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Article *in* Fisheries Management and Ecology · April 2017

DOI: 10.1111/fme.12222

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ORIGINAL ARTICLE

WILEY Fisheries Management and Ecology

Distribution of economically important fish larvae (Characiformes, Prochilodontidae) in the Central Amazonia, Brazil

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Funding information
Mamirauá Institute for Sustainable Development (MISD); Laboratory of Biology and Aquatic Organisms (LABIO-UFPA)

Abstract

The spatio-temporal patterns of three species of Prochilodontidae larvae that are intensely used as fishery resources in Central Amazonia are analysed. Sampling was conducted during 2011 at four stages of the hydrological cycle (flood, high water, falling and low water phases). Sixteen collecting stations were located in different habitats (mouths of lake channels, "barrancos," sandbars and the main river channel) along the Solimões and Japurá rivers. A total of 4,322 Prochilodontidae larvae were collected during this investigation, with most captures occurring in the Japurá River (76.3% of larvae), while only 23.7% of the samples were caught in the Solimões River. Most captures occurred during rising water, indicating a strong reproductive seasonality in these three species. Rainfall and water level, along with dissolved oxygen, water temperature and electric conductivity, determined the larvae's spatio-temporal distribution. These results confirm the importance of várzea areas along white water rivers for the conservation, preservation and maintenance of heavily used fishery resources in the Brazilian Central Amazonia.

KEYWORDS
fishery resources, white water rivers, variation, várzea

1 | INTRODUCTION

Fish of the family Prochilodontidae, such as jaraquis (*Semaprochilodus insignis* Jardine & Schomburgk and *Semaprochilodus taeniurus* Val.), and curimatás (*Prochilodus nigricans* Agassiz), belong to a group of neotropical Characiformes of high commercial importance and are intensively fished in the Amazonian region (Santos-Filho & Batista, 2009).

These species show high interannual variation in the fish landing statistics and are highly important economically. They represent approximately 60% of the total fish landed in markets of the region (Ferraz & Barthem, 2016; Ferraz, Lima & Amaral, 2012; Ruffino, 2004; Viana, 2004) and are the main source of dietary protein for most of the local riverine populations (Ferraz et al., 2012; Queiroz, 1999).

For more than a decade, curimatás and jaraquis have been overfished, but in some parts of the Amazon, stocks may now be recovering (Barthem & Fabré, 2004). The decrease in number observed for these fish is probably a result of intense fishing pressure associated with weak recruitment, caused by unfavourable environmental conditions such as the intensity of the flooding periods (Souza, Camargo & Camargo, 2012). Others stressors, such as deforestation of riparian forests, dam construction, agricultural expansion and, more recently, climate change (Chaves, Carvalho, Ponte, Ferreira & Zacardi, 2017; Fearnside, 2006), may also be important. Thus, the development of sustainable fishery management, especially for species of high economic importance, depends on a better understanding of their population dynamics, biology, recruitment patterns, spawning habits and early development (Santos & Santos, 2005).

Lack of knowledge on temporal and spatial patterns of larval occurrence can have dramatic adverse consequences on the quality and effectiveness of fishery management. Although the reproductive strategies of fishes are a result of long-term natural evolution, the actual timing of spawning and larval production can determine the success of recruitment (Nakatani et al., 2001).

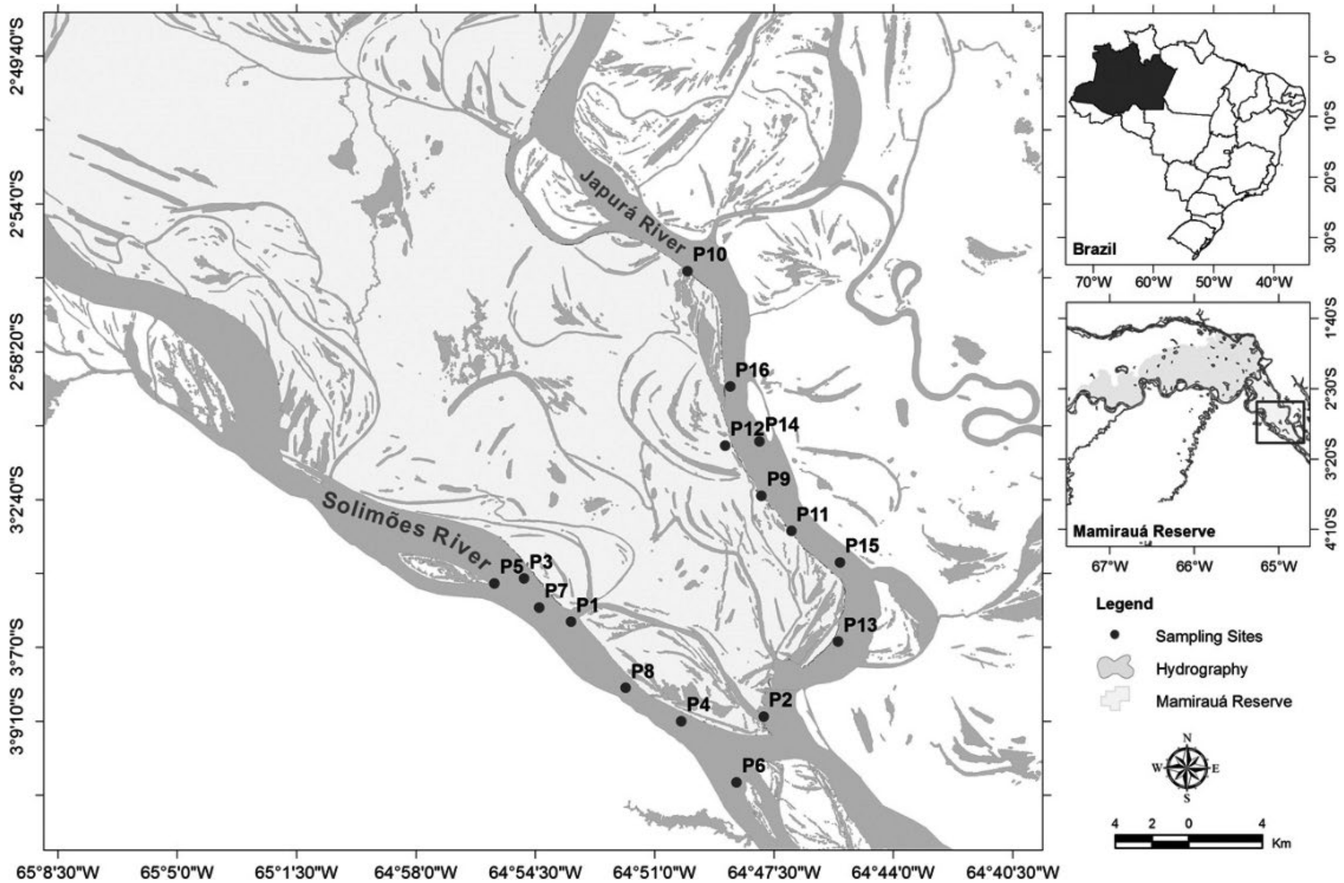

FIGURE 1 Location of the study area, with the sampling stations distributed alongside the Solimões and Japurá rivers, Central Amazonia, Brazil

Understanding of the phenology of fish spawning in neotropical freshwater ecosystems, such as the Amazon basin, depends on the life history strategies of the species, the availability of resources and the interactions of regional environmental variation patterns related to the hydrological cycle and seasonality (Camargo, Giarrizzo & Isaac, 2015; Lima & Araújo-Lima, 2004; Ponte, Ferreira, Bittencourt, Queiroz & Zacardi, 2016; Ruffino & Isaac, 1995). These factors regulate the composition, abundance and distribution of species within and among biological communities (Gomes & Agostinho, 1997; Junk, Bayley & Sparks, 1989; Menge & Sutherland, 1987; Winemiller, 1989). In addition, temporal factors such as seasonality of water quality, rainfall and the annual flood pulse in tropical floodplain rivers may determine the reproduction of migratory fishes during rising waters, ensuring the drift of eggs and larvae to nursery areas inside the várzea, where they shelter and feed, acquiring appropriate conditions for their survival and development into juveniles (Carolsfeld, Harvey, Ross & Baer, 2003; Leite & Araújo-Lima, 2002; Leite, Silva & Freitas, 2006; Mounic-Silva & Leite, 2013).

Such temporal patterns need to be understood to provide reliable evaluation of fish status and accurate basis for planning, and ensure healthy, well-managed fisheries (Booth, 2000; Shuai et al., 2016). However, in the Amazon, studies of ecology and distribution the fish larvae remain scarce; exceptions are the studies of Oliveira and Araújo-Lima (1998), Oliveira (2000), Araújo-Lima, Silva, Petry, Oliveira and Moura (2001), Lima and Araújo-Lima (2004), Oliveira and Ferreira (2008), Mounic-Silva and Leite (2013), Ponte et al. (2016), Zacardi and Ponte (2016) and Chaves et al. (2017) focusing on species of greater economic interest.

This paper aims to contribute to filling this gap through the study of the spatial and temporal variation patterns of the larvae of *S. taeniurus*, *S. insignis* and *P. nigricans* and to establish their relationship to key environmental variables in the middle Solimões and lower Japurá rivers' area. This information can support decisions about habitat management, conservation and sustainable management of these highly exploited fishery resources in Central Amazonia.

2 | MATERIAL AND METHODS

2.1 | Study area

The study area is in the middle portion of the Solimões River and the lower portion of the Japurá River, around the Mamirauá Sustainable Development Reserve–MSDR (03°08′S, 64°45′W and 02°36′S, 67°13′W), near the town of Tefé, in the State of Amazonas, Brazil (Figure 1).

The Solimões and Japurá rivers are white water rivers, following the classification of Sioli (1984), and determine the limnology of the region of the study. The waters of the Solimões River are richer in dissolved organic ions and show a greater level of suspended sediments from erosion processes. Along its course, the Japurá River receives approximately five black water rivers, making it different from the Solimões in terms of its chemical composition and current velocity. Both rivers are well-mixed and show little temperature stratification (Henderson, 1999). Hydrodynamic factors, the characteristics of undissolved sediments, erosion processes and the transport and deposition of the sediments cause annual morphological variations in the rivers and their banks.

Annual rainfall totals approximately 2,850 mm and shows distinct seasonality. Normally, the high water season (May to July), the falling water season (August and September) and the low water season (October and November) are short and followed by a long period of gradual flooding (December to April) (Ramalho et al., 2009). The annual mean temperature is 29.5°C, varying by 1.8°C through the year (Ayres, 2006).

2.2 | Sampling

Fish larvae were captured in 16 georeferenced sampling stations (Figure 1), distributed as eight sampling points in middle Solimões River and eight sampling points in lower Japurá River, representing the different habitat types present, including mouths of lake channels (P1, P2, P9 and P10), "barrancos" (river reaches encased between high banks with relatively accelerated and turbulent flow and high erosion) (P3, P4, P11 and P12), sandbars (P5, P6, P13 and P14) and central channels of the two rivers (P7, P8, P15 and P16).

Sampling was conducted in 2011 during four phases of the hydrological cycle (flooding, high water, falling and low water). Samples were collected on the surface of the water and eight metres deep, during the day and at night, using a conical plankton net (300 µm mesh) which was moved horizontally through the water. A flowmeter was used to obtain the volume of filtered water. A total of 64 samples were collected for each phase of the hydrological cycle, totalling 256 samples at the end of the study.

During each sampling, the net was dragged for approximately 5 min by a boat moving at low speed against the current. All samples were preserved in formalin 10% and stored in labelled containers. Simultaneously, the limnological parameters, including the surface temperature of the water (°C), dissolved oxygen concentration (mg/L), electrical conductivity (µS/cm) and hydrogen-ionic potential (pH), were measured at the same sampling sites. All the measurements were taken using digital meters. Data on the pluviometric index and fluviometric level of the river were provided by the meteorological station of the Mamirauá Reserve, stored in the Mamirauá Institute data bank (http://www. mamiraua.org.br/fluviometrico).

All biological samples were examined in the laboratory, using a stereoscopic microscope. The larvae were quantified and identified based on their morphology, using the work of Araújo-Lima (1985) and Araújo-Lima and Donald (1988) as references. Individuals were separated according to their developmental stage (pre-flexion, flexion and post-flexion) according to the terminology of Nakatani et al. (2001).

2.3 | Data analyses

For distribution analyses, larvae were standardised to the volume of 10 m^3 of filtered water, following Tanaka (1973), and modified by Nakatani et al. (2001). A bifactorial ANOVA was used to examine for temporal variation of mean larval density (flood, high water, falling water and low water periods), spatial variation between rivers (Solimões and Japurá) and differences between habitats (mouths of lake channels, barrancos, sandbars and central channels of the rivers). Collecting stations and sampling times were used as parameters.

Mean densities were log-transformed for parametric tests (Peters, 1986). Tukey's *a posteriori* test was used whenever significant differences were found in the overall ANOVA, at $p < .05$. STATISTICA 7.0 was used for all analyses.

Distribution patterns were analysed according to the variation in species densities at the moment of collection and in the sampled habitats. These abundances were tested to examine the possible effects of abiotic parameters summarised using principal component analysis (PCA), using the software PC-ORD 5.21 (McCune & Mefford, 2006). All limnological data, except pH, were log-transformed. Pearson correlations based on the scores of the PCA axes were used to examine the effect of abiotic variables on larval distribution. Finally, Surfer 9.0 ® was used to create maps that show the spatial distribution of fish larvae.

3 | RESULTS

A total of 4322 Prochilodontidae larvae were collected during this study, with the highest density registered in the flood period (23.15 larvae/10 m^3 for the Solimões River). In the low water season, only 6.17 larvae/10 m^3 were recorded. The Japurá River showed an inverse pattern with peak density occurring in the low water season (29.89 larvae/10 m^3), with the density in the flood season at 21.25 larvae/10 m^3 (Figure 2). No Prochilodontidae larvae were caught during periods of high and falling water. The list of Characiformes larvae captured in the study area can be viewed in Supplementary Material (Table 1 - annex).

Higher densities of *S. taeniurus* larvae were observed in the flood period (21.78 larvae/10 m^3) than the low water period (9.39 larvae/10 m^3). This differed from the pattern for *P. nigricans*, which showed highest density in the low water period (16.19 larvae/10 m^3) than the flood period (12.03 larvae/10 m^3). There was a statistically significant difference in the mean density of larvae according to the period of the hydrological cycle (ANOVA; $F = 1.777$; $p = .01$). However, there was no significant difference according to type of habitat sampled (ANOVA; $F = 0.823$; $p = .31$).

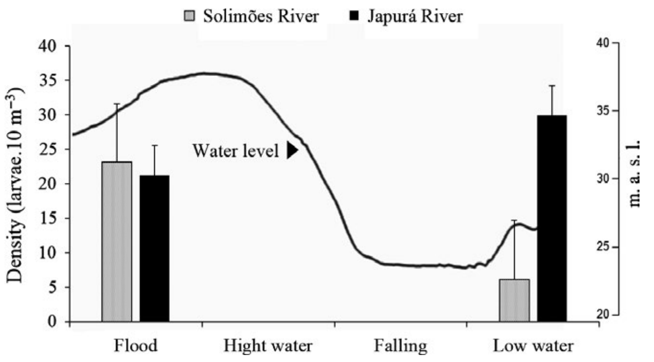

FIGURE 2 Mean density and standard error of Prochilodontidae larvae at different parts of the 2011 hydrological cycle, and water level variation, in the Solimões and Japurá rivers, Central Amazonia, Brazil. (m.a.s.l = metres above sea level)

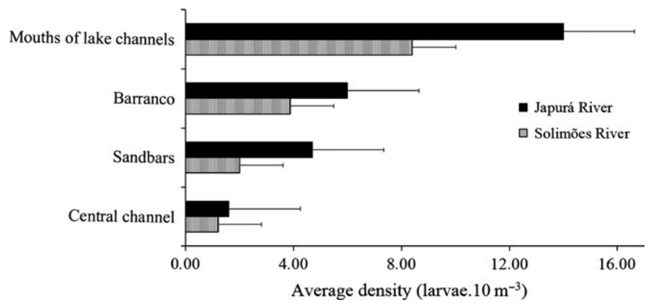

FIGURE 3 Mean distribution and standard error of Prochilodontidae larvae in different habitats along the Solimões and Japurá rivers, Central Amazonia, Brazil

In both rivers, individuals were captured in the larvae-yolk developmental stage and in the pre-flexion stage, a stage at which the larvae show pigmented eyes, mouth either formed or in the final stages of formation, vestigial or absent yolk sac, and well-developed pectoral fins (without rays) and embryonic fins. Larvae were not found at more advanced developmental stages (flexion and post-flexion).

Among the identified larvae, 76.3% (n = 3,297) occurred in the Japurá River and 23.7% (n = 1,025) in the Solimões River. Higher densities were found at stations at the mouths of lake channels and at barrancos than stations at sandbars and central channels of the rivers (Figure 3).

No significant differences were found among the habitats of the Solimões River (ANOVA; F = 3.73; p = .11), but significant differences were found for the Japurá River (ANOVA; F = 16.01; p = .01). The Tukey test showed that the areas around the mouths of lake channels had significantly higher larvae densities.

The larvae of *P. nigricans*, *S. insignis* and *S. taeniurus* exhibited broad spatial distribution and were captured at all sampling stations. The predominant larvae were jaraqui (64.5% of captured individuals). *S. taeniurus* occurred at higher density in the mouths of lake channels (P1–6.62 larvae/10 m^3 and P10–10.07 larvae/10 m^3), and barrancos (P3–2.86 larvae/10 m^3 and P12–3.40 larvae/10 m^3) in the sampled areas (Figure 4). However, high densities of *S. insignis* were restricted to areas at the mouths of lake channels (P1–6.65 larvae/10 m^3 and P10–4.90 larvae/10 m^3) in relation to the other sampling stations in both rivers (Figure 5).

The larvae of *P. nigricans* accounted for 35.5% of the samples, with 1,534 individuals captured. They showed a distribution like those of other prochilodontids, also occurring at the mouths of lake channels, especially P2 (3.35 larvae/10 m^3), which is located at the junction of both rivers (Figure 6).

The only limnological parameters that showed any variation were conductivity and pH, which were lower in the Japurá River than in the Solimões River (Table 1).

The first two axes of the principal component analysis (PCA) with the environmental variables explained 99.4% of variation in the data. Water temperature and dissolved oxygen were positively correlated to PC1. Electric conductivity, fluviometric level and pluviometric index were positively correlated with PC2, while pH was negatively correlated (Table 2).

In the second axis, there was a longitudinal gradient between the *S. taeniurus* larvae with areas around the mouths of lake channels in both rivers during the flood period correlated with the electric conductivity and fluviometric level and pluviometric index (Figure 7). *S. insignis* and *P. nigricans* larvae were more correlated with habitats at the mouths of lake channels and barrancos on the shore of the Japurá River in the low water period, influenced by dissolved oxygen and water temperature. pH was not associated specifically with species group or habitat.

TABLE 1 Minimum and maximum values of limnological parameters measured in different habitats along the Solimões and Japurá rivers, during the study period

	Solimões River				Japurá River			
HABITATS	T°	OD	Cond.	pH	T°	OD	Cond.	pH
Mouth of lake channel	28.03–30.78	2.28–5.84	90–143	6.93–7.53	27.20–30.12	2.13–6.10	43–92	6.78–7.40
Barranco	28.10–29.79	4.40–6.86	129–138	7.10–7.65	28.87–30.45	4.68–6.80	40–91	6.90–7.40
Sandbars	28.10–29.71	2.35–6.20	115–129	7.09–7.60	28.53–29.05	3.93–6.57	44–91	7.00–7.40
Central channel	27.96–29.40	2.59–6.70	86–130	7.09–7.63	27.35–27.78	3.08–7.19	38–91	6.78–7.30

T°= water temperature (°C), OD= dissolved oxygen (mg/L), Cond.= conductivity (µS/cm) and pH.

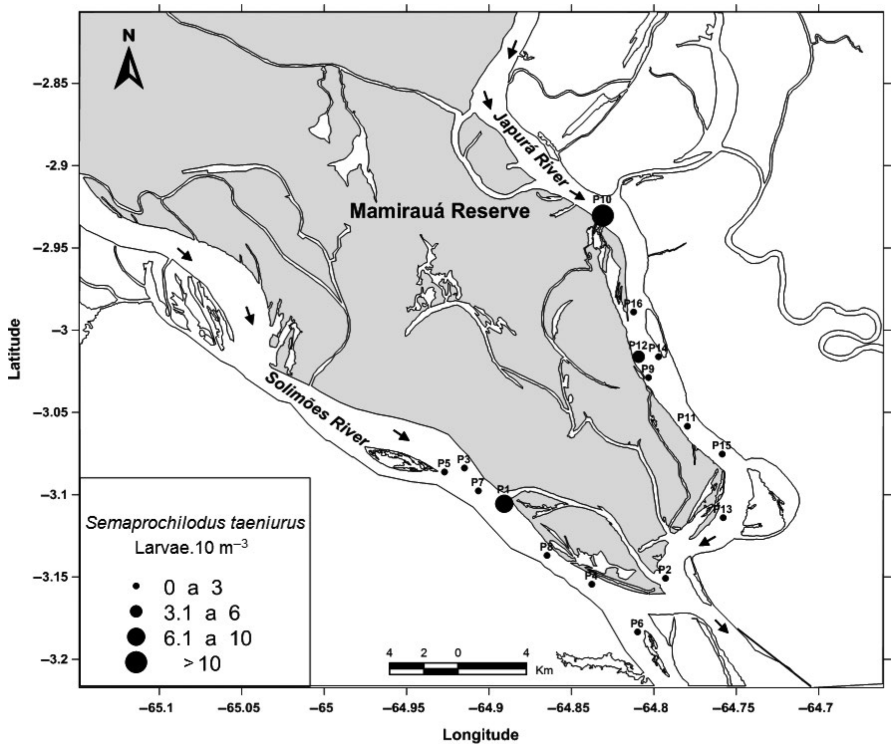

FIGURE 4 Spatial distribution of *S. taeniurus* larvae in habitats present along the Solimões and Japurá rivers, Amazonia

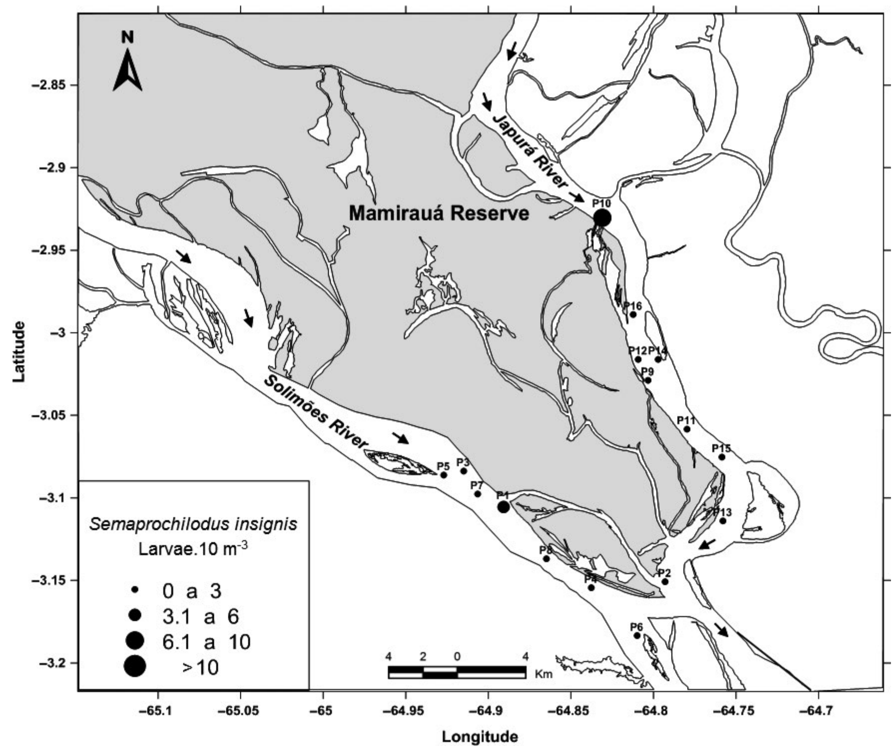

FIGURE 5 Spatial distribution of *S. insignis* larvae in habitats present along the Solimões and Japurá rivers, Amazonia

4 | DISCUSSION

The abundance of Prochilodontidae larvae in the samples confirms the planktonic habits of these species and their dispersion in white water rivers. Other studies (Leite et al., 2006; Sánchez-Botero & Araújo-Lima, 2001) reported the occurrence of larval and immature individuals colonising lakes, channels and floating meadows in várzea habitats during the flood period. Together with these results, these observations indicate that the larvae and adults of these species occupy diverse habitats and water bodies at different stages of their life cycle.

Several studies in Central Amazonia found that the regulation of fish biological cycles, their gonadal development and their reproduction are related to fluctuations in water level, which is considered

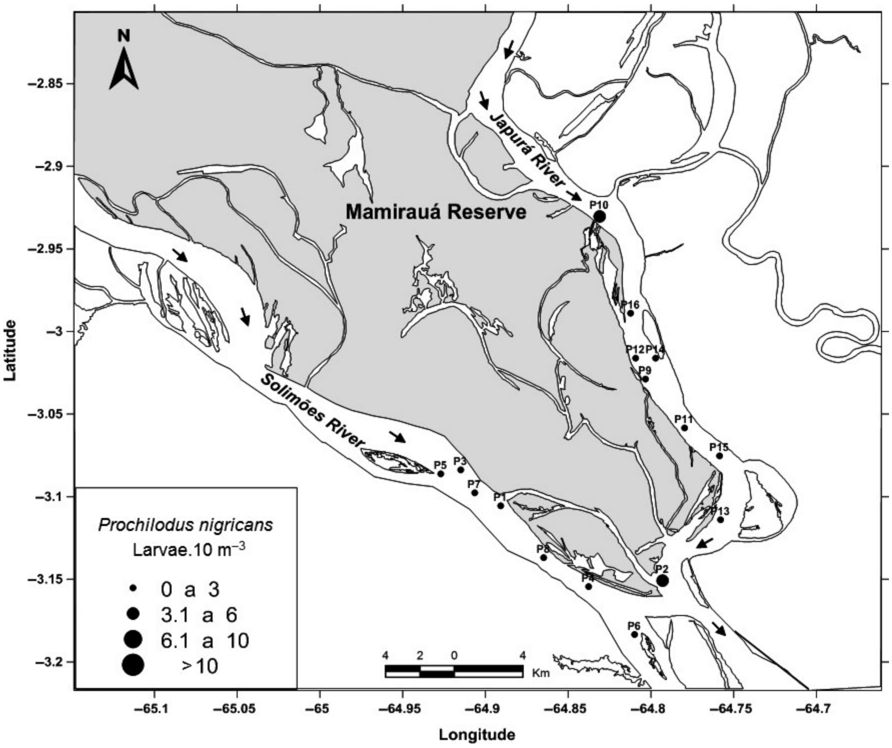

FIGURE 6 Spatial distribution of curimatá (*P. nigricans*) larvae in the habitats present along the Solimões and Japurá rivers, Amazonia

TABLE 2 Results of principal component analysis (PCA) applied to summarise the environmental and biological variables obtained in the moments of the hydrologic cycle and points of collection during the year 2010, in the Central Amazon

Variables	PC1 (86.57%)	PC2 (12.86%)
Fluviometric level	−0.130	0.457
Pluviometric index	−0.130	0.457
Water temperature	0.292	−0.256
Dissolved oxygen	0.215	−0.257
pH	−0.108	−0.475
Electric conductivity	−0.139	0.439
S. taeniurus	0.945	−0.317
S. insignis	0.985	−0.144
P. nigricans	0.857	0.515

the most important stimulus for spawning (Lowe-McConnell, 1999; Santos, 1982). These phenomena are usually linked to the beginning of the rainy season and the inundation period, which lead to high food availability and, consequently, favour the survival and development of larvae and juveniles (Leite et al., 2006; Lowe-McConnell, 1999; Menezes & Vazzoler, 1992). While the larvae have yolk sacs, they are transported by currents in the main river channels until they are carried to the várzea areas, where they obtain their first exogenous food source (Leite & Araújo-Lima, 2002).

The low occurrence of the yolk sac larvae in this study was possibly because that this is the shortest larval developmental stage, occurring soon after spawning and hatching. However, the presence of this stage, together with the high abundance of larvae in the pre-flexion stage, suggests that the sampling areas were located near reproductive sites. Therefore, the shores and flooded marginal areas of the Solimões and Japurá rivers can be characterised as areas of retention and growth for the early stages of these species of fish. These data indicate the occurrence of reproductive activities along these rivers, highlighting the importance of these habitats in the maintenance of natural fish stock and the importance of management actions for such sites.

The high abundance of larvae captured during rising water can be interpreted as evidence of the reproduction season of these species, as the curimatás (*P. nigricans*) and the jaraquis (*S. insignis* and *S. taeniurus)* are species that only migrate for short distances for reproduction. They initiate their gonadal maturation process when water levels in the rivers start to rise, and wait for the first rains to disperse along the várzea tributaries and lakes to spawn in the nutrient-rich, white water rivers of the Solimões/Amazonas basin (Barthem & Fabré, 2004; Batista & Lima, 2010; Ribeiro & Petrere, 1990; Vieira, Fabré, Sousa & Araújo, 2002). Other authors such as Junk et al. (1989), Humphries, King and Koehn (1999) and Leite and Araújo-Lima (2002) emphasise that rising water levels allow for the expansion of the aquatic environment and permit access to specific foraging, reproductive and growth sites, thus favouring larval development.

Undoubtedly, newly inundated várzea areas allow for better growth conditions and increase the probability of larval survival (Leite & Araújo-Lima, 2002; Leite et al., 2006; Mounic-Silva & Leite, 2013). The higher number of Prochilodontidae larvae captured in the Japurá River may be related to the geomorphological characteristics of this tributary, which presents a complex mosaic of water bodies with many "furos" (channels that interconnect with the internal bodies of water of the várzea) which make these mosaics excellent environments for larval development.

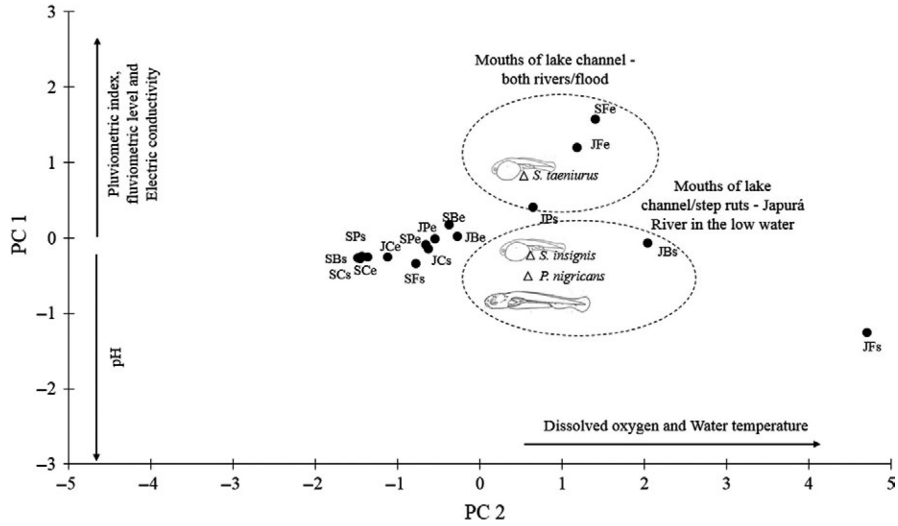

FIGURE 7 Principal component analysis of physical and chemical parameters and sampling locations and larval density. (J) Japurá River, (S) Solimões River, (F) mouths of lake channel, (B) barrancos, (P) sandbars, (C) central channels rivers, (e) flood and (s) low water

The high densities of larvae in areas at the mouths of lake channels and barrancos are consistent with the results of Oliveira and Araújo-Lima (1998) and Oliveira (2000). These authors also found a higher quantity of Characiformes larvae by the shores, and a lower density in the central channel of the Amazon River. This distribution pattern seems to be linked to trophic aspects of rivers and is common to this group. Leite and Araújo-Lima (2002) found the highest concentrations of larvae containing food in their digestive tracts in areas of recent inundation, where food is abundant. These areas normally occur in the mouth of the channels that connect lakes to rivers, as well as by the river shores, during the first months of inundation.

The concentration of the larvae at the mouths of lake channels and barrancos may also be associated to the reproductive strategies of these species. Large schools of adult *Semaprochilodus* spp. are reported to undertake extensive migrations in the Negro River, the largest black water tributary in the Amazon basin, for spawning at the junction of Solimões/Amazonas (Ribeiro & Petrere, 1990). Vieira et al. (2002) also observed this pattern and identified the spawning habitats of jaraquis in several rivers of the Amazonian region, such as mouth of streams (black water emptying into white water rivers), the mouth of rivers (junctions of small black water rivers and white water rivers) and lake channels (habitats that connect the lake water to white water rivers).

The physiochemical factors recorded here are consistent with the results of Affonso, Queiroz and Novo (2011) for several water bodies at the same area. These authors found that the Japurá River exhibits lower conductivity, temperature, turbidity and pH when compared to the Solimões River, but higher dissolved oxygen, particularly during the low water period.

The areas at the mouths of lake channels and barrancos, where larvae were concentrated, also had the highest values of dissolved oxygen and conductivity, as well as higher temperature at the time of lowest fluviometric levels. There is a close relationship between environmental factors (temperature, dissolved oxygen, pH, electric conductivity, nutrient availability and photoperiod) and the spatio-temporal distribution of fish eggs and larvae, as shown in other studies, such as those by Ziober, Bialetzki and Matheus (2012), Lopes, Garcia, Reynalte-Tataje, Zaniboni-Filho and Nuñer (2014), Ponte et al. (2016), Suzuki and Pompeu (2016), Zacardi and Ponte (2016) and Chaves et al. (2017). The seasonal variation in these environmental factors is probably what leads to more favourable conditions for spawning, survival and larval development (Baumgartner, Nakatani, Gomes, Bialetzki & Sanches, 2008).

However, Fisher (1978) and Forsberg, Devol, Richey, Martinelli and Santos (1988) reported that variations in dissolved oxygen, temperature, electric conductivity and pH are probably secondary factors in the effective spawning that occurs in the flooding period in the main channel of the Amazon River, due to its stable temperature and oxygen conditions. Other variables such as food availability, predation and competition (Harvey, 1991; Pavlov, Mikheev, Lupandin & Skorobogatov, 2008; and even adult foraging strategies (Reynalte-Tataje, Nakatani, Fernandes, Agostinho & Bialetzki, 2011) also are among those that may affect larval spatio-temporal distribution.

The highest density of organisms occurred when several biotic and abiotic factors acted together to favour the natural sequence of processes that lead to spawning, hatching, larval dispersal and larval maturation. The volume of larvae captured at the mouths of lake channels, near the Mamirauá Reserve, indicates that these habitats are areas of colonisation and dispersal for the initial phases of *P. nigricans*, *S. insignis* and *S. taeniurus*. They originate from reproductive sites along the Solimões and Japurá rivers at the start of the flooding period and end of the low water period. This confirms the relevance of these habitats and the importance of preserving them as protected areas. These are important sites for the conservation, preservation and maintenance of these fishery resources that are highly utilised in Central Amazonia.

ACKNOWLEDGMENTS

The authors thank the Mamirauá Institute for Sustainable Development (MISD) for financial support, and the Laboratory of Biology and Aquatic Organisms (LABIO-UFPA) and the Ichthyoplankton Ecology Laboratory (LEI-UFOPA) for technical support. We thank Dr. Andréa Bialetzki and Dr. Rosseval Galdino Leite for their help in identifying the collected material. Finally, we thank our field assistants, Jonas Oliveira Martins and Franciney Martins for their support during field collections, and the staff at the logistical section of MISD.

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How to cite this article: Zacardi DM, Bittencourt SCS, Nakayama L, Queiroz HL. Distribution of economically important fish larvae (Characiformes, Prochilodontidae) in the Central Amazonia, Brazil. *Fish Manag Ecol*. 2017;00:1–9. https://doi.org/10.1111/fme.12222