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The effects of water retention time and watershed features on the limnology of two tropical reservoirs in Brazil

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Abstract

Although reservoirs are similar to natural lakes in many respects, such driving forces as water retention time and watershed features can play important roles in the limnology of manmade lakes. With the goal of investigating how these factors influence the limnology of tropical reservoirs, physical and chemical variables were measured at four sampling sites in two reservoirs in southern Brazil, from June 2002 to June 2003. Funil Reservoir is located in one of the most-populated areas in the country, in the Paraíba do Sul river basin, which drains and drastically influences the water quality of the reservoir. In contrast, Lajes Reservoir is located in a well-preserved area, with its water retention time varying from six to 30 times longer than for Funil Reservoir. Funil Reservoir is a turbid (median euphotic zone = 4.3 m), eutrophic reservoir (median total phosphorus (TP) = 3.1 μM), with a high phytoplankton biomass (median chlorophyll-*a* concentration = 10.0 $\mu g\ L^{-1}$). In contrast, Lajes Reservoir is a transparent (median euphotic zone = 9.2 m), mesotrophic water system (median TP = 1.0 μM), with a low phytoplankton biomass (median chlorophyll-*a* = 1.9 $\mu g\ L^{-1}$). Both reservoirs were stratified during the summer months, but isothermy was only observed in Funil Reservoir. Because of its short water retention time, Funil Reservoir is a much more dynamic system than Lajes Reservoir, with a pronounced temporal pattern related to changes in its water column and its phytoplankton biomass. Spatial heterogeneity is more evident in Lajes Reservoir, mainly as a consequence of its location in a preserved area, long water retention time and the presence of net cages for fish culture in the waterbody. The typical spatial zonation found in reservoirs, related to nutrient sedimentation and light availability, however, is more evident in Funil Reservoir than in Lajes Reservoir. Despite the similarities between these two water systems, which are in the same geographical region with similar climate, and are comparable in size, the distinct watershed features and water retention time are responsible for marked differences between these reservoirs.

Key words

eutrophication, manmade lakes, seasonal variability, spatial heterogeneity.

INTRODUCTION

Construction of large reservoirs in Brazil began in the early 1900s. Brazil is today a reservoir-orientated country in which 85% of its energy comes from hydroelectricity (Tundisi *et al.* 1993; Nogueira *et al.* 1999). Many of these reservoir systems are located at the southeast region of Brazil, where the demand for electric power is high because of the intense industrial activity and high human population density that characterize this region. Furthermore, these reservoirs have multiple uses, including water supply, irrigation, aquaculture and recreation, thereby increasing the importance of studies on these systems.

A reservoir can be viewed as a very dynamic lake, in which a significant portion of its volume possesses characteristics and functions biologically similar to rivers

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(lotic water systems) (Wetzel 1990). The lotic influence can be responsible for longitudinal patterns in reservoirs, creating three distinct regions that can be defined on the basis of their physical, chemical and biological characteristics. The initial zone, the region of the reservoir furthest from the dam, is known as the riverine zone. It is characterized by an intense inflow of nutrients and reduced primary production, as a result of high turbidity. As the sedimentation and light availability increase as the water moves further into the reservoir, primary production also increases in the second region, known as a transition zone. Finally, in the lentic zone of the reservoir at the dam end, nutrient limitation caused by intense sedimentation can inhibit phytoplankton growth (Tundisi 1999; Kalff 2001). Several factors influence the size and limits between these regions, including morphometry, thermal stratification, geographical location and water retention time. The effect of water retention time on the longitudinal pattern of reservoirs was elucidated by Straškraba (1999), who observed that the entire reservoir could become a riverine zone when its water retention time is short, or else can be converted into a lacustrine zone when the water retention time lengthens. The retention time influences not only the longitudinal, but also the vertical patterns observed in a reservoir. It also seems to be the most useful variable for *a priori* prediction of stratification (Straškraba 1999).

Despite very significant advances on limnology in recent decades, eutrophication remains one of the foremost problems to be addressed in order to protect freshwater and coastal marine ecosystems (Schindler 2006; Smith *et al.* 2006). The multiple uses of reservoirs in Brazil, and the increasing human activity in watersheds, have accelerated the eutrophication process in these waterbodies. Due to the high population density and intense industrial activity, the water quality in many reservoirs in southeast Brazil has been degraded by high inputs of nutrients, toxic heavy metals and polycyclic aromatic hydrocarbons (Figueredo & Giani 2001; Branco *et al.* 2002; Calijuri *et al.* 2002; Marinho & Huszar 2002; Rocha *et al.* 2002; Rodgher *et al.* 2005). Funil and Ribeirão das Lajes (Lajes) reservoirs are located in southeastern Brazil, and experience similar climatic conditions. These two reservoirs, however, have distinct watershed features that influence their trophic states. The Paraíba do Sul River, which drains and receives waste from the most-populated area in the country, is the main tributary draining to Funil Reservoir. In contrast, Lajes Reservoir is located in a preserved region of tropical rain forest. Its water retention time, which can be six to 30 times higher for Lajes Reservoir than for Funil Reservoir over the course of the annual cycle, is another important difference between the two waterbodies.

Accordingly, the aim of this study was to evaluate the role of water retention time and watershed features on the limnological characteristics of both reservoirs. The hypothesis is that the seasonal and spatial patterns of the limnological variables are especially related to: (i) water retention time, which will influence mixing patterns and longitudinal heterogeneity; and (ii) watershed characteristics, which are the most important factors affecting the trophic state of each reservoir, and which promote distinct conditions between the reservoirs.

METHODS

Study site

The main morphometrical features of Funil Reservoir (22°30′S, 44°45′W, altitude 440 m, Cwa in the Köppen system) and Lajes Reservoir (22°43′S, 44°46′W, altitude 410 m, Aw in the Köppen system) are summarized in Table 1. Funil Reservoir was constructed at the end of the 1960s, by the damming of the Paraíba do Sul River. As it drains and receives waste from one of the main Brazilian industrial areas crossing part of the São Paulo and Rio de Janeiro States, this river has a large influence on the reservoir's water quality. Consequently, the reservoir has experienced dramatic eutrophication in recent decades, resulting in frequent and intense cyanobacterial blooms (Klapper 1998; Branco *et al.* 2002; Rocha *et al.* 2002). On the other hand, Lajes Reservoir was constructed at the beginning of the 1900s, and is located in a preserved area with tropical rain forests occupying >50% of the total watershed area of 305 km^2 (GEROE 1995). The main tributary is the Piraí River, which enters the reservoir through the Tócos Tunnel. The Tócos Tunnel is a 7-km, under-rock pipeline that transports water from Tócos Reservoir (0.59 km^2) in the Piraí Creek watershed, which lies in a farming region and receives waste from a small village (Guarino *et al.* 2005). Although both systems are primarily hydropower reservoirs, they are also used for industrial supply, irrigation, aquaculture and recreation. In regard to their limnological characteristics, another important difference between the

Table 1. Main physical features of Funil and Lajes reservoirs

	Funil Reservoir	Lajes Reservoir
Area (km^2)	40.0	38.9
Volume (m^3)	890×10^6	450×10^6
Maximum depth (m)	70	40
Mean depth (m)	22	15
Residence time (days)	10–50	297
Main tributary	Paraí ba do Sul River	Piraí River

two reservoirs is their water retention times, with that of Lajes Reservoir being six to 30 times higher than for Funil Reservoir. Furthermore, a Nile tilapia (*Oreochromis niloticus* Linnaeus) net-pen culture project was developed in one bay of Lajes Reservoir, beginning in 2002.

Field sampling

Water samples were taken monthly between June 2002 and June 2003 at four sampling sites in each reservoir. For Funil Reservoir, sampling site 1 is located close to the influent river, sites 2 and 3 are intermediate in the reservoir, and site 4 is located close to the dam. For Lajes Reservoir, sampling site 1 is located close to the river, site 2 is in an intermediate location, site 3 is located close to the net-cages, and site 4 is located near the dam (Fig. 1). Samples for physical, chemical and biological features were taken at a subsurface depth at all sampling sites. Furthermore, a vertical profile taken at sampling site 4 of each reservoir was sampled with a Van Dorn bottle at four sampling depths (1% light depth; 12 m in Funil Reservoir; 15 m in Lajes Reservoir and 30 m in both reservoirs). Water temperature, pH, electrical conductivity and dissolved oxygen (DO) concentrations were measured *in situ* with a YSI 6920 multisensor probe. Water transparency was estimated by the Secchi disk (SD) extinction depth.

Sample and data analysis

Water samples were collected for analysis of total phosphorus (TP) and total nitrogen (TN) concentrations. Samples also were filtered through Whatman GF/C filters, in order to analyse the water for dissolved nutrient concentrations, including soluble reactive phosphorus (SRP), ammonium ($\mathrm{NH_4^+}$-N), nitrate ($\mathrm{NO_3^-}$-N) and nitrite ($\mathrm{NO_2^-}$-N). Laboratory analysis was performed on the preserved water samples within 15 days of their collection, using standard spectrophotometric techniques. The TP and SRP concentrations were determined with the ascorbic acid method. $\mathrm{NO_3^-}$-N and $\mathrm{NO_2^-}$-N concentrations were determined by cadmium reduction of the samples,

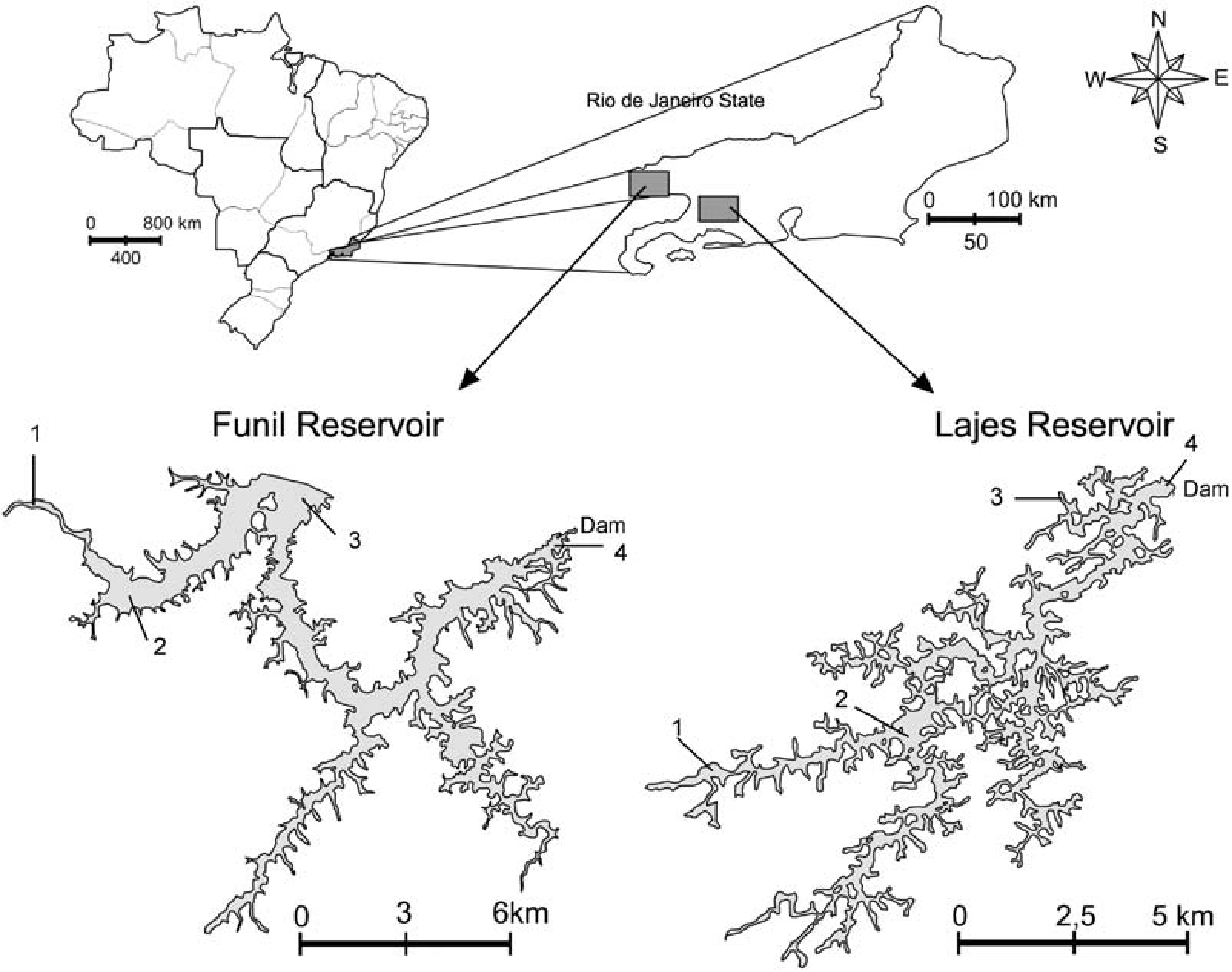

Fig. 1. Maps of Funil and Lajes reservoirs, showing the sampling sites.

followed by the colorimetric determination of NO_2^--N and NH_4^+-N concentrations with the phenolhypochlorite method (Wetzel & Likens 1990). The dissolved inorganic nitrogen (DIN) concentration was calculated as the sum of the NH_4^+-N, NO_3^--N and NO_2^--N concentrations. The chlorophyll-*a* concentrations were determined by the Colorimetric Method, after extraction with 90% acetone (Lorenzen 1967). The euphotic zone (z_{eu}) was defined as 2.7 times the Secchi disk extinction (Cole 1994). The mixing zone (z_{mix}) was identified from the temperature profiles. The resilience of the vertical structure was assessed by the Wedderburn number (Imberger & Hamblin 1982). In regard to the temporal dynamics, the data were analysed on the basis of the median value of the vertical profile at sampling site 4. In regard to longitudinal patterns, the data for the surface waters of sampling sites 1 to 4 were considered.

The data were analysed using the Stat-View® for Windows (SAS Institute Inc., Cary, NC, USA) version 5.0 software package. Differences between periods and stations were assessed using the non-parametric Kruskal–Wallis test. The reservoir trophic states were assessed on the basis of criteria from Vollenweider and Kerekes (1980) and Salas and Martino (1991). Principal component analysis (PCA) was performed on all log $(x + 1)$-transformed physical and chemical data (except pH), in order to summarize the seasonal and spatial patterns for Funil and Lajes reservoirs, and also to identify the main driving forces related to the variability observed in each reservoir. The data used in this latter analyses were lake water level (only for Funil Reservoir), water temperature, pH, electrical conductivity, euphotic zone ($_{Zeu}$), mixing zone ($_{Zmix}$, only for Funil Reservoir), dissolved oxygen concentration (only for Lajes Reservoir), dissolved inorganic nutrient concentrations (SRP and DIN) and chlorophyll-*a*. Correlations between the first two axes and the variables were considered significant when the distances to the centre of the plane were $d > \sqrt{2/n}$ (where n = number of variables) (Legendre & Legendre 1998). The PCA was performed in PC-Ord 4.0. The climate data were obtained from the National Institute of Meteorology. Data on the reservoirs' water levels, inflows and outflows were obtained from the Furnas Centrais Elétricas LTDA (Funil) and Light S.A. (Lajes). The maximum chlorophyll-*a* concentration supported by the bioavailable phosphorus and nitrogen capacity was calculated according to the method of Reynolds (1992; see also Reynolds & Maberly 2002; Diaz *et al.* 2007).

RESULTS

The study year was divided into periods corresponding to the mixing pattern and chlorophyll-*a* concentration at sampling site 4 (see session temporal variability). Four periods were identified for Funil Reservoir, including (I) June–October 2002; (II) November–December 2002; (III) III January–March 2003; and (IV) April–June 2003. Three periods were identified for Lajes Reservoir, including (I) June–September 2002; (II) October 2002–March 2003; and (III) April–June 2003. According to the regional climate characteristics, the study year exhibited a typical dry season during the winter, and a wet season during the summer (Fig. 2).

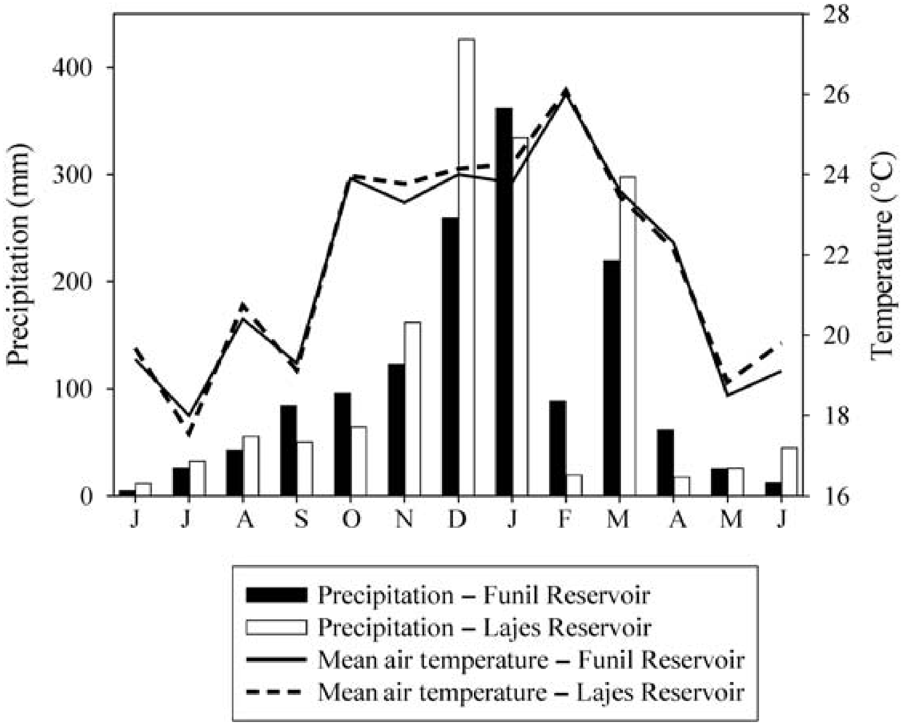

Fig. 2. Monthly precipitation and mean air temperatures in Lajes and Funil reservoirs during the study period.

The median air temperature and precipitation were higher ($P < 0.05$) in periods II and III for Funil Reservoir (28.8 and 29.4 °C, 191 and 219 mm, respectively), and during period II for Lajes Reservoir (32 °C and 297.4 mm). The net water flow was negative during most of the year and positive ($P < 0.05$) only during the wet-warm months, including period II for Funil Reservoir (15 $m^3 s^{-1}$) and period II for Lajes Reservoir (6.6 $m^3 s^{-1}$). During the beginning of period III, corresponding to the higher inflow months, an uncommon surface outflow occurred in Funil Reservoir (Fig. 3). As the spillways in Funil Reservoir are located near the bottom, this unusual outflow had drastic effects on the temporal variability.

Temporal variability

Although both reservoirs were stratified at sampling site 4 during the warm months, different water mixing patterns were observed (Fig. 4). Funil Reservoir was thermally stratified during periods II and III, with a significant increase in the water surface temperature from 22.3 °C in period I, to 27.0 °C in period III ($P < 0.05$). Various degrees of mixing occurred during the other periods, and the water column was isothermal at the end of period I and during period IV (Fig. 4). The z_{mix} median ranged from 4.5 m in period III, to 12.0 m in period IV ($P < 0.05$), reaching 30 m during some months in periods I and IV. Lajes Reservoir was strongly stratified in period II, but was not totally mixed during the coldest months (Δ temperature = 2.6 and 2.8 in periods I and III, respectively) (Fig. 4). Although a complete water turnover was not observed during this study period, z_{mix} deepened in period I (12.0 m) and in period III (8.0 m), maintaining the hypolimnion. To assess the influence of wind on the degree of water column stability in Lajes Reservoir, two contrasting situations were considered: (i) December 2002, with higher air temperatures, a thermocline depth of 6 m, and the maximum wind velocity of 4.7 m s^{-1}; and (ii) June 2003, with lower air temperatures, a thermocline at 18 m and a maximum wind velocity of 3 m s^{-1}. The Wedderburn number was >1 in both situations (2.36 and 1.03).

Differences in light availability also were observed in both reservoirs. Funil Reservoir is a turbid water system, with a low z_{eu} (annual median: 4.3 m). In contrast, the water transparency is high in Lajes Reservoir (annual median: 9.2 m). Low values of z_{eu} were observed in Funil Reservoir during stratification in period II (1.5 m), corresponding to periods of higher phytoplankton biomass (Fig. 4). High water transparency was observed in period IV (8.1 m), when the biomass was reduced ($P < 0.05$). In contrast, the z_{eu} for Lajes Reservoir decreased from 9.5 m, during the stratified period (II), to 8.1 m in period III, when the reservoir was mixing.

The dissolved oxygen concentration profile indicates a chemical stratification in Funil Reservoir only in period I (Fig. 4). Although there was a slight decrease in the oxygen concentration from the surface to the bottom, anoxic conditions were not observed. For Lajes Reservoir, a high oxygen saturation was registered at the surface in periods I and II. Anoxic conditions were observed <20 m in

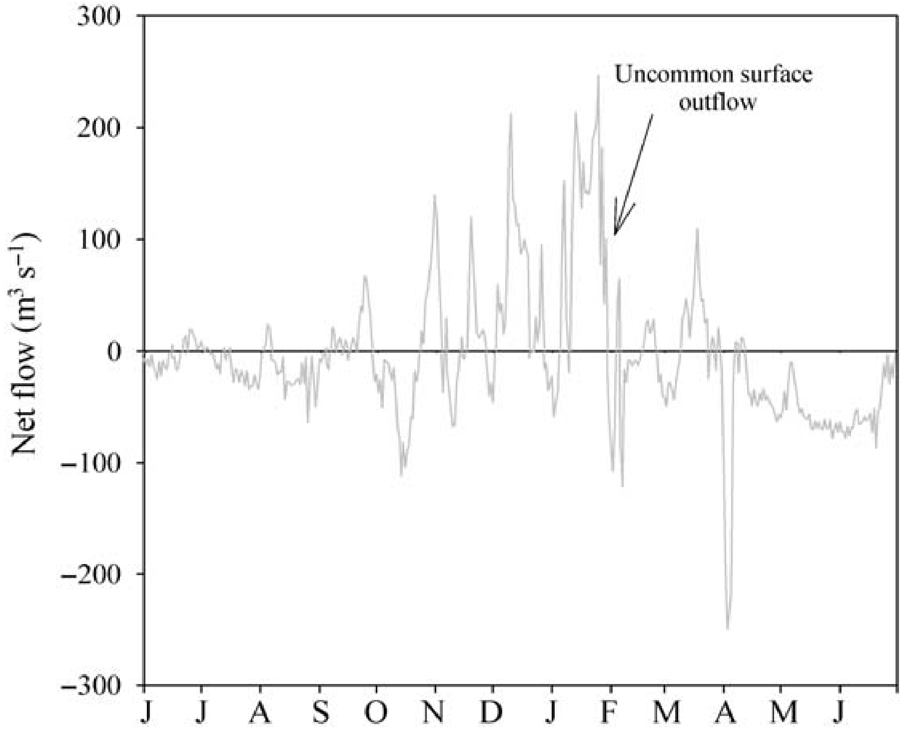

Fig. 3. Net flow in Funil Reservoir during the study period.

periods II and III (Fig. 4). The pH in Funil Reservoir was alkaline at the surface, especially in periods I and III, with the entire water column being slightly acidic at the end of III and beginning of IV, reaching higher values in period II (8.7). In Lajes Reservoir, the pH ranged from slightly acidic near the bottom, to slightly alkaline at the surface. The electrical conductivity in Funil Reservoir increased significantly ($P < 0.001$), from 75.2 µS cm^{-1} in period I, to 90.5 µS cm^{-1} in IV. High values were observed in the deeper waters, especially in periods III and IV (Fig. 4). In contrast, the electrical conductivity in Lajes Reservoir was low, especially at the surface, and somewhat higher near the bottom, especially in period III ($P < 0.05$) (Fig. 4).

Funil Reservoir exhibited high to slightly high nutrient concentrations throughout the year (Fig. 5). The SRP concentrations were high throughout the year, decreasing only in period III (median = 0.6 µM). The DIN concentration was ≈20 µM in all periods, exhibiting a strong stratification pattern, with higher concentrations at the surface and decreasing vertically (Fig. 5). The DIN represented 81% of the TN, and NO_3^--N was the most important form of dissolved nitrogen in Funil Reservoir (91% of the total DIN). Thus, a large quantity of nitrogen was available for phytoplankton utilization in Funil Reservoir. For Lajes Reservoir, the median SRP concentration varied from 0.6 µM in period II, to 0.7 µM in III. The DIN was well distributed through the water column throughout the study period (Fig. 5), varying from 2.3 µM in period II, to 3.9 µM in period III ($P < 0.05$). The DIN contributed only 11% of the TN. The NH_4^+-N and NO_3^--N fractions comprised 49% and 45%, respectively, of the total DIN.

The chlorophyll-*a* concentration in Funil Reservoir was high, especially in period II (median: 26.9 µg L^{-1}, $P < 0.001$). Although a peak occurred in December (78.3 µg L^{-1} at the surface), the chlorophyll-*a* concentration abruptly declined in periods III (1.6 µg L^{-1}) and IV (0.5 µg L^{-1}) (Fig. 5). In Lajes Reservoir, the chlorophyll-*a* concentrations were low during the study period. Intermediate values were observed during period I (1.7 µg L^{-1}), and a decrease during period II (0.9 µg L^{-1}), during which the reservoir was strongly stratified. The chlorophyll-*a* concentration increased again in period III (2.1 µg L^{-1}) (Fig. 5).

Spatial variability

Although sampling site 1 was typically lotic in both reservoirs, the longitudinal patterns were dissimilar, reflecting the peculiarities of each system. For Funil Reservoir, the water temperature ($P < 0.05$), pH ($P < 0.05$) and $_{Zeu}$ ($P < 0.05$) increased. The TP ($P < 0.05$), SRP ($P < 0.005$), TN ($P < 0.0001$) and DIN ($P < 0.0005$) decreased between sites 1 to 4, characterizing the typical pattern of these regions in reservoirs. With increased light availability and high

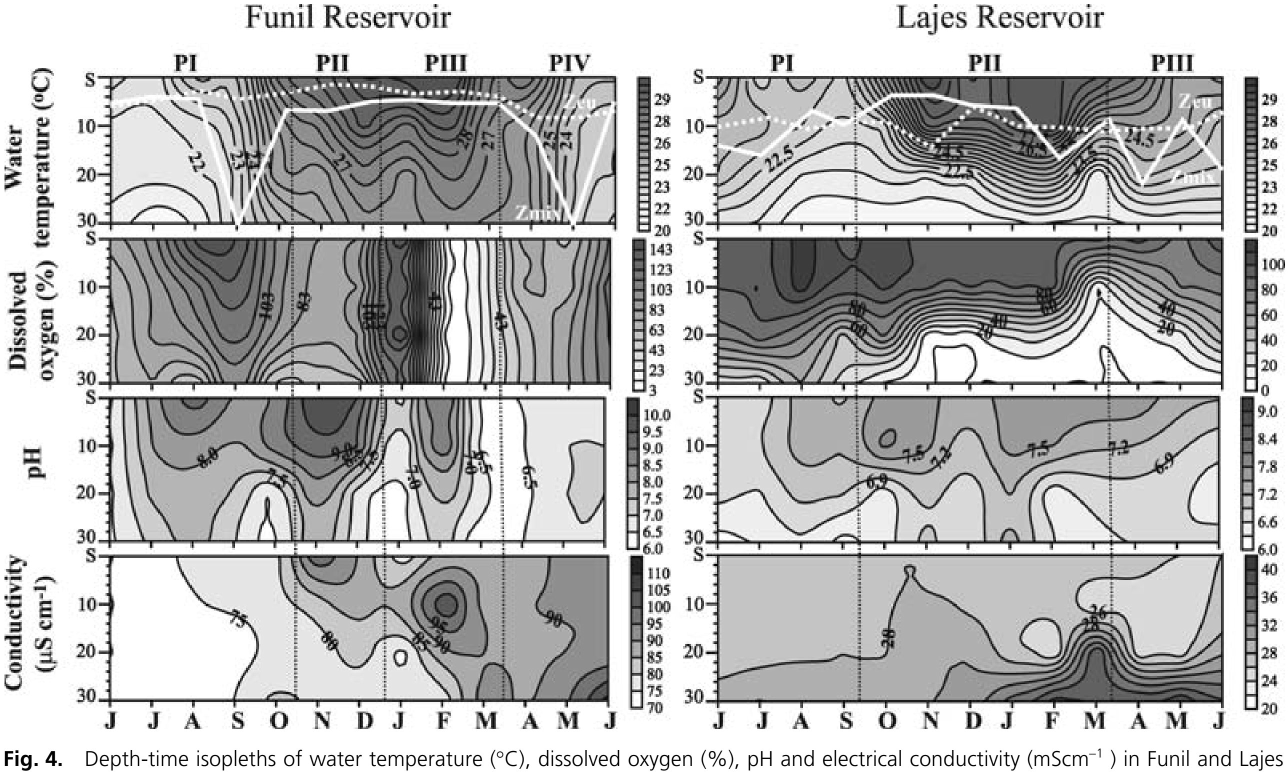

Fig. 4. Depth-time isopleths of water temperature (°C), dissolved oxygen (%), pH and electrical conductivity (mScm^{-1}) in Funil and Lajes reservoirs during the study period.

nutrient concentrations at sampling site 2, the maximum chlorophyll-*a* concentration was observed in this transition zone (168.9 μg L^{-1}) ($P < 0.05$). A decreased concentration was observed again at sites 3 and 4, which comprise the lentic zone (Table 2). For Lajes Reservoir, this pattern was observed from sampling sites 1 to 2, with an increased water temperature ($P < 0.05$) and $_{\text{Zeu}}$ ($P < 0.05$), and decreased nutrient concentrations ($P < 0.05$). The presence of fish net-cages at site 3 directly influenced the water quality observed at site 4, where an increased nutrient concentration and decreased light availability was observed. Consequently, the mean chlorophyll-*a* concentration was higher at sampling sites 3 and 4, in the lentic zone of the reservoir (Table 2).

Temporal × spatial variability

The PCA indicated a higher temporal influence on the gradient of variables for Funil Reservoir than for Lajes Reservoir. The long water retention time for Lajes Reservoir, however, was responsible for its remarkable longitudinal variability (Fig. 6).

The total variance explained by the first two axes in Funil Reservoir was 49.5%, with eingenvalues $\gamma_1 = 3.1$, $\gamma_2 = 2.3$, $\gamma_3 = 1.3$ and $\gamma_4 = 1.2$. Generally, the second axis grouped samples from mixed, clear and cold periods on the upper side (I and IV), and samples from stratified, turbid and warm periods (II and III) on the lower side. The main variables positively correlated to axis 1 were electrical conductivity (0.65), water level (0.52) and z_{eu} (0.48). The z_{eu} (0.53) was also the main variable correlated to axis 2. The plot illustrates the main temporal pattern, grouping samples in four defined periods. Low precipitation during period I was responsible for less dilution and, consequently, high inputs of SRP. The increase in biomass grouped samples from the end of period I and period II on the lower left. Period II is clearly related to the high chlorophyll-*a* concentrations and increased pH. The increases in temperature and water level related to high precipitation characterized period III, also with a high DIN concentration. The complete mixing in period IV caused decrease in biomass, which was related to the increased $z_{\text{eu-}}$.

For Lajes Reservoir, the two main PCA axes explained 38.8% of the total data variability, with eingenvalues being: $\gamma_1 = 2.1$, $\gamma_2 = 1.8$, $\gamma_3 = 1.4$ and $\gamma_4 = 1.1$. The PCA grouped samples in relation to the longitudinal heterogeneity. Samples from site 1 were characterized by high input of SRP and an increase in pH and dissolved oxygen concentrations were observed in relation to sampling site 2. At the same site, electrical conductivity and water temperature were also high. The increased nutrient concentrations at site 3, attributed mainly to the fish net-cages, and a consequent increased biomass grouped samples from sampling site 3

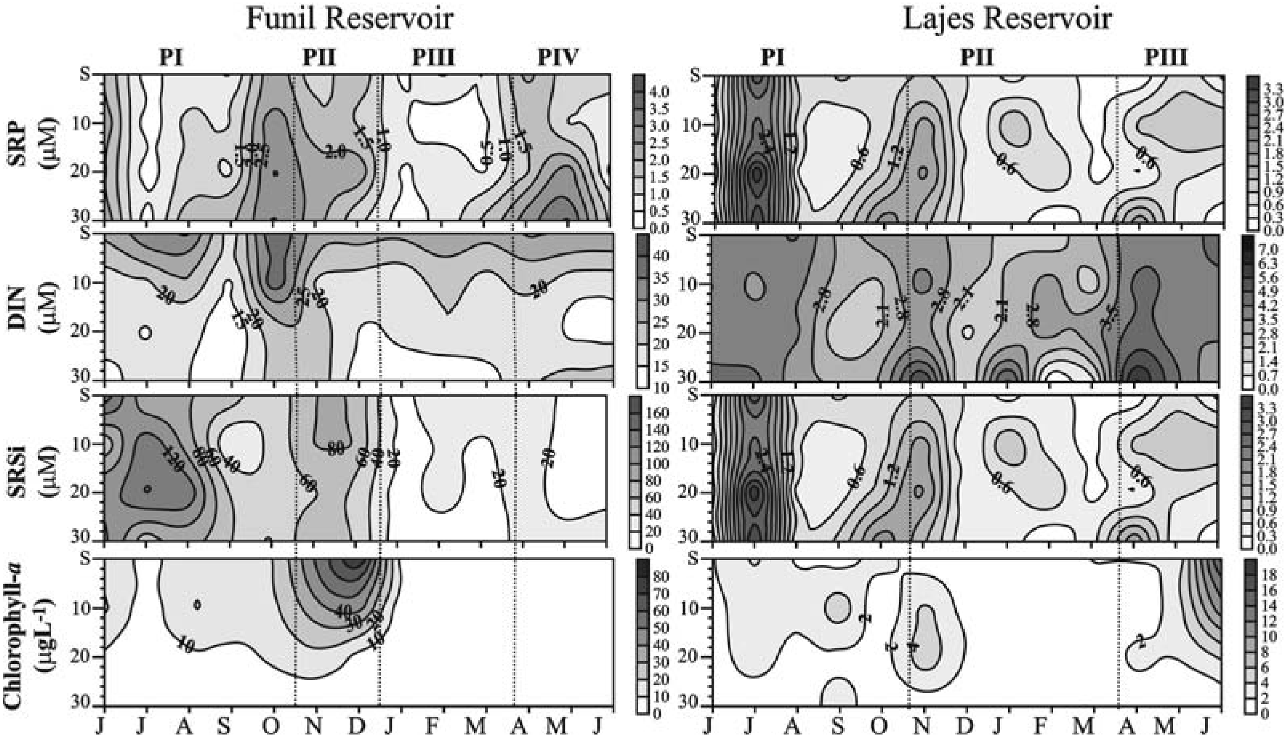

Fig. 5. Depth-time isopleths of soluble reactive phosphorus (SRP) (mM), dissolved inorganic nitrogen (DIN) (mM) and chlorophyll-*a* (mgL^{-1}) in Funil and Lajes reservoirs during the study period..

between sites 1 and 4. Samples from site 3 indicated intermediate conditions between sites 1 (higher nutrient concentrations, especially SRP) and 4 (light availability and chlorophyll-*a* concentration). The main variables positively correlated to axis 1 were DO concentration (0.63) and pH (0.59), while the DIN (0.83), SRP (0.45) and chlorophyll-*a* concentrations were the main variables associated with axis 2 (Fig. 6).

DISCUSSION

Lajes and Funil reservoirs are located in similar climate conditions, with patterns of temperature and precipitation leading to dry winters and wet summers. These features are very important in regard to the vertical structure of aquatic systems, which directly influences the dynamics of chemical and biological processes. From October to March, high temperatures were responsible for the stratification in both systems, being in accordance with other Brazilian deep-water systems, which are usually thermally stratified during the rainy-warm season and mixed during the dry-cold season (Henry 1995). However, while Funil Reservoir exhibited various degrees of mixing during periods I and IV, a complete turnover did not occur in Lajes Reservoir. During the study year, the decreased temperature was not sufficient to disrupt the thermocline in Lajes Reservoir, thereby merely deepening the mixing layer. As previously noted, this reservoir is located in a preserved area, and surrounded by dense vegetation, with the observed wind velocity during the study always being < 5 m s^{-1}. Even during the coldest period of the year, the wind was not sufficiently strong to cause a complete water turnover in the lake. The Wedderburn number was >1 in both situations (2.36 and 1.03), indicating that the wind force was insufficient to cause a complete mixing, even during the coldest period of the year. Moreover, the long water retention time also contributed to the long

Table 2. Median values and intervals of variation of limnological variables measured at the surface of sampling sites 1–4 in Funil and Lajes reservoirs

	Station 1		Station 2		Station 3		Station 4		General surface	
	Median	Range	Median	Range	Median	Range	Median	Range	Median	Range
Funil Reservoir										
WT (°C)	24.1	20.0–29.3	26.9	22.1–31.6	27.3	21.0–30.6	27.2	22.1–31.2	26.0	20.0–31.6
DO (%)	80.3	52–185.7	107.1	45.6–179.6	85.6	16.5–149.1	85.3	10.2–157.3	92.1	10.2–185.7
pH	6.2	5.9–8.9	7.4	5.6–9.9	8.4	6.1–9.8	8.2	6.1–9.3	7.0	5.6–9.9
Cond (µS cm^{-1})	80.8	64.6–107.6	88.3	71.5–97.0	85.5	69.7–95.8	85.9	69.3–99.3	85.9	64.6–107.6
$_{\mathrm{Zeu}}$ (m)	1.3	0.5–2.7	3.5	0.8–7.0	4.3	1.3–8.1	4.3	1.3–8.1	3.2	0.5–8.1
TP (µM)	3.5	2.9–25.6	3.9	1.3–14.1	2.5	0.8–8.3	1.9	0.8–22.0	3.2	0.8–25.6
SRP (µM)	1.7	0.4–12.3	1.5	0.1–3.2	1.2	0.3–2.7	1.1	0.3–2.4	1.2	0.1–12.3
TN (µM)	53.1	42.0–75.5	40.6	27.3–52.8	53.9	3.3–44.0	33.0	26.6–51.1	40.2	3.3–75.5
DIN (µM)	45.1	32.7–56.6	34.8	24.6–38.9	32.5	22.6–34.1	29.6	17.1–39.6	32.9	17.1–56.6
Chl (µg L^{-1})	1.1	0.1–62.4	12.1	1.6–168.9	6.1	0.5–54.5	5.9	0.2–78.3	5.2	1.1–168.9
Lajes Reservoir										
WT (°C)	24.1	17.1–27.7	27.1	22.5–30	27.7	22.7–30.3	26.1	22.6–29.6	25.3	17.1–30.3
DO (%)	94.5	84.0–113.5	96.2	78.1–117.1	96.5	71.0–117.7	93.2	75.9–113.9	94.8	71.0–117.7
pH	7.0	5.2–8.2	7.4	6.9–8.2	7.4	6.7–7.7	7.3	6.7–7.7	7.3	5.2–8.2
Cond (µS cm^{-1})	24.6	18.0–29.0	27.7	27.0–29.0	29.3	27.0–31.0	27.5	26.0–28.1	27.6	18.0–31.0
z_{eu} (m)	6.2	1.1–11.0	8.4	6.6–11.0	7.3	5.1–10.5	9.2	4.0–13.5	7.8	1.1–13.5
TP (µM)	1.0	0.6–2.5	0.4	0.2–1.6	1.0	0.4–2.2	0.8	0.4–2.4	1.0	0.2–2.5
SRP (µM)	0.6	0.3–1.3	0.4	0.1–1.9	0.8	0.2–1.8	0.6	0.2–3.0	0.6	0.1–3.0
TN (µM)	36.6	22.9–78.8	20.1	11.7–59.3	16.0	6.6–36.5	19.7	7.2–45.0	22.2	6.6–78.8
DIN (µM)	3.7	2.5–5.8	2.2	1.4–3.9	3.2	1.9–6.5	3.1	1.7–4.5	3.1	1.4–6.5
Chl (µg L^{-1})	0.8	0.2–4.9	2.5	1.0–6.7	3.0	0.8–8.2	1.9	0.7–16.6	2.1	0.2–16.6

Chl, chlorophyll-*a* concentration; Cond, electrical conductivity; DIN, dissolved inorganic nitrogen concentration; DO, dissolved oxygen concentration; SRP, soluble reactive phosphorus concentration; TN, total nitrogen concentration; TP, total phosphorus concentration; WT, water temperature; z_{eu}, euphotic zone.

stratification period in Lajes Reservoir. The influence of water retention time on the vertical stability of reservoirs was previously demonstrated by Straškraba (1999).

Many environmentally important variables for phytoplankton growth vary along the vertical gradient (Padisák 2003), and the importance of water mixing to the observed chemical and biological dynamics was critical to the definition of seasonality in Funil Reservoir. Different degrees of water mixing were clearly related to the seasonality of many variables throughout the water column. The high oxygen saturation throughout the water column, even during the stratification period, was not only related to the position of the spillways at a depth of 57.5 m, but also to the river flow close to the bottom, and which was responsible for atypical conditions at higher depths in the reservoir (Branco *et al.* 2002; Rocha *et al.* 2002). As the nutrient load to Funil Reservoir was high throughout the year, the stability of the water column, and the high temperatures during the summer months, were the main factors influencing the increased phytoplankton biomass in period II and the consequent increased pH. As the spillways in Funil Reservoir are located near the bottom of the dam, the regular outflow does not influence the euphotic zone and, consequently, the phytoplankton dynamics. As a result of high precipitation, however, an uncommon surface water outflow occurred at the beginning of period III, because of high precipitation, being responsible for eliminating the high surface biomass values.

Although complete water mixing was not observed in Lajes Reservoir, the increased oxygen saturation and SRP concentration in the hypolimnion, and even the chlorophyll-*a* concentration distribution along the water column, indicated water mixing in the epilimnion during periods I and III. Although the mixing layer deepened during period III, the hypolimnion persisted, as demonstrated by the observed anoxic conditions and higher electrical conductivity near the bottom of the lake. The deepening of the water mixing layer in Lajes Reservoir was especially well-defined by the profiles of DO, SRP, DIN and chlorophyll-*a* concentrations, and the electrical conductivity. The chlorophyll-*a* concentration in Lajes Reservoir was lower during the stratification period, and increased in period III, as a result probably of the increased nutrient concentrations (especially DIN).

The features of the watersheds of both reservoirs are of great importance, not only for light attenuation, but also in defining their chemical composition, and influencing their spatial heterogeneity. The Paraíba do Sul River is the main nutrient source for Funil Reservoir. Much of the phosphorus entering the reservoir is lost by sedimentation and adsorption, with 60% of the input being retained in the reservoir (ANEEL 1999). The influence of the Paraíba do Sul River on Funil Reservoir is evidenced by the high electrical conductivity, low water transparency, and high nutrient inputs, not only at sampling site 1, but also in determining the main limnological features of the entire

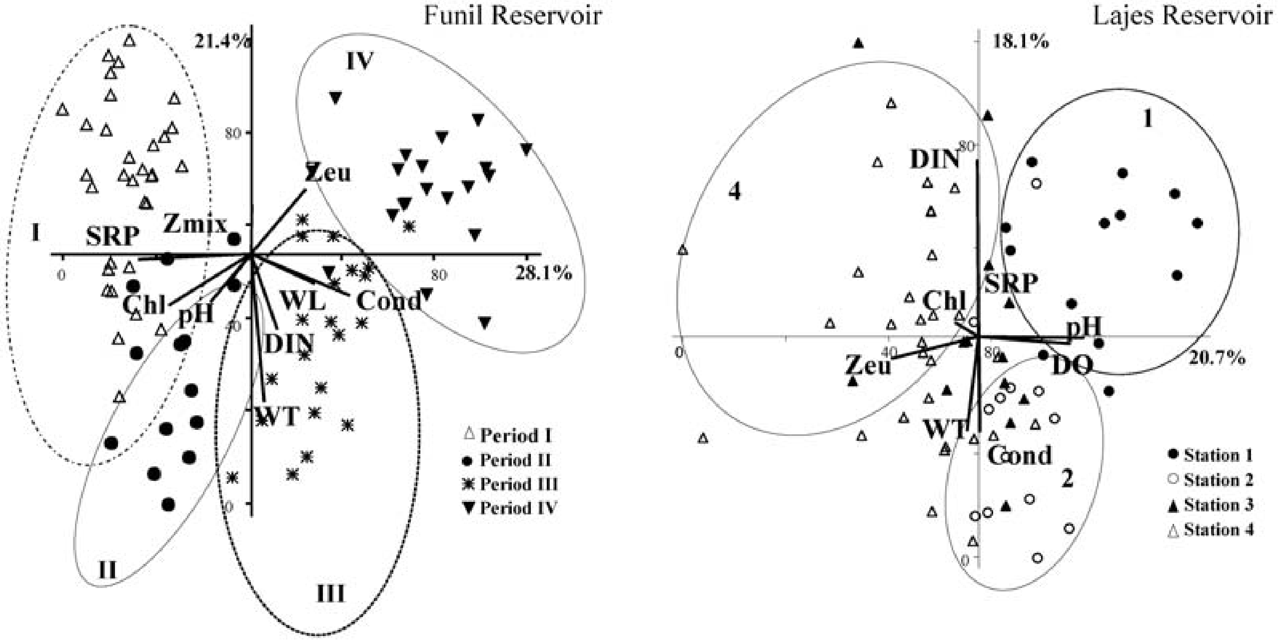

Fig. 6. Principal component analysis of Funil and Lajes reservoirs. WL, water level; WT, water temperature; Cond, electrical conductivity; DO, dissolved oxygen; z_{eu}, euphotic zone; z_{mix}, mixing zone; SRP, soluble reactive phosphorus; DIN, dissolved inorganic nitrogen; Chl, chlorophyll-*a*.

reservoir. Although the PCA illustrated a strong temporal pattern in Funil Reservoir, significant differences among the sampling sites also were observed in this study. These differences are attributed especially to the increased light availability, due to the sedimentation along the length of the reservoir, and the consequent increase in primary production. The abrupt decrease in river flows at sampling site 2, believed due to morphological characteristics, and the higher nutrient concentration at this site promoted cyanobacterial blooms, especially during the summer months. The lack of nutrient limitation, and the intense water flows from sampling sites 1 to 4, caused mainly by a low water retention time, also could be responsible for the high chlorophyll-*a* concentrations observed at sites 3 and 4. Thus, three different zones were clearly observed in Funil Reservoir. Sampling site 1 is influenced by lotic conditions, site 2 is in the transition zone, and sites 3 and 4 characterize the lentic zone. For aquatic ecosystems located in tropical and subtropical latitudes, the temporal variations are commonly induced by the seasonal pattern of precipitation and wind action (Nilssen 1984), which was true for Funil Reservoir in this study. The same pattern, however, was not responsible for differences between periods in Lajes Reservoir. The PCA results indicated that spatial heterogeneity was stronger than the seasonal variability for Lajes Reservoir. One of the main factors influencing the process of spatial compartmentalization in reservoirs is water retention time (Tundisi & Matsumura-Tundisi 1990). According to Kennedy and Walker (1990), maximum environmental gradients are expected in reservoirs with long water retention times, among other factors. A long water retention time is an important factor related to the spatial heterogeneity of large reservoirs. An example is Jurumirim Reservoir in Brazil (Nogueira *et al.* 1999), which has a surface area 10 times larger than Lajes Reservoir. In Lajes Reservoir, sampling sites 1 and 4 could be clearly distinguished. Intermediate conditions between lotic and lentic features, however, were noted at sites 2 and 3. In this case, the expected lotic–lentic gradient was less evident. While sampling site 1 has lotic features, and site 2 is located in the transition zone, the typical pattern of sedimentation and decreased primary production, in relation to the lentic zone, was not observed in this study. As expected, the nutrient concentrations decreased, and the light availability increased, from sampling sites 1 to 2. However the cultivation of Nile tilapia (*Oreochromis niloticus* Linnaeus) in fish net-cages at site 3 is an important factor related to the increased nutrient and chlorophyll-*a* concentrations and reduced light availability at sampling sites 3 and 4. This widespread activity is an important source of anthropogenic impacts in the reservoir, and the exclusion or control of fish populations to improve water quality has been suggested by some researchers (Starling *et al.* 2002; Lazzaro *et al.* 2003). Moreover, Nile tilapia can contribute to the eutrophication of a waterbody by both top-down and bottom-up forces. By supplying considerable quantities of nutrients, for example, the tilapia promote an increase in the biomass of rapidly growing algae (Figueredo & Giani 2005). Although site 3 is not located in the main channel, it directly affects the characteristics observed at site 4. In addition, because of its long water retention time, Lajes Reservoir has considerable potential to become eutrophic, thereby increasing the occurrence of cyanobacterial blooms.

Because of the main differences between these two reservoirs, their phytoplankton biomass also was dissimilar. Whereas the chlorophyll-*a* concentration peaked during the summer months in Funil Reservoir, low levels were observed in Lajes Reservoir during the entire year. Light and nutrients are the most important resources for phytoplankton growth. The importance of phosphorus and nitrogen in limiting algal biomass has been extensively demonstrated (Vollenweider & Kerekes 1980; Elser *et al.* 1990; Reynolds 2006). As light does not limit algal growth in Lajes Reservoir, which is highly transparent throughout the year, the nutrients appear to be the main limiting factors. The SRP and DIN concentrations can be 30 and seven times higher, respectively, in Funil Reservoir than in Lajes Reservoir. The distribution of the maximum observed chlorophyll-*a* concentrations, when plotted against the maximum concentration of SRP (Fig. 7), however, does not suggest a strong relationship between resource availability and biomass yield for these water systems. Moreover, the observed chlorophyll-*a* concentrations appeared to be low, in relation to the estimated available phosphorus. Using DIN as the predictor, the corresponding exercise (Fig. 7) also did not indicate nutrient limitation. The maximum observed chlorophyll concentration did come close to the estimated capacity, however, in a very few instances, especially for Lajes Reservoir. Based on this analysis, it appears the phytoplankton biomass is less than the maximum capacity of SRP and DIN for both water systems. Despite the high algal biomass observed in Funil Reservoir, competition between the main species and light limitation can interfere with the maximum expected chlorophyll-*a* concentrations for this system. The growth of phytoplankton in Lajes Reservoir, however, seems to be limited by nutrients other than phosphorus and nitrogen, or by a combination of macro- and micronutrients. Although the role of trace nutrients alone, or in combination with phosphorus and nitrogen, has been demonstrated (Frey & Small 1980;

Stoddart 1987; Sterner 1994); this topic requires further investigation for tropical freshwater systems. The zooplankton community seems to be limited by the scarce food availability and fish predation (Dias *et al.* 2005). Thus, the role of micro- and macronutrients in regard to phytoplankton growth in Lajes Reservoir must be further investigated, mainly because this is one of the few relatively well-preserved reservoirs in Brazil. Understanding these mechanisms is an important tool to prevent eutrophication of these water systems.

Eutrophication and increasingly frequent cyanobacterial blooms in Funil Reservoir have been occurring since the end of the 1970s (FEEMA 1991; Rocha *et al.* 2002). At that time, the TP and chlorophyll-*a* concentrations indicated a mesotrophic system. Today, however, the reservoir is completely eutrophic. Comparing these study data to those obtained over the past two decades (FEEMA 1991), the mean TP concentration increased three to six times, the DIN increased 10–25 times, and the maximum chlorophyll-*a* increased from 14 to 168.9 μg L^{-1}. Although Lajes Reservoir is still a mesotrophic system and exhibits good water quality compared to other Brazilian reservoirs, the water characteristics at sampling site 3, associated with the presence of fish net-cages, indicates possible changes in water quality, although other nutrients might be affecting phytoplankton growth in this water systems. Although Guarino *et al.* (2005) did not observe eutrophication in Lajes Reservoir, they also highlighted the fish net-cages as the main factor that might promote degradation of this system in the future.

In summary, the driving forces for Funil Reservoir (e.g. short water retention time; high nutrient input) were responsible for a more dynamic system, with high temporal variability and a typical zonation pattern. The Paraíba do Sul River influences not only the longitudinal pattern observed in the reservoir, but also the nutrient inputs and consequent phytoplankton biomass, especially the occurrence of cyanobacterial blooms. The preserved area around Lajes Reservoir, its long water retention time, and the presence of fish net-pens were responsible for the unusual characteristics observed in this water system. This preserved area not only maintains the historically low trophic state, but also influences the vertical water circulation pattern, preventing the effects of wind. The long water retention time also plays an important role in the low variability of the vertical pattern, which is

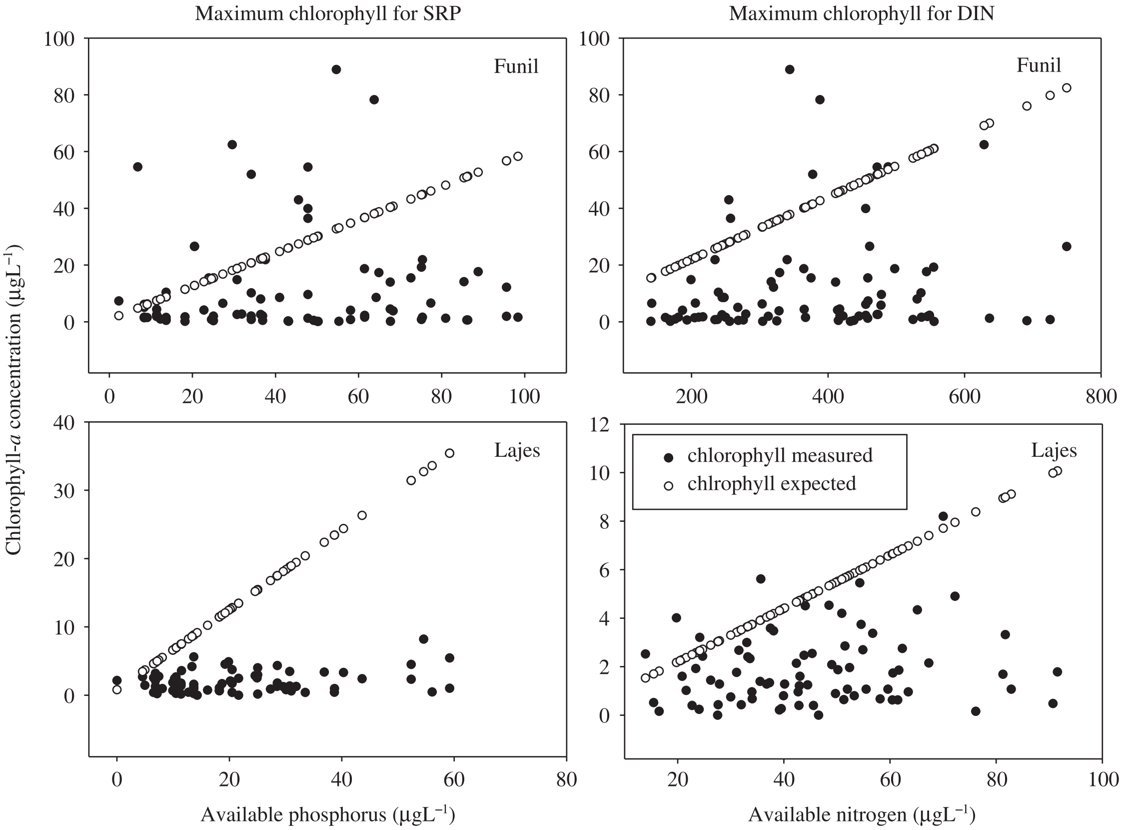

Fig. 7. Maximum chlorophyll-*a* for bioavailable phosphorus and dissolved inorganic nitrogen capacities (Reynolds, 1992) in Funil and Lajes reservoirs. DIN, dissolved organic nitrogen concentration; SRP, soluble reactive phosphorus concentration.

responsible for its important chemical and biological features. Spatial heterogeneity is an important feature of Lajes Reservoir, in which the presence of fish net-cages strongly influences the spatial dynamics of light, nutrients and chlorophyll-*a*. Even though located at the same geographical region, being of comparable size, and under similar climate conditions, the different watershed areas and water retention times are responsible for the observed differences between these systems.

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