ICHTHYOPLANKTON COMMUNITY IN LAGOONS OF THE TAPAJÓS AND TROMBETAS RIVERS, EASTERN AMAZON

Comunidade ictioplanctônica em lagoas dos rios Tapajós e Trombetas, Amazônia Oriental

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ABSTRACT

We evaluated the structure of the ichthyoplanktonic assemblage (taxonomic composition, abundance, developmental stages, and relationship with local environmental variables) in marginal lagoons located in the clearwater Tapajós and Trombetas rivers, Amazon Basin, Brazil during periods of high water (rising waters and flooding). Samples were collected by means of horizontal drags in the subsurface of the water with a plankton net (300 µm mesh). Sorting, counting, identification of biological material, and classification of embryonic and larval stages were performed under a stereoscopic microscope. A total of 122 eggs and 2,813 fish larvae were captured and distributed in nine orders, 18 families, 20 genera, and 26 species. Of these, more than 75% are considered sedentary or short-distance migrants and more than 50% are of commercial interest. The results revealed fluctuating patterns of abundance and species composition between the lagoons of the two rivers. The ichthyoplankton community in the lagoons consisted mainly of larvae of native pelagic fish belonging to the Engraulidae family and larvae of benthic fish such as Eleotridae, making up more than 85% of the individuals captured in the study area. In addition to these two groups, some larvae of piranha species (*Pygocentrus nattereri*) stood out due to their high densities in the Tapajós river lagoons and croaker larvae (*Plagioscion* spp.) in the Trombetas river lagoons. The highest larval densities were recorded during the night with significant variations recorded in species composition. The presence of all stages of larval development indicates that these biotopes enable growth and are essential for the biological recruitment of fish species in the region. The ichthyoplankton showed a low correlation with the limnological variables, however, the patterns of abundance and composition of fish larval assemblages in the lagoons of the Tapajós and Trombetas rivers were preliminarily elucidated, although additional work is needed to assess the effects on survival and recruitment.

Keywords: larval fish, composition, abundance, clear water, nursery.

RESUMO

Avaliamos a estrutura da assembleia ictioplanctônica (composição taxonômica, abundância, estágios de desenvolvimento e relação com variáveis ambientais locais) em lagoas marginais localizadas nos rios de águas claras Tapajós e Trombetas, Bacia Amazônica, Brasil durante os períodos de águas altas (enchente e cheia). As amostras foram coletadas por meios de arrastos horizontais na subsuperfície da água com rede de plâncton (malha 300 µm). A triagem, contagem, identificação do material biológico e a classificação dos estágios embrionário e larval foi realizado sob microscópio estereoscópico. Foram capturados 122 ovos e 2.813 larvas de peixes, distribuídas em 9 ordens, 18 famílias, 20 gêneros e 26 espécies. Destas, mais de 75% são consideradas como sedentárias ou migradoras de curta distância e mais de 50% são de interesse comercial. Os resultados revelaram padrões flutuantes de abundância e composição de espécies entre as lagoas dos dois rios. A comunidade ictioplanctônica nas lagoas consistiu principalmente de larvas de peixes pelágicos nativos pertencentes à família Engraulidae e larvas de peixes bentônicos como Eleotridae, perfazendo mais de 85% dos indivíduos capturados na área de estudo. Além desses dois grupos, algumas larvas de espécies de piranhas (*Pygocentrus nattereri*) se destacaram pelas elevadas densidades nas lagoas do rio Tapajós e larvas de pescadas (*Plagioscion* spp.) nas lagoas do rio Trombetas. As maiores densidades de larvas foram registradas durante o período noturno com variações significativas registrada na composição de espécies. A presença de todos os estágios de desenvolvimento larval indica que estes biótopos possibilitam o crescimento e são essenciais para o recrutamento biológico das espécies de peixes da região. O ictioplâncton apresentou baixa correlação com as variáveis limnológicas, no entanto, os padrões de abundância e composição das assembleias de larvas de peixes nas lagoas dos rios Tapajós e Trombetas foram elucidados preliminarmente, embora sejam necessários trabalhos adicionais, para avaliar os efeitos sobre a sobrevivência e recrutamento.

Palavras-chave: larvas de peixes, composição, abundância, águas claras, berçário.

INTRODUCTION

The alluvial plain of numerous tributaries of the Amazon River basin presents a complex system of marginal lagoons that occupy lateral depressions of the rivers and are periodically flooded and connected to each other, channels, or neighboring river systems (Souza Filho & Stevaux, 1997, Junk *et al.*, 2012). Thus, they form a landscape mosaic that sustains great biodiversity of species and is essential for the sustainability of the Amazonian fisheries resources (Soares *et al*., 2015; Hurd *et al.*, 2016; Zacardi, 2020). In these water bodies, biological processes and ecological functioning patterns are largely dependent on the hydrometric regime (flooding pulse), which promotes changes in the shape, size, and depth of the lagoons adjacent to the main river channel, contributing to the system homogenization (Junk *et al*., 2012.; Ortega *et al.*, 2015).

The expansion of flooding in the environment enables greater exchanges of water, sediments, minerals, and organisms between different biotopes, in addition to promoting physical and chemical changes such as changes in temperature, turbidity, and the input nutrients (Thomaz *et al*., 2007; Starr *et al.*, 2014). These factors govern, in part, the trophic state, composition, and growth of planktonic assemblages and other aquatic organisms, producing variations in the structure of fish communities and in ichthyoplankton distribution patterns (Tondato *et al*., 2010; Siqueira-Souza *et al*., 2016; Sahoo *et al*., 2017; Zacardi *et al.*, 2019). Marginal lagoons are recognized for their importance in maintaining regional biodiversity, either as natural breeding grounds for commercially valuable fish species (Ponte *et al*., 2019; Oliveira *et al*., 2022) or as a preferential habitat for non-migratory and small-scale species (Tondato *et al*., 2010; Beltrão & Soares, 2018).

However, climate change and expansion of anthropic activities (i.e., agricultural expansion, introduction of exotic species, overfishing, destruction of riparian forests to create pastures, pollution, fires, illegal mining, and damming of rivers) lead to several changes in the dynamics and configuration of drainage basins (Sodré *et al*., 2015; Sousa *et al*., 2021; Prestes *et al*.; 2022; Cajado *et al*., 2022). These interferences in the environment have direct consequences on fish communities and can directly affect migration, reproduction, spawning, larval development, and consequently, biological recruitment (Camargo & Camargo, 2012; Castello & Macedo, 2016; Oliveira *et al*., 2022; Pereira *et al*., 2023). In addition, such interference negatively reflects fishing productivity and causes socioeconomic impacts on the Amazonian populations that depend on these resources for their survival.

Despite the abundance of lagoons ecosystems in the Amazon region, relatively few studies on ichthyoplankton have been performed in these biotopes. Among these are Ponte *et al*. (2019), Zacardi *et al*. (2020), Reis *et al*. (2020), Zacardi and Ponte *et al*. (2021), and Oliveira *et al*. (2022). Except for the last one was carried out in the Juá lagoon (Tapajós river), all the others address composition and seasonality of the ichthyoplankton in floodplain lagoons of white-water systems, such as Solimões and Amazonas. Some lagoons along the Tapajós and Trombetas rivers have relatively well-known ichthyofauna (Silva *et al*., 2006; Soares, 2015; Soares *et al.*, 2015; Silvano, 2020), but with incomplete or non-existent information about species that use their waters as spawning grounds and nursery.

Ichthyoplankton studies provide a base of information involving major population changes of fish species and can serve as a sensitive indicator to monitor the potential effects of recruitment in lagoons, main river channels, and connected habitats such as the river-floodplain system (Amorim *et al.*, 2017, Gao *et al.*, 2018; Vorsatz *et al*., 2021), in addition to predicting the implications of human activities on the ecosystem and fisheries. Therefore, they represent an important component in the assessment of fish stocks. In this context, this study aimed to characterize the taxonomic composition and evaluate the abundance of fish larvae assemblages in lagoons, seeking to answer the following questions: 1) Is there a difference in taxonomic composition and abundance of fish larvae during the flooding phase in the marginal lagoons of the Tapajós and Trombetas rivers? 2) Are marginal lagoons in clearwater tributaries of the Amazon basin essential biotopes for development of early stages of the fish life cycle?

MATERIALS AND METHODS

STUDY AREA

The study area includes marginal lagoons in the floodplain of the Tapajós and Trombetas rivers - two clearwater tributaries of the Amazon River, Pará, Brazil (Table 1). The Tapajós River is a tributary of the right bank of the Amazon River, its watershed has about 764,183 km^2 and is located between latitudes 02°14’38” S and 14°67’38.4” S and longitudes 53°49’34” W and 60°8’42” W. It is formed by the union of the Juruena and São Manuel rivers (Teles Pires), is about 851 km long, carries few suspended materials, and has low conductivity and a pH that varies from 4.5 to 7.8 (Araújo *et al*., 2015). The Trombetas River is a tributary of the left bank of the Amazon River, its watershed has about 129,900 km^2 and is located between latitudes 02°36’36” N and 02°06’00” S and longitudes of 55°11’24” W and 59°02’24” W. It is formed by the union of the Poana and Anamu rivers that have their sources in region of the Acaraí and Tumucumaque mountains, with about 760 km in length between its river-source and mouth in the Amazon River (Ferreira, 1993; Mendel Junior 2022).

Seasonality of precipitation and flow regime is different between the sub-basins, as in the Tapajós river basin rainy season occurs between January and June, and dry season from July to December, and in the Trombetas river basin rainy season is from April to September, and dry season from October to March (Tomasella *et al*., 2013; Coutinho *et al*., 2019). The average annual rainfall is 2,100 mm but varies between 1,500 to 2,900 mm. In general, the region has a humid tropical climate with an average annual temperature between 26 and 27 °C (Hales & Petry, 2015).

In the Tapajós River, five lagoons were sampled (L1: Verde, L2: Piranha, L3: Tapari, L4: Juá, and L5: Mapiri) and in the Trombetas River four lagoons (L6: Caipuru, L7: Curupira, L8: Iripixi, and L9: Xiriri) (Figure 1). The lagoons are connected to the main rivers due to the increase in the water level and occupation of the floodplain during the floods, as they are subject to the average annual fluctuation of river levels (around five to six meters), with the highest levels fluvial registered in the months of May and June, and the smallest in the months of October and November. It is noteworthy that some lagoons receive drainage from streams with springs in areas of *terra firme* (areas that are not subject to flooding because they are located in a higher region of the Amazonian relief) and may be strongly influenced by white-waters rich in suspended material due to the backflow of the Amazon River, as is the case of the Mapiri and Juá lagoons at mouth of the Tapajós River, and Iripixi and Caipuru at mouth of the Trombetas River.

SAMPLING

Samplings were carried out in the flooding phase of the rivers in March 2020 (end of rising water) and May 2021 (flooding), during the day and night on board a local vessel through horizontal drags carried out in the subsurface of the water column (0 - 0.5 meters) at reduced speed (2 km/h) and constant for 10 minutes to increase the capture efficiency, using a conical plankton net (300 µm mesh), with flowmeter attached at mouth of the net to obtain the volume of filtered water. Triplicates were performed because in all lagoons three sections were defined, each with two sampling points: left margin (M1 and M2), middle (M3 and M4), and right margin (M5 and M6).

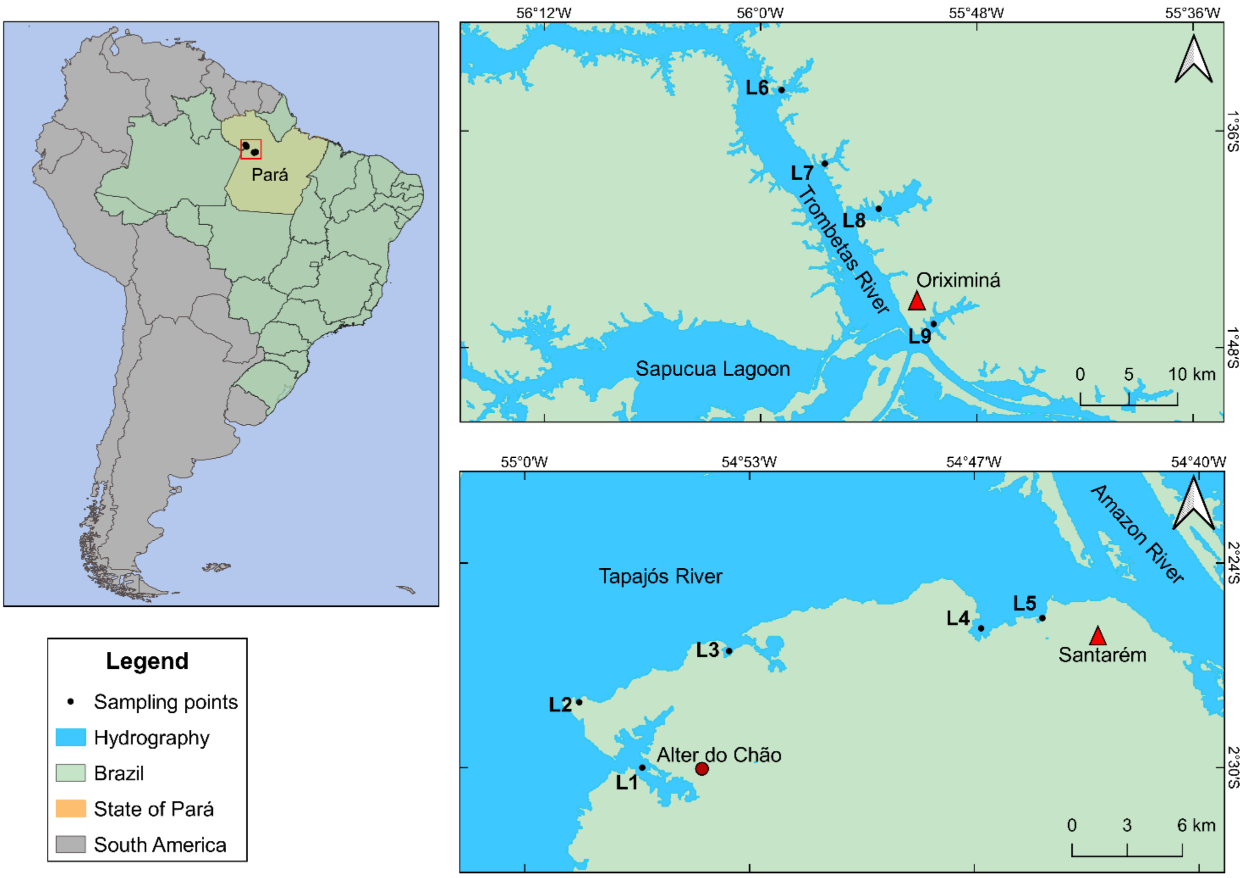

Figure 1: Location of sampled lagoons in the floodplain of the Tapajós and Trombetas rivers, Lower Amazon, state of Pará, Brazil. Tapajós River Lagoons: L1 = Verde Lagoon, L2 = Piranha Lagoon, L3 = Tapari Lagoon, L4 = Juá Lagoon, and L5 = Mapiri Lagoon. Trombetas River Lagoons: L6 = Caipuru Lagoon, L7 = Curupira Lagoon, L8 = Iripixi Lagoon, and L9 = Xiriri Lagoon).

Table 1. Geographical data on the location of marginal lagoons in the floodplain of the Tapajós and Trombetas rivers, Lower Amazon, state of Pará, Brazil.

River	Locality	Coordinates
Tapajós River	Tapari Lagoon	2°26’35” S/ 54°54’00” W
	Piranha Lagoon	2°28’05” S/ 54°58’24” W
	Juá Lagoon	2°25’55” S/ 54°46’36” W
	Verde Lagoon	2°30’00” S / 54°56’33” W
	Mapiri Lagoon	2°25’37” S/ 54°44’48” W
Trombetas River	Caipuru Lagoon	1°40’19” S/ 55°53’27” W
	Curupira Lagoon	1°33’44” S/ 55°58’50” W
	Iripixi Lagoon	1°46’42” S/ 55°50’24” W
	Xiriri Lagoon	1°37’49” S/ 55°56’26” W

After the draging, a eugenol solution (clove oil - 50 mg. L^{-1}) was added to each sample for 10 minutes, to anesthetize/euthanize the organisms present in it. Then, they were preserved in formalin diluted at 10% and placed in properly labeled 500 ml polyethylene bottles. The samples were transported for analysis at the Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores of the Universidade Federal do Oeste do Pará. The sampling effort totaled 216 final samples (9 lagoons x 3 sections x 3 points per section x 2 sampling times - day and night x 2 phases of the local hydrological cycle - rising waters and flooding).

Limnological variables such as water temperature (°C), dissolved oxygen (mg. L^{-1}), electrical conductivity (µS. cm^{-1}), hydrogen potential (pH) and turbidity (NTU) were obtained in loco concomitantly to the sampling drags using digital potentiometers. Water transparency (m) was measured through a Secchi disc. Ichthyoplankton were collected under permit Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) license number 72.330 issued based on the Normative Instruction number 154/2007.

Processing of samples

In the laboratory, the samples were washed and prepared for the sorting process, which consists of separating fish eggs and larvae from suspended material, debris and total plankton under a stereoscopic microscope using Bogorov plates with the aid of stylets, brushes, tweezers and Pauster pipettes. After sorting, the ichthyoplankton was quantified and the larvae identified at the lowest possible taxonomic level using specialized bibliographies and the regressive sequence of development technique, as recommended by Ahlstrom and Moser (1976) and described by Nakatani *et al*. (2001), which consists of identification through morphological, meristic and morphometric analysis from a sequence of individuals in different stages, from juveniles or more developed larvae to newly hatched larvae. Among the characters used for identification, the following were considered: body shape, pigmentation pattern, fin formation sequence, presence, or absence of barbels, relative position of the anal opening in relation to the body, eye diameter, digestive tract shape and for the swim bladder, number of myomeres, rays and fin spines (Figure 2).

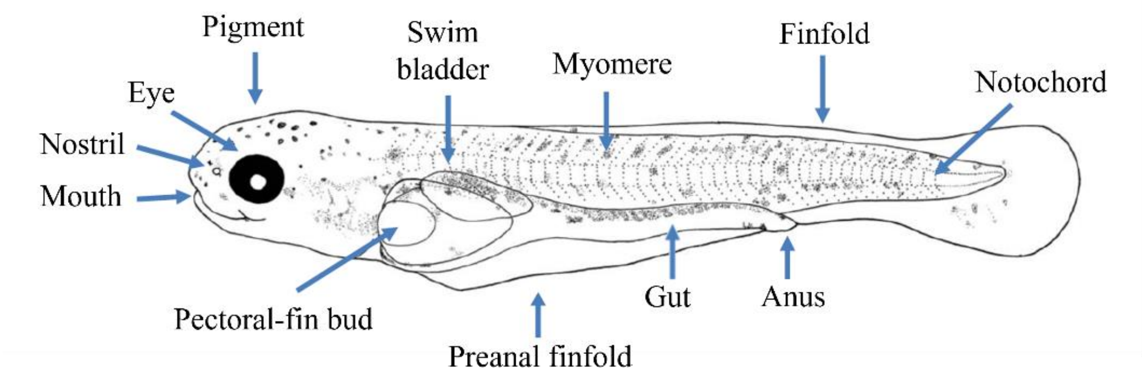

Figure 2. Illustration of a curimatá larva (*Prochilodus nigricans*) indicating the main structures observed for identification. Adapted from Silva *et al.* (2022).

Taxonomic classification of species followed Frickle *et al*. (2022) and classification of orders was presented in alphabetical order according to Betancur-R *et al.* (2017), except for Characiformes, in which the classification by Oliveira *et al.* (2011) and Achiridae (Girard *et al*., 2020). The larvae designated as "unidentified" corresponded to individuals with damaged structures and/or in a very early stage of development.

The eggs were classified as pelagic or free, considering the size of the perivitelline space (larger in migratory species and without parental care), demersal, with a greater amount of yolk and reduced perivitelline space, and adhesive, those that present structures in your chorion that help with stickiness. The eggs were classified according to the stages of embryonic development (Figure 3), proposed by Ahlstrom & Ball (1954) and modified by Nakatani *et al.* (2001): a) initial cleavage - stage in which the formation of the first cells occurs, including the stages of morula, blastula and gastrula; b) early embryo - stage in which embryo differentiation and tail formation occur; c) free tail embryo - stage in which the tail detaches from the yolk; and d) final embryo - stage in which the embryo is practically formed and ready for hatching.

The larvae were categorized according to the flexion of the final section of the notochord and the sequence of development of the fins and their support elements, comprising four stages (Figure 3): a) yolk-sac larval - from hatching to when the larvae have a complete eye or partially pigmented, opening of anus and mouth; b) pre-flexion - extends from the opening of the anus and mouth to the beginning of notochord flexion, with the appearance of the first support elements of the caudal fin; c) flexion - characterized by the beginning of flexion of the notochord with the appearance of the support elements of the caudal fin until its complete flexion and appearance of the pelvic fin bud; and d) post-flexion - from complete flexion of the notochord and appearance of the pelvic-fin bud until the complete formation of pectoral-fin rays and total absorption of the embryonic fin.

Individuals considered juveniles were those that showed complete formation of the rays of all fins, the appearance of scales until the first sexual maturation. The identified specimens were stored in properly identified glass vials containing 4% formaldehyde. The most complete individuals are being used as testimony specimens and deposited in the Collection of Fish Eggs and Larvae (CROLP) of the Universidade Federal do Oeste do Pará (UFOPA).

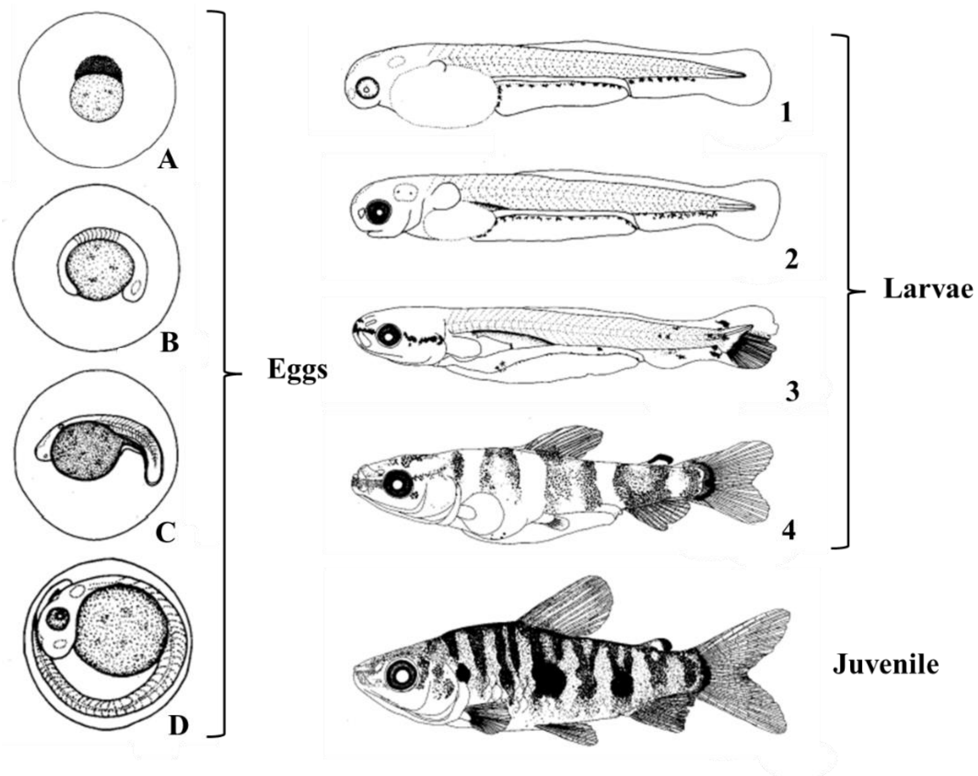

Figure 3. Illustration indicating the different periods and stages of early development of freshwater fish. Embryonic period: A - Early cleavage, B - Early embryo, C - Free tail embryo and C - Final embryo. Larval period: 1 - Yolk-sac larval, 2 - Pre-flexion, 3 - Flexion and 4 - Post-flexion, and juvenile individual. Adapted from Nakatani *et al*. (2001).

DATA ANALYSIS

Ichthyoplankton abundances were standardized for a volume of 10 m^{-3} of filtered water (number of organisms per 10 m^{-3}) as proposed by (Nakatani *et al*., 2001): $Y = (X/V) \times 10$, where Y represents the density of eggs or larvae in 10 m^{-3}, X represents the number of captured eggs or larvae, and V represents the volume of filtered water. For Principal Component Analysis (PCA), environmental data were subjected to z-score transformation to standardize variable scales (Gotelli & Ellison, 2013).

The PCA was used to reduce the dimensions of environmental variables and examine the existence of environmental differences between lagoons. Axes with eigenvalues greater than 1.0 were used for interpretation, according to the Kaiser-Guttman criterion. Only variables with score coefficients >0.4 were considered biologically important (Gotelli & Ellison, 2013). Permutation Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001) using Bray-Curtis similarity matrix and randomizations (9999 permutations) was used to verify the existence of differences in spatial distribution patterns (between lagoons and rivers) and temporal (day and night) on the composition and abundance of fish larval assemblages. A percentage similarity analysis (SIMPER) was conducted to emphasize the main taxa responsible for the formation of the delineated groups. Scatterplots and Spearman correlation tests were used to assess the correlation between environmental variables and egg and larvae density.

RESULTS

Of the total ichthyoplankton captured, 4.16% (n= 122) was represented by eggs belonging to the non-migratory category in the initial cleavage stage and obtained only in the Piranha lagoon near Alter-do-Chão (Santarém, state of Pará). The marginal lagoons of the Tapajós River contributed with 2,070 individuals and marginal lagoons of the Trombetas River with 743 individuals, totaling 2,813 larvae (95.84%), distributed in nine orders, 18 families, 20 genera and 26 species (Table 2). Of these, more than 75% are considered sedentary or short-distance migratory and more than 50% are larvae of species of commercial interest in the Amazonian region.

Table 2. Taxonomic composition and average density (ind.10m^{-3}) of ichthyoplankton captured in the marginal lagoons of the Tapajós and Trombetas rivers, state of Pará, Brazil.

Taxa	**N**	**Tapajós River Lagoons**				**Trombetas River Lagoons**				
		Juá	**Verde**	**Mapiri**	**Piranha**	**Taparí**	**Caipuru**	**Curupira**	**Iripixi**	**Xiriri**
CARANGIFORMES		-	-	-	-	-	-	-	-	-
ACHIRIDAE		-	-	-	-	-	-	-	-	-
Hypoclinemus mentalis	4	-	-	-	0.03	-	-	-	0.01	-
CHARACIFORMES		-	-	-	-	-	-	-	-	-
ANOSTOMIDAE		-	-	-	-	-	-	-	-	-
Schizodon fasciatus	1	-	-	-	0.01	-	-	-	-	-
CHARACIDAE	4	-	-	0.01*	-	0.08*	-	-	-	-
CTENOLUCIIDAE		-	-	-	-	-	-	-	-	-
Boulengerella cuvieri	2	-	-	-	-	-	-	0.02	-	-
CURIMATIDAE		-	-	-	-	-	-	-	-	-
Curimatella sp.	20	-	-	1.41	0.22	-	-	-	-	-
Psectrogaster amazonica	3	-	-	0.17	-	-	-	-	-	-
ERYTHRINIDAE		-	-	-	-	-	-	-	-	-
Erythrinus erythrinus	8	-	-	-	-	0.19	-	-	-	-
HEMIODONTIDAE	21	0.03*	-	-	0.18*	0.02*	-	0.03*	-	0.10*
Anodus elongatus	16	-	-	0.17	-	-	-	0.02	-	-
Hemiodus atranalis	3	-	-	0.04	-	-	-	0.01	-	-
Hemiodus immaculatus	4	0.03	-	0.05	-	-	-	-	-	-
Hemiodus microlepis	5	-	-	0.23	0.02	-	-	0.01	-	-
Hemiodus unimaculatus	5	-	-	0.13	-	-	-	-	-	-
SERRASALMIDAE		-	-	-	-	-	-	-	-	-
Pygocentrus nattereri	48	1.14	-	2.19	0.08	-	-	-	0.07	-
Serrasalmus sp.	52	-	-	0.70	0.02	-	-	-	-	-
TRIPORTHEIDAE		-	-	-	-	-	-	-	-	-
Agoniates halecinus	2	-	-	-	-	-	-	-	0.01	0.02
CLUPEIFORMES		-	-	-	-	-	-	-	-	-
ENGRAULIDAE		-	-	-	-	-	-	-	-	-
Engraulidae gen. sp.	1490	5.01	3.09	9.23	6.52	3.87	0.92	2.29	2.98	3.89
CYPRINODONTIFORMES		-	-	-	-	-	-	-	-	-
POECILIIDAE		-	-	-	-	-	-	-	-	-
Poecilia scalpridens	11	-	-	0.22	-	-	-	-	-	-
GOBIIFORMES		-	-	-	-	-	-	-	-	-
ELEOTRIDAE		-	-	-	-	-	-	-	-	-
Microphilypnus tapajosensis	945	3.53	2.38	21.60	4.96	1.94	0.47	0.77	4.71	3.06
Microphilypnus acangaquara	13	-	-	-	-	0.31	-	-	-	-
GYMNOTIFORMES		-	-	-	-	-	-	-	-	-
STERNOPYGIDAE		-	-	-	-	-	-	-	-	-
Eigenmannia sp.	1	-	-	-	-	0.02	-	-	-	-
INSERTAE SEDIS		-	-	-	-	-	-	-	-	-
SCIAENIDAE	8	-	-	-	-	-	-	0.05*	-	0.04*
Pachypops sp.	10	-	-	-	-	-	-	0.05	-	0.10
Plagisocion cf. *montei*	79	-	-	-	-	-	1.36	1.23	0.03	0.22
Plagioscion squamosissimus	16	0.01	0.56	-	-	-	-	0.03	0.01	0.02
SILURIFORMES	2	-	-	-	0.02*	-	-	-	-	-
AUCHENIPTERIDAE		-	-	-	-	-	-	-	-	-
Tatia cf. *melanoleuca*	2	-	0.02	-	-	0.02	-	-	-	-
DORADIDAE		-	-	-	-	-	-	-	-	-
Doradidae gen. sp.	1	-	-	0.01*	-	-	-	-	-	-

PIMELODIDADE		-	-	-	-	-	-	-	-	-
Hypophthalmus donascimientoi	2	-	-	-	-	-	-	-	-	0.03
Hypophthalmus edentatus	2	-	-	-	-	-	-	-	0.02	-
Pimelodus sp.	15	-	-	-	-	-	-	-	0.37	-
TETRAODONTIFORMES		-	-	-	-	-	-	-	-	-
TETRAODONTIDAE		-	-	-	-	-	-	-	-	-
Colomesus asellus	12	0.01	0.04	0.01	-	-	0.01	0.01	0.28	-
Unidentified	6	-	-	-	0.05*	-	0.18*	-	-	-
Eggs	122	-	-	-	1.33	-	-	-	-	-
Ichthyoplankton total	2,935	9.76	6.09	35.99	13.21	6.45	2.94	4.52	8.49	7.39

* Damaged larvae or in very early stages of development, making identification at lower taxonomic levels impossible.

The lagoons of both rivers share nine species (Figure 4). Some, such as *Schizodon fasciatus*, *Curimatella* sp., *Psectrogaster amazonica*, *Microphilypnus acangaquara*, *Poecilia scalpridens*, *Serrasalmus* sp., *Tatia* cf. *melanoleuca*, *Eigenmannia* sp., *Hemiodus immaculatus*, *H.unimaculatus*, *Plagioscion squamosissimus*, Doradidae gen. sp. and *Erythrinus erythrinus* were captured only in the Tapajós River lagoons. While *Agoniates halecinus*, *Boulengerella cuvieri*, *Hypophthalmus donascimientoi*, *H. edentatus*, *Pachypops* sp. occurred only in the lagoons of the Trombetas river. Individuals with damaged structures or in very early stages of development accounted for less than 1% of the collected material.

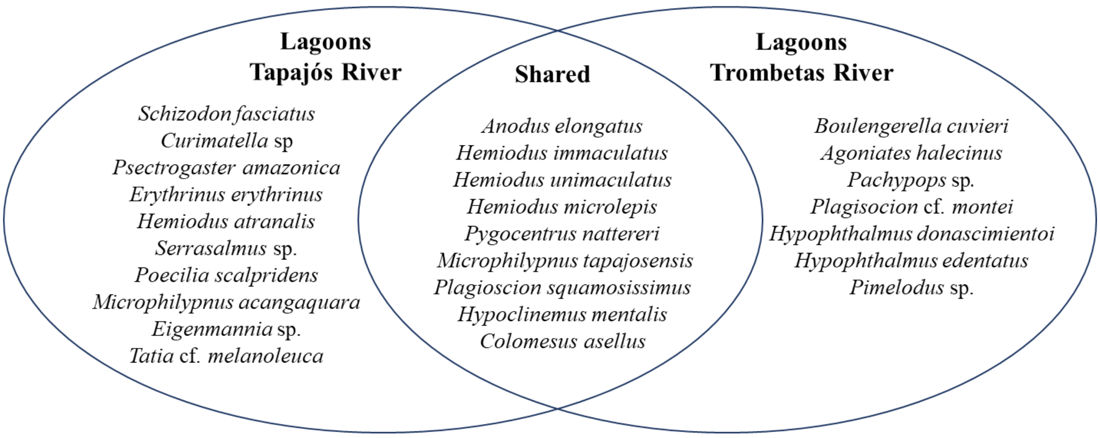

Figure 4. Larvae of fish species recorded in the marginal lagoons of the Tapajós and Trombetas rivers, Lower Amazon, state of Pará, Brazil

The larval density varied among the lagoons. In the Tapajós river lagoons, highest densities were recorded in the Mapiri (37.99 larvae.10m^{-3}) and Piranha (13.21 larvae.10m^{-3}), while in the Trombetas river lagoons, highest densities were in Iripixi (8.49 larvae.10m^{-3}) and Xiriri (7.39 larvae.10m^{-3}). The orders with the greatest diversity of families were the Characiformes and Siluriformes, which also had the greatest numerical abundance of species in the Tapajós River lagoons. In other hand, for Trombetas river lagoons, the order Characiformes was most diverse, and other orders presented similar numbers of families and species (between one and two species – Table 2). Although Characiformes and Siluriformes have greater taxonomic diversity, the orders Clupeiformes and Gobiiformes, represented by families Engraulidae and Eleotridae (*Microphilypnus* spp.), respectively, were the dominant groups, comprising more than 85% of individuals captured throughout study area (Figure 5). No significant difference was found in the variation of larval abundance of the two most abundant taxa among the lagoons studied in this period.

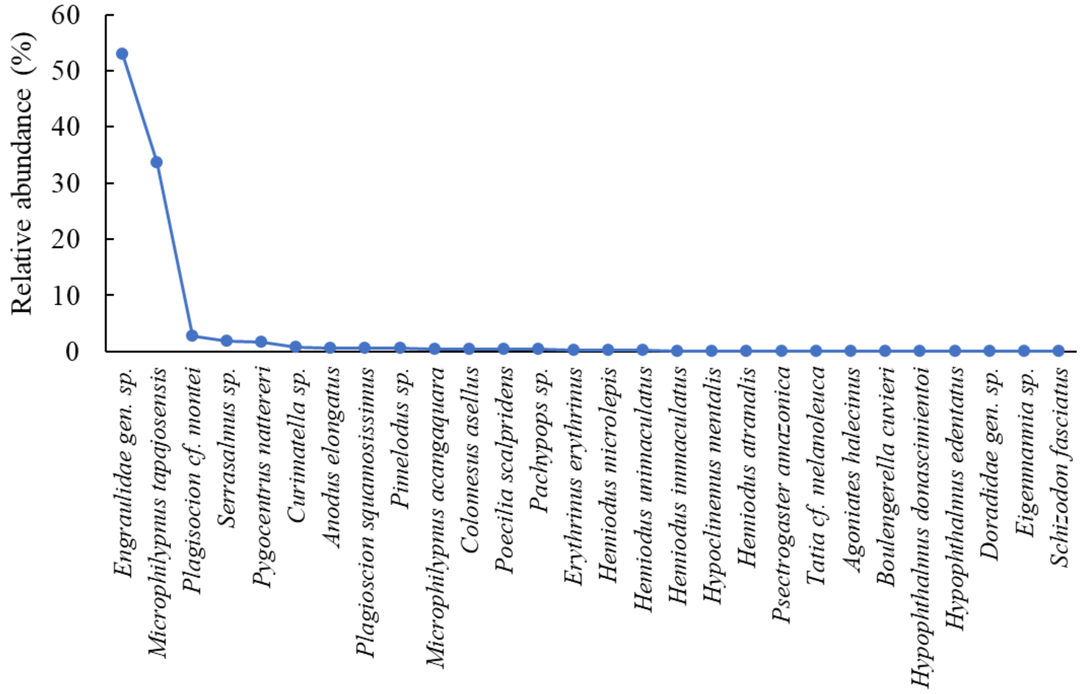

Figure 5. Ranking of the relative abundance of fish larvae taxa captured in the marginal lagoons of the Tapajós and Trombetas rivers, Lower Amazon, state of Pará, Brazil

The composition of the larval community was similar between the lagoons (Pseudo-F = 1.581; R^2 = 0.085; p =0.051), regardless of the river, with dominance of the species *M. tapajosensis* and Engraulidae gen. sp. Despite the high densities of these two groups, some species such as freshwater croaker (*Plagioscion* cf. *montei*) in the Caipuru, Curupira, and Xiriri lagoons, the pufferfish (*C. asellus*) in the Iripixi lagoon, the piranhas (*Pygocentrus nattereri*; *Serrasalmus* sp.) in the Juá, Mapiri, and Piranha lagoons and the little-pocomon (*M. acanguaquara*) also highlighted for their high densities (Figure 6).

The highest larval densities were recorded during the night (20.12 larvae.10m^{-3} *vs*. 1.73 larvae.10m^{-3} during the day) with significant variations in composition (Pseudo-F = 3452; R^2 = 0.023; p = 0.020). The greatest richness was recorded during nocturnal sampling and some species were exclusive to this period, such as for example *Psectrogaster amazonica*, *P. nattereri* and *Hypophthalmus edentatus*. However, *Poecilia scalpridens* and *Plagioscion squamosissimus* larvae were captured exclusively during the day in the lagoons, indicating that the larvae of some species tend to concentrate in the first layers of the water column during the daily shifts (active vertical migratory behavior).

Apart from the Juá, Verde, Mapiri, and Iripixi lagoons, all initial stages of development were recorded, with a greater contribution of larvae in flexion and pre-flexion (Figure 7). All identified yolk-sac larvae individuals belong to the Hemiodontidae family, which indicates that the lagoons are close to or are used as spawning areas by this group of fish.

Several species had more than two developmental stages captured in the lagoons: *M. tapajosensis*, *M. acangaquara*, Engraulidae gen. sp., *A. elongatus*, *C. asellus*, *H. atranalis*, *H. immaculatus*, *H. unimaculatus*, *H. mentalis*, *H. donascimentoi*, *Pachypops* sp., *P.* cf. *montei*, *P. nattereri*, *P. amazonica* and *Serrasalmus* sp., highlighting the relevance of these biotopes as appropriate places for the development of the initial life cycle of several species of fish (Figure 8).

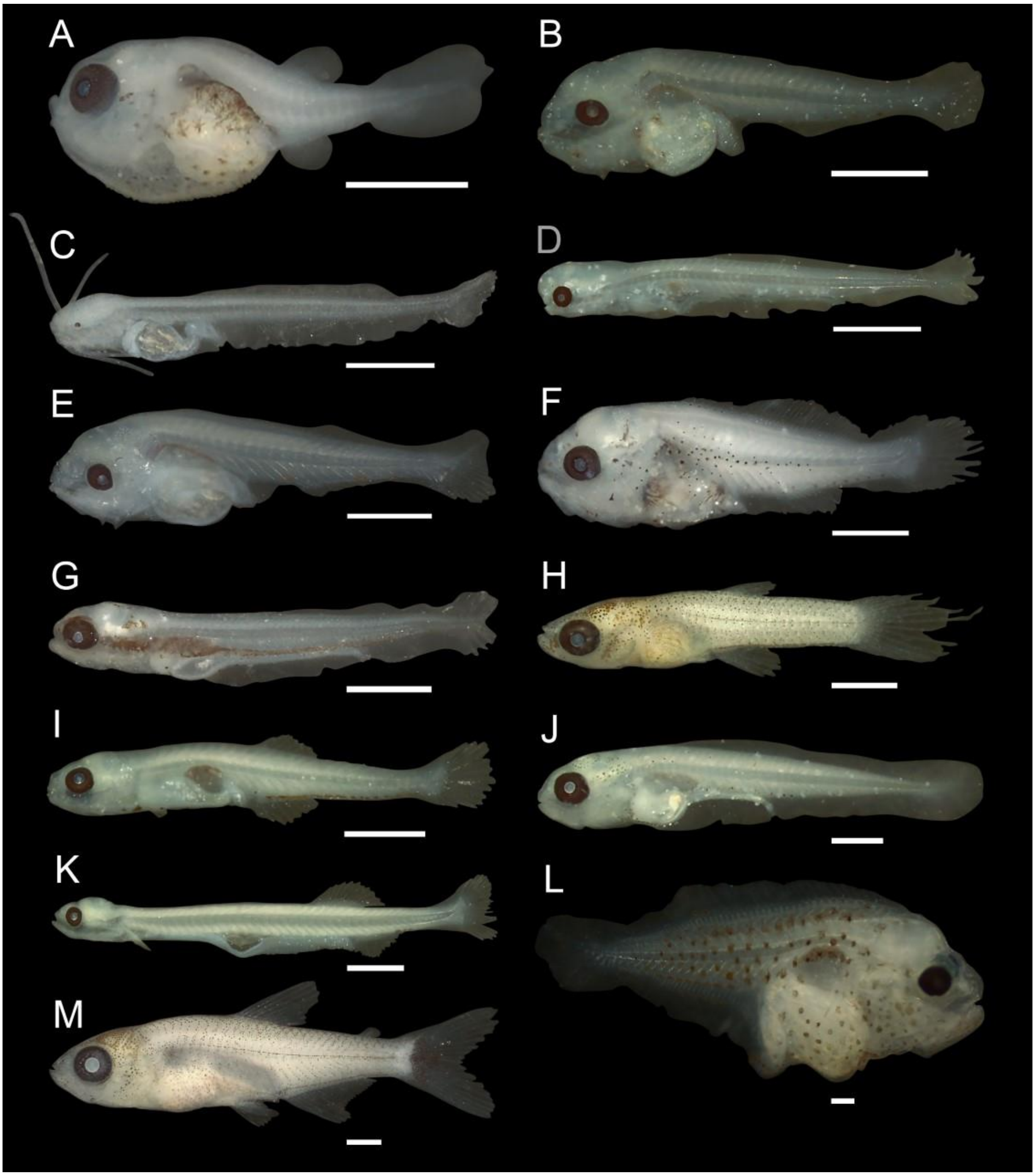

Figure 6. Images of some larval fish collected during samplings from lagoons, at the mouth of the Tapajós e Trombetas rivers, state of Pará, Brazil: A) *Colomesus asellus* - 3.48 mm; B) *Plagioscion squamosissimus* - 4.47 mm; C) *Hypophthalmus edentatus* - 4.93 mm: D) *Schizodon fasciatus* - 4.87 mm; E) *Plagioscion* cf. *montei* - 5.11 mm; F) *Pachypops* sp. - 5.08 mm; G) *Boulengerella cuvieri* - 5.14 mm; H) *Poecilia scalpridens* - 5.11 mm; I) *Microphilypnus tapajosensis* - 5.06 mm; J) *Pygocentrus nattereri* - 7.95 mm; K) Engraulidae - 7.29 mm; L) *Hypoclinemus mentalis* - 3.56 mm; M) Characidae - 10.89 mm.
Bars = 1 mm.

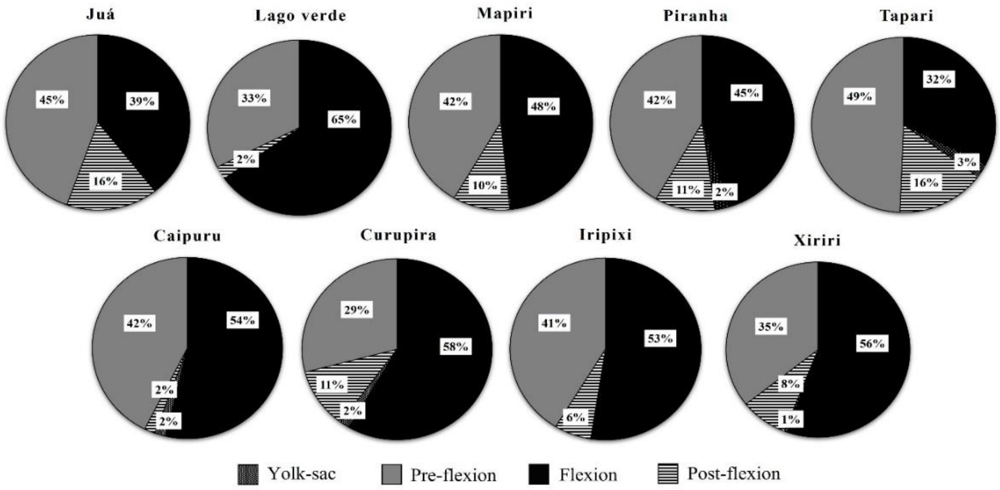

Figure 7. Relative contribution of early development stages captured in the marginal lagoons of the Tapajós and Trombetas rivers, Lower Amazon, state of Pará, Brazil

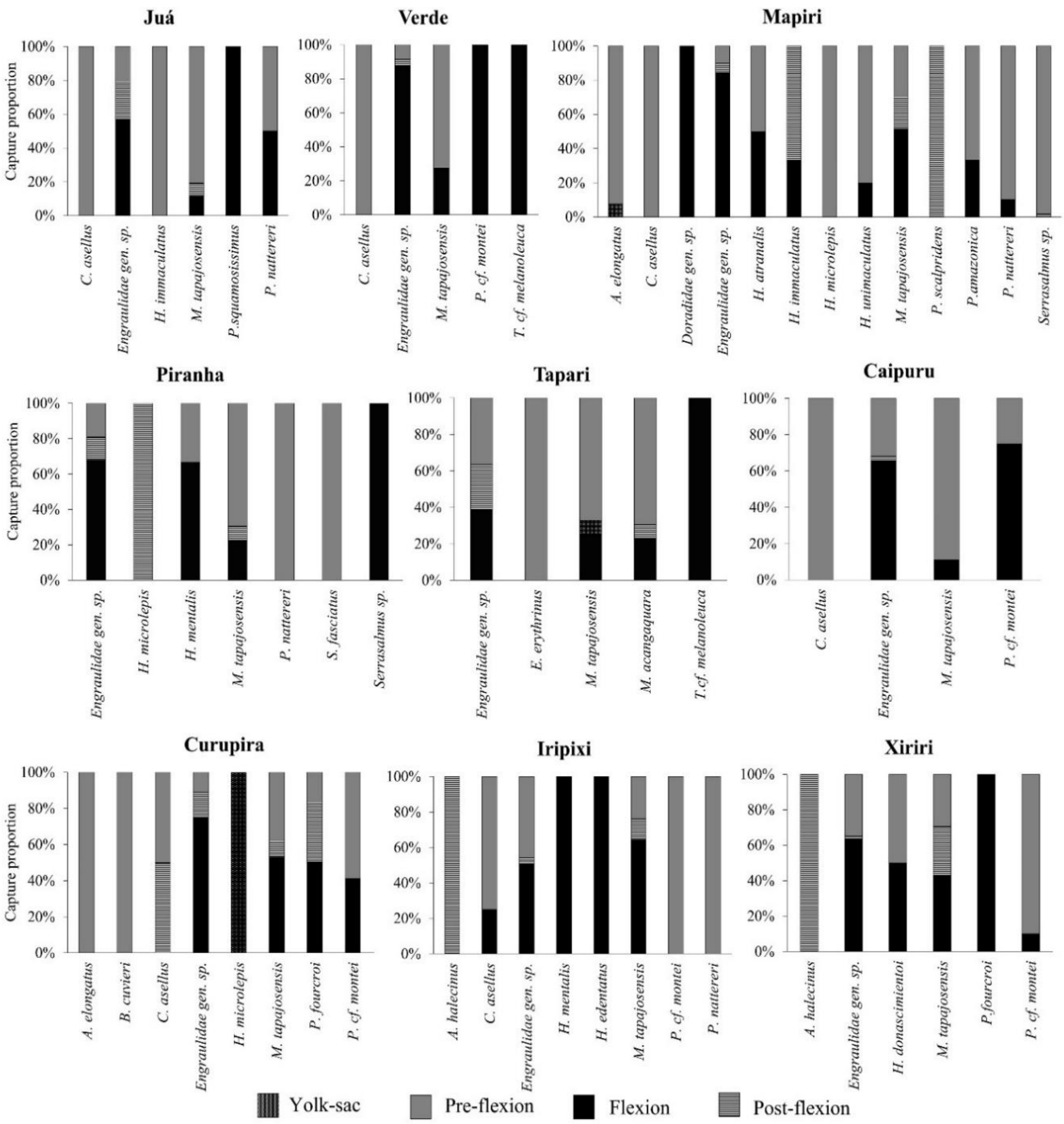

Figure 8. Relative proportion values of early developmental stages by captured taxa in the marginal lagoons of the Tapajós and Trombetas rivers, Lower Amazon, state of Pará, Brazil

The environmental variables measured during study showed little variability, showing limnological uniformity (Figure 9), being relatively hot (>28 °C), slightly acidic (< 7), low turbidity, high transparency (>150 cm) and good oxygenation (>5 mg. L^{-1}). It stands out the Itapari lagoon, which presented the lowest mean values of electrical conductivity, turbidity and pH, and the highest dissolved oxygen rate among the sampled points and lagoons (Table 3).

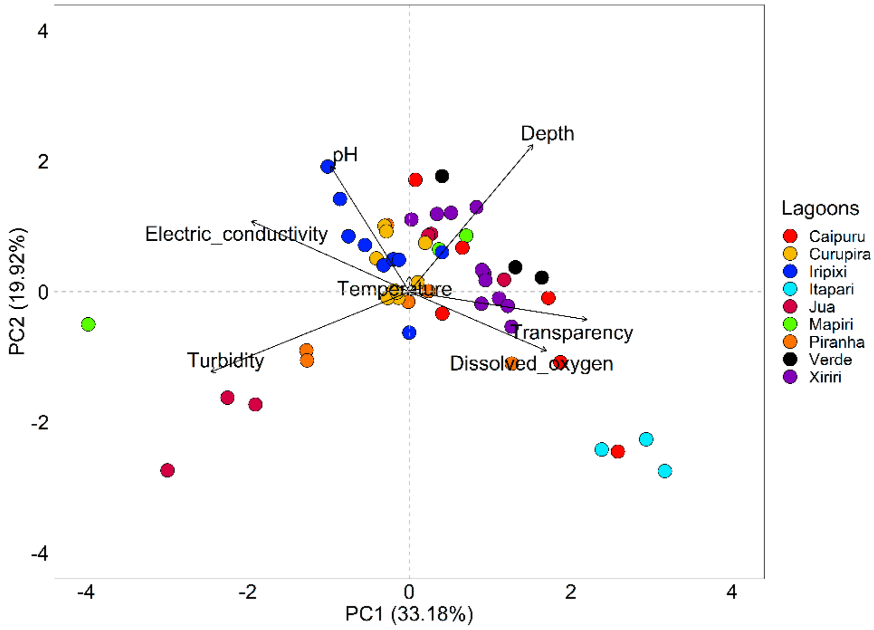

Figure 9. PCA analysis between the environmental variables measured along the sampling points in the marginal lagoons of the Tapajós and Trombetas rivers, Lower Amazon, state of Pará, Brazil

Table 3. Mean values of environmental variables measured along the sampling points in the marginal lagoons of the Tapajós and Trombetas rivers, Lower Amazon, state of Pará, Brazil

Environmental variables	Tapajós River Lagoons					Trombetas River Lagoons			
	Juá	Verde	Mapiri	Piranha	Taparí	Caipuru	Curupira	Iripixi	Xiriri
Electrical conductivity (µS. cm^{-1})	12.3	10.4	16.7	12.6	4.8	11.1	14.2	16.6	11.4
Temperature (°C)	29.8	29.9	29.9	29.6	30.3	30.7	31.7	31.8	31.6
pH	6.83	6.86	6.51	6.23	5.31	6.64	5.68	6.45	5.24
Dissolved oxygen (mg. L^{-1})	5.7	5.2	5.5	5.9	8.6	5.8	5.3	5.8	6.1
Turbidity (NTU)	3.79	4.01	4.38	4.47	1.98	2.37	2.59	3.88	3.79
Transparency (cm)	250	280	245	180	280	180	160	165	175
Depth (cm)	675	830	780	600	450	750	570	650	820

The ichthyoplankton showed a low correlation with the limnological variables measured in the lagoons during the flood periods (Figure 10). The variability of these factors occurs throughout the year and is linked to the seasonality of rainfall and water level fluctuations, which reinforces the importance of sampling covering longer period scales, covering all phases of the local hydrological cycle or months of the year instead than just during high waters.

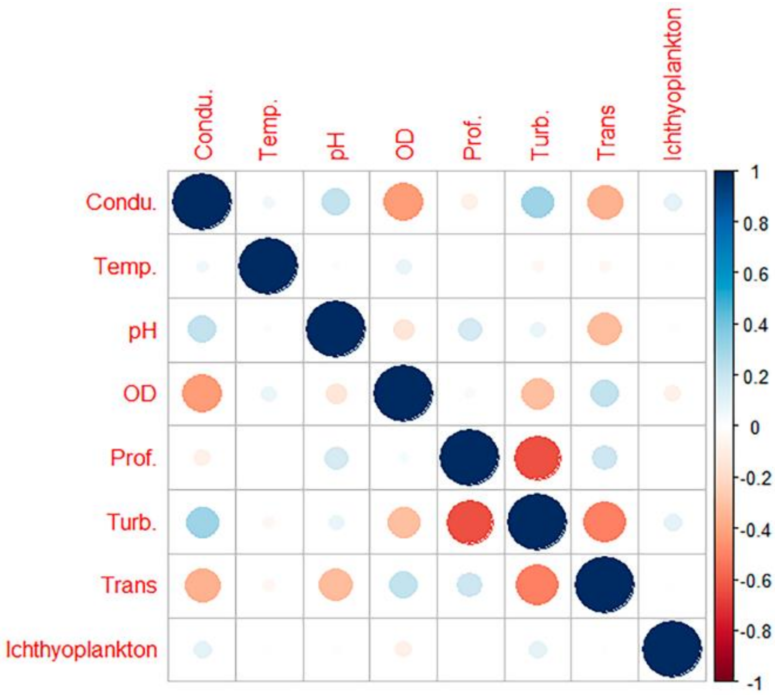

Figure 10. Spearman correlation between ichthyoplankton density and measured environmental variables in the marginal lagoons of the Tapajós and Trombetas rivers, Lower Amazon, state of Pará, Brazil.

DISCUSSION

Our results demonstrate that the larval community structure is similar between lagoons of the different drainages of clearwater rivers, dominated mainly by larvae of Engraulidae and Eleotridae. Although the taxonomic composition is similar, some species were exclusive to the lagoons of each river. The presence of larvae in all ontogenetic stages indicates that the marginal lagoons act as nurseries and recruitment sites for the fish species. The presence of eggs in Piranha Lagoon shows reproductive and spawning activity in the area. However, the absence of eggs in the other lakes may be related to the fact that the embryonic development of the resident fish species is relatively fast, seasonality and short reproductive periods, synchronous spawning, and in very specific places (Castro *et al*., 2002; Araújo, 2009).

The wide distribution of fish larvae occurring in all lagoons sampled demonstrates the importance of these biotopes adjacent to clearwater rivers as breeding and development sites for several species of fish. This occurs mainly for the small and resident species, with all their life cycle occurring within the floodplain and with great trophic importance for the aquatic environment, among other species of economic interest and exploited by artisanal fishing. The river-floodplain systems form aquatic and transitional habitats that favor the maintenance of considerable biodiversity, favoring the emergence of nursery areas (Luz *et al*., 2009). During floods, these marginal lagoons are flooded, forming habitats with distinct hydrological characteristics, with more lentic waters, the presence of aquatic macrophytes, and riparian vegetation on the banks, offering shelter and food (phytoplankton, zooplankton, periphyton, benthos) in abundance for the fish young (Mounic-Silva & Leite, 2013; Zacardi *et al*., 2020; Oliveira L. *et al*., 2020).

Regarding the taxonomic composition of the community, a predominance of larvae from some groups such as Clupeiformes and Gobiiformes was observed, and greater species richness was recorded for Characiformes and Siluriformes, in agreement with the diversity pattern for the Amazon basin and its tributaries (Lima & Araújo-Lima, 2004; Oliveira & Ferreira, 2008; Barletta *et al*., 2010; Zacardi *et al*., 2019). However, the composition and number of species varied between water bodies. This may be associated with the ecological characteristics of each group or species, making the low occurrence of larvae and/or the absence of some species in the samples common. The favorable conditions of oxygenation, depth, habitat complexity, foraging, and lentic environment offer advantages to small Characiformes (e.g., Hemiodontidae) and disfavor the presence of Siluriformes larvae which in general are bottom species and found mainly in river channels (Ferreira *et al*., 2016; Barthem *et al*., 2017; Chaves *et al*., 2017). The ichthyoplankton community collected in this study is considered common, with some species considered abundant in lagoons and river channels in the Lower Amazon and adjacent areas, directly reflecting on the structure of local adult fish assemblages and their life histories (Zacardi *et al*., 2017; Thompson *et al*., 2019; Ponte *et al*., 2019).

For example, the species *Microphilypnus* (Gobiiformes) have a long reproductive period, early sexual maturity, and a rapid generation replacement rate (Suzuki, 2016; Zacardi *et al*., 2019; Oliveira C. *et al*., 2020). For these reasons, it is a typical specie of opportunistic life history strategy, occupying the dominant population position in the larval stages during the reproductive period (Zacardi *et al*., 2019). Thus, the results indicated that the structure of the fish larvae community was also determined by the reproductive strategies and induced by the increase in the water level, which will probably guarantee a sufficient food supply and adequate environmental conditions for their descendants (Álvarez *et al*., 2012; Mendonça *et al*., 2015; Picapedra *et al*., 2018), indicating the importance of river-lagoon connectivity for the community structure (Yi *et al*., 2010; Ponte *et al*., 2019; Melo-Silva *et al*., 2022).

The highest densities of larvae captured at night and in the subsurface of the water column, configure a behavioral mechanism related to ontogenetic stages, food availability (nocturnal zooplankton migration), visual acuity, swimming capacity, strategy against predators or even to reduce intra and interspecific competition (Utne-Palm, 2010; Santin, 2012; Mendonça *et al*., 2015; Picapedra *et al*., 2018; Rosa *et al*., 2019). This behavioral mechanism is one of the most successful mechanisms in the life history of many fish species. (Picapedra *et al*., 2015; Zacardi, 2015). Thus, they allow these individuals to fulfill their ecological and physiological needs in the environment (Pareja-Carmona *et al*., 2014; Picapedra *et al*., 2018). Furthermore, the search for food and the escape from visual predators are some of the most important factors for the occurrence of this behavior, with the photoperiod being a stimulus for this biological event (Picapedra *et al*., 2015; Zacardi *et al*., 2017).

The marked presence of flexion and pre-flexion developmental stages for the species analyzed in this study suggests that the lagoons must safely allow for growth and recruitment maximization. The presence of larvae in less developed stages (yolk-sac larval and pre-flexion), indicates that reproduction sites, if they do not occur in the lagoon itself, possibly occur on the banks of the river channels, close to the entrance of the lagoons, mainly of migratory species. The reproduction of most fish that inhabit floodplains is highly seasonal, coincides with periods of high rainfall, and is closely related to water level fluctuations and flooding phases (Cantanhêde *et al*., 2016; Oliveira & Queiroz, 2017; Serrão *et al*., 2019; Zacardi *et al*., 2020; Carvalho *et al*., 2021). This ensures the access of larvae to suitable feeding and sheltering places and, consequently, success in recruiting and renewing stocks.

The Tapajós and Trombetas rivers have a long history of anthropic disturbances, including increased turbidity (sediment carry-over), pollution and contamination by tailings (Bauxite mining), mercury (illegal mining) among others, which modify the environmental characteristics and ecosystem functions (Nevado *et al*., 2010; Sodré *et al*., 2015; Freitas *et al*., 2019; Noronha Filho *et al*., 2021; Menezes *et al*., 2022; Montes *et al*., 2022). However, the presence of eggs, richness, and abundance of recorded larvae indicates the resilience of the local ichthyofauna. Thus, the ichthyofaunistic diversity and the size of natural stocks depend, to a large extent, on the conservation and integrity of these environments, which are crucial to enable the maintenance of fisheries, the life cycle of fish, and the abundance of species. In this way, it is recommended the establishment of a continuous monitoring system in the two rivers, their tributaries, and flood-prone marginal areas as an essential element of subsidy of data and information, fundamental requirements to guarantee safe interventions, and marking of possible mitigation measures.

We found that fish larvae were present in all lagoons sampled, with heterogeneous variation in richness and abundance. Our findings showed that the limnological conditions did not correlate and were not sufficient to determine patterns in the structure and distribution of ichthyoplankton in the analyzed period, since the lagoons presented similar characteristics during the flood. Although additional work is needed monthly, overall, the ichthyoplankton community in the lower reaches of the Tapajós and Trombetas rivers was revealed. Therefore, it is particularly important to study the patterns of fish larval assemblages and identify key functional groups with specific environmental sensitivities, as an alternative to formulating adequate policies to guarantee the protection and correct fisheries management for the region.

CONCLUSION

Despite the short seasonal scale, our results highlight the role of marginal lagoons as breeding, nursery, and growth sites for fish species of different ecological and migratory categories, confirmed by the presence of larvae in all stages of early development. Although the exclusive occurrence of species both in the lagoons of the Tapajós river, and only in the lakes of the Trombetas river, significant differences in composition were not observed. These biotopes are essential for maintaining the current levels of recruitment of fish species that support fisheries in the region and fundamental species as links in the aquatic trophic chain. Complementary studies should be carried out to better understand the reproductive strategy of the fish and the specific periods and places used for spawning. We call attention to the need to maintain the integrity of the lakes and the natural flow regime, aiming not only at the conservation of diversity but at a sustainability model that satisfactorily meets the level of production of fish stocks, which are, from a perspective of many impacts and anthropic changes along the basins, with direct repercussions on the river-lagoon flooding system.

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