Limnologica 55 (2015) 9–12

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

Phytoplankton and periphyton production and its relation to temperature in a humic lagoon

Patricia Rodríguez[a,*], Haydée Pizarro[b,c]

[a] Austral Centre for Scientific Research (CADIC-CONICET), Houssay 200, 9410 Ushuaia, Tierra del Fuego, Argentina
[b] Department of Ecology, Genetics and Evolution, University of Buenos Aires, C1428EHA, Buenos Aires, Argentina
[c] IEGEBA-CONICET, Buenos Aires, Argentina

ARTICLE INFO

Article history:
Received 3 July 2015
Received in revised form
18 September 2015
Accepted 26 October 2015
Available online 5 November 2015

Keywords:
Phytoplankton
Periphyton
Temperature seasonality
P–E curves
Humic lake
Shallow lake

ABSTRACT

To analyse the existence of interactive competition between phytoplankton and periphyton, we studied their photosynthesis–irradiance (P–E) response during one year in a humic lagoon. Lake production was dominated by phytoplankton, which followed seasonal changes in temperature. Periphyton primary production and algae biomass increased in winter, when phytoplankton biomass and production were lower. In this study we show that even in conditions of phytoplankton dominance, the habitat coupling between phytoplankton and periphyton can still be noticed.

Phytoplankton and periphytic algae are among the major producers in aquatic ecosystems. The relative importance of each community to lake primary production depends mainly on environmental conditions (e.g., light and nutrients), which in turn influence the net outcome of the interactive competition among them (Jäger and Diehl, 2014). Phytoplankton intercepts light before it reach periphyton, which recycles nutrients within their own matrix preventing thus their flux towards the water column (Hansson, 1988; Wetzel, 2005). Hence, when periphyton dominate primary production a clear-water state is established and phytoplankton dominance determine a turbid state (Moss, 1990; Genkai-Kato et al., 2012). In this study, we explored the contribution of phytoplankton and periphyton to whole-lake primary production on a seasonal basis in a turbid, humic shallow lake from the temperate zone in Argentina.

Grande Lake is a lagoon from the floodplain of the Paraná river (34°14′S, 58°52′W), which has been previously studied with special emphasis in algal community structure, trophic interactions and primary production (e.g., Rodríguez et al., 2011, 2012; Izaguirre et al., 2012). It is shallow with an area of 156 ha, mean depth ca. 0.7 m and maximum depth rarely exceeding 1 m. The lagoon has high concentrations of dissolved organic carbon, generally exceeding 15 mg L^{-1} (Aguilar Zurita, Unpubl. data).

The survey was carried out from April 2006 to March 2007 and samplings performed on a monthly basis, ca. 50 m away from the shoreline. The zone was free of aquatic plants during the study period. Water temperature, pH, dissolved oxygen and conductivity were measured with portable metres. Photosynthetic available radiation (PAR, 400–700 nm) was recorded with a submersible spherical quantum sensor LI-193SA (Li-Cor, Lincoln, USA) every 5 cm in the water column to calculate the vertical attenuation coefficient (k_d) and the mean irradiance integrated in the water column (E_{mean}) (Neale et al., 1991; Kirk, 2011). Water samples for chemical analysis were obtained with a tube sampler integrating water from the first centimetres and stored in plastic flasks in cold and dark conditions until processing within 24 h. Water samples were treated as described in Rodríguez et al. (2012) for absorbance and nutrient analyses. The absorption coefficient ($g440$) was calculated from absorbance measurements at 440 nm (Kirk, 2011). Dissolved inorganic nitrogen (DIN) represents the addition of the concentration of ammonia, nitrate and nitrite ions. Phytoplankton chlorophyll-*a* (Chl-*a*) was extracted with ethanol and determined spectrophotometrically (Jespersen and Christoffersen,

* Corresponding author. Tel.: +54 2901 422310x145; fax: +54 2901 430644.
E-mail addresses: patricia.rodriguez@cadic-conicet.gob.ar, aicirtap.rodriguez@gmail.com (P. Rodríguez).

http://dx.doi.org/10.1016/j.limno.2015.10.003
0075-9511/

1987). Depth integrated samples were taken, preserved with acid lugol iodine solution (1%) and counted in the laboratory under an inverted microscope (Utermöhl, 1958).

Periphton analyses were performed on artificial substrata (polycarbonate strips, 1 mm × 1.6 cm × 7.5 cm) that were allowed to colonize at 10 cm depth for one month as described in Rodríguez et al. (2012). For quantitative analyses of algal classes, Chl-*a*, and mass determinations, substrata were collected and transported to the laboratory in plastic zip-lock bags. Quantitative and Chl-*a* analyses were performed as described for phytoplankton, with the previous step of scraping 3 substrata. Dry weight (DW) and ash free dry weight (AFDW) determinations were performed in triplicate following standard protocols (APHA, 2005). The autotrophic index (AI) was estimated as the ratio AFDW/Chl-*a*. The P-E curves were performed by an in situ simulated deployment using the ^{14}C assimilation technique as described in Holm-Hansen and Helbling (1995) and full details of the methodology are given in Rodríguez et al. (2012).

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

$$P = E(aE^2 + bE + c)^{-1} \quad (1)$$

where P is Chl-*a* specific primary productivity (μg C (μg Chl *a*)$^{-1}$ h^{-1}), E is irradiance (μmol photon m^{-2} s^{-1}), and a, b and c are adjustment parameters. The initial slope or photosynthetic efficiency (α) and the maximum Chl-*a* specific photosynthetic rate (P_{max}) can be obtained from a, b and c as follows:

$$\alpha = \frac{1}{c} \quad (2)$$

$$P_{max} = \frac{1}{b + 2(ac)^{1/2}} \quad (3)$$

The irradiance corresponding to the onset of saturation (E_k) was calculated as $E_k = P_{max}/\alpha$ (Kirk, 2011). Hourly production rates were extrapolated to daily values employing a sinusoidal formula (McBride, 1992).

Spearman correlations were applied to pairs of physical, chemical and biological variables. Multiple regressions were conducted to explain phytoplankton and periphyton production with environmental variables with forward stepwise selection of variables. For phytoplankton, depth, pH, temperature, E_{mean}, DIN and soluble reactive phosphorus (SRP) were considered as independent variables. For periphyton, conductivity, temperature, $E_{10\,cm}$, DIN, SRP and phytoplankton Chl-*a* were included. The dependent variable was Log_{10} transformed to fulfil normality assumption when needed. Mann–Whitney U (M–W) testing was applied to look for differences among samples.

Water temperature followed a seasonal pattern, with the minimum observed in July (winter) and the maximum in January (summer) (Fig. 1). Water depth was ca. 40 cm during most of the study and increased towards the summer; conductivity increased during spring-summer, with values above 1000 μS cm^{-1} during all the study period (Table 1). The higher concentration of dissolved oxygen (DO) was registered in November during a bloom of filamentous cyanobacteria. Light integrated in the water column (E_{mean}) did not show significant differences among seasons. Instead, k_d followed a seasonal trend with lower values during winter, as supported by a positive correlation with water temperature (Table 2). The k_d generally was around ca. 4 m^{-1} but in October and November, during the cyanobacteria bloom, it was ca. 20 and 17 m^{-1}, respectively (Table 1). Absorption coefficient at 440 nm (*g*440) followed a seasonal trend, with higher values during spring-summer and was positively correlated with water temperature and k_d (Table 2).

Table 1
Mean, minimum and maximum (in parenthesis) values recorded at Grande Lake during the study period. DO = dissolved oxygen, E_{mean} = irradiance integrated in the water column, k_d = vertical attenuation coefficient of light, *g*440 = absorption coefficient at 440 nm, SRP = soluble reactive phosphorus, TP = total phosphorus, DIN = dissolved inorganic nitrogen, TN = total nitrogen, nd = not detectable.

water temperature (°C)	17.8 (5.8–27.5)
depth (m)	0.47 (0.37–0.68)
conductivity (μS cm^{-1})	1854 (1005–2580)
DO (mg L^{-1})	8.3 (3.6–14.3)
pH	8.6 (7.8–9.5)
E_{mean} (μmol photon m^{-2} s^{-1})	425 (309–577)
k_d (m^{-1})	7.8 (3.8–20.3)
*g*440 (m^{-1})	12.1 (3.7–27.9)
SRP (mg L^{-1})	0.24 (0.08–0.61)
TP (mg L^{-1})	0.69 (0.22–1.8)
DIN (mg L^{-1})	0.21 (nd–1.6)
TN (mg L^{-1})	1.8 (0.09–3.6)

The SRP concentrations were relatively high (Table 1) and did not show a seasonal pattern of variation; instead, TP showed a clear seasonal pattern with higher concentration during warmer months and was correlated to phytoplankton Chl-*a* (Table 2). DIN concentration tended to be lower towards the warmer months as supported by a negative correlation with water temperature (Table 2).

Phytoplankton abundances were higher in summer, with a maximum of 210,000 ind mL^{-1} in January, due to a bloom of the diatom *Cyclotella meneghiniana*. Lower abundances were observed in winter, with the minimum occurring in July (3300 ind mL^{-1}) and the assemblage being dominated by cryptophyceans. In October and November abundances were high (ca. 70,000 ind mL^{-1}) due to the bloom of several filamentous genera of cyanobacteria. The rest of the year the community was a mixed assemblage composed of different groups (diatoms, cryptophyceans, cyanobacteria, euglenoids and chlorophyceans). Phytoplankton Chl-*a* concentration followed a seasonal pattern and was positively correlated to water temperature and phytoplankton abundance (Table 2). Concentrations were variable, ranging from 22 μg L^{-1} (July) to 507 μg L^{-1}(November). Phytoplankton Chl-*a* was higher than periphyton chlorophyll-*a* (M–W test, $p < 0.001$); when expressed in area units, phytoplankton Chl-*a* ranged from 0.83 to 34 mg cm^{-2}.

Periphyton algae abundance were between 5750 ind cm^{-2} (October) to 112,000 ind cm^{-2} (March) without showing any seasonal pattern with diatoms the dominant group. Chlorophyll-*a* fluctuated between 0.5 μg cm^{-2} (September) and 4.5 μg cm^{-2} (April) and was correlated with periphyton abundance (Table 2). Dry weight (DW) and the ash free dry weight (AFDW) followed seasonal trends, with higher values during warmer months. DW values varied between 6.9 mg cm^{-2} (January) and 0.25 mg cm^{-2} (June). The highest AFDW value (5.2 mg cm^{-2}) was observed in January and the lowest (0.2 mg cm^{-2}) in June. Significant multiple regression analysis showed that AFDW was mainly determined by water temperature (T) as follows: AFDW = 0.045 T − 0.77 (p = 0.005; R^2 = 0.6). The AI indicated a more autotrophic periphyton in winter (97), and more heterotrophic during summer (3330), when light attenuation was higher. This last observation is supported by direct correlations with temperature and k_d (Table 2).

Phytoplankton maximum photosynthetic rate (P_{max}) did not follow temperature seasonal variations (Fig. 1A). Photosynthetic efficiency (α) ranged from 0.005 to 0.04 mg C m^2 s (mg Chl *a* μmol photon h)$^{-1}$ in January and March, respectively, and varied similarly to P_{max}. The irradiance at the onset of saturation (E_k) was higher than E_{mean} twice, during May and August (winter), when phytoplankton was potentially light-limited. On the other hand, phytoplankton production integrated in the water column (P_{ph}) followed a seasonal pattern (Fig. 1B), and water temperature (T) significantly explained its variation (P_{ph} = 0.044 T; p = 0.015; R^2 = 0.7).

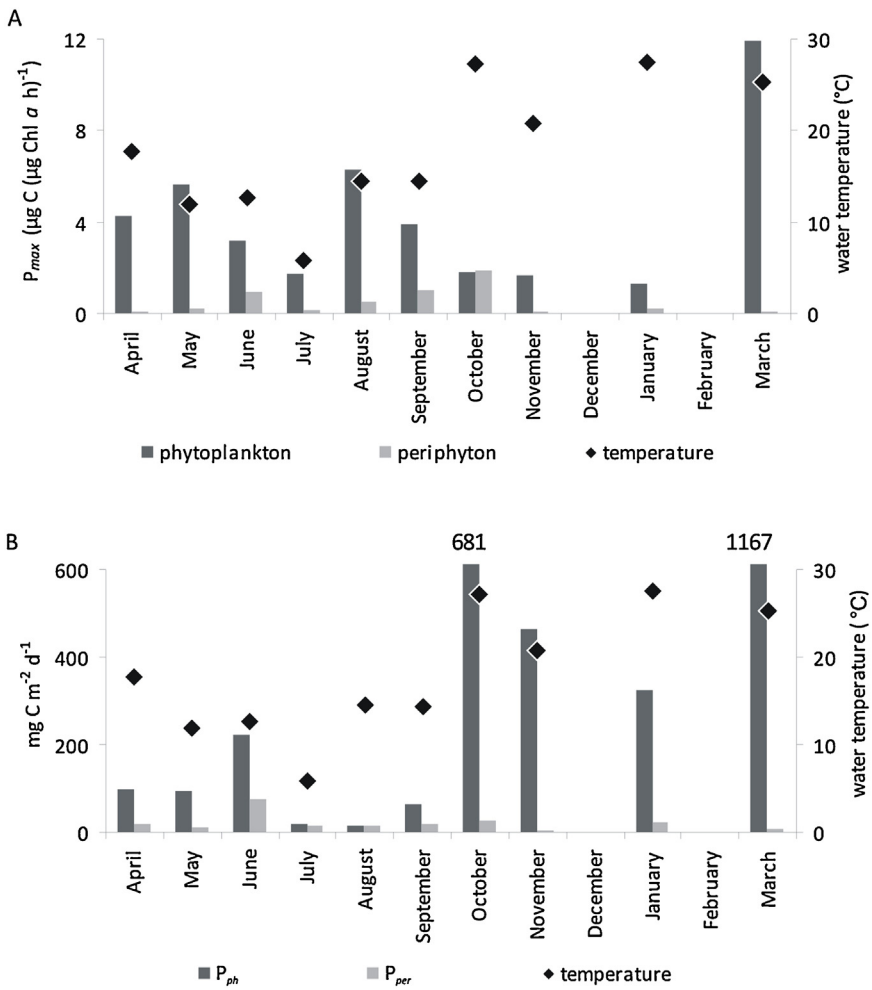

Fig. 1. (A) Phytoplankton and periphyton maximum photosynthetic rate, (P_{max}, left axis) and water temperature (right axis) during the study period, and (B) daily primary production per area unit for phytoplankton (P_{ph}) and periphyton (P_{per}) and water temperature. No data is available for December and February.

Table 2
Spearman correlation coefficient and p values for significant ($p < 0.05$) correlations among environmental and biological variables. k_d = vertical attenuation coefficient of light, *g*440 = absorption coefficient at 440 nm, TP = total phosphorus, DIN = dissolved inorganic nitrogen, *ph*Chl-*a* = phytoplankton chlorophyll *a*, *ph*density = phytoplankton total density, *per*Chl-*a* = periphyton chlorophyll *a*, *per*density = periphyton total density, AFDW = ash free dry weight, P_{ph} = phytoplankton production integrated in the water column.

	k_d	*g*440	TP	DIN	*ph*Chl-*a*	*per*Chl-*a*	AFDW
water temperature	0.60; 0.01	0.85; 0.001	0.85; 0.001	−0.63; 0.01	0.73; 0.001		0.71; 0.01
k_d		0.77; 0.003					0.78; 0.002
*ph*Chl-*a*	0.66; 0.004		0.71; 0.01				
*ph*density	0.54; 0.03				0.66; 0.001		
*per*density						0.85; 0.0002	
P_{ph}				−0.56; 0.03	0.80; 0.0004		

P_{ph} was positively correlated to phytoplankton Chl-*a* and inversely correlated to DIN (Table 2). The estimated annual rate of primary production for phytoplankton was ca. 132 gC m^{-2}.

Periphyton maximum photosynthetic rate (P_{max}) was lower than phytoplankton P_{max} (M–W, $p = 0.0001$) (Fig. 1A). The photosynthetic efficiency (α) was also lower for periphyton (M–W, $p = 0.0001$) and ranged from 0.0001 µg C m^2 s (µg Chl *a* µmol photon h)$^{-1}$ in November to 0.008 µg C m^2 s (µg Chl *a* µmol photon h)$^{-1}$ in October. Both periphyton P_{max} and α did not show any seasonal trend and fluctuated similarly during samplings. The E_k for periphyton was lower than irradiance at 10 cm once, in October; thus, periphyton was potentially light limited because of the massive growth of pelagic Cyanobacteria. Despite non significant statistics results, periphyton production (P_{per}) showed higher values during colder months (Fig. 1B), when the community was more autotrophic accordingly to the AI. Annual P_{per} was estimated to be ca. 7 gC m^{-2} and daily rates were higher for phytoplankton than periphyton (M–W, $p < 0.05$). Primary production per area unit was not inversely correlated between communities.

In this study we show that phytoplankton dominated primary production in a humic shallow lake and that pelagic production was driven by temperature seasonality. Nevertheless, periphyton algae biomass and production increased when phytoplankton abundances and production were lower, suggesting thus the existence of a competitive interaction between both communities.

Optical variables such as k_d and *g*440 as well as phytoplankton Chl-*a* concentrations and abundances emphasises that Grande Lake was phytoplankton dominated during the study period. Under

these conditions, it could be expected that phytoplankton growth would prevent, owing to light limitation, the development of periphyton. However, we detected light limitation in periphyton once, whilst for phytoplankton we detected light limitation twice. Besides, E_k values for both communities were similar and generally high; the lowest was observed for phytoplankton during winter (July, 63 μmol photon m^{-2} s^{-1}), when the algae assemblage was mainly composed of cryptophyceans, known to tolerate low light intensities (Lepistö and Holopainen, 2003; Rodríguez and Pizarro, 2007). High E_k values could be indicating that the water column is frequently mixed given that the lake is shallow and not wind sheltered. Thus, the organisms are continuously exposed to high irradiances from the upper layer of the water column.

The maximum photosynthetic rate, P_{max}, was higher for phytoplankton which implies that phytoplankton had a higher growth rate compared to periphyton. Accordingly, phytoplankton was also more efficient at using light as indicated by higher α values. Allende et al. (2009) studied the P–E relationship in a turbidity gradient of shallow lakes from the Pampa plain and found that phytoplankton P_{max} was higher in turbid lakes in comparison to clear vegetated lakes. Hence, higher P_{max} in turbid shallow lakes than in clear ones might be expected in the same climatic region.

During the study period phytoplankton was strongly influenced by temperature and to a lesser extent, by DIN availability. Interestingly, under these conditions, periphyton still showed a slight response to phytoplankton growth and production, suggesting that the interactive competition between communities could be inferred even in conditions of an almost suppressed periphyton development. The autotrophic fraction of periphyton developed better during the colder months, with lower phytoplankton biomass and production. Another possible explanation for the low biomass and production of periphyton, besides light and nutrient competition with phytoplankton, is predation by for example, Chironomidae larvae, very frequent in the substrata (pers. obs.). As AFDW was mainly related to heterotrophic biomass (e.g., herbivores and bacteria) during most of the year, predation cannot be ruled out as a possible mechanism behind the observed responses in periphyton.

We are thankful to our colleagues from the limnology laboratory for their assistance in the field and to Dr María Solange Vera for her help in the laboratory too. The authors wish to thank to Dr Sonia Brugel who revised the English and commented on the manuscript and also to Dr Stefan Woelfl and two anonymous reviewers whose comments helped to improve the manuscript. This study was supported with grants from the Argentinean Agency of Scientific and Technological Promotion, ANPCyT (PICT 536), the University of Buenos Aires(X195, X815) and the National Scientific and Technical Research Council from Argentina, CONICET (PIP 5355).

References

Allende, L., Tell, G., Zagarese, H., Torremorell, A., Pérez, G., Bustingorry, J., Escaray, R., Izaguirre, I., 2009. Phytoplankton and primary production in clear-vegetated, inorganic-turbid, and algal-turbid shallow lakes from the pampa plain. Hydrobiologia 624, 45–60.

APHA, American Public Health Association, 2005. Standard Methods for the Examination of Water and Wastewaters, 21st ed. Centennial Edition. APHA, American Water Works Association, Water Environmental Federation, Washington, DC.

Eilers, P.H.C., Peeters, J.C.H., 1988. A model for the relationship between light intensity and the rate of photosynthesis in phytoplankton. Ecol. Modell. 42, 199–215.

Genkai-Kato, M., Vadeboncoeur, Y., Liboriussen, L., Jeppesen, E., 2012. Benthic-planktonic coupling, regime shifts, and whole-lake primary production in shallow lakes. Ecology 93, 619–631.

Hansson, L.A., 1988. Effects of competitive interactions on the biomass development of planktonic and periphytic algae in lakes. Limnol. Oceanogr. 33, 121–128.

Holm-Hansen, O., Helbling, E.W., 1995. Técnicas para la medición de la productividad primaria en el fitoplancton. In: Alveal, K., Ferrario, M.E., Oliveira, E.C., Sar, E. (Eds.), Manual de métodos ficológicos. Universidad de Concepción, Concepción, Chile, pp. 329–350.

Izaguirre, I., Sinistro, R., Schiaffino, M.R., Sánchez, M.L., Unrein, F., Massana, R., 2012. Grazing rates of protists in wetlands under contrasting light conditions due to floating plants. Aquat. Microb. Ecol. 65, 221–232.

Jäger, C.G., Diehl, S., 2014. Resource competition across habitat boundaries: asymmetric interactions between benthic and pelagic producers. Ecol. Monogr. 84, 287–302.

Jespersen, A.M., Christoffersen, K., 1987. Measurements of chlorophyll-*a* from phytoplankton using ethanol as extraction solvent. Arch. Hydrobiol. 109, 445–454.

Kirk, J.T.O., 2011. Light and Photosynthesis in Aquatic Ecosystems, third ed. University Press, Cambridge, UK.

Lepistö, L., Holopainen, A.L., 2003. Occurrence of Cryptophyceae and katablepharids in boreal lakes. Hydrobiologia 502, 307–314.

McBride, G.B., 1992. Simple calculation of daily photosynthesis by means of five photosynthesis-light equations. Limnol. Oceanogr. 37, 1796–7808.

Moss, B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201, 367–377.

Neale, P., Talling, J.F., Heaney, S.L., Reynolds, C.S., Lund, J.W., 1991. Long time series from the English Lake District: irradiance-dependent phytoplankton dynamics during the spring maximum. Limnol. Oceanogr. 36, 751–760.

Rodríguez, P., Pizarro, H., 2007. Phytoplankton productivity in a highly coloured shallow lake of a South American floodplain. Wetlands 27, 1153–1160.

Rodríguez, P., Tell, G., Pizarro, H., 2011. Epiphytic algal biodiversity in humic shallow lakes from the Lower Paraná River Basin (Argentina). Wetlands 31, 53–63.

Rodríguez, P., Vera, M.S., Pizarro, H., 2012. Primary production of phytoplankton and periphyton in two humic lakes of a South American wetland. Limnology 13, 281–287.

Utermöhl, H., 1958. Zur vervollkommnung der quantitativen phytoplankton-methodik. Mitt. Int. Ver. Theor. Angew Limnol. 9, 1–38.

Wetzel, R.G., 2005. Periphyton in the aquatic ecosystem and food webs. In: Azim, M.E., Verdegem, M.C.J., van Dam, A.A., Beveride, M.C.M. (Eds.), Periphyton: Ecology, Exploitation and Management. CABI Publishing, Oxfordshire, UK, pp. 51–69.