__Original Research Article__

Influence of limnological processes and water level variation on the biodiversity of Brazilian Amazon lakes: an ecological approach

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ABSTRACT

This research makes a brief review of the limnology of lakes in wetlands in the Western Amazon, associating physical-chemical and morphological aspects to the biodiversity of black-waters lakes and whitewaters lakes. Lakes in these areas can show different patterns of vertical stratification, both in dissolved oxygen concentration and temperature. Furthermore, there are different mixing patterns. These events depend mainly on the way lakes connect to rivers, the time and extent of flooding, as well as the water levels variation. The availability of nutrients, particularly of phosphate, controls the biodiversity of the lakes and it is directly related with the thermal stratification and oxygen level in water column. In general, the most of the Amazon floodplain lakes can be classified as polymictic. Nevertheless, there are lakes of black-waters with trend to meromixy with permanent stratification. Under these conditions, stratification of other limnological variables also occurs, e.g., pH and electrical conductivity. Consequently, black-waters lakes systems with high species richness result in contrast to whitewaters lakes systems with lower species richness and high abundance of specimens.

Keywords: black-waters; whitewaters; water level variation; floods and ebbs cycles (FEC); richness of species; Amazon floodplain

1. INTRODUCTION

One of the most common characteristics of the shallow floodplain lakes in the Amazon region is their polymeric nature, which produces a variety of effects on the associated biological communities [1,2]. Most lakes are characterized by a daily stratification cycle linked to the daytime pattern of heat and wind exchange, with the daily extent of vertical mixing defined by seasonal variation in water depth [3]. Várzea lakes tend to have a longer stratification time during flood periods, in contradiction to the polymictic pattern of the low water period. Due to the high water temperature and aquatic productivity in these lentic systems, a rapid depletion of oxygen concentrations in the hypolimnion can eventually be observed, with an increase in the production rates of methane and hydrogen sulfide gases [4-6].

Several studies have been showed on the daily mixing and stratifying processes of the water column in Tropical lakes, however, most of these studies are isolated, and they represent an only lentic system. Diel studies provide important details of mixing and stratifying events and are particularly important in Amazon lakes where metabolic processes proceed at accelerated rates. These studies are essential to understand the ecological processes in the Amazon flood-plain lakes.

This review compares and discuss the different limnological aspects of whitewaters and black-waters of Central Amazon lakes, in special the physical and chemical processes of stratification related with the biodiversity of these systems. Diverse limnological parameters including nutrients, bathymetry and morphometry were measured in daily profiles in the last decade at the Western Amazon and compared with the classics works. In the same way, the variations of levels during flood and ebb cycles (FEC) and the possible interrelation of these variations with the biotic environment were observed.

2. MATERIAL AND METHODS

Diverse fluvial lakes belonging to the Amazon and Negro River (Fig. 1) basins were studied at 0.5 meters (m) intervals from the surface to bottom on a daily basis between 2001 and 2017. The limnological parameters temperature of the air and water (ºC), pH, dissolved oxygen (DO mg/l), oxygen saturation (OS %), electrical conductivity (EC μS_{25}/cm), and total dissolved sediment (TDS mg/l) were measured with WTW OXI and LF 197 electrodes. Transparency (m) was determined with Secchi disc. Total density (TD) of the water was determined for each 1 m depth for all FEC, and the density (D_z) of water due to temperature (T) was obtained from a table modified from [7] and contrasted with density calculated according to Martin and McCutcheon [8] (equation 1).

$$D_z = \left[1 - \frac{T + 288.9414}{508929.2\,(T + 68.12963)} (T - 3.9863)^2 \right] \quad \text{(Eq. 1)}$$

Were: D_z is density of water in a depth ($g.cm^{-3}$)

PAR radiation measurements were made with a Quantum Radiometer LI-COR Li-250 and sensor sub-aquatic LI-COR Li-192SA and the results were utilized to calculate euphotic zone (Z_{eu}) and attenuation coefficient (K). Nutrients P-total and P-PO_4 (P µg/L) were determined by the traditional colorimetric analytical method. Bathymetric and morphometric analyses were made with sonar (Eagle). Wind speed (Uw m/s) and rainfall data (mm/y) were obtained from a weather station of the University of Amazonas (UFAM) and water level variation from hydrological databank at the Manaus harbor between 2001–2017. The vertical thermal variation (ΔT) was studied for the FEC (flood, flood-peak, ebb, and dry) in association with morphometric and hydrological data. The thermal differences for black-waters and whitewaters lakes in the Central Amazon were also compared. All the samplings and analytical determinations followed the suggestions and proceeds from International Biological Program to Aquatic Systems [9-11].

Figure 1: Black-waters lakes (1) and Whitewaters lakes (2) in wetlands of the Amazon, respectively on the banks of the Negro and Amazon rivers. (Source: CNES/©2022Google modified by QGIS 2.18 GNU published by the Free Software Foundation).

3. RESULTS AND DISCUSSION

It has been suggested that many shallow tropical lakes stratify and mix on a daily basis [12,13]. However, in the Amazon, stratification and mixing events in floodplain lakes vary throughout the year, mostly because of the seasonal changes in depth and lake morphology [14]. The depth and the water surface area of the Amazon lakes changes according to the variation in the FEC of the main rivers (e.g., Negro and Amazon Rivers). In lakes in floodplain areas, those changes are more evident. In Calado Lake, a medium-sized (2 – 8 km^2) whitewater floodplain lake, depth ranges from 2 to 12 m [15], indicating an increment of

500% in the high-waters periods. In the meantime, in Poraquê Lake, a small sized (≈0.3 km^2) whitewater lake, depth ranges from 0.3 to 5.5 m [16], meaning an increment >1,800% according to the rise and fall of the waters in the Solimões (Amazon) River.

When floodplain lakes are very shallow and up to 4 meters deep, they stratify during the day but become isothermal and mix at night. In contrast, when the lakes become deeper, the nocturnal-mixing event tends to be limited to the surface layers only, and just the bottom layers remain stratified [3,14,17,18]. In Calado Lake, when the lake is more than 6 m deep, waters from hypolimnion became anoxic for extended periods. These events were also recorded by the authors (unpublished data) in the largest floodplain lakes in the Amazon (e.g, Cabaliana Lake with 16,000 hectares – not the biggest) whose depth ranges from 0.6 m to 15 m during the mentioned cycles (FEC), indicating a variation of 2,500% in your water column.

Lakes that were monitored in a daily cycle of 24 hours from surface to the bottom revealed a maximum temperature variation of 2.5 ºC and 9% of oxygen saturation (O.S.), respectively (Fig. 2A), resulting in a weak stratification of the water column. The low water period tends to overlap with the "summer" or regional dry season which is less rainy and has less cloud cover than during the "winter" or regional rainy season that occurs during practically the entire flood period. In general, the frequency of mixing to the bottom varies during the year, and the most of the whitewater floodplain lakes on Amazon can be classified as polymictic. Those trends can influence significantly in the biological distribution, especially in the abundance of species [19,20]. In fact, only the adapted species of fishes get to stay in the lakes during the critical periods of low oxygen concentrations.

Moderate sized and small island lakes, which are directly connected to the Amazon River, such as Camaleão Lake in Marchantaria Island, and Acari, Araçá, Comandá, Praia and Tracajá lakes all in Risco Island (160 km^2), tend not to stratify during the high water period because of the inflow of the fluvial water. In Camaleão Lake, Junk *et al*. [19] detected the presence of H_2S and anoxia from the bottom up to a depth of 1 – 2 meters, particularly during the high water periods. In Castanho Lake, Schmidt [17,21] observed that when the lake was more than 5 meters deep, the deeper layers became anoxic and H_2S was detected. Melack and Fisher [15] observed when floodplain lakes exceed 5 meters, thermal stratification persists, and the hypolimnion tends to become anoxic. In the island lakes, in the last decade, were observed in 24 hours from surface to the bottom variations higher than 3.5 ºC of temperature and 60% in the O.S. (Fig. 2B). In várzea lakes such as Calado and Poraquê and lakes inside the fluvial islands there are interference of the fluvial dynamics

(FEC), not just modifying the morphology of the connection channel (*paraná*) and of the own lake, as well as altering the chemical and physical-chemical composition of its interior body waters periodically.

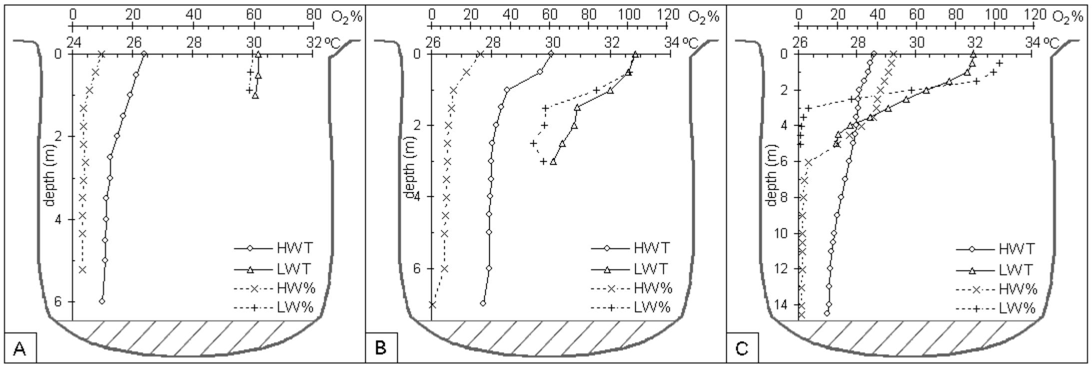

Figure 2: Profiles trends of temperature and oxygen saturation to 2A- whitewaters floodplain várzea lakes, 2B- island floodplain lakes and 2C- Tupé black-water Lake. HWT= high water temperature; LWT= low water temperature; HW%= high water O_2 saturation and LW%= low water oxygen saturation.

There is much less information available on the thermal and chemical regimes of black-waters lakes, nevertheless, the shallow Cristalino Lake, a small black-water lake connected to the Negro River, apparently has a similar diurnal-mixing pattern as whitewater lakes [3]. The authors observed that in Cristalino Lake, during the low water period, saturated surface oxygen levels throughout the day dropped slightly at night and in the bottom levels (4.2 meters) only a little lower than surface concentrations. According to [20], in black-waters lakes the oxygen depletion tends to be much less pronounced in relation to the várzea lakes. There are, however, some black-water lakes that show that the circulation does not reach the whole water column, differentiating them to the other Amazon lakes. Tupé Lake, for example, a narrow and dendritic black-water lake (0.67 km^2) located at the Negro River is a submerged and deeply cut “V-shaped valley” or “Ria” lake [22], where numerous igarapés-of-forest flow into the lake, and the lake is directly connected to the Negro River for most of the time, and is isolated only in the low water periods. It is isolated only in periods of low water when the level of the Rio Negro, at the Manaus harbor, is 19 meters above sea level or lower.

The depth in the deepest site of the lake ranges from 0.5 to 14.5 m indicating an increase of 2,800% in the high-water periods. During the FEC 2001-2017, were observed in 24 hours from surface to the bottom significant variations of the temperature and O.S. (ΔT = 4.7 ºC and ΔOS = 105% in low waters and ΔOS = 48% in high waters, Fig. 2C). Other authors observed also the same tendency [23-25]. The vertical temperatures differences are even more pronounced, particularly during the low water period. Tupé Lake is an example of an atypical black-water lake that can be classified as Meromictic Lake with permanent stratification and the main factor that contributes to maintain meromixy is the morphology-morphometry of the lake. Reiss [23] reports that Tupé Lake was clearly stratified both in terms of temperature and dissolved oxygen (DO) throughout the year and that, even at low water, Tupé Lake turned over infrequently. This author also suggested that, unlike other years when the lake apparently turned over more than once, during the study period, Tupé Lake “underwent” a phase of thermal meromixy — a condition of permanent stratification of water masses in lakes. Rai and Hill [24] suggested that Tupé Lake qualifies as a thermally stratified tropical lake, and classify it as an oligomictic lake.

The fact is if mixing to the bottom does occur, and there is no real evidence that it does, it might occur in high water seasons, during the *friagem* (cooldown – brief cooling period). This phenomenon can basically occur when the South Pole's cold fronts reach the Amazon Region bringing with them a very unusual turbulence between wind and convective cooling [20,26], but not when the lake is shallow. During to *friagem* phenomena in lakes, many fishes died due to low levels of oxygen and mainly by the high levels of H_2S in the water column. In Amazon lakes, the distribution of dissolved elements in water column, especially $P\text{-}PO_4$, is directly associated to the concentration of oxygen and the thermal stratification process.

In the stratified black-waters lakes, as the Tupé Lake, the levels of dissolved nutrients are extremely low [17,23,24], especially of $P\text{-}PO_4$ and P-total, ranging between 6 and 30 µg/L for medium conductivity of 9 μS_{25}/cm (authors unpublished results). Therefore, the low phosphate liberated in the primary production zone (euphotic zone) by the decomposition has to be quickly incorporated by the trophic cascade chain. In stratified whitewater lakes, the precipitation of the nutrients is more intense due to adsorption of the phosphates by clays contend Fe^{3+} and Al^{3+} and by the iron ions dissolved or associated $[Fe(OH).H_2O_5]^{2+}$. Studies on macrophytes decomposition and primary production of the phytoplankton in whitewaters, especially in flood areas, demonstrate that the macronutrients (N, P, Na, K, Ca and Mg) liberated in water column are fast and partially absorbed by the biota, resulting in increase of the biomass [20,21,25,27,28].

This succession of interferences from FEC in thermal and physical-chemical stratification, as well as in the stratification of available nutrients, makes up a flow that controls biodiversity in the Amazon. The FEC phenomenon or, in other words, the water level variation, is the main function of forces in the Amazon floodplain. This function can promote several environmental conditions with periodical alterations in the fauna e flora [28], and multiples and intensives alterations among the aquatic and terrestrial phases. As a consequence, high rates of decomposition of the organic matter, in special in the whitewaters, contribute to the dispersion of nutrients in the Amazon floodplain. The connectivity between flooded areas, natural channels (*paranás*), lakes, rivers and swamps represent a gradient of direct and indirect interactions (Fig. 3) that according to [20,26,28] it is of great ecological and economic importance with reflexes for the communities. The interactions are so complex that the forest does not survive without the aquatic system surface, and the last does not survive without the forest.

The rhythm of the annual variation of the water level imposes on the species that inhabit the forest, as well as on the rivers and lakes, seasonal variations that can draw different physiognomies in the Amazonian landscape. Biogeochemical and FEC share a close relationship with each other. Therefore, the biogeochemical cycle in the Amazon varies with the annual cycle of water level variation. This one always presents a monomodal curve with a maximum level frequently in June. The cycle is continuous and normally ends and starts again in October. That is, at the end of each ebb phase a new flood of a new cycle starts again, which is completed in the following year. This sequence of events occurs every year and presents temporal changes, in the speed of variation of the water level and in the amplitude of the variation each year. At the maximum and minimum levels, there are almost always brief interruptions in the variation of these levels (from 1 to 6 days and an average of 3.3 days, from 2001 to 2017) in the variation of these levels. Variations are recurrent, have bio-ecological implications, among others, and occur as a result of changes in climate.

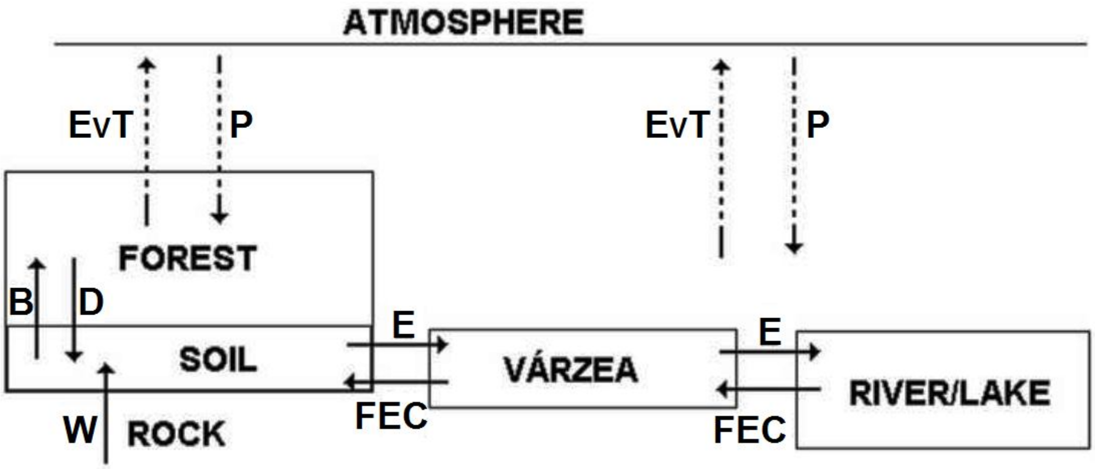

Figure 3: Input and output of elements to the Amazonian flood ecosystems. EvT= evapotranspiration; P= precipitation; B= incorporation of nutrients by the vegetal biomass; D= decomposition; W= weathering; E= erosion; FEC= floods and ebbs cycles rich in nutrients.

The biodiversity in Amazon lakes is associated to the availability of nutrients in the water-column. There is a relationship between nutrients and the presence of different habitats inside the lakes. The black-waters lakes are composed by channels, igapós, sandy beaches, waterfalls, rocky substrate, dendritic channels and banks of firm sand. In that great diversity of habitats, the process of co-evolution of the forest and fauna produced a system of high diversity of species, especially fishes, with populations size reduced due to limitation of resources (nutrients, Fig. 4). In the other hand, in the whitewater lakes, the abundance of nutrients stimulates the growth of the populations (absolute abundance). This will promote increased interactions and high competition rate for space between species, reducing the possibility of new species to be introduced. According to [19,20,28] the “flood pulse” (floods and ebbs cycles - FEC) in the várzea contributes to the abundance of aquatic organisms, including plankton, and planktivorous and piscivorous fish. In central Amazonia, under the influence of the whitewaters floodplain, the flood gradient acts as driving force for natural selection, strongly favoring the differentiation (characteristic) between species [20,28]. Changes in the ecological attributes of populations are an important component of ecological speciation [28]. In igapó areas, influenced by the black waters flood pulse from Negro River basin, the low concentration of nutrients acts as a drive force of ecological attributes, directly interfering with the diversity and abundance of the aquatic and terrestrial flood species [20,28-30].

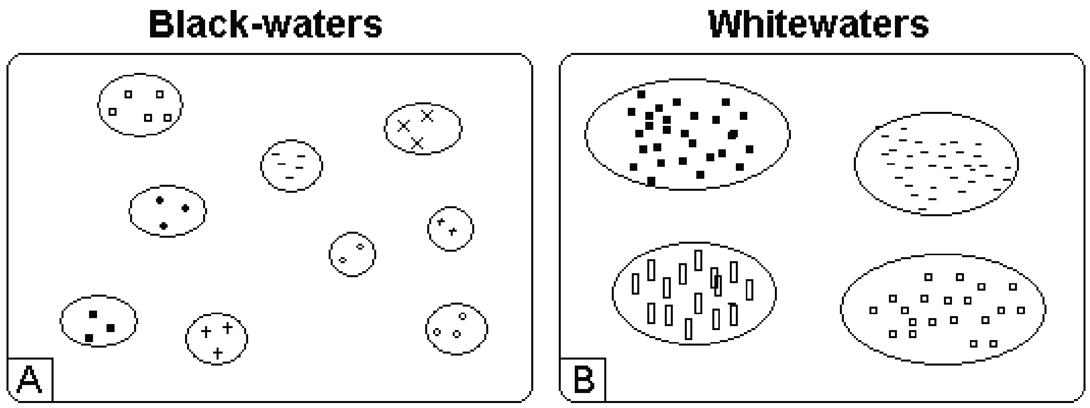

Figure 4: A) Richness or density of species (nº of species by area or volume); B) abundance or absolute density (total nº of organisms by area or volume).

CONCLUSION

There is a strong link between hydrology, morphology, FEC and stratification trends in Amazonian lakes, especially in the western Amazon plain during flood periods. In general, floodplain lakes can be classified as polymictics lakes. However, there are situations of partial and total meromixis, especially in black-waters lakes, mostly located in the Negro River basin. In Lake Tupé, due to its “V-shaped” morphology and the strong connection with the forest streams, the flow of cooler currents of these streams contributes to permanent meromixy trends with strong physical (temperature), physicochemical (conductivity, pH) and chemical (nutrients in general) stratification. From a biological point of view, both in abundance and in species richness, these limnological differences addressed in this study especially differentiate whitewater lentic systems from the black-water ones. Particular events within the FEC, such as the temporary stoppage of floods at the peak of floods and during floods and ebbs, certainly exert a great influence on the quality of water in the floodplain under the forest, on the forest, on the fauna and local aquatic flora as well as species behavior. Thus, in addition to the data discussed in this work, a particular ecological approach to these events will be of great importance, as well as their interrelationship with climate variations. There is no information on these events in the literature.

CONSENT

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ETHICAL APPROVAL

This section is not applicable in this manuscript.

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