



Article Exploring the Drivers of Spatiotemporal Patterns in Fish Community in a Non-Fed Aquaculture Reservoir

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Abstract: Non-fed aquaculture is an important contributor to low environmental impact protein production. However, knowledge of spatiotemporal patterns of the fish community in non-fed fishery systems remains limited, despite their ecological importance for sustainable aquaculture and fisheries. To elucidate the status of the fisheries and their critical drivers in non-fed fishery systems, hydroacoustic surveys were conducted seasonally in Hongchaojiang Reservoir in two seasons (spring and autumn) of two consecutive years: 2018 and 2019. Results showed that the average fish density in Hongchaojiang Reservoir was 121.6 ind./1000 m³. Fish communities varied significantly between geographical locations and seasons. On the temporal scale, fish densities in October were higher than those in April. On the spatial scale, fish densities were higher in the upstream (S1 and S3) than those in the midstream (S2, S4, S5, S6), while the density of S7, S8 and S9 in the downstream was the lowest. Trophic level index, zooplankton, chlorophyll-a, and phytoplankton play vital roles in fish distributional patterns, while the target strength, which reflects fish body size, was highly associated with water temperature, dissolved oxygen, total organic carbon, and phytoplankton. These results suggest that the spatiotemporal distribution of the fish community in Hongchaojiang Reservoir was jointly influenced by biotic and abiotic variables of water bodies, and highlight the importance of water nutrient levels and food availability in shaping fish distribution in the nonfed aquaculture system. This study should improve our understanding of ecological patterns and dominant drivers in fish stocks and provide information for successful sustainable management in non-fed purification fisheries.

Keywords: spatiotemporal variations; acoustics; fish density; environmental variables; non-fed aquaculture

1. Introduction

The phenology of many species has been shaped by individual optimal decisions in response to predictable patterns of food availability in space and time [1]. It is particularly true for fish inhabiting freshwater areas, where survival and breeding success depends on the ability to adjust behavior timing to spatiotemporal patterns in food availability [2,3]. However, the construction of large dams and reservoirs in freshwater ecosystems modifies river-channel morphology and leads to habitat fragmentation, known as the 'barrier effect', and food availability shifts in space [4,5]. These activities additionally contribute to



Citation: Wang, G.; Sang, S.; Zhou, Z.; Wang, D.; Chen, X.; Li, Y.; Guo, C.; Zhou, L. Exploring the Drivers of Spatiotemporal Patterns in Fish Community in a Non-Fed Aquaculture Reservoir. *Diversity* **2023**, *15*, 886. https://doi.org/ 10.3390/d15080886

Academic Editor: Paolo Pastorino

Received: 5 June 2023 Revised: 16 July 2023 Accepted: 21 July 2023 Published: 26 July 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). freshwater ecosystem instability and vulnerability, such as environmental deterioration and eutrophication due to the decomposition of important quantities of submerged plant material [6,7]. Importantly, as long as food webs and trophic interactions vary closely with the biogeochemical transformations and nutrients providing, species that can complete their life cycle in the new environment and take advantage of the available food resources will achieve their full potential for proliferation, which acts as an engine powering shifts the fish community composition and spatiotemporal distribution of fish stocks [8,9].

As a novel remedy, non-fed aquatic systems are applied to alleviate potential problems, which mediates a multitude of services such as cleaning the water, creating freshwater habitats, offering unfed services, and biodiversity conservation [10,11]. Specifically, fish assemblages rely solely on the natural food available to meet their nutritional needs and there will be no supplementation with pellet feed, eventually changing patterns of food availability. To date, the non-fed systems are widely utilized in marine aquaculture, which is successfully carried out with essential seaweeds, shellfish, mussels, oysters, and algae [12–14]. In freshwater, a non-fed system is applied to the development of juvenile freshwater fish, highly fertilized earthen ponds, and freshwater fish aquaculture in huge dams, e.g., carp [15,16], which was gradually being recognized as an effective solution for restoring eco-system function and livelihoods. Additionally, the artificial stocking of suitable fish in local fisheries changes the composition of the fish community to alter the aquatic environment and restore ecological balance [12,17]. For instance, filter-feeding fishes such as silver carp and bighead carp are important species in non-fed-based multispecies polycultures where they maintain the water quality and improve the production of the system by grazing on natural food [18,19]. It is unclear which component resulted in the benefit of the complicated system. Secondly, fundamental properties of the environment that affect the composition and spatiotemporal distribution of the fish community have been reported in numerous previous studies, which are important for the processes and functioning of sustainable systems [20,21]. The interaction of abiotic factors and species interaction networks of plankton structure are predictors of community structure, and, furthermore, the overall interaction may be the linchpin for understanding these effects. To the best of our knowledge, the potential changes in the fish community in non-fed culture systems triggered by biotic and abiotic factors have not been studied.

To better understand the composition, density, and three-dimensional distribution of fish communities in fisheries, hydroacoustic technology is often used in conjunction with conventional fishery stock assessment approaches. A quantitative echosounder can be utilized to quantify the acoustic parameters of the density and spatial dispersion of fish schools [22–24]. With this non-invasive method, surveys of fishery resources across a large area can be undertaken quickly and efficiently [25,26]. Therefore, the hydroacoustic methodology is increasingly utilized as a scientific evaluation method in the research of fish resources and ecology.

The Hongchaojiang Reservoir was originally one of the typical large aquaculture reservoirs. With the recent expansion of aquaculture production, aquaculture effluents result in eutrophication and environmental degradation, which increasingly reduces ecosystem productivity and resilience of ecosystems [27–31]. High concentrations of inorganic anions, such as phosphates, nitrates, and ammonia, coupled with organic nitrogen and/or heavy metals have been found in the sediment of the water body [32]. Enrichment of such aquatic ecosystems is usually followed by alterations in the phytoplankton community's structure, eventually creating artificially unbalanced and high-trophic ecosystems [30,33,34]. Along food chains, aquatic organisms have a robust response to modification. To curb eutrophication and restore the unbalanced aquatic ecosystems, it has been proposed to imitate lake-like conditions, and in 2012, the non-fed fishery system was introduced as an applicable mitigation approach. By introducing filter-feeding fish such as *Hypophthalmichthys molitrix* and *Hypophthalmichthys nobilis* into the reservoir and designing fishing areas, an efficient method has been devised and performed to slow down water eutrophication and maintain the ecosystem's stability [28,35]. However, the results after recovering processes

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and their functional importance have not yet been evaluated. Furthermore, the operational management of aquatic ecosystems requires a methodology that can provide objective and reproducible information on cycles and trends in water quality and fish assemblages [12,36]. Therefore, accurate environmental indicators, spatiotemporal distribution patterns of fish resources, and their responses to the dynamic changes in water variables are crucial for the management and sustainable development and utilization of fishery resources in local reservoirs [37].

The aim of this study was to (1) test patterns of fish communities' distribution in the Hongchaojiang Reservoir habitats after human intervention; and (2) determine whether local biotic and abiotic variables serve as potential drivers in the new aquatic ecosystem. In a non-fed aquatic ecosystem, affected by eutrophication, multiple uses of reservoir resources impact the fish communities and fisheries production. Logically therefore, we hypothesized that trophic level and food availability could play a vital role in driving the spatiotemporal distribution pattern of fishery assemblages.

2. Materials and Methods

2.1. Study Area

The study was performed at Hongchaojiang Reservoir in the Guangxi Zhuang Autonomous Region, China (21°52′5″ N, 109°7′35″ E). To reduce the risks of eutrophication and algal blooms, non-fed aquaculture was implemented in the reservoir, with abundant filter-feeding fish such as *Hypophthalmichthys molitrix* and *Hypophthalmichthys nobilis* stocked from 2012 [27,29,38].

2.2. Hydroacoustic Surveys

The hydroacoustic system was a SIMRAD EY60 echosounder with a split-beam transducer (an opening angle of 7° at -3 dB). The hydroacoustic surveys were carried out during daylight hours (6:00 to 18:00) in April, October 2018, and April, October 2019, respectively. Before each survey, the SIMRAD EY60 was calibrated with the original 13.7 mm diameter standard W–Cu metal sphere to eliminate the effect of water environment variations in each navigation on the acoustic detection and to obtain an accurate echo signal [39]. During the surveys, the transducer was mounted vertically on the right side of a 15 m fishing boat and positioned at a depth of 50 cm. The echosounder was controlled by Simrad ER 60 acquisition software (version 2.4.0), which provided a real-time display and stored acoustic raw data (Figure 1). Simultaneously, the geographical coordinates were recorded by a GPS (MX-500 GPS) connected to the processor, with a 0.012 m resolution accuracy. The survey was conducted on zigzag transect lines at a vessel speed of 8–10 km/h.

To understand the fish composition in Hongchaojiang Reservoir, fish samples were collected from S2, S3, S6, S7 and S9 using both gill nets and cage nets (Figure S1). Each sampling site was set up with 5 cage nets (the net frame was 33 cm in height, 45 cm in width, and 0.7 cm in mesh) that were 25 m long and 3-gill nets (the net height was 1.5 m and the mesh size was 6 cm, 8 cm, and 10 cm, respectively) that were 60 m long. All the sampling nets were placed at 7:00–9:00 p.m. and collected at 7:00–9:00 a.m. the next day, with the duration being about 12 h. All fishes caught were identified as species according to Freshwater Fishes of Guangxi, China (second edition) [40]. All individuals were counted and then weighed.

2.3. Plankton Collection and Water Quality Monitoring

Plankton samples were collected by a polymethyl methacrylate sampler from different water layers (the surface, the middle and the bottom). The phytoplankton samples (1 L) were fixed with 1% Lugol's solution and stored in a dark box at room temperature [41]. Species were enumerated with the Utermöhl method using microscopy [42], with a minimum of 500 units counted in each sample. The biovolumes of phytoplankton were estimated based on the provided geometric shapes and mathematical equations [43]. Phytoplankton biomass (mg/L) was estimated through their biovolumes [41]. Zooplankton samples (20 L) were filtered through a 64 μ m pore-size net and preserved with formaldehyde in the field [44]. The zooplankton were identified and counted using microscopes. Zooplankton biomass (mg/L) was estimated through their biovolumes [45]. The estimation of zooplankton biovolume and biomass was similar to that of phytoplankton.



Figure 1. The screen capture shows the echogram from Simrad EY60 echo sounder monitoring the aquatic habitat in Hongchaojiang Reservoir. (**A**) Single target position. This field gives you detailed information about single fish; (**B**) Single target histogram. This field offers an analysis of fish size distribution presented in a histogram; (**C**) The echograms show echoes from targets between the surface and bottom of the detected area. The red lines are echoes from the reservoir bottom. The blue lines are echoes from gas bubbles, near water's surface. Targets give detailed information about fish target strength and fish length.

During hydroacoustic surveys, water quality variables and food organisms in the reservoir were monitored simultaneously. Nine monitoring sites were settled in the reservoir during the experiment to collect these data (Figure S1), including water temperature (WT, °C), transparency (SD, cm), pH, dissolved oxygen (DO, mg/L), total phosphorus (TP, mg/L), total hardness (TH, mg/L), total nitrogen (TN, mg/L), NO₂-N (mg/L), NO₃-N (mg/L), NH₃N (mg/L), COD_{Mn} (mg/L), chlorophyll-a (mg/m³), total organic carbon (TOC, mg/L), and biomass of phytoplankton and zooplankton. Among them, water temperature, pH, dissolved oxygen, and transparency were all measured and recorded on site with a YSI PRO PLUS being used in measuring water temperature, pH and dissolved oxygen, and a 20 cm diameter Secchi disk being used in measuring transparency (SD). For other monitoring items, 1 L water samples were taken back to the laboratory, and the measurement was conducted in accordance with the environmental quality standard for water (GB3838-2002). In addition, the trophic status of each site was evaluated with the trophic level index (TLI) [46], based on Chl-a, TP, TN, SD and COD_{Mn} as follows:

 $TLI = 0.4612 \times TLI(Chl-a) + 0.2987 \times TLI(TP) + 0.0004 \times TLI(TN) + 0.1496 \times TLI(SD) + 0.0901 \times TLI(COD_{Mn}) \times TLI(COD_{Mn}) \times TLI(Chl-a) + 0.2987 \times TLI(TP) + 0.0004 \times TLI(TN) + 0.1496 \times TLI(SD) + 0.0901 \times TLI(COD_{Mn}) \times TLI(SD) + 0.0901 \times$

TLI(TP) = 10(9.436 + 1.624lnTP)TLI(TN) = 10(5.453 + 1.694lnTN)TLI(SD) = 10(5.118 - 1.94lnSD)

 $TLI(COD_{Mn}) = 10(0.109 + 2.661lnCOD)$

2.4. Data Processing and Analysis

Sonar 5 (version 6.0.3, Lindem Data Acquisition, Oslo, Norway) post-processing software was used to convert and analyze the acoustic data. The noise threshold of 40logR was set to -60 dB during conversion. Bottom detection in Sonar 5 was utilized to automatically identify the bottom of the reservoir, but obvious errors were corrected manually. To exclude the near-field and dead zones, acoustic data were only evaluated between the range of 1.5 m from the transducer and 0.5 m above the bottom layer. The acoustic data from each transect were cleaned of noise (bubbles, trash, bottom structures, etc.) using an appropriate threshold and manual deletion, leaving only the target echoes for further analysis.

Concerning sonar parameters for data processing, the TS threshold for this study was set to 60 dB, the lowest echo length was set to 0.6 and the maximum echo length was set to 1.8, with a maximum difference of 0.5; Maximum Gain Compensation for the cross-section was set to 6 dB [47]. The method of echo counting was used to determine the bulk density of fish. The empirical formula TS = 20 log L - 71.9 dB was used to determine the relationship between fish target strength (TS) and fish length (L) [48].

Principal component analysis (PCA) is an ordination method that can be used to identify the underlying structure of multivariate datasets. Accordingly, the relationship between biotic and abiotic environmental variables was subjected to it. The PCA procedure involved several analytical steps. All the parameters selected for PCA analysis were then Ln (x + 1)-transformed to get normalized data. The number of PCs to be retained is determined by the scree plot criterion. For the final PCA, the first two components of the PCA were selected and the parameters showing high variability and gradient across the dataset were chosen. All procedures were performed using R package "ade4" [49]. To further examine the spatial and seasonal variations of fish communities, ANOVA was used to test the differences in mean density with Tukey's HSD post hoc tests ($\alpha = 0.05$) for multiple comparisons. Linear regression was used to analyze the relationship between each environmental variable and fish density. A multiple regression model with variance decomposition analysis (relaimpo v2.2-6, R-package) was used to estimate the importance of measured environmental factors in explaining the distribution of fish density and TS. All these analyses were performed using R 3. 5. 1 [50].

3. Results

3.1. Spatial and Temporal Variations of Water Quality

Environmental variables in the sampled reservoir (Table 1) showed that water quality in Hongchaojiang Reservoir was in moderate-eutrophication status. Spatiotemporal variations of 18 environmental parameters are shown in Figure 2. WT, TOC, NH₃N, COD_{Mn} and Phytoplankton biomass were highly correlated with each other and negatively associated with DO, pH, and NO₃N. They are associated with axis 1, which accounts for 28.51% of the overall variation. A similar inverse association appeared between TLI, zooplankton, chlorophyll-a and transparency (Trans) along axis 2, explaining 21.70% of total variance (Figure 2A). All environmental factors exhibited significant seasonal and spatial gradients: in the spatial variations, a trend was presented with a gradient change from upstream (S1, S3) to midstream (S2, S4, S5, S6, S7) to downstream (S7, S8, S9) (Figure 2B); in seasonal variations, April (Spring) is characterized by low temperatures, high dissolved oxygen concentrations, TP, and TN, whereas October (Autumn) is characterized by high temperatures and low DO, pH (Figure 2C). There is no significant difference in the interannual variations of environmental conditions.

Variables	Mean	Min.	Max.	S.D.
WT	26.96	20.90	30.50	2.88
pН	7.84	6.41	9.18	0.76
DO	8.18	4.31	10.22	1.74
Trans	89.61	50.00	145.00	24.86
TH	10.80	7.01	27.90	3.80
TP	0.02	0.00	0.07	0.01
TN	0.65	0.12	1.35	0.29
NO2N	0.01	0.00	0.05	0.01
NO3N	0.30	0.01	0.98	0.27
NH3N	0.23	0.04	0.95	0.19
COD _{Mn}	3.14	1.49	4.89	0.69
Chl-a	22.42	8.43	43.05	10.03
TOC	3.85	2.00	7.13	1.30
TLI	51.84	44.31	62.04	4.56
phytoplankton	11.55	1.94	47.64	9.69
zooplankton	3.35	1.69	4.65	0.86

Table 1. The biotic and abiotic variables in Hongchaojiang Reservoir.

Note: Water temperature (WT, °C), pH, dissolved oxygen (DO, mg/L), transparency (Trans, cm), total phosphorus (TP, mg/L), total hardness (TH, mg/L), total nitrogen (TN, mg/L), NO2N(NO₂-N, mg/L), NO3N(NO₃-N, mg/L), NH3N(NH₃N, mg/L), COD_{Mn} (mg/L), chlorophyll-a (Chl-a, mg/m³), total organic carbon (TOC, mg/L), biomass of phytoplankton (phytoplankton, mg/L) and biomass of zooplankton (zooplankton, mg/L).



Figure 2. Principal Component Analysis of environmental variables. (**A**) Correlation and score of environmental variables. (**B**) Scatter diagram of sites variations of environmental variables. (**C**) Scatter diagram of seasonal variations of environmental variables. The variables are referred to Table 1.

3.2. Spatiotemporal Patterns in Fish Community

A total of 19,878 fish, comprising 29 species, representing 11 families and 25 orders, were collected by netting catches. Among them, *Oreochromis niloticus* dominated the reservoir fish community in both quantity and biomass, accounting for 61.71% and 57.76%, followed by *Toxabramis houdemeri* which accounted for 32.74% and 10.9%, respectively (Table S1).

Compared to limited net catches, acoustic data showed the apparent spatiotemporal patterns of fish density. The mean fish density of the reservoir was 121.6 ind./1000 m³. Significant differences were observed in the annual (F = 204.5; p < 0.01), seasonal (F = 314.5; df = 1; p < 0.01) and spatial (F = 121.0; df = 8; p < 0.01) distributions of the fish density in the reservoir (Table 2). Also, significant differences were observed in the seasonal (F = 751.304; df = 1; p < 0.01) and spatial (F = 21.219; df = 8; p < 0.01) distributions of the TS in the reservoir, but no significant difference was found between different years (Table 2).

Table 2. ANOVA statistics of different factors on fish density and target strength (TS).

Index	Factors	Df	Sum Sq	Mean Sq	F-Value	Pr (>F)	Significance
Density	year	1	2,546,212	2,546,212	204.5	$<2 \times 10^{-16}$	***
Density	season	1	3,915,494	3,915,494	314.5	$<\!\!2 imes 10^{-16}$	***
Density	zone	8	12,049,387	1,506,173	121.0	$<\!\!2 imes 10^{-16}$	***
TS	year	1	1	1	0.168	0.682	/
TS	season	1	6268	6268	751.304	$<\!\!2 imes 10^{-16}$	***
TS	zone	8	1416	177	21.219	$<\!\!2 imes 10^{-16}$	***

Note: *** *p* values < 0.001, statistically highly significant.

Spatially, the fish density of S1 and S3 in the upstream was higher than that of S2, S4, S5 and S6 in the midstream, while the density in S7, S8 and S9 in the downstream was the lowest. The maximum density was found at S3 upstream with an average density of 335.48 ind./1000 m³, the minimum was at S8 downstream with an average density of 26.27 ind./1000 m³ (Table S2; Figure 3). This spatial distribution is negatively correlated with the water depth, as revealed by hydroacoustics (*R*-pearson = -0.45; *p* < 0.01) (Figure 4).



Figure 3. Fish densities at different sites of Hongchaojiang Reservoir during 2018–2019. The measured fish density was transferred by Log10 (X + 1).



 $t_{\text{Student}}(2290) = -24.19, p = 2.60 \times 10^{-115}, \hat{r}_{\text{Pearson}} = -0.45, \text{Cl}_{95\%}$ [-0.48, -0.42], $n_{\text{pairs}} = 2292$

Figure 4. Relationship between fish density and depth in Hongchaojiang Reservoir during 2018–2019. Fish densities are log10 (X + 1)-transformed. Top: test statistic (t), level of significance (p), effect size (coefficient of correlation r), confidence interval of effect size (CI), and sample size (n_{paris}). Blue line: Linear regression. Gray band: 95% confidence interval.

Temporally, fish density in October was higher than in April, whilst the density increased drastically in October 2018 (Table S3; Figure 5).

3.3. Relationships between Environmental Conditions and Fish Community

Correlation analyses suggested that the trophic-level index (TLI) was most substantially connected with the spatiotemporal distribution of fish community ($R^2 = 0.36$, p = 0.003). In addition, zooplankton biomass ($R^2 = 0.33$, p = 0.006), chlorophyll-a ($R^2 = 0.32$, p = 0.009), and phytoplankton biomass ($R^2 = 0.28$, p = 0.02) were positively correlated with fish density (Figure 6). The mean target strength (TS), which reflects the fish size distribution, was strongly positively associated with dissolved oxygen ($R^2 = 0.50$; p < 0.001), but highly negatively associated with total organic carbon (TOC) ($R^2 = 0.58$; p < 0.001), phytoplankton density ($R^2 = 0.40$, p < 0.001) and water temperature ($R^2 = 0.39$; p = 0.002) (Figure 6).

For fish density, the measured variables can explain 84.95% of the variations, among which zooplankton (18.63%), phytoplankton (15.89%), TLI (11.93%), chlorophyll-a (8.64%) and TP (8.24%) contributed the most (Figure 7A). For TS, the measured variables could explain 89.07% of the variations, among which water temperature (18.78%), TOC (18.46%), dissolved oxygen (14.74%), and phytoplankton (12.52%) played significantly large roles compared to others (Figure 7B).



Figure 5. Seasonal variations of fish density in Hongchaojiang Reservoir during 2018–2019. The measured fish density was transferred by Log10 (X + 1).



Figure 6. Linear regression of fish density, mean fish target strength and their significant environmental variables. (Chl-a: chlorophyll a; Phylo: phytoplankton; TLI: trophic-level index; Zoop: zooplankton; TOC: total organic carbon; WT: water temperature). Gray band: 95% confidence interval.



Figure 7. Contributions of biotic and abiotic environmental variables to (**A**) fish density and (**B**) mean TS (fish target strength) by multiple regression model. $R^2 = 84.95\%$ for fish density and 89.07% for TS, metrics are normalized to sum to 100%.

4. Discussion

To date, there still has been little research on the patterns of fish community structure and environmental variables in non-fed culture systems, which is essential information for the regulation and management of sustainable aquaculture and fisheries [12,15,51]. In this study, water quality, food organisms, and fish community in Hongchaojiang Reservoir were investigated using hydroacoustic and netting data. The results showed that the distribution of fish in the non-fed culture system was not random in time and space, and exhibited significant inter-seasonal and spatial variability. The highest fish densities occurred in autumn and in the reservoir's upper basin. These results are consistent with the variation of environmental variables, in accordance with some natural reservoirs or rivers [52,53]. Spatial variations in the fish community structure were usually caused by changes in habitat features along the longitudinal gradient, whereas seasonal variability in fish community structure was often attributed to flood-related changes in habitat characteristics, and the seasonal population growth of fish species [19]. Based on the above consistency, the spatiotemporal difference in environmental variables is an important driver of the spatiotemporal variation of fish community structure in the Hongchaojiang Reservoir.

According to the relationship between environmental variables and fish density, the TLI (trophic-level index), a measure of the nutrient status of lakes or reservoirs, showed the greatest positive correlation on the spatiotemporal distribution of fish community in Hongchaojiang Reservoir. Slightly eutrophic waters with high trophic levels could improve fish resources to some extent [54,55]. By comparing reservoirs in different trophic states, Godlewska et al. (2003) found that reservoirs in a eutrophic state had higher fish densities. Furthermore, zooplankton, chlorophyll-a and phytoplankton also have significant and favorable effects on the distribution of fish density [56]. The ability of phytoplankton and zooplankton to serve as natural food for fish has a direct impact on the fishery resources of the reservoir, and chlorophyll-a in the reservoir reflects the primary productivity level of the water body [57–59]. Through food-chain transmission and bottom-up effects to higher trophic levels, primary productivity can provide abundant food for organisms at different trophic levels in the water, which subsequently affects fish production [60–62]. In this study,

phytoplankton and zooplankton are the direct food sources of filter-feeding fishes (e.g., *H. molitrix* and *H. nobilis*) in the reservoir. The increase in phytoplankton and zooplankton biomass can improve the number of filter-feeding fish resources, which will ultimately increase the number of carnivorous fish, e.g., mandarin fish. Based on previous studies, the significant decrease in fish density from upstream to downstream confirmed the high nutrient levels upstream. Temporally, fish densities were higher in autumn (October) than in spring (April), perhaps due to warmer temperatures in autumn compared to spring. Seasonal environmental factors influence the growth of plankton, resulting in a seasonal pattern of fish abundance [63]. It is also likely related to fish reproduction that the increase in recruitment population owing to fish reproduction causes the autumn density to be greater than the spring density.

In addition, dissolved oxygen, TOC, phytoplankton, and water temperature were found to have significant effects on fish size. Firstly, dissolved oxygen in water was a variable that directly affected the size of fish. An area with a higher concentration of dissolved oxygen is more conducive to large-sized fish, with a large oxygen requirement to carry out various metabolic processes [64]. Therefore, the area with dissolved oxygen content is often the preferred habitat for large-sized fish. In contrast, higher phytoplankton density, as the primary net producer, create favorable conditions for a massive proliferation of primarily small-sized sedentary species (i.e., those that do not migrate) which have a high reproductive potential and short longevity and for which the availability of food resources is high [65,66]. Similarly, the TOC reflects the amount of organic matter in the water. Oxygen consumption in the process of decomposition of organic matter results in the decrease in dissolved oxygen in waters. Due to the more aerobic characteristics of the growth of relatively large-sized fish, the TS of fish has a significant negative correlation with TOC. Water temperature is also considered to be an important driving variable for fish distribution, which is capable of shaping fish distribution by influencing dissolved oxygen content or food organisms in water. An appropriate increase in water temperature within the range of the physiological limit of fish is conducive to the survival and rapid growth of small fish [67]. Therefore, the water with relatively high water temperature is generally the area where juvenile fish often do their activities [17]. It is also in accordance with the similar causes of seasonal differences. In total, these drivers intently present a clear proof that the size and density of fish are closely related to food availability, and even the trophic level directly determines its distribution pattern.

In this study, we found the dominance of *Oreochromis niloticus*. A possible explanation might be that previous cage culture and reservoir eutrophication have created more favorable growth conditions for the species. Studies have confirmed that the phytophagouspreferred Oreochromis niloticus spread quickly in eutrophic water, and curb algae biomass by promoting the cycling of P and N in water [68]. Consistent with this, previous studies have also shown that tilapia are efficient consumers of cyanobacteria due to their low stomach pH (pH < 1) [69–71]. Similarly, phytophagous-preferred, and pelagic fish, such as Toxabramis houdemeri, were dominant in the reservoir under these suitable growth conditions. At the same time, released filter-feeding fish, such as silver carp and bighead, have a mesh-filtering apparatus and directly remove algae > 10 μ m from the water column [71]. The fish composition found in this study may be partly explained by effective conservation strategies based on the restocking of freshwater fishes, which typically involves either stock enhancement, aimed to maintain fish populations at a stable level, or multiple releases to increase both the number of recruits and the spawning biomass [72,73] These phenomena suggest that strong interaction among biotic and abiotic factors, as well as fish community structure in non-fed aquaculture systems appear to play a positive role in reducing water trophic levels. In management, it could be considered as one effective method to mitigate impacts caused by dams and associated reservoirs on fish diversity and fish stocks, with fish stocking, fish farming, and fishery control in non-fed reservoirs.

However, there are also some potentially negative impacts. As exotic fishes, tilapia may share a common food niche with local species, and native species that reproduce in

the ecosystem will have to struggle to coexist with tilapia [74]. Given the high survival rate of tilapia, the ecological consequences of tilapia invasion and establishment in such aquatic ecosystems can be severe [75]. The impact of alien fishes in the non-fed aquaculture systems should not be underestimated, and their relationship with native species and ecological balance needs to be further studied.

5. Conclusions

In this study, the spatiotemporal distribution of the fish community exhibits strong synergistic effects with the aquatic environment, where the greater abundance occurred in autumn and in the upper basin of the Hongchaojiang Reservoir. The spatiotemporal distribution of fish communities was jointly influenced by biotic and abiotic variables of water bodies, highlighting the importance of water nutrient levels and food availability in shaping fish distribution in the non-fed aquaculture system. Based on our findings, both natural (e.g., TLI, DO, TOC, food organisms) and human (e.g., alien species control, anthropogenic stock enhancement) factors may need to be considered when establishing aquatic conservation strategies and priorities in non-fed aquatic systems.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d15080886/s1: Figure S1: Location of Hongchaojiang reservoir and sampling sites. Black lines indicate separated sampling sites; Table S1: Composition of the fish assemblages in Hongchaojiang reservoir; Table S2: Statistics of fish density (ind./1000 m³) and target strength (TS, dB) in different investigated sites; Table S3: Statistics of fish density (ind./1000 m³) and target strength (TS, dB) in different investigated seasons.

Author Contributions: Conceptualization, Z.Z., C.G. and L.Z.; data curation, G.W., S.S., Z.Z., X.C., L.Z. and Y.L.; formal analysis, G.W. and S.S.; funding acquisition, L.Z.; investigation, G.W., S.S., Z.Z., D.W., X.C. and C.G.; methodology, G.W., S.S., X.C., C.G., D.W., L.Z. and Y.L.; project administration, D.W., L.Z.; resources, C.G., L.Z. and Y.L.; software, G.W., S.S. and X.C.; supervision, C.G.; validation, S.S., Z.Z. and Y.L.; visualization, G.W. and L.Z.; writing—original draft, G.W.; writing—review and editing, C.G. and L.Z. All authors have read and agreed to the published version of the manuscript.

Funding: Guangxi Science and Technology Major Project (No. AA17204095-8), the National Key Research and Development Program of China (No.2020YFD0900504), and Science and Technology Planning Project of Guangzhou City (No.PM-ZX913-202104-127\202002030345).

Institutional Review Board Statement: All the experimental protocols concerning the handling of fish were in accordance with the requirements of the Animal Ethics Committee at the South China Agricultural University, China (approval ID: SYXK-2019-0136).

Data Availability Statement: Data are available on request from the corresponding authors.

Acknowledgments: We would like to thank anonymous fishermen for their help in the acoustic survey and fish sampling.

Conflicts of Interest: This is an original submission that has not been published before and that is not currently under review at any other publication outlet. No conflict of interest exist in the submission of this manuscript, and the manuscript is approved by all authors for publication.

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