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Bacterioplankton and phytoplankton production in seven lakes in the Middle Rio Doce basin, south-east Brazil

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Abstract

The purpose of this study was to measure the phytoplankton production (PP) and bacterial production (BP) simultaneously in seven lakes in the middle Rio Doce basin (southeast Brazil) during the dry and the rainy seasons. Limnological monitoring was conducted from 1999 to 2001 as well as both PP (radioactive carbon fixation) and BP (^{3}H-Leucine incorporation) in four specific depths (100%, 10%, 1% of incident radiation, and aphotic zone). Furthermore, trophic state of the lakes was analyzed, considering the index proposed by Salas and Martino (1991) and Carlson (1977). In general, some parameters increased during the rainy season such as pH, conductivity, chlorophyll and total nitrogen. In the period of 1999/2000, the rain caused PP reduction in the lakes, excepting Carioca and Águas Claras Lake, but in the years 2000/2001, the lakes did not show a similar pattern. In contrast, the rainy season of both years caused an expressive bacterioplankton production enhancing. Using Salas and Martino index, we observed that some lakes were affected by the seasonal runoff, therefore the typologie of these lakes changed from oligotrophic to mesotrophic conditions, otherwise considering the Carlson index all lakes were classified as eutrophic in both dry and rainy seasons. Indeed, Salas and Martino index demonstrated to be more appropriate to determine the trophic status of the lakes. Finally, our data indicate that until now, in spite of the lakes location, protected and unprotected area, the lakes still maintain their natural characteristics.

Keywords: Lakes; Trophic state; Phytoplankton; Bacterioplankton; Primary production; Bacterial secondary production

Introduction

The study of trophic interactions between bacterioplankton and phytoplankton as well as the relations between these communities and the abiotic matrix has experienced considerable progress with the studies conducted by Pomeroy (1974) and Azam et al. (1983). Afterwards, some studies have indicated an existence of a coupling between bacteria and phytoplankton (Cole et al., 1988; Lind et al., 1997; Ochs et al., 1995), since algal carbon exudate might be the principal source for bacterial production. Nevertheless, bacterioplankton

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community also utilizes a considerable part of the dissolved organic carbon (DOC) available within aquatic ecosystems, besides absorbing inorganic nutrients thus competing with phytoplankton community (Hobbie, 1988). In addition, the importance of terrigenous carbon (Cole & Pace, 1994; Wetzel, 1995; Jonsson et al., 2001; Biddanda & Cotner, 2002; Pålsson et al., 2005) and aquatic macrophyte carbon have been reported (Rooney & Kalff, 2003; Huss & Wehr, 2004) to lake metabolism, which support secondary production. Indeed, the relative importance of each mechanism responsible for the regulation of bacterioplankton production (BP) within a lake (Kisand et al., 1998; Tammert et al., 2005).

Even now, studies focusing simultaneously on phytoplankton and bacteria remain scarce in tropical aquatic ecosystems (Carvalho et al., 2003) and there are questions in relation to the several and complex mechanisms which regulate functioning and diversity of planktonic and interactions between algae-bacteria communities (Le et al., 1994; di Sierve et al., 1995; Mariazzi et al., 1998; Reche et al., 1998). However, it is plausible to assume that nutrients concentration, mainly C, N and P, constitutes an important factor determining primary and secondary production in tropical lakes.

We have investigated the bacterioplankton production (BP) and phytoplankton production (PP) in protected and unprotected lakes, situated in the middle Rio Doce basin (southeast Brazil). We have considered that PP varies seasonally (dry and rainy seasons), as well as BP, resulting in changes of BP/PP ratio. Lower temperatures and the higher input of allochthonous material during the rainy season might influence the autotrophic and the heterotrophic activities. The relationship between bacterioplankton and PP has not been investigated in the lakes of this area yet.

The initial knowledge of these lakes began in the decade of 70 and an important detailed description of the lake systems in the area could be found by Tundisi and Saijo (1997). Some of these lakes, about 40, are located inside the Rio Doce State Park (Minas Gerais State) and are included in one of the largest Brazilian freshwater systems which are composed by about 140 lakes. This area is biologically significant as a water source for human population and for biological diversity that represents a refuge for fauna and flora.

Limnological data were determined for the understanding of factors that controls the bacterioplankton/phytoplankton relationship. The trophic state of the lakes was analyzed considering the index proposed by Salas and Martino (1991) and Carlson (1977), in as much as typology is an important tool for lake management and the development of strategies for conservation and its implementation.

Studied area

This investigation was carried out in lakes of Rio Doce State Park (Parque Estadual do Rio Doce, PERD) and its surroundings, including areas exposed to different anthropogenic impacts (domestic and industrial effluents; cattle raising). The State Park is surrounding by large plantations of *Eucalyptus* spp. and degraded pastureland. The PERD was founded in 1944 and it is located in the middle stretch of the Rio Doce basin (southeast Brazil) with an area c. 36,000 ha (19°29′24″–19°48′18″S; 42°28′18″–42°38′30″W), and protects the largest remnant of the original Atlantic forest in the State of Minas Gerais (Fig. 1).

According to Köppen system (1936), the climate can be classified as tropical wet and dry (A_w), with a rain season in the summer and a dry season during the months of May, June, July and August. The annual mean precipitation and the annual mean temperature are about 1300 mm and 23 °C, respectively (CETEC, 1978).

About 40 lakes were found inside the PERD area which does not show any communication with the Doce River, covering about 9% of the State Park area (Petrucio and Barbosa, 2004), situated about 300 m above the sea level. The park limits are defined by Doce River and Piracicaba River on the east and north, respectively. The Timóteo and Mariliéria districts delineate the park extension on the west and by south through Dionísio district.

Ultisol, eutrustox and alfisols are the most representative kinds of soils found in the park area (Silva Jr. et al., 1995). The relief is dominated by soft contours, as hills and sedimentary flat valleys, with altitude varying from 230 to 515 m. About 21% of the area of the Park corresponds to flat relief, whereas, lightly and strongly undulated montains represent 39% and 34%, respectively (CETEC, 1982).

Two lakes were selected within the PERD (Dom Helvécio and Carioca) and five lakes in its surroundings (Amarela, Águas Claras, Barra, Jacaré, and Palmeirinha). Dom Helvécio Lake is the largest and deepest lake of the system (6.87 km^2; 32.5 m) open to tourism and offering fishing, swimming, and rowing. Carioca Lake (0.13 km^2; 11.8 m) is not open to the public, exhibiting more preserved conditions. Among the lakes of the surroundings, Amarela Lake is the smallest and shallowest (0.11 km^2; 2.0 m) and colonized by a dense community of floating and submerged macrophytes. Águas Claras Lake is situated in an area of eucalyptus plantation, demonstrating low human impact and oligotrophic features. Palmeirinha Lake suffers direct influence of a charcoal plant and Barra Lake and Jacaré Lake, besides surrounded by eucalyptus plantations also holds fishing clubs, receive intermittent loads of untreated domestic sewage (Petrucio and Barbosa, 2004).

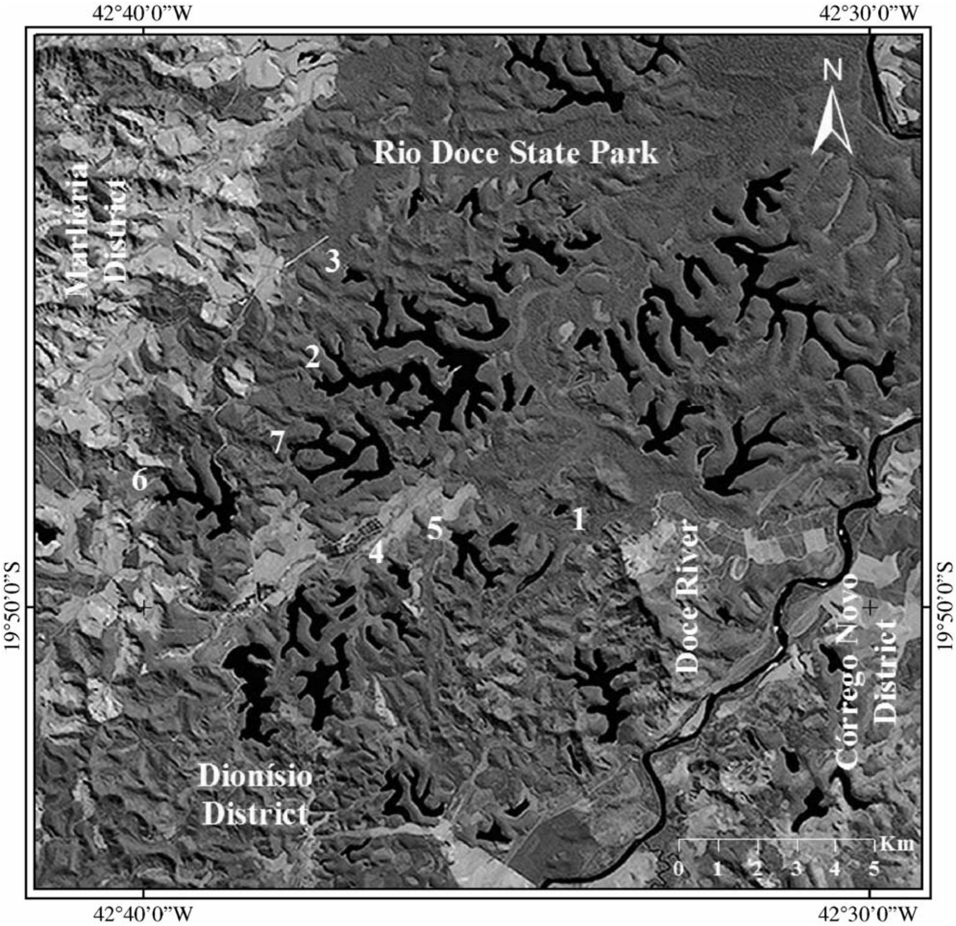


Fig. 1. Location of sampling sites in the middle of Rio Doce basin (MG, Brazil).

Materials and methods

Samplings were performed in 1999–2001, during dry (July 1999 and 2000) and rainy periods (February 2000 and 2001) always during morning hours and at a central station in each lake. A light profile (radiometer Li-Cor, model Li-193SA) along the water column was characterized in each lake and determined four sampling depths (100%, 10%, 1% of light incident and one point in aphotic zone) for production estimates. Water temperature, conductivity, pH and dissolved oxygen (DO) were measured in situ with a multiprobe (Horiba, model U-22) and total alkalinity by titration (Mackereth et al., 1978).

Water samples from the above mentioned depths were carried to the laboratory to determine DOC (TOC-5000 Shimadzu), total nitrogen (Mackereth et al., 1978) and total phosphorus (Golterman et al., 1978). Chlorophyll-*a* concentrations were measured after filtration onto glass fibre membranes (Schleicher & Schuell GF 50-A) and extraction with 90% acetone (Lorenzen, 1967).

PP was measured using the ^{14}C technique (Steemann-Nielsen, 1952). In situ incubations were carried out in dark and in transparent 70-ml-bottles, for 3–4 h with $NaH_{14}CO_3$ (0.5 ml/2 μCi) at 100%, 10%, 1% of light incident and the aphotic zone. In the laboratory, two subsamples from each bottle were taken (initial, dark and transparent). Activity (dpm) was measured in Bray cocktail (Bray, 1960) in a Liquid Scintillation Analyzer (Packard, Tri-carb 2100TR).

Immediately after sampling, BP from 100%, 10%, 1% of light incident and the aphotic zone was measured in the laboratory by incubating 1.3 ml water samples ($n = 3$) in the dark with L-[4,5-^{3}H] Leucine (TRK 510, 142Ci/mmol), final concentration of 10 nM, for 40 min at 25 °C. Carbon incorporation was estimated after multiplying protein (estimated through leucine incorporation) by 0.86 (Smith & Azam, 1992). Activity (dpm) and it was measured in Bray cocktail (Bray, 1960) in a Liquid Scintillation Analyzer (Packard, Tri-carb 2100TR).

Principal component analysis (PCA) was applied and the following variables were used in the matrix:

temperature, pH, conductivity, DO, total alkalinity, TP, TN, DOC and Chl *a*. The effects of seasons (dry × rainy season) upon BP and PP, as well as the interaction between both factors and nutrient concentrations, were tested with a factorial ANOVA.

Results

The summer sampling, which corresponds to the rainy season in Brazil, was especially marked by the enhancing of water temperature, conductivity, alkalinity, and chlorophyll, but some variable did not show the same trend (Table 1). For instance, the variation between the summer and winter pH and oxygen values was negligible, in spite of the slight increase of maximal values during the rainy season. Phosphorus and DOC concentration were similar in both seasons; otherwise precipitation (summer) had a positive effect on chlorophyll and nitrogen concentration. In Amarela Lake, the nitrogen concentration was about two-fold higher in summer than in winter. Other lakes had a smaller improvement of nitrogen concentration, even so it was considerable, and e.g., in Dom Helvécio Lake the nitrogen concentration increased nearly 20%.

The results indicated that the water temperature was not influenced by the lake depht. We observed high temperatures in the shallow Amarela Lake (1.5 m) and in the deep Dom Helvécio Lake (25 m), but all lakes exhibited thermal stratification. In winter, temperatures below 25 °C prevailed. As the solar energy increases from autumn through summer, the lakes started getting warm, revealing high water temperatures (an increase on average of 5 °C). Besides, Amarela Lake showed a pronounced difference between minimal and maximal temperature values in the dry season, keeping high water temperature during the rainy season. However we obtained the higher temperatures in other lakes as Palmeirinha (31.0 °C) and Jacaré (31.4 °C).

The pH varied from 5.2 at Palmeirinha Lake in the dry season to 7.8 at Jacaré Lake in the rainy season. However, comparing the seasons (dry and rainy), we could not distinguish a considerable difference of pH values, but the highest pH values were measured during summer, following the alkalinity tendency, suggesting higher microbial decomposition in the water column. It seems that anthropogenic forces did not have effect on the pH, since preserved and unpreserved lakes showed similar values of pH.

The alkalinity in all lakes was low, demonstrating the soft characteristic of water, since the lake water comes mainly from precipitation and from the runoff of the basin. We observed a substantial increase due to the precipitation, as long as, the alkalinity was two times lower in the dry season than in the rainy one. Total alkalinity was higher at Amarela Lake (1.1 meq $CO_2\,l^{-1}$) and lower values (0.1 meq $CO_2\,l^{-1}$) were found in Carioca, Palmeirinha, and Dom Helvécio Lakes.

In summer, the DO concentration decreased approximately 20%, excepting Dom Helvécio Lake situated in the protected area. In this case, the oxygen concentration in summer was 30% higher than in winter. In some lakes, the measured oxygen concentration was near to the anoxy (Carioca and Palmeirinha Lakes). The variation in DO concentration occurred seasonally and with depth; we founded in all lakes over-saturation of oxygen in the water surface, but in some ecosystems in the deeper areas, the DO was depleted.

Chlorophyll concentration fluctuated over the annual cycle; low values occured in the winter and high values in the summer, excepting Carioca Lake, which was not influenced by the season. Summer observations were about three times higher than in winter. The minimal chlorophyll-*a* concentration was measured at Barra Lake during the dry season (1.9 $\mu g\,l^{-1}$) and the maximal at Amarela Lake during the rainy period (260.9 $\mu g\,l^{-1}$).

Phosphorus, nitrogen and DOC concentration were influenced by either dry and rainy seasons, but in distinct ways without a clear tendency. In most of the lakes, total phosphorus and DOC concentration reduced during the summer, especially, in Dom Helvécio and Águas Claras Lakes. Nevertheless, in average we have not observed a strong variation in phosphorus concentration. In Amarela Lake, phosphorus concentration varied from 12.6 to 61.6 $\mu g\,l^{-1}$ in the dry season and from 14.0 to 59.2 $\mu g\,l^{-1}$ in the rainy season. Indeed, nitrogen seems to be more affected by the season than phosphorus and DOC. In Amarela Lake, in the winter, nitrogen concentration was two times lower than in summer. For the other lakes, nitrogen concentration decreased between 10% to 50%.

The highest N and P concentrations were recorded in deeper layers and during the stratification period and all lakes showed a clear phosphorus limitation ($N_{total}/P_{total} > 9$) except for a single value recorded in Barra Lake during the rainy period of 2001 at depth corresponding to 1% of incident light.

Considering the Salas and Martino index, the trophic state of the lakes varied considerably (Table 2). For instance, Dom Helvécio, Águas Claras, Jacaré and Barra were classified as oligotrophic in both dry and rainy seasons. However, Carioca and Palmeirinha Lakes exhibited oligotrophic conditions during the dry season becoming mesotrophic during the rainy season and the shallow Amarela Lake was classified invariably as mesotrophic. On the other hand, the Carlson index indicated all lakes as eutrophic.

Depth profiles for phytoplankton and bacterial production are shown, respectively in Table 2. Primary production was not related to the depth or the light incident. We have measured the lowest phytoplankton

Table 1. Minimal and maximal values, during dry and rainy seasons from 1999 to 2001, of depth, temperature, pH, electrical conductivity, dissolved oxygen, chlorophyll-*a*, and nutrient concentrations in seven lakes of middle Rio Doce basin

Lakes	Max. depth (m)	Temp. (°C)	pH	Conductivity ($\mu S\,cm^{-1}$)	D.O ($mg\,l^{-1}$)	Alkalinity ($meq\,l^{-1}$)	Chl-*a* ($\mu g\,l^{-1}$)	Tot-P ($\mu g\,l^{-1}$)	Tot-N ($\mu g\,l^{-1}$)	DOC ($mg\,l^{-1}$)	N/P
Dry[a]											
Amarela	1.5	18.5–26.0	5.6–6.7	59–111	1.8–6.6	0.3–0.7	3.2–40.1	12.6–61.6	617–1.206	4.7–9.3	13.9–54.5
Dom helvécio	25.0	22.5–25.2	5.4–6.0	34–55	0.9–6.5	0.1–0.4	2.9–7.2	6.5–16.7	674–1.181	3.5–4.9	62.3–107.5
Carioca	8.0	20.4–24.7	5.4–6.3	25–46	2.8–7.3	0.1–0.3	18.7–76.6	22.4–35.8	269–2.058	4.8–5.6	12.1–65.2
Palmeirinha	6.0	21.6–24.8	5.2–6.7	31–48	1.7–8.5	0.1–0.3	25.8–131.5	9.1–26.9	546–1.257	6.2–7.4	31.6–124.7
Águas Claras	8.0	21.8–24.5	5.5–6.7	33–64	4.7–9.0	0.2–0.3	16.8–33.9	11.6–29.5	363–957	5.9–7.3	24.8–47.7
Jacaré	9.0	21.3–24.1	5.4–7.2	31–63	5.0–9.3	0.2–0.3	6.4–24.9	18.7–29.7	312–841	5.3–6.2	14.6–36.7
Barra	8.0	21.6–24.5	5.6–6.6	46–73	2.4–8.1	0.2–0.5	1.9–25.9	18.6–25.6	660–1.194	3.6–5.8	25.8–59.8
Rainy[a]											
Amarela	2.0	26.5–29.4	5.6–6.6	73–435	0.5–6.9	0.7–1.1	23.0–260.9	14.0–59.2	343–3.019	6.8–20.1	8.9–64.3
Dom helvécio	30.0	23.0–30.9	5.9–7.4	36–93	0.6–9.0	0.3–0.5	8.0–78.1	2.1–12.7	270–2.015	0.6–3.9	31.3–200.1
Carioca	10.0	23.0–30.5	5.7–7.4	27–125	0.0–7.7	0.2–0.7	8.6–79.7	10.4–40.1	213–2.320	2.9–6.1	20.4–75.5
Palmeirinha	7.0	25.8–31.0	5.3–7.2	28–135	0.0–7.0	0.2–0.5	9.6–179.1	11.9–43.2	326–2.232	2.8–11.0	27.2–55.0
Águas Claras	9.0	25.6–30.5	5.5–6.9	39–155	2.4–8.4	0.3–0.6	9.8–137.4	3.0–19.6	337–1.688	5.5–7.0	31.8–111.6
Jacaré	9.0	26.4–31.4	5.8–7.8	35–151	0.5–8.9	0.3–0.5	9.4–63.6	12.6–25.2	395–1.333	3.8–6.9	20.8–81.0
Barra	8.0	26.0–30.9	5.7–7.7	41–105	0.7–6.6	0.3–0.8	10.4–39.8	13.4–34.8	171–1.928	3.9–12.0	6.9–55.4

[a]Precipitation varied between 0.0 mm (July 1999, 2000) and 59.2 mm (January 2000) (data obtained from Instituto Mineiro de Gestão das Águas–IGAM/SIMGE).

Table 2. Trophic state of seven lakes in the middle of Rio Doce region (south-east Brazil) during July 1999–January 2001

Lake	Trophic state index			
	Salas and Martino (1991)		Carlson (1977)	
	Dry	Rainy	Dry	Rainy
Amarela	Mesotrophic	Mesotrophic	Eutrophic	Eutrophic
Dom Helvécio	Oligotrophic	Oligotrophic	Eutrophic	Eutrophic
Carioca	Oligotrophic	Mesotrophic	Eutrophic	Eutrophic
Palmeirinha	Oligotrophic	Mesotrophic	Eutrophic	Eutrophic
Águas Claras	Oligotrophic	Oligotrophic	Eutrophic	Eutrophic
Jacaré	Oligotrophic	Oligotrophic	Eutrophic	Eutrophic
Barra	Oligotrophic	Oligotrophic	Eutrophic	Eutrophic

production at Dom Helvécio Lake ($0.3\,mg\,C\,m^{-3}\,h^{-1}$) during the rainy period of 2001 and the highest at Carioca Lake ($747.4\,mg\,C\,m^{-3}\,h^{-1}$) during the dry period of 2000. In general, the phytoplankton assemblage of the lakes had a higher production in the seasons of 2000/2001 than during the period of 1999/2000. In 1999/2000, in average, the less productive was Jacaré Lake ($2.2\,mg\,C\,m^{-3}\,h^{-1}$, rainy season) and Palmeirinha Lake was the most productive ($69.1\,mg\,C\,m^{-3}\,h^{-1}$, dry season), but in 2000/2001, these same lakes had a primary production of 46.5 and $41.5\,mg\,C\,m^{-3}\,h^{-1}$, respectively. In the first sampling period, the lakes had higher production in the dry season, excepting Carioca and Águas Claras Lake. This pattern changed in 2000/2001 when the rainy caused an enhancing of the primary production, principally in Jacaré and Amarela lakes, where the PP increased about 2.5 and 3.2, respectivelly, contrasting with Carioca and Barra lakes. In these lakes, the PP was higher in the dry season.

In contraposition to PP, we observed that most of the lakes had lower BP production in 2000/2001 than in 1999/2000. In average, the decrease of BP was near to 25% whereas PP increased 2.3 times during the same period. However, in Carioca and Barra Lakes, BP production increased from 0.34 to $0.63\,mg\,C\,m^{-3}\,h^{-1}$ and from 0.18 to $0.30\,mg\,C\,m^{-3}\,h^{-1}$, respectively. We measured the lower and higher secondary production in the shallow Amarela Lake in the rainy season of 1999/2000, 0.5 and $3{,}520.2\,\mu g\,C\,m^{-3}\,h^{-1}$ (Table 3).

In general, the rain caused a considerable enhancing on bacterial production, excepting for Amarela Lake in 1999/2000, where the BP production increased from 1.02 to $1.05\,mg\,C\,m^{-3}\,h^{-1}$, and for Carioca Lake in 2000/2001. In this case, the BP decreased from 0.86 to $0.40\,mg\,C\,m^{-3}\,h^{-1}$. The effect of the rainy season on plankton of the PERD lakes is more evident observing the BP/PP ratio (Table 4). In 1999/2000, no effect was observed in the Águas Claras and Carioca lakes, contrasting with other lakes as Dom Helvécio, Palmeirinha and Jacaré, where the ratio was significantly improved. Otherwise, comparing the dry and rainy seasons of 2000/2001, all lakes presented an increasing in BP/PP ratio, excepting Amarela Lake.

The result of PCA analysis is shown in Fig. 2 and the sampling periods were treated separately. For the period 1999/2000, the first two axes (principal component 1 and 2) of the PCA explained 70% of the total data variance. DO concentration was negatively with the first axis and conductivity, alkalinity, chlorophyll-*a*, total phosphorus, and dissolved carbon positively (43%). Temperature and BP were positively correlated with axis 2 (27%) (Fig. 2A). In the period of 2000/2001, the first two axis of the PCA explained 51% of total variance and we observed two groups. The first group, alkalinity and total nitrogen was positively correlated with the first axis (28%), whereas, the second group, chlorophyll-*a* and primary production was positively correlated with axis 2 (23%) (Fig. 2B).

In the first period (1999/2000) the effect of seasonality was well marked with the formation of two distinct groups: the first formed by the lakes during the dry period and the second one, with the lakes in the rainy period (Fig. 2C). However, in the second period (2000/2001) such division was not observed since all lakes were close to the origin and exhibited low percentage of explanation (Fig. 2D).

Discussion

The lakes are characteristically warm-monomictic with destratification beginning in May, exhibiting isothermal conditions in winter (July/August) and starting to stratify again in late September (spring), affecting, in the water column, the distribution pattern of DO and nutrient concentrations (Barbosa et al., 1989). As observed in other water bodies in both temperate and tropical zone, this phenomenon occurs because of the increase of water temperature in response to seasonal changes in air temperature and radiant heating. The sun radiation warms the upper water layers causing the lake stratification and the nutrients

Table 3. Phytoplankton production and bacterioplankton production measured in seven lakes of the middle Rio Doce basin (Minas Gerais. Brazil) at four depths during the dry and the rainy seasons[a]

	Amarela		Dom Helvécio		Carioca		Palmeirinha		Águas claras		Jacaré		Barra	
Phytoplankton production ($mg\,C\,m^{-3}\,h^{-1}$)														
Light incident (%)	Dry season/1999 and rainy season/2000													
100	5.8	**17.3**	9.0	4.9	23.8	28.7	47.1	20.5	7.4	7.6	15.7	3.0	50.4	26.3
10	**18.9**	15.0	15.3	**14.4**	**69.2**	27.1	91.2	21.4	**23.5**	4.4	**52.2**	**5.1**	**58.7**	26.6
1	10.9	1.1	**70.0**	3.7	41.1	**218.5**	**100.7**	**76.1**	20.5	**39.7**	8.9	1.0	18.9	**64.8**
0	7.6	0.8	0.3	1.1	22.1	11.3	1.7	0.6	4.6	29.5	17.9	1.4	4.0	2.5
	Dry season/2000 and rainy season/2001													
100	**51.7**	**151.7**	15.4	**28.0**	523.5	**16.3**	**107.4**	24.7	35.7	16.9	34.6	57.8	153.2	**35.5**
10	29.9	146.8	**24.9**	15.2	**747.4**	14.4	58.1	43.3	**70.4**	24.4	**35.0**	**108.9**	**179.1**	35.4
1	24.4	127.9	1.5	3.5	19.8	3.9	24.9	**177.8**	7.0	40.6	7.2	35.2	6.70	6.7
0	31.6	11.7	3.1	0.4	15.6	2.1	3.8	0.5	0.4	**46.8**	4.5	1.5	1.5	3.0
Bacterioplankton production ($\mu g\,C\,m^{-3}\,h^{-1}$)														
Light incident (%)	Dry season/1999 and rainy season/2000													
100	754.4	0.5	179.1	525.3	**654.9**	451.6	**680.2**	**1094.5**	125.4	525.3	**111.6**	451.6	**200.3**	**690.5**
10	632.8	10.3	**294.5**	609.0	123.0	452.2	47.2	764.1	**791.1**	609.0	97.5	452.2	3.3	12.5
1	**1337.9**	**3520.2**	240.6	**748.9**	37.7	**877.4**	24.2	585.4	383.7	**748.9**	28.6	**877.4**	16.7	351.0
0	1373.3	683.7	198.6	29.2	75.7	34.3	46.1	461.9	331.2	29.2	31.2	34.3	58.6	125.2
	Dry season/2000 and rainy season/2001													
100	325.0	577.2	**11.7**	**459.6**	**1840.6**	**1270.9**	**140.1**	**951.9**	**119.6**	285.2	**182.1**	**1115.5**	**244.7**	**1118.9**
10	199.2	52.8	5.3	86.1	109.2	133.8	82.7	281.5	8.3	499.6	8.5	106.9	68.6	193.0
1	292.1	674.4	5.0	19.9	283.0	120.5	40.9	256.6	20.1	**905.8**	39.2	133.4	50.8	602.5
0	**377.1**	**1272.0**	7.6	61.4	1220.7	62.7	33.8	548.3	7.2	901.7	26.9	33.3	75.0	118.7

[a]Maximal values in bold.

Table 4. Bacterioplankton/phytoplankton production ratio (BP/PP), during dry and rainy periods in seven lakes in the middle of Rio Doce basin (south-east Brazil)

Lake	1999/2000		2000/2001	
	Dry	Rainy	Dry	Rainy
Amarela	0.095	0.123	0.009	0.006
Dom Helvécio	0.010	0.079	0.001	0.013
Carioca	0.006	0.006	0.002	0.043
Palmeirinha	0.003	0.025	0.002	0.008
Águas Claras	0.029	0.024	0.001	0.020
Jacaré	0.003	0.173	0.003	0.007
Barra	0.002	0.010	0.001	0.025

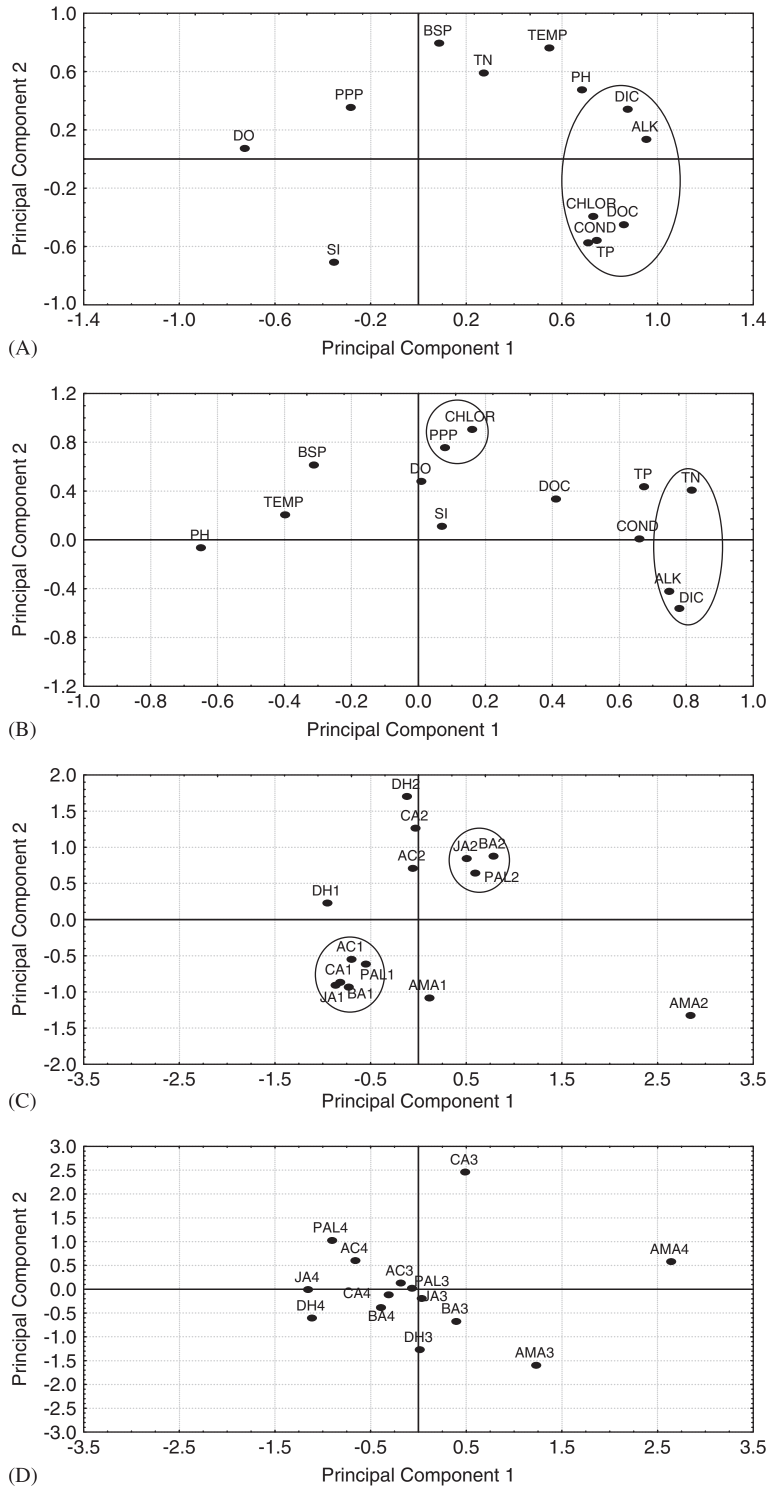
Values represent the average of the incubations at four depths (100%, 10%, 1% of light incident and aphotic zone).

regenerated in the deeper layers of the water column by heterotrophic organisms remain in the cold water. Considering the lakes do not have any communication with Doce River and, i.e., the inflow from a tributary does not exist and they are shallow, we assume that in the PERD area the wind is the principal force to mix the water column in these continental lakes, promoting isothermal conditions, influencing the primary and secondary production.

The production of the lakes

Previous estimations of PP in Carioca Lake (Barbosa & Tundisi, 1980; Barbosa et al., 1989) reported values between 0.08 and 10.9 $mg\,C\,m^{-3}\,h^{-1}$ for the dry period (winter) and between 0.03 and 1.25 $mg\,C\,m^{-3}\,h^{-1}$ in the rainy season. Tundisi et al. (1997) measured primary production rate varying from 0.1 to 1.7 $mg\,C\,m^{-3}\,h^{-1}$ in Dom Helvécio Lake; from 0.4 to 14.6 $mg\,C\,m^{-3}\,h^{-1}$ in Carioca Lake; from 4.7 to 65.5 in Amarela Lake and from 0.1 to 2.3 $mg\,C\,m^{-3}\,h^{-1}$ in Jacaré Lake, during the dry season. These values were similar to those observed by Henry et al. (1997) in Carioca and Dom Helvécio Lakes.

We have observed similar pattern (higher production rates during the dry season), when the lakes are destratified and the availability of nutrients is greater along the water column. Nevertheless, this tendency was not common for all lakes, mainly during the period of



*AMA = Amarela; DH = Dom Helvécio; CA = Carioca; PAL = Palmeirinha; AG = Águas Claras; JA = Jacaré; BA = Barra..
**1 = first sampling dry 1999; 2 = rainy 2000; 3 = dry 2000; 4 = rainy 2001.
***TEMP = temperature; PH = pH; COND = conductivity; DO = dissolved oxygen, ALK = total alkalinity, TN = total nitrogen; TP = total phosphorus; DOC = dissolved organic carbon; CHLOR = Chlorophyll a; BP = bacterial production; PP = primary production.

Fig. 2. Correlation of biotic and abiotic parameters with the first two axes of principal component analysis (A, B) and score distributions of lakes sampled in dry and rainy seasons along the first two principal components axes (C, D).

2000/2001 and the magnitude of primary production can vary considerable. In the dry period of 2000, phytoplankton production in Carioca Lake reached 747.4 mg C m^{-3} h^{-1}, decreasing to 16.3 mg C m^{-3} h^{-1} in the next season. High primary production has been reported for tropical lakes, about 290 mg C m^{-3} h^{-1} (Erikson et al., 1998), but Brazilian reservoirs have shown to be more productive (Calijuri and Dos Santos, 2001). Our results indicate a significant increase of the PP of all lakes in the last decade, even considering only the sampling time. In average, from 1999/2000 to 2000/2001, the primary production increased nearly three times, indicating the conspicuous anthropogenic influence on the lakes, even those located in the State Park area, leading to the eutrophication, as suggested by Tundisi and Saijo (1997).

The highest carbon fixation rates were recorded at depths corresponding to 10% and 1% of light incident of 1999/2000 period for both seasons, whereas, some lakes such as Amarela and Palmeirinha (Table 3) had high primary production at the superficial layer water. The occurrence of photo-inhibition at the surface layers was observed in some of these lakes, as demonstrated previously by Barbosa and Tundisi (1980). Even though, solar radiation, which includes photosynthetically active radiation (PAR) and UV radiation, which is able to degrade photolytically refractory DOC, becoming it available to primary producers. This excessive UV radiation can cause substantial damage on phytoplankton organisms (Arts & Rai, 1997; Sinha & Häder, 2002; Hernando & Ferreyra, 2005). However, the effect of solar radiation on phytoplankton and bacterioplankton still remain unclear (Xenopoulos & Schindler, 2003).

The BP recorded was high, reaching 3.5 mg C m^{-3} h^{-1} and can be considered high when compared with the ones recorded in temperate for oligotrophic and eutrophic lakes (Kisand et al., 1998; Furtado et al., 2001), temperate for humic lakes (Jonsson et al., 2001; Drakare et al., 2002) or tropical lagoons (Furtado et al., 2001). However, they are in the same magnitude that those measured by Petrucio et al. (2005) and Petrucio and Barbosa (2004) in rivers and lakes, respectively, in the middle Rio Doce basin and by Erikson, Vammen, Zelaya, and Bell (1999) in the tropical Lake Xolotlán (Nicaragua).

Our results indicated there was not a coupling between phytoplankton and bacterioplankton and no positive correlation was observed between nutrient concentrations and bacterial production. However, it is more common to observe correlation between nutrients and PP (Le et al., 1994; Vrede, 1996).

In contrast to PP, the rainy season (summer) had a marked stimulating effect on bacterioplankton. This fact and the uncoupling between PP and BP implies that the dominance of plankton community changed as a result of the season, corroborating Pomeroy and Wiebe (2001), then, the summer can be characterized as heterotrophic season and the winter as autotrophic season, explaining the higher values of BP/PP in the rainy season (Table 4).

We do not know exactly the mechanism that controls the BP and PP in the lakes yet, which has distinguishable characteristics, but more detailed and long-term studies are necessary since changes in the precipitation patterns of the region with significant consequences for the effects of seasonality as observed for the second year of sampling. Indeed, BP/PP ratio did not vary systematically with the depth.

However, nutrient condition is important since the TP/TN ratio influence the biomass and the diversity of the phytoplankton assemblage and the relationship bacteria-phytoplankton depend of the species composition (Kõiv & Kangro, 2005) and the BP/PP ratio is often used as an index to determine the amount of carbon fixed by phytoplankton that is processed by heterotrophic bacteria (Van Wambeke et al., 2002). In addition, the relatively high BP/PP ratios during the rainy season suggest that bacterioplankton production was more dependent on external nutrients input from the watershed than PP.

The trophic state of the lakes

Various indices are accessible for evaluating the trophic state of inland lakes. Carlson index (Carlson, 1977) has been widely used to determine the nutrient conditions of lakes temperate, mainly in North America, which exhibit stratification during the summer and it was developed from data obtained by reservoir sampling. This index is based on measurements of three limnological variables, which are highly correlated and are an estimation of algal biomass, using a logarithmic base 2. The values calculated were always between 50 and 60 TSI. In this situation, the lakes would keep slight eutrophic conditions with low values of light penetration, low algal diversity, low oxygen concentration, mainly, on the bottom during the heat months.

However, the facts mentioned above are not verified in the PERD lakes. During the sampling, usually, the light penetrated up to 5 m even in the rainy season (summer in Brazil) and the hypolimnion still remained oxygenated, excepting the deep Dom Helvécio Lake. Furthermore, the water column of the lakes was frequently oversaturated and phosphorus concentration, which was similar to that suggested by Esteves (1998) and Wetzel (1983) for mesotrophic lakes.

On the other hand, Salas and Martino index (Salas & Martino, 1991) was more appropriated to determine the trophic level and most of the lakes were classified as oligotrophic during the dry and rainy seasons. The trophic classification is based mainly in the geometric mean of total phosphorus concentrations recorded in *c*. 35 lakes and reservoirs in the tropics, defining the following categories: 21.3 = oligotrophic, 39.6 = mesotrophic, and 118.7 = eutrophic.

Our results indicate that despite of the same origin and age, the evolution of the middle Rio Doce lakes reflects distinct processes within each lake resulting in different trophic states. In addition, the rainy season, when it is expected high water temperature and consequently an increase of primary and secondary production, produced different effects on the trophic level of the lakes. For instance, the lakes might be separated in three distinct groups. The first group constituted by the shallow Amarela Lake, which had mesotrophic conditions in both seasons, showing higher nutrient concentration, an abundant macrophyte community (11 species identified so far) and high bacterioplankton production. The second group was characterized by the lakes classified as oligotrophic during the dry season, becoming mesotrophic during the rainy season (Carioca and Palmeirinha lakes) and the fourth included the deepest lakes (Dom Helvécio, Águas Claras, Jacaré, and Barra lakes), which were oligotrophic in both seasons. This group was characterized by lowest values of PP, excepting Barra Lake, which is situated between Jacaré Lake and D. Helvécio Lake (Fig. 1). Then, we might argue that this was due to intrinsic characteristics of each lake since the lakes were influenced by the same microclimate conditions and Barra and Jacaré Lakes are surrounded by eucalyptus plantations, receiving intermittent loads of untreated domestic sewage, but showed different result.

Finally, the Salas and Martino index demonstrated to be more appropriate to determine the trophic status of the lakes, which are submitted to anthropogenic forces driving them to the eutrophication and we did not observe significant differences in trophic state and production among lakes situated in protected and non protected areas.

Despite the uncoupling, the seasons (rainy/dry) influenced phytoplankton and bacterioplankton productions, but in an opposite way, i.e., during the summer the heterotrophic metabolism increased, decaying in the winter, when the phytoplankton became more active.

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