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Freshwater Phytoplankton of Argentina

Phytoplankton of the Paraguay and Bermejo rivers

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With 7 figures and 1 table

Abstract: This article deals with the phytoplankton of the Paraguay and Bermejo rivers, with emphasis on the spatial and temporal patterns of its composition, density, biomass, diversity and community size structure. The phytoplankton of the Paraguay River is characterized by the dominance of small Chlorophyceae and Cryptophyceae, with a gradual increase in Bacillariophyceae towards its confluence with the Paraná River. In the northern stretch, where the Pantanal drains, Bacillariophyceae exceptionally share the dominance with Chlorophyceae and Euglenophyceae. Small Chlorophyceae prevail in transparent waters, whereas *Aulacoseira* (*A. granulata* and *A. herzogii*) predominates throughout the main channel, in relation with a higher turbulence and lower water transparency. Density, biomass, diversity and species richness present an inverse relationship with the hydrometric level. Such variables are positively correlated with water temperature, and present a decrease from north to south in relation to increased suspended solids and conductivity and decreased water transparency. The Bermejo River, which is a main tributary of the Paraguay River in its lower section, is the main determinant of the sharp decrease in the main variables of the phytoplankton in the low Paraguay.

Keywords: phytoplankton, diversity, functional group, Paraguay, Bermejo

Introduction

Plankton dynamic in rivers is controlled by hydrological and hydrodynamic factors, such as discharge and/or water residence time (Reynolds & Descy 1996). Phytoplankton not only is affected by these factors, but also is susceptible to light limitation due to the high turbidity caused by resuspension of solids in turbulent waters. In deep and turbid rivers, the low light regime can thus contribute to the dominance of large diatoms (Reynolds 1994, Rojo et al. 1994). Light conditions may also affect the distribution of phytoplankton size structure. However, in spite of their importance in physiological and ecological processes of the com-

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munity, the size structures and functional groups of phytoplankton have been little explored. Besides, most of this research has been carried out in temperate environments of the northern hemisphere (Chételat et al. 2006), but tropical and subtropical environments, mainly the large South American rivers, are less studied (Uherkovich 1984, O'Farrell & Izaguirre 1994, O'Farrell et al. 1996, Train & Rodrigues 2004, Devercelli 2006, 2010, Zalocar de Domitrovic 1999, 2007, Zalocar de Domitrovic et al. 2007).

The first studies on phytoplankton along the Paraguay River include a comparison between sections and hydrological phases (Zalocar de Domitrovic 1999, 2002), and a detailed analysis in the area close to its confluence with the Paraná River (Bonetto et al. 1981). The size fractions and functional groups of phytoplankton of this river have been analysed along the river channel from the Pantanal to the Delta of Paraná River (Zalocar de Domitrovic 2007). In the Bermejo River, the research has been carried out in the lower section, about 20 km before its mouth (Bonetto et al. 1984).

This article integrates phytoplankton information of the Paraguay and Bermejo rivers, with emphasis on the spatial and temporal patterns of its composition, biomass and size structure. The influence of both rivers is based on the most outstanding limnological features of the Paraná-Paraguay system (Devercelli et al., 2014) and the Chaco-Pampean plain (Zalocar de Domitrovic et al., 2014).

Paraguay River

The Paraguay River (Fig. 1), which has a catchment area of 2.6 x 10^6 km^2 and a very regular discharge, averaging 4550 m^3 (Soldano 1947), is the largest tributary (~ 2550 km) of the Paraná River. It is scarcely disturbed by human activities. The main channel is largely unregulated, with one dam located on a secondary tributary (Frutos et al. 2006). Based on geomorphological and hydrological characteristics, the Paraguay River has two sections: the upper reach (Section 1), which extends from its headwaters in the Matto Grosso (Brazil) to the Apa River confluence and flows through the Pantanal, a great wetland between 140000 and 200000 km^2 (OEA 1971, Tricart & Frecaut 1983), and the lower section or main channel (Section 2), which extends from the Apa to the Paraná River and is not influenced by the Pantanal (Soldano 1947, Neiff 1990). The Pilcomayo River, its longest western tributary, flows into the Paraguay after losing most of its water discharge in the Chaco Plain (Bucher et al. 1993). The Bermejo River, originated in the eastern sector of the Argentine-Bolivian Andes, flows into the Paraguay River 100 km before its confluence with the Paraná River. It supplies more than 60% of the suspended inorganic material to the Lower Paraguay (Drago & Amsler 1988) and causes a high ionic content of the water, with conductivity values between 310 and 850 $\mu S\ cm^{-1}$ (Bonetto et al. 1984). The Bermejo causes modifications in the physical, chemical and biotic characteristics of the Lower Paraguay (Bonetto et al. 1981).

The Paraguay River basin is located in a tropical region. Flooding is distinctly seasonal. During the rainy period (December to March), the lakes and tributary rivers are connected with the main channel of the upper stretch. In the low water phase, some shallow lakes are isolated and their surfaces can be reduced by a factor of four or more in years of drought (Hamilton et al. 1997, Frutos et al. 2006). The high water phase of the river may be delayed by 4 to 6 months after the summer rains, due to the slow passage of floodwaters through the

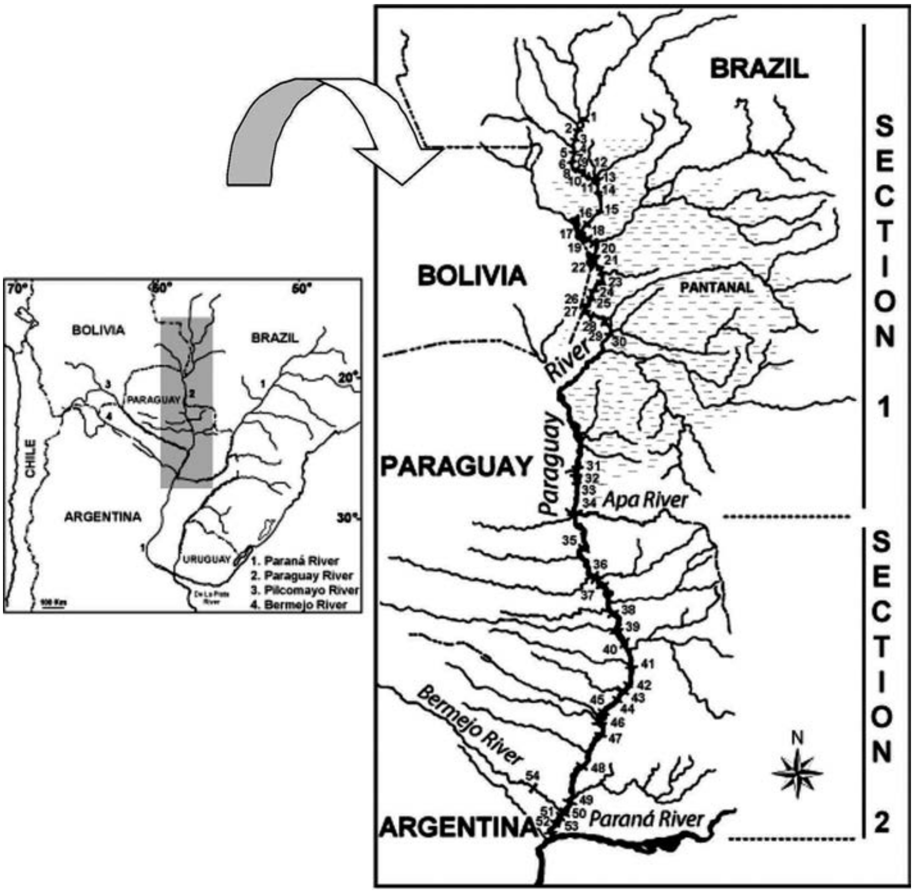

Fig. 1. Location map of the Paraguay and Bermejo rivers showing the sampling sites. Sites 1 to 34: Section 1 (Pantanal); Sites 35 to 53: Section 2 (Paraguay River: main channel). Site 54: Bermejo River (sampling site in its lower stretch).

Pantanal (Hamilton et al. 1996). The latter causes a 'sponge' effect, regulating the river flux downstream, before it reaches the Paraná River.

Abiotic variables. The information of the Paraguay River here presented is based on seasonal and longitudinal river samplings carried out in June–July 1995 (winter) and December 1995–January 1996 (summer) (Zalocar de Domitrovic 1999, 2002). The main environmental variables evaluated are summarized in Table 1. The wide range of variation recorded in the abiotic variables in the upper section is probably related to the fluctuation of the hydrometric levels in the environments of the Pantanal. The presence of vegetated environments, characterized by a high content of organic matter, influences the physical and chemical composition of the tributaries that flow through this sector before reaching the main channel (Da Silva & Esteves 1995, Hamilton et al. 1995, 1996, 1997). In particular, the decrease in pH values and dissolved oxygen is common in lotic waters flowing through wetlands, as large inundated

Table 1. Mean values (± S.D.) of some environmental variables measured in the Paraguay River (1995–1996). U: Mann-Whitney U test (only parameters which are significantly different within section 1 and 2 are indicated); n = number of samples; *** = p less than 0.001; ** = p between 0.001 and 0.01; * = p between 0.01 and 0.05, lw: low waters, hw: high waters (Zalocar de Domitrovic 2002).

	Winter		Summer	
	Section 1 LW	Section 2 HW	Section 1 HW	Section 2 LW
	n = 17	N = 6	N = 22	N = 15
Temperature (ºC)	24.6 (1.3)	*** 19.8(0.9)	30.7 (1.1)	29.8 (1.7)
Sd (cm)	61.8 (35.8)	58.8 (19)	23.9 (11.7)	23.1 (6.8)
pH	6.6 (0.3)	6.5 (0.2)	6.3 (0.5)	*** 7.6 (0.3)
DO (%)	72 (24)	66 (8)	58 (22)	*** 79 (11)
Cond (μS cm^{-1})	40.2 (6.7)	*** 87.5 (12)	61.1 (14)	*** 147.5 (151)
TSS (mg l^{-1})	20.2 (10.4)	55.8 (65.4)	39.4 (27.7)	* 249.5 (499)
$NO_3 + NO_2$ (μg l^{-1})	42 (34)	42 (8)	15 (10.8)	24 (19)
TP (μg l^{-1})	43.3 (19.4)	** 66.7 (9)	60.1 (21.9)	62.5 (11.7)

areas substantially modify the hydrological and limnological characteristics (Mitchel 1973, Rzóska 1974, Talling 1976, Payne 1986, Welcomme 1986).

In the study periods mentioned above, nitrogen and inorganic phosphorus concentrations of the Paraguay River were lower than those recorded in the High Paraná River by Pedrozo et al. in 1988. Hamilton et al. (1997) attributed the scarcity of nutrients of the Paraguay River to the presence of wetlands in its headwaters, where processes such as sedimentation, biotic assimilation and denitrification are usually important (Hamilton & Lewis 1987, Engle & Melack 1993). Likewise, the high transparency of the Paraguay River waters is explained by the sedimentation of suspended solids in the Pantanal during floods (Bucher et al. 1993), as it has been described in the fluvial range of the Taquarí River floodplain before reaching the Paraguay (Hamilton et al. 1998).

Phytoplankton. In the periods here analyzed, phytoplankton showed spatial and seasonal variations along the Paraguay River. Density and biomass were higher in the Pantanal (Section 1) than in the lower stretch (Section 2), where the river flows into the Paraná River (Fig. 2). Biomass was significantly higher in the main channel only in summer. The positive and highly significant correlation found between density, biomass and water temperature ($r_s = 0.46$; $p < 0.001$) may explain the higher values in summer than in winter. Minimum density and biomass mean values were recorded in the lower Paraguay, downstream the confluence with the Bermejo River. In each river section, seasonal differences related to regional hydrology were reflected in the phytoplankton.

In the Pantanal (Section 1), significantly high density of Chlorophyceae (M-W U test = 93; $p < 0.01$) and biomass of Bacillariophyceae (M-W U test = 154; $p < 0.05$) occurred in high waters as compared with low waters. In the lower stretch of the main channel (Section 2) total biomass showed significant differences between high and low waters (M-W U test = 10; $p < 0.01$), in response to increases in Bacillariophyceae, Cyanobacteria and Chlorophyceae in summer (low waters). Chlorophyceae and Cryptophyceae (smaller than 20 µm) predominated along the river channel (Figs. 3 and 4). These groups accounted for 79–93%

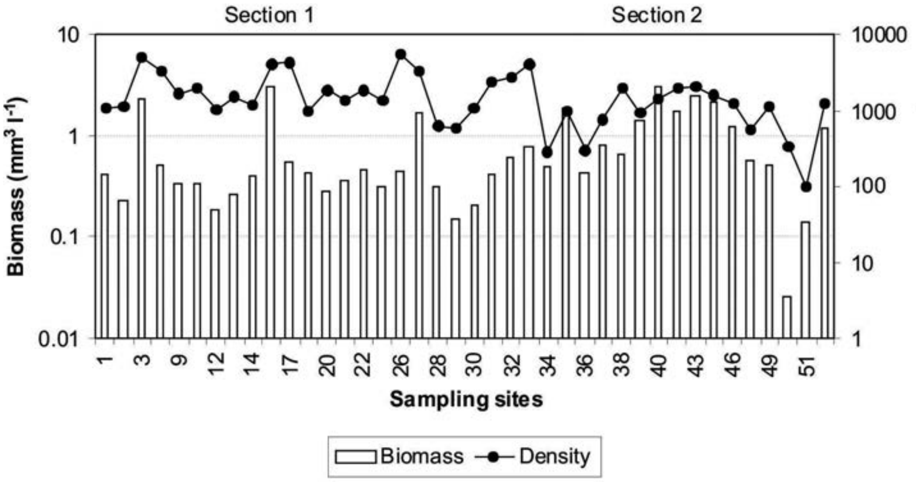

Fig. 2. Average values of phytoplankton density and biomass in the Paraguay River. The horizontal axis indicates the number of sampling sites. Section 1 (Pantanal): 1–33, Section 2: 34–53 (main channel). For sampling sites see Figure 1.

of the total density, with a high proportion of invasive C-strategists (Reynolds 1988, 2006). The dominant species belong to four functional groups (Reynolds et al. 2002): X1 (*Choricystis minor*, *Monoraphidium contortum*, *Nephrochlamys subsolitaria*), X2 (*Chloromonas gracilis, Rhodomonas minuta)*, J (*Crucigenia quadrata*, *Scenedesmus ecornis*) and Y (*Cryptomonas marssonii*, *C. ovata*). These groups are characterized by a high turnover rate, which allows them to survive in conditions of horizontal flow and high turbulence, but also have good strategies to exploit areas of reduced flow (Reynolds 2000), which may simultaneously occur in the transversal section. In the periods studied, the abundance of these taxa decreased downstream, in relation to a decrease in water transparency, which was significantly correlated with suspended solids ($r_s = -0.629$; $p < 0.001$). This scenario is consistent with the pattern described by Bonetto et al. (1979, 1981) for the Lower Paraguay and the initial reach of the Middle Paraná. The low transparency caused by the high content of sediments brought by the Bermejo to the lower section negatively affected density (Fig. 5), biomass and phytoplankton composition, reducing diversity and species richness (Zalocar de Domitrovic 2002).

In the Pantanal, the high density of the fraction smaller than 20 µm (functional groups X1, X2, J and Y) had an important contribution (60–90%) to biomass (Figs. 3 and 4). The larger fraction, with the greatest axial linear dimension (GALD) exceeding 100 µm, contributed to 42% of the biomass and was represented by *Dolichospermum planctonicum* (H_1), *Eudorina elegans* (G), *Synedra* sp. (D) and *Euglena oxyuris* (W1). Downstream the Pantanal region (main channel), Bacillariophyceae dominated and species with GALD exceeding 100 µm prevailed (Fig. 4). This is characterized by the dominance of *Aulacoseira granulata* and its morphotypes (P) and is accompanied in summer by the S-strategists (acquisitives) *Dolichospermum spiroides* and *D. planctonicum* (H_1). Bacillariophyceae gradually increased towards the lower section and were represented by *A. granulata*, *A. herzogii* (P), *Cyclotella meneghiniana* and *Discostella stelligera* (C). *A. granulata* prevailed when water transparency was

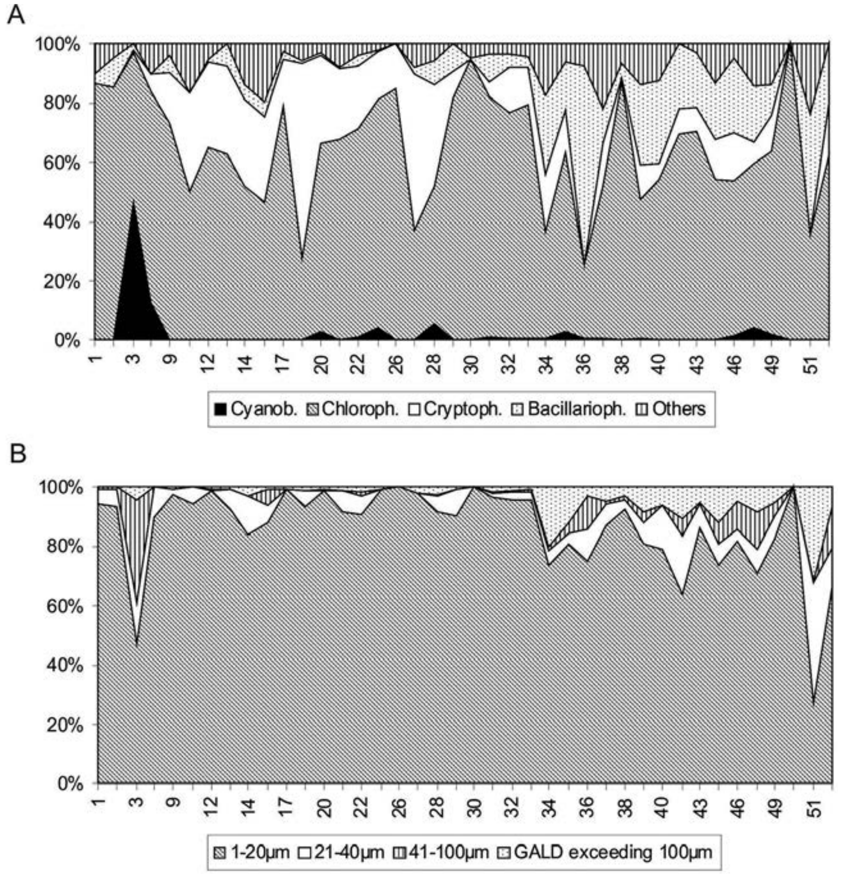

Fig. 3. Relative density of taxonomic groups (**A**) and size fractions grouped according to the GALD (**B**) of phytoplankton in the Paraguay River during the summer sampling (1995–1996). GALD: greatest axial linear dimension.

low (r_s = –0.304; p = 0.003). The low light requirements of Bacillariophyceae (Richardson 1984) would explain the predominance of *A. granulata* in turbid rivers as the Bermejo and in the lower section of the Paraguay. These taxa are not only morphologically adapted, but also physiologically prepared for rapid fluctuations of light conditions in the mixing water column (Kilham & Kilham 1975, Dokulil 1983, O'Farrell et al. 2001). Turbulence and high mixing waters are essential conditions for the development of the R-strategist *A. granulata* (Reynolds 2000). The low depth and turbulence of the tributaries that flow through the Pantanal would explain the low density of this species in the upper section. In Section 2 (main channel), the density of the fraction with GALD exceeding 100 µm (*A. granulata*) increased, while Chlorophyceae and Cryptophyceae (GALD 1–20 µm) decreased. In contrast to that observed for Bacillariophyceae, which have low light requirements, Chlorophyceae markedly diminished after the confluence of the Bermejo River as water transparency reduction would affect its high light requirements (Richardson et al. 1983, Richardson 1984). Small

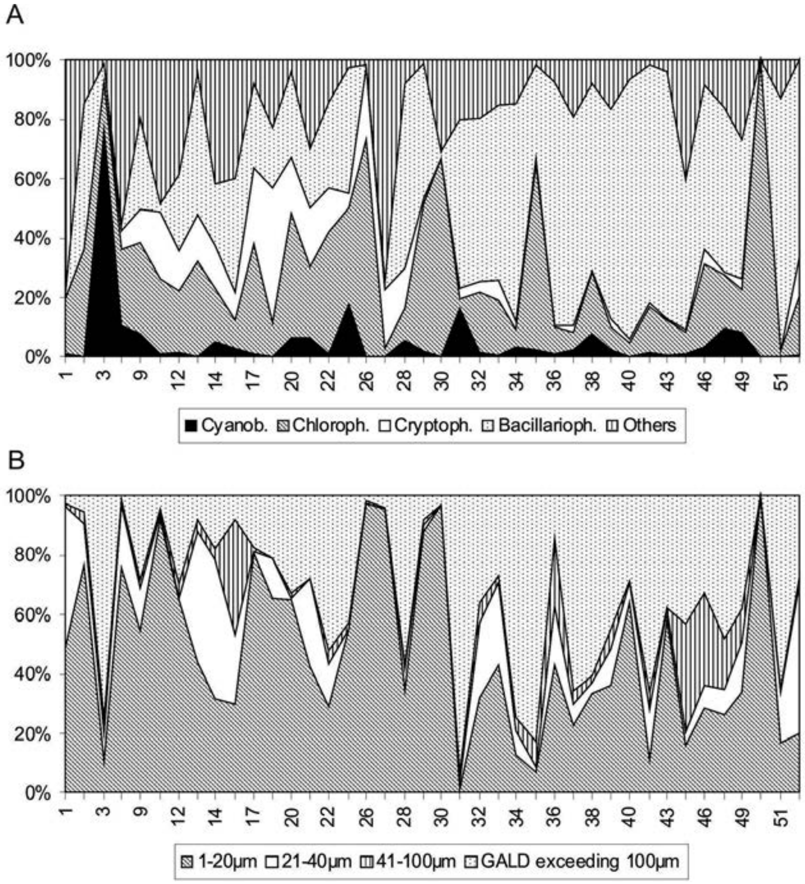

Fig. 4. Relative biomass (biovolume) of taxonomic groups (**A**) and size fractions grouped according to the GALD (**B**) of phytoplankton in the Paraguay River during summer sampling (1995–1996). GALD: greatest axial linear dimension.

Chlorophyceae prevailed in periods of higher water transparency, in agreement with that pointed out by Richardson et al. (1983). These nanoplanktic algae have a high specific affinity for nutrients (Malone 1980, Riegman et al. 1993), belong to the category of C-strategists, and are characterized by their high metabolic rate and high surface area/volume relationship (Reynolds 1988, 2006).

The discontinuity of the physical and chemical characteristics of the waters and of the main phytoplankton variables in the course of the Paraguay River is not consistent with the idea of the 'longitudinal gradient' in natural rivers (Vannote et al. 1980).

Diversity (H) varied between 2.8 and 5 in winter and between 1.5 and 4.9 in summer, and presented a slight inverse relationship with the hydrometric level of each section, with a decreasing tendency towards the south. The H based on biomass varied between 0.8 and 4.9 and between 1.5 and 4.6 in the winter and summer, respectively and presented a wide variability in the upper section, with a tendency similar to that of the H based on density, in the

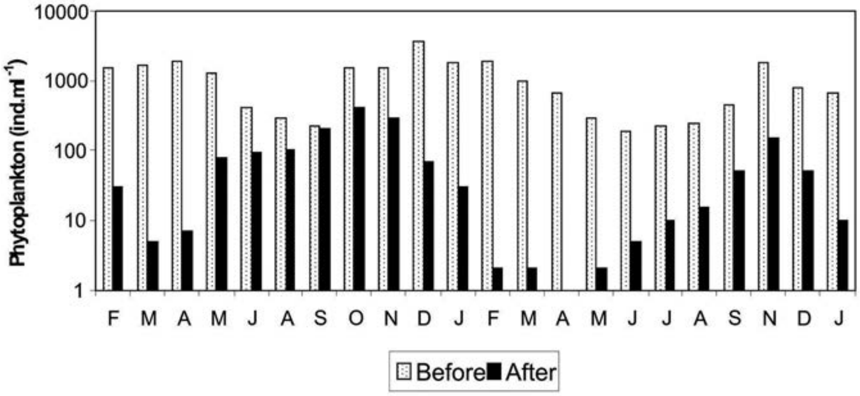

Fig. 5. Phytoplankton density of the Paraguay River before and after the Bermejo River mouth, between February 1978 and January 1979 (Bonetto et al. 1981, Zalocar de Domitrovic unpubl.).

middle and lower sections. Minimum values of H were recorded after the confluence with the Bermejo River in the lower section. Species richness varied between 4 and 105 taxa per sample. Minimum values were recorded in the lower section, near the mouth of the Bermejo River, and maximum values were found in the area of the Pantanal.

Fluvial plankton is characterized by the high number of sporadic species (Margalef 1983), as it has been observed in the Paraguay River, particularly in the Pantanal. The analysis carried out in June–July 1995 and December 1995–January 1996 revealed a total of 600 taxa: 572 in the upper section (Pantanal) and 129 downstream, up to the Paraguay confluence with the Paraná River. Downstream the Pantanal (main channel), there was a predominance of potamoplanktic species. The greatest variety of taxa corresponded to Chlorophyceae (mainly Chlorococcales), followed by Euglenophyceae, Bacillariophyceae and Xanthophyceae. The number of algal species was three times higher in the Paraguay River than in the Paraná (Zalocar de Domitrovic 1999). Although these two rivers presented many species in common, the Paraguay was characterized by a higher diversity of Chlorophyceae, Bacillariophyceae, Euglenophyceae and Xanthophyceae.

The high number of taxa in the upper section contrasts with the low number in the area of confluence with the Paraná, 10º higher in latitude, where the number of species was reduced to a fourth part. In this respect, limnological variables other than the latitudinal factor (Huston 1995), such as reduction of water transparency and water retention time, are determinant of biodiversity. Some authors were interested in relating the number of species found in rivers of temperate regions with that found in rivers of tropical regions (Rojo et al. 1994), but did not find a statistically significant relationship between species richness and latitude. The development of one of the largest wetlands in the world in the Paraguay River basin, which is associated with a great environmental heterogeneity, may explain the high algal diversity at these latitudes (Zalocar de Domitrovic 2002).

Bermejo River

The Bermejo River is an affluent of the lowest stretch of the Paraguay River. It is 1.450 km long, draining a basin of 135.000 km^2. Its sources are located in the eastern Andes Chain, in Bolivia and Argentina, and in the Argentine Puna (Iriondo & Paira 2007). The High Basin (between 21º13’-25º02’S and 63º47’-65º46’W) presents altitudes between 300 and 5.000 m and extreme temperatures between –15º and 46ºC. Local orographic processes determine intense summer precipitations (600–1.000 mm annually). In this section, the river receives all its affluent. In the Low Basin, the river runs through the Chaco-Pampean plain along 800 km, without receiving any affluent until it flows into the Paraguay River (Fig. 1).

The mean annual discharge of the Bermejo River is 600 m^3 s^{-1}, and the hydrological regime follows the precipitation pattern. The low water phase occurs from May to December, with minimum discharges of about 40 m^3 s^{-1} recorded during October. The flood period lasts from January to April, with maximum discharges around 2.000 m^3 s^{-1} during February (Soldano 1947). The uneven relief with scarcely developed soils on easily eroded sandstones and the marked seasonality of precipitations at the High Basin of the Bermejo River contribute to a high rate of solid transport (10^8 t year^{-1}). Phosphorus is transported mainly in particulate form. Pedrozo & Bonetto (1987) found that between 86 and 99% of the total dissolved phosphorus (TDP) was present in the form of soluble reactive phosphorus (SRP). The intense rains originated in the high basin are responsible for the floods in the mid and low sections, causing overflows on both margins. The high concentration of suspended solids reduces markedly the water transparency, creating unfavourable conditions for phytoplankton development.

Phytoplankton. Between February 1978 and January 1979 (Bonetto et al. 1984), the density and diversity of phytoplankton was low, showing a clear inverse relationship with the flux and load of suspended solids (Fig. 6). The highest density (33–170 ind. ml^{-1}) was

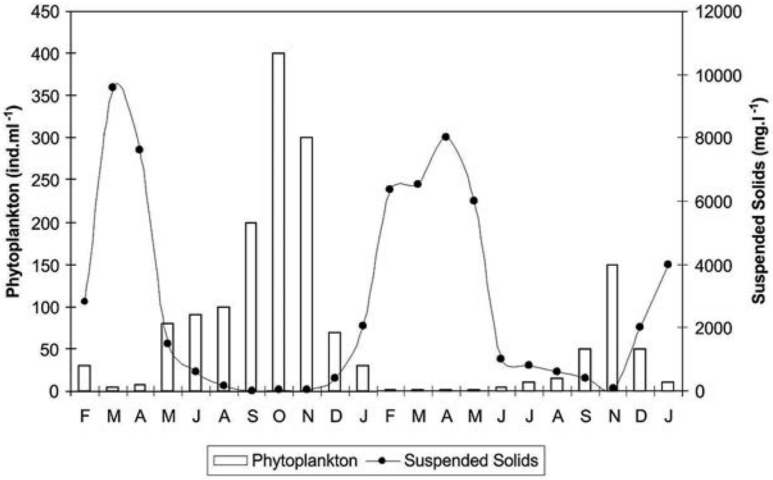

Fig. 6. Phytoplankton density (ind. ml^{-1}) of the Bermejo River in relation to suspended solids (mg l^{-1}), between February 1978 and January 1979 (Bonetto et al. 1984).

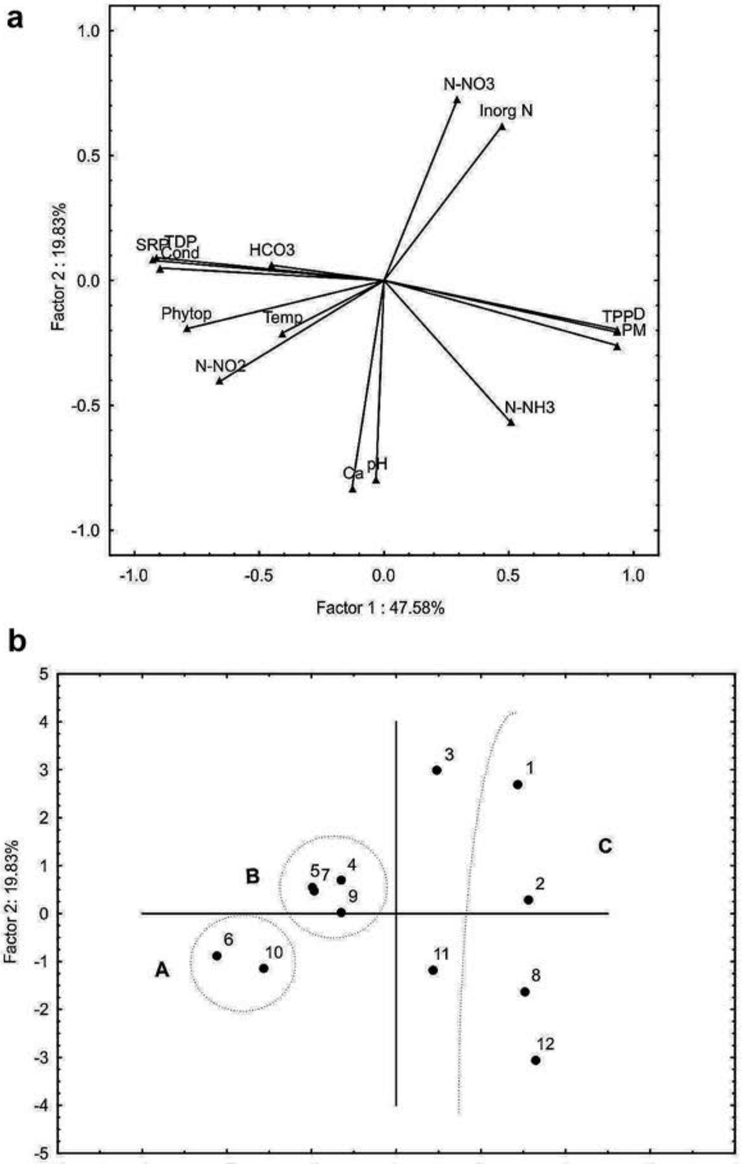

Fig. 7. a) Representation of the first two axes of the Principal Component Analysis using data of phytoplankton density and abiotic variables. **b)** Position of the samples in the space dimensioned by the first two principal components. A: Low waters (discharge less than 70 m^3 s^{-1}), B: Mid-waters (discharge between 200 and 600 m^3 s^{-1}), C: High waters (discharge exceeding 1200 m^3 s^{-1}).

recorded during the low water period (May to December), in relation with a higher water transparency (Secchi disk depth between 7 and 15 cm).

Bacillariophyceae and Chlorophyceae were the most frequent groups. The former was represented by *Aulacoseira granulata* and its morphotypes (functional group P). Chlorophyceae were characterized by low densities of *Monoraphidium contortum* (X1), *Scenedesmus ecornis*, *Desmodesmus communis*, *Monactinus simplex*, *Pediastrum duplex* (J) and *Chloromonas* spp. (X2). During high water periods (January to April), the Secchi disk depth never exceeded 1 cm and density was lower than 4 ind. ml^{-1}, with few diatom specimens and some Chlorococcales. Cryptophyceae were frequently recorded with species of *Cryptomonas* and *Chroomonas*. There were sporadic contributions of Euglenophyceae such as *Euglena* sp. (W1), *Trachelomonas* spp. and *Strombomonas* spp. (W2). Cyanobacteria were recorded during low water periods and high temperatures with *Cylindrospermopsis raciborskii* (S_N), *Dolichospermum* sp. and *Anabaenopsis arnoldii* (H1) as the main contributors.

Chlorophyll *a* was undetectable during high waters and increased up to 3 mg L^{-1} during the low water period. Primary production of phytoplankton also showed maximum values during low water periods (30 mg C m^{-2}, October 1978), in coincidence with the highest phytoplankton density (Pedrozo & Bonetto 1987).

In the ordination of the samples (Principal Component Analysis) of the lower Bermejo River the first three factors explained 78% of the total variation in the data. Factor I (49% of the variance) was positively correlated with suspended particulate matter (PM), discharge (D), and total particulate phosphorus (TPP) and negatively correlated with TDP, SRP, conductivity and total phytoplankton (Fig. 7 A). Factor II (19%) was positively correlated with nitrates (N-NO_3) and inorganic N, and negatively correlated with pH and Calcium. No de-finite groups merged from this ordination according to the first two axes. Nevertheless, a hydrological gradient, starting with high water samples arranged on the right (January to April) towards low water samples located on the left (May to December), was observed (Fig. 7 B)

Final remarks

The Paraguay River presents different physical and chemical characteristics in its longitudinal dimension that are reflected in the phytoplankton development. Density and specific diversity decrease and changes in composition occur from the Pantanal to the Lower Paraguay River, mainly influenced by the high spatial heterogeneity and water residence time related to the Pantanal floodplain, and the marked transparency decrease caused by suspended solids input from the Bermejo River to the Lower Paraguay. The predominance of Bacillariophyceae and Chlorococcales in the Paraguay, and Bermejo, as in the Paraná (see Devercelli et al., 2014), represents a general characteristic of large rivers. The Pantanal Section is enriched with groups typical of floodplain water bodies (Euglenophyceae, Chlorophyceae, Bacillariophyceae and Xanthophyceae). Nevertheless, when extreme turbid conditions prevail at the Lower Paraguay and at the Bermejo, Chlorophyceae sensitive to light depletion diminish their contribution. The hydrosedimentological regime plays a steering role in the phytoplankton dynamics of these large South American rivers.

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