

Janette NOVERAS¹, Kedma C. YAMAMOTO², Carlos E.C. FREITAS²

RESUMO

Avaliamos a diversidade e a distribuição de espécies de peixes em dois habitats: floresta alagada e água aberta de lagos do rio Negro. Três amostragens foram realizadas em quatro lagos do Arquipélago de Anavilhanas, em 2009 e 2010. Em geral, a diversidade de espécies foi maior na floresta alagada e durante a noite. A análise de correspondência indicou que predadores estavam mais ativos a noite nos dois habitats. Onívoros, filtradores e detritívoros foram mais capturados durante o dia.

PALAVRAS-CHAVE: prefência por habitats, diversidade de espécies de peixes, lagos de águas pretas

Use of the flooded forest by fish assemblages in lakes of the National Park of Anavilhanas (Amazonas, Brazil)

ABSTRACT

We evaluated diversity and distribution of fish species in two habitats: flooded forest and open water of lakes of Rio Negro. Each of four lakes within the Anavilhanas Archipelago was sampled three times from 2009-2010. Species diversity generally was higher in flooded forests and at night, according to correspondence analysis. Predators were most active at night, but showed no preference between the flooded forest and open water habitats. Omnivores, filter feeders, and detritivores were most active during the day.

KEYWORDS: habitat preference, fish species diversity, black-water floodplain lakes

¹ Biology Department, Washington & Lee University , Lexington, VA 24450, USA, email: noverasjl11@mail.wlu.edu

² Departamento de Ciências Pesqueiras, Universidade Federal do Amazonas Av. Gen. Rodrigo Otávio, 3000. 69077-00 – Manaus, Amazonas Email: cefreitas@ufam.edu.br



Studies of fish assemblages in Amazonian black-water environments mainly have focused on the composition and structure of these communities (Saint-Paul *et al.* 2000; Soares and Yamamoto 2005) and on the diversity and trophic relations of pelagic (Goulding *et al.* 1988) and benthic fish (Garcia 1995). Recently, Freitas *et al.* (2010) reviewed the factors that may explain fish diversity in Amazonian floodplain lakes, including those that are in black-water systems. The hypothesis that species diversity is mediated by spatial heterogeneity has been evaluated for floodplain lakes of the rivers Araguaia (Tejerina-Garro *et al.* 1998) and Solimões-Amazonas (Petry *et al.* 2003; Siqueira-Souza and Freitas 2004) but not for lakes in Amazonian black-water rivers.

We aimed to characterize diversity as well as temporal and spatial distribution of fish species in typical floodplain lakes of an Amazonian black water river. We examined the use of the flooded area with the following objectives: (a) to identify which fish species utilize the flooded forest and which utilize the open water (b) to compare the use of the two types of environments by fish species during diurnal and nocturnal periods and (c) to compare trophic levels of fish that show preference for habitat and/or time of activity.

We conducted our study in the lakes of the Anavilhanas National Park located in the inferior stretch of the Rio Negro, approximately 40 km upstream of Manaus, Amazonas. We sampled fish in four lakes within the reserve: Prato, Arraia,

Canauiri Grande, and Canauiri Pequeno (Figure 1). Our sample was composed of three separate sampling events completed in September 2009, June 2010, and July 2010. All samples were taken when the water level was high enough to create a perimeter of submerged flooded forest habitat around the lake. Each lake was sampled during two consecutive days by two periods: at morning between 0700 and 0900 hours and at night between 1700 and 1900 hours, corresponding to dawn and dusk when fish are most active. The fishing gear consisted of eight gill nets, each 25 m long by 2 m deep with mesh size ranging from 30 to 100 mm totaling a capture area of 400 m². Gill nets were set both in the open water and within the flooded forest of each lake. Sampling duration was two hours, after which the nets were recovered. This sampling strategy was chosen to avoid damage to the nets by dolphins and crocodiles, as conducted by Saint-Paul et al. (2000).

We measured diversity (H²), richness (S), and evenness (J) using Paleontological Software (PAST) for the two different habitat types and times. We applied a detrended correspondence analysis (Manly 2005) to determine trophic associations, with units consisting of time and habitat type, using the program Statistica. The collected fish were classified using Ferreira *et al.* (1998), Santos *et al.* (2004), Santos *et al.* (2006) e Soares *et al.* (2011). Since carnivorous species are known to exhibit various trophic functions, we chose to split them into two groups, based on main prey: piscivore for the



Figure 1 - Study area with indication of sampled lakes: Canauari Pequeno, Canauari Grande, Prato and Arraia.



species which exploit fish as its main prey and carnivore for the species which eat fish, insects, and other invertebrates. By the same criterion, kind of preferred prey, we grouped zooplanktivorous and phitoplanktivorous species in the same trophic classification – planktivore, as employed by Zavala-Camin (1996). Herbivores, on the other hand, were excluded from the analysis because of low representation.

We collected 1,216 individuals representing 64 species and five orders: Chariciformes, Siluriformes, Clupeiformes, Perciformes, and Gymnotiformes. Of these, 746 individuals were caught during a single falling water period (2009) while the remaining 470 individuals were caught over two flood water periods (2009 and 2010). Characiformes and Siluriformes were the dominant orders. Samples taken from the open water habitat of lakes resulted in a greater number of fish than those from the flooded forests, but fish abundance in samples done at dusk were only slightly higher than those done at dawn (Table 1). However, diversity showed a distinct pattern, with species richness higher at the flooded forest than at the lake (t = -5.488, p < 0.000) and higher at night than at morning (t = -2.280, p = 0.021).

The total sample yielded 35 species of omnivores, 7 detritivores, 10 carnivores, 11 planktivores and 46 piscivores, which are employed as descriptors in the detrended correspondence analysis. The first two axes of DCA were generated with more than 96% of inertia (Figure 2). According



Figure 2 - Detrended Correspondence Analysis using trophic level and units composed by time and habitat (LakeM: open water at morning; LakeN: open water at night; ForestM: flooded forest at morning; ForestN: flooded forest at night).

Table 1- Ecological parameters for habitat and time samplings

Parameter	Lake	Flooded Forest	Morning	Night
Number of individuals (N)	877	337	494	535
Species Richness (S)	30	41	41	49
Shannon Index (H')	2.435	2.912	2.92	3.08
Evenness (J)	0.716	0.784	0.786	0.791

List of species caught by year, habitat and time, including its trophic level.

			20	009		2010			
		La	ike	Floode	d Forest	La	ke	Flo	oded Forest
Species	Trophic level	07:00	19:00	07:00	19:00	07:00	19:00	07:00	19:00
Acestrorhynchus microlepis (Jardine, 1841)	Piscivore	0	0	0	0	0	0	2	4
Ageneiosus polystictus Steindachner, 1915	Piscivore	0	0	0	1	0	0	0	1
Ageneiosus ucayalensis Castelnau, 1855	Piscivore	20	24	1	2	48	41	1	5
Ageneiosus vittatus Steindachner, 1908	Piscivore	0	0	0	0	0	1	0	0
Agoniates halecinus Müller & Troschel, 1845	Carnivore	16	8	2	2	0	0	0	0
Anchovia surinamensis (Bleeker, 1865)	Planktivore	1	0	0	0	2	0	0	0
Anodus orinocensis (Steindachner, 1887)	Omnivore	0	0	0	1	0	0	0	0
Anodus sp.	Omnivore	0	0	3	0	0	0	0	0
Argonectes longiceps (Kner, 1858)	Omnivore	0	0	5	2	0	0	0	0
Astrodoras asterifrons (Kner, 1853)	Omnivore	8	7	0	0	0	1	0	0
Auchenipterichthys longimanus (Günther, 1864)	Omnivore	0	0	0	25	0	0	0	0
Auchenipterus nuchalis (Spix & Agassiz, 1829)	Omnivore	0	0	1	0	0	0	0	0
Boulengerella lucius (Cuvier, 1816)	Piscivore	0	1	7	0	0	0	0	0
<i>Brachyplatystoma capapretum</i> Lundberg & Akama, 2005	Piscivore	0	0	0	0	4	17	0	0
Brachyplatystoma filamentosum (Lichtenstein, 1819)	Piscivore	3	2	0	0	11	4	0	0
Brycon sp.	Omnivore	0	0	7	2	0	0	0	0
Bryconops alburnoides Kner, 1858	Omnivore	1	0	0	0	0	0	0	0
Calophysus macropterus (Lichtenstein, 1819)	Piscivore	1	0	0	0	1	2	0	0



List of species caught by year, habitat and time, including its trophic level.

		2009				2010				
	Omnivore	Lake		Flooded Forest		Lake		Flooded Forest		
Centrodoras hasemani (Steindachner, 1915)		0	0	0	0	4	2	0	0	
Centrodoras sp.	Omnivore	6	5	0	0	10	22	0	0	
Centromochlus macracanthus Soares-Porto, 2000	Omnivore	1	0	0	0	1	0	0	0	
Cetopsis coecutiens (Lichtenstein, 1819)	Carnivore	1	0	0	0	3	2	0	0	
Cichla temensis Humboldt, 1821	Piscivore	0	0	0	2	0	0	0	1	
Hemiodus immaculatus Kner, 1858	Piscivore	0	0	38	14	0	0	27	14	
Hemiodus sp.	Omnivore	0	0	0	1	0	0	0	0	
Hemiodus unimaculatus (Bloch, 1794)	Piscivore	0	0	3	2	0	0	0	0	
Hypophthalmus edentatus Spix & Agassiz, 1829	Planktivore	7	3	0	0	0	0	7	8	
Hypophthalmus fimbriatus Kner, 1858	Planktivore	0	0	0	4	0	0	4	1	
lypophthalmus marginatus Valenciennes, 1840	Planktivore	193	49	0	0	2	2	3	4	
<i>lisha amazonica</i> (Miranda Ribeiro, 1920)	Piscivore	0	1	0	0	0	0	0	2	
aemolyta taeniata (Kner, 1858)	Omnivore	0	0	4	2	0	0	2	3	
Leporinus affinis Günther, 1864	Carnivore	0	0	0	0	0	0	0	1	
eporinus fasciatus (Bloch, 1794)	Omnivore	3	0	0	0	0	0	0	0	
icengraulis batesii (Günther, 1868)	Carnivore	7	2	0	0	0	0	0	0	
oricariichthys nudirostris (Kner, 1853)	Detritivore	0	0	0	0	1	1	0	0	
oricariichthys sp.	Detritivore	0	0	0	0	3	0	0	0	
Netynnis hypsauchen (Müller & Troschel, 1844)	Omnivore	0	0	1	0	0	0	0	0	
Vemadoras elongatus (Boulenger, 1898)	Omnivore	2	5	0	0	4	4	0	0	
Vemadoras sp	Omnivore	1	0	0	0	0	0	0	0	
Opsodoras morei (Steindachner, 1881)	Omnivore	16	9	0	0	4	2	0	0	
Opsodoras ternetzi Eigenmann, 1925	Omnivore	1	4	0	0	44	47	0	0	
Pellona flavipinnis (Valenciennes, 1837)	Piscivore	42	21	2	2	2	3	3	17	
Pimelodina flavipinnis Steindachner, 1876	Piscivore	0	0	1	0	2	1	0	0	
Pinirampus pirinampu (Spix & Agassiz, 1829)	Piscivore	11	12	0	0	2	3	0	3	
Plagioscion montei Soares & Casatti, 2000	Piscivore	0	0	0	1	0	0	0	0	
Plagioscion squamosissimus (Heckel, 1840)	Piscivore	33	31	1	6	8	9	4	10	
Potamorhina latior (Spix & Agassiz, 1829)	Detritivore	0	0	0	1	0	0	0	0	
Rhamphichthys rostratus (Linnaeus, 1766)	Carnivore	0	0	0	0	1	0	0	0	
Raphiodon vulpinus Agassiz, 1829	Piscivore	0	0	1	3	0	0	1	1	
Rhytiodus microlepis Kner, 1858	Herbivore	0	0	0	0	0	0	0	2	
Semaprochilodus insignis (Jardine, 1841)	Detritivore	0	0	0	15	0	0	1	1	
Semaprochilodus taeniurus (Valenciennes, 1821)	Detritivore	0	0	0	0	0	0	1	0	
Serrasalmus altispinis Merckx, Jégu & Santos, 2000	Piscivore	0	0	1	3	0	0	0	0	
Serrasalmus elongatus Kner, 1858	Piscivore	0	0	0	0	0	0	0	1	
Serrasalmus gouldingi Fink & Machado-Allison, 1992	Piscivore	0	0	3	1	0	0	7	5	
Serrasalmus rhombeus (Linnaeus, 1766)	Piscivore	0	0	1	0	0	0	0	1	
Serrasalmus sp.	Piscivore	0	0	1	0	0	0	0	0	
atia intermedia (Steindachner, 1877)	Omnivore	0	0	0	4	0	0	0	0	
etragonopterus chalceus Spix & Agassiz, 1829	Omnivore	0	0	0	1	0	0	0	0	
Friportheus angulatus (Spix & Agassiz, 1829)	Omnivore	0	0	1	6	0	0	1	0	
Jaru amphiacanthoides Heckel, 1840	Omnivore	0	0	0	1	0	0	0	0	
rotal		374	184	84	104	157	164	64	85	



to the first dimension, the species composition of samplings taken at the flooded forest (morning and night) and at the lake (night) are more diverse than those taken at the lake in the morning. Piscivore species are most closely associated with the flooded forest in both periods (morning and night) and with the lake at night rather than with the lake in the morning. Carnivore species, on the other hand, are most closely linked to the lake in the morning. The second dimension shows that carnivores and piscivores are mostly present at night but are found in the flooded forest nearly as much as they are in the lake. Meanwhile, omnivores, planktivores and detritivores occur mostly during the morning in both habitat types.

Our results support the claim that higher diversity exists in the aquatic terrestrial transition zone (ATTZ) more so than in either adjacent habitat type (Junk et al. 1989). This is in part because the ATTZ possesses diverse habitat, refuge and food resources, creating the opportunity for several ecological niches. High diversity at night suggests that more species (i.e. carnivorous predators) are active after dark. Gear avoidance does not appear to have had a role in the lower levels of diversity associated with morning capture since the difference between the number of individuals sampled in the morning and in the night is small. Carnivorous species (carnivores and piscivores) were found more often at night, according to the correspondence analysis, further supporting the observed high nocturnal diversity. In contrast, omnivores, which represent a more generalist trophic level, are associated with the morning along with planktivores and detritivores. Such correlations demonstrate a distinct time division between carnivorous species and other trophic levels. The fact that predators contribute most to species richness suggests that, as in many ecosystems, they are integral in preventing herbivore overabundance through a top-down trophic cascade (Estes et al. 2011), corroborating the importance of piscivory in tropical systems (Rodríguez and Lewis 1997; Súarez et al. 2001).

ACKNOWLEDGEMENTS

We thank Professor Lawrence E. Hurd of Washington and Lee University (Virginia, USA) for his comments and help in editing the English in this manuscript.

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Recebido em: 29/09/2011 Aceito em: 17/01/2012