

Diversity and spatio-temporal distribution of the ichthyoplankton in the lower Amazon River, Brazil

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ABSTRACT

The present study investigated (i) the taxonomic composition of the larval fish fauna of the lower Amazon River, (ii) the structure of the larval assemblage, and (iii) the relationship between the abundance of the ichthyoplankton and environmental variables, in order to evaluate the importance of this river sector as spawning and nursery grounds for the region's fish species. Data were collected monthly between January and December 2013 during the day and at night sampling cycles. A total of 2,295 fish eggs and 46,298 larvae were collected, quantified and classified larvae in 63 taxa. These larvae belonged to species with a variety of reproductive strategies. Individuals at a very early stage of development made up 92% of the specimens collected. High densities of larvae were recorded between January and March, corresponding to the breeding season of most of the species exploited by local fisheries. This peak in density was associated with the period in which rainfall, river water levels, and dissolved oxygen concentrations all peaked, while pH and electrical conductivity reached their lowest levels. The results of the present study confirmed that a number of different fish species use the margins of the lower Amazon river as spawning grounds and nurseries, as well as dispersal routes. This emphasizes the importance of these areas for the reproduction of local fish species and the maintenance of their populations, and highlights the need for the preservation of these areas and the more effective regulation of the closed season.

Keywords: Amazon; distribution; fish eggs and larvae; environmental variables; conservation.

Diversidade e distribuição espaço-temporal do ictioplâncton no trecho inferior do rio Amazonas, Brasil

RESUMO

Este trabalho teve como objetivo (i) caracterizar a composição taxonômica larval da ictiofauna, (ii) analisar a estrutura da assembleia larval e (iii) verificar a relação da abundância do ictioplâncton com as variáveis ambientais, avaliando a importância do trecho inferior do rio Amazonas, como sítios de desova e desenvolvimento para as espécies de peixes da região. As coletas foram realizadas mensalmente de janeiro a dezembro de 2013, em ciclos de amostragem diurna e noturna. Um total de 2.295 ovos e 46.298 larvas de peixes foram capturados, quantificados e as larvas classificadas em 63 táxons. Essas larvas pertenciam a várias espécies caracterizadas por diferentes estratégias de reprodução. Indivíduos em estágio muito inicial de desenvolvimento perfizeram 92% das capturas. Elevadas densidade de larvas foram registradas entre os meses de janeiro a março, correspondendo à época de reprodução da maioria das espécies de peixes explorados pela pesca na região. Elevadas abundâncias do ictioplâncton foram relacionadas com os momentos em que o ambiente apresenta maiores valores de oxigênio dissolvido, índice pluviométrico e nível fluviométrico, e baixos valores de pH e condutividade elétrica. Os resultados obtidos neste trabalho confirmam que várias espécies de peixes, utilizam as áreas marginais do trecho inferior do rio Amazonas como área de desova, dispersão e berçário, ressaltando assim a sua importância para a reprodução e, conseqüentemente, para a manutenção das espécies de peixes amazônicos, evidenciando a necessidade de sua preservação, além de monitoramento para evitar a pesca durante o período reprodutivo.

Palavras-chave: Amazônia, distribuição, ovos e larvas de peixes, variáveis ambientais, conservação.

Introduction

The ichthyoplankton is made up of fish eggs and larvae, and represents a fundamentally important group for the understanding of fish biology and ecology (NAKATANI et al., 2001), being essential for the maintenance, monitoring and administration of fishery stocks (REYNALTE-TATAJE et al., 2013; ZACARDI et al., 2014), as well as the establishment of measures for the management (KING et al., 2003; SUZUKI et al., 2013) and sustainability of these resources (SHUAI et al., 2016).

The initial stages of fish development not only represent a critical recruitment phase (SAMPEY et al., 2004), but are also characterized by distinct morphology and spatio-temporal patterns of abundance and distribution different from those of the adults. This variation in larval distribution reflects their

interactions with a number of biotic and abiotic factors (ZIOBER et al., 2012; SILVA; LEITE, 2013; SUZUKI; POMPEU, 2016), which makes the understanding of these patterns essential for the interpretation of species ecology and population dynamics (NAKATANI et al., 2001).

In the initial phases of their life cycle, freshwater fish exploit a wide variety of environments, ranging from main river channels to a diversity of floodplain habitats (HUMPHRIES et al., 1999; LIMA; ARAÚJO-LIMA, 2004; JIMENEZ-SEGURA et al., 2010; MOUNIC-SILVA; LEITE, 2013), such as channels, lakes, macrophyte beds, as well as the water column itself (ARAÚJO-LIMA; OLIVEIRA, 1998; ZACARDI, 2014).

These floodplain areas provide the larvae with an ample diversity of habitats and feeding resources to support their development (LEITE; ARAÚJO-LIMA, 2002; SILVA; LEITE, 2013),

and these environments may constitute key nursery areas for a number of commercially-important species, both sedentary and migratory. Given their importance for the survival and development of these species, impacts to the structure of these habitats may affect fishery productivity by altering recruitment, abundance, and ultimately, species composition and distribution (LOPES et al., 2014; BARZOTTO et al., 2015).

More comprehensive studies on of the composition, distribution and variation in the structure of the ichthyoplankton community of the lower Amazon, together with spawning patterns, in order to better understand the use of these environments by regional fauna ichthyoplanktonic. Given these considerations, the present study described the species composition and abundance of the ichthyoplankton of the study area, and analyzed the spatio-temporal variation in the density of these organisms in relation to the seasonal fluctuations in certain specific environmental variables.

Material and methods

Study area

The present study focused on the Marrecas Island complex on the lower Amazon River, located between latitudes 2°12'41"S and 2°18'52"S, and longitudes 54°45'42"W and 54°43'11"W (Figure 1), adjacent to the city of Santarém, in the Brazilian state of Pará. The local hydrodynamics and unconsolidated sediments, together with the cycles of erosion, transportation and deposition of these sediments, provoke systematic annual morphological modifications of the river margin and its bed.

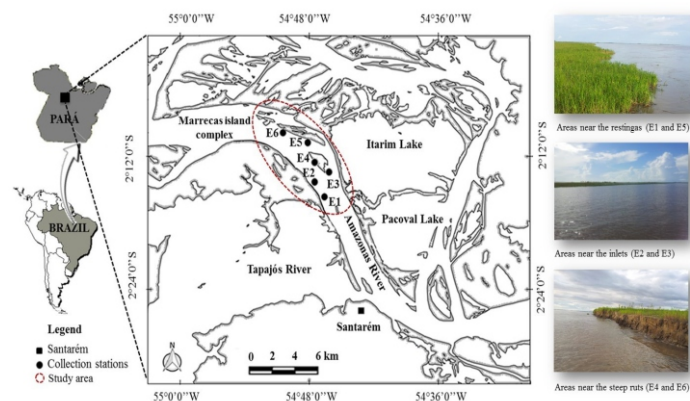


Figure 1. Location of the study area, showing the data sampling sites (●) and habitats in the Marrecas Island complex on the lower Amazon River in Pará, Brazil.

The local climate is classified as the *Am* type in the Köppen system, that is, rainy tropical, with a restricted annual temperature range and mean monthly precipitation of over 60 mm. Mean air temperature is approximately 27.7°C and relative humidity, 86%, varying little during the year, while annual rainfall is approximately 2000 mm, distributed in two distinct seasons, with a rainy season between December and June, and a dry, or less rainy season from July to November (COSTA et al., 2013).

Data collection

Samples were collected monthly between January and December 2013, at six georeferenced sampling stations selected randomly from areas representative of the restinga

swamp (E1 and E5), inlets (E2 and E3) and steep ruts (E4 and E6). The samples were taken both diurnal and nocturnal periods, with 12 samples being collected per month, resulting in a total of 144 samples over the course of the year.

At each station, samples were collected using five-minute horizontal trawls of the subsurface of the water column, with a conical-cylindrical plankton net with a 60 cm circular mouth and 300 µm mesh equipped with a mechanical flowmeter (General oceanic) to measure the volume of water filtered. The samples were treated with benzocaine (250 mg/L), and then preserved in 10% formalin buffered with calcium carbonate, and stored in labelled polyethylene flasks for transportation to the laboratory.

During the collection of the biological material, four parameters - water temperature (T°), dissolved oxygen (DO), pH and electrical conductivity (Cond.) - were measured *in loco* using portable digital meters. Precipitation index (PI) were obtained from the National Waters Agency's (ANA) hydro-meteorological station (0025000) located in the municipality of Santarém (Lat. -2.4322 and Long. -54.7575) and the waterlevel (FL) were provided by the Directorate of Hydrography and Navigation - DHN (Brazilian Navy).

Data analysis

In the laboratory, the samples were sorted, with the eggs and larvae being separated from the detritus and the rest of the plankton under a stereoscopic microscope using tweezers. The eggs and larvae were then quantified and identified to the lowest possible taxonomic level based on their morphological, meristic and morphological characteristics, using the specialist literature of Araújo-Lima (1985), Araújo-Lima and Donald (1988), Araújo-Lima (1991), Araújo-Lima et al. (1993), Nakatani et al. (2001), Oliveira et al. (2008), and Leite et al. (2007). The taxonomic classification of the orders and families was based on the Check List of the Freshwater Fishes of South and Central America, CLOFFSCA (REIS et al., 2003), except for the Characiformes, for which the classification of Oliveira et al. (2011) was used, with the genera and species being listed in alphabetical order.

The eggs were classified in the following development stages (following NAKATANI et al., 2001): (a) early cleavage: formation of the first cells; (b) early embryo: differentiation of the embryo; (c) tail-free: tail separated from the vitellus, and (d) late embryo: embryo fully formed.

The larvae were also distinguished by their degree of development, following Ahlstrom and Ball (1954), as modified by Nakatani et al. (2001): (a) vitelline stage: recently hatched, including larvae with the eye completely or partially pigmented, and the opening of the mouth and anus fully formed; (b) pre-flexion: from the opening of the mouth and anus to the initial flexing of the notochord, with the appearance of the first supports of the caudal fin; (c) flexion: between the initial flexing of the notochord and the appearance of the caudal fin supports to the complete flexing of the notochord and the appearance of the pelvic fin bud, and (d) post-flexion: flexing of the notochord and budding of the pelvic fin finalized, to the complete formation of the rays of all the fins.

The reproductive strategy of each species was classified according to the schemes of Barthem and Fabr e (2004),

Soares et al. (2008) and Neuberger (2010), who group the species in broad categories - migratory and non-migratory - based on the gonadal maturation stage, relative fecundity, diameter of the oocytes, duration of the breeding season, and migratory behavior.

The number of larvae of the taxa identified at each station was converted into a density of larvae per 10m³ of water filtered, following Tanaka (1973). The assumptions of normality and homoscedasticity were verified using the Shapiro-Wilk and Levene tests, respectively, run in SYSTAT v. 12.0 (WILKINSON, 2007). The density data and the environmental variables (except pH) were log-transformed (log (x +1)) to stabilize and normalize the variances (PETERS, 1986).

A two-way analysis of variance (ANOVA) was used to investigate the significance of the spatial (sampling stations) and temporal (months) variation in the mean ichthyoplankton density, considering the stations and months as factors. The Tukey test was applied whenever significant (P < 0.05) differences were detected.

A Principal Components Analysis (PCA) was used to verify the similarities in the environmental variables among sampling stations, based on the monthly values recorded during the study period. The principal components retained for interpretation were those that showed eigenvalues higher than 1.0 (one), according to the criteria of Keiser-Gutman (JACKSON, 1993). The relationship between species densities and the environmental variables were evaluated using the Pearson correlation (MCCUNE; MEFFORD, 2006). All the analyses were run in STATISTICA 7.0 (STATSOFT, 1999).

Results

Environmental variables

It was observed a single annual flood pulse (Figure 2), with four phases: flood (December to April), high water (May / June), ebb (July to September) and low water (October / November).

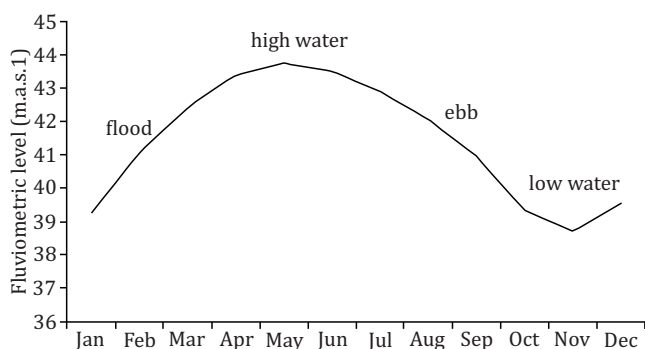


Figure 2. Hydrological cycle of the lower Amazon River at Santarém in Pará (Brazil) in 2013 (m.a.s.l. = meters above sea level).

No marked variation was recorded in water temperature (°C), dissolved oxygen (mg/L), pH or electrical conductivity (µS/cm) at the sampling stations. Temperatures were higher towards the end of the ebb phase (October), and lowest during the flood phase, in March (Figure 3A). Dissolved oxygen concentrations increased progressively during the flood phase, but began to decrease at the transition between the high water and ebb phases (June and July) and remained low until the beginning of the next flood phase, in November (Figure 3B). The pH showed small oscillations with more alkaline values at the end of the ebb phase (August and

September) and at low water, in October (Figure 3C). Electrical conductivity increased at the beginning of the flood phase (November, December and January), then decreased in February, March and April, and during high water, in May and June (Figure 3D).

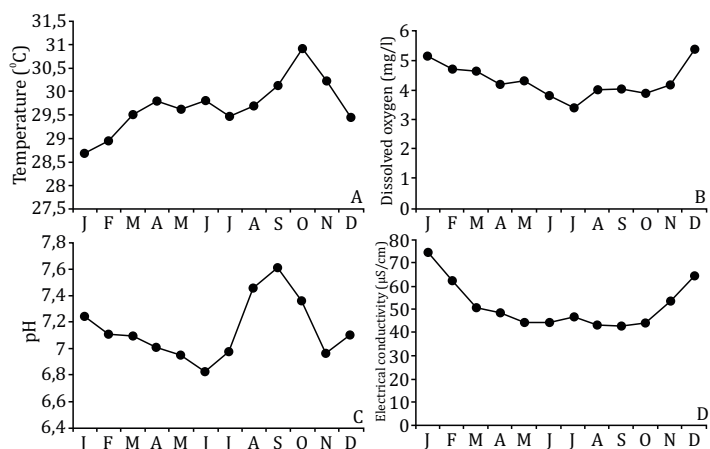


Figure 3. Mean values recorded for (A) surface water temperature, (B) dissolved oxygen, (C) pH, and (D) electrical conductivity recorded at the sampling stations on the lower Amazon River in Pará, Brazil.

Composition and abundance of the ichthyoplankton

During the study period, a total of 1,295 fish eggs and 46,298 larvae were collected at the six sampling stations. The larvae were classified in 63 taxa, distributed in eight orders, 20 families, 33 genera and 45 identified species (Table 1 - Supplementary Material). Overall, 2.86% of the specimens could not be identified due to structural damage or being in an early, indeterminate stage of development.

The Characiformes was the order with the greatest species richness and abundance, contributing 74.13% of the identified specimens, followed by the Clupeiformes (11.28%), Siluriformes (9.35%) and Perciformes (2.16%). The four other orders (Tetraodontiformes, Pleuronectiformes, Symbranchiformes and Beloniformes) together contributed less than 1% of the specimens collected. The predominant Characiformes families were the Characidae, Anostomidae and Curimatidae, which together contributed more than 93% of the larvae and more than 98% of all the Characiformes captured (Figure 4), making these families the most common in the study area.

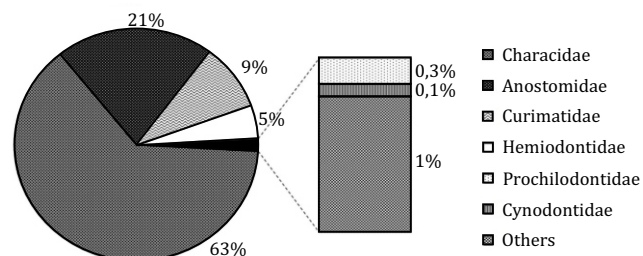


Figure 4. Taxonomic composition of the fish larvae collected on the lower Amazon River, relative to the Characiformes families, based on the total number of specimens collected.

The samples indicated the occurrence in the study area of a number of commercially-important migratory species, such as the silver prochilodus, *Semaprochilodus taeniurus* (Valenciennes, 1817), flag tail prochilodus, *Semaprochilodus insignis* (Jardine; Schomburgk, 1841), matrinxã, *Brycon amazonicus* (Spix; Agassiz, 1829), black prochilodus, *Prochilodus nigricans* Agassiz, 1929, common pacu, *Mylossoma aureum* (Spix; Agassiz, 1829), silver pacu, *Mylossoma duriventre* (Cuvier, 1817),

the hatchet fish, *Tripurtheus auritus* (Günther, 1864), South American silver croaker, *Plagioscion squamosissimus* (Hechel, 1840), catfish of the genera *Brachyplatystoma* and *Pseudoplatystoma*, as well as a number of curimatids (toothless characins), hemiodon-tids (halftooths) and anostomids (aracus and pias). The migratory breeding strategy was the most common among the larvae caught, according to the ichthyoplankton specimens identified (Table 1 - Supplementary Material).

Spatio-temporal variation in the ichthyoplankton

The results of the ANOVA indicated significant differences between the densities of eggs ($F=1,77$; $P=0,02$) and larvae ($F=2,51$; $P=0,01$), with an abundance of larvae always above the eggs in all analyzed stations (Figure 5A). However, it has not found significant differences in the spatial distribution of variation ($P>0,05$). The greatest abundance of ichthyoplankton was recorded during the first months of the flood phase (Figure 5B). The ANOVA confirmed that the abundance of both eggs ($F=2,63$; $P=0,01$) and larvae ($F=3,00$; $P=0,02$) varied significantly among months, peaking in January and February (Tukey, $P<0,05$), with 10.44 and 12.87 org.10m⁻³, respectively.

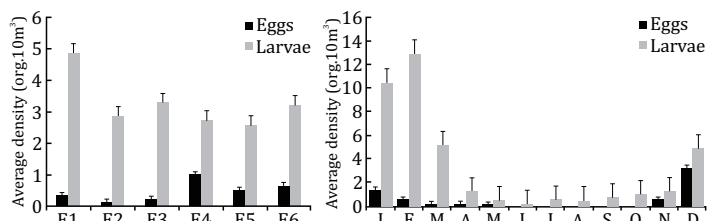


Figure 5. Spatial (A) and temporal (B) variation in the mean ichthyoplankton density (and the standard error) in 2013, in the Marrecas Island complex on the lower Amazon River in Pará, Brazil.

The larvae of the pacus of the genus *Mylossoma* (Characiformes) predominated in the samples, with 40.93% of the specimens collected ($N=18,948$), of which, just over half (9,838 specimens) were *M. duriventre* and 9,110 were *M. aureum*, with peaks of density being recorded in January and February, coinciding with the greatest abundance of migratory Characiformes larvae. The Siluriformes larvae were most abundant during the subsequent months to peak in Characiformes reproduction (March and April). By contrast, the abundance of Clupeiformes peaked during the low water phase, in November (Figure 6).

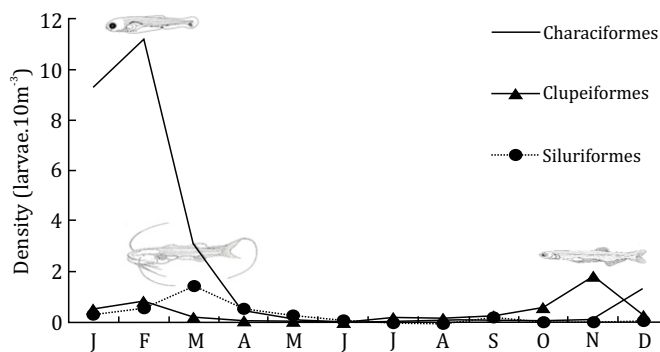


Figure 6. Monthly variation in the density of the larvae of the principal ichthyoplankton groups (Characiformes, Clupeiformes and Siluriformes) recorded in 2013, in the Marrecas Island complex on the lower Amazon River in Pará, Brazil.

The highest plankton densities (eggs and larvae) were recorded during the night-time period (Figure 7). The difference between day-time and night-time samples was significant for both eggs ($F=3,12$; $P=0,04$) and larvae ($F=2,76$; $P=0,02$).

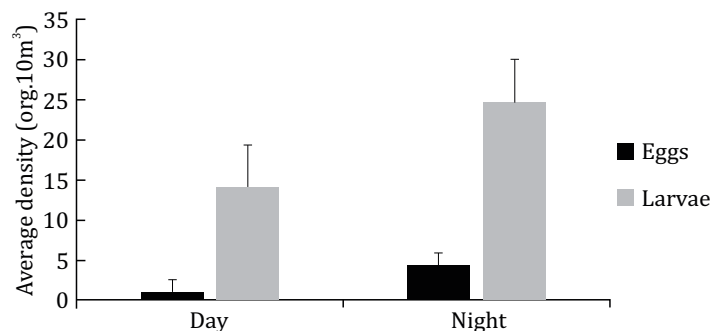


Figure 7. Day/night variation in the mean density (and standard error) of the ichthyoplankton collected in 2013 in the Marrecas Island complex on the lower Amazon River in Pará, Brazil.

Some species were only encountered during a certain part of the day. *Belonion apodion* Collette, 1966, *Colossoma macropomum* (Cuvier, 1817), *Piaractus brachypomus* (Cuvier, 1818), *Hydrolycus scomberoides* (Cuvier, 1819), *Microphilypnus amazonicus* Myers, 1927, *Brachyplatystoma rousseauxii* (Castelnau, 1855), *Brachyplatystoma platynemum* Boulenger, 1898, *Platynemichthys notatus* (Schomburgk, 1841), *Tatia* sp. and *Synbranchus marmoratus* Bloch, 1795 were only collected during the night-time period. Trichomycteridae larvae were the only group collected exclusively during the diurnal samples, indicating a possible vertical migration pattern in the distribution of these organisms.

Most (73%) of the eggs were in the initial cleavage stage, and the larvae in the early stages of development were also more numerous than those in the later stages. Larvae in the pre-flexion stage were the most abundant (81% of the total collected), followed by vitelline larvae (11%), and those in the flexion (7%) and post-flexion (1%) stages (Figure 8). Significant spatio-temporal differences were found only in the pre-flexion stage in the inlet samples ($F=5,42$; $P=0,01$) and during the flood phase (January: $F=4,18$; $P=0,01$ and February: $F=2,16$; $P=0,00$).

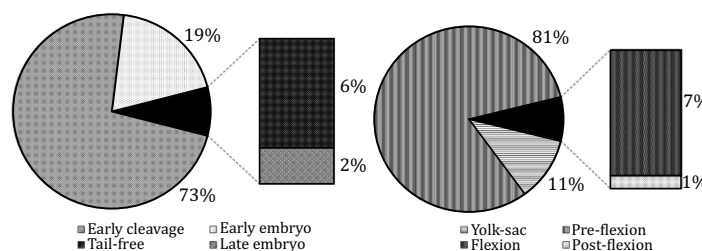


Figure 8. Relative contribution of the different development stages to the ichthyoplankton samples collected in 2013 in the Marrecas Island complex on the lower Amazon River in Pará, Brazil.

Relationship between of ichthyoplankton abundance and environmental variables

In the Principal Components Analysis (PCA) only axes 1 and 2 had eigenvalues close to 1.0 and were retained for interpretation. Together, these two axes, explained 68.58% of the total variability in the data, reflecting a temporal gradient (Table 2).

Table 2. Pearson correlation between environmental parameters at the sampling stations and months of the study period.

Environmental variables	Pc1	Pc2
Temperature	-0,857	-0,280
Dissolved oxygen	-0,353	0,629
pH	-0,600	-0,168
Electrical conductivity	0,094	0,869
Pluviometric index	0,871	0,283
Water level	0,709	-0,630

The ordination of the data revealed that the first axis (PC1) was correlated positively with the strong rains and rising river levels recorded during the first months of the year, while the opposite pattern was observed in the pH and temperature. The electrical conductivity and dissolved oxygen showed a positive correlation in the second axis (PC2), coinciding with the months of Amazon River flood (Figure 9).

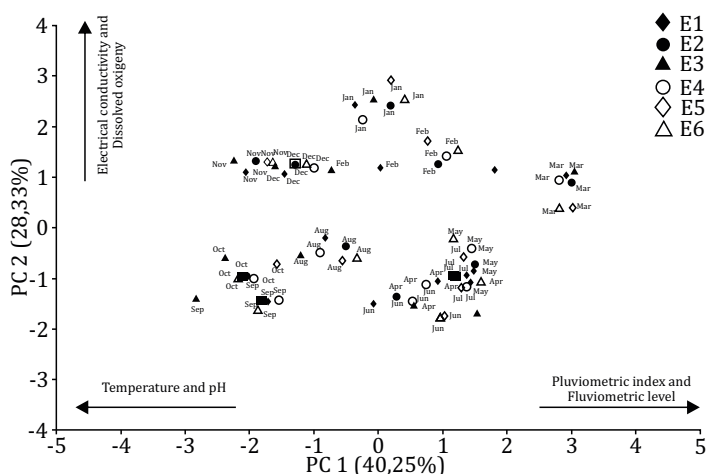


Figure 9. Results of the PCA of the abiotic variables recorded each month at the sampling station on the lower Amazon River, between January and December 2013.

The graphic analysis indicated spatio-temporal differences among the sampling stations. The data indicate that the highest densities of eggs and larvae coincided with the highest rainfall, fluvial discharge and dissolved oxygen concentrations, and lowest levels of electrical conductivity and pH. Only dissolved oxygen and rainfall correlated positively with egg density, while the density of larvae was related to the level of the river, and negatively with electrical conductivity (Table 3). The lowest densities were recorded at all the sampling stations in June, when dissolved oxygen, pH and electrical conductivity were all at their lowest levels.

Table 3. Pearson correlation coefficients (R) between environmental variables and the log-transformed [log(x+1)] densities of fish eggs and larvae recorded on the lower Amazon River in Santarém, Pará (Brazil). The probabilities associated with the R values and shown in parentheses. ns*= not significant (P<0.05).

Variables	T ^o	DO	pH	Cond.	PI	FL
Egges	-0,19(ns*)	0,21(0,003)	0,08(ns*)	0,023(ns*)	0,01(0,004)	0,16(ns*)
Larvae	-0,34(ns*)	0,06(ns*)	0,11(ns*)	-0,40(0,001*)	0,04(ns*)	0,32(0,004)

Discussion

The study area encompasses the lotic environment of the lower Amazon River, where the rivers cape is dominated by a complex of channels and islands, with numerous floodplain lakes. This environmental complexity is reflected in the marked heterogeneity of habitats that is fundamental to the diversity of the local ichthyoplankton community.

The predominance of Characiformes and the species diversity of Siluriformes were typical of Amazonian fish communities (LIMA; ARAÚJO-LIMA, 2004; OLIVEIRA; FERREIRA, 2008; BARLETTA et al., 2010). The preponderance 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.

One preoccupying finding of the present study was the low densities of *C. macropomum* larvae, although this may have been the result of a sampling bias, given that the tambaqui

probably spawns in “paused” water dominated by dead trees and eroded banks, or at the edges of banks of floating reeds (ARAÚJO-LIMA; GOULDING, 1998), areas typically dominated by calm and relatively clear waters, ideal for the survival of the fertilized eggs. However, one other possible explanation is that the local *C. macropomum* stocks have been depleted to critical levels. Additional research will be needed to determine whether the species is present in the study area, but spawning in discrete habitats (ARAÚJO-LIMA; GOULDING, 1998; COSTA et al., 1999) or whether its local stocks are threatened by overfishing, as observed in other parts of the Amazon basin (SOUSA; FREITAS, 2011; CORREIA; FREITAS, 2013).

In the present study, some species were rare or absent from the samples due to their specific ecological characteristics, such as the formation of sedentary breeding pairs, which build nests in backwaters or in rocks at the margins of rivers and lakes, where they actively raise a relatively small number of offspring, impeding their collection in plankton trawls. Despite this, the presence of the larvae of a large number of the region's commercially-valuable migratory fish, emphasizes the importance of the study area for the spawning, development, and dispersal of these species.

The relatively low densities of eggs in comparison with the larvae throughout the study area may be related to the comparatively rapid development of the embryos, given the relatively short time available to the majority of species for the dispersal of their eggs and larvae by river currents (ARAÚJO-LIMA, 1994; CARDOSO, et al., 1995; NAKATANI, et al., 2001). Even so, the predominance of eggs in the initial cleavage stage, as well as recently-hatched and pre-flexion larvae, indicates that the spawning grounds were very close to the study area.

The results of the present study indicate that the species most valued and harvested by local fisheries (e.g., *Semaprochilodus taeniurus*, *S. insignis*, *Brycon amazonicus*, *Prochilodus nigricans*, *Mylossoma aureum*, *M. duriventre*, *Piaractus brachypomus*, *Curimata amazonica*, *C. inornata*, and *Hypophthalmus* spp.) are reproductively active during the closed season defined for the lower Amazon by the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA). This period lasts from November 15th to March 15th, coinciding with the river's early flood phase.

A number of studies have shown that reproduction in the fish fauna of the várzea floodplains are highly seasonal (ARAÚJO-LIMA; OLIVEIRA, 1998; HUMPHRIES et al., 1999; CASTRO et al., 2002; HUMPHRIES et al., 2002; KING et al., 2003), coinciding with the beginning of the rainy season and the flood pulse, the period characterized by the greatest abundance of feeding resources, which favors the growth and development of the larvae and juveniles (WERNER, 2002; ARAÚJO-LIMA; RUFFINO, 2003). This guarantees survival, and emphasizes the importance of the study area for the recruitment of these species.

For the majority of the migratory Characiformes, however, the peak of the flood waters appears to signal the end of the breeding season, which would account for the low densities of larvae recorded in the late flood phase and at high water. The high water phase is short, with little variation in water levels, and a predominance of aquatic environments on the floodplain. This is when the larvae reach the juvenile phase, are well dispersed in the environment and feeding most intensely, ready to face the environmental pressures of the ebb

phase, as noted by Suzuki et al. (2004), Nascimento and Nakatani (2006) and Bailly et al. (2008) in other Brazilian basins. Ziober et al. (2012) refer to the EFHs (Essential Fish Habitats) proposed by Bilkovic et al. (2002) as a spatial component (bodies of water and substrates used for feeding, reproduction, spawning and growth) of fundamental importance for the administration of fisheries and the management of fishery resources.

In the study area, the density of eggs was higher at the sampling stations located in the steep ruts areas at the margins of the islands, which are relatively turbulent, and are affected by erosive processes and the washing of their sediments downstream. The spatial distribution of the larvae was completely opposite, with the highest densities being found in the restinga swamps and inlets, probably due to the low current velocity of these environments, which facilitates the sedimentation of fine particles, increases the availability of refuges, and may also provide better conditions for foraging and development, as indicated by Werner (2002) and Houde (2002) for other environments in which low current velocities are one of the primary factors determining the selection of habitats by fish larvae. A similar pattern was observed in the Baía River in Mato Grosso do Sul (Brazil) by Bialecki et al. (2005) and by Zacardi (2014) on the middle Solimões River, in the Central Amazon basin.

The longitudinal gradient indicates that eggs were probably derived from spawns in local areas or upriver, which the newly-hatched larvae developing as they drift down the principal channel of the river, indicating that the study area may be an important spawning ground and nursery for many fish species. On the middle Solimões, Zacardi (2014) observed that the vast majority of the larvae collected in the principal channel of the river were in the initial stages of development, and that the subsequent stage (post-flexion and juveniles) were found primarily in flooded areas of the várzea swamp, concluding that these areas are used as nurseries by most of the local fish fauna. This indicates the existence of a large number of Essential Fish Habitats (EFHs) along the length of the Solimões/Amazonas River, including the várzea floodplains (channels and lakes), which are fundamentally important for the maintenance of the fish stocks of the Amazon basin.

While no systematic pattern of spatial distribution was found in the present study, it is important to note that the distance from the spawning ground to the nursery areas may represent a limitation for the recruitment of the species, given that the risk of mortality increases over longer distances, due to the physical damage experienced during the drifting process, as well as the reduced access to feeding resources (ZIOBER et al. 2012).

Many studies in tropical rivers have recorded larger numbers of larvae during the nocturnal period, and in the sub-surface layer of the water column, irrespective of the limnological conditions (ARAÚJO-LIMA et al., 2001, BIALETZKI et al., 2004). This tendency tends to increase as the larvae develop. This behavior may have evolved to minimize intra and interspecific competition (SANTIN et al., 2004) and is probably related to the shift in the availability of feeding resources caused by the migration of the zooplankton, as well as the avoidance of visually-oriented predators. The present study also found a pattern of this type, with significant differences

being found in the abundance of specimens between day- and night-time samples.

The high concentrations of larvae recorded at all collection points and over the first months of flooding show the great functionality that these habitats on the shores of the main river channel play in the early life cycle of the Amazon fish populations. In general, high concentrations of fish eggs and larvae these in marginal areas of the river are related to spawning in the main channel, which increases the probability of the transportation of the larvae to the várzea floodplain, favoring their dispersal (ARAÚJO-LIMA; OLIVEIRA, 1998, THOMAZ et al., 2007). During the flood phase, these floodplains provide a wide variety of environments, and a greater supply of refuges and feeding resources for the larvae (LEITE; ARAÚJO-LIMA, 2002; LIMA; ARAÚJO-LIMA, 2004), maximizing the chances of the development, survival and recruitment of migratory species during the initial phases of their life cycle, satisfying the biological and ecological needs of the fish populations.

The importance of the influence of environmental factors on fish breeding patterns was emphasized by the synchrony of these variables with the distribution of the fish eggs and larvae, which may help guarantee the development and survival of these species during the initial stages of their life cycle (NASCIMENTO; NAKATANI, 2006). The positive correlations between the density of eggs and rainfall levels, and between the density of larvae and river water levels, and the fact that the highest densities were recorded in the months when these abiotic variables and dissolved oxygen were increasing (January and February) may indicate that these conditions may trigger spawning.

A relationship between environmental factors and the spatio-temporal distribution of the fish eggs and larvae has been demonstrated in a number of studies, such as those of Baumgartner et al., (2008), Viana and Nogueira (2008), Gogola et al. (2010), Ziober et al. (2012), Ferreira et al. (2016), Suzuki and Pompeu (2016), Ponte et al. (2016) and Chaves et al. (2017). This seasonal variability may thus guarantee favorable conditions for spawning, and the survival and development of the larvae, Second Nakatani et al. (2001) given that spawning depends not only on the condition of the female, but also adequate environmental conditions during the maturation and fertilization of the eggs.

High dissolved oxygen concentrations appear to be necessary for the adequate development of fish eggs (WERNER, 2002), although Fisher (1978) and Fosberg et al. (1988) concluded that the variation in dissolved oxygen concentrations, temperature, electrical conductivity and pH probably all play a secondary role in the activation of the spawning observed during the flood phase, in the principal channel of the Amazon River, due to its stable temperature and oxygen levels. Other variables, such as the availability of feeding resources, predation and competition (HARVEY, 1991; PAVLOV et al., 2008), and even the foraging strategy of the adults (REYNALTE-TATAJE et al., 2011), may also influence the spatio-temporal variation in the distribution of the larvae. The higher density of fish eggs and larvae during periods of low pH reflects the fact that some species prefer slightly acidic environments with low electrical conductivity, as reported by Nascimento and Nakatani (2006).

Conclusion

Based on the results of the present study on the lower Amazon River between January and December 2013, it is possible to confirm that the marginal zones along the Amazon River channel of this area are important for the spawning, retention, and development of the region's fish fauna, and that the larvae produced by migratory fish species are probably transported to the innumerable areas of the floodplain that are most adequate for the development of the larvae.

Overall, the main channel of the Amazon River appears to be the most appropriate environment for their production of most species, reinforcing the need to uphold the integrity of this environment in the face of anthropogenic pressures, and emphasizing the importance of the adoption of management strategies designed to guarantee the preservation of natural fishery stocks. The current measures in place for the protection of the region's most exploited fishery resources should also be reviewed, as well as the monitoring of fishing practices during the breeding season.

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Supplementary Material

Table 1. Species list and average density (individuals.10 m⁻³) of the ichthyoplankton collected in 2013 in the Marecas Island complex on the lower Amazon River in Pará, Brazil. *Specimens identified only to order; **Specimens identified only to family; N=total number of individuals; RA=Relative Abundance; RS =Reproductive Strategy; M=Migratory; NM=Non-migratory.

TAXA	N	RA(%)	Months of the year (2013)												RS
			J	F	M	A	M	J	J	A	S	O	N	D	
BELONIFORMES															
Belonidae															
<i>Belonion apodion</i>	1	<0.01	-	-	-	<0.01	-	-	-	-	-	-	-	-	NM
CHARACIFORMES*															
Anostomidae**															
<i>Leporinus</i> sp.	1343	2.90	0.13	0.49	0.25	0.13	0.04	-	-	-	-	<0.01	0.03	<0.01	M
<i>Schizodon fasciatus</i>	5005	10.81	0.59	2.31	1.13	0.03	<0.01	<0.01	-	-	-	<0.01	0.12	0.13	M
<i>Rhytioides microlepis</i>	13	0.03	0.01	<0.01	-	-	-	-	-	-	-	-	-	-	M
Characidae**															
<i>Brycon amazonicus</i>	7	0.02	<0.01	<0.01	<0.01	-	-	-	-	-	-	-	-	-	M
<i>Colossoma macropomum</i>	3	0.01	-	<0.01	-	-	-	-	-	-	-	-	-	-	M
<i>Mylossoma duriventre</i>	9838	21.25	3.27	3.18	0.93	0.08	0.01	<0.01	0.01	0.01	0.01	0.01	0.35	0.32	M
<i>Mylossoma aureum</i>	9110	19.68	3.84	1.55	0.07	<0.01	-	-	-	0.01	0.01	0.01	1.95	0.60	M
<i>Piaractus brachipomus</i>	13	0.03	-	-	<0.01	<0.01	0.01	<0.01	-	-	-	-	-	-	M
<i>Triportheus auritus</i>	117	0.03	-	-	<0.01	<0.01	0.01	<0.01	-	-	-	-	-	-	M
<i>Triportheus</i> spp.	2621	5.66	0.46	1.32	0.12	0.02	0.01	-	<0.01	0.11	0.10	0.03	0.08	0.04	M
Curimatidae**															
<i>Potamorhina altamazonica</i>	1040	2.25	0.14	0.38	0.28	0.01	<0.01	-	-	-	-	-	-	0.01	M
<i>Potamorhina latior</i>	21	0.05	-	0.01	0.01	<0.01	-	-	-	-	-	-	-	-	M
<i>Psectrogaster amazonica</i>	2000	4.32	0.27	1.09	0.20	0.04	0.02	-	0.08	-	-	<0.01	0.01	<0.01	M
<i>Psectrogaster rutiloides</i>	13	0.03	-	0.01	<0.01	-	<0.01	-	-	-	-	-	-	<0.01	M
Cynodontidae															
<i>Hydrolycus scomberoides</i>	6	0.01	<0.01	-	<0.01	-	-	-	-	-	-	-	-	-	M
<i>Raphiodon vulpinus</i>	87	0.19	0.02	0.04	0.01	0.01	<0.01	-	-	-	-	-	<0.01	0.01	M
Hemiodontidae**															
<i>Anodus elongatus</i>	852	1.84	0.12	0.30	0.03	0.01	-	-	<0.01	0.01	0.02	<0.01	0.09	0.15	M
<i>Hemiodus</i> sp.	742	1.60	0.20	0.20	0.01	<0.01	-	-	<0.01	0.01	0.05	0.01	0.08	0.04	M
Prochilodontidae															
<i>Prochilodus nigricans</i>	58	0.13	-	0.02	-	-	-	-	-	-	-	-	0.02	-	M
<i>Semaprochilodus insignis</i>	50	0.11	<0.01	0.02	<0.01	-	-	-	-	-	-	-	0.02	<0.01	M
<i>Semaprochilodus taeniurus</i>	38	0.08	<0.01	0.02	<0.01	<0.01	-	-	-	-	-	-	<0.01	<0.01	M
CLUPEIFORMES*															
Engraulidae**															
<i>Engraulis</i> spp.	1866	4.03	0.08	0.14	0.03	0.01	<0.01	0.01	0.12	0.07	0.13	0.39	0.79	0.06	-
Pristigasteridae															
<i>Pellona</i> spp.	3064	6.62	0.40	0.67	0.12	0.05	0.01	<0.01	0.05	0.03	0.04	0.18	0.99	0.13	M
PERCIFORMES															
Sciaenidae															
<i>Plagioscion squamosissimus</i>	910	1.97	0.02	0.03	0.03	0.08	<0.01	<0.01	0.06	0.07	0.17	0.16	0.03	0.01	NM
<i>Plagioscion aratus</i>	64	0.14	-	-	-	0.02	<0.01	0.01	0.01	0.01	0.01	-	<0.01	<0.01	NM
<i>Pachypops furcraeus</i>	1	<0.01	<0.01	-	-	-	-	-	-	-	-	-	-	-	NM
<i>Pachypops schomburgkii</i>	23	0.05	-	-	<0.01	0.01	-	-	<0.01	-	-	-	<0.01	-	NM
PLEURONECTIFORMES															
Acharidae**															
<i>Acharius</i> spp.	8	0.02	-	-	-	<0.01	-	-	<0.01	-	-	-	<0.01	-	NM
SILURIFORMES															
Auchenipteridae**															
<i>Tatia</i> sp.	2	<0.01	-	-	<0.01	-	-	<0.01	-	-	-	-	-	-	NM
<i>Trachelyopterus galeatus</i>	10	0.02	-	-	<0.01	<0.01	<0.01	-	-	<0.01	-	-	-	-	NM
Cetopsidae															
<i>Cetopsis coecutiens</i>	53	0.11	0.01	<0.01	0.02	-	-	-	-	<0.01	-	-	-	-	NM
Doradidae**															
<i>Pimelodella cf. cristata</i>	1	<0.01	-	-	-	-	<0.01	-	-	-	-	-	-	-	M
Loricaridae**															
<i>Loricaria</i> spp.	4	0.01	<0.01	-	-	-	-	-	-	-	-	<0.01	-	-	NM
Pimelodidae**															
<i>Brachyplatystoma filamentosum</i>	18	0.04	<0.01	<0.01	0.01	<0.01	-	<0.01	<0.01	-	-	<0.01	-	-	M
<i>Brachyplatystoma juruensis</i>	5	0.01	<0.01	<0.01	<0.01	<0.01	0.08	-	<0.01	-	-	-	-	-	M
<i>Brachyplatystoma platynemum</i>	1	<0.01	-	-	<0.01	-	-	-	-	-	-	-	-	-	M
<i>Brachyplatystoma rousseauxii</i>	14	0.03	-	-	-	-	-	-	-	-	-	<0.01	-	-	M
<i>Brachyplatystoma tigrinum</i>	14	0.03	<0.01	-	0.01	<0.01	-	-	-	-	-	-	-	-	M
<i>Brachyplatystoma vaillantii</i>	2	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	M
<i>Pimelodus blochii</i>	1331	2.87	0.16	<0.01	0.31	0.18	0.10	0.01	0.01	-	-	-	<0.01	-	M
<i>Hypophthalmus edentates</i>	27	0.06	-	-	<0.01	0.01	0.01	-	<0.01	-	-	-	-	-	M
<i>Hypophthalmus fimbriatus</i>	57	0.12	-	-	<0.01	0.02	0.01	-	<0.01	<0.01	0.01	<0.01	-	-	M
<i>Hypophthalmus marginatus</i>	82	0.18	<0.01	0.01	0.01	0.01	0.01	<0.01	0.01	<0.01	0.01	-	<0.01	-	M
<i>Platynemichthys notatus</i>	2	<0.01	-	-	<0.01	<0.01	-	-	-	-	-	-	-	-	M
<i>Pseudoplatystoma punctifer</i>	1648	3.56	0.09	-	0.72	0.14	0.03	0.02	<0.01	-	-	-	-	-	M
<i>Pseudoplatystoma tigrinum</i>	81	0.17	0.01	-	0.02	0.01	0.02	<0.01	<0.01	-	-	-	-	-	M
<i>Pseudoplatystoma</i> spp.	259	0.56	0.02	-	0.07	0.10	0.01	-	-	-	-	-	<0.01	-	M
<i>Sorubum lima</i>	254	0.55	0.01	<0.01	0.13	0.02	0.01	<0.01	-	-	-	-	-	-	M
Trichomycteridae**															
<i>Trichomycterus</i> spp.	2	<0.01	-	-	<0.01	-	-	-	-	-	-	-	-	<0.01	0
SYNBRANCHIFORMES															
Synbranchidae															
<i>Synbranchus marmoratus</i>	1	<0.01	-	-	<0.01	-	-	-	-	-	-	-	-	-	NM
TETRAODONTIFORMES															
Tetraodontidae															
<i>Colomesus asellus</i>	95	0.21	<0.01	0.02	0.05	<0.01	-	<0.01	-	-	<0.01	-	-	-	NM
UNIDENTIFIED															
	1323	2.86	0.47	0.23	0.17	0.04	0.03	0.01	0.01	0.04	0.04	0.02	0.12	0.09	-
EGGS															
	2295	4.96	1.32	0.33	0.11	0.02	<0.01	-	-	-	-	-	0.46	3.18	-