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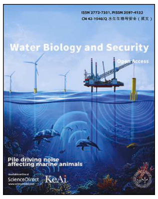

Research Article

Nitrate, water temperature, conductivity, and transparency drive littoral phytoplankton species composition and biovolume in two reservoirs in the Xingu river

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ABSTRACT

Ecological interactions in the littoral zone maintain water quality, biodiversity, and ecological services in freshwater ecosystems. Phytoplankton occupy a central position in the ecosystem due to their sensitivity to environmental changes and ecological importance for ecosystem functioning. Here, we aimed to evaluate dissimilarity in physicochemical characteristics and phytoplankton composition of the littoral zone in two reservoirs of the Belo Monte Hydroelectric Complex. We also investigated the physicochemical factors determining spatial variation in the composition, richness, and biovolume of littoral phytoplankton in the environments studied. The physical and chemical characteristics of the water displayed distinct patterns in the Xingu and Intermediate reservoirs, which drove phytoplankton biovolume and species composition. However, the richness of phytoplankton species was similar in the two reservoirs. More specifically, phytoplankton biovolume and species composition were influenced by nitrate, temperature, conductivity, and transparency. Our study increases understanding of the environmental factors determining spatial variation of littoral phytoplankton communities in reservoirs. This data improves understanding of littoral zones in reservoirs and highlights the importance of littoral phytoplankton in maintaining water quality and ecosystem services in these waterbodies.

1. Introduction

Freshwater ecosystems, including streams, rivers, and lakes, are complex systems where interactions between biotic and abiotic components determine their functioning and maintain their natural conditions (Jones and Reynolds, 1985; Sohani, 2016; Wang et al., 2021a; Xu et al., 2023). However, several anthropic activities have transformed these natural freshwater systems into artificial ones, such as reservoirs. When a reservoir is created, the river is dammed, which modifies several physical and chemical characteristics such as the hydrology, water quality, and overall habitat for species (Forsberg et al., 2017; Wojciechowski et al., 2017; Bertassoli et al., 2021; Wang et al., 2021a; Araújo et al., 2024). These alterations ultimately affect the biodiversity and dynamics of biological communities, thus affecting the ecosystem services offered by these systems (Bertassoli et al., 2021; Wang et al., 2021a; Berdugo et al., 2021).

Another change observed in the creation of reservoirs is related to the littoral and pelagic zones because their differences become more evident when the river is transformed into an artificial lake (Tundisi and Matsumura-Tundisi, 2011). In lakes, the pelagic zone refers to the open area, away from the shore, extending from the surface to the depth where sunlight can no longer penetrate, and is less influenced by the banks and with greater influence from the bottom of the lake's (Gregory et al., 1991; Wetzel, 2001). In contrast, the littoral zone of aquatic

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systems encompasses the area from the shore to the depth where light penetrates sufficiently to allow photosynthesis in the substrate (Gregory et al., 1991; Wetzel, 2001; Silveira et al., 2024). The littoral zone exhibits a strong interaction between water and land and is more complex and dynamic than the pelagic zone (Gregory et al., 1991; Naiman and Décamps, 1997; Wetzel, 2001; Reynolds, 2003; Silveira et al., 2024).The biological interactions in the littoral zone maintain water quality, biodiversity, and ecological services in freshwater systems (Gregory et al., 1991; Naiman and Décamps, 1997; Wetzel, 2001; Kalff, 2002; Silveira et al., 2024). Changes in these natural environmental characteristics, such as nutrients and water flow due to reservoir creation, act as filters, allowing only certain species or groups of organisms to establish themselves in those habitats (Hutchinson, 1957). Thus, understanding the responses of organisms to environmental changes such as reservoir creation increases knowledge about ecological interactions and disruptions in ecosystem services (Case and Gilpin, 1974; Abonyi et al., 2021; Shi et al., 2023).

The littoral zone of stagnant water bodies is functionally important due to its high temporal and spatial variability and its contribution to the recruitment of aquatic species and the maintenance of aquatic biodiversity (Lemly and Dimmick, 1982; Schiemer et al., 1995; Silveira et al., 2024). The littoral areas of freshwater systems are considered ecotones (Schiemer et al., 1995), providing habitat, food, and breeding sites for various communities of aquatic organisms (Lemly and Dimmick, 1982; Schiemer et al., 1995; Naiman and Décamps, 1997; Silveira et al., 2024). Additionally, the littoral zone of water bodies is underrepresented in limnological research, with the main focus of ecological studies being on pelagic areas (Silveira et al., 2024).

In a broader ecological context, two fundamental processes structure communities in different ecosystems; one is related to environmental filters acting at different time and spatial scales (Soininen and Heino, 2007; Leibold et al., 2004, 2022; Borics et al., 2021), while the other is related to the dispersal capacity of species that also plays a significant role in shaping communities at spatial and temporal scales (Leibold et al., 2004; Heino et al., 2015). In this context, phytoplankton, an important primary producer in freshwater, is widely studied for its role in describing diversity and community patterns that are shaped by complex interactions between environmental factors and trophic interactions (Jones and Reynolds, 1985; Abonyi et al., 2021). These organisms efficiently respond to environmental changes, such as eutrophication and climate change, and support biomonitoring strategies and water quality management (Faquim et al., 2021; Shi et al., 2023).

Different studies highlight the central role of physicochemical factors as regulators of the structure and composition of phytoplankton communities (Jones and Reynolds, 1985; Reynolds, 1998, 2006; Kruk et al., 2002; Mutshinda et al., 2016; Borics et al., 2021; Faquim et al., 2021; Zhang et al., 2023). These factors, such as nutrients (nitrogen and phosphorus), temperature, pH, dissolved oxygen, and parameters related to underwater light availability such as turbidity, transparency, euphotic zone depth, and total dissolved solids (TDS), are mainly responsible for the diversity, biomass, and dynamics of the phytoplankton community in aquatic environments (Reynolds, 1998, 2006; Devercelli et al., 2016; Shi et al., 2023; Mohanty et al., 2023).

Knowledge of the interactions between phytoplankton and physical-chemical parameters in the coastal zones of reservoirs has advanced. For example, in the Rybinsk Reservoir, the dynamics of the phytoplankton community were linked to the effects of thermal and water level regimes over a temporal gradient across different reservoir zones (Sakharova and Korneva, 2018). In another study conducted in a reservoir in the Philippines, the composition of phytoplankton and zooplankton communities in the littoral zone was linked to water quality (Alpecho et al., 2024). Similarly, in Lake Constance, located in the northern Alps, the exchange between littoral and pelagic phytoplankton communities was examined across several stations over two years (Schweizer, 1997).

However, several gaps remain, particularly regarding the processes and mechanisms linked to phytoplankton in the littoral zones of reservoirs. To conserve these environments and maintain ecosystem functionality, it is crucial to anticipate future changes by investigating local environmental filters and assembly processes that determine community composition (Reynolds, 2003). Community assembly processes can be understood as a set of filters operating at different spatial and temporal scales that collectively define the structure and composition of communities (Reynolds, 2003). Our study explores the phytoplankton community assembly processes that shape the distribution and composition of littoral phytoplankton species across spatial scales and investigates the influence of local environmental filters and spatially structured processes as key drivers of community assembly in littoral areas.

Continuous research is essential to deepen knowledge on this topic, improve water quality management, preserve biodiversity, and ensure the sustainability of aquatic ecosystems in the face of ongoing environmental changes on the planet (Thomaz et al., 2020; Wang et al., 2021a). The importance of these studies lies not only in their scientific value but also in their practical applications in the conservation and management of water resources (Latrubesse et al., 2017; Guo et al., 2017; Thomaz et al., 2020). This is because the phytoplankton community plays an essential role in ecosystem services such as nutrient cycling and biomass and oxygen production, among others.

Thus, this study aimed to answer the following questions: Is there a dissimilarity in the physical-chemical characteristics and phytoplankton composition of the littoral zone between two reservoirs? Second, how does the spatial variation of physical-chemical parameters affect the composition, richness, and biovolume of the littoral phytoplankton community in two Amazonian reservoirs? We will address these questions by studying two reservoirs that comprise the Belo Monte Hydroelectric Complex on the Xingu River and evaluating phytoplankton species composition, biovolume, water nutrients, pH, total suspended solids, temperature, conductivity, light availability, dissolved oxygen, and depth.

We expect that: (i) the physical-chemical factors of water and the structure of the littoral phytoplankton community will differ between the two reservoirs because these reservoirs differ in water flow and water residence time, leading to different habitat characteristics and suitability for different species; (ii) the composition and biovolume of the phytoplankton community in both reservoirs will be influenced by pH, nutrient concentration, temperature, turbidity, dissolved oxygen concentration, and electrical conductivity, with different ranges of these variables expected across reservoirs, favoring certain species over others; finally, (iii) environmental filtering (water physicochemical characteristics) at each site will be the main driver structuring the littoral phytoplankton community.

2. Material and methods

2.1. Study area

This study was conducted during the dry season, the Amazonian summer, at 22 points distributed along the two reservoirs of the Belo Monte Hydroelectric Complex (3°7′40″S, 51°46′33″W) in September 2022. Thirteen sites were in the Xingu Reservoir (RX) and nine in the Intermediate Reservoir (RI). The sampling sites were distributed along the littoral zone of both reservoirs. The littoral zone consists of an area near the shore of the water body where light penetrates to the bottom, allowing photosynthesis in the substrate (Gregory et al., 1991; Wetzel, 2001; Kalff, 2002).

The Belo Monte Hydroelectric Complex is located in the Volta Grande do Rio Xingu (Bertassoli et al., 2021; Araújo et al., 2024) (Fig. 1). The Xingu River is one of the main clearwater tributaries on the right bank of the Amazon River, with a drainage area of approximately 500,000 km^2 (Sioli, 1984; Bertassoli et al., 2021; Araújo et al., 2024). The

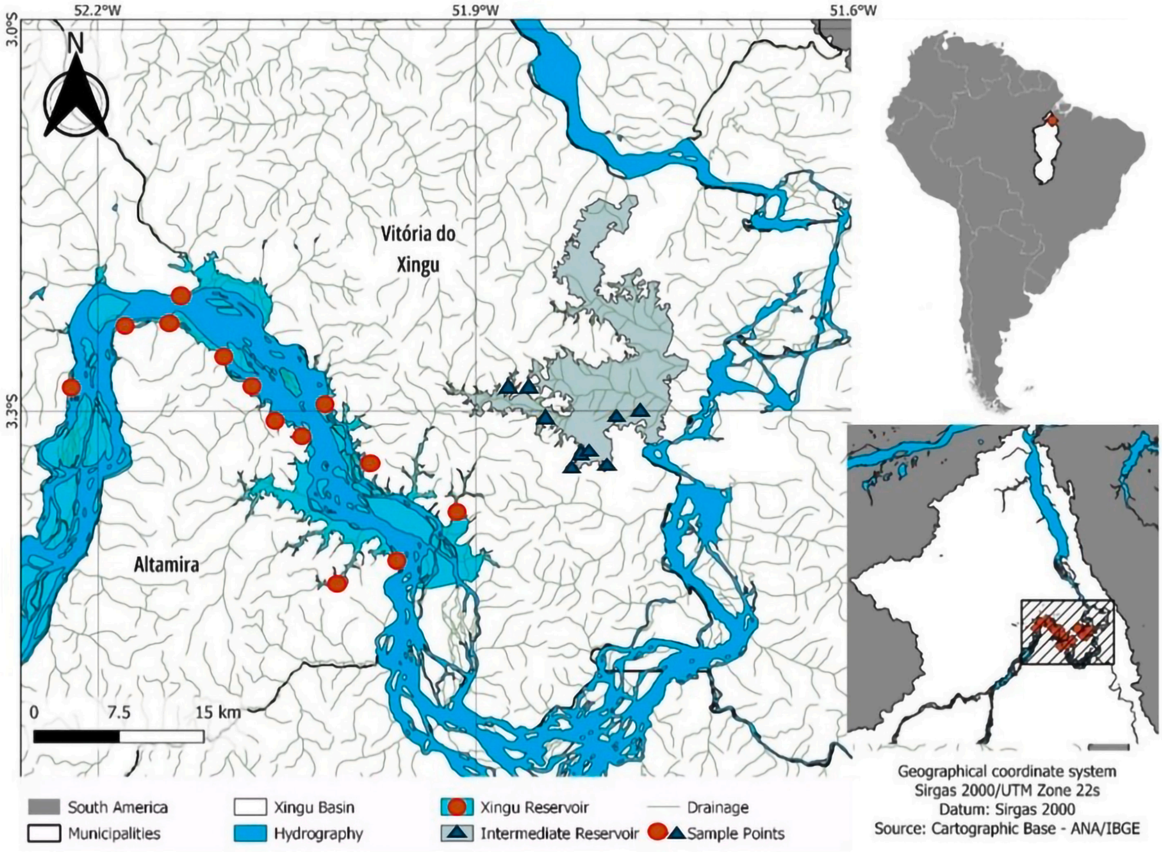

Fig. 1. Location of the reservoirs associated with the Belo Monte Hydroelectric Complex on the Xingu River. Sampling sites are shown with circles and triangles.

Belo Monte Hydroelectric Complex represents a run-of-river dam model (Bertassoli et al., 2021; Utsunomiya et al., 2024; Araújo et al., 2024) and includes the Pimental Site, where the main dam is located, forming the RX in the original riverbed with an area of 382 km^2 (Bertassoli et al., 2021; Araújo et al., 2024); and the Belo Monte Site, which forms the RI, with a lake covering approximately 134 km^2 of flooded area. This area is where most of the turbines and power generation structures are located. The complex was constructed in a valley of forest and upland areas and is supplied by water diverted from the main channel of the Xingu River via a diversion channel (Bertassoli et al., 2021; Utsunomiya et al., 2024; Araújo et al., 2024).

2.2. *Sampling of physical and chemical characteristics*

The physical and chemical variables of the water were measured at each point distributed in the littoral zone of the RI and RX reservoirs of the Belo Monte Hydroelectric Complex on the Xingu River. In situ measurements were performed using a multiparameter digital probe (U-50 - HORIBA) and included the following parameters: electrical conductivity (COND μS/cm), water temperature (WT °C), dissolved oxygen (DO mg/L), pH, turbidity (TURB NTU), total suspended solids (TSS), and oxidation-reduction potential (ORP). Water transparency (TRAN-cm) and depth (PROF-cm) were measured with a Secchi disk. Water samples were also collected directly from the river using high-density polyethylene bottles to determine the concentrations of phosphate (PO_4 mg/L), nitrate (NO_3 mg/L), and nitrite (NO_2 mg/L). Samples were stored in a cooler with ice and later preserved in the laboratory with 6 mg of thymol (Prado et al., 2004). Water sample analyses were performed at the Laboratory of Sustainable Systems Analysis (LASS) of EMBRAPA Amazônia Oriental using ion exchange liquid chromatography (Madden et al., 2002; Haddad, 2004) with a Proeminence Shimadzu instrument.

2.3. *Phytoplankton sampling and identification*

Phytoplankton samples were also collected in the littoral zone of the RI and RX reservoirs of the Belo Monte Hydroelectric Complex on the Xingu River. We used two sampling methods, one qualitative and another quantitative. Qualitative sampling was performed with a plankton net of 20 μm mesh to collect organisms in a concentrated form and then fixed with 4 % formalin (Bicudo and Bicudo, 2004). These samples supported the taxonomic identification and morphometric analysis of the cells of phytoplankton organisms, which was performed using an Olympus® BX 41 binocular microscope equipped with an image capture system and a NOVA® X-CAM BK17070847 camera. Quantitative sampling consisted of collecting water samples directly from the subsurface of the water column using a 300 mL collection bottle and then fixing samples with 4 % acetic Lugol's solution (Bicudo and Bicudo, 2004). This sampling is used to quantify cells and individuals of the phytoplankton community.

The preparation for quantifying phytoplankton samples followed the Utermöhl sedimentation method (Utermöhl, 1958), and the sedimentation time was 1 h per milliliter of sedimented content (Lund et al., 1958). Phytoplankton (cells) were quantified using an Olympus® Tokyo inverted microscope, utilizing the Utermöhl counting chamber with fields distributed randomly (Uhelinger, 1964). The counting limit was based on quantifying at least 100 individuals of the most abundant species with a significance level of $p < 0.05$ (Lund et al., 1958). Biovolume was calculated by multiplying the cellular density per ml by the average cellular volume, considering the average size of 20–30 individual samples of each recorded taxon (Hillebrand et al., 1999), and was expressed in mm^3/L. After determining the specific biovolume of the biotic matrix (species), we retained the taxa that contributed at least 5 % of the total biovolume per sample unit (Kruk et al., 2002) for statistical analyses.

Cyanobacteria and microalgal taxa were identified based on specialized literature. The nomenclature was reviewed following guidelines of the *Algaebase* database (Guiry and Guiry, 2024) and considering the principles of the International Code of Nomenclature for Algae, Fungi, and Plants (Turland et al., 2018).

2.4. Statistical analysis

Before statistical analyses, the values of physicochemical variables, except for pH, were standardized due to different units of measurement (mean equal to 0 with standard deviation equal to 1) (Hastie et al., 2009). To assess the dissimilarity of physicochemical characteristics between reservoirs (RX and RI), we used permutational multivariate analysis of variance (PERMANOVA) with 999 permutations and significance values calculated by the Monte Carlo test ($p < 0.05$). Using the environmental data matrix, we compared the physical-chemical characteristics between the reservoirs using multivariate dispersion homogeneity tests (PERMDISP) (Anderson and Walsh, 2013), using the euclidean distance (Legendre and Legendre, 1998; Anderson, 2001, 2017) and the "adonis" function from the "vegan" package (Oksanen et al., 2024). Each reservoir (RX and RI) constituted the categorical variable.

To compare differences in species richness (S) and the total biovolume of each taxon between reservoirs, independent *t*-tests were conducted. Assumptions of the test were verified, and when necessary, the variables were log $(x + 1)$ transformed. When the assumptions of the parametric test were not met, we used the non-parametric Mann-Whitney *U* test (Hart, 2001). Regarding the dataset containing the biovolume of descriptive phytoplankton species ($\geq$5 % of the total algae biovolume per sample), before statistical analysis, the data were transformed using a log-chord transformation. This technique combines logarithmic transformation, which makes the taxon distributions more symmetrical and reduces the importance of very abundant taxa, with chord transformation, which produces an asymmetrical double-zero coefficient (Legendre and Borcard, 2018).

Subsequently, to visualize the species composition of the littoral phytoplankton community at different sampling points in the two reservoirs (RX and RI), Principal Coordinates Analysis (PCoA) was used with a Euclidean distance matrix (Legendre and Legendre, 1998; Anderson, 2001) consisting of biovolume data obtained from morphometric measurements of taxa. Following this, the structure of the phytoplankton community between the two reservoirs (RX and RI) was evaluated using Permutational Multivariate Analysis of Variance (PERMANOVA), using the Euclidean distance matrix (Legendre and Legendre, 1998; Anderson, 2017) with the "adonis" function from the "vegan" package (Oksanen et al., 2024).

To analyze the relationship between phytoplankton species and physicochemical data, we performed a Redundancy Analysis (RDA) (Legendre and Legendre, 1998), considering the two reservoirs as a categorical variable. For this purpose, all physicochemical variables were standardized except for pH. Multicollinearity among physicochemical variables was assessed using a threshold Variance Inflation Factor (VIF) of 10. A final model was selected, including only variables with significant effects ($p < 0.05$) obtained using the "ordistep" function from the "vegan" package (Oksanen et al., 2024). The significance of the final global RDA model was tested by implementing the permutation ANOVA test (Legendre and Legendre, 1998). For this analysis, we used the "rda" function from the "vegan" package (Oksanen et al., 2024). All analyses were performed using the R Project (R Core Team, 2024).

3. Results

3.1. Physicochemical characteristics of the littoral zone in the two reservoirs

The depth in the littoral zone varied from 93 to 552 cm in the RX and 89–698 cm in the RI. The transparency average was 130.69 cm in the RX and 128.69 cm in the RI (Table 1); the water temperature averaged 30.79 °C in the RX and 31.19 °C in the RI. The pH was neutral in both reservoirs, with an average of 6.98 and 6.94 in RX and RI, respectively. The main form of inorganic nitrogen was NO_3, with an average of 0.09 mg/L in the RX and 0.18 mg/L in the RI. NO_2 and PO_4 were undetectable in all samples (Table 1).

The physical and chemical characteristics of the water exhibited distinct patterns between the RX and RI (Pseudo-F = 2.1807; $p = 0.007$) (Table 2 and Fig. 2). The variances in both reservoirs were homogeneous, indicating similar levels of heterogeneity in the physicochemical conditions across the two evaluated reservoirs (PERMDISP: F = 1.703; $p = 0.188$; Fig. 2).

3.2. Richness, biovolume, and composition of phytoplankton

A total of 134 phytoplankton morphospecies were recorded across the two reservoirs of the Belo Monte Hydroelectric Complex, distributed among nine taxonomic classes: Cyanophyceae (39 taxa), Chlorophyceae (22 taxa), Trebouxiophyceae (2 taxa), Zygnematophyceae (30 taxa), Euglenophyceae (7 taxa), Dinophyceae (5 taxa), Cryptophyceae (3 taxa), Coscinodiscophyceae (3 taxa), and Bacillariophyceae (19 taxa). The highest species richness was found in RX, with a total of 104 taxa, while the RI recorded a total richness of 62 taxa. The RX had an average richness of 23 taxa per sampling point (standard deviation = ± 7 taxa), whereas the RI had an average richness of 18 taxa (±8 taxa). When comparing the richness between the two reservoirs, no significant difference was observed ($t = -1.594$, df = 15.78; $p = 0.1307$).

Table 1
Summary of environmental data analyzed, including depth (Dep), water transparency (TRASP), water temperature (WT), electrical conductivity (COND), dissolved oxygen (DO), turbidity (TURB), oxidation-reduction potential (ORP), nitrate (NO_3), nitrite (NO_2), and orthophosphate (PO_4). The minimum value recorded (Min), maximum value recorded (Max), standard deviation to mean (SD), and coefficient of variation (CV) are presented.

	DEP	TRANSP	WT	COND	pH	DO	TURB	ORP	NO_3	NO_2	PO_4
	cm	cm	°C	µS/cm		mg/L	NTU	mV	mg/L	mg/L	mg/L
Xingu Reservoir											
Min	93.00	93.00	29.81	0.02	6.25	9.20	4.51	148.00	0.00	0.00	0.00
Max	552.00	190.00	32.51	0.02	7.30	12.96	922.00	272.00	0.44	0.00	0.00
Mean	212.92	130.69	30.79	0.02	6.98	10.66	79.89	231.46	0.09	0.00	0.00
SD	141.83	27.33	0.97	0.00	0.30	1.09	253.06	32.70	0.15	0.00	0.00
CV	0.67	0.21	0.03	0.03	0.04	0.10	3.17	0.14	1.72	0.00	0.00
Intermediate Reservoir											
Min	89.00	57.00	30.22	0.02	6.45	8.93	2.23	235.00	0.00	0.00	0.00
Max	698.00	240.00	32.62	0.03	7.59	25.80	20.30	275.00	0.21	0.00	0.00
Mean	204.62	128.69	31.19	0.02	6.94	11.93	33.48	214.36	0.18	0.00	0.00
SD	185.64	57.76	0.65	0.00	0.37	5.26	6.91	15.37	0.07	0.00	0.00
CV	0.91	0.45	0.02	0.24	0.05	0.44	0.21	0.07	0.39	0.00	0.00

Table 2
PERMANOVA based on the Distance Matrix to investigate significant differences in physicochemical data between the two reservoirs of the Belo Monte Hydroelectric Complex on the Xingu River.

	Df	R^2	F	*p*
RX vs RI	1	0.098	2.1807	0.007
Residual	20	0.901		
Total	21	1		

The total phytoplankton biovolume recorded for the two reservoirs was 113.67 mm^3/L. In the RX, the phytoplankton biovolume was 87.49 mm^3/L, accounting for 76.97 % of the total biovolume across both reservoirs, while in the RI, the total biovolume was 26.18 mm^3/L, representing 23.03 % of the total biovolume for both reservoirs. The Heterokontophyta taxa exhibited the highest aggregated biovolume, contributing 41.28 % in the RX and 1.25 % in the RI. Cyanobacteria ranked second, contributing 12.48 % of the total biovolume in the RX and 17.51 % in the RI. The Charophyta taxa displayed the third highest biovolume, with 19.33 % in RX and 0.6 % in RI. The remaining taxonomic groups contributed less than 5 % to the total biovolume (Fig. 3). Phytoplankton biovolume differed significantly between the two reservoirs ($w = 24$, $p = 0.02$; Fig. 4).

The composition of the 32 phytoplankton species with contributions greater than 5 % in the sample differed between the two reservoirs (Pseudo-F = 2.2164; $p = 0.001$; Table 3; Fig. 5). Of these, 17 species were found in both reservoirs, 10 species occurred exclusively in the RX, and 5 species were found only in the Intermediary Reservoir, indicating a restricted occurrence to a specific environment (Fig. 6).

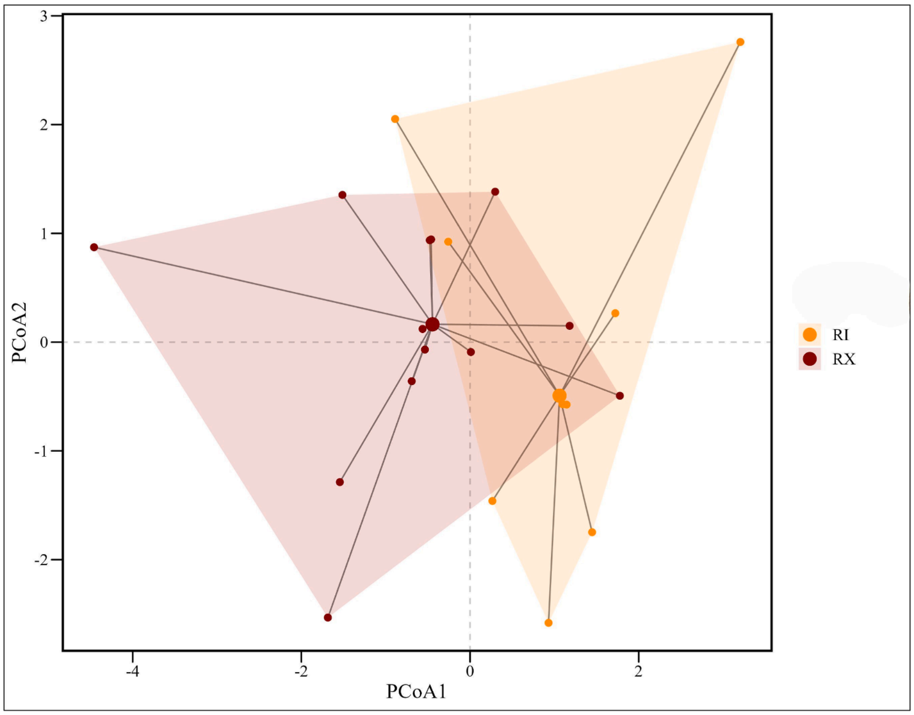

Fig. 2. PcoA analysis of the dissimilarity between the two reservoirs of the Belo Monte Hydroelectric Complex, investigated based on patterns of physical and chemical characteristics of the water. Caption: RI = Intermediate Reservoir, and RX = Xingu Reservoir.

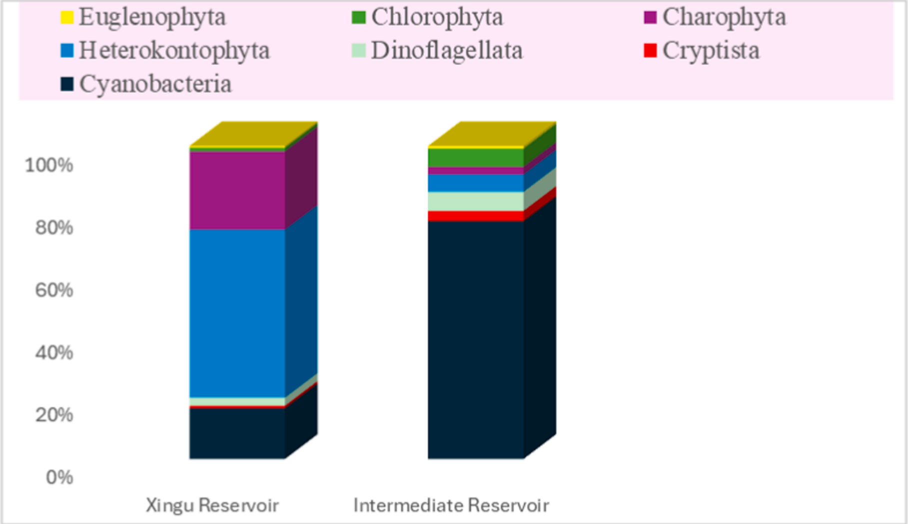

Fig. 3. Relative Biovolume (%) of the main taxonomic groups (Phylum) of Littoral Phytoplankton in the Two Reservoirs of the Belo Monte Hydroelectric Complex.

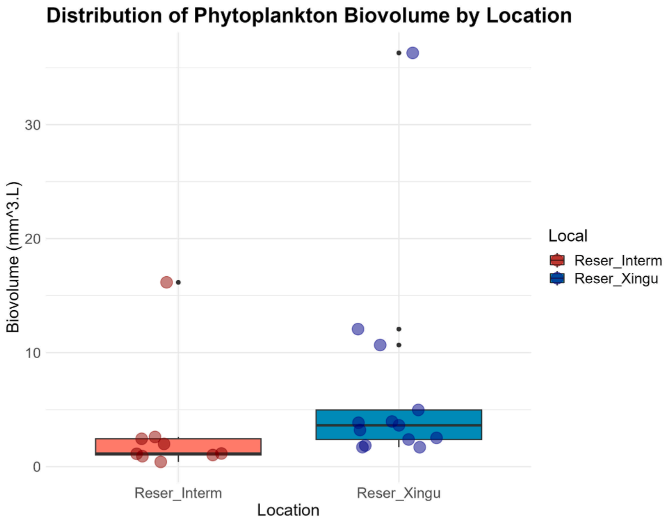

Fig. 4. Distribution of total phytoplankton biovolume in relation to the Xingu and Intermediary reservoirs of the Belo Monte Hydroelectric Complex. Legend: Reser_Interm = Intermediate Reservoir, Reser_Xingu = Xingu Reservoir.

Table 3
PERMANOVA showing significant differences in biovolume data for the 32 species between the Xingu (RX) and Intermediate (RI) Reservoirs.

	Df	R2	F	*p*
RX vs RI	1	0.099	2.216	0.001
Residual	20	0.900		
Total	21	1		

3.3. *Physical-chemical factors and the composition and biovolume of species*

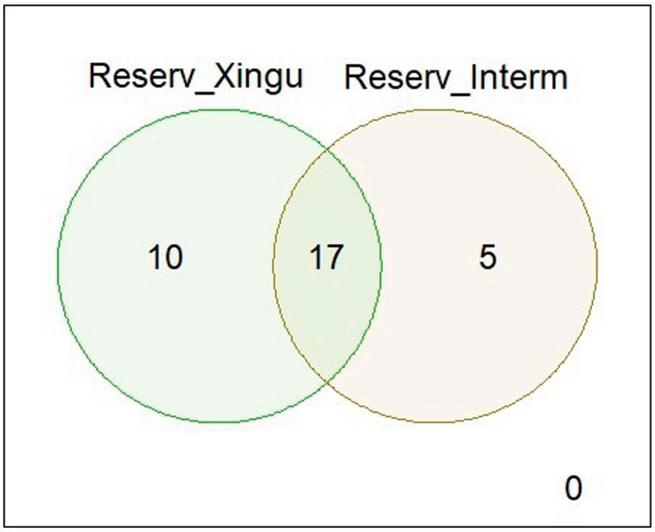

Fig. 6. Venn Diagram Showing the number of Common and Exclusive species in Xingu and Intermediate reservoirs. *Legend*: Reser_Xingu = Xingu Reservoir; Reser_Interm = Intermediate Reservoir.

Redundancy analysis (RDA) indicated that species composition was related to the physical and chemical variables analyzed (F = 2.277; *p* = 0.001). The first two axes of the RDA explained 25.73 % of the variability in the composition of the phytoplankton community in the reservoirs. The variable selection procedure highlighted NO_3 having a positive and significant relationship with axis 1, and temperature (WT) and conductivity (COND) negatively associated with axis 1 (Table 4). Axis 2 had a positive and significant association with water transparency (TRASP) (Table 4). Thus, the species *Aulacoseira granulata*, *Gonatozygon brebissonii,* and *Cryptomonas brasiliensis* tend to have greater biovolume in sites with higher NO_3 values (Fig. 7). The taxa *Dolichospermum planctonicum* and *Oscillatoria peronata* tend to have greater biovolume in sites with higher temperatures. The species *Anagnostidinema amphibium* has greater biovolume in places with greater electrical conductivity;

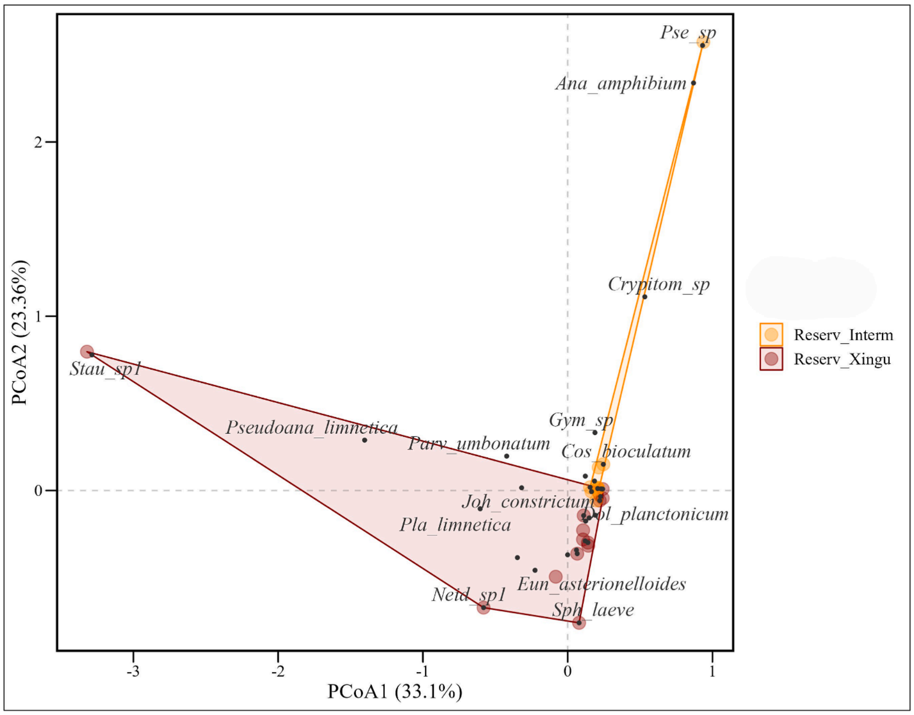

Fig. 5. Ordering of samples based on the sharing of phytoplankton species by type of treatment, summarized by Principal Coordinate Analysis (PCoA). Legend: Reser_Interm = Intermediate Reservoir, Reser_Xingu = Xingu Reservoir, *Ana_amphibium = Anagnostidinema amphibium, Aph_annulata = Aphanocapsa annulata, Joh_constrictum = Johanseninema constrictum, Dol_planctonicum = Dolichospermum planctonicum, Merism_convoluta = Merismopedia convoluta, Osc_perornata = Oscillatoria perornata, Phorm_sp1= Phormidium* sp1, *Pla_limnetica= Planktolyngbya limnetica, Pseudoana_limnetica = Pseudanabaena limnetica, Pse_sp = Pseudanabaena* sp, *Cryp_marssonii = Cryptomonas marssonii, Crypitom_sp= Cryptomonas* sp, *Cryp_brasiliensis = Cryptomonas brasiliensis, Gony_sp = Gonyaulax* sp, *Gym_sp= Gymnodinium* sp, *Parv_umbonatum = Parvodinium umbonatum, Peridin_amazonica = Peridiniopsis amazonica, Aul_brasiliensis = Aulacoseira brasiliensis, Aul_granulatav= Aulacoseira granulata, Aul_sp = Aulacoseira* sp, *Cos_bioculatum = Cosmarium bioculatum, Gon_brebissonii= Gonatozygon brebissonii, Sph_laeve= Sphaerozosma laeve, Coel_pulchrum = Coelastrum pulchrum, Har_reticulata = Hariotina reticulata, Oed_sp = Oedogonium* sp, *Rad_skujae = Radiococcus skujae, Eug_viridis= Euglena viridis, Eun_asterionelloides = Eunotia asterionelloides, Stau_sp1 = Stauroneis* sp1, *Neid_sp1= Neidium* sp1, *Pin_sp= Pinnularia* sp.

Table 4
Variable loading values (contribution of each variable to the formation of the RDA1 and RDA2 axes).

Variable	RDA1	RDA2
WT	**−0.743**	−0.234
COND	**−0.591**	0.485
NO_3	**0.648**	0.096
TRANSP	0.039	**0.273**

while *Planktolingbia limnetica* and *Eunotia asterionelloides* present greater biovolume in places with greater water transparency (Fig. 7).

4. Discussion

4.1. Physicochemical characteristics of the littoral zone of the two reservoirs in the Belo Monte Hydroelectric Complex

The results obtained in this study describe the physicochemical characteristics of the littoral zone of the two reservoirs that comprise the Belo Monte Hydroelectric Complex and support the initial hypothesis of environmental dissimilarity between the two reservoirs. Our findings are consistent with those of other studies that assess and characterize natural and anthropogenic processes related to water physicochemical parameters (Covino et al., 2022; Wolf et al., 2022; Xu et al., 2023).

The physicochemical characteristics of water in large rivers reflect historical anthropogenic and natural processes (e.g., temperature changes, rainfall patterns, weathering, and crustal materials) (Covino et al., 2022; Wolf et al., 2022; Xiong et al., 2022). These characteristics are reflected in the different spatial patterns of the physicochemical conditions observed in the Xingu and Intermediate reservoirs. For example, the damming of the Pimental site impounded the original river channel in the Volta Grande do Xingu region (Bertassoli et al., 2021; Araújo et al., 2024) that was originally a rocky system with channels. Currently, it forms the RX and redirects water to the RI, where the Belo Monte dam is located (Bertassoli et al., 2021; Utsunomiya et al., 2024; Araújo et al., 2024). The RI area was previously covered by tropical forest, pastures, plantations, and secondary and pioneer vegetation, with a small portion comprising urban and mining areas (Bertassoli et al., 2021). These characteristics can be reflected in the differences observed between the two reservoirs.

Furthermore, the different patterns in pH, conductivity, total dissolved solids, water temperature, oxidation-reduction potential, NO_3, dissolved oxygen, turbidity, and depth between the two evaluated reservoirs, may be related to the geological setting, historical land use events, and the operational and functional conditions of each reservoir (Latrubesse et al., 2017; Wolf et al., 2022). Studies have shown an association between physicochemical characteristics of fluvial systems with geomorphological factors and morpho-dynamic processes, which are implicated in erosion and deposition processes in pluvial systems (Latrubesse et al., 2017; Forsberg et al., 2017; Covino et al., 2022; Wolf et al., 2022). Also, hydroelectric operations can alter the physical and chemical characteristics of water including dissolved oxygen levels, sediment, nutrient concentrations, metals, pesticides, and greenhouse gas emissions (Bertassoli et al., 2021; Bao et al., 2023; Araújo et al., 2024).

4.2. Phytoplankton structure and the water's physicochemical parameters

The littoral zone of an aquatic ecosystem reflects the dynamic interaction between land and water and significantly contributes to the structuring processes of aquatic communities (Gregory et al., 1991; Naiman and Décamps, 1997; Kalff, 2002). Due to its location at the interface between land and water, the littoral zone exhibits distinctive environmental characteristics, particularly related to land use (Gregory et al., 1991; Wetzel, 2001; Kalff, 2002; Wolf et al., 2022; Xiong et al., 2022).

Understanding the assembly processes that shape communities in ecotone environments (Schiemer et al., 1995; Silveira et al., 2024), such as the littoral zone of aquatic systems, is crucial for predicting and

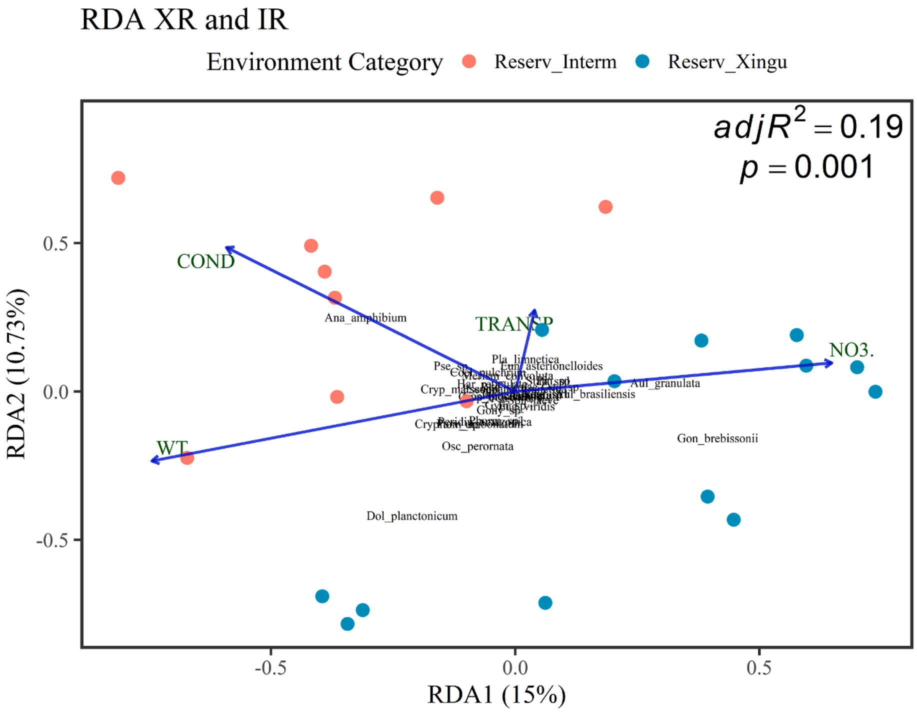

Fig. 7. Redundancy Analysis (RDA) between phytoplankton species and physicochemical parameters of the reservoirs of the Belo Monte Hydroelectric Complex. Legend: Reser_Interm = Intermediate Reservoir, Reser_Xingu = Xingu Reservoir, WT = water temperature, COND = Electric conductivity, NO_3 = nitrate TRANSP = transparency; *Ana_amphibium = Anagnostidinema amphibium, Aph_annulata = Aphanocapsa annulata, Joh_constrictum = Johanseninema constrictum, Dol_planctonicum = Dolichospermum planctonicum, Merism_convoluta = Merismopedia convoluta, Osc_perornata = Oscillatoria perornata, Phorm_sp1= Phormidium* sp1, *Pla_limnetica= Planktolyngbya limnetica, Pseudoana_limnetica = Pseudanabaena limnetica, Pse_sp = Pseudanabaena* sp, *Cryp_marssonii = Cryptomonas marssonii, Crypitom_sp= Cryptomonas* sp, *Cryp_brasiliensis = Cryptomonas brasiliensis, Gony_sp = Gonyaulax* sp, *Gym_sp= Gymnodinium* sp, *Parv_umbonatum = Parvodinium umbonatum, Peridin_amazonica = Peridiniopsis amazonica, Aul_brasiliensis = Aulacoseira brasiliensis, Aul_granulatav= Aulacoseira granulata, Aul_sp = Aulacoseira* sp, *Cos_bioculatum = Cosmarium bioculatum, Gon_brebissonii= Gonatozygon brebissonii, Sph_laeve= Sphaerozosma laeve, Coel_pulchrum = Coelastrum pulchrum, Har_reticulata = Hariotina reticulata, Oed_sp = Oedogonium* sp, *Rad_skujae = Radiococcus skujae, Eug_viridis= Euglena viridis, Eun_asterionelloides = Eunotia asterionelloides, Stau_sp1 = Stauroneis* sp1, *Neid_sp1= Neidium* sp1, *Pin_sp= Pinnularia* sp.

anticipating future changes in species distributions and community composition due to ongoing climate change on the planet (Schiemer et al., 1995; Dodds et al., 2013; Wang et al., 2021a; Silveira et al., 2024).

Although several studies have explored the relationship between water physicochemical factors and phytoplankton composition in the littoral regions of reservoirs (Lemly and Dimmick, 1982; Schweizer, 1997; Sakharova and Korneva, 2018; Silveira et al., 2024; Alpecho et al., 2024), references to the role of spatially structured environmental filtering processes in understanding phytoplankton species' responses and changes in reservoir littoral zones are still scarce. To address this knowledge gap, we applied the habitat model, incorporating environmental filters as proposed by Reynolds (2003), to investigate the main drivers and assembly processes affecting phytoplankton community composition.

The habitat model combined with environmental filtering provides a framework in which organisms' survival requirements and evolutionary traits are presented within the context of environmental conditions which drives the structure of community assembly. This approach takes into consideration the physiological attributes of organisms that are candidates to thrive in the system (Reynolds, 2003; Borics et al., 2021). In this way, the filter identifies the traits most likely to provide survival benefits to organisms capable of adjusting to habitat restrictions (Jones and Reynolds, 1985; Reynolds, 2003, 2006; Borics et al., 2021).

We emphasize that our results map the spatial gradient of physicochemical water conditions in the littoral zone to the organizational structure of ecological factors, which we describe here as the main drivers of the community assembly process that operate at the habitat scale and influence the composition of phytoplankton in the coastal region of these environments. Logically, these findings are based on years of study of the ecology and dynamics of phytoplankton, which allowed us to highlight important points in the spatial dynamics of phytoplankton. This also allowed for the role of the spatially structured environmental filtering process on community assembly and regulation of phytoplankton in the coastal region of the two reservoirs of the Belo Monte Hydroelectric Complex on the Xingu River to be discerned.

In our study, although we did not evaluate the directional dispersion processes of phytoplankton between the RX and RI reservoirs, our results found an environmental difference between coastal zones of the two reservoirs that was accompanied by a difference in community composition between the environments evaluated. This allows us to attribute a significant contribution of environmental filters in the community structuring of phytoplankton, and that these processes are spatially structured in the Belo Monte Hydroelectric Complex. Thus, we can suggest that passive dispersion between the connected reservoirs would tend to homogenize the local communities, and that this would mask the effect of the action of environmental filters (Heino et al., 2015; Bortolini et al., 2020; Borics et al., 2021). As this was not observed, findings corroborated our hypotheses of the structuring of the riverine phytoplankton community based on locally acting environmental filters.

We observed a similarity in the richness of littoral phytoplankton species between the reservoirs. However, when comparing the species composition and biovolume, we observed differences between reservoirs; the RX, for example, presented a higher phytoplankton biovolume than the RI. Also, in RX, the highest biovolumes were associated with Bacillariophyceae and Zygnematophyceae, while in RI, Cyanophyceae were predominant. These patterns in community structure indicate that the environmental conditions in each reservoir acted as filters, selecting different species with adaptations and attributes that allowed them to thrive in those environments (Reynolds, 1998, 2003, 2006; Borics et al., 2021).

The dominance in biovolume of Cyanobacteria in the RI agrees with reports from different studies that demonstrated that these organisms are often dominant under various environmental conditions (Reynolds et al., 1987; Robarts and Zohary, 1987; Jakubowska et al., 2013; Wang et al., 2021b) due to their adaptive strategies that often give them competitive advantages (Reynolds et al., 1987; Wang et al., 2021b). These characteristics are related to their metabolic activity, ability to regulate fluctuation in the water column, variability in size and shape, potential cyanotoxin production, and ability to form large blooms, among others (Robarts and Zohary, 1987; Suikkanen et al., 2004; Jakubowska et al., 2013; Wang et al., 2021b).

Our results from the RDA also confirmed the importance of physicochemical factors structuring the littoral phytoplankton composition, as reported in other studies (Kalff, 2002; Shi et al., 2023). The scientific literature highlights those physicochemical parameters, such as nutrients, temperature, light, and conductivity, are crucial for the structuring of phytoplankton communities (Jones and Reynolds, 1985; Reynolds, 1998; Shi et al., 2023; Mohanty et al., 2023). In our study, littoral phytoplankton was associated with nitrate (NO_3), temperature, conductivity, and transparency. More specifically, *Aulacoseira granulata*, *Gonatozygon brebissonii*, and *Cryptomonas brasiliensis* exhibited higher biovolume in sites with elevated NO_3 concentrations. It is important to note that NO_3 is one of the soluble forms of nitrogen in water and plays a critical role in the synthesis of proteins and other biomolecules within algal cells (Bhadury et al., 2011; Hutchins and Tagliabue, 2024). Additionally, diatoms have a high silica requirement and possess robust genetic mechanisms that facilitate rapid nutrient uptake (Bhadury et al., 2011; Kumar et al., 2022). Thus, *Aulacoseira* can be favored by increased nutrient concentrations and become dominant in the environment (Kumar et al., 2022; Hu et al., 2023). The taxa *Gonatozygon* spp. also exhibit high adaptability to nutrient concentrations (Jones and Reynolds, 1985; Reynolds, 2006) and *Cryptomonas* is known for its rapid growth and efficient nutrient absorption (Jones and Reynolds, 1985; Reynolds, 2006; Kruk et al., 2010). These characteristics of each genus could explain the observed distribution pattern in sites with higher NO_3 concentrations.

Regarding other variables, the taxa *Dolichospermum planctonicum* and *Oscillatoria peronata*, both Cyanobacteria, exhibit higher biovolume in sites with elevated temperatures. This observation is consistent with other studies highlighting the preference of cyanobacteria for warmer waters, as their growth rates increase under higher temperatures (Robarts and Zohary, 1987; Segura et al., 2018). This temperature-related growth advantage is also associated with buoyancy regulation, an adaptive mechanism that enhances the competitive ability to access resources such as nutrients and light (Reynolds, 2006; Kruk et al., 2010, 2021). The species *Anagnostidinema amphibium* showed greater biovolume in areas with higher electrical conductivity, indicating a preference for waters with elevated concentrations of dissolved ions, which may reflect higher salinity or pollution conditions (Jones and Reynolds, 1985; Reynolds, 2006). *Planktothrix limnetica* and *Eunotia asterionelloides* exhibited higher biovolume in sites with greater water transparency, suggesting that these species may benefit from increased light availability, facilitating their establishment and dominance. The enhanced light conditions support photosynthesis, providing the energy necessary for growth and reproduction (Jones and Reynolds, 1985; Reynolds, 2006; Souza et al., 2022).

Although the relationship between physical and chemical factors in water and cyanobacterial blooms is well documented in the literature (Reynolds et al., 1987; Robarts and Zohary, 1987; Suikkanen et al., 2004; Jakubowska et al., 2013; Fukushima et al., 2017; Wang et al., 2021b), the proliferation of these organisms in the coastal zone of reservoirs demands increasing attention in scientific studies, with an emphasis on identifying the main drivers and implementing sustainable solutions to control these algae, both from an environmental and public health point of view (Lemly and Dimmick, 1982; Wang et al., 2021b; Silveira et al., 2024). By tracking temperature and conductivity in this study as the factors that favored Cyanobacteria in the RI, we drew attention to potential blooms. The proliferation of Cyanobacteria in the coastal regions of reservoirs represents a major ecological concern, as these areas are subject to the effects of environmental changes induced by human activities (Gregory et al., 1991; Naiman and Décamps, 1997; Yang et al., 2017) and, therefore, are directly influenced by elevated nutrient concentrations and climate change (Gregory et al., 1991; Naiman and Décamps, 1997; Yang et al., 2017; Silveira et al., 2024; Alpecho et al., 2024). Cyanobacteria have a significant competitive advantage over other phytoplankton organisms because they have characteristics that make them adaptive to different environmental conditions, which allow them to thrive over other phytoplankton groups in response to environmental changes (Reynolds et al., 1987; Robarts and Zohary, 1987; Jakubowska et al., 2013; Wang et al., 2021b).

We highlight the importance of local environmental filtering in controlling phytoplankton composition and diversity (Borics et al., 2021). This is supported by the "habitat model" approach described by Reynolds, (2003), which characterizes the relationship between gradients and resource availability for phytoplankton community structure (Jones and Reynolds, 1985; Reynolds, 1998, 2006). The environmental filtering model generally represents the filter, while the habitat represents the filtering element (Reynolds, 2003; Borics et al., 2021). Thus, local species selection is considered crucial in shaping community structure (Borics et al., 2021). By understanding these fundamental principles of phytoplankton ecology, our results reveal a significant association between physical-chemical characteristics and the species distribution of the littoral phytoplankton community in reservoirs.

5. Conclusions

The physicochemical characteristics of the water, such as NO_3 concentrations, temperature, conductivity, and transparency, structured the phytoplankton biovolume, with distinct variations between the two reservoirs. Therefore, the effects of physicochemical variables on phytoplankton community structure highlighted the importance of local environmental filtering processes in regulating the composition and biovolume of the littoral phytoplankton in the studied reservoirs. These findings are grounded in Reynolds' habitat model, which explains the relationship between environmental gradients and phytoplankton community structure.

Furthermore, it is crucial to understand and conserve the littoral zone and littoral phytoplankton to promote reservoir sustainability and ensure the continuity of essential ecosystem services for both society and aquatic life. We recommend implementing continuous monitoring programs to track spatial changes and seasonal variation in phytoplankton and environmental parameters, as well as prevent future issues with algal and cyanobacterial blooms. Finally, this study contributes to the understanding of the ecological dynamics of littoral phytoplankton in reservoirs, providing valuable insights for future research and effective management of aquatic ecosystems of this nature.

CRediT authorship contribution statement

Dilailson Araújo de Souza: Methodology, Writing – original draft, Data curation, Writing – review & editing, Conceptualization, Formal analysis. **Francieli de Fátima Bomfim:** Supervision, Validation, Writing – original draft, Conceptualization, Visualization, Writing – review & editing, Formal analysis. **Daniela Santana Nunes:** Validation, Conceptualization, Visualization, Data curation, Investigation, Writing – review & editing, Formal analysis, Methodology. **Thiago Bernardi Vieira:** Methodology, Validation, Writing – review & editing, Conceptualization, Visualization, Formal analysis. **Juliana Feitosa Felizzola:** Visualization, Data curation, Writing – original draft, Formal analysis, Methodology, Writing – review & editing, Investigation, Validation, Conceptualization. **Karina Dias-Silva:** Supervision, Formal analysis, Validation, Investigation, Writing – review & editing, Project administration, Conceptualization, Visualization, Methodology, Resources, Data curation.

Declaration of competing interest

All authors declare that they have no known competing financial interests or personal relationships that could have influenced the work developed in this article.

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Appendix A. Supplementary data

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References

Abonyi, A., Descy, J.P., Borics, G., Smeti, E., 2021. From historical backgrounds towards the functional classification of river phytoplankton sensu Colin S. Reynolds: what future merits the approach may hold? Hydrobiologia 848, 131–142. https://doi.org/10.1007/s10750-020-04300-3.

Alpecho, B.C., Duya, M.R.M., Mendoza, N.Y.B., Magbanua, F.S., 2024. Littoral phytoplankton and zooplankton communities in a tropical reservoir: Pantabangan Reservoir, the Philippines. J. Plankton Res. 46, 272–281. https://doi.org/10.1093/plankt/fbae006.

Anderson, M.J., 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef: Statistics Reference Online, pp. 1–15. https://doi.org/10.1002/9781118445112.stat07841. Wiley.

Anderson, M. e, Walsh, D., 2013. PERMANOVA, ANOSIM, and the mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol. Monogr. 83, 557–574. https://doi.org/10.1890/12-2010.1.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070 x.

Araújo, K.R., Sawakuchi, H.O., Bertassoli, D.J., Bastviken, D., Pereira, T.S., Sawakuchi, A., 2024. Operational effects on aquatic carbon dioxide and methane emissions from the belo monte hydropower plant in the xingu River, eastern Amazonia. Sci. Total Environ. 946, 174100. https://doi.org/10.1016/j.scitotenv.2024.174100.

Bao, J., Twardek, W.M., Zhang, C., Li, W., Mi, X., Zhang, D., Wu, J., Jiang, H., Cook, S., Duan, M., 2023. Mitigating the cumulative effects of hydropower and climate change on riverine fishes. Rev. Fish Biol. Fish. 33, 915–930. https://doi.org/10.1007/s11160-023-09766-7.

Berdugo, M., Vidiella, B., Solé, R.V., Maestre, F.T., 2021. Ecological mechanisms underlying aridity thresholds in global drylands. Funct. Ecol. 36, 4–23. https://doi.org/10.1111/1365-2435.13962.

Bertassoli, D.J., Sawakuchi, H.O., Araújo, K.R., Camargo, M.G.P., Alem, V.A.T., Pereira, T.S., Krusche, A.V., Bastviken, D., Rico, J.E., Sawakuchi, A.O., 2021. How green can amazon hydropower be? Net carbon emission from the largest hydropower plant in Amazonia. https://doi.org/10.1126/sciadv.abe1470.

Bhadury, P., Song, B., Ward, B.B., 2011. Intron features of key functional genes mediating nitrogen metabolism in marine phytoplankton. Mar. Genom. 4, 207–213. https://doi.org/10.1016/j.margen.2011.06.002.

Bicudo, C.E. de M., Bicudo, D. de C., 2004. Amostragem Em Limnologia, second ed. São Paulo.

Borics, G., Abonyi, A., Salmaso, N., Ptacnik, R., 2021. Freshwater phytoplankton diversity: models, drivers and implications for ecosystem properties. Hydrobiologia 848, 53–75. https://doi.org/10.1007/s10750-020-04332-9.

Bortolini, J.C., da Silva, P.R.L., Baumgartner, G., Bueno, N.C., 2020. Environmental filters influencing phytoplankton taxonomic structure in cascade reservoirs. Rev. Bras. Bot. 43, 405–412. https://doi.org/10.1007/s40415-020-00604-9.

Case, T.J., Gilpin, M.E., 1974. Interference Competition and Niche Theory (Population dynamics/adaptive strategies/resource Gradients.

Covino, T., Riveros-Iregui, D.A., Schneider, C.L., 2022. Geomorphology imparts spatial Organization on hydrological and biogeochemical fluxes. In: Shroder, J., Jack), F. (Eds.), Treatise on Geomorphology, second ed. Academic Press, Oxford, pp. 53–67.

Devercelli, M., Scarabotti, P., Mayora, G., et al., 2016. Unravelling the role of determinism and stochasticity in structuring the phytoplanktonic metacommunity of the paraná river floodplain. Hydrobiologia 764, 139–156. https://doi.org/10.1007/s10750-015-2363-5.

Dodds, W.K., Perkin, J.S., Gerken, J.E., 2013. Human impact on freshwater ecosystem services: a global perspective. Environ. Sci. Technol. 47, 9061–9068. https://doi.org/10.1021/es4021052.

Faquim, R.C.P., Machado, K.B., Teresa, F.B., et al., 2021. Shortcuts for biomonitoring programs of stream ecosystems: evaluating the taxonomic, numeric, and cross-taxa congruence in phytoplankton, periphyton, zooplankton, and fish assemblages. PLoS One 16. https://doi.org/10.1371/journal.pone.0258342.

Forsberg, B.R., Melack, J.M., Dunne, T., et al., 2017. The potential impact of new Andean dams on amazon fluvial ecosystems. PLoS One 12. https://doi.org/10.1371/journal.pone.0182254.

Fukushima, M., Tomioka, N., Jutagate, T., et al., 2017. The dynamics of pico-sized and bloom-forming Cyanobacteria in large water bodies in the mekong river basin. PLoS One 12. https://doi.org/10.1371/journal.pone.0189609.

Guiry, M.D., Guiry, G.M., 2024. Algae Base. World-wide electronic publication. http://www.algaebase.org. (Accessed 2 June 2024).

Gregory, S.V., Swanson, F.J., Mckee, W.A., Cummins Reviewed, K.W., 1991. An Ecosystem Perspective of Riparian Zones.

Guo, W., Zhu, Y., Fu, Z., et al., 2017. Influences of environmental factors on biomass of phytoplankton in the northern part of Tai Lake, China, from 2000 to 2012. Environ. Monit. Assess. 189. https://doi.org/10.1007/s10661-017-6318-3.

Haddad, P.R., 2004. Ion chromatography. Anal. Bioanal. Chem. 379, 341–343. https://doi.org/10.1007/s00216-004-2572-7.

Hastie, T., Tibshirani, R., Friedman, J., 2009. The Elements of Statistical Learning: Data Mining, Inference, and Prediction.

Heino, J., Melo, A.S., Bini, L.M., 2015. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. Freshw. Biol. 60, 223–235. https://doi.org/10.1111/fwb.12502.

Hillebrand, H., Dürselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. J. Phycol. 35, 403–424. https://doi.org/10.1046/j.1529-8817.1999.3520403.x.

Hu, C., Guo, K., Wu, N., Liu, Q., Liu, Q., Yang, W., Wang, C., 2023. How do multidimensional traits of dominant diatom aulacoseira respond to abiotic and biotic factors in a river delta system? J Environ Manage 327. https://doi.org/10.1016/j.jenvman.2022.116858.

Hutchins, D.A., Tagliabue, A., 2024. Feedbacks between phytoplankton and nutrient cycles in a warming ocean. Nat. Geosci. 17, 495–502. https://doi.org/10.1038/s41561-024-01454-w.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22 (0), 415–427. https://doi.org/10.1101/sqb.1957.022.01.039.

Jakubowska, N., Paweł Zagajewski, P., Gołdyn, R., 2013. Water blooms and cyanobacterial toxins in Lakes. Pol. J. Environ. Stud. 22, 1077–1082.

Jones, R.I., Reynolds, C.S., 1985. The ecology of freshwater phytoplankton. J. Ecol. 73. https://doi.org/10.2307/2260522.

Kalff, J., 2002. Limnology: Inland Water Ecosystems. Prentice Hall, California.

Kruk, C., Devercelli, M., Huszar, V.L., 2021. Reynolds functional Groups: a trait-based pathway from patterns to predictions. Hydrobiologia 848, 113–129. https://doi.org/10.1007/s10750-020-04340-9.

Kruk, C., Huszar, V.L.M., Peeters, E.T.H.M., Bonilla, S., Costa, L., Lürling, M., Reynolds, C.S., Scheffer, M., 2010. A morphological classification capturing functional variation in phytoplankton. Freshw. Biol. 55, 614–627. https://doi.org/10.1111/j.1365-2427.2009.02298.x.

Kruk, C., Mazzeo, N., Lacerot, G., Reynolds, C.S., 2002. Classification schemes for phytoplankton: a local validation of a functional approach to the analysis of species temporal replacement. J. Plankton Res. 24, 901–912. https://doi.org/10.1093/plankt/24.9.901.

Kumar, C., Ghosh, A., Yash, B.P., 2022. Unusual abundance of bloom forming aulacoseira spp. diatom populations in an anthropogenically impacted stretch of lower part of the River Ganga. Environ. Res. Commun. 4. https://doi.org/10.1088/2515-7620/ac60ea.

Latrubesse, E.M., Arima, E.Y., Dunne, T., et al., 2017. Damming the rivers of the amazon basin. Nature 546, 363–369. https://doi.org/10.1038/nature22333.

Legendre, P., Borcard, D., 2018. Box–Cox-Chord transformations for community composition data prior to beta diversity analysis. Ecography 41, 1820–1824. https://doi.org/10.1111/ecog.03498.

Legendre, P., Legendre, L., 1998. Numerical Ecology, second ed. Elsevier, Amsterdam, p. 784.

Leibold, M.A., Holyoak, M., Mouquet, N., et al., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x.

Leibold, M.A., Rudolph, F.J., Blanchet, F.G., et al., 2022. The internal structure of metacommunities. Oikos. https://doi.org/10.1111/oik.08618.

Lemly, A.D., Dimmick, J.F., 1982. Phytoplankton communities in the Littoral zone of Lakes: observations on structure and dynamics in oligotrophic and eutrophic systems. Oecologia 54, 359–369. https://doi.org/10.1007/BF00380005.

Lund, J.W.G., Kipling, C., Le, C.E.D., 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11, 144–170. https://doi.org/10.1007/BF00007865.

Madden, J.E., Shaw, M.J., Dicinoski, G.W., Avdalovic, N., Haddad, P.R., 2002. Simulation and optimization of retention in ion chromatography using virtual column 2 software. Anal. Chem. 74, 6023–6030. https://doi.org/10.1021/ac020280w.

Mohanty, T.R., Tiwari, N.K., Das, B.K., Swain, H.S., Jhonson, C., Banerjee, T., 2023. Riverine connectivity influences the phytoplankton ecology in the open floodplain wetland of the lower river Ganga. Environ. Monit. Assess. 195. https://doi.org/10.1007/s10661-023-11983-3.

Mutshinda, C.M., Finkel, Z.V., Widdicombe, C.E., Irwin, A.J., 2016. Ecological equivalence of species within phytoplankton functional groups. Funct. Ecol. 30, 1714–1722. https://doi.org/10.1111/1365-2435.12641.

Naiman, R.J., Décamps, H., 1997. The ecology of interfaces: riparian zones. Annual Reviews 28, 621–658. https://doi.org/10.1146/annurev.ecolsys.28.1.621.

Oksanen, J., Simpson, G.L., Blanchet, F.G., et al., 2024. Package "vegan" title community ecology package. R package version 2, 6–8.

Prado, R.B., Tavares, S.R. de L., Bezerra, F.B., Rios, L. da C., Escaleira, V., 2004. Manual Técnico De Coleta, Acondicionamento, Preservação E Análises Laboratoriais De Amostras De Água Para Fins Agrícolas E Ambientais, 1a ed.

R Core Team, 2024. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. Avaliable in: https://www.R-project.org. (Accessed 10 June 2024).

Reynolds, C.S., 2003. Pelagic community assembly and the habitat template. Bocconea 16, 323–339.

Reynolds, C.S., 1998. Phytoplankton and Trophic Gradients. Kluwer Academic Publishers.

Reynolds, C.S., 2006. The Ecology of Phytoplankton. Cambridge University Press.

Reynolds, C.S., Oliver, R.L., Walsby, A.E., 1987. Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. N Z J Mar Freshwater Res 21, 379–390. https://doi.org/10.1080/00288330.1987.9516234.

Robarts, R.D., Zohary, T., 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming Cyanobacteria. N Z J Mar Freshwater Res 21, 391–399. https://doi.org/10.1080/00288330.1987.9516235.

Sakharova, E.G., Korneva, L.G., 2018. Phytoplankton in the Littoral and pelagial zones of the rybinsk reservoir in years with different temperature and water-level regimes. Inland Water Biol 11, 6–12. https://doi.org/10.1134/S1995082918010157.

Schiemer, F., Zalewski, M., Thorpe, J.E., 1995. The Importance of Aquatic-Terrestrial Ecotones for Freshwater Fish, 1rd ed. Springer, Dordrecht, p. 264. https://doi.org/10.1007/978-94-017-3360-1.

Schweizer, A., 1997. From littoral to pelagial: comparing the distribution of phytoplankton and ciliated protozoa along a transect. J. Plankton Res. 19 (7), 829–848. https://doi.org/10.1093/plankt/19.7.829. July 1997.

Segura, A.M., Sarthou, F., Kruk, C., 2018. Morphology-based differences in the thermal response of freshwater phytoplankton. Biol. Lett. 14. https://doi.org/10.1098/rsbl.2017.0790.

Shi, J., Ni, L., Liu, J., Xu, C., Zhang, J., Chen, X., 2023. Spatiotemporal distribution of phytoplankton community structure and its relationship with environmental factors in Hongze Lake, China. Urban Clim. 52. https://doi.org/10.1016/j.uclim.2023.101746.

Silveira, M.H., Crossetti, L.O., Rosa, L.M., Cavalcanti, J.R., Cardoso, L.S., Motta-Marques, D., Rodrigues, L.R., 2024. Short-term responses of littoral phytoplankton in a large shallow subtropical lake. An. Acad. Bras. Cienc. 96 (3), 1–19. https://doi.org/10.1590/0001-3765202420220870.

Sioli, H., 1984. The amazon and its main affluents: hydrography, morphology of the river courses, and river types. In: Sioli, H. (Ed.), The Amazon, Monographiae Biologicae, vol. 56. Springer, Dordrecht. https://doi.org/10.1007/978-94-009-6542-3_5.

Sohani, S., 2016. A review of phytoplankton ecology in freshwater Rivers and Lakes of India. IJSTE -International Journal of Sci. Technol and Eng. 3 (6), 19–21.

Soininen, J., Heino, J., 2007. Variation in niche parameters along the diversity gradient of unicellular eukaryote assemblages. Protist 158, 181–191. https://doi.org/10.1016/j.protis.2006.11.002.

Souza, D.A., Kraus, C.N., Burliga, A.L., et al., 2022. Understanding the effects of environmental heterogeneity on the morphofunctional structure of the phytoplankton community during the hydrological year in an amazon floodplain lake, Brazil. Limnology 23, 275–286. https://doi.org/10.1007/s10201-021-00685-9.

Suikkanen, S., Fistarol, G.O., Granéli, E., 2004. Allelopathic effects of the Baltic Cyanobacteria nodularia spumdigena, Aphanizomenon flos-aquae and Anabaena lemmermannii on algal monocultures. J. Exp. Mar. Biol. Ecol. 308. https://doi.org/10.1016/j.jembe.2004.02.012.

Thomaz, S.M., Naselli-Flores, L., Fontaneto, D., Martens, K., 2020. Preface: emerging trends in aquatic ecology III. Hydrobiologia 847, 1565–1570. https://doi.org/10.1007/s10750-020-04218-w.

Tundisi, J.G., Matsumura-Tundisi, T., 2011. Limnology. Rd, 1 ed. CRC Press, Londres. https://doi.org/10.1201/b11386.

Turland, N.J., Wierse, M.H., Barrie, F.R., Greuter, W., Herendeen, P.S., Wolf-Henning, S. K., Li, K.D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M. J., Smith, G.F., 2018. International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code). Koeltz Botanical Books, pp. 1–159. https://www.iaptglobal.org.

Uhelinger, V., 1964. Étude statistique des méthodes de dénombrement planctonique. Arch. Sci. 17, 121–223.

Utermöhl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Internationale Vereinigung für Theoretische und Angewandte Limnologie. Mitteilungen 9, 1–38. https://doi.org/10.1080/05384680.1958.11904091.

Utsunomiya, R., Beveridge, C., Lobo, G., Assahira, C., Moretto, E.M., Athayde, S., 2024. Dewatering the xingu River: hydrological alterations and biocultural connections among the arara Indigenous people in the Volta Grande region, Brazilian amazon. Reg. Environ. Change 24. https://doi.org/10.1007/s10113-024-02230-7.

Wang, J., Soininen, J., Heino, J., 2021a. Ecological indicators for aquatic biodiversity, ecosystem functions, human activities and climate change. Ecol. Indic. 132. https://doi.org/10.1016/j.ecolind.2021.108250.

Wang, Z., Akbar, S., Sun, Y., et al., 2021b. Cyanobacterial dominance and succession: factors, mechanisms, predictions, and managements. J Environ Manage 297. https://doi.org/10.1016/j.jenvman.2021.113281.

Wetzel, R.G., 2001. Limnology: Lake and River Ecosystems, rd:3 ed. Academic Press, San Diego, p. 1006. https://doi.org/10.1016/B978-0-08-057439-4.50002-2.

Wojciechowski, J., Heino, J., Bini, L.M., Padial, A.A., 2017. The strength of species sorting of phytoplankton communities is temporally variable in subtropical reservoirs. Hydrobiologia 800, 31–43. https://doi.org/10.1007/s10750-017-3245-9.

Wolf, S., Esser, V., Lehmkuhl, F., Schüttrumpf, H., 2022. Long-time impact of a large dam on its downstream river's morphology: determined by sediment characteristics, pollutants as a marker, and numerical modelling. J. Sed. Environ. 7, 403–424. https://doi.org/10.1007/s43217-02200103-9.

Xiong, F., Chen, Y., Zhang, S., Xu, Y., Lu, Y., Qu, X., Gao, W., Wu, X., Xin, W., Dianchen, G.D., Lian-Shin, L., 2022. Land use, hydrology, and climate influence water quality of China's largest river. J Environ Manage 318. https://doi.org/10.1016/j.jenvman.2022.115581.

Xu, Y., Wang, L., Tang, Q., Naselli-Flores, L., Jeppesen, E., Han, B.-P., 2023. The relationship between phytoplankton diversity and ecosystem functioning changes with disturbance regimes in tropical reservoirs. Ecosystems 26, 752–767. https://doi.org/10.1007/s10021-022-00791-4.

Yang, M., Grace, J., Geng, X., et al., 2017. Carbon dioxide emissions from the littoral zone of a Chinese reservoir. Water (Switzerland) 9. https://doi.org/10.3390/w9070539.

Zhang, M., Lv, X., Dong, J., et al., 2023. Multiple habitat templates for phytoplankton indicators within the functional group system. Hydrobiologia 850, 5–19. https://doi.org/10.1007/s10750-022-05024-2.