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Spatial and seasonal variability of ichthyoplankton in the middle Solimões and lower Japurá rivers, Central Amazon, Brazil

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Abstract. This study aimed to evaluate the spatial and seasonal variability of ichthyoplankton, in addition to verifying the predominant composition and reproductive strategy of the species identified in the middle Solimões and lower Japurá rivers, in the vicinity of the Mamirauá Sustainable Development Reserve - MSDR, Central Amazon. The collections were carried out in different habitats (mouth of lake channels, ravines, sandbanks and main channel of rivers), in day and night sampling cycles using subsurface and midwater trawls (eight meters deep). Larvae of several migratory and commercially important fish species were recorded, such as *Semaprochilodus* spp. 'jaraquis', *Brycon amazonicus* 'matrinxã', *Prochilodus nigricans* 'curimatá', *Mylossoma* spp. 'pacus', *Triportheus auritus* ‘long sardine’, *Plagioscion squamosissimus* 'pescada branca', catfish of the *Brachypatystoma* spp. genus, *Pseudoplatystoma* spp. and *Calophysus macropterus* 'piracatinga', among many curimatids 'branquinhas', hemiodontids 'charutinhos' and anostomids 'aracus and piaus', predominantly individuals in the preflexion phase. A spatial distribution pattern was found, in which the larvae of Characiformes were abundant near the margin, mainly in areas near the mouths of lake channels, while the Siluriformes were predominant in the main channel of the two rivers. There was no variation in the distribution of fish eggs and larvae between the analysed rivers, sampling periods (day and night) and strata of the water column (subsurface and midwater). Nonetheless, there was hidrological seasonality among the habitats. MSDR and its diversity of environments (coves, sandbanks, lakes, channels, holes, floating herbs, flooded forest) are suitable places for reproduction and initial development of various species of Amazonian fish.

Key words: Fish larvae, Hidrologic seasonality, Mamirauá reserve, Nursery, Varzea.

Resumo: **Variabilidade espacial e sazonal do ictioplâncton no médio rio Solimões e baixo rio Japurá, Amazônia Central, Brasil.** Este estudo teve como objetivo avaliar a variabilidade espacial e sazonal do ictioplâncton, além de verificar a composição e a estratégia reprodutiva predominante das espécies identificadas no trecho médio do rio Solimões e baixo rio Japurá, no entorno da Reserva de Desenvolvimento Sustentável Mamirauá - RDSM, na Amazônia Central. As coletas foram realizadas em diferentes habitats (desembocaduras de canais, áreas de barrancos, bancos de areia e no canal central dos rios), em ciclos de amostragem diurno e noturno por meio de arrastos subsuperficiais e de meia-água (oito metros de profundidade). Foram registradas larvas de diversas espécies de peixes migradores e de importância comercial, com predominância de indivíduos em fase de pré-flexão. Foram registradas larvas de diversas espécies de peixes migradores e de importância comercial, tais como *Semaprochilodus* spp. (jaraquis), *Brycon amazonicus* (matrinxã), *Prochilodus nigricans* (curimatá), *Mylossoma* spp. (pacus), *Triportheus auritus* (sardinha comprida), *Plagioscion squamosissimus* (pescada branca), bagres do gênero *Brachypatystoma* spp., *Pseudoplatystoma* spp. e *Calophysus macropterus* (piracatinga), além de diversos curimatídeos (branquinhas), hemiodontídeos (charutinhos) e anostomídeos (aracus e piaus), com predominância de indivíduos em fase de pré-flexão. Verificou-se um padrão distribuição espacial de larvas no qual o grupo dos Characiformes foi abundante nas margens, principalmente em áreas próximas as desembocaduras de canais de lago, enquanto o grupo dos Siluriformes foi predominante no canal central dos dois rios. Não foi registrada variação na distribuição da abundância de ovos e larvas entre os rios analisados, turnos de amostragem (diurno e noturno) e estratos da coluna d’água (subsuperfície e meia-água), entretanto foram constatadas entre os habitats e a sazonalidade hidrológica. A RDSM e sua diversidade de ambientes (enseadas, bancos de areia, lagos, canais, furos, herbáceas flutuantes, floresta alagada) constituem locais adequados para reprodução e desenvolvimento inicial de várias espécies de peixes amazônicos.

Palavras-chave: Larvas de peixes, Sazonalidade hidrológica, Reserva Mamirauá, Berçário, Várzea.

Introduction

The Amazon has extensive wetlands that present a high biological productivity and generate high fish biomass, representing one of the most important environments of the Amazon basin for continental fishing that is practiced in various environments, such as lakes, lowland channels and in the river channel (Isaac *et al.* 2016, Goulding *et al.* 2019, Zacardi 2020). In this context, the Mamirauá Sustainable Development Reserve (MSDR), located at the confluence of the Solimões and Japurá rivers, is the largest Brazilian protected area dedicated to exclusively protecting the Amazon floodplain environment, consisting of an area of approximately 1,124,000 hectares of flooded forests (Queiroz 2005). An environment of great importance both in ecological and socioeconomic terms, and extensive ecosystem services that deserve special attention and conservation of biodiversity in the region (Moura *et al.* 2016, Lima & Peralta 2017, Valsechi *et al.* 2017, Zacardi *et al.* 2020a).

The studies on the dynamics of ichthyofauna in the Mamirauá Reserve, overall, suggest that many species have a lacustrine habit and/or have a known association of parts of their life cycle with flooded environments (Queiroz & Camargo 2008, Castello, 2008a, b, Zacardi *et al.* 2020a). The hydrological seasonality is the key factor that significantly acts on the organization of fish communities (Chaves *et al.* 2008, Queiroz *et al.* 2010, Zacardi 2014, Bittencourt *et al.* 2020). However, there is still a lack of information on the ecology of the early stages of the life cycle of the vast majority of the species in the region. Besides, there is a lack of data to support estimates on the maintenance of the balance of natural stocks, which depend primarily on the integrity of spawning, development and growth areas for individuals, as well as knowledge about the distribution and dispersion of fish eggs and larvae.

The main ecological dynamics of the floodplain is the "flood pulse", i.e. the annual expansion of water bodies, integrating the natural fields and forests in the aquatic ecosystem (Garcez *et al.* 2010, Junk *et al.* 2012, Wittmann & Junk 2016). Most freshwater fish species perform annual reproductive migrations and total spawn in the period of rising waters. This alternation of the hydrological regime is one of the factors that influences the reproductive processes of fish and dispersion of eggs and larvae, altering the composition and abundance according to seasonal and spatial changes (Ponte *et al.* 2016, 2017, Zacardi *et al.* 2017A, c, Ponte *et al.* 2019, Chaves *et al.* 2019).

Overflow allows the offspring to access new habitats, offering various environments for foraging, protection and survival of larvae and development of fish juveniles during the flood period (Mounic-Silva & Leite 2013, Pinheiro *et al.* 2016, Zacardi *et al.* 2019, 2020a, Cajado *et al.* 2020a, Oliveira *et al.* 2020), especially those of greatest economic importance (Ponte *et al.* 2016, Zacardi *et al.* 2017a, Carvalho *et al.* 2018). Thus, the understanding of these processes together with the development of ichthyoplankton studies provide evidence about the period and location of spawning, nursery and recruitment areas (Suzuki *et al.* 2009, Oliveira *et al.* 2015, Zacardi *et al.* 2017a, Mounic-Silva *et al.* 2019).

Currently, the pressure on the middle Solimões river on fishery resources of great economic importance such as migratory fish (Batista *et al.* 2012), the high consumption of fish carried out by local populations (Ferraz *et al.* 2012, Ferraz & Barthem 2016) and the numerous environmental changes of local and regional scale, such as deforestation and hydroelectric constructions, cause significant losses of habitats that are essential for feeding, spawning and growth (Arantes *et al.* 2017, Castello *et al.* 2017, Lopes *et al.* 2020, Vasconcelos *et al.* 2020). Therefore, the lowland of the Mamirauá Reserve is an essential alternative for the conservation and preservation of several species, preventing the collapse in natural stocks, besides being responsible for ensuring food security and local economic development. Thus, the aims of this work were to identify the composition, to determine the abundance, and to evaluate the spatial and seasonal variation of the ichthyoplankton community in different habitats found in the middle Solimões and lower Japurá rivers, a region adjacent to the Mamirauá Sustainable Development Reserve, in Central Amazon.

Material and Methods

The study was carried out during four phases of the hydrological cycle of 2011 (rising waters, full flood, receding waters and drought), in 16 stations: mouth of lake channels (P1, P2, P9 and P10), ravines (P3, P4, P11 and P12), sandbanks (P5, P6 , P13 and P14) and main channel of rivers (P7, P8, P15, and P16), located in the middle stretch of the Solimões and lower Japurá rivers, and distributed around the Mamirauá Sustainable Development Reserve - RDSM (03°08'S, 64°45'W and 2°36'S, 67°13'W) in the state of Amazonas, Central Amazon (Fig.1).

This area has hydrodynamics marked by the flood pulse, with four well-defined seasonal phases rising waters (December to April), full flood (May to mid-July), receding waters (mid-July to September) and drought (September to November) (Ramalho *et al.* 2009). It has an average flood range in the region around 10.8 m (Wittmann *et al.* 2004, Affonso *et al.* 2011). This change in water level is probably the most important of the environmental changes in the region, affecting the life cycle of local fauna and flora, as well as human activities (Queiroz 2005, Moura *et al.* 2016).

The marginal regions of these two rivers are prone to periodic floods, the intensity varies according to the annual cycles of rainfall, which reach a mean of approximately 2,850 mm. Most of the precipitation is concentrated between January and April, but, so far, no month has been observed with precipitation below 60 mm or above 450 mm. The climate in the region is hot and humid, with the highest temperatures reached in the dry months - October and November - with monthly mean ranging from 30º to 33ºC, during this moment beaches and sandbanks are formed along the banks and in the gutter main of the middle Solimões river and low Japurá. The average minimum temperatures range between 21º and 23ºC (INMET 2012, Aleixo & Silva Neto 2015, 2019). In the rising waters, there is a greater amount of rainfall and smaller thermal amplitude. In the receding waters, this amplitude increases, reaching higher levels in the drought, when the lowest rates of monthly precipitation are also recorded (SCM 1996).

The captures occured during day and night, by horizontal trawling in two strata of the water column (subsurface and midwater - approximately 8 m), using conical-cylindrical plankton nets (300 µm mesh), with a coupled flowmeter. For the depth sampling the net was equipped with a manual system to open and close at the bottom of the river, stabilized by a depressor weighing 20 kg and vertically pulled. All biological material sampled was submitted to benzocaine (250 mg/L) and then fixed in a formalin solution at 10%, packed in 500 mL polyethylene containers, properly labeled and transported for laboratory analysis. In the laboratory, ichthyoplankton was sorted, quantified and the larvae identified, at the lowest possible taxonomic level, based on morphological, meristic and morphometric characteristics, using specialized bibliography: Araújo-Lima (1985); Araújo-Lima and Donald (1988); Nascimento and Araújo-Lima (1993); Araújo-Lima *et al.* (1993); Araújo-Lima (1994); Nascimento and Araújo-Lima (2000); Nakatani *et al.* (2001); Leite *et al.* (2007); Oliveira *et al.* (2008) and Orsi *et al.* (2016). Moreover, some species identification was confirmed by experts. The taxonomic framework was based on Nelson *et al.* (2016), for orders and families, except in Characiformes in which the classification of Oliveira *et al.* (2011) was used, in alphabetical order of genera and species.

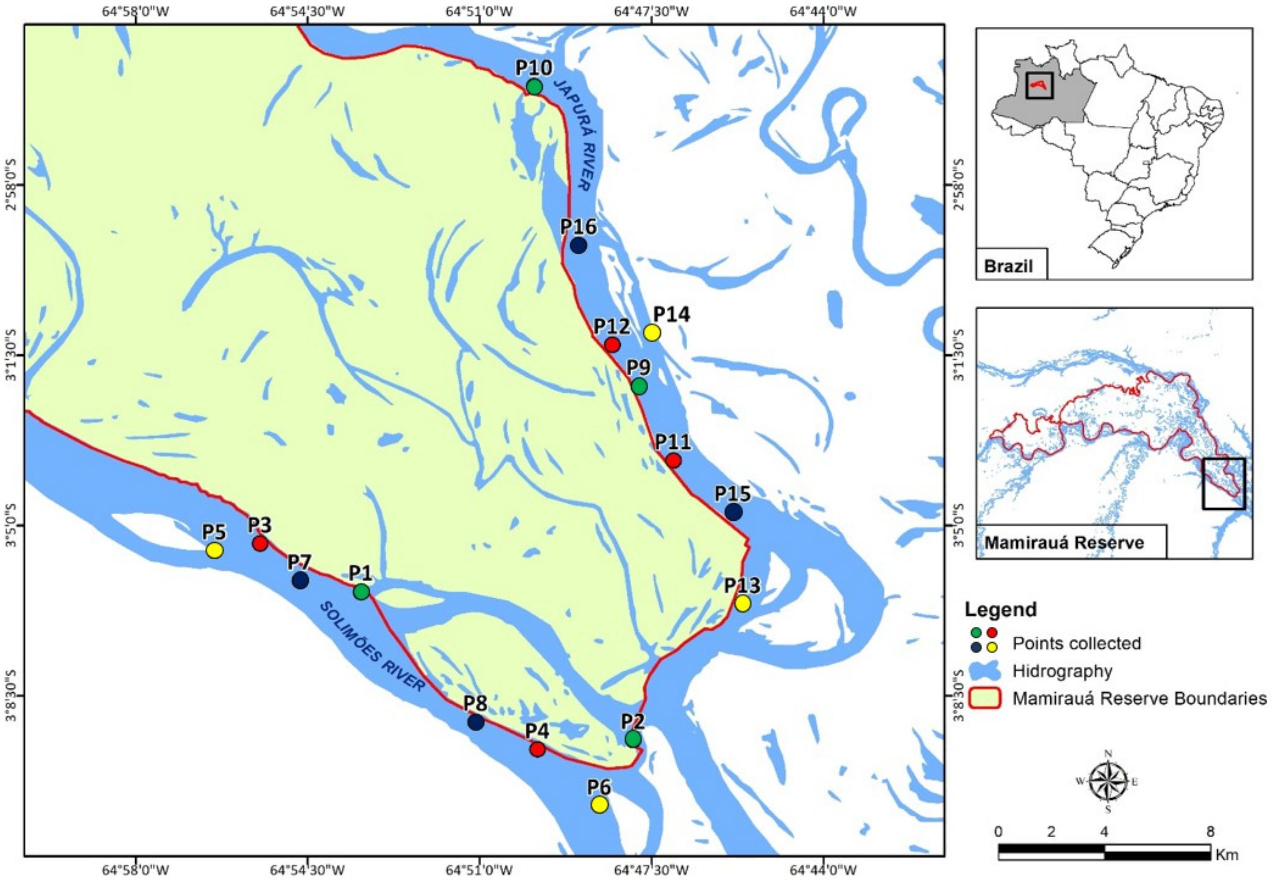

Figure 1. Location of the study area, highlighting the sampling stations distributed in the middle stretch of the Solimões and lower Japurá rivers, in sites near the mouth of lake channels (Green circles: P1, P2, P9 and P10), ravines (Red: P3, P4, P11 and P12), sandbanks (Yellow: P5, P6, P13 and P14) and main channel of rivers (Blue: P7, P8, P15 and P16), around the southeast portion of the Mamirauá Sustainable Development Reserve, Central Amazon, Brazil.

Four stages of larval development were established for classification of the analyzed material: (i) yolk-sac, (ii) preflexion, (iii) flexion, and (iv) postflexion, according to the terminology described by Nakatani *et al.* (2001). Individuals with damaged structures, or in very early stage of development, were classified as unidentified. For the classification of the species regarding their reproductive strategy, the works of Barthem and Fabré (2004), Granado-Lorencio *et al.* (2005), Soares *et al.* (2008) and Neuberger (2010) were used, which group the species into large comprehensive categories, such as M (= migratory) and NM (= non-migratory) according to the stage of gonadal maturation, relative fecundity, oocytes diameter, duration of reproductive period and migratory behavior of species.

The abundance of captured eggs and larvae was standardized to $10m^{-3}$ of filtered water, according to Nakatani *et al.* (2001). The assumptions of normality (Shapiro-Wilk test) and homocedasticity (Levene test) were not met and, therefore, only non-parametric analyzes were adopted. To verify significant differences in the density of eggs and larvae (response variable) due to (1) the of rivers (Solimões and Japurá rivers), (2) habitats (mouth of lake channels, ravines, sandbanks and main channel of rivers), (3) periods (daytime and nighttime), (4) water column strata (subsurface and midwater) and (4) hydrological phases (rising waters, full flood, receding waters and drought) - considered as predictor variables, Kruskal-Wallis analyss was performed. Dunn test was applied *a posteriori* to detect the differences ($p < 0.05$). All analyzes were performed using R Statistic version 4.0.1 software.

Results

During the study period, 1,050 eggs were captured in cleavage and initial embryo phases, with high relative abundance recorded for the Japurá river (64%), when compared to the Solimões river (36%). Regarding larvae, the middle stretch of the Solimões river recorded 28,362 individuals and lower Japurá river recorded 48,888, totaling 77,250 fish larvae captured and classified in seven orders, 21 families, 33 genera and 43 species (Table I). Of the species total, 76% were classified as reproductive migratory, and about 70% are of commercial interest in the middle Solimões region. Unidentified individuals accounted for 2.63% of the collected material.

Table I - Classification and mean density (individual.$10m^{-3}$) of fish larvae captured in the different habitats in the middle Solimões and lower Japurá rives, surrounding the Mamirauá Sustainable Development Reserve in the Central Amazon, Brazil. **N** = total number of individuals, **CI** = X - commercial importance and (*) high importance, **RS** = reproductive strategy (M = migratory and NM = non-migratory), **A** = mouths of lake channels, **B** = ravines, **C** = sandbanks e **D** = main channel of rivers.

Higher taxa and species	N	CI	RS	Solimões River				Japurá River			
				A	B	C	D	A	B	C	D
Beloniformes											
Belonidae											
Strongylura timucu (Walbaum, 1792)	1		NM	-	-	-	-	-	-	-	< 0.01
Clupeiformes	347			0.06	0.26	0.06	-	0.41	0.28	0.14	< 0.01
Engraulidae	259			0.06	< 0.01	< 0.01	< 0.01	0.13	0.07	0.14	0.03
Pristigasteridae											
Pellona spp.	1499		M	0.40	0.32	0.14	0.06	1.05	0.82	0.80	0.07
Characiformes	6082			1.01	0.75	0.98	4.14	2.41	1.27	1.11	1.47
Anostomidae	4434			1.15	1.05	0.81	0.59	4.06	1.22	2.14	0.10
*Rhytiodus microlepi*s Kner, 1858	37		M	0.02	0.04	< 0.01	0.02	0.03	< 0.01	< 0.01	-
Characidae	3			-	-	-	-	< 0.01	-	< 0.01	-
Brycon amazonicus (Spix; Agassiz, 1829)	296	X*	M	0.11	0.24	0.09	0.04	0.10	0.10	0.08	0.02
Serrasalmidae											
Colossoma macropomum (Cuvier, 1817)	3	X*	M	< 0.01	-	-	< 0.01	-	-	-	-
Mylossoma aureum (Spix; Agassiz, 1829)	1383	X	M	1.42	0.59	0.21	0.01	0.53	0.39	0.33	0.02
Mylossoma albiscopum (Cuvier, 1817)	9591	X*	M	3.87	3.76	2.27	0.69	6.50	3.80	4.66	0.22
Myleus sp.	3			-	< 0.01	-	< 0.01	-	-	-	-
Triportheidae											
Triportheus auritus (Günther, 1864)	1410	X*	M	1.06	1.32	0.11	0.06	0.42	0.63	0.19	< 0.01
Triportheus spp.	7407	X	M	6.70	2.53	0.71	0.36	3.42	3.16	2.33	0.07
Cynodontidae											
Cynodon gibbus (Agassiz,1829)	2		M	-	-	-	-	< 0.01	< 0.01	-	-
Hydrolycus cf. *scomberoides* (Cuvier, 1819)	267		M	0.20	0.28	0.09	0.04	0.11	0.06	0.04	0.01
Raphiodon vulpinus Agassiz, 1829	79		M	0.02	0.04	0.07	0.03	0.02	0.02	0.04	0.01
Curimatidae	711			0.06	0.41	0.04	< 0.01	0.54	0.21	1.15	0.01
Potamorhina altamazonica (Cope, 1878)	4280	X*	M	2.32	1.06	3.33	2.94	1.29	0.85	1.79	0.18
Potamorhina latior (Spix; Agassiz, 1829)	783	X*	M	1.05	1.50	0.12	< 0.01	0.17	< 0.01	< 0.01	0.04
Psectrogaster amazonica Eigenmann; Eigenmann, 1889	24658	X	M	7.07	9.40	7.90	4.60	19.09	5.64	17.97	0.59
Psectrogaster rutiloides (Kner, 1858)	7	X	M	-	-	-	-	0.02	-	-	-
Erythrinidae											
Hoplias cf. *malabaricus* (Bloch, 1794)	4	X	NM	-	-	< 0.01	-	< 0.01	-	-	< 0.01
Hemiodontidae	2807		NM	1.26	0.99	0.18	0.03	3.52	1.07	0.78	0.04
Prochilodontidae	23			-	-	0.01	-	0.02	-	-	-
Prochilodus nigricans Agassiz, 1829	1525	X*	M	0.29	0.28	0.25	0.04	0.60	0.28	0.26	0.04
Semaprochilodus insignis (Jardine; Schomburgk, 1841)	1213	X*	M	0.67	0.15	0.09	0.03	0.67	0.15	0.09	0.03
Semaprochilodus taeniurus (Valenciennes, 1817)	1574	X*	M	0.87	0.43	0.22	0.09	1.34	0.60	0.39	0.04
Perciformes											
Eleotridae											
Mycrophilypnus amazonicus (Myers, 1927)	52		NM	-	0.08	0.01	0.01	0.01	0.01	0.01	< 0.01
Sciaenidae											
Plagioscion squamosissimus (Hechel, 1840)	1810	X*	NM	0.22	0.35	0.21	0.54	0.54	0.22	0.32	0.42
Pachypops fourcroi (Lacepède, 1802)	7		NM	-	-	-	-	-	0.01	-	-
Pleuronectiformes											
Achiridae											
Hipoclinemus mentalis (Günther, 1862)	2		NM	-	-	-	-	< 0.01	-	< 0.01	-
Siluriformes	215			-	0.08	0.07	0.06	0.13	0.02	-	0.09
Auchenipteridae	338			0.08	0.12	0.09	0.15	0.18	0.05	0.02	0.18
Trachelyopterus galeatus (Linnaeus, 1766)	1		NM	< 0.01	-	-	-	-	-	-	-
Tatia sp.	1		NM	-	-	-	-	-	-	-	< 0.01
Cetopsidae											
Cetopsis coecutiens (Lichtenstein, 1819)	35		NM	0.02	0.02	< 0.01	0.04	0.01	0.01	< 0.01	< 0.01
Doradidae	10			-	-	-	-	0.01	< 0.01	-	< 0.01
Pimelodidae	354		-	0.07	0.15	0.05	0.08	0.07	0.06	0.04	0.08
Brachyplatystoma spp.	136	X	M	0.09	0.20	0.01	0.04	0.04	0.02	< 0.01	0.02
Brachyplatystoma filamentosum (Lichtenstein, 1819)	243	X	M	0.10	0.04	0.05	0.30	0.07	< 0.01	-	0.07
Brachyplatystoma juruense (Castelnau, 1855)	186	X	M	0.05	0.07	0.05	0.13	0.03	0.01	-	0.03
Brachyplatystoma tigrinum (Britski, 1981)	7	X	M	-	0.02	-	< 0.01	< 0.01	-	-	< 0.01
Brachyplatystoma rousseauxii (Castelnau, 1855)	12	X*	M	0.01	-	< 0.01	< 0.01	-	-	-	-

Higher taxa and species	N	CI	RS	Solimões River				Japurá River			
				A	B	C	D	A	B	C	D
Brachyplatystoma vailantii (Valenciennes, 1840)	3	X	M	-	< 0.01	-	-	-	-	-	< 0.01
Calophysus macropterus (Lichtenstein, 1819)	2	X*	M	-	-	-	-	-	< 0.01	-	-
Hypophthalmus edentatus Spix; Agassiz, 1829	27	X*	M	0.01	< 0.01	-	< 0.01	< 0.01	< 0.01	0.03	< 0.01
Hypophthalmus fimbriatus (Schneider, 1783)	433	X*	M	0.13	0.12	0.02	0.11	0.14	0.21	0.04	0.10
Hypophthalmus marginatus Valenciennes, 1840	477	X*	M	0.08	0.06	0.01	0.05	0.07	0.06	0.04	0.22
Paulicea luetkeni (Steindachner, 1875)	1		M	-	-	-	-	-	-	-	< 0.01
Platynematichthys notatus (Schomburgk, 1841)	16	X	M	0.01	-	-	< 0.01	< 0.01	-	< 0.01	< 0.01
Pimelodus gr. *blochii* (Valenciennes, 1840)	459	X*	-	0.22	0.50	0.07	0.11	0.12	0.17	0.06	0.07
Pinirampus pirinampu (Spix, 1829)	5		M	-	-	-	-	-	0.04	-	-
Pseudoplatystoma punctifer (Castelnau, 1855)	248	X*	M	0.26	0.11	0.22	0.58	0.01	0.01	0.05	0.04
Pseudoplatystoma tigrinum (Valenciennes, 1840)	136	X*	M	0.21	0.01	-	0.09	< 0.01	-	< 0.01	< 0.01
Sorubim lima (Bloch; Schneider, 1801)	83	X	M	0.03	0.04	0.02	0.05	0.04	< 0.01	0.02	0.01
Trycomycteridae	2		-	< 0.01	-	-	-	-	-	-	-
Tetraodontiformes											
Tetraodondidae											
Colomesus asellus (Müller; Troschel, 1848)	45		NM	0.01	0.02	0.01	-	0.03	0.04	0.04	0.01

Table I. Continued from previous page.

The orders with the highest number of families were Characiformes and Siluriformes, which also presented high numerical predominance of species. These two orders represented about 85% of the species and 94% of the captured and identified individuals, recording the highest richnesses (18 and 19, respectively) and composing the dominant groups, the Characidae and Pimelodidae families were the most representative in the study area.

Among the captured individuals, there were several migratory and commercially important species, such as *Semaprochilodus* spp. (“jaraquis”), *Brycon amazonicus* (“matrinxã”), *Prochilodus nigricans* (“curimatá”), *Mylossoma* spp. (“pacus”), *Triportheus auritus* (“sardinha comprida”), *Plagioscion squamosissimus* (“pescada branca”), catfish of the genus *Brachyplatystoma*, *Pseudoplatystoma* e *Calophysus macropterus* (“piracatinga”), as well as several curimatids (“branquinhas”), hemiodontids (“charutinhos”) and anostomids (“aracus” and “piaus”).

Regarding the identified taxa, Characiformes was more abundant in the mouth of lake channels with rivers (10.57 larvae.10m^{-3}; 45% of the total collected in this habitat), while Siluriformes was more abundant in the main channel of rivers (0.72 larvae.10m^{-3}, 53% of the total collected in this habitat). Sandbanks presented the lowest species richness (26 to 27) for both rivers and the highest values (30 to 32) were found for the mouth of lake channels and in the main channels of Solimões e Japurá rivers. The rising waters contributed to the higher values of richness when compared to the other phases of the hydrological cycle (Table II).

The predominance of larvae in the preflexion phase, followed by yolk-sac, flexion and postflexion were recorded in both rivers (Fig. 2). No significant differences were recorded in egg (Kruskal-Wallis; Chi^2= 0.4425; p= 0.5059) and larvae density (Kruskal-Wallis; Chi^2= 1.6420; p= 0.2000) between the two studied rivers. However, there were significant differences in egg (Kruskal-Wallis; Chi^2= 11.084; p=0.0113) and larvae density variation (Kruskal-Wallis; Chi^2= 8.385; p=0.0386) among the

Table II. Species richness found in the habitats and different phases of the hydrological cycle, in the middle Solimões and lower Japurá rivers, in the vicinity of the Mamirauá Sustainable Development Reserve, Central Amazon, Brazil.

Habitats	Solimões river	Japurá river
Mouths of channels	30	32
Ravines	29	28
Sandbanks	26	27
Channel of rivers	30	32
Hydrological cycle		
Rising waters	30	31
Flood	19	19
Receding waters	15	21
Drought	21	22

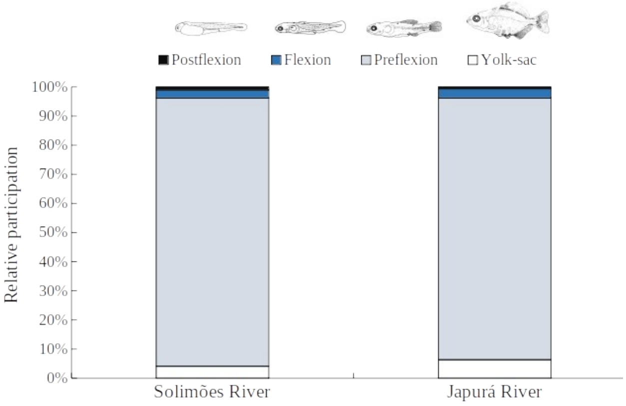

Figure 2 - Relative participation (%) of the initial stages of development of the larvae captured in the middle Solimões and lower Japurá rivers, in the vicinity of the Mamirauá Sustainable Development Reserve, in the Central Amazon, Brazil.

analyzed habitats, with the highest densities observed in the confluence zones of the lakes channels with rivers (Dunn test, $p < 0.05$), both in the middle Solimões and in the lower Japurá rivers (Fig. 3).

Significant differences were found for eggs (Kruskal-Wallis; Chi²= 12.176; $p < 0.0001$) and larvae (Kruska1-Wallis; Chi²= 8.213; p= 0.0003) density in relation to the four moments of the hydrological cycle, with peaks of abundance recorded in the rising waters in both rivers (Dunn test, $p < 0.05$), always with eggs abundance much lower than larvae (Fig. 4).

Numerically, the highest values of abundance of fish eggs and larvae were recorded on the subsurface of the water column during the night period (Fig. 5). But, no statistically significant difference was found between daytime and nighttime (Kruskal-Wallis; Chi²= 0.0113; $p < 0.9154$ - eggs; Chi²= 0.0993; $p < 0.7527$ - larvae), nor between the water column strata (Kruskal-Wallis; Chi²= 0.7218; $p < 0.3956$ - eggs; Chi²= 2.8235; $p < 0.0929$ - larvae). Overall, this demonstrates a homogeneous distribution of ichthyoplankton over the daily periods and strata of the water column.

Discussion

The study area is in a wetland region with evident seasonality of the rainfall cycle and flood pulse, which provides great variation in ichthyoplankton densities over time. This fact is evident by observing that the highest values of species richness and density of fish eggs and larvae occurred during the increase in river water level, which confirms the rising waters phase as the moment of greater reproductive activity of fish in the Solimões-Japurá rivers sub-basin. This proves the importance of the surroundings of the Mamirauá Reserve and its numerous adjacent water bodies and habitats (presence of marginal channels, holes and lakes, and dense coverage of macrophytes on the shores), as proper places to spawning and with favorable conditions to the initial development for various species of fish, including migratory and great economically important species, such as

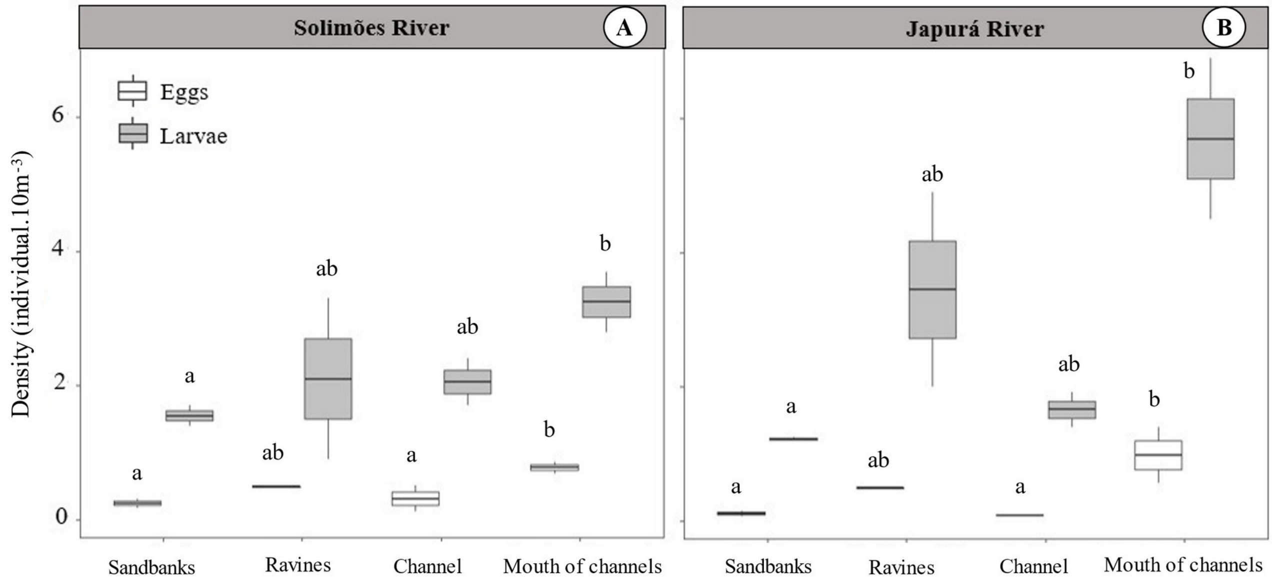

Figure 3 - Spatial variation of ichthyoplankton in the middle Solimões and lower Japurá rivers in different studied habitats, in the vicinity of the Mamirauá Sustainable Development Reserve, in the Central Amazon, Brazil.

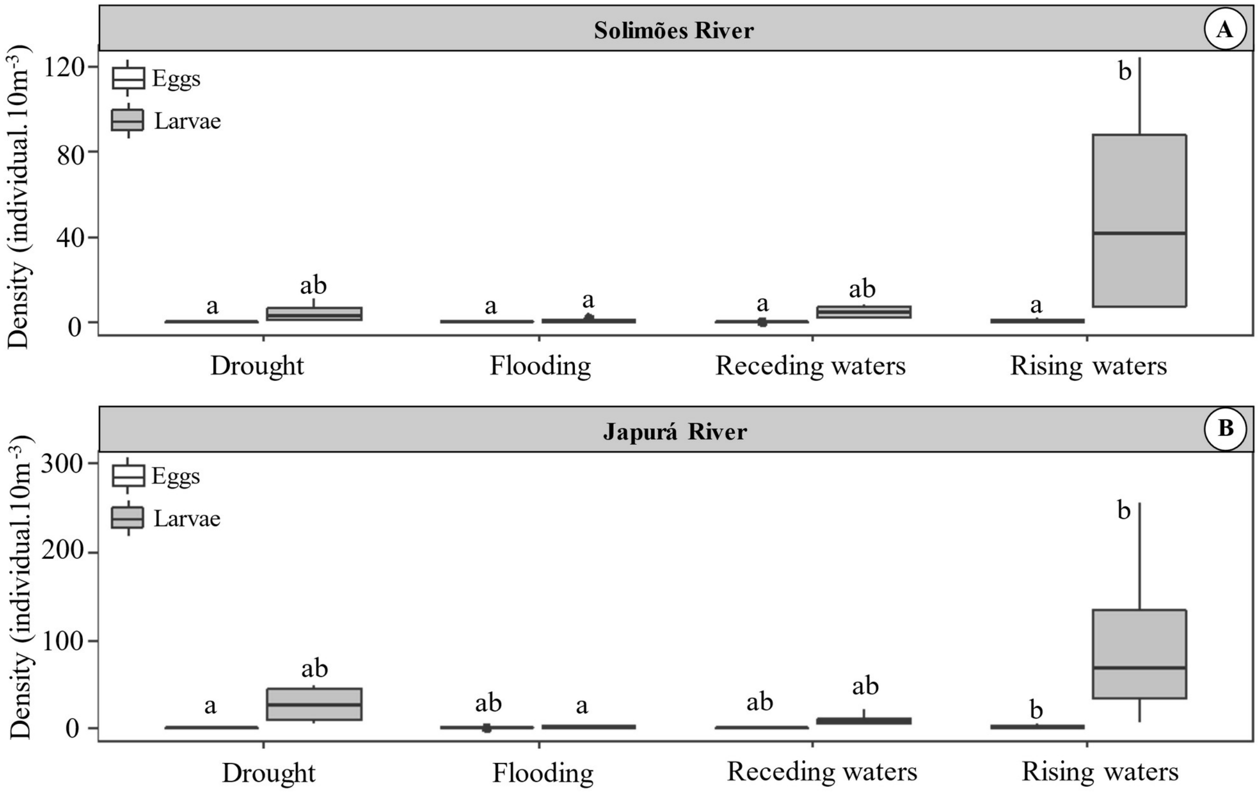

Figure 4. Seasonal variation of fish eggs and larvae density on the middle Solimões and lower Japurá rivers, in the four moments of the local hydrological cycle, in the vicinity of the Mamirauá Sustainable Development Reserve, in the Central Amazon, Brazil.

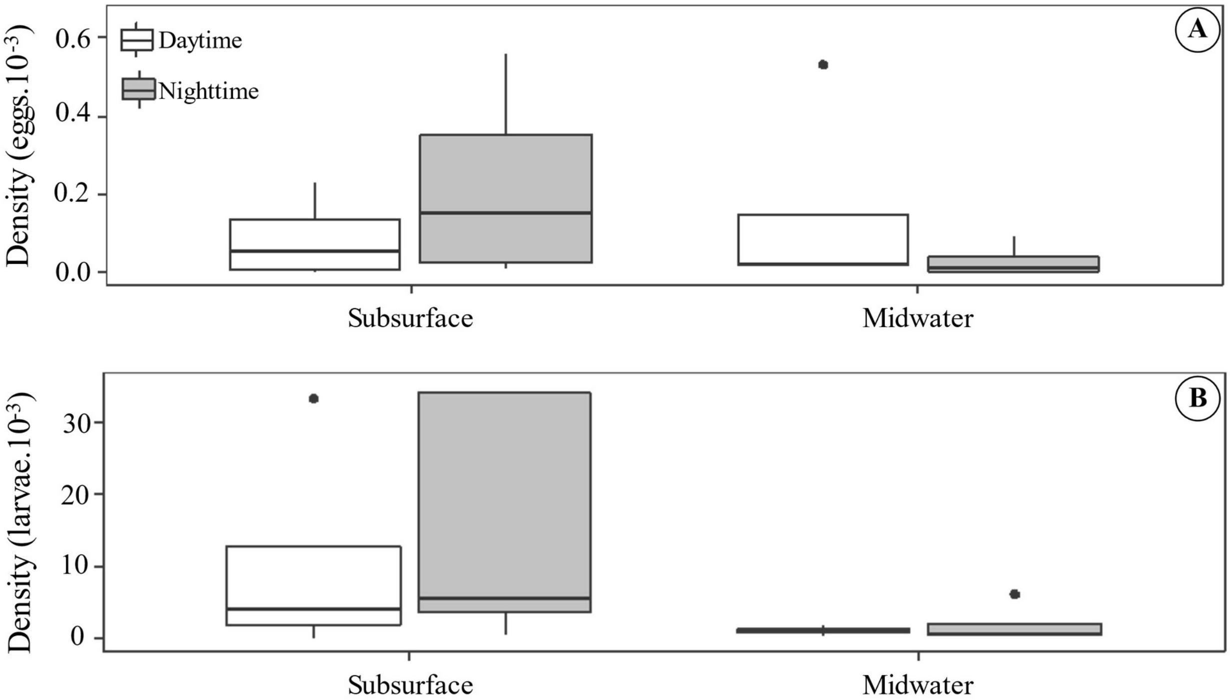

Figure 5. Variation of fish eggs and larvae density between the two water column strata (midwater and subsurface) and between sampling periods (day and night), in the middle Solimões and lower Japurá rivers, in the vicinity of the Mamirauá Sustainable Development Reserve, in the Central Amazon, Brazil.

Semaprochilodus insignis, *S. taeniurus*, *Brycon amazonicus*, *Prochilodus nigricans*, *Mylossoma aureum*, *M. albiscopum*, *Triportheus auritus*, *Plagioscion squamosissimus*, *Pseudoplatystoma punctifer*, *P. tigrinum* and *Hypophthalmu*s spp., as well as several anostomids (*Schizodon* spp. and *Leporinus* spp.), curimatids (*Psectrogaster* spp. and *Potamorhina* spp.), hemiodontids (*Anodus* spp. and *Hemiodus* spp.) and engraulids.

The composition and abundance of captured fish larvae assemblies corroborate the parameters described for the Amazon basin, where the reproduction of most fish species (Ostariophysi), occurs during rising water levels, verified by the large number of plankton larvae drifting in the rivers of white water (Araújo-Lima & Oliveira 1998, Lima & Araújo-Lima 2004, Barletta *et al*. 2010, Ferreira *et al.* 2016, Zacardi *et al*. 2017a, b, c, Cajado *et al*. 2020a, b). Several fish species of Characiformes, Siluriformes, Clupeiformes and Perciformes occupy different aquatic environments during the stages of their life cycle. According to several authors, the biological, physical and chemical conditions of the environments are the factors that probably play the most important role in reproduction and provide characteristics of spawning and/or nursery areas (Barthem & Fabré 2004, Oliveira & Ferreira 2008, Zacardi 2014, Zacardi *et al*. 2017b, Ponte *et al.* 2017, 2019, Chaves *et al*. 2019, Zacardi *et al.* 2020a).

The moving behavior of adult migratory fish coming out of tributaries and floodplains lakes, and remaining close to the margins to spawn (Ribeiro & Petrere 1990), may be a strategy for larvae to group themselves close to future-flooded areas where they will find shelter and food (Leite & Araújo-Lima 2002, Cajado *et al*. 2020a, Oliveira *et al*. 2020). An example is the mouth of lake channels, that function as important areas of stimulus for spawning, colonization zone and larval dispersion between the river-plain system, a scenario already observed by Zacardi and Ponte (2016), Ponte *et al.* (2016, 2019), Zacardi *et al.* (2017a, 2020a).

The presente data showed that Siluriformes larvae in the Solimões/Japurá river sub-basin occupy more central and deeper areas. This pattern may happen because these larvae do not use the same food resources and the same shelter sites as Characiformes larvae, which occupy the newly flooded areas as a nursery (Pinheiro *et al.* 2016, Goulding *et al.* 2019, Oliveira *et al*. 2020, Bittencourt *et al*. 2020). However, there is still a great lack of knowledge bout the real dynamics of the life cycle of these organisms throughout the Amazon Basin (Chaves *et al.* 2017). Furthermore, as in this research, other studies conducted in several Amazonian rivers also recorded low density values of Siluriformes larvae compared to those of Characiformes (Araújo-Lima & Oliveira 1998, Lima & Araújo-Lima 2004, Zacardi *et al*. 2017c, Cajado *et al.* 2020a, b). The methodology adopted (plankton net) may have influenced and undersampled the Siluriformes, since several representatives of this order spawn at the headwaters of the numerous tributaries of the Amazon basin, and not in their middle or lower stretches. Thus, their eggs and larvae drift long distances through the bottom of the river's main channel until they reach the estuary areas (Barthem & Goulding 1997, Leite *et al*. 2007, Barthem *et al.* 2017). Nevertheless, the methodology used in this study tends to sample larvae that derive in the subsurface and midwater, capturing to a lesser extent the individuals present in the benthic habitat of rivers.

Regarding the stratified distribution of larvae during the day and night in rivers of muddy waters such as the Solimões and Japurá rivers, the data corroborate the studies of Araújo-Lima and Oliveira (1998) and Ponte *et al.* (2016), which also did not verify a significant difference in the density of fish larvae in day and night samples, nor between water column strata. Most of the captured larvae were still in the early stages of development, with little visual acuity, mouths still in formation, embryonic fins and, therefore, with low natatory capacity. According to Oliveira and Araújo-Lima (1998) and Bialetzki (2002) larvae at this stage are dispersed laterally and vertically by the hydrodynamics of rivers and emphasize the importance of currents in the process of development and distribution of ichthyoplankton.

However, the presente results differ from Cajado *et al*. (2018), who found variation in the space-temporal distribution of the density of *Brycon amazonicus* larvae (Characiformes) in the lower stretch of the Solimões river, with the highest recorded abundances on the subsurface of water during the night, evidencing active vertical migration behavior of this species. Other specific and characteristic patterns of vertical and daily distribution were also observed by Ferreira *et al.* (2016), Zacardi *et al.* (2017b) and Chaves *et al.* (2017). This indicates that some species, during the larval phase, can modulate their drift between the water column strata, even in turbid and suspended particles-rich environments and, consequently, present differences in abundance in sampling during the day and night.

It is evident, therefore, that the structure of the ichthyoplankton of the middle Solimões and lower Japurá rivers is influenced by several intrinsic and extrinsic factors such as different environments and, habitats, as these can be used by numerous species, especially those of regional economic interest, to complete their life cycle, regardless of their development phase (Ponte *et al*. 2016, Zacardi *et al*. 2017a, Cajado *et al*. 2018, Zacardi *et al*. 2020 a, b, Bittencourt *et al*. 2020). The information presented on the ichthyoplankton community in the stretch of the middle Solimões and lower Japurá rivers are pivotal (and must be used) to identify potentialities, limitations, ecological dynamics and relative importance of water bodies and their habitats in the biological recruitment of the main species of ichthyofauna. Especially those of greater economic interest, which can be better managed and sustainably used based on the subsidies of this information.

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