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**Effects of dam operation on stability, species interactions, and the
mechanisms underlying the synchrony of fish in reservoirs**

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2020

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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 Doutor em Ciências Ambientais.
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*Dedico ao meu espaço
multivariado de amor e
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De qualquer forma, você continuará assim. Vivendo como dá. E enquanto der. Procurando esticar o encontro que alegra e abreviar o que entristece. E a vida que vale a pena? Só pode ser uma. A sua. Esta mesma que você está vivendo desde que nasceu. Mas com tudo. Seus encontros, certamente. Mas também seus sonhos, suas ilusões, seus medos e esperanças.

(Clóvis de Barros Filho)

Efeitos do modo de operação da barragem sobre a estabilidade das interações e os mecanismos de sincronia das espécies de peixes em reservatórios

RESUMO

A construção de barragens está entre os principais impactos antropogênicos em ambientes de água doce. A primeira consequência dos barramentos é a formação de um reservatório à montante, que representa um ambiente completamente modificado, em relação ao rio natural. Impactos secundários, como as variações no nível da água, também podem ser considerados outros tipos de distúrbio. Embora vários estudos investigaram os processos que ocorrem em reservatórios, existe uma lacuna a respeito dos efeitos do modo de operação da barragem sobre o estado dos ecossistemas. A maioria das barragens é projetada para operar sob dois modos: acumulação (ACU) e fio d'água (FDA). Esses modos alternativos resultam em variações temporais muito distintas, com reservatórios ACU apresentando flutuações rápidas, enquanto reservatórios FDA possuem volume relativamente constante. Do mesmo modo, essa diferença na dinâmica temporal do nível da água provavelmente afeta a estabilidade desses ecossistemas. A fim de investigar como o modo de operação da barragem pode afetar a estabilidade temporal dos ambientes de água doce, foram utilizadas comunidades de peixes de dois reservatórios do rio Iguaçu, que operam sob modos diferentes. A hipótese testada foi que o reservatório ACU seria menos estável, considerando a heterogeneidade ambiental criada pelas variações frequentes no nível da água, e as interações entre as espécies seriam menos importantes para a estrutura da comunidade de peixes. Na primeira abordagem, o foco foi na estabilidade em termos da habilidade em resistir e se recuperar (i.e., resistência e resiliência) aos distúrbios. Na segunda abordagem, dados empíricos e simulações foram utilizados para verificar quais mecanismos (interações entre espécies, ou estocasticidade ambiental/demográfica) seriam subjacentes à sincronia das comunidades de peixes. Ao contrário do esperado, os resultados mostraram que o reservatório FDA foi menos estável do que o reservatório ACU e os mecanismos subjacentes à sincronia das espécies coincidiram entre os reservatórios, mas com papéis opostos. Mais especificamente, a dinâmica temporal imposta pela operação do reservatório FDA provavelmente enfraqueceu as relações espécie-ambiente, o que levou a uma comunidade menos estável. Embora os resultados sejam consistentes, são apenas indícios primários e as relações de causa-e-efeito entre o modo de operação da barragem e a estabilidade dos ecossistemas requer investigações futuras.

Palavras-chave: Competição interespecífica. Processos de nicho. Estocasticidade ambiental. Barramento. Manejo de reservatórios. Rio Iguaçu.

Effects of dam operation on stability, species interactions, and the mechanisms underlying the synchrony of fish in reservoirs

ABSTRACT

The construction of dams is among the main anthropogenic impacts in natural freshwater systems. The first consequence of impoundments is the formation of reservoirs upstream, which represents a completely new environment compared to the natural river. In addition to this primary impact, the variations in the reservoir water level may be considered another facet of disturbances. Although several studies investigated the processes that occur in reservoirs, there is a shortfall regarding the effects of the dam operation scheme on ecosystem health. Most dams are designed to operate under two almost contrasting schemes: storage (STR) and run-of-river (ROR). These alternative operation schemes result in very different temporal variations, with STR reservoirs presenting rapid fluctuations while ROR reservoirs have a relatively constant volume. Likewise, this difference in the temporal dynamics of water level likely affects the stability of these ecosystems. In order to investigate how the dam operation scheme could affect the temporal stability of freshwater ecosystems, we used the fish communities from two reservoirs in the Iguaçu River that operate under contrasting schemes. The hypothesis was that the STR reservoir would be less stable, considering the environmental heterogeneity created by frequent water level variations, and the interactions among species would be less important for the structure of the resident fish community. In the first approach, the focus was on stability in terms of the ability to resist and recover (i.e., resistance and resilience) to disturbances. In the second approach, empirical data and simulations were used to assess which mechanism (species interactions, environmental or demographic stochasticity) underlie the synchrony of fish communities. Contrary to the expectation, the results showed the ROR reservoir as less stable than the STR, and the mechanisms underlying species synchrony coincided between reservoirs but played opposite roles. More specifically, the temporal dynamics imposed by ROR operation may have weakened the species-environment relationships, which led to a less stable community. Although the results were consistent, they were only primary evidence and such cause-effect relationships between dam operation and its effects on ecosystem stability require further investigations.

Keywords: Interspecific competition. Niche processes. Environmental stochasticity. Impoundment. Reservoir management. Iguaçu River.

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1 INTRODUCTION

The modifications of natural habitats are among the primary causes of biodiversity decline and the loss of ecosystem functions (Fischer & Lindenmayer, 2007; Haddad et al. 2015). The construction of dams is among the major causes of landscape alterations in freshwater environments (Dudgeon et al. 2006) with notable effects immediately upstream (Baxter 1977; Dudgeon et al. 2006; Agostinho et al. 2004; Gubiani et al. 2010).

In rivers, once reservoirs for energy production are formed, the variations in water level resulting from the discharge control imposed by dams are considered disturbances with the potential to affect primary production, nutrient cycling, and the structure of biotic communities (Miranda et al. 2010). Therefore, directly or indirectly, these artificial variations in water level likely affect all aquatic organisms, from primary producers (phytoplankton, periphyton, and macrophytes), through consumers (zooplankton and aquatic invertebrates), to top predators such as fish (Miranda 2001; Kolding & van Zwieten 2012). For fish, variations in water level are assumed as the main abiotic disturbances and are intimately related to the spatial and temporal dynamics of species (Agostinho et al. 2007).

The way that most dams are operated can be classified into two main types: accumulation and run-of-river. The main difference between these operation schemes is related to the water retention-release strategy. Those dams operated under accumulation retain and release large amounts of water in the short-term, depending on the discrete demands of energy and variations in rainfall within a couple of weeks. Conversely, dams operated under run-of-river release virtually the same amount of water that flows from upstream, thus keeping a relatively constant water volume. This difference in operation is thereby fundamental for determining distinct patterns of variation of the reservoir water level.

Nowadays, the decision on the construction of dams and whether dams will operate under a given scheme is widely grounded on technical information about the potential for power supply and biogeophysical processes, with little contribution of local and regional biological requirements (Poff & Hart, 2002). This discrepancy probably emerges from the absence of robust data to evaluate the ecological consequences of

different dam operation strategies, especially when there is no specific legislation for each project (Winemiller et al. 2016).

For ecologists, it seems intuitive that the temporal dynamics of water level variations affect the population- and community-level dynamics of biological groups. Thus, it is possible to evaluate changes in these dynamics under frameworks that consider the ability of communities to resist and recover from disturbances (i.e., resistance and resilience; Ives et al. 2003) and the degree at which the abundances of species vary similarly across time (i.e., synchrony; Loreau and de Manzacourt, 2008). Here, I used approaches based on time-series to evaluate differences in the relationships among species, considering two reservoirs with contrasting operation schemes, assuming that it may act as one of the major drivers of community stability and the synchrony among species. These aspects were investigated from two approaches as follows.

First, time-series with standardized samplings were used to estimate parameters describing the stability of fish assemblages in terms of resistance and resilience, aiming at differences coinciding with each dam's operation scheme. Community stability was assessed using five metrics as obtained through first-order Multivariate Autoregressive Models (MAR(1); Ives et al. 2003). The hypothesis tested was that the higher frequency and intensity of water level variations that are inherent to the reservoir operated under accumulation would result in a less stable fish assemblage, thus potentially less able to resist and recover from disturbances. The comparative results support the rationale that the different dam operation schemes likely affect fish assemblages.

Second, simulation experiments were employed to investigate which mechanisms were responsible for the synchrony of fish species in each studied reservoir. Empirical information was used to calibrate population parameters and run simulations where each of the main underlying mechanisms were artificially manipulated (González & Matorell, 2013; Merow et al. 2014; Tredenick et al. 2017). Comparative results of simulations for each reservoir, separately, showed that different mechanisms may act on fish assemblages under different environmental conditions, which are directly dependent on the dam operation. Finally, this work is a primary and fundamental contribution to understand the potential (beneficial or not) effects of the variations of water level that is inherent to each dam operation scheme and thereby should be accounted for when planning and managing rivers.

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2 STORAGE OR RUN-OF-RIVER RESERVOIRS: EXPLORING THE ECOLOGICAL EFFECTS OF DAM OPERATION ON STABILITY AND SPECIES INTERACTIONS OF FISH ASSEMBLAGES

ABSTRACT

Water level variation has an important role in the biology of fish species, driving behavior, feeding, and reproduction both in natural and modified environments. In reservoirs, different dam operation schemes result in alternative patterns of water level fluctuations. Storage (STR) reservoirs accumulate water and can vary the water level unpredictably, whereas this variation is more discrete in run-of-river (ROR) reservoirs. For this reason, ROR reservoirs are commonly presumed to be less environmentally harmful than STR reservoirs. We used multivariate autoregressive models (MAR) to compare the stability and species interactions of fish assemblages from two reservoirs under alternative operation schemes, using long-term data (15 years). We hypothesized that the lower variability of water level in the ROR reservoir would coincide with a more stable fish assemblage than in the STR reservoir. Contrary to our expectation, the MAR properties related to resilience and resistance indicated that the fish assemblage from the ROR was less stable than that from the STR reservoir. This suggests that the absence of water level variation limits the potential direct (movement and reproduction of fish) and indirect (primary production and nutrient input) benefits for fish that arise from the temporal environmental heterogeneity. Most importantly, this study highlights the need to reexamine the implications of ROR reservoirs on the health of aquatic communities. At least for fish, management actions should include varying the water level in a regime as similar as possible to the natural flow regime of the river, in order to improve the state of assemblages.

Keywords: Impoundment, Reservoir management, Water level variation, Reservoir cascade, Adaptive management, Multivariate autoregressive models.

2.1 Introduction

The construction of dams is among the main anthropogenic impact in natural freshwater systems (Dudgeon et al. 2006), with well-documented effects on river reaches both upstream and downstream (Baxter 1977; Dudgeon et al. 2006; Agostinho et al. 2004a; Gubiani et al. 2010; Reynalte-Tataje et al. 2012; Yan et al. 2015). Beyond landscape modification, environmental changes include increased evaporation and greenhouse gases emissions, nutrient and sediment retention, and hydrologic regime shift (Poff et al. 1997; Ney 1996; Agostinho et al. 2008; FitzHugh and Vogel 2011; Zhao et al. 2012). Upstream from the dam, the formation of the reservoir produces more conspicuous physical changes through the conversion of a lotic environment into a semi-lentic one, where spatial variations in longitudinal (water flow and sedimentation rates) and vertical (light penetration, thermal, and productivity stratification) gradients arise and drive subsequent biotic changes (Kimmel et al. 1990; Agostinho et al. 2004a; 2008).

Once a reservoir is filled, the water level variations that arise from dam operation are considered environmental disturbances with potential to affect productivity, nutrient cycling, and the structure of the biota (Miranda et al. 2010). Thus, directly or not, artificial water level variations may affect all aquatic organisms, from primary producers (phytoplankton, periphyton, and aquatic macrophytes), through consumers (zooplankton and aquatic invertebrates), to top predators such as fish (Miranda 2001; Kolding and van Zwieten 2012). For fish assemblages, these variations are recognized as the main disturbances in reservoirs and are closely related to their spatial and temporal dynamics (Agostinho et al. 2007; Lima et al. 2017). Thus, it is important to fully understand the impacts of dams on all aquatic organisms, considering their current expansion and especially when the legislation is not specific for each type of dam project (Winemiller et al. 2016).

Most dams and associated reservoirs are operated under two schemes: storage (STR) and run-of-river (ROR). The main difference between these operation schemes is related to the water retention–release strategy. Dams operated under STR retain and release large amounts of water according to energy demands and variation in rainfall; this is the commonest operation scheme throughout the world (International Energy Agency 2012). Conversely, dams operated under ROR release almost the same amount of water that they receive upstream. Because of this retention–release equivalence, these dams

usually create reservoirs with large amounts of standing water and only discrete variations in water level. This contributes to the general belief that ROR reservoirs are less harmful to resident aquatic communities than STR reservoirs (Paish 2002; Bilotta et al. 2016). However, there is a lack of long-term comparative studies of how dam operation (STR or ROR) may affect the biota of reservoirs (Anderson et al. 2014), especially in the Neotropics, where reservoirs are common features in the landscape (Agostinho et al. 2007; 2016). Understanding how each operation scheme affects fish assemblages within the associated reservoirs may provide scientific grounding for planning and adaptive management of hydroelectric facilities.

Decisions on the construction and operation scheme of dams are based on wide information regarding energy production and physiochemical processes, and on narrow information about local and regional biological requirements (Poff and Hart 2002). When a reservoir cascade (contiguous impoundments within the same river) is designed, STR reservoirs are usually placed at the beginning of the cascade, while ROR reservoirs are placed in the middle and lower parts (see the cases of Tennessee, Tietê, and Madeira rivers; Miranda et al. 2008; Petesse and Petrere 2012; Cella-Ribeiro et al. 2017). This design causes several detrimental synergic effects on communities (Stanford and Ward 2001; Miranda et al. 2008; Santos et al. 2016; Liu et al. 2017), but allows the operator to control water intake and to maximize energy production (see Appendix A for a summary of the reservoir cascade from the Paraná River basin in Brazil). Therefore, we were motivated to assess how different dam operation schemes could imply alternative temporal dynamics of biological communities.

Considering impoundments as permanent impacts on rivers, we intended to assess the potential effects of the operation scheme (STR and ROR) on fish. Here, we evaluated the stability of fish assemblages through time, considering variations in the abundance of species and potential interactions among them. Variations in water level were considered as disturbances because they have a recognized potential to shape fish assemblages, even in altered systems such as reservoirs (Poff and Schmidt 2016; Lima et al. 2017; Baumgartner et al. 2017). Therefore, reservoirs under lower water level variation (as in ROR) might be considered as presenting fewer disturbances than reservoirs with higher water level fluctuations (as in STR).

The main objective of this study was to compare the stability (in terms of resilience and resistance) and species interactions of fish assemblages from reservoirs

with different operation schemes, using long-term data with temporal trends in species abundances. To achieve this objective, we used the Salto Santiago (STR) and the Salto Osório (ROR) reservoirs as models; both in the Iguaçu River, and studied over 15 years (from 2003 to 2017). It is important to clarify that our purpose was to compare the stability of fish assemblages, not to categorize them as stable or unstable. Thus, we hypothesized that fish assemblages from the reservoir with higher water level variations (STR) would be less stable than the reservoir with lower water level variations (ROR). This decreased stability would emerge due to the contribution of the unpredictable environmental heterogeneity inherent to water level variation. In contrast, we may predict that the absence of substantial water level variations, characteristic to ROR reservoirs, could coincide with a more stable community. Therefore, reservoirs under ROR operation scheme would be more resilient and resistant to disturbances. We hope that our findings may serve as scientific grounding for an adaptive evidence-based management of dams and associated reservoirs. The potential effects (beneficial or not) of water level variations inherent to the operation scheme directly affects the resident fish assemblages, and therefore must be considered in planning and management.

2.2 Material and methods

2.2.1 Study Area

We surveyed two reservoirs from the Iguaçu River, Paraná River Basin, in Southern Brazil (Fig. 1). These reservoirs are third and fourth in a cascade of six large impoundments, taking advantage of the several falls that existed in this river. Along with particular physical differences like dam height and length, retention time, and reservoir length, area, and volume (Table 1), one main difference between the two reservoirs is in the water level variation (standard deviation from the operational level: $\sigma_{STR} = 6.09$ m and $\sigma_{ROR} = 0.62$ m; Fig. 2).

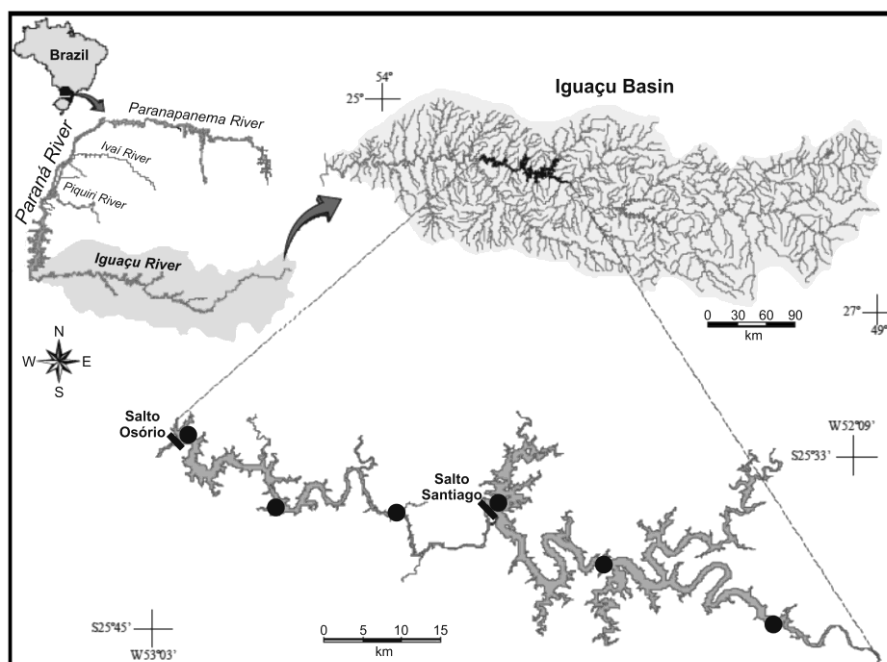


Fig. 1 Location of the sampling sites (black circles) within the two studied reservoirs operated under storage (STR; Salto Santiago) and run-of-river (ROR; Salto Osório) from the Iguaçu River, Paraná River basin

Table 1 – Detailed information of the two studied reservoirs in the Iguaçu River, Paraná River basin. Source: ENGIE Brasil Energia (www.engie.com.br)

Feature	Operation scheme	
	Storage	Run-of-river
Acronym	STR	ROR
Name	Salto Santiago	Salto Osório
Location (lat/long)	25°36'S/52°37'W	25°32'S/53°02'W
In cascade (order)	3 rd	4 th
Year (operation begin)	1980	1975
Installed capacity (MW)	1,420	1,078
Dam height (m)	80	56
Dam length (m)	1,400	795
Average annual flow (m ³ /s)	902	937
Maximum level (m a.s.l.)	508	398
Operational level (m a.s.l.)	506	397
Minimum level (m a.s.l.)	481	389
Length (km)	80	70
Area (km ²)	208	55
Maximum volume (m ³)	6,7 x 10 ⁹	1,1 x 10 ⁷
Average depth (m)	35	25,5
Raw slope (m)	106	72
Retention time (days)	51	16

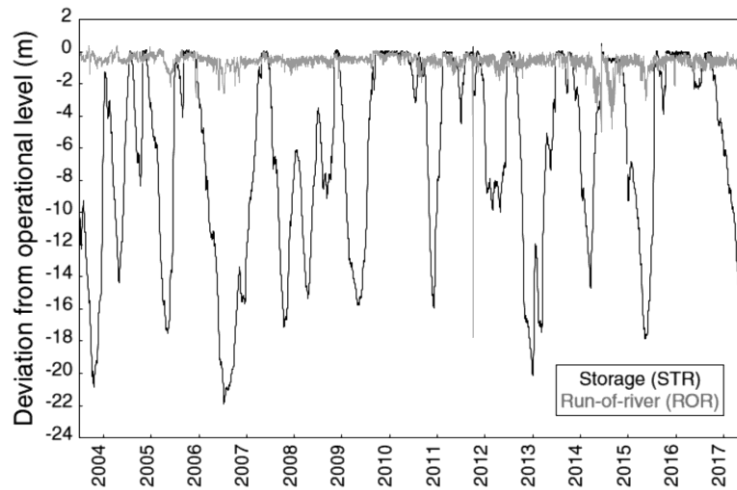


Fig. 2 Deviations from the operational water level of the reservoirs operated under storage (STR; Salto Santiago; operational level = 506 m a.s.l.) and the run-of-river (ROR; Salto Osório; operational level = 397 m a.s.l.) schemes, in the Iguaçu River, during the sampling period (2003–2017). Source: National Water Agency (Agência Nacional de Águas—ANA; www.ana.gov.br)

The Iguaçu River has a characteristic fish fauna, with elevated species endemism (Garavello et al. 1997; Abell et al. 2008), and both reservoirs inherited very similar assemblages from the former river after damming (80% of shared species between reservoirs from a total of 30 species in our data). Moreover, both reservoirs occupy a well-defined canyon-shaped valley, although with considerable differences in the reservoir volume (both overall and depending on the water level), and in the flooded area (Fig. 1). The two reservoirs have corresponding biogeography, and so the differences in community stability are expected to result mostly from water level-related environmental variations and species interactions than from compositional changes. Thus, we believe that these two reservoirs present a quasi-experimental opportunity to evaluate the effects of dam operation on fish assemblages. An important constraint of our experimental design lies in the use of only a single pair of reservoirs, so generalizations arising from our findings should be carefully evaluated.

2.2.2 Sampling and Data Preparation

Fish were collected bimonthly over 15 years, from July 2003 to May 2017. Surveys were carried out in three sites along each reservoir (Fig. 1). These covered the

longitudinal variation across fluvial, transitional, and lacustrine zones, following the zonation concept proposed by Thornton et al. (1990). To capture fish, we used a strongly standardized effort on both reservoirs. Identical sets of gillnets with a wide variety of mesh sizes (ranging from 2.4 to 16 cm between opposite knots; 12 gillnets and three trammel nets) were set near the margins (littoral), the surface (pelagic), and the bottom (bathypelagic) of each sampling site, during 24 h (littoral areas were sampled after May 2006). After sampling, fish were taken to the field laboratory, identified following Garavello et al. (1997), Reis et al. (2003), Graça and Pavanelli (2007), and Baumgartner et al. (2012), and counted. The abundances were indexed by the catch per unit of effort (CPUE; number of individuals/1000 m² of gillnets/ 24 h).

To conduct the analyses and address the proposed hypothesis, we organized one dataset for each reservoir with all information available. Both datasets were organized in samples \times species matrices, with the three sites pooled into one sample (i.e., the abundances of all three sites in a given sampling month were summed). We did this because we were interested in the overall temporal trend of each reservoir, thus treating each site separately would create undesired within-reservoir spatial variation. All variables were log-transformed to approximate the relationships to linear (following recommendations from Ives et al. 2003) and standardized (deseasoned Z-score) to allow for inferences between communities from model results (Poulos and Chernoff 2017). To avoid strong influences of species with very low abundances (or frequently absent) and because our analytical approach is sensitive to zeroes, we used only species that occurred in at least 75% of samples (15 out of 29 species for the STR reservoir and 17 out of 25 species for the ROR reservoir). These selected species were also the most abundant in each reservoir (unpublished data).

2.2.3 Data Analysis

The stability and species interactions of the fish communities from the reservoirs with different operation schemes were inferred through properties of first-order multivariate autoregressive models (MAR(1); Judge et al. 1985; Reinsel 1997), as proposed by Ives et al. (2003). To accomplish this, we used the package “MAR1” (Scheef 2013) in the R Environment (R Core Team 2017). Autoregressive models are statistical

tools that use linear combinations of previous observations to model the target variable. The most common type of autoregressive models is the first-order version (AR(1)), where a given value of the target variable depends on a single previous observation of itself, plus a random error. The MAR(1) model is a multivariate extension of AR (1) that incorporates the previous observation of all variables in the dataset as linear predictors of the target variable. In ecology, it means that the observed abundance of a species (i.e., the state of the target variable) depends on the previous abundances of itself and of all possible interactions with other species within the same environment. This analysis identifies a community state considered as stable (stationary state), with known variability, and estimates parameters based on the relationship with a temporary state (transition state). This is a multivariate approach recognized as suitable to analyze community stability and ecological interactions from time-series data (Ives et al. 2003; Scheef 2013; Poulos and Chernoff 2017).

The general matrix equation of MAR(1) model follows Ives et al. (2003)

$$\mathbf{X}_t = \mathbf{A} + \mathbf{B}\mathbf{X}_{t-1} + \mathbf{E}_t$$

where \mathbf{X}_t is a $p \times 1$ vector of log-transformed abundances of a variable at time t , \mathbf{A} is a $p \times 1$ vector of constants, \mathbf{B} is the interaction matrix, a $p \times p$ matrix where each element gives the effect of the interaction between the abundances of every pair of groups, \mathbf{X}_{t-1} is a $p \times 1$ vector of log-transformed abundances at time $t-1$, and \mathbf{E}_t is a $p \times 1$ vector of process errors with multivariate normal distribution. This model is essentially a set of multiple regressions solved simultaneously while accounting for autocorrelation in time-series data (Ives et al. 2003). An advantage of MAR(1) is that, after fitting these models, we can retrieve some estimators that represent different measures of stability of the communities (Table 2). Equations, parameters estimations, properties, and their relationship with stability are well described in Ives et al. (2003), but we provide interpretations and expectations in Table 2.

Table 2 – Summary of the stability attributes, their metrics, parameters and properties from the first-order multivariate autoregressive model (MAR(1); Ives et al., 2003). Along each description, there is the expectation in a more stable community and the expectations for each dam operation scheme [storage (STR) or run-of-river (ROR)] from the theoretical hypothesis

Stability Attribute	Metric	Parameter	Property	Higher stability	Expected	
					STR	ROR
Resilience	Variance	$\det(\mathbf{B})^{2/p}$	Community variability (interactions) in relation to environmental variability (stochastic)	Low	↑	↓
Resilience	Return rate	$\max(\lambda_{\mathbf{B}})$	Rate of return from the transition mean to the mean of the stationary state	Low	↑	↓
Resilience	Return rate	$\max(\lambda_{\mathbf{B} \otimes \mathbf{B}})$	Rate of return from the transition variance to the variance of the stationary state	Low	↑	↓
Resistance	Reactivity	$-\text{tr}[\boldsymbol{\Sigma}]/\text{tr}[\mathbf{V}_{\infty}]$	Expected difference between the stationary and the transition states	Low	↑	↓
Resistance	Reactivity	$\max(\lambda_{\mathbf{B}/\mathbf{B}}) - 1$	Species interaction-only reactivity	Low	↑	↓

All parameter estimations were based on the interaction matrix \mathbf{B} , which represents the estimated interaction coefficients among the abundances of all fish species in the environment. Since stability itself is a broad concept that encompasses many components of temporal dynamics (Ives and Carpenter 2007), we focused on two components of temporal stability: resilience and resistance. We assessed these two components using three metrics that directly assess community stability: variance and return rate (to quantify resilience), and reactivity (to quantify resistance). These three metrics were quantified using five parameters extracted from MAR(1) models, as described below and in Table 2.

To quantify stability as community variance (i.e., resilience), we used the variance of the stationary distribution relative to the variance of the process error that drives stochasticity ($\det(\mathbf{B})^{2/p}$). This parameter quantifies the differences in interactions among variables (community variability) in relation to the variability of the stochastic processes (environmental variability). To quantify community stability as return rate (i.e., resilience), we used the maximum eigenvalue ($\max(\lambda_{\mathbf{B}})$) and the maximum eigenvalue of the Kronecker product ($\max(\lambda_{\mathbf{B} \otimes \mathbf{B}})$) of the interaction matrix \mathbf{B} . These parameters estimate the rate at which the mean and the variance of the transition state, respectively, converge to mean and variance of the stationary state. Finally, to assess community

stability as resistance (i.e., reactivity), we used the expectation of the difference between the stationary and the transition state $-\text{tr}[\Sigma]/\text{tr}[\mathbf{V}_\infty]$, and the reactivity based only on species interactions ($\max(\lambda_{\mathbf{B},\mathbf{B}}) - 1$). These two parameters depict the short-term dynamics of the community and continuously quantify the changes between previous and actual states of the community. When the variance of interaction coefficients is larger than the process errors (stochastic), the system is less stable. Increased values of these parameters indicate higher reactivity, which leads to a system that over-responds to disturbances, and is thus less stable (Table 2). Models were fit using a random search procedure for the best-fit model and the top ten models (lowest Akaike information criteria - AIC-score) were retained. The final parameters were obtained using least-squares estimation and the confidence intervals for each parameter were calculated using bootstraps on the residuals matrix with 2000 runs (Ives et al. 2003). Note that the interpretation of the value and signal of each parameter is not directly related to their ecological meaning.

2.3 Results

The species' abundances, indexed by the CPUE, varied across the studied years with higher overall abundances in the STR reservoir (mean \pm standard deviation of CPUE = 2112.66 ± 1187.82 Ind./1000 m² of gillnets/24 h), than in the reservoir under ROR operation scheme (818.34 ± 359.68 Ind./1000 m² of gillnets/24 h; Fig. 3). Most of the abundance peaks occurred in or near the summer (October–March), and coincided for both reservoirs especially in the years 2006–2007 and 2012–2013, although abundance peaks also occurred in 2008–2009, 2009–2010, and 2010–2011 for the STR reservoir. The stronger peaks in abundance seen in the STR reservoir were mostly seen when water levels were high in the reservoir. Most of these abundance peaks occurred within the reproductive period for most species, which is also in summer (see the shaded areas in Fig. 3), or slightly after as in 2004–2005 and 2011–2012.

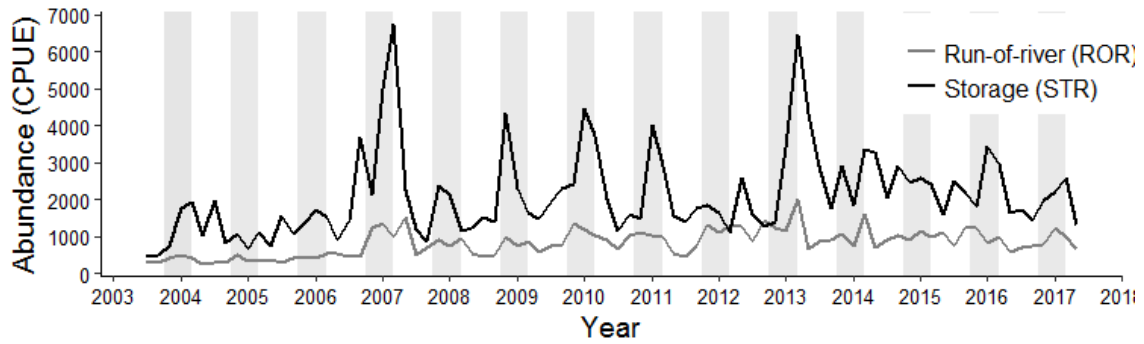


Fig. 3 Temporal trends in the total abundance (CPUE; Ind./1000 m² of gillnets/24 h) of the most abundant species in the reservoirs operated under storage (STR; Salto Santiago) and run-of-river (ROR; Salto Osório) schemes, in the Iguazu River, during the sampling period (2003–2017). Shaded areas represent the reproductive period of most species (October–March)

Considering the properties of the MAR(1) models related to community stability in terms of resilience and resistance to disturbances, the ROR reservoir was considered less stable than the STR reservoir (comparison of values and confidence intervals in Table 3). Apart from the parameter relating the variance of stationary process to stochastic variation ($\det(\mathbf{B})^{2/p}$) and that related to the difference between stationary and transition states $-\text{tr}[\mathbf{\Sigma}]/\text{tr}[\mathbf{V}_{\infty}]$, all others ($\max(\lambda_{\mathbf{B}})$, $\max(\lambda_{\mathbf{B} \otimes \mathbf{B}})$, and $\max(\lambda_{\mathbf{B}/\mathbf{B}}) - 1$) suggested a less stable community in terms of species interactions and self-dependence in the reservoir under the ROR operation scheme. For the return rate from transition to stationary state, the return rates of the mean ($\max(\lambda_{\mathbf{B}})$) and the variance ($\max(\lambda_{\mathbf{B} \otimes \mathbf{B}})$) were higher for the ROR reservoir, which indicates a longer elapsed time to shift between states, thus a less resilient system. In agreement, one parameter related to reactivity ($\max(\lambda_{\mathbf{B}/\mathbf{B}}) - 1$) also indicated the ROR reservoir as more reactive (i.e., less resistant) than the STR reservoir. Considering the estimated parameters for species covariance ($\text{tr}[\mathbf{V}_{\infty}]$) and process errors ($\text{tr}[\mathbf{\Sigma}]$), both suggested a higher variability of the interactions in the ROR reservoir (Table 3).

Table 3 – Stability measures using properties of first-order multivariate autoregressive models (MAR(1); Ives et al., 2003), for reservoirs under storage (STR) and run-of-river (ROR) operation schemes. Above: values of the best-fit (top 10 lowest-AIC models) and bootstrapped 95% confidence intervals from the MAR(1) models fit for each reservoir using log-transformed species abundances through time as variables. Below: the traces of the covariance (\mathbf{V}_∞) and process-error matrices ($\mathbf{\Sigma}$), and the percent and cumulative explained variance by the largest five eigenvalues of the species-interaction matrix \mathbf{B} . Table 2 provides a more detailed description of each parameter, their interpretation and the expected comparative values under each dam operation scheme.

Parameter	STR	ROR	Stability Attribute	Property Summary
$\det(\mathbf{B})^{2/p}$	0.13 [0.01, 0.15]	0.07 [0.00, 0.12]	Resilience	Stationary state variance
$\max(\lambda_{\mathbf{B}})$	0.69 [0.20, 0.72]	0.77 [0.31, 1.18]	Resilience	Return rate of the mean
$\max(\lambda_{\mathbf{B} \otimes \mathbf{B}})$	0.48 [0.10, 0.68]	0.59 [0.56, 0.79]	Resilience	Return rate of the variance
$-\text{tr}[\mathbf{\Sigma}]/\text{tr}[\mathbf{V}_\infty]$	-0.69 [-0.91, -0.23]	-0.67 [-0.89, -0.11]	Resistance (reactivity)	Expected difference between stationary and transition states
$\max(\lambda_{\mathbf{B}/\mathbf{B}}) - 1$	0.24 [0.04, 0.51]	0.88 [0.69, 1.07]	Resistance (reactivity)	Variability of the stationary state relative to stochastic process
$\text{tr}[\mathbf{V}_\infty]$	14.15 [11.82, 16.55]	16.41 [13.75, 19.15]		
$\text{tr}[\mathbf{\Sigma}]$	9.74 [7.86, 11.69]	10.94 [8.83, 13.14]		
Eigenvalues	% Expl. % Cum.	% Expl. % Cum.		
	21.17 24.29	22.70 23.24		
	15.35 17.09	19.05 19.34		
	15.26 17.09	16.46 13.91		
	15.26 15.15	14.23 13.91		
	14.29 15.15	14.23 12.05		

The patterns of the interactions among species' abundances suggested an effect of the operation scheme on species interactions (Fig. 4). When comparing the observed number of significant abundance-related interaction coefficients, in relation to the potential total number of interactions, the STR (0.19) had an almost similar proportion of significant interactions compared to the ROR reservoir (0.18). However, although 13 species were common among the most abundant in both reservoirs, only three interaction coefficients were shared between the two assemblages [*Astyanax bifasciatus* (Abif) – *Astyanax lacustris* (Alac); *Astyanax gymnodontus* (Agym) – *Crenicichla iguassuencis* (Cigu); Cigu–*Odontesthes bonariensis* (Obon); Fig. 4]. Analyzing the nature of species' abundance interactions, the ROR reservoir had more significant negative interaction coefficients (total of 16 interactions) than the STR reservoir (total of ten interactions). The identity of those species with the highest numbers of significant interaction coefficients also differed between reservoirs. In the reservoir under STR operation, *A. lacustris*, *Rhaphiodon vulpinus*, *Oligosarcus longirostris*, *O. bonariensis*, and

Apareiodon vittatus were those with more significant interaction coefficients. In contrast, those species with higher numbers of significant interactions from the ROR reservoir were *O. bonariensis*, *Astyanax minor*, *Pimelodus britskii*, *Glanidium ribeiroi*, *Bryconamericus ikaa*, and *Astyanax dissimilis* (Fig. 4).

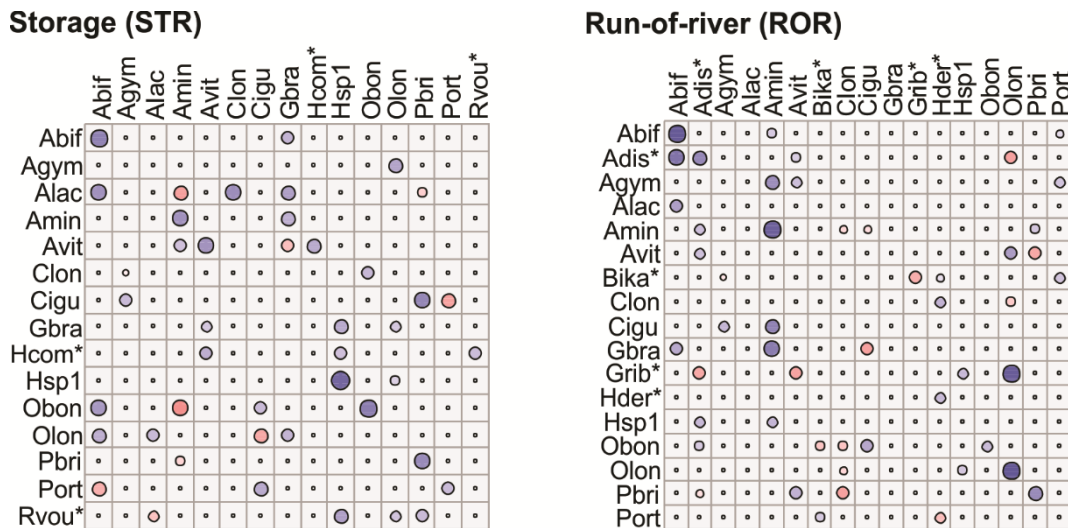


Fig. 4 Interaction coefficients indicating the effect of each column on each row, among the most abundant species in the reservoirs operated under storage (STR; Salto Santiago) and run-of-river (ROR; Salto Osório) schemes, in the Iguazu River, during the sampled period (2003–2017). Blue circles indicate positive interactions, whereas red circles indicate negative interactions. Larger circles represent stronger interactions. Species that were among the most abundant only in one reservoir are marked with (*). See Appendix B for species names and codes

2.4 Discussion

We observed differences in stability (characterized as resilience and resistance) and species interactions between the fish assemblages from two reservoirs operated under alternative water-release schemes. This outcome suggests a potential effect of dam operation scheme on the temporal stability of fish assemblages. Contrary to our expectation, the absence of large water level variations did not coincide with a more stable fish community in the ROR reservoir. The ROR presented lower resilience and lower resistance (i.e., higher reactivity) than the STR reservoir. In addition, the interactions among species (i.e., their mutual effects on each other's abundances) were clearly

different between the two reservoirs, thus suggesting that the dam operation scheme may have influenced the assemblage-level dynamics among fish species. Moreover, the number of positive significant interaction parameters was lower for the ROR reservoir, suggesting a less reciprocal community in terms of species contributing to each other's abundances.

The lower stability of the ROR reservoir may be due to different factors directly and indirectly related to the influence that water level variability has on the abundance and dynamics of fish species. Directly, fluctuations in water level affect the timing and physiological condition for the reproduction of fish (Vazzoler 1996; Wootton et al. 1996; Matthews 1998). Even in artificial systems such as reservoirs, the rise in the water level before the reproductive period is fundamental to trigger and synchronize fish reproduction, increasing cohorts, abundances, and biomass for the following year (Agostinho et al. 2007). However, if floods occur during or immediately after the reproductive period, it may compromise or even eliminate the young-of-the-year from natural populations (Agostinho et al. 2004b; 2007; Kahl et al. 2008). Particularly in reservoirs, the resident fish species are selected from the original species pool by their ability to thrive in lentic environments. Those species that depend on the annual variations of the hydrologic cycles, usually migratory, may then become locally extinct (Fernando and Holčík 1991; Gomes and Miranda 2001; Agostinho et al. 2008). However, most species from the two reservoirs studied herein still appear to benefit from water level variations.

The water level variations that could provide better conditions for fish feeding and reproduction are virtually absent in ROR reservoirs, and this condition seems to result in a less stable fish assemblage. We may credit the general belief in ROR reservoirs as more environmentally friendly to the intuition that these environments are less prone to disturbances arising from water level variations. In addition, the seeming equivalence between the amount of water that enters upstream in the reservoir and the discharge downstream of the dam supports the idea that the river flow is preserved. Although our experimental design is not so strong, it provides evidence against the concept that a less disturbed environment, as ROR reservoirs, provides better conditions for fish assemblages in reservoirs.

Indirectly, fluctuations in water level create important environmental heterogeneities both internally and on reservoir borders. Internally, for Neotropical

reservoirs (including those studied here), it has been documented that fish biomass is maintained mainly by detritus generated from primary production by phytoplankton (Piana et al. 2005). In the reservoirs studied herein, the largest proportion of the assemblages were composed of planktivorous species. Particularly in the ROR reservoir, the light penetration is decreased (Bortolini et al. 2019), and it may be that fish avoid the deeper waters because of low oxygen concentrations caused by stratification. This avoidance prevents fish from feeding on the detritus provided by dead phytoplankton. Thus this fraction of the sediment that could enhance stocks of detritivorous and other fish species is potentially not incorporated into the reservoir food web.

On the reservoir borders, the cyclical emersion and immersion of littoral areas allows riparian vegetation to develop, bringing nutrients and terrestrial and aquatic insects into the reservoir food web when the water level rises, increasing the production of all trophic levels (Agostinho et al. 1999, 2007; Coulter et al. 2019). This phenomenon is similar to the “trophic upsurge” phase (Kimmel and Groeger 1986; Kimmel et al. 1990) that is inherent to the process that forms reservoirs. This process can be systematically repeated (artificially or otherwise) with the intention of increasing the input of nutrients and organic matter from the terrestrial surroundings (Miranda et al. 2010; Poff and Schmidt 2016). Both internal and bordering effects of water level variation are fundamental to the maintenance of primary producers in reservoirs (Agostinho et al. 1999; Piana et al. 2005; Kolding and van Zwieten 2012), and reduced water level variation may prevent reservoirs from experiencing these potential benefits.

The stabilization of reservoirs is well reported and the mechanistic process that leads to biotic stabilization is well understood (Agostinho et al. 2007, 2016). Although there is no consensus on the time that a reservoir needs to achieve such a stable state (Petere 1996), we believe that the studied reservoirs have already been through this process (STR and ROR reservoirs were 39 and 44 years old, respectively). Petere (1996) characterized stabilization as the processes related to compositional and structural changes in fish and other communities following the physical, chemical, and hydrological changes promoted by the formation of the reservoir. We should here clarify the difference between this definition and how the term stability was used in the analysis in this study. Based on Petere’s (1996) definition, reservoirs achieve a stable state through major shifts in community composition, but which have detrimental effects on fish stocks in the long term. In our case, higher stability is defined as increasing the ability of communities to

resist and recover from disturbances; thus higher stability represents a preferable state. In sum, the process related to fish communities reaching a stable state after reservoir filling, as described in Petrere (1996), is important during the early stages of a reservoir's lifespan because environmental stochasticity may hinder species to find habitats in which they could live and reproduce. Our definition of stability is also important because "stable" freshwater communities and ecosystems are able to be more resistant and resilient to disturbances. Higher stability is preferable because less stable communities may be more vulnerable to environmental stressors.

The ROR reservoir suffered a very steep drawdown in 2011 (Baumgartner et al. 2017), with water level dropping up to 20 m in a few days. After the drawdown, almost all species increased in abundance. This benefit was attributed to the triggering and synchronizing effect of water level change on fish reproduction, and also to an increase in fish movement (Baumgartner et al. 2017). Although this is a very important event in the recent years of the dataset, we do not believe that the drawdown caused a permanent shift in community state because the changes were related to species abundance rather than species composition or dominance (for details, see Baumgartner et al. 2017). Particularly, the discrete nature of that event corroborates the results of this study regarding the importance of water level variation for fish assemblages.

There were also some factors that should be accounted for when interpreting the fact that the ROR reservoir was less stable. First, the ROR reservoir is nearly four times smaller than the STR. This difference in size suggests that local extinction risks and spatial forcing processes are intensified in the smaller (ROR) reservoir (Allen and Holling 2002). Second, the STR reservoir has an important major tributary (the Cavernoso River), which is believed to be an important contributor to fish abundance and reproduction in this reservoir (Baumgartner et al. 2016). These two differences are certainly potential additional explanations of the differences in stability among the studied reservoirs and should be considered, in addition to dam operation scheme, when interpreting our results.

Regardless of the theoretical approach, fluctuations in water level may provide perturbations that prevent stabilization of reservoirs and increase the abundances and diversity of fish (Miranda et al. 2010; Agostinho et al. 2016). From our results, there is evidence to suggest that water level variations also confer the ability to resist and return to a stable state after a disturbance. Specifically, the lower stability of the ROR reservoir is more important than the comparative higher stability of the STR reservoir. As our main

conclusion, the evidence herein suggests that our belief that ROR reservoirs are less threatening to the resident fauna must be promptly reconsidered. Counterintuitively and in opposition to our expectation, the absence of large water level variations coincided with a less resilient and less resistant system in terms of temporal dynamics and species interactions.

2.4.1 Research Needs

The results we show here are restricted to a single pair of reservoirs. The next step would be to assess if this is a consistent pattern among comparable reservoirs with different operational schemes. We reiterate the importance of long-term studies, which have the ability to provide fundamental ecological insights considering the temporal variation of communities (Magurran et al. 2010). We also suggest that this knowledge gap could be filled using spatial replication of our approach with available data from other reservoirs. Together these could provide the grounding for evidence-based environmental management and energy planning.

Ideally, experimental manipulations of the reservoir discharge pattern would be the best scenario to elucidate the direct effects of dam operation on fish. These experiments would allow for the exclusion of confounding effects such as those described above and many others. Unfortunately, due to the integrated nature of national energy production, these experimental trials are not feasible, at least at a large temporal and spatial extent. One alternative for this restriction would be before–after comparisons in those reservoirs where a major shift in operation occurred. These opportunities would provide stronger experimental designs to infer causality related to reservoir operation than was possible here.

2.4.2 Implications for Management

We can conclude and propose some evidence-based management actions for reservoirs, based on three premises: (i) we may expect a higher biological diversity when

disturbances occur at an intermediate frequency and intensity (Grime 1973; Connell 1978); (ii) water level variation is the major cyclical disturbance in freshwater ecosystems and is a major driver of the structure of aquatic communities (Agostinho et al. 2016); and (iii) our results suggested that the absence of greater water level variations led to a less stable community in terms of resilience and resistance to disturbances (Fig. 5). The absence of natural water level-related environmental variability, which is artificially imposed on ROR reservoirs, seems to create a less stable structure of the fish community. The most common designs, with ROR reservoirs at intermediate positions within the reservoir cascade, might actually result in less stable systems right in the middle of large connected river systems. Moreover, the construction of ROR impoundments in small rivers under the assumption that these schemes have less environmental impacts may need to be reexamined.

For management, as already proposed by Poff and Schmidt (2016), Baumgartner et al. (2017), Coulson et al. (2019), and many others, artificial water level variations may be important to prevent the physical and biological effects of long-term aging on reservoirs, especially in ROR schemes. Regarding the reproductive cycle of most species, water level variations (especially rising) before this period is a potential enhancer of fish abundances through its direct and indirect effects on fish movement, feeding, reproduction, and recruitment. Therefore, we could integrate artificial water level variations into planning and management of reservoirs, especially for those that experience a long time with a static water level. If these actions are respectful to the reproductive cycle of fish, the yet underexplored potential of these water level variations may benefit all aquatic communities in reservoirs.

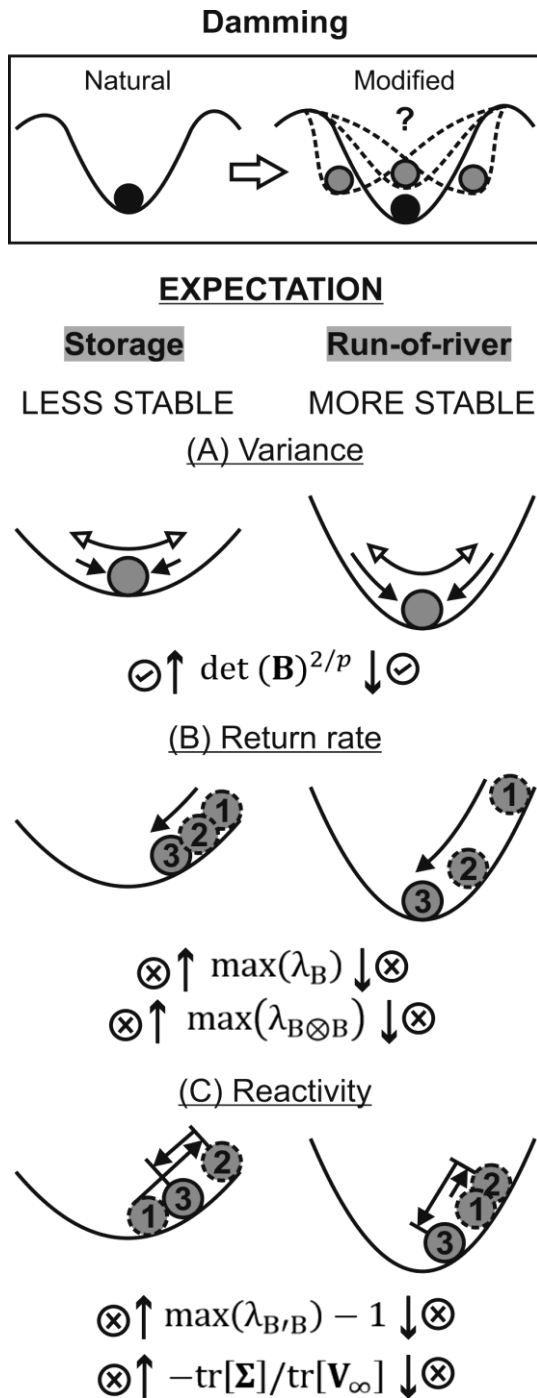


Fig. 5 The unpredictability of changes in system state resulting from damming, hypothetical differences in stability expected between systems with different operation schemes, and the MAR(1) properties used as measures of stability. Black and gray balls represent the states of natural and modified systems, respectively. (A) Stability measure based on the variance of the system (oscillation of the ball). Under the same disturbance (white arrow), more stable systems have stronger forces to return to the stationary state (bottom of the bowl) than less stable systems. (B) Stability measure based on the return rate of the system (speed in returning from the transition state to the stationary state). More stable systems return faster to the stationary state than less stable systems. (C) Stability measure based on the reactivity of the system (the effect—change in the ball position—presented by a system following a disturbance). In more stable systems, the change from stationary state to transition state is shorter than in less stable systems (the ball moves less in more stable systems). The arrows on the sides of each parameter indicate the expected difference in values when comparing two systems. Equations for parameters calculation (variance: Eqs. 22 and 23; return rate: Eqs. 19 and 21; reactivity: Eqs. 25 and 26) are in the original paper from which the figure was modified (Ives et al. 2003). The positive and negative checks in the side of each arrow indicate whether the expected and the observed comparative values matched in our study

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APPENDIX A - The reservoirs in the Paraná River basin

This figure is a summary of the river network from the Paraná River basin, along with all build (64), under construction (5), and projected (2) reservoirs. There are 31 built reservoirs under each operation scheme (storage and run-of-river). All cascade of reservoirs (contiguous impoundments in the same river) begin with a storage reservoir, except for the Verde River. Run-of-river reservoirs are usually placed in the middle of each cascade, which is particularly the cases of Grande, Tietê, Paranapanema, and Iguaçú rivers. This design allows for the production of energy using water control from the storage reservoirs.

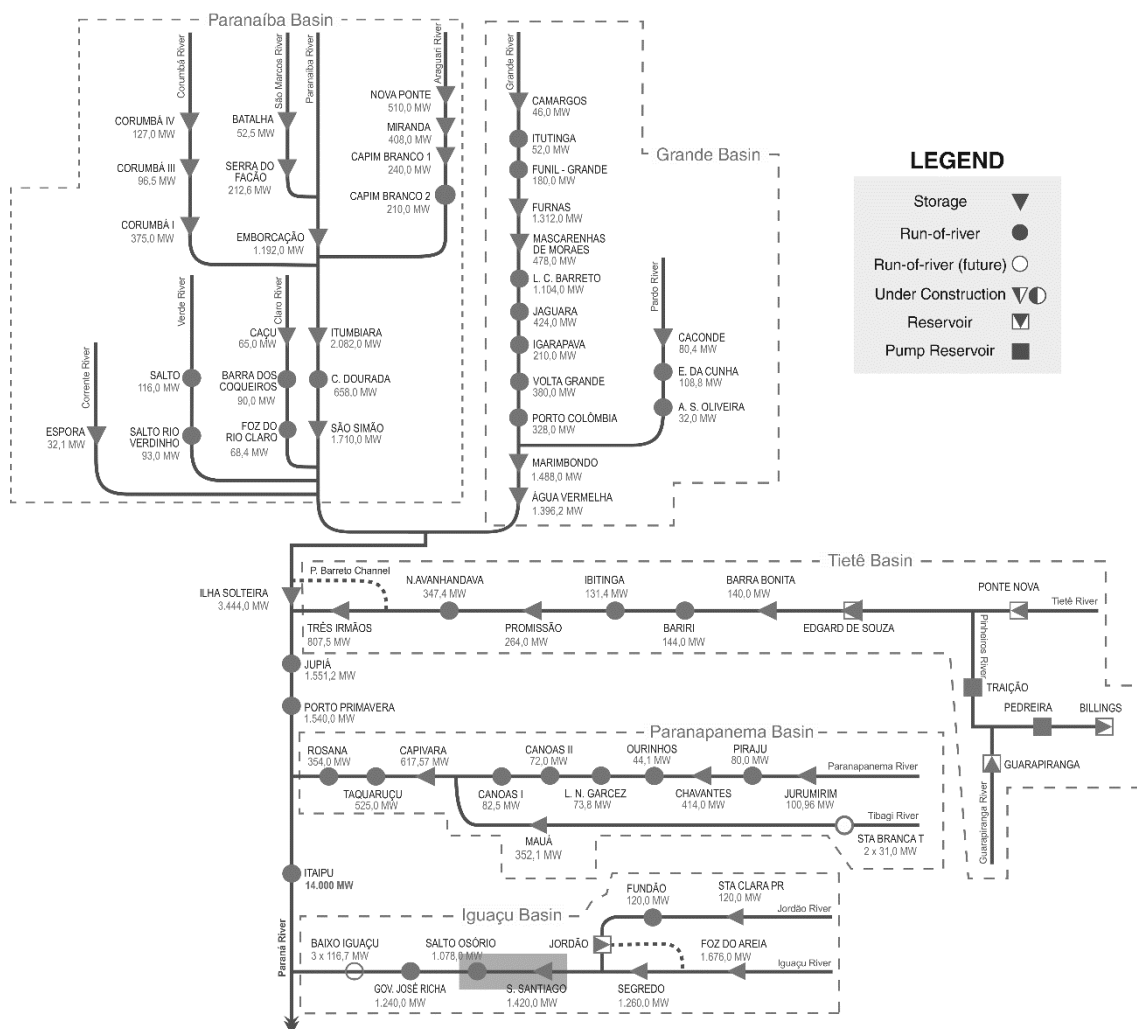


Figure S1 – Schematic representation of the reservoir cascade from the Paraná River basin, in Brazil. The shaded area is where the two studied reservoirs (Storage - Salto Santiago; Run-of-river – Salto Osório) are located. Source: Operador Nacional do Sistema – ONS (www.ons.org.br).

APPENDIX B - Species codes used in the analyses

Species	Code
<i>Astyanax bifasciatus</i>	Abif
<i>Astyanax dissimilis</i>	Adis
<i>Astyanax gymnodontus</i>	Agym
<i>Astyanax lacustris</i>	Alac
<i>Astyanax minor</i>	Amin
<i>Apareiodon vittatus</i>	Avit
<i>Bryconamericus ikaa</i>	Bika
<i>Crenicichla iguassuensis</i>	Cigu
<i>Corydoras longipinnis</i>	Clon
<i>Geophagus brasiliensis</i>	Gbra
<i>Glanidium ribeiroi</i>	Grib
<i>Hypostomus commersoni</i>	Hcom
<i>Hypostomus derbyi</i>	Hder
<i>Hoplias</i> sp. 1	Hsp1
<i>Odonthestes bonariensis</i>	Obon
<i>Oligosarcus longirostris</i>	Olon
<i>Pimelodus britskii</i>	Pbri
<i>Pimelodus ortmanni</i>	Port
<i>Rhamdia voulezi</i>	Rvou

3 SPECIES INTERACTIONS OR ENVIRONMENTAL STOCHASTICITY? MECHANISMS CONTRIBUTING TO THE SYNCHRONY OF FISH SPECIES IN RESERVOIRS UNDER DIFFERENT DAM OPERATION SCHEMES

ABSTRACT

Dams and reservoirs have been constructed worldwide to meet demands for energy and water supplies, and their effects on aquatic ecosystems have been investigated extensively. Dam operation schemes (water releases) affect reservoir water levels with potential effects on fish assemblages, but the mechanisms driving variation in fish population dynamics are poorly understood at present. There is already substantial evidence for the negative relationship between ecosystem stability and the temporal community-level synchrony, although the relative importance of each underlying mechanism is context-dependent. Using 11 years of fish survey data from two reservoirs, empirically-derived demographic parameters, and simulation experiments, we investigated the relative roles of three major drivers of synchrony in population dynamics: environmental stochasticity, species interactions, and demographic stochasticity. The two reservoirs have different operation designs that affect water level fluctuations: storage (STR) with infrequent, large-magnitude changes, and run-of-river (ROR) with frequent small-magnitude variations. By simulating the removal of each potential mechanism one at a time and in combination, we found that disabling environmental stochasticity and species interactions were more influential for the synchrony of fish communities, although with opposite contributions depending on the reservoir considered. We also found that the effect of demographic stochasticity was inconclusive for both reservoirs. Our study suggested that fish species synchrony is influenced by different mechanisms in reservoirs with different operations and therefore hydrologic regimes. Findings have implications not only for ecological theory, but also for balancing energy and water supply needs with fisheries and biodiversity conservation under alternative water retention-release strategies.

Keywords: niche differentiation; interspecific competition; reservoir management; fish assemblage; impoundment; inverse modelling; stability

3.1 Introduction

Modifications in natural habitats are among the primary causes of biodiversity decline and loss of valued ecosystem services (Fischer and Lindenmayer, 2007; Haddad et al. 2015). In fluvial ecosystems, the most pervasive habitat modification is dam construction, whether for water supply, flood control, energy production and/or recreation (Vörösmarty et al. 2010; Lehner et al. 2011; Poff and Schmidt, 2016). River impoundments usually result in major changes to fluvial ecosystems by converting lotic habitats into a series of lentic stretches (Agostinho et al. 2016; Maavara et al. 2020), and it is intuitive that the species without pre-adaptations to explore the newly formed environment will not thrive (Agostinho et al. 2016; Winemiller et al. 2016).

Fish are a highly diverse group of aquatic vertebrates occupying several habitats and trophic positions, from primary consumers to top-predators (Nelson et al, 2016). Thus, this group can be used as a good indicator of the overall state of riverine ecosystems, with species responding to environmental variation at various temporal and spatial scales (Holmlund and Hammer, 1999; Hoeinghaus et al. 2009; Arantes et al. 2019). In reservoirs associated with dams, the fish species that are mostly affected by the habitat constraints imposed by fragmentation are usually large-bodied, perform intermediate to long migrations for reproduction, and have long life cycle (Agostinho et al. 2016). In opposite, the species that thrive in lentic waters are small-sized, usually sedentary and opportunistic. These species benefit from the high availability of food resources and the steady flow, especially during the early years of the reservoir (Gomes and Miranda, 2001; Agostinho et al., 2016).

In rivers where dams are permanent impacts, fluctuations in reservoir water level can be considered as short-term disturbances with potential effects on productivity and the organization of aquatic communities (Miranda et al. 2010). Riverine species are pre-adapted to the natural hydrological variation, which tends to be seasonally predictable in the wet/dry tropics (Lowe-McConnell, 1987). Annual flood pulses drive the dynamics of riverine habitats and resources, as well as the ecology of fish and other aquatic organisms (Junk et al. 1989). Precisely for fish, flood pulses increase their movement and are determinants of dispersal, reproduction, and recruitment for many species, narrowing their relationship with the environment. However, the hydrological dynamics of reservoirs are mostly contingent upon energy demands and rainy patterns (Ngor et al.

2018), which is remarkably different from natural variations of rivers and its consequences are still not fully understood.

In addition to other characteristics, dams are designed to operate under two almost contrasting schemes that mostly explain the variations in reservoir water level: storage (STR) and run-of-river (ROR). Storage reservoirs retain water during rainy periods and release it for electricity generation as the seasonal or daily demand follows, whereas run-of-river reservoirs release virtually the same amount of water that flows from upstream. These alternative operation schemes result in very different temporal patterns of water level variations, with STR reservoirs presenting rapid fluctuations while ROR reservoirs have a relatively constant volume. Therefore, this temporal difference has recognized effects on vertical and longitudinal environmental conditions of reservoirs, with presumable effects on fish (Bilotta et al. 2016; Baumgartner et al. 2020). The consequences of the construction of dams have been extensively documented in the literature (Agostinho et al. 2016; Turgeon et al. 2019), hitherto there is insufficient information regarding the effects of dam operation on ecosystem dynamics.

We can investigate how communities change in time through the lens of the synchrony of species, evaluating at which degree the temporal trajectories of the abundances of the populations relate to each other (Loreau and de Manzacourt, 2008). Synchronous communities may result when species share similar responses to temporal variation, whereas asynchronous (i.e., compensatory) communities usually emerge from independent trajectories of populations along time (Gonzalez and Loreau, 2009; de Manzacourt et al. 2013). Theoretical approaches have identified three main drivers of community-level (a)synchrony: environmental stochasticity, species interactions, and demographic stochasticity (Loreau and de Manzacourt, 2008; 2013). Environmental stochasticity assumes that abiotic conditions vary in random or deterministic (e.g., seasonal) patterns across time (Loreau and de Manzacourt, 2008). When community responses to the environment are similar and intrinsically strong, environmental stochasticity may have a synchronizing role, with species responding similarly to abiotic changes (Gonzalez and Loreau, 2009). In this sense, long-term variations in environmental conditions (e.g., yearly changes in temperature or rainfall patterns) may largely increase the degree of community synchrony, if we consider that populations are large (thereby reducing the potential effect of demographic stochasticity) and interspecific interactions are weak (Loreau and de Manzacourt, 2008; Thibault et al.

2012). In opposite, we may expect that community synchrony may decrease as the proportion of species that respond independently to environmental variations increase (Loreau and de Manzacourt, 2008).

Species interactions influence community-level synchrony when intense negative interactions (e.g., competition) results in strong asynchrony (Loreau and de Manzacourt, 2013). In opposite, species interactions may have a synchronizing role in communities where interactions are strong but species mostly benefit from each other (Tredennick et al. 2017), and even when species direct responses to environmental variations are independent (Houlalan et al. 2007). There is also a specific inverse relationship between community synchrony and stability, in which more stable ecosystems require some form of temporal niche partitioning among species (Loreau and de Manzacourt, 2008; Craven et al. 2018). This niche differentiation underlies asynchronous fluctuations in populations, so that species may compensate for each other through time.

Ultimately, demographic stochasticity underlies variations related to individual-level survival, growth, and reproduction rates across years (Loreau and de Manzacourt, 2008). Stochastic shifts in these rates impose fluctuations in populations driven by self-regulatory random events, which leads to a negative relationship between demographic stochasticity and community-level synchrony. The effect of demographic stochasticity also depends on population size: larger populations are less likely to suffer from fluctuations related to individual-level differences (Tredennick et al. 2017). Therefore, considering that (i) dams are already a common feature in the landscape worldwide, (ii) the construction of these facilities is still increasing in several countries (Winemiller et al. 2016; Zarfl et al. 2019), and (iii) dam operation determines the hydrologic dynamics of reservoirs, we assume that understanding the relative effects of these factors underlying the synchrony (or asynchrony) of species is of foremost importance to predict the impacts of dam operation on ecosystem state.

A frequent approach to disentangle the drivers of species synchrony is through experiments (Loreau and de Manzacourt, 2013; Venail et al. 2013; Tredenninck et al. 2017). However, experiments using entire reservoirs are nearly unfeasible because of several confounding factors and the problematic of assigning treatments and true replicates, despite being monumental. A genuine solution to this research constraint is to resort to modelling approaches, which are built on realistic assumptions and are promising techniques to deal with population- and community-level complex ecological

questions (Otto and Day, 2011). Essentially, some of these models can be described by sets of equations that capture the dynamics of local populations, known as vital rates. These vital rates portray the individual-level probabilities of survival, growth, and reproduction, to make projections and inferences on the temporal dynamics of populations and thereby communities (Merow et al. 2014; White et al. 2016). Conveniently, we can reconstruct these vital rates using empirical population time-series data on suitable descriptors of organisms (e.g., body size) and environmental factors (González and Martorell, 2013; González et al. 2016). With these vital rates at hand, we can then project the temporal trajectories of interacting populations to simulate scenarios where drivers of synchrony are manipulated, such as in simulation experiments.

Here, we aimed to investigate the relative influence of environmental stochasticity, species interactions, and demographic stochasticity on the community-level synchrony of fish communities from reservoirs under alternative hydrologic regimes owing to each dam operation scheme. To achieve our objective, we first use long-term data on population size-structures and inverse modelling to reconstruct the equations that describe vital rates for species from both reservoirs, considering the environment and species interactions as covariates of these rates. Second, we use these empirically-derived equations to build dynamic multi-species models that successfully reproduce community dynamics (González and Martorell, 2013; Merow et al. 2014), to perform simulation-based experiments disabling each essential driver of community synchrony (species interactions, and environmental and demographic stochasticity) one at a time and in combination. Intuitively, we could then evaluate how the inclusion or the removal of a given mechanism affects community synchrony. For instance, if community-level synchrony changes more if environmental stochasticity is removed than when species interactions are dropped, we may infer that this community is more sensitive to environmental changes, and this can be mainly attributed to dam operation scheme, once it governs the environmental conditions of the ecosystem. In our argumentation, we explore our results in light of the theoretical predictions on the expected patterns of each mechanism related to community stability.

3.2 Methods

3.2.1 Fish data

We used long-term data on fish communities obtained from two reservoirs with contrasting operation schemes (storage and run-of-river), located in the Iguazu River, Southern Brazil (Appendix A; Figure S1; described in detail in Baumgartner et al. 2020). The long-term data came from a monitoring program conducted since 2003 in three sites along each reservoir, using a standardized sampling protocol. In this study, we used an 11-year subset of this data (from June 2006 to May 2017) in which the sampling method (number of gillnets and exposure time) was equal across all sites (for details, see Baumgartner et al. 2020). Because our methods required population-level data to be summarized on a yearly basis (see *Inverse estimation of vital rates*), we grouped data from June to May as a one-year period, which covers an entire reproductive cycle for most fish species (Baumgartner et al. 2016; de Oliveira et al. 2019). Therefore, each sampling year (hereafter sometimes referred to as ‘year’ for convenience) was composed of a census including six bimonthly surveys comprising three sites in each reservoir.

Because our analytical approach is particularly limited due to data constraints, such as missing data or only a few individuals from species (González et al. 2016), we were able to model only the dominant species from each reservoir. We considered as dominant those species that occurred in all bimonthly surveys, with at least 15 individuals per sample, and at least 5,000 individuals in total. These species were six for the STR reservoir (*Astyanax bifasciatus*, *Astyanax gymnodontus*, *Astyanax lacustris*, *Astyanax minor*, *Oligosarcus longirostris*, and *Pimelodus britskii*) and four for the ROR reservoir (*A. bifasciatus*, *A. minor*, *O. longirostris*, and *P. britskii*). For each captured individual, we obtained data on body size by measuring the standard length (the distance from the tip of the snout to the posterior end of the vertebral column) and used it as a continuous state variable. Because data on standard length was mandatory for every single individual, we excluded those records reporting damages on body parts, especially in the head and the caudal fin.

3.2.2 Calculating observed synchrony

With all the available data, we assembled one abundance-based dataset for each reservoir with the number of captured individuals for each species (columns) and year (rows). We then calculated the observed community-wide synchrony using the statistic proposed by Loreau and de Manzacourt (2008), available in the ‘synchrony’ package (Gouhier and Guichard, 2014) in the R Environment (v. 3.6.1; R Core Team, 2019) as:

$$\varphi_x = \frac{\sigma_{x_T}^2}{\left(\sum_{i=1}^n \sigma_{x_i}\right)^2} \quad (1)$$

In this equation, the community-wide synchrony of population sizes (φ_x) is calculated as the ratio between the community-level temporal variance ($\sigma_{x_T}^2$) and the equivalent aggregate of all population-level standard deviations (σ_{x_i}). This statistic is a standardized metric that drops to 0 (perfect asynchrony) when all species (i.e., population sizes) are perfectly uncorrelated through time, and peaks at 1 (perfect synchrony), when all abundances are perfectly correlated. We chose this statistic because it is a very flexible measure that can be readily applied to empirical and simulated data since it makes no assumptions on the variance and distribution of species abundances (Loreau and de Manzacourt, 2008).

3.2.3 Environmental data and gradients

Along with each fish collection at each site, we also recorded field data on electric conductance ($\mu\text{S}/\text{cm}$ at 25°C), dissolved oxygen (mg/L), pH, and water temperature ($^\circ\text{C}$), with portable devices, and transparency with a Secchi disk (cm). We also collected water and quantified chlorophyll- α ($\mu\text{g}/\text{L}$) in the laboratory using a spectrophotometer (Golterman et al. 1978). These variables affect the biology of freshwater fish through direct and indirect influences on habitat condition, metabolism, and behavior (Matthews, 1998; Jackson et al. 2001), thus we considered all of them as important to our environmental gradients. Fortunately, although there were a few missing values for some variables (see Appendix A; Table S1), we were able to fill these blank cells through the

imputation of the missing values, conducted using the routine named Multivariate Imputation by Chained Equations (MICE), available in package ‘mice’ (van Buuren and Groothuis-Oudshoorn, 2011). This approach considers every environmental variable as predicted by all others in the dataset and generates predictions for the missing values anywhere in the data.

For modeling purposes (see *Inverse estimation of vital rates*), we had to build environmental gradients with a number of observations that matched the yearly data for fish population sizes. Therefore, we averaged the environmental variables across sampling sites and survey months, thus having a single value for each year. This averaging was conducted using a Principal Coordinates Analysis (PCoA) based on Euclidean dissimilarities, as calculated from normalized (i.e., centered) variables. From the first axis of this ordination (PCoA 1; Appendix A; Fig. S2-S3), we then extracted the scores of the centroids for each sampling year and considered as the generic environmental gradient to use in the subsequent analyses. All these procedures were repeated for each reservoir, separately.

3.2.4 Schooling effect

The formation of schools is a common group strategy in teleost fish related to defense against predators and foraging optimization (Pitcher, 1986; Hemelrijk et al. 2015). These formations are also important determinants of competition and reproduction in many fish species (Ioannou et al. 2017) and are likely formed by more than one species when there is a phylogenetic resemblance among them (Ward et al. 2002). Here, we used the broad concept of schooling in fish to derive a variable that described the intra- (i.e., self-regulatory) and inter-specific (i.e., competition and/or predation) interactions among species at the population level (Herbert-Read et al. 2011). We quantified the positive and negative relationships within and among species in a given community using a classical density-dependent component that we referred to as the ‘schooling effect’. Therefore, we calculated the time-varying schooling effect for each species as:

$$w_{i,t} = \sum_{j=1}^s (n_{j,t} \alpha_{ij}) \quad (2)$$

where the schooling effect on species i at a given time t ($w_{i,t}$) is the sum across all species for the product between the log-transformed abundance of the j -th species at time t ($n_{j,t}$) and the interaction coefficient (α_{ij}), which portrays the effect of species j on i . This formulation considers both intra-specific (α_{ii}) and inter-specific ($\alpha_{ij}, \forall i \neq j$) interactions. The coefficients of the interaction matrices (see Appendix A; Table S2-S3) were obtained using the time-series approach to detect causality in multi-species data as proposed by Sugihara et al. (2012) and Ushio et al. (2018).

3.2.5 Inverse estimation of vital rates

To build dynamic models representing the temporal trends of the studied communities, we had to reconstruct the vital rates of fish populations. This procedure has been successfully applied to fish data (e.g., Fournier et al. 1998; Gosh et al. 2012; White et al. 2016), which makes the estimates obtained from inverse modelling reliable at a fair accuracy (González et al. 2016). We conducted the reconstruction using the likelihood approach as described in González and Martorell (2013), in which the population structure (n) changes over time as a function of a continuous state variable such as body size (x), that determines the rates of survival (s), growth (g), and recruitment (f_1 and f_2). In our modelling, we extended the approach of González et al. (2016) and treated the vital rates as changing over time by including the effect of an environmental forcing factor (i.e., the environmental gradient; h) and the schooling effect (w), which yielded the following full model:

$$n_{t+1}(y) = \int [s(x, h, w) \cdot g(y, x, h, w) + f_1(x, h, w) \cdot f_2(y, h, w)] \cdot n_t(x, h, w) dx \quad (3)$$

where $s(x, h, w)$ describes the survival probability of an x -sized individual; $g(y, x, h, w)$ represents the probability of an individual of changing from size x to y at each time step; $f_1(x, h, w)$ depicts the number of newborns produced by an x -sized individual at each time step; and $f_2(y, h, w)$ portrays the size-distribution of the newborns. All these equations (s , g , f_1 , and f_2) were dependent on the time-varying environment (h) and the schooling effect (w).

Because there are many structures that can describe how vital rates interact to produce size structures (Ranta et al. 2008; Merow et al. 2014; Plard et al. 2019), we used a reductionist version of the original structured population model from Easterling et al. (2000), with the following simple equations:

$$\begin{aligned}
 s(x, h, w) &= \text{logistic}(\beta_1 + \beta_2 \cdot x + \beta_3 \cdot h + \beta_4 \cdot w) \\
 g(y, x, h, w) &= \text{Normal}(\mu = \beta_5 + \beta_6 \cdot x + \beta_7 \cdot h + \beta_8 \cdot w, \sigma = \exp(\beta_9 \cdot \ln(10))) \\
 f_1(x, h, w) &= \exp(\beta_{10} + \beta_{11} \cdot x + \beta_{12} \cdot h + \beta_{13} \cdot w) \\
 f_2(y, h, w) &= \text{Normal}(\mu = \beta_{14} + \beta_{15} \cdot h + \beta_{16} \cdot w, \sigma = \exp(\beta_{17} \cdot \ln(10)))
 \end{aligned} \tag{4}$$

As it is clear in these equations, the four vital rate regressions and their temporal dynamics are determined by 17 parameters ($\beta_1, \dots, \beta_{17}$). We did not consider the interactions among x , h , and w for simplicity because it would inflate the number of parameters to be estimated. The inverse routine consists of estimating these parameters using time-series data of empirical abundances and size-structures as inputs (González et al. 2016).

If all parameters for vital rate regressions were estimated separately, we would be ignoring biological rules and result in unrealistic population dynamics. Therefore, all β s were estimated simultaneously, which was a costly computational procedure conducted in two steps. First, we used the Differential Evolution Adaptive Metropolis (DREAM; Vrugt et al. 2009), an algorithm based on Markov Chain Monte Carlo (MCMC) to find a multivariate likelihood surface area, both unimodal and with a positive gradient, where the solutions with the highest likelihood ratio can be searched for the combination of parameters. Second, we implemented an Automated Differentiation Model Builder (ADMB; Fournier et al. 2012) to find the mode of this surface area, which yielded an optimal combination of parameters that best reproduce the observed population dynamics (González et al. 2016).

Because the DREAM+ADMB search is as exhaustive as the amount of data, and exploratory trials suggested identifiability issues (i.e., finding more than one combination of parameters that yielded the same population structures), we had to define reasonable priors for each parameter to assist the inverse modelling and avoid biologically unrealistic

vital rates. We used different priors depending on the modeled species for all parameters, but restricted those related to environmental stochasticity (β_3 , β_7 , β_{12} , and β_{15}) and species interactions (β_4 , β_8 , β_{13} , and β_{16}) to an interval between -0.5 and 0.5, as suggested by González and Matorell (2013). This decision was fundamental to preserve the comparative properties of models in terms of numeric scales among species and to prevent potential over-responses to the environment and/or species interactions during simulations.

The inverse modelling was conducted using source code in C++ language, integrated into R using package ‘Rcpp’ (Eddelbuettel et al. 2011). The MCMC algorithm was run using the package ‘dream’ (Guillaume and Andrews, 2012) and the identified surface was used as the starting point to ADMB using package ‘R2admb’ (Bolker et al. 2012).

3.2.6 Dynamic multi-species models

After estimating the vital rate parameters for each species from both reservoirs, the next step was to build the multi-species models. For this task, we used two models: an Integral Projection Model (IPM) and an Individual-Based Model (IBM). Both IPMs and IBMs are flexible approaches that can represent a wide range of temporal dynamics within any desired level of biological realism (Merow et al. 2014; DeAngelis, 2018).

We initialized models using the average yearly abundance for each species (six for STR and four for ROR) across the sampled years. The models were then projected forward using the survival regression to determine if individuals may live to the next step, the growth regression to update the body size of individuals, and the fecundity regressions to determine the number and size of the newborns that should be added to each local population. To include the time-dependent environmental variation, we sampled a random number between -1 and 1 from a uniform distribution at each time step to represent the environmental gradient (h in Eq. 3 and 4), since parameters were calibrated using the scores from an ordination (see *Environmental data and gradients*). The density-dependent schooling effect (w in Eq. 3 and 4) was calculated for each species using the interaction matrix and the updated abundances of species at every time step. During simulations, a modification in the survival functions was required to approach biological

realism. Because some survival probabilities were asymptotic at one (Appendix A; Fig. S6-S15), meaning that the largest individuals for a given species had zero probability of mortality, we truncated the survival probabilities at 0.9 during simulations. We considered all models as spatially implicit for facilitation and we ran models for each reservoir independently.

3.2.7 Simulation experiments

To achieve our objective of investigating the roles of environmental stochasticity, species interactions, and demographic stochasticity on the synchrony of fish communities from reservoirs under alternative dam operations, we conducted simulation experiments removing each of these three drivers one-by-one and in combination. To remove environmental stochasticity, we set the parameters related to the environmental gradient (β_3 , β_7 , β_{12} , and β_{15}) to zero; this scenario preserves the species interactions within communities. To remove species interactions (i.e., schooling effect), we set the off-diagonals of interaction matrices to zero, which eliminated the inter-specific effects while preserving the intra-specific coefficients. Finally, to remove the effects of demographic stochasticity, we used IPMs instead of IBMs because IPMs do not include demographic stochasticity and this is inherent to IBMs. We opted to remove these effects on species synchrony using the procedures above, instead of modulating (i.e., gradually decreasing their effects) each of them, because our estimation with inverse modelling does not guarantee that there are no mixed-effects among them at some discrete degree (González et al. 2016). Thus, pulling out these mechanisms under controlled simulations may give a clearer perspective on how each one was related to synchrony, within each community.

Once we determined how drivers of synchrony should be disabled, we conducted the simulation experiments under the following seven ‘treatments’: (1) IBM with environmental stochasticity and species interactions (all drivers enabled); (2) IPM with environmental stochasticity and species interactions (demographic stochasticity removed); (3) IBM with environmental stochasticity (species interactions removed); (4) IBM with species interactions (environmental stochasticity removed); (5) IPM without environmental stochasticity (species interactions only); (6) IPM without species

interactions (environmental stochasticity only); and (7) IBM without environmental stochasticity and species interactions (demographic stochasticity only).

Each IPM was run for 2,000 time-steps after 500 burn-in runs. We then calculated the community-level synchrony for 100 randomly selected 30 time-steps sections of each IPM. Simulations using IBM were run for 30 time-steps and repeated 100 times for each simulation experiment. Those IBMs in that any species went extinct due to demographic stochasticity were discarded and repeated until all species were alive at the end of simulations. For both models, we treated time as discrete (this is inherent to IPMs but we only allowed IBMs to move forward when the fates of all living individuals were simulated at each time step). The main codes for the simulations described in the *Methods* section have been stored in a GitHub repository ([link to GitHub repository](#)). A summary of the analytical procedures is portrayed in Fig. 1.

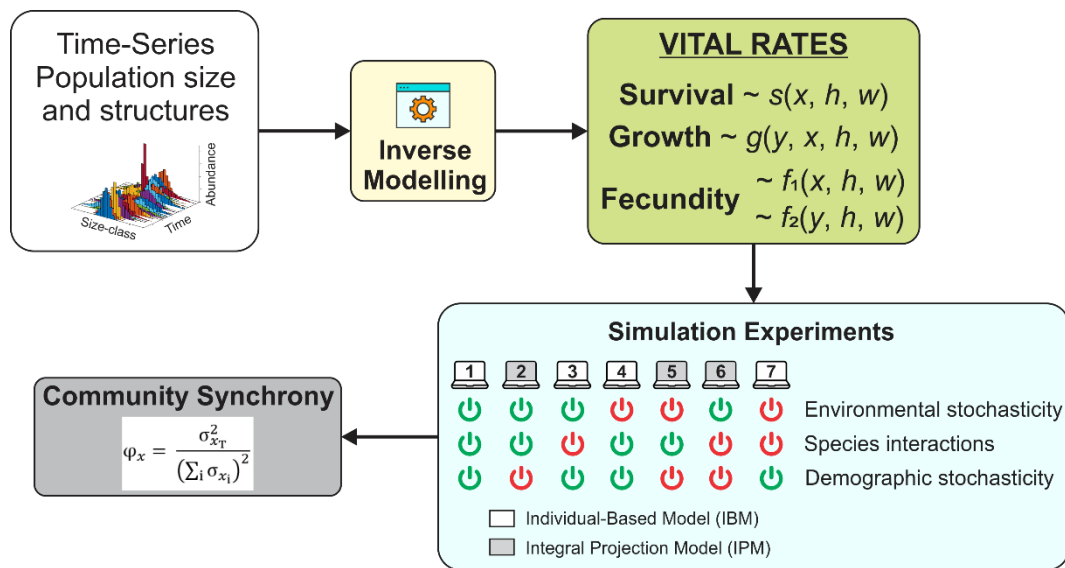


Figure 1 – Diagram of our analytical procedures. See *Methods* for details. This workflow was repeated for each reservoir, separately.

3.3 Results

The observed synchrony of species abundances for the STR reservoir was 0.45 (999 randomizations; one-tailed P -value < 0.01), with mean pair-wise correlation among species at 0.27, whereas the observed synchrony for the ROR reservoir was 0.53 (one-tailed P -value = 0.01) and mean pair-wise correlation among species of 0.35. Numerically, both values were stronger than expected by chance and the observed synchrony, for the STR reservoir, was slightly lower than that for the ROR reservoir.

The simulation experiments showed that removing different drivers of species synchrony (or their combination) resulted in distinct among-species temporal trends between the two reservoirs (Fig. 2; see also Appendix A; Fig. S16-S29 for simulated population structures). For the STR reservoir (Fig. 2a), removing species interactions had the largest perceived effect on synchrony, leading to a clearly more synchronous community when it was the only driver removed (“-SI”) and when it was removed along with environmental stochasticity (“-SI -ES”). However, in relation to simulations with all mechanisms enabled (“All Drivers”), removing environmental stochasticity alone (“-ES”) lowered species synchrony, although only slightly. In addition, disabling demographic stochasticity apparently did not affect the overall synchrony. We were also able to identify that the empirical value for synchrony (red circle in Fig. 2a) was closer to the simulation experiment considering all drivers as operating on the community-level dynamics.

Considering the ROR reservoir (Fig. 2b), there was a high variability depending on the driver of species synchrony that was disabled, alone or in combination. Compared to the simulations considering the influence of all three drivers on the temporal dynamics (“All Drivers”), removing environmental stochasticity alone (“-ES”) was the only condition in which community synchrony increased. In opposite, disabling demographic stochasticity alone (“-DS”) led to the lowest community synchrony, apparently. However, evaluating the simulations removing species interactions only (“-SI”), we noted that there was a synchronizing effect of species interactions, which can be interpreted as a tradeoff between the synchronizing effect of species interactions and the desynchronizing effect of environmental stochasticity. The empirical value for synchrony (red circle in Fig. 2b) roughly deviated from the expectation under the influence of all drivers and was closer to those simulations including only environmental stochasticity (“-DS -SI”).

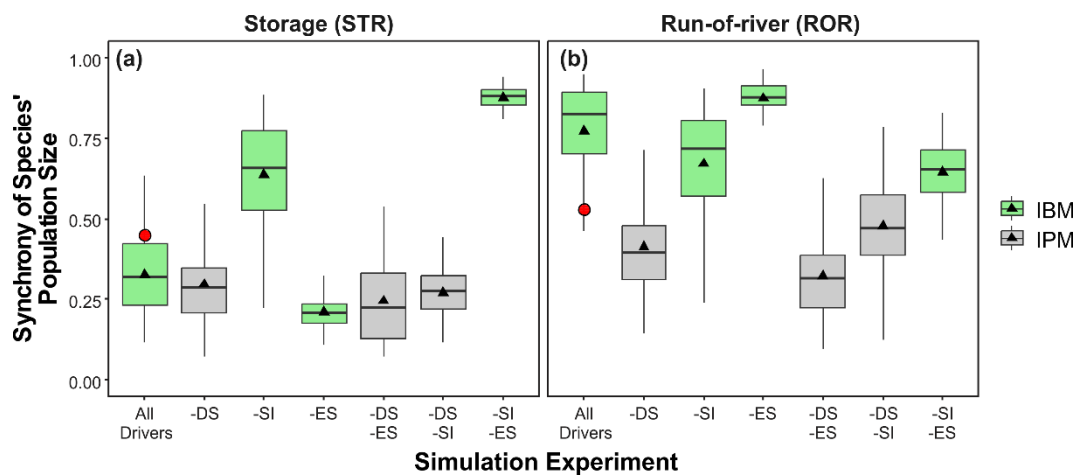


Figure 2 – Community-level synchrony of species' population sizes from simulation experiments. Synchrony was calculated for simulations with demographic stochasticity, species interactions, and environmental stochasticity (“All Drivers”), without demographic stochasticity (“-DS”), without species interactions (“-SI”), without environmental stochasticity (“-ES”), demographic and environmental stochasticity removed (only species interactions; “-DS -ES”), demographic stochasticity and species interactions removed (only environmental stochasticity; “-DS -SI”), and species interactions and environmental stochasticity removed (only demographic stochasticity; “-SI -ES”). Red circles represent the observed synchrony, while black triangles represent the mean synchrony values for each simulation experiment. For details, see *Simulation experiments*.

3.4 Discussion

The results produced by the models are in agreement with our overall expectation about different dam operation schemes, coinciding with divergent underlying mechanisms of community synchrony, and consequently stability. Findings suggest an effect of the water level variation regime on temporal fluctuations of the abundance of fish species in the long-term, which support that we are investigating dam operation schemes as an imperative factor underlying stability of reservoirs. Considering the results for both reservoirs, the mechanisms that were more influential for the community-level synchrony were fluctuations in environmental features (environmental stochasticity) and cross-regulating effects among species (species interactions), with an uninformative contribution of species-specific random events (demographic stochasticity). Thus, our analysis provides initial evidences for the causal relationship between dam operation schemes and ecosystem stability, although we also confirm that it was arduous to decipher

the mechanisms of species synchrony from time series (Loreau and de Manzacourt, 2008; Tredennick et al. 2017).

3.4.1 Drivers of synchrony in the storage reservoir

For the STR reservoir, disabling species interactions from simulations increased species synchrony (Fig. 2a), which underlines that the structure of interactions among species had a desynchronizing effect on the fish assemblage. Assuming that more stable communities tend to have asynchronous dynamics (Loreau and de Manzacourt, 2008; Craven et al. 2018), our results suggest that inter-specific interactions may have a stabilizing role in this reservoir. Theoretical predictions generalize that decreased synchrony, in communities where interactions are important, emerges from negative relationships among species (Loreau and de Manzacourt, 2008; Tredennick et al. 2017). These interactions result in non-independent but asynchronous fluctuations in populations, with differences in species' population sizes changing primarily from variations in the abundances of co-occurring predators or competitors (Pianka, 1974; Houlihan et al. 2007).

Particularly, interactions among species become important at multi-species communities when factors such as different trophic levels (Bauer et al. 2014) and resource overlap (Vasseur and Fox, 2007) are likely to influence community dynamics. Once our modeled species from the STR reservoir were composed of both potential predators and competitors, and inter-specific interaction coefficients were far from weak (Appendix A; Table S2), we may conclude that species interactions had a stabilizing role in this community by creating temporal asynchronous dynamics. Furthermore, recent work evidenced that those *Astyanax* species, which had potential to compete for food, actually exhibit strong niche segregation (Pini et al. 2019) and are included in the feeding spectrum of the modelled predator species (Novakowski et al. 2007; Pereira et al. 2016). These evidences have then tempted us to infer that perhaps trophic interactions have a more important role than competition on increasing community-level stability in the STR reservoir.

The removal of environmental stochasticity decreased community-level synchrony in simulations for the STR reservoir, which suggests a synchronizing effect of

the environmental forcing factors. Two pieces of evidence allow us to suggest that this result is closely related to this operation scheme. First, the theory states that species tend to fluctuate similarly in non-constant environments because communities exhibit positive environmental correlations, especially when other factors are not strong enough to overcome the environmental responses (Loreau and de Manzacourt, 2008; de Manzacourt et al. 2013). Second, evolution delivered riverine fish to an intimate relationship with water level variations (Matthews, 1998; Agostinho et al. 2004). The evolutionary adjustments for feeding and reproduction of many fish species are directly dependent on seasonal water level fluctuations that provide food and physiological triggers for migration and reproduction (Lowe-McConnell, 1987; Correa and Winemiller, 2014; Wootton and Smith, 2014). Thus, we are able to argue that variations in the water level of reservoirs are fundamental for the temporal dynamics of nutrient input and fish movement (Thomaz et al. 2007; Agostinho et al. 2016), as well as their absence may compromise these processes (Gubiani et al. 2007; Ngor et al. 2018). Given that similar responses to the environment are theoretically inherent to less stable communities (Loreau and de Manzacourt, 2008), we may therefore conclude that there is a reasonable tradeoff between the synchronizing (destabilizing) role of environmental stochasticity and the desynchronizing (stabilizing) role of species interactions on the fish community of the STR reservoir.

There was no clear difference among simulations with and without demographic stochasticity for the STR reservoir. This similarity raised questions on the uninformative potential of these results. In thesis, demographic stochasticity is expected to decrease community synchrony (Loreau and de Manzacourt, 2008) but those simulations including only this mechanism yielded very high synchrony values (Fig. 2a), which somehow indicates large local populations (Tredennick et al. 2017). These facts led us to assume that the effect of demographic stochasticity on the synchrony of fish community from the STR reservoir may be nearly negligible and the dynamics of fish populations are likely determined only by environmental stochasticity and species interactions.

3.4.2 Drivers of synchrony in the run-of-river reservoir

Results for simulations manipulating the mechanisms related to synchrony for the ROR were not intuitive at first glance and deserved a thorough examination. Apparently, removing demographic stochasticity and species interactions decreased synchrony, with the former causing the strongest shift when compared with the simulations including all drivers (Fig. 2b). Dropping environmental stochasticity, in turn, was the only condition where community-level synchrony increased. For convenience, and hopefully clearance, we will discuss these results in reverse.

Under the coating of theory, environmental stochasticity is expected to play a desynchronizing role when species exhibit different responses to a temporarily variable environment, especially when interspecific interactions are weak (Yachi and Loreau, 1999; Loreau and de Manzacourt, 2008). In the ROR reservoir, water level fluctuations that may benefit and synchronize fish communities (as described previously) are only discrete and do not respect any seasonal pattern, which is common for reservoirs under this operation scheme (Bilotta et al. 2016; Baumgartner et al. 2020). Studies report that species that thrive in reservoirs operated under ROR are independent of seasonal hydrologic variations to complete their life cycle (Fernando and Holčík, 1991; Ngor et al. 2018; Perôncio et al. 2019), owing to the virtually constant water level. This hydrologic condition may result in species that can respond independently to stochastic events related to the abiotic state of the environment, thus suggesting a clear desynchronizing effect of environmental stochasticity. Furthermore, we may argue that these findings suggest that the long-term effects of the ROR operation scheme (the ROR reservoir was more than 30 years old) have weakened the species-environment relationships in terms of seasonal flood pulses and the longitudinal process that are inherent to natural freshwater environments.

Accompanying the predictable effects on the life cycle and spatial distribution of aquatic organisms, flood pulses also modify physical and chemical characteristics along reservoirs (Thornton et al. 1990; Maavara et al. 2020). In natural rivers, the spatial and temporal dynamics created by water level variations can be described as large waves that vary in shape, amplitude, frequency, and wavelength, which travels through the river body and governs the local and river-scale nutrient dynamics (*sensu* Humphries et al. 2014). This concept summarizes biogeochemical processes, nutrient cycling, trophic

interactions, and spatial distribution of organisms into a robust model that accurately predicts the longitudinal processes determining fish composition (Gido et al. 2002; Humphries et al. 2014). When applied to impounded rivers, this wave concept predicts that reservoirs attenuate river waves through barriers to flow, weakening most of the main factors controlling spatial and temporal dynamics (Thornton et al. 1990; Humphries et al. 2014).

Specifically for the ROR reservoir, the most important variables related to the generic environmental gradient, which was used for model parametrization, were chlorophyll- α and water transparency (Appendix A; Table S4). This means that the ecosystem primary productivity, surrogated by these variables, was quite relevant for the limnology (i.e., biogeochemistry) of this reservoir, matching the empirical evidence observed by Bortolini et al. (2019). Those biogeochemical processes related to primary productivity are essential in reservoirs (Maavara et al. 2020) and there is a clear role of dam operation on the nutrient dynamics of reservoirs, as conceptualized by the wave concept (Humphries et al 2014). In this sense, our results suggest that the hypothesis of a neutralizing effect of the long-term absence of water level variations, on the species-environment relationships, seems defensible and robust.

The next most important driver of community synchrony for the ROR reservoir was species interactions, identified as playing a synchronizing role on fish community. More synchronous species' trajectories, driven by species interactions, assume that negative inter-specific relationships such as predation and competition are weak or neutral (Loreau and de Manzacourt, 2008; de Manzacourt et al. 2013). Theoretical and empirical work defends that communities in which predation and competition do not cause populations to compensate for each other through time are less stable, although they assume that these interactions should be strong (Tilman, 1988; Chu and Adler, 2015; Tredennick et al. 2017). The compensatory pattern explains the increased ecosystem stability because species are less likely to be uniformly affected by disturbances (Loreau and de Manzacourt, 2008).

Our results do not contradict the idea that more stable communities arise when species compensate for each other through time. Instead, we have evidence to suggest that the inter-specific interactions, that may cause the fish assemblage from the ROR reservoir to achieve a more stable condition, were likely affected by the dam operation scheme. Although several pieces of evidence are still necessary, we may speculate that

the relatively constant environment resulting from this dam operation scheme probably caused fish to follow temporal trajectories dictated by discrete species-specific responses to environmental features. The fact that potential negative interactions among species were not affecting their relative performance over time advocates in favor of this rationale.

Finally, while theory foretells that random population fluctuations driven by stochastic individual-level processes act as a stabilizing factor (Lande et al. 2003; Loreau and de Manzacourt et al. 2008), we had an apparent overall synchronizing effect of demographic stochasticity on the ROR community (Fig. 2b; IBMs with higher synchrony values than IPMs). Nevertheless, we judge this result with caution as it is probably a misleading outcome arising from the unbalanced tradeoff between environmental stochasticity and species interactions (when demographic stochasticity was dropped, at least one of these mechanisms were enabled). This interpretation is endorsed if we focus on simulations considering demographic stochasticity as the only active mechanism (“-SI -ES” in Fig. 2b), which yielded the highest synchrony values considering experiments with only one driver as active.

3.5 Final considerations

Responses to the fluctuating environment and how species interact with each other were the most important mechanisms underlying community-level synchrony of the two studied impoundments, which exhibit contrasting dam operation schemes. There was a tradeoff between these two mechanisms in determining the (a)synchronous dynamics of each fish community, although with opposite contributions. We also found that the effect of demographic stochasticity was nearly indistinguishable for both reservoirs. Results for the STR reservoir showed a strong desynchronizing effect of species interactions, with a supporting synchronizing effect of environmental variations, whereas the results for the ROR reservoir revealed opposite effects of the same mechanisms. Observed synchrony was qualitatively similar between reservoirs with empirical values closer to simulations including all three drivers for the STR reservoir, whereas the results for the ROR were more variable and demanded thorough evaluation.

We must still be conservative and consider that temporal synchrony may arise from non-unique combinations of driving mechanisms (Ranta et al. 2008). However, the results that we produced allow us to argue that there is likely a mismatch between the biological requirements of local populations and the energy demands that dictates dam operation, especially the relatively constant volume or ROR reservoirs. Assuming this analogy as correct, and the evidence that the longitudinal dynamics of reservoirs can still be controlled by dam operation (Miranda and Dembkowski et al. 2015), considering varying the flow regimes under water releasing schedules with annual or seasonal ups and downs becomes fundamental for preserving local- and watershed-scale ecosystem processes, especially for reservoirs operated under ROR. Determining these schedules must consider the requirements of fish species and catchment features that are inevitably context-dependent, but we believe that our results should unroll further investigation. We envision that the effects of dam operation scheme on aquatic communities and ecosystem stability should be better disentangled if our findings inspire more work considering large spatial scales and a gradient of operation schemes.

3.6 Caveats

Along with the clear distinction regarding the water level variations owing to each operation scheme, the two reservoirs differ in terms of dam height and length, flooded area, volume, and residence time (Baumgartner et al. 2020). In our argumentation, ignoring such differences probably masks critical factors that underpin community-level synchrony. This is why our results should be complemented before defining a causal relationship between dam operation scheme and ecosystem stability.

Like any model, ours have limitations as well. We are compelled to acknowledge that although we used highly controlled models and simulations to rule out the effects of some of the most important mechanisms that operate on community synchrony, we must be conservative regarding the generalizations arising from these findings. Assuming a causal relationship between each dam operation scheme and the results that we produced should be a consequence of further investigations. From our findings, we expect readers to be reasonable and only admit a correlation between the relative roles of species

interactions and environmental and demographic stochasticity on the community-level synchrony, and the dam operation schemes. We also recognize that our sampling design is restricted to only two reservoirs. However, this constraint does not invalidate our conclusions because models were constructed considering empirical data, which certainly accounts for the individual contexts of each reservoir and their respective intrinsic processes.

Many studies have been conducted aiming at understanding the processes underlying species' synchrony in communities, most of them focusing on plants (Loreau and de Manzacourt, 2013; Chu et al. 2016; González et al. 2016; Tredenninck et al. 2017). This bias towards terrestrial sessile organisms creates a shortfall for cross-literature comparisons of our findings concerning freshwaters, especially for fish. We have also to consider the interactions among each of the three drivers of community synchrony in the inverse modelling procedures (interactions among x , h , and w in Eq. 4). However, our prognosis on the identifiability of model parameters was not encouraging and we decided to model the vital rates within the narrowest simplicity.

Another fact that deserves observations is that reconstructing the vital rates of species using highly-parametrized models proved challenging. Without defining tight prior bounds, the model occasionally converged for combinations of parameters that resulted in biologically unrealistic population dynamics, which translates into too artificial populations. In addition, some parameters (especially those modulating the environmental stochasticity and species interactions) reached the initially provided bounds for many species, meaning that some effects of the among-species and environmental effects might have been underestimated. Therefore, the estimation of the vital rates should not be transferred to another context but that of this study.

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APPENDIX A – Details of methods and model outputs

Table S1 – Number of missing values imputed using the Multivariate Imputation by Chained Equations (MICE) for each environmental variable in our dataset (for details, see section *Environmental data and gradients* in the manuscript).

	Electric conductance ($\mu\text{S}/\text{cm}$ at 25°C)	Dissolved oxygen (mg/L)	pH	Water temperature ($^\circ\text{C}$)	Transparency (cm)	Chlorophyll- α ($\mu\text{g}/\text{L}$)
Storage (STR)	1	0	1	1	1	3
Run-of-river (ROR)	0	0	1	0	0	5

Table S2 – Interaction coefficients among the six modeled species from the storage (STR) reservoir (Salto Santiago, Iguaçu River, Brazil).

	<i>A. bifasciatus</i>	<i>A. gymnodontus</i>	<i>A. lacustris</i>	<i>A. minor</i>	<i>O. longirostris</i>	<i>P. britskii</i>
<i>A. bifasciatus</i>	-0.10	0.38	0.00	-0.08	0.42	0.00
<i>A. gymnodontus</i>	0.16	0.22	0.00	0.00	0.00	0.00
<i>A. lacustris</i>	0.00	0.00	0.19	0.00	0.26	0.00
<i>A. minor</i>	0.46	0.00	0.00	0.53	0.00	0.00
<i>O. longirostris</i>	0.00	0.00	0.00	0.00	-0.01	0.00
<i>P. britskii</i>	0.15	0.00	0.00	0.20	0.00	0.44

Table S3 – Interaction coefficients among the four modeled species from the run-of-river (ROR) reservoir (Salto Osório, Iguaçu River, Brazil).

	<i>A. bifasciatus</i>	<i>A. minor</i>	<i>O. longirostris</i>	<i>P. britskii</i>
<i>A. bifasciatus</i>	0.42	0.47	0.55	0.00
<i>A. minor</i>	0.27	0.29	0.29	0.00
<i>O. longirostris</i>	0.001	-0.07	-0.27	0.00
<i>P. britskii</i>	0.00	0.00	0.00	-0.04

Table S4 – Spearman's rank correlation between the first axes of the Principal Coordinates Analysis (PCoA) applied to the Euclidean dissimilarities, calculated from normalized environmental data (electric conductance, dissolved oxygen, pH, water temperature, transparency, and chlorophyll- α), for the two reservoirs operated under storage (STR; Salto Santiago) and run-of-river (ROR; Salto Osório) from the Iguaçu River, Brazil. These variables are the most responsible for the environmental gradient used in inverse modelling (see *Environmental data and gradients* in the manuscript for details).

Environmental variable	STR	ROR
Electric conductance ($\mu\text{S}/\text{cm}$ at 25°C)	0.25	-0.08
Dissolved oxygen (mg/L)	-0.49	-0.48
pH	0.69	0.51
Water temperature ($^\circ\text{C}$)	0.10	-0.26
Transparency (cm)	-0.39	-0.67
Chlorophyll- α ($\mu\text{g}/\text{L}$)	-0.68	-0.73

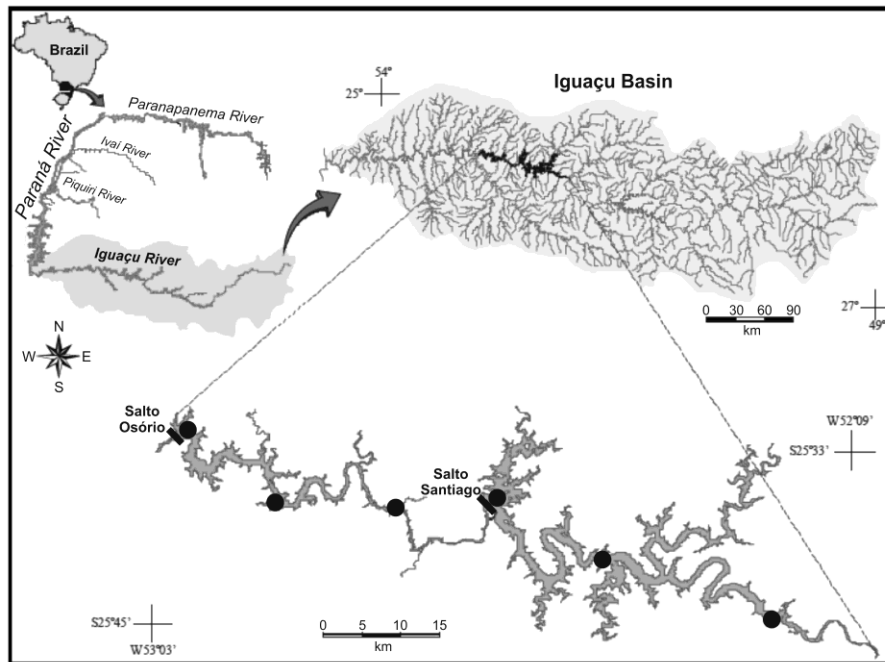


Figure S1 – Location of the sampling sites (black circles) from the two reservoirs operated under Storage (STR) and Run-of-river (ROR), from the Iguazu River, Paraná Basin, Brazil.

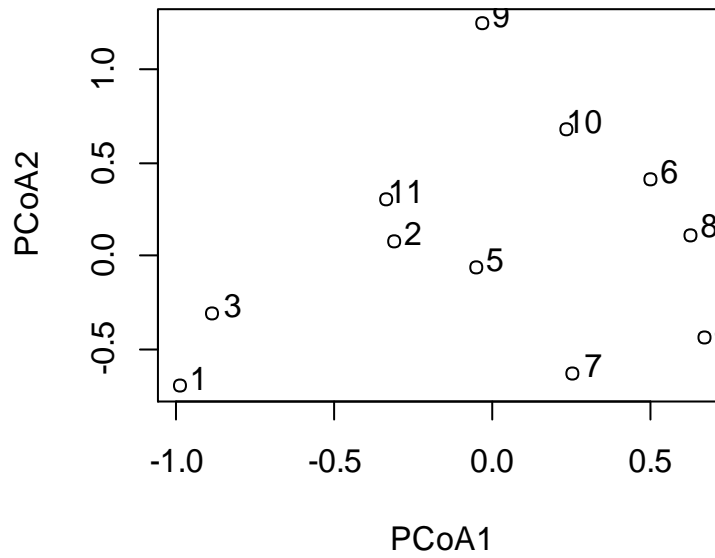


Figure S2 – Principal Coordinates Analysis (PCoA) with Euclidean dissimilarities applied to the environmental variables (electric conductance, dissolved oxygen, pH, water temperature, transparency, and chlorophyll- α) from the Storage (STR) reservoir. Each point in the plotting panel represents the centroid for a given sampling year. The PCoA 1, which explained 25.21% of total variation, was used as the environmental gradient for estimating the time-varying vital rates.

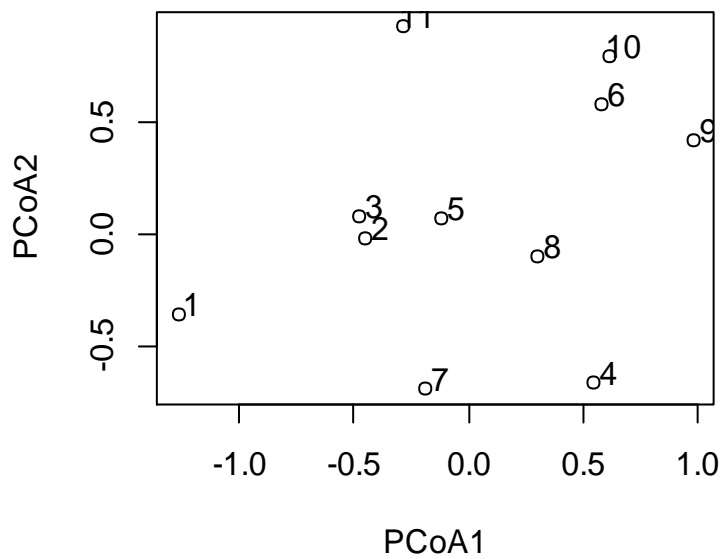


Figure S3 – Principal Coordinates Analysis (PCoA) with Euclidean dissimilarities applied to the environmental variables (electric conductance, dissolved oxygen, pH, water temperature, transparency, and chlorophyll- α) from the Run-of-river (ROR) reservoir. Each point in the plotting panel represents the centroid for a given sampling year. The PCoA 1, which explained 28.46% of total variation, was used as the environmental gradient for estimating the time-varying vital rates.

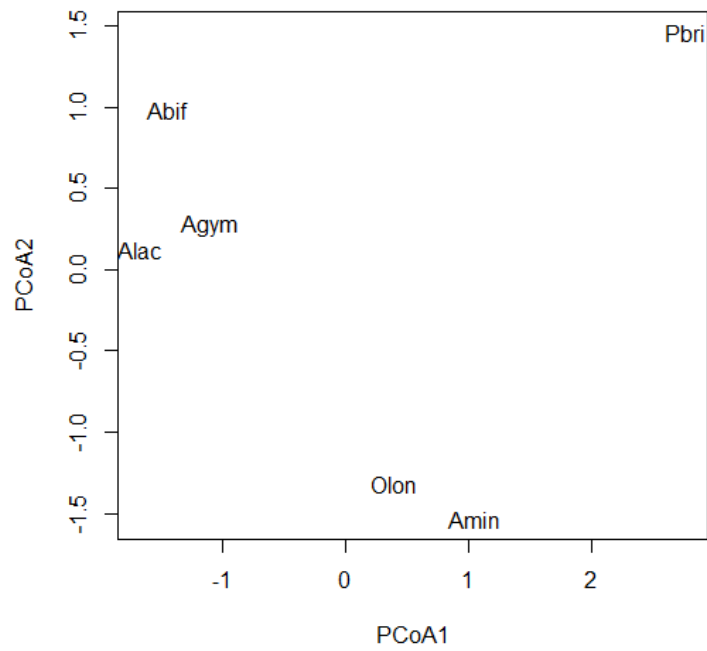


Figure S4 - Principal Coordinates Analysis (PCoA) with Euclidean dissimilarities applied to the vital rates of the six modelled species from the Storage (STR) reservoir.

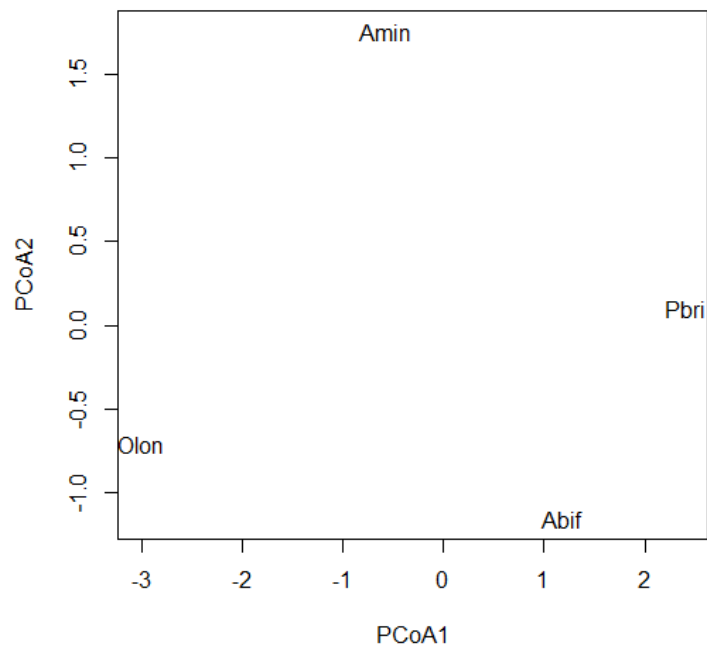


Figure S5 - Principal Coordinates Analysis (PCoA) with Euclidean dissimilarities applied to the vital rates of the four modelled species from the Run-of-river (STR) reservoir.

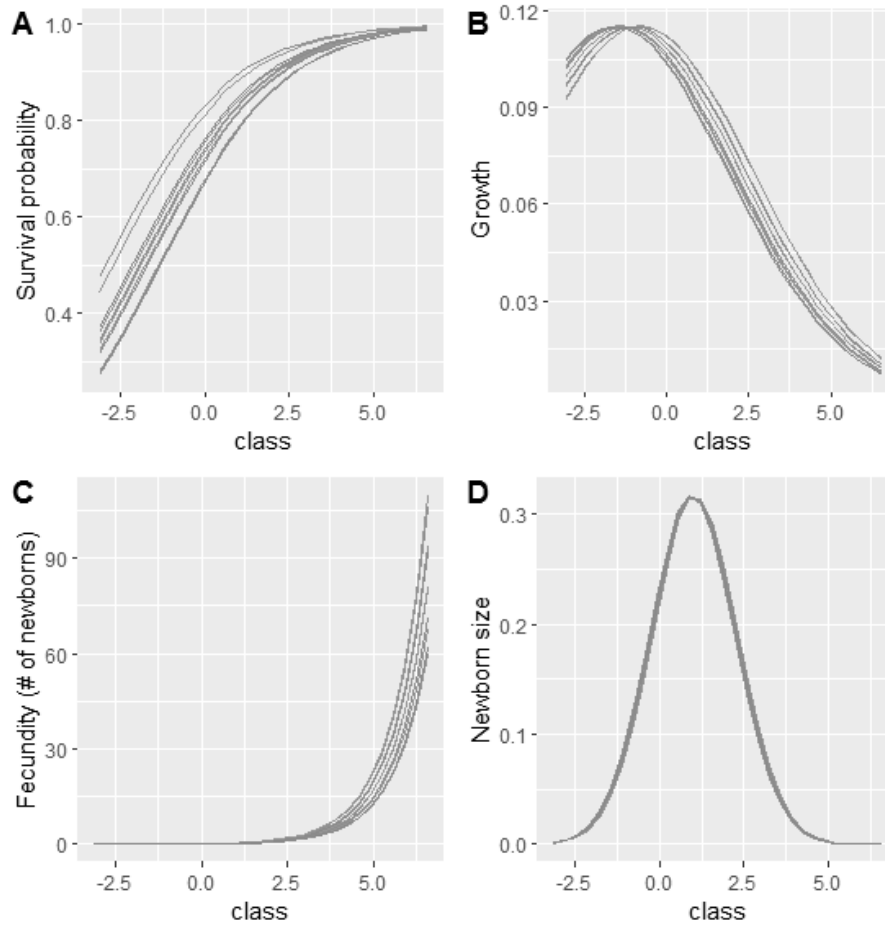


Figure S6 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Asyanax bifasciatus* with population-level data from June 2006 to May 2017 from the storage (STR) reservoir (Salto Santiago, in the Iguaçu River, Brazil).

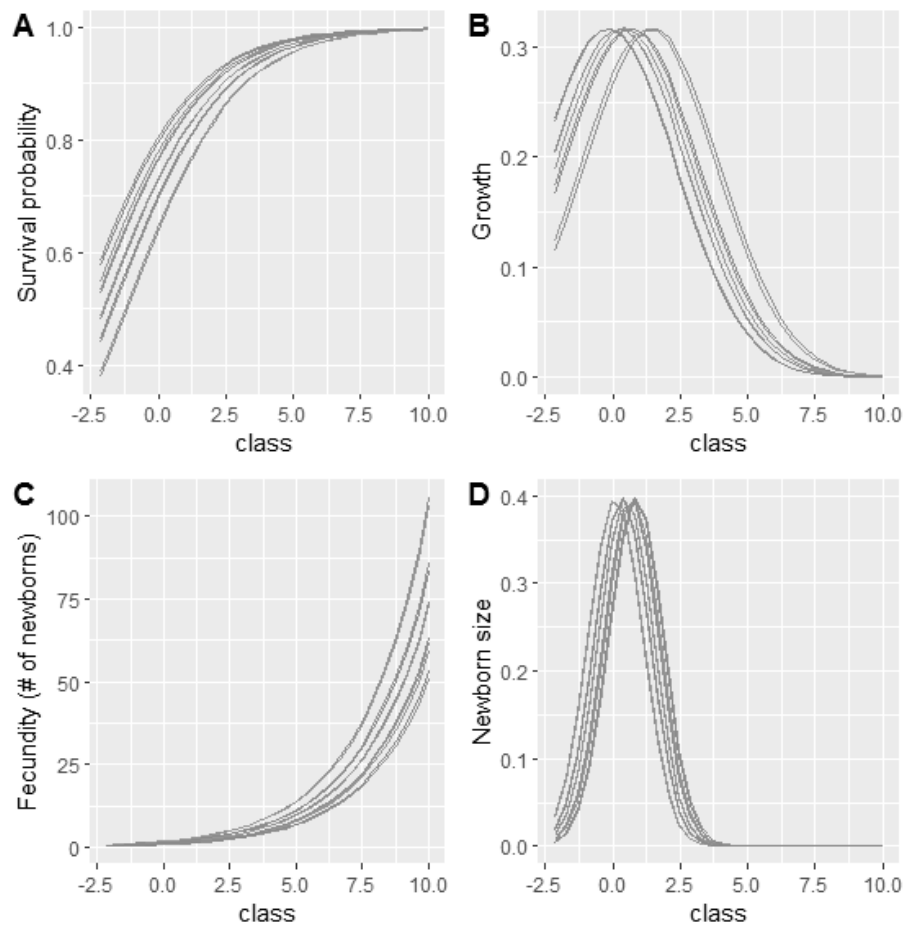


Figure S7 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Asyanax gymnodontus* with population-level data from June 2006 to May 2017 from the storage (STR) reservoir (Salto Santiago, in the Iguaçu River, Brazil).

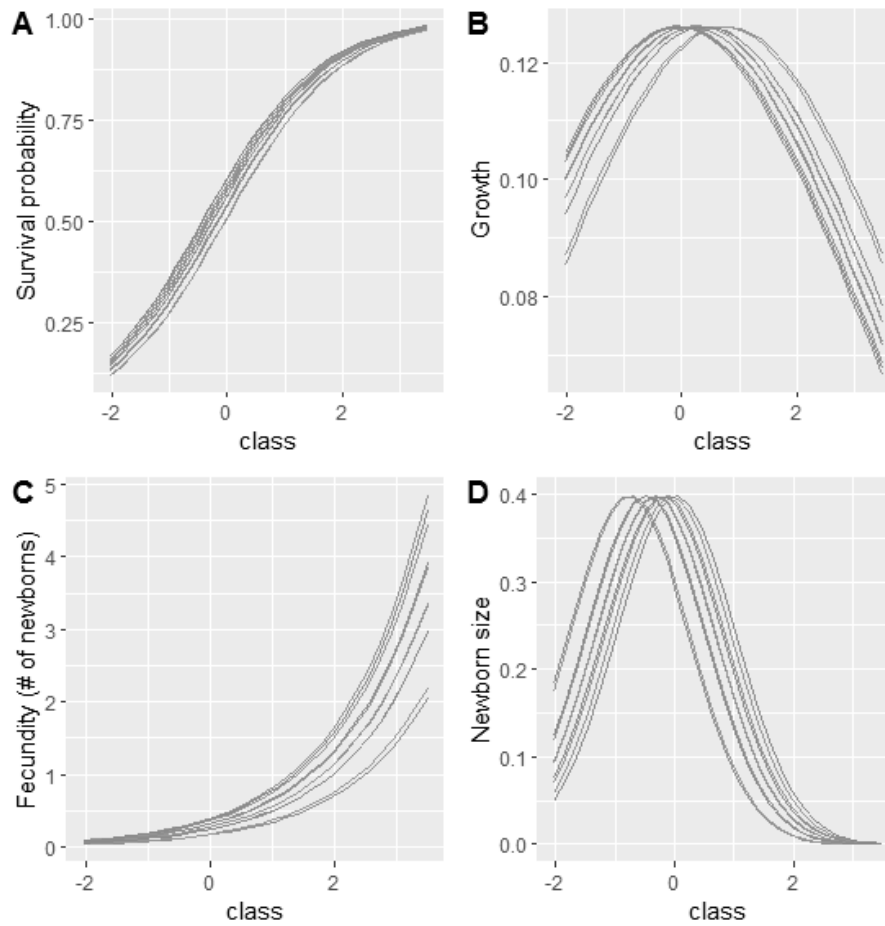


Figure S8 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Asyanax lacustris* with population-level data from June 2006 to May 2017 from the storage (STR) reservoir (Salto Santiago, in the Iguaçu River, Brazil).

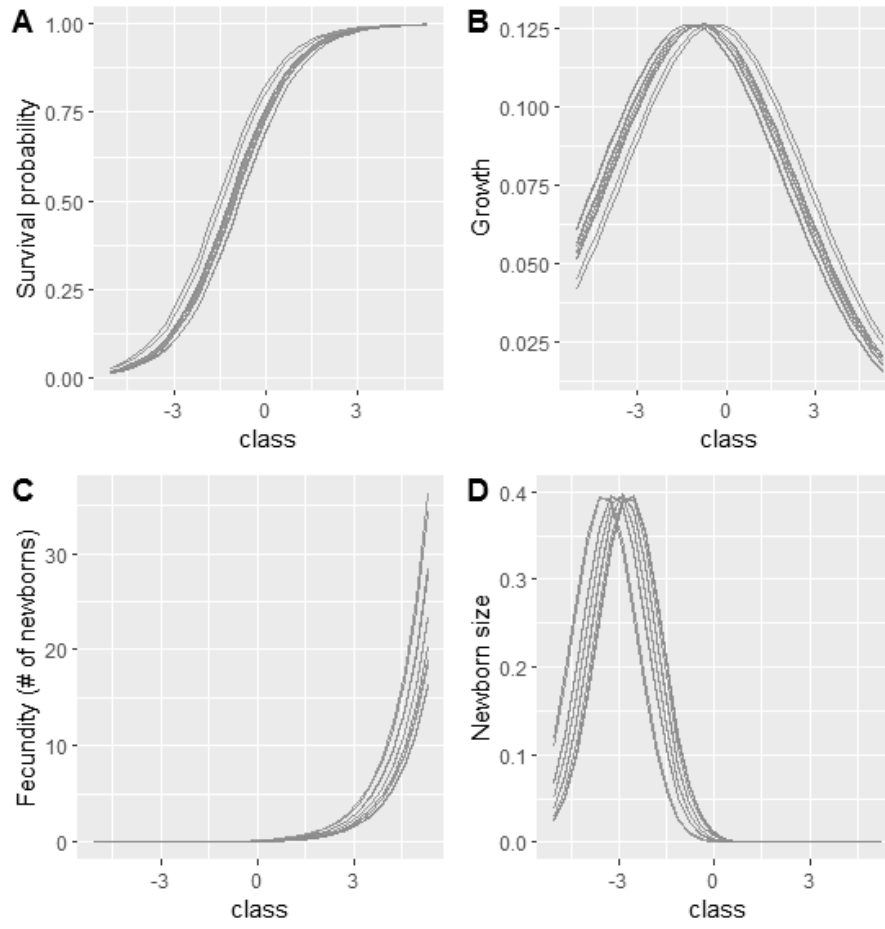


Figure S9 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Asyanax minor* with population-level data from June 2006 to May 2017 from the storage (STR) reservoir (Salto Santiago, in the Iguaçu River, Brazil).

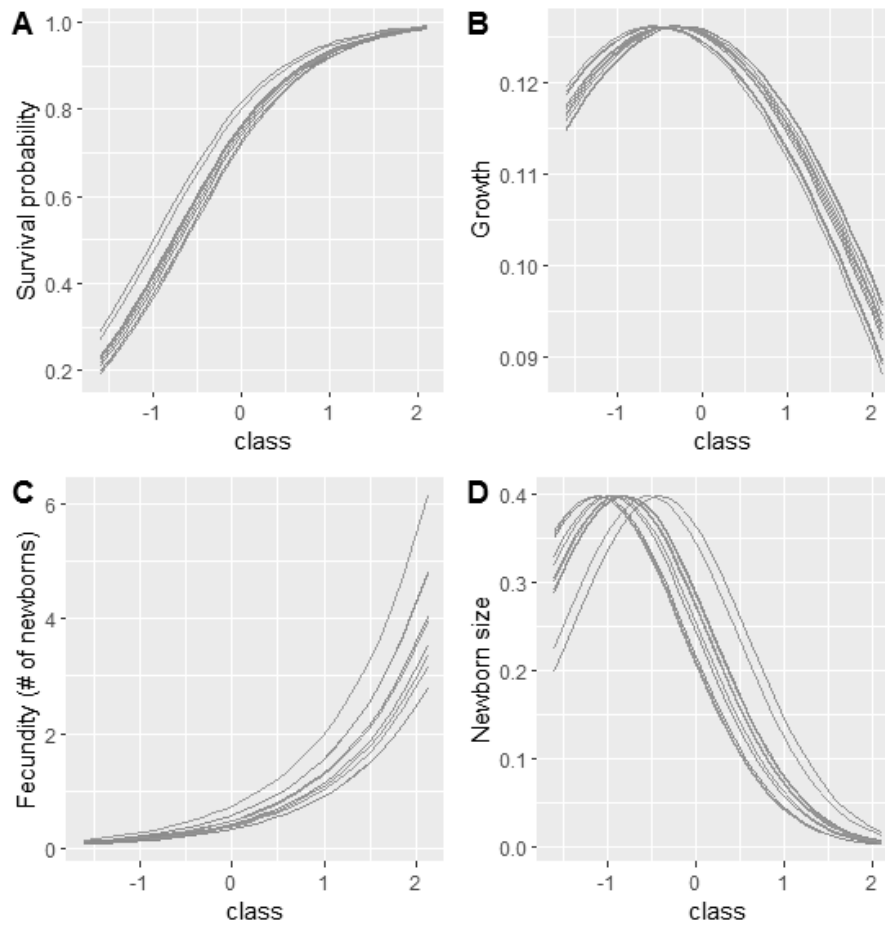


Figure S10 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Oligosarcus longirostris* with population-level data from June 2006 to May 2017 from the storage (STR) reservoir (Salto Santiago, in the Iguaçu River, Brazil).

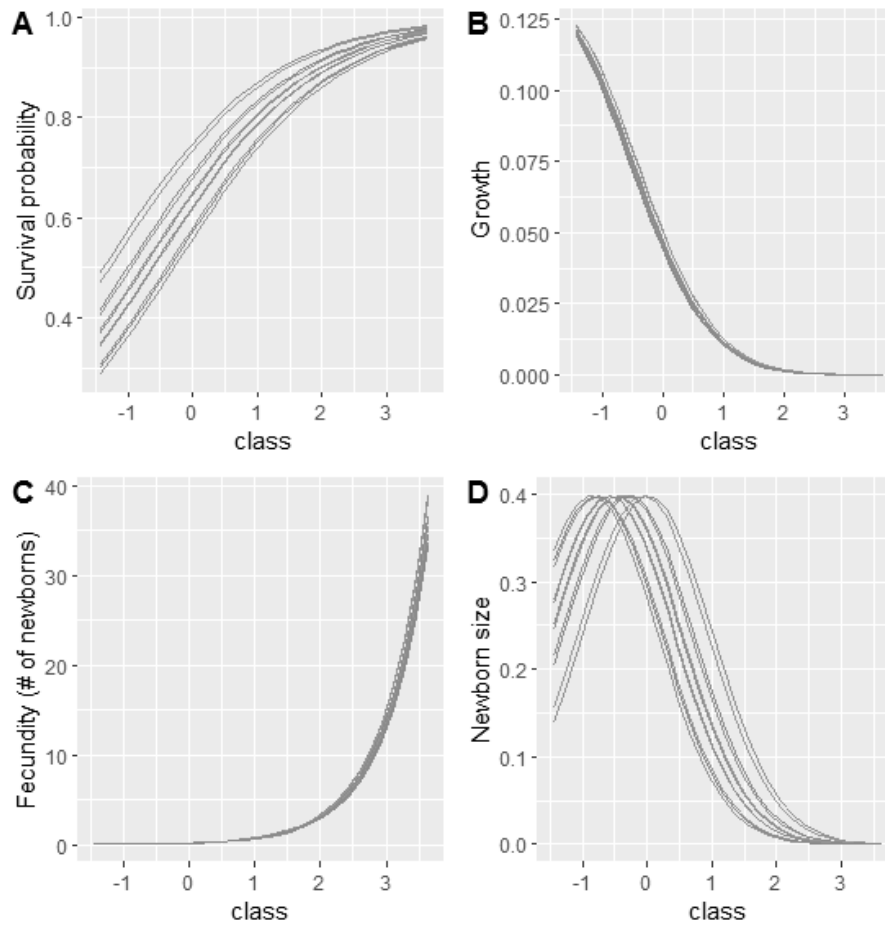


Figure S11 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Pimelodus britskii* with population-level data from June 2006 to May 2017 from the storage (STR) reservoir (Salto Santiago, in the Iguaçu River, Brazil).

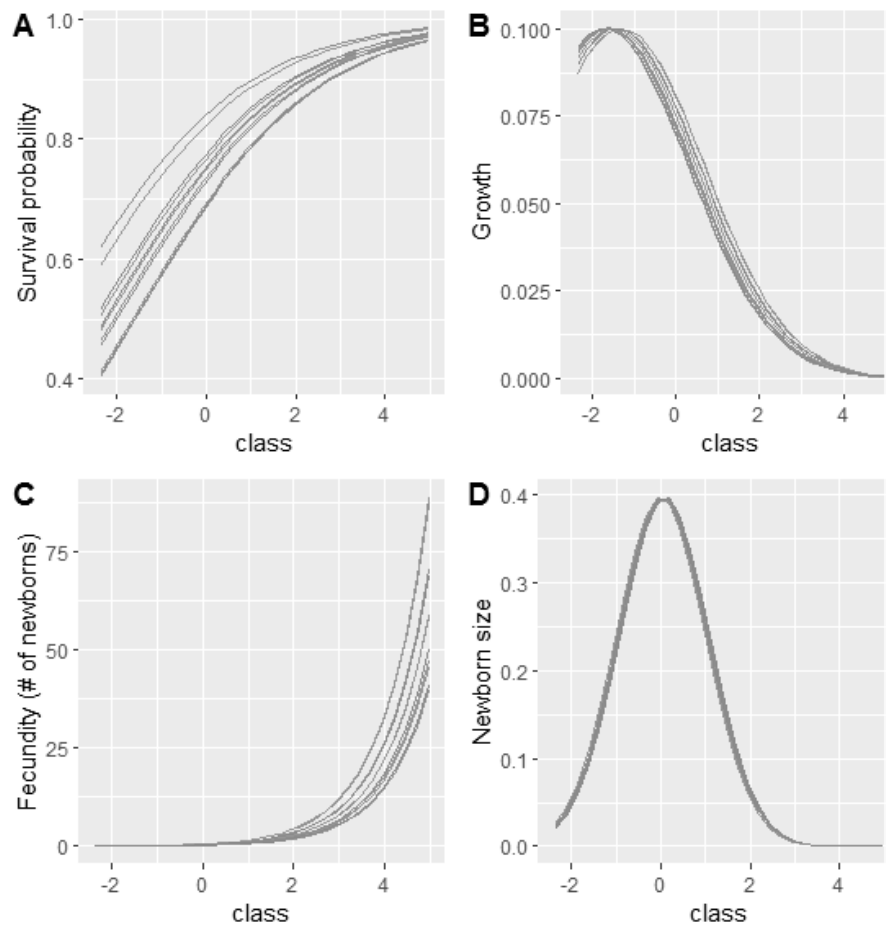


Figure S12 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Astyanax bifasciatus* with population-level data from June 2006 to May 2017 from the run-of-river (ROR) reservoir (Salto Osório, in the Iguaçu River, Brazil).

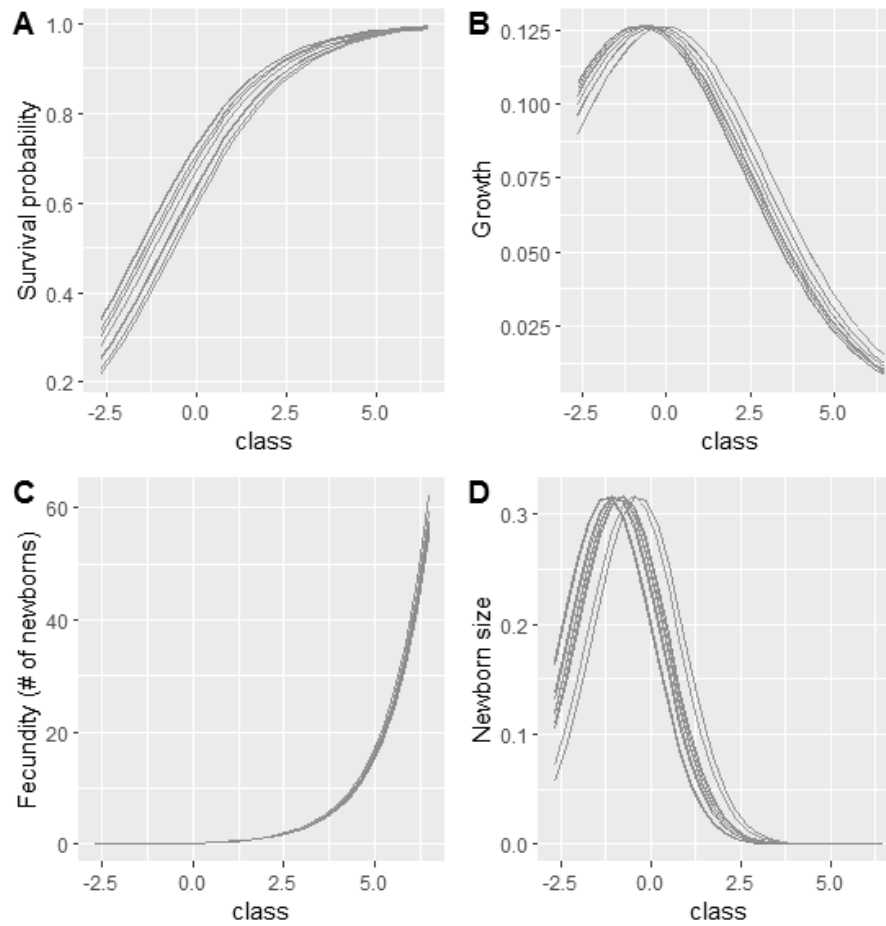


Figure S13 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Astyanax minor* with population-level data from June 2006 to May 2017 from the run-of-river (ROR) reservoir (Salto Osório, in the Iguazu River, Brazil).

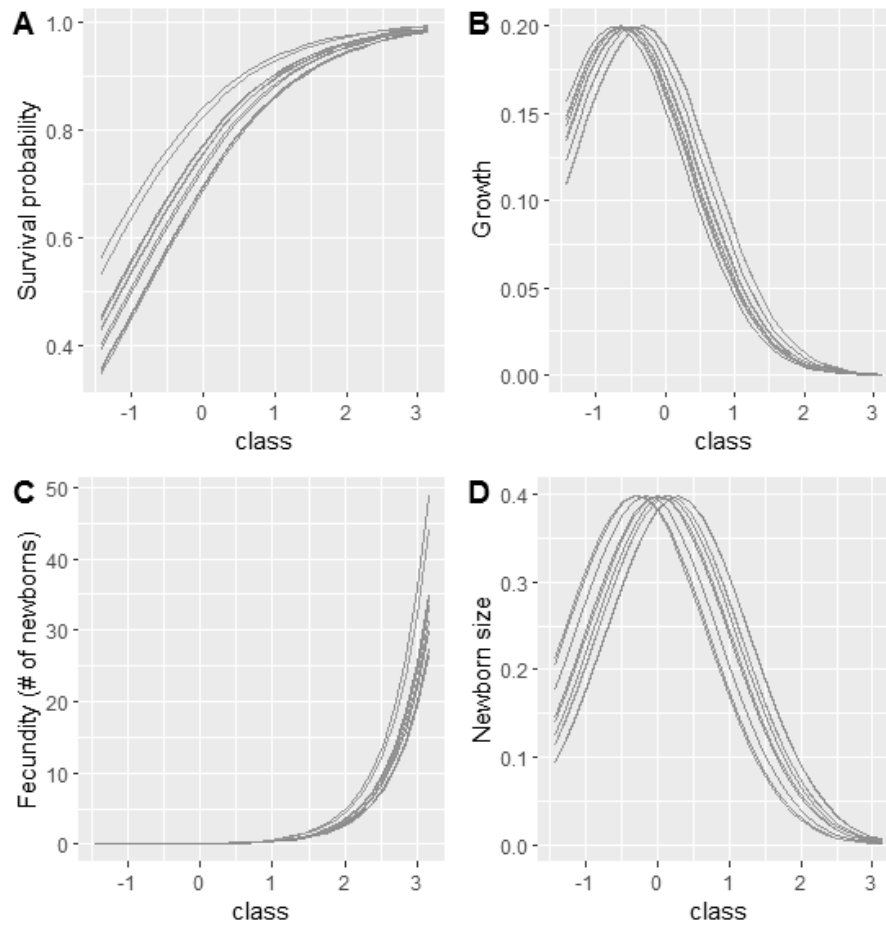


Figure S14 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Oligosarcus longirostris* with population-level data from June 2006 to May 2017 from the run-of-river (ROR) reservoir (Salto Osório, in the Iguaçú River, Brazil).

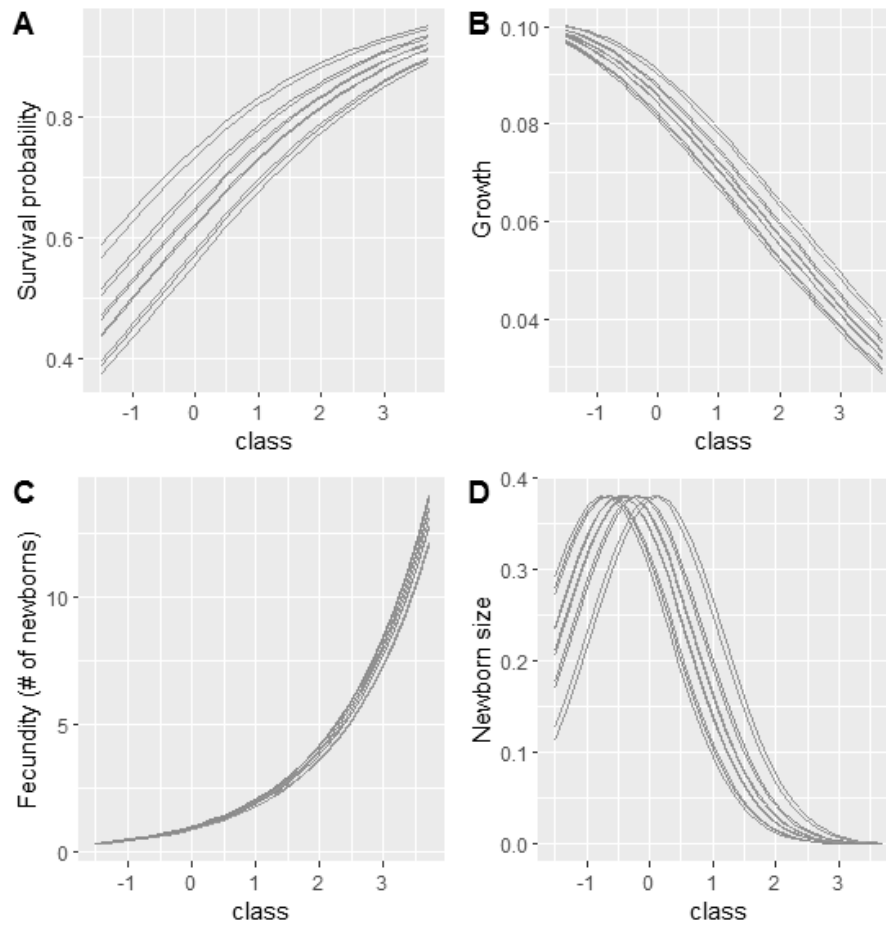


Figure S15 – Reconstructed vital rates (A: survival, B: growth, C: number of newborns, D: size distribution of newborns), using inverse modelling for *Pimelodus britskii* with population-level data from June 2006 to May 2017 from the run-of-river (ROR) reservoir (Salto Osório, in the Iguaçu River, Brazil).

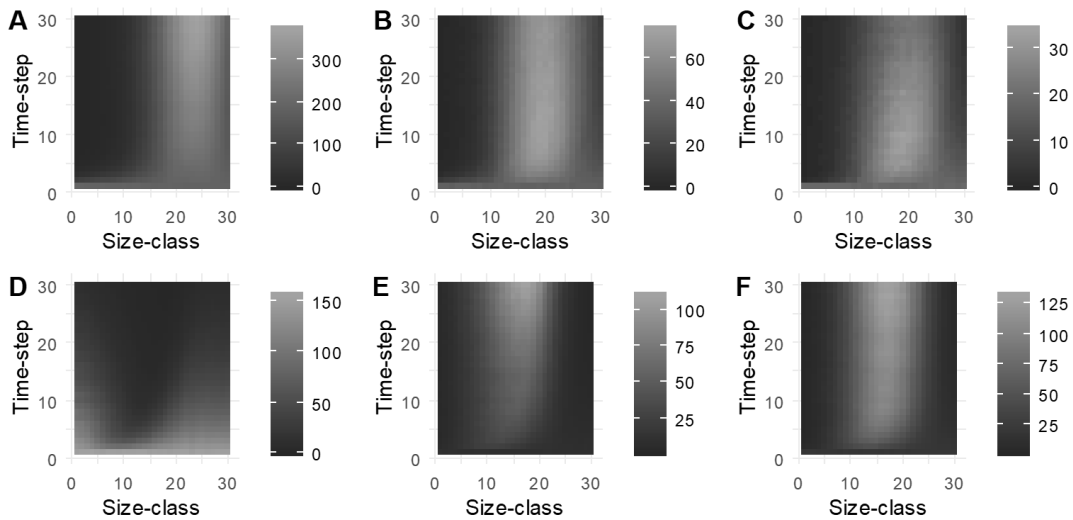


Figure S16 - Simulated population-level size structures in all time steps for the six modeled species in the first simulation experiment (All Drivers) from the Storage (STR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax gymnodontus* (B), *Astyanax lacustris* (C), *Astyanax minor* (D), *Oligosarcus longirostris* (E), and *Pimelodus britskii* (F).

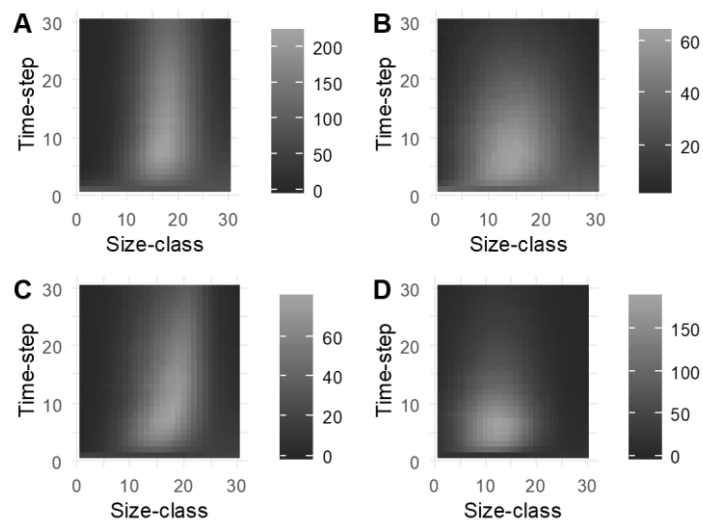


Figure S17 - Simulated population-level size structures in all time steps for the four modeled species in the first simulation experiment (All Drivers) from the Run-of-river (ROR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax minor* (B), *Oligosarcus longirostris* (C), and *Pimelodus britskii* (D).

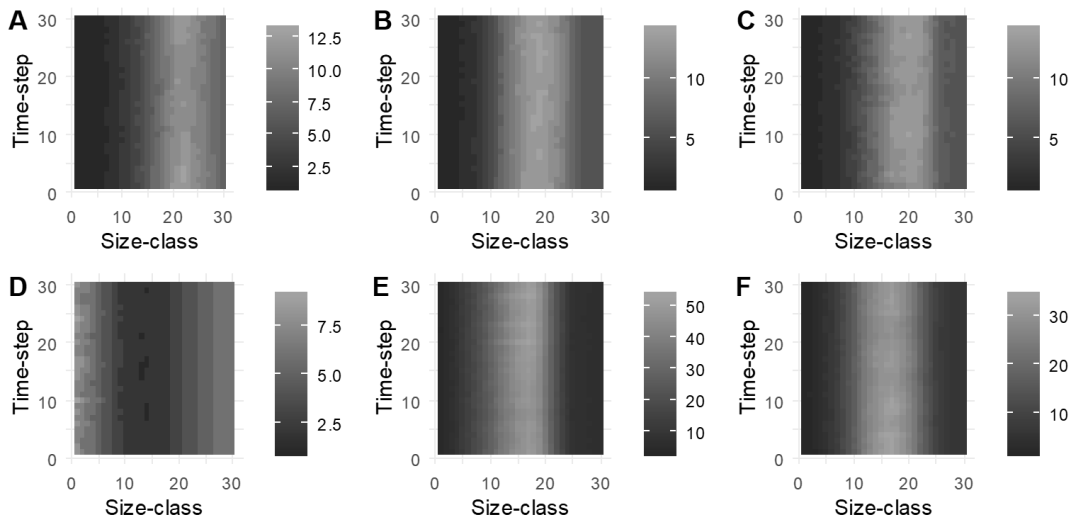


Figure S18 - Simulated population-level size structures in all time steps for the six modeled species in the second simulation experiment (-DS; without demographic stochasticity) from the Storage (STR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax gymnodontus* (B), *Astyanax lacustris* (C), *Astyanax minor* (D), *Oligosarcus longirostris* (E), and *Pimelodus britskii* (F).

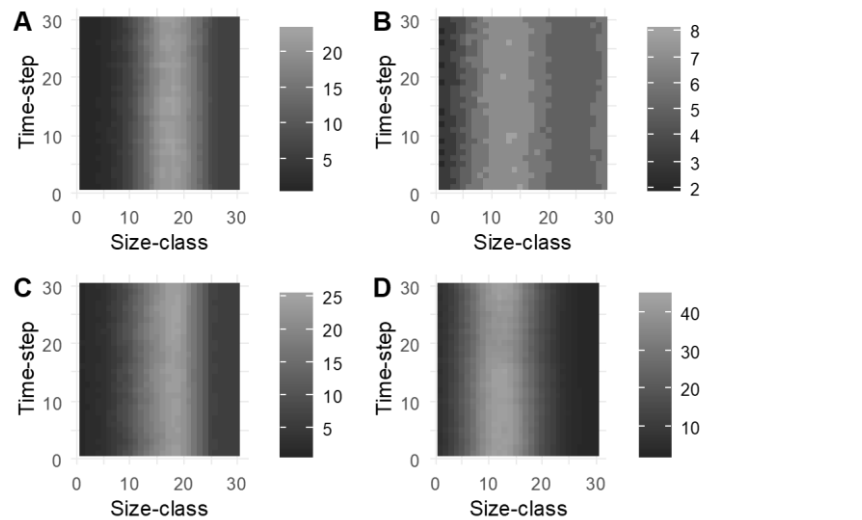


Figure S19 - Simulated population-level size structures in all time steps for the four modeled species in the second simulation experiment (-DS; without demographic stochasticity) from the Run-of-river (ROR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax minor* (B), *Oligosarcus longirostris* (C), and *Pimelodus britskii* (D).

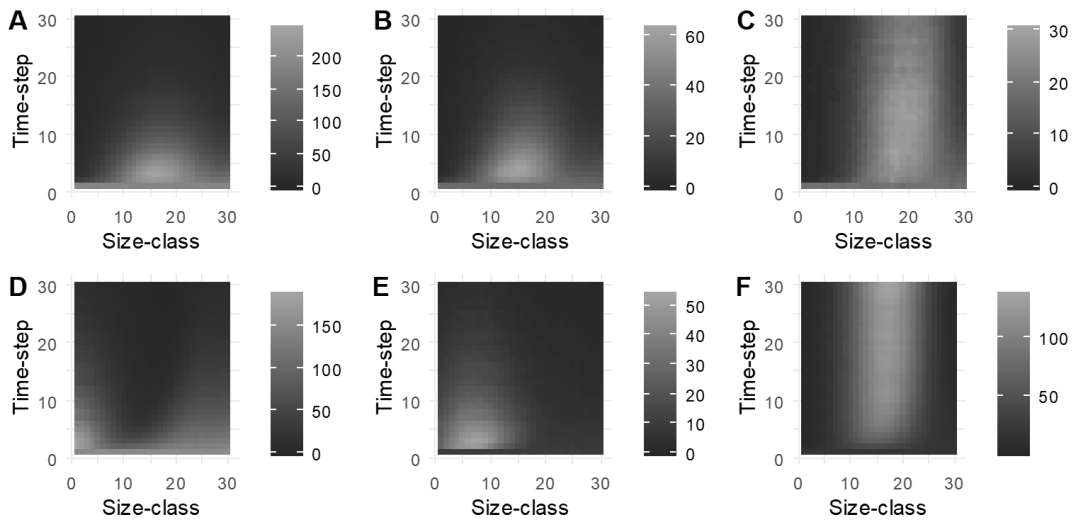


Figure S20 - Simulated population-level size structures in all time steps for the six modeled species in the third simulation experiment (-SI; without species interactions) from the Storage (STR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax gymnodontus* (B), *Astyanax lacustris* (C), *Astyanax minor* (D), *Oligosarcus longirostris* (E), and *Pimelodus britskii* (F).

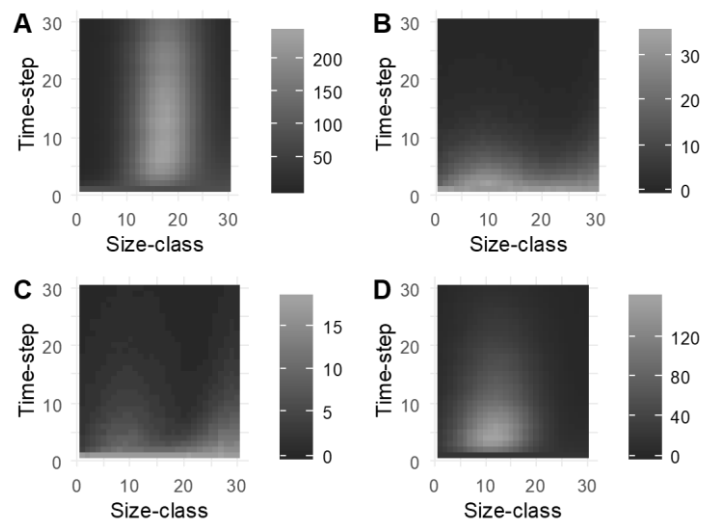


Figure S21 - Simulated population-level size structures in all time steps for the four modeled species in the third simulation experiment (-SI; without species interactions) from the Run-of-river (ROR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax minor* (B), *Oligosarcus longirostris* (C), and *Pimelodus britskii* (D).

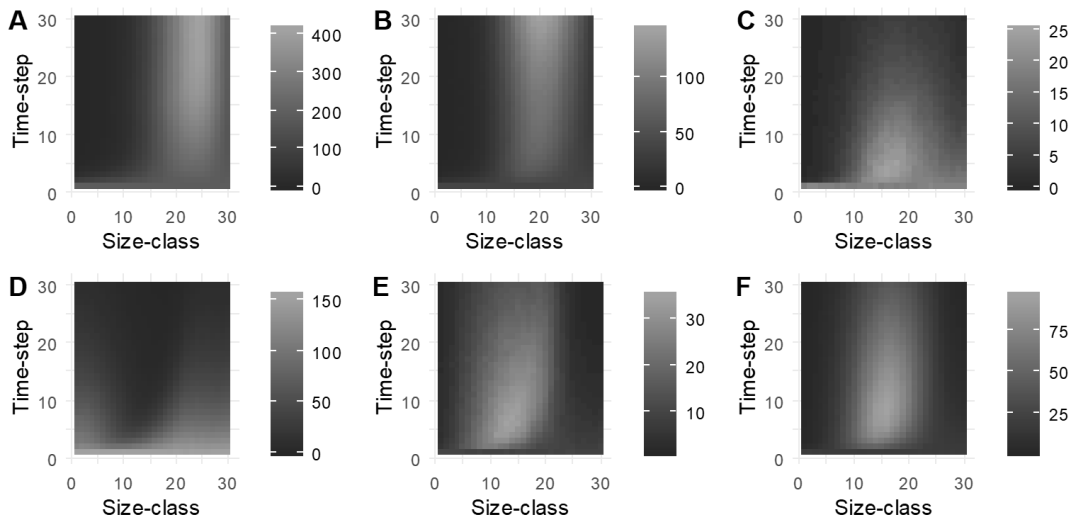


Figure S22 - Simulated population-level size structures in all time steps for the six modeled species in the fourth simulation experiment (-ES; without environmental stochasticity) from the Storage (STR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax gymnodontus* (B), *Astyanax lacustris* (C), *Astyanax minor* (D), *Oligosarcus longirostris* (E), and *Pimelodus britskii* (F).

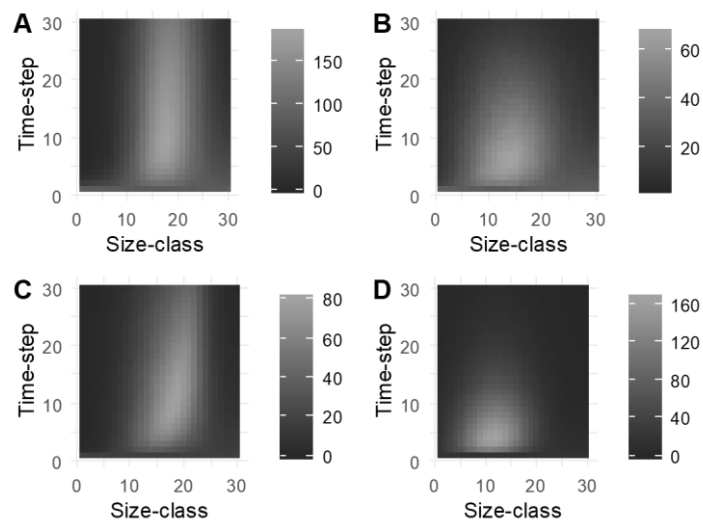


Figure S23 - Simulated population-level size structures in all time steps for the four modeled species in the fourth simulation experiment (-ES; without environmental stochasticity) from the Run-of-river (ROR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax minor* (B), *Oligosarcus longirostris* (C), and *Pimelodus britskii* (D).

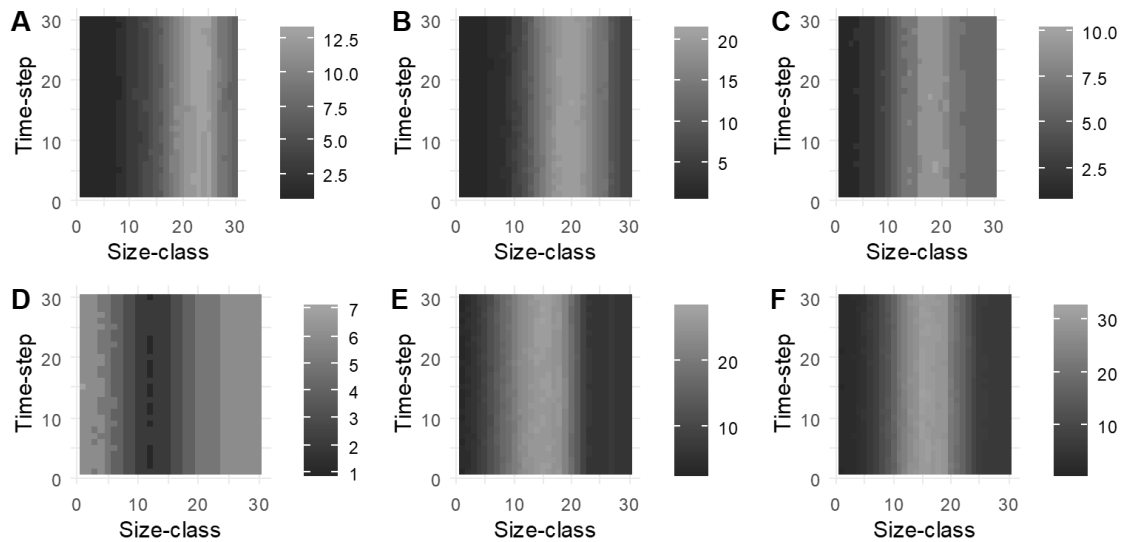


Figure S24 - Simulated population-level size structures in all time steps for the six modeled species in the fifth simulation experiment (-DS -ES; without demographic and environmental stochasticity) from the Storage (STR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax gymnodontus* (B), *Astyanax lacustris* (C), *Astyanax minor* (D), *Oligosarcus longirostris* (E), and *Pimelodus britskii* (F).

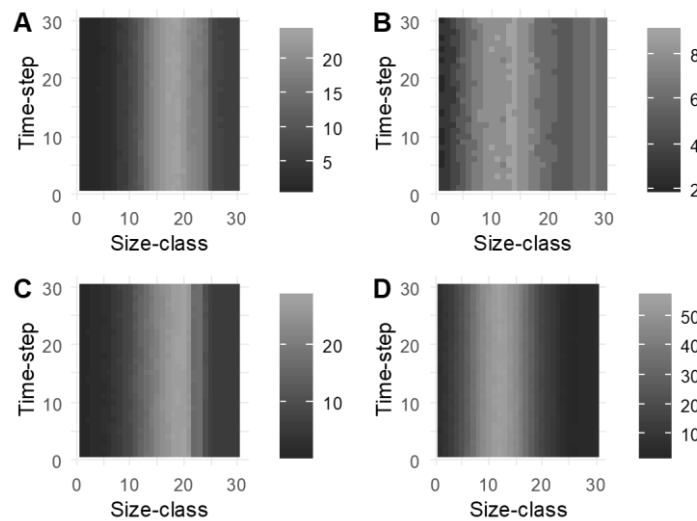


Figure S25 - Simulated population-level size structures in all time steps for the four modeled species in the fifth simulation experiment (-DS -ES; without demographic and environmental stochasticity) from the Run-of-river (ROR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax minor* (B), *Oligosarcus longirostris* (C), and *Pimelodus britskii* (D).

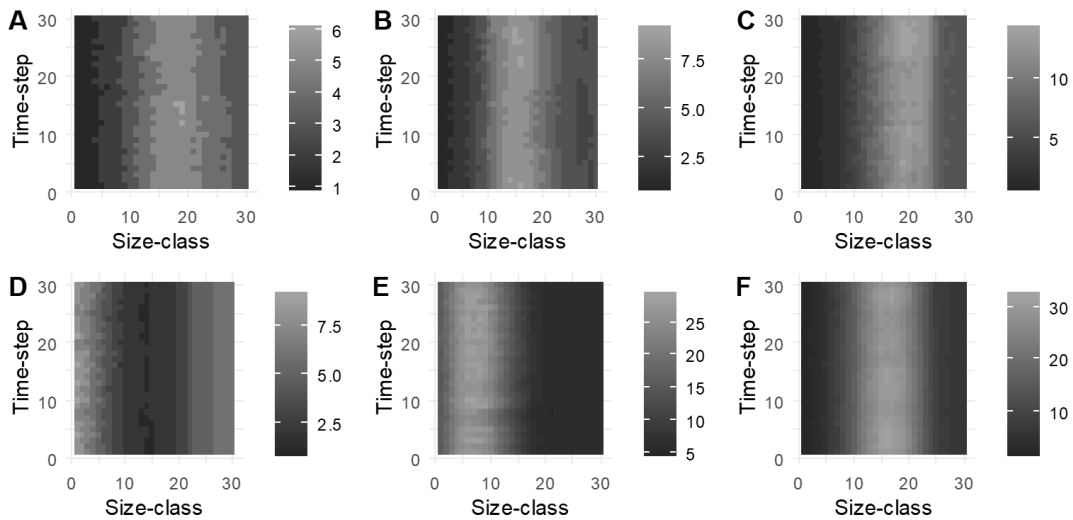


Figure S26 - Simulated population-level size structures in all time steps for the six modeled species in the sixth simulation experiment (-DS -SI; without demographic stochasticity and species interactions) from the Storage (STR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax gymnodontus* (B), *Astyanax lacustris* (C), *Astyanax minor* (D), *Oligosarcus longirostris* (E), and *Pimelodus britskii* (F).

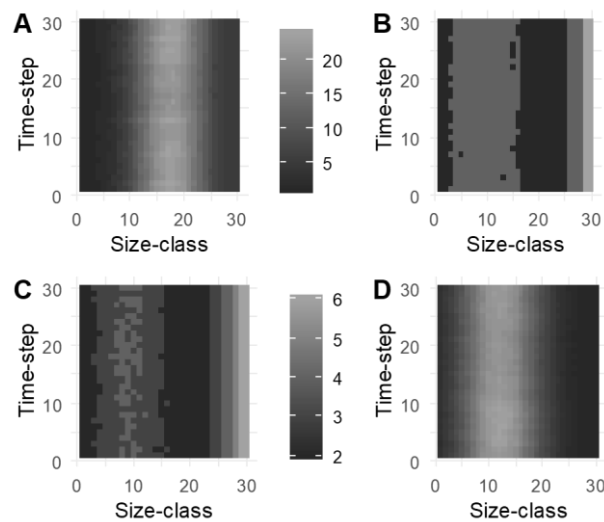


Figure S27 - Simulated population-level size structures in all time steps for the four modeled species in the sixth simulation experiment (-DS -SI; without demographic stochasticity and species interactions) from the Run-of-river (ROR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax minor* (B), *Oligosarcus longirostris* (C), and *Pimelodus britskii* (D).

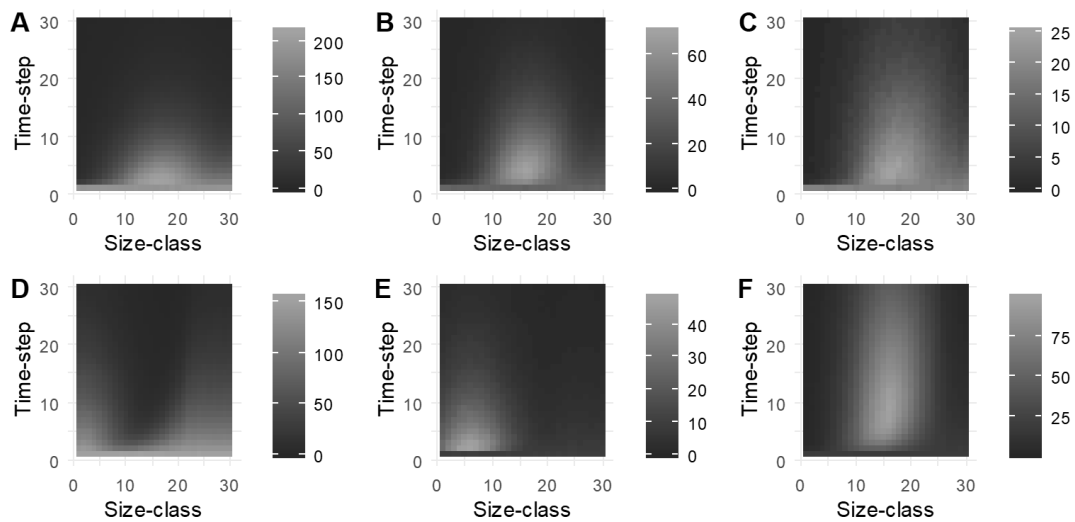


Figure S28 - Simulated population-level size structures in all time steps for the six modeled species in the seventh simulation experiment (-SI -ES; without species interactions and environmental stochasticity) from the Storage (STR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax gymnodontus* (B), *Astyanax lacustris* (C), *Astyanax minor* (D), *Oligosarcus longirostris* (E), and *Pimelodus britskii* (F).

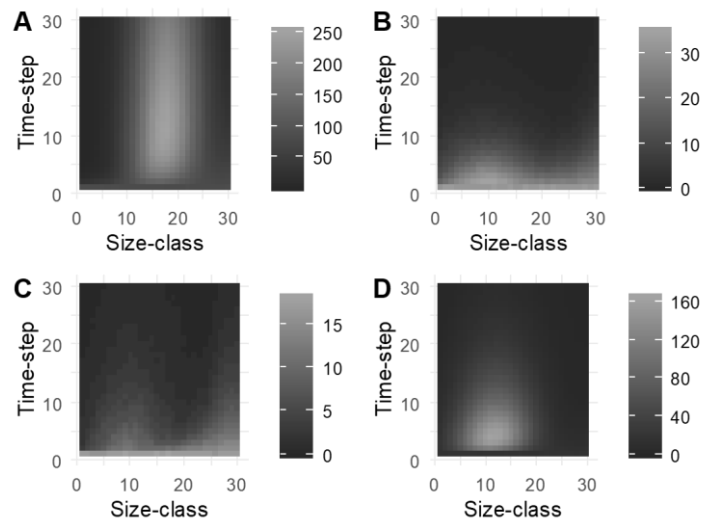


Figure S29 - Simulated population-level size structures in all time steps for the four modeled species in the seventh simulation experiment (-SI -ES; without species interactions and environmental stochasticity) from the Run-of-river (ROR) reservoir. Simulated species are *Astyanax bifasciatus* (A), *Astyanax minor* (B), *Oligosarcus longirostris* (C), and *Pimelodus britskii* (D).

4 CONCLUDING REMARKS

It was possible to identify different patterns related to the stability of fish assemblages, which coincided with alternative dam operation schemes. Simply put, the two studied reservoirs presented different parameters related to stability in terms of resistance and resilience to disturbances, suggesting that the reservoir operated under run-of-river as less stable than that operated under accumulation. The underlying mechanisms that had stronger effects on the synchrony of fish species coincided between the reservoirs, although with opposite contributions.

More specifically, it was also possible to argue that the species-environment relationships have been likely weakened in the reservoir operated under run-of-river as a result of the temporal dynamics imposed by dam operation, which coincided with a less stable fish assemblage. The results regarding the underlying mechanisms of the differences in stability properties also reinforce this rationale. However, it is important to highlight that the evidence herein is only primary information on the potential direct effects of the dam operation scheme on ecosystem stability and species interactions. Identifying the causal relationships and the relative roles of the main factors is a task for further extensive and intensive assessments, combining several reservoirs (larger spatial scale) comprising a range between the two contrasting operation schemes.