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Scientific Article



The flood pulse regulates the longitudinal distribution of fish assemblages in the amazonian floodplain lakes

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ABSTRACT

The present study evaluated the incidence of fish species in Cujubim Lake in Porto Velho (Rondônia, Brazil) concerning periods of flood and low water. For this, we used experimental fisheries, with ichthyofauna samplings carried out in the years 2019 and 2020, which resulted in 2,508 specimens. For quantifying the ecological data, we analyzed Shannon-Weaver diversity, species richness, Simpson dominance and Pielou evenness. The predominant fish orders were Characiformes and Siluriformes, and the species Anchovia aff. surinamensis was the most abundant (N=809/35.49%). Diversity indicators were similar across all sectors (S1=the lower margin - end, S2=center and S3=mouth of the lake). Only the levels of richness and abundance were lower in the S3 sector, despite the importance of this habitat as a link to the Madeira River, which indicates transient diversity, followed by active selection of the S1 and S2 sectors in the lake by most fish. Limnological data, such as those of temperature (30.30 \pm 1.20°C), conductivity (35.82 \pm 5.98 μ S cm⁻¹), dissolved oxygen (7.38 \pm 3.56 mg L⁻¹) and pH (6.70±0.54), were within the acceptable levels for tropical fish. The non-metric multidimensional scaling (NMDS) analysis showed the ordering of parameters by sector and species with greater affinity for each environmental attribute, in which dissolved oxygen (NMDS1=-0.720; r²=0.862 and p=0.043) and electrical conductivity stood out. Thus, it can be concluded that the behavior of the fish diversity of Cujubim Lake is affected both seasonally and longitudinally.

Keywords: seasonality; fish ecology; amazon fisheries; migration.

O pulso de inundação regula a distribuição longitudinal das assembleias de peixes nos lagos de várzea amazônicos

RESUMO

O presente estudo avaliou a incidência de espécies de peixes no lago Cujubim em Porto Velho (Rondônia, Brasil), com os períodos de cheia e seca. Para tal, utilizou-se de pescarias experimentais, com coletas da ictiofauna realizadas nos anos de 2019 e 2020, totalizando 2.508 peixes amostrados. Na quantificação dos dados ecológicos, foram aplicados os métodos de Shannon-Weaver para diversidade, riqueza, dominância de Simpson e equabilidade de Pielou. As ordens predominantes foram Characiformes e Siluriformes, sendo a espécie Anchovia aff. surinamensis a mais abundante (N=809, 35,49%). Os indicadores de diversidade foram semelhantes em todos os setores (S1=a margem inferior - extremidade, S2=centro e S3=entrada do lago). Somente a riqueza e a abundância foram menores no setor S3, mesmo com a importância desse hábitat como conexão com o rio Madeira, indicando diversidade transitória, seguida de seleção ativa dos setores S1 e S2 pela maioria dos peixes no lago. Os dados limnológicos, como temperatura (30,30±1,20°C), condutividade (35,82±5,98 µS cm⁻¹), oxigênio dissolvido (7,38 \pm 3,56 mg L⁻¹) e pH (6,70 \pm 0,54), estiveram de acordo com a média aceitável para peixes tropicais. A análise de escalonamento multidimensional não métrico (NMDS) evidenciou a ordenação dos parâmetros por setor e espécies com maior afinidade para cada atributo ambiental, no qual se destacaram o oxigênio dissolvido (NMDS1=-0,720; r²=0,862 e p=0,043) e a condutividade elétrica. Assim, pode ser concluído que o comportamento de colonização da diversidade de peixes do lago Cujubim é afetado de forma sazonal e longitudinal.

Palavras-chave: sazonalidade; ecologia de peixes; pesca amazônica; migração.

INTRODUCTION

Fishing is one of the main economic activities developed in the northern region of Brazil, and the rivers provide the main source of animal protein consumed by many riverine communities and large urban centers (Lima et al., 2012). However, this activity is not only limited to food production, but also to numerous forms of behavioral interactions between man, environment and ichthyofauna (Daaddy et al., 2016), which, as a result, dictate the daily life of the Amazonian populations that depend on the capture of these animals as a means of livelihood (Lira and Chaves, 2016).

However, with the decrease in the size of fish and fish stocks of commercial interest (Viana, 2013; Barthem et al., 2019), fishing becomes an unstable activity and causes insecurity regarding the use of this resource in cultural and economic terms (Santos and Santos, 2005). In addition, hydroelectric projects also negatively impact fisheries, since they affect the characteristic flood pulse of rivers (Junk and Mello, 1990; Almeida et al., 2020), and modify the behavior of the fish species that colonize or leave these environments during their migration processes for reproduction or feeding (Lewinsohn and Prado, 2002; Cintra et al., 2013; Scanferla and Suaréz, 2016).

However, the flood pulse is recognized as the main influencer of the behavior of aquatic biota in the rivers of the Amazon basin, mainly by seasonally connecting and separating the various flooded environments, which interferes with the structure of the fish communities that reside therein (Hurd et al., 2016).

The richly diverse Amazonian fish species present differentiated characteristics in their forms and habits that contrast with the abundance of rivers and lakes that make up this ecosystem (Leal et al., 2018). However, these environments, when modified abruptly, also affect artisanal fisheries and cause great losses to the sector (Souza et al., 2015). Thus, it is understood that the dispersal flow of fish assemblages is responsible for the replenishment processes of natural fish stocks, and this has relevance not only in the maintenance of biodiversity, but also economically and in regards to the subsistence of fishing and riverine communities (Issac et al., 1996; Lima et al., 2012). This is especially important because the empirical knowledge these communities have on the environment that are directly related to the ichthyofauna behavior, which is a strong point to the riverine, obtains the most success with small-scale fishing (Doria et al., 2008; Moraes, 2011).

Information on the ecological processes and colonization of fish assemblages in aquatic environments permits the construction of a more accurate understanding of how fish communities organize themselves in a given environment, especially where they maintain their reproductive and dispersal processes (Doria et al., 2012; Inomata and Freitas, 2018; Lopes and Freitas, 2018). Therefore, it is necessary to comprehend the diversity indicators of the fish assemblages that exist in a given area, especially in the large lakes of lowland regions, which annually go through flood (period of low fishing productivity) and low water (period of high fishing productivity) phases (Agripino and Maurizio, 2013). Thus, these facts affect the behavior of fish species that colonize or leave the floodplains, since this knowledge can directly influence the optimization of fishing activity and the management of fishing resources by local communities (Lewinsohn and Prado, 2002; Doria et al., 2008).

In order to understand the structures of fish assemblages and their longitudinal distribution in lowland environments, the present study tested the hypothesis that the diversity indices of ictic communities of the Cujubim Lake do not change seasonally (flood and low water phases) in the different sectors within the lake (mouth, central part and lower shore of the lake). Given the above, it is understood that studies on the diversity indices of fish assemblies in flooded areas that form the slow environments of the Amazon have become indispensable for the correct understanding of the interaction of biota in flood environments. These studies encourage the correct management and conservation of the fishery resources of the Amazon basin, especially those of interest to artisanal fishers who depend on this livelihood to maintain their families.

MATERIAL AND METHODS

Study area

Cujubim Lake is located in the western portion of the northern Brazilian region, comprising an approximate area of 2,195.26 hectares. It is located on the right bank of the Madeira River (geographical coordinates 8° 36' 14" S, 63° 40' 44" W), and, in a straight line, is 38 km from Porto Velho, the capital city of the state of Rondônia (Figure 1).

Data collection

Experimental fisheries were carried out in the periods of flood in 2019 (March and October) and low water in 2020 (February and October), according to the authorization issued by the Chico Mendes Institute-ICMBio under license number 66945-2. For the sampling of the fish, we used batteries of fixed and drift nets, which were made of monofilament nylon, 4 m high by 20 m long,



Figure 1. Location of Cujubim Lake, the area where this research was developed. S1, S2 and S3 represent the sectorization of the lake, which correspond to the lower margin (end), center and mouth of the lake, respectively.

tied side by side, with different sizes (40, 60, 80 and 100 mm, between opposite knots). During the fisheries, a cast net was also used (mesh of 8 cm between opposite knots, thread of 0.50 mm, 20 m diameter with a height of 2.50 m). The nets were arranged at the end, central part and shore of Cujubim Lake, where they were kept submerged for 24 hours. Each battery of nets was inspected for fish samples at 06:00 p.m., 00:00, 06:00 a.m. and 12:00. The cast net was used for 30 minutes after the inspections of the nets.

The sampled fish were separated by time and place of collection and were packed in plastic bags with handles. Each individual was euthanized by spinal cord section (CFMV, 2012), once the research project was approved by the Ethics Committee for Animal Use (CEUA) of the Federal University of Rondônia (UNIR), under registration 018/2019. While in the sampling location, the standard length (cm) and total weight (g) of each specimen were measured with the aid of an ichthyometer (cm) and precision scale (0.01 g), respectively. The collected individuals were identified in the field by professionals and experts in fish identification. Only the species that were difficult to identify were stored in polystyrene boxes and transported to the Ichthyology and Fisheries Laboratory at UNIR for further identification (rare species were identified and listed in the LIP-UNIR fish collection). During the nychthemeral period, the physical and chemical parameters of the lake water, i.e., temperature (°C), dissolved oxygen (mg L-1), hydrogenionic potential (pH) and electrical conductivity (µS cm⁻¹) were measured with the aid of a multi-parameter probe (AKSO model 8603).

Analysis of abiotic and biotic data

The analysis of the physicochemical parameters of the water occurred in two manners. The first involved the use of descriptive statistics, using the calculations of mean and standard deviation, in order to verify the acceptable environmental levels for fish of tropical environments, and the second involved an analysis of variance (ANOVA) to verify possible differences between the means of the variables according to each sector within the lake and between the hydrological phases of flood and low water. When the assumptions of normality and homogeneity were met, the Tukey test was applied to identify which groups differed. The Kruskal-Wallis test was also used for nonparametric data.

The limnological, seasonality and abundance data of the fish species were analyzed by using non-metric multidimensional scaling analysis (NMDS) to determine the minimum number of dimensions necessary for the ordering of data based on Bray-Curtis dissimilarity between the samples, according to Legendre and Legendre (1998). The analysis was carried out using the Vegan statistical package (Oksanen, 2013) in the computer program R (R Development Core Team, 2010).

Estimates of species diversity

The estimated diversity indices were those of Shannon (Shannon, 1948), Pielou evenness or equity (Magurran, 1988), Simpson

dominance (Simpson, 1949) and numerical species richness. The Shannon index was calculated using the Equation 1:

$$H=-\sum pi * Lnpi, \tag{1}$$

Where:

pi=ni/N;

ni=the number of individuals of species I;

N=the total number of individuals in the sample, i.e., the relative proportion of each species by the total of individuals in the sample.

The Pielou equity for the samples was calculated using the Equation 2:

$$E = \frac{H'}{LnS}$$
(2)

Where:

H'=the Shannon index;

LnS=the natural logarithm of the number of registered species (Magurran, 1988).

With the inverse concept to the diversity, the Simpson dominance index (D) was calculated using the Equation 3:

$$\sum p_i^2$$
(3)

Which is the sum of the abundances relative to the square.

The data on the fish communities distributed by sectors were added together and separated according to the sample areas indicated by seasonality and sector, totaling six groups of samples. These data were arranged in dominance-diversity curves (Whittaker, 1965), according to relative abundance rankings, which were described in logarithmic proportions (Magurran, 1988) to compare the results of theoretical diversity with the composition of abundances in a longitudinal manner in Cujubim Lake. For Log_{10} scale plotting, relative abundances were expressed in permille, rather than percentage, or gross values, in order to avoid the problem of plotting logarithmic values when the gross abundance of a given species was equal to one.

Fish communities underwent tests of data agreement between dispersion curves and theoretical modeling, through least-squares regression analysis, with the aid of the statistical software package MyStat (Systat Software Inc., 2020). The observed r² (squared multiple r) patterns were indicated as evidence of adherence of abundance distributions among species by sector (Fattorini, 2005). $p \le 0.05$ were recognized as relevant for related data.

RESULTS

A total of 2,508 fish were collected, belonging to five orders, 18 families and 92 species (Table 1). The order Characiformes was found to be the dominant order with 1,241 individuals, which belong to 40 species, followed by Clupeiformes with 997

Taxanamy		Flood pha		ase	low v	ow water phase			
Taxonomy	Cod	S1	S2	S3	S1	S2	S3	- (RF; %)	Migratory
Characiformes									
Anostomidae									
Anostomoides laticeps (Eigenmann 1912)	Al	1	1		1	3	1	0.28	Yes
Anostomoides passionis (Santos and Zuanon 2006)	Ap		3					0.12	Yes
Leporinus friderici (Bloch 1794)	Lf				2	4		0.24	Yes
Megaleporinus trifasciatus (Steindachner 1876)	Mlt				4	2	2	0.32	Yes
Rhytiodus argenteofuscus (Kner 1858)	Ra	1						0.04	Yes
Schizodon fasciatus (Spix and Agassiz 1829)	Sf		2		26	13	14	2.19	Yes
Bryconidae									
Brycon cephalus (Günther 1869)	Bcp	1				2		0.12	Yes
Brycon amazonicus (Spix and Agassiz 1829)	Ba				1	1		0.08	Yes
Brycon sp.	Bc				2			0.08	Yes
Characidae									
Cynopotamus juruenae (Menezes 1987)	Cj	2						0.08	Yes
Poptella compressa (Günther 1864)	Pc				4	1		0.20	Yes
Roeboides affinis (Günther 1868)	Raf	11	22		3	5	1	1.67	Yes
Roeboides myersii (Gill 1870)	Rm	2	5					0.28	Yes
Tetragonopterus chalceus (Spix and Agassiz 1829)	Tc	1						0.04	Yes
Curimatidae									
Curimata inornata (Vari 1989)	Ci		4	1	13	1	5	0.96	Yes
Curimatella alburna (Müller and Troschel 1844)	Ca			2				0.08	Yes
Curimatella dorsalis (Eigenmann and Eigenmann 1889)	Cd	1	7					0.32	Yes
Curimatella meyeri (Steindachner 1882)	Cm				3			0.12	Yes
Potamorhina altamazonica (Cope 1878)	Pa	15	30	10	4	30	5	3.75	Yes
Potamorhina latior (Spix and Agassiz 1829)	Pl	33	21	25	1	25	2	4.27	Yes
Psectrogaster amazonica (Eigenmann and Eigenmann 1889)	Psa		1	1	4	8		0.56	Yes
Psectrogaster rutiloides (Kner 1858)	Pr	11	10	5	17	15	1	2.35	Yes
Erythrinidae									
Hoplias malabaricus (Bloch 1794)	Hml	1			2		1	0.16	No
Hemiodontidae									
Anodus elongatus (Agassiz 1829)	Ae			7	4	20		1.24	Yes
Anodus orinocensis (Steindachner 1887)	Ao	3	1					0.16	Yes
Hemiodus microlepis (Kner 1858)	Hmc					1	1	0.08	Yes
Hemiodus sp.	Hs		1	4				0.20	Yes
Hemiodus unimaculatus (Bloch 1794)	Hu		4			4		0.32	Yes
Prochilodontidae									
Prochilodus nigricans (Spix and Agassiz 1829)	Pn	3		3	33	6		1.79	Yes
Semaprochilodus insignis (Jardine 1841)	Si		1		111	18	149	11.12	Yes
Semaprochilodus taeniurus (Vallenciennes 1817)	St	2						0.08	Yes

Table 1. Taxonomic list and abundance of fish species by sectors and seasonal period of Cujubim Lake, Porto Velho, Brazil.

Continue...

Table 1. Continuation.

Taxanamy		Flood phase		ase	low water phase			_ (DE, 0/)	Migrotory
	Cou	S1	S2	S3	S1	S2	S3	- (KF; 70)	wingratory
Serrasalmidae									
Serrasalmus maculatus (Kner 1858)	Sm					1		0.04	No
Serrasalmus rhombeus (Linnaeus 1766)	Sr				1	2	1	0.16	No
Serrasalmus spilopleura (Kner 1858)	Ss	1					1	0.08	No
Mylossoma aureum (Spix and Agassiz 1829)	Ma	2						0.08	No
Mylossoma duriventre (Cuvier 1818)	Md			1	1			0.08	No
Triportheidae									
Triportheus albus (Cope 1872)	Ta	2		1	2	9	13	1.08	Yes
Triportheus angulatus (Spix and Agassiz 1829)	Tag	18	13	2	48	79	114	10.93	Yes
Triportheus elongatus (Günther 1864)	Te	34	17	14	9	6	7	3.47	Yes
Triportheus sp.	Ts		1	6				0.28	Yes
Clupeiformes									
Engraulidae									
Jurengraulis juruensis (Boulenger, 1898)	Jj				8	11	21	1.59	Yes
Lycengraulis batesii (Günther 1868)	Lb	3	7					0.40	Yes
Anchovia aff. surinamensis (Bleeker 1865)	As	134	183	38	235	263	37	35.49	Yes
Pristigasteridae									
Pellona castelnaeana (Valenciennes 1847)	Plc					1		0.04	Yes
Pellona flavipinnis (Valenciennes 1836)	Pf	13	25	8	7	3		2.23	Yes
Perciformes									
Cichlidae									
Caquetaia spectabilis (Steindachner 1875)	Cs				1			0.04	No
Chaetobranchopsis orbicularis (Steindachner 1875)	Cho				1			0.04	No
Chaetobranchus flavescens (Heckel 1840)	Chf				3		1	0.16	No
Cichla pleiozona (Kullander and Ferreira 2006)	Ср	1			2	1	1	0.20	No
Crenicichla aff. lenticulata (Heckel 1840)	Ccl	1						0.04	No
Crenicichla reticulata (Heckel 1840)	Cr		1					0.04	No
Geophagus cf. altifrons (Heckel 1840)	Gat	2	4					0.24	No
Geophagus megasema (Heckel 1840)	Gm	2	1		2		1	0.24	No
Geophagus sp. aff. altifrons (Heckel 1840)	Gsa				1			0.04	No
Satanoperca acuticeps (Heckel 1840)	Sa	3	2					0.20	No
Satanoperca cf. jurupari (Heckel 1840)	Scj	2						0.08	No
Satanoperca jurupari (Heckel 1840)	Sj	4			1		5	0.40	No
Sciaenidae									
Plagioscion squamosissimus (Heckel 1840)	Ps	3	2	3	3	1	6	0.72	Yes
Pleuronectiformes									
Achiridae									
Hypoclinemus mentalis (Günther 1862)	Hmt	1	1	-			1	0.12	Yes

Table 1. Continuation.

Terrenewa		Flood phase		ase	low water phase					
Taxonomy	Cod	S1	S2	S3	S1	S2	S3	· (RF; %)	Migratory	
Siluriformes						-				
Auchenipteridae										
Ageneiosus apiaka (Ribeiro et al. 2017)	Aa		2					0.08	Yes	
Auchenipterichthys logimanus (Günther 1864)	Alg	1	1					0.08	Yes	
Auchenipterus aff. nuchalis (Spix and Agassiz 1829)	An		4			1		0.20	Yes	
Trachelyopterus galeatus (Linnaeus 1766)	Tgl	3						0.12	Yes	
Doradidae										
Amblydoras affinis (Kner 1855)	Aaf		1					0.04	No	
Leptodoras cf. praelongus (Myers and Weitzman 1956)	Ltp		9					0.36	No	
Hemidoras morrisi (Eigenmann 1925)	Hm		1	1		1		0.12	No	
Nemadoras elongatus (Boulenger 1898)	Ne			1				0.04	No	
Nemadoras hemipeltis (Eigenmann 1925)	Nh					1		0.04	No	
Nemadoras humeralis (Kner 1855)	Nhu		1					0.04	No	
Opsodoras boulengeri (Steindachner 1915)	Ob						1	0.04	No	
Opsodoras stuebelii (Steindachner 1882)	Os	1						0.04	No	
Ossancora punctata (Kner 1855)	Op	2	1	1				0.16	No	
Oxydoras niger (Valenciennes 1821)	On	1	1		1	1		0.16	No	
Trachydoras paraguayensis (Eigenmann and Ward 1907)	Тр					1		0.04	No	
Loricariidae										
Hypostomus cochliodon (Kner 1854)	Hc	2	1					0.12	No	
Hypostomus gr. Cochliodon	Htc		1					0.04	No	
Hypostomus plecostomus (Linnaeus 1758)	Нр						1	0.04	No	
Pterygoplichthys pardalis (Castelnau 1855)	Ptp				13			0.52	No	
Pterygoplichthys lituratus (Kner 1854)	Ptl				2					
Loricariichthys maculatus (Bloch 1794)	Lm	1	8					0.36	No	
Loricariichthys nudirostris (Kner 1853)	Ln				8		1	0.36	No	
Loricariichthys sp.	Lc	4	1	1	2	1	1	0.40	No	
Rineloricaria cf. castroi (Isbrücker and Nijssen 1984)	Rc	2	4					0.24	No	
Squaliforma emarginata (Valenciennes 1840)	Sqe		1					0.04	No	
Pimelodidae										
Pimelodus blochii (Valenciennes 1840)	Pb	15	14	5	12	13	17	3.03	Yes	
Pimelodus cf. tetramerus (Ribeiro and Lucena 2006)	Plt	2		7				0.36	Yes	
Pseudoplatystoma punctifer (Castelnau 1855)	Рр	1						0.04	Yes	
Sorubim elongatus (Littmann, Burr, Schmidt and Isern 2001)	Se	1	1	1	1	1	2	0.28	Yes	
Sorubim lima (Bloch and Schneider 1801)	Sl	1	1	3				0.20	Yes	
Hemisorubim platyrhynchos (Valenciennes 1840)	Hpt						1	0.04	Yes	
Hypophthalmus edentatus (Spix and Agassiz 1829)	He	9		1		1	1	0.48	Yes	
Hypophthalmus marginatus (Valenciennes 1840)	Hmr					1		0.04	Yes	
Total		360	423	152	599	558	416		2,508	

Migratory: confirmation of whether it is a migratory fish species or not; Cod: Species identifier code; S1: the lower margin – end; S2: center; S3: mouth of the lake; RF %: Relative frequency (Santos and Jegu, 1996; Reis et al., 2003; Carolsfeld et al., 2004; Garcia, 2005; Baumgartner et al., 2012; Queiroz et al., 2013a, 2013b, 2013c; Ribeiro et al., 2017; Froese; Pauly, 2019; Myers et al., 2020).

individuals distributed in five species, and Siluriformes with 206 individuals and 33 species (Table 1).

In both periods, sectors S1 and S2 presented the highest species richness, 47 species in the flood phase and 41 in the low water phase for S1. For S2, 45 species occurred in the flood phase and 39 in the low water phase (Table 2). Sector S3 presented the lowest species richness in both phases, with 26 species in the flood phase and 32 species in the low water phase (Table 2).

The distribution of relative abundance among species resulted in greater Pielou evenness (E) and consequent lower dominance of Simpson dominance (D) in S3 during the flood phase (Table 2). On the other hand, in the low water phase, there was lower equity and greater dominance in the S2 sector (Table 2). This indicates the sub-dominance of *Anchovia surinamensis* (47.1% of relative abundance) in the low water phase in S2 and its lower dominance (25.0% of relative abundance) in S3 during the flood phase. *A. surinamensis* (Clupeiformes) was also the most abundant species in the other communities (37.2% in S1, in the flood phase; 43.3% in S2, in the flood phase; 39.2% in S1, in the low water phase), except in Sector S3 during the low water phase, when *Semaprochilodus insignis* (Characiformes) presented the highest number of records (35.8%). The difference in the relative abundance of these two species, as well as of Potamorhina altamazonica, Potamorhina latior, Triportheus angulatus, Triportheus elongatus (Characiformes) and Pellona flavipinnis (Clupeiformes), was the main factor related to the variations in the parameters of evenness and dominance among the sectors and between seasons.

The combination of the species richness and the evenness recorded resulted in low variation of the Shannon diversity index among sectors and between seasons (Table 2), with values between 2.054 and 2.613. This occurred because the sample of sector S3 during the flood phase, which presented the lowest species richness (S=26), also presented the highest Pielou equity (0.800), resulting in an intermediate Shannon index value compared to the other samples (Table 2). Thus, the lowest Shannon index was recorded in the S3 sample in the low water phase, which is when the second lowest species richness occurred, combined with the lowest equity, or the highest dominance.

The graphical interpretation of the abundance rankings (Whittaker, 1965) of the ichthyocenoses sampled indicates that sector S3 could present a lower diversity than sectors S1 and S2 in the low water phase (Figure 2A), while presenting great overlapping in the floods (Figure 2B). However, the analyses performed in order to check the adherence of the real rankings to different theoretical models of abundance distribution were

Table 2.	Fish	assemblage	diversity	indices b	v sector.	in C	uiubim	Lake.
		webe the tenge			,			

	Cujubim Lake (Sectors according to the hydrological period)								
Indices		Flood phase		Low water phase					
	S1	S2	S 3	S1	S2	S 3			
S	47	45	26	41	39	32			
Н'	2.613	2.460	2.605	2.297	2.155	2.054			
D	0.167	0.207	0.116	0.203	0.253	0.219			
Е	0.679	0.646	0.800	0.618	0.588	0.593			

S: species richness; H': Shannon diversity; D: Simpson dominance; E: Pielou equability; S1: the lower margin - end of the lake; S2: center of the lake; S3: mouth of the lake.



S1: the lower margin - end; S2: center; S3: mouth of the lake.

Figure 2. Abundance rankings in each sector in the period of (A) low water and (B) flood, for the years 2019 and 2020, in Cujubim Lake.

inconclusive, since in all sectors there was statistically significant adherence mainly to the geometric series model and secondarily to the log series model (Table 3), and without a consistent pattern when compared to the other diversity parameters.

The analysis of variance (ANOVA) indicated significant differences among the means of limnological variables for the phases of low water and flood in Cujubim Lake (Kruskal-Wallis, $H_{(1;251)}=43,5164, p<0.05$). However, among the sectors, only temperature showed variation (ANOVA, F=2.953, df=8, p<0.05) in the phases of low water (p=0.014) and flood (p=0.005) (Table 4).

After processing 719 permutations, the ordering of ichthyofauna and environmental data in NMDS revealed a distinct separation of fish groups in the flood and low water phases, with high dissimilarity among species in sectors of the lake in the flood, and Sector 3 is highlighted. During the low water phase, there was a grouping of species from all sectors, aligned positively to the values of electrical conductivity and secondarily to dissolved oxygen and negatively to pH (Figure 3). When we tested the relationships, variables such as pH, conductivity and temperature showed no significant differences, and only dissolved oxygen was decisive for the composition of the communities (NMDS1=-0.7205; r²=0.862 and p=0.043).

During the flood phase, sectors S1 and S2 formed another extremely cohesive group of species, partially aligned with increased pH (Figure 3), while sector S3 was positioned in isolation with a high NMDS2 axis value. This indicates a different ichthyofauna composition and low relationship with the variables, but possibly a secondary relationship with low dissolved oxygen levels.

In Sector S3, during the flood phase, there was a record of a group of less common species in the other treatments, especially the Characiformes *Curimatella alburna*, *Hemiodus*



S1: the lower margin – end of the lake; 2: center of the lake; 3: mouth of the lake; F: flood phase; L: low water phase; TC: temperature in degrees Celsius; DO: dissolved oxygen; EC: electrical conductivity; pH: hydrogenionic potential; *the other codes represent the fish species and are shown in Table 1.

Figure 3. Distribution of fish assemblages in the NMDS dimensional matrix (stress=0.102), in different seasonal, environmental groups and among the sectors of Cujubim Lake*.

Theoretical	Statistical		Flood phase		Ι	low water phas	se
models	parameters	S1	S2	S3	S1	S2	S 3
Geometric series	r^2	0.99	0.95	0.96	0.93	0.88	0.94
	Р	0.000	0.017	0.025	0.003	0.008	0.000
Log Series	r^2	0.59	0.52	0.67	0.55	0.49	0.85
	Р	0.004	0.013	0.004	0.007	0.016	0.015

Table 3. Regression analysis results for the actual distributions of abundances of species in Cujubim Lake sectors with the theoretical models of geometric series and log series.

 r^2 : an indicator of the adherence (relationship) of the real data to each model; *p*-value: significant relationships (when $p \le 0.05$) between the real data and the theoretical model; S1: the lower margin - end; S2: center; S3: mouth of the lake.

Table 4. Analysis of the average±standard deviation values of the limnological parameters of Cujubim lake using seasonal sectors and phases.

Environmental		Flood phase		Ι			
parameters	S1	S2	S 3	S1	S2	S 3	р
pН	6.44±0.52	6.42±0.54	6.39±0.57	6.88±0.54	7.02±0.51	7.07±0.55	*
T °C	30.30±0.81	30.30±0.73	30.35±0.78	29.99±1.93	30.26±1.63	30.60±1.34	*
DO mg L ⁻¹	9.14±4.71	8.72±4.22	8.56±3.89	7.16±3.73	5.74±2.50	4.94±2.28	*
EC µS cm ⁻¹	37.91±7.82	37.77±7.94	37.81±7.89	34.11±4.89	33.55±3.75	33.77±3.60	*

T °C: Temperature in degrees Celsius; DO: dissolved oxygen; EC: electrical conductivity; \pm : standard deviation. Equal letters on the same line have no significant differences by the Tukey test, among the lake's sectors (S1 = the lower margin - end, S2 = center and S3 = mouth of the lake); **p*-value: significant differences (p≤0.05) between the seasonal averages (flood and low water phase).

sp., Triportheus sp., and the Siluriformes Nemadoras elongatus, Pimelodus tetramerus and Sorubim lima, which explains the isolation of the community by NMDS. From the point of view of connectivity, the S3 sector is precisely the most exposed to species exchange with the Madeira River during the flood phase, which would explain the differences, such as limnological differences, in ichthyofauna composition.

DISCUSSION

The Madeira River is considered one of the main tributaries of the Amazon River basin, contributing approximately half of the sediments transported along its route in this region (Farias et al., 2010; Doria et al., 2012). Its territorial extent covers an estimated area of 1.4 million km² (Rapp Py-Daniel, 2007), and it contains a number of natural environments such as lakes and micro-basins that are distributed in its surrounding areas (Fearnside, 2014). The flood pulse governs the dynamics of the waters in the floodplains of the Amazonian rivers, so that they connect and disconnect various environments, such as rivers and lakes in periods of flood and low water phase (Junk et al., 1989; Hurd et al., 2016). During the flood phase of the rivers, several species of migratory fish take advantage of the expansion of the waters to carry out their dispersal movements between the flooded environments that function as access routes to the lakes and contribute to the processes of immigration and emigration when they colonize or leave their environments during the hydrological cycle (Fernandes, 1997; Hurd et al., 2016).

This factor corroborates the results presented herein, since there was seasonal differentiation of the composition of fish communities for each sector of Cujubim Lake, which correlated with environmental variables, such as electrical conductivity, dissolved oxygen and pH, and which were also seasonally distinct. Similarly, conductivity is one of the four structuring factors of the ichthyofauna of the Orinoco flood plain lake, and it has a direct relationship with transparency, depth and surface area (Rodríguez and Lewis Jr., 1997). In the low water period, the shoals may have clustered in response to the contraction of the aquatic environment, which makes them more vulnerable to natural predators and fishing; therefore, they present greater wealth and abundance by virtue of easy access and capture (Silvano et al., 2000).

Most species of Neotropical fish (Lowe-McConnell, 1999), including those from the Amazon region (Barletta et al., 2010; Freitas et al., 2015), belong to the order of Characiformes, which were also predominant in the present study, with 40 species sampled. Such abundance is linked to eating habits, reproduction and adaptations to varied environments (Saint-Paul et al., 2000; Pouilly et al., 2004; Siqueira-Souza and Freitas, 2004). Sequentially, the Siluriformes, the order of the "big catfish", predominated with 33 species, and these are of great importance for commercial and subsistence fisheries in the Amazon region (Santos et al., 2009). These are followed by the orders of Perciformes, Clupeiformes and Pleuronectformes, with a total of 5 orders and 2,508 individuals sampled.

Species richness values (S) were higher in the sectors farthest from the mouth of the lake, S1 and S2, which also presented more uniform richness values for the low water and flood phases. The S3 sector, which is more closely linked with the Madeira River, presented the lowest values of species richness and abundance of individuals both in the low water phase and in the flood phase. We expected, for the flood phase, that there would be an increase in species records due to the exchange of populations with the Madeira River. In the channels that connect lakes to the Solimões River, Freitas and Garcez (2004) recorded both resident species as opportunistic species in temporary colonization, since they are migratory species (Galacatos et al., 2004; Gutierrez and Pinill, 2016; Röpke et al., 2016).

However, for the same type of channels, Sousa and Freitas (2008) considered that the direction of water flow, limnological conditions and the concentration of predators are stress factors that define the structure of the remaining ichthyofauna. In the present study, the S3 sector presented the lowest mean dissolved oxygen, especially in the low water phase, slightly higher temperatures, in addition to a greater pH variation between the low water phase and the flood phase, as examples of variables that can cause species displacement, thus influencing the local composition of ichthyofauna (Milani et al., 2010; Rebouças et al., 2014). During the low water phase, when there is no connection to the Madeira River, the S3 sector responded to the same environmental variables and showed alignment with the composition of the other sectors, as demonstrated by the ordering of the NMDS analysis. In this situation, sector S3 presented a set of species in common with the other sectors, but with less abundance, and which resulted in a lower record of species richness, presumably due to the active selection of other habitats by the ichthyofauna (Moura and Val, 2019).

The low attractiveness of sector S3 in the selection of habitats by fish extends to the flood phase, since the lowest values of abundance and species richness are maintained, even with the inclusion of different species, some of which are "visitors" or migratory. Consequently, this resulted in the differentiated pattern recorded through the NMDS analysis for the S3 sector during the flood phase, whose ordination indicates the lowest correlations with the environmental variables that were measured. This is consistent with the transient character of the fish passage through the S3 sector, followed by the active selection of the other sectors. It is during the flood phase that the fish take advantage of the situation to disperse through the mosaic of habitats between the river and floodplain (Lowe-McConnell, 1979; Rodríguez and Lewis Jr., 1997), which is intense in Amazonian rivers (Goulding et al., 1988). During the low water phase, Arrington and Winemiller (2006) recorded high determinism in the selection of mesohabitats in coastal areas and marginal lakes of the Orinoco River. Thus, the fish

may be using the S3 sector as a link during the flood phase, but most of the time they select other habitats to stay in, due to the greater adequacy of environmental variables, such as those recorded herein, which results in lower density, if we consider the indication of low capture success.

Therefore, the connection of habitats (Cujubim Lake – Madeira River) provided by the S3 sector is consistent with the implications of the flood pulse concept (Junk et al., 1989), and is the means by which the species exchange is propagated throughout the lake, including in sectors S1 and S2. As a result, the composition of the ichthyofauna on a micro-scale, in each stretch of the lake and in each period of the year, is due to the selection of habitats; although the composition of the ichthyofauna of the isentence and in the medium term, is dependent on the connectivity with the Madeira River via the flood pulse, which implies great importance for the S3 sector, as a link for regional fish diversity (gamma diversity) (Rincón, 1999; Oliveira and Goulart, 2000; Buhrnheim, 2002; Oliveira et al., 2005).

The ichthyofauna that actively selects sector S3 in Cujubim Lake presents good distribution of relative abundances among the component species when compared to sectors S1 and S2, which is represented by similar equity and dominance indices (low water phase) or even better (flood phase) than that recorded in S1 and S2. Therefore, even with less species richness at the time of collection, it was not possible to differentiate local diversity of the S3 sector from the others, regardless of the diversity approaches that were applied. Thus, the lower species richness of S3, as a gross indicator of local alpha diversity, needs to be measured with the following possible caveats: due to the effect of lower local fish density, which disfavors records; and the temporary increase in transient species. Both factors are able to explain the local diversity and the diversity indicators presented, even with lower recorded species richness.

The low variation in all indicators of diversity between sectors is understandable considering that they are contiguous environments, though with high connectivity between the contiguous environments. However, different physical and chemical gradients along the mesoscale were formed between the sectors of Cujubim Lake, which may represent different dimensions of the niche for each species, and cause the differences in the composition of the recorded communities (Cottenie, 2005; Beisner et al., 2006; Ferrareze et al., 2014). Thus, of all the species of the lake, in addition to the species entering annually from the Madeira River, each of the populations could be more conspicuous in a certain range of local environmental gradients (Magalhães et al., 2002).

The species that presented the greatest numerical abundance was *A. surinamensis*, which represented about 35% of the individuals collected in both phases, followed by *S. insignis*, with approximately 11%, and *T. Angulatus*, with 10% of the total captured. These species perform migrations and make up a large part of the 94% of migratory species found in the lake. This

predominance indicates the effectiveness of the flood pulse in maintaining diversity in these environments, which is a pattern similar to that found in studies already carried out in tropical lakes in the Amazon region (Junk, 1993; Sousa and Freitas, 2008; Silva et al., 2021).

The abundance rankings approach corroborates the overlap of diversity indicators in this study. We can infer that the high number of rare species, which occurred in all samples, limits the application of this approach, since this did not coincide with what was expected for the classical models of abundance distribution, although it is important as a record of local alpha diversity (Nogueira et al., 2008).

The analyses of environmental parameters presented acceptable results regarding pH levels (6.39-7.07), and these are values that are within the standards observed in tropical environments for survival of aquatic species with small variation according to seasonal changes (Ribeiro et al., 2005; Lima et al., 2008; Faria et al., 2013; Oliveira et al., 2018). Temperature averages varied seasonally between 29 and 31°C. According to Boyd and Tucker (1998) and Faria et al. (2013), the ideal climate conditions for the development of tropical fish are between 25 and 32°C, showing another positive factor for the permanence of the species in the lake. Dissolved oxygen levels ranged from 4.94 to 9.14 mg L⁻¹, and are ideal for the species survival, since other studies indicate values above 5 mg L-1 as desirable for these environments (Lachi and Sipaúba-Tavares, 2008; Faria et al., 2013). For electrical conductivity, the values were from 33.55 to 37.91 µS cm⁻¹, also within the parameters indicated by Diemer et al. (2010) that range from 20 to 150 μ S cm⁻¹.

In summary, all the environmental parameters analyzed showed seasonal differences, but not always among the sectors. The NMDS analysis allowed these differences to be expressed more clearly, and the ordering took place by grouping similar values, showing the dispersion of species by sector (habitat selection), linked to environmental parameters (Gurgel-Lourenço et al., 2015). NMDS revealed that dissolved oxygen was paramount in the permanence of fish species in the study area, and equated to conductivity; factors that stand out together in the S1 sector, during the flood phase. The parameter-sector order allowed for the visualization of species with greater affinity to environmental conditions, and showed the species that were more adapted to available oxygen levels, milder temperatures, pH and higher conductivity. In the low water phase, the temperature naturally rises and the organic matter becomes abundant, which can influence the levels of dissolved oxygen in the water (Silva et al., 2008; Silva et al., 2017). This was observed in the axes of the analysis, and the incidence of certain fish species in this period due to their adaptation to these environmental conditions is noticeable (Centofante and Melo, 2012). The increase in conductivity in the sectors may be related to the rainy season (Fraga et al., 2012), in which the rocky sediments of the rivers undergo weathering, and distribute ions throughout the basin (Silva et al., 2008) and, consequently, cause higher conductivity.

CONCLUSION

The results showed that the levels of water quality and species diversity remained within the limits considered as ideal for the permanence and cultivation of tropical freshwater fish species. There were small changes among the sampling sectors and significant variations from one season to another. Sector S3, near the mouth of the lake, was the least selected by the ichthyofauna, thus presenting the lowest abundances, and consequently lower records of species richness. Even so, its diversity was almost indistinguishable in relation to sectors S1 and S2, which is probably due to the importance of S3 as a link to regional fish diversity (gama), and is governed by flood pulses. Factors, such as relatively high conductivity, increased dissolved oxygen and species diversity, are also directly linked to the phenomenon of flood pulse, which is the most important environmental factor for the natural maintenance of biodiversity in the study area. Thus, it was found that the fish diversity of Cujubim Lake has a seasonal and longitudinal behavior for colonization of the studied lake.

CONFLICT OF INTERESTS

Nothing to declare.

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AUTHOR'S CONTRIBUTIONS

Sousa, R.G.C.: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing–original draft, Writing–review & editing. Oliveira, N.S.: Data curation, Investigation, Methodology, Writing – original draft Writing. Rosa, F.R.: Conceptualization, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing.

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