



Phytoplankton of the Paraná River Basin

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With 8 figures and 2 tables

Abstract: We summarize the information on the phytoplankton of the Paraná River in the Argentine stretch, comparing the density, biomass, functional groups and diversity studies of the mainstem and floodplain since the 70's. We described the Yacyretá Reservoir and its impact downriver since it started operating in 1994. The spatio-temporal changes of the phytoplankton are associated to the hydrosedimentological regime. Regular variations in the hydrological phases and shorter permanent fluctuations are essential for phytoplankton maintenance, since they allow the lateral exchange with zones of higher algal accumulation in the main channel and with the floodplain. During ordinary hydrological cycles, the mainstem shows a typical potamoplankton, dominated by *Aulacoseira granulata* and, alternatively, with sub-dominance of Chlorococcales, Cryptophyceae at the Middle and Lower Stretch, Cyanobacteria abound at Yacyretá Reservoir and downriver at the High and the beginning of the Middle Stretch. The disruption of Yacyretá Reservoir produces profound changes in the High Paraná phytoplankton evidenced in increased density and replacement of dominant species; Cryptophyceae replaced the Bacillariophyceae. Since 2001, water transparency increased and phosphorus concentration decreased, as well as the density and diversity of phytoplankton. Since 2004, an increase in Cyanobacteria was observed with bloom of *Microcystis aeruginosa* that extended 220 km downstream of the dam. Anomalous hydrological cycles, related to the ENSO phenomenon produced changes in phytoplankton density and structure. During El Niño, the system maintains a relative homogeneous phytoplankton assemblage, although mean density values are significantly lower than those registered in ordinary hydrological periods. La Niña provokes a more drastic change in the community, due to the disruption in the exchange with the alluvial valley. The river-floodplain connectivity is essential for the maintenance of phytoplankton diversity.

Keywords: potamoplankton, Paraná, Yacyretá, floodplain

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Introduction

The Río de la Plata Basin includes the Paraná, Paraguay, Uruguay, and La Plata rivers with their tributaries. The Paraná River, with a drainage area of $2.8 \times 10^6 \text{ km}^2$ and 3740 km of length (15° to 35° S) is the second largest catchment of South America (Fig. 1). It flows from North to South along a complex hydrological gradient, with tropical climate at the headwaters, subtropical warm-temperate at the Paraguay River region and temperate at its mouth (OEA 1969). Longitudinally, it is divided in four stretches (Soldano 1947, Bonetto 1986) as follows:

The headwater begins with the junction of the Paranaíba and Grande Rivers in Brazil. This Upper Stretch flows over basalts and sandstones covered by lateritic soils rich in iron and aluminum oxides, and it is interrupted by a series of rapids and falls, and important tributaries coming mainly from the East. The High Paraná Stretch is emplaced in Argentine territory, downriver the Itaipú Reservoir. Its hydrological regime has been altered by several Brazilians dams constructed during the seventies (Bonetto et al. 1989, Rosin et al. 2009), and the Itaipú and Yacyretá Reservoirs at the proper stretch in 1982 and 1994, respectively. The high water transparency that characterized this reach (1–1.5 m) augmented up to 2 m after Yacyretá Dam started operating.

The Middle Stretch is the section starting at the Paraguay River confluence, occupied by islands that remain emergent during the ordinary floods and by a fringe-floodplain (Drago 1989). The river becomes turbid, water transparency diminishes and conductivity and phosphorus concentrations increase due to the high suspended materials transported through the Paraguay River from the Bermejo River. They are swept away from the Andean sedimentary rocks rich in carbonates (see Zalocar de Domitrovic et al., 2014). Mean suspended solids of 175 mg L^{-1} (range: 58–609) were registered at the Middle Stretch (García de Emiliani & Devercelli 2003) and 143 mg L^{-1} (range: 10–743) at the Lower Stretch (O'Farrell et al. 1996). The waters from the High Paraná with different lithology flow by the left bank whereas the Paraguay waters flow by the right, and both keep unmixed until 300–400 km downriver, depending on the hydrological phase. Fifty to 70% of the Middle Paraná suspended solid content is supplied by the Bermejo, while 65 to 80% of the water discharge belongs to the Upper Paraná (Drago 1984, Orfeo & Stevaux 2002, Depetris et al. 2003). In the transversal section, the floodplain is constituted by a diversity of waterbodies arising from a variety of hydrodynamic processes.

The Middle Stretch is fringed along its right bank by a wide floodplain (6–40 km) that comprises thousands of permanent and temporary water bodies of different morphology, vegetation gradient, macrophytes cover and connectivity degree with the mainstem (Drago 1989). At the Lower Paraná Stretch (from Diamante to Río de La Plata), the alluvial plain changes to the left bank and experience a marked enlargement. A large formation of islands determines a complex network of small, broad and winding lotic courses, covered by a subtropical gallery forest wetland. Many of them are small, shallow and sometimes turbid. Downriver Rosario City, the Lower Paraná divides in two main arms, the Paraná de Las Palmas and the Paraná Guazú, which delimit a vast Delta of around 15000 km^2 , 320 km long and more than 60 km wide, joining the Uruguay River at the mouth to form the Río de La Plata (Bonetto & Wais 1990). A description of the Middle Paraná could be found in Iriondo

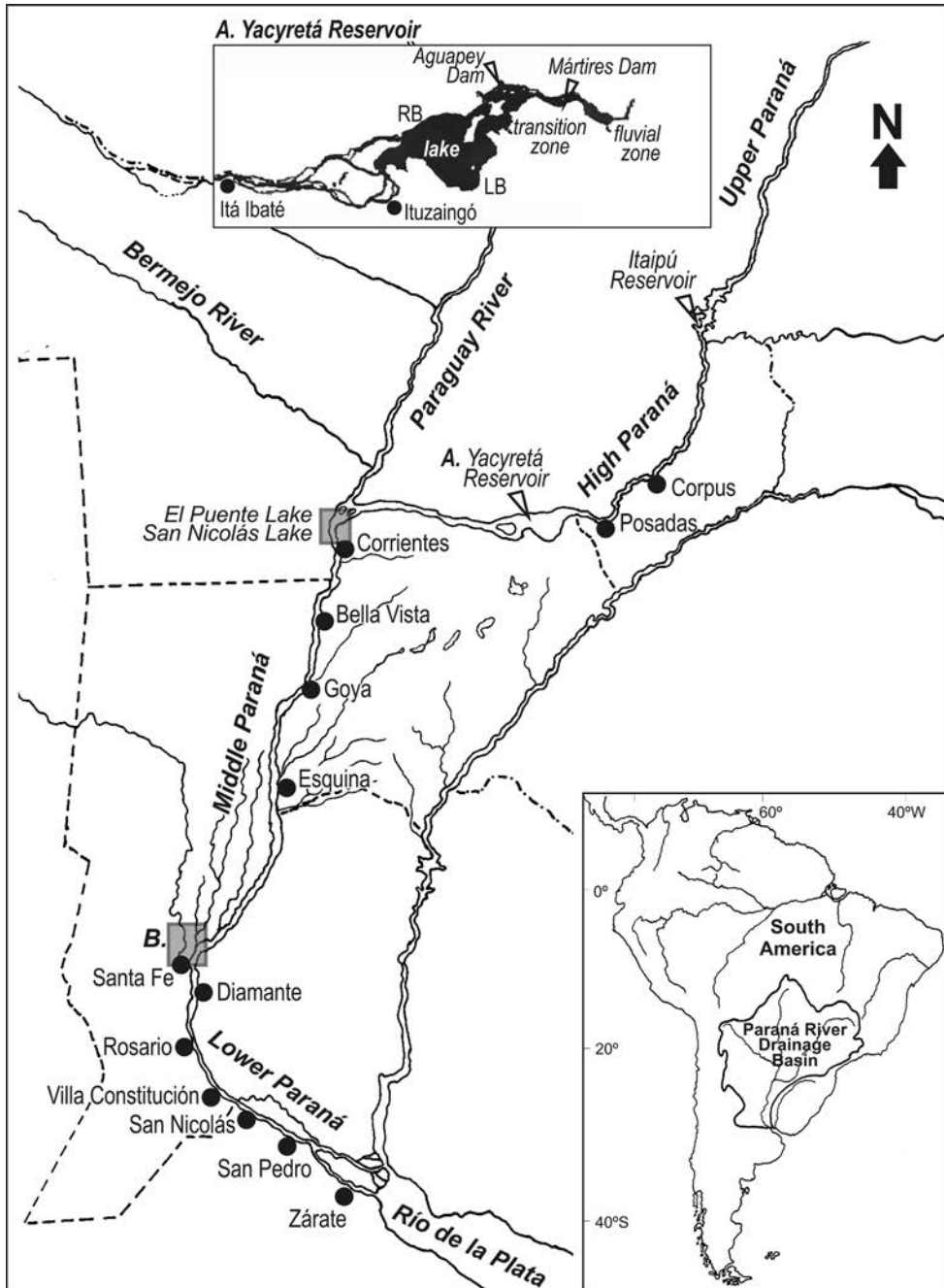


Fig. 1. Paraná River drainage basin and its location in South America. **A.** Detail of Yacyretá Reservoir. **B.** Emplacement area of the rivers Correntoso, Colastiné, Colastinecito, San Javier, Chipá, Conchillas and Mendieta, and El Tigre and Matadores lakes.

et al. (2007), and of the Lower Stretch in O'Farrell et al. (1996). In Table 1 there is a detail of the Paraná environmental conditions at the different stretches.

The pulsatic dynamic is the predominant force that integrates the mainstem and the floodplain in a unique and integrated system with constant exchange of energy and matter (Junk et al. 1989, Neiff 1990). The hydrological connectivity among waterbodies, which depends mainly in the topographic rather than in the horizontal position, enables the exchange in the lateral gradient. Pulses of high and low water discharges that occur with an interannual variability alternate with other permanent minor fluctuations. Hydrological regularities are shown through long-term studies but they cannot be determined as a hydrological variability tendency (Neiff 1996) such as in the Orinoco or Amazon large rivers. Extreme hydrological phases in the Paraná River are coupled with the world extended hydroclimatic phenomenon 'El Niño-Southern Oscillation' (ENSO) that occurs with a variable frequency (Depetris et al. 1996, Camilloni & Barros 2003). Extreme floods correspond to situations of completely inundated alluvial valley, whereas during extreme drought floodplain waterbodies are isolated from the main channel and many of them dry up (Drago 1989).

The phytoplankton of the Paraná Argentine stretch has been studied since the 70's. Several researches have analysed algal responses during different hydrological phases (Bonetto et al. 1982, Zalocar de Domitrovic & Vallejos 1982, O'Farrell et al. 1996, 1998, Mercado 1999, Mercado & Gomez 1999, Izaguirre et al. 2001, Zalocar de Domitrovic 2003, Unrein 2002, Unrein et al. 2010), including extreme hydrological conditions (García de Emiliani & Devercelli 2003, Devercelli 2006, 2010). There are some general reviews (Bonetto & Wais 1990), whereas the studies carried out in the Middle Stretch are summarized in García de Emiliani (1990) and Zalocar de Domitrovic et al. (2007a).

Potamoplankton of the Paraná River mainstem: the longitudinal gradient

The basin geomorphology, the morphology of the mainstem, and the characteristics and extension of the lateral floodplain are important features that must be taken into account for the longitudinal characterisation of the potamoplankton. In addition, tributaries confluence or impoundments disruption, as depicted by the Serial Discontinuity Concept (Ward & Stanford 1995), may influence phytoplankton longitudinal transport and its development downriver.

Physical factors play a steering role in phytoplankton dynamics as in other large rivers (Descy 1993, Reynolds & Descy 1996, Wehr & Descy 1998, Lewis et al. 2000, Salmaso & Zignin 2010). 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 environment. Thus, the hydrosedimentological regime is a macrofactor that conducts phytoplankton behaviour and explains a highly significant proportion of algal assemblage variations (Zalocar de Domitrovic et al. 2007a, Devercelli 2010). Hydrological fluctuations allow lateral exchanges and recruitment of organisms from the floodplain (Reynolds & Glaister 1993). The pulsing of water discharge is the major force that determines the degree of connectivity and such exchanges (Junk et al. 1989, Neiff 1990). 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).

The Paraná mainstem shows a typical potamoplankton, characterized by low density and biovolume (García de Emiliani 1990, Zalocar de Domitrovic 2007). Mean annual biovolume (between 0.1 and 1.7 mm³ L⁻¹) and density (Table 1) varied along the longitudinal gradient. The high species and functional group richness are due to several fluvial species jointly with a high number of sporadic species, which are mostly incorporated from floodplain environments during hydrological fluctuations. On the other hand, the strong selectivity conditions of the main flow (high turbidity and turbulence, low water residence time) are responsible of the low functional diversity and the high abundance of only few species. The predominance corresponds to R-strategist species (acclimating), adapted to variations in turbulence and light intensity, followed by C- or R-C- strategist species with high metabolic rate (Bonetto et al. 1982, García de Emiliani 1990, O'Farrell et al. 1996, Zalocar de Domitrovic et al. 2007a).

The phytoplankton of the Paraná mainstem is dominated by centric Bacillariophyceae. *Aulacoseira granulata* and its bioforms, belonging to the functional group P of Reynolds et al. (2002) classification, is the most important species (Zalocar de Domitrovic & Maidana 1997), followed by *Cyclotella meneghiniana* and other centric diatoms (C). The subdominance corresponds to functional groups of Chlorococcales (mainly X1 and J). An increment in centric diatoms is observed in the longitudinal gradient accompanied by a parallel diminution in Cyanobacteria contributions (Zalocar de Domitrovic et al. 2007a) (Fig. 2).

At the High Paraná mainstem, the mentioned predominance in density and biovolume of P was found followed by C and D (*Synedra* spp.) (Zalocar de Domitrovic & Vallejos 1982). The chlorococcalean were mainly represented by X1 (*Nephrochlamys subsolitaria*, *Monoraphidium contortum*, *M. pusillum*), J (*Scenedesmus* spp., *Desmodesmus* spp., *Coelastrum* sp., *Actinastrum hantzschii*, *Monactinus simplex*, *Stauridium tetras*) and F (*Dictyosphaerium ehrenbergianum*, *Oocystis lacustris*). As a particular feature of this stretch, Cyanobacteria groups S_N (*Cylindrospermopsis raciborskii*), S1 (*Planktolyngbya limnetica*) and

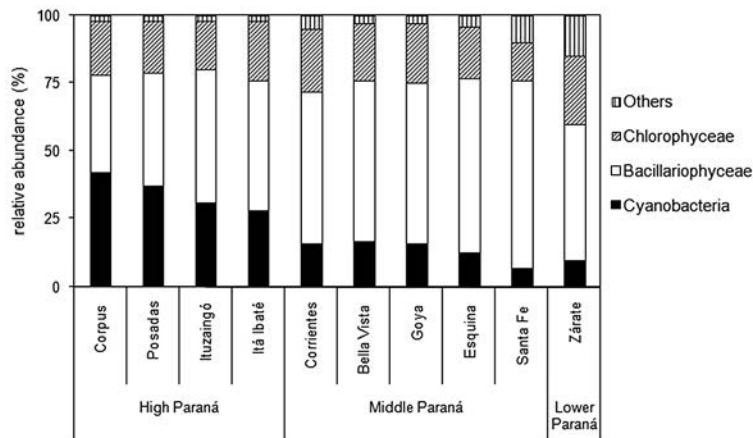


Fig. 2. Variation of the main taxonomical groups along Paraná River mainstem. The locations of the sampling stations are indicated in Figure 1 (Zalocar de Domitrovic et al. 2007b, García de Emiliani & Devercelli 2003, O'Farrell et al. 1996).

Table 1. Mean values of environmental characteristics and phytoplankton density along the mainstem of the Paraná River at the different stretches. LB: left bank; RB: right bank; LW: low-waters; HW: high-waters; ELW: extreme low-water; EHW: extreme high-water.

Sites/dates	Discharge (m ³ s ⁻¹)	Temp (°C)	Sd (cm)	pH	DO (mg L ⁻¹)	Cond (µS cm ⁻¹)	Density (ind. ml ⁻¹)	
HIGH PARANÁ (a)								
Posadas								
Aug. 1994–Jul. 1995	15641	24	65	7.3	8.1	44.4	420	
Candelaria								
Sept. 2001–Aug. 2002	12363	24.6	139	7.02	7.9	49.7	319	
April 2006–April 2008	13394	23.8	190	7.1	8.3	50.9	146	
Yacyretá Reservoir								
Aug. 1994–July 1995	wd	25	115	7.4	8.0	44.7	820	
Sept. 2001–Aug. 2002	wd	23.8	191	7.2	8.3	48	905	
April 2006–April 2008	wd	24.6	230	7.4	8.6	51.4	1226	
Ituzaingó								
Aug. 1994–July 1995	wd	24	107	7.3	10.6	42.7	597	
Itá Ibaté								
Sept. 2001–Aug. 2002	wd	24.1	150	7.2	8.3	50.2	343	
April 2006–April 2008	wd	23.7	200	7.3	8.4	51.3	298	
MIDDLE PARANÁ								
Corrientes LB / RB (b)								
March 1981–March 1982	LW	17153	21.3–21.4	61–19	7.2–7.3	8.4–6.9	52–126	1379–454
	HW	22349	27.1–27.6	21–7	7.1–7.6	13–8.6	50–123	344–352
June 1995–June 1996	LW	wd	24.3–24.4	48–18	7.6–7.1	8.0–7.1	48–106	1443–432
	HW	wd	25.9–26.1	69–11	6.9–7.0	7.6–6.2	60–121	880–392
Bella Vista LB / RB								
March 1981–March 1982	LW	wd	20.3–20.9	41–229	7.3–7.3	8.8–8	65–100	758–403
	HW	wd	26.7–27.0	12–6	7.1–7.4	7.4–7	56–93	169–193
Goya LB / RB								
March 1981–March 1982	LW	wd	20.3–20.5	32–24	7.4–7.4	8–7.7	74–96	703–444
	HW	wd	26.7–26.7	11–9	7.2–7.4	7–6.8	60–97	229–145
Esquina LB / RB								
March 1981–March 1982	LW	wd	20.6–20.4	26–19	7.3–7.4	8–8	76–99	466–323
	HW	wd	26.1–26.1	16–11	7.0–7.3	9–9	70–90	183–164
Santa Fe (c)								
Nov. 1977–Nov. 1978	LW	12218	21.2	28.5	7.6	8.3	90	565
	HW	17186	27.8	17	7.5	6.6	75	224
June 1984–March 1986	LW	13000	23.3	19.9	7.5	8.3	103	1095
	HW	18000	20.7	25.9	7.2	8.3	88	667
Nov. 1997–Nov. 1998	EHW	21444	22.4	36	7.2	7.1	66	194
Nov. 1999–Nov. 2000	ELW	11000	23	21.8	7.5	8.7	99	655
LOWER PARANÁ								
Paraná de las Palmas (d)								
March 1995–April 1996		5100	20.7	20.6	7.1	wd	137	450
Rosario–Brazo Largo (e)								
April 2003–April 2004		wd	20.5	24.5	7.4	8.3	156	402

Table 1. cont.

Sites/dates	Discharge (m ³ s ⁻¹)	Temp (°C)	Sd (cm)	pH	DO (mg L ⁻¹)	Cond (µS cm ⁻¹)	Density (ind. ml ⁻¹)
Villa Constitución (f)							
April 1996–Febr. 1997	wd	21.7	29.5	7.3	9.8	125	552

References: a) Meichtry de Zaburlín 1999, 2002, Meichtry et al. 2007. b) Zalocar de Domitrovic 2007, Zalocar de Domitrovic et al. 2007b. c) García de Emiliani & Devercelli 2003, Devercelli 2006, 2010, unpublished. d) Mercado & Gómez 1999. e) O'Farrell 1996, 1998.

H1 (*Dolichospermum spiroides*), followed in importance and prevailed during the warm periods, even at high waters; no bloom formations were here recorded.

At the beginning of the Middle Stretch, contrasting chemical and physical compositions along the river cross-section remains for about 400 km downstream of the Paraguay River confluence (Bonetto & Orfeo 1984). The different water sources of the High Paraná that flows by the left bank and the Paraguay River waters that flows by the right are reflected by higher water transparency and dissolved oxygen in the former, and higher suspended solids, conductivity and phosphate concentrations in the latter.

Phytoplankton also presents different characteristics at both banks. At the right bank, the prevailing functional group P is associated in minor proportion with B (*Aulacoseira alpigena*, *A. herzogii*) and C. The diminution of Bermejo's suspended solids input during fall and winter allows for the development of S1, J, Y, X1 and X2. On the other hand, the left bank is characterized by comparatively higher phytoplankton density and richness. This asymmetrical distribution persists during the entire annual hydrological cycle and may even continue for about 400 km downriver Paraguay's confluence. The lowest density value and the greatest transversal differences are observed during the Bermejo flood period. From a total of 143 taxa, 59 corresponded to the left bank, 36 to the right and 26 appeared at both sides (Zalocar de Domitrovic et al. 2007b). The functional group richness was also higher at the left bank than at the right (19 vs. 11). Groups P, X1 and J contributed to more than 50% of the total density, and only P to 50% of the total biovolume. The Shannon-Wiener diversity index showed significant differences between the two margins ($p = 0.009$), with again higher values at left (2.9–4.1) as compared to right bank (1.2–3.7).

After Yacyretá Dam started operating in 1994, evidences of important impacts on the biota were observed (Domitrovic et al. 1994, Meichtry de Zaburlín 1999, Garrido 1999, Peso & Bechara 1999, Neiff et al. 2000). As the interruption of the river flow diminishes the current velocity and increments the water residence time, higher algal development and changes in species composition (Meichtry de Zaburlín 1999, 2002) were observed. The phytoplankton structure of the right bank remained unchanged during the last 40 years (1970–2010), but a year after the river's damming (1995–1996) the phytoplankton structure of the left bank 220 km down Yacyretá, changed significantly in comparison with 1970–1980 period (Fig. 3). Cyanobacteria ($p = 0.001$) and diatoms ($p = 0.035$) notably diminished, whereas Cryptophyceae ($p = 0.001$) and Chlorophyceae ($p = 0.006$) augmented (Zalocar de Domitrovic et al. 2007b). In the same way, functional groups P, S_N, S1 and H1 presented lower proportion, while Y (*Cryptomonas marssonii*, *C. ovata*), X2 (*Plagioselmis nannoplanctica*, *Chloromonas acidophila*, *Chlamydomonas leptobasis*), X1 (*Choricystis minor*, *Chlorella vulgaris*,

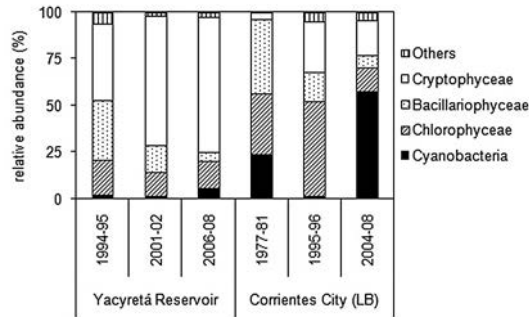


Fig. 3. Variation of the main taxonomical groups at Yacyretá Reservoir and downriver at the Paraná mainstem left bank (LB) before and after the impoundment (Meichtry de Zaburlín et al. 2007, Zalocar de Domitrovic et al. 2007b, unpubl. data).

Nephrochlamys subsolitaria, *Monoraphidium contortum*, *M. pusillum*) and J (*Scenedesmus ecornis*) increased their contributions.

The Detrended Correspondence Analysis (DCA) reflects the mentioned differences before and after the impoundment (Fig. 4). In the first axis (eigenvalue = 0.79), samples from the left bank (waters from High Paraná) collected during pre-impoundment period are located to the right of the gradient. *Aulacoseira alpigena* and especially *A. granulata* predominated also at the right bank (waters from Paraguay River) in all the samples of the pre and post-impoundment periods (Fig. 4, Groups 2 and 4). Samples from Group 3 correspond to the left bank of the post-impoundment period and are allocated in the negative region of Factor 1, which is related to numerous species of Chlorophyceae, Cryptophyceae, Chrysophyceae, Bacillariophyceae and Euglenophyceae. Some common taxa to both periods (pre and post-impoundment) occupy an intermediate position in the gradient. Ten years after, in Yacyretá (February to April 2004), and in coincidence with a prolonged drought, the first bloom of *Microcystis aeruginosa* registered in the reservoir was swept downwaters, magnifying by the left bank up to Corrientes City. Contrarily, no blooms were observed at the right bank due to the influence of Bermejo high waters and suspended solids (Zalocar de Domitrovic & Forastier 2007). Blooms of minor magnitude and persistence were observed between December and April of the next years (2005 to 2008). Before 2004, *M. aeruginosa* was detected in lower percentage in net samples. This species classified in functional group M dominated alternatively with Y, X2 and X1, and in scarce proportion with P, E (*Mallomonas* sp.), MP (pennate diatoms) and the Euglenoids W1 and W2. During *Microcystis* blooms (2004–2008 summer periods), the cyanotoxin analysis performed with HPLC, determined the presence of Microcystins (Zalocar de Domitrovic et al. 2009, Forastier et al. 2010).

Downriver, near Santa Fe City (31°42'S–60°29'W), no significant differences were found in abiotic characteristics and phytoplankton between both banks because turbulence at this stretch is high enough to maintain a relative homogeneity. Some variations are only observed among the banks and the centre in periods of alluvial plain drainage (Devercelli 2006). The dominance of *Aulacoseira granulata* diminished during prolonged low water phases (Devercelli 2010). This could be attributed to the reduction of the mainstem-floodplain interactions at low connectivity periods and, in consequence to the reduction of organisms' recruitment

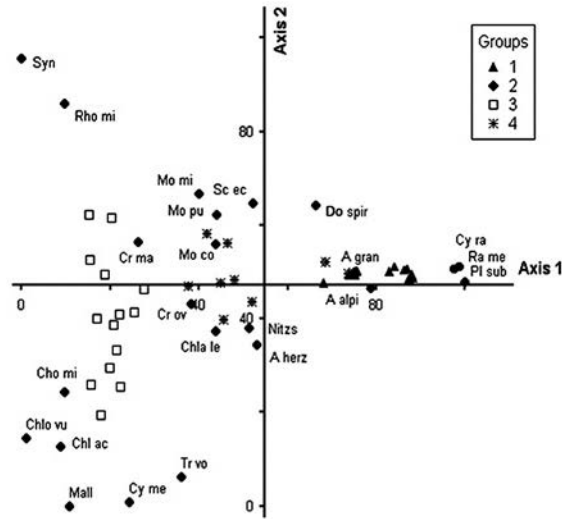


Fig. 4. Detrended Correspondence Analysis (DCA) of phytoplankton species and samples (groups), before and after Yaciretá impoundment. Factor 1 shows the order of the species between the periods of the pre and post-impoundment. Groups 1 and 2 show samples taken during 1970–80 (pre-impoundment period), and Groups 3 and 4 represent samples collected during 1995–96 (post-impoundment period). From Zalocar de Domitrovic et al. (2007b).

Abbreviations: *Dolichospermum spiroides* (Do spir); *Aulacoseira alpigena* (A alpi); *A. granulata* (A gran); *A. herzogii* (A herz); *Chlamydomonas acidophila* (Chl ac); *Ch. leptobasis* (Chla le); *Chlorella vulgaris* (Chlo vu); *Chorycistis minor* (Cho mi); *Cryptomonas marsonii* (Cr ma); *C. ovata* (Cr ov); *Cyclotella meneghiniana* (Cy me); *Cylindrospermopsis raciborski* (Cy ra); *Mallomonas* sp. (Mall); *Nephrochlamys subsolitaria* (Mo co); *Monoraphidium minutum* (Mo mi); *M. pusillum* (Mo pu); *Nitzschia* sp. (Nitzs); *Planktolyngbya limnetica* (Pl sub); *Raphidiopsis mediterranea* (Ra me); *Rhodomonas minuta* (Rho mi); *Scenedesmus ecornis* (Sc ec); *Synura* sp. (Syn); *Trachelomonas volvocina* (Tr vo).

from adjacent storage zones (Reynolds & Glaister 1993) where the diatom was found. A distinct feature of this stretch is the great development of Cryptophyceae (X2 and Y), that share alternatively the sub-dominance with green algae and even dominated during periods of extreme drought. *Cryptomonas* spp. and *Plagioselmis nannoplanctica* are the principal contributors, the former mainly during high waters and the latter during low waters. In addition, registers of the filamentous diatom *Skeletonema* cf. *subsalsum* (D) were found only at this stretch since 1999 (Devercelli 2006).

The Lower Paraná was sampled along 400 km at several stations (near Rosario City, San Nicolás, San Pedro, Zárate and Brazo Largo) from April 1993 to April 1994 (O'Farrell et al. 1996). 370 taxa and density concentrations between 59 and 964 ind. ml⁻¹ were found. Maximum density and species diversity coincided with spring, when high transparency and low water discharges occurred. The centric diatoms contribution to total density (mainly *Aulacoseira granulata*) varied between 47 and 83%. Pennate diatoms and green algae appeared alternatively as subdominant, with up to 28 and 24% of total density, respectively. At high Secchi depth and low water period, Chlorococcales increased in abundance. Euglenoids and Cyanobacteria were rarely important and never exceeded 13% of total contribution. The most

common Cyanobacteria species were Nostocales: *Dolichospermum* spp., *Aphanizomenon* spp. and *Raphidiopsis mediterranea* (O'Farrell et al. 1996). Phytoplankton vertical distribution at San Nicolás and San Pedro showed no differences in the water column, whereas some contrasts were found in the cross-section (O'Farrell et al. 1998). At San Nicolás the algal composition was different at both banks. The left bank presented higher algal density and significant increase in Zygnematophyceae, attributable to the bank differences in depth, morphology and influence of floodplain waterbodies. On the other hand, a more homogeneous phytoplankton distribution in the cross-section was found at San Pedro. A similar density range (186–969 ind. ml⁻¹) was observed near Villa Constitución City during 1996 (Unrein 2002). At the Paraná de Las Palmas, Mercado & Gómez (1999) also found the lowest density values during the flooding period, and the highest during the low water phase (13 and 1822 ind. ml⁻¹, respectively; Mercado, unpubl. data).

Yacretá Reservoir: addressing river discontinuity

It is the largest reservoir built in the Argentine stretch, with a mean area of 1140 km² (67 km length and 30 km wide), 7000 hm³ of volume and 6–7 m of mean depth (maximum = 23 m). The water residence time is lower than 15 days, and the water level is relatively stable. It receives the Mártires Stream at the Argentine left bank, charged with urban effluents, and the Aguapey Stream that runs by a wide rural alluvial valley at the right bank (Fig. 1). Its waters are continuously mixed, with homogeneous temperature and dissolved oxygen distribution in the water column. The longitudinal pattern for reservoirs proposed by Thornton (1990) occurring along a continuum from the river inflow to the dam, is observed at Yacretá. A fluvial, transition and lacustrine zone are distinguished, each possessing unique physical, chemical, and biological properties.

At the Reservoir filling phase in 1994, water transparency varied between 0.75 and 1.13 m and the total phosphorus range was 0.047–0.095 mg L⁻¹ in 1998. During 2001, transparency increased significantly (maximum > 4 m), whereas total phosphorus diminished (0.018–0.024 mg L⁻¹) in accordance with water discharge diminution due to the additional effect of the filling of Puerto Primavera Dam at the Brazilian Upper Stretch (Meichtry de Zaburlín et al. 2007, 2013, Souza Filho 2009).

Phytoplankton density varied in a wide range (52 and 15708 ind. ml⁻¹). The lower mean densities were found at the fluvial and transition zones throughout the study period that did not exceed 500 ind. ml⁻¹. Higher values in these stations (512 ± 181 ind. ml⁻¹) were registered after the first year of operation (1994–1995), with a decreasing trend since the stabilization of the impoundment (2001–2002). Higher densities were observed during low waters, characterized by a high water residence time and transparency, whereas lower densities occurred at high waters related to turbidity and solid increments. From 1994 to 2006, functional groups P and C dominated at the fluvial zone and the flagellates X2 and Y subdominated. At the transition zone, P and C dominated during the first period, changing to Cryptophyceae after 2001. Chlorophyceae were present in lower proportion, mainly groups F (*Sphaerocystis schroeteri*, *Mucidosphaerium pulchellum*) and X1 (*Monoraphidium arcuatum*, *M. contortum*, *M. tortile*). The Cyanobacteria groups M (*Microcystis aeruginosa*), H1 (*Dolichospermum circinalis*, *D. spiroides*) and L_o (*Chroococcus minutus*, *Ch. limneticus*) presented high density during

spring and summer, especially at periods of low discharges. In the lake, since 1994, higher densities were registered at the left bank characterized by higher water residence time than the right one. Cryptophyceae predominated over diatoms that are more affected by sedimentation processes due to current velocity diminution (Fig. 3). Chlorophyceae contributed poorly to total density and were mainly represented since 2002 by *Sphaerocystis Schroeteri*, *Mucidosphaerium pulchellum* (F) and small flagellates such as *Chlamydomonas* spp. and *Carteria* spp. (X2). Cyanobacteria increased its density since 2002, with the development of potentially toxic species such as *Microcystis aeruginosa* and *Dolichospermum circinalis*. The first bloom of *M. aeruginosa* that affected all the reservoir was registered during the summer and autumn 2004, and it was extended to the Paraná mainstem (Zalocar de Domitrovic & Forastier 2007, Meichtry de Zaburlín et al. 2007, 2013). Blooms of lower intensity and duration occurred particularly at high water retention zones and during low water periods (e.g. April 2005, December 2006).

Minor dams are naturally formed at the mouth of Mártires (left bank) and Aguapey Streams (right bank) (Fig. 1), where density ranged between 160–4630 and 320–12124 ind. ml⁻¹, respectively. Cryptophyceae was the dominant group followed by Euglenophyceae that is favoured by the high organic matter and nutrient concentrations, and by green algae belonging to X1, G and J. At Mártires Dam, the high turbidity limited phytoplankton density (inversely correlated with water color, $r = -0.667$, $p < 0.05$). At Aguapey Stream, density was positively correlated with water temperature ($r = 0.25$, $p < 0.05$), total phosphorus ($r = 0.47$, $p < 0.01$) and ammoniac nitrogen ($r = 0.83$, $p < 0.001$). Density diminished down the reservoir (Itá Ibaté) with values lower than 500 ind. ml⁻¹, where Cryptophyceae dominate the phytoplankton density and Bacillariophyceae subdominate, except during periods of Cyanobacteria blooms.

Extreme hydrological periods

During the extreme floods and droughts in the Paraná River triggered by the ENSO phases, the connectivity degree between the alluvial valley and the mainstem is significantly affected and, in consequence, the phytoplankton dynamics. During extreme floods, diminution in conductivity, suspended and dissolved solid concentrations are observed due to dilution. On the other hand, the significant enhancement of nitrogen chemical species and the less accentuated increment in phosphate concentrations, reveal nutrient inflow from the inundated floodplain area. The effect of the sedimentary pulse of the Bermejo River may be intensified during extreme droughts since no dilution occurs, thus causing a simultaneous increment in conductivity, suspended and dissolved solids (Devercelli 2010).

In comparison with ordinary hydrological periods, algal density and biovolume are lower at El Niño and higher at La Niña (Table 1) (Fig. 5), whereas rare and sporadic phytoplanktonic species increase in number at both periods. The typically dominant large filamentous diatoms are replaced by small flagellate unicells belonging to Y and X2, favoured by their high surface:volume ratio and metabolic activity. The colonizer species of group X2, sensible to mixing and light depletion, are more abundant during the drought phase, where the 'lenticated' mainstem allows the unusual development of these flagellates. The dominance of cryptomonads, especially at El Niño phase, reflects their capacity to compensate the increasing

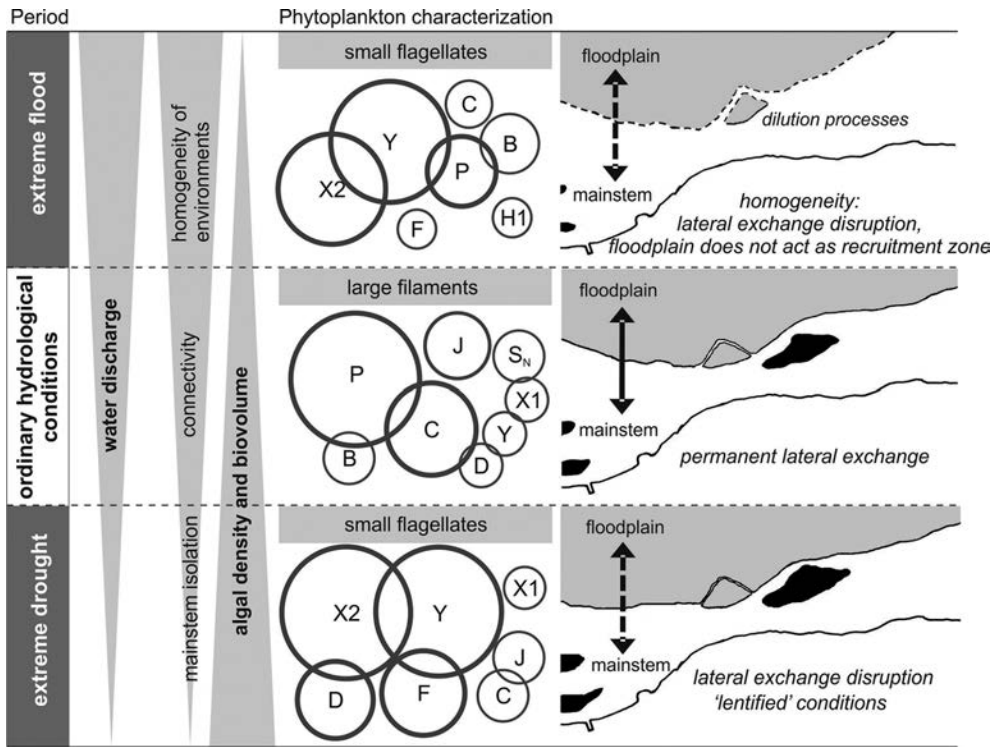


Fig. 5. Scheme summarising the main environmental conditions (water discharge, connectivity and mainstem-floodplain interactions) and the principal phytoplankton attributes (abundance, life forms and functional groups) during ordinary and anomalous hydrological conditions. The size of the circles indicates the contribution of the main functional groups. The arrows indicate the mainstem-floodplain interactions (dashed line: lateral exchange disruption; continuous line: permanent lateral exchange). From Devercelli (2010).

dilution effect with high reproduction rates, and its capacity to grow under heterogeneous flow and light climate (Reynolds 1997). Even though they are not commonly dominant in large rivers (Rojo et al. 1994), they also presented high densities at the beginning of an intense flood (Anselmi de Manavella 1986). Another distinct feature, is that specimens of group D (small centrics and *Skeletonema cf. subsalsum*), which are more edible and with lower sedimentation rates than P, are the major components of Bacillariophyceae during La Niña.

The two main axes defined in a PCA based on density (Fig. 6) of functional groups explained 56% of total variance, and describe an environmental gradient determined by the hydrological conditions. The diatom assemblage A-C-P as well as groups J and S_N appeared associated to the ordinary hydrological conditions (neutral period) with a high disperse sample ordination. Groups D, F, X2 and Y were directly related with La Niña drought. MP and X1 showed an intermediate arrangement between La Niña and ordinary periods. Only B was directly related to El Niño flood because the other groups presented significantly lower density at this period.

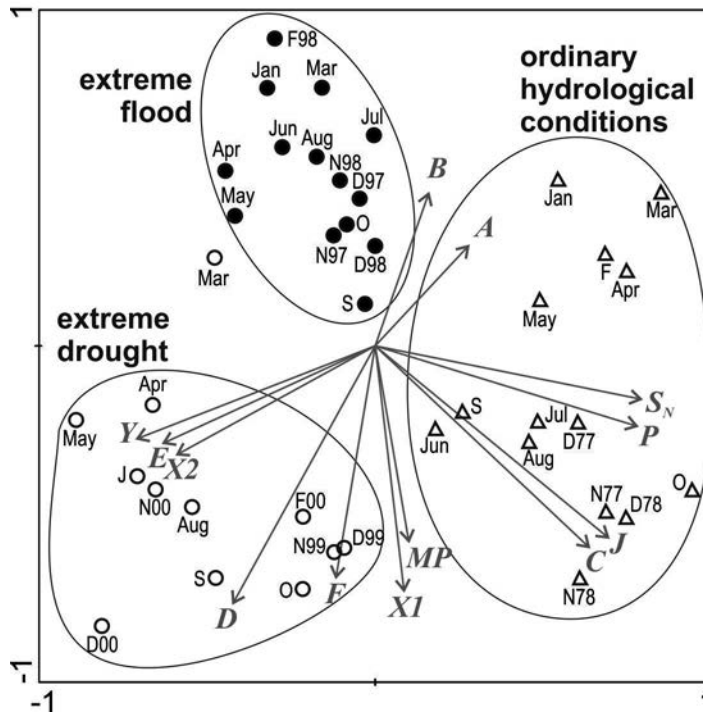


Fig. 6. First and second axes of PCA based on density of functional groups. Functional group vectors are represented with arrows and samples with a symbol (ordinary hydrological conditions, 1977–1978 = Δ ; extreme flood influenced by El Niño event, 1997–1998 = \bullet ; extreme drought influenced by La Niña, 1999–2000 = \circ) and the corresponding month abbreviated with the beginning letters. From Devercelli (2010).

The marked decrease of groups P and C during both anomalous periods, results from different processes. On one hand, sedimentation may be accentuated due to the lower turbulence during drought constituting a negative factor for maintaining in suspension these large-celled diatoms (Hötzel & Croome 1996, O'Farrell et al. 2001). On the other hand, *A. granulata* was probably not able to compensate the losses due to dilution by increasing its growth rate during floods, and may also have been retained by the vegetation and topographic obstacles through water displacement in the plain as it was observed in the Orinoco River (Lewis et al. 2000). However, the decrease of the inoculums from adjacent waterbodies 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. 2007a).

Phytoplankton of the Paraná River floodplain: trends in the lateral dimension

A high diversity of waterbodies with different limnological characteristics are found in the alluvial plain (Table 2). River-floodplain interactions determine gradual changes of the environmental and biotic features in the lateral dimension that depend on the amplitude and intensity of the hydrological phases and the connectivity degree (Neiff 1996, Thomaz et al. 2007). In general, an increase in transparency as well as a diminution in depth, pH, dissolved oxygen, suspended solids, nitrate and phosphate concentrations in the water column is observed from the mainstem towards the more isolated waterbodies of the Paraná River (Unrein 2002, Maine et al. 2004).

The environments of the Paraná floodplain sustain variable biomasses of floating macrophytes. *Eichhornia crassipes* (the water hyacinth) is the most important in terms of coverage, biomass and productivity. It normally forms cohesive floating meadows which may cover 20–100% of the available surface (Neiff & Poi de Neiff 1984). This vegetation produces profound changes in the physical and chemical water (Carignan & Neiff 1992).

A high denitrification rate prevails towards the floodplain due to low levels of dissolved oxygen in both water and sediment, and to high organic matter concentration. The quick uptake of the river DIN by macrophytes, algae and bacteria also explains this abrupt decrease of DIN from the river to the floodplain (Carignan & Neiff 1992, Unrein 2010) as in other large river systems (Hamilton & Lewis 1987, Forsberg et al. 1988, Engle & Melack 1993). As regards phosphorus, this element is bounded to sediments, suspended solids and iron, and a high percentage of retention was also observed in macrophytes roots, especially in *Eichhornia crassipes* (Poi de Neiff et al. 1994, Maine et al. 2004). Although higher or similar SRP concentration was found between the river and the floodplain in the Middle and Lower Paraná, a consistent increase of this nutrient towards the floodplain was reported in the bottom (Pedrozo et al. 1992, Bonetto et al. 1994, Villar et al. 1998). It may be rapidly released and transformed into bioavailable orthophosphate when it is subject to the acidic conditions or low dissolved oxygen concentrations prevailing in the floodplain (Pedrozo et al. 1992, Villar et al. 1998).

Phytoplankton concentration (density and biomass) also increase with the decreasing connectivity to the mainstem and the increasing water residence time (e.g. El Puente → San Nicolás lakes; Table 2). Izaguirre et al. (2001) found a clear segregation of the most abundant algae populations from the river towards the floodplain. The heterogeneity of the floodplain waterbodies determines a wide refuge for fluvial algal storage as they offer better environmental conditions for algal development than the turbid and turbulent mainstem. *Aulacoseira granulata* and other centric diatoms decreased towards the lenitic systems (Izaguirre et al. 2001), but mainly pennate diatoms, Chlorophyceae, Cryptophyceae and Euglenophyceae could be found during isolation. The main functional groups are X1, Y, J, W1, W2 and D. During floods, taxonomic and functional richness is reduced and resembles the mainstem potamoplankton (P and C, and lower contributions of X1 and J) due to the homogenization effect of floods (Thomaz et al. 2007).

The daily rate of change in alluvial plain environments is higher during connection periods (with a strong increase at the beginning of the pulse: maximum 0.33 day^{-1}) than during

Table 2. Mean values of environmental variables and phytoplankton attributes in the Paraná River floodplain lakes. H: species diversity; Rich.: richness; Ec: *Eichhornia crassipes*; Schi: *Schoenoplectus californicus*; Az: *Azolla filiculoides*; Le: *Lemma minima*.

Site-coordinates/ period	Z (m)	Temp (°C)	Secchi (cm)	pH	DO (mg L ⁻¹)	Cond (µS cm ⁻¹)	Nitrate (mg L ⁻¹)	SRP (mg L ⁻¹)	Density (ind.ml ⁻¹)	H (bit.ind ⁻¹)	Rich	Vegetation (% main spp.)
LEEVE PONDS												
Catay 27°25'S 58°45'W (a)												
isolation	2.51	28.4	34	7.4	8	75	wd	wd	898	4.1	51	25% <i>Polygonum</i>
connection	3.34	24.2	37	7.1	6	55	wd	wd	310	3.2	75	sp.
Turbia 27°25'S 58°45'W (a)												
isolation	0.57	29	7	7.6	6	118	wd	wd	660	3.1	69	Without vegetation
connection	2.14	23	47	7.1	5	112	wd	wd	382	3.1	62	90%
Bañado Chouí 27°30'S 58°55'W (b)												
isolation	0.7	24.9	0.29	6.2	1.6	95	wd	wd	3137	2.3	88	<i>Panicum grumosum</i>
connection	2.2	24.8	0.26	7	5.1	85	wd	wd	357	3.5	22	40–50%
Perdida 27°30'S 58°55'W (b)												
isolation	3.06	24.5	0.35	6.8	5.7	65	wd	wd	149	3	11	<i>Polygonum acuminatum</i>
connection	5.45	23.9	0.23	7.2	8.2	80	wd	wd	76	2.2	12	
OXBOW LAKES												
El Puente Sur 27°27'S 68°51'W (c)												
isolation	1.54	22.13	26.0	6.2	5.57	153	0.014	0.045	2350	3.22	43	30–80%Ec
connection	2.3	24.58	26.5	6.8	0.65	244	0	0.426	1217	4.32	70	
El Puente Norte 27°27'S 68°51'W (c)												
isolation	1.87	22.4	59.4	6.1	3.29	151	0.002	0.037	3343	3.91	44	45–95%Ec
connection	2.36	24.4	27	6.6	0.36	250	0	0.449	1251	3.54	44	
San Nicolás 27°27'S 68°51'W (c)												
isolation	1.1	23.1	35.6	6.1	3.59	195	0.001	0.034	4571	3.82	59	50–95%Ec
connection	1.77	23.7	24.8	6.2	0.41	294	0.002	0.593	2755	3.22	42	
Los Matadores 31°41'S 60°42'W (d)												
isolation	1.6	20.8	20	7.9	9.62	wd	0.13	0.06	2890	3.4	73	
connection	3.00	17.5	29	6.9	7.88	wd	0.4	0.15	603	3.3	80	

Table 2. cont.

Site-coordinates/ period	Z (m)	Temp (°C)	Secchi (cm)	pH	DO (mg L ⁻¹)	Cond (µS cm ⁻¹)	Nitrate (mg L ⁻¹)	SRP (mg L ⁻¹)	Density (ind.ml ⁻¹)	H (bit.ind ⁻¹)	Rich	Vegetation (% main spp.)
El Niño period	2.86	22.2	54	7.2	5.6	88	2.3	0.1	429	3.59	118	50-0% <i>Ec</i>
<i>La Niña</i> period	1.89	20.8	76	7.2	6.2	206	2.2	0.08	4199	3.69	101	30-50% <i>Ec</i>
El Tigre (e)												
isolation	1.22	22.5	0.53	7	6.73	201	0.02	0.064	8032	3.60	117	20-30% <i>Ec</i>
connection	2.44	13.38	1.08	6.8	7.23	171	0.12	0.270	2213	3.07	78	
El Niño period	2.2	21.8	74	7.2	6.41	107	2.32	0.188	548	3.36	103	95-20% <i>Ec</i>
<i>La Niña</i> period	0.57	24.6	32	6.9	3.12	271	2.2	0.118	1294	4.05	42	90-100% <i>Ec</i>
Reserve Otamendi 34° 10' S 58° 48' W (f)												<i>Sch-Az-Le</i>
Relictual oxbow lake 1	wd	13.8	wd	6.5	0.05	2049	0.341	wd	~50000	wd	25	100%
Relictual oxbow lake 2	wd	14.5	wd	6.5	0.02	3012	0.355	wd	~30000	wd	30	100%
Relictual oxbow lake 3	wd	14.6	wd	6.3	0.2	1837	0.423	wd	~10000	wd	40	100%
Shallow lake: littoral	wd	20.7	wd	6.9	4.9	1845	0.053	wd	~32000	wd	45	50%
pelagial	wd	21.2	wd	7.6	7.3	1327	0.074	wd	~28000	wd	30	10%
Small pond	wd	16.2	wd	6.3	1.5	3527	0.093	wd	428432	wd	30	

References: a) Zalocar de Domitrovic 1990. b) Zalocar de Domitrovic 1992. c) Zalocar de Domitrovic 2003. d) García de Emiliani 1997, unpublished. e) García de Emiliani 1993, unpublished. f) Izaguirre et al. 2004.

isolation (lower than 0.1 day^{-1}) (García de Emiliani 1997, Zalocar de Domitrovic 2003), which suggests a great environmental variability (Reynolds 1992) and a higher velocity of biogeochemical processes (Esteves 1988).

The lotic waterbodies

In addition to the connectivity degree with the mainstem, the phytoplankton dynamics of the lotic waterbodies of the Paraná River floodplain changes in relation to its size. Rivers of different order of magnitude, classified according to their mean water discharge in medium- (Colastiné: $1840 \text{ m}^3 \text{ s}^{-1}$ and San Javier: $595 \text{ m}^3 \text{ s}^{-1}$) and small-sized rivers (Conchillas: $80 \text{ m}^3 \text{ s}^{-1}$, Chipá: $53 \text{ m}^3 \text{ s}^{-1}$, Colastinecito: $30 \text{ m}^3 \text{ s}^{-1}$ and Mendieta: $20 \text{ m}^3 \text{ s}^{-1}$) were studied at the Middle stretch during 1984–1985 in comparison with the large-sized mainstem ($16000 \text{ m}^3 \text{ s}^{-1}$).

The increasing species richness from the mainstem towards smaller rivers is mainly due to the increasing number of sporadic species. Density varied more in the small- and medium size anabranches ($186\text{--}2992 \text{ ind. ml}^{-1}$ and $306\text{--}3219 \text{ ind. ml}^{-1}$, respectively) than in the mainstem ($252\text{--}1663 \text{ ind. ml}^{-1}$). Algal density was always higher during periods of low waters, but especially in the rivers less connected with the mainstem (Chipá, Conchillas, Mendieta and San Javier). The side channels, with lower dilution power and less connected with the mainstem can recruit algae from lakes and ponds with higher biomass. The higher exchange of organisms occurs during the flood pulse, as well as during small water level fluctuations (Junk et al. 1989). Mean density in side channels is inversely related to the connectivity degree with the mainstem as they offer better conditions for algal growth. The increasing $z_{\text{eu}}/z_{\text{mix}}$ relationship as depth decreases is the most favorable environmental change for algal growth, particularly in low waters, when the water residence time is higher.

The similar phytoplankton composition observed in the different floodplain rivers is due to their high connectivity. Most abundant and typically fluvial species are Bacillariophyceae, Cryptomonadales and Chlorococcales. Bacillariophyceae density varied in a wider range in small ($44\text{--}2431 \text{ ind. ml}^{-1}$) and medium ($37\text{--}2726 \text{ ind. ml}^{-1}$) secondary channels as compared with the mainstem ($170\text{--}1433 \text{ ind. ml}^{-1}$). During the low-water phase, *Aulacoseira granulata* dominated with mean percentages increasing towards the mainstem (small-size rivers: 53%; medium-size rivers: 55%; the mainstem: 62%). Its contribution decreased strongly during high waters in the side-channels (32 and 36% in medium and small, respectively), whereas it remained high in the mainstem (55%). Cryptophyceae was ubiquitous with higher contributions in floodplain (20%) than in the mainstem (10%), and with increasing densities during the high water phase when they could become dominant during the initial stages of the main flood pulse. *Cryptomonas erosa* and *C. brasiliensis* were mainly responsible for the high water peaks, whereas *Plagioselmis nannoplanctica* increased its participation during low waters. Cyanobacteria, mainly represented by *Raphidiopsis mediterranea* and *Dolichospermum spiroides*, registered the highest densities during the low-water phase.

The lenitic waterbodies

A wide variety of lenitic waterbodies are found in the Paraná floodplain as regards limnological and physical features (Table 2). Floods are the most important disturbances for phytoplankton. The intensity and characteristics of the impact may be extremely variable as a result of the interaction between river waters and different local environmental conditions such as the lake topographic position, type of connection with the river (García de Emiliani 1997), lake morphometry, water residence time, chemistry, macrophytes coverage and biomass (Zalocar de Domitrovic 1993, 2003, O'Farrell et al. 2003, Izaguirre et al. 2001, 2004) and biological interactions (Sinistro et al. 2007, Sinistro 2010).

Density, biomass, diversity and specific richness of phytoplankton are higher during isolation when high water residence time represents more time for algae reproduction. On the other hand, the intrusion of river waters represents a disturbance for lenitic algal population during connection periods added to the river water dilution effect and changes in waterbodies limnological conditions.

During the flooding, the river 'sows' the floodplain with nutrient and vegetative and reproductive algal cells that may develop when appropriate conditions occur, contributing to biodiversity conservation. The concept of 'ecological memory' (sensu Padisák 1992), applied to fluvial phytoplankton (Rojo et al. 1994), indicates that river is receptor and distributor of such species memory when interacting with the floodplain. On the contrary, the floodplain contributes with more abundant algal populations to the river, acting as storage zone. The gradual increase in algal concentration as water level decreases, and the alternation of dominant taxonomic groups could be interpreted as a 'gradual hydroclimatic change' conducted by internal processes (Huszar & Reynolds 1997), analogous to the 'gradual climatic change' proposed by Wilson (1994).

In the El Puente and San Nicolás lakes, located at the beginning of the Middle Stretch, Chlorophyceae show high density in both hydrological phases. The predominance corresponds to functional groups X2 (*Chlamydomonas leptobasis*, *Ch. microspheara*, *Plagioselmis nannoplantica*), X1 (*Nephrochlamys subsolitaria*, *Monoraphidium contortum*, *Schroederia antillarum*, *Choricystis cylindracea*, *Chlorella vulgaris*) and Y (*Cryptomonas marssonii*, *C. ovata*). These species, due to their small size, are not dominant in biomass. Only exceptionally both groups (Chlorophyceae and Cryptophyceae) can reach an important percentage of biomass when, in addition to their high density, they are associated to other large species, such as *Pyrobotrys squarrosa* (G), during the connection period, or *Cryptomonas rostratiformis* (Y), during the isolation period.

In Los Matadores Lake, directly connected to a secondary channel, phytoplankton composition is similar to that of the river, but density is approximately three times higher. In general, Cryptophyceae dominate in high waters and Bacillariophyceae (mainly centric forms of *Aulacoseira granulata*, *A. distans* and *Cyclotella meneghiniana*) dominate in low waters coinciding with high temperatures.

In an isolated lake, El Tigre, phytoplankton density shows marked variations between the connection and isolation periods. Chlorophyceae dominate the phytoplankton and is replaced by Cryptophyceae during connection periods. In this situation, phytoplankton density and composition are similar to those of the river. Sporadic high densities of Chrysophyceae, Euglenophyceae and Dinophyceae, related to variations in the hydrometric level and nutrient

availability, alternate. The former is associated to an activation of statospores, probably distributed by the river (i.e. *Synura echinulata*, *Mallomonas* spp. and *M. akrokomos*). In contrast, high biovolume of S-strategists and nitrogen fixing Cyanobacteria (*Dolichospermum planctonicum*) predominate after a prolonged isolation.

As regards Cyanobacteria, blooms of Chroococcales and Nostocales species are observed, the latter during nitrogen limitation periods. Interestingly, nostocaleans nitrogen-fixing blooms are not frequent at the beginning of the Middle Stretch and at the Lower Stretch even though N-limitation is likely to occur in the floodplain (Carignan & Neiff 1992, Pedrozo et al. 1992). Unrein et al. (2010) found that low pH values, frequently found in the floodplain may limit the development of these algae.

In general, there is a predominance of nanoplanktic organisms (2–20 μm), C-strategists, mainly Chlorophyceae and Cryptophyceae. They fluctuate through time and alternate with larger R- and S-strategists (20–100 μm) that increase during isolation with a rapid and ‘explosive’ growth (Chrysophyceae), or slow and gradual growth (e.g. dinoflagellates, Euglenophyceae or Cyanobacteria) during decreasing water phases. During the isolation phases, ‘microsuccessions’ are registered, which start with C-strategists dominance and pulses of S-strategists, with species belonging to different taxonomic groups, controlled by their particular nutritional requirements. These successional processes are interrupted and reverted by the flooding or even by pulses of low magnitude. The intrusion of river waters is perceived as an intense disturbance by the phytoplankton, and allowing the input of fluvial species such as Cryptophyceae and Bacillariophyceae (García de Emiliani 1993).

Phytoplanktons from the vegetated ponds are commonly dominated by Cryptophyceae, Euglenophyceae, Chlorophyceae and Chrysophyceae in some cases, while diatom species are mainly tychoplanktic or potamoplanktic during river floods (Zalocar de Domitrovic 1990, 1992, 1993, Unrein 2002). Euglenoids (W1 and W2) reach important biomass percentages, particularly in environments rich in organic matter and in those isolated and macrophytes covered such as the San Nicolás Lake (Table 2).

The abundant floating macrophytes of three relictual oxbow lakes (ROLs) located at the Otamendi Natural Reserve of the Lower Paraná Stretch (O’Farrell et al. 2003, Izaguirre et al. 2004), generated a severe reduction in light penetration, almost anoxic conditions and high nitrate and phosphate concentrations. Such characteristics determined a particular algal flora constituted by Cyanobacteria (groups S, Z, L_o) and several diatoms (mainly *Achnanthes hungarica*) responsible of more than 90% of total density. These species are probably mixotrophic regarding their capacity to grow in extremely poor light intensities and tolerate very low oxygen contents. Total algal density ranged between 797 and 45233 ind. ml⁻¹ in the ROLs and algal biomass varied from 1.3 to 18.5 mm³ l⁻¹ (O’Farrell et al. 2003). On the other hand, the existence of areas free of floating vegetation in a near shallow lake allows the dominance of euplanktic taxa in the open waters with many small green algae, accompanied by flagellates belonging to Cryptophyceae, Euglenophyceae and Dinophyceae (Izaguirre et al. 2004) (Fig. 7). In this sense, the algal assemblages strongly change in the lateral gradient with differences among the permanently vegetated ROLs and the larger shallow lake temporally covered by macrophytes. Poor light penetration triggered by macrophytes cover constituted the leading factors in the selection of algal species in this wetland. Changes in algal density and biomass were more pronounced in the shallow lake than in the ROLs. An alternative dominance of *Cryptomonas* spp., *Peridinium*

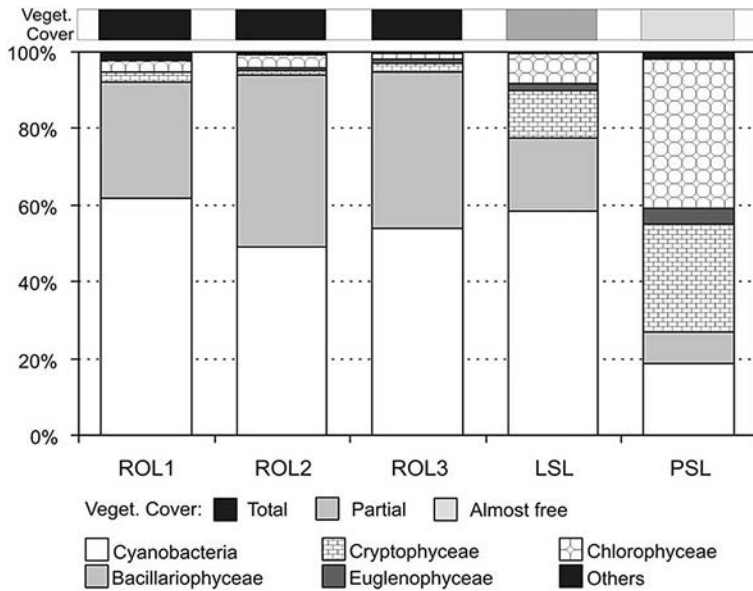


Fig. 7. Mean percentages of the algal classes in relation to vegetation cover at the relictual oxbow lakes (ROL) and the shallow lake (LSL: littoral zone; PSL: pelagial zone) located at the Lower Paraná Stretch (Otamendi Natural Reserve). From Izaguirre et al. (2004).

spp., *Euglena* spp., *Monoraphidium* spp., Oscillatoriales and Chroococcales occurred in the shallow lake, with a consequent replacement of the groups Y, Lo, W1, X1, S2, K and F. Variation in the macrophytic cover of the small pond accounted for the fluctuations in its algal composition. When the cover was complete, the assemblages resembled those of the ROLs, whereas when its surface was free of plants, they were more similar to those of the shallow lake (O'Farrell et al. 2003). The differences in light conditions determine a morphology response at the community level (O'Farrell et al. 2007). The strong light constrained environments were characterized by high surface:volume ratio ($S/V > 2$) organisms, non-flagellated or small proportion of unicellular flagellates. This pattern was different to that registered in well illuminated sites where longer and larger organisms, with a smaller S/V and frequently flagellated predominated (O'Farrell 2007).

Phytoplankton trophic interactions were poorly explored in the Paraná floodplain. An experimental study using mesocosms in the main shallow lake analyzed the impact of zooplankton on phytoplankton and the microbial assemblages (Sinistro et al. 2006). A significant zooplankton grazing on the nanophytoplankton fraction (3–30 μm) was observed, whereas large algae (filamentous Cyanobacteria, colonial Chlorophytes and large diatoms) increased, suggesting that they were not actively grazed by zooplankton. However, this algae fraction decreased at the end of the experience when the abundance of large herbivores increased. A trophic cascade effect on the lower levels of the microbial community composed by copepods-microzooplankton-heterotrophic nanoflagellates-picoplankton was also indicated (Sinistro et al. 2006).

In other field experiments, a bottom-up effect due to nutrient release from sediments (mainly total phosphorus) was observed on phytoplankton, whereas experiments with the presence of omnivorous-planktivorous fish (*Jenynsia* sp.) exerted a strong predation pressure on zooplankton (top-down) evidenced by a marked decrease in mesozooplankton abundance (Sinistro 2010). In this sense, this author hypothesized that phytoplankton regulation by zooplankton might be weaker in warm temperate systems than in temperate ones as it was proposed by von Rückert & Giani (2008).

Extreme hydrological phases

The influence of extreme hydrological phases on phytoplankton structure and density is pronounced in the more isolated waterbodies, many only receiving lotic influence during extreme floods. During one of these phases induced by El Niño event, the phytoplankton density of the Correntoso River located at the Middle Paraná Stretch, decreased four times in comparison with the mainstem and, in particular, Bacillariophyceae decreased almost one order of magnitude in relation to the ordinary period. In the connected Los Matadores Lake, density was also notably reduced in relation to ordinary periods, and was similar to those of the Correntoso River and the mainstem. In the more isolated El Tigre Lake, mean density decreased one order of magnitude in relation to the ordinary period. The dominant groups at both lakes are replaced by Cryptophyceae (García de Emiliani, unpubl. data).

The highest density in Los Matadores Lake was registered during the extreme drought, La Niña, whereas density values were intermediate at El Tigre Lake with dominance of Chlorophyceae, and sub-dominance of Cryptophyceae. In this period, the most drastic changes in phytoplankton were produced due to the scarce water level of this environment, silted by vegetation. High biovolume (*S*-strategists) and nitrogen fixing Cyanobacteria (*Dolichospermum planctonicum*) predominate in this isolated lake, if the isolation time is enough to reach high succession stages.

The extreme floods affect community density and structure. The permanence of species representative of ordinary hydrological periods and the rapid recovery of the identity of these environments when water level decreases, suggest a temporary alteration of the community that cannot be interpreted as a severe disturbance (Sparks et al. 1990). In contrast, in environments that are generally isolated from the mainstem, the flooding is perceived as an intense disturbance due to the profound changes produced by El Niño, being more severe during La Niña.

Conclusion

About 800 taxa were observed in the phytoplankton of the Paraná sub-basin over forty years of study. The contribution of the number of species is summarized in Figure 8. The largest contribution to species richness corresponds to Chlorococcales. This group is followed in importance by Bacillariophyceae in the mainstem and by Euglenophyceae in the floodplain.

Phytoplankton dynamics is driven by the hydrosedimentological regime. Regular variations in the hydrological phases and shorter permanent fluctuations are essential for

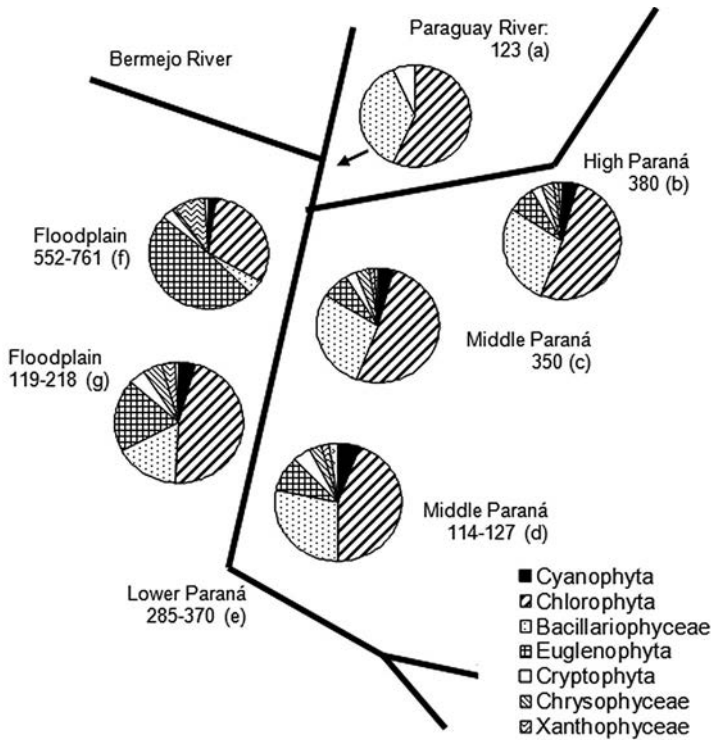


Fig. 8. Number of taxa and their relative contribution (%) to each taxonomical group at the Paraná River mainstem and floodplain, and at Paraguay River lower stretch. From Zalocar de Domitrovic (2005). References: (a): Zalocar de Domitrovic 2002; unpubl. data; (b-c): Zalocar de Domitrovic et al. 2007b, unpubl. data, (d): García de Emiliani 1997, García de Emiliani & Devercelli 2003; (e): O'Farrell et al. 1996, 1998; (f): Zalocar de Domitrovic 2003; (g) García de Emiliani 1993, 1997.

phytoplankton maintenance, since they allow the lateral exchange with floodplain waterbodies with higher algal accumulation. The numerous and diverse waterbodies located in the lateral extensive floodplain play a more important role for the exchange of organisms than the longitudinal dimension. Even though, a discontinuity such as the imposed by the Yacyretá Reservoir emplacement, may significantly affect the phytoplankton structure.

During isolation, floodplain waterbodies show clear differences with the mainstem due to their higher number of species, diversity, density and biovolume, and the occurrence of autogenic processes. The connection period produces a relative homogeneity between the mainstem and the floodplain, which depends on the extent and duration of the flood.

Figure 5 summarises the features of the main environmental conditions and phytoplankton attributes during the different hydrological events. Anomalous hydrological periods such as an extreme and prolonged drought or a flood provoke changes in the structure and abundance of the potamoplankton. These changes during extreme flooding or isolation are mainly attributed to the loss of a regular exchange of organisms with floodplain areas that do not act as exchange zones of organisms any more. Extreme hydrological phases constitute a

disturbance for phytoplankton populations (Sparks et al. 1990, Lake 2003). C-strategists and species adapted to live in heterogeneous conditions (C-R-strategists) are favoured against the typical R-strategists that predominate during ordinary hydrological conditions. The typical P and C groups of the Paraná River shift to the small and high-metabolic X2 and Y.

It is very important to preserve the connectivity among waterbodies and to avoid engineering constructions that impede the natural flowing of running waters. River regulation is perceived as a disruption of the natural fluvial dynamic that maintains potamoplanktic diversity and environmental health of large rivers (Ward et al. 1999).

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