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Community structure and biodiversity of benthic macroalgae in the Shengsi Archipelago of the East China Sea

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Introduction: This study focused on benthic macroalgal communities in the Shengsi Archipelago, East China Sea, a region jointly influenced by pronounced environmental heterogeneity driven by the interplay of the Yangtze River diluted water and the Taiwan Warm Current, and intensive mussel aquaculture. The aim was to characterize spatial patterns in community structure across environmentally distinct zones and to compare contemporary macroalgal assemblages with historical records to identify potential long-term shifts in community composition.

Methods: A field survey was conducted in May 2025 at 30 intertidal stations, spanning from estuary-influenced nearshore areas to offshore island environments. The composition, biomass, and abundance of macroalgal species were quantified, and α -diversity indices and taxonomic distinctness (Δ^+) were calculated. Contemporary spatial patterns were compared with historical data from the same region to assess long-term shifts in community structure and functional-group dominance.

Results: A total of 43 benthic macroalgal species were recorded, with Rhodophyta representing the dominant taxonomic group. Macroalgal communities exhibited a clear “west–low, east–high” spatial pattern, with extremely low biomass and phylogenetic clustering in estuary-proximal areas, and higher biomass, species richness, and taxonomic uniqueness in offshore waters. Comparisons with historical data indicated an over 80% decline in average biomass on natural reefs since 2010, accompanied by a shift in dominance from canopy-forming *Sargassum* to opportunistic *Ulva australis*. Mussel aquaculture zones were associated with relatively high diversity and structural complexity.

Discussion: The results highlight the dominant role of water-mass-driven environmental differentiation in structuring benthic macroalgal communities in the Shengsi Archipelago while also revealing a compensatory role of mussel aquaculture under conditions of natural reef degradation. The study provides important baseline information for evaluating the ecological status and conservation of macroalgae in highly modified estuarine–island systems.

KEYWORDS

community structure, environmental heterogeneity, macroalgae, mussel aquaculture, Shengsi Archipelago, taxonomic distinctness

Introduction

Benthic macroalgae inhabiting rocky shores and reefs in intertidal and shallow subtidal zones constitute a fundamental component of coastal island ecosystems (Chi et al., 2017; Ford et al., 1999). As primary producers, macroalgae play pivotal roles in carbon fixation, nutrient cycling, and the formation of three-dimensional habitats that support diverse assemblages of fishes and invertebrates (Komatsu and Tatsukawa, 1999; Zou and Gao, 2002; He et al., 2015). However, macroalgal-dominated habitats are increasingly being threatened by the combined pressures of ocean warming, coastal eutrophication, acidification, and intensified human activities (Adey and Steneck, 2001; Peng et al., 2009; Zhang et al., 2022). In many temperate and subtropical regions, these pressures have been associated with pronounced ecological changes, including the decline of canopy-forming brown algae and their replacement by low-biomass, opportunistic turf-forming species (Kautsky et al., 1986; Benedetti-Cecchi et al., 2001; Sun et al., 2010). Such shifts have been linked to reduced habitat complexity, biodiversity loss, and weakened ecosystem resilience, underscoring the need for assessments of macroalgal communities across complex environmental gradients.

The Shengsi Archipelago, located at the interface between the Yangtze River (Changjiang) Estuary and the East China Sea, represents a hydrographically heterogeneous and ecologically sensitive island system (Wang et al., 2024). This region lies at the convergence of nutrient-rich, low-salinity riverine waters and high-salinity offshore currents influenced by the Taiwan Warm Current and the Yellow Sea Coastal Current (Liu, 2013; Wang et al., 2024). Consequently, there is pronounced spatial heterogeneity in salinity, turbidity, and nutrient availability across relatively short distances from the western islands near the estuary to the more oceanic eastern islands (Zhang et al., 2008b; Bi et al., 2018). Historically, such environmental heterogeneity has supported diverse macroalgal communities and positioned the archipelago as a biogeographical transition zone between warm-water and cold-temperate floras (Zhou and Yang, 2001; Liu, 2013). In recent decades, however, long-term changes in sediment discharge and nutrient inputs from the Yangtze River have altered the coastal conditions, imposing increasing stress on benthic macroalgae (Yang et al., 2006; Bi et al., 2018; Zhan et al., 2024).

In addition to natural river–sea gradients, the Shengsi Archipelago has been subject to intensive human modification, particularly through the expansion of marine aquaculture (Xiong and Wu, 2024). The waters surrounding Gouqi Island host one of the largest mussel (*Mytilus coruscus*) raft farms in China (Huang et al., 2017; Shen et al., 2025). The ecological implications of these artificial floating structures remain controversial. While high-density aquaculture may enhance nutrient availability, alter hydrodynamics, and increase shading near the seabed, it may also create novel habitats by providing attachment substrates in the upper water column, where light conditions are more favorable than in turbid nearshore waters (Bao et al., 2020). As a result, aquaculture-associated habitats may support macroalgal assemblages that differ from those on adjacent natural reefs (Huang et al., 2017; Bao et al.,

2020). Understanding how such artificial structures interact with natural environmental variability to shape the spatial patterns of macroalgal communities is essential for evaluating ecological trade-offs in intensively utilized island systems.

Despite the ecological and economic importance of the Shengsi Archipelago, previous investigations in this region have largely focused on individual islands or descriptive species inventories (Zhou and Yang, 2001; Lin et al., 2012). Studies that explicitly integrate river–sea environmental differentiation with habitat differences between natural reefs and aquaculture-associated structures remain scarce. Moreover, most available research has relied primarily on traditional diversity metrics that do not account for phylogenetic relationships among species and may be sensitive to uneven sampling effort (Huang et al., 2017). Taxonomic distinctness indices, such as average taxonomic distinctness ($\Delta+$), provide a complementary approach by incorporating evolutionary relatedness and offering robust indicators of community structure under varying degrees of anthropogenic influence (Warwick and Clarke, 1995; Zhang et al., 2025).

In this study, we conducted a spatially explicit survey of benthic macroalgal communities at 30 intertidal stations across the Shengsi Archipelago. By integrating community composition, biomass, abundance, diversity indices, and taxonomic distinctness metrics, we aimed to (1) characterize the spatial patterns in macroalgal community structure across environmentally distinct zones shaped by differential water mass influence and aquaculture activity, (2) compare macroalgal assemblages between natural reefs and aquaculture-associated habitats, and (3) examine the structure and taxonomic composition of macroalgal communities under combined natural and anthropogenic influences. This cross-sectional assessment provides a snapshot of macroalgal biodiversity and community organization in a dynamic estuarine–island system, offering baseline data for future monitoring and management of coastal “underwater forests” in the East China Sea.

Materials and methods

Study area and sampling sites

The Shengsi Islands (30°40′–30°52′ N, 122°26′–122°50′ E) are located in the northeast of the Zhoushan Archipelago, Zhejiang Province, China. This region is situated at the confluence of the Yangtze River estuary, the Jiangsu-Zhejiang coastal current, and the Taiwan Warm Current. The location creates a complex hydrographic environment characterized by significant gradients in nutrient levels and significant variation in turbidity (Wang et al., 2024).

Thirty intertidal sampling stations were established across the archipelago to investigate the spatial patterns of macroalgal diversity (Figure 1; Supplementary Table 1). The approximate centroid distances between adjacent areas are 22 km (A–B), 17 km (B–C), and 29 km (A–C). The study area was divided into three sectors based on the dominant water masses influencing each zone:

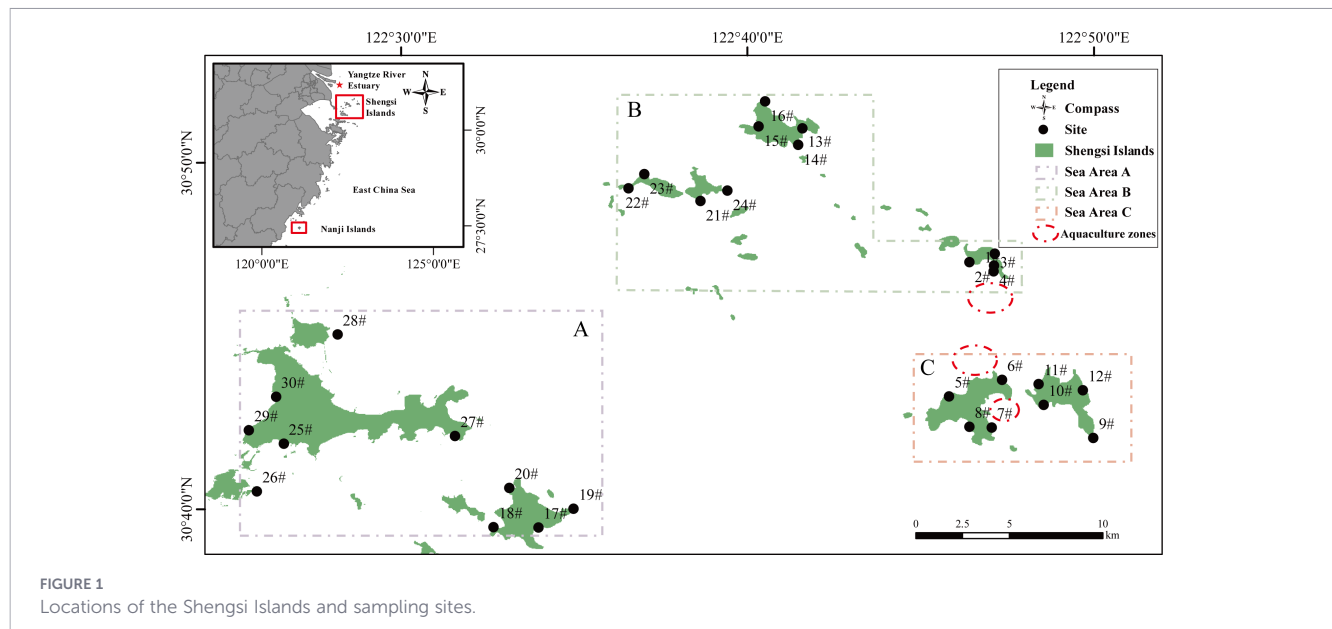


FIGURE 1
Locations of the Shengsi Islands and sampling sites.

Sea Area A (Western) comprised the islands closest to the Yangtze River mouth (e.g., Huanglong and Main Shengsi Island) and was characterized by lower salinity and higher turbidity.

Sea Area B (Central) comprised the Huaniao and Lvhu islands and represented a transition zone.

Sea Area C (Eastern) comprised the Shengshan and Gouqi islands and was characterized by the highest salinity and water transparency among the three areas. However, this area also hosts the mussel (*M. coruscus*) farming zone, and bivalve excretion contributes additional dissolved inorganic nitrogen and phosphorus to the local waters (Bao et al., 2020).

Key environmental parameters were measured synchronously at each station during the field survey (Supplementary Table 2). Intensive aquaculture zones were concentrated north of Station 5, south of the 6–7–8 station area, and south of Stations 1–4 around Bixia Island. The farms were dominated by *M. coruscus*, with a smaller contribution from *Mytilus galloprovincialis*.

Sample collection and processing

The field survey was conducted from May 11 to 15, 2025. At each station, three replicate quadrats (25 cm × 25 cm) were placed on rocky substrate within the mid-intertidal zone where macroalgal coverage was visually representative of the surrounding area. All macroalgae within the quadrats were scraped from the substrate, washed *in situ* to remove sediment and epiphytes, and then blotted on absorbent paper before being returned to the laboratory in sampling bags for species identification and fresh-weight determination using an electronic balance (accuracy 0.01 g). The entire survey was conducted in accordance with the Marine Survey Specifications (First Institute of Oceanography et al., 2007a, b).

Taxonomic identification was based on the classification systems and diagnostic descriptions provided in *Flora Algarum Sinicarum Aquae Dulcis et Maris Sinensis* (Chinese Algal Flora) (Tseng, 2000; Xia, 2004; Ding and Luan, 2013) and the *Color Atlas of Marine Algae in Zhejiang* (Hang and Sun, 1983). Scientific names

and higher-level classifications were subsequently checked and updated according to AlgaeBase (<https://www.algaebase.org>).

Biomass was expressed as fresh weight and later standardized to g m⁻² based on quadrat area. Abundance was recorded as the number of individuals (or discrete thalli/ramets, depending on the taxon morphology) per quadrat and standardized to ind m⁻².

Community structure and biodiversity indices

The importance of each species within the community was assessed using the dominance index (Y) calculated by McNaughton's formula (Liao, 2021): $Y = (N_i/N) f_i$, where N_i is the biomass of species i , N is the total biomass of all species, and f_i is the frequency of occurrence of species i across the quadrats. A species was considered dominant when $Y \geq 0.02$.

To evaluate the α -diversity of macroalgal communities, the following indices were calculated for each station:

The Shannon-Wiener diversity index (H'): $H' = -\sum (P_i) (\ln P_i)$, where P_i is the proportion of the i -th species.

Pielou's evenness index (J'): $J' = H'/\ln S$, where S is the total number of species.

Margalef's richness index (D): $D = 1 - \sum \ln P_i^2$, where P_i is the proportion of species i 's biomass relative to the total biomass at the sampling site (Wang et al., 2025).

An UpSet plot was constructed using the UpSetR package in R to visualize the intersection and uniqueness of species compositions across the three sea areas in order to identify cosmopolitan species and those restricted to specific environmental gradients. The spatial distributions of biomass, abundance, and diversity indices were visualized using ArcGIS 10.8 (ESRI, USA). Inverse Distance Weighting and Kriging interpolation were employed to generate continuous surface maps. Cluster analysis was performed to evaluate the similarity of algal communities among the 30 stations. The Bray-Curtis similarity coefficient was calculated from a matrix of square-root transformed biomass data. Hierarchical clustering was

performed using the group average method. Community similarity between sampling sites was assessed using Sorenson's similarity coefficient based on shared species composition, consistent with classical plant community similarity metrics.

Taxonomic distinctness analysis

Taxonomic distinctness was analyzed to assess phylogenetic diversity based on the Linnean hierarchy (phylum, class, order, family, genus, and species). Three primary indices were calculated using PRIMER v7 (Plymouth Routines in Multivariate Ecological Research): taxonomic diversity/distinctness (Δ^*), average taxonomic distinctness (Δ^+), and variation in taxonomic distinctness (Δ^+) (Clarke and Warwick, 2001; Warwick and Clarke, 1995).

These indices quantify the average path length between taxa on a Linnean hierarchical tree and are relatively robust to unequal sampling effort compared to raw richness. A master species list for the Shengsi Islands was compiled for randomization tests (1,000 permutations). Funnel plots were generated to visualize whether the observed and expected values at each station fell within the 95% confidence intervals of the regional species pool.

Statistical analysis

The differences in biomass, abundance, and diversity indices among the three sea areas were analyzed using one-way analysis of variance (ANOVA), followed by Duncan's multiple range test for *post-hoc* comparisons. The data were tested for normality and homogeneity of variances prior to analysis. Non-metric multidimensional scaling (NMDS) based on the Bray-Curtis similarity matrix was performed to visualize community similarity, and the significance of spatial grouping was tested using analysis of similarities (ANOSIM). All statistical analyses and visualizations (box plots, stacked bars, and UpSet plots) were conducted using SPSS 26.0 and R software (v.4.3.2) with the ggplot2, UpSetR, and vegan packages as well as PRIMER v.7. A significance level of $p < 0.05$ was applied for all tests.

Results and discussion

Community composition and spatial distribution patterns

The algal community of the Shengsi Archipelago exhibited a distinct taxonomic structure dominated by warm-temperate and subtropical elements. A total of 43 benthic macroalgal species belonging to four phyla and 30 genera were identified (Figure 2A). The community structure was dominated by the phylum Rhodophyta, which accounted for the highest diversity with 26 species (60.47%), followed by Heterokontophyta, Phaeophyceae (10 species, 23.26%) and Chlorophyta (six species, 13.95%). In comparison, Cyanobacteria exhibited the lowest diversity with only one species (2.33%). The dominance of Rhodophyta across all sea areas is consistent with the floral characteristics of the East China Sea, such as in the adjacent Dongtou (Wang et al., 2012) and Nanji archipelagos

(Wang et al., 2025). The Feldmann R/P ratio (Rhodophyta/Heterokontophyta (Phaeophyceae) species number; Feldmann, 1937) for the entire survey was 2.6 (26/10), falling within the warm-temperate range (2.0–4.0), which is broadly consistent with a warm-temperate floristic affinity. Red algae typically exhibit higher speciation rates and broader vertical distributions in intertidal zones than other phyla in such warm-temperate regions (Tseng, 1983; Zhou and Yang, 2001).

In terms of ecological dominance, the community was driven by a mix of opportunistic green algae and canopy-forming brown algae. The five most abundant species were *Ulva australis* (dominance index, $Y = 0.156$), *Sargassum fusiforme* ($Y = 0.089$), *Sargassum thunbergii* ($Y = 0.043$), *Scytosiphon lomentaria* ($Y = 0.032$), and *Chondria crassicaulis* ($Y = 0.021$) (Supplementary Table 3). The co-dominance of ephemeral *Ulva* species and perennial *Sargassum* species suggests that the region is currently in a transitional state, subject to both eutrophication pressures (Fan et al., 2014) and the remnant presence of perennial *Sargassum* canopy communities historically dominant in this region (Lin et al., 2012; Bi et al., 2018).

The macroalgal community exhibited significant spatial heterogeneity in biomass and abundance, revealing a complex pattern driven by the differential influence of riverine and oceanic water masses, together with localized anthropogenic interventions such as mussel aquaculture (Figures 2B, C; Supplementary Tables 4, 5). In contrast to a simple linear gradient, the distribution of biomass showed a distinct “west-low, east-high” trend. The lowest average biomass was recorded at Station 25 (35.64 g·m⁻²) in Sea Area A (east of Huanglong Island) (Figure 2B), the area most strongly influenced by the Yangtze River diluted water. This western zone exhibited the highest turbidity and lowest salinity among the three sea areas (Supplementary Table 2), reflecting the strong influence of suspended sediment and low-salinity riverine plume from the Yangtze River (Wang et al., 2024). The high turbidity in this area severely attenuates photosynthetically active radiation, restricting the vertical distribution and growth rates of perennial canopy-forming algae such as *Sargassum*, which matches historical observations of algal decline in turbid nearshore waters of the Ma'an Archipelago (Zhou and Yang, 2001; Bi et al., 2018). In addition to light limitation, intensified coastal reclamation and port construction over the past two decades have physically disturbed the intertidal substrate in the western Shengsi Islands, further reducing suitable habitat for macroalgal colonization (Chi et al., 2023).

In contrast, the highest average biomass was recorded at Station 7 (1875.36 g·m⁻²) located in Sea Area C (west of Gouqi Island) (Figure 2B). The exceptionally high biomass in Sea Area C, particularly around Gouqi Island, can be attributed to the combined effects of improved water transparency (associated with reduced influence of the Yangtze River plume) and extensive mussel (*M. coruscus*) aquaculture (Shen et al., 2025). Gouqi Island is a national center for mussel farming, and the aquaculture rafts and infrastructure may exert a fertilization effect due to the excretion of dissolved inorganic nitrogen and phosphorus by bivalves, thereby relieving nutrient limitation for macroalgae (Bao et al., 2020; Wang et al., 2024). Furthermore, other stations in Sea Area C (e.g., Stations 5 and 6) maintained relatively high biomass (Figure 2B), suggesting that the high macroalgal biomass in this area results from the

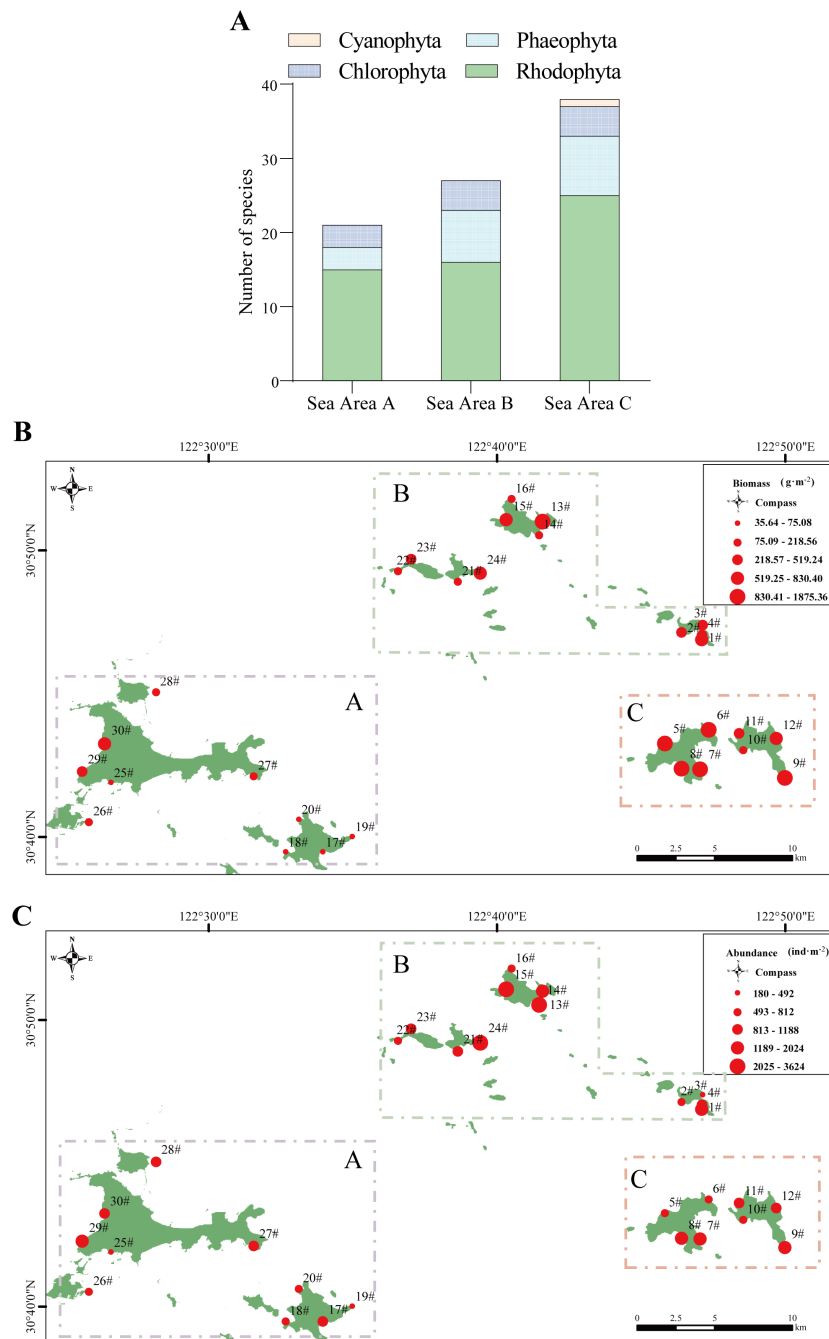


FIGURE 2

Spatial patterns of benthic macroalgal composition, biomass, and abundance across the Shengsi Archipelago. (A) Species richness of benthic macroalgae belonging to different phyla in the three sea areas. (B) Spatial distribution of average macroalgal biomass at the 30 sampling stations. (C) Spatial distribution of average macroalgal abundance at the 30 sampling stations.

combined effects of favorable light conditions associated with the Taiwan Warm Current and nutrient enrichment from intensive mussel aquaculture (Zhang et al., 2008a; Liu, 2013; Costanzo et al., 2001). However, no pre-aquaculture baseline data are available for this region, and the relative contributions of natural oceanographic conditions versus aquaculture-derived nutrients to the observed biodiversity remain to be disentangled. The elevated dissolved inorganic nitrogen concentration in Sea Area C ($0.421 \pm 0.089 \text{ mg}\cdot\text{L}^{-1}$; Supplementary Table 2), which exceeded that in the

transitional Sea Area B ($0.12 \pm 0.02 \text{ mg}\cdot\text{L}^{-1}$) despite the greater distance from the estuary, provides direct evidence that aquaculture-derived nutrient enrichment contributes substantially to the high macroalgal biomass in this area. More broadly, stable isotope studies have demonstrated that macroalgal tissues effectively integrate nitrogen from multiple anthropogenic sources, including aquaculture effluents, through shifts in tissue $\delta^{15}\text{N}$ signatures (Costanzo et al., 2001; Viana and Bode, 2013). In the Gouqi Island farming zone specifically, Shen et al. (2025) confirmed

through ^{13}C stable isotope tracing that sessile macroalgae on mussel rafts actively assimilate dissolved inorganic carbon under the nutrient-enriched conditions created by bivalve excretion. These findings collectively suggest that the high macroalgal abundance and diversity in Sea Area C reflect not only favorable oceanic light conditions but also the fertilization effect of aquaculture-derived nutrients, which may support a wider range of species by alleviating nutrient limitation across different functional groups.

Interestingly, the spatial pattern of abundance (Figure 2C) was decoupled from biomass, revealing a complex non-linear response to environmental gradients. The highest average abundance was observed at Station 24 (3624 ind. m^{-2}) in the transitional Sea Area B (Lvhu Island). This high individual abundance, coupled with moderate biomass, indicates a community dominated by small-sized r-strategists (e.g., filamentous *Ulva* and *Cladophora* species) (Sousa, 1979; Littler and Littler, 1980). This suggests that the transitional waters provide sufficient nutrients for rapid recruitment and proliferation (Fan et al., 2014) but lack the stability required for large canopy species to establish dominance (Connell, 1978).

Stations in Sea Area A exhibited relatively low biomass and abundance, with Station 25 recording the lowest values in the entire survey. The high turbidity and sedimentation stress characteristic of this estuarine-influenced zone are known to inhibit macroalgal settlement, growth, and survival on rocky substrata (Airolidi, 2003), which likely accounts for the lower macroalgal biomass generally observed in this area. Within-zone variation among stations (e.g., Stations 26 and 29 supported somewhat higher biomass; Supplementary Table 4) may reflect local-scale differences in microhabitat conditions that were not captured by our area-level environmental measurements. Meanwhile, the eastern offshore stations (Sea Area C) maintained high biomass with moderate abundance, a characteristic of mature communities structured by K-strategists (e.g., *S. fusiforme*). These organisms occupy more space per individual and are able to competitively exclude smaller ephemeral species (Steneck et al., 2002). Thus, the archipelago displays a shift from stress-inhibited assemblages in the west, to opportunistic-proliferating communities in the transition zone, and finally to competition-structured forests in the east.

Community similarity and clustering patterns

The similarity analysis of benthic macroalgal communities revealed distinct spatial clustering that reflected the interplay between natural environmental gradients and anthropogenic aquaculture activity. The hierarchical cluster analysis, based on the Bray-Curtis similarity of species biomass, classified the 30 sampling stations into three statistically significant groups (ANOSIM, $p < 0.05$) (Figure 3A). Pairwise tests confirmed significant separation between Group 1 and Group 2 ($R = 0.297$, $p = 0.004$) and between Group 1 and Group 3 ($R = 0.600$, $p = 0.001$), while Groups 2 and 3 showed partial overlap ($R = 0.137$, $p = 0.067$), consistent with their shared oceanic influence. While these clusters generally corresponded to the geographic gradient from the estuary to the open sea, they also highlighted the influence of local habitats.

Group 1 comprised stations from the western Sea Area A (e.g., Stations 17, 18, 19, 20, 25, and 26). Geographically, these stations are located closest to the Yangtze River Estuary and are subject to the strongest influence of Yangtze River-diluted water (Wang et al., 2024). The high turbidity and lower salinity in this region act as a severe environmental filter, homogenizing the community structure by restricting it to a limited set of stress-tolerant species (Airolidi, 2003). Consequently, the stations within this group exhibited high within-group similarity but low similarity to the offshore groups, highlighting a distinct “estuarine community” characterized by low species richness and the dominance of opportunistic green algae (Lin et al., 2012).

The offshore stations were assigned to Groups 2 and 3, representing communities in the clearer, highly saline waters influenced by the Taiwan Warm Current (Liu, 2013). Notably, Group 3 clustered with Stations 2 and 4 (Bixia Island in Sea Area B) and with Stations 6, 7, and 8 (Gouqi Island in Sea Area C). Although Bixia Island is geographically positioned in the eastern portion of the archipelago, its relatively sheltered location between the main island groups exposes it to the influence of the Jiangsu-Zhejiang Coastal Current, making its hydrographic conditions more transitional than those of the more oceanic Shengshan-Gouqi area; it was therefore assigned to Sea Area B. Nevertheless, the clustering of

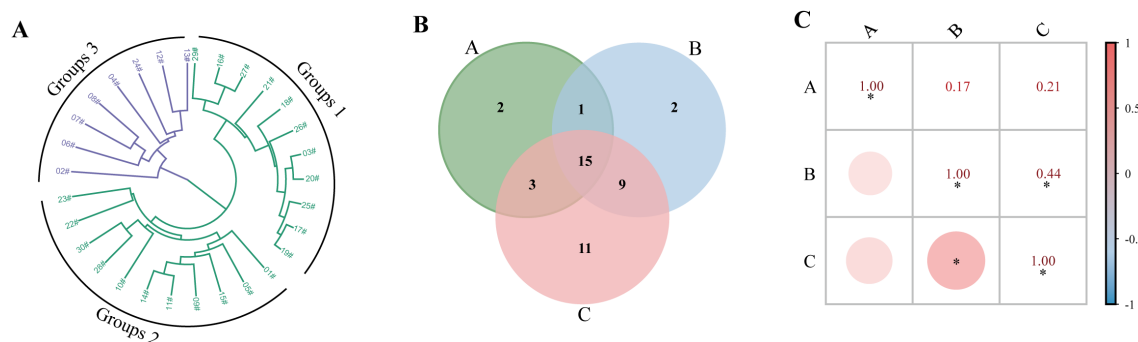


FIGURE 3

Community similarity and spatial distribution patterns of benthic macroalgae in the Shengsi Archipelago. (A) Hierarchical cluster dendrogram of 30 sampling stations based on Bray-Curtis similarity of biomass data. (B) Venn diagram illustrating the number of unique and shared species among three sea areas. (C) Heatmap of pairwise similarity indices between the three sea areas, with the color gradient indicating the degree of floristic overlap. The numbers represent the similarity between different sea areas, * $P < 0.05$.

Stations 2 and 4 with the Gouqi Island stations suggests that aquaculture activities surrounding Bixia Island may override the background hydrographic differences, exerting a “habitat homogenization” effect (Forrest et al., 2009). The presence of bivalve metabolic byproducts creates a nutrient-rich microenvironment that favors similar algal assemblages (Huang et al., 2017; Bao et al., 2020).

A Venn diagram analysis identified a robust “core community” comprising 15 cosmopolitan species common to all three zones (Figure 3B; Supplementary Table 6). These widespread species, including the dominant *U. australis*, *S. thunbergii*, and *Corallina officinalis*, accounted for a significant proportion (34.88%) of the total biodiversity. Their broad distribution indicated high phenotypic plasticity and euryhaline traits. For example, *U. australis* was recorded at 28 of the 30 stations across the full salinity (27.99–32.20 PSU) and turbidity (Secchi depth 0.36–5.30 m) ranges of the archipelago (Supplementary Table 4), consistent with the well-documented euryhaline tolerance of *Ulva* species (Fan et al., 2014). Similarly, *S. thunbergii* occurred in all three sea areas despite marked differences in environmental conditions. These traits enable such species to tolerate the wide fluctuations in salinity and turbidity characteristic of the Yangtze estuary (Zhang et al., 2008ab). In terms of pairwise similarity, Sea Areas B and C exhibited the highest overlap (Figure 3C; Supplementary Table 6), sharing 24 species, consistent with their similar oceanic hydrographic conditions. Conversely, Sea Area C hosted the highest number of unique species (11 species) that were absent in other areas, including *Petalonia fascia*, *Dictyota coriacea*, and *Laurencia* sp. Under the Ecological Evaluation Index (EEI) framework (Orfanidis et al., 2003, 2011), these species span different ecological status groups: *Dictyota coriacea* and *Laurencia* sp. are thick perennial or corticated taxa classified as late-successional species (ESG I), indicative of relatively undisturbed conditions, whereas *Petalonia fascia*, a sheet-form brown alga, belongs to the opportunistic group (ESG II). The co-occurrence of both ESG I and ESG II taxa exclusively in Sea Area C suggests that this offshore environment supports a functionally diverse community encompassing multiple successional stages, in contrast to the western zones where only ESG II opportunistic species persist. Unlike the opportunistic green algae found in the nearshore, the ESG I taxa among these unique species are typically stenohaline and sensitive to sedimentation (Airoldi, 2003). Previous studies in the Ma'an Archipelago have indicated that high turbidity and sediment deposition can inhibit the settlement of *Sargassum* zygotes and reduce the photosynthetic efficiency of subtidal macrophytes (Bi et al., 2018). The offshore waters of Sea Area C are buffered by the high-salinity Taiwan Warm Current, which maintains greater transparency and stable salinity (Liu, 2013; Zhang et al., 2008b). Therefore, the survival of these sensitive taxa in Sea Area C confirms that the eastern offshore waters, buffered by the Taiwan Warm Current, preserve the structural integrity of the East China Sea's native algal flora, which has been largely filtered out in the turbid western zones.

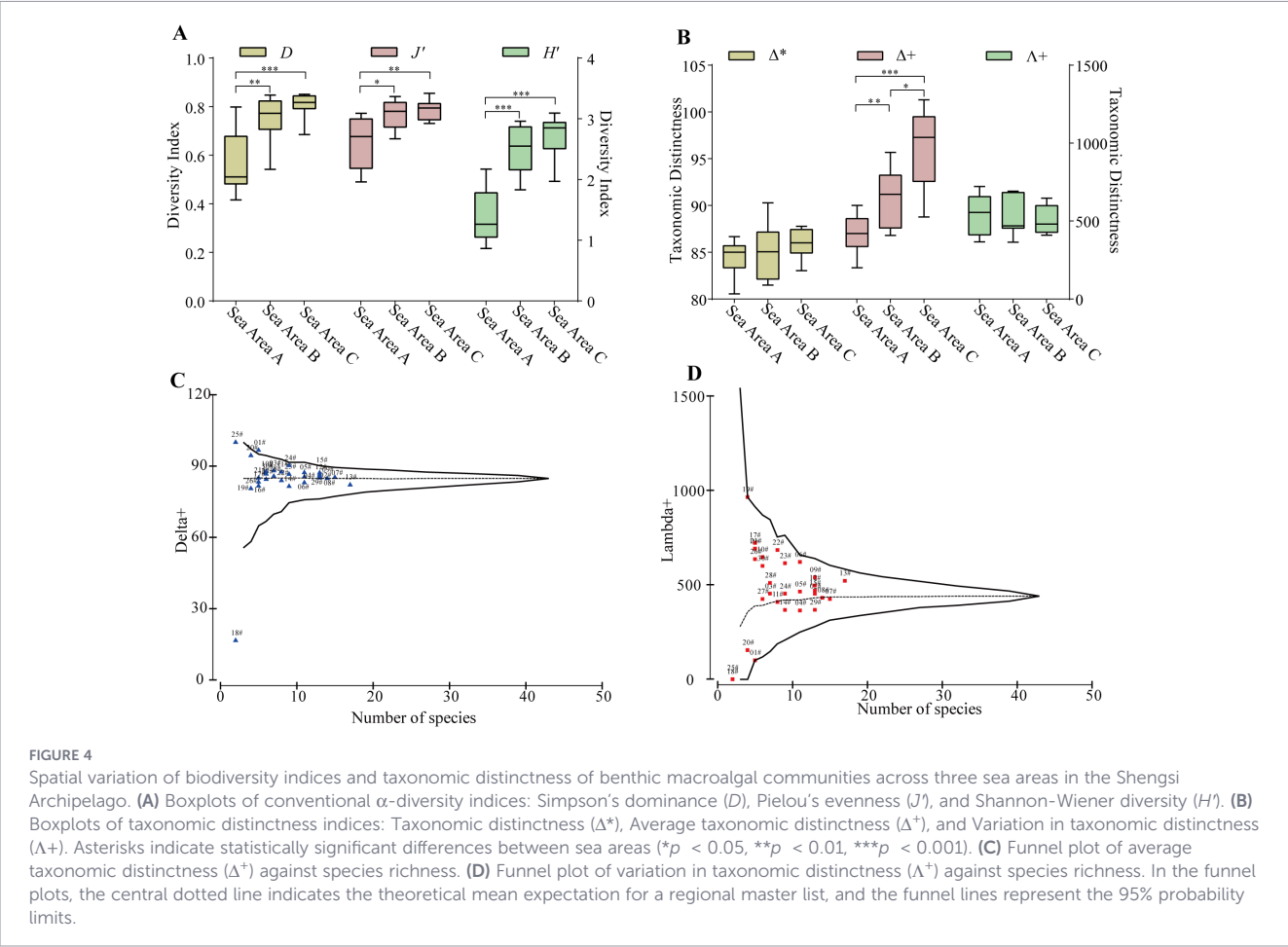
α -diversity and taxonomic characteristics

The α -diversity indices, including Shannon-Wiener (H'), Pielou's evenness (J'), and Simpson's dominance (D), showed a

clear increasing trend from the nearshore to the offshore waters. Sea Area A (nearshore) was characterized by the lowest biodiversity (Figure 4A). Specifically, the lowest Shannon index was recorded at Station 18 ($H' = 0.864$), followed by Station 25 ($H' = 0.943$) (Supplementary Table 7). While both stations exhibited low diversity, they reflected distinct ecological responses to estuarine stress. The low diversity at Station 18 was driven by the over-dominance of stress-tolerant opportunistic species (e.g., *Ulva australis*). Although Station 18 is far from the aquaculture zones, Sea Area A receives elevated dissolved inorganic nitrogen from the Yangtze River plume (Supplementary Table 2), creating nutrient-enriched but severely light-limited conditions. Under such conditions, fast-growing opportunistic *Ulva* species are favored over slower-growing perennial taxa (Fan et al., 2014). In contrast, Station 25 recorded the lowest values for both biomass and abundance across the entire archipelago. This indicated that severe environmental filtering—likely due to extreme turbidity and scouring from the Yangtze River plume—exceeded the tolerance limits of most species, preventing even opportunistic taxa from proliferating and resulting in a structurally depauperate community (Bi et al., 2018).

In contrast, Sea Area C (offshore) maintained the highest biodiversity levels, with the maximum Shannon-Wiener index recorded at Station 8 ($H' = 3.095$), located west of Gouqi Island, followed closely by Station 15 ($H' = 2.962$) and Station 5 ($H' = 2.957$) (Supplementary Table 7). Notably, Station 8, with the highest biodiversity, is located within the mussel (*M. coruscus*) aquaculture zone of Gouqi Island (Shen et al., 2025). The community at Station 8 exhibited both high species richness and evenness. Among these, *U. australis* and *C. crassicaulis* are nutrient-tolerant species capable of rapid nitrogen uptake under enriched conditions (Fan et al., 2014), while perennial canopy-forming species such as *S. fusiforme*, *S. thunbergii*, and *S. vachellianum* co-occurred at the same site (Supplementary Table 4). This is consistent with evidence that moderate nutrient enrichment by invertebrates, including bivalves, can increase macroalgal diversity by alleviating nutrient limitation (Bracken and Nielsen, 2004), suggesting that the local aquaculture environment sustains a complex assemblage comparable to, or exceeding, that of natural offshore reefs (Huang et al., 2017; Bao et al., 2020).

The analysis further elucidated the phylogenetic structure of the communities (Figure 4B). The average taxonomic distinctness (Δ^+), defined as the average path length between species in the Linnaean taxonomic tree, was significantly higher in Sea Area C than in Sea Area A ($p < 0.001$). This indicated that the offshore communities in Area C were not only species-rich but also phylogenetically diverse, composed of species from distantly related lineages (e.g., a balanced mix of Heterokontophyta (Phaeophyceae), Rhodophyta, and Chlorophyta). Conversely, the lower value in Sea Area A suggested a “phylogenetic clustering” effect, where the estuarine environment filters out sensitive lineages, leaving behind a community composed of closely related species (mostly within the genus *Ulva* or *Grateloupia*) that share similar physiological traits to cope with the stress of sedimentation (Warwick and Clarke, 1995; Zhang et al., 2025). Furthermore, a cluster analysis of diversity indices (Table 1) classified the stations into three groups with distinct ecological characteristics. Group 3, primarily consisting of offshore areas (e.g., Stations 2, 4, 7, and 8), exhibited the highest average Shannon index ($H'_{\text{mean}} = 2.780$) and high taxonomic



differentiation (Δ^* mean = 85.28). These stations are all located in proximity to intensive mussel aquaculture zones, where bivalve-derived nutrient enrichment may promote macroalgal diversity by alleviating nutrient limitation (Bracken and Nielsen, 2004). In addition, these stations are distributed across separate islands (Bixia and Gouqi islands), each subject to distinct local environmental conditions such as wave exposure, substrate type, and current regime, which may contribute to the high taxonomic differentiation observed among them. In contrast, Group 1, dominated by nearshore stations (e.g., Stations 17, 18, and 19), exhibited the lowest average diversity (H' mean = 1.546), consistent with a simplified estuarine stress community (Lin et al., 2012).

To assess ecological health and detect potential anthropogenic disturbances, taxonomic distinctness indices were plotted against species richness using 95% probability funnels (Figure 4C). The majority of stations from the offshore Sea Areas B and C, including those located within intensive mussel aquaculture zones (e.g., Station 8), were within the 95% confidence limits. This indicated that the phylogenetic breadth at these stations remains within the expected range for the regional species pool. However, in the absence of time-series environmental data since the establishment of mussel farms, the possibility that native species have been progressively replaced by opportunistic or stress-tolerant taxa

TABLE 1 Taxonomic diversity indices of major benthic algae in the Shengsi Archipelago.

Group 1			Group 2			Group 3		
Site	Δ^*	H'	Site	Δ^*	H'	2#	85.043	2.656
3#	88.095	2.172	1#**	96.667	1.298	4#	85.455	2.863
16#	81.667	1.160	5#	87.273	2.957	6#	83.030	2.816
17#	83.333	1.243	9#	85.684	2.783	7#	85.238	2.890
18#*	16.667	0.864	10#	87.778	1.972	8#	84.799	3.095
19#	80.556	1.287	11#	87.500	2.413	12#	86.325	2.905
20#	94.444	1.153	14#*	81.481	2.405	13#*	82.108	2.894
21#	85.000	1.833	15#	87.179	2.962	24#**	90.278	2.118
25#**	100.000	0.943	22#	83.929	2.447			
26#	85.000	1.732	23#	86.574	2.797			
27#	84.444	1.838	28#	85.714	2.171			
29#	85.043	2.783	30#	86.667	1.266			
Δ^* mean = 80.386			Δ^* mean = 86.950			Δ^* mean = 85.284		
H' mean = 1.546			H' mean = 2.315			H' mean = 2.780		

*Indicates the station with the minimum within-group classification difference index; **indicates the station with the maximum within-group classification difference index.

cannot be excluded (Huang et al., 2017; Bao et al., 2020). In contrast, Station 18 was a distinct outlier, falling significantly below the 95% probability funnel. This indicates a severe loss of phylogenetic diversity, as the community comprises several closely related species (e.g., opportunistic green algae). This degradation is likely driven by the combined effects of high turbidity from the Yangtze River plume and local coastal engineering activities (Bi et al., 2018; Chi et al., 2023).

Historical evolution of macroalgal communities in Gouqi Island

A temporal comparison of macroalgal communities in Gouqi Island from 2010 to 2025 revealed significant ecological restructuring, characterized by a transition from a mature climax community to a simplified, opportunistic-dominated system (Table 2). Historically, the intertidal zone in 2010–2011 supported a stable “underwater forest” ecosystem dominated by large perennial brown algae (*Sargassum* spp.) and calcified red algae (*Corallina officinalis*) with a large spring biomass (>8195.00 g·m⁻²) and high biodiversity (87 species) (Lin et al., 2012). However, the present study (2025) indicates a severe functional regression of this natural community. The current average biomass in natural reefs (1486.44 g·m⁻²) represents a precipitous decline of more than 80% compared to historical peaks (Lin et al., 2012). This collapse is further evidenced by a shift in dominance. While the community was historically anchored by perennial canopy-forming species, the present study demonstrated that the opportunistic green alga *Ulva australis* has become dominant (*Y* = 0.156), surpassing perennial *Sargassum* species (Supplementary Table 3). The elevation of ephemeral, r-selected *Ulva* species, coupled with the collapse in overall biomass, is a classic indicator of ecosystem retrogression driven by long-term environmental stresses such as coastal eutrophication and ocean warming.

The extensive mussel aquaculture activities in the region appear to play a critical yet compensatory role in the severe degradation of natural habitats. Historical surveys of mussel culture rafts (2014–2016) demonstrated that these floating structures supported significantly higher species richness (70 species) and a peak spring biomass of 12,599.35 g·m⁻², nearly 10 times that of the current natural reefs (Huang et al., 2017; Bao et al., 2020). This is consistent with our observation at Station 8, located within the aquaculture zone, which maintained the highest relative biomass and diversity in the present survey (Figure 2B; Supplementary Table 7).

These findings suggest that aquaculture infrastructure functions as an “artificial refuge” for macroalgae amid benthic habitat deterioration (Huang et al., 2017). The mechanism likely involves the provision of suspended vertical substrates that allow macroalgae to grow in the upper water column, escaping the severe light limitation caused by high turbidity near the seabed—a primary stressor in the Yangtze River estuary (Bao et al., 2020). Furthermore, nutrients excreted by mussels may locally alleviate nutrient limitation, fostering “oasis” conditions for algal growth (Zhang et al., 2008a; Wang et al., 2024). Station 8 retained the protected species *Sargassum vachellianum* that has largely vanished from other natural shorelines. This indicates that, while natural reefs are shifting toward turf-dominated, degraded states, aquaculture zones may inadvertently serve as reservoirs for regional algal germplasm, preserving the functional structure of historical “marine forests” that can no longer persist on the natural benthos.

Conclusion

This study has provided a comprehensive, spatially explicit assessment of benthic macroalgal communities across the Shengsi

TABLE 2 Variation in taxonomic composition of macroalgal communities in Gouqi Island from 2010 to 2025.

Survey period/habitat	Total species	Phylum	Number of species/ (percentage)	Dominant species	Biomass (g·m ⁻²)*	Data source
2010.08–2011.0 (Natural intertidal zone)	87	Rhodophyta	60 (69.0%)	<i>Sargassum thunbergii</i> , <i>Corallina officinalis</i> , <i>Sargassum horneri</i> , <i>Ulva australis</i>	> 8195.00	Lin et al. (2012)
		Heterokontophyta (Phaeophyceae)	17 (19.5%)			
		Chlorophyta	17 (19.5%)			
2014.04–2015.01 (Mussel culture rafts)	70	Rhodophyta	38 (54.3%)	<i>Ulva australis</i> , <i>Grateloupia livida</i> , <i>Sargassum horneri</i> , <i>Undaria pinnatifida</i>	12,599.35	Huang et al. (2017)
		Heterokontophyta (Phaeophyceae)	21 (30.0%)			
		Chlorophyta	11 (15.7%)			
2015.12–2016.01 (Mussel rafts vs. Natural reefs)	42	Rhodophyta	28 (66.7%)	<i>Grateloupia livida</i> , <i>Ulva australis</i> , <i>Bryopsis plumosa</i> , <i>Sargassum horneri</i>	No information on spring biomass.	Bao et al. (2020)
		Heterokontophyta (Phaeophyceae)	6 (14.3%)			
		Chlorophyta	8 (19.0%)			
2025.05 (Present Study) (Natural intertidal zone, #5–8)	21	Rhodophyta	11 (52.4%)	<i>Ulva australis</i> , <i>Sargassum fusiforme</i> , <i>Sargassum thunbergii</i> , <i>Sargassum vachellianum</i>	1486.44	This Study
		Heterokontophyta (Phaeophyceae)	8 (38.1%)			
		Chlorophyta	2 (9.5%)			

*Survey information from spring.

Archipelago, revealing how the differential influence of riverine and oceanic water masses and intensive mussel aquaculture jointly shape community structure, biodiversity, and ecological quality. Our results demonstrated a clear west–east differentiation from severely stressed, low-biomass and phylogenetically clustered assemblages near the Yangtze River Estuary to species-rich, structurally complex, and taxonomically diverse communities in offshore waters, with the latter also strongly influenced by nutrient enrichment from mussel aquaculture. Historical comparisons further indicated a pronounced long-term degradation of natural intertidal reefs, with an >80% decline in biomass since 2010 and a shift from perennial, canopy-forming *Sargassum* forests to opportunistic *Ulva*-dominated assemblages. Notably, mussel aquaculture zones, particularly around Gouqi Island, supported relatively high macroalgal biomass, α -diversity, and taxonomic distinctness, suggesting that suspended farming structures may function as refuges for macroalgal diversity under conditions of benthic habitat deterioration. By integrating conventional diversity metrics with taxonomic distinctness indices, this study has highlighted the value of phylogenetically informed approaches to analyzing the status of highly modified coastal ecosystems. We acknowledge that the present study is based on a single spring survey, which limits our ability to capture seasonal dynamics and inter-annual variability. The observed spatial patterns should therefore be interpreted as a spring snapshot rather than a year-round characterization. Future studies incorporating multi-seasonal sampling are needed to fully understand the temporal stability of the community patterns reported here. Overall, our findings suggest that the future conservation and restoration of “underwater forests” in estuarine–island systems such as the Shengsi Archipelago will require management strategies that explicitly consider both large-scale water-mass-driven environmental differentiation and the ecological roles—both negative and compensatory—of aquaculture-associated habitats.

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

LW: Data curation, Writing – original draft. WX: Data curation, Writing – original draft, Methodology. QL: Writing – original draft,

Funding acquisition, Project administration, Supervision. HC: Funding acquisition, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work 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.2026.1814340/full#supplementary-material>

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