Importance of protection strategies in the conservation of the flagship species “dourado” *Salminus brasiliensis* (Characiformes: Bryconidae)

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In the upper Paraná River floodplain, the populations of *Salminus brasiliensis* have been subjected to several anthropic impacts, such as overfishing, the blocking of migratory routes by dams, and regulation of the flood regime. Its populations have disappeared or become depleted in most rivers in this basin. These populations are the target of protection measures aimed at restoring them. This study evaluated the abundance of this species in the upper Paraná River floodplain over a 26-year time series in sites under different degrees of protection. Despite the overall decrease in the abundance of *S. brasiliensis* across the region, the less impacted sites have higher abundances and exhibited a slower decline in the probability of occurrence. Over time, populations in less impacted sites also exhibited improved fish condition. Some protected areas in the upper Paraná River have had a mitigation effect by lowering the velocity of population decline and representing a constant source of propagule production for other areas. Our results reinforce the notion that populations threatened with low abundances take a long time to effectively recover their stocks. Thus, besides evaluating species conservation strategies, long-term studies are essential to subsidize management measures, such as fisheries regulations.

Keywords: Dams, Endangered native species, Migratory fish, River-floodplain system, Upper Paraná River floodplain.

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Na planície de inundação do alto rio Paraná, as populações de *Salminus brasiliensis* têm sido submetidas a diversos impactos antrópicos, como sobrepesca, bloqueio de suas rotas migratórias por barragens e regulação do regime de cheias. Essas populações desapareceram ou se esgotaram na maioria dos rios dessa bacia, sendo alvo de medidas de proteção para restaurá-las. O objetivo deste trabalho foi avaliar a abundância da espécie na planície de inundação do alto rio Paraná ao longo da série temporal de 26 anos em locais sob diferentes graus de proteção. Apesar da diminuição geral na abundância de *S. brasiliensis* em toda a região, os locais menos impactados possuem maiores abundâncias e exibiram um declínio mais lento na probabilidade de ocorrência. Com o tempo, as populações em locais menos impactados apresentaram aumento na condição dos peixes. Algumas áreas de proteção no alto rio Paraná têm efeito mitigador, diminuindo a velocidade de declínio populacional, representando fonte de propágulos para as demais áreas. Nossos resultados reforçam a ideia de que populações ameaçadas com baixas abundâncias levam muito tempo para recuperar seus estoques. Assim, além de avaliar as estratégias de conservação das espécies, estudos de longo prazo são essenciais para subsidiar medidas de manejo, como a regulamentação da pesca.

Palavras-chave: Barragens, Espécies nativas ameaçadas de extinção, Peixes migradores, Planície de inundação do alto rio Paraná, Sistema rio-planície de inundação.

INTRODUCTION

The loss of natural habitats due to the expansion and rapid growth of the human population (8–10 billion by 2050; United Nations, 2022) has increased habitat degradation and fragmentation (Zhao *et al*., 2019; Dias *et al*., 2021), which are among the main causes of biodiversity loss (Gorenflo, Brandon, 2006; Newbold *et al*., 2015). Freshwater ecosystems have been considered the most impacted worldwide due to human population growth, which has resulted in the increased use and regulation (*e.g.*, flood control) of freshwater resources (Grill *et al*., 2015; Mekonnen, Hoekstra, 2016; Winemiller *et al*., 2016; He *et al*., 2019). Notably, dam construction causes changes in freshwater ecosystems that can have several pervasive impacts on fish community structure (Agostinho *et al*., 2016; Dias *et al*., 2020). In addition to blocking fish migration routes, dams also alter river flow regimes (Agostinho *et al*., 2004; Winemiller *et al*., 2016) and cause changes in abiotic conditions, such as increased water transparency due to sediment and nutrient retention (Roberto *et al*., 2009). Dams also facilitate the establishment of non-native species (Johnson *et al*., 2008) and limit species dispersal (Agostinho *et al*., 2004, 2007a; Affonso *et al*., 2015). The synergism of these impacts affects the maintenance of migratory species in freshwater ecosystems.

The large spatial scale involved in the reproductive processes of migratory fishes makes them sensitive to anthropogenic pressures. Additionally, the reproductive cycles of migratory fishes are synchronized with the variation of the hydrological regimes of rivers (Junk *et al*., 1989; Agostinho *et al*., 2004; Oliveira *et al*., 2020; Silva *et al*., 2020).

Notably, fish require free river stretches to migrate to the uppermost regions of the basin, spawn, and allow their eggs and larvae to drift to flooded areas downstream for development (Nakatani *et al*., 2001; Wantzen, Junk, 2006). Thus, flood control by dams affects the reproduction and recruitment of migratory fishes (Ferguson *et al*., 2011; Oliveira *et al*., 2015, 2020). Moreover, since these species often reach large body sizes, they are the target of intensive fishing, which has caused depletion in many of their stocks (Agostinho *et al*., 2004). Additionally, some migratory piscivores are key species that regulate food chains through top down-control (Ruaro *et al*., 2019). Thus, maintaining a viable population of these species is pivotal for ensuring the balance and functioning of freshwater ecosystems (Meretsky *et al*., 2011).

Besides their impact on ecosystem functioning, the slow population growth rates resulting from their life histories (prolonged longevity, late maturation, and long generation time), as well as their restricted distribution ranges, make migratory fish species a priority for conservation (Pelicice *et al*., 2017; Wang *et al*., 2019). Among the fish species in the upper Paraná River floodplain that fit this description, we highlight the "dourado" *Salminus brasiliensis* (Cuvier, 1816), which has a vulnerable status on the threatened species list (Abilhoa, Duboc, 2004) and is of high fisheries importance. Since *S. brasiliensis* is considered a symbol of the regional fishery (Hoeinghaus *et al*., 2009), it has been used as a flagship in conservation strategies for not only conserving the species in question but also its ecosystem and the less-charismatic species within it via an umbrella strategy (Dietz *et al*., 1994; Oliveira *et al*., 2018; Ruaro *et al*., 2019).

Notably, *S. brasiliensis* presented taxonomic synonymy with *Salminus maxillosus* when the genus was reviewed by Lima *et al*. (2003). *Salminus brasiliensis* stands out for being the largest species among the Bryconidae (former Characidae) and plays an important ecological role because it is one of the largest predators within the environments in which it occurs (Zaniboni-Filho *et al*., 2017). The distribution of this species includes southern South America in the Paraná, Paraguay, and Uruguay rivers (de la Plata River basin), the Laguna dos Patos drainage, and the Chaparé and Mamoré rivers (Amazon basin) (Reis *et al*., 2003; Graça, Pavanelli, 2007). Although a large portion of the original *S. brasiliensis* distribution has been intensively regulated by dam cascades, the upper Paraná River still has an extensive floodplain and tributaries that are free of dams, which is important for maintaining populations of this and other migratory species (Agostinho *et al*., 2004; Affonso *et al*., 2015).

Among the measures aimed at protecting this and other endangered fish species, establishing protected areas (*e.g*., parks and other types of reserves; Roque *et al*., 2018) and controlling fishing exploitation stand out. Protected areas often export resources and individual organisms that can bolster populations outside reserve boundaries (Hunter, Gibbs, 2007). In the Paraná River basin, fishery control measures are based on laws prohibiting fishing for endangered native species (*i.e*., Law nº 19789/2018 – Government of the State of Paraná; Law nº 22/2018 – Government of the State of Mato Grosso do Sul), the capture and consumption of undersized fish (*i.e*., Federal law nº 9605/1998), and fishing during spawning periods (*i.e*., Federal law nº 7653/1988), as well as laws facilitating the passage of fish across dams (Agostinho *et al*., 2002) and catch and release fishing (*i.e*., Portaria IAP nº 211/2012 – Government of the State of Paraná).

Such conservation measures intend to increase population abundance. However, increasing fish abundance also depends on the fitness and reproductive success of the individuals as determined by their ability to avoid predators, foraging success, and response to environmental variability (Toïgo *et al*., 2006; Hilborn *et al*., 2017). Some of these features might manifest in the individual health condition (Schulte-Hostedde *et al*., 2005; Stevenson, Woods, 2006; Gubiani *et al*., 2020). Besides changes in abundance, determining whether populations are successful in obtaining resources for growth and allocating resources for reproduction is important information for assessing whether a population is maintaining itself in the environment. For threatened populations, such assessments are essential since the main objective of conservation biology is to ensure the long-term maintenance of species (Hunter, 2001; Primack, 2006).

In this context, the general objective of this paper was to evaluate variations in the abundance of an extinction-vulnerable species (*S. brasiliensis*) the last remaining stretch of the upper Paraná River floodplain over 26 years and consider areas with different levels of conservation/degradation. We expected that a decreasing trend in the abundance of *S. brasiliensis* in a highly altered river (HA – Paraná River) over this period has been directly affected by the construction of dams. In contrast, within rivers that have been less altered (LA – Ivinhema River), protected by parks (*i.e.*, with more restricted uses, not regulated by dams), and even moderately altered (MA – Baía River; partially controlled by a dam and containing a less restrictive protected area), we expected an increase in *S. brasiliensis* abundance. We also expected a strong relationship between the abundance of species and the water level of the LA river. Moreover, we expected the probability of occurrence of this species and its young-of-the-year individuals to increase in the LA river. Additionally, we tested whether the abundance of *S. brasiliensis* in the more impacted sites (*i.e.*, HA and MA rivers) depends on the abundance of the more preserved river (*i.e.*, LA river) since it is expected that rivers with more restricted protection can represent a constant source of propagules for other rivers. Finally, we expected that adults with better body and reproductive conditions would be more frequent in the LA river.

MATERIAL AND METHODS

Study area. The dam-free remnant of the upper Paraná River floodplain extends from the Porto Primavera Dam (closed in 1998) to the Itaipu reservoir (closed in 1982) 230 km downstream and includes tributaries, anastomosed channel networks, and floodplain lakes (Fig. 1). This stretch plays a fundamental role in maintaining fish populations and regional aquatic biological diversity (Agostinho *et al*., 2001; Luz-Agostinho *et al*., 2008). The Paraná River basin is considered the basin most heavily regulated by dams in South America (Souza Filho *et al*., 2004). Moreover, its flood pulse can be considered irregular when compared to other large tropical rivers (Thomaz *et al*., 2004). The construction of the Porto Primavera Dam modified water levels, reducing average levels downstream of the dam by 14% (Stevaux *et al*., 2009) and consequently reducing connectivity among biotopes during critical periods (Agostinho *et al*., 2009). However, the flood pulse remains primarily responsible for the seasonality and dynamics of the biotic communities of the floodplain and its associated habitats (Agostinho *et al*., 2004, 2009; Thomaz *et al*., 2007).

At the end of the last century, this stretch was covered by conservation units with various degrees of use restrictions (Agostinho *et al*., 2004): Environmental Protection

Area of the Islands and floodplains of the Paraná River (Área de Proteção Ambiental das Ilhas e Várzeas do Rio Paraná, 1,000,310 hectares of extension), which is included in the sustainable use category (Agostinho, Gomes, 2002); Ilha Grande National Park (Parque Nacional de Ilha Grande, 78,800 hectares) (Decree s/n., September 30, 1997); Ivinhema River State Park (Parque Estadual das Várzeas do Rio Ivinhema, 70,000 hectares) (Decree 9.278, December 17, 1998). Despite the creation of these environmental protection areas and conservation units, this region still has several anthropogenic impacts that cause habitat degradation and biodiversity loss (*i.e.*, pollution, habitat destruction, deforestation, non-native species introduction, overfishing, and – most critically – the construction and operation of dams for hydroelectric purposes).

The upper Paraná River floodplain is characterized by three main rivers (Fig. 1): Paraná (highly altered – HA), Baía (moderately altered – MA), and Ivinhema (less altered – LA). Notably, the Paraná River exerts a predominant influence on the river dynamics of the entire floodplain (Rocha *et al.*, 2001).

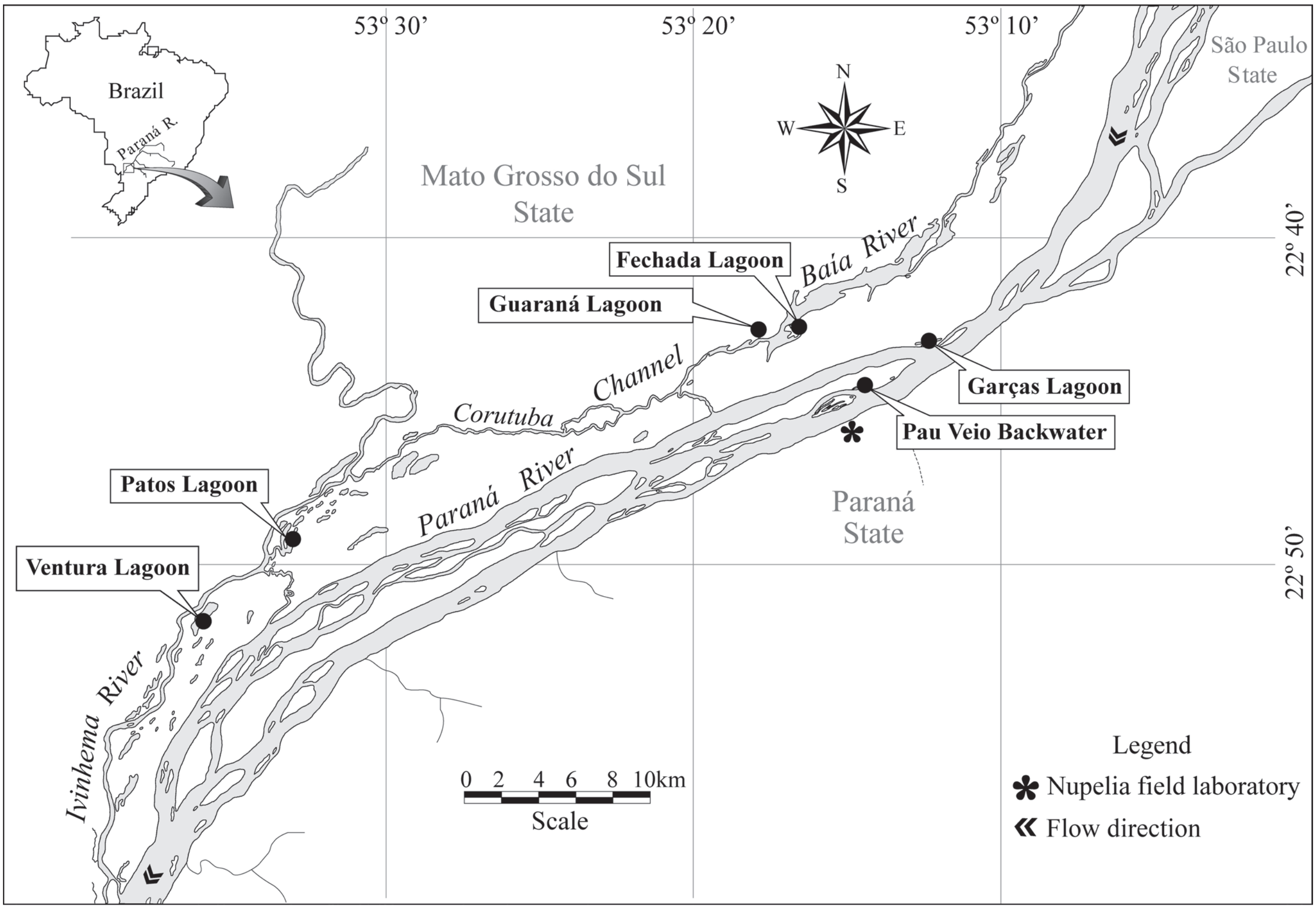

FIGURE 1 | Protected areas and sampling stations in the upper Paraná River floodplain. Paraná River (highly altered – HA), Baía River (moderately altered – MA), and Ivinhema River (less altered – LA).

Sampling sites. Individuals of *S. brasiliensis* were collected during two periods over 26 years: before and after the construction of the Porto Primavera Dam. Before period: Fish were sampled monthly from October 1986 to September 1988 and March 1992 to February 1993, and then every two months from March 1994 to February 1995. The sampling was conducted at different sampling sites located in each river: Paraná (highly altered – HA): two sampling sites; Baía (moderately altered – MA): seven sampling sites; Ivinhema (less altered – LA): three sampling sites. For each river, a connected lake, an isolated lake, and the main river channel were sampled. After period: quarterly sampling was conducted for 19 years (from 2000 to 2018) at nine sampling sites located in each river (Paraná, Baía, and Ivinhema). For each river, a connected lake, an isolated lake, and the main river channel were sampled (Fig. 1). Fish were caught using a set of gillnets of different mesh sizes (3, 4, 5, 6, 7, 8, 10, 12, 14, and 16 cm between opposite knots), which remained exposed for 24 h and were checked at 8:00, 16:00, and 22:00 h. Captured fish were anesthetized with 5% benzocaine, sacrificed, identified according to Ota *et al.* (2018), measured [standard length (SL); cm], weighed [weight (W); g], and eviscerated. The gonads were analyzed to identify the sex and determine the stage of gonadal maturation (Vazzoler, 1996; Brown-Peterson *et al*., 2011). Individuals of *S. brasiliensis* with a total length < 28.3 cm were considered young-of-the-year (YOY; Oliveira *et al*., 2015). Some individuals of this species were deposited as vouchers in the ichthyological collection at Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (NUP), Universidade Estadual de Maringá, Maringá, Brazil (NUP 20110608025, NUP 2011061502, NUP 2010092002, NUP 2011081901, NUP 2010030301). Fish abundance was expressed in catch per unit effort (CPUE: individuals/1,000m^2 gillnets during 24 h). This study was conducted as part of a long-term ecological research project (Site 6) supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Hydrologic data were provided by the National Water Agency (Agência Nacional das Águas – ANA; Sistema Nacional de Informações Sobre Recursos Hídricos – SNIRH) and obtained through daily water level measurements (WL; cm in relation to the operation of the Hydrometric Station at 231.8 m a.s.l.) conducted at a gauging station in the Paraná River (Estação Hidrométrica de Porto São José; register number: 64575000/ANA). The used time series was composed of the arithmetic mean of daily WL for the months when fish were collected.

Condition factor and gonadal index. To estimate the investment of individuals in growth, we considered their body weight-body length relationships. Variation in this relationship or condition factor (K) provides information on weight loss/gain, which can be related to the use of food resources and foraging success. The condition factor equation is presented as follows (Ricker, 1975): $K = W/LS^b$, where W is the individual body weight, LS is the standard length, and *b* was determined to fit ordinary least square models (OLS) regressing the natural logarithm of body weight on the natural logarithm of body length. The condition factor was calculated for males and females separately while excluding the weight of the gonads and stomach. Juvenile individuals (< 21.4 cm for males and < 28.3 cm for females; Barbieri *et al*., 2001; Oliveira *et al*., 2015) were also excluded.

The gonadal index [GI; (GI = G/W^b)] (Vazzoler, 1996) evaluates the relationship between gonad weight (G) and body weight (W) and is frequently employed to compare reproductive condition across individuals or different groups of individuals of the same species. The GI was calculated separately for males and females within each river. The parameter *b* was determined to fit OLS regressing the logarithm of gonad weight on the logarithm of body weight through OLS models.

Data analysis. Negative binomial models were fitted for modeling total abundance (CPUE) and the probability of occurrence of the species (All) and young-of-the-year individuals (YOY). The probability of occurrence was computed as the number of samples in which species and YOY were detected each year. Then, we tested whether the abundance of *S. brasiliensis* differed before (1986 – 1995) and after (2000 – 2018) the Porto Primavera Dam closure and the creation of protected areas in the region. That is, we tested for differences in abundance among sampling periods (before-after) and the interaction with the river (predictor variables). We also determined whether the abundance was related to water level (cm). In these models, the response variables were the count of individuals per sample while controlling the sampling effort through a covariate.

A cross-correlation and a Granger causality test were conducted to test whether the abundance of *S. brasiliensis* in the most impacted sites (*i.e*., the Baía and Paraná rivers) depends on their abundance in the most preserved river (LA; Ivinhema River). In the cross-correlation, we searched for significant correlations between the temporal series of *S. brasiliensis* for each pair of sites. Cross-correlation allowed us to search for which extent of time two temporal series display concordant behavior. Although this method is often used to infer possible causal relations, it has been found to have a limited ability to determine the direction of causality. Thus, the Granger causality test seems more suitable for detecting causal relationships in ecological questions (Detto *et al*., 2012; Damos, 2016). Thus, we used the temporal series of the Ivinhema River as a predictor variable of the temporal series of the Baía and Paraná rivers in the cross-correlation. The cross-correlation protocol (Dean, Dunsmuir, 2016) was used to test the correlation among temporal series exhibiting autocorrelation. Overall, a procedure known as prewhitening first estimates a significance limit for the cross-correlations. Then, it fits an autoregressive model for the bivariate (each pair of rivers) time series to remove the autocorrelation from at least one of the temporal series and avoid significant spurious correlations. After identifying the lags of time at which significant cross-correlation between pairs of time series is detected, the Granger causality test was carried out. The Granger test was employed to investigate whether prior abundance in the LA river (Ivinhema River) predicted abundance at posterior samplings in the other two rivers. To make the results interpretable in terms of lags of time, only the period with quarterly sampling was considered (2004 – 2016).

Finally, an interaction effects ANCOVA model was fitted to test whether individuals in the most conserved river exhibited better body and reproductive conditions. The ANCOVA models were considered for females and males separately. These models allow for an evaluation of the homogeneity of slopes among rivers (*e.g*., whether individuals in some rivers gain more weight with increasing length than others). Differences in K values among rivers and periods were tested via two-way ANOVA. The same analysis was performed for the gonadal index (GI).

All analyses were performed in ‘R’ software (R Development Core Team, 2020) using the packages ‘MASS’ (Venables, Ripley, 2002) and ‘car’ (Fox, Weisberg, 2019) for model fitting as well as ‘DHARMa’ (Hartig, 2022) to analyze models’ residuals and fit.

RESULTS

Total abundance and the probability of occurrence of *S. brasiliensis* and young-of-the-year individuals. Over the 26 years of sampling, 872 *S. brasiliensis* individuals (492 females, 296 males, and 84 unidentified) were captured in the upper Paraná River floodplain. The surveyed rivers displayed a similar temporal trend in abundance variation: a decline from a high value between 1986 and 1995, an increase from low abundance between 2000 and 2009, and a posterior decrease (Fig. 2A). Before the construction of Porto Primavera Dam, the abundances were distributed more evenly over the three rivers. After the construction of dam, the Ivinhema River began to stand out by often exhibiting the highest abundances.

The less altered sites (LA; Ivinhema River) had a higher abundance, which was 75% higher than the moderately altered (MA; Baía River) and 50% higher than the highly altered (HA; Paraná River) sites. When tested for differences in abundance among periods

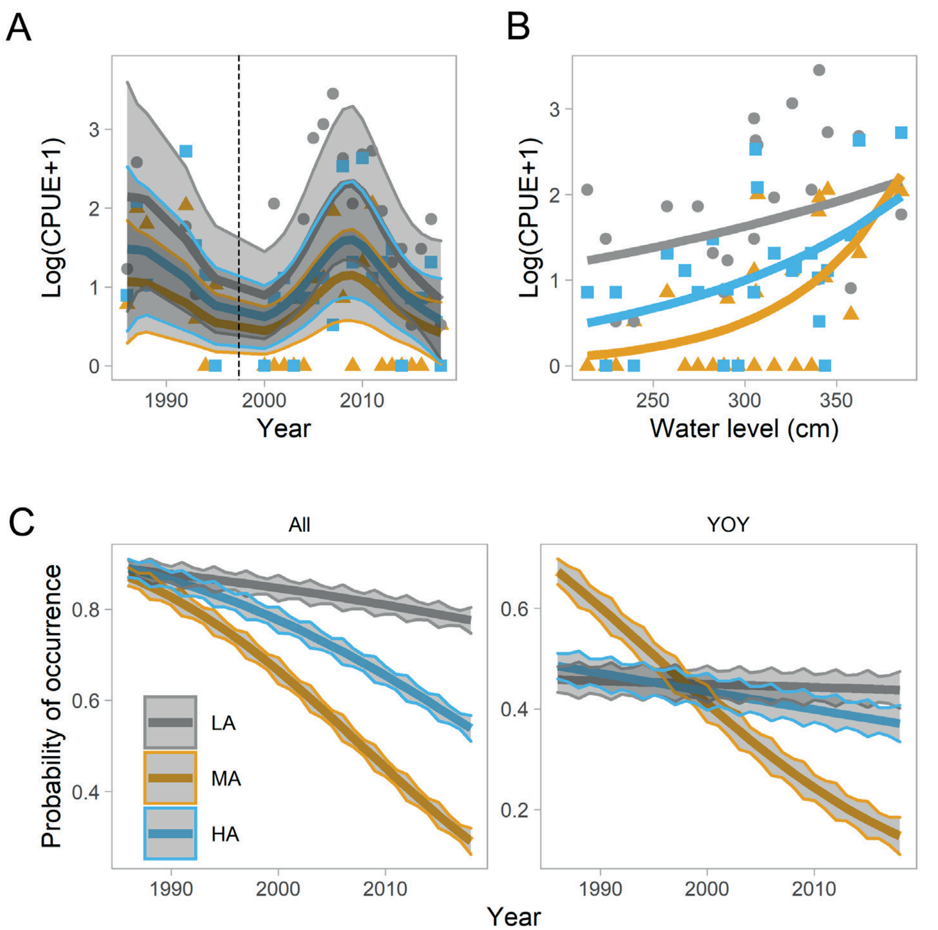

FIGURE 2 | *Salminus brasiliensis* in three rivers of the upper Paraná floodplain. **A.** Temporal trend in abundance – dashed line indicates the year in which the Porto Primavera Dam began to operate; **B.** Relationship between water level and abundance (CPUE). The less altered (LA) river has a weaker relationship between water level and young-of-the-year abundance. HA – highly altered (Paraná River), MA – moderately altered (Baía River), and less altered – LA (Ivinhema River); **C.** Probability of occurrence of the species (All) and young-of-the-year (YOY).

(before and after the construction of the Porto Primavera Dam), only the interaction (River x Period) was significant. The abundance mainly differed among periods due to a decrease in the MA and HA rivers, whereas the LA river maintained a higher abundance over time (Fig. 2A). However, after the closure of the Porto Primavera Dam, the LA river accounted for 68% of the CPUE, reducing at a rate of -0.11 each year (R^2 = 0.24; P < 0.001). No significant reduction trends were observed in MA (slope = -0.03; R^2 = 0.04; P = 0.09) or HA (slope = -0.01; R^2 = -0.01; P = 0.65). For all sites, the abundance of *S. brasiliensis* was positively related to water level. Nevertheless, contrary to our expectation, the relationship was stronger for the MA river (Fig. 2B).

The probability of occurrence of *S. brasiliensis* and the YOY showed a decline for all the rivers. These declines were larger in the MA river (All = -0.09; YOY = -0.08) and smaller in the LA river (All = -0.02; YOY = -0.002) (Fig. 2C).

Cross-correlation and Granger causality test. Cross-correlation showed that the temporal series of the MA and HA rivers had higher correlations with the LA river at negative lags of time (Fig. 3). Then, abundances in the MA and HA rivers could be in response to past changes in abundance within the LA river. The lag 1 (12 months) had a higher correlation for both rivers. However, the Granger causality test found that only the abundance in the HA river in response to the abundance in the LA river was significant (Tab. 1).

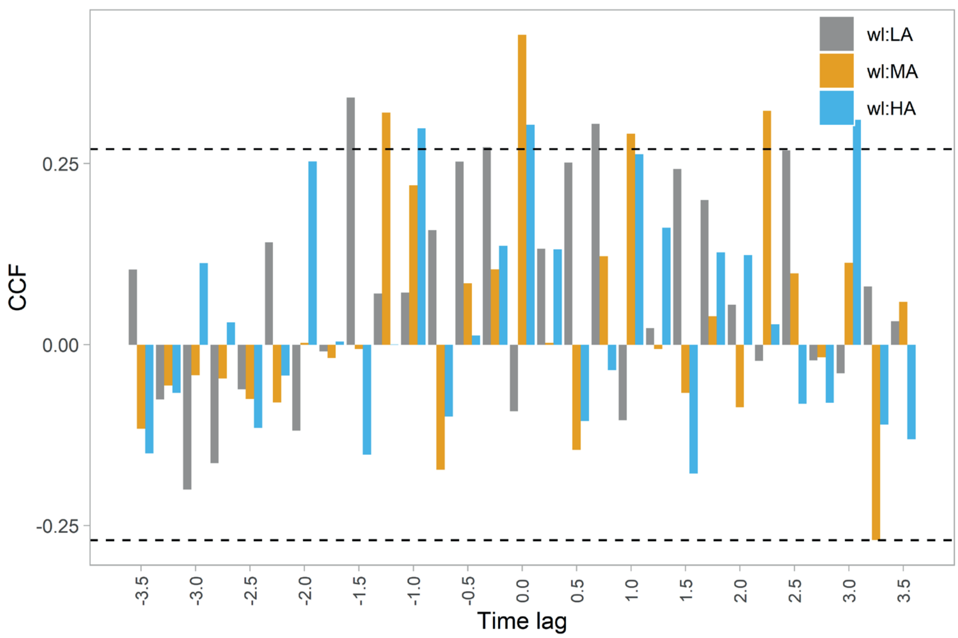

FIGURE 3 | Cross-correlations between the temporal abundance series of the less altered (LA) and moderately altered (MA) rivers (LA:MA) and the LA and HA rivers (LA:HA). As sampling was conducted quarterly. A 0.25 lag is equal to three months. HA: Paraná River; MA: Baía River; LA: Ivinhema River). CCF = cross-correlation coefficient. After the prewhitening protocol correlations, < -0.27 and > 0.27 were considered significant (dashed line).

Condition factor and gonadal index. To investigate variation in K, 344 females and 137 males were considered. For females, the slope of the body weight x body length relationship was steepest in the MA river (b = 3.32), indicating that females in this river gained weight faster with increasing length (Fig. 4A). However, as shown by the ANOVA test, larger females (in length and weight) and individuals with higher K values were found in the LA river (Fig. 4B). For males, the slope of the body weight x body length relationship was also steeper in the MA river (b = 3.40) (Fig. 4D). Higher K values were observed in the HA river and lower in the MA river (Fig. 4E). However, the K values increased over time in the LA river but remained stable in the HA river for both sexes (Figs. 4C, F).

For both sexes, GI values showed similar patterns to those observed for K (Fig. 5). For females, GI was higher in the LA river (Fig. 5B). Moreover, an increase in GI over time was observed in the LA river for both sexes (Figs. 5C, F). The MA river had the lowest GI values and the smallest increase over time (Figs. 5B, C, E, F).

TABLE 1 | Granger test of causality. The upper row shows if the abundance in the HA – highly altered (Paraná River) and MA – moderately altered (Baía River) rivers have a causal relation with the abundance in the LA – less altered (Ivinhema River). The lower diagonal shows the inverse direction in causality. Bold letters indicate significant causality.

		Response temporal series		
	River	**LA**	**HA**	**MA**
Explanatory temporal series	LA	–	**F = 3.66; P < 0.01**	F = 1.59; P = 0.20
	HA	F = 0.07; P = 0.80	–	F = 0.10; P = 0.74
	MA	F = 3.53; P = 0.07	F = 0.10; P = 0.76	–

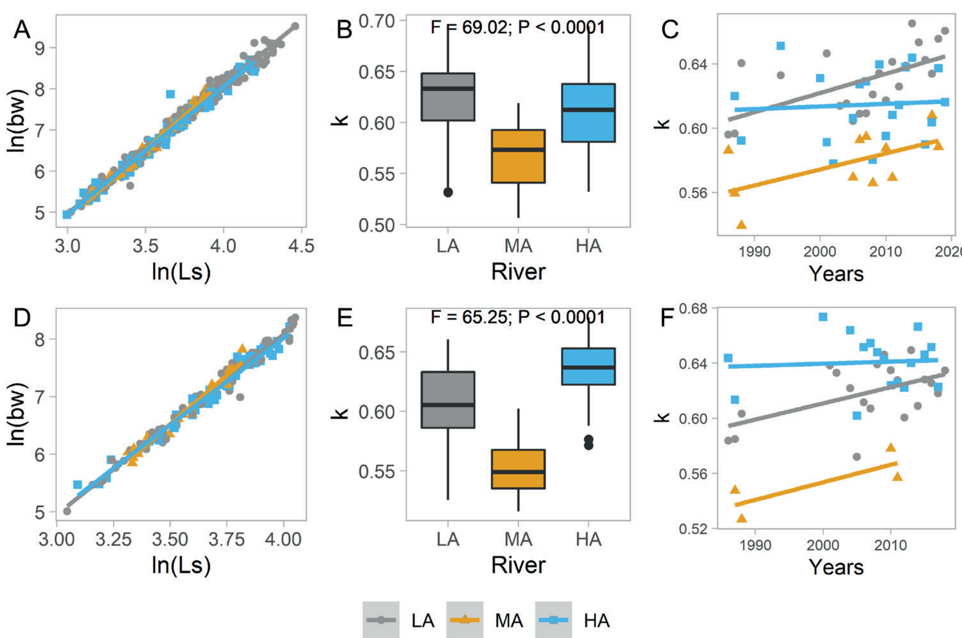

FIGURE 4 | ANCOVA interaction effects for the relationship between body weight (bw) and body length (Ls) for female (**A**) and male (**D**) *Salminus brasiliensis*. Mean condition factor (K) for female (**B**) and male (**E**) *S. brasiliensis* by river (HA – highly altered; MA – moderately altered; LA – less altered). Condition factor (K) for female (**C**) and male (**F**) *S. brasiliensis* over time. K was measured as the relationship between ln(bw)/ln(Ls^3.13) for females and ln(bw)/ln(Ls^3.10) for males.

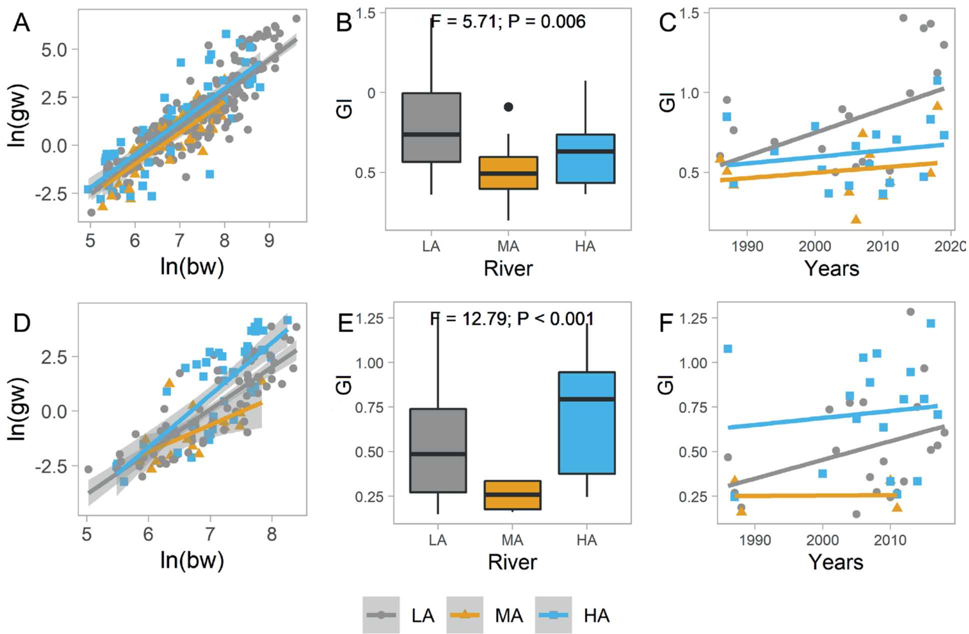

FIGURE 5 | ANCOVA interaction effects for the relationship between gonad weight (gw) and body weight (bw) for female (**A**) and male (**D**) *Salminus brasiliensis*. Mean gonadal index (GI) for female (**B**) and male (**E**) *S. brasiliensis* by river (HA – highly altered; MA – moderately altered; LA – less altered). GI for female (**C**) and male (**F**) *S*. brasiliensis over time. GI was measured as the relationship between ln(gw)/ln(bw^1.25) for females and ln(gw)/ln(bw^1.07) for males.

DISCUSSION

Despite an overall decrease in the abundance and occurrence of *S. brasiliensis* across the studied region, we found that the less impacted sites hold higher abundances and exhibited a slower decline in the probability of occurrence. Over time, populations in less impacted sites also exhibited increased fish condition (K and GI). Our results imply that the protection of some areas in the upper Paraná River has had a sound effect by reducing the velocity of *S. brasiliensis* decline.

The stocks of migratory species have diminished in many rivers due to overfishing and habitat modifications caused by dams (Agostinho *et al*., 2004). *Salminus brasiliensis*, an emblematic example of this, is the most valuable species in artisanal and sport fishing in the upper Paraná River (Agostinho *et al*., 2005). Notably, even before the construction of the Porto Primavera Dam, a decrease in the abundance of this species was related to overfishing (Petrere Jr., 1996; Petrere *et al*., 2002; Agostinho *et al*., 2007b) since there was an absence of protected areas or laws that prohibited *S. brasiliensis* fishing during that period. Additionally, before the construction of the Porto Primavera Dam, the Paraná River was one of the most dammed rivers in South America and its floodplain had already been impacted by other forms of flow control made by the reservoir cascade (Agostinho *et al*., 2007a, 2016).

The creation of the "Parque Estadual das Várzeas do Rio Ivinhema" was a compensatory action due to the impacts of the Porto Primavera Dam. Moreover, this was accompanied by a ban on fishing of *S. brasiliensis*. In conjunction with the law regulating punishments for environmental crimes (Law nº 9605/1998), these actions likely caused the observed increase in the abundance of *S. brasiliensis* observed between 2005 and 2013. Moreover, successive years of drought (*e.g*., 2000 – 2001) increased the effects of the El Niño-Southern Oscillation (ENSO) in the La Niña phase (Grimm *et al*., 2000), concentrating fishes due to lower hydrologic levels in the sample sites. This favored the feeding of piscivorous and consequently increased their body condition factor, which could have increased the abundance of piscivorous fishes in the floodplain (Pereira *et al*., 2017). While such an increased fish density provides abundant and available food for piscivores over the short term (Luz-Agostinho *et al*., 2008; Pereira *et al*., 2017), food resources may become limiting for piscivorous species over more extended periods (Medeiros, Arthington, 2014).

The Porto Primavera Reservoir could be the primary driver of negative trends in the most impacted rivers (*i.e*., the MA and HA rivers). It directly regulates the seasonal fluctuation of floods for the Paraná River (HA river) and indirectly regulates the same for the Baía River (MA river) (Agostinho *et al*., 2007b). The absence of lasting floods has led to a recruitment failure and a reduction in the total abundance of *S. brasiliensis* in regulated rivers (Oliveira *et al*., 2015, 2020). Nonetheless, the probability of occurrence decreased across the three rivers, implying that regional pressures can also affect the populations in the LA river. For instance, the main migratory route of *S. brasiliensis* includes the main channel of the Paraná River, which is highly modified by upstream dams and thus retains sediments and nutrients (Roberto *et al*., 2009). Also, this channel is occupied by visually orientated alien piscivores (Peacock bass) that have better performance in capturing prey in clear waters (Ortega *et al*., 2020). Moreover, clear water reduces the chance of larvae from undammed tributaries surviving predation when arriving in the channel (Agostinho *et al*., 2016).

Previous studies have shown high densities of migratory species larvae in the Ivinhema River (LA river) (Baumgartner *et al*., 2004; Reynalte-Tataje *et al*., 2011; Barzotto *et al*., 2015; Rosa *et al*., 2019). Thus, the LA river constitutes an important available route for migratory species in this last lotic stretch of the Paraná River within Brazilian territory (Reynalte-Tataje *et al*., 2011; Affonso *et al*., 2015). Thus, *S. brasiliensis* reproduction in this stretch contributes to maintaining fish stocks — even in the HA river — considering a lag of 12 months. This appears to be congruent with the sink-source model (Pulliam, 1988; Marques *et al*., 2018), whereby the LA tributary is a propagule source whereas the HA tributary is a propagule sink. These results reinforce the importance of preserving free rivers without flood control to maintain the reproduction and recruitment of migratory species (Agostinho *et al*., 2001; Sanches *et al*., 2006; Reynalte-Tataje *et al*., 2011) and the important role of protected areas as propagule sources for surrounding areas (Hunter, Gibbs, 2007).

Migratory fish are high-quality habitat indicators (McDowall, Taylor, 2000) because they require specific environmental resources (*e.g*., spawning, nursery, and feeding areas) and large stretches of unimpeded river to complete their reproductive life cycles. One way to evaluate environmental quality is to measure some parameters of the target population, such as condition indexes (*e.g*., K and GI; Le Cren, 1951; Chang, Navas, 1984; Gubiani *et al*., 2020). The K of *S. brasiliensis* assemblages in the LA and MA rivers increased over time, with the LA river having the highest K values. This result supports our prediction that the river with the most effective protection will present better environmental quality and thus individuals in better nutritional condition. On the other hand, the assemblages of the HA river had a similar body condition between periods and maintained a constant nutritional condition after the hydroelectric dam closure. These results were likely due to the impacts caused by seasonal flood control.

Moreover, female *S. brasiliensis* of the MA river gained more weight with every centimeter grown. However, the population of the LA river had adults with the largest body lengths and heaviest gonads. As a strategy for maintaining their offspring, females from the MA and HA rivers must allocate more energy to developing their gonads at the expense of body growth and reproducing at shorter lengths (Audzijonyte, Richards, 2018). Under more favorable environmental conditions, the assemblage of the LA river can allocate its energy to body growth over time, thus favoring a larger body size than other populations. The presence of larger *S. brasiliensis* individuals in the LA river corroborates the results of Lopes *et al*. (2020) and demonstrates the effectiveness of protected areas and fishing prohibition laws (Laws nº 7653/1988 and nº 9605/1998) since larger fish are the target of commercial and recreational fishing.

Considering the conservation strategies for this freshwater fish species in the upper Paraná River floodplain over the past 26 years, the abundance of *S. brasiliensis* has generally declined, with a lower level of population decline observed in the most preserved river. Therefore, the implemented conservation strategies must be reinforced and monitored to avoid population decrease and local extinction. Furthermore, the conservation of the LA river also likely favors other migratory fish species. In this sense, the *S. brasiliensis* fishing prohibition law that came into force at the end of 2018 in Mato Grosso (Law nº19789/2018) and Paraná (Law nº22/2018) for 5 and 8 years, respectively, should only be suspended after studies can prove an increase in the abundance of this species in the region.

Most importantly, an ideal scenario involves the combination of protected areas and regulating the fishery and flood management in the upstream reaches to provide suitable conditions for reproduction. Moreover, all involved stakeholders should cooperate in developing conservation strategies. Our results reinforce the notion that fish populations with low abundances recover very slowly. Thus, long-term studies on this topic are essential to applying appropriate management measures, proposing relevant laws, and verifying the effectiveness of species conservation strategies.

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AUTHORS' CONTRIBUTION

Rosa Maria Dias: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.
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Mirtha Amanda Angulo-Valencia: Investigation, Validation, Visualization, Writing-review and editing.
Angelo Antonio Agostinho: Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing-review and editing.

ETHICAL STATEMENT

Samples were collected after obtaining all required permissions from the Ministério do Meio Ambiente [Brazilian Environmental Ministry (MMA), the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Sistema de Autorização e Informação em Biodiversidade (SISBIO)] (license number: 22442–1; authentication code: 3263346). This study was approved by the Committee for Ethical Conduct on Animal Use and Experimentation at the Universidade Estadual de Maringá (CEUA; technical advice nº 1420221018/2018).

COMPETING INTERESTS

The authors declare no competing interests.

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