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Community Dynamics of Fish Larvae in Coastal Zhejiang: Seasonal Variations in Spatiotemporal Distribution and Environmental Driving Factors

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Abstract: The coastal waters of Zhejiang feature a complex aquatic environment and abundant biological resources, creating an ideal habitat for various fish species. However, the systematic monitoring of fish larvae in these offshore waters is limited. This study collected 24,232 fish larvae using large plankton nets during April and November 2022, as well as February and July 2023, and identified 93 species, primarily warm-temperate and warm-water species, with a peak occurrence in summer. The dominant species include *Larimichthys croceus*, *Sebastiscus marmoratus*, *Lateolabrax japonicus*, and *Odontamblyopus lacepedii*, among others, and these species exhibit frequent seasonal changes. Fish larvae are typically found to be aggregated along estuaries and bays in spring, autumn, and summer, while in winter, they tend to shift towards areas near the boundaries of motor trawler fisheries areas. Our cluster analysis revealed spatial heterogeneity in the community structure, driven by an abundance of dominant and important species. Our Mantel tests and canonical correspondence analysis (CCA) identified seawater temperature and salinity as core drivers of the aggregation and distribution of fish larvae, interacting with factors such as the chlorophyll-a concentration, water turbidity, water depth, and dissolved oxygen. This research provides a scientific basis for the dynamic monitoring of spawning grounds and effective management of fishery resources in Zhejiang's coastal waters.

Keywords: fish larvae; spatiotemporal distribution; community structure; environmental driving factors; Zhejiang coastal waters

Key Contribution: This study provides data on the composition and seasonal variation of fish larvae assemblages in the coastal waters of Zhejiang, while further investigating the key driving factors that influence their spatial distribution patterns and community structure. The findings not only enrich the ecological monitoring data of fish larvae in the offshore waters of Zhejiang but also lay a foundation for future assessments of the responses of fish larvae communities to a wider range of environmental drivers. This has significant implications for the conservation of fishery resources.

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1. Introduction

Fish provide nearly 20% of the animal protein intake for approximately half of the global population [1]. The East China Sea is one of the highest-yielding marine areas in the world and serves as an important natural fishing ground for China, with an annual catch of nearly 600 $\times$ 10^4 t [2,3]. The coastal waters of Zhejiang are situated on the continental shelf of the East China Sea, bordered to the north by the Yangtze River estuary in Shanghai and to the south by the southern end of the Qixing Islands at the Zhejiang–Fujian border. It includes numerous islands such as the Zhoushan Archipelago, Ma'an Islands, and Dongtou Islands, and connects to various water systems including Hangzhou Bay, Xiangshan Bay, Jiaojiang River, and the Oujiang River, resulting in a complex geographical landscape. The perennial invasion of the Taiwan Warm Current and the Kuroshio Current provides nutrients and abundant food organisms, making it an ideal spawning, feeding, and habitat environment for many marine organisms [4,5]. Since the 1950s, marine fishery production in Zhejiang Province has continued to rise. With the continuous upgrading of marine fishing technology and the increasing demand for high-quality marine protein, marine fishery resources have been overexploited [6]. Simultaneously, the intensifying problem of seawater pollution has been exacerbated by climate change, the rapid expansion of marine aquaculture, and anthropogenic factors such as the discharge of polluted land-based wastewater [7]. According to the 2013 Zhejiang Provincial Marine Environmental Bulletin, the significant environmental issues in the coastal waters of Zhejiang include water pollution, eutrophication, and frequent occurrences of marine red tide events [8]. These challenges have resulted in the degradation of marine ecosystem structures, environmental threats, damage to marine functional zones, a decline in fishery resources, and even the risk of gradual depletion. Moreover, the fishing seasons for many traditional economic fish species are steadily disappearing [9]. Various traditional commercial fish species are gradually disappearing [10]. Meanwhile, the main targets of fishing have shifted from traditional high-trophic-level resources to low-trophic-level resources. This shift has resulted in a simplification of fishery community structures and a trend towards smaller and younger fish in catches [11–13]. To protect the marine fishery resources along the coast, the Chinese government has designated trawl fishery ban areas in the Bohai Sea, Yellow Sea, and East China Sea. In 2017, the Zhejiang provincial government established ten spawning ground protection areas. By implementing measures such as setting fishing bans during specific periods in these protection areas, the duration of reproduction, spawning, and habitat use for important commercial fish species is extended. This approach helps to protect and monitor the dynamic changes in the resource status of these economically important fish species.

Fish larvae are important prey organisms and also predators of planktonic flora and fauna, playing a crucial role in the energy flow and material cycling within marine food webs [14]. Fish larvae are crucial for the replenishment of fishery resources and form the foundation of sustainable marine fishery development. Their distribution and abundance are likely influenced by multiple factors, including environmental conditions, coastal currents, and the reproductive strategies of the broodstock [15], with changes in larval resource abundance aiding in predicting the resource status, spawning grounds, and migratory routes of the broodstock [16–18]. Fish larvae are in the early life history stage of fish, and due to their sensitivity to environmental stressors and weak swimming abilities, they are strongly influenced by environmental factors [19]. In recent years, the number of fish larvae species in the north-central waters of Zhejiang Province has declined sharply, from 52 species in 2008 to 23 species in 2020, with frequent turnover of dominant species and traditional commercial fish being replaced by small, low-economic-value fish, reflecting the changing trends in fishery resource structure, with temperature, as a key environmental factor, playing a profound role in the diversity of these species [20]. In the southern waters of Zhejiang, the abundance of fish larvae was lowest in 2017–2018, with the dominant species and their distribution varying seasonally and being influenced by environmental factors such as the water depth, temperature, and salinity [21–23]. The Zhoushan Archipelago and its adjacent waters are also facing a decline in fish larvae species. The distribution of these larvae is primarily influenced by environmental factors, including temperature, salinity, chlorophyll-a, and turbidity. Recent studies have shown that the dominant larvae species in the region are shifting towards Gobiidae fish [24–26]. Studies in specific areas such as Xiangshan Bay and Ma'an Archipelago have revealed the richness and ecological habits of fish larvae species, emphasizing the importance of physical factors such as temperature and salinity, along with human interventions (such as artificial reefs) on fish larvae communities [27–29]. Additionally, as one of the important marine areas, the fish larvae community in Daiquyang is predominantly composed of species such as *Planiliza haematocheilus*, *Stolephorus chinensis*, and *Engraulis japonicus*. The distribution of these species is closely related to marine physical and chemical factors such as temperature, salinity, ammonia nitrogen, reactive phosphate, and suspended solids, reflecting the unique ecological characteristics of this area [30]. The Qixing Archipelago also has rich fish larvae resources, with 40 species identified, among which anchovies and *Stolephorus commersonnii* are the dominant species. The distribution of fish larvae in this area is not only directly affected by environmental factors such as dissolved oxygen but may also interact with physical processes and topographic features, such as island topography and ocean currents, jointly shaping a unique fish larvae community structure [31].

Currently, there is a lack of systematic surveys of fish larvae across all seasons in the offshore waters of Zhejiang, making further research particularly urgent. This study aims to describe the seasonal changes in the composition, resource density changes, and distribution of fish larvae. It also explores the main factors influencing the distribution of fish larvae communities and infers the spawning grounds of dominant species. The results of this study provide foundational data for establishing a comprehensive monitoring network for the coastal waters of Zhejiang, as well as for understanding the dynamic changes in fish larvae community composition and spawning ground distribution, thereby offering scientific support for the restoration and management of fishery resources.

2. Materials and Methods

2.1. Study Area and Stations

The survey area is located in the offshore waters of Zhejiang, in the East China Sea (120.50°~123.25° E, 27.00°~31.00° N). To investigate the seasonal variation characteristics of the species composition, aggregation distribution, and influencing factors of fish larvae, this study conducted surveys of fish larvae and environmental data across four periods: April 2022 (spring), November 2022 (autumn), February 2023 (winter), and July 2023 (summer). The sampling stations for all four cruises were identical, adding to a total of 83 stations in each cruise (Figure 1).

2.2. Sample and Data Collection

The sampling survey was conducted in accordance with the State General Administration of the Peoples Republic of China for Quality Supervision and Inspection and Quarantine (AQSIQ), including the Specifications for Oceanographic Surveys Part 6: Marine Biological Surveys GB/T 12763.6-2007 [32] and the Specifications for Marine Monitoring Part 7: Ecological Surveys for Offshore Pollution and Biological Monitoring GB 17378.7-2007 [33]. Ichthyoplankton samples were collected using a large zooplankton net with a mesh length of 280 cm, featuring an 80 cm mouth diameter and 0.505 mm mesh size. Each net mouth was equipped with a flowmeter to estimate the filtered water volume. The sampling was conducted via horizontally towing at speeds of 2–3 knots for 10 min per station. Concurrently, environmental parameters including the sea surface temperature

(SST), sea surface salinity (SSS), chlorophyll-a (Chl.a), turbidity (turb.), dissolved oxygen (DO), water depth (depth), and pH were measured using a multifunctional water quality analyzer (JFE-AAQ171, JFE Techno-Research Corporation, Tokyo, Japan) at each survey station. The collected fish larvae samples were preserved rapidly with 5% formalin solution mixed with seawater. At some survey stations, the samples were preserved with 95% ethanol solution.

Figure 1. Survey stations in the coastal waters of Zhejiang.

2.3. Sample Processing in the Laboratory

The collected fish larvae were brought back to the laboratory, where they were individually selected and placed into corresponding fresh 5% formalin solution or 95% ethanol solution for morphological and molecular identification. The fish larvae species were taxonomically identified using a Leica M205 C stereo microscope (Leica Microsystems, Wetzlar, Germany) following the taxonomic keys used by Okiyama [34] and Zhao [35]. The measurements, photography, and counting of the organisms were conducted at the highest possible taxonomic level. Based on the characteristic bending of the caudal fin notochord development in the fish [15], we classified the larvae into three stages: pre-flexion larvae, flexion larvae, and post-flexion larvae [34].

Samples that could only be identified to the family or genus level were recorded with their respective family or genus names, while those that could not be identified were labeled as indeterminate species. After capturing photographic records of fish larvae samples with indistinct morphological characteristics and fixed in 95% ethanol solution, they were sent to Shanghai Bioscience Biotechnology Co., Ltd. (Shanghai, China), for DNA extraction, amplification, and sequencing. The obtained sequences were subjected to a BLAST analysis against the NCBI database (National Center for Biotechnology Information, https://www.ncbi.nlm.nih.gov/, accessed on 20 November 2023) to determine their taxonomic classification.

2.4. Data Analysis

The abundance of the larval fish was standardized and reported in terms of individuals per cubic meter (ind/m^{-3}) [32]. The index of relative importance (IRI) was employed to determine the dominance of fish larvae species, calculated using the formula IRI = N% × F%. In this context, N% signifies the proportion of individuals of each species relative to the total number of fish species, whereas F% denotes the percentage frequency of occurrence for each species in the sampled population. Species with IRI > 500 were classified as dominant species, and those with 100 < IRI < 500 were considered important species [36,37]. Based on books such as *Zhejiang Marine Fishes* [35,38], the literature from scholars such as Wan [39], and websites such as the World Register of Marine Species (WoRMS) (https://www.marinespecies.org/, accessed on 23 November 2023), an ecological typology analysis was conducted on the fish larvae collected during the survey. The spatial and temporal distribution can reflect the aggregation trends of fish larvae in different seasons. A fish larvae density distribution map was generated using ArcGIS 10.8 software developed by Environmental Systems Research Institute in California, USA.

Prior to analyzing the community structure of the fish larvae, preprocessing of the raw data was conducted to reduce the impact of rare species on the community structure analysis. The fish larvae data were log (x + 1)-transformed. The Bray–Curtis similarity coefficient was used to obtain a similarity matrix among sampling points, which was utilized to generate a clustering dendrogram. The significance of differences between each clustering group was tested using a one-way similarity analysis (SIMPROF) with $\alpha = 0.05$. Nonmetric multidimensional scaling (NMDS) was employed to ordinate the fish larvae communities into points in a two-dimensional space [40]. An analysis of similarities (ANOSIM) was used to investigate the significance of differences in community structure among different station groups. The similarity percentage routine (SIMPER) was applied to analyze the contribution percentages of intra-group similarity and inter-group dissimilarity of the fish larvae, displaying their percentages. The analysis above was conducted using Primer 6.0 software developed by Quest Research Limited, located in Plymouth, UK.

The relationships between the fish larvae density and different environmental variables were preliminarily explored using a Mantel test for a correlation analysis. The Mantel statistic calculates values between matrices. The Bray–Curtis similarity index was used to generate the fish larvae biological matrix, and Euclidean distance was used to construct the environmental distance matrix, completed through the "linkET" package in R software version 4.2.2. A canonical correspondence analysis (CCA) of the fish larvae communities and environmental variables was conducted using the vegan package in R. Before conducting the CCA, variance inflation factors (VIF) were used to test for multicollinearity among the environmental factors, selecting explanatory variables with VIF values of less than 3. A VIF analysis was implemented using the "car" package in R software version 4.2.2.

3. Results

3.1. Composition of Fish Larvae

A total of 24,232 fish larvae from 93 species were collected over four surveys. The order Perciformes included 21 families and 60 species (64.52%), *Clupeiformes* represented 2 families and 8 species (8.60%), *Scorpaeniformes* consisted of 4 families and 6 species (6.45%), and *Pleuronectiformes* comprised 3 families and 5 species (5.38%). The abundance of fish larvae at the order level is shown in Figure 2a. The compositions of dominant and important species are illustrated in Figure 2b,c. The dominant species include *Larimichthys crocea*, *Sebastiscus marmoratus*, *Lateolabrax japonicus*, and *Odontamblyopus lacepedii*, while important species include *Engraulis japonicus*, *Planiliza haematocheilus*, and *Salanx ariakensis*. The fish larvae species observed in each season include *Harpodon nehereus*, *Amblychaeturichthys hexanema*, and *Odontamblyopus lacepedii*. The species composition table is provided in Table S1 of the Supplementary Materials.

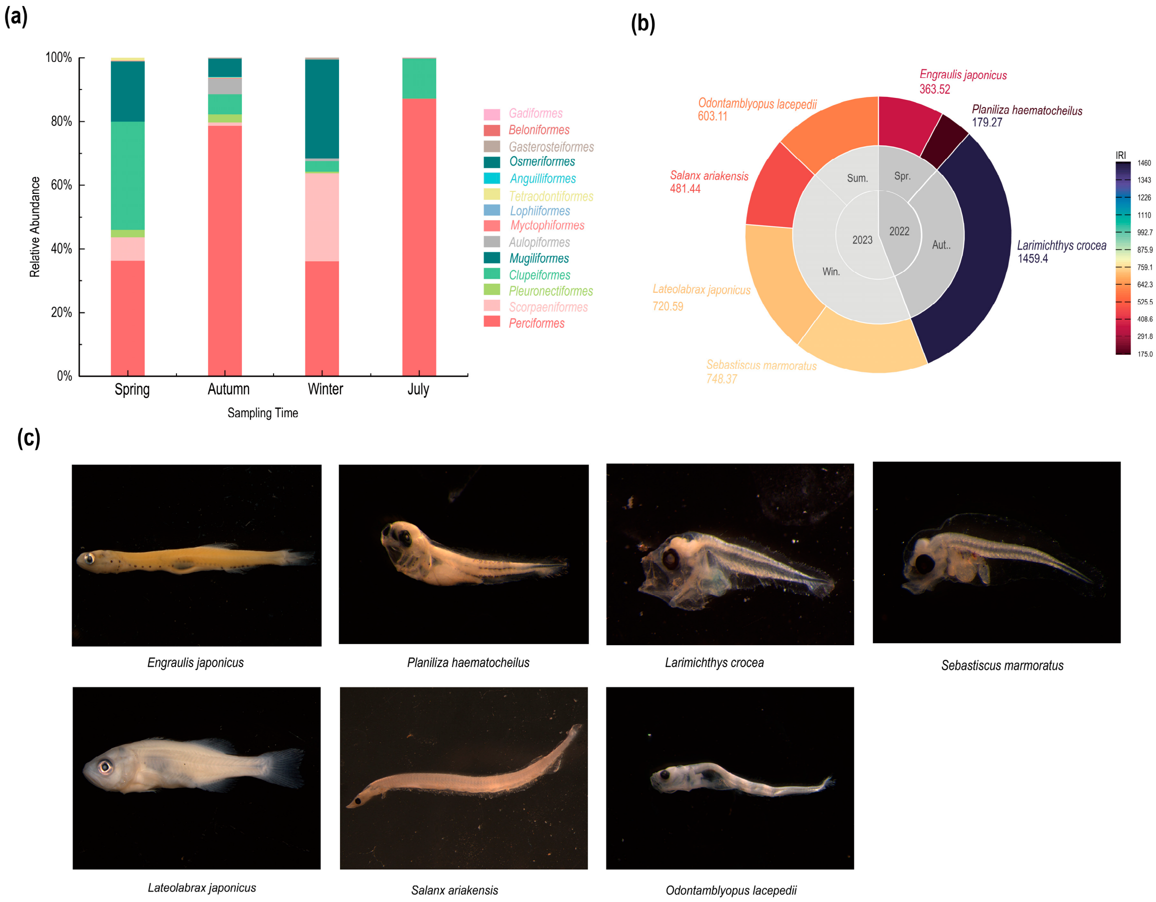

Figure 2. Fish larvae species composition: (**a**) abundance of fish larvae by taxonomic order; (**b**) composition of dominant and important species; (**c**) photographs of dominant and important species.

3.2. Seasonal and Spatial Distribution Patterns

The temporal distribution analysis revealed that the fish larvae resource density in the coastal waters of Zhejiang is highest in summer, followed by spring and autumn, and lowest in winter. Spatially, during spring, autumn, and summer, the fish larvae resource density along the coast is consistently higher than in areas near the boundaries of motor trawler fisheries and closed fishing areas, whereas in winter, the fish larvae resource density is higher in the southern seas compared to the northern seas (Figure 3).

In spring (April 2022), fish larvae were observed at 63 sampling stations, with an average density of 0.084 ind./m^3. The fish larvae were predominantly found aggregating in coastal bays and estuaries. The highest density was observed in the Yueqing Bay Estuary, primarily comprising species such as *Engraulis japonicus* and *Odontamblyopus lacepedii*. Additionally, the Xiangshan Bay Estuary showed aggregations dominated by *Odontamblyopus lacepedii*, *Planiliza haematocheilus*, and *Sebastiscus marmoratus*. Furthermore, they were more distributed in the Hangzhou Bay Estuary, mainly represented by *Planiliza haematocheilus* and *Odontamblyopus lacepedii*.

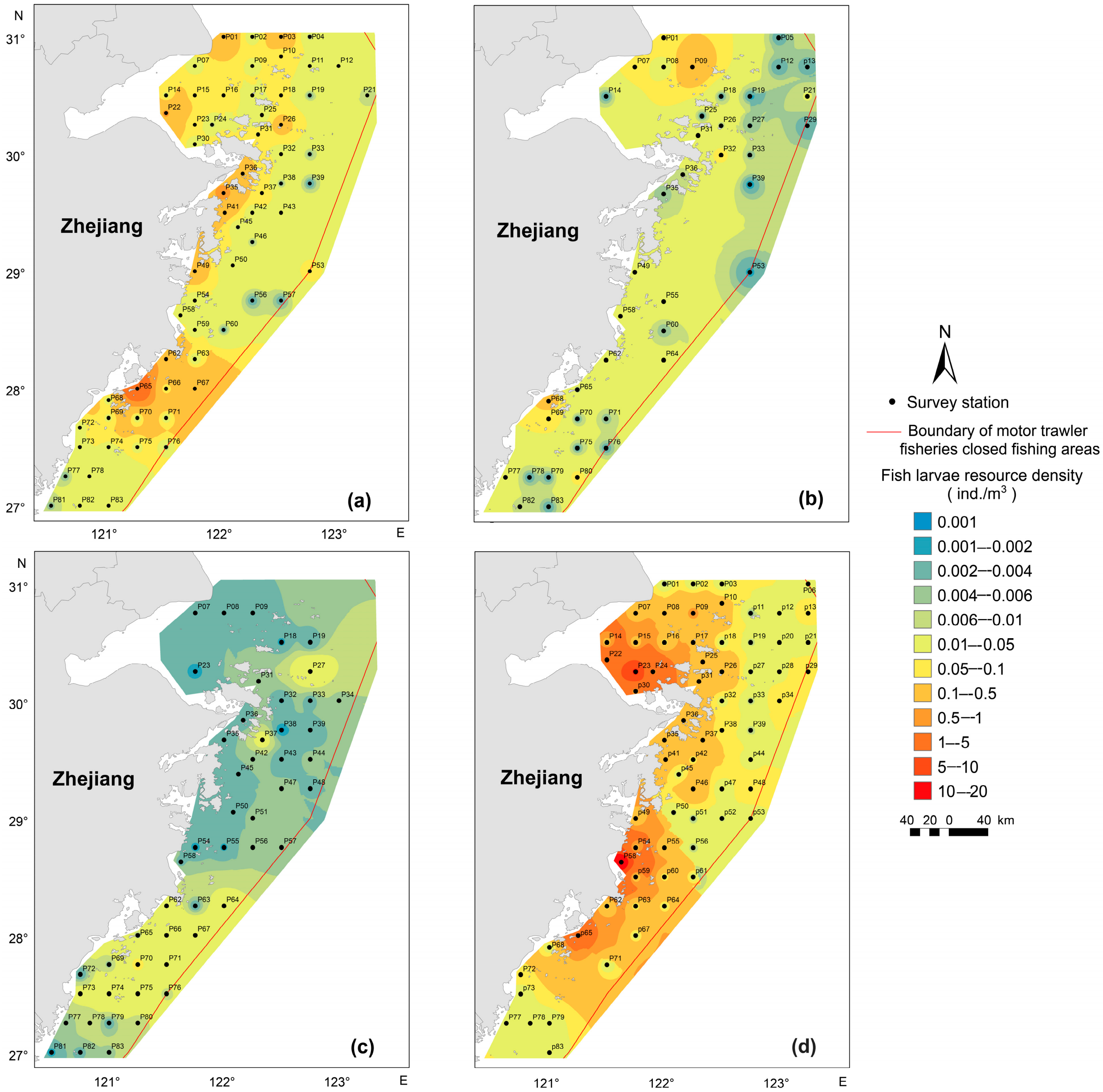

Figure 3. Spatial and temporal distribution of fish larvae in the coastal waters of Zhejiang: (**a**) April 2022, spring; (**b**) November 2022, autumn; (**c**) February 2023, winter; (**d**) July 2023, summer.

In autumn (November 2022), fish larvae were observed at 41 stations, with an average density of 0.0123 ind./m^3. The fish larvae were predominantly concentrated in the estuary of Hangzhou Bay, primarily comprising *Larimichthys crocea* and *Salanx ariakensis*, followed by the mouth of the Oujiang Estuary, mainly with *Larimichthys crocea*.

In winter (February 2023), fish larvae were observed at 50 sampling stations, with an average density of 0.0049 ind./m^3. The fish larvae were mainly found aggregating in the waters near the Dongtou Islands, predominantly species such as *Salanx ariakensis*.

Additionally, they were observed near the boundaries of motor trawler fisheries and closed fishing areas, primarily consisting of *Sebastiscus marmoratus* and *Lateolabrax japonicus*.

In summer (July 2023), fish larvae were observed at 69 sampling stations, with an average density of 0.48 ind./m^3. The fish larvae showed higher densities near coastal estuaries, with the highest density observed in the estuary of Jiaojiang Bay. The main species observed were *Odontamblyopus lacepedii*, *Trypauchen vagina*, and *Stolephorus commersonnii*. Additionally, significant densities were observed in the Hangzhou Bay Estuary, primarily comprising *Odontamblyopus lacepedii*, *Tridentiger barbatus*, *Periophthalmus magnuspinnatus*, *Coilia nasus*, and *Chaeturichthys stigmatias*. Furthermore, fish larvae were also abundant in the Yueqing Bay Estuary, mainly including *Stolephorus commersonnii*, *Setipinna taty*, and *Tridentiger barbatus*.

3.3. Community Structure

The clustering analysis results are presented in Figure 4. In spring, the SIMPROF test indicated that the community structure similarity across sampling sites was relatively high. Based on the clustering analysis, the sampling sites were classified into four groups at a similarity level of 13.23% (A: 16.1%; B: 13.23%; C: 19.61%; D: 17.48%). The ANOSIM analysis revealed significant differences among these groups (Global R = 0.705, p = 0.001), and the NMDS ordination showed reliable performance (stress = 0.16). The SIMPER analysis indicated that group A was primarily characterized by *Engraulis japonicus* and *Amblychaeturichthys hexanema*, contributing 52.31% and 46.78% to this group, respectively. Group B was predominantly characterized by *Planiliza haematocheilus* and *Sebastiscus marmoratus*, contributing 68.74% and 29.46% to this group, respectively. Group C was mainly characterized by *Planiliza haematocheilus*, contributing 87.26% to this group. Group D was characterized by *Sebastiscus marmoratus*, *Synechogobius ommaturus*, *Lateolabrax japonicus*, contributing 39.06%, 15.77%, and 15.48%, respectively. The SIMPER analysis table is provided in Table S2 of the Supplementary Materials.

In autumn, the SIMPROF test indicated that the community structures of some sampling sites differed significantly. Based on the clustering analysis, the sampling sites were classified into three groups at a similarity level of 17.86% (A: 17.86%; B: 52.99%; C: 19.60%). The ANOSIM analysis revealed significant differences among these three groups (global R = 0.943, p = 0.001), and the NMDS ordination performed well (stress = 0.01). The SIMPER analysis indicated that group A was primarily characterized by *Trichiurus lepturus*, contributing 100% to this group. Group B was predominantly characterized by *Harpodon nehereus*, contributing 100% to this group. Group C was characterized by *Larimichthys crocea*, contributing 92.02% to this group. The SIMPER analysis table is provided in Table S3 of the Supplementary Materials. In winter, the SIMPROF test indicated that the community structures of some sampling sites differed significantly. Based on the clustering analysis, the sampling sites were classified into three groups at a similarity level of 17.28% (A: 52.56%; B: 17.28%; C: 17.56%). The ANOSIM analysis indicated significant differences among these three groups (global R = 0.636, p = 0.001), with the NMDS ordination performing well (stress = 0.11). The SIMPER analysis showed that group A was characterized by *Salanx ariakensis*, accounting for 97.24% of the species.; group B by *Lateolabrax japonicus*, accounting for 93.82%; and group C by *Sebastiscus marmoratus*, accounting for 98.18%. The SIMPER analysis table is provided in Table S4 of the Supplementary Materials. In summer, the SIMPROF test indicated that the community structures of some sampling sites differed significantly. Based on the clustering analysis, the sampling sites were classified into five groups at a similarity level of 11.33% (A: 28.23%; B: 12.94%; C: 13.33%; D: 35.95%; E: 11.33%). The ANOSIM analysis indicated significant differences among the four groups (global R = 0.661, p = 0.001), and the NMDS ordination showed reliable results (stress = 0.15). The SIMPER analysis identified the following characteristic species and their respective contributions in each group. Group A featured *Periophthalmus magnuspinnatus* (40.24%), *Eupleurogrammus muticus* (15.6%), and *Coilia mystus* (14.4%). Group B comprised *Stolephorus commersonnii* (44.34%), *Odontamblyopus lacepedii* (25.27%), and *Tridentiger barbatus* (17.51%). Group C was characterized by *Omobranchus punctatus* (60.9%), and to a lesser extent *Odontamblyopus lacepedii* (14.54%). Group D was dominated by *Auxis rochei* (65.39%) and *Decapterus maruadsi* (34.61%). Group E included *Engraulis japonicus* (60.66%) and *Scomber japonicus* (21.05%) as its characteristic species. The SIMPER analysis table is provided in Table S5 of the Supplementary Materials.

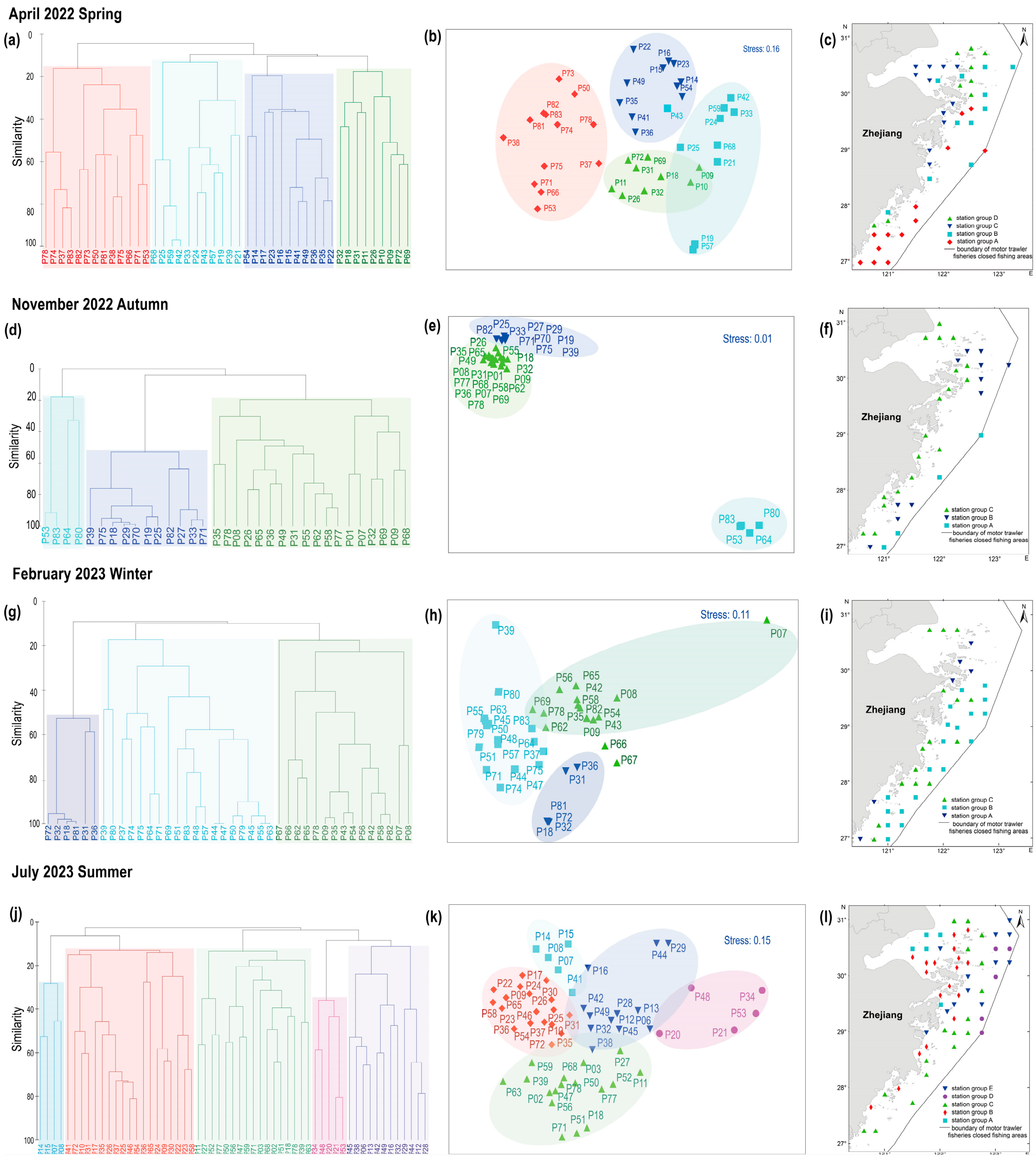

Figure 4. Community structure distribution of fish larvae in the coastal waters of Zhejiang: (**a**,**d**,**g**,**j**) cluster analysis of fish larvae community; (**b**,**e**,**h**,**k**) NMDS analysis of fish larvae community; (**c**,**f**,**i**,**l**) group distribution of fish larvae community.

3.4. Relationship Between Community Structure and Environmental Factors

3.4.1. Mantel Test

Figures 5a, 6a, 7a and 8a present the results of the Mantel test conducted between the fish larvae density and environmental data in April 2022. Significant correlations were found for pH (Mantel's r = 0.213, p = 0.001), DO (Mantel's r = 0.178, p = 0.001), and SSS (Mantel's r = 0.145, p = 0.003) with fish larvae. Additionally, SST (Mantel's r = 0.09, p = 0.018), Chl.a (Mantel's r = 0.116, p = 0.016), and turb. (Mantel's r = 0.116, p = 0.021) were also significantly associated. In November 2022 (Figure 6a), significant correlations were observed for depth (Mantel's r = 0.316, p = 0.001), SSS (Mantel's r = 0.236, p = 0.001), and SST (Mantel's r = 0.222, p = 0.002). For February 2023 (Figure 7a), SSS (Mantel's r = 0.146, p = 0.002) and pH (Mantel's r = 0.134, p = 0.006) showed significant positive correlations, while DO (Mantel's r = 0.105, p = 0.026) was also significantly correlated. Finally, in July 2023 (Figure 8a), significant correlations were noted for depth (Mantel's r = 0.225, p = 0.001), SSS (Mantel's r = 0.154, p = 0.002), and SST (Mantel's r = 0.079, p = 0.008). Statistical summary of explanatory variables is provided in Table S6 of the Supplementary Materials.

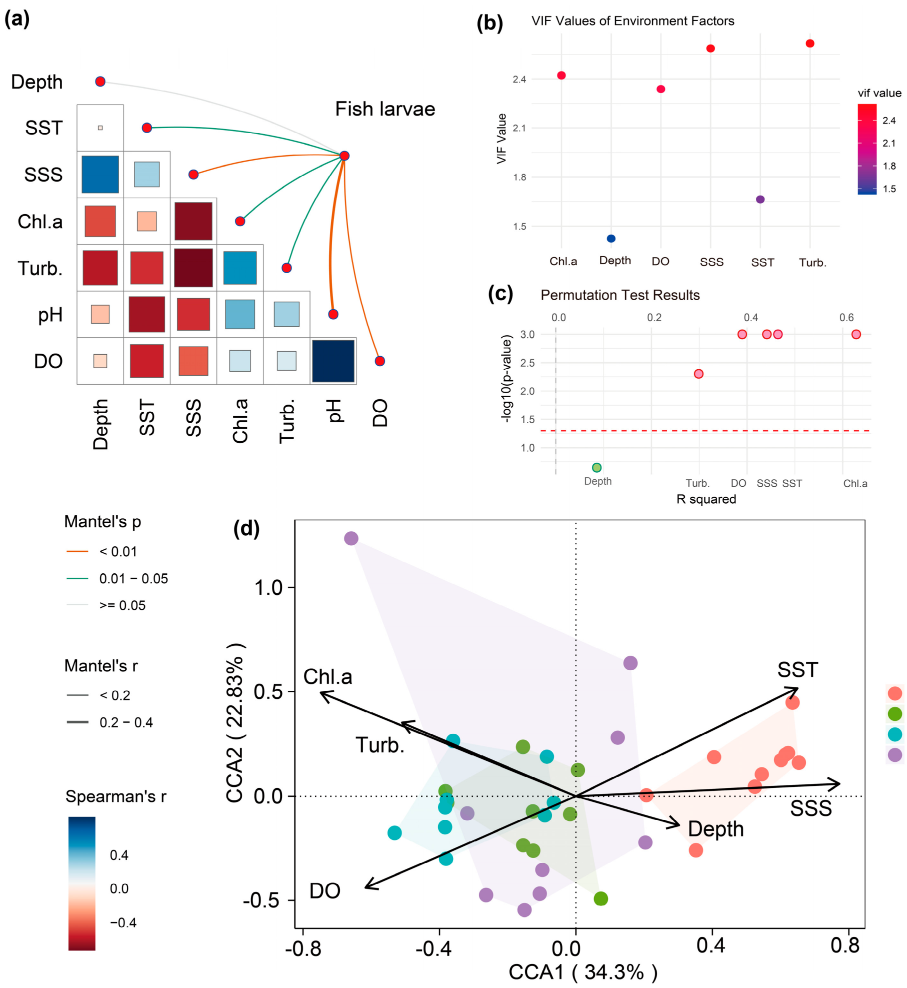

Figure 5. An analysis of the fish larvae community and environmental factors in April 2022: (**a**) Mantel test; (**b**) VIF analysis; (**c**) permutation test (pink represents significant results (p < 0.05), green represents non-significant results ($p \geq 0.5$)); (**d**) CCA.

3.4.2. CCA

The results of the CCA showed that SST and SSS have highly significant effects on the fish larvae community across all four seasons, with differences in environmental factors affecting each season. Summary of the significance of environmental variables. is provided in Table S7 of the Supplementary Materials. In spring (Figure 5), the two CCA axes collectively explained 57.13% of the variance between the fish larvae community and environmental variables. The fish larvae community was significantly influenced by SST, SSS, Chl.a, DO, and turb. ($p < 0.01$). Among them, group A was sensitive to SSS and SST, group B was primarily influenced by turb., group C was sensitive to DO and turb., and group D was sensitive to Chl.a.

In autumn (Figure 6), the two CCA axes collectively explained 81.08% of the variance between the larval fish community and environmental variables. The larval fish community was significantly influenced by Chl.a, SSS, depth, and SST ($p < 0.01$). Group A was primarily influenced by depth, group B was affected by SST, and group C was sensitive to Chl.a.

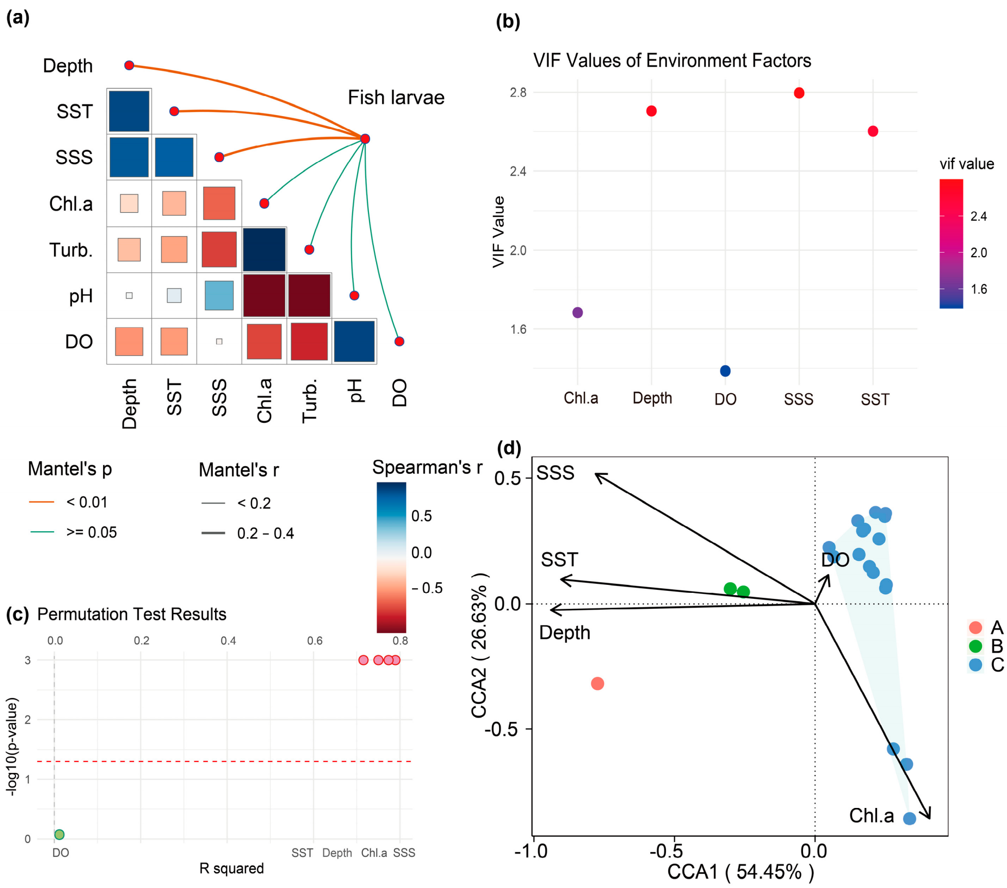

Figure 6. Analysis of fish larvae community and environmental factors in November 2022: (**a**) Mantel test; (**b**) VIF analysis; (**c**) permutation test (pink represents significant results ($p < 0.05$), green represents non-significant results ($p \geq 0.5$)); (**d**) CCA.

In winter (Figure 7), the two CCA axes collectively explained 84.44% of the variance between larval fish communities and environmental variables, with highly significant effects from SSS, SST, and depth ($p < 0.001$). Group A was sensitive to Chl.a and group B was influenced by a combination of depth, SST, and turb., while group C was primarily affected by turb. and Chl.a.

In summer (Figure 8), the two CCA axes collectively explained 63.34% of the variance between the fish larvae community and environmental variables. The larval fish community was significantly influenced by depth, SSS, SST, and DO ($p < 0.01$). Group A was primarily influenced by SST, group B was sensitive to Chl.a, group C was mainly affected by Chl.a and SSS, and group D was primarily influenced by DO and depth, while group E was impacted by a combination of DO, depth, and Chl.a.

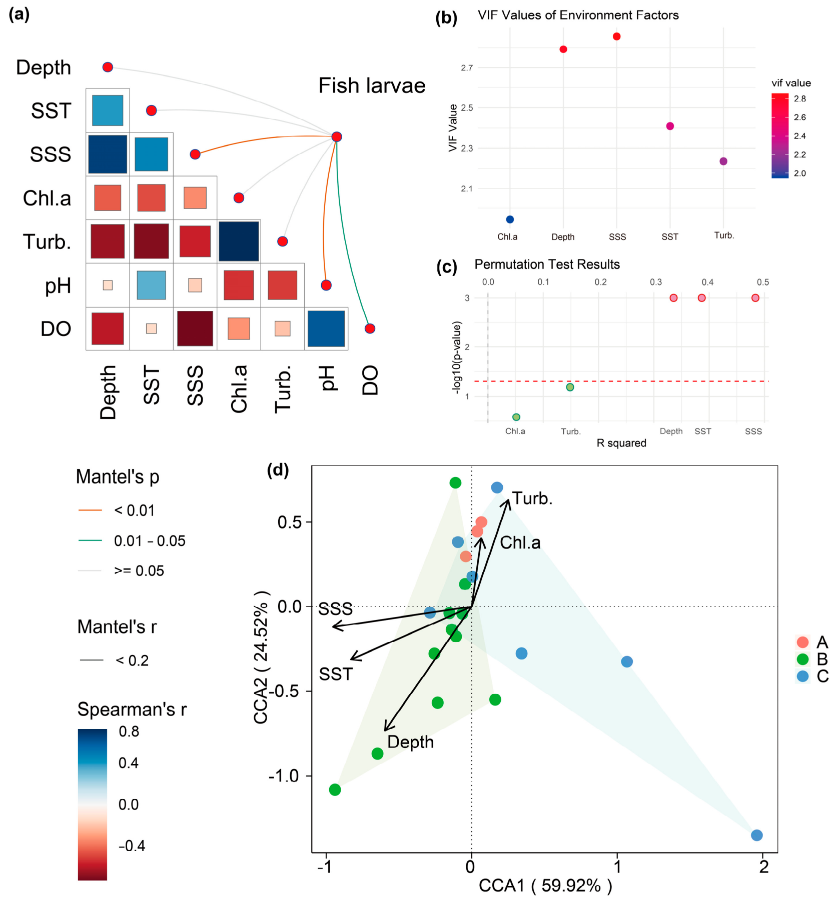

Figure 7. An analysis of fish larvae community and environmental factors in February 2023: (**a**) Mantel test; (**b**) VIF analysis; (**c**) permutation test (pink represents significant results ($p < 0.05$), green represents non-significant results ($p \geq 0.5$)); (**d**) CCA.

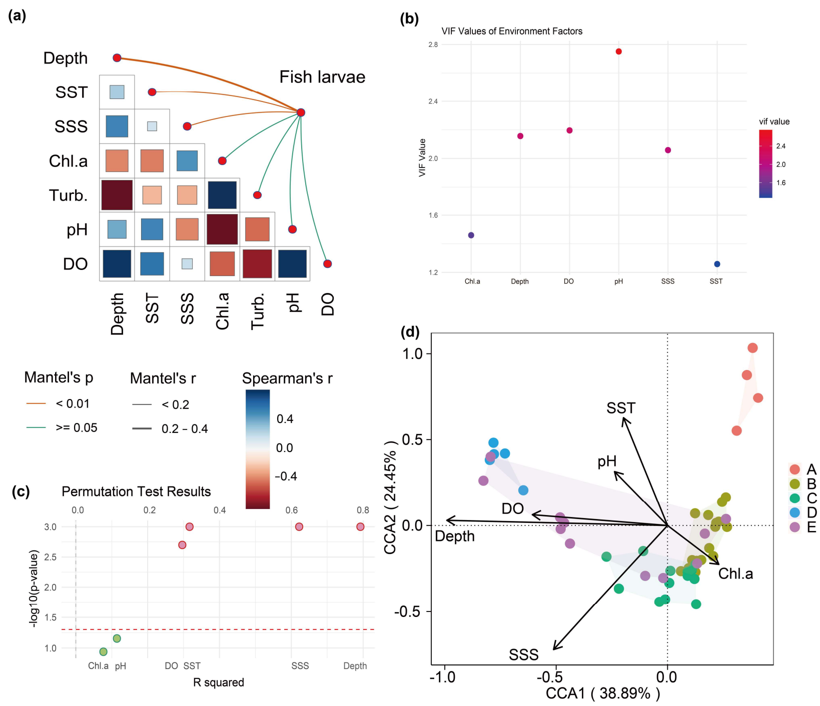

Figure 8. Analysis of the fish larvae community and environmental factors in July 2023: (**a**) Mantel test; (**b**) VIF analysis; (**c**) permutation test (pink represents significant results ($p < 0.05$), green represents non-significant results ($p \geq 0.5$)); (**d**) CCA.

4. Discussion

4.1. The Composition and Turnover of Fish Larvae Species

The fish larvae in the Zhejiang coastal waters are primarily warm-temperature and warm-water species. This distribution may be influenced by the Taiwan Warm Current and the Kuroshio Current, which potentially bring warm oceanic water into the region [41,42]. These oceanographic processes could contribute to the high abundance of warm-associated species, shaping the fish community structure in this temperate zone. The composition of fish larvae species and their resource density show significant seasonal variation. The peak period for fish larvae occurrence is in summer, followed by spring, with the respective species proportions being 69.89% and 39.78% and the resource density proportions being 82.49% and 14.55%. The average abundance of fish larvae in summer is 97.96 times higher than that in the season with the lowest abundance. We believe that the Zhejiang coastal waters are a crucial area for these fish species to return for spawning and reproduction during spring and summer.

The compositions of dominant species do not overlap across the four seasons. The dominant and important fish species in each season are primarily determined by their reproductive habits. *Engraulis japonicus* migrates to the coastal waters of Zhejiang for spawning each spring, with its spawning season typically occurring from April to June along the Zhejiang coast and in nearby waters [43]. *Planiliza haematocheilus* spawns in shallow seas or brackish estuarine areas during spring, with the larvae drifting into the coastal zone with the tides [44]. As a result, the larvae of both *Engraulis japonicus* and *Planiliza haematocheilus* are more frequently captured in spring. *Larimichthys crocea* is a coastal migratory fish with two spawning seasons each year, in spring and autumn. Our study indicates that autumn is a critical spawning period for *Larimichthys crocea* in the Zhejiang coastal region, as previously predicted [22–24]. In winter, the dominant species is *Sebastiscus marmoratus*, a euryhaline, reef-associated fish with a spawning season typically from February to July [45]. Another dominant species, *Lateolabrax japonicus*, is a nearshore, shallow-sea fish capable of multiple spawning events within a short period [46] [43]. In our study, *Lateolabrax japonicus* comprised 61.82% of the winter samples. *Salanx ariakensis* is an important species found in coastal bays and estuarine brackish waters. It spawns from November to December each year, and the larvae grow to 40–50 mm in length after 4–5 months. *Odontamblyopus lacepedii* is a warm-temperate, benthic fish that spawns twice a year, from February to April and from July to September. In our study, 396 larvae of *Odontamblyopus lacepedii* in summer accounted for 97.93% of the total number of larvae of this species, leading us to hypothesize that summer is the peak spawning period for this species.

4.2. Temporal and Spatial Distribution Characteristics of Fish Larvae Resource Density

The fish larvae in the coastal waters of Zhejiang often aggregate in nearshore areas, which may be closely related to the selection of breeding habitats for spawning parent pairs. The spawning adults of the main fish species, *Engraulis japonicus*, successively enter the coastal island and reef areas near Fujian's outer sea and central-southern Zhejiang to spawn [47]. The spawning adults of *Planiliza haematocheilus* mainly aggregate in estuarine brackish water or shallow sea areas, and the hatched larvae enter the coast for growth under the influence of tides [48]. *Sebastiscus marmoratus* exhibits strong settlement characteristics, typically residing in offshore areas with seaweed beds and rocky reefs. This species does not engage in long-distance migration but rather undertakes short-distance migrations in response to seasonal changes [45]. During the breeding season, *Larimichthys crocea* typically migrates to islands, estuaries, or shallow waters within the inner bay [3]. *Salanx ariakensis* migrates from the nearshore to spawn in estuarine brackish areas in autumn, with the adults dying after spawning. The hatched larvae then migrate from the estuary to the sea for overwintering in early winter [49]. The larvae of *Coilia nasus*, hatching after spawning, aggregate in estuarine brackish water and only start to migrate into the sea for growth and fattening in the second year. *Setipinna taty* typically spawns in shallow waters near estuaries. The spawning adults of *Stolephorus commersonnii* usually concentrate in nearshore shallow water areas to spawn [50]. The spawning adults of goby fish mainly inhabit shallow water areas of estuaries and coastal zones for spawning. Our research findings indicate that areas with high densities of fish larvae are typically found in estuaries and bays. We hypothesize that this is related to the distribution of food organisms and the presence of various water masses. Fish larvae possess predatory capabilities and limited migratory swimming abilities. In areas where prey organisms are abundant, fish larvae tend to decrease their cruising speed and remain in those waters [51]. A bay serves as a pivotal area where the land and ocean converge, including seawater, basins, and adjacent land areas, with its complex ecosystem structure integrating various coastal resources while being relatively fragile and ecologically sensitive [52]. Yueqing Bay, situated in southern Zhejiang Province, is the largest semi-enclosed bay in the region, serving as a critical habitat for the reproduction, feeding, and fattening of various marine organisms [53]. Xiangshan Bay, located in northern Zhejiang Province, is a narrow and elongated semi-enclosed bay that provides essential spawning, feeding, and fattening grounds for several migratory commercial fish species [54]. Hangzhou Bay, found in northeastern Zhejiang Province, serves as the estuary of the Qiantang River. This bay is influenced by runoff from both the Qiantang and Yangtze Rivers, as well as tidal currents from the East China Sea. It is characterized as a funnel-shaped estuary trending east–west, with strong tidal dynamics, complex hydrological conditions, and abundant planktonic resources [55]. The Oujiang River, located in southern Zhejiang Province, is the second largest river flowing into the sea in the region. Its runoff, combined with the Zhejiang–Fujian coastal currents and the Taiwan Warm Current, generates upwelling in offshore areas, resulting in abundant plankton [56]. In central Zhejiang Province, the Jiaojiang River is the third largest river entering the sea. It features an open-type estuary that extends outward in a funnel shape. The runoff from the Jiaojiang River supplies a rich array of forage organisms, making the Jiaojiang River Estuary, known as the Yushan Fishery, a prominent fishing ground that serves as both a spawning and feeding habitat for various fish species [57]. The southern waters of Zhejiang Province are dotted with numerous islands, which provide natural shelters and habitats for diverse marine life. Influenced by the Taiwan Warm Current, Zhejiang–Fujian coastal currents, and seabed friction, coastal upwelling [58] and onshore currents bring nutrients to the upper water layers, promoting the production of forage organisms.

4.3. Fish Larvae Communities and Environmental Driving Factors

NMDS was used to divide the survey stations into groups, forming distinct regional community structures. The ANOSIM analysis verified that there are significant differences in species composition among different fish larvae groups. The SIMPER analysis indicated that the characteristic species contributing to the similarities of fish larvae community structures across the four seasons are mainly the dominant and important species in those seasons. We believe that there is spatial heterogeneity in the community structure of the offshore waters of Zhejiang, and that spatial differences are mainly related to the species composition and abundance distribution of fish larvae. Differences in the abundance of dominant and important species result in distinct fish larvae assemblages. These assemblages demonstrate the aggregation of fish larvae communities along spatial gradients. This is consistent with the research findings of Nie Zhenlin [59] and Liang Hai [60]. We classified the fish larvae into four representative communities: coastal estuary communities, island

and reef communities along with their adjacent waters, communities near the motorized fishing vessel fishing ban line, and the communities surrounding the Zhoushan Islands and their adjacent waters. Based on the results of this study, we identified temperature and salinity as the dominant factors influencing the resource density of fish larvae. Additionally, factors such as chlorophyll-a, turbidity, depth, and dissolved oxygen also significantly contribute to the spatial heterogeneity of fish larvae community structures.

The coastal waters off Zhejiang belong to a subtropical monsoon climate with distinctive monsoon characteristics. In winter, influenced by the northeast monsoon, the coastal currents flow southward. In summer, due to the combined influence of the southwest monsoon and the Kuroshio Current, the coastal currents dissipate [61]. The Taiwan Warm Current and coastal water masses are strengthened in summer and weakened in winter under the influence of monsoons [62], while the Kuroshio Current exhibits the opposite trend. The Yangtze River diluted water and the Zhejiang–Fujian coastal current constitute the main components of the coastal water system, with the Yangtze River diluted water having a more widespread impact on the surveyed sea area. The low-salinity Yangtze River diluted water expands eastward in summer, and influenced by northerly winds in winter, turns southward to converge with the Zhejiang–Fujian coastal current [63]. The Taiwan Warm Current, located on the eastern side of the coastal current, is a significant component of the offshore currents in Zhejiang. Its velocity increases and flow width expands in summer, while it decreases and narrows in winter [64]. Consequently, under the influence of water masses such as the coastal currents, the Taiwan Warm Current, and the Kuroshio Current, the environmental factors in the offshore waters of Zhejiang exhibit considerable variability [4]. The temperatures show distinct seasonal characteristics [65,66]. In winter, the water temperature is uniformly distributed vertically, while summer sees the formation of a strong thermocline. Spring is marked by rising temperatures, whereas autumn experiences a decline, leading to complex and unstable temperature variations. The salinity also displays regional characteristics, primarily influenced by the Kuroshio Current and coastal waters. The coastal water masses are characterized by low salinity, contrasted with the high-temperature, high-salinity conditions of the Taiwan Warm Current and Kuroshio Current. The fluctuations between these high-salinity and low-salinity water masses significantly affect the salinity distribution in the surveyed sea area [67].

We found that Chl.a, turb., and DO are the primary environmental drivers influencing coastal estuarine communities. Meanwhile, the Pearson correlation coefficient in the Mantel test repeatedly verified the intimate relationship between Chl.a and turb., as well as DO. Chl.a typically serves as a direct indicator of phytoplankton biomass [68]. Abundant phytoplankton facilitates feeding and the aggregation of fish larvae. When the Chl.a concentrations are excessively high, this leads to the eutrophication of water bodies [69]. An increased biomass of phytoplankton and algae in seawater triggers marine disasters such as red tides [70]. The sharp increase in algae density makes the water turbid and shades the light, further exacerbating the turbidity. High turbidity affects the photosynthesis of aquatic plants and algae, and the decomposition of dead algae causes the consumption of a large amount of oxygen, exacerbating the deficiency of dissolved oxygen in the water [71,72]. Estuaries are strongly influenced by human activities such as the discharge of industrial wastewater and domestic sewage and the inflow of agricultural fertilizers, and they have poor water exchange capabilities. They are typically high-incidence areas for water eutrophication [73]. The coastal areas of Zhejiang are one of the important intensive regions for marine economic activities in China, where numerous aquaculture zones and industrial production areas converge. Notably, the coastal waters of Zhejiang have been in a state of large-scale eutrophication for a long time, with the frequency and scale of red tide outbreaks far greater than those in other coastal areas of China [74]. Therefore, human activities may alter the Chl.a, turb., and DO in the study area, thereby affecting the fish larvae communities in coastal estuaries.

The fish larvae communities in island reefs and their adjacent waters are sensitive to environmental factors such as Chl.a, turb., SST, and SSS. We speculate that this sensitivity is related to the habitat preferences of the major fish species and the unique geomorphology of the island reefs. The major fish larvae species in island reef communities, such as *Sebastiscus marmoratus*, *Synechogobius ommaturus*, *Lateolabrax japonicus*, *Odontamblyopus lacepedii*, and *Harpodon nehereus*, prefer to inhabit areas with rocky structures or muddy–sandy substrates [35]. The coastal water masses of Zhejiang and the Taiwan Warm Current form a coastal front with a large salinity gradient near the Zhejiang coast. An upwelling forms on the outer lower side of the coastal front, characterized by low temperature and high salinity [64]. The upwelling brings bottom nutrients to the surface [58], which favors the reproduction of primary producers, namely plankton, and is a necessary condition for the formation of fishing grounds [75]. Our study area includes the Wentai Fishing Ground and Yushan Fishing Ground, as well as the largest fishing ground in China, the Zhoushan Fishing Ground. Island reefs can alter the direction and speed of water currents, forming localized upwellings [76]. In the typical island reef area of the Zhoushan Islands off the coast of Zhejiang, upwellings exist throughout the year [77]. Therefore, environmental factors such as Chl.a and turb. become particularly important. The results of the CCA indicate that the fish larvae community near the mechanized fishing ban line is influenced by depth and DO. Depth affects fish communities through various factors, including temperature, salinity, light availability, DO levels, and food resources [78]. The primary species of fish larvae in this area, such as *Trichiurus lepturus*, *Decapterus maruadsi*, and *Auxis rochei*, typically spawn here. This region also includes the core zone of the East China Sea National Aquatic Germplasm Resources Protection Area, where *Trichiurus lepturus* and *Decapterus maruadsi* are recognized as key protected species.

5. Conclusions

In this paper, we systematically reported the species composition, aggregation patterns, and community structure of fish larvae in the coastal waters of Zhejiang Province during one annual cycle (spring, summer, autumn, and winter cruises). The results indicated that summer is the peak period for the occurrence of fish larvae, and due to the spawning habits of adult fish, there are significant differences in dominant and important species between seasons. Furthermore, our analysis also found that coastal estuary and bay entrances are the main aggregation areas for fish larvae, and in winter, these aggregation areas shift towards the waters near the mechanized fishing ban line. Further research has demonstrated that SST and SSS are critical drivers influencing the resource density of fish larvae. Together with the Chl.a, turb., depth, and DO, these factors contribute to the spatially heterogeneous distribution patterns of fish larvae communities. Moreover, these environmental variables prompt consideration of additional factors, such as monsoon variability, water mass dynamics, seabed topography, habitat selection preferences among fish larvae, food resource availability, and anthropogenic influences, all of which may significantly impact the aggregation and distribution of these fish populations. Therefore, in future research, we will delve deeper into the interaction mechanisms of these factors to gain a more comprehensive understanding. Overall, this study not only provides valuable monitoring data on the dynamic changes in fish community composition and spawning ground distribution in the coastal waters of Zhejiang Province but also lays a solid scientific foundation for the restoration, sustainable utilization, and management of fishery resources.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/xxx/s1: Table S1. Species composition of fish larvae in the coastal waters of Zhejiang. Table S2. A SIMPER analysis table for the station group of the fish larvae community in April 2022. Table S3. A SIMPER analysis table for the station group of the fish larvae community in November 2022. Table S4. A SIMPER analysis table for the station group of the fish larvae community in February 2023. Table S5. A SIMPER analysis table for the station group of the fish larvae community in July 2023. Table S6. Statistical summary of explanatory variables. Table S7. Summary of the significance of environmental variables.

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Institutional Review Board Statement: This study complies with the Specifications for Oceanographic Surveys Part 6: Marine Biological Surveys; the Specification for Marine Monitoring Part 7: Ecological Surveys for Offshore Pollution and Biological Monitoring; and the laws of China. The fish larvae samples were collected with a larva net, and the samples were dead when they were obtained. Ethical approval was not required for this study.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data are available from the corresponding author upon reasonable request.

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