Seasonality determines patterns of composition and abundance of ichtyoplankton in Maiká lake, Eastern Amazon

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Abstract. This study aimed to characterize ecological attributes of the ichthyoplankton related to the temporal distribution in the Maicá Lake, Santarém-Pará. The captures totaled 2,525 eggs and 6,961 larvae of fish, comprising 52 species from 10 orders. Ichthyoplankton distribution differed between the phases of the hydrological cycle, the highest density of eggs and larvae was recorded in the rising water phase, which corresponds to the reproduction season of most Amazonian fish exploited in the region. The composition of fish larvae species varied between phases of the hydrological cycle, and the larval density differed between all phases. This indicates that species have distinct reproductive behavior and recruitment period. The precipitation index, water level and electric conductivity were the environmental variables that affected the pattern of the temporal distribution of the larvae. The higher diversity and abundance of eggs and larvae captured during the study confirmed that the Maicá Lake is used as a natural spawning and nursery area by many non-migratory or reproductive migrant fish species. It highlights its importance for the reproduction and maintenance of fish in the Lower Amazon River. Therefore, natural resource planning and management measures should be considered priority actions for the lake's conservation and for the maintenance of the regional fishery stocks.

Key words: Biological recruitment, Conservation, Fish eggs and larvae, Nursery.

Resumo. A sazonalidade determina os padrões de composição e abundância do ictioplâncton no lago Maicá, Amazônia Oriental. Este estudo teve como objetivo caracterizar atributos ecológicos do ictioplâncton relacionados à distribuição temporal no lago Maicá, Santarém-Pará. No total, foram capturados 2.525 ovos e 6.961 larvas de peixes, distribuídos em 10 ordens e 52 espécies. A distribuição do ictioplâncton diferiu significativamente entre os momentos do ciclo hidrológico, sendo registradas as maiores densidades de ovos e larvas na enchente, respectivamente, correspondendo à época de reprodução da maioria dos peixes amazônicos explorados pela pesca na região. A estrutura das assembleias de larvas de peixes demonstrou que a mesma esteve influenciada pelo regime hidrológico e a densidade larval diferiu em todos os momentos, indicando que as espécies têm comportamento reprodutivo e período de recrutamento distintos. Das espécies identificadas, grande parte apresenta importância comercial e são consumidas pela população local. O índice precipitação, nível de água e a condutividade elétrica foram as variáveis ambientais que influenciaram o padrão de

distribuição temporal das larvas. Os resultados do estudo confirmam a utilização do lago Maicá, como área de desova e criadouro natural, para diversas espécies de peixes, ressaltando a sua importância para reprodução e manutenção dos peixes no trecho baixo do rio Amazonas. Portanto, medidas de planejamento e gestão de recursos naturais devem ser consideradas como ações prioritárias para a conservação do lago e para a manutenção dos estoques pesqueiros regionais.

Palavras-Chave: Recrutamento biológico, Conservação, Ovos e larvas de peixes, Berçário

Introduction

The floodplain areas of the Amazon basin are covered by an immense block of flooded rainforest interspersed by a complex ecosystem of whitewater rivers. This geomorphology provides important habitats such as streams, creeks, canals, lakes, sandbanks and many other formations, which undergo long and short-term seasonal modifications, such as sedimentation and erosion, which provide environments that are rich in nutrients and organic production (Garcez *et al.* 2010, Junk *et al.* 2012).

In this ecosystem, the alternation of the hydrological regime, also known as flood pulse, promotes physical and chemical alterations in the environment such as temperature, turbidity and nutrients (Thomaz *et al*. 2007, Barbosa *et al*. 2010), which affect the structure of aquatic communities (Silva *et al.* 2010). Thus, the flood pulse is considered the key factor in the determination of ecological working patterns and biodiversity (Junk *et al.* 2012, Ortega *et al.* 2015).

Within the varzea environments, there is a complex marginal lake system that forms a true mosaic with a great diversity of canals that branch and interconnect during the inundation period (Junk *et al.* 2010). The expansion of the lake environments during floods alters the shape, size and hydrological characteristics of the lakes; which influence the composition and distribution of aquatic communities, allowing access to different environments for foraging, spawning, protection for larvae and development of juveniles of many species of the ichthyofauna (Picapedra *et al.* 2015, Pinheiro *et al*. 2016, Ponte *et al*. 2019).

These lakes are widely acknowledged for their importance in the maintenance of regional biodiversity, either as natural breeding sites for species of economic interest (Leite *et al*. 2006, Zacardi *et al*. 2020a) or as a preferential habitat for sedentary and small-sized species (Bevilaqua & Soares 2014, Pinheiro *et al*. 2016). Hence, the integrity of such environments for the conservation and sustainability of fishery resources is vital (Petry *et al.* 2003, Goulding *et al.* 2019), besides these

lakes constitute an important data source for the rationalization of the use of water resources.

In the Maicá Lake, impacts caused by human activities have been observed in the landscape, such as the expressive reduction of the forest area (due to the expansion of the agricultural frontier), increasing disorderly urbanization, implementation of several agro-export projects (creation of a bulk port) and the intense pressure on the region's fishery stocks (Vaz *et al.* 2017). The disturbances caused by these anthropic actions directly affect reproduction, spawning, larval development and consequently, biological recruitment (Castello *et al.* 2011, Souza *et al.* 2012) and the maintenance of fish populations, which fail to replenish their natural stocks as they heavily rely on environmental quality (Mateus & Penha 2007, Zacardi *et al.* 2017d).

Therefore, knowing the composition, abundance and distribution of ichthyoplankton allows us to identify spawning areas and natural nursery sites, as well as to propose management and restoration actions for the fishery resources based on water use efficiency (Pompeu & Godinho 2003, Zacardi *et al.* 2020b). Hence, understanding the role of floodplain habitats for breeding and nursery areas is essential for the implementation of effective conservation policies. In this context, the study aimed to verify the taxonomic composition and identify temporal patterns in the occurrence of the ichthyoplankton community in Maicá Lake, in order to assist in the establishment of best practices for the sustainable use of the biodiversity of this lacustrine ecosystem, in view of the high degree of natural resources use. Hence, the main questions addressed in this work comprise: i) Do the ichthyoplankton assemblages in the Maicá Lake show seasonal pattern differences?; and ii) Which environmental factor affect the structure of ichthyoplankton assemblages in the lake?

Material and Methods

This study was carried out in the Maicá Lake (02° 43'79" S , 54° 16'93" W), approximately 5 km from the city of Santarém, state of Pará, which is

bordered by the Amazon River and the "paraná" Ituqui (side-arm of a large river, separated of the main channel by one or more islands) (Fig. 1). The lake has 161 km^2 of aquatic area and is in a floodplain region, lowlands are periodically flooded (Isaac & Cerdeira 2004). Throughout the year the average oscillation of the lake's water level is influenced by the flood pulse, thus determining the rising water (January to March), full flood (April to June), receding water (July to September) and drought (October to December) phases (Bentes *et al.* 2018). This environment is composed of lateral or "paranás" canals, "restingas", basins of central shallow lakes and flooded plains during the flood, which are exposed in the phase drought and at the upland.

The biological material was sampled monthly during the phases of the hydrological cycle of 2015, in nine georeferenced stations (supplementary material), with an average distance of 400 m between stations, in sampling cycles between 11 am and 6 pm and between 8 pm and 3 am, totalizing 18 samples per month and 216 samples at the end of the study.

Samples were collected using horizontal trawling in the subsurface of the water column, for approximately 5 minutes, using a conical plankton net (mesh 300 µm) equipped with a flowmeter to measure the volume of filtered water. The sampling was made with the assistance of a local vessel, at a low and constant speed, to ensure greater efficiency in the capture, keeping an average distance of 5 m from the shores of the lake. Subsequently, samples were submitted to benzocaine (250 mg.L^{-1}) and then fixed in 10% formalin solution, packed in 500 mL polyethylene containers, labeled and transported for laboratory analysis.

Water temperature (°C), pH, electric conductivity (µS.cm^{-1}) and dissolved oxygen (mg.L^{-1}) were recorded *in loco*, using a digital portable multi-parameter probe. Precipitation index (mm) data were obtained from the National Waters Agency's (ANA) hydro-meteorological station and water level (m) data were obtained from the Directorate of Hydrography and Navigation – DHN (Brazilian Navy) located in the municipality of Santarém.
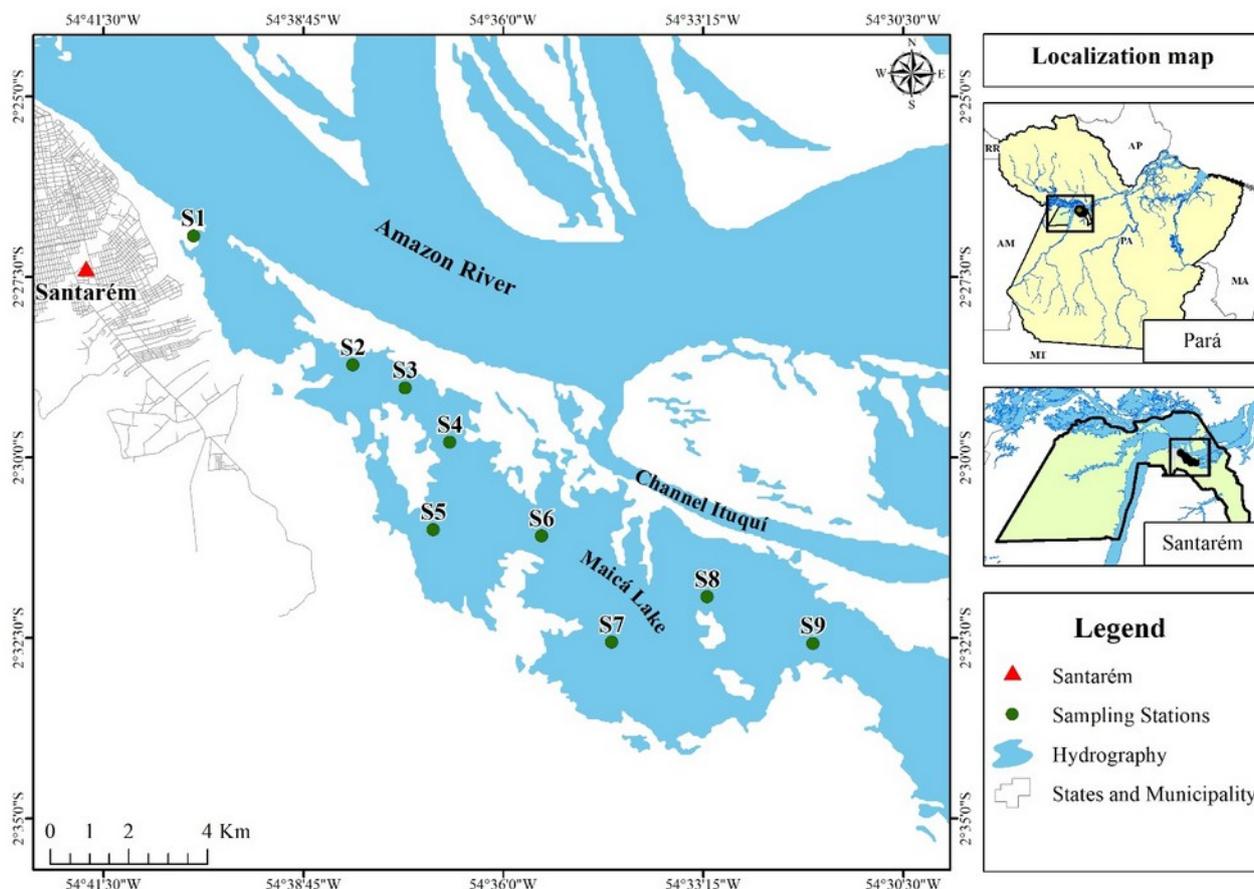
Figure 1 - Ichthyoplankton and physicochemical sampling stations location in the Maicá Lake, municipality of Santarém, state of Pará, Brazil, collected monthly during 2015.

In the laboratory, all samples were sorted, separating the eggs and larvae from the suspended material, debris, and total plankton, with the aid of tweezers and Petri dishes under a stereoscopic microscope. Subsequently, the eggs were classified according to the embryonic development and the larvae were identified at the lowest possible taxonomic level, based on the regressive development, sequence technique as described by Nakatani *et al.* (2001) and on the morphological, meristic, and morphometric characteristics, using specialized publications: Araújo-Lima & Donald (1988), Araújo-Lima (1991), Araújo-Lima *et al.* (1993), Nakatani *et al.* (2001), Leite *et al.* (2007) and Orsi *et al.* (2016). The taxonomic framework was based on Betancour-R *et al.* (2017), 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.

The eggs and larvae were classified according to the reproductive strategies in migratory (M) and non-migratory (NM) species, considering the criteria established by Nakatani *et al.* (2001) as the amount of yolk (higher in species with parental care) and the size of the perivitelline space (higher in migratory species without parental care) for the eggs. Whereas for larvae the classification was based on the information of adult fish, such as gonadal maturation stage, relative fecundity, oocyte diameter, duration of the reproductive period and migratory behavior, as recommended by Barthem & Fabré (2004), Granado-Lorencio *et al.* (2005), Soares *et al.* (2009) and Goulding *et al.* (2019).

For the temporal distribution analysis, the number of fish eggs and larvae captured in the monthly samples was converted to the density of organisms per 10 m^{-3} as proposed by Nakatani *et al.* (2001). The mean density values were obtained by the equation: $D = d/N$. Where: D = mean density values; d = density of collected organisms; N = sample number in each location. The relative abundance of each taxon was calculated by the expression: $Ar = N*100/Na$, being: Ar = relative abundance; N = total number of larvae of each sample; Na = total number of larvae in the sample.

The non-parametric test of Kruskal-Wallis (H) was performed (since the assumptions of normality (Shapiro-Wilk test) and homoscedasticity (Levene test) were not achieved) to verify differences in the mean density values of the fish eggs and larvae (response variables) among hydrological phase - rising water, full flood, receding water and drought - (predictor variables),. A permutational multivariate

analysis of variance (PERMANOVA) (Anderson 2001) was used with the matrix of Bray-Curtis similarity to verify the existence of differences in the patterns of temporal distribution (rising water, full flood, receding water and drought – predictor variables) in the composition of the larval fish assemblage (response variables),. A non-metric multidimensional scaling (NMDS) was used to graphically represent the variation in the composition of the larvae assemblage (Clarke *et al.* 2006), it was used with the matrix of Bray-Curtis similarity based on the larval density. An analysis of similarity percentages (SIMPER) (Clarke & Gorley 2006) was performed to identify the most influential species that best contributed to the similarity observed within the groups, and by the differences observed between the groups (dissimilarity). The analyses of Kruskal-Wallis (H), PERMANOVA, NMDS was performed in the R Statistic program version 3.4.4 (R Core Team 2016) using functions of the package "Vegan" (Oksanen *et al.* 2016) and the SIMPER in the PAST software version. 2.17.

The Detrended Canonical Correspondence Analysis (DCCA) was used to investigate the size of the environmental gradient. Since this gradient was linear, we opted for the Redundancy Analysis (RDA) to verify, in the ordering diagram, the main pattern of variation of density larval depending on the limnological variables, both logarithmized. Only the taxa that provided the greatest contribution to the dissimilarity between the groups outlined by the SIMPER analysis were included in the RDA. The forward selection model using a Monte Carlo permutation test was applied to identify the limnological variables that could better explain the variation in biological data ($p < 0.05$). Prior to the analysis, data on larval density and abiotic variables, except for pH, were standardized based on the log transformation ($\log (x + 1)$) to linearize the variance and reduce the effect of the scale difference. For this analysis, the CANOCO 4.5 software was used (Ter Braak & Smilauer 2002).

Results

A total of 2,525 eggs (26.60% of the total sampled organisms) 6.73% (N = 675) identified as eggs of migratory species and 73.27% (N = 1,850) of non-migratory species and 6,691 fish larvae (73.40%) were collected during the study. The larvae were classified into ten orders, 25 families, 40 genera and 52 species (Supplementary Material ANNEX I). More than 50% of the total of these species perform reproductive migrations, and

approximately 48% are non-migratory species. About 58% of the species are of commercial interest to the Lower Amazon.

The most abundant orders were Characiformes (41.79%), Clupeiformes (31.48%) and Perciformes (7.67%), the remaining orders each corresponding to less than 2% of the total abundance, 15% of sampled larvae were affected or at a very early stage of development, therefore, identification was not possible. The specimens of Serrasalmidae, Engraulidae and Sciaenidae families were the most representative in the study site.

Among the captured fish there were several migratory and non-migratory species of interest for both commercial fishing and subsistence, responsible for part of the food and source of income for many riverside families. Some examples of these species are: *Serrasalmus spilopleura*, *Roeboides* sp., *Squaliforma* sp., *Tatia* cf. *strigata*, *Gymnotus* sp., *Eignenmannia* sp., *Hypoclinemus mentalis*, *Anchoviella jamesi*, *Strongylura timucu*, *Colomesus asellus*, *Hemiodus unimaculatus*, *Plagioscion squamosissimus*, *Pellona flavipinnis*, *Mylossoma aureum*, *M. albiscopum* and *Leporinus* cf. *trifasciatus* (Supplementary Material ANNEX I, Fig. 2).

Analyzing the temporal variation of egg density, higher values were observed in the rising water phase: 9.86 (org.10m^{-3}), with a significant difference (H = 14.65; p = 0.00005) between phases. A similar pattern was observed in the larvae distribution, which differed significantly (H = 31.07; p = 0.0001) with higher larval density values 18.15 (org.10m^{-3}) in the same period (Fig. 3 A and B).

During the study, three increasing peaks of larval density were recorded: one related to the rising water, when the rainy season is initiated in the region and increases the water level in the lake (coinciding with the high capture of several individuals of species that perform reproductive migrations, such as Characiformes, with emphasis on the larvae of the "pacus" *M. aureum* (15.94 larvae.10m^{-3}) and *M. albiscopum* (7.89 larvae.10m^{-3}) that presented higher density values); another in the receding water with the predominance of *P. squamosissimus* larvae (3.52 larvae.10m^{-3}) (Perciformes - "pescada branca"); and the third in the drought with high capture of Engraulidae (17.08 larvae.10m^{-3}) (Clupeiformes - "manjubas").

Eggs in the early cleavage stage (EC - when the first cells are formed) had the highest abundances (98.65%) and were captured at all times in the hydrological cycle, which indicates that the spawning occurred close to the sampling areas. The stages of early embryo (EE - 1.27%, when the embryo is differentiated) and free tail stage (FT - 0.08%, when the tail is released from the yolk) were recorded in the full flood and receding water, however in low abundance and the final embryo (FE - when the embryo is completely formed and ready for eclosion) was not found in the samples (Fig. 4 A). Regarding larval development, individuals in the pre-flexion stage (PF - from the beginning of exogenous feeding until the beginning of notochord flexion, when supporting elements of the caudal fin appear) were more abundant during the rising water, full flood and receding water, representing 70.78% of the total captured, followed by larvae in flexion (FL - 22.52%, from the beginning of notochord flexion, when supporting elements of the caudal fin appear, until complete flexion of the notochord, the appearance of the pelvic fin bud and the beginning of dorsal and anal fin ray segmentation), postflexion (POF - 4.98%, from full notochord flexion, the appearance of the pelvic fin bud and the beginning of dorsal and anal fin ray segmentation until the full formation of the pectoral fin rays, absorption of the embryonic fin and the appearance of scales) and yolk-sac larva (YS - 1.72%, stage between hatching and the first exogenous feeding) (Fig. 4 B). The more developed stages were more frequent during the drought.

The NMDS demonstrated that the structure of larval fish assemblages was influenced by the hydrological regime (Fig. 5). It was confirmed by the PERMANOVA that recorded a significant difference in the structure of the composition of fish larvae in relation to the phases of the hydrological cycle (Pseudo F = 7.27; p = 0.0001), noting that the larval density significantly differed at all times (pairwise test: p = 0.0013), what indicated that the species have different reproductive behavior and recruitment period. The Characiformes larvae were the main contributors in the phase of rising water, the Perciformes in the receding water and the Clupeiformes in the drought; during the full flood, low densities of larvae were recorded (Table I), the dissimilarity recorded was 80.34% (SIMPER).

The RDA result indicated that the evaluated abiotic variables explained 60% of the biological variability (Supplementary Material ANNEX I). The first two axes explained 84.3% of the accumulated percentage variation of the species-environment relationship. On axis 1, *P. squamosissimus* larvae correlated positively with the water level during the receding water period. While on axis 2, the
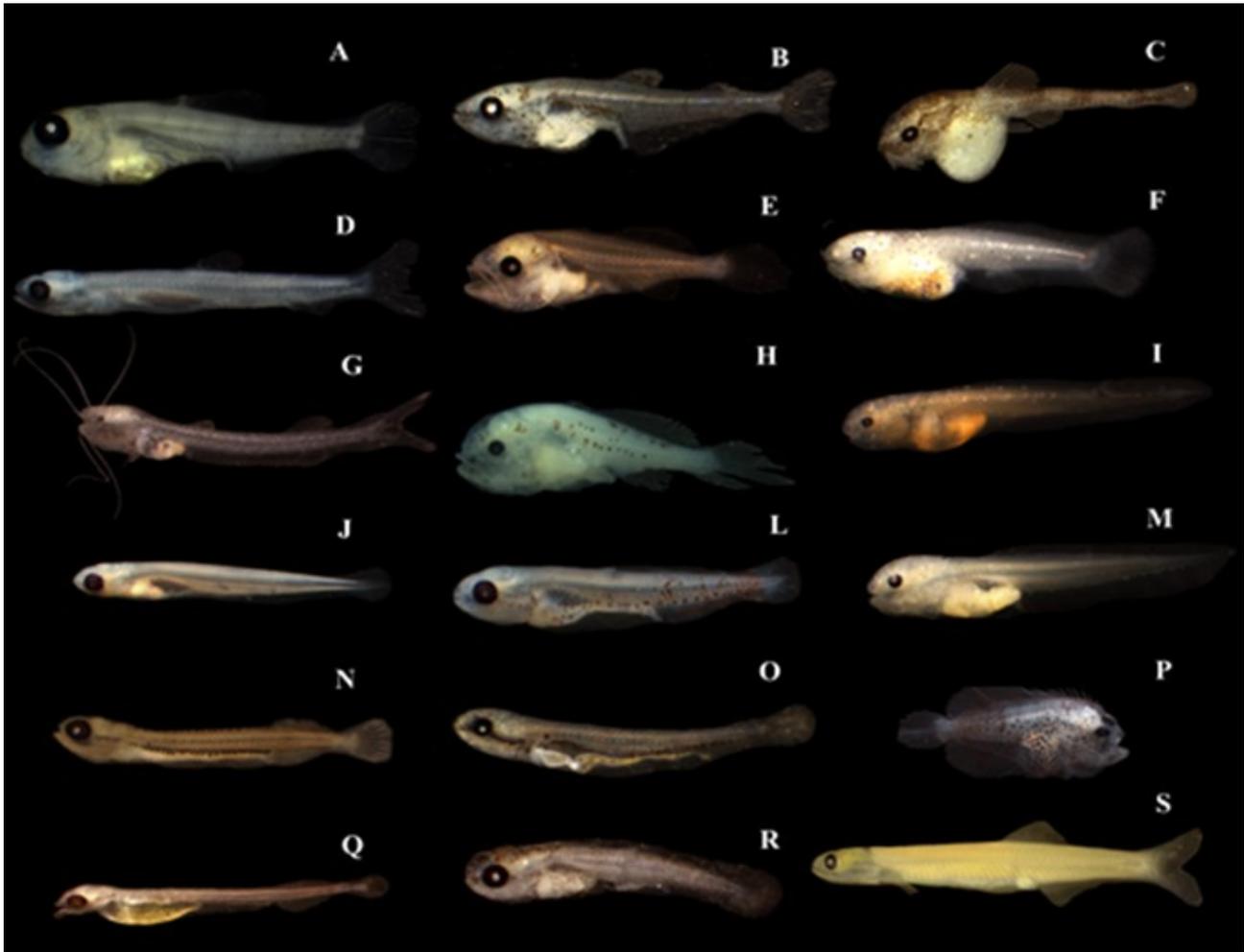
Figure 2 - Fish larvae captured in the Maicá Lake: **A-** *S. spilopleura* (25.7 mm), **B-** *Roeboides* sp. (23.1 mm), **C-** *Squaliforma* sp. (9.09 mm), **D-** *H. immaculatus* (10.69 mm), **E-** *P. squamosissimus* (9.3 mm), **F-** *Tatia* spp., (6.93 mm), **G-** *H. fimbriatus* (9.69 mm), **H-** *P. auratus* (6.02 mm), **I-** *Gymnotus* sp. (8.98 mm), **J-** *T. auritus* (8.63 mm), **L-** *M. aureum* (5.8 mm), **M-** *Eignenmannia* sp. (13 mm), **N-** *H. brederi* (8.19 mm), **O-** *L.* cf. *trifasciatus* (5.01 mm), **P -** *Hypoclinemus mentalis* (3.60 mm), **Q-** *S. timucu* (6.19 mm), **R-** *H. malabaricus* (6.80 mm), **S-** *A. jamesi* (25 mm).
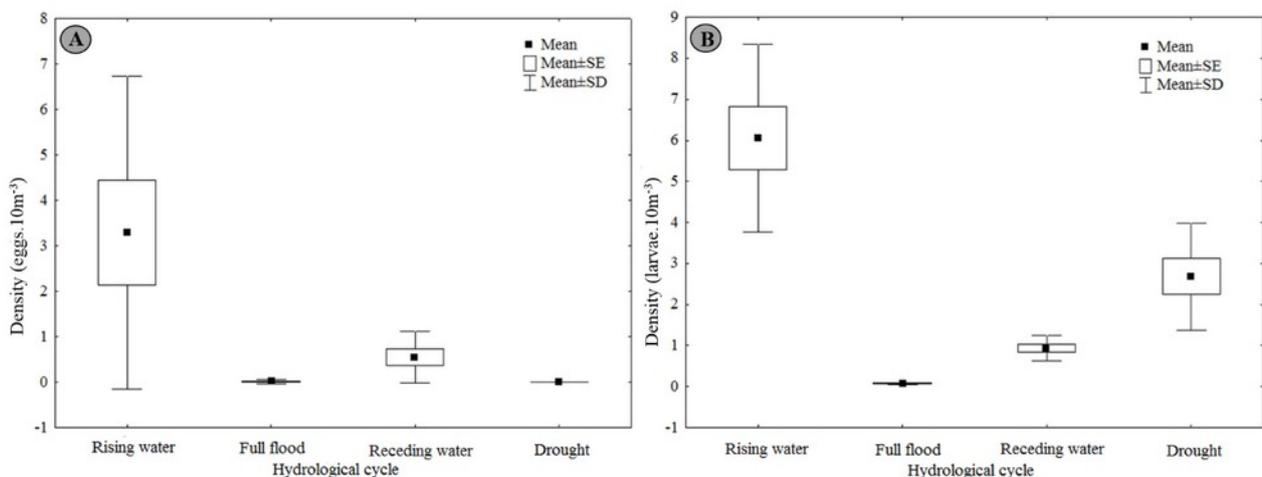
Figure 3 - Mean density and standard deviation of fish eggs (A) and larvae (B) captured in the Maicá Lake in the phases of the hydrological cycle of 2015.
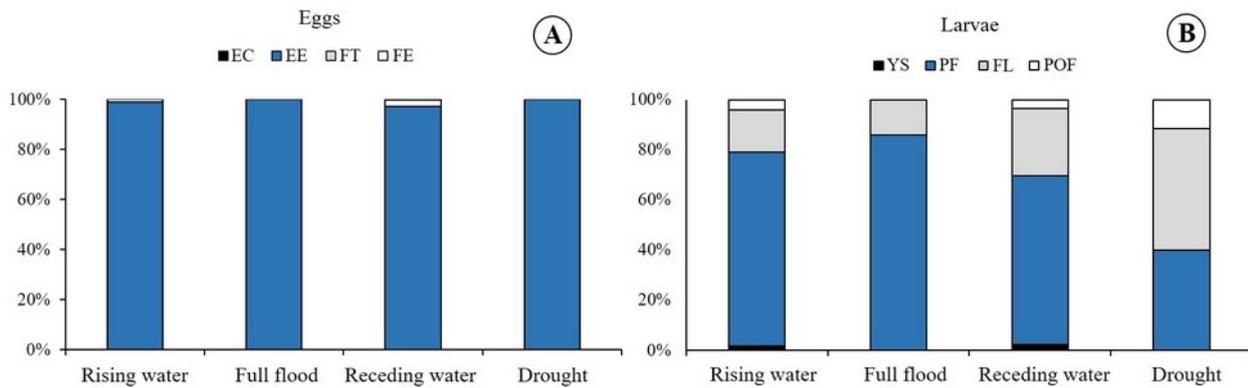
Figure 4 - Relative proportion (%) of the embryonic (A) and larval (B) stages captured in the four phases of the hydrological cycle in Maicá Lake in 2015, Santarém, Pará. EC - early cleavage , EE - early embryo, FT - free tail stage, FE - final embryo, YS - yolk-sac, PF - pre-flexion, FL - flexion and POF - postflexion.
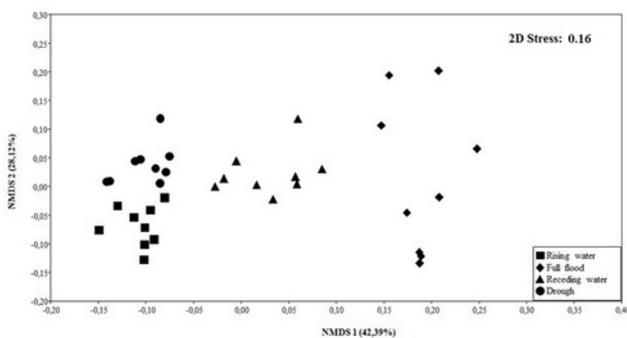
Figure 5 - Ordering of the two axes of the NMDS applied to the dissimilarity matrix with Bray-Curtis coefficient, based on the density and composition of the larvae assemblage, which were obtained at the Maicá Lake, Santarém, Pará. $F_{(1,20)}=5{,}76$, $p=0{,}03$.

Engraulidae larvae were positively associated with temperature and pH gradients during the drought and the larvae of *M. aureum* and *M. albiscopum* were associated with an increase in the precipitation index during rising water (Fig. 6). For the Monte Carlo test, the environmental variables that significantly influenced the larval distribution were the water level, precipitation index and electrical conductivity ($p = 0.001$).

Discussion

A large number of ichthyoplankton species were captured, comprising a set of species of great economic relevance for the region. That demonstrates the importance of these watercourses as a spawning and nursery area of various fish species that have found in this varzea lake, favorable conditions to their reproduction and early development. The sampling area should be considered an important corridor for the drift of migratory fish eggs and larvae spawning in the main

river channel and entering the lake during the flooding period, as for several other species that complete their entire life cycle in this environment.

The ichthyic composition found in the study area is in agreement with the expected pattern for floodplain environments of the Central (Saint-Paul *et al.* 2000, Freitas & Garcez 2004) and Eastern (Almeida 2010) floodplains in Brazil and the Amazonian floodplains in Colombia (Reginfo 2007) and Peru (Piraquive *et al.* 2015). In the Amazonian region, fish assemblages are predominantly represented by species of Characiformes, Clupeiformes, Siluriformes and Perciformes. This pattern differs from the composition found in the Uruguay and Paraná river basins with the predominance of Characiformes and Siluriformes larvae (Tondato *et al.* 2010, Reynalte-Tataje *et al.* 2012, Ortega *et al.* 2015).

The predominance of Characiformes in the ichthyoplankton composition has been reported by many authors in studies conducted in different floodplain lakes (Leite *et al.* 2006, Reynalte-Tataje *et al.* 2012, Ávila-Simas *et al.* 2014), this fact may be related to the wide distribution of the group and the greater diversity of fish species in Neotropical regions (Lévêque *et al.* 2008). This predominance of these taxa is nevertheless a characteristic of all South American river basins, although the exact species composition and diversity patterns vary considerably among the different watercourses (Zacardi *et al.* 2017c). Moreover, in this group there are small and sedentary fish species that have a generalist diet and high reproduction rates in several habitats. Furthermore, many species of this group complete their life cycle in lentic or low-speed environments (Bennemann *et al.* 2000, Azevedo 2010) as observed in the present study, in which

Table I. Results of the analysis of similarity percentages (SIMPER), indicating the taxa which more contributed (%) for dissimilarity (Dis) between the phases of the hydrological cycle, in the Maicá Lake. RIW = rising water, FF= full flood, REW= receding water and D = drought.

Taxa	RIW versus FF		RIW versus REW		FF versus REW		FF versus D		D versus REW	
	(%)	Dis	(%)	Dis	(%)	Dis	(%)	Dis	(%)	Dis
Characiformes										
M. aureum	28,85	27,89	27.38	23.54	33.81	20.19	-	-	28.03	26.76
M. albiscopum	18.09	22.15	15.66	14.73	20.88	12.47	-	-	17.43	20.18
Clupeiformes										
Engraulidade	22.92	17.49	17.14	13.47	13.46	8.35	15.67	33.29	21.14	16.63
Perciformes										
P. squamosissimus	-	-	11.47	9.86	-	-	39.28	13.28	-	-

more than 70% of eggs and almost 50% of larvae assemblages were composed of non-migratory individuals.

The highest density values of fish eggs and larvae recorded during the rising water phase show that many fish species are in full reproductive activity. Several authors associate this reproductive intensity with the elevation of the water level of the river's main channel, which in this period reaches or exceeds the limits of the margins (Ponte *et al.* 2017, Zacardi *et al.* 2017b, Cajado *et al.* 2018, Carvalho *et al.* 2018; Cajado *et al.* 2020a). This flood pulse strongly influences the life cycle of fish, as flooding makes it possible to explore newly available food sources and the heterogeneity of habitats (flooded forest, aquatic macrophyte banks, canals and floodplain lakes) that provide refuge and shelter for fish in their early stages of the life cycle (Tondato *et al.* 2010, Zacardi *et al.* 2017a, 2019; Oliveira *et al.* 2020).

The occurrence of planktonic fish eggs and larvae at different moments of the year is variable and reveals a seasonal sequence that depends on the periodicity in the annual gonadal maturation cycle of the species, as stated by Zacardi *et al.* (2014). However, the reproductive process is influenced by biological conditions (nutritional and physiological status of the breeders), environmental conditions (water temperature, photoperiod, flooding time), which maximizes fecundation and offspring development, and factors (increasing river levels, the direction and strength of the currents) that assist passive transport and the retention of organisms (Binder *et al.* 2011, Zacardi *et al.* 2014, Cajado *et al.* 2020b).

Another key factor to understand the presence of fish larvae in the environment is the abundance of plankton, the preferred food of these individuals, where the food predilection is delimited according to

the species and the larval development phase (Fosse *et al.* 2013). This occurs because during exogenous feeding, the passage from the vitelline to the pre-flexion phases (mouth and functional anus), the larvae have nutritional requirements that guarantee rapid growth and survival (Manetta *et al.* 2011, Neves *et al.* 2015). Thus, not one but a set of several variables are responsible for changes (fluctuations) in the distribution and qualitative and quantitative composition of ichthyoplankton in aquatic environments.

A high density of migratory Characiformes larvae was recorded during the elevation of the fluviometric level and rainfall index in the region, probably linked to the reproductive strategy of the "pacus" (*M. aureum* and *M. albiscopum*) (Oliveira 2000), that form shoals of fish and migrate during the region's heavy rains to spawn in the river's main channel and confluence zones with lakes channels (Granado-Lorencio *et al.* 2005, Zacardi *et al.* 2017c, 2018). This synchronism occurs to ensure maximum availability of food at early stages of development, maximizing larval growth and survival (Mounic-Silva & Leite 2013; Ponte *et al.* 2019).

The "pescada-branca" larvae (*P. squamosissimus* - Perciformes) had the highest densities recorded at receding water, corroborating the results of Rocha *et al.* (2006) and Carvalho *et al.* (2017) who found adult individuals with mature gonads in this same period, indicating that this phase of the hydrological cycle corresponds to the reproductive peak of the species, as observed by Chaves *et al.* (2019). However, the species presents parceled spawning, external fertilization, without parental care (Keith *et al.* 2000, Santos *et al.* 2006), and colonizes habitats, even in unfavorable environmental conditions and under high predation pressure, and it is commonly found in rivers,

reservoir and floodplain lakes (Bialetzki *et al*. 2004, Chaves *et al*. 2019).

Engraulidae (Clupeiformes), unlike "pacus" and "pescadas", had the highest densities during the drought. This group is represented by small individuals forming numerous shoals of fish, with reproduction recorded during the most extreme period of the hydrological cycle and the smallest available wetland (Le Guennec & Loubens 2004, Maciel 2010), presumably contributing to the strong recruitment of these species.

The composition of the fish larvae was different between the moments of the hydrological cycle, indicating the formation of structurally distinct groups characterized by the seasonal distribution of the species recorded during periods of the hydrological cycle, demonstrating that the assemblages of fish larvae have a strong interdependence with the hydrological regime. The variation in the composition of the ichthyofauna of lake systems had already been reported by Saint-Paul *et al.* (2000) and Soares *et al*. (2009), who observed that these environments are constituted both by sedentary and migratory species that perform short-distance reproductive migrations and usually spawn at different phases of the hydrological cycle, in the drought (Junk 2000, Magoulick & Kobza 2003) or at the beginning of the rising water (Duponchelle *et al.* 2007), as recorded in this study.

Whitewater rivers are considered favorable for the development of fish larvae due to the presence of a great diversity of habitats and high concentration of nutrients (Ponte *et al*. 2016, Cajado *et al*. 2018, Carvalho *et al*. 2018). However, some studies reported that in the main channel of these rivers there is not enough biological production to sustain the larvae throughout their different ontogenic stages (Gagne-Maynard *et al*. 2017, Zacardi *et al*. 2020a). Nonetheless, the annual flooding of the Amazonian lowland areas caused by whitewater rivers favors the entry and distribution of nutrients, sediments, and suspended particles, which generates an intense fertilization flow, increased primary and secondary productivity, and maintenance of the aquatic biota (Gopal, 1999, Feresin *et al*. 2010).

The rains also play a crucial role in inducing the increase in planktonic biomass, as they promote the resuspension of nutrients from the bottom of stagnant waters of the lakes and the transport of exogenous nutrients to aquatic environments, generating an accelerated increase in groups of phytoplankton and zooplankton (Costa *et al.* 2009).

For this reason, floodplain lakes are among the most productive natural systems on the planet and are vital for the maintenance of fishery resources (Pinheiro *et al.* 2016, Zacardi *et al.* 2018, 2020a, b) and biodiversity conservation (Aprile & Darwich, 2013, Goulding *et al.* 2019).

Thus, the connectivity of the lakes to the main river, the streams, the position of wetlands in the landscape, and the dynamics of floods are important factors that influence fish assemblages and their recruitment patterns in floodplain areas. In this context, environmental pressures and problems related to the use and availability of water resources may prevent the movement of organisms between different watercourses of the river-plain system and impair the colonization and retention of the early life cycle of fish species, whereas regional ichthyofauna depends on this connectivity to reach the feeding and shelter areas (Freitas *et al.* 2013, Arthington *et al.* 2015, Hurd *et al.* 2016). Therefore, the diversity and size of species' natural stocks, especially migratory ones, will depend on the conservation and integrity of this ecosystem (Petry *et al.* 2003, 2004, Zacardi *et al.* 2019).

According to Ziober *et al.* (2012), in floodplains, monthly variations in precipitation reflect changes in hydrometric levels and promote changes in abiotic variables that can influence the fish community. The high pH values during the drought may be related to the greater photosynthetic activity and the increase in phytoplanktonic biomass that tend to raise the pH values due to the removal of carbon dioxide from the system (Schmidt, 1973, Brito *et al.* 2014), but this can vary depending on the area within the lake.

The rainfall regime presents marked seasonality with a dry and rainy season at different times of the year. It has a direct relationship with phytoplanktonic biomass, suspended material, and dissolved oxygen and an inverse relationship with water temperature and transparency (Angelis *et al.* 2004, Bastos *et al.* 2005). According to Nascimento and Nakatani (2006), in different regions of Brazil, some species of fish show a preference for environments with slightly acidic pH and low electrical conductivity. For Bialetzki (2002), pH can also act secondarily in fish reproduction, inducing individuals to spawn. After all, several authors report that the reproductive activity of neotropical fish is strongly linked to the abiotic variations that occur in aquatic ecosystems (Gogola *et al.* 2010, Ziober *et al.* 2012, Zacardi & Ponte, 2016, Zacardi *et al.* 2017a, c).

Regarding the relation between the environmental variables and the larvae distribution, it was evident that the precipitation, the water level and the electrical conductivity exert a strong influence on the larvae of *M. aureum*, *M. albiscopum*, *P. squamosissimus* and Engraulidae. This relation of the variables with fish larvae in inland aquatic environments, subjected to seasonal flooding, has been demonstrated by several studies (Tan *et al*. 2010, Ren *et al*. 2016, Chaves *et al*. 2019). This increase in the water level and rainfall acts as an environmental trigger, a regulating factor of the spawns of various fish species (Worthington *et al*. 2014), which can accelerate or delay this process and affect the incubation of eggs, development of the larvae, as well as the growth and survival of these individuals (Nakatani *et al*. 2001, Batista & Lima 2010).

In general, a typical seasonal variation pattern of ichthyoplankton found in Maicá Lake was observed, occurring at different stages of the hydrological cycle, showing that many species of fish have their reproductive period influenced by water level oscillation. The lake has an important role in maintaining the fish community that uses this environment temporarily or permanently during its life cycle and is widely exploited by the local population as a source of protein and income alternative for fishers and other users. Nevertheless, the conservation of this environment can be subsidized by the implementation of a natural resource's management plan, fundamental for ecosystem balance and renewal of fishery stocks.

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Seasonality determines patterns of composition and abundance of ichtyoplankton in Maiká lake, Eastern Amazon

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Table I. Taxonomic composition and average density of ichthyoplankton (Org.10m^{-3}) captured from January to December 2015, in the Maicá Lake, Lower Amazon, Pará. N = absolute number of individuals; RIW= rising water, FF = full flood, REW= receding water, D = drought; EI = economic importance (†); RS = reproductive strategy (M = migratory species, NM = non-migratory species); Conservation status = CS (LC =Least-Concern, DD = Data deficient).

Order/Family/Species	Common name	N	CS	Mean density				EI	RS
				RIW	FF	REW	D		
Beloniformes									
Belonidae									
Strongylura timucu (Walbaum, 1792)	peixe agulha	3	LC	<0.01	-	0.03	-		NM
Hemiramphidae									
Hyporhamphus brederi (Fernández-Yépez, 1948)	peixe agulha	2	DD	-	-	0.45	-		NM
Characiformes*		137		0.20	0.26	0.16	<0.01		
Acestrorhynchidae									
Acestrorhynchus falcirostris (Cuvier, 1819)	peixe cachorro	2		0.02	0.02	-	-		NM
Anostomidae			LC						
Leporinus cf. *trifasciatus* (Steindachener, 1876)	aracu	15	LC	0.17	<0.01	-	-	†	M
Rhytiodus microlepis Kner, 1858	aracu pau de vaqueiro	4	LC	0.06	-	-	-	†	M
Schizodon fasciatus Agassiz, 1829	aracu-comum	54	LC	0.43	0.03	0.02	-	†	M
Characidae**		56		0.41	0.38	0.04	-		
Hyphessobrycon pulchripinnis Ahl, 1937	piaba	2	LC	0.07	-	-	-		NM
Hyphessobrycon sp.	piaba	85	DD	0.03	1.03	0.01	-		NM

Taxon	Common name	N	Status						
Roeboides sp.	zé-do-ó	1	DD	0.02	-	-	-		NM
Curimatidae**		15		0.15	-	-	-		
Potamorhina altamazonica (Cope, 1878)	branquinha	30	LC	0.36	0.04	-	-	†	M
Potamorhina latior Spix & Agassiz, 1829	branquinha-comum	6	LC	0.06	0.02	-	-	†	M
Psectrogaster amazonica Eigenmann & Eigenmann, 1889	branquinha	32	LC	0.39	0.03	-	-	†	M
Cynodontidae									
Cynodon gibbus Spix & Agassiz,1829	peixe-cachorro	2	LC		-	0.02	-	†	M
Raphiodon vulpinus Agassiz, 1829	peixe cachorro	4	LC	0.06	-	-	-	†	M
Erythrinidae									
Hoplias cf. *malabaricus* (Bloch, 1794)	traíra	29	LC	0.28	0.06	0.01	-	†	NM
Hemiodontidae									
Anodus elongatus Agassiz, 1829	charutinho	27	LC	0.19	0.01	0.04	0.02	†	M
Hemiodus unimaculatus (Bloch, 1794)	charutinho	142	LC	0.79	-	0.44	0.10	†	M
Prochilodontidae									
Semaprochilodus insignis (Jardine & Schomburgk, 1841)	jaraqui escama-grossa	5	LC	0.06	-	-	-	†	M
Semaprochilodus taeniurus (Valenciennes, 1817)	jaraqui escama-fina	1	LC	0.00	0.03	-	-	†	M
Serrasalmidae**		100		1.09	-	-	-		
Myleus sp.	pacu	5	DD	0.03	0.04	-	-	†	NM
Mylossoma aureum (Agassiz, 1829)	pacu-manteiga	1,421	LC	15.94	-	-	-	†	M
Mylossoma albiscopum Cope, 1872	pacu-comum	616	LC	7.89	0.01	0.29	-	†	M
Serrasalmus spilopleura Kner, 1858	piranha-amarela	12	LC	0.11	0.03	-	-	†	NM
Serrasalmus rhombeus (Linnaeus, 1766)	piranha preta	50	LC	0.53	0.09	0.03	-		NM
Triportheidae									
Triportheus auritus (Gunther, 1864)	sardinha comprida	9	LC	0.07	-	<0.01	-	†	M
Triportheus angulatus Spix and Agassiz, 1829	sardinha papuda	122	LC	0.76	-	0.39	0.04	†	M
Clupeiformes									
Engraulidae**		1,762		8.37	0.35	1.07	17.08		
Anchoviella guianensis (Eigenmann, 1912)	manjuba	14	LC	0.15	0.04	-	0.10		NM
Anchoviella jamesi (Jordan & Seale, 1926)	manjuba	68	LC	0.72	-	-	0.14		NM
Anchoviella juruasanga Loeb, 2012	manjuba	37	LC	0.28	-	0.01	0.42		NM
Lycengraulis batesii (Günther, 1868)	manjuba	61	LC	0.51	-	<0.01	0.83		M
Pristigasteridae									
Pellona castelnaeana (Valenciennes, 1847)	apapá-amarelo	10	LC	0.04	-	-	<0.01	†	M
Pellona flavipinnis (Valenciennes, 1836)	apapá-branco	218	LC	2.07	-	0.07	0.45	†	M
Gobiiformes									
Eleotridae									
Microphilypnus tapajosensis Caires, 2013	pacamãozinho	1	DD	-	0.02	-	-		NM
Gymnotiformes									
Gymnotidae									
Gymnotus sp.	sarapó	1	DD	0.01	-	0.04	-		NM
Sternopygidae									

Eignenmannia sp.	sarapó	19	DD	0.17	0.08	-	-		
Perciformes									
Sciaenidae									NM
Plagioscion cf. *auratus* (Castelnau. 1855)	pescada preta	13	LC	-	-	0.10	-	†	NM
Plagioscion squamosissimus (Heckel, 1840)	pescada branca	521	LC	0.50	0.35	3.52	0.15	†	NM
Pleuronectiformes									
Achiridae**		103		0.02	0.01	0.75	-		
Hypoclinemus mentalis (Günther, 1862)	sôlha	5	LC	0.04	-	<0.01	-		NM
Siluriformes		17		0.15	0.06	3.21	-		
Auchenipteridae**		5		0.03	0.04	-	-		
Ageneiosus cf. *dentatus* Kner, 1857	mandubé	1	LC	0.01	-	-	-	†	M
Auchenipterus cf. *nuchalis* (Spix and Agassiz, 1829)	cangati	4	LC	0.03	0.04	-	-		M
Tatia cf. *strigata* Soares-Porto, 1995	cangati	11	LC	0.02	0.09	0.02	-		NM
Trachelyopterus galeatus (Linnaeus, 1766)	cangati	3	LC	0.04	-	-	-		NM
Loricariidae									
Squaliforma sp.	bodó	2		0.02	-	-	-		NM
Pimelodidae**		6		0.04	0.02	-	-		
Hypophthalmus fimbriatus Kner, 1858	mapará	5		0.04	0.03	-	-	†	M
Hypophthalmus marginatus Valenciennes, 1840	mapará	5		-	-	0.05	-	†	M
Pimelodus blochii Valenciennes, 1840	mandi	12		0.05	0.10	-	-	†	M
Pseudoplatystoma punctifer (Castelnau18,55)	surubim	14		0.08	-	-	-	†	M
Pseudoplatystoma tigrinum (Valenciennes, 1840)	caparari	2		0.02	-	-	-	†	M
Sorubim lima (Bloch and Schneider, 1801)	bico-de-pato	2		0.01	-	-	-	†	M
Trichomycteridae									
Paravandellia sp.	candiru	4		0.01	-	0.03	-		NM
Synbranchiformes									
Synbranchidae									
Synbranchus marmoratus Bloch, 1795	muçum	16		0.16	0.07	-	-		NM
Tetraodontiformes									
Tetraodontidae									
Colomesus asellus (Müller & Troschel, 1848)	baiacu	50		0.08	0.10	0.23	<0.01		NM
Unidentified		959		6.32	0.40	4.24	4.77		
Larvae total		6961		18.15	1.3	5.1	13.12		
Migratory eggs		675							
Non-migratory eggs		1850							
Eggs total		2525		9.86	0.11	0.41	0.35		

* Larvae identified up to Order level

** Larvae identified up to the Family level

Supplementary matter ANNEX II:
Seasonality determines patterns of composition and abundance of ichtyoplankton in Maiká lake, Eastern Amazon

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Geographic coordinates of the sampling stations in the Maicá Lake, near the city of Santarém, in the region of the Lower Amazon, Pará.

Sampling stations	Latitude (S)	Longitude (W)
E01	02°26'55.69"	54°40'15.69"
E02	02°28'42.94"	54°38'04.25"
E03	02°29'01.87"	54°37'21.14"
E04	02°29'47.09"	54°36'44.34"
E05	02°30'59.64"	54°36'58.00"
E06	02°31'13.64"	54°35'28.63"
E07	02°32'33.23"	54°34'30.79"
E08	02°31'55.37"	54°33'11.93"
E09	02°32'34.28"	54°31'44.65"

Results of the redundancy analysis (RDA) associating the larvae densities and the environmental variables obtained during the phases of the hydrological cycle of 2015, in the Maicá Lake, Santarém, Pará. *Correlation values.

	Axis		
	RDA1	**RDA2**	**RDA3**
Eigenvalues	0.323	0.183	0.089
Species-environment correlations	0.919	0.792	0.744
Cumulative percentage variance			
of species data	32.3	50.6	59.5
of species-environment relation	53.9	84.3	99.2
Sum of all eigenvalues			1
Sum of all canonical eigenvalues			0. 600
Correlation			
Precipitation index	0.0682	-0.7017*	0.6857
Water level	0.6879	-0.5391*	0.4604
Water temperature	-0.2530	0.8406	-0.3431
Dissolved oxygen	-0.0064	0.2683	-0.8591
pH	-0.6729	0.5821	0.1639
Electrical conductivity	0.1698	0.0840	-0.9602*

Mean ± standard deviation and maximum and minimum amplitudes (between brackets) of abiotic variables collected monthly during 2015 in the Maicá Lake, Santarém, Pará.

Abiotic variables	Phases of the hydrological cycle			
	Rising water	**Full flood**	**Receding water**	**Drought**
Electrical conductivity (μS.cm^{-1})	17.55 ± 4.35 (20.61 – 2.57)	16,05 ± 1,28 (17,53 -15,28)	21,81 ± 2,02 (23,83-19,79)	36,03± 6,73 (40,96 -28,36)
Water temperature (°C)	29,43 ± 0,55 (30,02 - 28,93)	28,89 ± 0,60 (29,56 -28,39)	29,91 ± 0,51 (30,42 -29,41)	32,15 ± 1,32 (33,38 -30,76)
Dissolved oxygen (mg/L)	6,63 ±0,62 (7,24-6,00)	6,69 ± 0,61 (7,34 -6,12)	4,64 ± 0,81 (5,55 -4,00)	4,48 ± 0,54 (5,10 -4,12)
pH	5,83 ± 0,17 (5,93-5,63)	5,70 ± 0,07 (5,78 -5,65)	5,53 ± 0,32 (5,90 -5,33)	7,47 ± 0,32 (7,84 -7,24)
Precipitation index (mm)	313,5 5± 82,5 (405,15-44,90)	398,00 ± 123,85 (471,0-255,0)	63,53 ± 99,13 (178,0 -6,0)	2,60± 4,50 (7,80 -0,00)
water level (m)	41,14 ± 1,11 (42,25-40,02)	43,60 ± 0,29 (43,77 -43,27)	42,55 ± 0,94 (43,38 -41,53)	37,90 ± 0,84 (38,87 -37,32)