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Do phytoplankton fractions < 20 μm dominate in tropical reservoirs independent of their trophy?

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ABSTRACT

Do phytoplankton fractions < 20 μm dominate in tropical reservoirs independent of their trophy?

A spatial and temporal evaluation was made of the contribution of phytoplankton fractions (> 100 μm, 50-100 μm, 20-50 μm, 1.2-20 μm and < 1.2 μm) to total primary production in two shallow tropical reservoirs with different trophy, Ninféias (mesotrophic) and Garças (hypertrophic), located in southeastern Brazil. Material was collected for 14 consecutive months, from November 2000 to December 2001, at different depths. At Ninféias Reservoir, both the total and fractioned production were distinct during rain and dry periods and stratification and mixing processes, which promoted nutrient homogenisation in the system. Light intensity was an inhibitory agent, mainly at the more superficial layers of the reservoir. The phytoplankton fractions varied both spatially and temporally, but algae < 20 μm (nanoplankton) always dominated. At Garças Reservoir, the primary production values were usually greater than those of Ninféias Reservoir, whereas the fractioned production was dominated by algae between 1.2 and 20 μm and was virtually restricted to the reservoir layer between the surface and a depth of 0.5 m. Light was the limiting factor in the latter system as well as the phytoplankton blooms that lasted for the entire study period, affecting light penetration and reducing the extension of the euphotic zone to 0.59 m depth. The primary production temporal variation was influenced by stratification and mixing processes at Ninféias Reservoir. This influence was practically null at Garças Reservoir. The permanent stratification of Garças Reservoir restrained total production to its superficial layer. At Ninféias Reservoir, production was greater at the superficial layer, but the contribution of the lower layers was significant due to the extensive euphotic zone and the occurrence of photo inhibition. Nanoplankton was the most photosynthetically efficient and productive fraction in the latter reservoir, independent of the system's trophy. At Garças Reservoir, light availability was the primary limiting factor, favouring micro and nanoplankton production at the surface. At Ninféias Reservoir, the limiting factors were stratification and mixing processes acting on light and nutrient availability. During the mixing period, however, there was a better distribution of different primary production fractions along the water column.

Key words: Fractioned primary production, shallow tropical urban reservoir, total primary production, trophy.

RESUMEN

¿Dominan las fracciones del fitoplancton < 20 μm en los embalses tropicales con independencia de su estado trófico?

El presente trabajo es una evaluación espacial y temporal de la contribución de las diferentes fracciones del fitoplancton (> 100 μm, 50 a 100 μm, 20-50 μm, 1.2 a 20 μm y < 1.2 μm) al total de la producción primaria en dos embalses tropicales poco profundos, con diferente nivel trófico: Ninféias (mesotrófico) y Garças (hipertrófico), ubicados en el sureste de Brasil. El material fue recogido durante 14 meses consecutivos, entre Noviembre de 2000 y Diciembre de 2001, a diferentes profundidades. En el embalse Ninféias, tanto la producción total como por fracciones, fueron muy diferentes durante los períodos de lluvia y sequía y durante la estratificación y mezcla, que promovió la homogeneización de los nutrientes en el sistema. La intensidad de la luz actúa como un agente inhibidor, sobre todo en las capas más superficiales del embalse. Las diversas fracciones de fitoplancton varían tanto espacial como temporalmente, pero las algas de menos de 20 μm (nanoplancton) dominaron siempre. En el embalse Garças, los valores de producción primaria fueron generalmente mayores que los del embalse de Ninféias, mientras que la producción estaba dominada por las algas de entre 1.2 y 20 μm y se limitaba prácticamente a la capa entre la superficie y 0.5 m de profundidad. La luz fue el factor limitante en este sistema, así como el bloom de fitoplancton durante el período de estudio, afectando a la penetración de la luz y la reducción de la zona eufótica a 0.59 m de *profundidad. Las variaciones temporales en la producción primaria estaban relacionadas con los procesos de estratificación y mezcla en Ninféias. En Garças esta influencia es prácticamente nula, su estratificación permanente restringía la producción a su capa superficial. Aunque la producción en Ninféias también fue mayor en la capa superficial, la contribución de las capas inferiores fue significativa debido a la extensa zona eufótica. El nanoplancton fue la fracción más eficiente y con mayores valores de producción en Ninféias, independiente de su estado trófico. Durante el período de mezcla, sin embargo, hubo una mejor distribución de las diferentes fracciones de la producción primaria a lo largo de la columna de agua. En Garças, la disponibilidad de luz fue el factor limitante para la producción primaria, favoreciendo la producción de micro y nanoplancton en la superficie.*

Palabras clave: *Producción primaria fraccionada, embalse urbano tropical poco profundo, producción primaria total, estado trófico.*

INTRODUCTION

Studies on primary production are essential for aquatic ecosystem characterisation and for allowing the determination of trophic status, which can be affected by anthropogenic action, interfering with water quality (Berman *et al.* 1995).

The phytoplankton productivity vertical distribution is directly affected by allochthonous factors such as light intensity and water transparency, which directly influence phytoplankton photosynthesis through the available energy quality and quantity and, indirectly, through the control of nutrient availability produced by the water stratification and mixing processes. In the same way, phytoplankton position in the water column may be related to community autochthonous factors such as cell-specific density (cell size and shape), which can generate different vertical profiles of phytoplankton productivity (Harris 1978).

Phytoplankton can be divided into size classes that have different physical properties. Picoplankton have the greatest surface:volume ratio compared with nano- and microplankton (Lewis 1976) and may, consequently, more efficiently assimilate nutrients than nano- and microplankton (Lafond *et al*. 1990). Smaller cells usually have greater growth potential (Bruno *et al*. 1983), greater biomass productivity and lower sinking rates (Stockner *et al*. 1987). Picoplankton is, however, the dominant size class in several environments all over the world, both in marine and oligotrophic freshwater environments (Adame *et al*. 2008).

Callieri & Stockner (2002) demonstrated the importance and need for more studies on picoplankton because this fraction may provide clues for carbon production in aquatic systems, including the extreme systems such as those that are frozen or extremely hot.

APP (autotrophic picoplankton, 0.2-2 μm) contributes, according to Sieburth *et al.* (1978), to carbon fixation, with 1-90 % of the total primary production in marine environments and 16-70 % in freshwater environments (Stockner 1988). However, ecological data on fractioned phytoplankton and knowledge of the contribution of each fraction in lacustrine and marine environments are still scarce worldwide, especially for tropical environments.

In Brazil, Tundisi *et al.* (1997) studied four systems of the Doce River Valley (Carioca Pond, Amarela Pond, Dom Helvécio Lake and Jacaré Lake), focusing on total primary production and nanoplankton responses to light intensity variation along the water column at four different times of day. About the total primary production and that of the 20 μm fraction, but for Barra Bonita Reservoir alone there are the studies by Oliveira (1997), Calijuri *et al*. (1999) and Moschini-Carlos & Pompêo (2001).

Emphasis should be put on Roland’s (1998) paper, which compared the participation of different phytoplankton fractions in the productivity of two coastal lagoons with distinct trophies in the State of Rio de Janeiro. Roland (2000) also studied different phytoplankton fractions in impacted and non-impacted parts of

Batata Lake, Pará State, and their participation in the system's total production, observing that the small algae (< 1-35 μm) contributed less to the total production and that those greater than 35 μm were responsible for most of the total production. It is important to mention that algae smaller than 20 μm contributed between 70 and 100 % of the total density during water lowering, low waters and flooding.

Studies have shown that the nanoplankton (< 20 μm) contribution is between 60 and 90 % of the primary production and of the phytoplankton biomass (Roland 1998). However, despite the nanoplankton fraction well-known importance, its contribution to the carbon flux remains poorly investigated in tropical freshwater environments.

In summary, most publications worldwide discuss total primary production, focusing on its spatial and temporal distribution and its relationships with the dominant limnological features. Also, knowledge of tropical phytoplankton productivity of marine environments (including the estuarine) is far greater than that of freshwaters. Finally, the fractioned production in freshwater is almost completely unknown, and what is known is mostly based on the fractionation of chlorophyll *a* (Beaty & Parker 1996).

The present study is an absolutely pioneering work for Brazil, and it aims to evaluate both the spatial and temporal scales of the contributions of different phytoplankton fractions (micro, nano and pico) towards total primary production in two reservoirs with different trophies (one mesotrophic and the other hypertrophic).

STUDY AREA

The reservoirs studied are located in the PEFI, Parque Estadual das Fontes do Ipiranga, Municipality of São Paulo, southeast Brazil (23°38′08″ S-23°40′18″ S, 46°36′48″ W-46°38′00″ W). The Parque has altitudes between 770 and 825 m, and the total area is 526.38 ha. The climate is tropical, and the wind speed is usually low (< 2.5 m s^{-1}). Locally called Ninféias Pond (23°38′18.95″ S, 46°37′16.3″ W) and Garças Pond (23°38′40.6″ S, 46°37′28.0″ W), both systems are, in fact, shallow, warm polymictic reservoirs according to Lewis' classification. A stable stratification is found in summer, and mixing events are more frequent in winter. Ninféias Reservoir's maximum depth is 3.6 m, its maximum length is 187 m, its maximum width is 52.6 m, its volume is 7170 m^3, and its mean residence time is 7.2 days. Garças Reservoir's maximum depth is 4.7 m, its maximum length is 512 m, its maximum width is 319.5 m, its volume is 88.156 m^3, and its mean residence time is 45.4 days. Garças Reservoir is hypertrophic, and Ninféias Reservoir is mesotrophic (D. Bicudo *et al*. 2002).

MATERIAL AND METHODS

Fractioning

The metrical limits used to separate the phytoplankton communities of both systems into size classes were those in Reynolds (1997): microplankton (> 20-100 μm), nanoplankton (< 20-1.2 μm) and picoplankton (< 1.2 μm).

The filtration system consisted of the association of a funnel with cloths of different meshes (Roland 1998) and glass filters, with each system having its own filter set. The separation of phytoplankton size classes was performed by using sequential filtering. The water samples were pre-filtered using monofilament nylon meshes and, immediately after fractioning, by Millipore (mixed cellulose esters) filter membranes of distinct porosities to obtain the microplankton (20-100 μm) and nanoplankton (< 20 μm). The filters then followed the regular analytical procedures for the determination of radioactive carbon (^{14}C) and chlorophyll *a*. To obtain picoplankton (< 1.2 μm), the water samples were directly filtered using Millipore 1.2 μm filter membranes.

Radioactive carbon ^{14}C method

Primary production was determined by using the ^{14}C method according to Steemann-Nielsen (1952), as described in Vollenweider (1974) and Gargas (1975).

The samples were incubated in clear and dark flasks, with 1 ml of $NaH^{14}CO_3$ (radioactivity equivalent to 5 μCi) at the same depths from which material was collected. The samples were collected with a van Dorn sampler, and they were placed horizontally in a proper rack for 3 hours while attached to the support (Teixeira 1973). Afterwards, the samples were taken to the laboratory in isoprene boxes containing ice for further filtration using adequate meshes and filters (Millipore HA, 25 mm diam., 0.45 μm diam. pore). After filtration, dry filters were stocked in a dryer and used for the final determination.

The determination of ^{14}C radioactivity in the filters was processed at the Universidade de São Paulo, after filter dissolution in Bray scintillating liquid (Bray, 1960). Radioactivity values were in counts per minute (CPM) in a liquid Packard model C2425 scintillator.

The Gargas (1975) equation was used to calculate the final amounts of assimilated carbon. To calculate photosynthetic efficiency, it was assumed that 1 mg of carbon is equal to 9.4 cal (Jonasson 1973). The photosynthetic efficiency was calculated according to Vollenweider (1974).

Nutrients and chlorophyll *a*

The samplings were performed monthly from November 2000 to December 2001 at the deepest parts of both reservoirs (Garças Reservoir 4.7 m, Ninféias Reservoir 3.2 m). The samples were taken at 5 depths at Garças Reservoir (subsurface, 1 m, 2 m, 3 m and at about 30 cm from the sediments) and at 4 depths at Ninféias Reservoir (subsurface, 1 m, 2 m and at about 30 cm from the sediments). The water samples ($n = 2$) were gathered with a van Dorn sampler and were transferred to acid-rinsed bottles. In the field, the temperature, pH and conductivity were measured using standard electrodes. The thermal profile was measured every 10 cm. Water transparency was determined by the Secchi disc and euphotic zone (Z_{eu}) according to Cole (1983). The following variables were determined on the sampling day: dissolved oxygen (Winkler modified by Golterman *et al*. 1978), alkalinity (Golterman & Clymo 1969), free CO_2, HCO_3^- and CO_3^- (Mackereth *et al*. 1978), soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) (Strickland & Parsons 1960), total phosphorus (TP) (Valderrama 1981), NO_2^- and NO_3^- (Mackereth *et al*. 1978), NH_4^+ (Solorzano 1969), total nitrogen (TN) (Valderrama 1981) and soluble reactive silica (SRS) (Golterman *et al*. 1978).

To determine the chlorophyll *a* concentration, pigment extraction was done with 90 % ethanol as the organic solvent (Sartory & Grobbelaar 1984).

Statistical analyses

A one-way ANOVA was used to test the differences in contribution of the plankton fractions in the temporal scale. The ANOVA was performed using the MINITAB program (version 14.1). Tukey's multiple comparison technique was adopted to calculate the significance of the differences among the size-fractioned plankton. A CCA (Canonical Correspondence Analysis) was used to evaluate the combined main environmental variables and the fractioned phytoplankton production at both spatial and seasonal scales at the Garças and Ninféias reservoirs. A Monte Carlo Test proved that the correlation among the biological and abiotic matrices was statistically significant (axes 1 and 2, $p = 0.01$).

RESULTS

Limnological features

Ninféias Reservoir is a shallow, slightly turbid system. Light reached the bottom during most of the study period, with $Z_{euaver.} = 2.3$ m for a system with $Z_{max} = 3.2$ m (Fig 1). Table 1 shows the reservoir's limnological features during the present study period. During most months sampled, the underwater radiation went down to a 1.5 m depth. Thermal stratification was observed from January to April and from September to December, whereas a period of mixing took over from May to July (Fig. 2), the Z_{mix} reaching a 2.5-m depth in July. During the mixing period, the DO vertical distribution demonstrated the presence of chemical stratification from January to April and from October to December, although always with anoxia at the bottom (Fig. 3).

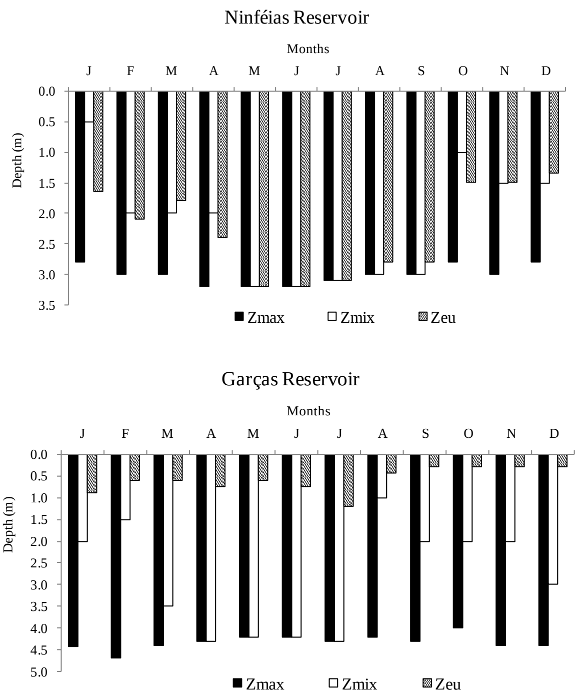

Figure 1. Depth of euphotic zone (Z_{eu}), mixing zone (Z_{mix}) and maximum depth (Z_{max}) at the Ninféias and Garças reservoirs during the study period. *Profundidad de las zonas eufótica (Z_{eu}), de mezcla (Z_{mix}) y profundidad máxima (Z_{max}) de los embalses Ninféias y Garças durante el período de estudio.*

Garças Reservoir is a shallow, highly turbid system, with light penetrating just a few centimetres and $Z_{euaver.}$ = 0.5 m for a system with

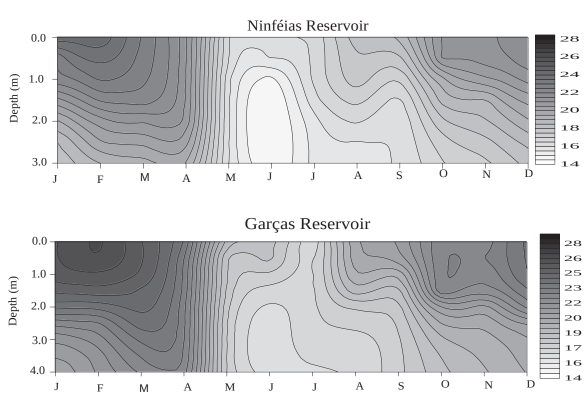

Figure 2. Depth and time diagram of temperature (°C) isolines at the Ninféias and Garças reservoirs during the study period. Note different scales. *Diagrama de profundidad y tiempo de las isolíneas de temperatura (°C) de los embalses Ninféias y Garças durante el período de estudio. Nótese las diferentes escalas.*

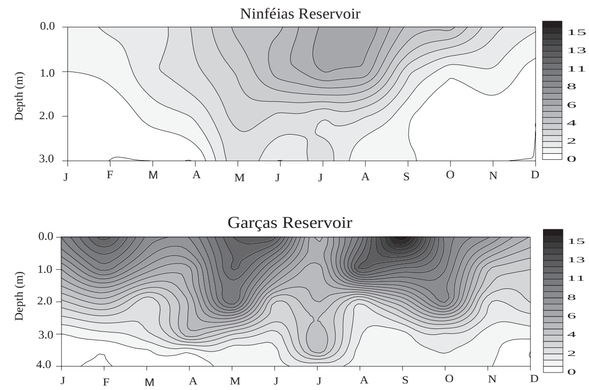

Figure 3. Depth and time diagram of dissolved oxygen (mg L^{-1}) isolines at the Ninféias and Garças reservoirs during the study period. *Diagrama de profundidad y tiempo de las isolíneas de oxígeno disuelto (mg L^{-1}) de los embalses Ninféias y Garças durante el período de estudio.*

Z_{max} = 4.5 m (Fig. 1). Table 1 shows the reservoir's limnological features during the present study period. Thermal stratification was observed during most of the sampled months, except for July, when Z_{mix} reached 3 m deep (Fig. 2). The DO vertical distribution also showed chemical stratification during the entire study period, with greater values at the surface and anoxia at the bottom (Fig. 3).

Phytoplankton chlorophyll *a*

Phytoplankton chlorophyll *a* showed a homogeneous distribution from May to July at Ninféias

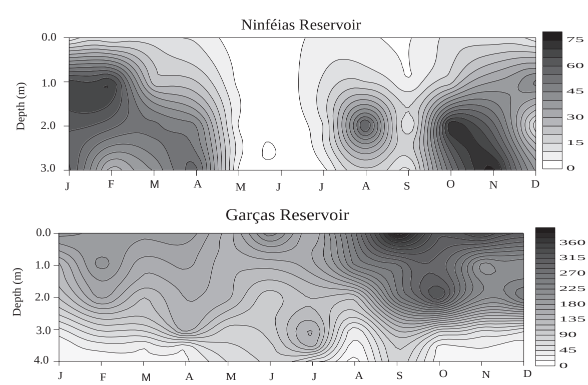

Figure 4. Depth and time diagram of the phytoplankton chlorophyll-a (μg L^{-1}) isolines at the Ninféias and Garças reservoirs during the study period. Note different scales. *Diagrama de profundidad y tiempo de las isolíneas de clorofila a (μg L^{-1}) del fitoplancton de los embalses Ninféias y Garças durante el período de estudio. Nótese las distintas escalas.*

Table 1. Limnological features average values for Ninféias (mesotrophic) and Garças reservoirs (hypertrophic). *Valores promedios de las características limnológicas de los embalses Ninféias (mesotrófico) y Garças (hipertrófico).*

	J	F	M	A	M	J	J	A	S	O	N	D
Garças Reservoir												
pH	7.5	7.9	6.9	6.8	7.3	7.5	7.3	7.7	7.8	8.2	7.5	7.8
Conductivity (μS cm^{-1})	248.2	267.4	255.3	316.7	219.1	230.1	222.3	234.9	250.9	222.6	245.6	240.7
Turbidity (NTU)	21.8	25.2	21.8	22.9	16.5	17.8	17.9	18.0	20.9	21.5	20.9	23.7
Alcalinity (mEq L^{-1})	1.4	2.2	1.8	2.3	1.4	1.1	1.0	0.9	0.9	2.3	1.2	1.3
DO (mg L^{-1})	3.3	4.6	3.4	4.2	6.5	4.5	4.4	4.6	5.8	5.4	2.8	2.2
Free CO_2	26.7	39.2	42.5	53.5	11.1	5.4	22.5	8.5	6.3	14.6	15.3	18.9
N-NO_2 (μg L^{-1})	11.8	4.4	8.3	29.6	30.8	14.4	32.6	25.0	13.5	2.3	6.8	7.6
N-NO_3 (μg L^{-1})	1.5	40.3	10.0	62.5	75.3	73.1	82.0	90.0	36.5	0.0	0.0	0.1
N-NH_4 (μg L^{-1})	6256.4	6762.6	4039.5	10619.1	2814.2	4613.2	3957.8	3944.3	2521.7	3355.9	5555.0	4606.9
TN (μg L^{-1})	4124.2	2681.3	6602.1	12488.9	4203.6	19323.5	5755.4	9614.5	5143.6	4535.0	3951.7	3747.4
P-PO_4 (μg L^{-1})	25.4	36.4	28.1	55.4	0.2	0.3	3.6	59.0	4.1	59.5	112.4	123.4
TDP (μg L^{-1})	50.3	56.9	56.7	91.9	19.4	15.1	27.0	100.9	25.4	100.3	147.2	46.9
TP (μg L^{-1})	503.5	312.4	316.3	378.8	166.4	179.9	175.9	260.9	258.7	440.6	488.7	509.5
Silicate (mg L^{-1})	3.9	2.8	3.6	3.0	2.3	1.2	2.1	1.6	2.2	2.2	2.5	3.6
Ninféias Reservoir												
	J	F	M	A	M	J	J	A	S	O	N	D
pH	6.1	6.1	6.1	6.2	6.1	6.3	6.4	6.4	6.4	6.1	6.3	6.1
Conductivity (μS cm^{-1})	84.4	95.6	164.3	105.1	56.1	58.0	53.1	52.2	59.4	73.3	91.9	80.6
Alcalinity (mEq L^{-1})	16.6	16.4	15.3	14.8	16.8	15.0	13.8	14.4	14.2	16.9	14.4	14.0
Turbidity (NTU)	0.5	1.0	0.8	1.0	0.4	0.3	0.3	0.3	0.3	1.0	0.5	0.6
DO (mg L^{-1})	0.6	0.6	1.2	1.8	3.5	3.5	4.4	3.9	2.2	1.3	1.2	0.5
Free CO_2	44.7	87.6	75.7	69.9	27.4	16.9	10.9	11.6	12.5	78.6	28.0	45.5
N-NO_2 (μg L^{-1})	4.5	11.4	10.1	9.4	8.0	3.9	6.0	0.8	2.0	10.3	4.8	7.7
N-NO_3 (μg L^{-1})	7.9	42.8	6.2	27.3	106.3	21.3	6.1	0.0	1.3	64.4	2.9	3.7
N-NH_4 (μg L^{-1})	269.1	265.0	681.6	879.7	27.1	91.8	40.3	57.6	11.5	507.5	687.8	332.4
TN (μg L^{-1})	210.6	579.2	654.7	1248.6	295.9	376.3	310.0	367.5	541.7	687.8	23.3	266.1
P-PO_4 (μg L^{-1})	4.2	3.6	0.6	0.0	0.0	0.0	0.0	0.0	0.0	8.8	18.7	2.7
TDP (μg L^{-1})	13.7	21.1	17.0	17.1	4.9	3.9	5.0	5.5	4.7	8.8	18.7	18.3
TP (μg L^{-1})	36.4	39.1	28.2	40.0	22.3	18.4	13.4	60.3	22.7	50.2	54.6	43.1
Silicate (mg L^{-1})	4.1	3.1	2.8	3.3	2.7	2.3	2.9	2.2	3.0	2.7	4.2	7.1

Reservoir, but it was highly heterogeneous during the remaining study period (Fig. 4). Emphasis must be put on the occurrence of the greater biomass values in the lower layers of the reservoir, with its greatest value measured in October at a depth of 3 m (78 μg L^{-1}). At Garças Reservoir, the superficial layers always presented the greatest biomass values, especially in September (406 μg L^{-1}).

Total primary production

The total primary production followed, in general, the underwater radiation penetration in the water column in both reservoirs, exponentially decreasing with increasing depth (Figs. 5-6).

At Ninféias Reservoir, the total primary production presented a heterogeneous vertical distribution during the period January-March and August-December, tending, however, to homogeneity from May to July (Fig. 7). In contrast, Garças Reservoir's total primary production presented a heterogeneous vertical distribution during the entire study period, except for July, when it showed a slight homogeneity. It was also verified that production was detected at the bottom of Ninféias Reservoir for several months (February-March, August and November). However, photo-

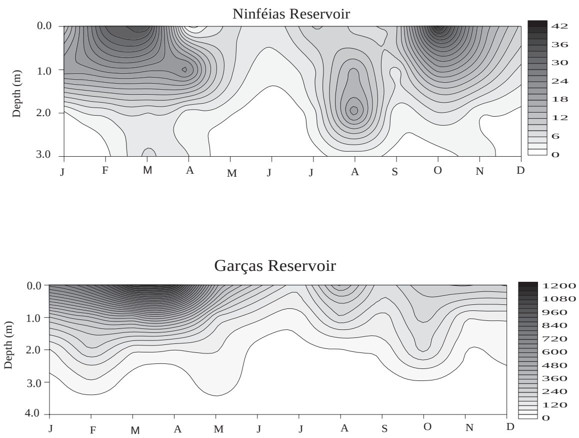

Figure 5. Total primary production values (mgC L^{-1} h^{-1}) along the water column of the Ninféias and Garças reservoirs during the study period. Note different scales. *Valores de producción primaria total (mgC L^{-1} h^{-1}) a lo largo de la columna de agua de los embalses Ninféias y Garças durante el período de estudio. Nótese las diferentes escalas.*

synthetic activity at Garças Reservoir was only detected down to a 2 m depth.

Vertical scale values smaller than those measured for the deepest layers were detected in January, April and August at the surface of Ninféias Reservoir. These results indicate the occurrence of photo-inhibition at the surface of the system, but a similar condition was not observed at Garças Reservoir. In the latter reservoir, the average values of primary production decreased steadily from 0.5 m down to the bottom of the system during all months sampled (Fig. 7).

Based on the total primary production maximum and average values, it was observed that

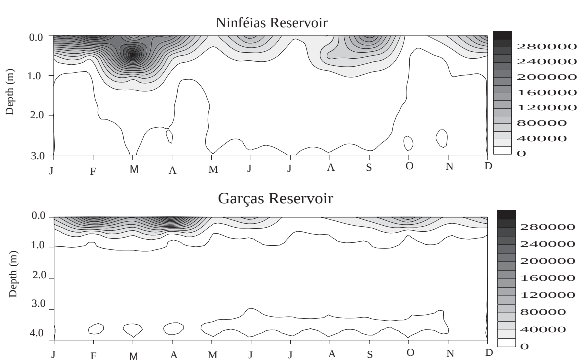

Figure 6. Depth and time diagram of underwater radiation (μmol s^{-1} m^{-2}) isolines at the Ninféias and Garças reservoirs during the study period. *Diagrama de profundidad y tiempo de las isolíneas de radiación subacuática (μmol $s^{-1}m^{-2}$) de los embalses Ninféias y Garças durante el período de estudio.*

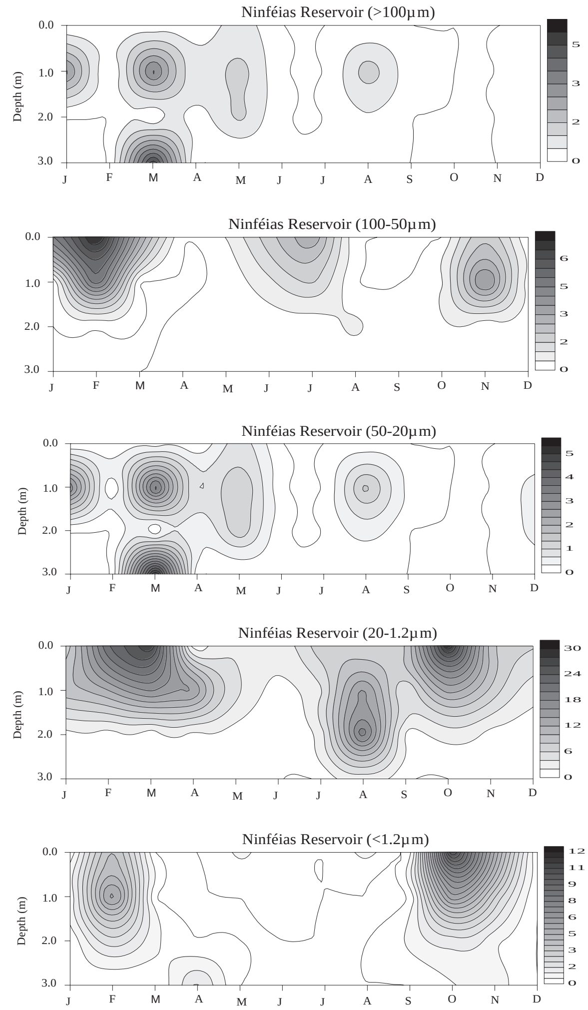

Figure 7. Fractionated primary production (mgC L^{-1} h^{-1}) of cells > 100 μm, 50-100 μm, 20-50 μm, 1.2-20 μm and < 1.2 μm along the water column of Ninféias Reservoir during the study period. *Producción primaria fraccionada (mgC L^{-1} h^{-1}) de células > 100 μm, 50-100 μm, 20-50 μm, 1.2-20 μm y < 1.2 μm a lo largo de la columna de agua del embalse Ninféias durante el período de estudio.*

the surface was the reservoir layer presenting the greatest production in both systems studied. Garças Reservoir's superficial layer was 31.6 times more productive than that of Ninféias, with the maximum values registered in April and October (respectively, 1618.5 mgC m^{-3} h^{-1} and 40.9 mgC m^{-3} h^{-1}).

The total primary production showed a positive and significant correlation with underwater solar radiation at Garças Reservoir (r = 0.64-0.97). At Ninféias Reservoir, there was no significant correlation in January, April and August (< -0.3), but there was a positive and significant correlation (r = 0.78-0.94) during all other months studied.

Fractioned primary production at Ninféias Reservoir (mesotrophic)

Regarding spatial and temporal scales, it was noted that the primary production rate of microplankton > 100 µm was greater at the deeper layers (> 1 m), mainly in March (Fig. 7). For total primary production, however, that of algae > 100 µm varied by 9 % on average, its greatest contribution being measured in March (71 % at the bottom).

Microplankton measuring 50 to 100 µm presented higher primary production rates at the surface (Fig. 7), with the greatest values being registered in January (4.5 mgC m^{-3} h^{-1}) and February (7.2 mgC m^{-3} h^{-1}). The production of 50-100 µm microplankton was, as a rule, greater at the surface than at all other depths of the reservoir. On the annual scale, the production amplitude varied from 1.7 mgC m^{-3} h^{-1} at the reservoir surface to 0.11 mgC m^{-3} h^{-1} at its bottom. For total primary production, fractions above the contribution varied from 6.1 to 14.5 %.

Microplankton measuring 20-50 µm showed greater primary production values between depths of 0.5 and 1.5 m, with the greatest occurring in April (10.8 mgC m^{-3} h^{-1}) and January 2001 (8.7 mgC m^{-3} h^{-1}) at a 1-m depth (Fig. 7). The total primary production of the present fraction varied from zero to 76 %, its greatest contribution being observed in March at a 3-m depth.

Among all phytoplankton fractions studied, that of nanoplankton (1.2-20 µm) presented the greatest primary production values (Fig. 7) in most sampling units collected. This fraction production peak was observed at the surface of the system in October and March, respectively, at 29.9 mgC m^{-3} h^{-1} and 27.6 mgC m^{-3} h^{-1}. In relation to total primary production, nanoplankton contribution varied from 21 to 100 % (average 56 %).

The lowest primary production values at Ninféias Reservoir were due to the picoplankton, *i.e.*, to the algae < 1.2 µm (Fig. 7). The greatest value (10.6 mgC m^{-3} h^{-1}) was detected at the reservoir's surface in October. Regarding total primary production, the picoplankton contributed 6.7 at the reservoir bottom to 7.5 % at the surface, with its greatest contribution (40 %) registered in February at a 2 m depth.

The primary production of different phytoplankton fractions was significantly distinct (ANOVA: $F = 19.00$, $p > 0.0000$), but only that of nanoplankton (1.2-20 µm) was considered significantly different from all the others according to the Tukey test ($p > 0.05$). Also, the primary production of the mixing period at Ninféias was less, but the nanoplankton maintained their high representation.

Photosynthesis efficiency at the Ninféias Reservoir reached its maximum of 2.65 % in October for an average primary production of 0.36 % (Tab. 2).

Table 2. Photosynthetic efficiency relative values for Ninféias (mesotrophic) and Garças reservoirs (hypertrophic). *Valores de eficacia fotosintética relativa para los embalses Ninféias (mesotrófica) y Garças (hipertrófica).*

	Ninféias Reservoir (mesotrophic)					Garças Reservoir (hipertrophic)				
	> 100	100-50	50-20	< 20	< 1.2	> 100	100-50	50-20	< 20	< 1.2
January	0.00	0.00	0.00	0.00	0.00	0.00	5.57	43.87	68.76	5.20
February	0.00	0.00	0.00	0.02	0.00	0.00	0.24	0.52	3.95	0.00
March	0.01	0.00	0.02	0.03	0.00	0.00	0.50	1.16	2.70	0.36
April	0.00	0.01	0.00	0.04	0.01	0.00	0.43	0.23	0.71	0.00
May	0.00	0.02	0.03	0.12	0.00	0.09	0.54	0.54	1.32	0.00
June	0.00	0.00	0.03	0.05	0.00	0.00	0.08	0.25	0.76	0.00
July	0.05	0.01	0.02	0.13	0.00	0.12	0.75	1.20	3.40	0.16
August	0.00	0.01	0.00	0.01	0.00	0.00	0.07	0.35	0.53	0.39
September	0.00	0.07	0.03	0.23	0.00	0.00	1.21	0.68	4.25	1.80
November	0.07	0.00	0.00	1.08	0.00	0.00	1.85	0.46	2.36	0.13
October	0.00	0.00	0.01	0.02	0.00	0.00	0.12	0.20	1.23	0.18
December	0.12	0.00	0.42	2.13	0.00	0.00	0.00	0.00	0.91	0.00

For the distinct fractions, it was observed that the greatest efficiency was that of the 1.2-20 μm fraction, which presented its maximum (0.29 %) in October.

Fractioned primary production at Garças Reservoir (hypertrophic)

At Garças Reservoir, microplankton > 100 μm presented their greatest primary production in February at the system's surface (306 mgC m^{-3} h^{-1}), with the production detected only at the surface layer during the warmer months of the year (Fig. 8). The contribution of the latter fraction to total primary production varied from 10.9 to 1.9 %.

The primary production of microplankton fraction 50-100 μm showed an average value of 77.9 mgC m^{-3} h^{-1} at the surface, but it gradually decreased towards the reservoir bottom (Fig. 8). This fraction's greatest contributions were registered in January (157.6 mgC m^{-3} h^{-1}) and March at the reservoir surface (263.05 mgC m^{-3} h^{-1}), and they decreased vertically down to a 2-m depth from January to September. In relation to the total primary production, microplankton contribution varied between 0 and 29 %, particularly in March.

The microplankton fraction 20-50 μm presented a clear vertical distribution down to a 2-m depth from January to May (Fig. 8). This fraction's maximum production occurred in January (207 mgC m^{-3} h^{-1}) and March (359.9 mgC m^{-3} h^{-1}). Compared to the total primary production, this fraction's contribution varied from zero to 39 %.

Nanoplankton (1.2-20 μm) was the most representative fraction at Garças Reservoir in terms of total primary production, at both the vertical and temporal scales (Fig. 8). This fraction's maximum production value (852.5 mgC m^{-3} h^{-1}) was registered in April at the surface. June and July were the months of least total primary production. The nanoplankton, however, maintained their greatest representativeness among all fractions. In regard to total primary production, the nanoplankton contribution was 60.8-85.8 %.

The picoplankton (< 1.2 μm) primary production was detected only in January (17.3 mgC m^{-3} h^{-1}) and August (13.24 mgC m^{-3} h^{-1}) at the surface. Compared with the total primary production, this fraction's contribution was greatest at 3 %, and it was the least representative of all fractions in the reservoir (Fig. 8).

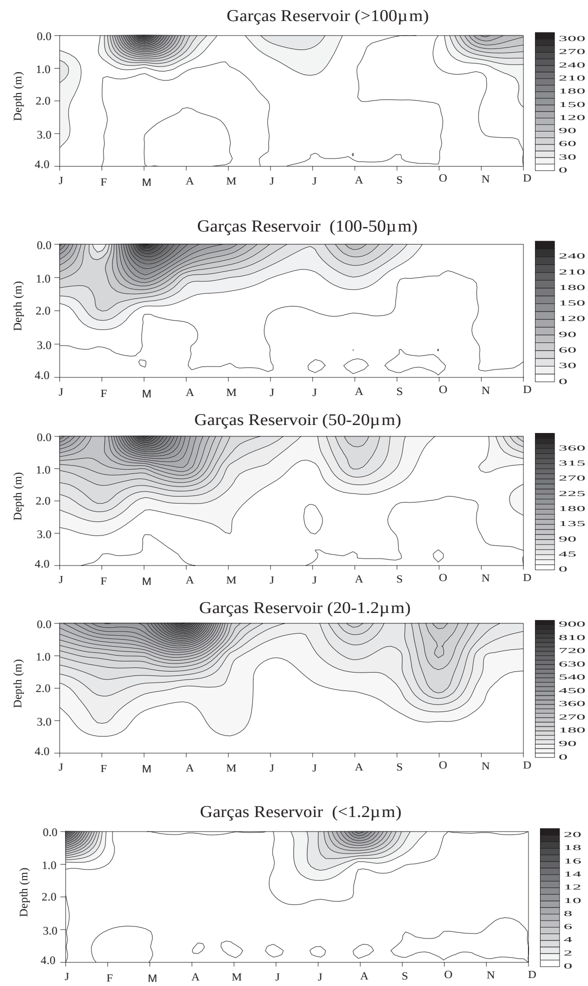

Figure 8. Fractionated primary production (mgC L^{-1} h^{-1}) of cells > 100 μm, 50-100 μm, 20-50 μm, 1.2-20 μm and < 1.2 μm along the water column of Garças Reservoir during the study period. *Producción primaria fraccionada (mgC L^{-1} h^{-1}) de células > 100 μm, 50-100 μm, 20-50 μm, 1,2-20 μm y < 1,2 μm a lo largo de la columna de agua del embalse Garças durante el período de estudio.*

Comparatively, the most representative fraction in terms of total primary production was that of nanoplankton, followed by that of microplankton 20-50 μm (21-100 %), > 100 μm (0-53 %) and 50-100 μm (0-39 %).

The primary production of phytoplankton fractions was considerably different (ANOVA: $F = 7.48$, $p = 0.000$), but only nanoplankton (1.2-20 μm) showed a significantly different production when compared with the production of all other fractions according to the Tukey test ($p > 0.05$). The nanoplankton contribution to total primary production was the greatest (52.7-97.6 %). The total annual production of Garças Reservoir was 111.9 gC m^{-2} yr^{-1}, from which 81.2 gC m^{-2} yr^{-1} represented that of the nanoplankton, with 80 % of the total photosynthetic efficiency.

The photosynthetic efficiency at Garças Reservoir presented an exceptional value of 112.16 % in November (Tab. 1). During the entire remaining period, however, these values varied from 0.99 to 7.82 %. Considering the distinct phytoplankton fractions, it was observed that the greatest efficiency was that of nanoplankton (67 %), followed by microplankton 50-20 µm (3.6 %) and microplankton 50-100 µm (1 %). During most months studied, however, the nanoplankton always showed the greatest photosynthetic efficiency.

Canonic correspondence analysis

A CCA was performed with 4 environmental variables and the primary production of 5 plankton fractions (Fig. 9). The eigenvalues of axis 1 ($\lambda = 0.096$) and axis 2 ($\lambda = 0.037$) explained 28.2 % of the total data variation. The Monte Carlo test demonstrated that the correlation between biological and abiotic matrices was statistically significant for axes 1 and 2 ($p = 0.01$). The

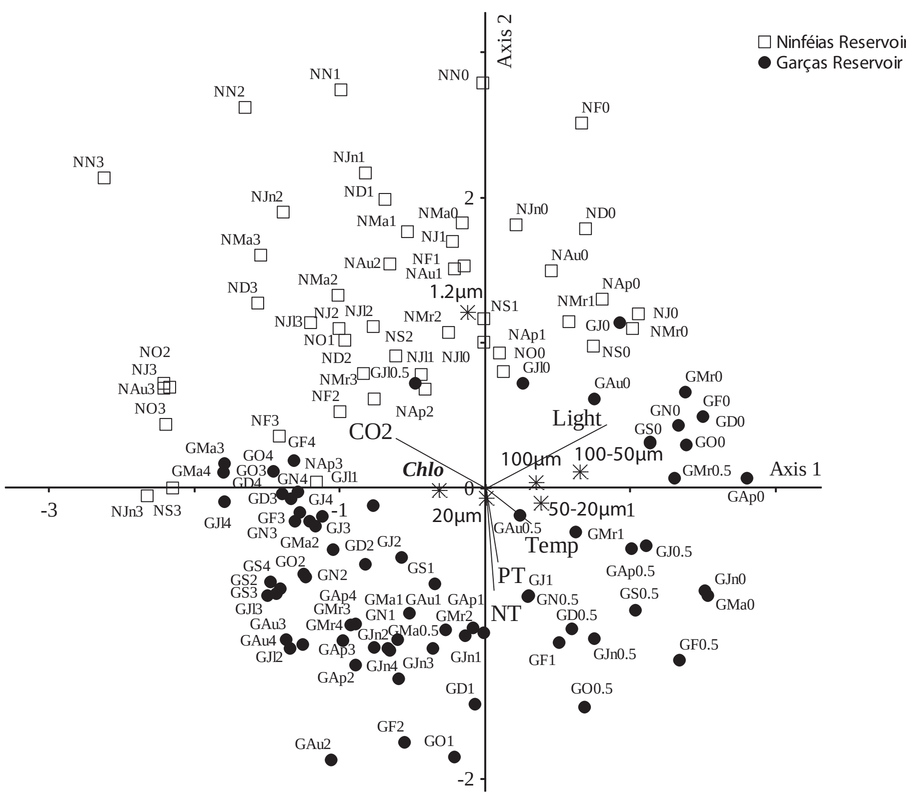

Figure 9. CCA ordination of the Garças and Ninféias reservoirs' sampling units based on phytoplankton biomass and primary production data (5 fractions and 5 environmental variables). Abbreviations: *sampling units* = first letter indicates the reservoir (N = Ninféias, G = Garças), second letter the calendar month, and the number the sampled depth (0 = surface, 0.5 m, 1 m, 2 m, 3 m and 4 m); *Vectors*: NT = total nitrogen, PT = total phosphorus, luz = light; Temp = temperature. *Ordenación por el ACC de las muestras de los embalses Garças y Ninféias con base en datos de biomasa y producción primaria del fitoplancton (5 fracciones y 5 variables ambientales). Abreviaciones: unidades de muestreo = primera letra indica el embalse (N = Ninféias, G = Garças), segunda letra, mes del año y el número, la profundidad muestreada (0 = superficie, 0.5 m, 1 m, 2 m, 3 m and 4 m); Vectores: NT = nitrógeno total, PT = fósforo total, luz = luz; Temp = temperatura.*

Table 3. Canonic coefficient and Pearson correlation of environmental variables with CCA axes 1 and 2. *Coeficiente canónico y correlación de Pearson de las variables ambientales con los ejes 1 y 2 del ACC.*

	Canonic coeficient		Pearson Correlation	
Variable	Axis 1	Axis 2	Axis 1	Axis 2
Total nitrogen	0.295	0.928	0.015	−0.829
Total phosphorus	0.031	0.491	0.010	−0.634
Free CO_2	−0.234	0.566	−0.606	0.352
Light	0.879	0.628	0.839	0.490
Temperature	0.319	0.503	0.429	−0.254

canonic coefficients for axis 1 showed that light availability was the most important environmental variable for ordination along that axis (Tab. 3).

The environmental variables correlated to axis 1 pointed to a spatial gradient. The sample units of the Garças and Ninféias reservoirs' more superficial layers were ordinated at the positive side of the axis; all others were at its negative side. The microplankton fraction's (50-100 μm and 20-50 μm; $r > 0.6$) primary production was correlated to Garças Reservoir's more superficial layers, whereas that of the picoplankton was more correlated to the Ninféias Reservoir's more superficial layers. The nutrient concentration (NT and PT) and free CO_2 weighted considerably towards the ordination of axis 2, thus distinguishing the two reservoirs. It was also noted that there was a great affinity of the picoplankton fraction to the Ninféias Reservoir's sampling units, whereas the nanoplankton fractions showed a low correlation to the canonic axes due to their great participation in the reservoirs and their strata.

DISCUSSION

The Ninféias and Garças reservoirs are small, shallow tropical reservoirs located in the same basin, though they present highly distinct limnological conditions. Ninféias Reservoir is mesotrophic (D. Bicudo *et al*. 2002), and during the entire study period it showed an extensive euphotic zone, stratification and mixing for different periods. Garças Reservoir, in contrast, is hypertrophic (Bicudo *et al.* 2005), and it has presented three different limnological phases since 1997 (Bicudo *et al.* 2007, Fonseca & Bicudo 2008, Crossetti & Bicudo 2008). The present sampling period occurred after the removal of 90 % of the water surface macrophytes, which Bicudo *et al*. (2007) called phase III (September 1999 to December 2004). This phase was characterised by abrupt limnological changes in the system, which led to a significant increase in chlorophyll *a*, TP, pH and SRP and a drastic decrease in water transparency, free CO_2 and DO at the deepest layers of the reservoir (Bicudo *et al.* 2007, Crossetti & Bicudo 2008). In the present study, Garças Reservoir was identified as having a permanent thermal and chemical stratification, high phytoplankton biomass and light penetration not surpassing a depth of 0.5 m.

The total primary production presently registered for the two reservoirs confirms their trophic classification of D. Bicudo *et al*. (2002, 2007) calculated according to the Carlson Trophic State Index, as modified by Toledo. The average primary production at Ninféias Reservoir was 262.78 mgC m^{-2} day^{-1}, and at Garças Reservoir, it was 5675.45 mgC m^{-2} day^{-1}. According to Likens (1975), a system is oligotrophic when its production is in the 50-300 mgC m^{-2} day^{-1} range, is mesotrophic in the 250-1000 mgC m^{-2} day^{-1} range and is eutrophic in the 600-8000 mgC m^{-2} day^{-1} range.

Primary production in tropical systems is, in general, much greater than in temperate systems, mainly because of the phytoplankton's high photosynthesis capacity in the first systems (Amarasinghe & Vijverberg 2002). Referring to tropical systems, the primary production at Ninféias Reservoir presented values nearly identical to those registered for shallow mesotrophic systems in Tundisi *et al*. (1997), but greater than those registered for shallow oligotrophic systems in Pompêo (1996) or deep systems in Tundisi *et al*. (1997). In contrast, the production registered for Garças Reservoir (hypertrophic) was greater than that referred to for eutrophic lakes in Tundisi (1983). Consequently, based on primary production, the Ninféias and Garças reservoirs were classified as mesotrophic and hypertrophic, respectively.

Spatially, the total primary production at Ninféias Reservoir (mesotrophic) was greater at the upper layers. However, due to the extended euphotic zone, the lower layers were also metabolically active. Photo inhibition may explain the high primary production in the lower layers in January, April and August. Photo inhibition at the surface of a tropical system has already been registered by Henry *et al.* (1998) and Jureidini *et al.* (1983) and of a temperate system by Taylor & Gebre-Mariam (1989). At a temporal scale, despite good light penetration, underwater radiation intensity decreased during the mixing period, and, as a consequence, the total primary production also substantially decreased. Consequently, the present results indicate that light availability was not considered a primary production-limiting factor, but at the temporal scale, the stratification and mixing processes controlled primary production in the reservoir.

Garças Reservoir's euphotic zone was restricted to a few centimetres due to the very intense cyanobacteria bloom, which decreased light availability to the lower layers. According to D. Bicudo *et al.* (2007), the cyanobacteria's permanent bloom maintains the reservoir's degraded steady state. Under such hypertrophic conditions, the reservoir's superficial layer is responsible for the system's total primary production. At the temporal scale, during the cooler months (June and July), there was a decrease of primary production due to lower solar radiation intensity, particularly in July (reduction of 89 %). Consequently, the permanent thermal and chemical stratification was controlled and kept by the intense cyanobacteria bloom (D. Bicudo *et al.* 2007), thus making light availability the limiting factor, which is fundamental for primary production at both the spatial and the temporal scales. Other studies in tropical reservoirs also point out light availability as the limiting factor for primary production (Calijuri *et al.* 1999, Oliveira 1997).

In the present study, nanoplankton effectively registered the best fraction in terms of primary production and photosynthetic efficiency, independent of the system's trophy at the superficial layer of Garças Reservoir, whereas picoplankton were at the superficial layer of Ninféias Reservoir. Also, microplankton were more abundant at Garças Reservoir and picoplankton at the Ninféias Reservoir. The annual total primary production at Garças Reservoir was 111.9 gC m^{-2} yr^{-1}, from which 81.2 gC m^{-2} yr^{-1} represented the nanoplankton production, and the photosynthetic efficiency was 80 % of the total. However, the distribution of the fractioned primary production varied considerably at both the temporal and the spatial scales in the two reservoirs.

The total primary production at Ninféias Reservoir was directly related to exponential light attenuation, being affected by the stratification and mixing regimen that, in turn, interfered with the plankton fraction distribution. The lower layers (< 1 m) were considered metabolically active, and the primary production of the nanoplankton, together with that of the > 100 μm and the 50-20 μm microplankton, were very much representative. The high photosynthetic biomass below a 1-m depth also suggested the high metabolism of the lower layers in January, April and August, with the greatest total primary production occurring in the 1-m layer due to photo inhibition at the surface. Under the latter condition, micro- and nanoplankton were the fractions responsible for most of the primary production. In general, nanoplankton dominated in terms of production, followed by the 20-50 μm microplankton, 50-100 μm microplankton, picoplankton (< 1.2 μm) and, finally, > 100 μm microplankton (nano $\rightarrow$ $\text{micro}_{20-50\ \mu m}$ $\rightarrow$ $\text{micro}_{50-100\ \mu m}$ $\rightarrow$ pico $\rightarrow$ $\text{micro}_{>100\ \mu m}$).

Garças Reservoir's superficial layers were responsible for almost the entire primary production because the euphotic zone was restricted to a few centimetres and the light penetration was significantly reduced by the enormous phytoplankton biomass (cyanobacteria blooms). The primary production detected at the bottom of the reservoir was approximately 1 %, due, most probably, to the heterotrophic bacterioplankton activity. As a rule, nanoplankton also dominated in terms of primary production, followed by the 20-50 μm microplankton, 50-100 μm microplankton, picoplankton (< 1.2 μm) and, finally, >100 μm microplankton (nano $\rightarrow$ $\text{micro}_{50-100\ \mu m}$ $\rightarrow$ $\text{micro}_{20-50\ \mu m}$ $\rightarrow$ pico $\rightarrow$ $\text{micro}_{>100\ \mu m}$).

Crossetti & Bicudo (2008) reported the dominance of *Planktothrix agardhii* (Gomont) Komárek & Anagnostidis from January to

March, followed by multi-specific blooms of Cyanobacteria (*Aphanizomenon gracile* (Lemmermann) Lemmermann, *Microcystis panniformis* Komárek *et al*., *Microcystis aeruginosa* (Kützing) Kützing, *Cylindrospermopsis raciborskii* (Woloszyńska) Seenayya & S. Raju and *Planktothrix agardhii*) from April to September and, again, the dominance of *Planktothrix agardhii* in November and December at Garças Reservoir (Fonseca & Bicudo 2010, Crossetti & Bicudo 2008). *Planktothrix agardhii* presented filaments of a large range of sizes (26-269 μm long), consequently being included in the fractions from nano- to microplankton. The primary production of different phytoplankton fractions usually reflects the species composition at the reservoir's superficial layers and that, during the cyanobacteria's multispecies bloom described in Crossetti & Bicudo (2008), the primary production comprised the contributions of different phytoplankton fractions.

Comparing the influence of stratification and mixing processes on the primary production of the different plankton fractions, it was observed that the reservoir trophy defined the plankton metabolism. On one side, the stratification and mixing processes at Ninféias Reservoir affected the primary production of distinct fractions differently. Despite the high primary production of the nanoplankton during the mixing period, there was an increase in the microplankton's primary production, probably due to the plankton resuspension, whereas the reservoir lower layers were metabolically active during the stratification months.

During the period May-September 2001, the Z_{eu} reached the two reservoirs' greatest depths, coinciding with the mixing of the water column, suggesting a displacement of organisms along the water column. Phytoplankton displacement in the water column is also affected by the cell's morphological characteristics and the organism's size, but high radiation intensity may also act as a photo inhibitor at the reservoir surface, pushing production to the lower depths (Fig. 9).

In contrast, at Garças Reservoir, the stratification was permanent, and it maintained high primary production only in the superficial layers, where the plankton fraction's production was variable. Along the entire study period, Z_{eu} showed at the Garças Reservoir an average depth of 0.59 cm, reaching its maximum depth (1.20 m) in July 2001, the greatest primary production values being measured within that reservoir layer. During the same period, Z_{mix} also reached its greatest depths associated with the lower temperatures and the greatest system stability (Fig. 9). Small individual cells were much more efficient during this period.

Photosynthetic efficiency allows comparison among different systems because it relates biomass concentration, primary production and local radiation in terms of percentages (Tilzer & Amazaza 1975). Comparatively, photosynthetic efficiency was much greater at Garças Reservoir than at the Ninféias Reservoir, with nanoplankton being the most efficient fraction in the two reservoirs.

In summary, the primary production temporal variation was influenced by stratification and mixing processes at Ninféias Reservoir, but that influence was practically null at Garças Reservoir. In terms of spatiality, the permanent stratification of Garças Reservoir restrained the total production to its superficial layer, whereas at Ninféias Reservoir, production was greater at the superficial layer, although the contribution of the lower layers was also significant. At Ninféias Reservoir, the lower layers were active in terms of metabolism due to the extended euphotic zone and to the occurrence of photo inhibition. In this reservoir, nanoplankton was the most photosynthetically efficient and productive fraction, independent of the system's trophy. At Garças Reservoir, light availability was the primary production limiting factor, favouring micro and nanoplankton production at the surface. In contrast, the primary production-limiting factors at Ninféias Reservoir were the stratification and mixing processes, which interfered with light and nutrient availability. During the mixing period, there was a better distribution of different primary production fractions along the water column. Consequently, in both tropical systems studied, the results suggest that reservoir trophy determined photosynthetic efficiency and total primary production, but it was not intimately associated with a specific plankton fraction.

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