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Phytoplankton of the Chaco-Pampean Plain

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With 3 figures and 2 tables

Abstract: This article summarizes the characteristics of phytoplankton of the Chaco-Pampean Plain between the Pilcomayo River (25°15'S; 57°45'W) and the Lower Salado River (31°39'S; 60°45'W) towards the Paraguay-Paraná system. This subtropical area has a climate gradient from east (wet) to west (arid). Rivers and streams have a seasonal regime, with floods in autumn and dry periods at the end of winter. These hydrological fluctuations appear to be the driving forces of the phytoplankton community. During low waters (flow reduction and increase in salinity), diversity is reduced and density of euryhaline species is increased. The highest algal development in this area was observed during the extraordinary low water period of La Niña. In occasions of environmental stability and high temperatures, water blooms of *Anabaenopsis arnoldii*, *A. nadsonii* and *Nodularia harveyana* have been recorded.

The lenitic environments of the western region (arid) show marked fluctuations in extension and depth and may dry during periods of scarce precipitations. Phytoplankton density is low and represented by small Chlorococcales and Euglenophyceae. Water blooms of *Dolichospermum* spp. and *Cylindrospermopsis raciborskii* are frequent. Shallow lakes and wetlands of the eastern region (wet), which have presence of macrophytes and high organic matter, are dominated by Cryptophyceae, Chlorococcales and a wide variety of species of Euglenophyceae and diatoms. The Ramsar Site called 'Humedales Chaco' has the greatest diversity of species in this region.

Keywords: Chaco, phytoplankton, hydrological fluctuations, floodplain

Introduction

The phytoplankton studies of the Chaco region include studies of the aquatic environments of the northeast of the Chaco-Pampean plain (Fig. 1). This plain constitutes part of the region called Great Chaco, which comprises Argentina (50%), Bolivia (25%), Paraguay (20%) and Brazil (5%), and is characterised by forests, savannas, and extensive swamps, which pro-

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Fig. 1. Geographical location of the study area in Chaco Region. **Lotic environments** – 1: Negro Stream, 2: He He Stream, 3: Inglés Stream, 4: Monte Lindo Stream, 5: Pilagá Stream, 6: San Hilario Stream, 7: Salado Stream, 8: Canguí Chico Stream, 9: Oro River, 10: Quiá Stream, 11: del Tres Stream, 12: Guaycurú River, 13: Tragadero River, 14: Salado North River, 15: Negro River, 16: Palometa Stream, 17: Saladito Stream, 18: Tapenagá River, 19: Amores Stream, 20: Saladillo Stream, 21: Salado River. **Lenitic environments** – A, B, C: Reservoirs, D: Cocherek marsh, E: El Sábalo marsh, F: La Rica marsh, G: El Lobo marsh, H: El Morocho marsh, I: Patí marsh, J: Cuatro Diablos marsh, K: Barranqueras lake, L: El Puente Sur lake, M: El Puente Norte lake, N: San Nicolás lake.

vide a marked climatic and biogeographic identity (Iriondo & Paira 2007). The region has a subtropical climate, with an east-to-west climatic gradient. In the east, precipitations exceed 1200 mm annually, decreasing towards the west to values lower than 500 mm annually in the driest area (Bruniard 1981). The number of aquatic environments decreases in the same direction and their hydric balance is regulated by the rainy seasons (Patiño & Orfeo 1986).

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The Chaco plain has little topographic variation (slope ranging from 0.30 to 0.40 m/ 1000 m). Three rivers flow across the region: Juramento-Salado, Bermejo and Pilcomayo, all of which have their high basins in the Andean Mountains. When going into the Chaco plain, they form alluvial fans through obturations and migrations of their channels. There are several fluvial basins in the eastern region of these fans (numbered from 1 to 20 in Fig. 1). These environments, with definite channels, are connected to the Bermejo and Pilcomayo rivers when they overflow during floods. In this way, there is overlapping in areas of contact between hydric subsystems, which connect through wetlands or transfluences while they come close to the Paraguay or Paraná rivers. Water infiltration in this sector is almost null and the low slope prevents the exit of the hydric excess; thus, the formation of permanent and temporary water bodies, covered by marshy and floating vegetation, is favoured. This area mixes up with the alluvial plain of the Paraguay and Paraná rivers, called Humedales Chaco (Ramsar site), which joins the Jaaukanigás Ramsar site towards the south. Both sites constitute a continuous wetland corridor (Paraguay-Paraná fluvial corridor) of about 450 km (Neiff et al. 2005, Oakley et al. 2005).

The Juramento-Salado, Bermejo and Pilcomayo rivers have Andean origin. The last two are tributaries of the Paraguay, whereas the Salado River is a tributary of the Middle Paraná River (Fig. 1). The Pilcomayo River forms the border between Argentina and Paraguay. In the low-water period (March-November), the river diminishes its flow and forms extensive wetlands. It is currently in process of avulsion: the lower section of the channel gradually clogs with sand and silt, and the water overflows into the plain (Iriondo & Paira 2007). In high waters (December–February), overflow occurs and the water returns to a defined channel, until it flows into the Paraguay River. Nevertheless, its influence on the hydrology of the Paraguay River is negligible (Bucher et al. 1993).

In this article, we analyse the phytoplankton of the lower stretch of the Salado River and a group of 20 autochthonous fluvial courses, as well as 14 lenitic environments of the western and eastern Chaco region during contrasting hydrological conditions. The influence exerted by the Bermejo on the Paraguay River (Zalocar de Domitrovic et al., 2014) and Paraná River (Devercelli et al., 2014) deserves a separate study. The Pilcomayo River is not included because phytoplankton studies are still lacking.

Lotic environments

Salado River (Lower stretch). The Lower Salado River (Fig. 1, Site 21) comprises a drainage area of 29700 km² with a mean water discharge of 146 m³ s⁻¹; it has a meandering channel with scarce gradient and a current velocity ranging between 0.1 and 0.3 m s⁻¹ (Devercelli 2008). This stretch receives the urban and rural runoff waters as well as the rainfall excess from the surrounding settlements. The river has high concentration of dissolved (TDS ~ 2 g L⁻¹) and suspended (TSS ~ 0.16 g L⁻¹) solids, with predominance of the finest fraction (< 1 μ m), deriv-

Environ-	Width	Z	Temp	Sd	pН	DO	Cond	Nitrate	PO_4	Ammo-
ments	(m)	(m)	(°C)	(m)		(mg L ⁻¹)	(µS cm ⁻¹)	(µg L ⁻¹)	(µg L ⁻¹)	$(\mu g L^{-1})$
1. Negro	Stream	. /	. /	~ /		(8 -)	(100 000)	(10-)	(18-)	(10-)
LW	22	1.5	19	1.7	7	0.5	245	20	10	60
HW	30	2.5	22	0.46	6.5	0.3	240	11.5	140	410
2. He-He	Stream									
LW	5	0.5	26.2	0.5	8.5	5.2	11000	98	190	160
HW	20	2.5	21.5	wd	6.7	3.2	350	43	125	365
3. Inglés S	Stream									
LW	7	1.0	25.2	0.04	8	4.7	1050	464	170	200
HW	50	wd.	22.8	wd	7.1	6.3	420	12	135	425
4. Monte	Lindo Str	eam								
LW	23	2.2	27.5	wd	8.4	wd	3200	1200	160	80
HW	60	4.0	22	0.04	7.9	wd	460	131.3	280	285
5. Pilagá S	Stream									
LW	8	0.8	25.6	0.08	7.2	6.2	120	344	40	315
HW	50	5.0	21.7	0.07	6.9	8.3	210	102.3	310	100
6. San Hil	lario Strea	am								
LW	wd	1.7	25	wd	7.8	6.8	95	424	50	85
HW	20	5.5	22	wd	7.5	wd	82	75	20	75
7. Salado	Stream									
LW	14	2.3	wd	0.12	8	5.6	1150	464	305	200
HW	23	2.3	25.5	wd	7.8	wd	350	35	230	262
8. Canguí	Chico St	ream								
LW	1	0.2	24.2	0.31	7.3	0.8	93	125	670	200
HW	8	0.5	18.7	wd	7.6	3	220	62	720	355
9. Oro Riv	ver									
LW	10	1	25	0.34	7	8.5	1650	180	400	100
HW	35	4	24	wd	7.8	4.5	285	92.5	960	135
10. Quiá S	Stream									
LW	5	2	wd	wd	wd	wd	wd	wd	wd	wd
HW	11	wd	24.8	0.26	7.8	5	510	wd	wd	wd
11. Del Ti	res Strean	n								
LW	24	0.8	23.9	0.07	7	0.44	480	wd	wd	wd
HW	wd	1.1	wd	0.44	7.3	0.5	wd	wd	wd	wd
12. Guayo	curú Rive	r								
LW	8	2.8	25.3	wd	8.4	4.9	450	218	900	425
HW	18	3	23.2	wd	7.8	8.3	355	35	130	270
13. Traga	dero Rive	r								
LW	14	1.2	25	0.11	7.4	5.4	2650	485	330	500
HW	40	4.5	24	wd	6.7	7.6	95	30	60	200

Table 1. Summary of environmental variables of lotic environments of Chaco Region. wd: without data.

Table 1. co	ont.									
Environ- ments	Width	Ζ	Temp	Sd	pН	DO	Cond	Nitrate	PO_4	Ammo- nium
	(m)	(m)	(°C)	(m)		(mg L ⁻¹)	(µS cm ⁻¹)	(µg L ⁻¹)	$(\mu g L^{-1})$	(µg L-1)
14. Salado	North R	liver								
LW	40	0.9	25	0.14	7	5.1	6500	212	1405	300
HW	52	3	19.6	23.4	7.6	6.16	140	51	164	164
15. Negro	River									
LW	wd	wd	23	0.34	8.7	wd	1186	79	538	wd
HW	wd	wd	21.3	0.18	7.6	wd	442	68	527	wd
16. Palom	eta Strea	m								
LW	21	0.7	26	0.07	7.2	5.6	190	244	290	250
HW	36	3.5	wd	wd	7	wd	90	41	210	180
17. Saladi	to Strean	1								
LW	14	1.2	22	0.13	8.9	6.3	13000	130	145	80
HW	27	3	wd	wd	6.9	wd	160	21	75	165
18. Tapen River	agá									
LW	12	0.8	26	0.07	8	8.1	1700	520	160	490
HW	30	4.5	23	0.2	6.8	wd	90	71.2	340	190
19. Amore	es Stream	1								
LW	20	3	26	0.05	7.5	8.1	1400	188	240	540
HW	37	5	23	0.08	6.7	wd	180	92	20	215
20. Saladi	llo Stream	m								
LW	wd	wd	17.3	0.1	7.7	8.9	2530	1.79	0.8	24
HW	wd	wd	25.8	0.13	7.1	5.2	502	1.95	1.38	12
21. Salado	River									
extreme drought	wd	2.86	28.9	0.28	8.2	11.1	6250	323	100	64
neutral period	wd	4.94	20.9	0.18	7.9	8.5	2881	55	47	120

Phytoplankton of the Chaco-Pampean Plain 85

ing in permanent turbid waters. The high salinity (> 3 g L⁻¹), conductivity (~ 3000 μ S cm⁻¹) and slightly alkaline waters (pH ~ 8) are caused by the input of chlorinated ground waters and the washout of saline soils (Maglianesi & Depetris 1970).

The phytoplankton density ranges are typical of eutrophic systems, favoured by the high nutrient availabilities and organic matter concentrations (García de Emiliani & Devercelli 2004, Devercelli 2008). During the 2004–2005 period, the mean density (51832 ind ml⁻¹), biovolume (13.63 mm³ L⁻¹) and chlorophyll-*a* concentrations (39.3 mg m⁻³) were high (Table 1), and the hydrological fluctuations appeared to be the driving forces of phytoplankton dynamics. Low-water periods favoured algal growth due to the higher water residence time, lower flushing and decreased dilution. In contrast, the lowest algal development coincided with high waters (inverse correlation with water level: $r_s = -0.41$; p < 0.01). Moreover, abundance and biovolume were inversely related to water velocity ($r_s = -0.43$; p < 0.01) and

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directly related to transparency ($r_s = 0.50$; p < 0.01). Regarding nutrients, only biovolume was weakly related to phosphate concentrations ($r_s = -0.24$; p < 0.05).

The diatoms *Entomoneis paludosa*, *Chaetoceros* cf. *whigamii* and *C. muelleri* are characteristic of this river, as they are indicators of high conductivity (Zalocar de Domitrovic & Maidana 1997). Chlorophyceae (chlorococcaleans > volvocaleans), Bacillariophyceae (centric > pennate), Euglenophyceae and Cyanobacteria constitute the bulk of the phytoplankton density and biovolume. The phytoplankton size structure is composed mainly of species with a maximum linear dimension (MLD) smaller than 20 µm (mean values= 35002 ind ml⁻¹ and 4.9 mm³ L⁻¹). Small organisms, such as *Cyclotella meneghiniana*, *Actinocyclus normanii, Nitzschia acicularis* (functional group C, here in after codon are indicated with capital letters), *Entomoneis paludosa*, *Skeletonema* spp. (D), chlorococcalean species (X1), *Pteromonas* sp. and *Carteria* sp. (X2), are dominant. The slow flow and organic enrichment in the river facilitate the thriving of Cyanobacteria (L_o and minor contributions of H1, K and S_N) and large Euglenophyceae (W1 and W2) as regards biovolume. The main functional groups are correlated with physical factors such as water level (X1: $r_s = -0.55$; X2: $r_s = -0.65$; p < 0.01), current velocity (X1 and X2: $r_s = -0.45$; p < 0.01), water temperature and transparency (X1 and X2: $r_s = 0.64$; p < 0.01).

The assemblage formed by C-D diatoms and X1 chlorococcaleans has been repeatedly found in small enriched lowland rivers (Descy 1987, Gosselain et al. 1994, Yang et al. 1997, Leland et al. 2001, Salmaso & Braioni 2007, 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). Groups X1 and X2 comprise opportunistic species of small size and rapid reproduction that can counterbalance the losses caused by the unidirectional flow and the physical restrictions typical of the mainstem (Reynolds & Descy 1996, Chételat et al. 2006). The high surface:volume ratio of *Merismopedia tenuissima* (L_0) has been recognized as a successful strategy for maximizing the harvesting of light in turbid systems (O'Farrell et al. 2007). The remaining groups of Cyanobacteria and Euglenophyceae probably came from floodplain lakes and marshes and encountered favourable growth conditions in the river, namely low water velocities and high trophic status. The participation of these phytoplankton groups is rare in lotic systems of this temperate region and the existing records correspond to low-flow, saline, eutrophic and organically polluted rivers (Loez & Salibián 1990, del Giorgio et al. 1991, Conforti et al. 1995, Bauer et al. 2002, O'Farrell et al. 2002, Mercado 2003).

The highest algal development was observed during the extraordinary low water period known as La Niña (November–December 1999), which coincided with high temperatures (Emiliani & García de Emiliani 2003, Devercelli 2008) (Fig. 2). Unicellular Volvocales (60%, mainly *Pyramimonas minima*, *Nephroselmis minuta* and *Chlamydomonas* spp.), together with a unicellular (non-identified) Chrysophyta, constituted the dominant functional group during this period, (X2) (Fig. 3). The reduction in flow, together with an increase in water transparency, facilitated the appearance of accumulations of algae, such as a *Chlamydomonas* spp., not commonly observed in this environment. Larger Chlorococcales (43%), belonging to groups F (*Oocystis parva*) and J (*Coelastrum* spp.), and euglenoids from the group W1, characteristic of small organically enriched ponds, were important in terms of biovolume (Reynolds et al. 2002). The density of Cyanobacteria was high at the beginning of the low water period (Pre Niña), doubling in one order of magnitude those observed in other studies



Fig. 2. Temporal variations in biovolume of phytoplankton (circles) in the Salado River, in relation to the hydrometric level (line) during the different stages of a period influenced by La Niña (September 1999–February 2001).



Fig. 3. Temporal variations in density and biovolume of the main functional groups in the Salado River during the different phases of the period influenced by La Niña (September 1999–February 2001) and a neutral hydroclimatic period (December 2004–August 2005).

(García de Emiliani & Devercelli 2004). The assemblage was composed of species of groups L_o (*Merismopedia tenuissima*), K (*Aphanocapsa delicatissima*) and S1 (*Limnothrix planctonica*), with different ecophysiological and morphological characteristics. The first two groups are colonies composed of small cells, CS-strategists, sensitive to profound mixing and flow velocity (Reynolds et al. 2002). In contrast, filamentous S1 are adapted to mixing and low light intensity. During this low-water period (La Niña), sporadically occurring species (*Anabaenopsis arnoldii* and *A. nadsonii*) proliferated. The development of Cyanobacterial blooms in this type of rivers would be associated with periods of low flow and high temperatures (Philips et al. 2007), and prolonged periods without rains. This was also observed in December 2007 with a *Microcystis aeruginosa* bloom in the right margin of the Salado River (Devercelli, pers. obs.).

Autochthonous fluvial systems. About 20 small lowland rivers and streams (Fig. 1, Sites 1 to 20) have been studied in the Chaco-Pampean plain (Zalocar de Domitrovic et al. 1986, Devercelli & Peruchet 2008). Most of these streams and rivers are turbid and characterised by high conductivity caused by the phreatic saline input (Table 1). Salinity has large seasonal fluctuations. In high waters, salt concentration does not exceed 0.3 g L⁻¹ (e.g. Guay-curú River), while in low waters, a maximum of 10 g L⁻¹ (e.g. Saladito Stream) was recorded (Lancelle et al. 1986); conductivity reflects such variations, ranging between 82 and 15500 μ S cm⁻¹, respectively. During low waters, the Tragadero, Salado North, and Tapenagá rivers, and Palometa, Saladito, Amores, and Saladillo streams have high concentrations of chlorides, sulfates and sodium, while chlorides and sodium prevail in the He-He Stream in the north. In parallel with a reduction in flow and an increase in salinity, phytoplankton diversity is reduced as the density of euryhaline species is increased (Zalocar de Domitrovic et al. 1986).

In the Salado Norte River (Fig. 1), there is a dominance of *Gymnodinium balticum* and *Protoperidinium achromaticum* (Y), dinoflagellates characteristic of salinised continental waters. In the Tragadero and Tapenagá rivers, and Palometa, Saladito, Amores, and Saladillo streams (Fig. 1), the phytoplankton is composed of *Nitzschia reversa* (D), *Cyclotella meneghiniana* (C), *Surirella striatula*, *S. ovalis*, *S. ovata* (TD) and *Campylodiscus clypeus* (MP). Higher chlorophyll-*a* concentrations have been found in the Saladillo Stream during low waters as compared with high waters (mean = 71 vs. 25.1 mg m⁻³), with a negative correlation with the hydrometric level (p < 0.01; r = -0.76), and a positive correlation with conductivity (p < 0.01; r = 0.83) (Devercelli & Peruchet 2008). In the He-He Stream, which has a mean conductivity of 11000 μ S cm⁻¹, the phytoplankton assemblage is composed of *Nitzschia reversa*, *Bacillaria paradoxa* (D), *Entomoneis alata*, *Plagiotropis lepidoptera*, *Surirella striatula* (MP) and *Glenodinium balticum* (Y) (Zalocar de Domitrovic et al. 1986).

In streams north of the Tragadero River (Fig. 1), except the He-He Stream, the water is rich in bicarbonate, sodium and calcium and conductivity does not exceed 2400 μ S cm⁻¹ (e.g. Monte Lindo Stream) in low waters (Lancelle et al. 1986). Among those with conductivities less than 500 μ S cm⁻¹, on the one hand there is a group with dense cover of aquatic macrophytes (between 70 and 100%), such as Negro, Canguí Chico and Del Tres streams, and on the other hand a group with less than 5% vegetation or total lack of vegetation, such as San Hilario and Quiá streams, and Pilagá and Guaycurú rivers. In both cases, similar taxa of Bacillariophyceae, Euglenophyceae and Cryptophyceae or Cyanobacteria predominate. A greater variety of taxa and functional groups of phytoplankton were observed by Zalocar

de Domitrovic et al. (1986) in vegetated streams. This was probably because of the reduction in turbidity and the greater heterogeneity of microhabitats offered by macrophytes. In other environments with moderately low conductivity (e.g. Oro and Tapenagá rivers), these authors observed amphitolerant freshwater species of Chlorophyceae, Bacillariophyceae and Euglenophyceae. Alternation of high and low salinity causes fluctuations in the phytoplankton composition and abundance, and species differ in their tolerance to the current environmental conditions.

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In the Negro and Salado Norte rivers, Bacillariophyceae, Cryptophyceae and Chlorophyceae are regularly observed in a higher frequency. In occasions of environmental stability and high temperatures, water-blooms of *Anabaenopsis circularis* and *Nodularia harveyana* have been recorded in the Salado Norte River and in the Negro River, respectively. Both species are heterocystons (N-fixers), and show no correlation with the concentration of the main macronutrients (Zalocar de Domitrovic, pers. obs.).

The high-water period is characterized by fluvial overflow and the transfluence of basins. A reduction in phytoplankton density (between 15 and 289 ind. ml⁻¹ in the Oro River and the Negro Stream, respectively) and a slight increase in diversity (between 1.9 and 4.3) are observed (Zalocar de Domitrovic et al. 1986). Probably there is incorporation and/or exchange of phytoplankton species. The existence of flooded areas causes water flow retardation, thus increasing the residence time and water transparency, both of which favour algal development.

The highest density has been recorded in vegetated environments (e.g. Negro Stream), where the functional groups S_1 (*Planktolyngbya limnetica*, *P. contorta*), W1 (*Euglena* spp.) and W2 (*Trachelomonas* spp.) predominate (Zalocar de Domitrovic et al. 1986). In non-vegetated streams, the best represented groups are Y (*Cryptomonas erosa*, *C. ovata*, *C. marsonii*, *Chroomonas* sp.), X2 (*Rhodomonas minuta*), X1 (*Monoraphidium contortum*, *M. pusillum*), J (*Scenedesmus* spp.), D (*Ulnaria acus*, *Nitzschia* sp.) and TD (*Surirella* sp., *Pinnularia* sp.).

The effects of flooding on density and diversity of river plankters show variations according to their origin, the sampling sites and the species involved (Hynes 1970). The number of species is high in most water courses, being higher in the Salado Norte River than in the Negro River (Zalocar de Domitrovic et al. 1986). Although both rivers originate in extense flooding areas, the influence area of the Salado Norte River is twice that of the Negro River and shows more frequent overflows and biotic inputs from the basin environments and from surrounding areas. In both rivers, Cryptophyceae (Y), which are flagellate algae that can move in the water column towards favourable conditions of light and/or nutrients (Reynolds 2006), are dominant. The dominance of Cryptophyceae in high waters has been observed in most fluvial courses of this region (García de Emiliani & Anselmi de Manavella 1983, 1989, Zalocar de Domitrovic et al. 1986).

In general, rivers and streams of the Chaco region drain a high concentration of salts towards the Paraguay and Paraná rivers; although these inputs do not reach levels that markedly affect the water quality of the Paraná River, which is the last receptor (see Devercelli et al., 2014). However, the salinity of these autochthonous courses is much higher than that of the affluents of the left margin of the Paraná River for the same latitude (Lancelle et al. 1986).

Lenitic environments

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Western Chaco region. This is an arheic area. The phytoplankton studies in this area have been carried out in a scarce number of isolated water bodies (Fig. 1: Sites A–C), most of which are temporary, constructed as water reservoirs (for agricultural and/or cattle raising use), with scarce depth (maximum 1.20 m) and turbid waters (Secchi disk 10–30 cm), and without vegetation. Conductivity oscillates between 150 and 900 μ S cm⁻¹. These waterbodies show marked fluctuations in extension and depth and may dry totally during periods of scarce precipitations.

Phytoplankton density is low (lower than 200 ind. ml⁻¹) and represented by assemblages of small size algae such as *Chlorella* spp. and *Choricystis* sp. (X1). These algae alternate their dominance with *Euglena oxyuris*, *E. ehrenbergii*, *E. acus*, *Phacus longicauda*, *Ph. tortus*, *Ph. platalea* (W1), *Trachelomonas caudata*, *T. volvocina*, *T. armata*, *Strombomonas fluviatilis*, *S. ovalis*, and *S. treubii* (W2). Water blooms of *Dolichospermum* spp. occur exceptionally. However, there are frequent blooms of *Cylindrospermopsis raciborskii* (Zalocar de Domitrovic, pers. obs.).

Eastern Chaco region. This region is mostly humid and constitutes a large wetland or macrowetland. It includes small rivers and streams (previously described, Fig. 1, Sites 1 to 20), permanent and temporary lenitic environments and sectors of mainland (Neiff & Malvárez 2004).

Marshes. Numerous water bodies are included in an extense depressed surface called Great Subsouthern Lowlands, which extends from the south of the Negro River and drains into the Salado Norte River. Marshes are formed by rainfall (Ginzburg et al. 2005) and overflowing of rivers, and are covered by hydrophytes and helophytes adapted to the alternating conditions of dryness-flooding. Waters are turbid, due to the abundance of suspended solids of small particle size, showing almost null luminic permeability in the periods of great surface retraction. Water temperature is influenced by vegetation, which can sometimes cause stratification. pH fluctuates around the neutral point, with a tendency to the acid range. Dissolved oxygen is moderate or scarce, thus causing frequent situations of anoxia. Conductivity oscillates between 150 and 550 μ S cm⁻¹. Nutrient (mainly phosphate) and organic matter concentrations are high (Table 2) (CECOAL 1980).

In Cocherek, El Sábalo and La Rica marshes (Fig. 1), the phytoplankton density is lower than 500 ind. ml⁻¹ and is characterized by the predominance of Euglenophyceae (50–90%). There is a high number of species of euglenoids: *Euglena oxyuris, E. acus, Trachelomonas volvocina, T. armata, Phacus tortus, Ph. platalea, Strombomonas fluviatilis, S. diptera, S. tetraptera, S. gibberosa* and *S. treubii*. Chlorophyceae and Bacillariophyceae alternate the subdominance. Cyanobacteria and Xanthophyceae are scarcely represented. Numerous new species have been described for this area, which is almost unexplored from the taxonomic point of view (Tell & Zalocar de Domitrovic 1985, Zalocar de Domitrovic 1991, Conforti & Zalocar de Domitrovic 2003).

The marshes related to the fluvial courses between the Pilcomayo River and parallel 28° S (Fig. 1) show a plant coverage of hydrophytes and helophytes (Table 2), which reduces the light incidence and gives a high content of organic matter to the ground (Neiff 1986). The highest depth corresponds to the flood period that occurs by the end of summer and autumn. In

Table 2. Summary of env	ironmental v	ariables and	l vegetation (of lenitic er	nvironments.	. wd: withou	ıt data. nd: ne	on detectable.	
Environments and	Ζ	Temp	Sd	μd	DO	Cond	Nitrate	Phosphate	Macrophytes
sampling periods	(m)	(0 [°] C)	(m)		$(mg L^{-1})$	$(\mu S \text{ cm}^{-1})$	$(\mu g L^{-1})$	$(\mu g L^{-1})$	species more frecuent
Western Chaco Region									
A-C. Reservoirs	0.80 - 1.20	15-28	0.10 - 0.30	6.6–7.4	3.1-6.7	150 - 900	0.11 - 0.71	0.60 - 1.4	Without vegetation
1999–2001									
Eastern Chaco Region									
D. Cocherek Marsh	0.20-1.00	18–25	0.10-0.20	6.3–7.6	39.9–70.6	190–510	1.11–2.90	1.13-513	Cyperus giganteus Thalia multiflora
E. El Sábalo Marsh	0.30-1.10	17–24	0.10-0.33	6.6–7.1	52.9-89.4	180–550	1.18–2.72	1.32–320	C. giganteus T. multiflora
F. La Rica Marsh	0.10-0.80	15-27	0.7–0.44	6.4–6.8	55.9–75.9	170–380	0.53–2.39	pm	C. giganteus T. multiflora
1979–1980									
G. El Lobo Marsh	0.80-1.20	18–25	0.21-0.22	6-6.3	0.3	100-105	nd-88	wd	C. giganteus T. multiflora
1984									
H. El Morocho Marsh	0.70–1.50	22–26.7	0.1-0.22	6.1-6.85	0.2	660L	25-140	bw	C. giganteus T. multiflora
1984									
I. Patí Marsh	0.45–1.50	19.5–20.1	0.01-0.11	6-6.4	0.7–5.2	75–137	72–150	bw	Leersia hexandra Ludwigia peploides
1984									
J. Cuatro Diablos Marsh	06.0-09.0	17.8–23	0.68	6.2	9	70	pm	pm	<i>Oplismenopsis</i> sp.
1904 K. Barrandheras Lake									
limnetic area vegetated area	0.90-2.3	12.2–28.5	0.30-0.50	7.3–8.5	0.11-10.6 0.0-5.9	300–540 330–580	0.17–0.62 0.24–0.66	0.09–851 0.09–110	Eichhornia crassipes (35–50%)

Phytoplankton of the Chaco-Pampean Plain 91

Table 1. cont.									
Environments and	Ζ	Temp	Sd	Hq	DO	Cond	Nitrate	Phosphate	Macrophytes
sampling periods	(m)	(O°)	(m)		$(mg L^{-1})$	$(\mu S \text{ cm}^{-1})$	$(\mu g L^{-1})$	$(\mu g L^{-1})$	species more frecuent
1978-1980									
L. El Puente Sur Lake									
isolation	1.60	14–28	50	6.2	5.6	153	nd–20	40-62	Eichhornia crassipes
connection	2.30	23–29	27	6.8	0.65	244	nd–27	92–775	(30-80%)
1995-1996									
M. El Puente Norte Lak	e								
isolation	1.87	13.9–27.5	59.4	6.1	3.29	151	nd–5	40-47	Eichhornia crassipes
connection	2.36	22–29	27	6.6	0.3	250	nd–7	147-1075	(45–95%)
1995-1996									
N. San Nicolás Lake									
isolation	1.10	13-28	26	6.18	3.6	195	nd–5	28-40	Eichhornia crassipes
connection	1.80	22–31	25	6.23	0.4	294	nd-12	204-1270	(50-95%)
1995-1996									

the isolated hydrological phase, marshes show scarce depth, neutral to acid waters, abundant vegetation, and low concentration of dissolved oxygen.

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Phytoplankton density is low, with abundance of epiphytic or benthic diatoms. Generally, the functional group TD, represented by a varied number of (tychoplanktic) species of the genera *Eunotia*, *Pinnularia*, *Gomphonema*, *Cocconeis* and the filamentous *Spirogyra* sp., *Oedogonium* sp. and *Mougeotia* sp., predominate. During low waters, phytoplankton shows its maximum density (between 650 and 1800 ind. ml⁻¹) and diversity (between 2 and 4.5). *Euglena* spp., *Phacus* spp., *Lepocinclis* spp. (W1), *Trachelomonas* spp., *Strombomonas* spp. (W2) and the previously mentioned taxa of group TD predominate (Zalocar de Domitrovic, pers. obs.).

Shallow lakes. The principal characteristic distinguishing the extense humid Chaco region is the large number of small, shallow and densely vegetated lakes; these include isolated and lakes periodically connected to the Paraguay and Paraná rivers during high waters (Fig. 1).

The isolated Barrangueras Lake is affected by river overflow only during extraordinary floods. It shows some characteristics of deltaic meanders of the Negro and Tragadero rivers (Poi de Neiff & Neiff, 1977). It has permanent turbid waters, mean depth of 0.90 m (Z_{max} = 2.30 m in rainy periods), and floating meadows of *Eichhornia crassipes* (50–60%), located along the border or dispersed, depending on wind direction. Its physical and chemical variables differ between limnetic and vegetated areas (Table 2). Dissolved oxygen is markedly low, with a decrease from the surface to the bottom at both sampling stations, generally showing anoxia in the vegetated area. In the limnetic area, pH oscillates between 7.3 and 8.5, showing values within the acid range in the vegetated littoral zone (Caro 1983). The wind acts as the driving force of water dynamics with direct influence on the phytoplankton. Density shows variations closely related to the movements of the floating meadows. Both areas have the same taxonomic groups, Chlorophyceae, Cryptophyceae, Bacillariophyceae and Euglenophyceae, in variable density (Zalocar de Domitrovic, pers. obs.). In the limnetic area, the community size structure is mainly composed of species with their greatest axial linear dimension smaller than 20 µm, C-strategist (invasive) phytoplankters belonging to the groups X1 (Monoraphidium contortum, Chlorella vulgaris), X2 (Rhodomonas minuta, *Chlamydomonas* sp.) and Y (*Cryptomonas* spp.). However, near the bottom, between 60 and 90 cm depth, Euglenophyceae belonging to the groups W1 and W2 predominate. The resuspension of benthic diatoms (TD) increases species richness (Zalocar de Domitrovic, pers. obs.). In the floating meadows, a great variety of Euglenophyceae dominate throughout the water column during stable conditions (without wind). At both sampling stations, there is an assemblage formed by W1 (Euglena variabilis, E. fusca, E. ehrenbergii) and W2 (Trachelomonas volvocina, T. armata, T. hemisphaerica, Strombomonas ovalis). Euglenophyceae are typical of environments rich in organic matter (usually with high coverage of macrophytes), where they reach high biomass. Cyanobacteria are recorded sporadically (Zalocar de Domitrovic, pers. obs.). Water blooms of Dolichospermum planctonicum (H1) are observed in spring, when nitrate is not detected and the concentration of phosphate is high (851 μ g L^{-1}). Transparency is low and pH is high as a result of a higher photosynthetic activity. The low N/P ratio indicates an intense denitrification, which would explain the development of N-fixer Cyanobacteria. Primary production (estimated through the ¹⁴C method) oscillates between 5.3 and 834 mg C m⁻² d⁻¹ (Caro 1983), with the maximum value recorded during the cyanobacterial blooms.

Periodically connected shallow lakes are observed in the Paraná River floodplain (Fig. 1, Sites L-N) during high water periods. Many of them are vegetated by *Eichhornia crassipes* (Table 2), and the number of floating meadows is comparatively larger than in other South American floodplain systems such as the Amazon or the Orinoco (Carignan & Neiff 1992). The frequency, duration, and timing of the connections vary with the river stage and with the topographic position of the lakes in relation to the main channel (see Devercelli et al., 2014). The input of lotic waters causes large changes in the physical and chemical characteristics of these environments and in the phytoplankton. In a study carried out in 1995 and 1996, the depth of the lakes (between 0.60 and 2.80 m) was positively correlated with the hydrometric level: $r_{p} = 0.331$; p < 0.05 (Zalocar de Domitrovic 2003). In the flood phase, the strong dissolved oxygen demand is due to the organic matter degradation caused during the isolation phase, whereas the increase in conductivity is related to a greater influence of the waters of the Paraguay River (see Zalocar de Domitrovic, 2014). Nutrient enrichment during the flood phase has been described as a common process in floodplains (Junk 1982). High phosphate and inorganic nitrogen (as ammonium) concentrations are explained by the release from the sediments (Pedrozo et al. 1992) and the decomposition of organic matter accumulated on the floodplain during the dry season, respectively. Maximum concentrations of nitrites and nitrates in the initial isolation phase coincide with the decrease in *Eichhornia crassipes* biomass (Carignan & Neiff 1992).

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During the isolation phase of 1995–1996, density and biovolume of phytoplankton were high in relation to the connection phase. Both attributes showed significant differences (p < 0.05) between phases. The rate of community change was lower during the isolation phase than during connection; there were differences in density (M-W U test = 43; p < 0.001) and biomass (p < 0.001) between both phases (Zalocar de Domitrovic 2003). Chlorophyceae and Cryptophyceae were dominant in all the shallow lakes (Puente Sur, Puente Norte and San Nicolás; Fig. 1). Small C-strategist phytoplankters grouped in X2 (*Chlamydomonas leptobasis, Ch. microsphaera, Rhodomonas minuta*), X1 (*Chlorella vulgaris, Choricystis cylindracea, Nephrochlamys subsolitaria, Monoraphidium contortum, Schroederia antillarum*) and Y (*Cryptomonas marssonii, C. ovata, C. erosa, C. rostratiformis*) predominated. Chlorophyta, with biovolumes between 27 and 697 µm³, showed a low biomass. However, in the initial isolation phase in San Nicolás Lake, *S. antillarum* (X1) increased in density and biomass. When the connection phase began, *Pyrobotris squarrosa* (G) increased Chlorophyceae biomass.

In the same study by Zalocar de Domitrovic (2003), Euglenophyceae showed low density, and their contribution to biomass increased after the lotic influence. Groups W1 (*Euglena sanguinea, E. spathirhyncha, E. viridis*) and W2 (*Trachelomonas volvocina, T. volvocinopsis, T. cervicula*) stood out. In general, biomass of Euglenophyceae was represented by a wide variety of species of *Euglena, Trachelomonas, Phacus, Lepocinclis* and *Strombomonas* at both phases. The high organic matter brought by the vegetation and the high nutrient concentration (Carignan & Neiff 1992) may explain the qualitative predominance of Euglenophyceae (Reynolds et al. 2002). Cyanobacteria were scarce during the isolation phase, with the presence of group MP (*Oscillatoria* spp.) and L_o (*Chroococcus* sp. and *Merismopedia teuissima*). During the connection phase, there was an increase in this group with species belonging to L_o (*Merismopedia teuissima*), K (*Aphanocapsa elachista*) and M (*Microcystis pulverea, M. aeruginosa*). A low percentage of species with heterocytes from H1 was observed (*Trichormus ellipsosporus, T. naviculoides*). Even though Cyanobacteria are not

frequent in the Paraguay-Paraná rivers floodplain (Zalocar de Domitrovic et al. 2007), they predominated in biomass in some samplings during the connection phase, probably because they were able to tolerate the physical and chemical conditions found in the floodplain during that period (Carignan & Planas 1994).

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Bacillariophyceae, Chrysophyceae, Xanthophyceae and Dinophyceae were represented during the isolation phase by groups D (*Synedra* sp.), E (*Synura* sp.), J (*Tetraediella jovetti*, *Isthmochloron lobulatum*) and L_o (*Peridinium* spp.) (Zalocar de Domitrovic, pers. obs.). The presence of large dinoflagellates and Chrysophyceae can be related to nutrient enrichment, which may result either in the rapid growth (e.g., *Synura* sp. or *Mallomonas* sp.) or slow growth of Dinophyceae and Euglenophyceae (S-strategists), with species of large size that prevailed in biomass over other algae. Dominance of Chrysophyceae also seems to depend on the presence of cysts. The proliferation of *Synura* spp. when flood waters decrease is a phenomenon known in some shallow lakes of the Paraná River floodplain (Zalocar de Domitrovic et al. 2007).

Diversity oscillated between 1.9 and 4.8 during the isolated phase and between 1.6 and 5 during the connection phase. Species richness was related to the connectivity degree with the fluvial system. In El Puente Sur Lake, with greater lotic-lenitic interaction time, diversity showed differences between both phases (p < 0.05) (Zalocar de Domitrovic 2003). During the connection phase, the highest diversity and species richness seemed to be related to environmental conditions favourable for growth and to the effects caused by the horizontal dragging of species previously accumulated in the floodplain.

Desmidiaceae are scarcely represented in the Paraguay-Paraná floodplain, but are characteristic of other tropical and subtropical systems (Rojo et al. 1994), such as the Amazon and Uruguay, where a high floristic richness is developed (Uherkovich 1976, Tell et al. 1994, see also O'Farrell & Izaguirre, 2014). From the total taxa recorded in the three shallow lakes, 18% are common to those of the Paraná River and 48% to those of the Paraguay River basins. The similarity with the former is due to Chlorophyceae whereas Euglenophyceae explains the correspondence with the latter.

In the source of the middle section of the Paraná River floodplain there are environments with conditions analogous to those of many environments of the Upper Paraguay basin (waters rich in organic matter, low oxygen content, acid waters, important coverage of aquatic macrophytes, etc.). The similarity in composition (mainly Euglenophyceae) between the Paraguay River Pantanal and these floodplain environments could be attributed to the transport of species by the Paraguay River (Zalocar de Domitrovic 2002). These species, as vegetative cells or cysts, would act as a potential inoculum in the floodplain when environmental conditions are favourable for their development. In this way, the concept of "ecological memory" (*sensu* Padisák 1992) also applies to fluvial phytoplankton (Rojo et al. 1994). Thus, while interacting with the floodplain, in each flood, the river acts as a receptor and distributor of such species memory.

Concluding remarks

Hydrology clearly exerts an overall impact on the phytoplankton composition via its effects on water chemistry, horizontal dragging and exchange of algae during floods, water residence

time and aquatic vegetation coverage. The hydrological and salinity fluctuations in the small rivers and streams that flow across the Chaco region are selective factors in the density and composition of phytoplankton. The wetlands of the East Chaco region, including the shallow lakes of the Paraguay-Paraná floodplain, are sources of biodiversity conservation. This Ramsar Site 'Humedales Chaco' has the greatest diversity of species in the Chaco-Pampean region.

References

- Bauer, D. E., Conde, M. E. & Gómez, N. (2002): Phytoplankton of a small lowland stream related to water quality and hydraulic discontinuities. Arch. Hydrobiol. **153**: 421–442.
- Bucher, E. H., Bonetto, A., Boyle, T. P., Canevari, P., Castro, G., Huszar, P. & Stone, T. (1993): Hidrovía: Examen inicial ambiental de la vía fluvial Paraguay-Paraná. – Humedales para Las Americas, Manomet, Masssachusetts, Buenos Aires.
- Caro, P. M. (1983): Produccion primaria del fitoplancton de la laguna Barranqueras, provincia del Chaco, República Argentina. Historia Natural **3**(12): 125–134.
- Carignan, R. & Planas, D. (1994): Recognition of nutrient and light limitation in turbid mixed layers: three approaches compared in the Paraná floodplain (Argentina). – Limnol. Oceanogr. 39: 580–596.
- Carignan, R. & Neiff, J. J. (1992): Nutrient dynamics in the floodplain ponds of the Paraná River (Argentina) dominated by the water hyacinth *Eichhornia crassipes*. – Biogeochemistry 17: 85–121.
- CECOAL (Centro de Ecología Aplicada del Litoral) (1980): Investigaciones relativas a la producción y ecología de plantas acuáticas de valor forrajero y sobre calidad de aguas en los Bajos Submeridionales (Subsistema Chaco). Consejo Federal de Inversiones-CECOAL.
- Chételat, J., Pick, F. R. & Hamilton, P. B. (2006): Potamoplankton size structure and taxonomic composition: influence of river size and nutrient concentrations. – Limnol. Oceanogr. 51: 681–689.
- Conforti, V., Alberghina, J. & Gonzalez Urda, E. (1995): Structural changes and dynamics of the phytoplankton along a highly polluted lowland river of Argentina. – J. Aquat. Ecosyst. Health 4: 59–75.
- Conforti, V. & Zalocar de Domitrovic, Y. (2003): Ultrastructural study of *Strombomonas* (Euglenophyta) from the province of Chaco (Argentina). Bol. Soc. Argent. Bot. **38**: 5–12.
- Del Giorgio, P. A., Vinocur, A. L., Lombardo, R. J. & Tell, G. (1991): Progressive changes in the structure and dynamics of the phytoplankton community along a pollution gradient – a multivariate approach. – Hydrobiologia 224: 129–154.
- Descy, J. P. (1987): Phytoplankton composition and dynamics in the River Meuse (Belgium). Arch. Hydrobiol. Suppl. **78**: 225–245.
- Devercelli, M. (2008): Ecología del fitoplancton en la cuenca inferior del río Salado: desarrollo algal en zonas de retención hidráulica y transporte de algas suspendidas en el flujo principal. – Tesis de Doctorado. Universidad de Buenos Aires, Argentina.
- Devercelli, M. & Peruchet, E. (2008): Trends in chlorophyll-*a* concentration from urban water bodies within different man-used basins. Annales de Limnologie Int. J. Limnol. **44**: 75–84.
- Devercelli, M., Zalocar de Domitrovic, Y., Forastier, M. E. & Meichtry de Zaburlín, N. (2014): Phytoplankton of the Paraná River. Adv. Limnol. **65**: 39–65.
- Emiliani, F. & García de Emiliani, M.O. (2003): Predicción de la calidad bacteriológica de las aguas naturales en ambientes urbanos. Influencia de El Niño-Oscilación Sur. – Rev. Argent. Microbiol. 35: 8–18.
- García de Emiliani, M. O. & Anselmi de Manavella, M. I. (1983): Fitoplancton de los principales cauces y tributarios del valle aluvial del Río Paraná: tramo Goya-Diamante. III. – Rev. Asoc. Cienc. Nat. Litoral 14: 217–237.
- García de Emiliani, M. O. & Anselmi de Manavella, M. I. (1989): Fitoplancton y variables ambientales en la cuenca del río Saladillo (Santa Fe, Argentina). Rev. Bras. Biol. **49**: 957–967.

García de Emiliani, M. O. & Devercelli, M. (2004): Estructura y dinámica del fitoplancton de un río tributario (Salado) y cauces secundarios de río Paraná (Santa Fe, Coronda y El Vado) en el área de confluencia (Santa Fe, Argentina). – Rev. Facultad de Bioquímica y Ciencias Biológicas **8**: 23–42.

Ginzburg, R., Adámoli, J., Herrera, P. & Torrilla, S. (2005): Los humedales del Chaco: Clasificación, inventario y mapeo a escala regional. – Miscelánea **14**: 121–138.

Gosselain, V., Descy, J. P. & Everbecq, E. (1994): The phytoplankton community of the River Meuse, Belgium: seasonal dynamics (year 1992) and the possible incidence of zooplankton grazing. – Hydrobiologia **289**: 179–191.

Hynes, H. B. N. (1970): The ecology of running waters. - Liverpool University Press, Liverpool.

- Iriondo, M. & Paira, A. R. (2007): Physical Geography of the Basin. In: Iriondo, M., Paggi, J. C. & Parma, J. (eds.): The middle Paraná River. Limnology of a subtropical wetland, pp. 7–31. Springer, Berlin.
- Junk, W. J. (1982): Amazonian floodplains: their ecology, present and potential use. Rev. Hydrob. Trop. **15**: 285–301.
- Lancelle, H. G., Longoni, A. C., Ramos, A. O. & Cáceres, J. R. (1986): Caracterización físico-química de ambientes acuáticos permanentes y temporarios del Chaco Oriental. – Ambiente Subtropical 1: 73–91.
- Leland, H. V., Brown, L. R. & Mueller, D. K. (2001): Distribution of algae in the San Joaquin River, California, in relation to nutrient supply, salinity and other environmental factors. – Freshwat. Biol. 46: 1139–1167.
- Loez, C. & Salibian, A. (1990): Première donées sur le phytoplancton et les caractéristiques physicochimiques du Rio Reconquista (Buenos Aires, Argentine): une rivière urbaine polluée. – Rev. Hydrobiol. Trop. 23: 283–296.
- Maglianesi, R. & Depetris, J. P. (1970): Características químicas de las aguas del río Salado Inferior (provincia de Santa Fe, República Argentina). – Physis 30(80): 19–32.
- Mercado, L. M. (2003): A comparative analysis of the phytoplankton from six pampean lotic systems (Buenos Aires, Argentina). Hydrobiologia **495**: 103–117.

Neiff, J. J. (1986): Sinópsis ecológica y estado actual del Chaco Oriental. – Ambiente Subtropical 1: 5–35.

- Neiff, J. J. (1996): Large rivers of South America: toward the new approach. Verh. Internat. Verein. Limnol. 26: 167–180.
- Neiff, J. J., Iriondo, M. H. & Carignan, R. (1994): Large tropical south American wetlands: an overview. – In: Link, G. L. & Naiman, R. J. (eds.): The ecology and management of aquatic-terrestrial ecotones, pp. 156–165. Proceedings Book, Univ. of Washington, Seattle.
- Neiff, J. J. & Malvarez, A. I. (2004): Grandes Humedales Fluviales. In: Malvarez, A. I. & Bo, R. F. (ed.): Bases ecológicas para la clasificación e inventario de humedales en Argentina. Pp. 77–85. Buenos Aires.
- Neiff, J. J., Poi de Neiff, A. & Casco, S. (2005): Importancia ecológica del corredor fluvial Paraguay-Paraná como contexto de manejo sostenible. Humedales fluviales de América del Sur. – In: Peteán, J. & Capato, J. (eds.): Fundación Proteger, UICN, pp. 193–210. Proteger Ediciones 2.
- Oakley, L. J., Prado, D. & Adámoli, J. (2005): Aspectos biogeográficos del corredor fluvial Paraguay-Paraná. – Miscelánea 14: 245–258. Ediciones Magna, Tucumán.
- O'Farrell, I. & Izaguirre, I. (2014): Phytoplankton of the middle and lower stretches of the Uruguay River. Adv. Limnol. **65**: 113–126.
- O'Farrell, I., Lombardo, R. J., de Tezanos Pinto, P. & Loez, C. (2002): The assessment of water quality in the Lower Luján River (Buenos Aires, Argentina): phytoplankton and algal bioassays. Environ. Pollut. **120**: 207–218.
- O'Farrell, I., de Tezanos Pinto, P. & Izaguirre, I. (2007): Phytoplankton morphological response to the underwater light conditions in a vegetated wetland. Hydrobiologia **578**: 65–77.
- Padisák, J. (1992): Seasonal succession of phytoplankton in a large shallow lake (Balaton, Hungary) a dynamic approach to ecological memory, its possible role and mechanisms. – J. Ecol. 80: 217–230.
- Patiño, C. & Orfeo, O. (1986): Aproximación al conocimiento del proceso de erosión del suelo en el Chaco Oriental. – Ambiente Subtropical 1: 47–59.

- Pedrozo, F., Diaz, M. & Bonetto, C. A. (1992): Nitrogen and phosphorus in the Paraná river floodplain waterbodies. – Arch. Hydrobiol./Suppl. 90: 171–185.
- Philips, E. J., Hendrickson, J., Quinlan, E. L. & Cichra, M. (2007): Meteorological influences on algal bloom potential in a nutrient-rich blackwater river. – Freshwater Biol. 52: 2141–2155.
- Poi de Neiff, A. S. G. & Neiff, J. J. (1977): El pleuston de *Pistia stratiotes* de la Laguna Barranqueras (Chaco, Argentina). Ecosur **4**: 69–101.
- Reynolds, C. S. (2006): Ecology of phytoplankton. Cambridge Univ. Press, Cambridge.
- Reynolds, C. S. & Descy, J. P. (1996): The production, biomass and structure of phytoplankton in large rivers. Arch. Hydrobiol. Suppl. 113, Large Rivers **10**: 161–187.
- Reynolds, C. S., Huszar, V., Kruk, C., Naselli-Flores, L. & Melo, S. (2002): Towards a functional classification of the freshwater phytoplankton. – J. Plankton Res. 24: 417–428.
- Rojo, C., Alvarez Cobelas, M. & Arauzo, M. (1994): An elementary, structural analysis of river phytoplankton. – Hydrobiologia 289: 43–55.
- Salmaso, N. & Braioni, M. G. (2007): Factors controlling the seasonal development and distribution of the phytoplankton community in the lowland course of a large river in Northern Italy (River Adige). – Aquat. Ecol. 42: 533–545.
- Soares, M. C. S., Huszar, V. & Roland, F. (2007): Phytoplankton dynamics in two tropical rivers with different degrees of human impact (southeast Brazil). – River Res. Appl. 23: 698–714.
- Tell, G., Izaguirre, I. & O'Farrell, I. (1994): Ecological and taxonomical remarks on the desmid flora of the Lower Uruguay river basin (Argentina) Bibliotheca Phycologica **96**: 1–141. Cramer, Berlin, Stuttgart.
- Tell, G. & Zalocar de Domitrovic, Y. (1985): Euglenophyta pigmentadas de la provincia del Chaco (Argentina). Nova Hedwigia **41**: 353–391.
- Tracanna, B. C. & Lacoste, E. N. (1988): Algas de aguas continentales de la Argentina, IX. Ficoflora de Formosa. – Lilloa 37: 61–93.
- Uherkovich, G. (1976): Algen aus den Flüssen Rio Negro und Rio Tapajós. Amazoniana 5: 465-515.
- Yang, J. R., Basu, B. K., Hamilton, P. B. & Pick, F. R. (1997): The development of a true riverine phytoplankton assemblage along a lake-fed lowland river. – Archiv Hydrobiol. 140: 243–260.
- Zalocar de Domitrovic, Y. (1991): *Strombomonas* (Euglenophyta) nuevas o raras de la Argentina. Cryptogamie, Algologie **12**: 271–281.
- Zalocar de Domitrovic, Y. (2002): Structure and variation of the Paraguay river phytoplankton in two periods of its hydrological cycle. Hydrobiologia 472: 177–196.
- Zalocar de Domitrovic, Y. (2003): Effect of fluctuations in the water level on phytoplankton development in three lakes of the Paraná River floodplain (Argentina). Hydrobiologia **510**: 175–193.
- Zalocar de Domitrovic, Y., Devercelli, M. & García de Emiliani, M. O. (2007): Phytoplankton. In: Iriondo, M., Paggi, J. C. & Parma, J. (eds.): The middle Paraná River. Limnology of a subtropical wetland, pp. 175–203. Springer, Berlin.
- Zalocar de Domitrovic, Y. & Maidana, N. I. (1997): Taxonomic and ecological studies of the Paraná River diatom flora (Argentina). – Bibliotheca Diatomologica **34**: 1–122. Cramer, Berlin, Stuttgart.
- Zalocar de Domitrovic, Y., Vallejos, E. R. & Pizarro, H. (1986): Aspectos ecológicos de la ficoflora de ambientes acuáticos del Chaco Oriental (Argentina). – Ambiente Subtropical 1: 92–111.
- Zalocar de Domitrovic, Y., Devercelli, M. & Forastier, M. E. (2014): Phytoplanktion fo the Paraguay and Bermejo rivers. Adv. Limnol. **65**: 67–80.