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Delineation of estuarine ecological corridors using the MaxEnt model to protect marine fishery biodiversity

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Ecological corridors (ECs) are important management tools to protect biodiversity by linking fragile habitats, especially for highly mobile organisms. ECs in terrestrial landscapes work as passages on land or in water. However, the significance of ECs to migratory species in estuaries has not been well elucidated. Based on annual fishery investigation in the Yangtze estuary and their dominance index rank, three of the top five species, including *Larimochthys polyactis*, *Coilia mystus*, and *Gobiidae*, exhibited absolute dominance in spring during the past 5 years. The temporal and spatial density variance of *C. mystus* supported its short-distance migration pattern. Redundancy analysis and the MaxEnt model predicted optimum habitats for *C. mystus*. *C. mystus* larvae survival was significantly related to salinity, total nitrogen, pH, reactive silicate, dissolved oxygen, surface water temperature, and chlorophyll-a in May and to salinity, surface water temperature, permanganate index, suspended particles, total nitrogen, and total phosphorus in August. The MaxEnt model predicted a broader longitudinal distribution range from offshore to the upstream freshwater area but narrower latitudinal distribution in the southern branch in May than in August. Finally, we delineated migratory corridors connecting optimum habitats for *C. mystus* using the least-cost route method. Optimum habitats close to the coastlines in the south branch might play a significant role in maintaining population or community connectivity in the Yangtze estuary. Our findings provide a perspective and method to quantify and facilitate the harmonious development of socioeconomy and fishery biodiversity conservation.

KEYWORDS

ecological corridors, biodiversity, Yangtze Estuary, *Coilia mystus*, MaxEnt model, fish conservation

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Abbreviations: ECs, ecological corridors; YRE, Yangtze River Estuary; SS, suspended particles; DO, dissolved oxygen; N, total nitrogen; P, total phosphorus; Si, reactive silicate; Temp, estuarine surface water temperature; COD_{Mn}, permanganate index; Chla, chlorophyll-a; depth, water column depth; RDA, redundancy analysis.

Introduction

Ecological corridors (ECs) are landscapes linking spatially isolated and dispersed patches in a linear or strip-like distribution, which are constructed for the movement of individuals such as tigers (Seidensticker et al., 2010), fishes (Benson et al., 2007), birds (Klaasen, 1996; Tong et al., 2012), and butterflies (Runge et al., 2015). They also serve as a buffer with certain similarities to habitual kernels benefiting the recovery and adaptation of native species (Lawler et al., 2013; Degteva et al., 2015; McGuire et al., 2016; Keeley et al., 2018). Such landscapes play important roles in sustaining and restoring biodiversity (Hilty et al., 2019) by promoting the flow of energy and materials and genetic exchange in terrestrial environments (Miklos et al., 2019), freshwater systems (Bastian et al., 2015; Hauer et al., 2016), and marine environments (Gillanders et al., 2003; Cowen and Sponaugle, 2009), or a transboundary of the above-mentioned environments. The methods for investigating ECs (Weeks, 2017; Balbar and Metaxas, 2019) have grown steadily during the past several years. Subsequently, more tools are available to project and map ECs in systematic conservation planning, such as the circuit theory (McRae, 2006), graph theory (Urban and Keitt, 2001), least-cost route method (McRae et al., 2016), and individual-based model (Allen et al., 2016). In general, the following aspects are crucial for modeling ECs: the movement behavior of objectives, the physical conditions of their habitats, the degree of disturbances or pressures, and the persistence and adaptation of objectives. To date, global actions have been taken to sustain ecological connectivity by constructing marine protected area networks (Carr et al., 2017). Most of them are based on specific investigating datasets about objectives; for example, specific megafauna or birds migrating across varied jurisdictions, entire passages, or rivers for anadromous or catadromous fish species. However, research on defining the importance of ECs in fishery biodiversity by projecting the dispersion and distribution of model species in estuaries is lacking.

Estuarine ecosystems are located at the ecological intersection between terrestrial and marine ecosystems. They are socioeconomically and ecologically important benefiting from the economic, demographic, natural resource, transportation, and other advantages (Levin et al., 2001; Cowen and Sponaugle, 2009). In recent years, estuarine ecosystems have been considerably altered by global climate change (Gillanders et al., 2011; Scanes et al., 2020) and intense anthropogenic activities (Wang et al., 2022), such as important habitat reclamation, upstream dam construction (Ferguson et al., 2011), overfishing since the 1990s (Wang et al., 2022), spawning and nursing habitat deterioration, and migratory corridor breakdown (Cowen and Sponaugle, 2009). The coupled effects of natural and human activities have altered the temperature, salinity, pH, and nutrients as well as the heterogeneity of seawater characteristics (depending on the mixing process of fresh and salty water) (Pelage et al., 2021). Additionally, it has adversely accelerated the mixing process and promoted the fragmentation of the physical and chemical properties of water columns (Wu and Wu, 2018). Such variance has driven changes in the physiology, morphology, and genetics of marine organisms (Finn, 2007; Johnston and Roberts, 2009; Garcia and Barria de Cao, 2018). For example, ammonia nitrogen and cadmium could be toxic to fish and may decrease their survival rates and biodiversity (Schram et al., 2014). Ocean acidification has changed the preference of catadromous barramundi for tropical estuarine mangroves (Rossi et al., 2018). Spatial heterogeneity in salinity, temperature, and turbidity gradients have increased in estuaries, simultaneously leading to changes in preferred habitats for some marine organisms or different life history stages of the same marine organism. In past decades, some fishes that are highly dependent on estuarine habitats have been decimated; for example, tapertail anchovies (*Coilia nasus*) migrates from the sea to the river (Jiang et al., 2014), the Yangtze River dolphin migrates in the descending river (Zhu et al., 2009), and Chinese sturgeon (Wang et al., 2018) larvae require the brackish water of the estuary to balance body fluid osmolality.

Migration is a characteristic developed by fishes in the process of phylogeny and a long-term adaptation of fish to the environment, which enables the population to obtain more favorable conditions for survival and reproduction (Planes et al., 2009; Christie et al., 2010; Sykes and Shrimpton, 2010). Anadromous fishes live in the ocean but spawn in the middle or upstream of rivers. In contrast, catadromous fishes live in freshwater and spawn in the ocean. They have strict adaptations to the ecological conditions of their habitat (Hanson et al., 2010; Wang et al., 2012; Wang et al., 2018; Chaparro-Pedraza and de Roos, 2019). Eggs and larvae play an important role in energy transfer in the marine ecosystem, and their survival rate and the amount of remaining stock determine the abundance of population replenishment resources (Botsford et al., 2009; Saenz-Agudelo et al., 2010; D'Aloia et al., 2015). Hence, eggs and larvae are indispensable elements in the study of sustainable use of fish resources and important indicators for evaluating fish migration (Almany et al., 2017). In recent years, the eutrophication of estuarine waters and increase in pollutant discharges have led to a significant decrease in the suitability of estuarine fish habitats. The larval survival rate and species replenishment have continued to decrease, especially for the migratory fishes. Hence, it is essential to identify the migratory pathways of key species in estuaries and to protect marine biodiversity by maintaining the connectivity of organisms and their habitats. In this study, we aimed to (1) construct a theoretical framework for identifying key migratory species in estuaries; (2) test the suitability of the MaxEnt model to predict optimal habitats and construct resistance surfaces for migratory fish species; and (3) delineate or identify ECs as the minimum management space to maintain population connectivity.

Materials and methods

Study site and ichthyoplankton sampling

The Yangtze River Estuary (YRE) is the largest estuary in China, with three-order bifurcations and four outlets for significant volumes of freshwater discharge from the Yangtze River to the East China Sea (Figure 1A). The annual average water temperature is 15°C–16°C. The YRE is a medium-intensity tidal estuary with regular half-day tides outside the mouth and informal half-day shallow tides inside the mouth. From offshore to upstream of the YRE, the duration of flood tide decreases gradually, whereas that of the ebb tide increases and is longer than that of the flood tide. The tidal range of the southern branch of the YRE decreases upstream. The YRE is located in a subtropical monsoon climate zone with oceanic and monsoon characteristics and an annual average precipitation of approximately 1,030 mm, which is mostly concentrated in June and September. A large amount of freshwater carries sediment discharge into the sea, which influences the water quality, hydrologic dynamics, and topography (Wu et al., 2011; Wu et al., 2013). Furthermore, socioeconomic development, including fishing; shipping; and corresponding channel maintenance, pollutant emission, and coastal reclamation, has led to marine ecological degradation and biodiversity extinction through a trophic cascade or habitat destruction.

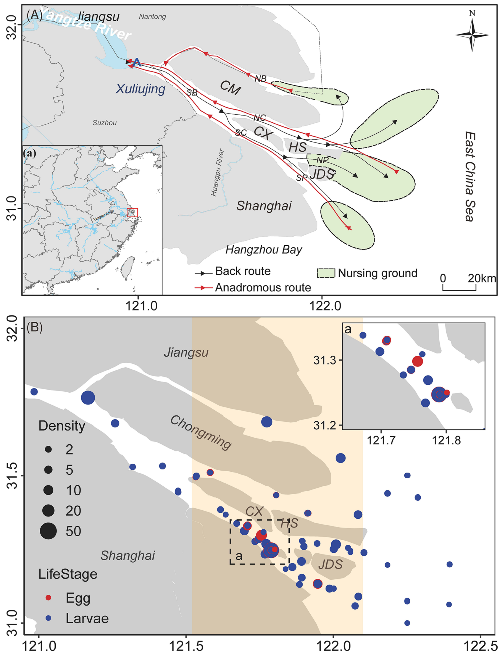

FIGURE 1
Coilia mystus community at Yangtze estuary. **(A)** Migration pattern of *C mystus*; **(B)** spatial density distribution of *C mystus* eggs and larvae. Unit of density: ind./m^3. NB, north branch; SB, south branch; NC, north channel; SC, south channel; NP, north passage; SP, south passage; CM, Chongming Island; CX, Changxing Island; HS, Hengsha Island; JDS, Jiuduansha Island.

Fish species were surveyed once in spring and summer from 2017 to 2021 during the East China Sea monitoring campaign. In our study area, 65 sites were investigated during each campaign (Figure S1). Ichthyoplankton samples were collected using two kinds of beam trawl: I-trawl and a large plankton trawl. I-trawl is the shallow water type, with a 145 cm length, 50 cm horizontal opening, 0.2 m^2 net mouth area, and 0.505 mm screen silk aperture. The I-trawl was trawled once from the bottom to the surface layer at each site. The larvae density of each site was equal to the number of larvae in the sample divided by the volume of the water column, which was defined by the water depth and net mouth area. The large plankton trawl had a net with 280 cm length, 80 cm horizontal opening, 0.5 m^2 mouth area, and 0.505 mm screen silk aperture. Larvae density was equal to the number of larvae in the sample divided by the swept area, which was defined by boat speed, trawling time, and the net mouth area. The collected samples were fixed and preserved with a 37% formaldehyde solution. The species were identified and counted using a stereoscopic microscope (Nikon SMZ25, Japan) based on the external morphology of fish eggs and larvae and the individual morphology, tissues, organs, and phylogenetic characteristics at different development stages. The dominance of the main fish species (Y, Li et al., 2022) was calculated using the following equation: $Y=n_i/N\times f_i$ where n_i represents the number of individuals of species i, f_i is the frequency of species i in each site, and N is the total number of individuals hauled in the campaign. From the five most dominant fish species, only the short-distance migratory species, anchovy (*Coilia mystus*), was selected for the following analysis.

C. mystus is a short-distance anadromous fish that mainly inhabits coastal shallow water or offshore. Its migratory behavior has been inferred from otolith microchemical analysis (Yang et al., 2006a; Yang et al., 2006b; Jiang et al., 2012; Jiang et al., 2014; Yang et al., 2019; Vu et al., 2022). In general, the breeding period of *C. mystus* in the Yangtze estuary is from April to September, including the primary spawning season of May and the minor spawning season of August (Hu et al., 2021). In late April, a small number of sexually mature fishes migrate upstream to the brackish water or freshwater areas of the Yangtze estuary to spawn, and some migrate to Zhenjiang, Jiangsu (Zeng and Dong, 1993). The surviving larvae grow in the deep water around Chongming Island and return to the sea in winter (Zeng and Dong, 1993; Yang et al., 2019). Studies on the feeding habits of *C. mystus* indicated that they mainly fed on crustacean plankton, including Copepods, Mysids, and Decapoda, especially *Acanthomysis longirostris*, *Schmackeria poplesia*, *Tortanus vermiculus*, and *Labidocera euchaeta* (Liu and Xu, 2011). Compared with long-distance migratory species, the growth and reproduction of *C. mystus* are more dependent on the marine environment of the Yangtze estuary. Hence, we used *C. mystus* as the study object to reference the biodiversity conservation of native resident species and short-distance migratory species.

We monitored the environmental factors influencing the community assemblage or distribution of marine fish species. Environmental factors included the concentration of suspended particles (SS), dissolved oxygen (DO), total nitrogen (N), total phosphorus (P), reactive silicate (Si), salinity, estuarine surface water temperature (Temp), pH, permanganate index (COD_{Mn}), chlorophyll-a (Chla), and water column depth (depth). Salinity, water temperature, and depth were measured *in situ* using a conductivity–temperature–depth (CTD) automatic recording analyzer (SBE25plus, Sea-Bird Electronics, Inc. USA). Seawater samples were collected in 5 L bottles from 0.5 m below the surface and at the bottom of each site to measure the other eight physicochemical factors. DO was measured using the iodometric titration method. The water nutrients, including P, Si, and N, were analyzed using an automatic continuous flow analyzer (QuAAtro, SEAL Analytical GmbH, Germany). pH was monitored by a pH meter (JENCO 6010M, JENCO International, Inc. USA). COD_{Mn} was measured using the alkaline permanganate method, and Chla was measured using fluorescent spectrophotometry (Agilent Cary Eclipse, Agilent Technologies, Inc. USA). SS samples were filtered by preweighted Whatman GF/F microfiber filters (25 mm) (Gao et al., 2019) and weighted by an electronic scale (QUINTIX224-1CN, Sartorius Aktiengesellschaft, Germany); its concentration was determined using the SS weight divided by the sampling volume.

Predicting potential optimal habitats of migratory species

Maximum entropy (MaxEnt) is a program for modeling species niches and spatial distributions from presence-only species records (Elith et al., 2010). From a set of environmental data and known species occurrence, the model expresses a probability distribution where given grids predict the suitability of conditions for the species by comparing the conditions between present locations and the study area. This model has been widely used in predicting the likely distribution of species in terrestrial (Lamb et al., 2008; Yates et al., 2010) and marine ecosystems (Tittensor et al., 2009; Verbruggen et al., 2009). Considering the complex habitat biogeographical features of *C. mystus*, the MaxEnt model may be an effective approach to predict their preferred habitats. MaxEnt analysis was performed using the open-source Java software MaxEnt 3.4.1 (Phillips et al., 2006; Phillips et al., 2017). We selected 75% of fishery survey datasets as the training samples to establish the prediction model and the remaining 25% as the test samples to verify the model. Two performance metrics were chosen: (1) the receiver operating characteristic curve, which evaluates the trade-off between prediction sensitivity and specificity and (2) the associated area under the curve, which presents the values of approximately 0.5 representing a random prediction, and values closer to 1 indicate a better performance of the model (Mantas et al., 2022). The analysis was repeated 10 times and averaged to obtain the final simulation results. The prediction results were imported into ArcGIS 10.2 (ESRI, Redlands, California, USA) and converted to a raster format to generate distribution probability prediction maps. Here, we defined the areas with species distribution probability greater than 90% as optimal habitats.

Optimal habitats located at the Yangtze estuarine mouth or offshore were defined as source patches, and those located at upstream freshwater or brackish water area were defined as sink patches. These definitions refer to the two possible behavior patterns of *C. mystus*. First, *C. mystus* adults migrate from offshore source habitats to upstream sink habitats to spawn, where the source and sink patches correspond to the feeding ground and spawning ground, respectively. Second, *C. mystus* egg and larvae have little motor ability, and they drift back and forth with flood and ebb tides between offshore and freshwater areas. Here, source and sink patches represent the origin and destination areas of larvae drifting with the flood tide, respectively.

Delineation of ecological corridors

Ecological resistance refers to the biotic and abiotic factors in a recipient ecosystem that limits population growth (D'Antonio and Thomsen, 2004). Ecological processes such as animals crossing the landscape carry the property of overcoming spatial resistance, which can be measured in terms of accessibility, cost distance, and minimum cumulative resistance. All these measures of resistance can be considered the extensions of the spatial distance concept. In this study, a graph theory algorithm was used to extract animal migration corridors (Pinto and Keitt, 2009). First, the relationship between the model species and the environmental elements was tested using the canonical correspondence analysis, and the explanatory rate values of the environmental factors in the habitats were analyzed. We selected salinity, DO, and surface water temperature with phosphorate concentrations in May and Chla in August to construct a resistance surface. The weights of selected explanatory environmental factors were calculated based on $y=(a+b)/2$, where a was the predicted contribution value of an environmental factor and b was their explanatory rate in canonical correspondence analysis. Second, kriging interpolation was used to rasterize the point environmental datasets to obtain the resistance surface.

Based on the rasterized resistance surface, the path of cumulative minimum cost distance from the source to the sink patches was generated. The gravity center of source and sink patches were extracted using conventional tools. The cost distance tool was used to calculate the cumulative cost distance from each pixel to the specified source. The cost backlink tool was used to define the direction in which any pixel extends the minimum cost path to the specified source. The cost path tool was used to generate the path with the smallest cumulative cost distance. Finally, 500-m-wide buffer zones were constructed for the theoretical least-cost route to eliminate the spatial redundancy of corridors delineated by the least-cost route method.

Statistical analysis

The nonparametric Kruskal–Wallis test followed by a *post hoc* comparison was used to analyze the temporal and spatial differences between the average values of life-history characteristics (density, abundance, and maximum and minimum body length) of *C. mystus* larvae and eggs. Redundancy analysis (RDA) was performed to assess the linear relations between multiple dependent and independent variables in a matrix, which was then incorporated into principal component analysis (Xia, 2020). We used the RDA of life-history characteristics on the environmental factors to extract key factors explaining variations in the investigated sites. This statistical analysis was performed using the statistical software package R (R Core Team, 2014).

Results

Dynamics of fish communities in the Yangtze River Estuary

The YRE is an important spawning and nursery ecosystem for some species. According to the fishery survey of the YRE in May during 2017–2021, this area was dominated by estuarine and marine fishes until 2020; however, freshwater fishes of the family Cyprinidae reached the top five in 2021 (Table 1). Among them, marine fish *Larimochthys polyactis*, migratory fish *C. mystus*, and estuarine fish *Gobiidae* exhibited absolute dominance in spring during the past 5 years. *C. mystus* larvae or eggs were detected in the Xuliujing hydrological station located upstream of the YRE. Nonetheless, the larvae density around Changxing Island and Jiuduansha Shoal was 2–10 folds higher than offshore and upstream freshwater areas (Figure 1B). Hence, we speculated that *C. mystus* inhabits coastal or offshore areas and migrates upstream to freshwater or brackish water areas during the breeding season. Their larvae grow around Chongming Island and then migrate back to the sea (Figure 1A). *C. mystus* has two breeding periods: May is the primary reproductive period, and August is secondary. These life-history characteristics were proven by larger larvae density in May (Wilcoxon test, $P < 0.001$) than in August. In particular, the density of *C. mystus* larvae increased significantly from 2020 to 2021 (Figure 2, right panel; Wilcoxon test, $P < 0.001$), which may benefit fishery production.

Linking life-history characteristics of *C. mystus* with environmental variables

RDA was used to correlate the life-history characteristics of *C. mystus* with environmental variables. A total of 11 explanatory variables were considered in this study, including five hydrological variables: Temp, pH, salinity, depth, and DO and six chemical factors: Chla, COD_{Mn}, and the contents of N, P, Si, and SS. Forward selection revealed that the correlation between key factors and the life-history characteristics of *C. mystus* in two breeding seasons varied profoundly (Table S1). In May, 7 of the 11 variables were significant in RDA: salinity, N, pH, Si, DO, surface water temperature, and Chla. However, in August, six variables were significant: salinity, Temp, COD_{Mn}, SS, N, and P.

The first and second axes of the RDA plot demonstrated 39.9% and 7.8% variations in the life-history characteristics of *C. mystus* larvae in May, respectively (Figure 3A; Table S2). The life-history

TABLE 1 Dominant species based on the offshore monitoring voyage in May from 2017 to 2021.

Species	**Y-dominance index**					**Ecotypes**
	2017	**2018**	**2019**	**2020**	**2021**	
Engraulis japonicus	0.0748	0.0119	0.0911	0.0084	/	Marine
Larimochthys polyatis	0.0403	0.0307	0.012	0.0283	0.0023	Marine
Coilia mystus	0.0126	0.0034	0.0109	0.1215	0.0296	Short-distance migration
Gobiidae	0.0006	0.0245	0.0568	0.0137	0.0393	Estuarine
Stolephorus	0.0005	/	/	/	/	Marine
Liza haematocheila	/	0.0238	/	/	/	Estuarine
Callionymidae	/	/	0.0018	/	/	Marine
Cynoglossus sp.	/	/	/	0.0062	/	Estuarine
Cyprinidae	/	/	/	/	0.0122	Freshwater
Cynoglossus semilaevis	/	/	/	/	0.0038	Estuarine

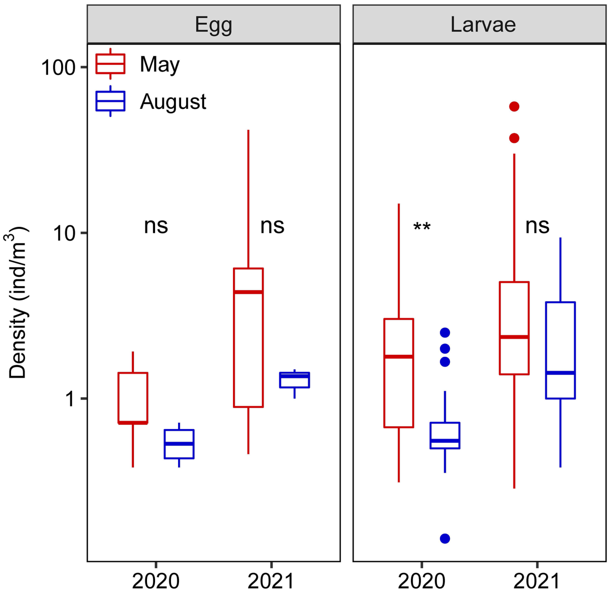

FIGURE 2
Mean density of *C. mystus* eggs and larvae in May and August of 2020 and 2021 at the Yangtze estuary. 'ns' indicates no significance between compared groups; ** indicates $P < 0.01$.

characteristics of *C. mystus* were positively correlated with Chla, N, Si, P, DO, and surface water temperature, whereas pH and salinity negatively contributed to *C. mystus* growth. In August, the first and second axes of the RDA plot demonstrated 17.2% and 9.2% variations in the life-history characteristics of *C. mystus* larvae, respectively (Figure 3B; Table S2). Three chemical factors, P, N, and COD_{Mn}, and two physical factors, Temp and SS, were positively correlated with *C. mystus* growth. Moreover, *C. mystus* growth was negatively correlated with salinity in May.

Optimal habitats of *C. mystus* and its migratory corridors in the Yangtze River Estuary

The average area under the curve values of the model training datasets were 0.983 and 0.971 in May and August, respectively (Figures 4A, B), indicating an accurate prediction of the optimal occurrence of *C. mystus* produced by the MaxEnt model. The predicted *C. mystus* occurrence hotspots with suitability larger than 0.90 were widely spread in the YRE, where the total area of the hotspots reached 89.9 and 271.2 km^2, accounting for 0.41% and 1.53% of the study area in May and August, respectively (Figures 4C, D; Table S3). In May, the predicted occurrence hotspots were mainly concentrated in the south branch (Figure 4C); however, they were almost homogeneously distributed in the south and north branch in August (Figure 4D).

The resistance values were 104.73–165.69 in May (Figure 5A) and 47.49–95.93 in August (Figure 5B), generally decreasing from offshore to upstream of the Yangtze River. ECs delineated in this study showed high spatial variances between May and August. Specifically, almost all ECs were concentrated in the south channel, especially around Jiuduansha Shoal (Figure 5A); however, ECs were almost homogeneously spread in the YRE in August (Figure 5B). Furthermore, most ECs were distributed along the coastlines of Changxing Island, Jiuduansha Shoal, and Hengsha Island. The main nodes among EC interactions were accumulated at western Changxing and Chongming islands and around Jiuduansha Shoal, indicating potential conservation priority for YRE fishery biodiversity protection.

Discussion

Life-history characteristics of *C. mystus* and its fitness to environmental forcing

The life-history characteristics of species are a result of natural evolution and ecological adaptation. The documented spawning ground of *C. mystus* was in the maximum turbidity zone in the YRE (Hu et al., 2021). Our study extended the spawning ground to the Xuliujing hydrologic station (Figure 1B). This extension may indicate two characteristics of short-distance migratory species. First, adults migrating to the upstream freshwater area were an active selection. Runoff is an unneglectable factor controlling larvae

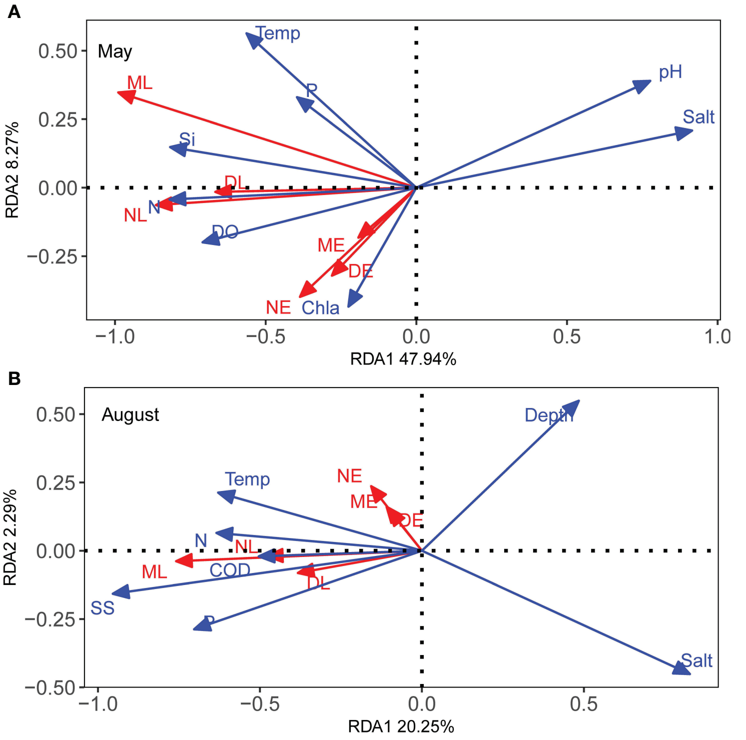

FIGURE 3
Redundancy analysis of the effect of environmental variables (blue arrows) on the life-history characteristics (red arrows) of *C mystus* in May **(A)** and August **(B)**. The response variables include the density, abundance, and mean body length of *C mystus* larvae (*in abbr.* DL, NL, and ML, respectively) and egg (*in abbr.* DE, NE, and ME, respectively). Total variation explained by the redundancy analysis model was 56.21% **(A)** and 22.54% **(B)**. Si, reactive silicate; N, total nitrogen; P, total phosphorus; SS, suspended particles; Salt, salinity; Temp, temperature of surface water.

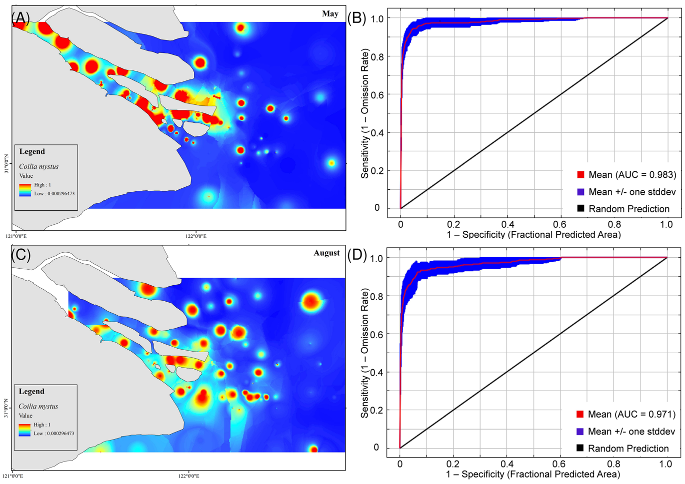

FIGURE 4
Predicted optimal distribution of *C mystus* through the MaxEnt model. **(A, C)** Potential geographical distribution of *C mystus* in Yangtze Estuarine during the May **(A)** and August **(C)** breeding season. **(B, D)** Area under the curve result of MaxEnt modeling (10 runs) for May **(B)** and August **(D)**.

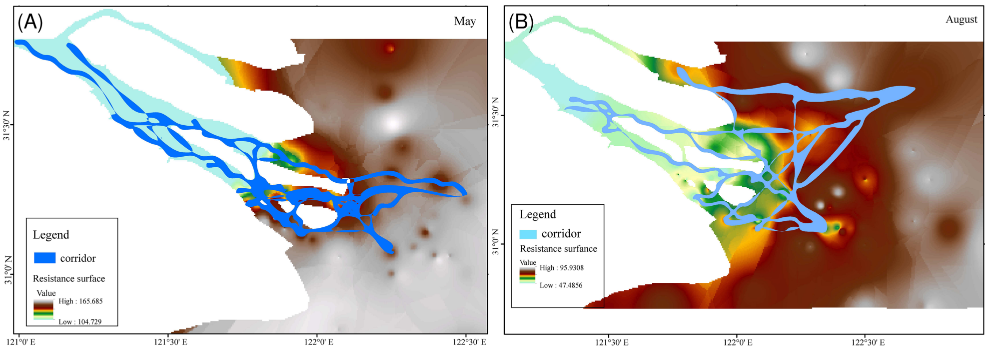

FIGURE 5
Theoretical migratory corridors of C *mystus* based on the least-cost route analysis in May **(A)** and August **(B)**.

drift. If the spawning ground is close to the estuary front, egg and larvae might be carried into the adjacent sea by the tide, where it will be difficult for them to survive because decreased sea water temperature might inhibit the hatching of eggs, and most larvae may become food sources for other fishes. Therefore, some adults would migrate upstream to freshwater, with weak tide and low salinity. Nonetheless, physiological characteristics may be the key factor controlling the migratory distance of *C. mystus*. Compared with long-distance migratory species *C. nasus*, *C. mystus* allocates most of the body lipid for gonadal development and rapidly consumes trunk lipid (Wu et al., 2017). Moreover, when migrating across a large salinity gradient, *C. mystus* needs to evolve the ability to rapidly regulate the equilibration of fluid osmotic pressure, potentially raising the cost of population maintenance. Second, some *C. mystus* adults spawn in the estuary front area, and their larvae drift upstream with tides. In this case, some unknown physiological characteristics may be developed to adapt the ebb and flow tide to sustain their spatial distribution. Some species in the Penaeus family could sense the increase or decrease in water pressure at a depth of 8 m to conduct directional migration. During a flood tide, they enter the estuary along the tide but swim to the bottom to avoid being carried out of the estuary during an ebb tide (Vance and Pendrey, 2008; Wolanski, 2017). Constricted by traditional investigation approaches and the natural characteristics of most marine fish species, providing direct evidence about their migration patterns, life-history characteristics, or adaptative evolution is challenging. Advancements in animal tracking and environmental DNA technology enable greater data collection on migratory behavior and environmental suitability assessment (Xu et al., 2018; Thalinger et al., 2019; Yatsuyanagi and Araki, 2020). Collecting more data using advanced technologies to protect more extinct or dominant species is necessary.

Based on RDA, salinity, COD_{Mn}, SS, N, P, pH, Si, DO, Temp, and Chla may considerably affect the breeding and migratory behavior of *C. mystus*. Among them, physical factors such as salinity, Temp, SS, and DO are correlated with the survival or growth of marine species (Spares et al., 2012; Walsh et al., 2013); however, chemical factors such as Chla, N, P, Si, and COD_{Mn} have not been studied adequately. Higher N, P, and Si promote algal growth, and increased Chla indicates high algal bioactivity. Algae produce large amounts of oxygen through photosynthesis and increase the DO content of the water column. As primary producers, the healthy growth of phytoplankton provides the material basis for fish growth and reproduction. Hence, detecting a positive relationship between Chla, N, P, Si, and *C. mystus* growth is reasonable.

The optimum environmental conditions for *C. mystus* larvae were as follows: salinity, 5‰–12‰; temperature, 20°C–28°C; and DO concentration, 5.2–8.0 mg/L (Hu et al., 2021), indicating that any event causing environmental variables beyond the range of biological adaptation may lead to biodiversity reduction. For example, saltwater intrusion can carry sexually mature *C. mystus* to freshwater through the north branch or to brackish water through the south branch. If the upstream freshwater runoff is low, the tide upwells, and brackish water expands upstream, providing a broad survival space for *C. mystus* larvae; such causality may account for the broader longitudinal distribution of the larvae in May than in August. However, the natural ecosystem is more complex because of the non-linear relationship among all biotic and abiotic factors for the fitness of organisms. Hence, it is necessary to study their fitness to the dynamics of certain or coupled variables.

Marine fishery biodiversity protection through ecological corridors

The YRE is rich in fish biodiversity, supporting 46 freshwater fishes, 53 estuarine sedentary and migratory fishes, and 48 marine fishes (Zhuang et al., 2006). Life-history characteristics revealed that the dominant species varied from season to season, which included *Engraulis japonicus*, *C. mystus*, *Anchoviella commersonii*, *Gobiidae*, and *Liza haematocheilus* in spring; *C. nasus*, *C. mystus*, and *Stolephorus chinensis* in summer; *Salanx ariakensis*, and *Benthosema pterotum* in autumn; and *Neosalanx jordani* in winter. Most of these dominant species act as secondary consumers relying on organic detritus or primary consumers (including zooplankton such as copepods, branchiopods, and benthic invertebrates). To date, only a few studies have reported the interspecific competition in the fish community; hence, we speculate that anthropogenic and environmental stressors that directly affect food and habitat quality severely influence the marine fish biodiversity of the YRE.

We investigated the 17 larvae of marine, estuarine, freshwater, and migratory fishes in the YRE during the past few years (Table 1). The spatial distribution of larvae did not match that of adults, which is consistent with the functional orientation of the YRE as migratory passage, spawning, nursing, and feeding grounds. Most larvae species distributed in the maximum turbidity zone developed under the coupled effects of freshwater discharge, tides and currents, the mixture of freshwater and saltwater, and suspended sediment transportation (Shen et al., 1992). Marine fishes use the YRE as a nursing and feeding ground because the convergence of various water masses brings in rich nutrients, and long-distance migratory species need to regulate the equilibration of fluid osmotic pressure here. Some freshwater species, such as those from the Cyprinidae family, can be detected due to complex hydrodynamics here. For example, freshwater discharge from Huangpu River (Figure 1A) southward into the sea along the coastal waters of Shanghai forms a fresh flume. Sometimes, saltwater intrusion might increase salinity in waters near Changxing Island and western Chongming Island. Considering the diversity in the marine species community, their habitat utilization, and the complexity of the marine environment, our study on the short-distance migratory *C. mystus* may provide a breakthrough for researching multispecies habitat utilization and conservation.

C. mystus, a typical short-distance migratory fish in the YRE, mainly lives in the nearshore area. *C. mystus* migration began during the spawning period from the nearshore sea area with 25‰ salinity to the estuarine front area with approximately 4% salinity. Some adults migrated further anadromous to the freshwater. Fish larvae were mainly distributed near Jiuduansha Shoal (Figure 1A), which displays a mixture of brackish and fresh waters with the most intense tidal influence. Affected by tides and runoff, the distribution of *C. mystus* eggs in May was closer to the upstream of the YRE, whereas that in August was closer to the periphery with 4‰–10‰ salinity. In general, migration is an important adaptive evolutionary strategy for fishes to maintain population genetic diversity. Compared with fishes in uniform habitats, migratory fishes need to span different habitats. Highly suitable patches, also called source and sink patches in our study, are important nodes and ecological stepping stones for their migration. The quantity, quality, and connectivity of source and sink patches directly determine whether the species can successfully migrate to their destinations. This study further showed that the estuarine front area was an important ecological aid for anadromous migration, with a larger number of nodes and density of ECs in May and August in this area.

In conclusion, in this study, three priority areas were identified, including the maximum turbidity zone located at the estuarine mouth and two brackish water confluence areas located around Changxing Island and western Chongming Island (Figure 1B). Among these priority areas, *C. mystus* might prefer migrating through the southern branch, especially the south channel in the May breeding season (Figure 5A), but without any bias in August (Figure 5B). Furthermore, most theoretical corridors are distributed along the coastlines except those in the offshore area, which might infer the more important role of islands in fishery production and biodiversity protection. Aside from that, theoretical ECs also ensure the connectivity of some important nature reserves, such as the *C. nasus* germplasm resource protection area at western Chongming Island, YRE Chinese sturgeon Nature Reserve to eastern Chongming Island, and some important wetlands located at Chongming Island, Jiuduansha Shoal, and Nanhui Shoal. ECs also provide an accessible approach to fishery management and biodiversity conservation. On one hand, theoretical ECs provide a least-cost movement route for fish migration and inhabitation, indicating that migratory species can sustain their population connectivity at the least cost. On the other hand, from a social management perspective, imposing a ban on an entire estuary is unnecessary, and differential measures must be taken in corridors and priority areas to facilitate the harmonious development of socioeconomic and biodiversity conservation, especially for the high-traffic YRE.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

YH, LZ, XZ, and XJ designed research; SL and YW contributed field samples collection and species classification; YH and LZ analyzed data and wrote the paper; All authors contributed to discussion of the content, and reviewed the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.966621/full#supplementary-material

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