

SPATIAL DIVERSITY OF ICHTHYOPLANKTON IN THE LOWER STRETCH OF THE AMAZON RIVER, PARÁ, BRAZIL

Ruineris A. CAJADO*, Lucas S. OLIVEIRA, Maria A.L. SUZUKI, and Diego M. ZACARDI

*Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores, Instituto de Ciências e Tecnologia das Águas,
Universidade Federal do Oeste do Pará, Santarém, Pará, Brasil*

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Background. This study analyzed the variation of abundance and spatial distribution of fish eggs and larvae sampled from December 2017 to April 2018 along approximately 23 km in the downstream/upstream direction (departing from the city of Santarém) in the lower stretch of the Amazon River, with emphasis on gradients: vertical (subsurface and depth) and horizontal (in the mid channel and the shore proximity).

Materials and methods. Fish eggs and larvae were collected at six sampling stations, each representing the mid channel, the shore proximity areas, and both the subsurface (by means of horizontal trawling) and the depth of 10 meters (by means of a conical plankton net with a mesh size of 300 μm).

Results. During the sampling period, a total of 62 eggs and 8188 fish larvae were collected. The larvae represented seven orders, 21 families, 29 genera, and 46 species-level taxa: *Strongylura timucu*, *Leporinus* sp., *Rhytidodus microlepis*, *Schizodon fasciatus*, *Schizodon vittatus*, *Brycon amazonicus*, Characidae gen. sp., *Potamorhina altamazonica*, *Potamorhina latior*, *Psectrogaster amazonica*, *Psectrogaster rutiloides*, *Rhaphiodon vulpinus*, *Anodus elongatus*, *Hemiodus immaculatus*, *Hemiodus microlepis*, *Hemiodus unimaculatus*, *Prochilodus nigricans*, *Semaprochilodus insignis*, *Semaprochilodus taeniurus*, *Mylossoma albiscopum*, *Mylossoma aureum*, *Piaractus brachipomus*, *Triporthesus auritus*, *Triporthesus* spp., *Rhinosardinia amazonica*, Engraulidae gen. sp., *Pellona castelnaeana*, *Pellona flavipinnis*, *Microphilypnus* sp., *Plagioscion squamosissimus*, *Trachelyopterus galeatus*, *Tatia* sp., Cetopsidae gen. sp., Doradidae gen. sp., Heptapteridae gen. sp., *Brachyplatystoma filamentosum*, *Brachyplatystoma juruense*, *Brachyplatystoma* sp., *Calophrys macropterus*, *Hypophthalmus marginatus*, *Pimelodus blochii*, *Pseudoplatystoma punctifer*, *Pseudoplatystoma tigrinum*, *Sorubim elongatus*, *Sorubim lima*, *Colomesus asellus*. Among them, 65% perform reproductive migrations and about 80% are of commercial interest in the region of the lower Amazon River. Regarding the spatial variation, the egg concentration was uniform and no significant differences were observed. For the larvae, there was both a horizontal (t -test, $df = 4$, $t = 23.827$, $P < 0.001$), and vertical (t -test, $df = 4$, $t = 4.086$, $P = 0.015$) spatial variation, with the highest abundance values recorded in the shore proximity areas and in the subsurface of the water column.

Conclusion. The studied environment functions as an important mechanism of exchange between spawning zones and nursery sites. Any alteration in these areas can certainly modify the composition, abundance, and distribution of the ichthyoplanktonic community and affect the processes of biological recruitment of fishery resources in the region.

Keywords: eggs and larvae, freshwater fish, dispersion area, migratory species, eastern Amazon

INTRODUCTION

Fishing in the lower Amazon River is one of the most traditional and important activities for the regional economy; it supplies food, occupation, and income for the local citizens. This activity relies on the exploitation of about 62 commercial categories** of fish (Ruffino et al. 2012, Zacardi et al. 2014, Corrêa et al. 2018). However, the presently observed high rates of capture were mainly restricted to a small number of these species, usually the migratory species, that are considered of great economic value, and fished in the shore proximity of the main

channel of the Amazon River and its extensive floodplain (Almeida et al. 2006, Batista et al. 2012, Lima J.L. et al. 2016, Cruz et al. 2017, Rabelo et al. 2017, Vaz et al. 2017, Goulding et al. 2019)

Despite the importance and the great potential that fishing activity represents for the region, the data on fishing resources are insufficient, especially regarding the mechanisms of species recruitment, which may be better understood using studies of composition, abundance, and distribution of eggs and larvae of fish, that can provide information on and local spawning and nursery sites

* Correspondence: R.A. Cajado, Laboratório de Ecologia do Ictioplâncton, Instituto de Ciências e Tecnologia das Águas, Universidade Federal do Oeste do Pará, Santarém, Pará, Brazil, phone: +559321014996, e-mail: (RAC) ruineris.cajado@gmail.com, (LSO) lucasmcpa@gmail.com, (MALS) cidaatm@hotmail.com, (DMZ) dmzacardi@hotmail.com, ORCID: (RAC) 0000-0002-7047-0302, (LSO) 0000-0002-1631-0498, (MALS) 0000-0001-5598-7314, (DMZ) 0000-0002-2652-9477.

** A set of species of the same genus or the same family with a common name.

(Nakatani et al. 2001, Zacardi et al. 2017c). These studies also allow scientists to identify which species complete their lifecycles in the region (Goulding 1981).

Nonetheless, the emergence of ichthyoplankton is related to the annual cycle of sexual maturation of adult fishes. This cycle depends on favorable environmental conditions for fertilization and is regulated by the interaction of several biotic (physiological factors of the species, presence of potential predators, and availability of appropriate food) and abiotic processes (heavy local rains and the rise of water level) (Ferreira et al. 2016, Zacardi and Ponte 2016, Ponte et al. 2017, Zacardi et al. 2018). It is during this flooding period that a rise in the number of eggs is observed and newly hatched larvae adrift in the main channel of the Amazon River, with a gradual reduction in the subsequent phases of the hydrological cycle (Chaves et al. 2016, 2019, Zacardi et al. 2017b, 2017c).

Studies conducted in the central Amazon, by Zacardi et al. (2017a), confirmed that the flooding period is the most relevant for the spawning of prochilodontids. The marginal zones, also known as *áreas de várzea*, of the middle Solimões and the lower Japurá rivers, are used as spawning areas and the channels connecting lakes and river are used as main dispersal routes, transporting larvae to the inner areas of the floodplain, such as lakes and great floating vegetation mats. Additionally, Oliveira and Araújo-Lima (1998), while studying spatial variation of larvae of pacu, *Mylossoma aureum** and *M. albiscopum* sensu Mateussi et al. (2018) in the shore proximity areas of the Solimões River, observed a different and stratified distribution among the two species, in which *M. aureum* was more abundant close to the surface, whereas *M. albiscopum* was predominant in deeper waters, suggesting active larval behavior.

These examples indicate that data on vertical and horizontal patterns of fish larvae spatial distribution are crucial not only for the understanding of ecological processes but also in providing more realistic estimates of the abundance of ichthyoplankton in several strata of the water column,

since samples that integrate only the most superficial part of the water underestimate, for example, groups that live in the deepest layers. However, little is known about variations in the abundance and distribution of ichthyoplankton in the low stretch of the Amazon River, State of Pará.

Therefore, the aim of this study was to evaluate the spatial variation of fish eggs and larvae, highlighting their vertical and horizontal distribution patterns. Additionally, the taxonomic composition of ichthyoplankton and reproductive strategies of the species are provided, expanding the knowledge about this planktonic community in the region of the lower Amazon River, an aspect of great importance to assist environmental management actions that enable the maintenance and conservation of fishery stocks.

MATERIALS AND METHODS

Study area. This study was carried on the lower stretch of the Amazon River, upstream of the Tapajós confluence zone near the city of Santarém, between 02°23'41.4"S, 054°43'23.4"W and 02°14'43.3"S, 054°45'11.1"W (Fig. 1), in the western part of the State of Pará. The sampling stretch was approximately 23 km long, in six sampling stations arranged on the Amazon River that comprised sections in the mid channel of the river (S2, S4, and S6) and in the shore proximity (S1, S3, and S5), constantly subjected to erosion processes caused by the strong river current.

Sampling procedures. The biological material was sampled monthly, from December 2017 through April 2018, a period of higher reproductive activity of migratory or non-migratory Amazonian fish species (Zacardi et al. 2017c). The samples were taken on board of a local vessel, with a standardized capture time in five minutes of horizontal trawl at low speed and against the current of the river, in order to increase the capture efficiency.

The trawl fishery, in the middle of the river and near the shore, occurred during the day (0700 h to 1700 h) in two strata of the water column, the subsurface (0–1 m) and the depth of 10 m. Eggs and larvae were collected with a 1.80 m long conical plankton net (300 µm mesh size) with the

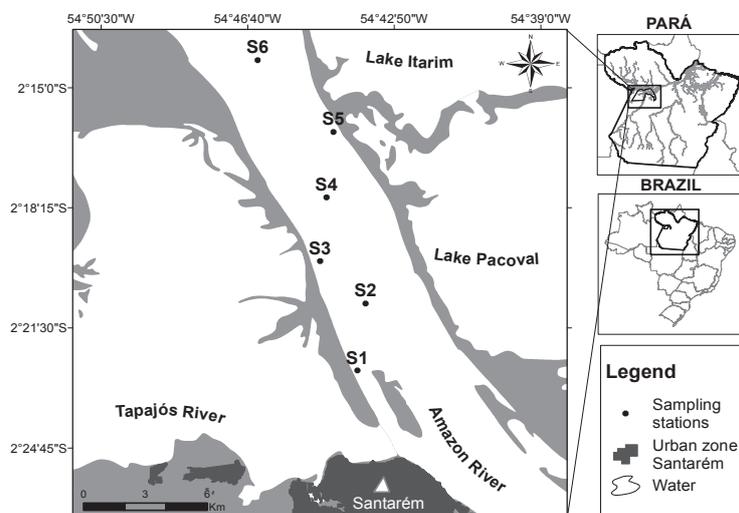


Fig. 1. Location of the study area with the sampling stations along the lower Amazon River, Santarém, Pará, Brazil

* The full authorities of species are given in Material and methods section.

mouth opening of 60 cm, and with flowmeter coupled and centralized to the mouth of the net to obtain the volume of filtered water. It is noteworthy that the sampling stations (E1, E3, and E5) to the shore proximity were characterized according to the topography, hydrodynamics and depth. Thus, we kept a minimum distance of 5 and a maximum distance of 15 m from the margin to avoid the influence of vegetation and depths below 10 m that could compromise the methodological processes according to Zacardi (unpublished*).

The depth samples consisted of the submersion of the net with an open loop cable placed around to the rim of the net mouth, stabilized by a 20 kg anchor and vertically driven by means of cables by the side of the vessel. After reaching the trawl time the cable was collected, closing the loop and interrupting the water inlet and rotation of the flowmeter, as described by Zacardi (unpublished**). The sampling effort totaled 60 samples.

After each trawl, the biological material was submitted to benzocaine solution for anesthesia ($250 \text{ mg} \cdot \text{L}^{-1}$ for at least 10 min of exposure), preserved in 10% formalin solution, packaged in polyethylene pots of 500 mL, labeled, and transported for analysis and storage in the Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores of the Instituto de Ciências e Tecnologia das Águas, of the Universidade Federal do Oeste do Pará (UFOPA), in Santarém, Pará.

Samples processing. 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, such as Araújo-Lima (1985, 1991), Araújo-Lima and Donald (1988), Araújo-Lima et al. (1993), Nascimento and Araújo-Lima (2000), Nakatani et al. (2001), Leite et al. (2007), and Oliveira et al. (2008). The validity of species names was verified according to the Eschmeyer's Catalog of Fishes (Fricke et al. 2019). The classification of families was presented in alphabetical order and followed Betancur-R et al. (2017). The larvae classified as "unidentified" corresponded to individuals with damaged structures and/or at a very early stage of development, rendering correct identification impossible.

The species classification according to their reproductive strategy was based on Barthem and Fabré (2004), Granado-Lorencio et al. (2005), and Soares et al. (2008), which grouped the species into large broad categories, such as M (migratory) and NM (non-migratory) in accordance to the gonadal maturation stage, relative fecundity, the diameter of oocytes, duration of the reproductive period and migratory behavior of adult individuals.

The identified specimens were stored in 10 mL glass vials, containing 4% formalin solution and labeled, to constitute a reference collection in the Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores – UFOPA.

Data analysis. For the analysis of variation in the spatial distribution, the density of ichthyoplankton was standardized for a volume of 10 m^{-3} of filtered water (No. of individuals $\cdot 10 \text{ m}^{-3}$), as proposed in Nakatani et al. (2001). The assumptions of normality and homoscedasticity were verified by the Shapiro–Wilk and Levene tests, respectively. The paired-sampled Student's *t*-test was used to compare the mean values of the densities and to evaluate the differences between the spatial variations in the concentrations of eggs and larvae in accordance to the vertical (subsurface and depth) and horizontal (mid channel and shore proximity areas) (Zar 1996).

To examine the variation in the spatial distribution (horizontal and vertical) of the composition of the on the fish larval community, a non-metric multidimensional scaling analysis (NMDS) was performed with the species density data. The similarity matrix was calculated based on Euclidean distance. A similarity analysis (ANOSIM) was used to evaluate possible significant differences in community composition between the analyzed environments. To emphasize the main species responsible for the formation of the outlined groups, a percentage similarity analysis (SIMPER) was performed, which is one of the main methods used to interpret the significant differences existing after ANOSIM (Clarke and Gorley 2006). For NMDS, only the taxa identified at a species level were considered, except for Engraulidae and Auchenipteridae, which were considered as a taxon due to their relevant abundance in the samples and short information on the description of larval stages of the species of these families.

These analyses were performed with the statistics al program PRIMER v. 6 (Clarke and Gorley 2006).

RESULTS

Taxonomic composition. A total of 62 eggs (0.75% of the total of sampled organisms) and 8188 fish larvae (99.25%) were collected during the presently reported study. The larvae were distributed in seven orders, 21 families, 29 genera, and 46 species-level taxa: *Strongylura timucu* (Walbaum, 1792), *Leporinus* sp., *Rhytiodus microlepis* Kner, 1858, *Schizodon fasciatus* Spix et Agassiz, 1829, *Schizodon vittatus* (Valenciennes, 1850), *Brycon amazonicus* (Agassiz, 1829), Characidae gen. sp., *Potamorhina altamazonica* (Cope, 1878), *Potamorhina latior* Spix et Agassiz, 1829, *Psectrogaster amazonica* Eigenmann et Eigenmann, 1889, *Psectrogaster rutiloides* (Kner, 1858), *Rhaphiodon vulpinus* Spix et Agassiz, 1829, *Anodus elongatus* Agassiz, 1829, *Hemiodus immaculatus* Kner, 1858, *Hemiodus microlepis* Kner, 1858, *Hemiodus unimaculatus* (Bloch, 1794), *Prochilodus nigricans* Spix

* Zacardi D.M. 2014. Abundância e distribuição espaço-temporal de ovos e larvas de peixes de interesse econômico no médio Rio Solimões e baixo Rio Japurá, Amazônia Central, Brasil. [Abundance and spatiotemporal distribution of eggs and larvae of fish of economic interest in the middle Rio Solimões and lower Japurá River, Central Amazon, Brazil.] Doctoral dissertation, Universidade Federal do Pará, Brazil. [In Portuguese.]

et Agassiz, 1829, *Semaprochilodus insignis* (Jardine, 1841), *Semaprochilodus taeniurus* (Valenciennes, 1821), *Mylossoma albiscopum* (Cope, 1872), *Mylossoma aureum* (Spix et Agassiz, 1829), *Piaractus brachypomus* (Cuvier, 1818), *Triportheus auritus* (Valenciennes, 1850), *Triportheus* spp., *Rhinosardinia amazonica* (Steindachner, 1879), Engraulidae gen. sp., *Pellona castelnaeana* Valenciennes, 1847, *Pellona flavipinnis* (Valenciennes, 1837), *Microphilypnus* sp., *Plagioscion squamosissimus* (Heckel, 1840), *Trachelyopterus galeatus* (Linnaeus, 1766), *Tatia* sp., Cetopsidae gen. sp., Doradidae gen. sp., Heptapteridae gen. sp., *Brachyplatystoma filamentosum* (Lichtenstein, 1819), *Brachyplatystoma juruense* (Boulenger, 1898), *Brachyplatystoma* sp., *Calophysus macropterus* (Lichtenstein, 1819), *Hypophthalmus marginatus* Valenciennes, 1840, *Pimelodus blochii* Valenciennes, 1840, *Pseudoplatystoma punctifer* (Castelnaud, 1855), *Pseudoplatystoma tigrinum* (Valenciennes, 1840), *Sorubim elongatus* Littmann, Burr, Schmidt et Isern, 2001, *Sorubim lima* (Bloch et Schneider, 1801), *Colomesus asellus* (Müller et Troschel, 1849). The detailed list with the taxonomic arrangement is given in Table 1. Some 65% of the above-mentioned species-level taxa perform reproductive migrations and about 80% of the species are of commercial interest in the region of the lower Amazon River. Damaged individuals or at very early stages of development composed fewer than 1% of the sampled material.

Fish larvae of the orders Characiformes and Siluriformes represented the largest numbers of families (nine and five, respectively). They comprised 68% of the total number of species and more than 80% of the captured and identified individuals, registering the largest species richness and composing the groups of highest numerical abundance. Species belonging to the families Serrasalminidae (21.5%), Anostomidae (17.9%), Curimatidae (15.2%), Engraulidae (7.6%), and Pimelodidae (4.6%) were the most prevalent in the study area (Table 1).

Reproductive strategies. The presence of many migratory species was recorded in the collected material. Migratory species are important for commercial purposes as well as for subsistence, composing part of the diet of many riverside communities. Some examples of these migratory fish and their respective Portuguese common names (in brackets) are *Semaprochilodus taeniurus* (jaraqui

de escama fina), *Semaprochilodus insignis* (jaraqui de escama grossa), *Prochilodus nigricans* (curimatá), *Brycon amazonicus* (matrinxã), *Mylossoma aureum* (pacu comum), *Mylossoma albiscopum* (pacu manteiga), *Piaractus brachypomus* (pirapitinga), *Triportheus auritus* (sardinha comprida), *Pellona flavipinnis* (apapá branco), *Pellona castelnaeana* (apapá amarelo), and catfishes of genus *Brachyplatystoma* (dourada, piramutaba, filhote) and *Pseudoplatystoma* (surubim, caparari), in addition to several curimatids (branquinhas) and hemiodontids (cubius, oranas, charutinhos).

Analyzing the embryonic development, it was noted that most of the sampled eggs (92%) had ample perivitelline space (space between the chorion and the vitelline membrane) characteristic of migratory species, and all stages of development were observed: the initial cleavage (20%), the initial embryo (19%), the free tail embryo (29%), and the final embryo (32%). The captured larvae also presented all phases of development, with a larger contribution of individuals in the pre-flexion stage (91%), followed by flexion (5%), vitelline larval (3%), and post-flexion (1%).

Horizontal distribution pattern. The highest egg density was found in the marginal region, with 1.03 (eggs $\cdot 10\text{ m}^{-3}$), although no significant difference was observed in the spatial distribution from the horizontal section of the river ($P > 0.05$). However, there was a significant difference in the density of larvae (t -test, $df = 4$, $t = 23.827$, $P < 0.001$), with the highest concentration of individuals (139.51 larvae $\cdot 10\text{ m}^{-3}$) registered in the marginal region of the river (Fig. 2).

Characiformes and Siluriformes larvae (most abundant groups in the study area) occurred on both the shore proximity areas and mid channel, with the highest densities recorded in the shore proximity areas with 94.71 larvae $\cdot 10\text{ m}^{-3}$ and 12.71 larvae $\cdot 10\text{ m}^{-3}$, respectively, but a significant variation in horizontal distribution was recorded only for Characiformes larvae (t -test, $df = 4$, $t = 3.986$, $P = 0.016$).

Vertical distribution pattern. Regarding the vertical distribution, the highest egg (0.74 eggs $\cdot 10\text{ m}^{-3}$) and larvae (123.6 larvae $\cdot 10\text{ m}^{-3}$) densities were found in the subsurface stratum of the water column (Fig. 3A). However, only the larvae densities showed a significant difference between the strata (t -test, $df = 4$, $t = 4.085$, P

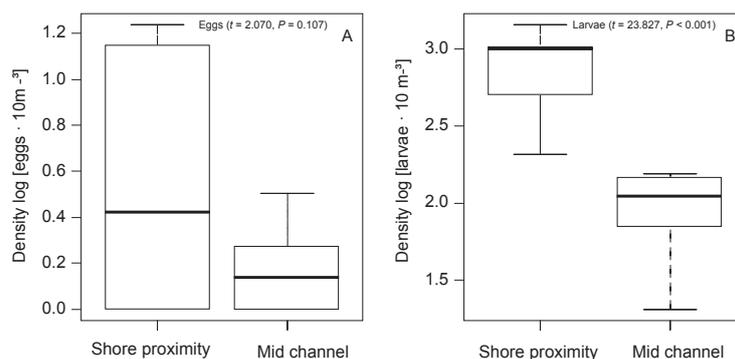


Fig. 2. Density of fish eggs (A) and larvae (B) in the marginal sector and in the mid channel of the Amazon River

Table 1

Species list and the mean density (individuals · 10 m⁻³) of fish larvae sampled in habitats and microhabitats of the Lower Amazon River, close to the city of Santarém, Pará, Brazil

Higher taxa and species	N	CI	RS	Density			
				SS	SD	CS	CD
BELONIFORMES							
Belonidae							
<i>Strongylura timucu</i> (Walbaum, 1792)	1		NM	—	—	0.01	—
CHARACIFORMES							
Anostomidae							
<i>Leporinus</i> sp.	15	+	M	0.13	—	0.20	—
<i>Rhytidodus microlepis</i> Kner, 1858	50	+	M	1.15	0.06	0.03	0.02
<i>Schizodon fasciatus</i> Spix et Agassiz, 1829	1333	+	M	36.89	4.17	2.27	0.69
<i>Schizodon vittatus</i> (Valenciennes, 1850)	67	+	M	2.55	1.40	0.11	—
Bryconidae							
<i>Brycon amazonicus</i> (Agassiz, 1829)	7	++	M	0.50	—	0.05	—
Characidae							
Characidae gen. sp.	3		—	—	—	—	0.02
Curimatidae							
<i>Potamorhina altamazonica</i> (Cope, 1878)	741	+	M	16.03	3.65	2.41	0.30
<i>Potamorhina latior</i> Spix et Agassiz, 1829	15	+	M	0.49	0.02	—	0.05
<i>Psectrogaster amazonica</i> Eigenmann et Eigenmann, 1889	484	+	M	10.59	1.93	0.88	0.37
<i>Psectrogaster rutiloides</i> (Kner, 1858)	7	+	M	0.12	—	0.01	0.06
Cynodontidae							
<i>Rhaphiodon vulpinus</i> Spix et Agassiz, 1829	18		M	0.37	0.11	0.01	—
Hemiodontidae							
<i>Anodus elongatus</i> Agassiz, 1829	200		NM	6.27	0.27	0.57	—
<i>Hemiodus immaculatus</i> Kner, 1858	34	+	NM	2.07	0.03	0.14	0.02
<i>Hemiodus microlepis</i> Kner, 1858	162	+	NM	11.35	0.13	0.19	0.09
<i>Hemiodus unimaculatus</i> (Bloch, 1794)	30	+	NM	0.55	0.14	0.16	—
Prochilodontidae							
<i>Prochilodus nigricans</i> Spix et Agassiz, 1829	57	++	M	1.29	0.19	0.05	—
<i>Semaprochilodus insignis</i> (Jardine, 1841)	3	++	M	0.03	0.02	—	—
<i>Semaprochilodus taeniurus</i> (Valenciennes, 1821)	5	++	M	0.10	—	0.06	—
Serrasalminidae							
<i>Mylossoma albiscopum</i> (Cope, 1872)	1259	++	M	38.02	16.80	2.03	1.56
<i>Mylossoma aureum</i> (Spix et Agassiz, 1829)	498	++	M	11.81	7.91	1.34	0.58
<i>Piaractus brachypomus</i> (Cuvier, 1818)	3	++	M	—	0.14	—	—
Triporthidae							
<i>Triporthus auritus</i> (Valenciennes, 1850)	10	++	M	5.88	1.87	1.05	0.12
<i>Triporthus</i> spp.	220	+	M	0.27	0.12	0.04	0.02
CLUPEIFORMES							
Clupeidae							
<i>Rhinosardinia amazonica</i> (Steindachner, 1879)	3		—	0.08	—	—	—
Engraulidae							
Engraulidae gen. sp.	624		—	25.36	1.46	3.81	0.13
Pristigasteridae							
<i>Pellona castelnaeana</i> Valenciennes, 1847	149	+	M	3.88	0.36	0.34	0.14
<i>Pellona flavipinnis</i> (Valenciennes, 1837)	240	+	M	7.22	1.00	0.79	—
GOBIIFORMES							
Eleotridae							
<i>Microphilypnus</i> sp.	4		NM	—	—	0.08	—
PERCIFORMES							
Sciaenidae							
<i>Plagioscion squamosissimus</i> (Heckel, 1840)	226	++	NM	4.19	1.13	2.73	0.23

Table 1. cont.

Higher taxa and species	N	CI	RS	Density			
				SS	SD	CS	CD
SILURIFORMES	102		—	1.70	0.24	0.56	0.25
Auchenipteridae	392		—	10.63	1.64	0.97	0.07
<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)	1		NM	0.03	—	—	—
<i>Tatia</i> sp.	1		NM	—	0.02	—	—
Cetopsidae							
Cetopsidae gen. sp.	9		—	0.10	0.06	0.03	0.04
Doradidae							
Doradidae gen. sp.	7		—	0.17	0.06	—	—
Heptapteridae							
Heptapteridae gen. sp.	17		—	0.05	0.49	0.01	—
Pimelodidae	5		—	—	—	—	0.08
<i>Brachyplatystoma filamentosum</i> (Lichtenstein, 1819)	5	++	M	0.05	0.06	—	0.07
<i>Brachyplatystoma juruense</i> (Boulenger, 1898)	19	+	M	0.14	0.08	0.15	0.05
<i>Brachyplatystoma</i> sp.	4	+	M	0.05	0.04	—	—
<i>Calophysus macropterus</i> (Lichtenstein, 1819)	162	++	M	4.98	0.79	0.37	0.12
<i>Hypophthalmus marginatus</i> Valenciennes, 1840	19	++	M	0.17	0.09	0.05	0.10
<i>Pimelodus blochii</i> Valenciennes, 1840	13	+	M	0.12	0.08	—	0.11
<i>Pseudoplatystoma punctifer</i> (Castelnau, 1855)	95	++	M	2.26	1.25	0.08	0.18
<i>Pseudoplatystoma tigrinum</i> (Valenciennes, 1840)	29	++	M	0.24	0.25	0.13	—
<i>Sorubim elongatus</i> Littmann, Burr, Schmidt et Isern, 2001	3	+	M	0.73	0.26	0.15	0.02
<i>Sorubim lima</i> (Bloch et Schneider, 1801)	29	+	M	0.12	0.01	0.01	0.05
TETRAODONTIFORMES							
Tetraodontidae							
<i>Colomesus asellus</i> (Müller et Troschel, 1849)	26		NM	0.82	0.08	0.19	0.03
Not identified	80		—	0.03	0.83	—	0.02
Eggs	62		—	1.43	0.63	0.06	0.17
Total larvae	8188						

N = total number, CI = commercial importance (+) and high commercial importance (++), RS = reproductive strategy (M = migratory and NM = non-migratory), SS = Shore proximity/Subsurface, SD = Shore proximity/Depth, CS = mid Channel/Subsurface, and CD = mid Channel/Depth.

= 0.015) (Fig. 3B). No significant differences ($P > 0.05$) were found between the subsurface and depth samples in the distribution of Characiformes and Siluriformes larvae, the most representative orders captured in this study.

Larvae composition variation between environments.

The results from the ordination analysis (NMDS) indicated the existence of distinct groups of fish larvae among the sampled environments, mainly confirming that the community structure is influenced by the horizontal (shore proximity areas and mid channel) and vertical (subsurface and depth) distribution. By analyzing the NMDS graph a horizontal grouping can be observed: Group I (mostly formed by the sites located in the shore proximity areas) (SS, SD) and group II (mostly formed by the sites located on the mid channel) (CS, CD) (Fig. 4). The community composition of fish larvae was significantly different between the sampled environments (ANOSIM, $R = 0.121$; $P = 0.001$). Also, through SIMPER analysis, a high dissimilarity was observed between the studied environments

(>75%). The taxa that most influenced the differences between the sampling sites were Engraulidae and species of the migratory Characiformes group, such as the “pacus” (*M. albiscopum* and *M. aureum*), the “aracus” (*S. fasciatus*) and the “branquinhas” (*P. amazonica* and *P. altamazonica*). These individuals were more abundant in the shore proximity areas and subsurface of the water column.

DISCUSSION

The most abundant taxa found in the study area represent migratory species highly valuable in regional fisheries, due to the flavor of their meat, such as the serrasalmids of the order Characiformes and the pimelodids of the order Siluriformes, with high representativeness in the markets of the region (Ferreira et al. 1998, Lima K.F. et al. 2016, Sousa unpublished*). The dominance of Characiformes larvae followed by Siluriformes and other less abundant orders such as Clupeiformes and Perciformes corroborate the results of several other works of fish larvae in rivers

* Sousa K.N.S. 2017. Feira do pescado – síntese de cinco anos de monitoramento participativo do desembarque pesqueiro (2011–2015) Santarém-PA. [Fish market—Synthesis of five years of participatory monitoring of fishing landings (2011–2015) Santarém-PA.] Relatório Técnico. Universidade Federal do Oeste do Pará (UFOPA), Santarém. [In Portuguese.]

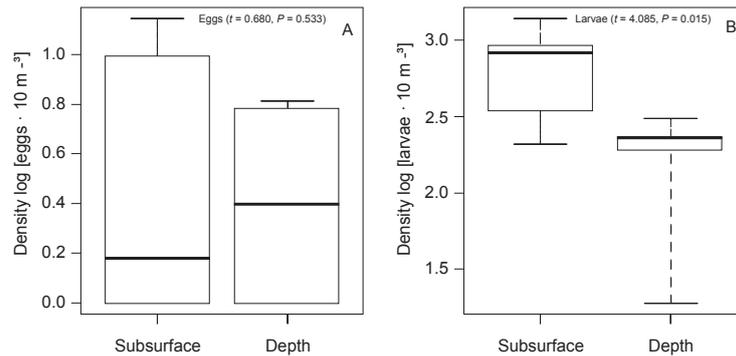


Fig. 3. Density of fish eggs (A) and larvae (B) between the two strata of the water column (subsurface and depth) in the lower Amazon River

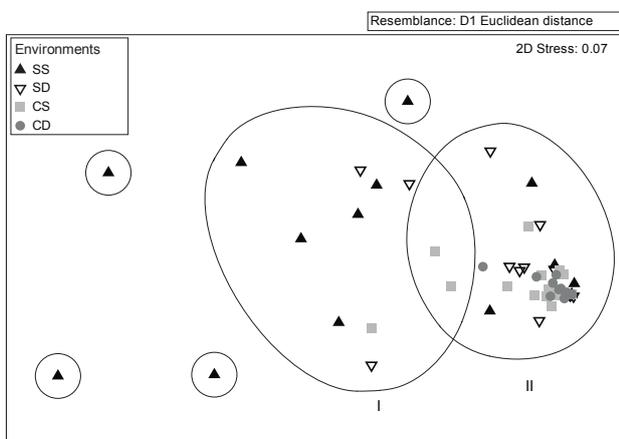


Fig. 4. Ordering resulting from non-metric multidimensional scaling analysis (NMDS) on the density of fish larvae based on Euclidean distance in the lower Amazon River, Santarém, Pará, Brazil (Stress = 0.07 and $R^2 = 0.121$) (SS = Shore proximity/Subsurface, SD = Shore proximity/Depth, CS = mid Channel/Subsurface, and CD = mid Channel/Depth); irregular circles represent groups I and II

in the Amazon basin (García-Dávila et al. 2014, Ochoa-Orrego et al. 2015, Zacardi and Ponte 2016, Zacardi et al. 2017c), being among the standards established by Barletta et al. (2010) for the Amazon. The composition of fish larvae assemblages follows the general pattern found in the South American basins, but with variations in abundance and number of species (Zacardi et al. 2017c).

An explanation for the higher abundance of larvae found in relation to eggs during the sampled period is the possible distance of the spawning sites in the region. Probably, these sites are located upstream from the selected sampling sites, so that the embryos can develop and the eggs hatch as they derive from the current, justifying the low capture of eggs. This process of drift is essential for reproductive success and, consequently, for the recruitment of fishery stocks. Additionally, because most of the captured individuals were in a pre-flexion stage (91%), added to the information that Characiformes larvae hatch between 12 and 20 hours after the egg laying

(Nakatani et al. 2001), and considering that the mean velocity of the current flow in the lower Amazon River at the beginning of the flooding season is $1.25 \text{ m} \cdot \text{s}^{-1}$ (Filizola et al. 2009), it is possible that a large portion of the captured larvae originated from spawns which occurred at approximately 60 km from the study area.

Another factor that may have contributed to the low amount of eggs is associated with the short time span between incubation and hatching. This process is relatively short, for most species that disperse eggs and larvae by the river current, and it decreases the time of exposure of eggs in the environment (Araújo-Lima and Oliveira 1998, Nakatani et al. 2001). Finally, the last possibility may be related to sampling problems, such as capture efficiency due to speed filtration, as suggested by Oliveira and Araújo-Lima (1998). Nonetheless, the records of eggs in the cleavage phase and initial embryo indicate the origin of local spawns, signaling that the study area presents favorable environmental conditions to reproduction.

The high numbers of larvae of migratory and economic interesting species captured in the region corroborates the results found by Zacardi et al. (2017a, 2017b, 2017c). It could be explained by the fact that these fish are rheophilic, mainly spawning in whitewater rivers when the water level rises. This can be a trigger for reproduction, as, when the water level rises, there is an increase in the concentration of nutrients, turbidity, and oxygenation of the water, offering favorable environmental conditions for the reproduction of many of these species. At the same time as when the water level rises, there is an increase in the concentration of nutrients, turbidity, and oxygenation of the water, offering favorable environmental conditions for the reproduction of many of these species. Thus, it is noteworthy that despite the current scenario of overexploitation of fishery resources, many species are able to recruit locally, even under heavy fishing pressure.

The predominance of larvae, especially Characiformes, in the marginal zone of the lower Amazon River, had already been cited by Araújo-Lima and Oliveira (1998) and Zacardi et al. (2017a) in samplings in the Solimões/Amazon River, in the central Amazon, and by Ponte et al. (2017)

and Zacardi et al. (2018) for the study area, indicating a horizontal distribution pattern of these organisms.

This agglomeration of the larvae in the shore proximity areas may be related to the favorable conditions that these regions provide to the growth of some species that can complete their early development in this section of the river. Or, because it is a strategic zone for the transport of eggs and newly hatched larvae to the breeding areas, in lakes and floodplain channels, carried by the currents of flood waters (Ponte et al. 2016, Zacardi et al. 2017a). The success in the transport of ichthyoplankton to suitable growth areas has a crucial role in the availability of future juveniles and subsequent recruitment for the adult population. In this regard, the shore proximity areas act as an intermediary between the riverbed and the growth areas, and their conservation is essential for the management of fishing and maintenance of fishery resources.

Regarding the vertical distribution of ichthyoplankton, results indicate that the larvae modulate their behavior as to the strata of the water column. Significant differences and variations of abundances were found, with higher numbers of larvae in the subsurface layer when compared with the depth samples. According to Power (1984), the position of the larvae in the water column can be attributed to their buoyancy regulated by the swim bladder, swimming capacity or by the sense of orientation.

The majority of large groups of Amazonian fishes have floating or semi-floating eggs and planktonic larvae, which favors drift and dispersion in the most superficial layers of the water column (Leite et al. 2007, Pareja-Carmona et al. 2014). Thus, this stratified behavior presents adaptive advantages, such as maintaining the position in relation to the horizontal distribution (Thomaz et al. 2007), food assurance (Pavlov et al. 2008), a mechanism to minimize intra-specific competition (Santin et al. 2004, Picapedra et al. 2015), and refuge against predators (Zacardi et al. 2017c), or even by the influence of hydrological factors such as transport and retention (Araújo-Lima and Oliveira 1998). The hydrodynamic movements of the river, the spawning sites, and the active larval behavior are the main causes of the stratified distribution of the larvae in the water column (Ponte et al. 2016). However, this variation and its probable causes are not well understood and certainly work differently for each species.

The NMDS results showed that species composition varied among sampled environments, mainly between the shore proximity areas and mid channel, suggesting that the presence of distinct landscapes and disparities in the natural characteristics of the environments throughout the system are responsible for structuring ichthyoplanktonic communities, as observed by Zacardi (2014b, 2017c) and Ponte et al. (2019). Therefore, it is of utmost relevance to consider in management plans the interactions between the environments, as well as the heterogeneities of habitats occurring in the various sectors of the Amazon River. This because the abundance of fish species and the successful biological recruitment of stocks, especially migratory Characiformes, is dependent on the conservation of marginal river sectors.

CONCLUSIONS

The position of the eggs in the water column allows us to identify preferences in the places of laying since eggs do not have their own mechanisms that change their position and therefore are dependent on the hydrodynamic patterns of currents and buoyancy. In the presently reported study, no significant difference was observed in the concentration of eggs in the different strata of the river.

The results allowed us to understand the importance of the use of marginal regions, of the lower Amazon River, as an aggregation and larval dispersion area for countless fish species and as an important mechanism of exchange between spawning zones and nursery sites. The data also indicated the best capture sites that should be favored in the sampling of ichthyoplanktonic studies along the river channel, according to the strata and sections of the water column.

Therefore, any alteration in this stretch of the river can safely modify the composition and specific abundance of the ichthyoplanktonic community and affect processes of energy exchange in the environment and the recruitment of the ichthyofauna. It emphasizes the importance of maintaining this environment's integrity and adopting management actions focused on the conservation of natural stocks and the sustainability of regional fishery resources.

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