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The contribution of water hyacinth (*Eichhornia crassipes*) and zooplankton to the internal cycling of phosphorus in the eutrophic Pampulha Reservoir, Brazil

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Abstract

The contribution of zooplankton and the water hyacinth, *Eichhornia crassipes*, to the internal cycling of phosphorus was investigated in Pampulha Reservoir, in the shallow and eutrophic Pampulha Reservoir. In the last 20 years, algal blooms, as well as outbreaks of the macrophyte, have been observed with increasing frequency. Previous investigations have suggested that phosphorus is the limiting nutrient controlling the plant production in this ecosystem. A restoration program is currently underway aiming at the complete removal of external nutrient input. Therefore, the knowledge of the magnitude of some internal metabolic processes would be desirable in order to estimate the time lag that would be necessary for the recovery of water quality. The production and loss of macrophyte biomass was monitored in limnocurrals between May 1994 and April 1995. The zooplankton was also monitored during this period at a central sampling point. The biomass losses of macrophytes were followed in marked plants during their growing season. The P-content of macrophyte biomass was also measured monthly. Excretion rates of zooplankton collected in the reservoir were determined using short time experiments at the laboratory. This study demonstrated that zooplankton was more important for the P-cycling during the dry season when it was able to recycle a maximum of 26% d^{-1} of total phosphorus in lake water. The macrophyte contribution was more important during the rainy season (especially at the end of the rainy season). In April 1995, the macrophytes were able to recycle as much as 26% d^{-1} of the total phosphorus present in the water. At this time of the year, both communities recycled more than 40% d^{-1} of the total phosphorus available in water. Therefore, it was demonstrated that zooplankton and macrophytes play a key role in the internal cycling of a limiting nutrient in this reservoir.

Introduction

Eutrophication is typically characterized by the biomass increase of primary producers, such as phytoplankton, peryphyton and macrophytes in response to increased nutrient inputs (Hutchinson, 1973). However, eutrophication rates may vary significantly among lakes having different ecological constraints with otherwise comparable external nutrient inputs (Henrickson et al., 1980; Christoffersen et al., 1993). Most eutrophication models were mostly based on the role played by external inputs of nutrients, while the sediments would be the most important source for the nutrient internal load (Zauke et al., 1992). Recent investigations have demonstrated the importance of biotic feedback in the phosphorus cycles of aquatic ecosystems (Carpenter et al., 1992).

There is some evidence that tropical lakes be-

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come eutrophic with less nutrient input than temperate ecosystems (Pinto-Coelho, 1994). This difference possibly could be explained by the hypothesis asserting that internal biotic processes play a more important role in tropical ecosystems. Recent investigations have shown that the existence of high production of certain tropical ecosystems is based on a highly efficient nutrient recycling between autotrophs and heterotrophs (Thomas & Atkinson, 1997). These processes favor a rapid recycling of limiting nutrients. Nevertheless, the potential role of internal biological processes in nutrient cycling has been studied mostly in temperate areas (Bartell, 1981; Ejsmont-Karabin, 1990; Gutelmakher & Makartseva, 1990). Only a few recent investigations have demonstrated the importance of internal processes in nutrient cycling in some tropical lakes. These processes are basically the nutrient regeneration of zooplankton and biomass decomposition of macrophytes (Pieczynska, 1990; Pinto-Coelho et al., 1997).

The traditional strategy of lake recovery is based on reductions of external input of nutrient and sediment dredging top layers of sediment (Kleeberg & Kozerski, 1997). Some investigations have demonstrated that many lakes have maintained eutrophic conditions for long periods, despite of the reductions in external P-loading, (Jeppsen et al., 1991). The rate of recovery will depend not only on the hydrological and morphometric characteristics of the reservoir itself, but also on the knowledge of the factors influencing the internal cycling of limiting nutrients (Stephen et al., 1997).

Phosphorus has long been recognized as the most critical nutrient limiting primary producers in many lakes (e.g. Schindler, 1977). There is evidence that this element should be limiting in several tropical lakes and reservoirs (Henry & Tundisi, 1983; Pinto-Coelho, 1994). Additionally, some studies have also demonstrated that macrophytes and zooplankton can contribute significantly to phosphorus release in eutrophic and hypertrophic lakes (Stephen et al., 1997; Pinto-Coelho et al., 1997).

Water hyacinth, *Eichhornia crassipes* (Mart.) Solms., is an aggressive aquatic weed throughout its range in virtually all tropical and subtropical areas of the world (Center & Spencer, 1981). This species usually has high production rates reaching values as high as 40 t ha^{-1} y^{-1} (Debusk et al., 1981). Water hyacinth vegetation also provide a favorable habitat for mosquitoes (Sucharit et al., 1981) which are vectors of diseases such as malaria, encephalitis and filariasis. Also freshwater snails, like *Biomphalaria*, intermediate hosts for schistosomiasis, have been found attached to the roots of these plants (Brönmark, 1989). In spite of all these problems associated with this macrophyte, there is a scarcity of studies concerning field determinations of production and losses and, especially, those concerning the biomass turnover (Gopal, 1987).

The objective of this paper was to evaluate the potential role in the internal cycling of phopshorus of the macrophyte,*E. crassipes*, and zooplankton in a small tropical ecosystem in Brazil, the Pampulha Reservoir. The P-release from the macrophyte was estimated from data of biomass loss and P-content. The potential role of the zooplankton community was estimated by means of the experimental determination of excretion rates multiplied by the integrated biomass of zooplankton in the lake at a given date. The P-release rates were directly measured in short-term experiments using zooplankton fresh collected from the reservoir.

Study area

The Pampulha Reservoir has a surface area of 2.4 km^2 and a volume of 12 mio m^3. The maximum depth is 17 m and the mean depth is 6 m. This reservoir is located in the northern part of Belo Horizonte (19° 55′ 09″ S, 43° 56′ 47″ W), the fourth largest city in Brazil. Despite the small size, the reservoir is of great significance. Constructed in 1938, it is the pivotal element in a series of architectural projects conceived by Oscar Niemeyer, who later projected Brasília, the capital of Brazil. Additionally, an important ecological reserve, as well as several other sport, tourist and leisure facilities are also available in the catchment basin of this reservoir.

Since the 1970s, this reservoir has been suffering from eutrophication caused by the input of untreated sewage water. At first, algal blooms were recorded and, in the mid 1980s, the macrophyte water hyacinth (*Eichhornia crassipes)* appeared in the lake, rapidly, covering large areas (Giani et al., 1988; Greco, 1996). In the early 1990s, the city administration started regular macrophyte removal campaigns. However, the macrophyte removal cleared the ‘ecological space’ for Cyanobacteria. After the water hyacinth removal began, the lake has been suffering frequent blooms of *Microcystis* especially *M. aeruginosa* and *M. flos-aquae*. These algae generally bloom during the dry

season which begins in May and ends in October. A restoration project is currently underway, which will provide the region with a wastewater treatment plant and a system of sewage channels that will remove most of the input of wastewater which is still flowing into the lake.

The climate of the region is classified as tropical B-2 type with moderate hydric deficit (Ferreira, 1992). Mean monthly air temperatures usually range from 18 (May–July) to 28 °C (October–February). It can be described by the prevalence of two clearly marked seasons that can be divided according to rainfall pattern: (a) a dry season which extends from May to October and a (b) rainy season extending from November through March. Annual mean precipitation ranges from 1400 to 1600 mm, mostly restricted to the wet season.

Methods

Zooplankton and macrophyte were collected monthly from April 1994 to April 1995. Replicate samples of water and zooplankton were collected at a sampling station with 6 m depth located in the central region of the lake. After studying the horizontal distribution of plankton in the reservoir for some years, Giani et al., (1988) proposed this point as representative for assessing water quality in the whole lake. The macrophyte *E. crassipes* was collected at a sampling site located next to one of the two channels which collect the inflow of the Ressaca/Sarandi streams. These are the largest tributaries of the reservoir, collecting the bulk of polluted water originated in the watershed.

Water samples were taken with a Hydro-Bios Van Dorn bottle and transferred to 0.5 l plastic bottles, that were placed in a thermos box with ice. At the laboratory, they were frozen for later orthophosphate determinations. Replicate zooplankton samples were drawn using a 5.1 l Clarke-Juady plankton trap at four different depths covering the whole water column. Organisms were quickly rinsed into plastic vials using filtered cold tap water and preserved with formalin solution (buffered to pH 7.0, 4% final concentration) containing 0.1 ml of Bengal Rose. The samples were completely enumerated using a 25 ml plexiglass counting chamber. A Leica 3M stereo-microscope equipped with a SONY CCD IRIS video camera and a high resolution SAMSUNG color monitor was used, under 40× magnification. The lengths of all individuals were measured using a calibrated ocular micrometer in order to estimate their biomass using allometric equations:

$$B = a.L^b, \tag{1}$$

where a and b are specific parameters, B = biomass in μg dry weight and L = length in mm. The coefficients a and b are specific for each organism were taken from the literature (Bottrell et al., 1976; McCauley, 1984; Masundire, 1994).

Phosphorus excretion rates were determined at the laboratory between 1994 and 1996, covering different phases of the seasonal cycle. On the day of each experiment, samples of zooplankton were collected from the reservoir with vertical hauls using a 90 μm mesh conical net, 80 cm in diameter. Animals were gently transferred to a thermos flask containing lake water. After measuring the water column temperatures with a YSI thermistor and taking a 10 l sample of lake water (0.5 m) with a Van Dorn sampler, the zooplankton was rapidly transported to the laboratory (20 min).

In the laboratory, the lake water was filtered through 20 μm mesh filters. The filtrate was immediately transferred to a 20 l aquarium and aerated for 15 min to achieve full oxygen saturation. In some experiments, a solution containing a mixture of antibiotics – penicillin (0.12 g/l) and streptomycin (0.24 g/l) – was added to the water in order to avoid nutrient uptake by bacteria. The water of the aquarium was syphoned to the experimental vessels which consisted of 500 ml borosilicate bottles with a large opening. The zooplankton from thermos flask was subsampled using a 20 ml Stempel pipette and the content of this pipette was added to the experimental vessels. The control vessels received no zooplankton. Five replicates were considered for each treatment. The following treatments were considered: different incubation times (2,4 and 6 h.), different times of day (day and night), and different illumination conditions (0–1300 lux). The experimental vessels were kept in incubation cabinets, where the temperature (24 °C ± 1 °C) and illumination conditions were controlled with precision. Special care was taken to check the number of dead animals at the beginning and at regular intervals throughout the incubation time. The number of dead animals was found to be minimal especially when short incubations (2 h.) were performed.

At the end of the incubation time, the content of each bottle was filtered through an inox gauze (90 μm) and was immediately deep frozen. The next day, the zooplankton samples were freeze dried using an Edwards freeze dryer coupled to a Edwards-RV8 vacuum

pump. The dried biomass was gravimetrically determined using a high precision Mettler microbalance. The remaining water in the experimental vessels was collected for further nutrient determinations. A 250 ml aliquot was vacuum filtered using a GF 50 Schleicher & Schüll glass fiber filter, 47 mm in diameter. The water samples were frozen (−25 °C) for later orthophoshate determination by a spectrophotometric method (Murphy & Riley, 1962) using a Shimadzu UV 1201 spectrophotometer. The phosphate release of zooplankton (Ep in mg P–PO_4 gdw h^{-1}) was estimated according to the following formula:

$$\mathrm{EP} = \frac{P_z[\text{mg P-PO}_4.l^{-1}] - P_c[\text{mg P-PO}_4.l^{-1}]}{\text{Biomass [g DW}.l^{-1}].t[\text{h}]}, \quad (2)$$

where EP is the orthophosphate excretion rate of zooplankton in mgP–PO_4.g dry weight h^{-1}. $[P]_z$ and $[P]_c$ are the concentrations of dissolved orthophosphate from zooplankton and control bottles, respectively. Biomass is the zooplankton biomass in dry weight and t is the incubation time. The 'phosphorus release' due to the whole zooplankton community was estimated according to the following expression:

$$\begin{aligned}\mathrm{ZP_i} &= (B_i[\mathrm{gDWm^{-2}}].\mathrm{EP_d} \\ &[\mathrm{mgP-PO_4.gDW.h^{-1}}].\mathrm{DL_i[h]}) \\ &+ (B_i[\mathrm{g.DW.m^{-2}}].\mathrm{Ep_n} \\ &[\mathrm{mgP-PO_4.gDW.h^{-1}}].\mathrm{NL_i[h]}), \end{aligned} \quad (3)$$

where ZP_i is the estimated phosphorus return rate in mg P–PO4 m^{-2} d^{-1} due to the zooplankton community, B_i is the integrated zooplankton biomass at each sampling date and EP_d and Ep_n are the excretion rates of zooplankton during the day and night, respectively. DL and NL are the day and night length in hours for each date. Both estimates of excretion rates are based on laboratory experiments.

The temporal dynamics of the macrophyte *E. crassipes* was assessed in plants kept in five floating limnocurrals of 9.0 m^2 (15 m × 3 m) each. These structures were fixed in the sediments by means of wood sticks. *E. crassipes* individuals were transferred to each limnocurral in April 1994. The specimens were small, with leaves showing dilated petioles. A ramet was a plant individual with one or more expanded leaves with a root. The initial density in each stand was 85 ramets m^{-2}. A subsample of 38 ramets was marked in each limnocurral using metal labels. All the leaves from these ramets were marked with colored PVA-based glue, in order to determine the rates of leaf losses between two successive samplings. At each sampling date, the number of healthy, senescent and dead leaves was recorded. Senescent leaves were those with more than 50% of leaf area without green pigments. Each new ramet was identified and received a metal etiquette. One of the limnocurrals was used for the analysis of the seasonal variation in plant biomass and density. At each sampling date, three samples were taken using a 0.25 m^2square frame made of PVC tube, according to Westlake (1965). For the determination of dry weight, the ramets were separated and dried in a cabinet at 70 °C. After being dried and weighed, the plants were mechanically grounded. The phosphorus content was determined using the colorimetric method proposed by Murphy & Riley (1962). The results were expressed as percent phosphorus related to the sample biomass.

The estimation of biomass loss by demographic analysis was done according to the equation:

$$\mathrm{BL_i} = N_i.[N \text{ ramets.m}^{-2}.\text{d}^{-1}].X_i[\text{gDW}], \quad (4)$$

where BL_i is the biomass loss in g DW. $m^{-2}.d^{-1}$, N_i is the number of ramets (or leaves) lost per $m^{-2}.d^{-1}$ and X_i is the average dry weight (of ramets or leaves) on each sampling occasion (i).

The phosphorus released by the macrophyte community was estimated according to the following product:

$$\mathrm{MP_i} = \mathrm{BL_i}[\mathrm{gDW.d^{-1}}].\mathrm{P_i}[\mathrm{mgP-PO_4.gDW^{-1}}], \quad (5)$$

where MP is the phosphorus release due to macrophytes in mg P–PO_4.m^{-2}.d^{-1}. BL_i is the daily biomass loss of macrophytes and P_i is the mean phosphorus content of macrophytes on each sampling date (i).

Results

Total phosphorus

As a eutrophic reservoir, Pampulha lake is characterized by high phosphorus concentrations. These concentrations however suffered strong seasonal oscillations. They were higher during the dry season of 1994 reaching an annual maximum in October, when a integrated concentration of 1.05 g P–PO_4.m^{-2} was recorded (Figure 1). These concentrations decreased soon after the first heavy rains that occurred in

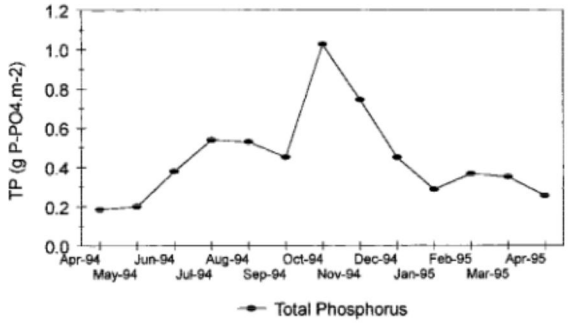

Figure 1. Integrated concentrations of total phosphorus (TP) in Pampulha Reservoir between April 1994 and April 1995.

November and December. The phosphorus availability remained at lower levels until April 1995.

Zooplankton

Zooplankton biomass also showed a clear seasonal pattern, with higher biomass occurring during the dry season, especially during the months of June, August and September (Figure 2). The biomass of mesozooplankton remained at high levels (> 2.0 g dw m^{-2}) during all the 'core months' of the dry season, between June and September. The biomass maximum occurred in June, with nearly 4.0 g of dry weight per square meter. Larger organisms were dominated by cladocerans such as *Diaphanosoma birgei* (Korinek, 1981), *Daphnia gessneri* (Herbst, 1967) and *D. laevis* (Birge, 1878). Copepods were the second most important group. The cyclopoid *Thermocyclops decipines* (Kiefer, 1929) was the leading organism, but the calanoid *Scolodiaptomus corderoi* (Wright, 1936) was also present, although at low densities (Figure 2a).

Microzooplankton was dominated by *Bosmina longirostris* (O.F. Müller, 1785) which occurred between July and November 1984 and *Ceridaphnia cornuta* (Sars, 1886) that was abundant during the rainy season (Figure 2b). Several rotifers were present, among them the most important were *Brachionus calyciflorus* (Pallas, 1766), *Keratella cochlearis* (Gosse, 1851), *K. tropica* (Apstein, 1907) and *K. americana* (Carlin, 1943), but with low abundance and biomass (data not represented). The two dominant organisms of Microzooplankton, *B. longisrostris* and *C. cornuta* exhibited different seasonal peaks in biomass registered in September 1994 (0.18 g dw m^{-2}) and in March 1995 (0.33 g dw m^{-2}), respectively (Figure 2b).

Zooplankton excretion

Since several factors potentially affect the experimental determination of nutrient excretion rates by zooplankton, a series of experiments were performed with the objective to evaluate the effect of some factors known to affect these rates. The effects of daytime and illumination conditions were examined on two different occasions (Figure 3a). Higher excretion rates were obtained with incubations conducted in the morning hours using illuminated experimental vessels. Under these conditions average excretion rates ranged between 0.6 and 0.8 mg $P–PO_4$ gDW h^{-1}. Both experiments were performed in the early dry season, in April 1994 and again in May 1996. The zooplankton community was dominated by large cladocerans (*Daphnia* and *Diaphanosoma*) on both occasions.

Excretion rates were also strongly affected by the metabolism of free living bacteria, since these organisms are capable of absorbing large quantities of orthophosphate within short periods of time. The addition of antibiotics to the experimental vessels produced higher P-excretion rates, as observed in the incubations conducted on April 26, 1995 (Figure 4a). During this time of the year, the zooplankton was strongly dominated by *Daphnia laevis* (Figure 4b). Longer incubation times also affected the determination of release rates of phosphorus by zooplankton. The highest Figure of all experiments, 1.57 mg $P–PO_4$ g dry weight of zooplankton. h^{-1}, was obtained when the incubation time was the shortest (2 h.), with the addition of antibiotics (Figure 4). This maximum was recorded in June 13, 1996, when zooplankton was dominated by *Daphnia laevis*, *Diaphanosoma birgei* and *Thermocyclops decipiens* (Figure 4b).

In the view of the above data, we considered two estimates of P-release by the zooplankton community. For the daytime, we considered a conservative estimate of P-release of 1.05 mg $P–PO_4$ g DW h^{-1}, obtained in experiments conducted on April 26, 1995, with an incubation time of 2 h, conducted between 10:00 h and 12:00 h a.m., using illuminated experimental vessels containing antibiotics (Figure 4a). For the night hours, we took an excretion rate of 0.49 mg $P–PO_4$ g DW h^{-1} based on experiments conducted on May 24, 1996, between 19:00 and 21:00 h, in the dark, using vessels with antibiotics (Figure 3a).

The contribution of the zooplankton to the internal cycling of phosphorus in Pampulha Reservoir was found to be relevant (Figure 5). The phosphorus release rates due to the zooplankton community ranged

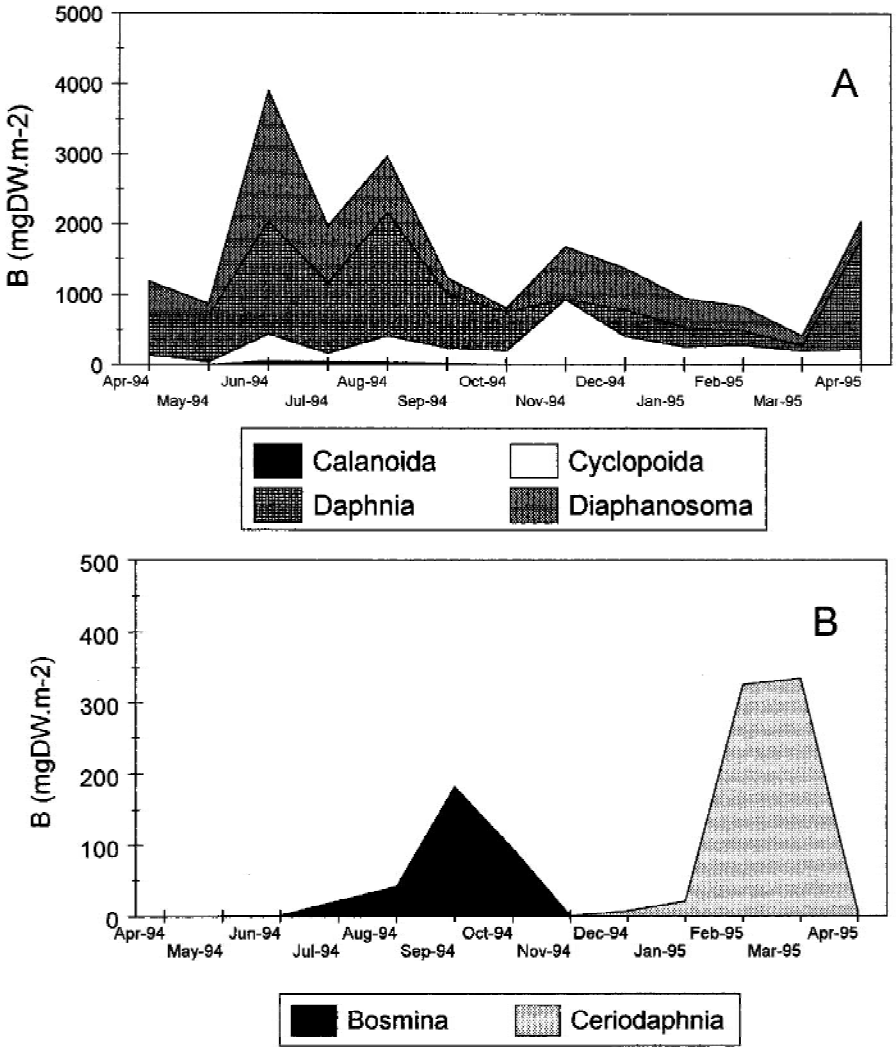

Figure 2. (a) Mesozooplankton biomass (mg d w m^{-2}) in Pampulha Reservoir, between April 1994 and April 1995; (b) microzooplankton biomass (mg d w m^{-2}) in Pampulha Reservoir between April 1994 and April 1995.

from 22 to 99 mg $P–PO_4$ m^{-2} d^{-1}. This amplitude was obtained if only the higher excretion rate of 1.05 mg $P–PO_4$ g DW h^{-1} was applied to Equation (3). This range became more restricted, 16–70 mg $P–PO_4$ m^{-2} d^{-1}, if the different values for day and night incubations were used. As expected, the highest figures were obtained in June 1994, during the dry season, when the zooplankton biomass peaked in the lake, dominated by large cladocerans (*Diaphanosoma* and *Daphnia*).

Macrophytes

The temporal dynamics of *E. crassipes* was also affected on a seasonal basis. The population began to increase in density in the limnocurrals in September 1994, when ramet density was about 65 ramets m^{-2}. This value more than doubled in December (156 ramets m^{-2}). In the lake, the macrohyte population also expanded its biomass vigorously during this period. The temporal pattern of biomass loss was associated with plant population growth. Leaf and ramet losses were minimal during the dry season, ranging from 1.0 to 2.0 g DW m^{-2} d^{-1} (Figure 6a). However, in November 1994, loss values increased to nearly 4.0 g DW m^{-2} d^{-1}. Leaf losses were higher than ramet losses, reaching an annual maximum of 25.0 g DW m^{-2} d^{-1} in April 1995. The ramet loss began

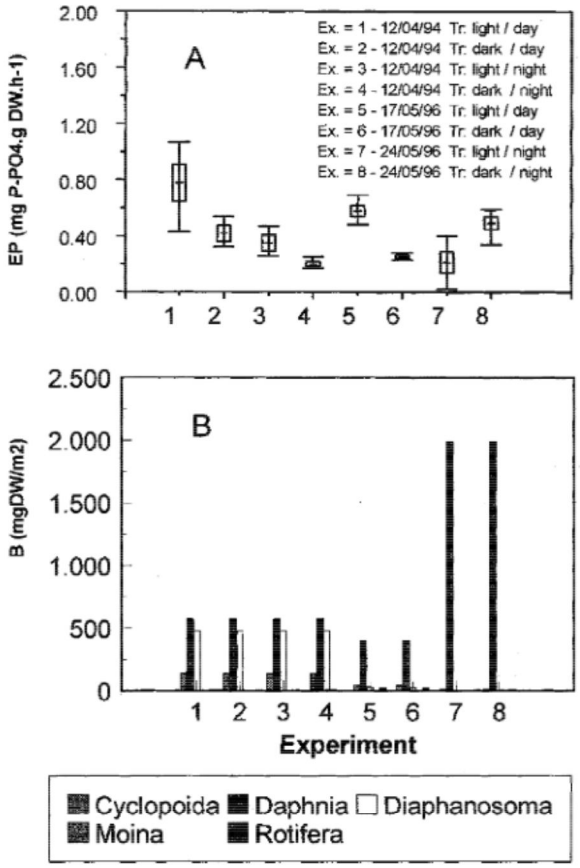

Figure 3. (a) Excretion rates of phosphorus (EP in mg $P–PO_4$ gDW h^{-1}) by the zooplankton community of Pampulha Reservoir: effect of time of the day and illumination. Mean, standard error and maximum and minimum values are given. (b) zooplankton biomass (B) in the reservoir on each day of the experiment.

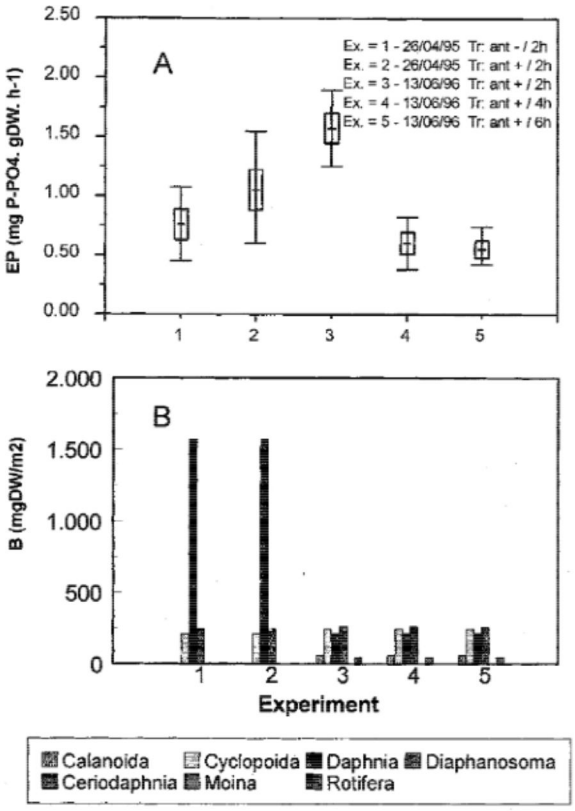

Figure 4. (a) Excretion rates of phosphorus (EP in mg $P–PO_4$ gDW h^{-1}). Mean, standard error and maximum and minimum values are given by the zooplankton community of Pampulha Reservoir: effect of the addition of antibiotics (exps 1 and 2) and incubation time (exps. 3,4,5); (b) zooplankton biomass (B) in the reservoir on each day of the experiment.

to increase somewhat later during the rainy season, in January 1995, reaching a seasonal maximum of 14.2 g DW m^{-2} d^{-1} in March 1995.

Since on each occasion we had taken plant samples to determine their phosphorus content, we could estimate the phosphorus release based on updated data of phosphorus content. The P-content fluctuated between 0.10 and 0.37% of macrophyte dry weight. It was somewhat higher during the growing season, when it remained above 0.20%. The phosphorus release due to *E. crassipes* showed negligible values during the dry season, ranging from 0.0 to 4.0 mg $P–PO_4$ m^{-2} d^{-1}. However, there was a steep increase in P-release, soon after the onset of the population growth, shorter after the beginning of the rainy season in November 1994. The phosphorus release due to the biomass loss of leaves of *E. crassipes* reached a maximum of 57 mg $P–PO_4$ m^{-2} d^{-1} (Figure 6 b). The phosphorus regenerated from ramets reached 33 mg $P–PO_4$ m^{-2} d^{-1}, in March 1995.

Comparison of P released by zooplankton and E. crassipes

The zooplankton had a higher impact on P-cycling during the dry season, when its biomass peaked in the lake. In June 1994, it was able to cycle daily as much as 100 mg $P–PO_4$ m^{-2} d^{-1} (Figure 7a). The macrophyte population began to release higher quantities of phosphorus as soon as the biomass losses increased. A seasonal maximum of 90 mg $P–PO_4$ m^{-2} d^{-1} was found in March 1995. These contributions could also be calculated as ratios of total phosphorus in the lake. The daily percentiles of recycled orthophosphate from lake water due to zooplankton varied between 2 and 26% d^{-1} during the study period. (Figure 7b).

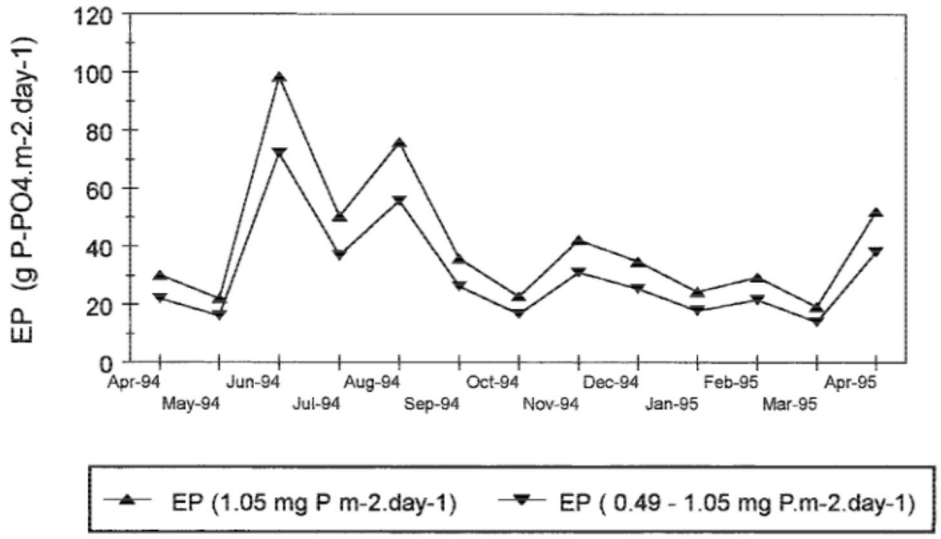

Figure 5. Phosphorus release (EP, mg P–PO_4 m^{-2} d^{-1}) due to the zooplankton community in Pampulha Reservoir between April 1994 and April 1995. The two curves were obtained using the following estimates of excretion rates: EP = 1.05 mg P–PO_4 g d w h^{-1} (higher curve) and EP = 1.05 mg P–PO_4 g d w h^{-1} (day) and 0.49 mg P–PO_4 g d w h^{-1} (night) (lower curve).

These estimations become more modest if we consider the combined excretion rates for different times of day. The highest value would be 18% d^{-1} instead of 26% d^{-1}. As expected, the estimate of P-release due to the biomass turnover of the macrophyte *E. crassipes* reached a maximum during the rainy season, between November 1994 and April 1995. The maximum rare of P-release was close to 26% d^{-1}, obtained in March of 1995, also at the end of the growing season (Figure 4b).

Discussion

The objective of this investigation was to compare P-release due to the macrophyte *E. crassipes* and zooplankton. The way these organisms release phosphorus into the water column is quite different since the former are primary producers and the latter ones are consumers. The zooplankton from Pampulha Reservoir is composed of microcrustaceans and rotifers and the dominance of large cladocerans (*Daphnia* and *Diaphanosoma* and *Moina*) has increased recently (Pinto-Coelho, 1998). The basic endproducts of their excretory activity are CO_2, NH_4 and P–PO_4 (Peters & Lean 1973; Mayzaud, 1976; Alcaraz et al., 1994). Recent investigations have stressed the potential impact that zooplankton excretion may have on whole lake chemistry, not only affecting the nutrient availability but also determining nutrient ratios such as N:P ratios (Urabe et al., 1995).

Macrophytes, like other plants, are normally seen as a P-sink rather as a P-source. However, one of the most striking features of the macrophyte *E. crassipes* is its high biomass turnover rates (Gopal, 1994). Therefore, the basic idea of this article was to compare the magnitude of these two processes: zooplankton excretion and biomass turn over of *E. crassipes* using the phosphorus as a common unit of comparison. Although these are quite different processes, they may have similar ecological significance, since they are two major ways by which biotic phosphorus is returning to lake water.

P-release by zooplankton

In this study, the P-release of the zooplankton community was based on two specific biomass excretion rates, 1.05 and 0.49 mg P–PO_4 g DW h^{-1}, for the daytime and night hours, respectively. Despite being high excretion rates, they are still comparable to other studies available in the literature (Pinto-Coelho et al., 1997). Lehman (1980b) found rates varying between 0.58 and 0.83 mg P–PO_4 g DW h^{-1} obtained with *Daphnia*, at 20 °C. Jacobsen & Comita (1976) measured phosphorus excretion rates as high as 0.75 mg P–PO_4 g DW h^{-1} using *Daphnia pulex*, in incubations varying between 2 and 24 h. *Mesocyclops*

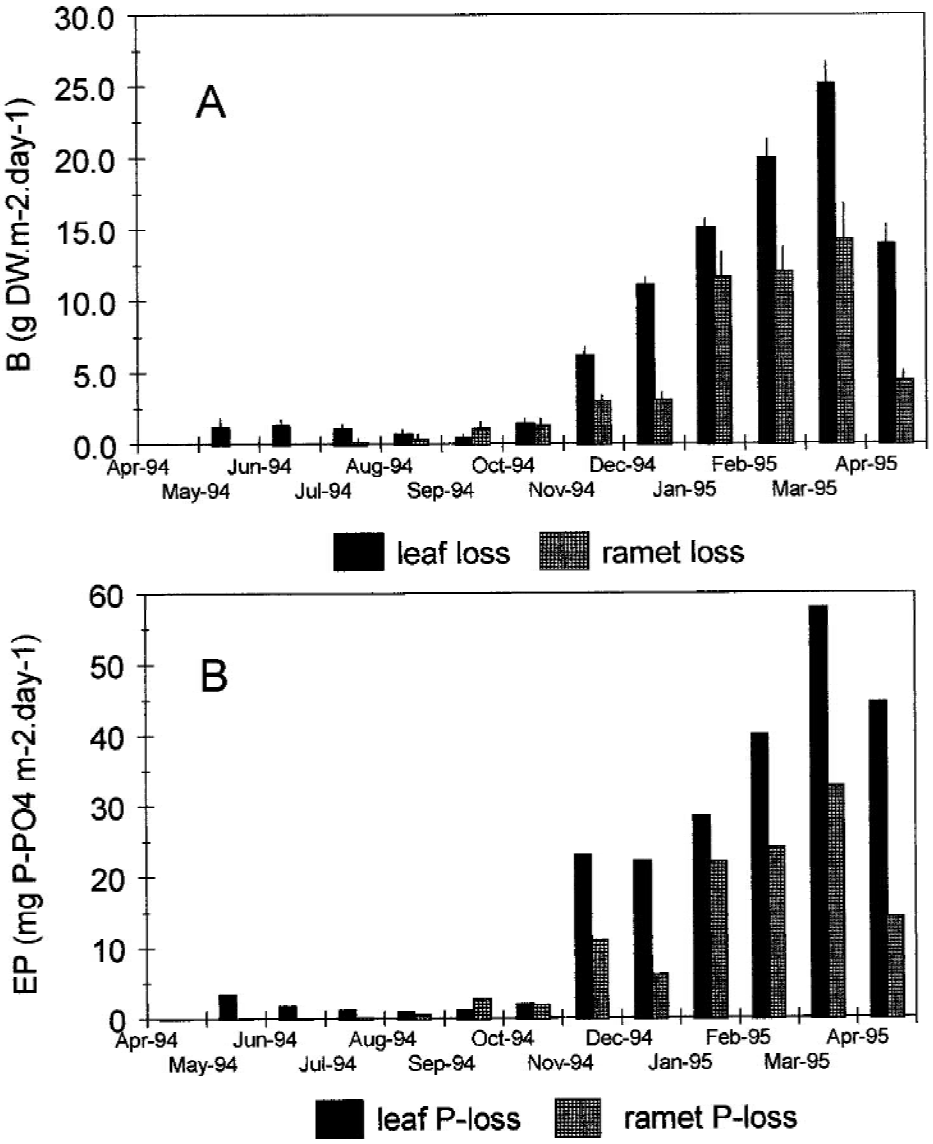

Figure 6. (a) Biomass loss (means and standard errors) of leaves and ramets of *E. crassipes* in Pampulha Reservoir, between April 1994 and April 1995; (b) Phosphorus release (mg $P–PO_4$ m^{-2} d^{-1}) due to leaves and ramets of *E. crassipes* in Pampulha Reservoir between April 1994 and April 1995.

leuckati is able to release 0.7 mg $P–PO_4$ g DW h^{-1} (Ejsmont-Karabin, 1984).

The calculations of Equation (3), in which the specific biomass excretion rates for day and night time are multiplied to the integrated biomass permitted estimating the contribution of zooplankton to the internal cycling of phosphorus in this reservoir. The release of phosphorus by the zooplankton community was found to vary between 10 and 47 mg $P–PO_4$ m^{-2} d^{-1}. This is a conservative estimation since this range was based on estimations using two different excretion rates for day and night, respectively. If we do not consider the lower excretion rates obtained for the night incubations, this range would be 22–99 mg $P–PO_4$ m^{-2} d^{-1}.

Several factors affect the experimental determination of phosphorus excretion by zooplankton: water temperature, nutritional status of organisms, nutrient uptake by bacteria and algae are the most commonly cited factors (La Row et al., 1975; Gophen, 1976;

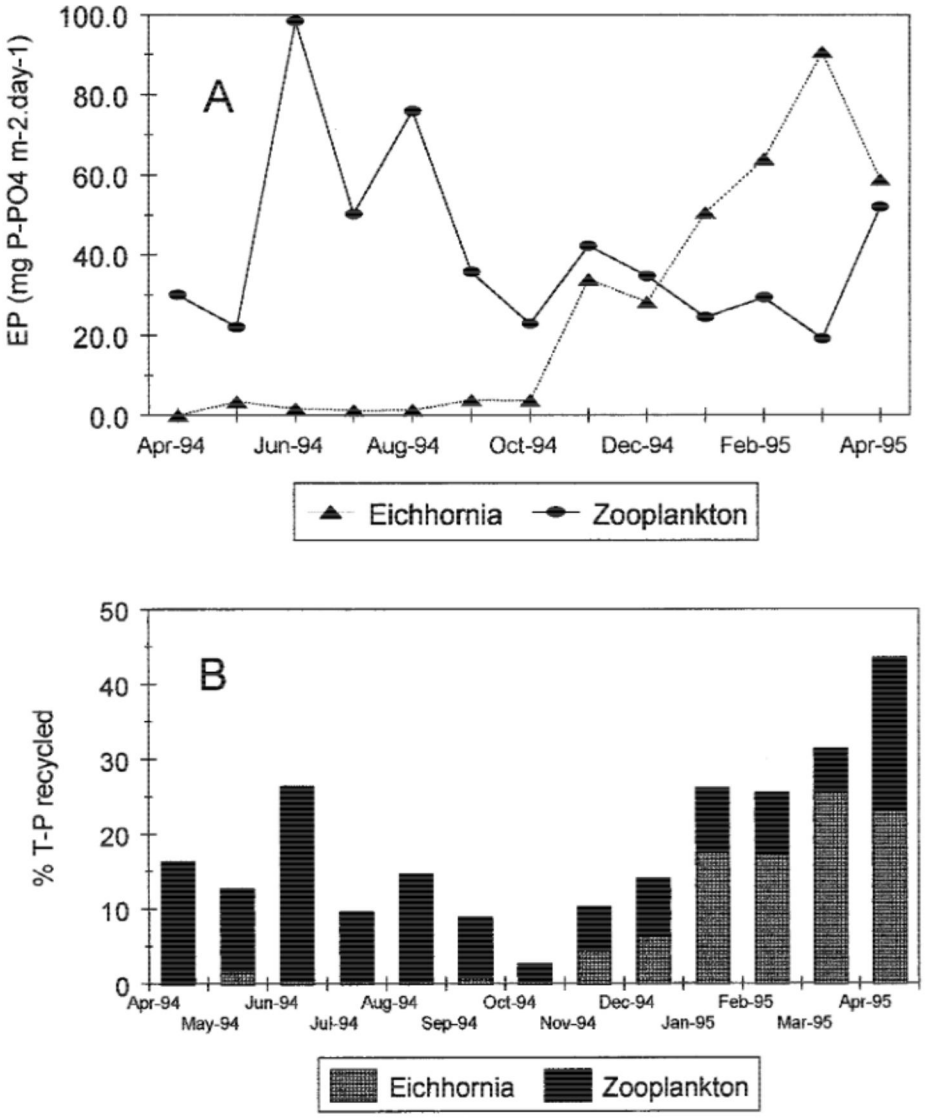

Figure 7. (a) Phosphorus release rates of the zooplankton community and the macrophyte *Eichhornia crassipes* in Pampulha Reservoir expressed as mgP–PO_4 m^{-2} d^{-1}; (b) Relative contributions (% Total Phosphporus – TP) of zooplankton and *E. crassipes* to the internal cycling of total phosphorus in Pampulha Reservoir between April 1994 and April 1995.

Ejsmont-Karabin, 1984; Conner & Wetzel, 1992). All experiments were run using a germination cabinet under controlled conditions of temperature and illumination. The temperature of the experiments was set to be as close as possible to the temperature found in the lake, at the time and depths where the water and plankton samples were drawn. The nutritional status of organisms is another major source of variation. Starved organisms usually have lower excretion rates (Ejsmont-Karabin, 1984). Algae and bacteria are important food sources for zooplankton and eliminating these particles by filtration would have caused starvation. In order to avoid the effect of increasing starvation of organisms during the experiments, we considered only short time incubations (2). Our experiments using different incubation times showed that excretion rates suffered a noticeable decrease at incubation times of 4 and 6 h.

The nutrient uptake of algae and bacteria may be the most important source of bias in the excretion experiments. It was already demonstrated that these organisms are able to uptake nutrients as soon as that

are released by zooplankton (Lehman, 1980a, b). In order to reduce possible interference of nutrient uptake by algae and bacteria, we took two different measures. First of all, we eliminated larger algae (net phytoplankton) by filtering the water to be used in the experimental vessels through a 20 μm mesh filter. Therefore, only nanoplanktonic algae were kept inside the vessels. Second, we added a mixture of two antibiotics to eliminate nutrient uptake by bacteria. The counting of bacterial colonies on Agar plates from different treatments demonstrated that this procedure completely eliminated bacterial activity in the vessels containing antibiotics. Since the excretion rates of phosphorus were significantly higher in the experimental units with antibiotics, it was demonstrated the crucial role of bacteria as a sink source for released zooplankton phosphorus. To evaluate the role of nutrient uptake by nannoalgae, we ran experiments under different illumination regimen and at different times of day. These experiments showed that P-release of zooplankton was consistently lower at night or in the dark vessels. This lower P-excretion values at night or in the dark may be the result of increased nutrient uptake by nannoalgae under these circumstances. However, these differences may also reflect diel rhythms in the metabolic activity of zooplankton.

Since we could not completely overcome the influence of nutrient uptake by nannoalgae, we used two estimates of P-release. It is quite possible that the lower excretion rates at night were affected by nutrient uptake by nannoalgae. Thus, we considered only the higher excretion rates obtained in our morning experiments for the calculation of the impact of zooplankton on P-recycling in the reservoir. On the other hand, it is also possible that these differences may reflect important diel rhythms of the zooplankton community. Nevertheless, it was demonstrated that this community has a large impact on the internal cycling of phosphorus in this lake, even considering the lower excretion rates.

P-release of E. crassipes

Estimations of P-release due to *E. crassipes* in Pampulha Reservoir during the growing season varied between 28 and 90 mg $P–PO_4$ m^{-2} d^{-1}. These figures are also high considering other studies. In some English lakes situated in the Norfolk Broads, for instance, Stephen et al. (1997) found P-release rates varying from 8 to 16 mg $P–PO_4$ m^{-2} d^{-1} from sediment containing rooted macrophytes. These estimations were somewhat higher in other English lakes situated in Chesire Meres, (10–32 mg $P–PO_4$ m^{-2} d^{-1}). Reddy & DeBusk (1991) measured the decomposition rates of *E. crassipes* in Lake Apopka, in Florida and found P-release rates varying from 16 to 19 kg P ha^{-1} y^{-1} (i.e. 4.4–5.2 mgP m^{-2} d^{-1}).

The maximum P-release of *E. crassipes* was observed during the growing season. The increase in biomass loss coincided with the increase in plant density. This is probably due to the morphological and physiological shifts suffered by the individuals as plant density increases. Under these circumstances, there is an overall replacement of small floating leaves with expanded petioles by longer leaves without expanded petioles (Geber et al. 1992). This density increase also causes physiological shifts in the plants. Increased density increases shading. The light limitation can reduce the internal levels of giberellines causing morphological changes and an overall decrease in ramet production (Methy & Roy, 1993). Light limitation also causes leaves to die faster than leaves of the same age submitted to favorable conditions of luminosity (White, 1979). All of these modifications suffered by plants living at high densities are probably self-regulating mechanisms controlling population growth (Center & Spencer, 1981). On the other hand, they also explain why the increase in the biomass loss of *E. crassipes* was associated with increased density.

The P-release estimation based on biomass turnover rates may involve some overestimation. It is well known that several plants re-allocate essential nutrients from moribund leaves (Larcher, 1980). This estimation was based on the P-content of living leaves and thus, it is quite possible that the real P-release due to the macrophytes could be somewhat lower. In *E. crassipes*, the leaves become senescent gradually and are decomposed while still attached to the plant. Therefore the plant has time for the translocation of nutrients (Center & Van, 1989). Nutrient translocation is an energy consuming process, and it is an important feature for plants living under stressing conditions imposed by severe nutrient limitation, as those faced by plants in tropical rain forests or savannas. However, since this plant is typically well adapted to eutrophic environments. It is unlikely that nutrient translocation should be an adaptive advantage for plants living in such environments.

Another important mechanism causing some interference with the nutrient release from dead tissue of macrophytes is microbial immobilization. Reddy &

DeBusk (1991) observed that microbial retention of phosphorus from macrophytes caused an acute reduction of C:P ratios of detrital biomass attached to the root zone of *E. crassipes* in the first 40 days of observations. Nevertheless, these microbial community attached to the root zone of *E. crassipes* is a key factor for the decomposition of these macrophytes, since decomposition rates are faster in the root zone of hyacinth mats than at the sediment water interface (Reddy & DeBusk, 1991). As an example, the microbial flora and fauna attached to young *E. crassipes* plants required only 26 days to recycle its biomass completely in other lakes (Singhol et al., 1993). The decomposition rate will depend strongly on the prevailing metabolism of the attached microbes: aerobic respiration, facultative anaerobic respiration and anaerobic respiration. The aerobic respiration, however, may be the major metabolic pathway of biomass decomposition of dead macrophyte tissue in the root zone (Reddy & DeBusk, 1991).

Conclusions

The higher excretion rates of zooplankton and biomass turnover rates of macrophytes found in this study indicate that the zooplankton community and the macrophyte *E. crassipes* may be the keystone organisms in the internal cycling of phosphorus in Pampulha reservoir. On some occasions, like at the end of the rainy season, both communities were able to recycle as much as 43% d^{-1} of the available phosphorus in lake water. Furthermore, it was also clear that there was a time lag between the maximum of return rates of phosphorus due to these communities. Zooplankton released more phosphorus during the dry season when its biomass was high, whereas the water hyacinths released more phosphorus at the end of their growing season when biomass turnover peaked. This period coincided with the end of the rainy season and a low zooplankton biomass.

The temporal differences in maximum P-release due to zooplankton and macrophytes possibly have important consequences. The regular monitoring program over several years has shown that the phosphorus concentrations in the water usually reach a minimum at the end of the rainy season (Pinto-Coelho, 1998). At this time, the water hyacinth population is recycling more phosphorus. Therefore, the decomposition of macrophyte biomass is not only a major source of phosphorus for the existing biota in the reservoir, but is possibly the most important source of regenerated phosphorus during some periods of the year.

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