Spatiotemporal Patterns of Eggs of Bartail Flathead, *Platycephalus indicus* in Coastal Southern Yellow Sea

Sanny Tri Utami, Zhenjiang Ye*, Wenchao Zhang and Yixiao Zhang

ABSTRACT

The distribution of fish spawning grounds is a key factor influencing larval transport, growth, mortality, and early recruitment success. Understanding the spatiotemporal patterns of fish egg distribution provides a scientific foundation for comprehending population fluctuations. This study investigated the spawning patterns and environmental impacts on the egg distribution of *Platycephalus indicus* in the Southern Yellow Sea (SYS). Data were collected from 27 ichthyoplankton survey cruises conducted during the spawning season from 2013 to 2018 in the coastal waters of the Southern Yellow Sea waters. A two-stage generalized additive model (GAM) was used to analyze the spatiotemporal distribution patterns of eggs and their non-linear relationships with environmental factors, including sea surface temperature (SST), salinity (SSS), water depth, longitude, and latitude. Results indicated that spawning mainly occurred from April to July, peaking in May. GAM analysis identified SST, longitude, latitude, and water depth as significant predictors of egg presence, explaining 34.5% of the variance (AIC = 835.22). For egg abundance, SST, SSS, water depth, longitude, latitude, and offshore distance were key predictors, accounting for 55% of the variance (AIC = 778.73). SST was the most influential variable for both presence and abundance, showing a positive correlation with SST below 17 °C and a negative correlation above this threshold. Optimal egg abundance occurred between 15 °C and 19 °C. High egg concentrations were found in nearshore waters. These findings emphasize the importance of monitoring SST and protecting nearshore spawning grounds to support the conservation and management of *P. indicus* in the Southern Yellow Sea.

Keywords: Egg distribution, Generalized additive model (GAM), *Platycephalus indicus*, Sea surface temperature, Southern Yellow Sea

INTRODUCTION

Understanding the early life history of fish, particularly the spatial and temporal distribution of eggs, is essential for studying fish population dynamics (Köster *et al*., 2001; Zhou *et al*., 2011). A key factor influencing fish population dynamics in aquatic environments is the success of the recruitment process (Secor *et al*., 2009; Soeth *et al*., 2019). Fish are highly vulnerable during early life stages, making the timing and location of egg deposition critical for their survival and early recruitment (Chen, 2022), ultimately influencing the number of individuals recruited into the adult population (Rijnsdorp *et al*., 2009). Different fish species employ various spawning strategies, selecting optimal spawning times and habitats to maximize replenishment success (Zhang *et al*., 2021). Across regions, the spatiotemporal distribution of fish eggs is intricately linked to oceanographic conditions and the geographical distribution of larvae (Alvarez *et al*., 2001; Kim *et al*., 2005; Sassa

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and Konishi, 2015). The interaction of these factors ensures that fish eggs are distributed in areas where conditions are favorable for their development. The dispersal of eggs and larvae often reflects the influence of oceanographic factors (Zheng *et al*., 2022). In particular, sea surface temperature (SST) is strongly correlated with spawning events and fish egg density (Takasuka *et al*., 2007; Mazloumi *et al*., 2017; Yu *et al*., 2020). Additionally, the distribution of fish eggs and larvae is significantly influenced by surface currents, water depth, tidal mixing, and salinity, highlighting the crucial role of environmental factors in determining the success of early-stage survival (Hao *et al*., 2003; Wei *et al*., 2016a; Song *et al*., 2019; Tan *et al*., 2023).

Platycephalus indicus (Linnaeus, 1758), commonly known as the bartail flathead, predominantly inhabits the demersal zone and is widely distributed across the Northwestern Pacific region, including the Japan and China Seas (Chen *et al*., 2020; Furuhashi *et al*., 2021; Zheng *et al*., 2023). This species holds significant economic value in the fisheries of these regions, particularly in China, where it is extensively harvested for consumption (Zheng *et al*., 2022a). The population dynamics of *P. indicus* exhibit regional trends, with an increase observed in the Yellow Sea and a decline in the Bohai Sea (Zheng *et al*., 2022b; Zheng *et al*., 2023). The Yellow Sea serves as a critical distribution area and spawning ground for this species. However, while previous studies have mainly focused on its morphology, growth, sexual maturity, and species distribution (Chen and Gao, 2017; Masuda *et al*., 2000; Ding *et al*., 2020; Hara and Sunobe, 2021), the spatiotemporal distribution patterns of this species' eggs in the Yellow Sea, particularly the influence of environmental factors on their distribution, remain poorly understood. Notably, the distribution of *P. indicus* in Chinese waters reflects seasonal migratory patterns, with populations migrating to the waters near Cheju Island during the overwintering period (Qin and Gao, 2012). As temperatures rise in spring and summer, *P. indicus* returns to the coastal areas of the Yellow Sea, where its reproductive strategies are closely tied to these migration patterns (Gray and Barnes, 2015). In the Southern Yellow Sea (SYS), *P. indicus* eggs are predominantly found during spring and summer, particularly in Haizhou Bay (Li *et al*., 2017).

During summer, the Yellow Sea Cold Water Mass (YSCWM) exerts significant influence on the waters of the SYS (Liu *et al*., 2021). Seasonal thermal stratification in the SYS begins at the end of spring, intensifies during summer, and dissipates by autumn (Wei *et al*., 2016a). This process plays a crucial role in fish spawning, alongside regional tidal fronts and upwelling events (Hao *et al*., 2003; Guo *et al*., 2020). The coastal waters of the SYS are regarded as vital spawning and nursery grounds for numerous fish species, including *P. indicus* (Qun *et al*., 2012; Li *et al*., 2015; Cheng *et al*., 2019; Jiang *et al*., 2019). This region not only supports capture fisheries but also sustains critical spawning habitats, underlining the importance of studying the spatiotemporal distribution of fish eggs, particularly in relation to environmental changes (Matta *et al*., 2010). Climate change scenarios predict a northward shift in suitable spawning grounds for various fish species, further emphasizing the need for in-depth studies on these shifts (Zhang *et al*., 2022). Understanding these patterns is essential, as changes in environmental variables may significantly alter the suitability of spawning habitats in the SYS. Currently, the spatiotemporal distribution patterns of *P. indicus* eggs and their relationship to resource supplementation remain poorly understood.

In this study, we analyzed the spatiotemporal distribution of *P. indicus* eggs in the SYS based on surveys conducted during the spawning seasons from 2013 to 2018. The aim of this analysis was to investigate the impact of environmental factors on egg distribution and to provide crucial baseline information for anticipating how spawning habitats may respond to climate-driven ocean changes, thereby supporting scientific understanding of resource dynamics and conservation of *P. indicus*.

MATERIALS AND METHODS

Survey area, cruises and stations

Field surveys were conducted in the SYS during the spring and summer seasons from 2013 to 2018, comprising a total of 27 cruises (Figure 1, Table 1). A stratified and systematic sampling design was employed during six cruises in 2013, while a fixed-station design was applied in the subsequent 21 cruises between 2014 and 2018. The survey areas encompassed the potential spawning grounds of *P. indicus* within the study region (31°60' N–36°51' N, 119°15' E–122°38' E). Ichthyoplankton samples were collected during daylight hours using a large plankton net (net mouth diameter: 80 cm; net length: 280 cm; mesh size: 505 µm). Towing was carried out at a speed of approximately 3 knots for 10 min in the surface layer, at an estimated depth of less than 1 meter at each sampling station. A flow meter was attached to the mouth of the net to quantify the volume of filtered water. Immediately after collection, ichthyoplankton samples were preserved in a 5% seawater formaldehyde solution and transported to the laboratory for morphological species identification and analysis. Temperature, salinity, and depth were measured at each station using a CTD (Model: XR-420).

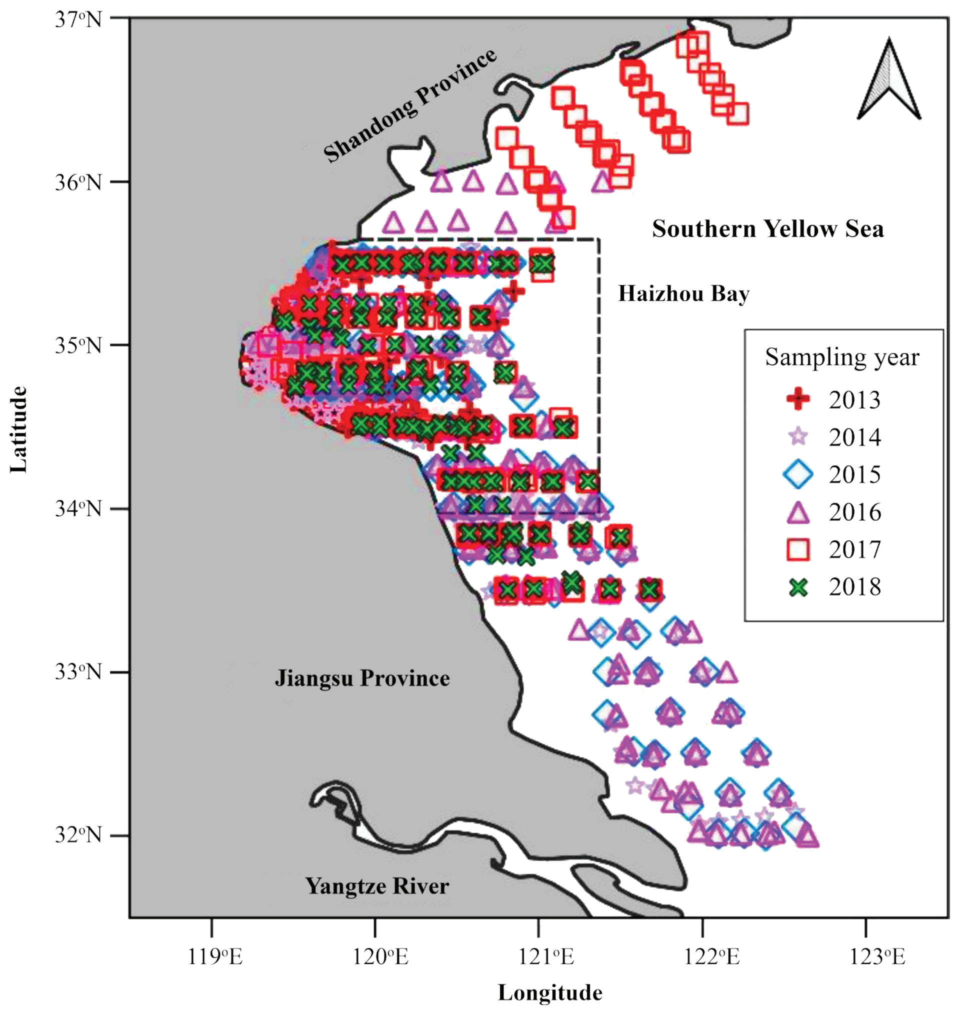


Figure 1. Survey cruises and sites in the coastal Southern Yellow Sea (SYS) during the spring and summer (2013–2018).

Table 1. Details of cruises, survey areas, and number of stations for ichthyoplankton surveys in the coastal Southern Yellow Sea (2013–2018).

Duration of cruises	Latitude (N)	Longitude (E)	Number of stations
23–24 April 2013	34°30'–35°34'	119°18'–120°15'	51
10–12 May 2013	34°30'–35°25'	119°17'–120°15'	70
15–16 May 2013	34°25'–35°29'	119°34'–120°51'	18
23–25 May 2013	34°30'–35°28'	119°15'–120°15'	73
6–8 Jun 2013	34°30'–35°31'	119°15'–120°14'	65
21–23 Jun 2013	34°30'–35°25'	119°15'–120°10'	70
6–8 Jul 2013	34°30'–35°29'	119°15'–120°10'	71
12–16 May 2014	33°60'–35°36'	119°17'–120°50'	94
25–30 Jun 2014	33°60'–35°01'	119°15'–121°20'	29
15–18 Jul 2014	33°60'–35°01'	119°16'–121°20'	29
12–23 Aug 2014	32°15'–35°30'	119°28'–122°29'	81
15–24 May 2015	32°00'–35°30'	119°30'–122°28'	91
23–24 Jun 2015	34°45'–35°31'	119°35'–120°49'	28
2–17 Jul 2015	34°45'–35°30'	119°35'–120°50'	28
20–23 Jul 2016	31°60'–35°31'	119°30'–122°39'	90
3–11 Aug 2016	32°01'–36°01'	119°17'–122°38'	75
21–26 Apr 2017	33°30'–35°32'	119°26'–121°41'	49
11–22 May 2017	34°57'–36°51'	119°21'–122°08'	37
24–29 May 2017	33°29'–35°32'	119°30'–121°01'	48
7–11 Jun 2017	35°47'–36°49'	120°49'–122°13'	20
18–29 Jun 2017	33°29'–36°39'	119°28'–121°51'	64
25–29 May 2018	33°31'–35°30'	119°27'–121°40'	46
7–12 Jun 2018	33°30'–35°31'	119°27'–121°41'	49
22–28 Jun 2018	33°30'–35°31'	119°26'–121°41'	49
6–10 Jul 2018	33°30'–35°30'	119°27'–121°41'	47
19–20 Jul 2018	33°43'–35°04'	119°38'–120°55'	25
6–8 Aug 2018	33°42'–35°15'	119°36'–120°55'	31

Data analysis

A two-stage generalized additive model (GAM) was employed in this study to explore the relationship between the spatiotemporal distribution of eggs and environmental factors (Yang *et al*., 2018; Fu *et al*., 2024). This approach was chosen due to the high prevalence of zero values in egg abundance data, as the GAM can effectively reduce the impact of zero catches and improve predictive accuracy (Jensen *et al*., 2005; Jie *et al*., 2019). Compared to traditional linear models or generalized linear models (GLMs), GAM offers better performance in capturing nonlinear relationships, particularly in ecological studies (Potts and Rose, 2018).

During the 27 cruises conducted from 2013 to 2018, *P. indicus* eggs were found at 276 stations out of a total of 1,428 sampling stations. Egg abundance was calculated by multiplying the number of eggs by 100 and dividing by the filtration volume at each station. The resulting abundance data were then log-transformed (log (n+1)) for further analysis (Zarrad *et al*., 2013). Egg abundance data and surface environmental parameters, including water depth (m), distance from shore (km), sea surface temperature (SST) (°C), sea surface salinity (SSS) (‰), and the geographical coordinates (longitude and latitude), were analyzed to explore the spatiotemporal distribution pattern of the fish eggs.

Multicollinearity among environmental variables was assessed using the Variance Inflation Factor (VIF), with a threshold set at 3. Variables exceeding this threshold were excluded from further analysis (Zarrad *et al*., 2013; Daoud, 2018). In the two-stage GAM, the model was used to fit the relationship between the number of fish eggs and the predictive factors (Equation 1):

$$\hat{y} = \hat{d} \times \hat{q} \qquad \text{(Equation 1)}$$

Where:

$\hat{y}$ is the number of eggs laid,
$\hat{d}$ is the abundance of fish eggs when they appear
$\hat{q}$ is the probability of fish eggs appearing.

The first stage of the GAM determined the probability of occurrence of *P. indicus* eggs in the study area, addressing the influence of zero data using a binomial distribution (classification: presence/absence) (Equation 2). In the second stage of the model, only positive fish egg data (presence) were modeled as a function of environmental covariates with a Gaussian error distribution (Equation 3):

$$\text{GAM 1: } \operatorname{logit}(p) = \alpha + \sum_{i=1}^{n} s_i(x_i) + \varepsilon \qquad \text{(Equation 2)}$$

Where:

p = occurrence of eggs [0/1], binomial distribution
logit(p) = log-odds of egg occurrence
α = intercept term
$s_i(x_i)$ = smooth function (e.g., spline) of the i^{th} predictor variabl (e.g., SST, salinity, depth, etc)
n = number of predictor variables
ε = error term (residual)

$$\text{GAM 2: } Y = \alpha + \sum_{i=1}^{n} s_i(x_i) + \varepsilon \qquad \text{(Equation 3)}$$

Where:

Y = abundance of fish eggs [log(n+1)], Gaussian distribution
α = intercept term
$s_i(x_i)$ = smooth function (e.g., spline) of the i^{th} predictor variabl (e.g., SST, salinity, depth, etc)
n = number of predictor variables
ε = error term (residual)

The best-fitting model was selected based on the Akaike Information Criterion (AIC) (Equation 4), with the model yielding the lowest AIC value being chosen for the study (Akaike, 1974). All analyses were conducted using R software (version 4.2.1), with the mgcv package applied for model implementation.

$$AIC = 2k - 2\ln(L) \qquad \text{(Equation 4)}$$

Where:

k = number of estimated parameters in the model
L = maximum value of the likelihood function for the model.

RESULTS AND DISCUSSION

Spatiotemporal pattern of Platycephalus indicus eggs in the SYS

P. indicus eggs were found from April to July, with the highest abundance recorded in May. No eggs were detected in August. In late April, only a small number of eggs were collected from Haizhou Bay and the southern part of the survey area. As water temperatures increased in May, *P. indicus* entered its peak spawning period, and the distribution of eggs expanded from south to north, gradually covering the entire survey region. By June, the number of eggs in the southern part of the survey area had significantly decreased, while a considerable number of eggs remained in the northern region. By July, the spawning season had largely ended, with only a few eggs detected at specific stations in Haizhou Bay (Figure 2).

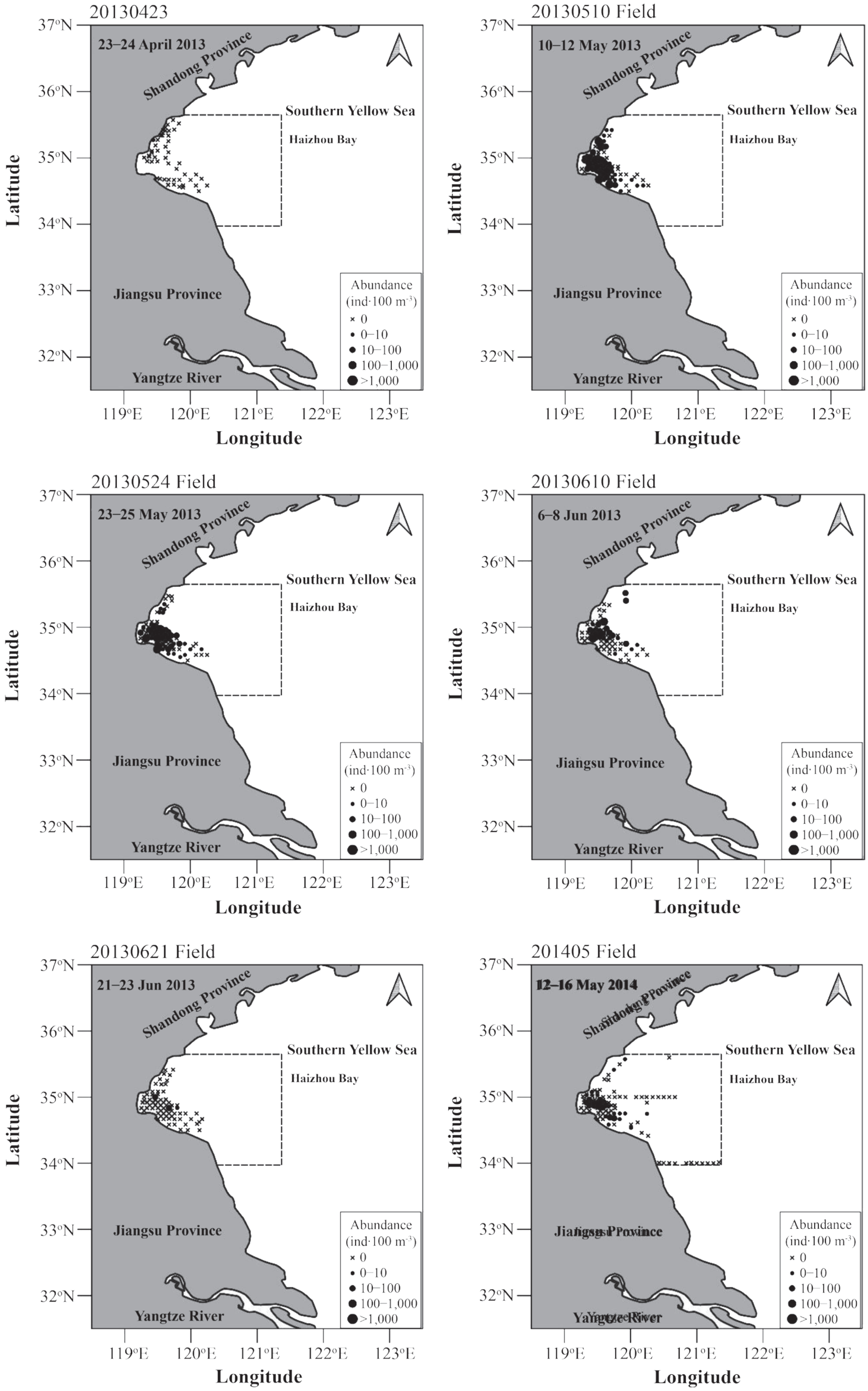
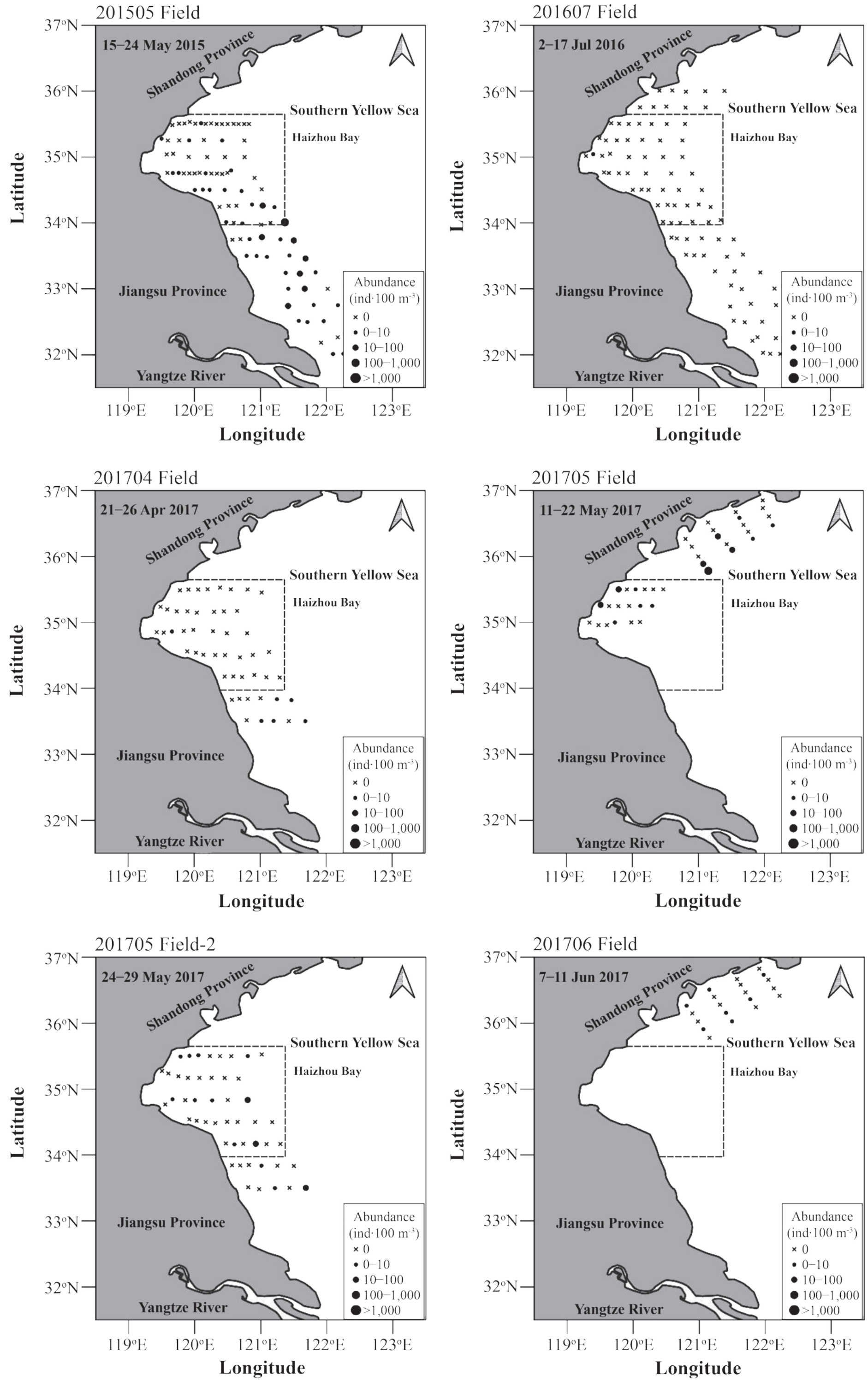


Figure 2. Spatial distribution and abundance of *Platycephalus indicus* eggs across various survey cruises (2013–2018).



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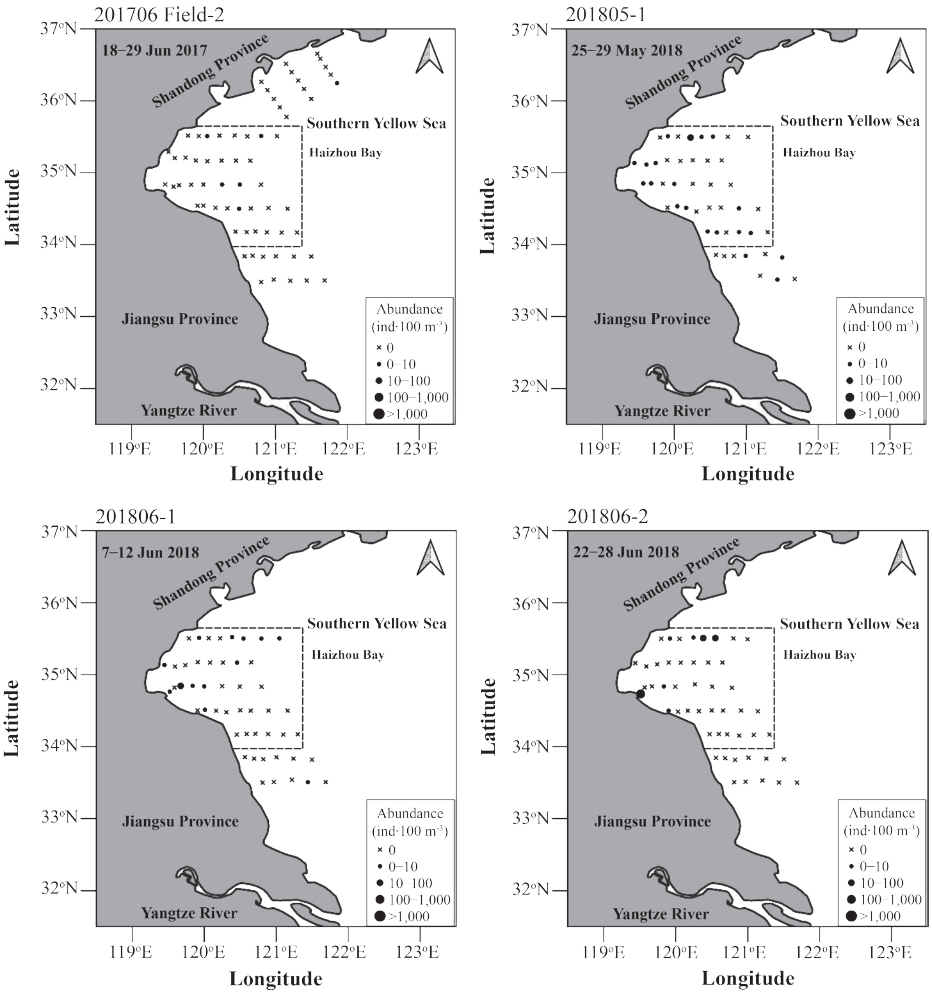

Figure 2. Cont.

Monthly variations in SST showed a gradual increase from April to July, reflecting a typical seasonal warming trend, with an overall mean of 20.80 °C (Figure 3a). Salinity values remained relatively stable across the sampling months, averaging 29.79‰, with the highest mean SSS recorded in April (Figure 3b). A distinct outlier in May (27.11‰) suggests possible freshwater intrusion, though it did not significantly influence the monthly average. Water depth at the sampling stations remained relatively consistent throughout the study, with monthly averages ranging from 14 m to 18 m (Figure 3c). Offshore distance varied widely, especially in April when sampling covered the broadest spatial extent from coastal to offshore zones. In contrast, sampling in July was limited to a single mid-range station located 7.45 km from shore (Figure 3d).

Among the environmental variables measured when eggs were found, sea surface temperature (SST) ranged from 10.46 °C to 25.00 °C, sea surface salinity (SSS) ranged from 17.11‰ to 32.11‰, water depth ranged from 10.47 m to 28.17 m, and the offshore distance from the shore ranged from 2.11 km to 107.95 km (Table 2, Figure 3). The SYS serves as a key seasonal spawning ground for many fish species due to favorable spring-summer conditions, including rising SST, water column stratification, and increased primary productivity. The spawning strategy of *P. indicus* involves adapting to different environmental conditions to optimize egg production and survival rates. This includes timing spawning and selecting specific areas that provide optimal conditions for egg development (Alvarez *et al*., 2001; Rehberg-Haas *et al*., 2012).

The results of this study show that spawning of *P. indicus* occurs from late April to early July, with a peak in May. Spawning gradually shifts from south to north, which is similar to the breeding patterns of other fish species in coastal China waters, such as the small yellow croaker (*Larimichthys polyactis*) (Jiang *et al*., 2019), Japanese anchovy (*Engraulis japonicus*) (Zhang *et al*., 2021), and blue-spotted mackerel (*Scomber australasicus*) (Kasai *et al*., 2008). This pattern is attributed to the gradual increase in water temperature from south to north during the spring and summer months. In spring, as the water temperature rises along the Yellow Sea coast, plankton proliferates in large numbers, providing abundant biological food for larvae. This attracts various fish species, including *Larimichthys polyactis*, *Chelon haematocheilus, Konosirus punctatus, Hexagrammos otakii, Cynoglossus joyneri, Cleisthenes herzensteini,* and *P. indicus*, which spawn in the area (Li *et al*., 2017; Jie *et al*., 2019; Liu *et al*., 2019). Unlike these species that spawn in the SYS during April to July, *P. indicus* spawns from January to March in the Persian Gulf (Mohammadikia *et al*., 2014) and from April to May in the Khuzestan Coastal Waters (Hashemi *et al*., 2012). These differences in spawning periods may be linked to regional variations in water temperature and breeding season. Our study suggests that *P. indicus* eggs primarily appear in shallow coastal waters at depths of less than 30 meters during spring and summer, particularly in Haizhou Bay and its adjacent waters in the central part of the study area. This is consistent with the spawning behavior of other coastal species in the region (Li *et al*., 2015).

Table 2. Egg density and environmental variables (surface sea temperature: SST; salinity: SSS; water depth) recorded during each survey cruise conducted from 2013−2018.

Year	Cruise	Egg density (ind·100 m^{-3})	SST (^{O}C)	SSS (‰)	Water depth (m)	Offshore distance (km)
2013	Late April	0.786	10.46	29.67	10.20	2.17
2013	Early May	5,042.788	15.25±1.42	29.27±0.77	11.09±4.11	12.46±6.93
2013	Late May	4,737.438	17.60±1.29	29.34±0.55	11.86±3.76	16.47±8.85
2013	Early June	1,848.086	18.60±0.98	29.12±0.55	11.59±5.74	20.83±8.07
2013	Late June	103.784	22.61±0.85	29.19±0.37	12.77±7.69	24.48±9.66
2014	Middle May	11.576	15.60±1.28	30.63±0.48	16.14±3.46	20.44±8.46
2015	Late May	498.421	16.81±1.10	30.35±1.00	16.13±5.19	52.28±29.01
2016	Early July	2.358	23.68*	30.32*	16.28*	7.45*
2017	Late April	4.960	13.59±0.50	30.55±1.08	14.72±4.80	69.32±31.55
2017	Early May	938.825	14.89±0.69	31.10±0.70	23.58±5.08	40.42±20.37
2017	Late May	51.578	18.05±1.04	30.75±0.86	22.19±4.89	40.50±28.31
2017	Early June	13.083	19.29±0.84	32.07±0.05	23.20±9.46	38.95±24.83
2017	Late June	4.378	22.85±1.11	30.74±0.83	27.05±6.33	49.65±19.26
2018	Late May	66.618	17.58±0.90	28.35±4.65	20.13±7.15	41.04±27.18
2018	Early June	79.156	20.45±0.59	30.12±1.48	22.66±10.16	42.83±29.19
2018	Late June	367.878	22.21±1.46	30.26±1.36	22.49±11.87	28.29±21.51

Note: *Values without standard deviations indicate single observations

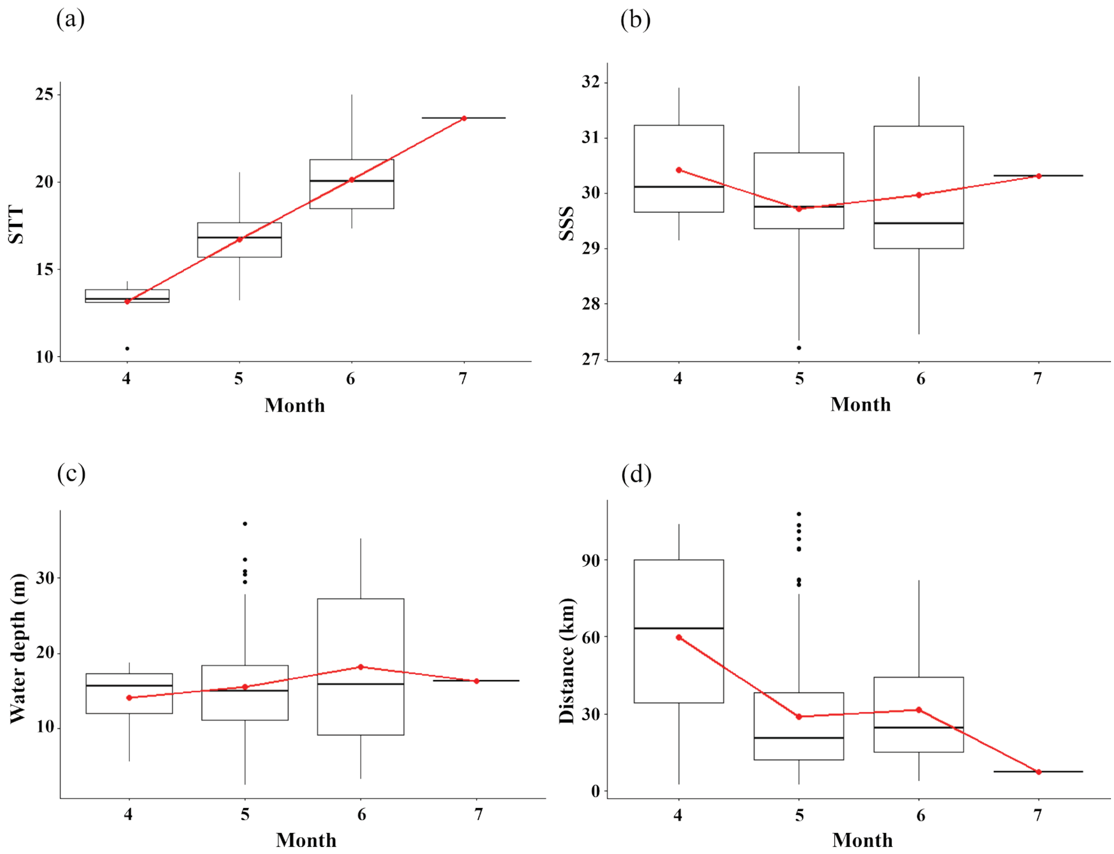

Figure 3. Monthly environmental variables during egg collection. Black dots represent outliers beyond the range. The red line connects the monthly means, illustrating the average shift in sampling distance over time. Stations without egg presence were excluded.

The relationship between egg distribution and environmental factors

The results of the VIF test indicated that variables that SST, SSS, longitude, latitude, and water depth exhibited VIF values below 3, indicating the absence of multicollinearity issues. Therefore, these variables were retained for subsequent analysis.

The results of the two-stage GAM are presented in Figure 4 and 5, respectively. The first stage of the GAM analysis revealed that the environmental variables influencing the presence of *P. indicus* eggs included SST, longitude, latitude, and water depth (Deviance explained: 34.5%, AIC = 835.22). Among these variables, SST emerged as the most significant factor, showing a positive correlation up to 17 °C and a negative correlation beyond that. The optimal SST range for the presence of *P. indicus* eggs was around 17 °C (Figure 4a). Eggs were primarily found in specific areas, particularly within the latitude range of 33.5 °N–36.0 °N, suggesting a geographic hotspot for spawning activity (Figure 4b). The relationship between egg presence and water depth was weakly negative, as indicated by the nearly flat smooth curve and wide confidence intervals across the depth range of 2 to 35 m, reflecting a limited contribution of this variable to the model (Figure 4c). In the second stage of the GAM, the environmental variables influencing egg abundance included SST, SSS, longitude, latitude, and water depth (Deviance explained: 55%, AIC = 778.73) (Table 3). Egg abundance exhibited a positive

Table 3. Selection model results for the two-stage of GAM.

Model	Resource used for GAM	The selection model	AIC	Deviance explained (%)	Sample size (n)
The presence of fish eggs distribution (p)	Regular GAM	Presence eggs~s(SST)+s(SSS)+s(lon, lat)+s(depth)	835.97	34.7%	1,250
		Presence eggs~s(SST)+s(lon, lat)+s(depth)	**835.22**	**34.5%**	**1,250**
		Presence eggs~s(SST)+s(lon, lat)	836.52	34.0%	1,250
		Presence eggs~s(SST)+s(depth)	856.35	30.4%	1,250
		Presence eggs~s(SST)	866.01	29.1%	1,250
The abundance of fish eggs distribution (B)	Regular GAM	**Abundance eggs~s(SST)+s(SSS)+s(lon, lat)+s(depth)**	**778.73**	**55.0%**	**276**
		Abundance eggs~s(SST)+s(lon,lat)+s(depth)	792.55	49.9%	276
		Abundance eggs~s(SST)+s(lon, lat)	796.17	48.0%	276
		Abundance eggs~s(SST)+s(depth)	879.33	10.0%	276
		Abundance eggs~s(SST)	890.58	4.23%	276

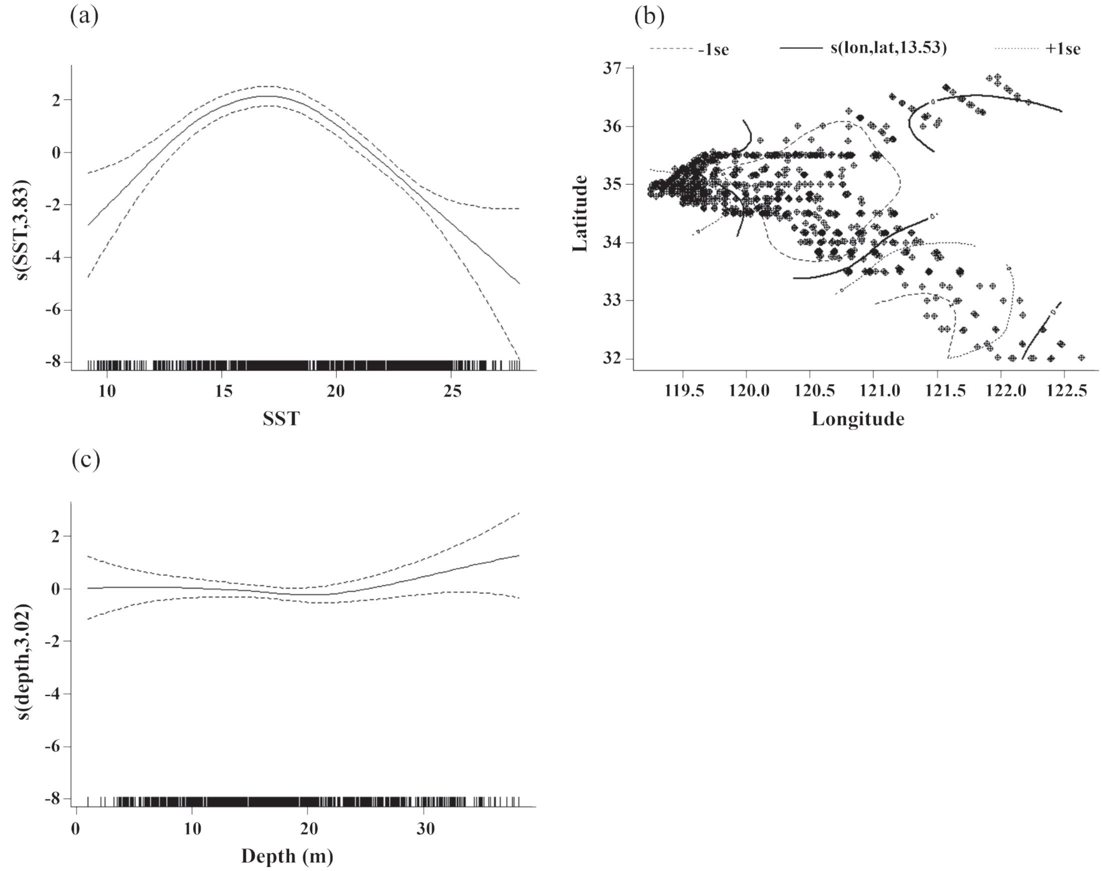

Figure 4. Effect of environmental variables on predicted fish egg occurrence based on the first-stage GAM results (a–c). The solid black line represents the smoothed effect of each variable on egg presence (a–c), while the dashed lines indicate the 95% confidence intervals (±1 standard error) (a–c). Tick marks along the x-axes denote the distribution of observed values at the sampling stations (a–c). Black dots represent the actual sampling locations used in the spatial panel (b).

correlation with SST below 17 °C and a negative correlation beyond this value (Figure 5a). SSS showed a non-linear effect, with optimal salinity range (SSS) for egg abundance was approximately 29.72‰, and a positive correlation above this value, followed by a significant number (Figure 5b). Spatially, egg abundance exhibited a stronger correlation with latitude, particularly between 34.0 °N–35.5 °N, while longitude had a generally low correlation with egg abundance (Figure 5c). Moreover, the smooth term for water depth indicates that eggs were predominantly found at depths between 10–20 m, with higher abundance centered around 15 m (Figure 5d). A suitable marine environment is essential for fish spawning, and small changes in the temperature of spawning grounds can significantly affect recruitment success. Our research indicates that sea surface temperature (SST) plays a crucial role in the occurrence and abundance of fish eggs, with the optimal SST for egg occurrence around 17 °C (Figure 4a, 5a). Environmental temperature significantly influences the embryonic development of fish and the survival rate of eggs (Alvarez *et al*., 2001; Yu *et al*., 2020). Several studies have highlighted that fish eggs are more likely to be found in specific temperature ranges rather than salinity (Davies *et al*., 2015; Sogawa *et al*., 2019). Therefore, in this study, temperature is identified as the most important factor influencing the appearance and abundance distribution of

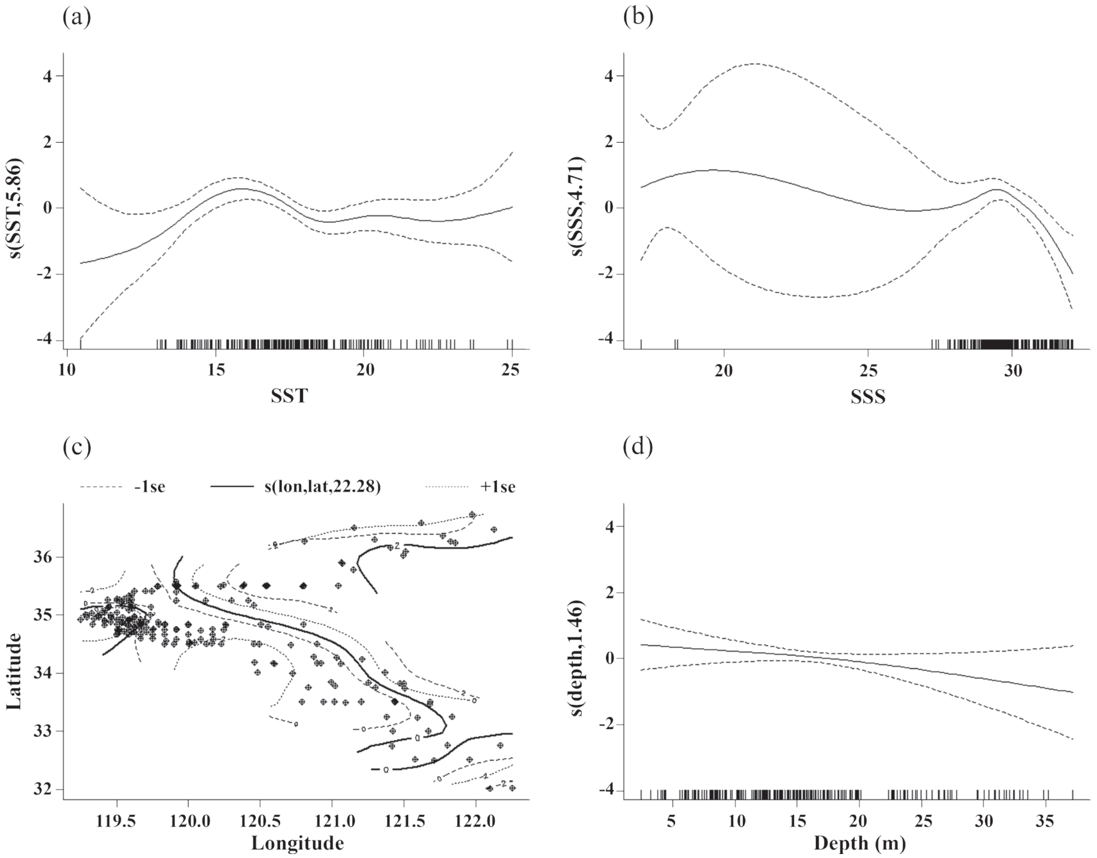

Figure 5. Effect of environmental variables on estimated fish egg abundance based on the second-stage GAM results. The solid black line represents the smoothed effect of each variable on egg presence (a–d), while the dashed lines indicate the 95% confidence intervals (±1 standard error) (a–d). Tick marks along the x-axes denote the distribution of observed values at the sampling stations (a, b, d). Black dots represent the actual sampling locations used in the spatial panel (c).

eggs. While salinity did not significantly affect the presence of eggs, it was the second most significant environmental variable affecting egg abundance. This underscores the importance of seawater salinity, in addition to temperature, in influencing the development of fish embryos (Tan *et al*., 2023).

Wind, tidal mixing, and river discharge are the primary factors influencing coastal hydrodynamic processes, such as upwelling and frontal dynamics, which result in variations in the vertical structure of hydrodynamics. Haizhou Bay and its adjacent waters are located near the Yangtze River Estuary to the south, with several rivers, including the Guanhe, Longwang, Qingkou, and Linhong Rivers, discharging into the sea near the coast. These hydrodynamic conditions influence the distribution of fish eggs in the coastal waters.

During spring and summer, increased river runoff driven by seasonal precipitation alters salinity patterns in coastal waters. Results from the two-stage GAM analysis indicated that salinity was influential variable for egg abundance (Table 3, Figure 5b). In line with this, salinity levels showed a declining trend over the months (April: 30.11‰, May: 29.72‰, June: 29.52‰) and increased again in July (30.31‰) (Figure 3b), and this change may affect egg abundance and distribution significantly.

The study area is significantly influenced by oceanographic phenomena, particularly the Tidal Mixing Front (TMF) (Lü *et al*., 2010) and the Yellow Sea Cold Water Mass (YSCWM) (Huang *et al*., 2018). As water depth increases, the influences of the lower water layer associated with the YSCWM intensifies, increasing the temperature difference between the upper and lower water layers. In spring, the water velocity and flow direction often differ vertically, with the upper layer flowing away from the shore and the lower layer moving toward the shore. This phenomenon becomes more pronounced in summer, when strong coastal upwelling occurs (Jiang *et al*., 2024). TMF, water flow direction difference in the vertical structure and related vertical stratification can influence fish egg transport and retention near spawning habitats. In the present study, fish egg sampling was conducted in surface waters. Previous study in the Shandong Peninsula region have shown that some pelagic fish eggs can gradually ascend and tend to accumulate near the surface within several hours post-spawning (Iseki and Kiyomoto, 1997; Wan *et al*., 2008). These findings support the assumption that surface-collected eggs during daytime surveys reflect recent spawning events and are appropriate for examining the relationship between spawning dynamics and environmental conditions. This may be attributed to the physiological advantages conferred by optimal SST, as temperature directly influences fish egg development, accelerating embryonic growth and improving survival rates (Koenker *et al*., 2018). These hydrodynamic may affect the fish egg distribution, but this was not further explored in the present study and could be addressed in future research.

P. indicus eggs were primarily found in shallow waters, and the GAM results indicated a weak negative correlation between water depth and egg abundance. The higher primary productivity in shallow waters (Wei *et al*., 2016b) may be another important factor contributing to this pattern.

The dynamic oceanographic conditions along the SYS coast and their effects on egg distribution, larval transport, and early recruitment success of nearshore spawning fish are important subjects for future research. A more detailed understanding of the spatiotemporal distribution of fish eggs, reproductive strategies, and early-stage resource replenishment in *P. indicus* is crucial for predicting stock dynamics and for the effective management and protection of fishery resources.

CONCLUSIONS

This study provides a comprehensive analysis of the spatiotemporal distribution of *P. indicus* eggs in the SYS and their environmental drivers. The findings reveal that sea surface temperature (SST) is the most influential factor, with egg occurrence and abundance being positively correlated with SST below 17 °C and negatively correlated above this threshold. The main spawning season occurs between April and July, reaching its peak in May. Egg abundance was highest in nearshore waters, emphasizing the importance of coastal habitats for the early life stages of *P. indicus*. These insights contribute not only to a better understanding of the reproductive ecology but also provide valuable baseline information for anticipating how spawning habitats may shift in response to climate-driven ocean changes. This study therefore provides a scientific basis for the conservation and management of *P. indicus* in the region.

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