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Research Paper

Mapping the macrozoobenthic communities in the Yellow Sea and the East China Sea using community distribution model*

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Abstract The continental shelves of Yellow Sea and East China Sea harbor complex macrozoobenthic communities, and they are shaped by unique hydrographic features such as the Yellow Sea Cold Water Mass and the Kuroshio. To address the lack of full-coverage spatial baselines for these ecologically critical assemblages, we constructed a continental shelf-scale community distribution model (CDM). By integrating community point data from benthic trawl surveys conducted between 2000 and 2015 with benthic environmental data from Bio-ORACLE, we developed CDMs based on binomial generalized linear model (GLM) and multi-algorithm ensemble species distribution models (SDMs). Spatial probability distribution maps of communities were generated at a resolution of 0.5° and subsequently integrated into a comprehensive map of the most probable macrozoobenthic community distribution across the study area. The results indicate: (1) model predictions exhibit high consistency with observed distributions (GLM: 90.4%; ensemble SDM: 91.3%); (2) depth and temperature are dominant environmental drivers, and cold-water mass communities exhibited significant negative correlations with temperature, while East China Sea communities display coast-to-offshore zonation patterns along depth gradients; (3) CDMs demonstrate robust extrapolation capabilities in data-sparse regions, such as the northern Yellow Sea and offshore areas of the East China Sea, and successfully predicted the community distributions. This study provided continuous distribution maps of macrozoobenthic community distributions in the Yellow and East China Seas, validated the applicability of CDMs in complex shelf ecosystems with a valuable tool for biodiversity conservation and marine management in this region.

Keyword: macrozoobenthos; community structure; community distribution modeling

1 INTRODUCTION

Macrozoobenthos refers to benthic animals that inhabit the surface of the seabed or within the sediment and are retained when samples are sieved through a 0.5-mm mesh (Lalli and Parsons, 1997; Li, 2011; Walag, 2022). These include mollusks, crustaceans, polychaetes, echinoderms, and other groups. As an important functional component of marine ecosystems, macrozoobenthos play a critical role in material cycling and energy flow (Snelgrove, 1998; Hinz et al., 2004; Montie and Thomsen, 2023)

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and serve as a link between benthic and pelagic ecosystems (Griffiths et al., 2017). They exhibit relatively fixed living ranges, with some species leading sessile lifestyles and having long life cycles. Their delayed response to adverse environmental conditions makes them more susceptible to the profound impacts of environmental changes (Li et al., 2007). Different species display varying tolerances and sensitivities to stressors, allowing the species composition, population dynamics, and community structure of macrozoobenthos to integrate and reflect environmental changes over extended periods (Josefson et al., 2009).

Detailed and comprehensive marine environmental and biological survey data serve as the foundation for marine ecological protection and management decisions (Reiss et al., 2015). However, due to the complexity of marine environments, sparse or missing biological survey data are common. Predictive spatial modeling based on environmental parameters offers a new approach for mapping the large-scale distribution of marine organisms (Guisan and Thuiller, 2005; Cheung et al., 2009). Species-level modeling, which involves modeling the distribution of individual species, is the most commonly used strategy for predictive spatial biodiversity modeling (Bentlage et al., 2013) and has increasingly been applied to study the impact of climate change on marine organism distributions (Singer et al., 2017; Zhang et al., 2019; Chen et al., 2021; Xu et al., 2022; De Cubber et al., 2023). Community distribution models (CDMs), which predict the spatial distribution of biological communities and their responses to environmental changes, are more suitable for ecosystem management than species distribution models (SDMs).

The Yellow Sea (YS) and the East China Sea (ECS), located in the northwest Pacific continental shelf area, exhibit unique benthic biogeographic patterns shaped by complex hydrodynamic processes (e.g., the Kuroshio system, the Yellow Sea Cold Water Mass (YSCWM), and the Changjiang (Yangtze) River Diluted Water). Extensive research has been conducted on macrozoobenthic communities in these seas. Liu and Xu (1963) first established the macrozoobenthic fauna of the YS and ECS. Zhang et al. (2016a, b) compared macrozoobenthic community data from the YS over nearly 50 years (1959 and 2007), revealing significant disturbances and changes in the macrozoobenthic community structure of the YS. Large-scale distribution maps of macrozoobenthic communities are crucial for long-term monitoring, protection planning, and decision support for benthic ecosystem. Xu et al. (2020) analyzed 60 years of survey data from the South YS and ECS, finding that communities in the YSCWM area were relatively stable, while those in other regions exhibited significant spatiotemporal changes. However, there remains a lack of research on the spatial distribution of communities covering the entire YS and ECS. This study utilized binomial generalized linear model (GLM) and multi-algorithm SDMs to construct CDMs for macrozoobenthos in the YS and ECS, aiming to: (1) establish a full coverage spatial distribution map of macrozoobenthic communities in the YS and ECS; (2) analyze key environmental driving factors; (3) verify the feasibility of the CDM in predicting data-blind areas.

2 MATERIAL AND METHOD

2.1 Study area and data collection

The study area encompasses the primary sea regions of the Yellow Sea (YS) and East China Sea (ECS) (25.18°N–38.93°N, 119.28°E–127.20°E; Fig.1a). The seabed topography in this region gradually deepens from northwest to southeast and is predominantly influenced by the Kuroshio and the YSCWM. Macrozoobenthic data were collected during benthic trawl surveys conducted in the YS and ECS between 2000 and 2015. Sampling was performed using an Agassiz trawl (with a mouth size of 1.5 m×0.5 m), where the mesh size progressively decreased from 2 cm at the mouth to 0.7 cm at the cod end. Samples were preserved in 75% ethanol, and species identification was subsequently completed in the laboratory. Environmental layers were extracted from the Bio-ORACLE 3.0 database (Tyberghein et al., 2012; Assis et al., 2024). Based on ecological relevance to macrozoobenthos, 23 benthic environmental variables were initially selected.

2.2 Data analysis

2.2.1 Environmental data

To match the resolution to station intervals, raster data were resampled from 0.05° to 0.5° spatial resolution. Variance Inflation Factor (VIF) was calculated using the usdm R package (Naimi et al., 2014), retaining variables with VIF<10 to avoid multicollinearity. Finally, twelve benthic environmental variables were ultimately used: depth (DEPTH), mean of ocean temperature (BTM), range of sea-water salinity (BSR), range of sea-water velocity

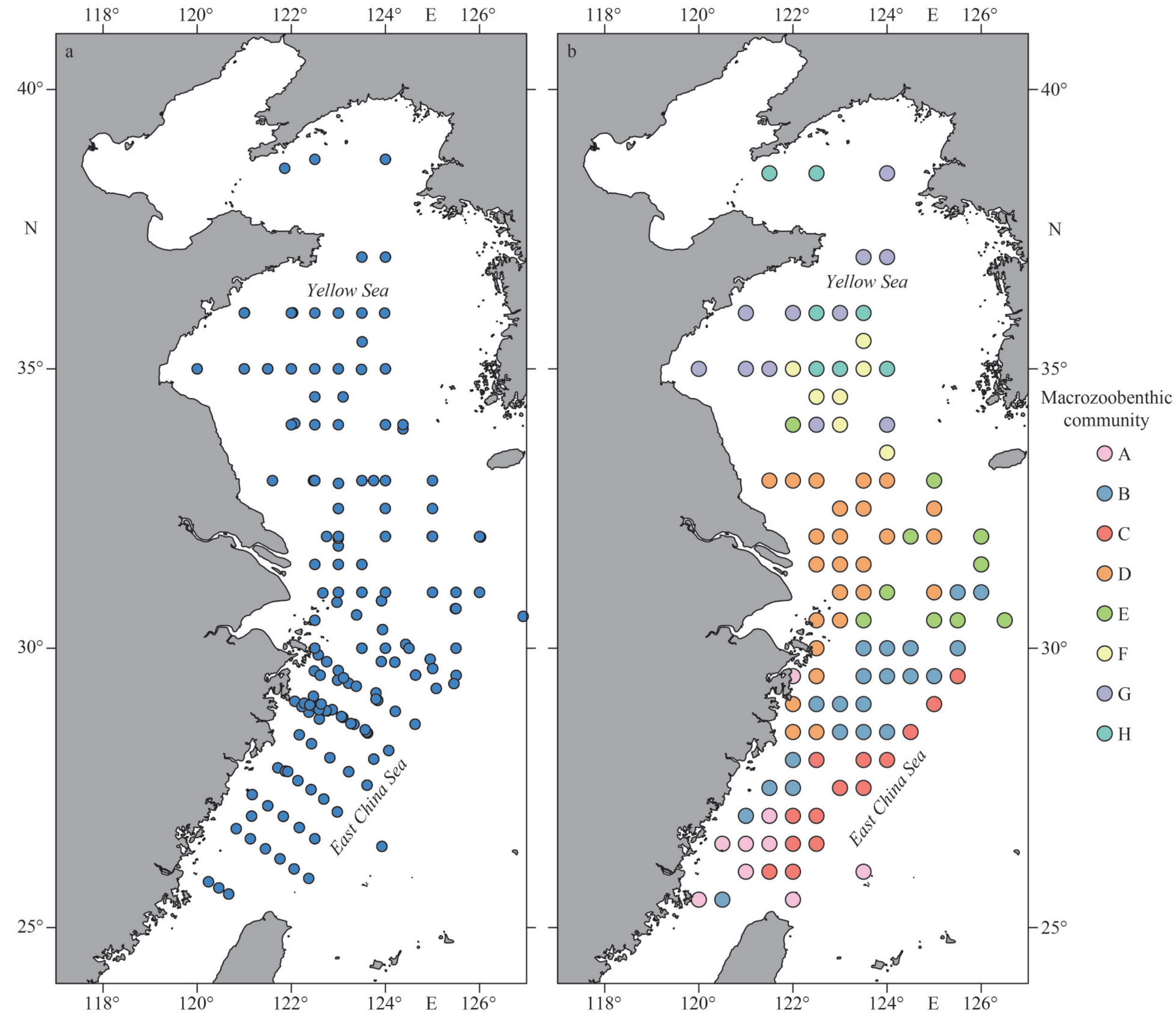

Fig.1 Sampling sites during 2000–2015 (a) and eight macrozoobenthic communities (A–H) defined by Zhang et al. (2023) in the Yellow Sea and East China Sea during 2000–2015 (b)

(BVR), mean of sea-water direction (BDM), range of sea-water direction (BDR), mean of nitrate (BNM), range of phosphate (BPhoR), range of silicate concentration (BSiR), range of dissolved iron concentration (BFeR), range of total phytoplankton (BPhyR), and range of sea-water pH (BpHR).

2.2.2 Community distribution model (CDM)

In this study, the community clustering results established by Zhang et al. (2023) were adopted as the response variable for community distribution modeling. Specifically, the eight communities (Fig.1b) were defined based on species presence/absence data from 0.5° grids, using a Sørensen dissimilarity matrix combined with Ward hierarchical clustering (Zhang et al., 2023). The coordinates of these communities are provided in Supplementary Table S1.

Spatial modeling of community-level biodiversity employs three strategies: assemble first, predict later; predict first, assemble later; and assemble and predict together (Ferrier and Guisan, 2006). The "Assemble First, Predict Later" strategy involves an initial step where biological survey data are processed (via classification, ordination, or aggregation) to define community-level units or characteristics. This study followed the "Assemble First, Predict Later" framework, employing the presence/absence of each community as the response variable and environmental factors as explanatory variables. Two methods were employed to construct CDMs. Based on the approach proposed by Mamede et al. (2022), a GLM with a binomial distribution and a clog-log link function was utilized. Significant terms ($P \leq 0.05$) were retained via backward stepwise selection, and spatial autocorrelation in residuals was assessed using Moran's *I* test, followed by adjustment of autocorrelated variables (Bivand and Wong, 2018). The "pROC" package (Robin et al., 2011) was used to calculate the AUC for evaluating model performance. Probability maps for the presence of each macrozoobenthic community were generated using CDM expressions and environmental layers. These individual community maps were then integrated to produce the most probable community distribution map.

Following Butler and Sanderson (2022), who constructed predictive maps of plant communities under the assumption that each community, like individual species, requires distinct ecological conditions, this study applied common species distribution modeling techniques. Specifically, the biomod2 package version 4.2-4 (Thuiller et al., 2023) was used, integrating seven modeling algorithms—generalized boosting model (GBM), generalized additive model (GAM), classification tree analysis (CTA), artificial neural network (ANN), flexible discriminant analysis (FDA), multiple adaptive regression splines (MARS), and random forest (RF)—with their respective default parameters. Target community stations were defined as truly present, while all others were treated as truly absent. Community data were randomly partitioned, with 75% allocated to the training set and the remaining 25% reserved for testing. To assess model accuracy, ten random cross-validations were performed for each model. Single-model algorithm performance was evaluated using true skill statistics (TSS) (Allouche et al., 2006) and the area under the receiver operating characteristic (ROC) (Fielding and Bell, 1997) curve (AUC). Models with AUC and TSS values≥0.7 (Hosmer and Lemeshow, 2000) were selected, and an ensemble model was constructed using the average probability method. Variable importance assessments and environmental variable response curves were generated to identify key environmental factors influencing macrozoobenthic community distributions. Finally, the ensemble model was used to predict the current distribution of each community and produce the final composite map. All analyses were conducted in R 4.2.3 (The R Core Team, 2023).

3 RESULT

3.1 Macrozoobenthic community characteristic

The eight communities (A–H) delineated by Zhang et al. (2023) exhibit distinct biogeographic patterns (Fig.1b). In the Yellow Sea, three communities (F, G, H) occupy overlapping zones, with Group F (7 stations, 19 species) dominated by the brittle star *Ophiura sarsii vadicola*, Group G (11 stations, 46 species) represented by *Stegophiura sladeni*, *Ophiura sarsii vadicola*, and *Crangon hakodatei*, and Group H (7 stations, 18 species) featuring *Ophiura sarsii vadicola* as the key species. In the southern Yellow Sea and East China Sea, three communities display coast-to-offshore distribution: Coastal Group D (25 stations, 59 species) with dominant shrimp *Palaemon gravieri* and goby *Amblychaeturichthys hexanema*; Transitional Group B (21 stations, 66 species) characterized by shrimp *Plesionika izumiae* and crab *Charybdis bimaculata*; Offshore Group C (14 stations, 71 species) dominated by crab *Charybdis bimaculata* and shrimp *Metapenaeopsis provocatoria*; Group A (9 stations, 30 species) with key species *Alpheus japonicus* and *Atypopenaeus stenodactylus*; and Offshore Jiangsu Group E (10 stations, 31 species) featuring *Solenocera melantho*. The coordinates of these communities are listed in Supplementary Table S1.

3.2 Community distribution predicted by the binomial GLM

The CDMs constructed using binomial GLM and their predictive performance metrics are summarized in Table 1. The presence of each macrozoobenthic community was effectively explained by distinct environmental predictors. The sign of each parameter coefficient for the environmental variables indicated either positive or negative correlations. All CDMs exhibited high predictive performance, with AUC>0.9. Additionally, the percentage of deviance explained was greater than 50%, confirming a strong model fit to the data.

By calculating the occurrence probability of each community using the binomial GLM (Fig.2; Supplementary Fig.S1), we generated a predicted map highlighting the highest occurrence probabilities for each community. These maps were then integrated to produce the final predicted distribution of the most likely macrozoobenthic communities in the YS and ECS (Fig.3).

The CDM predictions showed 90.4% agreement with empirically observed communities. These results indicate that at a spatial resolution of 0.5°, the CDMs accurately captured the current distribution patterns of macrozoobenthic communities under the prevailing climate conditions.

Table 1 Expression and predictive ability evaluation of community distribution models (CDM) constructed by generalized linear model (GLM) of binomial distribution

Community	CDM expression	AUC	Deviance explained (%)
A	-26.969 326+0.149 182DEPTH+1.477 506BTM+0.019 992BDR+1.016 882BNM+ 15.847 341BPhoR–73.042 233BpHR	0.979	62.3
B	2.040+0.232DEPTH+1.281BTM–4.580BSR–21.173BVR–0.017BDM+11.045BPhoR–2.207BPhyR	0.958	62.8
C	-26.593 2–0.277 6DEPTH	0.993	82.9
D	-21.260 5+0.177 8DEPTH+0.752 1BTM+21.681 9BVR+0.011 7BDR+14.513 8BPhoR+0.363 3BPhyR	0.981	74.7
E	-38.624 75–0.454 21DEPTH+3.000 96BSR–119.014 73BVR+0.030 60BDM–0.023 16BDR– 30.958 85BPhoR–1.624 78BSiR+268.547 76BpHR	0.976	71.9
F	-14.021 34–0.119 40DEPTH–0.639 42BTM+44.920 93BpHR	0.971	57.7
G	-12.650 7–0.406 2DEPTH–0.914 1BTM+2.174 4BSR–36.537 4BVR–1.418 7BNM– 21.392 2BPhoR–1 657.160 6BFeR+80.226 5BpHR	0.961	58.2
H	8.543 2–0.785 4BTM–3.430 1BSR+13.842 4BpHR	0.957	52.9

AUC: area under ROC curve; DEPTH: depth; BTM: mean of benthic ocean temperature; BSR: range of benthic sea-water salinity; BVR: range of sea-water velocity; BDM: mean of sea-water direction; BDR: range of sea-water direction; BNM: mean of nitrate; BPhoR: range of phosphate; BSiR: range of silicate concentration; BFeR: range of dissolved iron concentration; BPhyR: range of total phytoplankton; BpHR: range of sea-water pH.

In the YS, three primary communities (F, G, and H) were identified, with their spatial distributions negatively correlated with mean benthic water temperature (Table 1). Communities F and G represent cold-water assemblages in the YS, covering the three cold centers of the YSCWM and occupying most of the YS region (Figs.2 & 3). Community H occupied smaller patches, primarily distributed on the east side of Dalian Bay and to the east of community F. In the southern YS and the ECS, communities D, B, and C are distributed from coastal areas to offshore regions and from northwest to southeast (Fig.3). Depth was the single environmental variable significantly associated with the spatial distribution of community C (Table 1). Community E is mainly distributed in the outer seas off eastern Jiangsu and Zhejiang provinces, while community A is mainly distributed along the coast of Fujian Province.

3.3 Community distribution predicted by ensemble SDM

The prediction of community distribution was conducted using ensemble SDMs. The evaluation of model prediction ability and the importance of environmental variables are shown in Table 2. The SDM-based CDM demonstrated high predictive performance for each community. Notably, the models for communities E and F exhibited AUC and TSS values of 1, likely due to the limited number of distribution points, which may have led to overfitting. Therefore, predictions for these rare communities should be interpreted with caution until independently validated. Benthic ocean temperature was identified as the most critical environmental variable influencing the distributions of communities A, G, and H, whereas depth played the dominant role in shaping the distributions of communities B and C. For communities D, E, and F, the most important environmental variables were salinity, sea-water velocity, and dissolved iron concentration, respectively. Using the ensemble CDM, the occurrence probabilities of each community were predicted (Fig.4; Supplementary Fig.S2), and the final predicted maps with the highest occurrence probabilities for each community were generated through superimposition and calculation (Fig.5). The ensemble community model predictions showed a high consistency of 91.3% with the actual survey results, confirming the model's robust predictive ability at a spatial resolution of 0.5°. Communities G and H predominantly occupied the northern YS, while communities D, B, and C exhibited a gradient distribution extending from nearshore to offshore areas and progressing from northwest to southeast in the southern YS and ECS (Fig.5).

4 DISCUSSION

4.1 CDM prediction and environmental variable

This study, by integrating actual survey data of macrozoobenthic communities with benthic

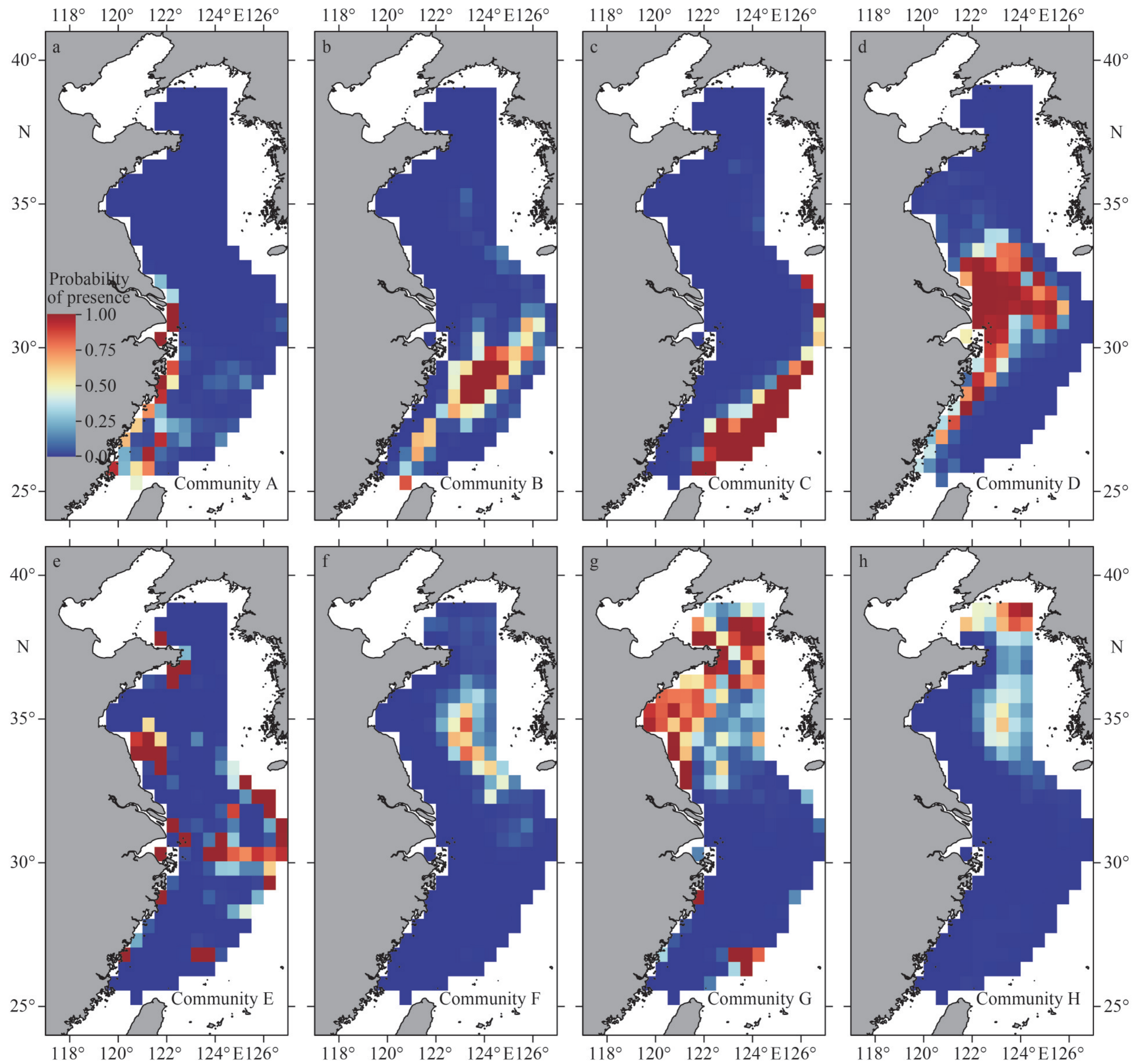

Fig.2 Maps of the presence probabilities for eight macrozoobenthic communities (A–H) in the study area generated using binomial GLM

environmental data, verified for the first time in the YS and the ECS the predictive efficacy of CDMs for macrozoobenthic communities.

Depth and temperature are key explanatory variables in CDMs constructed using binomial GLM and ensemble SDMs. Depth plays a role in marine ecosystems analogous to altitude in terrestrial environments (Gogina et al., 2010), acting as a physical driver for many marine environmental variables (e.g., light conditions, productivity, temperature, dissolved oxygen, etc.) and fundamentally influencing benthic organism distribution. This explains why depth is more likely retained during model selection rather than its correlated variables.

The YSCWM is a unique hydrological phenomenon in the YS (Yu et al., 2006). The YSCWM consists of three cold centers: northern YS, western southern YS, and eastern southern YS. Despite seasonal movements, these cold centers maintain relatively low water temperatures year-round with stable temperature variations (Yu et al., 2006). In this study, community G's distribution encompasses the northern YS cold center and the western southern YS cold center, while communities H and F are primarily influenced by the eastern southern YS cold center. The CDM constructed using binomial GLM reveals that the spatial distributions of the three YS communities are significantly negatively

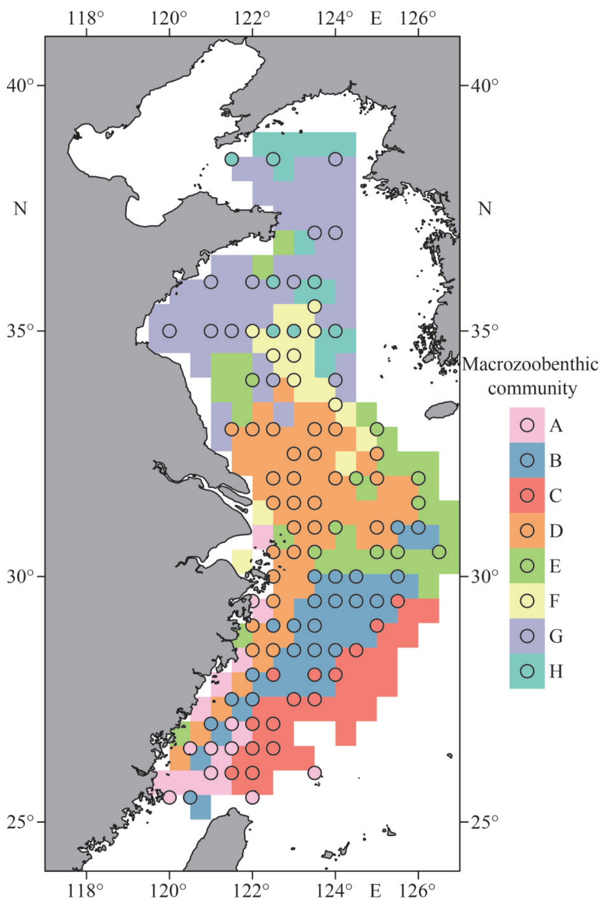

Fig.3 The observed distribution of eight macrozoobenthic communities (A–H) within the study area and the most likely distribution predicted by the binomial GLM

Circles represent the observed spatial distribution of the communities, while the continuous layer indicates the most probable predicted distribution of the communities.

Table 2 Predictive ability (AUC_{EM} and TSS_{EM}) and environmental variables importance (EVI)

Community	AUC_{EM}	TSS_{EM}	Environmental variable	Variable importance
A	0.993	0.989	BTM DEPTH BSR BpHR	0.17 0.15 0.15 0.14
B	0.987	0.887	DEPTH BNM BSiR	0.15 0.08 0.08
C	0.999	0.989	DEPTH BSR	0.49 0.02
D	0.993	0.947	BSR DEPTH	0.51 0.04
E	1	1	BVR BpHR BSiR	0.55 0.48 0.47
F	1	1	BFeR BDM BPhoR	0.14 0.09 0.07
G	0.979	0.978	BTM	0.92
H	0.988	0.968	BTM	0.43

TSS: the true skill statistics; AUC: area under the receiver operating characteristic curve; DEPTH: depth; BTM: mean of benthic ocean temperature; BSR: range of benthic sea-water salinity; BVR: range of sea-water velocity; BDM: mean of sea-water direction; BDR: range of sea-water direction; BNM: mean of nitrate; BPhoR: range of phosphate; BSiR: range of silicate concentration; BFeR: range of dissolved iron concentration; BPhyR: range of total phytoplankton; BpHR: range of sea-water pH.

correlated with benthic water temperature (Table 1). Furthermore, SDM-based environmental variable importance analysis indicates that benthic water temperature is a critical factor affecting the distributions of communities G and H (Table 2). These findings demonstrate that the CDMs developed in this study effectively characterize the relationship between community distribution and environmental variables, exhibiting high predictive feasibility.

Both GLM- and SDM-based CDMs delineated three communities (D, B, and C) distributed from north to south and nearshore to offshore in the southern YS and ECS (Figs.3 & 5). Coastal shallow waters are directly influenced by terrestrial climate and receive substantial freshwater input from the Changjiang River, forming significant temperature-salinity gradients. Hydrological conditions (temperature, salinity, etc.) in this area exhibit marked seasonal fluctuations, resulting in predominantly eurythermal and euryhaline macrobenthic species (Liu et al., 1986). Offshore areas are dominated by the warm and saline Kuroshio and Taiwan Warm Current, where macrobenthic organisms are mainly warm-water species. Environmental variable importance analysis (Table 2) shows that key factors influencing community distributions are salinity (nearshore community D), depth (transition community B), and depth (offshore community C), indicating that depth is the dominant factor shaping community distribution at large spatial scales.

4.2 Predictive feasibility and application of CDM

This study adopted the assemble first, predict later strategy, which is advantageous for rapidly identifying current community type distributions (Ferrier, 2002). This strategy is prioritized for two main reasons: (1) ecological coherence—pre-defined communities (Zhang et al., 2023) represent

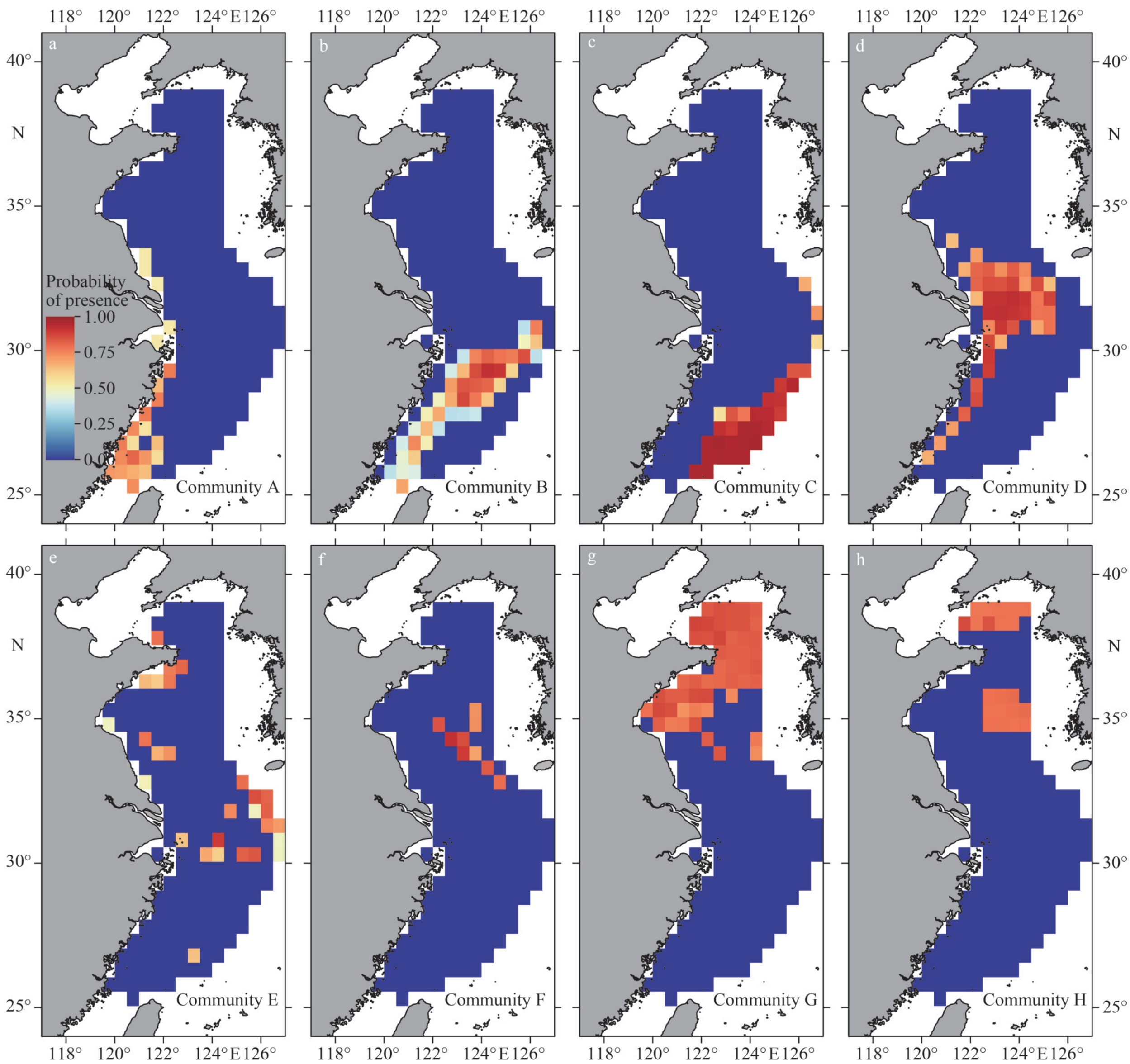

Fig.4 Maps of the presence probabilities for eight macrozoobenthic communities (A–H) in the study area generated using ensemble SDM

empirically validated stable assemblages within the YS and ECS continental shelf ecosystem; and (2) computational efficiency—modeling directly at the community level reduces data dimensionality, enhances computational efficiency, and preserves the original species combination patterns. However, this strategy assumes future community compositions remain consistent with present ones and is unsuitable for predicting future changes or newly formed communities. Climate change may induce fundamental shifts in community composition (e.g., altered species interactions), reducing reliability for predicting communities under future climate scenarios. Therefore, this study utilized CDMs only to predict current community distributions in the YS and ECS. Predicted community distribution maps exhibited high consistency with observed distributions (90.4% for binomial GLM and 91.3% for ensemble SDMs). Additionally, both CDMs successfully predicted community distributions in data-sparse regions such as the northern YS and offshore ECS, demonstrating their ability to extrapolate community distributions through environmental variables and provide theoretical support for ecologically undersampled areas. Notably, community distribution prediction maps should complement, not replace, actual observations of macrobenthic community structure (Degraer et al., 2008). The most probable

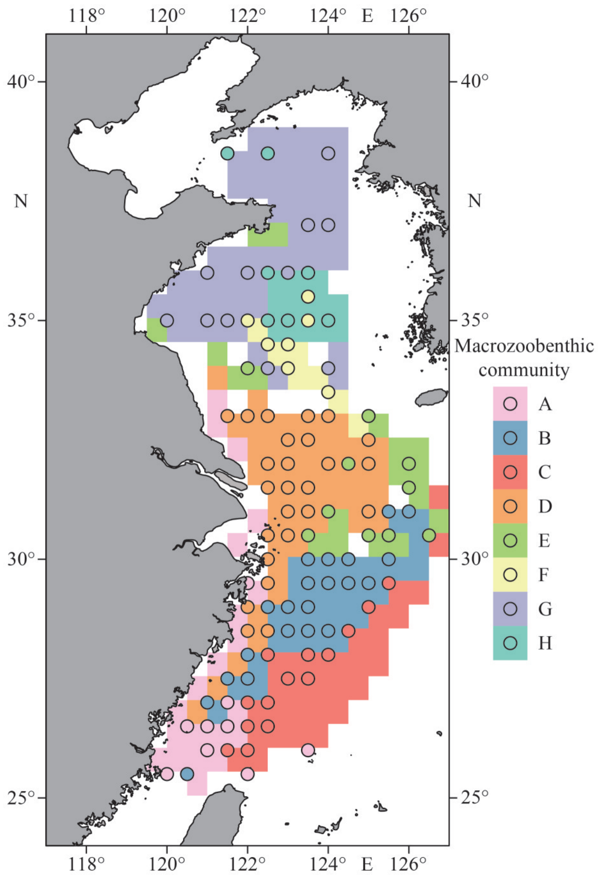

Fig.5 The observed distribution of macrozoobenthic communities within the study area and the most likely distribution predicted by the ensemble SDM

Circles represent the observed spatial distribution of the communities, while the continuous layer indicates the most probable predicted distribution of the communities.

community distribution map generated in this study serves as an essential tool for biodiversity conservation and ecological reserve planning in the YS and ECS.

5 CONCLUSION

This study establishes the first continental shelf-scale CDMs for macrozoobenthos in the YS and ECS, integrating trawl survey data (2000–2015) with Bio-ORACLE environmental variables through binomial GLM and ensemble SDMs. Key results demonstrate: (1) >90% predictive accuracy across methods, enabling continuous distribution mapping of eight communities; (2) depth and temperature as dominant controls, with cold-water communities (G, H, F) negatively correlating to temperature while East China Sea communities (D, B, C) showing coast-to-offshore depth zonation; (3) robust extrapolation in data-sparse regions (northern YS/offshore ECS), validating CDMs for biodiversity mapping gaps. This spatial baseline supports marine protected area design and monitoring, though the "assemble first, predict later" strategy limits applicability to climate-driven community reassembly scenarios. CDM maps thus complement empirical observations for enhanced benthic ecosystem monitoring.

6 DATA AVAILABILITY STATEMENT

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Electronic supplementary material

Supplementary material (Supplementary Table S1 and Figs.S1–S2) is available in the online version of this article at https://doi.org/10.1007/s00343-025-5223-9.