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Spatial Variation in the Composition and Diversity of Fishes Inhabiting an Artificial Water Supply Lake, Eastern China

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With the intensification of eutrophication, many artificial water supply lakes that act as a biological filter for water diverted from rivers have been built to alleviate water scarcity in Eastern China. In this study, we selected Lake Yanlong, a representative artificial water supply lake in Yancheng City, as our experimental lake to explore how the community composition of fishes changed among different habitat types and assess potential consequences for effective water treatment. From October 2015 to October 2020, we conducted quarterly surveys of fish communities and environmental factors in the Mangshe River (MR; water for lake) compared to four different water treatment zones of Lake Yanlong (PZ, the pretreatment zone with inlet from the MR; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone with outlet to urban waterworks). A total of 16,339 individual fish belonging to 11 families and 49 species were collected. Six of the eight dominant species observed across zones were small-bodied fishes. Despite reduced fish species richness, the relative abundance and biomass of fishes tended to be higher in Lake Yanlong relative to the MR. The Shannon-Wiener diversity index, Pielou evenness index, Simpson's diversity index all decreased from the MR to the DZ in the following sequence: MR < PZ < EZ < SZ < DZ. Analysis of similarities and similarity percentage analysis confirmed that fish communities differed significantly among zones and *Coilia ectenes*, *Carassius auratus*, *Pseudobrama simony*, *Hemiculter leucisculus*, and *Hemiculter bleekeri* were the major differentiating species. Mantel's test and redundancy analysis revealed that water depth, aquatic vegetation coverage, and phytoplankton concentrations were the major factors determining the spatial distribution of fishes when moving from the MR to the DZ of Lake Yanlong. Stocking piscivorous fish can be used as an effective measure to control the abundance of prolific small-bodied fishes in Lake Yanlong. The details backing these findings are important for understanding how the community composition of fishes among habitat types in Lake Yanlong influence water quality, and to develop suitable biomanipulation strategies for the management of fish resources and maintaining proper function of these artificial water supply lakes.

Keywords: fish community, fish biodiversity, artificial water supply lake, Lake Yanlong, regulation strategies

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INTRODUCTION

Eutrophication, caused by both natural and anthropogenic disturbance, is a pervasive problem facing surface water bodies (Smith and Schindler, 2009; Bhagowati and Ahamad, 2018) and has been an important topic for academic and social debate over the past few decades (Bonsdorff, 2021). The middle and lower reaches of the Yangtze River Basin (MLYRB) contains the majority of shallow lakes in China, with 651 lakes larger than 1 km^2 and 18 lakes larger than 100 km^2, accounting for about 1/3 of the total surface area of lakes in China (Zhang et al., 2019; Tang, 2020). With rapid socioeconomic development and the acceleration of urbanization since the 1980s, industrial and agricultural pollution as well as discharge of domestic sewage has resulted in the eutrophication of most lakes in the MLYRB (Zhu et al., 2019; Tang, 2020; Zou et al., 2020). Increasing levels of eutrophication pose a great threat to drinking water quality and human health (Qin et al., 2010; Moal et al., 2019), which has become an important ecological and socioeconomic problem in the MLYRB, particularly in the Eastern Plain of China (EPC) (Zou et al., 2020).

To alleviate this risk, the central and local governments of China have launched a series of water pollution control projects over the last decade (Guo et al., 2019), including the construction of artificial water supply lakes that act as a biological filter for water diverted from rivers within the EPC (Cai et al., 2019). Compared to natural lakes in the region, these artificial water supply lakes are often characterized by short construction time, small area, simple and unstable ecosystem structure, and are prone to degradation by human activities (e.g., improper fisheries management) (Cai et al., 2019; Li S. et al., 2021). Moreover, water quality and other ecosystem components (e.g., fish communities and extent of submerged aquatic vegetation) within these artificial lakes are affected by shifts in the environmental conditions of the rivers that feed them (Cai et al., 2019). There has been extensive research aimed toward developing restoration strategies for maintaining ecosystem function in natural lakes within the MLYRB [e.g., Taihu Lake (Wang et al., 2019) and Dongting Lake (Li B. et al., 2021)]. However, maintaining proper ecosystem function and identifying effective restoration strategies for artificial water supply lakes is much less common, despite their importance for protecting human health in the EPC. Therefore, it is necessary to understand the physical and biological characteristics of these artificial lakes, how different components work together to maintain core ecosystem functions and delivery of goods and services (e.g., purification of drinking water), and to establish effective restoration strategies that are suitable for these lakes given their unique properties when compared to natural lakes.

As the largest group of vertebrates and the primary mid- to upper-trophic level consumers in freshwater ecosystems, fish play important roles in the functioning of lakes by affecting the physical environment, trophic interactions, and community dynamics (Mello et al., 2009; Jeppesen et al., 2010). Under some circumstances, by consuming small zooplanktivorous fish, piscivorous fish can reduce grazing pressure on zooplankton communities, which in turn can increase grazing pressure on phytoplankton to an extent that improves water clarity—a more desirable state for many lakes that can also help support submerged macrophyte production (Mehner et al., 2004). Filter-feeding fish can also control undesirable cyanobacterial blooms by grazing phytoplankton directly (Xie and Liu, 2001). Alternatively, an unbalanced fish community can have a negative impact on water quality and lake ecosystem function (Cai, 2017; Guo et al., 2022). For example, the overabundance of herbivorous fish can precipitate submerged macrophyte loss in shallow lakes through over-grazing (Zhen et al., 2018). Often affected by overfishing and habitat loss, piscivorous fish in most MLYRB lakes and rivers have dramatically declined over the past decades, which has led to the proliferation of small-bodied fishes (Mao et al., 2011; Cai et al., 2019). Most of these small-bodied fish in the MLYRB feed on zooplankton (especially cladocerans and copepods), leading to increased phytoplankton biomass and reduced water clarity (Zhang, 2005). Furthermore, some studies demonstrated that declines in fish species diversity and the proportion of piscivorous fish present in aquatic ecosystems were accompanied by the deterioration of water quality (Karr, 1981, 1991; Karr et al., 1986). Given the strong roles fish play in aquatic ecosystem function, fish community structure has been regarded as an important ecological indicator and suitable for assessing the status of aquatic ecosystems (Oberdorff et al., 2001).

The physical environment can also have reciprocal effects on the composition and spatial distribution of fish communities through a variety of mechanisms (Geheber and Piller, 2012; Cote et al., 2013). Previous studies demonstrated that water velocity, macrophytes, water depth and trophic state were the primary factors mediating fish community dynamics (Brinsmead and Fox, 2002; Mehner et al., 2005; Li et al., 2010). For example, river fishes are generally more slender-bodied, and have smaller fins than fishes occupying lakes to reduce lotic drag (Brinsmead and Fox, 2002). In a survey of Xiaosihai Lake, China, areas with greater submerged macrophyte coverage supported a higher biomass and abundance of small fish (Li et al., 2010). Moreover, the coverage of submerged macrophytes is strongly correlated to water depth and trophic state, whereby deep or eutrophic lakes are often devoid of submerged macrophytes needed to support certain species of fish (Jeppesen et al., 1990). Thus, the composition and spatial distribution of fish communities are shaped by both environmental factors and biotic interactions, which could have consequences for ecosystem function (Mehner et al., 2005; Mehner and Brucet, 2021). Understanding these complexities may help inform proper restoration strategies in degraded lakes. However, the interdependencies among fish and the physical environment within artificial water supply lakes of the MLYRB are poorly studied.

The design and construction of artificial water supply lakes are tailored toward water treatment for human consumption. As a result, water quality and the physical habitat available for fish can vary from the inlet (where water is pumped from adjacent rivers) to the outlet as water travels through different purification zones of the lakes. Therefore, the community composition of fishes could vary along this gradient. Lake Yanlong (33°20′N, 120°1′E), built in 2012 and located at the intersection of the lower Yangtze River Basin and the lower Huaihe River Basin, is the first artificial water supply lake in the ECP and represented an ideal system for studying fish distribution and community composition (Zuo et al., 2015). The lake collects raw water from its waterhead river—the Mangshe River (MR)—through a pump station, and finally supplies water to the urban waterworks once traveling through four distinct purification zones: the pretreatment zone (PZ), the emergent macrophyte zone (EZ), the submerged macrophyte zone (SZ), and finally the deep purification zone (DZ). In this study, we conducted a quarterly survey of the fish community and environmental factors within each distinct purification zone of Lake Yanlong (PZ, EZ, SZ, DZ), as well as the adjacent Mangshe River (MR) from October 2015 to October 2020. We aimed to explore: (1) how fish species composition and diversity differed between Lake Yanlong and the Mangshe River; (2) the key environmental factors that could differentiate the fish community of the Mangshe River from Lake Yanlong as well as the distribution of fishes within the lake; and (3) suitable biomanipulation strategies for the management of fish resources and water quality in these artificial water supply lakes.

MATERIALS AND METHODS

Study Area

The Mangshe River is 43 km long and drains a basin area of 64,000 ha. It flows through the northern Lixiahe Plain of Jiangsu Province and used to be the primary drinking water source for residents of Yancheng City. The water quality of MR fluctuates throughout the year, and is typically classified between levels III to IV according to the environmental quality standards for surface water in China (GB3838-2002, Ministry of Environmental Protection of China, 2002). Additionally, the MR usually shows characteristics of organic pollution during summer (Zuo et al., 2015). In order to ensure the safety of drinking water for residents of Yancheng city, Lake Yanlong, an artificial water supply lake collecting raw water from the MR, was built in June 2012. After replacing the MR as the main source of drinking water in Yancheng City with Lake Yanlong, drinking water quality has improved and has become more stable (Zuo et al., 2015).

Lake Yanlong (210.9 ha) is a complex ecosystem exhibiting both wetland- and reservoir-type features and includes four distinct purification zones (**Figure 1**). Water enters the PZ first, which pretreats water from the MR mainly by means of precipitation, oxygenation and exposure to an established biofilm, and is characterized by relatively deep depths (mean ± SE; 3.25 ± 0.30 m) and relatively short water residence times as water moves through at measurable velocities (0.07 ± 0.04 m/s). Water enters the EZ second, which purifies water through assimilation, absorption and transformation of pollutants by emergent macrophytes (mainly *Phragmites australis* and *Typha orientalis*), and is characterized by relatively shallow depths (0.78 ± 0.19 m) and a high spatial coverage of emergent plants (86.3% ± 46.3%). Water enters the SZ third, which further purifies water through absorption and transformation of pollutants by submerged macrophytes (mainly *Myriophyllum verticillatum*, *Ceratophyllum demersum,* and *Vallisneria natans*). The DZ is the last purification zone before water exits the lake via a pumping station, which like the PZ, purifies water mainly through the settling of particulates, but is deeper (4.75 ± 0.22 m) and encompasses the largest surface area and storage capacity (4.2×10^6 m^3) of all zones. These four distinct purification zones are separated by sluices, which act as obstacles to fish movement among zones. The main characteristics of the five different zones (MR, PZ, EZ, SZ, and DZ) are shown in **Table 1** (Ren, 2021; Guo et al., 2022).

To help support a clear-water state in Lake Yanlong, which can bolster macrophyte production, biomanipulation was used. Different types of native piscivorous fish were stocked in each purification zone of Lake Yanlong from 2017 through 2020 to consume small-bodied fishes. By the end of June 2020, a total of 3.2×10^4 individual topmouth culter *Culter alburnus*, 3.3×10^4 individual mandarin fish *Siniperca chuatsi*, 2.0×10^4 individual catfish *Clarias gariepinus* and 1.87×10^4 individual snakehead fish *Channa argus* were stocked into the lake. Species and numbers stocked varied among zones to account for differences in surface area and habitat characteristics (**Table 2**).

Fish Sampling

A total of nine standard fish sampling sites (one site both for MR and PZ, two sites both for EZ and SZ, and three sites for DZ) were established across the MR and all purification zones of Lake Yanlong. The number of sites within each zone reflected the relative size of each region. Fishes were sampled quarterly from October 2015 to October 2020 using multi-mesh monofilament gill nets. The design of the gill nets was modified according to the standard method (Appelberg, 2000). Each net consisted of twelve 2.5 m long × 1.5 m tall mesh panels placed in random order (8.5, 4.0, 12.5, 2.0, 11.0, 1.6, 2.5, 4.8, 3.1, 1.0, 7.5, and 6.0 cm stretch measure). Three nets (two pelagic surface nets and one benthic net) were set in series at each sampling site overnight (12–15 h) for three consecutive nights each season (January, April, July, October). Fishes were separated and identified to the species level, and individually measured for total length to the nearest 1 mm and body weight to the nearest 0.01 g. We calculated the species richness, mean quarterly catch per unit effort in both numerical ($CPUE_N$; ind./m^2/12 h) and biomass ($CPUE_B$; g/m^2/12 h) terms. Small-bodied fishes were defined by having an age-at-first-maturity of less than 2 years (Cai et al., 2019). Each fish species was classified for feeding type (omnivorous, piscivorous, planktivorous, or herbivorous) and propensity for movement (migratory and resident) according to Ni and Wu (2006).

Environmental Variables

On each sampling occasion, eleven environmental variables were measured in conjunction with fish sampling at each sampling site (**Table 1**). Dissolved oxygen (DO; mg/L) and surface water temperature (WT;°C) were monitored using a YSI ProPlus meter (Thermo Fisher Scientific Company, Waltham, United States). Water depth (WD; m) was measured using a Speedtech SM-5 Portable Depth Sounder. Turbidity (NTU) was measured using a Hach 2100P portable turbidity meter. Chemical oxygen demand (COD_{Mn}; mg/L), total nitrogen (TN; mg/L) and total phosphorus (TP; mg/L) were determined according

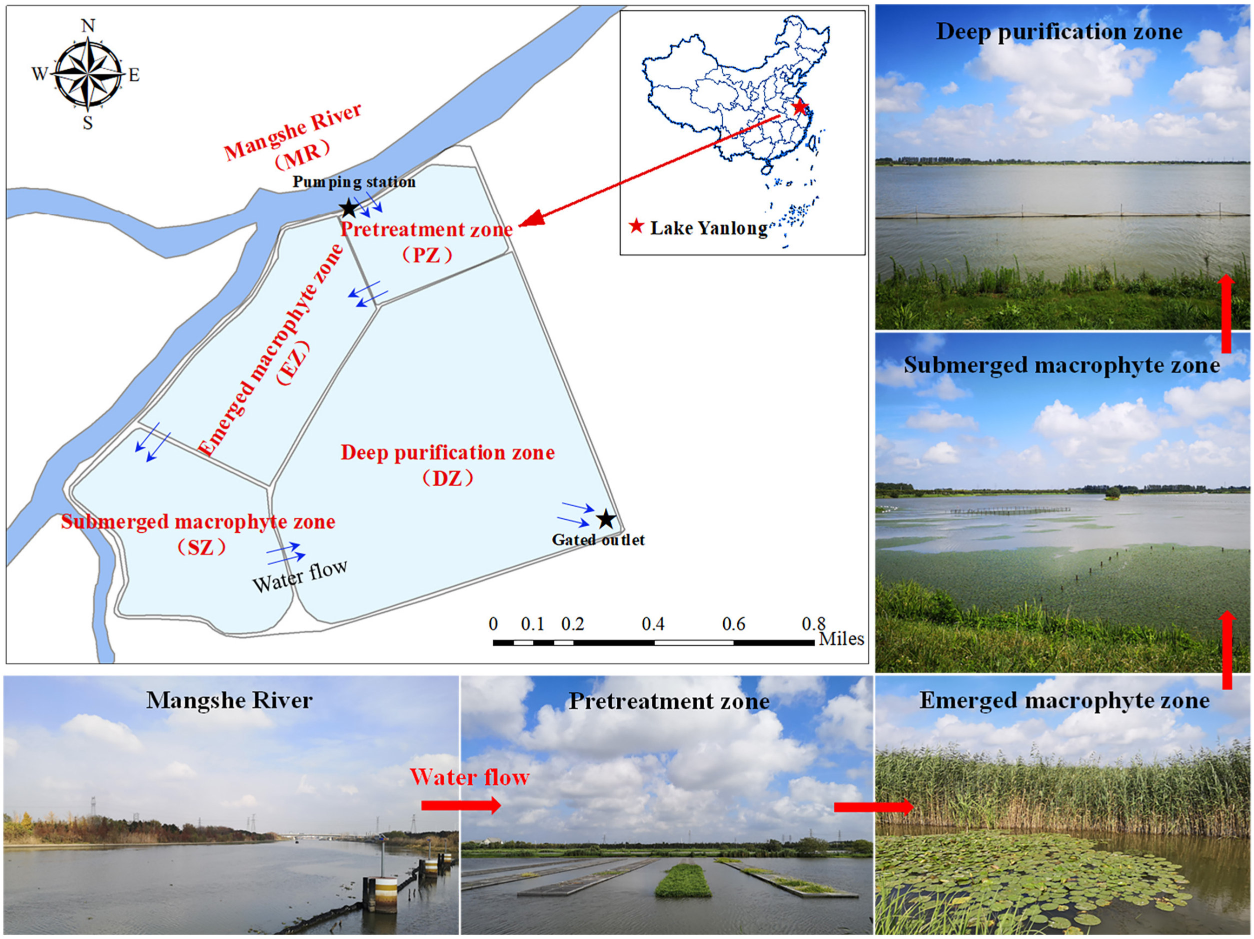

FIGURE 1 | Pictures and map of the Mangshe River (MR) and Lake Yanlong, showing the distribution of different purification zones (PZ, the pretreatment zone; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone).

TABLE 1 | Annual means (±SE) of physicochemical parameters measured in the Mangshe River (MR) and different purification zones of Lake Yanlong (PZ, the pretreatment zone; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone).

Zones	MR	PZ	EZ	SZ	DZ
Area (ha)	–	20.3	41.3	40	109.3
Water depth (WD; m)	2.88 ± 1.50	3.25 ± 0.30	0.78 ± 0.19	1.43 ± 0.51	4.75 ± 0.22
Water temperature (WT; °C)	20.6 ± 8.9	21.0 ± 9.5	18.3 ± 10.7	20.6 ± 8.2	20.5 ± 8.2
Transparency (cm)	31.7 ± 10.0	27.6 ± 11.1	36.6 ± 10.8	39.1 ± 6.4	46.7 ± 16.1
Total phosphorus (TP; mg/L)	0.23 ± 0.08	0.25 ± 0.08	0.21 ± 0.05	0.20 ± 0.08	0.12 ± 0.04
Total nitrogen (TN; mg/L)	1.83 ± 0.57	2.05 ± 0.98	1.89 ± 0.69	1.46 ± 0.57	1.42 ± 0.85
Chemical oxygen demand (COD_{Mn}; mg/L)	5.74 ± 1.31	6.38 ± 1.38	6.25 ± 1.23	6.00 ± 0.98	5.31 ± 0.60
Dissolved oxygen (DO; mg/L)	5.54 ± 3.07	6.51 ± 2.59	7.67 ± 2.75	5.23 ± 3.78	8.62 ± 2.35
Chlorophyll-α (Chl-α; μg/L)	26.32 ± 15.34	36.56 ± 12.82	42.66 ± 15.32	38.46 ± 19.67	32.67 ± 22.00
Water velocity (m/s)	0.10 ± 0.07	0.07 ± 0.04	0.06 ± 0.04	0.05 ± 0.03	0.02 ± 0.02
Coverage of aquatic vegetation (%)	2.1 ± 1.2	5.6 ± 3.6	86.3 ± 46.3	12.1 ± 8.8	1.5 ± 0.8

to the standard methods described in American Public Health Association [APHA] (1992). Chlorophyll-α concentration (Chl-α; μg/L) was determined using a fluorimeter with methanol extraction of the filtrate (Holm-Hansen and Riemann, 1978). The biomass of aquatic vegetation (BAV; g/m^2) was recorded using a grass collection sampler (Guo et al., 2022). Family-specific zooplankton (NZ; ind./L) and phytoplankton density (NP; ind./L) were estimated following the standard methods described in Dumont (2002) and Paredes and Montecino (2011), respectively.

TABLE 2 | The total number and individual size of piscivorous fish species stocked annually into the four purification zones of Lake Yanlong (PZ, the pretreatment zone; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone) from 2017 to 2020.

Stocking		2017		2018			2019				2020			
		SZ	DZ	EZ	SZ	DZ	PZ	EZ	SZ	DZ	PZ	EZ	SZ	DZ
Topmouth culter	Number (10^3 ind.)	3.0	3.0	–	3.0	3.0	4.0	2.0	3.0	2.0	2.0	2.0	2.0	3.0
	Size (cm)	8∼10	8∼10	8∼10	8∼10	8∼10	3∼5	3∼5	3∼5	3∼5	3∼5	3∼5	3∼5	3∼5
Mandarin fish	Number (10^3 ind.)	1.0	4.0	2.0	1.0	4.0	1.0	2.0	2.0	4.0	2.0	2.0	3.0	5.0
	Size (cm)	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15
Catfish	Number (10^3 ind.)	1.0	3.0	1.0	1.0	1.5	0.5	2.0	1.0	2.0	1.0	1.0	2.0	3.0
	Size (cm)	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15
Snakehead fish	Number (10^3 ind.)	1.0	1.5	1.0	1.0	1.5	0.5	1.0	1.0	2.0	1.0	1.0	2.0	3.0
	Size (cm)	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15	8∼15

Species Diversity Indices

The following indices were calculated for each sampling occasion and used to quantify fish species diversity and rank the relative importance of each species among the MR and different purification zones of Lake Yanlong:

(i) Shannon–Wiener diversity index (H_N) (Shannon and Weaver, 1949)

$$H_N = -\Sigma[P_i \times lnP_i] \tag{1}$$

(ii) Pielou evenness index (J) (Pielou, 1975)

$$J = H_N/lnS \tag{2}$$

(iii) Simpson diversity index (D) (Whittaker, 1972)

$$D = 1 - \Sigma {P_i}^2 \tag{3}$$

(iv) Simpson dominance index (λ) (Simpson, 1949)

$$\lambda = \Sigma {P_i}^2 \tag{4}$$

(v) The index of relative importance (IRI) (Pianka, 1971)

$$IRI_i = (N_i\% + W_i\%) \times F_i \times 10000 \tag{5}$$

where Pi is the proportional abundance of species i referenced to the total number of fish individuals sampled; S is the total number of species; N_i is the numerical percentage of species i; W_i is the biomass percentage of species i; and F_i is the percent frequency of occurrence of species i. When IRI_i is larger than 1000, this species is defined as the dominant species (Yang et al., 2018).

Data Analysis

Differences in Fish Community Composition and Diversity

Potential differences in mean diversity indices (H_N, J, D, λ) and the relative abundance and biomass ($CPUE_N$ and $CPUE_B$) of different fishes observed from October 2015 to October 2020 among the four purification zones of Lake Yanlong and of the MR were tested using multiple non-parametric, one-way ANOVA's (Kruskal–Wallis tests) implemented in the R package "coin" (Hothorn et al., 2008). The different zones (averaging across sampling quarters) represented the fixed factor. Where applicable, Wilcoxon tests were used for *post hoc* comparisons and to determine which zones differed using the "rstatix" package (Kassambara, 2021). Moreover, we used one-way analysis of similarity (ANOSIM) to identify the significance of observed differences in fish community composition and then used similarity percentage analysis (SIMPER) to explore the discriminating species of fish within communities among zones using the "vegan" package (Oksanen et al., 2022).

Environmental Effects on Fish Community Composition

Spearman correlation analyses and Mantel's tests were used to explore the relationship between different environmental variables and the dominant fish species in each purification zone and the MR by using quarterly measurements, also implemented in R using package "linkET" (Huang, 2022). Redundancy analysis (RDA; provided within the "vegan" package) was then used to identify the key environmental factors that could explain differences in the abundance of dominant species among zones. Prior to these analyses, variance inflation factors (VIFs) were adopted to examine multicollinearity among environmental factors. Collinear environmental variables detected by forward-backward selection were excluded until all remaining variables had VIFs less than 5 (Gou et al., 2021). In addition, hierarchical partitioning (HP) and permutation analyses were performed to acquire the independent explanation power and variance of each environmental factor using the "rdacca.hp" package (Lai et al., 2022). Environmental variables were standardized to a mean of zero and unit variance by the "decostand" function in the "vegan" package. Lastly, $CPUE_N$ of dominant species were $\log_{10}(x + 1)$ transformed prior to analysis (James and McCulloch, 1990).

Effect of Stocking Piscivorous Fish on Small-Bodied Fishes and Species Diversity

To assess the effect of stocking of piscivorous fishes on small-bodied fishes and fish community diversity, we compared mean relative abundance and biomass values ($CPUE_N$ and $CPUE_B$) of small-bodied fishes and fish diversity indices (H_N, J, D) among the four purification zones of Lake Yanlong before (data from October of 2015 and 2016) and after (data from October of 2017, 2018, 2019, and 2020) stocking of piscivorous fishes occurred. For this analysis, we used Mann-Whitney tests implemented in the R package “stats” (R Core Team, 2021).

All statistical analyses and figures were made using R software (Version 4.1.2). Differences were considered significant at an α level of 0.05 (i.e., p-value < 0.05) for all tests.

RESULTS

Species Composition and Richness

In total, 16,339 individual fish belonging to 11 families and 49 species were collected from all purification zones of Lake Yanlong and the MR between October 2015 and October 2020 (**Supplementary Table 1**). Fish species richness was highest in the MR (39 species), followed by the SZ (31 species), the EZ (30 species), and richness was lowest in the DZ (22 species). The 49 fish species were divided into resident fish (39 species) and migratory fish (10 species) based on their propensity for movement. The species richness of migratory fish (e.g., *Elopichthys bambusa* and *Squaliobarbus curriculus*) in the MR was the highest (10 species), but decreased greatly after entering Lake Yanlong (five species in PZ; four species in EZ; six species in SZ; four species in DZ). Compared to migratory fish, resident fish (e.g., *Coilia ectenes* and *Pseudobrama simony*) were more prolific in the four purification zones of Lake Yanlong, especially in the EZ (26 species) and SZ (25 species), which reflected the transition from riverine to wetland- and reservoir-type habitats (**Figure 2**). Based on typical food items ingested, these 49 fish species were also classified into four trophic guilds: omnivores (23 species), piscivores (14 species), planktivores (7 species) and herbivores (5 species). For omnivorous fish, species richness differed between MR and the other four zones, being highest in MR (22 species), and lowest in DZ (8 species); For piscivorous fish, species richness was highest in EZ (12 species), followed by MR (7 species), and only 6 species each for PZ, SZ and DZ; For planktivorous fish, species richness was highest in SZ (6 species), followed by MR (5 species) and DZ (5 species), and only 1 species each for EZ; For herbivorous fish, species richness was highest in EZ, SZ and MR (each with 5 species), followed by PZ (4 species), and DZ (3 species) (**Figure 2**).

Distribution of Dominant Species

A total of eight dominant species (*IRI* > 1,000) were identified among the MR and four purification zones. Six of the eight dominant species (*P. simony*, *Carassius auratus*, *Hemiculter leucisculus*, *C. ectenes*, *Hemiculter bleekeri* and *Toxabramis swinhonis*) were small-bodied fishes that feed primarily on zooplankton, algae and plants debris. In addition, the total number of dominant species identified varied among zones, being highest in the PZ (five dominant species), followed by EZ (four dominant species), DZ (three dominant species), SZ (two dominant species), and was lowest in the MR (one dominant species). In the MR, only *H. bleekeri* met conditions for dominance (*IRI* = 1323.0), and represented 10.0% of the total numerical catch across study years. In the PZ, *P. simony* (*IRI* = 3168.3) and *C. ectenes* (*IRI* = 2217.5) were the most dominant species, accounting for 16.5% and 12.5% of the total catch biomass across years, respectively. *C. auratus* (*IRI* = 5243.3), *P. simony* (*IRI* = 6232.0) and *C. ectenes* (*IRI* = 5092.7) were the most dominant species in the EZ, SZ and DZ, respectively. Lastly, *H. leucisculus* was relatively common in the PZ, EZ, SZ and DZ, while *T. swinhonis* and *Cyprinus carpio* only met conditions for dominance in the PZ and EZ, respectively (**Table 3**).

Diversity Indices and Relative Abundance and Biomass

There were significant differences in the diversity indices (H_{N}, J, D, λ) and relative abundance and biomass ($\mathrm{CPUE_N}$ and CPUE_B) among the MR and four purification zones when averaging across study quarters (Kruskal–Wallis test, $p < 0.05$ for all cases) (**Table 4**). In terms of the diversity indices, H_{N}, J and D of the fish communities all showed a decreasing trend from the MR to DZ and followed the progression of: MR < PZ < EZ < SZ < DZ. Conversely, λ showed the opposite pattern (**Figure 3**). In terms of relative abundance and biomass, $\mathrm{CPUE_N}$ and CPUE_B both increased from the MR to Lake Yanlong. These values were lowest in the MR (9.6 ± 1.1 ind./m^2/12 h and 387.1 ± 60.5 g/m^2/12 h, respectively), and highest in the EZ (35.4 ± 5.1 ind./m^2/12 h and 1895.7 ± 318.2 g/m^2/12 h, respectively) (**Figure 4** and **Supplementary Table 2**).

Dissimilarity and Differentiating Species Among Fish Communities

The ANOSIM analysis confirmed that fish community composition differed significantly among zones ($R = 0.429$, $P < 0.001$). Dissimilarity of fish was greatest between the MR and SZ (averaged 83.9%), followed by MR and EZ (83.8%), MR and DZ (83.0%), EZ and DZ (81.7%), and was lowest between PZ and SZ (71.6%) (**Table 5**). According to the SIMPER analysis, *C. ectenes*, *C. auratus*, *P. simony*, *H. leucisculus,* and *H. bleekeri* were the major differentiating species among zones. Specifically, *C. ectenes* had a higher contribution than the other differentiating species in the MR vs. DZ, PZ vs. DZ, EZ vs. DZ, and SZ vs. DZ. Contributions of *C. ectenes* for these comparisons were 30.4, 25.2, 20.7, and 28.1%, respectively. The species *C. auratus* had a higher contribution than the other differentiating species in the MR vs. EZ, PZ vs. EZ and the EZ vs. SZ, with contributions of 22.0, 18.3, and 22.2%, respectively. Next, *H. bleekeri* had a higher contribution in the MR vs. PZ and the PZ vs. SZ, with corresponding contributions of 19.8 and 18.2%, respectively. Lastly, *P. simony* had a higher contribution in the MR vs. SZ (30.9%) (**Table 5**).

Environmental Effects on Fish Community Composition

The results from Mantel's test comparing environmental variables to the relative abundance of dominant species indicated that WD was significantly correlated with the $\mathrm{CPUE_N}$ of *C. auratus* ($r = 0.08$), *C. carpio* ($r = 0.09$), *P. simony* ($r = 0.20$) and *C. ectenes* ($r = 0.25$). Further, BAV was significantly correlated with the $\mathrm{CPUE_N}$ of *P. simony* ($r = 0.13$) and CCA ($r = 0.31$), while NP was significantly correlated with the $\mathrm{CPUE_N}$ of *T. swinhonis* ($r = 0.20$) and *C. ectenes* ($r = 0.18$) ($p < 0.05$ for all

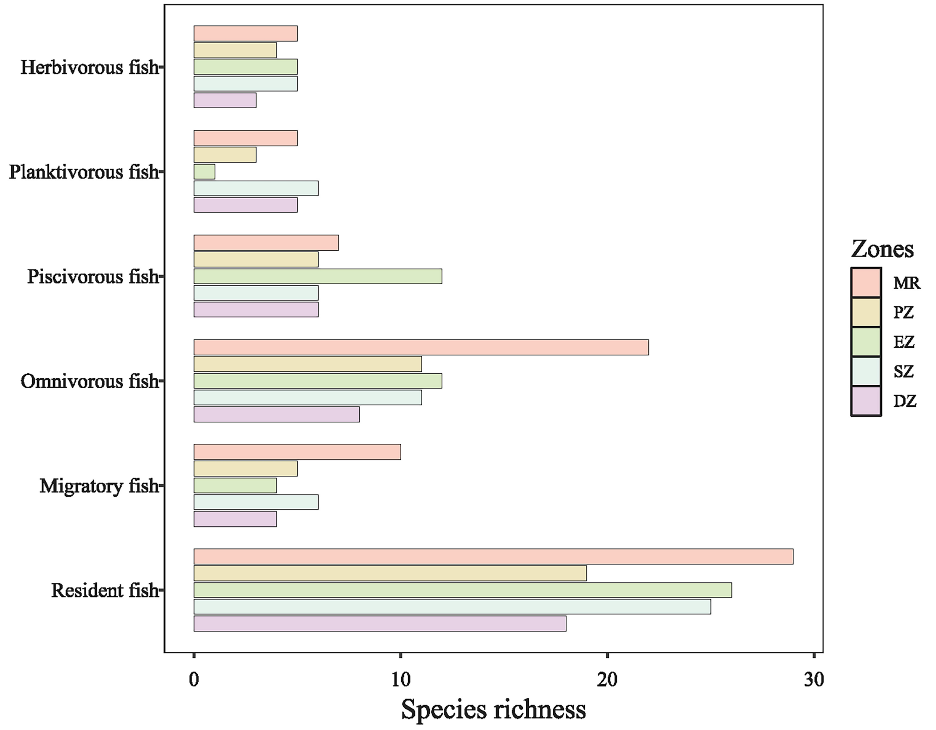

FIGURE 2 | The total number of fish species sampled (i.e., species richness) parsed into different different feeding types (omnivores, piscivores, planktivores, and herbivores) and propensity for movement (migratory or resident) among the Mangshe River (MR) and different purification zones of Lake Yanlong (PZ, the pretreatment zone; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone).

TABLE 3 | The percent relative abundance (*N*%) and biomass (*W*%) and the index of relative importance (*IRI*) of dominant fish species sampling from the Mangshe River (MR) and from different purification zones of Lake Yanlong (PZ, the pretreatment zone; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone).

Scientific name	Code	MR			PZ			EZ			SZ			DZ		
		N%	*W*%	*IRI*	*N*%	*W*%	*IRI*	*N*%	*W*%	*IRI*	*N*%	*W*%	*IRI*	*N*%	*W*%	*IRI*
P. simony	PSI	1.6	0.7	84.5	17.6	16.5	**3168.3**	15.2	5.1	**1754.7**	45.8	16.6	**6232.0**	8.8	5.0	765.3
C. auratus	CAU	3.3	2.3	275.7	1.1	9.4	374.6	24.3	28.1	**5243.3**	3.4	1.8	228.0	8.5	23.0	**2980.9**
H. leucisculus	HLE	5.7	1.4	442.9	16.7	8.9	**2012.3**	23.7	3.4	**2528.5**	16.6	4.7	**1999.7**	11.2	4.2	**1367.8**
C. ectenes	CEC	7.4	1.9	466.1	13.4	12.5	**2217.5**	0.0	0.0	–	3.5	0.7	259.4	43.9	10.1	**5092.7**
H. bleekeri	HBL	10.0	4.9	**1323.0**	19.6	12.2	**1816.0**	7.4	2.0	687.7	3.9	1.4	333.9	11.7	2.9	888.3
C. mongolicus	CMOO	4.3	3.0	450.0	7.5	3.8	892.5	4.6	5.7	755.5	1.8	2.5	241.6	5.6	2.4	802.8
T. swinhonis	TSW	1.6	0.3	91.7	13.8	4.2	**1416.9**	0.0	0.0	–	2.0	0.3	57.3	5.8	1.3	353.9
C. carpio	CCA	0.6	2.4	36.6	0.2	3.0	45.6	2.4	16.6	**1393.2**	0.2	0.4	8.3	0.0	0.9	5.0

N%, percentage based on total catch number of fish across study years; W%, percentage based on total catch biomass of fish across study years; IRI, index of relative importance; Code, fish code. Bold numbers indicate the dominant species.

cases). Spearman correlation analyses using the 11 environmental variables measured showed that WD was significantly negatively correlated with COD_{Mn} ($r = -0.24$, $p < 0.05$) and significantly negatively correlated with BAV ($r = -0.68$, $p < 0.001$). The variable BAV was also significantly negatively correlated with NP ($r = -0.23$, $p < 0.05$). Alternatively, we observed significant positive correlations among most of the nutrient indices (i.e., TN, TP, COD_{Mn}) and Chl-α (**Figure 5**).

The RDA model was significant ($p < 0.001$), indicating the existence of a relationship among environmental variables and the spatial distribution of dominant species. The model described 53.2 and 24.5% of variation in species distribution data along the first and second RDA axes (**Figure 6A**). All environmental variables (WT, WD, TN, TP, COD_{Mn}, Chl *a*, Turbidity, DO, BAV, NZ and NP) were selected for using in the RDA (VIFs were < 5 for all variables). According to the HP analysis and permutation tests, WD, NP and BAV explained 35.66, 19.08, and 15.13% of the total variation in fish community composition (all species) among zones, respectively. These were the same

TABLE 4 | Detailed information on results from the non-parametric, one-way ANOVA (i.e., Kruskal–Wallis test) models evaluating potential differences in the mean catch per unit effort of fishes [in both numerical ($CPUE_N$) and biomass ($CPUE_B$) terms] and the fish community diversity metrics (H_N, J, D, λ) among habitat zones.

Variables	Statistical parameters		
	χ^2	*df*	*P*
$CPUE_N$	18.495	4	<0.001
$CPUE_B$	17.213	4	0.002
H_N	22.109	4	<0.001
J	16.621	4	0.002
D	19.327	4	<0.001
λ	18.818	4	<0.001

environmental variables that explained the abundance of dominant fish species among zones ($P_{HP} < 0.01$ for WD, $P_{HP} < 0.05$ for NP and BAV) (**Figure 6B**). In addition, *C. ectenes* preferred habitats (principally the PZ and DZ) with deeper water depths and lower aquatic vegetation cover, while *H. bleekeri* preferred deep habitats within the MR that lacked phytoplankton. Alternatively, *P. simony*, *C. carpio,* and *C. auratus* were found in shallow habitats (principally the EZ and SZ) with abundant aquatic vegetation (**Figure 6A**).

Effects of Stocking Piscivorous Fish on Small-Bodied Fishes and Fish Community Diversity

There were significant differences in mean relative abundance and biomass of all small-bodied fishes combined (25 species) among the four purification zones of Lake Yanlong before ($CPUE_N$: 49.72 ± 1.01 ind./m^2/12 h; $CPUE_B$: 2342.40 ± 148.44 g/m^2/12 h) and after ($CPUE_N$: 17.65 ± 2.62 ind./m^2/12 h; $CPUE_B$: 381.74 ± 64.49 g/m^2/12 h) stocking of piscivorous fishes (Mann–Whitney test, $P < 0.001$ for all case) (**SupplementaryTable 3**). In addition, the fish community diversity indices (H_N, J, D) increased significantly among the four purification zones of Lake Yanlong before ($H_{N:}$ 1.32 ± 0.15, $J_{:}$ 0.64 ± 0.07, $D_{:}$ 0.61 ± 0.06) and after ($H_{N:}$ 1.66 ± 0.10, $J_{:}$ 0.72 ± 0.04, $D_{:}$ 0.76 ± 0.04) stocking of piscivorous fishes (Mann–Whitney test, $P < 0.05$ for all case) (**Supplementary Table 3**).

DISCUSSION

Spatial Patterns in Fish Community Composition

The species composition, diversity, relative abundance and biomass of fishes among shifting habitat types from the Mangshe

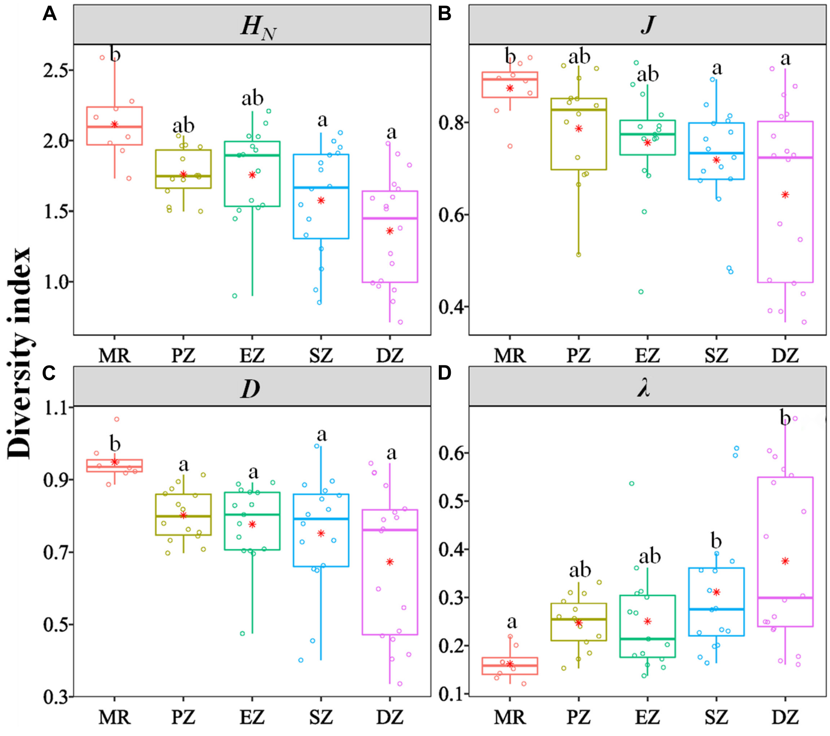

FIGURE 3 | Box and whisker plots characterizing the distribution of different indices [**(A)** Shannon–Wiener diversity index H_N, **(B)** Pielou evenness index J, **(C)** Simpson diversity index D, **(D)** Simpson dominance index λ] characterizing the biodiversity of fish communities inhabiting the Mangshe River (MR) and different purification zones of Lake Yanlong (PZ, the pretreatment zone; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone). Different letters above bars denote significant differences among zones. Asterisks represent mean values.

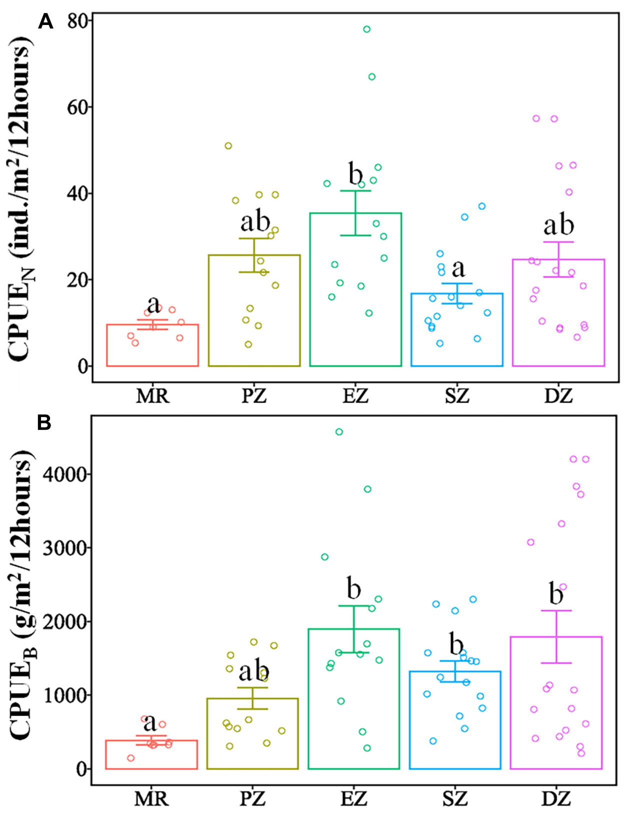

FIGURE 4 | Mean catch per unit effort (CPUE$_N$ and CPUE$_B$) of all fish species combined sampled from the Mangshe River (MR) and different purification zones of Lake Yanlong (PZ, the pretreatment zone; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone) **(A,B)**. Letters above bars denote significant differences among zones. Error bars represent 1 SE.

River to the outlet of Lake Yanlong were distinctly different. Compared to the Mangshe River, fish species richness in the four purification zones of Lake Yanlong was reduced, especially species of migratory fish (e.g., *E. bambusa* and *S. curriculus*). Migratory fish—those that spawn in rivers and migrate to lakes for feeding, growth and maturation—have been severely limited for key habitats for fulfilling their life history over the past several decades as a result of fragmentation imposed by the extensive construction of hydraulic engineering projects (Zhou et al., 2014; Liao et al., 2018). Similar to river-reservoir ecosystems created by dams, Lake Yanlong is connected to the Mangshe River by a large pumping station, which can block migratory channels and still negatively affect the reproduction and growth of migratory fish despite providing additional lake-type habitat that could otherwise be utilized by these fish if accessible (Bai et al., 2020).

Despite reduced species richness, the relative abundance and biomass of fishes tended to be higher in Lake Yanlong relative to the adjacent Mangshe River. Lake Yanlong is a newly constructed ecosystem formed through artificial excavation. It is still in the early stages of ecological development, and some potential niches remain vacant (Cai et al., 2019). Small-bodied fishes (e.g., *P. simony*, *H. leucisculus,* and *C. auratus*) introduced from the Mangshe River are considered r-strategists (or opportunistic strategists), which can quickly occupy vacant ecological niches. These fishes were able to increase in abundance quickly and became the dominant species after entering Lake Yanlong due to the lack of natural enemies (Cai et al., 2019; Jeschke et al., 2019). In this study, six of the eight dominant species observed across purification zones were small-bodied fishes, with *C. auratus*, *P. simony,* and *C. ectenes* accounting for 28.1, 45.8, and 43.9% of the CPUE$_N$ of fishes in the EZ, SZ, and DZ, respectively. High abundances of small-bodied fishes can reduce species diversity within fish communities and affect the complexity and stability of ecosystems (Lima et al., 2016; Liu et al., 2017). Some studies demonstrated that the overabundance of small-bodied fishes and declines in overall fish diversity were accompanied by the deterioration of water quality (Karr, 1981, 1991; Karr et al., 1986; Yu et al., 2021). Moreover, the present study revealed a significant reduction in the Shannon–Wiener diversity index, the Pielou evenness index and the Simpson's diversity index of fishes inhabiting the Mangshe River versus Lake Yanlong. Therefore, it is essential to seek appropriate strategies that help enhance the biodiversity of artificial water supply lakes in order to maintain proper ecosystem function.

Environmental Effects on Fish Community Composition

A wide range of studies have shown that the spatial distribution and composition of fish communities are influenced by both biotic (e.g., competition and predation) and abiotic factors (e.g., nutrient levels and habitat heterogeneity) (Li et al., 2010; Liu et al., 2017; Cai et al., 2019; Whiterod et al., 2021). Mantel's tests and the RDA model all revealed that water depth, aquatic vegetation coverage, and phytoplankton concentrations were the major factors determining the spatial distribution of fishes when moving from the Mangshe River to the DZ of Lake Yanlong. The present study also showed that water depth was the most important abiotic factor influencing fish distribution, as it influenced ecological conditions present within the water column (e.g., food availability and light penetration), which has been important in other related studies (Keast, 1978; Mehner et al., 2005; Fernandes et al., 2010; Li et al., 2010; Cai et al., 2019). Benthivorous fish (i.e., *C. carpio* and *C. auratus*) preferred to live in relatively shallow habitat, principally within the EZ and SZ, while pelagic fish (i.e., *C. ectenes*) generally inhabited deeper water, principally within the PZ and DZ. Phytoplankton is the primary food source for many planktivorous and omnivorous fish species, and can affect the spatial distribution of fishes by modifying the trophic state of and dissolved oxygen concentrations within the water column (McClatchie et al., 1997; Amarasinghe et al., 2012). In this study, the distribution of *H. bleekeri*, *C. ectenes*, and *T. swinhonis* was closely related to the abundance of phytoplankton. A previous study revealed that *H. bleekeri* preferred flowing water habitats that lacked phytoplankton (Li et al., 2020). Conversely, *C. ectenes* and *T. swinhonis* are very common zooplanktivorous fish within the MLYRB, and are better suited for living in habitats with abundant

TABLE 5 | Average dissimilarity and corresponding differentiating species of fish among the Mangshe River (MR) and different purification zones of Lake Yanlong (PZ, the pretreatment zone; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone).

Group	Average dissimilarity (%)	Discriminating species 1	Contribution (%)	Discriminating species 2	Contribution (%)	Discriminating species 3	Contribution (%)
MR-PZ	79.87	HBL	19.77	PSI	15.30	HLE	13.47
MR-EZ	83.82	CAU	22.00	PSI	14.78	HLE	14.58
MR-SZ	83.91	PSI	30.93	HBL	15.25	HLE	10.24
MR-DZ	82.98	CEC	30.37	HBL	15.41	HLE	7.85
PZ-EZ	76.78	CAU	18.29	HLE	13.80	HBL	12.52
PZ-SZ	71.62	HBL	18.17	PSI	17.71	HLE	14.60
PZ-DZ	73.03	CEC	25.20	HBL	17.41	PSI	13.39
EZ-SZ	76.25	CAU	22.19	PSI	17.23	HLE	14.48
EZ-DZ	81.70	CEC	20.74	CAU	17.04	PSI	12.55
SZ-DZ	80.58	CEC	28.05	PSI	21.61	HLE	9.35

Species codes can be referenced in ***Table 3****.*

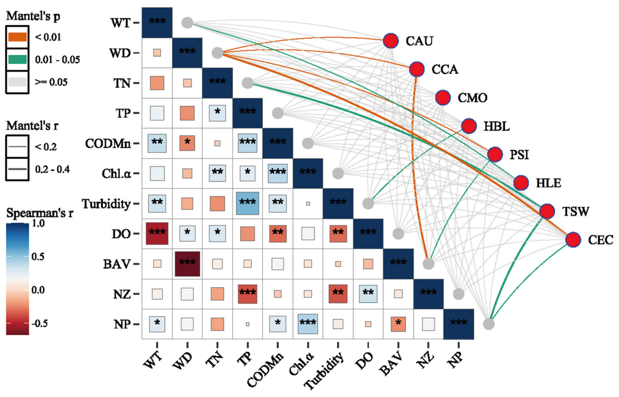

FIGURE 5 | Results from Spearman correlation analyses and Mantel's tests assessing associations among different environment variables and among environmental variables and the dominant species of fish sampled from the Mangshe River (MR) and different purification zones of Lake Yanlong (PZ, the pretreatment zone; EZ, the emergent macrophyte zone; SZ, the submerged macrophyte zone; DZ, the deep purification zone). WT, water temperature; WD, water depth; TN, total nitrogen; TP, total phosphorus; COD_{Mn}, chemical oxygen demand; Chl-α, Chlorophyll-α concentration; DO, dissolved oxygen; BAV, biomass of aquatic vegetation; NZ, density of zooplankton; NP, density of phytoplankton; CAU, *Carassius auratus*; CCA, *Cyprinus carpio*; CMO, *Culter mongolicus*; HBL, *Hemiculter bleekeri*; PSI, *Pseudobrama simony*; HLE, *Hemiculter leucisculus*; TSW, *Toxabramis swinhonis*; CEC, *Coilia ectenes*; * = $0.01 < p < 0.05$, ** = $0.001 < p < 0.01$, *** = $p < 0.001$.

plankton (Liu et al., 2008), so their association to phytoplankton in this study was not surprising.

The biomass of submerged aquatic vegetation was also a key factor affecting the distribution of fishes within Lake Yanlong, which is in accordance with other studies (Li et al., 2010; Massicotte et al., 2015; Cai et al., 2019). Generally, the density of fish, especially small-bodied fish, is positively correlated with the biomass of submerged aquatic vegetation (Cai et al., 2019). Extensive studies have shown that aquatic vegetation can affect the distribution of small-bodied fishes in the following ways: (1) providing abundant food resources for small fish (such as periphytic algae, invertebrates, and plant detritus) (Schneck et al., 2011; Massicotte et al., 2015); (2) the branches and leaves of different aquatic plants often interweave to form complex habitat, which can provide refuge for small fish (Clark et al., 2003; Kovalenko et al., 2012); and (3) the stems and leaves of aquatic plants can provide suitable spawning substrate for fish that produce either adhesive or semi- adhesive eggs (Su and Yao, 2002).

Strategies for Manipulating Fish Community Composition in Artificial Water Supply Lakes

Aforementioned studies and results from the present study indicate that the fish community in Lake Yanlong has undergone the process of miniaturization (i.e., over-abundance of small-bodied fishes), which has implications for ecosystem function, and is a common problem facing other artificial water supply lakes. Planktivorous small-bodied fishes (especially *T. swinhonis* and *C. ectenes*) in the MLYRB can exert heavy grazing pressure on the zooplankton community, leading to the release of phytoplankton, declines in water clarity and submerged macrophyte productivity, and loss of primary ecosystem function (i.e., purification of drinking water for humans) (Post and McQueen, 1987). Traditional biomanipulation, which aims to reduce the biomass of small-bodied fishes by stocking piscivorous fish, thus protecting large-bodied zooplankton capable of controlling phytoplankton, has been carried out extensively in temperate and subtropical lakes (Beklioglu et al., 2003; Mehner et al., 2004; Li et al., 2018). Based on the principle of traditional biomanipulation, we stocked native piscivorous fish (including *C. alburnus*, *S. chuatsi*, *C. gariepinus* and *C. argus*) into each purification zone of Lake Yanlong from 2017 through 2020. Our results revealed that the abundance and biomass of overabundant small-bodied fishes have declined significantly since biomanipulation started in 2017, indicating that the long-term stocking of piscivorous fish can effectively control small-bodied fishess. This in turn has supported environmental conditions more suitable for stimulating submerged macrophyte production and more efficient water purification. Some previous studies

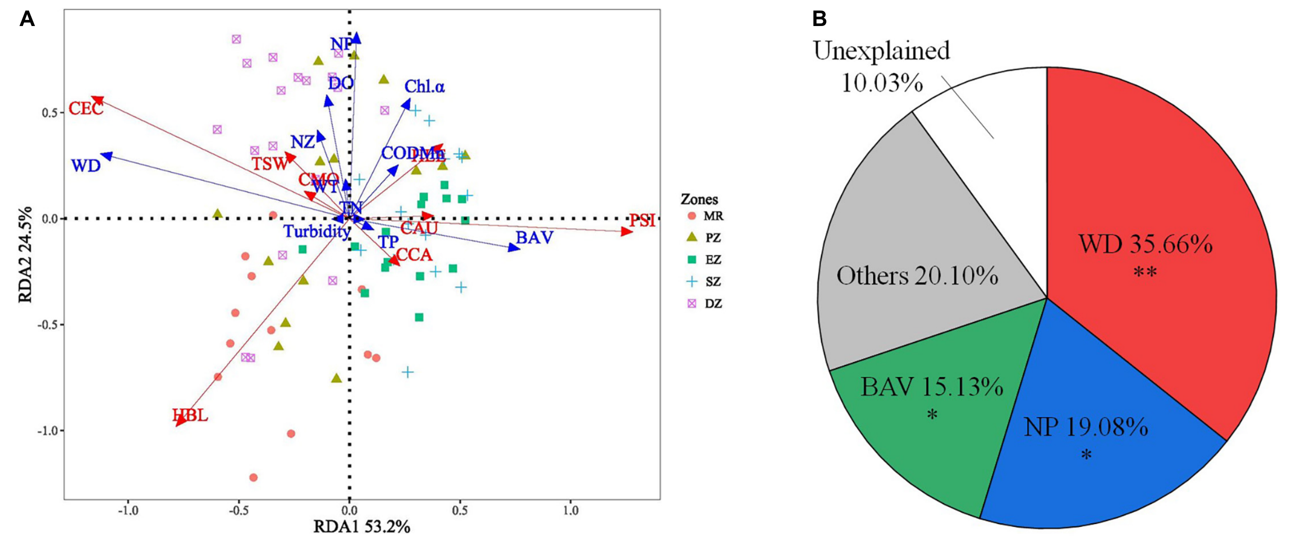

FIGURE 6 | Results from the redundancy analysis (RDA) identifying the key environment variables explaining differences in the relative abundance of dominant fish species among the Mangshe River (MR) and purification zones of Lake Yanlong **(A)**. The pie chart **(B)** describes results from the hierarchical portioning analysis (HP) characterizing the amount of independent explanatory power of each key environmental variable identified. WT, water temperature; WD, water depth; TN, total nitrogen; TP, total phosphorus; COD_{Mn}, chemical oxygen demand; Chl-α, Chlorophyll-α concentration; DO, dissolved oxygen; BAV, biomass of aquatic vegetation; NZ, density of zooplankton; NP, density of phytoplankton; CAU, *Carassius auratus*; CCA, *Cyprinus carpio*; CMO, *Culter mongolicus*; HBL, *Hemiculter bleekeri*; PSI, *Pseudobrama simony*; HLE, *Hemiculter leucisculus*; TSW, *Toxabramis swinhonis*; CEC, *Coilia ectenes*, * = $0.01 < p < 0.05$, ** = $0.001 < p < 0.01$.

arrived at the same conclusion (Jeppesen et al., 1997; Li et al., 2018).

Stocking of piscivorous fishes started 5 years after the construction of Lake Yanlong was completed (2012). During this period, small-bodied fishes occupied most of the ecological niches available in the lake. Because small-bodied fish were already well established before stocking was initiated, they could have limited the early growth and survival of piscivorous fish, necessitating the need for repeated stocking efforts. In addition, previous studies demonstrated that repeated biomanipulation (such as stocking piscivorous fish or removing benthivorous and zooplanktivorous fishes) was necessary for achieving and maintaining desired effects over the long-term in shallow eutrophic lakes (Søndergaard et al., 2008; Li et al., 2018; Setubal and Riccardi, 2020; Guo et al., 2022).

Although stocking of piscivorous fish positively influenced aquatic ecosystem function in the present study, stocking piscivores could have unintended consequences worth noting. For example, the unintentional introduction of non-native species and or genetic hybridization that could reduce overall biodiversity (Buoro et al., 2016; Cucherousset et al., 2020). Therefore, we propose three mitigation strategies for the management of fish resources and improving the water quality of artificial water supply lakes. First, the stocking of piscivorous fish should be carried out immediately after artificial lakes are built and subsequently maintained for the long-term. Second, different types of piscivorous fish should be selected according to the characteristics of different habitats present within the lakes. For example, shallow habitats were more suitable for benthic-oriented piscivorous fish (e.g., *S. chuatsi*, *C. gariepinus,* and *C. argus*), while deep water habitats were more suitable for pelagic-oriented piscivores (e.g., *C. alburnus*). Third, the piscivorous species stocked should be native to avoid potential ecological hazards caused by non-native species and genetic hybridization. Although piscivorous fish played a key role in controlling small-bodied fish in Lake Yanlong, the utility of stocking piscivorous fish for improving water quality should be further verified in other artificial water supply lakes.

CONCLUSION

This study provided basic information on the composition, relative abundance and biomass, and diversity characteristics of fish communities occupying distinct habitat zones extending from the Mangshe River through to the outlet of Lake Yanlong. We confirmed that water depth, the amount of submerged aquatic vegetation and phytoplankton concentrations were the primary factors determining the spatial distribution of fishes along this gradient of artificially constructed habitat types. Based on the effects of stocking piscivorous fish in Lake Yanlong from 2017 to 2020, we suggest that the long-term stocking of piscivorous fish can effectively control small-bodied fishes. However, the species of piscivorous stocked should be tailored to habitat conditions present within the different purification zones of Lake Yanlong.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

CG: investigation, data analysis, and writing – original draft. SL: investigation, resources, and data curation. WL: methodology, resources, and writing – review and editing. CL: methodology and writing – review and editing. TZ: resources and funding acquisition. JL: resources, writing – review and editing, and supervision. LL: resources and data curation. JS: investigation and data curation. XC: investigation and writing – review and Editing. AH: resources and writing – review and editing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.921082/full#supplementary-material

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