On the relation amongst limnological factors and fish abundance in reservoirs at semiarid region

Relação entre características limnológicas e abundância de peixes em reservatórios da região semiárida

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Abstract: Aim: To evaluate possible nycthemeral and seasonal temporal patterns in fish assemblage associated with limnological aspects and biotic factors in two reservoirs in semarid Northeastern Brazil. Methods: Fish were sampled with gillnets in nycthemeral cycles throughout the dry and rainy season in two reservoirs (Paulo Sarasate/PS and Edson Queiroz/EQ). The stomach contents of the predator species were surveyed. The limnological variables were submitted to principal components analysis, while their relation to fish abundance was determined by canonical correspondence analysis. Temporal patterns in relative fish species abundance were detected with nMDS. Results: Temperature and dissolved oxygen levels segregated the reservoirs physico-chemically. Turbidity and chlorophyll-a levels differed between seasons, and the relative abundance of species differed between the reservoirs. Predators were more abundant in PS, while detritivores were more abundant in EQ. Triportheus signatus and Plagioscion squamosissimus were the most abundant species in both reservoirs. In general, predator abundance was positively associated with high temperature and dissolved oxygen (PS>EQ) and negatively associated with turbidity. The activity patterns of P. squamosissimus could not be explained by fluctuations in environmental variables. Non-predators tended to cluster around the vectors chlorophyll-a, pH and turbidity. Predators had a more diversified diet in PS in accordance with food availability, while predators in EQ ate only fish and shrimp. Nycthemeral patterns varied for the same species depending on the reservoir. Generally, in PS predators were more active during daylight hours while non-predators were more active after dark. However, in EQ predators and non-predators displayed similar nycthemeral activity patterns. Regardless of the reservoir, predators were more abundant in the rainy season. No seasonal trend was observed for non-predators. Conclusions: Limnological differences between PS and EQ influenced temporal species abundance patterns. The species distribution was determined by predation conditions and physiological attributes.

Keywords: physical and chemical variables; daily patterns; diet; predation; fish stocking.

Resumo: Objetivo: Avaliar os possíveis padrões temporais nictemerais e sazonais na assembleia íctica em relação a aspectos limnológicos e fatores bióticos em dois reservatórios no semiárido Nordeste do Brasil. Métodos: Peixes foram amostrados com redes de espera em ciclos nictemerais nos períodos seco e chuvoso em dois reservatórios (Paulo Sarasate /PS e Edson Queiroz /EQ). O conteúdo estomacal das espécies predadoras foi avaliado. As variáveis limnológicas foram submetidas a uma PCA, enquanto suas relações com a abundância de peixes foi determinada por uma CCA. Padrões temporais relativos à abundância de espécies de peixes foram detectados com nMDS. Resultados: Temperatura e oxigênio dissolvido segregaram fisico-quimicamente os reservatórios. Níveis de turbidez e

clorofila-a diferiram entre os períodos do ano, e a abundância relativa das espécies diferiram entre os reservatórios. Predadores foram mais abundantes no PS, enquanto detritívoros foram mais abundantes no EQ. Triportheus signatus e Plagioscion squamosissimus foram as espécies mais abundantes em ambos os reservatórios. No geral, a abundância de predadores foi positivamente relacionada com altas temperaturas e oxigênio dissolvido (PS>EQ) e negativamente associada com turbidez. Os padrões de atividades de P. squamosissimus não podem ser explicados por flutuações nas variáveis ambientais. Espécies não predadoras tenderam a se agruparem aos vetores clorofila-a, pH e turbidez. Predadores apresentaram dieta mais diversificada no PS de acordo com a disponibilidade de alimento, enquanto predadores no EQ consumiram somente peixe e camarão. Padrões nictemerais variaram para algumas espécies dependendo do reservatório. Em geral, no PS predadores foram mais ativos durante as horas iluminadas do dia, enquanto não predadores foram mais ativos após o escurecer. Entretanto, no EQ predadores e não predadores mostraram padrões nictemerais de atividades similares. Independentemente do reservatório, predadores foram mais abundantes no período chuvoso. Nenhuma tendência sazonal foi observada para espécies não predadoras. Conclusões: Diferenças limnológicas entre PS e EQ influenciaram padrões temporais na abundância das espécies.

Palavras-chave: variáveis físicas e químicas; padrões diários; dieta, predação; estocagem de peixes.

1. Introduction

Covering 969,000 km², the semiarid region of Northeastern Brazil is subject to recurrent and severe droughts (Ab'Sáber, 2003). Thus, over the decades measures have been taken to store water, especially by building reservoirs, which eventually become ecologically heterogeneous and complex environments (Araujo-Lima et al., 1995; Agostinho et al., 1999; Ferrareze et al., 2014; Novaes et al., 2014) capable of sustaining fish communities and fishing (Paiva et al., 1994).

The fish assemblage of these reservoirs is the result of the adaptation of the original community (of the caatinga, Rosa et al., 2003) to the new environment (Agostinho et al., 1999; Loureiro-Crippa & Hahn, 2006; Cantanhêde et al., 2008) and of the introduction of new species. Fish survival and successful adaptation depend on the trophic conditions of the reservoir and on the availability of food, shelter and adequate spawning grounds (Agostinho et al., 1999; Oliveira & Goulart, 2000).

Fish move within a reservoir in accordance with temporal factors (diurnal/nocturnal habits, seasons, and fluctuations in water level) and spatial factors (lotic, lentic, littoral and pelagic zone). In other words, fish assemblages in reservoirs are regulated by environmental fluctuations (abiotic factors) and/or by biotic interactions (Coutant, 1985; Gido & Matthews, 2000; Jackson et al., 2001).

The ecology of fish assemblages in reservoirs in Northeastern Brazil has been little investigated. Thus, the objective of this study was to investigate daily and seasonal temporal patterns in fish assemblage of two reservoirs in the Brazilian

semiarid, considering limnological aspects, trophic characteristics and abundance of species.

2. Material and Methods

2.1. Study area

The study was conducted in two major reservoirs in the middle Acaraú River basin (Ceará, Brazil): the Paulo Sarasate reservoir (PS), located in the Varjota municipality, and the Edson Queiroz reservoir (EQ), located in the municipality of Santa Quitéria. The Acaraú River basin covers an area of 14,427 km², corresponding to 15% of the territory of the state of Ceará (Figure 1). Built in 1958, PS has a storage capacity of 891 million m³ and a surface area of 96.25 km². The reservoir, which is considered eutrophic, has a dendritic drainage pattern, a maximum and average depth of 34 m and 10.4 m, respectively, and a hydraulic retention time of 1.43 year. Built in 1987 in the Groaíras River (tributary of the Acaraú River), EQ has a storage capacity of 254 million m³, a surface area of 26.60 km², an average depth of 9.4 m and a hydraulic retention time of 3.12 years (Figueirêdo et al., 2007; Ceará, 2010). Currently, 23 communities are settled in the vicinity of these two reservoirs, including approximately 600 active subsistence fishermen (Batista, unpublished data).

According to the Köppen classification, the regional climate may be identified as BSw'h' (hot semiarid). The region has an annual rainfall of 800 mm and two annual seasons (dry and rainy, FUNCEME, 2012). The rainy season extends from early January to the end of May (Figure 2).

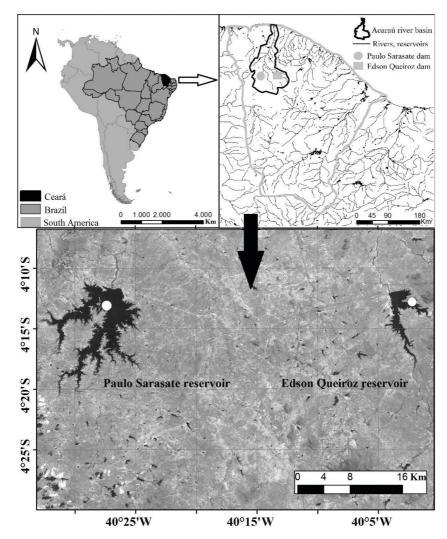


Figure 1. Location of the Paulo Sarasate (PS) and the Edson Queiroz (EQ) reservoirs in the semiarid middle Acaraú river basin (Ceará, Northeastern Brazil) with the respective fish sampling sites (white dots).

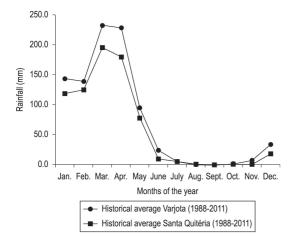


Figure 2. Historical average monthly rainfalls (1988-2011) in the municipalities Varjota and Santa Quitéria (Ceará, Northeastern Brazil) where the Paulo Sarasate and the Edson Queiroz reservoirs are located, respectively. Source: FUNCEME (2012).

2.2. Procedures

The fish fauna of each reservoir was sampled on four occasions, twice in the rainy season and twice in the dry season. Sampling occurred in January 2011 (rainy 1), March 2012 (rainy 2), July 2010 (dry 1) in both reservoirs, in August 2011 (dry 2) in PS, and in October 2011 (dry 2) in EQ. The physical and chemical properties of the water (temperature, dissolved oxygen, pH, conductivity, salinity, total dissolved solids, turbidity and chlorophyll-a) were measured at a depth of 4-7 m by staff from COGERH (Companhia de Gestão dos Recursos Hídricos) using a multiparameter water quality instrument (YSI 6600 V2 Sonde) at the location and time of fish sampling.

A fish sampling area was defined in the sublittoral zone of each reservoir (PS: 4°14′03″S 40°27′40″W; EQ: 4°13′27″S 40°02′08″W) at a

depth of 4 to 7 m. Nineteen floating gillnets were deployed at mid-water depth in nycthemeral cycles, with samplings at six-hour intervals: morning (6h-12h), afternoon (12h-18h), evening (18h-0h) and night (0h-6h). The mesh size varied from 3 to 12 cm between opposite knots, with net sections mounted in random order (shoreline covered: 400m, with standardized effort for both systems: 690 m²/24h. Samples were collected under license number 23837-1 from the MMA (Ministério do Meio Ambiente) and ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade). Voucher specimens were deposited in the fish collection of a public university (Coleção Ictiológica da Universidade Federal do Rio Grande do Norte). The collected species were identified to the lowest possible taxon based on Kullander (1983), Britski et al. (1984), Vari (1989, 1991), Ploeg (1991), Castro & Vari (2004), Malabarba (2004), Kullander & Ferreira (2006), Britski et al. (2007), Oyakawa & Mattox (2009) and Silva (2009). The species Hypostomus jaguribensis (Fowler, 1915) was identified with the assistance of Dr. Pedro Hollanda Carvalho.

Predator species were dissected and the stomach was fixed in 70% alcohol. Trophic guilds were identified analyzing the stomach contents and calculating the alimentary index (IAi) (Kawakami & Vazzoler, 1980) based on volume and frequency of occurrence of items. To determine the volume of the food items, the area occupied by the items on millimeter paper in a Petri dish was multiplied by the items' height measured with a digital caliper. The guilds of the non-predators species were determined from the available literature.

2.3. Data analysis

The environmental variables were combined by Principal Components Analysis (PCA) in order to reduce the dimensionality of the data and describe the relations among the variables. PCA was based on a Pearson correlation matrix of the environmental variables following log-transformation of the data, except for pH. The component axes retained for interpretation were selected with the broken-stick model (Jackson, 1993). Thus, only axes with eigenvalues greater than the eigenvalues generated by the broken-stick model were interpreted.

A Canonical Correspondence Analysis (CCA) was performed to detect correlations between environmental variables and fish abundance. The analysis used variables with a variance inflation factor under 10 (Gross, 2003). The axes were selected with the Monte Carlo test based on

999 permutations at α =0.01 (Quinn & Keough, 2002). These methods made it possible to determine the influence of environmental variables on fish assemblage patterns and to evaluate the potential of certain groups (or guilds) of fish for use as indicators of environmental conditions. The fish abundance data were transformed with the Hellinger distance (Legendre & Gallagher, 2001).

To evaluate seasonal (dry/rainy) and 24-hour fish assemblage distribution patterns, the collected abundance data were analyzed with the PerMANOVA (Anderson, 2001), with the Bray-Curtis dissimilarity. Differences between the treatments were tested with the Monte Carlo method, with 999 permutations at α =0.05. Subsequently, based on Bray-Curtis dissimilarities, non-metric Multidimensional Scaling (nMDS) was performed for log-transformed 24-hour matrixes x abundance and for season x abundance, selecting the dimensions generating the least stress (McCune & Grace, 2002). All statistical analyses were handled with the software R version 2.11.1 (R Foundation for Statistical Computing, 2010).

3. Results

3.1. Environmental variables

The first two PCA axes (Figure 3a) explained 69.8% of the total variation in reservoir-related environmental data (Table 1). Axis 1 (47.7%) was positively influenced by conductivity, total dissolved solids (TDS), salinity, temperature and negatively influenced by dissolved oxygen (DO). Since the first three variables displayed a high level of redundancy (Figure 3a), the two variables with the smallest loadings (conductivity and salinity) were excluded from further analysis. Temperature and DO appeared to promote physical and chemical segregation between the reservoirs since these variables were generally higher for PS than for EQ (Table 1 and Figure 3a). Chlorophyll-a, pH and turbidity were the most influential variables in Axis 2 (22.1%), although did not segregate the reservoirs.

When seasonality was added to the analysis, segregation due to physical and chemical variations became more evident in PCA (Figure 3b). Thus, temperature, turbidity and chlorophyll-*a* concentrations were greater in PS during the first dry season covered by the study (dry 1), but remained unchanged in EQ (Figure 3b). Despite seasonal variation, chlorophyll-*a* levels where consistently high in both PS and EQ, characterizing eutrophic/supereutrophic (CHLOR.a >2.96 µg.L⁻¹) to hypereutrophic (CHLOR.a >7.46 µg.L⁻¹) conditions.

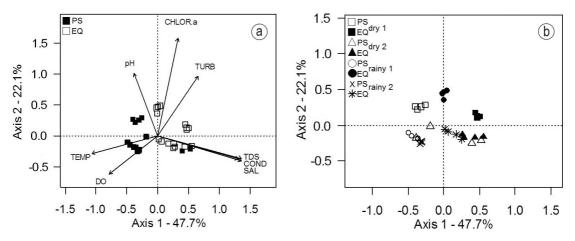


Figure 3. Principal Components Analysis using limnological variables for the Paulo Sarasate (PS) and Edson Queiroz (EQ) reservoirs: (a) differences between reservoirs, (b) temporal variation in reservoirs. TEMP: temperature, DO: dissolved oxygen, pH: hydrogen potential, COND: conductivity, SAL: salinity, TDS: total dissolved solids, TURB: turbidity, CHLOR.a: chlorophyll-a.

Table 1. Average values and standard deviations of the physical and chemical properties of water collected in the Paulo Sarasate reservoir (PS) and the Edson Queiroz reservoir (EQ). TEMP: temperature, DO: dissolved oxygen, pH, COND: conductivity, SAL: salinity, TDS: total dissolved solids, TURB: turbidity, CHLOR.a: chlorophyll-a.

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PS	dry 1	rainy 1	dry 2	rainy 2
TEMP (°C)	28.60 ± 0.30	28.10 ± 0.90	28.60 ± 1.00	28.90 ± 0.70
DO (mg.L ⁻¹)	7.30 ± 1.50	4.23 ± 1.90	7.65 ± 1.50	3.24 ± 3.00
рН	8.40 ± 0.30	7.00 ± 0.40	8.00 ± 0.40	7.70 ± 0.40
COND (µS.cm ⁻¹)*	208.00 ± 1.70	249.00 ± 39.70	209.00 ± 4.00	228.00 ± 2.30
SAL (ppt)*	0.09 ± 0.00	0.11 ± 0.02	0.09 ± 0.00	0.10 ± 0.00
TDS (mg.L ⁻¹)*	120.00 ± 0.00	150.00 ± 0.02	120.00 ± 0.00	130.00 ± 0.00
TURB (NTU)	12.00 ± 0.90	13.40 ± 2.50	5.40 ± 0.70	3.50 ± 1.20
CHLOR.a (µg.L ⁻¹)	29.00 ± 2.00	7.80 ± 0.80	4.60 ± 0.60	3.60 ± 0.90
EQ				
TEMP (°C)	27.00 ± 0.70	28.10 ± 0.60	28.50 ± 0.70	28.20 ± 0.60
DO (mg.L ⁻¹)	2.62 ± 1.30	5.60 ± 2.50	2.76 ± 1.30	3.77 ± 2.60
рН	7.50 ± 0.10	7.60 ± 0.50	8.80 ± 0.40	8.00 ± 0.50
COND (µS.cm ⁻¹)*	264.00 ± 1.10	283.00 ± 0.00	234.00 ± 3.30	257.00 ± 2.20
SAL (ppt)*	0.12 ± 0.00	0.12 ± 0.00	0.10 ± 0.00	0.11 ± 0.00
TDS (mg.L ⁻¹)*	160.00 ± 0.00	170.00 ± 0.00	140.00 ± 0.00	150.00 ± 0.00
TURB (NTU)	11.60 ± 4.20	16.70 ± 1.40	16.40 ± 1.00	8.80 ± 3.50
CHLOR.a (µg.L⁻¹)	32.50 ± 3.40	8.60 ± 0.50	31.80 ± 1.60	6.30 ± 1.40
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^{*}Variables excluded from the CCA analysis due to high colinearity and redundancy.

3.2. Fish assemblage

A total of 1,626 specimens were collected from the two reservoirs, representing 17 fish species, nine families and three orders (Table 2). The sample included predators (41.2%), detritivores (23.5%) and species classified in other guilds (35.3%). In this study, *Cichlasoma orientale* and *Trachelyopterus galeatus* were classified as predators since they prey on small fishes in addition to their preferred diet of invertebrates. The stomach contents of the predators covered the following categories: fishes,

shrimp (genus *Macrobrachium*), insects (Coleoptera, Diptera larvae, Hymenoptera, Odonata nymph, Trichoptera larvae), other invertebrates (Arachnida, Chilopoda, Gastropoda) and plant matter (leaves and twigs) (Table 2).

The two reservoirs differed with regard CPUE (Catch Per Unit Effort) values: CPUE $_{\rm PS}$ was 59.5 individuals/ $100 {\rm m}^2/24 {\rm h}$ and CPUE $_{\rm EQ}$ 101.9 individuals/ $100 {\rm m}^2/24 {\rm h}$. Relative abundance of species in each trophic guild also was different (Table 3). Thus, predators were more diverse and abundant in PS than in EQ, while

Table 2. Fish species collected in the Paulo Sarasate (PS) and Edson Queiroz (EQ) reservoirs, with their relative abundance (N%) and trophic guilds. Trophic guilds of non-predatory species were obtained from the studies on the species or congeners: (1) Mérona & Rankin-de-Mérona (2004), (2) Montenegro et al. (2011), (3) Castro & Vari (2004), (4) Montenegro et al. (2010), (5) Gurgel et al. (2005), (6) Pinto et al. (2011), (7) Mazzoni et al. (2010), (8) Silva (2009).

N%								
Taxon	PS	EQ	Trophic guild	Voucher				
CHARACIFORMES								
Curimatidae								
Psectrogaster rhomboides Eigenmann e	0.15	0.31	Detritivore (1)	UFRN 903-905				
Eigenmann, 1889								
Steindachnerina cf. notonota (Miranda Ribeiro, 1937)	0	0.10	Detritivore (2)	UFRN 902				
Prochilodontidae								
Prochilodus brevis Steindachner, 1874	1.40	11.94	Detritivore (3)	UFRN 895-896				
Anostomidae								
Leporinus spp.	1.86	3.67	Omnivore (4)	UFRN 920-927				
Characidae								
Astyanax bimaculatus (Linnaeus, 1758)	0	0.31	Omnivore (5)	UFRN 897				
Astyanax fasciatus (Cuvier, 1819)	1.24	5.55	Omnivore (5)	UFRN 898-901				
Triportheus signatus (Garman, 1890)	56.80	68.03	Insectivore (6)	UFRN 906-907				
Erythrinidae								
Hoplias spp.	2.64	0.42	Piscivore	UFRN 930-933				
SILURIFORMES								
Loricariidae								
Hypostomus jaguribensis (Fowler, 1915)	0.31	0.73	Detritivore (7)	UFRN 891-894				
Auchenipteridae								
Trachelyopterus galeatus (Linnaeus, 1766)	0.68	0	Omnivore	UFRN 909				
PERCIFORMES								
Sciaenidae								
Plagioscion squamosissimus (Heckel, 1840)	27.64	7.06	Carnivore	UFRN 928-929				
Cichlidae								
Cichla monoculus Spix and Agassiz, 1831	3.72	1.36	Carnivore	UFRN 912-917				
Cichlasoma orientale Kullander, 1983		0	Carnivore	UFRN 918-919				
Crenicichla menezesi Ploeg, 1991		0.10	Carnivore	UFRN 910-911				
Oreochromis niloticus (Linnaeus, 1758)	0.15	0.42	Omnivore (8)	UFRN 908				

Table 3. Dominance (by abundance) of fish species in the reservoirs of Paulo Sarasate (PS) and Edson Queiroz (EQ). Bold: predators, D: detritivore, E: endemic to the Brazilian semiarid, I: introduced species. Among the captured species, 41.2% are endemic to the Brazilian semiarid region and 17.6% were introduced (Gurgel-Lourenço et al., 2013).

	PS		EQ
N	Species	N	Species
1°	Triportheus signatus ^E	1°	Triportheus signatus ^E
2°	Plagioscion squamosissimus	2°	Plagioscion squamosissimus
3°	Cichla monoculus	3°	Prochilodus brevis ^{D,E}
4°	Hoplias spp.	4°	Astyanax fasciatus
5°	Cichlasoma orientale [⊑]	5°	Leporinus spp.
	Leporinus spp.	6°	Cichla monoculus
6°	Crenicichla menezesi	7°	Hypostomus jaguribensis ^{D,E}
7°	Prochilodus brevis ^{D,E}	8°	Oreochromis niloticus
8°	Astyanax fasciatus		Hoplias spp.
9°	Trachelyopterus galeatus	9°	Astyanax bimaculatus
10°	Hypostomus jaguribensis ^{D,E}		Psectrogaster rhomboides ^{D,E}
11°	Psectrogaster rhomboides ^{D,E}	10°	Steindachnerina cf. notonota ^{D,E}
	Oreochromis niloticus		Crenicichla menezesi

detritivores were more diverse and abundant in EQ than in PS. *Triportheus signatus* and *Plagioscion squamosissimus* were the most abundant species in both reservoirs (Table 3).

In the CCA analysis we used the most important variables with low colinearity according to PCA (temperature, DO, turbidity, pH and chlorophyll-a). The first two axes explained 73.9% of the variance in species abundance (Figure 4). The sum of all the canonical axes was significant when the Monte Carlo test was applied (pseudo-F=1.869; p=0.01).

According to the CCA analysis, the predators Crenicichla menezesi, Cichla monoculus, Cichlasoma orientale and Hoplias spp. were favored by high temperatures and DO levels, especially in PS, while T. galeatus was the only predator species positively associated with turbidity (Figure 4). On the other hand, a number of non-predators, including Astyanax fasciatus, Hypostomus jaguribensis, Leporinus spp., Prochilodus brevis and Steindachnerina cf. notonota, were associated with the vector turbidity and, to a lesser degree, chlorophyll-a and pH. Astyanax bimaculatus and T. signatus were associated with the same vectors, with emphasis on chlorophyll-a (Figure 4). The distribution of these species is primarily dependent on temperature, DO, turbidity, pH and chlorophyll-a levels.

Predators in PS consumed primarily fish and insects, followed by shrimp, other invertebrates and plant matter. In EQ, the same predator species had less diversified diets, eating mainly shrimp and fish (Figure 5).

Significant differences were found for both temporal cycles investigated (seasonal and nycthemeral) (PerMANOVA, seasonal: p=0.008; nycthemeral: p=0.02). According to the nMDS test (stress=0.18), the two reservoirs have different and unique nycthemeral patterns. Generally speaking, in PS many of the predators (C. menezesi, C. orientale, Hoplias spp. and T. galeatus) were particularly active in the morning and in the afternoon (Figure 6a), while the predators C. monoculus and P. squamosissimus were uniformly active throughout the 24-hour period. The non-predator species A. fasciatus, H. jaguribensis, Leporinus spp., O. niloticus, P. brevis, P. rhomboides and T. signatus were more active after dark (evening and night) (Figure 6a). In EQ, nycthemeral activity patterns were similar for predators and non-predators. All predators displayed homogenous activity throughout the 24-hour period. The same was true for the non-predator species A. fasciatus, A. bimaculatus, H. jaguribensis, Leporinus spp., O. niloticus, P. brevis, P. rhomboides, S. cf. notonota and T. signatus (Figure 6a). Regardless of the reservoir, predators were more abundant in the rainy season. No seasonal trend was observed for non-predator species (Figure 6b).

In EQ, the diversity of predators was smaller (*C. orientale* and *T. galeatus* were not observed) and *C. menezesi* and *Hoplias* spp. were less abundant in

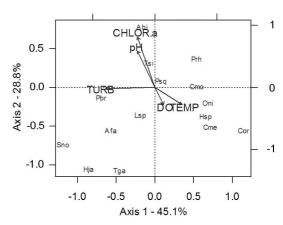


Figure 4. CCA ordination with fish species and limnological variables of the Paulo Sarasate (PS) and Edson Queiroz (EQ) reservoirs. Variables: TEMP: temperature, DO: dissolved oxygen, pH: hydrogen potential, TURB: turbidity, CHLOR.a: chlorophyll-a. Species: Abi: Astyanax bimaculatus, Afa: Astyanax fasciatus, Cme: Crenicichla menezesi, Cmo: Cichla monolucus, Cor: Cichlasoma orientale, Hja: Hypostomus jaguribensis, Hsp: Hoplias spp., Lsp: Leporinus spp., Oni: Oreochromis niloticus, Pbr: Prochilodus brevis, Prh: Psectrogaster rhomboides, Psq: Plagioscion squamosissimus, Sno: Steindachnerina cf. notonota, Tga: Trachelyopterus galeatus, Tsi: Triportheus signatus.

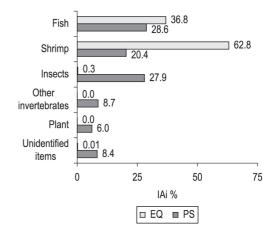


Figure 5. Feed items consumed (IAi%) by predator fish species from the Paulo Sarasate (PS) and Edson Queiroz (EQ) reservoirs.

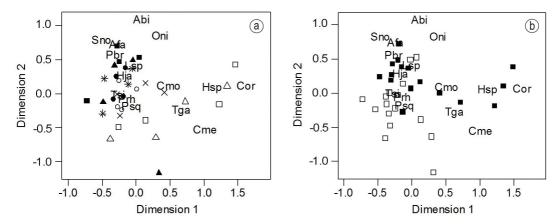


Figure 6. nMDS (stress = 0.18). (a) time at the reservoirs: PS: [Δ] morning, [□] afternoon, [x] evening, [0] night, EQ: [▲] morning, [■] afternoon, [*] evening, [●] night; (b) season in PS and EQ: [□] dry season [■] rainy season. Species: Abi: Astyanax bimaculatus, Afa: Astyanax fasciatus, Cme: Crenicichla menezesi, Cmo: Cichla monolucus, Cor: Cichlasoma orientale, Hja: Hypostomus jaguribensis, Hsp: Hoplias spp., Lsp: Leporinus spp., Oni: Oreochromis niloticus, Pbr: Prochilodus brevis, Prh: Psectrogaster rhomboides, Psq: Plagioscion squamosissimus, Sno: Steindachnerina cf. notonota, Tga: Trachelyopterus galeatus, Tsi: Triportheus signatus.

relation to PS. The only abundant predators in EQ were *P. squamosissimus* and *C. monoculus*, which feed almost entirely on shrimp (98.7% and 89.9%, respectively). Thus, in the more turbid waters of EQ, non-predator species were active 24 hours a day (Table 3).

4. Discussion

With indices between 250 mm (rainy season) and 0 mm (dry season), rain was scarce throughout the study period, leading to decreased water levels in both PS and EQ and, consequently, increased temperature, TDS and chlorophyll-a levels. These three variables, which were particularly high in PS, provided the best explanation for the observed limnological variation. Such conditions appear to favor predators since these were more diverse and abundant in PS, displaying diurnal activity patterns (especially in the rainy season). Non-predators were invariably more active nocturnally, regardless of season and reservoir.

The limnological characteristics of PS and EQ were typical of semiarid regions: high temperatures, accumulation of nutrients and saline concentration. The high TDS values observed were likely associated with the low water levels in the reservoirs (average depth: PS=10.4 m; EQ=9.4 m), favoring sediment resuspension, increasing turbidity and reducing the photic zone (Secchi depth <1 m) (Bouvy et al., 2000; Eskinazi-Sant'Anna et al., 2007; Sousa et al., 2008). With pH values around 8 and high chlorophyll-*a* levels, especially in the

dry season, the two reservoirs may be considered eutrophic or hypereutrophic (Bouvy et al., 2000; Huszar et al., 2000; Eskinazi-Sant'Anna et al., 2007). In addition, large amounts of nutrients are washed into the reservoirs due to intense soil erosion and discharge of wastewater from nearby settlements (Ceará, 2009; Barbosa et al., 2012).

Predators were more active during the day in PS, where temperatures and DO levels were higher and turbidity was lower. These variables are related to physiological aspects (Rantin & Johansen, 1984; Coutant, 1985; Petry et al., 2007) influencing mobility. In addition, predation tactics appeared to rely mostly on eyesight since the most important diet component was small, free-swimming invertebrates which are most easily captured in daylight, when the influence of turbidity is smallest (La Porta et al., 2010; Brejão et al., 2013; Jönsson et al., 2013). However, this association was not observed for the predator *P. squamosissimus*, which appeared to be more generalist and less restricted by specific environmental conditions. Conversely, non-predator species were most abundant in turbid, oxygen-poor and chlorophyll-rich environments. Some of these species thrive in hypoxic environments due to their ability to absorb oxygen through the digestive tract (Hypostomus) or dermal lip protuberances (Astyanax, Triportheus) (Winemiller, 1989a; Armbruster, 1998; Podkowa & Goniakowska-Witalińska, 2003; Scarabotti et al., 2011).

Species of the genus *Hoplias*, classified as ambush predators, were most abundant in PS and

most active during the day, preying primarily on fish. The large amount of aquatic macrophytes in PS (personal observation) very likely facilitates ambushing the prey (Petry et al., 2010). *Plagioscion squamosissimus* differed from the general pattern observed for predators in PS by the absence of temporal fluctuations in activity and the almost exclusive preference for shrimp (97.2%), an abundant food item in the reservoirs. In contrast, the preference of non-predators for nocturnal activity is likely explained by the lower incidence of predation after dark and by the migration of zooplankton towards the surface (Moreira & Odinetz Collart, 1993; Costa et al., 2009; Previattelli et al., 2005).

The National Department for Drought Relief (DNOCS) stocked PS and EQ with allochthonous shrimp of the genus *Macrobrachium* in order to boost fisheries (of both shrimp and their predators) (Gurgel & Fernando, 1994; Paiva et al., 1994). The new species adapted very quickly (Paiva et al., 1994; Sampaio et al., 2007) and has become the main energy source for non-native predators in these ecosystems, especially generalists such as *P. squamosissimus* and *C. monoculus* (Paiva et al., 1994; Hahn & Fugi, 2007; Costa et al., 2009).

In both reservoirs, predators were less abundant in the dry season, with the exception of P. squamosissimus. In this season, habitats and shelters become scarcer, making it more difficult for ambush predators (Hoplias and Crenicichla) to ambush their prey (Winemiller & Jepsen, 1998; Brejão et al., 2013; Montenegro et al., 2013). In addition, Cichla and Cichlasoma, both of which are common in coastal regions (Oliveira et al., 2005; Beltrão et al., 2009), also become less abundant in the dry season. In contrast, non-predator species generally displayed no seasonal patterns, although migrating species such as Leporinus spp., P. brevis and Curimatidae tend to become more abundant in the rainy season during the annual spawning season (Gurgel et al., 2012; Peressin et al., 2012; Silva Filho et al., 2012; Araújo et al., 2013). The low abundance of these species in PS and EQ may be associated with isolation from adjacent water courses due to the absence fish ladders in the dams (Antonio et al., 2007).

Only three of the species observed in this study -- O. niloticus, P. squamosissimus (both non-native) and T. signatus (native) -- are adapted to the pelagic zone to the extent they are capable of feeding, reproducing and/or finding shelter in this compartment (Nakatani et al., 1993; Agostinho et al., 1999; Höfling et al., 2000; Santos et al., 2003; Silva,

2009), although they all regularly forage in the littoral zone as well (Fernando & Holcík, 1991; Gurgel & Fernando, 1994; Agostinho et al., 1995). Based on this, one would expect these species to be abundant in relation to other species. Nevertheless, few specimens of *O. niloticus* were captured, despite the fact that the species is both eurythermal and euryhaline, factors which have made it a successful colonizer of reservoirs throughout Northeastern Brazil (Silva, 2009).

DNOCS periodically restocks PS and EQ with fish, especially juvenile tilapias (Gurgel-Lourenço et al., 2013). The small number of O. niloticus captured in this study may be explained by the inefficiency of gillnets used to catch this species (Petrere Junior et al., 2007; Lazzaro et al., 2003). On the other hand, Petrere Junior et al. (2007) demonstrated the high predation pressure to which newly stocked tilapia juveniles are subject in the absence of parental care. This view appears to be supported by the inverse relation between predator richness/abundance and the abundance of *O. niloticus* observed in this study. Thus, although stocking efforts have been greater in PS than in EQ (Gurgel-Lourenço et al., 2013), the tilapia was less abundant there. However, since the deeper zones of the reservoirs were not sampled for this study, our findings remain to be confirmed by further investigations.

Some species thrive under eutrophic conditions, such as T. signatus, a benthonic-pelagic filter feeder that was abundant in both reservoirs partly due to the absence of pelagic predators (Gomes & Miranda, 2001; Ab'Sáber, 2003; Rosa et al., 2003), with the possible exception of P. squamosissimus. However, this predator may be hampered by the low visibility of the relatively turbid reservoir water (La Porta et al., 2010; Jönsson et al., 2013). The species' almost total reliance on shrimp (PS-EQ average: 97.9%), not unlike that of its marine relatives and ancestors (Souza et al., 2008), may explain its successful adaptation to PS and EQ. Thus, while the population of P. squamosissimus is sustained by Macrobrachium sp., the population of T. signatus is favored by the abundance of insects and zooplankton characteristic of eutrophic environments (Eskinazi-Sant'Anna et al., 2007; Hahn & Fugi, 2007; Pereira et al., 2011; Pinto et al., 2011).

Small fish species with short life cycles tend to be abundant in eutrophic environments due to the large supply of food (Agostinho et al., 1999). Astyanax fasciatus and Hoplias spp. were inversely related with regard to abundance, indicating predator/prey interaction. In fact, 95.9% of the diet of the trahiras was on small fishes. In some cases it was possible to identify the species Astyanax spp. as part of the stomach contents. In addition, due to greater diversity and abundance of predators, the effect of piscivory was stronger in PS (Paiva et al., 1994; Jackson et al., 2001; Mazzeo et al., 2010; Petry et al., 2010). On the other hand, the activity patterns observed in PS for Hoplias spp. may be related to abiotic factors such as hypoxia: trahiras (Hoplias spp.) were less active at night when DO levels decrease in macrophyte-rich habitats (which are numerous in PS). In response, sometime after dark trahiras (Hoplias spp.) leave their daytime feeding grounds (Saint-Paul & Soares, 1987; Frodge et al., 1990; Yamanaka, 2013).

Detritivorous species were more abundant in EQ, where *P. brevis* was the third-most abundant species. This species possibly benefits from the presence of submerged bushes and trees (absent from PS). Generally, the terrestrial vegetation growing in areas flooded after the construction of a dam provides food and shelter for extended periods (Winemiller and Jepsen, 1998; Agostinho et al., 1999; Gois et al., 2012).

The peacock bass (tucunaré) and its close relatives (genera Cichla, Cichlasoma and Crenicichla) and the silver croaker (pescada) (P. squamosissimus) are visual predators (Costa et al., 2009; Kovalenko et al., 2010; Elvidge & Brown, 2012). The former prefer the shallower areas of the reservoir, while the latter occupies a wider range of habitats, including the pelagic zone (Gurgel et al., 1994; Araujo-Lima et al., 1995; Williams et al., 1998; Oliveira et al., 2005; Costa et al., 2009; Kovalenko et al., 2010). The coexistence of these predators may be facilitated by habitat partition, as in the case of Hoplias malabaricus and C. menezesi, both ambush predators found in dense macrophyte beds (Paiva et al., 1994; Sánchez-Botero & Araujo-Lima, 2001; Elvidge & Brown, 2012; Brejão et al., 2013). In addition, the ample availability of shrimp potentially reduces competition for food between introduced predator species (C. monoculus and P. squamosissimus) and native predators (Hoplias spp and C. menezesi). Likewise, in macrophyte beds, which are rich in fish and invertebrates (Takeda et al., 2003; Sánchez-Botero et al., 2007), resources may be partitioned between native predators. Thus, while trahiras (Hoplias spp.) were essentially piscivorous (95.9%), C. menezesi primarily fed on insects

(78.8% in PS). Finally, a considerable percentage of juvenile peacock bass (50%) have been reported to consume invertebrates associated with vegetation in PS (*like* Winemiller, 1989b), which is endowed with abundant littoral vegetation. The capture of juvenile peacock bass (average: 63.7%) and silver croaker (pescada) (average: 32%) in both reservoirs (unpublished data) is an indication of natural recruitment since neither species has been restocked in PS or EQ since at least 2003 (Gurgel-Lourenço et al., 2013).

5. Conclusion

Limnological differences between the reservoirs Paulo Sarasate (PS) and Edson Queiroz (EQ) influenced fish activity patterns temporally, reflecting a differentiation of fish species distribution related to appropriate conditions of predation, physiological attributes and stocking with non-native species. Thus, proper fishing resource management requires evaluating the long-term consequences of damming up rivers in semiarid regions and the consequences of introducing new species into the local fish assemblage.

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