http://dx.doi.org/10.1590/1519-6984.14712 Original Article

Fish assemblage in a semi-arid Neotropical reservoir: composition, structure and patterns of diversity and abundance

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Received July 31, 2012 – Accepted March 7, 2013 – Distributed May 31, 2014
(With 8 figures)

Abstract

The aim of this study was to analyse the composition, structure and spatial and temporal patterns of diversity and abundance of the ichthyofauna of the Santa Cruz Reservoir in semi-arid Brazil. Data were collected quarterly at eight sampling locations on the reservoir between February 2010 and November 2011 using gillnets from 12- to 70-mm mesh that were left in the water for 12h00min during the night. We evaluated the composition, structure and assemblage descriptors (Shannon-Wiener diversity index and equitability, respectively) and catch per unit effort by the number (CPUEn) and biomass (CPUEb) of the ichthyofauna. The 6,047 individuals (399,211.6 g) captured represented three orders, ten families and 20 species, of which four belonged to introduced species. The family Characidae was the most abundant with a total of 2,772 (45.8%) individuals captured. The species-abundance curve fit the log-normal model. In the spatial analysis of diversity, there were significant differences between sampling sites in the lacustrine and fluvial regions, and the highest values were found in the lacustrine region. In the temporal analysis of diversity, significant differences were also observed between the rainy and dry seasons, and the higher values were found during the dry season. Equitability followed the same spatiotemporal pattern as diversity. The Spearman correlation was significantly negative between diversity and rainfall. A cluster analysis spatially separated the ichthyofauna into two groups: one group formed by sampling sites in the fluvial region and another group formed by the remainder of the points in the lacustrine region. Both the CPUEn and CPUEb values were higher at point 8 (fluvial region) and during the rainy season. A two-way ANOVA showed that the CPUEn and CPUEb values were spatially and temporally significant. We conclude that the spatial and temporal trends of diversity in the Santa Cruz reservoir differ from those of other Brazilian reservoirs but that the fish community composition and spatiotemporal patterns of abundance were similar.

Keywords: transposition, São Francisco River, Eastern Northeast Atlantic Basin, Apodi/Mossoró River, dam.

Assembleia de peixes de um reservatório no semiárido Neotropical: composição, estrutura e padrões de diversidade e abundância

Resumo

O objetivo desse trabalho foi analisar a composição, estrutura e os padrões espacial e temporal de diversidade e abundância da ictiofauna do reservatório de Santa Cruz, no semiárido brasileiro. As coletas ocorreram trimestralmente em oito pontos do reservatório entre fevereiro de 2010 e novembro de 2011, com rede de espera e malhas entre 12 a 70mm, expostas por 12h00min na água no período noturno. Foram analisados a composição, estrutura e os descritores da assembleia (índice de diversidade de Shannon-Wiener, equitabilidade), CPUEn (número) e CPUEb (biomassa) da ictiofauna. Foram capturados 6.047 indivíduos (399.211,6g) pertencentes a três ordens, 10 famílias e 20 espécies, sendo quatro espécies introduzidas. A família Characidae foi a mais abundante com 2.772 (45,8%) dos indivíduos capturados. A curva de abundância-espécie se ajustou ao modelo log-normal. Na abordagem espacial da diversidade, houve diferenças estatísticas entre os pontos da região fluvial e região lacustre, sendo os maiores valores encontrados nos pontos da região lacustre. Na abordagem temporal da diversidade, também foram observados diferenças estatísticas entre as estações de chuva e seca, sendo os maiores valores encontrados na estação da seca. A equitabilidade seguiu o mesmo padrão espaço-temporal da diversidade. A correlação de Spearman foi significativa e negativa entre a diversidade e a pluviosidade. A análise de cluster separou espacialmente a ictiofauna em dois grupos: um formado pelos pontos da região fluvial e outro formado pelos demais pontos do compartimento lacustre. Tanto as valores da CPUEn e CPUEb foram maiores no ponto 8 (compartimento fluvial) e na estação da chuva. ANOVA *two-way* foi significativa no espaço e no tempo nos valores da CPUEn e CPUEb. Concluímos que os padrões espacial e temporal de diversidade no reservatório de Santa Cruz foram diferentes de outros reservatórios brasileiros, enquanto a composição da ictiofauna e os padrões espaço-temporal de abundância apresentaram padrões similares.

Palavras-chave: transposição, Rio São Francisco, Bacia Atlântico Nordeste Oriental, Rio Apodi/Mossoró, açude.

Introduction

Semi-arid regions comprise 7% of the Brazilian territory and include the northern Southeast region and 70% of the Brazilian Northeast (Leal et al., 2003). The semi-arid climate is characterised by high temperatures and low (250-500 mm) and irregular annual rainfall (Maltchik, 1999). These aspects are responsible for the annual and interannual instability of the rain patterns and, while associated with high rates of surface water evaporation, constitute intermittence and seasonal processes affecting the river network ecosystem of this region. These environmental characteristics led to the formation of a national policy of regional water security based on the accumulation of water during favourable conditions from the construction of reservoirs (Paiva et al., 1994).

Although they benefit human populations by providing water for consumption, agricultural activities, small industrial ventures, local subsistence fishing and, more recently, cage aquaculture, the construction of these reservoirs is one of the main threats to aquatic ecosystems (Nilsson et al., 2005). The reservoirs cause changes in the water quality, flow and habitat conditions, reduce the biodiversity and modify ecological and biological processes, such as reproduction and the recruitment of species with different life history patterns (Petry et al., 2003; Agostinho et al., 2004, 2008; Gao et al., 2010; Yang et al., 2012). The fish assemblage in reservoirs is a result of the combination of the species previously present in the river and the species introduced after impoundment (Fernando and Holčík, 1991; Agostinho et al., 2007). Furthermore, the structure of the new fish assemblage may exhibit a longitudinal gradient (river-dam) of species distribution that may vary in terms of composition, abundance and diversity (Matthews et al., 1989; Okada et al., 2005).

Although the semi-arid region has a high density of water supply reservoirs (ANA, 2006), studies regarding the diversity and structure of the fish assemblies in these ecosystems are fragmented, recent and scarce (Texeira and Gurgel, 2005; Marinho et al., 2006; Montenegro et al., 2012), and the spatial and temporal patterns of diversity and the abundance of the ichthyofauna in these ecosystems are unknown. This gap in knowledge about the northeastern reservoirs contrasts with the knowledge about reservoirs in other regions of Brazil, especially in southern and southeastern Brazil, where many studies have been conducted and the diversity and abundance patterns of the ichthyofauna are well-known (Carvalho et al., 1998; Agostinho et al., 1999; Araújo and Santos, 2001; Oliveira et al., 2004; Hoffmann et al., 2005; Britto and Carvalho, 2006; Silva et al., 2006; Smith and Petrere Junior, 2008; Terra et al., 2010).

Thus, based on such peculiarities as climate, hydrology, intermittency of rivers and different water uses combined with biogeographical aspects, we can ask if the composition, structure and spatiotemporal patterns of the diversity and abundance of the ichthyofauna of reservoirs in semi-arid regions different from those of reservoirs in other regions of Brazil? Guided by this question, the objective of the present study was to describe the composition and structure of the fish assemblage and analyse the spatial (longitudinal gradient) and temporal (rainy vs. dry season) patterns of diversity and abundance of the ichthyofauna in a semi-arid reservoir, the Santa Cruz Reservoir, which is formed by the intermittent Apodi/Mossoró River. A relevant point of the present study is the fact that the Apodi/Mossoró River and, consequently, the Santa Cruz Reservoir, are linked to receive the transposing waters of the São Francisco River (Brasil, 2004). Thus, knowledge of the structure of the ichthyofauna will be important to facilitate the evaluation of the unforeseen effects that the transfer of the São Francisco River could have on the ichthyofauna of this drainage basin.

Material and Methods

Study area

Part of northeastern Brazil is located in the Eastern Northeast Atlantic basin, which occupies an area of 287,348 km^2, where the predominant vegetation is the caatinga with fragments of Atlantic Forest, as well as small areas of cerrado and coastal and insular biomes, which are currently under heavy human pressure. Among the small watersheds located inside of the Eastern Northeast Atlantic basin is the Apodi/Mossoró River, which has an area of 4,246 km^2 and is the main river of the basin with 22 reservoirs that supply water for human consumption and agriculture and livestock use (Almeida et al., 2006). The average annual rainfall in this watershed is 750 mm and is concentrated between the months of February and June. The Santa Cruz dam (05°45’45’’ S, 37°48’00’’W) is the largest of the water supply reservoirs in this watershed, and it is located in the municipality of Apodi (Figure 1). This reservoir, which was built in 2002 with the purpose of providing water for the supply and irrigation of the Apodi Valley, occupies an area of 34.13 km^2 and has a maximum capacity of six million cubic metres (SEMARH, 2009).

Data collection

Data collection occurred quarterly from February 2010 to November 2011 at eight sites in the reservoir (Figure 1). According to Henry-Silva et al., (2013), sites 1 to 6 are in the lacustrine region of the reservoir, whereas points 7 and 8 are in the fluvial region. Sampling involved the use of gillnets with 12 to 70 mm mesh between adjacent knots; the nets were 15 m long and 1.8 to 2m high. They were set at 17h00min and were removed at 05h00 min the following day with a fish collection at 22h00 min.

The specimens captured were stored in plastic bags and identified by sampling point. The samples were transported to the biology laboratory of the Federal Institute of Education, Science and Technology of Rio Grande do Norte (Instituto Federal de Educação, Ciência e Tecnologia do Rio Grande do Norte – IFRN), Apodi Campus, where they were prepared and identified to the lowest taxonomic level by the use of specialised literature

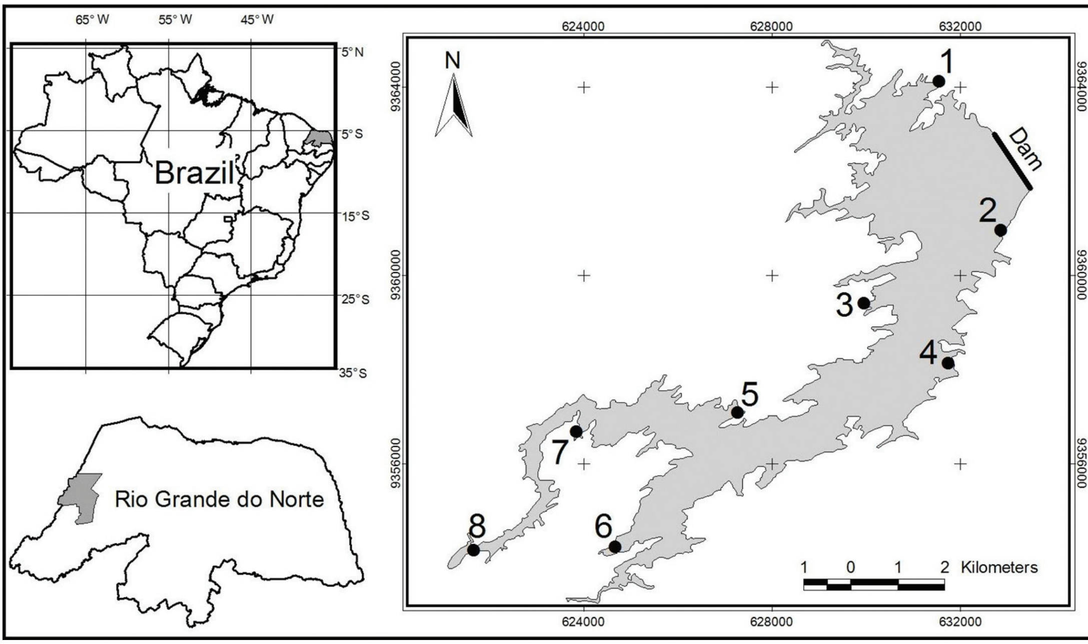

Figure 1. Location of the Santa Cruz Reservoir in the Apodi/Mossoró drainage basin, showing the eight sampling sites.

(Rosa et al., 2003). After identification, the specimens were separated by species and counted, and the routine biometric data collected were standard length (Lp) in centimetres and weight (Wt) in grammes. The identification of the material was confirmed by taxonomists from the Federal University of Paraíba (Universidade Federal da Paraíba – UFPB) and deposited in the ichthyological collection of the institution (catalogue number UFPB 8933 to 8997).

Data analysis

Our approach was temporal and spatial, and in our temporal analysis, the data were grouped by seasons: rainy (February to May) and dry (August to November). The number of individuals and the relative frequency of species by family were calculated. The species richness of the Santa Cruz Reservoir was estimated by the jackknife method; the Shannon-Wiener diversity index (H') and the Peilou index of equitability (J), using the numerical abundance of the species captured (Krebs, 1999; Gotelli and Colwell, 2001; Maurer and McGill, 2011), were estimated by site and season. The Whittaker-plot model with abundance data transformed to ln+1 was created and fitted to the best species-abundance model (geometric series, logarithmic series, truncated series or broken stick) (Magurran, 1988).

The spatial and temporal abundances of the assemblage were determined by Catch per Unit Effort (CPUE) by numbers (CPUEn) and biomass (CPUEb) using the following calculation: CPUE = C/*f*, where C = capture in number or biomass and *f* = effort m^2*h. The CPUE data were standardised as catch per 1000 m^2*24 h.

The following statistical analyses were performed. i) A two-way ANOVA was used to spatially and temporally compare H'. ii) The Spearman correlation coefficient was calculated between rainfall and reservoir volume, as well as the temporal H' data. The monthly rainfall and volume data of the reservoir used in these analyses were obtained from the sites of the Agricultural Research Corporation of Rio Grande do Norte (Empresa de Pesquisa Agropecuária do Rio Grande do Norte – EMPARN)(http://www.emparn.rn.gov.br/contentproducao/aplicacao/emparn/pesquisa/gerados/meteorologia.asp) and the State Secretary of the Environment and Water Resources (Secretaria Estadual de Meio Ambiente e Recursos Hídricos – SEMARH) (http://www.semarh.rn.gov.br/contentproducao/aplicacao/semarh/sistemadeinformacoes/consulta/cBaciaSitVolumetrica_Detalhe.asp?CodigoEstadual=00), respectively. iii) A cluster analysis was used to classify the sampling points using the data related to the numerical abundance of fish. A dendrogram was created using the Bray-Curtis dissimilarity index, and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) method was used as the clustering method. iv) A two-way ANOVA followed by Tukey's HSD test was used to compare the values of CPUEn and CPUEb, which were transformed (ln+1) to meet the assumptions of normality and homogeneity of variance and were tested, respectively, by the Shapiro-Wilk's and Levene tests.

Results

Fish assemblage composition and structure

During the study, 6,047 individuals were captured with a total biomass of 399,211.6 g. Twenty species were documented, belonging to sixteen genera, ten families and three orders (Table 1). The order Characiformes was the most representative with respect to the number of species

Table 1. Codes for species definition, scientific names and respective common names, abundance of individuals (N) and biomass (B), total, per year and per season of the year, of the species captured in the Santa Cruz Reservoir, Apodi/Mossoró River.

Code	Taxonomic Group	Vulgar names		Year 2010		Year 2011	
			N(B) total	Rainy N(B)	Dry N(B)	Rainy N(B)	Dry N(B)
	CHARACIFORMES						
	Characidae						
sp01	*Astyanax fasciatus*	Lambari; piaba	40(252.8)	28(180.3)	8(52.5)	-	4(19.9)
sp02	*Astyanax* gr. *bimaculatus*	Lambari, piaba	73(447.2)	20(159.0)	41(225.5)	-	12(62.6)
sp03	*Moenkausia dichroura*	Lambari corintiano	1,939(11,033.9)	1,342(7,387.6)	361(2,241.0)	3(62.8)	227(1,344.4)
sp04	*Moenkausia costae*	Piaba	202(894.3)	50(213.2)	139(621.0)	3(14.0)	10(46.13)
sp05	*Triportheus signatus*	Sardinha	518(32.205,2)	105(5,410.2)	87(5,138.7)	135(9,721.1)	191(11,935.1)
	Prochilodontidae						
sp06	*Prochilodus brevis*	Curimatã	32(8,382.6)	8(2,337.0)	3(1,400.0)	9(2,692.0)	12(1,653.6)
	Curimatidae						
sp07	*Curimatella lipidura*	saguiru	1,413(59,276.8)	254(9,218.6)	214(9,118.4)	803(34,192.6)	142(6,747.5)
	Anostomidae						
sp08	*Leporinus piau*	Piau três pintas	119(18,716.7)	16(4,021.0)	6(1,541.8)	33(6,593.1)	64(6,560.8)
sp09	*Leporinus taeniatus*	Piau	2(70.6)	-	-	-	2(70.6)
	Erythrinidae						
sp10	*Hoplias* gr. *malabaricus*	Traíra	112(48,201.9)	29(13,937.0)	19(9,730.8)	28(11,341.1)	36(13,192.9)
	SILURIFORMES						
	Auchenipteridae						
Sp11	*Parauchenipterus galeatus*	Cangati	155(19,287.9)	51(7,027.0)	27(3,366.3)	57(6,612.5)	20(2,281.9)
	Heptapteridae						
Sp12	*Pimelodella* sp.	Anequim	1(8.0)	1(8.0)	-	-	-
	Loricariidae						
Sp13	*Hypostomus* cf. *papariae*	Cascudo	496(85,822.4)	113(20,765.0)	71(13.254.9)	180(28,540.7)	132(23,261.9)
sp14	*Loricariichthys derbyi*	Cascudo Chinelo	34(2,451.2)	11(1,174.0)	5(503.5)	10(380.0)	8(393.6)
	PERCIFORMES						
	Sciaenidae						
Sp15	*Plagioscion squamosissimus**	Pescada	759(93,794.2)	346(40,917.3)	169(15,694.8)	168(22,947.4)	76(14,234.7)
	Cichlidae						
Sp16	*Cichlassoma orientale*	Acará	3(791.8)	-	1(299.8)	1(222.3)	1(269.5)
Sp17	*Cichla monoculus**	Tucunaré	95(12,806.7)	13(1,080.7)	38(5,626.9)	21(2,567.6)	23(3,531.4)
Sp18	*Crenicichla menesezi*	Jacundá	49(1,836.2)	12(481.0)	22(743.0)	8(182.2)	7(429.8)
Sp19	*Oreochromis niloticus**	Tilápia, Pilato	4(2,395.0)	-	3(1,453.4)	1(938.6)	-
Sp20	*Astronotus ocellatus**	Cará	1(535.3)	-	-	1(535.3)	-

*introduced species.

with ten documented species. Four introduced species were recorded, all of which belonged to the order Perciformes: *P. squamosissimus* (Sciaenidae), *C. kelberi*, *O. niloticus* and *A. ocellatus* (Cichlidae). The families Characidae and Cichlidae had the highest number of species, with five species captured. However, the family Characidae was the most abundant with 2,772 individuals, which represented 45.8% of all of the individuals captured (Figure 2).

The number of species estimated by the jackknife method was S = 23 (19-26, 95% CI). The species abundance curve (Whittaker plot), represented in decreasing order, showed that *M. dichroura* (sp04), *C. lepidura* (sp07), *P. squamosissiumus* (sp16), *T. signatus* (sp05) and *Hypostomus* cf. *paparie* (sp13) were the most abundant species, and *O. niloticus* (sp19), *C. orientale* (sp16), *Leporinus* sp. (sp09), *Pimelodella* sp. (sp12) and *A. ocellatus* (sp20) were the most rare (Table 1 and Figure 3). The species-abundance model that best fit the data was the log-normal distribution ($c^2 = 7.066 < c^2_{0.05:5} = 11.07$), which estimated the number of species in the assemblage as S* = 20.8.

Diversity: spatial and temporal patterns

In the spatial analyses, the highest values of diversity and equitability were obtained at sites 4 (H' = 2.398 bits/ind and J = 0.885) and 1 (H' = 2.147 bits/ind and J = 0.837). The lowest diversity and equitability values were found at sites 8 (H' = 1.641 bits/ind and J = 0.579) and 7 (H' = 1.582 bits/ind and J = 0.558 (Figure 4). In the temporal analyses, the highest diversity and equitability values were found during the dry season: dry/2010, H' = 2.107 bits/

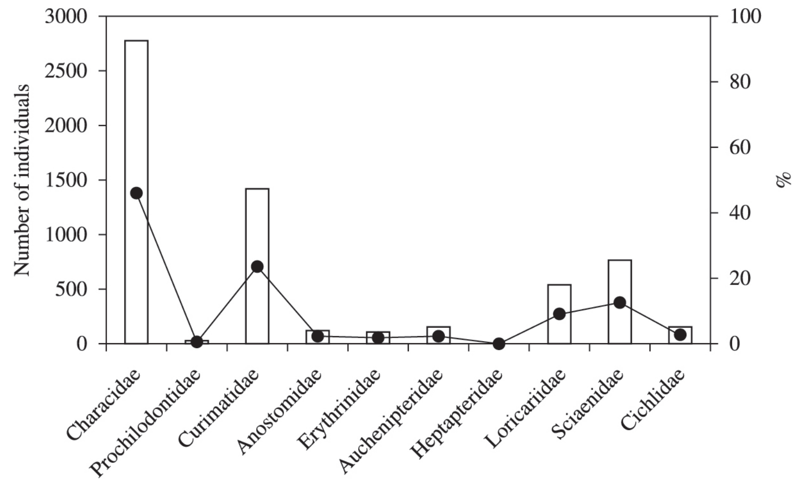

Figure 2. Number (bars) and relative frequency (solid line) of individuals captured by family in the Santa Cruz Reservoir, Apodi/Mossoró River.

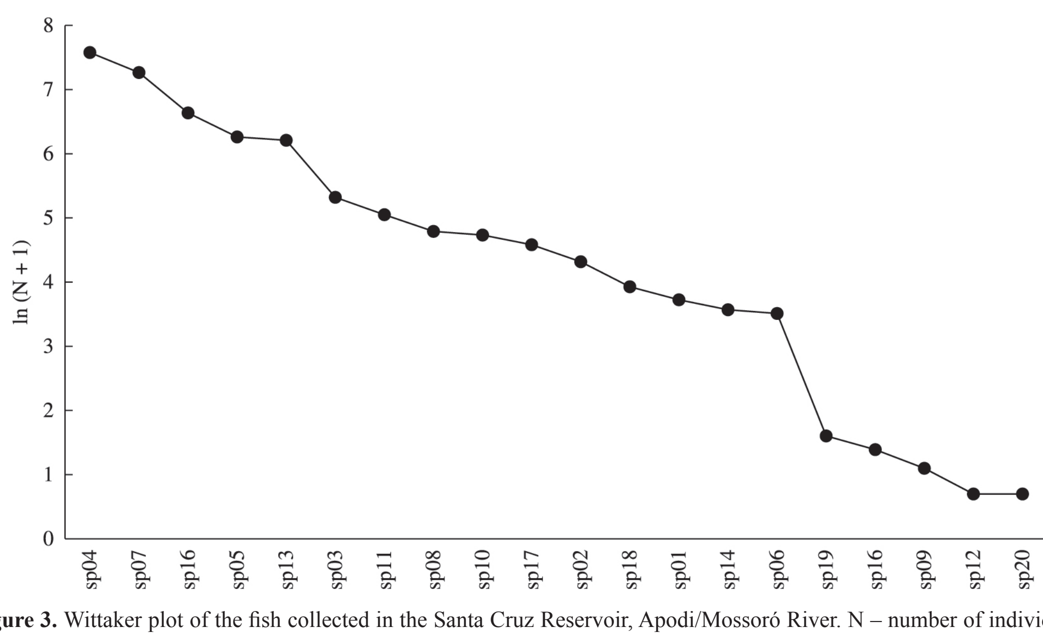

Figure 3. Wittaker plot of the fish collected in the Santa Cruz Reservoir, Apodi/Mossoró River. N – number of individuals per species.

ind and J = 0.743; dry/2011, H' = 2.260 bits/ind and J = 0.762; rainy/2010, H' = 1.556 bits/ind and J = 0.564; H' = 1.555 bits/ind and J = 0.561 (Figure 5). The two-way ANOVA indicated no significant differences (Table 2).

Figure 6 shows the temporal variation in rainfall in the municipality of Apodi and the level of the Santa Cruz Reservoir. The Spearman correlation analysis between diversity and rainfall was significantly negative (r_s = –0.826, $p<0.05$), whereas there was no correlation with the level of the reservoir (r_s = –0.514, p=0.265).

The cluster analysis between the sampling sites determined two separate groups (Figure 7). Group 1 consisted of sites 7 and 8, which were located at the mouth of the Apodi/Mossoró River in the Santa Cruz Reservoir, and group 2 consisted of the rest of the sampling sites.

Spatial and temporal catch per unit effort (CPUE)

The greatest spatial measures of CPUEn and CPUEb were obtained at sites 7 and 8, and the greatest temporal measurements of CPUEn and CPUEb were obtained during the rainy season (Figures 8a, b). The two-way ANOVA indicated a significant difference ($p<0.05$) between the sites and between the seasons and in the interaction with CPUEn, due to high capture recorded in sites 7 and 8 in the rainy season of 2010. For the CPUEb data, the two-way ANOVA was significant ($p<0.05$) between sites and seasons but was not significant for the interaction between the two (Table 3).

Discussion

Fish assemblage composition and structure

The composition of the ichthyofauna of the Santa Cruz reservoir followed the pattern of reservoirs in Brazil and other countries; it consists of a combination of species present in the dammed river and introduced species, of small and medium size (Fernando and Holčík, 1991; Agostinho et al., 2007). Of sixteen the native species observed in this study, fourteen are documented for the

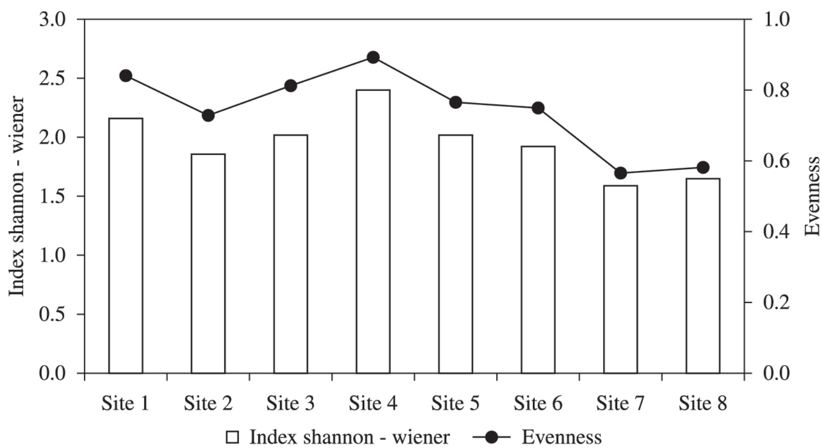

Figure 4. Shannon-Wiener diversity index (bars) and equitability (solid line) for each sampling site in the Santa Cruz Reservoir, Apodi/Mossoró River.

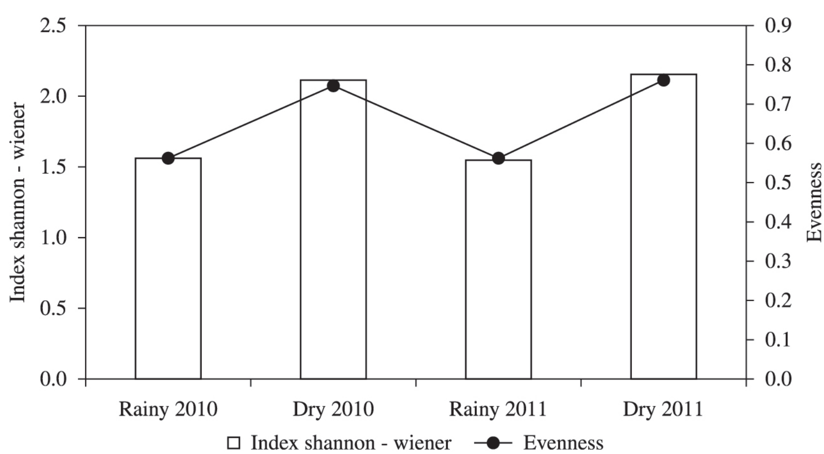

Figure 5. Shannon-Wiener diversity index (bars) and equitability (solid line) for each season of the year in the Santa Cruz Reservoir, Apodi/Mossoró River.

Table 2. Result of the two-way ANOVA for the data of Shannon-Wiener diversity index in the Santa Cruz Reservoir, Apodi/Mossoró River.

Effect	d.f	MS	F	p
Site	7	0.06	0.765	0.620
Season	3	0.02	0.320	0.811
Site x Season	21	0.12	1.410	0.188
Error		0.08		

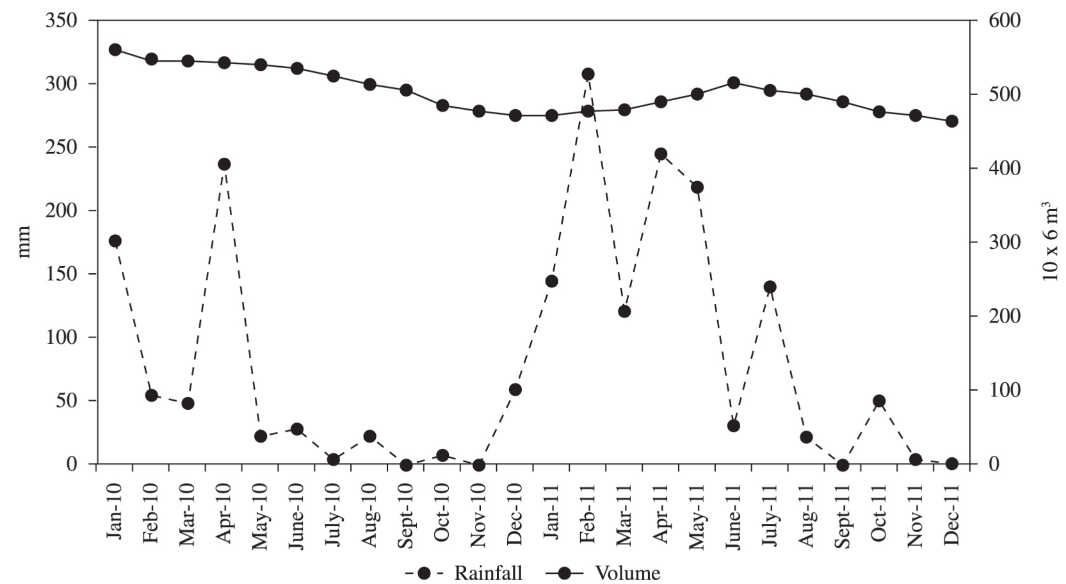

Figure 6. Rainfall data for the municipality of Apodi and volume of the Santa Cruz Reservoir in the Apodi/Mossoró River during the study period. Source: rainfall – EMPARN; Reservoir volume – SEMARH

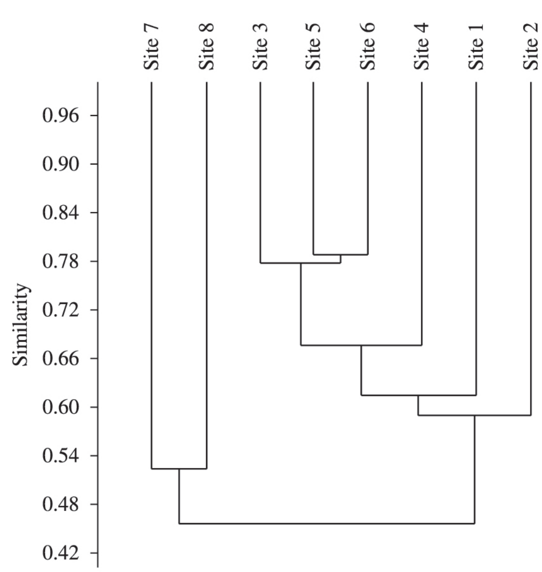

Figure 7. Dendrogram of the sampling sites grouped according to numerical abundance of the fish species in the Santa Cruz Reservoir, Apodi/Mossoró River (r_{coph} = 0.88).

Apodi/Mossoró River in the urban stretch of the river in the municipality of Mossoró, which is approximately 80 km downstream from the reservoir (Gavilan-Leandro, 2003), or were documented in other rivers of the Eastern Northeast Atlantic basin, where the Apodi/Mossoró River is located (Rosa et al., 2003). Thus, these species probably occurred in the stretch where the Santa Cruz Reservoir is located before the dam was built. Some species were widely introduced in northeastern Brazil after the 1950s in public reservoirs by the National Department of Works Against Droughts (Departamento Nacional de Obras Contra as Secas – DNOCS) with the goal of increasing recreational fishing and small local ponds and include such species as *P. squamosissimus*, *Cichla monoculus* and *O. niloticus* (Fontenele and Peixoto, 1978; Gurgel and Oliveira, 1987; Leão et al., 2011). Given that it is a recent reservoir and given the extensive knowledge of damage that introduced species cause to the environment, these species probably invaded the Santa Cruz Reservoir through escape and/or inundations of small private ponds during reservoir filling and/or illegal introduction because there are no documented introductions of these species into the reservoir. These

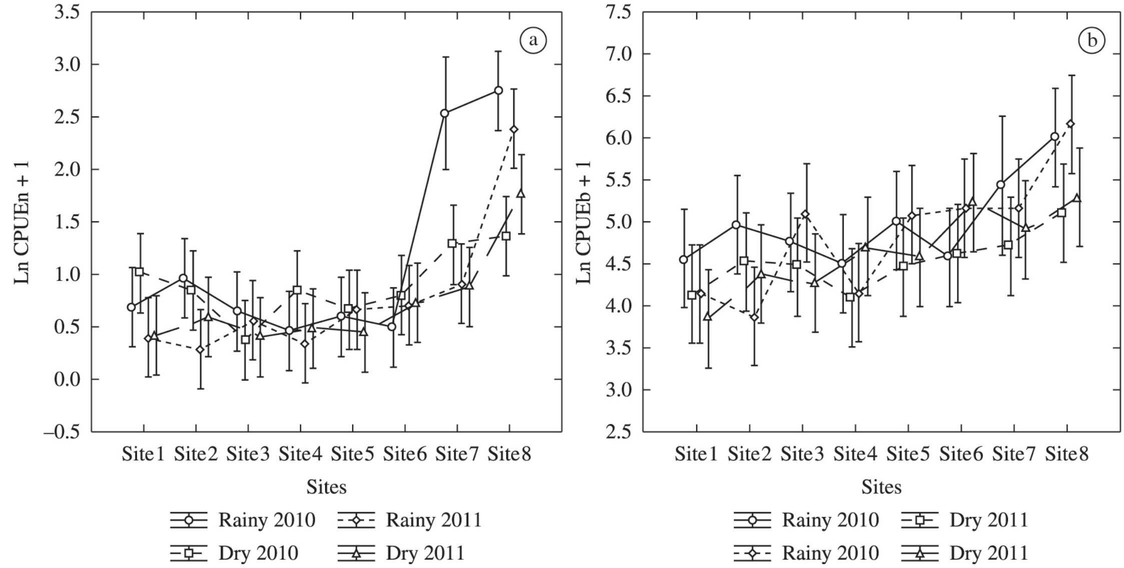

Figure 8. Spatiotemporal variation of the data of capture per unit effort (CPUE) transformed by Ln (x+1). a) Number (CPUEn) and b) biomass (CPUEb) in the Santa Cruz Reservoir, Apodi/Mossoró River.

Table 3. Results of the two-way ANOVA for the transformed data of the catch per unit effort (CPUE) by number (CPUEn) and biomass (CPUEb) in the Santa Cruz Reservoir, Apodi/Mossoró River.

Variable	Effect	d.f	MS	F	p
Ln (CPUEn +1)	Site	7	2.42	35.65	<0.001
	Seasons	3	0.51	7.59	<0.001
	Site x seasons	21	0.23	3.43	<0.001
	Error	31	0.06		
Ln (CPUEb +1)	Site	7	1.69	10.32	<0.001
	Seasons	3	0.65	3.95	0.019
	Site x seasons	21	0.21	1.28	0.256
	Error	31			

CPUEn: Shapiro-Wilk's test, p=0.641; Levene test, p=0.701. CPUEb: Shapiro-Wilk's test, p=0.598; Levene test, p=0.550.

results suggest that *P. squamossisimus* and *C. monoculus* are established in the reservoir and perform all stages of their life cycles in this ecosystem, unlike *O. niloticus* and *A. ocellatus*, which are not established in the reservoir. However, the expansion of tank aquaculture activities in the reservoir and the eventual escape of individuals during all stages of management of this activity have led *O. niloticus* to be a potential invader of this ecosystem, which may cause negative effects on the reservoir (Attayde et al., 2007). Two species were documented for the first time in the Apodi/Mossoró River and in the Eastern Northeast Atlantic basin: *M. dichrora* and *L. taeniatus.* Given that these species have been documented in the rivers of other watersheds in northeastern Brazil (Rosa et al., 2003), we believe that the absence of these species is related to the lack of ichthyofauna monitoring in the Apodi/Mossoró River.

Studies in reservoirs have shown that some species of the family Characidae are abundant in reservoirs, mainly the species known as "lambaris" and/or "piabas", especially in the years following dam construction (Agostinho et al., 1999). *M. dichroura,* which was the most abundant Characidae, is a small fish with high feeding flexibility that feeds primarily on aquatic and terrestrial insects (Silva and Hahn, 2009) and is able to complete its life cycle in lentic environments (Cassimiro et al., 2011). These characteristics probably favour the high abundance of this species. Other Characidae species, such as *M. costae*, *A. bimaculatus* and *A. fasciatus*, were moderately abundant.

This study documented 20 species in the Santa Cruz Reservoir. This value was similar to the values estimated by the jackknife and log-normal methods (23 and 20.8 species, respectively). Brazilian reservoirs are characterised by low species richness (Agostinho et al. 2008), with the main reason being that the Brazilian ichthyofauna has few species adapted to the lentic environments characteristic of reservoirs (Fernando, 1992). The number of species documented in the Santa Cruz Reservoir corresponds to the number of species documented in Brazilian hydroelectric reservoirs (Agostinho et al. 2007).

The log-normal model of species abundance was the model that best fit the data of the Santa Cruz Reservoir. In this model, most of the species were moderately abundant and coexisted under conditions of partial competition instead of direct competition with adaptations that promoted niche differentiation without competitive exclusion (Magurran, 1988). Thus, species that occupy the same trophic guild are likely to be separated by space and occupy different areas of the reservoir or have a distinct seasonal competitive capacity that favours coexistence with population fluctuations throughout the year. Furthermore, it is expected that the species have smaller ecological niches because they are more specialised. Further investigations are necessary to confirm these hypotheses. Other fish assemblies in Brazilian rivers and reservoirs have also been fit to the log-normal model (Baginski et al., 2007; Smith and Petrere Junior, 2008; Smith et al., 2009). Although the results should be analysed with caution, the absence of high dominance by a few species in the Santa Cruz Reservoir suggests that this ecosystems does not show high levels of other anthropogenic disturbances, such as organic pollution.

Diversity: spatial and temporal patterns

Reservoirs can be spatially separated into three different compartments – fluvial, transition and lacustrine – that have different limnological characteristics and may influence the spatial distribution of fish in the reservoirs (Agostinho et al., 1999). Little is known about the limnological dynamics and spatial compartmentalisation of the reservoirs of northeastern Brazil, which are mostly formed by intermittent rivers. The first limnological studies of the Santa Cruz Reservoir showed that the reservoir had only two compartments, specifically, fluvial and lacustrine, which could vary in extent depending on the season (rainy or dry) (Henry-Silva et al., 2013). According to these authors, sampling sites 7 and 8 of the current study would be in the fluvial compartment of the reservoir, while the rest of the sampling sites would be in the lacustrine compartment. The cluster analysis divided the fish assemblage of the Santa Cruz Reservoir into two groups: the first consisted of the sites in the fluvial compartment, and the second consisted of the sites of the lacustrine compartment. Furthermore, the sites in the fluvial compartment had lower values of equitability and diversity, which was significantly different compared with the sampling sites of the lacustrine compartment. Based on these results, it is evident that the ichthyofauna of the fluvial and lacustrine compartments differed in their numerical composition and diversity. Limnological variables strongly influence the structure of ichthyofauna in reservoir environments (Suzuki et al., 1997), and the different limnological characteristics between the fluvial and lacustrine compartments of the Santa Cruz Reservoir were probably important factors in the spatial structure of the ichthyofauna, although other factors should not be overlooked.

Although there was no statistical difference, the spatial pattern of diversity found in the Santa Cruz Reservoir diverges from the patterns of reservoirs in other regions of Brazil, where the highest values of numerical diversity occur in the fluvial compartments (Araújo and Santos, 2001; Oliveira et al., 2004; Britto and Carvalho, 2006; Carvalho et al., 1998; Smith and Petrere Junior., 2008; Terra et al., 2010). The high dominance by the species *C. lepidura*, *P. squamosissimus*, *M. dichroura*, *T. signatus* and *L. piau* in the fluvial compartment reduces the values of the Shannon-Wiener diversity index and equitability in the Santa Cruz Reservoir. Because these species are not migratory, with the exception of *L. piau*, it is reasonable to propose that the fluvial compartment provides better conditions for these species to survive and complete their life cycles. In contrast, the species dominance was lower in the lacustrine compartment, and the species *H.* cf. *paparie* and *P. galeatus* were the most abundant.

In the temporal analyses, the numerical diversity was not significantly different in the Santa Cruz Reservoir, although greater diversity and equitability during the dry periods, but there was a significant negative correlation between diversity and rainfall. Temporal variation in the fish assemblies of reservoirs is low because the composition of species in these environments is formed by species that are tolerant of the changes caused by the dam (Matthews, 2000). Studies in several hydroelectric reservoirs have not found different values of diversity between the rainy and dry seasons (Castro, 1997; Silva et al., 2006; Smith and Petrere Junior, 2008). The high dominance by certain species in the Santa Cruz Reservoir, such as *H.* cf. *paparie*, *P. galeatus*, *C. lepidura*, *M. dichroura*, *P. squamosissimus* and *T. signatus*, could have led to the low level of diversity observed during the rainy period.

Catch per unit effort (CPUE): spatial and temporal patterns

The CPUEn and CPUEb values were significantly different along the spatial gradient, and the highest values were found in the fluvial sampling sites (sites 7 and 8). Similar results were found in reservoirs in other regions of Brazil (Carvalho et al., 1998; Araújo and Santos, 2001; Britto and Carvalho, 2006; Petesse et al., 2007; Terra et al., 2010). The species that contributed the most to the high CPUE values in the fluvial compartment sampling sites were *C. lepidura*, *M. dichroura*, *P. squamosissimus* and *T. signatus*. Several reasons that may explain the high capture of species in the fluvial compartment are i) a greater number of micro-habitats, which offer species more resources such as available prey and shelter from predators and ii) better environmental conditions for species to perform vital activities.

In the temporal approach, the CPUEn and CPUEb values were higher during the rainy periods, and these results are in agreement with those found in other reservoirs (Terra et al., 2010; Agostinho et al., 2004). In freshwater environments, even in artificial environments, such as reservoirs, inundation of the adjacent terrestrial areas during the rainy period could cause alterations in the abundance of fish populations, due to a greater availability of food resources for the fish (Lowe-McConnel, 1999), that may also explain the significant result for the interaction site x season for CPUEn. In the Santa Cruz Reservoir, *A. fasciatus*, *H.* cf. *paparie*, *P. galeatus*, *C. lepidura*, *M. dichroura*, *P. squamosissimus* and *T. signatus* increased in abundance during the rainy periods. These species are characterised as opportunistic and have high dietary flexibility (Hahn and Fugi, 2007), and in the Santa Cruz Reservoir, the inundation of the adjacent terrestrial areas during the rainy season probably benefits these species, which can efficiently explore the newly available and increased resources.

According to the results of this study, the Santa Cruz Reservoir has similarities and differences from reservoirs in other region of Brazil formed by perennial rivers. The number of species, the composition of the ichthyofauna and the spatial and temporal patterns in CPUEn and CPUEb found in the Santa Cruz Reservoir were similar to other reservoirs. The spatial structure of the fish assemblage in the Santa Cruz Reservoir was also similar to other Brazilian reservoirs with differences between the fluvial and lacustrine compartments. For the spatial and temporal patterns in diversity, the results observed in the Santa Cruz Reservoir were different because a greater diversity in other Brazilian reservoirs is found in the fluvial regions but not in the lacustrine regions, as was found in the present study. Furthermore, the results suggest that biotic factors, such as competition and limnological characteristics of the reservoir, were important in the spatial structure of the fish assemblage of the Santa Cruz Reservoir, although more specific studies are necessary to address these questions further.

Acknowledgements – We thank the financial support agencies, the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ) and Fundação de Apoio a Pesquisa do Estado do Rio Grande do Norte (FAPERN), agreement nº 68.0025/2005/7– CNPq/FAPERN.

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