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Environmental impact on marginal coastal benthic communities within the Jeju Island, South Korea temperate transition zone

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Aim of study: Marine climatic transition zones are boundary areas of major climate zones, here the boundary between the subtropical and temperate zones. They present areas containing high abundance of organisms living at the limit of their physiological tolerance. These marginal populations are particularly sensitive to changes in their environment. As such, marine climatic transition zones are excellent natural playgrounds for climate change-related hypothesis testing, especially with respect to marine habitat response to ocean warming. The marginal biogenic habitats around Jeju Island, South Korea, which lies within the temperate transition zone, have gradually changed from macroalgal-dominated to hard coral-dominated habitats. Understanding the specific abiotic environmental factors that influence the distribution of the marginal populations in temperate transition zones (i.e., species at their occurrence limit) is crucial to predicting and managing temperate zone habitat changes caused by climate change. This study aims to identify the specific abiotic environmental factors that contribute to explaining the current spatial distribution of the declining temperate and expanding subtropical foundation species in Jeju waters.

Methods: Coverage and composition of sessile benthic communities were determined by photo-quadrat analysis at two depths (10 m and 15 m) at three sites along the island's south, east, and north coasts in May and November 2022. Divergences in community composition between sites were characterized in light of ten quantitative environmental parameters.

Results: Our results show that sessile foundation communities vary significantly at different sites around the island. While the south is defined by high-latitude hard corals, predominately *Alveopora japonica*, the east is defined by the temperate canopy-forming macroalga *Ecklonia cava*, and the north is characterized by coralline algae. Winter sea surface temperature, water transparency, nutrient concentration, and water movement were statistically the most impactful environmental factors determining which foundation species constitute each distinct benthic community.

Conclusion: This study provides valuable baseline information on the impacts of abiotic environmental factors on marine sessile communities in a temperate transition zone.

KEYWORDS

barren grounds, climatic transition area, environmental control, foundation species, high-latitude hard corals, kelp forest, marginal populations, ocean warming

1 Introduction

Marine climatic transition areas are geographically located between two separated climate zones, but they display a combination of characteristics from both. This leads to a high environmental variability that promotes the co-occurrence of different marine communities (Ferro and Morrone, 2014; Shimabukuro et al., 2023). These communities are considered marginal communities, describing the fact that they experience environmental conditions near their physiological limit, which makes them particularly vulnerable to changes in environmental conditions, biotic interactions, and local extinctions (Kawecki, 2008; Wernberg et al., 2016; Agostini et al., 2018; Soares, 2020). Jeju Island, the southernmost region of South Korea (33°23.75' N, 126°33.42' E), is a temperate transition zone, as it is part of the Temperate Northern Pacific ecoregion, but exhibits subtropical characteristics due to the Kuroshio Current, a massive, subtropical current that brings warm, oligotrophic waters to the region (Sakamoto et al., 2005; Spalding et al., 2007; Wu et al., 2012). In fact, Jeju Island lies between two climatic zones with alternating influence depending on the season: the “polar dry” in winter and “tropical/subtropical moist” (due to a short monsoon) in summer (Shimabukuro et al., 2023). Additionally, Jeju Island is frequently affected by typhoons (Park et al., 2006; Lee K.-T. et al., 2023). Over the past half a century, the coastal waters of Jeju, and the Korean mainland in general, have recorded a rise in annual sea surface temperature (SST) by +1.23°C, 2.5 times the global average (Belkin, 2009; Wu et al., 2012; Hobday and Pecl, 2014; Han and Lee, 2020; Tang et al., 2020). Takatsuki et al. (2007) reported an increase in Jeju winter SST by 2.1°C per century from the early 20th century until 2007, while Kim T. et al. (2022) reported a rise in Jeju winter SST of 3.6°C over the last 36 years (compared to just 0.7°C in summer). This trend is associated with an increase in heat wave- and typhoon-frequency and -intensity (Oouchi et al., 2006; Park et al., 2006; Lee S. et al., 2023), highlighting Jeju Island’s significant position as a climate change hotspot (Hobday and Pecl, 2014). All these circumstances lead to a large portion of Jeju’s marine life being highly susceptible to environmental changes, especially benthos with limited mobility and dispersal abilities, such as sessile species.

Although biotic interactions, anthropogenic pressures, and general environmental conditions all determine benthic marine community composition, including species distribution and

diversity dynamics (Sousa, 1984; Hillebrand, 2004; Campbell et al., 2014; Pinsky et al., 2020), water temperature is largely accepted as a primary factor in structuring species distribution (Sunday et al., 2012; Tanaka et al., 2012; Ribas-Deulofeu et al., 2023). Therefore, marine climatic transition zones are expected to undergo severe changes in their biogenic habitats as a consequence of global ocean warming. Changes in marine community composition, detrimental to native temperate species, such as increasing numbers of species with tropical affinities and species of turf-forming algae, have already been observed in high-latitude areas worldwide, for example, in the Atlantic Ocean along the Portuguese continental coast (de Azevedo et al., 2023), the west Pacific Ocean and East China Sea along the Japanese coast (Yamano et al., 2011), and the Indian Ocean along the western Australian coast (Wernberg et al., 2016). This settlement of subtropical and tropical species in temperate ecosystems also raises concerns about the management of marine systems, as it may be too difficult to return to previous states (Hobbs et al., 2006; Bejer et al., 2014; Makino et al., 2014; Pecl et al., 2017). Moreover, prominent changes in foundation species, such as a kelp species, can have cascading consequences for the entire community (Vergés et al., 2014) by altering biotic interactions and modifying the habitat, hence the goods and services the ecosystem provides (Kang, 2010; Pecl et al., 2017; Aguilar et al., 2022). Until the late 1980s, Jeju Island’s benthic ecosystem was dominated by temperate kelp forests, especially the native species *Ecklonia cava* (Kang, 2010). This foundation species plays a critical role for associated organisms, providing shelter, food, and nursery grounds (Steneck et al., 2002; Filbee-Dexter and Wernberg, 2018). The fishing industry in South Korea, especially on Jeju Island, relies heavily on kelp forest habitats to sustain economically valuable species (Kang, 2010, 2011; Hwang et al., 2013). Previous changes in canopy-forming algae coverage have reportedly decreased commercial animal species catches (Serisawa et al., 2004; Kang, 2010). Currently, the *E. cava* population around Jeju Island is declining and being replaced by a variety of species, especially crustose coralline algae (CCA), leading to the formation of a habitat type known as “barren grounds” (Kim, 2006; Kang, 2010). This phenomenon, called “getnoguem” in Korea, is similar to “isoyake” in Japan (Fujita, 2010; Lee et al., 2022). Barren grounds are characterized by large areas of bare rock, extensively covered by CCA, and exhibiting low biodiversity (Serisawa et al., 2004; Kang, 2010; Uribe et al., 2015). Around Jeju Island, barren ground

coverage has increased by nearly 11% over a 5-year period between 1998 and 2003, at which point it was covering 4541 hectares of coastal seafloor (Kim, 2006).

This study aims to investigate the distribution of marine benthic communities in Jeju waters with regard to local environmental conditions. As such, focus was laid on dominant sessile macrofoundation species, such as canopy-forming algae (characterizing kelp forests), coralline and turf-forming algae (characterizing barren grounds), hard corals (characterizing high-latitude coral habitats), soft corals (characterizing soft coral beds), and sponges and bryozoans (characterizing sessile invertebrate macrofauna habitats). To determine how site-specific local stressors and hydrographic parameters may influence marginal marine communities, three sites from different parts of the island were chosen to ensure an extensive range of biotic and abiotic data. At each site, sessile communities at two specific water depths were analyzed to determine potential depth-related changes in species coverage and composition, as depth is directly correlated with light and nutrient availability and, as such, impacts the vertical zonation of many marine benthic species, especially photosynthetic organisms and organisms sensitive to nutrient flux and chlorophyll content, respectively (Kang and Kim, 2012; Muir et al., 2015). This study provides valuable insights into the primary abiotic environmental factors that can structure coastal benthic communities on an annual scale in a marine climatic transition zone.

2 Materials and methods

2.1 Study site

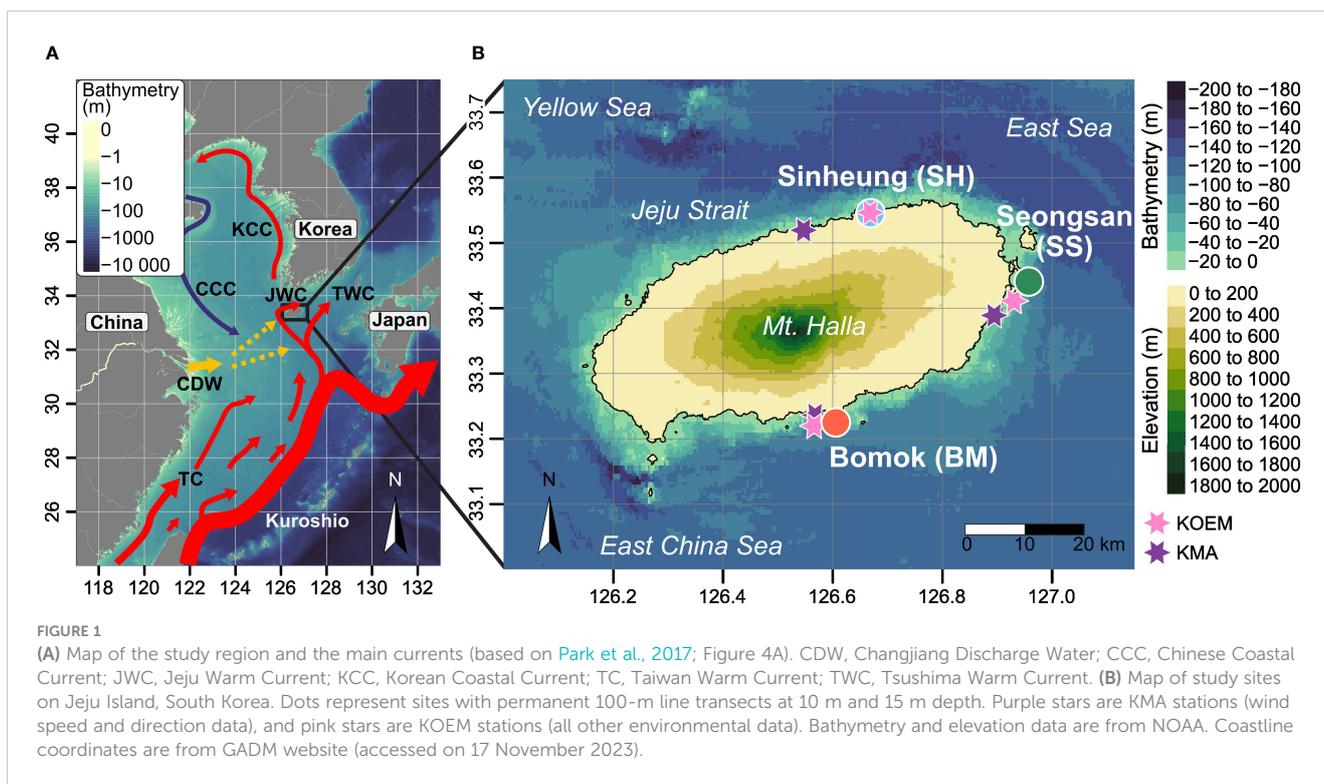
This study was conducted at three sites around Jeju Island: Sinheung (SH) in the northeast (33°33.5173' N, 126°39.1891' E), Seongsan (SS) in the east (33°27.2356' N, 126°56.5033' E), and Bomok (BM) in the south (33°14.2995' N, 126°35.3935' E) (Figure 1B). Globally, Jeju Island is surrounded by the Yellow Sea in the east, the East/Japan Sea in the west, and the East China Sea in the south (Figure 1). Jeju Island's marine environment is strongly influenced by the Kuroshio Current (Figure 1A), which is characterized by high temperature, high salinity, and low dissolved oxygen values (Park, 1986; Choe, 1988). Specifically, the Tsushima Warm Current (TWC; Figure 1A), a warm and saline surface branch of the Kuroshio Current, which originates at 31°N and flows northward reaching the southern coast of Jeju Island, has a strong influence during summer (Lie et al., 1998; Hur et al., 1999; Cha and Moon, 2020). The majority of the TWC passes southeast of the island, flowing eastward up to the Tsushima Strait, while a minor branch flows westward and turns clockwise in the Jeju Strait as Jeju Warm Current (Teague et al., 2003; Cha and Moon, 2020) (Figure 1A). However, coastal circulation is primarily driven by tidal currents, particularly in the Jeju Strait, north of the island (Cha and Moon, 2020). These regional impacts are measurable, leading to distinct environmental conditions between the north and the south of the island, with a conspicuous thermal north/south gradient expressed by average annual water temperatures of $18.8 \pm 4.5^\circ\text{C}$ and

$20.0 \pm 4.6^\circ\text{C}$, respectively (average SST from 2004 to 2022; Korea Marine Environment Management Corporation, <http://data.kma.go.kr/>, accessed on 08 March 2023). Despite these local differences, environmental conditions present a strong seasonality. In winter, the coastal waters are mainly influenced by strong and cold Siberian winds, cooling down the water column (Hur et al., 1999). In summer, the fresh discharge of the China-based Changjiang River combined with the summer monsoon accentuates the stratification of Jeju waters by reducing sea surface salinity (Park, 1986; Hur et al., 1999) (Figure 1A). Despite the natural differences in water mass-driven conditions, each site is, in varying degrees, affected by locality-specific anthropogenic stressors. The northern SH site is located within proximity of three fish farms (distance of 890 m to 1331 m), while the eastern SS site is far from any obvious artificial effluents. The southern BM site is just 350 m from a sewage treatment plant.

2.2 Environmental variables

All abiotic environmental variables applied in this study were extracted from publicly available websites. Hydrographic variables are available from the Korea Marine Environment Management Corporation website (KOEM, n.d.), while meteorological variables are available from the website of the Korean Meteorological Administration (KMA, n.d.). Data from 2004 (beginning of systematic record at the sites) to 2022 were used. Hydrographic variables (KOEM data) were collected quarterly (i.e., February, May, August, November; one data point each) by boat survey from coastal surface waters at each site (1.5–2.5 km from the coastline) (Figure 1B). KOEM parameters were measured using a CTD-rosette sampler followed by laboratory analyses (Korea Marine Environment Management Corporation, 2019). KMA variables were recorded hourly at each site from ground atmospheric observatories (Synopsis Weather Observations - ASOS program). Consequently, for meteorological variables, the monthly average for February, May, August, and November, respectively, was computed to also gain one data point for each month. Recording locations closest to the coordinates of our respective sampling site were chosen (indicated by stars on the map; max. distance to study site: 10 km; Figure 1B).

A total of 10 variables were chosen for statistical analyses, 9 hydrographic variables and 1 meteorological variable: Chlorophyll *a* (Chl*a*; $\mu\text{g L}^{-1}$), Dissolved Inorganic Nitrogen (DIN; $\mu\text{g L}^{-1}$), Dissolved Inorganic Phosphate (DIP; $\mu\text{g L}^{-1}$), Dissolved Oxygen (DO; mg L^{-1}), pH, Salinity (PSU), Suspended Organic Matter (SOM; mg L^{-1}), Sea Surface Temperature (SST; $^\circ\text{C}$), Transparency (m) (from KOEM); and Wind Speed (WS; m s^{-1}) (from KMA). An additional 4 variables were considered for discussion purposes: Nitrite (NO_2^- ; $\mu\text{g L}^{-1}$), Nitrate (NO_3^- ; $\mu\text{g L}^{-1}$), Ammonia (NH_4^+ ; $\mu\text{g L}^{-1}$) (from KOEM); and Wind Direction (WD; degrees) (from KMA). Nutrient concentration-related variables (DIN, DIP, NO_2^- , NO_3^- , NH_4^+) were converted to $\mu\text{mol L}^{-1}$ based on the corresponding molar masses to facilitate comparisons to the literature. Wind speed and direction were used as proxies for water movement and surface currents (Charlier, 2005; Skirving et al., 2006).



2.3 Benthic community

Two surveys were carried out by scuba diving in May and November 2022, respectively. These months were chosen to avoid extreme summer and winter environmental values, in order to reduce seasonal variations in the data set and obtain a representative picture of benthic communities by site. Indeed, May and November show temperatures close to the annual average (Supplementary Table 1), and this study focuses on dominant foundation macro-species at each site, all of which have a perennial life cycle and an overall annual stable coverage (Haroun et al., 1989; Vieira et al., 2016). At each site, permanent 100-m line transects were installed at 10 m and 15 m depth, respectively, parallel to the coastline following each isobath. The 10 m and 15 m depths were chosen according to the vertical distribution of dominant benthic species around Jeju Island (Supplementary Table 2) and to avoid intertidal and sand bottom zones, respectively. The transects were installed in a “zigzag” fashion to cover a wider area (Supplementary Figure 1). Along the transects, 100 photos (1 x 1 m) were taken at each site and depth using an underwater camera (Sony ILCE-7RM3A with underwater housing; maximum resolution of 7952 x 5304 pixels). The “zigzag”-scheme ensures that the one photo taken at every meter of the respective permanent transect does not overlap with the next. The camera was mounted on a tetrapod quadrat to maintain a constant distance from the substrate and ensure comparable pictures. At the SH-10m site, data are missing for the November 2022 survey because typhoon Hinnamnor destroyed the permanent line transect at that depth in September 2022.

Dark, blurred, and poorly framed images were excluded from the photo stack ($n = 12$ in May, and $n = 8$ in November). From the

remaining photos, 30 images (i.e., replicates) were randomly selected using the “base::sample” function in R from each “site-depth-month” group (e.g., BM-10m-May; hereafter called “group”) for image annotation. The PhotoQuad® software (version 1.4; Trygonis and Sini, 2012) was used to identify and quantify benthic organisms and bare substrate in each group following our benthic community categories (Supplementary Table 3). The relative percentage cover of the benthic community in each photo-quadrat was estimated using the software’s stratified random points count tool (Figure 2). On each image, a point was randomly placed on each of the 100 grid cells (i.e., 100 points), and the underlying benthic organism and substrate type (i.e., sand, gravel and rock) was identified to the lowest possible taxonomic level (Supplementary Table 3; except for coralline and turf algae) based on visual information, such as texture, color, and shape. Taxonomic identification was mainly based on fieldwork taxonomic books of Jeju and Japanese coasts (Masuda et al., 1986; Sugihara et al., 2014; Kim M.-S. et al., 2022). Indeterminate annotations and motile benthic organisms, such as asteroids and other echinoderms, polychaetes, holothurians, bivalves, and gastropods were removed before statistical analyses. Sand, gravel, and rock annotations were grouped in the “Substrate” category, which was included in the analysis as the only non-biological component because of its essential role in habitat characterization. Based on the overall species percentage distribution in our data set, a species or non-biological component was described as “major” when its coverage was greater than 2.5% in a group. “Dominance” was defined as a coverage over 25% by a single species or category in a group (e.g., BM-10m-May), following Reimer et al. (2021). All remaining species (cover < 2.5%) were merged into the “Other” category. Coverages were reduced to 100% at the group level. As the dense

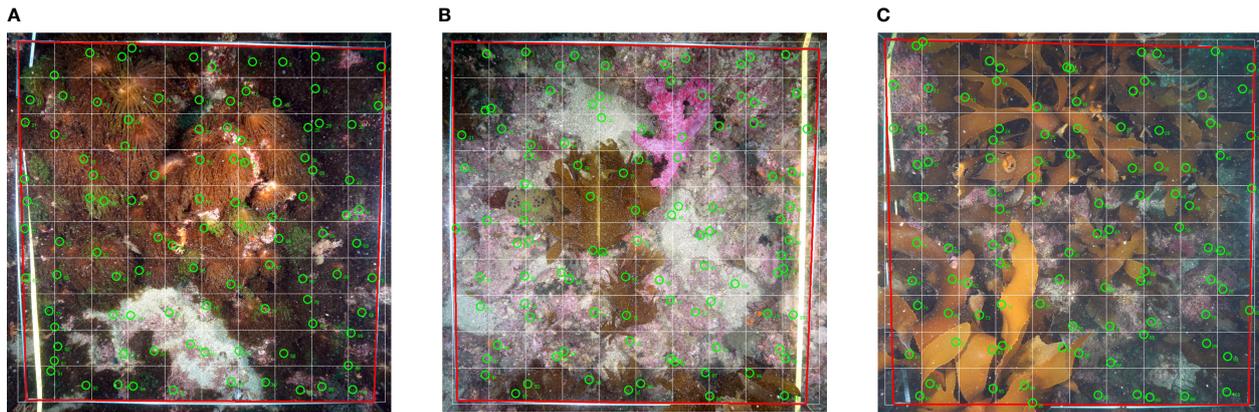


FIGURE 2

Examples of photo-quadrat annotations on PhotoQuad® of (A) Bomok site at 15 m, (B) Sinheung site at 15 m, and (C) Seongsan site at 15 m, in May. The stratified random points count method (100 points per image) was used to assess the relative percentage cover (%) of benthic communities.

kelp cover obstructs the vision of underlying species, this photo-quadrat method cannot be used to study species-specific coverages and biodiversity in the presence of canopy-forming algae, and percentage cover data have been interpreted cautiously. All species categories used to classify benthic communities in the image annotations are listed in [Supplementary Table 3](#).

2.4 Statistical analyses

All statistical analyses were performed using R (version 4.3.0).

2.4.1 Environmental variables

Statistical analyses were carried out for each month independently (i.e., February, May, August, and November, corresponding to four time series of 18 points each) to eliminate seasonal variability in the results. Each monthly time series was then detrended using linear regression to remove the inter-annual trend, thus obtaining each site's "average" environmental conditions and avoiding masking spatial variability. The median of each monthly time series was summed with the regression's residuals ([Supplementary Figure 2](#)). The resulting data (hereafter called "environmental data") were used in further statistical analyses.

A Principal Component Analysis (PCA) was performed on the ten standardized abiotic variables selected to assess spatial divergences in environmental conditions. The PCA distance biplot (i.e., scaling 1) was used to visualize the most impactful environmental variables contributing to the spatial data ordination. Furthermore, to test the effect of space (i.e., site) and time (i.e., year) on environmental conditions, a non-parametric Multivariate Analysis of Variance (PERMANOVA; `vegan::adonis2`) was carried out ([Anderson, 2001](#)). A Kruskal-Wallis test (KW) was performed on each variable to specifically determine which environmental parameters vary according to the factor "site" ([Kruskal and Wallis, 1952](#)). When the test was significant, a Dunn's post-hoc test with a

Bonferroni correction for multiple comparisons was performed ([Dunn, 1964](#)).

2.4.2 Benthic community

Multivariate analyses were conducted at the species level. The percentage cover matrix of the benthic community was transformed using Hellinger's method to reduce the weight of rare and absent species ([Legendre and Gallagher, 2001](#)).

To investigate which spatiotemporal factor (i.e., "site", "depth", and "month") statistically influences benthic communities the most, partial Redundancy Analysis (pRDA) was carried out ([Legendre and Legendre, 2012](#)). The pRDA searches for the variability in the community matrix explained by a single, main explanatory factor (i.e., the constraining factor) by removing the variability induced by additional explanatory variables (i.e., the conditioning factors). In this study, the factors "site" (i.e., BM, SH, SS), "month" (i.e., May, November), and "depth" (i.e., 10 m, 15 m) were each, in turn, considered as the main explanatory factor, resulting in three pRDA models. The RDA_x axes indicate the proportion of variation explained by the pRDA model, while PC_x axes indicate the proportion of variation in the residuals (which is not explained by any model). After each pRDA, a permutation test ($n_{\text{perm}} = 999$) was used to test for the analysis' significance and each RDA axis' significance. In addition, the effect of each spatiotemporal factor without interaction (i.e., "site", "depth", and "month", respectively) on the percentage cover of the benthic community was tested using PERMANOVA. The test was performed using the Hellinger distances of the percentage cover matrix, with 9999 permutations. For the factor "site", as it contains three levels, as soon as a significant difference between benthic communities was detected, a post-hoc, pairwise PERMANOVA test (`pairwiseAdonis::pairwise.adonis`) with Bonferroni significance correction was conducted to identify which site was responsible for the difference. The role of biotic interactions in shaping benthic communities was excluded from the scope of this paper.

TABLE 1 (A) PERMANOVA test results from Euclidean distance matrix of the 10 standardized environmental data. (B) Pairwise PERMANOVA test results for the factor "site".

| (A) | Month | Factors | R ² | F Statistics | P-value |
|----------|----------|-----------|----------------|--------------|------------------|
| | February | Site | 0.140 | 11.536 | 0.0001 |
| | | Year | 0.641 | 5.869 | 0.0001 |
| | May | Site | 0.073 | 5.614 | 0.0001 |
| | | Year | 0.692 | 5.904 | 0.0001 |
| | August | Site | 0.078 | 6.209 | 0.0001 |
| | | Year | 0.697 | 6.188 | 0.0001 |
| | November | Site | 0.214 | 17.320 | 0.0001 |
| | | Year | 0.564 | 5.073 | 0.0001 |
| (B) | Month | Pairs | R ² | F Statistics | Adjusted P-value |
| February | | BM vs. SS | 0.105 | 4.214 | 0.0003 |
| | | BM vs. SH | 0.175 | 7.647 | 0.0003 |
| | | SH vs. SS | 0.039 | 1.471 | 0.478 |
| May | | BM vs. SS | 0.059 | 2.260 | 0.047 |
| | | BM vs. SH | 0.075 | 2.928 | 0.002 |
| | | SH vs. SS | 0.032 | 1.207 | 0.830 |
| August | | BM vs. SS | 0.077 | 2.994 | 0.014 |
| | | BM vs. SH | 0.065 | 2.494 | 0.034 |
| | | SH vs. SS | 0.034 | 1.265 | 0.762 |
| November | | BM vs. SS | 0.136 | 5.648 | 0.0003 |
| | | BM vs. SH | 0.263 | 12.868 | 0.0003 |
| | | SH vs. SS | 0.072 | 2.802 | 0.024 |

Factor "site": Bomok (BM), Sinheung (SH), Seongsan (SS); factor "year": from 2004 to 2022. The P-values were adjusted using Bonferroni correction for multiple comparisons. Significant P-values ($P \leq 0.05$) are highlighted in boldface type.

3 Results

3.1 Environmental variables

To determine and illustrate the weight of each abiotic variable in setting the environmental conditions around Jeju Island, PERMANOVA, KW tests, and PCA were applied. Environmental variables clearly clustered according to sites, with distinct seasonal differences, largest between November and February (Table 1A; Figure 3). In November, clustering appeared along the primary PCA axis only, while in February, clustering appeared along primary (PC1: 20.9% of the variance) and secondary (PC2: 17.4% of the variance) axes, representing 38.3% of the total February variance (Figures 3A, D). The first principal component in the November graph (PC1: 29.4% of variance) was related to salinity, SST, transparency, DIN, DIP, and WS. In the February graph, the first principal component was related to SST and DIP, and the second principal component was related to WS and transparency. The driving environmental variables of the site variability, therefore, are

season-dependent, consisting of temperature (SST), phosphorus levels (DIP), WS, and transparency in February, and salinity, SST, phosphorus and nitrogen levels (DIP and DIN), transparency, and WS in November. Although no distinct site-specific clustering was discernible in May and August in the PCA, the PERMANOVA, KW, and Dunn tests indicated significant differences (Figures 3B, C, 4; Table 1): in August, DO was lower at SH (mean \pm SD = 7.3 ± 0.7 mg L⁻¹) than at BM (7.6 ± 0.6 mg L⁻¹) and SS (7.7 ± 0.7 mg L⁻¹), while in May, the DIN concentration was lower at SS (median = 0.7 μ M) than at BM (1.1 μ M) and SH (1.0 μ M) (Supplementary Table 1). WS was always significantly lower at BM, especially in November and February (Figure 4E). The wind directions also differed between sites and months (Supplementary Figure 3). In February and November, strong north-westerly winds dominated at SS and SH (February mean \pm SD = 3.5 ± 0.1 m s⁻¹ and 3.7 ± 0.1 m s⁻¹, respectively), with maximal gusts of up to 4.2 m s⁻¹ and 4.3 m s⁻¹, respectively (Supplementary Figures 3B, C). In contrast, BM was subject to light winds, mainly from the north (max. 3.2 m s⁻¹; mean \pm SD = 2.4 ± 0.1 m s⁻¹) (Supplementary Figure 3A). In May and August, the wind regime shifted. BM experienced winds from the southwest and the northeast, while wind directions at SS and SH were similar and highly variable (Supplementary Figure 3).

Regardless of season (i.e., months), BM was consistently distinct from SS and SH (Table 1B). Specifically, November and February DIN and DIP concentrations were significantly lower at BM (November mean \pm SD = 1.2 ± 0.8 μ M and 0.07 ± 0.06 μ M, respectively) than at SH (November mean \pm SD = 1.8 ± 0.9 μ M and 0.09 ± 0.05 μ M, respectively) (see also Figure 4 and Supplementary Table 1). November and February transparency and SST were significantly higher at BM (November mean \pm SD = 12.6 ± 2.7 m and $21.5 \pm 1.7^\circ$ C, respectively) than at SS (November mean \pm SD = 10.4 ± 2.2 m and $20.5 \pm 1.2^\circ$ C, respectively) and SH (November mean \pm SD = 8.8 ± 1.5 m and $19.5 \pm 1.3^\circ$ C, respectively). In contrast, SS and SH exhibited generally similar environmental conditions (Table 1B). However, although no statistically significant trend in nutrient concentration-related measurements (i.e., DIP, DIN, NO₂⁻, NO₃⁻, and NH₄⁺) could be established, it is noteworthy that the mean November concentrations were consistently highest at SH (Supplementary Table 1).

3.2 Benthic community

Forty-six benthic taxa and one non-biological component were identified, 16 of which were considered major (percentage cover > 2.5%) (Supplementary Tables 3, 4). All three sites were dominated (percentage cover > 25%) by a single species or category (Figure 5). Generally, the wide range of species coverage percentages (Supplementary Table 5) combined with very high standard deviations (when compared to the mean percentage cover of each species by group; Supplementary Table 4) mirror a patchy distribution of benthic species. Sixteen species were present at all three sites in variable percentages, including coralline algae, turf-forming algae, and the encrusting rhodophytes *Peyssonnelia* sp. and *Hildenbrandia* sp. that had high coverages at all three sites (Supplementary Tables 4, 6). However, regardless of depth and

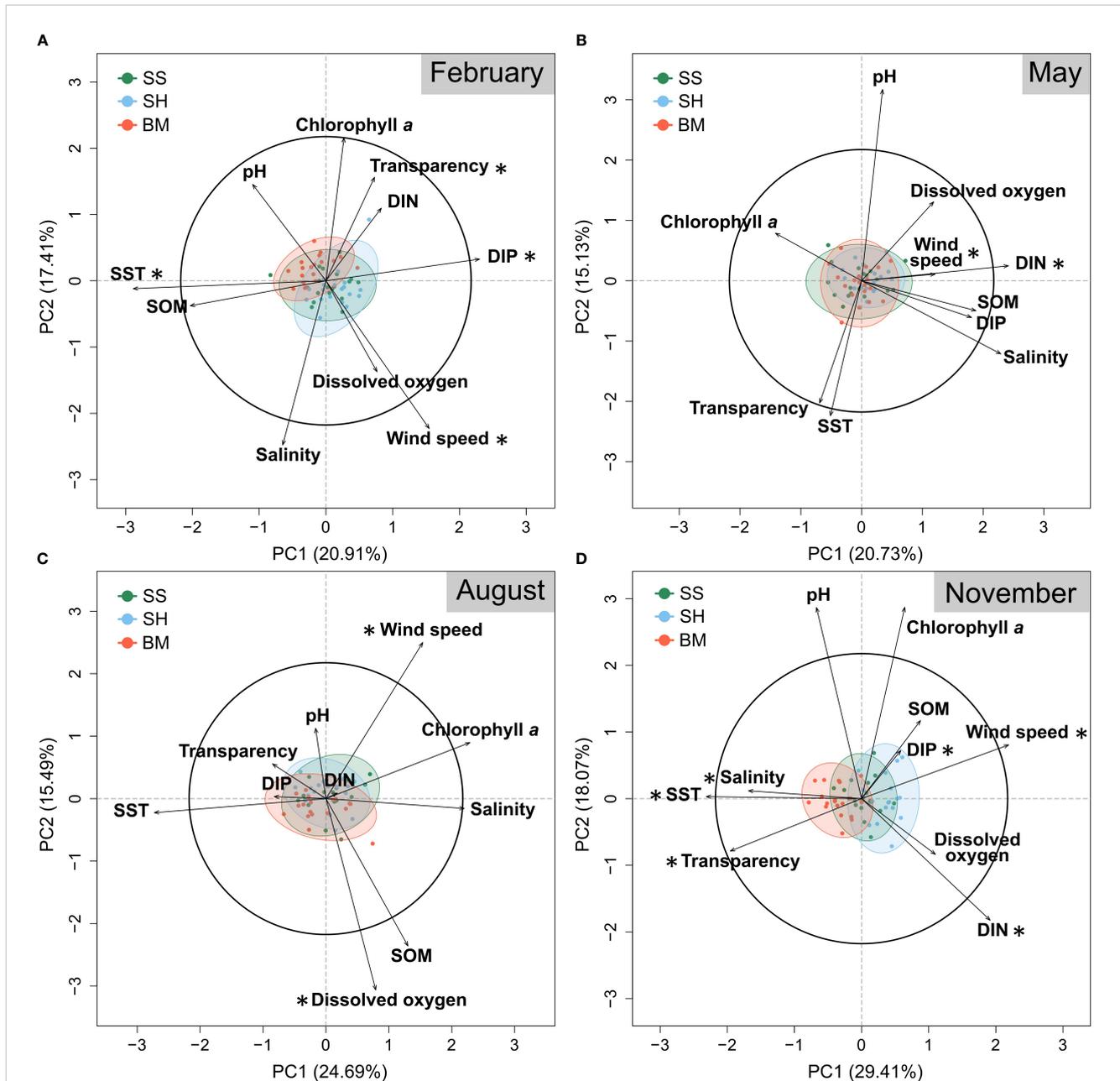


FIGURE 3

Principal Coordinate Analysis (PCA) biplot – scaling 1 – of the standardized environmental data from 2004 to 2022 of (A) February, (B) May, (C) August, and (D) November. Each dot represents a year. Red: Bomok (BM); Blue: Sinheung (SH); and Green: Seongsan (SS). The ellipses are the square-root chi-squared density distributions of objects with quantile = 0.95. The black asterisks indicate significantly different variables according to sites using the non-parametric Kruskal-Wallis test. The black circle is the equilibrium circle of descriptors. DIN, Dissolved Inorganic Nitrogen; DIP, Dissolved Inorganic Phosphate; SOM, Suspended Organic Matter; SST, Surface Seawater Temperature.

season, coralline algae species strongly dominated at SH, with CCA showing coverages between 7.5% and 62.0% per image and geniculate coralline algae between 0% and 51.0%. At SS and BM, respectively, CCA coverage ranges of 0–48.3% and 4.0–57.0%, and geniculate coralline algae coverage ranges of 0–35.4% and 0–42.9% were recorded (Supplementary Table 5). Interestingly, SH had the lowest coverage of bare substrate (mean \pm SD = 2.5 \pm 3.5%) compared to SS and BM (5.6 \pm 8.5% and 5.3 \pm 7.6%, respectively). SH also showed highest coverage percentages in recorded bryozoans (max. 6.5%) and sponges (max. 12.5%), as

well as sponge diversity (7 species) (Supplementary Tables 4, 5). At BM, only 4 Porifera species (max. 1.1%), and at SS, only 3 Porifera species (max. 6.7%) were recorded (Supplementary Tables 4, 5). Additionally, highest diversity in soft and fire corals was recorded from SH, including one species of sea anemone (*Heteractis* sp., max. 2.2%), one species of thick-polyp-bearing soft coral (*Dendronephthya gigantea*, max. 36.1%), and two species of fire corals (*Solanderia* sp., max. 1.1%; *Aglaophenia pluma*, max. 6.7%) (Supplementary Table 5). At SS, although environmentally most similar to SH, no soft corals were recorded. At BM, two species of

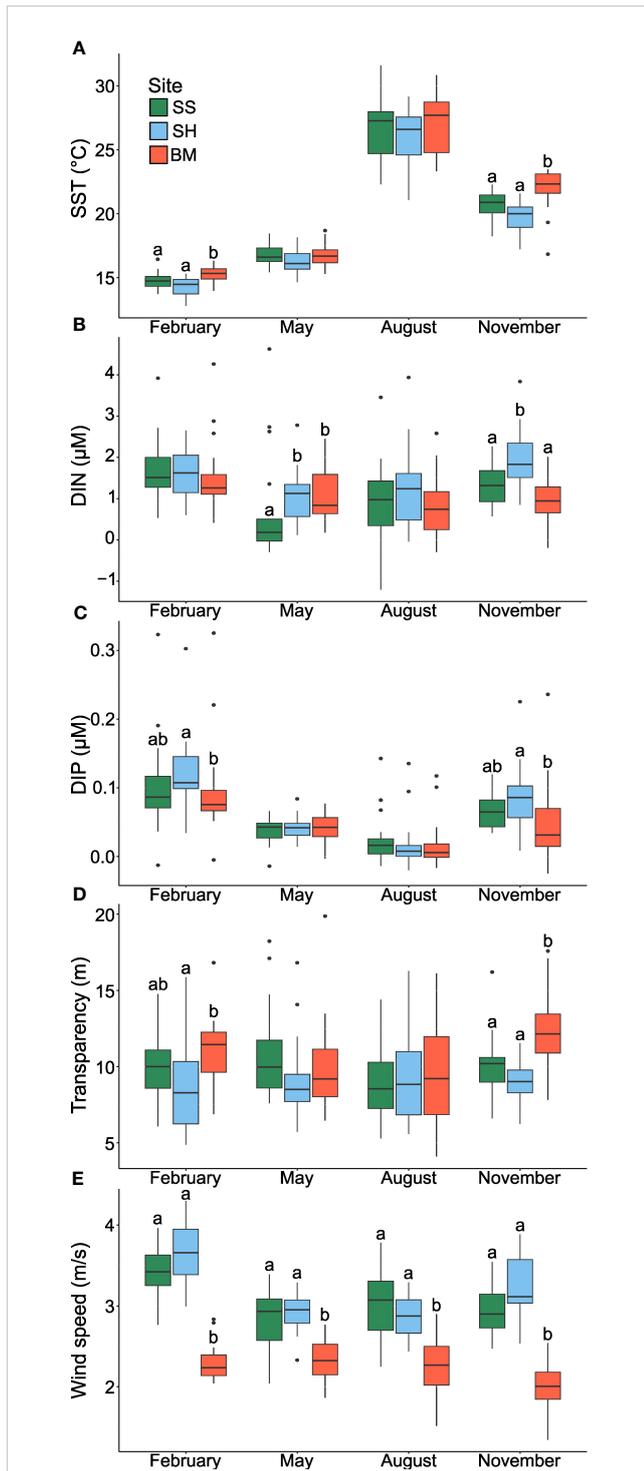


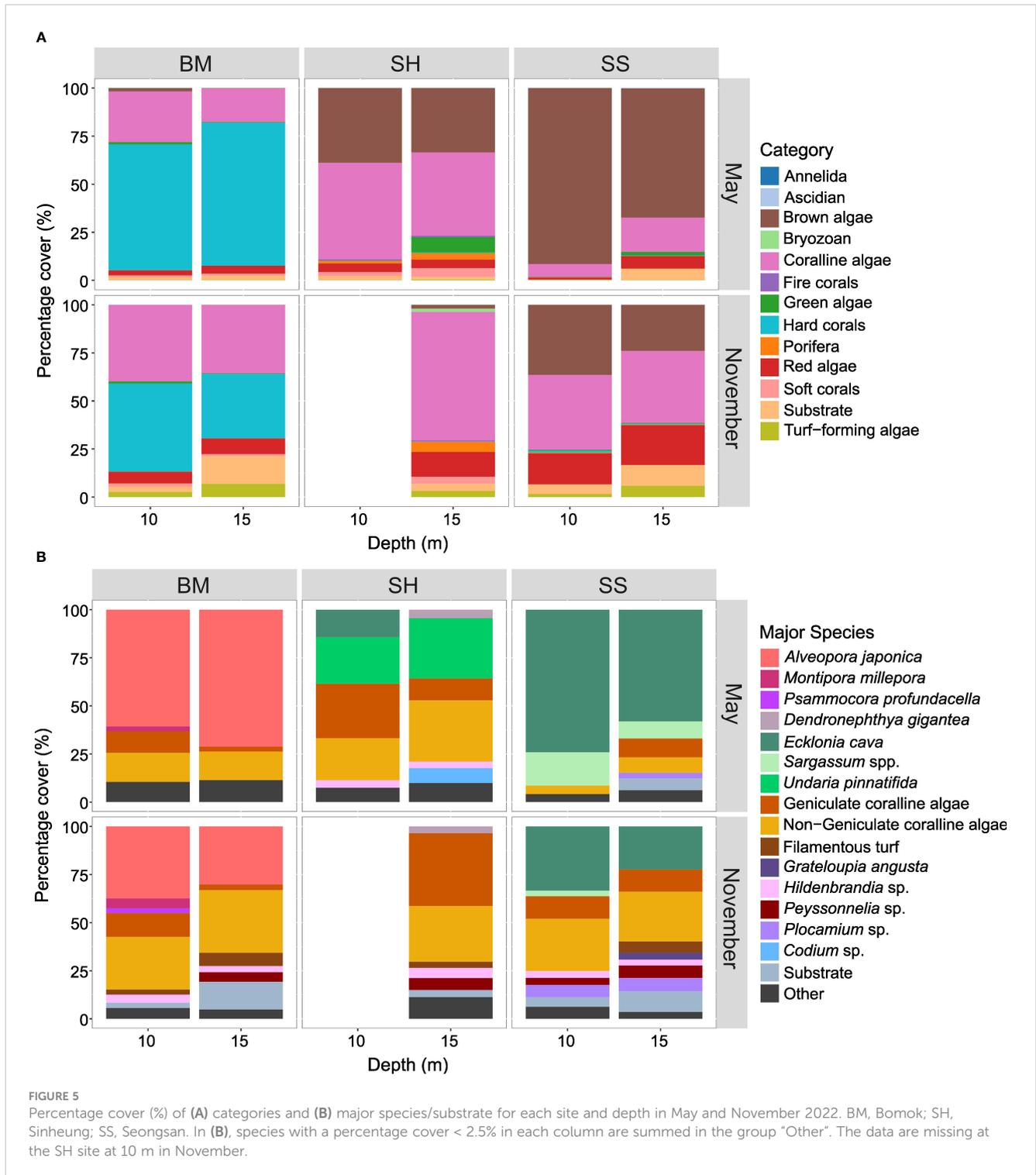
FIGURE 4
Boxplots by month and site of (A) Surface Seawater Temperature (SST, °C), (B) Dissolved Inorganic Nitrogen (DIN; μM), (C) Dissolved Inorganic Phosphate (DIP; μM), (D) transparency (m), and (E) wind speed (ms⁻¹). Red: Bomok (BM); Blue: Sinheung (SH); and Green: Seongsan (SS). Letters indicate the results of the non-parametric pairwise Dunn test in cases where the Kruskal-Wallis test was significant.

sea anemone were recorded (*Entacmaea* sp., max. 10.3%; *Heteractis* sp., max. 4.1%) (Supplementary Table 5). Scleractinian hard corals were present at all three sites, although the highest diversity (4 species) and, by large, the highest coverage percentage (sum by site

= 54.7 ± 25.1%) were recorded from BM, followed by SS (3 species; sum by site = 0.5 ± 1.9%), and SH (2 species; sum by site = 0.06 ± 0.5%) (Supplementary Table 4). At BM at both depths, *Alveopora japonica* dominated by over 60% in May and 30% in November (Figure 5B; Supplementary Table 4). Recently, it has been suggested that there are three cryptic species of *Alveopora japonica* corresponding to their Japanese, Korean and Taiwanese distributions respectively (Kang et al., 2020). At SS at both depths, canopy-forming brown algae (*Ecklonia cava* and *Sargassum* spp.) dominated by over 65% in May and 23% in November. At SH at both depths, coralline algae (geniculate coralline algae and CCA) dominated by over 40% in May and 66% in November (only 15 m depth data available). These differences in dominance are highlighted by multivariate analyses, showing a clear difference in benthic percentage cover between sites (Figure 6A; Tables 2, 3).

The pRDA results showed that the greatest proportion of variance in the benthic community cover was explained by the factor “site” (50.3%), followed by “month” (8.0%) and “depth” (1.3%), while 40.0% of the variance remained unexplained by these factors (Figure 6; Table 2). All three pRDA models were significant (Table 2; p-value = 0.001). However, the variability explained by the pRDA model (RDA axis) was far greater than that of the residuals (PC axis) for “site” only, where the first two canonical axes were significant (Table 2A; RDA1 = 39.6%, RDA2 = 16.1%). The inter-site variability observed in the benthic community was explained primarily by the species *E. cava*, *Plocamium* sp., and *Sargassum* spp. (i.e., macroalgae species) which were representative of SS, opposed on the first axis to *A. japonica* (i.e., scleractinian hard coral) representing BM. *Undaria pinnatifida*, coralline algae, and *D. gigantea* (i.e., macroalgae and soft coral species, respectively) represented SH on the second axis (Figure 6A). The PERMANOVA test showed an F-statistic and R² of more than two times higher for sites than for months and depths, although all three factors significantly influenced the benthic community (Table 3A). The benthic communities of BM and SS were the most distinct, followed by BM and SH, then SH and SS (Table 3B; Figure 6A).

The benthic compositions of BM and SS exhibited differences between May and November (Figure 5; Table 3), mainly characterized by a decrease in the percentage cover of the dominant taxa (i.e., *E. cava* and *A. japonica*), an increase in coralline algae, and the emergence of filamentous turf, *Hildenbrandia* sp. and *Peyssonnelia* sp. as major species. At SS, the rhodophytic macroalgae *Grateloupia angusta* and *Plocamium* sp. had higher coverages in November. At SH, the canopy-forming algae *E. cava* and *U. pinnatifida* and the chlorophyte *Codium* sp. were present at non-negligible coverages only in May (mean ± SD between depths = 8.2 ± 12.8%, 27.8 ± 21.4%, and 3.9 ± 6.4%, respectively) (Figure 5B; Supplementary Table 4). At all three sites, the coverage of substrate was constantly higher in November than in May. These observations are supported by the pRDA “month” model (RDA1 = 16.7%; Figure 6B), where *A. japonica*, *E. cava*, *U. pinnatifida*, and *Sargassum* spp. were indicative of May, while substrate, coralline and turf algae, *Hildenbrandia* sp., *Plocamium* sp., and *Peyssonnelia* sp. were linked to November. Note that SH data from November at 10 m depth are missing.



There were slight differences in benthic percentage cover between depths (Figures 5, 6C; Table 3). Indeed, the variation explained by the factor "depth" was five times lower than the proportion of variance in the residuals ($PC1 = 17.9\%$; $RDA1 = 3.1\%$). Regardless of months and sites, only macroalgae species and substrate were responsible for the variability observed across depths. For instance, *U. pinnatifida*, *Sargassum* spp., *E. cava*, and geniculate coralline algae were representative of the 10 m depth,

while *Plocamium* sp., *Peyssonnelia* sp., *Codium* sp., filamentous turf and CCA converged to 15 m depth (Figure 6C). Specifically, at BM, at 10 m, geniculate coralline algae, hard coral species *Montipora millepora* and *Psammocora albopicta*, sea anemone *Entacmeae* sp., and chlorophyte species *Cladophora wrightiana* had higher coverage than at 15 m, contrary to rhodophyte *Peyssonnelia* sp. and sea anemone *Heteractis* sp. (Supplementary Table 4). At SS, the coverages of canopy-forming brown algae were

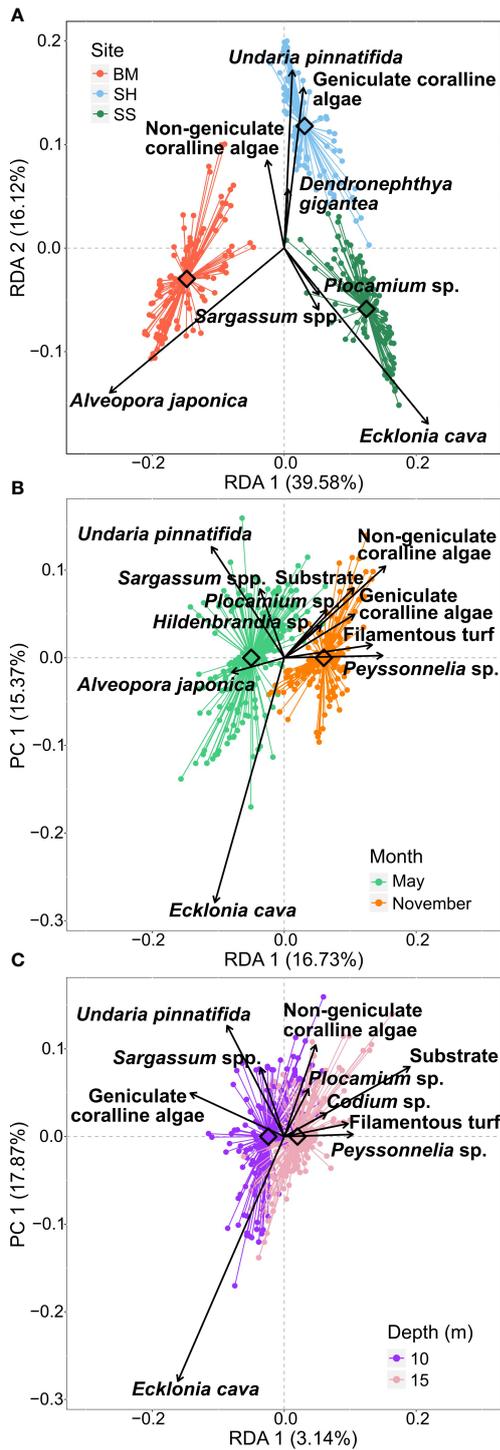


FIGURE 6
 Partial Redundancy Analysis (pRDA) of Hellinger transformed percentage cover data. The constraining factor is (A) "site", (B) "month", and (C) "depth". For each graphic, the influence of the two other factors was removed (conditioning factors). The diamond is the centroid of each group. Each dot represents a photo-quadrat. In (A) – Red: Bomok (BM); Blue: Sinheung (SH); and Green: Seongsan (SS). In (B) – Light green: May 2022; and Orange: November 2022. In (C) – Purple: 10 m depth; and Pink: 15 m depth. Table 2 reports the pRDA models' details and the permutation test results.

TABLE 2 Complementary pRDA results of Figure 6.

| (A) | Model result | Inertia | Proportion (%) |
|---------------------|---------------|--------------|----------------|
| Figure 6A ("site") | Total | 0.497 | 1.000 |
| | Conditioned | 0.048 | 0.097 |
| | Constrained | 0.250 | 0.503 |
| | Unconstrained | 0.199 | 0.400 |
| Permutation test | | F Statistics | P-value |
| Figure 6A ("site") | RDA Model | 204.31 | 0.001 |
| | RDA 1 | 290.36 | 0.001 |
| | RDA 2 | 118.26 | 0.001 |
| (B) | Model result | Inertia | Proportion (%) |
| Figure 6B ("month") | Total | 0.497 | 1.000 |
| | Conditioned | 0.258 | 0.519 |
| | Constrained | 0.039 | 0.080 |
| | Unconstrained | 0.199 | 0.400 |
| Permutation test | | F Statistics | P-value |
| Figure 6B ("month") | RDA Model | 65.319 | 0.001 |
| | | | |
| (C) | Model result | Inertia | Proportion (%) |
| Figure 6C ("depth") | Total | 0.497 | 1.000 |
| | Conditioned | 0.292 | 0.587 |
| | Constrained | 0.006 | 0.013 |
| | Unconstrained | 0.199 | 0.400 |
| Permutation test | | F Statistics | P-value |
| Figure 6C ("depth") | RDA Model | 10.533 | 0.001 |
| | | | |

The constraining factor is (A) "site" (i.e., Bomok, Sinheung, Seongsan), (B) "month" (i.e., May, November), and (C) "depth" (i.e., 10 m, 15 m). The influence of the two other factors was removed (conditioning factors). The first table is the pRDA model result. The second table is the result of the permutation test to test the significance of the pRDA model and each RDA axis. Significant P-values ($P \leq 0.05$) are highlighted in boldface type.

higher at 10 m than at 15 m, contrary to the trends recorded for rhodophytes *G. angusta*, *Peyssonnelia* sp., and *Plocamium* sp., as well as the substrate category. At SH, the soft coral *D. gigantea*, CCA, Porifera, turf-forming algae, and rhodophytes *Peyssonnelia* sp. and *G. angusta* were more abundant at 15 m depth, contrary to kelp species *E. cava*.

4 Discussion

This study quantified abiotic environmental variations at three sites around Jeju Island and investigated accompanying community dynamics of sessile benthos. Hard corals dominated in the TWC-influenced, low-energy (i.e., less windy), southern BM; canopy-forming brown algae dominated in less TWC-influenced, high-

TABLE 3 (A) PERMANOVA test results from Euclidean distance matrix of Hellinger transformed percentage cover data of all species. (B) Pairwise PERMANOVA test results for the factor "site".

| (A) | Factors | R ² | F Statistics | P-value |
|-----|-----------|----------------|--------------|------------------|
| | Site | 0.500 | 203.280 | 0.0001 |
| | Month | 0.086 | 70.156 | 0.0001 |
| | Depth | 0.013 | 10.533 | 0.0001 |
| (B) | Factors | R ² | F Statistics | Adjusted P-value |
| | BM vs. SS | 0.508 | 245.953 | 0.0003 |
| | BM vs. SH | 0.425 | 153.435 | 0.0003 |
| | SH vs. SS | 0.314 | 95.044 | 0.0003 |

Factor "site": Bomok (BM), Sinheung (SH), Seongsan (SS); factor "month": May, November; and factor "depth": 10 m, 15 m. The P-values were adjusted using Bonferroni correction for multiple comparisons. Significant P-values ($P \leq 0.05$) are highlighted in boldface type.

energy, eastern SS; and coralline algae dominated in shallow, strongly tide-influenced, more eutrophic, northern SH.

First, it was found that the level of environmental distinctness between sites varied with season, being strongest in November and February, respectively, while being weakest in May and August. Consequently, the distinct environmental setting at each site was subject to seasonal variations. The TWC, a branch of the warm, saline, and oligotrophic Kuroshio Current, shows seasonal variability, intensifying in summer (i.e., reaching further north than in winter), with a current velocity that can vary by 20 cm s^{-1} between July and January (Takikawa and Yoon, 2005; Cha and Moon, 2020). Additionally, Changjiang River discharge (termed Changjiang Diluted Water, CDW) from the Chinese mainland arrives at Jeju Island in the southwest. Then, driven by southerly summer winds, the CDW encompasses the whole island, peaking in July and August (Park, 1986; Kim et al., 2009; Park et al., 2011; Kwon et al., 2018). Therefore, during summer, environmental heterogeneity around the island is further reduced as CDW adds fresh, warm, oligotrophic water to the TWC-dominated coastal surface waters. Moreover, increased precipitation during the summer monsoon season further homogenizes surface water properties around the island (Kwon et al., 2020). In winter, however, the weakened TWC only reaches the south of Jeju Island, increasing the SST by up to 2°C at BM compared to SS and SH. Cha and Moon (2020) even reported a winter temperature gradient of 6°C between the northwest (12°C) and the southeast (18°C), compared to just 3°C in summer (25°C and 28°C , respectively). Additionally, in winter, the east and north are subject to strong northerly wind bursts, impacting currents, surface mixing layer, SST, nutrient supply and turbidity, while Mt. Halla, a nearly 2000 m high volcano situated near the center of the island, acts as a wind-breaker, sheltering the south from these strong, northerly winter gusts (Jacobs et al., 2000; Nishihara and Terada, 2010; Cho et al., 2013). Hence, environmental conditions between sites were most similar in summer and most different in winter. Considering that in our benthic community data, the factor "month" explained only a comparably low proportion of variability in sessile community coverages (pRDA = 8.0% between May and November), these environmental winter differences may play a key

role in structuring benthic community around the island. However, a more in-depth study, including high time-resolution data to detect seasonal patterns, is necessary to confirm this assumption.

Second, the recorded site-specific sessile benthic compositions around Jeju Island were consistent with the observed local environmental conditions and topography. It was found that all three sites showed a distinct sessile benthic composition. Each site was dominated by one foundation species or category, which reflected local abiotic conditions. While all our study sites showed the presence of hermatypic scleractinian coral species, BM was characterized by highest coverage and species diversity, including *A. japonica*, *M. millepora*, *P. profundacella*, and *P. albopicta*. Generally, the southern coastal marine area is steep and deep, while winds are milder (see Figure 1 bathymetry). In addition, the tidal energy contribution is low ($< 30\%$), while the majority of prevailing environmental conditions are determined by the specific water properties of the TWC (i.e., saline, warm, oligotrophic) passing Jeju Island (Hur et al., 1999; Cha and Moon, 2020). Such hydrographic and topographic features may promote a comparably oligotrophic environment. Although the nutrient concentration at BM may show a localized peak due to the presence of a sewage treatment plant near the sampling site, environmental data from the exact sampling site are currently lacking. In addition, the consistent supply of oligotrophic TWC waters may soften direct impacts of the sewage treatment plant. As high nutrient concentrations can benefit corals' competitors and hinder coral physiological processes (Harriott and Banks, 2002; Manzello et al., 2014; Kwon et al., 2020), more oligotrophic conditions could favor the thriving of hard coral species at BM. Moreover, this low-energy habitat and the influence of the TWC lead to significantly higher winter SST and transparency readings. At BM, the mean SST and transparency in February were over 15°C and 10 m, respectively, contrary to SH and SS. Subtropical hard coral richness and abundance are more sensitive to minimum temperatures and short-term thermal variability (Sommer et al., 2018), which is in line with Jeju's hard coral thermal optimums (see Supplementary Table 2). For instance, temperatures between 10°C and 15°C can induce *A. japonica* bleaching and reduction of its basal metabolism, although without being lethal (Higuchi et al., 2020; Keshavmurthy et al., 2021). Recently, it was showed that three cryptic species of *Alveopora japonica* corresponding to Japanese, Korean and Taiwan distributions existed (Kang et al., 2020). Moreover, McIlroy et al. (2019) reported that 80% of the maximum productivity of five subtropical coral species, including one *Montipora* species, was maintained at temperatures between 15.7°C and 32°C , with their optimal temperatures always being greater than 20°C , which fall within the annual temperature range of BM. Additionally, photosynthetic symbionts-carrying hard corals thrive better in high transparency waters where there is more sunlight (De'ath and Fabricius, 2010; Muir et al., 2015), while the reduction in suspended particles can promote coral recruitment by decreasing the abrasion effect (Gilmour, 1999; Gove et al., 2015). However, habitats dominated by *A. japonica* (percentage cover $> 25\%$) have been identified at Biyangdo, northwest of Jeju Island (Denis et al., 2014). Although the environmental conditions at this site are unknown, they are likely to differ from those at BM, and

additional controlling factors could explain this hard coral outbreak (see Kwon et al., 2020). The low coverage of canopy-forming algae and other non-encrusting macroalgae species at BM (< 2.5%) can favor the growth of hermatypic scleractinian corals by decreasing competition stress, abrasion and dislodgment (Coyer et al., 1993; Miller and Hay, 1996; Tuckett et al., 2017; De Vargas Ribeiro et al., 2022). Interestingly, a few decades ago, the perennial canopy-forming brown alga *E. cava* thrived at BM (Chung et al., 1998; Ribas-Deulofeu et al., 2023). Meanwhile, in our study, *E. cava* was not found at the BM site, while it was present at the SH site and dominated the SS site. Tuckett et al. (2017) reported a shift in ecosystems in Western Australia from temperate canopy-forming algae to hard coral species with warm water affinities. They attributed this shift to a competitive release caused by kelp decline resulting from heatwaves and global warming. Indeed, temperate kelps, such as *E. cava*, are heat-sensitive (Wernberg et al., 2011, 2016) (Supplementary Table 2) and, like hard corals, may be limited by water temperature in winter. The optimal water temperature for *E. cava* growth during winter is 15–18°C, while water temperatures above 20°C in summer can inhibit growth, although promoting reproductive potential (Yokohama et al., 1987; Kim et al., 2016). At SS, mean SST in February and May were nearly 15°C and 17°C, respectively, lying within the range of *E. cava*'s optimal temperature. Moreover, the high-energy environment caused by strong winter winds could contribute to the persistence of kelp forests at SS. Water motion is key in promoting and aiding kelp forest growth by dislodging grazers (Denny and Gaylord, 1996) and increasing nutrient availability and uptake (Hurd et al., 1996; Nishihara and Terada, 2010). *E. cava* is well-equipped to handle these physical disturbances due to its finger-like holdfasts and large thalli, which help to attach itself firmly to the substrate (Kang et al., 2011; Kang and Kim, 2012; Lee K.-T. et al., 2023). Therefore, climate change-related events, such as the intensification of the KWC (i.e., increased SST and oligotrophy) (Wu et al., 2012; Kim et al., 2022a), could promote the expansion of high-latitude hard coral communities along the southern coastline towards east and west, while driving a decline in eastern temperate kelp forests. On the north of the island, the coastal marine area is flat and shallow, the wind speed is high, and tidal energy is prevalent (> 90%) in setting local environmental conditions (Cha and Moon, 2020). Results showed that DIN and DIP concentrations were significantly higher at SH than at BM, and generally, all nutrient concentration-related variables were consistently highest at SH, especially the November measurements. This may be due to a combination of reasons, such as topography hindering quick dilution, increased input through aquaculture wastewater, and inefficient biological uptake by marine organisms. Indeed, nutrient availability in Jeju's coastal waters is strongly related to land-based, anthropogenic activities, such as land-operated fish farms which are present in the vicinity of SH. Wastewater from land-operated fish farms accounts for up to 95% of the seawater ammonium (Kwon et al., 2022), increasing coastal DIN and DIP concentrations (Choi et al., 2021), and generally contributes significantly to the nitrogen budget in the coastal waters of Jeju (Koh et al., 2013; Kim et al., 2022b). Sea water enriched in ammonium is preferred by coralline algae, which dominate SH

(Nguyen et al., 2020; Kwon et al., 2022). Moreover, geniculate coralline algae have lower nitrogen amounts in their tissue than brown algae (e.g., *E. cava*, *U. pinnatifida*), hence incorporating less total nitrogen (Choi et al., 2021). Although, throughout the year, SH showed similar environmental conditions to SS, SH was not dominated by *E. cava*. Canopy-forming algae populations of *U. pinnatifida* and *E. cava* were present at SH but showed much lower coverage percentages than in SS and were only recorded in May. High nutrient concentrations due to sewage effluents can inhibit the germination and photo efficiency of brown algae (Doblin and Clayton, 1995; Scherner et al., 2012), but this substantial difference in benthic composition compared to the abiotic environmental similarity of these sites suggests that other factors may hold a key role in shaping these benthic ecosystems. Overgrazing by sea urchins and other invertebrates is known to cause decrease in kelp forests (Kang, 2010; Bekkby et al., 2015; Ling et al., 2015), and a high abundance of such grazers at SH compared to SS could explain the low coverage of canopy-forming algae despite the apparent favorable environmental conditions. Such information is not reported in Jeju's literature, and personal observations did not attest to high abundance of grazers. Still, additional ecological factors, such as intensity and frequency of extreme weather-related events (Smale and Wernberg, 2013) and biotic interactions (Negri et al., 2001; Tebben et al., 2015), can all hold essential roles in shaping benthic communities, and additional study including these parameters is warranted. Additionally, DO measurements were significantly lowest at SH, especially in August, which may be caused, in parts, by the elevated nutrient levels, as increased nitrogen and phosphorous content lowers the amount of dissolved oxygen in the water (Dodds, 2006). The overall lower water quality at SH mirrored in the high coverage percentages and diversity of Bryozoa, Porifera, and soft corals. Sponges and bryozoans have been found in large species numbers and percentage cover on hard bottoms of highly disturbed environments, and especially bryozoans are reported to thrive in low light conditions, while soft corals can tolerate high eutrophication and sedimentation environments (Corriero et al., 2007; Baum et al., 2016; Evseeva and Dvoretzky, 2023). In contrast to the southern coast, the benthic community composition in the northern coastal waters may be more influenced by topography and additional localized anthropogenic stressors rather than natural abiotic parameters. Similarly, the impact of global warming on the community composition of the northern barren grounds may be comparably low, as CCA communities are less sensitive to rising SST (Krieger et al., 2023).

Third, water depth did not much influence any of the observed community dynamics, although depth is directly correlated with light and nutrient availability and, as such, impacts the vertical zonation of marine benthic species (Kang and Kim, 2012; Muir et al., 2015). Generally, photosynthetic species, such as canopy-forming brown algae and hermatypic scleractinian species, always showed higher coverages at the shallower depth. At BM, the hard corals *M. millepora*, *P. profundacella*, and *P. albopicta*, and geniculate coralline algae were more abundant at 10 m depth. As light is a major limiting factor in high-latitude ecosystems, particularly in winter, hard corals carrying photosynthetic

symbionts living above 30° latitude tend to thrive best in shallow areas that receive more sunlight (Muir et al., 2015). Interestingly, there was no depth-related trend in the coverage of *A. japonica*. This may be because the reported depth range of this species around Jeju Island is much wider than those of *M. millepora* and *P. profundacella* (5–25 m and < 10 m, respectively; Sugihara et al., 2014). Geniculate coralline algae usually dominate at shallower depths (1–10 m depth; Kang et al., 2023) because of their higher tolerance to wave action. Similarly, the photosynthetic brown algae *E. cava* and *Sargassum* spp. showed decreasing coverages with depth at SH and SS. These species exhibited maximum abundances at depths between 6 m and 10 m in Jeju waters, explained by their higher light demand and lower tolerance to strong physical forces (Kang et al., 2023). On the contrary, encrusting red algae (e.g., CCA and *Peyssonnelia* sp.) and *G. angusta* have increasing coverages with depth due to their lower demand for light (Kang et al., 2023). At SH, the soft coral *D. gigantea* was more abundant at 15 m depth (coverage ≈ 4% in May and November), which may be explained by its non-photosynthetic lifestyle, i.e., not requiring sunlight for energy acquisition, and its generally high stress-tolerance to sedimentation, turbidity, and eutrophication (De'ath and Fabricius, 2010; Powell et al., 2014; Baum et al., 2016; Lalas et al., 2023). These traits enable *D. gigantea* to thrive in poorer quality waters while avoiding increased competition at shallower depths. Likewise, the sampling months accounted for a minor part of the variability observed in the benthic community. For instance, the decrease in canopy-forming algae and high-latitude hard corals at SS and BM, respectively, can be attributed mainly to, in the absence of other extreme events, destruction by super typhoon Hinnamnor, which reached Jeju Island in September 2022. Lee K.-T. et al. (2023) reported a 42% loss of *E. cava* at 10 m and 34% at 15 m in September 2022 compared to May 2022 at SS, which is coherent with our results. This decline in canopy density has led to an artificial increase in the percentage cover of underlying species in November, such as rhodophytes *Plocamium* sp. and *G. angusta*. Similarly, the seasonal decline of *A. japonica* at BM by roughly half its coverage from May (61% at 10 m; 71% at 15 m) to November (37% at 10 m; 30% at 15 m) was also likely caused by typhoon Hinnamnor. Numerous dead and bleached *A. japonica* were observed on photo-quadrats in September 2022, right after Hinnamnor had hit. At the same time, the increase at all three sites and two depths of turf-forming algae, substrate, red algae, and coralline algae may have been promoted by space, light, and resources availability, as well as species-specific invasion capacity of a newly disturbed area (Sousa, 1984; Airoldi, 1998; Kim T. et al., 2022). Life history traits can also contribute to this observed monthly divergence (Darling et al., 2012). Whereas the dominant *E. cava* and *A. japonica* have a perennial life cycle and are known to have an overall annual stable coverage (Haroun et al., 1989; Vieira et al., 2016), *U. pinnatifida* is an annual species living as macroscopic, diploid sporophyte from January to July, and the rest of the year, as microscopic, haploid gametophyte (Schiel and Thompson, 2012). In its microscopic stage, its presence cannot be identified by image analysis, which can explain its absence in the November results. This study investigated the current spatial variability in Jeju's benthic

communities and local environmental conditions, and seasonal variability of these marginal ecosystems needs further assessment.

5 Conclusion

Marine climatic transition zones are emerging as geographic hot spots of scientific interest in climate warming-related ocean changes. Increasing temperatures threaten the survival of the heat-sensitive temperate species living at the limit of their physiological tolerance while driving the arrival and expansion of species with warmer climate affinities. Therefore, benthic habitats of marine climatic transition areas are subject to extensive faunal turnover, driven by an interplay of extinction, outbreak, and migration events.

This study greatly improved the understanding of Jeju benthic community dynamics on an annual scale and demonstrated the importance of considering environmental parameters in understanding benthic community distribution in climatic transition zones. It clearly suggests that a combination of hydrographic, meteorological, and topographic parameters structures coastal benthic communities in the temperate transition zone of Jeju Island. Statistically, winter water temperature, nutrient concentration, water motion (derived from wind speed and direction), and transparency were the most significant in setting the particular environmental conditions around the island. These local environmental conditions were congruent with the distribution, composition, and coverage of sessile foundation species.

Although the underlying drivers of Jeju benthic communities need to be further investigated, our study suggests that site divergence in winter environmental conditions may play a significant role. Higher spatio-temporal resolution abiotic and biotic data are needed in future studies to improve our understanding of marginal benthic community dynamics. Moreover, experimental research is necessary in the mostly overlooked, temperate transition zone of Jeju to investigate the controlling factors of these marginal communities further. Having such information will help clarify the role of ecological variables in driving biogenic habitat shifts, assessing how each affects sessile communities, including, among others, effects on the physiology of foundation species, antagonistic and synergistic relationships, and food web interactions.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

GP: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. AJ: Conceptualization, Validation, Visualization, Writing – review & editing. K-TL: Data

curation, Investigation, Methodology, Writing – review & editing. LP: Formal analysis, Investigation, Visualization, Writing – review & editing. H-SY: Investigation, Project administration, Writing – review & editing. YS: Investigation, Validation, Writing – review & editing. H-SP: Funding acquisition, Project administration, Resources, Writing – review & editing. D-HK: Funding acquisition, Project administration, Resources, Writing – review & editing. TK: Conceptualization, Data curation, Investigation, Methodology, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1345518/full#supplementary-material>

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