Abiotic variability among different aquatic systems of the central Amazon floodplain during drought and flood events

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Abstract

This paper examines water properties from lakes, (depression lakes, sensu Junk et al., 2012), channels (scroll lakes with high connectivity, sensu Junk et al., 2012) and paleo-channels (scroll lakes with low connectivity-sensu Junk et al., 2012, locally called *ressacas*) located in Mamirauá Sustainable Development Reserve, in Central Amazon floodplain, Amazonas, Brazil. We analysed surface temperature, conductivity, pH, dissolved oxygen, turbidity, transparency, suspended inorganic and organic matter, chlorophyll-a, pheophytin, total nitrogen, total phosphorus, organic and inorganic carbon in 2009 high water phase, 2009 and 2010 low water phases. Multivariate statistical analyses of 24 aquatic systems (6 *ressacas*, 12 lakes and 6 channels, 142 samples) were applied to the variables in order to: 1) quantify differences among aquatic system types; 2) assess how those differences are affected in the different phases of the hydrological year. First, we analysed the entire set of variables to test for differences among phases of the hydrological year and types of aquatic systems using a PERMANOVA two-way crossed design. The results showed that the all measured limnological variables are distinct regarding both factors: types of aquatic systems and hydrological phases. In general, the magnitude and amplitude of all variables were higher in the low water phase than in the high water phase, except for water transparency in all aquatic system's types. PERMANOVA showed that the differences between aquatic system's types and hydrological phases of all variables were highly significant for both main factors (type and phase) and for the type x phase interaction. Limnological patterns of Amazon floodplain aquatic systems are highly dynamic, dependent on the surrounding environment, flood pulse, main river input and system type. These patterns show how undisturbed systems respond to natural variability in such a diverse environment, and how distinct are those aquatic systems, especially during the low water phase. Aquatic systems in Mamirauá floodplain represent limnological patterns of almost undisturbed areas and can be used as future reference for comparison with disturbed areas, such as those of the Lower Amazon, and as a baseline for studies on the effects of anthropogenic influences and climate change and on Amazon aquatic ecosystem.

Keywords: limnology, natural aquatic systems, Central Amazon, Mamirauá Reserve.

Variabilidade abiótica entre os diferentes sistemas aquáticos da planície de inundação da Amazônia central durante eventos de seca e cheia

Resumo

Esse trabalho investiga as propriedades da água de lagos (lagos de depressão, sensu Junk et al., 2012), canais (*scroll lakes* com alta conectividade, sensu Junk et al., 2012) e paleo canais *(scroll lakes* com baixa conectividade - sensu Junk et al., 2012, localmente chamados de *ressaca*) localizados na Reserva de Desenvolvimento Sustentável Mamirauá (RDSM), na planície de inundação da Amazônia Central, Amazonas, Brasil. Analisaram-se temperatura, condutividade, pH, oxigênio dissolvido, turbidez, e transparência da água na superfície e coletaram-se amostras de água na superfície para a determinação de material orgânico e inorgânico em suspensão, clorofila-a, feofitina, nitrogênio e fósforo total, carbono orgânico e inorgânico dissolvido, em duas fases da hidrógrafa, água alta em 2009, e água baixa em 2009 e 2010. Análises de estatística multivariada de 24 sistemas aquáticos (6 *ressacas*, 12 lagos e 6 canais, 142 amostras) foram realizadas para: 1) quantificar as diferenças entre os tipos de sistemas aquáticos; 2) determinar como essas diferenças são afetadas nas diferentes fases do ano hidrológico. Primeiramente foram analisadas todas as variáveis para testar as diferenças entre as fases do ano hidrológico e dos tipos de sistemas aquáticos utilizando o teste pareado cruzado PERMANOVA. Os resultados mostraram que todas as variáveis limnológicas medidas são distintas em

relação a ambos os fatores: tipos de sistemas aquáticos e fases da hidrógrafa. Em geral, a magnitude e amplitude de todas as variáveis foram maiores na fase seca do que na cheia, com exceção da transparência da água em todos os tipos de sistemas aquáticos. Os resultados da PERMANOVA mostraram que as diferenças entre os tipos de sistemas aquáticos e as fases da hidrógrafa para todas as variáveis foram altamente significativas para ambos os fatores (*tipo e fase*) e ainda para a interação *tipo x fase*. Os padrões limnológicos dos sistemas aquáticos da planície de inundação Amazônica são altamente dinâmicos, dependente do ambiente ao redor, do pulso de inundação, do rio principal e do tipo de sistema. Os sistemas aquáticos da planície de inundação de Mamirauá representam os padrões limnológicos de áreas não perturbadas e podem servir como futura referência para comparação com as propriedades dos sistemas aquáticos de áreas perturbadas, como as do Baixo Amazonas. Podem ser também utilizados como linha de base para estudos dos impactos antropogênicos e das mudanças climáticas sobre os ecossistemas aquáticos Amazônicos.

Palavras-chave: limnologia, sistemas aquáticos naturais, Amazônia Central, Reserva Mamirauá.

1. Introduction

The Amazon floodplain composes a mosaic of forests, lakes, channels, and paleo-channels seasonally flooded by the main rivers (Junk, 1997). The paleo-channels are remnants of stream channels, which have been buried by sediments and covered by vegetation, or even partially filled by recent sedimentation, becoming shallower. This formation is very common and widespread in the Amazonian "várzea", and can become completely dry during the low water period. These aquatic systems provide a variety of habitats for many animal and plant species (Junk and Silva, 1997) acting as food sources, nesting and refuge for many fish species (Sanchez-Botero and Araújo-Lima, 2001).

The periodic flooding changes the proportion of suspended and dissolved component inputs into floodplain aquatic systems and modifies its physical-chemical conditions (Melack and Forsberg, 2001). Besides that, due to sedimentation and particulate matter transport, those systems suffer constant change of their morphometric features (along with limnology and hydrology characteristics) (Junk et al., 1989).

During the high water phase, the water chemistry tends to be more homogeneous; all the lakes become interconnected with channels and rivers due to the large volume of water entering the floodplain (Thomaz et al., 2007). In contrast, during the low water phase, the lakes become isolated with poor or no connection to channels and rivers turning into actual lentic systems, influenced by their local immediate environment. In spite the fact that Affonso et al. (2011) described differences in lake limnology between river margins in this study area, the differentiation among lakes regarding water properties was much larger during the low water phase. This pattern has already been documented in different types of floodplain lakes in South America (Carvalho et al., 2001), and specifically in floodplain lakes at Pantanal (Abdo and Silva, 2004), and at Amazon region (Forsberg et al., 1988; Barbosa et al., 2010; Almeida and Melo, 2009; Brito et al., 2014). Several studies carried out in Mamirauá lakes not included in the present study (Henderson, 1999; Queiroz, 2007). Affonso et al. (2011) and Pedro et al. (2013) noted similar patterns for conductivity, temperature, dissolved oxygen and water transparency, with lower variable values during flood and higher variable values during drought (except for water transparency). Several studies assessed the spatial and temporal variations

of limnological features of Amazonian floodplain lakes (Melack and Fisher, 1990; Moreira-Turcq et al., 2003; Aufdenkampe et al., 2007; McClain and Naiman, 2008; Almeida and Melo, 2009; Affonso et al., 2011). However, other aquatic systems such as channels and paleo-channels (Junk, 1997), which are the dominant feature of the Mamiraua floodplain, have been missing in the literature.

In this paper, we examined water properties of different aquatic systems which were operationally divided into lakes, channels, and the local called *ressacas* located in Mamirauá Sustainable Development Reserve, in Central Amazon floodplain, Amazonas, Brazil. According to Castello (2008) *ressacas* are shallow water bodies with large and open mouths that may dry up during the dry season, whereas lakes and channels retain water throughout the hydrological year. Those aquatic system types are described in methods and can be roughly related to the lake typology proposed by Junk et al. (2012). What is named Lake in this paper actually refers to "Depression Lakes" which are nearly round and oval lakes (sometimes a coalescence of depressions) which occupy depressions on the floodplain an can be more or less connected to main channels and rivers. Lakes named as channel lakes and *ressacas* in the present paper refers to the Scroll lake type, which is related to the scroll-bar crests and swale topography and occupies ancient active channels in the floodplain (Junk et al., 2012). The channels are Scroll lakes with higher connectivity to flowing channels and rivers and *ressacas* are Scroll lakes with smaller connectivity, which during the low water phase can become swamps. This lake classification was carried out in order to identify how lake morphology and origin affects chemical and physical properties of aquatic system in two hydrological phases: high and low water. For that, chemical and physical variables measured in 24 aquatic systems (6 *ressacas*, 12 lakes and 6 channels, a total of 142 samples) (2009 and 2010) were submitted to statistical analyses in order quantify the differences among aquatic system types and to assess how those differences are affected at different hydrological phases.

2. Material and Methods

2.1. Study area and sampling campaign

The study area is located in Mamirauá Sustainable Development Reserve (MSDR), in western Amazon, near Tefé municipality (570 km distant from Manaus), in

Amazonas State. This region is a floodplain formed in the confluence between Japurá and Solimões rivers and subjected to an average annual variation of 10 m in the water level measured within the reserve (Ramalho et al., 2009). During the high water, channels, lakes and rivers remain interconnected, whereas during the low water, only the main river and channels keep their connection (Ayres, 1993; Ramalho et al., 2009; Affonso, 2012). The high water phase starts generally in May and finishes in mid-July, when the highest water levels are registered. The receding water season extends from July to September, when the low water season starts, until to reach the lowest level in the end of October. With the beginning of the rainy season, the water level starts a slow increase reaching its highest rate when the increased water level from Solimões is under influence of the Andes melting and precipitation (Junk et al., 1989). The rainy season is characterized by low solar radiation due to high cloud cover (Ceballos et al., 2004; Affonso, 2012).

The area is characterized by high temperatures with average annual climatological normal ranging from 28 °C to 30 °C, with maximum monthly normal ranging from 33 °C to 35 °C in August and minimum monthly normal ranging from 20 °C to 22 °C in June and July (INMET, 2011). The highest precipitations are concentrated between December and May (Ramalho et al., 2009) when it can reach climatological normal of a total of 300 mm during the wettest years. In average, during the rainy season, there are 20 days during which daily precipitation exceeds 1 mm. Data from MSDR indicates that yearly precipitation in the reserve is in average 3000 mm. The lakes sampled in this study are distributed within the floodplain stretched between Japurá and Solimões Rivers and consists of white water rivers ("várzea") habitats. Successive erosion and deposition processes along the geological history of the floodplain created a complex mosaic of permanent and temporary lakes which are well described in Junk et al. (2012). The annual variation of water level which in normal years reaches 10 m responds for various degrees of connectivity between the different lakes and the main rivers (Ayres, 1993; Henderson, 1999; Queiroz, 2005; Queiroz, 2007; Ramalho et al., 2009).

There are three main aquatic system types in the Mamirauá reserve: lakes, channels and *ressacas*. The channels transport water from the rivers and from main channels to lower order aquatic environment within the floodplain. The lakes vary in shape and size, and retain water and lose connection to the main channel during low water phase. "Ressaca" is a shallow channel, which is flooded during the high water phase and may or may not dry completely during the low water phase (Affonso, 2012).

We carried out three sampling campaigns, two in 2009 during both high (5/20 to 06/11) and low (11/11/ to 12/10) water level, and one in 2010 during the low (08/29 to 09/07) water level (Figures 1 and 2). These hydrological phases were selected to represent extremes of water level in the region. Initially, the sampling campaigns were

carried out during the 2009 hydrological year, but as in 2010, there were early signs of an extreme event of drought in the Amazon floodplain (Marengo et al., 2011; Marengo et al., 2013), another mission was included to assess the impact of those extreme events on the limnology of the different lake types.

According to the hydrological monitoring data system of the Eastern Amazon (CPRM, 2009; IDSM, 2011) the hydrological period of 2008/2009 corresponded to the second highest record (38.33 m above sea level) in the historical data (from 1990 to 2010) in the studied area (Ramalho et al., 2009). Therefore, during the campaign of 2009, the sampling sites were subjected to an extreme flooding episode. Furthermore, the 2010 dry season was considered one of the driest, ranking as the fifth low water level observed in the period (Marengo et al., 2013). This paper analyses limnological data acquired during two historical, extreme and opposite events and data acquired during a below average but still normal low water event (Marengo et al., 2011; Marengo et al., 2012; Marengo et al., 2013).

The following variables were measured: water temperature (°C), dissolved oxygen (mg.l⁻¹), turbidity (NTU), electrical conductivity (µS.cm⁻¹) and pH at around 50 cm below the surface using an YSI multi-parameter probe (YSI samples). We also collected water samples for laboratory determination of the following parameters: suspended inorganic and organic matter (mg.l⁻¹); chlorophyll-a (µg.l⁻¹), pheophytin (µg.l⁻¹), total nitrogen (mg.l⁻¹), total phosphorus (µg.l⁻¹), organic and inorganic carbon (mg.l⁻¹).

For chlorophyll-a, pheophytin and suspended inorganic and organic matter, water samples were filtered in the field (Whatmann GF / C fiberglass filter (0.5-0.7 mm)) and stored in silica gel at 0 °C until further analysis in laboratory according to Nush (1980) and Wetzel and Likens (1991) methodology, respectively. Total phosphorus and nitrogen were determined according Valderrama (1981) and Golterman et al. (1978), in that order, and organic and inorganic carbon was according to Eaton et al. (1995).

Sample size varied in the different hydrological phases and among aquatic systems types (Table 1) due to changes in open water depth.

Table 1. Number of samples per aquatic system types in different phases of the hydrograph.

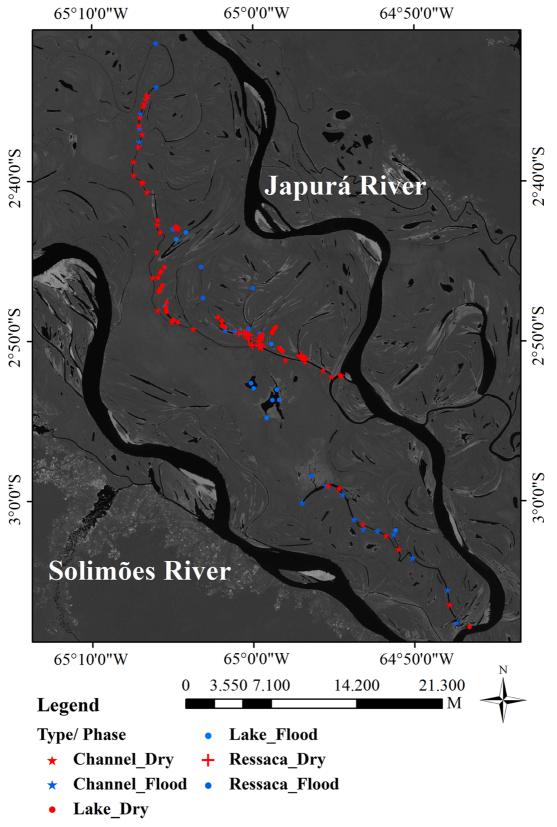| Hydrograph phase/date	High water	Low water
Aquatic system type	05/20/09 to 06/11/09	11/11/09 to 12/10/09 and 08/29/10 to 09/07/10
Lake	14	38
Channel	17	45
"Ressacas"	10	14
Total	41	116

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Figure 1. Study area and sample points per aquatic system in each hydrological phase. Japurá and Solimões Rivers are shown.

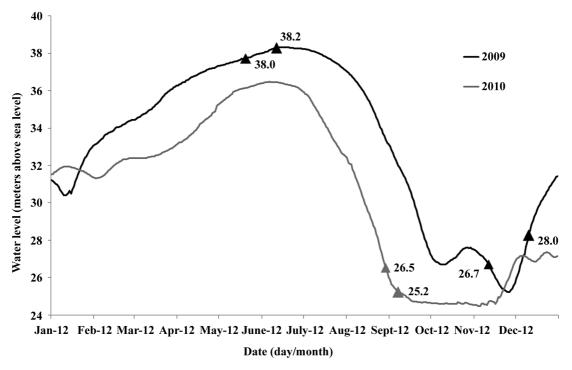*Braz. J. Biol., 2015, vol. 75, no. 4, suppl. 1, pp. S60-S69*

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Figure 2. Water level variation (above sea level) during 2009 and 2010 field campaigns and the respective water level in the beginning and end of each field mission.

2.2. Data analysis

In order to test for differences in the variables as a function of hydrological phases and aquatic systems types PERMANOVA (Permutational Multivariate Analysis of Variance) two-way crossed design (Anderson, 2001) was applied. PERMANOVA is suitable for statistical analysis with different number of samples per station, such as in this study because it calculates a pseudo-F (based on permutations) which is equal to the F statistic of traditional ANOVA and it does not assume the normality of the distribution (Anderson, 2001).

Thus, aquatic system types (with 3 levels: lake (l), channel (c) and *ressaca* (r)) and hydrological year phases (with 2 levels: low and high water phase) were treated as fixed factors to test the statistical significant differences among systems and phases using both, the entire set of variables (multivariate approach) and each variable separately (univariate approach).

Variables were log (x+1) transformed to retain information on relative concentrations but also to reduce differences in scale among the variables. Data was normalized and a resemblance matrix based on the Euclidean distance was performed as part of the statistical test routine. PERMANOVA was performed using 999 permutations of residuals under a reduced model. In addition, significant terms and interactions were examined through pair-wise comparisons to identify which pairs of aquatic environmental types and phases were significantly different.

Differences between aquatic systems types and phases were also examined using a Canonical Analysis of Principal Coordinates (CAP). This is a multivariate constrained ordination technique in which an initial principal coordinate analysis (PCO) is used to reduce the number of axes, followed by a canonical discriminant analysis on the PCO to maximize the separation between predefined groups (in this case: aquatic system type and hydrological phase).

3. Results

The magnitude and amplitude of all variables were higher in the low water phase than in the high water phase, except for water transparency in all the aquatic system types (Table 2). The multivariate analyses indicated that both effects are highly significant (*types*: pseudo-$F = 13.9$, p<0.001 and *phases*: pseudo-$F = 212.8$, p<0.001) and also for their interaction (*type x phase*: pseudo-$F = 13.0$, p<0.001).

All variables displayed significant difference between hydrological phases for all aquatic system type, except for total phosphorus and pH in lakes. However, looking into differences among aquatic system types according to a given hydrological phase, it can be observed that during the high water phase, the mean value of all variables tend to be similar. The amplitude between them is very low, when compared to the low water phase. The mean of the lakes, however were slightly warmer and with higher concentrations of dissolved oxygen, chlorophyll,

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Table 2. Two-way PERMANOVA results on the effects of aquatic system types and hydrological phases on the measured variables in Mamirauá Sustainable Development Reserve.

Variables	Type	Hydrological Phases		High × Low
		Lowwater	High water	
Secchi (m)	Lake	$0.43_{(0.1-1)}$ r*	$1.7_{(0.8-2.4)}$	*
	Channel	$0.40_{(0.15-0.9)}$ r*	$1.7_{(1.0-2.4)}$	*
	Ressaca	$0.14_{(0.05-0.3)}$ l,c*	$1.73_{(1.3-2.8)}$	*
pH	Lake	$7.01_{(6.21-8.52)}$ c*,r*	$6.85_{(6.76-6.96)}$ r*	ns
	Channel	$7.29_{(6.81-8.06)}$ l*	$6.84_{(6.74-6.98)}$	*
	Ressaca	$7.33_{(6.88-8.13)}$ l*	$6.76_{(6.35-6.87)}$ l*	*
Electrical Conductivity ($\mu S.cm^{-1}$)	Lake	$85.21_{(54-123)}$ c*,r*	$115.29_{(105-123)}$ c+	*
	Channel	$231.02_{(78-291)}$ l*,r*	$110.53_{(107-112)}$ l+,r*	*
	Ressaca	$326.89_{(260-378)}$ l*,c*	$116.5_{(112-119)}$ c*	*
Turbidity (NTU)	Lake	$43.19_{(2.7-137.1)}$ r*	$6.33_{(3.1-13.3)}$	*
	Channel	$51.93_{(5.8-224.5)}$ r*	$6.97_{(3.6-13.4)}$	*
	Ressaca	$185.25_{(18.1-565)}$ l*,c*	$7.81_{(3.2-11.9)}$	*
Dissolved Oxygen ($mg.l^{-1}$)	Lake	$5.12_{(2.34-9.18)}$	$2.59_{(1.44-6.98)}$	*
	Channel	$6.12_{(1.86-14.02)}$	$2.3_{(1.4-3.2)}$	*
	Ressaca	$4.55_{(0.72-8.47)}$	$2.04_{(0.86-2.46)}$	+
Temperature (°C)	Lake	$31.52_{(29.89-34.14)}$	$27.27_{(26.7-28.8)}$ c*	*
	Channel	$31.32_{(28.8-33.26)}$	$26.62_{(26.5-27.02)}$ l*r*	*
	Ressaca	$30.76_{(27.98-33.91)}$	$27.06_{(26.6-27.4)}$ c*	*
Suspended Inorganic Material ($mg.l^{-1}$)	Lake	$16.49_{(1.52-73.29)}$ r*	$0.78_{(0.05-2.69)}$	*
	Channel	$17.1_{(2.81-61.43)}$ r*	$0.98_{(0.13-3)}$	*
	Ressaca	$139.83_{(7.82-590.39)}$ l*,c*	$1.02_{(0.21-2.29)}$	*
Suspended Organic Material ($mg.l^{-1}$)	Lake	$19.63_{(4.47-202.96)}$ r+	$1.06_{(0.24-1.7)}$	*
	Channel	$12.28_{(2.31-27.86)}$ r*	$1.3_{(0.8-2)}$	*
	Ressaca	$31.07_{(3.39-77.94)}$ l+,c*	$1.10_{(0.31-1.55)}$	*
Chlorophyll ($\mu g.l^{-1}$)	Lake	$118.68_{(10.48-2061.29)}$ c+	$0.34_{(0.16-0.81)}$	*
	Channel	$198.65_{(23.3-2589.23)}$ l+	$0.26_{(0.11-0.38)}$	*
	Ressaca	$86.99_{(15.42-262.74)}$	$0.26_{(0.13-0.56)}$	*
Pheophytin ($\mu g.l^{-1}$)	Lake	$17.86_{(5.63-95.59)}$	$0.26_{(0.05-0.60)}$	*
	Channel	$16.16_{(1.35-39.91)}$ r*	$0.17_{(0.0-0.42)}$ r+	*
	Ressaca	$28.13_{(8.76-60.27)}$ c*	$0.33_{(0.11-0.64)}$ c+	*
Nitrogen ($mg.l^{-1}$)	Lake	$1.26_{(0.23-10.31)}$ r*	$0.21_{(0.10-0.30)}$ c+	+
	Channel	$1.62_{(0.04-4.07)}$ r*	$0.15_{(0.03-0.25)}$ l*	*
	Ressaca	$2.66_{(1.73-3.76)}$ l*,c*	$0.18_{(0.13-0.31)}$	*
Phosphorus ($\mu g.l^{-1}$)	Lake	$123.78_{(38.05-897.31)}$ c*,r*	$108.14_{(52.94-179.42)}$	ns
	Channel	$230.08_{(89.16-701.81)}$ l*,r*	$102.44_{(52.5-172.5)}$	*
	Ressaca	$461.28_{(161.57-1094.89)}$ l*,c*	$105.41_{(50.68-150.5)}$	+
Dissolved Inorganic Carbon ($mg.l^{-1}$)	Lake	$5.56_{(0.49-10.42)}$ c*,r*	$7.84_{(3.56-9.42)}$ r+	+
	Channel	$22.3_{(6.96-31.6)}$ l*,r+	$7.81_{(6.6-9.1)}$ r*	*
	Ressaca	$29.3_{(24.49-40.04)}$ l*,c+	$9.18_{(8.76-9.58)}$ l+,c*	*
Dissolved Organic Carbon ($mg.l^{-1}$)	Lake	$6.47_{(3.49-10.8)}$ c*,r*	$4.49_{(2.02-5.99)}$	*
	Channel	$14.15_{(1.85-22.94)}$ l*,r#	$5.06_{(3.6-6.3)}$ r+	*
	Ressaca	$16.67_{(11.56-23.39)}$ l*,c#	$4.04_{(3.87-4.38)}$ c+	*

ns = non-significant. # = $p<0.05$. + = $p<0.01$. * = $p<0.001$. Letters indicates significant differences among aquatic system types them (r: ressaca, l: lake, c: channel). High × Low: refer to comparisons among hydrological phases (two-way PERMANOVA, pairwise test). Mean, minimum and maximum values are shown.

nitrogen and phosphorus, but lower turbidity, suspended inorganic and organic matter concentrations during this phase (Table 2).

The two-sample PERMANOVA tests showed that, during the high water, the differences for each variable, among aquatic systems types were statistically significant for pH (*ressaca x lakes*), electrical conductivity (*lake x channel; channel x ressaca*), temperature (*lake x channel; channel x ressaca*), pheophytin (*channel x ressaca*), nitrogen (*lake x channel*), dissolved inorganic (*lake x ressaca, channel x ressaca*) and organic carbon (*channel x ressaca*). The variability during low water phase, however, was much higher between aquatic system types, than in the high water phase. During the low water *ressaca* systems displayed the highest mean values in almost all variables. The lakes, on the other hand, had lower values in the majority of the variables (pH, electrical conductivity, suspended inorganic matter, turbidity, nitrogen, phosphorus and organic and inorganic carbon). Total phosphorus, dissolved inorganic and organic carbon and electrical conductivity showed variation between all aquatic system types (*lake x channel, lake x ressaca and channel x ressaca*).

Figure 3 shows CAP results for all chemical and physical variables for both high and low water phases. CAP 1 showed limnological distinction between low and high water phase samples. High water samples, as mentioned before, are characterized by lower values for all variables in contrast to low water samples which has higher values with the exception of transparency. CAP 2 revealed, the aquatic system type structure within the low water phase, with channel and *ressacas* having higher values than lakes for almost all variables. The graphic clearly shows two clusters, one composed by lakes, and other by both channels and *ressacas*. We drew a black circle in the figure
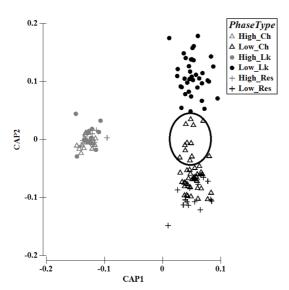
to highlight the channels which, depending of the sampling station location display limnological features resembling those of the lake type. Actually, the channel type of aquatic system during low water occupies a wide range along CAP2, having a clear superposition with *ressacas* and in the other extreme values closer to lakes. Examining those particular samples, they correspond to water bodies that lost their connection with the main rivers during the low water phase, what explain their resemblance with lakes.

4. Discussion

The results showed that the chemical and physical variables displayed large differences between hydrological phases and among aquatic systems. These results are in agreement with results of a comparative study about the effects of water level on selected limnological variables in lakes of eight floodplain systems of South America, including Upper and Middle Paraná River, Amazon River among others (Carvalho et al., 2001). In spite of the fact that the study was based on data gathered in the literature, the authors provided information on the uncertainties related to differences in measurement protocols and other error sources. The authors have reported large differences between water level phases regarding the average values of key variables such as alkalinity, chlorophyll-a, total phosphorus, total nitrogen, oxygen saturation disregarding the different floodplains. According to them, during the low water phase, the coefficient of variation of the limnological variables is much higher than that observed during the high water phase, what supports the hypotheses that it homogenizes the aquatic environment. In a study carried out in the Upper Paraná River floodplain to examine the impact of upstream reservoirs on different types of lakes and channels (Roberto et al., 2009), the authors analyzed sampling series conducted during high water levels of the year 2002 and 2008 and reported that similarity among the floodplain habitats increased during the high water phase. They also reported the trend of decreasing Total phosphorus concentration in lakes during the high water phase. According to them, this was indicated by negative correlations between Paraná river water level and total-P in lakes. They reported a wide range of several limnological variables such as oxygen concentration, alkalinity, total nitrogen among others and attribute that to water-level fluctuations, because they are affected by changes in depth and water velocity.

Similar results were reported by Mayora et al. (2013) in a study carry out to understand spatial variability of phytoplankton and abiotic variables in different phases of the Paraná River hydrology. According to their results, there were significant differences among hydrological phases and sites. Similarly of what was observed in the present study, the highest values of the limnological variables were observed during the low water phase. They observed that the high water had a homogenizing effect on chlorophyll-a, but the same trend was not observed for all limnological variables. Different time lags between the hydrological

Figure 3. Canonical analysis of principal coordinates (CAP) of high and low water samples of lakes (lk), channels (Ch) and ressacas (Rs), in Mamirauá Sustainable Development Reserve.

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pulse and the sedimentological pulse maybe responsible for large differences in turbidity during the high water phase.

Forsberg et al. (1988) sampled 51 lakes located within 5 km from their associated rivers and connected to them during the sampling missions. Among the largest rivers connected to the sampled lakes are Solimões, Negro, Amazonas, Jataí, Juruá, Japurá and Trombetas. Data collections were carried out during high and low water phases, which were roughly define as mid-March and Mid-September respectively. According to their results during the high-water phase, the lake alkalinity was similar to the contributing rivers, except for lakes such as Coari and Tefé, which are characterized by large local drainage basins (larger than 2,500 km^2). At low water, the influence of the rivers on the floodplain lakes properties was reduced. According to the authors, many of the lakes became isolated or drained into the rivers. The alkalinity levels in many lakes were much lower than the rivers, suggesting dilution from local inputs. The alkalinity differences between lakes and parent rivers varied substantially suggesting that local factors were much more important to lake chemistry than the previous input from the rivers.

The concentrations of dissolved nitrogen and total phosphorus declines as the water river enters the lakes at the high water, which may be related to nitrogen uptake by phytoplankton and sedimentation of phosphorus adsorbed in suspended particles. During low water, however, the size of the local drainage affected the patterns of total phosphorus and nitrogen concentration in relation the parent rivers. Other studies (Abdo and Silva, 2004; Almeida and Melo, 2009) and in Mamirauá lakes (Henderson, 1999; Queiroz, 2007; Pedro et al., 2013) although not comparing hydrological phases, their results point to smaller water property variation during high water.

The limnological variability among aquatic system types and among hydrological phase's points out to the complexity of the floodplain environment as pointed out by Mayora et al. (2013). The lakes are influenced by two main rivers, being one under the influence of the northern hemisphere climatic conditions, and one under the influence of the western Amazonia climatic conditions during the sampling campaigns.

Time lags between the Solimões floodpulse and the Japurá may vary inter-annually and increase or decrease the connectivity between the different types of aquatic systems and those parent rivers. Another aspect, to take into consideration, mainly regarding the similarity among lakes during the high water level, is the extreme conditions of flooding during the field mission, when the lakes were submitted to the second highest water level registered in the records. During the high water phase, all the aquatic systems became connected with the main channels and rivers, due to the huge volume of water entering into the floodplain. In this case, only few variables (the most conservative) displayed a clear distinction among the aquatic system types because the water from the main rivers overrode local factors such as lake shape, depth and degree of connectivity. Another important aspect

regarding the homogenization of lake limnological features during high water is the spatial distribution of lakes, the presence of connecting channels and their mesohabitat characteristics (Junk et al., 2012). Lakes may be flooded by overland flow or by connecting channels. The flood wave in the overland flow will be modulated by the type of vegetation surrounding the lakes.

5. Conclusions

Limnological patterns of Amazon floodplain aquatic systems are highly dynamic, dependent on the surrounding environment, on the flood pulse, the parent river input and system type. These patterns show how undisturbed systems respond to natural variability in such a diverse environment, and how distinct are those aquatic systems, especially during the low water phase.

Aquatic systems in Mamirauá floodplain represent limnological patterns of natural waters of undisturbed areas and which may be used as future reference for comparison with disturbed areas, such as the Lower Amazon.

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