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Spatio-Temporal Dynamics of Fish Early-Life Stages and Their Ecological Drivers in Xiangshan Bay, China

Mengya Zhang [1,2,3], Tiejun Li [1,2], Zhouting He [1,2], Yingjun Jiang [3], Dong Wang [1,2,*] and Yuanming Guo [1,2]

[1] Institute of Ocean and Fisheries Research, Zhejiang Ocean University, Zhoushan 316000, China; alanre603@163.com (M.Z.); litiejun1982@126.com (T.L.); hezht513@163.com (Z.H.); 13515806306@163.com (Y.G.)
[2] Zhejiang Marine Fisheries Research Institute, Zhoushan 316000, China
[3] College of Fisheries, Zhejiang Ocean University, Zhoushan 316000, China; 18757175359@163.com
* Correspondence: h01159@zjou.edu.cn

Abstract

To investigate the dynamic characteristics of early fish life stages and their association with environmental factors in Xiangshan Bay, China, two surveys were conducted in the springs of 2023 and 2024 to collect fish eggs and larvae. A total of 21,221 eggs and 10,730 larvae of 23 species belonging to 5 orders and 13 families were collected. Dominant species identified from eggs included *Scomberomorus niphonius*, *Konosirus punctatus*, and *Pennahia argentata*, while dominant species of larvae included *Engraulis japonicus*, *Planiliza haematocheilus*, and *Rhinogobius giurinus*. Species diversity analysis showed that the diversity was higher in spring 2023 (H' = 1.13) but decreased in spring 2024 due to the outbreak of dominant species (H' = 0.86). Cluster analysis and non-metric multidimensional scaling ordination analysis revealed significant regional differentiation in the community structure of fish eggs and larvae between the springs of 2023 and 2024. Mantel test correlation and redundancy analyses indicated that temperature, salinity, dissolved oxygen, and chlorophyll-a concentration were the main environmental factors influencing the distribution of fish eggs and larvae. This study elucidates spatio-temporal patterns and environmental response mechanisms of early fish life stages in Xiangshan Bay, providing scientific support for the conservation and sustainable utilization of fishery resources in the National Fishery Germplasm Resource Reserve.

Keywords: Germplasm Resource Reserve; fish eggs; larvae; species composition; environmental factors

1. Introduction

Egg and larval (juvenile) stages are critical early-life history periods for fish. Fish egg and larval abundance, distribution, and survival not only directly determine the annual recruitment of fish resources but also serve as vital indicators for fishery resource potential and aquatic ecosystem health [1,2]. Individuals at these early stages exhibit significant adaptive changes in ecology, morphology, behavior, and habitat selection. Eggs and larvae are highly sensitive to environmental variability; because they possess limited swimming ability, they cannot effectively avoid adverse conditions, predators, or areas of low prey density. Consequently, natural mortality during these early stages can exceed 99% [3,4]. Therefore, a thorough understanding of spatio-temporal dynamics of early fish life stages and their relationship with environmental factors is crucial for evaluating ecosystem health and developing effective fisheries management strategies [5].

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Xiangshan Bay is one of the three major semi-enclosed bays in Zhejiang Province, China, alongside Sanmen Bay and Yueqing Bay, and is characterized by a relatively stable hydrological environment. It is connected to the open sea through only three waterways and is sheltered from external oceanic disturbances by the Zhoushan Archipelago on its eastern side. This stability offers low-disturbance habitats conducive to the development of early-life stages of fish, making it an important spawning habitat, feeding ground, and migratory corridor for various economically valuable fish species. However, in recent years, fishery resources in Xiangshan Bay have shown a marked decline. High-intensity fishing has caused a sharp decrease in the populations of species such as *Scomberomorus niphonius*, which show catch rates per vessel continuously declining. Meanwhile, severe eutrophication driven by excess inorganic nitrogen and phosphorus [6], combined with environmental pollution characterized by heavy metals such as copper and zinc [7], has altered aquatic community structures. Local studies indicate that these environmental stressors have significantly structured macrobenthic assemblages [8], reflecting broad-scale habitat deterioration and a decline in ecosystem quality. Consequently, the quantity and quality of fish populations have significantly declined. Larval fish are key contributors to fishery resource replenishment and thus are crucial for understanding the changes in fish populations. Thus, studying their distribution in Xiangshan Bay will provide essential data and theoretical support for identifying the mechanisms behind fluctuations of the bay's fishery resources.

Community structure stability is closely tied to the ecological niche differentiation of dominant species. Dominant species, through processes such as regulating resource competition and predator–prey relationships, dominate local species composition and functional characteristics of the community. Fluctuations in abundance of dominant species are often important signals of community succession [9]. In nearshore bay ecosystems, fish community structure is influenced by various environmental factors and exhibits significant spatial heterogeneity. Inshore areas are highly affected by terrestrial inputs and are rich in nutrients but experience substantial environmental fluctuations. Inshore fish communities are dominated by species that are euryhaline, eurythermal, and tolerant to pollution. In contrast, central waters have more stable hydrological conditions and abundant prey organisms. Central waters serve as key spawning grounds for various economically important fish species and show the highest community diversity and abundance. Finally, offshore areas are significantly influenced by open-ocean tides and have high salinity, and their communities are dominated by early-life individuals of eurythermal and migratory species (e.g., Scombridae fish). This three-zone spatial differentiation pattern is an adaptive response of fish to the environmental conditions of different regions [10,11].

The early-life stages of fish are highly sensitive to environmental factors such as temperature, salinity, nutrients, and hydrodynamics [12]. Water temperature is key for regulating the early developmental rate of fish, directly affecting egg incubation periods and larval survival rates. Different species have specific optimal temperature ranges, and abnormal fluctuations in temperature can lead to a reorganization of the early stage fish community structure [13]. Salinity also determines their spatial distribution range by influencing the osmoregulatory capacity of early-life stages. The salinity gradient between nearshore low-salinity areas and offshore high-salinity areas is one of the core factors driving the spatial differentiation of early-stage fish resource communities [14]. The abundance and composition of prey organisms like zooplankton directly affect the feeding success of larvae. Prey scarcity can result in slowed growth and increased mortality rates in larvae, subsequently influencing recruitment [15]. Water depth affects spawning ground selection by altering microenvironmental conditions such as light and current speed. Most fish species tend to spawn in shallow marine areas with depths of 5–15 m to increase

early-stage survival rates [16,17]. Nutrient concentrations (e.g., nitrogen and phosphorus) affect the abundance of prey organisms by regulating phytoplankton growth, thus exerting an indirect regulatory effect on the structure of early fish resource communities [18,19].

Xiangshan Bay serves as a vital spawning ground for numerous economically valuable species. Understanding the interannual variability of these spawning assemblages and their quantitative response to environmental drivers is essential. In this study, we analyze the species composition, spatio-temporal distribution patterns, and diversity characteristics of fish eggs and larvae, based on continuous surveys conducted in the waters of Xiangshan Bay during the springs of 2023 and 2024. Furthermore, we quantify the relationship between the distribution of these early-life stages and key environmental factors. These results are critical for evaluating the efficacy of the National Aquatic Germplasm Resource Conservation Zone and formulating science-based conservation strategies.

2. Materials and Methods

2.1. Overview of the Study Area

Xiangshan Bay, located in the southeastern part of Ningbo City, Zhejiang Province, China, is a narrow, semi-enclosed bay that stretches from inland in the southwest to the ocean in the northeast [20]. The area is characterized by high primary productivity and abundant food resources, making it a crucial "three fields and one corridor" [21] for various economically important fish species. Due to its unique ecological services, Xiangshan Bay was designated a National Aquatic Germplasm Resource Conservation Area for the Blue Spotted Mackerel by the Ministry of Agriculture in 2011 (No. 3, Agricultural Fisheries Development [2011]) to protect the reproductive ecology and the sustainability of germplasm resources of key economic fish species such as *S. niphonius* and *Pampus argenteus* [22].

2.2. Survey Stations and Sampling Methods

The survey area is located within the Xiangshan Bay Germplasm Resource Conservation Area and its adjacent waters in Zhejiang Province. Two surveys for fish eggs and larvae were conducted in April 2023 and April 2024 within the area defined by the coordinates 29.4–29.7° N and 121.5–122.0° E (Figure 1). Simple Random Sampling was used to establish the sampling stations in the surveys, and there were 16 stations in 2023 and 13 stations in 2024. Collection and analysis of fish eggs and larvae followed guidelines outlined in the Marine Survey Standards [23] and Marine Monitoring Standards [24]. Fish eggs and larvae were collected by a macroplankton net (mouth diameter 50 cm, mouth area 0.196 m^2, mesh size 0.505 mm). At each survey station, the net was towed horizontally at the surface against the current at an average vessel speed of 3 knots for a duration of 10 min, and a calibrated flow meter was mounted in the net opening to capture the filtered water volume. Vertical profiles of temperature, salinity, and pH were simultaneously recorded from an RBRconcerto^3 C.T.D instrument (RBR, Ottawa, ON, Canada). For the purpose of this study, surface environmental variables were calculated as the average values within the upper 3 m of the water column.

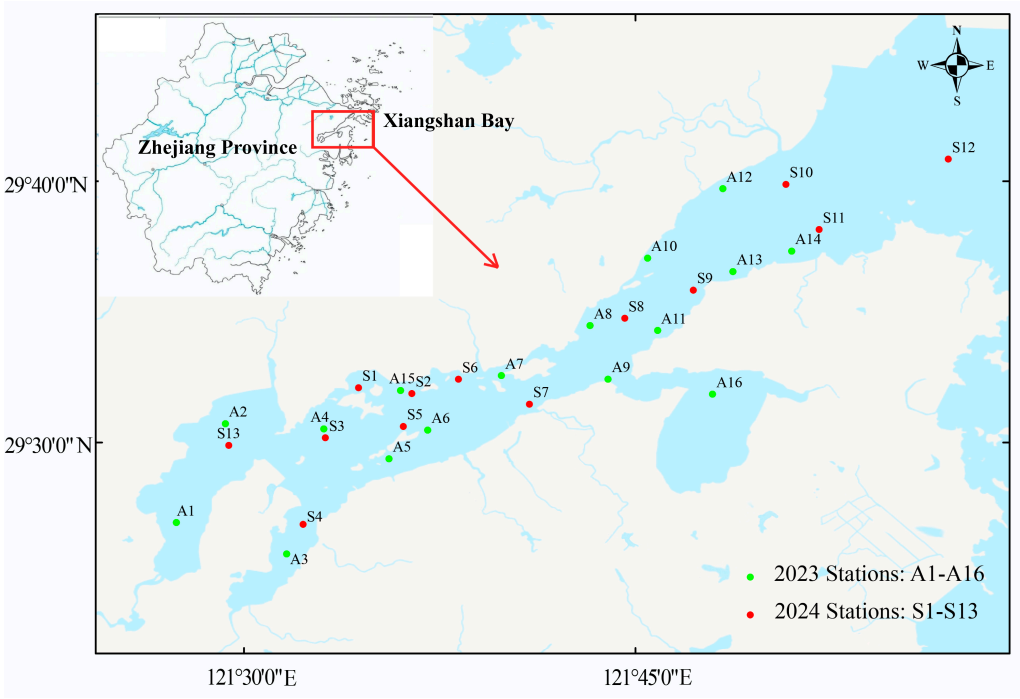

Figure 1. Map of the Survey Sampling Stations in Xiangshan Bay in Spring 2023 and Spring 2024.

2.3. Sample Processing and Analysis

Collected fish eggs and larvae were fixed with 5% formaldehyde (Shenyang, China) on site and stored in wide-mouth bottles. Impurities and non-target organisms were removed in the laboratory and samples were taxonomically identified and counted under a stereomicroscope (Leica Microsystems, Wetzlar, Germany). Species identification was mainly conducted with reference to the following publications: *Fish Eggs and Larvae in the Coastal Waters of China*, *Fish Eggs, Larvae and Juveniles in the Coastal Waters of China and Adjacent Areas*, *Atlas of Early Stage Fishes in Japan*, *Marine Fishes of Zhejiang*, and *Fishes of the Yangtze Estuary* [25–29]. The classification of fish egg types, thermal adaptation traits, and ecological types of larvae was primarily based on *Iconography of Fishes in the Yellow Sea and Bohai Sea* and *Fishery Resources of Fujian Province* [28–31]. The quantitative statistics of fish eggs and larval fish were made up of the number of individuals obtained at each sampling station, with the units expressed as eggs and individuals, respectively.

2.4. Data Statistical Analysis

2.4.1. Egg and Larval Fish Density

The distribution density of fish eggs or larval fish per unit volume of seawater is calculated using the following formula [23]:

$$Ga = \frac{Na}{S \times L \times C} \quad (1)$$

where

Ga represents the resource density of fish eggs or larval fish, with units of individuals per cubic meter (ind/m^3);

Na is the number of fish eggs or larval fish, with units of individuals (ind);

S is the actual mouth area of the sampling net, in square meters (m^2);

L is the number of rotations of the flowmeter;

C is the flowmeter calibration value (C = 0.3).

2.4.2. Calculation of Dominant Species

The Index of Relative Importance (IRI) was used to calculate the dominant species of fish eggs and larval fish [32]:

$$IRI = N\% \times F\% \times 10^4 \quad (2)$$

where

$N\%$ represents the proportion of each fish egg or larval fish resource density relative to the total resource density;

$F\%$ represents the frequency of occurrence of each fish egg or larval fish;

Species with $IRI > 1000$ are considered dominant species, while species with $IRI = 100 - 1000$ are considered important species [33].

2.4.3. Diversity Indices

The Margalef Species Richness Index [34], Shannon-Wiener Diversity Index [35], and Pielou Evenness Index [36] were used to analyze the variations in larval fish diversity.

The Margalef Species Richness Index is:

$$D = \frac{(S-1)}{\ln N} \quad (3)$$

The Shannon-Wiener Species Diversity Index is:

$$H' = -\sum P_i \ln P_i \quad (4)$$

The Pielou Evenness Index is:

$$J' = \frac{H'}{\ln S} \quad (5)$$

where

S represents the number of larval fish species;

P_i is the proportion of the i-th larval fish species relative to the total number of individuals;

N is the total number of larval fish individuals.

2.4.4. Structure Analysis

The community structure of fish eggs and larval fish was analyzed using Primer 5.0 software. Data were subjected to a fourth-root transformation to mitigate the impact of extreme values on analyses. Hierarchical cluster analysis using unweighted pair group method with arithmetic mean (UPGMA) and non-metric multidimensional scaling (NMDS) were performed based on the Bray–Curtis similarity matrix. The effectiveness of the NMDS ordination was evaluated using the stress coefficient (Stress): a Stress value ≤ 0.05 indicates excellent NMDS ordination, $0.05 < \text{Stress} \leq 0.1$ suggests the ordination is generally reliable, $0.1 < \text{Stress} < 0.2$ indicates a moderate level of reliability, and Stress ≥ 0.2 implies the ordination lacks interpretative significance [37]. Analysis of similarity (ANOSIM), a non-parametric multivariate method, was also applied and key contributing species were quantified through SIMPER analysis.

2.4.5. Environmental Factor Analysis

A species data matrix was constructed using the resource densities of fish eggs and larvae with an occurrence frequency $\geq 2\%$ in the survey months. To eliminate the differences in orders of magnitude in resource densities across species, a log(x + 1) transformation was applied to the density data for all fish eggs and larval fish [38]. To meet the assumption of normal distribution, environmental variables including Sea Surface Temperature (SST), Sea Surface Salinity (SSS), Dissolved Oxygen (DO), Chlorophyll-a (Chl.a), Water Depth (Dep), and

Total Suspended Solids (TSS) were subjected to log(x + 1) transformation [39,40]. Spatial predictors (Longitude [Lon] and Latitude [Lat]) and pH were used in their original scale without transformation. A Mantel test was conducted using the R package linkET (version 0.0.7.4) in R (version 4.3.2) to analyze the correlation between community composition and environmental factors. Additionally, the relationship between species abundance and environmental factors was further explored using Canoco 5.0 software to identify the impact of different environmental factors on distribution. Prior to ordination analysis, a detrended correspondence analysis (DCA) was performed based on species abundance data. The appropriate ordination method was selected based on the gradient length (LGA). Redundancy analysis (RDA) was used when LGA < 3, canonical correspondence analysis (CCA) was applied when LGA > 4, and either method could be employed when 3 < LGA < 4. In this study, RDA was ultimately used to quantify the response of different fish egg and larval fish species to environmental factors [41].

3. Results

3.1. Species Composition and Abundance

A total of 21,221 fish eggs and 10,730 larval fish were collected during the two surveys, representing 5 orders, 13 families, and 23 species (Table S1). In 2023, 7764 fish eggs and 9594 larval fish were collected, representing 4 orders and 9 families. Among these, the most diverse order was Perciformes, with 5 families identified, Clupeiformes with 2 families, Scorpaeniformes with 1 family, and Mugiliformes with 1 family. In 2024, 13,457 fish eggs and 1136 larval fish were collected, representing 4 orders and 9 families. Perciformes was again the most diverse order with 4 families identified, followed by Clupeiformes with 2 families, Pleuronectiformes with 2 families, and Mugiliformes with 1 family. Species such as *S. niphonius*, *Konosirus punctatus*, and *Planiliza haematocheilus* were collected in both the springs of 2023 and 2024 (Figure 2).

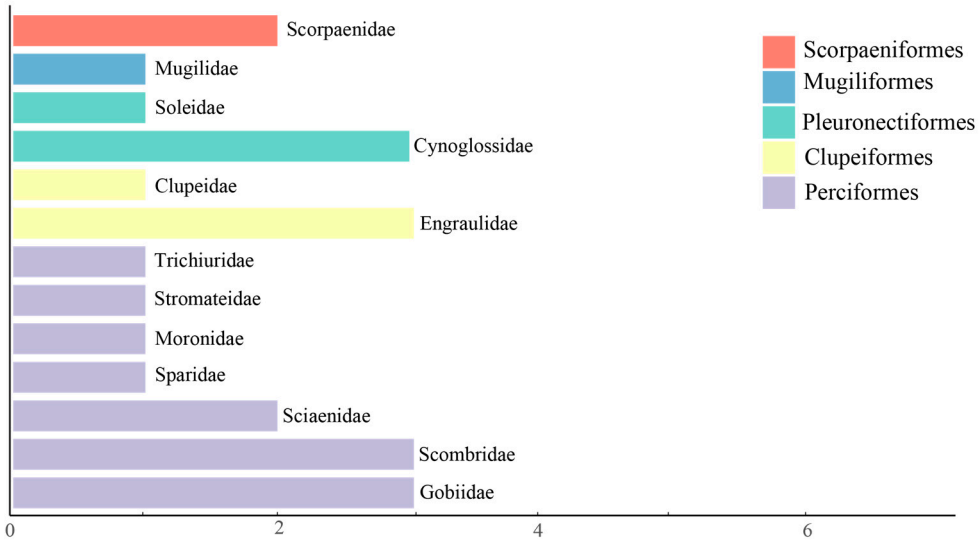

Figure 2. Distribution of the number of larval fish species in different families (grouped by order).

Larval fish in Xiangshan Bay were predominantly warm-temperate species, including *S. niphonius*, *Engraulis japonicus*, and *Coilia mystus*. The coastal waters of Xiangshan Bay were mainly characterized by benthic and mid-lower larval fish, such as *Rhinogobius giurinus*, *Trichiurus lepturus*, and *P. haematocheilus* (Table S1).

3.2. Analysis of Dominant Species Variation and Species Diversity

In 2023, the dominant species of fish eggs were *K. punctatus*, *S. niphonius*, and *T. lepturus*, while the dominant larval fish species were *E. japonicus* and *P. haematocheilus*. In

2024, the dominant fish egg species were *K. punctatus* and *Pennahia argentata*, with the dominant larval fish species being *R. giurinus* and Engraulidae sp. Meanwhile, the fish species diversity index (H') in the study area decreased from 1.13 in spring 2023 to 0.86 in spring 2024. This decrease is closely associated with the outbreak of dominant species such as *K. punctatus* and *P. argentata*. The evenness index (J') showed no significant interannual difference ($p > 0.05$), ranging from 0.63 in 2023 to 0.62 in 2024. This indicates that the community evenness remained in a stable state between the two years. However, the richness index (D) declined sharply from 0.79 in 2023 to 0.54 in 2024, showing a significant difference in community richness between the years (Figure 3).

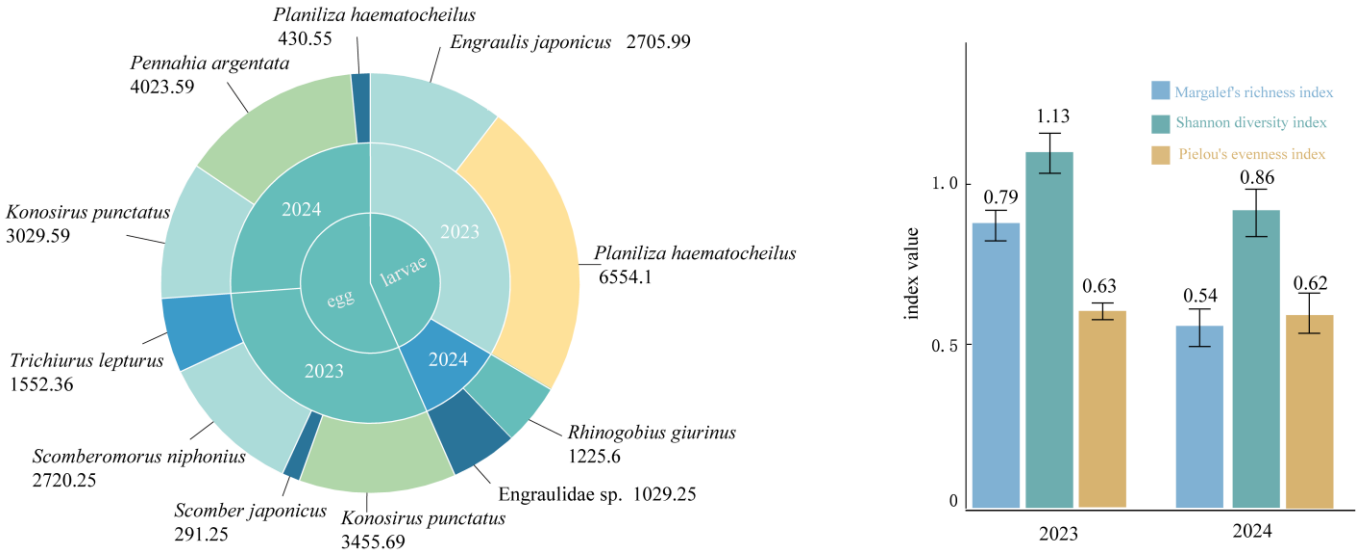

Figure 3. Dominant species (with numbers representing the Index of Relative Importance, IRI) and species diversity indices of fish eggs and larval fish in Xiangshan Bay (2023–2024).

3.3. Spatial Distribution of Fish Eggs and Larval Fish

A total of 7764 fish eggs and 9594 larval fish were collected from all 16 stations surveyed in 2023. The three stations with the highest fish egg counts were sites 9, 16, and 6 (Figure 4), with 1083, 805, and 792 fish eggs captured, accounting for 13.9%, 10.4%, and 10.2% of the total fish eggs collected in 2023. The highest fish egg density reached 1.9 ind./m^3, while the lowest was 0.14 ind./m^3. The average density was 1 ind./m^3. The species with the highest egg counts in 2023 included *K. punctatus*, *T. lepturus*, and *S. niphonius*. Larval fish counts in the survey areas ranged from 4 to 2385 individuals. The three stations with the highest larval fish catches from the horizontal tow nets were sites 9, 6, and 11, with 2385, 1766, and 1499 individuals captured, accounting for 24.9%, 18.4%, and 15.6% of the total larval fish caught that year. The highest larval fish density was 3.97 ind./m^3, while the lowest was 0.01 ind./m^3. The species with the highest larval fish counts were *P. haematocheilus* and *E. japonicus* (Figure 4).

In 2024, 13 sampling stations were surveyed, yielding 13,457 fish eggs and 1136 larval fish. Fish eggs were collected at 11 of the stations, with an appearance frequency of 84.6%. The three stations with the highest egg counts were Stations 8, 7, and 13, which captured 3372, 2100, and 2012 eggs, accounting for 25.0%, 15.6%, and 15.0% of the total egg count in 2024. The highest egg density recorded was 4.33 ind./m^3, with an average density of 1.45 ind./m^3. The most abundant egg species were *K. punctatus* and *P. argentata*. The number of larval fish in 2024 surveys ranged from 0 to 713 individuals. The three stations with the highest larval fish counts were Stations 9, 11, and 10, with 713, 186, and 128 larvae captured. The highest

larval fish density reached 0.95 ind./m^3. The species with the highest larval fish numbers were Engraulidae sp. and *R. giurinus* (Figure 4).

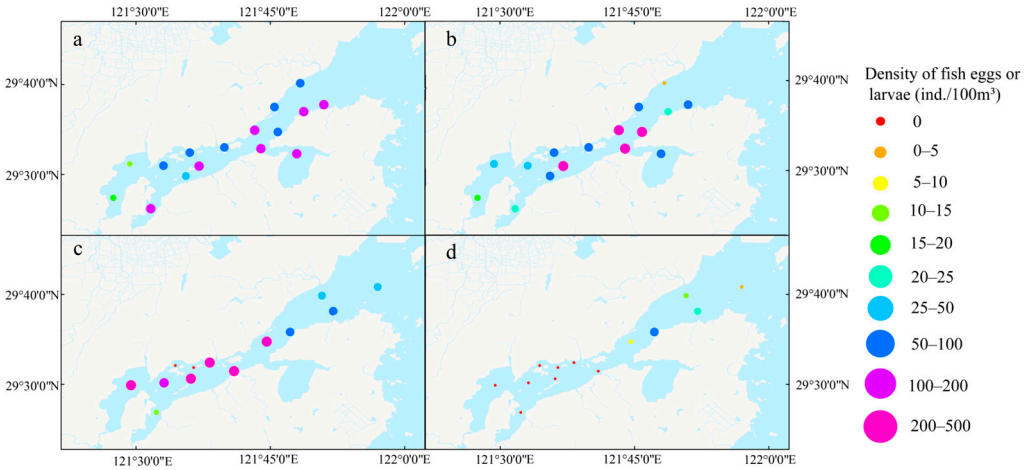

Figure 4. Spatiotemporal Distribution of Fish Egg and Larval Fish Resource Densities in Xiangshan Bay. (**a**) Horizontal Tow Net Fish Eggs in 2023; (**b**) Horizontal Tow Net Larval Fish in 2023; (**c**) Horizontal Tow Net Fish Eggs in 2024; (**d**) Horizontal Tow Net Larval Fish in 2024.

3.4. Community Structure Analysis

The fish egg and larval fish counts collected from various stations in Xiangshan Bay were analyzed using Primer 5.0 for similarity clustering and NMDS tests. To minimize statistical errors, stations 1 and 2 in 2024 were excluded from both egg and larvae analysis as neither fish eggs nor larvae were collected at these stations. The community structure of both fish eggs and larval fish during the springs of 2023 and 2024 exhibited significant grouping patterns, with a strong correlation between site distribution and community grouping.

The results of the clustering analysis (Figure 5) show that in 2023, all stations can be divided into three groups (A, B, and C) with a similarity index of 58.69%. The ANOSIM test revealed significant differences among the three groups (Global $R = 0.71$, $p = 0.001$), indicating distinct regional differences in the community structure of fish eggs and larval fish in 2023. The NMDS ordination stress coefficient (stress < 0.2) suggests that the NMDS plot provides a good representation. The SIMPER analysis indicated that Group A is primarily located along the nearshore coastal area, with the dominant species being *Scomber japonicus* and *S. niphonius*, contributing 72.44% cumulatively. Group B is mainly found in the western nearshore area of the bay, with the key species being *E. japonicus*, *K. punctatus*, and *T. lepturus*, contributing 67.26% in total. Among these, *E. japonicus* is the dominant species, contributing 31.69% within the group. Group C is mainly located in the central area of the study zone, with species such as *P. haematocheilus*, *K. punctatus*, *E. japonicus*, and *S. niphonius* contributing 84.08% cumulatively. The average dissimilarity between Group A and Group B is 51.95%, primarily due to the absolute dominance of *S. niphonius* and *S. japonicus* in Group A (with an abundance of 316 for *S. japonicus*, far exceeding the abundance of 26.2 in Group B). Further, the absence of *E. japonicus*, a core species in Group B, from Group A and the dominance of *T. lepturus*, in Group B contributes to the observed differences. The dissimilarity between Group A and Group C is 52.58%, mainly because *P. haematocheilus*, *K. punctatus*, and *E. japonicus* dominate Group C, whereas they are less abundant in Group A. The average dissimilarity between Group B and Group C is 41.31%, with the difference mainly attributed to the dominance of *P. haematocheilus*, *K. punctatus*, and *S. niphonius* in Group C.

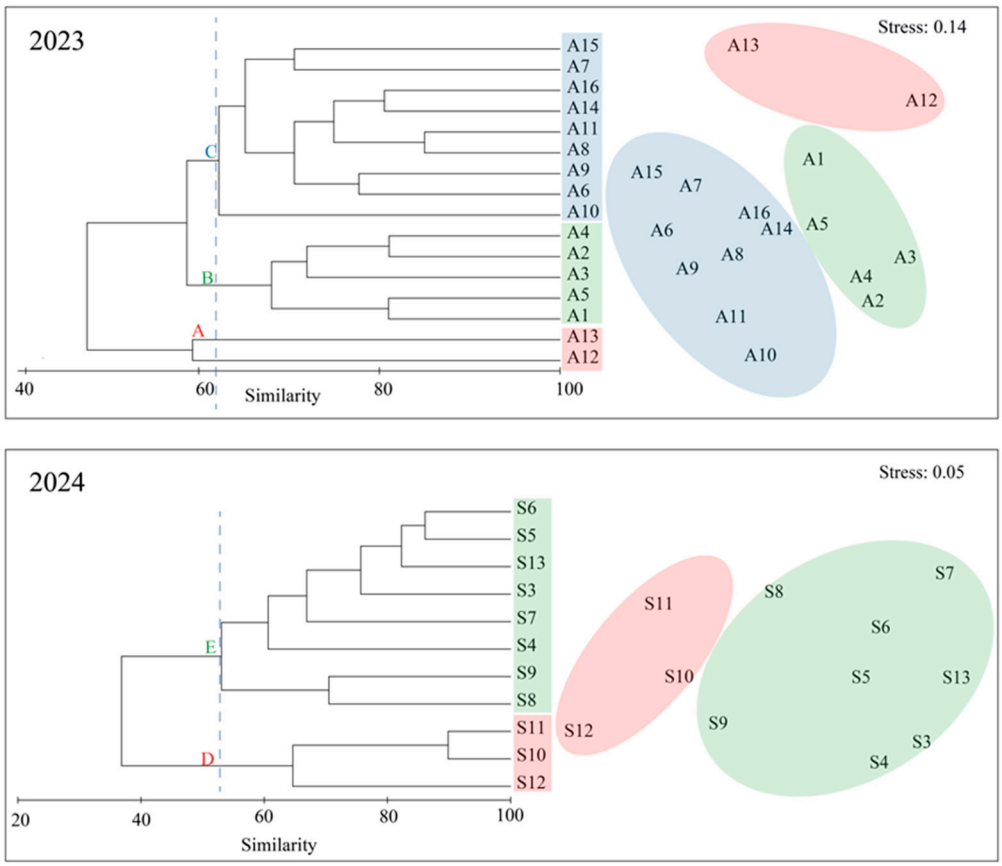

Figure 5. Cluster analysis and NMDS ordination of fish egg and larval fish survey stations in Xiangshan Bay during 2023–2024.

The cluster analysis results (Figure 5) indicate that all stations in 2024 can be divided into two groups, D and E, based on a similarity index of 51.0%. The similarity test (ANOSIM) reveals a borderline significant difference between the two groups (Global $R = 0.849$, $p = 0.06$). The NMDS ordination plot stress coefficient is < 0.2, indicating that the NMDS plot has good representativeness. SIMPER analysis shows that Group D is primarily located in the nearshore area of Xiangshan Bay, with the main contributing species being *P. haematocheilus*, *R. giurinus*, and *P. argentata*, which together account for 78.34% of the cumulative contribution of species. Group E is mainly distributed in the central and nearshore areas of the study area, where *P. argentata* and *K. punctatus* dominate, with a cumulative contribution rate of 92.24%. Community structure analysis shows significant ecological differentiation between Groups D and E, with a dissimilarity of 73.05%. This is reflected in the inverted species abundance gradient: the abundance of *P. argentata* in Group E (789.88) is 29.6 times that in Group D (26.67), while the abundance of *P. haematocheilus* in Group D (336.67) is 36.1 times that in Group E (9.38).

3.5. Analysis of Environmental Factor

Environmental conditions in Xiangshan Bay exhibited significant interannual variability (Table 1). Statistical analyses revealed that SST, SSS, and chlorophyll-a concentrations were significantly lower in 2024 compared to 2023 ($p < 0.05$). In contrast, TSS and COD were significantly higher in 2024 ($p < 0.05$). No statistically significant differences were observed for pH, Dep, or DO between the two years ($p > 0.05$).

Table 1. Environmental variables in Xiangshan Bay during the springs of 2023 and 2024.

Environmental Variables	2023 (Mean ± SD)	2024 (Mean ± SD)	*t*-Value	*p*-Value
Sea Surface Temperature (°C)	17.77 ± 1.94	14.35 ± 0.94	6.072	<0.001
Sea Surface Salinity (‰)	27.41 ± 0.96	24.42 ± 0.78	8.889	<0.001
Chlorophyll-a (μg/L)	4.67 ± 3.69	0.98 ± 0.31	4.044	0.001
Total Suspended Solids (mg/L)	18.36 ± 12.95	84.82 ± 93.89	−2.332	0.041
COD (mg/L)	0.70 ± 0.15	0.83 ± 0.10	−2.715	0.012
pH	8.03 ± 0.06	8.07 ± 0.05	−1.967	0.061
Water Depth (m)	13.29 ± 6.46	16.72 ± 7.49	−1.234	0.232
Dissolved Oxygen (mg/L)	9.43 ± 0.28	9.45 ± 0.59	−0.084	0.935

The results of the Mantel test analysis (Figure 6) show that, in 2023, the distribution of fish eggs was significantly positively correlated with Dep ($p < 0.05$), while the distribution of larval fish was significantly positively correlated with Lat and pH ($p < 0.01$). In 2024, the distribution of fish eggs was significantly positively correlated with SST, SSS, TSS, Lon and Lat ($p < 0.01$), while the distribution of larval fish was significantly positively correlated with Dep and TSS ($p < 0.05$), and highly significantly positively correlated with SST, SSS, DO, as well as Lon and Lat ($p < 0.01$).

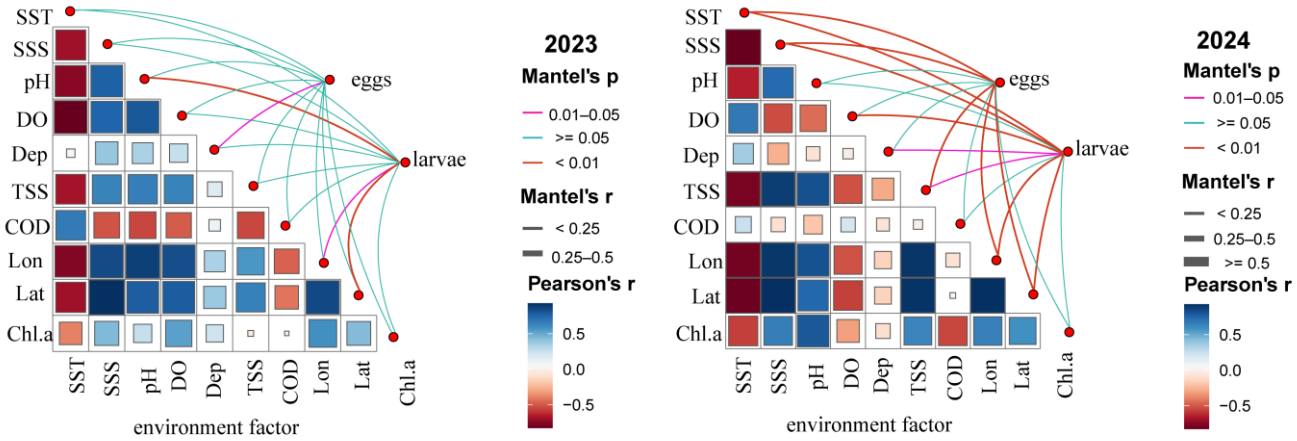

Figure 6. Correlation Analysis Between Fish Eggs, Larval Fish and Environmental Factors (2023–2024).

In 2023, Lon was excluded due to high multicollinearity (VIF > 10). The RDA results indicated that five environmental factors, selected via forward selection with Monte Carlo permutation tests, explained 58.9% of the variance in the relationship between fish egg and larval fish species and environmental conditions (Figure 7). The eigenvalues of the first and second RDA axes were 0.2629 and 0.1321, respectively, with correlation coefficients of 0.8619 and 0.7677 with environmental factors. The Monte Carlo permutation test indicated that both the overall model and the separation along the first canonical axis were statistically significant (First axis: $F = 3.6$, $p = 0.044$; All axes: $F = 1.9$, $p = 0.026$). The primary environmental factors influencing the distribution of fish eggs and larval fish in Xiangshan Bay were Dep, SSS, and DO. The first axis was negatively correlated with Dep, SSS, and DO, while the second axis was positively correlated with Lat, SSS, and Dep. The results also indicated that the distributions of *S. niphonius* and *P. haematocheilus* were positively correlated with chlorophyll-a and Dep and influenced by SSS and DO. Conversely, the distributions of *T. lepturus* and *E. japonicus* showed a negative correlation with SSS, chlorophyll-a, DO, and Dep.

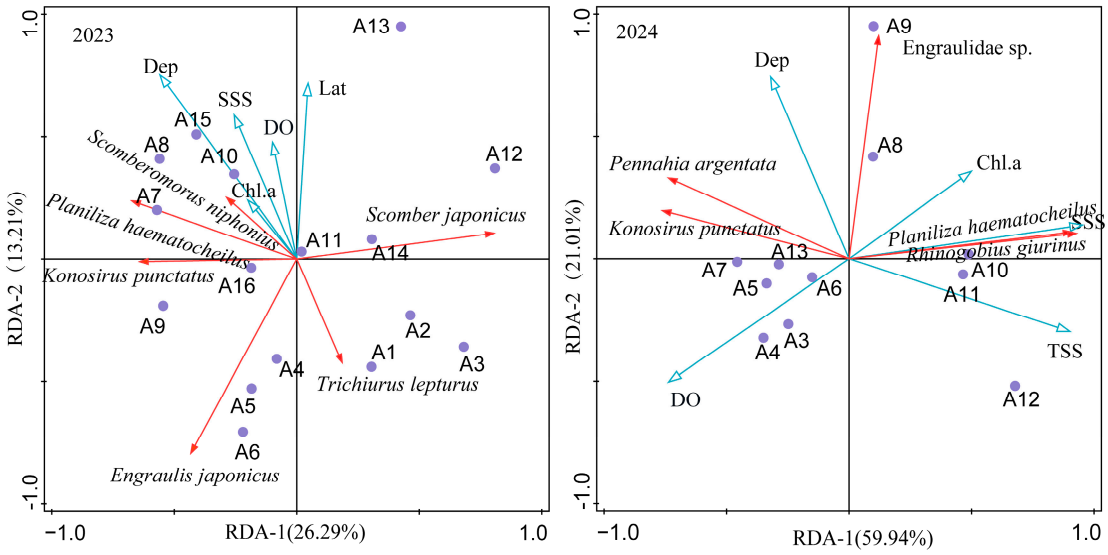

Figure 7. Redundancy Analysis (RDA) of Fish Eggs, Larval-Fish and Environmental Factors.

In the collinearity analysis for 2024, SST, Lon, and Lat were excluded due to high multicollinearity. The RDA results indicated that five environmental factors, selected via forward selection with Monte Carlo permutation tests, explained 81.6% of the variance in the relationship between fish egg and larval fish species and environmental variables (Figure 7). The eigenvalues for the first axis (RDA-1) and the second axis (RDA-2) were 0.5994 and 0.2101, with correlations to the environmental factors of 0.9499 and 0.9288. The Monte Carlo permutation test indicated that both the overall model and the separation along the first canonical axis were statistically significant (First axis: $F = 6.6$, $p = 0.018$; All axes: $F = 4.4$, $p = 0.002$). The primary environmental factors influencing the distribution of fish eggs and larval fish in Xiangshan Bay included SSS, Dep, DO, chlorophyll-a, and TSS. On the first ordination axis, SSS and TSS were positively correlated, while Dep and DO were negatively correlated. On the second ordination axis, Dep, SSS, and chlorophyll-a were positively correlated, while TSS and DO were negatively correlated. The species *P. haematocheilus* and *R. giurinus* showed a positive correlation with TSS and SSS, and a negative correlation with DO and Dep. The Engraulidae sp. were primarily influenced by Dep and chlorophyll-a. *P. argentata* and *K. punctatus* exhibited a positive correlation with Dep and DO, and a negative correlation with TSS, SSS, and chlorophyll-a.

4. Discussion

4.1. Composition and Spatiotemporal Distribution Characteristics of Fish Eggs and Larvae

This study was conducted in Xiangshan Bay with two research cruises focusing on the collection of fish eggs and larvae. A total of 21,221 fish eggs and 10,730 larvae were collected, identified as belonging to 5 orders, 13 families, and 23 species (Table S1). Perciformes was the most species-rich order, with 7 families and 12 species, accounting for 52.2% of the total species. This result is similar to previous findings in the Xiangshan Bay area, where Perciformes represented 53.0% (18 species), as well as in the neighboring Oujiang River estuary, where it accounted for 58% of the catch [42,43]. The dominant fish egg species included *S. niphonius*, *K. punctatus*, *P. argentata*, and *T. lepturus*, while the dominant larval species were *E. japonicus*, *P. haematocheilus*, and *R. giurinus*. This composition is very similar to survey results from adjacent Sanmen Bay waters, where Perciformes also dominated, representing 43% of the assemblage [44].

Fish eggs and larval fish collected during the two surveys were dominated overall by warm-temperate and warm-water species. This phenomenon is closely related to the

geographical and hydrological conditions of Xiangshan Bay. As a typical semi-enclosed bay, it exhibits minor salinity fluctuations and is located in a warm-temperate marine area influenced by a subtropical monsoon climate. Meanwhile, under the continuous influence of the Taiwan Warm Current and Kuroshio Current, high-temperature oceanic water continuously flows into the bay providing a suitable habitat and breeding environment for warm-temperate and warm-water fish species [45]. Xiangshan Bay has higher water temperatures and more stable salinity than the adjacent Hangzhou Bay, resulting in significant differences in larval fish community structure between the two regions. Hangzhou Bay is affected by diluted water from the Yangtze River and has low and highly fluctuating salinity resulting in the estuarine fish Coilia mysticetus as the dominant group. In contrast, Xiangshan Bay is dominated by warm-temperate fish including *K. punctatus* and gobiids [46–48]. Previous studies have shown that warm-temperate and warm-water species account for more than 80% of the larval fish in Xiangshan Bay, and their distribution is significantly correlated with water temperature ($p < 0.01$). For instance, typical warm-temperate and warm-water species such as *K. punctatus* (25.8%), *Chaeturichthys stigmatias* (23.9%), and *P. haematocheilus* (19.2%) were identified as dominant species in 2015 surveys, which further supports the regional ecological characteristics observed in this study [42].

There are significant interannual differences in the high-density areas of fish eggs and larvae in Xiangshan Bay. In the spring of 2023, high-density zones for both fish eggs and larvae exhibited a relatively concentrated distribution, with the high-density area of larvae being more concentrated in nearshore and central bay waters. In the spring of 2024, a significant spatial shift occurred in the high-density zones of fish eggs, and the distribution of the high-density area for larvae also differed from 2023. However, in both years, high-density zones of fish eggs and larvae in the study area still showed similar spatial correlation in the central and nearshore regions (Figure 4).

Xiangshan Bay is an important spawning ground and early developmental habitat for fish. Lou et al. [49] showed that in the spring, fish eggs were more concentrated in the nearshore and central region, while larvae were more concentrated in the central stations of the bay. In this study, the distribution of fish eggs in spring was relatively wide, but larvae were more inclined to aggregate in nearshore and mid-bay areas. This is mainly related to the reproductive habits and early developmental needs of dominant species such as *S. niphonius* and *K. punctatus*, whose peak spawning periods occur in the spring. Song et al. [50] found that *S. niphonius* eggs in Xiangshan Bay appeared from early April to early June, with a peak spawning period from mid-April to early May. *S. niphonius* yolk-sac larvae and pre-flexion larvae were mostly found in deeper waters, while post-flexion larvae and juveniles tended to be distributed in shallower nearshore waters. This is mainly related to the feeding habits of *S. niphonius* whose larvae and juveniles are predatory and primarily feed on fish larvae (98.6% of their diet), with *K. punctatus*, gobiids, and *P. haematocheilus* being their core prey. This makes them highly dependent on the abundance of prey organisms [51]. The nearshore areas of the East China Sea serve as spawning and nursery grounds for prey fish such as *K. punctatus*, gobiids, and *P. haematocheilus*, providing rich prey resources in the spring [52–54].

4.2. Community Structure Characteristics of Fish Eggs and Larvae

Since the mid-20th century, the structure of fisheries resources in the East China Sea has shown a trend of shifting towards smaller, lower-trophic level fish species [55]. Overfishing has led to a sharp decline in the population of high-trophic level fish, altering the flow of energy and nutrient cycling within these ecosystems and creating more ecological space and resources for smaller, lower-trophic level species [56]. This study reveals that in the waters of Xiangshan Bay, the dominant species of fish eggs and larval fish are mainly

mid- to small-sized fish such as *E. japonicus*, *P. haematocheilus*, and *R. giurinus*. In contrast, traditional high-trophic level economically important fish species such as *Larimichthys crocea* and *Larimichthys polyactis* have relatively low abundances and constitute a small portion of the fish community. The reduction in high-trophic level fish is likely closely related to increased fishing pressure and environmental changes in the bay in recent years, including factors such as nutrient input and fluctuations in water temperature. Cluster and NMDS ordination analyses revealed that the community structure of fish eggs and larvae in Xiangshan Bay exhibited significant interannual differentiation (Figure 5). The core dominant species were mainly warm-temperate and warm-water taxa, which are highly sensitive to environmental changes such as SST and SSS. Their compositional turnover and abundance fluctuations directly drove the interannual differentiation of the community [57]. The ecological grouping of the community showed a distinct trend of functional differentiation: in 2023, mid-upper layer fish dominated, with high species richness and density in the concentrated distribution areas of dominant species; in 2024, the community exhibited a significant tendency toward mid-lower and benthic habitats, and the abundance proportion of relevant species increased remarkably. The community's adaptive strategies to the Xiangshan Bay habitat have undergone a significant shift with functional differentiation being primarily driven by the ecological niche adaptation of dominant species and environmental selection. Further analysis with environmental factors indicates that the interannual turnover of dominant species is highly coupled with the synergistic variation in SSS, SST, TSS, and chlorophyll-a content. This synergy represents the core driving mechanism behind community functional differentiation. In 2023, the dominant species' distribution was concentrated in areas exhibiting high stability and high productivity characteristics. In these areas, SSS remained stable between 27.0 and 28.4‰, SST was within the optimal range of 16–19 °C, the average chlorophyll-a concentration reached 4.67 μg/L, and the TSS concentrations at most stations were below 30 mg/L. The high chlorophyll-a content indicates abundant phytoplankton biomass, which provides a rich food source for zooplankton. Meanwhile, the favorable SST and SSS conditions ensured high egg hatching rates and larval fish survival, supporting the reproductive needs of mid-upper layer filter-feeding and zooplankton-feeding species such as *K. punctatus*, *S. niphonius*, and *E. japonicus*, making them the dominant groups in the community [58,59].

In 2024, the environmental conditions in the study area underwent significant changes compared to the previous year. Specifically, SSS, SST, and chlorophyll-a concentrations decreased significantly, while the concentration of TSS increased substantially. These low-SSS, low-SST, high-TSS, and low-productivity environmental conditions significantly constrained the early development of mid-upper layer species. The eggs and larvae of mid-upper layer fish species are mostly pelagic, and high-TSS concentrations can lead to reduced feeding efficiency and even suffocation or death. Additionally, the low-SSS and low-SST conditions fall outside their optimal survival range. In contrast, species from the mid-lower layer or benthic layer, such as *P. argentata*, Cynoglossidae species, and *R. giurinus*, exhibit stronger environmental adaptability with increased tolerance for low-SSS and low-SST conditions. Moreover, high-TSS environments create lower visibility that reduces predation risk. These species also have a diet comprising benthic detritus or small benthic organisms, making them less affected by the decline in plankton biomass [60,61]. As a result, mid-lower and benthic layer species became dominant groups under the shifted environmental conditions in 2024.

4.3. Correlation Between Fish Eggs, Larval Fish, and Environmental Factors

The distribution patterns of fish during their early developmental stages are coregulated by multiple environmental factors. Studies from different marine regions have

confirmed that temperature, salinity, chlorophyll-a, and total suspended particles are key factors influencing community structure [62–64]. In spring, optimal temperatures enhance the embryonic metabolic rate of fish eggs and improve the feeding activity and swimming abilities of larval fish, thus providing a physiological foundation for their early growth and development [65]. Salinity directly affects the maturation of reproductive cells, fertilization rates, and enzyme activity involved in embryo hatching by regulating the osmotic pressure balance in fish eggs and larval fish [66]. At the larval stage, fish have underdeveloped respiratory systems and much lower tolerance to hypoxic environments than adult fish. Sufficient dissolved oxygen can ensure the normal performance of their basic life activities, while also enhancing feeding conversion rate and stress resistance [67,68]. As an important indicator of phytoplankton biomass, increased chlorophyll-a content signifies a richer food base, which is conducive to the growth and survival of larval fish [69]. During the survey, some areas of Xiangshan Bay were influenced by land-based inputs, causing a gradual trend toward eutrophication [70].

As a typical direct gradient analysis method, redundancy analysis (RDA) fundamentally involves regressing each computational step against environmental variables to quantitatively elucidate the coupling relationships between fish community structure and environmental factors [71]. In this study, RDA results indicated that fish egg distribution was strongly associated with chlorophyll-a and TSS, reflecting their close relationship with the early-stage dietary requirements and survival strategies of fish. Specifically, the eggs of mid-upper layer species, such as *S. niphonius*, *S. japonicus*, *K. punctatus*, and Engraulidae sp., showed higher correlations with chlorophyll-a, which is a key indicator of phytoplankton biomass and directly reflects the potential availability of first-feeding prey (e.g., zooplankton larvae). Given that eggs rapidly transition to the larval stage post-hatching and require timely and suitable food, these species tend to concentrate in areas with optimal chlorophyll-a levels that support subsequent larval feeding [72,73].

Conversely, the eggs of mid-lower or benthic layer species, such as *P. haematocheilus*, *P. argentata*, and *R. giurinus*, were influenced by TSS. TSS exerts a complex, dual ecological effect on fish early-life stages. Moderate levels can provide essential physical shelter, enhancing survival probability by reducing visual detection by predators. Additionally, TSS can adsorb nutrients from the water column, supporting phytoplankton growth and indirectly optimizing prey distribution [74]. However, excessive concentrations of TSS can be detrimental. High turbidity may impair the visual feeding efficiency of larvae and cause mechanical damage to delicate gill tissues, thereby negatively impacting their growth and survival [75,76]. For larvae, deeper areas generally maintain more stable thermal conditions, mitigating physiological stress from extreme temperature fluctuations. Additionally, lower hydrodynamic disturbance in deeper waters ensures more uniform prey distribution and lower predator densities, providing safer nursery habitats [77].

5. Conclusions

This study reveals the dynamic changes in early fish resources and their environmental driving forces in Xiangshan Bay during spring. The results show that the community of fish eggs and larval fish in this water area is dominated by warm-temperate species but exhibits significant interannual turnover. In 2023, mid-upper layer fish such as *S. niphonius* and *E. japonicus* were the dominant species, while in 2024, the dominant species shifted to mid-lower and benthic fish including *P. argentata* and *R. giurinus*, accompanied by a decline in species diversity. SSS, DO, and chlorophyll-a are the main positive factors affecting community distribution, while high TSS concentration has a significant negative impact on pelagic species and is an important environmental driver leading to the benthic shift in community structure in 2024. Based on these findings, adaptive management strategies are

recommended, including strictly regulating coastal engineering activities (e.g., dredging) during critical spawning periods to prevent harmful turbidity levels. Furthermore, the significant interannual environmental variations observed underscore the necessity of long-term monitoring to adjust conservation measures in response to extreme hydrological fluctuations. The findings of this study clarify the regulatory role of environmental factor fluctuations in the fish recruitment process of estuarine bays, providing a scientific basis for evaluating the ecological functions of the *S. niphonius* National Aquatic Germplasm Resource Reserve and ensuring the sustainable conservation of fishery resources.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d18020113/s1, Table S1: Species Composition of Fish Eggs and Larval Fish in Xiangshan Bay (2023–2024).

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