Thus, integrated studies of meiofauna and macrofauna could provide data contributing to the efficient management and conservation of benthic ecosystems. Moreover, both communities should be examined in evaluations of the effects of disturbance in marine environments (Whomersley et al., 2009; Patrício et al., 2012). However, integrated investigations of meiofauna and macrofauna are relatively rare, due to methodological differences in the collection, counting, and taxonomic classification of these communities, particularly those containing small organisms (Whomersley et al., 2009; Frontalini et al., 2011).

Our aim was to investigate the spatial distribution of macrofaunal and meiofaunal assemblages to provide a more comprehensive tool for the quality assessment of intertidal mudflat environments on the southern coast of Korea. We hypothesized that the meiofauna and macrofauna taxonomic diversity, density, and assemblage composition would 1) reflect different variability patterns depending on natural environmental factors and their interaction with anthropogenic disturbance and 2) such patterns were consistent along hydrological and sedimentary gradients in the study area. Furthermore, we sought to identify major environmental factors that determine the variability of both size-class assemblages.

In June and July 2021, we examined the transformations occurring in natural and altered assemblages, focusing on intertidal meiofaunal and macrofaunal assemblages, along the southern coast of Korea. The indented, ria-type western south coast of Korea has 281 $km^2$ of wide intertidal flats and numerous semi-enclosed embayments, rocky shores, and offshore islands (Koh and Khim, 2014; Kwon et al., 2022). In order to reflect the characteristics of the intertidal flat on the southern coast of Korea, five stations were selected along the study region by referring to the Korea Marine Environment Management Corporation (KOEM, 2021; Fig. 1). All five stations (S1: Jindo, S2: Haenam, S3: Wando, S4: Boseong, S5: Suncheon), where abiotic and biotic samples collected, were intertidal mudflats with similar environmental characteristics being sheltered depositing shores (Fig. 1, Table S1). All stations had agricultural land nearby, and there were sources of freshwater inflow of various sizes. Especially, S4 and S5 are the stations designated as wetland protected area (Ministry of Oceans and Fisheries, 2003a; Ministry of Oceans and Fisheries, 2003b). In addition, Yeoja Bay, where S4 and S5 are located, is a semi-closed inner bay that accumulates organic matter and terrestrial organic pollutants through the inflow of fresh water as well as domestic sewage, factory wastewater, livestock wastewater, and agricultural water (Park and Kweon, 2001; Wollheim et al., 2008; Park and Cheong, 2013; Lee et al., 2019; Lim, 2015; Kwon et al., 2022).

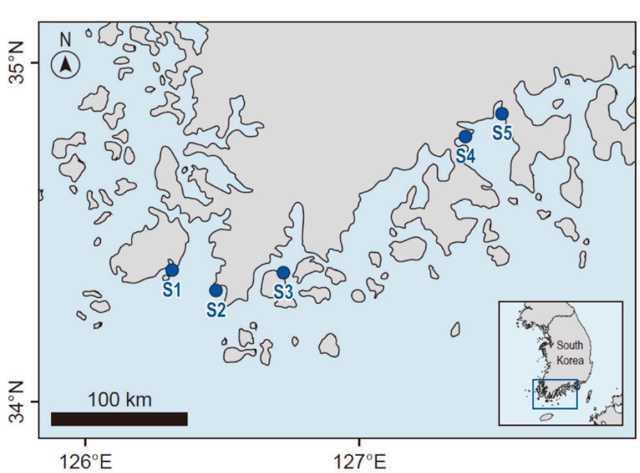


**Fig. 1.** Map of the study area and sampling station (S1–S5) locations.

Macrofaunal and abiotic data (e.g., species abundance and sediment properties) were obtained from the national marine ecosystem monitoring program (KOEM, 2021). To ensure that samples represent the entire population and are not biased, all abiotic and biotic samples were surveyed by random collection at each station. We randomly collected abiotic-biotic samples at least 1 m apart per replicates at each station. The collection and analyses of abiotic-biotic samples were conducted in accordance with the program's protocol (Ministry of Oceans and Fisheries, 2013).

At least nine macro-meiofauna replicates were collected and analyzed at each station. Macrofaunal samples were collected using a can core (10 depth × 25 width × 30 height cm). Sediment from the can core were filtered on the ground using a standard 1-mm-mesh sieve. The residue was fixed in a plastic sample bottle with 10 % neutral formalin solution diluted with seawater and transported to the laboratory. The samples were refiltered at the laboratory using a standard 0.5-mm-mesh sieve. The macrofauna were separated from the residue and identified to species level.

Three sediment replicates were collected at each station using a plastic core to the top 2 cm of the sediment and transferred to the laboratory. All sediment samples were analyzed according to the standard protocols of the Ministry of Oceans and Fisheries (2018a). These determined proportions of sediment types (gravel, sand, silt, and clay), mean grain size (MG), sorting, water content (WC), loss on ignition to measure organic content (LOI), and concentrations of acid volatile sulfides (AVS), total organic carbon (TOC), and heavy metals [arsenic (As), cadmium (Cd), chromium (Cr), copper (Cu), mercury (Hg), nickel (Ni), lead (Pb), iron (Fe), zinc (Zn), lithium (Li), cobalt (Co), and aluminum (Al)]. According to the marine environmental standard (Ministry of Oceans and Fisheries, 2018b), the Li correction formula was applied to the Cu and Zn values before analysis. Furthermore, an assessment was made to ascertain whether the concentration of heavy metals surpassed the threshold effect limit (a precautionary criterion; Ministry of Oceans and Fisheries, 2018b).

Meiofaunal samples were collected and analyzed directly at each sampling station. Meiofaunal samples were collected using a plastic syringe corer in 10-$cm^2$ surface areas at 0–3 cm depth. All meiofaunal samples were transferred to the laboratory on ice. Each meiofaunal sample was fixed with 99.9 % ethyl alcohol and separated by centrifugation (Burgess, 2001). The extraction procedure was performed at least three times to ensure that all organisms had been removed from the sediments. The meiofauna were counted and identified to the highest taxonomic level following Schmidt-Rhaesa (2020) under a stereomicroscope (M165C; Leica).

Seawater variables including salinity, sea surface temperature (SST), pH, dissolved oxygen concentration (DO) were collected and measured at low tide level using a YSI probe (ProQuatro Multiparameter Meter; Xylem, USA).

Univariate and multivariate statistical analyses were performed using a permutational multivariate analysis of variance (PERMANOVA) package (PRIMER-E, UK) with the PRIMER software (v. 7.0.21; Clarke and Gorley, 2015). The relative abundances of meiofauna and macrofauna were standardized according to the total number of taxa in each sample and square-root transformed to obtain homoscedasticity (Anderson et al., 2008). The converted meiofaunal and macrofaunal data were averaged by sampling station and used for the production of respective Bray–Curtis similarity matrices (Anderson et al., 2008). Benthos spatial variability was explored using PERMANOVA and the Monte Carlo method (Anderson, 2001a). Permutational analysis of multivariate dispersion (PERMDISP) was performed to examine the PERMANOVA assumption of homogeneity multivariate dispersion (Anderson et al., 2008).

Bray–Curtis similarity matrices were also used to construct nonmetric multidimensional scaling ordination (nMDS) and cluster plots, to which the similarity percentages test was applied. The matrices, made with converted unaveraged meiofaunal and macrofaunal data, were used to construct distance-based linear models (DistLMs; Anderson, 2001b; McArdle and Anderson, 2001; Anderson et al., 2008). Correlations between abiotic variables were examined using Draftsman plots, and only variables with correlation coefficients <0.7 were included in the DistLMs to avoid collinearity. The DistLMs were used to determine the extent to which differences in meiofaunal and macrofaunal assemblage variability patterns could be explained by habitat-related factors. Significant explanatory variables were selected for inclusion in a multivariate regression model using a forward stepwise procedure, and the best models for the meiofaunal and macrofaunal assemblages were selected using the Akaike information criterion (AIC) and the AIC with second-order correction, respectively (Schwarz, 1978; Chambers and Hastie, 2017). Distance-based redundancy analysis (dbRDA) plots were used to visualize the DistLM results.

Community analyses were performed to identify assemblage structure using the following ecological indices: the Shannon–Wiener diversity index (Pielou, 1969), Pielou's (1975) evenness index, the Margalef (1958) richness index, and McNaughton's (1967) dominance index. These indices were calculated by DIVERSE routine in the PRIMER software.

Twenty-five environmental variables showed significant spatial variations among stations (PERMANOVA: df = 4, pseudo-$F$ = 10.06, $p$ = 0.001; Table 1). The heterogeneity of variance of the environmental data was confirmed (PERMDISP: Pseudo-$F$ = 7.85, $p$ = 0.003). Summary statistics for the major environmental variables are provided in Table 2.

The salinity was highest at S2 (33.53 psu), followed by S3 (33.14 psu), S1 (31.42 psu), S4 (29.54 psu), and S5 (14.44 psu). The SST was highest at S1 (29.6 °C), followed by S5 (28.3 °C), S4 (27.0 °C), S2 (24.9 °C), and S3 (23.0 °C). The seawater pH was consistent among stations (mean, 7.92 ± 0.29; range, 7.47–8.22). The seawater DO concentration was lowest at S2 (1.79 mg/L), indicating hypoxia, and highest at S5 (5.57 mg/L). The DO concentration showed strong positive and negative correlations with the pH ($r$ = 0.76, $p$ < 0.001) and salinity ($r$ = −0.73, $p$ > 0.05), respectively (Table S2).

Sediment sorting indicated that various particle sizes of sediment are mixed (2–4 Ø) at all stations, with the highest mean value calculated for S3 (3.24 ± 0.43 Ø). The MG exceeded 4 Ø at all stations. The sediment at S1, S2, and S3 was sandy mud (50–75 % mud). S3 had the least mud content, followed by S1. The sediment at S4 and S5 had a mud-dominated bottom fraction (> 98 % mud), with a higher mud content at the former. Mean AVS concentrations were below the threshold value at all stations (Table S3).

Variables related to the sediment organic matter content (LOI and TOC) correlated positively with the silt and clay contents, MG, WC, and most heavy metal concentrations ($r$ > 0.7, $p$ < 0.001; Table S2) and negatively with the gravel ($r$ = −0.47 and −0.46, respectively; both $p$ > 0.05) and sand (both $r$ = −0.89, $p$ > 0.05) contents (Table S2). The sediment WC, LOI, and TOC content were higher at S4 and S5, which had higher mud contents than at S1–S3 (Fig. 2). The LOI exceeded the threshold of United States at S4, S5, and parts of S1 and S2 (Tables S3 and S4). The TOC content exceeded the threshold of Canada, in some parts of S5 (Canadian Council of Ministers of the Environment, 1995).

Heavy metal concentrations in the sediments varied among stations. All except that of Al were highest at S5. With the exception of the Cu and Al concentrations, the heavy metal concentrations showed strong positive correlations with each other and with sediment variables such as the TOC content and MG ($r$ > 0.7; Table S2). The concentrations were within the threshold effect limit at all stations, with the exception of the As and Ni in some parts of S5 (Tables S3 and S4).

In total, 13 meiofaunal taxa were identified (Table S5). Nematoda was the most dominant taxon (80.46 %), followed by copepods (13.30 %) and copepod nauplii (3.45 %). The meiofaunal density was greatest at S4 (859 ± 338 individuals/10 $cm^{-2}$) and least at S2 (237 ± 112 individuals/10 $cm^{-2}$; Fig. 3). PERMANOVA indicated that the meiofaunal density and assemblage composition, but not the taxonomic diversity, differed significantly among stations; PERMDISP did not confirm heterogeneity of variance for any of these variables (Table 1). The taxonomic diversity and evenness were greatest at S4 (0.82 ± 0.20 and 0.74 ± 0.19, respectively) and the least at S2 (0.20 ± 0.22 and 0.19 ± 0.10, respectively; Table S6). In the taxa richness, S1 was the highest (0.48 ± 0.20) and S2 was the lowest (0.36 ± 0.31). The dominance index was highest for S5 (0.98 ± 0.03) and lowest for S4 (0.92 ± 0.09), but did not differ significantly among stations. The nMDS and cluster analyses revealed differences in meiofaunal assemblages among stations, with the clustering of S1, S3, and S5 and no clustering of S2 or S4 (Fig. 4a).

In total, eight macrofaunal taxa (mean, 15 species/station) were identified (Table S5). The top three phyla were Annelida (79.52 %), Mollusca (10.57 %), and Arthropoda (7.65 %). All three of the most dominant species were Annelida. *Polydora* sp. was the most dominant species (21.25 %), followed by *Aphelochaeta monilaris* (12.35 %) and *Scoletoma longifolia* (6.20 %). PERMANOVA indicated that the taxonomic composition, diversity, and density differed significantly among stations, although PERMDISP suggested that the effect of station was due to the heterogeneity of variance (Table 1). Taxonomic diversity and richness were greatest at S3 (2.07 ± 0.44 and 3.21 ± 1.29, respectively).

**Table 1**
Summary of environmental and macrofaunal and meiofaunal assemblage characteristics.

| | PERMANOVA | | | | | | PERMDISP | |
|---|---|---|---|---|---|---|---|---|
| Target | Term | df | P-F | ECV | Sqrt | *P* | P-F | *P* |
| **Environment** | St | 4 | 10.06 | 14.38 | 3.79 | **0.001** | 7.85 | **0.003** |
| | Res | 37 | | 13.27 | 3.64 | | | |
| **Meiofauna** | | | | | | | | |
| Taxon composition | St | 4 | 10.69 | 151.87 | 12.32 | **0.001** | 1.76 | 0.27 |
| | Res | 37 | | 131.02 | 11.45 | | | |
| Taxon diversity | St | 4 | 1.20 | 2.51 | 1.59 | 0.337 | 2.92 | 0.051 |
| | Res | 37 | | 105.57 | 10.28 | | | |
| Density | St | 4 | 8.98 | 114.3 | 10.69 | **0.001** | 0.13 | 0.984 |
| | Res | 37 | | 119.73 | 10.94 | | | |
| **Macrofauna** | | | | | | | | |
| Taxon composition | St | 4 | 3.28 | 874.37 | 29.57 | **0.001** | 1.64 | 0.324 |
| | Res | 37 | | 3211.3 | 56.67 | | | |
| Taxon diversity | St | 4 | 7.38 | 119.63 | 10.94 | **0.001** | 1.07 | 0.676 |
| | Res | 37 | | 156.68 | 12.52 | | | |
| Density | St | 4 | 2.90 | 139.33 | 11.80 | **0.01** | 2.56 | 0.187 |
| | Res | 37 | | 613.17 | 24.76 | | | |

PERMANOVA, permutational multivariate analysis of variance; PERMDISP, permutational analysis of multivariate dispersion; df, degrees of freedom; P-F, pseudo-*F*; ECV, estimated components of variation; Sqrt, square root of the ECV; St, station; Res, Residual; Bold values, $p$ < 0.05.

**Table 2**
Summary of the selected environmental variables in the intertidal mudflat on the southern coast of Korea.

| | All | | | Station (Mean (± SD)) | | | | |
|---|---|---|---|---|---|---|---|---|
| | Min | Max | Mean (± SD) | S1 | S2 | S3 | S4 | S5 |
| Surface of seawater | | | | | | | | |
| Salinity (psu) | 14.4 | 33.5 | 28.1 (± 7.3) | 31.4 | 33.5 | 33.1 | 29.5 | 14.4 |
| pH | 7.5 | 8.2 | 7.9 (± 0.3) | 8.2 | 7.7 | 8.0 | 7.5 | 8.1 |
| SST (°C) | 23.0 | 29.6 | 26.9 (± 2.5) | 29.6 | 24.9 | 23 | 27.9 | 28.3 |
| DO (mg/L) | 1.8 | 5.6 | 3.6 (± 1.3) | 3.7 | 1.8 | 4.0 | 2.5 | 5.6 |
| Sediment | | | | | | | | |
| MG (Ø) | 0.1 | 8.8 | 6.7 (± 2.4)4 | 5.9 (± 2.7) | 6.9 (± 2.4) | 4.1 (± 2.3) | 8.0 (± 0.3) | 8.4 (± 0.3) |
| Sorting (Ø) | 0.4 | 3.8 | 2.7 (± 0.6) | 2.1 (± 0.9) | 2.9 (± 0.3) | 3.2 (± 0.4) | 2.7 (± 0.1) | 2.5 (± 0.1) |
| Gravel (%) | 0.0 | 37.4 | 2.1 (± 7.2) | 1.3 (± 4.0) | 0.2 (± 0.4) | 8.2 (± 14.0) | 0.0 (± 0.0) | 0.0 (± 0.0) |
| Sand (%) | 0.0 | 97.7 | 19.2 (± 29.9) | 31.9 (± 46.1) | 23.2 (± 34.8) | 40.0 (± 16.4) | 1.7 (± 3.0) | 0.3 (± 0.2) |
| Silt (%) | 0.0 | 69.3 | 46.2 (± 20.1) | 42.2 (± 31.3) | 40.3 (± 19.3) | 35.6 (± 21.3) | 57.7 (± 2.5) | 53.2 (± 4.9) |
| Clay (%) | 0.0. | 52.1 | 32.6 (± 15.5) | 24.6 (± 17.5) | 36.3 (± 16.7) | 16.2 (± 6.7) | 40.6 (± 3.6) | 46.4 (± 5.0) |
| WC (%) | 25.0 | 66.4 | 46.8 (± 13.8) | 39.4 (± 13.9) | 49.9 (± 15.6) | 35.0 (± 5.8) | 57.9 (± 7.8) | 52.6 (± 11.4) |
| LOI (%) | 0.9 | 8.8 | 5.3 (± 2.4) | 3.3 (± 1.9) | 4.3 (± 1.7) | 3.2 (± 0.6) | 7.0 (± 0.6) | 8.1 (± 0.4) |
| AVS (mg/g) | 0.0 | 0.3 | 0.0 (± 0.1) | 0.0 (± 0.0) | 0.0 (± 0.0) | 0.1 (± 0.1) | 0.0 (± 0.0) | 0.0 (± 0.1) |
| TOC (%) | 0.2 | 1.1 | 0.7 (± 0.3) | 0.5 (± 0.3) | 0.7 (± 0.3) | 0.5 (± 0.1) | 0.8 (± 0.1) | 1.0 (± 0.1) |
| Heavy Metal | | | | | | | | |
| Li (mg/kg DW) | 26.8 | 79.3 | 62.0 (± 14.7) | 54.1 (± 20.0) | 63.5 (± 20.2) | 53.6 (± 11.8) | 67.7 (± 2.5) | 71.9 (± 3.0) |
| Cr (mg/kg DW) | 8.4 | 102.9 | 69.2 (± 25.6) | 52.8 (± 32.5) | 71.2 (± 18.9) | 44.3 (± 9.8) | 85.2 (± 5.9) | 93.1 (± 4.3) |
| Ni (mg/kg DW) | 3.5 | 50.5 | 28.7 (± 10.5) | 21.0 (± 12.8) | 27.7 (± 9.5) | 21.3 (± 4.7) | 35.0 (±5.0) | 38.3 (± 4.9) |
| Li-Cu (mg/kg DW) | 5.2 | 9.1 | 7.1 (± 0.9) | 6.7 (± 1.0) | 7.2 (± 0.3) | 6.4 (± 1.1) | 7.2 (± 0.8) | 7.8 (± 0.5) |
| Li-Zn (mg/kg DW) | 14.1 | 49.7 | 43.6 (± 6.1) | 37.3 (± 9.7) | 41.6 (± 5.0) | 45.0 (± 2.3) | 45.7 (± 1.0) | 47.5 (± 1.7) |
| As (mg/kg DW) | 2.9 | 15.0 | 9.1 (± 3.6) | 6.9 (± 3.0) | 8.0 (± 3.0) | 6.4 (± 1.0) | 11.1 (± 2.7) | 12.7 (± 3.3) |
| Cd (mg/kg DW) | 0.0 | 0.1 | 0.1 (± 0.0) | 0.1 (± 0.0) | 0.0 (± 0.0) | 0.1 (± 0.0) | 0.1 (± 0.0) | 0.1 (± 0.0) |
| Pb (mg/kg DW) | 10.5 | 32.4 | 21.5 (± 4.5) | 17.4 (± 5.2) | 20.3 (± 4.6) | 20.9 (± 3.1) | 23.0 (± 1.3) | 25.5 (± 3.1) |
| Al (%) | 2.6 | 7.9 | 5.3 (± 1.4) | 4.6 (± 1.5) | 5.2 (± 1.5) | 4.9 (± 0.7) | 6.7 (± 1.0) | 5.0 (± 1.1) |
| Fe (%) | 1.1 | 4.3 | 3.0 (± 0.9) | 2.4 (± 1.0) | 2.8 (± 1.1) | 2.3 (± 0.4) | 3.5 (± 0.2) | 3.9 (± 0.3) |
| Hg (mg/kg DW) | 0.0 | 0.1 | 0.0 (± 0.0) | 0.0 (± 0.0) | 0.0 (± 0.0) | 0.0 (± 0.0) | 0.0 (± 0.0) | 0.1 (± 0.0) |

SD, standard deviation; S, station; SST, sea surface temperature; DO, dissolved oxygen; MG, mean grain size; WC, water content; LOI, loss on ignition; AVS, acid volatile sulfide; TOC, total organic carbon; DW: dry weight. S1: Jindo, S2: Haenam, S3: Wando, S4: Boseong, S5: Suncheon.

Evenness was greatest at S1 (0.78 ± 0.08) and least at S5 (0.58 ± 0.25; Table S6). The nMDS and cluster analyses showed clear differences between two groups of stations (Fig. 4b).

The dbRDA plots showed that differences in abiotic variables affected the spatial patterns of the meiofaunal and macrofaunal assemblages (Fig. 5). The DistLM showed that sediment-related variables (the MG, the percentage of silt and clay, WC, LOI, and TOC), the SST, DO concentration, pH, salinity, and concentrations of heavy metals (Li, Cr, Ni, Zn, As, Cd, Pb, Fe, and Hg) at all stations affected the spatial variation in the meiofauna assemblage composition (Fig. 5a, Table 3). Sediment-related variables and heavy metal concentrations significantly affected macrofaunal assemblage composition at all stations (Fig. 5b, Table 3). The group of sediment-related variables contributed to the best model solution for the composition of both assemblages (Table 3).

In this study, a group of sediment-related variables (the MG, the percentage of silt and clay, WC, LOI, and TOC) correlated with each other and was the major factor influencing the spatial variability of meiofaunal and macrofaunal assemblages off the southern coast of Korea. Many previous studies have also revealed correlations among environmental variables (Swan and Palmer, 2000; Danovaro et al., 2002; Martins et al., 2013; Schückel et al., 2013; Semprucci et al., 2019). For example, fine-grained sediments have been shown to have higher organic matter content and heavy metal concentrations than coarser-grained sediments (Cho et al., 1999; Martinez-Garcia et al., 2015), as the increasing grain surface area and ion exchange capacity with decreasing MG facilitates the adsorption of these materials (Kim et al., 2005). Thus, the silt and clay contents are regarded as related to the distribution and accumulation of contaminants such as organic matter and heavy metals, and WC is affected by the mud content and is closely related to the organic matter and heavy metal contents (Cho et al., 1999; Li et al., 2000; Lee et al., 2019).

Moreover, the density of macrofauna was similar at S4 and S5, but different meiofaunal densities (half that of S4 at S5) (Fig. 3a and 3b), possibly due to the presence of more pollution that adversely affected benthic organisms at S5 (Josefson et al., 2009); the AVS, TOC, Ni, and As concentrations exceeded thresholds in some parts of this station. In addition, mean LOI values reflected severe pollution at S5 and moderate pollution at S4. Physically disturbed seashore environments were marked by high meiofaunal abundance and low DO (Sun et al., 2014). S4 showed results consistent with this previous study. S4 had the highest meiofauna abundance among all study stations and showed the second lowest DO (Fig. 2 and 3a).

S5 had the highest DO and lowest salinity concentration among our stations due to freshwater inflow from several tributaries and a large lake; the other stations were not located near an estuary or had inflow from single streams. Moreover, the polychaeta *Hediste japonica*, common in brackish water (Kim et al., 2016), was the most dominant species at S5, with the highest dominance index and lowest diversity index. The bivalve *Potamocorbula laevis* and the 260 polychaete *Nephtys chemulpoensis*, the species with the greatest density in sediments with high mud contents (Seo and Hong, 2004), were also dominant in S5. *N. chemulpoensis* was also dominant at S4, as were the polychaetes *Prionospio japonica* and *Heteromastus filiformis*, which are highly tolerant of organic pollution (Word, 1978; Borja et al., 2000; Wi et al., 2014).

The sediments at S1–S3 were sandy and muddy, with poor sorting that seemed to affect the benthic assemblages, in line with previous findings (Parr et al., 2007). Sediment sorting was worst and macrofaunal density was greatest at S3, followed by S2 and S1. The effect of poor sorting on the meiofaunal density is also consistent with previous findings (Urban-Malinga et al., 2004). The SST was lowest at S3 which likely contributed to the high macrofaunal and meiofaunal densities, as low SST cause less environmental stress (McLachlan and Defeo, 2017; Celentano et al., 2019).

The polychaetes *Polydora* sp., *Aphelochaeta monilaris*, and *Scoletoma* (*Lumbrineris*) *longifolia* were the dominant macrofaunal species at S3; these opportunistic species are known to adapt to various organic rich environments (Pearson, 1978; Wu, 1982; Jung et al., 2007; Yoon et al., 2009; Johansen et al., 2018). However, the organic matter and heavy

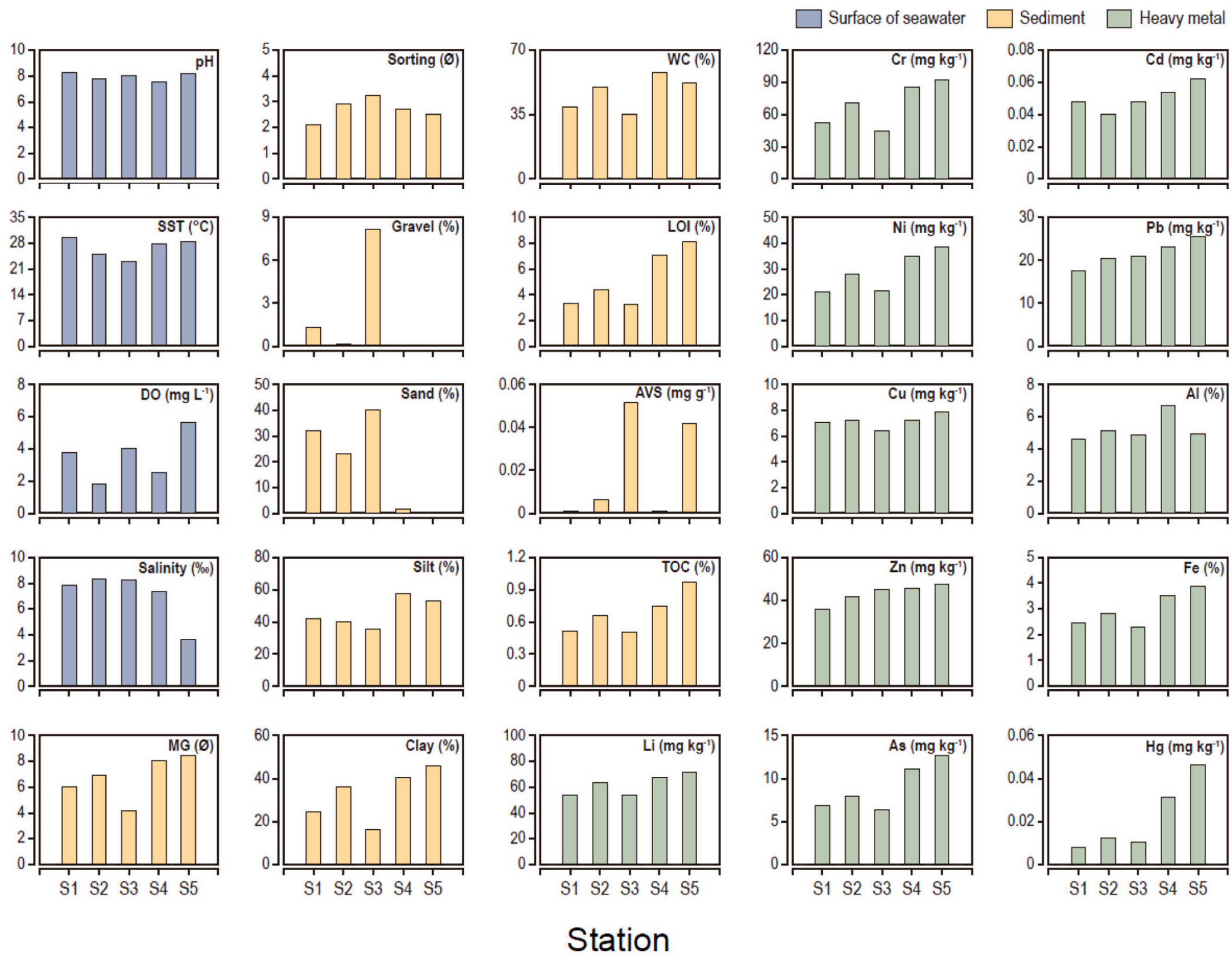


**Fig. 2.** Spatial variation in environmental variables among stations. Cu and Zn values are Li corrected. Surface of seawater (pH, SST, DO, Salinity); Sediment (MG, Sorting, Gravel, Sand, Silt, Clay, WC, LOI, AVS, TOC); Heavy metal (Li, Cr, Ni, Cu, Zn, As, Cd, Pb, Al, Fe, Hg).

metal concentrations were lowest at S3 among all stations; thus counterintuitively, opportunistic species dominated the low-pollution zone. Recent bioturbation by meiofauna and macrofauna may have reduced contamination at S3, releasing pollutants from the sediment (Bradshaw et al., 2006). Moreover, nematodes used metal-binding proteins to absorb heavy metals such as Cr, Cu, and Zn into their tissues and remove them from sediment (Monserrat et al., 2003).

S2, with the second worst sorting level, had the second greatest macrofaunal density (but little meiofaunal density) among all stations. Copepods were less common at this station than at other stations, as the most dominant macrofaunal species was a bivalve (*Laternula gracilis*). Ólafsson et al. (1993) noted that copepods are less abundant when bivalves are present due to competition for food resources. Similarly, the presence of the amphipod *Sinocorophium sinensis*, the second most dominant species at S2, negatively affected the presence of nematodes (Sundelin and Elmgren, 1991). These factors explain the low meiofaunal density at S2 relative to the other stations, and illustrate how meiofaunal assemblages can be influenced by macrofaunal assemblages. Moreover, the LOI exceeded the intermediate pollution threshold in half of the areas tested at S2, which might also have contributed to the low meiofaunal density. In addition, the low meiofaunal density at S2 might be attributable to hypoxia. Meiofauna are more sensitive than macrofauna to hypoxia, among other environmental changes; the sudden onset of hypoxia causes rapid reductions in their abundance and diversity (Patrício et al., 2012; Kim et al., 2020). In addition, *L. gracilis* which the most dominant macrofauna at S2 was included in the same subterclass Euheterodonta as the hypoxic-tolerant bivalve *Theora fragilis* (Table S5).

The meiofaunal density at S1 was more than twice that at S2, perhaps at least in part because the LOI exceeded the intermediate pollution threshold in one part of S1. Moreover, hypoxia was absent and macrofaunal species that adversely affect the presence of meiofauna were not dominant at S1 as they were at S2. However, the macrofaunal density was the lowest among stations, affected by the very poorly sorted sediment. The most dominant species at S1 was polychaete *Nephtys polybranchia*, which occurs in sediments containing gravel and sand with low organic content (Park et al., 2000). *H. filiformis*, the second most dominant species at S1, appears in muddy sediments and is highly tolerant of organic pollution (Borja et al., 2000; Park et al., 2000). The LOI and TOC content at S1 were below threshold levels, and the sediment was sandy mud containing some gravel. Thus, the two species, which are often present in environments with opposing characteristics, were found together at S1. The third dominant species at S1 was the mussel *Arcuatula senhousia*. The effects of the presence of mussels on meiofauna are not consistent (Austen and Thrush, 2001; Norling and Kautsky, 2007; Gestoso et al., 2013).

In general, our results indicate that the integrated analyses of both meio-macrofauna assemblages would improve the power of explanation to distinguish the spatial variation of benthic community structure on intertidal mudflats (Table 3). Although sediment-related factors are predominant for both faunal size classes, the DistLMs results indicated

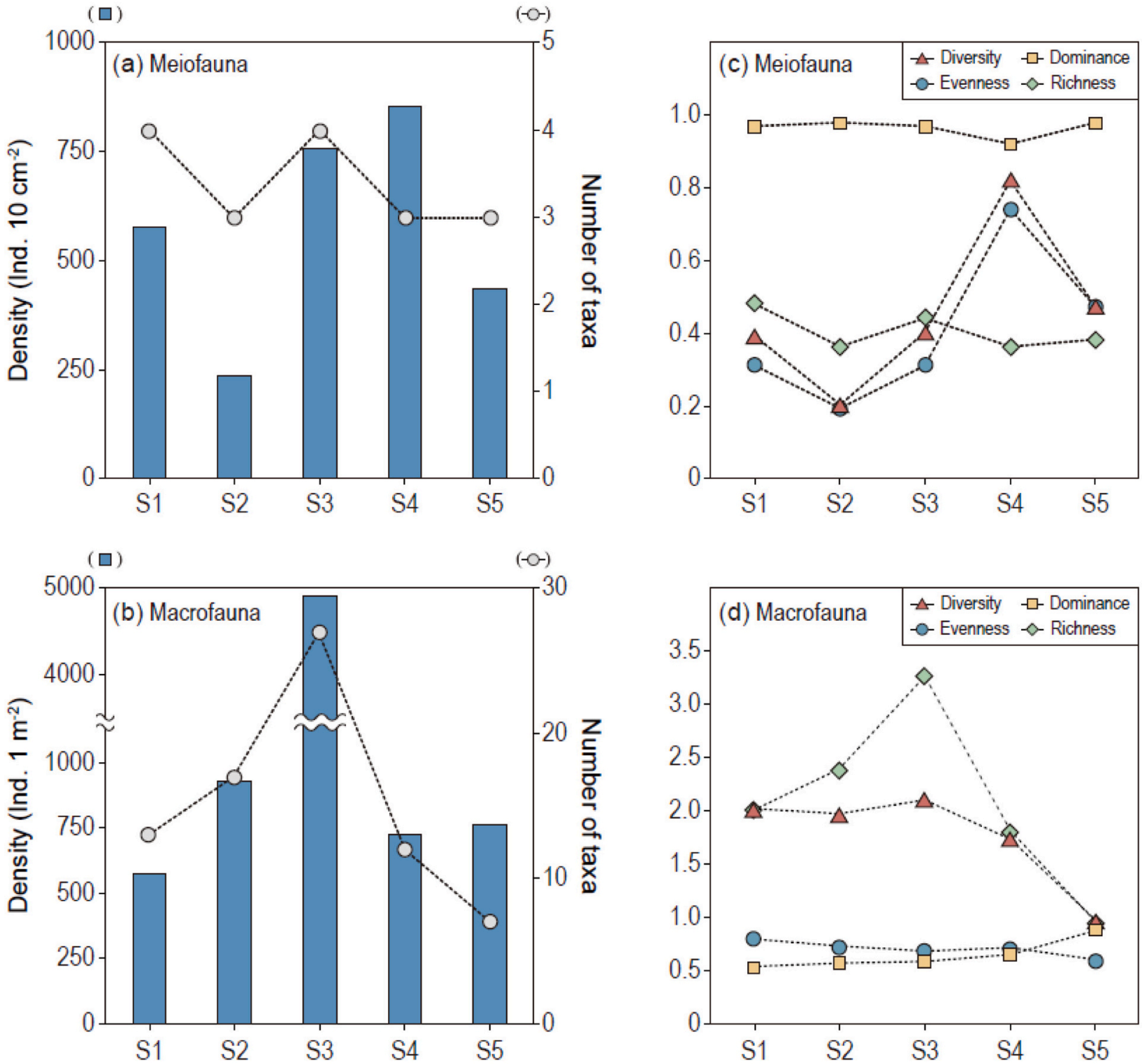


**Fig. 3.** Meiofaunal and macrofaunal density (a, b) and ecological indices (c, d).

that the meiofaunal assemblages were more sensitive to various environmental variables than the macrofaunal assemblages. Previous studies had also revealed that meiofauna assemblages directly respond to natural and/or anthropogenic environmental change (Kim et al., 2020). Apart from sediment related variables, moreover, heavy metals were the second predominant factor that determined both meio and macrofaunal assemblage composition. Our results indicate that both natural factors (sediment properties, etc.) and anthropogenic stresses (e.g., heavy metals) can simultaneously influence patterns of benthic community composition and structure (Bae et al., 2018; Kim et al., 2020).

Marine benthic ecosystems exhibit environmental heterogeneity across various spatial and temporal scales, which significantly impact species diversity (Gallucci et al., 2020). In the context of marine benthic communities, small-scale environmental heterogeneity (cm to few meters) is primarily driven by habitat variations created by biological processes and interactions among organisms. Conversely, larger-scale heterogeneity (>10 km) is predominantly influenced by environmental factors rather than biotic features (Moens et al., 2013). For example, within a given habitat, meiofauna, particularly nematodes, are more susceptible to the effects of localized variability compared to larger, more mobile macrofauna (Schratzberger et al., 2008). Conversely, macrofauna are more likely to be influenced by larger-scale environmental heterogeneity, such as hydrodynamic conditions and positioning along the shoreline (Eckman, 1983). Additionally, while both substrate identity and the surrounding environment play significant roles in shaping the structure of smaller-sized meiofauna, larger-scale changes in the surrounding ecosystem have a greater impact on macrofauna. These findings underscore the importance of incorporating ecological studies and impact assessments that consider both local and regional diversity (Gallucci et al., 2020).

This study characterized the spatial distribution of meiofaunal and macrofaunal assemblages only in intertidal mudflats on the western south coast of Korea. Therefore, this study can provide fundamental ecological insights for understanding the spatial distribution of meiofaunal and macrofaunal assemblages and aid in the development of management strategies to mitigate sustainable coastal management in intertidal mudflats on the western south coast of Korea. The meiofauna and macrofauna density, diversity, and assemblage composition differed

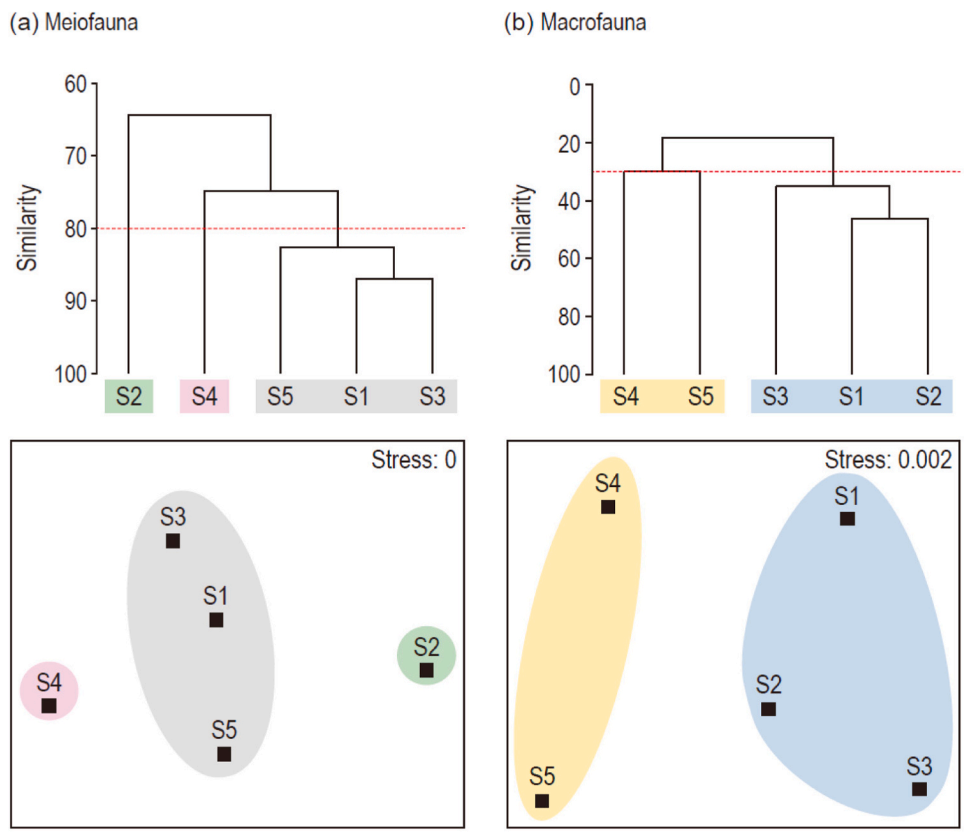


**Fig. 4.** Non-metric multidimensional scaling and cluster plots based on the Bray-Curtis similarity index of the average meiofaunal (a) and macrofaunal (b) abundance.

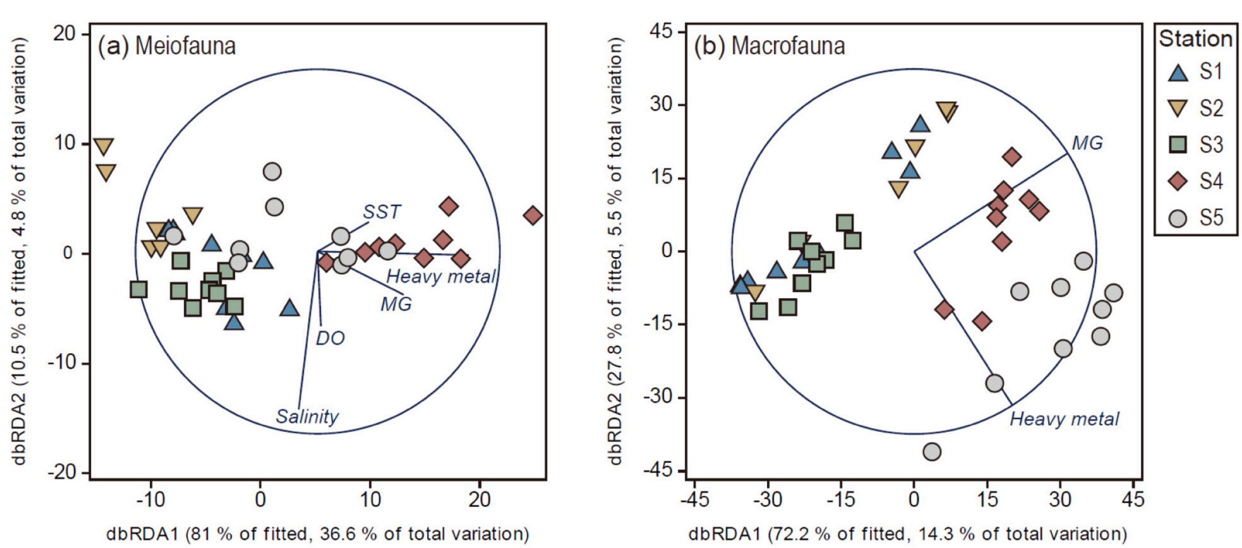


**Fig. 5.** Two-axis distance-based redundancy analysis (dbRDA) plots of relationships between biological variables [(a) meiofauna and (b) macrofauna] and environmental variables.

significantly among sampling stations. The spatial differences in benthic assemblages might be due to the interaction of site-specific environment (e.g., sediment properties, salinity, and heavy metals) and biological factors (meio-macro interaction). Our results revealed that meio and macrofauna can provide different but complementary types of information, depending on natural environmental factors and anthropogenic disturbance. Therefore, integrated analysis of micro to macro faunal groups should be considered for future environmental monitoring and assessments in coastal environments, elsewhere. Additional research is needed to characterize the spatiotemporal variation in meiofaunal and macrofaunal assemblages at the entire intertidal flat on southern coast of Korea.

**Table 3**
Results of DistLM analysis used to explore the relationship between meiofauna and meio-macrofauna and environmental variables.

| | Meiofauna | | | | | Macrofauna | |
|---|---|---|---|---|---|---|---|
| | Heavy Metal[1] | Salinity[2] | DO[3] | SST[4] | Sediment[5] | Heavy Metal[1] | Sediment[5] |
| V | | | | | | | |
| **AIC (c)** | 228.28 | 222.62 | 221.27 | 219.63 | **218.48** | 344.95 | **343.91** |
| **P-F** | 7.72 | 7.80 | 3.16 | 3.35 | 2.81 | 6.02 | 3.25 |
| ***P*** | **0.002** | **0.001** | **0.025** | **0.015** | **0.044** | **0.001** | **0.001** |
| **Cum**. | 0.16 | 0.30 | 0.36 | 0.41 | 0.45 | 0.13 | 0.20 |
| B.S. | | | | | | | |
| **AIC (c)** | **218.48** | | | | | **343.91** | |
| $\mathbf{R^2}$ | 0.45 | | | | | 0.20 | |
| **V** | 5 | | | | | 2 | |

*P* values were obtained using 999 permutations of residuals under the best model (for meiofauna, forward selection based on the AIC; for macrofauna, forward selection based on the AICc). Bold font indicates significant values and best solutions. V, variable; DO, dissolved oxygen; SST, sea surface temperature; AIC(c), Akaike information criterion (with second-order correction); P—F, pseudo-*F*; Cum., Cumulative; B.S., best solution.

[1] Li, Cr, Ni, Zn, As, Cd, Pb, Fe, and Hg.

[2] Salinity.

[3] DO and pH.

[4] SST.

[5] Mean grain size, silt content, clay content, water content, loss on ignition, total organic carbon.

## CRediT authorship contribution statement

**Jeong Won Kim**: Conceptualization, Investigation, Formal analysis, Data curation, Visualization, Writing - original draft.
**Hyeong-Gi Kim**: Conceptualization, Methods development, Writing - original draft, Writing - review & editing, Project administration, Funding acquisition, Supervision.
**Hyein Kim**: Formal analysis, Data curation, Writing - review & editing.
**Stephen John Hawkins**: Investigation, Formal analysis, Data curation.
**In-Soo Seo**: Investigation, Formal analysis, Data curation.
**Chul-Woong Oh**: Conceptualization, Investigation, Formal analysis, Data curation, Writing - review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The authors do not have permission to share data.

## Acknowledgments

This work was supported by the National Research Foundation of Korea (NRF) grant funded by the Korea government (MSIT) (No. 2021R1C1C1010084) and (No. 2022R1A4A1033825). Also, this research was supported by Korea Institute of Marine Science & Technology Promotion (KIMST) funded by the Ministry of Oceans and Fisheries (20220150), Republic of Korea. The authors would also like to acknowledge the contributions of data from the “National Marine Ecosystem Monitoring Program”, funded by the Ministry of Oceans and Fisheries (MOF) of the Republic of Korea.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2023.115377.

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