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Physicochemical characterization of the white, black, and clearwater rivers of the Amazon Basin and its implications on the distribution of freshwater stingrays (*Chondrichthyes*, *Potamotrygonidae*)

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Abstract: This study characterizes the spatial physicochemical variation of the surface water in the main stems of three important rivers in the Amazon Basin and its influence on the distribution of freshwater stingrays. The Amazon River is circumneutral pH ($\text{pH } 6.6 \pm 0.2$), high conductivity ($44.8 \pm 24.8 \mu\text{S/cm}$) and solute-rich (total dissolved solid, $\text{TDS} = 23.9 \pm 17.8 \text{ mg/l}$) in relation to the Negro River. The Negro River is blackwater (black or tea-colored), acidic ($\text{pH } 4.5 \pm 0.9$), low conductivity ($17.0 \pm 15.2 \mu\text{S/cm}$) and solute-poor ($\text{TDS} = 7.1 \pm 6.7$), while the Tapajós River is a clearwater river with physicochemical characteristics ($\text{pH } 6.5 \pm 0.4$; conductivity = $14.4 \pm 13.1 \mu\text{S/cm}$; $\text{TDS} = 7.7 \pm 5.6 \text{ mg/l}$) lying between those of the Amazon and Negro rivers. The longitudinal variability of the water of these rivers was attributed to the discharges of their tributaries, which come from different geological provinces. The distribution of the Family *Potamotrygonidae* was interpreted as a result of the physicochemical differences between bodies water. Thus, the physicochemical characterization of the main water types in the Amazon Basin may act as a hydrological barrier (or hydrological filter) for the dispersal of potamotrygonid rays.

Key words: Amazon River, Negro River, Tapajós River, potamotrygonid, hydrological barrier

Resumo: Caracterização físicoquímica dos rios de água branca, preta e clara da Bacia Amazônica e suas implicações para a distribuição das arraia de água doce (*Chondrichthyes*: *Potamotrygonidae*). Este estudo descreve o perfil espacial das variáveis físicas e químicas da água em três importantes rios da bacia Amazônica. A água branca do Rio Amazonas possui pH circumneutro ($\text{pH } 6,6 \pm 0,2$), elevada condutividade elétrica ($44,8 \pm 24,8 \mu\text{S/cm}$) e rica em sólidos totais dissolvidos ($\text{TDS} = 23,9 \pm 17,8 \text{ mg/l}$) em relação ao Rio Negro. O Rio Negro possui água preta, ácida ($\text{pH } 4,5 \pm 0,9$), baixa condutividade ($17,0 \pm 15,2 \mu\text{S/cm}$) e pobre em sólidos dissolvidos totais ($\text{TDS} = 7,1 \pm 6,7 \text{ mg/l}$). As águas claras do Rio Tapajós possuem características físicas e químicas ($\text{pH } 6,5 \pm 0,4$; condutividade = $14,4 \pm 13,1 \mu\text{S/cm}$; $\text{TDS} = 7,7 \pm 5,6 \text{ mg/l}$) intermediárias entre o Rio Amazonas e Rio Negro. Nestes rios, a variabilidade longitudinal dos valores de pH, condutividade e TDS da água foi atribuída às descargas dos seus tributários, os quais se originam de diferentes províncias geológicas. A distribuição das arraia de água doce da família *Potamotrygonidae* foi interpretada como o resultado das diferenças entre os tipos de águas. Portanto, as características físicas e químicas das águas da bacia Amazônica podem agir como barreiras ou filtros hidrológicos para a dispersão das espécies de potamotrigonídeos.

Palavras-chave: Rio Amazonas, Rio Negro, Rio Tapajós, potamotrigonídeos, barreira hidrológica

Introduction

The Amazon Basin is the largest world's hydrographic system, covering an area of 6,879,761

km^2 . The basin is drained by the 7,025 km Amazon River. The Amazon's average annual discharge of $220,000 \text{ m}^3 \text{ s}^{-1}$ comprises about 20% of the Earth's

superficial freshwater (Molinier et al. 1997). From the headwaters to its mouth in the Atlantic Ocean, the Amazon River is fed by more than 1,000 tributaries from different geological regions; thus, the physicochemical characteristics of the rivers in the Amazon Basin reflect the soil properties of the provinces they drain (Salati & Vose 1984, Konhauser et al. 1994).

Alfred Russel Wallace (1853) was the first to classify the Amazon and its tributaries into white, black, and clearwater rivers types. However, this classification was based only on color. Sioli (1984) showed that these waters are chemically and physically heterogeneous. Whitewater rivers (such as the Amazon and Madeira rivers) have a characteristic muddy color, relatively high concentrations of dissolved solutes, an alkaline to neutral pH, and a high sediment load originating from Andean regions (Konhauser et al. 1994, Alcour et al. 2003). Blackwater rivers (for example, the Negro and Uatumã rivers) are black or tea-colored due to a high concentration of dissolved organic carbon, have negligible suspended sediment loads and medium transparencies, are very dilute in dissolved ions, and are usually acidic (Rickey et al. 1990). Other characteristics of blackwater include extremely weathered sandy podzolic soil, bed stability, and low erosion (Klückler et al. 2000). Finally, clearwater rivers (for example, the Tapajós and Xingu rivers) are relatively transparent and olive-green in color, typically have lower dissolved sediment loads (as well as ion loads), exhibit low values for electric conductivity, and range from acidic to alkaline (pH 5-8). These rivers usual drain the weathered soil of the Precambrian Shield which explains their low dissolved sediment loads (Sioli 1984, Konhauser et al. 1994).

As a result of these differences between aquatic environments, the Amazon Basin is a mosaic of different water types connected by the main stem of the Amazon River. Therefore, it has been hypothesized that hydrographic conditions form a strong hydrographic barrier constraining the dispersion of fish acting as selective forces that drive allopatric speciation (Lovejoy & Araújo 2000, Hubert & Reno 2006, Willis et al. 2007). In the case of the Amazon main stem, it serves as a major corridor for the dispersal of aquatic biota among different water types. However, the main channel of the Amazon River may not be a free dispersal corridor but rather a zoogeographical filter for the interchange of fish species, at least for freshwater stingray species (Potamotrygonidae) such as those that occur in the Casiquiare River, which acts as a

corridor and geographical filter for fish dispersion between the Orinoco and Amazon basins (Winemiller et al. 2008).

Potamotrygonids are endemic to South America and are the only extant elasmobranch family restricted to a freshwater environment. The family Potamotrygonidae comprises three genera: *Paratrygon*, *Plesiotrygon*, and *Potamotrygon*. *Paratrygon* is monotypical, represented by *Paratrygon aiereba* Müller & Henle 1841 and is widely distributed in all water types, both in the Amazon River and Orinoco River. *Plesiotrygon* is also monotypical, represented by *Plesiotrygon iwamae* Rosa, Castello & Thorson 1987 which occurs in the Amazon River drainage, but is usually distributed only in the main stem and marginal lakes of the Amazon River (Rosa et al. 1987). *Potamotrygon* contains 18 described species, most of them restricted to a single river and its tributaries (Rosa et al. 2008). For example, *Potamotrygon leopoldi* Castex & Castello 1970 and *Potamotrygon henlei* Castelnau 1855 are endemic to the Xingu and Tocantins Rivers and its tributaries, respectively. Both rivers are typically classified as clearwater. However, *Potamotrygon* sp. (an undescribed specie known as cururu ray) is endemic to the acidic, ion-poor, and blackwater of the Negro River. In contrast, *Potamotrygon motoro* Müller & Henle 1841 and *Potamotrygon orbignyi* Castelnau 1855 are widespread in different water types of the Amazon Basin (Martin 2005). This clearly shows that potamotrygonid species show marked allopatric distribution patterns; four of them are widely distributed throughout the Amazon Basin, and several species are restricted to a single river and its tributaries. Recently, studies have revealed large genetic differentiation between several populations of potamotrygonids, suggesting that the river may be a barrier to gene flow (Toffoli et al. 2008).

The goal of this study was to characterize the physicochemical variables along the longitudinal gradient in the main stem of the Amazon (whitewater), Negro (blackwater), and Tapajós (clearwater) rivers and to discuss the geographical pattern of potamotrygonid species distribution in the context of environmental differences to evaluate the potential of Amazonian basin water to function as a geological barrier that drives allopatric speciation.

Material and Methods

Water and stingray sampling was carried out in the Amazon River, Negro River and Tapajós River (Fig. 1) during the high water period (May-June) of 2007 and 2008.

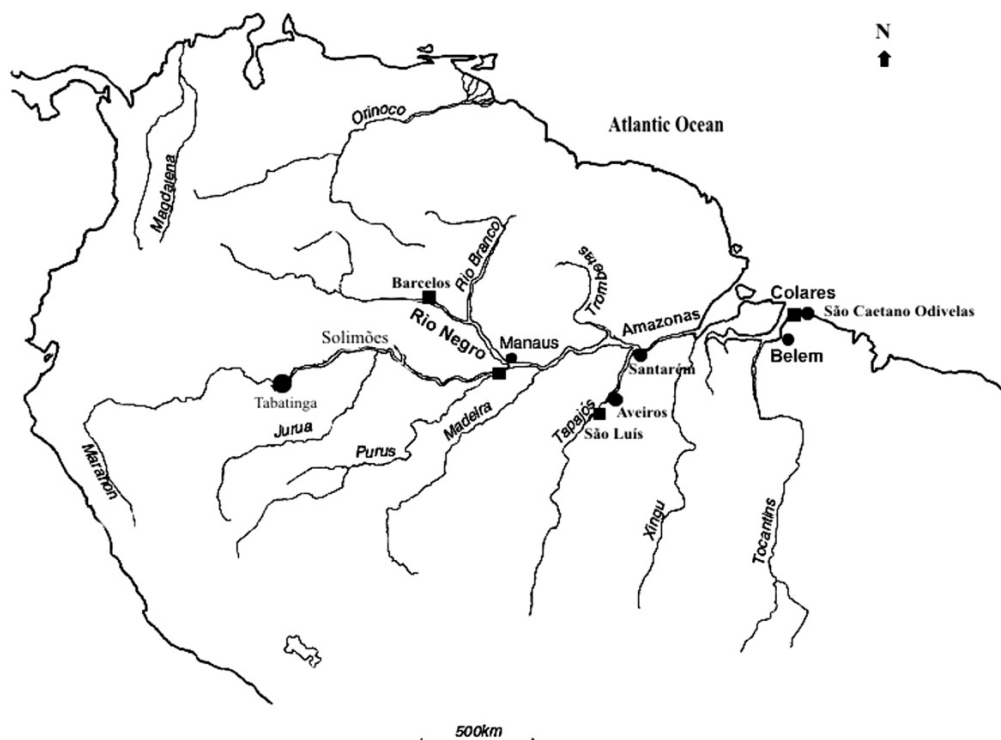


Figure 1. Study area. The names of the main stem and major tributaries are shown. Cross-sectional composites were performed on the main stem of the Amazon River (whitewater type, from São Caetano de Odivelas/Colares to Manaus), the Negro River (blackwater type, from Manaus to Barcelos), and the Tapajós River (clearwater type, from Santarém to the São Luís do Tapajós rapids). The fishing sampling are shown as black squares.

Study area - For the Amazon River, water samples were collected upstream river from town of São Caetano de Odivelas and Colares Island ($0^{\circ}44'$ S; $48^{\circ}00'$ W) near to Manaus City at the confluence of the Solimões (Lower Solimões) and Negro rivers ($03^{\circ}08'$ S; $59^{\circ}55'$ W), a distance of 1,540 kilometer. In the Amazon Basin, the water upstream from this confluence of the Amazon River is known as the Solimões River (Upper, Middle and Lower Solimões), while downstream from this confluence (the main stem) the river is named the Amazon River (Upper, Middle and Lower Amazon). Both the Solimões and Amazon rivers are typically whitewater types. The Amazon River receives a volumetrically high amount of blackwater (from the Negro, Urubu and, Uatumã rivers) and clearwater (from the Trombetas, Tapajós, and Xingu rivers) and has only one important whitewater tributary, the Madeira River. The water at the region of São Caetano de Odivelas and Colares Island is typically brackish and affected by daily tides. It is also influenced on a seasonal basis by the hydrological pulse of the Amazon River.

For the Negro River, the samples of water were collected from the river mouth at Manaus

($3^{\circ}29'$ S; $59^{\circ}55'$ W) upstream to the Middle Negro River (Mariuá Archipelago) at Barcelos ($0^{\circ}41'$ S; $63^{\circ}09'$ W). The sample comprised a span of 480 kilometer. The Negro River extends approximately 1,700 kilometer, and its basin spreads over an area of 715,000 km², which represents 14% of the total Brazilian Amazon Basin. It is the largest and most important source of blackwater.

For the Tapajós River, water samples collected on the main stem of the Tapajós River were conducted along a stretch of 312 kilometers from the mouth of the Tapajós River at Santarém ($2^{\circ}25'$ S; $54^{\circ}53'$ W) upstream to the rapids in the village of São Luís do Tapajós ($4^{\circ}19'$ S; $56^{\circ}03'$ W). The Tapajós River is 851 kilometer long, with many rapids and waterfalls that extend over 500 kilometer. The São Luís do Tapajós Rapids are the most important of these geological barriers.

Water sampling - Water sampling was carried out along the main stem of the Amazon River ($n = 67$ sites), the Negro River ($n = 54$ sites), and the Tapajós River ($n = 37$ sites). Four sub-samples were collected manually using a polyethylene flask beneath the water's surface. The measured distance between each site collection was

calculated using a Garmin Plus III global position system. Field measurements of physicochemical parameters were analyzed immediately after the collection of samples from each site. The pH values, electrical conductivity ($\mu\text{S}/\text{cm}$), total dissolved solid (TDS, mg/l), and salinity (psu) were measured using a Consort C535 multiparameter analyzer.

Stingray - Stingrays were collected in the Amazon River (a whitewater system), near Colares Island in Marajó Bay ($0^{\circ}55' \text{ S}$; $48^{\circ}17' \text{ W}$) and Lake Janauacá ($3^{\circ}21' \text{ S}$; $60^{\circ}15' \text{ W}$). In the Negro River (a blackwater system), rays were collected between the Arirahá River ($0^{\circ}30' \text{ S}$; $63^{\circ}32' \text{ W}$) and the Cuiuni River ($0^{\circ}45' \text{ S}$; $63^{\circ}06' \text{ W}$). In the Tapajós River (a clearwater system), rays were collected near the town of Aveiros ($3^{\circ}38' \text{ S}$; $55^{\circ}20' \text{ W}$) and in the São Luís do Tapajós rapids ($4^{\circ}25' \text{ S}$; $56^{\circ}15' \text{ W}$). The rays were caught during rising and high water levels. Hook and line, throw-net, beach seine, harpoons, and a long line were used to capture the stingrays (an effort of five hours per day). Species determination was carried out according to Rosa (1985). In this study was considered only the presence and absence of the potamotrygonid species collected in each river sampled. Herein, in this issue forward the species of the genus *Paratrygon* and *Plesiotrygon* are cited as full names, while for the genus *Potamotrygon* is abbreviated.

Statistical analysis - All data are reported as the means \pm standard deviation (sd). To perform the correlation between pH and electric conductivity parameters, the conductivity data were log-transformed prior to performing analysis.

Results

The variations of physicochemical characteristics in the Amazon River along the stretch upstream from the Amazon estuary to confluence of the Negro and Solimões rivers are shown in the Figure 2. The physicochemical patterns were similar values in both years sampled (2007 and 2008). In general, an increase of the conductivity and total dissolved solids (TDS) was observed along the stretch studied. But, the pH values showed little spatial variation along the stretch studied, except in the sites near the margin in confluences with acidic rivers such as the Guamá River ($1^{\circ}30' \text{ S}$; $48^{\circ}31' \text{ W}$) and the Negro River ($3^{\circ}04' \text{ S}$; $59^{\circ}40' \text{ W}$), which is characterized by a strong variation from acidic (pH 4 - 5) to slightly neutral (pH 6 - 7) water. At the Amazon River mouth, the physicochemical variables were relatively high near Colares Island (pH 6.3 ± 0.3 ; conductivity $104.3 \pm 0.3 \mu\text{S}/\text{cm}$, and TDS $67.0 \pm 0.2 \text{ mg}/\text{l}$). In these locations, the Amazon River water is strongly influenced by seawater from the

Guyana Current (an ascendant of the South Equatorial Atlantic Current). *P. scobina* Garman 1913 and *P. orbignyi* are common potamotrygonid species found in the Colares Island (Marajó Bay, Amazon River mouth), while *Paratrygon aiereba* is occasionally captured. In the Lake Janauacá (Lower Solimões/Upper Amazon), the occurrence of *Paratrygon aiereba*, *P. motoro*, *P. scobina*, and *P. orbignyi* was also recorded in this study.

The Negro River was characterized by high heterogeneity in its physicochemical parameters, except in its mid-channel and around of the island, which was typically homogeneous and characterized by acidic with low conductivity and diluted water (very low TDS values). The river-margin was highly heterogeneous in its physicochemical variables; at the Mariuá Archipelago this was largely due to the discharge of the Demini and Branco rivers (Fig. 3). In the flooded forest, the electrical conductivity was negatively related to pH value ($n = 15$, $r^2 = 0.80$, $p < 0.05$ in May-June 2007; $n = 21$, $r^2 = 0.72$, $p < 0.05$ in May-June 2008) (Fig. 4). The flooded forest (locally know as the igapó forest) was characterized by acidic water (pH 3.7) and is the preferential habitat of two potamotrygonids, *Potamotrygon* sp. (cururu ray) and *P. motoro*. The rays *Paratrygon aiereba*, *P. orbignyi*, and *P. schroederi* Fernández-Yépez 1958 showed a preference for habitats near the beaches of the islands in the mid-channel of the Negro that exhibited highly water quality (i.e. highly transparent and oxygen-rich water, $5.1 \pm 0.6 \text{ mg}/\text{l}$).

At its mouth the Tapajós River is constrained by the water of the Amazon River. Consequently, its physicochemical parameters are strongly affected by the whitewater of the Amazon River, and it exhibits high pH, conductivity, and TDS values until 50 kilometer upstream. In general, the clear water of the Tapajós River was relatively homogeneous along the stretch studied (Fig. 5), except for the high conductivity and TDS values recorded in Aveiros ($3^{\circ}38' \text{ S}$; $55^{\circ}20' \text{ W}$). Physicochemically, the water of the Tapajós River exhibited characteristics lying between those of the Amazon and Negro rivers waters (see Fig. 4). The fauna of elasmobranch between São Luís do Tapajós Rapids and Aveiros was characterized by *Paratrygon aiereba*, *P. motoro*, and *P. orbignyi* (these species are also commonly found in the Amazon and Negro rivers). A summary of the physicochemical variables on the surface water of the three Amazonian rivers studied (the Amazon, Negro and Tapajós rivers) is shown in Table I, as well as the potamotrygonid species that occur in each river.

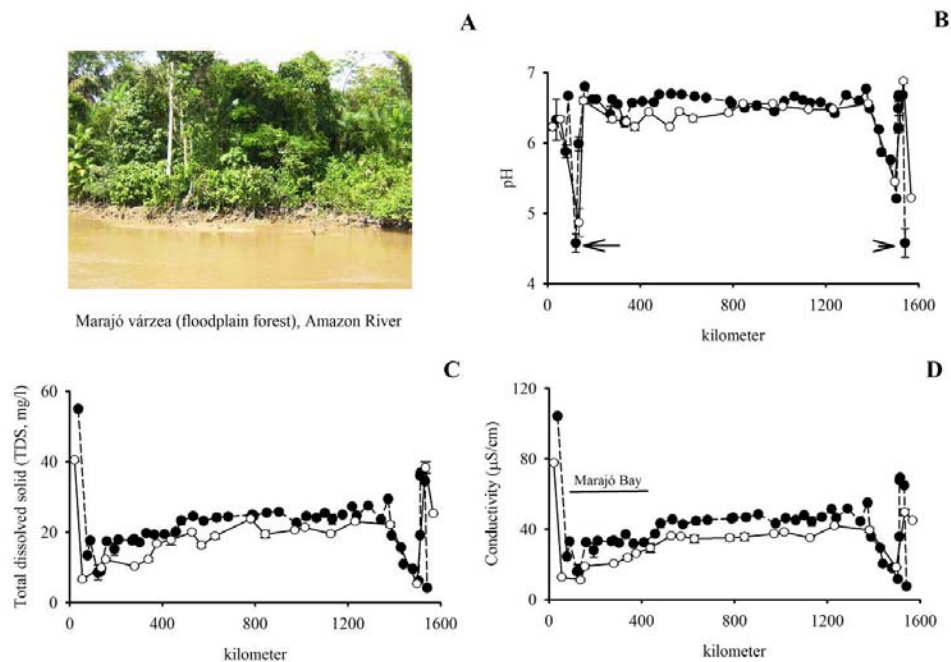


Figure 2. The Amazon River (a whitewater river): longitudinal trends along a 1,540 kilometer stretch of the Amazon River main stem from Manaus (at the confluence of the Solimões and Negro rivers) to Colares Island (Amazon estuary), showing a general view of Marajó Várzea (A); values of pH (B), total dissolved solids (C), and conductivity (D) along the same river stretch in 2007 (closed circles) and 2008 (open circles) during increasing water levels. In (B), note the low pH value at the confluence of the Negro River (arrowhead) and the Guamá River (arrow), which are both acidic tributaries.

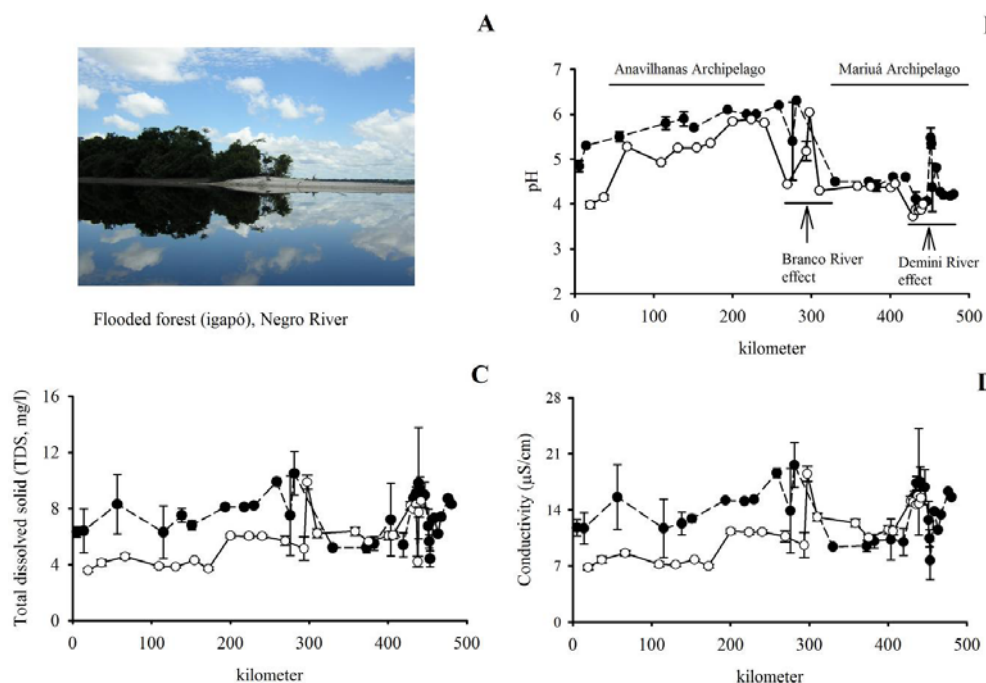


Figure 3. Longitudinal trends along a 480 kilometer stretch of the Negro River (a blackwater system) main stem from Manaus (at the confluence of the Solimões and Negro rivers) to Barcelos (Mariuá Archipelago), showing the igapó flooded forest (A), longitudinal variation in the pH (B), total dissolved solids (C), and conductivity (D) during increasing water levels in 2007 (closed circles) and 2008 (open circles).

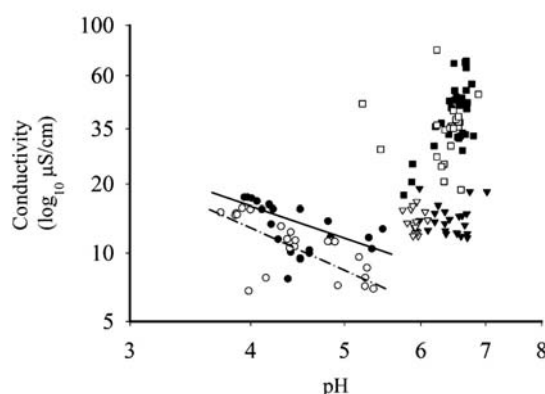


Figure 4. Relationship between electric conductivity (log-transformed values) and pH from data collected in 2007 (closed symbols) and 2008 (open symbols) during increasing water levels of the Amazon River (squares), Negro River (circles) and Tapajós River (inverted triangles). Note that the physicochemical characteristic of the Tapajós River is intermediate between the Amazon and Negro rivers. In the Negro River, a negative correlations were observed both in 2007 (solid line; $n = 15$; $r^2 = 0.80$; $p < 0.05$) and 2008 (dash line; $n = 21$; $r^2 = 0.72$; $p < 0.05$).

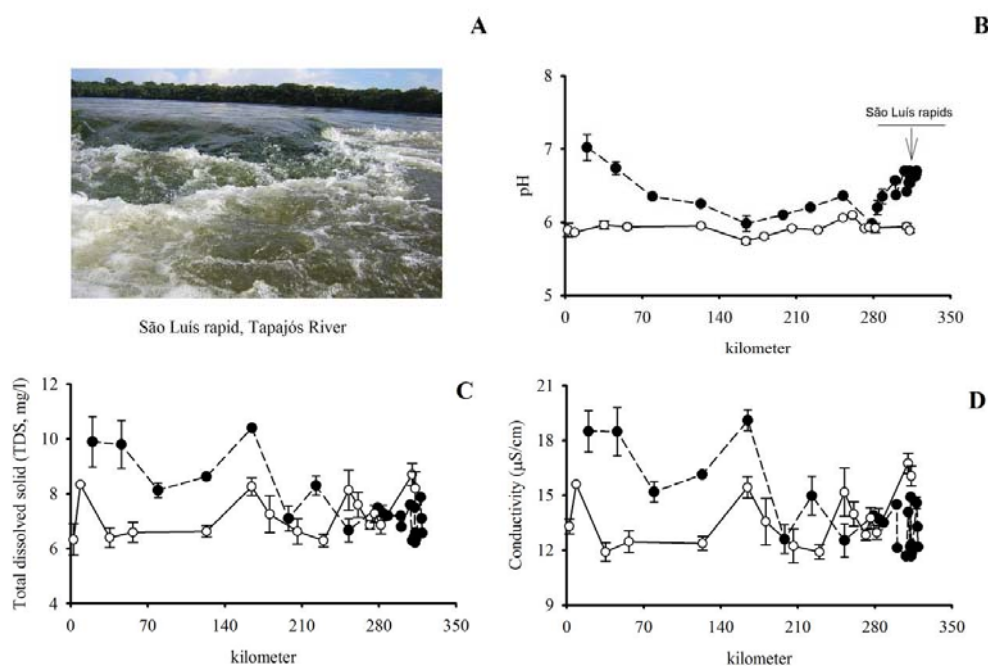


Figure 5. Longitudinal transect along a 312 kilometer stretch of the Tapajós River main stem from Santarém (at the confluence of the Amazon and Tapajós rivers) to Itaituba: São Luís do Tapajós rapids in (A), and pH (B), total dissolved solids (C), and conductivity (D) during increasing water levels in 2007 (closed circles) and 2008 (open circles).

Table I. A summary of physicochemical variables (mean \pm sd; min – max; number of samples) and occurrences of potamotrygonid species in the Amazon River, Negro River and Tapajós River.

Rivers	pH	Conductivity (μ S/cm)	TDS (mg/l)	Potamotrygonidae
Amazon River	6.6 \pm 0.2 (6.0 - 6.8) n = 40	44.8 \pm 24.8 (17.4 - 104.3) n = 40	23.9 \pm 17.8 (8.8 - 55.0) n = 40	<i>Paratrygon aiereba</i> [#]
				<i>Plesiotrygon iwamae</i> *
				<i>Potamotrygon motoro</i> [#]
				<i>Potamotrygon orbignyi</i> ^{#&}
				<i>Potamotrygon scobina</i> ^{#&}
				<i>Potamotrygon ocellata</i> *
				<i>Potamotrygon humerosa</i> *
Negro River	4.5 \pm 0.9 (3.7 - 6.4) n = 15	17.0 \pm 15.2 (7.7 - 35.4) n = 15	7.1 \pm 6.7 (4.4 - 19.4) n = 15	<i>Potamotrygon constellata</i> *
				<i>Paratrygon aiereba</i> [#]
				<i>Potamotrygon motoro</i> [#]
				<i>Potamotrygon orbignyi</i> [#]
				<i>Potamotrygon</i> sp. 1, n.sp. (cururu ray) [#]
Tapajós River	6.5 \pm 0.4 (6.0 - 8.0) n = 23	14.4 \pm 13.1 (11.7 - 25.2) n = 23	7.7 \pm 5.6 (6.2 - 13.3) n = 23	<i>Potamotrygon schroederi</i> [#]
				<i>Paratrygon aiereba</i> [#]
				<i>Potamotrygon</i> sp. 2, n. sp. (P14-Itaituba ray) [¥]
				<i>Potamotrygon</i> sp. 3, n. sp. (jabuti ray) [¥]
				<i>Potamotrygon</i> sp. 4, n. sp. ^{#@}
				<i>Potamotrygon motoro</i> [¥]
				<i>Potamotrygon orbignyi</i> [#]

[#]Occurrence recorded *in situ*; *Occurrence according to Compagno & Cook (1995); [&]Collected in the Amazon estuary; [¥]M.L.G. Araújo, personal communication; [@]New species (n. sp.) according M.R de Carvalho (personal communication).

Discussion

In the Amazon Basin, the annual water-level fluctuation is seasonally dependent (Junk, 1997). The average flooding amplitude is about 10 m and the flooding occurs during the rainy season between May and June and corresponds to the maximum monthly Amazon River discharge to the Atlantic Ocean (Ffield 2007, Birkett *et al.* 2002). At this time, the main stem of the Amazon River receives a high volume of water from different tributaries (Martinelli *et al.* 1993). Consequently, the river demonstrates physicochemical variables along its longitudinal gradient. Furthermore, during the years in which the inundation period is more severe, such as in 2008, a consistent dilution in the dissolved

solutes was observed. As a result, some limnological variables were reduced.

Except for pH values, there was a clear longitudinal decrease in conductivity and TDS values downstream. The Amazon River receives volumetrically high discharges of highly diluted water from the Negro, Urubu, and Uatumã rivers (all blackwater types) and the Trombetas, Tapajós, and Xingu rivers (all clearwater types). According to Santos & Ribeiro (1988), the Solimões River shows a consistent dilution in its major nutrients along a stretch from Tabatinga (Upper Solimões River, Brazil-Colombia border) until Santarém (Middle Amazon), at the mouth of the Tapajós River. This is consistent with the hypothesis in which dissolved

nutrients originating in the Andean headwaters exhibit a dilution effect downstream, where large-scale variations are controlled largely by the relative contribution of larger diluted tributaries (Richey *et al.* 1990). There is no well-defined pattern for pH values; this variable often breaks down at the river-margin after the confluence of acidic rivers like the Negro, Urubu, Uatumã, and Guamá. The slight longitudinal variation in pH along the Amazon main stem may reflect the maintenance of conservative dissolved characteristics such as alkalinity, which originates in the Andes and alluvial foreland rivers and is present primarily in the main stem. These waters thus avoid the acidification effect farther downstream that occurs as a result of the input of the larger acidic tributaries cited above.

Two main channels comprise the estuary of the Amazon River. The southward channel constitutes a long bay named Marajó Bay at the confluence of the Pará and Tocantins rivers. During the dry season, Marajó Bay is strongly affected by seawater due to the reduced discharge of the Amazon, Tocantins and Guamá Rivers. As a result, the water of Marajó Bay is a typically brackish environment. In contrast, freshwater habitats extend to Colares Island during the rainy period. The waters along the main stem at Marajó Bay are then more diluted compared to the northward channel of the Amazon River at the Marajó Archipelago. According to Charvet-Ameida *et al.* (2005), the Colares region is characterized by a high population density of freshwater stingrays, mostly represented by four species: *Plesiotrygon iwamae*, *Paratrygon aiereba*, *P. orbignyi*, and *P. scobina*. The latter two stingrays were the most abundant species (96%) in Soure region (Amazon estuary), near of Colares Island (Almeida *et al.* 2009). During the dry season, most areas in the Marajó Bay exhibit brackish characteristics, including Colares Island, where salinity increases from 0.1 during the rainy season to 7 psu during the dry season due to the simultaneous discharge reduction of the Amazon and Tocantins rivers (Almeida 2003). According to several authors, potamotrygonids do not disappear completely from this area (Charvet-Almeida *et al.* 2002, Charvet-Almeida *et al.* 2005; Almeida *et al.* 2009). However, there is evidence of effects on fauna of elasmobranch composition during seasonal periods, in which some species are more tolerant to increases in environmental salinity than others. *Paratrygon aiereba* may be less tolerant to salinity than *P. scobina* and *P. orbignyi* (Charvet-Almeida *et al.* 2005). According to Almeida *et al.* (2009), *P. orbignyi* is the most salt tolerant species found at the mouth of the Amazon. These authors recorded the

occurrence of this species in the brackish water of the Soure region in Marajó Bay (Amazon River mouth), which conductivity and salinity levels were as high as 20,800 $\mu\text{S}/\text{cm}$ and 12.4 psu. However, despite the occurrence of *P. orbignyi* in the Soure region, the salt water (salinity >18 psu) of São Caetano de Odivelas (which is only 20 kilometer downstream from Colares Island and 40 kilometer west of the town of Soure) may act as a geographical barrier for potamotrygonids. Thus, an imaginary line between Colares Island and Soure region may be the distributional limits of potamotrygonids in the southern channel of the Amazon estuary during the rainy season.

In spite of the controversial phylogenetic relationships within the Potamotrygonidae family *Plesiotrygon iwamae* is a sister-species of *Potamotrygon* sp. “cururu ray” (Toffoli *et al.* 2008). The former is typically found in the main stem of the Amazon River and is absent in the clearwater of the Tapajós River and the blackwater of the Negro River, while the cururu ray, however, is endemic to the acidic blackwater of the Negro River. It has been widely hypothesized that the absence of any paleogeological event to explain the allopatric speciation between these species led several authors to describe the differences among water types as a geographic barrier driving speciation (Toffoli *et al.* 2008).

The Negro River is known as one the most extreme aquatic environments in the world. The waters are typically acidic and ion-poor with low conductivity and very few dissolved solids. Moreover, the conductivity is associated with a H^+ concentration, as observed by Furch *et al.* (1982). During the rainy season, the water of the Negro River spreads into the forest, forming a habitat locally known as Igapó forest. Igapó forest is characterized by submersed litter, acidic and tea-colored water, and a low dissolved oxygen concentration. Interestingly, this is the preferential habitat of the most common potamotrygonids of the Negro River, the cururu ray. The cururu ray exhibits an unusual epithelial morphology in their gills (Duncan *et al.* 2010) and physiological traits to tolerate acidic and diluted water (Wood *et al.* 2002). *Paratrygon aiereba*, *P. schroederi*, and *P. orbignyi* are commonly found in the shallow water near the beaches of the Negro River islands. The occurrence of *Paratrygon aiereba*, *P. schroederi*, and cururu ray in the Negro River Basin indicates that an ancient lineage of potamotrygonid was well established in this area, and this evidence suggests that some habitats in the Negro River may be hydrographical relics of the paleo-Amazon-Orinoco River in which

the potamotrygonid ancestor has evolved during the Miocene (65-23 million of years ago). There is substantial evidence that the ancestor of *P. motoro* was responsible for the dispersion and radiation of potamotrygonids in different bodies of water in the Amazon Basin (Toffoli *et al.* 2008). This species is widely distributed in the Amazonian rivers surveyed, which suggests a high degree of phenotypic plasticity due to the capacity to osmoregulation in a wide range of ion concentrations, as reported for *Paratrygon aiereba* (Duncan *et al.* 2009).

In the Tapajós River, *Paratrygon aiereba*, *P. motoro*, and *P. orbignyi* are sympatric and syntopic species. In addition, there are at least three undescribed endemic species in the clearwater of the Tapajós River (Marcelo de Carvalho, personal communication). One of these species may be constrained by the whitewater of the Amazon River at the mouth of the Tapajós River and by the rapids at the village of São Luís do Tapajós. It is important to emphasize the absence of volumetrically significant tributaries in the stretch of water that extends from the river mouth to the São Luis do Tapajós rapids. This absence could explain the relative homogeneity in the physicochemical parameters along the same stretch (except near the town of Aveiros, whose variations could be associated with local pollution or mining).

In general, the Tapajós River is a clearwater river and may be physicochemically characterized as exhibiting an intermediary pattern lying between those of the Amazon River and the Negro River water types. The Amazon River is whitewater river that is solute-rich and with a slightly alkaline to neutral pH, while the Negro River is a blackwater (or tea-colored) river that is acidic and solute-poor. This difference between water types could help to explain the zoogeographical distribution of the family Potamotrygonidae in the Amazon Basin, thus facilitating a better understanding of the role of the rivers as geographic barriers or even as selective corridors for the dispersion of potamotrygonid rays.

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