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Influence of the Kuroshio Current on the benthic communities in the southern seas of Korea☆

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ABSTRACT

The Kuroshio Current, a major western boundary current in the North Pacific, intrudes into the southern seas of Korea through the Tsushima Warm Current (TWC) and exerts strong influence on benthic ecosystems. From 2015 to 2024, we assessed seasonal variability in hydrography, sediments, and benthic macrofauna. Summer conditions featured warmer surface waters (27.8 °C), lower dissolved oxygen, and more organic-rich, coarse sediments. Benthic communities showed clear seasonality, with all community metrics highest in spring, lowest in winter, and intermediate in summer and autumn. Sediments were mainly sandy silt and silty sand, dominated by polychaetes, with higher species density and biomass observed in summer and autumn. Bottom temperature was modestly related to richness and density, while biomass declined with surface warming. These patterns closely resemble observations from other Kuroshio-affected regions, including seasonal oxygen depletion and organic enrichment on the East China Sea shelf, enhanced nutrient flux and benthic shifts off Taiwan, and polychaete-dominated assemblages in southern Japan. The convergence of these features across Kuroshio-influenced margins provides evidence that the benthic ecosystems of Korea are directly shaped by the hydrographic and biogeochemical forcing of the Kuroshio system.

1. Introduction

The Kuroshio Current, a prominent western boundary current originating from the North Equatorial Current, plays a critical role in the North Pacific circulation system (Chen et al., 2021). Driven by planetary rotation and prevailing wind systems, it transports substantial volumes of warm, saline water poleward along the western Pacific margin, influencing regions including Philippines, Taiwan, and Japan (Chang and Oey, 2012; Zheng et al., 2016). With velocities exceeding 2 m/s and transport rates estimated to be between 20 and 55 Sverdrup (Sv)—comparable to the Gulf Stream—the Kuroshio plays a vital role in regional and basin-scale climate regulation (Kawakami et al., 2023; Nakano et al., 2008; Zhang et al., 2021). Its associated mesoscale variability significantly influence on hydrographic conditions and nutrient distributions, making the current a key component in sustaining marine biodiversity and shaping the ecological dynamics of East Asia marginal seas (Bai et al., 2018; Jung et al., 2017; Lee et al., 2009).

The Kuroshio Current exhibits distinct physical properties that distinguish it apart from surrounding Pacific waters at comparable latitudes (Nan et al., 2015; Wei et al., 2016; Yatsu et al., 2013). Characterized by elevated temperatures and salinity, its waters possess a stratified vertical structure, consisting of a warm, shallow surface layer overlaying a colder, deeper water mass (Chang et al., 2004; Giordani et al., 2006; Nagai et al., 2012). The transition between these layers—the thermocline—is often sharply defined and plays a crucial role in regulating the vertical distribution of marine organisms (Wang et al., 2016). Importantly, the Kuroshio is neither a uniform nor steady flow; it displays pronounced mesoscale variability, including eddies and a meandering path (Chen et al., 2022; Hurlburt et al., 1996; Miyazawa et al., 2004; Zhang et al., 2001). These dynamic features significantly influence local hydrographic conditions and modulate nutrient fluxes. They also affect the dispersal patterns of plankton and the early life stages of marine organisms, thereby structuring the ecology of adjacent marine ecosystems (Bonilla et al., 2005; Ji et al., 2010). Therefore, a

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comprehensive understanding of the Kuroshio, including its origin, trajectory, physical structure, and variability is essential for elucidating the broader ecological processes governing the East Asian marginal seas (Lee et al., 2020). In particular, these far-reaching effects provide the environmental foundation for the structure and function of benthic ecosystems in the southern seas of Korea (Chertoprud et al., 2015; Macias et al., 2024; Rebstock and Shil Kang, 2003; C. I. Zhang et al., 2007).

In the southern Hyūga-nada region of Japan, the intrusion of the Kuroshio induces strong internal waves and turbulent mixing, which transport subsurface nitrate into the euphotic zone and thereby enhance local productivity (Durán Gómez and Nagai, 2022). Along eastern Taiwan, the Kuroshio mediates nutrient exchanges at the sediment–-water interface, regulating benthic nutrient cycling (Chen et al., 2017), while in the southern sector, intense bottom currents redistribute sediments and alter benthic habitats (Das et al., 2021). Beyond these physical processes, the Kuroshio exerts profound influences on marine biodiversity and community structure. In the East China Sea, branches of the Kuroshio delineate benthic fish assemblages into coastal, transitional, and Kuroshio-associated groups, with gradients of temperature, oxygen, and sediment grain size acting as key determinants of species composition (Xu et al., 2019). Furthermore, an eDNA-based study off the Japanese coast demonstrated that small pelagic fishes such as sardine, anchovy, and mackerel, aggregate around the Kuroshio Front, with their distributions controlled by temperature, dissolved oxygen, and prey availability (Yu et al., 2023). The intensification of the Kuroshio has been linked to major shifts in productivity, climate, and benthic ecosystem evolution in the northwestern Pacific. It also exerts broad ecological effects across Japan, Taiwan, and the Philippines through its connection to the Indo-Pacific circulation system, including the Indonesian Throughflow and the West Pacific Warm Pool (Gallagher et al., 2009).

The southern seas of Korea constitute a complex and biologically productive marine ecosystem shaped by the interplay between large-scale oceanographic forces and localized environmental features (Kang et al., 1999; Kim et al., 1998; Lee et al., 2006). A prominent influence in this region is the Tsushima Warm Current (TWC), a northeasterly branch of the Kuroshio Current that transports warm, saline waters into the area (Tian et al., 2008; Yun et al., 2017). The region is further characterized by broad continental shelf, intricate coastlines punctuated by numerous islands and embayments, and the interaction of diverse water masses (Lie and Cho, 1994; Park et al., 2013; Yoshikawa et al., 2010). In addition to the TWC, coastal currents, riverine freshwater inputs, and seasonal atmospheric forcing contribute to the creation of a heterogeneous and dynamic marine environment (Hirose et al., 2006; Watanabe et al., 2006; Yabe et al., 2021). These physical and oceanographic factors collectively determine spatial environmental variability, thereby influencing the distribution, composition, and abundance of marine biota, including the benthic communities that form the central focus of this study (Kitamura et al., 1999; Takata et al., 2019; Tanaka, 2008).

Previous studies have extensively documented the biodiversity of the southern Korean marine environment, encompassing a wide range of taxonomic groups from phytoplankton to fish (Kang et al., 2019; Khim et al., 2021). In particular, considerable research has focused on the distribution and community structure of benthic invertebrates across diverse habitats and depth gradients in the region (Kim et al., 1993; Park and Huh, 2018; Seo et al., 2014). Moreover, environmental factors such as sediment type, water depth, and organic matter content have been identified as key drivers shaping benthic community structure, with several investigations highlighting their significant influence on species distribution patterns and ecological functioning (Igeta et al., 2023; Ko et al., 2008; Lee et al., 2012).

Several studies have begun to explore the influence of the Kuroshio Current on the southern seas of Korea, focusing primarily on the seasonal variability and intrusion of the TWC (Bae et al., 2017; Park et al., 2013; Yabe et al., 2021). Studies have tracked TWC dynamics and their impact on local temperature and salinity regimes within the region (Seo et al., 2013; Shin et al., 2022). Furthermore, investigations have examined the relationship between the TWC and the distribution of pelagic organisms, including commercially significant fish species and plankton communities (Tian et al., 2006; Yatsu et al., 2013). Notably, a regime shift observed in the TWC ecosystem around the late 1980 s involved marked changes in species composition and habitat distribution (Tian, 2002).

The direct and indirect effects of the Kuroshio system, particularly the TWC, on the benthic ecosystems of the southern seas of Korea remain underexplored. Consequently, the primary objective of this study was to comprehensively elucidate the influence of the Kuroshio Current system on the benthic ecosystem structure and function in this region. To address knowledge gaps regarding temporal dynamics, we examined interannual and seasonal variations in species abundance and biomass over a decade, relating these biological metrics to spatial differences in environmental parameters. This study aims to provide a baseline for future ecological assessments and conservation efforts under changing environmental conditions.

2. Materials and Methods

2.1. Study area

The seasonal ocean circulation patterns in the study area are characterized by distinct summer and winter hydrographic regimes (Fig. 1). During summer, the northeastward-flowing Kuroshio Current flows along the Ryukyu Trench, accompanied by a stronger intrusion of the TWC and coastal currents such as the Cheju Warm Current (CWC). In contrast, winter is marked by the southward influence of the Yellow Sea Coastal Current (YSWC) and freshwater input from the Changjiang Diluted Water (CDW), both of which play significant roles in shaping the physical environment of the southeastern East Sea and the eastern South Sea of Korea.

This study assessed the influence of the Kuroshio Current system on the benthic ecosystem in the southern seas of Korea by analyzing seasonal oceanographic and biological data collected over a 10-year period, from 2015 to 2024. The study area encompassed the southeastern East Sea and the eastern South Sea of Korea (34°–37°N, 128°–131°E). Sampling stations were situated at depths ranging from approximately 30 to 110 m, a region benthic ecological variability is strongly influenced by the seasonal branching and fluctuation of the Kuroshio Current and its derivatives (Fig. 1). Benthic environmental and biological data were obtained from 36 sampling stations distributed across the southeastern East Sea and the eastern South Sea. At each station, measurements of physical oceanographic parameters were measured, and benthic macrofaunal samples were systematically collected to characterize seasonal and spatial variability.

2.2. Sample processing

The surveys were conducted from 2015 to 2024 at an average depth of 71.6 m, with a total of 20 surveys conducted twice each year to reflect seasonal variability. Benthic samples were collected using a Smith–McIntyre grab sampler with a sampling area of 0.1 m^2; two replicates were obtained at each station. Replicates were merged to derive macrobenthos density at each station. The collected sediment was passed through a 1-mm-mesh sieve, and the retained macrofauna were fixed in 10 % buffered formalin solution for subsequent taxonomic analysis. In parallel, surface sediment samples (within the top 1 cm) were collected and immediately stored at − 20 °C for subsequent analysis of total organic carbon (TOC) and sediment grain size composition. In the laboratory, the retained benthic organisms were sorted and identified to the species level using a stereomicroscope. All environmental variables were categorized by season to assess temporal variability. Seasonal differences in each parameter were visualized using boxplots.

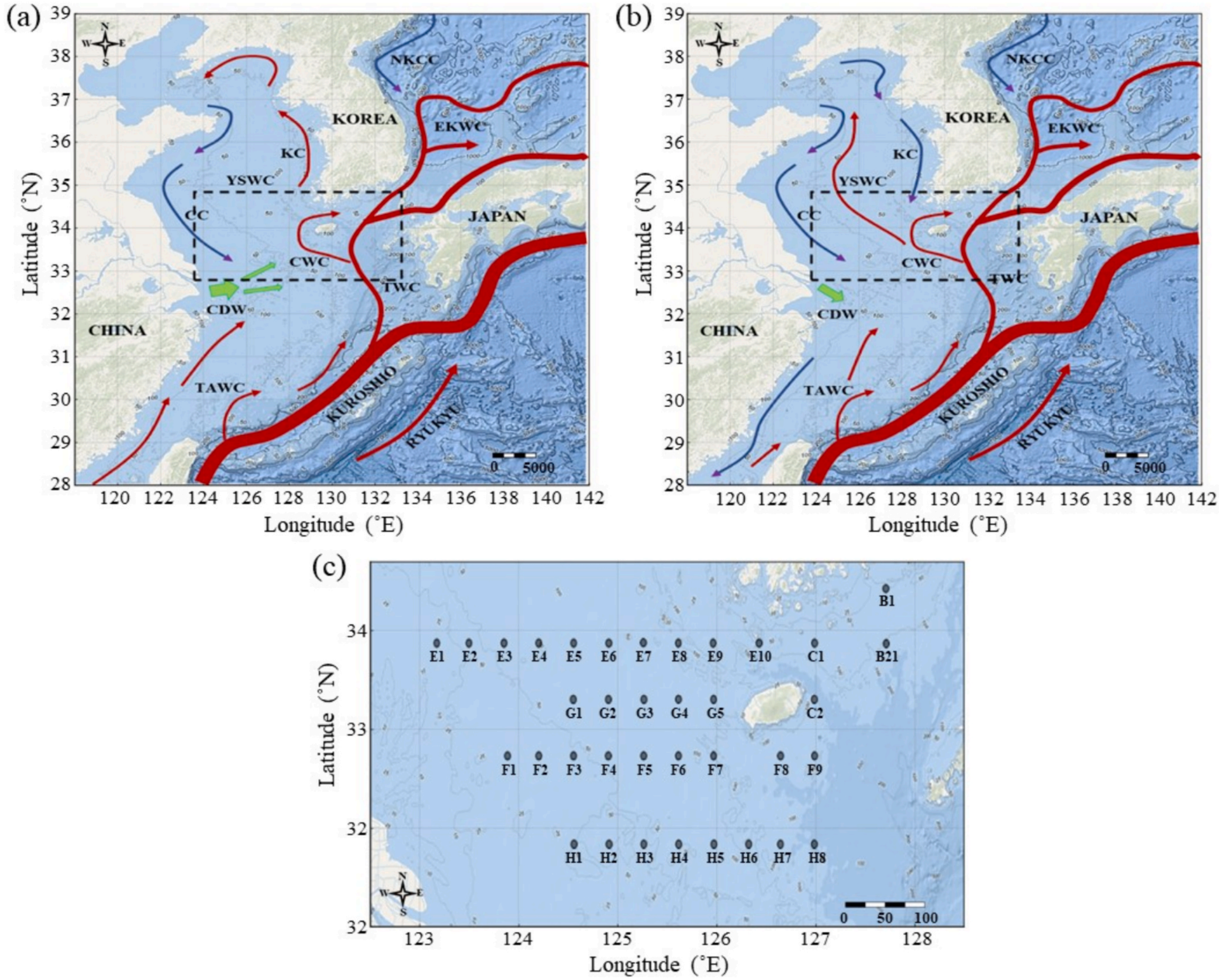

Fig. 1. Seasonal surface current systems in the East China Sea and the southern seas of Korea during summer (a) and winter (b), and the spatial distribution of benthic sampling stations in the study area (c). Abbreviations: TWC, Tsushima Warm Current; CDW, Changjiang Diluted Water; KC, Kuroshio Current; NKCC, North Korea Coastal Current; EKWC, East Korea Warm Current; YSWC, Yellow Sea Warm Current; CWC, Cheju Warm Current; TAWC, Taiwan Warm Current; CC, Coastal Current.

Seawater temperature, depth, salinity, and dissolved oxygen (DO) were recorded in situ using a CTD profiler (model SBE 911, Sea-Bird Electronics, Bellevue, WA, USA). For sediment granulometry, organic matter was first oxidized by treating the samples with a 10 % hydrogen peroxide (H_2O_2) solution, followed by drying at 100 °C. Residual salts and biological materials were subsequently removed by rinsing with deionized water, after which the cleaned sediments were dried and weighed. For fine particle analysis, subsamples containing grains < 63 μm were treated with a sodium hexametaphosphate solution to promote dispersion and were analyzed using a SediGraph 5120 (Micromeritics, Norcross, GA, USA). Total organic carbon (TOC) content was determined after removing carbonates by adding 0.1 N HCl to oven-dried (50 °C, 48 h) sediments, followed by analysis using a CN analyzer (TOC-5000A, Shimadzu, Kyoto, Japan).

2.3. Data processing

Species abundance data were normalized to individuals per m^2 and then compared among stations. To investigate spatial and temporal variations in community composition, the data were fourth-root transformed to reduce the influence of highly dominant species. Community classification and ordination were performed using cluster analysis and non-metric multidimensional scaling (nMDS) based on Bray–Curtis similarity matrices. These multivariate analyses were conducted using PRIMER v6 with the PERMANOVA + add-on (Plymouth Marine Laboratory, Plymouth, UK).

2.4. Indicator species analysis

Indicator species analysis was performed following the method of Dufrêne and Legendre, 1997 to identify species that are characteristic of specific years or seasons (Dufrêne and Legendre, 1997). This method integrates two components, specificity and fidelity, to quantify the degree to which a species is representative of a particular temporal group. The indicator value (IndVal) for each species was calculated as IndVal = 100 × A × B, where specificity (A) represents the proportional abundance of a species in a specific year relative to its overall abundance across all years and fidelity (B) denotes the consistency of the species' occurrence within a specific year. An IndVal score approaching 100 indicates that a species is both highly abundant and consistently present in a specific year or season, thereby serving as a strong ecological indicator for that period.

2.5. Regression analysis

Linear regression analyses were conducted to evaluate the relationships between water temperatures and benthic community parameters. Both surface and bottom water temperatures were treated as independent variables, while benthic community metrics, including species richness, density, the Shannon–Wiener diversity index (H′), and biomass, were used as dependent variables. Separate regression models were fitted for surface and bottom temperature data against each biological parameter. For each model, the linear regression equation (F(x) = a + bx), coefficient of determination (r2), and p-value were calculated to assess the strength and statistical significance of the relationships. Although many models yielded relatively low r^2 values, linear regression was employed because it allows for the identification of general trends and provides ecologically meaningful insights into how temperature variability may influence benthic community structure. Furthermore, several models produced statistically significant results, supporting the interpretation of consistent patterns.

2.6. Taxonomic distinctness analysis

To investigate the relationship between benthic species richness and taxonomic diversity, three metrics were calculated for each benthic macrofaunal community sample collected from the study area: number of species, average taxonomic distinctness (Delta +), and taxonomic distinctness variance (Lambda +). Delta + represents the average taxonomic distance between all possible pairs of species in a sample, while Lambda + measures the variance of these distances, reflecting taxonomic dispersion. Both indices were calculated based on a hierarchical taxonomic framework constructed from all identified taxa, using the World Register of Marine Species (WoRMS), encompassing levels ranging typically from the species to family level and above.

All calculations of Delta + and Lambda+, as well as the funnel plot construction and associated permutation tests, were performed using PRIMER v6 with the PERMANOVA + add-on (Plymouth Marine Laboratory, UK). Variance patterns in Lambda + were assessed to evaluate consistency in taxonomic structure across samples, and Levene's test was applied to test for homogeneity of variances among groups.

2.7. Correlation analysis

To explore the relationships between benthic macrofaunal assemblages and environmental gradients, a distance-based redundancy analysis (db-RDA) was performed as a constrained ordination method (Legendre and Andersson, 1999). This approach is particularly suitable for ecological data, as it accommodates non-Euclidean dissimilarities and circumvents the assumption of strictly linear species–environment responses that may bias traditional RDA. Prior to analysis, environmental variables were square-root transformed to reduce skewness, and variable selection was carried out by excluding highly correlated pairs (Spearman's $\rho > 0.6$, $p < 0.05$). To identify the most influential predictors of community composition, a distance-based linear model (DistLM; Clarke and Gorley, 2006) was applied. A Bray–Curtis similarity matrix was constructed for the faunal data, whereas standardized Euclidean distance were employed for the environmental dataset (Clarke and Gorley, 2006; Legendre and Legendre, 2012).

Spearman correlation coefficients were calculated separately for each season (spring, summer, autumn, and winter) to examine the linear relationships between individual environmental and sediment variables and the abundance of each benthic macrofaunal taxon. Significance levels ($P < 0.05$, $P < 0.01$, $P < 0.001$) were interpreted based on raw p-values. The correlation coefficients (r-values) ranged from − 1 to + 1, with values near + 1 indicating strong positive correlations, values near − 1 indicating strong negative correlations, and values near 0 representing weak or no linear relationships (SigmaPlot 13; Systat Software Inc., San Jose, CA, USA.

3. Results

3.1. Seasonal variability in environmental parameters

Surface and bottom water properties exhibited clear seasonal cycles driven by the TWC. Surface water temperature peaked in summer (27.8 °C) and decreased in winter (13.8 °C), while bottom temperatures showed limited seasonal variability but remained consistently higher during summer (14.7 °C) (Fig. 2). Seasonal differences in bottom water temperature were statistically significant (ANOVA, $F = 18.75$, $p < 0.0001$). Salinity also exhibited significant seasonal variability, with relatively lower values in summer and elevated levels in spring and winter (ANOVA, $F = 5.26$, $p = 0.0016$). Dissolved oxygen (DO) concentrations declined in summer and autumn, reflecting the development of seasonal stratification and organic matter deposition at the seabed under the intensified influence of the TWC. Sediment characteristics also responded to seasonal forcing: coarser sediments and higher TOC accumulation wers observed in summer, conditions typically associated with enhanced organic matter input and reduced benthic oxygen availability. Current velocity revealed distinct seasonal variations, characterized by a marked intensification during the summer months. The highest median velocity (23 cm/s) and greatest variability were recorded in summer, coinciding with the seasonal intensification of the TWC. In contrast, spring showed the lowest median speed of 13 cm/s, indicating relatively stable flow conditions.

3.2. Benthic community abundance and diversity

Seasonal variation was evident in all community parameters. In spring, species richness (47.1 species), density (780 ind./m^2), and biomass (63.1 g/m^2) reached their highest values, indicating favorable conditions for abundant assemblages (Fig. 3). During summer, richness and density declined to 26.8 species and 521 ind./m^2, respectively, with reduced biomass (41.8 g/m^2). Autumn exhibited intermediate values, with 36.0 species, a density of 625 ind./m^2, and a biomass of 46.1 g/m^2, suggesting a partial recovery after summer. In winter, all parameters reached their lowest levels (30.0 species, 442 ind./m^2, and biomass of 27.8 g/m^2), reflecting less favorable conditions for benthic communities.

3.3. Spatial variation in sediment type

The composition of surface sediments in the study area is presented in a ternary diagram (Fig. 4), with each point representing a single sediment sample. The vertices of the triangle denote 100 % sand, silt, and clay, respectively, and the relative position of each point indicates the proportional contribution of these three fractions. Most samples were clustered within the sandy silt to silty sand region, suggesting that sediments are predominantly composed of moderate amounts of sand (average: 30.7 %), silt (average: 54.1 %), and clay (average: 15.3 %). Gravel content was negligible across all samples. This sediment composition indicates that the study area is dominated by fine-grained substrates, which provide suitable conditions for deposit-feeding organisms. Such sedimentary conditions are known to support high macrofaunal abundance and diversity in other Kuroshio-influenced shelf regions.

3.4. Linear relationships between water temperature and benthic community parameters

Linear regression analyses revealed several significant relationships between water temperature and benthic community parameters (Fig. 5). Species richness showed a weak but statistically significant negative relationship with surface water temperature, described by the equation $F(x) = 46.2838 - 0.5541x$ ($r^2 = 0.0205$, $p = 0.0305$). In contrast, a significant positive relationship was found between species richness and

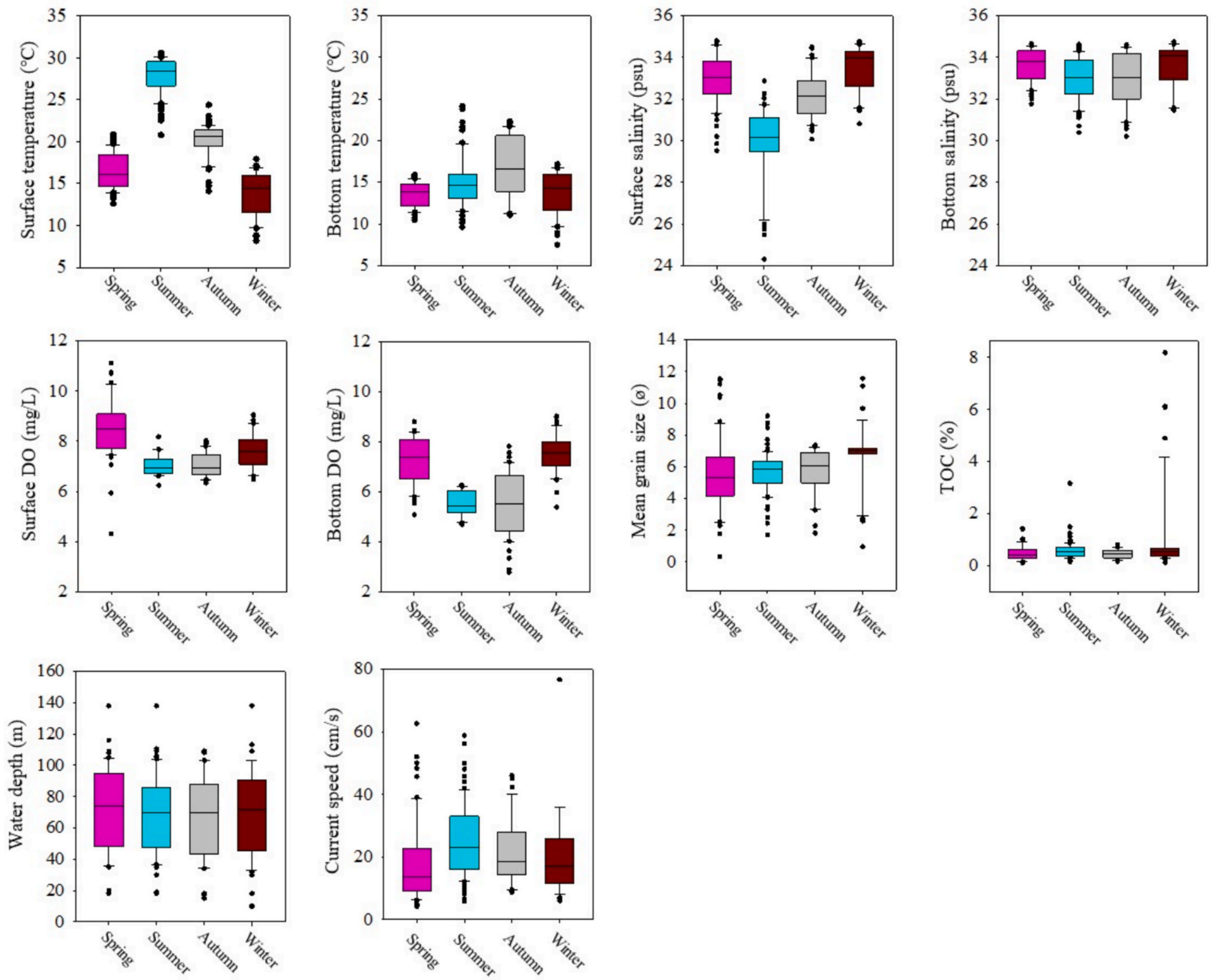

Fig. 2. Seasonal variation in environmental parameters measured in the southern seas of Korea. Boxplots represent surface and bottom water temperature (°C), salinity (psu), dissolved oxygen (DO, mg/L), mean grain size (φ), total organic carbon (TOC, %), water depth (m), and current speed (cm/s) across four seasons: spring, summer, autumn, and winter.

bottom temperature ($F(x) = 20.8456 + 0.9542x$, $r^2 = 0.0167$, $p < 0.0001$). Benthic density (ind./m2) exhibited no significant association with surface temperature ($F(x) = 736.109 - 6.6300x$, r2 = 0.0055, p = 0.5369), but a significant positive relationship was observed with bottom temperature ($F(x) = 205.448 + 26.734x$, r2 = 0.0244, $p < 0.0001$). For the Shannon–Wiener diversity index (H′), surface temperature showed a non-significant negative relationship ($F(x) = 3.2114 - 0.0203x$, r2 = 0.0286, p = 0.1949), whereas a weak but statistically significant positive relationship was found with bottom temperature ($F(x) = 2.5069 + 0.0196x$, r2 = 0.0073, $p < 0.0001$). Benthic biomass (g/m2) showed a highly significant negative relationship with surface temperature ($F(x) = 57.8720 - 0.5808x$, r2 = 0.0016, $p < 0.0001$), while no significant relationship was detected with bottom temperature ($F(x) = 58.8917 - 0.8736x$, r2 = 0.0010, p = 0.7174). Overall, these results suggest that bottom temperature exerted stronger control on species richness and density, while surface temperature was more closely linked to biomass variation. Although many of these relationships were statistically significant due to the large sample size, the consistently low r^2 values (<0.03) indicate very weak explanatory power, suggesting that temperature explained only a small fraction of the variability in benthic community parameters.

3.5. *Temporal dynamics of dominant species*

Heatmap analysis combined with hierarchical clustering revealed distinct temporal patterns in benthic macrofaunal taxa collected from 2015 to 2024 in the southern seas of Korea (Fig. 6). Dominant species such as *Lumbrineris* sp. and *Goniada japonica* maintained consistently high abundance across seasons and years, indicating their stable presence in the community. In contrast, *Terebellides* sp. showed recurrent seasonal peaks in summer, while *Capitella capitata* exhibited a sharp increase in autumn 2020, suggesting episodic or disturbance-driven occurrences. Taxa clustered into groups based on abundance trajectories, with some maintaining a low but stable presence, and others displaying sporadic or seasonally concentrated high points.

3.6. *Taxonomic structure patterns*

The relationships between species richness and taxonomic distinctness indices were assessed using funnel plots (Fig. 7). In the scatter plot of species richness versus Delta+, most data points fall within the 95 % confidence funnel, indicating that the average taxonomic distinctness generally conforms to expectations under random sampling. However,

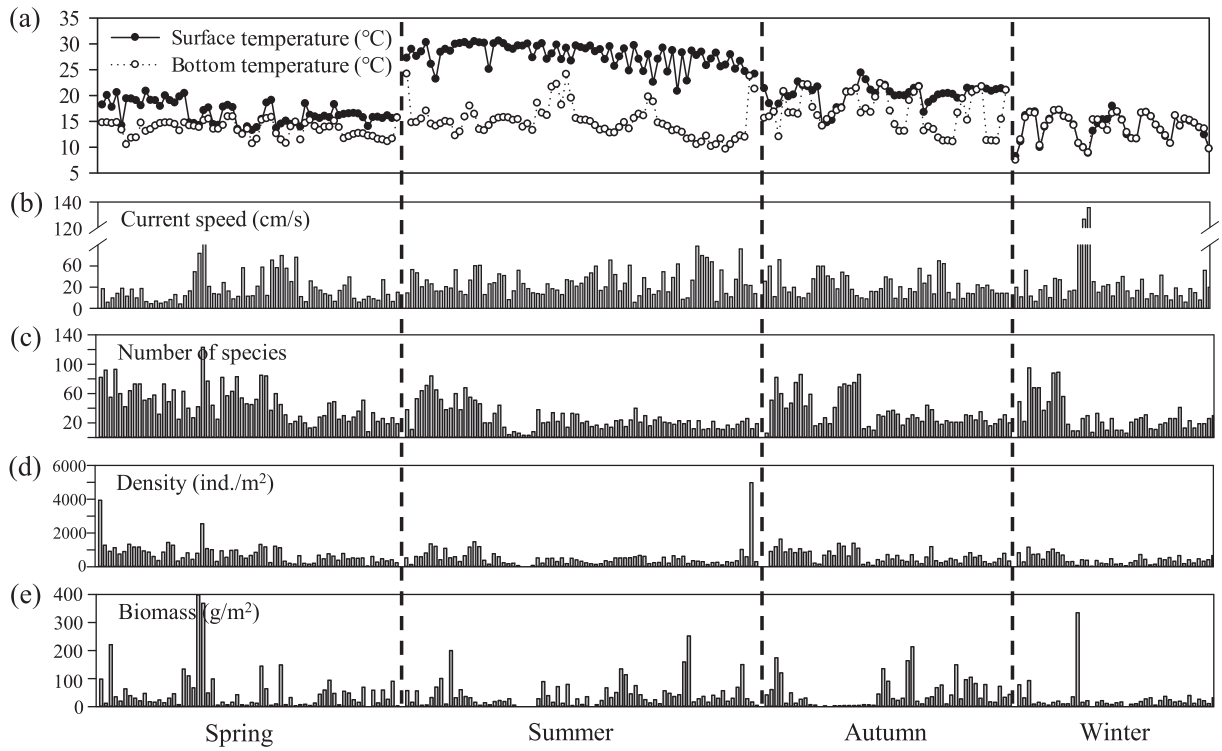

Fig. 3. Temporal variation in hydrographic and benthic community parameters from spring to winter in the southern seas of Korea. (a) surface and bottom water temperatures (°C), (b) current speed (cm/s), (c) number of species, (d) macrobenthos density (ind./m^2), and (e) biomass (g/m^2).

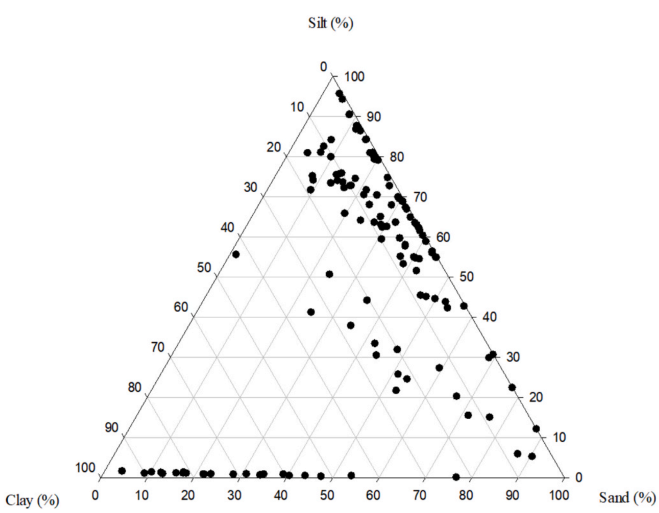

Fig. 4. Ternary diagram of surface sediment composition based on percentages of sand, silt, and clay in the southern seas of Korea.

several points—primarily those in the lower richness range—fall below the lower confidence limit, suggesting strong taxonomic clustering within those communities. A few points lie above the upper limit, representing communities with greater-than-expected taxonomic breadth. Similarly, the plot of species richness against Lambda + showed comparable results. Most observations are distributed within the expected range, but a number of blue triangles and red circles fall outside the funnel at both high and low richness levels. These outliers indicate unusually high or low variation in taxonomic distinctness, potentially associated with he tuneven representation of higher-level taxa.

3.7. Indicator value analysis

Indicator value analysis identified key benthic macrofaunal taxa that were strongly associated with specific sampling groups, as visualized in the bubble plot (Fig. 8). Each bubble represents the relative indicator value of a species within a particular group, with larger bubbles indicating higher IndVal scores. Several species, including *Lumbrineris* sp., *Yoldiella squamaeformis*, *Notomastus latericeus*, and *Apionsoma (Apionsoma) misakiana*, showed high indicator values across multiple groups, suggesting broad ecological relevance or consistent association with varying environmental conditions. In contrast, species such as *Praxillella pacifica*, *Prionospio* sp., and *Ampelisca naikaiensis* displayed high IndVal scores in specific groupings, indicating strong fidelity and specificity to those habitats or temporal phases. *Terebellides horikoshi*, *Ampharete finmarchica*, and *Amphipholis* sp. showed sporadic yet marked indicator values, suggesting episodic environmental suitability or recruitment pulses. Species such as Nematoda unid. and *Raeta pulchella* had uniformly low indicator values, reflecting either generalist traits or low detectability. Overall, these results indicate that some taxa function as consistent indicators of the TWC-influenced environments, while others respond opportunistically to episodic habitat changes, underscoring the mixed stability and variability of benthic assemblages in the study area.

3.8. Seasonal correlations analysis

Seasonal correlation analysis revealed significant relationships between environmental factors and benthic macrofaunal species abundance (Figs. 9, 10). Among the environmental parameters, total organic carbon (TOC), mean grain size (Mz), and salinity exhibited strong and consistent correlations with multiple species across seasons. TOC showed significantly positive correlations with several species during spring and autumn, including *Lumbrineris* sp. and *Ophelina acuminata*. In contrast, Mz and silt content were negatively correlated with the same species, particularly in spring and summer. *Lumbrineris* sp. showed consistently negative correlations with temperature, salinity, and Mz

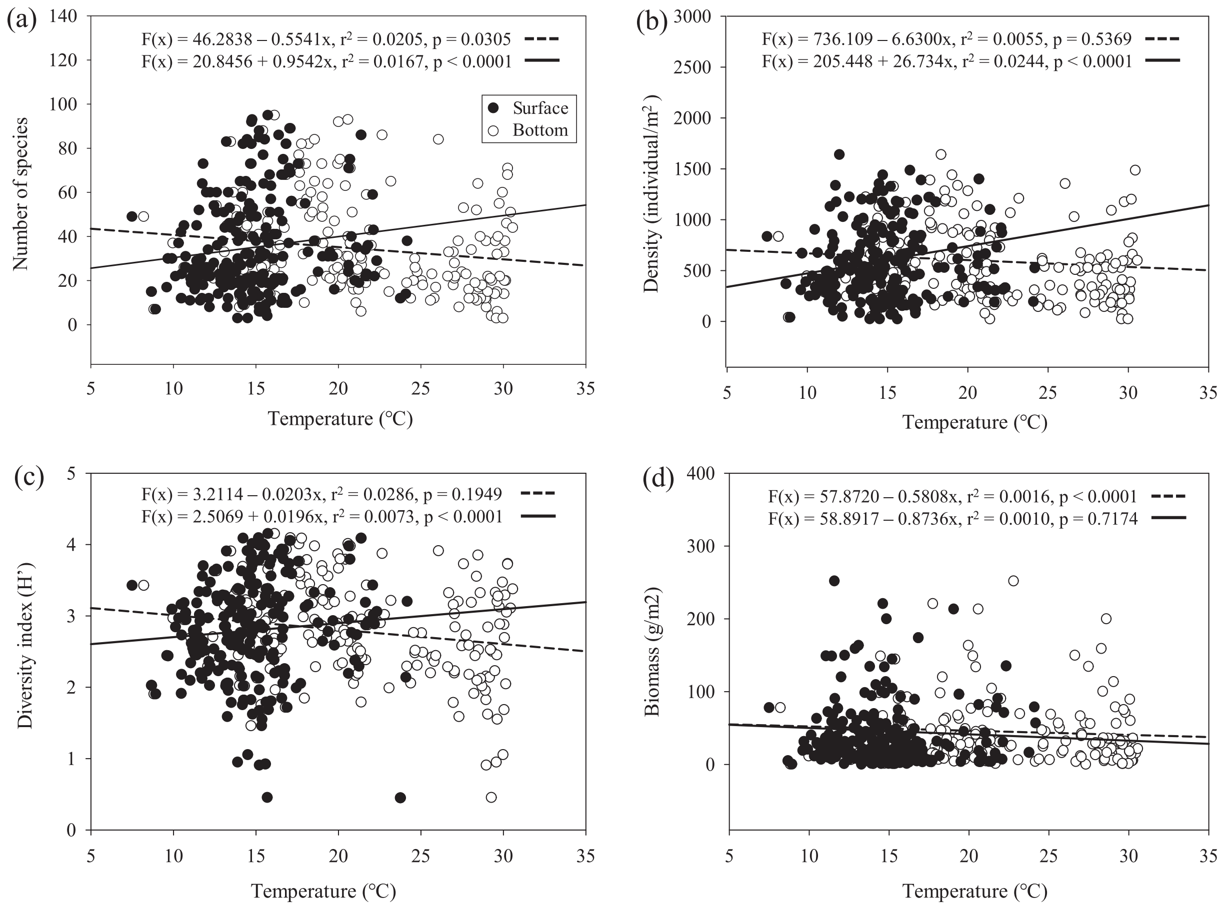

Fig. 5. Relationships between water temperature (°C) and benthic community parameters in the southern seas of Korea. (a) number of species, (b) density (ind./m2), (c) Shannon–Wiener diversity index (H′), and (d) biomass (g/m2).

across all seasons, with many coefficients reaching high statistical significance ($p < 0.001$). *Apionsoma misakiana* and *Raeta pulchella* displayed positive correlations with sand and TOC, particularly during summer and autumn. These results suggest that benthic species show different habitat associations: some taxa appear to be influenced by organic enrichment and sediment texture, while others display broader tolerance or opportunistic patterns.

4. Discussion

The hydrographic and sedimentary parameters observed in this study are consistent with conditions reported in regions influenced by the Kuroshio Current system. The relatively warm bottom waters (summer average: 14.7 °C) and stable salinity values (30.2–34.6 psu) align with the characteristics of the TWC, a branch of the Kuroshio (Hsueh, 2000; Qiu and Miao, 2000). In addition, seasonal declines in dissolved oxygen and the enrichment of organic matter during summer reflect stratification processes commonly associated with Kuroshio-driven circulation (Chang et al., 2004; Sun et al., 2016). Together, these features indicate that the southern Korean coastal waters are directly shaped by the broader Kuroshio Current system. Within this hydrographic framework, our results demonstrate that seasonal changes in benthic macrofaunal assemblages are strongly mediated by variability associated with the TWC. Elevated bottom temperatures and reduced dissolved oxygen in summer promoted organic matter deposition and hypoxic conditions near the seabed, favoring tolerant taxa such as *Apionsoma (Apionsoma) misakiana* and *Raeta pulchella* (Chang et al., 2004). By contrast, autumn mixing alleviated oxygen stress and supported higher species richness. This seasonal oscillation highlights how benthic communities respond not only to surface productivity cycles but also to physical–biogeochemical interactions regulated by the Kuroshio system (Nakada and Hirose, 2009; Polovina et al., 2006).

The environmental conditions recorded in this study (mean surface temperature of 20 °C and bottom temperature of 13.8 °C) were consistent with values reported near the Kuroshio bifurcation zone. Furthermore, these values were comparable to observations from the East China Sea shelf and southern Japanese waters (Guo et al., 2013; Masuda, 1982; Xu et al., 2022). Seasonal intensification of the TWC, together with freshwater input from the Yangtze River, likely contributed to the relatively low salinity observed in summer (Watanabe, 2007). The warm current influencing the southern Korean coast generally weakens upon entering Korean waters but strengthens again through the Korea Strait, with marked seasonal intensification during summer (Chang et al., 2004; Huh, 1982; Shin et al., 2022). These hydrographic patterns indicate that the southern seas of Korea are strongly influenced by the dynamics of the Kuroshio system. These effects extend northward into the East Sea where interactions with the Liman Current affect ecosystem structure and fisheries resources (Tian et al., 2011; Zhang et al., 2004). Although regression analyses showed low explanatory power ($r^2 < 0.1$), a key contrast emerged: surface water temperature was significantly correlated with benthic parameters ($p < 0.0001$), whereas bottom temperature was not. This disparity highlights the importance of pelagic–benthic coupling, suggesting that benthic communities here are primarily regulated by surface-driven primary productivity and organic matter flux rather than by local bottom temperatures.

Sediment composition in the study area, dominated by sandy silt and silty sand, exhibited seasonal enrichment of organic matter, particularly during summer. These conditions favored deposit feeders, while

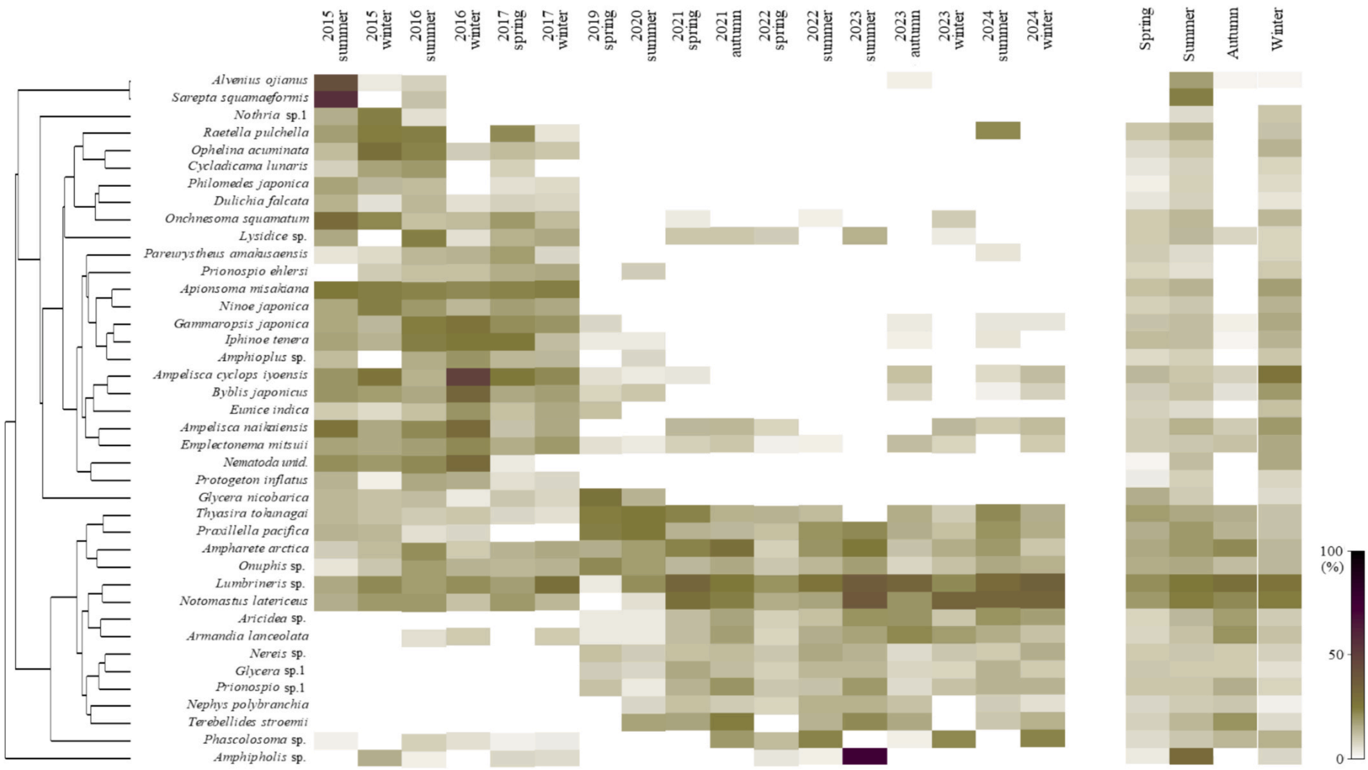

Fig. 6. Heatmap and hierarchical clustering of dominant macrobenthos species in the southern seas of Korea. A color scale legend is added to indicate relative abundance (%).

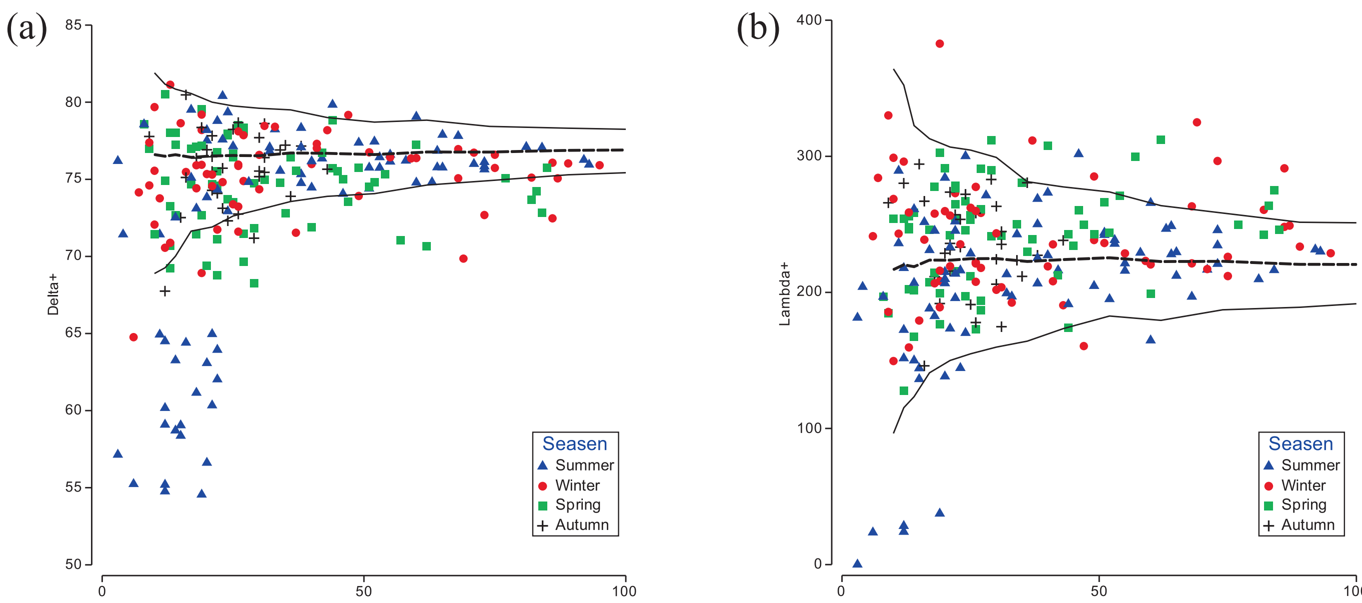

Fig. 7. Funnel plots of species richness versus taxonomic distinctness indices in benthic macrofaunal communities. (a) Average taxonomic distinctness (Delta$^+$) and (b) variation in taxonomic distinctness (Lambda$^+$) plotted against the number of species.

suspension feeders became more abundant in autumn when vertical mixing replenished oxygen and food resources. Predatory taxa such as *Lumbrineris* sp. maintained stable dominance across seasons, demonstrating ecological plasticity under fluctuating conditions (Fauchald and Jumars, 1979; Jumars et al., 2015; Manokaran et al., 2013). The dominance of sandy silt indicates intermediate sediment stability, but resuspension under stronger currents and enhanced organic deposition during stratification likely modulate species composition and trophic structure. Together, these functional responses and sedimentary processes emphasize that benthic community variability cannot be explained by species counts alone. It requires consideration of feeding strategies and habitat dynamics shaped by hydrographic forcing (Shou et al., 2018; Xu et al., 2017).

The benthic responses documented here are consistent with studies in other Kuroshio-influenced regions. In Taiwan, strong intrusions of the Kuroshio onto the shelf restructure benthic assemblages through

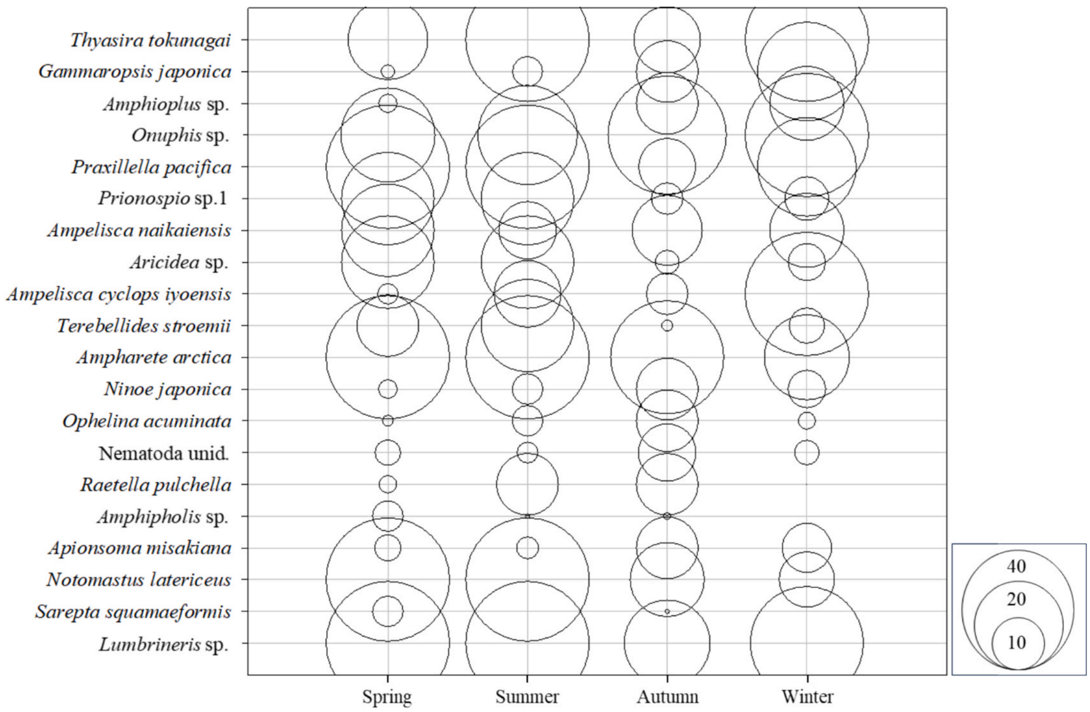

Fig. 8. Seasonal variation in Indicator Value (IndVal) scores of dominant macrobenthos species in the southern seas of Korea.

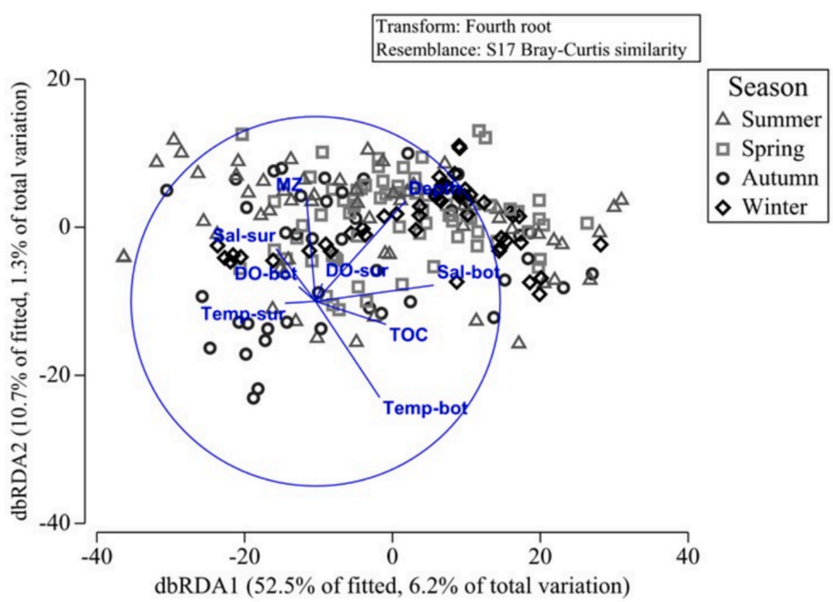

Fig. 9. Distance-based redundancy analysis (db-RDA) biplot of the macrobenthos samples and environmental variables (arrows).

sediment redistribution and nutrient exchanges at the sediment–water interface (Chen et al., 2021; Das et al., 2021; Wei et al., 2016). Similarly, in the East China Sea, gradients of temperature, oxygen, and sediment grain size determined by Kuroshio branches shape macrofaunal and demersal fish communities (Nan et al., 2015; Xu et al., 2019; Zhang et al., 2007). Along southern Japan, Kuroshio-induced internal waves deliver subsurface nitrate to the euphotic zone, stimulating primary productivity and indirectly modifying benthic habitats (Durán Gómez and Nagai, 2022; Guo et al., 2013). These parallels suggest that the processes observed in Korean waters are part of a broader set of Kuroshio-driven mechanisms, while the persistence of dominant species reflects a regionally specific outcome.

Polychaetes were the most dominant taxonomic group, accounting for 35 % of species and 38 % of total abundance, a pattern also observed in other Kuroshio-influenced shelves. Several species, including *Praxillella pacifica*, *Ampelisca naikaiensis*, and *Apionsoma (Apionsoma) misakiana* showed increased abundance in summer, coinciding with elevated bottom temperatures and stratification. Among these, *Apionsoma (Apionsoma) misakiana* and *Raeta pulchella* were consistent indicators of warm, saline conditions and may serve as bioindicators of the TWC influence (Chen et al., 2020; Kurihara et al., 2011; Shou et al., 2018). This dominance is likely linked to the high ecological plasticity of polychaetes, supported by their diverse feeding strategies and tolerance to fluctuating oxygen and organic matter conditions, which enable them

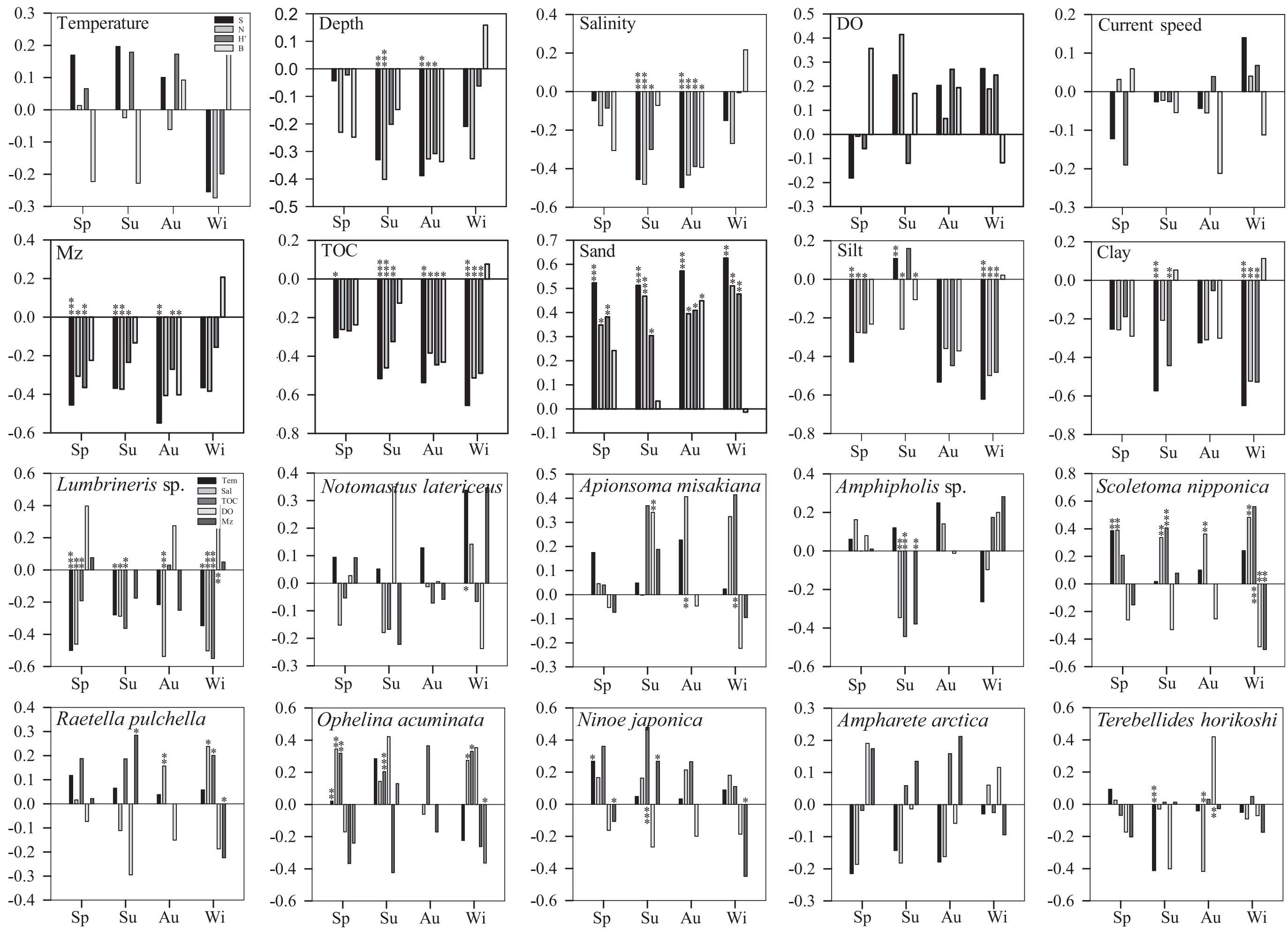

Fig. 10. Seasonal correlation analysis between environmental variables and dominant benthic macrofaunal species in the southern seas of Korea (*p < 0.05, **p < 0.01, *p < 0.001).

to thrive across heterogeneous benthic environments (Fauchald and Jumars, 1979; Jayaraj et al., 2008; Kim and Yu, 2022). Beyond their general ecological plasticity, polychaetes are known to recruit successfully under high current velocity regimes (Pagliosa, 2005) and to tolerate hypoxic and organically enriched conditions (Dauer et al., 1992; Pearson and Rosenberg, 1978). These traits provide mechanistic support for their consistent dominance across diverse and dynamic benthic habitats.

Beyond seasonal variability, our decade-long dataset revealed subtle but consistent increases in warm-water taxa and reductions in cold-water species. These trends suggest biogeographic shifts under ongoing climate warming. These patterns are in line with poleward expansions of warm-water fauna reported in other Kuroshio regions (Gallagher et al., 2009; Xu et al., 2018). Such changes imply that future alterations in the TWC transport and stratification may reshape benthic functional guilds. Specifically, deposit feeders may expand under higher organic loading, while suspension feeders may respond to altered mixing regimes. Ultimately, these trends could transform ecosystem functioning, biodiversity, and trophic interactions in the southern seas of Korea (Shin et al., 2022; Yatsu et al., 2013). Although the observed patterns were consistent with hydrographic conditions shaped by the Kuroshio system, benthic communities are also strongly influenced by local hydrography, sedimentation, and anthropogenic disturbance. These local-scale processes may buffer or modulate the expression of large-scale current signals, suggesting that the influence of the Kuroshio should be interpreted in conjunction with site-specific variability.

The indicator taxa identified in this study also reflect specific ecological traits. For instance, *Lumbrineris* sp. is a carnivorous polychaete capable of inhabiting diverse sediment types, while *Apionsoma misakiana* is a deposit feeder frequently associated with warm and saline conditions. These traits are consistent with their higher abundance during summer stratification, suggesting a mechanistic link between species ecology and the hydrographic patterns observed. It should be noted that although IndVal identified several taxa as significant indicators, no multiple-testing correction was applied. As a result, some associations may represent false positives, and these findings should therefore be interpreted with caution.

This study provides valuable insights into benthic community dynamics under the influence of the Kuroshio Current system, supported by broad spatial coverage. However, several limitations should be noted. The absence of stratification by depth zone, sediment type, or current pathways constrains causal interpretation. This limitation is further compounded by limited temporal resolution and the lack of direct hydrodynamic measurements or modeling of TWC intrusion events, constrain causal interpretation. The benthic community patterns observed here should not be interpreted as direct effects of the TWC, but rather as being consistent with hydrographic conditions shaped by TWC-modified water masses. Some of the observed variability may therefore reflect sampling heterogeneity rather than current-driven effects. Future studies incorporating stratified sampling designs, higher-resolution temporal monitoring, and direct current validation (e.g., ADCP measurements, satellite-derived SST anomalies, or current modeling), combined with experimental and modeling approaches, will be essential. These approaches are necessary to disentangle ecological responses from site-specific variability and to strengthen predictive capacity.

5. Conclusion

This study establishes that benthic macrofaunal communities in the southern seas of Korea are regulated by seasonal hydrographic variability and the broader influence of the Tsushima Warm Current (TWC), a branch of the Kuroshio system. Variations in temperature, dissolved oxygen, and sediment composition exerted a direct influence on species richness, density, and biomass, while functional group responses elucidated mechanistic links between organic enrichment, oxygen availability, and feeding strategies. Furthermore, indicator and correlation analyses identified key taxa, such as *Lumbrineris* sp. and *Apionsoma misakiana*, as bioindicators of TWC-influenced environments. Comparisons with other Kuroshio-affected regions underscore both shared processes and unique regional outcomes, and long-term trends in warm- and cold-water taxa point to ongoing community shifts under climate warming. Collectively, these findings provide critical mechanistic insights into how western boundary currents shape benthic ecosystems and emphasize the need for continued monitoring and integrative approaches to enhance predict capabilities under evolving oceanographic conditions.

CRediT authorship contribution statement

Sang Lyeol Kim: Writing – original draft, Formal analysis, Data curation. **Hyung-Gon Lee:** Investigation, Data curation. **Kyung-Hee Oh:** Investigation. **Kongtae Ra:** Investigation. **Ok Hwan Yu:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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.

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Data availability

Data will be made available on request.

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