Abundance and diversity of phytoplankton in the Paraná River (Argentina) 220 km downstream of the Yacyretá reservoir

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(With 4 figures)

Abstract

Patterns in the temporal composition, abundance and diversity of the phytoplankton community of the Paraná river prior to and after the initial filling phase of the Yacyretá reservoir are analyzed. The study site is located 220 km downstream from the Yacyretá reservoir and 30 km downstream from the confluence with the Paraguay river. Because both rivers remain separate and unmixed at the study site, we compared the possible effects of the impoundment on both river banks (left and right banks) in hydrological periods with similar duration and magnitude of the low and high water phases. Physical and chemical conditions measured on the right bank (water from the Paraguay river) were similar at both periods (pre and post-impoundment) whereas conductivity, pH and orthophosphate concentration increased on the left bank (water from the High Paraná river and Yacyretá reservoir) after the impoundment. Changes in phytoplankton density and diversity were observed only in samples collected from water flowing from the reservoir (left bank). The density of Chlorophyceae (*Chloromonas acidophila*, *Chlamydomonas leptobasis*, *Choricystis minor*, *Chlorella vulgaris*, *Scenedesmus ecornis*, *Monoraphidium minutum*, *M. contortum* and *M. pusillum*) and Cryptophyceae (*Rhodomonas minuta*, *Cryptomonas marssonii* and *C. ovata*) increased while Cyanophyceae (*Cylindrospermopsis raciborskii*, *Raphidiopsis mediterranea* and *Planktolyngbya subtilis*) and Bacillariophyceae (*Aulacoseira granulata* and its bioforms) decreased compared to previous studies conducted on the left bank of the Paraná river. Phytoplankton collected from the right bank of the river did not differ in pre and post- impoundment samples because they originate from the Paraguay river, which remains relatively unaffected by human activities.

Keywords: temporal and spatial variation, diversity, large rivers, pre and post-impoundment.

Abundância e diversidade do fitoplâncton do Rio Paraná (Argentina) 220 km a jusante do Reservatório de Yacyretá

Resumo

Estudaram-se os padrões temporais de composição, abundância, e diversidade da comunidade fitoplanctônica do Rio Paraná, antes e depois da fase inicial de fechamento do reservatório de Yacyretá (períodos pré e pós-fechamento). A área de estudo está localizada 220 km a jusante do reservatório de Yacyretá e 30 km a jusante da confluência dos Rios Paraná e Paraguai. Considerando que as águas destes rios permanecem sem se misturar no local de estudo, os possíveis efeitos do fechamento da barragem foram comparados em ambas as margens (direita e esquerda), durante as fases de águas altas e baixas de períodos hidrológicos de duração e magnitude semelhantes. As condições físico-químicas medidas na margem direita (águas do Rio Paraguai) foram similares em ambos os períodos (pré e pós-fechamento), observando-se aumento nos valores da condutividade, pH e concentração de ortofosfato na margem esquerda (águas do alto Rio Paraná e do reservatório de Yacyretá) no período pós-fechamento. Alterações na densidade e composição da comunidade fitoplanctônica foram observadas somente em amostras coletadas de águas provenientes do reservatório (margem esquerda). As densidades de Chlorophyceae (*Chloromonas acidophila*, *Chlamydomonas leptobasis*, *Choricystis minor*, *Chlorella vulgaris*, *Scenedesmus ecornis*, *Monoraphidium minutum*, *M. contortum* e *M. pusillum*) e Cryptophyceae (*Rhodomonas minuta*, *Cryptomonas marssonii* e *C. ovata*) incrementaram-se, no entanto houve diminuição das densidades de Cyanophyceae (*Cylindrospermopsis raciborskii*, *Raphidiopsis mediterranea* e *Planktolyngbya subtilis*) e Bacillariophyceae (*Aulacoseira granulata* e suas bioformas), se comparadas a estudos prévios desenvolvidos nesta margem. O fitoplâncton coletado nos períodos pré e pós-fechamento na margem direita não mostrou diferencas por se originar no Rio Paraguai, que permanece relativamente pouco afetado pelas atividades humanas.

Palavras-chave: variação espacial e temporal, diversidade, grandes rios, pré e pós-fechamento.

1. Introduction

The impoundment of a river determines a series of modifications in its physical, chemical and biological characteristics observed from the filling stage until reaching a relative stability. This period is very variable and can last up to twenty years in some tropical reservoirs (Balon and Coche, 1974). Differences in the water residence time, temperature, transparency and nutrient level produce changes in the quali-quantitative phytoplankton composition (Tundisi, 1993), which can be seen up to 350 km downstream from the dam (Petts, 1984).

The Paraná river basin, with a drainage area of 2.6×10^6 km^2 and 3,965 km length is the second largest catchment of South America, shared by Brazil, Bolivia, Paraguay and Argentina (Orfeo and Stevaux, 2002). Several reservoirs (approximately 23), situated in cascade (Bonetto et al., 1989), occupy its main channel, mainly in Brazil (Upper Paraná). The construction of Yacyretá in the High Paraná, one of the largest impoundments built in Argentina, was finished in April 1990, although the first turbine did not start operating until September 1st, 1994. This had an important impact on aquatic communities of the reservoir (Garrido, 1999; Meichtry de Zaburlín, 1999; Peso and Bechara, 1999; Neiff et al., 2000) and downstream from it (Domitrovic et al., 1994).

The aim of this study is to analyze the variations in abundance and diversity of the phytoplankton on both banks of the Paraná river, 30 km downstream from the confluence with the Paraguay and 220 km downstream from the reservoir. We also analyzed pre- and post-impoundment phytoplankton for both banks (1980-1981 and 1995-1996) in relation to environmental variables.

Our hypothesis is that phytoplankton abundance and diversity on the left bank have changed following the impoundment of the Yacyretá reservoir.

1.1. Study site

The Yacyretá reservoir is located on the High Paraná river (27° 28' S and 56° 44' W) near Ituzaingó (Argentina) and Ayolas (Paraguay). During the initial filling phase (water level = 76 m a.s.l), the reservoir had a retention time of less than 20 days. Its main morphometric characteristics are: length of 66.5 km; surface area of 1,600 km^2 at 82 m above sea level; volume of 21,000 hm^3; maximum depth of 35 m and maximum width of 21 km.

The study site (Figure 1) is located 220 km downstream from the reservoir near Corrientes city (27° 30' S and 58° 55' W), where the river is approximately 1,200 m wide. At this site, the Paraná river flows as a typical floodplain river with an irregular hydrological regime. Thirty kilometers upstream from this site, the Paraguay

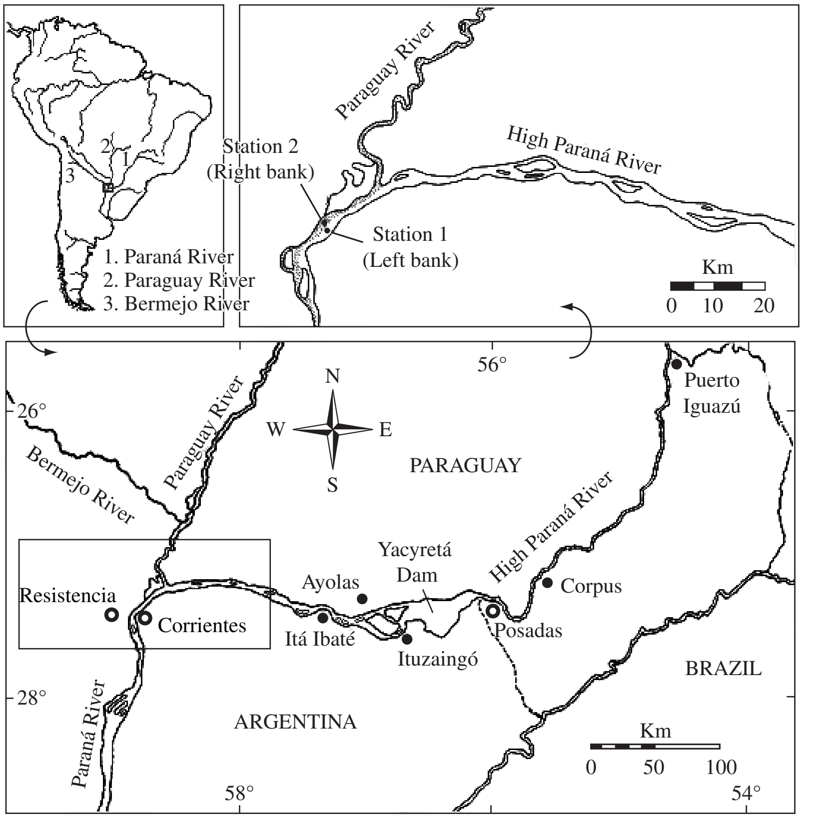

Figure 1. Location map of the study site showing the two sampled stations in the Paraná river. Station 1: left bank, associated with water from the High Paraná river and the Yacyretá dam. Station 2: right bank, associated with water from the Paraguay river.

river merges with the High Paraná. Both rivers remain unmixed until they reach 200-300 km downstream. The Paraguay river drains the Pantanal and 100 km before the study site receives the high suspended load of the Bermejo river (3 to 10 g litter) which drains Andean sedimentary rocks rich in carbonates. The Upper Paraná (Brazil) flows over basalts and sandstones covered by lateritic soils rich in iron and aluminum oxides. These different watershed lithologies are reflected in the contrasting chemical and physical composition of both rivers. At the confluence, the annual discharge of the Paraná river increases from 11,983 to 16,941 $m^3 s^{-1}$, and the discharge of suspended sediment increases from 5.1 x 10^6 to 118.7 x 10^6 $tons.year^{-1}$ (Orfeo and Stevaux, 2002).

The water level of the Paraná river at Puerto Corrientes fluctuated between 2.04 (44.33 m a.s.l.) and 5.79 m (48.18 m a.s.l.) between 1995-1996 and between 2.35 (44.74 m a.s.l.) and 6.88 m (49.27 m a.s.l.) prior to the Yacyretá impoundment (1980-1981). There were no significant differences in the water level of the Paraná river at Puerto Corrientes between both periods.

As comparative data, a limnological study (including information on phytoplankton) was carried out in the current dam area and 220 km downstream, near Corrientes city from 1980 to 1981, i.e., before the construction of the dam (Bonetto et al., 1982).

2. Methodology

Monthly (exceptionally fortnightly) samplings were carried out at two stations located near both banks of the Paraná river from April 1995 (7 months after the Yacyretá started operating) to May, 1996.

Single subsurface samples were taken with a Van Dorn sampler approximately 150 m from each bank and fixed with Lugol's solution for phytoplankton counts. Counts were carried out using an inverted microscope with the same methods (Lund et al., 1958; Utermöhl, 1958) and by the same operators as the 1980-1981 pre-impoundment work. Specific diversity (H') was estimated using the Shannon-Wiener index (Shannon and Weaver, 1963) from the density data (bits $ind.^{-1}$). Specific richness (SR) refers to the number of algal taxa registered in each sample in the Utermöhl counting chambers.

At each sampling station, *in situ* measurements of water temperature, transparency (25 cm diameter Secchi disk), pH (digital pH meter Metrohm A G Herisau), electrical conductivity (conductometer YSI 33 SCT) and dissolved oxygen (oxygen meter YSI 54 A) were carried out. Analyses of dissolved nutrients (NO_3 + NO_2 and orthophosphate) were performed according to APHA (1981) on filtered (Whatman GF/C) samples by the staff of the Chemical Laboratories at the Centro de Ecología Aplicada del Litoral.

Results obtained near both banks of the river (Station 1 vs. Station 2) between 1995-1996 and those obtained before the dam operation (1980-1981) were compared using the Wilcoxon matched pairs test (Steel and Torrie, 1988). The ordination of environmental variables was performed by Principal Component Analysis (PCA). Before computation, the data, except pH, were log transformed to stabilize the variance.

The pre and post-impoundment phytoplankton densities of both banks were analyzed using Detrended Correspondence Analysis (DCA). Subsequently, a forward stepwise multiple regression analysis was used to examine the relationship between species abundance and the DCA axes. For this, the sample scores which are weighed mean species scores of the two first axes of DCA (dependents variables) and eight abiotic variables (independents variables): water level, temperature, Secchi disk, dissolved oxygen, pH, conductivity, nitrite+nitrate concentration and orthophosphate concentration were analyzed. Twenty three species, reaching a relative abundance greater than 10% and/or samples frequency greater than 30%, were included in the analysis (Legendre and Legendre, 1983; Zalocar de Domitrovic, 1999).

3. Results and Discussion

3.1. Environmental variables

In both periods (pre and post-impoundment), mean annual values of transparency (Secchi disk) and dissolved oxygen were significantly higher at Station 1 (left bank, water from the High Paraná river). On the other hand, mean values of conductivity and orthophosphate concentration were significantly higher at Station 2 (right bank, water from the Paraguay river) (Table 1).

The first three axes of a Principal Component Analysis (PCA) of abiotic variables accounted for 75% of the total variance. The first axis (37%) was negatively correlated with conductivity (Cond) and positively correlated with transparency (Sec) and dissolved oxygen (Ox). Axis 2 was negatively correlated with nitrite+nitrate concentration (N). The pH was positively correlated with axis 3. The first principal component scores contrasted Station 1 (left bank, water from the High Paraná river) with Station 2 (right bank, water from the Paraguay river), the former having relatively high values of transparency and dissolved oxygen. Station 2 (right bank) was characterized by more conductivity and concentration of nutrients (Figure 2).

Physical and chemical conditions measured at Station 2 (right bank) in the pre-impoundment period were, in general, similar to those registered post-impoundment. On the other hand, conductivity, pH and orthophosphate concentration at Station 1 (left bank, water from the High Paraná and Yacyretá dam) increased significantly ($p < 0.05$) after the impoundment (Table 1).

3.2. Phytoplankton

3.2.1. Comparison of phytoplankton between Station 1 (left bank) and Station 2 (right bank) of the river

Between 1995-1996, phytoplankton density was higher at Station 1 (between 588 and 2,598 $ind.mL^{-1}$) than at Station 2 (between 88 and 1,322 $ind.mL^{-1}$) (Figure 3).

The Paraná river community at Station 1 (left bank) included eight taxonomic groups: Cyanophyceae,

Table 1. Mean annual values, standard deviation (S.D.) and the results of the Wilcoxon test (*Z*) evaluating the difference between Station 1 (left bank) and Station 2 (right bank) for each environmental variable. p <0.05 are in bold; *n* = number of samples.

	Pre-impoundment			**Post-impoundment**		
	Station 1 (*n* = 14)	**Station 2 (*n* = 14)**	***Z* (p)**	**Station 1 (*n* = 14)**	**Station 2 (*n* = 14)**	***Z* (p)**
Temperature (°C)	29.1 (4.05)	29.2 (4.21)	0.711 (0.109)	28 (2.57)	28 (2.57)	- -
Secchi disk (cm)	115 (28.2)	44 (14.7)	3.296 **(0.001)**	82 (11.8)	41 (11.87)	3.296 **(0.001)**
pH	7.5 (0.12)	8.3 (0.39)	0.902 (0.367)	8.0 (0.31)	7.4 (0.19)	2.731 **(0.006)**
Dissolved oxygen (% saturation)	149 (15.6)	104 (13.6)	3.296 **(0.001)**	110 (6.67)	93 (6.11)	3.296 **(0.001)**
Conductivity ($\mu S.cm^{-1}$)	65 (9.9)	180 (22.1)	3.296 **(0.001)**	66 (6.8)	140 (19.9)	3.296 **(0.001)**
Nitrite + Nitrate ($\mu g.L^{-1}$)	1.3 (0.32)	1.7 (0.42)	1.572 (0.116)	0.5 (0.15)	0.7 (0.19)	3.059 **(0.002)**
Orthophosphate ($\mu g.L^{-1}$)	0.14 (0.03)	0.48 (0.10)	3.296 **(0.001)**	0.5 (0.15)	0.7 (0.19)	3.059 **(0.002)**

Chlorophyceae, Euglenophyceae, Cryptophyceae, Dinophyceae, Bacillariophyceae, Chrysophyceae and Xanthophyceae. At Station 2 (right bank), only five taxonomic groups were registered. No Dinophyceae, Chrysophyceae and Xanthophyceae were detected. Most phytoplankton groups showed statistically significant differences between the two river banks: Chlorophyceae (Z = 3.170, p = 0.001), Cryptophyceae (Z = 3.170, p = 0.001) and Euglenophyceae (Z = 3.233, p = 0.001).

The highest phytoplankton density corresponded to Chlorophyceae, Bacillariophyceae and Cryptophyceae. The first group (Chlorophyceae) was best represented at Station 1 (between 27 and 73%) with small flagellated and coccoid forms (*Chloromonas acidophila*, *Chlamydomonas leptobasis*, *Choricystis minor*, *Chlorella vulgaris*, *Scenedesmus ecornis*, *Monoraphidium minutum*, *M. contortum* and *M. pusillum*), while the second one (Bacillariophyceae) was observed at Station 2 (between 0.4 and 97%) with *Aulacoseira granulata* (and its bioforms), *A. alpigena* and *A. herzogii*. Cryptophyceae (with *Rhodomonas minuta*, *Cryptomonas marssonii* and *C. ovata*) were present in all samples collected on the left bank (between 7 and 56%), but were not always detected on the right bank (0-38%).

The Shannon-Wiener diversity index (*H'*) showed significant differences between the two stations (Z = 2.605, p = 0.009), with higher values at Station 1 (Range = 2.9-4.1 $bits.ind.^{-1}$) compared to Station 2 (Range = 1.2-3.7 $bits.ind.^{-1}$). Equitability varied from 65 to 79% and from 52 to 100% in the left and right banks, respectively.

Species richness (number of taxa) ranged between 19 and 47 taxa per sample on Station 1 and between 3 and 18 taxa per sample on Station 2. These values were significantly different (Z = 3.296, p = 0.001).

Between 1995-1996 (post-impoundment), the species composition was not homogeneous between the two river banks (Table 2). Out of a total taxa of 143, there were 69 exceeding a relative abundance of 1%. Fifty seven taxa corresponded to Station 1 (left bank) and 36 to Station 2 (right bank), with 26 species in common between both river banks.

Differences registered between the two banks in the physical and chemical variables, as well as in the phytoplanktonic community, are likely related to the influence exerted by the Bermejo river (Andean origin, mineralized waters and high content of suspended solids) on the lower reach of the Paraguay river, which flows along the right bank of the Paraná river at our study site (Bonetto et al., 1982; Bonetto and Orfeo, 1984). The tendency for higher phytoplankton densities at Station 1 (left bank) was similar to what was reported in pre-impoundment studies. Although some common algal species were observed on both banks, in general, taxa from the right bank corresponded to those brought by the Paraguay river, while those from the left bank corresponded to those brought from the High Paraná river (Zalocar de Domitrovic and Vallejos, 1982; Zalocar de Domitrovic, 1999; 2002).

3.2.2. Comparison between phytoplankton abundance before and after the impoundment of Yacyretá

At Station 1 (left bank), Chlorophyceae were the dominant group in 1995-1996, followed by Cryptophyceae, showing a statistically significant increase in density in relation to studies carried out previously to the construction of the dam (Z = 2.731; p = 0.006 and Z = 3.233; p = 0.001, respectively). Before Yacyretá, dominant groups were Chlorophyceae and/or Cyanophyceae and Bacillariophyceae (Bonetto et al., 1982). There was a

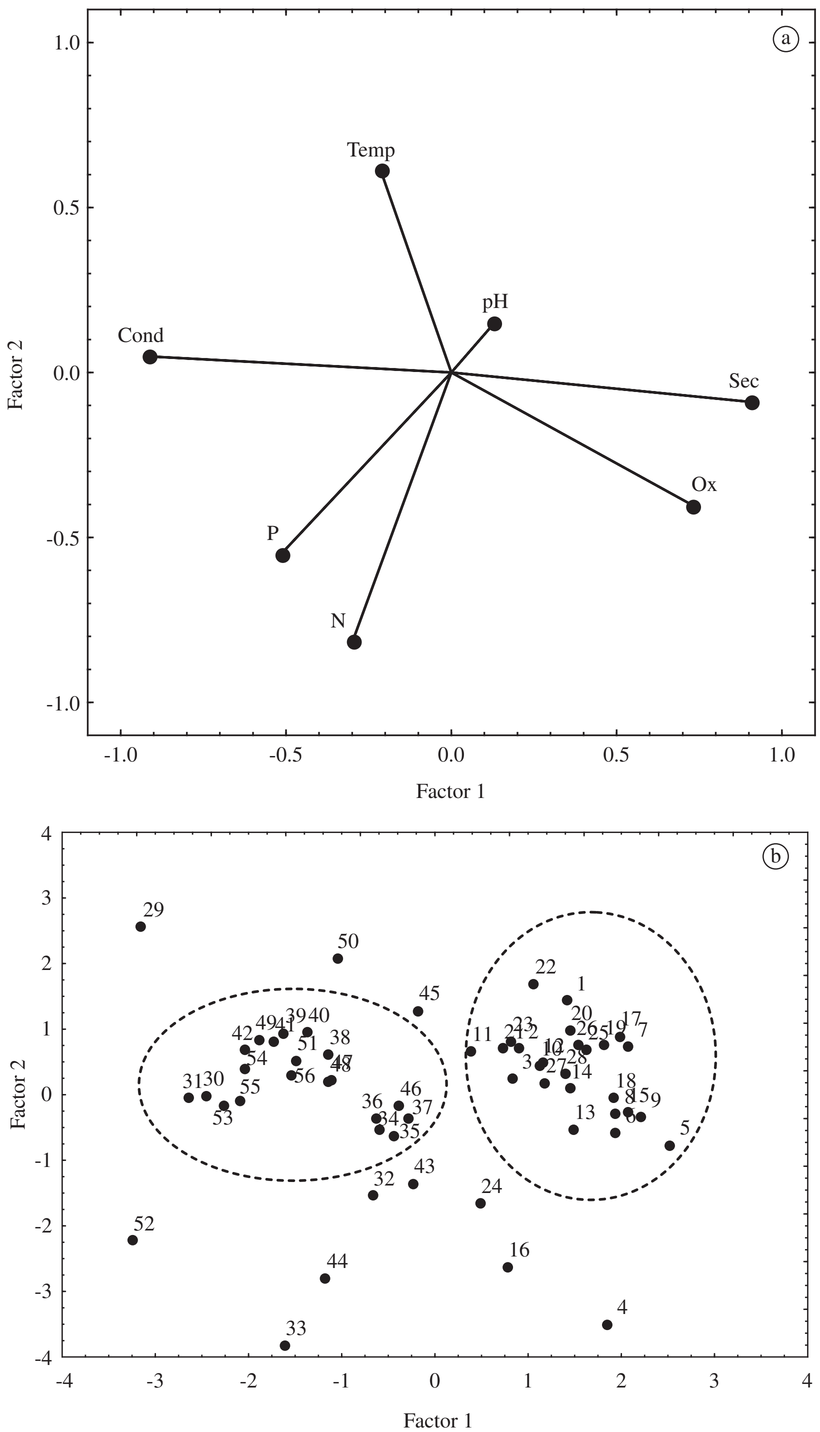

Figure 2. PCA based on abiotic variables. a) Position of vectors of environmental variables in the reduced space of the first two main components. Temp: temperature, Ox: dissolved oxygen (% saturation), Sec: Secchi depth, Con: conductivity, N: nitrite+nitrate concentration, P: orthophosphate concentration; and b) Position of 56 samples in the space dimensioned by the first two principal components. 1-28: Station 1 (1-14: pre-impoundment samples, 15-28: post-impoundment samples), 29-56: Station 2 (29-42: pre-impoundment samples, 43-56: post-impoundment samples).

surprising reduction in the abundance of Cyanophyceae ($Z = 3.295$; $p = 0.001$) and Bacillariophyceae ($Z = 2.103$; $p = 0.035$) in the post-impoundment period. The latter (Bacillariophyceae) was in the third place of importance at Station 1 and continued to dominate Station 2, where the phytoplanktonic community in general did not show statistically significant differences in relation to pre-impoundment levels.

The Detrended Correspondence Analysis (DCA) of phytoplankton species and samples, before and after impoundment is shown in Figure 4. Eigenvalues were 0.79 and 0.23 for axis 1 and 2 respectively and lengths of gradients were 3.56 and 2.06 S.D. Total variance ("inertia") in the species data was 2.62. Factor 1 shows the order of the species between the periods of the pre and post-impoundment. The first two groups (Groups 1 and 2) show samples taken during the pre-impoundment period, and Groups 3 and 4 represent samples collected during the post-impoundment period. In the first axis, samples from Station 1 (waters from High Paraná) collected during pre-impoundment period are located to the right of the gradient and are distinguished by species: *Cylindrospermopsis raciborskii*, *Raphidiopsis mediterranea*, *Planktolyngbya subtilis*, *Aulacoseira granulata* and *A. alpigena.* The two last species of diatoms, especially *A. granulata*, was predominant in Station 2 (water from Paraguay river), in all the samples of the pre and post-impoundment periods (Groups 2 and 4). Samples from Group 3 correspond to Station 1 (left bank) of the post-impoundment period and are allocated in the negative region of Factor 1, which is related to many species of Chlorophyceae (*Chlorella vulgaris*, *Chlamydomonas acidophila*, *Choricystis minor*), Cryptophyceae (*Cryptomonas marssonii*, *C. ovata*), Chrysophyceae, diatoms and Euglenophyceae (see Table 2). Some common species of both periods (pre and post-impoundment) occupy an intermediate position in the gradient.

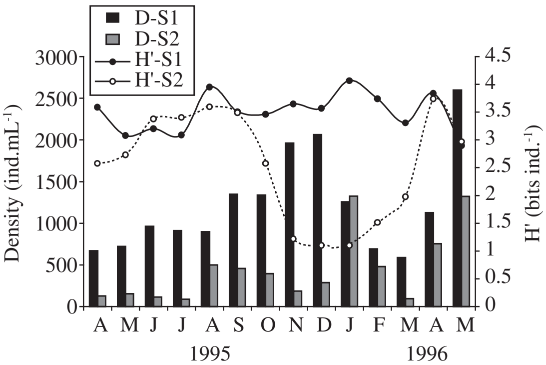

Figure 3. Variations in density (D) and diversity (H'= Shannon-Wiener index) of phytoplankton in the two stations sampled in the Paraná river. S1: Station 1 (left bank, associated with water from High Paraná river and the Yacyretá dam); S2: Station 2 (right bank, associated with water from the Paraguay river).

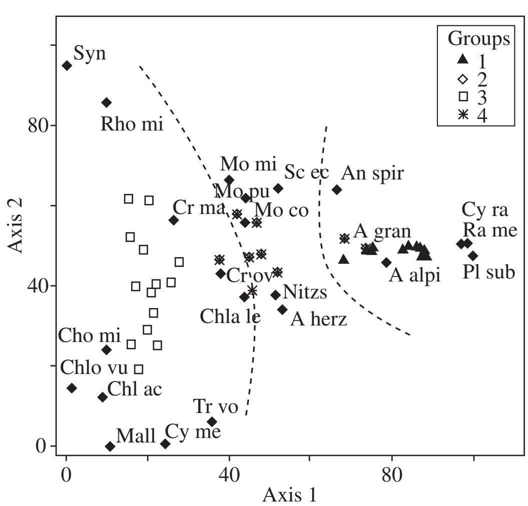

Figure 4. Detrended Correspondence Analysis (DCA) of phytoplankton species (●) and samples (groups), before and after impoundment. Group 1: Station 1, pre-impoundment, Group 2: Station 2, pre-impoundment, Group 3: Station 1, post-impoundment, Group 4: Station 2, post-impoundment. The letters represent abbreviated names of the species according to Table 2.

Multiple regression reveals that three variables (pH, Secchi disk and conductivity) explain 39% of the variability of species for axis 1 and pH explain 6% for Axis 2 (Table 3).

When comparing our results for Station 1 (left bank) with those of Meichtry de Zaburlín (1999) on the left side of the Yacyretá reservoir, Chlorophyceae and Cryptophyceae densities show significant differences ($Z = 3.296$; $p = 0.001$ and $Z = 2.542$; $p = 0.011$, respectively). Lentic Desmidiaceae and Euglenophyceae were not detected downstream from the reservoir probably because of selection mechanisms typical of lotic waters (Reynolds, 1999).

The replacement of lentic plankton associations by lotic ones downstream from reservoirs was observed in small rivers like the Loire in France (Lair and Reyes-Marchant, 1997). In large rivers, like the Paraná, they are probably detected to short distances downstream from the reservoir. A high percentage of algae cannot be detected by count methods in the study area, but downstream they could act as "memory species" (*sensu* Padisák, 1992), being a potential inocula for the colonization of lentic floodplain environments (Zalocar de Domitrovic, 2002; 2003).

In the Salto Grande reservoir of the Uruguay river, Quirós and Luchini (1982) and O'Farrel and Izaguirre (1994) observed the reduction in the number of plankton species downstream from the reservoir.

Petts (1984) indicated that reservoirs are an important source of plankton for a river. The high phytoplankton density 220 km downstream from Yacyretá corresponds to what was pointed out by several authors who registered a high algal density downstream from some dams, as far as 350 km from them (Talling and Rzóska, 1967; Hynes, 1970; Hammerton, 1972; Literáthy et al., 2002).

Although nutrient enrichment usually favours the development of Cyanophyceae during the first year of resevoir operation (Petts, 1984), there was a quantitative reduction of this group in Yacyretá, as well as down-

Table 2. List of algae recorded in the Paraná river (pre and post-impoundment periods) and accounting for more than 1% of total phytoplankton density. S1: Station 1 (Left bank, water from High Paraná river), S2: Station 2 (Right bank, water from Paraguay river); ■: >100 ind.mL^{-1}, □: 50-100 ind.mL^{-1}, +: <50 ind.mL^{-1}. Abbrev.: Abbreviated names of species used in DCA of Figure 4.

	Abbrev.	Pre		Post	
		S1	S2	S1	S2
CYANOPHYCEAE					
Anabaena planctonica Brunnth.			+		+
Anabaena spiroides Kleb.	An spir	□		+	
Cylindrospermopsis raciborskii (Wolosz.) Seen. & Subba Raju	Cy ra	■			
Merismopedia tenuissima Lemm.		+	+	+	+
Planktolyngbya subtilis (W. West) Anagn. & Kom.	Pl sub	■			
Raphidiopsis mediterranea Skuja	Ra me	■			
CHLOROPHYCEAE					
Volvocales					
Chlamydomonas leptobasis Skuja	Chla le	+		■	
Chlamydomonas microsphaera Pasch. & Jahoda		+	+	+	+
Chloromonas acidophila (Nygard) Gerloff & Ettl	Chl ac	+	+	■	+
Chloromonas gracilis (Matwienko) Ettl		+	+	+	+
Eudorina elegans Ehr.		+	+	+	+
Chlorococcales					
Actinastrum hantzschii Lagerh.		+	+	+	+
Ankistrodesmus gracilis (Reinsch) Kors.		+		+	
Ankyra judayi (G. M. Smith) Fott		+	+	+	+
Chlorella vulgaris Beij.	Chlo vu	+		■	
Choricystis cylindracea Hind.				+	
Choricystis minor (Skuja) Fott	Cho mi	+	+	■	+
Coelastrum microporum Näg. in A. Braun		+		+	
Crucigenia quadrata Morr.		+	+	+	+
Crucigenia rectangularis (Näg.) Kom.				+	
Dictyosphaerium ehrenbergianum Näg.		+		+	
Dictyosphaerium tetrachotomum Printz		+		+	
Didymocystis bicellularis (Chod.) Kom.		+		+	
Micractinium bornhemiense (Conr.) Kors.		+		+	+
Monoraphidium contortum (Thur.) Kom.-Legn.	Mo co	□	+	■	+
Monoraphidium minutum (Näg.) Kom.-Legn.	Mo mi	+	+	■	+
Monoraphidium pusillum (Printz) Kom.-Legn.	Mo pu	□	+	■	+
Oocystis marssonii Lemm.		+		+	
Pediastrum duplex Meyen		+		+	
Pediastrum simplex Meyen		+		+	
Pediastrum tetras (Ehr.) Ralfs		+		+	
Scenedesmus acuminatus (Lagerh.) Chod.		+	+	+	+
Scenedesmus ecornis (Ehr.) Chod.	Sc ec	+	+	■	+
Scenedesmus quadricauda (Turp.) Bréb. sensu Chod.		+	+	+	+
Sphaerocystis planctonica (Kors.) Bourr.				+	
Sphaerocystis schroeteri Chod.		+		+	

	Abbrev.	Pre		Post	
		S1	S2	S1	S2
Tetraedron caudatum (Corda) Hansg.				+	
Tetrastrum heteracanthum (Nordst.) Chod.		+	+	+	
EUGLENOPHYCEAE					
Euglena sp.		+	+	+	+
Phacus sp.			+		+
Strombomonas ensifera (Daday) Defl.			+		+
Strombomonas jaculata (Palmer) Defl.			+		+
Strombomonas maxima (Skv.) Defl.			+		+
Strombomonas ovalis (Playf.) Defl.		+	+		+
Strombomonas verrucosa var. *zmiewika* (Swir.) Defl.		+	+	+	+
Trachelomonas volvocina Ehr.			+		+
BACILLARIOPHYCEAE					
Centrales					
Actinocyclus normanii (Greg. ex Grev.) Hust.				+	
Aulacoseira alpigena (Grun.) Krammer	A alpi	□	□		
Aulacoseira granulata (Ehr.) Simonsen	A gran	■	■	□	■
Aulacoseira herzogii (Lemm.) Simonsen	A herz		□		□
Cyclotella meneghiniana Kütz.	Cy me	□	□	+	+
Discostella stelligera Houk & Klee		+	+	+	+
Pennales					
Craticula cuspidata (Kütz.) Mann		+		+	
Eunotia monodon Ehr.			+		+
Gomphonema augur var. *turris* (Ehr.) Lange-Bertalot		+	+	+	
Gyrosigma acuminatum (Kütz) Rabh.		+		+	
Nitzschia acicularis W. Smith	Nitzs	+	+	+	+
Surirella guatimalensis Ehr.		+		+	
Synedra sp.		+	+		+
Synedra goulardii Bréb.		+		+	+
Tryblionella victoriae Grunow		+	+	+	+
Ulnaria ulna (Nitzsch) Compère		+	+	+	
CHRYSOPHYCEAE					
Synura sp.	Syn		+	+	
Mallomonas sp.	Mall	+		+	
XANTHOPHYCEAE					
Goniochloris tripus Pascher				+	
Pseudostaurastum lobulatum (Nag.) Chodat				+	
DINOPHYCEAE					
Peridinium sp.			+	+	
CRYPTOPHYCEAE					
Rhodomonas minuta Skuja	Rho mi	+	+	■	
Cryptomonas sp.		+	+	+	+
Cryptomonas ovata Ehr.	Cr ov	+	+	■	
Cryptomonas marssonii Skuja	Cr ma	+	+	■	+

Table 3. Results of fitting a multiple regression model to describe the relationship between two first axes of DCA (sample scores which are weighed mean species scores) and eight independent variables: water level, temperature, Secchi disk, disolved oxygen, conductivity, nitrite+nitrate concentration and orthophosphate concentration.

Parameter	Estimate	Standard error	Adjusted R^2 (%)
Dependent variable: Axis 1			
Constant	2.60613	0.423062	0.00
pH	-0.18794	0.0387045	22.76
Secchi disk	-0.218115	0.0534318	27.70
Conductivity	-0.38841	0.116557	39.28
Dependent variable: Axis 2			
Constant	0.37305	0.114122	0.00
pH	-0.0328465	0.0156024	5.87

stream from it, near Corrientes. It is important to point out the increase in Cryptophyceae, which dominated in the reservoir (Meichtry de Zaburlín, 1999), and subsequently reduced their density significantly by half 220 km downstream ($Z = 2.542$, $p = 0.011$). This algal group (Cryptophyceae) alternating with Bacillariophyceae and Cyanophyceae was observed in reservoirs on tributaries of the Paraná (Barbosa et al., 1999; Ludwig et al., 1997). Marked changes in the dominant algal species were also observed in other reservoirs (Magrin and Matsumura-Tundisi, 1997; Marinho et al., 1993).

The most important factor controlling the development of reservoir-phytoplankton would be the residence time of the reservoir water which, during these studies, was approximately 6 days.

In the Ohio river (the largest tributary of the Mississippi river), Sellers and Bukaveckas (2003) suggest that the presence of water regulation structures substantially alters spatial and temporal patterns in light intensity and that these effects have important consequences for phytoplankton production. Short residence times are a parameter that in fact summarizes the effect of river circulation through the reservoir (Armengol et al., 1999).

Conditions observed in the reservoir by Meichtry de Zaburlín (1999) such as the increase in suspended matter and the decrease in water transparency would directly affect the generation time necessary for a complete development of algal populations (Wetzel, 1973). Cryptophyceae (of small size, high surface/volume relationship and good nutrient competitors) with a high generation rate (C-strategists *sensu* Reynolds, 1988) were predominant in such conditions, which are compatible with what was observed by various authors for reservoirs with a high renovation rate (Calijuri et al., 1999; Hynes, 1970; Petts, 1984; Tundisi, 1990). In this algae group, *Cryptomonas* is one of the species that tolerates vertical high-frequency vertical disturbances well (Reynolds, 1987). In tropical reservoirs, very short residence times can favour the development of picophytoplankton (Tundisi, 1993). In oligotrophic reservoirs, the dominance of Chlorophyceae and Bacillariophyceae, in relation to Cyanophyceae, which are usually abundant in eutrophic reservoirs, was observed (Tundisi et al., 1993). *Cylindrospermopsis raciborskii* and *Microcystis aeruginosa* (Cyanophyceae) were the two common species in the Itaipú reservoir (Andrade et al., 1988) and High Paraná river course in previous studies (Bonetto et al., 1982; Zalocar de Domitrovic and Vallejos, 1982); however, they were scarcely represented during the post-impoundment period. These species were characteristics of eutrophic reservoirs in the Tieté river, a tributary of the Upper Paraná (Barbosa et al., 1999).

Calijuri et al. (1999) indicated the dominance of Cyanophyceae (*Microcystis* spp. and *Pseudanabaena* spp.) in Salto Grande (Americana, SP, Brazil), an eutrophic reservoir of the Atibaia river, where high urban and industrial densities produce an increasing deterioration of the water quality. Low nutrients concentration in the Yacyretá reservoir, even in the filling stage (Neiff et al., 2000), and the short residence time, may explain the scarcity of Cyanophyceae in the studied sector.

Dominant algal groups, in the High Paraná river (Brazil-Argentina) before the Yacyretá dam, were Bacillariophyceae, Chlorophyceae and/or Cyanophyceae (CECOAL, 1977; EBY, 1979; Zalocar de Domitrovic and Vallejos, 1982; Andrade et al., 1988). When comparing studies conducted near Ituzaingó (High Paraná) with those carried out after by Meichtry de Zaburlín (1999) in the same sampling area, there was an increase in phytoplankton density. The changes occurring in the phytoplankton community downstream from the reservoir in the period of maturity are very variable and depend on several factors including morphometry, climate, physical and chemical properties of water, residence time, biological interactions and their location in the river gradient. The existence of numerous reservoirs in the Paraná have caused great discontinuities in the potamoplankton, interrupting the natural *continuum* (Vannote et al., 1980). By regulating river flow, reservoirs may have cascading effects on downstream lakes (Barbosa et al., 1999; Dumont, 1999) and the ecological changes that happen downstream from the reservoir depend on its location in the *continuum* according to the serial discontinuity concept (SDC) introduced by Ward and Stanford (in Petts, 1989).

4. Conclusions

Physical and chemical conditions measured on the right bank (water from Paraguay river) were similar at both periods (pre and post-impoundment) whereas conductivity, pH and orthophosphate concentration increased on the left bank (water from High Paraná river and Yacyretá reservoir) after the impoundment.

The density, structure and specific diversity of phytoplankton of the Paraná river showed statistically significant differences between water under the influence of the High Paraná river (Station 1) and that under the influence of the Paraguay river (Station 2).

The phytoplankton of Station 2 (right bank) did not show significant differences in relation to pre-impoundment studies (Zalocar de Domitrovic and Vallejos, 1982; Bonetto et al., 1982), as expected since the Paraguay river (which flows along this bank) remains little affected by human activities and originates in the Pantanal, one of the largest wetlands of the world. In contrast, phytoplankton abundance and structure at Station 1 (water from the High Paraná river) showed marked changes after the creation of the Yacyretá dam. There were significant increases in Chlorophyceae and Cryptophyceae densities, whereas Cyanophyceae and Bacillariophyceae decreased in relation to their pre-impoundment levels (Zalocar de Domitrovic and Vallejos, 1982; Bonetto et al., 1982).

The presence of the Yacyretá reservoir in the High Paraná river causes considerable changes in the density and structure of phytoplankton communities. Although phytoplankton variations would be influenced by the hydrological regime of the river and to associated factors, the increase in phytoplankton density appears to be related to the short residence time of the water in the reservoir and to favorable environmental conditions for observed 220 km downstream from Yacyretá.

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References

ANDRADE, LF., BRUNKOW, RF., XAVIER, CF. and DOMÍNGUEZ, LL., 1988. Fitoplancton e características físico-quimicas do reservatorio de Itaipu, Paraná-BR. In TUNDISI, JG (ed.), *Limnologia e manejo de represas*. Monografías en Limnología Vol. I, Tomo 1. Universidade de Sao Paulo, Escola de Engenharia de Sao Carlos, Centro de Rec. Hídricos e Ecol. Aplic., Brazil, pp. 205-268.

APHA (AMERICAN PUBLIC HEALTH ASSOCIATION), 1981, *Standard methods for the examination of water and wastewater*. APHA, AWWA & WPCF, Washington, 1134p.

ARMENGOL, JJ., GARCIA, C., COMERMA, M., ROMERO, M., DOLZ, J., ROURA, M., HAN, BH., VIDAL, A. and SIMEK, K., 1999. Longitudinal processes in canyon type reservoirs: the case of Sau (N.E. Spain). In TUNDISI, JG. and STRAŠKRABA, M. (eds.), *Theoretical Reservoir Ecology and its application*. International Institute of Ecology (Sao Carlos, SP, Brazil), Brazilian Academy of Sciences (Rio de Janeiro, RJ, Brazil) and Backhuys Publishers (Leiden, The Netherlands).

BALON, EK. and COCHE, AG., 1974. *Lake Kariba. A man-made tropical ecosystem in Central Africa*. Dr. W. Junk bv Publishers. The Hague. 767p.

BARBOSA, FAR., PADISÁK, J., ESPÍNDOLA., ELG., BORICS, G. and ROCHA, O., 1999. The cascading reservoir continuum concept (CRCC) and its application to the river Tietê-basin, São Paulo State, Brazil. In TUNDISI, JG. and STRAŠKRABA, M. (eds.), *Theoretical Reservoir Ecology and its application*. International Institute of Ecology (Sao Carlos, SP, Brazil), Brazilian Academy of Sciences (Rio de Janeiro, RJ, Brazil) and Backhuys Publishers (Leiden, The Netherlands).

BONETTO, AA. and ORFEO, O., 1984. Caracteres sedimentológicos de la carga en suspensión del río Paraná entre confluencia y Esquina (Prov. de Corrientes). *Rev. Asoc. Arg. Petro-Sedim*, vol. 15, no. 3-4, p. 51-61.

BONETTO, AA., WAIS, I. and CASTELLO, HP., 1989. The increasing damming of the Paraná basin and its effects on the lower reaches. *Regulated Rivers: research and management*, vol. 4, no. 4, p. 333-346.

BONETTO, AA., ZALOCAR de DOMITROVIC, Y. and VALLEJOS, ER., 1982. Contribución al conocimiento del fitoplancton del Paraná Medio. I. *Ecosur*, vol. 9, no. 18, p. 189-212.

CALIJURI, MC., DEBERDT, GLB. and MINOTI, RT., 1999. A produtividade primária pelo fitoplâncton na Represa de Salto Grande (Americana-S.P.). In HENRY, R. (ed.), *Ecologia de reservatórios: Estrutura, Função e Aspectos Sociais*. FAPESP, FUNDIBIO, Botucatú, S.P., Brazil.

CECOAL (CENTRO DE ECOLOGÍA APLICADA DEL LITORAL), 1977. *Estudios ecológicos en el área de Yacyretá*. Informe de Avance Nº 2, Corrientes, Argentina. 204p.

DOMITROVIC, HA., BECHARA, JA., JACOBO, R., FLORES QUINTANA, CI. and ROUX, JP., 1994. Mortandad de peces en el río Paraná provocada por sobresaturación de gases: causas y lesiones. *Revista de Ictiología*, vol. 2/3, no. 1/2, p. 49-54.

DUMONT, HJ., 1999. The species richness of reservoir plankton and the effect of reservoirs on plankton dispersal (with particular emphasis on Rotifers and Cladocerans). In TUNDISI, JG. and STRAŠKRABA, M. (eds.), *Theoretical Reservoir Ecology and its application*. International Institute of Ecology (Sao Carlos, SP, Brazil), Brazilian Academy of Sciences (Rio de Janeiro, RJ, Brazil) and Backhuys Publishers (Leiden, The Netherlands).

EBY (ENTIDAD BINACIONAL YACYRETÁ),1979. *Estudios ecológicos en el área de Yacyretá*. Informe de Avance Nº 3, Buenos Aires, Argentina. 153p.

GARRIDO, GG., 1999. Composición y abundancia del zooplancton en dos estaciones de muestreo del embalse de Yacyretá, Argentina en las primeras etapas después del llenado a cota 76 m s.n.m. *Revista de Ictiología*, vol. 7, p. 27-35.

HAMMERTON, D., 1972. The Nile River-a case history. In WARD, JV. and STANFORD, JA (eds.), *River Ecology and Man*. Plenum Press, New York.

HYNES, HBN., 1970. *The ecology of running waters*. Liverpool University Press. Liverpool. 555p.

LAIR, N. and REYES-MARCHANT, P., 1997. The potamoplankton of the middle Loire and the role of the "moving littoral" in downstream transfer of algae and rotifers. *Hydrobiologia*, vol. 356, no. 1-3, p. 33-52.

LEGENDRE, L. and LEGENDRE, P., 1983. *Numerical Ecology*. Elsevier Scientific Publishing Company. Amsterdam. 419p.

LITERÁTHY, P., KOLLER-KREIMEL, V. and LIŠKA, I., 2002. (eds.), *Joint Danube Survey.* Technical Report of the International Commission for the Protection of the Danube River (ICPDR), Vienna/Austria. 261p.

LUDWIG, TV., CECY, IT., RIBEIRO, LH., FLORES, TL., ATAB, D. and SILVA, S., 1997. Phytoplankton and some abiotics parameters in Segredo Hydroelectric Power Plant Reservoir during one year (Paraná State, South Brazil). *Ver. Internat. Verein. Limnol.*, vol. 26, Parte 2, p. 520-521.

LUND, JWG., KIPLING, C. and LE CREN, ED., 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia*. vol. 11, no. 2, p. 143-170.

MAGRIN, AGE. and MATSUMURA-TUNDISI, T., 1997. Phytoplankton assemblages in the Samuel Reservoir (Rondônia State, Brazil) during the filling phase. *Ver. Internat. Verein. Limnol.*, vol. 26, Parte 2, p. 529-534.

MARINHO, MM., HUSZAR, VLM. and SAMPAIO-PINTO, GF., 1993. Estrutura da comunidade fitoplanctônica da lagoa de Juturnaíba, Araruama, RJ, Brasil: Uma comparacao entre os períodos anterior e posterior à construção da barragem no río São João. *Rev. Brasil. Biol.*, vol. 53, no. 3, p. 453-467.

MEICHTRY DE ZABURLÍN, N., 1999. La comunidad fitoplanctónica durante las primeras etapas de llenado del embalse de Yacyretá, Argentina. *Revista de Ictiología*, vol. 7, p. 15-26.

NEIFF, JJ., POI DE NEIFF, ASG., PATIÑO, CAE. and BASTERRA DE CHIOZZI, I., 2000. Prediction of colonization by macrophytes in the Yacyretá reservoir of the Paraná river (Argentina and Paraguay). *Rev. Brasil. Biol.*, vol. 60, no. 4, p. 615-626.

O'FARREL, I. and IZAGUIRRE, I., 1994. Phytoplankton ecology and limnology of the river Uruguay Lower Basin (Argentina). *Arch. Hydrobiol.*, vol. 1/2, p. 155-179.

ORFEO, O. and STEVAUX, J., 2002. Hydraulic and morphological characteristics of middle and upper reaches of the Paraná River (Argentina and Brazil). *Geomorphology*, vol. 44, no. 3/4, p. 309-322.

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.*, vol. 80, no. 2, p. 217-230.

PESO, J. and BECHARA, JA., 1999. Estructura del zoobentos del embalse de Yacyretá, Argentina en dos estaciones de muestreo, antes y después del llenado a cota 76 m s.n.m. *Revista de Ictiología*, vol. 7, p. 37-47.

PETTS, GE., 1984. *Impounded rivers: Perspectives for ecological management*. J. Wiley & Sons, Chichester, UK, 325p.

PETTS, GE., 1989. Perspectives for ecological management of regulated rivers. In GORE, JA. and PETTS, GE (eds.), *Alternatives in regulated river management*. CRC Press, Inc., Florida.

QUIRÓS, R. and LUCHINI, L., 1982. Características limnológicas del embalse de Salto Grande, III: Fitoplancton y su relación con parámetros ambientales. *Rev. Asoc. Cienc. Nat. Litoral*, vol. 13, p. 49-66.

REYNOLDS, CS., 1987. The response of phytoplankton communities to changing lake environments. *Schwiz. Z. Hydrol.*, vol. 49, no. 2, p. 220-236.

REYNOLDS, CS., 1988. Functional morphology and the adaptive strategies of freshwater phytoplankton. In SANDGREN, CD (ed.), *Growth and reproductive strategies of freshwater phytoplankton*. Cambridge University Press, Cambridge.

REYNOLDS, CS., 1999. Phytoplankton assemblages in reservoirs. In TUNDISI, JG. and STRAŠKRABA, M. (eds.), *Theoretical Reservoir Ecology and its application*. International Institute of Ecology (Sao Carlos, SP, Brazil), Brazilian Academy of Sciences (Rio de Janeiro, RJ, Brazil) and Backhuys Publishers (Leiden, The Netherlands).

SELLERS, T. and BUKAVECKAS, PA., 2003. Phytoplankton production in a large, regulated river: A modeling and mass balance assessment. *Limnol. Oceanogr.*, vol. 48, no. 4, p. 1476-1487.

SHANNON, CE. and WEAVER, W., 1963. *The mathematical theory of communication*. Illinois University Press, Urbana. 177p.

STEEL, GD. and TORRIE, JH., 1988. *Bioestadística: principios y procedimientos*. McGraw-Hill, México. 622p.

TALLING, JF. and RZÓSKA, J., 1967. The development of plankton in relation to hydrological regime in the Blue Nile. *J. Ecol.,* vol. 55, no. 4, p. 637-662.

TUNDISI, JG., 1990. Distribuição espacial, seqüência temporal e ciclo sazonal do fitoplâncton em represas: fatores limitantes e controladores. *Rev. Brasil. Biol.*, vol. 50, no. 4, p. 937-955.

TUNDISI, JG., 1993. Represas do Paraná Superior: limnologia e bases científicas para o gerenciamento. In BOLTOVSKOY, A. and LÓPEZ, HL. (eds.). *Conferencias de Limnología*. Instituto de Limnología "Dr. R. A. Ringuelet".

TUNDISI, JG., MATSUMURA-TUNDISI, T. and CALIJURI, MC., 1993. Limnology and management of reservoirs in Brazil. In STRAŠKRABA, M., TUNDISI, JG. and DUNCAN, A. (eds.), *Comparative reservoir limnology and water quality management*. Kluwer Academic Publishers, The Netherlands.

UTERMÖHL, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Int. Ver. Limnol.*, vol. 9, no. 1, p. 1-38.

VANNOTE, RL., MINSHALL, GW., CUMMINS, KW., SEDELE, JR. and CUSHING, CE., 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.*, vol. 37, no. 1, p. 130-137.

WETZEL, RG., 1973. Primary production. In WHITTON, BA. (ed.), *River Ecology*. Blackwell Scientific Publications, Oxford.

ZALOCAR DE DOMITROVIC, Y., 1999. *Estructura y dinámica del fitoplancton en la cuenca del eje potámico Paraguay-Paraná (Argentina).* Thesis, Universidad Nacional de Córdoba. Córdoba, 375p.

ZALOCAR de DOMITROVIC, Y., 2002. Structure and variation of the Paraguay river phytoplankton in two periods of its hydrological cycle. *Hydrobiologia*, vol. 472, no. 1-3, p. 177-196.

ZALOCAR de DOMITROVIC, Y., 2003. Effect of fluctuations in water level on phytoplankton development in three lakes of the Paraná river floodplain (Argentina). *Hydrobiologia*, vol. 510, no. 1-3, p. 175-193.

ZALOCAR de DOMITROVIC, Y. and VALLEJOS, ER., 1982. Fitoplancton del río Alto Paraná. Variación estacional y distribución en relación con factores ambientales. *Ecosur*, vol. 9, no. 17, p. 1-28.