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Estimation of estuarine habitat degradation and its influence on the reproduction process of the crab *Eriocheir sinensis* in the Yangtze River Estuary

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Abstract

Background The provision of habitat for fishery species in estuaries is highly valued and represents one of the most challenging ecosystem service values to quantify. However, quantifying this value is challenging due to complex relationships between habitat change, ecological processes, and environmental variations. This study aims to estimate estuarine habitat degradation and its impact on the reproduction process of the crab *Eriocheir sinensis* by characterizing the changes in breeding habitat and investigating relationships between the species and its habitat in the Yangtze River Estuary.

Methods A species distribution model recently developed was applied to estimate the extent and quality of breeding habitat changes from 2014–2021. The intrinsic (physiological) and external (structural) reproductive attributes of the breeding process were measured to assess the effects of habitat change. The relationships among habitat change, reproductive attributes and environmental factors were analyzed to understand the underlying driving forces of habitat degradation for breeding process by multivariate statistical analysis.

Results About 34.24% of essential habitat was lost, mainly in highly suitable areas due to reclamation and waterway construction. Habitat degradation significantly affects female distribution and their reproductive processes, particularly gonad development during the pre-reproductive period and fecundity during the reproductive period, without altering population structure. These results indicated that the main ecological function served by the highly suitable breeding ground was the provision for development of gonad and improvement of fecundity. Increases of salinity and turbidity, caused by hydrodynamic changes from large-scale waterway construction, were identified as the environmental determinants contributing to cumulative habitat degradation. These influences ultimately led to a decrease in the fecundity of *E. sinensis*.

Conclusions Our research sheds light on the quantification of habitat degradation in the Yangtze River Estuary and its implications for the reproduction process of *E. sinensis,* which can serve as a foundation for assessing and quantifying the ecosystem service values provided by these breeding grounds. This information is valuable

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for policymakers and resource managers in making informed decisions regarding habitat conservation and the sustainable utilization of fishery resources.

Keywords Fishery habitat provision, Breeding habitat degradation, Reproductive process, Estuarine ecosystem services, Sustainable fisheries management

Introduction

Estuaries are well-known to provide important fishery habitats (breeding, nursery and feeding habitat) for numerous commercially and ecologically important fish, crabs, and reptile species. Despite the importance of estuaries as fish habitat, estuaries are highly dynamic and have been subject to a wide range of environmental and anthropogenic stressors (Ladd et al. 2019). Changes in sediment supply, hydrology, sea level rise, human activity in intertidal habitats, and land management in adjacent areas can have detrimental effects on estuarine water quality and habitat extent, resulting in substantial habitat alteration and degradation. Since many important fishery species exhibit specific habitat preferences (Fodrie and Levin 2008; Seitz et al. 2014) or localized movement behavior (Munsch et al. 2017), continued habitat degradation and loss may negatively impact fishery population within estuaries (Chesney et al. 2000; Seitz et al. 2014; Sundblad et al. 2014).

The provision of habitat for fishery species in estuaries is highly valued and represents one of the most challenging ecosystem service values to quantify (Barbier et al. 2011). The difficulty arises from the fact that fish utilize estuarine habitats in diverse ways, influenced by various factors such as species, life stage, time of year (Scott et al. 2000). Moreover, the habitat change is a cumulative (and possibly interactive) effects of natural environmental variability and negative anthropogenic activities (Barbier et al. 2011). Consequently, it becomes crucial to accurately characterize changes in the spatial area or quality of specific fishery habitats; also, it requires tracing how the changes in habitat influence the quantities and qualities of the ecosystem functions or processes (Barbier et al. 2011).

The spatial extent of habitat and its associations with fishery population play a primary and important role in the conservation of sustainable fisheries management. Numerous studies have demonstrated correlations between estuarine habitat extent and local fishery production (Rochette et al. 2010; Sundblad et al. 2014; Swadling et al. 2022). The reduction or fragmentation of habitat can lead to a decline in species abundance over time until a new equilibrium level is reached. However, estimating the quality of habitat remains challenging due to the complex life histories of fishery species and the extensive spatiotemporal variability of habitat variables. The species distribution model (SDM) has been widely used in the past decade to identify fishery species habitat (O'Connor et al. 2012; Wagner et al. 2020; Yang et al. 2017; Zhang et al. 2019). Techniques in statistical and machine learning have been applied in SDMs, ranging from classical statistical models (Potts and Rose 2018) to machine learning algorithms (Rees et al. 2021; Scott et al. 2000). Recently, a SDM was developed, which combines species life history analysis and the effective use of remote-sensing predictors from Landsat data, to provide high capability in fishery habitat mapping (Zhang et al. 2022).

To analyze the species or community responses to habitat change, previous studies mostly relied on the structural metrics of fish communities such as species richness, diversity, and composition. However, these metrics focus on external characteristics and fail to measure the intrinsic ecological processes critical to supporting resilient and robust fishery stocks, such as feeding, reproduction, nutrient cycling, and secondary biomass production (West and Zedler 2000). To complement structural metrics, functional metrics are necessary for a comprehensive understanding of the fish–habitat links underlying these processes (Fu et al. 2013). Several functional metrics have been utilized to evaluate movement, breeding, and feeding processes relevant to target species, including fish movement metrics such as residence time, rate of movement, tortuosity of movement, and area of use (Caldwell and Gergel 2013; Freedman et al. 2016), physiological metrics such as body weight, body length, gonad and hepatopancreas status (Colpo and Lopez-Greco 2017), and diet metrics such as stomach contents and stable isotopes (Eduardo et al. 2020). However, there has been limited research on the effects of habitat change on each of these processes, as the effects are cumulative or interactive, and the relationships are often confounded. Effective management requires disentangling the cumulative or interactive effects on each process, as mitigation strategies may vary depending on the primary cause of degradation (Bonin et al. 2011).

The Yangtze River, known as the largest river in China and the third largest in the world, originates in the Tibetan Plateau and flows more than 6000 km through 11 provinces and municipalities of China, before entering the East China Sea near Shanghai. The Yangtze watershed is one of the intensely industrial areas, and the major lakes along the Yangtze River, such as Taihu Lake, Chaohu Lake, and Dongting Lake, deteriorated to the inferior V class (Wang et al. 2022c). Many hydro dams are built on the river, including the Three Gorges Dam as the world's largest hydro-electric power station, which have significant impacts on economic growth, water flow, sediment, fishery immigration, etc. (Huettmann and Regmi 2020). For example, dam/barrier construction in upstream rivers would change the sedimentation flow, which is expected to have an adverse impact on foraging and spawning fish habitat, by changing even a few centimeters of sediment layer over the natural substrata (Guo et al. 2023). The Yangtze River delivers huge amount of water and sediment to the Yangtze River Estuary (YRE) and the marginal East China Sea, providing a significant contribution to the global terrestrial flux (Zhuang et al. 2013). The YRE is the largest estuary on the Pacific coast, and its massive discharge creates a highly productive ecosystem. Also, this region is the contact zone between the Yangtze River freshwater and the Pacific ocean saltwater, and coupled with the many river and ocean processes, which are essential in the global water and nutrients cycle (Zhu and Shukla 2016). Moreover, as climate change coming up unabated, this region is one of the most susceptible areas to changes of monsoon and tides, sea level rise, brackish water intrusion and ocean acidification (Huettmann and Regmi 2020). The YRE is also a critically important and sensitive habitat, providing valuable resources for biodiversity. It serves as a major stopover for migratory birds along the western Pacific coast and is also a breeding and feeding ground for numerous fishery species (Zhuang et al. 2013). As the YRE is located adjacent to the megacity of Shanghai, human activities exert substantial pressures on the coastal wetlands. For example, it is heavily affected by the new seawall, invasive species, overfishing, sewage, the global car industry, globalization, urban planning, entertainment parks, farming, reclamation, electrification, airports and a certain air quality management (Ma et al. 2014). These have led to significant changes in the ecological environment of the estuary area, including alterations in water sediment, river morphology, saltwater intrusion, water quality deterioration, wetland shrinkage, and species replacement (Zhuang et al. 2013). These changes have resulted in coastal ecosystem degeneration and consequent decreases or loss in ecosystem services. The impact on fish species residing in the estuary is particularly severe, and fishery resources and biodiversity significantly declined in this region over the past decades (Zhuang et al. 2013). The restoration of the ecological environment of the YRE becomes a major priority, especially with the launch of the "10-year fishing ban" plan (TYFB) from January 2021 (The TYFB aims at recovering the fish stocks and aquatic biodiversity across the Yangtze River Basin. According to the plan, all activities concerning harvesting of natural fishery resources are prohibited within specified areas, including the mainstream of the Yangtze River, the two remaining river-connected large lakes, Lake Poyang and Lake Dongting, seven important tributaries, 332 aquatic life reserves, and other important waters.) and the issuance of the Yangtze River Protection Law by Chinese government on March 1, 2021. (The Yangtze River Protection Law aims to protect and restore the ecological environment of the Yangtze River and promoting sustainable development in the Yangtze River Economic Belt. The YRE serves as the most important ecological barrier for the Yangtze River Economic Belt and has an extremely important strategic position in the overall regional development.)

The objective of this study was to estimate estuarine habitat degradation and its impact on the reproduction process of fishery species, by investigating the links between a representative fishery species, the Chinese mitten crab (*Eriocheir sinensis*) and its breeding habitat in the YRE. *E. sinensis* is an ecologically and commercially important fishery species in the YRE, characterized by its wide distribution, environmental tolerance, rapid growth, high reproductive capacity, broad diet, and gregarious behavior (Li et al. 2011). Furthermore, it also represents a typical deteriorating fishery resource in the YRE, with annual yields plummeting from 46.3 to 2.0 tons due to overfishing and habitat degradation (Xue et al. 2016). The conservation of *E. sinensis* is one of the main concerns of environmental managers in the YRE. In this study, we firstly estimated the habitat distribution of *E. sinensis* over the past decade using our newly developed SDM (Zhang et al. 2022). This allowed us to quantify the extent and quality of habitat change based on the modeled distribution. Then, the reproduction process of *E. sinensis* at berry stage was focused on and both intrinsic (physiological) and external (structural) reproductive attributes were measured to assess the effects of habitat change on reproduction process in the breeding ground. Lastly, the relationships among habitat, reproductive attributes, and environmental factors were analyzed to understand the underlying driving forces of habitat degradation and the degradation mechanism influencing the breeding process. By examining the linkages among species, habitat, and environment, we aimed to gain a clear understanding of how habitat change influences the reproduction process, beyond the commonly observed relationships between two individual components. From a management perspective, this study could provide the basis for the qualification of ecosystem service values and the specific scientific suggestions for the successful restoration project.

Materials and methods

Study area

The YRE is a large estuary divided by Chongming Island into two branches (North Branch and South Branch) (Fig. 1). In terms of ecological functioning, the YRE serves as crucial grounds for spawning, feeding, and nursing grounds of various commercially valuable species, such as *E. sinensis* (Taxonomic Serial Number, TSN 99058), *Coilia ectenes* (TSN 678262) and *Muraenesox cinereus* (TSN 161296). Additionally, it serves as essential migration corridors for endangered and rare species like *Acipenser sinensis* (TSN 550555) and *Myxocyprinus asiaticus* (TSN 639710) (Geng et al. 2018; Ma et al. 2020). Historically, the YRE held immense importance as traditional fishing grounds, fostering the breeding of the "five major fisheries", such as *C. ectenes*, *Hemisalanx prognathus* (TSN 623667) and *E. sinensis*, and yielding significant social and economic benefits (Zhuang et al. 2013). However, over time, the fishery habitats within the YRE have experienced continuous degradation due to extensive human activities. The operation of the Three Gorges Dam in 2003 has notably reduced the sediment flow from the Yangtze River by 70% (Yang et al. 2015). Another major project, the deep waterway project (DWP), which stands as China's largest estuarine hydraulic engineering endeavor, has brought about significant alterations in the regional hydrodynamics, thereby modifying the ebb flow diversion between the North and South Branches (Pan et al. 2012). In particular, large-scale reclamation occurs between the edge of the high watermark to around 2-m water depth, covering the most critical coastal wetland areas and tidal flats. As this coastal zone contains important spawning and hatching habitats for economically important fish species, the overall effect of reclamation is a net loss of fishery habitat. An estimated 1259 km^2 of intertidal flats have been reclaimed between 1953 and 2010, primarily due to the urban expansion for Shanghai (Chen et al. 2018). On the other hand, along with the rapid increase of population, industrial and agriculture development, the YRE and the water areas have been facing emerging water quality deterioration, heavy metal pollution and ecological and environmental risks, especially under the global warming, ocean acidification and hypoxia circumstances (Chong et al. 2022; Hu et al. 2022).

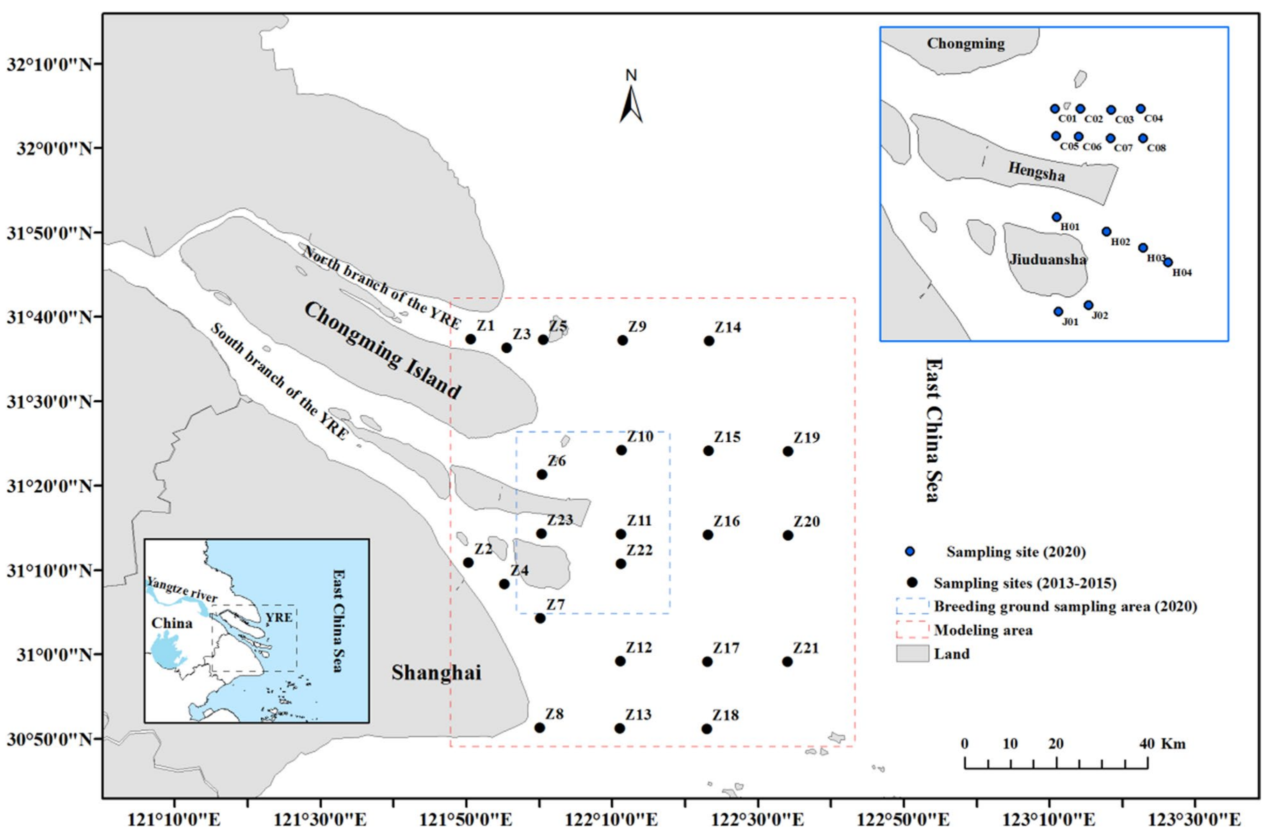

Fig. 1 Study area and sampling sites

Field sampling and measurement of reproductive attributes

E. sinensis is a catadromous species, spending 16 to 18 months in freshwater during the juvenile and immature stages before migrating downstream to brackish water when sexually mature to spawn in estuaries (Rudnick et al. 2005). The YRE plays an important role in serving as a breeding ground for *E. sinensis* (Geng et al. 2018). The breeding season of *E. sinensis* includes four distinct stages: mating, spawning, berry and hatching, among which berry stage lasts longest from November to March. Thus, field sampling was focused on the berry stage and conducted during two periods in 2020 (12.06–12.16 and 12.21–12.28) at 14 sampling sites located in areas where stable populations of *E. sinensis* were found (depicted by the blue frame in Fig. 1). These sites included eight sites near Chongming island (C01–C08), four sites near Hengsha island (H01–H04) and two sites near Jiuduansha shoal (J01–J02). At each site, three gillnets (1.6 m in height, 100 m in length, with 10 cm mesh) were deployed to catch the crabs. The gillnets were set during low tide and retrieved approximately seven hours later at high tide. A total of 1471 crabs were collected, including 452 females and 1019 males. Based on anatomical reproductive status (Xuan et al. 2016), female crabs were further divided into 291 mated females (Fig. 2a) and 161 ovigerous females (Fig. 2b). Considering the proportion of mated and ovigerous females, the early December (12.06–12.16) was designated as the pre-reproductive period (Pre-R), as over 90% of the sampled females were mated and prepared to oviposit. The late December period (12.21–12.28) was considered as the reproductive period (R), since the proportion of ovigerous crabs turned to above 90% (Table 1). Subsequently, female crabs were mainly measured and weighed to focus on the reproductive process, while physiological measurements for males were excluded, except for abundance and the male-to-female ratio. The indices of female and male abundance and the male-to-female ratio served as the external (structural) reproductive attributes (Table 2). During the Pre-R stage, the gonads of most mated females were fully developed, but no fertilized eggs were present. In contrast, during the R stage, the fertilized egg mass got developed while the gonads were depleted. According to the *t*-test results, there were no differences in carapace width (CW), carapace length (CL), body weight (BW) and hepatopancreas weight (HW) between the Pre-R and R female groups (Table 3). Therefore, ovigerous females in the R period were considered part of the same mated group during the Pre-R period. Subsequently, intrinsic (physiological) reproductive

Fig. 2 Anatomical diagram of different reproductive statuses of *Eriocheir sinensis*, **a** mated state: the seminal receptacles have an amount of sperm stored in it; **b** ovipositing state: ovipositing in the abdominal limbs, no or little gonad tissue remains and the ovulation process has been completed

Table 1 Reproductive periods of *Eriocheir sinensis* based on the proportion of ovigerous females and the mated crabs throughout the sampling time

Period	Sampling time	Mated crab	Ovigerous crab	Proportion of mated crabs (%)	Proportion of ovigerous crabs (%)	Males	Male to female ratio
Pre-reproductive (Pre-R)	12.06–12.16	276	16	94.5	5.5	671	2.3
Reproductive (R)	12.21–12.28	15	145	9.4	90.6	348	2.2

Table 2 The measurements of reproductive attributes and related indices of *Eriocheir sinensis*

Reproductive attributes	Reproductive indices	Measurements
The abundance of females and males	Female	The number of female crabs caught by gillnet per net per day (ind/(net·d))
	Male	The number of male crabs caught by gillnet per net per day (ind/(net·d))
	Male/female	The ratio of male to female
The general status of females	Carapace width (CW)	The width of the crab carapace measured across the widest point (mm)
	Carapace length (CL)	The length of the crab carapace from the base to the eye orbit (mm)
	Body weight (BW)	The wet weight of crab (g)
The status of the females' hepatopancreas	Hepatopancreas weight (HW)	The wet weight of females' hepatopancreas (g)
	Hepatosomatic index (HSI)	HSI (%) = HW/BW × 100%
The status of the mated females' gonads	Gonadosomatic weight (GW)	The wet weight of mated females' ovaries (g)
	Gonadosomatic index (GSI)	GSI (%) = GW/BW × 100%
The status of ovigerous females' fertilized egg mass	Absolute fecundity (AF)	The wet weight of fertilized egg masses (g)
	Relative fecundity (RF)	RF (%) = AF/BW × 100%

Table 3 Difference comparison of physiological measurements of reproductive attributes between Pre-R and R female groups by *t*-test (mean and standard deviation)

Indices	Female crab	
	Pre-R	R
CW (mm)	58.28 ± 3.66^a	59.43 ± 9.34^a
CL (mm)	53.54 ± 3.04^a	57.10 ± 8.45^a
BW (g)	95.47 ± 17.58^a	103.67 ± 35.25^a
GW (g)	13.53 ± 3.87	–
HW (g)	4.89 ± 0.84^a	6.39 ± 2.89^a
AF (g)	–	20.44 ± 7.49

Different letters indicate statistically significant differences between means ($p < 0.05$), according to Duncan's test ($\alpha = 0.05$)

Different superscripts of values in each row indicate significant differences ($p < 0.05$), while the same superscripts indicate no significant differences

attributes were calculated, encompassing the general status of females, the status of the females' hepatopancreas, the status of the mated females' gonads, and the status of ovigerous females' fertilized egg mass. The relevant indices and their measurements are presented in Table 2. Among these indices, the indices of the hepatopancreas can reflect the status of energy and nutrient for reproductive and oviposition activities, as the hepatopancreas serves as a vital energy storage tissue in crustaceans, responsible for nutrient absorption and storage. The indices of the gonads and fertilized egg mass reflect the spawning capability and are widely employed to assess the reproductive performance of crustaceans (Colpo and Lopez-Greco 2017; Huang et al. 2022).

Abiotic factors were measured during the gillnet placement at each sampling site. The salinity (SAL, ppt), dissolved oxygen (DO, mg L^{-1}) were measured using an in situ multi-parameter water quality analyzer (Proplus, YSI). The transparency or turbidity (nephelometric turbidity units, NTU, cm) of surface water was measured using a portable Secchi disk. The depth of water (DEP, m) at each sampling site was measured using a single beam bathymeter (Bathy-500MF, SyQwest).

SDM modeling of *E. sinensis* habitats in 2014 and 2021

To quantify the extent and quality of habitat change of *E. sinensis*, the habitat distributions of *E. sinensis* over nearly ten years were estimated by using our newly developed SDM, and then the complex relationships between habitat degradation and the reproductive processes of *E. sinensis* could be investigated based on this. The basic model of the SDM model is defined as:

$$Y = \alpha + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \varepsilon,$$

where Y is a matrix of presence/absence (1/0) or count data of *E. sinensis*, α and β are the true intercept and slope parameters for environmental explanatory variables, and x is the main environmental explanatory variables as the fixed effects to species. The ε parameter represents here the random effect at the site level to account for spatial autocorrelation between sites with repeated measures.

With this SDM model, the essential habitat of *E. sinensis* in the berry stage was firstly modeled by with Landsat data from February 21, 2014 (Zhang et al. 2022). The biological dataset for the model was derived from large-scale regular surveys conducted between late February to May from 2013–2015 (Geng et al. 2018). Field measurements were collected from a total of 23 sampling stations, strategically positioned across the YRE to cover potential crab habitats (depicted by the red frame in Fig. 1). The DO, total suspended sediments (SST), sea surface temperature (TSS) and depth were selected as environmental explanatory variables of SDMs, as they were potential critical environmental factors and can be calculated from Landsat images or auxiliary data. The explanatory and predictive powers of our SDM modeling demonstrated satisfactory, which were measured by area under the curve (AUC) (Pearce and Ferrier 2000) and Tjur's R^2 (Tjur 2009) values, particularly in the occurrence model with satisfied explanatory power (Tjur $R^2 = 0.57$, AUC = 0.95) and predictive power (Tjur $R^2 = 0.39$, AUC = 0.89) (Zhang et al. 2022). Moreover, the α and β parameter estimates were shown to accurately represent the true posterior distribution from the Markov Chain Monte Carlo (MCMC) convergence diagnostics. To avoid yielding biased parameter estimates, the Bayesian approach-MCMC chains were applied by using trace plots of parameters with 7500 samples over 2 chains, a thinning of 5 and burn-in of 2500 samples, and the MCMC convergence and mixing were good in all SDMs and revealed no sign of autocorrelation (Zhang et al. 2022). Therefore, the output and the inferences drawn from the model can be considered reliable. Accordingly, the predict functions and corresponding estimated parameters from the best-fit model were employed to predict the relative index of occurrence (RIO) of *E. sinensis* using Landsat data from March 28 in 2021. This date was chosen to align closely with the sampling period in 2020 and the month of the SDM modeling conducted in 2014. Thus, the habitat changes of *E. sinensis* breeding grounds can be compared with the modeling results in 2014 and 2021. The fitting and prediction of the SDM models were conducted using the R-package Hmsc (Tikhonov et al. 2020). The more detailed steps of the modeling can be referred to our previous article (Zhang et al. 2022) or Additional file 1, and the model code and datasets are available online in Figshare.

Statistical analysis of habitat change on reproduction process

To examine the effects of habitat change on the breeding process, the sampling sites were classified into different habitat groups based on the RIO values obtained from habitat predictions. Subsequently, differences in reproductive attributes data were clustered and compared among these habitat groups using a one-way analysis of variance (ANOVA). Multiple comparisons were conducted using post hoc Duncan tests, and a significance level of $p < 0.05$ was considered indicative of a significant difference. To meet the assumptions of ANOVA, the data were log-transformed after testing for homogeneity of variances. ANOVA analysis and the creation of column diagrams were performed using SigmaPlot 22.0 (OriginPro 2021).

Although ANOVA was effective in differentiating large differences in reproductive attributes among habitat groups, it was insufficient for investigating the complex relationships between reproductive attributes, habitat changes, and environmental variations. Therefore, two multivariate statistical analyses (the redundancy analysis, RDA, and the variation partitioning analysis, VPA) were used to interpret the responses of the reproductive attributes across a range of habitat or environmental change. RDA was utilized to analyze the changes in reproductive attributes along continuous gradients of habitat or environmental changes. If the habitat or environmental determinants provided satisfactory explanations for a set of reproductive attributes in RDA, VPA was subsequently performed to determine the importance of each variable, the amount of variation it explained, and the extent of shared effects (Borcard et al. 1992). The VPA could summarize their explanations for multiple reproductive variables, elucidate the determinants of the breeding process, and indicate the proximity and similarity between sites. Two sets of explanatory variables were tested: the habitat change group and the environmental group (DEP, SAL, NTU and DO). These variables were evaluated against the 15 reproductive attributes listed in Table 2, which served as the response variables for all 14 sampling sites. The multivariate statistical analyses were conducted using the CANOCO 5.1 program package (Ter Braak and Šmilauer 2012).

Results

Habitat change of *E. sinensis* breeding grounds

Both habitat models in 2014 and 2021 yielded satisfactory results, allowing the RIO to be categorized into five habitat suitability levels for breeding using the Jenks natural breaks classification. The habitats of breeding ground were classified as follows: (1) very lowly (< 0.35), (2) lowly (0.35–0.43), (3) moderately (0.43–0.50), (4) highly (0.50–0.60), and (5) very highly suitable (> 0.60) habitats (Fig. 3). A comparison of potential accessible areas for *E. sinensis* (RIO > 0.35) reveals habitat loss and degradation in the breeding ground of *E. sinensis.* The areas from lowly to highly suitable habitat have significantly diminished and become fragmented between the two periods. The areas of high RIO (> 0.5) show that the *E. sinensis* mainly occurs in the subtidal zones adjacent to the wetlands of Dongtan Island, Hengsha Island, and Nanhui tidal flat. The most substantial habitat loss occurred in the highly suitable areas (RIO: 0.5–0.6), which encompassed 2312.73 km^2 as essential breeding grounds. However, after seven years, 34.24% of the essential habitat was lost and degraded to

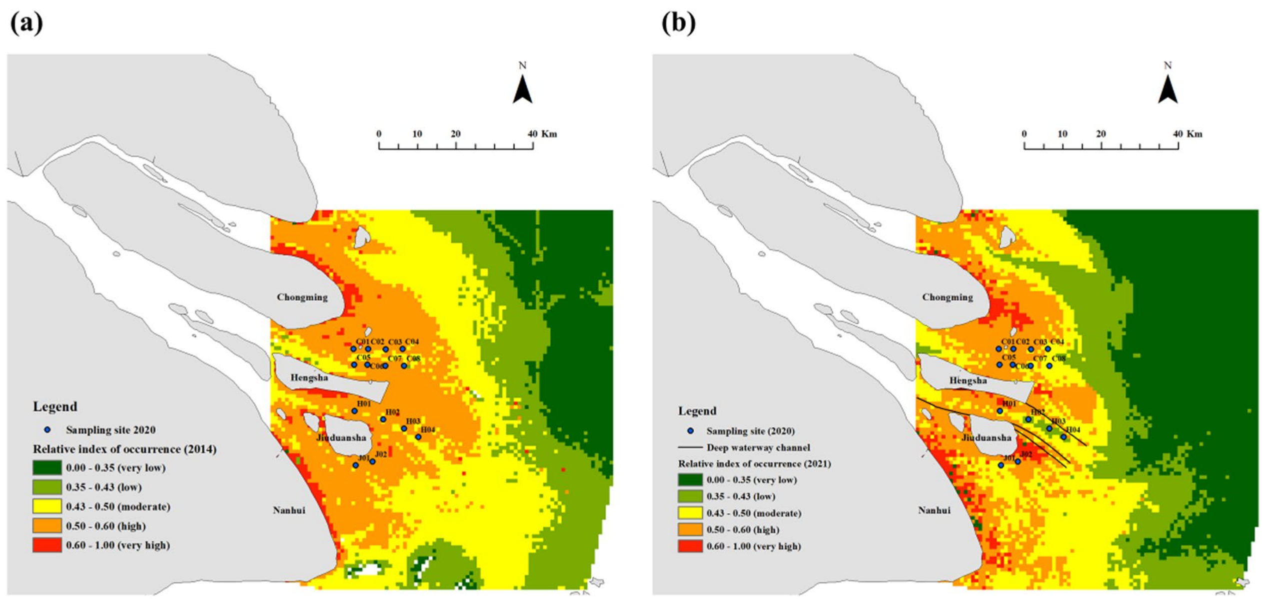

Fig. 3 SDM modeling of RIO of *E. sinensis* at berry stage in **a** 2014 and **b** 2021

Table 4 Habitat suitability for *E. sinensis* in the YRE

Scenario	RIO	Areas (km^2)	Percentage lost (%)
Very highly suitable habitat			
2014	0.60–1.00	185.76	−3.6
2021	0.60–1.00	192.47	
Habitat loss		−6.71	
Highly suitable habitat			
2014	0.50–0.60	2312.73	34.24
2021	0.50–0.60	1520.83	
Habitat loss		791.90	
Moderately suitable habitat			
2014	0.43–0.50	2410.02	28.24
2021	0.43–0.50	1729.37	
Habitat loss		680.65	
Lowly suitable habitat			
2014	0.35–0.43	1603.01	15.90
2021	0.35–0.43	1348.16	
Habitat loss		254.85	
Very lowly suitable habitat			
2014	0.00–0.35	1351.38	−111.69
2021	0.00–0.35	2860.74	
Habitat loss		−1509.36	

the moderately or lowly suitable habitat (Table 4). All 14 sampling sites in 2020 were initially distributed in the highly suitable areas, but most of these sites shifted to the lower suitable areas, with the exception of C01, C02, C05, C06, J02 (Fig. 3). The moderately and lowly suitable areas also experienced significant degradation, resulting in losses of approximately 28.24% and 15.90%, respectively (Table 4). The core area of breeding ground undergone minimal change, with a percentage change of only 3.6% in the very highly suitable habitat areas (from 185.76 to 192.47 km^2).

Responses of reproductive attributes to habitat suitability degradation

According to the distribution of habitat suitability modeled in 2021, the 14 sampling sites were located within three habitat classes. Specifically, C01, C02, C05, C06, J02 were distributed in the highly suitable areas; C03, C04, C07, C08, H01, J01 were in the moderately suitable areas, and H02, H03, H04 were in the lowly suitable areas (Fig. 3). Thus, differences in reproductive attributes of *E. sinensis* were analyzed to examine the effects of habitat degradation among three groups (Fig. 4). Since most metrics did not show differences between Pre-R period and R period, the measurements from both periods were combined for analysis (Table 3). However, it should be noted that some metrics were unique to either the Pre-R or R period, such as GW and GSI were the specific metrics in pre-R period, and AF and RF were in R period. The results showed that there was a significant effect of habitat degradation on several reproductive attributes among the three habitat groups (Fig. 4). Specifically, only the abundance of females exhibited a significant difference among the highly, moderately and lowly suitable groups. Other structural metrics, such as the abundance of males, the ratio of male to female, displayed more complex variations. This suggests that habitat quality primarily affects

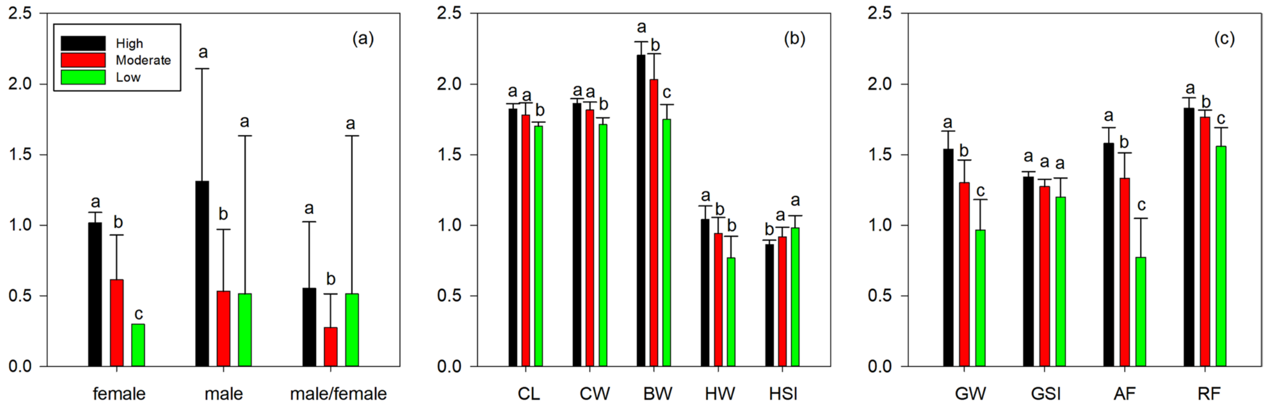

Fig. 4 Variation of the reproductive attributes of *E. sinensis* among the highly, moderately and lowly suitable habitat groups (mean and 95% confidence interval) **a** changes in the structural metrics, **b** the basis status of females and hepatopancreas, **c** the status of the gonads and fertilized egg mass (*CW* carapace width, *CL* carapace length, *BW* body weight, *HW* hepatopancreas weight, *HSI* hepatosomatic index, *GW* gonadosomatic weight, *GSI* gonadosomatic index, *AF* absolute fecundity, *RF* relative fecundity). Different letters indicate statistically significant differences between means ($p < 0.05$), according to Duncan's test ($\alpha = 0.05$)

the distribution of females rather than males, considering the relatively stable ratio of male to female (2.2–2.3:1) observed during both periods. Among the physiological metrics, BW, GW, AF, and RF were significantly different among the three groups, while CL, CW, HW, HSI, GSI showed no conspicuous variation throughout the three groups. This indicates that habitat quality influences the development of body weight, with differences mainly arising from the development of gonads in the Pre-R period and the development of egg mass in the R period. Furthermore, the impact on fecundity in the R period appears to be greater than gonad development, as the significantly different RF suggests that the variations in egg mass exceed the increase in body weight, while the stable GSI indicates the increases in gonad and body weight are proportional across the three groups. The lack of significant variations in HW and HSI also indicates that the primary ecological function served by the highly suitable breeding ground is providing suitable conditions for gonad development and enhancing fecundity levels, rather than storing and accumulating energy, as habitat degradation has no significant impact on the hepatopancreas status.

Relationship among reproductive attributes, habitat changes and the environmental variations

Two groups of indices were used to quantify the habitat conditions and investigate their relationships with the breeding process: (1) habitat degradation index (HDI), which was calculated from the differences between two RIO values and aimed to reflect the cumulative effects of habitat change; (2) environmental factors measured during field sampling, including SAL, DEP, NTU, DO, which were assumed to reflect the present habitat condition.

The reproductive variables were primarily sieved by Mantel tests, which used Monte Carlo permutations with a forward stepwise selection procedure (999 iterations). Variables that showed significant influence from HDI or environmental factors (e.g., $p < 0.05$) were considered for subsequent RDA and VPA. The selected significant variables included female abundance, RF, CL, BW, AF, CW, GW and HW. Most of these variables exhibited significant differences among the three habitat groups as shown in Fig. 4.

Monte Carlo tests of all RDAs (Fig. 5a–c) indicated that all the canonical axes were significant ($p < 0.05$), suggesting relatively strong relationships between species–habitat, species–environment and habitat–environment. The eigenvalues of first axes accounted for 60.6%, 59.8% and 39.0%, respectively. Subsequently, a VPA ordination diagram was created to assess the variance in reproductive variables explained by each of the two habitat condition sets independently, as well as the combined effect of the two sets. The VPA revealed that the variation partitioning was significant ($p < 0.01$) for the HDI (group I) and the intersection group (group III). The intersection group explained the most variability (42.7%, $p = 0.02$), followed by HDI group (14.5%, $p = 0.04$), and the environment group explained the least (5.1%, $p = 0.69$). The VPA, considering the intersection effects of HDI and environmental factors, accounted for 65.8% of the variance in the reproductive attributes with the first axes (Fig. 5d). Both RDA and VPA results consistently identified HDI, SAL and NTU as key determinant factors for the reproductive attributes of *E. sinensis* (Fig. 5a–d). However, the VPA provided an improved explanation by considering the intersection effects of the two sets compared to analyzing each set separately. The aggregations of habitat site

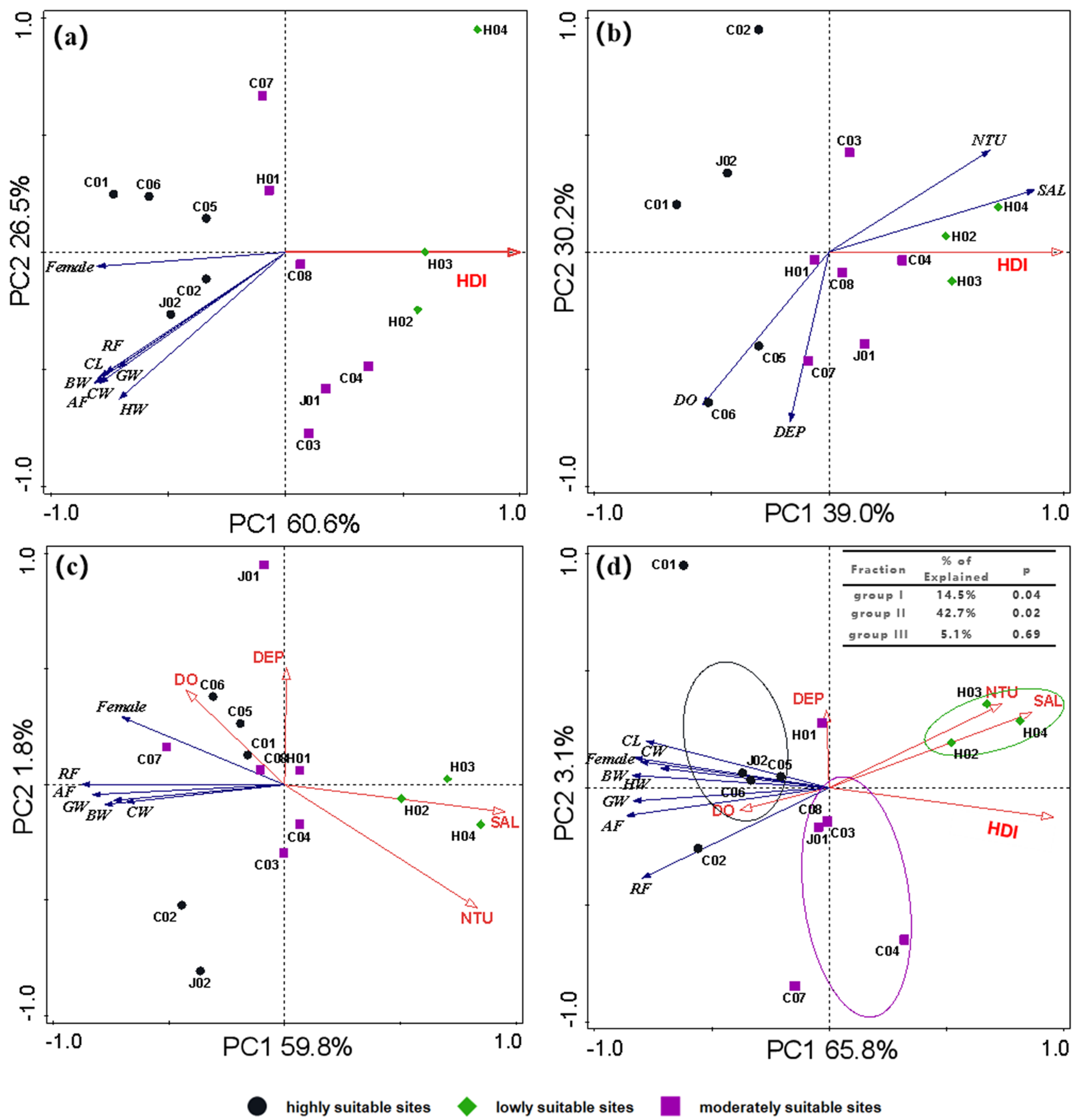

Fig. 5 Results of the RDA and VPA displaying significant predictors of the species–habitat–environment linkages. Displayed are the first and second extracted axes. **a** The RDA based on HDI accounted for 60.6% (the eigenvalue of first axes) of the variance in the determinant reproductive variables. **b** The RDA based on HDI accounted for 39.0% of the variance in the environmental variables. **c** The RDA based on first canonical axe of environmental factors (SAL and NTU were main contributors) accounted for 59.8% of the variance in determinant reproductive variables. **d** The VPA based on the three groups accounted for 65.8% of the variance in the determinant reproductive variables

groups in VPA also yielded clearer relationships between habitat and reproductive attributes compared to the RDAs, highlighting the stronger association between the two.

Specifically, in the VPA analysis, the reproductive variables demonstrated a negative correlation with HDI, SAL and NTU, while DEP and DO showed weaker correlations with reproductive variables, as shown in Fig. 5d. The environmental factors (SAL and NTU) mainly influenced the RF based on the angle between the arrows representing reproductive attributes and the opposite extension of the arrows representing NTU and SAL. On the other hand, habitat degradation (HDI) primarily influenced female abundance, BW, and CW based on the angle between the arrows representing reproductive attributes and the opposite extension of the HDI arrow. The close angle between HDI arrow and SAL and NTU arrows suggested that these two environmental variations were the main drivers of habitat degradation. By envelop mapping of the three classes of habitats suitability, it was observed that the lowly suitable sites were located closely with HDI, SAL and NTU, while the highly suitable sites were clustered around DO (Fig. 5d).

Discussion

The role of habitat degradation estimation

The breeding ground of *E. sinensis* in the YRE has experienced significant habitat loss and degradation. This study quantitatively estimated the extent of this habitat degradation with a newly developed SDM model. The results of the SDM model provided satisfactory predictions, allowing for a visual display of the magnitude of habitat loss and the degree of degradation (Fig. 3). Notably, the most substantial losses occurred in the essential breeding grounds, where highly suitable areas decreased by 34.24% (Table 4). These areas are predominantly located near the Dongtan Island, Hengsha Island, and Nanhui tidal flat (Fig. 3). It is noted that many of these areas are ecologically fragile and currently subjected to intensive anthropogenic pressures, mainly the reclamation (Xue et al. 2016) and the deep waterway construction (Wan et al. 2014). The simulation SDM method is effective and convenient, which can be simulated on the complex estuarine scale through remote sensing data (Zhang et al. 2022). Despite the advantages of SDM models, we acknowledged that the SDMs may be not comprehensive enough due to the limited number of field sampling points, the sampling design limitations and the restrictive inversion from remote sensing data, as some important environmental variables could not be included due to the limited availability of Landsat predictors (e.g., salinity, water current). Therefore, the explanatory power (T_{jur} $R^2=0.57$) and predictive power (T_{jur} $R^2=0.39$) were relatively low, which will lead to uncertainty in the estimation of species distribution. Also, there are some outlier pixels distributing in the modeled areas, which may originate from the uncertainties and outliers of the input remote sensing inversions. In this respect, the improvement of field sampling, the precise inversion methods and the model updating are needed further. Nevertheless, the resulting habitat distribution of the breeding grounds can meet the basis for analyzing the reproductive process. The estimation of fishery habitat degradation helps in the conservation and management of fishery resources, which allows for the identification of areas that are most affected by degradation and helps prioritize conservation efforts (Brown et al. 2019; Taylor and Creighton 2018).

From a policy conservation perspective, the important role of fish habitat in sustaining healthy fish stocks is increasingly being recognized (Lewin et al. 2006). Many fishery habitat assessment has been performed by focusing mainly on seagrass, mangroves, coral reefs and macroalgae habitats in shallow vegetated or hard bottom area (Brown et al. 2019). However, the habitat degradation has not been well addressed across other offshore aquatic landscapes as the extent or rates of habitat degradation/loss are not well known (Minns et al. 2011). In consequence, the relationship between fish habitat degradation and the fishery species is difficult to investigate, and the researches of habitat-driven mechanisms for fishery resources are limited. Methods of habitat trends, such as SDM models, are needed to properly attribute causes of fisheries dynamics and are likely to raise importance of habitat protection for fisheries management (Bradley et al. 2020).

Impacts of habitat degradation on reproductive process

Until now, there has been limited evaluation or targeted restoration of the habitat status for fishery species (Brown et al. 2019), particularly with regard to relating specific processes highly affected by degradation. In this study, significant variations in several reproductive attributes were observed among the three site groups in ANOVA (Fig. 4), such as the female, BW, GW, AF and RF. These findings were largely consistent with the determinants identified through RDA and VPA analyses (Fig. 5). These results confirm the significant influence of habitat degradation on the reproductive process of *E. sinensis,* mainly the intrinsic (physiological) process. Specifically, habitat degradation influenced GW in the Pre-R period and AF in the R period, suggesting that highly suitable breeding grounds primarily serve as critical habitats for gonad development and fecundity improvement. Conversely, as evidenced by the absence of significant differences in the male/female ratio, habitat degradation may not significantly impact the external population structure, as the sex-ratio is one of population structure parameters. This suggests that habitat degradation predominantly affects female distribution rather than male distribution, highlighting the increased vulnerability of females to breeding habitat changes during the reproductive process.

Since the 1980s, the annual yield of Chinese mitten crabs has experienced a sharp decline due to overfishing and habitat deterioration (Chen and Du 2017). Recent efforts in proliferation and release programs, along with the implementation of the TYFB and the Yangtze River Protection Law, have been conducted to recover fish stocks and biodiversity resources and promote the economic efficiency. The implementation of TYFB is having a great influence on the local fisheries in the early period, such as the trophic level and body size structure of the fish community were reported in the way of recovery (Feng et al. 2023). However, it remains unclear whether the expected goal of recovering fish stocks and biodiversity can be achieved solely through TYFB as overfishing might not be the only important factor threatening the Yangtze ecosystem (Wang et al. 2022a). Researchers have suggested that insistence on fishing ban is necessary but not sufficient for full biodiversity recovery, and other measures are needed, such as habitat restoration and species-focused stocking (Feng et al. 2023; Wang et al. 2022b). Moreover, the potential economic growth problems alongside should be cautiously considered, especially in the face of habitat degradation. For example, can measures such as fishing proliferation and release programs support for the sustainable development of fishery resources and protection of estuarine ecosystem without restoration of deteriorated habitat? The stock of *E. sinensis* has been improved by increasing the number of adult generation in the short term (Wu et al. 2020). In the case of reproductive process affected by the accumulation of habitat degradation, the survival and development of the next generation of young crabs could been detrimentally affected. Thus, such effect remains uncertain in the long term, meanwhile the influences of the releasing stocks may further produce risks for estuarine ecosystem. Xu et al. (2022) stated that although proliferation and release of fishery species had a positive effect on the short-term restoration of fishery resources, it can lead to a decreased ecological stability if the species are not keystone species, and ecosystems can become less resilient to natural disturbance. Therefore, our study provides some perspectives to ensure the long-term sustainability of fishery resource, as well as the protection of the fishery habitat, with a better understanding of ecosystem functions and processes. The clarification of reproductive process impaired by habitat degradation could optimize the management measures, such as fishery ecological compensation, reasonable proliferation and release, and protection of the health and reproductive capacity of fishery resource populations (Xu et al. 2022). In addition, the restorations of habitat will be more conducive to the persistence of ecosystem restoration in the long term (Hartig et al. 2019).

Mechanism of deterioration and restoration suggestions

Previous studies have often explored the relationship between habitat conditions and reproductive attributes through group comparisons or linear regression methods (Colpo and Lopez-Greco 2017; Huang et al. 2022; Lv et al. 2022; Wu et al. 2013). While these methods can identify key driving forces, they may not fully capture the impact of gradual variations or cumulative effects on different stages of ecological processes (Barbier et al. 2011). The application of multivariate analysis methods could solve this problem to deeply explore its influence mechanism and subsequent evaluation. Especially the VPA provided the best explanations, offering a clearer understanding of the relationship between habitat and reproductive attributes (Fig. 5d).

According to the VPA analysis (Fig. 5d), the combined interaction of the accumulative HDI and the SAL and NTU variables emerged as the primary determinant of the reproductive process of *E. sinensis.* Further analysis of the confounded interaction from the RDA results revealed that these two environmental variables were the main drivers of habitat degradation (Fig. 5b), leading to a decrease in gonad development and fecundity levels. These findings align with previous physiological experiments. For example, Huang et al. (2022) examined salinity thresholds in female *E. sinensis* reproductive characteristics, demonstrating that egg production, reproductive index and fecundity of *E. sinensis* reached their peak and declined when salinity exceeded 18 ppt. Physiological experiments have also shown that ovigerous *E. sinensis* prefers waters with moderate turbidity (10–23 cm) (Jiang et al. 2014), and high turbidity waters (especially from dredging operation) can imperil spawning rate and the larval of crabs (Araujo et al. 2020). The estuarine environmental gradients of salinity and suspended sediment concentration were verified to be compressed and the gradients became steeper by the hydrodynamic evolutions due to the DWP project and the corresponding bathymetry transformation in the North Passage (Wan et al. 2014). Given that there is no evidence of a decrease in precipitation, or an increase in evapotranspiration, it is reasonable to attribute the increasing trend in water salinity and turbidity to hydrological constructions in the YRE (Yang et al. 2010). The deterioration mechanism thus could be implied as the reproductive process is negatively influenced by the accumulative habitat degradation primarily driven by increased water salinity and turbidity (SAL and NTU) resulting from large-scale waterway construction. Understanding this degradation mechanism can provide a targeted scientific basis for subsequent management and restoration efforts. For example, a variety of measures for the restoration of estuarine and coastal fisheries habitats have implemented in Asia, North America, Europe (Blaber 2013; Gittman et al. 2016; Hutchings and Post 2013; Ma et al. 2017; Schaberg et al. 2019), such as wetland restoration and conservation, shoreline protection and restoration, water quality improvement, establishment of no-fishing zones and protected areas, etc. Most of these measures are aimed at preserving and rehabilitating aquatic habitats to support the sustainable utilization of fisheries resources, especially in shallow vegetated or hard bottom areas. While for the restoration of offshore fisheries habitats, particularly in areas affected by large engineering projects, like the areas in this study, the measures, such as the construction of artificial reefs (Xu et al. 2022), water quality enhancement, port and waterway management, sediment control and remediation (Elliott et al. 2016), should be paid more attention to and suggested as the specific restoration recommendations according to the related degradation mechanism in the future.

Conclusion

This study models the habitat change of *E. sinensis* over a span of nearly 10 years, which could be a basis for estimating habitat degradation and analyzing its impact on the reproduction process of *E. sinensis*. It can be seen that habitat deterioration was serious and has not improved yet. Additionally, by examining both the intrinsic (physiological) and external (structural) reproductive attributes of *E. sinensis*, the effects of habitat degradation on breeding process were investigated. The findings indicate that habitat degradation in the breeding grounds has a significant impact on the reproductive process of *E. sinensis*, particularly during the development of gonads in the Pre-R period and on the fecundity level in the R period. However, it may not significantly affect the external population structure, such as the male/female ratio. The findings about the changes in breeding habitat and their impacts on the reproductive process of *E. sinensis* could help managers in other regions benefit from understanding the specific habitat needs during the reproductive stage, which can inform targeted management strategies. The deterioration mechanism of the breeding habitat implies that accumulative habitat degradation primarily stems from increased water salinity and turbidity resulting from large-scale waterway construction. These findings offer insights for the conservation of fishery resources for managers globally by understanding the reproductive habitat requirements, assessing habitat degradation and restoration, and emphasizing the restoration of essential habitats to control key biological processes.

In the future, rehabilitation measures should be suggested according to the specific condition of habitat degradation, particularly in areas where hydrological and sedimentary engineering have been implemented. The relationship between habitat degradation and the current practices of proliferation and release should be further investigated. Additionally, the study emphasizes the need to quantify ecosystem service values provided by breeding grounds. The significant explanatory power of HDI for reproductive attributes suggests its usefulness in quantifying the ecological services or functions of breeding grounds for fishery resources. Such quantitative assessments of ecological functions can help quantify the lost value caused by habitat degradation in the following studies and make informed decisions about conservation and sustainable resource utilization. Furthermore, the study highlights that the essential breeding grounds have suffered the most damage, and migration channels and connectivity have been fragmented. The impact of these factors on the breeding population of the Chinese mitten crab requires further investigation.

Abbreviations

YRE	Yangtze River Estuary
TYFB	10-Year fishing ban
SDM	Species distribution model
DWP	Deep waterway project
Pre-R period	Pre-reproductive period
R period	Reproductive period
CW	Carapace width
CL	Carapace length
BW	Body weight
HW	Hepatopancreas weight
HSI	Hepatosomatic index
GW	Gonadosomatic weight
GSI	Gonadosomatic index
AF	Absolute fecundity
RF	Relative fecundity
SAL	Salinity
DO	Dissolved oxygen
NTU	Nephelometric turbidity units
DEP	Depth of water
AUC	Area under the curve
ANOVA	Analysis of variance
RDA	Redundancy analysis
VPA	Variation partitioning analysis
RIO	Relative index of occurrence
HDI	Habitat degradation index

Supplementary Information

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Additional file 1. SDM modeling process.

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Author contributions

TZ: conceptualization, methodology, data and modeling analyses, writing—original draft preparation, funding acquisition. ND: resources, data analysis, investigation. ZG: resources, investigation, funding acquisition. SW: resources, investigation. YG: resources, investigation. GY: resources, investigation. XH: resources, data analysis. TZ: resources, writing—review and editing. FZ: writing—review and editing, supervision, funding acquisition. PZ: writing—review and editing, supervision.

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Availability of data and materials

The model input data, model code and the simulation results that support the findings of this study are available in Figshare with the identifier (https://figshare.com/articles/dataset/The_model_input_data_model_code_and_the_simulation_results_from_SDM_modelling_of_E_sinensis_habitats_in_2014_and_2021/23984001).

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
The authors confirm that they have no conflicts of interest to disclose concerning this publication.

Competing interests
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