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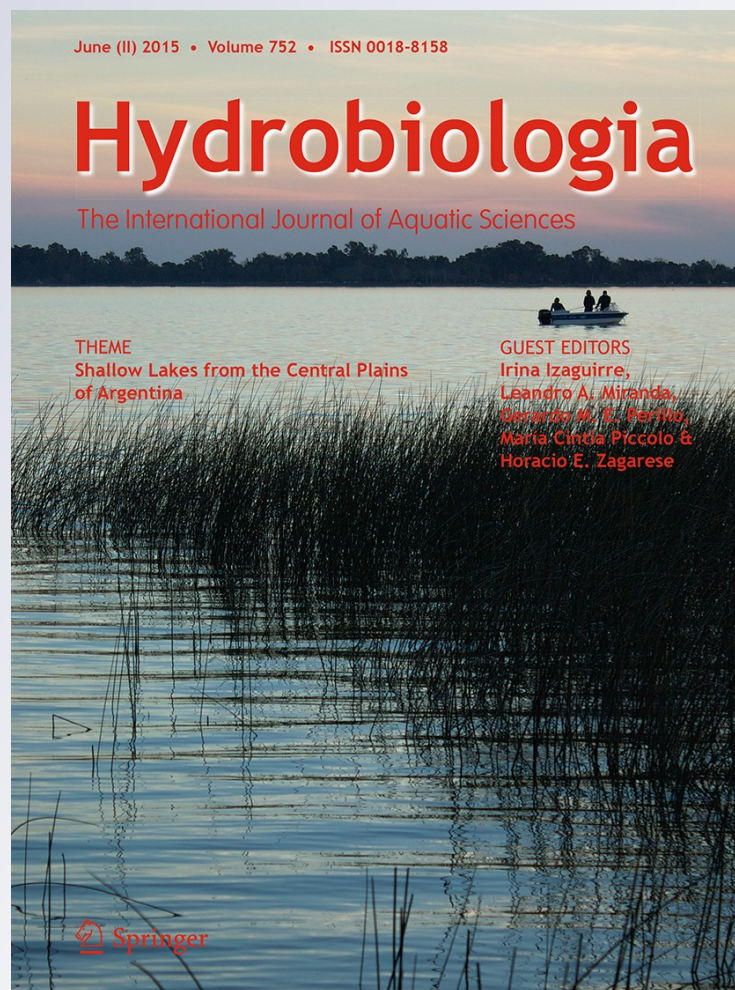
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# Estimation of ecosystem metabolism from diel oxygen technique in a saline shallow lake: La Salada (Argentina)

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**Abstract** Studies based on continuous monitoring of diel changes in dissolved oxygen concentration allow the estimation of ecosystem metabolism and provide a measure of the overall trophic processes of an ecosystem. In this study, net ecosystem production (NEP), community/ecosystem respiration ( $R$ ), and gross primary production (GPP) rates were estimated in relation to physicochemical and climatic variables for 18 months in La Salada, a saline shallow lake. Net autotrophic conditions prevailed during the study period (NEP:  $64.05 \pm 44.22 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ). GPP and  $R$  were positively correlated and were

synchronized on a daily timescale, with GPP typically greater than  $R$ . Principal component analysis revealed that monthly rates of GPP,  $R$ , and NEP responded, as expected, to temperature and light seasonal patterns. Water level and conductivity fluctuations, because of evapoconcentration and water management, were relevant as a driver of the physicochemical and biological characteristics of the lake. In saline lakes as La Salada, an adequate management of water resources will be relevant to maintain the ecosystem equilibrium and the quality of its resources.

**Keywords** Shallow lake · Lake metabolism · Saline lake · Time series

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## Introduction

Studies based on high frequency measurements of dissolved oxygen concentrations (DO) are becoming increasingly available and are a widely accepted method to examine ecosystem metabolism of aquatic systems, particularly in lakes (Cole et al., 2000; Gelda & Effler, 2002; López-Archilla et al., 2004; Lauster et al., 2006; Staher & Sand-Jensen, 2007; Laas et al., 2012). The continuous monitoring of diel changes in DO concentrations allows the estimation of temporal dynamics of gross primary production (GPP), ecosystem respiration ( $R$ ), and net ecosystem production (NEP) (i.e.,  $GPP - R$ ), which in turn provides relevant information in relation with the global carbon cycle (Laas et al., 2012; Solomon et al., 2013). GPP and  $R$  are the major metabolic pathways by which organic matter is produced and decomposed. Ecosystem metabolism provides a measure of the overall activity of an ecosystem, summarizing the biogeochemical and trophic processes and determining the efficiency of resource processing (Whittaker et al., 1975).

Odum (1956) proposed NEP as a measure of the trophic status of an ecosystem. The ecosystem can be classified in one of two possible states. When  $GPP/R > 1$  or  $NEP > 0$ , the system is considered as net autotrophic, so it can support and export organic material and/or accumulate it within the ecosystem. When  $GPP/R < 1$  or  $NEP < 0$ , it is classified as net heterotrophic, which implies that  $R$  is subsidized with allochthonous material imported from outside the ecosystem boundaries (Cole et al., 2000). Changes in GPP,  $R$ , and NEP were registered among lakes and over time within them and are the result of a combination of several factors. Supply of allochthonous organic material from the surrounding landscape and its subsequent degradation results in negative NEP values (Sand-Jensen & Staehr, 2007, 2009). Also, changes in the concentration of total phosphorus (TP), phytoplankton chlorophyll (Chl  $a$ ), and dissolved organic carbon (DOC) are reflected in long-term changes in ecosystem metabolism (Sand-Jensen & Staehr, 2007, 2009). Autotrophic lakes typically have high TP, high Chl  $a$ , and low DOC concentrations, whereas the more heterotrophic systems have low TP,

low Chl  $a$ , and high DOC (Hanson et al., 2003; Sand-Jensen & Staehr, 2007). Increasing DOC also enhances light attenuation in the water column which promotes net heterotrophic conditions due to GPP decrease (del Giorgio & Peters, 1994; Scully & Lean, 1994; Morris et al., 1995; Krause-Jensen & Sand-Jensen, 1998; Robarts & Waiser, 1998). In addition, nutrients and food web structure can interact to determine whether lakes and reservoirs are net sources or sinks for CO<sub>2</sub> by stimulating net production (Schindler et al., 1997; Pace & Cole, 2000) and increasing sedimentation rates (Flanagan et al., 2006). Also, climate variability influences lake temperatures and establishes strong stratification, promoting differences in the levels of light, oxygen, and nutrients throughout the water column (Staher & Sand-Jensen, 2007; Coloso et al., 2011; Laas et al., 2012).

About 75% of saline lakes are located in endorheic watersheds (Meybeck, 1995); therefore, as they are enclosed basins, all materials (i.e., nutrients, organic matter, salts) received and produced by these systems largely remain within the basin and are not exported downstream (Jones & Deocampo, 2003). Nevertheless, an unidentified percentage of these materials may be lost by infiltration into groundwater. As a result, saline lakes typically can support highly active biological communities (Hammer, 1981; Melack, 1981; Williams, 1981) with direct consequences in ecosystem metabolism rates. Also, high pH conditions in combination with elevated DOC concentrations and salt may bind phosphate (PO<sub>4</sub>) in prairie saline lakes, rendering PO<sub>4</sub> unavailable to phytoplankton (Waiser & Robarts, 1995). On the other hand, phytoplankton biomass (and GPP) is significantly less in saline lakes for a given TP concentration when compared to freshwater lakes (Campbell & Prepas, 1986; Robarts et al., 1992; Evans & Prepas, 1997). For all these reasons, the ecosystem metabolism of saline lakes may be significantly different from freshwater systems and requires special attention.

The hydrology of aquatic ecosystems is considered a significant factor in any water-body process (Wetzel, 2001). Shallow and deep lakes show different functional behaviors, depending on their morphology (Serruya, 1990; Mitsch and Gosselink, 2000). Shallow lakes are the most abundant lake types in the global landscape (Downing et al., 2006; Diovisalvi et al., 2014). Those located in the Pampean Region (Argentina) are mostly polymictic with high nutrient levels, ranging from eutrophic to highly hypertrophic

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(Quirós & Drago, 1999). The water renewal time and salinity are highly variable (Quirós et al., 2002; Echaniz et al., 2006) and depend mainly on local and regional precipitation and evaporation cycles. However, they also may be affected by infiltration into groundwater. The reduction in the extent of saline lakes due to climate variability and use of water are coupled with increased salinity (Williams, 1999, 2002), which affects the role of saline lakes in carbon cycling by reducing the active gaseous exchange surface. Also, alterations in precipitation patterns result in wetter climates with more export of DOC to lakes (Freeman et al., 2001), whereas shorter water retention times allow less time for degradation and hence, higher standing stocks of DOC (Hinton et al., 1997; Schindler et al., 1997; Tranvik & Jansson, 2002). GPP is thus strongly influenced by latitude, lake size, insolation, and nutrient availability (Tranvik et al., 2009). These factors have direct consequences on the aquatic communities and, consequently, on ecosystem metabolism (López-Archilla et al., 2004; Laas et al., 2012; Staher et al., 2012). Based on the significant differences between freshwater and saline lakes and the relative small number of studies in temperate and saline shallow lakes, the overall aim of this study was to determine the temporal dynamics and regulation of the ecosystem metabolism in La Salada

lake, located in the South of the Pampean region (Argentina). The results will allow comparison with other shallow and saline lakes worldwide and establish a precedent for future studies in this region which has a significant number of similar lakes.

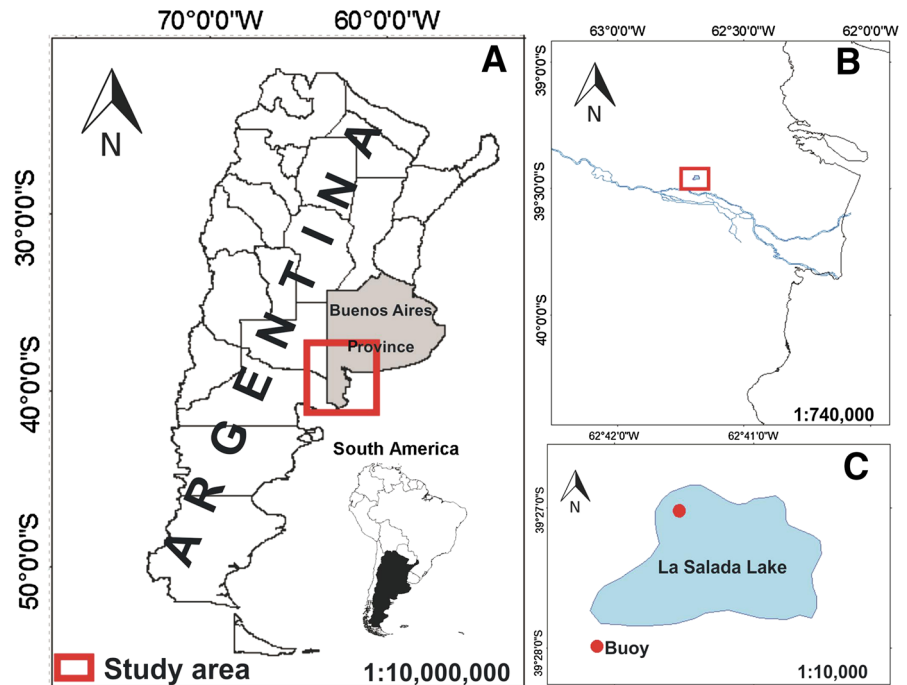
## Materials and methods

This study combines hydrological and physicochemical surveys covering 18 months from September 2012 to February 2014. This is the first data set based on a long-term monitoring program made on the lake (and in the whole country as well). The surveys included both monthly sampling (from October 2012 to January 2014), and high-frequency data (from September 2012 to February 2014) obtained with an instrumented buoy moored in the deepest part of the lake (Fig. 1C).

### Study site

La Salada ( $39^{\circ}27'S$ ,  $62^{\circ}42'W$ ) is a saline shallow lake located in the South of the Buenos Aires Province, Argentina (Fig. 1A, B). It is a small, shallow, and polymictic lake, with a total surface area of  $4\text{ km}^2$  and a mean depth of 2.5 m. Its main affluent is a channel

**Fig. 1** Location map of **A** the study area, **B** La Salada Lake, and **C** the buoy and sampling station



derived from the Colorado River. Water Authorities maintain and control the water level depending on the region water availability and crop irrigation needs. However, there is no outflow, and it behaves as an endorheic system where water loss is due to evaporation and possible groundwater infiltration.

The climate of the region is cold temperate and mostly dry, although characterized by wet and dry cycles that depend on the annual rate of rainfall. Annual atmospheric temperature values are between 14–20°C, with pronounced summers and winters, and moderate springs and autumns. The higher precipitation normally occurs in spring and summer, with an average annual rainfall of 518 mm (Scian, 2000). The dominant winds in the region are from the NW and, because of the lack of geographical barriers, they exert their influence all year long, being able to produce abrupt climate variability in the system.

#### Monthly physicochemical and biological measurements

Previous to defining a sampling site, vertical profiles of electrical conductivity, turbidity, DO, water temperature, and salinity were measured in situ using a HORIBA-U10 multiparameter probe along transects crossing the lake. This preliminary study allowed us to define the spatial homogeneity of most variables. Therefore, a unique sampling station was established close to the buoy.

Water for nutrient concentrations analysis was taken with a Van Dorn bottle at 0.5 m depth. Water samples were filtered through Whatman GF/F filters. Total phosphorus (TP) and total dissolved phosphorous (TDP) were estimated following APHA (1998). Particulate phosphorous ( $P_{\text{part}}$ ) was calculated as the difference between TP and TSP. Total organic nitrogen ( $N_{\text{org}}$ ) and total dissolved nitrogen (TDN) was determined by the semi-micro-Kjeldahl method (APHA, 1998). Particulate nitrogen ( $N_{\text{part}}$ ) was calculated as the difference between  $N_{\text{org}}$  and TSN.

Total suspended solids, also referred as seston, were determined by weighting the residue resulting from the filtration of a water sample through a membrane filter (0.45  $\mu\text{m}$ ) according to APHA (1998). Chlorophyll *a* (Chl *a*) concentration was estimated by an spectrophotometric method, with a SLM model 4800 fluorometer, using 90% acetone as the extraction solvent (Marker et al., 1980). Water

transparency was estimated with a Secchi disk. To assess the effect of rainfall on physicochemical values like salinity and metabolism rates, precipitation values were obtained from a meteorological station located 10 km from La Salada (INTA- Hilario Ascasubi <http://rian.inta.gov.ar/>). Considering that the region has very little relief and mostly devoid of forests, the values of this weather station can be considered as representative of the lake area.

#### High-frequency data

Continuous measurements of water and meteorological variables were obtained from September 2012 to February 2014. In 2012, a buoy (EMAC—Estación de Monitoreo Ambiental Costero) was moored approximately in the lake's deepest point. DO concentration, water temperature, water level, electrical conductivity, Chl *a* concentration, and turbidity were measured at 0.5 m depth. Also, air temperature and wind speed and direction were obtained from a meteorological station located on the buoy (2.10 m in height). To examine possible water temperature differences, a temperature sensor was deployed at a height of 0.1 m from the bottom (heretofore considered as bottom temperature sensor). All measurements were taken at 10 min intervals. Data is available on the web site <http://emac.iado-conicet.gob.ar/>.

#### Estimation of metabolism

Estimation of the ecosystem metabolism was based on the equations proposed by Odum (1956) and the guidelines presented in Staehr et al. (2010a), with modifications for saline and high wind environments based on Ho et al. (2006). Hourly NEP ( $\text{NEP}_h$ ) ( $\text{mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ ) was calculated as

$$\text{NEP}_h = \Delta\text{DO} - \frac{F}{z} \quad (1)$$

where  $\Delta\text{DO}$  is the change in DO concentration,  $F$  is the diffusive oxygen exchange of gas with the atmosphere, and  $z$  is the daily mean water depth. Our study differed from those in stratified lakes as we employed the daily mean depth ( $z$ ) instead of the mixing depth. This was determined on the basis of the shallow depth of the lake, the shape of the basin (flat and free from obstacles), and the continuous wind action, all of

which determine a polymictic condition (Scheffer, 1998; Quirós et al., 2002; Echaniz et al., 2006) for La Salada.  $F$  ( $\text{mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ ) was calculated as

$$F = k(\text{DO} - \text{DO}_{\text{sat}}) \quad (2)$$

where  $\text{DO}_{\text{sat}}$  is the concentration of oxygen in equilibrium with the atmosphere and  $k$  is the coefficient of oxygen exchange at a given temperature. As in this region high winds are prevalent, the coefficient  $k$  was computed from the Schmidt number ( $S_c$ ) and the gas piston velocity ( $k_{660}$ ), with a correction for high wind environments, using a 1/2 coefficient instead 2/3 (Ho et al., 2006)

$$k = k_{660} \left( \frac{S_c}{660} \right)^{\frac{1}{2}} \quad (3)$$

Also, as the Schmidt number is dependent on water temperature and salinity, to avoid errors, it was calculated at each time step using the DO-specific equation of Wanninkhof (1992), but using the coefficients for seawater instead of freshwater for this saline lake.

$$S_c = 1953.4 - 128.0T + 3.9918T^2 - 0.046527T^3 \quad (4)$$

The  $k_{660}$  was estimated based on the gas piston velocity ( $k_{600}$ ) proposed by Cole & Caraco (1998) as a function of wind speed at 10 m above the lake surface ( $U_{10}$ ), but with a correction for high wind environments.

$$k_{660} = (2.07 + 0.215U_{10}^{1.7})/100 \quad (5)$$

As the wind speed in the buoy is measured at  $h = 2.10$  m above the water ( $U_{2.1}$ ),  $U_{10}$  was calculated from the relationship given by Smith (1985), assuming a neutrally stable boundary layer

$$U_{10} = aU_{2.1} \quad (6)$$

where  $a$  is a correction factor given by

$$a = 1.4125h^{-0.15} \quad (7)$$

For calculation of GPP,  $R$ , and NEP, the fraction of the day when there was daylight (*dayfraction*) was calculated, in radians, from latitude and date of measurements, according to Iqbal (1983). Daytime NEP ( $\text{NEP}_{\text{daytime}}$ ), corresponding to NEP occurring during photosynthesis, was estimated as the mean

hourly NEP rate taking place between sunrise and sunset extrapolated over day length (Cole et al., 2000)

$$\text{NEP}_{\text{daytime}} = \text{mean NEP during daylight} \times \text{dayfraction} \times 24 \text{ h} \quad (8)$$

To calculate respiration ( $R$ ), we assumed that at night there is no photosynthesis; therefore,  $\text{GPP} = 0$  and  $R$  during nighttime is equal to NEP during nighttime. Also, we assumed that  $R$  during nighttime was equal to  $R$  during daytime (e.g., Staehr et al., 2010a, b; Laas et al., 2012). Hourly respiration rates ( $R_{\text{hr}}$ ), derived from changes in DO concentration during nighttime were extrapolated over a 24-h period to calculate respiration during the day ( $R_{\text{day}}$ ). So, respiration during daytime (sunrise-sunset) was calculated from mean  $\text{NEP}_{\text{hr}}$  during darkness ( $R_{\text{hr}}$ ) extrapolated over a day length

$$R_{\text{daytime}} = R_{\text{hr}} \times 24 \text{ h} \times \text{dayfraction} \quad (9)$$

$$R_{\text{day}} = R_{\text{hr}} \times 24 \text{ h} \quad (10)$$

Finally, since NEP during daytime is the result of the balance between GPP and  $R_{\text{daytime}}$ , GPP is the change in DO concentration due to  $\text{NEP}_{\text{daytime}}$  added to  $R_{\text{daytime}}$

$$\text{NEP} = \text{GPP} - R_{\text{day}} \quad (11)$$

$$\text{GPP} = \text{NEP}_{\text{daytime}} + R_{\text{daytime}} \quad (12)$$

Metabolism rates were daily integrated ( $\text{day}^{-1}$ ). Also, volumetric values of GPP,  $R$ , and NEP were multiplied by the daily  $z$  of the lake to get surface units ( $\text{m}^2$ ).

### Statistical analysis

Relationships between monthly variables were analyzed using correlation coefficients (Pearson or Spearman) and Principal Component Analysis (PCA) with SPSS and XLSTAT statistical software, respectively. Normality was examined by means of the Kolmogorov–Smirnov test (Zar, 1996). High-frequency data were spectrally analyzed using Fast Fourier Transform to define any potential periodicity of the variables (Bendat & Piersol, 2000). Previously, the original 10-min time series were filtered with a Butterworth filter with 1-h cutoff period. Further analysis was made applying wavelets (using the

Morlet model) to define the occurrence of the peak energy for each variable considered (Torrence & Compo, 1998). In all cases, we employed the Signal Processing and Wavelet Toolboxes both under Matlab® environment.

**Results**

**Physicochemical and biological variables**

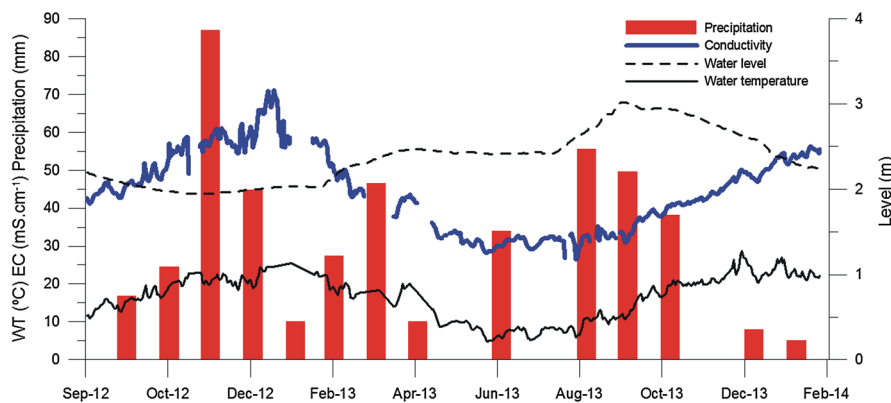
During the study period, rainfall was moderate. Maximum values were registered in September 2013 (55.5 mm) and December 2012 (87.0 mm) (Fig. 2). Water level fluctuated between 2 and 3 m (Table 1; Fig. 2). There were two significant inputs because the Water Authority opened the gates so water from the Colorado River entered in the lake. Unfortunately, they do not have an adequate control of the volume sent by this channel to the lake. The inputs correspond to the rainier seasons, one in February and another in August, both in 2013.

Winds predominate from NW and mean velocity was 24.7 km h<sup>-1</sup>, reaching over 100 km h<sup>-1</sup> in August 2013. Wind speed above 40 km h<sup>-1</sup> for several hours is a common feature in the region, allowing the development of short, steep waves. Time series of water temperature measured at the buoy varied between 7.0°C (July 2013) and 23.7°C (December 2013) following seasonal variability (Fig. 2). Similarly, bottom water temperature ranged between 8.0°C (July 2013) and 23.8°C (December 2013).

Water temperature from surface and bottom were strongly positively correlated ( $r = 0.99, P < 0.01$ ), this further supports the fact that the lake is not stratified. The pH (Table 1) was alkaline with little fluctuations. Conductivity was high (mean value of 44.7 mS cm<sup>-1</sup>) and highly fluctuating, showing a notable increase from winter to summer (Table 1;

**Table 1** Mean ± standard deviation (SD), minimum and maximum values of monthly meteorological, limnological and metabolic variables of La Salada Lake for the period September 2012–February 2014

Parameters	Mean ± SD	Minimum	Maximum
Wind speed (km h <sup>-1</sup> )	24.7 ± 4.8	11.1	31.0
Bottom water temperature (°C)	16.7 ± 6.1	8.0	23.8
pH	9.9 ± 0.3	9.3	10.5
Conductivity (mS cm <sup>-1</sup> )	44.7 ± 10.5	30.2	63.4
Salinity	34.0 ± 5.4	20.9	52.0
Turbidity (NTU)	28.5 ± 8.7	17.0	49.7
Secchi depth (m)	1.5 ± 0.6	0.6	2.9
Seston (mg L <sup>-1</sup> )	36.6 ± 28.1	6.0	89.0
TP (µg L <sup>-1</sup> )	100.3 ± 91.2	36.1	298.0
TSP (µg L <sup>-1</sup> )	74.8 ± 67.1	20.0	230.3
P <sub>part</sub> (µg L <sup>-1</sup> )	25.5 ± 33.5	4.0	120.0
N <sub>org</sub> (mg L <sup>-1</sup> )	5.262 ± 2.501	0.005	7.414
TSN (mg L <sup>-1</sup> )	3.500 ± 1.701	0.004	5.264
N <sub>part</sub> (mg L <sup>-1</sup> )	1.762 ± 1.192	0.001	4.166
DO (mmol O <sub>2</sub> m <sup>-2</sup> )	270.1 ± 59.8	174.1	376.8



**Fig. 2** Monthly precipitation values and conductivity, water surface temperature (water temperature) and water level daily values for the study period. Data discontinuities correspond to

periods of sensor cleaning and calibration. Bottom water temperature is not represented here as it is basically indistinguishable from the surface temperature



Fig. 2). It was negatively correlated with water level ( $r = -0.66$ ,  $P < 0.01$ ) and positively with water temperature ( $r = 0.87$ ,  $P < 0.01$ ). We also converted conductivity to salinity using the UNESCO (1981) conversion method considering the influence of temperature. This parameter was also high (mean value of 34) and fluctuating (Table 1). Despite the effect of high wind in vertical mixing, the lake presented high transparency for most part of the year, with a mean Secchi depth of 1.5 m and a mean turbidity of 28.5 NTU (Table 1). Also, seston concentrations were in agreement with the high transparency values, with a mean value of  $36.6 \text{ mg L}^{-1}$  (Table 1).

In general, nutrient concentrations were high and widely fluctuating. Mean value of TP was  $100.3 \text{ } \mu\text{g L}^{-1}$  (Table 1). Phosphorus concentrations (TP, TSP and  $P_{\text{part}}$ ) showed negative correlations with pH ( $r = -0.693$ ,  $r = -0.63$  and  $r = -0.70$ , respectively,  $P < 0.05$ ). Mean value of  $N_{\text{org}}$  was  $5.26 \text{ mg L}^{-1}$  (Table 1). The rest of nutrient values are presented in Table 1. Chl *a* concentration obtained from monthly measurements showed a mean value of  $8.6 \text{ } \mu\text{g L}^{-1}$ , and ranged between  $1.3 \text{ } \mu\text{g L}^{-1}$  (November 2013) and  $18.2 \text{ } \mu\text{g L}^{-1}$  (June 2013) with minimum values in spring and maximum values in winter (Fig. 3). It was positively correlated with TP concentration ( $r = 0.74$ ,  $P < 0.05$ ) and negatively correlated with light hours ( $r = -0.63$ ,  $P < 0.05$ ) and water temperature ( $r = -0.72$ ,  $P < 0.01$ ). High-frequency measurements of Chl *a* concentrations obtained at the buoy (Fig. 3) were slightly similar ( $r = 0.63$ ,  $P < 0.05$ ), with a mean value of  $6.8 \text{ } \mu\text{g L}^{-1}$ . This variable varied between  $2.7 \text{ } \mu\text{g L}^{-1}$  (January 2014) and  $17.9 \text{ } \mu\text{g L}^{-1}$  (September 2012). Also, similar significant correlations were found as happened with monthly Chl *a* except for conductivity ( $r = -0.38$ ,  $P < 0.01$ ), water level

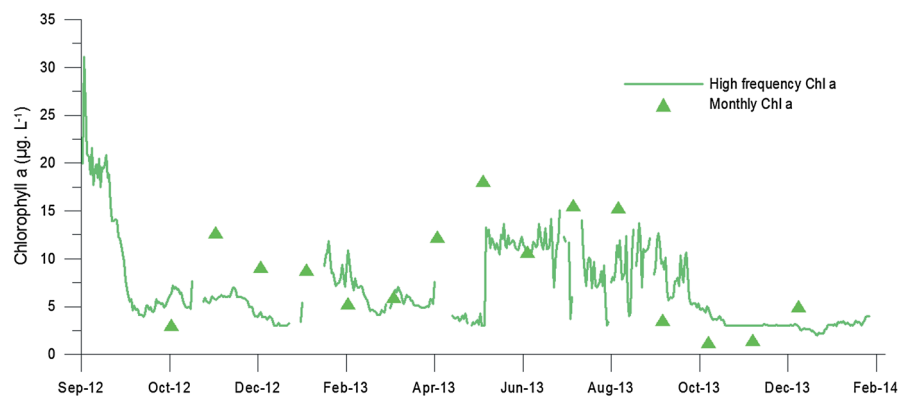
( $r = -0.9$ ,  $P < 0.05$ ), GPP ( $r = -0.19$ ,  $P < 0.01$ ) and NEP ( $r = -0.25$ ,  $P < 0.01$ ). DO concentration presented a mean value of  $270 \text{ mmol O}_2 \text{ m}^{-2}$  (Table 1). Data discontinuities corresponded to periods of sensor cleaning and calibration.

### Lake metabolism

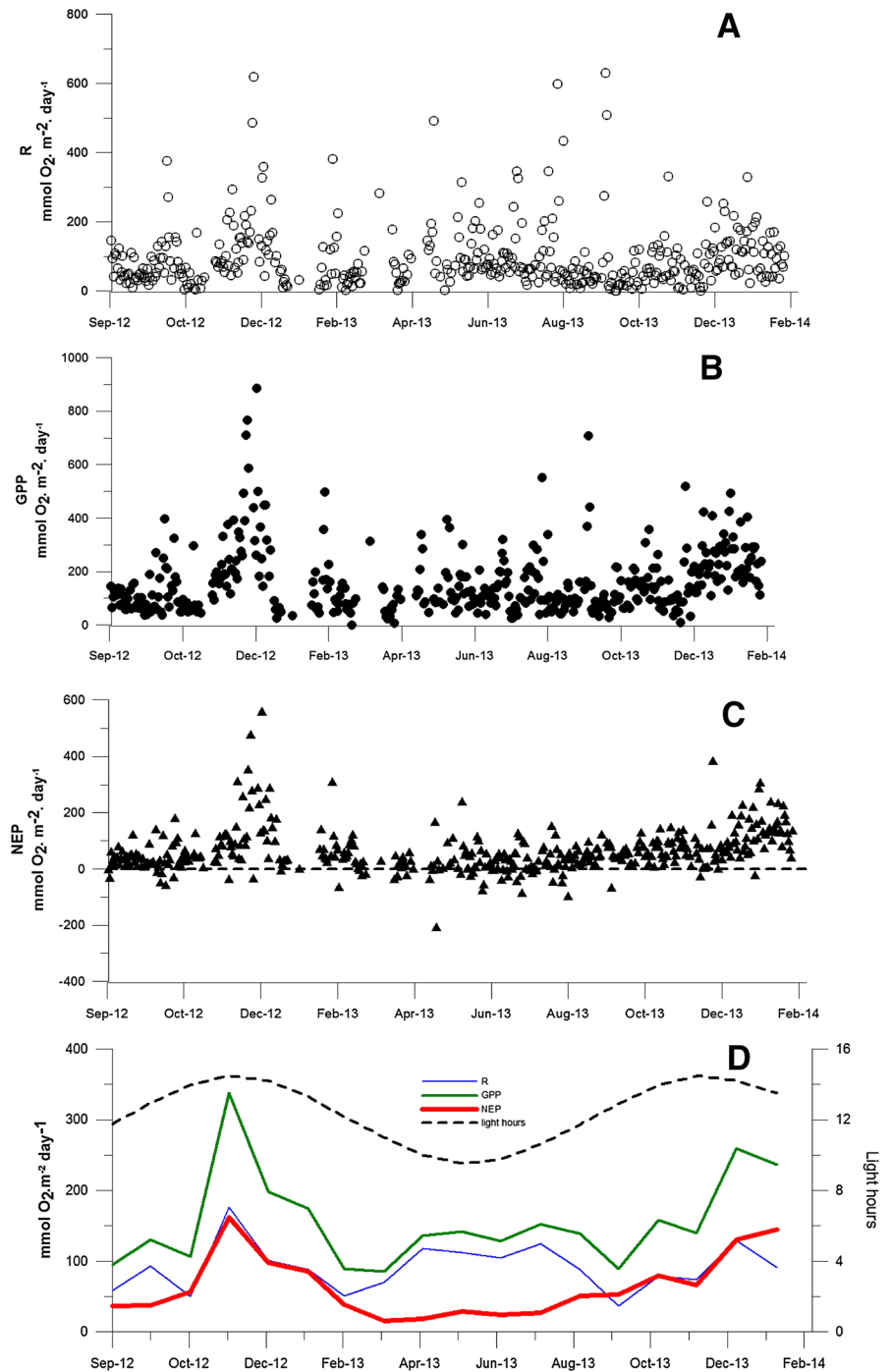
Rates of GPP and *R* showed daily and seasonal variations, with GPP exceeding *R* during the study period (Fig. 4). Monthly GPP ranged between  $85.6 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$  in April 2013 and  $338.3 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$  in December 2012, without a regular pattern throughout the study period. GPP increased in summer (January–February) and during the last months of autumn and winter (May–August 2013), while decreased at the beginning of autumn (March–April 2013) and in spring. February 2014 showed higher rates of GPP with respect to the previous year, when the Water Authority opened the channel to allow water inflow. In contrast, in August 2013, when the channel was opened again, GPP increased. Temporal variation in *R* followed a similar pattern and was positively correlated to GPP ( $r = 0.814$ ,  $P < 0.01$ ), but remaining below GPP during the study period (Fig. 4D). The minimum monthly *R* value was  $36.6 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$  in early spring (October 2013) and the maximum was  $176.4 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$  in late spring (December 2012).

NEP monthly values varied between  $15.5 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$  April 2013 and  $161.8 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$  in December 2012. Net heterotrophy ( $\text{NEP} < 0$ ) occurred in some sparse days during the study period (Fig. 4C), but predominated in the during autumn–winter season, when mean NEP values were below 0, varying between  $-0.9$

**Fig. 3** Monthly and high-frequency measurements of Chl *a* concentration during the study period. Data discontinuities correspond to periods of sensor cleaning and calibration



**Fig. 4** Calculated daily values of *R* (A), GPP (B) and NEP (C) and monthly values of *R*, GPP, NEP and light hours (D) in La Salada Lake during the study period



and  $-206.8 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ . If we average monthly NEP values for the study period, the lake presented net autotrophic conditions and the annual NEP rate was  $>0$ , with a mean value of  $64.1 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ .

#### Regulation of lake metabolism

Monthly rates of GPP, *R*, and NEP were regulated by temperature, light, conductivity, Chl *a* concentration,

water level, and wind action; therefore, we used these variables to integrate a PCA. The first three factors defined in the PCA correlation matrix explained 82.9% of the total variance. All the main variables are well represented in Axis I, except *R* (Axis II) and wind speed (Axis III) (Table 2). Three major groups are detected from a PCA plot for the first two factors (Fig. 5). The first group (Group I) includes summer months with higher NEP values, and high *R*, GPP, and conductivity values. In contrast, the second group (Group II), corresponding to autumn–winter months, is characterized by lower NEP and GPP values but with higher *R* and Chl *a* values. The third group (Group III) was characterized by the lowest or near to

the average NEP, GPP, and *R* values from the study period, which corresponded to spring (Fig. 5B).

NEP values showed that the net autotrophic conditions are related to increasing water temperature ( $r = 0.32$ ,  $P < 0.01$ ) and light hours ( $r = 0.32$ ,  $P < 0.01$ ), high conductivity values ( $r = 0.32$ ,  $P < 0.01$ ), and wind effect ( $r = 0.42$ ,  $P < 0.01$ ). In contrast, a negative relationship was found between NEP and water level and Chl *a* concentrations ( $r = -0.11$ ,  $P < 0.05$  and  $r = -0.25$ ,  $P < 0.01$ ). From May to September 2013, when the lake presented the highest water level and Chl *a* concentration, NEP values were lower. However, NEP increased with respect to the previous months (March–April 2013). These months are represented in Group II from PCA analysis (Table 2; Fig. 5B).

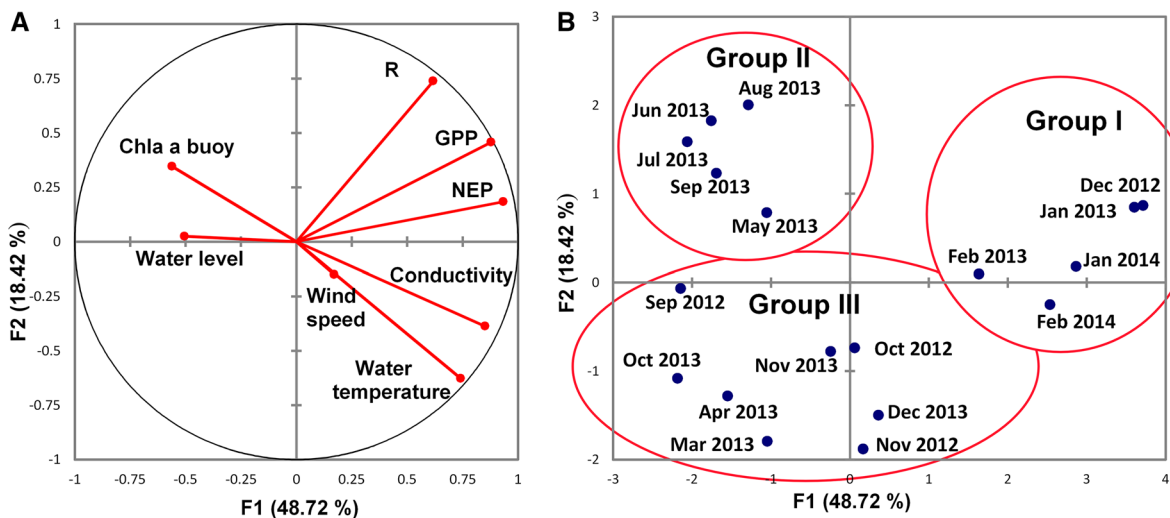
**Table 2** Principal component analysis: correlations between variables and factors

	Factors		
	I	II	III
Wind speed	0.171	-0.151	<b>0.569</b>
Water level	-0.504	0.025	<b>0.747</b>
Water temperature	<b>0.742</b>	-0.628	0.072
Conductivity	<b>0.851</b>	-0.388	-0.318
Chl <i>a</i> buoy	-0.560	0.345	-0.489
<i>R</i>	0.618	<b>0.738</b>	0.141
GPP	<b>0.879</b>	0.457	0.098
NEP	<b>0.933</b>	0.183	0.053

Boldface type indicates the major factor loadings on each axis

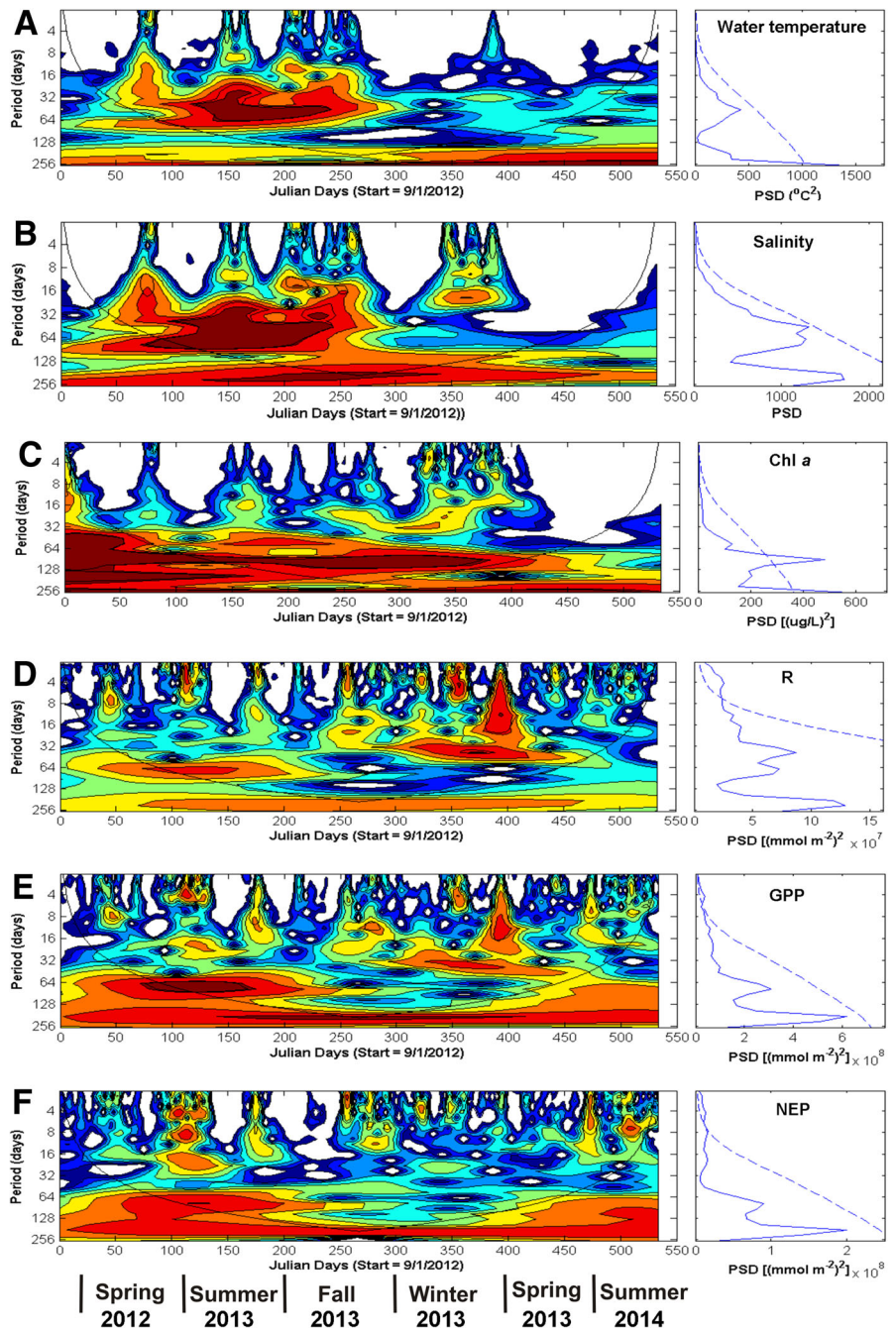
Time series analysis

Employing wavelet analysis to some of the time series measured and calculated during the study period allowed the identification of the changes in both the weather and lake conditions. Air temperature was similar for spring and summer months in both years; the fact that the water level in the lake was 50% higher in the last measurement period (Fig. 2) induced lower heat content in the water column which is reflected in the wavelet structure at periods of 32 and 64 days (Fig. 6A). Salinity (Fig. 6B) had more energy during the first summer at the same periods. Chl *a* had an even power distribution until the beginning of spring 2013



**Fig. 5** Principal Component Analysis plots for factors I and II: **A** main monthly physicochemical variables and metabolism rates and **B** studied months

**Fig. 6** Wavelet analysis plot of **A** water temperature, **B** salinity, **C** Chl *a*, **D** *R*, **E** GPP, and **F** NEP. *White areas* in the wavelet graphs correspond to periods where data is lacking due to sensor cleaning and calibration. PSD means power spectral density. The contours are at normalized variances of 0.0625, 0.125, 0.25, 0.5, 1, 2, 4, 8, and 16. Curved line represents the 95% confidence interval; therefore, all information below the curve is considered not significant



(Fig. 6C) concentrated in a 128-day period, but become stronger during the winter period. Unfortunately, we have high-frequency data only for one winter which does not allow further analysis if the process was unique or it could be repeated annually.

*R* (Fig. 6D), GPP (Fig. 6E), and NEP (Fig. 6F) all have peaks more or less concomitantly with the peak in temperature and salinity for the summer 2012–2013. They coincide in a 64-day period. However, both *R* and GPP have a secondary peak in late

winter and early spring 2013 but in a 32-day period which does not appear for NEP.

## Discussion

### Lake metabolism

Rates of ecosystem metabolism obtained from continuous oxygen measurements in La Salada Lake showed large variations on a daily basis and across seasons during the study period (Fig. 4). The general annual balance shows a net autotrophic state, with a NEP annual rate  $>0$  (NEP  $64 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ). From the studies that have dealt with ecosystem metabolism in shallow lakes, only a few were developed in saline environments. If La Salada NEP results are compared with previous studies developed in these systems, similar and also higher values were attained (e.g., Reati et al., 1997; Florín & Montes, 1998), but all of this measures were made at low frequency and only for a few months, mainly in summer. In comparison with freshwater lakes located in northern temperate regions, where high-frequency measurements are available, similar values were observed (e.g., Staher & Sand-Jensen, 2007). Nevertheless, in most of these systems, metabolism rates were calculated for summer periods and their values are lower than that estimated in this study (e.g., Laas et al., 2012). Finally, if La Salada is compared with other shallow lakes located at similar latitudes like Rotoiti and Rotorua (New Zealand) (Solomon et al., 2013), similar  $R$  and GPP values were observed, but with an annual NEP rate  $<0$ . These results suggest that La Salada is a highly productive lake in comparison with other lakes from temperate regions of the world.

A similar pattern between  $R$  and GPP rates was found (Fig. 4) and in agreement with other studies,  $R$  and GPP were positively correlated (Staher & Sand-Jensen, 2007; Laas et al., 2012; Solomon et al., 2013). Also, wavelet analysis results suggested a strong coupling between  $R$  and GPP, showing the same peaks in summer and winter seasons, unlike NEP which only presents a summer peak (Fig. 6D–F). Solomon et al. (2013) indicates that  $R$  was tightly coupled to GPP at a daily scale in oligotrophic and dystrophic lakes, and more weakly coupled in mesotrophic and eutrophic lakes, where substantial production escapes immediate respiration, and it is, instead, buried or exported

(Caraco & Cole, 2004). A possible reason for this is that  $R$  is coupled to GPP because, except at short timescales, autotrophs and heterotrophs organisms cannot collectively respire more autochthonous primary production than the autotrophs organisms produce (Solomon et al., 2013). Analysis of the data plotted in Fig. 4A, B suggested a daily coupling between  $R$  and GPP instead of a weekly coupling expected for a eutrophic system, with high nutrient concentrations. Cole et al. (2000) affirmed that when GPP rates exceed the rates of  $R$  above  $80 \mu\text{mol O}_2 \text{ L}^{-1}$ , a lake can be considered as net autotrophic. Along the study period, GPP exceeded  $R$  in much larger values, especially in the summer season (Fig. 4D), suggesting that  $R$  is supported mainly by the organic compounds originally produced by photosynthesis.

### Regulation of lake metabolism

The observed seasonal patterns were those usually expected as a result of variations in light and temperature. These observations were reflected in the PCA results (Table 2; Fig. 5) and the positive correlations found between metabolic rates and light and temperature values. This is also in agreement with other metabolism studies where summer peaks are common (Cole et al., 2000; López-Archilla et al., 2004; Staher & Sand-Jensen, 2007; Laas et al., 2012; Solomon et al., 2013). The integrated analysis of time series and correlation between metabolic rates and physicochemical variables demonstrated that most of the processes were strongly affected by the higher energy contained in the temperature, specifically during the summer 2012–2013 (Fig. 6A). In addition, during this period, water level was particularly low and therefore, the differences in the ecosystem behavior can be also attributed to the volume of the lake. Metabolic rates showed a significantly negative relationship with water level (Table 2; Fig. 5B) and positive with conductivity or salinity (Figs. 5B, 6B). The latter indicates higher evaporation rates and a concomitant increase in salinity through evapoconcentration which resulted in strong effects on the physical, chemical, and biological characteristic of the lake as it was observed in other studies (i.e., Hammer, 1986; Evans & Prepas, 1996; Williams, 1998; Anderson & Stedmon, 2007).

Changes in Chl  $a$  concentrations related to temperature, water level fluctuations, and consequent

conductivity variability have an important role in the regulation of ecosystem metabolism for this saline lake. In other studies, an increase in Chl *a* concentrations was reflected in increases of GPP and *R* rates (López-Archilla et al., 2004; Staher & Sand-Jensen, 2007; Laas et al., 2012; Solomon et al., 2013) but in this study, a negative correlation between daily measurements of Chl *a* and metabolic rates was found. This could be explained due to the higher Chl *a* values registered in winter months (Figs. 3, 5B, 6C), which was reflected in a small increment of *R* and GPP rates, but no large enough as during summer peaks. A literature analysis suggests that in lakes with high TP, high Chl *a*, and low DOC concentrations, net autotrophic conditions are expected (Hanson et al., 2003; Sand-Jensen & Staher, 2007). Considering nutrient concentrations, NEP > 0 conditions are commonly found in nutrient-rich productive aquatic ecosystems (del Giorgio & Peters, 1994; Schindler et al., 1997; Pace & Cole, 2000). The NEP rates found in this study are in agreement with our expectations according to the TP concentrations from La Salada (Table 1), but no respect to Chl *a* concentrations. Other possible cause is that the effect of DOM recalcitrance over nutrient availability for autotrophs might play an important role in the ecosystem metabolism for La Salada, reducing the expected phytoplankton productivity for these nutrient values. This situation was reflected in the positive relationship between Chl *a* and TP, and the negative one between TP and pH. Chl *a* concentrations were not as high as expected in comparison with Northern temperate lakes, but are in agreement with concentrations expected for saline alkaline lakes (Waiser & Robarts, 1995; Evans & Prepas, 1997; Waiser & Robarts, 2004).

The fact that GPP and *R* followed a similar pattern over time (Fig. 4), but with GPP above *R*, implies that La Salada produces significantly more organic material by photosynthesis than it is able to degrade. Therefore, most of this organic matter could be respired by bacteria and zooplankton and the excess may either be exported to adjacent systems or accumulate within the system in the sediment or as DOM in the water. Cole et al. (2000) affirm that when planktivorous fish dominate the food web, large zooplanktons are rare and nutrient enrichment produces positive values of NEP. Since in La Salada Lake, planktivorous fish are present (*Argentinian silverside*) and zooplanktons are dominated by

small-size zooplanktons, especially rotifers as *Brachionus plicatilis* (Alfonso et al., 2013) then, NEP > 0 conditions are expected, and this is in agreement with the results observed in this study; however, further studies will be needed in order to complete this assumptions.

Allochthonous input of DOM via streams is an important source of supplementary energy to community *R* (Staher et al., 2010b). In La Salada, two important water inputs coming from the main channel were observed during the study period (Fig. 2), one in February 2013 and another in August 2013. An increment in daily *R* and GPP rates was observed following these water inputs, and then NEP values changed from positive to negative, mainly in summer, where negative NEP values were already detected previous to the water input. This suggests that the supply of new organic material and phytoplankton organisms from the river would promote *R* and GPP, respectively. However, not static evidence was found. In addition, this was not reflected in the monthly metabolism rates (Fig. 4), highlighting the importance of high-frequency measurements and human management of water level fluctuations in connection. These are important factors to take into account in the development and maintenance of equilibrium in La Salada Lake as in other shallow and saline lakes.

## Conclusions

The present research in the saline and alkaline shallow lake La Salada revealed that temperature and conductivity variations due to evapoconcentration play an important role in the physicochemical and biological characteristics of the system. Also, the annual and interannual variation of water level seems to be a major factor influencing the ecological processes in the system. Although La Salada is characterized by high nutrient concentrations, they would not be totally available, because DOC has a recalcitrant effect in saline alkaline systems. Nevertheless, general NEP annual balance shows a net autotrophic state. Metabolism rates are within the values expected for a saline lake, being more productive than other temperate lakes, where unlike La Salada, metabolism measurements were performed mostly on free ice periods (spring-summer). Allochthonous input of DOM via

streams seems to be an important source of supplementary energy to community *R* which was reflected in daily metabolism rates, highlighting the importance of high-frequency measurements. Conductivity variability is an important key that influences the development and maintenance of equilibrium in the ecosystem, and it is strongly linked to natural water level fluctuations due to evapoconcentration and human management of water resources. They are important factors to take into account in La Salada Lake as in other shallow saline lakes. Future studies are needed to analyze the interactions between water level fluctuations and management, input of organic matter, trophic interactions, and how they affect metabolism rates in saline environments.

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