

Fish Fauna in Oxbow Lakes of the Middle Purus River in the Neotropical Region of the Amazon Rainforest**Fauna de peixes em lagos de meandro abandonado no Médio Rio Purus na região Amazônica Neotropical**

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ABSTRACT

The effect of the flood pulse directs productivity and interactions of biota in abandoned oxbow lakes, as these habitats provide refuge from predators and serve as nurseries and feeding grounds for many fish species. The present study was conducted in twelve oxbow lakes with varying degrees of connectivity, located in the floodplain of the Middle Purus River in Brazil. 8.647 individuals were collected among 157 species. Lakes with high hydrological connectivity were shown to have the largest richness of species (131 species), while lakes with medium connectivity had slightly smaller richness (123 species), and lakes with low connectivity had even less (113 species). The results show high diversity in lakes that are attributed different connectivity, thereby indicating the importance of studies focused on oxbow lakes that contribute with relevant information on the composition of fish species in the Middle Purus River.

Keywords: Hydrological connectivity, floodplain, lake conservation, community of fishes, Purus microregion.

RESUMO

O efeito do pulso de inundação direciona a produtividade e as interações da biota em lagos de meandro abandonado, uma vez que estes habitats oferecem refúgio de predadores e servem como viveiros e locais de alimentação para muitas espécies de peixes. O presente estudo foi conduzido em doze lagos de meandro abandonado com diferentes graus de conectividade, localizados na planície de inundação do Médio Rio Purus no Brasil. 8.647 indivíduos foram coletados entre 157 espécies. Os lagos com alta conectividade hidrológica mostraram ter a maior riqueza de espécies (131 espécies), enquanto os lagos com conectividade média tinham uma riqueza ligeiramente menor (123 espécies), e os lagos com baixa conectividade tinham ainda menos (113 espécies). Os resultados mostram uma grande diversidade em lagos aos quais são atribuídas diferentes conectividades, indicando assim a importância de estudos focados em lagos de meandro abandonado que contribuem com informações relevantes sobre a composição das espécies de peixes no Médio Rio Purus.

Palavras-chave: Conectividade hidrológica, planície de inundação, conservação dos lagos, comunidade de peixes, microrregião Purus.

1 INTRODUCTION

The river basins of South America are home to the largest diversity of fish in the world (REIS et al., 2003; ALBERT et al., 2011; REIS et al., 2016, LEVÊQUE et al., 2007), with the Amazon River Basin being the world's richest fluvial system (ALBERT; REIS, 2011; REIS et al., 2016). This richness is associated to multiple aspects, such as historical and biogeographical factors, as well as the immensely large river basins and their geomorphological complexity that generate a wide variety of aquatic ecosystems (GOULDING et al., 2003). Among the main drainage basins of the Amazon rainforest, the Purus River Basin (PRB) located in Southwestern Amazonia features an abundant richness of fish fauna. During periods of high rainfall, areas around the riverbanks are affected by large floods that can reach up to approximately 200,000 km² (JUNK, 1993). PRB features a sinuous asymmetrical system, and due to hydro-sedimentation processes, the formation

of oxbow lakes occurs (WETZEL, 1993; ESTEVES, 2011). These ecosystems have connecting watercourses which become directly connected to the main river channel primarily during the flood season. This dynamic is influenced by the hydrological pulse, considered a key factor in the ecological functioning of these inundation areas (BUNN; ARTHINGTON 2002; JUNK et al., 2014).

Oxbow lakes are nutrient-rich and provide a fertile environment for nurseries of fish larvae, thus contributing to increased survival rates, where several fish species benefit from the food diversity created by lateral expansions of the river (GOULDING, 1980; STASS; NEUMANN, 1994; CASTELLO, 2008; AGOSTINHO et al., 2009). However, there is ever-increasing evidence that the structure and functioning of the Amazonian freshwater ecosystems are being gradually altered by anthropogenic activities (ALHO et al., 2015; ALMEIDA et al., 2016; BRUMMETT et al., 2016), which in turn affect the overall dynamic ecology of the system, such as energy flow and fish migration (BRUMMETT et al., 2016).

Thus, information on fish assemblages that occur in oxbow lakes of the Middle Purus River is an important resource for gathering data on the richness of fish species, thereby contributing to the knowledge and conservation of the ichthyofauna of the Amazon Rainforest. Considering that the existing studies on fish species in the Purus river basin are concentrated in the upper Purus River and lower Purus River (RAPP-PY-DANIEL; DEUS, 2003; DUARTE et al., 2013), the oxbow lake system is of central importance for studies related to the ichthyofauna. In this context, the present study describes fish fauna inhabiting twelve oxbow lakes of the Middle Purus River, and evaluate the influence of hydrological connectivity in the number of species of fish between the hydrological periods. As is the first study ever conducted in these environments, it aims to fill the current knowledge gap and contribute with more information on the ichthyofauna of the Purus River drainage basin. This data may lead to important information useful for the conservation and management of the lakes, taking into account their great economic, social and ecological importance to the region of the Amazon Rainforest.

2 MATERIALS AND METHODS

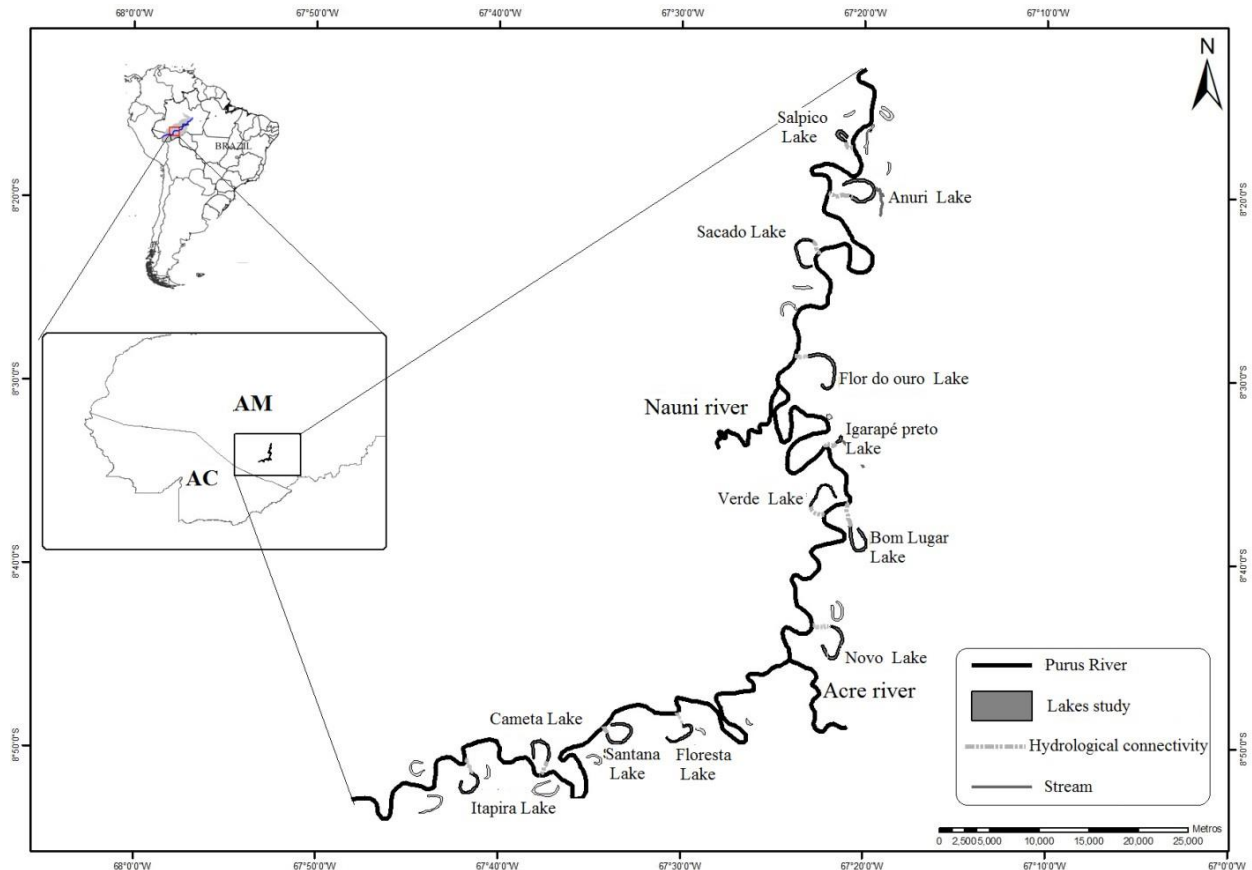
2.1 METHODS

Study Area

The Rio Purus river basin is located in the Southwestern Amazon Rainforest and is comprised of a total area of 376.000 km² (TRANCOSO, 2009). The Purus River features an asymmetrical sinuous system and, due to hydro-sedimentation processes, numerous oxbow lakes have formed (LATRUBESSE, 1992). The region has a distinct seasonal cycle, resulting in two

periods: the wet season, which extends from the month of November until March; and the drought season, from May to September/October. Twelve oxbow lakes in the Rio Purus river basin are located between the municipalities of Boca do Acre ($8^{\circ} 42'39.75''\text{S}/67^{\circ}23'20.40''\text{W}$) and Pauini ($7^{\circ}44'33.32''\text{S}/67^{\circ}01'20.35''\text{W}$), Amazonas State, Brazil (Fig.1).

Figure 1. Oxbow Lakes located in the Middle Purus River in the western Amazon Rainforest, Boca do Acre, AM.



Specimen Collection and Data Analysis

The specimens were collected during the wet, mid and dry seasons in the months of February, May and September of 2012 (ICMBio n° 11185-1), using twelve sets of seine nets 80m long and 4m high, with mesh sizes of 1.5 cm, 2.5 cm, 3.5 cm, 4.5 cm, 5.5 cm, 6.5 cm, 7.5 cm, 8.5 cm, 9.5 cm, 10.0 cm, 11.0 cm, and 12.0 cm between opposite nodes, placed for 24 hour periods (checked after 4 hours). Each group of nets was laid parallel to the lake margins in locations with banks of aquatic macrophytes in order to capture fish of different sizes. The collected fish were properly anesthetized and placed in plastic bags with 5% formaldehyde and subsequently taken to the Ichthyology Laboratory of the Federal University of Acre, where they were identified with the aid of the bibliography (BUCKUP et al., 2007; CASTRO; VARI, 2004; CALCAGNOTTO et al., 2005; FINK; FINK 1996; GÉRY, 1997; SILVANO, 2001) and, when necessary, with the assistance

of experts in each group. Voucher specimens were fixed in 10% formalin, preserved in alcohol 70°GL and deposited in the fish collection of the Federal University of Acre (MUFAC), Acre state, Brazil.

Additionally, the following characteristics of the lakes were recorded: surface area (ha), depth (m), hydrogenionic potential (pH), dissolved oxygen (% Sat), conductivity ($\mu\text{S.cm1}$), water temperature ($^{\circ}\text{C}$), transparency (m) (Table 1). For each pond, the total number of individuals and the numerical percentage (%), richness of species (S) and Shannon-Wiener diversity (H') were calculated. The Analysis of Variance (ANOVA) was used to verify differences in richness between lakes with distinct hydrological connectivity levels and hydrological cycle phase (Factor) and, when significant, was applied a post-hoc Tukey test to identify which levels were different. The calculations were made using the PAST 3.16 statistical software program (HAMMER et al., 2001).

3 RESULTS

A total of 8.647 individuals among ten orders, 33 families and 157 species were collected. The most representative orders were Characiformes and Siluriformes (71 species, 45.22% and 58 species, 36.94%, respectively) (Fig. 2). Of the Characiformes order, the most abundant species were *Moenkausia* sp. (817 individuals, 9.45%), *Psectrogaster amazonica* (626 individuals, 7.24%) and *Pygocentrus nattereri* (435 individuals, 5.03%) (Fig.3). Of the Siluriformes order, the most representative species were *Auchenipterus nuchalis* (244 individuals, 2.82%), *Hypoptopoma gulare* (170 individuals, 1.97%) and *Hypoptopoma thorocotum* (138 individuals, 1.60%) (Table 2 e Fig.3). However, the least diverse orders were Cichliformes and Gymnotyformes (Fig. 2A). The least abundant species were *Agamyxis pectinifron*, *Osteoglossum bicirrhosum*, *Phractocephalus hemioliopeterus*, *Boulengerella maculate*, *Chalceus epakros*, *Abramites hypselonotus*, *Steatogenys* cf. *duidae*, *Synbranchus marmoratus* (Table 2 e Fig.4).

In lakes with high connectivity, a total of 2.612 individuals were collected, the most abundant species being *Pygocentrus nattereri* (249 individuals, 9.53%) and *Psectrogaster amazonica* (262 individuals, 10.03%). It is worth noting that these lakes showed the greatest richness (131 species). The lake with the highest abundance of fish with high connectivity was Bom Lugar, with 899 individuals collected. However, it presented the lowest richness (65 species) and least diversity ($H' = 3.22$), in contrast to Lake Anuri, which showed the greatest richness (86 species) and was also the most diverse ($H' = 3.73$) (Table 3).

In lakes of medium connectivity, a total of 3.066 individuals were collected with a richness of 123 species. The predominant species were *Moenkausia* sp. (268 individuals, 8.74%) and

Psectrogaster amazonica (246 individuals, 8.02%). Lake Cometa was the most abundant, with a total of 1,006 captured individuals, while Lake Santana presented a lesser abundance of 633 individuals, although it featured the greatest richness and diversity ($S = 79$ and $H' = 3.94$, respectively) (Table 3). In low-connectivity lakes, 2,969 individuals were collected, the dominant species being *Moenkausia* sp. (543 individuals, 18.29%) and *Hemigrammus* sp. (191 individuals, 5.59%), with a richness of 113 species. Lake Itapira was the most abundant with 1,412 collected individuals, featuring the greatest richness (73 species), but the smallest diversity ($H' = 2.79$). Lake Floresta presented the least abundance (324 individuals) and a richness of 58 species, but had the highest diversity ($H' = 3.71$) (Table 3).

We found significant differences in species richness ($F=3.57$; $P = 0.006$) among the lakes communities with different connectivity levels during the hydrological cycle phases. This occurred mainly between lakes with high and low connectivity ($P = 0.01$) and medium and high connectivity ($P = 0.001$) during drought, high and medium connectivity ($P = 0.001$) and high and low connectivity during flood. We found a variation in lakes with high connectivity in flood and ebb periods ($P = 0.005$), flood and drought ($P = 0.006$), in lakes with low connectivity between flood and drought ($P = 0.04$) and flood and ebb ($P = 0.03$).

Figure 2. Number of species and cumulative number of species for each taxonomic order of the oxbow lakes located in the Middle Purus River in western Amazon Rainforest.

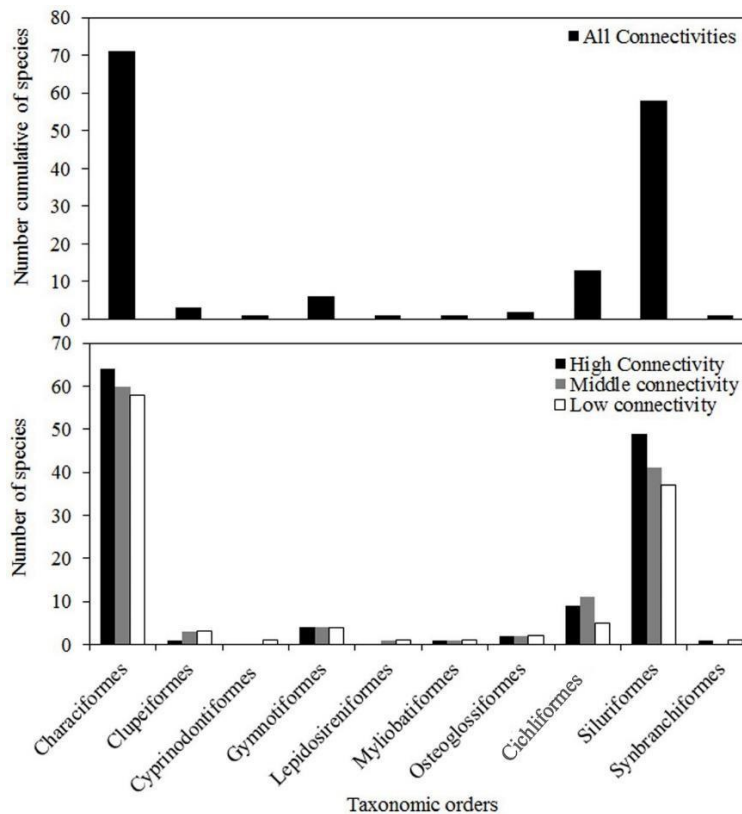


Figure 3. Fishes Species of the Oxbow Lakes located in the Middle Purus River in Western Amazon Rainforest, Boca do Acre, AM, Brazil. (A) *Auchenipterus nuchalis*; (B) *Psectrogaster amazonica*; (C) *Moenkausia* sp.; (D) *Potamorhina altamazonica*; (E) *Hypoptopoma thorocotum*; (F) *Hypoptopoma gulare*; (G) *Pygocentrus nattereri*; (H) *Hemigrammus* sp.

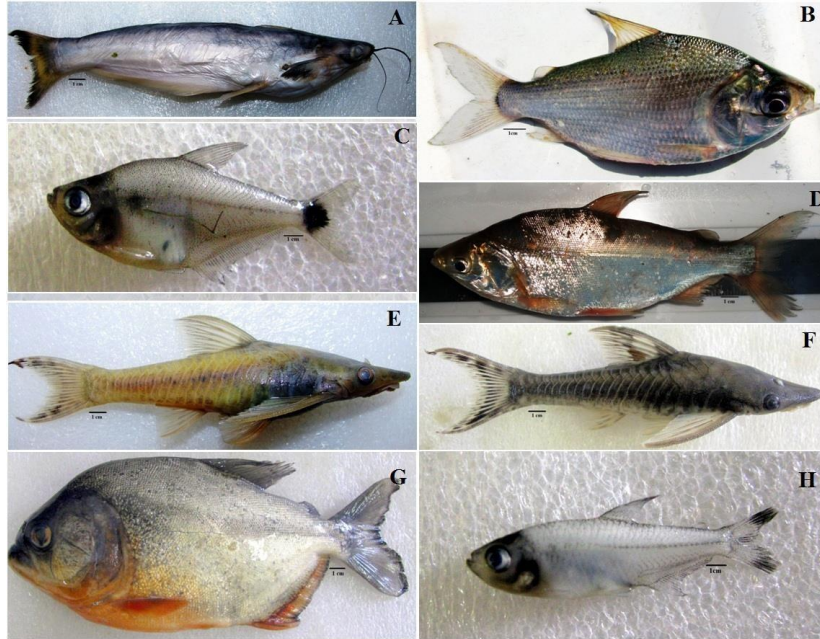


Figure 4. Fishes Species of the Oxbow Lakes located in the Middle Purus River in Western Amazon Rainforest, Boca do Acre, AM, Brazil. (A) *Agamyxis pectinifron*; (B) *Osteoglossum bicirrhosum*; (C) *Phractocephalus hemioliopterus*; (D) *Boulengerella maculata*; (E) *Chalceus epakros*; (F) *Steatogenys* cf. *duidae*; (G) *Abramites hypselonotus*; (H) *Synbranchus marmoratus*.

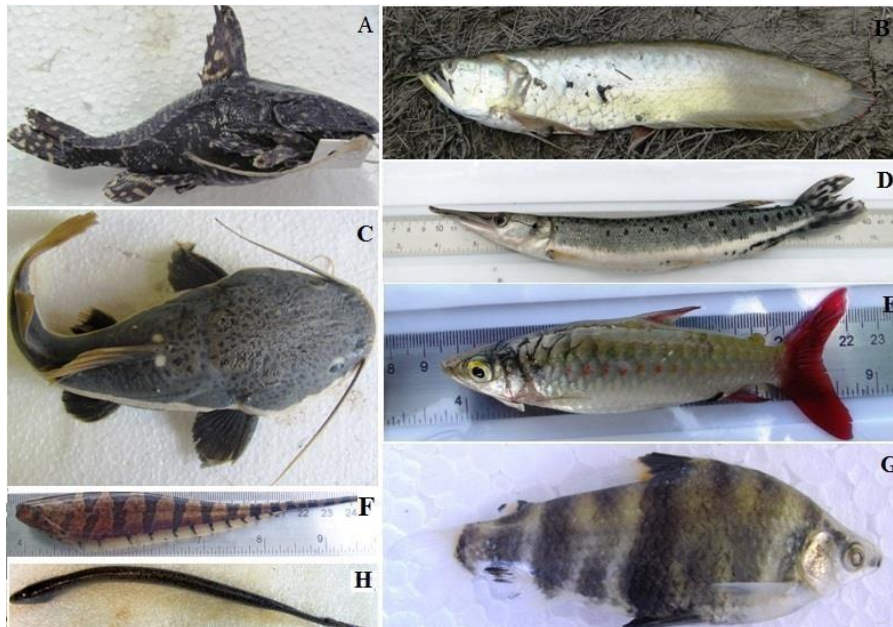


Table 1. Average and standard deviation of the abiotic variables of the oxbow lakes in the Middle Purus River. B.L=Bom Lugar; IG.=Igarapé Preto; SAC=Sacado; AN=Anuri; CA=Cameta; Sant=Santana; FO=Flor do Ouro; ITA=Itapira; FLO=Floresta; LN=Lake Novo and LV=Lake Verde.

Lakes	Area (ha)	Depth (m)	pH	DO (%)	Cond (µS.cm1)	Temp (C°)	Transp. (m)	Latitude (S)	Longitude (W)
AN	172 ±8.7	19.3 ±5.9	6.3 ± 0.21	40.6±21.5	39.8 ±11.4	24.4 ± 1.6	40 ±15	8°20'0.32"	67°20'40.26"
BL	123 ±7.5	19.1 ±6.1	6.4 ±0.93	52.4 ±27	86.2±19.2	27.6 ± 2.8	37±8.8	8°38'51.49"	67°20'37.32"
CA	90 ±8.7	14 ±4.4	6.5 ± 0.25	54.7 ±30.7	85.1 ±17.8	30.5 ± 2.2	63 ±2.2	8°50'19.13"	67°38'28.0"
FO	145 ±10.7	17 ±5.4	6.2 ± 0.77	45.3 ±17.5	98.4 ±18.3	26.3 ± 1.4	53 ± 18	8°28'39.28"	67°23'28.97"
FLO	70 ±11.3	13 ±5.5	6.5 ±0.71	65.9 ±31.9	163.5±92.7	29.8 ± 3.1	31 ± 10	8°48'51.03"	67°30'53.67"
IG	14 ±7.1	10 ±5.7	6.6 ±0.40	44.3±28.5	50.7±18.9	28.2 ± 1.9	35 ±19	8°33'20.82"	67°21'32.41"
ITA	82 ±10.2	13 ±6.1	6±0.81	62.3 ±17.8	100.1±23.2	26.5±1.9	40 ± 22	8°51'44.69"	67°41'22.89"
LN	133 ±10.5	14 ±4.1	7.2±0.81	45.3±8.2	126.3 ±45	28.7±3.9	33 ± 6	8°37'16.57"	67°22'29.12"
LV	51 ±10.7	8.8 ±3.6	6.1 ±2.37	69.3±31.5	97.1 ± 35	27± 2.5	33 ± 14	8°44'36.06"	67°22'49.03"
SAC	73 ±9.9	14 ± 6	6.3±0.54	50.3 ±27	44.1 ±15	28.4±3.5	24 ± 3	8°26'29.6"	67°23'48.35"
SALT	54 ± 9	15 ± 6.1	5.7 ±0.80	50.7 ±25	41.5 ±16	25.5 ±1.8	31 ± 10	8°16'50.06"	67°21'14.43"
SANT	124 ±9.3	16 ± 5.9	6.8±86	65.6±40	109 ±16.4	31.4 ± 2.2	49 ± 15	8°49'34.62"	67°33'11.9"

Table 2. List of fish species, with voucher specimens, collected in oxbow lakes of the Middle Purus River, Boca do Acre, AM.

Total individuals per site; total of individuals per biotope; richness per site; richness per biotope; Shannon_H. BL=Bom Lugar, IG=Igarapé Preto, SAC=Sacado, AN=Anuri, CA=Cameta, SANT=Santana, FO=Flor do Ouro, ITA=Itapira, FLO=Floresta, LN=Lake Novo and LV=Lake Verde.

Order/Family/Species	BL	IG	SAC	NA	CA	SANT	FO	SALP	ITA	FLO	LN	LV	Voucher
Characiformes													
Acestrorhynchidae													
<i>Acestrorhynchus microlepis</i> (Jardine, 1841)	3	17	2	7			4		3	2	44		845
Alestidae													
<i>Chalceus epakros</i> Zanata & Toledo-Piza, 2004				4				8	2				876
Anostomidae													
<i>Abramites hypselonotus</i> (Günther, 1868)				6									873

<i>Anostomoides laticeps</i> (Eigenmann, 1912)	6	2	1		7	3		4	3		6	3	811
<i>Anostomus trimaculatus</i> (Kner 1858)		5											909
<i>Laemolyta varia</i> (Garman, 1890)		3			4		2			4	6		826
<i>Leporinus friderici</i> (Bloch, 1794)	41	31	3	9	35	34	14	3	20	9	28	20	800
<i>Leporinus obtusidens</i> (Valenciennes, 1847)				2	10	8	2		13	2		1	801
<i>Leporinus pellegrinii</i> (Steindachner, 1910)					7	3							936
<i>Leporinus trifasciatus</i> (Steindachner, 1876)						6	1			1	2		856
<i>Rhytiodus microlepis</i> (Kner, 1858)			4										924
<i>Schizodon fasciatus</i> Spix & Agassiz, 1829	78	30	8	4	14	9	5	4	17	4	30	7	816
Characidae													
<i>Aphyocharax alburnus</i> (Günther, 1869)		10		4	4		2		2			2	946
<i>Brachyhalcinus cf. copei</i> (Steindachner, 1882)	8	7	5	1		2	8	3	17			2	848
<i>Brycon cf. falcatus</i> Müller & Troschel, 1844					8								898
<i>Bryconops affinis</i> (Günther, 1864)					2					2			902
<i>Colossoma brachypomum</i> (Cuvier 1817)	6		8	4		2	2				5		888
<i>Colossoma macropomum</i> (Cuvier, 1816)	2	2				2	2				2	5	905
<i>Ctenobrycon hauxwellianus</i> (Cope, 1870)	6					15	17					19	854
<i>Gymnocorymbus thayeri</i> Eigenmann, 1908				3			4	2					925
<i>Hemigrammus</i> sp.	2	1		5	19	13	5		189			2	802
<i>Hemigrammus neptunus</i> Zarske & Géry, 2002												7	921
<i>Metynnis cf. hypsauchen</i> (Müller & Troschel, 1844)				22									867
<i>Metynnis cf. argenteus</i> Ahl, 1923	2			5				1		2			868
<i>Moenkhausia</i> sp.	6				236	15	17		524			19	806
<i>Moenkhausia intermedia</i> Eigenmann, 1908		2				20			23		1		792
<i>Moenkhausia oligolepis</i> (Günther, 1864)					3	3		2	2				853
<i>Mylossoma aureum</i> (Spix & Agassiz, 1829)	4				7	7	3		12		3		865
<i>Mylossoma duriventre</i> (Cuvier, 1818)	7	2	17	22	86	33	16	7	29	3	2	2	799
<i>Piaractus brachypomus</i> (Cuvier, 1818)	4					2							919
<i>Prionobrama filigera</i> (Cope, 1870)				2	6	2						13	871

<i>Pristobrycon</i> sp1.		1			7								866
<i>Pygocentrus nattereri</i> Kner, 1858	26	57	49	117	19	4	75	48	17	7	11	5	815
<i>Roebooides myersii</i> Gill, 1870	11	12	3	9	5	15	9	16	6	11	11	7	786
<i>Tetragonopterus argenteus</i> Cuvier, 1816		1	3			4					6	2	891
<i>Tetragonopterus chalceus</i> Spix & Agassiz, 1829	22	5	4	1	5		4	1		2		2	900
<i>Triportheus albus</i> Cope, 1872	12	17	3	21	30	12	21	25	58	24	63	8	807
<i>Triportheus angulatus</i> (Spix & Agassiz, 1829)				4	8	14	7	12	36	18	4		779
<i>Triportheus elongatus</i> (Günther, 1864)			5	3	3	2	3						851
<i>Triportheus</i> cf. <i>rotundatus</i> (Jardine, 1841)	10	9	23		34	35	8	13	29		7	15	803
Ctenoluciidae													
<i>Boulengerella maculata</i> (Valenciennes, 1850)		2			1	10				2			894
Curimatidae													
<i>Curimatella meyeri</i> (Steindachner, 1882)	11	3	2	5	6		22	1	3	7	11	2	837
<i>Cyphocharax</i> sp1.				4			4						945
<i>Potamorhina altamazonica</i> (Cope, 1878)	82	9	31	11	16	4	16	56	2	8	143	13	810
<i>Potamorhina</i> cf. <i>pristigaster</i> (Steindachner, 1876)	16	2		3			4	3				18	847
<i>Potamorhina lator</i> (Spix & Agassiz, 1829)	10	21	22	26	32	16	28	23	35	10	6	20	820
<i>Psectrogaster curviventris</i> Eigenmann & Kennedy, 1903					5			8	2				878
<i>Psectrogaster rutiloides</i> (Kner, 1858)	31	16	52	17	6	6	7	120	2	16	47	3	809
<i>Psectrogaster amazonica</i> Eigenmann & Eigenmann, 1889	174	29	21	38	56	21	33	136	6	7	84	21	789
<i>Psectrogaster essequibensis</i> (Günther, 1864)			1	7	5	2	4			6	1	1	805
<i>Steindachnerina bimaculata</i> (Steindachner, 1876)	2	3	3				5	1	3	2			840
<i>Steindachnerina guentheri</i> (Eigenmann & Eigenmann, 1889)	102	2	16	24	11	8	1	11	8	5	52	2	833
<i>Steindachnerina</i> cf. <i>notograptos</i> Lucinda & Vari, 2009	20	4	1		2		1		1	11	4		841
<i>Steindachnerina</i> sp1.				4									932
Cynodontidae													
<i>Hydrolycus scomberoides</i> (Cuvier, 1819)			1		3							2	920
<i>Rhaphiodon vulpinus</i> Spix & Agassiz, 1829	3	2	3		4	1		4	4		2		793

Erythrinidae

Hoplias malabaricus (Bloch, 1794) 9 7 8 5 7 4 7 4 10 11 6 9 824

Hoplerythrinus unitaeniatus (Spix & Agassiz 1829) 1 2 879

Gasteropelecidae

Carnegiella marthae (Myers, 1927) 5 2 9 1 8 2 1 11 2 2 814

Gasteropelecus cf. sternicla (Linnaeus, 1758) 6 926

Hemiodontidae

Anodus elongatus Agassiz, 1829 3 1 5 2 12 12 8 5 4 2 15 7 817

Bivibranchia cf. fowleri (Steindachner, 1908) 2 6 6 2 6 4 4 2 13 2 808

Prochilodontidae

Prochilodus nigricans Spix & Agassiz, 1829 6 4 2 6 9 10 1 2 14 17 24 15 822

Semaprochilodus taeniurus (Valenciennes, 1821) 1 1 4 1 2 1 857

Serrasalminidae

Serrasalmus cf. altispinis Merckx, Jégu & Santos, 2000 6 4 5 4 26 5 2 2 15 870

Serrasalmus cf. altuvei Ramírez, 1965

Serrasalmus eigenmanni Norman, 1929 2 13 3 933

Serrasalmus elongatus Kner, 1858 2 3 8 2 844

Serrasalmus maculatus Kner, 1858 8 6 4 2 2 877

Serrasalmus rhombeus (Linnaeus, 1766) 2 2 14 2 6 882

Serrasalmus cf. spilopleura Kner, 1858 4 2 2 2 889

Clupeiformes 2 2 14 2 6 882

Engraulidae

Lycengroulis botesii (Günther, 1868) 29 1 24 778

Pristigasteridae

Pellona castelnaeana Valenciennes, 1847 1 3 789

Pellona flavipinnis (Valenciennes, 1837) 1 1 4 5 3 2 31 2 3 3 785

Cyprinodontiformes**Rivulidae**

Rivulus compressus (Henn, 1916) 6 970

Gymnotiformes										
Apterodontidae										
<i>Apterodontus albifrons</i> (Linnaeus, 1766)	2	8							908	
Gymnotidae										
<i>Gymnotus carapo</i> Linnaeus, 1758						5			911	
Hypopomidae										
<i>Steatogenys duidae</i> (La Monte, 1929)				4				4	907	
Rhamphichthyidae										
<i>Rhamphichthys rostratus</i> (Linnaeus, 1766)		8		2	8				897	
Sternopygidae										
<i>Eigenmannia macrops</i> (Boulenger, 1897)			3		7		12		892	
<i>Eigenmannia virescens</i> (Valenciennes, 1836)	1			2	25		2	2	835	
Lepidosireniformes										
Lepidosirenidae										
<i>Lepidosiren paradoxa</i> Fitzinger, 1837				4				12	819	
Myliobatiformes										
Potamotrygonidae										
<i>Potamotrygon motoro</i> (Müller & Henle, 1841)	1		1		9		1	2	935	
Osteoglossiformes										
Arapaimatidae										
<i>Arapaima gigas</i> (Schinz, 1822)		6			5	7	4	4	6	787
Osteoglossidae										
<i>Osteoglossum bicirrhosum</i> (Cuvier, 1829)		1	1			4	5	3	8	934
Cichliformes										
Cichlidae										
<i>Apistogramma linkei</i> Koslowski, 1985				5		2			904	
<i>Astronotus crassipinnis</i> (Heckel, 1840)						3			788	
<i>Astronotus ocellatus</i> (Agassiz, 1831)					4				929	
<i>Chaetobranchopsis orbicularis</i> (Steindachner, 1875)	1			1					944	

<i>Chaetobranchius flavescens</i> Heckel, 1840	5	2	2									922	
<i>Cichla ocellaris</i> Bloch & Schneider, 1801	2				7	4	2		6		3	812	
<i>Cichla monoculus</i> Bloch & Schneider, 1801	2	6	2	2					3			931	
<i>Cichlasoma</i> sp1.				6	11		4		5		2	943	
<i>Geophagus jurupari</i> (Quoy & Gaimard, 1824)				5								849	
<i>Heros severus</i> Heckel, 1840					4	2			9		6	855	
<i>Mesonauta festivus</i> (Heckel, 1840)				3		2						864	
<i>Satanoperca jurupari</i> (Heckel, 1840)			3		8	3	3		9	2		942	
Scianidae													
<i>Plagioscion squamosissimus</i> (Heckel, 1840)	1	2	4	5	7	1	4	5	8	2	3	823	
Siluriformes													
Auchenipteridae													
<i>Ageneiosus brevifilis</i> (Valenciennes, 1840)	2			3						4		869	
<i>Ageneiosus uranophthalmus</i> Ribeiro & Rapp Py-Daniel, 2010	4			6			1					825	
<i>Ageneiosus vittatus</i> Steindachner, 1908	4	1	2									906	
<i>Auchenipterichthys coracoideus</i> (Eigenmann & Allen, 1942)	5			41	2		8				3	827	
<i>Auchenipterus osteomystax</i> (Miranda Ribeiro, 1918)	3		5	7	3	3		2		8		784	
<i>Auchenipterus nuchalis</i> (Spix & Agassiz, 1829)	19	25	10	62	20	37	19	27	11	12	2	941	
<i>Centromochlus cf. heckelii</i> (De Filippi, 1853)	3			7								831	
<i>Parauchenipterus galeatus</i> (Linnaeus, 1758)					7	8						930	
<i>Trachelyopterus striatulus</i> (Steindachner, 1877)	19	5	3		2	2	5	1	6		3	2	796
Callichthyidae													
<i>Brochis splendens</i> (Castelnau, 1855)	5									5	12	913	
<i>Dianema longibarbis</i> Cope, 1872	2								1	2		861	
Cetopsidae													
<i>Cetopsis coecutiens</i> (Lichtenstein, 1819)				4								846	
Doradidae													
<i>Agamyxis pectinifrons</i> (Cope, 1870)	6		4								1	915	

<i>Anadoras regani</i> (Steindachner, 1908)	2			1	2							895
<i>Astroadoras asterifrons</i> (Kner, 1853)									3			928
<i>Hassar</i> sp.					12			9				794
<i>Nemadora humeralis</i> (Kner, 1855)	8	3	22	2		11		1		1		828
<i>Nemadoras elongatus</i> (Boulenger 1898)	1	2		2	2	1	2	1			2	782
<i>Nemadora</i> sp1.			1		1	22						838
<i>Oxydoras niger</i> (Valenciennes, 1821)	3		2		4				3	2		890
<i>Platydoras</i> cf. <i>armatulus</i> (Valenciennes, 1840)	2	4	3							2		916
<i>Platydoras costatus</i> (Linnaeus, 1758)	8	6										918
<i>Rhinodoras gallagheri</i> Sabaj Pérez, Taphorn & Castillo, 2008	13			2						1	2	832
Heptapteridae												
<i>Pimelodella picta</i> (Steindachner, 1876)	1			4				4			6	880
Loricariidae												
<i>Ancistrus ranunculus</i> Muller, Rapp Py-Daniel & Zuanon, 1994	1	4		2		4	1	2	1			850
<i>Dekeyseria</i> cf. <i>amazonica</i> Rapp Py-Daniel, 1985	6	1	4	2	4	2	5	2	2	4	9	783
<i>Hemiodontichthys acipenserinus</i> (Kner, 1853)	6											927
<i>Hypoptopoma thorocotum</i> (Günther, 1868)	9		5	16	33	16	12	11	11	25		791
<i>Hypoptopoma gulare</i> Cope, 1878	22	8	9	4	22	34	23	15	10	15	8	804
<i>Hypostomus</i> cf. <i>plecostomus</i> (Linnaeus, 1758)	1	6	1		2	2	1	3				830
<i>Hypostomus pagei</i> Armbruster, 2003			8									875
<i>Hypostomus pyrineusi</i> (Miranda Ribeiro, 1920)			4				2		2			903
<i>Hypostomus</i> sp.1	1				2		2	2		1		885
<i>Hypostomus</i> sp.2								2		1		852
<i>Loricariichthys nudirostris</i> (Kner, 1853)				1			3	2	13			887
<i>Loricariichthys</i> cf. <i>platymetopon</i> Isbrücker & Nijssen, 1979			1	8	4		4	5		9	5	797
<i>Loricariichthys anus</i> (Valenciennes, 1836)					2							899
<i>Peckoltia bachi</i> (Boulenger, 1898)								8				863
<i>Pseudorinelepis genibarbis</i> (Valenciennes, 1840)	3	2					1					914

<i>Pterygoplichthys disjunctivus</i> (Boulenger, 1895)	1	2				6	3	2	1			940	
<i>Rineloricaria cf. parva</i> (Boulenger, 1895)	11	8	3	2	9	11	6		2	2	2	829	
<i>Sturisoma nigrirostrum</i> Fowler, 1940	6			8				5				917	
<i>Sturisoma</i> sp1.		2			3							939	
Pimelodidae													
<i>Brachyplatystoma vaillantii</i> (Valenciennes, 1840)						8	4					839	
<i>Calophysus cf. macropterus</i> (Lichtenstein, 1819)	8	2			4		1					938	
<i>Hemisorubim platyrhynchus</i> (Valenciennes, 1840)		5			4	5		1				923	
<i>Hypophthalmus edentatus</i> Spix & Agassiz, 1829	9	2	4	5	6	4	3	3	6	1	77	795	
<i>Leiarius marmoratus</i> (Gill, 1870)			2	1	3	3						893	
<i>Phractocephalus hemioliopus</i> (Bloch & Schneider, 1801)			6	4						1		912	
<i>Pimelodina flavipinnis</i> Steindachner, 1876						5			3			881	
<i>Pimelodus albicans</i> (Valenciennes, 1840)			4	5	8	2	4	4	2	5	9	937	
<i>Pimelodus blochii</i> Valenciennes, 1840	9		3	7	12	4		2	3		1	4	813
<i>Pimelodus maculatus</i> Lacepède, 1803				3						2		860	
<i>Pimelodus</i> sp1.		2										834	
<i>Pinirampus pirinampu</i> (Spix & Agassiz 1829)	1								2	1		2	818
<i>Pseudoplatystoma fasciatum</i> (Linnaeus, 1766)		4		1		2	2				4	3	843
<i>Pseudoplatystoma tigrinum</i> (Valenciennes, 1840)		2	4	1		2	3			1	2	2	862
<i>Surubim lima</i> (Schneider, 1801)	2		8	2	8	8	5		5	9	4	4	781
Synbranchiformes													
Synbranchidae													
<i>Synbranchus marmoratus</i> Bloch, 1795						3						2	859

Table 3. Composition of fish fauna in twelve oxbow lakes of the Middle Purus River. Total individuals per site, total of individuals per biotope, richness per site, richness per Biotope and Shannon_H. BL=Bom Lugar; IG=Igarapé Preto; SAC=Sacado; AN=Anuri; CA=Cameta; SANT=Santana; FO=Flor do Ouro; ITA=Itapira; FLO=Floresta; LN=Lake Novo and LV=Lake Verde.

Hydrological connectivity	Lakes	Number of individuals	Individuals by biotope	Species richness	Richness by biotope	Shannon_H
High connectivity	BL	899	2612	65	131	3.22
	IG	496		67		3.64
	SAC	535		68		3.64
	NA	682		86		3.73
	CA	1006		75		3.4
Medium connectivity	SANT	633	3066	79	123	3.94
	FO	704		79		3.77
	SALP	723		62		3.09
	ITA	1412		73		2.79
Low connectivity	FLO	324	2969	58	113	3.71
	LN	847		59		3.19
	LV	386		59		3.7

4 DISCUSSION

Overall, the oxbow lakes of the Middle Purus River have a high diversity of fish, which may be associated primarily with different degrees of hydrological connectivity. This connectivity, caused by expansions of the river banks due to hydrological pulse, does in fact provide a richness of habitats for countless species and consequently an increase in fish diversity. Similar aspects were also observed by Crampton (2011) who evaluated ecological perspectives of the diversity and distributions of Neotropical fish. Another central factor relevant to fish diversity in lakes and environmental heterogeneity is the presence of banks of aquatic macrophytes, as they provide shelter against possible predators, as well as breeding grounds and feeding locations for the ichthyofauna. Moreover, the vast diversity of fish identified in the lakes might reveal evolutionary processes in the dispersion of species, where the most adapted tend to achieve greater success in colonization. Albert and Reis (2011) maintain that ecological processes have a direct correlation with the diversification of fish species, mainly in river basins of the Neotropics, with special emphasis on the Amazon River Basin.

The Purus River is one of the main ecosystems of the Neotropical region and, according to Silva et al. (2010), is characterized by a variety of environments which directly influences increased fish diversity. Another important factor influencing the richness of species in lake systems is the flood pulse, which accelerates nutrient cycling, resulting in increased food resources during the wet season, thus enabling countless species to thrive in their habitats (JUNK et al., 2012). For instance,

lakes with high hydrological connectivity showed greater fish diversity, evidencing the importance of the hydric balance in the movement and colonization of fish species. While studying flood plain areas in Central Amazon, Junk (1997) showed that the river's hydrological connection enables the movement of species between different habitats. In the present study, oxbow lakes that lost connectivity during low hydrological levels showed a decrease in the richness of fish species, strongly indicating the influence of the river's hydric pulse over the fish community, and which in turn entails changes in the physical, chemical and biological characteristics of the oxbow lakes.

Among the main orders identified in the lakes with varying degrees of connectivity, the Characiformes and Siluriformes were predominant, both in species and abundance. This dominance pattern follows a common model found in many studies conducted in Amazon environments (LOWE-McCONNELL, 1987; SABINO; ZUANON, 1998; CLARO-GARCÍA, 2013; REIS et al., 2016). For example, previous studies conducted in the Purus River, such as that of Anjos et al. (2008) and Duarte et al. (2013), reported Characiformes and Siluriformes as being the dominant orders and a common standard in this Neotropical region. Ecological aspects such as different feeding tactics (LOWE-McCONNELL 1987; MÉRONA; RANK-DE-MÉRONA, 2004), reproductive strategies (WINEMILLER, 1989), as well as the ability to adapt and survive (JUCÁ-CHAGAS, 2004) may be key factors influencing the large abundance of Characiformes and Siluriformes orders in flood plain environments and oxbow lakes. These fish groups are attributed great ecological importance in aquatic ecosystems, such as for instance, balancing the structure of food webs (LOWE-McCONNELL, 1987; ARRINGTON; WINEMILLER, 2003; CORRÊA et al., 2012), energy flow and seed dispersal (WEISS et al., 2016).

Moenkhausia sp. and *Psectrogaster amazônica* being examples of the most representative species in the lakes may be related to adaptation capability, reproductive rate and environmental structure—the presence of aquatic macrophytes and food availability, for instance. For example, *Moenkhausia* sp. individuals were captured in lakes with the presence of aquatic macrophytes, which corroborates with the findings of Suçuarana et al. (2016) who captured a large number of individuals of this species in oxbow lakes. In fact, macrophytes offer fish structural complexity and food availability, as well as shelter against possible predators (GRENOUILLET et al., 2002; AGOSTINHO et al., 2003; PADIAL et al., 2009). The species *Psectrogaster amazônica*, for instance, migrate to lake environments that may be favorable to their reproductive behavior and the physical-chemical characteristics of the water (FERNANDES, 1997). Moreover, basal species such as curimatideos are especially significant to the food chain (CORRÊA et al., 2008).

Piranhas (Characidae: Serrasalminae) are among the main predators of the Neotropical freshwater ecosystems (ALMEIDA et al., 1998). Represent a large percentage of the number of individuals and of the total Osteichthyes biomass in the ecosystems where they inhabit (MAGOLECCIA, 1970). What can justify the large number of individuals in the *Pygocentrus nattereri* captured in the lakes. *Pygocentrus nattereri* is one of the most abundant fish species in floodplain lakes in the Amazon, as observed in studies of Mérona and Bittencourt (1993) and Bevilaqua et al. (2010).

It is worth mentioning that lakes with greater abundance of fish species and low richness, such as the lakes Novo, Cameta and Floresta, show evidence of anthropic impacts, namely reduced riparian forest. According to Oberdorff et al. (2015), the loss of riparian forest can cause strong variations in the diversity and composition of the ichthyofauna, thus causing ecological imbalance. Moreover, it is important to emphasize that these environments in the middle region of the Purus River are essential for maintaining fishing grounds of various species such as *pseudoplatystoma fasciatum* and *pseudoplatystoma tigrinum*. Thus, the present study shows the importance of developing knowledge of the ichthyofauna in abandoned oxbow lakes, thereby contributing with relevant information on the composition and diversity of the fish species in the Middle Purus River. However, the lack of studies in this region hinders more precise assessments of these ecosystems and, for that reason, the presented data are important for achieving a better understanding of the ichthyofauna in these environments. Future studies that address various ecological aspects, such as reproductive aspects and trophic interactions, may provide a better understanding of the ecology of the species in these important ecosystems.

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