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Flood pulse influence on phytoplankton communities of the south Pantanal floodplain, Brazil

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Abstract

Four sites situated on the Pantanal floodplain (Paraguay River and floodplain) were sampled throughout the annual cycle, mainly during the rising water period, with the aim of evaluating the effects of the flood pulse on the composition and population densities of the phytoplanktonic communities. Comprehensive water chemistry data were collected. Eighty-two taxa were found, numerically dominated by Chlorophyceae (23 taxa). Cryptophyceae (principally *Cryptomonas brasiliensis*) occurred in all samples, and were responsible for 47–58% of the phytoplankton abundance in the studied area. Highest phytoplanktonic population density was at the rising water period, when the limnological changes are most marked as the river water first enters into contact with the floodplain. During this period, when intense decomposition occurs, the Cryptophyceae decreased and the Euglenophyceae increased, except at site 1 (Castelo Lake), where this group were more stable during the year, representing 35–56% of the phytoplankton. In the falling water period (September and October), the phytoplankton was also represented by Bacillariophyceae and Cyanophyceae. In the Pantanal, the great abundance and sometimes dominance of Cryptophyceae, may be due largely to adverse conditions for the development of other groups; the former are adapted to low availability of dissolved nutrients, and high water transparency, such conditions prevailing during the high water period.

Introduction

The Pantanal, an extensive floodplain of approximately 140 000 km^2 (Figure 1), has a great diversity of aquatic habitats. Some are connected to the Paraguay River, such as the big marginal lakes ('baías') and some are not, such as the saline lakes ('salinas') and the smaller, numerous, shallow freshwater lakes that may disappear when the water level drops. Drainage in the Pantanal floodplain is made by countless small drainage canals locally knows as 'vazantes' and 'corixos'. The former are of moderate declivity, without a defined channel, while the latter are well-defined and of longer extension (Carvalho, 1986).

These environments are influenced by the flooding of the Paraguay River and its tributaries, by surface flow or by groundwater. Water level fluctuations and flooding periods (the flood pulse) change the hydrochemistry of the Paraguay River, due to the interactions between the terrestrial and aquatic systems. River water contact with the plains results in dissolved oxygen decreases, supersaturation of free CO_2 and CH_4, and introduction of suspended solids and nutrients. Elevated concentrations of dissolved inorganic carbon and low levels of inorganic particulate matter, as well as algae give the water a black color. Precipitated oxidized iron compounds become abundant in the surface waters, along with increased concentrations of Mn, Co, Hg, Ni, B, I and Rb.

When the flooding is in the rising water phase, all of these alterations promote a natural phenomenon of water quality deterioration locally known as 'Dequada'. Depending on the magnitude of the event, an expressive amount of fish dies due to respiratory stress (Calheiros & Ferreira, 1997; Calheiros

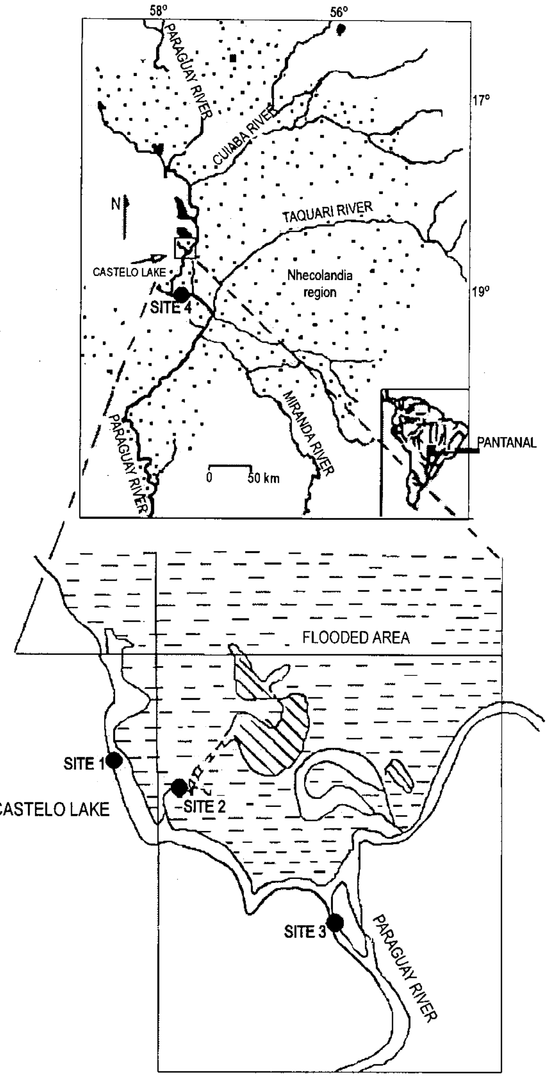

Figure 1. Location of the Pantanal wetland and Castelo Lake, Brazil. The full circles indicate the sampling sites. Source: Calheiros & Hamilton (1998).

& Hamilton, 1998; Hamilton et al., 1995, 1997; Resende, 1992).

The flood pulse is the main factor influencing the phytoplankton communities of floodplains (Bayley, 1991, Junk & Da Silva, 1995; Junk et al., 1989). Phytoplankton species composition and abundance change in response to the duration and intensity of the hydrological and water chemistry alterations. This fact has been observed in floodplain studies of the Parana River, in Brazil and Argentina (Garcia de Emiliani, 1990; Train & Rodrigues, 1997), in the Orinoco River basin, in Venezuela (Hamilton & Lewis, 1987), and in the Amazon River, Brazil (Engle & Melack, 1993; Fisher & Parsley, 1979).

Despite the extension and richness of habitats in the Pantanal floodplain, little is known about the phytoplankton taxonomy and ecology. Such knowledge is restricted mainly to lakes in the northern part of the Pantanal. These shallow lakes have clear, turbulent waters, many macrophytes, low to moderate ionic concentrations, and are with or without river connections. Lists of species for various water bodies of the Mato Grosso (northern Pantanal) have been provided by De-Lamonica Freire (1985, 1989a,b, 1992), De-Lamonica Freire et al. (1992), De-Lamonica Freire & Heckman (1996), Menezes (1986, 1989), Dias (1989), Menezes & Fernandes (1989), Lima (1990) and Figueiredo (1991).

With regard to ecological studies, the temporary environments of the northern Pantanal have been studied by Heckman et al. (1996). They have high ionic concentrations (conductivity up to 600.0 μS cm^{-1}), high pH (e.g., 9.0), supersaturation of dissolved oxygen (400%), and temperatures of up to 40.0°C. Under these conditions, seasonally alternating intense 'blooms' of Euglenophyceae (*Euglena sanguinea, Euglena gracilis*), Chlorophyceae and Zygnemaphyceae have been observed.

Among the northern Pantanal lakes, a turbulent lake, 1.8–2.3 m in depth, without a connection to the Cuiabá River, was found to have abundant colonial cyanobacteria as the dominant group (Silva, 1990). In the southern Pantanal, a deeper lake, 5.0–6.0 m in depth, and connected to the Paraguay River, was found to have an abundance of the classes Bacillariophyceae, Zygophyceae and Chlorophyceae (Espíndola et al., 1996).

Also in the southern Pantanal, lakes of the 'Nhecolândia' region (Figure 1), without a direct connection with any river, and with rainfall apparently their main source of water, have great hydrochemical variety, varying from freshwater to saline, the latter with high ionic concentration (conductivity above 2000.0 μS cm^{-1}), high pH (e.g., 9.8), and high primary productivity. The phytoplankton has been as yet poorly studied, with, at present, only qualitative data being available. In the freshwater lakes, Zygnemaphyceae, Euglenophyceae and filamentous Chlorophyceae and Cyanophyceae are prominent (Ferreira & Mattos, personal communication; Mourão, 1989), while in the saline lakes, only species of Cyanophyceae (families Chroococcaceae, Nostococaceae and Oscillatoriaceae) have been found (Mourão, 1989).

The river tributaries and oxbow lakes are fed every year by floods of the main rivers, and have high concentrations of sediments, low phytoplankton biomass, and abundance of Chlorophyceae and Bacillariophyceae (Oliveira & Calheiros, 1998; Silva, 1990).

Besides taxonomic studies, other works have focused mainly on differences between the dry and wet seasons. Studies on the variation of community structure and dynamics in relation to the flood pulse are new to this region. The aim of the present study was to analyze the influence of the changes in the physical and chemical properties of the water occurring during different phases of the hydrological cycle, with emphasis on the rising water period, on phytoplankton community structure, in part of the River Paraguay, and its floodplain.

Study area

The Paraguay River runs from north to south collecting the waters of large tributary rivers on the left margin, including the Cuiabá, Taquari and Miranda. On the right margin, there is a series of river-connected extensive lakes such as Castelo Lake, surrounded by higher land. Our study area is a portion of the Paraguay River, including the latter lake (Figure 1).

In the study area, flooding is seasonal and is usually delayed by about 3 months in relation to the rainfall in the north. Due to the time required to move down through the floodplain, this flood water only reaches the area between April and June, when rainfall has already stopped in the northern part. Flooding occurs as a result of river overflows, local precipitation, or a combination of both processes (Calheiros & Ferreira, 1997).

The direction of the water flow depends on the hydrological phase, going towards the river in the falling/dry phases, going from the river in the rising phase, before running again towards the river during the period of the full flood, after the whole system coalesces. The Paraguay River fluctuation level is unimodal, varying from 2 to 5 m during the year. This river is the deepest of the region (mean of 8.6 m).

Generally, the floodplain waters are shallow (1–2 m) but with substantial flow. The lakes are shallower than the rivers (3–6 m), although they usually retain water during the dry season (Hamilton et al., 1995). Castelo Lake is located north of Corumbá City (18° 34′ S and 57° 34′ W), on the right margin of the Paraguay River, in an extensive vegetated area. It receives floodplain water from numerous drainage channels and/or through the river mouth, when river level is higher than that of the lake, and also from other diffuse points (Calheiros & Hamilton, 1998). During the high water phase, aquatic plants colonize the floodplain, dying during the dry phase. Part of this material is carried to the lake by the subsequent flood. Floating and submerged aquatic vegetation, with many roots, are very abundant (Hamilton et al., 1995; Pott et al., 1989, 1992), and include *Utricularia* sp., *Cabomba piauhyensis*, *Ludwigia* sp., *Eichornea azurea*, *E. crassipes*, *Scirpus cubensis*, *Salvinia* sp., *Cyperus giganteus*, *Thypha dominguensis*, and *Pontederia cordata*.

The climate is hot and humid in the summer and cold and dry in the winter, with distinct dry and wet seasons, resulting in seasonal flooding and desiccation of the extensive plain. Greater rainfall occurs from November to March (Soriano, 1997). The litology consists of alluvial sediments of the Pantanal formation, in loamy and sandy phase, in alternate and discontinuous formations (Amaral Filho, 1986).

Materials and methods

Is this study, the following sites were sampled: Site 1, Castelo Lake (18° 34′ S and 57° 34′ W); site 2, a drainage channel (‘corixo’) of the Castelo Lake floodplain; site 3, Paraguay River on the outflow of Castelo Lake; and site 4, Paraguay River near Corumbá City (18° 59′ S and 57° 42′ W) (Figure 1).

Sampling was conducted during rising water (March to May), as well as at the end of the dry season (February), during high water (July) and during falling water (October), during 1996. Monthly sampling (January to December) was also conducted at station 4.

Subsurface water samples were taken with a Van Dorn bottles. Water temperature, dissolved oxygen, pH and conductivity were measured with portable potentiometers (DIGIMED). Total alkalinity was analyzed by the Gran titration method (Gran, 1952) and free CO_2 was calculated according to Kempe (1982). Chlorophyll *a*/phaeopigments was analyzed by method of Marker et al. (1980). Transparency of water were obtained using Secchi disc. Total suspended solids, and organic matter (%) was determined by the gravimetric method (APHA, 1985). Total nitro-

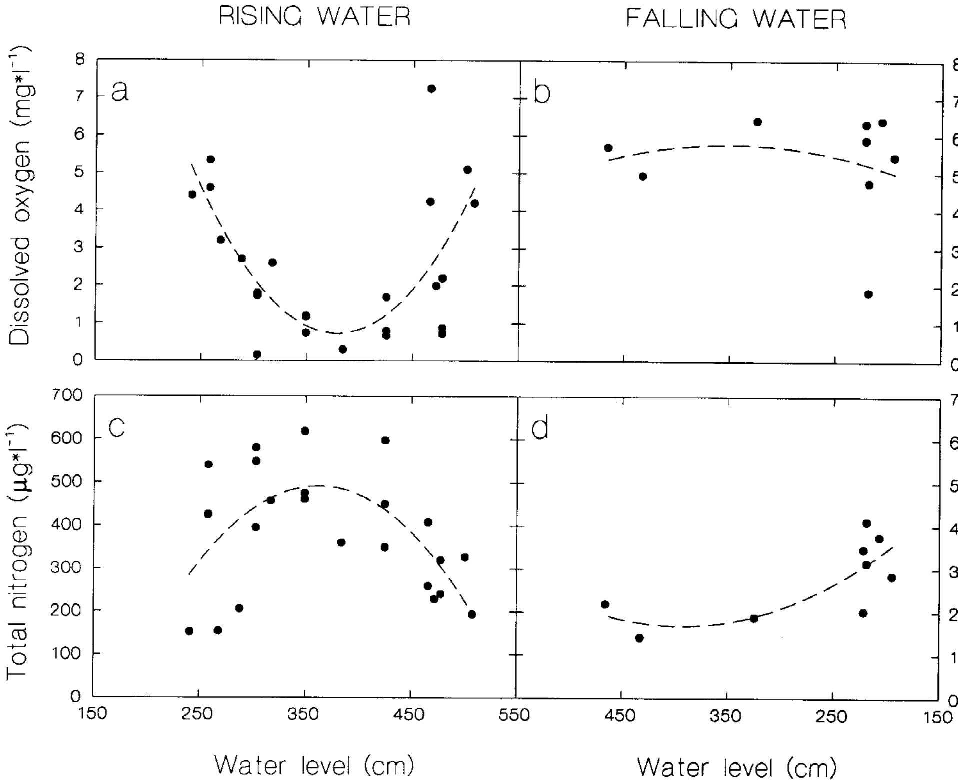

Figure 2. Relationship between dissolved oxygen (a,b), total nitrogen (c,d) and water level in the rising and falling waters phase in the Paraguay River and flooded area.

gen and phosphorus (TN and TP) and PO_4^{3-}, were analyzed by colorimetric analysis, as described by Mackereth et al. (1978) and Wetzel & Likens (1991). NO^{3-} and NH^{4+}were analyzed by colorimetric analysis by flux injection (Krug et al., 1983; Nobrega et al., 1991; Zagatto et al., 1981).

Hydrometric level data of the Paraguay River were obtained from daily readings carried out by the Brazilian Navy on the limnimetric rule, downriver at Ladário City, near Corumbá (19° 02′ S and 57° 33′ W).

Sub-samples for analysis of the phytoplankton community were fixed with acetic lugol solution. Aliquots from these sub-samples were analyzed quantitatively, according to Uthermöhl (1958), using an inverted Zeiss microscope. Individuals (cells, colonies, cenobies and filaments) were counted in at least 150 alleatory fields. Dominant and abundant species were established by the approach described in Huszar (1994).

ANCOVA was used to test the influence of water level and phase on dissolved oxygen, total nitrogen, and total phosphorous concentrations, and water transparency, as well as phytoplankton abundance (Wilkinson, 1990). Dissolved oxygen can be considered a good indicator of water quality, while the remaining three chemical and physical variables directly influence phytoplankton communities. Data from all four sites were pooled.

Results and discussion

Abiotic factors

The magnitude of the flood of the previous year and the amount of rain in the upper basin, which determine the extension of the flooding on the floodplain, govern the intensity of the annually occurring hydrochemical changes (Hamilton et al., 1997). In 1996, the magnitude of such changes was intermediate between 1994 and 1995, occurring mainly in the flood area and in a small section of the Paraguay River. The maximum flood was in June, reaching 5.08 m (Figure 4e).

Temperatures of about 29.0°C were registered in the rising water phase (Table 1). Concentrations of

Table 1. Variation in limnological variables during the study period in the Paraguay River and floodplain. Mean values during rising water phase (I) and high, falling and dry phases (II). n = 7 (floodplain) and n = 13 (Paraguay River)

Variables	Site 1	Site 2	Site 3	Site 4
	I–II	I– II	I–II	I– II
Water temperature (° C)	28.9–25.7	28.4–26.3	28.8–27.2	28.9–27.3
Dissolved oxygen (mg l^{-1})	1.1–5.8	0.6–3.6	1.7–5.4	1.9–4.9
Alkalinity (μeq l^{-1})	318.3–567.2	368.5–607.1	270.0–540.4	318.2–527.4
Free CO_2 (mg l^{-1})	11.7–4.5	15.5–9.9	6.8–6.2	10.0–10.9
pH	6.4–7.1	6.3–6.8	6.5–6.9	6.5–6.7
Conductivity (μS cm^{-1})	52.5–54.4	47.6–51.5	41.8–52.3	46.8–45.5
Chlorophyll *a* (μg l^{-1})	1.6–nd	2.2–nd	1.5–nd	1.9–3.1
Phaeopigment (μg l^{-1})	6.0–6.8	2.2–nd	3.4–nd	4.0–4.2
Water transparency (m)	0. 8–0.7	0.8– 1.2	1.0–0.5	0.8–0.9
Total suspended solids (mg l^{-1})	25.2–37.8	31.4–31.3	10.8–31.2	37.7–42.0
Organic matter (%)	37.3–24.9	37.9–35.3	28.0–21.8	31.0–20.7
Total nitrogen (μg l^{-1})	486.0–382.4	447.0–365.8	446.8–368.6	313.1–227.8
NO_3^- (μg l^{-1})	19.4–nd	2.6–6.5	19.9–19.0	26.6–26.4
NH_4^+(μg l^{-1})	51.2– nd	10.7–67.1	63.3–5.7	17.8–22.2
N:P ratio (dissolved forms)	20.3–0.5	16.0–6.6	6.7–1.3	18.6–3.0
Total phosphorus (μg l^{-1})	9.9–59.7	51.0–90.0	51.4–55.9	53.7–84.7
PO_4^{3-}(μg l^{-1})	5.5–22.5	6.7–11.39	11.1–17.8	7.2–12.2

nd, not detected

dissolved oxygen oscillated from 0.6 mg l^{-1} (5.4% of saturation) to 5.8 mg l^{-1} (62.1% of saturation) in the flooded area and from 1.7 mg l^{-1} (22.5% of saturation) to 5.4 mg l^{-1} (70.6% of saturation) in the Paraguay River. In both areas, the dissolved oxygen concentration was lower during rising water, influenced by water level (r^2 = 0.470; P = 0.001); the influence of water level during falling water was not significant (P = 0.927) (Figure 2a,b).

During the rising water period, there was a decrease in pH, alkalinity and conductivity (except at site 4 for the latter), while increases in free CO_2 concentrations were observed at sites 1, 2 and 3. Chlorophyll *a* concentrations were consistently low (mean values less than 3.2 μg l^{-1}) and concentrations of phaeopigments generally greater than those of chlorophyll *a* (Table 1).

The recorded concentrations of particulate N and P are low as compared to other rivers (Meybeck, 1982, 1988). Figure 2c,d shows the relationship between total nitrogen (dissolved and particulate) and water level. The greatest influxes of TN occurred during the flooding when the river level was around 3.5 m. The increase of TN in the rising water period was significantly related with water level (r^2 = 0.358; P = 0.009, Figure 2c) and was probably a result of decomposition of submerged inorganic matter, as recorded by Calheiros (1995). TN tended to increase during the falling water period, but the relationship was not significant (P = 0.089, Figure 2c,d).

Total phosphorous concentration was directly related to the variations in water level (r^2 = 0.503; $P<0.001$), with lower values during high water (Figure 3a). Dilution effects seem to be very important for phosphorous in this system during the high water phase.

The ratio of dissolved N:P, during the rising water phase, was close to the ideal supply range (10–20) of these nutrients for algae (Bochart, 1996; Reynolds, 1984) varying from 6.7 to 20.3, while in the other phases this ratio were smaller (0.5–6.6) (Table 1).

Suspended solids concentrations were higher in the river than in the flooded area. In the latter area, water transparency was, in general, greater than 70 cm (Table 1). Transparency was significantly related with water level (r^2 = 0.899; $P<$ 0.001). In the river, the period of highest concentrations of solids, with reduced water transparency (<40 cm), was during low water (Figure 3b).

Table 2. Phytoplanktonic genera and species recorded in the Paraguay River and floodplain during the study period

NOSTOCOPHYCEAE	CRYTPOPHYCEAE
Anabaena circinalis Rabenhorst 1852	*Cryptomonas brasiliensis* Castro, Bicudo & Bicudo 1991
Anabaena sp.	*Cryptomonas* sp.
Chroococcus sp.	*Chroomonas* sp.
Coelosphaerium confertum W. & G.S. West, 1896	
Gloeocapsa sp.	CHLOROPHYCEAE
Merismopedia punctata Meyen, 1893	*Ankistrodesmus gracilis* (Reinsch) Korsikov 1953
Merismopedia sp.	*Actinastrum hantzschii* Lagerheim 1882
Microcystis aeruginosa Kützing, 1846	*Closteriopsis* sp.
Oscillatoria sp. 1	*Coelastrum microporum* (Nageli) Bohlin 1987
Oscillatoria sp. 2	*Crucigenia tetrapedia* (Kirch.) W. & G.S. West 1902
	Crucigeniella pulchra (Nageli) Bohlin 1897
EUGLENOPHYCEAE	*Dictyosphaerium ehrenbergianum* Nag. 1949
Euglena acus Ehrenberg, 1838	*D. pulchellum* Wood 1872
E. spirogyra Ehrenberg, 1838	*Eudorina elegans* Ehr. 1904
Euglena sp.	*Eutetramorus fottii* (Hind.ák) Komárek 1979
Phacus orbicularis Huebner 1886	*Golenkinia radiata* Chodat 1894
P. tortus (Lemm.) Skv. 1928	*Keratococcus bicaudatus* (A. Braun) Boye-Petersen
P. suecicus (Lemm.) Pascher & Lemm. 1913	*Lagerheimia chodati* Bernard 1908
P. verrucoso (Lemm.) Deflandre 1927	*Micractinium pusillum* Fresenius 1858
Phacus sp.	*Monoraphidium arcuatum* (Kors) Hind. 1970
Strombomonas acuminata (Schm.) Defl. 1930	*M. griffithii* (Nygaard) komarková-Legnerová 1983
S. ensifera (Daday) Deflandre 1930	*M. tortile* (W. et G.S. West) Kom.-Legll. 1969
S. fluviatilis (Lemm.) Deflandre 1930	*Oocystis lacustris* Chodat 1897
Strombomonas sp.	*Pediastrum tetras* (Ehr.) Ralfs 1844
Trachelomonas acanthophora Stokes 1894	*Scenedesmus acuminatus* (Lagrheim) Chodat 1902
T. cervicula Stokes 1890	*S. denticulatus* Lagrheim 1882
T. estriada Stokes 1899	*Scenedesmus* sp1
T. hispida (Pet.) Stein emend. Deflandre 1926	*Scenedesmus* sp2
T. similis Stokes 1890	
T. oblonga Lemm. 1899	ZYGNEMAPHYCEAE
T. volvocina Ehr. 1838	*Closterium* sp1
T. volvocinopsis Swir. 1914	*Closterium* sp2
Trachelomonas sp1	*Cosmarium* sp.
Trachelomonas sp2	*Staurastrum tringularis* Meyen, 1884
	Staurastrum sp.
BACILLARIOPHYCEAE	*Staurodesmus* sp.
Aulacoseira distans (Ehr.) Simonsen 1979	*Xanthidium* sp.
Aulacoseira herzogii (Lemm.) Simonsen 1910	
A. granulata var. *angustissima* (O.F. Müller) Simon. 1979	DINOPHYCEAE
A. granulata var. *granulata* (Ehr.) Simonsen 1979	*Peridinium* sp.
Cyclotella meneghiniana kützing 1844	
Eunotia curvata	XANTHOPHYCEAE
Eunotia sp.	Isthmochloron gracile (Reinsch) Skuja 1949
Navicula sp. 1	
Navicula sp. 2	CHRYSOPHYCEAE
Nitzschia sp.	*Dinobryon divergens* Imhof 1887
Urosolenia longiseta (Zach.) Round & Crawford 1990	*D. sertularia* Ehr. 1835
Thallassiosira weisflogii (Grun.) Fryxell & Hasle 1991	*Mallomonas* sp.

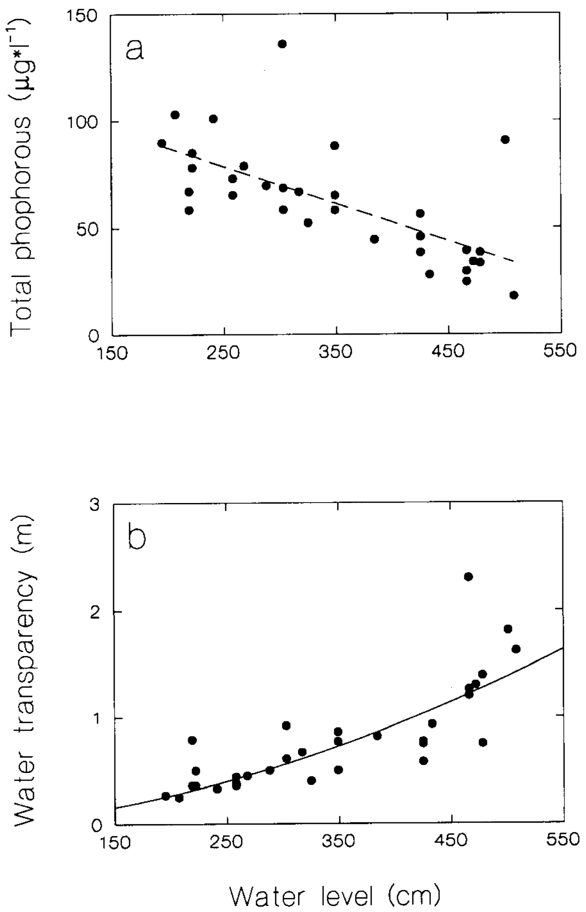

Figure 3. Relationship between total phosphorus (a), transparency of water (b) and water level in the rising and falling water phases in the Paraguay River and flooded area.

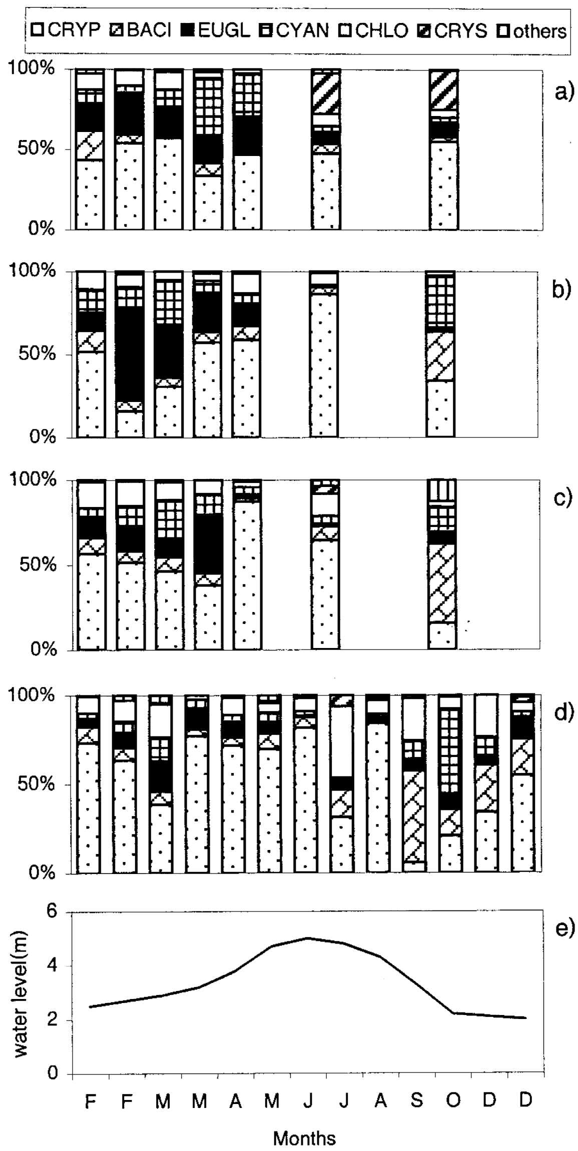

Figure 4. Fluctuations in the phytoplankton community composition (percent of total density) at sites 1 (a), 2 (b), 3 (c) and 4 (d). (e) shows the variation in the water level of the River Paraguay.

Phytoplankton community

Whenever possible, identification was made to the genus or species level, with 82 taxa being recorded, distributed in the classes Chlorophyceae (23), Euglenophyceae (22), Bacillariophyceae (12), Nostocophyceae (10), Zygnemaphyceae (seven), Cryptophyceae (three), Chrysophyceae (three), Xanthophyceae (one) and Dinophyceae (1) (Table 2). Although presenting greater species richness, the Chlorophyceae had low abundance (Table 2, Figure 4).

In the flooded area (sites 1 and 2), there was a prevalence of Cryptophyceae (Figure 4a,b), in contrast to the Amazon and Parana environments. In the former, an abundance of Chlorophyceae and Zygnemaphyceae has been found (Fisher & Parsley, 1979; Huzsar, 1994), while, in the latter, Bacillariophyceae and Chlorophyceae were found to be dominant (Train & Rodrigues, 1998). In lentic environments of the Pantanal, dominance of Cyanophyceae has been recorded in the northern part, and of Bacillariophyceae and Chlorophyceae, in the south (Lima, 1996 and Espíndola et al., 1996, respectively).

The phytoplankton composition of the Paraguay River (sites 3 and 4), was quantitatively dominated most of the year by the class Cryptophyceae (*Cryptomonas brasiliensis*, *Cryptomonas* sp. and *Chroomonas* sp.). During the falling water period (September and October), the classes Bacillariophyceae (*Aulacoseira distans* and *A. granulata*) and Cyanophyceae (*Merismopeida punctata*, *Merismopedia* sp., *Oscillatoria* sp., *Gloeocapsa* sp.) were especially abundant (Figure 4c,d).

The Paraguay River was found to have a phytoplankton composition similar to other floodplain rivers such as the Parana, the Amazon and the Orinoco, the only observed differences being basically in species abundance. In the latter rivers, there is a greater abundance of Bacillariophyceae, with a prominence of *Aulacoseira granulata*, Chlorophyceae and Cyanophyceae (Garcia de Emiliani, 1990; Huszar, 1994; Oliveira et al., 1994; Weibezahn et al., 1990). In the Parana River, Cryptophyceae has also been recorded as being quantitatively and qualitatively important, mainly at the junction of the Paraguay and Parana Rivers (Argentina), occasionally alternating in dominance with Chlorophyceae and Cyanophyceae.

Cryptophyceae are small cells (6–10 μm), with reduced surface/volume ratios. According to Reynolds (1984), such nanoplankton has high metabolic activity and high production/biomass ratios, indicating a high degree of adaptability and efficiency in the use of nutrients under extreme conditions of brightness. The biology of these algae is poorly known; according to Klaveness (1988), they are opportunistic, developing mainly under adverse conditions such as heterotrophic environments. The biomass contribution of these algae is very low, explaining the low chlorophyll *a* concentrations found in this study (Table 1).

A decrease in Cryptophyceae density was observed during the rising and falling water periods, except at site 1 (Castelo Lake), where this group were more stable during the year, representing 35–56% of the phytoplankton (Figure 4a).

In the rising water period, the Euglenophyceae (*Trachelomonas volvocina* and *T. volvocinopsis*) were the second largest group with regard to species richness and abundance, followed by Chlorophyceae and Cyanophyceae (Figure 4a–d). The Euglenophyceae was particularly well represented at site 2, coinciding with low values of dissolved oxygen and high quantities of inorganic matter and nutrients. This group is also considered opportunistic, living in heterotrophic environments that have low levels of dissolved oxygen (Figure 2a,b).

In the high water phase, Cryptophyceae was a dominant group in all the environments. In the Paraguay river, this group was substituted by Chlorophyceae in one sample (end of high water phase), returning to dominance the following month (Figure 4d).

In the falling water phase, at sites 2, 3 and 4, there was an accentuated decrease of Cryptophyceae density, and a dominance of Bacillariophyceae (*Aulacoseira granulata* and *A. distans*) and Cyanophyceae (*Gloeocapsa* sp. and *Oscillatoria* sp.) (Figure 4b–d), probably associated with greater mixing of the water column, due to climatological factors (wind and precipitation), as also observed by Train & Rodrigues (1998) in the Parana River. In Castelo Lake, Chrysophyceae (*Dinobryon sertularia* and *D. divergens*) was the second most abundant phytoplanktonic group in this period (Figure 4a).

In floodplain rivers, biomass and productivity of phytoplankton generally increase from the main river to the secondary rivers and marginal ponds (Garcia de Emiliani, 1990). In the present study, the following densities were found: 143 040 (dry period) to 531 620 ind. l^{-1} (rising water) in Castelo Lake (site 1), 170 180 (rising water) to 301 210 ind. l^{-1} (also rising water) at the drainage Channel (site 2), and 23 000 (high water) to 272 000 ind. l^{-1} (rising water) in the Paraguay River (sites 3 and 4) (Figure 5). Cryptophyceae was responsible for density peaks in all of the cases, except in the falling water period for the Paraguay River, when Bacillariophyceae (*Aulacoseira distans*) prevailed.

The density of phytoplakton was influenced by water level (r^2 = 0.226; $P<0.001$), with significant increases during the rising and falling water phases (water level 3–4 m). Both rising and falling water periods represent occasions of augmented plain–river interaction and greater availability of nutrients, from the river to the plains during rising water and the opposite during falling water, thereby perhaps explaining the increases in phytoplankton biomass during these periods in the river.

In the flooded area (sites 1 and 2), a peak was observed in the rising water phase. However, at site 2, high phytoplanktonic density was also observed during high water (Cryptophyceae) and falling water (abundance of Cryptophyceae, Bacillariophyceae and Cyanophyceae).

In the river, phytoplankton density peaks were observed in the rising water phase, with abundance of Cryptophyceae and Euglenophyceae, and, in the falling water, with abundance of Bacillariophyceae (Figure 4d,e). Similarly, Espíndola et al. (1996) found, in a lake of the region, highest abundance in the beginning of the rising water period.

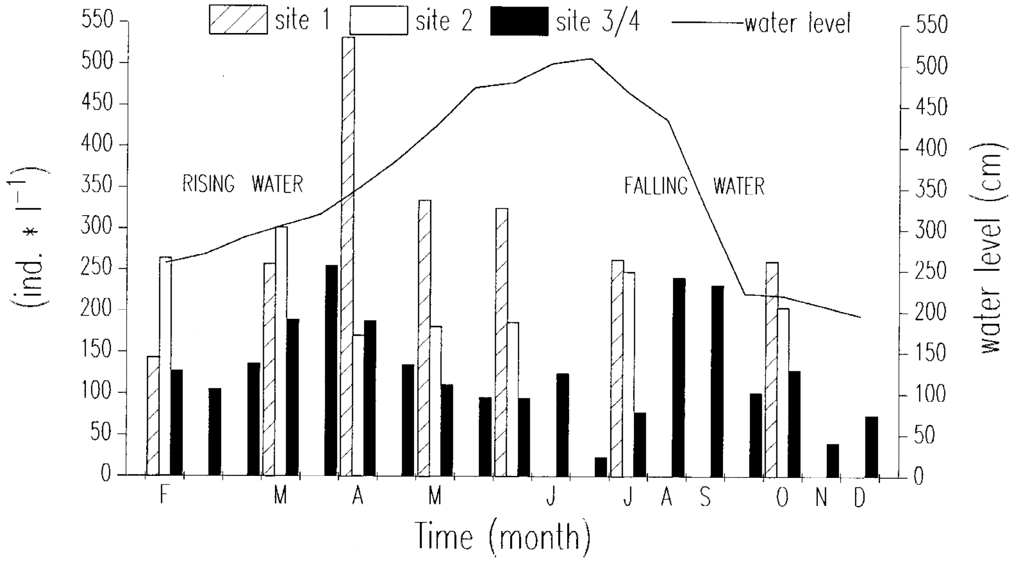

Figure 5. Fluctuations in the total abundance of the phytoplankton at sites 1, 2, 3 and 4. Sites 3 and 4 were plotted together. The line shows the variation in the water level of the River Paraguay.

Table 3. Comparison between minimum and maximum values of phytoplanktonic densities and chlorophyll *a* concentrations of the Paraguay, Parana and Orinoco Rivers

Local	Density (ind. l^{-1})		Chlorophyll *a* ($\mu g\ l^{-1}$)
	Min.	Max.	
Paraguay River, Brazil[1]	40 000	272 000	<1.0–5.0
Paraguay River, Argentina[2]	1 200 000		
Parana River, Brazil[3]	73 600	901 000	2.5
Parana River, Argentina[2]	340 000	1 400 000	2.0–24.0
Orinoco River, Venezuela[4]	65	68 145	<1.0

Sources: (1) This study; (2) Garcia de Emiliani (1990); (3) Train & Rodrigues (1998); (4) Wiebezahn et al. (1990).

The phytoplankton densities obtained in the present study for the Paraguay River are low but, in general, are in the range of those obtained for similar systems such as the Parana, Amazon and Orinoco Rivers (Garcia de Emiliani, 1990; Train & Rodrigues, 1998; Weibezhan et al., 1990) (Table 3). However, in other environments of the Pantanal floodplain, higher densities have been recorded, with values of 300 000–860 000 000 ind. l^{-1} (Espíndola et al., 1996; Lima, 1996).

In the Orinoco and Parana Rivers, the amount of transported sediments is greater during high water, resulting in lower water transparency and phytoplankton density. In the Paraguay river, the opposite is the case, with larger transport of sediments occurring during low water, and reduced water transparency and phytoplankton density (Table 1 and Figures 3b and 5).

Zooplankton grazing in the Paraguay River may have an influence on the phytoplankton populations, because, during the rising water period, the zooplankton population was found to be low (<50 000 ind. l^{-1}), increasing to approximately 550 000 ind. l^{-1}, in the falling water period (unpublished data).

The floodplain environments analyzed in this study are permanently flooded and in communication with the Paraguay River. Due to these characteristics, the composition and abundance of the phytoplankton communities are very similar in both river and floodplain areas. It is not possible to clearly observe species input from the floodplain to the river or vice-versa. However, there was a density increase in the falling water period in the Paraguay River that could be attributed to a contribution from the plains. The same was found for zooplankton, which develop a greater abundance during the falling water period (unpublished data).

The occurrence and, in many cases, dominance of Cryptophyceae in lotic and lentic Pantanal environments, seem to be related to adverse conditions for the development of other groups, such as reduced availability of dissolved nutrients (Hamilton et al., 1995; Heckman, 1994), and elevated water transparency during high water.

In the Parana River, this group seems to be especially associated with lotic environments, having high suspended solids concentrations, during high water periods (Garcia de Emiliani, 1990; Oliveira et al., 1994; Train & Rodrigues, 1998).

The great abundance of Cryptophyceae observed in the present study shows a peculiarity of the Paraguay River in relation to other tropical rivers. As the dynamics of a system such as this, governed by the hydrological regime, are very complex, studies on the phytoplankton community should be continued in order to verify if this pattern repeats in other years; 1996 exhibited low nutrient concentrations as compared to the results of a 5-year study (1994–1998) (Calheiros & Oliveira, in preparation).

Conclusions

In this study of a complex environment of the Paraguay River's floodplain, the Cryptophyceae were found to be abundant. The flood pulse influence on the phytoplankton community was expressed mainly in the dominance of the more resistant and tolerant nanoplanktonic species (classes Cryptophyceae and Euglenophyceae), as a result of the heterotrophic conditions which develop. The observed patterns in the Pantanal differ from other similar environments, probably as a result of external influences on the extensive floodplain (140 000 km^2), in which the Paraguay River is inserted. The rivers of the plain affect the floodplain but also are affected by it.

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References

Amaral Filho, Z. P., 1986. Solos do Pantanal Mato-Grossense. In EMBRAPA-DDT (eds), Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal — 1. In Anais do 1° Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal. Embrapa-CPAP, Documentos 5: 91–104.

APHA, 1985. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, Washington, 1268 pp.

Bayley, P. B., 1991. The flood pulse advantage and restoration of river–floodplain systems. Regulated Rivers Res. Manage. 6: 75–86.

Bochart, M. A., 1996. Nutrients. In Stevenson R. J., M. L. Bothwell & R. L. Lowe (eds), Algal Ecology, Freshwater Benthic Ecosystems. Academic Press, New York: 183–227.

Calheiros, D. F., 1995. Baia do Castelo: exemplo de funcionamento de uma lagoa marginal ao rio Paraguai (Pantanal-MS). In Resumos do VI Congresso Brasileiro de Limnologia, São Carlos, SP: 87.

Calheiros, D. F. & C. J. Ferreira, 1997. Alterações limnológicas no rio Paraguai ('Dequada') e o fenômeno natural de mortandade de peixes no Pantanal Mato-Grossense-MS. Corumbá, Embrapa-CPAP, Bol. Pesq. 7: 48.

Calheiros, D. F. & S. K. Hamilton, 1998. Limnological conditions associated with natural fish kills in the Pantanal Wetland of Brazil. Verh. int. Verein. Limnol. 26: 2189–2193.

Calheiros, D. F. & M. D. Oliveira. Pesquisa Limnológica no Pantanal: uma revisão. Acta Limnol. Brasil. In Anais. do 2° Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal. Embrapa-CPAP, Documentos, in press.

Carvalho, N. O., 1986. Hidrologia da Bacia do Alto Paraguai. In EMBRAPA-DDT (eds), Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal — 1. In Anais. do 1° Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal. Embrapa-CPAP, Documentos 5: 43–49.

De-Lamonica-Freire, E. M., 1985. Desmídioflórula da Estação Ecológica da Ilha Taiamã, Município de Cáceres, Mato Grosso. Tese de Doutorado em Ecologia. Instituto de Biociências, USP, São Paulo, 538 pp.

De-Lamonica-Freire, E. M., 1989a. Catálogo das Algas Referidas para o Estado de Mato Grosso, Brasil, 1. Rev. brasil. Biol. 49: 671–677.

De-Lamonica-Freire, E. M., 1989b. Catálogo das Algas Referidas para o Estado de Mato Grosso, Brasil, 2. Rev. brasil. Biol. 49: 679–689.

De-Lamonica-Freire, E. M., 1992. Desmídias filamentosas (Zygnemaphyceae, Desmidiales) da Estação Ecológica da Ilha Taiamã, Mato Grosso, Brasil. Acta limnol. Brasil. 4: 315–325.

De-Lamonica-Freire, E. M. & C. W. Heckman, 1996. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: III. The algal communities in the Pantanal of Mato Grosso, Brazil, with a comprehensive list of the know species and revision of two desmid taxa. Int. rev ges. Hydrobiol. 81: 253–280.

De-Lamonica-Freire, E. M., C. E. D. M. Bicudo, & A. A. J. De Castro, 1992. Algal Flora of the Poconé Pantanal, State of Mato Grosso, Brazil. I. Euglenaceae. Rev. brasil. Biol. 52: 141–149.

Dias, I. C. A., 1989. Chlorophyta filamentosas do Município de Cáceres e arredores, Mato Grosso, Brasil. Acta bot. Brasil. 3: 3–12.

Engle, L. D. & J. M. Melack, 1993. Consequences of riverine flooding for seston and the periphyton of floating meadows in an Amazon floodplain lake. Limnol. Oceanogr. 38: 1500–1520.

Espíndola, E. G., T. Matsumura-Tundisi & I. H. Moreno, 1996. Estrutura da comunidade fitoplanctônica da lagoa Albuquerque (Pantanal Matogrossense). Mato Grosso do Sul, Brasil. Acta limnol. Brasil. 8: 13–27.

Figueiredo, D. M., 1991. Levantamento Taxonônico da Família Eunotiaceae (Bacillariophyceae) do Pantanal de Poconé, Município de Poconé, Mato Grosso, Brasil. Monografia de Graduação. Instituto de Biociências, UFMT, Cuiabá, 58 pp.

Fisher, T. R. Jr. & P. E. Parsley, 1979. Amazon lakes: water storage and nutrient stripping by algae. Limnol. Oceanogr. 24: 547–553.

Garcia de Emiliani, M. O., 1990. Phytoplankton ecology of middle Parana River. Acta limnol. Brasil. 3: 392–417.

Gran, G., 1952. Determination of the equivalence point in potentiometric titrations, Part II Analyst 77: 661–671.

Hamilton, S. K. & W. M. Lewis Jr., 1987. Causes of seasonality in the chemistry of a lake on the Orinoco River floodplain, Venezuela. Limnol. Oceanogr. 32: 1277–1290.

Hamilton, S. K., S. J. Sippel & J. M. Melack, 1995. Oxygen depletion and carbon and methane production in waters of the Pantanal wetland of Brazil. Biogeochemistry 30: 115–141.

Hamilton, S. K., J. S. Sippel, D. F. Calheiros & J. M. Melack, 1997. An anoxic event and other biogeochemical effects of the Pantanal wetland on the Paraguay River. Limnol. Oceanogr. 42: 257–272.

Heckman, C. W. 1994. New limnological nomenclature to describe ecosystem structure in the tropical wet-and-dry climatic zone. Arch. Hydrobiol. 130: 385–407.

Heckman, C. W., B. R. S. Trindade & E. L Hardoim, 1996. Environmental conditions in the Pantanal of Mato Grosso in relation to natural Euglenophyte populations. Jpn. J. Limnol. 57: 119–132.

Huszar, V. L. M., 1994. Fitoplâncton de um lago amazônico impactado por rejeito de bauxita (Lago Batata, Pará, Brasil): Estrutura da comunidade, flutuações espaciais e temporais. Tese de Doutorado em Ecologia. Universidade Federal de São Carlos, 219 pp.

Junk, W. J. & C. J. da Silva, 1995. Neotropical floodplains: a comparison between the Pantanal of Mato Grosso and the Large Amazonian river floodplains. In: Tundisi, J. G., C. E. M. Bicudo & T. Matsumura-Tundisi (eds), Limnology in Brazil. ABC/SBL, Rio de Janeiro: 195–217.

Junk, W. J., P. B. Bayley & R. E. Sparks, 1989. The flood pulse concept in river–floodplain systems. In Dodge, D. P. (ed.), Proceedings of the International Large River Symposium (LARS). Can. Spec. Publ. Fish. Aquat. Sci. 106: 110–127.

Kempe, S. 1982. Long term records of CO_2pressure fluctuations in fresh waters. Mitt. Geol. Palaont. Inst. Univ. Hamburg. SCOPE/UNEP Sonderband, 52: 91–332.

Klaveness, D., 1988. Ecology of the Cryptomonadida: a first review. In Sandgren, C. D. (ed.), Growth and Reproductive Strategies of Freshwater Phytoplankton. Cambridge University Press, New York: 105–133.

Krug, F. J., B. F. Reis, M. F. Giné, E. A. G. Zagatto, J. R. Ferreira & A. O. Jacintho, 1983. Zone trapping in the injection anlysis. Spectrophotometric of flow level of ammonium ion in natural waters. Analyt. chim. Acta, 151: 39–48.

Lima, D., 1990. Diatomáceas (Bacillariophyceae, Centrales) do Pantanal de Poconé, Estado de Mato Grosso, Brasil: contribuição ao seu conhecimento. Monografia de Graduação. Instituto de Biociências, UFMT, Cuiabá, 50 pp.

Lima, D., 1996. Estrutura das comunidades zooplanctônica e fitoplanctônica do Lago Recreio – Pantanal de Barão de Melgaço-MT. Dissertação de Mestrado em Ecologia. UFSCar, São Carlos, 440 pp.

Mackereth, F. Y. H., J. G. Heron & J. J. Talling, 1978. Water analysis: some revised methods for limnologists. Freshwat. Biol. Assoc. 36, 120 pp.

Marker, A. F. H., E. A. Nusch, H. Rai & M. Rieman, 1980. The measurement of photosynthetic pigments in freshwaters and standardization of methods: conclusions and recommendations. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14: 91–106.

Menezes, M., 1986. Ficoflórula da Chapada dos Guimarães e arredores, Mato Grosso, Brasil: Euglenaceae pigmentadas (Euglenophyceae). Rickia 13: 87–93.

Menezes, M. & V. O. Fernandes, 1989. Euglenaceae (Euglenophyceae) pigmentadas do noroeste do Estado de Mato Grosso, Brasil: municípios de Barra do Bugres, Cáceres, Juína e Porto Espiridião. Hoehnea 16: 35–55.

Meybeck, M., 1982. Carbon, nitrogen, and phosphorus transport by world rivers. Am. J. Sci. 282: 401–450.

Meybeck, M., 1988. How to establish and use world budgets of riverine materials. In Lemran, A. & M. Meybeck (eds), Physical and Chemical Weathering in Geochemical Cycles. Kluwer, Dordrecht: 247–272.

Mourão, G. M., 1989. Limnologia comparativa de três lagoas (duas 'baías' e uma 'salina' do Pantanal da Nhecolândia, MS. Dissertação de Mestrado em Ecologia e Recursos Naturais. Universidade Federal de São Carlos, São Carlos,135 pp.

Nobrega, J. A. M. & A. A. Alberici, 1991. Flow injection spectrophotometric determination of ammonium in natural waters. J. Chem. Educ. 68: 966–972.

Oliveira, M. D. & D. F. Calheiros, 1998. Transporte de nutrientes e sólidos suspensos na bacia do rio Taquari, Pantanal sul, Brasil. Acta limnol. Brasil. 10: 35–45.

Oliveira, M. D., S. Train, L. C. Rodrigues, 1994. Levantamento preliminar do fitoplâncton de rede (exceto Zignemaphyeceae) do rio Parana, Munícipio de Porto Rico, Parana, Brasil. Rev. Unimar 16: 155–174.

Pott, V. J., N. C. Bueno, R. A. C. Pereira, S. M. Salis & N. L Vieira, 1989. Distribuição de macrófitas aquáticas numa lagoa na Fazenda Nhumirim, Nhecolândia, Pantanal, MS. Acta bot. Brasil. 3 (Suppl.): 153–168.

Pott, V. J., N. C. Bueno & M. P. Silva, 1992. Levantamento florístico e fitossociológico de macrófitas aquáticas em lagoas da Fazenda Leque, Pantanal, MS. In Anais do 8° Congr. SBSP: 91–99.

Resende, E. K. de. 1992. Manejo de recursos pesqueiros no Pantanal Matogrossense. In Agostinho, A.A. & E. Benedito-Cecílio (eds), Situação atual e perspectivas da Ictiologia no Brasil. Documentos do IX Encontro Brasileiro de Ictiologia. UEM, NUPELIA, SBA: 97–105.

Reynolds, C. S., 1984. The Ecology Of Freshwater Phytoplankton. Cambridge University Press, New York, 384 pp.

Reynolds, C. S., 1988. Functional morphology and the adapative strategies of freshwater phytoplankton. In Sandgren, C.D. (ed.), Growth and Reproductive Strategies of Freshwater Phytoplakton. Cambridge University Press, New York: 388–433.

Silva, G. A., 1990. Composição e abundância do fitoplâncton durante as fases de cheia e seca na bacia do rio Miranda, MS. Monografia de Graduação. Universidade Federal do Mato Grosso do Sul, Corumbá,48 pp.

Soriano, B. M. A., 1997. Caracterização climática de Corumbá – MS. Embrapa-CPAP. Bol. Pesq. 11: 25 pp.

Train, S. & L. C. Rodrigues, 1997. Distribuição espaço-temporal da comunidade fitoplanctonica. In Vazzoler, A.E.A.M., A.A. Agostinho & N.S. Hahn (eds), A planície de inundação do alto rio Parana: Aspectos físicos biológicos e socioeconômicos. EDUEM, Maringá, 105–115 pp.

Train, S. & L. C. Rodrigues, 1998. Temporal fluctuations of the phytoplankton community of the Baía River, in the upper Parana River floodplain, Mato Grosso do Sul, Brazil. Hydrobiologia 361: 125–134.

Uthermol, H., 1958. Zur Vervollkommmung der quantitativen phytoplankton-methodic. Mitt. int. Ver. Limnol. 9: 1–39.

Wetzel, R. G. & G. E. Likens, 1991. Limnological Analyses, 2 edn. Springer-Verlag, New York, 391 pp.

Wiebezahn, F.H., H. Alvarez & W. M. Lewis Jr., 1990. El Río Orinoco como Ecossistema. Editorial Galac, Caracas, 430 pp.

Wilkson, L., 1990. SYGRAPH: The system for graphics. Evanston, IL: SYSTAT, Inc.

Zagatto, E. A. G., A. O. Jacintho, B. F. Reis, F. J. Krug, H. Bergamin F, L. C. R. Pessenda, J. Mortatti & M. F. Giné, 1981. Manual de análises de plantas e águas empregando sistemas de injeção em fluxo. Universidade de São Paulo/CENA, Piracicaba, 45 pp.