



OPEN Early life stage fish community structure and environmental drivers in offshore waters of Liaoning Province, Yellow Sea

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Early life stages of marine fishes play a critical role in shaping recruitment variability and population dynamics, yet the environmental processes structuring ichthyoplankton communities remain poorly understood in many marginal seas. Here, we investigated the seasonal dynamics of early life stage (ELS) fish assemblages and their environmental drivers in the offshore waters of Liaoning Province in the northern Yellow Sea using monthly ichthyoplankton surveys conducted from April to December 2021. Community structure and environmental relationships were examined using multivariate statistical analyses, and species distribution models were applied to project potential spawning habitats of the dominant species *Engraulis japonicus* under future climate scenarios. A total of 36 fish species were recorded, with spawning activity peaking between May and August. The ichthyoplankton assemblage exhibited pronounced seasonal succession characterized by shifts in dominant species composition and community structure. Temperature-related variables, particularly surface and bottom temperature, together with bottom salinity and depth, were identified as primary environmental drivers shaping the spatial and temporal organization of ELS fish communities. Distribution modelling further indicated that suitable spawning habitats for *E. japonicus* may expand under low-emission climate scenarios (RCP 2.6) but show increasing instability and potential contraction under moderate (RCP 4.5 and 6.0) and high emission scenarios (RCP 8.5). Our results demonstrate that environmental gradients and seasonal hydrographic variability jointly structure ichthyoplankton communities in the northern Yellow Sea, while future climate change may substantially alter spawning habitat availability for key pelagic species. These findings provide new insights into the mechanisms linking environmental variability and early life stage fish dynamics and highlight potential risks to regional fisheries resources under ongoing climate change.

Keywords Early life stage, Community structure, Dominant species, *Engraulis japonicus*, Environmental factors, SDMs

Early life stage (ELS) encompasses the initial phases of a fish's life cycle, specifically including the stages of eggs and larvae. Fish at ELS typically have limited swimming capabilities. Consequently, their growth, development, and survival are more susceptible to marine environmental shifts than those of adult fish¹. This period is also characterized by the highest mortality rate within a fish's life cycle. The status of ELS is a pivotal indicator of fish population health and sustainability, reflecting the reproductive scale and population growth rate. The condition of ELS fish also mirrors changes in the age structure and size distribution of fish populations²³. These aspects are crucial to understand the dynamics and long-term viability of marine ecosystems, providing essential insights for effective fisheries management and conservation.

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The offshore waters of the Liaoning Province of China in the Yellow Sea experience a complex interplay of oceanic currents and water masses. The Liaonan Coastal Current, the Yellow Sea Cold Water Mass⁴, and the Yellow Sea Warm Current converging in this region creates a dynamic marine environment with considerable nutrients and organic matters along the coast^{5,6}. This area consequently serves at important habitats for many marine fish species and one of the crucial fishing grounds in northern China⁷. Since the 1990 s, fish community in this area has exhibited a pronounced shift from medium and large economic categories toward small-sized mesopelagic and epipelagic with lower trophic levels^{8–10}. Currently, *Engraulis japonicus* is the predominant fish species in the system as well as the principal component of the ELS fish communities in this area¹¹.

Over several decades, ELS fish research in the offshore waters of the Liaoning Province in the Yellow Sea has yielded important insights into fish reproductive patterns, population structure, and ecological drivers^{12,13–17,18} (Table 1). Studies carried out in the late 1950 s only focused on *E. japonicus*, mapping its major spawning areas and seasonal distributions¹². In the subsequent decades, studies broadened to examine ELS fish community structure and its relationship with environmental factors¹⁸. However, most surveys were limited to specific regions or seasons, and thus lacked a comprehensive understanding of broader ecological processes. More recently, with improvements in bottom-trawl and ichthyoplankton surveys, preliminary spatial and temporal distribution models of ELS fish resources have been established^{15,17}. However, uneven station coverage and data limitations still leave uncertainties regarding the ecological dynamics between nearshore and offshore waters. While some studies have explored habitat-specific physical and biological conditions¹⁶, gaps remain in understanding how habitat variability impacts early-stage growth and survival. Notably, the importance of nearshore spawning grounds to resource renewal gained attention in surveys from 2014 to 2018¹¹ (Table 1), yet long-term dynamics and potential climate impacts require further assessment.

Despite the significant insights gained from decades of surveys on ELS fish in the coastal waters of Liaoning Province, the Yellow Sea, and the Bohai Sea, several unresolved issues still remain. Previous studies have provided important information on fish reproductive patterns, habitat characteristics, and the ecological factors influencing their distribution. Firstly, most existing studies have concentrated on nearshore areas, resulting in a lack of understanding of the dynamics in offshore waters, which complicates a comprehensive understanding of the ecosystem’s complexity. Secondly, while some research has explored environmental factors such as temperature and salinity, their specific impacts on ELS fish community structure are not yet fully understood. It is crucial to delve deeper into how these environmental conditions influence fish growth and survival. Additionally, the potential impacts of climate change on fish spawning and survival rates require further investigation, especially considering how rising water temperatures and changing currents may have profound effects on fish populations. To address these gaps, future long-term monitoring and comprehensive analyses are needed to improve our understanding of community dynamics and to provide a scientific basis for ecological management and conservation.

The distribution and survival of ELS of fish can be influenced by various physical and chemical factors such as tides, dissolved oxygen, and water temperature^{20–24}. Amidst the backdrop of global climate warming, the average global seawater surface temperature (SST) has witnessed an increase of 0.67 °C since the early 20th century²⁵. The Yellow Sea became warmer at a faster rate, with the annual average SST climbing by a substantial 1.0 °C over the period from 1957 to 2011 (Belkin 2009). Additionally, the warming trend persisted in the Yellow Sea from 2012 to 2018²⁶. Continued warming has brought considerable challenges to the marine ecosystem²⁷, affecting the spawning grounds of various fish stocks, especially *E. japonicus*, in the coastal waters of the Yellow Sea. It is important to evaluate such spawning grounds under various climate change scenarios for understanding fishery population dynamics and sustainable utilization of fish stocks. This research utilized data from a monthly ichthyoplankton survey in the north Yellow Sea from April to December, 2021, to unveil the structure and distribution pattern of ELS fish community in the coastal water of the north Yellow Sea. It also predicts the

Year	Survey content	Main purpose	References
1959	Twelve cruises for <i>E. japonicus</i> eggs and larvae monthly surveys in the Yellow and Bohai Seas	Assessment of fishing resources and habitat conditions of <i>E. japonicus</i> in the Yellow and Bohai Seas	Ruan ¹²
1985–1986	Thirteen cruises for fishery resource bottom trawl and habitat assessments in the Yellow Sea	Studies of ichthyoplankton to support fishery life	Wan and Jiang ¹⁸
1987–1988	Three cruises for spawning ground surveys in the nearshore areas of the Yellow Sea	Determination and monitoring of spawning grounds	Wan and Jiang ¹⁸
1998	Two cruises for bottom-trawling surveys in the northern Yellow Sea, including fixed station observations and sampling for the hydrological environment, primary productivity, fish eggs, and larvae, as well as plankton surveys.	Investigation of the physical and chemical environment that supports marine biological resources and their habitats	Qiu et al. ¹⁵
1998–2000	Five cruises for studying zooplankton species, abundance, and distribution, as well as fish eggs and larvae in the Yellow and Bohai Seas	Researching the physicochemical environment of marine biological resources and their habitats	Zhao et al. ¹⁷
2009	Four cruises for surveying fish eggs and larvae in the nearshore area of the North Yellow Sea	Concentrated study on fish egg and larval populations in the nearshore region	Yu et al. ¹⁹
2009–2010	Four cruises exploring ecological foundation for enhancing fishery resources and fish egg and larval surveys in key waters of the Yellow and Bohai Seas	Investigating enhancement strategies for fishery resources through understanding key water habitats	Shan et al. ¹⁶
2014–2017	Ten cruises for spawning ground surveys and fish egg and larval investigations in the nearshore waters of the northern Yellow Sea	Longitudinal studies on fish egg and larval dynamics in specific regions of interest	Cui et al. ¹¹

Table 1. Summary of historical surveys on early life stage (ELS) fish in the offshore waters of the Liaoning Province in the Yellow Sea.

effect of climate change under various scenarios on the spatial distribution of potential spawning grounds for dominant species such as the *E. japonicus* in the study area.

Research methods

Data acquisition

The ichthyoplankton survey was conducted monthly in the coastal waters of Liaoning province, China, in the northern Yellow Sea. The survey schedule was designed based on the seasonal occurrence patterns of ichthyoplankton and previous investigation experience in the study area (Table 1). Spawning activity, as well as the abundance of fish eggs and larvae, is generally low during winter. In addition, sea ice, strong winds, and rough sea conditions frequently occur from January to March, making offshore investigations difficult and unsafe. Therefore, the surveys were conducted from spring to winter, with the December investigations considered representative of winter conditions and sufficient to cover the major spawning and nursery periods of most species. A total of seven cruises were carried out during April 16–23, May 27–June 2, July 20–26, August 16–27, September 10–16, October 18–November 6, and December 8–18. During each cruise, 20 distinct stations were surveyed (Fig. 1).

Marine survey sampling methods and sample analysis procedures followed the guidelines outlined in the “Specification for Oceanographic Surveys Part 6: Marine Biological Survey” (GB/T 12763.6–2007). Fish eggs and larvae were collected using a large plankton net made of 36GG (mesh size 0.505 mm) silk gauze, with a mouth diameter of 0.80 m and a length of 2.70 m. The net was used for horizontal trawling, with a 10-min surface trawl at each station and a towing speed of 2 knots mile/h, and a flowmeter was attached to the mouth of the net to calculate the volume of water filtered. The specimens were fixed with a 5% seawater formalin solution. This study did not involve breeding, rearing, surgical manipulation, or prolonged live holding of animals. The main ethical consideration was the collection and preservation of wild ichthyoplankton specimens, and sampling was restricted to the minimum necessary to achieve the study objectives while minimizing habitat disturbance. All procedures were approved by the Institutional Animal Care and Use Committee of the Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences.

Water temperatures and salinities are measured using a Seabird 19 plus from the United States or a CTD 60 M from Sea & Sun Technology of Germany. The surface layer was identified as the water column from the surface down to 0.5 m, while the bottom layer was the water column within 0.5 m above the seafloor. The bathymetric depth at each station was determined using the echo sounder on ship. Surface chlorophyll-a (Chl-a) samples were collected by using a water sampler to collect 500 ml of surface seawater, which was then filtered onto a glass fiber filter membrane (with a pore size of 0.7 µm), and the samples were immediately stored and frozen at −20 °C.

The taxa of the ichthyoplankton, zooplankton, and phytoplankton were identified taxonomically by using the traditional morphological method. The developmental stages of fish eggs included cleavage, gastrula, embryo, hatching, and dead eggs, while the developmental stages of juvenile fish included prelarvae, postlarvae, and juveniles. The scientific names of the species referred to the World Register of Marine Species (WoRMS, <https://>

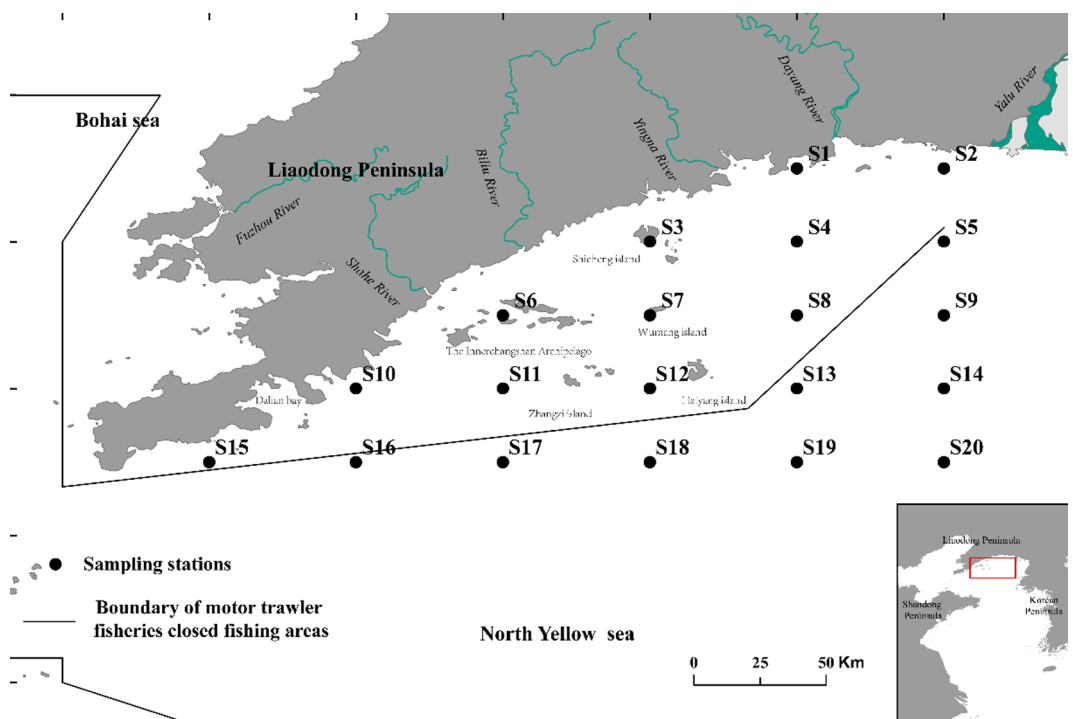


Fig. 1. The sampling stations in offshore waters of the Liaoning Province in the north Yellow Sea.

www.marinespecies.org/). After eliminating debris and ichthyoplankton, the residual wet weight of zooplankton is determined using a balance accurate to 0.001 g. Chl-a was extracted using a 90% acetone solution at -20°C for 12 h from the glass fiber filter membrane, and the concentration of Chl-a was then measured with a Turner Designs Trilogy fluorometer.

Species dominance and ecological density

Using Pinkas' Relative Importance Index (IRI), species dominance was evaluated as an indicator²⁸. Given that fish eggs and larvae are small in size, biomass was not considered in the calculations, and the formula was simplified as follows:

$$IRI = N\% \times F\% \quad (1)$$

In Formula 1, $N\%$ represents the percentage of the abundance of a particular fish egg or larva species relative to the total abundance accounting for the month, and $F\%$ represents the occurrence frequency of that species. Species with $IRI \geq 1000$ are defined as dominant species, species with $100 \leq IRI < 1000$ are defined as important species, species with $10 \leq IRI < 100$ are defined as common species, species with $1 \leq IRI < 10$ are defined as general species, and species with $IRI < 1$ are defined as rare species.

The density of fish eggs (D) or larvae (i.e., number per unit volume of filtered water, ind/ m^3) was calculated as:

$$d = R \times q \quad (2)$$

$$D = \frac{N}{d \times \pi \times r^2} \quad (3)$$

where d represents the distance covered by the trawl net during each station's water filtration, in meters; R represents the difference in the readings of the flow meter, rounded to the nearest whole number; q represents the ratio of distance covered by the flow meter to the number of revolutions, in meters/round, and is assumed to be 0.4²⁹; and r represents the radius of the trawl net opening, in meters.

Monthly variation in community structure and its relationship to environmental factors

The species turnover rate reflects the changes in fish eggs and larvae species between different months⁸, which was calculated as:

$$E = \frac{A}{(A + B)} \quad (4)$$

where E represents the species turnover rate, A represents the number of different species between months, and B represents the number of species that remain the same between months.

Cluster analysis and NMDS were performed using Primer 5.0 software to analyze changes in the community structure of fish eggs and larvae between months. The significance of differences between groups was tested using analysis of similarities (ANOSIM), and the reliability of NMDS results was tested using stress coefficients^{30,31}. SIMPER analysis was used to identify the most important typical species within groups and the most important divergent species between groups based on the average dissimilarity contribution rate and the average similarity contribution rate³².

The relationship between fish eggs or larvae communities and environmental factors was analyzed using the Mantel test for correlation analysis, based on the "linkET" package in R. The dominant species and some important species of fish eggs and larvae during the survey period were selected as the early life stage fishery resources. The selected environmental factors included depth, SST, wet weight of zooplankton (WW), seawater surface salinity (SSS), seawater bottom temperature (SBT), seawater bottom salinity (SBS), and chlorophyll-a (Chl-a).

Additionally, constrained ordination analysis was applied using Canoco 5.0 software to study how different species respond to changes in environmental conditions. Data from May to August were selected for constructing the species matrices because this period corresponded to the main spawning season in the study area, during which the richness and abundance of fish eggs and larvae were relatively high. In contrast, samples collected in April and September–December contained relatively few species and individuals, which could have introduced excessive zero values and reduced the reliability of the multivariate analyses. Therefore, distinct species matrices for fish eggs and larvae were independently constructed for each sampling station using data collected from May to August 2021. Only species that occurred with a minimum occurrence frequency of 5% were included in the species matrices for these sampling periods. Prior to conducting the analysis, a $\log(x + 1)$ transformation was implemented on the species matrices to fulfill the prerequisites of the analytical methods being used³³. The environmental factors considered for analysis were SST, SBT, SSS, SBS, depth, and seawater surface Chl-a. A preanalysis procedure, where a $\log(x + 1)$ transformation was applied to all variables, except for Chl-a^{34,35}, was undertaken to ensure that the environmental data conformed to a normal distribution.

Modeling the spawning grounds of the most dominant species, *E. japonicus*

E. japonicus was identified as the most dominant fish species, based on extensive surveys in the study area from 1959 to 2017^{12–19}. Referencing the historical surveys, the details are presented in Table 1. This study focused on the records of *E. japonicus* eggs, specifically within the months of May to September, as a strategic choice to mitigate the variability associated with random sampling locations. Additionally, only one distribution record

was retained within each grid cell (5'×5', approximately 9.2 km×9.2 km) to minimize sampling bias and spatial autocorrelation among the distribution sites^{36,37}. Subsequently, a binary dataset indicating species absence or presence (0–1 data) was compiled to facilitate model construction and to evaluate its predictive accuracy.

SDMs were developed to model the spawning grounds of *E. japonicus* (i.e., its egg distribution), using package Biomod2 in R program, while 10 types of modeling algorithms were explored, including Generalized Linear Model (GLM)³⁸, Generalized Additive Model (GAM)³⁹, Artificial Neural Network (ANN)⁴⁰, Maximum Entropy (Maxent)⁴¹, Classification Tree Analysis (CTA)^[63], Random Forest (RF)⁴², Flexible Discriminant Analysis (FDA)³⁹, Gradient Boosting Machine (GBM)⁴³, Multivariate Adaptive Regression Splines (MARS)^[63], and Stepwise Regression Estimation (SRE)⁴⁴. The performance of the 10 algorithms were determined through a five-fold cross-validation. Two common metrics, the area under the receiver operating characteristic curve (AUC) and the true skill statistics (TSS), were used to assess the accuracy of the models^{41,44}.

Nine environmental factors were considered as explanatory variables for the SDMs, average seawater surface temperature (AMSST, °C), average seawater average chlorophyll-a concentration (Chl-a, mg/m³), average dissolved oxygen concentration (Oxy, mol/m³), average water depth (Depth, m), average offshore distance (Landis, Km), average sea surface pH (pH), average sea surface water velocity (Vel, m/s), and average primary productivity (Prip, g/m³/day). The spatial resolution of the environmental factors was consistent with the resolution of species distribution dataset (5'×5'). The Depth and Landis data were obtained from the Global Marine Environmental Dataset (<http://gmed.auckland.ac.nz>), while the other marine environmental data were obtained from the Bio-ORACLE v2.0 dataset (<https://www.bio-oracle.org/>). It should be noted that the “current” environmental conditions used in the SDM were derived from the averaged climate data for 2000–2014 rather than the survey year 2021. This mismatch may introduce some uncertainty into habitat predictions, but the long-term averaged dataset was adopted to reduce the influence of short-term environmental anomalies and to maintain consistency with future climate projections. For model prediction, current climatic conditions were represented by the average climate data from the years 2000 to 2014.

Future environmental data include two time periods (2040–2050, 2090–2100) and four Representative Concentration Pathway (RCP) scenarios: RCP2.6, RCP4.5, RCP6.0, and RCP8.5. The data were sourced from the Bio-ORACLE v2.0 dataset, accessible at <https://www.bio-oracle.org/>. The study assumes that the Depth and Landis parameters within the research area will remain constant.

For model validation, this study adopted a variance inflation factor (VIF) cutoff at 4⁴⁵, and set a condition number (κ) limit at 100, to address multicollinearity and ensure model accuracy. Additionally, the committee averaging approach was employed to integrate the selected models, and thus refine the predictive accuracy of all models and address their inherent limitations^{46,47}. The habitat suitability range predicted by the models is from 0 to 1 000, where 0 represents the lowest probability of occurrence (i.e., 0), and 1000 represents the highest probability of occurrence (i.e., 1). Habitat suitability is graded into four levels based on predicted probabilities: 0–250 for low, 250–500 for moderate, 500–750 for high, and 750–1 000 for optimal habitats.

Results

Composition, dominant species, spatiotemporal distribution of fish eggs and larvae

From April to December 2021, seven surveys in Liaoning's Yellow Sea waters collected 71 202 fish eggs and 1 027 larvae. Among these, 36 fish species were identified, including 27 species of eggs and 17 species of larvae, belonging to 8 orders and 24 families. On the basis of the temperature preferences of the spawning adults, 18 species were classified as warm temperature (50.0%); 10 species were classified as warm water (27.8%); and eight species were classified as cold temperature (22.2%) (Table 2). With regard to the spawning types of the gravid fishes, 27 species were found to produce pelagic eggs (75%); six species produced adhesive eggs (16.7%); and three species were ovoviparous (8.3%) (Table 2). From the temporal distribution of the early life stage fish resource species, the highest number of fish egg species was observed in May and June, while the highest number of larval fish species was observed in July. Throughout the period from April to December, *E. japonicus* eggs and larvae had the highest occurrence frequency (Table 3).

The spatial distribution of fish eggs (Fig. 2) and larvae (Fig. 3) varies with changes in SST and SSS. The density of fish eggs was low in April, peaking in May and June, primarily concentrated around the estuaries of the Yalu and Dayang Rivers. In July, fish eggs were concentrated from the Yalu River estuary to the Yingna River estuary, with a significant density decrease at the Dayang River estuary. In August, the spawning center shifted southward to the offshore area south of the Yalu River estuary and the southwestern waters of Zhangzi Island. The distribution of larvae reached its annual peak in July, mainly concentrated in the Yalu River and Dayang River estuaries. After September, the density of both fish eggs and larvae significantly decreased and tended to distribute more evenly.

Community structure of fish eggs and larvae and their environmental correlation

During the study period, the species composition of fish eggs and larvae showed significant monthly variation (Table 4). Overall, the turnover rates for fish eggs and larvae exhibited a clear trend of change across different months. To further analyze, cluster analysis was conducted (Fig. 4a), and the ANOSIM test results indicated significant differences among the groups (fish eggs: $R = 1$, $P < 0.05$; larvae: $R = 1$, $P < 0.01$). These results were consistent with the NMDS analysis (Fig. 4b), with a stress value of less than 0.1 (Bray et al., 1957). After SIMPER analysis³², species with a similarity contribution rate and a dissimilarity contribution rate greater than 4% were selected as representative species and key distinctive species (Table 5).

The results of the Mantel test indicate significant correlations between the seven environmental factors and the dominant species of fish eggs and larvae (Fig. 5). The CCA analysis⁴⁹ shows that during the warming period from May to August, SST and SBS are important factors influencing the community structure of fish eggs (Fig.

Species	Egg type	Thermal preferences	4	5–6	7	8	9	10–11	12
<i>E. japonicus</i>	Pel	WT	○	○●	○●	○●	○●	○●	
<i>T. kammalensis</i>	Pel	WW		○	○				
<i>K. punctatus</i>	Pel	WW		○					
<i>S. elongata</i>	Pel	WT			○	○			
<i>P. brevipinnis</i>	adh	WT				●			
<i>S. Schlegeli</i>	ovo	WW						●	
<i>H. mohnikei</i>	ovo	WT					●		
<i>P. haematocheilus</i>	Pel	WT		○●					
<i>S. pinguis</i>	Pel	WT				○			
<i>L. maculatus</i>	Pel	WT						○	●
<i>S. japonica</i>	Pel	WW			○●	○●	○●		
<i>D. maruadsi</i>	Pel	WW			○●	○			
<i>S. aureovittata</i>	Pel	WT			○				
<i>C. hippurus</i>	Pel	WW				○			
<i>L. polyactis</i>	Pel	WT		○					
<i>P. argentata</i>	Pel	WW		○	○				
<i>P. major</i>	Pel	WT		○					
<i>T. japonicus</i>	Pel	WT			○	○	○		
<i>E. muticus</i>	Pel	WT				○			
<i>S. japonicus</i>	Pel	WW		○	○●				
<i>S. nipponius</i>	Pel	WT		○					
<i>A. tapeionosoma</i>	Pel	WW				○			
<i>G. mororanus</i>	adh	WT			●				
<i>A. personatus</i>	Adh	CT	●						
<i>A. emmion</i>	Adh	CT							●
<i>C. richardsoni</i>	Pel	WT		○					
<i>C. beniteguri</i>	Pel	WT		○	○	○●	○●		
<i>C. joyneri</i>	Pel	WT			○	○	○		
<i>C. herzensteini</i>	Pel	CT		○		○	○	○	
<i>P. herzensteini</i>	Pel	CT	○						
<i>P. cornutus</i>	Pel	WT						○●	
<i>K. bicoloratus</i>	Pel	CT							○
<i>P. olivaceus</i>	Pel	WT		○					
<i>S. schlegelii</i>	ovo	CT		●	●				
<i>H. otakii</i>	Adh	CT							●
<i>A. agrammus</i>	Adh	CT							●

Table 2. Species composition of fish eggs and larvae community in offshore waters of the Liaoning Province in the Yellow Sea from April to December 2021. Note: “○” means the presence of fish eggs, “●” means the presence of fish larvae; Pel: Pelagic, Adh: adhesion (the eggs with adhesive egg filaments), ovo: ovoviviparity. Thermal preferences refer mainly to those of the corresponding spawning adults. According to the literature on fish faunal classification based on thermal preferences⁴⁸⁶⁴, the species listed in this table were classified into three thermal types: warm temperate species (WT), warm water species (WW), and cold temperate species (CT).

6a, $P < 0.05$), explaining 54.4% of the community variance. The CCA analysis for larvae reveals that WW is the main driving factor, accounting for 74.82% of the variance (Fig. 6b). Additionally, the correlation coefficients between species and environmental factors in the CCA analysis exceed 0.60, indicating that the results effectively reveal the relationships between the abundance of fish eggs and larvae and the environmental factors.

***E. japonicus* spawning habitat suitability dynamics across climate change scenarios**

The comprehensive review indicated that *E. japonicus* eggs were found at 76 distinct stations. By contrast, no evidence of these eggs was noted at six stations throughout the survey years. Ultimately, 54 distribution points for *E. japonicus* eggs were identified (Fig. 7). These points were combined with six nonexistent points to form an absence-presence dataset (0–1 data), which was used for model construction and accuracy assessment. Finally, five environmental factors that have a considerable effect on the distribution of *E. japonicus* eggs in the northern Yellow Sea were selected for modeling analysis: AMSST, AMSSS, Depth, Landis, and Vel.

Among the 10 predictive models for *E. japonicus* spawning habitat suitability, all but the CTA model have proven to be highly effective. This study selected models based on criteria of Total Sum of Squares (TSS) over

Month	Fish eggs		Fish larvae	
	Species	IRI	Species	IRI
April	<i>E. japonicus</i>	345.9*	<i>A. personatus</i>	526.3*
	<i>P. herzensteini</i>	180.5*		
May–June	<i>E. japonicus</i>	9576.2**	<i>E. japonicus</i>	1479.3**
July	<i>E. japonicus</i>	5520.8**	<i>E. japonicus</i>	2940.1**
	<i>S. japonica</i>	1029.0**	<i>S. japonicus</i>	145.2*
August	<i>E. japonicus</i>	2129.4**	<i>E. japonicus</i> <i>S. japonica</i>	2801.4** 127.3*
	<i>S. japonica</i>	403.4*		
	<i>C. valenciennei</i>	115.7*		
September	<i>E. japonicus</i>	1624.1**	<i>E. japonicus</i>	3459.2**
	<i>S. japonica</i>	244.9*		
	<i>C. valenciennei</i>	335.1*		
	<i>C. joyneri</i>	128.9*		
	<i>C. herzensteini</i>	193.3*		
October–November	<i>P. cornutus</i>	3577.8**	<i>E. japonicus</i>	1731.7**
			<i>P. cornutus</i>	611.2*
December	<i>K. bicoloratus</i>	6666.7**	<i>H. osotakii</i>	9809.9**
Annual	<i>E. japonicus</i>	3792.3**	<i>E. japonicus</i>	1455.2**
			<i>H. otakii</i>	342.2*

Table 3. Dominant and important species of eggs and larvae community in offshore waters of the Liaoning Province in the Yellow Sea from April to December 2021. Note: “**” means dominant species, “*” means important species.

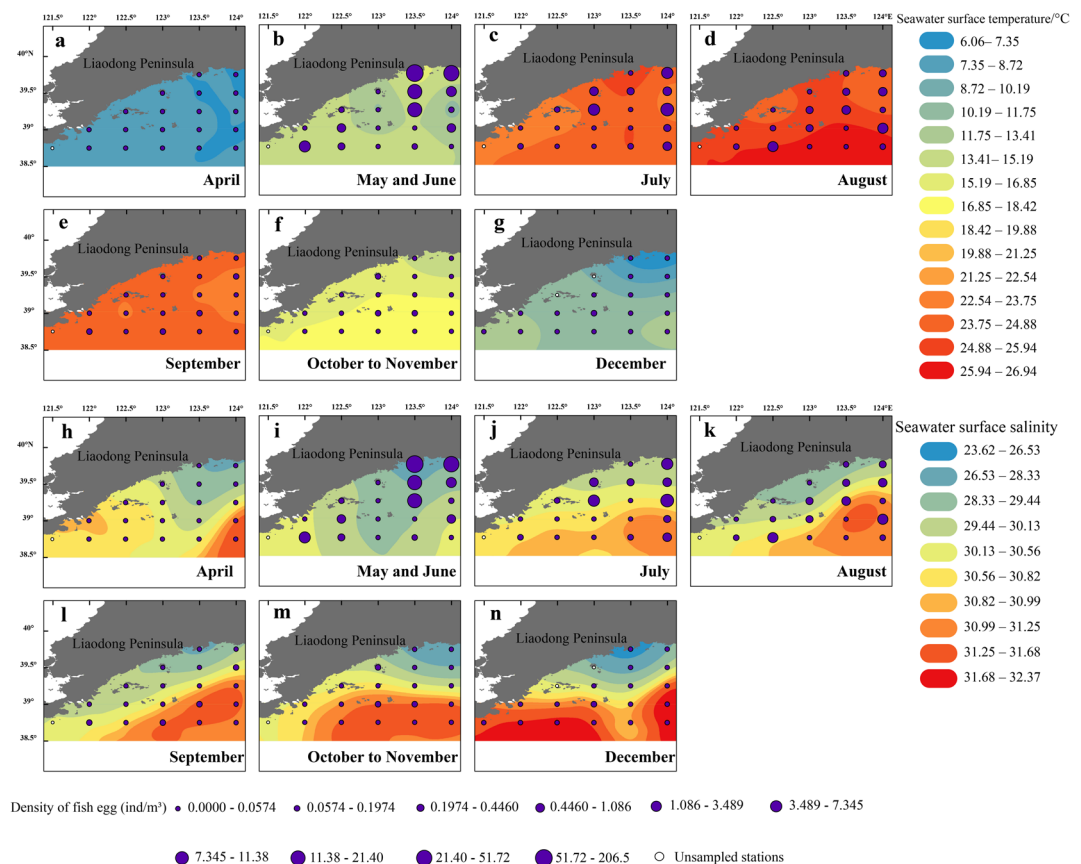


Fig. 2. Fish egg density and its monthly variation with SST (**a to g**) and SSS (**h to n**) in offshore waters of the Liaoning Province in the Yellow Sea from April to December 2021.

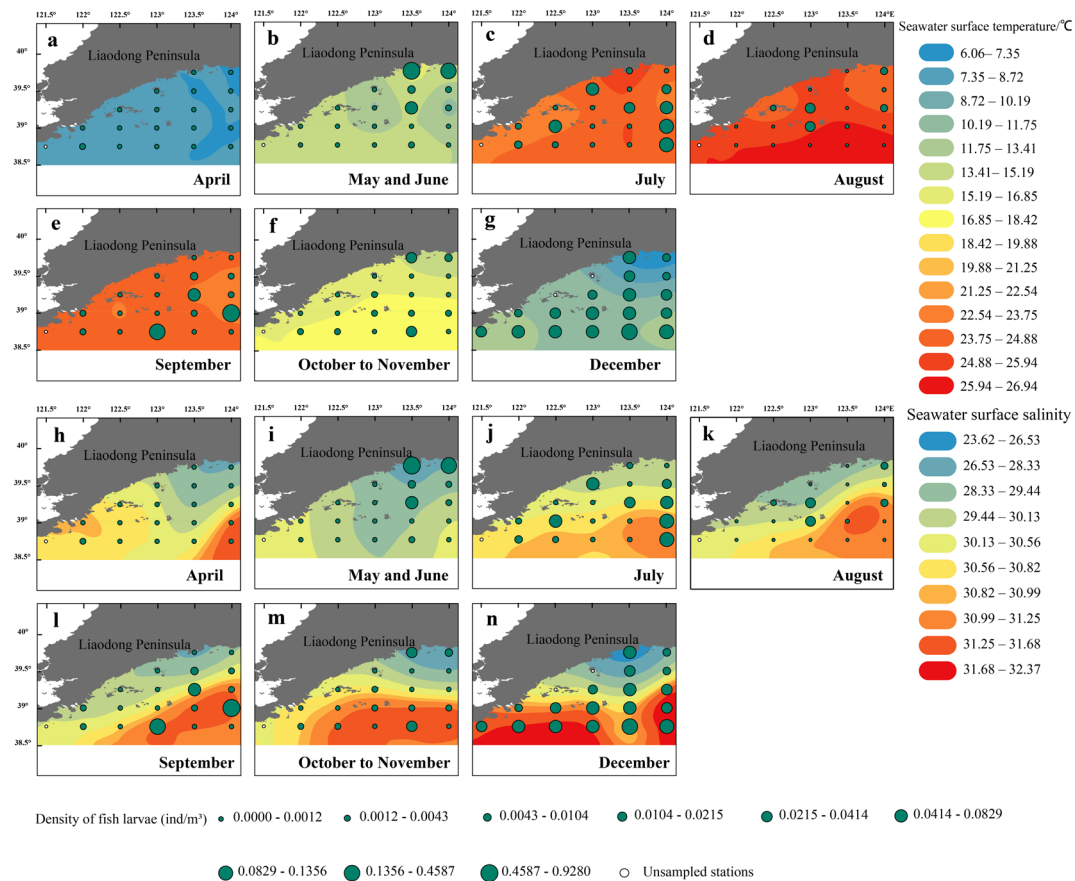


Fig. 3. Fish larvae density and its monthly variation with SST (a to g) and SSS (h to n) in offshore waters of the Liaoning Province in the Yellow Sea from April to December 2021.

Month	April	May–June	July	August	September	October	Nov–Dec
April		98.12	98.11	94.44	98.16	90.70	98.56
May–June	99.95		53.31	72.85	30.28	90.43	98.75
July	99.73	90.67		70.97	61.38	89.43	98.32
August	99.36	96.90	79.57		74.63	70.93	97.32
September	89.85	99.69	98.07	94.03		90.91	98.13
October	97.75	99.98	99.92	99.71	96.73		96.39
Nov–Dec	94.50	99.99	99.89	99.72	95.90	95.65	

Table 4. Monthly species turnover rates (%) for fish eggs (the lower triangular portion) and larvae (the upper triangular portion).

0.4 and Area Under the Curve (AUC) over 0.7 to minimize prediction uncertainty. Consequently, ANN, FDA, GAM, GBM, GLM, MARS, Maxent, RF, and SRE were selected to construct an ensemble model for further analysis. The ensemble model had an average TSS of 0.666 and an AUC of 0.906.

Under the current climate scenario, environmental factors exert varying influences on the spawning habitat suitability for *E. japonicus* (Fig. 8). Under the different climate scenario, the distribution proportions and average suitability of suitable habitats for *E. japonicus* spawning grounds are shown in Table 6. Under current climate conditions, the optimal suitable spawning grounds for *E. japonicus* are predominantly found situated north of 39°N, extends along the nearshore from 122.5°E to 124°E, specifically from the Yalu River Estuary to the Danyang and Yingna River Estuaries (Fig. 9a). Under the RCP2.6 scenario, from 2040 to 2050, highly suitable habitats for anchovy spawning grounds show a trend of shifting from the coast towards the east (Fig. 9b). In 2090–2100, there is little change compared to the 2050 s (Fig. 9f). Under the RCP4.5 scenario, habitat distribution from 2040 to 2050 is similar to that under RCP2.6 (Fig. 9c). However, by 2090–2100, the area of highly suitable habitats decreases, and the average habitat suitability further declines compared to the 2050 s (Fig. 9g). Under the RCP6.0 scenario, from 2040 to 2050, highly suitable habitats expand eastward compared to current conditions (Fig. 9d). By 2090–2100, the area of highly suitable habitats shrinks significantly, and average suitability also declines

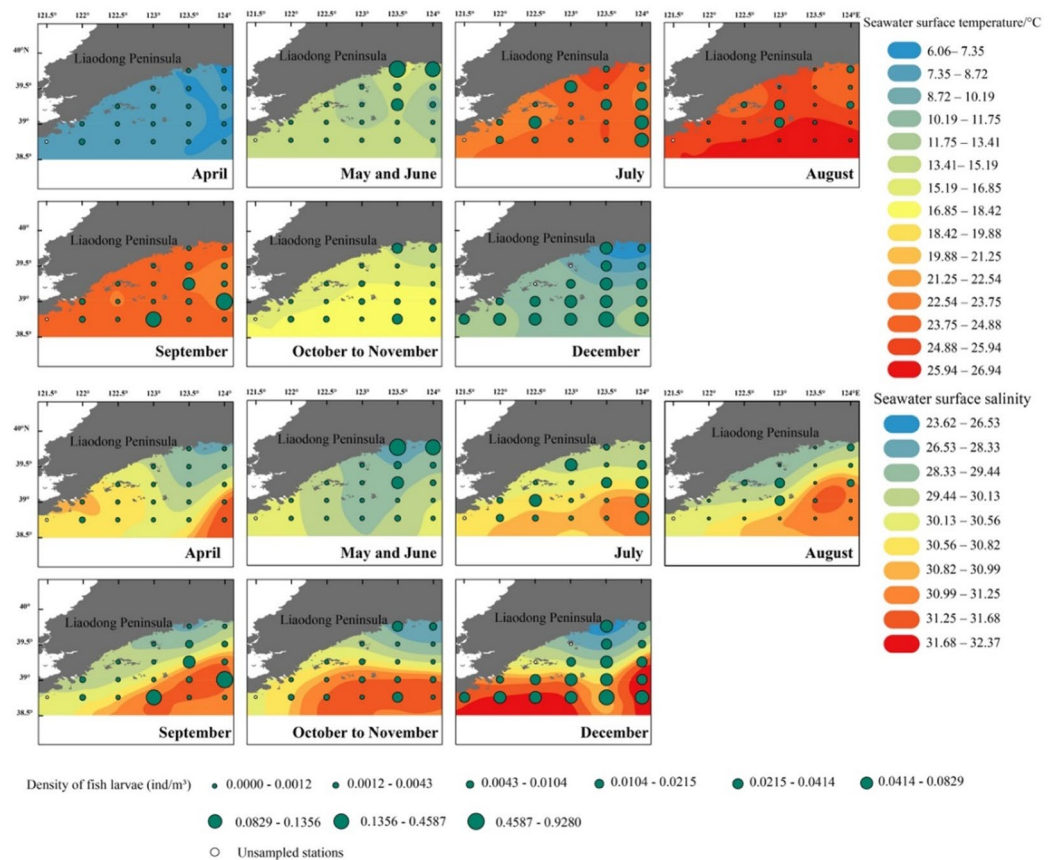


Fig. 4. Monthly scale clustering diagram (a, c) and NMDS ordination diagram (b, d) of fish eggs and larvae from April to December 2021 (a, b Based on the abundance of fish eggs; c, d Based on abundance the of fish larvae).

sharply compared to the 2050 s (Fig. 9h). Under the RCP8.5 scenario, from 2040 to 2050, the proportion of highly suitable habitats increases significantly compared to current conditions, although the average suitability slightly decreases (Fig. 9e). By 2090–2100, medium and high suitability habitats dominate, with a small proportion of highly suitable areas and a notably low average suitability, showing a sharp decline compared to the 2050 s (Fig. 9i).

Discussion

Current status of early life stage fish community structure in the offshore waters of Liaoning Province in the Yellow Sea

During the survey period from April to December 2021, many fish eggs and larvae were collected each month, and the period from May to August accounted for 98.51% of the total annual catch, indicating the concentrated spawning period for fish. Consistent with the findings of Wan and Jiang¹⁸ and Wan et al.⁵⁰, the peak spawning period occurs in May and June, with the central spawning grounds located in the northern part of the Haiyang Island fishing ground. Regarding the annual variation in species composition of the early stage fish resources, *E. japonicus* prevails as the primary fish egg contributor from May through September but also reigns supreme within the larval fish community. In addition to *E. japonicus*, the species composition of other early life stage fish resources exhibited a noticeable seasonal and monthly shift. Although the succession patterns of larval fish assemblages are delayed relative to the spawning of fish eggs, both exhibit an overall trend of inter-monthly changes in species composition in relation to SST fluctuations. From April to August, as SST rises, the dominant or key species gradually shift from cold-temperate species to warm-water or warm-temperate species. Conversely, after September, with the decrease in SST, the dominant or important species gradually transition back to cold-temperate species.

The early life stages of fish, such as fish eggs and larvae, are vital indicators of the brood fish population⁵¹. A comprehensive survey from 1985 to the present indicates that *E. japonicus* eggs and larvae have consistently been predominant in the coastal waters of Liaoning Province in the Yellow Sea^{18,19,51}. This species dominates, especially during its peak spawning period in May and June, indicating stable spawning grounds in the area. Since the 1990s, the Yellow Sea has experienced substantial fishing pressure due to the widespread use of midwater trawling for *E. japonicus*, resulting in a notable decline in the species' population, especially between 2010 and 2017^{19,52}. Since 2017, a strict seasonal fishing moratorium, implemented by national fisheries authorities from

Category	RS	KDS				
Fish eggs	<i>P. herzensteini</i>	April	<i>E. japonicus</i>	<i>S. japonica</i>	<i>P. cornutus</i>	<i>E. japonicus</i>
	<i>E. japonicus</i>		<i>K. punctatus</i>	<i>C. beniteguri</i>	<i>L. maculatus</i>	<i>P. argentata</i>
			<i>P. argentata</i>	<i>E. japonicus</i>		<i>K. punctatus</i>
		92.03	May-June	<i>K. punctatus</i>	<i>E. japonicus</i>	<i>E. japonicus</i>
	<i>P. argentata</i>			<i>E. japonicus</i>	<i>P. argentata</i>	<i>P. argentata</i>
	<i>E. japonicus</i>			<i>P. argentata</i>	<i>K. punctatus</i>	<i>K. punctatus</i>
	<i>E. japonicus</i>	85.3	70.95	July-Sept	<i>P. cornutus</i>	<i>S. japonica</i>
	<i>C. beniteguri</i>				<i>S. japonica</i>	<i>E. japonicus</i>
	<i>S. japonica</i>				<i>P. argentata</i>	<i>C. beniteguri</i>
	<i>P. cornutus</i>	83.96	91.86	88.13	Oct-Nov	<i>P. cornutus</i>
	<i>L. maculatus</i>					<i>K. bicoloratus</i>
	<i>K. bicoloratus</i>	100	100	100	100	December
Larvae		April	<i>E. japonicus</i>	<i>E. japonicus</i>	<i>E. japonicus</i>	<i>H. otakii</i>
	<i>A. personatus</i>		<i>S. schlegelii</i>	<i>S. japonica</i>	<i>P. cornutus</i>	<i>A. agrammus</i>
	<i>E. japonicus</i>	100	May-July	<i>S. schlegelii</i>	<i>E. japonicus</i>	<i>H. otakii</i>
	<i>S. schlegelii</i>			<i>S. japonica</i>	<i>P. cornutus</i>	<i>E. japonicus</i>
	<i>S. japonica</i>	100	55.76	Aug-Sept	<i>P. cornutus</i>	<i>H. otakii</i>
	<i>E. japonicus</i>				<i>S. japonica</i>	<i>E. japonicus</i>
	<i>C. beniteguri</i>					<i>K. bicoloratus</i>
	<i>E. japonicus</i>	100	77.85	66.67	Oct-Nov	<i>P. cornutus</i>
	<i>P. cornutus</i>					
	<i>H. otakii</i>	100	100	100	100	December
	<i>A. agrammus</i>					

Table 5. Representative species of each community group, intergroup differentiating species, and average dissimilarity rate of fish egg and larval fish between different community groups. Note: RS represents representative species, key dissimilarity species (KDS) on the diagonal represents the key species contributing to the dissimilarity between communities, average dissimilarity below the diagonal indicates the average level of dissimilarity between communities.

May 1 to September 1, has considerably aided the species’ recovery by aligning with their primary spawning season. From 2017, surveys have documented a sharp rise in egg density, culminating in 2021 with record highs, signaling a notable rebound in early life stage of *E. japonicus*. The eggs and larvae of *D. maruadsi*, seldom documented in past studies, were first captured in the July 2021 survey. Predominantly located in the deeper waters south of the survey area, these findings coincide with the results of a bottom trawl survey. Between October and November, a notable population of zero-age *D. maruadsi* young was observed in the same sea area. These observations preliminarily confirm the existence of a spawning and nursery habitat for *D. maruadsi* along the southern coast of Ocean Island. By contrast, *K. punctatus* did not emerge as a primary species in the 2021 survey possibly due to its classification as an estuarine and bay-pawning species¹⁹. The limited number of nearshore estuary survey stations in this investigation may have resulted in its infrequent collection. The survey data indicate substantial shifts in the early life stage fish species composition, with a noticeable transition from *E. japonicus*, *K. punctatus*, *Scomberomorus niphonius*, and *S. japonicus* in the late 20th century⁵⁰ to the current dominance of *E. japonicus* and *H. otakii*. A considerable downturn was observed in the early life stage presence of historically important economic species, such as *S. niphonius* and *S. japonicus*, with their occurrence rates falling well below previous highs. Moreover, the early life stage populations of *Larimichthys polyactis* and *Trichiurus japonicus* have not demonstrated a substantial recovery, indicating a continued conservation concern for these species.

Spatiotemporal dynamics of early life stage fish communities and environmental correlates in the offshore waters of Liaoning Province in the Yellow Sea

The survey revealed a distinct seasonal succession in fish egg and larval fish communities. While fish egg species showed similar composition and low turnover from July to September, and larval fish species were similar from May to July and August to September, other months exhibited considerable monthly turnover in fish egg and larval fish composition. The reasons are as follows: first, the occurrence of fish and the various stages of their life cycle are primarily controlled by physiological responses regulated by water temperature⁵³. In their early life stages, fish lack the abilities to actively select external environment, with their distribution passively controlled by parental reproductive activities. Water temperature plays a key role in inducing gonadal development and inducing fish to spawn and reproduce⁵⁴. Driven by water temperature variations, fish species with varying thermal preferences sequentially inhabit in the offshore waters of Liaoning Province in the Yellow Sea for spawning and reproduction. The typical species of the community reached their spawning periods in succession

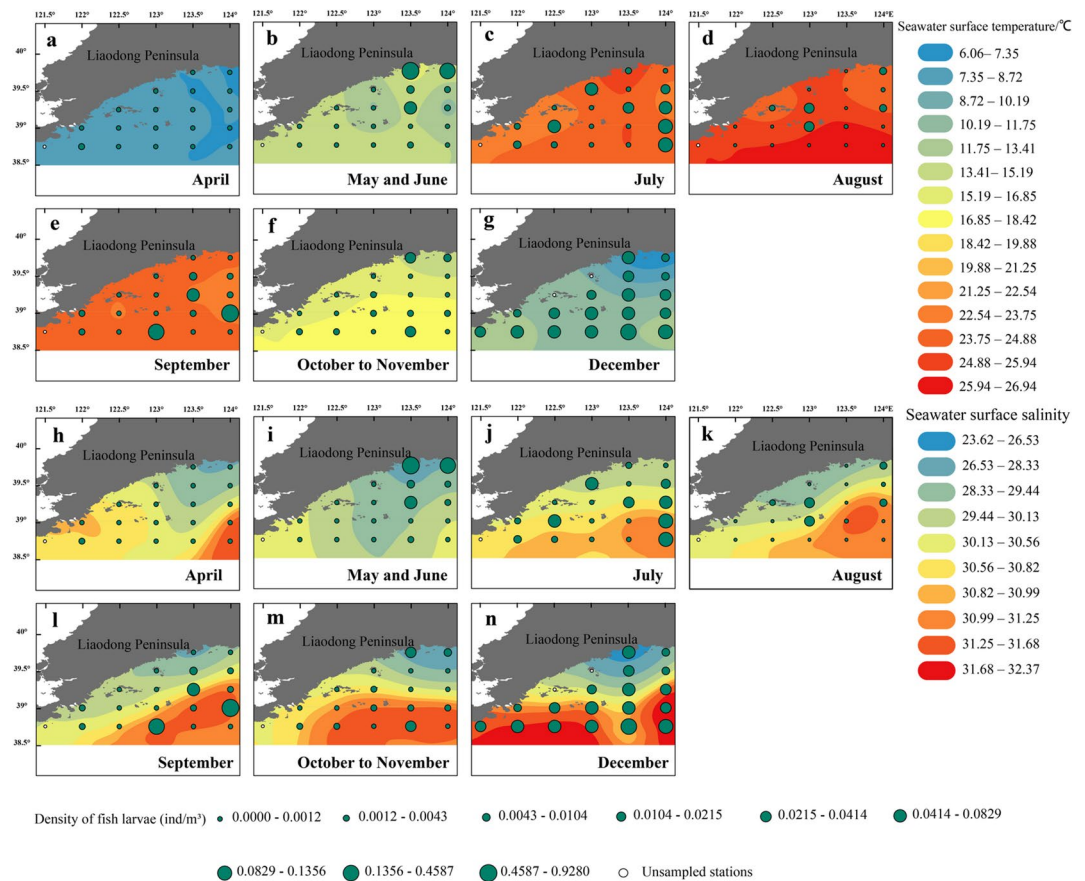


Fig. 5. Mantel test correlation analysis between fish eggs (a) and larvae (b) communities and environmental factors in the offshore waters of Liaoning in the Yellow Sea from May to August 2021 (SST: seawater surface temperature; SSS: seawater surface salinity; SBT: seawater bottom temperature; SBS: seawater bottom salinity; Depth: sea water depth; WW: wet weight; Chla: chlorophyll a).

with the change in water temperature, spawning in the sea area alternately, thus forming the annual succession of fish egg and larval fish community structures.

In the distribution of early fish resources in marine areas, the low-temperature and dry season predominantly inhabits the nearshore areas with low salinity, typically around estuaries. Conversely, during the high-temperature, wet season, a discernible trend of migration toward the southern offshore regions is characterized by increased salinity. Adult fish choose breeding sites that boost offspring survival, aligning hatching with prey abundance over evolutionary time. This alignment results in an uneven spread of early life stage fish, shaped by prey density in specific regions⁵⁵. Salinity also serves as a critical hydrological factor influencing fish spawning activities and the concentration of early life history of fish resources. Its effect is especially pronounced near the geographical limits of spawning areas, often referred to as thermal thresholds. High (or low) SST paired with correspondingly high (or low) SSS is beneficial for boosting the potential for successful recruitment; conversely, a mismatch where high (or low) SST is coupled with low (or high) SSS can diminish the likelihood of successful fish recruitment^{56,68}.

During the spring dry season of April and the months of May-June, when water temperatures are low, the distribution of fish eggs is closely related to the position of the tidal front during the warming period⁵⁷. Considering the distribution of tidal fronts, a clear characteristic is the SST cold water band. The bottom cold water is involved in transfrontal circulation and mixed with tide and wind actions to form surface cold water in the upper mixed layer, where the convergence and entrainment effects in the frontal zone are more likely to cause fish eggs to congregate and form dense patches^{57–59}. The survey found fish eggs aggregate at the cold-warm water interface in May-June, while high temperatures and rainfall in July-August create a coastal salinity gradient, prompting many fish to migrate offshore for improved spawning. The study revealed a positive correlation between the egg distribution of the warm-temperate benthic fish *C. joyneri* with SBT and SBS. The distribution of larvae *S. japonica* has been found to exhibit a significant positive correlation with SBT, a finding that corroborates the results of Zhang et al⁶⁰.

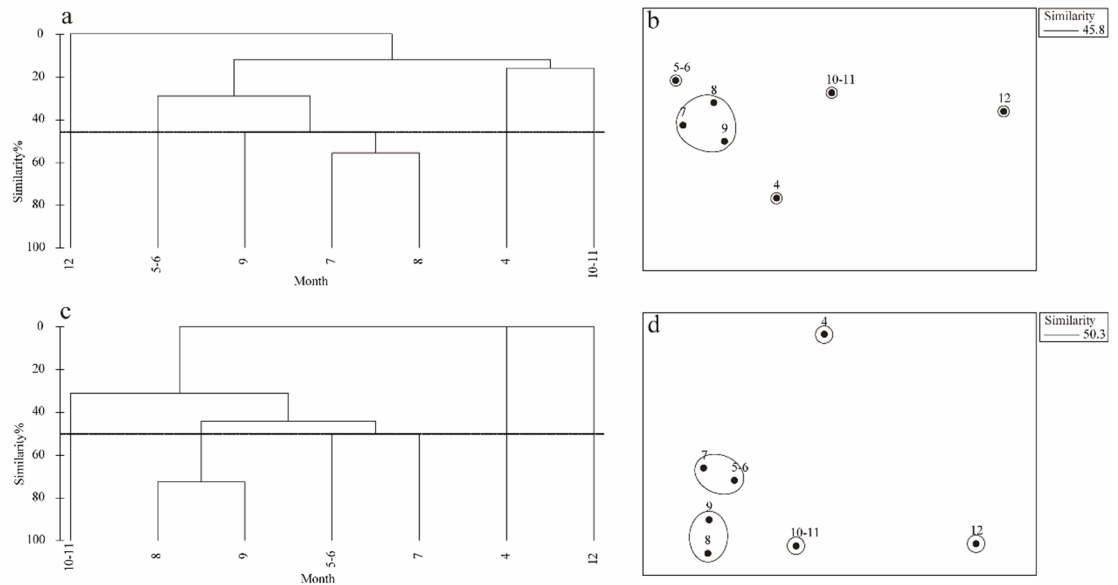


Fig. 6. CCA ordination of fish eggs (a) and larvae (b) distribution with environmental factors from May to August in offshore waters of the Liaoning Province in the Yellow Sea (SST: seawater surface temperature; SSS: seawater surface salinity; SBT: seawater bottom temperature; SBS: seawater bottom salinity; Depth: sea water depth; WW: wet weight; Chla: chlorophyll a).

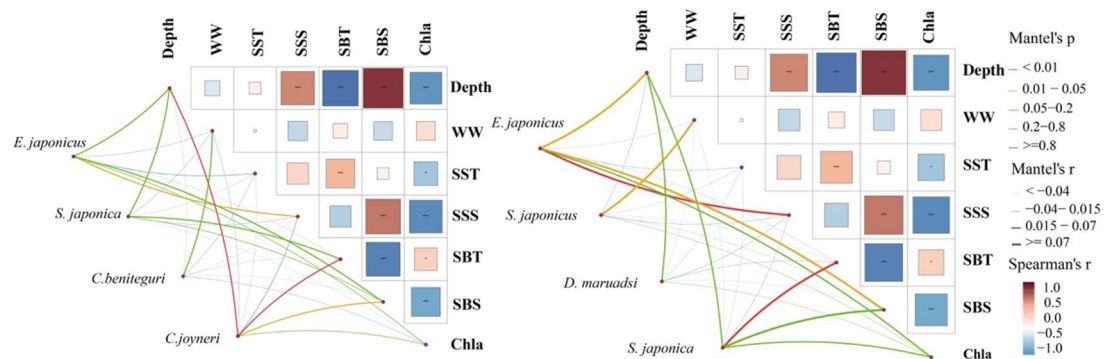


Fig. 7. Absence-presence records of *E. japonicus* eggs in offshore waters of the Liaoning Province in the Yellow Sea from 1998 to 2017.

Response of potential *E. japonicus* spawning grounds under different climate change scenarios in the offshore waters of Liaoning Province in the Yellow Sea

Global warming is expected to exert diverse influences on the distribution of potential *E. japonicus* spawning habitats in the offshore waters of Liaoning Province in the Yellow Sea. The SDMs have revealed that the main environmental factors dictating the spatial distribution of potential *E. japonicus* spawning ground are Depth, the Landis, and the AMSST. Under the current climate scenario, the Depth within the range of 10–40 m and Landis beyond 0.3 km show a negative correlation with the habitat suitability, for potential *E. japonicus* spawning grounds. The AMSST between 12.7 °C and 14 °C is deemed optimal for the spawning grounds of *E. japonicus*, with coastal regions in the marine area showing a marked increase in habitat suitability. Under the condition where greenhouse gas emissions are controlled (RCP2.6 scenario), a continuous trend of expansion is observed in the distribution of potential *E. japonicus* spawning grounds within the marine area. With greenhouse gas emissions stabilized under the RCP4.5 and RCP6.0 scenarios, suitable *E. japonicus* spawning habitats may see a temporary expansion by the 2050s, yet the overall trend points toward a fluctuating decline. In the event of sustained high levels of greenhouse gas emissions (RCP8.5 scenario), the optimal spawning habitats for *E. japonicus* in the marine environment are at risk of disappearing, which would profoundly compromise the area's importance as a key spawning ground for the species. Furthermore, across diverse climate change scenarios, the potential spawning grounds for anchovies in the marine environment exhibit a trend of expansion toward the eastern seaboard. In the 2050s under the RCP6.0 scenario, new spawning sites have been identified in the outer

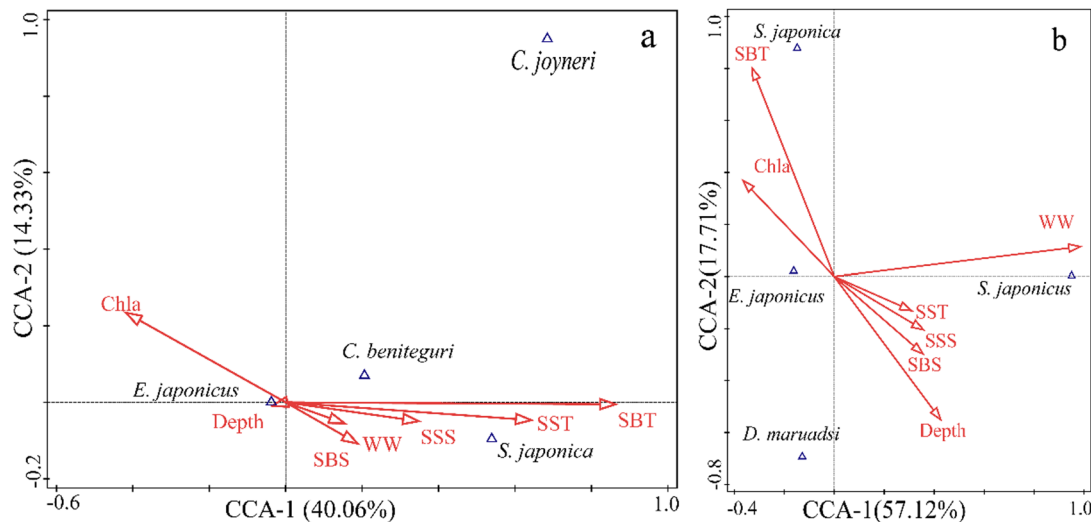


Fig. 8. The trend of distribution suitability of *E. japonicus* eggs with environmental factors in offshore waters of the Liaoning Province in the Yellow Sea (a: Sea water depth; b: Offshore distance; c: Annual mean seawater surface salinity; d: Annual mean seawater surface temperature; e Seawater surface velocity).

Period	Climate scenarios	Lowly suitable habitat/%	Moderately suitable habitat/%	Highly suitable habitat/%	Extremely suitable habitat/%	Average suitability
current	-----	35.90	23.40	13.52	27.18	899.14
2050s	RCP2.6	0.00	32.66	35.27	32.08	870.68
	RCP4.5	0.00	32.66	35.27	32.08	870.68
	RCP6.0	0.14	33.82	25.54	40.49	905.47
	RCP8.5	0.00	33.09	37.45	29.46	859.01
	RCP2.6	0.00	33.82	31.93	34.25	876.78
2100s	RCP4.5	0.00	33.53	38.32	28.16	843.20
	RCP6.0	0.00	34.69	40.49	24.82	818.60
	RCP8.5	0.00	47.02	52.69	0.29	760.00

Table 6. Average spawning habitat suitability range of *E. japonicus* across climate change scenarios in offshore waters of the Liaoning Province in the Yellow Sea. Note: The average suitability is the average value of the predicted suitability for Extremely suitable habitat.

waters to the south of the Yalu River estuary. The ongoing increase in sea surface salinity could be a pivotal factor driving this shift.

Data integrity is essential for ensuring the accuracy of model predictions^{61–67}. In this study, some of the anchovy egg records are sourced from historical survey literature. Given the constraints of the marine survey station locations, survey frequencies, and intervals from previous investigations, obtaining high-precision records of the distribution of anchovy eggs is challenging. Consequently, the study employs model simulations to create synthetic pseudoabsence data. The model optimization process remains open to further enhancement. Implementing long-term, high-resolution surveys that encompass the full spawning season of *E. japonicus* is a potent strategy for remarkably elevating the quality of the data obtained.

Conclusion

The concentrated spawning period for fish species in the offshore waters of Liaoning Province in the Yellow Sea is from May to August, with a peak spawning period occurring between May and June. The primary spawning grounds are situated around the estuaries of the Dayang River and the Yalu River. Fish with different spawning habits and temperature preferences take turns using these waters as spawning or nursery grounds. In addition to the similar composition of fish egg species and a reduced rate of species turnover between July and September, and the similar composition of juvenile fish species and a reduced rate of species turnover between May and July and between August and September, a considerable monthly turnover in the composition of fish eggs and juvenile fish is observed in other months. Cold-temperate species such as *P. herzensteini*, *H. otakii*, *Kareius bicoloratus* and *A. personatus* are the predominant early life stage resources from September to April spanning the autumn to early spring; *E. japonicus* is the main dominant species during the peak spawning period, with other early life stage resource species showing considerable monthly composition changes; the area also serves as a spawning and nursery ground for *D. maruadsi*. The integrated SDMs based on the Biomod2 framework can effectively

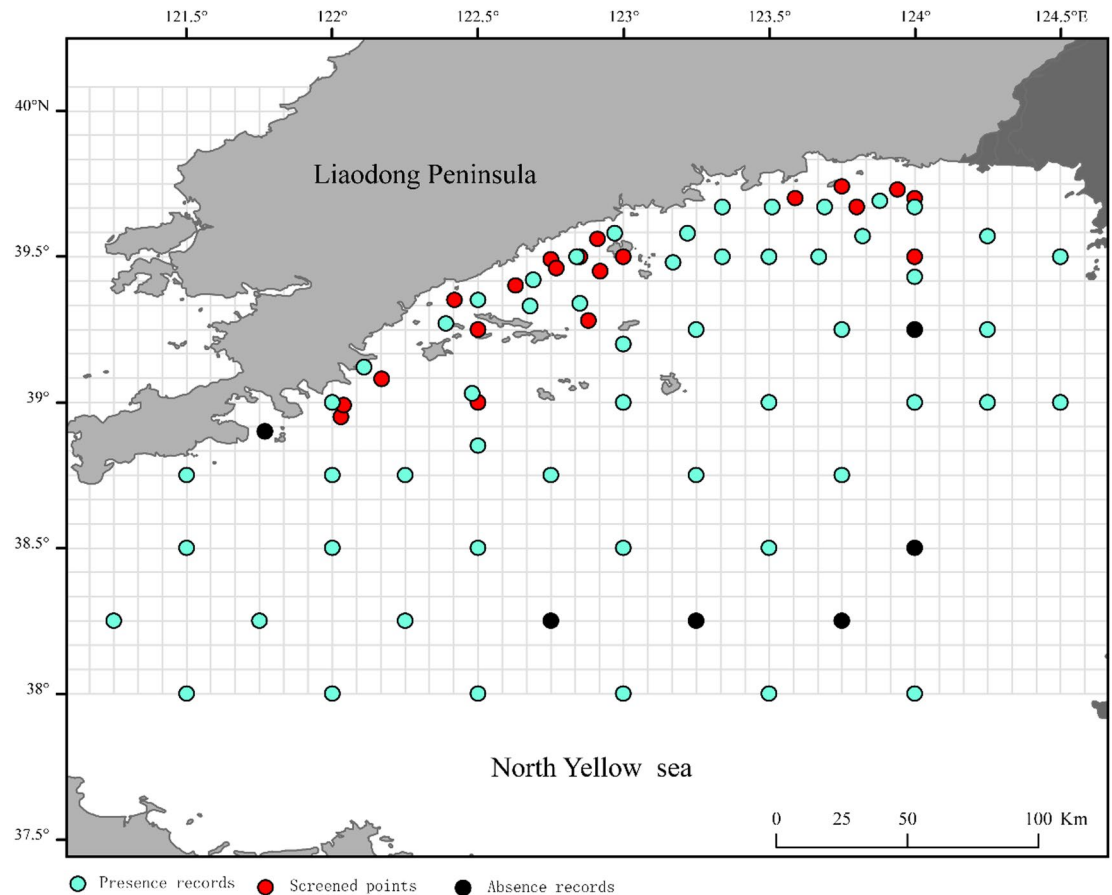


Fig. 9. Forecasting the habitat suitability for spawning to the *E. japonicus* under various climate scenarios in offshore waters of the Liaoning Province in the Yellow Sea (Panel a shows the current climate conditions; panels b and f show RCP2.6; panels c and g show RCP4.5; panels d and h show RCP6.0; and panels e and i show RCP8.5. Panels b–e represent 2040–2050, and panels f–i represent 2090–2100.).

predict the spatial distribution patterns of potential *E. japonicus* spawning grounds under different climate change scenarios in the offshore waters of Liaoning Province in the Yellow Sea. Depth, Landis, and AMSST are the main environmental factors influencing the spatial distribution of potential *E. japonicus* spawning grounds in this region. The spawning grounds of *E. japonicus* characterized by their coastal distribution characteristics, demonstrate varying degrees of extension toward the eastern side of the marine area, as influenced by four different climate change scenarios. They show a continuous expansion in the RCP2.6 scenario, fluctuating contractions in the RCP4.5 and RCP6.0 scenarios, and severe damage in the RCP8.5 scenario.

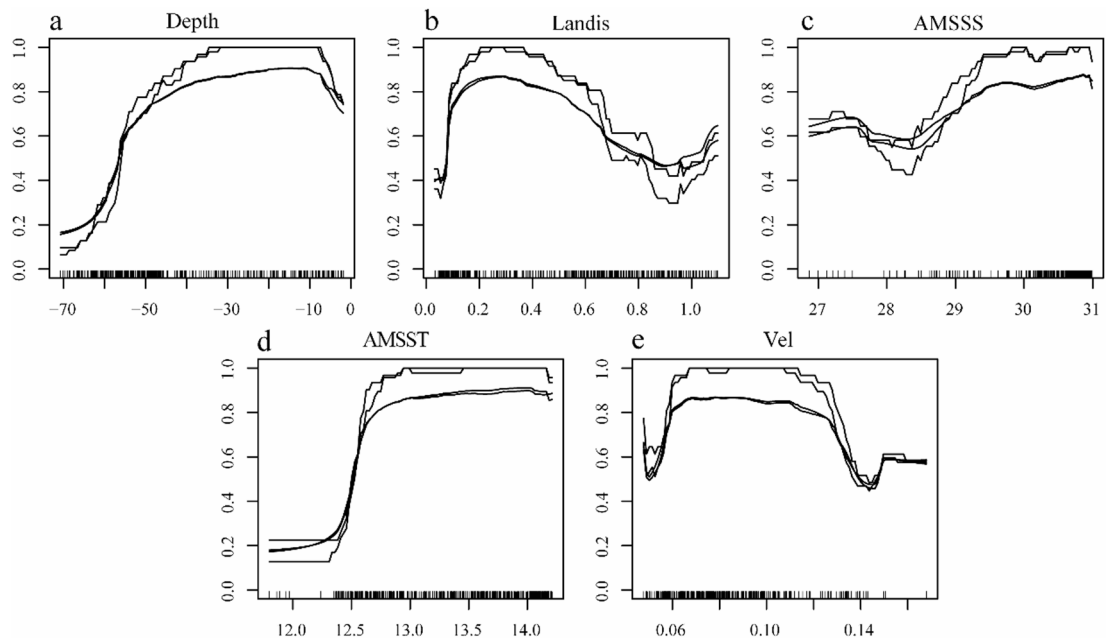


Fig. 10. The trend of distribution suitability of *E. japonicus* eggs with environmental factors in offshore waters of the Liaoning Province in the Yellow Sea (**a**: Sea water depth; **b**: Offshore distance; **c**: Annual mean seawater surface salinity; **d**: Annual mean seawater surface temperature; **e** Seawater surface velocity).

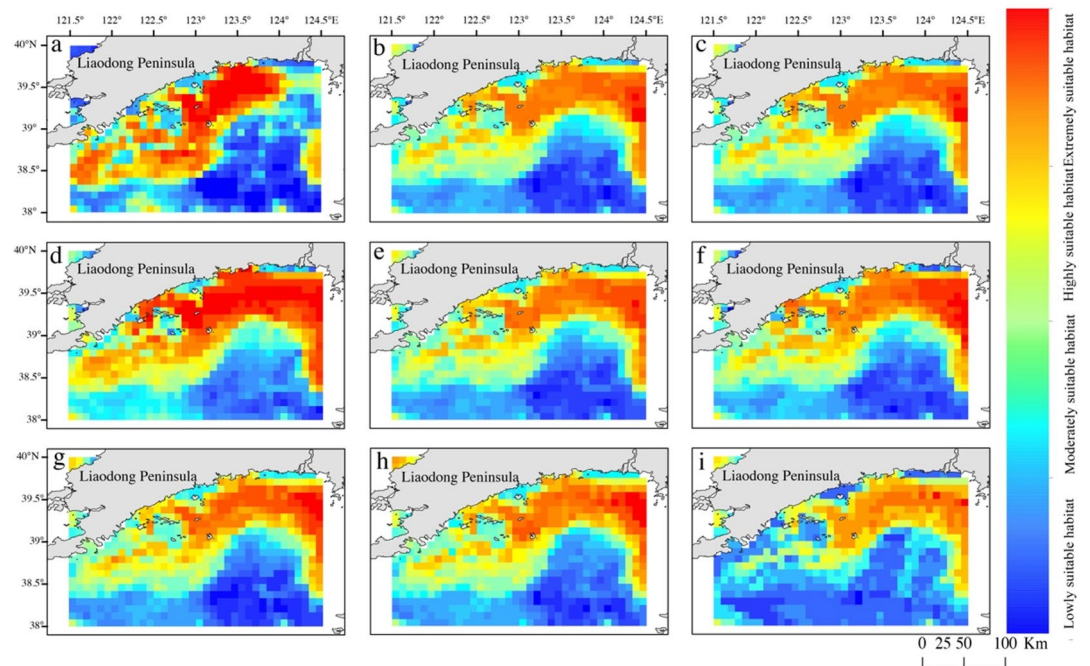


Fig. 11. Forecasting the habitat suitability for spawning to the *E. japonicus* under various climate scenarios in offshore waters of the Liaoning Province in the Yellow Sea (Panel **a** shows the current climate conditions; panels **b** and **f** show RCP2.6; panels **c** and **g** show RCP4.5; panels **d** and **h** show RCP6.0; and panels **e** and **i** show RCP8.5. Panels **b–e** represent 2040–2050, and panels **f–i** represent 2090–2100.).

Data availability

Data will be made available upon individual request (contact: corresponding author).

Appendix A. Supplementary data

The scientific names of the species refer to the World Register of Marine Species (WoRMS, <https://www.marinespecies.org/>).

The Depth and Landis data were obtained from the Global Marine Environmental Dataset (<http://gmed.auckland.ac.nz>), while the other marine environmental data were obtained from the Bio-ORACLE v2.0 dataset (<https://www.bio-oracle.org/>).

The data were sourced from the Bio-ORACLE v2.0 dataset, accessible at <https://www.bio-oracle.org/>.

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****Xuening Li (Co-first author 1)**** : Conceptualization, Collection of sample, Formal analysis, Methodology, Validation, Investigation, Writing – original draft. ****Peidong Cui (Co-first author 2)**** : Conceptualization, Code writing, Formal analysis, Methodology, Validation, Visualization, Writing – original draft. ****Qingpeng Han**** and ****Xiaodong Bian**** : Data curation, Identification of sample, Fund acquisition, Project administration, Resources, Supervision, and Writing—review and editing. ****Ming Sun**** : Fund acquisition, Resources and Supervision. ****Xun Li**** : Participate in the original draft writing. ****Xilong Xu**** : Participate in the original draft writing.

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Declarations

Competing interests

The authors declare no competing interests.

Ethics approval

This study did not involve breeding, rearing, surgical manipulation, or prolonged live holding of animals. The main ethical consideration was the collection and preservation of wild ichthyoplankton specimens, and sampling was restricted to the minimum necessary to achieve the study objectives while minimizing habitat disturbance. All procedures were approved by the Institutional Animal Care and Use Committee of the Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences.

Additional information

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