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Structure and variation of the Paraguay River phytoplankton in two periods of its hydrological cycle

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Abstract

The structure and distribution of the Paraguay River phytoplankton (between 16° 03′ and 26° 53′ S and between 57° 13′ and 58° 23′ W was studied during June–July/95 and December/95–January/96. Phytoplankton density values were lower in winter (mean value between 731 and 878 ind. ml^{-1}) in summer (between 1113 and 1876 ind. ml^{-1}), and mean biomass (biovolume) ranged between 0.215 and 0.372 $mm^3\ l^{-1}$ and between 0.586 and 1.223 mm^3 respectively. In all, 332 algal taxa were identified: 298 in the upper section (Pantanal) and 143 in the middle and lower sections. They pertained to the Cyanophyta, Chlorophyta, Euglenophyta, Cryptophyta, Pyrrhophyta, Bacillariophyceae, Chrysophyceae and Xanthophyceae. Small Chlorophyta (*Chloromonas gracilis*, *Choricystis minor, Crucigenia quadrata, Scenedesmus ecornis, Monoraphidium contortum* and *M. minutum*) and Cryptophyta (*Cryptomonas marssonii, C. ovata* and *Rhodomonas minuta*) dominated. Bacillariophyceae (genera *Aulacoseira* and *Cyclotella*) increased in the lower section of the river. Biomass was dominated by centric forms of the genus *Aulacoseira* (*A. granulata* and its morphotypes, and *A. herzogii*). The diversity index varied between 1.99 and 5.0 bits ind.$^{-1}$ in winter and between 1.49 and 4.87 bits ind.$^{-1}$ in summer. Species richness (between 4 and 105 taxa per sample) showed a decrease in north–south direction. The presence of one of the largest wetlands of the world may explain the high algal diversity in the upper section. The Bermejo River, with highly mineralized waters and a high content of suspended solids, causes a strong discontinuity in the lower section of the main course, viz, a decrease in water transparency and in the density, biomass, diversity and species richness values of phytoplankton, before its waters meet the Paraná River.

Introduction

Most phytoplankton investigations in lotic environments around the world were carried out in the temperate zone, mainly in Europe (Rojo et al., 1994). The study of phytoplankton of tropical rivers with large floodplains is still fragmentary and its knowledge restricted to monographs by Rzóska (1976), Sioli (1984) and A. A. Bonetto (1976) for the Nile, Amazon and Paraná Rivers, respectively.

South America is characterized by a huge fluvial net, which is why Margalef (1983) called it the 'river country' In spite of this fact, only few studies on phytoplankton ecology in these fluvial ecosystems exist. Most information comes from the Amazon and Orinoco basins (Uherkovich, 1984; Vásquez & Sánchez, 1984; Sánchez & Vásquez, 1986; Lewis, 1988; Putz & Junk, 1997). In the La Plata basin, studies were carried out on the Argentinian section of the Paraná and Uruguay Rivers (Zalocar de Domitrovic & Vallejos, 1982; A. A. Bonetto et al., 1982; Bonetto et al., 1983; García de Emiliani, 1990; O'Farrell & Izaguirre, 1994; Tell et al., 1994; Zalocar de Domitrovic & Maidana, 1997; Zalocar de Domitrovic, 1999), but there are no previous phytoplankton studies on the Paraguay River. Partial results are known for only part of the lower section of the river (Bonetto et al., 1981).

The Paraguay River harbours one of the largest wetlands in the world within its basin (Neiff, 1990). Recent investigations of algal communities in some

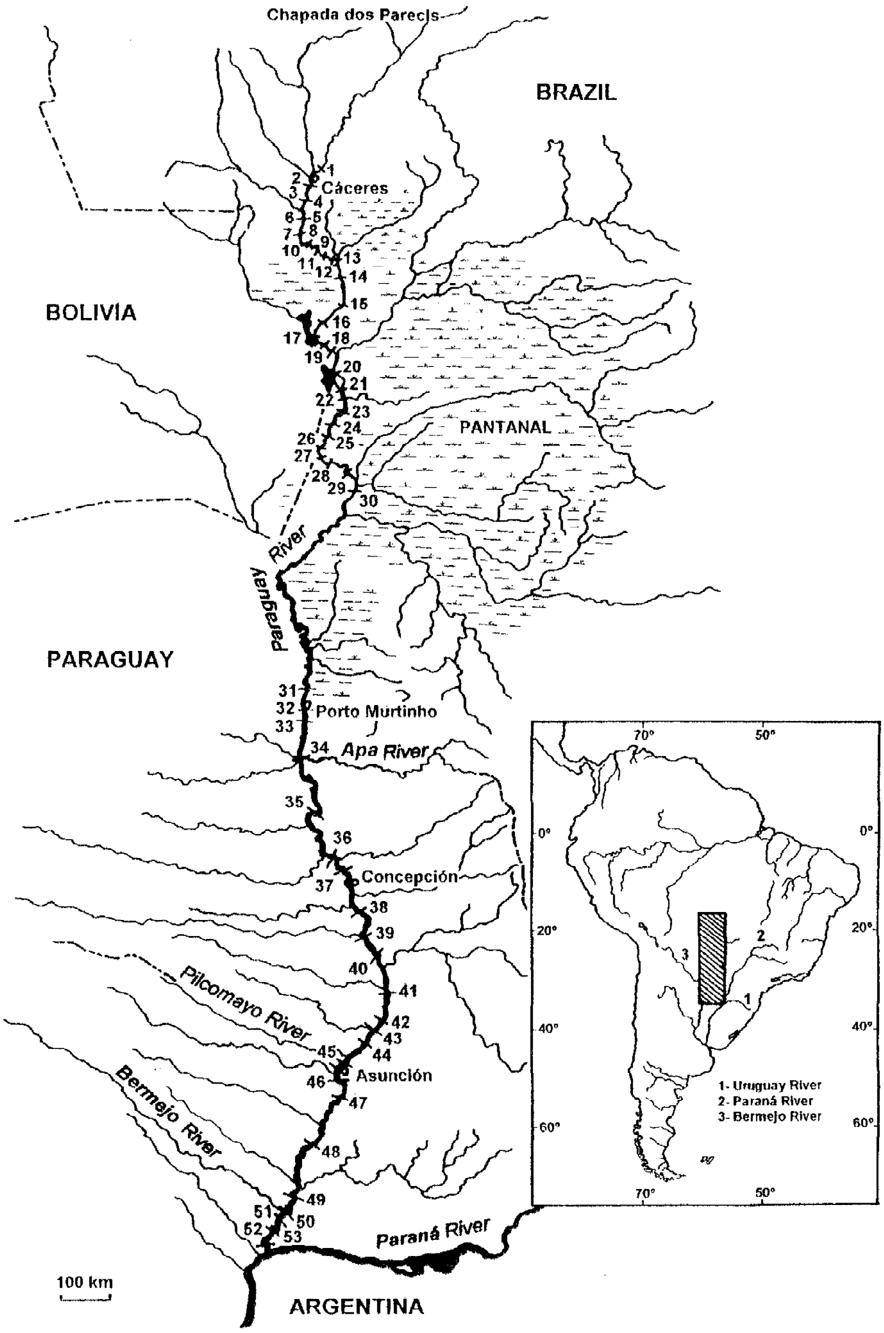

Figure 1. Location map of the Paraguay River showing the sampling stations. Numbers 1–34: Section 1 (Upper Paraguay or feeding basin); Numbers 35–53: Section 2 (Middle Paraguay: numbers 35–47, Lower Paraguay: numbers 48–53). References are shown in Table 1.

wetlands north of the Pantanal of Mato Grosso (Brazil) revealed a high local biological diversity (De-Lamónica-Freire, 1992; De-Lamónica-Freire & Heckman, 1996).

It is generally accepted in phytoplankton ecology that the biological number of species increases downstream, suggesting that a river is a continuum (Vannote et al., 1980). In tropical rivers, such as the Paraguay, the longitudinal gradient can be distorted by geographic heterogeneities: wetland development, and input of turbid waters (coming from the Andes). River sections adjacent to wetlands are expected to have higher biodiversity. These hypotheses were tested on the Paraguay River to study the influence of the Pantanal. Abundance, biomass, diversity and species richness of phytoplankton were analyzed in relation to environmental variables during two periods of the hydrological cycle.

Study area

The study area includes the main channel of the Paraguay River along more than 2000 km of navigation, between the basin (Cáceres Port) and the Paraná River (between 16° 03′ and 26° 53′ S and between 57° 13′ and 58° 23′ W) (Fig. 1).

Similarly to other rivers of the La Plata basin (e.g. Paraná, Uruguay), the Paraguay River has a predominant north–south direction, with neutral to slightly acid waters and sediments from geological erosion of the Brazilian shield (Neiff, 1996). It is one of the more important tributaries of the Paraná River; however, it remains not much affected by anthropic activities.

The Paraguay River rises in the central region of the Mato Grosso (Brazil), in the Chapada dos Parecis high plain, which separates this hydrographic basin from the great Amazonian basin (A. A. Bonetto, 1994). It has a length of 2550 km, with a basin of 1100 000 km^2 and a very regular discharge, averaging 4550 m^3 (Soldano, 1947).

This river harbours one of the largest wetlands of the world, occupying a surface of 140 000–200 000 km^2 (OEA, 1971; Tricart & Frecaut, 1983). The largest part of this region (Pantanal) is found in Brazil, with smaller areas in the west of Bolivia and Paraguay. In this sector, the river bed runs by the west side, collecting the water of various tributaries and the non-canalized influx of this large floodplain. Margins are plain, with low drainage capacity. Floodings from the Paraguay River and the tributaries cover large extensions and produce a gradual drainage downstream (Arduino, 1990).

Based on geomorphological and hydrological characteristics, Soldano (*op. cit.*) divided the Paraguay River into two sections: 1 – Upper section or basin (from the source to the Apa River), and 2 – The discharge channel (from the Apa River to the confluence with the Paraná River). The latter was subdivided into Middle Paraguay (from the Apa River to Itá Pirú Point, 47 km south of Asunción, Paraguay) and Lower Paraguay (between Itá Pirú Point and the confluence with the Paraná River).

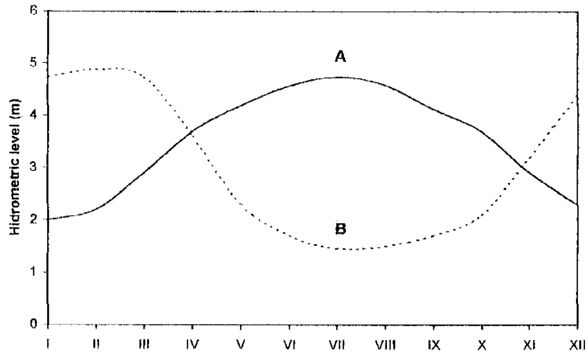

Figure 2. Inter-annual variation patterns in the hydrometric level (in meters) of the Paraguay River, showing the 'sponge' effect of the Pantanal. (A) after the Pantanal, (B) before the Pantanal. Data taken from Soldano (1947).

According to Troll's seasonal classification (OEA, 1969), the Paraguay River basin belongs to a tropical area. The upper section has summer rains (7–9 months), changing gradually to the middle and lower sections with no rainy season (9–12 months). The mean rain value in the basin is approximately 1350 mm per year. There are more rains (November–March) in the north than in the southeast of the Pantanal. In this region, floods are differently seasonal and they tend to unbalance after the rains, due to the slow passage through the Pantanal (Hamilton et al., 1996). The latter performs a 'sponge' effect, regulating the river flux downstream and slowing from 4 to 6 months the flood wave, before the arrival to the Paraná River (Fig. 2).

The longitudinal slope of the basin is very reduced, so the river shows a very stable regime throughout the annual cycle, although presenting a modification of phases between the upper and lower river. In the latter, near the confluence with the Paraná River, the hydrological regime gets more irregular due to the discord with that of the tributaries (Pilcomayo and Bermejo), which have summer floods. The Bermejo River (of 'white water' *sensu* Neiff, 1990), originated in the east sector of the Argentine-Bolivian Andes, has a high content of suspended solids, giving to the Lower Paraguay more than 60% of the suspended inorganic matter (Drago & Amsler, 1988). The Bermejo waters have a high ionic content, with conductivities between 310 and 850 $\mu S\ cm^{-1}$ (A. A. Bonetto et al., 1984). This produces modifications in the physical, chem-

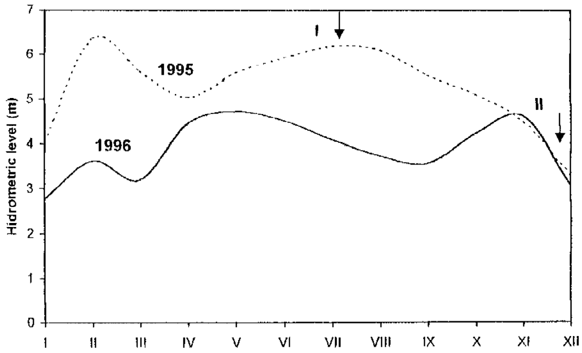

Figure 3. Hydrometric level (in meters) of the Paraguay River downstream of the Pantanal, in the middle section (Pilcomayo Port), during the years 1995 and 1996. Arrows indicate the two sampling periods. I: winter sampling (June–July/95), II: summer sampling (December/95–January/96).

ical and biotic characteristics of the Lower Paraguay (Bonetto et al., 1981).

Materials and methods

Two sections were considered for the study of the Paraguay River: 1 – Pantanal and 2 – Discharge channel. Two seasonal samplings were carried out (June–July/95 and December/95–January/96), in winter and summer, respectively. During the first sampling, the Pantanal was in low waters and the discharge channel in high waters. The inverse situation was found during the second sampling (Fig. 3).

Fifty three sampling sites were established in the central area of the river bed (Fig. 1, Table 1). At each site, phytoplankton subsuperficial samples were collected. For the taxonomic analysis of phytoplankton, samples were taken with a 25 μm mesh size plankton net and fixed in 4% formalin. For the quantitative analysis, 300 cm^3 samples were taken and fixed in Lugol's solution using glacial acetic acid for flagella conservation. Density and biomass were estimated following methods by Utermöl (1958) and Lund et al. (1958), using an inverted microscope. To calculate biomass (biovolume), species were approximated to simple geometric or combined forms (Edler, 1979; Rott, 1981). Species diversity (H') was estimated using the Shannon–Wiener index (Shannon & Weaver, 1963) from the density data (bits ind.$^{-1}$). Species richness (SR) was referred to the number of algal taxa in each sample. The taxonomic name of phytoplankton groups follows that of Bold & Wynne (1985).

At most sampling stations, *in situ* measurements of water temperature, transparency (using a 25 cm diameter Secchi disk), pH (Metrohm A G Herisau digital pH meter), electric conductivity (YSI 33 SCT conductometer) and dissolved oxygen (YSI 54 A oxygen meter) were carried out.

The analysis of nitrogen (NO_3+NO_2), total phosphorus, and those of suspended solids were carried out by staff of the Chemical and Edaphology Laboratories of the CECOAL, following techniques by APHA (1981).

Environmental variables were correlated using the Spearman Rank Order Correlations index (Steel & Torrie, 1988). A Mann–Whitney U test (M–W) (Sokal & Rohlf, 1979) was used to test for differences between groups of seasonal samples (high waters vs low waters) and spatial samples (section 1 vs section 2). A multivariate analysis studied the group of abiotic variables in relation to phytoplankton abundance, total biomass, diversity index and species richness. For the Principal Component Analysis (PCA), the MVSP program (Multi-Variate Statistical Package), version 2.1 (Kovach, 1986–1993), was run.

Results

Abiotic variables

In Table 2, the arithmetic mean and standard deviation of environmental variables in the Pantanal and in the discharge channel of the Paraguay River are shown in relation to the hydrometric levels.

In winter, there were significant differences in water temperature between the two sections of the river (M–W U test = 0; $p<0.001$), being higher in the Pantanal. Conductivity (M–W U test = 0; $p<0.001$) and total P concentration (M–W U test = 11.5; $p<0.01$) also showed significant spatial variation (with lower values in the Pantanal).

In summer, a higher number of abiotic variables showed significant differences between the two sections of the river (Table 2). At the south (between the Pantanal and the confluence with the Paraná River), there was an increase in electric conductivity (M–W U test = 0; $p<0.001$), dissolved oxygen (M–W U test = 0; $p<0.001$), pH (M–W U test = 6; $p<0.001$) and suspended solids (M–W U test = 99; $p<0.05$).

Water transparency, although did not show significant differences between both sections of the river, was negatively correlated with suspended solids ($r_s = -0.53$; $p<0.001$).

Table 1. References of sampling stations (N: number, location and date) in the Paraguay River, pointed out in the map of Figure 1. I: winter sampling (June–July/95); II: summer sampling (December/95–January/96); w. d.: without data

N	G.P.S. Location	Date	
1	Cáceres (upstream) 16° 03′ 44″ S; 57° 48′ 24″ W	07/12/95	II
2	Cáceres (Center) 16° 03′ 56″ S; 57° 41′ 23″ W	26/06/95 (07/12/95)	I(II)
3	Cáceres (in front of Yat Club) 16° 02′ 42″ S; 57° 40′ 47″ W	07/12/95	II
4	Cáceres, Randón Port; 16° 04′ 28″ S; 57° 42′ 05″ W	26/06/95	I
5	Upstream mouth of Jaurú River; 16° 22′ 19″ S; 57° 46′ 04″ W	27/06/95	I
6	km 2083; 16° 41′ 57″ S; 57° 50′ 39″ W	28/06/95	I
7	km 2066; 16° 43′ 08″ S; 57° 45′ 10″ W	28/06/95	I
8	km 2049 (Bracinho stream) 16° 55′ 59″ S; 57° 26′ 01″ W	28/06/95 (08/12/95)	I(II)
9	km 2032 (upstream mouth of Bracinho stream) 16° 50′ 54″ S; 57° 35′ 49″ W	28/06/95 (08/12/95)	I(II)
10	km 2122 (downstream mouth of Jaurú River) 16° 24′ 32″ S; 57° 46′ 58″ W	28/06/95 (09/12/95)	I(II)
11	km 2025; 16° 51′ 24″ S; 57° 34′ 29″ W	28/06/95	I
12	Mouth of Sararé stream; 16° 58′ 13″ S; 57° 23′ 19″ W	08/12/95	II
13	In front of mouth Sararé stream; 16° 58′ 17″ S; 57° 23′ 28″ W	08/12/95	II
14	Taiamá (right bank) 16° 51′ 31″ S; 57° 33′ 51″ W	09/12/95	II
15	Taiamá (Center) 16° 50′ 38″ S; 57° 35′ 08″ W	09/12/95	II
16	km 1795; w.d.	01/07/95	I
17	In front of Gaíba lake (Bolivia) 17° 43′ 16″ S; 57° 43′ 16″W	01/07/95 (09/12/95)	I(II)
18	km 1782; 17° 44′ 58″ S; 57° 36′ 56″ W	01/07/95	I
19	km 1749 (upstream mouth of Cuiaba River) 17° 52′ 47″ S; 57° 28′ 41″ W	01/07/95 (13/12/95)	I(II)
20	Upstream of Fazenda Amolar; 18° 00′ 11″ S; 57° 27′ 22″ W	14/12/95	II
21	Downstream of Fazenda Amolar; 18° 00′ 11″ S; 57° 27′ 22″ W	14/12/95	II
22	Fazenda Amolar; 18° 32′ 29″ S; 57° 29′ 06″ W	14/12/95	II
23	km 1726; 17° 50′ 08″; 57° 30′ 00″ W	01/07/95	I
24	km 1570; w.d.	02/07/95	I
25	3,5 km upstream of Corumbá; w.d.	11/12/95	II
26	In front of Cáceres lake (Bolivia) 18° 58′ 51″ S; 57° 44′ 15″ W	11/12/95	II
27	Tamengo channel; 18° 58′ 44″ S; 57° 43′ 06″ W	07/07/95 (11/12/95)	I(II)
28	Ladario Port; 19° 00′ 01″ S; 57° 35′ 44″ W	07/07/95 (11/12/95)	I(II)
29	Taquarí River mouth; 19° 14′ 33″ S; 57° 13′ 34″ W	15/12/95	II
30	Manga Port; 19° 15′ 42″ S; 57° 14′ 17″ W	15/12/95	II
31	Murtinho Port (right bank) 21° 43′ 00″ S; 57° 54′ 53″ W	11/07/95 (05/12/95)	I(II)
32	Murtinho Port (Center) 21° 43′ 00″ S; 57° 54′ 53″ W	11/07/95 (05/12/95)	I(II)
33	Murtinho Port (left bank) 21° 43′ 00″ S; 57° 54′ 53″ W	05/12/95	II
34	Apa River mouth; 22° 03′ 07″ S; 58° 00′ 11″ W	06/12/95	II
35	Pinasco Port; 22° 39′ 22″ S; 59° 52′ 47″ W	08/12/95	II
36	Aquidaban River mouth (right bank) 23° 05′ 37″ S; 57° 37′ 33″ W	08/12/95	II
37	Aquidaban River mouth (left bank) 23° 07′ 11″ S; 57° 37′ 55″ W	08/12/95	II
38	Sete Puntas River mouth; 23° 40′ 05″ S; 57° 23′ 07″ W	09/12/95	II
39	Monte Lindo River mouth; 23° 54′ 39″ S; 57° 18′ 13″ W	09/12/95	II
40	San Pedro River mouth; 24° 06′ 07″ S; 57° 13′ 01″ W	09/12/95	II
41	Negro River mouth; 24° 25′ 33″ S; 57° 10′ 03″ W	09/12/95	II
42	Villa Hayes River mouth; 25° 06′ 47″S; 57° 31′ 40″W	10/12/95	II
43	Confuso River mouth; 25° 08′ 36″ S; 57° 32′ 26″ W	10/12/95	II
44	Upstream Asunción Port; 25° 13′ 49″ S; 57° 34′ 51″ W	10/12/95	II
45	Pilcomayo Port (right bank) 25° 22′ 03″ S; 57° 38′ 55″ W	22/06/95	I
46	Pilcomayo Port (left bank) 25° 22′ 03″ S; 57° 38′ 55″ W	22/06/95 (04/12/95)	I(II)
47	Dalmacia; 25° 39′ 10″ S; 57° 44′ 25″ W	23/06/95	I
48	Formosa; 26° 03′ 27″ S; 57° 56′ 15″ W	23/06/95 (04/12/95)	I(II)
49	Colonia Cano; 26° 51′ 45″ S; 58° 22′ 29″ W	05/12/95	II
50	Bermejo River mouth; 26° 51′ 37″ S; 58° 23′ 08″ W	05/12/95	II

Continued on p. 182

Table 1. Continued.

N	G.P.S. Location	Date	
51	Bermejo Port; 26° 52′ 09″ S; 58° 22′ 52″ W	25/06/95 (05/12/95)	I(II)
52	Downstream mouth of Bermejo River; 26° 53′ 32″ S; 58° 22′ 14″ W	06/12/95	II
53	25 km downstream mouth of Bermejo River; w.d.	26/06/95	I

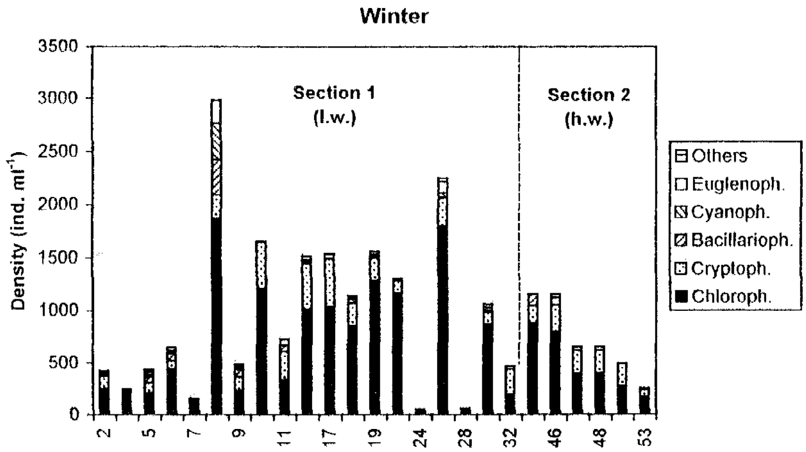

Figure 4. Spatial variations in phytoplankton density (ind. ml^{-1}) in the Paraguay River during the winter sampling (June–July/95). Others: Pyrrhophyta + Chrysophyceae + Xanthophyceae; l.w.: low water; h.w.: high water.

Marked seasonal variations were found in each section of the river for water temperature, pH and concentration of nitrites+nitrates (M–W U test, Table 3).

Phytoplankton

In Figures 4–7, phytoplankton showed clear seasonal variations. A positive and highly significant correlation between density, biomass and water temperature ($r_s = -0.46$; $p<0.001$) may explain higher values in summer than in winter (Table 4).

Spatial variation along the Paraguay River revealed a higher density of phytoplankton in the Pantanal (mean density between 878 and 1876 ind. ml^{-1}) than in the discharge channel (between 731 and 11113 ind. ml^{-1}) (Table 5, Figs 4 and 5). Biomass did not show significant differences between both sections of the river in winter, with means of 0.372 and 0.215 mm^3 l^{-1}, for sections 1 and 2, respectively (Fig. 6). In summer, biomass was significantly higher in section 2 (mean = 1.233 mm^3 l^{-1}) than in section 1 (mean = 0.586 mm^3 l^{-1}) (Table 5, Fig. 7).

In each section of the river, seasonal differences (related to regional hydrology) were reflected in the phytoplanktonic community (Table 6). In the Pantanal, total density showed statistically significant differences between high and low waters (M–W U test = 113; $p<0.01$). These differences were produced by Chlorophyta (M–W U test = 93; $p<0.01$), very abundant in summer (high waters). In this sampling, an increase in pennated diatoms (*Synedra* sp.) produced seasonal differences in Bacillariophyceae biomass (M–W U test = 154; $p<0.05$).

In section 2 of the river, there was a higher variation in density and biomass of phytoplankton groups (Table 6). Total biomass showed significant differences between high and low waters (M–W U test = 10; $p<0.01$), produced by an increase in Bacillariophyceae, Cyanophyta and Chlorophyta biomass in summer (low waters). In parallel, Bacillariophyceae, Cyanophyta, Cryptophyta and the other groups (Pyrrhophyta+Chrysophyceae+Xanthophyceae) increased their density, showing significant differences between winter and summer samplings (M-W U test, Table 6).

There was a high density of Chlorophyta and Cryptophyta (Figs 4 and 5). The first one predominated throughout the river in both samplings, with representatives of unicellular Volvocales (*Chloromonas gracilis*) and Chlorococcales (*Choricystis minor,*

Table 2. Mean values (±S.D.) of some environmental variables measured in the Paraguay River. U: Mann–Whitney U test (only parameters which are significantly different between sections 1 and 2 of the river have been indicated); n = number of samples

Environmental variables	Winter			Summer		
	Section 1 low water ($n = 17$)	Section 2 high water ($n = 6$)	U value	Section 1 high water ($n = 22$)	Section 2 low water ($n = 15$)	U value
Temperature (°C)	24.6 (1.3)	19.8 (0.9)	0***	30.7 (1.1)	29.8 (1.7)	
Secchi disk (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)	6***
Dissolved oxygen (% saturation)	72 (24)	66 (8)		58 (22)	79 (11)	0***
Conductivity (μS cm^{-1})	40.2 (6.7)	87.5 (12)	0***	61.1 (14)	147.5 (151)	0***
Suspended Solids (mg 1^{-1})	20.2 (10.4)	55.8 (65.4)		39.4 (27.7)	249.5 (499)	99*
$N0_3$+$N0_2$ (μg l^{-1})	42 (34)	42 (8)		15 (10.8)	24 (19)	
TP (μg l^{-1})	43.3 (19.4)	66.7 (9)	11.5**	60.1 (21.9)	62.5 (11.7)	

*** = $p < 0.001$; ** = $0.001 < p < 0.01$; * = $0.01 < p < 0.05$

Table 3. Mann–Whitney U test for environmental variables between low and high waters in the sections 1 and 2 of the Paraguay River. Only parameters which are significantly different between low and high waters have been indicated. n = number of samples

Environmental variables	Section 1 ($n = 39$)		Section 2 ($n = 21$)	
	U value	p value	U value	p value
Temperature (°C)	0	***	0	***
Secchi disk (cm)	25	***	7	**
pH	75.5	**	1	***
Dissolved oxygen (% saturation)	102	*	8	**
Conductivity (μS cm^{-1})	22.5	***	20	*
NO_3+NO_2(μg l^{-1})	90.5	**	16.5	*
TP (μg l^{-1})	87.5	**		

*** = $p < 0.001$; ** = $0.001 < p < 0.01$; * = $0.01 < p < 0.05$.

Table 4. Spearman rank correlations coefficients between environmental variables and phytoplankton attributes in the Paraguay River ($n = 60$ observations)

	Density	Biomass	Diversity	Species richness
Temperature	0.45***	0.46***	0.05	0.02
Secchi disk	0.01	−0.03	0.20	0.27*
pH	−0.14	0.25*	0.15	0.18
Dissolved oxygen	−0.16	0.07	0.13	0.02
Conductivity	0.08	0.32**	0.00	−0.04
Suspended solids	−0.27*	−0.03	−0.12	−0.20
Nitrites+Nitrates	−0.33**	−0.32**	0.17	0.10
Total Phosphorus	0.05	0.25*	−0.04	−0.10
Latitude	−0.16	0.10	−0.16	−0.19

*** $= p < 0.001$; ** $= 0.001 < p < 0.01$; * $= 0.01 < p < 0.05$

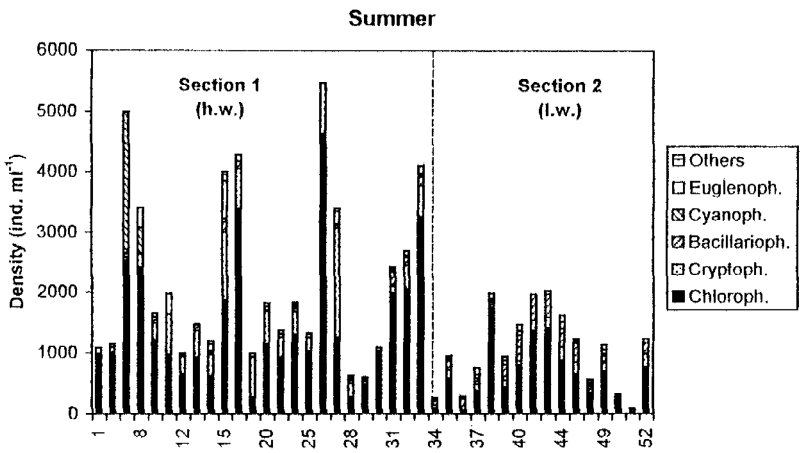

Figure 5. Spatial variations in phytoplankton density (ind. ml^{-1}) in the Paraguay River during the summer sampling (December/95–January/96). Others: Pyrrhophyta + Chrysophyceae + Xanthophyceae; l.w.: low water; h.w.: high water.

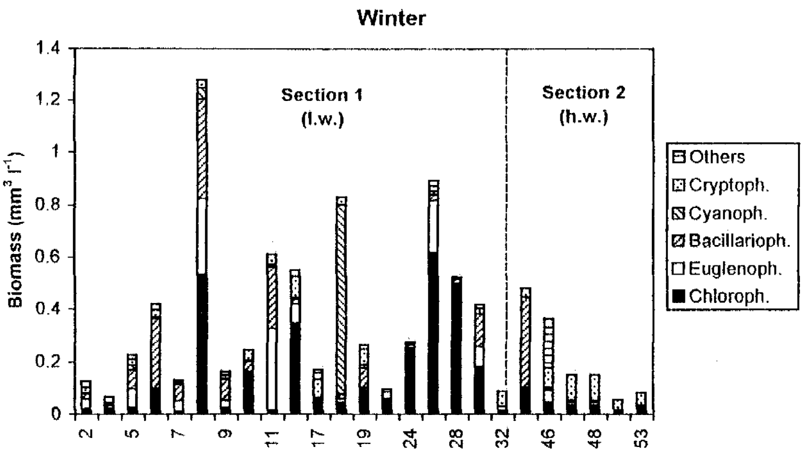

Figure 6. Spatial variations in phytoplankton biomass (mm^3 l^{-1}) in the Paraguay River during the winter sampling (June–July/95). Others: Pyrrhophyta + Chrysophyceae + Xanthophyceae; l.w.: low water; h.w.: high water.

Table 5. Mean values (±S.D) of phytoplankton density (D: ind. ml^{-1}); biomass (B: mm^3 l^{-1}); diversity index (bits $ind.^{-1}$); species richness (number of taxa for sample). U: Mann–Whitney U test (only parameters which are significantly different between sections 1 and 2 of the river have been indicated); n = number of samples; Other Groups: Pyrrhophyta + Chrysophyceae + Xanthophyceae

Phytoplankton		Winter			Summer		
		Section 1 low water (n = 17)	Section 2 high water (n = 6)	U value	Section 1 high water (n = 22)	Section 2 low water (n = 15)	U value
Chlorophyta	D	604	488		1,233	702	96*
		(548)	(287)		(806)	(492)	
	B	0.139	0.042		0.111	0.211	
		(0.170)	(0.033)		(0.083)	(0.288)	
Cryptophyta	D	161	191		315	106	84**
		(134)	(63)		(276)	(80)	
	B	0.027	0.065	16**	0.051	0.029	
		(0.022)	(0.028)		(0.069)	(0.039)	
Bacillariophyceae	D	42	20		69	211	71**
		(79)	(44)		(68)	(137)	
	B	0.085	0.064		0.181	0.824	55***
		(0.108)	(0.137)		(0.250)	(0.746)	
Euglenophyta	D	29	25		91	31	
		(52)	(28)		(151)	(28)	
	B	0.059	0.013		0.122	0.048	
		(0.095)	(0.017)		(0.252)	(0.052)	
Cyanophyta	D	28	0	6*	136	8	
		(81)	(0)		(498)	(10)	
	B	0.049	0	6*	0.100	0.023	
		(0.174)	(0)		(0.378)	(0.019)	
Other Groups	D	14	6	6*	32	55	
		(13)	(15)		(42)	(61)	
	B	0.012	0.031	6*	0.021	0.088	
		(0.011)	(0.076)		(0.029)	(0.219)	
Total	D	878	731		1,876	1,113	107*
		(765)	(363)		(1,248)	(630)	
	B	0.372	0.215		0.586	1.223	96*
		(0.318)	(0.170)		(0.708)	(0.899)	
Diversity index		3.8	3.2		3.5	3.8	
		(0.6)	(1.1)		(0.6)	(0.9)	
Species richness		41	27	11**	35	39	
		(12)	(10)		(14)	(17)	

*** = $p<0.001$; ** = $0.001 < p < 0.01$; * = $0.01 < p < 0.05$

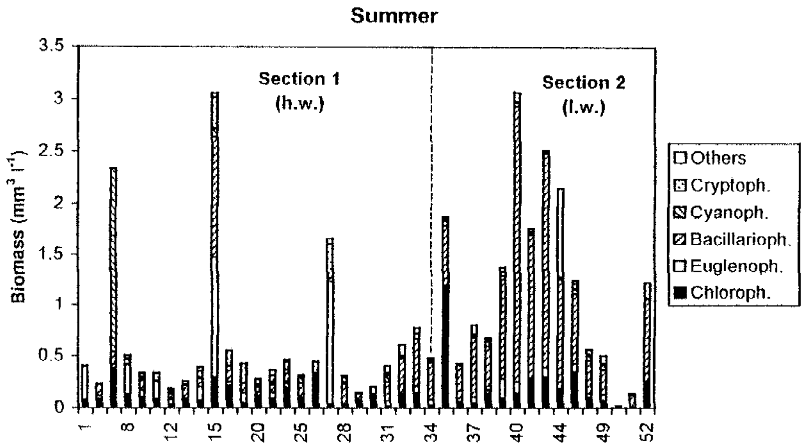

Figure 7. Spatial variations in phytoplankton biomass ($mm^3\ l^{-1}$) in the Paraguay River during the summer sampling (December/95–January/96). Others: Pyrrhophyta + Chrysophyceae + Xanthophyceae; l.w.: low water; h.w.: high water.

Table 6. Mann–Whitney *U* test for phytoplankton groups between low and high waters in sections 1 and 2 of the Paraguay River. Only parameters which are significantly different between low and high waters have been indicated. D: density (ind. ml^{-1}); B: biomass ($mm^3\ l^{-1}$); n = number of samples; Other Groups: Pyrrhophyta + Chrysophyceae + Xanthophyceae

Phytoplankton		Section 1 ($n = 39$)		Section 2 ($n = 21$)	
		U value	*p* value	*U* value	*p* value
Chlorophyta	D	93	**		
	B			16	*
Cryptophyta	D			16.5	*
Bacillariophyceae	D			10	**
	B	154	*	9	**
Cyanophyta	D			6	**
	B			6	**
Other Groups	D			17	*
Total	D	113	**		
	B			10	**
Species richness		109.5	**		

*** = $p<0.001$; ** = $0.001<p<0.01$; * = $p<0.05$

Table 7. Number of taxa of the major phytoplankton groups in the Paraguay River. In brackets: number of taxa downstream of the Bermejo River

	Section 1	Section 2	Common taxa in both sections	Total
Cyanophyta	14	9 (2)	7	16
Chlorophyta	136	70 (17)	57	149
Euglenophyta	70	18 (0)	10	78
Bacillariophyceae	56	33 (11)	24	65
Chrysophyceae	2	2 (0)	1	3
Xanthophyceae	10	3 (0)	2	11
Cryptophyta	6	6 (2)	6	6
Pyrrhophyta	4	2 (0)	2	4
Total	298	143 (32)	109	332

Crucigenia quadrata, Scenedesmus ecornis, Monoraphidium contortum and *M. minutum*). Cryptophyceae were represented by *Cryptomonas marssonii*, *C. ovata* and *Rhodomonas minuta*. Bacillariophyceae of genera *Aulacoseira* (*A. granulata* and its morphotypes, *A. herzogii*) and *Cyclotella* (*C. meneghiniana* and *C. stelligera*) showed a gradual north-south increase in density (and biomass), mostly found in section 2 of the river, particularly in summer (low waters) (Fig. 7).

In the Pantanal, biomass of Cyanophyta (with *Anabaena planctonica*), Chlorophyta (with *Eudorina elegans*), Euglenophyta (with *Euglena oxyuris*) and Bacillariophyceae (with *Synedra* sp. and *Aulacoseira granulata*) predominated (Table 5, Figs 6–7).

Bacillariophyceae was the only algal group which showed statistically significant differences in density (M–W *U* test = 268; $p<0.05$) and biomass (M–W *U* test = 253; $p<0.05$) between the two sections of the river.

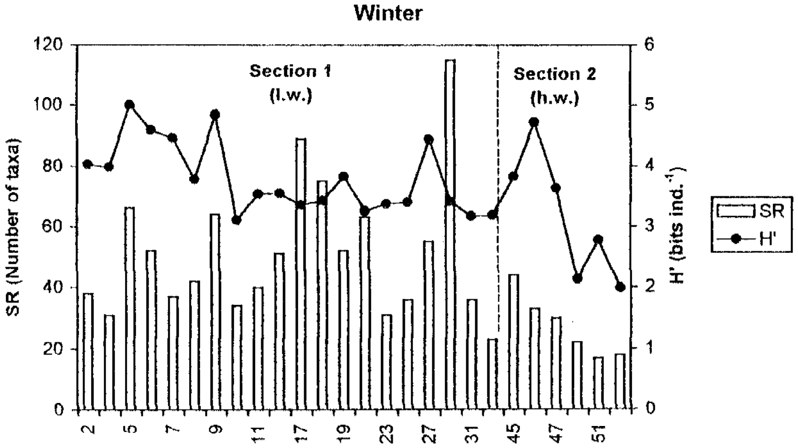

Figure 8. Variations in diversity index (H': bits ind.$^{-1}$) and species richness (SR: number of taxa for sample) of phytoplankton registered in the Paraguay River during the winter sampling (June–July/95). l.w.: low water; h.w.: high water.

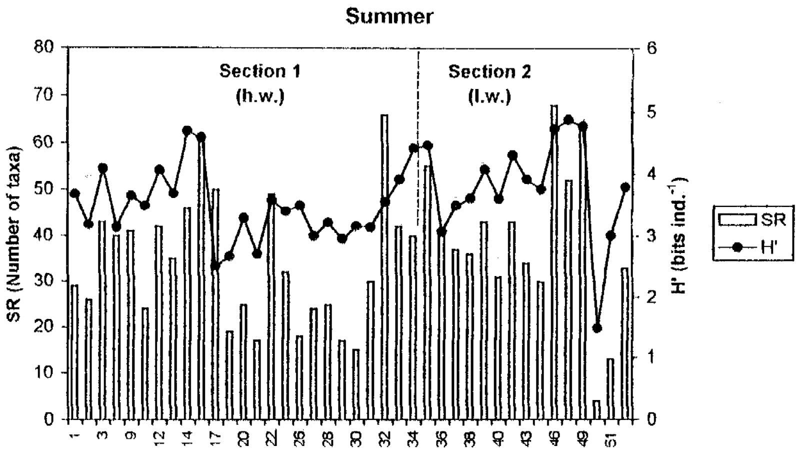

Figure 9. Variations in diversity index (H': bits ind.$^{-1}$) and species richness (SR: number of taxa for sample) of phytoplankton registered in the Paraguay River during summer sampling (December/95–January/96). l.w.: low water; h.w.: high water.

Diversity index (H') showed similar mean values in both sections (between 3.5 and 3.8 in section 1 and between 3.2 and 3.8 bits ind^{-1} in section 2) (Table 5, Figs 8 and 9). Although a reductional tendency was observed towards the south (Fig. 8) in winter, there were no statistically significant differences in H' between both sections of the river.

Species richness (SR) showed significant longitudinal variations in winter (M–W U test = 11; $p<0.01$), with a higher number of taxa in the Pantanal. In summer, mean SR value was similar in both sections of the river, probably because the Pantanal was in a flood phase. In section 1, there were significant differences in the number of taxa between high and low waters (M–W U test = 109.5; $p<0.01$). Although an inverse relationship between SR and hydrometric level was observed, low SR values (as for H') were recorded at the Bermejo River and higher values were found in the Pantanal (Table 5, Figs 8 and 9).

There was no significant variation in the total number of taxa along the river. Variation in the specific composition of groups integrating phytoplankton was significant. Cyanophyta and Euglenophyta, for example, were best represented in the Pantanal. These algae, with appropiate conditions in this sector (high temperatures for the former, abundant organic matter for the latter) might be brought from different environments by the tributaries. The reduction in density and

Table 8. List of algal taxa found in the Paraguay River with relative abundance higher than 2%. Section 1: feeding basin (Pantanal), Section 2: discharge channel (between the Pantanal and the confluence with the Paraná River)

	Section 1	Section 2
CYANOPHYTA		
Anabaena planctonica Brunnth.	X	
A. spiroides Kleb.	X	X
Aphanocapsa elachista West & G. S. West	X	
Cylindrospermopsis raciborskii (Wolosz.) Seen. & Subba Raju	X	
Merismopedia tenuissima Lemm.	X	X
Planktolyngbya contorta (Lemm.) Anagn. & Kom.	X	
P. subtilis (W. West) Anagn. & Kom.	X	
CHLOROPHYTA		
Volvocales		
Chlamydomonas microsphaera Pasch. & Jahoda	X	X
Chloromonas acidophila (Nygaard) Gerloff & Ettl	X	
Ch. gracilis (Matwienko) Ettl	X	X
Coccomonas platyformis Jane	X	
Eudorina elegans Ehr.	X	
Gonium pectorale Müller	X	
Pteromonas rectangularis Lemm.	X	
Chlorococcales		
Actinastrum hanzschii Lagerh.	X	X
Ankistrodesmus gracilis (Reinsch) Kors.	X	
Ankyra judayi (G. M. Smith) Fott	X	X
Chlorella ellipsoidea Gern.	X	
Choricystis cylindracea Hind.	X	X
Ch. minor (Skuja) Fott	X	X
Coelastrum microporum Näg. *in* A. Braun		X
Crucigenia mucronata (G. M. Smith) Kom.	X	
C. quadrata Morr.	X	X
C. tetrapedia (Kirchn.) West & G. S. West	X	
C. rectangularis (Näg.) Kom.	X	
Dictyosphaerium ehrenbergianum Näg.	X	X
D. tetrachotomun Printz	X	X
Didymocystis bicellularis (Chod.) Kom.	X	
Golenkinia radiata Chod.	X	
Kirchneriella lunaris (Kirchn.) Moeb.	X	
Micractinium bornhemiense (Conr.) Kors.	X	X
M. pusillum Fres.	X	
Monoraphidium contortum (Thur.) Kom.-Legn.	X	X
M. irregulare (G. M. Smith) Kom.-Legn.	X	X
M. minutum (Näg.) Kom.-Legn.	X	X
Oocystis marssonii Lemm.	X	
Pachycladella umbrina (G. M. Smith) Silva		X
Paradoxia multiseta Svir.		X
Pediastrum duplex Meyen	X	
P. simplex Meyen	X	X
P. tetras (Ehr.) Ralfs	X	

Continued on p. 189

Table 8. Continued.

	Section 1	Section 2
Scenedesmus acuminatus (Lagerh.) Chod.	x	x
S. bicaudatus Dedus.	X	
S. brasiliensis Bohl.		x
S. ecornis (Ehr.) Chod.	X	X
S. quadricauda (Turp.) Bréb. *sensu* Chod.	X	X
Schroederia antillarum Kom.	X	X
Schroederiella africana Wolosz.	X	
Selenodictyon brasiliense in Uherk. & Schmidt	X	
Sphaerocystis planctonica (Kors.) Bourr.		X
S. schroeteri Chod.	X	X
Tetrachlorella alternans (G. M. Smith) Kors.	X	
Tetraedron caudatum (Corda) Hansg.		X
Tetrastrum heteracanthum (Nordst.) Chod.	X	X
Treubaria schmidlei (Schrod.) Fott & Kovac.	X	X
T. setigera (Arch.) G. M. Smith	X	X
Zygnematales		
Closterium gracile Bréb.	X	X
Cl. setaceum Ehr.	X	X
Desmidium aptogonum Bréb.	X	
Staurastrum boergesenii (Boerg.) Racib.	X	
St. leptocladum Nordst.	X	
St. quadrangulare var. *longispina* Börg.	X	
Staurodesmus cuspidatus (Bréb.) Teil.	X	
Teilingia wallichii var. *borgei* (Grönbl.) Först.	X	
Mougeotia sp.	X	
EUGLENOPHYTA		
Euglena sp.	X	
E. acus Ehr.	X	
E. allorgei Defl.	X	
E. oxyuris Schmarda	X	
E. tripteris (Duj.) Klebs	X	
Lepocinclis capito Wehrle	X	
L. ovum (Ehr.) Lemm.	X	
L. pseudonayalii Tell & Zalocar	X	
Phacus agilis Skuja	X	
Ph. minutus (Playf.) Pochm.	X	
Strombomonas ensifera (Daday) Defl.	X	
Str. jaculata (Palmer) Defl.	X	X
Str. maxima (Skv.) Defl.	X	X
Str. ovalis (Playf.) Defl.	X	X
Str. treubii (Wol.) Defl.	X	
Str. verrucosa var. *zmiewika* (Swir.) Defl.	X	X
Trachelomonas abrupta var. *minor* Defl.	X	
Tr. acanthophora Stokes	X	
Tr. armata var. *steinii* Lemm. emend Defl.	X	
Tr. cervicula Stokes	X	
Tr. curta da Cunha emend Defl. var. *curta*	X	
Tr. curta var. *minima* Tell & Zalocar	X	
Tr. gracillima Balech & Dast.	X	

Continued on p. 190

Table 8. Continued.

	Section 1	Section 2
Tr. multifacies Yacubson & Bravo	X	
Tr. rugulosa Stein emend Defl.	X	
Tr. sculpta Balech	X	
Tr. varians Defl.	X	
Tr. volvocina Ehr. var. *volvocina*	X	X
Tr. volvocina var. *derephora* Conr.	X	
BACILLARIOPHYCEAE		
Centrales		
Actinocyclus normanii (Greg. ex Grev.) Hust.		X
Aulacoseira granulata (Ehr.) Simonsen	X	X
A. herzogii (Lemm.) Simonsen	X	X
Cyclotella meneghiniana Kütz.	X	X
C. stelligera Cl. & Grun.	X	X
Pennales		
Cocconeis placentula var. *acuta* Meist.	X	
Eunotia sp.	X	
Eunotia bilunaris (Ehr.) Mills	X	
E. didyma var. *gibbosa* (Grun.) Hust.	X	X
E. monodon Ehr.	X	
Gomphonema augur var. *turris* (Ehr.) Lange-Bertalot	X	X
Gyrosigma acuminatum (Kütz.) Rabh.	X	X
Navicula cuspidata (Kütz.) Kütz.	X	
Nitzschia sp.	X	
N. acicularis W. Smith	X	
N. levidensis var. *victoriae* (Grun.) Cholnoky	X	
Pinnularia acrosphaeria W. Smith	X	
Surirella guatimalensis Ehr.	X	X
Synedra sp.	X	
S. goulardii Bréb.	X	
S. ulna (Nitzsch) Ehr.	X	X
CHRYSOPHYCEAE		
Synura sp.	X	X
Mallomonas sp.	X	X
XANTHOPHYCEAE		
Goniochloris tripus Pascher	X	X
Tetraedriella jovetii (Bourr.) Bourr.	X	
Tetraplektron torsum (Skuja) Dedus. Sceg.		X
Pseudostaurastum lobulatumn (Näg.) Chodat	X	X
PYRRHOPHYTA		
Peridinium sp.	X	
CRYPTOPHYTA		
Rhodomonas minuta Skuja	X	X
Cryptomonas sp.	X	
C. ovata Ehr.	X	X
C. marssonii Skuja	X	X

specific composition of phytoplankton in the discharge channel may reflect the own elimination factor of the water current.

The presence of a greater variety of tichoplanktonic species in the Pantanal than in the discharge channel, particularly during the flood, evidences their incorporation from other communities of lentic and vegetated areas where they were brought by running waters and/or during floods. Potamoplanktonic species predominated between the Pantanal and the area of confluence with the Paraná River.

In sample analysis, there was a total of 332 algal species pertaining to the Cyanophyta (5%), Chlorophyta (45%), Euglenophyta (23%), Cryptophyta (2%), Bacillariophyceae (20%), Chrysophyceae (1%), Xanthophyceae (3%) and Pyrrhophyta (1%). 298 taxa were represented in the upper section of the river and 143 taxa were found in the discharge channel. In both sections of the river, there were 109 species in common, and 34 different taxa were incorporated in section 2 (Table 7). Greatest variety of species corresponded to Chlorophyta (mainly Chlorococcales), followed by Euglenophyta, Bacillariophyceae and Cyanophyta (Table 8).

Many species were below the detection limits of the counting method, as seen by the greater variety of taxa (approximately 600) observed during the analysis of samples concentrated with a plankton net, where relative abundance of each algal group was similar to that recorded in the quantitative samples.

Relationship of phytoplankton with environmental variables: principal component analysis (PCA)

A PCA tested phytoplankton variation in relation to abiotic variables along the river. The first three factors explained 53% of the total variation in data (Table 9).

In sample ordering according to the first two axes, no completely homogeneous groups were found. A general gradient from right to left, starting from samples from the northern sector (most of the Pantanal) towards those from the southern sector (the last part of the Paraguay River) was observed.

Factor I (24% of the variance) was positively correlated with phytoplankton abundance (TD), mainly of Chlorophyta (CH), Euglenophyta (EU), Cryptophyta (CR), Cyanophyta (CY) and other algal groups (O). It was also positively correlated with total phytoplankton biomass (TB) and water temperature (T), but negatively correlated with suspended solids (SS) and dissolved oxygen (OX) (Fig. 10).

Table 9. Eigenvalues, total variance, cumulative variance and eigenvectors coefficients of three factor of the Principal Component Analysis using abiotic variables and phytoplankton data of the Paraguay River

Factor	I	II	III
Eigenvalues	4.4987	3.2274	2.2898
Total variance (%)	23.6775	16.9864	12.0517
Cumulative eigenvalues	4.4987	7.7261	10.0160
Total variance (cumulative %)	23.6775	40.6639	52.7156
Eigenvector coefficients			
Total density (**TD**)	0.8501	0.0758	0.2695
Total biomass (**TB**)	0.6432	0.5385	0.1010
Cyanophyta density (**CY**)	0.3426	0.0016	−0.1082
Chlorophyta density (**CH**)	0.7450	0.0744	−0.2838
Euglenophyta density (**EU**)	0.6137	−0.1840	−0.2394
Cryptophyta density (**CR**)	0.5859	−0.2655	−0.2754
Bacillariophyceae density (**BA**)	0.4215	0.6857	0.2916
Other Groups density (**O**)	0.4874	0.4403	0.0276
Diversity index (**H**)	0.4415	0.0625	0.7213
Species richness (**SR**)	0.5052	0.0424	0.6545
Latitude (**L**)	−0.3198	0.6655	0.0031
Temperature (**T**)	0.4594	0.4749	−0.2887
Secchi disk (**S**)	0.0977	−0.4189	0.2480
pH (**pH**)	−0.2743	0.8026	0.2998
Conductivity (**C**)	−0.3979	0.5480	−0.4457
Dissolved oxygen (**OX**)	−0.4298	0.3379	0.3778
$N0_3$+$N0_2$ (**NI**)	−0.2333	−0.2176	0.3510
T P (**TP**)	0.1982	0.1690	−0.2068
Suspended solids (**SS**)	−0.5191	0.4166	0.4527

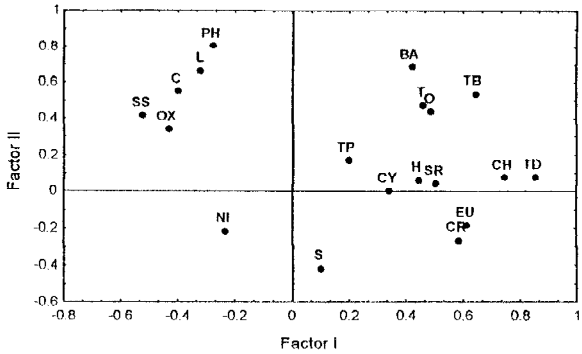

Figure 10. Representation of two first axes of the Principal Component Analysis using abiotic variables (T, water temperature; S, Secchi disk; pH; C, conductivity; OX, dissolved oxygen; NI, nitrites+nitrates; TP, total phosphorus; SS, suspended solids; L, latitude) and phytoplankton data (TD, total density; TB, total biomass; CY, Cyanophyta density; CH, Chlorophyta density; EU, Euglenophyta density; CR, Cryptophyta density; BA, Bacillariophyceae density; O, other groups density; H, diversity index; SR. species richness).

Factor II (17% of variance) was positively correlated with pH, Bacillariophyceae density (BA), latitude (L) and conductivity (C), and negatively correlated with water transparency (S).

Factor III (not represented) showed similar information to that of axis I but with a highly positive correlation with diversity index (H') and species richness (SR).

Total density, abundance of main phytoplankton groups (except diatoms), total biomass, H' and SR were high with higher water temperature, with generally higher values in summer, and mainly in the Pantanal. Suspended solids and dissolved oxygen, were lower in section 1 than in section 2 of the river. pH, conductivity and diatoms density increased from the basin towards the confluence with the Paraná River. Water transparency decreased after the mouth of the Bermejo River.

Discussion

Variation in abiotic variables and phytoplankton in the upper section of the river may be strongly influenced by Pantanal's wetlands, where floods are not produced simultaneously but in a north–south geographical gradient, modifying the hydrological and limnological characteristics of the Paraguay River. Vegetated environments, with a high content of organic matter, influence the physical an chemical composition of tributaries (Da Silva & Estéves, 1995; Hamilton et al., 1995, 1996, 1997). For example, pH and dissolved oxygen show lower values in the Pantanal section than in the discharge channel (Table 2). This agrees with studies by Mitchell (1973), Rzóska (1974), Talling (1976), Neiff (1977), Payne (1986) and Welcomme (1986) for lotic waters in wetlands.

Concentration of suspended solids and conductivity showed larger fluctuations in section 2 of the river, particularly during the summer, as a result of the seasonal differences in the discharge of the tributaries. Smaller fluctuations in section 1 of the river may indicate greater stability. Low concentrations of suspended solids in the Pantanal are attributed, to their precipitation to the bottom during floods caused by the decrease in the current velocity of the river (Bucher et al., 1993), as happens in the fluvial net of the Taquarí River floodplain before reaching the Paraguay River (Hamilton et al., 1998).

Although the general tendency along a water course is the increase in mineralization (Margalef, 1983), the increase in electric conductivity and suspended solids in section 2 of the river was mainly due to the tributaries, as the Bermejo River, with a high content in suspended solids and high mineralization (A. A. Bonetto et al., 1984).

Density, biomass, diversity index and species richness of phytoplankton generally showed an inverse relationship with the hydrometric level. This inverse relationship is widely known for phytoplankton density (Rojo et al., 1994), but references for biomass (expressed as cell volume), diversity and species richness in relation to the hydrometric level are scarce for most studies in lotic environments.

Water temperature and concentration of suspended solids explained spatial and temporal changes of phytoplankton in the river. Density and biomass of phytoplankton were positively correlated to water temperature and negatively correlated to suspended solids, which was also found for other South American rivers (del Giorgio et al., 1991; O'Farell, 1993; O'Farell & Izaguirre, 1994).

The slight correlation among the rest of the abiotic variables and phytoplankton attributes could be masked by the effect produced by the horizontal water flux. When a flood phase begins, phytoplankton density, biomass and other attributes generally show great differences when comparing different sampling stations in the same river, and between the river and the floodplain (Zalocar de Domitrovic & Vallejos, 1982; A. A. Bonetto et al., 1982).

The abundance of small Chlorophyta and Cryptophyta, with a gradual increase of Bacillariophyceae at the lower section of the Paraguay River, is a common tendency in most lotic environments (Reynolds, 1994).

The predominance of Bacillariophyceae, as well as a great variety of species of Chlorococcales (Chlorophyta), represents a general characteristic in diverse rivers of the world (Whitton, 1975; Hynes, 1976; Talling, 1976; Kuzmin, 1979; Zalocar de Domitrovic & Vallejos, 1982; A. A. Bonetto et al., 1982; Vásquez & Sánchez, 1984; Dumont, 1986; Walker, 1986; Finlayson et al., 1990; Zalocar de Domitrovic & Maidana, 1997). However, the low number of Desmidiaceae species (Chlorophyta) in the Paraguay River contrasts with what was shown in some tropical rivers by Payne (1986), O'Farrel & Izaguirre (1994) and Rojo et al. (1994).

Low light requirements of Bacillariophyceae (Richardson, 1984) may explain the predominance of *Aulacoseira granulata* in rivers so turbid as the Bermejo and in the low section of the Paraguay River

(Bonetto et al., 1981, and this study). The taxa of this genus are not only morphologically adapted, but also physiologically prepared for rapid fluctuations of light conditions in mixing levels of the water column (Kilham & Kilham, 1975; Dokulil, 1983). This species, adjusted to the so-called R-strategists (Reynolds, 1988), is usually related to a higher turbulence and the extense mixing of water is essential for its development, that is why it dominates in large rivers. The low depth and turbulence of the tributaries that meet in the Pantanal could explain the low density of this species in the upper section.

In this study, the lack of statistically significant differences between specific richness and latitude agrees with what was shown by Rojo et al. (1994), when comparing rivers of temperate and tropical zones.

Pantanal's environments contributed significantly to the floristic composition of plankton in the upper section of the Paraguay River. In contrast, in the discharge channel, the algal input from tributaries was not significant, predominating true potamoplanktonic species in the main course.

A high proportion of tichoplanktonic species (from the limnoplankton, benthos, and/or periphyton) characterize the plankton of a fluvial system (Margalef, 1983; Reynolds, 1994). Species observed in the Pantanal and in the high part of section 2 of the river may probably be related to the variety of microhabitats along gradients. Part of this complexity of microhabitats may be generated by diverse macrophytes found in environments of the Pantanal (Hamilton et al., 1995), from where part of the algal species may be carried downstream by lotic waters. Several authors (Zalocar de Domitrovic, 1990, 1992, 1993; Train, 1998) indicated floodplain aquatic environments as sources of biodiversity conservation, where vegetation contributes with a greater variety of niches for aquatic organisms. Although there are no data previous to this study, samples taken in low and high waters of the Paraguay River indicate a consistent tendency towards an increase in different microhabitats, more marked during high waters by the effect of the horizontal dragging of lentic waters in the Pantanal.

In most of section 2 of the river, the predominance of potamoplanktonic species is due to morphological and hydrological characteristics, different to those of the Pantanal; in section 2, the river runs at a higher velocity, has a greater depth and does not go through wetlands as in section 1. Unidirectional flux, continuous turbulence and periodic changes in turbidity of a lotic system are accentuated downstream of the Pantanal. Thus, in this section and until running into the Paraná River, along more than 1500 km, there was a decrease in phytoplankton abundance and changes in the qualitative integration, reducing the number of species to almost half, decreasing even more at the Bermejo River (Table 7). Our observations in this last part of the section greatly differ from those of Bonetto et al. (1981), who found a higher number of species (135) during a 12-month sampling. In the Bermejo River, with a similar sampling intensity, however, a total of 67 taxa were recorded (A. A. Bonetto et al., 1984). Differences in the number of species between that study and ours could be due to the fact that this study included only two seasonal samplings. This agrees with Huszar (1996) and Train (1998), who argued that such differences are more related to effort and sampling intensity, counting methods and taxonomic experience than to temporal variations. It is probable that the number of species of the Paraguay River would be higher than that showed in this study.

When comparing this study with another one carried out for the Paraná River in similar study periods and hydrological phases, however, the number of algal taxa of the Paraguay River was three times higher than that of the Paraná River (Zalocar de Domitrovic, 1999). The Paraguay River was characterized by a higher variety of Chlorophyta, Euglenophyta and Xanthophyceae.

In the Paraguay River, environmental discontinuities, such as the proportion of wetlands in the heads and the input of tributaries carrying suspended solids into the discharge channel, may form a spatial-temporal pattern of distribution and abundance of phytoplankton. In this study, there was no longitudinal succession (characterized by an increase in 'information' *sensu* Margalef, 1961) from the heads to the mouth of the river. That is to say, phytoplankton had a cumulative effect on taxa towards the upper section. This is not consistent with the River Continuum Concept (Vannote et al., 1980).

In this study, it is difficult to conclude on the causes of the higher species richness found in the Pantanal section. In the context of publications which explain biodiversity at a biosphere level (Huston, 1995), this result could be attributed to the fact that the Pantanal is found in a low latitude strip, in a tropical area and with high temperatures. We should also add the presence of a greater development and variety of wetlands which occupy a surface larger than those of the High basin of the Paraná River and of other great South American rivers (Neiff et al., 1994).

The Paraguay River, with one of the largest wetlands in the world, may explain the high algal diversity at these latitudes.

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References

APHA (American Public Health Association), 1981. Standard methods for the examination of water and wastewater, 15th edn. APHA, AWWA & WPCF, Washington: 1134 pp.

Arduino, G., 1990. Hidrología de Ia cuenca del rio de La Plata. Interciencia 15: 373–377.

Bold, H. C. & M. J. Wynne, 1985. Introduction to the algae. Prentice-Hall, Inc., Englewood Cliffs, New Jersey: 720 pp.

Bonetto, A. A., 1976. Calidad de las aguas del río Paraná. Introducción a su estudio ecológico. INCYTH-PNUD-ONU, Santa Fé: 202 pp.

Bonetto, A. A., 1994. Austral rivers of South America. In Margalef, R. (ed.), Limnology Now: A paradigm of Planetary Problems. Elsevier Science, New York: 425–471.

Bonetto, A. A., Y. Zalocar de Domitrovic & E. R. Vallejos, 1982. Contribución al conocimiento del fitoplancton del Paraná Medio. I. Ecosur 9: 189–212.

Bonetto, A. A., Y. Zalocar, F. L. Pedrozo & C. A. Bonetto, 1984. Contribución al conocimiento limnológico del río Bermejo en su tramo inferior. Ecosur 11: 61–74.

Bonetto, C. A., A. A. Bonetto & Y. Zalocar, 1981. Contribución al conocimiento limnológico del río Paraguay en su tramo inferior. Ecosur 8: 55–88.

Bonetto, C. A., Y. Zalocar de Domitrovic & E. R. Vallejos, 1983. Fitoplancton y producción primaria del Alto Paraná. Physis Sec. B 41: 81–93.

Bucher, E. H., A. A. Bonetto, T. P. Boyle, P. Canevari, G. Castro, P. Huszar & T. Stone, 1993. Hidrovía: Examen inicial ambiental de Ia via fluvial Paraguay-Paraná. Humedales para Las Americas, Manomet: 74 pp.

Da Silva, C. J. & F. A. Estéves, 1995. Dinâmica das caracteristicas limnológicas das baias Porto de Fora e Acurizal (Pantanal de Mato Grosso) em funçâo da variaçâo do nivel da água. In Estéves, F. A. (ed.), Oecologia Brasiliensis, Vol. I: Estructura, funcionamento e manejo de ecossistemas brasileiros. Instituto de Biologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro: 47–60.

De-Lamónica-Freire, E. M., 1992. Desmídias filamentosas (Zygnemaphyceae, Desmidiales) da estação ecológica da Ilha de Taiamâ, Mato Grosso, Brasil. Acta Limnol. Bras. 4: 315–325.

De-Lamónica-Freire, E. M. & C. W. Heckman, 1996. The seasonal succession of biotic communities in wetlands of the tropical wey-and-dry climatic zone: III. The algal communities in the Pantanal of Mato Grosso, Brazil, with a compreensive list of the known species and revision of two desmid taxa. Int. Rev. ges. Hydrobiol. 81: 253–280.

del Giorgio, P. A., A. Vinocur, R. J. Lombardo & G. Tell, 1991. Progresive changes in the structure and dynamics of the phytoplankton community allong a polution gradient in a lowland river: a multivariate approach. Hydrobiologia 224: 129–1 54.

Dokulil, M., 1983. Mezcla y tamaño de las células y su relación con la productividad primaria. In Bahamonde N. & S. Cabrera (eds), Embalses, Fotosíntesis y Productividad Primaria. Programa sobre el hombre y la biosfera, UNESCO, Santiago de Chile: 127–134.

Drago, E. C. & M. L. Amsler, 1988. Suspended sediment at a cross section of the Middle Paraná River: concentration, granulometry and influence of the main tributaries. Int. Assoc. Sci. Hydrology 174: 381–396.

Dumont, H. J., 1986. The Nile river system. In Davies, B. R. & K. V. Walker (eds), The Ecology of River Systems. Dr W. Junk Publishers, Dordrecht: 61–74.

Edler, L. (ed.), 1979. Recommendations for Marine Biological Studies in the Baltic Sea; Phytoplankton and Chlorophyll. UNESCO, The Baltic Marine Biologist 5: 1–38.

Finlayson, C. M., I. D. Cowie & B. J. Bailey, 1990. Characteristics of a seasonally flooded freshwater system in monsoonal Australia. In Whigham, D. F., R. E. Good & J. Kvet (eds), Wetland Ecology and Management: Case Studies. Kluwer Academic Publishers, Dordrecht: 141–162.

García de Emiliani, M. O., 1990. Phytoplankton ecology of the Middle Paraná River. Acta Limnol. Bras. 3: 391–417.

Hamilton, S. K., O. Correa De Souza & M. E. Coutinho, 1998. Dynamics of floodplain inundation in the alluvial fan of the Taquari river (Pantanal, Brasil). Verh. int. Ver. Limnol. 26: 916–922.

Hamilton, S. K., S. J. Sippel & J. M. Melack, 1995. Oxygen depletion and carbon dioxide and methane production in waters of the Pantanal wetland of Brazil. Biogeochemistry 30: 115–141.

Hamilton, S. K., S. J. Sippel & J. M. Melack, 1996. Inundation patterns in the Pantanal Wetland of South America determined from passive microwave remote sensing. Arch. Hydrobiol. 137: 1–23.

Hamilton, S. K., S. J. Sippel, D. F. Calheiros & J. M. Melack, 1997. An anoxic event and other biogeochemical effects of the Pantanal wetland on the Paraguay river. Limnol. Oceanogr. 42(2): 257–272.

Huston, M. A., 1995. Biological diversity. The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge: 681 pp.

Huszar, V. L. M., 1996. Floristic composition and biogeographical aspects of the phytoplankton of an amazonian lake (lake Batata, Pará, Brazil). Acta Limnol. Bras. 8: 127–136.

Hynes, H. B. N., 1976. The Ecology of Running Waters. Liverpool University Press, Liverpool: 555 pp.

Kilham, S. S. & P. Kilham, 1975. *Melosira granulata* (Ehr.) Ralfs: morphology and ecology of cosmopolitan freshwater diatom. Verh. int. Ver. Limnol. 19: 2716–2721.

Kovach, W. L., 1986–1993. MVSP Plus. Version 2.1. Users' Manual. Kovach Computing Services, U. K: 55 pp.

Kuzmin, G. V., 1979. Algae: A phytoplankton of the Volga. In Mordukhai-Boltovskoi, Ph.D. (ed.), The River Volga and its Life. Dr W. Junk Publishers, The Hague: 137–170.

Lewis, Jr., W. M., 1988. Primary production in the Orinoco river. Ecology 69: 679–692.

Lund, J. W. G., C. Kipling & E. D. Le Cren, 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11: 143–170.

Margalef, R., 1961. Communication of structure in planktonic populations. Limnol. Oceanogr. 6: 124–128.

Margalef, R., 1983. Limnología. Omega, Barcelona: 1010 pp.

Mitchell, D. S., 1973. Supply of plant nutrient chemicals in lake Kariba. In Ackermann, W. C., G. F. White & F. B. Worthington (eds), Man-made Lakes: Their Problems and Environmental Effects. American Geophysical Union, Washington: 165–169.

Neiff, J. J., 1977. Investigaciones ecológicas en el complejo de la laguna Iberá en relación a diversas formas de aprovechamiento hídrico. Seminario sobre medio ambiente y represas, OEA 1: 70–88.

Neiff, J. J., 1990. Ideas para la interpretación ecológica del Paraná. Interciencia 15: 424–441.

Neiff, J. J., 1996. Large rivers of South America: toward the new approach. Verh. int. Ver. Limnol. 26: 167–180.

Neiff, J. J., M. H. Iriondo & R. Carignan, 1994. Large tropical south american wetlands: an overview. In Link, G. L. & R. J. Naiman (eds), Proceedings of the International workshop on The Ecology and Management of Aquatic-Terrestrial Ecotones. University of Washington, Seattle: 156–165.

OEA, 1969. Cuenca del Río de la Plata. Estudio para su planificación y desarrollo. Inventario de datos hídrológicos y climatológicos. Secretaría General de la Organización de Estados Americanos, Washington: 272 pp.

OEA, 1971. Cuenca del Río de la Plata. Estudio para su planificación y desarrollo: inventario de datos hidrológicos y climatológicos. Secretaría General de la Organización de Estados Americanos, Washington: 169 pp.

O'Farrell, I., 1993. Phytoplankton ecology and limnology of the Salado river (Buenos Aires, Argentina). Hydrobiologia 271: 169–178.

O'Farrel, I. & I. Izaguirre, 1994. Phytoplankton ecology and limnology of the river Uruguay lower basin (Argentina). Arch. Hydrobiol. 99: 155–179.

Payne, A. I., 1986. The Ecology of Tropical Lakes and Rivers. John Willey, New York: 301 pp.

Putz, R. & W. J. Junk, 1997. Phytoplankton and periphyton. In Junk, W. J. (ed.), The Central Amazon Floodplain: Ecology of a Pulsing System. Springer, Berlin: 207–222.

Reynolds, C. S., 1988. Functional morphology and the adaptive strategies of freshwater phytoplankton. In Sandgren, C. D. (ed.), Growth and Reproductive Strategies of Freshwater Phytoplankton. Cambridge University Press, Cambridge: 388–433.

Reynolds, C. S., 1994. The long, the short and the stalled: on the attributes of phytoplankton selected by physical mixing in lakes and rivers. Hydrobiologia 289: 9–21.

Richardson, K., 1984. Fisiología del fitoplancton. In Bahamonde, N. & S. Cabrera (eds), Embalses, Fotosíntesis y Productividad Primaria. Programa Sobre el Hombre y la Biosfera, UNESCO, Santiago de Chile: 123–126.

Rojo, C., M. Alvarez Cobelas & M. Arauzo, 1994. An elementary, structural analysis of river phytoplankton. Hydrobiologia 289: 43–55.

Rott, E., 1981. Some results from phytoplankton counting intercalibrations. Schweiz Z. Hydrol. 43: 34–61.

Rzóska, J., 1974. The upper Nile swamps, a tropical wetland study. Freshwat. Biol. 4: 1–30.

Rzóska, J. (ed.), 1976. The Nile: Biology of an Ancient River. Dr W. Junk Publishers, The Hague: 417 pp.

Sanchez, L. & E. Vasquez, 1986. Estudio estacional y longitudinal de la hidroquímica y fitoplancton en una sección del bajo Orinoco (Venezuela). Mem. Soc. Cienc. Nat. La Salle 46: 69–93.

Shannon, C. E. & W. Weaver, 1963. The Mathematical Theory of Communication. Illinois University Press, Urbana: 177 pp.

Sioli, H. (ed.), 1984. The Amazon (Monographie biologicae), Vol. 56. Dr W. Junk Publishers, The Hague: 763 pp.

Sokal, R. & F. J. Rohlf, 1979. Biometría. Principios y métodos estadísticos en la investigación biológica. Blume, Madrid: 832 pp.

Soldano, F., 1947. Régimen y aprovechamiento de la red fluvial Argentina. Cimera, Buenos Aires: 277 pp.

Steel, G. D. & J. H. Torrie, 1988. Bioestadística: principios y procedimientos. McGraw-Hill, México: 622 pp.

Talling, J. F., 1976. Phytoplankton: composition, development and productivity. In Rzóska, J. (ed.), The Nile: Biology of an Ancient River. Dr W. Junk Publishers, The Hague: 385–402.

Tell, G., I. Izaguirre & I. O'Farrel, 1994. Ecological and taxonomical remarks on the Desmid flora of the Lower Uruguay River Basin (Argentina). Bibliotheca Phycologica 96, J. Cramer, Berlin: 141 pp.

Train S., 1998. Flutuaçôes temporais da comunidade fitoplanctônica do sub-sistema rio Baía-lagoa do Guaraná, planície de inundaçâo do Alto rio Paraná (Bataiporâ, Mato Grosso do Sul). Escola de Engenharia de Sâo Carlos, Universidade de Sâo Paulo, Brasil: 189 pp. (Tesis doctoral).

Tricart, J. & R. Frecaut, 1983. Le Pantanal: un exemple de plaine on le raseau hydrographique est mal defini. In Fuschini Mejia M. C. (ed.), Hidrology of Large Flatlands. Proceedings of the Olavarria Symposium, Volume III. UNESCO, Buenos Aires: 1475–1513.

Uherkovich, G., 1984. Phytoplankton. In Sioli, H. (ed.), The Amazon; Limnology and Landscape Ecology of a Mighty Tropical River and its Basin. Dr W. Junk Publishers, Dordrecht: 295–310.

Utermöhl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitt. int. Ver. Limnol. 9: 1–38.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The River Continuum Concept. Can. J. Fish. aquat. Sci. 37: 130–137.

Vásquez, E. Z. & L. Sánchez, 1984. Variación estacional del plancton en dos sectores del río Orinoco y una laguna de inundación adyacente. Mem. Soc. Cienc. Nat. La Salle 121: 11–33.

Walker, K. F., 1986. The Murray-Darling. In Davies, B. R. & K. F. Walker (eds), The Ecology of River Systems. Dr W. Junk Publishers, Dordrecht: 631–659.

Welcomme, R. L., 1986. The Niger System. In Davies, B. & H. Walker (eds), The Ecology of River Systems. Dr W. Junk Publishers, Dordrecht: 9–23.

Whitton, B. A., 1975. Algae. In Whitton, B. A. (ed.), River Ecology. California University Press, Berkeley: 81–105.

Zalocar de Domitrovic, Y., 1990. Efecto de las fluctuaciones del nivel hidrométrico sobre el fitoplancton en tres lagunas isleñas en el área de confluencia de los ríos Paraná y Paraguay. Ecosur 16: 13–29.

Zalocar de Domitrovic, Y., 1992. Fitoplancton de ambientes inundables del río Paraná (Argentina). Estudio comparativo entre áreas libres y vegetadas. Rev. Hydrobiol. trop. 25: 177–188.

Zalocar de Domitrovic, Y., 1993. Fitoplancton de una laguna vegetada por *Eichhornia crassipes* en el valle de inundación del río Paraná (Argentina). Amb. Subtrop. 3: 39–67.

Zalocar de Domitrovic, Y., 1999. Estructura y dinámica del fitoplancton en la cuenca del eje potámico Paraguay-Paraná (Argentina). Tesis doctoral, Facultad de Ciencias Exactas, Físicas y Naturales de la Universidad Nacional de Córdoba, Córdoba: 375 pp.

Zalocar de Domitrovic, Y. & N. I. Maidana, 1997. Taxonomic and ecological studies of the Paraná River diatom flora (Argentina). Bibliotheca Diatomologica 34, J. Cramer, Berlin: 122 pp.

Zalocar de Domitrovic, Y. & E. R. Vallejos. 1982. Fitoplancton del río Alto Paraná. Variación estacional y distribución en relación a factores ambientales. Ecosur 9: 1–28.