Effect of fluctuations in water level on phytoplankton development in three lakes of the Paraná river floodplain (Argentina)

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Abstract

The effect of fluctuations in water level on phytoplankton development (abundance, biomass, size structure, taxonomic composition, species diversity and rate of community compositional change) in three vegetated lakes of the Paraná River floodplain (27° 27′ S; 58° 55′ W) were studied. Between September 1995 and June 1996 there were two inputs of lotic water. Ordering of physical and chemical parameters (Principal Component Analysis) allowed the differentiation of two phases: I) without lotic influence (limnophase) and II) with lotic influence (potamophase). Two-hundred fifty-eight algal taxa were identified, of which Euglenophyceae showed the highest number of taxa (65% of total). Small Chlorophyceae and Cryptophyceae (C-strategists) predominated in density in both periods. During potamophase, the input of nutrients from a flood event produced an increase in algal biomass and a shift in phytoplankton composition from a Chlorophyceae (C-strategists), to a Cyanophyceae and Euglenophyceae (S-strategists), dominated comunity. Bacillariophyceae, Chrysophyceae, Dinophyceae and Xanthophyceae were best represented during limnophase. All phytoplankton attributes showed significant differences between phases (limnophase vs potamophase) but not among lakes. These results support the hypothesis that hydrology (floods) clearly exerts an overall impact on the phytoplankton community composition in lakes of the Paraná River floodplain. Hydrology effects the lake water chemistry, conditioned by the isolation time prior to a flood, the horizontal dragging and exchange of algae during floods, and the water residence time and aquatic vegetation coverage.

Introduction

In floodplains aquatic environments the flood pulse is the most important environmental parameter, determining the existence, productivity and interactions of the biota (Junk et al., 1989; Van den Brink et al., 1994; Welcomme, 1985; Bonetto, 1994; Junk, 1997; Putz & Junk, 1997). Pulses, represented by phases of floods and droughts, constitute what Neiff (1996) called a hydrosedimentological pulse. He differentiated a limnophase, when floodplain environments remain isolated from the river, from a potamophase, a flood period with drastic changes in the physical, chemical and biotic characteristics (Neiff, 1990).

Although floods produce the most important disturbances in these systems, the impact on the phytoplanktonic community can be variable as a result of the interaction between river waters and local environmental conditions, such as the degree of connection between these environments, the distance from the main course, the topographic position, the morphometry of lakes, the water residence time, and the type and percentage of aquatic vegetation coverage (García de Emiliani, 1980; Zalocar de Domitrovic, 1990, 1992). Comparative studies between open and vegetated areas show the presence of a higher number of algal species in the littoral vegetated zone than in the limnetic area (Zalocar de Domitrovic, 1993). Ecological studies of phytoplankton in South American floodplains, such as the Amazon (Uherkovich, 1984; Day & Davies, 1986; Huszar, 1994), Orinoco (Vásquez & Sánchez, 1984) and Paraná (Train & Rodrigues, 1997, 1998; Zalocar de Domitrovic, 1990,

1992, 1993; García de Emiliani, 1980, 1993, 1997), are scarce.

An important aspect of the Paraná River that differentiates it from other South American rivers (e.g., Amazonas and Orinoco) is the irregularity of its hydrological regime, with 1 to 3 floods per year and level fluctuations between 2 and 6 m (Carignan & Neiff, 1992). Low water periods can have short and rapid increases in the discharge, while high water periods can have periods of relatively low water level. The irregular hydrological regime makes it is difficult to predict phytoplankton abundance based on the fluctuations of the stage (Train & Rodrigues, 1998; Zalocar de Domitrovic, 1990; García de Emiliani, 1980).

Recent studies of the phytoplankton in the Paraná River floodplain include aspects such as biovolume, seasonal succession, morphology and phytoplankton size structure. Train (1998), in an Upper Paraná lake, observed different adaptive strategies of algal development (*sensu* Reynolds, 1988a), noting abundance of C-strategists and R-strategists (high surface area/volume ratios) in potamophase and of S-strategists (low surface area/volume ratios) in limnophase. García de Emiliani (1993), in a shallow lake of the Middle Paraná River floodplain, showed seasonal sub-sequences during stable periods, similar to what was observed in temperate lakes. In this respect, she considered a flood as an event analogous to spring circulation, and isolation, analogous to summer stratification. This suggests that seasonal changes in phytoplankton would result from the interaction between processes of true successional development and disturbances of intermediate frequency (Reynolds, 1988b).

To widen phytoplankton investigations, a study of the structure and variations during high waters (potamophase) and low waters (limnophase) in a normal hydrological cycle (with two flood pulses) was conducted in three environments in the middle section of the Paraná River floodplain, a sector influenced by Paraguay River waters and with limnological characteristics which are different from those downstream. Phytoplankton were analyzed based on abundance, diversity, species richness attributes, biovolume, size structure and rate of community change in relation to regional hydrology and main environmental variables. Concepts of algal succession and some aspects of biodiversity maintenance and variability of algal species in relation to the hydrological cycle are discussed.
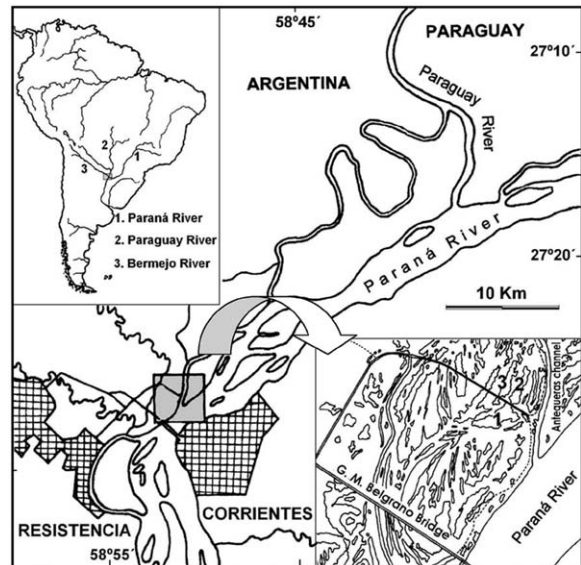

Figure 1. Geographic location of studied lakes on the right bank of the Paraná River floodplain. Station 1: Puente Sur lake, Station 2: Puente Norte lake, Station 3: San Nicolás lake.

Study area

Three lakes in the Paraná River fringing floodplain, 30 km downstream of its confluence with the Paraguay River (27° 27′ S; 58° 55′ W), were selected for study. In normal hydrological cycles of the Paraná River (below 6 m), as in this study, these environments are under the influence of the Lower Paraguay, which flows on the right margin, covering a distance of approximately 300 km (Bonetto, 1994). The Lower Paraguay River, in turn, receives the input of the Bermejo River with mineralized waters and loaded with sediments, giving to this sector of the floodplain particular limnological features. The waters flow slowly due to the presence of small islands, other vegetated water bodies and roads (e.g., General Manuel Belgrano Bridge).

Figure 1 shows the selected lakes, called 'Puente Sur', 'Puente Norte' and 'San Nicolás' (Stations 1, 2 and 3, respectively). The input of lotic waters is indirect, i.e., through other water bodies of the floodplain. In the Puente lake, during the study period, flood occurred first in the southern sector, which was connected during floods with the northern sector. Flood in the San Nicolás lake occurred almost simultaneously with Station 2, through the Antequeras channel from the northern sector.

A distinct characteristic of these lakes is the coverage of floating macrophytes, with the water hyacinth (*Eichhornia crassipes* (Mart.) Solms) as the domin-

Table 1. Morphometric characteristics and percentage of floating aquatic vegetation coverage in the three lakes of the Paraná River floodplain.

Station	1	2	3
Name	Puente Sur	Puente Norte	San Nicolás
Depth range (meters)	1.0–2.75	1.50–2.80	0.60–1.85
Maximum length (meters)	1000	800	500
Maximum width (meters)	300–500	200–300	100
Closest distance to the river (meters)	500–1000	500–1000	1050–1600
River stage level for connection (meters)	4.80	5.0	5.10
Lotic-lenitic interaction time (days)	7–14	4–12	3–11
Coverage of *Eichhornia crassipes* (%)	30–80	45–95	50–95

Table 2. Spearman rank correlation coefficients between the attributes of phytoplankton (D: density, B: biomass, $H'D$: species diversity based on density, $H'B$: species diversity based on biomass, SR: species richness) and physicochemical parameters ($n = 51$ observations). *** $= p < 0.001$; ** $= 0.001 < p < 0.01$; * $= 0.01 < p < 0.05$

	D	B	$H'(D)$	$H'(B)$	SR
Water level (m)	−0.066	0.049	0.296*	0.326*	0.231
Depth (m)	−0.510***	−0.270*	0.244	0.180	0.100
Temperature (°C)	−0.011	−0.170	−0.161	−0.121	−0.248
Dissolved oxygen (% sat.)	0.597***	0.431**	−0.057	−0.078	0.077
Secchi disk (cm)	0.232	0.350*	0.283*	0.161	0.334*
Conductivity (μS cm^{-1})	−0.299*	−0.380**	−0.178	0.084	−0.239
pH	−0.286*	−0.196	0.084	0.243	−0.038
NH$_4$ (μg l^{-1})	−0.311*	−0.115	0.180	0.122	0.091
NO$_3$+NO$_2$ (μg l^{-1})	0.267	0.240	−0.308*	−0.238	−0.111
PO$_4$ (μg l^{-1})	−0.415**	−0.435**	−0.119	0.144	−0.122
Suspended solids (mg l^{-1})	−0.470***	−0.205	−0.046	0.056	0.040

ant species in biomass and productivity (Neiff, 1986). This species forms cohesive floating meadows, which acts to reduce water column mixing through wind action, and in turn deposits important quantities of organic matter at the bottom, both of which produce changes in the limnological characteristics (Bonetto et al., 1984; Carignan & Neiff, 1992). The percentage of lake coverage is variable (20–100%); biomass usually increases from October to March and decreases to 50 % of its annual maximum during the cold season (April to September) (Carignan & Neiff, 1992).

A summary of the morphometric characteristics and the percentage of vegetation coverage for each lake is shown in Table 1. Figure 2 shows the stage of the Paraná River at Puerto Corrientes, the mean depth of lakes and the entrance level of lotic waters when connected.

The study includes 17 surveys at each station, from September 1995 to June 1996. During this period the river had two flood pulses of small duration and intensity, with maximum levels of 5.20 and 5.80 m, respectively. Lotic–lenitic interaction time in both pulses oscilated between 3 and 7 days during the first pulse, and between 11 and 14 days during the second pulse. Survey periodicity was determined by fluctuations of the Paraná River.

Methodology

Subsurface samples were taken in the open water compartment, i.e., outside the vegetation belt. Water were collected with a Van Dorn sampler and were fixed with Lugol's acidified solution. In order to study the species composition of phytoplankton, additional
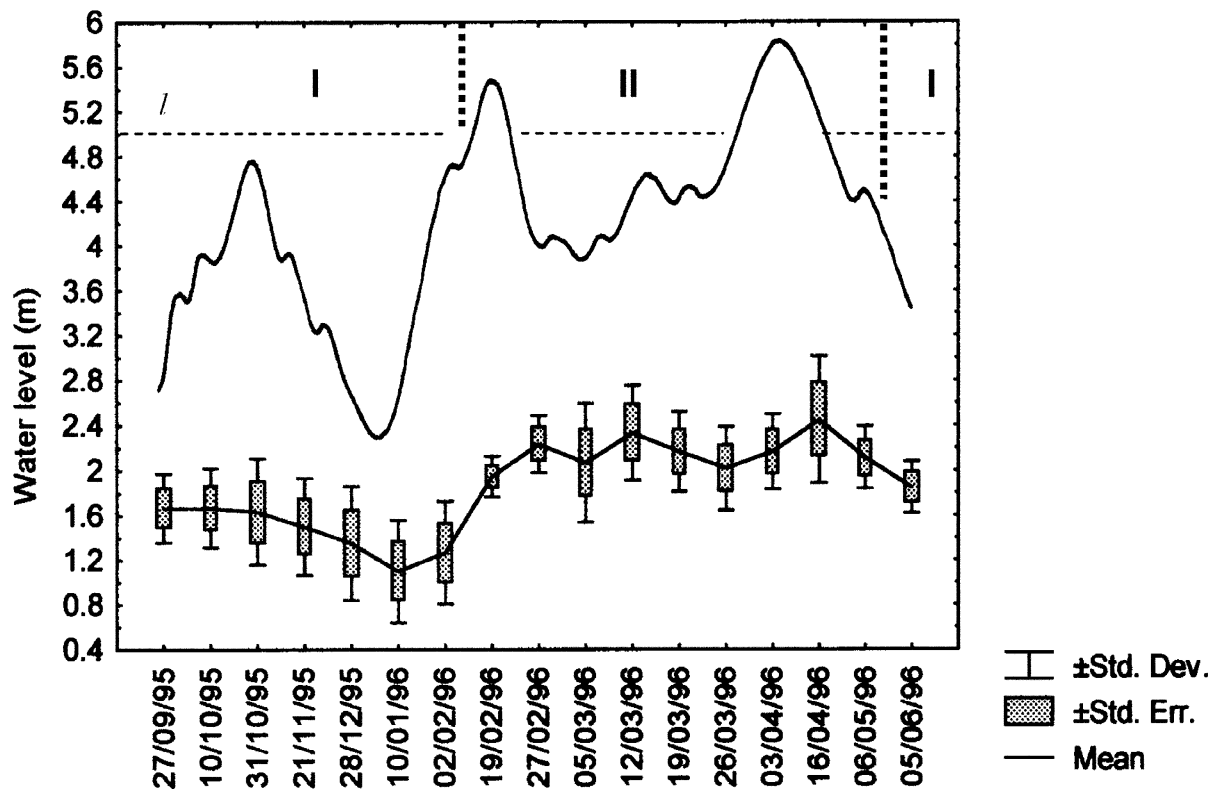
Figure 2. Variations in depth of lakes (Mean, S.D., S.E.) and water level of Paraná River (Puerto Corrientes) during the study period. *l*: overflow. I: limnophase, II: potamophase.

samples were taken with a 25 μm mesh size plankton and fixed in 4% formalin. Density was estimated with the methods of Utermöhl (1958) and Lund et al. (1958) using an inverted microscope. To calculate biomass (biovolume), the species were approximated as simple geometric or combined forms (Rott, 1981; Edler, 1979). Species diversity (H') was estimated using the Shannon–Wiener Index (Shannon & Weaver, 1963) from the density (bits ind.$^{-1}$) and biomass (bits mm^{-3}) data. Species richness was referred to the number of algal taxa registered in each sample in the counting chambers.

The algae were grouped taking into account their greatest axial linear dimension (GALD) (Lewis, 1976). Size groups were selected with the following criterium: group G1 >1–20 μm; group G2 >20–40μm; group G3 >40–100 μm and group G4 >100 μm. The rate of community compositional change (σ) was calculated according to Lewis (1978) as the summed-difference method based on biomass measures.

At each one of the sampling stations, *in situ* measurements of water temperature, transparency (with a Secchi disk of 25 cm diameter), pH (digital pH meter Metrohm A G Herisau), electrical conductivity (conductometer YSI 33 SCT) and dissolved oxygen (oxygen meter YSI 54 A) were carried out. Analyses of dissolved nutrients (nitrogen (NH_4, NO_3+NO_2) and phosphorus (PO_4)) and of suspended solids were carried out by staff of the Chemical and Edaphology Laboratories of the Centro de Ecología Aplicada del Litoral. They were carried out from filtered samples, using Whatman GF/C glass fiber filters, according to APHA (1981).

To classify all samples, abiotic variables were processed with ordering techniques using Principal Component Analysis (PCA) (Legendre & Legendre, 1979). To compare lakes (Stations 1, 2 and 3) and periods (limnophase vs potamophase), non-parametric statistics (Mann–Whitney U test) were used (Sokal & Rohlf, 1979). Abiotic variables were correlated with main phytoplankton attributes using Spearman's correlation coefficient (Steel & Torrie, 1988).

Results

Abiotic variables

Depth of lakes oscillated between 0.60 and 2.80 m, with minimum values during isolation (Fig. 2). Depth was positively correlated with stage of the Paraná River ($r_s = 0.331$; $p < 0.05$).

Physical and chemical characteristics of waters did not have significant differences among stations; however, there were significant differences between periods. A multivariate analysis of these parameters (with 51 observations) showed large changes in abiotic variables with the input of lotic waters. The first two factors of PCA explained 53% of the total variation in data. Percentages of variance estimated for factors 1 and 2 were 36 and 16%, and their eigenvalues 4.0 and 5.8, respectively. The first factor was positively correlated with conductivity (COND), orthophosphate concentration (P) and stage of the Paraná River (HL), and negatively correlated with percentage of dissolved oxygen saturation (OX) and water transparency (SEC). The second factor was positively correlated with depth (DEPTH) and negatively correlated with water temperature (Fig. 3A).

Sample ordering enabled the formation of two groups (Fig. 3B). Group I included the first 7 surveys (the initial isolation stage) and the final survey at the end of the study, this period, not disturbed by lotic waters, was called 'without lotic influence' or limnophase *sensu* Neiff (1990). Group II includes surveys 8 to 16, taken when environments were under the influence of two floods from the Paraná River. This period was called 'with lotic influence' or potamophase *sensu* Neiff (1990), lasting 43 days, during which the physical and chemical characteristics were maintained even after the flood waters had retired.

Phytoplankton

(a) Density, biomass, diversity and specific composition

Mean values for phytoplankton density and biomass had higher values in limnophase (3400 ind. ml^{-1} and 2.03 mm^3 l^{-1}, respectively) than in potamophase (1700 ind. ml^{-1} and 0.86 mm^3 l^{-1}, respectively) (Figs 4 and 5). Although both attributes recorded an increase from Station 1 towards Station 3, there were no significant differences among stations. However, there were significant differences in density at Stations 1 and 3, and in biomass at Station 3 between both periods (limnophase vs potamophase).

The first input of flood waters produced changes, not only in the physical and chemical characteristics of water, but also in phytoplankton. During the first three weeks of potamophase, there was a decrease in density, biomass, diversity and changes in specific composition. Afterwards, there was a recovery of the community (with an increase in attributes mentioned above) until the following input of flood waters during which phytoplankton were only slightly diluted.

Density and biomass were positively correlated with the percentage of dissolved oxygen saturation, and negatively correlated with depth, electrical conductivity of water and concentration of orthophosphates (Table 2). Only biomass was positively correlated with water transparency ($r_s = 0.377$; $p < 0.5$), while density was negatively correlated with pH ($r_s = -0.292$; $p < 0.5$), concentrations of suspended solids ($r_s = -0.469$; $p < 0.001$) and ammonium ($r_s = -0.314$; $p < 0.5$).

In Table 3, mean ($\pm$ SD) values for density and biomass of main phytoplankton groups during limnophase and potamophase are summarized, as well as those which showed significant differences between both periods (Mann–Whitney U test) (Table 4).

Phytoplankton was represented by a total of 258 taxa, distributed into eight algal groups: Cyanophyceae (3%), Chlorophyceae (19%), Euglenophyceae (65%), Bacillariophyceae (7%), Chrysophyceae (1%), Xanthophyceae (2%), Dinophyceae (1%) and Cryptophyceae (2%) (Table 5).

Chlorophyceae was the dominant group in density in all environments and in both periods (Fig. 6). It had higher abundance during potamophase, with percentages greater than 60%. Small unicellular forms of Volvocales (*Chlamydomonas leptobasis* and *Ch. microsphaera*) and Chlorococcales (*Chlorella vulgaris*, *Choricystis cylindracea*, *Monoraphidium minutum*, *M. contortum* and *Schroederia antillarum*) predominated in this group. Chlorophyceae did not dominate in terms of biovolume due to the small size of taxa (biovolumes between 27 and 697 μm^3). An exception was observed during limnophase, on December 28, 1995, when *Schroederia antillarum* was dominant (more than 50% of total phytoplankton) in density and biomass. During the first two weeks of potamophase, at Stations 1 and 2, *Pyrobotris squarrosa* (of larger biovolume) was added to the species mentioned before, thus increasing the biomass of this group.

Cryptophyceae were second most abundant, particularly during limnophase. *Cryptomonas*, *Chroomonas* and *Rhodomonas* were the genera in this

A

B
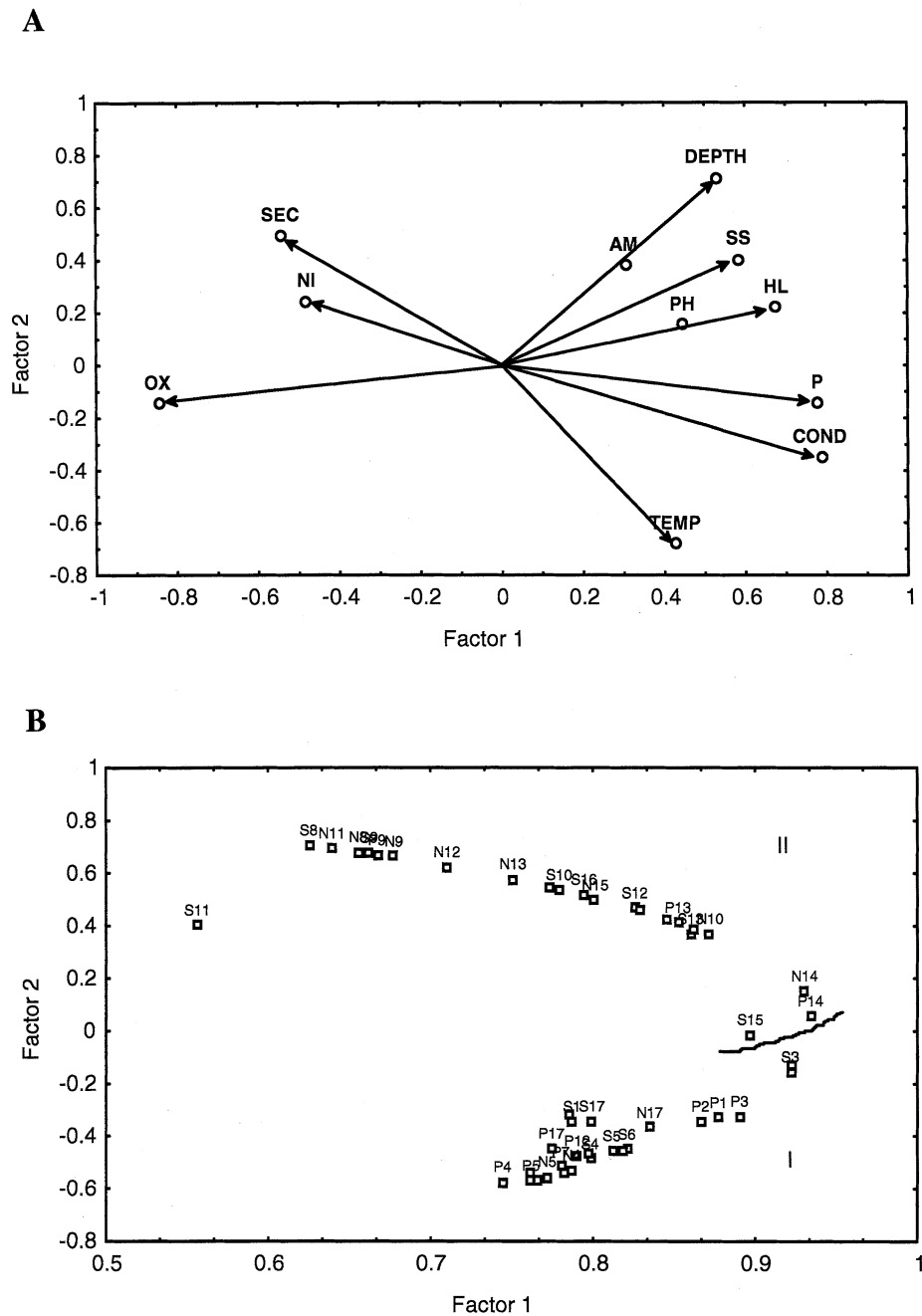
Figure 3. PCA based on abiotic variables. (A) Position of vectors of environmental variables in the reduced space of the first two principal components. DEPTH: depth, TEMP: temperature, OX: disolved oxygen (% saturation), SEC: Secchi disk, COND: conductivity, PH: pH, HL: water level, SS: suspended solids, AM: ammonium concentration, NI: nitrites+nitrates concentration; P: orthophosphate concentration. (B) Position of the 51 samples in the space dimensioned by the first two principal components. I: limnophase, II: potamophase. S: Station 1 (Puente Sur), P: Station 2 (Puente Norte), N: Station 3 (San Nicolás). 1: 27/09/95, 2: 10/10/95, 3: 31/10/95, 4: 21/11/95, 5: 28/12/95, 6: 10/01/96, 7: 02/02/96, 8: 19/02/96, 9: 27/02/96, 10: 05/03/96, 11: 12/03/96, 12: 19/03/96, 13: 26/03/96,14: 03/04/96, 15: 16/04/96, 16: 06/05/96, 17: 05/06/96.

Table 3. Mean values (±S.D.) of density (D, ind. ml^{-1}) and biomass (B, mm^3 l^{-1}) of phytoplankton during limnophase (I) and potamophase (II) periods, in three lakes of the Paraná River floodplain. nI = 8 observations; nII = 9 observations.

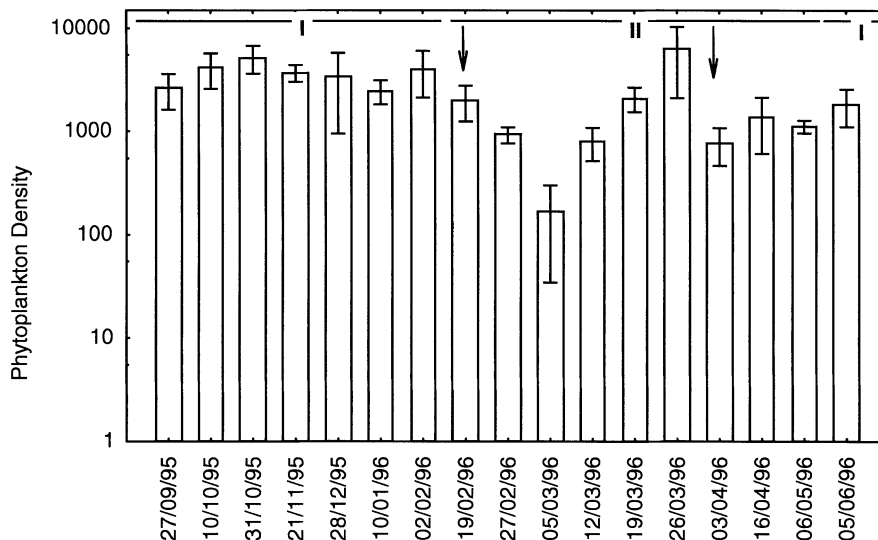|		Station 1		Station 2		Station 3	
		I	II	I	II	I	II
Cyanophyceae	D	11	123	4	93	104	56
		(11)	(117)	(11)	(178)	(236)	(110)
	B	0.002	0.182	0.0003	0.027	0.003	0.062
		(0.003)	(0.485)	(0.0004)	(0.027)	(0.005)	(0.122)
Chlorophyceae	D	1,193	596	1,902	672	2,399	740
		(680)	(428)	(1,717)	(822)	(1,829)	(695)
	B	0.186	0.118	0.172	0.085	2.358	0.080
		(0.157)	(0.094)	(0.155)	(0.105)	(6.110)	(0.068)
Euglenophyceae	D	65	213	273	206	256	457
		(80)	(209)	(284)	(166)	(244)	(889)
	B	0.128	0.342	0.654	0.388	0.773	0.695
		(0.167)	(0.469)	(0.815)	(0.464)	(1.038)	(1.256)
Cryptophyceae	D	590	225	766	230	1,550	1,483
		(332)	(259)	(713)	(366)	(1,117)	(3,775)
	B	0.169	0.078	0.167	0.063	0.501	0.322
		(0.171)	(0.097)	(0.142)	(0.087)	(0.627)	(0.776)
Dinophyceae	D	58	3	87	6	26	3
		(124)	(5)	(80)	(12)	(19)	(6)
	B	0.233	0.034	0.134	0.006	0.020	0.003
		(0.525)	(0.088)	(0.100)	(0.015)	(0.014)	(0.007)
Bacillariophyceae	D	36	21	159	17	68	15
		(42)	(17)	(268)	(21)	(54)	(27)
	B	0.029	0.018	0.035	0.013	0.068	0.011
		(0.028)	(0.009)	(0.045)	(0.021)	(0.042)	(0.019)
Chrysophyceae	D	380	26	120	10	121	8
		(844)	(33)	(133)	(14)	(97)	(13)
	B	0.243	0.033	0.075	0.007	0.098	0.003
		(0.592)	(0.047)	(0.078)	(0.011)	(0.110)	(0.007)
Xanthophyceae	D	16	10	32	16	46	4
		(28)	(8)	(31)	(36)	(38)	7
	B	0.007	0.011	0.013	0.006	0.013	0.002
		(0.018)	(0.019)	(0.015)	(0.016)	(0.013)	(0.003)
Total	D	2.350	1.217	3.343	1.251	4.571	2.755
		(724)	(740)	(2.783)	(1.158)	(921)	(4.685)
	B	0.997	0.815	1.250	0.596	3.835	1.178
		(0.814)	(0.664)	(1.093)	(0.594)	(2.127)	(2.046)

Figure 4. Mean values ($\pm$ S.E.) of phytoplankton density (ind. ml^{-1}) in lakes of the Paraná River floodplain. I: limnophase, II: potamophase. (Arrows: input of lotic waters).

group having the most abundant taxa (*C. marssonii, C. ovata, C. erosa* and *C. rostratiformis*). *Cryptomonas marssonii* and *C. ovata* were dominant in density and/or biovolume in all environments. However, *C. rostratiformis* was important in terms of biovolume, particularly after the fourth week since the first input of lotic waters.

Euglenophyceae had low density. However, their contribution to biomass was important in most environments, particularly after the first two inputs of flood waters (Fig. 7). The association of species of *Trachelomonas*, represented by forms with smooth loricae (*T. volvocina* + *T. volvocinopsis* + *T. cervicula*), was dominant in all environments. At Station 2, this association shared the dominance with two species of *Euglena*: *E. sanguinea*, in limnophase, and *E. spathirhyncha*, in potamophase. At Station 3, subdominance corresponded to *E. viridis*, during potamophase. When there were no dominant species or associations, most of the biomass of this group was represented by a wide variety of species of the genera *Euglena, Trachelomonas, Phacus, Lepocinclis* and *Strombomonas*.

Cyanophyceae were scarcely represented during limnophase but were important in potamophase, after the two inputs of flood waters. At Stations 1 and 2, density and biomass of this group showed significant differences between both periods (Table 4). Most important species were colonial forms of *Merismopedia tenuissima, Aphanocapsa elachista, Microcystis*

pulverea and *Microcystis aeruginosa*. Heterocytous species (e.g., *Trichormus ellipsosporus* and *T. naviculoides*) were only observed in low percentages at Stations 1 and 3. However, during the initial isolation, these species were below the detection limits of the counting method, and only non-heterocytous forms of genera *Planktothrix, Chroococcus* and *Merismopedia* could be observed.

Bacillariophyceae, Chrysophyceae, Dinophyceae and Xanthophyceae were best represented during limnophase (Table 3, Figs 6 and 7). Bacillariophyceae, characterized by pennated forms (*Synedra* sp.), reached higher density and biomass at Stations 2 and 3. Chrysophyceae, with the genus *Synura*, dominated in density and biovolume in only one survey (on June 5, 1996), taken during limnophase. Dinophyceae, with *Peridinium* sp., were important in terms of biomass at the end of the initial isolation, on December 28, 1995. Xanthophyceae, with low percentages in all environments, were represented by a low number of species.

Species diversity based on density (H'D) and biomass (H'B) showed a similar variation pattern, with mean values of 3.65 bits ind.$^{-1}$ and 3.45 bits mm^{-3} in limnophase and 3.72 bits ind.$^{-1}$ and 3.88 bits mm^{-3} in potamophase, respectively (Figs 8 and 9). Species richness (SR) varied from 33 to 68 taxa during limnophase, and from 21 to 78 taxa during potamophase (Fig. 10). All attributes were slightly higher at Stations 2 and 3 during limnophase, and at Station 1 during pot-
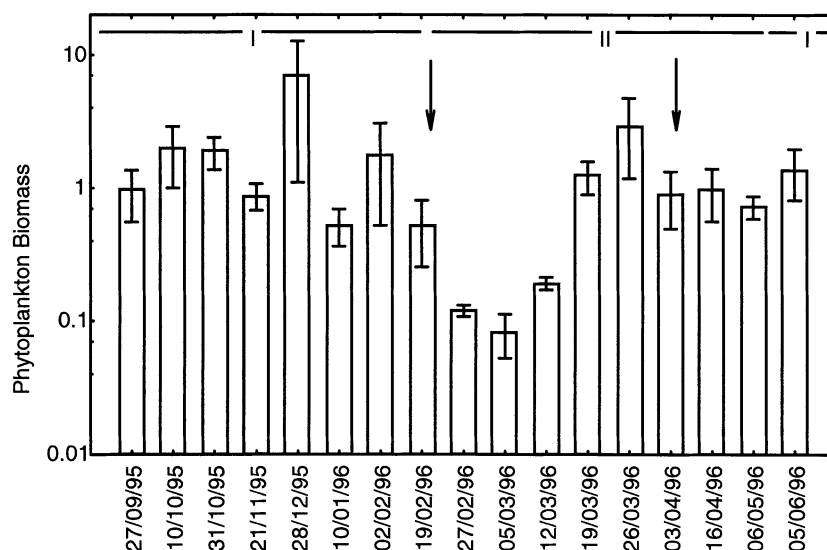
Figure 5. Mean values (± S.E.) of phytoplankton biomass (mm^3 ml^{-1}) in lakes of the Paraná River floodplain. I: limnophase, II: potamophase. (Arrows: input of lotic waters).

amophase. H' and SR (as well as density and biomass) did not show significant differences among stations. However, there were significant differences between phases, for H'D at Station 1 (M–W U test = 12; $p < 0.05$), and for SR at Station 3 (M–W U test = 14.5; $p < 0.05$).

(b) *Size groups (GALD)*

Size groups did not show significant differences among stations nor between periods. Generally, nannoplanktonic taxa from group G1 (>1–20 μm) predominated (Fig. 11). During limnophase, this group predominated at the three stations, and, at stations 2 and 3, it alternated with algae from groups G2 (>20–40 μm) and G3 (>40–100 μm). During potamophase, the contribution of larger size taxa (groups G2, G3 and G4) increased in relation to limnophase.

The greatest contribution to group G1 was by Chlorophyceae (unicellular coccoid and flagellated forms) and Cryptophyceae (*Cryptomonas* spp.). Group G2 was represented by Cryptophyceae (*Cryptomonas rostratiformis*), Chrysophyceae (*Synura* sp.) and Euglenophyceae (*Euglena* spp., *Trachelomonas* spp.). Groups G3 and G4 were primarily represented by Euglenophyceae and Bacillariophyceae.

(c) *Rate of community change (σ)*

Rate of community change (σ) had lower values during limnophase than in potamophase (Fig. 12). There were highly significant differences between both peri-

ods for density (M–W U test = 43; $p < 0.001$), as well as for biomass (M–W U test = 48; $p < 0.001$).

During limnophase, modification rate had similar values for both attributes (density and biomass), oscillating between 0.035 and 0.125 day^{-1}, with minima from December 28, 1995 to January 10, 1996 (samples 5 and 6). This period corresponded to the season where these environments had most isolation and shallowest depths.

From the beginnings of potamophase, there was a progressive increase of rate of community change until reaching maximum values two weeks after the first input of flood waters, on February 19, 1996 (sample 8). Variation in σ based on density showed a pattern similar to that of biomass. Maximum values were 0.235, 0.333 and 0.332 day^{-1} for density (not represented), and 0.271, 0.314 and 0.278 day^{-1} for biovolume at Stations 1, 2 and 3, respectively (Fig. 12). During the rest of potamophase, while stage was decreasing in all environments, thus remaining isolated from the river, there was a gradual decrease of the modification rate with a slight increase, when the second input of flood waters occurred (on April 3, 1996; sample 14), after which it continued to decrease as a new isolation began.

Table 4. U values (Mann–Whitney U Test) for density (D) and biomass (B) of total and taxonomic groups of phytoplankton in three lakes (Station 1, 2 and 3) of the Paraná River floodplain. Only groups which are significantly different within limnophase and potamophase have been indicated (*** $= p < 0.001$; ** $= 0.001 < p < 0.01$; * $= 0.01 < p < 0.05$); $n =$ number of observations.

Phytoplankton	Station 1 ($n = 17$)		Station 2 ($n = 17$)		Station 3 ($n = 17$)	
	D	B	D	B	D	B
Cyanophyceae	13*	6 **	13*	11*	34	22
Chlorophyceae	15*	22	20	28	14	14*
Euglenophyceae	16	23	33	28	34	29
Cryptophyceae	11*	16	17	20	13*	17
Dinophyceae	11*	12*	3.5**	3**	5**	6**
Bacillariophyceae	36	29	19	21	12*	10
Chrysophyceae	7**	23	13.5*	19	3***	2***
Xanthophyceae	27	16	22	20.5	9**	13*
Total	10*	29	18	18	15*	15*

Discussion and conclusion

Structure and composition of phytoplanktonic community were influenced by the hydrosedimentological regime. Participation of lotic waters, with two inputs or disturbances, produced large changes in physical and chemical characteristics of waters and in the phytoplanktonic community, particularly during the first flood, which occurred after a prolonged isolation.

Strong dissolved oxygen demand, which characterized potamophase, is due to organic matter degradation, produced during the initial isolation (of approximately 5 months). Hypoxia was recorded in most water bodies of the Middle Paraná (Carignan & Neiff, 1992; Bechara, 1996), Upper Paraná (Thomaz et al., 1992a, c) and Amazon floodplains (Schmidt, 1973a, b; Rai & Hill, 1982; Lópes et al., 1983; Odinetz Collart & Moreira, 1989). The increase in electrical conductivity of water in this period is related to a greater influence of waters from the Paraguay River (which in turn are influenced by waters of the Bermejo River).

Nutrient enrichment during potamophase is described as a common process in floodplains (Junk, 1982; Margalef, 1983; Fisher, 1978; Schmidt, 1973a; Santos, 1980; Lópes et al., 1983; Furch & Junk, 1997; Hamilton & Lewis, 1987; Bonetto, 1975). In this study, high phosphorus concentrations (as orthophosphates) and inorganic nitrogen (as ammonium) are related to liberation from the sediments (Pedrozo et al., 1985/6, 1992; Schmidt, 1973a; Setaro & Melack,

1984) and to decomposition of organic matter accumulated on the floodplain during the dry season (Junk, 1982; Melack & Fisher, 1990; Thomaz et al., 1992a, c). Maximum concentrations of nitrites and nitrates in the initial isolation coincided with the decrease of *Eichhornia crassipes* (Carignan & Neiff, 1992).

The negative correlation between phytoplankton abundance and stage was described for lentic environments of the potamic axis Paraguay–Paraná (Zalocar et al., 1982; Zalocar de Domitrovic, 1990, 1992, 1993; García de Emiliani, 1979, 1980, 1993, 1997) and at the Brazilian section of the Upper Paraná River (Train, 1998). The relationship is similar for biomass, expressed as chlorophyll *a* (Thomaz et al., 1992b, c; Train & Rodrigues, 1997) and biovolume (García de Emiliani, 1993, 1997; Train, 1998; Zalocar de Domitrovic, 1999; Huszar, 1994).

The low rate of community compositional change during limnophase (lower than 0.1 day^{-1}), indicates a greater environmental stability, related to a higher complexity in the community organization. High σ during potamophase (with a maximum of 0.33 day^{-1}), suggests environmental variability (Reynolds, 1992), maybe indicating a higher rates of biogeochemical processes, characteristic of tropical environments (Estéves, 1988).

Table 5. List of algae recorded in the three lakes of the Paraná River floodplain with percentages higher than 5% of total phytoplankton and/or in more than 40% of samples.

CYANOPHYCEAE

Anabaena planctonica Brunnth.
Aphanizomenon sp.
Aphanocapsa delicatissima West & G.S. West
A. elachista West & G. S. West
Chroococcus minutus (Kütz.) Näg.
Merismopedia tenuissima Lemm.
Microcystis aeruginosa Kütz.
M. pulverea (Wood) Forti
M. viridis (A. Braun) Lemm.
Planktothrix sp.
Planktolyngbya subtilis (W. West) Anagn. & Kom.
Trichormus ellipsosporus (Fritsch) Kom. & Anagn.
T. naviculoides (Fritsch) Kom. & Anagn.

CHLOROPHYCEAE

Volvocales

Chlamydomonas conferta Korsch.
Ch. leptobasis Skuja
Ch. microsphaera Pasch. & Jahoda
Chloromonas acidophila (Nygaard) Gerloff & Ettl
Ch. gracilis (Matwienko) Ettl
Coccomonas platyformis Jane
Dysmorphococcus variabilis Takeda
Eudorina elegans Ehr.
Gonium pectorale Müller
Pteromonas sp.
P. rectangularis Lemm.
Pyrobotrys squarrosa (Kors.) Kors.

Chlorococcales

Ankistrodesmus gracilis (Reinsch) Kors.
Ankyra judayi (G.M. Smith) Fott
Chlorella ellipsoidea Gern.
Ch. vulgaris Beij.
Choricystis cylindracea Hind.
Coelastrum microporum Näg. in A. Braun
Crucigenia quadrata Morr.
Dictyosphaerium tetrachotomum Printz
Kirchneriella lunaris (Kirchn.) Moeb.
Micractinium pusillum Fres.
Monoraphidium contortum (Thur.) Kom.-Legn.
M. komarkovae Nyg.
M. minutum (Näg.) Kom.-Legn.
M. pusillum (Printz) Kom.-Legn.
Oocystis lacustris Chod.
Pediastrum duplex Meyen
P. simplex Meyen
Scenedesmus ecornis (Ehr.) Chod.
S. quadricauda (Turp.) Bréb. *sensu* Chod.
Schroederia antillarum Kom.
S. setigera (Schröd.) Lemm.
Sphaerocystis planctonica (Kors.) Bourr.
Tetrachlorella alternans (G.M. Smith) Kors.
Tetraedron caudatum (Corda) Hansg.
Tetrastrum elegans Playf.
T. heteracanthum (Nordst.) Chod.

EUGLENOPHYCEAE

Euglena sp. 1
Euglena sp. 2
Euglena acus Ehr
E. allorgei Defl.
E. bonettoi (Tell & Zalocar) Couté & Théréz.
E. ehrenbergii Klebs
E. fusca (Klebs) Lemm.
E.gaumei All. & Lef.
E. gracilis Klebs
E. oxyuris Schmarda
E. oxyuris f. *minima* Bourr.
E. proxima Dang.
E. rostrifera Johnson
E. sanguinea Ehr.
E. spathirhyncha Skuja
E. viridis Ehr.
Lepocinclis caudata da Cunha
L. salina Fritsch
L. pseudonayalii Tell & Zalocar
L. spirogyra Kors.
Phacus sp. 1
Phacus sp. 2
Phacus agilis
Ph. angulatus Pochm.
Ph. anomalus Fritsch & Rich
Ph. brevicaudatus (Klebs) Lemm.
Ph. glaber (Defl.) Pochm.
Ph. hamatus Pochm.
Ph. longicauda (Ehr.) Duj.
Ph. obolus Pochm.
Ph. onyx var. *symetrica* Tell & Zalocar
Ph. orbicularis Hübn.
Ph. pyrum (Ehr.) Stein
Ph. stokesii Lemm.
Ph. tortus (Lemm.) Skv.
Strombomonas argentinensis García de Emil.
Str. diptera Zalocar & Tell
Str. ensifera (Daday) Defl.
Str. fluviatilis (Lemm.) Defl.
Str. gibberosa (Playf.) Defl. var. *gibberosa*
Str. gibberosa var. *longicollis* (Playf.) Defl.
Str. girardiana (Playf.) Defl.
Str. girardiana var. *triondulata* Tell & Zalocar
Str. jaculata (Palmer) Defl.
Str. maxima (Skv.) Defl.
Str. ovalis (Playf.) Defl.
Str. rotunda (Playf.) Defl.
Str. schauinslandii (Lemm.) Defl.
Str. treubii (Wol.) Defl.
Str. verrucosa (Daday) Defl. var. *verrucosa*
Str. verrucosa var. *argentinensis* Tell & Zalocar
Str. verrucosa var. *borystheniensis* (Roll) Defl.
Str. verrucosa var. *zmiewika* (Swir.) Defl.
Trachelomonas abrupta var. *minor* Defl.
Tr. armata (Ehr.) Stein var. *armata* f. *armata*
Tr. armata var. *armata* f. *inevoluta* Defl.

Table 5. continued.

Tr. armata var. *steinii* Lemm. em. Defl.
Tr. caudata Ehr.) Stein
Tr. cervicula Stokes
Tr. curta da Cunha em. Defl. var. *curta*
Tr. curta var. *minima* Tell & Zalocar
Tr. dastuguei Balech
Tr. gracillima Balech & Dast.
Tr. hemisphaerica García de Emil.
Tr. hispida (Perty) Stein em. Defl.
Tr. intermedia Dang.
Tr. kellogii Skv. em. Defl.
Tr. magdaleniana Defl.
Tr. naviculiformis Defl.
Tr. oblonga Lemm. var. *oblonga*
Tr. oblonga var. *umbilicophora* Defl.
Tr. planctonica var. *flexicollis* Balech
Tr. planctonica var. *oblonga* Drez.
Tr. pulcherrima var. *minor* Playf.
Tr. pusilla Playf.
Tr. robusta Swir. em. Defl.
Tr. rugulosa Stein em. Defl.
Tr. scabra var. *coberensis* Defl.
Tr. sculpta Balech
Tr. sydneyensis Playf.
Tr. sydneyensis var. *grandicollis* Defl.
Tr. sydneyensis var. *oblonga* Playf.
Tr. varians Defl. var. *varians*
Tr. varians f. *acuminata* Defl.
Tr. volvocina Ehr.
Tr. volvocina var. *derephora* Conr.
Tr. volvocina var. *punctata* Playf.
Tr. volvocinopsis Swir.
Tr. woycickii Koczw.

BACILLARIOPHYCEAE

Centrales
Aulacoseira granulata (Ehr.) Simonsen
A. herzogii (Lemm.) Simonsen
Cyclotella meneghiniana Kütz.

Pennales
Amphipleura lindheimeri Grun.
Capartogramma crucicula (Grun. ex Cl.)
Ross
Cymbella tumida (Bréb.) V. Heurck
Eunotia sp.
E. didyma var. *curta* Hust.
E. formica Ehr.

E. minor (Kütz.) Grun. *in* V. Heurck
E. pectinalis f. didymodon (Grun.) A. Berg
Fragilaria construens (Ehr.) Grun.
Gomphonema augur var. turris (Ehr.) Lange-Bertalot
G. parvulum Kütz.
Gyrosigma acuminatum (Kütz.) Rabh.
Navicula capitata Ehr.
Nitzschia sp.
N. acicularis W. Smith
N. reversa W. Smith
Pinnularia sp.
P. gibba var. *parva* (Ehr.) Hust.
P. latevittata var. *domingensis* Cl.
P. viridis (Nitzsch) Ehr.
Surirella robusta Ehr.
S. tenera Greg.
Synedra sp. 1
Synedra sp. 2
S. ulna (Nitzsch) Ehr. var. *ulna*
S. ulna var. *contracta* Ostr.

CHRYSOPHYCEAE
Synura sp.
Mallomonas sp. 1
Mallomonas sp. 2

XANTHOPHYCEAE
Chlorogibba allorgei Bourr.
Goniochloris sculpta Geitler
G. tripus Pascher
G. fallax Fott
Tetraedriella jovetii (Bourr.) Bourr.
Tetraplektron torsum (Skuja) Dedus. Sceg.
Tetraplektron torsum var. *longispinum* Théréz.
Pseudostaurastrum lobulatum (Nag.) Chodat

DINOPHYCEAE
Peridinium sp.

CRYPTOPHYCEAE
Rhodomonas minuta Skuja
Chroomonas caudata Geitler
Cryptomonas ovata Ehr.
C. erosa Ehr.
C. marssonii Skuja
C. gracilis Skuja
C. reflexa Skuja
C. rostratiformis Skuja

Conceptual aspects of phytoplankton periodicity and response to gradual environmental changes

According to the concepts of ecological succession applied to phytoplankton by Reynolds (1980, 1988b), and considering both floods as a disturbance factor (*sensu* Reynolds et al., 1993), there was a phytoplanktonic succession between floods for 43 days, with an autogenic development of the community. The first flood (after a prolonged isolation) produced marked physical and chemical changes and the phytoplanktonic community began a new ('shifted') succession.

During the first week after the succession began, associations of small flagellated green algae from group G1 (*Chloromonas acidophila* and *Chlamydomonas leptobasis*) predominated in density (C-
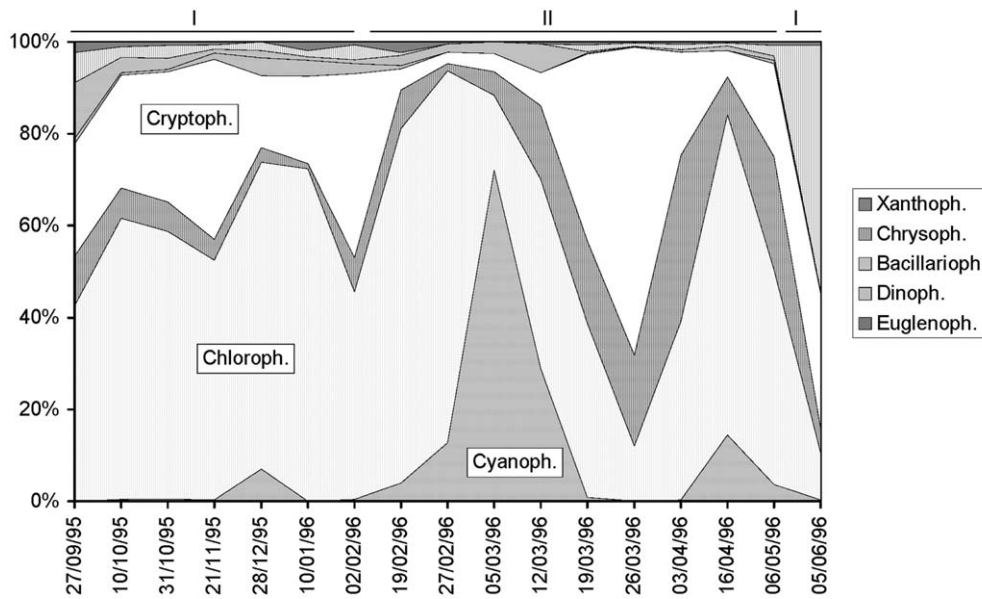
Figure 6. Relative density (%) of the main taxonomic groups of phytoplankton. I: limnophase, II: potamophase.
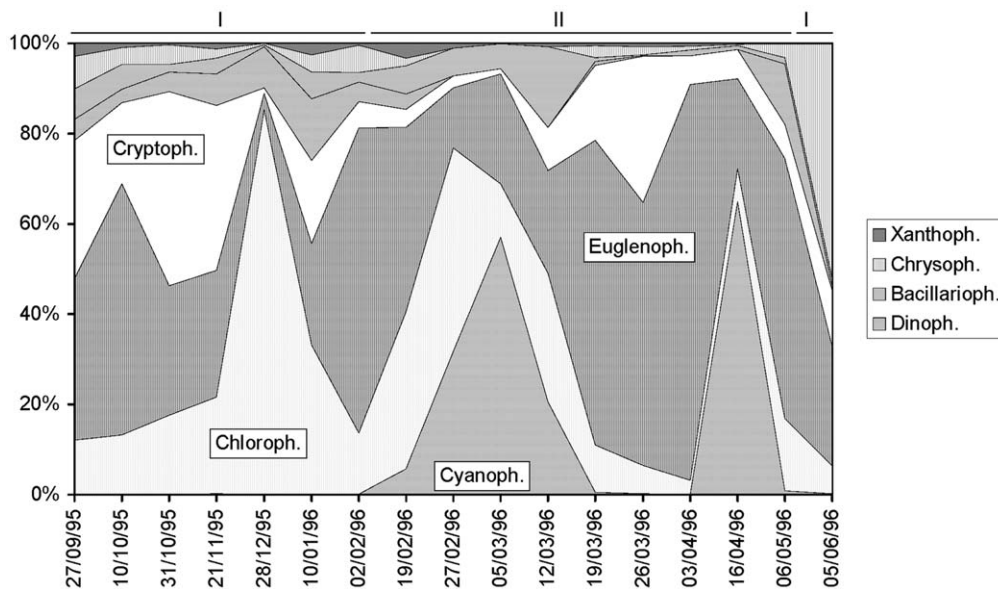

Figure 7. Relative biomass (%) of the main taxonomic groups of phytoplankton. I: limnophase, II: potamophase.

strategists), accompanied by others from groups G3 and G4, which were less abundant but with larger biomass (*Pyrobotris squarrosa* and *Eudorina elegans*). During the second week, there was an increase in colonial Cyanophyceae, with *Merismopedia tenuissima* predominating in density and biomass, and to a lesser extent *Aphanocapsa* and *Microcystis*. Between the third and fifth weeks, associations of Chlorophyceae continued dominating, while Cryptophyceae

increased. In parallel, there was a gradual increase in biomass of Euglenophyceae (S-strategists) until the second flood. During this last flood, the community showed a 'reversion' phenomenon. The composition of species was similar to that observed before, during the first two weeks after the first flood.

The presence of Dinophyceae and Chrysophyceae during isolation can be related to nutrient enrichment, resulting in the rapid growth (Chrysophyceae),
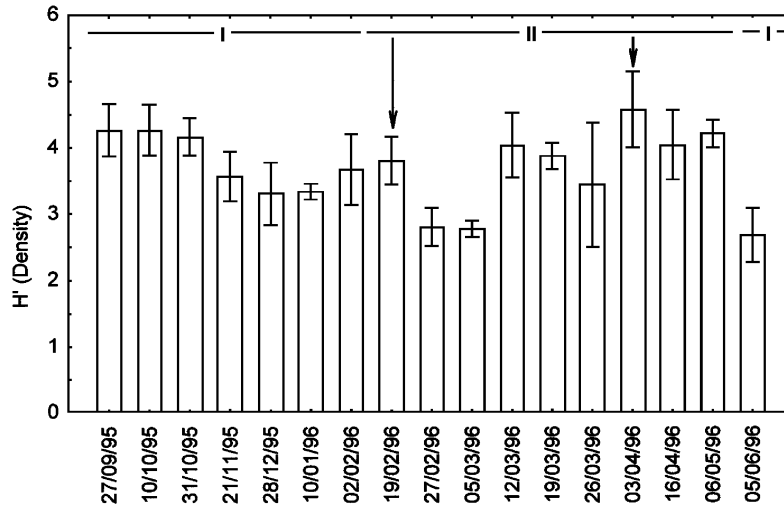
Figure 8. Mean values (± S.E.) of diversity ($H'D$) based on phytoplankton density (bits ind.$^{-1}$) in lakes of the Paraná River floodplain. I: limnophase, II: potamophase. Arrows: input of lotic waters.
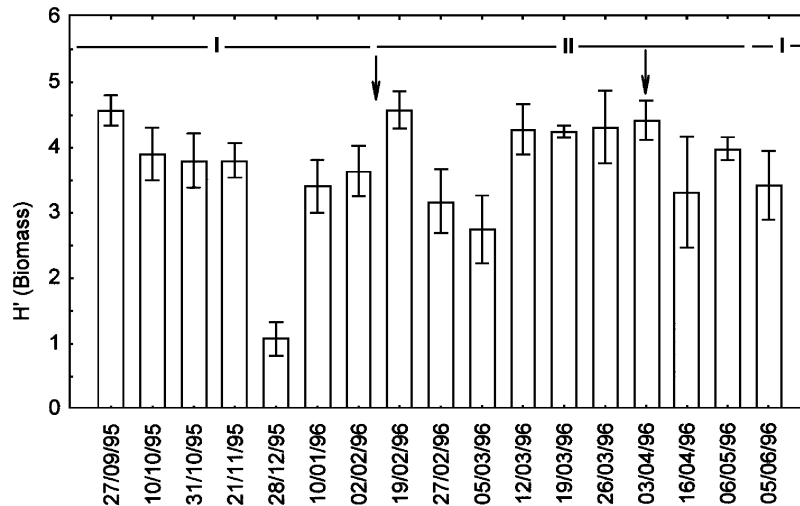

Figure 9. Mean values (± S.E.) of diversity ($H'B$) based on phytoplankton biomass (bits mm^{-3}) in lakes of the Paraná River floodplain. I: limnophase, II: potamophase. Arrows: input of lotic waters.

or slow, gradual growth (Dinophyceae and Euglenophyceae) of these groups. Dominance of Chrysophyceae of the genus *Synura* would also depend on the presence of cysts. The proliferation of this group when flood waters decrease is a phenomenon known in some ponds of the Middle Paraná River (García de Emiliani, 1979; Zalocar de Domitrovic, 1990). Dinophyceae and Euglenophyceae, in contrast, incorporate nutrients slowly and gradually, increasing their size and prevailing over other algae at the end of the succession (S-strategists). The disappearance of dinoflagellates during the first two weeks after the first input of flood

waters would indicate their sensitivity to modifications in physical and chemical variables. Such disappearance would probably be related to high ammonium concentrations recorded at this moment, because they have low growth rate when this element (more than nitrate) is the nitrogen source (Lindström, 1991).

During the first two weeks of potamophase, the scarcity of Cryptophyceae, which are usually dominant or subdominant in these environments during flood periods (García de Emiliani, 1980, 1993, 1997; Zalocar de Domitrovic, 1990, 1992, 1993; Train, 1998), was remarkable. An important increase in Crypto-
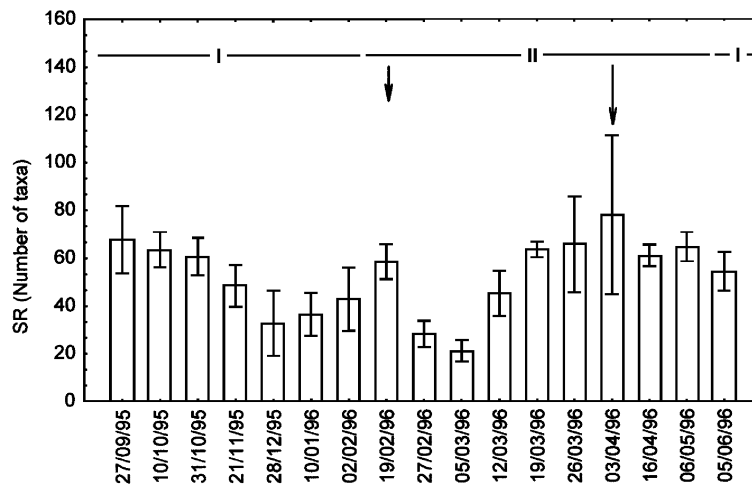
Figure 10. Mean values (± S.E.) of species richness (SR) of phytoplankton in lakes of the Paraná River floodplain. I: limnophase, II: potamophase. Arrows: input of lotic waters.

phyceae was observed from the first week in relation to an 'improvement' in the physical and chemical conditions of waters.

Cyanophyceae are not very frequent in the Paraná River floodplain (García de Emiliani, 1993, Zalocar de Domitrovic, 1993). However, in this study, they predominated during the first two weeks of potamophase, probably because they were able to tolerate physical and chemical conditions found in the floodplain during that period (Carignan & Planas, 1994).

In this study, during potamophase, highest diversity and number of algal species would be related not only with environmental conditions favourable for their growth but also with the effects produced by the horizontal dragging of *information* (*sensu* Margalef, 1961) previously accumulated in the rest of the floodplain. These results differ from those of other studies with high water levels (higher than 7 m) or extraordinary floods where H′ and SR were found in very low values (Zalocar de Domitrovic, 1992).

García de Emiliani (1993), based on Reynold's concept (1988), suggested that seasonal changes of phytoplankton in lakes are best interpreted as the interaction between true successional development and intermediate disturbance. An interesting aspect about periodicity of phytoplankton was proposed by Huszar & Reynolds (1997) for a floodplain lake of the Amazon basin. They demonstrated that *gradual climate change*, in Wilson's (1994) sense, also has a planktonic analogue. In this respect, I agree with Huszar & Reynolds, who demonstrated how one successional pathway can be supplanted by another one in

response to a gradual change in the hydrographic environment ('hydroclimate'), and not as a consequence of wholly internally-driven processes. It is logical to think that gradual changes of 'hydroclimate' in great river floodplains constitute a preponderant factor to understand certain patterns of phytoplankton periodicity.

Considerations on the specific richness and structure of the phytoplanktonic community

At the source of the Middle Paraná River, the environments that receive the influence from Paraguay River waters have generally the qualitative predominance of Euglenophyceae (Zalocar de Domitrovic, 1993; this study). In contrast, those environments that receive a greater influence from the Upper Paraná River have a higher number of species of Chlorophyceae Chlorococcales (Zalocar de Domitrovic, 1990, 1992).

These lakes are different from others of tropical and subtropical environments (e.g., Amazon and Uruguay basins), where Desmidiaceae (Chlorophyceae) stand out because of their floristic richness (Uherkovich, 1976). Some authors (e.g., Rojo et al., 1994) described this algal group as characteristic of tropical and subtropical environments. However, in the Paraná River floodplain, Desmidiaceae are scarcely represented.

The qualitative predominance of Euglenophyceae in these environments could be related to the important quantity of organic matter brought to the system by vegetation and to the high nutrient concentration (Carig-
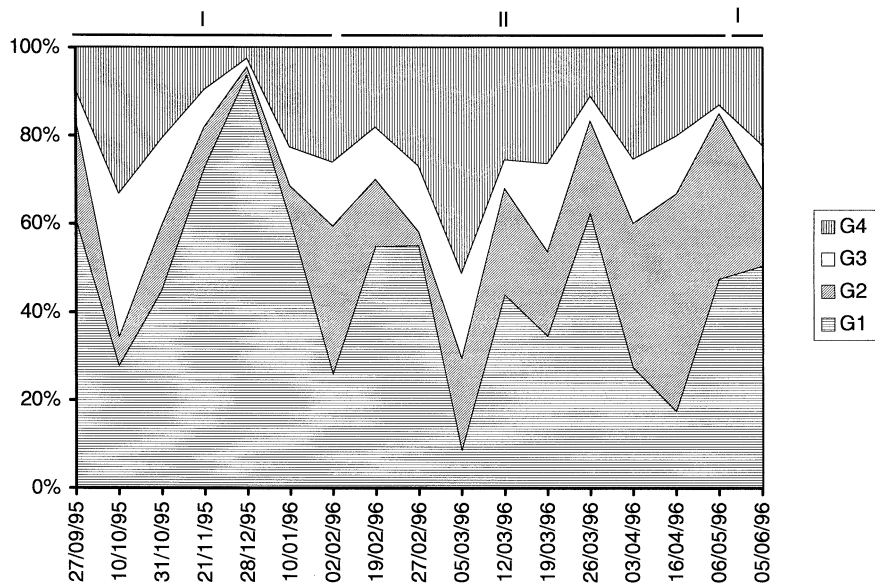
Figure 11. Variation in relative biomass of phytoplankton ($mm^3 ml^{-1}$) grouped by size, according to GALD. G1: >1–$20 \mu m$, G2: >20–$40 \mu m$, G3: >40–$100 \mu m$, G4: $>100 \mu m$. I: limnophase, II: potamophase.

nan & Neiff, 1992), which favour the development of this group (Huber-Pestalozzi, 1955).

From the total taxa recorded at the three lakes, 18% of them were common to the Paraná River and 48% to the Paraguay River basin. The greatest similarity with the former was found for Chlorophyceae and, with the latter, for Euglenophyceae.

In the source of the middle section of the Paraná River floodplain there are environments with analogous conditions to many environments of the Upper Paraguay basin (waters rich in organic matter, low content of dissolved oxygen, acid pH, important coverage of aquatic macrophytes, etc.).

The similarity in the species composition (mainly Euglenophyceae) between the Paraguay River's Pantanal and the floodplain environments could be attributed to the transport of those species by Paraguay River waters (Zalocar de Domitrovic, 2002). These species, as vegetative cells or as spores or cysts, would act as a potential inoculum in the floodplain when environmental conditions would be favourable for their development. In this way, the concept of 'ecological memory' (*sensu* Padisák, 1992) also applies to fluvial phytoplankton (Rojo et al., 1994). Thus, the river, while interacting with the floodplain, in each flood, acts as a receptor and distributor of 'memory' species.

Neiff (1996) pointed out pulse hydrodynamics as regulators of biocenosis in great rivers, where both phases constitute powerful factors of selection in the distribution and abundance of plants and animals. Several authors (Train, 1998; Zalocar de Domitrovic, 1992) indicated floodplain aquatic environments as sources of biodiversity conservation, where vegetation contributes with a greater variety of niches for aquatic organisms. Neiff et al. (1994) considered these environments, of great 'ecological plasticity', as important biodiversity reservoirs.

Finally, these results support the hypothesis that hydrology (floods) clearly exerts an overall impact on the phytoplankton community composition in lakes of the Paraná River floodplain, via its effects on the lake water chemistry (conditioned by the isolation time prior to a flood), the horizontal dragging and exchange of algae during floods, the water residence time and aquatic vegetation coverage.

Acknowledgements

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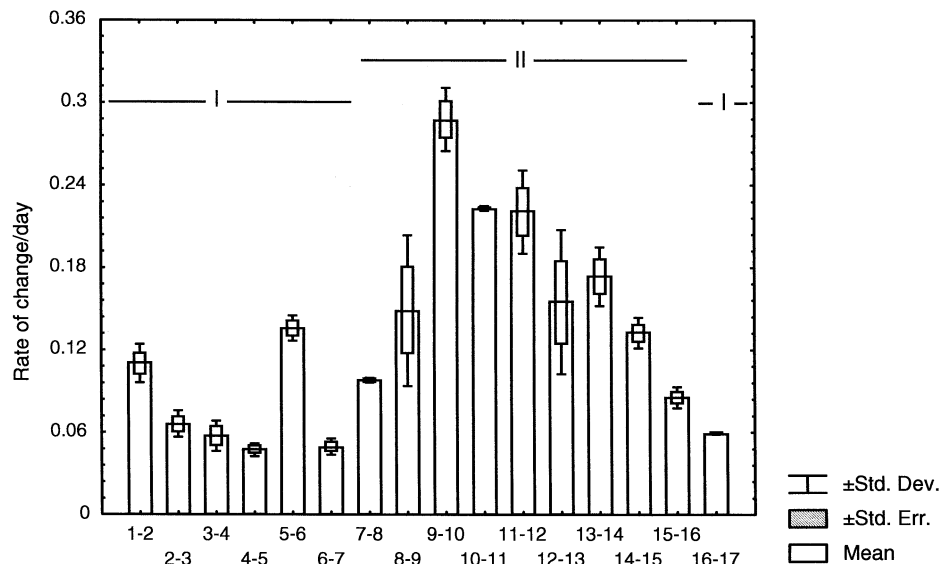
Figure 12. Rate of community change based on phytoplankton biomass in lakes of the Paraná River floodplain. I: limnophase, II: potamophase.

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