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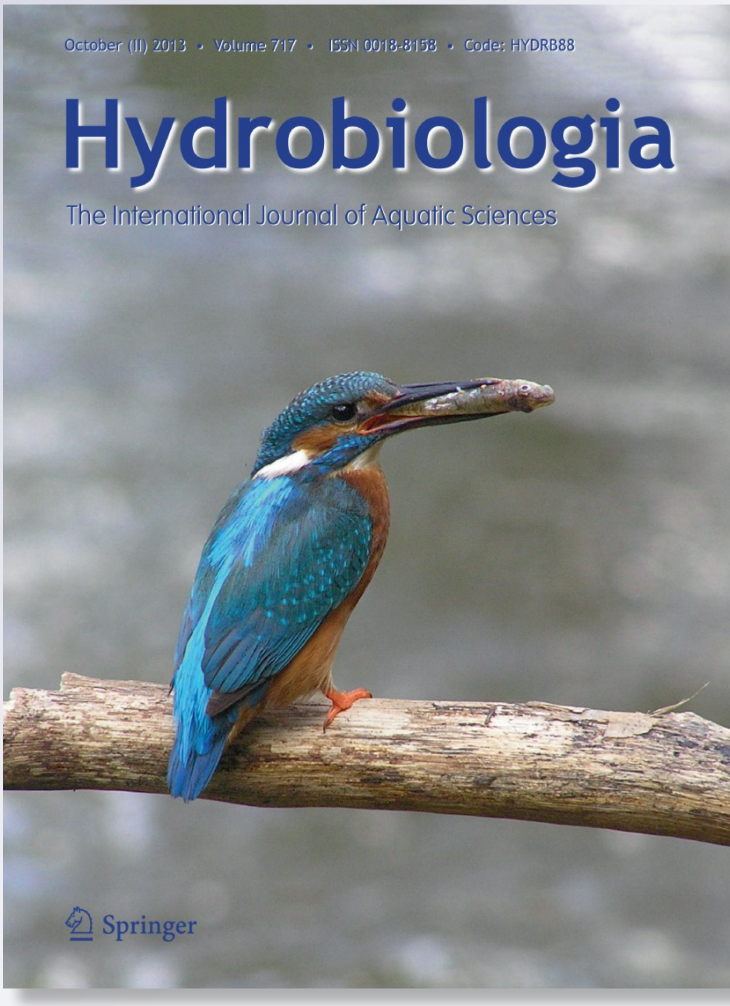

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PRIMARY RESEARCH PAPER

Spatial variability of chlorophyll-*a* and abiotic variables in a river–floodplain system during different hydrological phases

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Abstract Chlorophyll-*a* (Chl-*a*) and abiotic variables were measured in the main channel and floodplain waterbodies of the Middle Paraná River to analyse the system dynamics and to assess their spatial variability during different hydrological phases, including an extreme flood. We wanted to test that the flood does not always have a homogenising effect in a river–floodplain system. An explanatory model for Chl-*a* was performed according to Akaike's Information Criterion (AIC), and the relation of water level with the coefficient of variation (CV) among sites for each variable was explored. The model explained 64% of Chl-*a* variability. Water level, depth:euphotic zone ratio (Z_d:Z_{eu}) (inverse correlation) and conductivity (direct correlation) were the significant explicative variables. The CV of Chl-*a* decreased with flood from the main channel to the floodplain, but for turbidity, Z_d:Z_{eu}, pH, dissolved oxygen, soluble reactive phosphorus and Chl-*a*:pheophytin-*a* ratio, it increased. However, within the floodplain, CV of turbidity, Z_d:Z_{eu} and pH decreased during flood. These suggest that the homogenising effect frequently observed during inundation cannot be generalised and that the floodplain may maintain its identity even during flood. The extreme flood and its overlap with the warm season and sedimentological pulse probably contributed to the heterogeneity in the spatial gradient.

Keywords Phytoplanktonic chlorophyll-*a* · Large floodplain river · Spatial heterogeneity/homogeneity · Hydrological fluctuations

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G. Mayora (✉) · M. Devercelli · F. Giri
Instituto Nacional de Limnología (INALI, CONICET-UNL), Ciudad Universitaria – Paraje "El Pozo" sin número, C.P. 3000 Santa Fe, Argentina
e-mail: gpmayora@inali.unl.edu.ar

M. Devercelli · F. Giri
Facultad de Humanidades y Ciencias (FHUC, UNL), Ciudad Universitaria – Paraje "El Pozo" sin número, C.P. 3000 Santa Fe, Argentina

Introduction

River–floodplain systems are characterised by a wide range of temporal and spatial heterogeneity (Neiff, 1996; Tockner et al., 1999, 2010; Lewis et al., 2000; Ward et al., 2002). The hydrological fluctuations, which integrate the main channel and the floodplain in a dynamic unit, are mainly responsible for the system complexity and enable the lateral exchanges of materials and organisms between both (Junk et al., 1989; Neiff, 1990). The abiotic variables are subject to pulses of high and low water discharges that steer changes in suspended and dissolved organic and inorganic matter and, therefore, in turbidity, conductivity, pH and nutrient concentrations (Unrein, 2002;

Maine et al., 2004; Depetris, 2007; Rodrigues et al., 2009). The biota is also adjusted to the pulse dynamics and is able to tolerate the hydrologically fluctuated environment (Amoros & Bornette, 2002).

Phytoplankton is an important pelagic component of the aquatic systems since it allows the flux of organic carbon through the planktonic food web (Araujo-Lima et al., 1986; Lewis et al., 2000; Thorp & Delong, 2002). The dynamics of chlorophyll-*a* (Chl-*a*) concentration, as a good proxy of phytoplankton biomass, was largely found to be regulated by water discharge in large rivers (Soballe & Kimmel, 1987; Reynolds & Descy, 1996; Lewis et al., 2000; Zalocar de Domitrovic et al., 2007; Salmaso & Zignin, 2010). In floodplain waterbodies, the inundation occasions changes due to the entrance of lotic waters with different physicochemical qualities. Dilution processes and the decrease of water residence time negatively affect phytoplankton development (García de Emiliani, 1997; Zalocar de Domitrovic, 2003). Simultaneously, organic matter decomposition increases with the flooding of littoral litterfall and desiccated macrophytes (Lewis et al., 2000). The extent of the water level reached mainly depends on the connectivity degree to the main channel (Neiff, 1990; Tockner et al., 1999; Depetris, 2007).

During isolation, local conditions trigger a specific dynamic action at each floodplain waterbody that results in changes in pH and dissolved oxygen (DO) concentration, and both variables could influence the bioavailability of nitrogen (N) and phosphorus (P). Denitrification and the consequent decrease of nitrate (NO_3^-) take place mainly under DO depletion, while nitrification occurs mainly during aerobic conditions (Chen et al., 1972; Conzonno, 2009). On the other hand, high pH favours the retention of phosphate (PO_4^{3-}) in the sediment by apatite formation (calcium bound P), and high DO favours its adsorption onto Fe(OOH) (iron-bound P), especially at low pH values (Bonetto et al., 1994; Golterman, 1995; Villar et al., 1998). The relation of both NO_3^- and PO_4^{3-} with phytoplankton development is firmly entrenched (Vollenweider, 1968; Rhee, 1978; Brett et al., 1999; Chrzanowski & Grover, 2001; Kisand et al., 2001). Nevertheless, the evidence of its dependence on nutrients at floodplain lakes is not at all clear since the hydrological regime simultaneously affects water physicochemical quality, residence time and the export of algal biomass (Zalocar de Domitrovic, 2003). In addition, algal senescence, sedimentation or herbivory may also affect phytoplankton concentration (Bidle & Falkowski, 2004; Lucas et al., 2009; Silveira et al., 2010).

Differences in the floodplain lateral dimension are more evident during isolation periods (Hamilton & Lewis, 1990). Thomaz et al. (2007) claimed that such variability decreases with increasing water levels, suggesting that floods increase similarity among waterbodies not only within the floodplain but also between the main channel and the floodplain. There are several examples supporting this trend (e.g. O'Farrell et al., 1996; Unrein, 2002; Maine et al., 2004; Roberto et al., 2009). Extreme floods that correspond to completely inundated alluvial valley situations (Depetris, 2007) are expected to increase the homogeneity. Nevertheless, the effects of hydrological connectivity cannot be reduced to a simple gradient (Amoros & Bornette, 2002) and exceptions to the rule may be found.

The goal is to test the hypothesis that the flood does not always have a homogenising effect in a river–floodplain system. To address this issue, Chl-*a* and abiotic variables in the main channel and floodplain waterbodies of the Middle Paraná River were studied during different hydrological phases, including an extreme flood, in order to: (a) analyse the dynamics of limnological variables in the system and then develop a model that explains Chl-*a* concentrations; and (b) analyse the effect of water level on the spatial variability from the main channel to the floodplain gradient, as well as within the floodplain gradient. Understanding the functioning of limnological variables in an almost pristine large floodplain river may be interesting in a scenario of hydrological changes that could potentially lead to various biogeochemical implications (Hamilton, 2010).

Materials and methods

Study area

The Paraná River (Fig. 1a) drains an area of 2.6×10^6 km^2 along its 4,400 km length (Depetris & Kempe, 1993). The Middle stretch extends from its confluence with the Paraguay River (27°29′S; 58°50′W) to the city of Diamante (Argentina) (32°4′S; 60°32′30″W). It has a well-defined main channel of variable width (0.4–8 km) and several anabranches. It

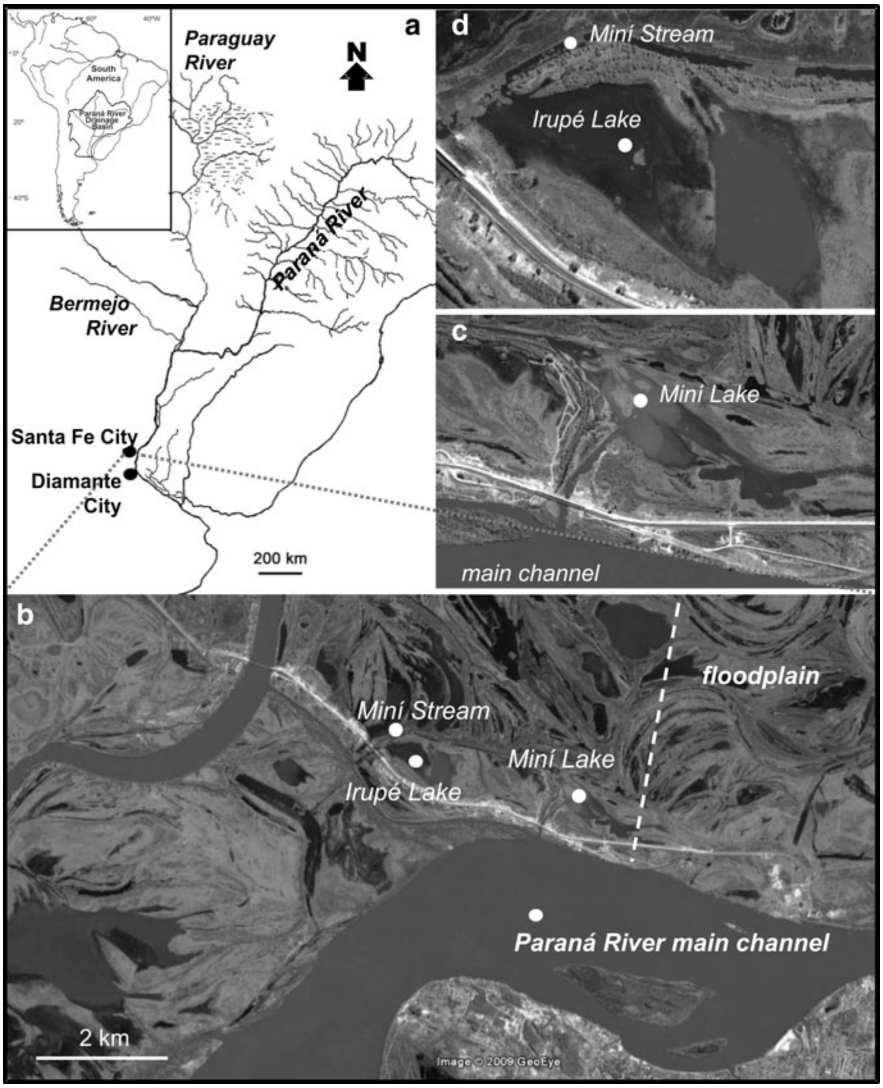

Fig. 1 **a** Drainage basin and main tributaries of the Paraná River and location of the study area. **b** Sampling sites location. **c** Detail of the Miní Lake and its connection to the Middle Paraná River main channel. **d** Detail of the Miní Stream and its connection to the Irupé Lake. Sampling sites are indicated by *circle*

is fringed along its right bank by a 6–40-km-wide floodplain (13,000 km^2), comprising thousands of permanent and temporary waterbodies (Paira & Drago, 2007). The annual average discharge is 16,000 m^3 s^{-1} mainly supplied by the Upper Paraná. This discharge corresponds to 3.40 m of hydrometric level at the Paraná Harbour Station Gauge. High (>3.40 m) and low (<3.40 m) water phases occurring with interannual variability and extreme high (>5 m) and low (<2.62 m) water phases are observed with variable frequency. Suspended solids (mean concentration = 276 mg l^{-1}), most of them (~50–70%) coming from the Bermejo Basin through the Paraguay River, are mainly responsible for the Middle Paraná River turbidity. The study sites were located near the city of Santa Fe (31°42′34″S; 60°29′7″W) in a transversal section that includes the main channel and floodplain waterbodies of the Middle Paraná River (Fig. 1b). The Miní Lake is directly and permanently connected to the main channel by a 0.65-km-long channel (Fig. 1c). The Irupé Lake is connected to the fluvial system by the Miní Stream, and it is isolated during periods of extreme droughts (Fig. 1d).

Samplings and laboratory analysis

Samplings were carried out approximately fortnightly from December 2009 to December 2010, during morning hours. The waterbodies depth (Z_d), water temperature (thermometer), transparency (Secchi disc depth, SD), pH, conductivity (Hanna portable water checkers) and water current velocity (at the lotic waterbodies with a current meter AOTT C20) were measured in situ.

Samples for DO determinations by Winkler's method (APHA, 1992) and 5 l of water samples for physical and chemical analyses were transported on ice to the laboratory. Turbidity was spectrophotometrically estimated at 450 nm wavelength with an HACH DR 2000 spectrophotometer. A variable volume (200–2,500 ml) of water was filtered through Whatman GF/F glass-fibre filters with a vacuum pump. From the filtrate water, $N–NO_3^-$ (principle of reduction with metallic cadmium) and soluble reactive phosphorus (SRP) (ascorbic acid method) were determined using chemical sets from the HACH Company and measured at 400 and 880 nm, respectively, with an HACH DR 5000 spectrophotometer. Chl-*a* and pheophytin-*a* (Pheo-*a*) were extracted from the filters with acetone (90%) macerating into a glass grindex and storing at 4°C for 6–12 h in the dark. The extracts were filtered and measured with a spectrophotometer at 750, 664, 665 and 430 nm, and at 665 and 750 nm after acidification with HCl 0.1 N (Lorenzen, 1967 in APHA, 1992).

Data analysis

Daily atmospheric pressure and hydrometric level at the Paraná Harbour Gauge were obtained from Centro de Informaciones Meteorológicas (UNL). Data were separated into hydrological phases according to the water level and the flooding degree of the alluvial valley (Drago, 1989). The DO saturation percentage (%DO) was calculated taking into account the gas solubility coefficient according to temperature and atmospheric pressure to assess the prevalence of autotrophic or heterotrophic conditions. The depth of the euphotic zone (Z_{eu}) was estimated using the index proposed for turbid waters where SD is multiplied by a 3.5 factor (Koenings & Edmundson, 1991). The Z_d:Z_{eu} ratio was calculated as a measure of light availability in the water column. The Pheo-*a*:Chl-*a* ratio was calculated and considered as an indicator of algal physiological state (APHA, 1992). Margalef's pigment index (MI), which estimates the proportion of Chl-*a* in relation to the total concentration of photosynthetic pigments, was calculated as the ratio of the acetone extract optical density at 430 and 665 nm (Margalef, 1960) during the period March–December 2010.

Normality was checked with Kolmogorov–Smirnov test and homogeneity of variances with Bartlett test. Spearman's correlation coefficients were calculated among all measured variables. Kruskal–Wallis with Dunn's post test was used to compare differences among the study sites.

A nested analysis of variance was conducted to evaluate the variation of the Chl-*a* concentration in the spatial gradient during the different hydrological phases (hydrological phases nested within sites as fixed factors) and Tukey HSD test was applied to detect significant differences. Data were ln-transformed to fulfil the assumptions of normality and homogeneity of variance. Multiple regression analyses were performed to propose the model that best explains the Chl-*a* variation. All the variables measured were considered in the analyses. Multicollinearity problems were sorted taking into account the correlations among variables and the variance inflation factor (VIF). Akaike's Information Criterion (AIC) was used as a method for model selection (-2*log-likelihood $+ k*npar$, where *npar* represents the number of parameters in the fitted model, and $k = 2$). The influence of each variable to the resulting AIC model was checked removing a variable by time and comparing the resulting model with the AIC model by ANOVA. Both, nested ANOVA and multiple regression models were conducted with R software (R Development Core Team, 2008).

Coefficient of variation (CV) of each variable were obtained among all sites (main channel to floodplain gradient) and excluding the main channel (floodplain gradient). In order to analyse both spatial gradients, simple linear regressions among water level and CV were performed and significant relationships were tested with Spearman's correlation coefficients. The mentioned statistical analyses were computed with PAST 1.76 software.

Results

System dynamics and main controlling factors of Chl-*a* and abiotic variables

Hydrological conditions changed from a potamophase that was differentiated in an extreme high-water phase (e-HW, December 2009–March 2010) and an ordinary high-water phase (o-HW, March–June 2010), to a limnophase or low-water period (LW) that lasted till the end of the study (Fig. 2). Maximum water temperatures coincided with the e-HW period (Fig. 2).

Changes among phases (Fig. 3) and sites (Table 1) were observed. The most turbid period was the potamophase at the main channel and the limnophase at the floodplain. A peak of turbidity (150 FTU) was observed at the main channel after the major flooding that coincided with maximum conductivity value (170.3 μS cm^{-1}, March 29). Both turbidity and the Z_d:Z_{eu} ratio increased with water level at the main channel (direct correlations: $P < 0.05$ and $P < 0.01$, respectively, Table 2), whereas it showed the opposite trend at the floodplain (inverse correlations: $P < 0.01$). During LW, conductivity tended to increase (inverse correlation with water level at all sites: $P < 0.05$, except at the Miní Stream), and the pH values were circumneutral and slightly acidic during potamophase. Only at the Irupé Lake, the pH was negatively correlated to water level ($P < 0.05$). DO and %DO depletions were registered at high temperatures during e-HW, especially at the floodplain waterbodies where it decreased down to 2 mg l^{-1} and 22%, respectively (inverse correlations with water level and temperature, $P < 0.05$).

Higher N–NO_3^- concentrations were recorded during LW (inverse correlations with water level at the main channel: $P < 0.01$, and Miní Lake: $P < 0.05$). Positive relations were also registered with DO and pH at some of the floodplain sites ($P < 0.01$). Contrarily, SRP concentrations decreased during LW

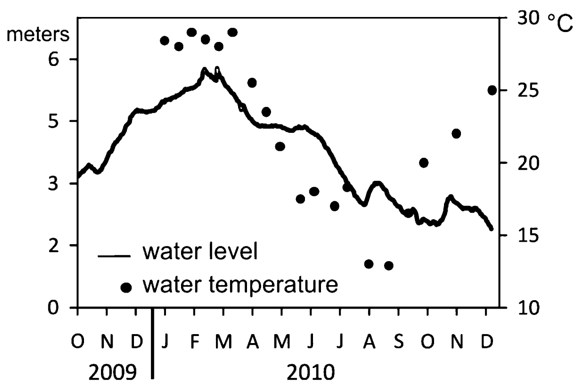

Fig. 2 Water level (Paraná Harbour Station Gauge) and temperature at the Middle Paraná River main channel. Sampling dates coincide with the values of water temperature

(positive correlations with water level at the main channel, $P < 0.05$).

The main channel differed significantly from the other study sites because of its higher turbidity ($P < 0.05$), Z_d:Z_{eu} ratio, pH and DO concentrations, and lower transparency ($P < 0.01$). Chl-*a* concentration increased in the lateral gradient from the main channel to the more isolated Irupé Lake. The nested ANOVA showed differences among sites' hydrological phases ($F = 9.2379$, DF = 8, $P = 4.238e^{-08}$), as well as sites ($F = 16.6697$, DF = 3, $P = 6.298e^{-08}$). The highest concentrations occurred during the LW phase. The main channel particularly differed from the floodplain waterbodies with the lowest concentration (Table 3).

The AIC criterion showed that the best model that explained the Chl-*a* dynamic in the fluvial system was ln Chl-$a = -8.39114 - 1.23754$ (ln water level) + 0.64777 (ln water temperature) + 1.41360 (ln pH) + 1.41241 (ln conductivity) − 0.01736 (ln SRP) − 0.2217 (ln N–NO_3^-) − 0.36298 (ln Z_d:Z_{eu}) with a $r^2 = 0.64$, F-statistics = 13.37, DF = 7–52, and a P value of $1.008e^{-09}$. From these seven variables retained by the multiple regression model, only water level, Z_d:Z_{eu} (inverse correlation) and conductivity (direct correlation) significantly explained Chl-*a* concentrations. The ANOVA comparing models revealed that water temperature, pH, N–NO_3^- or SRP could be removed from the model ($P > 0.05$) without changing the explanatory power, but the elimination of more than one variable was not supported by the analysis (Table 4).

As regards the Pheo-*a*:Chl-*a* ratio, it tended to decrease from the main channel to the floodplain. Both the main channel and the Miní Stream were significantly different from the lakes ($P < 0.05$). At the main channel, the MI was positively correlated to water level and turbidity ($P < 0.05$), and negatively to Chl-*a* concentration ($P < 0.01$). As regards the floodplain, in the Irupé Lake it was negatively correlated to water level ($P < 0.01$) and positively to turbidity ($P < 0.05$).

Spatial variation of limnological variables in relation to water level

Regarding the spatial gradient of limnological variables from the main channel to the floodplain (Fig. 4A), a positive relation was observed between water level and the CV of turbidity ($r = 0.544$;

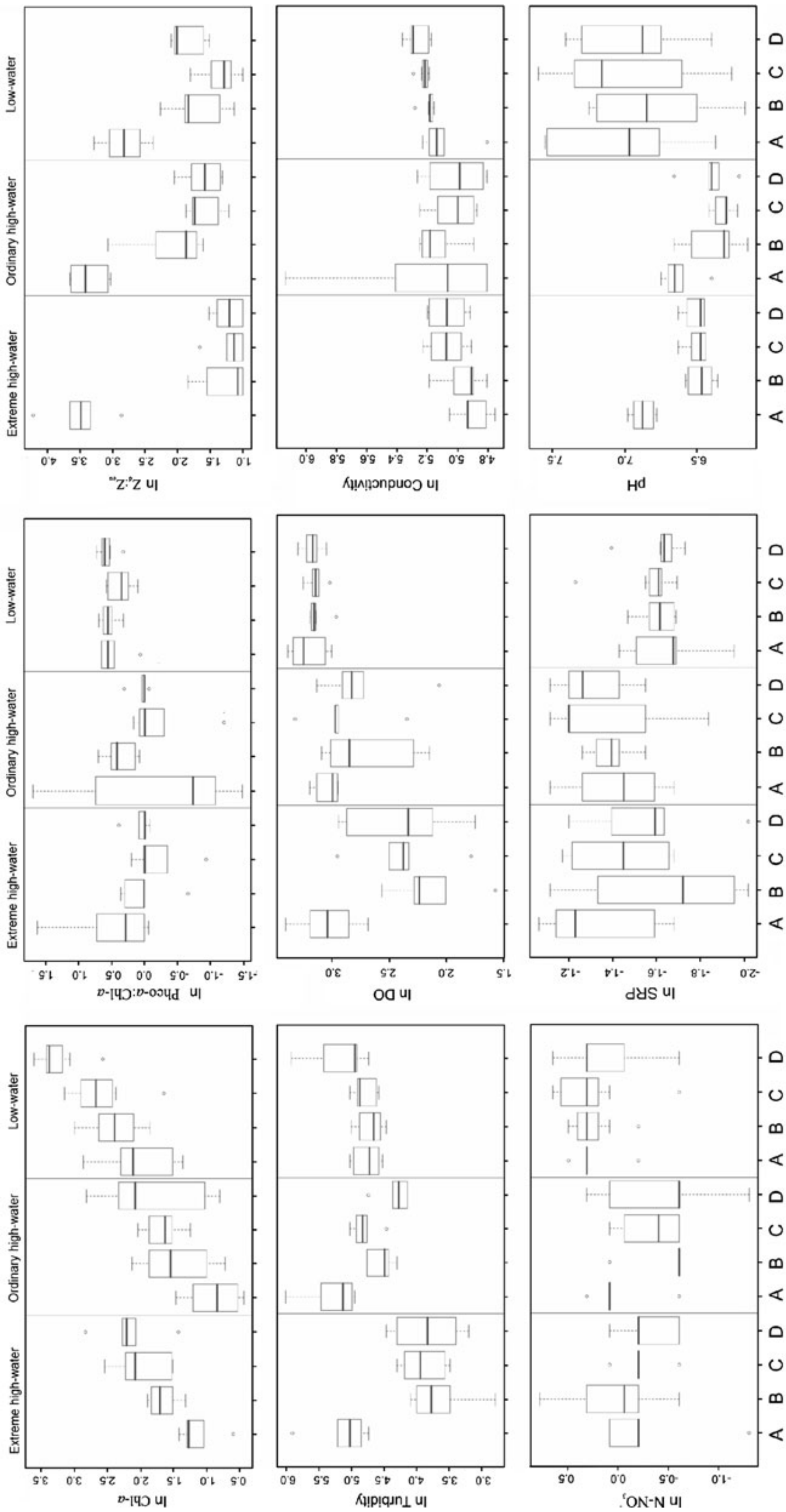

Fig. 3 *Box plots* of the main limnological variable distributions for Middle Paraná River main channel (*A*), Miní Stream (*B*), Miní Lake (*C*) and Irupé Lake (*D*) at the different hydrological phases, period December 2009–2010

Table 1 Mean values and range of limnological variables at the Middle Paraná River main channel, Miní Stream, Miní Lake and Irupé Lake, period December 2009–2010

	Main channel	Miní Stream	Miní Lake	Irupé Lake
Current velocity (m s^{-1})	0.94 (0.1–1.34)	0.31 (0.19–0.48)		
Temperature (°C)	22.2 (12.9–29)	21.3 (13–29)	21.3 (12–29.5)	21 (11–30)
Depth (m)	7.8 (5.1–11.3)	3.7 (1.2–6.5)	2.6 (0.7–5.5)	3.5 (1.3–5.3)
SD (cm)	26 (11–41)	63 (23–175)	58 (23–150)	66 (18–168)
Z_d:Z_{eu}	10.0 (4.0–25.0)	2.3 (1.0–8.0)	1.5 (1.0–2.4)	1.9 (1.0–3.0)
Turbidity (FTU)	62 (34–150)	31 (6–55)	37 (12–56)	41 (9–138)
Conductivity (µS cm^{-1})	62 (43–170)	61 (45–72)	61 (48–73)	62 (45–79)
pH	6.9 (6.4–7.6)	6.6 (6.2–7.3)	6.6 (6.2–7.6)	6.6 (6.2–7.4)
DO (mg l^{-1})	8.1 (4.9–11.1)	5.9 (1.8–9)	6.6 (2.2–10.3)	6.4 (2.1–9.9)
%OD	91.6 (62.7–140)	63.6 (22.2–100.6)	72.0 (27.6–99.7)	69.5 (26.9–99.9)
N–NO_3^- (µg l^{-1})	400 (100–600)	394 (200–800)	382 (200–700)	344 (100–700)
SRP (µg l^{-1})	88 (52–127)	81 (49–121)	87 (59–121)	84 (49–121)
Chl-*a* (µg l^{-1})	1.6 (0.0–6.5)	2.8 (0.8–7.4)	3.6 (1.3–8.6)	5.7 (0.8–13.6)
Pheo-*a* (µg l^{-1})	0.9 (0.1–2.3)	1.0 (0.1–2.2)	0.7 (0.0–2.3)	1.5 (0.3–4.6)
Pheo-*a*:Chl-*a*	1.1 (0.0–8.8)	0.4 (0.1–0.6)	0.2 (0.0–0.5)	0.2 (0.0–0.4)
MI	2.3 (1.9–2.7)	2.0 (1.6–2.4)	2.1 (1.6–2.3)	2.0 (1.9–2.4)

$P < 0.05$), Z_d:Z_{eu} ratio ($r = 0.749$; $P < 0.01$), pH ($r = 0.58$; $P < 0.05$), DO ($r = 0.83$; $P < 0.01$), SRP ($r = 0.62$; $P < 0.01$), MI ($r = 0.627$; $P < 0.05$) and Pheo-*a*:Chl-*a* ratio ($r = 0.647$; $P < 0.01$). Within the floodplain gradient (Fig. 4B), the relation of water level was also positive with the CV of DO ($r = 0.569$; $P < 0.05$) and SRP ($r = 0.524$; $P < 0.05$), while the relation between water level and the CV of turbidity ($r = -0.553$; $P < 0.05$), Z_d:Z_{eu} ratio ($r = -0.519$; $P < 0.05$) and pH ($r = -0.618$; $P < 0.01$) reversed the tendency. The CV of Chl-*a* was inversely related to water level at both spatial scales, but with statistical significance only within the floodplain gradient ($r = -0.581$; $P = 0.011$).

Discussion

The hydrosedimentologic pulse as the main actor of the fluvial system

Similar to what has been observed in other large floodplain rivers, in the Paraná System the hydrological fluctuations modify the river–floodplain interactions determining changes in the environmental features (Junk et al., 1989; Neiff, 1996; Tockner et al., 2010). Water level was associated to the variation of most limnological variables although in some cases these associations were different and even opposite in the main channel when compared to the floodplain (Table 2).

The extreme flood largely increased the connectivity degree between the floodplain and the main channel. Its effect was coupled with the sedimentary pulse, which happens due to the inflow of waters enriched with suspended solids supplied by the Bermejo River (Depetris, 2007), and was evidenced by turbidity and conductivity peaks. DO depletion and low pH, especially at the floodplain, characterised the potamophase. Increments in organic matter decomposition due to the vegetation flooding were reported to trigger such conditions (Pagioro & Thomaz, 1999; Rocha et al., 2009) which could be accentuated if they coincided with high temperature (Tockner et al., 2010), as in the present work. The lowest N–NO_3^- concentrations are in agreement with the DO depletion that allows the prevalence of denitrification. The incorporation of SRP from large areas of inundated soil and from Bermejo's River input could explain their highest concentration. High load of calcium bound P is transported with the sedimentary pulse to the Middle Paraná River which is redistributed as

Table 2 Spearman correlation coefficients among limnological variables at the Middle Paraná River main channel, Miní Stream, Miní Lake and Irupé Lake, period December 2009–2010

	Variable	Water level	Turbidity	Z_d:Z_{eu}	Conductivity	DO	$N–NO_3^-$	SRP	Chl-*a*
Main channel	Water level		0.492	**0.616**	−0.477		**−0.658**	0.506	−0.533
	Temperature					−0.493			
	Turbidity			**0.778**					**−0.641**
	MI	0.604	0.719						**−0.738**

	Variable	Water level	Temperature	Z_d:Z_{eu}	Conductivity	pH	$N–NO_3^-$	SRP
Miní Stream	Depth							0.485
	Turbidity	**−0.764**		0.524	0.476			
	pH						**0.759**	
	DO	**−0.837**	**−0.792**					
	%DO	**−0.853**	**−0.714**					
	Chl-*a*	**−0.695**				0.519	0.56	

	Variable	Water level	Temperature	Turbidity	Conductivity	pH	$N–NO_3^-$	MI
Miní Lake	Depth			**−0.778**	−0.458		**−0.643**	
	Turbidity	**−0.641**						
	Conductivity	−0.565				**0.597**		
	DO	**−0.765**	**−0.753**				**0.628**	
	%DO	**−0.660**	−0.581					
	$N–NO_3^-$	−0.532						
	Chl-*a*	−0.53			**0.631**	**0.724**		
	Pheo-*a*:Chl-*a*							0.642

	Variable	Water level	Temperature	Turbidity	Conductivity	$N–NO_3^-$	MI
Irupé Lake	Water level						**−0.705**
	Depth						**−0.714**
	Turbidity	**−0.841**			**0.618**		0.663
	Z_d:Z_{eu}	**−0.72**		**0.788**			
	Conductivity	−0.501		**0.618**			
	pH	−0.508		0.458		**0.704**	
	DO	**−0.774**	**−0.766**				
	%DO	**−0.695**	−0.565				
	SRP			−0.536			
	Chl-*a*	**−0.641**			**0.733**		
	Pheo-*a*:Chl-*a*			**0.635**			

Only variables with statistically significant correlations are shown. Bold and normal letters indicate $P < 0.01$ and $P < 0.05$, respectively

iron-bound P by accessing the floodplain lakes with lower pH, and released to the water under DO depletion (Pedrozo & Bonetto, 1987; Maine et al., 2004).

In relation to the limnophase, lower SRP and higher $N–NO_3^-$ concentrations were observed. However, during all hydrological phases their values far exceeded those indicated as limiting for phytoplankton (Reynolds, 2006) and increments in algal biomass were more related to the better hydrological conditions. As shown by the AIC regression model, a highly significant proportion of phytoplankton biomass was explained by water level variations, followed by Z_d:Z_{eu} ratio and conductivity (64%). The negative

Table 3 Tukey HSD test results to determine differences in Chl-*a* concentrations among the study sites and hydrological phases

	Mean diff	*P*
Study site		
Irupé Lake versus Miní Stream	0.5846581	**0.046069**
Miní Lake versus Miní Stream	0.2472671	0.6823677
Main channel versus Miní Stream	−0.536106	0.1078373
Miní Lake versus Irupé Lake	−0.337391	0.4197556
Main channel versus Irupé Lake	−1.1207641	**0.0000422**
Main channel versus Miní Lake	−0.7833731	**0.0068561**
Hydrological phase		
LW versus o-HW	1.1220485	**0.0000001**
e-HW versus o-HW	0.2790156	0.2761241
e-HW versus LW	−0.8430329	**0.0000171**

Statistically significant values ($P < 0.05$) are indicated with bold letters

Table 4 Single term deletions based on AIC model

	Df	Sum	RSS	AIC	*F*	p
Water level	1	2.3382	15.629	−66.715	9.1486	**0.0038617**
Temperature	1	0.9571	14.247	−72.266	3.7448	0.0584188
pH	1	0.1252	13.415	−75.876	0.4899	0.4870911
Conductivity	1	1.7051	14.995	−69.196	6.6714	**0.0126502**
SRP	1	0.0008	13.291	−76.435	0.0031	0.9559656
$N–NO_3^-$	1	0.3159	13.606	−75.029	1.2359	0.2713738
Z_d:Z_{eu}	1	3.4445	16.735	−62.611	13.4769	**0.0005701**

Values of $P > 0.05$ indicate that the variable could be removed from the model without changing the explanatory power

relation found between Chl-*a* and water level has been previously reported for large rivers and their floodplains (Soballe & Kimmel, 1987; Descy, 1993; O'Farrell et al., 1996; Reynolds & Descy, 1996; Wehr & Descy, 1998; Gruberts, 2007; Zalocar de Domitrovic et al., 2007; Lucas et al., 2009; Devercelli, 2010). The increment in water residence time and the more favourable hydraulic conditions for algal growth that took place during hydrological isolation allowed a higher phytoplankton development; whereas the intrusion of lotic waters during the potamophase was reflected in the algal biomass decrease due to dilution and decrease in water residence time. Accordingly, the potamophase differed significantly in Chl-*a* concentration from the LW phase, whereas the e-HW and o-HW phases presented a similar effect (no statistical significance between both). In addition, variations in Chl-*a* among phases were more pronounced at the floodplain since hydrology caused more drastic changes for environmental conditions and for lenitic algae than at the main channel.

Light is a major resource for phytoplankton. The lower proportion of light in the mixed layer or in the water column (when depth is almost coincident with the mixed layer) is expected to negatively affect algae (Loverde-Oliveira & Huszar, 2007) as shown by the multiple regression model (Z_d:Z_{eu} ratio, negative relation). The improvement in hydrological and light conditions for algal development at the main channel during the LW phase was also reflected by the better algal physiological state (lower MI, and positively correlated to water level). MI, indicative of the proportion of accessory pigments, was found to increase under stress conditions and with bad algal physiological state (Margalef, 1965).

Even though conductivity represents bicarbonate and ion concentrations that positively affect photosynthesis (Rocha et al., 2009), its positive relation with Chl-*a* in the AIC model seems to be more related to an inverse relation with water level. Other variables that were selected by the model (temperature, pH, $N–NO_3^-$ and SRP) were not significantly associated with Chl-*a*. The positive effect of temperature on algal growth was not observed due to the stronger negative effect of high waters level. As regards pH, it has no direct causal relationship with phytoplankton biomass but algal

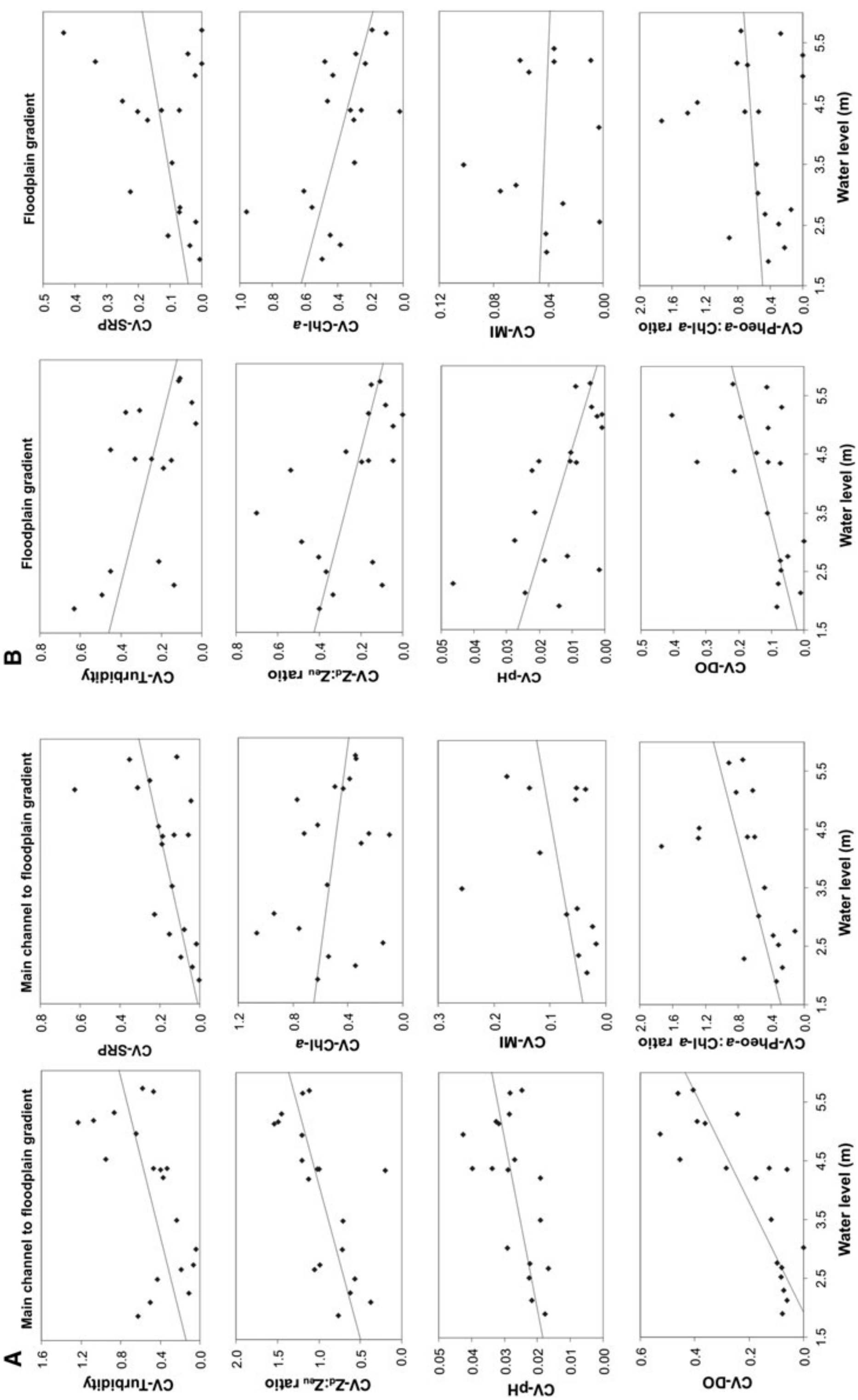

Fig. 4 CV of turbidity, Z_d:Z_{eu} ratio, pH, DO, SRP, Chl-*a*, MI and Pheo-*a*:Chl-*a* ratio from the main channel to floodplain gradient (**A**) and in the floodplain gradient (**B**) plotted against the water level

photosynthesis or respiration could change its values. No significant correlations with N–NO_3^- and SRP were found as it happens in other systems with ample nutrients, where it is likely that Chl-*a* production is more limited by physical factors (Reynolds & Descy, 1996; Reynolds, 2000; Stanković et al., 2012). In Huszar et al.'s (2006) review, poor relationships between Chl-*a* and total N and P were found. Rocha et al. (2009) proposed that algal biomass association with P may exist in small spatial scales in the Upper Paraná System but it disappears if a larger scale is considered, whereas the inverse relationship between NO_3^- and Chl-*a* suggested that phytoplankton significantly affects this nutrient. The explanation seems unsuitable for the Middle Paraná System, where higher nutrient concentrations and lower algal biomass were observed in comparison with the Upper Paraná stretch.

Spatial homogeneity is not the only possible trend of flooding

In the present work, decreasing trends were found in the spatial gradient from the main channel towards the floodplain for pH, DO, N–NO_3^-, Z_d:Z_{eu} and Pheo-*a*:Chl-*a* ratios, as well as increasing trends for Chl-*a*, in agreement with other reports (O'Farrell et al., 1996; Izaguirre et al., 2001; Unrein, 2002; Maine et al., 2004; Zalocar de Domitrovic et al., 2007; Cardoso et al., 2012). The flood had a homogenising effect on Chl-*a* from the main channel to the floodplain gradient and within the floodplain gradient, as observed in other studies (Thomaz et al., 2007; Cardoso et al., 2012). However, for most of the physical and chemical variables, a higher heterogeneity was observed during flood. Thus, results are not in agreement with the general idea that flood exerts exclusively a homogenising effect on the limnological variables in a river–floodplain system. It could be explained by the differential effect of the hydrosedimentological pulse on limnological variables at each site. As regards turbidity, the enhancement of particle sedimentation at the floodplain (high transparency) coincided with the arrival of the sediment pulse at the main channel (high turbidity) during flood, increasing spatial heterogeneity. On the other hand, sediment resuspension at the floodplain favoured by the reduction of lakes depth (ca. 1 m) during LW resembles the main channel turbidity values. A similar effect was observed for the Z_d:Z_{eu} ratio. With respect to pH and DO, the sharper decline at the floodplain than at the main channel increased spatial differentiation during flood. The greater heterogeneity of SRP during potamophase would be associated with the different contribution of the inundated floodplain and the Bermejo River to each site. The more heterogeneous values of both MI and the Pheo-*a*:Chl-*a* ratio during the potamophase may be due to the spatial heterogeneity of light conditions and their effect on algal physiological state (Furusato & Asaeda, 2009), and to the microscopic parts of decaying macrophytes that influence the results of the pigment analysis.

The heterogeneity in the main channel to floodplain gradient during periods of high water level was probably increased due to the extreme nature of the flooding, and its overlap with the warm season and sedimentological pulse. But when considering the floodplain gradient, turbidity, Z_d:Z_{eu} ratio and pH kept the accepted pattern of greater homogeneity during the flood (Thomaz et al., 2007). In this regard, it could be assumed that, even though the system operates as a whole, the floodplain presents a particular identity.

The effect of flood for limnological variables is too complex for reducing it to a unique pattern. The results show that exceptions to the rule could be found: the homogenising effect of inundation cannot be generalised to all variables and situations. The complexity of the functioning of large floodplain rivers demands that the spatial scale should be considered in relation to hydrological phases in order to fully understand their dynamics. In addition, waterbodies rarely act independent from each other and their conditions are highly dependent on hydrological fluctuations and the connectivity between the main channel and the floodplain (Henry et al., 2011).

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