

# Primary production of phytoplankton and periphyton in two humic lakes of a South American wetland

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**Abstract** Seasonal primary productivities of periphyton and phytoplankton were compared in Grande Lake (GL) and a relict oxbow lake (ROL) in winter 2006 and summer 2007. GL was free of floating plants on the sampling dates and covered over 80 and 100% of the ROL surface in winter and summer, respectively. The  $^{14}\text{C}$  assimilation technique was used to obtain the  $P$ - $E$  curves of phytoplankton and periphyton on artificial substrata. The periphytic maximum photosynthetic rate ( $P_{\max}$ ) was higher in the ROL in winter and summer, being better adapted to low irradiances than those in the GL. Phytoplankton and periphytic algae were light-limited in the ROL in summer due to complete coverage by floating macrophytes. In summer,  $P_{\max}$  and  $\alpha$  values for periphyton in the ROL were higher than those for phytoplankton, and were even higher than in GL. In turn,  $P_{\max}$  and  $\alpha$  values for phytoplankton in Grande Lake were higher than those for periphyton due to improved light conditions and the presence of algae that were adapted to movement through the water column. These results suggest that the complete coverage by floating macrophytes restricted phytoplankton productivity and allowed the development of a periphytic community that was better adapted to low-light conditions.

**Keywords** Periphytic algae · Phytoplankton · Primary production · Humic shallow lakes · Floodplain wetland

## Introduction

Among the factors that influence primary production in humic lakes, light plays a crucial role in the development of microbial communities, and may become a limiting resource for primary production (Karlsson et al. 2009). In particular, light attenuation is known to be even higher in the water columns of shallow, vegetated, colored lakes due to the presence of floating macrophytes, which can reduce surface irradiance by up to 98% (O'Farrell et al. 2009). Aquatic plants also act as a source of colored organic matter for water bodies because they release humic substances that are formed during the decomposition process (Kirk 1994). This organic matter, which imparts a yellow-brownish color to the water, restricts light penetration and hence the amount of light received by organisms (Eloranta 1999). In regard to phytoplankton production in temperate lakes, Torremorell et al. (2009) found a strong correlation between incident light and water temperature, while Rodríguez and Pizarro (2007) observed seasonal changes in temperature and species composition. Furthermore, Kirk (1994) reported an increase in the maximum light-saturated photosynthetic rate per unit of biomass with increasing temperature for phytoplankton, benthic algae, and macrophytes.

Algae in the phytoplankton and periphyton communities play an important role in wetland productivity. They are responsible for carbon fixation, and are involved in the sequestration of essential nutrients such as nitrogen and phosphorus, making them available for consumers (van der

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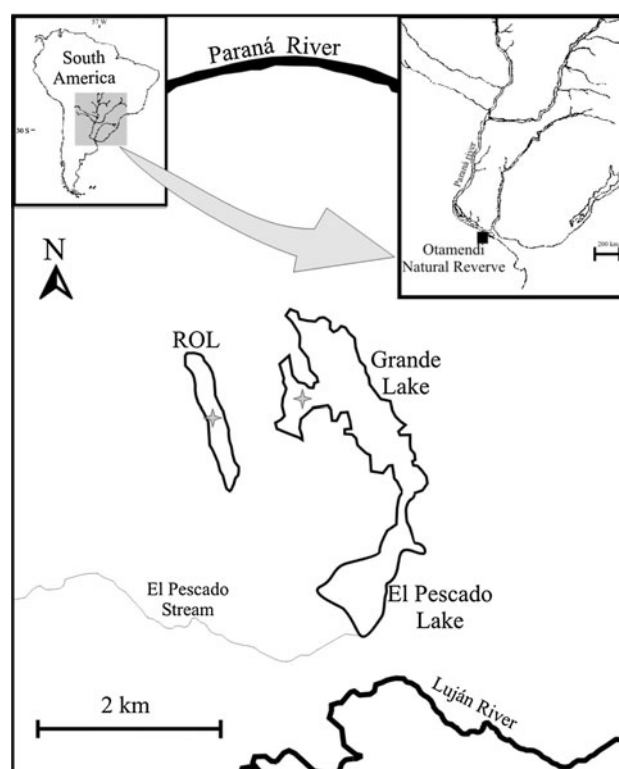
Valk 2007). Periphytic algae account for a large proportion of the production in clear and shallow water bodies (Dodds et al. 1999), and can outcompete phytoplankton under certain conditions (Liboriussen and Jeppesen 2003). The transfer of energy to higher trophic levels is likely to be dominated by the benthic habitat in clearwater lakes and by the pelagic habitat in humic water bodies (Ask et al. 2009; Karlsson and Sävström 2009).

There are some studies that deal with phytoplankton productivity in temperate zones of South America (e.g., Allende et al. 2009; Rodríguez and Pizarro 2007; Torremorell et al. 2009), but much less attention has been paid to periphyton productivity and comparisons between those communities. The objective of the present work was to compare the primary production characteristics of periphyton and phytoplankton from two humic shallow water bodies of a wetland in the Paraná River floodplain, employing photosynthetic parameters derived from  $P-E$  curves. These two environments showed different light conditions because of differences in humic acid content and coverage of free-floating macrophytes. Comparisons were made in summer and winter, since the water bodies from this region usually have marked seasonal trends in environmental and community characteristics.

#### Study area

The two water bodies selected for this study are shallow lakes with contrasting limnological characteristics: a relict oxbow lake (ROL, 17 ha, maximum depth 0.5 m, mean depth 0.3 m) and Grande Lake (156 ha, maximum depth 0.7 m, mean depth 0.5 m). Both are located in the floodplain of the Otamendi Natural Reserve in Argentina, which extends over approximately 3000 ha (34°14'S, 58°50'W) (Fig. 1). These water bodies are rich in humic substances, with summer mean dissolved organic carbon concentrations being ca. 28 mg L<sup>-1</sup> for Grande Lake and 50 mg L<sup>-1</sup> for the ROL (Rodríguez and Pizarro 2007). Bottom sediments are loosely packed owing to the deposition of large amounts of organic matter. The macrophyte community is characterized by stands of emergent plants such as *Schoenoplectus californicus* and *Typha latifolia* and floating plants of different sizes such as *Pistia stratiotes*, *Ricciocarpus natans*, *Azolla filiculoides*, *Wolffiella oblonga*, and *Lemna minima* (Rodríguez and Pizarro 2007). The latter form a dense floating carpet that cover the entire surface of the water body or are restricted to the littoral zone, depending on the seasonality and/or the morphometric characteristics of the systems.

The climate of the region is humid-temperate because of the influence of the Río de La Plata River. There is strong seasonality between summer and winter; the annual mean air temperature was about 17.3°C for the period



**Fig. 1** Map of the study area. Four-pointed stars indicate the sampling points at ROL and Grande Lake

2004–2007. January was the warmest month, with maximum and mean temperatures of 37 and 29.3°C, respectively, while July was the coldest month, with minimum and mean temperatures of -3 and 6.5°C, respectively. Mean rainfall during the study period was 1200 mm (data provided by the Estación Experimental Agropecuaria INTA Delta del Paraná).

#### Methods

Samplings in the two water bodies were carried out in winter (July) 2006 and summer (January) 2007. The ROL was 80 and 100% covered by floating plants in winter and summer, respectively, while they were absent from Grande Lake in both seasons.

Measurements of environmental variables were performed in situ at each sampling point. Depth was recorded with a meter stick. Water temperature, pH, and conductivity were assessed with a Hanna HI 991301 portable meter, and dissolved oxygen with a Hanna HI 9143 oximeter (Woonsocket, RI, USA). Photosynthetically available radiation (PAR, 400–700 nm) was measured with a submersible spherical quantum sensor (LI-193SA, Li-Cor, Lincoln, NE, USA) every 5 cm in the water column to calculate the vertical attenuation coefficient ( $k_d$ )

(Kirk 1994). The mean irradiance integrated over the water column ( $E_{\text{mean}}$ ) was calculated as follows (Helbling et al. 1994):

$$E_{\text{mean}} = E_0(1 - e^{-k_d z})(k_d z)^{-1},$$

where  $E_0$  is the subsurface irradiance and  $z$  is the depth. The incoming atmospheric radiation was measured with the same equipment. To avoid light reflecting from the different surfaces present where the measurements were taken, we placed a black frame just below the spherical sensor.

Water samples for chemical analysis were obtained by integrating the water column with a tube sampler (1 m height,  $\varnothing = 10$  cm), and were kept in plastic flasks under cold and dark conditions until processing (which occurred within 24 h of sampling). To estimate the humic content of the water, its absorbance at 440 nm was measured after filtering the water through polycarbonate filters 0.2  $\mu\text{m}$  in pore size, and the absorption coefficient ( $g_{440}$ ) was calculated (Kirk 1994). The phenate method was used for ammonia, the cadmium reduction method was used for total nitrogen and nitrate + nitrite, and the stannous chloride method was used for total phosphorus and phosphate (APHA 2005). Total fractions of both nitrogen and phosphorus were determined after the simultaneous digestion of nitrogen and phosphorus compounds (APHA 2005). The dissolved inorganic nitrogen concentration (DIN) was obtained as the sum of the ammonia and nitrate + nitrite fractions. Dissolved inorganic carbon (DIC) was determined from the alkalinity by Gran titration, pH, and temperature (Stumm and Morgan 1996).

### Phytoplankton

Samples for chlorophyll *a* were taken, integrating the water column with a sampler about 1 m in length and 10 cm in diameter. They were then transferred into 1 L plastic bottles and preserved under dark and cold conditions until filtration was performed (on the same sampling day). Samples were filtered through Whatman GF/F fiber glass filters (0.7  $\mu\text{m}$  nominal pore size,  $\varnothing = 47$  mm). The filters were stored at  $-20^\circ\text{C}$  until the extraction of pigments with ethanol (60–70°C); the extracts were kept overnight at 4°C and darkness. The absorbance was then measured at 665 and 750 nm in a spectrophotometer before and after acidification with HCl 0.1 N (Nusch 1980). For comparative purposes, we expressed the phytoplankton chlorophyll *a* values in area units by assuming that 100  $\mu\text{g L}^{-1}$  equals 100  $\text{mg m}^{-2}$ , considering an average water depth of 1 m (Goldsborough and Robinson 1996).

The production versus irradiance curves ( $P$ – $E$ ) were obtained for each sampling using the  $^{14}\text{C}$  assimilation technique (Holm-Hansen and Helbling 1995). Incubations (2 h) were carried out in the field on clear and sunny days

around noon. Water samples with 1  $\mu\text{Ci}$  (Grande Lake) and 2  $\mu\text{Ci}$  (ROL)  $\text{NaH}^{14}\text{CO}_3$  (PerkinElmer Life Sciences, Inc., Wellesley, MA, USA) added were incubated in clear Plexiglas bottles (62.5 mL, sharp cut-off at 400 nm) that were placed inside a container filled with water (0.75  $\text{m}^3$ ). Both the incubation time and the amount of radioactive material added had previously been assayed for these lakes and shown to be optimal for obtaining a  $P$ – $E$  saturation curve. The bottles were exposed in duplicate to 6 or 7 irradiances ranging between 0 and 100% of the incident light, which was achieved using meshes of neutral attenuation consisting of weaves with different pore sizes that were combined to allow the differential passage of light through them. Two dark bottles per lake were also incubated, and assimilation values were obtained by subtracting those of the clear bottles. Bottles were transported under cool and dark conditions to the laboratory.

In the laboratory, samples were filtered onto Whatman GF/F fiber glass filters (0.7  $\mu\text{m}$  nominal pore size,  $\varnothing = 47$  mm); the filters were then placed in scintillation vials in an atmosphere saturated with HCl for one night. The scintillation cocktail (Opti-phase Hi Safe 3, Perkin-Elmer Life Sciences, Inc.) was added, and the radioactivity incorporated by the algae was measured using a Beckman LS-6500 liquid scintillation counter (Brea, CA, USA). To determine the specific radioactivity in the sample, 1 mL of the incubated water and three drops of 0.1 N NaOH were mixed with the scintillation cocktail, and measured as described previously.

The parameters of the  $P$ – $E$  curves were fitted by iteration to the following equation (Eilers and Peeters 1988):

$$P = (aE^2 + bE + c)^{-1},$$

where  $P$  is the primary productivity [ $\mu\text{g C}$  ( $\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$ ],  $E$  is the irradiance ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ), and  $a$ ,  $b$ , and  $c$  are adjustment parameters. The initial slope ( $\alpha$ ) and maximum productivity rate ( $P_{\text{max}}$ ) can be expressed as a function of the parameters  $a$ ,  $b$ , and  $c$  as follows:

$$\alpha = 1/c$$

$$P_{\text{max}} = 1/(b + 2(ac)^{1/2}).$$

The irradiance corresponding to the onset of saturation ( $E_k$ ) was calculated as  $E_k = P_{\text{max}}/\alpha$  (Kirk 1994). Phytoplankton production per unit area in the water column ( $P_A$ ) was calculated by integrating the productivity–depth curve. Depth was obtained from the equation of irradiance versus depth ( $E = E_0 e^{-k_d z}$ ) (Kirk 1994).

### Periphyton

All periphyton measurements were performed on artificial substrata that periphyton were allowed to colonize for a

month prior to measurements. Before the experiments, we tested whether one month was sufficient time to obtain a mature periphytic community. Substrata consisted of polycarbonate strips (1 mm thick  $\times$  15 mm wide  $\times$  75 mm long) held submerged about 10 cm below the surface of the water using an ad hoc device. The chlorophyll *a* concentration was obtained using the same methodology described for phytoplankton (with the previous step of scraping the material from the substrata). Measurements were run in triplicate.

To construct the *P*–*E* curves of periphyton, the incubations were run on the same day and within the same device employed for phytoplankton. Substrata were placed in tubes filled with water filtered through a 15  $\mu$ m pore net, and 2  $\mu$ Ci  $\text{NaH}^{14}\text{CO}_3$  were added to each tube from Grande Lake and ROL. Incubations (2 h) were run in duplicate for each light attenuation. One face of each polycarbonate strip was scraped off, and the opposite face was exposed to light during the incubation period. In the laboratory, the periphyton from the light-exposed face was removed and subjected to the same analytical procedure as described for phytoplankton.

To investigate whether the community grew under light-limiting conditions due to the depth at which the substrata were incubated (10 cm), the periphytic  $E_k$  value was compared with the irradiance at a depth of 10 cm ( $E_{10\text{cm}}$ ). Also, the production per unit area at 10 cm ( $P_{A\ 10\text{cm}}$ ) was estimated.

## Results

Even though the coverage of floating macrophytes fluctuated in Grande Lake throughout the year, they were completely absent from the sampling area when the measurements were carried out. Conversely, the ROL was 80 and 100% covered with floating plants in winter and summer, respectively. In Grande Lake, dissolved oxygen values were higher in winter than in summer (10.5 and 3.6  $\text{mg L}^{-1}$ , respectively), while they were consistently low (3.3  $\text{mg L}^{-1}$ ) or undetectable in the ROL due to the high development of floating plants (Table 1).

Light intensity fluctuated among seasons in the study area; atmospheric light intensity during summer averaged 1700  $\mu\text{mol m}^{-2}\text{s}^{-1}$ , while that in winter was ca. 1200  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . In Grande Lake, the fluctuation in  $E_0$  (subsurface underwater light intensity) followed the pattern of higher values in summer and lower in winter (ca. 1600 and 780  $\mu\text{mol m}^{-2}\text{s}^{-1}$  for summer and winter, respectively). In the ROL, the observed  $E_0$  values responded to the coverage by floating plants (420 and 73  $\mu\text{mol m}^{-2}\text{s}^{-1}$  in winter and summer, respectively). The light penetration

**Table 1** Environmental variables measured in Grande Lake and the ROL at the winter and summer samplings

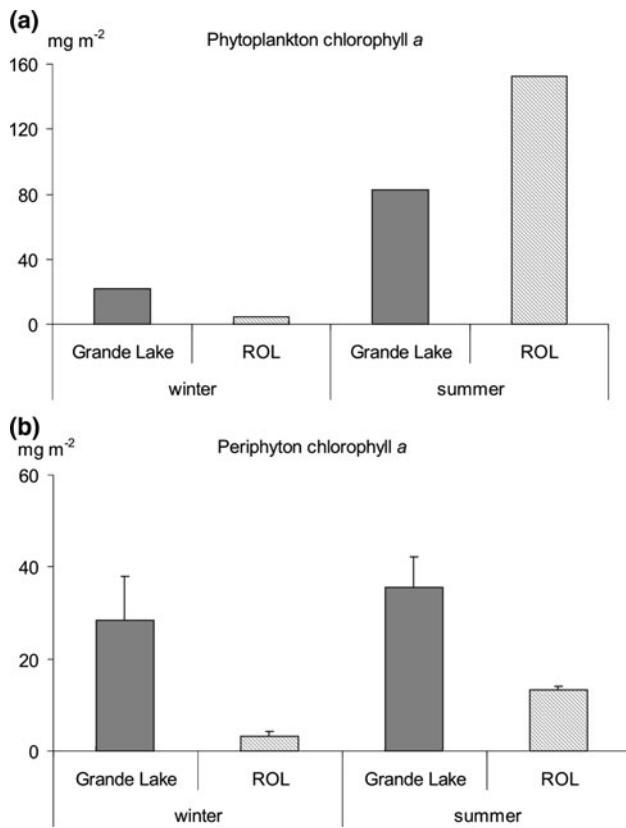
	Winter		Summer	
	Grande Lake	ROL	Grande Lake	ROL
Floating plant coverage (%)	0	80	0	100
Water depth (m)	0.4	0.2	0.7	0.3
Conductivity ( $\mu\text{S cm}^{-1}$ )	1900	2900	1300	1070
Dissolved oxygen ( $\text{mg L}^{-1}$ )	10.5	3.3	3.6	ND
Water temperature ( $^{\circ}\text{C}$ )	6	6	25.3	23
pH	8.8	7.6	8.1	7.3
$E_{\text{mean}}$ ( $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ )	476	297	290	23
$g_{440}$ ( $\text{m}^{-1}$ )	8	15	16	18
$k_d$ (PAR) ( $\text{m}^{-1}$ )	4	12	8	12
DIN ( $\text{mg L}^{-1}$ )	0.09	0.5	ND	0.04
Total N ( $\text{mg L}^{-1}$ )	0.1	0.6	3	3.5
Dissolved P ( $\text{mg L}^{-1}$ )	0.1	0.5	0.2	0.13
Total P ( $\text{mg L}^{-1}$ )	0.2	0.5	0.7	1.1

ND not detected

integrated in the water column ( $E_{\text{mean}}$ ) at both lakes was higher in winter, particularly for Grande Lake, probably because the humic content in summer was twice that in winter, as indicated by the  $g_{440}$  values. Moreover, the total coverage of floating plants in summer contributed to greater light attenuation in the ROL. The  $k_d$  in Grande Lake was higher in summer than in winter, probably due to the stronger development of phytoplankton during the warm season. No seasonal differences in  $k_d$  were observed for the ROL (Table 1).

The DIN concentrations were higher in the ROL than in Grande Lake, and in both water bodies the DIN concentrations were lower in summer while total N followed the opposite trend. Dissolved phosphorus concentrations in Grande Lake were higher in summer than in winter, while the opposite trend was observed for the ROL. Total phosphorus concentrations were higher in summer at both sampling sites (Table 1).

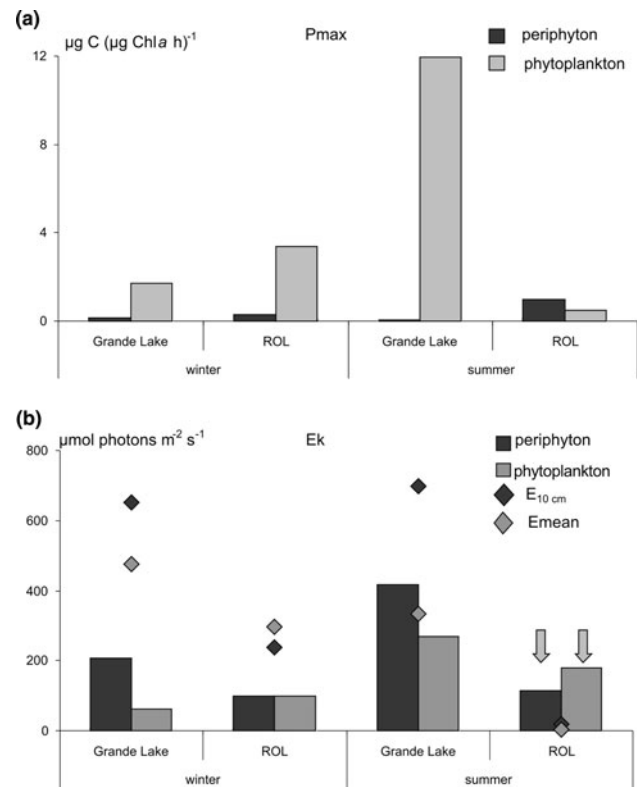
The phytoplanktonic chlorophyll *a* showed its maximum and minimum values in the ROL, ranging from 4.3  $\text{mg m}^{-2}$  in winter up to 152  $\text{mg m}^{-2}$  in summer; at this latter time point it was almost twofold that for Grande Lake (83  $\text{mg m}^{-2}$ ), despite the fact that floating plant coverage was 100% in the ROL (Fig. 2a). Periphytic chlorophyll *a* was higher in Grande Lake (Mann–Whitney test,  $p = 0.002$ ); it was higher in summer in both water bodies, with a maximum value of 36  $\text{mg m}^{-2}$  in Grande Lake (Fig. 2b). With the exception of the winter sampling in Grande Lake, the phytoplankton chlorophyll *a* values were generally higher than the periphytic ones.



**Fig. 2** **a** Phytoplankton and **b** periphyton chlorophyll *a* concentrations in Grande Lake and the ROL during the study period

### Primary production

The photosynthetic parameter  $P_{\max}$  was higher for phytoplankton than for periphyton, except in the summer in the ROL. The values fluctuated between 0.06 and 12  $\mu\text{g C } (\mu\text{g Chl } a \text{ h})^{-1}$  for periphyton and phytoplankton, respectively, with an extreme value being recorded in the summer in the Grande Lake (Fig. 3a). Photosynthetic efficiency ( $\alpha$ ) followed the same spatial and seasonal trend as  $P_{\max}$ . The minimum and maximum values were recorded for Grande Lake; the former [ $0.0002 \mu\text{g C m}^2 \text{ s } (\mu\text{g Chl } a \mu\text{mol photons h})^{-1}$ ] corresponded to periphyton in summer, and the latter [ $0.04 \mu\text{g C m}^2 \text{ s } (\mu\text{g Chl } a \mu\text{mol photons h})^{-1}$ ] to phytoplankton in summer. Likewise, the minimum (63  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) and maximum (418  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) light intensities at the onset of saturation ( $E_k$ ) were obtained for Grande Lake: the former was observed for phytoplankton in winter, and the latter for periphyton in summer. The light intensities that reached the phytoplankton and periphyton ( $E_{\text{mean}}$  and  $E_{10\text{cm}}$ , respectively) were higher than  $E_k$ , except in summer in the ROL, when the light intensities received by both communities were lower than their respective  $E_k$  values, suggesting light limitation (Fig. 3b).



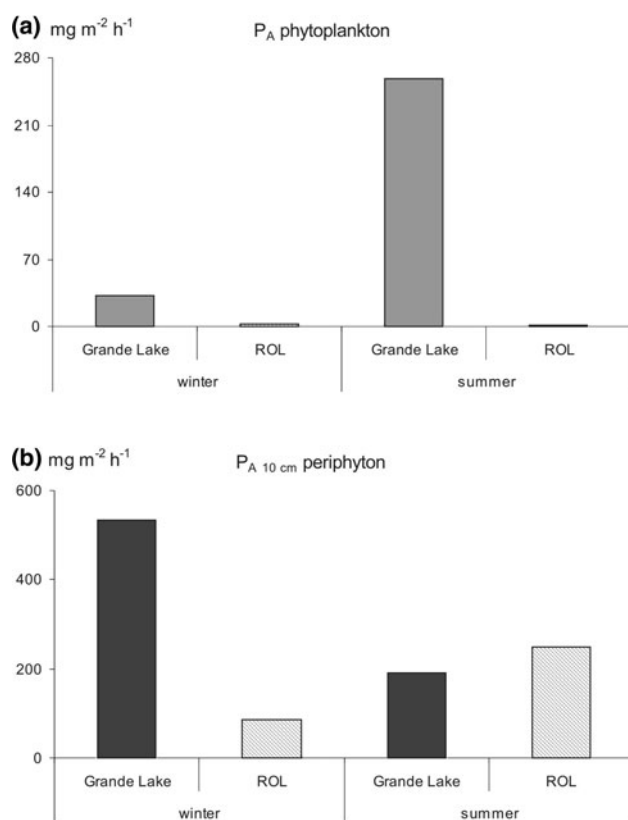
**Fig. 3** Values of photosynthetic parameters: **a**  $P_{\max}$  and **b**  $E_k$  for phytoplankton and periphyton in both water bodies during the study period; bars represent the parameter  $E_k$ , diamonds represent  $E_{\text{mean}}$  and the light intensity at a depth of 10 cm ( $E_{10\text{cm}}$ ), and arrows indicate the occurrence of light limitation

The primary production per unit area ( $P_A$ ) of phytoplankton in Grande Lake showed a clear seasonal pattern, with the maximum occurring in summer (258  $\text{mg C m}^{-2} \text{ h}^{-1}$ ) and the minimum in winter (32  $\text{mg C m}^{-2} \text{ h}^{-1}$ ). Values were lower in the ROL than in Grande Lake for both seasons (2.7 and 1  $\text{mg C m}^{-2} \text{ h}^{-1}$  for winter and summer, respectively) (Fig. 4a). Periphyton at a depth of 10 cm ( $P_{A 10\text{cm}}$ ) showed its maximum value in Grande Lake in winter (530  $\text{mg C m}^{-2} \text{ h}^{-1}$ ) and its minimum value in the ROL in winter (86  $\text{mg C m}^{-2} \text{ h}^{-1}$ );  $P_{A 10\text{cm}}$  was higher in the ROL in summer (250  $\text{mg C m}^{-2} \text{ h}^{-1}$ ), despite the light limitation (Fig. 4b).

### Discussion

Grande Lake is the largest water body in the wetland, and its maximum effective length exceeds that of the ROL. Based on these characteristics, the wind plays a major role in mixing the water column. This fact may have prevented floating plants from covering the surface completely during the study period; those found were small and generally restricted to the littoral zone. Comparing the production





**Fig. 4** a  $P_A$  values for phytoplankton and b  $P_A$   $_{10\text{cm}}$  values for periphyton in both lakes during the study period

rates of phytoplankton and periphyton in Grande Lake, it could be argued that periphyton was the dominant community in winter (530 vs. 32  $\text{mg C m}^{-2} \text{h}^{-1}$ , periphyton and phytoplankton, respectively), and phytoplankton was dominant in summer (190 vs. 258  $\text{mg C m}^{-2} \text{h}^{-1}$ , periphyton and phytoplankton, respectively). The scarcity of available substrata for colonization (mainly composed of stands of *Schoenoplectus californicus* and *Typha latifolia* restricted to the shore, and accompanied by some floating plants) restricts us from making that statement. Thus, our results show that even when phytoplankton was the dominant community in this lake, periphyton had the potentiality to overcome phytoplankton productivity rates when nutrients and light competition were less important, as in winter. Moreover, we also observed the same trend regarding chlorophyll *a* concentration. This pattern was also observed by Hansson (1992) along a productivity gradient of Swedish and Antarctic lakes.

On the other hand, the morphometric characteristics of the ROL (small and more wind-sheltered) favored the extension of macrophyte cover. Surprisingly, full plant coverage of the ROL in summer reduced light to almost 98% of atmospheric incident levels, but did not seem to affect phytoplankton chlorophyll *a*. One possible explanation would be that wind-induced changes in floating

plant coverage during the days prior to sampling allowed the development of the algal community. Hence, the characteristics of the phytoplankton at sampling would reflect the past history of plant cover fluctuations. This result also shows that light limitation of phytoplankton did not restrict algal growth, indicating that other factors (e.g., nutrients, wind-induced displacement of plants) may influence the development of phytoplankton.

In the ROL, floating macrophytes provide available substrata for periphytic growth (Rodríguez et al. 2011), and despite our suspicion that this macroscopic community was the dominant producer, the microbial primary production at this site was driven by periphytic algae. We can make this assertion considering that periphytic production rates were one or two orders of magnitude higher than those of phytoplankton in this lake (86 vs. 2.7  $\text{mg C m}^{-2} \text{h}^{-1}$  in winter and 250 vs. 1  $\text{mg C m}^{-2} \text{h}^{-1}$  in summer, periphyton and phytoplankton, respectively).

Comparatively, phytoplankton and periphyton were more productive in Grande Lake, while periphyton made efficient use of light in the ROL, especially when floating plants covered the entire surface of the water body. In the studied water bodies, planktonic and periphytic algae were fairly well acclimatized to the light-limited conditions resulting from the high humic content and the presence of floating macrophytes. The most representative algal groups in this study were the cryptophyceans in the phytoplankton, the diatoms in the periphyton, and the cyanobacteria in both communities (data not shown). These groups, which have developed morphological and/or physiological adaptations to cope with low light levels, have also been found in similar and even more light-limited habitats (Lepistö and Holopainen 2003; Lepistö et al. 2004; Putz 1997; van Dam et al. 1994; Vincent 2000; Wynn-Williams 2000).

Phytoplankton production obtained by integrating the water profile was higher in Grande Lake than in the ROL, probably due to improved light conditions. The  $P_A$  values for phytoplankton from Grande Lake are similar to those reported previously for the same water body (Rodríguez and Pizarro 2007), and lower than those estimated for a less humic lagoon at a comparable latitude (Torremorell et al. 2009). The  $E_k$  values for phytoplankton in both lakes were similar to those reported by Kirk (1994) for a wide range of environments.

Regarding the periphyton, the  $P_A$   $_{10\text{cm}}$  values were within the range of those recorded for water environments in the Amazonian watershed (Putz 1997), and  $E_k$  values fell in the range 100–400  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , typical of attached communities (Hill 1996). In summer, both of the studied communities that inhabited the ROL experienced light limitation ( $E_k < \text{in situ irradiance}$ ), in concomitance with complete surface coverage by floating macrophytes. The phytoplankton of Grande Lake could withstand the

fluctuating light regime possibly because it was composed of species that were able to move through the water column in search of light (flagellated cryptophytes in winter and filamentous cyanobacteria, which regulate their buoyancy, in summer). The fact that the periphytic algae in the ROL showed higher  $P_{\max}$  and  $\alpha$  values than the phytoplankton may indicate that they are better adapted to this light-limited environment.

The present results suggest that the phytoplankton and periphyton in the studied water bodies were adapted to the environmental conditions through a combination of morphological and/or physiological features. Periphytic algae grown under low-light conditions caused by a high humic content and an increased coverage of floating plants (ROL) were more efficient; while phytoplankton and periphyton grown under a fluctuating light regime (Grande Lake) were more productive.

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