Modeling chlorophyll-*a* and dissolved oxygen concentration in tropical floodplain lakes (Paraná River, Brazil)

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(With 3 figures)

Abstract

The need for prediction is widely recognized in limnology. In this study, data from 25 lakes of the Upper Paraná River floodplain were used to build models to predict chlorophyll-*a* and dissolved oxygen concentrations. Akaike's information criterion (AIC) was used as a criterion for model selection. Models were validated with independent data obtained in the same lakes in 2001. Predictor variables that significantly explained chlorophyll-*a* concentration were pH, electrical conductivity, total seston (positive correlation) and nitrate (negative correlation). This model explained 52% of chlorophyll variability. Variables that significantly explained dissolved oxygen concentration were pH, lake area and nitrate (all positive correlations); water temperature and electrical conductivity were negatively correlated with oxygen. This model explained 54% of oxygen variability. Validation with independent data showed that both models had the potential to predict algal biomass and dissolved oxygen concentration in these lakes. These findings suggest that multiple regression models are valuable and practical tools for understanding the dynamics of ecosystems and that predictive limnology may still be considered a powerful approach in aquatic ecology.

Keywords: model, chlorophyll-*a*, oxygen, floodplain lakes.

Predição das concentrações de clorofila-*a* e oxigênio dissolvido em lagoas da planície de inundação do Alto Rio Paraná

Resumo

O objetivo desse estudo foi o de construir modelos para predizer as concentrações de clorofila-*a* e oxigênio dissolvido em lagoas da planície de inundação do Alto Rio Paraná. Para tanto, foram selecionadas 25 lagoas na planície de inundação. O critério de Akaike (AIC) foi utilizado para a seleção dos modelos. Posteriormente, os modelos foram validados utilizando dados independentes obtidos nas mesmas lagoas. As variáveis que explicaram significativamente as concentrações de clorofila-*a* (52%) foram pH, condutividade elétrica, material em suspensão (relação positiva) e nitrato (relação negativa). As variáveis que melhor explicaram as concentrações de oxigênio dissolvido (54%) foram pH, área das lagoas, nitrato (relação positiva), temperatura da água e condutividade elétrica (relação negativa). A elevada capacidade preditiva desses modelos foi demonstrada através da utilização de dados independentes. Esses resultados demonstraram que a limnologia preditiva continua sendo uma importante área de pesquisa na ecologia aquática.

Palavras-chave: modelo, clorofila-*a*, oxigênio, lagoas.

1. Introduction

The need for prediction is now widely recognized and frequently articulated as an objective of research programs in aquatic sciences. Predictions are required to anticipate the future state or dynamics of a system (temporal predictions), to characterize a new place (spatial predictions), and to characterize a new circumstance (altered systems) (Pace, 2001). The empirical limnology school advocates prediction mainly in the form of regression models (Rigler, 1982; Rigler and Peters, 1995; Gomes and Miranda, 2001; Pace, 2001), using a small number of variables, but with a long-term data set.

An intuitive premise for ecological modeling is that interacting abiotic variables create environmental gradients that shape the spatial patterns of natural populations. In general, phytoplankton is the major source of pelagic carbon, and its abundance can be estimated through chlorophyll-*a* concentration. The relationship between nutrients and chlorophyll-*a* concentration in aquatic systems has yielded insights on nutrient limitation and is a valuable management tool (Peters, 1986).

Regression and correlation analysis are widely used in water quality management as supplementary tools for

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dynamic models. These types of relationships can be used to improve estimations of chlorophyll-*a* and oxygen concentration in tropical aquatic ecosystems (e.g., Huszar et al., 2006). For instance, the Upper Paraná River floodplain (Paraná River, Brazil) is characterized by its high heterogeneity of aquatic habitats and diversity of organisms (Agostinho and Zalewski, 1995; Agostinho et al., 2004; Aoyagui and Bonecker, 2004). However, few predictive models have been described for this system (e.g., Thomaz et al., 2001) or for other Neotropical floodplains.

Chlorophyll and oxygen are relevant parameters in tropical and sub-tropical river-floodplain systems. Phytoplankton (indexed by chlorophyll concentration) constitute an important carbon source for fish (e.g., Araújo-Lima et al., 1986; Lopes et al., 2007; Hoeinghaus et al., 2008), despite the apparent predominance of macrophytes in river-floodplain systems (Hoeinghaus et al., 2007). In addition, phytoplankton can develop conspicuously in floodplain lakes, leading to eutrophic conditions, especially during low-water periods (Carvalho et al., 2001; Rodrigues et al., 2002). Similarly, oxygen is important for aquatic fauna in floodplains, where extreme seasonal fluctuations in oxygen concentration are observed (Thomaz et al., 1992). This gas is also considered one of the most important abiotic factors affecting fish (Crampton, 1998; Agostinho et al., 2004; 2007; Soares et al., 2006) and invertebrate distribution (Bonecker and Lansac-Tôha, 1996; De Melo et al., 2004). Decreased oxygen concentration during rising and high waters can lead to fish kills in floodplain habitats (Hamilton et al., 1997).

In this study, we used an extensive spatial (25 lakes) and temporal (4 samples per year) data set obtained in lakes of the Upper Paraná River floodplain to identify predictors or environmental forcing functions that could explain chlorophyll-*a* and dissolved oxygen concentrations. This stretch of the Paraná River and its remnant floodplain (the last stretch within Brazil) are key for maintaining the unique biological diversity of this river in the Brazilian territory, already threatened by numerous human impacts (e.g., flow regulation; Agostinho and Zalewski, 1995; Agostinho et al., 2004). We also tested the predictions of the models with independent data sets (validation), to evaluate the potential of these models. Finding models that represent causal relationships is fundamental to determine the most important variables linked to primary production and eutrophication (indexed by chlorophyll) and the integrity of bodies of water for wildlife (indicated by dissolved oxygen). These models represent important tools to predict the future state of the upper Paraná River floodplain, providing insight into possible management actions aimed at conservation.

1.1. Study area

The Paraná basin covers a large area of the Brazilian territory (~802,150 km²). Several dams were built during the last three decades in the Paraná River and in its main tributaries. In the upper portion, the Paraná River presents a floodplain (5-20 km wide), which represents the last undammed stretch within Brazil. Three conservation units were recently created in this region, which is vital for biodiversity conservation of biological diversity and ecological functioning of this large river. The Paraná and its floodplain remnant are also one of the Brazilian sites belonging to the Long Term Ecological Research Program (LTER).

The data set used includes 25 lakes located in the Upper Paraná River floodplain. These lakes belong to three different ecoregions, determined by the river that affects each most intensively: the Paraná, Baía or Ivinheima rivers (Figure 1). Some lakes are permanently connected with a river whereas others are connected only during high water periods (usually from December to March), due to overflow; however, communication through ground water is constant. Morphometric and limnological characteristics varied intensely among lakes (Thomaz et al., 2004a; Table 1).

2. Methods

Water samples were taken in different seasons (February, May, August and November 2000), about 10 cm below the surface. Sampled lakes were shallow (depth < 2 m), except during high water periods when depths reached ~4-5 m. However, vertical mixing is common in these shallow lakes and stratification in physicochemistry is rarely found (Thomaz et al., 1992; Rodrigues et al., 2002; Rocha and Thomaz, 2004). Thus, surface samples are adequate to characterize water quality.

For all 25 lakes, we obtained data for 19 morphometric and limnological variables: lake area (meters), water depth (meters), Secchi disc depth (meters), pH and electrical conductivity (μS.cm^{-1}; digital portable potentiometers), dissolved oxygen (mg.L^{-1}) and temperature (°C; digital portable YSI), turbidity (NTU; portable turbidimeter LaMotte) and total alkalinity (μEq.L^{-1}; Gran titration; Carmouze, 1994). All these variables were measured during samplings.

Sub-samples were filtered (Whatman GF/C membranes) and used to quantify chlorophyll-*a* (spectrophotometer, after acetone extraction; Golterman et al., 1978) and total seston (mg.L^{-1}; gravimetry) concentrations. Total nitrogen concentrations (μg.L^{-1}) were obtained after oxidation of the organic and inorganic nitrogen to N-nitrate, which was reduced to N-nitrite and examined in a spectrophotometer with a Flow Injection Analysis system (Zagatto et al., 1981). Nitrate and nitrite levels (μg.L^{-1}) were determined spectrophotometrically with a Flow Injection Analysis System (Zagatto et al., 1981). N-ammonium concentrations (μg.L^{-1}) were measured spectrophotometrically according to Mackereth et al. (1978). Total phosphorus (μg.L^{-1}), reactive phosphate (μg.L^{-1}) and dissolved phosphate (μg.L^{-1}) were determined in a spectrophotometer after ascorbic acid-mo-
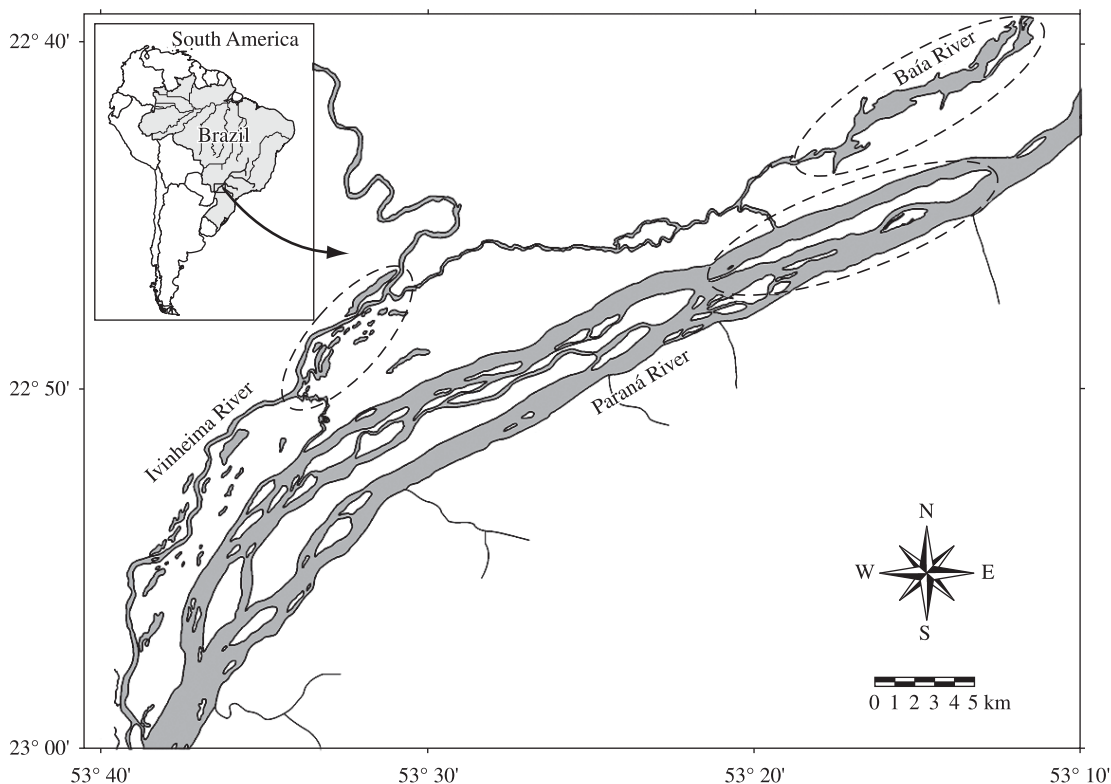
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Figure 1. Study area in the Upper Paraná River floodplain. The lakes studied are connected to the Paraná, Baía and Ivinheima rivers; they are located within the dashed circles.

lybdate reaction (Golterman et al., 1978). A Shimadzu TOC 5000 apparatus measured dissolved organic carbon (DOC; mg.L^{-1}).

2.1. Data analysis

Before analyses, all data, except pH, were log-transformed to meet the assumptions of regression analysis. Multiple regression analysis was performed to obtain models that predicted chlorophyll-*a* and dissolved oxygen concentrations, taking into account the other limnological variables as predictor variables (see Table 1 for the list of variables).

To circumvent multicollinearity problems, strongly correlated predictors (e.g., total seston and turbidity, electrical conductivity and total alkalinity) were not included in the same model. Thus, considering the different pairs of correlated variables, only the ones with the highest predictive power were retained in the multiple regression models. After this first step, a total of ten variables were retained to model chlorophyll-*a* and dissolved oxygen concentrations by different combinations of these variables as predictors: lake area (Area), temperature (Temp), pH, electrical conductivity (EC), total seston (TS), total phosphorus (TP), Nitrate (N-NO$_3$), nitrite (N-NO$_2$), N-ammonium (NH$_4$) and dissolved organic carbon (DOC).

The best models were selected using the model selection approach (Burhnham and Anderson, 1998). Akaike's Information Criterion (AIC) is a recent tool that has been widely used as a criterion for model selection in ecology, but it is rarely applied to limnological data. Basically, AIC is defined as:

$$AIC = -2Ln[L(x|M_i)] + 2K \qquad (1)$$

where $Ln[L(x|M_i)]$ is the log-likelihood of data x given the model M_i; K is the number of parameters in the model. This measure combines the goodness of fit of a model to data and the number of estimated model parameters (complexity).

In particular, we examined Δ_i, the difference between AIC for any particular model and the minimum AIC for the best, most parsimonious model (best fit and complexity). As a rule of thumb, $\Delta_i > 4$-7 suggests that a model does not have strong empirical support (Burnham and Anderson, 1998).

We validated the resulting models using independent data obtained in 2001 in the same lakes. Computer software for analyses included the open-source R and Statistica. Due to the high number of possible models (a total of ten variables considered), only the best one (lower AIC) is presented.

Table 1. Mean, standard deviation (SD), minimum (min) and maximum (max) values of each variable obtained in lakes connected to the rivers (Ivinhema, Baia and Paraná) in the Upper Paraná River floodplain (DO = dissolved oxygen; TS = total seston; DOC = dissolved organic carbon).

Variables	Ivinhema River			Baia River			Paraná River		
	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max
Area (m)	41.22 (42.77)	2.30	113.80	8.11 (8.66)	0.36	27.20	6.75 (5.96)	0.06	14.10
Depth (m)	2.96 (0.84)	1.00	4.25	2.36 (0.49)	1.80	4.00	1.16 (0.52)	0.20	2.25
Temperature (ºC)	23.77 (3.71)	17.20	28.50	24.21 (4.09)	18.10	31.80	24.52 (4.04)	19.20	32.60
Secchi depth (m)	0.56 (0.46)	0.10	2.40	0.97 (0.44)	0.20	2.00	0.65 (0.28)	0.20	1.20
pH	6.67 (0.53)	5.74	8.62	6.34 (0.55)	5.72	8.85	6.5 (0.34)	5.97	7.47
Electrical conductivity ($\mu S.cm^{-1}$)	42.88 (12.44)	22.00	95.00	32.92 (10.51)	22.60	75.40	59.84 (16.91)	33.20	107.50
Alkalinity ($\mu Eq.L^{-1}$)	281.02 (161.27)	12.45	697.60	266.25 (205.62)	52.12	870.30	477.34 (277.24)	8.99	1187.00
Turbidity (NTU)	39.33 (45.02)	0.59	217.00	12.49 (14.98)	2.00	67.60	22.83 (21.72)	4.10	91.40
DO ($mg.L^{-1}$)	6.37 (1.42)	3.18	8.88	4.80 (1.99)	1.50	10.87	4.60 (2.14)	0.34	8.35
TS ($mg.L^{-1}$)	14.47 (10.82)	0.00	46.00	8.85 (7.83)	2.30	34.50	17.43 (14.04)	3.07	53.33
chlorophyll-a ($\mu g.L^{-1}$)	14.89 (25.11)	0.00	143.34	10.25 (14.9)	1.82	89.56	18.71 (16.75)	2.46	60.07
Nitrate ($\mu g.L^{-1}$)	59.22 (82.23)	0.00	355.00	28.72 (86.86)	0.00	485.95	23.36 (48.57)	0.00	195.32
Nitrite ($\mu g.L^{-1}$)	1.87 (2.0)	0.00	10.00	1.13 (0.91)	0.00	4.05	1.28 (1.04)	0.00	3.26
N-ammonium ($\mu g.L^{-1}$)	6.96 (12.38)	0.00	66.18	4.20 (9.16)	0.00	45.38	9.34 (19.79)	0.00	88.32
Total-N ($\mu g.L^{-1}$)	425.66 (184.61)	205.00	879.61	421.57 (183.52)	164.57	902.50	375.82 (187.14)	165.28	922.00
Ortho-P ($\mu g.L^{-1}$)	6.88 (9.68)	0.00	48.22	3.73 (5.51)	0.00	25.73	2.78 (2.96)	0.00	7.81
Dissolved-P ($\mu g.L^{-1}$)	16.49 (15.02)	2.33	78.74	15.49 (24.85)	0.55	144.23	12.66 (9.56)	1.98	42.23
Total-P ($\mu g.L^{-1}$)	90.25 (185.43)	9.03	1170.62	51.89 (48.97)	12.19	289.57	58.17 (39.96)	9.77	141.10
DOC ($mg.L^{-1}$)	8.56 (5.83)	2.82	28.94	7.64 (3.20)	3.65	20.01	4.47 (2.11)	2.16	11.22

3. Results

Overall, sampled lakes presented a wide range of morphometrical and limnological conditions (Table 1). Mean values of dissolved oxygen, nitrate, nitrite, total nitrogen, reactive phosphate, total phosphate and turbidity were higher in lakes of the Ivinheima River. Lakes of the Paraná River showed higher values of electrical conductivity, alkalinity and ammonium, whereas those of the Baía river had the highest mean Secchi depth and intermediate values for most of the remaining variables (Table 1).

Following the AIC criterion, the best, most parsimonious model (fit and complexity), to predict chlorophyll-*a* concentration was:

$$\log (Chlor) = -3.747 + 0.422 \,(pH) + 0.528 \log (EC) + 0.682 \log (TS) - 0.191 \log (N\text{-}NO_3) \qquad (2)$$

with AIC = 198.2; Δ_i = 34.1; n = 97; R^2 = 0.52; F = 36.89; $p < 0.001$.

Predictor variables that significantly explained chlorophyll-*a* concentration were pH, electrical conductivity (EC), total seston (TS) (positive correlations) and nitrate (N-NO$_3$) (negative correlation) (Table 2).

This model explained 52% of the total variation in levels of chlorophyll-*a* in these lakes. Residual analysis indicated that this model was adequate for describing chlorophyll-*a* (Figure 2a). Therefore, this is an indication that the resulting model is adequate to predict chlorophyll-*a* concentrations in the Paraná River floodplain lakes.

The best, most parsimonious model to predict dissolved oxygen concentration was:

$$\log (DO) = 2.92265 + 0.30255 \,(pH) + 0.06172 \log(Area) - 0.60086 \log (Temp) + 0.03999 \log (N\text{-}NO_3) - 0.36633 \log (EC) \qquad (3)$$

with AIC = 12.132; Δ_i = 7.673; n = 89; R^2 = 0.54; F = 21.76; $p < 0.001$.

Predictor variables that significantly explained dissolved oxygen concentration were pH, lake area (Area) and nitrate (N-NO$_3$) (positive correlations), and water temperature (Temp) and electrical conductivity (EC) (negative correlations) (Table 3). Overall, this model explained 54% of the total variation in dissolved oxygen

concentration in these lakes. Similarly to chlorophyll, there was no trend in residuals along the oxygen concentration gradient (Figure 2b). Thus, the proposed model is adequate to predict dissolved oxygen concentration in the Paraná River floodplain lakes.

To test the predictive power of both models, we used an independent data set obtained in the same lakes in 2001. We observed a significant relationship between chlorophyll-*a* concentrations estimated through the model and the chlorophyll-*a* concentrations measured independently in 2001 (r = 0.50; p < 0.001; n = 50) (Figure 3a). A significant relationship was also observed between dissolved oxygen concentrations estimated through the model and concentrations measured independently in 2001 (r = 0.75; p < 0.001; n = 43; Figure 3b). Therefore,

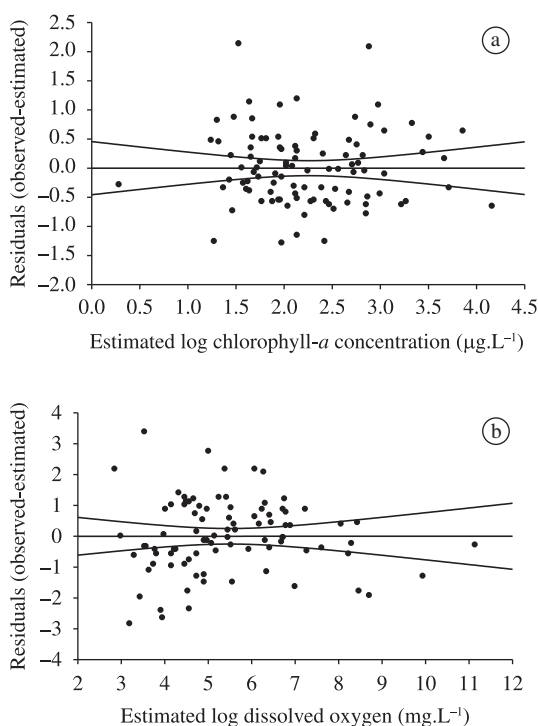**Figure 2.** a) Relationship between residuals and estimated values of chlorophyll-*a;* and b) oxygen concentrations.

Table 2. Results of a multiple regression analysis of chlorophyll-*a* concentration against pH, electrical conductivity (EC), total seston (TS) and nitrate (N-NO$_3$).

Predictor variables	B	t (92)	p
Intercept	–3.747	–3.575	0.00056
pH	0.421	3.231	0.0017
log EC	0.527	2.646	0.0095
log TS	0.682	7.584	<0.0001
log N-NO$_3$	–0.191	–5.805	<0.0001

Table 3. Results of a multiple regression analysis of dissolved oxygen concentration against pH, lakes area (Area), water temperature (Temp), nitrate (N-NO$_3$) and electrical conductivity (EC).

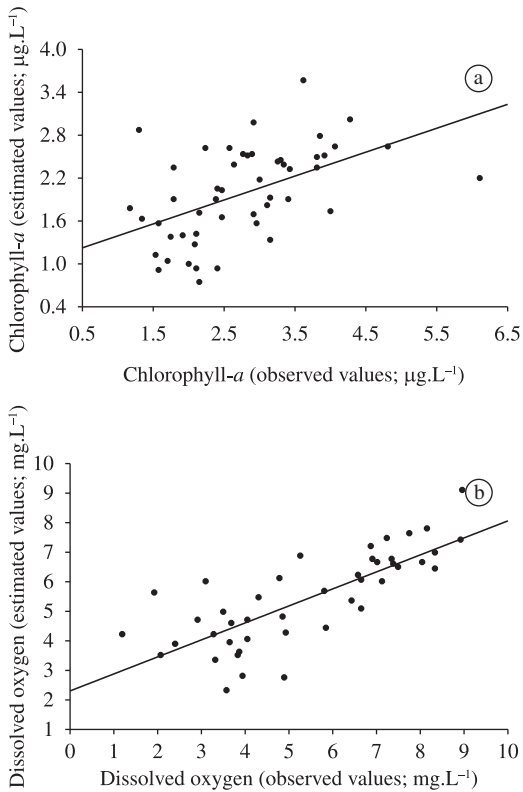| Predictor variables	B	t (84)	p
Intercept	2.92265	4.174	<0.001
pH	0.30255	5.672	<0.001
log Area	0.06172	2.942	0.004
log Temp	–0.60086	–3.549	<0.001
log N-NO$_3$	0.03999	3.017	0.003
Log (EC)	–0.36633	–4.540	<0.001

Figure 3. a) Relationship between chlorophyll-*a* concentrations estimated through the model and those measured in 2001; and b) between the oxygen concentrations estimated through the model and those measured in 2001 in the same lakes.

independent validation also indicated that both models have potential to predict algal biomass and dissolved oxygen concentration in these lakes.

4. Discussion

The hydrological regime, together with temperature, wind and photosynthetically active radiation (PAR) are considered the main driving forces in river-floodplain systems (Junk et al., 1989; Thomaz et al., 2007). The Paraná River floodplain lakes were characterized by high variability in most of the limnological variables. At a large spatial scale, differences in the limnology of these lakes are mainly determined by the river to which they are connected, i.e., the Paraná, Baía or Ivinheima rivers (Carvalho et al., 2003; Thomaz et al., 2004a). On the other hand, lakes are also affected by local functioning forces, such as inputs from small tributaries, depth, colonization by aquatic macrophytes and source of organic substrate and nutrients traveling from the floodplain into the lakes (Thomaz et al., 2007). Both coarse and finer scale factors contribute to the great variety of limnological features found in this study.

In general, the great majority of empirical studies relating phytoplankton to nutrients use data obtained from temperate lakes (Peters, 1986; Kalff, 2002), although a few investigations using this approach studied tropical and sub-tropical freshwater ecosystems (Attayde and Bozelli, 1998; Huszar et al., 2006; Chellappa et al., 2008). It is well known that phytoplankton biomass, expressed as chlorophyll-*a* concentration, is affected by nutrients, mainly phosphorus, both in temperate (e.g., Dillon and Rigler, 1974; Rigler and Peters, 1995; Van Nieuwenhuyse and Jones, 1996; Bryhn et al., 2007) and tropical and subtropical (Attayde and Bozelli, 1998; Huszar et al., 2006) freshwater ecosystems. In the Upper Paraná floodplain, phosphorus also limits microbial activity (Thomaz et al., 2001) and free-floating macrophytes (Kobayashi et al., 2008). However, our findings suggest that only 11% of the variation in chlorophyll-*a* concentration was explained by phosphorus concentration. The weak chlorophyll-phosphorus relationship may be explained by at least two non-mutually exclusive causes. First, previous studies of microbial organisms and macrophytes examined the short temporal period in only a few lakes, connected to the Paraná River, which presented low phosphorus concentrations (Thomaz et al., 2004a). This suggests that phosphorus may be important in some lakes, but its importance disappears when the entire floodplain is considered. Thus, by incorporating a large-spatial scale data set, including several lakes, as we did in this investigation, it is possible to add another perspective to those previous studies. Second, phosphorus was highly correlated with turbidity (log TP-log turbidity: $r = 0.49$; $p < 0.001$; $n = 97$). Thus, phosphorus concentrations in the floodplain lakes have a temporal synchrony with water turbidity, and underwater radiation may hide the relationship between phosphorus and phytoplankton biomass. A similar pattern has been described to explain the weak relationship between total phosphorus and chlorophyll-*a* in Paraná River basin reservoirs (Pagioro et al., 2005).

In our analysis, the best predictors of chlorophyll-*a* concentration in Paraná floodplain lakes were pH, electrical conductivity, total seston and nitrate. In fact, this model had higher R^2 ($R^2 = 0.52$) than the model generated based only on total phosphorus ($R^2 = 0.11$). In agreement with our results, a principal component analysis (PCA) demonstrated that pH, electrical conductivity, total seston and nitrate are responsible for the spatial ordination of lakes (Rocha and Thomaz, 2004). This result has been supported by Van Nieuwenhuyse and Jones (1996), Attayde and Bozelli (1998), and Gomes and Miranda (2001), who explain chlorophyll-*a* concentration by physical, chemical and biological variables, such as grazing pressure induced by zooplankton.

Although the model explained substantial variability in the data set, we wondered if its application would be valuable and if the multiple regression approach is a practical tool for understanding the dynamics of chlorophyll-*a* in lakes. One of our objectives was to test the model using an independent data set (obtained in 2001). In fact, the correlation ($r = 0.52$) between predicted val-

ues (model) and independent data demonstrated the substantial predictive power of the model.

Although it is difficult to determine cause and effect through an exploratory approach such as that used in this paper, we believe that some inferences are possible. The positive relationship between chlorophyll-*a* and pH, for example, can be readily explained by photosynthesis, since CO_2 assimilation increases pH values (Wetzel, 2001). The positive relationship between electrical conductivity and chlorophyll-*a* concentration could also be a causal mechanism, since bicarbonate, which is significantly related to conductivity in the Paraná basin (Thomaz et al., 1992), can influence photosynthesis and phytoplankton biomass. Sediment resuspension can also transfer nutrients and ions from sediment to the water, increasing the electrical conductivity (Thomaz et al., 2004a). In addition, nutrients are transported from other floodplain features to lakes during high water and rainy seasons. In general, electrical conductivity can be considered a surrogate for the concentration of nutrients in the water, which directly influences phytoplankton biomass. The positive relationship between chlorophyll-*a* concentration and total seston suggests that phytoplankton per se is an important component of seston in these lakes. The absorption of nitrate (NO_3^-) by the phytoplankton community has been widely discussed, mainly with regard to daylight conditions (Thomaz et al., 2004a). The negative relationship between nitrate and chlorophyll corroborates this idea, and suggests that, in fact, phytoplankton significantly affects nitrate. This variable is considered an important determinant of phytoplankton biomass in some lakes of the Upper Paraná floodplain (Train and Rodrigues, 2004).

Predicting dissolved oxygen concentration in floodplain lakes is necessary, since this gas is one of the main determinants of fish and invertebrate distributions in floodplain ecosystems (e.g., Bonecker and Lansac-Tôha, 1996; De Melo et al., 2004; Crampton, 1998; Soares et al., 2006). Indeed, during high water levels, when allochthonous influence increases, low oxygen concentration in the water column can affect aquatic biota, especially fish (Hamilton et al., 1997; Crampton et al., 1998; Carvalho et al., 2001). The main sources of oxygen for the Paraná floodplain lakes are the atmosphere and algal photosynthesis, since these lakes are poorly colonized by submerged macrophytes (Thomaz et al., 2004b). The loss of this gas occurs through decomposition of organic matter (substantial in the Paraná floodplain; Pagioro and Thomaz, 1999), transfer from the water to the atmosphere, respiration and oxidation of metal ions (e.g., iron and manganese; Wetzel, 2001). Thus, several variables may influence water oxygen in lakes.

According to model selection, certain variables were important to predict oxygen concentrations in the Paraná River floodplain lakes (lake area, temperature, pH electrical conductivity and nitrate). Lake area is an important feature in determining the dynamics of some limnological variables (such as wind/wave activity) that can distribute oxygen within the water column. In fact, this variable explained approximately 16% of oxygen concentration variability. Empirical studies demonstrate that large lakes exposed to wind have a more uniform oxygen distribution in the water column (Panosso and Kubrusly, 2000). Indeed, smaller lakes are more influenced by margins and, consequently, are subject to higher allochthonous organic matter input (edge effects). The continuous input and decomposition of allochthonous detritus, produced in the aquatic terrestrial transitional zone (ATTZ), tends to decrease the oxygen concentrations even in periods of autotrophy (Carvalho et al., 2001).

Electrical conductivity was negatively associated with oxygen concentration, but this relationship is probably indirect, since this variable reflects decomposition processes. Increases in decomposition rates and decreases in oxygen usually occur during high water periods, when decomposing organic matter input to the lakes increases (Taniguchi et al., 2004; Thomaz et al., 2004a; Townsend, 2006). This process rapidly leads to a change in water quality, an increase of ions due to the leaching of detritus and a decrease of dissolved oxygen due to microbial respiration (Godshalk and Wetzel, 1978; Carvalho et al., 2005; Bianchini et al. 2008; Cunha-Santino et al., 2008). In addition, oxygen depletion promotes the release of ions from sediment (e.g., reactive phosphorus), increasing electrical conductivity. As discussed previously, photosynthetic rates may increase water pH and dissolved oxygen concentration. Thus, the relationship between oxygen and pH is also an indirect effect of phytoplankton photosynthesis. In the Paraná River floodplain lakes, higher pH values are frequently obtained during the low water phase when chlorophyll-*a* and dissolved oxygen concentrations are higher (Thomaz et al., 2004a; Rocha and Thomaz, 2004). The positive relationship between nitrate and dissolved oxygen can be explained by the dependence of the nitrification process on oxygen supply (Wetzel, 2001).

There is a direct effect of temperature on the solubility of gases, in particular dissolved oxygen (Wetzel, 2001). In addition, there is a direct temperature effect on decomposition rates due to microbial activity. According to the Van T' Hoff rule, an increase in temperature can cause a two- to three-fold increase in bacterial activity, and consequently decrease dissolved oxygen concentrations. The negative effect of temperature on oxygen concentration reflected by the predictive model corroborates other studies that showed that high temperatures found in tropical and subtropical aquatic ecosystems are responsible for rapid detritus breakdown (Esteves and Barbieri, 1983; Carvalho et al., 2005), further enhancing oxygen depletion.

Models built to predict chlorophyll-*a* and dissolved oxygen concentrations in the Paraná River floodplains lakes, explained most of the variability of the data, as proven by multiple regression analysis and posteriori validation with an independent data set. Despite significant correlations between predicted and measured

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concentrations of chlorophyll-*a* and dissolved oxygen, 48% of the total variability of the former and 46% of variability in the latter remained unexplained by the proposed models. Therefore, this type of model may be useful for estimating both variables, but application of these models should be conducted with great caution. Other possible factors not considered in our models but that could contribute to explain chlorophyll-*a* concentrations in these lakes are herbivory, difference in chlorophyll-*a* concentration between algal populations (Attayde and Bozelli, 1998), water turbulence and sedimentation of algal cells adsorbed with clay. Similarly, other potential variables explaining oxygen are water column mixing, concentration of metals and bacterial densities.

In conclusion, these findings suggest that predictive limnology may be considered a powerful approach in aquatic ecology, even considering the unexplained variability found in these models. Multiple regression models can be valuable and practical tools for understanding the dynamics of ecosystems if these models meet certain requirements such as simplicity, general applicability and validity. We believe that our models meet these requirements and could be used to study other tropical floodplain lakes. The models proposed here are also a valuable tool to predict future trends with regard to chlorophyll-*a* and oxygen concentrations in the Paraná River floodplain lakes, which are rapidly changing due to human interference (Agostinho et al., 2008). It would be difficult to propose measures related to all important variables included in our models, but at least two of them deserve attention due to indicated roles in future broad-scale floodplain management. First, it seems that nitrogen is driving phytoplankton productivity in lakes and consequently, attempts to control eutrophication should focus first on this nutrient. Second, lake area was an important predictor of oxygen concentration and thus, efforts to reduce fish mortality derived from anoxia (e.g., by increasing the connection between lakes and the main river channel) should focus on smaller lakes. Thus, these predictions are useful to identify patterns and also to manage ecosystem function following disturbances.

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