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ÉLIDA JERONIMO GOUVEIA

**Variations in fishing landings from the Itaipu Reservoir:** relationships with life history and upstream hydrological regime

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Tese apresentada ao Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais do Departamento de Biologia, Centro de Ciências Biológicas da Universidade Estadual de Maringá, como requisito parcial para obtenção do título de Doutora em Ecologia e Limnologia.

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Coorientador: Prof. Dr. Diego Corrêa Alves

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*“Eu sou o sonho dos meus pais  
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*Vitória é sonho dos olhares  
Que nos aguardam nos lares  
Crendo que na volta somos mais.”*

***(Leandro Roque de Oliveira)***

## **Variações nos desembarques pesqueiros do reservatório de Itaipu: relações com os traços de história de vida e regime hidrológico a montante**

### **RESUMO**

As hidrelétricas são frequentemente apontadas como uma das principais causas da perda de biodiversidade e, conseqüentemente, da redução dos serviços ecossistêmicos. As modificações físicas, químicas e biológicas provocadas pelos represamentos favorecem diferentes espécies de peixes com base em seus traços de história de vida, selecionando aquelas com maior plasticidade ou com pré-adaptações às condições dos *habitats* represados. Investigou-se os impactos do represamento sobre os rendimentos pesqueiros do reservatório de Itaipu e em trechos a montante deste reservatório, com base em 32 anos de monitoramento. Buscou-se avaliar a relação entre os traços funcionais dos peixes registrados nos desembarques pesqueiros e a variação espacial e temporal dos locais estudados. Os resultados constataram que a montante apresentou maior abundância na maioria dos traços avaliados. Essa região mostrou alta similaridade dos traços com a região fluvial, enquanto a zona transição apresentou similaridade com a região lacustre, indicando que os desembarques pesqueiros são influenciados pelos traços funcionais das espécies, os quais variam na escala temporal e espacial. Analisou-se as mudanças no regime hídrico da planície de inundação do alto rio Paraná, antes e após a construção da hidrelétrica Porto Primavera, a fim de compreender como os padrões de inundação influenciam os desembarques pesqueiros das espécies migradoras do reservatório de Itaipu, considerando diferentes intervalos temporais. Essa análise revelou diferenças significativas nas métricas hidrológicas após o funcionamento da Usina Hidrelétrica de Porto Primavera. Coletivamente, esses resultados ilustram a variabilidade espacial e temporal dos desembarques pesqueiros no reservatório de Itaipu e montante, destacando os efeitos prejudiciais da operação da usina hidrelétrica a montante na sustentabilidade dos estoques pesqueiros nas áreas avaliadas. Diferentes padrões de cheias afetam os rendimentos das espécies migradoras, com efeitos significativos observados entre 2 e 4 anos subsequentes. Entre as principais contribuições desta tese, destaca-se a integração de dados em ampla escala sobre os desembarques pesqueiros no reservatório de Itaipu e montante. Evidenciou-se que a composição dos desembarques pesqueiros é dependente das características funcionais, as quais variam em escalas espacial e temporal. Uma importante abordagem adotada foi o uso de descritores hidrológicos baseado no índice *Indicator of Hydrological Alteration*, aplicados para caracterizar os padrões de cheias na planície de inundação situada a montante do reservatório de Itaipu, área essencial para a desova e o desenvolvimento das espécies migradoras. Ademais, foram analisados os efeitos dos diferentes tipos de cheias sazonais dessa planície sobre os rendimentos pesqueiros do reservatório de Itaipu e a montante.

**Palavras-chave:** Planícies de inundação; pesca; peixes migradores; regime hidrológico; represamento; traços funcionais.

# **Variations in fishing landings from the Itaipu Reservoir: relationships with life history and upstream hydrological regime**

## ***ABSTRACT***

Hydroelectric dams are frequently identified as one of the main drivers of biodiversity loss and, consequently, the reduction of ecosystem services. The physical, chemical, and biological modifications caused by damming favor different fish species based on their life-history traits, selecting those with greater plasticity or pre-adaptations to the conditions of impounded habitats. This study investigated the impacts of damming on fishery yields in the Itaipu Reservoir and upstream stretches, based on 32 years of monitoring. It aimed to assess the relationship between the functional traits of fish recorded in landings and the spatial and temporal variation of the studied locations. The results showed that the upstream region had higher abundance in most evaluated traits. This area exhibited high trait similarity with the fluvial region, while the transition zone showed greater similarity with the lacustrine region, indicating that fish landings are influenced by the functional traits of species, which vary over space and time. Changes in the hydrological regime of the Upper Paraná River floodplain were also analyzed before and after the construction of the Porto Primavera hydropower plant, to understand how flood patterns influence the landings of migratory species in the Itaipu Reservoir, considering different temporal intervals. This analysis revealed significant differences in hydrological metrics following the operation of the Porto Primavera Hydropower Plant. Collectively, these findings illustrate the spatial and temporal variability of fish landings in the Itaipu Reservoir and upstream, highlighting the harmful effects of upstream dam operations on the sustainability of fish stocks in the assessed areas. Different flood patterns affect the yields of migratory species, with significant impacts observed between two and four years afterward. Among the main contributions of this thesis is the large-scale integration of data on fishery landings in the Itaipu Reservoir and upstream areas. It was found that the composition of fish landings depends on functional traits, which vary across spatial and temporal scales. A key approach adopted was the use of hydrological descriptors based on the *Indicator of Hydrological Alteration* index, applied to characterize flood patterns in the floodplain located upstream of the Itaipu Reservoir—an area essential for the spawning and development of migratory species. Furthermore, the effects of different seasonal flood types in this floodplain on fishery yields in the Itaipu Reservoir and upstream were analyzed.

**Keywords:** Floodplain; fishing; migratory fish; hydrological regime; damming; functional traits.

Tese elaborada e formatada conforme as normas das publicações científicas:

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## 1 GENERAL INTRODUCTION

The transformation of lotic environments into lentic ones, resulting from the construction and operation of hydroelectric dams, is a globally recognized issue (DUGAN et al., 2010; WINEMILLER et al., 2016). The effects of these changes are predominantly negative, including biodiversity loss (WINEMILLER et al., 2016), alterations to the natural hydrological regime (POFF et al., 1997; HUMPHRIES et al., 2024), retention of sediments and nutrients (AGOSTINHO et al., 2016; FANTIN-CRUZ et al., 2016; LI et al., 2021), river fragmentation (NILSSON et al., 2005; PELICICE et al., 2015), and, consequently, damage to ecosystem services (PETRERE, 1996; HOEINGHAUS et al., 2009). These impacts can be categorized into three orders, as proposed by Petts (1980). The first order refers to changes in water flow and habitat modification (TUNDISI et al., 1991; POFF et al., 1997). The second order involves changes in the physical and chemical components of water, especially due to nutrient discharge, with considerable effects on the benthic community (TUNDISI et al., 1993; BRANDIMARTE et al., 2008; CUNHA et al., 2016). The third order, in turn, manifests over time, with significant effects on fish assemblages (AGOSTINHO et al., 1999), resulting in the reorganization of aquatic communities to adapt to the new environment (HAVEL et al., 2015).

In large reservoirs, fish assemblages vary in richness and abundance according to the longitudinal zonation pattern, which includes the fluvial, transitional, and lacustrine zones (AGOSTINHO et al., 1999; OLIVEIRA et al., 2004; OKADA et al., 2005). This zonation is evidenced by differences in water flow characteristics, sedimentation processes, and water residence time (KENNEDY & WALKER, 1990; AGOSTINHO et al., 2007). The fluvial zone generally presents abiotic characteristics like those of a lotic environment, with high water flow, elevated nutrient concentrations, and greater species richness (BAUMGARTNER et al., 2018), while the transitional zone is an ecotone between fluvial and lacustrine zones, displaying intermediate characteristics between lotic and lentic systems, with moderate water flow and intermediate species richness. The lacustrine zone, in turn, exhibits typical lake-like features, with low water flow and lower species richness (KIMMEL et al., 1990).

Considering the temporal scale, fish assemblages are also influenced by the trophic phases of reservoirs. After the filling period, the reservoir enters the heterotrophic phase (upsurge period), characterized by an increase in nutrient concentrations and, consequently, an intensification of primary production (KIMMEL & GROEGER, 1986). Over time, this production declines, marking

the post-heterotrophic phase (depression period) (CUNHA et al., 2016). This shift in reservoir productivity directly affects fish abundance and species richness, leading to a significant decline in diversity, replacement of migratory species by sedentary ones, an increase in non-native species, and a predominance of more generalist trophic strategies over the years (GOMES & MIRANDA, 2001; PELICICE & AGOSTINHO, 2009; ORSI & BRITTON, 2014).

In the upstream sections of reservoirs, the effects on fish assemblages are related to the lack of gene flow between downstream populations, resulting in dysconnectivity and potential loss of genetic diversity (BLANCHET et al., 2010; HORREO et al., 2011). In the downstream section, the impacts of reservoirs are even more pronounced, especially for migratory species, due to the control of the flood regime and the blockage of migratory routes caused by hydroelectric dams (AGOSTINHO et al., 2008; HUMPHRIES et al., 2024), with negative consequences for the recruitment of these populations (OLIVEIRA et al., 2018; KEPPELER et al., 2022).

In disturbed ecosystems, such as reservoirs, life history traits—including trophic, reproductive, and habitat use traits—have been widely used to assess functional responses to environmental changes (VASCONCELOS et al., 2014; GRANZOTTI et al., 2018; GANASSIN et al., 2024). Trophic traits, for instance, are influenced by variations in the trophic state throughout the reservoir and over the time since impoundment. During the heterotrophic (upsurge) phase, the increase in nutrients and primary production favors the abundance of herbivores, insectivorous omnivores, and piscivores due to the greater availability of food resources (HAHN & FUGI, 2007). In contrast, during the nutrient decline (depression) phase, there is a selection for opportunistic trophic traits (HAHN et al., 1998; DELARIVA et al., 2013). On the other hand, reproductive guilds—especially long-distance migratory species, which have more conservative constraints in relation to damming—show a significant decline within the first years following reservoir formation, particularly in the lacustrine zone of a reservoir (BARTHEM, 1991; OKADA et al., 2005; AGOSTINHO et al., 2016; LOURES & POMPEU, 2018).

The decline of migratory species in reservoirs has a direct and significant impact on one of the key ecosystem services: fisheries (AGOSTINHO et al., 2007; HOEINGHAUS et al., 2009). This ecosystem service is crucial for artisanal and riverside fishers, who depend on it for their survival and economic subsistence (DORIA et al., 2021; SANTOS & PELICICE, 2023). With the installation and operation of hydroelectric dams, migratory species typically larger and of higher commercial value, which sustain fishery yields are progressively eliminated from the inner

segments of reservoirs (D'AVILLA et al., 2021), being replaced by non-migratory species that often lack the same commercial value (AGOSTINHO et al., 2016; SANTOS & PELICICE, 2025). This results in changes in the composition of the catch and the market value of fish species (LIMA et al., 2020). In this context, free flowing upstream stretches of rivers play a fundamental role in mitigating the negative impacts on migratory species (DA SILVA et al., 2015), especially when floodplain areas are present (AGOSTINHO & ZALEWSKI, 1995; MIRANDA et al., 2014). Floodplain environments are regulated by seasonal flood pulses (JUNK et al., 1989), which act as triggers for migration and spawning (VAZZOLER, 1996), and also provide suitable conditions for the drift of eggs and the development of larvae and juveniles (BALCOMBE et al., 2007; SUZUKI et al., 2009), which later contribute to fish stocks in areas near reservoirs (MAKRAKIS et al., 2012).

Given the various impacts that hydroelectric dams have on fish assemblages, this dissertation aimed to investigate the effects of impoundments on fishery yields in the Itaipu Reservoir and its upstream region. It is composed of two chapters, both based on fishery monitoring data from the Itaipu Reservoir and its upstream areas. The first chapter aimed to assess the spatial and temporal variation in the composition of fish landings, considering life history traits (trophic and reproductive). The second chapter focused on evaluating changes in the hydrological regime of the Upper Paraná River floodplain before and after the construction of the Porto Primavera Hydroelectric dam, seeking to identify its impacts on the fishery yields of migratory species in the Itaipu Reservoir.

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## 2 SPATIAL AND TEMPORAL VARIATIONS IN THE COMPOSITION OF LANDINGS FROM PROFESSIONAL FISHING IN THE ITAIPU RESERVOIR, ACCORDING TO FUNCTIONAL TRAITS

### ABSTRACT

Large reservoirs exhibit different longitudinal and temporal gradients, which influence the selection of functional traits of fish adapted to each of these strata. In this context, this study aimed to assess the spatial and temporal variation in the composition of fish landings in the Itaipu Reservoir and upstream, based on trophic, reproductive, and habitat use functional traits. To this end, fish landing data from 1987 to 2018 were used, sourced from the reservoir zones (fluvial, transition, and lacustrine) and the upstream area. To analyze the variation in the abundance of functional traits (feeding, reproductive, and habitat use) across space and time, a Multivariate Generalized Linear Model (GLM). The results indicated that the upstream area showed higher abundance for all traits, except for planktivorous. Trophic traits showed variations in abundance, with a notable decline in planktivorous in the reservoir and an increase in herbivorous across all studied sites. Regarding reproductive traits, long-distance migratory species showed a decline early on, especially in the more internal zones, while non-migratory species exhibited variation in abundance across the evaluated sites, with a tendency for an increase in the fluvial zone. On the other hand, some traits prevailed over time in all studied areas, with a significant increase in herbivores, parental care, and internal fertilization. In contrast, a decline in planktivorous was observed, along with the absence of parental care and external fertilization. The results suggest that the composition of fishing landings is dependent on functional traits, which vary according to the spatial and temporal characteristics within the reservoir and upstream.

**Keywords:** damming, environmental filter, fish, life strategy, Upper Paraná.

### 2.1 Introduction

The construction and operation of hydroelectric dams represent significant threats to biodiversity at various levels of organization (Agostinho et al. 2005; Poff and Zimmerman, 2010). The impacts of dams have been widely studied, especially on fish assemblages, with records of reductions in richness and abundance of several native species (Agostinho et al. 2008; Turgeon et al. 2019), increases in non-native species (Loures and Pompeu, 2018; Orsi and Britton, 2014), and changes in the composition of functional traits of the communities (Arantes et al. 2019; Santos et al. 2017). The intensity of these impacts seems to vary throughout the dammed area and become more pronounced over time (Agostinho et al. 2007a).

Impoundments lead to marked changes in habitats, especially in relation to water velocity, depth, substrate type, and shelter availability, generating spatial gradients of physical, chemical and biological nature, from the upper lotic stretches to the more lentic ones near the dam

(Agostinho et al. 1999; Kimmel et al. 1990). In large reservoirs, changes in water dynamics lead to changes in sediment transport and deposition processes, creating a longitudinal gradient that includes fluvial, transition and lacustrine zones, differing not only in water flow, but also in nutrient load, transparency and productivity (Agostinho et al. 2007a; Kimmel et al. 1990). In this gradient, the pristine characteristics of the stretches upstream of the reservoir's backwater are gradually lost towards the dam. It is expected that different species will colonize the environment in distinct ways, with those that are more generalist or have pre-adapted to lake conditions reaching the innermost stretches and those that are more specialized advancing only in the zones that maintain more similarity with the upstream habitats (Agostinho et al. 1999; Gomes and Miranda 2001). These longitudinal gradients, together with the vertical strata, select different groups of species that manage to adapt and persist in each area (Baumgartner et al. 2018).

In terms of temporal variation, reservoirs undergo changes in trophic status, altering the availability and composition of food resources (Mérona et al. 2003). Thus, the new environmental conditions directly influence the process of selecting trophic strategies during and after colonization of the new environment (Agostinho et al. 2007a; Costa et al. 2024). In the first few years after the formation of a reservoir, the incorporation of organic matter and nutrients from the flooded areas leads to an increase in productivity and abundance of allochthonous food resources (heterotrophic phase), which is expected to be reflected in the abundance of herbivorous, insectivorous, and omnivorous, especially smaller species, which consequently favors the proliferation of piscivorous (Delariva et al. 2013; Pereira et al. 2016). Over time, with the trophic depletion of a reservoir, a general reduction in fish richness and abundance is expected, especially in the lacustrine zone (Agostinho et al. 2016; Gomes and Miranda, 2001). The age of the reservoir is one of the determining factors in the predominance of some functional traits over others (Santos et al. 2017). Thus, older reservoirs tend to have a greater abundance of species with omnivorous habits, multiple spawning and parental care, while younger reservoirs tend to be dominated by herbivorous species, with total spawning and medium size (Muniz et al. 2019).

In dammed environments, it is expected that the fish assemblage is structured according to these spatial and temporal gradients (Agostinho et al. 2016; Oliveira et al. 2005; Santos et al. 2010). Identifying the patterns of responses to these changes using the trophic and/or reproductive traits exhibited by fish species has been considered promising (Dias et al. 2020; Sousa et al. 2021; Vasconcelos et al. 2014), as it provides an integrated view of functional changes (Austen et al.

1994) and allows predictions about the success of species groups in the new environment as well as important inferences about losses of ecosystem services (Moillot et al. 2013; Naem et al. 2019).

In fact, the analysis of variations in the biomass of functional traits allows us to go beyond understanding the loss of ecological roles, in other words, it is possible to measure the impact of ecosystem services such as fisheries production (Petrere Jr. 1996), which is fundamental for generating income and food security for part of the riverside population (Arantes et al. 2023; Santos et al. 2018). Migratory species, which are usually larger, have higher commercial value and enjoy greater market acceptance, are highly vulnerable to damming (Dugan, 2008; Hoeinghaus et al. 2009). Therefore, their reduction or elimination in reservoirs results in significant socio-economic impacts for riverside communities and fishermen, who depend on these stocks for their livelihoods (Agostinho et al. 2007a; Lima et al. 2020).

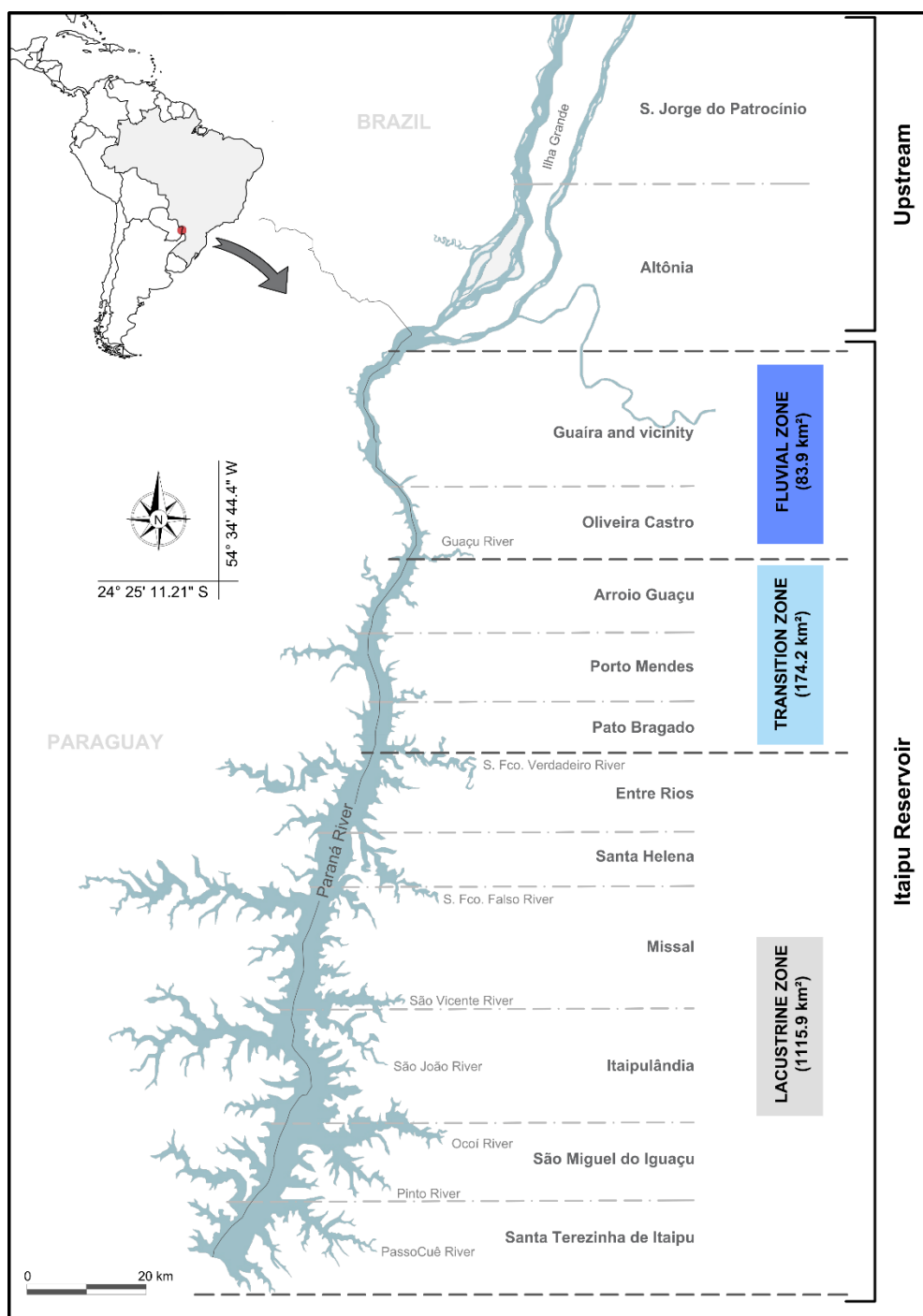
In this context, considering that functional traits are determining factors in the response of fish populations in reservoirs, this study aimed to evaluate the spatial and temporal variation in the composition of fish landings in the Itaipu reservoir and upstream according to trophic, reproductive, and habitat use functional traits. It is expected that (i) the trophic traits will show different responses depending on the availability of resources in the different locations and over time; (ii) the reproductive traits should also respond in a varied way, with a sharp decline in the long-distance migrator trait in all areas of the reservoir, especially in the innermost stretches, where the expected predominance is that of non-migrants, and these trends should increase over the years; (iii) in relation to the other functional traits, also with non-random distribution along the reservoir zones and the un-dammed upstream stretches, with more generalist traits, such as sedentary species, with parental care, pelagic habit, having a greater contribution in the innermost stretches.

## **2.2 Methods**

### **2.2.1 Study area**

The Itaipu reservoir is located on the border between Brazil and Paraguay and was formed in 1982. It covers an area of approximately 1,350 km<sup>2</sup>, has a mean depth ranging from 22m, and a retention time of 40 days (29 days in the main channel). Longitudinally, this reservoir is divided into 12 fishing areas across three zones: fluvial (Guaíra, Guaíra and vicinity, Oliveira Castro), transition (Arroio Guaçu, Porto Mendes, Pato Bragado), and lacustrine (Entre Rios, Santa Helena, Missal, Itaipulândia, São Miguel do Iguaçu, Santa Terezinha de Itaipu). This study focused on the

three zones of the Itaipu reservoir and a 46 km section upstream of the reservoir (Okada et al. 2005) (Figure 1).



**Figure 1.** Map of the Itaipu Reservoir highlighting the longitudinal gradient, including the fluvial, transition, and lacustrine zones, as well as the fishery areas (modified from Okada et al. 2005).

### 2.2.2 Fish data

Fishing in the reservoir began in 1985, the third year after the hydroelectric dam started operation. However, the landing monitoring data collected by Nupélia (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura) began in January 1987 and continued until 2018 (except for 1994). The data were collected through a network of fishermen's associations and colonies, using forms filled out by artisanal fishermen. These fishers employed various artisanal fishing gear commonly employed in artisanal fishing, including gill nets, cast nets, long lines, and hooks. The questionnaires recorded the number of fishing effort (number of fishing days), species caught, total weight (kg) of all individuals of the species in the sampled month, and date of capture. Three primary variables were extracted from these records: fisher identification, capture effort (fisher/day), and the weight (kg) of each species caught. The common names of the species present in the questionnaires were replaced with scientific names, according to the specialized literature (Dagosta et al. 2024; Pavanelli et al. 2023).

### 2.2.3 CPUE and Classification of Functional Traits

Species abundance was indexed by Catch per Unit Effort (CPUE;  $\text{kg.fisher}^{-1}.\text{day}^{-1}$ ) for each species. The CPUE was calculated as the ratio of the catch (kg) of each species to the specific effort (fisherman/day) in each month. The specific effort refers to the fishing effort directed toward each stock, considering that fishing activity in the Itaipu Reservoir is multi-species, using various types of equipment. This makes it difficult to apply a single fishing effort across all stocks. An algorithm was therefore developed to classify each fisherman as a fisherman of a particular species or not. Only fishermen who caught specimens of a specific species in at least five months of the time series were considered regular fishers of that species. Thus, the fishing effort of these fishermen was counted for that species in all the months they fished, regardless of whether or not they caught the species. In contrast, if a fisherman was not classified as a regular fisherman of the species (i.e., did not catch that species in at least five months), their effort was only counted in the months they caught the species, and not in the other months. It should be noted that counting the effort of all fishermen for all species would underestimate CPUE, since not all fishermen catch all species, since they use different fishing strategies. On the other hand, considering only the effort in the months in which there was a catch would overestimate the CPUE, since it would disregard zero catches (when the fisherman went fishing but didn't catch any of that species).

The fish assemblage of the Itaipu Reservoir was grouped into functional traits related to feeding (planktivorous, piscivorous, omnivorous, invertivorous, insectivorous, herbivorous,

detritivorous). In addition, other functional characteristics related to reproductive traits were considered, such as non-migratory and long-distance migratory, the presence or absence of parental care, type of fertilization (internal or external), and habitat use, including position in the water column (pelagic, demersal and benthopelagic) (Appendix A – Table S1). The classification of species into trophic and reproductive traits and habitat use was based on information extracted from specialized literature and Fish Base (Froese & Pauly, 2024).

The trophic traits were defined as follows: detritivorous, made up of species that feed on detritus of organic and inorganic origin; herbivorous includes species that consume algae and higher plants, such as fruit, leaves and seeds; planktivorous is made up of species that feed on phytoplankton and zooplankton; insectivorous is made up of species that consume aquatic and terrestrial insects at different stages of development; invertivorous includes species that consume benthic organisms such as amoebas, microcrustaceans, small molluscs, algae and insect larvae; omnivore involves species that consume items of plant origin (from algae to plants) and animal origin (from invertebrates to fish); and piscivorous is made up of species that consume whole or fragmented fish. Meanwhile, reproductive traits were classified into two categories: non-migratory, which includes sedentary and/or short-distance migratory species that migrate laterally; and long-distance migratory, made up of species that migrate at least 100 km.

#### 2.2.4 Data Analysis

To assess the variation in abundance (Indexed by the mean CPUE) of the functional traits related to feeding, reproduction, and habitat use on both spatial and temporal scales, the Multivariate Generalized Linear Model (GLM) was used, with a Tweedie distribution and a power parameter set to 1.1. This resulted in a distribution similar to a Poisson-Gamma composite distribution, which has a positive mass at zero but continuous behavior for the rest of the distribution. The CPUEs (abundances) of each species were defined as the response variable, while the zones (upstream: baseline, fluvial, transition, and lacustrine) and their interaction with the year (year - initial year) were considered predictor variables. Additionally, the functional traits were included as interacting predictor variables, enabling the conduct of a fourth-corner analysis. The month variable was also included as a random variable in the model to mitigate temporal dependence. The inclusion of the year variable as "year - initial year" allows the main effects of the zones to be assessed in year zero, which marks the start of the study, approximately five years after the reservoir was formed and two years after fishing activity began. The figures were created

using *ggplot2* package. To complement the information provided in Figures 2 and 3, which illustrate mean abundance, Tables S2 (Appendix B) and S3 (Appendix C) have been included in the Supplementary Material, containing the standard deviation values that could not be plotted in the figures. The analyses were conducted using R software, version 4.2.2 (R Development Core Team, 2020).

## 2.3 Results

During the study period, 63 fish species were recorded (Appendix A – Table S1). In general, the region upstream of the reservoir exhibited the greatest abundance for all traits and years, except for planktivorous, for which the upstream zone showed the least relative importance, followed by the fluvial zone (Figures 2 and 3). Another general pattern observed was in abundance of the traits between the upstream and fluvial zones, although with more pronounced interannual fluctuations in the upstream zone. In contrast, the variation trends in the transition and lacustrine zones were more similar to each other (Figures 2 and 3).

At the beginning of the study, that is, five years after the start of the Itaipu Reservoir operation, only planktivorous showed high abundance across all zones of the reservoir, while there was a decline in piscivorous, omnivorous, invertivorous, and herbivorous in all zones (Figures 2 and 4). On a broader temporal scale, i.e., over the entire study period, only planktivorous and herbivorous exhibited consistent patterns of abundance variation, with a pronounced decline in the former and an increase in the latter (Figures 2 and 4).

The other trophic traits varied between zones and different years in such a way that omnivorous showed a slight increasing trend in all reservoir zones, whereas invertivorous increased only in the lacustrine zone during certain periods (Figure 2). Piscivorous and detritivorous continued to exhibit fluctuations, with a declining trend in the upstream and fluvial zones during intermediate years and a subsequent increase (Figure 2).

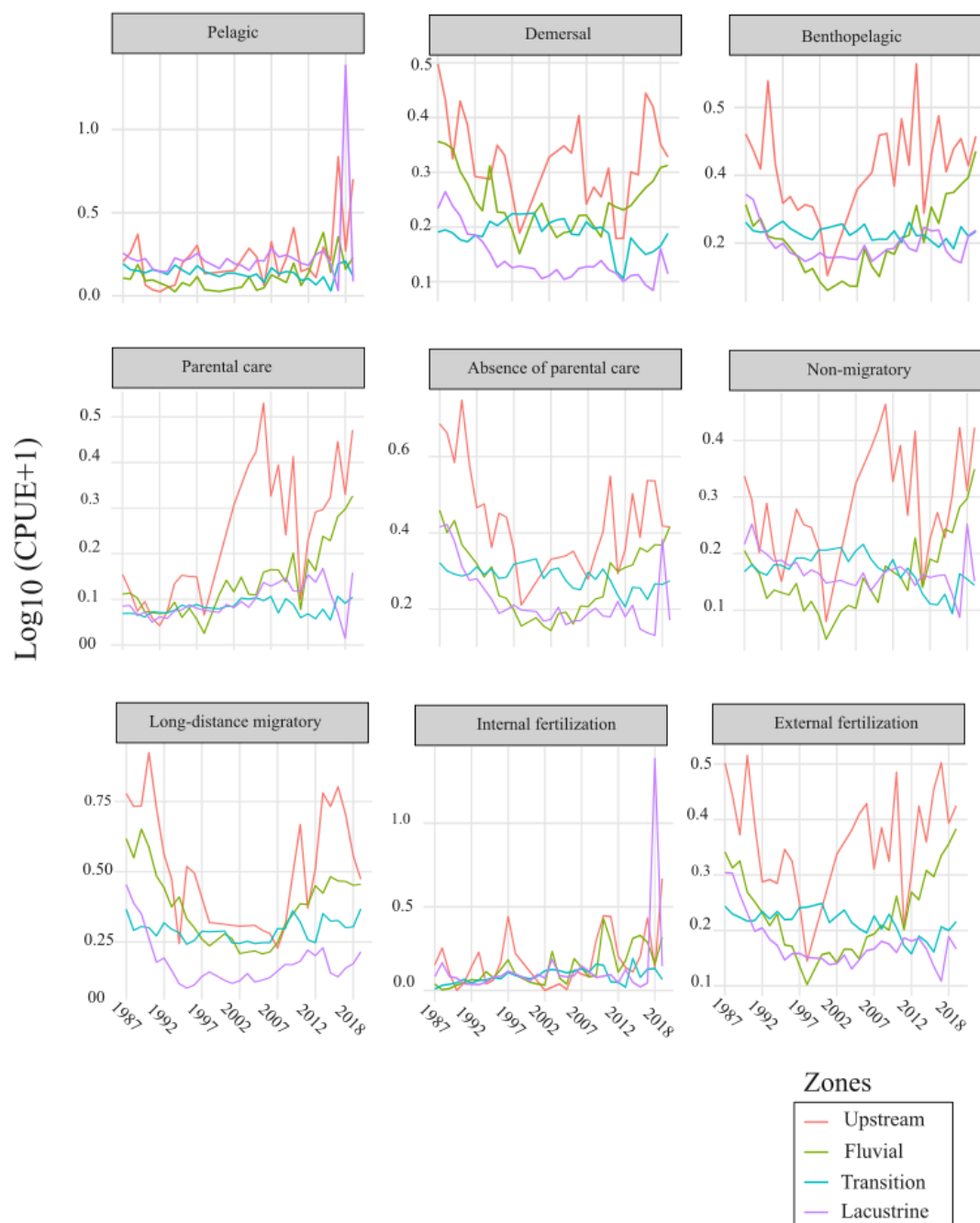


**Figure 2.** Mean abundance (CPUE) of different trophic functional traits across the zones of the Itaipu Reservoir and the upstream area over time

Reproductive strategies exhibited distinct responses to the early years of impoundment. Long-distance migratory species showed less fluctuation in the transition zone, while in the lacustrine zone, they experienced a decline during the first years of landing monitoring and remained low for the rest of the period. In the fluvial zone, no changes in abundance were observed compared to the upstream segment, with variation trends similar to those in the upstream zone, where the lowest values were observed between 1995 and 2007 (Figures 3 and 4). Conversely, a declining trend of non-migratory species was observed over time in the transition and lacustrine zones, while an increase was noted in the fluvial zones (Figures 3 and 4).

The demersal, benthopelagic, parental care, and internal fertilization traits showed an increasing trend across all locations (i.e., in the reservoir zones and upstream). On the other hand,

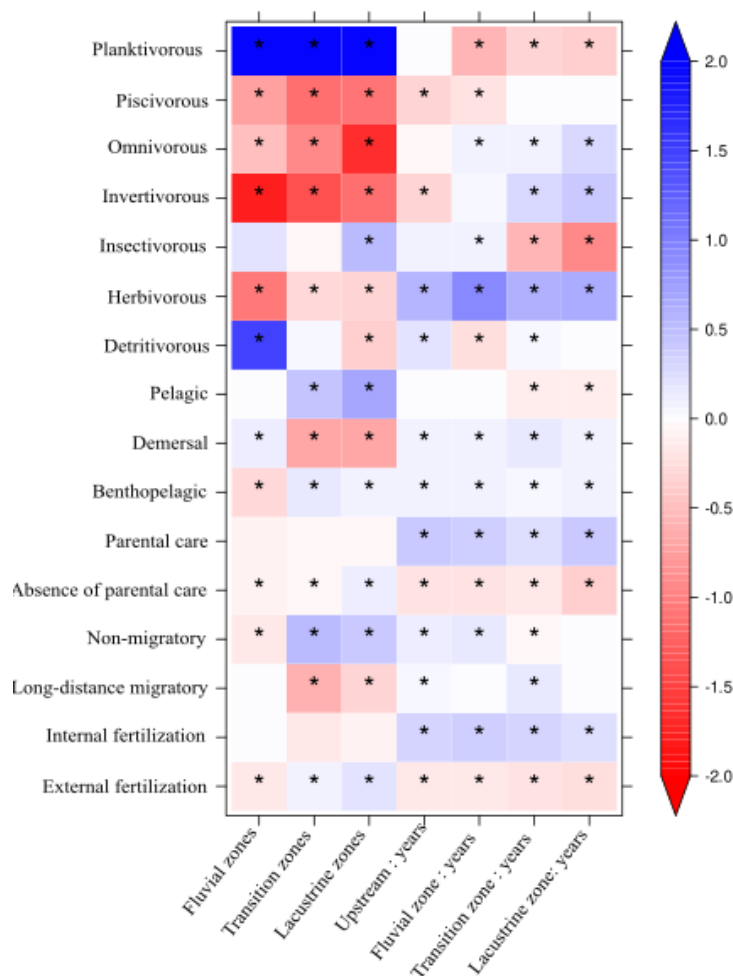
a slight declining trend was observed for species without parental care and with external fertilization in the same zones, although an increasing trend was recorded in the final years for the upstream and fluvial zones (Figures 3 and 4).



**Figure 3.** Mean abundance of different reproductive and habitat use traits across the zones of the Itaipu Reservoir and the upstream area over time

Based on the results of the fourth-corner analysis, we can interpret the main effects of each reservoir zone when compared to the baseline (control), which is the Paraná River upstream of the reservoir, at the start of the study, i.e., in 1987 (5 years after the reservoir formation and 2 years after fishing began) (Figure 4). Furthermore, the interaction between the zones and year allows for the assessment of temporal trends over the study period in each zone separately. Overall, the fourth-corner analysis indicated that the trophic, reproductive, and habitat use functional traits exhibited a certain pattern of responses, with the predominance of significant negative effects in the reservoir zones when compared to the upstream area at the start of the study, particularly in the more inland zones (Figure 4). These results are corroborated by the temporal profiles presented in Figures 2 and 3, which also showed higher abundances for most traits upstream, as previously mentioned. Exceptions to this pattern include planktivorous, which showed higher abundances in the reservoir (at the beginning of the study), and pelagic and benthopelagic traits, non-migratory species, and external fertilization, which exhibited higher abundances in the transition and lacustrine zones when compared to upstream and also to the fluvial zone (Figure 4). Traits that did not show significant spatial variation at the start of the study were insectivorous (only an increase in the lacustrine zone), parental care, and internal fertilization.

Regarding temporal trends, some traits showed a significant increasing trend across the entire study area, such as herbivorous, parental care, and internal fertilization. In contrast, planktivorous traits, absence of parental care, and external fertilization showed significant negative temporal trends (Figure 4). It is noteworthy that although planktivorous exhibited significantly higher abundances in the reservoir zones compared to upstream at the beginning of the study, a temporal decline in these abundances was also evident (only within the reservoir), resulting in similar abundances across all zones by the end of the study, with slightly higher values in the lacustrine zone (Figures 3 and 4).



**Figure 4.** Fourth-corner model showing paired relationships between functional traits and different locations across a broad temporal scale. Colors represent the direction and magnitude of the associations: blue indicates positive relationships and red indicates negative relationships. Asterisks (\*) denote statistically significant associations compared to the baseline category, which serves as a reference in the model.

## 2.4 Discussion

The results of this study indicate that the fluctuations in fishing landings in the Itaipu Reservoir, monitored from 1987 to 2018, exhibited distinct patterns of variation in space and time, depending on the functional trait considered. The reservoir zones (fluvial, transition, and lacustrine) showed lower abundance in all traits (except for planktivorous) compared to the lotic upstream section, which features habitats with characteristics closer to the original. The trophic traits displayed varied responses over time, with planktivorous and invertivorous being more

abundant in the more interior areas of the reservoir, although with opposite trends of variation over time. Detritivorous, insectivorous, and omnivorous, on the other hand, were less abundant in the fishing catches from the lacustrine zone. Meanwhile, herbivorous species showed an increasing trend in all areas. Regarding reproductive traits, the expected patterns were already evident in the first decade of monitoring, with a sharp decline in migratory species in the more internal zones of the reservoir (lacustrine and transition). The other traits, such as habitat use and reproductive traits (parental care, fertilization), exhibited more stable patterns across the zones on a broader scale.

The trophic traits showed great variability in the abundance of fishery landings in the reservoir landings, especially during the first decade of the Itaipu operation. This phenomenon can be primarily attributed to the heterotrophic state that characterizes recent reservoirs and leads to marked changes in the composition of available trophic resources (Agostinho et al. 1999; Hahn et al. 1998), being influenced by the degree of instability in dam operation (Agostinho et al. 2007a). The initial high yield of planktivorous across all reservoir zones, but particularly in the more interior zones, was solely due to the high capture of *Hypophthalmus oreamaculatus*, a planktivorous species favored by pre-adaptations to open areas of this environment (eye position, pelagic eggs, body shape) and by the high availability of plankton in the early years (Abujanra and Agostinho, 2002; Hahn et al. 1998). On the other hand, in subsequent years, this species showed a marked decline in all zones of the reservoir, possibly due to predation pressure by *P. squamosissimus*, overfishing (Ambrósio et al. 2001), and reduced reservoir productivity as a result of upstream drought years (1997 to 2007).

Herbivorous, with low catch in the first two decades of the reservoir, showed consistent temporal increases across all zones, with the initially low values being due to the low catches of *Brycon orbignyanus* and *Piaractus mesopotamicus*, two migratory species known to be among the most affected by damming (Agostinho and Zalewski, 1995). In subsequent years, this trait increased across all studied areas, including upstream of the reservoir, likely due to the major floods that characterized some years of this period (2007, 2010, and 2016) (Oliveira et al. 2020). Moreover, during this period, the increase of two herbivorous anostomids from the genus *Schizodon* was observed (see Appendices G, H, I, J). The higher abundance of this trait upstream is due to the greater contribution of allochthonous items from riparian vegetation (Sá-Oliveira et al. 2014).

Piscivorous declined in the early years across all zones, with the decline being more pronounced in the upstream and fluvial zones, which showed some recovery in the last decade of monitoring. The interior zones of the reservoir exhibited less pronounced variations, which could be attributed to the greater availability of prey species, which are smaller, more abundant species in these sections (Luz-Agostinho et al. 2006; Pereira et al. 2016). The reduction in the fluvial zone was associated with the decline of long-distance migratory species such as *Salminus brasiliensis*, *Pseudoplatystoma corruscans*, *Hemisorubim platyrhynchos*, and *Zungaro jahu* (see Appendix D), which also declined upstream due to the scarcity of floods, upon which they depend (Oliveira et al. 2020). In the interior areas of the reservoir, no significant differences were observed in subsequent years due to the contribution of *P. squamosissimus* (see Appendices E and F), which became dominant in the reservoir (Benedito Cecilio et al. 1997).

Omnivorous showed an abundance gradient from the upstream section to the lacustrine zone. Despite considerable fluctuations in the upstream lotic section, this trait was consistent throughout the entire period. This trait is considered opportunistic, with high trophic plasticity, and is usually one of the most abundant in reservoirs (Lazaro et al. 2003; Mérona and Vigouroux, 2006), especially in older ones (Agostinho et al. 2007a; Ganassin et al. 2024). Moreover, variations in the yield of this trait can be attributed to the fact that it is mainly composed of small species, in addition to *Pterodoras granulosus*, a large species that significantly contributed to this trait, with an expressive increase in the Itaipu Reservoir and upstream (Oliveira et al. 2005).

Invertivorous showed considerable fluctuations in yield over the years in the upstream section of the reservoir, with a declining trend in the last decade. This trend was the opposite of those observed in the more interior zones of the reservoir, especially in the lacustrine zone. The increase of this trait in the landings from the more interior areas of the reservoir is attributed to the proliferation of species such as *Satanoperca setepele* in the transition zone and *Geophagus sveni* in the lacustrine zone (see Appendices I and J), both introduced from the Tocantins River basin. The availability of benthic organisms may be related to the success of this trait. Although the diversity and even the density of benthic species decrease towards the dam, some groups pre-adapted to the trophic conditions of the reservoir may become dominant, explaining the increase of this trait in the lacustrine zone (Jorcin et al. 2009; Takahashi et al. 2008).

Insectivorous (*Auchenipterus osteomystax*, *Crenicichla* spp., *Gymnotus inaequilabiatus*, and *Rhamphichthys hahni*) were sporadic in the fishery landings upstream and across all reservoir

zones during the first two decades of the Itaipu Reservoir. Their proliferation upstream was followed by an increase in the fluvial zone. It is possible that the greater interface between the terrestrial and aquatic environments in the river and the upper section of the reservoir allows a higher contribution of allochthonous resources, whereas in the more interior, wider, and deeper zones, the contribution of insects is more limited (Agostinho et al. 2007a; Delariva et al. 2013).

The decline in detritivorous yield, which was evident in the first decade of the reservoir across all zones, was more pronounced in the fluvial zone and was associated with the decline of the genus *Hypostomus* and migratory species such as *Prochilodus lineatus* and *Rhinelepis aspera*. Many local species of the genus *Hypostomus* and *Rhinelepis aspera* are rheophilic and feed on rocky substrates, so the decline in yield can be attributed to changes in their habitats, both due to changes in water dynamics and the sediment deposition-induced alterations (Pagioro and Thomaz, 2002). *Rhinelepis aspera* and *P. lineatus*, on the other hand, are affected by changes in the flood regime of the upstream reservoirs and overfishing (Gomes and Miranda, 2001; Okada et al. 2005).

On the other hand, we expected that reproductive strategies would show consistent responses in the early years of Itaipu's operation, and this was observed. Migratory species experience a decline in these environments due to structural modifications and alterations in water flow caused by hydropower plants (Agostinho et al. 1999; Dugan et al. 2010). The replacement of migratory species by sedentary ones leads to a decrease in fishery yield, particularly in the more interior zones of reservoirs, where species pre-adapted to lacustrine environments are typically dominant (Gomes and Miranda 2001; Hoeinghaus et al. 2009). The decline of migratory species was also observed in the upstream region of the reservoir, despite the presence of the floodplain of the Upper Paraná River, a crucial environment for the maintenance of this group (Agostinho et al. 2004; Agostinho et al. 2007b). However, this floodplain is located downstream of Porto Primavera hydropower plant, which interferes with flooding patterns (Oliveira et al. 2020), directly impacting the fishery yield of areas near the Itaipu Reservoir (Gomes and Agostinho 1997; Okada et al. 2005; Gouveia et al. unpublished data). In contrast, an increase in the abundance of non-migratory traits, while long-distance migratory species declined across all sites, especially in the lacustrine zone, as previously reported in the literature (Agostinho et al. 2007a; Arantes et al. 2023; Lima et al. 2020). Species with opportunistic characteristics, such as sedentary species, tend to colonize reservoirs more easily, primarily due to their trophic plasticity (Hahn and Fugi, 2007).

A trend of increase was observed in some functional traits exclusive to certain species, such as parental care and internal fertilization, across all sites studied during the last monitored decade. Parental care is a common reproductive strategy in reservoirs, serving to ensure success in these disturbed environments (Agostinho et al. 2016; Santos et al. 2017). In the upstream sections, this increase can be explained by the abundance of species exhibiting these traits, such as *Loricariichthys platymetopon*, *Pterygoplichthys ambrosetii*, *Satanoperca setepele*, and *Astronotus crassipinnis* (see Appendix G). On the other hand, although internal fertilization did not show consistent patterns in the early years of the reservoir's operation, a marked increase in this strategy was observed across all zones, particularly in the lacustrine zone. This increase is likely related to the rise of *Auchenipterus osteomystax* (see Appendices H and I), which became significant in the reservoirs (Agostinho et al. 2007a). The increase in demersal and benthopelagic traits, as well as the decline in traits such as absence of parental care and external fertilization, may have been influenced by other functional traits, as most species listed in the fishery landings share these characteristics.

The results allow us to conclude that the response of the stocks that sustain fishing landings to the changes imposed by damming is trait-dependent; that is, the characteristics of the new habitats, regardless of their position in space or time, influence groups of species with different life strategies in different ways. Thus, the composition of landings, in terms of life history, will be differentiated according to the spatial or temporal gradient considered. Temporal variation in resource availability, as well as the spatial distribution of habitats altered by the damming process, imposes different ecological pressures on species with varying adaptations. This, in turn, creates a dynamic mosaic of species dominance in fishing landings across time and space.

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### 3 FOUR TYPES OF FLOODS IN THE UPPER PARANA RIVER AFFECT FISHERIES YIELD OVER THE NEXT 2-4 YEARS IN ITAIPU RESERVOIR

#### ABSTRACT

Migratory fish frequently sustain fishery yields, especially species reliant on floodplains that provide diverse habitats and trophic resources essential for juveniles development. However, hydroelectric dams have altered natural flows, modified flood patterns, and negatively impacted fishes that rely on floodplains. We investigated changes in the natural hydrological regime before and after the construction of a hydroelectric dam and examined how flood patterns in a floodplain downstream affected fishery yields with delays of 1-5 years. We used three decades of hydrological records and fisheries yield data for seven migratory fish species. We observed changes in hydrological conditions before and after the construction of the hydroelectric dam, with the pre-dam years showing higher values in extreme magnitudes, duration, and flood intensity. In contrast, post-dam years exhibited high rates of change in the water conditions (rising, falling, and reversals). Four flood patterns were identified: small, medium, erratic, and large, with the erratic pattern showing the greatest fluctuation in the hydrological indicators. Differences in the fisheries, seemingly reliant on flooding, were apparent 2-4 years post-flood, particularly for large floods. In conclusion, our results emphasize the need for hydroelectric projects to consider the ecological needs of migratory species when regulating discharges, to ensure the survival and maintenance of these populations in floodplains of dammed rivers.

**Keywords:** floodplain | reservoirs | migratory species | artisanal fishery | hydrological alteration | upstream

#### 3.1 Introduction

The flow regime is a primary determinant of aquatic ecosystem health (Poff et al. 1997). Alterations to natural flow regimes represent one of the greatest threats to aquatic biodiversity (Dudgeon et al. 2006). Socioeconomic programs of development, such as hydropower and flood control projects, have drastically altered flow regimes globally (Grill et al. 2019). These changes affect crucial flood attributes such as duration, timing, magnitude, frequency, and rates of variation, which directly influence the dynamics of aquatic ecosystems and the organisms that depend on them (Richter et al. 1996; Agostinho et al. 2004; Kennen et al. 2008; Belmar et al. 2013).

Dams reduce the intensity or even eliminate natural floods, disrupting natural hydrologic pulse cycles crucial for many aquatic organisms (Standford and Ward 1992; Stone et al. 2017). This impact is particularly pronounced in floodplain systems, where high water levels lead to the inundation of large areas (Junk et al. 1989). Flow regulation compromises this expansion and precludes lateral connectivity between the river and diverse aquatic habitats in floodplains

(Miranda et al. 2014). Consequently, nutrient cycling is disrupted, and organisms are denied access to vital environments for feeding, spawning, and development (Wang et al. 2016; Ely et al. 2020).

Changes in flow regimes caused by dams have direct impacts on fish assemblages both downstream and upstream (Arantes et al. 2019). Upstream effects include declines in fish abundance and species richness along the river's length and at different water depths (Agostinho et al. 2016), reductions in native species populations (Orsi and Britton 2014), changes in trophic group dynamics and abundance (Miranda et al. 2019; Santos et al. 2020), functional and taxonomic homogenization (Vitule et al. 2012), a decrease in migratory species (Agostinho et al. 2003; Zydlewski et al. 2023) and introduction of non-native species (Júlio Jr. et al. 2009). Downstream, the effects are mainly related to the blocking of migratory routes, which prevent migration, spawning, and access to essential habitats for fish development and recruitment (Antonio et al. 2007; Pompeu et al. 2012). Additionally, river fragmentation leads to population isolation, limiting gene flow among population strata (Zarri et al. 2022). Beyond flow regulation, reservoirs also trap sediments and nutrients, affecting water transparency and reducing productivity downstream (Agostinho et al. 2016). On the other hand, altered hydrological and environmental conditions can facilitate the invasion of non-native fish species downstream (Gois et al. 2015).

Fish reproduction is among the most impacted traits by the formation and operation of reservoirs (Mims and Olden 2012; Vasconcelos et al. 2014; Arantes et al. 2021). The patterns of fish assemblages that emerge from damming reveal an increased prevalence of species with lacustrine traits (Gomes and Miranda 2001), while long-distance migratory species are extirpated (Agostinho et al. 2016). The latter group experiences severe disruption of its reproductive dynamics (Suzuki et al. 2011), due to changes in discharge regimes and physical barriers imposed by dams (Mims and Olden 2012; Pelicice et al. 2015). These changes disrupt natural flood cycles, which are a key trigger for migration and spawning (Bailly et al. 2008). Consequently, populations of migratory species tend to decline, particularly when the regulation of floods pulses by dams fail to provide suitable habitats for juvenile development and for subsequent recruitment (Agostinho et al. 2004; Suzuki et al. 2009; Oliveira et al. 2015; Oliveira et al. 2020).

The decline of high-value migratory species in reservoirs compromises essential ecosystem services, particularly fish production (Petrere et al. 2002; Arantes et al. 2023), which is crucial for the subsistence of local communities in some regions (Lima et al. 2020). This decline can be observed by the replacement of the economically valuable migratory species by lower trophic level

species with reduced economic value (Hoeinghaus et al. 2009). Fish productivity within reservoirs varies spatially, according to the characteristics of longitudinal segments within the reservoir. Lacustrine zones near the dam, for example, tend to be less productive, and offer unfavorable environmental conditions for migratory species. Conversely, the riverine zones in the upper reaches of a reservoir, where some river conditions persist, typically exhibit higher yields of migratory species (Petrere 1996; Okada et al. 2005).

This study examines the hydrologic regime of the Upper Paraná River floodplain. We focus on the impact of the altered discharge from Porto Primavera Dam immediately upstream, which directly affects the downstream flood patterns crucial for migratory species. We utilize data from a hydrologic station downstream of that dam, alongside artisanal fishing statistics collected from the Itaipu Reservoir and its upstream reaches, which are all downstream from the floodplain. The aim was to evaluate how flood patterns in the Upper Paraná River floodplain relate to fishing yields, both within the Itaipu Reservoir (fluvial and transition zones) and in the river reach immediately upstream, using hydrologic indicators. We address two specific objectives. First, characterize the natural (pre-dam) and altered (post-dam) flow regime of the Upper Paraná River floodplain, using hydrologic indicators. Second, assess the influence of different flood types on migratory species fisheries, considering time lags and spatial variations across the three spatial reaches, including two reaches within the Itaipu Reservoir and one reach in the Paraná River just upstream of Itaipu Reservoir, included in the lower section of the floodplain. For this second objective, the hypothesis postulates that different flood patterns differentially influence the migratory fishery yield due to species-specific ecological requirements, accounting for recruitment time lags and distribution effects.

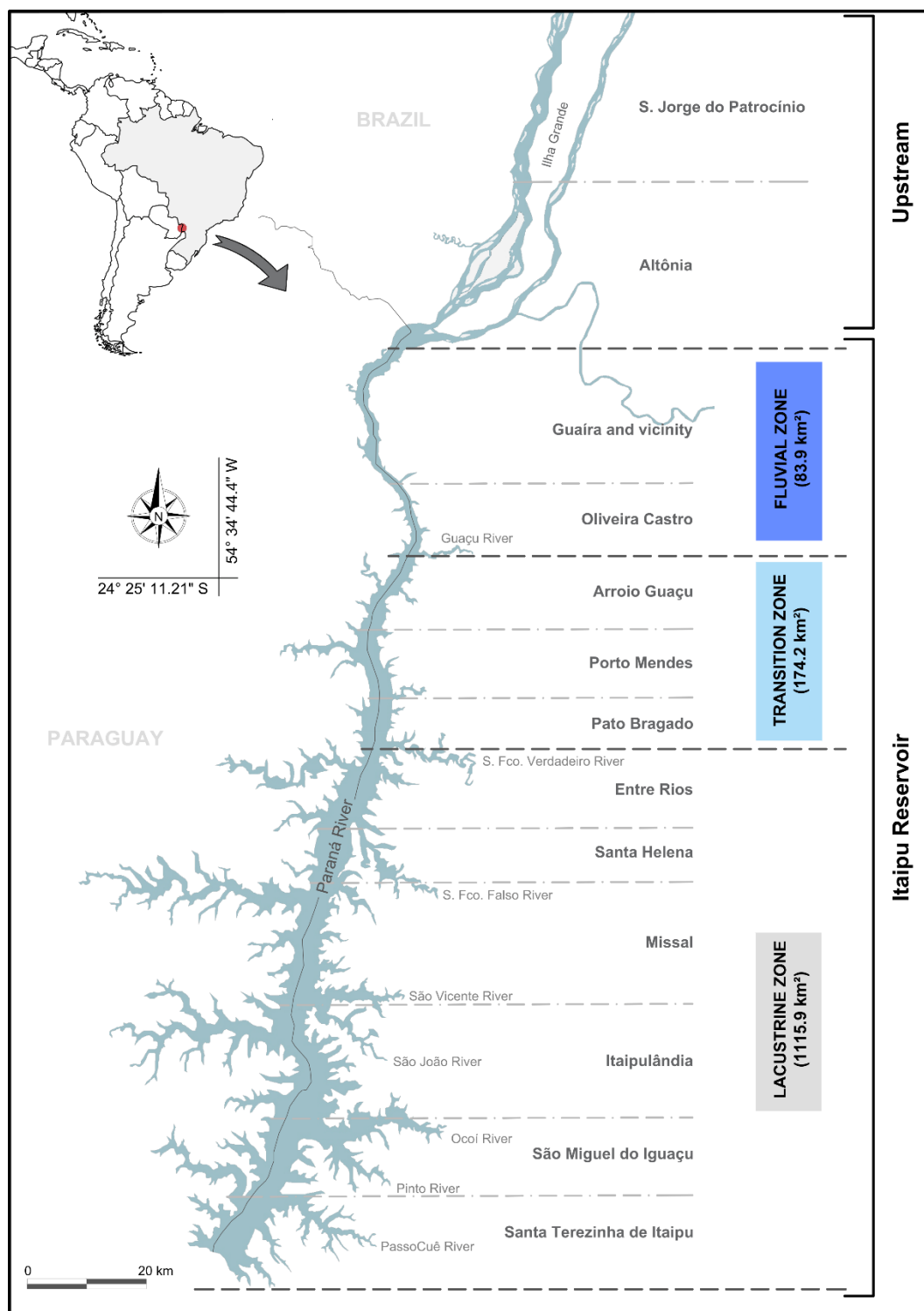
## **3.2 Methods**

### **3.2.1 Study area**

The Paraná River Basin is the third largest river basin in South America (Orfeo and Stevaux 2002), covering an area of 2,600,000 km<sup>2</sup> across Brazil, Argentina and Paraguay territory. Within Brazil, the Paraná River is among the most fragmented river systems in the world (Nilsson 2005). The Upper Paraná River floodplain, a 230-km un-dammed stretch, lies between the Porto Primavera Reservoir upstream and the Itaipu Reservoir downstream. This floodplain, at the confluence of the Baía, Paraná, and Ivinhema rivers, along with secondary channels and floodplain lakes, is crucial for development migratory species (Stevaux 1994; Agostinho et al. 2004). Others undammed lateral tributaries, such as the Ivaí, Piquiri, and Iguatemi, are especially important for

the conservation of fish with these life strategies. The Porto Primavera Reservoir is the newest and largest in the region. It was formed in 1998, with a surface area of 2,250 km<sup>2</sup>, a total volume of 18,500 x 10<sup>6</sup> m<sup>3</sup>, and an average residence time of 33.9 days (Souza Filho et al. 2004). In the drainage basin above Porto Primavera Reservoir, including its lateral tributaries, there are dozens other reservoirs (Julio Jr et al. 2009). The Itaipu Reservoir was formed in 1982, covers an area of approximately 1,350 km<sup>2</sup>, has a total volume 29,000 x 10<sup>6</sup> m<sup>3</sup>, and an average residence time of 40 days (29 days in the main channel).

The Itaipu Reservoir is often characterized by a longitudinal gradient, with three relatively distinct zones: lacustrine, transition, and fluvial, which differ in terms of productivity, physical, and chemical characteristics (Agostinho et al. 1999). This study focused on the transition and fluvial zones of Itaipu Reservoir and on the floodplain downstream of Porto Primavera Reservoir. These two zones are compared with a 46-km section of the floodplain downstream of Porto Primavera Reservoir (Figure 1). The three sections were included because they support migratory species but differ in flow and other physical characteristics, attracting different species and possibly provide different fisheries.



**Figure 1** - Map of the Itaipu Reservoir highlighting the longitudinal gradient, including the fluvial, transition and lacustrine zones, as well as the fishery areas (modified from Okada et al. 2005).

### 3.2.2 Characterization of flood patterns in the floodplain

To characterize flooding, daily discharge ( $\text{m}^3/\text{s}$ ) were obtained from the National Water Agency (ANA – National System of Information on Water Resources – SNIRH), specifically from the Porto São José Meteorological Station (64575001/22533018). This station is located approximately 49 km downstream from the Porto Primavera dam and 189 km upstream from Itaipu Reservoir. Only data collected from October to March were used to characterize a ‘flood year’, as this period represents the spawning period for most migratory fishes and coincides with the elevated river level (Gomes and Agostinho 1997). Discharge estimates were used to compute various hydrological indicators based on the Indicator of Hydrological Alteration (IHA) procedure, developed by the U.S. Nature Conservancy (<http://www.nature.org>) and widely applied in aquatic environments (Zhou et al. 2020). The IHA computes 32 hydrological indicators that highlight five primary characteristics of hydrological regimes including frequency, magnitude, timing, rate of change, and duration. These characteristics are critical for understanding biological processes such as population dynamics and species migration (Richter et al. 1996).

While the IHA primarily addresses stream fluctuations, several of its indicators are relevant for characterizing floodplain inundation and were included in this study (Table 1). These indicators were computed using the *IHA* package in R (Law 2013). Furthermore, four additional attributes were calculated: flood intensity, defined as the maximum October-March river level; flood duration, defined as the total number of days within October-March when the river level exceeded 450 cm (the onset of floodplain inundation, as determined by Comunello et al. (2003); and median quarterly discharge for the October-December and January-March periods, representing the early and late spawning season, respectively (Table 1).

**Table 1** Hydrological descriptors based on the Indicator of Hydrological Alteration (IHA) procedure, used to characterize different flood patterns

| Indicator       | Definition                                                                                                                                                     | Min     | Mean     | Max      | CV    |
|-----------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------|---------|----------|----------|-------|
| 1-day min       |                                                                                                                                                                | 4322.61 | 5950.7   | 7357.39  | 0.12  |
| 1-day max       |                                                                                                                                                                | 9157.32 | 15172.4  | 22477    | 0.26  |
| SFD 1-day       |                                                                                                                                                                | 2888.99 | 9221.7   | 18999.3  | 0.40  |
| 3-day min       |                                                                                                                                                                | 4481.89 | 6173.55  | 7929.68  | 0.13  |
| 3-day max       |                                                                                                                                                                | 9020.55 | 14891.6  | 24827.2  | 0.26  |
| SFD 3-day       | -Magnitude of extreme flow events:                                                                                                                             | 2489.18 | 8718.09  | 18642.3  | 0.43  |
| 7-day min       | Maximum and Minimum flow                                                                                                                                       | 4812.07 | 6524.88  | 8471.58  | 0.13  |
| 7-day max       | -SFD: seasonal flow difference:                                                                                                                                | 8549.23 | 14390.4  | 24509.2  | 0.28  |
| SFD 7-day       | maximum – minimum for each                                                                                                                                     | 2003.4  | 7865.51  | 17893.5  | 0.49  |
| 30-day min      | variable.                                                                                                                                                      | 5109.20 | 7173.94  | 9837.35  | 0.12  |
| 30-day max      |                                                                                                                                                                | 7891.41 | 12471.3  | 20480.9  | 0.27  |
| SFD 30-day      |                                                                                                                                                                | 1088.91 | 5297.32  | 13606.9  | 0.61  |
| 90-day min      |                                                                                                                                                                | 5524.29 | 10755.4  | 10755.4  | 0.12  |
| 90-day max      |                                                                                                                                                                | 7372.50 | 10285.3  | 14686.83 | 0.18  |
| SFD 90-day      |                                                                                                                                                                | 376.56  | 2429.3   | 6274.35  | 0.67  |
| Base flow index | 7-day minimum flow mean/mean flow for year                                                                                                                     | 0.47    | 0.72     | 0.87     | 0.11  |
| Minimum day     | Day of flood season with minimum flow                                                                                                                          | 4       | 54.85    | 181      | 0.87  |
| Maximum day     | Day of flood season with maximum flow                                                                                                                          | 105     | 141.64   | 179      | 0.13  |
| SFD day         | Seasonal flow difference: maximum – minimum day                                                                                                                | -51     | 86.79    | 164      | 0.59  |
| Fall rate       | Measures the average daily increase in flow over a given period. It reflects how quickly the flow decreases                                                    | -560.95 | -374.26  | -140.63  | -0.29 |
| Rise rate       | Measures the average daily decrease in flow over a given period. It represents how quickly the flow increases                                                  | 190.52  | 359.77   | 523.77   | 0.29  |
| Reversals       | The number of times the flow direction changes (from increasing to decreasing and vice versa) within each period                                               | 27      | 65.97    | 93       | 0.22  |
| Flood Duration  | Calculated as the total number of days the river level remained above 450 cm                                                                                   | 0       | 27.85    | 103      | 0.97  |
| Flood Intensity | Defined as the maximum annual level recorded in the river (cm)                                                                                                 | 334     | 567.38   | 791      | 0.18  |
| Early season    | Magnitude of Median Quarterly: characteristic of the flow regimes from the perspective of median quarterly of October, November, December                      | 5544.12 | 8002.96  | 12083.13 | 0.13  |
| Late season     | Magnitude of Median Quarterly: characteristic of the flow regimes from the perspective of median quarterly of January, February, March (equivalent to 1 year). | 6952.13 | 10219.06 | 14699.6  | 0.19  |

### 3.2.3 Fisheries Data

From January 1987 to December 2018, the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia) of the State University of Maringá, with support from Itaipu Binacional, conducted monthly fisheries monitoring. This monitoring encompassed two sections of the Itaipu Reservoir - the fluvial and transition zones – and the Paraná River upstream of this reservoir. Fisheries data were obtained through a network of fisher associations and colonies, using questionnaires completed by artisanal fishers. These fishers employed various fishing gears commonly employed in artisanal fishing, including gill nets, cast nets, longlines, and hooks. The questionnaires recorded the number of fishing effort (number of fishing days), species caught, total weight (kg) of all individuals of the species in the sampled month, and date of capture. Three primary variables were extracted from these records: fisher identification, capture effort (fisher/day), and the weight (kg) of each species caught. These variables were used to estimate monthly yield as catch per unit of effort (CPUE;  $\text{kg.fisher}^{-1}.\text{day}^{-1}$ ) for individual migratory species, serving as a proxy for abundance. The common names of the species present in the questionnaires were replaced with their scientific names, according to the specialized literature (Pavanelli et al. 2023; Dagosta et al. 2024).

The multispecies nature of the Itaipu Reservoir fishery, combined with the use of diverse gear types, makes the accurate determination of species-specific fishing effort challenging. To minimize this, an algorithm was developed to classify individual fishers. A fisher was designated as a species-specific fisher if they recorded catches of that species in at least five distinct months. Thus, their fishing effort was accounted for every month they fished, regardless of whether they caught that particular species in each instance. On the other hand, when a fisher did not meet this criterion (i.e., fewer than five months with catches), their effort was only considered for the months in which they actually captured the species. This approach addresses two potential biases in CPUE calculation. Simply accounting for the effort of all fishers across all species would underestimate CPUE, as varied fishing strategies lead to species-specific targeting. Conversely, considering only the effort in months when a capture occurred would overestimate CPUE, by ignoring periods of zero catches (when a fisher failed to capture the target species).

This study evaluated migratory species with consistent annual abundance records throughout the study period: *Piaractus mesopotamicus* (Holmberg, 1887), *Prochilodus lineatus* (Valenciennes, 1836), *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829), *Pterodoras*

*granulosus* (Valenciennes, 1821), *Rhinelepis aspera* (Spix & Agassiz, 1829), *Salminus brasiliensis* (Cuvier, 1816), and *Zungaro jahu* (Ihering, 1989). Other migratory species, while present in the fishery, were excluded due to inconsistent annual targeting, rare catches, or abundance likely driven by stocking programs rather than natural recruitment.

The fisheries of Itaipu Reservoir were significantly impacted by its impoundment (Okada et al. 2005; Agostinho et al. 2007). The fisheries exhibited the standard boom-and-bust often associated with impounding rivers, as well as the reservoir filling period during which reservoirs typically experience a heterotrophic phase (Agostinho et al. 1999). This phase is characterized by an increase in nutrients, which promotes greater primary productivity (Okada et al. 2005; Agostinho et al. 2008). Preliminary analyses of the fishery data indicated catch rates for most species declined precipitously in the decade after impoundment of Itaipu Reservoir, leveling off for most species around the mid-1990s, as suggested by exploratory change-point regression analyses. Thus, for this study we only considered the fisheries in the 23 years from 1995 to 2018, as earlier data likely confounded the effect of impoundments with the effect of floods, and data beyond 2018 were not available.

### 3.2.4 Data Analysis

To assess changes in the flow regime of the Upper Paraná River floodplain, we compared 34 years of flood indicators (1985-2018), consisting of 14 years pre-impoundment and 20 years post-impoundment. Beginning with a year-by-flood IHA indicator table, a similarity matrix was built with a Euclidian coefficient and subjected to a permutation analysis of variance (PERMANOVA) (Anderson 2014). Prior to similarity computation, as needed some indicators were square-root transformed to reduce dispersion, and all indicators were normalized (zero mean and unit variance) to place them on the same scale. The PERMANOVA tested if the selected flow regime indicators differed after the dam was closed. If they did, we analyzed the differences graphically using box plots. We applied K-means cluster analysis on the similarity matrix to further characterize the hydrological regime as defined flood types. We used the Elbow Method to determine the optimal number of clusters based on the within-cluster sum of squares (WSS). A Hartigan-Wong clustering algorithm was implemented, which updates centroids as data points are reassigned to different clusters during the estimation. Lastly, we used the Wald-Wolfowitz runs test to determine if the sequence of floods was random or showed some type of sequential pattern.

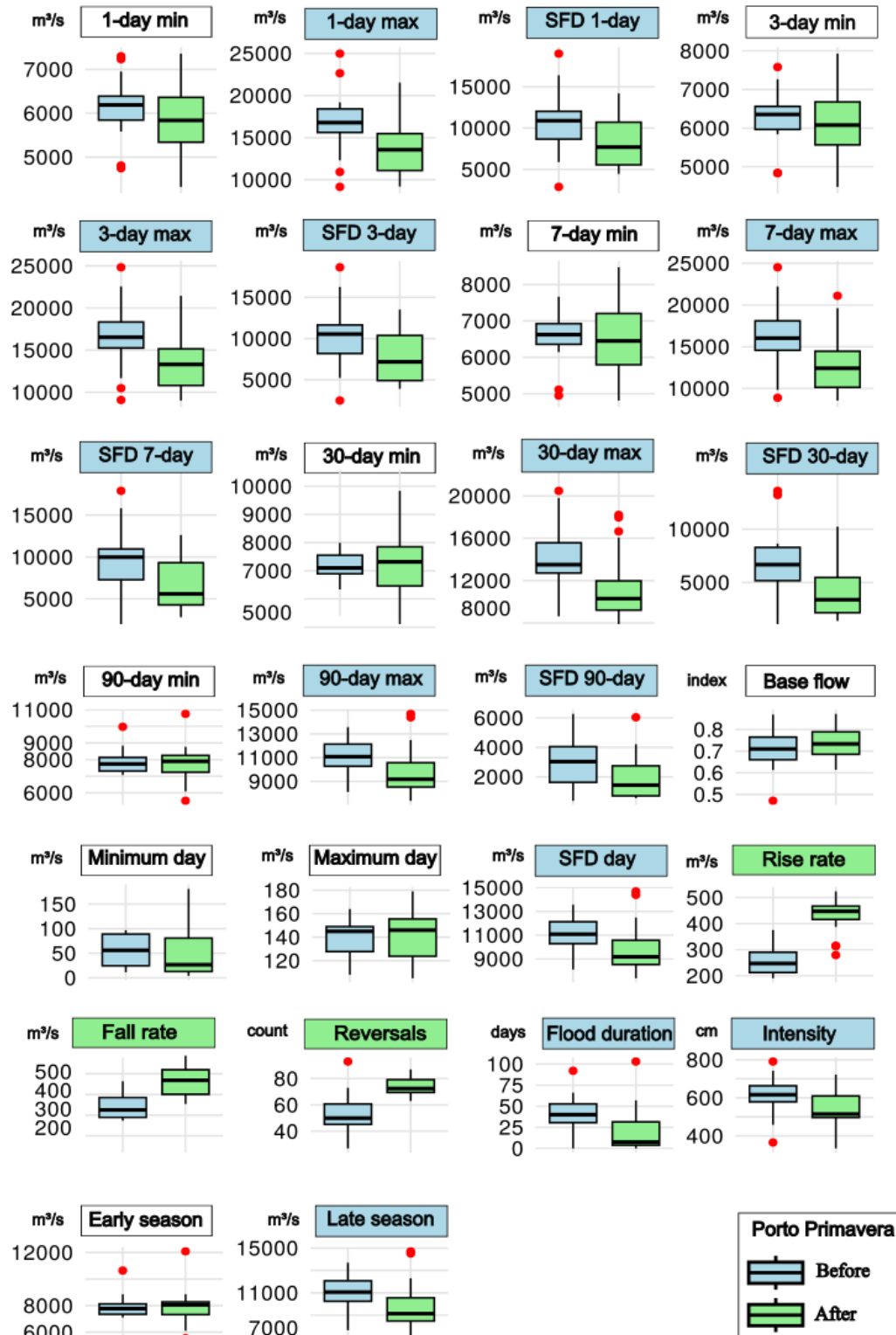
To test hypothesis that fish representation in the fisheries depends on the characteristics of the flood, we tested if species catch rates (CPUE) differed among the flood types assembled with the K-means clustering. A similarity matrix was generated using a Euclidean coefficient, starting with a year-by-species catch-per-effort table that was compiled using annual fishery averages. Before computing similarity, catch rates underwent a square-root transformation to diminish dispersion and then normalized (zero mean and unit variance) by species to place all fisheries in the same scale. A PERMANOVA was performed on this similarity matrix to determine whether the water regime types were linked to fishery yield (seven species). Besides water flood type, a class variable in the PERMANOVA included spatial section (upstream, fluvial, transition), and the interaction between flood type and section, to estimate if the effect of flood type depended on section. Local ecological knowledge indicates that juveniles spend roughly 1-2 years in the floodplain before starting to disperse into adjacent rivers and the reservoir downstream where they begin entering the fishery (Gomes and Agostinho 1997). Thus, the PERMANOVA was repeated five times, each with an added year lag, to assess the impact of the flood type on the fishery 1-5 years post-event. We projected no flood influence early and late, but some influence in the intervening years. We also projected that different species would dominate the fishery in different years post flood, due to differential recruitment pace, and dwindling effects 5 years post-event as the effects of a flood begin to fade or become intertwined with recruitment from subsequent floods. It was not possible to examine the interplay of consecutive flood types because it would require a longer time series than the 23 years currently available. If statistically significant ( $p < 0.05$ ) effects were identified by the PERMANOVA, we used radar charts to provide a visual representation of the flooding patterns at different delays and their effects on the capture of different species. Lastly, if the PERMANOVA identified a section effect, post-hoc pairwise tests were applied for multiple group comparisons.

All analyses were performed in R software, version 4.2.2 (R Development Core Team, 2022). Cluster analysis was performed with the k-means function, both from the stats package. The adonis function was used for PERMANOVA, and pairwise comparisons were made with the pairwise.adonis function, available in the *vegan* package. To graphically show distribution of hydrological indicators box plots were created using *ggplot2* package. Similarly, to graphically demonstrate the effects of different flood patterns on species abundance, radar charts were created

using the *fmsb* package (Nakazawa 2019). The Wald-Wolfowitz runs test was performed using the *tseries* package.

### 3.4 Results

Our findings demonstrated that the construction of the Porto Primavera Dam altered the hydrologic regime of the floodplain downstream. This was revealed by the PERMANOVA analysis, which showed significant global differences in the hydrologic indicators between the years before and after the construction of the dam ( $pseudo-F = 3.84$ ;  $p = 0.05$ ). Most indicators contributed to the global difference. Specifically, 14 of the 26 indicators evaluated exhibited higher levels before the dam, three after the dam, and nine showed no significant difference (Figure 2). Pre-dam flood regimes were distinguished by significantly higher 1-, 3-, 7-, 30-, and 90-day maximum flows, as well as greater flow differences. Furthermore, indicators such as SFD-day, flood duration, flood intensity, and late-season flow were higher before the dam filling. Post-dam, rise rate, fall rate, and flow reversals exhibited a notable increase. No substantial differences were apparent for minimum flow indicators (1-, 3-, 7-, 30-, and 90-day minima), base flow, early season flow, minimum day, or maximum day. The Indicators of Hydrologic Alteration (IHA) identified the flow alterations resulting from Porto Primavera Dam operation, with changes primarily reflected in reductions of maximum flow values.



**Figure 2** | Hydrological Indicators of the Upper Parana Floodplain before and after the Porto Primavera Dam. The boxes with metric names are color coded as light blue if higher before the

dam, green if higher after the dam, and uncolored if no obvious difference (see Table 1 for hydrological variables).

The hydrologic indicators were separated into four unique clusters by the Hartigan-Wong algorithm ( $pseudo-F = 34.9$ ;  $p < 0.001$ ). Each cluster represents a distinct flood pattern (Table 2). The four clusters were named considering their mean metric scores. The first cluster, *small floods*, represented mild inundations characterized by low intensity, rapid increase, short duration, and high rates of reversals. This type of flood exhibited low minimum and low maximum values, indicating a smaller magnitude and extent of floods. The second cluster, *medium floods*, were distinguished by longer duration and intensity, with a moderate impact on the hydrologic regime. The third cluster, *large floods*, were marked by high intensity and prolonged duration, with high flow peaks. Lastly, the fourth cluster, *erratic floods*, exhibited significant seasonal fluctuations in hydrologic indicators, including intermediary day maxima (1-, 3-, 7-, 30-, 90-day), seasonal flow difference, and late season. These floods were characterized by short duration and low intensity, yet they were marked by high fall rates, indicating rapid drops in water levels. In all, 26% of the floods were categorized as small, 26% as medium, 18% as large, and 30% as erratic. All the small floods occurred after Porto Primavera Reservoir was completed, whereas the medium, large, and erratic floods occurred before and after installation of the dam (Table 2). Figure S1 illustrates the flood categories and their associated patterns. The Wald-Wolfowitz runs test revealed the four types of floods occurred randomly over years (Wald-Wolfowitz  $Z = 0.2$ ,  $p = 0.85$ ).

**Table 2** | Clusters of Hydrological Descriptors by Year and Characterization of Flood Patterns

| Clusters       | Years                                                               | Variables                                                                                                                                                                                                                                                                                                    |
|----------------|---------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Small floods   | 2000; 2003; 2008;<br>2012; 2014; 2016;<br>2017; 2018                | <ul style="list-style-type: none"> <li>• High: Min day, reversals, rise rate.</li> <li>• Low: 1, 3, 7, 30, 90 -day min, 1, 3, 7, 30, 90-day max, SFD of 1, 3, 7, 30, 90-day, max day, SFD of max and min day, flood duration, intensity, OND, JFM, fall rate.</li> <li>• Middle: Base index flow.</li> </ul> |
| Medium floods  | 1993; 1995; 1997;<br>1999; 2005; 2007;<br>2011; 2013                | <ul style="list-style-type: none"> <li>• High: 1, 3, 7 and 30-day min, base flow index, max day, SFD of 7-day, flood duration, intensity, fall rate.</li> <li>• Middle: Reversals, rise rate</li> </ul>                                                                                                      |
| Erratic floods | 1987, 1988; 1990;<br>1991; 1994; 1998;<br>2001; 2002; 2004,<br>2015 | <ul style="list-style-type: none"> <li>• Middle: 1, 3, 7, 30, 90 -day max, SFD of 1, 3, 7, 30, 90 -day, fall rate, max day, JFM.</li> </ul>                                                                                                                                                                  |

|              |                                       |                                                                                                                                                                                                                                                                                                     |
|--------------|---------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Large floods | 1989; 1992; 1996;<br>2006; 2009; 2010 | <ul style="list-style-type: none"> <li>• High: 1, 3, 7, 30, 90-day min, 1, 3, 7, 30, 90-day max, SFD 1, 3, 7, 30, 90-day, SFD max and min day, OND, JFM, fall rate.</li> <li>• Low: Base index flow, min day, reversals, rise rate</li> <li>• Middle: max day, flood duration, intensity</li> </ul> |
|--------------|---------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|

In relation to the hypothesis that different flood patterns differentially influence the fishery yield of migratory fish, the PERMANOVA analyses demonstrated significant effects of flood patterns across several of the five time lags, and effects of spatial zones. In all the five delays tested, the spatial zones consistently showed significant effects on species, suggesting there were differences in fishery catches across spatial zones. Pairwise PERMANOVA showed that fisheries composition in the transition zone was different from that in the fluvial and the upstream zones, but that there were no statistical differences between the fluvial and upstream zones except with the 3-year lag, when all zones differed (Table 3). In general, the transition zone tended to have lower catches of most species but higher catches of *P. lineatus*. Moreover, there were no significant interactions ( $p > 0.76$ ) between zone and flood type, suggesting that the effect of the flood type was consistent across spatial zones. Because of the absence of interaction, the results that follow focus on flood types and delayed impacts and disregard spatial zones.

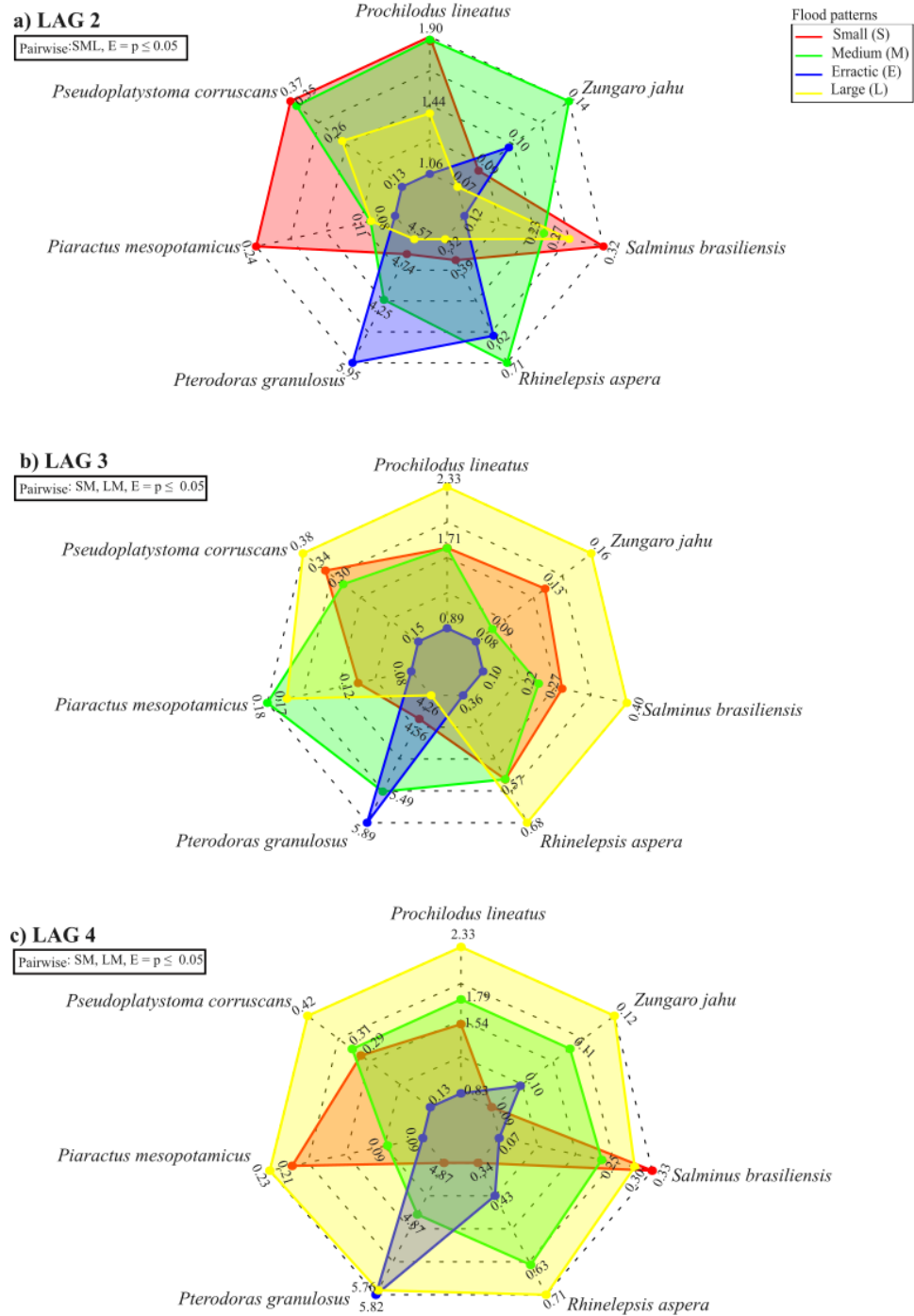
Flood types significantly influenced fisheries yield in subsequent years. While no effect were detected with the a 1-year delay ( $pseudo-F = 1.1$ ;  $df = 3$ ;  $p = 0.37$ ) or the 5-year delay ( $pseudo-F = 1.1$ ;  $df = 3$ ;  $p = 0.31$ ), significant effects were observed for the 2-year delay ( $pseudo-F = 2.00$ ;  $df = 3$ ;  $p = 0.04$ ), 3-year delay ( $pseudo-F = 6.1$ ;  $df = 3$ ;  $p < 0.01$ ), and 4-year delay ( $pseudo-F = 3.4$ ;  $p < 0.01$ ). Pairwise comparisons for 2-, 3-, and 4-year delays indicated that erratic flood types produced distinct fisheries yield compared to small, medium, and large floods ( $t \geq 1.6$ ;  $p \leq 0.05$ ). Moreover, for the 3- and 4- year delays, small and medium floods showed similar yields ( $t \geq 1.0$ ;  $P \geq 0.28$ ), as did medium and large floods ( $t \geq 1.2$ ;  $P \geq 0.08$ ). However, small and large floods resulted in significantly distinct yields ( $t \geq 1.7$ ;  $P \leq 0.03$ ). These findings corroborate local ecological knowledge, which suggests that flood patterns become noticeable approximately two years after the flood. The findings also indicate these effects persist for 2 to 4 years but diminish or become obscured by subsequent floods by the fifth year. Lastly, the analysis showed that small and large floods produced contrasting fishery yields, with medium floods yielding intermediate results (Table 3).

**Table 3** | Results of the PERMANOVA analysis showing the effects of flood type, zone, and their interaction over 5-year delays (lag) on the yield of migratory species in the fisheries. For the flood types S = small flood, M = medium flood, L = large flood, and E = erratic flood. For the zones F = fluvial, U = upstream, and T = transition. In the pairwise tests, floods not separated by a comma resulted in fishery yields that were not significantly different ( $p > 0.05$ ).

| Lag | Test     | Flood type      |             | Zone            |             | Flood type*Zone |          |
|-----|----------|-----------------|-------------|-----------------|-------------|-----------------|----------|
|     |          | <i>Pseudo-F</i> | <i>P</i>    | <i>Pseudo-F</i> | <i>p</i>    | <i>Pseudo-F</i> | <i>P</i> |
| 1   | overall  | 1.1             | 0.37        | 8.3             | <0.01       | 0.4             | 0.99     |
|     | pairwise |                 |             | FU, T           | $\leq 0.05$ |                 |          |
| 2   | overall  | 2.0             | 0.04        | 9.2             | <0.01       | 0.5             | 0.98     |
|     | pairwise | SML, E          | $\leq 0.05$ | FU, T           | <0.05       |                 |          |
| 3   | overall  | 6.1             | <0.01       | 21.1            | <0.01       | 0.8             | 0.76     |
|     | pairwise | SM, LM, E       | $\leq 0.05$ | F, U, T         | <0.05       |                 |          |
| 4   | overall  | 3.4             | <0.01       | 10.2            | <0.01       | 0.6             | 0.92     |
|     | pairwise | SM, LM, E       | $\leq 0.05$ | FU, T           | <0.05       |                 |          |
| 5   | overall  | 1.1             | 0.31        | 8.5             | <0.01       | 0.4             | 0.99     |
|     | pairwise |                 |             | FU, T           | <0.05       |                 |          |

The fisheries were influenced by the flood pattern and by the time elapsed since those events (Figure 3). Erratic floods generally resulted in lower post-flood fishery yield, across all time delays, and for most of the seven migratory species studied, except for *P. granulosus*, which appeared to flourish in erratic floods.

Otherwise, different flood patterns favored distinct migratory species in varying ways and across different time delays. Large floods generally had longer-lasting impacts than small floods, as evidenced by their greater representation in catches 3-4 years post flood. Furthermore, the area of the radar charts representing small flood impacts tended to shrink with increasing time lags (Figure 3a-c), but the area representing major flood tended to expand, suggesting that large floods had longer-term repercussions. Lastly, large floods tended to benefit a wider range of species 3-4 years post floods, compared to small floods, which benefitted fewer, while erratic floods benefitted the fewest species.



**Figure 3|** Radar plot illustrates the contribution of flood patterns with a two-year delay (Lag 2) (a), three-year delay (Lag 3) (b), and four-year delay (Lag 4) to the abundance of migratory species.

### 3.4 Discussion

The operation of the Porto Primavera hydropower plant significantly modified the water flow of the Paraná River, resulting in substantial changes to the flood regime downstream in the

Upper Parana River floodplain. Prior to reservoir operation, the floodplain experienced more intense and prolonged floods, followed by slower recession rates, reflecting a natural flood pattern. This natural flood regime is crucial for maintaining floodplain dynamics and productivity (Junk et al. 1989; Junk et al. 2021), as it promotes habitat connectivity (Thomaz et al. 2007), increase the availability of trophic resources (Quirino et al. 2018; Bianchi-Costa et al. 2023), and provides essential environments for the development for various organisms. For migratory species, these floods act as a trigger for migration and spawning, facilitate eggs and larvae drifting (Carolsfeld et al. 2003) and ensure the survival and recruitment of young-of-the-year (Suzuki et al. 2009; Górski et al. 2011), thus supporting future fishery stocks (Makrakis et al. 2012).

Conversely, following the Porto Primavera operation, the controlled water flows led to smaller flood with rapid rise rate, high fall rate and more frequent flow reversals, significantly altering the flooding patterns of the Upper Paraná River floodplain (Stevaux et al. 2009). These observed flow alterations likely result from the Porto Primavera Reservoir operation, a common characteristic of reservoirs that homogenize flows by flood retention and extended water release. Artificial discharges from the hydroelectric facility are likely influencing aspects of the erratic flood patterns. However, it is important to acknowledge that such erratic flood events occurred both prior to and after the dam filling. Consequently, it is plausible that these erratic flood elements, unless generated by dams upstream of the Porto Primavera Reservoir, may be integral to natural flood regimes.

Changes in extreme flow magnitudes, particularly reductions in maxima, impact the dynamics of species with different reproductive patterns (Granzotti et al. 2018; Oliveira et al. 2020), especially migratory species (Agostinho et al. 2004; Oliveira et al. 2015). These species depend on an ideal period to initiate the spawning process (Baran and Myschowoda 2009). The reduced flows and unnatural discharges from the Porto Primavera may interfere with environmental signals, creating confusion and resulting in reduced migration or reproductive failures (Larinier et al. 2001; Sanches et al. 2006). Premature migration, induced by disrupted environmental cues, may result in excessive energy expenditure, as species may need time and resources to wait for the ideal spawning conditions, compromising migratory success (Baras and Lucas 2001). Conversely, late migration can expose them to adverse conditions, leading to reproductive failures (Welcomme and Halls 2004). Additionally, the reduction in maximum flows

restricts the amount of floodplain inundation, limiting critical habitats for juvenile fish (Agostinho et al. 2007; Opperman et al. 2010).

The study revealed that different flood patterns affected the yields of various species in distinct ways, depending on delay periods. These results are consistent with the established understanding that migratory species, particularly those dependent on floodplains, are strongly associated with the annual flood regime (Welcomme 1985). Consequently, interannual variation in the flood regimes directly influences species abundance, biomass, survival, growth and recruitment. These factors, in turn, ultimately determine fishery yields over multiple subsequent years, considering the species-specific recruitment rates and timeframes (Agostinho et al. 2004).

Small floods, characterized by short duration and low magnitude, although beneficial to some species, have a dissipating effect in subsequent years. These floods primarily influenced the abundance young-of-the-year (Oliveira et al. 2015) and early juvenile stages, with diminishing effects in subsequent years. We hypothesize that most species are adapted to small and medium floods, modalities already prevalent before the dam's filling. In the years when these types of floods occurred, most took place in October, coinciding with the onset of migration of many species (Agostinho et al. 2003).

Erratic floods exhibited high variability in hydrological metrics, with intermediate values in the magnitude of extreme events (1-, 3-, 7-, and 30-day minima), fall rates, and magnitude in late season. This flood pattern was featured by years with short or absent floods, primarily occurring from January onward (Suzuki et al. 2009). These years coincided with the filling period of the Porto Primavera Reservoir, which may explain the variability of these floods (Stevaux et al. 2009; Souza Filho et al. 2016). This flooding pattern favored mostly *P. granulosus* a species that spawns later, between January and March, compared to other species (Agostinho et al. 2003). Moreover, this species utilizes a variety of reproductive habitats, including floodplains, lateral tributaries of the Itaipu Reservoir, and even the reservoir itself (Makrakis et al. 2007).

Large floods, characterized by high intensity and duration, featured elevated flow peaks in both periods (October-December and January-March). These floods significantly impacted fisheries, with increased yields observed for six of seven study species (excluding *P. granulosus*) three years after spawning. After a 4-year delay, all study species showed significant yield increases, indicating the lasting and widespread impact of large floods on the ecosystem. Large floods are positively associated with higher young-of-the-year recruitment, as they promote

increased habitat diversity, greater trophic resources availability, and enhanced juvenile survival, due to larger body sizes at lagoon departure, thus reducing the risk of predation (Suzuki et al. 2009; Oliveira et al. 2020).

These flood patterns reflect flow regulation by hydroelectric dams, balancing energy production with natural flow, which is crucial for migratory fish survival. Alterations in flood timing and duration directly affect species recruitment and survival, with prolonged floods yielding the most favorable outcomes by enhancing habitat diversity and food availability, leading to significant increases in young-of-the-year abundance (Oliveira et al. 2015).

In summary, the results showed that there were differences in the hydrological indicators before and after the operation of the Porto Primavera hydroelectric plant. The post-dam period was characterized by a higher flow change rate, which is one of the main impacts that such projects have on watercourses. We also observed spatial differences in the fishery yield of migratory species, with the transition zone tending to have lower yields compared to the riverine and upstream zones. These results suggest a decline in suitable habitats within the reservoir. Our study also demonstrated that different flood patterns benefit different species. Large floods, characterized by high intensity and prolonged duration, were the most beneficial to all species after 3 and 4 years of flooding. These findings highlight the need for hydroelectric projects balancing the operational needs of the system with the ecological needs of migratory species and other organisms living in dammed environments.

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#### 4 FINAL CONSIDERATIONS

A long-term series of fish landing data from the Itaipu Reservoir was evaluated, highlighting the impacts of impoundment on fisheries. The results demonstrated significant effects on species' functional traits and emphasized the influence of flood pulses from the upstream

floodplain on the fish landings of migratory species. The findings indicated that the composition of fish landings in the Itaipu Reservoir and its upstream reaches is influenced by spatial and temporal gradients. Species with different functional traits were selected according to the characteristics of the distinct reservoir zones. In the reaches that still preserve original lotic characteristics, such as the upstream area, higher abundance was observed for all functional traits compared to the reservoir zones. This underscores the importance of impounded reaches for maintaining fish assemblages, as well as their role in ecosystem service provision, considering that the high variability in the abundance of certain traits was offset by the presence of other functionally redundant species. Changes were also found in the hydrological descriptors of the Upper Paraná River floodplain following the onset of operations at the Porto Primavera Dam. Prior to dam operation, flood regimes were characterized primarily by high maximum discharges. After dam operation began, however, an increase was observed in the rates of rise, fall, and reversal of flows, indicating greater instability in flood types. In terms of migratory fish landings, differences were observed across zones, with the transition zone (within the reservoir) showing lower catches compared to the upstream (fluvial and lotic) zones, reinforcing the impact of impoundment on these populations. The results also indicated that different flood types benefited different migratory species, with large floods characterized by higher intensity and duration being more beneficial to all species, particularly three to four years after the event. These findings have important implications for fish conservation and fishery sustainability in the region. The results reinforce the importance of incorporating the ecological requirements of fish assemblages into dam operations. Such measures are crucial not only for maintaining biodiversity but also for ensuring the resilience and continuity of fishing activities, which are essential for the communities that depend on them.

**APPENDIX A - Table S1.** Functional traits of species captured in the Itaipu Reservoir and upstream.

**Table S1.** Functional traits of species captured in the Itaipu Reservoir and upstream. Trophic: Pl = Planktivorous, Pis = Piscivorous, Om = Omnivorous, Ins = Insectivorous, Inv = Invertivorous, He = Herbivorous, De = Detritivorous. Habitat use: Pel = Pelagic, De = Demersal, Be = Benthopelagic. Reproductive: PC = Parental care, Nm = non-migratory, LD = Long distance migratory, IF = Internal fertilization, EF = External fertilization.

|                                                                   |    | Trophic                                                                                                      |    |     |     |    |    | Habitat use           |    |    |    | Reproductive                                      |    |    |    |
|-------------------------------------------------------------------|----|--------------------------------------------------------------------------------------------------------------|----|-----|-----|----|----|-----------------------|----|----|----|---------------------------------------------------|----|----|----|
|                                                                   |    | Abujanra & Agostinho (2002);<br>Delariva et al. (2013); Norma et al.<br>(1998; 2000); Oliveira et al. (2005) |    |     |     |    |    | Froese & Pauly (2024) |    |    |    | Agostinho et al. (2004);<br>Froese & Pauly (2024) |    |    |    |
| Species                                                           | Pl | Pis                                                                                                          | Om | Ins | Inv | He | De | Pel                   | De | Be | PC | Nm                                                | LD | IF | EF |
| <b>Myliobatiformes</b>                                            |    |                                                                                                              |    |     |     |    |    |                       |    |    |    |                                                   |    |    |    |
| <i>Potamotrygon</i> sp.                                           |    | X                                                                                                            |    |     |     |    |    |                       |    | x  | x  | x                                                 |    | x  |    |
| <b>Cypriniformes</b>                                              |    |                                                                                                              |    |     |     |    |    |                       |    |    |    |                                                   |    |    |    |
| <i>Cyprinus carpio</i> Linnaeus, 1758                             |    |                                                                                                              | x  |     |     |    |    |                       |    | x  |    | x                                                 |    |    | x  |
| <b>Characiformes</b>                                              |    |                                                                                                              |    |     |     |    |    |                       |    |    |    |                                                   |    |    |    |
| <b>Acestrorhynchidae</b>                                          |    |                                                                                                              |    |     |     |    |    |                       |    |    |    |                                                   |    |    |    |
| <i>Acestrorhynchus lacustris</i> (Lütken, 1875)                   |    | X                                                                                                            |    |     |     |    |    |                       |    | x  |    | x                                                 |    |    | x  |
| <b>Anostomidae</b>                                                |    |                                                                                                              |    |     |     |    |    |                       |    |    |    |                                                   |    |    |    |
| <i>Leporinus</i> spp.                                             |    |                                                                                                              |    |     |     | x  |    |                       |    | x  |    | x                                                 |    |    | x  |
| <i>Megaleporinus macrocephalus</i><br>(Garavello & Britski, 1988) |    |                                                                                                              | x  |     |     |    |    |                       |    | x  |    |                                                   | X  |    | x  |
| <i>Megaleporinus</i> spp.                                         |    |                                                                                                              | x  |     |     |    |    |                       |    | x  |    |                                                   | X  |    | x  |
| <i>Schizodon</i> spp.                                             |    |                                                                                                              |    |     |     | x  |    |                       |    | x  |    | x                                                 |    |    | x  |
| <b>Bryconidae</b>                                                 |    |                                                                                                              |    |     |     |    |    |                       |    |    |    |                                                   |    |    |    |
| <i>Brycon hilarii</i> (Valenciennes, 1903)                        |    |                                                                                                              | x  |     |     |    |    |                       |    | x  |    |                                                   | X  |    | x  |
| <i>Brycon orbignyanus</i> (Valenciennes,<br>1850)                 |    |                                                                                                              |    |     |     | x  |    |                       |    | x  |    |                                                   | X  |    | x  |
| <i>Salminus brasiliensis</i> (Cuvier, 1816)                       |    | x                                                                                                            |    |     |     |    |    |                       |    | x  |    |                                                   | X  |    | x  |
| <b>Acestrorhamphinae</b>                                          |    |                                                                                                              |    |     |     |    |    |                       |    |    |    |                                                   |    |    |    |
| <i>Astyanax lacustris</i> (Lütken, 1875)                          |    |                                                                                                              | x  |     |     |    |    |                       |    | x  |    | x                                                 |    |    | x  |
| <b>Characinae</b>                                                 |    |                                                                                                              |    |     |     |    |    |                       |    |    |    |                                                   |    |    |    |

|                                                          |   |   |   |   |   |   |   |   |
|----------------------------------------------------------|---|---|---|---|---|---|---|---|
| <i>Galeocharax gulo</i> (Cope, 1870)                     | x |   |   | x |   | x |   | x |
| Cynodontidae                                             |   |   |   |   |   |   |   |   |
| <i>Rhaphiodon vulpinus</i> Spix & Agassiz, 1829          | x |   |   | x |   | x | x | x |
| Erythrinidae                                             |   |   |   |   |   |   |   |   |
| <i>Hoplerethrinus unitaeniatus</i> (Agassiz, 1829)       | x |   |   | X |   |   | x | x |
| <i>Hoplias</i> spp.                                      | x |   |   |   |   | x | x | x |
| Hemiodontidae                                            |   |   |   |   |   |   |   |   |
| <i>Hemiodus orthonops</i> Eigenmann & Kennedy, 1903      |   |   | x |   | x |   | x | x |
| Prochilodontidae                                         |   |   |   |   |   |   |   |   |
| <i>Prochilodus lineatus</i> (Valenciennes, 1837)         |   |   | x |   | x |   | X | x |
| Serrasalminae                                            |   |   |   |   |   |   |   |   |
| <i>Colossoma macropomum</i> (Cuvier, 1818)               | x |   |   |   | x |   | X | x |
| <i>Metynnis lippincottianus</i> (Cope, 1870)             | x |   |   | x |   | x | x | x |
| <i>Myloplus tiete</i> (Eigenmann & Norris, 1900)         |   | x |   |   | x |   | x | x |
| <i>Piaractus mesopotamicus</i> (Holmberg, 1887)          |   | x |   | x |   |   | X | x |
| <i>Serrasalmus</i> spp.                                  | x |   |   | X |   | x | x | x |
| Gymnotiformes                                            |   |   |   |   |   |   |   |   |
| Gymnotidae                                               |   |   |   |   |   |   |   |   |
| <i>Gymnotus inaequilabiatus</i> (Valenciennes, 1839)     |   | x |   |   | x | x | x | x |
| Rhamphichthyidae                                         |   |   |   |   |   |   |   |   |
| <i>Rhamphichthys hahni</i> (Meinken, 1937)               | x |   |   |   | x | x | x | x |
| Siluriformes                                             |   |   |   |   |   |   |   |   |
| Auchenipteridae                                          |   |   |   |   |   |   |   |   |
| <i>Ageneiosus</i> spp.                                   | x |   |   | X |   |   | x | x |
| <i>Auchenipterus osteomystax</i> (Miranda Ribeiro, 1918) |   | x |   |   | x |   | x | x |

|                                                               |   |   |   |   |   |   |   |
|---------------------------------------------------------------|---|---|---|---|---|---|---|
| <i>Trachelyopterus galeatus</i> (Linnaeus, 1766)              | x |   | x |   | x |   | x |
| Callichthyidae                                                |   |   |   |   |   |   |   |
| <i>Hoplosternum littorale</i> (Hancock, 1828)                 |   | x |   | x |   | x |   |
| Clariidae                                                     |   |   |   |   |   |   |   |
| <i>Clarias gariepinus</i> (Burchell, 1822)                    | x |   |   | x |   | x |   |
| Doradidae                                                     |   |   |   |   |   |   |   |
| <i>Pterodoras granulosus</i> (Valenciennes, 1821)             | x |   | x |   |   | X |   |
| Loricariidae                                                  |   |   |   |   |   |   |   |
| Hypostominae                                                  |   |   |   |   |   |   |   |
| <i>Hypostomus auroguttatus</i> Kner, 1854                     |   |   | x |   | x |   |   |
| <i>Hypostomus commersoni</i> Valenciennes, 1836               |   |   | x |   | x |   |   |
| <i>Hypostomus derbyi</i> (Haseman, 1911)                      |   |   | x |   | x |   |   |
| <i>Hypostomus microstomus</i> Weber, 1987                     |   |   | x |   | x |   |   |
| <i>Hypostomus regani</i> (Ihering, 1905)                      |   |   | x |   | x |   |   |
| <i>Hypostomus ternetzi</i> (Boulenger, 1895)                  |   |   | x |   | x |   |   |
| <i>Megalancistrus parananus</i> (Peters, 1881)                |   |   | x |   | x |   |   |
| <i>Pterygoplichthys ambrosetii</i> (Holmberg, 1893)           |   |   | x |   | x |   |   |
| Loricariinae                                                  |   |   |   |   |   |   |   |
| <i>Loricaria</i> sp.                                          |   |   |   |   |   |   |   |
| <i>Loricariichthys platymetopon</i> Isbrücker & Nijssen, 1979 |   |   | x |   | x |   |   |
| <i>Loricariichthys rostratus</i> Reis & Pereira, 2000         |   |   | x |   | x |   |   |
| Rhinelepininae                                                |   |   |   |   |   |   |   |
| <i>Rhinelepis aspera</i> Spix & Agassiz, 1829                 |   |   | x |   |   | X |   |
| Rhamdiinae                                                    |   |   |   |   |   |   |   |
| <i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)                  | x |   |   | x |   | x |   |
| Pimelodidae                                                   |   |   |   |   |   |   |   |



|                                                     |   |   |   |   |
|-----------------------------------------------------|---|---|---|---|
| <i>Plagioscion squamosissimus</i> (Heckel,<br>1840) | x | x | x | x |
|-----------------------------------------------------|---|---|---|---|

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**APPENDIX B - Table S2.** Mean abundance, standard deviation (SD), minimum, and maximum of trophic functional traits captured in the Itaipu Reservoir and upstream.

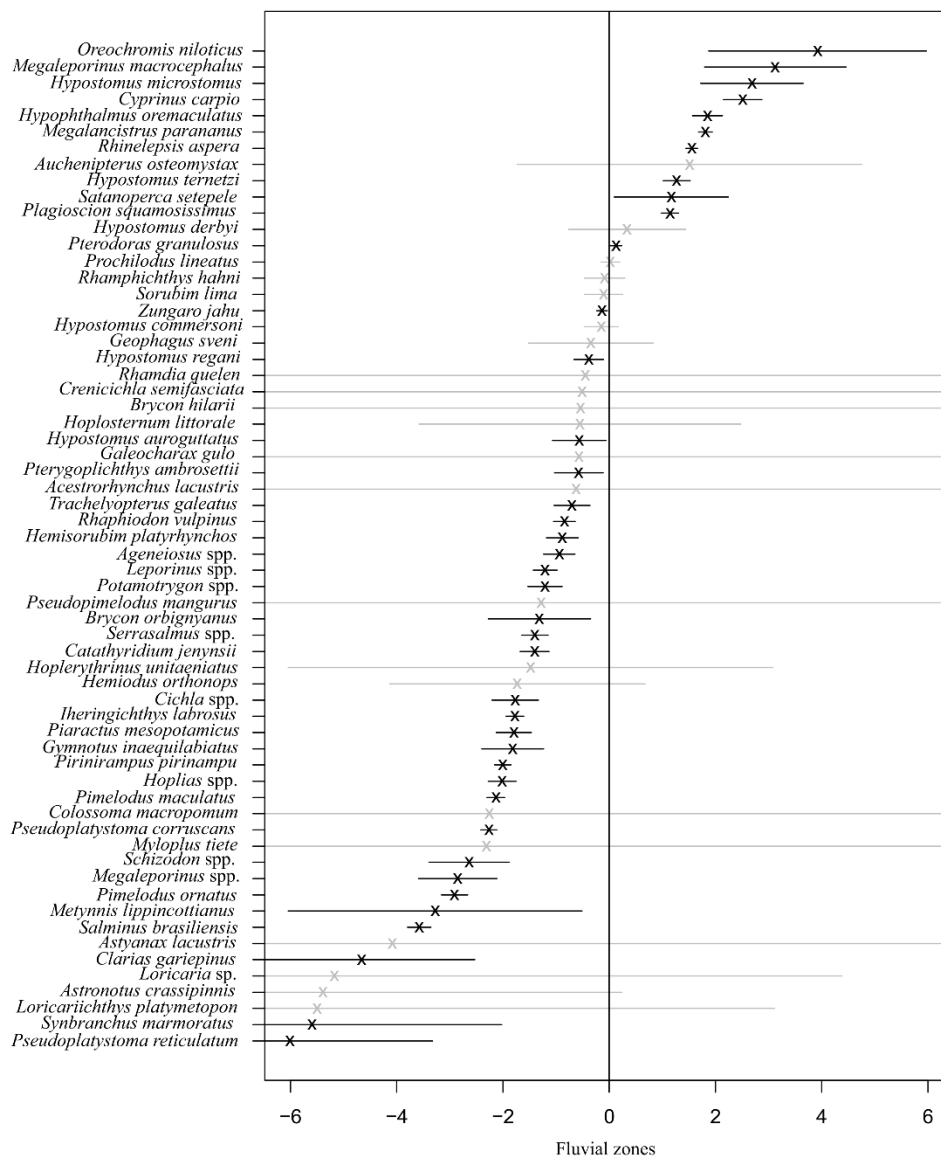
|               |         | Upstream | Fluvial | Transition | Lacustrine |
|---------------|---------|----------|---------|------------|------------|
| Planktivorous | Mean    | 0.12     | 0.32    | 1.86       | 2.72       |
|               | SD      | 0.35     | 0.65    | 1.58       | 2.90       |
|               | Minimum | 0        | 0       | 0          | 0          |
|               | Maximum | 3.8      | 6.16    | 8.57       | 16.07      |
| Piscivorous   | Mean    | 0.91     | 0.25    | 0.34       | 0.32       |
|               | SD      | 3.8      | 0.59    | 0.64       | 0.68       |
|               | Minimum | 0        | 0       | 0          | 0          |
|               | Maximum | 133      | 10      | 6.12       | 7.27       |
| Omnivorous    | Mean    | 1.70     | 1.07    | 0.54       | 0.27       |
|               | SD      | 3        | 2.44    | 1.33       | 0.52       |
|               | Minimum | 0        | 0       | 0          | 0          |
|               | Maximum | 28.2     | 21.28   | 18.2       | 5          |
| Invertivorous | Mean    | 0.45     | 0.06    | 0.12       | 0.18       |
|               | SD      | 1.05     | 0.25    | 0.14       | 0.21       |
|               | Minimum | 0        | 0       | 0          | 0          |
|               | Maximum | 12.5     | 6.88    | 0.75       | 1.92       |
| Insectivorous | Mean    | 9.85     | 2.11    | 0.08       | 0.17       |
|               | SD      | 16.2     | 7.32    | 0.38       | 1.16       |
|               | Minimum | 0        | 0       | 0          | 0          |
|               | Maximum | 115      | 108.5   | 5.10       | 19.09      |
| Herbivorous   | Mean    | 0.44     | 0.12    | 0.20       | 0.14       |
|               | SD      | 1.99     | 0.27    | 0.36       | 0.32       |
|               | Minimum | 0        | 0       | 0          | 0          |
|               | Maximum | 48       | 3.10    | 6          | 6.51       |
| Detritivorous | Mean    | 0.33     | 0.37    | 0.27       | 0.13       |
|               | SD      | 1.03     | 0.89    | 0.99       | 0.64       |
|               | Minimum | 0        | 0       | 0          | 0          |
|               | Maximum | 16.7     | 10.48   | 17.8       | 13.85      |

**APPENDIX C - Table S3.** Mean abundance, standard deviation (SD), minimum, and maximum of habitat use, and reproductive functional traits captured in the Itaipu Reservoir and upstream.

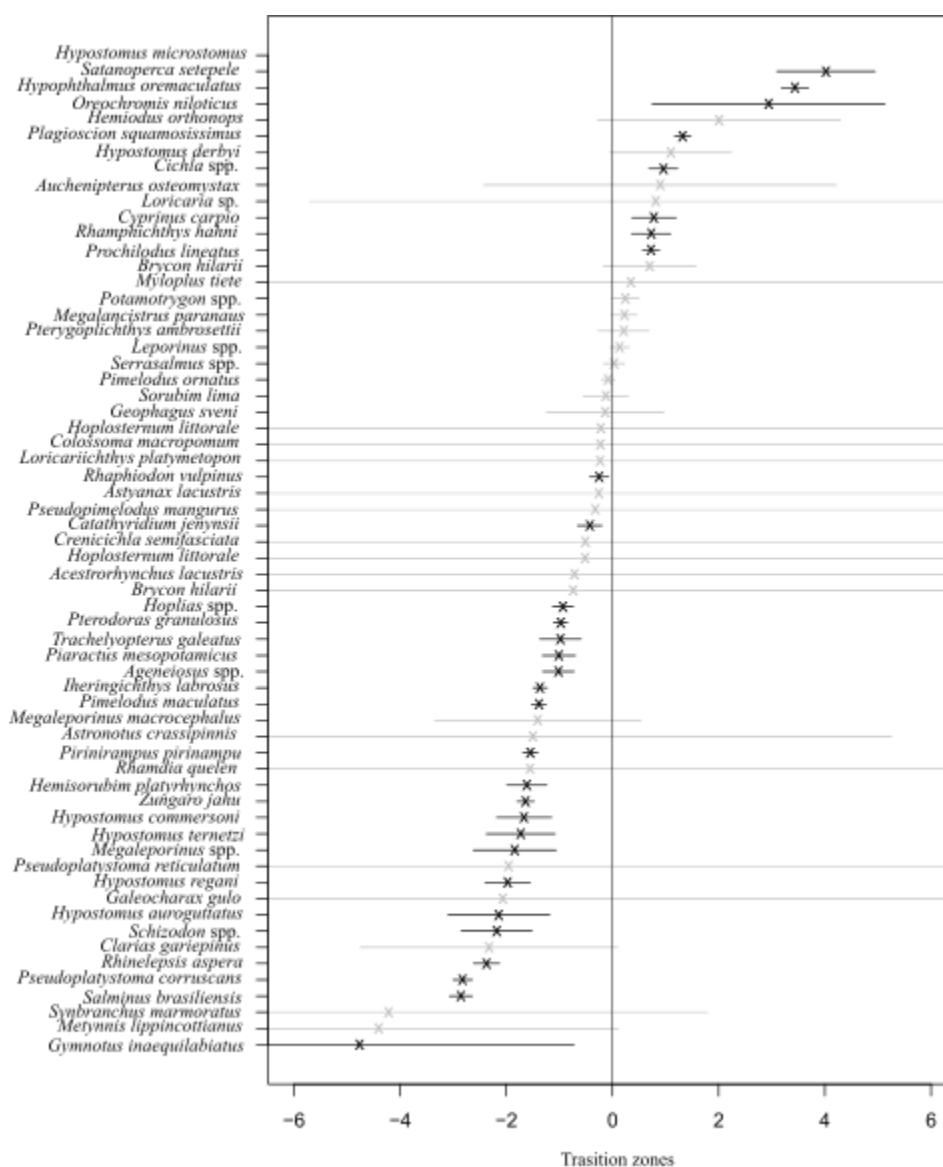
|                              |                         | Upstream | Fluvial | Transition | Lacustrine |       |
|------------------------------|-------------------------|----------|---------|------------|------------|-------|
| Position in the water column | Pelagic                 | Mean     | 0.98    | 0.16       | 0.155      | 0.25  |
|                              |                         | SD       | 7.03    | 0.61       | 0.173      | 0.27  |
|                              |                         | Minimum  | 0       | 0          | 0          | 0     |
|                              |                         | Maximum  | 133     | 10         | 2.36       | 5     |
|                              | Demersal                | Mean     | 0.80    | 0.54       | 0.35       | 0.25  |
|                              |                         | SD       | 2.10    | 1.57       | 0.99       | 0.90  |
|                              |                         | Minimum  | 0       | 0          | 0          | 0     |
|                              |                         | Maximum  | 30.5    | 21.3       | 18.2       | 16.1  |
|                              | Benthopelagic           | Mean     | 1.37    | 0.44       | 0.39       | 0.31  |
|                              |                         | SD       | 5.32    | 2.41       | 0.92       | 0.83  |
|                              |                         | Minimum  | 0       | 0          | 0          | 0     |
|                              |                         | Maximum  | 115     | 109        | 17.9       | 19.1  |
| Parental care                | Absence                 | Mean     | 1.07    | 0.579      | 0.534      | 0.399 |
|                              |                         | SD       | 3.48    | 1.52       | 1.16       | 1.03  |
|                              |                         | Minimum  | 0       | 0          | 0          | 0     |
|                              |                         | Maximum  | 133     | 21.3       | 18.2       | 16.1  |
|                              | Presence                | Mean     | 1.01    | 0.327      | 0.09       | 0.123 |
|                              |                         | SD       | 5.04    | 2.44       | 0.190      | 0.426 |
|                              |                         | Minimum  | 0       | 0          | 0          | 0     |
|                              |                         | Maximum  | 115     | 109        | 2.70       | 19.1  |
| Fertilization                | Non-migratory           | Mean     | 0.94    | 0.31       | 0.26       | 0.28  |
|                              |                         | SD       | 4.75    | 1.91       | 0.63       | 0.88  |
|                              |                         | Minimum  | 0       | 0          | 0          | 0     |
|                              |                         | Maximum  | 133     | 109        | 8.57       | 19.1  |
|                              | Long-distance migratory | Mean     | 1.30    | 0.89       | 0.61       | 0.28  |
|                              |                         | SD       | 2.48    | 2          | 1.43       | 0.75  |
|                              |                         | Minimum  | 0       | 0          | 0          | 0     |
|                              |                         | Maximum  | 28.2    | 21.3       | 18.2       | 13.9  |
| Internal                     | Mean                    | 0.322    | 0.49    | 0.108      | 0.115      |       |
|                              | SD                      | 1.02     | 2.01    | 2.88       | 0.36       |       |
|                              | Minimum                 | 0        | 0       | 0          | 0          |       |
|                              | Maximum                 | 10.3     | 109     | 5.11       | 5.59       |       |

|          |         |      |      |      |      |
|----------|---------|------|------|------|------|
| External | Mean    | 1.09 | 0.22 | 0.38 | 0.30 |
|          | SD      | 4.36 | 0.89 | 0.96 | 0.87 |
|          | Minimum | 0    | 0    | 0    | 0    |
|          | Maximum | 133  | 13.1 | 18.2 | 19.1 |

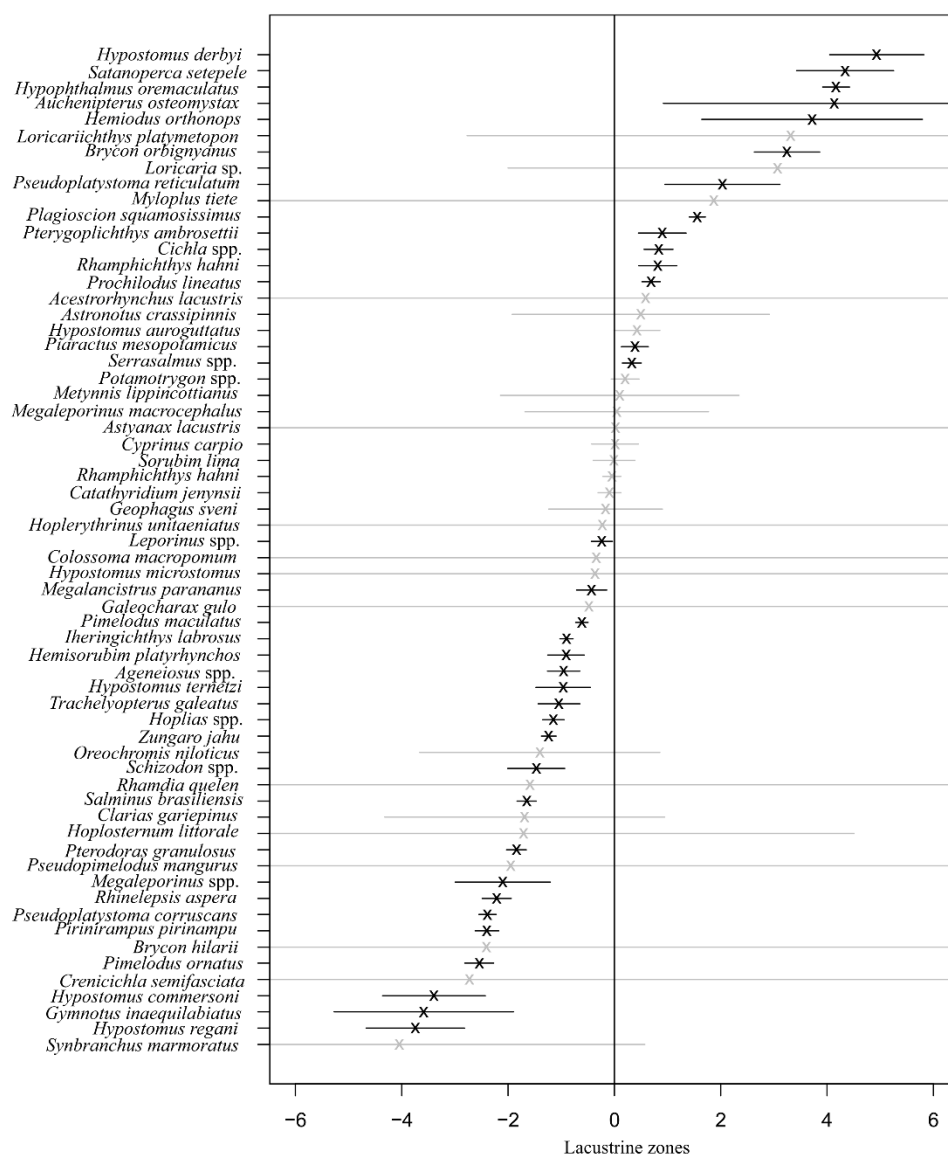
**APPENDIX D - Figure S1.** Estimates of the specific coefficients for the fluvial zone in the early years (five years after the start of the Itaipu Reservoir operation).



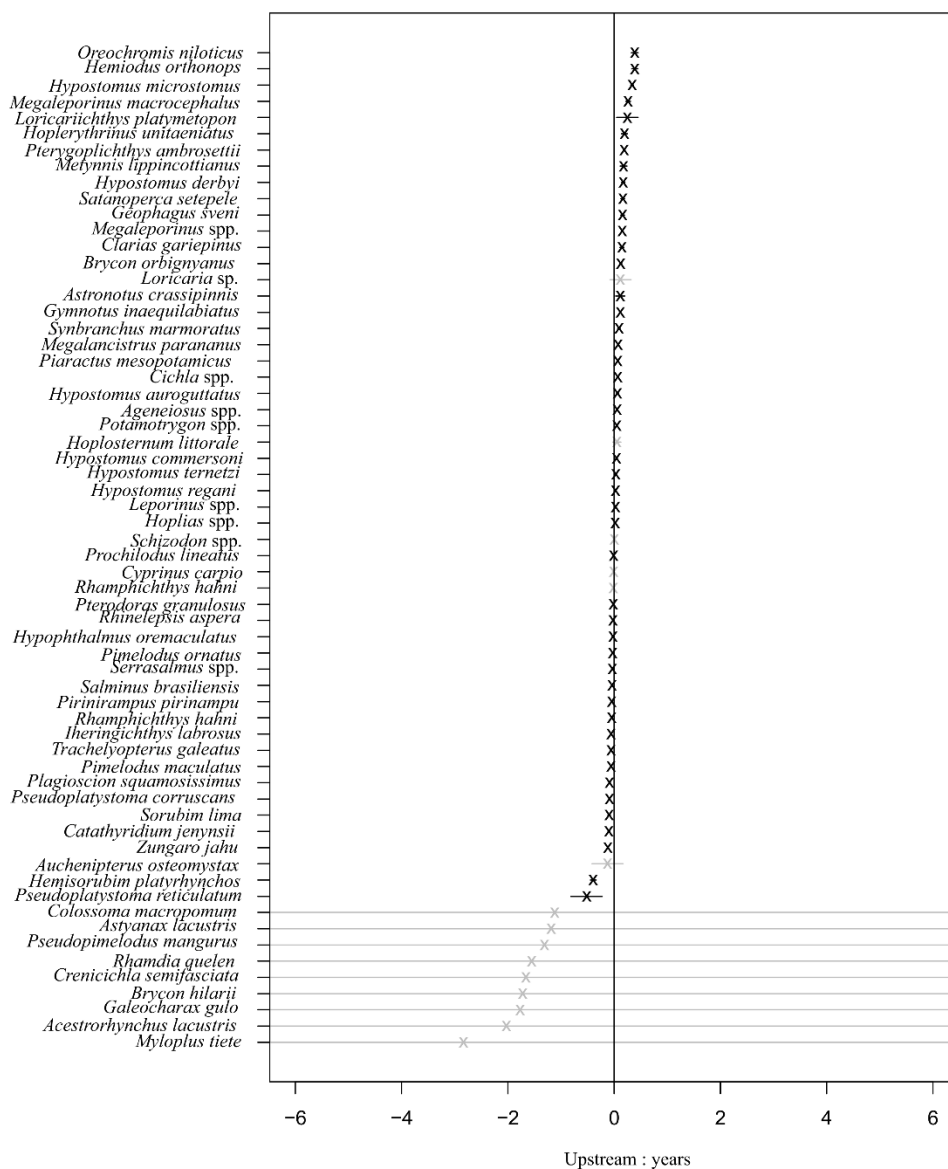
**APPENDIX E - Figure S2.** Estimates of the specific coefficients for the transition zone in the early years (five years after the start of the Itaipu Reservoir operation).



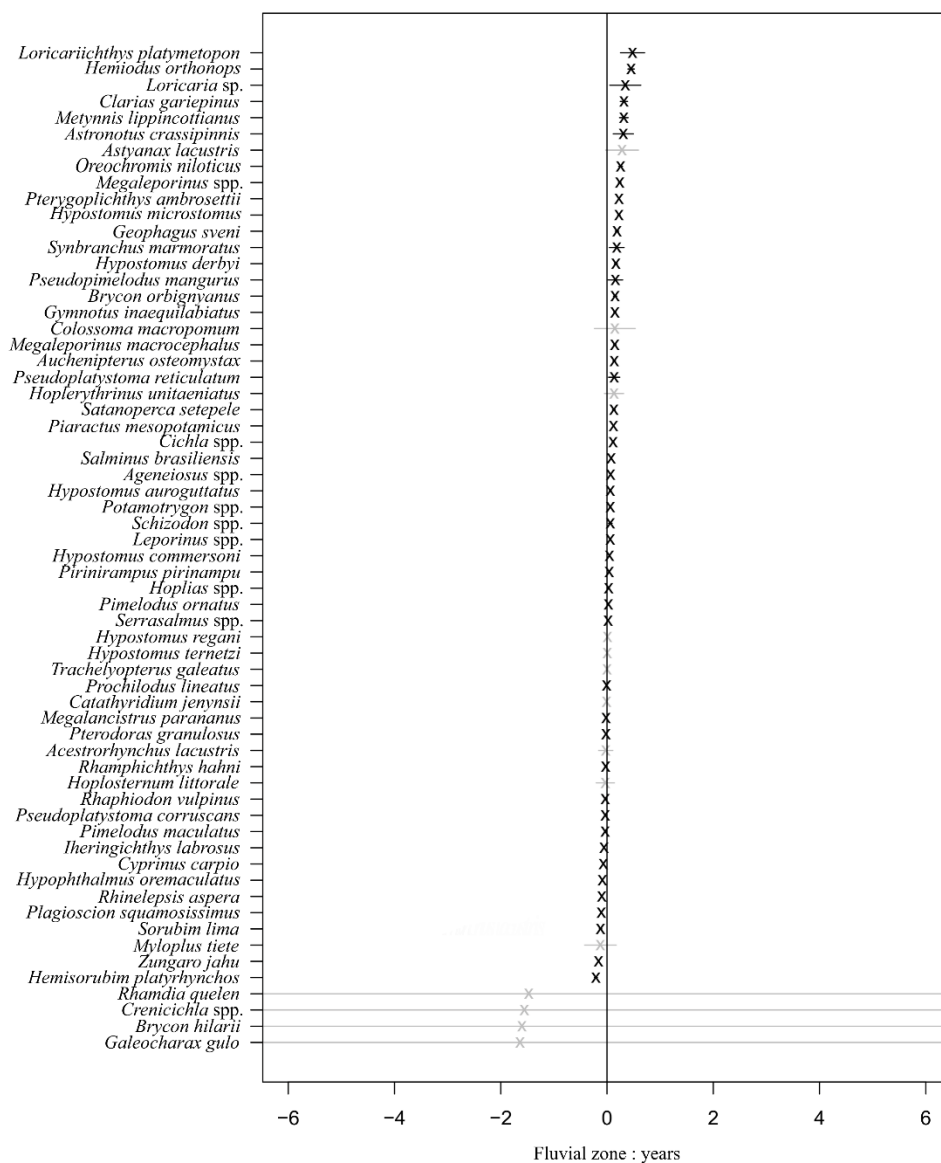
**APPENDIX F - Figure S3.** Estimates of the specific coefficients for the lacustrine zone in the early years (five years after the start of the Itaipu Reservoir operation).



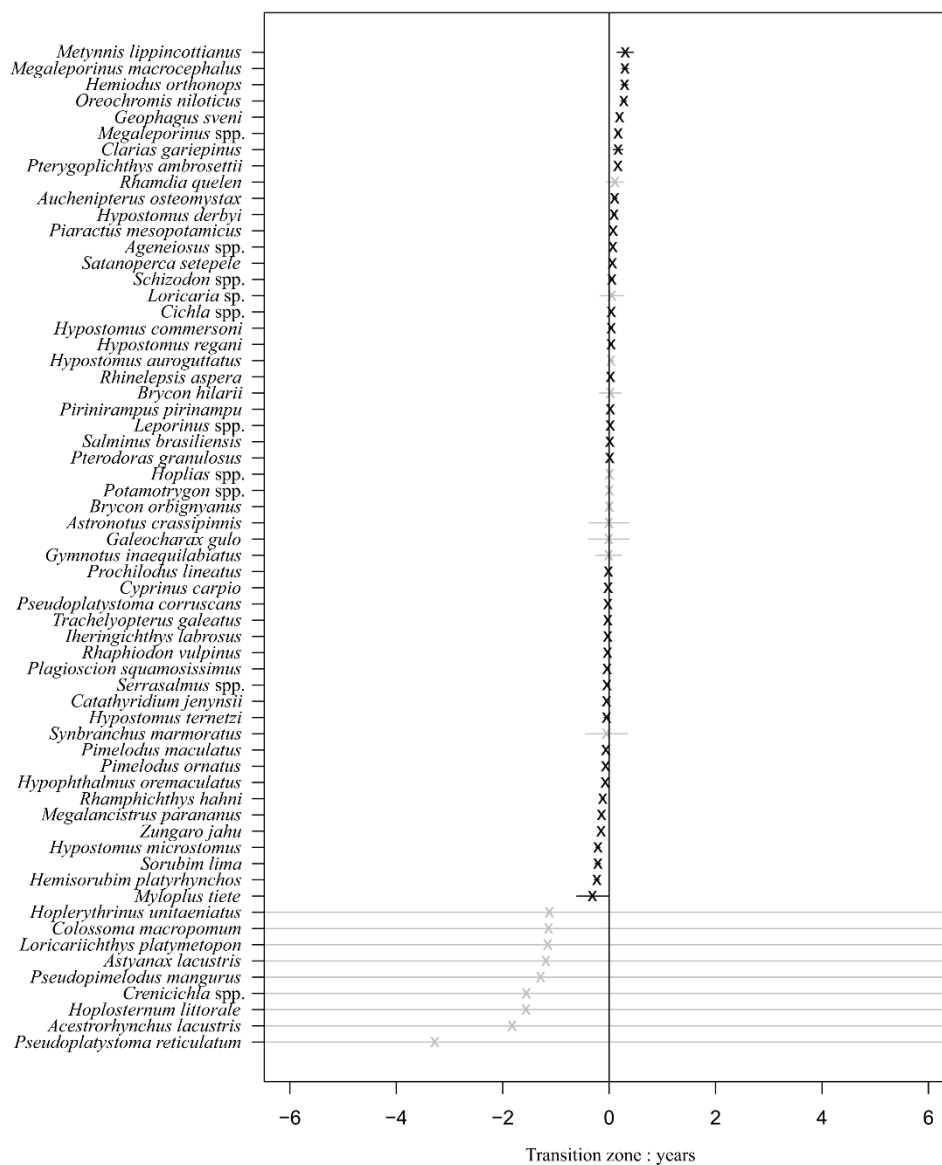
**APPENDIX G - Figure S4.** Estimates of the specific coefficients for the upstream subsequent years to the early years.



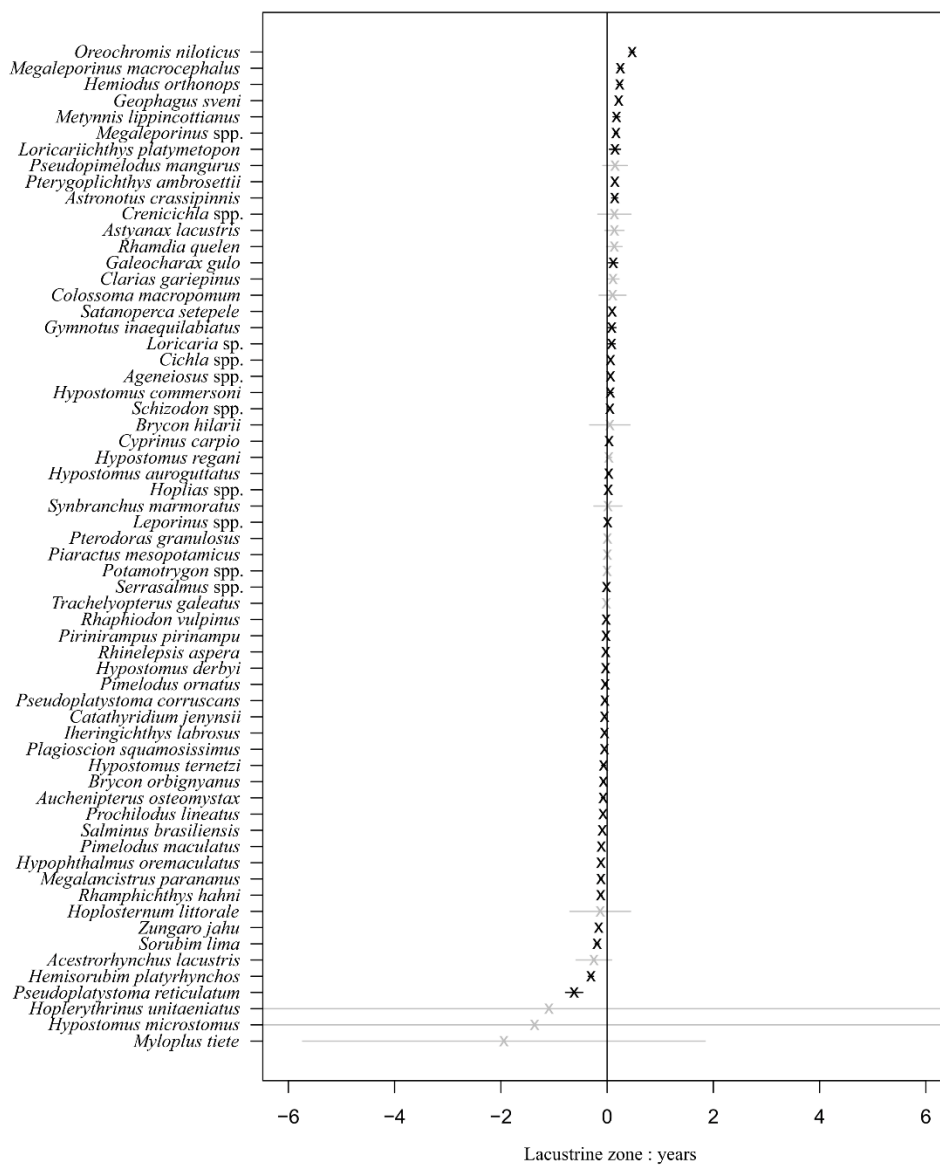
**APPENDIX H - Figure S5.** Estimates of the specific coefficients for the fluvial subsequent years to the early years.



**APPENDIX I - Figure S6.** Estimates of the specific coefficients for the transition subsequent years to the early years.



**APPENDIX J - Figure S7.** Estimates of the specific coefficients for the lacustrine subsequent years to the early years.



**APPENDIX K - Figure S8** Hydrological Indicators (square root transformed) and different flood patterns of the Upper Parana Floodplain.

