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Recruitment of migratory Characiforms in the different wetland habitats of Central Amazonia: Subsidies for sustainable fisheries management

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Abstract

By promoting the biological recruitment of relevant natural resources, wetlands offer a major ecosystem service. This study investigates the importance of wetland habitats of the central Amazon basin as sites for spawning and/or initial development of seven of the most important commercial Characiforms fish species. In order to confirm this importance, samples of the eggs, larvae, and juveniles of these fish species were collected during the four seasonal phases of the hydrological cycles of 2010 and 2011, in different aquatic environments of the wetland ecosystem in the central Amazon. The results confirmed that the flooding phase is the most important for the spawning of these species, and that they preferred to use the marginal areas of the central Amazon as spawning grounds. The larvae of these species colonize the confluence zone of the rivers and the mouths of the floodplain channels, principally during the initial stages (pre-flexion) of their ontogenetic development. The channels that connect the lakes to the rivers are the main dispersal route for the larvae, especially those in advanced stages of development (flexion/post-flexion), towards the internal of the wetland habitats, such as the lakes and large mattresses of floating vegetation. The different wetland habitats of this region provide an extremely important ecosystem service, playing a critical role in the recruitment of commercially-valuable fish species, and thus require adequate protection and management to ensure the continuity of fisheries and natural stocks.

KEYWORDS
amazonian floodplains, ecosystem services, fish larvae, fishery resources, food provisioning, Mamirauá Reserve

1 | INTRODUCTION

In the Amazon region, fisheries play a fundamental role in cultural, economic and social dimensions. In addition to providing jobs and income, fishing is the main source of animal protein for the riverside populations (Lima, Doria, & Freitas, 2012; Serrão et al., 2019). A number of fish species are exploited commercially in the Amazon region, including migratoty Characiforms (Cardoso & Freitas, 2008; Doria, Ruffino, Hijazi, & Cruz, 2012). These species represent the bulk of the catch disembarked in the region's principal urban centers in both Brazilian Amazon (Ferraz, Lima, & Amaral, 2012; Siebert & Silva, 2019) and in the neighboring countries (Carvajal-Vallejos, Van-Damme, & Muñoz, 2011; Van-Damme, Carvajal-Vallejos, Rua, Cordova, & Becerra, 2011).

Some of these species perform reproductive migrations, for which they move from oligotrophic lakes and rivers to spawn in the region's major white water rivers, which contain high concentrations of nutrients and suspended solid particles (Goulding et al., 2019; Jiménez-Segura, Palacio, & Leite, 2010). This reproductive strategy is based on an annual cycle, which is generally linked to the increase in rainfall at the headwaters of the rivers, and the resulting increase in the water level of the main rivers (Bayley, Castello, Batista, & Fabré, 2018; Bednarski, Miller, & Scarnecchia, 2008). The flood pulse results in the expansion of aquatic habitats and increase in the connectivity of these habitats form the wetland ecosystem, representing a significant part of the entire Amazon.

The considerable heterogeneity of habitats found along the floodplains of the major rivers in the tropics – as in the case of the wetland habitats of the Amazon basin – allows a wide diversity of fishes to exploit these habitats in distinct ways during their life cycles (Chaves, Oliveira, Cajado, Ponte, & Zacardi, 2019; Humphries, King, & Koehn, 1999; King, Humphries, & Lake, 2003). Over the past few years, increasing pressure from fisheries has progressively threatened the resources of the Amazonian wetlands (Castello, McGrath, & Beck, 2011; Souza, Camargo, & Camargo, 2012).

This process may lead to increasing ecological imbalances and, eventually, the collapse of the fishery stocks exploited by traditional local populations and even by commercial fleets (Tregidgo, Barlow, Pompeu, Almeida Rocha, & Parry, 2017). Increasing fishery pressures on these stocks may also result in intense socio-economic impacts on the populations that depend on these resources for their livelihood. As indicated in previous studies, these marginal flooded habitats of tropical wetlands provide important ecosystem services, including the maintenance of fishery stocks, which may be lost through the degradation of these environments and the inadequate exploitation of their resources (Renó, Novo, & Escada, 2016; Strand et al., 2018).

The principal objective of the present study was to describe and understand the role of the wetland environments, and their different aquatic habitats, for the recruitment and development of the different ontogenetic phases of seven commercially-important Characiforms species, among the most important fishery resources of the central Amazon basin. The study also provides essential information for the understanding of the relationships that exist among these environments, and their limnological conditions, which will contribute to the regulation, conservation, and management of these environments, these fisheries and other natural resources.

2 | MATERIALS AND METHODS

The study area is located near the town of Tefé (between 03°08′S, 64°45′W and 02°36′S, 67°13′W), in the Brazilian state of Amazonas, one of the main fishery regions of the central Amazon basin (Figure 1), located between the Middle Solimões River and the Lower Japurá River. The samples were collected in a number of different environments, including lakes and channels.

The mattresses of aquatic vegetation and the open waters of the lakes and channels of the wetland ecosystem were surveyed within the Mamirauá Sustainable Development Reserve (MSDR), both samples occurred during the years 2010 and 2011. In addition, the main channels of the Middle Solimões and Lower Japurá rivers were also sampled but only during the year 2011.

The eggs, larvae, and juveniles of the targeted migratory Characiforms species were collected during the four principal phases of the hydrological cycle (flooding, high water, falling, and low water) of 2010 and 2011. Samples were collected in 34 points located distributed in the open waters of lakes, channels, and rivers during both diurnal and nocturnal periods, in both deep and subsurface depths of the water column, using horizontal trawls of a conical-cylindrical plankton net (300 μm mesh) equipped with a flowmeter, to measure the volume of water filtered. The organisms collected were stored in labeled flasks containing 10% formalin.

Samples from aquatic macrophytes mattresses were collected at 18 randomly-selected points located on the margins of the lakes and in the channels that interconnect them. The samples were collected using a 500 μm mesh net fixed to a rectangular frame of 1.5 × 1.0 m, as described by Nakatani et al. (2001). The samples were standardized by sampling effort, and three mixed beds of vegetation of a similar size and configuration were sampled independently at each point. The license for the collection of biological samples was granted by SISBIO/ICMBio/MMA, in the special license 23741-1, issued in accordance with Normative Instruction 154/2007.

In the laboratory, the samples were processed, the number of eggs and larvae were determined, and the ontogenetic development stages of eggs were classified in early cleavage, early embryo, tail-free and late embryo, is the larvae were classified in larval yolk sac, pre-flexion, flexion and post-flexion, according to the terminology of Nakatani et al. (2001) for both cases. The larvae in the samples were quantified and then identified to the lowest taxonomic level as possible, based in specialized literature.

The juveniles in the samples were rinsed in running water, quantified, identified, and transferred to 70% alcohol for conservation. The specimens were identified using the taxonomic keys specific and when necessary confirmed by specialists. The density of the eggs and larvae was standardized to a volume of 10 m^3 of filtered water, as in Nakatani et al. (2001). The larval densities and limnological parameters were log-transformed ($\log (x + 1)$) to meet normality. The assumptions of normality and homoscedasticity were verified using the Shapiro-Wilk and Levene tests, respectively.

The spatial variation in the density of the fish and their developmental stages was evaluated using a factorial ANOVA, in which the environments were considered as independent factors and each developmental stage was included as a dependent variable. The samples were only included in the analyses if they contained at least one specimen of the study species. Then a posteriori Tukey test was applied whenever significant ($p < .05$) difference was found. The STATISTICA 7.0 software was used for all analyses.

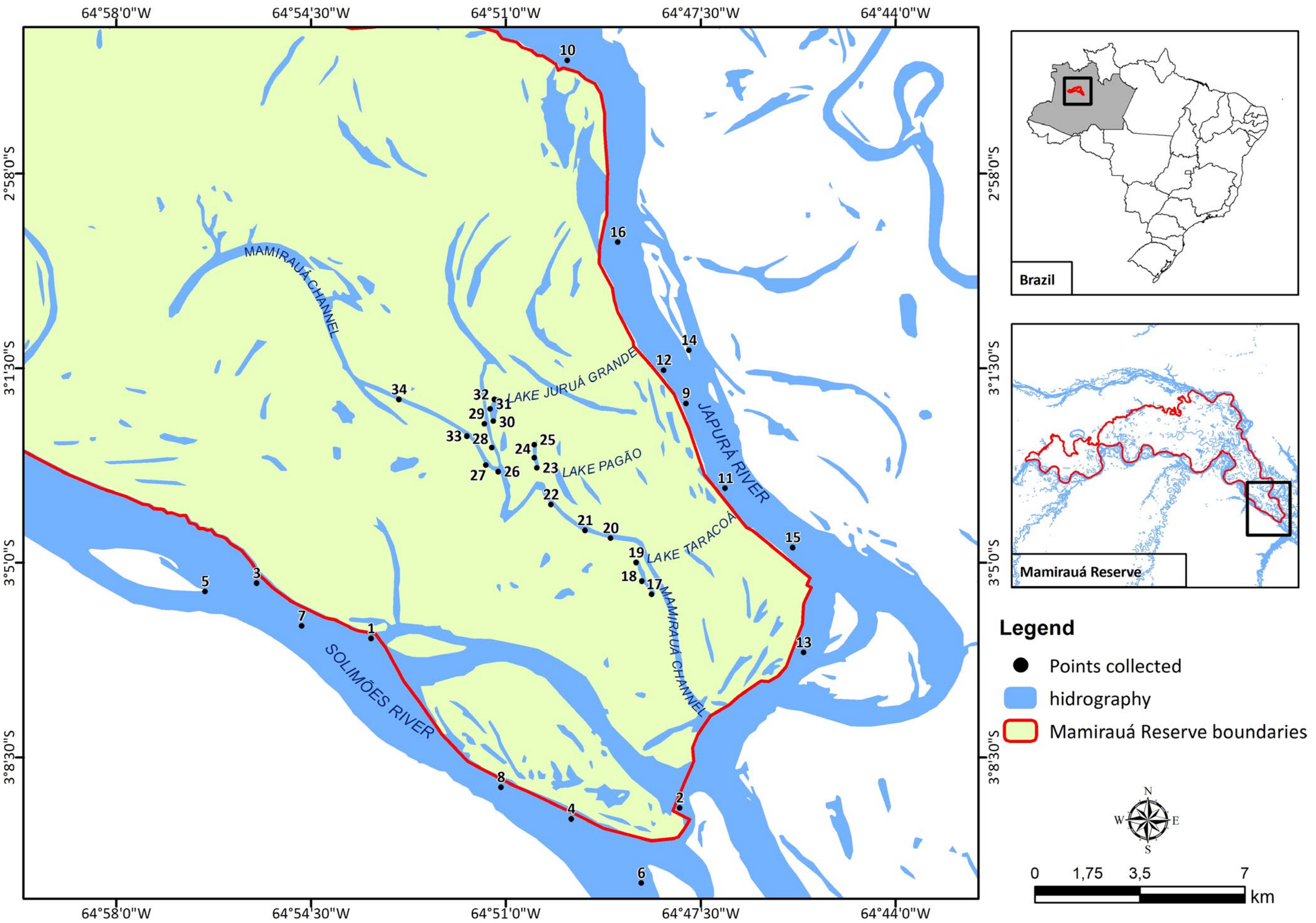

FIGURE 1 Location of the study area, showing the sample collecting points (●) in and around the Mamirauá Reserve in the central Amazon basin, in the Brazilian state of Amazonas

3 | RESULTS

A total of 1,846 eggs, 90,154 larvae, and 2,339 juvenile fishes were collected during this study. The specimens classified in 11 orders, 35 families, 105 genera, and 122 species (Supporting information). Overall, 16,886 of the larvae and juveniles were identified as belonging to the study species *Brycon amazonicus*, *Mylossoma albiscopum*, *Triportheus auritus*, *Semaprochilodus taeniurus*, *Semaprochilodus insignis*, *Prochilodus nigricans*, and *Colossoma macropomum*, representing 18.72% of all the specimens collected (Figure 2).

The largest number of eggs was recorded in the main river environments, in the marginal areas of the Middle Solimões and Lower Japurá (56.88% of the total) during the flooding period. The remaining 43.12% were found in floating macrophytes inside the wetlands. The eggs collected in the rivers had a mean diameter of three mm and ample perivitelline space, which is typical of the migratory Characiforms. Most of the specimens were in a state of initial cleavage (76.82%) or initial embryo development (11.37%). Less commonly, embryos were collected in the final stage of development (10.37%) or the free-tail stage (1.44%). No significant ($p > .05$) spatial variation was found in the density of eggs nor among the developmental phases collected in the different aquatic habitats.

The main river channels had the highest densities of larvae, as well as the greatest abundance, with 89.55% of the total number of individuals captured. The open waters of the channels had the second highest abundance (6.26%), followed by the lakes (2.27%), and lastly, the submerged root zone of the mattresses of aquatic macrophytes (1.92%). No significant difference was found in the mean density of larvae among the different habitats sampled. A significant difference was found, however, among the different stages of ontogenetic development ($F = 1.65$; $p = .011$) in the different sampled areas, with a greater contribution of the initial, pre-flexion phase in the areas of confluence between the channels and the main rivers.

The seven study species presented a distinct pattern of distribution of their different developmental stages, with a greater abundance of pre-flexion larvae being found in the main rivers, with the subsequent stages (flexion and post-flexion) predominating in the wetland lakes and channels, while the post-flexion stage was also abundant in the submerged mattresses of aquatic macrophytes (Figure 3). The juveniles of *M. albiscopum*, *T. auritus*, *S. insignis*, *S. taeniurus*, and *P. nigricans* were the most common inside the macrophytes found in the marginal areas of the channels. The juveniles of *B. amazonicus* and *C. macropomum* were not found in this habitat.

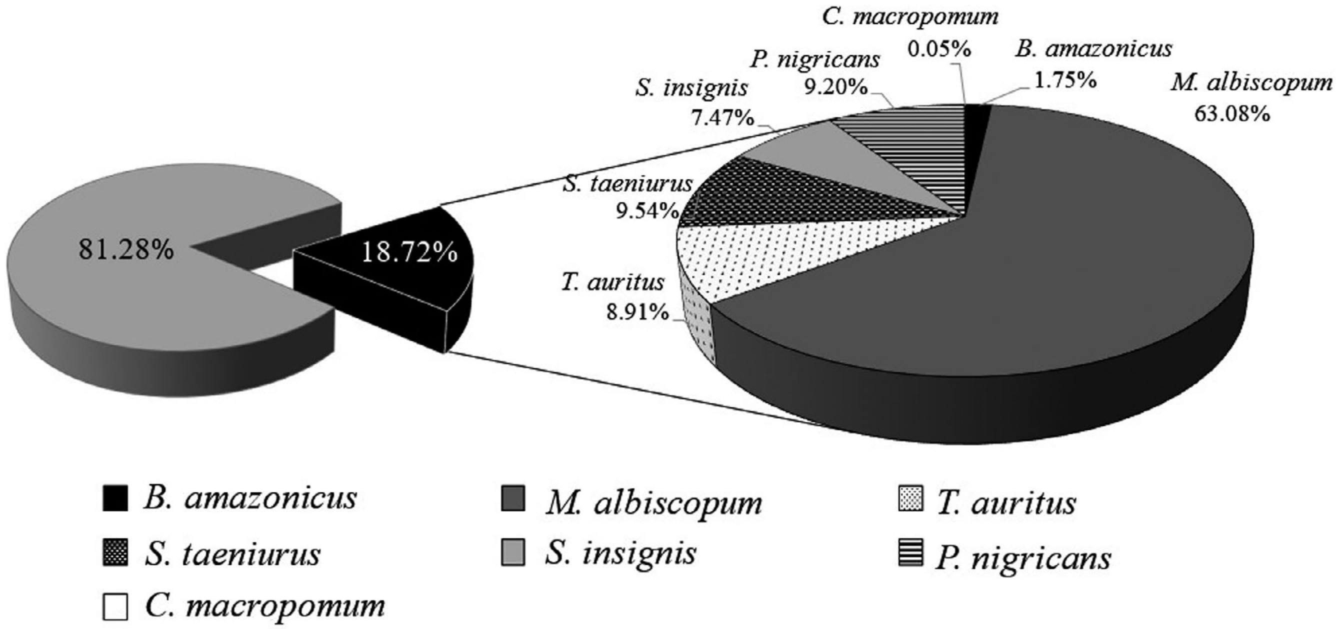

FIGURE 2 Total abundance of the larvae and juveniles of the Characiforms species collected during the present study in the central Amazon basin, highlighting the relative abundance of the study species

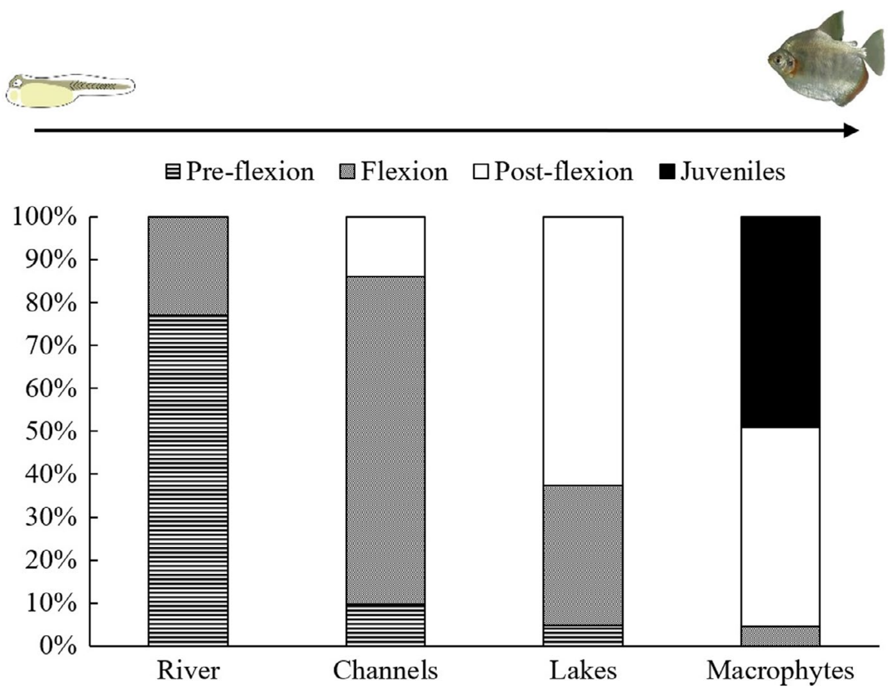

FIGURE 3 Relative abundance of the different development stages of the Characiforms species analyzed during the present study of the different wetland habitats environments of the Mamirauá Sustainable Development Reserve and adjacent areas of the Middle Solimões and Lower Japurá rivers in the central Amazon basin

4 | DISCUSSION

The rivers, lakes, channels, and macrophyte mattresses in the area of the Mamirauá Reserve were important sites for the recruitment of the region's principal commercially-important migratory Characiforms species. The overexploitation of some of the most important fishery resources in the Amazon basin had already been recorded by Petrere (1983) and subsequently by other authors, such as Araújo-Lima and Goulding (1998), and more recently, by Lopes, Catarino, Lima, and Freitas (2016). The target species of the present study are intensively exploited in many parts of the Amazon basin (Correia & Freitas, 2013; Mounic-Silva & Leite, 2013), in Brazil and neighboring countries. In the region of the Mamirauá Reserve, however, these species (with the possible exception of *C. macropomum*) are not yet being overfished, indicating that they are being successfully recruited locally, despite the pressure from local fisheries.

In the Amazon basin, the beginning of the rainy season, when the rivers start to flood, is considered to be the spawning period of most of the migratory Characiforms species, given the higher nutrient concentrations, and the increased turbidity and oxygenation of the water, conditions that favor the reproduction of many of these species (Ponte, Ferreira, Bittencourt, Queiroz, & Zacardi, 2016; Zacardi, Chaves, Ponte, & Lima, 2017; Zacardi, Ponte, et al., 2017). These conditions also favor the movement of these species to their spawning areas, which are generally located in areas where the channels connect with white-water rivers (Zacardi, Bittencourt, Nakayama, & Queiroz, 2017; Zacardi & Ponte, 2016). This combination of factors supports the development and transportation of the recently-hatched larvae to the areas in which they develop, in the wetland lakes and channels, carried by the currents of the flooding waters (Oliveira, Cajado, Santos, Suzuki, & Zacardi, 2020; Ponte, Oliveira, & Zacardi, 2019).

The presence of larvae at a given development stage in specific habitats may be linked to environmental conditions, the presence of competitors, their susceptibility to predation, and the abundance and availability of feeding resources (King et al., 2003; Picapedra, Sanches, & Lansac-Tôha, 2018). The use of lakes and channels as zones of growth and development is probably related to the reduced water current speeds found in these environments, which facilitate the sedimentation of fine particles, leading to an increase in the availability of feeding resources and refuges, and, possibly, optimal conditions for their development (Goulding et al., 2019; Oliveira et al., 2020; Zaniboni-Filho, Schulz, & Ross, 2003). These conditions allow the species to reach a body size that offers more protection from predation, maximizing survival, and characterizing these environments as areas appropriate for the development of the commercially-valuable fish species studied here.

The availability of feeding resources is considered to be a primary factor determining the establishment and initial development of fishes on the floodplains of the Solimões/Amazon basin, and may account for their preferences for some specific types of habitat (Silva-Soares & Leite, 2013). This habitat selectivity may not be related to one or two specific factors, but rather to a set of chemical, physical, and biological conditions of the target habitats, as observed in previous studies (Bertolo et al., 2012; Reynalte-Tataje, Hermes-Silva, Silva, Bialetzki, & Zaniboni-Filho, 2008; Zacardi, Ponte, et al., 2017).

The large numbers of larvae found at the flexion stage of development in the channel that connects the Japurá River to a number of lakes within the study area makes this body of water an important dispersal route for the drifting larvae. It transports the larvae from the spawning grounds, probably in adjacent stretches of the Japurá to areas appropriate for their initial development, in the lentic environments of the floodplain where they reach the beds of aquatic macrophytes located in the lakes (Figure 4), which indicates that the ideal conditions for the development of the larvae are found inside the different wetland habitat, rather than the principal rivers.

The distribution pattern of fish larvae and juveniles recorded in the present study, with the migratory Characiforms spawning in the white-water tributaries, rich in nutrients, and the pelagic eggs developing and hatching while drifting, was observed in many previous studies (Araújo-Lima & Oliveira, 1998; Goulding, 1980). A number of authors have, nevertheless, questioned the generalization of this model, citing the role of the diversity of habitats found along the main river channels, which may provide adequate conditions for the development of the larvae, mainly in marginal areas (Humphries et al., 1999; King et al., 2003), reality observed in *Brycon* larvae collected during sampling only in the margin river channel.

The wetlands form a natural nursery environment for the larvae of the migratory Characiforms that spawn in the adjacent rivers, reinforcing the importance of these habitats and the whole of the floodplain for the maintenance and preservation of this fish fauna, in addition to monitoring to prevent fishing during the reproductive period. A pattern observed here and in many other important wetlands worldwide (Ren, He, Song, Cheng, & Xie, 2016). Therefore, ensuring its reproductive success of these species means maintaining a balanced ecological sturct.

The conservation of these important floodplain areas within the Amazon basin will be essential to guarantee the biological recruitment process (reproduction, growth, and establishment) of

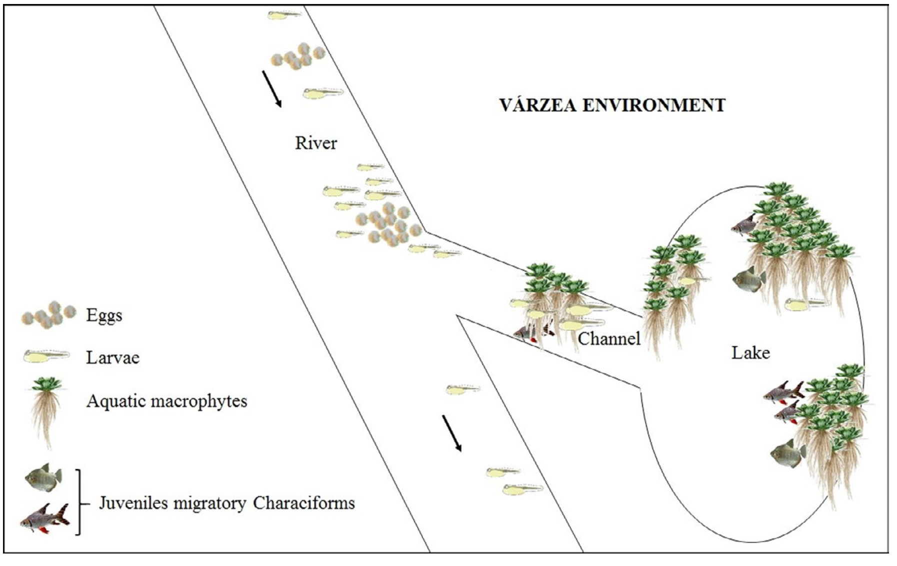

FIGURE 4 Schematic model of the spatial distribution of the spawning and development of the commercially-important migratory Characiforms of the region of the middle Solimões River in the central Amazon basin

countless fishery stocks, as well as the production of food and economic resources for a large part of the region's human population. The natural balance of the dynamics of this system is thus fundamental to the continuity of the ecosystem services it provides for traditional local communities (Barbosa, Atkison, & Dearing, 2016; Caballero-Serrano et al., 2017; Sukhdev, 2008). The protection and conservation of these areas provides a number of benefits, direct or indirect to the wellbeing of local human populations (Hueting, Reijnders, Boer, Lambooy, & Jansen, 1998). New goods, additive values and opportunities may be generated by the adequate protection and management of these areas, and their stocks of juveniles of fisheries resources.

Given the high levels of consumption of fish from the Amazon basin the importance of fisheries for the region and the existing fishing pressures (Correia & Freitas, 2013; Sousa & Freitas, 2011), to conserve fishery resources, and to ensure the sustainability of this activity in different wetland habitats, such as those of the Middle Solimões and Lower Japurá rivers, will depend on the implementation of effective management measures represent the only effective way to guarantee the long-term provision of services by these ecosystems (Macedo & Castello, 2015; Wilcox, 2008).

The management of fishery stocks on a local scale by artisanal fishing communities appears to be one of the most viable alternatives for the conservation of fishery resources and the organization of local economic activities (Hallwass & Silvano, 2016; Keppeler, Hallwass, & Silvano, 2017). These are extremely effective strategies given that they emphasize food security, environmental education, and environmental protection, integrated with the participation of local communities and/or societies, on a number of different levels. Other strategies, which include the creation of protected areas, with the potential for the provision of ecosystem services and the regulation of the major commercial fishery fleets of the Amazonian countries, will be also important for the reinforcement of the sustainability of these ecosystem services, guaranteeing that these Amazonian environments are preserved, and will be available for future generations, as already occurs in other floodplain areas (Barzotto, Sanches, Bialetzki, Orvati, & Gomes, 2015; Keppeler et al., 2017; Rosa, Silva, & Bialetzki, 2019).

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DATA AVAILABILITY STATEMENT

We authors authorize the availability of the research data presented.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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