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PHYTOPLANKTON ECOLOGY OF THE MIDDLE PARANÁ RIVER

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RESUMO - ECOLOGIA DO FITOPLÂNCTON NO RIO MÉDIO PARANÁ

Efetua-se uma revisão crítica sobre a ecologia do fitoplâncton do rio principal e dos ambientes lóticos e lênticos da planície aluvial.

As comunidades fitoplanctônicas do rio Médio Paraná estão fortemente condicionadas pelo regime hidro-sedimentológico. As variações temporais do fitoplâncton estão mais influenciadas por este fator do que pelas flutuações nas condições químicas. Não há evidências de que os nutrientes limitem a produção. A elevada turbidez da água limita o crescimento das algas no braço principal do Rio Paraná.

No vale do Rio Médio Paraná a biomassa e a produtividade do fitoplâncton aumenta a seguinte ordem: rio principal, rios secundários e lagoas marginais. Neste último tipo de ambiente, o fitoplâncton está também controlado pela dinâmica hidro-sedimentológica do rio. A cheia das lagoas constitui um processo de intensa mudança inicial nas condições físico-químicas e biológicas. Entretanto, uma característica não menos importante é o particular dinamismo destes ambientes durante os períodos de isolamento. Os fatores climáticos provocam alterações

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abruptas e repentinas das condições abióticas do meio e freqüentes mudanças na composição, densidade e produtividade do fitoplâncton.

A planície aluvial tem um papel importante na manutenção da produtividade do ecossistema do rio Médio Paraná.

ABSTRACT - PHYTOPLANKTON ECOLOGY OF THE MIDDLE PARANÁ RIVER

A critical review of the phytoplankton ecology of the Paraná river mainstream and the lotic and lentic environments of its alluvial plain is carried out.

Phytoplankton communities of the Middle Paraná mainstream are heavily conditioned by the hydrosedimentologic regime. Temporal changes in phytoplankton are influenced more by this factor than by physico-chemical variations. There is no evidence that nutrients limit production. Algal growth is limited by high turbidities in the Middle Paraná mainstream.

In the Middle Paraná flood valley, biomass and phytoplankton productivity increase in the following order: mainstream, secondary channels and alluvial ponds. In these latter environments the phytoplankton is also controlled by the hydrosedimentologic dynamics of the river. The flooding of the floodplain ponds constitutes an intense initial change in the physical, chemical and biological conditions. Nevertheless, its particular dynamism during isolation periods is another important characteristic. Climatic factors cause sudden changes in the environmental conditions and frequent variations in composition, density, and productivity of phytoplankton.

The floodplain plays an important role in maintaining the productivity of the Middle Paraná ecosystem.

INTRODUCTION

A synthesis of ecological information about the Middle Paraná flood valley, on the basis of published and unpublished papers, field experiments, observations, and discussions among other researchers, is presented.

This paper may be complemented by data on the general ecology of the river system including phytoplankton (BONETTO et alii, 1969; BONETTO, 1975; 1976; QUIRÓS & CUCH, in press) already known, as well as by summaries of papers dealing with phytoplankton through 1981 (GARCÍA de EMILIANI & PEROTTI de JORDA, 1982).

MIDDLE PARANÁ MAINSTREAM

Longitudinal distribution

The phytoplankton of the Middle Paraná mainstream shows some variations along the 707 km from the confluence of the Paraguay and Upper Paraná rivers (km 1240) up to Diamante City (km 533).

Quantitative fluctuations are initially associated with the different water qualities of the Upper Paraná (left bank) and the Paraguay (right bank). Both rivers waters flow for 200-300 km (Goya-Diamante stretch), until they mix completely. Population density and structural composition of phytoplankton at Corrientes City (km 1208) has a heterogeneous distribution in cross-section, due to this lack of mixing (BONETTO et alii, 1979; BONETTO, 1983).

In the first stretch (Corrientes-Goya/Esquina), the structural composition of the communities is intermediate between that of the main rivers which form the Middle Paraná; the average population density decreases downstream (Tab. 1). In the second stretch (up to Diamante

Table 1 - Mean values for phytoplankton populations along the Middle Paraná mainstream, Paraguay and Upper Paraná rivers.

RIVER	PARAGUAY	UPPER PARANÁ	MIDDLE PARANÁ* I(2)				MIDDLE PARANÁ II	
Stretch	La Herradura(1) km 60	Itá Ibaté(3) km 1308	Corrientes km 1208	Bella Vista km 1060	Goya km 967	Esquina km 853	Hernandarias(4) km 689	Paraná(5,6) km 601
Density (ind.ml^{-1})	1200	505	744	485	478	340	567	520
Diatomophyceae (%)	71	48	56	59	59	64	60	63
Chlorophyceae (%)	22	22	23	21	22	19	9	12
Cryptophyceae (%)	3	0.5	3	1	1	1	10	12
Cyanophyceae (%)	2	28	16	18	16	14	5	7
Specific diversity (bits.ind.$^{-1}$)					3.23(4)	3.42(4)	3.60	3.61

* river-km 0: Río de la Plata

(1) BONETTO et alii, 1981 (II/78 - XII/79)
(2) BONETTO et alii, 1982 (III/81 - III/82)
(3) BONETTO et alii, 1983 (VI/78 - IV/80)
(4) GARCÍA de EMILIANI, 1981b, 1985 (XII/81 - IV/82)
(5) GARCÍA de EMILIANI, unpubl. data (III/81 - VIII/82)
(6) SCHIAFFINO de MARTA, unpubl. data (I/78 - I/79)

City, km 533) phytoplankton density is more stable and its structural composition changes little from the first stretch; there is a higher relative abundance of Cryptophyceae and Chlorophyceae; while transverse distribution is homogeneous.

Along the Middle Paraná reach, Diatomophyceae is the dominant class. Among these, centric diatoms of the genus *Melosira* are most abundant. Some species of this group, typical of the Upper Paraná, are detected only at Corrientes (left bank) (Tab. 2). Others are present in the Middle Paraná as well as in the Upper Paraná and Paraguay rivers (ZALOCAR de DOMITROVIC & VALLEJOS, 1982; BONETTO et alii, 1981; 1983).

Chlorophyceae are generally subdominant and are noteworthy for species richness (principally Chlorococcales). The number of species appears to increase downstream. Cyanophyceae, subdominant or dominant in the Upper Paraná, diminishes in relative importance downstream and rarely attains high densities in the Middle Paraná reach. Cryptophyceae are quantitatively and qualitatively important in the last stretch, where they occasionally alternate in dominance with Chlorophyceae. Other classes of algae (Zygophyceae, Ulothrycophyceae, Xanthophyceae, Dinophyceae, Chrysophyceae and Euglenophyceae) are present sporadically in low densities.

These structural features, especially the dominance of centric diatoms in the lotic phytoplankton are commonly observed (WHITTON, 1975; HYNES, 1976). The abundance of *Melosira* has also been observed in other rivers of the Rio de la Plata Basin (QUIRÓS & LUCHINI, 1982; di PERSIA & NEIFF, 1986; BONETTO et alii, 1981; 1983; ZALOCAR de DOMITROVIC & VALLEJOS, 1982), and of the world (GREENBERG, 1964; LACK, 1971; TALLING, 1976; LAM, 1979; KUZMIN, 1979; SHIEL et alii, 1982; WELCOMME, 1986). Even when differences in the species composition among rivers are observed, a common characteristic is the abundance of

Table 2 - Common species along the Middle Paraná mainstream, near Corrientes City and Paraná City.

ALONG MAINSTREAM(1,2)	CORRIENTES (km 1208)(1)	PARANÁ (km 604)(2)
	DIATOMOPHYCEAE	
Melosira granulata *M. distans* *M. herzogii* *Cyclotella meneghiniana* *Fragilaria construens* *Rhizosolenia eriensis* *Attheya zachariasi* *Nitzschia actinastroides* *Nitzschia* spp *Synedra* spp *Navicula* spp *Cymbella* spp	*Melosira pseudogranulata* *M. agassizii* *M. dickiei* *Biddulphia laevis* (l.b.) *Hydrosera whampoensis* (l.b.) *Terpsinoe musica* (l.b.) *Tetracyclus* sp (r.b.)	
	Chlorophyceae	
Monoraphidium *M. contortum* *M. griffithii* *Scenedesmus quadricauda* *S. acuminatus* *S. smithii* *Schroederia setigera* *Micractinium pusillum* *Sphaerocystis schroeteri* *Crucigenia quadrata* *Crucigeniella rectangularis* *Tetrastrum staurogeniaeforme* *Dictyosphaerium ehrenbergianum* *Tetraedron minimum*	*Chlamydomonas* sp *Oocystis lacustris* *Errerella bornhemiensis*	*Ankistrodesmus falcatus* *A. gracilis* *Chlamydomonas* spp *Scenedesmus ecornis* *S. intermedius* *S. bicaudatus* *Oocystis* spp *Actinastrum hantzschii* *Coelastrum microporum* *Crucigenia tetrapedia*
	Cyanophyceae	
Raphidiopsis mediterranea *Anabaena spiroides*	*Lyngbya limnetica*	*Anabaenopsis raciborskii*
	Cryptophyceae	
Chroomonas acuta *C. minuta* *Cryptomonas ovata*	*Cryptomonas* sp	*Cryptomonas pusilla* *C. marsonii* *C. erosa* *C. curvata*

l.b. = left bank

r.b. = right bank

(1) BONETTO et alii, 1979; BONETTO et alii, 1982

(2) GARCÍA de EMILIANI, 1981b, 1985 and unpubl.data; SCHIAFFINO de MARTA, 1981; ANSELMI de MANAVELLA, 1986.

forms capable of keeping themselves suspended during strong turbulence (e.g., *Melosira*), and of quick reproduction (e.g., several Chlorococcales, Volvocales, *Anabaena* and *Melosira*) (MARGALEF, 1983).

Available data indicate the presence of 200 taxa. Nevertheless, taking into consideration that complete lists have not been published, that the algae listed were observed in sedimented samples of low volume (Utermöhl, generally between 10 and 30 ml), and that parallel observations of concentrated material recorded additional taxa, it is concluded that the species richness of the mainstream is greater. The few available data suggest that richness as well as specific diversity increase downstream (Tab. 1).

As regards chlorophyll a and primary productivity (Tab. 3), not many data are available which permit

Table 3 - Mean values of chlorophyll a concentration and primary productivity of phytoplankton along the Middle Paraná mainstream.

	CORRIENTES(2) km 1208		ESQUINA(2) km 853	PARANÁ(3) km 601
	l.b.	r.b.		
Chlorophyll a ($mg.m^{-3}$)	10	9.4	6.6	8
Productivity ($mg\ C.m^{-2}.d^{-1}$)	80(1) 400	30(1) 180	200	109

l.b.: left bank

r.b.: right bank

(1) BONETTO et alii, 1979 (II/78 - VIII/79, C^{14} method)

(2) BONETTO, 1983 (IV/81 - I/82, C^{14} method)

(3) PEROTTI de JORDA, 1984 (I/78 - I/79, oxygen method)

estimation of average values representative of successive stretches of the river, and their comparative value is limited. Most determinations were carried out at the initial and final stretches of the Middle Paraná (Corrientes and Paraná Cities, respectively) during different annual hydrologic cycles. Besides, different methodologies to determines primary productivity were used.

Additional determinatios of photosynthetic pigments as well as of primary productivity are needed. Besides, regarding this last parameter it would be useful to review the methodology for the interference supposed to be produced by keeping water from the turbulent river in bottles and for its later exposure in a constantly illuminated area. Other environmental factors (great concentration of suspended solids and high oxygenation) as well as the low concentration of phytoplankton renders inadvisable use of the oxygen method. Usually, the differences among bottles fall below the resolution limit of the method.

Complementary information about the longitudinal distribution of the phytoplankton was obtained during a sampling trip carried out in the Middle Paraná under stable mid-waters (13-18 September 1975; water level at Paraná Harbor: 1.50-1.57 m). The principal results permitted differentiation of two zones upstream and downstream from Goya (I and II, Tab. 4). The zone showed greater fluctuation of values and significantly lower means than the second. The contribution of some important tributaries at each point (outlets) was principally observed in the first reach (SCHIAFFINO de MARTA, 1981; PEROTTI de JORDA, 1980a).

Summing up, the phytoplankton of the Middle Paraná mainstream shows longitudinal variations that may in part be due to different supplies from the major and minor tributaries and from the floodplain. Undoubtedly, contributions from the alluvial plain increase

Table 4 - Mean values for phytoplankton population along the Middle Paraná mainstream. Stretch I: Corrientes-Goya; stretch II: Goya-Diamante.

Stretch:	I	II
Density(1) (ind.ml^{-1})	210	274
Chlorophyll a(2) ($mg.m^{-3}$)	3.8	5.9
Gross production(2) (mg $C.m^{-3}.h^{-1}$)	32	83
Respiration(2) (mg $C.m^{-3}.h^{-1}$)	18	26
Specific diversity(3) ($bits.ind.^{-1}$)	3.5	3.96

(1) SCHIAFFINO de MARTA, 1981

(2) PEROTTI de JORDA, 1980a (laboratory experience, oxygen method)

(3) GARCÍA de EMILIANI (unpubl. data)

qualitatively and quantitatively downstream as its width increases possibly having cumulative effect.

On the other hand, it has to be taken into consideration, as MARGALEF (1983) points out, that the potamoplankton is affected by changes in environmental conditions which may alternately favor different species, impeding the formation of a stable community. A typical fluvial plankton should exist in rivers having about two months renewal time, and the plankton should reach higher density in the lower stretches. Even though the residence time of water in the Middle Paraná mainstream is short

(5-20 days), the data given in Tab. 1 and 2 suggest the existence of a real potamophytoplankton. This consists of a set of common species detected alog its mainchannel, with the addition of others (surely coming from the alluvial plain or tributaries) which may be developing in the river channel. It must also be kept in mind that in the calculation of water age, the interference of the alluvial plain, where the water flow is considerably delayed, has not been estimated.

It is concluded that phytoplankton variations downstream are a consequence of the successional process and the increase of the floodplain contribution. It should be interesting to quantify the independent effects of these factors through samplings of adequate design.

Temporal distribution

The structure of the phytoplankton varies slowly through time in the uppermost Middle Paraná (Corrientes-Antequera, km 1208) as in its lower stretch (Toma Aguas Corrientes, Paraná, km 604) (Tab. 5).

Table 5 - Range of annual variation and mean values for phytoplankton population in two cross-sections of the Middle Paraná mainstream.

CROSS-SECTION:		CORRIENTES-ANTEQUERA (km 1208)				TOMA AGUA CORRIENTES		
		Corrientes (l.b.)		Antequera (r.b.)		Paraná (km 601)		
Dominance		Diatomophyceae		Diatomophyceae		Diatomophyceae		
Subdominance		Chloro.-Cyano.		Chloro.-Cyano.		Chloro.-Crypto.		
		range	mean	range	mean	range	mean	
Density (ind.ml^{-1})	(1)	85-2500	852	80 -1600	651	50 -2550	255	(3)
	(2)	230-2330	1143	150 - 920	414		532	(4)
Chlorophyll *a* (mg.m^{-3})	(2)	2- 18	10	5.2- 16	9.5	2.8- 17.3	5.3	(3)
							7.6	(4)
Productivity	(1)	3- 285	80	2 - 120	30	1 - 800	94	(3)
(mg C.m^{-2}.d^{-1})	(2)	10-1000	400	10 - 580	180		109	(4)
Annual production							34.4	(3)
(g C.m^{-2}.year^{-1})							39.9	(4)

l.b.: left bank r.b.: right bank

(1) BONETTO et alii, 1979 (period: II/78 - VIII/79)
(2) BONETTO, 1983 (period: III/81 - II/82)
(3) year 1977, (4) year 1978, in PEROTTI de JORDA, 1984 (oxygen method)

The dominant class, Diatomophyceae (mainly centric diatoms) has a greater relative abundance during winter-apring. The subdominant class (seldom attaining dominance) is Chlorophyceae, principally in autumn and early spring. Cyanophyceae has a greater participation during spring-summer. They are occasionally dominant in Corrientes (on the left bank) though generally they occupy third place. Cryptophyceae are sometimes dominant in the last stretch, though they are better represented in winter.

The specific composition of phytoplankton undergoes temporal variations, but not enough data are available to establish a pattern of succession.

Differences in annual ranges of variation and mean values of quantitative descriptors of the phytoplankton (Tab. 5) are fundamentally attributable to the hydrosedimentologic regime. The highest values were found during low water (late winter - early spring) and the lowest during high water agrees with similar observations for other river systems (SCHMIDT, 1970; LACK, 1971; EGBORGE, 1974; TALLING, 1976; KUZMIN, 1979; WELCOMME, 1986). During annual flooding, the phytoplankton density decreases by dilution and by the unfavorable effect of other environmental changes (greater current velocity, turbulence and turbidity) (BONETTO, 1986).

This generalization, even when it constitutes a reasonable explanation for hydrologic cycles that diverge little from an average level hydrograph (BONETTO et alii, 1979; BONETTO, 1983 and year 1977 in PEROTTI de JORDA, 1984), is not applicable to other hydrologic behaviors. For instance, at the Toma Aguas Corrientes cross-section in Paraná City (through which flows 85% of the valley water discharge), there was no inverse correlation between water level and phytoplankton density during a period in which river level fluctuated frequently (every 30-35 days, Fig. 1).

In the same zone, a positive correlation between phytoplankton density and water level was detected during and extraordinary flood (ANSELMI de MANAVELLA, 1986) (Fig. 2).

The above examples may be explained considering:
a) the coincidence of favorable factors such as water transparency and temperature during the high water periods (Fig. 2). As regards transparency it must be considered that the discharge peaks are often produced before suspended sediments peak (DRAGO & AMSLER, 1981). On the other hand, both factors have a negative influence during low water periods (Fig. 1). The different combinations of the three factors considered (water regime behavior, temperature and turbidity) explain much of the seasonal variation in the phytoplankton density.
b) the particular influence of the floodplain on the main river channel which depends on the frequency, intensity and range of water level changes. During "normal" water levels, part of the floodplain may be covered by 1.5 m of water, up to 2.5 m during annual floods and up to 4.5 m during exceptional floods (NEIFF, 1986). In the example of Fig. 1 and in hydrologic cycles which do not substantially differ from average, the greatest contribution from flood plain to river is seen when water level sharply decreases (e.g.: February-March, September-October, November-December/1978, Fig. 1). During and exceptional flood the contribution from the alluvial plain to the main river channel is greater due especially to the encompassing of alluvial flats that are not annually flooded. Furthermore, the lengthening of the high water period supports the productive processes in the flooded plain versus in the mainstream. The progressive transference should explain the high densities of phytoplankton in the main river channel during the second period of Fig. 2.

If we analyze the absolute abundance of the phytoplankton we can study its variations independently of the dilution effect. WELCOMME (1986) points out that lower

Figure 1 - Annual variation of water level (fine line), phytoplankton density (heavy line) and absolute abundance of phytoplankton (bars) in the Middle Paraná mainstream (km 601).

Figure 2 - Fluctuations of water level (fine line), phytoplankton density (heavy line) and absolute abundance of phytoplankton (bars) in the Middle Paraná mainstream (km 601) during an exceptional flood.

absolute abundance of phytoplankton during floods is due to factors that make conditions less favorable for growth, and not obviously to dilution. Nevertheless, in the example of Fig. 1, increments in absolute abundance were observed when water levels sharply decreased (independently of the hydrometric stage), and low values during the period of low waters (May-June). In the example of Fig. 2, a direct relation among discharge and density and absolute abundance of the phytoplankton was verified. After periods of stable hydrometric levels, in mid as in high water, the same absolute abundance occurred: 3.5 ind.sec^{-1} for hydrometric levels of 1.57 m and 4.12 m at Paraná Harbor (SCHIAFFINO de MARTA, 1981 & GARCÍA de EMILIANI, 1985, respectively).

Changes within each annual hydrologic cycle with respect to the mid kimnogram (pulses within each water stage, fluctuation range of the water level, duration of each water stage, and climatic periods constitute important elements that must be considered in the analysis of the water level - phytoplankton abundance relationships.

The effects of temperature are not easily identified because flow changes normally occur at the same time. The relationship between phytoplankton development and nutrient concentration is not verified either. Nevertheless, an analysis of multiple correlation (Toma Aguas Corrientes cross-section, Paraná) explained 49% of the chlorophyll <u>a</u> variance due to the effect of the discharge and water temperature. The percentage rose to 71% when nitrates and phosphates were included (GARCÍA de EMILIANI E PEROTTI de JORDA, 1982).

The rate of carbon fixation depends mostly upon phytoplankton density. Daily productivity per unit area shows variation related to phytoplankton abundance, water transparency, solar radiation, and water temperature. At the Toma Aguas Corrientes cross-section (Paraná) 74.8% of daily productivity variation was explained by the action of these factors (GARCÍA de EMILIANI & PEROTTI de JORDA, 1982).

At Corrientes City (km 1208) the environmental features differ markedly from one bank to the other. The right bank transports a large load of suspended solids coming from the Bermejo River through the Paraguay River during its annual flood period. Therefore, turbidity is the principal limiting factor on productivity, principally on the right bank (BONETTO et alii, 1982; BONETTO, 1983) (Tab. 5).

Some studies of the impact of projected man-made lakes on the Middle Paraná River (SMIRNOV, 1984) predicted strong increments in the phytoplankton due to increased water transparency and slower water movement, since nutrients would not be limiting.

MIDDLE PARANÁ FLOODPLAIN

The wide alluvial valley is a composite floodplain with a set of structurally and functionally diverse environments (DRAGO, in this volume; BONETTO, 1975; 1976; 1986).

In the Middle Paraná hydrosystem, the general tendency is for average biomass and phytoplankton productivity to increase in the following order: mainstream, side-arm channels and alluvial ponds. The relative influence of tributaries depends on the particular characteristics of the respective drainage basins and on the floodplain zone where they flow into the river.

Lotic environments

In a comparative sampling of different types of water courses (Goya-Diamante stretch, km 967 - km 533) during mid and high waters (Tab. 6), it was found that dominance relationships among algal groups were mantained,

Table 6 - Mean discharge, composition and mean values for phytoplankton populations in the Middle Paraná mainstream, secondary channels and tributary courses (Stretch Goya-Diamante) and annual average in secondary courses near Paraná City.

		GOYA - DIAMANTE (km 967-533)			SECONDARY COURSES (km 601)			
		MAINSTREAM	SECONDARIES C.	TRIBUTARIES	Santa Fe	Coronda	Correntoso	Cordobés
Discharge	mw	8733	248	16	1170	947	61	24
(m^3.sec^{-1})	hw	12000	475	25				
Dominance		Diatomophyceae	Diatomophyceae	Diato.-Chloro.	Diatomophyceae			
Subdominance		Crypto-Chloro.	Crypto.-Chloro.	Crypto.-Eugle.	Chlorophyceae			
Density	mw	726	1360	1600	740	640	637	677
(ind.ml^{-1})	hw	222	804	2100				
Chlorophyll *a*	mw	7.2	21	21	9.7	11.6	12.1	12.6
(mg.m^{-3})								
Absolute abundance(1)								
ind.10^{11}.sec^{-1}	mw	63	3.4	0.3	8.6	6.1	0.4	0.2
	hw	28	3.8	0.5				
mg chlor.*a* .sec^{-1}	mw	63000	5300	420	11349	10985	738	302

Data from García de Emiliani,1985; Perotti de Jorda,1981,1982,1985 and Schiaffino de Marta,1977.
(1) Calculated from García de Emiliani,1985.
mw : mid-water stage hw : high water stage

and the relative abundance of the most important classes varied little. Tributaries were characterized by a greater representation of Euglenophyceae and Chlorophyceae (GARCÍA de EMILIANI, 1985).

On the other hand, quantitative parameters show greater variation related to the discharge of the different types of river channels and the water stage. It is apparent that in spite of the strong discharge differences among river courses, the abundance of phytoplankton does not vary in the same proportion.

Canonical correlation analysis (GARCÍA de EMILIANI, 1988) revealed that discharge fluctuations (inversely related to conductivity and pH) are closely and inversely associated to the total phytoplankton, Euglenophyceae, Chlorophyceae and Dinophyceae concentrations. The relation with *Melosira* is direct and more significant in mid waters whereas *Cryptomonas* is inversely associated during high waters.

A study on the annual cycle simultaneously carried out in Paraná side-arms of different discharge near Santa Fe and Paraná Cities (km 601) demostrated no significant differences in average values of cell concentrations and chlorophyll a among the different secondary channels (PEROTTI de JORDA, 1981) (Tab. 6).

Analysis of annual variation of quantitative descriptors showed a similar behavior to that already shown for the main stream with respect to the water regime: maximum in low waters (early spring) and minimum in high waters (summer-autumn). Furthermore, the range of variation in phytoplankton abundance was similar in different anabranches (170-1400 ind.ml^{-1} and 2-24 mg chlorophyll a . m^{-3}) and did not differ from values for the mainstream. Regarding the dominance structure (Diatomophyceae - Chlorophyceae), only one change was observed during low water in the rivers with minor discharges, where Chlorophyceae dominated (SCHIAFFINO, 1977).

Factors explaining temporal variation of chlorophyll a in each anabranch were: discharge, temperature, transparency, nitrates, phosphates, and silica. The effect of water temperature was greater (30%) in the river with low water discharge than in the river with high discharge (12%). The joint effect of all these variables explained more than 75% of variance in chlorophyll a in each anabrach (PEROTTI de JORDA, 1981).

Lentic environments

The lentic water bodies of the Middle Paraná floodplain vary considerably in morphology and hydrology, as well as in their physical, chemical and biological characteristics.

The phytoplankton of "standing" waters along the Middle Paraná floodplain is little known. Data from a study of 21 ponds made during a sampling trip along 700 km between the Paraguay River outlet and Diamante City, during mid-waters showed a wide variation in phytoplankton densities (148-8500 ind.ml^{-1}), chlorophyll a concentrations (2-48 $mg.m^{-3}$), specific diversity (0.4-3.8 $bits.ind^{-1}$), dominant class (Cryptophyceae, Chrysophyceae, Chlorophyceae or Euglenophyceae), and specific composition. Differences among alluvial ponds were attributable principally to different levels in phytoplankton microsuccession, which begins with the isolation of lentic water bodies. It was concluded that the number of ponds studied was not enough to demostrate latitudinal differences (GARCÍA de EMILIANI, 1979; PEROTTI de JORDA, 1980b).

A greater knowledge of these shallow waterbodies (maximum depth less than 6 m and with different macrophyte covers) was obtained from water bodies located near the Cities of Paraná and Corrientes (Tab. 7).

Table 7 - Composition and range of annual variation for phytoplankton populations in lentic waterbodies of the Middle Paraná floodplain.

	P O N D S		O X B O W S	
	Los Matadores(1)	Las Chilcas(2)	Corrientes(3)	Paraná(4)
Volume (m^{-3})	51000	185000	200000	12000
Mean depth (m)	1.5	0.8	4	0.7
Dominance	Crypto.-Diatomo.	Chloro.-Crypto.	Crypto.	
Subdominance	Chlorophyceae	Diatomo.-Cyano.	Eugleno.	
Density (ind.ml^{-1})	800 - 5500	300 - 60000	100 - 1060	
Chlorophyll a ($mg.m^{-3}$)	2 - 50	1 - 120		1 - 100
Productivity (mg $C.m^{-2}.d^{-1}$)	500 - 1250	310 - 3600	40 - 560	

(1) GARCÍA de EMILIANI, 1980; PEROTTI de JORDA, 1977 (oxygen method)
(2) HUSZAR, unpubl. data (oxygen method)
(3) BONETTO et alii, 1984 (C^{14} method)
(4) PEROTTI de JORDA, 1982 (oxygen method)

Phytoplankton density, composition and productivity in these environments are heavily conditioned by the major event, the flood. Usually, in the Middle Paraná floodplain the ponds are isolated in winter-spring (July-November) and flooded in summer and autumn (January-June).

Some permanent waterbodies may be in communication with the main river or its anabranches during a great part of the year. In Los Matadores Pond, connected 90% of the year, with a marginal belt of macrophytes, temporal changes in phytoplankton were influenced more by water level fluctuations (accounting for 68% of variance of phytoplankton density) than by temperature variations (19%) (GARCÍA de EMILIANI, 1980). A principal components analysis applied to a set of 10 attributes (depth, water temperature, pH, primary productivity, specific diversity, and concentrations of nitrates, phosphates, silica, cells and chlorophyll a) allowed two factors to be defined: lotic influence (58.3% of variance) and seasonal cycle (16.4%) (GARCÍA de EMILIANI & DEPETRIS, 1982). During high water stages, the permanent lotic influence caused an increase in the volume of the pond's stored water and, hence, of characteristics inherent in the incoming water (i.e., lower pH, primary productivity and specific diversity, higher nutrient concentrations, and lower concentrations of planktonic algae and chlorophyll a). With lower water level, the pond exhibited a more lentic behaviour, becoming totally isolated for 10 days. Phytoplankton abundance and productivity increased rapidly and nutrients were depleted. Blooms of *Anabaena* were observed along the shore. During the greater part of the year, Cryptophyceae and Diatomophyceae dominated, but when the lotic influence decreased, Chrysophyceae, Chlorophyceae, and Cyanophyceae succeeded. Temporal changes in phytoplankton composition were related to lotic influence and temperature (GARCÍA de EMILIANI, 1981a).

An example of the effect of water residence time in the ponds on phytoplankton abundance and productivity is Las Chilcas Pond (50% of the year with indirect connection and sparse shore line vegetation) (Tab. 7). The quality of river water entering the pond was modified due to its displacement across the floodplain: part of its sestonic load and oxygen content was lost, it was acidified, and organic matter was added. Furthermore, during the long spring-summer isolation period, nutrients became quickly mineralized and inmobilized, causing sudden changes in phytoplankton composition, abundance and productivity. The higher productivity values were obtained during a spring bloom of Cyanophyceae (October).

Also frequent in the Middle Paraná floodplain are the oxbow lakes, partially or totally covered by a carpet of macrophytes. One of them located on the right bank of the mainstream at latitude of Corrientes City, and isolated from the mainstream during September-November, showed changes strongly conditioned by the water regime of the river. During the low stage, *Eichhornia crassipes* covered the pond area almost completely (90%), providing effective wind protection. These circumstances favored development of termal stratification and oxygen depletion. Highest phytoplankton density was observed during September at the surface but decreased with depth. Primary productivity, together with nutrients, increased until November. Both phytoplankton density and productivity showed low values during the cloudy winter (June-July), coinciding with high water level. The inflow of river water reduced the carpet of *Eichhornia* to 50%, increased the oxygen content, and simultaneously diluted the organic matter content and phytoplankton (BONETTO et alii, 1984).

In another pond near Paraná city, generally isolated for 20 months and with an indirect connection for 4 months, partially covered by *Eichhornia crassipes*, variations in the concentration of chlorophyll a were studied. Variations were closely associated with water temperature (r = 0.71) and somewhat less with transparency. During the long isolation period the phytoplankton was controlled principally by water temperature. During the period of high waters (January-April), macrophytes drifted towards the river and the pond acquired the characteristics of the incoming water. During this period chlorophyll a concentration was controlled by turbidity (PEROTTI de JORDA, 1982).

Available information about the Middle Paraná phytoplankton is still insufficient to reach a conclusive synthesis about some important aspects of its structure and functioning. Much more ecological research is required before we can hope for a coherent picture, because the wide floodplain greatly increases the ecological complexity of the hydrosystem.

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