Comparative limnology of South American floodplain lakes and lagoons

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ABSTRACT. The primary purpose of this study was to compare different lagoons from eight floodplains in South America (Amazon, the Upper Paraná, the Middle Paraná, Mogi-Guaçu, Araguaia, Pantanal, São Francisco and Orinoco floodplains). Secondly, the effect of water level upon selected limnological variables (important and frequently used variables in limnological studies) was evaluated. Data were obtained from published articles and dissertations. Some unpublished data from Upper Paraná, Amazon and Araguaia floodplains were also used. Despite the general differences among the floodplains such as climate, geology and limnological characteristics of the main river, certain constant patterns were found. Oxygen concentration was always higher during low water phase and, in general, the lagoons have an acid water independently of the period. By comparing the Amazon, Paraná and Araguaia floodplains, whose data are more abundant, high variability in chemical factors was found during the low water phase when measured by the variation coefficient. This result supports the hypothesis that the flood pulse acts as a regional process that increases similarity among the lagoons.

Key words: comparative limnology , floodplains, lagoons.

RESUMO. Limnologia comparada de lagos e lagoas de planícies de inundação da América do Sul. O objetivo principal deste estudo foi comparar diferentes lagoas de oito planícies de inundação da América do Sul (planícies do Amazonas, Alto Paraná, Médio Paraná, Moji-Guaçu, Araguaia, Pantanal, São Francisco e Orinoco). Posteriormente, foi avaliado o efeito do nível da água sobre as variáveis limnológicas selecionadas (variáveis importantes e freqüentemente utilizadas nos estudos limnológicos). Os dados foram obtidos de artigos publicados e dissertações. Também foram utilizados alguns dados inéditos das planícies do Alto Paraná, Amazônia e Araguaia. Apesar das diferenças nos climas, aspectos geológicos e características limnológicas dos rios principais das planícies, alguns padrões limnológicos foram observados. As maiores concentrações de oxigênio foram observadas durante o período de águas baixas, e em geral todas as lagoas apresentam baixos valores de pH, independentemente do período hidrológico. Comparando-se apenas as planícies do Amazonas, Alto Paraná e Araguaia, que possuem o maior número de dados, a maior variabilidade limnológica, medida pelo coeficiente de variação, foi encontrada durante o período de águas baixas. Este resultado corrobora a hipótese de que a inundação age como um processo regional, aumentando a similaridade entre as lagoas.

Palavras-chave: limnologia comparada, planícies de inundação, lagoas.

Lagoons are important physiographic elements in floodplain landscapes. Their importance may be evaluated in various ways. First, they are very numerous. For example, the floodplain along the Amazon main stem in Brazil occupies 92,400 km^2, of which 11% is covered with lakes (Sippel *et al*., 1992). Floodplain lagoons are also imperative as nursery habitats for many species of fish, some of them with high economical value (Agostinho *et al*., 1997). Floodplain lagoons differ with respect to origin, limnology, hydrology and morphometric features. Thus, given the high environmental heterogeneity among floodplain lagoons, one could expect high beta diversity (Ward and Stanford, 1995;

Neiff, 1996; Tockner *et al*., 1999; Ward *et al*., 1999; Bini *et al*., 2001). High beta diversity (among lagoons) and high alpha diversity (within lagoons) contribute towards the high biodiversity of floodplain ecosystems (Agostinho *et al*., 2000).

The annual hydrological regime of the main rivers has been recognized as the primary factor accounting for temporal limnological changes in floodplain lagoons (Junk *et al*., 1989; Neiff, 1990). The entrance of nutrients from different sources (main river, sediment and decomposing vegetation) and the environmental reset promoted by floods, maintain the floodplains immature, which might explain the high productivity rates found in these environments (Junk and Welcomme, 1990).

Their relative degree of isolation permits one to consider floodplain lagoons as discrete units. This facilitates the compilation of independent data and the identification of general limnological patterns. Several studies have been carried out on large (e.g., Sioli, 1984; Hamilton *et al*., 1990; Bozelli, 1992; Vazzoler *et al*., 1997; Calheiros and Hamilton, 1998) and small lagoons (e.g., Camargo and Esteves, 1995). Nevertheless, few investigations have tried to summarize and analyze general predictions applicable to this class of ecosystems as a whole (Melack and Fisher, 1990; Esteves, 1998a).

Herein, we compiled and compared data from lagoons of different South American floodplains. We also evaluated the effect of the hydrological level on a selected set of variables. Our goal has been to identify limnological patterns common to floodplain lagoons on a continental scale.

Material and methods

In this paper, data were used from lagoons in the floodplains of the following rivers: Amazon, Trombetas, Negro (hereafter called Amazon floodplains), Upper Paraná (in the states of Paraná and Mato Grosso do Sul), Middle Paraná (Argentina), Mogi-Guaçu (state of São Paulo), Araguaia (state of Goiás), Paraguay (hereafter called Pantanal Matogrossense; state of Mato Grosso), São Francisco (state of Minas Gerais) and Orinoco (Venezuela). Description of these floodplains is found in Table 1 and elsewhere (Sioli, 1984; Santos *et al*., 1989; Melack and Fisher, 1990; Depetris and Paolini, 1991; Carignan and Neiff, 1992; Junk and Furch, 1993; Vazzoler *et al*., 1997).

Thirty-five studies, published between 1967 and 2000, were consulted for the compilation of our data (Table 2). When the same lagoon was investigated more than once, an average value was employed. The following variables were included in our analyses: total nitrogen, total phosphorus, electrical conductivity, pH, alkalinity, water transparency, dissolved oxygen and chlorophyll-*a*. Chemical analytical methods varied, however all of them were basically based upon the procedures described below.

Table 1. Geographical coordinates (midpoints), months of high and low water level, and water level range (maximum-minimum values) of eight floodplains

Floodplains	Localization	High Water	Low Water	Range (m)
Orinoco	S 07° 00'; W 67° 30'	Jun - Oct	Dec - Apr	5.5
Araguaia	S 13° 15'; W 50° 36'	Sep - Apr	Apr - Aug	5.6
Mogi-Guaçu	S 21° 36'; W 47° 50'	Dec - Mar	May - Sep	2.5
Pantanal	S 19° 30'; W 57° 30'	Dec - May	Jun - Oct	2.8
Amazon	S 02° 00'; W 62° 30'	Feb - Jul	Sep - Dec	9.0
São Francisco	S 16° 00'; W 44° 30'	Dec - Mar	Apr - Oct	-
Middle Paraná	S 31° 00'; W 60° 00'	Jan - Jun	Aug - Nov	3.8
Upper Paraná	S 23° 00'; W 54° 00'	Jan - May	Jun - Nov	3.5

Table 2. List of papers used to obtain the data. The number of lagoons analyzed by each author is also shown

Floodplains	Authors/year	Lagoons analyzed (number)
Amazon	Almeida (2000); Camargo and Miyai (1988); Day and Davies (1986); Hardy (1992); Huszar and Reynolds (1997); Ibañez (1998); Irmler (1975); Keppeler (1999); Reiss (1977); Ribeiro and Darwisch (1993); Santos (1980); Schmidt (1973); Wissmar *et al.* (1981).	1
Amazon	Bozelli (1992); Rai (1978); Tundisi *et al.* (1984)	2
Amazon	Forsberg *et al.* (1988)	51
Amazon	Furch (1984); Sendacz and Costa (1991)	3
Amazon	Hardy (1980); Marlier (1967)	5
Amazon	Rai and Hill (1980)	24
Mogi- Guaçu	Camargo and Esteves (1995); Nogueira *et al.* (1996)	1
Pantanal	Calheiros and Hamilton (1998)	1
Pantanal	Mourão *et al.* (1988)	62
Orinoco	Hamilton and Lewis Jr. (1987); Rodríguez and Betancour (1999)	1
Orinoco	Hamilton *et al.* (1990)	2
Orinoco	Rodríguez and Lewis Jr. (1997)	20
Araguaia	Tejerina- Garro *et al.* (1998)	12
Middle Paraná	Emiliani (1993)	1
Middle Paraná	Neiff *et al.* (1994)	2
São Francisco	Dabés (1995)	5
Upper Paraná	Thomaz (1991)	4
Upper Paraná	Unpublished data (P. de Carvalho)	20
Araguaia	Unpublished data (L.G. Oliveira)	18
Amazon	Unpublished data (B. Robertson)	19

Total nitrogen was determined by the method of persulfate digestion with the transformation of nitrogen into N-nitrate. Total phosphorus determinations followed the hydrolysis of unfiltered samples and their reaction with a molybdate-antimony solution. Afterwards, total nitrogen and total phosphorus concentrations were measured by standard spectrophotometric procedures. In some studies total nitrogen was estimated by summing total Kjeldahl nitrogen and nitrate concentrations. Electrical conductivity and pH values were obtained by potentiometers. Total alkalinity was measured by acidification (Gran titration or titration down to pH 4.35). Water transparency was measured with a Secchi disc. Dissolved oxygen concentrations were determined by Winkler titration or by oxygen meters. Spectrophotometric or fluorometric methods were used to determine chlorophyll-*a* concentrations.

Two descriptive statistics were used to compare floodplains. Means and standard errors, per floodplain and water phase (high and low water periods), of each variable, were estimated as measures of central tendency and variation, respectively. Water phases were defined by the use of the period classification described in the studies. In the Mogi-Guaçu River floodplain, values of pH, conductivity, water transparency and dissolved oxygen were available for only one lagoon. In this case, a temporal mean (± standard error) was estimated.

Results

High variability on chemical factors was found both among floodplains and between water phases (Figures 1 and 2). Range values (maximum minus minimum values) of alkalinity (3,908 μEq/L), total phosphorus (246 μg/L) and chlorophyll-a (88 μg/L) highlight this variability.

The lowest mean of water transparency was found in the Araguaia floodplain. More transparent waters were found in the Amazon, Mogi-Guaçu and Orinoco floodplains (Figure 1A). Low pH values (below neutrality) were found in all floodplain lagoons (except at Araguaia during low water period) (Figure 1B). Dissolved oxygen was usually undersaturated and the lowest dissolved oxygen saturations were found in the Pantanal floodplain (7%). The lowest oxygen saturations were observed during high water periods in all floodplains (Figure 1C).

Mean alkalinity values for all floodplains were lower than 450 μEq/L. The highest mean value (1,106.5 μEq/L) was recorded in Amazonian floodplain lagoons during the low water phase (Figura 1D). High ionic concentrations were found in Pantanal and Amazon floodplains, independently of the water phase, as shown by the electrical conductivity measurements. The lowest values (≤ 25 μS/cm) were obtained, in general, in the High Paraná, Mogi-Guaçu, São Francisco and Araguaia floodplains (Figura 2A).

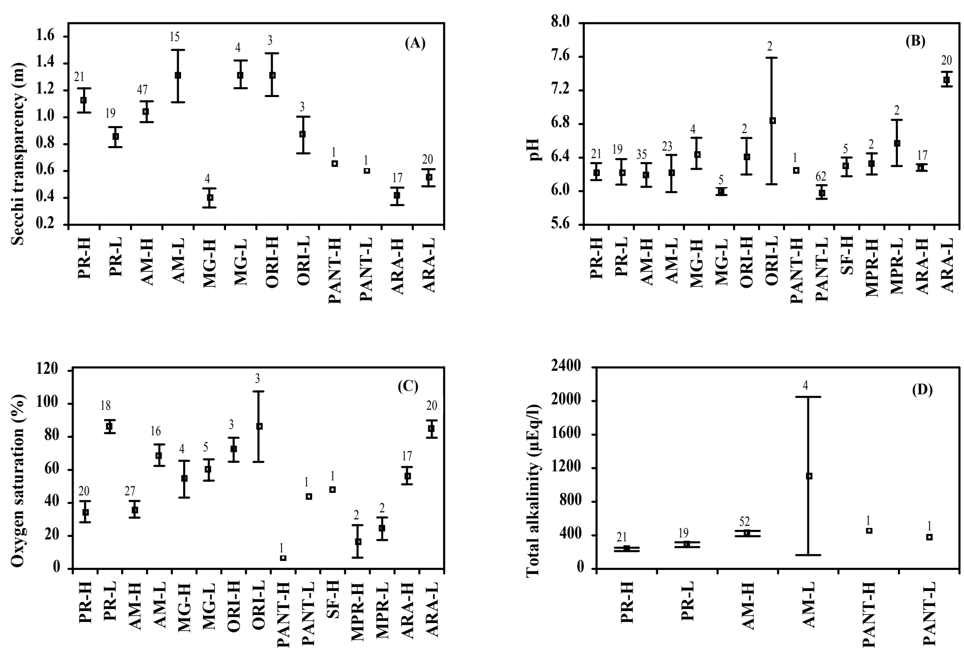

Figure 1. Mean values of water transparency (A), pH (B), oxygen saturation (C) and alkalinity (D) estimated for different South America floodplain lakes and lagoons. Vertical bars indicate standard error. (PR = Paraná, AM = Amazon, MG = Mogi-Guaçu, ORI = Orinoco, PANT = Pantanal, SF = São Francisco, ARA = Araguaia, MPR = Middle Paraná, and H = high water and L = low water levels). The numbers showed above each whisker correspond to the number of lagoons analyzed.

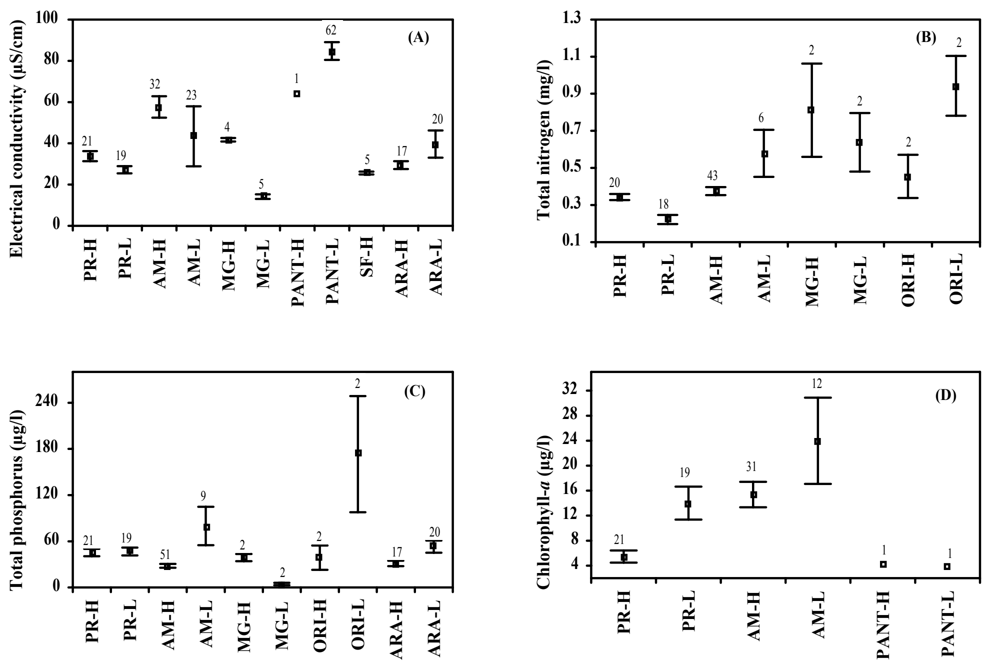

Figure 2. Means values of electrical conductivity (A), total nitrogen (B), total phosphorus (C) and chlorophyll-*a* (D). See Figure 1 for other details

The highest total nitrogen and phosphorus concentrations were obtained in Orinoco floodplain lagoons during low water period (Figure 2B e 2C). The greatest mean differences between water phases in nutrient concentrations were also found in this floodplain (0.49 mg/L for total nitrogen and 134.5 μg/L for total phosphorus), whereas the lowest mean differences (0.12 mg/L and 1.40 μg/L, for total nitrogen and total phosphorus, respectively) were obtained in the High Paraná lagoons.

The Amazon floodplain lagoons presented the highest chlorophyll-*a* concentration (mean of 24 μg/L). In the floodplains with available data, the highest mean concentrations were found in the low water phase (Figure 2D).

There are sufficient data for the Upper Paraná, Amazon and Araguaia floodplains to compare the variability (measured by the coefficient of variation) found in the two water phases. With the exception of dissolved oxygen, the highest rate in lagoon variability was observed during the low water phase.

Discussion

The limnological variability among lagoons on the same floodplain during the two water phases points to the influence of several driving forces operating on a local scale, such as, local rains, influence of small tributaries and variation in the lagoons' morphometry (fetch, depth and area). Due to the wide latitudinal range covered by our survey (2º to 30º S), floodplain variability may be best explained by regional factors, such as climate, geology and the limnological profile of the main rivers basins.

On a continental scale, the estimated electrical conductivity values are within the range expected for South American waters and these values are lower than the ones found in temperate water bodies (Gibbs, 1970; Payne, 1986).

The lowest water transparency values occurred in the Araguaia floodplain. This may be explained by severe erosive processes in the headwaters due to intensive deforestation, mining and erosion susceptibility of natural soil. On the other hand, in the Upper Paraná floodplain also located downstream regions of intensive land use, high Secchi disc values are common. In this case, upstream reservoirs trap most of the particulate matter transported by the river (Agostinho *et al.*, 1995; Bini, 1997; Barbosa *et al.*, 1999).

The predominance of low pH values may be expected in floodplain lagoons because these systems usually have a low redox potential, as indicated by the undersaturated dissolved oxygen values (see below). It is possible to infer that in some floodplains (Paraná and Amazon), the decomposition of organic matter is a more likely explanation for low pH values, since the main rivers are more alkaline and the input of river water during the floods does not alter the pH significantly. Additionally, these ecosystems are subject to high inputs of humic compounds from surrounding areas (Thomaz *et al*., 1992a), which tend to reduce pH. Finally, the rivers draining pre-Cambrian regions (e.g. Trombetas River), with very low pH values (mean of 5.7), may influence the pH of their floodplain lagoons (Panosso and Kubrusly, 2000). Thus, despite the overall low pH, at least two factors (local decomposition and geology of drainage basin) may explain such a discovery.

The average oxygen saturation was lower than 100 % in all floodplains. This result emphasizes the general heterotrophic condition (Production/ Respiration < 1.0) of floodplain lagoons. The continuous input and decomposition of allochthonous detritus, produced in the aquatic terrestrial transitional zone (ATTZ), tends to decrease oxygen concentrations even in periods of autotrophy. The heterotrophic condition is especially evident during high water periods, when the allochthonous influence is accentuated. During such phases, the water column can become anoxic leading to death of fish. Such events are well described in Pantanal ("dequada"; see Calheiros and Hamilton, 1998) and Amazonian lagoons ("friagem"; see Esteves, 1998b).

Despite the different underwater light regimes and nutrient concentrations in the lagoons, oxygen concentrations were always higher during the low water periods. This may indicate an increase of primary production relative to heterotrophic processes. During this period, autotrophy (P/R > 1.0) has been registered (Rai and Hill, 1980; Paes da Silva and Thomaz, 1997) and oxygen saturation may occasionally reach values higher than 100% (Thomaz *et al*., 1997).

The predominance of high values of phytoplankton biomass (as indicated by chlorophyll-*a* concentrations) and productivity during low water phases in floodplain lagoons is a well-described pattern in lagoons of the Amazon (Schmidt, 1973; Rai and Hill, 1984; Huszar, 2000; Roland, 2000) and Paraná (Thomaz *et al*., 1992a, 1997, Train and Rodrigues, 1998) floodplains. This pattern may be explained by key factors related to primary production. For example, high total nitrogen, high total phosphorus and high Secchi disc values were found in the low water period. During this phase, lagoons are shallow and diel mixing is common (Melack and Fisher, 1983; Tundisi *et al*., 1984; Lansac-Tôha *et al*., 1995; Paes da Silva and Thomaz, 1997; Panosso and Kubrusly, 2000). Diel mixing, higher light penetration (Thomaz, 1991) and fertilization due to sediment resuspension, are the main causes of such increments in phytoplankton primary production and biomass during low water phases. Conversely, the lowest concentrations of chlorophyll-*a* were recorded in the Pantanal floodplain, which is influenced by the poor nutrient waters of the Paraguay River (Hamilton *et al*., 1997). Thus, similar to other aquatic ecosystems, nutrients and light are the main factors influencing phytoplankton biomass variation in floodplain lagoons.

Based upon total nitrogen and total phosphorus concentrations, floodplain lagoons may not be classified into a single trophic category. Most of the lagoons may be classified between oligotrophic and mesotrophic, according to total nitrogen (Wetzel, 1983), and between mesotrophic and eutrophic, according to total phosphorus (Esteves, 1998b).

Various processes may account for temporal variations in macronutrients and ionic concentrations (Thomaz *et al*., 1992a, 1997; Camargo and Esteves, 1995) in floodplain lagoons. During high water periods, the more likely processes responsible for lagoons enrichment are fertilization by the main river (Schmidt, 1973; Fisher, 1978; Hamilton and Lewis Jr., 1987; Camargo and Esteves, 1995) and decomposition of aquatic and ATTZ vegetation (Schmidt, 1973; Rai and Hill, 1980; Santos, 1980; Barrios, 1996; Pagioro and Thomaz, 1999). On the other hand, dilution is expected when main river waters are poor in nutrients (Braun, 1952 in Schmidt, 1973; Thomaz *et al*., 1992b). Nutrient dilution in floodplain lagoons is also expected in regulated rivers (for example, in Paraná River; Agostinho *et al*., 1995).

Peaks of nitrogen and phosphorus during low water phases are also common (Amazon, Orinoco and Araguaia floodplains; Figure 2). In this case, local processes like resuspension of bottom sediments from wind action, increased by the small depths of the lagoons (as a rule, lower than 3 meters) (Schmidt, 1973; Junk, 1984; Melack and Fisher, 1990; Thomaz *et al*., 1997; Panosso and Kubrusly, 2000) is a parsimonious explanation for such results. Small tributaries entering the floodplain (Thomaz *et al*., 1992a) as well as biological activities, such as nitrogen fixation (Howard-Williams *et al*., 1989), sediment revolving by cattle (Pagioro *et al*., 1997) and fish (Junk, 1984), may also contribute towards nutrient increase during low water periods.

Some variables, such as alkalinity and electrical conductivity, may be considered conservative and may be successfully used to trace the water origin (Devol *et al*., 1987; Forsberg *et al*., 1988). Thus, the highest variability in alkalinity and electrical conductivity values in the Amazon floodplain lagoons are associated with the different water chemistry of the main rivers, which drain regions with different geological properties (Furch, 1984; Sioli, 1984; Junk and Furch, 1993). This is a well-known pattern for the Amazon and the comparison with other South American floodplains, with less variability, highlights the fact.

The effects of local rain on ionic and nutrient concentrations depend on the region or the time of year, such as the beginning or the end of the rainy season. In some floodplains (Paraná, Amazon and Mogi-Guaçu), ionic concentrations were higher during the low water phase and in others (Pantanal and Araguaia) the opposite pattern was found. The lack of temporal patterns with respect to nutrients and electrical conductivity may reflect the combination of possibilities mentioned above. Thus, the influence of water level variation on lagoon nutrient concentrations is still an open question.

Processes acting on different scales may influence the limnological variability of floodplain lagoons. During low water periods, the overall degree of hydrological connectivity is reduced. Thus, it is expected that lagoons are more susceptible to the influence of local processes (local rains, wind/fetch, anthropogenic influence and edge effects), which enhance limnological variability among them. On the other hand, the higher hydrological connectivity during high water periods may increase the similarity among floodplain environments. In the present survey results support the hypothetical prediction that floods increase the similarity of floodplain environments. This pattern has been found for zooplankton in the Trombetas River floodplain (Bozelli, 1992) and also for abiotic factors in the Upper Paraná River by Thomaz *et al*. (1997), who referred to it as the "homogenization effect". Since then, this prediction has been successfully corroborated by independent data (Veríssimo, 1999; Bozelli, 2000).

Given the patterns that emerged from the analysis performed in this study, comparative limnology may be still considered a powerful approach in aquatic ecology. However, the paucity of data is a caveat that constrains further general predictions.

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