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Larval Fish Spatiotemporal Dynamics of Different Ecological Guilds in Yangtze Estuary

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Abstract: Estuaries, as important fish nursery habitats, usually include a variety of larval fishes of different ecological guilds and exhibit complicated changing environmental conditions. We carried out a survey to examine the spatiotemporal dynamics of different ecological guild larval fishes and their relationships with environmental factors in the springs and summers from 2018 to 2020 in the Yangtze Estuary (China). The aims of the study were to provide detailed information on the characteristics of the larval fish assemblage and to explore the spatiotemporal variation in different ecological guild species and the effects of environmental variables on assemblage structure. More than 140,000 fish larvae from 26 families and 99 species were gathered during the six cruises, with the spring being the most prolific. The assemblage was dominated by a few species and was divided into three ecological guilds. Engraulidae was the most abundant family, followed by Cyprinidae and Gobiidae. *Hemiculter bleekeri* (freshwater), *Pseudolaubuca sinensis* (freshwater), *Coilia mystus* (brackish water), and *Engraulis japonicas* (marine) were the predominant species. Seasonal variations in larval fish assemblage structure were closely influenced by temperature, and the fluctuation in salinity mainly determined the spatial distribution of the larval fish community. Freshwater flows also played an important role in shaping the larval fish assemblage structure and dynamics. The conclusions improve the understanding of the ecological dynamics of larval fish assemblages in environmentally heterogeneous areas and may be applicable to other estuary ecosystems.

Keywords: fish larvae; assemblage structure; environmental factors; the Yangtze Estuary

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1. Introduction

Estuaries are transitional regions between freshwater and the sea that are known to play an important role as fish nurseries throughout the world [1–3]. The high primary and secondary productivities in estuaries support a great abundance and diversity of larval fishes [4]. The dynamics of freshwater inflows can also cause dramatic fluctuations in the estuarine environment (such as the salinity gradient), which can alter the fish community structure [5,6]. Fish larvae in an estuary are the foundation for the sustainable use of fishery resources, as their survival influences recruitment [7]. An understanding of the temporal and spatial patterns of larval fish in estuaries is valuable for conservation and management; this can also provide fundamental information to establish protected areas and ban fishing seasons [8].

The numerous fish species that use estuaries are highly variable and exhibit a diversity of community structures [9]. Estuarine larval fish can either originate from within the estuary or from marine or freshwater environments [10,11]. The estuarine usage functional group comprises four categories: marine, estuarine, diadromous, and freshwater [12]. The larvae are generally divided into four ecological guilds in the Yangtze Estuary, including freshwater, brackish water, coastal, and marine [13]. Brackish water species can live in both freshwater and saltwater areas and generally use the estuary as a habitat. These include the above estuarine species (Gobiidae) and diadromous species (Engraulidae) [13,14]. Furthermore, temperate estuarine larval assemblages are dominated by estuarine species and, depending on the season, by diadromous spawners or freshwater [11,15]. Environmental conditions influenced the abundance and diversity of larval fish in different functional groups [16]. For example, González-Ortegón et al. (2012) showed that marine species tended to be more abundant in dry years in the Guadalquivir estuary [17]. Larval fish are more sensitive to environmental changes than adults [18,19]. Highly dynamic environments occur in estuarine systems, which are caused by a variety of physical processes [20]. Therefore, the survival of larval fish could be influenced by environmental conditions, including salinity, temperature, turbidity, dissolved oxygen, depth, sediment characteristics, and hydrographic events [4,21]. River freshwater inflows also play a very important role in determining the larval fish community in the estuary [17]. Variations in salinity and freshwater inputs are interdependent and seasonally related [22]. The spatial and temporal variation in the habitats of larval fish has been widely studied in estuarine ecology, including tropical estuaries [20,22,23] and temperate estuaries [11,24]. The succession of larval fish assemblages in temperate estuaries is mainly caused by seasonal fluctuations in environmental factors, such as temperature [25]. It was shown that salinity and freshwater flows played major roles in modeling the larval fish assemblage structure in tropical estuaries [26]. The temperature was presumably related to the adult fish spawning periods [27]. Salinity was found to be an important factor in the diversity of estuarine fish composition, and freshwater flows were identified as a contributing factor in the characterization of fish assemblages in different seasons [22].

The Yangtze Estuary is the largest estuary in China, and its environmental characteristics are particularly complicated and varied [14,28]. For example, the annual average salinity of the north branch is about ten times greater than that of the south branch [29]. About 100 larval fish species have been found in the Yangtze Estuary, which serves as an important nursery ground for fish [13,30]. The dominant larval fish families mainly include Clupeidae, Engraulidae, and Gobiidae. The seasonal variation in the abundance of larval fish varies drastically, usually peaking in the spring and summer [14,30,31]. It may be an adaptation of the dominant species to avoid fierce competition and make full use of the habitat resources in the Yangtze Estuary [32,33]. The larval fish assemblage structure and dynamic changes in the Yangtze River estuary are closely related to the seasonal changes in environmental conditions [33–35]. Two studies found that salinity, temperature, chlorophyll a, and total suspended particulate matter were the major environmental conditions affecting the larval fish assemblages in the study areas [36]. The dynamics of freshwater flows lead to changes in environmental conditions, which may alter the proportion of larval fish from different ecological guilds. Previous studies, however, have primarily focused on the south branch and outside the mouth of the Yangtze Estuary [4,16], leaving out high-density sampling data for a variety of water profiles, including the south and north branches. Therefore, it is still not clear how the freshwater flows affect the seasonal changes in the number of larval fish from different ecological groups inside the Yangtze Estuary.

This study conducted a high-spatial-resolution larval fish survey in the Yangtze Estuary in the springs and summers from 2018 to 2020. We divided the larval fish into different ecological guilds to reveal the dominant species and their relationship with environmental conditions. We further explored the dynamics of the dominant species of different ecological guilds and the special distinction of larval fish habitats in the complex hydrological environment of the Yangtze Estuary.

2. Materials and Methods

2.1. Study Area

The Yangtze Estuary is the biggest estuary in China, with special geographical conditions and specific environmental conditions. The estuary is mainly occupied by Chongming Island, and the area is divided into north and south branches (Figure 1). The south branch is bisected by two successive islands, Changxing and Hengsha Islands, forming the north and south channels. At the outermost end of the estuary, Jiuduansha Shoal divides the outflows to the north and south passage to the open sea. The different areas of the Yangtze Estuary are geographically similar, but their hydrological conditions are different, being under the influence of water masses such as the freshwater inflows of the Yangtze River, the offshore water mass, and the coastal current [28].

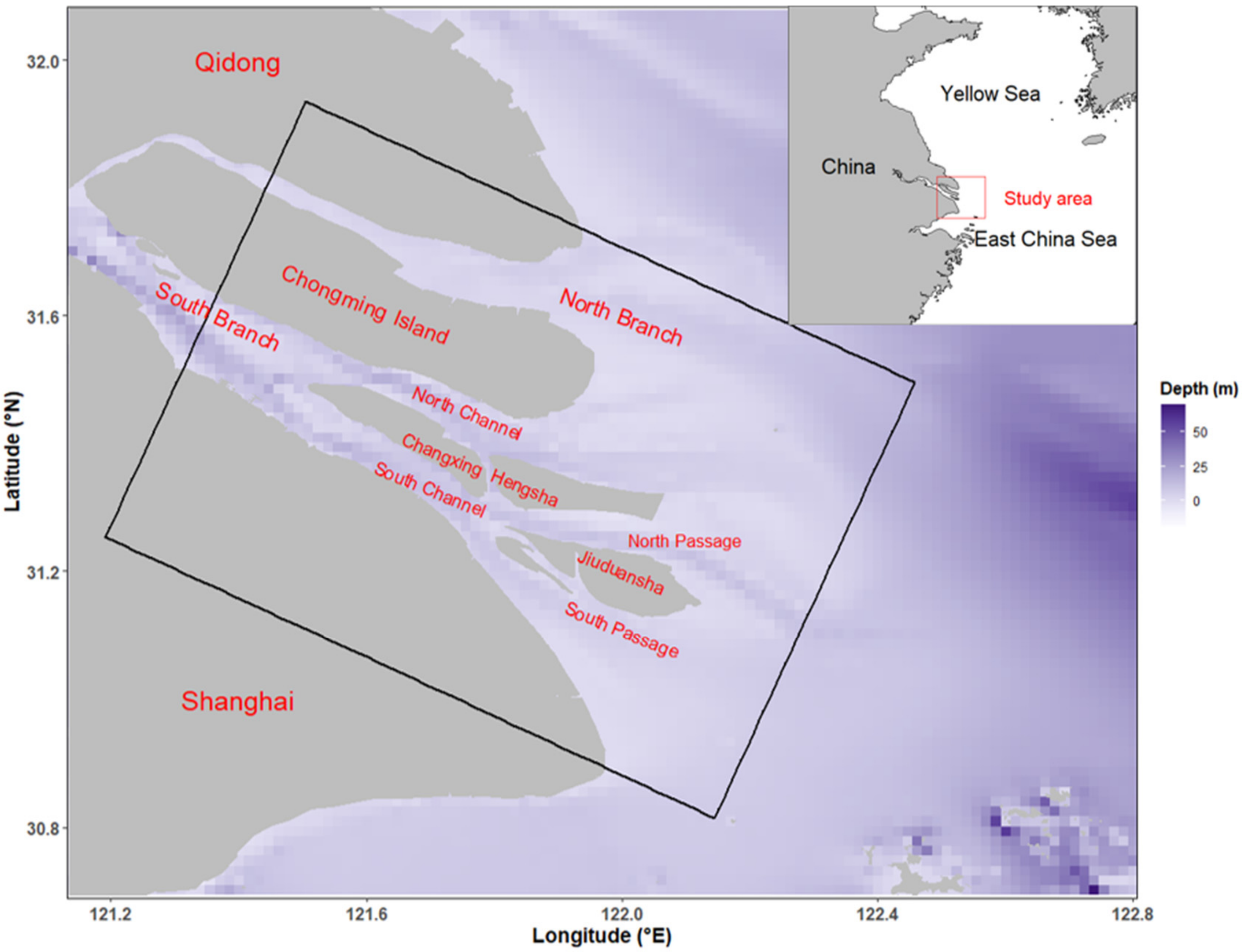

Figure 1. Location of study area in the Yangtze Estuary.

2.2. Sampling Surveys and Data Collection

A series of six surveys (June 2018, July 2018, May 2019, August 2019, May 2020, and August 2020) were conducted in the Yangtze River estuary (30.8° N–31.7° N, 121.3° E–122.5° E) based on a stratified random design between 2018 and 2020 (Figure 2). The study area can be separated into four regions: inside the north branch (A), inside the south branch (B), outside the north branch (C), and outside the south branch (D). Fifty-five stations from 182 grid cells per survey were scheduled for sampling. Grid cells had a resolution of 3′ × 3′. The number of stations in regions A, B, C, and D was 12, 10, 25, and 8, respectively. A total of 328 stations were investigated (50 stations in June 2018, 55 stations in July 2018, 57 stations in May 2019, 55 stations in August 2019, 56 stations in May 2020, and 55 stations in August 2020) (Appendix A, Figure A1). Sampling was performed during the daytime using a plankton net (0.505 mm mesh size, 80 cm in diameter, and 145 cm in length), towed horizontally under the surface for 10 minutes at a constant speed of 2–3 knots. The volume of water filtered during each tow was estimated using a digital flowmeter (Hydro Bios 438115) attached across the center of the net mouth. The depth, temperature, salinity, and chlorophyll a were measured using a Sea-bird 19plus V2 CTD. The Yangtze River inflows data measured at Datong station (117°37′ E, 30°46′ N) were acquired from the Changjiang Water Resources Commission of the Ministry of Water Resources (http://www.cjw.gov.cn accessed on 16 January 2022).

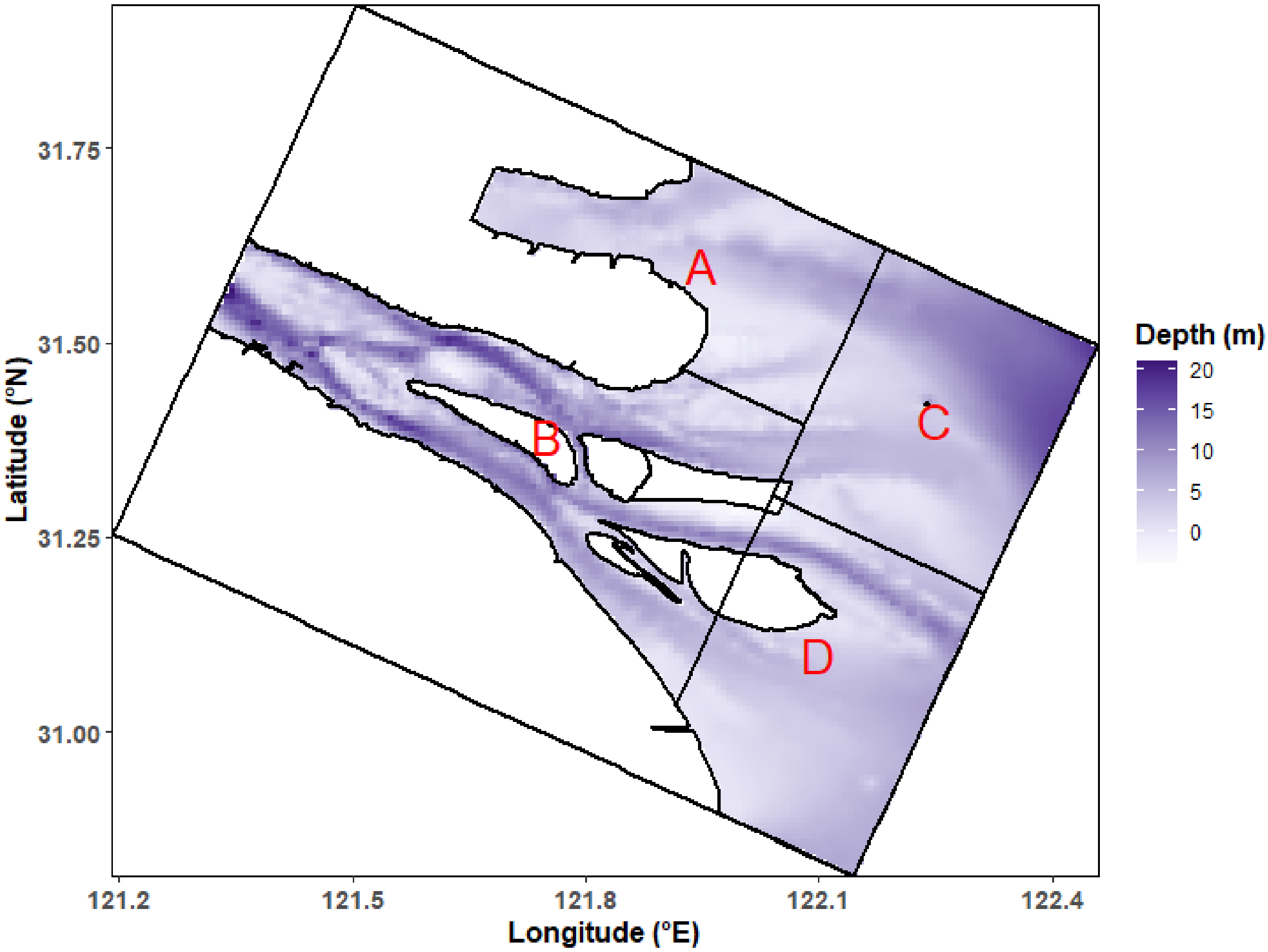

Figure 2. Stratified random sampling regions in the Yangtze Estuary.

The samples were preserved in 5% formaldehyde in seawater and transported to the laboratory for later analysis. All larvae were identified to the species level or to the lowest possible taxon based on existing literature [37–39]. The larval fish in the Yangtze Estuary were divided into three ecological guilds: freshwater (F), brackish water (B), and marine (M) (Figure 3) after combining the clustering results of our six cruises with the related literature [13,14].

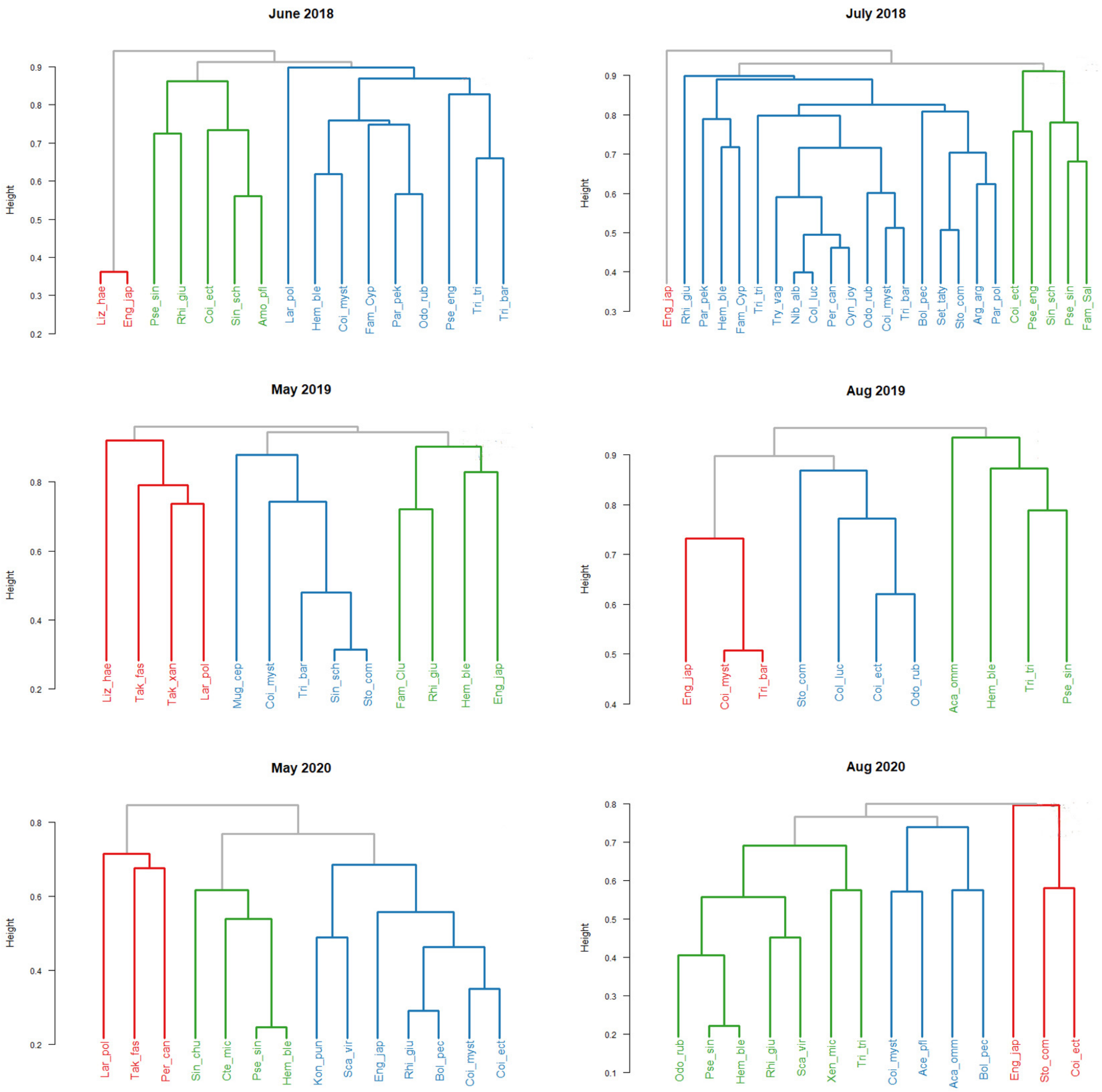

Figure 3. Hierarchical clustering for the species with occurrence >5% in each cruise (blue: brackish water; green: freshwater; red: marine).

2.3. Data Analyses

The abundance of larval fish was standardized and expressed as the total number of individual fish larvae per 100 m^3 by the volume of water filtered (ind./100 m^3). The dominant species in each ecological guild were determined using the Index of Relative Importance (IRI) developed by Zhu et al. (2002) [40]. Margalef's richness (D), the Shannon–Wiener index (H′), and Pielou's evenness (J′) were calculated for each station to show the diversity of larval fish in different ecological guilds [41]. Due to the multicollinearity of environmental factors, the variance inflation factor (VIF) test was used to select environmental factors. The VIF should be less than 10 (Wang et al., 2021). Longitude (Long), latitude (Lat), depth (Dep), sea surface temperature (SST), sea surface salinity (SSS), and sea surface chlorophyll a (SSChl) were selected.

Multivariate analysis methods were used to analyze the relationship between the larval assemblage and environmental factors [4,11]. Larval fish abundance data were first log-transformed as [log (x + 1)] before multivariate analysis to minimize the influence of extreme values [42]. Only species with an occurrence >5% for each cruise were included in the multivariate analysis to remove any undue effects of rare species on the analysis [11]. Distance measures that are non-Euclidean (such as Bray–Curtis or other ecologically meaningful measures) can be selected in distance-based redundancy analysis (db-RDA) [27]. In this study, a db-RDA with a Bray–Curtis distance measure was used to analyze the larval assemblage structure and the relationship of the assemblage structure to environmental characteristics (including Long, Lat, Dep, SST, SSS, and SSChl) for each year. A forward selection method was used to select significant explanatory variables (permutation p-values < 0.05) with 999 unrestricted permutations in db-RDA.

All the analyses were carried out with the R 64-bit (version 4.0.2, 64-bit) software (https://www.r-project.org accessed on 22 July 2020), using the package "vegan" for db-RDA analysis and the package "ggplot2" for figures and maps.

3. Results

3.1. Hydrographic Conditions

SST was the most variable parameter, whose mean value ranged between 21.93 °C and 29.14 °C in all six cruises (Table 1). Its value was lowest in May 2019 and highest in August 2020 (Table 1). The mean value of SST in May and August 2020 was higher than that in 2019 (Table 1). Generally, the SST value was higher in the south branch than in the north branch (Figure 4). The mean value of SSS ranged from 3.76 to 7.47, with the lowest value in June 2018 (Table 1). SSS showed an opposite pattern to that of SST, with a higher value in the north branch and a lower value in the south branch (Figure 4). In different months, the regions of low salinity were different, being larger in summer (June, July, August) and smaller in spring (May) (Figure 4). The mean value of SSChl ranged from 0.55 to 1.16 mg/m^3 (Table 1). In general, a higher SSChl value was observed outside the mouth of the estuary (Figure 4). The Yangtze River flows showed an upward trend from May to July and began to decline in August, which was the opposite trend to salinity (Figure 5). During our research period, the minimum value (597.3 million m^3) was reached in May 2020. Compared with 2019, the Yangtze River flow in May 2020 was smaller, but it was larger in August 2020.

3.2. The Composition and Abundance of Larval Fish

Overall, 145,434 larval fish were collected from 328 plankton tows. They belonged to 26 families and 99 taxa (Appendix A, Table A1). Of the 99 taxonomic groups, 90 taxa were identified to the genus or species level, 7 taxa were identified to the family level, and 2 taxa were unidentified (Appendix A, Table A1). Three families were predominant in the survey, accounting for 94.5% of the total abundance (Engraulidae, 61.0%; Cyprinidae, 17.8%; Gobiidae, 15.7%) (Appendix A, Table A1). The taxa in Gobiidae were the most numerous (25 species). The number of species in each ecological guild was relatively uniform, including freshwater species (27 species), brackish water species (35 species), and marine species (35 species). Clupeidae, Engraulidae, and Sciaenidae were identified as marine species, except *Konosirus punctatus*, *Coilia mystus*, and *Coilia ectenes*, which were brackish water species. Cyprinidae and Salangidae were identified as freshwater species. Most species of Gobiidae were brackish water species (Figure 3). The freshwater species mainly came from the Cyprinidae (e.g., *Pseudolaubuca sinensis*) and Salangidae (e.g., *Neosalanx tangkahkeii*) families. Brackish water species mainly included *Coilia nasus* and *Coilia mystus* from the Engraulidae family and *Boleophthalmus pectinirostris* and *Parachaeturichthys polynema* from the Gobiidae family. Marine species mainly came from the Engraulidae (e.g., *Engraulis japonicas*) and Sciaenidae (e.g., *Larimichthys polyactis*) families (Appendix A, Table A1).

Table 1. Mean values for depth (Dep, m), sea surface temperature (SST, °C), sea surface salinity (SSS), and sea surface chlorophyll a (SSChl, mg/m^3) sampled during six cruises in the Yangtze Estuary (±95% confidence interval).

Cruises	Dep	SST	SSS	SSChl	Stations	No. of Larvae
June 2018	7.70 ± 1.10	24.55 ± 0.30	3.76 ± 1.54	0.94 ± 0.16	50	7357
July 2018	7.71 ± 1.19	27.42 ± 0.39	5.56 ± 1.81	0.55 ± 0.07	55	16,964
May 2019	5.14 ± 1.10	21.93 ± 0.22	7.47 ± 2.28	0.88 ± 0.14	57	29,789
Aug 2019	7.99 ± 1.15	28.95 ± 0.23	5.70 ± 1.93	0.82 ± 0.15	55	2512
May 2020	7.05 ± 1.11	22.35 ± 0.23	7.38 ± 1.91	1.16 ± 0.15	56	82,650
Aug 2020	7.52 ± 1.29	29.14 ± 0.41	4.30 ± 1.87	0.88 ± 0.13	55	6162

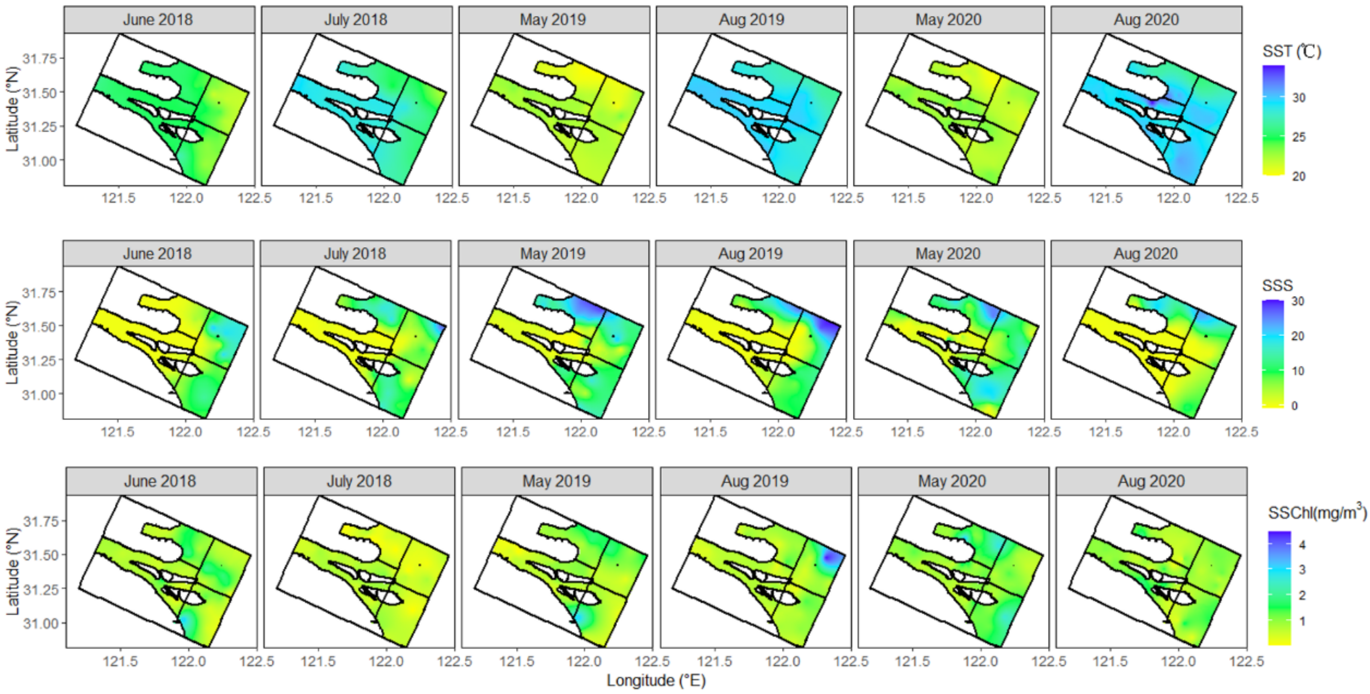

Figure 4. The distribution of environmental factors in the Yangtze Estuary (SST, sea surface temperature; SSS, sea surface salinity; SSChl, sea surface chlorophyll a).

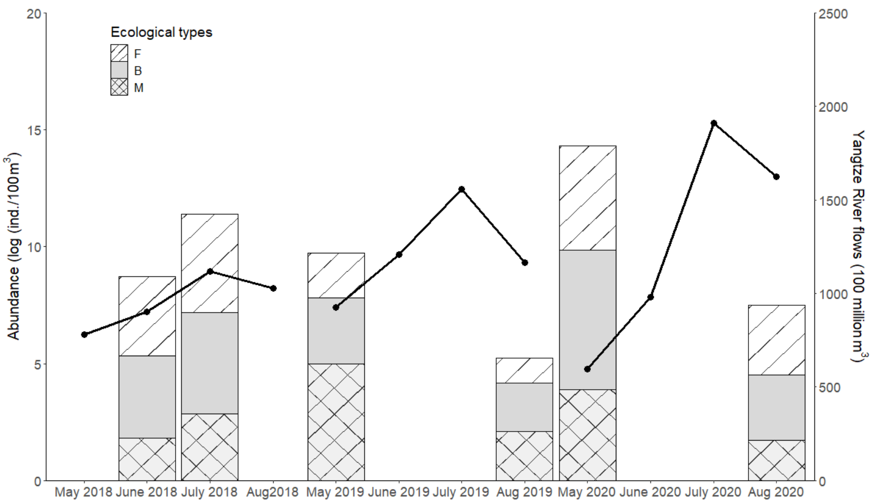

Figure 5. Mean abundance (log (ind./100 m^3)) of larval fish of different ecological guilds and the Yangtze River flows (100 million m^3) from May to August during 2018, 2019, and 2020 (bar plot for abundance of larval fish; line plot for Yangtze River flows).

The richness values were the lowest in 2019 and highest in 2018 (Table 2). The highest abundance values were found in spring (May) and the lowest occurred in summer (August). The fifth cruise (29,221.3 ind./100 m^3) was the greatest contributor to the total abundance (Table 2). Different change trends were found in the abundance of larval fish from different ecological guilds. The mean abundance of larval fish showed similar tendencies in freshwater species and brackish water species, while the abundance of marine species showed opposite tendencies (Figure 5). The abundance of marine species peaked in May 2019 (8409.8 ind./100 m^3), while brackish water species peaked in May 2020 (21,713.0 ind./100 m^3) (Table 2). In this study, IRI was used to determine the dominant species. Four species were the predominant species: *Hemiculter bleekeri*, *P. sinensis*, *C. mystus*, and *E. japonicas*, respectively (Table 3). *Boleophthalmus pectinirostris* turned into the dominant species only in May 2020, and *Odontamblyopus rubicundus* was dominant only in August 2020. *E. japonicas* was the only dominant species in May 2019. Over the six cruises, *H. bleekeri*, and *P. sinensis* showed nearly the same change trend (Figure 6). However, *C. mystus* (brackish water) accounted for the greatest proportion of the abundance in May 2020, while *E. japonicas* (marine) made up the greatest proportion in May 2019. Peak abundances of 14,112.0 ind./m^3 and 8263.0 ind./m^3 were recorded for *C. mystus* and *E. japonicas*, respectively.

Table 2. Abundance (ind./100m^3) and taxonomic richness (no. of taxa) of different ecological guilds sampled during six cruises in the Yangtze Estuary.

Ecological Guilds	Abundance (Taxonomic Richness)					
	June 2018	**July 2018**	**May 2019**	**Aug 2019**	**May 2020**	**Aug 2020**
Freshwater	1840.7 (17)	3676.4 (19)	384.3 (9)	155.6 (2)	4725.1 (9)	1081.1 (8)
Brackish water	1663.1 (18)	4116.8 (20)	957.0 (8)	447.4 (14)	21,713.0 (21)	923.4 (18)
Marine	313.2 (13)	961.5 (19)	8409.8 (12)	445.3 (9)	2783.2 (14)	305.1 (13)
Total	3817.0 (48)	8754.7 (58)	751.1 (29)	1048.3 (25)	29,221.3 (44)	2309.6 (39)

Table 3. IRI (IRI > 500) of dominant species of different ecological guilds in the Yangtze Estuary.

Species	Ecological Guilds	June 2018	July 2018	May 2019	Aug 2019	May 2020	Aug 2020
Hemiculter bleekeri	Freshwater	1884	-	-	-	-	1101
Pseudolaubuca sinensis	Freshwater	-	1196	-	-	-	797
Coilia mystus	Brackish water	1220	830	-	668	3769	-
Boleophthalmus pectinirostris	Brackish water	-	-	-	-	999	-
Odontamblyopus rubicundus	Brackish water	-	-	-	-	-	1194
Engraulis japonicas	Marine	-	-	5844	1824	-	-

3.3. Spatial Heterogeneity of Communities

All the ecological guilds were collected during each sampling cruise, but the spatial distribution of these ecological guilds differed. Freshwater species were mainly distributed in region B, with relatively high SST and low SSS (Figures 4 and 7). The brackish water species (e.g., *C. mystus*) were mainly distributed in region A in both 2018 and 2019. However, they extended to region D in 2020. Marine species were mainly distributed in region A and less distributed in region B (Figure 7). The spatial distribution patterns of the three diversity indices were relatively similar (Appendix A, Figure A2). In regard to marine species, it was shown that there was a different distribution pattern between the abundance and diversity index. The high diversity values were distributed in region A and region D, which meant that the marine larval fish in region D were diverse but low in abundance (Figures 7 and A2).

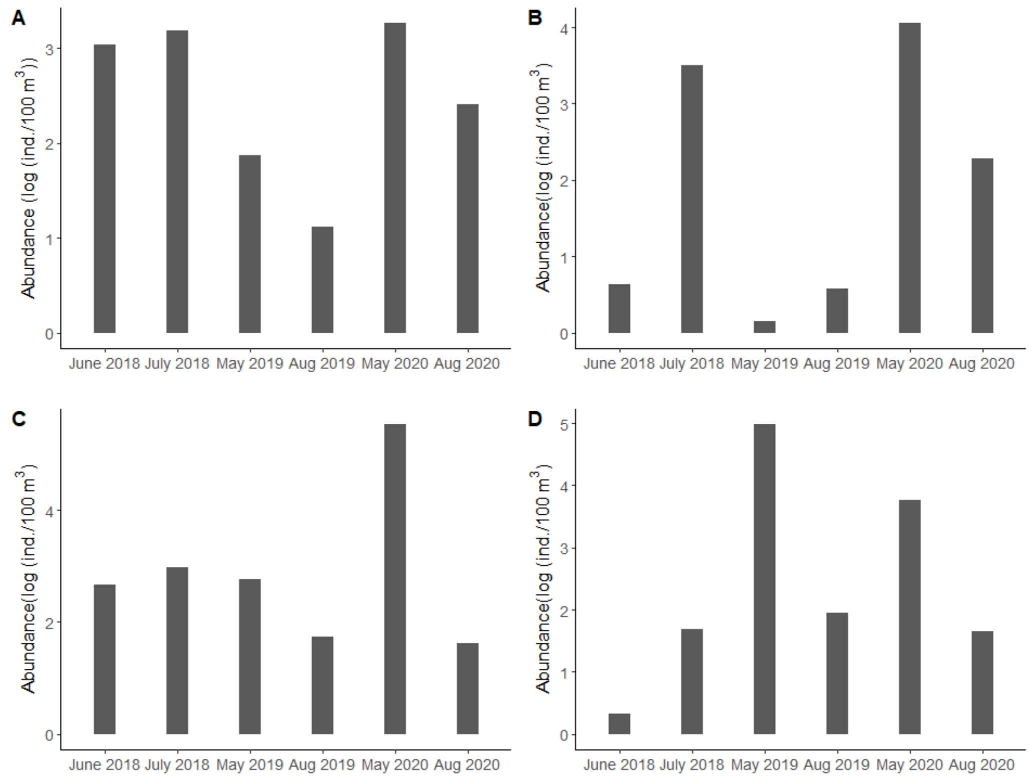

Figure 6. Mean abundance (log (ind. /100 m^3)) of four mainly dominant species collected during six cruises ((**A**), *Hemiculter bleekeri*; (**B**), *Pseudolaubuca sinensis*; (**C**), *Coilia mystus*; (**D**), *Engraulis japonicus*).

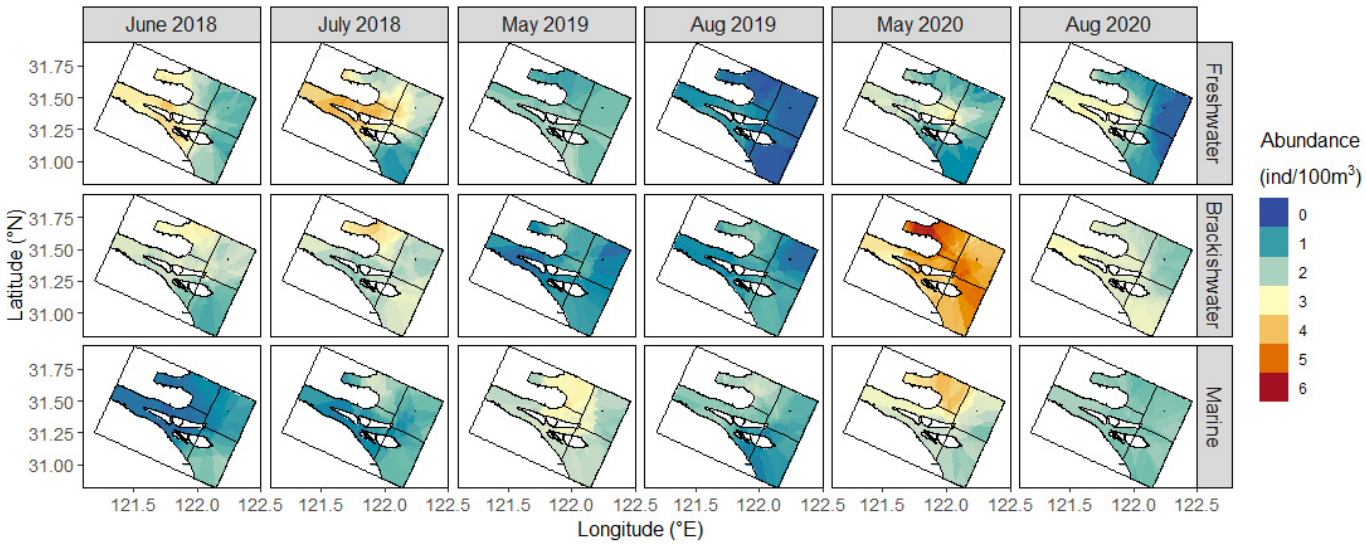

Figure 7. The distribution of abundance (log (ind./100 m^3)) of larval fish of different ecological guilds.

3.4. Relationship between Environmental Factors and Community Structure

The relationships between sampling sites, environmental variables, and the species collected were clarified in the db-RDA for each year (Figure 8). Superimposing the species abundance data enabled the identification of the species with the highest affinity to some environmental variables and sites. SST and SSS were significant in affecting the larval fish community structure in all three years ($p < 0.05$). Latitude, longitude, and SSChl, as well as latitude, longitude, and depth, were also included in 2018 and 2020, respectively. In all three years, the first axis was positively correlated with SST, and samples moved along the direction of SST. For the second axis, SSS exerted a negative effect. Different ecological guild species showed patterns with dispersed distribution, and freshwater species, brackish water species, and marine species moved along the direction of SSS. However, SST showed the opposite relationship with the second axis in 2019 (0.2640) and 2020 (−0.1536). The same state occurred in SSS with the first axis in 2019 (0.2357) and 2020 (−0.3051). Overall, the results indicate that SST is the key environmental variable influencing seasonal changes, and SSS is influencing the distribution of species in the larval fish community in the Yangtze Estuary.

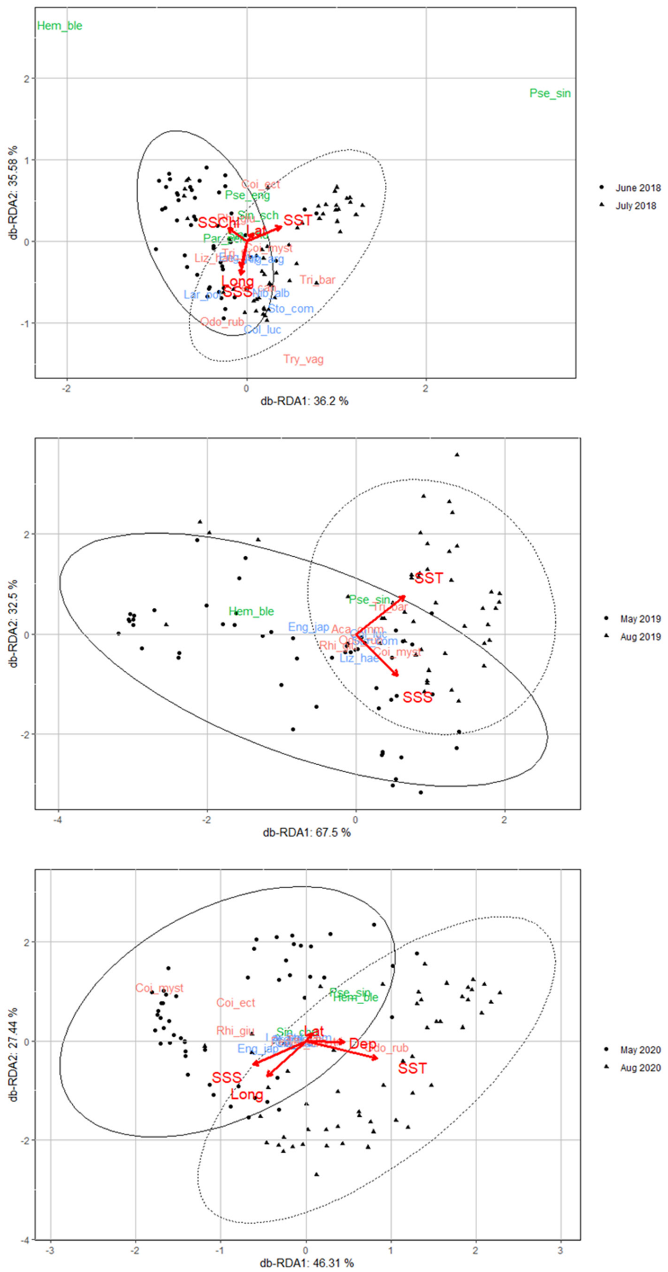

Figure 8. Ordination plot resulting from distance-based redundancy analysis (db-RDA) for the larval fish community using Bray−Curtis distance, examining the relationship between the sampling sites (points), the significant environmental variables (red arrows, $p < 0.05$), and species abundance (colored font: green for freshwater species, pink for brackish water species, and blue for marine species, only species with occurrence >5%). Environmental variables were latitude (Lat), longitude (Long), sea surface temperature (SST, °C), depth (Dep, m), sea surface salinity (SSS), and sea surface chlorophyll a (SSchl, mg/m^3).

4. Discussion

The environmental conditions of the Yangtze Estuary fluctuated across seasons and topography [28]. SSS in spring (May) was higher than that in summer (June, July, and August), whereas SST was the opposite. Interannual change in these environmental conditions was closely related to the rhythm of the river runoff [6]. The salinity gradients in many estuarine ecosystems can be seriously affected by freshwater flows [43]. The Yangtze Estuary is a complex estuarine system with a highly seasonal freshwater inflow, especially in summer [16,39]. In this study, the Yangtze River flows showed an upward trend from May to July and began to decline in August. The Yangtze Estuary, which is primarily influenced by Yangtze River flows, coastal currents, strong tides, and river bed landforms, also showed geographical variability in environmental influences [4]. Lower SST and higher SSS were found in the north branch, and the opposite situation was found in the south branch of the Yangtze Estuary [44]. The regulation function upstream of the Three Gorges Reservoir had a certain impact on the runoff of the Yangtze River [36]. The reduction in the freshwater discharge of the Yangtze River resulted in the significant retreat of the river plume and, consequently, saline water incursion [28]. Coastal currents affected the offshore area (i.e., regions C and D) (Figure 2). As a result, the complex environmental differences in our study were significant in the Yangtze Estuary.

This study used high-spatial-resolution larval fish survey data to reveal the dynamics of different ecological guilds of larval fish in a typical temperate estuary during the springs and summers of 2018, 2019, and 2020. Compared to large-scale studies, the variability of the larval fish assemblage can be better tested using fine-scale studies [4]. The 99 taxa and 145,434 individuals that make up our community are a good reflection. Moreover, the number of taxa and the abundance of larval fish in our study were higher than in previous studies carried out in adjacent areas of the Yangtze River Estuary, perhaps because of the different seasons that are studied. For example, in the spring seasons of 1999 and 2001, 32 species and 11,540 individuals of ichthyoplankton were recorded in adjacent areas of the Yangtze River Estuary [34]. From 2010 to 2012, only 26 species in 12 families were collected in spring [36].

In our study, three ecological guilds were classified (Figure 3). Previous literature on the larval fish assemblage in the Yangtze Estuary divided the species into four ecological guilds; however, three were found in our study, perhaps due to our focus on the mouth of the Yangtze Estuary [4,13,14]. Among the three ecological guilds, freshwater species are known to complete their life cycle in the freshwater part of the estuarine system (i.e., Clupeidae). However, some brackish water species complete their spawning in freshwater, and thereafter, the larvae move to the seawater, where adults are mainly marine inhabitants (i.e., *C. mystus*). Marine species are typically marine inhabitants, but for the development of larval and juvenile stages, they frequently move to estuarine systems. Therefore, the abundance and diversity distribution of different ecological guilds also provide information on the spatial and temporal dynamics in the study area. The results showed that the abundance and diversity distribution of different ecological guilds were relatively uniform, indicating that the spatial and temporal dynamics of the larval fish assemblage were caused by environmental heterogeneity in the Yangtze Estuary (Figures 7 and A2).

The view that estuaries are key nursery habitats for fish has been widely recognized. The fish communities are usually dominated by resident species belonging to the Gobiidae family and seasonal spawners such as species from the Engraulidae family [11,12]. The high abundances of fish from these families in estuaries are mainly due to the presence of several dominant species, as typically observed for adult fish communities [32,45,46]. Differences in the community of larval fish are mainly related to the abundance of dominant species of different ecological guilds. In the south branch of the Yangtze Estuary, the community was essentially characterized by the abundance of freshwater species, especially *H. bleekeri* and *P. sinensis*. For the north branch of the Yangtze Estuary, the abundance of brackish water species and marine species together influenced the differences in the community. *C. mystus* and *E. japonicas*, which belong to the Engraulidae family, comprise a large portion of the larval fish community in the Yangtze Estuary. *C. mystus* was responsible for the high abundance in May 2020. A previous study also showed higher egg production of *C. mystus* in the Yangtze Estuary [44]. However, the abundance of *E. japonicas* peaked in May 2019. The different interannual peak abundance values of *C. mystus* and *E. japonicas* shown in our study, as well as in other studies [4,36], may be due to niche overlap between the two species. Thus, a study on the niche overlap of the early life stage of *C. mystus* and *E. japonicas* is necessary to verify this inference and hypothesis. Moreover, the abundance of *C. mystus* peaked with higher SST (22.35 ± 0.23 °C) and lower SSS (7.38 ± 1.91), whereas the abundance of *E. japonicas* peaked with lower SST (21.93 ± 0.22 °C) and higher SSS (7.47 ± 2.28). The differences between *C. mystus* and *E. japonicas* may also be caused by optimal differential environments for growth during the early life stages. Thus, longer-term sampling series need to be collected to answer these questions. For example, do the shifts between *C. mystus* and *E. japonicas* occur rapidly? How do they relate to the environmental variables?

Similar to other estuaries (e.g., Lima estuary) [11,42], SST and SSS explained most of the environmental change experienced by the larval fish community. SST was found to be a significant environmental variable, likely due to its demonstrated role in larval fish survival [27]. Variations in temperature could manipulate the physiology and behavior of fishes and ultimately affect the abundance of selected fish [22]. In temperate estuaries, species usually peak in the spring and summer because of the interannual changes in temperature [14,25]. The db-RDA showed that samples moved along the direction of SST, which indicated that the temperature closely influenced the seasonal variations in larval fish assemblage structure. Salinity is also a key variable contributing to spatiotemporal variability in the assemblage structure of fish in estuaries [4]. Areas with different salinity support fish assemblages belonging to different ecological guilds. Moreover, low-salinity coastal systems considerably influence the hatching and development of fish at the early stage [36]. The abundance of the dominant species is also influenced by environmental variables, such as low salinities from high freshwater inflow limited bay anchovy (*C. mystus* and *E. japonicas*) production in the inshore area of the Yangtze Estuary [36].

Freshwater flow is also a significant factor influencing the relative abundance of larval fish [26]. Freshwater flows generate a gradational and dynamic estuarine environment, which consequently determines and alters the spatial patterns of larval fish assemblages along the salinity gradient [47]. In the Yangtze Estuary, Gao et al. (2018) indicated that freshwater flow is a major factor shaping the patterns of larval fish assemblages in the south branch [16]. Within the South branch of the Yangtze Estuary, larval fish occurred year-round and peaked from May to August, mainly influenced by temperate and freshwater flows [14,16]. In our study, the abundance of larval fish showed the opposite trend when the Yangtze River flows peaked, perhaps due to the influence of the retention effect of larval fish in the nursery ground. Unfortunately, the relationship between larval fish assemblage and freshwater flows could not be studied due to a lack of real-time freshwater flows during our investigation period. Further research is needed to investigate the effect of the freshwater flow on the estuary ecology.

5. Conclusions

In conclusion, the study showed that the larval fish assemblage in the Yangtze Estuary is composed of a few species with high abundance and a large number of other species, and it is structured according to environmental conditions. SST and SSS were the key variables influencing the larval fish species composition and abundance. In this study, the quantity of larval fish demonstrated the opposite tendency as the freshwater flow increased. The abundance, richness, and variety of species varied widely throughout the Yangtze Estuary's various regions. The regional distribution of the community of larval fish was mostly influenced by salinity variation. The community assemblage pattern may change to adapt in response to changes in various environmental variables.

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Appendix A

Table A1. Larval fish abundance and their occurrence in the Yangtze Estuary.

Family	Species	Code	EG	Total Abundance (ind. /100 m^3)	Occurrence in Samples
Megalopidae	*Megalops cyprinoides*		B	1.02	2
Clupeidae	*Sardinella zunasi*		M	13.93	2
	Sardinella spp.		M	57.12	6
	Ilisha elongate		M	24.21	4
	Konosirus punctatus	Kon_pun	B	97.44	12
	Clupeidae spp.		M	6.83	3
Engraulidae	*Engraulis japonicus*	Eng_jap	M	11,450.02	130
	Stolephorus commersonii	Sto_com	M	711.86	48
	Stolephorus spp.		M	6.44	2
	Setipinna taty	Set_taty	M	44.25	14
	Coilia mystus	Coi_myst	B	17,124.26	165
	Coilia ectenes	Coi_ect	B	3926.86	60
Salangidae	*Neosalanx tangkahkeii*		F	48.09	11
	Neosalanx jordani		F	6.32	2
	Protosalanx chinensis		F	23.75	3
	Neosalanx anderssoni		F	0.24	1
	Hemisalanx prognathus		F	4.73	2
	Salangidae spp.	Fam_Sal	F	104.99	9
Synodontidae	*Saurida elongata*		M	18.71	5
	Harpadon nehereus		M	12.26	6
Anguillidae	*Anguilla japonica*		M	0.46	1
Cyprinidae	*Elopichthys bambusa*		F	0.53	1
	Ctenopharyngodon idellus		F	1.70	2
	Mylopharyngodon piceus		F	3.49	3
	Cultrichthys erythropterus		F	3.20	5
	Parabramis pekinensis	Par_pek	F	40.10	23
	Hemiculter bleekeri	Hem_ble	F	4406.88	111
	Hemiculter spp.		F	21.57	1
	Pseudolaubuca sinensis	Pse_sin	F	4395.62	96
	Pseudolaubuca engraulis	Pse_eng	F	135.65	18
	Pseudorasbora parva		F	15.77	3
	Xenocypris microlepis	Xen_mic	F	25.56	11
	Squalidus argentatus		F	2.64	2
	Saurogobio dabryi		F	21.98	3
	Acheilognathin spp.		F	1.94	2

Table A1. *Cont.*

Family	Species	Code	EG	Total Abundance (ind. /100 m^3)	Occurrence in Samples
	Cyprinus carpio		F	0.60	1
	Carassius auratus		F	1.83	3
	Toxabramis swinhonis		F	3.46	3
	Cyprinidae spp.	Fam_Cyp	F	643.81	20
Siluridae	*Silurus asotus*		F	2.57	5
Hemirhamphidae	*Hyporhamphus intermedius*		M	0.57	1
Mugilidae	*Liza haematocheila*	Liz_hae	M	88.40	25
	Mugil cephalus	Mug_cep	B	42.56	4
Polynemidae	*Eleutheronema rhadinum*		B	0.24	1
Serranidae	*Lateolabrax maculatus*		B	33.58	22
	Siniperca chuatsi		F	133.97	27
	Siniperca scherzeri		F	46.43	25
Apogonidae	*Apogonichthys lineatus*		M	183.05	1
Sillaginidae	*Sillago sihama*		M	3.68	2
Sciaenidae	*Johnius belengerii*		M	0.47	1
	Nibea albiflora	Nib_alb	M	32.89	18
	Argyrosomus argentata	Arg_arg	M	60.45	21
	Argyrosomus japonicus		M	0.41	1
	Larimichthys polyactis	Lar_pol	M	265.41	30
	Collichthys niveatus		M	1.24	1
	Collichthys lucidus	Col_luc	M	131.87	30
	Miichthys miiuy		M	3.57	1
Pomadasyidae	*Hapaloyenys mucronatus*		M	0.88	2
Theraponidae	*Therapon* spp.		M	1.26	2
	Therapon jarbua		M	0.96	1
Blenniidae	*Omobranchus elegans*		M	1.99	4
	Blenniidae spp.		M	0.28	1
Zoarcidae	Zoarcidae spp.		M	1.19	1
Ammodytidae	*Ammodytes personatus*		M	1.27	2
Eleotridae	*Valenciennea* sp.		B	0.36	1
Gobiidae	*Acanthogobius flavimanus*		B	39.70	7
	Acanthogobius ommaturus	Aca_omm	B	61.87	40
	Amblychaeturichthys hexanema		B	24.13	14
	Amoya pflaumi	Amo_pfl	B	79.20	9
	Glossogobius olivaceus		B	7.08	5
	Lophiogobius ocellicauda		B	0.89	1
	Parachaeturichthys polynema	Par_pol	B	1907.09	14
	Pseudogobius javanicus		B	17.45	13
	Rhinogobius giurinus	Rhi_giu	B	1160.88	119
	Tridentiger barbatus	Tri_bar	B	503.16	77
	Tridentiger trigonocephalus	Tri_tri	B	84.23	43
	Boleophthalmus pectinirostris	Bol_pec	B	3443.26	66
	Periophthalmus cantonensis		B	80.59	27
	Scartelaos virids	Sca_vir	B	239.33	61
	Ctenotrypauchen chinensis		B	0.60	1
	Ctenotrypauchen microcephalus	Cte_mic	B	164.16	20
	Odontamblyopus rubicundus	Odo_rub	B	507.12	88
	Trypauchen vagina	Try_vag	B	142.26	24
	Polyspondylogobius sinensis		B	1.68	2
	Luciogobius guttatus		B	5.69	6

Table A1. *Cont.*

Family	Species	Code	EG	Total Abundance (ind. /100 m^3)	Occurrence in Samples
	Cryptocentrus filifer		B	18.03	10
	Amblychaeturichthys sciistius		B	0.37	1
	Acentrogobius pflaumii	Ace_pfl	B	67.93	30
	Acanthogobius lactipes		B	0.37	1
	Gobiidae spp.		B	23.89	3
Trichiuridae	*Trichiurus japonicus*		M	0.57	2
Stromateidae	*Pampus cinereus*		M	0.26	1
	Pampus echinogaster		M	0.70	2
Cynoglossidae	*Cynoglossus joyneri*	Cyn_joy	B	11.95	9
	Cynoglossus robutus		B	1.40	1
Tetraodontidae	*Takifugu fasciatus*	Tak_fas	M	81.90	29
	Takifugu xanthopterus	Tak_xan	M	8.69	4
	Unidentified spp1.			0.36	1
	Unidentified spp2.			45.08	7

Notes. EG, Ecological guild; M, Marine; B, Brackish water; F, Freshwater.

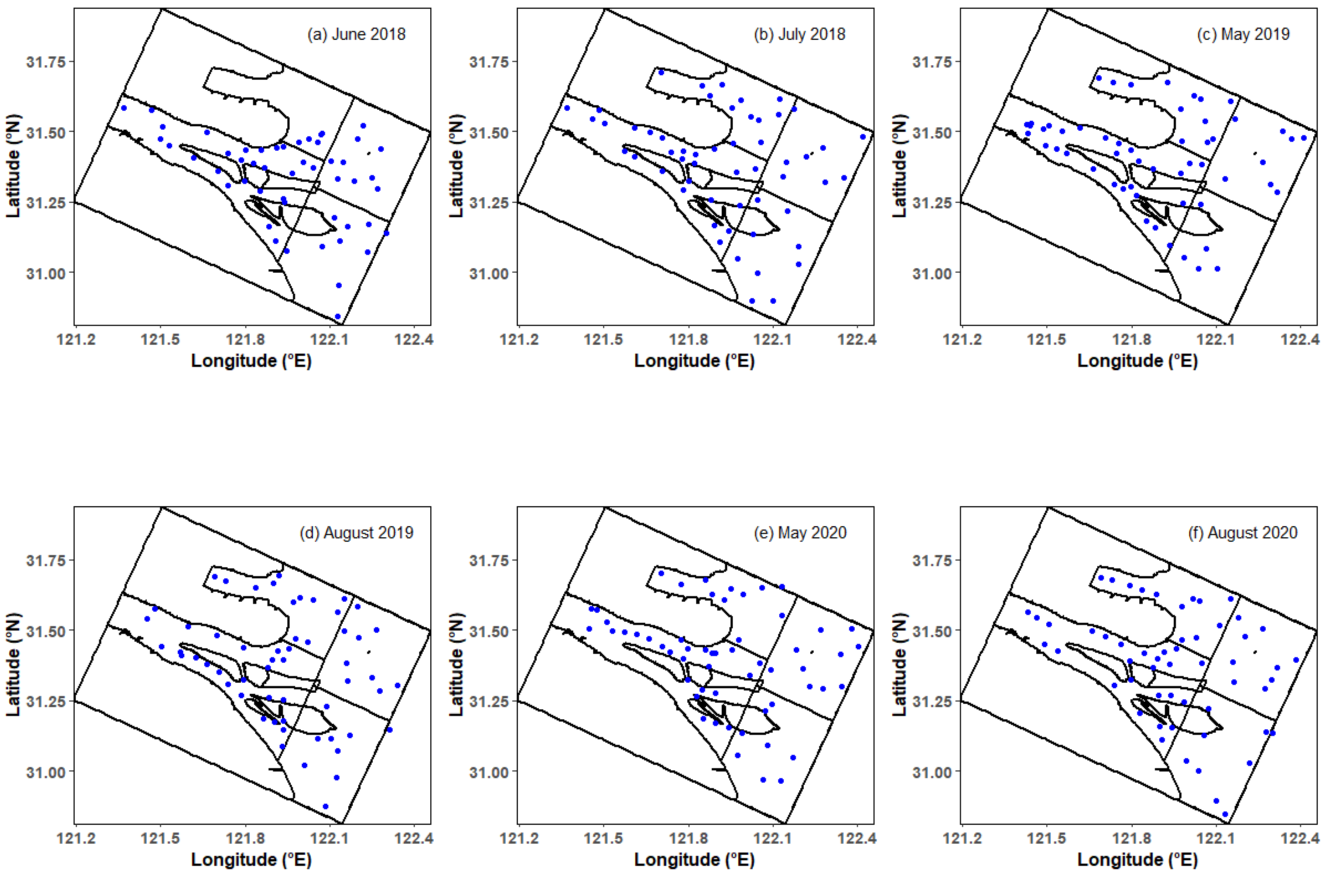

Figure A1. Sampling stations for six cruises in the Yangtze Estuary.

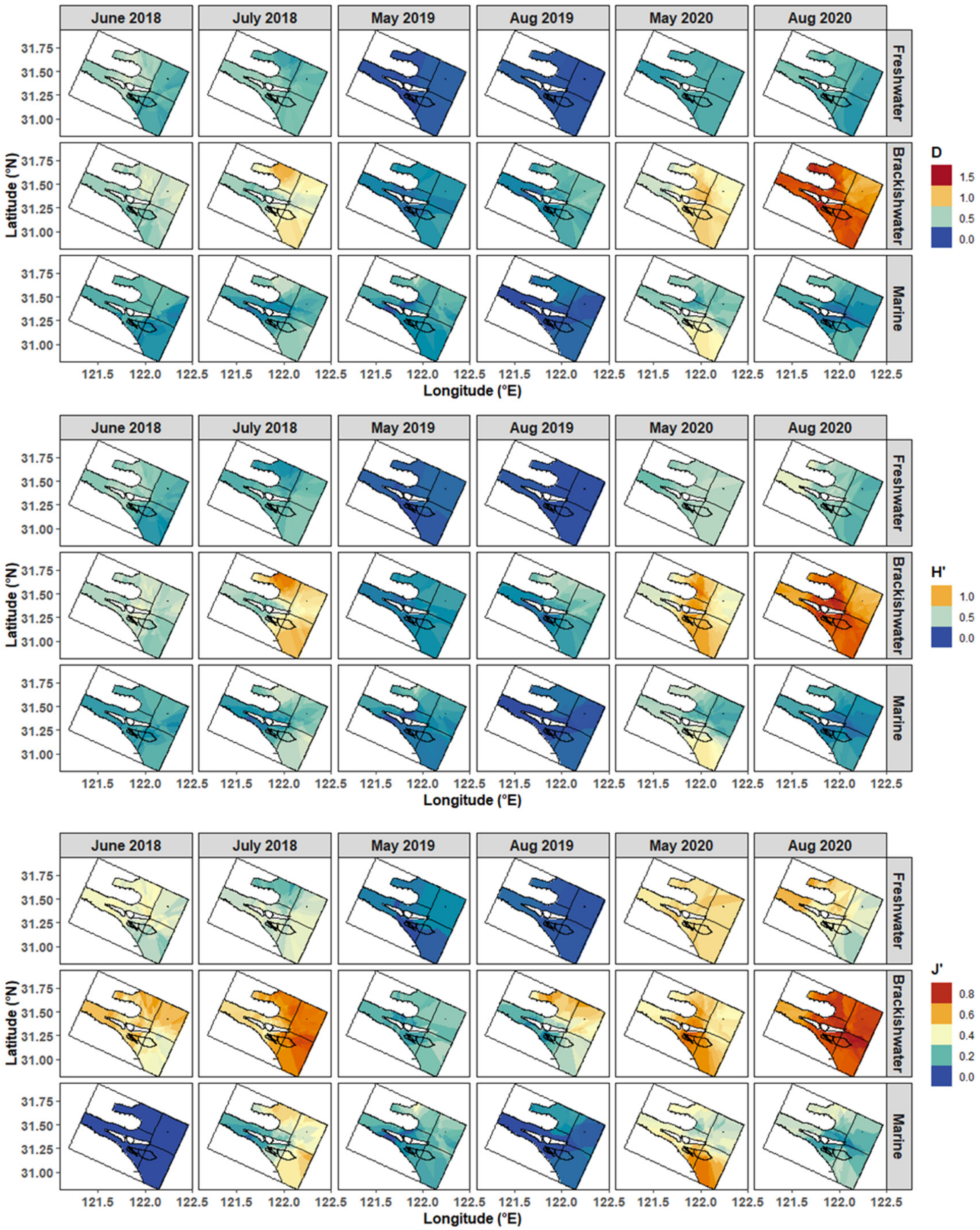

Figure A2. The distribution of Margalef's richness (D), Shannon–Wiener index (H'), and Pielou's evenness (J') with different ecological guilds in the Yangtze Estuary.

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