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Longitudinal Variations in Physiochemical Conditions and Their Consequent Effect on Phytoplankton Functional Diversity Within a Subtropical System of Cascade Reservoirs

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The social and environmental impacts of large dams are quantifiable and have been well documented, while small dams have often been presumed to be less environmentally damaging than large dams. The purpose of this study was to analyze longitudinal gradients in environmental, hydrodynamic variables and their impact on phytoplankton function, within a cascade of four reservoirs (XuanMiaoGuan, XMG; TianFuMiao, TFM; XiBeiKou, XBK; ShangJiaHe, SJH) and one reservoir bay (Huangbohe Bay, HBH), located from upstream to downstream in the Huangbo River, Hubei Province, China. Our results showed that water temperature, total nitrogen, and soluble silicate increased along the cascade reservoir system, while the concentration of dissolved oxygen and total phosphorus decreased. We identified 16 phytoplankton functional groups, and the predominant groups, including **D** (*Synedra* and *Stephanodiscus hantzschii*), **E** (*Dinobryon divergens*), **Lo** (Dinoflagellate: *Peridinium bipes* and *Peridiniopsis*), **X2** (*Chroomona*), and **Y** (*Cryptomonas*), changed longitudinally from up to down in the cascade reservoirs. The number of dominant functional groups increased along the longitudinal gradient, indicating that the function of the phytoplankton community was more stable. Functional group **D** was the dominant phytoplankton functional group among the four reservoirs, and **Lo** group was dominant except SJH. The phytoplankton functional groups in the HBH have been completely changed due to the backwater jacking of the main stream of the Yangtze River. Euphotic depth, suspended solids, and nutrients were apparently the key factors driving variations in phytoplankton functional groups among the reservoirs. Notably, the patterns we observed were not all consistent with the cascading reservoir continuum concept (CRCC) that typically characterizes large rivers. Thus, our findings contribute to the further theoretical development of the CRCC, which may not apply widely to all cascade systems.

Keywords: longitudinal heterogeneity, continuum, phytoplankton functional group, cascade reservoirs, Huangbo River

INTRODUCTION

River is the major conjunction of terrestrial and aquatic ecosystems and has important ecological functions such as water supply, flow regulation, and moderation of climate (Costanza et al., 1997; Cai et al., 2003). However, the constructed dam that fragmented the river ecosystem leads to modifications of the river's original conditions and water dynamics, resulting in changes in abiotic and biotic compartments (Zhao et al., 2017; Liu et al., 2020; Castro et al., 2021). Cascade reservoirs can maximize the utilization of water resources such as water supply, seasonal flood regulation, electricity production, and navigation (Rosenberg et al., 2000; WCD, 2000).

The cascade dams ignore the long-term environmental impacts (McCartney et al., 2000). Dams cause considerable changes in surrounding basins by disrupting the continuous gradient of the rivers (Nogueira et al., 2018; Xiao et al., 2019). Several hypotheses have been proposed to depict and interpret the longitudinal variations in physical, chemical, and biological attributes of river ecosystems. Various studies have shown that the longitudinal distribution of functional feeding groups only partially follows the Reservoir Continuum Concept (RCC) framework (Tomanova et al., 2007; Jiang et al., 2011; Jelil et al., 2021). In contrast, the serial discontinuity concept (SDC) emphasizes that non-free-flowing rivers, such as regulated streams, often have discontinuous changes in riverine geomorphology, as well as biological populations and communities (Ward and Stanford, 1983). The longitudinal connectivity has been severely disrupted by transformation of the rivers into cascade reservoirs (Miranda et al., 2008; Wu et al., 2010). Research of these aquatic systems has emphasized the isolated reservoirs, with no specific study focused on the spatial distribution along a single river basin (Miranda et al., 2008). Nevertheless, studies in such cascades considering step-like continuous systems are rare despite their obvious hydrological and suspected functional interconnectivity downstream. A subsequent addition to lotic theory, the cascading reservoir continuum concept (CRCC) shows connectivity since it deals with data concerning biotic and abiotic among the serial reservoirs (Barbosa et al., 1999; Da Silva et al., 2005). The downstream reservoirs are affected by the features of the upstream reservoirs. CRCC has provided some theoretical postulates about the effects of upstream reservoirs on the downstream ones. However, CRCC was proposed in the study of large rivers, and those concerning small cascade reservoirs are still rare.

Previous studies have considered the impact of cascade reservoirs from the aspects of water quality and biological community changes, and those concerning functional groups were rare (Rodgher et al., 2005; Perbiche-Neves and Nogueira, 2010; Nogueira et al., 2018; Wu et al., 2021). For example, the study on phytoplankton in cascade reservoirs has been carried out in Brazilian Iguacu River and Lancang-Mekong River in China (Li et al., 2013; Nogueira et al., 2018). As important primary producers in ecosystems, phytoplankton is considered to be a natural bioindicator for its complex and rapid responses to fluctuations in environmental conditions, and is well suited to study the impact of the construction of cascade reservoirs (Lewitus, 2002; Darchambeau et al., 2014; Wentzky et al., 2020). The Reynolds functional approach is more effective in evaluating the phytoplankton responses to changes in environmental conditions and has been widely used in the temperate and subtropical areas of the world (Kruk et al., 2002; Reynolds et al., 2002). But this approach in small cascade reservoirs is still not well documented, especially considering that they are not more important due to the social and environmental benefits (Wang et al., 2020; Zaidel et al., 2021). Consequently, the effects of these cascade systems on phytoplankton functional groups still require attention (Moura et al., 2013).

This study of phytoplankton ecology in reservoirs along the Huangbo River Basin (HRB) in Central China has two main objectives. First, a single river system is selected to study the impact of cascade reservoirs on phytoplankton functional groups. Moreover, our results are helpful to clarify the changing trend of phytoplankton functional groups in cascade reservoir system and enrich the CRCC theory.

MATERIALS AND METHODS

Investigation Area

Huangbo River, with a length of 162 km, is one of the first-grade branches between Three Gorges Reservoir and Gezhou Reservoir at the north shore of the Xiling Gorge of Yangtze River, located in Yichang, Hubei Province, China (30°42′–31°29′ N, 110°08′–111°34′ E; **Figure 1**). The HR drains a basin of 1931.5 km^2 and flows from north to south, entering the Yangtze River 1.5 km upstream of the Gezhou Dam. The region occupied by the HRB has a subtropical monsoon climate with a hot rainy summer. The mean annual temperature is 16.9°C, with the highest mean temperature in July and lowest in January; the annual frost-free period is 223–273 days; mean annual precipitation and runoff are approximately 1,101 mm and 28.4 $m^3 \cdot s^{-1}$, respectively (Wei et al., 2021).

The HR is a low-lying river that runs from the north to the south. It is canyon-shaped with the highest altitude at 1,962 m, lowest at 61.5 m, and a relative height of 1,895.5 m. A series of reservoirs, such as XuanMiaoGuan (XMG), TianFuMiao (TFM), XiBeiKou (XBK), and ShangJiaHe (SJH), were constructed in the HR to meet the demand for water for agricultural irrigation in eastern Yichang from 1966 to 2005. The total installed capacity of cascade hydropower stations reaches about 6.6×10^4 kW, and the total annual power generation is 2.2×10^8 kWh. After the impoundment of the Gezhouba Reservoir (GZBR) was filled to an altitude of 66 m above sea level in June 2003, the lower 10.4 km stretch of this river became Huangbohe Bay (HBH, a representative bay of GZBR), with a flow velocity of 1.8–3.6×10^{-3} $m \cdot s^{-1}$ (Bao et al., 2021). Basic habitat characteristics of the cascade reservoirs (Bay) of HRB are shown in **Table 1**.

Field Sampling

Samples were collected every 3 months during the dry (October, January) and rainy (April, July) seasons from 2011 to 2012. Collections were taken at 18 sampling stations distributed along

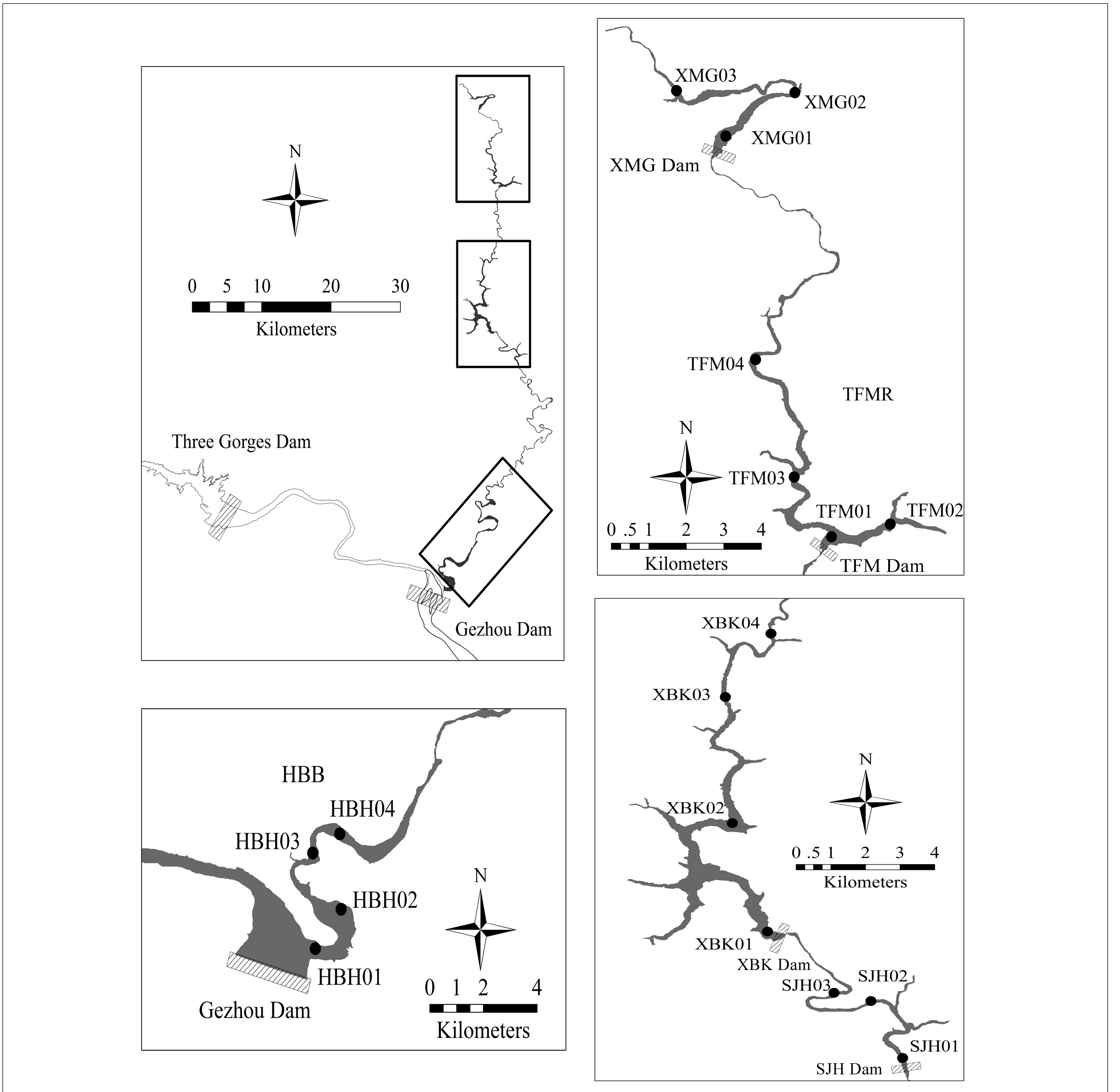

FIGURE 1 | The location of sampling sites in the cascade reservoirs of Huangbo River Basin.

different reservoirs of the main mid-lower course of the HRB. The selected stations are shown in **Figure 1**. Integrated water samples for analyses of water quality and phytoplankton community were collected at 0.5 m below the surface with a 5-L plexiglass water sampler. Excluding SJH in January due to bad weather and harsh road conditions, samples were collected at each site, resulting in a total of 69 samples. Water samples for nutrients were kept cool and shaded in acid-cleaned plastic containers, before being transported to laboratory. An Environmental Monitoring System probe (YSI 6600EDS, United States) was used to measure water temperature (WT) and dissolved oxygen (DO), pH, specific conductance (Cond), and turbidity (Turb) at 0.5 m below the water surface. Water depth was also measured by YSI 6600EDS. Water transparency was measured with Secchi Disk, and suspended solids were concentrated by filtering a known volume of water through a weighed pre-ignited glass fiber filter (Whatman type GF/C). An additional known volume of water was filtered through the GF/C for chlorophyll *a*

TABLE 1 | Basic habitat characteristics of the cascade reservoirs (Bay) of Huangbo River Basin.

	Damming year	Drainage area (km^2)	Normal water level (m)	Installed capacity ($10^7 m^3$)	Mean outflow (m^3/s)	Retention time (days)	Types
XMG	2005	380	495	3.9	5.6	50.7	Class B
TFM	1978	553.6	409	6.1	8.5	39.3	Class B
XBK	1991	862	322	16.1	12.3	115.5	Class B
SJH	1978	937	243.8	1.1	14.2	7.7	Class A
HBB	1981	1931.5	66.5	14.56	10.2	>20	Class B

Class A: residence time < 20 days was a fully mixed system with river characteristics.
Class B: 20 < residence time < 300 days can be grouped into intermediate system between rivers and natural lakes has both river-like and lake-like characteristics (Straškraba and Tundisi, 1999).

(chl. *a*) determination (Xu et al., 2009). All the filters were immediately placed in a dark cooler and stored at (−20°C) until the laboratory analysis.

Chemical Analyses and Phytoplankton Assemblages

In the laboratory, the following variables were measured. Different forms of nitrogen (TN, NO_3-N, NH_4-N), phosphorus (TP, PO_4-P), and silicon (SiO_2-Si) were measured using Skalar (San++, The Netherlands; Shen et al., 2014). Total organic carbon (TOC) and dissolved organic carbon (DOC) were measured using Shimadzu (TOC-VCPH, Japan). Suspended solids (TSS) and their two fractions, volatile (VSS) and non-volatile fractions (NVSS), were measured according to a Standard Operating Procedure for Total Suspended Solids Analysis (Xu et al., 2009). The Chl. *a* concentration was determined using a spectrophotometer (Shimadzu UV-1601, Japan) by measuring the absorbance of the extract at various wavelengths (750, 663, 645, and 630 nm; Cai, 2007).

Samples for phytoplankton analysis were preserved with 5% formalin and neutral Lugol's solution, then isolated through sedimentation for 48 h and concentrated to a final volume of 30 ml, and at least 100 random transects for over 300 cells of phytoplankton were counted in 0.1 ml under an Olympus CX21 microscope at 400 × magnification (Huang et al., 1999; Cai, 2007). Taxa identification was done according to Hu and Wei (2006) and John et al. (2002). Algal biomass was calculated using the approximation of cell morphology to regular geometric shapes, assuming that the fresh weight unit is expressed in mass, where 1 $mm^3 \cdot L^{-1}$ = 1 $mg \cdot L^{-1}$ (Huang et al., 1999; Wang et al., 2011). We combined species contributing > 5% to the total biomass into functional groups using the criteria of Padisák et al. (2009) and Shen et al. (2014).

Data Analysis

We calculated the euphotic zone depth (Zeu) as 2.7 times the Secchi depth (Cole, 1994). In the absence of stratification for small reservoirs, mixing depth (Zmix) was taken equal to the average depth of the reservoir (Naselli-Flores, 2000). The ratio between the euphotic and mixing depths (Zeu: Zmix) was used as a measure of light availability (Shatwell et al., 2012). Relative water column stability (RWCS) was calculated following Padisák et al. (2003): $RWCS = (D_b - D_s)/(D_4 - D_5)$, where D_b is the density of the bottom water, D_s is the water density at surface, a depth of 1 m was artificially considered "surface water." D_4 and D_5 are the densities of water at 4 and 5°C, respectively. Phytoplankton data were log(x + 1) transformed to reduce the effects of extreme values, and the relationship between functional groups and environmental factors was analyzed using the CANOCO 4.5 software (Lepš and Šmilauer, 2003; Shen et al., 2014). A forward selection of environmental factors was applied to avoid using collinear environmental factors in the same constrained ordination model. An initial detrended corresponded analysis suggested that redundancy analysis (RDA) should be used because the length of the first axis exceeded 3 SDs. The relationships between functional groups and environmental variables were also assessed by Pearson correlations with IBM SPSS Statistics 20.0 (IBM, Chicago, IL, United States).

RESULTS

Longitudinal Patterns of Physical and Chemical Properties

Reservoirs varied widely in most of the environmental variables. Significant differences in the nutrient parameters along the cascade reservoirs were observed during the sampling periods ($p < 0.01$; **Table 2**). TN (range from 0.94 to 2.71 $mg \cdot L^{-1}$) and SiO_2-Si (1.7 to 4.5 $mg \cdot L^{-1}$) showed a progressive increase in the last two reservoirs, especially HBH (**Figure 2A**), NO_3-N (0.79–2.05 $mg \cdot L^{-1}$), TOC (1.18–1.73 $mg \cdot L^{-1}$), and DOC (1.07–1.68 $mg \cdot L^{-1}$; except a little higher values in TFM) showed a slight increase from the upper part to the mid and lower sections of the cascade reservoirs, while TP and PO_4-P in the four upper reservoirs showed a slight decrease in this longitudinal pattern (**Table 1** and **Figure 2A**). As for the highest concentrations of nutrients, the mean concentrations of NH_4-N and TP were 45 and 123.9 $\mu g \cdot L^{-1}$, respectively. We found that changes in the water quality of the first three reservoirs are relatively stable, while HBH has decreased, which may be mainly affected by the backwater jacking of the main stream of the Yangtze River.

There was no significant variation among the four abiotic variables (WT, Cond, Zmix, and RWCS). Remarkable variations existed between the other physical variables (TSS, VSS, NVSS, pH, Turb, DO, Zeu and Zeu: Zmix) along the cascade system (**Table 2**). Surface WT increased slightly down the cascade (range from 17 to 20°C). DO decreased slowly from 7.4 to 5.3 ml. L^{-1} (**Figure 2B**). The mean specific conductance of the

TABLE 2 | The summary statistics of environmental variables and results of non-parametric test between the cascade reservoirs.

	XMG	TFM	XBK	SJH	HBB	p
TN ($mg{\cdot}L^{-1}$)	0.94 ± 0.12	1.31 ± 0.21	1.32 ± 0.32	1.85 ± 0.83	2.71 ± 0.64	< 0.01
NO_3-N ($mg{\cdot}L^{-1}$)	0.79 ± 0.1	1.11 ± 0.2	1.09 ± 0.19	1.61 ± 0.78	2.05 ± 0.42	< 0.01
NH_4-N ($mg{\cdot}L^{-1}$)	0.06 ± 0.06	0.07 ± 0.06	0.05 ± 0.03	0.06 ± 0.04	0.45 ± 0.55	< 0.01
TP ($\mu g{\cdot}L^{-1}$)	26.3 ± 11.1	24.3 ± 9.8	19.7 ± 6.8	19.1 ± 7.2	123.9 ± 51.6	< 0.01
PO_4-P ($\mu g{\cdot}L^{-1}$)	13.3 ± 7.9	11.2 ± 7.0	8.5 ± 5.5	9.1 ± 4.4	105.9 ± 45.2	< 0.01
SiO_2-Si ($mg{\cdot}L^{-1}$)	1.7 ± 0.5	1.9 ± 0.3	2.1 ± 0.4	3.3 ± 1.6	4.5 ± 2.3	< 0.01
TN: TP	41 ± 15	77 ± 35	61 ± 20	104 ± 37	23 ± 5	< 0.01
TOC ($mg{\cdot}L^{-1}$)	1.18 ± 0.25	1.45 ± 0.3	1.24 ± 0.11	1.62 ± 0.42	1.73 ± 0.29	< 0.01
DOC ($mg{\cdot}L^{-1}$)	1.07 ± 0.25	1.34 ± 0.22	1.20 ± 0.11	1.55 ± 0.42	1.68 ± 0.27	< 0.01
TSS ($mg{\cdot}L^{-1}$)	5.0 ± 2.3	5.4 ± 4.3	2.2 ± 1.2	4.3 ± 2.2	9.2 ± 7.3	< 0.01
VSS ($mg{\cdot}L^{-1}$)	2.7 ± 1.3	2.6 ± 1.5	1.5 ± 1.1	2.5 ± 1.0	2.5 ± 1.1	0.02
NVSS ($mg{\cdot}L^{-1}$)	2.4 ± 1.2	2.8 ± 3.0	0.8 ± 0.5	1.8 ± 1.4	6.7 ± 6.5	< 0.01
Water tempature (°C)	17.0 ± 6.5	18.1 ± 6.0	19.1 ± 6.1	19.8 ± 4.2	20.0 ± 6.8	0.78
Cond ($mS{\cdot}cm^{-1}$)	0.387 ± 0.03	0.402 ± 0.05	0.392 ± 0.02	0.410 ± 0.01	0.380 ± 0.06	0.18
pH	8.7 ± 0.8	8.8 ± 1.1	9.3 ± 1.1	8.0 ± 1.2	8.1 ± 1.0	< 0.01
Turb (NTU)	4.4 ± 3.8	4.5 ± 3.8	1.3 ± 1.6	2.9 ± 2.0	11.1 ± 11.1	< 0.01
DO ($ml{\cdot}L^{-1}$)	7.4 ± 1.6	7.0 ± 1.2	6.5 ± 0.7	6.4 ± 0.5	5.3 ± 1.4	< 0.01
Zeu (m)	5.1 ± 2.1	6.5 ± 3.3	10.2 ± 3.3	5.8 ± 3.1	3.4 ± 2.1	< 0.01
Zmix (m)	15.9 ± 16.5	13.2 ± 13.4	16.8 ± 16.6	5.1 ± 6.6	6.8 ± 1.6	0.15
Zeu: Zmix	1.1 ± 1.1	1.2 ± 0.9	1.5 ± 1.4	4.3 ± 4.3	0.53 ± 0.32	0.03
RWCS	138 ± 125	94 ± 92	114 ± 135	133 ± 100	72 ± 107	0.24
Chl *a* ($\mu g{\cdot}L^{-1}$)	12.4 ± 10.3	7.5 ± 6.6	4.0 ± 1.6	7.7 ± 4.3	6.3 ± 5.7	< 0.01
Density ($10^6 cells{\cdot}L^{-1}$)	7.4 ± 5.3	6.5 ± 9.2	1.1 ± 0.7	2.2 ± 1.4	1.3 ± 0.9	< 0.01
Biomass ($mg{\cdot}L^{-1}$)	4.5 ± 4.5	2.7 ± 2.7	0.7 ± 0.9	1.1 ± 0.5	0.6 ± 0.4	< 0.01

Results are the mean values and standard deviation (standard deviation for the entire data) for each reservoir during the period.
VSS, volatile suspended solids; NVSS, non-volatile suspended solids; Cond, specific conductance; Zeu, the euphotic zone depth; Zmix, mixing depth.

reservoirs was about 0.4 $mS{\cdot}cm^{-1}$. The highest RWCS was 409 in XBK in July, while the lowest (−2) in TFM in January. The mean suspended solids (TSS, VSS, and NVSS were 2.2, 1.5, and 0.8 $mg{\cdot}L^{-1}$, respectively) and Turb (1.3 NTU) were lower in the XBK. The highest value of Zeu (10.2 m) was recorded in the XBKR, for the longest retention time (115.5 days) in the cascade reservoirs (**Table 1**). Higher Zeu were always present in front of the dam in the four reservoirs (**Figure 2C**). The reservoirs (except HBH) showed stratification in April and July of 2012, with high light availability (Zeu: Zmix > 1), and the lowest value of Zmix was 1 m.

According to the results of principal component analysis (PCA; **Figure 3**), the first PCA axis explained 53.33% of the variance in the environmental variables, and the second axis explained 24.20% of the variance. The PCA results showed that all samples in each reservoir were separated independently into five groups by the phytoplankton density, DO, RWCS, pH, Zeu, WT, bottom WT, TN, SiO_2-Si, and TSS. Furthermore, distinct spatial pattern was detected in the PCA ordination diagram (**Figure 3B**).

Composition and Abundance of Phytoplankton

The 124 algal species identified in the cascading reservoirs are members of the following seven major taxonomic categories: Bacillariophyta (55), Chlorophyta (37), Cyanophyta (10 taxa), Cryptophyta (7), Pyrrophyta (10), Chrysophyta (3), and Euglenophyta (2). In the subtropical cascade reservoirs, 80 species were sorted into seven major taxonomic categories and belonged to 16 functional groups using the functional approach (>5% of the total biomass) described by Reynolds (1984) and Reynolds et al. (2002). The 43 descriptor species (>10% of the total biomass) were members of 13 functional groups (**Table 3**). The typical traits of these functional groups are exhibited in **Table 3**. Phytoplankton biomass was characteristically low and varied widely among reservoirs (**Figure 4**). Biomass ranged from 0.05 to 16.2 $mg{\cdot}L^{-1}$, with higher biomass in the upstream (XMG and TFM) and lower in the downstream (XBK, SJH, and HBH). Phytoplankton functional groups occurred in the cascade reservoirs, with one or more species contributing to their compositions (**Figure 4A**). Groups **D**, **E**, **Lo**, **X2,** and **Y** were classified as dominant phytoplankton functional groups (**Figure 4**).

The diatom of group **D** (*Synedra acus* and *S. hantzschii*) was the most important in quantity, sharing this importance with the dinoflagellates *P. bipes* and *Peridiniopsis* (*Peridiniopsis* sp., *Peridiniopsis kevei*, *Peridiniopsis penardiforme*, *Peridiniopsis cunningtonii*, *Peridiniopsis niei,* and *Ceratium hirundinella*) in group **Lo** of phytoplankton community in the XMG. Biomass was dominated by groups **Lo** (46.3%) and **D** (23.9%) upstream of the reservoir (XMG03). Group **D** also dominated in the TFM, XBK, and SJH with over 20% of the contribution. The dominant and co-dominant groups in the riverine zone of XBK

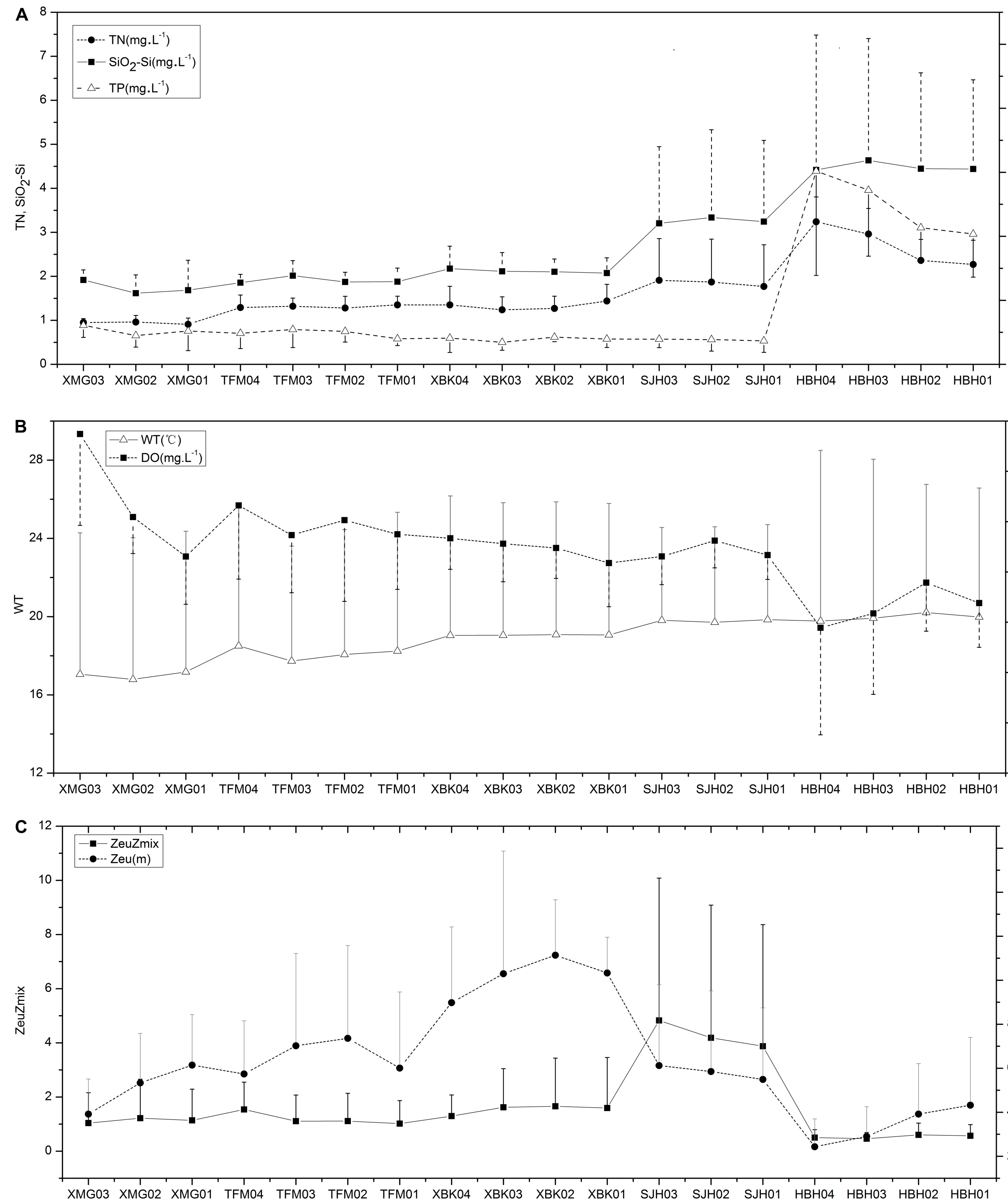

FIGURE 2 | Spatial variation of environmental variables in the cascade reservoirs **(A)** TN, SiO2-Si and TP; **(B)** WT and DO; **(C)** Zeu, Zmix and Zeu: Zmix.

were groups **D** (34.1%), **Lo** (16.9%), and **X2** (14.5%), formed by small *Chroomonas* (*Chroomonas acuta* and *Chroomonas caudate*) and Chlorophyta (*Pyramidomonas delicatula*, *Chlamydomonas reinhardtii*). The biomass of groups **X2** and **Lo** decreased while **D** increased downstream of the XBK reservoir; the dominance of **X2** and **Lo** groups was supplanted by the **D** group. In SJH, groups **Lo** and **D** dominated (28.4%, 20% of biomass) though the dominance of group **D** declined. Group **E** (*D. divergens*) and the crytophyceans in group **Y** (*Cryptomonas ovata*, *Cryptomonas erosa*, *Cryptomonas* sp.,

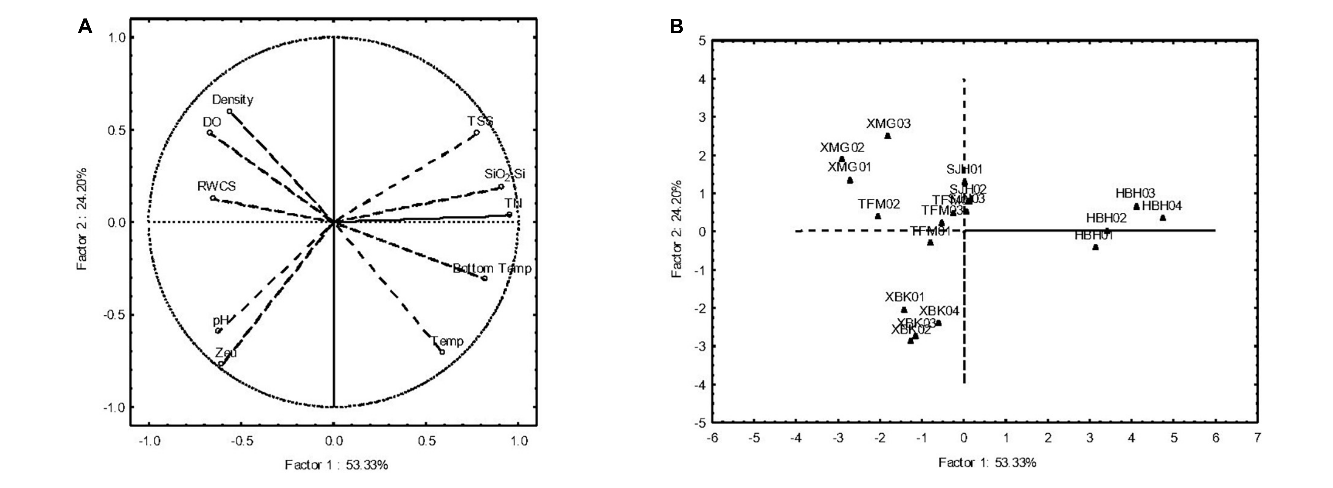

FIGURE 3 | Ordination diagram of PCA for environmental variables and phytoplankton community characteristics **(A)** and samples **(B)**.

TABLE 3 | Trait of phytoplankton functional groups detected in the cascade reservoirs quoted from Reynolds et al. (2002) and Padisák et al. (2009).

Functional group	Habitat template	Typical representatives	Tolerances	Sensitivities
B	Mesotrophic small- and mediumsized lakes with species sensitive to the onset of stratification	*Cyclotella* sp.; *Cyclotella ocellate; Cyclotella bodanica; Cyclotella stelligera; Cyclotella hubeiana; Stephanodiscus minutulus*	Light deficiency	pH rise, Si depletion
C	Mixed, eutrophic small-medium lakes	*Asterionella formosa*	Light, C deficiencies	Si exhaustion stratification
D	Shallow turbid waters including rivers.	*Synedra acus; Stephanodiscus hantzschii*	Flushing	Nutrient depletion
E	Usually small, shallow, base poor lakes or heterotrophic ponds	*Dinobryon divergens*	Low nutrients (resort to mixotrophy)	CO_2 deficiency
G	Nutrient-rich conditions in stagnating water columns; small eutrophic lakes and very stable phases in larger river-fed basins and storage reservoirs	*Pandorina morum*	High light	Nutrient deficiency
J	Shallow, mixed, highly enriched systems (including many low-gradient rivers)	*Tetraedron minimum; Scenedesmus bijugatus; Coelastrum microporum*	?	Settling into low light
Lo	Deep and shallow, oligo-eutrophic, medium to large lakes	*Peridinium bipes; Peridiniopsis penardiforme; Peridiniopsis* sp.; *Peridiniopsis cunningtonii; Peridiniopsis kevei; Peridiniopsis niei; Ceratium hirundinella; Peridiniopsis penardii var. robusta*	Segregated nutrients	Prolonged or deep mixing
MP	Frequently stirred up, inorganically turbid shallow lakes	*Oscillatoria* sp.; *Cocconeis placentula; Surirella* sp.	High turbidity, low light	Stratification nutrient depletion
P	Eutrophic epilimnia at higher trophic states	*Aulacoseira sulcate; Staurastrum gracil; Aulacoseira* sp.	Mild light and C deficiency	Stratification Si depletion
TB	Highly lotic environments (streams and rivulets)	*Aulacoseira varians; Cymbella pusilla; Cymbella ventricosa; Achnanthes linearis; Frustulia vulgaris*		
W1	Ponds, even temporary, rich in organic matter from husbandry or sewages	*Phacus* sp.	High BOD	Grazing
X2	Shallow, meso-eutrophic environments	*Chroomonas acuta; Chroomonas caudata; Pyramidomonas delicatula; Chlamydomonas reinhardtii*	Stratification	Mixing, filter feeding
Y	Wide range of habitats, which reflect the ability of its representative species to live in almost all lentic ecosystems when grazing pressure is low	*Cryptomonas ovata; Cryptomonas erosa; Rhodomonas lacustris; Cryptomonas coerulea; Cryptomonas* sp.	Low light	Phagotrophs

Cryptomonas coerulea, and *Rhodomonas lacustris*) were the high biomass contributors. In HBH, **Lo**, **X2** (*C. acuta*, *C. caudate*, *P. delicatula*, *C. reinhardtii*) and **Y** supplanted **D** group became dominant biomass contributors. Despite low biomass contributions, groups **MP** (*Oscillatori*a sp., *Cocconeis placentula,* and *Surirella* sp.) and **P** (*Aulacoseira sulcata*, *Aulacoseira*

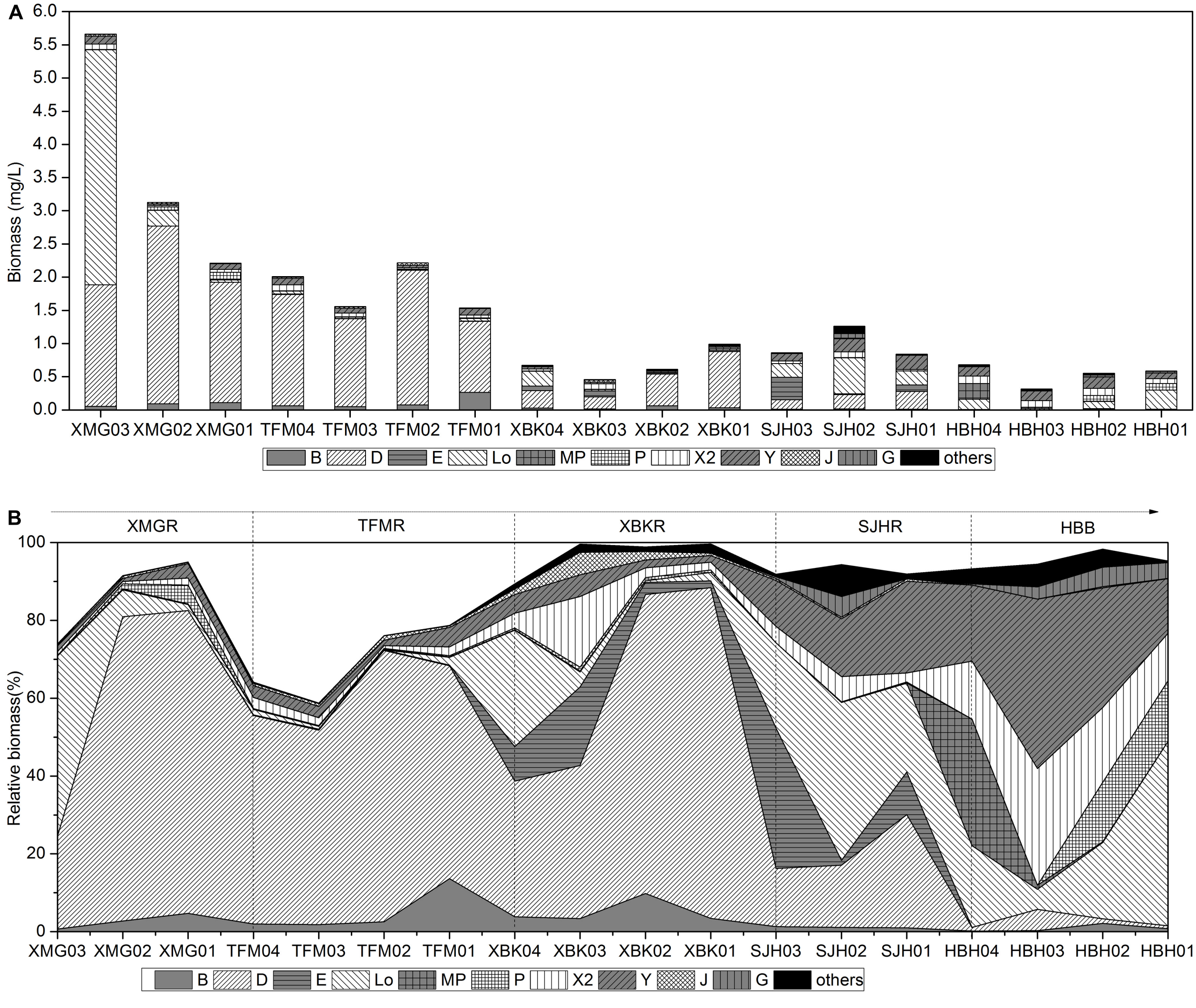

FIGURE 4 | Longitudinal variation of the biomass **(A)** and relative biomass (%) **(B)** of the main phytoplankton functional groups in the cascade reservoirs.

sp., and *Staurastrum gracile*) were also important as they were present in the upper reach (**MP**) and the river mouth region (**Figure 4A**).

Relationships Between Phytoplankton Functional Groups and Environmental Variables

Redundancy analysis was the appropriate method for linear ordination (gradient lengths of the first two axes are 2.73 and 2.88, respectively). The results of the RDA ordination for phytoplankton functional groups and environmental variables on axes 1 and 2 are shown in **Figure 5A**. The Monte Carlo test revealed that the first canonical axis and all canonical axes were significant (F = 52.32, p = 0.002; F = 9.94, p = 0.002; 499 random permutation).

The correlations for the first (0.84) and second (0.70) axes were high (**Table 4**), indicating a strong relationship between phytoplankton and selected environmental factors. All canonical axes cumulatively explained 99.43% of the total variation in RDA, and the first two redundancy axes jointly accounted for 97% of the species–environmental variables relation (axis 1: 78.0%; axis 2: 21.0%; **Table 4**). Nine significant variables of environmental data were screened by forward selection, DO (F = 28.98, p = 0.001), TN (F = 5.76, p = 0.005), TSS (F = 4.98, p = 0.007), NO_3-N (F = 5.44, p = 0.012), VSS (F = 4.82, p = 0.013), Cond (F = 4.48, p = 0.012), Zeu (F = 3.84, p = 0.022), SiO_2-Si (F = 3.54, p = 0.033), and RWCS (F = 3.37, p = 0.029). These variables accounted for 58.5% variance of species data for the first two axes (axis 1: 47.0%; axis 2: 11.5%). The first RDA axis was mainly positively correlated to DO (0.66) and negatively to TN (−0.50), NO_3-N (−0.50), and SiO_2-Si (−0.38). Axis 2 was positively correlated with VSS (0.26; **Figure 5A**).

The spatiotemporal dynamic changes of phytoplankton functional groups in cascade reservoirs of the Huangbo River were well presented in the RDA diagram (**Figure 5B**).

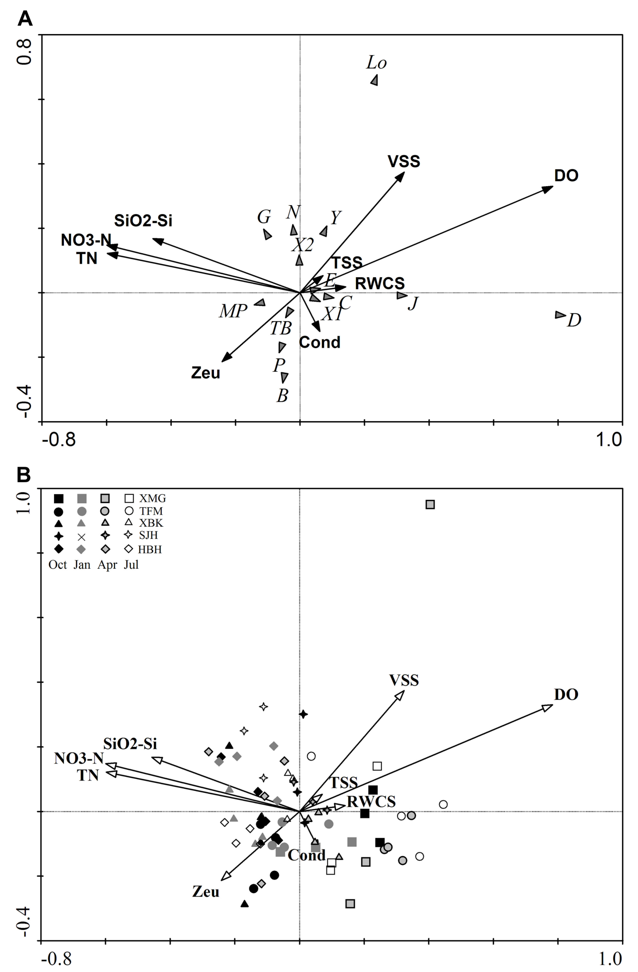

FIGURE 5 | Ordination diagram of RDA for environmental variables and phytoplankton functional groups **(A)** and samples **(B)**.

The first RDA axis illustrates differences between upstream and downstream regions. Upstream reservoirs showed high concentrations of DO while the downstream regions were characterized by high nitrogen nutrient levels (TN, NO_3-N, and SiO_2-Si). Pearson correlations found significant correlations ($p < 0.05$) between the biomass of main functional groups and most of the examined physicochemical factors (WT, DO, Zeu, nutrients, suspended solids, and hydrodynamic conditions; **Table 5**). The biomass of groups **X2** and **Y** was negatively correlated with Zeu and TN:TP ratio and positively correlated with WT, TOC, DOC, and VSS. Group **Y** was also positively correlated with TP, PO_4-P, and TSS and negatively correlated with pH and Zeu: Zmix. In contrast, the biomass of group **D** was positively correlated with DO and VSS and negatively correlated with nutrients (N, P, Si, and C). The significant environmental variables for group **Lo** were DO and VSS; for groups **MP** and **P,** significant environmental variables were WT, Turb, SiO_2-Si, TSS, and NVSS; for **E**, significant environmental variables were Zeu, Zeu: Zmix, and TN:TP ratios. Total phytoplankton biomass was significantly related to DO, Zeu, Zmix, TN, NO_3-N, SiO_2-Si, TSS, and VSS.

Significant differences in major environmental factors existed between different locations by RDA, which are not displayed in this study. In XMG, pH and DO were the principal environmental factors related to phytoplankton community and accounted for 73.4% variance of species data in the first two axes ($F = 12.4$, $p = 0.002$). In TFM, however, the central environmental factors changed into Zeu: Zmix, TN, RWCS, and Turb and explain 86% of the species data ($F = 17.3$, $p = 0.002$); SiO2-Si, NO_3-N, and Cond replaced the previous factors as the important factors in XBK with a probability are 59% ($F = 5.8$, $p = 0.008$). Phytoplankton growth is limited by Cond, pH, and Zeu: Zmix in SJH, where the phytoplankton could also be explained as 64% ($F = 4.5$, $p = 0.002$); No remarkable factor was selected in the RDA to explain phytoplankton distribution in HBH ($p > 0.05$).

DISCUSSION

Longitudinal Variations of Physicochemical Variables

It is reported that the capture of nutrients by reservoirs with low retention time along the basin would increase the nutrient level in the downstream of the cascade. In the Tietê River, Brazil, the uppermost reservoir in a series of nine impoundments captured most of the nutrients released from São Paulo, Brazil (Barbosa et al., 1999), and decreased linearly with descent down the cascade. In the Iguaçu River, Brazil, Da Silva et al. (2005) observed that nutrients decreased in a downstream direction while in Tennessee River, United States, nutrients increased (Miranda et al., 2008), but nutrient ratios changed, reflecting nutrient-specific gradients along the cascade reservoirs. The values of TP also showed a decreased gradient, while TN and SiO_2-Si increased along the longitudinal cascade reservoir system in the Huangbo River, China. The nutrient levels in the cascade reservoirs may be recorded as a result of specific watershed differences in morphometric features, retention time, hydrodynamic conditions, external loads, and retention by dams (Barbosa et al., 1999; Rodgher et al., 2005). Like nutrients, other water quality characteristics are affected by impoundments and exhibit gradients along cascade reservoirs. The values of DO displayed descending gradients in Tennessee River (Miranda et al., 2008) and Huangbo River; however, surface WT revealed an ascending gradient variation along the longitudinal cascading system in Tietê River (Barbosa et al., 1999), Iguaçu River (Da Silva et al., 2005), and Huangbo River.

The discontinuity also presented in the system, and there was a sharp decline in PO_4-P, TOC, DOC, and suspended solids in XBK, with the same trends for chl. *a*, density, and biomass of phytoplankton. In addition, the light condition and RWCS were also interrupted by dams. In general, the proposed concept of CRCC was partly verified in the reservoirs in Huangbo River unlike the established gradients in Tietê River, Tennessee River, and Iguaçu River (Barbosa et al., 1999; Da Silva et al., 2005; Miranda et al., 2008). In contrast, more attention from limnologists was paid to longitudinal patterns within reservoirs

TABLE 4 | Redundancy analysis results for phytoplankton functional groups and environmental variables.

	Eigen values	Species-environment correlations	Cumulative percentage variance		Sum of all canonical eigenvalues
			Species data	Species-environment relation	
Axis 1	0.470	0.838	47.0	78.0	
Axis 2	0.115	0.699	58.5	97.0	
Axis 3	0.009	0.598	59.4	98.6	
Axis 4	0.005	0.626	59.9	99.4	
					0.602

TABLE 5 | Significant Pearson correlations between the biomass of the 10 main phytoplankton functional groups and the biomass of total phytoplankton, and 20 environmental variables (n = 69).

	WT	Cond	pH	DO	Turb	Zeu	Zmix	Zeu: Zmix	TN	NO_3-N	TP	PO_4-P	TN: TP	SiO_2-Si	TOC	DOC	TSS	VSS	NVSS	RWCS
B			−0.24*				0.43**													
D				0.56**					−0.45**	−0.46**	−0.26*	−0.26*		−0.35**		−0.28*		0.21*		
E						0.22*		0.62**					0.43**							
J	0.41**	−0.29**		0.29**					−0.29**	−0.28**		0.03*						0.25*		0.47**
G			−0.34**															021*		
Lo				0.45**														0.32**		
MP	0.21*	−0.27*		−0.3**	0.43**				0.20*	0.23*				0.46**			0.41**		0.46**	
P	0.29**	−0.41**			0.43**	−0.24*								0.33**			0.37**		0.39**	0.40**
X2	0.21*					−0.24*							−0.31**		0.25*	0.22*		0.21*		
Y	0.24*		−0.46**			−0.39**		−0.21*			0.22*	0.22*	−0.36**		0.35**	0.32**	0.21*	0.14**		
Chl. *a*	0.41**	−0.40**		0.27*		−0.42**	−0.22*						−0.25*		0.31**	0.25*	0.33**	0.46**	0.25*	0.27*
Density	0.32**	−0.35**		0.52**		−0.40**			−0.29**	−0.29**			−0.26*		0.21*		0.36**	0.54**	0.27*	0.34**
Biomass				0.74**		−0.34**	−0.22*		−0.38**	−0.39**				−0.23*			0.24*	0.53**		

$p < 0.05$; $^{**}p < 0.01$.

than among reservoirs, leading to informational deficiencies in the literature (Miranda et al., 2008). As a consequence, we could not predict which limnological characteristic parameter will show continuous longitudinal gradients along the cascade reservoirs. Longitudinal gradients may reset and restart multiple times as the river travels through a different basin (Barbosa et al., 1999; Miranda et al., 2008). Thus, the exact patterns in Huangbo River may not apply directly to other cascade systems.

The Impact of Physiochemical Conditions on Phytoplankton

In the cascade reservoirs, physicochemical conditions were successfully described by the predominant coexistent phytoplankton species. We found that groups **D**, **E**, **Lo**, **X2,** and **Y** occurred in the cascade reservoir system, however, with relatively different contributions. **D** group was more important in the former three reservoirs, while **E**, **Lo,** and **Y** groups became more representative in XBK, SJH, and HBH. The relative biomass of **D** group decreased in SJH and HBH, while the **Lo**, **X2,** and **Y** groups increased along the longitudinal cascade reservoirs from upstream to downstream. In view of the above description, we concluded that the longitudinal distribution characteristics of phytoplankton in the cascade reservoirs of the Huangbo River could be summarized as groups **D** and **Lo** in XMG, only **D** in TFM, and **D**, **Lo**, **E** groups in XBK, while in SJH, the dominant groups were **Lo**, **D**, **E,** and **Y**, based on biomass changes of functional groups. Due to the influence of jacking from the mainstream of GZB, the phytoplankton in HBH has changed greatly compared with the four reservoirs and **Y**, **Lo,** and **X2** groups dominant in HBH, which was consistent with the study of Xiangxi bay (Wang et al., 2011).

D group was represented by lanceolate, pinnate diatoms (*Synedra*), and centric diatom (*S. hantzschii*), which were also the main contributors of the group on this occasion. **D** group was more important in the upper three reservoirs and exhibited a higher biomass over the reservoirs, commonly found in shallow, turbid waters, with species sensitive to nutrient consumption (Reynolds et al., 2002; Shen et al., 2014). Although the group typically occurs in spring (Yin et al., 2011), it was observed in the other seasons in our study. In fact, diatoms can become dominant in the flooding and mixed waters because dissolved silicate is replenished from deeper water (Stević et al., 2013; Yi et al., 2020). As a C-strategist, this small-celled and fast-growing species is tolerant of mixing and low light (Reynolds, 2006). In this study, group **D** was well adapted to high VSS though strongly negatively correlated with nutrients (C, N, P, and Si) and light conditions. As reported in the lower Salado River (Argentina), group **D** was also directly correlated with Cond in the region (Devercelli and Farrell, 2013).

Group **E**, with the representative species of *D. divergens*, can tolerate low nutrients (resort to mixotrophy) but is sensitive to CO_2 deficiency (Reynolds et al., 2002). This group is wildly distributed in the northern hemisphere and reported in moderately to very nutrient-rich ponds and lakes (John et al., 2002; Hu and Wei, 2006). However, the correlation analysis showed its significant relation with light availability and TN:TP ratio. Many different species of *Dinobryon* are distributed widely in different nutritional water, and most of them were recorded once and predominantly occurred in clear-water lakes and ponds with low nutrient contents, low temperature, and high transparency (Feng, 2008).

Groups **Lo** and **Y** became more representative in SJH and HBH. The **Lo** group mainly comprises dinoflagellates species in the reservoirs. The representative species of group **Lo** were *P. niei*, *P. bipes*, *C. hirundinella,* and *Peridiniopsis penardii* var. *robusta*. This group was usually observed in mesotrophic lakes, tolerated segregated nutrients, and sensitive to prolonged or deep mixing as emphasized by Reynolds et al. (2002). According to former research, most of the dinoflagellates were capable of using their slower swimming velocities to perform diel vertical migration where nutrient-depleted conditions occurred in aquatic ecosystems (Xu et al., 2010a; Shen et al., 2014). High temperature resulted in group **Lo** in a Mediterranean reservoir (Becker et al., 2010) and Lake Sakadaš along the Danube (Stević et al., 2013). In this study, group **Lo** had no significant correlation to WT and nutrients. Concerning *P. niei*, high abundances have been found in Danjiangkou Reservoir and Three Gorges Reservoir, leading to bloom in some periods (Xu et al., 2010b; Shen et al., 2014). This species can be a dominant species in winter and spring for a short time, and is widely distributed in waters whose trophic status varies from oligotrophic to eutrophic (Amorim and Moura, 2022).

The **Y** group was characterized by *C. ovata* and *C. erosa*, occurred in the system, and dominated in the downstream throughout the year. These two species have similar ecological requirements, which is well adapted to live in small, low light, and enriched lakes (Reynolds et al., 2002). The relatively high surface to volume ratio of cryptomonads facilitates their rapid absorption of nutrients and fast growth (Bovo-Scomparin and Train, 2008). The group Y was dominated by wide suitable habitat during the mixing period, where there was low grazing pressure and a quiet water body (Becker et al., 2010). In this study, group **Y** was characterized by low Zeu and TN:TP ratio, high concentration of TP, PO_4-P, TOC, and DOC. Thus, in HBH, lowest eutrophic depth and TN:TP ratio and the highest nutrients contribute to the high biomass. The results obtained from RDA analysis also showed a virtual correspondence to Rychtecký and Znachor, 2011 in the Římov Reservoir, Czech Republic, and a young canyon reservoir in Southwest China (Liao et al., 2020).

The habitat template for group **X2** is shallow, meso-eutrophic environment with species-tolerant stratification but sensitive to mixing regime and filter feeding (Padisák et al., 2009). The representative species of the group are *C. acuta* and *C. caudata*, existing in all waters along the Huangbo River. This group presented a high biomass only in the downstream area, but never became dominant in the cascade reservoirs except in HBH. These small unicellular flagellates are generally considered as "C" strategists with high surface/volume ratio (Bovo-Scomparin and Train, 2008), high intrinsic growth rates, and high metabolic activity and low light requirement in common (Grime, 1977; Reynolds, 1988). However, they differ in sedimentation velocity and silica requirement (Mieleitner and Reichert, 2008). **X2** group was positively correlated with VSS, nutrients (TN, NO_3-N, and SiO_2-Si), and negatively correlated with Zeu and Cond, which was not consistent with observations in the Middle Paraná River (Devercelli, 2006; Devercelli and Farrell, 2013). The present habitat for **X2** is well consistent with what RDA indicated and also with shallow eutrophic lakes of Huaihe River, China (Yi et al., 2020).

It is widely recognized that spatial heterogeneity plays a functional role in aquatic ecosystems (Dutilleul and Legendre, 1993; Becker et al., 2010), and phytoplankton communities are regulated mainly by hydrology, WT, the availability of light, nutrients, and mixing conditions (Costa et al., 2009; Rigosi and Rueda, 2012; Shen et al., 2014). In some reservoirs, although both internal and external variables determine the structure of the phytoplankton community, physical variables and hydrodynamics generally predominate (Rangel et al., 2012; Xu et al., 2021). Phytoplankton community structure was driven by light and nutrient, which have illuminated by Reynolds (2006). The results also highlighted the hydrodynamic conditions, light availability, mixing regime and nutrients as the main factors related to the phytoplankton functional groups in the cascade reservoirs. In terms of importance, nutrients seemed to play a more important role in the four reservoirs in this study. The results verified by the correlations between the biomass and environmental factors. The importance of environmental factors showed spatial differences in terms of influence. The major environmental factors shape phytoplankton in different waters for the main functional groups. Heterogeneity in the distribution of phytoplankton was clearly demonstrated as in Mangueira Lake (Crossetti et al., 2013). Reservoirs were traditionally considered as an independent system, separated from the surrounding watersheds and other parts of the river basin (Miranda et al., 2008). Despite the shortcomings of the paradigm, our research was restricted to five reservoirs in phytoplankton assemblages and physicochemical variables, and obvious longitudinal gradients were identified in the cascade reservoir system of the Huangbo River. In this study, the effects of the cascading dams on phytoplankton assemblages were obvious and more complex than those in a single reservoir (Amorim and Moura, 2022). The operations of cascade reservoirs can cause eutrophication of downstream reservoirs, longitudinal connectivity loss in RCC, and cascading and accumulation effects on phytoplankton communities.

CONCLUSION

Instead of seeing each part of the reservoir as independent, we regarded them as an interdependent system. For the spatial pattern, the biomass of functional groups was interfered by the strong influence of the dams, especially the series of dams in the study region. The number of dominant functional groups increased along the longitudinal gradient, indicating that the function of the phytoplankton community was more stable. Functional group **D** was the dominant phytoplankton functional group among the four reservoirs, and **Lo** group was dominant except SJH. Among the main environmental variables, the depth of euphotic layer, nutrients were the limiting factors of algae growth, and the effects of nutrients were apparently more important. Furthermore, the study confirmed that CRCC existed in the cascade reservoirs of Huangbo River, which were not completely consistent with it in large rivers. The phytoplankton functional groups in the HBH have been completely changed due to the backwater jacking of the main stream of the Yangtze River.

DATA AVAILABILITY STATEMENT

The original contributions presented in this study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

HS and QC conceived the ideas and designed the study. HS and LT sampled the phytoplankton. HS, LY, LT, and QC analyzed the data and led wrote the manuscript. All authors contributed, and approved it for publication.

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