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# Hydrodynamic Control of Plankton Spatial and Temporal Heterogeneity in Subtropical Shallow Lakes

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## 1. Introduction

During the last 200 years, many lakes have suffered from eutrophication, implying an increase of both nutrient loading and organic matter (Wetzel, 1996). An aspect that has often been neglected in freshwater systems is the fact that phytoplankton is often not evenly distributed horizontally in space in shallow lakes. Although the occurrence of phytoplankton patchiness in marine systems has been known for a long time (e.g., Platt et al., 1970; Steele, 1978; Steele & Henderson, 1992), phytoplankton in shallow lakes is often assumed to be homogeneously distributed. However, there are various mechanisms that may cause horizontal heterogeneity in shallow lakes. For example, grazing by aggregated zooplankton and other organisms may cause spatial heterogeneity in phytoplankton (Scheffer & De Boer, 1995). Submerged macrophyte beds may be another mechanism, through reduction of resuspension by wave action and allelopathic effects on the algal community (Van den Berg et al., 1998). For large shallow lakes, wind can be a dominant factor leading to both spatial and temporal heterogeneity of phytoplankton (Carrick et al., 1993), either indirectly by affecting the local nutrient concentrations due to resuspended particles, or directly by resuspending algae from the sediment (Scheffer, 1998). In the management of large lakes, prediction of the phytoplankton distribution can assist the manager to decide on an optimal course of action, such as biomanipulation and regulation of the use of the lake for recreation activities or potable water supply (Reynolds, 1999). However, it is difficult to measure the spatial distribution of phytoplankton. Mathematical modeling of a phytoplankton can be an important alternative methodology in improving our knowledge regarding the physical, chemical and biological processes related to phytoplankton ecology (Scheffer, 1998; Edwards & Brindley, 1999; Mukhopadhyay & Bhattacharyya, 2006).

Over the past decade there has been a concerted effort to increase the realism of ecosystem models that describe plankton production as a biological indicator of eutrophication. Most

of this effort has been expended on the description of phytoplankton in temperate lakes; thus, multi-nutrient, photo-acclimation models are now not uncommon (e.g., Olsen & Willen, 1980; Edmondson & Lehman, 1981; Sas, 1989; Fasham et al., 2006; Mitra & Flynn, 2007; Mitra et al., 2007). In subtropical lakes, eutrophication has been intensively studied, but only with a focus on measuring changes in nutrient concentrations (e.g., Matveev & Matveeva, 2005; Kamenir et al., 2007). A wide variety of phytoplankton models have been developed. The simplest models are based on a steady state or on the assumption of complete mixing (Schindler, 1975; Smith, 1980; Thoman & Segna, 1980). Phytoplankton models based on more complex vertical 1-D hydrodynamic processes give a more realistic representation of the stratification and mixing processes in deep lakes (Imberger & Patterson, 1990; Hamilton et al., 1995a; Hamilton et al., 1995b). However, the vertical 1-D assumption might be too restrictive, especially in large shallow lakes that are poorly stratified and often characterized by significant differences between the pelagic and littoral zones. In these cases, a horizontal 2-D model with a complete description of the hydrodynamic and ecological processes can offer more insight into the factors determining local water quality.

Currently, computational power no longer limits the development of 2-D and 3-D models, and these models are being used more frequently. Of the wide diversity of 2-D and 3-D hydrodynamic models, most were designed to study deep-ocean circulation or coastal, estuarine and lagoon zones (Blumberg & Mellor, 1987; Casulli, 1990). However, only a few models are coupled with biological components (Rajar & Cetina, 1997; Bonnet & Wessen, 2001).

In this chapter, we present the results of comparative modeling of two subtropical shallow lakes where the wind, and derived hydrodynamics, and river flow act as the main factors controlling plankton dynamics on temporal and spatial scales. The basic hypothesis is that wind and wind derived-hydrodynamics are the main factor determining the spatial and temporal distribution of plankton communities (Cardoso et al. 2003; Cardoso & Motta Marques, 2003, 2004a, 2004b, 2004c, 2009), in association with point incoming river flows.

The spatial heterogeneity of phytoplankton in Lake Mangueira is influenced by hydrodynamic patterns, and identifying zones with a higher potential for eutrophication and phytoplankton patchiness (Fragoso Jr. et al., 2008). The spatial patterns of chlorophyll-a concentrations generated by the model were validated both with a field data set and with a cloud-free satellite image provided by a Terra Moderate Resolution Imaging Spectroradiometer (MODIS) with a spatial resolution of 1.0 km.

### 1.1 Study areas

Itapeva Lake is the first (N→S) in a system of interconnected fresh-water coastal lakes on the northern coast of the state of Rio Grande do Sul, Brazil (Fig. 1). The lake has an elongated shape (30.8 km × 7.6 km) and a surface area of ≈125 km<sup>2</sup>, and is shallow, with a maximum depth of 2.5 m. The lake is oriented according to the prevailing wind direction (NE - SW quadrants), where the northern part is more constricted and consequently the water is more confined. Two rivers enter the lake: Cardoso River, in the northern part, and Três Forquilhas River in the southern part. The former is small and the flow was not important for the input; however, the contribution of the latter river was modeled and influenced the spatial pattern. Lake Mangueira (33°1'48"S 52°49'25"W) is a large freshwater ecosystem in southern Brazil (Fig. 2), covering a total area of 820 km<sup>2</sup>, with a mean depth of 2.6 m and maximum depth of

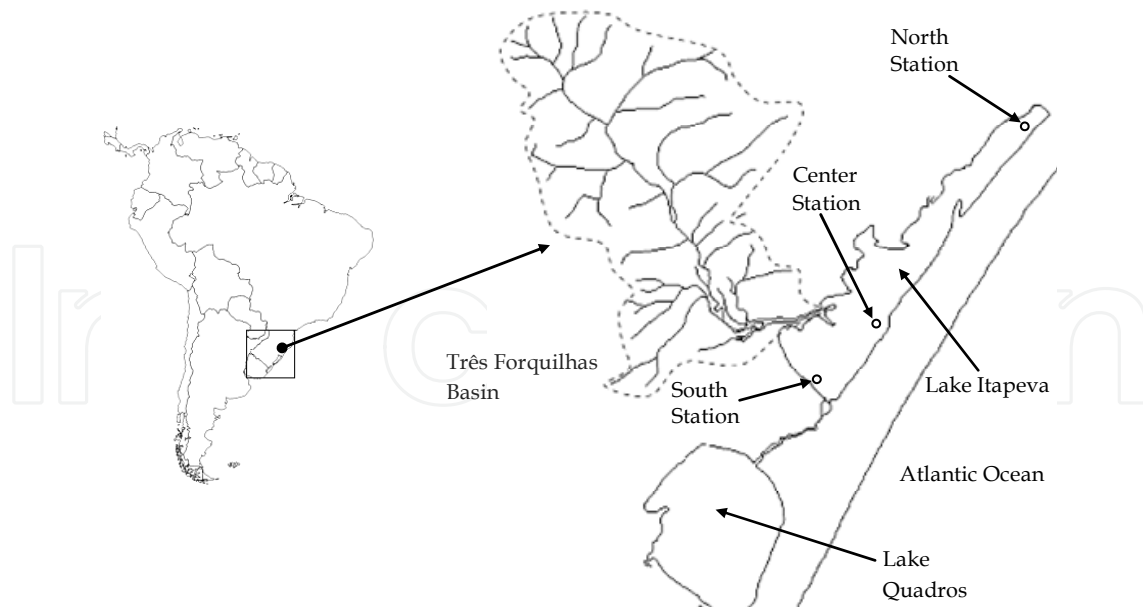


Fig. 1. Itapeva Lake in southern Brazil, with the three sampling points (North, Center and South).

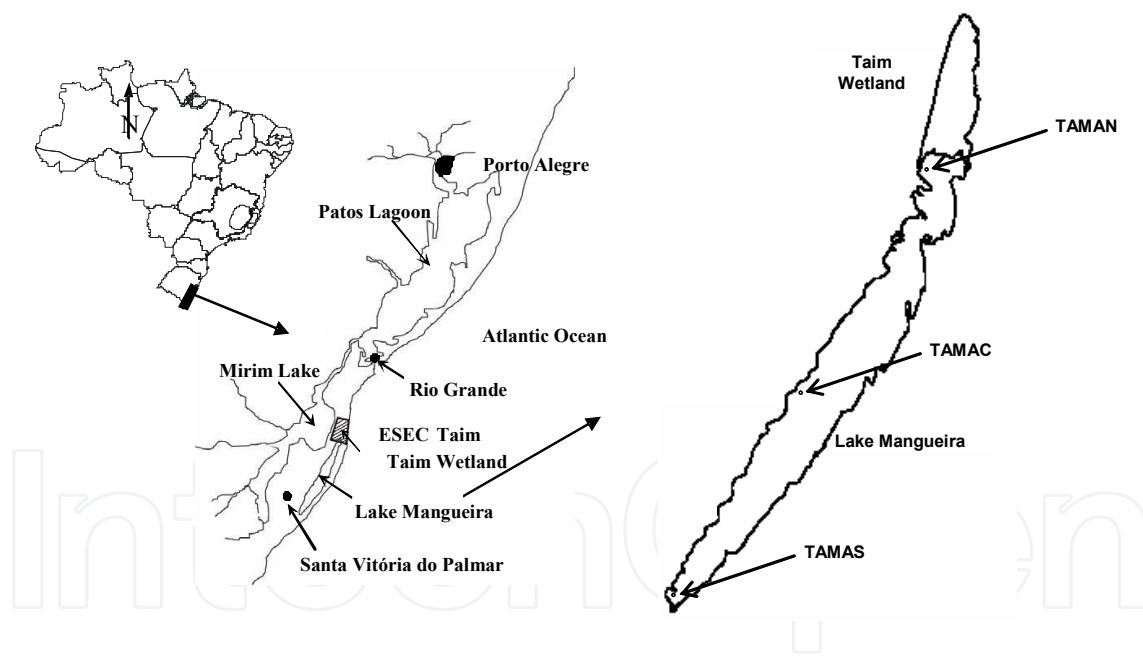


Fig. 2. Lake Mangueira in southern Brazil. The meteorological and sampling stations in the North, Center and South parts of Lake Mangueira are termed TAMAN, TAMAC and TAMAS, respectively.

6.5 m. Its trophic state ranges from oligotrophic to mesotrophic (annual mean  $\text{PO}_4$  concentration  $35 \text{ mg m}^{-3}$ , varying from  $5$  to  $51 \text{ mg m}^{-3}$ ). This lake is surrounded by a variety of habitats including dunes, pinus forests, grasslands, and two wetlands. This heterogeneous landscape harbors an exceptional biological diversity, which motivated the Brazilian federal authorities to protect part of the entire hydrological system as the Taim Ecological Station in 1991 (Garcia et al., 2006). The watershed (ca.  $415 \text{ km}^2$ ) is primarily used

for rice production, and many of the local waterbodies are used for irrigation, with a total water withdrawal of approximately  $2 \text{ L s}^{-1} \text{ ha}^{-1}$  on 100 individual days within a 5-month period, and a high input of nutrients from the watershed during the rice-production period.

## 2. Data base

The data from Itapeva Lake were gathered over more than one year (August 1998 – August 1999), at three fixed sampling stations (North, Center and South). Lake Mangueira has been sampled for several years, although for the modeling exercise reported here we used data also collected at three fixed sampling stations (North, Center and South) from 2000 to 2001.

The sampling protocol as well as some results were published previously by Cardoso & Motta Marques (2003, 2004a, 2004b, 2004c, 2009) for Itapeva Lake, and by Crossetti et al. (2007) and Fragoso Jr. et al. (2008) for Lake Mangueira.

Environmental data (air temperature, precipitation, wind velocity and wind direction) from the meteorological station (DAVIS, Weather Wizard III, Weather Link) installed at the Center point were recorded every 30 min (beginning 24 h before each sampling event) throughout the period. Based on the prevailing wind direction in each season, the effective fetch ( $L_f$  km) was calculated (Håkanson, 1981) for each sampling point using the map of the region on a 1:250 000 scale. An estimate was also made of the height of waves produced and the bottom dynamics, from wind velocity, depth and fetch (Håkanson, 1981).

Four sections were chosen to study seiches in the lake, one section for each region (North, Center and South), and one section running in the longest and most central direction. It was considered that the seiches occur at time intervals of over 120 min; to obtain this value, the length of the lake (fetch) in the direction of the seiche, the mean wind speed, and the time needed by the wind to cover this distance were considered. This time is the minimum time for seiche occurrence, i.e., it is the time needed by the wind to cover the fetch. In addition to evaluating the existence of seiches, the period was also studied using simulated values and an empirical equation. The period calculated empirically is based on the formula for a rectangular shape (Lopardo, 2002 as cited in Cardoso & Motta Marques, 2003).

Data for turbidity, temperature, dissolved oxygen, pH, and electrical conductivity from the YSI (Yellow Springs Instruments 6000 upg3) multiprobe installed at the three sampling points were recorded every 5 minutes during each seasonal campaign. Water level, direction and velocity were recorded every 15 minutes at the same locations.

Samples were collected during five seasonal campaigns: winter/98 (August 24–25/1998), spring (December 15–20/1998), summer (March 2–7 /1999), autumn (May 21–26/1999) and winter (August 14–19/1999). The water samples for plankton analyses were collected at three depths (surface, middle and bottom) during four shifts throughout the day (06:00, 10:00, 14:00 and 18:00 h), at 24-h intervals during the three days of each seasonal sampling. The water samples for analyses of solids, nitrogen and phosphorus (APHA, 1992) were collected and integrated into the water-column data during the same periods as the plankton sampling.

### 2.1 Modeling in Itapeva Lake

Modeling in Itapeva Lake was divided into two parts: watershed and lake modeling. First, we used two different hydrological models: a) to estimate the input from the Três Forquilhas basin, and b) to estimate the output from Itapeva Lake to the river downstream.

Subsequently, we used a 2-D hydrodynamic model to evaluate the roles of the Três Forquilhas inflow and wind effects on the hydrodynamics and mixture processes of the lake. For the watershed analysis we used the IPH2 model, a rainfall, runoff-lumped model developed at the Instituto de Pesquisas Hidráulicas (IPH). Its mathematical basis is the continuity equation composed of the following algorithms: (a) losses by evapotranspiration and interception by leaves or stems of plants; (b) evaluation of infiltration and percolation by Horton; and (c) evaluation of surface and groundwater flows (Tucci, 1998). The model works by regarding a drainage basin as series of storage tanks, with rainfall entering at the top, and being split between what is returned to the atmosphere as evaporation, and what emerges from the basin as runoff (stream flow). Depending on the number of tanks and the number of parameters controlling the passage of water between them, it can be made more or less complex.

For the output analysis we used the MOLABI model (Ecoplan, 1997), a water-budget model based on the Puls method, which represents the continuity equation applied to the whole lake. The input data is rainfall over the lake, inflows from the watershed, and groundwater flux estimated by the Darcy equation. Evaporation was estimated using the Penman method.

The hydrodynamic patterns in Itapeva Lake were modeled using the model IPH-A (2D; Borche, 1996). The main inputs of the model were: water inflow, wind, rainfall and evaporation, spatial maps (including waterbody, bathymetry, bottom and surface stress coefficient). This model was applied because Itapeva Lake is a polymictic environment with no significant difference among depths (surface, middle and bottom), neither for the physical and chemical data nor for the plankton communities. The model was run from January to December 1999.

## 2.2 Modeling in Lake Mangueira

For Lake Mangueira, we applied a dynamic ecological model describing phytoplankton growth, called IPH-TRIM3D-PCLake (Fragoso Jr. et al., 2009). Although this model can represent the three-dimensional flows and the entire trophic structure dynamically, in this study case we used a simplified version of the model consisting of three modules: (a) a detailed horizontal 2-D hydrodynamic module for shallow water, which deals with wind-driven quantitative flows and water levels; (b) a nutrient module, which deals with nutrient transport mechanisms and some conversion processes; and (c) a biological module, which describes phytoplankton growth in a simple way. An overview of the modeling processes is given in Fig. 3.

The hydrodynamic model is based on the shallow-water equations derived from Navier-Stokes, which describe dynamically a horizontal two-dimensional flow:

$$\frac{\partial \eta}{\partial t} + \frac{\partial [(h + \eta)u]}{\partial x} + \frac{\partial [(h + \eta)v]}{\partial y} = 0 \quad (1)$$

$$\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} + v \frac{\partial u}{\partial y} = -g \frac{\partial \eta}{\partial x} - \gamma u + \tau_x + A_h \nabla^2 u + f v \quad (2)$$

$$\frac{\partial v}{\partial t} + u \frac{\partial v}{\partial x} + v \frac{\partial v}{\partial y} = -g \frac{\partial \eta}{\partial y} - \gamma v + \tau_y + A_h \nabla^2 v - f u \quad (3)$$

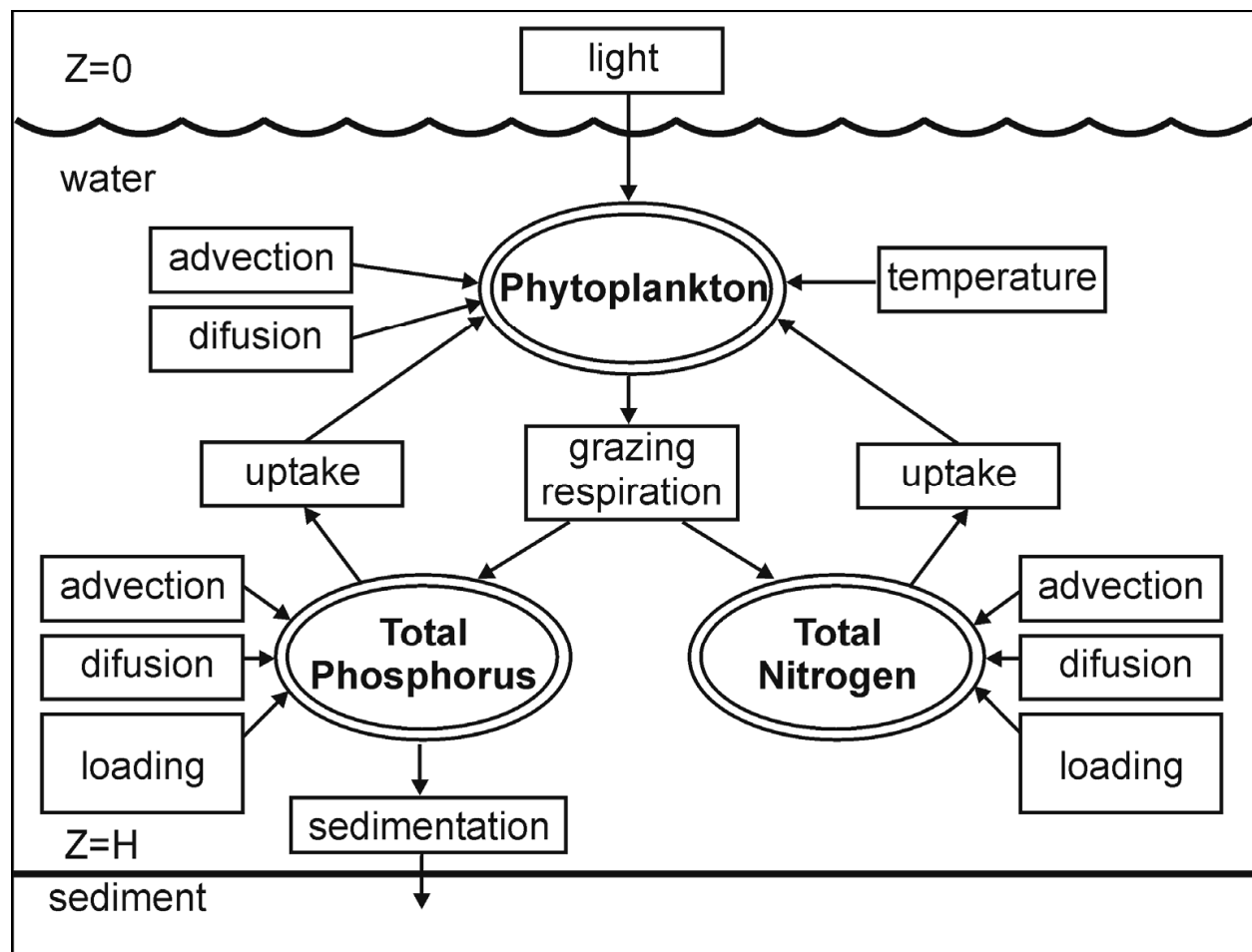


Fig. 3. Simplified representation of the interactions involving the state variables (double circle), and the processes (rectangle) used for the modeling of Lake Mangueira.

where  $u(x,y,t)$  and  $v(x,y,t)$  are the water velocity components in the horizontal  $x$  and  $y$  directions;  $t$  is time;  $\eta(x,y,t)$  is the water surface elevation relative to the undisturbed water surface;  $g$  is the gravitational acceleration;  $h(x,y)$  is the water depth measured from the undisturbed water surface;  $f$  is the Coriolis force;  $\tau_x$  and  $\tau_y$  are the wind stresses in the  $x$  and  $y$  directions;  $\nabla = \partial/\partial x \cdot \vec{i} + \partial/\partial y \cdot \vec{j}$  is a vector operator in the  $x$ - $y$  plane (known as nabla operator, or del operator);  $A_h$  is the coefficient of horizontal eddy viscosity; and  $\gamma = \frac{g\sqrt{u^2 + v^2}}{C_z}$  (Daily & Harleman, 1966) where  $C_z$  is the Chezy friction coefficient.

Usually, the wind stresses in the  $x$  and  $y$  directions are written as a function of wind velocity (Wu, 1982):

$$\tau_x = C_D \cdot W_x \cdot \|W\| \quad (4)$$

$$\tau_y = C_D \cdot W_y \cdot \|W\| \quad (5)$$

where  $C_D$  is the wind friction coefficient; and  $W_x$  and  $W_y$  are the wind velocity components ( $\text{m}\cdot\text{s}^{-1}$ ) in the  $x$  and  $y$  directions, respectively. Wind velocity is measured at

10 m above the water surface; and  $\|W\| = \sqrt{W_x^2 + W_y^2}$  is the norm of the wind velocity vector. We solved the partial differential equations numerically by applying an efficient semi-implicit finite differences method to a regular grid, which was used in order to assure stability, convergence and accuracy (Casulli, 1990; Casulli & Cheng, 1990; Casulli & Cattani, 1994).

The nutrient module includes the advection and diffusion of each substance, inlet and outlet loading, sedimentation, and resuspension through the following equation:

$$\frac{\partial(HC)}{\partial t} + \frac{\partial(uCH)}{\partial x} + \frac{\partial(vCH)}{\partial y} = \frac{\partial}{\partial x} \left( K_h \frac{\partial(HC)}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_h \frac{\partial(HC)}{\partial y} \right) + \text{source or sink} \quad (6)$$

where  $C$  is the mean concentration in the water column;  $H = \eta + h$  is the total depth; and  $K_h$  is the horizontal scalar diffusivity assumed as  $0.1 \text{ m}^2 \text{ day}^{-1}$  (Chapra, 1997). Equation 6 was applied to model total phosphorus, total nitrogen and phytoplankton. All these equations are solved dynamically, using a simple numerical semi-implicit central finite differences scheme (Gross et al., 1999a; 1999b) (Fig. 2). Thus, the mass balances involving phytoplankton and nutrients can be written as:

$$\frac{\partial(Ha)}{\partial t} + \frac{\partial(uHa)}{\partial x} + \frac{\partial(vHa)}{\partial y} = \mu_{\text{eff}} Ha + \frac{\partial}{\partial x} \left( K_h \frac{\partial(Ha)}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_h \frac{\partial(Ha)}{\partial y} \right) + \text{inlet/outlet} \quad (7)$$

$$\frac{\partial(Hn)}{\partial t} + \frac{\partial(uHn)}{\partial x} + \frac{\partial(vHn)}{\partial y} = -a_{na} \mu_{\text{eff}} Ha + \frac{\partial}{\partial x} \left( K_h \frac{\partial(Hn)}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_h \frac{\partial(Hn)}{\partial y} \right) + \text{inlet/outlet} \quad (8)$$

$$\frac{\partial(Hp)}{\partial t} + \frac{\partial(uHp)}{\partial x} + \frac{\partial(vHp)}{\partial y} = -a_{pa} \mu_{\text{eff}} Ha - k_{\text{phos}} p + \frac{\partial}{\partial x} \left( K_h \frac{\partial(Hp)}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_h \frac{\partial(Hp)}{\partial y} \right) + \text{inlet / outlet} \quad (9)$$

where  $a$ ,  $n$  and  $p$  are the chlorophyll-a, total nitrogen and total phosphorus concentrations, respectively;  $a_{na}$  is the N/Chla ratio equal to  $8 \text{ mg N mg Chla}^{-1}$ ;  $a_{pa}$  is the P/Chla ratio equal to  $1.5 \text{ mg N mg Chla}^{-1}$ , inlet/outlet represents the balance between all inlets and outlets in a control volume  $\partial x \partial y \partial z$ ; and  $k_{\text{phos}}$  is the settling coefficient.

The effective growth rate itself is not a simple constant, but varies in response to environmental factors such as temperature, nutrients, respiration, excretion and grazing by zooplankton:

$$\mu_{\text{ef}} = \mu_p(T, N, I) a - \mu_L a \quad (10)$$

where  $\mu_p(T, N, I)$  is the primary production rate as a function of temperature ( $T$ ), nutrients ( $N$ ), and light ( $I$ );  $\mu_L$  is the loss rate due to respiration, excretion, and grazing by zooplankton; and  $a$  is the chlorophyll-a concentration.

The hydrodynamic module was calibrated by tuning the model parameters within their observed ranges taken from the literature (Table 1). Nonetheless, the hydraulic resistance caused by the presence of emerged macrophytes in the Taim Wetland was represented by a



smaller Chezy's resistance factor than was used in other lake areas (Wu et al., 1999). Calibration and validation of the hydrodynamic parameters were done using two different time-series of water level and wind produced for two locations in Lake Mangueira (North and South).

Parameter	Description	Unit	Values /Ref.	
Hydrodynamic:				
1	$A_h$	Horizontal eddy viscosity coefficient	$m^{1/2} s^{-1}$	5 – 15 <sup>1</sup>
2	$C_D$	Wind friction coefficient	-	2e-6 – 4e-6 <sup>2</sup>
3	$C_Z$	Chezy coefficient	-	50 – 70 <sup>3</sup>
Biological:				
1	$G_{max}$	Maximum growth rate algae	day <sup>-1</sup>	1.5 – 3.0 <sup>4</sup>
2	$I_S$	Optimum light intensity for the algae	cal cm <sup>-2</sup> dia <sup>-1</sup>	100 – 400 <sup>5</sup>
3	$k'_e$	Light attenuation coefficient in the water	m <sup>-1</sup>	0.25 – 0.65 <sup>5</sup>
4	$\theta_T$	Temperature effect coefficient	-	1.02 – 1.14 <sup>6</sup>
5	$\theta_R$	Respiration and excretion effect coefficient	-	1.02 – 1.14 <sup>5</sup>
6	$k_P$	Half-saturation for uptake phosphorus	mg P m <sup>-3</sup>	1 – 5 <sup>7</sup>
7	$k_N$	Half-saturation for uptake nitrogen	mg N m <sup>-3</sup>	5 – 20 <sup>7</sup>
8	$k_{re}$	Respiration and excretion rate	day <sup>-1</sup>	0.05 – 0.25 <sup>8</sup>
9	$k_{gz}$	Zooplankton grazing rate	day <sup>-1</sup>	0.10 – 0.20 <sup>8</sup>

Sources: <sup>1</sup> White (1974); <sup>2</sup> Wu (1982); <sup>3</sup> Chow (1959); <sup>4</sup> Jørgensen (1994); <sup>5</sup> Schladow & Hamilton (1997); <sup>6</sup> Eppley (1972); <sup>7</sup> Lucas (1997); <sup>8</sup> Chapra (1997)

Table 1. Hydrodynamic and biological parameters description and its values range.

For the parameters of the phytoplankton module, we used the mean values for the literature range given in Table 1. To evaluate its performance, we simulated another period of 86 days, starting 12/22/2002 at 00:00 hs (summer). Solar radiation and water temperature data were taken from the TAMAN meteorological station, situated in the northern part of Lake Mangueira. Photosynthetically active radiation (PAR) at the Taim wetland was assigned as 20% of the total radiation, in order to represent the indirect effect of the emergent macrophytes on the phytoplankton growth rate according to experimental studies of emergent vegetation stands in situ. For the lake areas, we assumed that the percentage of PAR was 50% of the total solar radiation (Janse, 2005).

The resulting phytoplankton patterns were compared with satellite images from MODIS, which provides improved chlorophyll-a measurement capabilities over previous satellite sensors. For instance, MODIS can better measure the concentration of chlorophyll-a associated with a given phytoplankton bloom. Unfortunately, there were no detailed chlorophyll-a and nutrient data available for the same period. Therefore, we compared only the median simulated values with field data from another period (2001 and 2002).

### 3. Modeling results

#### 3.1 Itapeva Lake

In Itapeva Lake, wind action generated oscillations of the water level between the North and South parts of the lake. The meteorological and hydrological variables were characterized for daily and seasonal periods.

Simulations using a mathematical bidimensional horizontal hydrodynamic model succeeded in reproducing this phenomenon, and helped to calculate the synthesis of velocity and direction of the water. It was possible to confirm the complexity of the circulation in the lake and to distinguish different behaviors among the South, Center and North. Besides the similarities in morphometry between the Center and South parts, the flow from the Três Forquilhas River enters the center part of the lake and the prevailing N-NE winds move water toward the South part of the lake (Figs 4 and 5).

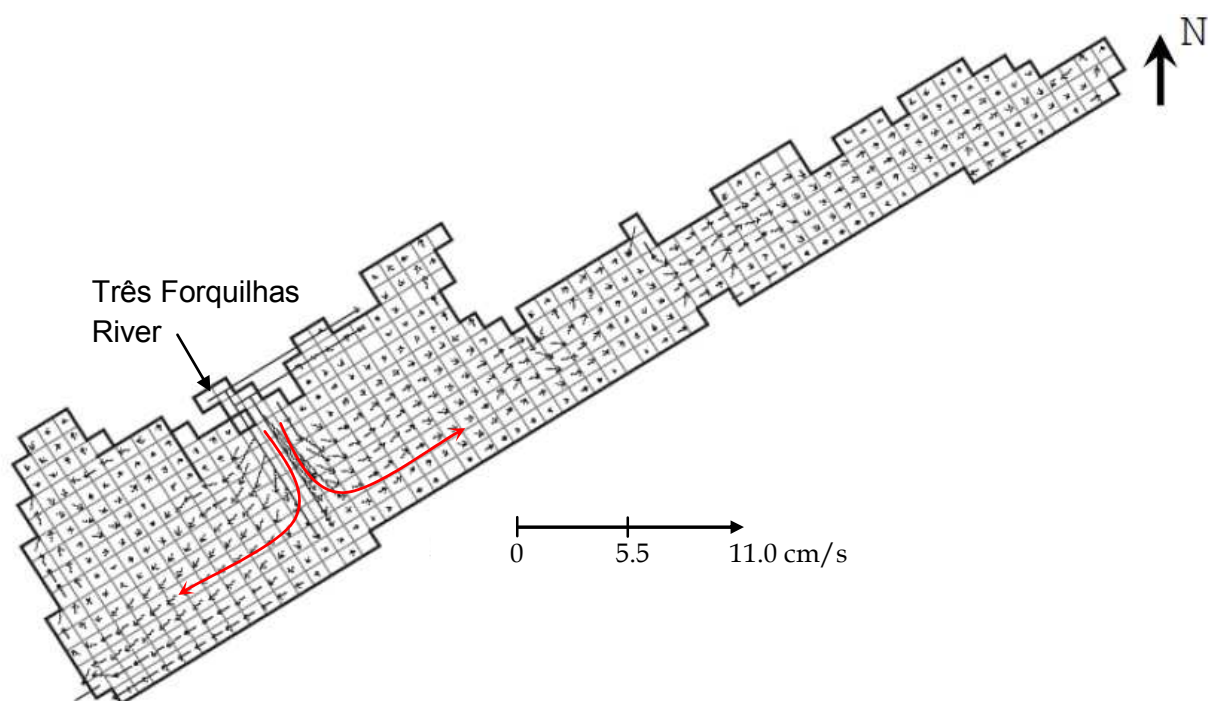


Fig. 4. Numerical simulation of the vertically averaged velocity field in Itapeva Lake during the combination of high-flow condition in the Três Forquilhas River and low wind speed. Red arrows indicate the direction of the prevailing currents.

The hydrological variables analyzed and modeled showed a quite characteristic seasonal behavior at each sampling point in Itapeva Lake, closely related to the velocity and direction of the wind. The water level responded to wind action in a very direct manner, since NE winds displaced water from north to south, along the main lake axis. Winds from the SW quadrant produced the opposite effect.

The environmental sources selected for the analysis were suspended solids and turbidity, due to their influence on many physical, chemical and biological factors. The results for hydrodynamics, such as water column and water velocity generated by the model for the sampling points, were used as the basis for the study of the environmental variations. The waves generated by wind action were the third source used to explain the variations of suspended solids and turbidity in the lake (Figs 6 and Table 2).

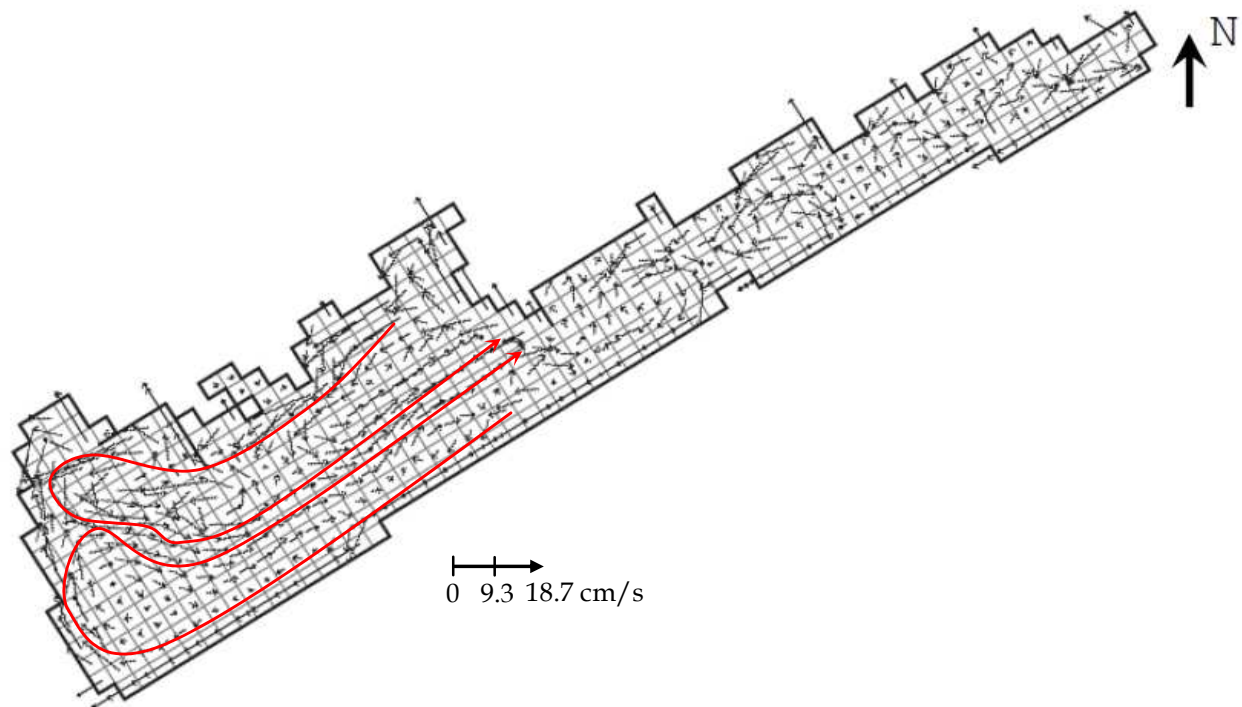


Fig. 5. Numerical simulation of the vertically averaged velocity field in Itapeva Lake during the combination of low-flow condition in the Três Forquilhas River and high wind speed from the Northeast quadrant (20/05/1999 - 21/05/1999). Red arrows indicate the direction of the prevailing currents.

The hydrodynamic variable explained 70% to 95% of the environmental variations for each seasonal campaign, using mean values for four-hour periods. Considering the entire lake and all seasonal campaigns, this explained 68% of the variation for turbidity and 49% for suspended solids. The hydrodynamic and environmental study were capable of evaluating that the changes in the water level as a function of runoff occur slowly, compared with the changes in the water level and seiches created by the effect of the wind on the lake. These variations in water levels and wind speeds have significant effects on the variability of the environmental variable tested.

Water Quality Variable	Hydrological Variable	South, Center and North					
		Mean	R	C1	C2	C3	error
Turbidity	12	4 hours	0.68	0.42	0.47	-	12.54
Suspended Solids	12	4 hours	0.49	0.43	0.27	-	63.63

Legend: Hydrological Variable - 1. water level (N), 2. water velocity (V); 3. wave height (H); 12- N-V; 13. N-H; 23. V-H; 123. N-V-H; R - correlation factor; C1, C2, C3 - N, V and H coefficients, respectively.

Table 2. Results of multiple regression between water quality variable (dependent variable) and hydrological variables (independent variable) in Itapeva Lake considering the three monitoring stations: South, Center and North.

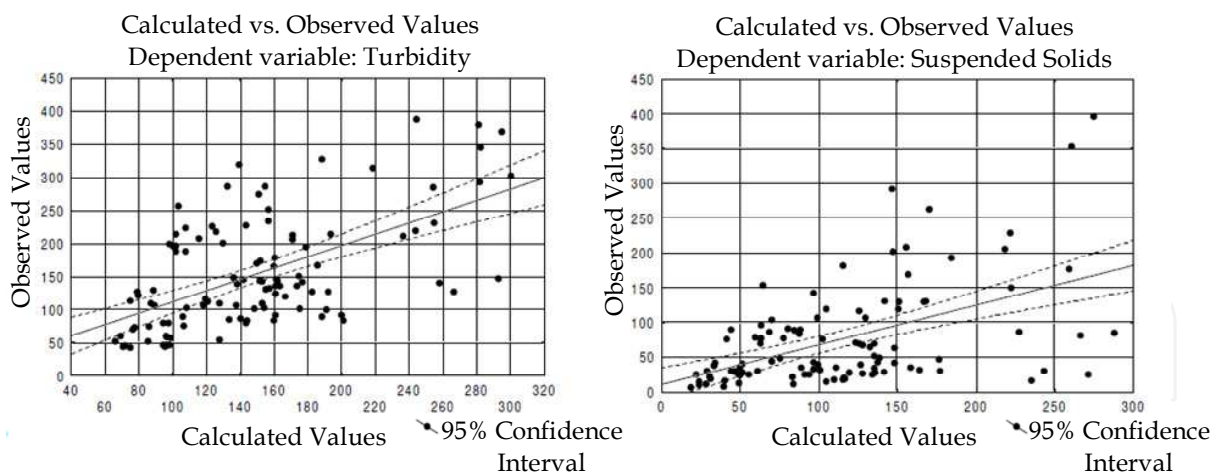


Fig. 6. Comparison between observed and calculated values for turbidity and suspended solids through multiple regression model using the three monitoring station along the Itapeva Lake.

### 3.2 Lake Mangueira

The simulated and observed values of water levels at two stations of Lake Mangueira during the calibration and validation period are shown in Fig. 7. An independent validation data set showed a good fit to the hydrodynamic module ( $R^2 \geq 0.92$ ). The model was able to reproduce the water level well in both extremities of Lake Mangueira. Wind-induced currents can be considered the dominant factor controlling transport of substances and phytoplankton in Lake Mangueira, producing advective movement of superficial water masses in a downwind direction. For instance, a southwest wind, with magnitude approximately greater than  $4\text{ms}^{-1}$ , can causes a significant transport of water mass and substances from south to north of Lake Mangueira, leading to a almost instantaneous increase of the water level in the northeastern parts and, hence the decrease of water level in southwestern areas (Fig. 7).

Our model results showed two characteristic water motions in the lake: oscillatory (seiche) and circulatory. Lake Mangueira is particularly prone to wind-caused seiches because of its shallowness, length (ca. 90 km), and width (ca. 12 km). These peculiar morphological features lead to significant seiches of up to 1 m between the south and north ends, caused by moderate-intensity winds blowing constantly along the longitudinal axis of the lake (NE-SW). Depending on factors such as fetch length and the intensity and duration of the wind, areas dominated by downwelling and upwelling can be identified (Fig. 8). For instance, if northeast winds last longer than about 6 h, the surface water moves toward the south shore, where the water piles up and sinks. Subsequently a longitudinal pressure gradient is formed and produces a strong flow in the deepest layers (below 3 m) toward the north shore, where surface waters are replaced by water that wells up from below. Such horizontal and vertical circulatory water motions may develop if wind conditions remain stable for a day or longer. The model was also used to determine the spatial distribution of chlorophyll-a and to identify locations with higher growth and phytoplankton biomass in Lake Mangueira. Fig. 9 shows the spatial distribution of the phytoplankton biomass for different times during the simulation period.

Specifically, in Lake Mangueira there is a strong gradient of phytoplankton productivity from the littoral to pelagic zones (Fig. 9). Moreover, the model outcome suggests that there

is a significant transport of phytoplankton and nutrients from the littoral to the pelagic zones through hydrodynamic processes. This transport was intensified by several large sandbank formations that are formed perpendicularly to the shoreline of the lake, carrying nutrients and phytoplankton from the shallow to deeper areas.

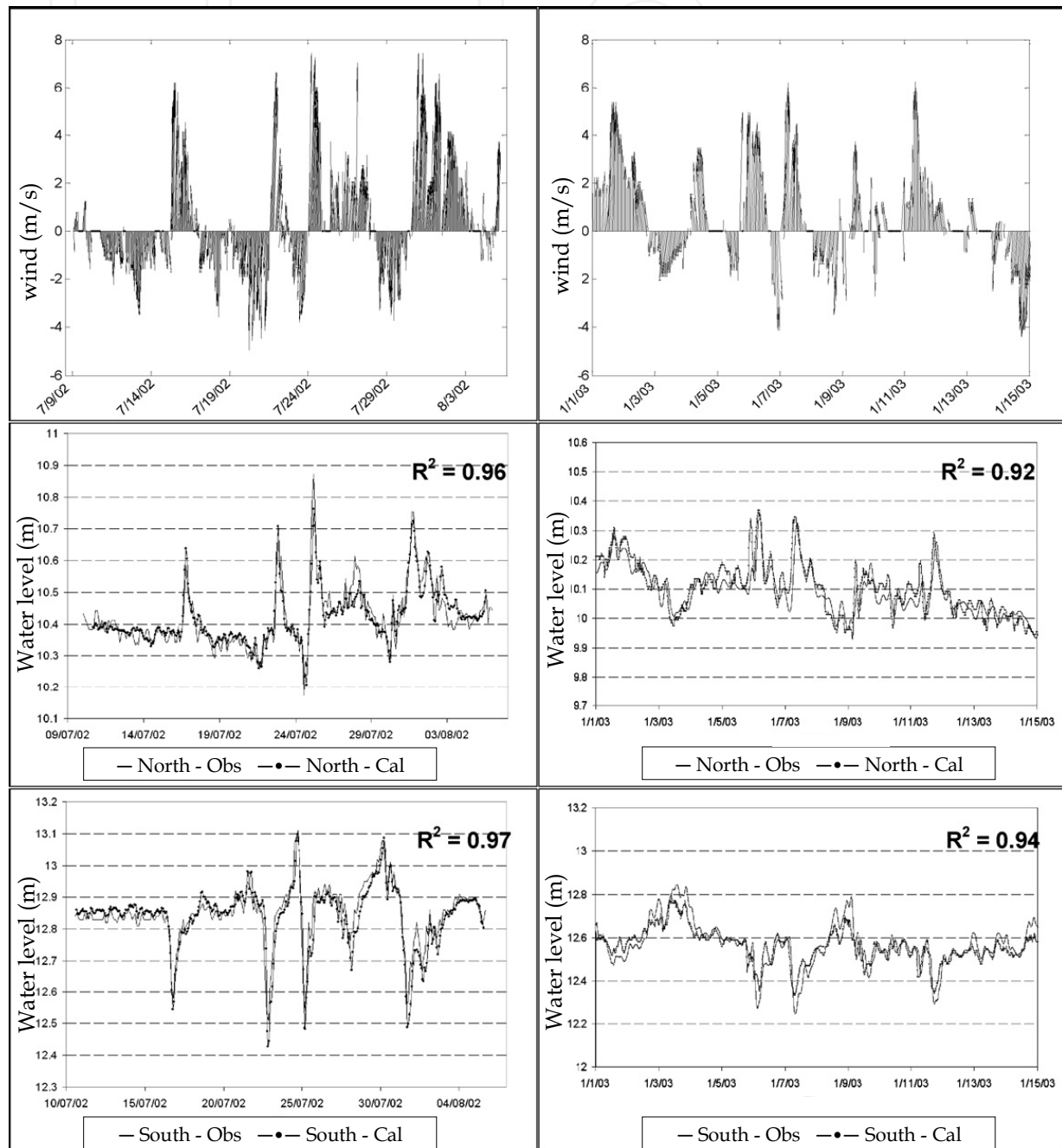


Fig. 7. Time series of wind velocity and direction on Lake Mangueira, and water levels fitted for the North and South parts of Lake Mangueira into the calibration and validation periods (solid line - observed, dotted line - calculated). Source: Frago Jr. et al. (2008).

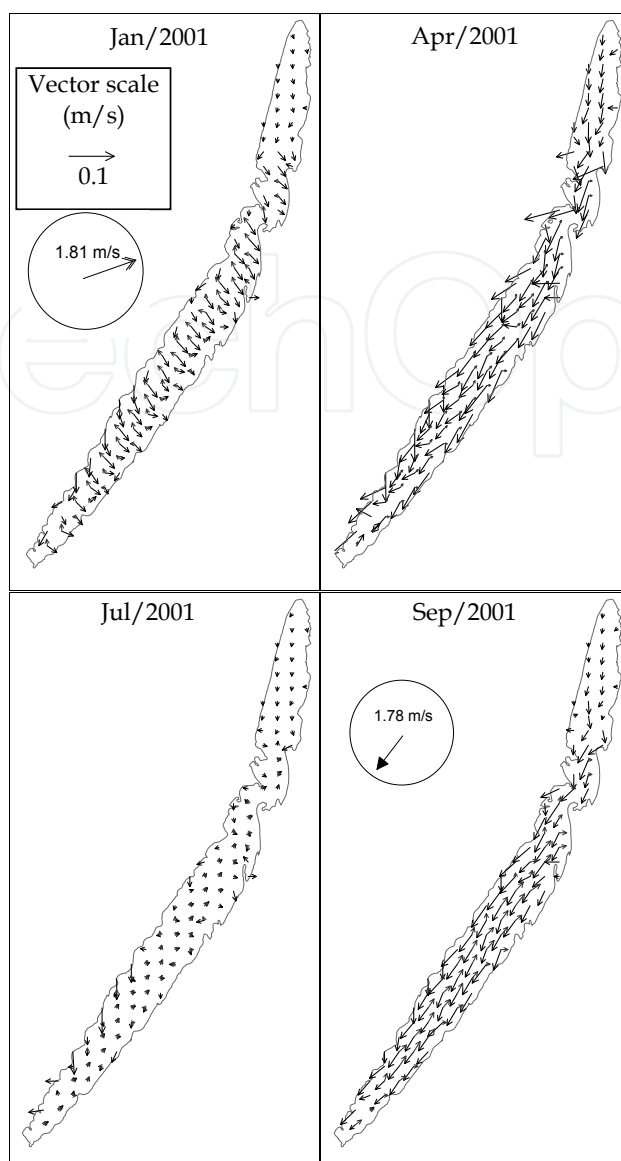


Fig. 8. Simulated instantaneous currents in the surface (black arrows) and bottom (gray arrows) layers of Lake Mangueira at four different instants. A wind sleeve (circle), in each frame, indicates the instantaneous direction and the intensity of the wind. Source: Fragoso Jr. et al. (2011).

In addition, it was possible to identify zones with the highest productivity. There is a trend of phytoplankton aggregation in the southwest and northeast areas, as the prevailing wind directions coincide with the longitudinal axis of Lake Mangueira. The clear water in the Taim wetland north of Lake Mangueira was caused by shading of emergent macrophytes, modeled as a fixed reduction of PAR.

After 1,200 hours of simulation (50 days), the daily balance between the total primary production and loss was negative. That means that daily losses such as respiration, excretion and grazing by zooplankton exceeded the primary production in the photoperiod, leading to a significant reduction of the chlorophyll-a concentration for the whole system (Fig. 9d; 9e).

We verified the modeled spatial distribution of chlorophyll-a with the distribution estimated by remote sensing (Fig. 10). The simulated patterns had a reasonably good similarity to the

patterns estimated from the remote-sensing data (Fig. 10a, b). In both figures, large phytoplankton aggregations can be observed in both the southern and northern parts of Lake Mangueira, as well as in the littoral zones.

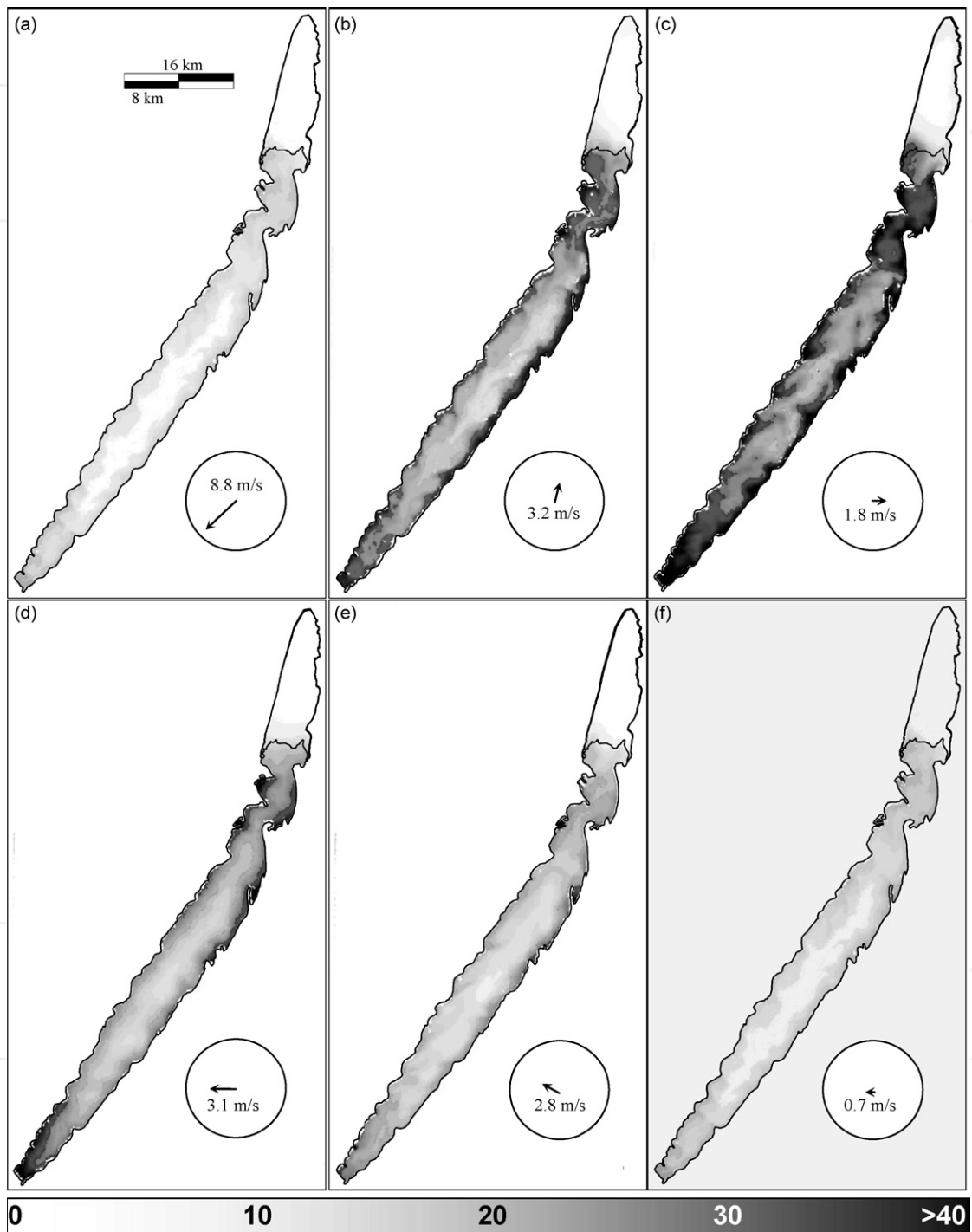


Fig. 9. Phytoplankton dry weight concentration fields in  $\mu\text{g l}^{-1}$ , for the whole system at different times: (a) 14 days; (b) 28 days; (c) 43 days; (d) 57 days; (e) 71 days; and (f) 86 days. The color bar indicates the phytoplankton biomass values. A wind sock in each frame indicates the direction and intensity of the wind. The border between the Taim wetland and Lake Mangueira is shown as well.

Unfortunately we did not have independent data for phytoplankton in the simulation period. Therefore we could only compare the median values of simulated and observed chlorophyll-a, total nitrogen and total phosphorus for three points in Lake Mangueira, assuming that the median values were comparable between the years. The fit of these variables was reasonable, considering that we did not calibrate the biological parameters of the phytoplankton module (see results in Fragoso Jr. et al., 2008). The lack of spatially and temporally distributed data for Lake Mangueira made it impossible to compare simulated and observed values in detail. However, the good fit in the median values of nutrients and phytoplankton indicated that the model is a promising step toward a management tool for subtropical ecosystems.

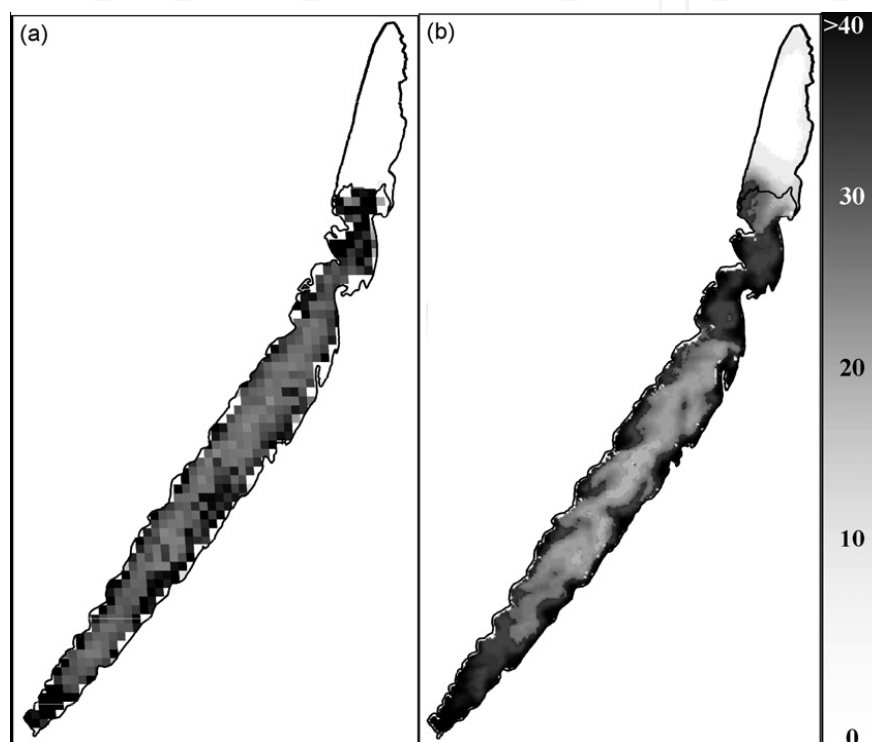


Fig. 10. Lake Mangueira: (a) MODIS-derived chlorophyll-a image with 1-km spatial resolution, taken on February 8, 2003; and (b) simulated chlorophyll-a concentration for the same date.

### 3.3 Hydrodynamic versus plankton

Hydrodynamic processes and biological changes occurred over different spatial and temporal scales in these two large and long subtropical lakes. Itapeva Lake (31 km long) is almost one-third the size of Lake Mangueira (90 km long), and therefore the hydrodynamic response is faster in Itapeva Lake. On a time scale of hours, we can see the water movement from one end of the lake to the other (e.g., from N to S during a NE wind and in the opposite direction during a SW wind). Because of this rapid response, the plankton communities showed correspondingly rapid changes in composition and abundance, especially the phytoplankton when the resources (light and nutrients) responded promptly to wind action. This interaction between wind on a daily scale (hours) and the shape of Itapeva Lake was a determining factor for the observed fluctuations in the rates of change for phytoplankton (Cardoso & Motta Marques, 2003) as well as for the spatial distribution of plankton



communities (Cardoso & Motta Marques, 2004a, 2004b, 2004c). The rate of change in the phytoplankton was very high, indicating the occurrence of intense, rapid environmental changes, mainly in spring.

Marked changes in the spatial and temporal gradients of the plankton communities occurred during the seasons of the year, in response to resuspension events induced by the wind (Cardoso & Motta Marques, 2009). These responses were most intense precisely at the sites where the fetch was longest. The increase in changes occurred as the result of population replacements in the plankton communities. Resuspension renders diatoms and protists dominant in the system, and they are replaced by cyanobacteria and rotifers when the water becomes calm again (Cardoso & Motta Marques, 2003, 2004a, 2004b). Thus, diatoms and protists were the general indicator groups for lake hydrodynamic, with fast responses in their spatial distribution. Wind-induced water dynamics acted directly on the plankton community, resuspending species with a benthic habit.

In Itapeva Lake, water level and water velocity induced short-term spatial gradients, while wind action (affecting turbidity, suspended solids, and water level) was most strongly correlated with the seasonal spatial gradient (Cardoso & Motta Marques, 2009). In Lake Mangueira, water level was most strongly correlated with the seasonal spatial gradient, while wind action (affecting turbidity, suspended solids, and nutrients) induced spatial gradients.

The Canonical Correspondence Analysis (CCA) suggested that some aspects of plankton dynamics in Itapeva Lake are linked to suspended matter, which in turn is associated with the wind-driven hydrodynamics (Cardoso & Motta Marques, 2009). Short-term patterns could be statistically demonstrated using CCA to confirm the initial hypothesis. The link between hydrodynamics and the plankton community in Itapeva Lake was revealed using the appropriate spatial and temporal sampling scales. As suggested by our results, the central premise is that different hydrodynamic processes and biological responses may occur at different spatial and temporal scales. A rapid response of the plankton community to wind-driven hydrodynamics was recorded by means of the sampling scheme used here, which took into account combinations of spatial scales (horizontal) and time scale (hours).

In both lakes, the central zone of the lake takes on intermediate conditions, sometimes closer to the North part and sometimes closer to the South, depending on the duration, direction and velocity of the wind. This effect is very important for the horizontal gradients evaluated, in relation to the physical and chemical water conditions as well as to the plankton communities. In Lake Mangueira, the South zone is characterized by high water transparency whereas the North zone is more turbid, because the latter is adjacent to the wetland and is influenced by substances originated from the aquatic macrophyte decomposition. In Itapeva Lake it was not possible to distinguish such clear spatial differences. The spatial variation is directly related to wind action, because the lake is smaller and shallower than Lake Mangueira. In addition, the prevailing NE winds and the influence of the Três Forquilhas River on Itapeva Lake make the central zone often similar to the South part. The high turbidity in Itapeva Lake is an important factor affecting the composition and distribution of the plankton communities. However, in Lake Mangueira the marked spatial differences between the North and South zones were important for the composition and distribution of the plankton, and the influence of the wind was more evident in the Center zone than in the two ends of the lake.

In Lake Mangueira, wind-driven hydrodynamics creates zones with particular water dynamics (Fragoso Jr. et al., 2008). The velocity and direction of currents and water level

changed quickly. Depending on factors such as fetch and wind, areas dominated by downwelling and upwelling could be identified in the deepest parts. We observed a significant horizontal spatial heterogeneity of phytoplankton associated with hydrodynamic patterns from the south to the north shore (littoral-pelagic-littoral zones) over the winter and summer periods. Our results suggest that there are significant horizontal gradients in many variables during the entire year. In general, the simulated depth-averaged chlorophyll-a concentration increased from the pelagic to the littoral zones. This indicated that a higher zooplankton biomass can exist in the littoral zones, leading, eventually, to stronger top-down control on the phytoplankton in this part of the lake. Moreover, as expected for a wind-exposed shallow lake, Lake Mangueira did not show marked vertical gradients. The field campaigns showed that the lake is practically unstratified, emphasizing the shallowness and vertical mixing caused by the wind-driven hydrodynamics. This complete vertical mixing, as expected, was noted for both the pelagic and littoral zones. However, we are still of the opinion that incorporation of horizontal spatially explicit processes associated with the hydrodynamics is essential to understand the dynamics of a large shallow lake. The occurrence of hydrodynamic phenomena such as the seiches between the extreme ends, in a very long and narrow lake, is important, since seiches function as a conveyor belt, accounting for the vertical mixing and transportation of materials between the two ends of the lake and between the wetlands in the North and South areas in Lake Mangueira. Seiches was very important to explain much of the spatial changes in Itapeva Lake.

#### 4. Conclusion

Recognition of the importance of spatial and temporal scales is a relatively recent issue in ecological research on aquatic food webs (Bertolo et al., 1999; Woodward & Hildrew, 2002; Bell et al., 2003; Mehner et al., 2005). Among other things, the observational or analytical resolution necessary for identifying spatial and temporal heterogeneity in the distributions of populations is an important issue (Dungan et al., 2002). Most ecological systems exhibit heterogeneity and patchiness over a broad range of scales, and this patchiness is fundamental to population dynamics, community organization and stability. Therefore, ecological investigations require an explicit determination of spatial scales (Levin, 1992; Hölker & Breckling, 2002), and it is essential to incorporate spatial heterogeneity into ecological models to improve understanding of ecological processes and patterns (Hastings, 1990; Jørgensen et al., 2008).

Water movement in aquatic systems is a key factor which drives resources distribution, resuspend and carries particles, reshape the physical habitat and makes available previously unavailable resources. As such processes, and communities change along and patterns are created in time and space. Ecological models incorporating hydrodynamics and trophic structure are poised to serve as thinking pads allowing discovering and understanding patterns in different time and space scales of aquatic ecosystems. In lake ecosystem simulations, the horizontal spatial heterogeneity of the phytoplankton and the hydrodynamic processes are often neglected. Our simulations showed that it is important to consider this spatial heterogeneity in large lakes, as the water quality, community structures and hydrodynamics are expected to differ significantly between the littoral and the pelagic zones, and between differently shaped lakes. Especially for prediction of the water quality (including the variability due to wind) in the littoral zones of a large lake, the incorporation

of spatially explicit processes that are governed by hydrodynamics is essential. Such information may be also important for lake users and for lake managers.

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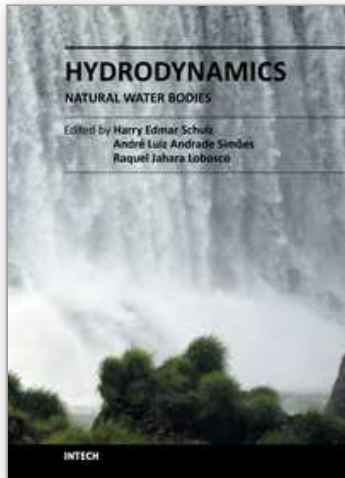
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## **Hydrodynamics - Natural Water Bodies**

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The knowledge of the characteristics of the fluids and their ability to transport substances and physical properties is relevant for us. However, the quantification of the movements of fluids is a complex task, and when considering natural flows, occurring in large scales (rivers, lakes, oceans), this complexity is evidenced. This book presents conclusions about different aspects of flows in natural water bodies, such as the evolution of plumes, the transport of sediments, air-water mixtures, among others. It contains thirteen chapters, organized in four sections: Tidal and Wave Dynamics: Rivers, Lakes and Reservoirs, Tidal and Wave Dynamics: Seas and Oceans, Tidal and Wave Dynamics: Estuaries and Bays, and Multiphase Phenomena: Air-Water Flows and Sediments. The chapters present conceptual arguments, experimental and numerical results, showing practical applications of the methods and tools of Hydrodynamics.

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