

Changes in phytoplankton morpho-functional groups induced by extreme hydroclimatic events in the Middle Paraná River (Argentina)

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Abstract The extreme hydrological fluctuations in the South American Paraná River are unequivocally coupled with El Niño-Southern Oscillation's (ENSO's) global climatic phenomenon. In order to identify phytoplankton changes triggered by periods of extraordinary flood (November 1997–1998) and drought (November 1999–2000), the main channel of the Middle stretch was monthly analysed and compared with neutral hydrological conditions (November 1977–1978). These results show that water discharge plays a stirring role on phytoplankton dynamics, and that light availability acts as an important selective force. Phytoplankton transport,

density, and biovolume were lower during El Niño and higher during La Niña ($P < 0.01$). A great development of small flagellate unicells belonging to morpho-functional groups **Y** (*Cryptomonas* spp.) and **X2** (*Chlamydomonas* spp., *Plagioselmis nannoplantica* and small Cryptophyceae) prevailed during both anomalous periods, accompanied by small centric diatoms and *Skeletonema* cf. *potamos* (**D**). This scenario significantly differs from those encountered during neutral conditions, where codon **P** (*Aulacoseira granulata*) dominated. The absence of these large filaments during drought and flood peaks could be explained by sedimentation processes in low waters, and by organisms' retention by obstacles after water displacement from the plain in high waters periods; however, the disruption of the inocula from floodplain areas to the main flow may be the most important factor in both periods. The hydroclimatic anomalies provoked changes in the phytoplankton structure of the Paraná River, favouring **X2** and **Y** functional groups instead of the typical **P** and **C**. The interruption of the constant feedback between the main channel and the floodplain water bodies due to low connectivity during droughts and the homogeneity of environment during floods, govern phytoplankton dynamics in this large river. The rapid occurrence of community reorganization after the conclusion of these events and the persistence of certain variations lead to the hypothesis that the magnitude and duration of extreme water discharges will determine the intensity and duration of changes.

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Introduction

El Niño-Southern Oscillation (ENSO) is a global climatic phenomenon positively correlated with pluvial anomalies strongly affecting the discharge patterns of rivers throughout the world (Kane, 2002; Wilby et al., 2008). In the Paraná River, the second largest hydrographical system of South America and fifth in the world, extreme hydrological events are unequivocally coupled with ENSO phases (Camilloni & Barros, 2003). The consequences are record floods (ENSO's warm phase, El Niño) and droughts (ENSO's cold phase, La Niña) that alternate with periods without anomalies (neutral conditions) (McPhaden et al., 2006). These extraordinary events produce changes on the river's physical and chemical conditions (Neiff, 1996). In this sense, they may act as disturbances for the biota by producing either gradual or discrete changes in a control factor. If it exceeds a critical threshold, the structure and functioning at population, community or ecosystem level will be affected (Sparks & Spink, 1998).

Phytoplankton assemblages of large rivers are strongly influenced by physical factors, mainly water discharge and the related hydrological variables (Descy, 1993; Stoyneva, 1994; Reynolds & Descy, 1996; Wehr and Descy, 1998; Salmaso & Braioni, 2007; Gruberts, 2007). Discharge fluctuations allow lateral exchanges and recruitment of organisms from river refuges, including zones within the river and adjacent water bodies (Reynolds & Glaister, 1993). In floodplain rivers, where the main channel and the alluvial valley are integrated components of a dynamic system, the pulsing of water discharge is the major force that determines the degree of connectivity and exchange of matter and organisms across a lateral gradient (Junk et al., 1989). These processes are fundamental for the maintenance of suspended algae in the mainstem where environmental conditions such as turbidity, turbulence, low residence time, and unidirectional flow physically constrain phytoplankton development (Reynolds, 2000).

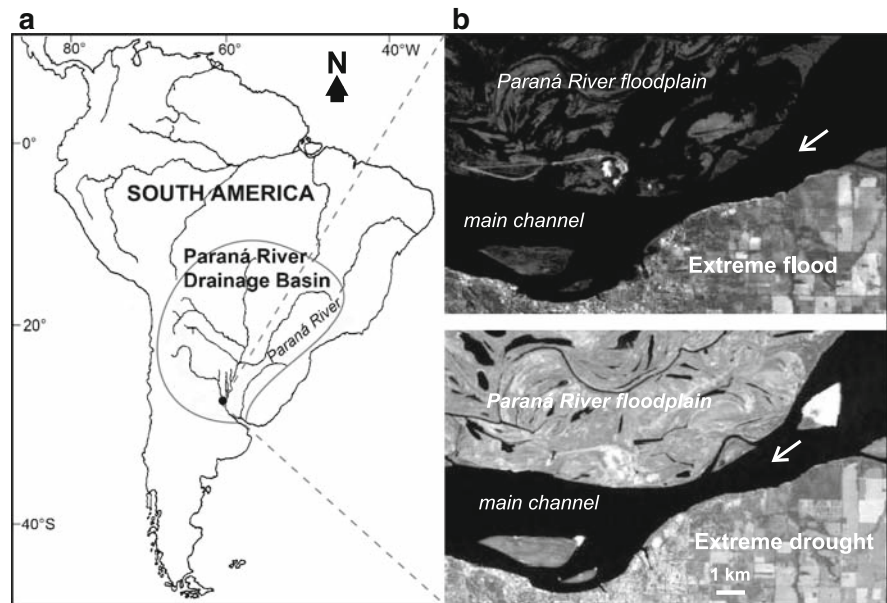
Several studies have analysed potamoplankton responses to neutral hydrological conditions in the Paraná River (Bonetto et al., 1982; García de Emiliani, 1990; O'Farrell et al., 1996; Zalocar de Domitrovic, 1999). These periods are characterised by alternatively high- and low-water phases, identified by the degree of connection between the main channel and the alluvial valley. In the Paraná River Middle stretch, when water discharges exceeds $21,700 \text{ m}^3 \text{ s}^{-1}$ or are below $13,700 \text{ m}^3 \text{ s}^{-1}$, anomalous hydrological conditions are triggered (Fig. 1b). Even though the magnitude and frequency of these extraordinary floods and droughts have been increasing in the last decades (Wilby et al., 2008), the understanding of their effects in large rivers is limited.

The aim of this work is to analyse the ecological effects of extreme discharge fluctuations on the phytoplankton of the mainstem of the Middle Paraná River. Extreme flood (November 1997 to December 1998) and drought periods (November 1999 to December 2000) are compared with historical data registered during neutral conditions (November 1977 to December 1978). Changes in algal density and biovolume are discussed as well as algal transport in order to illustrate differences among periods with markedly different dilution capacity. The community structure of life forms, taxonomic, and functional groups is analysed. The functional classification is performed according to Reynolds et al. (2002) proposal. Although it was primarily created for lentic water bodies, it was successfully applied in rivers (Devercelli, 2006; Borics et al., 2007; Soares et al., 2007) providing information that was recently included in algal habitat templates by Padisák et al. (2009).

Study area

The Paraná River flows from North to South along 3,800 km, draining an area of $2.6 \cdot 10^6 \text{ km}^2$ (Fig. 1a). The Middle stretch extends from its confluence with the Paraguay River ($27^\circ 29'S$; $58^\circ 50' W$) to Diamante City ($32^\circ 4'S$; $60^\circ 32' 30'' W$). It has a well-defined mainstem and multiple anabranches, with a length of 707 km, a slight slope ($3\text{--}5 \text{ cm km}^{-1}$), variable width (0.4–8 km) and a

Fig. 1 **a** Paraná River drainage basin and sampling site location (filled circle) **b**. Study area during extreme flood (May 1998) and drought (January 2000) periods. The arrows indicate the water flow direction. Landsat 5 satellite image from Lab. de Sedimentología archives, Facultad de Ingeniería y Ciencias Hídricas, UNL, Ing. M. Amsler



maximum depth of 45 m. It is fringed along its right bank by a 6–40 km wide floodplain (13,000 km²), comprising thousands of permanent and temporary water bodies (Drago, 2007). The annual average discharge is 16,000 m³ s⁻¹ mainly supplied by the Upper Paraná. It is a turbid river with a mean suspended solids concentration of 276 mg l⁻¹, most of them (50–70%) coming from the Bermejo Basin through the Paraguay River. The sedimentary pulse is not coupled with the hydrological pulse (Depetris et al., 2003). Samples were taken at a river nodal point, where 85% of the total river discharge drains (Drago, 2007). It constitutes a narrow and deep cross-section (Fig. 1b, 0.8–1.2 km width and 29 m maximum depth) situated 100 km upriver from Diamante City (31° 42' 34" S; 60° 29' 7" W).

Materials and methods

Samples were collected monthly from the centre of the Middle Paraná River mainstem from November 1997 to December 1998 (El Niño), November 1999 to December 2000 (La Niña, except on January and June 2000), and compared with historical data registered from November 1977 to December 1978 (neutral conditions). The similarity of the methods used for measuring environmental variables and the

taxonomic criteria in each period was checked. Daily water discharge values were obtained from Paraná Harbour gauge, located 25 km downstream of the studied area. Depth, subsurface water velocity (current meter), temperature, pH, conductivity, dissolved oxygen (water quality checker Horiba U-10) and water transparency (Secchi disk) were measured in situ. Subsurface water samples were carried on ice to the laboratory and filtered through Whatman GF/F filters for dissolved chemical analyses. Total suspended solids (SS) were determined by water sample filtration through porcelain filters and dried at 105°C to constant weight. Total dissolved solids (TDS) were analysed from the water filtrate and dissolved organic matter (DOM) was obtained by ashing to 550°C and weighting (Rodier, 1981). Nitrate and nitrite concentration (cadmium-cooper reduction followed by colorimetric analysis of nitrite), ammonium (indophenol-blue method), and soluble reactive phosphorus (SRP, ascorbic acid-molibdate method) were analysed following APHA (1992).

Subsurface phytoplankton samples were collected and fixed with Lugol's acidified solution (1%). Additional samples for taxonomic analysis were obtained with a 25 µm pore net and fixed with formaline (2%). Taking into account that these are the first data of algal biovolume in the study area, results of both density and biovolume are presented for their

comparison. Algal counts (cells, colonies and filaments) for density calculation (ind. ml^{-1}) were performed with inverted microscope (Utermöhl, 1958). Biovolumes ($\mu\text{m}^3 \text{ ml}^{-1}$) were calculated following Hillebrand et al. (1999) and Olenina et al. (2004); spines, flagella, and mucilage were excluded. A 35% and 65% was subtracted to pennate and centric diatom biovolumes, respectively, in order to consider the intracellular vacuoles (Round et al., 1990). Algal transport was obtained by multiplying density with water discharge (10^9 ind. s^{-1}). Life forms were classified into five categories: flagellate unicells, non-motile unicells, filaments, colonies, and coenobia (Reynolds, 1984). Species were sorted in the functional groups proposed by Reynolds et al. (2002) and Padisák et al. (2009).

Taxa and functional group diversity (density) was estimated according to Shannon and Wiener Index (Shannon & Weaver, 1949) using \log_2 . Normality and homogeneity of variances were checked with Kolmogorov–Smirnov and Bartlett tests, respectively. Spearman's correlation coefficients were calculated among all measured variables (species, major taxonomic groups and functional groups, versus environmental variables). Kruskal–Wallis with Dunn's post test was used to compare all study periods. The mentioned statistical analyses were computed with SPSS 10.5 and PAST 1.76 software. The ordination of functional groups in relation to samples was carried out by principal component analysis (PCA), applied to the correlation matrix performed by the CANOCO 4.5 software (ter Braak & Smilauer, 2002) on the basis of both density and biovolume data. Functional groups with mean contributions to total density or biovolume less than 1% were not included.

Results

Environmental characterization

Water discharge fluctuations during El Niño period (November 1997–1998) differed significantly from La Niña (November 1999–2000) and the neutral conditions (November 1977–1978) ($P < 0.001$, Fig. 2a). The extreme flood phase was registered from December 1997 to June 1998 (mean water

discharge: $23,618 \text{ m}^3 \text{ s}^{-1}$), with a decreasing water phase till August. The exceptional drought occurred from November 1999 to February 2000 ($11,526 \text{ m}^3 \text{ s}^{-1}$) with a slight discharge increment on February and a rising water phase from March to May 2000. The mid-water phase took place from June 2000 onwards. The neutral period registered ordinary discharge fluctuations with alternating high- and low-waters ($13,220 \text{ m}^3 \text{ s}^{-1}$). Similar water temperature patterns were evidenced among the study periods (Fig. 2b). River depth was about 17.6 and 26 m for the whole data set. Mean current velocity was 1.2 m s^{-1} for La Niña and the neutral period. The highest current velocity occurred at the beginning of the El Niño flood (1.7 m s^{-1} , November 1997) and it diminished with discharge increments (1.5 m s^{-1} , April 1998). For the whole data set, it was directly correlated to water discharge ($r = 0.51$, $P < 0.01$), and indirectly correlated to SS ($r = -0.37$, $P < 0.05$), TDS ($r = -0.54$, $P < 0.01$) and DOM ($r = -0.39$, $P < 0.01$). Moreover, water transparency was inversely correlated to SS and TDS ($r = -0.87$ and 0.54 , respectively, $P < 0.01$). During El Niño minimum SS and maximum water transparency values occurred, with significant differences as regards to the other periods ($P < 0.001$, Fig. 2c, d). The sedimentary pulse due to the solid input coming from the Bermejo River occurred on February in all the years here analysed. The SS increment was slight in February 1998, whereas it was higher during the other periods (February to April). DOM concentration differed significantly between neutral and anomalous periods ($P < 0.01$), with higher values during the former (Table 1). Dissolved oxygen concentrations were usually near saturation (80–118% of saturation), and the minimum value was recorded at the onset of the extreme flood (64%). The lowest conductivity and pH values were measured during El Niño, with significant differences in comparison with the other periods ($P < 0.001$, Fig. 2e, f). Both variables were inversely correlated to water discharge ($r = -0.78$ and -0.75 , $P < 0.01$, respectively).

Maximum nitrate, nitrite, and ammonium concentrations were registered at anomalous periods (Table 1), yet significant differences only occurred between the neutral and El Niño periods ($P < 0.01$). Nitrate contents increased progressively with water discharge increments at La Niña (April–May 2000) whereas at El Niño, higher values were observed

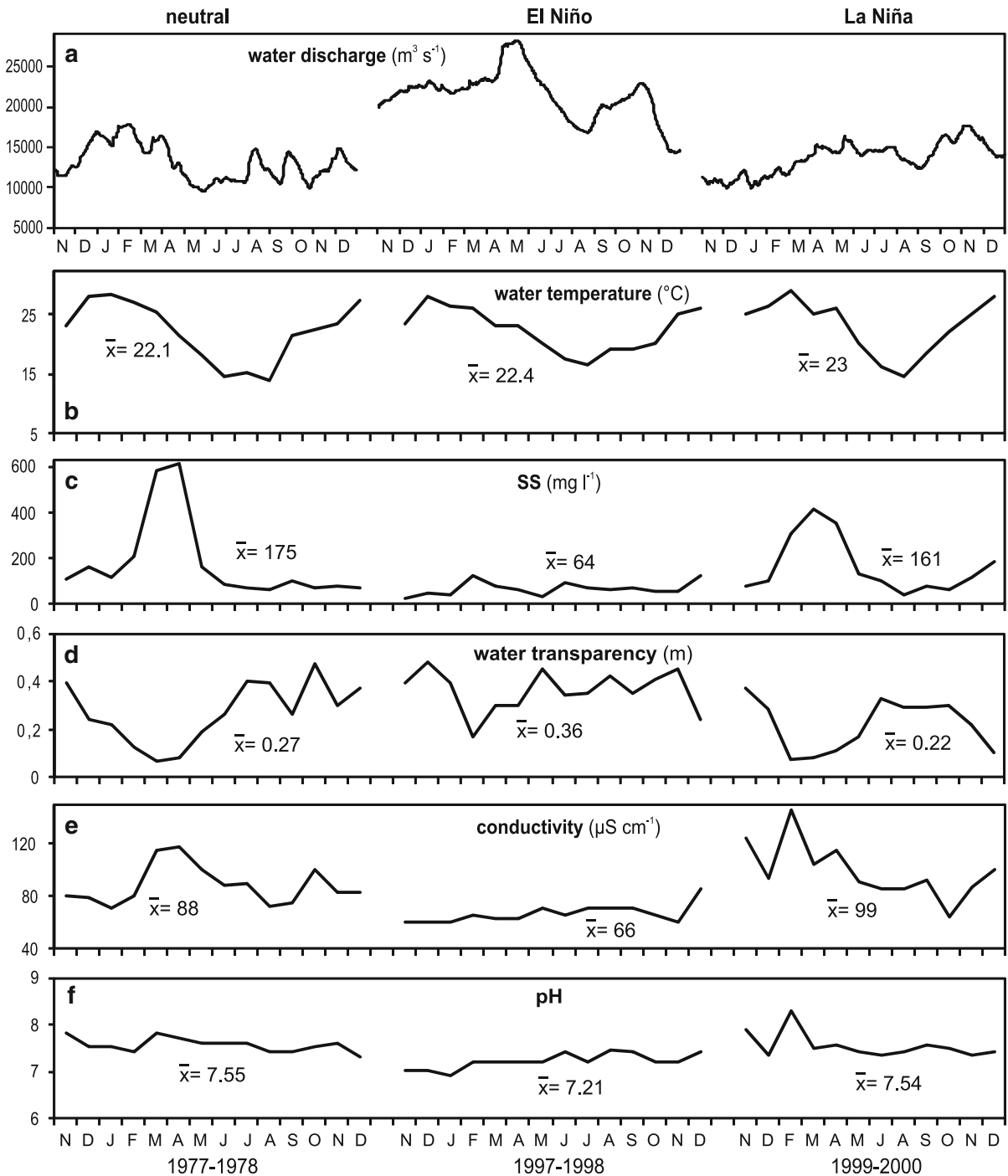


Fig. 2 Temporal variations of environmental conditions in the Middle Paraná River during the study periods. Mean values (\bar{x}) for each period are indicated

during the extreme flood phase (March–June 1998). Likewise, SRP concentrations were significantly higher at anomalous periods ($P < 0.05$), and the

maximum values were registered during La Niña increasing discharges (February–March, October–December 2000).

Table 1 Mean values (\bar{x}) and range of dissolved solids (TDS), dissolved organic matter (DOM) and nutrient concentrations measured in the Middle Paraná River during the study periods

	Neutral (1977–1978) \bar{x} (range)	El Niño (1997–1998) \bar{x} (range)	La Niña (1999–2000) \bar{x} (range)
TDS (mg l ⁻¹)	66 (43–91)	45 (9–62)	69 (49–115)
DOM (mg l ⁻¹)	20 (10–46)	12 (8–16)	13 (7–21)
Nitrate (mg l ⁻¹)	1.03 (0.16–2.38)	2.83 (0.44–6.16)	3.08 (0.04–8.8)
Nitrite (mg l ⁻¹)	0.01 (0.006–0.017)	0.03 (0.007–0.046)	0.02 (0.009–0.033)
Ammonium (mg l ⁻¹)	0.07 (0.01–0.26)	0.28 (0.03–1.26)	0.75 (0–4.84)
SRP (mg l ⁻¹)	0.07 (0.03–0.16)	0.10 (0.05–0.24)	0.36 (0.04–1.1)

Phytoplankton

Taxonomical and functional diversity

A total of 171 taxa were identified for the whole data set: 111 corresponded to La Niña, 104 to El Niño and 78 to the neutral period (see Appendix—Supplementary Material). No statistical differences were found among periods. Chlorophyceae and Bacillariophyceae achieved relevance in terms of species richness. The registered taxa were sorted into 24 functional groups, mainly **J**, **X1**, and **X2**.

The species diversity index ranged from 1.91 to 4, with average values between 3.27 and 3.43 considering all the periods (Fig. 3a). Diversity declined during La Niña event coincidentally to an SS concentration increase (February–April, December 2000), thus evidencing an inverse correlation to Secchi disk readings ($r = -0.77$, $P < 0.01$). At the extreme flood phase, minimum diversity values were observed (February–May 1998). Diversity presented frequent and pronounced temporal changes during the neutral period. Lowest values occurred after intervals of falling water discharges (March, July, October 1978) and in March it also coincided with SS increment. Phytoplankton diversity calculated on the basis of functional groups, showed a similar trend, but with values and averages lower than those of species diversity (Fig. 3a).

The whole community

Mean algal transport at the Middle Paraná River was lower during El Niño event and higher during La Niña, with intermediate values in the neutral period (Fig. 3b). It was inversely correlated to water

discharge for the whole data set ($r = -0.4$, $P < 0.05$). In accordance, density and biovolume followed the same pattern (Fig. 3c, d) and were also inversely correlated to water discharge ($r = -0.61$ and -0.62 , respectively, $P < 0.01$). The lowest algal transport, density, and biovolume were registered during the flood phase (January–June 1998), augmented with decreasing water phase and achieved higher values towards the end of that stage. Values during El Niño were statistically lower than at other periods ($P < 0.01$). As regards La Niña, the highest algal concentration was recorded at mid-waters (September–December 2000) and the lowest was observed from March to July 2000, in coincidence with the coupling of rising waters and high SS. The neutral period presented more frequent and pronounced fluctuations, with maximum and minimum values during low waters (October and May 1978, respectively) and increments of variable intensity after short periods of water drop (March, July, and December 1978).

Life forms, taxonomic, and functional groups

Cryptophyceae, Bacillariophyceae, and Chlorophyceae were the dominant groups as regards density and biovolume, followed by Chrysophyceae and Cyanobacteria. Ulotrichales, Zygnematales, Xantophyceae, Dinophyceae, and Euglenophyceae contributions to total phytoplankton concentration were less than 2%. Table 2 summarises the statistics for the main taxonomic and functional groups, and Fig. 4 shows the temporal variation of functional groups at the different study periods.

During El Niño flood period, the dominant life form in terms of density was flagellate unicells,

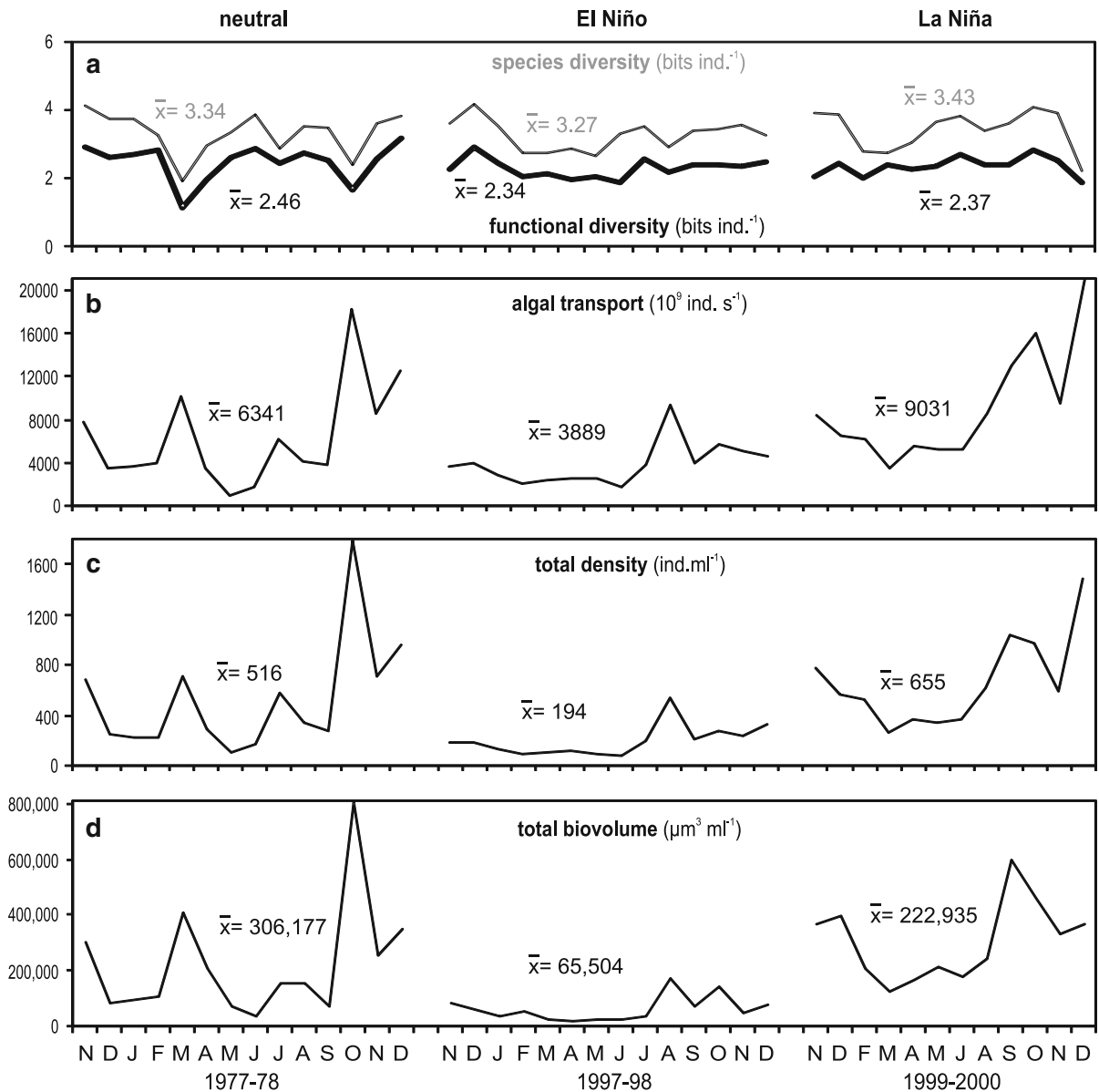


Fig. 3 Temporal variations of species and functional diversity (a), and total phytoplankton transport (b), density (c), and biovolume (d) in the Middle Paraná River during the study periods. Mean values (\bar{x}) for each period are indicated

grouped in **X2** (mainly *Plagioselmis nannoplanctica*, with minor proportions of *Chroomonas acuta*, *Cryptomonas pusilla*, and *Chlamydomonas* spp.) and **Y** (*Cryptomonas brasiliensis*, *C. erosa*, and *C. ovata*). The major contributions of the **X2-Y** assemblage were registered during the extreme flood pulse (March–June 1998), but higher **X2** density occurred during decreasing waters (correlation to water discharge: $r = -0.8$, $P < 0.01$). As regards biovolume,

large filaments forms and centric diatoms presented higher concentrations. Codon **P** (mainly *Aulacoseira granulata* and its bioforms) achieved high contributions through all the study period, except for the flood phase (January–June 1998) when even no occurrences were registered at the maximum water discharge (April–May 1998). Group **B** (*Aulacoseira italica*) was abundant from December 1997 to February 1998, and other groups such as **A** (*Cyclotella* cf. *glomerata*),

Table 2 Density and biovolume mean values (\bar{x}) and range for the main taxonomic and functional groups of the Middle Paraná River during the studied periods

	Density (ind.ml ⁻¹)				Biovolume (μm ³ ml ⁻¹)				
	Neutral (1977–1978) \bar{x} (range)	El Niño (1997–1998) \bar{x} (range)	La Niña (1999–2000) \bar{x} (range)	Neutral (1977–1978) \bar{x} (range)	El Niño (1997–1998) \bar{x} (range)	La Niña (1999–2000) \bar{x} (range)	Neutral (1977–1978) \bar{x} (range)	El Niño (1997–1998) \bar{x} (range)	La Niña (1999–2000) \bar{x} (range)
Bacillariophyceae	370 (42–1,528)	61 (14–160)	214 (28–981)	147,575 (22,511–686,762)	30,031 (5,516–87,913)	42,807 (9,829–94,670)			
<i>Aulacoseira granulata</i>	244 (18–1,280)	31 (0–107)	23 (0–89)	110,179 (11,701–615,483)	18,039 (0–78,116)	9,864 (0–32,536)			
Chlorococcales	56 (10–160)	7 (1–17)	42 (17–95)	26,484 (1,178–88,812)	5,500 (17–24,576)	61,086 (2,386–234,892)			
Volvocales	3 (0–8)	9 (1–21)	66 (9–151)	81 (1,178–88,812)	2,351 (19–78,82)	11,917 (1,024–37,515)			
Cryptophyta	35 (0–88)	109 (49–341)	227 (76–399)	6,459 (0–15,265)	17,043 (53,44–69,634)	147,333 (24,174–441,681)			
Codon									
A	4 (0–24)	10 (0–35)	0	3,812 (0–24,633)	3,244 (0–25,972)	0			
B	18 (0–96)	12 (0–30)	42 (0–26)	6,202 (0–33,654)	3,768 (0–10,704)	1,820 (0–11,426)			
C	64 (10–292)	5 (0–23)	15 (0–59)	22,112 (2,291–65,822)	1,506 (0–6,598)	12,268 (0–56,600)			
D	6 (0–15)	2 (0–8)	159 (0–963)	1,447 (0–12,257)	1,157 (0–12,366)	8,813 (0–52,055)			
F	5 (0–13)	2 (0–10)	19 (0–72)	733 (0–2,476)	3,273 (0–19,636)	46,446 (0–20,2048)			
J	36 (6–112)	1 (0–3)	6 (0–19)	22,523 (1,007–80,602)	1,063 (0–6,929)	12,624 (0–103,626)			
P	250 (24–1,288)	32 (0–107)	30 (0–96)	115,033 (18,981–629,359)	18,229 (0–78,116)	13,034 (0–40,322)			
S_N	24 (0–73)	1 (0–2)	1 (0–3)	23,806 (0–73,725)	180 (0–2,521)	175 (0–2,098)			
X1	16 (0–47)	4 (0–13)	18 (0–48)	3,469 (0–8,670)	1,164 (0–6,814)	2,914 (0–8,159)			
X2	24 (0–72)	68 (25–163)	194 (47–469)	940 (0–2,227)	8,571 (3,707–18,815)	37,647 (6,067–89,459)			
Y	14 (0–33)	52 (15–197)	137 (59–320)	5,600 (0–13,476)	11,397 (1,077–60,735)	144,182 (16,747–439,177)			

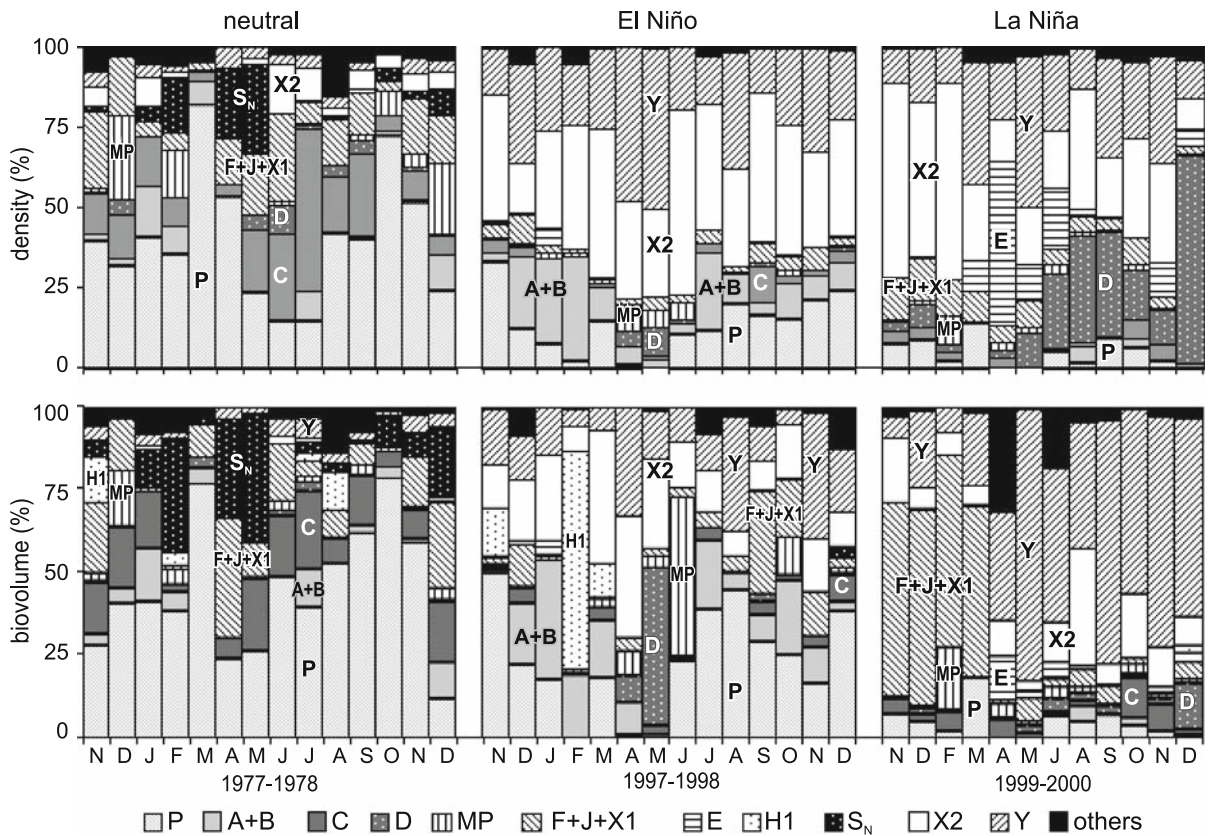


Fig. 4 Temporal variations in relative density and biovolume of functional groups in the Middle Paraná River during the study periods

C (*C. meneghiniana* and *Aulacoseira distans*) and **D** (*Actinocyclus normanii*) were present with scarce participation. Coda **A** and **P** were inversely correlated to water discharge ($r = -0.63$ and -0.82 , respectively, $P < 0.01$). Chlorococcales density was similar to Volvocales, yet the former presented higher biovolume. Groups **F**, **J**, and **X1** contributed poorly to total phytoplankton but persisted through all the study. This assemblage decreased its contribution during the flood and augmented progressively in the decreasing water phase. The presence of codon **E** with *Epipyxis* spp. in January 1998 as epiphyte of *Aulacoseira granulata* and *Cyclotella* cf. *glomerata* is worth highlighting.

In La Niña drought period, flagellate unicells represented by **X2** and **Y** were the main contributors to phytoplankton density and biovolume. **X2** dominated algal density during the drought phase (November 1999–February 2000) and was inversely correlated to SS ($r = -0.6$, $P < 0.05$). In terms of biovolume, group **F** provided the maximum contribution from December 1999 to March 2000 (mainly

Eutetramorus fottii, *Micractinium pusillum*, and *Dictyosphaerium ehrenbergianum*), which were inversely correlated to water discharge ($r = -0.84$, $P < 0.01$). The increasing waters (March–May 2000) and the enhancement of SS load-diminished phytoplankton development, and only cryptomonadals (**Y**) maintained high densities. Diatom contributors belonged mainly to the group **D** (*Skeletonema* cf. *subsalsum*, small centric (4–7 μm) and *Actinocyclus normanii*). This codon was inversely correlated to SS ($r = -0.52$ for density, $P < 0.05$) and depth ($r = -0.77$ and -0.71 for density and biovolume, respectively, $P < 0.01$). Increasing abundance of codon **E** (epiphytic and free living *Epipyxis* spp. and flagellated crysophytes, February 2000), **P** (March 2000), **W1** (April 2000), and **MP** (non-planktonic pennate diatoms, April–May 2000) were observed during rising waters. From August 2000 onwards, with mid-waters and diminution of SS concentration, algal density and biovolume increased due to the prevalence of groups **Y** and **X2** as responsible of the

phytoplankton bulk, and group **D** that was only important in terms of density.

The neutral period was characterised by the dominance of filamentous life forms in terms of density and biovolume. They were mainly represented by Bacillariophyceae belonging to codon **P**. At low-water phases and minimum hydrological fluctuations (May–July 1978), this group decreased its contribution and was replaced by **C** (*Cyclotella meneghiniana* in November–December and May 1978 and *Aulacoseira distans* in June–July 1978). Chlorococcales subdominated phytoplankton density (mainly in **J** and **X1**) with maximum concentrations during low-water discharges (November–December 1977, May–June 1978). The Cyanobacteria codon **S_N**, was important in terms of biovolume, especially during decreasing waters (February, April–May 1978).

Functional groups ordination in the environmental gradient

The two main axes of both PCA based on density and biovolume of functional groups (Fig. 5) explained 56 and 41% of total variance, respectively, and produced similar ordinations of samples and vectors. The

planes defined in both analyses describe an environmental gradient determined by the hydrological condition. Samples of El Niño period were clustered at the top left. Only codon **B** was directly related to these samples, probably because of the lower algal concentrations registered at this period. La Niña samples were arranged at the left bottom of the figure with groups **D**, **F**, **X2**, and **Y** strongly influenced by the drought conditions. Codon **E** (only for density PCA) and **MP** (only for biovolume PCA) were also displayed here. The neutral period was located at the right side of the PCA graphs with a highly disperse sample ordination. The diatom assemblage **A–C–P** as well as groups **J** and **S_N** appeared related to these samples. Coda **MP** (only for density PCA) and **X1** showed an intermediate arrangement between the samples of La Niña and neutral periods.

Discussion

In the Paraná River, water discharge and solid load regulate the changes of the physical and chemical variables (water velocity, transparency, pH, conductivity) acting as driving forces in the fluvial

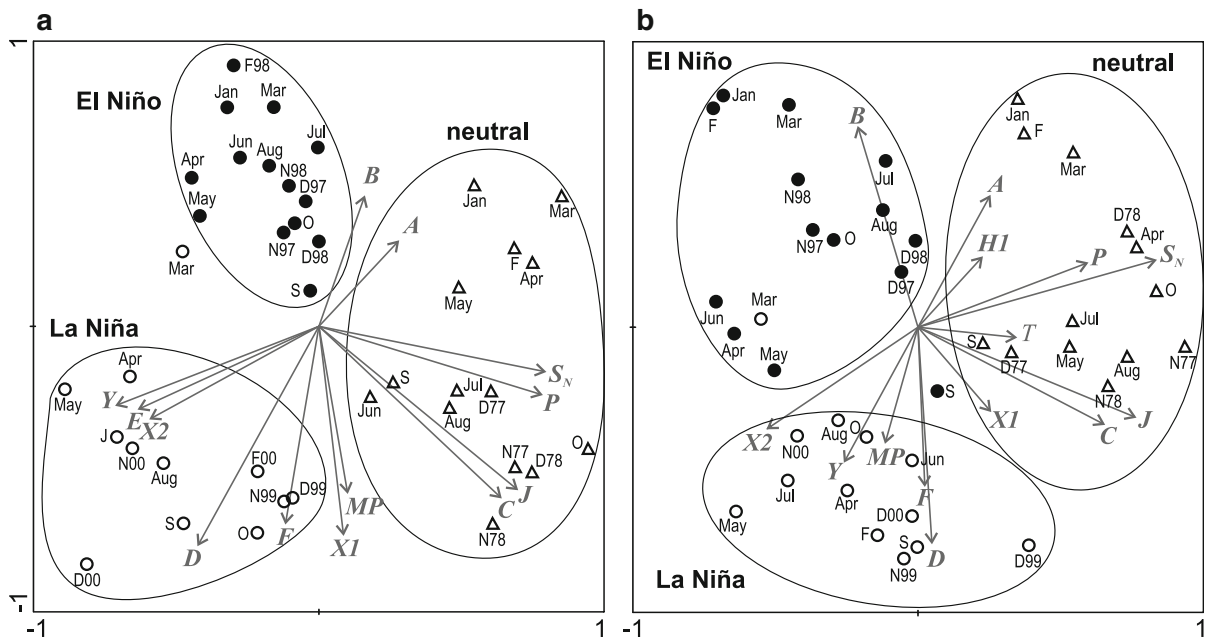


Fig. 5 First and second axes of both PCA based on density (a) and biovolume (b) of functional groups. Coda vectors are represented with arrows and samples with a symbol (neutral

conditions, 1977–1978 open triangle; El Niño, 1997–1998 filled circle; La Niña, 1999–2000 open circle) and the corresponding month abbreviated with the beginning letters

environment. Thus, the hydrosedimentological regime is a macrofactor that conducts phytoplankton behaviour and explains a highly significant proportion of algal assemblage variations as shown by the results analysed here and in previous works (García de Emiliani, 1990; Zalocar de Domitrovic et al., 2007). Grazing pressure is not a control factor in this system since the zooplanktonic community, mainly rotifers and nauplius, is scarce and small sized (José de Paggi & Paggi, 2007).

During neutral conditions, the Middle Paraná River phytoplankton is characterised by low densities and biovolumes. The dominance of centric Bacillariophyceae, mainly *Aulacoseira granulata* and its bioforms (functional group **P**) is typical of this river (Bonetto et al., 1982; García de Emiliani, 1990; O'Farrell et al., 1996; Zalocar de Domitrovic et al., 2007) and of other large rivers of the world (Rojo et al., 1994; Lewis et al., 1995). Jointly with codon **C**, they constitute the main groups of this fluvial system, as they are favoured by their capacity to survive under a low and fluctuating light climate (Reynolds, 1997). Chlorococcales (**J** and **X1**, small unicellular and coenobial species) are frequently found as subdominant (O'Farrell et al., 1996; Zalocar de Domitrovic et al., 2007), especially during low water phases (November–December 1977 and May–June 1978). Cyanobacteria are scarce, whereas in the Upper stretch higher concentrations are encountered, mainly due to the existence of numerous reservoirs (Zalocar de Domitrovic, 1999). Codon **S_N**, the main cyanobacteria contributor in the study area, is stimulated by its adaptation to turbid and mixed water columns (Reynolds, 1997). However, an increasing biovolume of the nostocalean **H1** is also observed during decreasing waters (February, April–May 1978) due to the input from adjacent water bodies. The high species diversity in this system is explained by the occurrence of several potamoplanktonic species in addition to a high number of sporadic species, which are mostly incorporated to the main channel after hydrological fluctuations. The comparatively lower functional diversity is due to the strong selectivity conditions influencing algal development in the main channel of large rivers (Reynolds, 2000).

A different scenario emerges during El Niño and La Niña anomalous periods. The extreme flood and drought events induce changes on the environmental conditions and, therefore on the phytoplanktonic

community. During the flood, an increased dilution of the physical and chemical water properties (conductivity, SS, TDS, DOM) occurs. Nitrate, nitrite, and ammonium concentrations are an exception to this pattern. The significant enhancement of nitrogen species and the less accentuated increase in SRP concentration during El Niño, reveal the nutrient inflow from the inundated floodplain area. On the other hand, the effect of the sedimentary pulse of the Bermejo River may be intensified since no dilution occurs during La Niña drought, thus causing a simultaneous increment in SS, TDS, DOM, and conductivity.

During the anomalous hydrological periods and, contrarily to neutral conditions, rare and sporadic phytoplanktonic species increase in number. Algal concentrations (transport, density and biovolume) are lower at El Niño and higher at La Niña. Minimum values occur in the extreme high-water pulse (January–June 1998). They augment progressively with decreasing waters, parallel to the recovery of the hydraulic conditions that are characteristic of the Paraná mainstem. Contrarily, high densities are recorded during the drought phase (November 1999–February 2000) under summer temperature, relatively high transparency, and retentiveness. High densities are also coupled with periods of river-floodplain connection, when a combined effect of small losses due to permanent mixing and a constant feedback between the main channel and adjacent water bodies occur (September–October 2000, and December 2000).

Another important distinctive feature of the anomalous periods is the great abundance of small flagellate unicells in opposition to the dominance of large filaments typical of the Paraná River. Coda **Y** (cryptomonadals) and **X2** (smaller cryptophytes and volvocaleans) are dominant, as they are both favoured by their high SA/V ratio and metabolic activity, with the consequent increments in light-harvesting capacity, nutrient uptake and high growth rate (Reynolds, 1997). The colonizer species of **X2**, sensitive to mixing and light depletion (Reynolds, 1997), are more abundant during the drought phase. The 'lenticated' main channel allows the unusual development of these flagellates that are capable to counteract sedimentation. The dominance of cryptomonadals, especially at El Niño, reflects their capacity to compensate the increasing dilution effect with a

high reproduction rate. The maintenance of high concentrations, either after a prolonged flood or a drought when floodplain-mainstem disconnection occurs, evidences reproduction within the river. This is possible due to their capacity to grow under heterogeneous flow and light climates, and to maintain in suspension (Reynolds, 1997). Even though they are not commonly dominant in large rivers (Rojo et al., 1994), there are registers of high densities at the beginning of the 1982–1983 floods in the Middle Paraná (Anselmi de Manavella, 1986). Moreover, their abundance in the River Paraná floodplain water bodies and in its secondary channels (García de Emiliani, 1990; Zalocar de Domitrovic, 1999), may

favour an initial recruitment to the main flow during El Niño.

The marked Bacillariophyceae decrease during anomalous periods, mostly groups **P** and **C**, results from different processes. On one hand, sedimentation may be accentuated due to the lower turbulence during droughts constituting a negative factor for large-celled diatoms that need certain mixing intensity to be maintained in suspension (Karim & Saeed, 1978; Hötzel & Croome, 1996; O’Farrell et al., 2001). Small centrics and *Skeletonema* cf. *subsalsum* (group **D**), which are more edible and have a low sedimentation rate, are the major component of Bacillariophyceae during La Niña. On the other hand, during floods

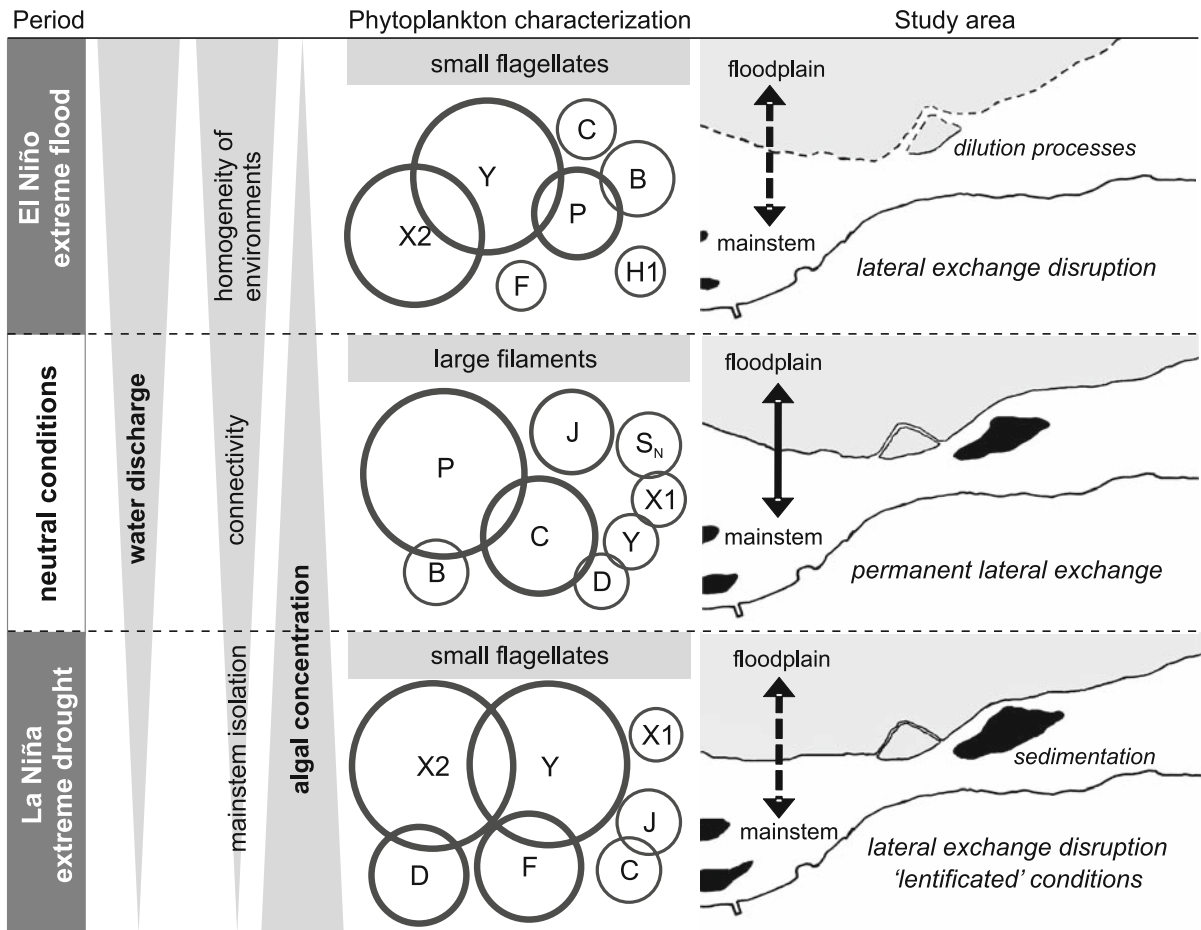


Fig. 6 Scheme summarizing the main environmental conditions (water discharge, connectivity, and mainstem-floodplain interactions in the study area) and the principal phytoplankton attributes (concentration, life forms and functional groups) during the study periods. The size of the circles indicates the

relative importance of the main functional groups. The arrows indicate the mainstem-floodplain interactions (*dashed line*: lateral exchange disruption; *continuous line*: permanent lateral exchange)

Aulacoseira granulata was probably not able to compensate the losses due to dilution by increasing its growth rate. These filamentous forms may also have been retained by the vegetation and topographic obstacles through water displacement in the plain. However, the decrease of the inoculum from adjacent water bodies to the main flow may be more important than the mentioned processes, as diatoms were registered in secondary channels and ponds directly connected with the mainstem (Zalocar de Domitrovic et al., 2007). A similar situation is observed at neutral conditions, during low water phases and minimum mainstem-floodplain interaction (March–July 1978), when *Aulacoseira granulata* diminishes its contribution. This reduces the recruitment of organisms from adjacent storage zones (Reynolds & Glaister, 1993) due to either the complete inundation of the alluvial valley during floods (homogeneity of environments) or the isolation of the main channel at droughts (low connectivity) (Fig. 6).

The causes of the maintenance of *A. granulata* populations in the main flow of large turbid rivers remains a conjecture, with some evidences of its origin in retention zones where they develop as eu- or meroplanktic (Reynolds, 1994). The presence of epiphytic *Epipyxis* spp. on diatom valves found in both anomalous periods could be an evidence of meroplanktic habits.

Figure 6 summarises the features of the main environmental conditions and phytoplankton attributes during the different hydrological events. The results here obtained show that the drought and the prolonged flood induced by the ENSO phenomena affect potamoplankton transport, density, biovolume, and specially the community structure of the Paraná River mainstem. These changes are mainly attributed to the loss of a regular exchange of organisms with floodplain areas with high water retention times that act as nurseries for fluvial species. The alteration of regular mainstem-floodplain interactions are key factors for structuring the potamoplankton. Extreme hydrological phases constitute a disturbance for phytoplankton populations (Sparks et al., 1990; Lake, 2003), and the biotic response to the prevailing environmental conditions depends on the capability of organisms to exploit extreme conditions (Sparks & Spink, 1998). The temporal analysis reveals that the phytoplankton structure will change according to the opportunity of the existing species to thrive, thus determining the

success of organisms of similar strategies. The typical **P** and **C** groups of the Paraná River shift to the small and high-metabolic **X2** and **Y**. It seems plausible that even if El Niño and La Niña provoke changes in the potamoplankton structure, the community may be rapidly re-structured when the event ends due to its high resilience, as asserted by Lake (2000) for stream communities. However, if such changes persist even when the anomalous periods conclude (particularly the scarce participation of *Aulacoseira* during La Niña), it could be hypothesised that the magnitude and duration of the extreme hydrological events may govern the intensity and duration of phytoplankton changes (Sparks et al., 1990).

Increasing frequency and magnitude of great floods and droughts are forecasted for the next decades as a consequence of climate change. Hard engineered defences are the most common practice in flood management. However, in accordance to the results here obtained, river regulation is perceived as a disruption of the natural fluvial dynamic that maintains potamoplanktonic diversity and environmental health (Ward et al., 1999). A shift towards a more holistic approach involving the whole fluvial system and risk-driven adaptability to climate change is urgently needed (Wilby et al., 2008).

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