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Factors affecting the structure and maintenance of phytoplankton functional groups in a nutrient rich lowland river

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ABSTRACT

The phytoplankton structure along the mainstem of the Lower Salado River (Argentina) was analysed in relation to the environmental variables and the influence exerted by the inflowing waters from the Paraná River (via El Vado Stream) and an adjacent floodplain shallow lake, between December 2003 and August 2004. Phytoplankton driving forces were explored using a functional approach. Small phytoplanktonic organisms with high metabolism and well adapted to live in mixed environments dominated (functional groups **C**, **D**, **X1**, **X2**), but the organic enrichment and slow flow also facilitated the thriving of Cyanobacteria ($\mathbf{L_O}$ and minor contributions of **H1**, **K**, $\mathbf{S_N}$) and large Euglenophyta (**W1**, **W2**) inflowing from adjacent sites. The longitudinal and temporal changes in the phytoplankton structure depended on the prevailing hydrological conditions. Three scenarios were identified as regards the complex hydrological interactions of the Paraná and Salado Rivers: (i) the *hydrological isolation* period (low waters) when the Salado had a homogeneous longitudinal pattern and high phytoplankton development; (ii) the period of *hydrological interactions with Salado River influence* (high waters) when the homogeneous longitudinal pattern extended to the stream, and algal growth in the river was counteracted by dilution and enhancement of water velocity, and (iii) the period of *hydrological interactions with Paraná System influence* characterised by a longitudinal discontinuity with lower phytoplankton concentrations downriver the Paraná inflow due to dilution. There were no evidences that the lake contributed with algal biomass to the downriver plankton during the study period.

Introduction

The importance of river's flow regime for sustaining biodiversity and shaping the fundamental ecological characteristics of riverine ecosystems is well recognised (Poff and Zimmerman 2010). The physical environment is the major controlling factor of the dynamics and structure of the phytoplankton of large rivers. Water discharge, channel retentivity, light penetration and temperature have been identified as the main selective potamoplankton mechanisms (Kiss 1994; Reynolds and Descy 1996; Reynolds 2000). Phytoplankton in these turbid, turbulent and deep systems is characterised by assemblages with low density and biomass and high richness due to the occurrence of many sporadic species. The prevalence is defined by organisms of high surface:volume ratio (small size or large with forms distant to the sphere) that allows high reproduction rates and captures low light intensities (Hynes 1970; Margalef 1978; Rojo et al. 1994; Reynolds and Descy 1996). Unicellular centric diatoms of the genera *Cyclotella*, *Thallassiosira* and *Stephanodiscus* dominate the phytoplankton of many lowland rivers (Kiss 1987; Descy 1987; Gosselain et al. 1994; Leland et al. 2001; O'Farrell et al. 2002). In the largest courses with high discharge such as the Nile (Rzóska et al. 1955; Sinada and Karim 1984), Orinoco (Carbajal-Chitty, 1993), Amazonas (Uherkovich 1984) and Paraná (O'Farrell et al. 2001; Zalocar de Domitrovic et al. 2007) the long filaments of *Aulacoseira* prevail in the deep water column. The morphological adaptations of species to live under low irradiance and permanently mixed conditions are supplemented by the production of accessory pigments that amplify the light absorption spectrum (Reynolds 2006), thus favouring their dominance in rivers. Other taxonomical groups sub- or co-dominate, particularly chlorococcaleans (Rojo et al. 1994; Schmidt et al. 1994), when discharge decreases and water transparency increases (Descy 1987).

The lowland rivers related to floodplains are additionally subject to the flood pulse influence (Junk et al. 1989; Neiff 1990), whereby the variations of the water level produce situations of connection and isolation between the mainstem and the adjacent environments. This behaviour allows a periodical and lateral exchange of water, suspended and dissolved matter, which shapes the biological communities. The flood pulse influence on phytoplankton has

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been clearly described in the Paraná and Paraguay Rivers (García de Emiliani 1990; de Oliveira and Fernandes Calheiros 2000; Zalocar de Domitrovic et al. 2007; Rodrigues et al. 2009).

The hydrodynamic interactions in the confluence area of water courses with different hydrological regime may also affect their physical, chemical and biological characteristics (O'Farrell et al. 2002; Piirsoo et al. 2008). Tributary inflows may influence water quality with the consequent downriver change. In particular, they act as source of organisms with greater species richness (Hudon 2000) and increasing biomass in the longitudinal gradient (Talling 1957; Kiss and Schmidt 1998; Istvánovics et al. 2010), or produce decreasing plankton abundance due to dilution effect (Scherwass et al. 2010).

In other lotic systems, biotic and chemical factors are indicated as the driving forces of potamoplankton dynamics (Basu and Pick 1996; Bahnwart et al. 1999; Ietswaart et al. 1999) due to the fact that nutrient and salinity conditions cause differences in species composition and abundance. Rivers with a high trophic status and water residence time support enhanced algal concentrations, populations commonly represented in lentic environments (e.g. euglenoids or cryptomonads) and even transitory proliferations of cyanobacteria in zones of retarded current (Webster et al. 2000; Everbecq et al. 2001; Tell et al. 2006). Abundance enhancement and species selection processes are also common in increasing salinity gradients (Greenwald and Hurlbert 1993; Janse Van Vuuren and Pieterse 2005; Bazzuri et al. 2010). Despite cyanobacteria and halophile diatoms thrive in such scenarios (Blinn and Bailey 2001; Oliver et al. 2010), no evident changes are registered for most phytoplanktonic groups (Pilkaitytë et al. 2004).

The Salado River is one of the most important saline tributaries of the Paraná River. It presents a high hydrological complexity in the stretch close to its mouth due to the inputs of El Vado Stream, whose discharge and water quality are determined by the hydrological variations of the Paraná River. The phytoplankton of this system was poorly studied even though it is emplaced between two highly populated urban settlements and it constitutes an important fluvial resource (Polla et al. 2008; Emiliani and García de Emiliani 2003; García de Emiliani and Devercelli 2004).

This paper aims to analyse the phytoplankton responses to environmental changes of the Lower Salado River and to identify its driving forces using a functional approach. The dynamic study of the phytoplankton ecology will focus on the strong hydrological changes and the quality of the mixing waters with adjacent water bodies (the El Vado Stream on the left margin and the Bedetti Shallow Lake on the right margin). We hypothesize that flow regime plays a key role in the determination of the functional structure of fluvial phytoplankton, and that hydrological interactions with adjacent systems exert further changes within the assemblages posing marked spatial discontinuities along the Lower Salado River system.

Study area

The Salado River is a saline tributary of the Paraná River. It flows north–south along 1500 km extending over 247,000 km^2. The lower stretch comprises a drainage area of 29,700 km^2 with a mean water discharge of 146 m^3 s^{-1}. The river has a meandering channel with scarce gradient and a velocity current ranging between 0.1 and 0.3 m s^{-1} (FICH-INA 1998). Mean mainstem width is of approximately 100 m; narrow levees separate the river from the floodplain located in the left margin. The river section close to its mouth flows between Santo Tomé (right margin) and Santa Fe (left margin) cities, and receives the El Vado Stream, finally draining into the Santa Fe River (secondary channel of the Paraná River) (Fig. 1a). The Lower Salado River receives the urban and rural sewage waters as well as the rainfall excess from the surrounding settlements; cattle are raised in its alluvial valley (Emiliani and González de Paira 1996).

The Bedetti shallow Lake, located in the right margin of the river, has a surface of ca. 150,000 m^2 and a maximum depth not exceeding 3.5 m when the water level of the Salado River at the INALI station indicates 4.88 m. The lake is isolated from the river at levels lower than 3 m and connected when it surpasses 3.5 m. It is fed by groundwater and flooding of the Salado River and also receives rain water city drainage through a pipe in its west margin (Emiliani and García de Emiliani 2003).

Material and methods

Sampling, in situ measurements and laboratory analysis

Samplings were monthly performed between December 2003 and August 2004, period which integrated the different hydrological conditions. Fig. 1a shows the sites established across two transversal transects (sites 1 and 3: centre, bottom, right margin, left margin) and in the centre (site 5) of the Salado River, in El Vado Stream (site 2) and in Bedetti Lake (site 4: limnetic and littoral). Depth, subsurface water velocity (current meter AOTT C20), temperature, pH (HANNA HI 1288), conductivity (Beckman RC19), dissolved oxygen (DO, YSI 55) and water transparency (Secchi disk) were measured in situ. Subsurface (Van Dorn horizontal sampler) and bottom (Ruttner sampler) water samples were transported on ice to the laboratory and filtered through Whatman GF/F filters for chemical analyses.

Nitrate (N-NO_3^-) and nitrite (N-NO_2^-) were analysed with the cadmium–copper reduction method, soluble reactive phosphorus (SRP) with the ascorbic acid-molibdate method, and total phosphorus (TP, non-filtered water samples) after acid persulfate digestion, using kits of reagents HACH, whereas ammonium (N-NH_4^+) was analysed using kits of Wienner Company, following the indications of APHA (1991). Chlorophyll-*a* was extracted with acetone 90% macerating into a glass grindex (90% acetone + 10% distilled water) and stored at 4 °C for 6–12 h in the dark. The extracts were filtered, and measured with spectrophotometer at 664–750 nm, and 665–750 nm after the acidification with 0.1 N HCl (APHA, op. cit.).

Subsurface phytoplankton samples were collected and fixed with Lugol's acidified solution (1%). Additional samples for taxonomic analysis were obtained with a 10 μm pore net and fixed with formaline (2%). Algal counts (cells, colonies and filaments) were performed according to Utermöhl (1958) reaching at least 100 specimens of the most frequent species. Whenever the application of this criterion was not possible, either due to low algal abundance or to high concentration of sediments, the necessary number of fields for a stabilisation of the number of species was counted as determined by the minimum area method.

Additional 5 l-water samples were collected at the sites located in the main flow of the rivers (1, 2 and 3) for the determination of suspended organic matter (SOM), dissolved organic matter (DOM), total suspended solid (TSS) and total dissolved solids (TDS). TSS were analysed in laboratory by sample filtration through porcelain filters and dried at 105 °C to constant weight, and SOM was obtained by ashing to 550 °C and weighted. The water filtrate was dried at ~105 °C, weighted for TDS determination, and also used for DOM estimation after ashing at 550 °C and reweighted (Rodier 1981).

Data analysis

Two hydrograms were analysed on the Salado River: one located upriver of the section studied (Esperanza Station) and another

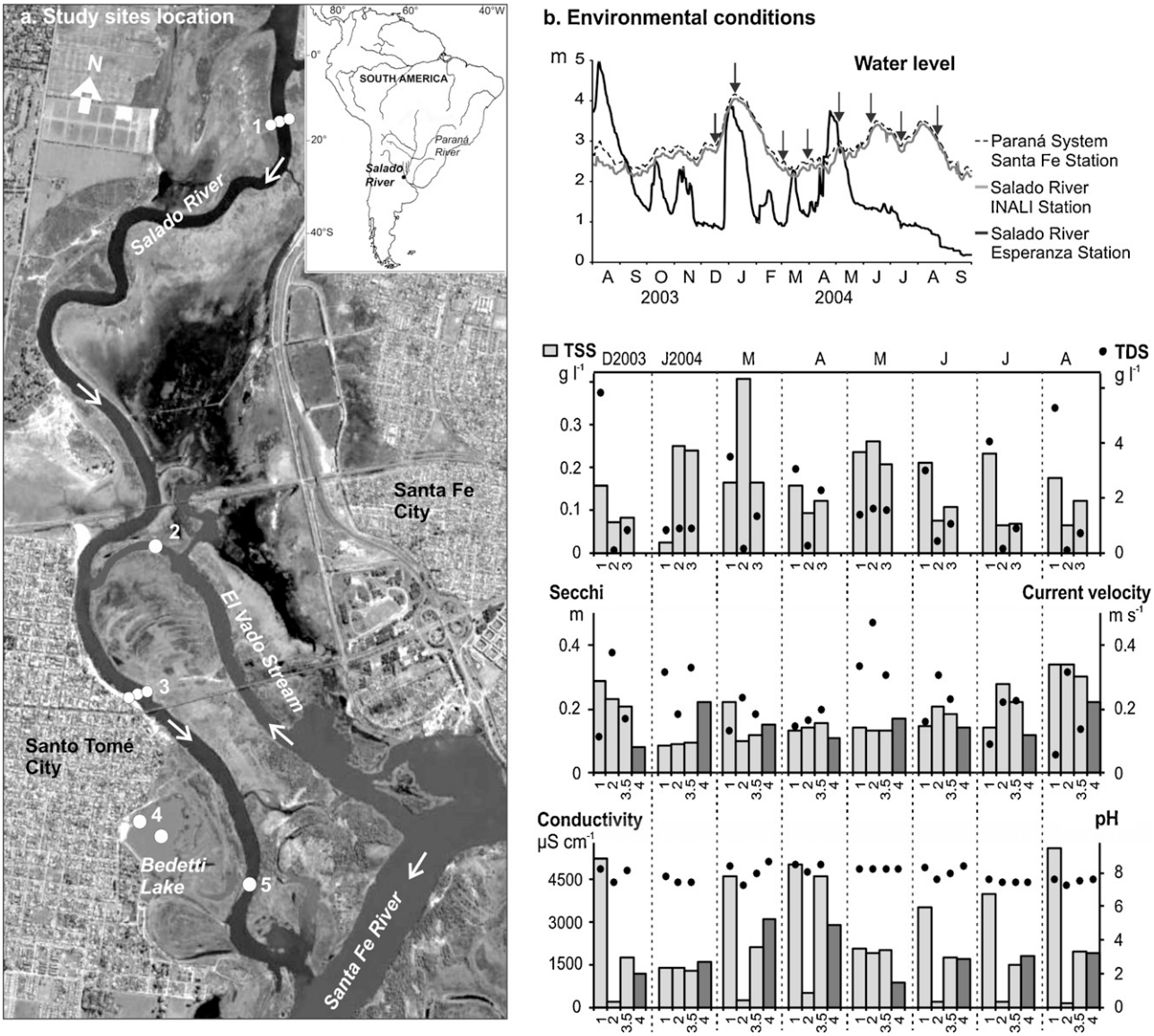

Fig. 1. (a) Study area and sampling sites location (O) in a satellite image (Google Earth): Salado River (sites 1, 3, 5), El Vado Stream (2) and Bedetti Lake (4). The arrows indicate the flow direction. (b) Temporal variation of the main environmental variables at the Salado River up (site 1: mean values, except for SS, TDS and current velocity that correspond to the value of the centre site) and down (3, 5: mean values) the connection of El Vado Stream (2) and at Bedetti Lake (4: mean values) during December 2003–August 2004. The sampling dates are indicated with arrows at the water level graph and with the first letter of the month in the others.

downriver from the inflow of the El Vado Stream (INALI Station). They were compared with the Paraná System hydrogram (Santa Fe Station, Centro de Informaciones Meteorológicas).

Results of both density (ind. ml^{-1}) and biovolume ($mm^3 l^{-1}$) are presented for their comparison. Biovolumes were calculated following Hillebrand et al. (1999). At least, 25 individuals were measured; 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 maximum linear dimensions (MLD, Lewis, 1976) were classified in the following ranges: 1–20 μm, 20–40 μm, 40–100 μm and > 100 μm. Species were sorted in the functional groups proposed by Reynolds et al. (2002) and Padisák et al. (2009).

Normality and homogeneity of variances were checked with Kolmogorov–Smirnov and Bartlett tests, respectively, in order to choose between parametric and non parametric techniques. Spearmanĭs correlation coefficients were calculated among all measured variables (species, major taxonomic groups and functional groups, versus environmental variables) (SPSS 13 software). Kruskal Wallis with Bonferroni's post test was used to analyse differences among the studied water systems (PAST 1.76 software).

A multivariate ordination method was performed to analyse the relationship between functional groups and environmental variables (software CANOCO 4.5). Detrended Correspondence Analysis suggested that a lineal method was appropriate since the gradient length of species did not exceed 3 standard deviations. Accordingly, Redundancy Analysis (RDA) were performed (ter Braak and Smilauer 2002), using biovolume of functional groups (square root-transformed) as the response variables, and all the limnological variables measured (standardised) as the explanatory variables. Functional groups with contributions to total biovolume lower than 1% were excluded. The forward selection option was used to identify the more significant subset of environmental variables for the first and for all axes, with Monte Carlo test under unrestricted model of 999 permutations.

Results

Abiotic conditions

The water discharge of the Salado River ranged between 13 and 290 $m^3 s^{-1}$ with a mean of 76 $m^3 s^{-1}$. The Salado water level fluctuations registered upriver the study stretch (Esperanza Station Gauge) were attenuated in the section closer to the river mouth (INALI Station) due to Paraná System influence (Santa Fe Station), as indicated by the high correlation of the latter two hydrograms ($p < 0.01$, $r = 0.99$) (Fig. 1b).

The values and temporal trends of the environmental variables analysed in the Salado River, El Vado Stream and Bedetti Lake are summarised in Table 1 and Fig. 1b. Water velocity of the Salado River was higher in the centre of the mainstem than in its margins ($p < 0.01$), but lower than in the El Vado Stream. Water transparency in both lotic systems was always lower than 0.38 m, and increased in December and August, inversely to the Salado water level and to TSS concentration ($p < 0.01$, $r = -0.73$ and -0.56, respectively). Even though mean TSS concentrations were high and similar in the river and the stream, their seasonal and spatial patterns differed. Contrarily, TDS, SOM, DOM, conductivity and pH were higher in the Salado River ($p < 0.01$); conductivity and pH were inversely related to the Paraná water level ($p < 0.01$, $r = -0.44$ and -0.54, respectively). Temperature remained higher than 24 °C till March and then decreased progressively up to 11 °C; DO concentrations were always near to saturation levels. Nutrient concentrations were high, though in El Vado Stream values were lower and less fluctuating. N-NO_3^- and SRP concentrations in the stream were directly correlated to the Salado water level ($p < 0.01$, $r = 0.61$ and 0.42) and N-NH_4^+ with the Paraná water level ($p < 0.01$, $r = 0.4$). Sites located at the bottom and the river left bank presented higher SRP concentrations.

In the Bedetti Lake the maximum depth never exceeded 3.5 m and the mean transparency was similar to the Salado River. The conductivity pattern was inversely related to the river discharge ($p < 0.05$, $r = -0.53$) with mean values lower than those of the river; pH was generally higher than 8. Mean temperature was 2–3 °C higher than in the river. N-NO_3^- and N-NO_2^- concentrations were significantly lower in the lake ($p < 0.01$), whereas TP concentrations were higher ($p < 0.05$).

Different situations were triggered in response to the Paraná and Salado water discharge fluctuations (Fig. 1b). On one hand, when low waters in the Salado coincided with Paraná high or middle waters (December 2003, March, June–August 2004), the El Vado Stream exerted its influence, especially downriver the Salado confluence: water velocities in the upriver stretch were lower (site 1) than downriver (3, 5) or in the El Vado (2); TSS, TDS, SOM, DOM, conductivity and pH were highest upriver the incoming waters from El Vado, minimum in this stream and intermediate in the lower stretch of the Salado River. Bedetti Lake was isolated from the river in December, whereas from July to August 2004 it was connected by low water inputs (water level ca. 3.5 m). Water transparency was lower in the lake and conductivity was similar to the downriver stretch of the Salado River.

On the other hand, the above mentioned discontinuities vanished during the periods of simultaneous water level increase in the Salado and Paraná Rivers (January 2004) producing mixing of both systems and material exchange. This caused a longitudinal homogeneity of TDS, SOM, DOM, conductivity, pH and transparency, which even extended to El Vado. DO concentrations were minimum and less than 4.5 mg l^{-1}. The water input from the river to the lake caused similar conductivities, whereas transparency increased and SRP concentration decreased. A similar situation of homogeneity was encountered on May 2004 as the high waters in the Salado River influenced El Vado's water quality, with similar environmental variables behaviour (except DO). No evidence of lotic influence on Bedetti Lake was observed. A different scenario occurred by April 2004 when both systems presented low water levels and the Salado River had longitudinally similar conditions. At this stage, the Bedetti Lake remained isolated from the river; conductivity values and water transparency became lower than in the Salado, and N-NO_3^- concentration increased.

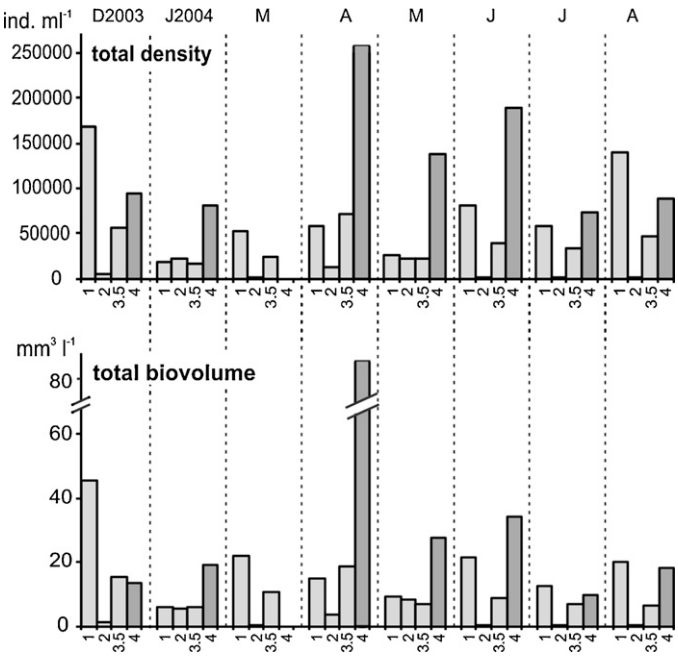

Fig. 2. Temporal variation of total phytoplankton density and biovolume at the Salado River up (site 1: mean values) and down (3, 5: mean values) the influence of El Vado Stream (2) and at Bedetti Lake (4: mean values) during December 2003–August 2004. The sampling dates are indicated with the first letter of the month.

Phytoplankton composition

A total of 289 taxa were identified in the Salado River, 200 in Bedetti Lake and 162 in the El Vado Stream. These were sorted in 25 coda according to the phytoplankton functional group classification (Table 2). Most species were comprised in the Chlorophyceae class, followed by Bacillariophyceae, Cyanobacteria and Euglenophyta. *Nitzschia acicularis*, *Chaetoceros muelleri* and a non identified Chrysophyceae (unicelular siliceous species of 4.5 μm diameter) were the most frequent species in the Salado River, whereas the flagellated *Plagioselmis nannoplanctica* and *Phacotus minusculus* were common in El Vado Stream. At Bedetti Lake, the most frequent taxa were *Chroococcus minimus* and the chlorococcaleans *Scenedesmus ecornis*, *Monoraphidium griffithi*, *M. contortum* and *Kirchneriella irregularis*.

Total phytoplankton trend

Phytoplankton chlorophyll-*a* concentration, density and biovolume in the Salado River were high with a wide variation range (Table 3). The highest values were observed in the bottom of the river and at the left bank, which is adjacent to the floodplain. These values were significantly lower in the El Vado Stream ($p < 0.01$).

Highest densities corresponded to low water periods of the Salado River (December 2003 and August 2004) and coincided with high biovolume only in December, as in August phytoplankton was dominated by small organisms (Fig. 2). The river presented lower phytoplankton concentrations during high waters (January and May 2004). Consequently, density was inversely correlated

Table 1
Mean values and ranges (between brackets) of limnological variables at Salado River, El Vado Stream and Bedetti Lake during December 2003–August 2004.

	Salado River	El Vado Stream	Bedetti Lake
Temperature, °C	20.9 (11–30)	21.19 (13–30)	23.9 (13–34)
Current velocity, m s^{-1}	0.2 (0–0.75)	0.28 (0.16–0.47)	
Depth, m	4.94 (3.8–6.2)	2.48 (1.5–4)	0.5 (0.45–0.5)
Secchi, m	0.19 (0.07–0.38)	0.19 (0.09–0.34)	0.2 (0.08–0.22)
TSS, g l^{-1}	0.15 (0.03–0.24)	0.16 (0.06–0.4)	
SOM, g l^{-1}	0.01 (0.001–0.02)	0.006 (0.001–0.01)	
TDS, g l^{-1}	2.28 (0.73–5.8)	0.46 (0.1–1.6)	
DOM, g l^{-1}	0.06 (0.01–0.15)	0.02 (0.009–0.05)	
Conductivity, μS cm^{-1}	2881 (852–5750)	601 (140–1900)	1888 (850–3100)
pH	7.97 (7.4–8.53)	7.58 (7.3–8.2)	8 (7.4–8.6)
DO, mg l^{-1}	8.5 (4–11.6)	7.89 (4.2–11)	10.3 (6–15)
N-NO_3^-, mg l^{-1}	0.55 (0.2–1)	0.46 (0.1–0.8)	0.3 (0.1–0.9)
N-NO_2^-, mg l^{-1}	0.02 (0.003–0.09)	0.01 (0.003–0.01)	0.005(0.003–0.01)
N-NH_4^+, mg l^{-1}	1.2 (0.09–8.8)	0.66 (0.08–1.78)	0.9 (0.13–2.72)
TP, mg l^{-1}	0.63 (0.1–1.9)	0.52 (0.23–0.95)	1.3 (0.5–3.5)
SRP, mg l^{-1}	0.47 (0.15–2.56)	0.26 (0.05–0.55)	0.6 (0.28–1.9)

with the Salado River water level while a weaker relation was evidenced with the Paraná, that correlated only with biovolume ($p < 0.01$) (Table 4). In El Vado, both variables were directly correlated with the Salado water level ($p < 0.01$, $r = 0.78$ and 0.89, respectively). Moreover, density and biovolume in the Salado River were inversely related with water velocity ($p < 0.01$) and directly with transparency ($p < 0.01$). Regarding nutrients, only biovolume was weakly related to SRP ($p < 0.05$) (Table 4).

A longitudinal pattern revealing decreased algal development in the river section downriver the inflow of the El Vado coincided with high water periods in the Paraná River (December 2003, March, June to August 2004) (Fig. 2). When the Salado River presented high waters (January and May), a relatively homogeneous longitudinal pattern extended to El Vado Stream. During hydrological isolation (April), the differentiation of water flows determined a homogeneous phytoplankton development along the Salado, though with lower abundance in the El Vado.

Bedetti Lake presented algal concentrations higher than in the lotic systems ($p < 0.01$); the highest values were observed in the isolation period, and the lowest in July in correspondence with low temperatures (Fig. 2). Density and biovolume in the lake were correlated with N-NO_3^- concentration ($p < 0.01$, $r = 0.91$; $p < 0.05$, $r = 0.81$, respectively).

Phytoplankton size structure and main taxonomical classes

In these aquatic systems the phytoplankton size structure was mainly composed by species with MLD smaller than 20 μm (Table 3). As regards biovolume, the contribution of species ranging between 20–40 μm and 40–100 μm was higher. The latter ranges had a higher participation in the lake from April on. The classes Chlorophyceae (chlorococcaleans > volvocaleans), Bacillariophyceae (centrics > pennates), Euglenophyta and the division Cyanobacteria characterised the phytoplankton of the studied water systems.

Phytoplankton functional groups

Functional groups **C**, **X2** and **X1** comprised the bulk of phytoplankton density and biovolume of the Salado River; $\mathbf{L_O}$ and **D** were also important in terms of density, whereas **W1** and **W2** in biovolume (Fig. 3). In December 2003, diatoms from codon **D** (small centric diatoms and *N. acicularis*) were high. Group **C** (*Cyclotella meneghiniana*, *Actinocyclus normanii*, *Chaetoceros* spp. and *Entomoneis paludosa*) increased with water level enhancement and maintained high values up to March 2004. After the phytoplankton depletion of May, group $\mathbf{L_O}$ (*Merismopedia tenuissima*) augmented during June–July. Groups **X1** (small Chloroccocales) and **X2** (mainly the volvocaleans *Carteria* sp., *Chlamydomonas* spp. and *Nephroselmis minuta*) presented constant contributions all along the study period: **X1** with higher values in December and August, and **X2** from July to August. Groups **W1** and **W2** (*Strombomonas gibberosa*, species of *Euglena* and encysted forms of this genus) contributed with a high percentage of the biovolume all over the study period, with greatest proportions between May and July. The Cyanobacteria $\mathbf{S_N}$ (*Raphidiopsis mediterranea*) and **K** (*Aphanocapsa holsatica*) were weighty in terms of biovolume.

In El Vado Stream, the algal functional group structure was quite similar to the Salado River (Fig. 3). Nevertheless, the group **X2** presented higher relative density and biovolume (%) and different composition (mainly *Carteria* sp., *Chlamydomonas* spp., *Pteromonas* sp. and *P. nannoplanctica*). The diatom assemblage was less important than in the Salado River with an increment of codon **B** in June. Group **F** was enhanced in biovolume, while **E** in density. The dominance in terms of biovolume of **W1** and **W2** from late March to May was produced by the previously mentioned species and by *Trachelomonas* spp., *Lepocinclis ovum* and *Monomorphina* sp. Small contributions of groups **Y** (cryptomonads) and **P** (*Aulacoseira granulata* and its bioforms) characterised this stream and had a marked biovolume increase in August. The January discharge mixing period determined the occurrence of group **P** in the Salado River.

In the Bedetti Lake, the contributions of **X1** and **F** were higher than in the lotic systems (Fig. 3). During March's lake isolation, groups **H1** (*Anabaenopsis arnoldii*), **K** (*Aphanocapsa planctonica*) and **S1** (*Planktolyngbya limnetica* and *Pseudanabaena* spp.) increased their densities, and groups **W1** and **W2** their biovolume.

In general terms, the main functional groups (**C**, **D**, **F**, $\mathbf{L_O}$, **X1**, **X2**, **W1**, **W2**) presented significantly higher density and biovolume in the Salado River than in El Vado Stream ($p < 0.01$), though **X2** and **X1** were even higher in the lake ($p < 0.01$).

Several functional groups were correlated with environmental variables, especially with water level and current velocity, as well as with water temperature, transparency and conductivity (Table 4). Accordingly, the forward selection option of RDA based on functional group biovolumes, reduced the environmental variability that significantly explained the phytoplankton to four variables: Paraná water level (Santa Fe Station), Salado water level (Esperanza Station), water temperature and conductivity (Monte Carlo permutation test for the first and for all axes: $p < 0.01$). The first two axes of the RDA accounted for 93.6% of the cumulative variance that explained the functional groups-environmental variation (axis 1: 65.1%; axis 2: 28.5%), and the sum of both eigenvalues was 34%. The longitudinal differences in the Salado River during *periods with influence from the Paraná System* (December 2003,

Table 2
List of the taxa and the functional group assigned (coda in bold letter) encountered in the Salado River (Riv), El Vado Stream (Str) and Bedetti Lake (La) with relative participation to total density of 0.2–1% (+), 1–3% (++) and 3–13% (+++) for the whole study period.

		Riv	Str	La
	Cyanobacteria			
	Chrococcales			
K	*Aphanocapsa delicatissima* W.et G.S. West	+	+	+
K	*A. holsatica* (Lemm.) Cronb.et Kom.	++	++	+++
K	*A. incerta* Cronb. et Kom.	+	+	+
K	*A. nubilum* Kom. et Kling	+	+	
K	*A. planctonica* (G.M.Smith) Kom.et Anag.	+	+	++
K	*Aphanothece nebulosa* Skuja	+	+	+
L_O	*Chroococcus minimus* (Keissler)Lemm.	+	+	++
L_O	*Coelosphaerium kuetzingianum* Näg.	+		+
L_O	*Merismopedia tenuissima* Lemm.	+++	+++	+++
M	*Microcystis aeruginosa* Kutz.	+	+	+
	Nostocales			
H1	*Anabaenopsis arnoldii* Aptekarj	+		+
H1	*Aphanizomenon aphanizomenoides* (Forti) Hor.et Kom.	+	+	+
	Oscillatoriales			
S1	*Planktolyngbya limnetica* (Lemm.) Kom.-Leg.et Cronb.			++
S1	*Pseudanabaena* cf. *acicularis* (Nyg.) Anag.et Kom.	+	+	++
S_N	*Raphidiopsis mediterranea* Skuja	+	+	
S2	*Spirulina* spp.	++	++	+++
	Chlorophyceae			
	Volvocales			
X2	*Carteria* sp.	+	++	+
X2	*Chlamydomonas spp.*	+	+++	+
X2	*C. asymmetrica* Kors.	+	+	+
X2	*C. microsphaerella* Pasch.et Jah.	+	+	+
X2	*Nephroselmis minuta* (Carter) H.-P.	++	+	++
X_{PH}	*Phacotus minusculus* Bourr.	+	++	+
X2	*Pteromonas* sp.	+	++	+
X2	*P. angulosa* Lemm.	+	+	+
X2	*P. limnetica* Hort.	+	+	+
X2	*Spermatozopsis exultans* Kors.	+	+	+
	Chloorococcales			
J	*Actinastrum hantzschii* Lagerh.	+	+	++
X1	*Chlorella minutissima* Fott et Novák.	+	+	+
X1	*Chlorococcum* spp.	++	+	++
F	*Dictyosphaerium ehrenbergianum* Näg.	+	+	+
F	*Ecdysichlamys* sp. G.S. West	+	+	
F	*Eutetramorus tetrasporus* Kom.	+	+	++
F	*Kirchneriella arcuata* G.M. Smith	+	+	++
F	*K. irregularis* (G.M.Smith) Kors.	+		++
F	*K. subcapitata* Kors.			+
X1	*Lagerheimia subalsa* Lemm.	+	+	+
X1	*Monoraphidium arcuatum* (Kors.)Hind.	+	+	++
X1	*M. circinale* (Nyg.) Nyg.	+	+	+
X1	*M. contortum* (Thur.) Kom.-Legn.	+	+	+
X1	*M. griffithi* (Berk.) Kom.-Legn.	+	+	+
X1	*M. komarkovae* Nyg.	+	+	+
X1	*M. minutum* (Näg.) Kom.-Legn.	++	++	+++
F	*Nephrocytium* sp.	++	++	+
F	*Oocystis parva* W. et G.S.West	+++	++	++
F	*Oocystis pusilla* Hansg.	+	+	+
F	*Raphidocelis mucosa* (Kors.) Kom.	+		+
J	*Scenedesmus acuminatus* (Lagerh.) Chod.	+	+	+
J	*S. ecornis* (Ehr.) Chod.	+	+	+
J	*Tetrastrum glabrum* (Roll) Ahls.et Tiff.	+	+	+
J	*T. staurogeniaeforme* (Schroed.)Lemm.	+	+	+
	Ulotrichophyceae			
T	*Geminellopsis* cf. *fragilis* Kors.	+	+	+
T	*Planctonema lauterbornii* Schmidle	+		+
	Bacillariophyceae			
C	*Actinocyclus normanii* (W.Greg.)Hust.	+++	++	+
P	*Aulacoseira granulata* (Ehr.) Sim.	+	+	+
D	Small centrics (<7 μm)	+++	+++	+++
C	*Chaetoceros* sp.	++		
C	*C. muelleri* Lemm.	++	++	+
C	*Cyclotella meneghiniana* Kütz	4	++	+
D	*Skeletonema potamos* (Weber) Hasle	+	+	
MP	*Craticula* sp.	+		+
MP	*Fragilaria construens* (Ehr.) Grun.	+	+	+
D	*Nitzschia acicularis* (Kütz.) W. Smith	+++	+	+
	Chrysophyta			
E	Chrysophyceae n.i.1	++	++	+
X2	Chrysophyceae n.i.2	+	+++	+
X2	*Chromulina* spp.	+	+	+

Table 2 (*Continued*)

		Riv	Str	La
E	*Epipyxis* sp.	+	+	+
E	*Mallomonopsis* sp.	+	++	+
X2	Haptophyceae n.i.	+++	+	+
	Xanthophyta			
J	*Goniochloris fallax* Fott	+	+	+
J	*Goniochloris mutica* (A.Braun) Fott	+	+	+
	Cryptophyta			
X2	*Chroomonas acuta* Uterm.	+	+	+
Y	*Cryptomonas curvata* Ehr.	+	+	
Y	*Cryptomonas ovata* Ehr.	+	+	+
X2	*Hemiselmis simplex* Butcher	+	+	+
X2	*Plagioselmis nannoplanctica* (Skuja)N.Lucas et Morr.	+	++	+
	Euglenophyta			
W1	*Euglena spp.*	+	+	+
W1	*Lepocinclis ovum* (Ehr.) Lemm.	+	+	+
W1	*L. texta* (Duj.) Lemm.	+	+	+
W1	*Monomorphina* sp.	+	+	+
W2	*Trachelomonas* spp.	+	+	+
W2	*Strombomonas gibberosa* (Playf.) Defl.	+		

Table 3
Mean values and ranges (between brackets) of chlorophyll-*a* (Chl-*a*), total density and biovolume and organisms with maximum linear dimension < 20 μm (MLD) at Salado River, El Vado Stream and Bedetti lake during December 2003–August 2004.

	Salado River				El Vado Stream	Bedetti Lake
	Centre	Right margin	Left margin	Bottom		
Chl-a mg m^{-3}	39.3 (9.4–99)	46.4 (10.7–112)	47.1 (10–112)	57.2 (14.7–105)	8.1 (0.11–19)	60.4 (29–102)
Total density ind. ml^{-1}	51,832 (8354–183,998)	46,070 (13,147–138,009)	56,998 (15,354–200,999)	80,711 (5358–187,966)	8507 (1267–22,332)	131,108 (69,100–307,459)
MLD < 20 μm ind. ml^{-1}	35,002 (7231–86,548)	30,954 (10,397–64,493)	39,591 (11,670–141,260)	53,279 (5358–128,533)	385 (0–1522)	75,207 (44,467–123,521)
Total biovolume mm^3 l^{-1}	13.63 (0.9–57)	11.41 (3–30)	13.90 (2.6–38)	18.73 (0.67–56)	2.5 (0.14–8.4)	29.8 (6.4–98)
MLD < 20 μm mm^3 l^{-1}	4.9 (0.59–19)	4.27 (1.7–9.1)	5.48 (1.78–15)	6.51 (0.67–12)	0.56 (0–3.7)	10.6 (3.56–36)

March, June–August 2004) that have been already indicated in previous paragraphs, are depicted in the separation of the sites located upriver (Fig. 4, white circles) and downriver (black circles) of the El Vado Stream inflow. A reduced variability was evidenced by the proximal positions of samples collected during periods of longitudinal homogeneity indicated with grey shade in the graph: Salado high waters, both systems high waters (*Salado River influence on El Vado* during May and January, respectively) and both systems low

Table 4
Spearman correlation coefficient and its level of significance (*$p < 0.05$; **$p < 0.01$) among limnological variables and chlorophyll-*a* (Chl-*a*), total density, biovolume and the most relevant functional groups of the Salado River during December 2003–August 2004.

	Water level		Current velocity	Temperature	Secchi	$N\text{-}NO_3^-$	$N\text{-}NH_4^+$	SRP	Conductivity	pH
	Paraná	Salado								
Chl-a	−0.52**	−0.30**	−0.42**		0.33**			0.48**	0.79**	0.54**
Density										
Total	−0.29**	−0.41**	−0.43**	−0.29**	0.50**				0.70**	0.39**
C	−0.49**		−0.30**	0.28*	0.26*		−0.39**	0.26*	0.68**	0.57**
D	−0.23*	−0.35**	−0.38**	−0.28*	0.55**				0.59**	0.40**
F	−0.25*	−0.35**			0.39**				0.54**	0.25*
P		0.41**		0.47**	−0.37**	0.42**	−0.41**			
X1	−0.29**	−0.55**	−0.41**	−0.32**	0.64**				0.58**	0.28*
X2		−0.62**	−0.30**	−0.60**	0.63**	−0.40**	0.32**		0.40**	
Y		0.27*		0.24*		0.33**				0.30**
Biovolume										
Total	−0.42**		−0.34**		0.32**			0.24*	0.70**	0.52**
C	−0.51**			0.51**		0.34**	−0.55**	0.30**	0.59**	0.58**
D	−0.38**	−0.27**	−0.29*		0.41*				0.53**	0.49**
F		−0.33**	−0.31*	−0.28*	0.40**				0.50**	0.26*
J		−0.33**		−0.24*	0.45**				0.54**	0.27*
P		0.35**		0.43**	−0.30**	0.39**	−0.34**			
X1		−0.55**	−0.41**	−0.39**	0.53**				0.49**	
X2		−0.40**	−0.22*	−0.30**	0.49**	−0.25*			0.42**	
Y		0.30**		0.26*		0.40**				0.36**
Number of samples	70	70	54	69	69	64	69	68	69	67

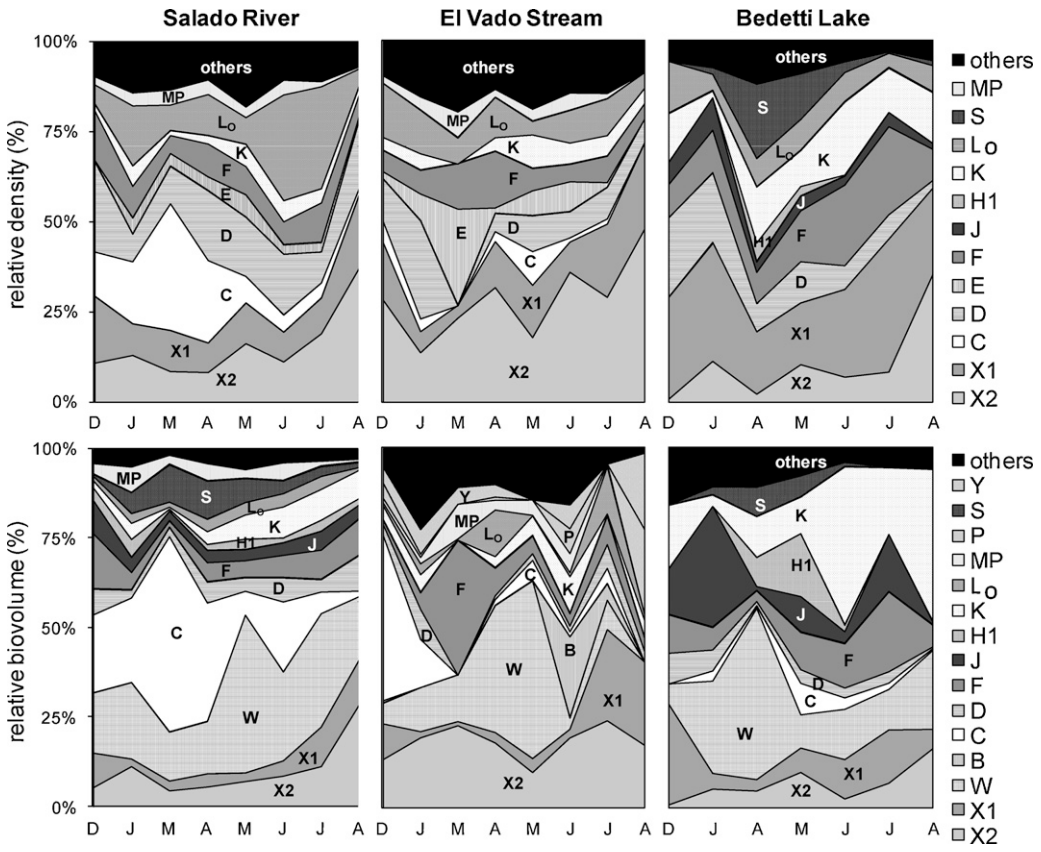

Fig. 3. Temporal variations of relative density and biovolume of functional groups (%) in the Salado River, El Vado Stream and Bedetti Lake during December 2003–August 2004. The sampling dates are indicated with the first letter of the month.

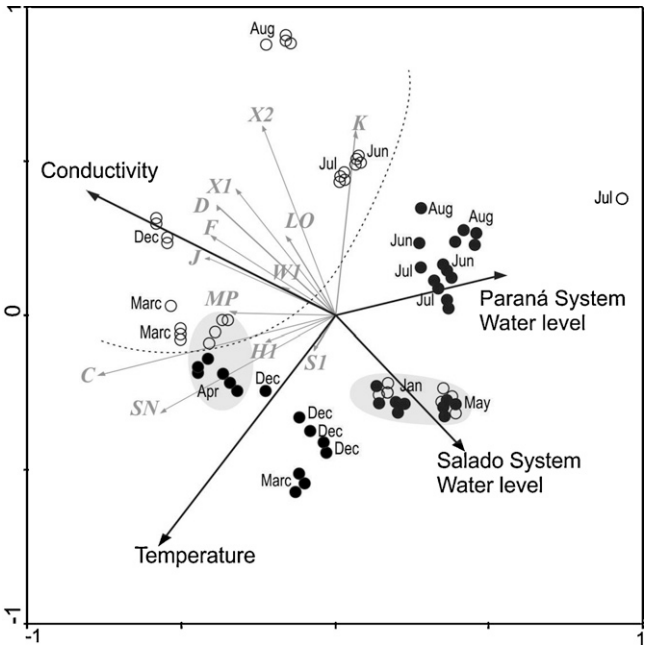

Fig. 4. First and second axes of the RDA based on biovolume of functional groups of the Salado River. Functional group vectors are represented with grey arrows, limnological variables with black arrows, and samples with the beginning letters of the corresponding month. White circles indicate upriver sites location (○: site 1). Black circles indicate downriver sites location (●: sites 3 and 5).

waters (*isolation period* on April). The length of the functional group vectors show that high biovolumes of **C**, **J**, **F**, **X1**, **D**, **X2** and **K** were positively related to the sites and periods characteristic of the Salado River (upriver localisation and April isolation period). They are inversely plotted to water level and directly to water conductivity. Group **C** and the Cyanobacteria **H1**, **S1** and $\mathbf{S_N}$ appeared to be most associated to increasing temperatures and to the isolation period, shown at the left bottom of the graph.

Discussion

Phytoplankton driving forces in this lowland river

Flow regime appears as the driving force affecting phytoplankton growth and assembly in the Salado River, as it is postulated in large rivers (Reynolds and Descy 1996). Low discharges favoured algal growth due to amelioration of the system's general conditions (lower water velocity associated to higher water residence time) that determined lower flushing and decreasing dilution. Conversely, algal abundance declined in response to enhanced water discharge, as it has been repeatedly observed along several world large rivers from different latitudes (Soballe and Kimmel 1987; García de Emiliani 1990; Lewis et al. 1995; Dokulil 1996; Kiss 1997; O'Farrell et al. 2002; Améziane et al. 2003; Salmaso and Braioni 2008; Rodrigues et al. 2009; Salmaso and Zignin 2010). The inflow of Paraná waters diluted phytoplankton cells and worsened the light climate in the Salado River, whereas the increase of water discharge in El Vado Stream enhanced the input of organisms from the river during high waters (January and May). Such enriching

effect has been also described for other rivers influenced by more productive systems (Istvánovics et al. 2010; Scherwass et al. 2010).

There are no evidences that Bedetti Lake contributed with algal biomass to the downstream river plankton during the study period; this is in agreement with observations from other river–lake systems (Basu et al. 2000; Twiss et al. 2010). Basu et al. (op. cit.) and Walks and Cyr (2004) postulated that the morphology of lake edges and the macrophytes presence can affect the export of lake plankton into streams. The duration of the lake–river connection and the selective forces that predominate in the main flow may also affect the survival of lenitic species in the river.

On the other hand, despite high temperature may have enhanced the positive effect of the hydrological condition on phytoplankton or even decreased its negative effect in the Salado River, it cannot be considered by itself a driving variable. Likewise, salinity and trophic status influenced species composition and supported an abundant phytoplankton but did not determine the phytoplankton temporal fluctuations. Correlation values with nutrients were low and concentrations largely exceeded those values considered to be limiting for phytoplankton growth (3–6 $\mu g\,P\,l^{-1}$ and 100 $\mu g\,N\,l^{-1}$, Reynolds 2006), as in many fluvial systems (Dokulil 1996; Kelly and Whitton 1998; Leland and Frey 2008; Salmaso and Zignin 2010). Even though phytoplankton biomass and mainly chlorophyll-*a* are predicted by phosphorus concentrations (Basu and Pick 1996; Van Nieuwenhuyse and Jones 1996; Dodds 2006; Piirsoo et al. 2007), in large rivers the role of nutrients is subordinated to the hydrology and associated variables (Kiss 1994; Reynolds and Descy 1996; Reynolds 2000; Salmaso and Zignin 2010). Finally, the grazing effect on algal losses was probably minor in this system due to the low abundance of zooplankton (José de Paggi and Paggi 1998). Moreover, the algae development of species smaller than 20 μm was indicated as evidence of the small importance of predation as a phytoplankton control (Chételat et al. 2006).

Phytoplankton along the complex spatial gradient

The confluence of rivers with different limnological characteristics introduces further heterogeneity in this aquatic system. The hydrological complexity of the Salado River in the stretch close to its mouth is produced by the overlap of the hydraulic and sedimentological actions of the Paraná System, via the El Vado Stream inflowing at its left margin.

The Salado River has high concentrations of dissolved (TDS $\sim 2\,g\,l^{-1}$) and suspended (TSS $\sim 0.16\,g\,l^{-1}$) materials, with predominance of the finest fraction (<1 μm) (García de Emiliani and Ruiz, unpublished). This derives in permanent turbid waters, since very low velocities and even small eddies are enough to keep these particles in suspension. The high conductivity ($\sim 3000\,\mu S\,cm^{-1}$) and slightly alkaline waters (pH ~ 8) caused by the input of chlorinated ground waters and the washout of saline soils characterise the area ecologically (Maglianesi and Depetris 1970). The occurrence of *E. paludosa*, *Chaetoceros* cf. *whigamii* and *C. muelleri* are an expression of the identity of the Salado River, as they are indicators of such high conductivities (Zalocar de Domitrovic and Maidana 1997). The water quality of the El Vado Stream was different, with TDS, conductivity and pH values lower and similar to those of the Paraná River ($\sim 0.06\,g\,l^{-1}$; $100\,\mu S\,cm^{-1}$ and 7, respectively) (García de Emiliani 1990). The constancy of *P. nannoplanctica* and the usual occurrence of *A. granulata* and its bioforms in this stream indicate its affiliation to the Paraná System: the former species is abundant in the Middle Paraná floodplain and in its mainstem, and the latter abound through all the Paraná mainstem (Zalocar de Domitrovic et al. 2007). Accordingly, the zooplankton development is similar to that of the Paraná secondary channels (José de Paggi and Paggi 1998).

Despite light limitation constrained further phytoplankton increase in the Salado River, the density, biovolume and chlorophyll-*a* concentrations correspond to eutrophic systems (Dodds 2006). Algal development was favoured by the high nutrients availabilities (mean $N\text{-}NO_3^- > 0.5\,mg\,l^{-1}$; $N\text{-}NH_4^+ > 0.8\,mg\,l^{-1}$; $SRP > 0.4\,mg\,l^{-1}$) and organic matter concentrations. Transport of organisms from upriver stretches was plausible due to their even higher trophic status and algal biomass (Devercelli and Peruchet 2008). Phytoplankton densities in El Vado Stream were significantly lower, just as in the other rivers influencing this water course (García de Emiliani and Devercelli 2004).

The connection of the Salado River increased the transparency, conductivity, pH and nitrogen concentrations of Bedetti Lake, but reduced the high phosphorus values observed during its isolation phase. The functioning of this system matches with floodplain lakes whose physical, chemical and biological changes depend on lotic influence (Thomaz et al. 2007). Notwithstanding, its longer water residence time determined significantly higher algal development and trophic level than in the river. Despite there was a floristic convergence with the Salado River as a result of their connection and similar water quality, the *Planktothrix-Oscillatoria-Planktolyngbya* assemblage only occurred in the lake. Coincidentally, this assemblage was also described for shallow enriched systems with unfavourable light conditions (Scasso et al. 2001; de Tezanos Pinto et al. 2007).

Phytoplankton presented a definite functional response to the complex spatial gradient here encountered. Small organisms, either with a high metabolism and non-mobile (**C**, **D**, **X1**) or mobile and well adapted to live in mixed environments (**X2**) dominated the Salado River. The slow flow and organic enrichment in the river facilitated the thriving of Cyanobacteria ($\mathbf{L_O}$ and minor contributions of **H1**, **K**, $\mathbf{S_N}$) and large Euglenophyta (**W1**, **W2**) inflowing from adjacent sites. The assemblage formed by **C–D** diatoms and **X1** chlorococcaleans has been repeatedly found in small enriched lowland rivers (Kiss and Szabó 1975; Descy 1987; Gosselain et al. 1994; Yang et al. 1997; Leland et al. 2001; Salmaso and Braioni 2008; Soares et al. 2007). The success of these groups in lotic systems relies on their tolerance to hydraulic stress and the morphological and physiological adaptations of diatoms to grow under low light intensities (Reynolds 2006); group **C** was better represented in the Salado, whereas **D** (small centric diatoms) in the El Vado Stream. Groups **X1** and **X2** were favoured in both water courses as they comprise opportunistic species of small size and rapid reproduction that can offset losses caused by unidirectional flow and the physical restrictions typical of the mainstem (Reynolds and Descy 1996; Gosselain et al. 1994; Chételat et al. 2006; Soares et al. 2007). The high surface:volume ratio of *M. tenuissima* ($\mathbf{L_O}$) was recognised as a successful strategy for maximising the harvesting of light in turbid systems (O'Farrell et al. 2007). The remaining groups of Cyanobacteria and Euglenophyta probably came from floodplain lakes and marshes and seemed to have encountered favourable growth conditions in the river, namely low water velocities and high trophic status, just as it was observed in other lowland water courses (Kiss and Ács 2002). The participation of these phytoplankton groups is rare in lotic systems of this temperate region and the existing records correspond to rivers with low flow, saline, eutrophic and organically polluted (Loez and Salibián 1990; del Giorgio et al. 1991; Conforti et al. 1995; Bauer et al. 2002; O'Farrell et al. 2002; Mercado 2003).

Diatoms were less abundant in Bedetti Lake though **X1** prevailed just like in other Paraná floodplain lakes (García de Emiliani 1997; Zalocar de Domitrovic 2003), accompanied by colonial organisms from **K** and **F**, usually well represented in short water columns due to their neutral buoyancy (Reynolds et al. 2002). Groups **W1**, **W2** and **S1** have longer generation times and thus, they dominated during the isolation period in agreement to the observations of Zalocar

de Domitrovic (2003) and Townsend (2006). The decrease of connectivity implies increased water residence time and therefore more time available for the development of more mature stages of the phytoplankton (Van den Brink et al. 1994; Jones and Elliot 2007).

Scenarios triggered by the hydrological interactions

The hydrological interactions of Salado and Paraná rivers affected the physical, chemical and biological characteristics of both systems as well as of the Bedetti Lake to which the Salado River is connected. This is summarised by three possible scenarios arising from the temporal dynamics and the grouping of samples performed by the multivariate analysis (Fig. 4).

During the *hydrological isolation* period the water bodies maintained their own identity. The Salado River had a homogeneous longitudinal pattern (depicted by the low dispersion of samples in the RDA plot) and comparatively higher suspended and dissolved solid concentrations, conductivity and pH than in the stream. The retarded flow decreased the restrictions for algal growth allowing high phytoplankton abundances in the Salado, mainly represented by functional groups **C** and **D**. The coupling of both high temperature (28 °C) and higher water residence time stimulated algal development in the lake, as it was observed in several floodplain water bodies during isolation phases (Huszar and Reynolds 1997; García de Emiliani 1997; Zalocar de Domitrovic 2003). Thomaz et al. (2007) and Kiss and Ács (2002) indicate that during isolation periods the biota follows different temporal patterns according to local lake factors, whereas during floods the river is responsible for driving the phytoplankton changes.

The period of *hydrological interactions with Salado River influence* was consequence of high waters in the river or in both fluvial systems. The homogeneous longitudinal pattern in the river (low dispersion of samples in the RDA plot) extended to the stream, showing similar water quality and phytoplankton concentrations. Algal growth in the river was counteracted by dilution and enhancement of water velocity, whereas the riverine input increased phytoplankton concentrations in the stream and, specially, of the euglenoids **W1** and **W2** in May. The flooding of the adjacent vegetated wetland resulted in a significant drop of DO concentration on January (summer); this event was previously explained in this basin by bacterial decomposition of submerged terrestrial vegetation on the banks and input of organic matter from the overflowed floodplain lakes (Emiliani and González de Paira 1996). The connection of the river with lake was not strong enough to modify the lake water quality on May as it did on January, and even during the latter period, the expected phytoplankton drop typical of floodplain lakes in these phases was not observed (Unrein 2002; Zalocar de Domitrovic 2003; Thomaz et al. 2007). The increments in the lake water transparency could have been a positive factor for algae to counteract losses due to the slow intrusion of lotic waters.

The *hydrological interactions with Paraná System influence* was characterised by a longitudinal discontinuity in the river with lower conductivity and phytoplankton concentrations downriver the Paraná inflow, as depicted by the separation of upriver and downriver samples in the RDA. Similar algal diminutions in lowland rivers were explained by the dilution caused by tributaries (Reynolds and Descy 1996; O'Farrell et al. 2002; Ohte et al. 2007; Piirsoo et al. 2008). This negative effect was enhanced on March by the high suspended solids transported through the stream, consequence of the sedimentological pulse of the Paraná (Drago and Amsler 1988). Likewise, the entrance of Paraná waters was reflected by the occurrence of *A. granulata* (**P**), cryptomonads (**Y**) and *P. nannoplanctica* (**X2**) in the Salado. Water quality and phytoplankton changes responding to the influence exerted by the Paraná River were also observed in other saline or high conductivity tributaries (García de Emiliani 1994; O'Farrell et al. 2002).

In conclusion, the hydrological complexity of the Salado Basin in its lower stretch affects the flow pattern, connectivity with adjacent floodplain systems and water quality of the river, thus influencing not only the structure of potamoplankton but also its functional composition.

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