LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2025, 1–12

doi: 10.1002/lno.70198

RESEARCH ARTICLE

Effects of oligotrophication on fish growth: Insights from a mesocosm experiment

Juliana Deo Dias,[1]* **Nadson Ressye Simões**,[2] **Claudia Costa Bonecker**,[3] **Angelo Antonio Agostinho**[3]

[1]Department of Oceanography and Limnology, Universidade Federal do Rio Grande do Norte, Natal, RN, Brazil; [2]Centro de Formação em Ciências Agroflorestais, Universidade Federal do Sul da Bahia, Ilhéus, BA, Brazil; [3]Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura (Nupelia), Universidade Estadual de Maringá, Maringá, PR, Brazil

Abstract

Human activities can frequently affect aquatic ecosystems in irreversible ways, with flow regulation and water quality being major concerns. Dams can promote the retention of sediments and nutrients, increase water transparency, and reduce primary productivity, all of which characterize the oligotrophication process. Although the beneficial effects of oligotrophication in eutrophic systems are well documented, the oligotrophication process caused by river impoundment can negatively affect aquatic communities in non-eutrophic systems. Our study aimed to assess the effects of oligotrophication on the specific growth rate of small-bodied fish. We hypothesized that the fish-specific growth rate would decrease under an oligotrophic scenario, due to bottom-up processes. We performed a full-factorial experiment with nine treatments, using three levels of inorganic turbidity crossed by three levels of nutrients, in mesocosms during 24 d. In each tank, we added plankton and 30 individuals of *Moenkhausia forestii*, a fish species with omnivorous feeding habits. The fish were weighed at the beginning and at the end of the experiment to calculate specific growth rates. We observed a significant interaction between inorganic turbidity and nutrients on the specific growth. The smallest reduction in growth rate occurred in treatments with intermediate turbidity and high nutrient levels (T2N3), and high turbidity and high nutrient levels (T3N3). Our results indicate that changes in inorganic turbidity and nutrients, coinciding with oligotrophication caused by river dams, would negatively affect fish growth, which could have severe implications for fishery production and irreversible impacts on aquatic ecosystems.

Human activities have significantly altered the availability of nutrients in both aquatic and terrestrial environments, leading to their degradation. In aquatic ecosystems, modification of natural river flow by impoundments is a common anthropogenic impact that can alter both the structural (i.e., richness and density of communities) and functional (i.e., organic production) components of the ecosystem. River impoundments modify the landscape, transforming lotic ecosystems into large artificial lakes, which can have a profound impact on nutrient cycling and organic matter production, which can influence aquatic food webs (Ward and Stanford 1995; Poff et al. 1997; Nilsson 2005; Agostinho et al. 2008; Hoeinghaus et al. 2009). The construction of river dams leads to an increase in sedimentation rates, which has significant consequences for the ecosystem, with the retention of nutrients and organic and inorganic particulate matter in the area located upstream of the dam (Barbosa et al. 1999; Agostinho et al. 2007). Sedimentation can be increased in cascade reservoirs, which are a series of

---

*Correspondence: juliana.dias@ufrn.br

Associate editor: Jens Nejstgaard

Special Issue: Mesocosms: Bridging the Gap Between In-situ and Laboratory Studies. *Edited by Christopher Cornwall, Christian Pansch-Hattich, Maren Striebel, Jens Nejstgaard and Deputy Editors Julia C. Mullarney, Steeve Comeau, and Elisa Schaum.*

reservoirs constructed along a river, or under conditions of prolonged water residence time in the reservoir area. This can result in a reduction in sediment load, inorganic turbidity, and concentration of nutrients, such as phosphorus and nitrogen (Barbosa et al. 1999; Agostinho et al. 2007). As a result, reservoirs function as sinks for phosphorus within the ecosystem (Stockner et al. 2000) and are one of the primary causes of oligotrophication in aquatic ecosystems.

Cultural oligotrophication resulting from river impoundments is an emerging environmental impact that proves difficult to reverse in aquatic ecosystems, since it alters the trophic structure and dynamics of the system (Manca and Ruggiu 1998; Bergman et al. 1999; Jeppesen et al. 2005; Milbrink et al. 2011; Hartwich et al. 2012; Lorenz et al. 2019). Despite its importance, studies evaluating the effects of oligotrophication as a result of river impoundment on aquatic biodiversity remain scarce, and most of these studies were performed in temperate latitudes (Stockner et al. 2000; Ludsin et al. 2001; Matzinger et al. 2007; Hartwich et al. 2012).

Throughout the process of oligotrophication, bottom-up effects are expected within the food web. Reduced nutrient concentrations lead to diminished primary production, causing shifts in secondary production (Finger et al. 2007, 2013; Dias et al. 2017; de Melo et al. 2019; Braz et al. 2020), and affecting planktivorous, detritivorous, and piscivorous fish production (Ney 1996; Manca and Ruggiu 1998; Jeppesen et al. 2005; Anderson et al. 2005; Finger et al. 2007; Milbrink et al. 2011; Lorenz et al. 2019; dos Santos et al. 2020). Consequently, the herbivorous food web may be replaced by the microbial food web, which is longer and has reduced energy flow, leading to lower biomass at higher trophic levels (Anders and Ashley 2007). Therefore, alterations in the limnological conditions induced by damming can trigger strong bottom-up effects within the ecosystem, modifying the base of the food web up to the higher trophic levels. On the other hand, oligotrophication can also yield ecological benefits, particularly when eutrophic systems shift toward oligotrophic conditions. In such cases, positive impacts include improved water quality (Müller et al. 2014), reduced cyanobacterial dominance with an increase in eukaryotic algae (Cabrerizo et al. 2020), and enhanced fish production (Gerdeaux et al. 2006).

The issue of dam-induced oligotrophication becomes even more severe when downstream segments are regulated mainly by natural flood regimes that supply sediment and nutrients. This is particularly evident in floodplains, where the flood regime is the main structuring force (Junk et al. 1989; Neiff 1990; Humphries et al. 2024). The natural variability of water flow sustains habitats and environmental conditions essential for the aquatic biota within floodplains (Agostinho et al. 2007; Winemiller et al. 2016). This phenomenon has been widely demonstrated in the Upper Paraná River floodplain, where alterations in the water flow caused by an upstream reservoir led to changes in hydrodynamics and physical, chemical, and biological variables within the ecosystem (Abujanra et al. 2009; Fernandes et al. 2009; Roberto et al. 2009; Bonecker et al. 2013).

Long-term ecological research conducted at the Upper Paraná River floodplain has revealed severe alterations in the limnological variables following dam construction, including a notable increase in water transparency and a decrease in nutrient concentration (Roberto et al. 2009), as observed for other aquatic ecosystems (Straskraba 1990; Nilsson 2005). Limnological variables are directly related to the oligotrophication processes induced by dams. This is due to the blockage of sediment loads flowing downstream, affecting ecosystems (Bovo-Scomparin et al. 2013). Additionally, there has been a decrease in the diversity of phytoplankton and zooplankton species in the floodplain over time. This decline is primarily attributed to changes in water transparency and nutrient concentration (Agostinho et al. 2013; Bovo-Scomparin et al. 2013; Bonecker et al. 2013; Rodrigues et al. 2015). Such changes have important implications for the ecosystem, given their role as crucial food resources for small-bodied fish (Carniatto et al. 2012). They, consequently, influence the fish community as well.

Considering the ecological implications previously described, as a result of the river impoundment and decrease in nutrients in the floodplain, we conducted a mesocosm experiment to evaluate the effects of water transparency (measured by inorganic turbidity) and inorganic nutrient concentration (measured by nitrate and phosphate) on the specific growth rate (measured by weight variation) of a small-bodied fish species, *Moenkhausia forestii* Benine, Mariguela & Oliveira, 2009. We hypothesized that the current oligotrophic scenario of the Upper Paraná River floodplain (higher water transparency or lower inorganic turbidity and lower nutrient concentration) would reduce the fish-specific growth rate. We predicted that, given the current oligotrophic scenario, there would be lower phytoplankton biomass and zooplankton density, resulting in reduced resource availability and, consequently, a decrease in the fish growth rate. The environmental conditions simulated in our experiment were modeled to replicate those observed in the field data of the Paraná River during the long-term monitoring of this site over the past 30 years (Roberto et al. 2009). In this sense, we used the floodplain of the Paraná River as a model to assess the impact of oligotrophication caused by river impoundment on fish, simulating a real ecosystem in a manipulative experiment.

Material and methods

Ethics statement

Our study was carried out in compliance with the Ethics Committee on the use of animals in experimentation (protocol number 123/2010) and Brazilian legislation, including all required permissions from Biodiversity Authorization and Information System (SISBIO) and Chico Mendes Institute for Biodiversity Conservation (ICMBio) under protocol number

22442-1. Endangered or protected species were not included in our study.

Long-term ecological data of the upper Paraná River floodplain

The floodplain (22°30′–22°00′S, 53°00′–53°30′W) is situated in the upper segment of the Paraná River basin, which ranks as the second largest basin in South America in terms of both length and drainage area (Agostinho et al. 2007). This floodplain between the Porto Primavera and Itaipu reservoirs encompasses a 230 km non-dammed stretch of the Paraná River. It is an ecosystem of great importance for Brazilian biodiversity, harboring many endemic species and over 4500 plant and animal species (Agostinho et al. 2013). Furthermore, it plays a pivotal role in maintaining fish populations, which are largely absent from the upstream dammed stretches of the basin.

The oligotrophication process of the Upper Paraná River floodplain has been documented over the past 30 years through the long-term ecological research program conducted by Maringá State University (Roberto et al. 2009; Agostinho et al. 2013; Rodrigues et al. 2015). From1986 to 1988, the mean water transparency (measured by Secchi disk depth) was 1 m (± 0.5 SD), and total phosphorus was 27 μg L^{-1} (± 1.2 SD). Between 1992 and 1995, the mean water transparency was 1.4 m (± 0.4 SD), and the mean total phosphorus concentration was 16 μg L^{-1} (± 9 SD). After the construction of the Porto Primavera reservoir in 1998, the mean water transparency increased to 3.9 m (± 1.6 SD), whereas total phosphorus decreased to 11 μg L^{-1} (± 9 SD) (values taken between 2000 and 2012). Further details regarding the limnological variation of this floodplain can be found in earlier studies (Roberto et al. 2009; Agostinho et al. 2013; Rodrigues et al. 2015).

Experimental design

Our mesocosm experiment was conducted at the Nupelia Advanced Research Base, situated within the Upper Paraná River floodplain in Brazil. The experimental design consisted of three distinct treatments of inorganic turbidity (T1 = 15 NTU; T2 = 25 NTU; T3 = 35 NTU) combined with three treatments of inorganic nutrient concentration (N1 = 100 μg NO_3 L^{-1} and 5 μg PO_4 L^{-1}; N2 = 240 μg NO_3 L^{-1} and 12 μg PO_4 L^{-1}; N3 = 360 μg NO_3 L^{-1} and 18 μg PO_4 L^{-1}). These combinations resulted in nine treatments, each replicated three times, resulting in 27 mesocosms. These treatments were established based on field data from the environmental monitoring program (PIAP-LTER) to replicate realistic scenarios of past and present environmental conditions within the floodplain.

We designed our mesocosms to mimic natural communities. Each mesocosm consisted of polyethylene tanks (1.16 m in base diameter, 1.51 m in top diameter, 0.8 m high) with 1000 L of water. The mesocosms were filled with water sourced from the Paraná River (filtered through a plankton net 40 μm mesh) and added a combination of phytoplankton and zooplankton species from various lakes associated with the Paraná River. This was done to replicate the diverse planktonic communities found in nature, particularly in the floodplain lakes. Phytoplankton biomass and zooplankton densities were similar to those recorded in long-term ecological research studies in lakes within the Upper Paraná River floodplain (Lansac-Tôha et al. 2009; Roberto et al. 2009). Phytoplankton was collected using a 20-μm plankton net and direct water sampling from the lake to ensure representation of the entire community, including small algae species (< 20-μm) not retained by the net. Zooplankton was sampled using plankton nets of different mesh sizes (45-μm and 68-μm). Both phytoplankton and zooplankton species were acclimatized together in tanks similar to those of the experimental units for 3 d. In each tank, 30 adult individuals of *M. forestii* were added. We established this density based on fish samplings conducted in the floodplain lakes prior to the experiment while also accounting for a margin to compensate for potential individual losses during the experiment. The fish were captured using seine nets with a mesh size of 0.4 cm from aquatic macrophyte banks, then acclimatized for 1 week in tanks and fed with plankton. This species was selected due to its omnivorous feeding habit, showing a preference for invertebrates such as chironomid larvae, cladocerans, and copepods. However, it also consumes vegetal resources such as algae, albeit to a lesser extent (Quirino et al. 2017).

Our experiment was conducted over 24 d, from November 6th to November 29th, 2014. Inorganic turbidity was controlled by adding sterile clay, and submerged pumps were used to prevent sedimentation. Based on previous tests, in treatment T1, no clay was added, while in treatments T2 and T3, 20 g and 40 g of clay were added, respectively. Differences in nutrient concentrations were maintained by adding 1 mL (N1), 2.4 mL (N2), and 3.6 mL (N3) of a solution containing inorganic nutrients (80 g NO_3 L^{-1} and 4 g PO_4 L^{-1}) every 3 d to avoid depletion over time. The mix of phytoplankton and zooplankton species (10 L) was added to each tank at the beginning of the experiment. Thus, the initial mean biomass of phytoplankton (measured as chlorophyll *a*) was 24 μg L^{-1} (± 8 SD) and the initial mean density of crustacean zooplankton was 17 ind L^{-1} (± 7 SD) in each tank. No difference among treatments was found for the initial biomass of phytoplankton (ANOVA, turbidity treatment, $F_{2,0.08} = 0.21$, $p = 0.81$; nutrients treatment, $F_{2,0.59} = 1.62$, $p = 0.22$; interaction, $F_{4,0.82} = 1.13$, $p = 0.37$) and initial density of crustacean zooplankton (turbidity treatment, $F_{2,0.52} = 0.64$, $p = 0.54$; nutrients treatment, $F_{2,0.21} = 0.26$, $p = 0.78$; interaction, $F_{4,1.02} = 0.63$, $p = 0.65$). We used artificial macrophytes (around 15% coverage) to create zooplankton refuges in each mesocosm, maintaining the same amount of cover to simulate the natural environment.

During the experiment, the fish were not provided with external food sources to ensure their reliance on plankton as the primary food source. No additional food sources were introduced in the tanks. Dead fish were not replaced in the tanks during the experiment to prevent any influence on the results, considering that the objective was to assess the effects of inorganic turbidity and nutrients, along with the bottom-up effect.

Biological communities (phytoplankton, crustacean zooplankton, and fish) were analyzed at the experiment's beginning and end. All fish were individually weighted using a precision balance (nearest 0.01 g). Water samples were sampled to determine chlorophyll *a* concentrations, a proxy for phytoplankton biomass ($\mu g\ L^{-1}$). Chlorophyll *a* concentrations were determined by filtering aliquots of water on glass fiber filters (Whatman GF/ F), 90% acetone extraction, and reading in a spectrophotometer (663 nm). Zooplankton was sampled by filtering 10 L of water through a 45-μm plankton net and fixed using a calcium carbonate-buffered formaldehyde solution. Crustacean zooplankton density (expressed as ind L^{-1}) was estimated by sub-sampling with a Hensen–Stempell pipette (2.5 mL) in Sedgewick–Rafter chambers, with at least 10% of the concentrated sample being counted. Cladoceran and copepod species were identified using specialized taxonomic literature (*see* Lansac-Tôha et al. 2009 for details). Fish-specific growth rate, defined as the instantaneous growth rate per unit time (Wootton 1998), was calculated based on variations of fish mass before and after the experiment ($g = \ln P_d - \ln P_a/24$ d, where: P_d and P_a are the mass at the end and at the beginning of the experiment, respectively). It is important to evaluate fish growth rates, considering that it represents an estimate of secondary production, allowing an inference of fish stocks.

Daily measurements of turbidity (nearest 1 NTU), water temperature (nearest 0.1°C), dissolved oxygen concentration (nearest 0.1 mg L^{-1}), pH (nearest 0.1), and electric conductivity (nearest 0.1 $\mu S\ cm^{-1}$) were measured in each experimental unit using a multiparameter probe (HORIBA U-21). Water samples were obtained at the end of the experiment to determine the nitrate and phosphate concentrations (nearest 0.1 $\mu g\ L^{-1}$) (Roberto et al. 2009). These samples were obtained to assess if the inorganic nutrients were absorbed by the algae.

Data analysis

Two-factor PERMANOVAs were used to test statistical differences in the limnological variables (daily measurements) among treatments (inorganic turbidity and nutrients). In the first two-factor PERMANOVA, we used water temperature, dissolved oxygen concentration, pH, and conductivity as the response matrix. In addition, to verify significant differences in turbidity among treatments, we performed a second two-factor PERMANOVA using all the above-mentioned limnological variables further to the turbidity ($n = 648$ samples) as the matrix response. We used Euclidean dissimilarity measures for this analysis, and each variable was previously standardized to zero mean and unit variance. The response matrix was continuous, while the explanatory variables were categorical. The calculation of pseudo-*F* and *p* values was based on 4999 permutations.

We performed two-way ANOVAs to compare phytoplankton biomass, crustacean zooplankton density, and fish-specific growth rate among treatments: inorganic turbidity (three different levels—T1, T2, and T3), nutrients (three different levels—N1, N2, and N3), as well as their interaction. Phytoplankton biomass and crustacean zooplankton density used as response variables in two-way ANOVAs were defined as the variation of these variables before and after the experiment (end—beginning/24 d). The response variables were continuous, while the explanatory variables were categorical. Post hoc Tukey HSD tests were used to compare means when significant effects were found. We log-transformed ($\log_2 = x + a$, where x is the response variable and a is a constant added to x to eliminate the negative values) phytoplankton biomass to meet assumptions of homoscedasticity and normality, which were met. For zooplankton density and fish-specific growth rate, it was not necessary to transform the data to meet the assumptions.

All analyses were performed in the R environment (R Core Team 2023), using packages "vegan" (Oksanen et al. 2017) for PERMANOVA and "stats" (R Core Team 2023) for ANOVA and post hoc Tukey HSD tests. Graphs were generated using the ggplot2 package (Wickham 2016). A *p*-value < 0.05 was considered indicative of statistical significance.

Results

Water temperature, dissolved oxygen concentration, pH, and conductivity did not show significant differences among treatments for turbidity (PERMANOVA, pseudo-$F = 1.54$; $p = 0.194$), nutrients (PERMANOVA, pseudo-$F = 1.66$; $p = 0.165$), and their interaction (PERMANOVA, pseudo-$F = 0.59$; $p = 0.739$). However, when inorganic turbidity was included in the response matrix, significant differences were observed among treatments for turbidity (PERMANOVA, pseudo-$F = 48.56$; $p < 0.001$), nutrients (PERMANOVA, pseudo-$F = 11.01$; $p < 0.001$), and the interaction (PERMANOVA, pseudo-$F = 7.51$; $p < 0.01$). These results highlight the differences in inorganic turbidity among treatments throughout the experiment. Table 1 shows the results of limnological variables during the experiment. Mean values of nitrate concentrations at the end of the experiment were 4.6 $\mu g\ L^{-1}$ (± 0.6 SD) in N1, 4.0 $\mu g\ L^{-1}$ (± 0.2 SD) in N2, and 4.3 $\mu g\ L^{-1}$ (± 0.4 SD) in N3; while phosphate concentrations were 7.4 $\mu g\ L^{-1}$ (± 4.9 SD) in N1, 11.2 $\mu g\ L^{-1}$ (± 7.0 SD) in N2, and 9.4 $\mu g\ L^{-1}$ (± 7.7 SD) in N3. Inorganic nutrients were absorbed by algae, as evidenced by the final concentrations being lower than the concentrations added every 3 d in each treatment.

Phytoplankton biomass (measured by chlorophyll *a* concentration before and after the experiment) differs significantly among treatments for nutrients ($F_{2,26.51} = 8.52$, $p = 0.002$), with higher values of chlorophyll *a* found in the treatment with the

Table 1. Mean values (± standard deviation) of limnological variables measured daily for 24 d and chlorophyll *a* concentration at the end of the experiment in different treatments. N = nutrient treatments, T = inorganic turbidity treatments.

Treatments	Turbidity (NTU)	Temperature (°C)	pH	Conductivity (μS cm^{-1})	Dissolved oxygen (mg L^{-1})	Chlorophyll *a* (μg L^{-1})
T1 × N1	18.39 ± 7.97	25.15 ± 1.50	8.47 ± 0.48	57.06 ± 2.30	6.88 ± 0.77	30.87 ± 10.59
T1 × N2	16.24 ± 10.44	25.09 ± 1.54	8.60 ± 0.57	59.23 ± 2.16	6.92 ± 0.98	32.31 ± 10.25
T1 × N3	20.88 ± 9.94	25.13 ± 1.50	8.80 ± 0.50	60.49 ± 1.87	7.04 ± 0.91	61.25 ± 14.55
T2 × N1	21.96 ± 6.77	25.16 ± 1.58	8.33 ± 0.38	56.70 ± 2.12	6.65 ± 0.80	24.48 ± 13.98
T2 × N2	23.50 ± 8.81	25.12 ± 1.56	8.40 ± 0.52	58.34 ± 1.54	6.83 ± 0.82	31.63 ± 12.95
T2 × N3	33.13 ± 12.22	25.08 ± 1.59	8.47 ± 0.48	59.41 ± 1.67	6.57 ± 0.62	58.22 ± 31.16
T3 × N1	28.98 ± 8.84	25.23 ± 1.50	8.35 ± 0.46	56.86 ± 1.66	6.51 ± 0.83	13.35 ± 2.78
T3 × N2	34.15 ± 11.04	25.13 ± 1.53	8.55 ± 0.67	55.97 ± 2.20	7.18 ± 0.20	38.01 ± 7.73
T3 × N3	33.16 ± 9.91	25.16 ± 1.64	8.51 ± 0.56	57.74 ± 1.49	6.55 ± 0.92	48.42 ± 10.15

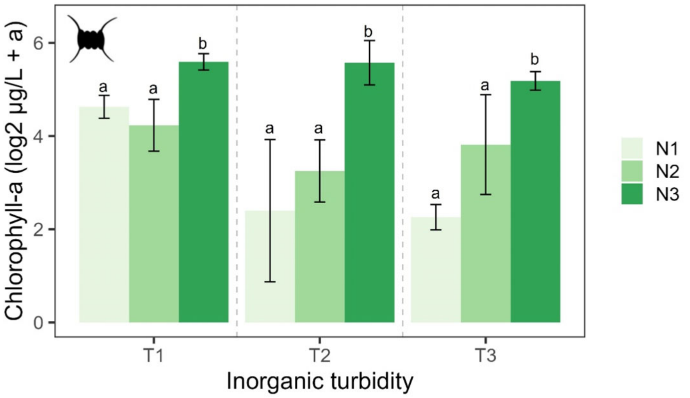

Fig. 1. Mean and standard error of the variation in phytoplankton biomass (difference between end and beginning chlorophyll *a* concentrations) after 24 d of the experimental conditions. Chlorophyll *a* concentrations are expressed as $\log_2(x + a)$, where x represents the response variable and a (= 13) is a constant added to prevent negative values. Different letters indicate significant differences among nutrient treatments (Tukey's HSD test < 0.05).

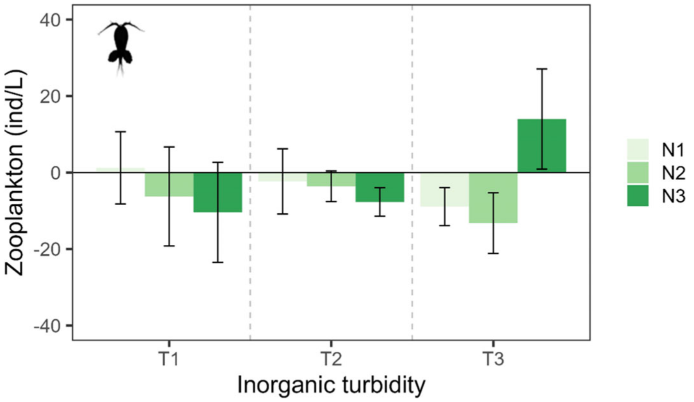

Fig. 2. Mean and standard error of variation in crustacean zooplankton density (difference between end and beginning) in different treatments after 24 d of the experimental conditions.

highest nutrient concentrations and lower values of chlorophyll *a* in the treatments with the lowest nutrient values (Tukey's HSD test < 0.05; Fig. 1). However, the turbidity treatments and the interaction between turbidity and nutrients had no significant effect on phytoplankton biomass (turbidity, $F_{2,6.88} = 2.21$, $p = 0.138$; interaction, $F_{4,5.50} = 0.88$, $p = 0.493$).

We identified a total of 21 species of crustacean zooplankton (7 cladoceran and 14 copepod species) in our experiment (Table S1). Mean zooplankton density before and after the experiment (17.5 ± 7.8 and 13.3 ± 13.2 ind L^{-1}, respectively) was consistent with those found in nature at the same floodplain lakes in 2000–2012 (6.9 ind L^{-1} ± 10.3 SD). In general, most treatments showed reduced zooplankton density at the end of the experimental conditions. Zooplankton density (variation before and after the experiment) did not differ among treatments (turbidity, $F_{2,1.08} = 0.43$, $p = 0.657$; nutrients, $F_{2,0.58} = 0.23$, $p = 0.796$; interaction, $F_{4,4.88} = 0.97$, $p = 0.447$). However, the higher zooplankton density was registered in the treatment with higher turbidity and nutrient concentration (Fig. 2).

Fish mass decreased in all treatments compared to the beginning of the experiment, and the maximum mortality rate per treatment was 2.22% (six fish per treatment, considering the three replicates) (Table 2). We observed a significant interaction between inorganic turbidity and nutrients on the fish growth rate (Table 3). The most pronounced reduction in fish growth rate was observed in treatments T1N3 and T3N1. These treatments differed significantly from T2N3 and T3N3 (Tukey's HSD test < 0.05), which exhibited the smallest reductions in growth rate over the course of the experiment. No significant differences were detected among the remaining treatments (Tukey's HSD test > 0.05) (Fig. 3).

Discussion

Our experiment revealed a significant interaction effect of inorganic turbidity and nutrient concentration on the specific growth rate of small-bodied fish. This suggests that the effects of nutrients on fish growth rates change with increasing inorganic turbidity. The most pronounced reduction in fish growth rates occurred in treatments with lower turbidity and highest nutrient concentration (T1N3) and higher turbidity and lowest nutrient concentration (T3N1). The interaction effect between inorganic turbidity and nutrient concentration on fish-specific growth rate is expected. Inorganic turbidity reduces light availability in the water column, thereby inhibiting or diminishing phytoplankton productivity (Finger et al. 2007, 2013; Bovo-Scomparin et al. 2013; Rodrigues et al. 2015), which may be aggravated when nutrient concentrations are low. This was corroborated in our experiment, considering that the lowest values of phytoplankton biomass were registered at the treatment T3N1, concomitantly with the low zooplankton density and lower fish growth rate. In this case, limitation of plankton food resources may explain the greater decrease in fish growth rate. Light attenuation caused by turbidity of allochthonous origin was considered the main cause of low productivity in an oligotrophic lake (Finger et al. 2007). This increase in inorganic turbidity and subsequent reduction in light availability can negatively impact fish foraging by reducing their ability to detect prey (Figueiredo et al. 2020; Ranåker et al. 2012; Turesson and Brönmark 2007). Furthermore, this reduction in prey detection can affect fish growth rates, as observed in our study. A recent meta-analysis study confirms that turbidity can negatively affect the prey capture rates of aquatic predators, regardless of their visual ability or body size (Ortega et al. 2020).

Low fish growth rates registered at the treatment with lower turbidity and higher nutrient concentration (T1N3) can be explained by turbidity caused by an increase in phytoplankton (organic turbidity) on fish foraging. In organic turbidity, the decrease in light availability, which can reduce the visual field of fishes and their foraging abilities, is primarily due to the absorption of wavelengths by phytoplankton, whereas in inorganic turbidity, it mainly occurs through scattering and deflection of light (Kirk 1985; Figueiredo et al. 2020). Organic turbidity can negatively affect fish foraging more than inorganic turbidity (e.g., Ranåker et al. 2012; Wellington et al. 2010). In a microcosm experiment also using *M. forestii*, Figueiredo et al. (2020) demonstrated that both organic and inorganic turbidity could negatively affect fish foraging. In our experiment,

Table 3. Output of factorial ANOVA for fish-specific growth rates (g) among experimental treatments. df = degrees of freedom. SS = sum of square. MS = mean square. Significant *p*-values (< 0.05) are indicated in bold.

	df	SS	MS	*F*-value	*p*-value
Turbidity	2	0.004	0.002	3.45	0.054
Nutrients	2	0.002	0.001	1.65	0.219
Turbidity × nutrients	4	0.010	0.003	3.95	**0.018**
Error	18	0.012	0.001	–	–

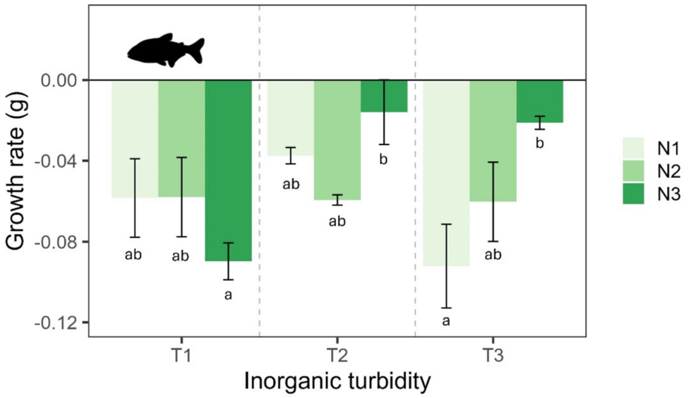

Fig. 3. Mean and standard error of fish specific growth rates of *Moenkhausia forestii* species in experimental treatments. Different letters indicate significant differences among treatments (Tukey's HSD test < 0.05).

Table 2. Mean values and standard deviation (SD) of the weight of *Moenkhausia forestii* before and after 24 d of the experimental conditions, number of fish (*n*), and mortality rate per treatment. N = nutrient treatments, T = inorganic turbidity treatments.

	Before			After			
Treatments	Weight (g)	SD	*n*	Weight (g)	SD	*n*	Mortality (%)
T1 × N1	0.77	0.03	90	0.72	0.01	84	2.22
T1 × N2	0.77	0.00	90	0.73	0.02	86	1.48
T1 × N3	0.80	0.02	90	0.73	0.02	89	0.37
T2 × N1	0.77	0.01	90	0.74	0.01	89	0.37
T2 × N2	0.80	0.07	90	0.75	0.07	90	0.00
T2 × N3	0.73	0.03	90	0.72	0.03	90	0.00
T3 × N1	0.81	0.03	90	0.74	0.02	90	0.00
T3 × N2	0.76	0.03	90	0.71	0.04	88	0.74
T3 × N3	0.78	0.02	90	0.76	0.02	90	0.00

phytoplankton biomass (measured by chlorophyll *a* concentration) was significantly higher in treatments with highest nutrient concentrations and was different from the other treatments (Table 1; Fig. 1).

An alternative explanation for the lowest fish growth rate in T1N3 treatment is a possible effect of resource availability (nutrients and light) on the increase in phytoplankton dominance. The theory of resource competition proposed by Tilman (Tilman 1982) suggests that a decrease in species diversity occurs when only a few species dominate, reducing the availability of resources. However, in the absence of resource limitation, some species may be favored and show an increase in density and biomass (Tilman 1977; Rothhaupt 1988; Dittrich et al. 2023). Despite the higher phytoplankton biomass registered in this treatment, the increase in water transparency (Interlandi and Kilham 2001; Flöder et al. 2002; Bovo-Scomparin et al. 2013; Rodrigues et al. 2015) and nutrient concentrations (Cottingham et al. 2004; Šorf et al. 2015) may have a negative effect on phytoplankton diversity (Smith et al. 2006; Elser et al. 2007), thus decreasing the heterogeneity of food resources for the other trophic levels. Therefore, the lower resource heterogeneity reduced density (zooplankton) and growth rate (fish) of the other trophic levels.

Intermediate levels of inorganic turbidity and higher nutrient concentrations (T2N3) favored a smaller reduction in the fish growth rate, contradicting our expectation that this rate would be higher in higher turbidity and nutrient concentration (T3N3). However, no significant differences were observed between T2N3 and T3N3 treatments (Tukey's HSD test > 0.05). One possible explanation is that besides decreasing light penetration, high inorganic turbidity may also be responsible for a decrease in predation rates because it reduces predator–prey encounter rates and serves as a visual refuge for planktonic organisms (De Robertis et al. 2003; Carter et al. 2010; Ortega et al. 2020). Studies have shown a reduction in prey capture rates with increasing turbidity, both under experimental conditions (De Robertis et al. 2003; Carter et al. 2010) with turbidity values (0–40 NTU) similar to those in our experiment (15–35 NTU) and through a meta-analytic approach (Ortega et al. 2020) that considers a broad range of turbidity variation. Thus, changes in predation rates may have favored the lower growth rate in high turbidity levels compared to the intermediate level. In experimental mesocosms, Figueiredo et al. (2015) showed that slight variations in turbidity levels, as those observed in our experiment (approximately 20 NTU), were not sufficient to change predation rates. On the other hand, the authors used larger-sized prey (ostracods) compared to planktonic organisms. However, these authors found that higher inorganic turbidity concentrations decreased predation rates.

Fish growth rate was negative across all treatments. One possible explanation for this result is potential stress induced by experimental conditions or by fish overpopulation combined with the fact that fish only had access to zooplankton. The absence of top predators in our experiment allows us to infer that the observed effect on fish-specific growth rate may be attributed to the environmental conditions maintained during the experimental period.

Phytoplankton is usually one of the first aquatic communities to react to environmental changes, and an increase in nutrient concentration favors their rapid growth and reproduction (Pan et al. 2014), enhancing their density, biomass, and primary productivity. Nutrient limitation otherwise negatively affects phytoplankton and declines energy transfer to higher trophic levels via bottom-up control (Van Donk 1997; Perhar et al. 2013; Pan et al. 2014). This can result in a loss of ecosystem services, such as fish production. Moreover, oligotrophic conditions could lead to a shift from the traditional short herbivorous food web to a longer microbial loop, characterized by a greater number of trophic levels and, therefore, lower energy transfer efficiency, affecting the higher trophic levels (Anders and Ashley 2007).

Although non-significant, zooplankton density reflected the environmental conditions present in the floodplain before reservoir construction (higher turbidity and nutrient concentrations). Under oligotrophic conditions, zooplankton productivity may decline due to food resource limitations (Finger et al. 2007). The non-significant differences observed for zooplankton density among treatments may possibly be attributed to fish predation pressure. Although the effect of predation was not controlled in our experiment (as it was not the primary goal), the zooplankton size structure was smaller in the treatments with higher transparency (data published in Braz et al. 2020 for the same experiment). This result supports the potential predation effect, as increased water transparency enhances the visual range of fish (Bramm et al. 2009). Intense predation can reduce the size structure of zooplankton (Brooks and Dodson 1965). Fish predation is an important factor influencing the zooplankton community, interfering both with population (body size and reproductive rates) and community attributes (biomass, density, and species diversity) (Iglesias et al. 2011, 2017).

The current scenario of environmental conditions in the last non-dammed stretch of the Paraná River is concerning. Cascade reservoir construction at the Paraná River basin has promoted profound alterations in biotic and abiotic variables through time (Fernandes et al. 2009; Roberto et al. 2009; Bovo-Scomparin et al. 2013; Bonecker et al. 2013; Rodrigues et al. 2015) and these alterations were intensified after the closure of Porto Primavera reservoir (Agostinho et al. 2004; Bonecker et al. 2009), which is closer to the floodplain. Fish density and richness in the floodplain located downstream of the Porto Primavera reservoir have significantly decreased since its closure (Agostinho et al. 2004, 2007; Fernandes et al. 2009). Impoundment of rivers is among the main anthropogenic causes of oligotrophication in aquatic ecosystems (Ney 1996; Stockner et al. 2000), and it is a process that is difficult to reverse or restore.

Few studies have investigated the effects of oligotrophication on higher trophic levels, such as fish (Jeppesen et al. 2005; Anderson et al. 2005; Matzinger et al. 2007; Milbrink et al. 2011; Lorenz et al. 2019). Our experiment evaluated the effects of inorganic turbidity and nutrients, coincident with the current scenario of oligotrophication at the last non-dammed stretch of the Paraná River and conditions present before Porto Primavera reservoir construction, on specific growth rates of small-bodied fish. Our hypothesis that the current oligotrophic scenario of the Upper Paraná River floodplain (higher water transparency or lower inorganic turbidity and lower nutrient concentration) would reduce fish-specific growth rate was not completely accepted. Intermediate and higher turbidity combined with higher nutrients (T2N3 and T3N3) favor a small reduction in the growth rate of *M. forestii*. It is expected that this result may be attributed to bottom-up mechanisms, influenced by higher food availability (plankton) in turbid and productive environments (Cottingham et al. 2004; Jeppesen et al. 2005; Anderson et al. 2005; Matzinger et al. 2007; Finger et al. 2013; Lorenz et al. 2019). In addition, we observed that the effects of nutrients on growth rate change with the increase in inorganic turbidity. This result has important consequences for higher trophic levels. In tropical and subtropical regions, fish communities are dominated by omnivorous, small-bodied species (Iglesias et al. 2011, 2017), which constitute an essential food resource for piscivorous fish. Consequently, alterations in environmental conditions mediated by bottom-up mechanisms may be responsible for a decrease in fish production and a consequent effect on fish stocks, reflected in economic, cultural, and social activities.

We observed the impacts of inorganic turbidity and nutrients on the growth rate of fish in a large dammed river in the tropical region. However, it is important to highlight that not all oligotrophication processes are negative for the aquatic ecosystem. In eutrophic systems that became oligotrophic, nutrient reduction and transparency increase can have positive impacts on fish species (Ludsin et al. 2001; Gerdeaux et al. 2006; Müller et al. 2014; Cabrerizo et al. 2020).

Our findings support previous studies that used time-series data. While manipulative experiments are prone to errors, since they usually cannot replicate all environmental conditions, our experiment aimed to replicate real scenario conditions related to the most crucial variables (nutrient concentration and turbidity) in order to achieve greater accuracy. Furthermore, experiments contribute to answering specific and direct hypotheses.

Our research indicates that changes in nutrient concentrations and water transparency, coinciding with the effects of river dams, can lead to a scarcity of plankton downstream, resulting in reduced fish growth. Long-term monitoring data (Agostinho et al. 2013; Bovo-Scomparin et al. 2013; Bonecker et al. 2013; Rodrigues et al. 2015) evidence our main results. These findings underscore the critical importance of conservation efforts to address the detrimental impact of oligotrophication on the preservation and sustainable functioning of affected aquatic ecosystems.

Author Contributions

Juliana Deo Dias: Conceptualization, methodology, validation, formal analysis, investigation, resources, data curation, writing – original draft, writing – review and editing, visualization, project administration, funding acquisition. Nadson Ressye Simões: Conceptualization, methodology, validation, formal analysis, writing – original draft, writing – review and editing, visualization. Claudia Costa Bonecker: Conceptualization, methodology, validation, resources, writing – original draft, writing – review and editing, visualization. Angelo Antonio Agostinho: Conceptualization, methodology, validation, resources, writing – original draft, writing – review and editing, visualization, supervision, funding acquisition.

Acknowledgments

We thank Kirk Winemiller and Luiz C. Gomes for their valuable suggestions. Juliana Deo Dias is grateful for CNPq post-doctoral scholarships (Process 560380/2010-0) and Claudia Costa Bonecker, Nadson Ressye Simões, and Angelo Antonio Agostinho for a productivity scholarship. We thank CNPq for financial support for the "Long-Term Ecological Research Program." We would like to thank B. T. Segovia, F. E. Amadeo, D. C. Amaral, T. X. Melo, A. Pineda, J. D. Latini, S. Rodrigues, and V. A. Capatti for invaluable help in the field and support while conducting the experiment. We also thank J. E. M. Braz for help with the laboratory analyses of the zooplankton. The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Conflicts of Interest

None declared.

Data Availability Statement

Data are available upon request.

References

Abujanra, F., A. Agostinho, and N. Hahn. 2009. "Effects of the Flood Regime on the Body Condition of Fish of Different Trophic Guilds in the Upper Paraná River Floodplain, Brazil." *Brazilian Journal of Biology* 69: 459–468. https://doi.org/10.1590/S1519-69842009000300003.

Agostinho, A. A., L. C. Gomes, C. C. Bonecker, and S. M. Thomaz. 2013. "Padrões de variação de longo prazo na planície de inundação do alto rio Paraná." In PELD—CNPq Dez anos do programa de pesquisas ecológicas de longa duração no Brasil: achados, lições e perspectivas, edited by M. Tabarelli, J. D. Hay, S. F. Ferrari, and L. A. Martinelli, 163–194. Editora Universitaria da UFPE.

Agostinho, A. A., F. M. Pelicice, and L. C. Gomes. 2008. "Dams and the Fish Fauna of the Neotropical Region: Impacts and Management Related to Diversity and Fisheries." *Brazilian Journal of Biology* 68: 1119–1132. https://doi.org/10.1590/S1519-69842008000500019.

Agostinho, A. A., F. M. Pelicice, A. C. Petry, L. C. Gomes, and H. F. Júlio. 2007. "Fish Diversity in the Upper Paraná River Basin: Habitats, Fisheries, Management and Conservation." *Aquatic Ecosystem Health and Management* 10: 174–186. https://doi.org/10.1080/14634980701341719.

Agostinho, A. A., S. M. Thomaz, and L. C. Gomes. 2004. "Threats for Biodiversity in the Floodplain of the Upper Paraná River: Effects of Hydrological Regulation by Dams." *Ecohydrology and Hydrobiology* 4: 255–256. http://repositorio.uem.br:8080/jspui/bitstream/1/5287/1/242.pdf.

Anders, P. J., and K. I. Ashley. 2007. "The Clear-Water Paradox of Aquatic Ecosystem Restoration." *Fisheries* 32: 125–128. https://doi.org/10.1577/1548-8446(2007)32[125:TWPOAE]2.0.CO;2.

Anderson, J. N., E. Jeppesen, and M. Sondergaard. 2005. "Ecological Effects of Reduced Nutrient Loading (Oligotrophication) on Lakes: An Introduction." *Freshwater Biology* 50: 1589–1593. https://doi.org/10.1111/j.1365-2427.2005.01433.x.

Barbosa, F. A. R., J. Padisák, E. L. G. Espindola, G. Borics, and O. Rocha. 1999. "The Cascading Reservoir Continuum Concept (CRCC) and Its Application to the River Tietê Basin, São Paulo State, Brazil." In Theoretical Reservoir Ecology and its Applications, edited by M. Tundisi and J. G. Straskaba, 425–437. International Institute of Ecology.

Bergman, E., L.-A. Hansson, A. Persson, et al. 1999. "Synthesis of Theoretical and Empirical Experiences From Nutrient and Cyprinid Reductions in Lake Ringsjön." *Hydrobiologia* 404: 145–156. https://doi.org/10.1023/A:1003788900521.

Bonecker, C. C., A. S. M. Aoyagui, and R. M. Santos. 2009. "The Impact of Impoundment on the Rotifer Communities in Two Tropical Floodplain Environments : Interannual Pulse Variations." *Brazilian Journal of Biology* 69: 529–537. https://doi.org/10.1590/S1519-69842009000300008.

Bonecker, C. C., N. R. Simões, C. V. Minte-Vera, F. A. Lansac-Tôha, L. F. M. Velho, and A. A. Agostinho. 2013. "Temporal Changes in Zooplankton Species Diversity in Response to Environmental Changes in an Alluvial Valley." *Limnologica* 43: 114–121. https://doi.org/10.1016/j.limno.2012.07.007.

Bovo-Scomparin, V. M., S. Train, and L. C. Rodrigues. 2013. "Influence of Reservoirs on Phytoplankton Dispersion and Functional Traits: a Case Study in the Upper Paraná River, Brazil." *Hydrobiologia* 702: 115–127. https://doi.org/10.1007/s10750-012-1313-8.

Bramm, M. E., M. K. Lassen, L. Liboriussen, K. Richardson, M. Ventura, and E. Jeppesen. 2009. "The Role of Light for Fish-Zooplankton–Phytoplankton Interactions During Winter in Shallow Lakes—A Climate Change Perspective." *Freshwater Biology* 54: 1093–1109. https://doi.org/10.1111/j.1365-2427.2008.02156.x.

Braz, J. E. M., J. D. Dias, C. C. Bonecker, and N. R. Simões. 2020. "Oligotrophication Affects the Size Structure and Potential Ecological Interactions of Planktonic Microcrustaceans." *Aquatic Sciences* 82: 59. https://doi.org/10.1007/s00027-020-00733-z.

Brooks, J. L., and S. I. Dodson. 1965. "Predation, Body Size, and Composition of Plankton." *Science* 150, no. 80: 28–35. https://doi.org/10.1126/science.150.3692.2.

Cabrerizo, M. J., M. I. Álvarez-Manzaneda, E. León-Palmero, et al. 2020. "Warming and CO_2 Effects Under Oligotrophication on Temperate Phytoplankton Communities." *Water Research* 173: 115579. https://doi.org/10.1016/j.watres.2020.115579.

Carniatto, N., R. Fugi, G. Cantanhêde, É. A. Gubiani, and N. S. Hahn. 2012. "Effects of Flooding Regime and Diel Cycle on Diet of a Small Sized Fish Associated to Macrophytes." *Acta Limnologica Brasiliensia* 24: 363–372. https://doi.org/10.1590/S2179-975X2013005000007.

Carter, M. W., D. E. Shoup, J. M. Dettmers, and D. H. Wahl. 2010. "Effects of Turbidity and Cover on Prey Selectivity of Adult Smallmouth Bass." *Transactions of the American Fisheries Society* 139: 353–361. https://doi.org/10.1577/T08-159.1.

Cottingham, K. L., S. Glaholt, and A. C. Brown. 2004. "Zooplankton Community Structure Affects How Phytoplankton Respond to Nutrient Pulses." *Ecology* 85: 158–171. https://doi.org/10.1890/02-0570.

de Melo, T. X., J. D. Dias, N. R. Simões, and C. C. Bonecker. 2019. "Effects of Nutrient Enrichment on Primary and Secondary Productivity in a Subtropical Floodplain System: An Experimental Approach." *Hydrobiologia* 827: 171–181. https://doi.org/10.1007/s10750-018-3763-0.

De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. "Differential Effects of Turbidity on Prey Consumption of Piscivorous and Planktivorous Fish." *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1517–1526. https://doi.org/10.1139/f03-123.

Dias, J. D., M. R. Miracle, and C. C. Bonecker. 2017. "Do Water Levels Control Zooplankton Secondary Production in Neotropical Floodplain Lakes?" *Fundamental and Applied Limnology* 190: 49–62. https://doi.org/10.1127/fal/2017/0869.

Dittrich, J., J. D. Dias, A. C. M. Paula, and A. A. Padial. 2023. "Experimental Nutrient Enrichment Increases Plankton Taxonomic and Functional Richness and Promotes Species Dominance Overtime." *Hydrobiologia* 850: 4029–4048. https://doi.org/10.1007/s10750-023-05285-5.

dos Santos, N. C. L., R. M. Dias, D. C. Alves, et al. 2020. "Trophic and Limnological Changes in Highly Fragmented Rivers Predict the Decreasing Abundance of Detritivorous Fish." *Ecological Indicators* 110: 105933. https://doi.org/10.1016/j.ecolind.2019.105933.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, et al. 2007. "Global Analysis of Nitrogen and Phosphorus Limitation of Primary Producers in Freshwater, Marine and Terrestrial Ecosystems." *Ecology Letters* 10: 1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x.

Fernandes, R., A. Agostinho, E. Ferreira, et al. 2009. "Effects of the Hydrological Regime on the Ichthyofauna of Riverine Environments of the Upper Paraná River Floodplain." *Brazilian Journal of Biology* 69: 669–680. https://doi.org/10.1590/S1519-69842009000300021.

Figueiredo, B. R. S., R. V. Granzotti, L. F. Fiori, C. L. Nieman, and E. Benedito. 2020. "Cascading Effects of Predation Risk Under High Organic and Inorganic Turbidity: Impacts on Individuals and Shoals of a Mesopredator Fish." *Aquatic Ecology* 54: 855–868. https://doi.org/10.1007/s10452-020-09782-w.

Figueiredo, B. R. S., R. P. Mormul, and E. Benedito. 2015. "Structural Complexity and Turbidity Do Not Interact to Influence Predation Rate and Prey Selectivity by a Small Visually Feeding Fish." *Marine and Freshwater Research* 66: 170. https://doi.org/10.1071/MF14030.

Finger, D., M. Schmid, and A. Wüest. 2007. "Comparing Effects of Oligotrophication and Upstream Hydropower Dams on Plankton and Productivity in Perialpine Lakes." *Water Resources Research* 43: 2007WR005868. https://doi.org/10.1029/2007WR005868.

Finger, D., A. Wüest, and P. Bossard. 2013. "Effects of Oligotrophication on Primary Production in Peri-Alpine Lakes." *Water Resources Research* 49: 4700–4710. https://doi.org/10.1002/wrcr.20355.

Flöder, S., J. Urabe, and Z. Kawabata. 2002. "The Influence of Fluctuating Light Intensities on Species Composition and Diversity of Natural Phytoplankton Communities." *Oecologia* 133: 395–401. https://doi.org/10.1007/s00442-002-1048-8.

Gerdeaux, D., O. Anneville, and D. Hefti. 2006. "Fishery Changes during re-Oligotrophication in 11 Peri-Alpine Swiss and French Lakes Over the Past 30 Years." *Acta Oecologica* 30: 161–167. https://doi.org/10.1016/j.actao.2006.02.007.

Hartwich, M., D. Martin-Creuzburg, K. O. Rothhaupt, and A. Wacker. 2012. "Oligotrophication of a Large, Deep Lake Alters Food Quantity and Quality Constraints at the Primary Producer-Consumer Interface." *Oikos* 121: 1702–1712. https://doi.org/10.1111/j.1600-0706.2011.20461.x.

Hoeinghaus, D. J., A. A. Agostinho, L. C. Gomes, et al. 2009. "Effects of River Impoundment on Ecosystem Services of Large Tropical Rivers: Embodied Energy and Market Value of Artisanal Fisheries." *Conservation Biology* 23: 1222–1231. https://doi.org/10.1111/j.1523-1739.2009.01248.x.

Humphries, P., E. Wohl, A. A. Agostinho, et al. 2024. "Flood Ecology." *Bioscience* 74: biae038. https://doi.org/10.1093/biosci/biae038.

Iglesias, C., N. Mazzeo, M. Meerhoff, et al. 2011. "High Predation Is of Key Importance for Dominance of Small-Bodied Zooplankton in Warm Shallow Lakes: Evidence From Lakes, Fish Exclosures and Surface Sediments." *Hydrobiologia* 667: 133–147. https://doi.org/10.1007/s10750-011-0645-0.

Iglesias, C., M. Meerhoff, L. S. Johansson, et al. 2017. "Stable Isotope Analysis Confirms Substantial Differences Between Subtropical and Temperate Shallow Lake Food Webs." *Hydrobiologia* 784: 111–123. https://doi.org/10.1007/s10750-016-2861-0.

Interlandi, S. J., and S. S. Kilham. 2001. "Limiting Resources and the Regulation of Diversity in Phytoplankton Communities." *Ecology* 82: 1270. https://doi.org/10.2307/2679988.

Jeppesen, E., J. P. Jensen, M. Søndergaard, and T. L. Lauridsen. 2005. "Response of Fish and Plankton to Nutrient Loading Reduction in Eight Shallow Danish Lakes With Special Emphasis on Seasonal Dynamics." *Freshwater Biology* 50: 1616–1627. https://doi.org/10.1111/j.1365-2427.2005.01413.x.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. "The Flood-Pulse Concept in River-Floodplain Systems." In Proceedings of the International Large River Symposium (LARS), edited by D. P. Dodge, 110–127. Canadian Special Publication of Fisheries and Aquatic Sciences.

Kirk, J. T. O. 1985. "Effects of Suspensoids (Turbidity) on Penetration of Solar Radiation in Aquatic Ecosystems." *Hydrobiologia* 125: 195–208. https://doi.org/10.1007/BF00045935.

Lansac-Tôha, F., C. Bonecker, L. Velho, et al. 2009. "Biodiversity of Zooplankton Communities in the Upper Paraná River Floodplain: Interannual Variation from Long-Term Studies." *Brazilian Journal of Biology* 69: 539–549. https://doi.org/10.1590/S1519-69842009000300009.

Lorenz, P., G. Trommer, and H. Stibor. 2019. "Impacts of Increasing Nitrogen : Phosphorus Ratios on Zooplankton Community Composition and Whitefish (*Coregonus macrophthalmus*) Growth in a Pre-Alpine Lake." *Freshwater Biology* 64: 1210–1225. https://doi.org/10.1111/fwb.13296.

Ludsin, S. A., M. W. Kershner, K. A. Blocksom, R. L. Knight, and S. A. Roy. 2001. "Life After Death in Lake Erie: Nutrient Controls Drive Fish Species Richness, Rehabilitation." *Ecological Applications* 11: 731–746. https://doi.org/10.1890/1051-0761(2001)011[0731:LADILE]2.0.CO;2.

Manca, M., and D. Ruggiu. 1998. "Consequences of Pelagic Food-Web Changes During a Long-Term Lake Oligotrophication Process." *Limnology and Oceanography* 43: 1368–1373. https://doi.org/10.4319/lo.1998.43.6.1368.

Matzinger, A., R. Pieters, K. I. Ashley, G. a. Lawrence, and A. WÜest. 2007. "Effects of Impoundment on Nutrient

Availability and Productivity in Lakes." *Limnology and Oceanography* 52: 2629–2640. https://doi.org/10.4319/lo.2007.52.6.2629.

Milbrink, G., T. Vrede, L. J. Tranvik, and E. Rydin. 2011. "Large-Scale and Long-Term Decrease in Fish Growth Following the Construction of Hydroelectric Reservoirs." *Canadian Journal of Fisheries and Aquatic Sciences* 68: 2167–2173. https://doi.org/10.1139/f2011-131.

Müller, B., R. Gächter, and A. Wüest. 2014. "Accelerated Water Quality Improvement During Oligotrophication in Peri-Alpine Lakes." *Environmental Science & Technology* 48, no. 12: 6671–6677. https://doi.org/10.1021/es4040304.

Neiff, J. J. 1990. "Ideas para la interpretacion ecologica del Parana." *Interciencia* 15: 424–441.

Ney, J. J. 1996. "Oligotrophication and Its Discontents: Effects of Reduced Nutrient Loading on Reservoir Fisheries." *American Fisheries Society Symposium* 16: 285–295.

Nilsson, C. 2005. "Fragmentation and Flow Regulation of the World's Large River Systems." *Science* 308: 405–408. https://doi.org/10.1126/science.1107887.

Oksanen, J., F. G. Blanchet, M. Friendly, et al. 2017. "*Package 'vegan'*." Community Ecology Package https://doi.org/10.1016/j.stemcr.2017.10.016.

Ortega, J. C. G., B. R. S. Figueiredo, W. J. da Graça, A. A. Agostinho, and L. M. Bini. 2020. "Negative Effect of Turbidity on Prey Capture for Both Visual and Non-Visual Aquatic Predators." *Journal of Animal Ecology* 89: 2427–2439. https://doi.org/10.1111/1365-2656.13329.

Pan, Y., Y. Zhang, and S. Sun. 2014. "Phytoplankton–Zooplankton Dynamics Vary with Nutrients: a Microcosm Study With the Cyanobacterium Coleofasciculus Chthonoplastes and Cladoceran Moina Micrura." *Journal of Plankton Research* 36: 1323–1332. https://doi.org/10.1093/plankt/fbu057.

Perhar, G., G. B. Arhonditsis, and M. T. Brett. 2013. "Modeling Zooplankton Growth in Lake Washington: A Mechanistic Approach to Physiology in a Eutrophication Model." *Ecological Modelling* 258: 101–121. https://doi.org/10.1016/j.ecolmodel.2013.02.024.

Poff, N. L., J. D. Allan, M. B. Bain, et al. 1997. "The Natural Flow Regime." *Bioscience* 47: 769–784. https://doi.org/10.2307/1313099.

Quirino, B. A., N. Carniatto, R. Guglielmetti, and R. Fugi. 2017. "Changes in Diet and Niche Breadth of a Small Fish Species in Response to the Flood Pulse in a Neotropical Floodplain Lake." *Limnologica* 62: 126–131. https://doi.org/10.1016/j.limno.2016.10.005.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Ranåker, L., M. Jönsson, P. A. Nilsson, and C. Brönmark. 2012. "Effects of Brown and Turbid Water on Piscivore–Prey Fish Interactions Along a Visibility Gradient." *Freshwater Biology* 57: 1761–1768. https://doi.org/10.1111/j.1365-2427.2012.02836.x.

Roberto, M., N. Santana, and S. Thomaz. 2009. "Limnology in the Upper Paraná River Floodplain: Large-Scale Spatial and Temporal Patterns, and the Influence of Reservoirs." *Brazilian Journal of Biology* 69: 717–725. https://doi.org/10.1590/S1519-69842009000300025.

Rodrigues, L. C., N. R. Simões, V. M. Bovo-Scomparin, et al. 2015. "Phytoplankton Alpha Diversity as an Indicator of Environmental Changes in a Neotropical Floodplain." *Ecological Indicators* 48: 334–341. https://doi.org/10.1016/j.ecolind.2014.08.009.

Rothhaupt, K. O. 1988. "Mechanistic Resource Competition Theory Applied to Laboratory Experiments With Zooplankton." *Nature* 333: 660–662. https://doi.org/10.1038/333660a0.

Smith, V. H., S. B. Joye, and R. W. Howarth. 2006. "Eutrophication of Freshwater and Marine Ecosystems." *Limnology and Oceanography* 51: 351–355. https://doi.org/10.4319/lo.2006.51.1_part_2.0351.

Šorf, M., T. A. Davidson, S. Brucet, et al. 2015. "Zooplankton Response to Climate Warming: a Mesocosm Experiment at Contrasting Temperatures and Nutrient Levels." *Hydrobiologia* 742: 185–203. https://doi.org/10.1007/s10750-014-1985-3.

Stockner, J. G., E. Rydin, and P. Hyenstrand. 2000. "Cultural Oligotrophication: Cases and Consequences for Fisheries Resources." *Fisheries* 25: 7–14. https://doi.org/10.1577/1548-8446(2000)025<0007:CO>2.0.CO;2.

Straskraba, M. 1990. "Limnological Particularities of Multiple Reservoir Series." *Archiv für Hydrobiologie. Beihefte. Ergebnisse der Limnologie* 33: 677–678.

Tilman, D. 1977. "Resource Competition Between Planktonic Algae: An Experimental and Theoretical Approach." *Ecology* 58: 338–348. https://doi.org/10.2307/1935608.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press.

Turesson, H., and C. Brönmark. 2007. "Predator–Prey Encounter Rates in Freshwater Piscivores: Effects of Prey Density and Water Transparency." *Oecologia* 153: 281–290. https://doi.org/10.1007/s00442-007-0728-9.

Van Donk, E. 1997. "Defenses in Phytoplankton against Grazing Induced by Nutrient Limitation, UV-B Stress and Infochemicals." *Aquatic Ecology* 31: 53–58. https://doi.org/10.1023/A:1009951622185.

Ward, J. V., and J. A. Stanford. 1995. "The Serial Discontinuity Concept: Extending the Model to Floodplain Rivers." *Regulated Rivers: Research and Management* 10: 159–168. https://doi.org/10.1002/rrr.3450100211.

Wellington, C. G., C. M. Mayer, J. M. Bossenbroek, and N. A. Stroh. 2010. "Effects of Turbidity and Prey Density on the Foraging Success of Age 0 Year Yellow Perch Perca

Flavescens." *Journal of Fish Biology* 76: 1729–1741. https://doi.org/10.1111/j.1095-8649.2010.02612.x.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag.

Winemiller, K. O., P. B. McIntyre, L. Castello, et al. 2016. "Balancing Hydropower and Biodiversity in the Amazon, Congo, and Mekong." *Science* 351: 128–129. https://doi.org/10.1126/science.aac7082.

Wootton, R. J. 1998. Ecology of Teleost Fishes. Kluwer Academic Publishers.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 26 July 2024
Revised 15 April 2025
Accepted 15 August 2025