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Spatiotemporal distribution patterns of macrobenthic communities and their relationship with environmental factors in the Shengsi Archipelago (Zhejiang, China)

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Abstract

Macrobenthic organisms are commonly employed as biomonitors for environmental risk assessment. In this study, we aimed to investigate the spatial and temporal patterns of the macrobenthic community, which is influenced by environmental factors of sediments and bottom water layer. We sampled a total of 12, 11, 10, and 11 stations in the Shengsi Archipelago during June 2010, August 2010, November 2020, and April 2021 respectively. A total of 124 species of macrobenthos were identified, with polychaetes being the dominant group. The abundance, biomass, and diversity indices exhibited no significant temporal differences. Similarly, biodiversity did not exhibit a clear spatial gradient, likely due to the small study area and the absence of significant differences in key factors such as depth. However, the stations with the lowest biodiversity values consistently appeared in the southwest region, possibly due to the impact of human activities. Significant differences in the macrobenthic community were observed between all months except between June and August, and mollusk *Endopleura lubrica* and polychaete *Sigambra hanaokai* were important contributors to these differences according to the results of the Similarity Percentages analysis. Suspended particulate matter (SPM) was identified as the primary driving factors of macrobenthic variability. In summary, the community structure underwent temporal changes influenced by complex current patterns, while biodiversity remained relatively stable. This study contributes to our understanding of the key environmental factors affecting macrobenthic communities and biodiversity. It also provides valuable data support for the long-term monitoring of macrobenthos and the environment in the Shengsi Archipelago.

Key words macrobenthic community, Shengsi Archipelago, distribution pattern, biodiversity, environmental factors

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1 Introduction

The Shengsi Archipelago occupies a unique geographical position, situated in the northern part of China's largest fishing ground, the Zhoushan Fishing Ground. The waters surrounding the Shengsi Archipelago display intricate hydrological characteristics, influenced by various water masses, including diluted freshwater from the Changjiang River, the seasonal Zhoushan upwelling (Hu and Zhao, 2007; Shen et al., 2020) and Zhe-Min Coastal Current (Zhang et al., 2022), as well as a branch of the Kuroshio Warm Current known as the Taiwan Warm Current (Hu and Zhao, 2007; Mao et al., 1964; Xu et al., 1983; Zhang et al., 2007b; Zhao, 1993; Fan et al., 2020, Yang et al., 2013). This complexity results in frequent material exchange and energy flow within the ecosystem,

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rendering it highly responsive to human activities and environmental changes. The physical and chemical attributes of water bodies, such as temperature, salinity, and nutrient concentrations, are linked to the influence of different water masses (Zhang et al., 2007a, 2007b). Furthermore, marine plankton, such as *Ortanus vermiculus* (Zhang et al., 2016), exhibit distinct patterns in various water masses. Unlike marine plankton, benthic organisms exhibit greater stability. However, similar to plankton, they can offer valuable insights into hydrological and marine environmental conditions. While previous research in the East China Sea has primarily focused on the influence of the Kuroshio Current (Xu, 2017; Xu et al., 2018), it is important to note that the waters surrounding the Shengsi Archipelago are also affected by the Changjiang River and upwelling. Although some studies have explored the macrobenthos in the vicinity of the Shengsi Archipelago (Zhoushan sea area), including their response to terrestrial organic matter (Jia et al., 2011) and the distribution of sediment heavy metals and petroleum hydrocarbons (Tang et al., 2021), very few previous studies have explored the relationships between the intricate temporal changes in current patterns and the structure of the macrobenthic community.

Marine macrobenthic organisms play a crucial role in marine ecosystems due to their richness and intricate ecological relationships, making them essential components of material cycling and energy flow (Li, 2011). These organisms contribute to environmental restoration and pollutant degradation through processes such as biodeposition and bioturbation (Li et al., 2017). Some macrobenthos species serve as indicators of marine environmental deterioration and are thus used to conduct environmental pollution assessments (Brey, 2012; Tian et al., 2009). Therefore, the dynamics of community pattern of macrobenthos can be used as a good indicator of environmental changes. For example, the macrobenthic communities in the Yellow Sea Cold Water Mass and the East China Sea, which are greatly influenced by the Kuroshio Current, exhibit significant variations (Liu et al., 1986; Xu et al., 2016, 2018). In these regions, macrobenthic species richness increases with depth and is higher closer to the Kuroshio mainstream area (Xu, 2017). Long-term monitoring in Mejillones Bay, northern Chile, has revealed that El Niño disturbances affect the Humboldt Current upwelling system, resulting in reduced macrobenthos abundance at a depth of 10 m but a remarkable increase in species diversity and abundance at greater depths due to elevated dissolved oxygen levels (Laudien et al., 2007). The intricate interactions between these physical processes and benthic communities have significant ecological, conservation, and climate change implications, underscoring the need for interdisciplinary research in this field to better understand and manage these critical marine ecosystems.

In this study, we hypothesized that various oceanic flow patterns significantly influence the community structure of macrobenthos. Therefore, our study aimed to analyze how these organisms respond to environmental changes induced by varying oceanic flow patterns. Specifically, the objectives of this study were to (1) analyze the spatiotemporal patterns of macrobenthic communities in the sea area of the Shengsi Archipelago; (2) investigate the response of macrobenthos to different environmental factors; (3) characterize the response of macrobenthic communities to complex currents.

2 Materials and methods

2.1 *Study area*

The study area is located near Sijiao Island, which is the primary island within the Shengsi Archipelago. Sijiao Island is located in the northern waters of Zhejiang Province, marking the easternmost island county in the province and the northernmost point of the Zhoushan Archipelago. Positioned within the East China Sea region, the study area lies to the east of Hangzhou Bay and southeast of the Changjiang River Estuary, with coordinates ranging from 30°24′N to 31°04′N and 121°30′E to 123°25′E. This region encompasses a total of 630 islands, comprising 28 inhabited and 602 uninhabited islands. In a preceding survey of marine environmental, it was discerned that the waters in the vicinity of Sijiao Island exhibited marked eutrophication, accompanied by a notable paucity in benthic species diversity (Zhang et al., 2014).

The study area is influenced by different current patterns during various seasons. In summer, the study area experiences eastward surface currents that carry diluted freshwater from the Changjiang River and northward upwelling of the Taiwan Warm Current along the continental shelf (Fan et al., 2020; Song et al., 2022b; Zhang and Wang, 2004; Zhang et al., 2007b), alongside occasional upwelling currents (He, 2017; Hu and Zhao, 2007; Jing et al., 2007; Shen et al., 2020; Yang et al., 2020; Zhou, 2021). In contrast, during winter, the influence of Changjiang River water weakens, and the Taiwan Warm Current dominates the entire water column (Zhang et al., 2007b), whereas upwelling currents become less frequent or absent (He, 2017; Hu and Zhao, 2007; Jing et al., 2007; Shen et al., 2020; Yang et al., 2020; Zhou, 2021). Meanwhile, the Zhe-Min Coastal Current emerges and exercises its influence over the region under the impact of the northeast monsoon (Zhang et al., 2022).

2.2 *Sampling design*

Sampling of macrobenthos in the Shengsi Archipelago was carried out in June and August of 2010, November 2020, and April 2021. Around Sijiao Island, a total of 12, 11, 10, and 11 stations were established in June, August, November, and April, respectively, as depicted in Fig. 1. At each sampling station, we conducted two samplings using the Van Veen grab sampler, which has a sam-

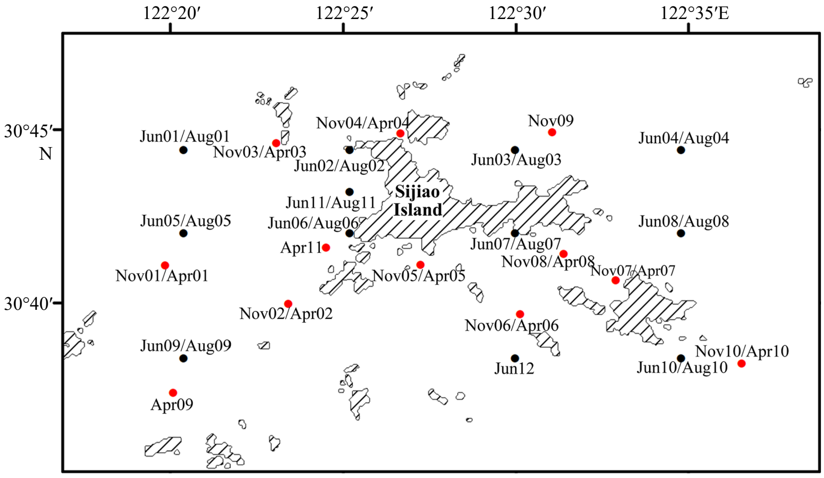

Fig. 1. Map of the distribution of the sampling stations in Shengsi Archipelago. The image labeled the identification numbers for the sampling stations, where Jun, Aug, Nov, and Apr represent different sampling times (June 2010, August 2010, November 2020, and April 2021, respectively).

pling area of 0.1 m^2, to collect macrobenthos samples. The biological samples were separated from sediment using a 500 μm mesh sieve and subsequently preserved in a 5% formaldehyde solution. In the laboratory, we identified the collected samples to the finest taxonomic level and counted them based on classification using a binocular stereoscopic microscope (Zeiss Stemi508, Germany). Subsequently, the samples were weighed based on classification using an electronic analytical balance (Sartorius BSA223S, Germany), with the results recorded to three decimal places.

Surface sediment samples (0–5 cm) were collected using the Van Veen grab sampler for the purpose of measuring sediment environmental variables. However, sediment sample collection was not conducted in April. At each sampling location, a portion of the sediment sample was analyzed for oxidation-reduction potential (Eh) using a pH meter (Orion 898, USA) which employed platinum electrodes for redox potentials and utilized a saturation calomel electrode as the reference electrode (Li et al., 2008). The remaining portion was preserved by freezing and transported back to the laboratory for subsequent analysis. In the laboratory, the sediment samples brought back were freeze-dried using a freeze dryer (Christ Delta1-24LSC). A portion of the freeze-dried sample was subjected to particle size analysis using a laser diffraction particle size analyzer (Malvern Mastersizer 3000) to determine the volume mean diameter (*D*) (Ding et al., 2016). Another portion of the sample was ground using a ball mill (TH-0.4L) and subsequently sieved through a 100-mesh sieve. Next, the sample was used for measuring the content of total organic carbon (TOC), total nitrogen (TN), sulfide, and trace metals. After undergoing pre-treatment, TOC and TN were quantified using an elemental analyzer (Elementar VarioMICROcube, Germany) (Zhao et al., 2023). The sulfide content was determined using the iodometric method (Wu et al., 2023). Trace metals, namely copper (Cu), lead (Pb), zinc (Zn), cadmium (Cd), chromium (Cr), arsenic (As), and mercury (Hg), were quantified using an inductively coupled plasma mass spectrometer (iCAP-Q, Thermo Fisher Scientific, USA) after pre-treatment of the samples (Zhao et al., 2023). Total phosphorus (TP) and the oil contents were measured separately using the phosphomolybdenum blue method (Lemanowicz et al., 2020) and fluorescence spectrophotomentric technology (Xie and Gan, 2010).

Seawater transparency was determined using a transparency disc visual method. Bottom water samples were collected in Niskin bottles equipped with a conductivity, temperature, and depth (CTD) sampler (Sea Bird 911 PLUS). Temperature, salinity, and depth were determined by CTD sampler. Chlorophyll *a* (Chl *a*) was quantified using fluorescence techniques with a Turner Designs 10-AU fluorometer (Zheng et al., 2022). However, Chl *a* measurements were not conducted in November and April. The pH and Chemical Oxygen Demand (COD) of water were respectively measured using a pH meter (Orion 898, USA) and the acidified potassium permanganate method (Goh and Lim, 2017). Dissolved oxygen (DO) was determined using iodometric titration (Xie, 2019). Reactive phosphate (PO_4^{3-}-P), nitrite nitrogen (NO_2^--N), nitrate nitrogen (NO_3^--N), and ammonium nitrogen (NH_3-N) were determined using methods including ascorbic acid reduction phosphomolybdenum blue method for PO_4^{3-}-P (Xu et al., 2022), diazo coupling method for NO_2^--N (Xu et al., 2022), zinc cadmium reduction method for NO_3^--N (Xu et al., 2022), and sodium hypobromite oxidation method for NH_3-N (Gao et al., 1980). Suspended particulate matter (SPM) concentration was quantified using a gravimetric method (Zhou et al., 2004).

2.3 *Data analyses*

The significance tests employed to identify differences in environmental variables among different months were selected based on the results of the homogeneity of variance test. Environmental variables were subjected to either a one-way ANOVA or a Kruskal-Wallis test, depending on whether they met the assumption of homogeneity of variance. The choice of the significance test for assessing pairwise differences in environmental variables between different months was determined by the results of the homogeneity of variance test. The least significant difference (LSD) test was used for variables that met the assumption, whereas Tamhane's T2 was used for those that did not. To describe the community structure of macrobenthos, species dominance (Y) was estimated as described by Chen et al. (1995) along with species diversity parameters, including the Margalef richness index (d), Shannon-Wiener diversity index (H') (Shannon, 1997), and Pielou evenness index (J) (Pielou, 1966). The relevant formulas for these parameters are as follows:

$$Y = P_i \times f_i, \tag{1}$$

$$d = (S-1)/\log_2 N, \tag{2}$$

$$H' = -\sum_{i=1}^{S} P_i \log_2 P_i, \tag{3}$$

$$J = H'/\log_2 S, \tag{4}$$

where $P_i = n_i/N$, P_i represents the proportion of the number of individuals or biomass of species i in relation to the total number of individuals or total biomass, whereas n_i and N represent the number of individuals for species i and the total number of individuals across all species, respectively. f_i represents the percentage ratio of occurrences of a given species in specific sample points to the total number of sample points, while S denotes the species richness. Furthermore, when the Y value of a particular species is greater than or equal to 0.02, that species is considered to be dominant (Chen et al., 1995).

The significance testing methods used to assess differences in abundance, biomass, S, d, H', and J of macrobenthos among all months align with the methods previously mentioned for testing environmental variables.

The dissimilarity and the key differentiating species of macrobenthic communities between different time points were analyzed using the Similarity Percentages (SIMPER) method. Analysis of Similarities (ANOSIM) was used to test the similarity of macrobenthic communities between different months. The outcomes of these two analyses were used to illustrate the variations in community structure across different months. Prior to the analysis, a square root transformation was applied to the abundance data. SIMPER analysis and ANOSIM tests were conducted using PRIMER 6 software (Zhou and Zhang, 2003).

For community-environment correlation analysis, dominant species, as well as environmental factors exhibiting significant differences between months, were selected for a forward selection analysis. According to the forward selection results, significant explanatory environmental variables ($p < 0.05$) and the abundance of dominant species were chosen for canonical correspondence analysis (CCA). The CCA was performed on the Canoco 5 software (Lai, 2013; Ter Braak and Smilauer, 2012).

3 Results

3.1 *Environmental variables*

Selected environmental variables deemed the most significant for this study have been presented in Table 1, and the remaining environmental variables were showed in Table S1. Most of the environmental variables examined in this study exhibited significant differences among different months ($p < 0.05$). Eh, TOC, TN, TP, Hg concentration, Cu concentration, Pb concentration, Zn concentration, As concentration, and D in surface sediments exhibited significant differences ($p < 0.05$), whereas the differences for Cd concentration and Cr concentration were not significant ($p > 0.05$). Water transparency, as well as water temperature, COD, pH, salinity, SPM, Chl *a* concentration, PO_4^{3-}-P concentration, NO_2^--N concentration, NH_3^--N concentration, and NO_3^--N concentration in the bottom water layer also exhibited significant differ-

Table 1. Temporal variations of environmental variables in the waters of Shengsi Archipelago

Environmental variable	June	August	November	April
Hg concentration/(mg·kg^{-1})	0.020 (0.001) ^{a}	0.020 (0.001) ^{a}	0.077 (0.014) ^{b}	no data
Pb concentration/(mg·kg^{-1})	25.4 (0.6) ^{a}	24.7 (0.6) ^{a}	19.9 (0.4) ^{b}	no data
As concentration/(mg·kg^{-1})	5.5 (0.1) ^{a}	5.6 (0.2) ^{a}	9.5 (0.6) ^{b}	no data
D/μm	9.8 (0.4) ^{a}	12.7 (0.8) ^{b}	11.6 (0.7) ^{ab}	no data
Depth/m	13.2 (1.8) ^{a}	17.5 (6.0) ^{a}	13.3 (1.9) ^{a}	13.7 (2.7) ^{a}
Temperature/℃	19.4 (0.1) ^{a}	25.1 (0.3) ^{b}	20.2 (0.1) ^{c}	16.3 (0.2) ^{d}
Salinity	20.6 (0.8) ^{a}	21.9 (0.7) ^{a}	27.2 (0.7) ^{b}	28.3 (0.7) ^{b}
SPM concentration/(mg·L^{-1})	40 (15) ^{a}	18 (2) ^{a}	235 (43) ^{b}	604 (90) ^{c}
Chl *a* concentration/(μg·L^{-1})	3.23 (0.77) ^{a}	15.61 (4.01) ^{b}	no data	no data

Note: The standard error for each value is indicated in brackets. Superscripts (a, b, c, d) are used to indicate whether there is a significant difference in the environmental variables among different months. Superscripts with the same letter indicate non-significant differences ($p > 0.05$), whereas different letters indicate significant differences ($p < 0.05$).

ences ($p < 0.05$), whereas the differences for water depth and DO were not significant ($p > 0.05$).

3.2 *Macrobenthic community*

3.2.1 *Species composition and dominant species*

In this study, a total of 124 species of macrobenthos were identified, comprising a combined count of 1 115 individuals, with an average density of 127 individuals per square meter (ind./m^2). The macrobenthic assemblages in the study area were primarily composed of polychaetes, followed by crustaceans and mollusks (Fig. 2a). The macrobenthic assemblages maintained a relatively consistent composition across different sampling times, with polychaetes dominating, followed by mollusks and crustaceans. Moreover, the stations Jun03, Aug04, Nov07/Apr07, and Apr05 exhibited the highest species richness values in June, August, November, and April, respectively, and the stations Jun09, Aug09, and Apr09 exhibited the lowest species richness, registering a value of only 3 species. The stations with the highest species richness were scattered around Sijiao Island, whereas those with the lowest species richness were concentrated in the southwest region, with the exception of November (Station Nov09) (Fig. S1). In summary, the results demonstrate spatial differentiation in species richness.

The *Y* value of each species was calculated based on the sampling time, designating species with $Y \geqslant 0.02$ as dominant species. As shown in Table 2, there were significant differences in the dominant species among different months, along with considerable variations in their abundance. Except for polychaete *Sternaspis chinensis*, which appeared as a dominant species in all four months, most species emerged as dominant species only once or twice. Moreover, when comparing dominant species between June and August versus November and April, the latter demonstrated higher diversity, with a larger proportion of polychaetes.

Notably, the mollusk *Endopleura lubrica* exhibited a significantly higher average abundance in August com-

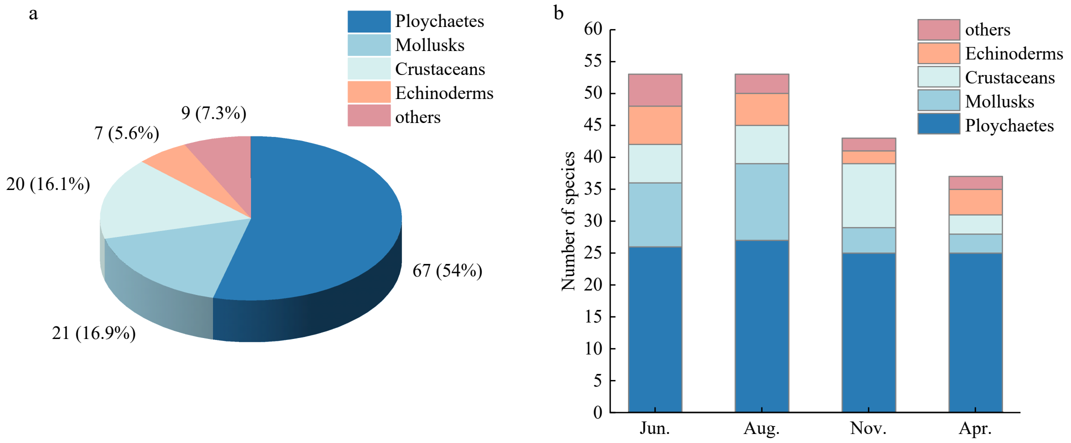

Fig. 2. Species richness (*S*) and their assemblage composition in Shengsi Archipelago. a. Macrobenthic assemblage composition in general. b. Temporal variation in macrobenthos diversity and assemblage composition. The ‘others’ category classification includes nemerteans, echiurans, and fish. Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020 and April 2021, respectively).

Table 2. Temporal variation in the average abundance of dominant species in Shengsi Archipelago

Dominant species	June	August	November	April
Aglaophamus dibranchis/(ind.·m^{-2})	6.7 (3.1)*	8.2 (4.2)*	0	0
Sternaspis chinensis/(ind.·m^{-2})	23.8 (7.9)*	14.5 (5.8)*	8.0 (2.7)*	9.1 (3.4)*
Eocylichna braunsi/(ind.·m^{-2})	5.8 (2.2)*	6.4 (3.2)	0.5 (0.5)	0.5 (0.5)
Endopleura lubrica/(ind.·m^{-2})	2.9 (1.1)	79.1 (54.2)*	0	0
Tharyx multifilis/(ind.·m^{-2})	0	0	11 (3.4)*	0
Nephtys oligobranchia/(ind.·m^{-2})	0	0	10.5 (3.7)*	5.9 (2.5)*
Sigambra hanaokai/(ind.·m^{-2})	0	0	29.5 (7.3)*	0.9 (0.6)
Prionospio sp./(ind.·m^{-2})	0	0	14.0 (4.8)*	0
Mediomastus sp./(ind.·m^{-2})	0	0	12.0 (5.6)*	0
Eriopisella sechellensis/(ind.·m^{-2})	0	0	10.0 (5.8)*	0
Amphiura vadicola/(ind.·m^{-2})	4.5 (1.8)	4.1 (2.4)	19.0 (15.8)*	8.6 (3.1)*
Lumbrineris japonica/(ind.·m^{-2})	0	0	0	4.5 (1.6)*
Dentinephtys glabra/(ind.·m^{-2})	0	0	0	9.5 (4.4)*
Heteromastus filiformis/(ind.·m^{-2})	0.8 (0.8)	0	0	11.8 (5.7)*

Note: The standard error for each value is indicated in brackets. The dominant species in the corresponding month are marked with *.

pared to other dominant species. This surge in abundance was linked to a substantial increase in occurrences of *E. lubrica* in stations Aug06 and Aug07, registering abundances of 190 ind./m^2 and 595 ind./m^2, respectively. In contrast, its abundance sharply declined or became undetectable at other stations during the same period (*E. lubrica* was most abundant in the Station Aug04, with only 8 ind./m^2).

3.2.2 *Abundance and biomass*

In the Shengsi Archipelago, the average abundance of macrobenthos was 127 ind./m^2, with polychaetes accounting for the largest proportion (56.0%). As illustrated in Fig. 3a, the ratio of the abundance of different groups varied significantly among different months. Particularly, the dominant position of polychaetes was replaced by mollusks in August, mainly due to the explosive proliferation of *E. lubrica*. Due to this abrupt increase in *E. lubrica* growth, the highest abundance value reached 755 ind./m^2 in Station Aug07, which was significantly higher than the highest values observed in other months, which were only 240 285 ind./m^2, and 150 ind./m^2, observed in stations Jun01, Nov08, and Apr05, respectively. The lowest abundance values were recorded in stations Jun05, Aug09, Nov04, and Apr01/Apr09, with corresponding values of 20 ind./m^2, 35 ind./m^2, 55 ind./m^2, and 40 ind./m^2. As shown in Fig. S2, except for June, the stations with the highest abundance values tended to be located on the south side of the island, while the station with the lowest abundance values concentrated in the southwest.

On the other hand, the average biomass of macrobenthos was 16.04 g/m^2, primarily contributed by echinoderms (36.2%). Although echinoderms were dominant in general, mollusks, and the ‘others’ category respectively dominated in August, November, and April (Fig. 3b). As mentioned earlier, the dominance pattern observed in August was due to the increase of *E. lubrica*, while the dominance in November and April resulted from the presence of large individuals of fishes, although they were less abundant. Examples include fish *Ctenotrypauchen microcephalus* in the Station Nov01 and fish *Odontamblyopus lacepedii* in the Station Apr01. The spatial distribution of biomass was irregular, and the stations with the highest and lowest biomass values did not follow similar spatial patterns in different months (Fig. S3).

In summary, the temporal fluctuations in the composition of abundance and biomass indicated changes in the community structure of macrobenthos. Unfortunately, it is noteworthy that, in this study, neither abundance nor biomass exhibited significant temporal differences (p > 0.05).

3.2.3 *Species diversity index*

The species diversity indices (d, H' and J) in June and November were higher than those in August and April (Fig. 4). However, the temporal variations in these indices did not reach statistical significance as a whole (p > 0.05). The highest d values in different months were distributed around the island, whereas the lowest values were located in the southwest region of the study area except in November (Fig. S4). Moreover, the highest H' values were not concentrated, whereas half of the stations with lowest values were still distributed in the southwest (stations Jun09 and Apr09) (Fig. S5). The distribution of J was generally uniform (Fig. S6), except for stations Aug06 and Aug07 when there was a high abundance of a single species.

3.2.4 *Community structure and stability*

According to the results of ANOSIM tests, macrobenthic communities exhibited the highest similarity between June and August, and, they cannot be differentiated statistically (R < 0, p > 0.05), as shown in Table 3. In contrast, the average dissimilarity of macrobenthic communities was higher among the other months, and intergroup differences were consistently more significant than intragroup differences (R > 0, p < 0.01).

The key differentiating species of the macrobenthic community between different months included *E. lubrica*, *S. chinensis*, echinoderm *Amphiura vadicola*, polychaete

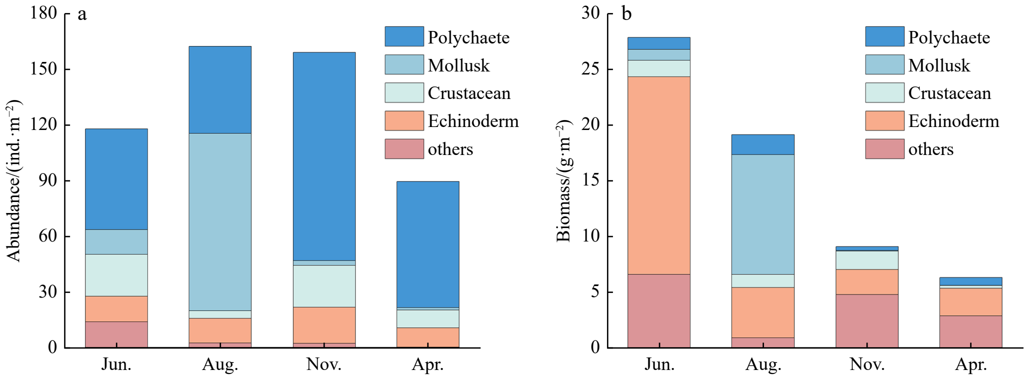

Fig. 3. Temporal changes in the average abundance (a), biomass (b), and their composition in the Shengsi Archipelago. Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020, and April 2021, respectively).

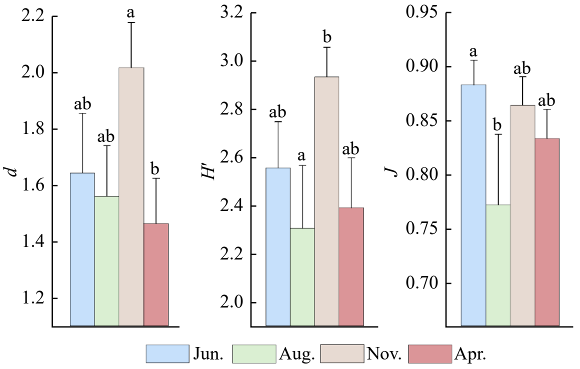

Fig. 4. Temporal variation in diversity indices of microbenthic community in the Shengsi Archipelago. Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020, and April 2021, respectively). *d*, *H'* and *J* represent the Margalef richness index, Shannon-Wiener diversity index, and Pielou evenness index, respectively. Different letters (a, b) indicate significant differences ($p < 0.05$) in these indices between different months.

Heteromastus filiformis, polychaete *Sigambra hanaokai*, polychaete *Prionospio* sp., and polychaete *Tharyx multifilis* (Table 4). *Sternaspis chinensis* and *A. vadicola* consistently exhibited characteristics of key differentiating species. *Sigambra hanaokai*, *Prionospio* sp., and *T. multifilis* only exhibited characteristics of key differentiating species between November and other months. Similarly, *H. filiformis* only exhibited characteristics of key differentiating species between April and other months.

3.3 *Biological-environmental relationship analyses*

To explore the correlation between community structure patterns and environmental factors, a forward selection analysis was conducted using the abundance of dominant species and environmental factors that exhibited significant differences between all months. According to the forward selection results, significant explanatory environmental variables ($p < 0.05$) and the abundance of dominant species were chosen for CCA (Fig. 5). SPM accounted for 31.0% of the community variation and was therefore identified as the primary driver of community variability. This parameter was followed closely by Hg, which accounted for 29.5% of the variation.

As shown in Fig. 5, macrobenthos can be categorized into three groups based on their responses to different environmental factors. The first group was primarily influenced by the positive effects of Pb (explaining 27.1% of the variation) and the negative effects of other factors. This group included mollusks such as *E. braunsi*, echinoderms such as *A. vadicola*, and various polychaetes such as *S. chinensis* and *A. dibranchis*. The second group was mainly influenced by the positive effects of SPM and the negative effects of Pb. This group included crustaceans such as crustacean *Eriopisella sechellensis* and polychaetes such as *T. multifilis* and *S. hanaokai.* The third group was primarily influenced by the positive effects of Hg. This group included polychaete species, among which polychaete *Nephtys oligobranchia*, *Prionospio* sp., and polychaete *Mediomastus* sp. were the most important.

Additionally, the relationship between sampling sta-

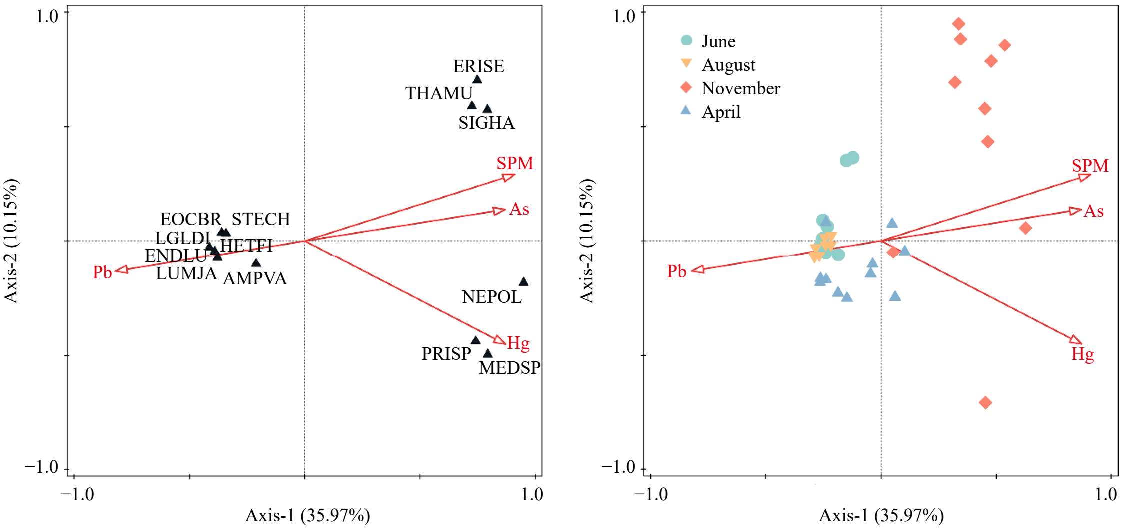

Fig. 5. CCA analysis results for community-environment correlation. The abundance of dominant species in the stations of Jun11, Aug02, Aug05 and Aug11 was 0. Therefore, these stations were omitted from the analysis. The abbreviations in the figure were formed using the first three letters of the genus name and the first two letters of the specific epithet. Polychaete *Sternaspis chinensis* is abbreviated as STECH, polychaete *Aglaophamus dibranchis* as AGLDI, mollusk *Eocylichna braunsi* as EOCBR, mollusk *Endopleura lubrica* as ENDLU, polychaete *Tharyx multifilis* as THAMU, polychaete *Nephtys oligobranchia* as NEPOL, polychaete *Sigambra hanaokai* as SIGHA, polychaete *Prionospio* sp. as PRISP, polychaete *Mediomastus* sp. as MEDSP, crustacean *Eriopisella sechellensis* as ERISE, echinoderm *Amphiura vadicola* as AMPVA, polychaete *Heteromastus filiformis* as HETFI, and polychaete *Lumbrineris japonica* as LUMJA.

Table 3. Average dissimilarity and ANOSIM analysis results of macrobenthic communities in the Shengsi Archipelago between different months

Groups	Average dissimilarity/%	*R*	*p*
Jun. and Aug.	83.37	−0.003	0.468
Jun. and Nov.	93.68	0.658	0.001^{***}
Jun. and Apr.	90.54	0.401	0.001^{***}
Aug. and Nov.	95.29	0.660	0.001^{***}
Aug. and Apr.	93.03	0.456	0.001^{***}
Nov. and Apr.	88.48	0.662	0.001^{***}

Note: Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020, and April 2021, respectively). $^{***}p < 0.001$ (extremely significant).

tions and environmental factors was also explained. The points corresponding to June and August were distributed in the second and third quadrants, with environmental conditions had comparable effects on macrobenthic communities in both June and August. In contrast, the points corresponding to April mainly falls within the first and fourth quadrants. The points for November were distributed on both sides of the vertical axis, with different site locations being influenced by distinct environmental factors. The points representing June and August exhibited a similar distribution pattern, indicating their higher similarity, whereas the points for November were scattered and noticeably deviated from those of other months. This aligns with the results of SIMPER analysis and the ANOSIM test.

4 Discussion

4.1 *Spatiotemporal variation of community structure*

Dominant macrobenthos species play a significant role in shaping the community structure and the environmental dynamics within marine ecosystems (Santos and Bloom, 1983; Yan et al., 2020). Changes in dominant species reflect variations in benthic community structure and the transformations within their respective environments (Fukumori et al., 2008). Within the pollution area created by the ‘Hebei Spirit’ oil spill, the dominant species and their abundance also underwent changes corresponding to shifts in the environment and the passage of time (Jung et al., 2017). In this study, many of the dominant species were collected only at specific times, indicating the presence of seasonal succession. In contrast, *S. chinensis* and *A. vadicola* were found in every month, as both of these species have a wide distribution and exhibit strong adaptability to varying temperature and salinity conditions. Furthermore, compared to August and June, there was a distinct increase in the abundance of polychaete species and dominant species number in November and April. Recent researches on macrobenthos in the Zhoushan sea area (Table S2) also reveal a notable upward trend in the quantity of dominant polychaete species, with polychaetes becoming the primary dominant species and *S. chinensis* being a widely distributed representative among them.

Additionally, polychaete *Aglaophamus dibranchis* and *N. oligobranchia* both belong to Nephtyidae. There exists a partial spatial overlap in the distribution range of both species, however, within the maritime expanse of China, *N. oligobranchia* exhibits a more northerly distribution range (Liu, 2008). In this study, *A. dibranchis* emerged as the dominant species in June and August and was absent in November and April, whereas the situation was reversed for *N. oligobranchia*. The phenomenon was the result of seasonal succession and interannual succession.

Particularly, an explosive proliferation of *E. lubrica* was observed in August, which may be attributed to the combined effects of temperature and upwelling. The promoting effects of both factors on the growth and development of mollusks have gained widespread recognition (Thiel, 1978). Simultaneously, the flood season of the Changjiang River and human activity provides a source of nutrients for the growth of mollusks.

The average abundance and biomass of macrobenthos in this study were 127 ind./m^2 and 16.04 g/m^2, respectively. These values are relatively higher compared to the findings of previous studies in the Zhoushan sea area (Table S2). Polychaetes were the primary contributors to species abundance, which was consistent with the findings of a previously reported macrobenthos survey conducted in the Zhoushan sea area from 2019 to 2020 (Song et al., 2022a). Moreover, in this study, the biomass was primarily composed of echinoderms, whereas cnidarians accounted for the majority of the biomass in the

Table 4. SIMPER analysis results: key differentiating species and their contribution rates

Key differentiating species	Jun. and Aug.	Jun. and Nov.	Jun. and Apr.	Aug. and Nov.	Aug. and Apr.	Nov. and Apr.
Endopleura lubrica/%	9.70	1.91	2.48	7.31	9.07	0
Sternaspis chinensis/%	7.68	5.75	7.50	4.56	5.91	4.03
Amphiura vadicola/%	4.39	4.31	5.17	4.21	5.07	5.56
Heteromastus filiformis/%	0.40	0.32	5.44	0	5.03	4.44
Sigambra hanaokai/%	0	9.05	0.77	8.55	0.72	9.06
Prionospio sp./%	0	4.93	0	4.68	0	5.30
Tharyx multifilis/%	0	4.79	0	4.52	0	5.14

Note: Only species with contributions ⩾ 4% in any given month are listed. Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020, and April 2021, respectively).

2019–2020 survey (Song et al., 2022a). Indices such as *d*, *H′*, and *J* serve as effective indicators of ecosystem biodiversity, and the biodiversity levels (*d*, *J*) in the Shengsi Archipelago are relatively higher compared to those within the Zhoushan sea area (Table S2). However, due to differences in calculation methods, *H′* cannot be directly compared across different studies.

4.2 *Biological-environmental relationships*

Marine environmental conditions play a crucial role in shaping the distribution and abundance characteristics of macrobenthos. Different environmental factors exert varying degrees of influence on different macrobenthic species. For instance, the growth of mollusk *Mactra veneriformis* is significantly affected by temperature and salinity conditions (Zou et al., 2018). Excessively high temperatures (⩾32℃) have been shown to significantly reduce the success rate of metamorphosis in echinoderm *Acanthaster cf. solaris* (Lang et al., 2023). Armonies et al. (2023) suggested that the degree of mixing between shell fragments and sandy sediment is a key influencing factor for the macrobenthic community in the North Sea.

In our study, SPM was the primary environmental factor driving variations in the community, similar to its role as the main driver for macrobenthos in the Yushan waters (Sun, 2021). Low concentrations of SPM can serve as a food source for benthic organisms, but high concentrations can lead to the mortality of filter-feeding bivalves, polychaetes, and sediment-feeding echinoderms (Xu et al., 2018) due to the clogging of their feeding apparatus (Nicholls et al., 2003). Furthermore, SPM can affect the primary productivity of phytoplankton in the water column (Li et al., 2023). In regions characterized by elevated SPM concentrations, the intensity of light may limit the primary productivity of the mid-water and bottom-water layers (Ning et al., 2004), indirectly impacting benthic organisms. In our CCA model, different species exhibited varying responses to SPM, indicating differences in the tolerance levels of these species to SPM concentrations. Previous research has shown a positive correlation between SPM and *S. chinensis* (Wu et al., 2015; Xu et al., 2018). However, in our study, a negative correlation between *S. chinensis* and SPM was observed, which could potentially be attributed to the SPM concentration in our study exceeding the threshold that *S. chinensis* can tolerate. Additionally, SPM significantly influenced the variation in community structure. By examining the SPM data for different months (Table 1) alongside the results from the SIMPER analysis and ANOSIM tests, we observed that the community structure and species composition in June and August, which did not exhibit significant differences in SPM, were more similar. Additionally, the concentrations of Hg did not reach the Effects Range-Low (ERL), representing the 10th percentile values below which adverse effects rarely occur (Macdonald et al., 1996). At the same time, dominant species showed similar or contrasting monthly fluctuations (Table 2). Thus, the explanatory power of Hg for the variation in macrobenthos may only have statistical significance rather than ecological significance, as Hg concentrations did not reach hazardous levels. However, the bioaccumulation role of macrobenthos may be overlooked, and further research is needed.

Salinity experiences significant fluctuations within estuarine areas and has a notable impact on the distribution of macrobenthos. However, it was not included in the CCA model due to its lack of statistically significant explanatory power. In this region, the influence of freshwater discharge from the Changjiang River results in lower salinity during summer and higher salinity during other seasons (Table 1). Salinity has been recognized as a primary environmental factor influencing macrobenthos abundance in Hangzhou Bay (Shou et al., 2012), the distribution of macrobenthos in the Jintang Island sea area (Yang et al., 2017), as well as the distribution of shrimp and crab species in the Pishan waters of Zhejiang Province (Jiang et al., 2021). Research conducted in the Zhoushan waters revealed significant positive correlations between Eco-Exergy-based indices and diversity indices (Huang et al., 2020), as well as species richness and abundance (Song et al., 2022b), with salinity. Huang et al. (2020) proposed that marine ecosystems farther away from the coastline tend to be more stable, with higher salinity and lower levels of nutrients and pollutants in the seawater. *Aglaophamus dibranchis* and *E. braunsi*, two of the most dominant species in this study, were mainly distributed in the estuary (Jia et al., 2017, 2022; Tian and Xu, 2015). The higher abundance of these two species during summer (June and August) compared to other times indicates their strong adaptability to lower salinity conditions.

Additionally, in many studies focusing on macrobenthic communities, water depth has been identified as a key influencing factor. Xu et al. (Xu, 2017; Xu et al., 2018) reported on the response of macrobenthic communities to the Kuroshio Current, where water depth was the primary influencing factor in the Kuroshio current area. Water depth was also a major factor influencing the distribution of macrobenthos in the South Yellow Sea (Xu et al., 2016). During jellyfish blooms, water depth remained a primary influencing factor for macrobenthos (Peng et al., 2014). In the southern Yellow Sea and the East China Sea, species diversity generally tended to increase first and then decrease with increasing water depth, which could be attributed to the edge effect of the transition from shallow-water to deep-water communities (Xu et al., 2020). Constrained by the absence of significant differences in depth, no spatial scale differentiation of macrobenthic communities was observed in this study.

In conclusion, SPM was identified as the primary environmental factor influencing macrobenthos in the Shengsi sea area. Additionally, factors such as salinity also had an impact on the macrobenthos in the region. Furthermore, the relatively consistent changes in water depth over time explained why macrobenthos, apart from dominant species, did not exhibit significant differences. The environmental factors influencing macrobenthos exhibit a certain degree of complexity and are susceptible to disturbances from factors such as marine regions, seasons, and ocean currents. Therefore, the study of the relationship between marine macrobenthos and environmental factors requires the accumulation of long-term data and continued in-depth research.

4.3 *Response of macrobenthic community to current patterns*

The temperature and salinity conditions in the study area, as shown in Table 1, exhibited a pattern of high temperature and low salinity with elevated nutrient concentrations during the summer, and low temperature and high salinity with reduced nutrient concentrations during the winter. This pattern is determined by the combined influence of the Changjiang River freshwater discharge and the Taiwan Warm Current. In the Zhoushan waters, the bottom water mass is influenced by the low-temperature, high-salinity bottom layer of the Taiwan Warm Current during the summer, whereas during the winter, it is influenced by the high-temperature, moderately high-salinity surface layer of the Taiwan Warm Current (Zhang et al., 2007b). Nutrients primarily originate from the Changjiang River freshwater discharge and diffuse southward with the Zhe-Min Coastal Current in winter (Zhang et al., 2022), and phosphate levels are jointly regulated by both the Changjiang River freshwater and the Taiwan Warm Current (Shi et al., 2003; Ye et al., 2017). Consequently, seasonal factors lead to the establishment of thermal and salinity conditions characterized by high temperature, low salinity, and elevated nutrient concentrations during the summer, while during the winter, they result in low temperature, high salinity, and reduced nutrient concentrations. Furthermore, the presence of upwelling during the summer leads to a significant increase in Chl *a* in the study area. Although data on Chl *a* for November and April were absent in this study, Jin and Zhuo (2017) reported that high Chl *a* levels in the Zhoushan waters occur during August. Temperature and salinity directly impact the growth of macrobenthos, whereas nutrients and Chl *a* levels affect the availability of food for these organisms. Therefore, our findings suggest that the seasonal variations in oceanic current patterns can significantly impact the environmental conditions that affect macrobenthic communities. The changing conditions resulting from these variations in oceanic currents can have a substantial influence on the composition and dynamics of macrobenthic communities.

However, the abundance, biomass, *S*, and diversity indices (*d*, *H*′, and *J*) of macrobenthos did exhibit some temporal variability, but the overall differences were not statistically significant. Similarly, the study by Xu et al. (2018) on the response of macrobenthic communities to the Kuroshio Current in the East China Sea also indicated a relatively stable species composition and insignificant monthly differences in diversity indices. Likewise, in the macrobenthic community of the southern Yellow Sea, significant differences were observed only in biomass among different months (Xu et al., 2016). In these studies, the dominant species exhibited some seasonal variations, indicating seasonal succession in the macrobenthic community (Xu et al., 2016, 2018). In this study, there were significant changes in the dominant species of macrobenthos overtime, highlighting that despite there were only minor fluctuations in other indices, there was a noticeable seasonal succession in the macrobenthic community within the study area.

Additionally, the macrobenthic community exhibited varying spatial distribution patterns in different months. However, the lowest values of various indices often occurred in the southwest region, which may be influenced by human activities (Qin et al., 2013; Zhu et al., 2020). During the summer (June, August), a blurred pattern of higher abundance in the north and lower abundance in the south was observed. Furthermore, by incorporating salinity data, it became evident that the salinity in the June exhibited a decreasing trend towards the north and an increasing trend towards the south. Therefore, the observed spatial distribution pattern could be attributed to the influence of freshwater discharge from the Changjiang River Estuary.

The macrobenthic community in the Shengsi Archipelago waters did not exhibit significant spatial differentiation in the east-west direction. However, research conducted on a broader spatial scale regarding the response of benthic communities to the Kuroshio Current reveals that the influence of the Kuroshio results in the clear differentiation of benthic communities along the Zhejiang coast into three distinct assemblages characterized by different dominant species (Xu et al., 2018). Additionally, Xu (2017) found that the closer the distance to the main current of the Kuroshio, the higher the species richness within benthic communities. In the East China Sea, benthic organisms are spatially divided into shallow-water and deep-water communities, with the highest abundance and species diversity occurring at depths of 50–60 m, and this phenomenon could be attributed to increased food availability brought by the Kuroshio Current or the edge effect of the transition zone between communities (Liu et al., 2020; Xu et al., 2020). These studies all indicate latitudinal variation in macrobenthic communities in this region.

In the East China Sea, the area where the influence of the Taiwan Warm Current predominantly observed is mainly deeper than the 50 m isobath (Su and Pan, 1989; Xue et al., 2018; Zeng et al., 2012; Zhu et al., 2009), while the area shallower than the 50 m isobath is controlled by the Zhe-Min Coastal Current in winter (Zeng et al., 2012). Furthermore, in the Zhoushan waters, the abundance, biomass, and biodiversity indices of macrobenthos exhibited an increasing trend from nearshore to offshore areas, influenced by terrestrial organic matter input (Jia et al., 2011). Limited by the small spatial scale, our study focused on the 10–20 m depth range of the study area, lacking the direct effect of the Kuroshio, and therefore there were significant differences just in community structure rather than biodiversity.

In summary, on the temporal scale, changes in environmental factors due to variations in oceanic current patterns did not seem to significantly impact macrobenthic biodiversity but rather influenced the community structure. On the spatial scale, the relatively limited spatial extent of this study and the consistent influence of oceanic currents may have contributed to the lack of significant spatial variation in macrobenthos, but in the southwest region, there was a zone characterized by low biodiversity values.

5 Conclusions

This study compared macrobenthic data in the Shengsi sea area and found that there were no significant differences in biodiversity at different times, but the changes in community structure were highly significant. By analyzing marine environmental factors and their relationship with the macrobenthic community, SPM was identified as the primary driving factor. At the scale of this study, changes in environmental factors influenced the community structure more than biodiversity. Additionally, many studies have observed an increasing trend in polychaetes within the macrobenthos of the Zhoushan sea area. Therefore, continuous monitoring of macrobenthos and the marine environment in this area is essential for better adaptation to environmental changes.

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Supplementary information:

Table S1. Temporal variations in mean and standard error of remaining environmental variables in the waters of Shengsi Archipelago.

Table S2. Abundance, biomass, diversity index, and dominant species of macrobenthos in the Zhoushan Sea area in recent years.

Fig. S1. Spatial distribution of the species richness (S) of macrobenthos at different times. Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020 and April 2021, respectively).

Fig. S2. Spatial distribution of abundance of macrobenthos at different times. Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020 and April 2021, respectively).

Fig. S3. Spatial distribution of biomass of macrobenthos at different times. Jun., Aug,. Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020 and April 2021, respectively).

Fig. S4. Spatial distribution of Margalef richness index (d) of macrobenthos at different times. Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020 and April 2021, respectively).

Fig. S5. Spatial distribution of Shannon-Wiener diversity index (H') of macrobenthos at different times. Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020, and April 2021, respectively).

Fig. S6. Spatial distribution of Pielou evenness index (J) of macrobenthos at different times. Jun., Aug., Nov., and Apr. represent different sampling times (June 2010, August 2010, November 2020, and April 2021, respectively).

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