Phytoplankton primary production in freshwater environments of Argentina

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With 1 figure

Abstract: In this article we review the existing knowledge about phytoplankton primary production (PPP) studies conducted in freshwater environments of Argentina, as well as the methodologies used to assess it. The large geographical and temporal differences in physical, chemical and biological characteristics of the aquatic bodies have resulted in a wide range of PPP values. This, together with the different methodologies and approaches used to assess PPP, precluded for the determination of spatial and temporal trends. In regard to PPP studies, and when looking at the water bodies in Argentina as a whole, it is evident that lakes have been scattered sampled; moreover, information about rivers and streams is scarce or virtually absent. These facts clearly highlight for the need of continuing (in some cases) or starting (in most of the cases) monitoring programs of PPP (as well as of related variables) to further assess the impacts of human activities on aquatic bodies i.e., as those occurring due to climate change.

Keywords: lakes, phytoplankton, primary production, rivers, Argentina

Introduction

Continental aquatic ecosystems (e.g., lakes, rivers, reservoirs, streams) are key quantitative components of the carbon cycle at either global or regional scales (Cole et al. 2007) having an important role in the sequestration, transport and mineralization of organic carbon (Battin et al. 2009) and accounting for an important share of the World´s carbohydrates production. In particular Argentina, the fourth largest country in America, has an important number of freshwater bodies that may contribute for a significant proportion of the World´s continental phytoplankton primary production (PPP).

Primary production essentially depends on the photosynthetic process which can be resumed as:

$$6\ CO_2 + 6\ H_2O \xrightarrow{h\nu} C_6H_{12}O_6 + 6\ O_2 \qquad \text{Eq. 1}$$

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This process is carried out by autotrophic organisms that in aquatic ecosystems include phytoplankton, phytobenthos, periphyton and macrophytes. In particular phytoplankton (diatoms, dinoflagellates, cyanobacteria and autotrophic flagellates) are very important primary producers in aquatic bodies. In a simplified description, phytoplankton are unicellular organisms that move passively in the water column and thus their distribution and physiology are strongly conditioned by changes in the physical (e.g., turbulence, radiation), chemical (e.g., nutrients) and biological environment (e.g., competitors, grazers).

In this article we will review our present knowledge about PPP in freshwater bodies of Argentina. Argentina has a wide latitudinal coverage and variable orography thus freshwater bodies differ in their geomorphology, chemistry and biology (Quirós 1988). In the following paragraphs we will present the status of the methodology used as well as of our knowledge about PPP in continental Argentinean waters.

Methodological approaches

According to the methodology used, primary production can be expressed either as gross or net. Gross primary production refers to the total amount of CO_2 fixed into carbohydrates without considering any losses during respiration. Net primary production refers to the total amount of carbohydrates formed during photosynthesis minus losses due to respiration. Primary production is usually expressed as carbon fixed per unit chlorophyll a (chl a) per hour, the so called assimilation number that is commonly expressed in mg C (mg chl $a)^{-1}$ h^{-1}. In the water column, the assimilation number varies along the euphotic zone so another way to express PPP is by integrating the carbon fixed in some portion of the water column (e.g., from the surface to the bottom of the euphotic zone) thus PPP has units of mg C m^{-2} d^{-1}. The term primary production refers to a rate of carbon fixation and should not be confused with biomass, which is the mass (in terms of carbon content) of living organisms in the ecosystem (in our case, phytoplankton) at a given time, expressed in units of mg C m^{-3}. In some cases, it has been wrongly considered chl a concentration as biomass, however chl a measurements are good estimates of biomass only when the ratio of carbon to chlorophyll a (C/chl a) is known. This is especially important when assessing the integrated production in the water column, as not only the concentration of chl a will change with depth but also it will C/chl a due to differential acclimation of the cells to solar radiation.

The most common method for measuring PPP consists in doing in situ incubations by hanging bottles with phytoplankton samples at different depths in the water column, and measuring the changes in oxygen or carbon over time. Alternatively, simulated in situ incubations can be done by using neutral density screens that simulate the attenuation of solar radiation with depth. In any case, these techniques have some limitations (e.g., do not exactly mimic turbulent motions and light fluctuations, grazing and nutrient regeneration are usually neglected, excreted carbon is not discriminated) (see details in Holm-Hansen & Helbling 1995) and therefore the values obtained do not exactly represent PPP, but rather some approximation of it. Several techniques have been used to measure PPP and they can be resumed as follows:

a) Carbon incorporation: The use of radiocarbon to measure photosynthetic rates (Steemann Nielsen 1952) assumes that fixation and reduction of $^{14}CO_2$ can be equated to the rate of uti-

lization of $^{12}CO_2$, except for a slight isotope discrimination factor. Inorganic carbon exists in various forms (CO_2, H_2CO_3, HCO_3^-, and CO_3^{-2}) and their relative abundances in the water are dependent upon factors such as pH, temperature, and salt content. There is a rapid equilibrium between these carbon species, so that if radiocarbon is added in any form, it equilibrates rapidly among the others. This is important as phytoplankton utilize different forms of inorganic carbon. In this technique, radiocarbon is generally introduced in the sample as labeled sodium bicarbonate ($NaH^{14}CO_3$) and, after the incubation period, the amount of radiocarbon incorporated as carbohydrates is determined by liquid scintillation techniques (Holm-Hansen & Helbling 1995). This method provides (depending on the incubation time) a value that lies between gross and net productivity. The stable isotope ^{13}C may be also used in a similar way as described above for ^{14}C. Since the isotope is not radioactive, the measurement of ^{13}C must be done using mass spectrometry.

b) Oxygen production: The oldest and most direct measurement of PPP is through the measurement of dissolved oxygen in light and dark bottles. The dark bottle provides the rate of respiratory consumption of organic substrates therefore, from the comparison of oxygen values obtained in the light and dark bottles it is possible to obtain the gross primary production. Oxygen may be measured by the classic Winkler titration method or with oxygen electrodes (if phytoplankton biomass is relatively high). Some of the limitations of this method are that it requires relatively long incubation periods and that it has low sensitivity for oligotrophic waters.

c) Measurements of chlorophyll *a* (chl *a*) fluorescence: This technique (and some variations of it) allows for the estimation of photosynthetic performance from light-stimulated changes of the photosystem II. Estimations of the capture of photons by light-harvesting pigments, light reactions, thylakoid electron transport rate (ETR), regulatory feedback processes and other variables can also be obtained using this technique.

d) Estimation from remote sensors: Sensors on remote platforms (airplanes or satellites) are capable of estimating the concentration of chl *a* in surface waters by measurements of spectral changes of the upwelling light. This, in conjunction with other remotely sensed data, is used in algorithms to estimate the rate of PPP in the water column. There are many limitations in this methodology, and the reliability of the estimates depend on various factors, such as the phytoplankton distribution in the euphotic zone, nutrient status of cells, C/chl *a*, mixing conditions, temperature, underwater radiation field, etc. As upwelling light recorded by remote sensors mostly comes from the upper few centimeters of the water column, satellite estimates of PPP are more reliable for temperate and polar waters, where chl *a* concentrations are generally the highest in surface waters. Remotely-sensed data however, has the advantage that it can cover large geographical areas and long periods of time.

Solar radiation and the underwater light climate

The Sun constitutes the source of radiant energy, providing a wide range of wavelengths – infrared (IR, 700–2100 nm), photosynthetic active radiation (PAR, 400–700 nm) and ultraviolet radiation (UVR, 280-400 nm, arbitrarily subdivided in UV-B (280–315 nm) and UV-A

(315–400 nm)). The relative proportions of these wavebands reaching the Earth's surface are 55% of IR and 45% of UVR + PAR. The distribution of solar radiation at the ground level is mostly variable due to geographical (i.e., latitudinal) factors (Blumthaler & Webb 2003) being the tropical regions those that register the maximum solar irradiances. This latitudinal dependence is clearly exemplified in studies carried out along Argentina that showed that the energy ratio of 305 nm to 340 nm in the tropical sites (i.e., Jujuy) was 3–4 times greater than in sub-Antarctic ones (i.e., Tierra del Fuego) at the same time of the year (Orce & Helbling 1997, Vernet et al. 2009). Besides, altitude plays a significant role in the radiation climate and so, locations in high altitudes (e.g., Puna) receive higher radiation levels than their sea level counterparts. This is especially evident in the UV-B range, as determined in studies carried out in the Alps that reported a 10% increase in UV-B every 1000 m of altitude (Blumthaler et al. 1992). Additionally, the penetration of solar radiation is conditioned by the amount and composition of gases present in the atmosphere and particularly, UV-B wavelengths are strongly absorbed by stratospheric ozone. Thus, as a result of the Antarctic ozone "hole", polar areas receive increased UV-B radiation, especially during springtime, a fact that may have important consequences for organisms (Helbling & Villafañe 2014). Due to the dynamics of the polar vortex, the Patagonia area is sporadically under the influence of the ozone "hole" and thus, events of increased UV-B radiation are commonly registered, although they are relatively short in duration (Helbling et al. 2005).

In the water column, solar radiation is further attenuated due to the absorption by the water itself, and several particulate and dissolved materials (Kirk 1994). Particulate materials include both those of inorganic (e.g., sediments) and organic (e.g., phytoplankton) origin, and dissolved materials resulting from the decomposition of organic matter (DOM) due to microbial activity. The overall result of the absorption of solar radiation by dissolved and particulate materials is the exponential decrease of irradiance as a function of depth as follows:

$$E_z = E_0 * e^{-k_\lambda z} \qquad\qquad\qquad \text{Eq. 2}$$

where E_z is the irradiance at a specific depth (z), E_0 is the irradiance at the surface and k_λ is the attenuation coefficient that depends on the wavelength and provides information on how transparent or opaque a particular water body is.

Given the large number and variety of water bodies in Argentina, it is difficult to establish clear patterns in regard to their optical properties. Still, some features are worth of highlighting: Andean lakes are generally deep and relatively transparent as determined not only by early Secchi disk depths measurements (reviewed by Quirós & Drago 1999) but also with underwater radiometers. However, there are also shallow lakes in this area, in which high amounts of DOM (due to the presence of macrophytes in the littoral) cause important attenuation of solar radiation (Bastidas Navarro et al. 2009a). Therefore, large variability in PAR attenuation coefficients (k_{PAR}) is determined in the Andean region: For example, Villafañe et al. (2004) obtained k_{PAR} values that varied from 0.15 to 0.46 m^{-1} (Lake Moreno and Lake Morenito, respectively). In shallow lakes, k_{PAR} values of 0.59, 0.43 and 0.50 m^{-1} were determined for lakes Escondido, Morenito and El Trébol, respectively (Bastidas Navarro et al. 2009b). Other comparative study (Pérez et al. 2007) determined k_{PAR} values of 0.09 and 0.22 m^{-1} for Lake Correntoso and Lake Mascardi Tronador, respectively; the largest lake of the area i.e., Lake Nahuel Huapi was characterized as one of the most transparent (k_{PAR}

= 0.10 m^{-1}). It should be noted however, that k_{PAR} is also variable within a particular water body, as for example the Lake Mascardi that received variable input of suspended solids of glacial origin in different sections of the lake (Modenutti et al. 1998, 2013a, Laspoumaderes et al. 2013). Recent studies have determined important changes in the in the penetration of solar radiation in the water column in lakes Espejo, Correntoso, Nahuel Huapi, Gutiérrez and Mascardi, following the eruption of the Puyehue volcano. The ash and pumice discharged by the volcano into these lakes resulted in an increase in total suspended solids from 1.5 to 8-folds, with the concomitant decrease in penetration of solar radiation (Modenutti et al. 2013a, b).

In contrast to those relatively clear lakes of the Andean region, extreme k_{PAR} values (~ 60 m^{-1}) were registered in lakes of the Chaco-Pampa Plain (Allende et al. 2009) which are relatively shallow and contain high amounts of dissolved solids (Quirós & Drago 1999) and particulate materials (Torremorell et al. 2009). High k_{PAR} values were determined in Lake Don Tomás in La Pampa Province i.e., 50–70 m^{-1} due to a persistent bloom of cyanobacteria (Fiorda Giordanino et al., unpubl. data). Still, important variability in the optical characteristics are also observed in this area, as seen in a comparative study carried out by Sánchez et al. (2013) who determined a k_{PAR} range from 3.3 (Lake Kakel Huincul) to 45.1 m^{-1} (Lake Yalca). In other sites in the Lower Paraná River floodplain, such as the Laguna Grande, k_{PAR} showed seasonal variations from 3.8 to 20.4 m^{-1} (Rodríguez & Pizarro 2007, Rodríguez et al. 2012a, b) whereas in a nearby relictual oxbow lake the k_{PAR} range was 2.4-30.2 m^{-1} (Rodríguez et al. 2012a, b). These seasonal variations in k_{PAR} following the annual succession of phytoplankton were also determined in the Lake Cacique Chiquichano (Chubut Province) in the Patagonian Plateau, where k_{PAR} values varied between 0.44 and 12.5 m^{-1} (Gonçalves et al. 2007, 2010, Fiorda Giordanino et al., unpubl. data). Finally, in studies carried out in the Peri-Pampean Sierras (i.e., Lake La Angostura) Helbling et al. (2006) determined values of k_{PAR} of 1.7 m^{-1} during the summer, however, Medina et al. (2010) found relatively higher penetration of solar radiation at the same study site, with 83–86% (PAR) of incoming irradiances at 0.30 m. These differences are attributed to the fact that the former study was performed during the rainy season thus higher amounts of terrigenous material were transported to the lake.

An important parameter in aquatic primary production studies is the determination of the depth of the euphotic zone (z_{eu}, the depth of 1% of surface irradiance) which is the area where net carbon fixation occurs. Because of their high transparency, Andean oligotrophic lakes are those that present the deepest euphotic zones e.g., Lake Moreno Oeste with a z_{eu} = 35 m (Modenutti et al. 2004) in contrast with lakes from the Chaco-Pampa Plain where z_{eu} was < 1 m (Allende et al. 2009), similarly as found in an early study carried out at Embalse de Río Tercero (i.e., 1–3 m in summer and 5 m in winter) (Romero et al. 1988). Other important parameter is the optical depth (i.e., $k*z_{eu}$ = 4.6) which is very useful at the time to compare different environments (i.e., waters that differ in their attenuation coefficient) as it is not possible to use the physical depth due to the differential distribution of phytoplankton in the water column (Villafañe et al. 2001). The determination of the epilimnion depth (z_{ep}) is also important for PPP studies, as it delimits the area where most of phytoplankton cells are generally retained. In general, and for freshwater environments, z_{ep} is mostly conditioned by temperature and it can be defined as the depth where its maximum gradient is found; z_{ep} can be highly variable, for example of 25 m in the Andean lakes (Pérez et al. 2007) and of 7.5 m in Lake La Angostura in the Peri-Pampean Sierras (Helbling et al. 2006). From an ecological

point of view, it is also important to calculate the mean irradiance received by phytoplankton within the epilimnion, as the cells are moving within it and thus they are exposed to changing irradiances while moving in the water column, as:

$$I_{m(\lambda)} = \frac{I_{0(\lambda)}[1 - \exp(-k_{d(\lambda)}z)]}{k_{d(\lambda)}z}$$ Eq. 3

where $I_{0(\lambda)}$ is the irradiance at the surface at a certain wavelength, $k_{d(\lambda)}$ the attenuation coefficient, and z the depth of the epilimnion.

Finally, photosynthesis versus irradiance relationships (P vs. E curves) are useful tools at the time to establish the photoacclimation status of cells. P vs. E curves are characterized by diverse parameters, i.e. α (the light limited slope of the P vs. E curve), E_k (the light saturation parameter, i.e. the intercept between the initial slope of the P vs. E curve and P_{max}), β (the photoinhibition parameter, i.e. the negative slope of the curve at high irradiances) and P_{max} (the maximum rate of carbon fixation, i.e. maximum production) (Sakshaug et al. 1997). These parameters depend on several factors such as the irradiance level at which samples are exposed and the incubation period, species composition, physiological status of cells, previous light history, as well as the temperature and CO_2 concentration (Kirk 1994, Sakshaug et al. 1997).

Current knowledge about phytoplankton primary production in freshwater environments of Argentina

Specifically, and for lakes in Argentina, Quirós & Drago (1999) have defined six geographical regions: Puna, Chaco-Pampa Plain, Peri-Pampean Sierras, Andean Patagonia, Patagonian Plateau, and Misiones Plateau and Brazilian Shield-related systems (Fig. 1), each with specific characteristics and patterns that will condition PPP in geographical as well as in seasonal scales. The country as a whole, unfortunately, has been largely under-sampled in regard to PPP studies. Moreover, and to the best of our knowledge, no PPP data are available for the Misiones Plateau–Brazilian Shield related systems (i.e., the Misiones Province). In the following paragraphs we will present the information available for water bodies of these geographical regions.

a) Puna: This region that includes the western part of Salta and Jujuy Provinces is characterized by high-altitude salt lakes –the so called "salares" and "salinas". Helbling et al. (unpubl. data) have evaluated the photosynthetic response to solar radiation of natural phytoplankton samples from Lake Pozuelos (northwestern Jujuy Province, 3,600 m a.s.l.) during winter. At this site, phytoplankton was well acclimated to the high irradiance conditions, and the inhibition of photosynthesis evaluated via measurements of chl *a* fluorescence was < 10%, even though the samples were exposed to solar radiation under the worst case scenario (i.e., at the surface of the water).

b) Chaco-Pampa Plain: The water bodies in this area, which includes the central, Northern and some Eastern portions of Argentina, present important heterogeneity, from the very
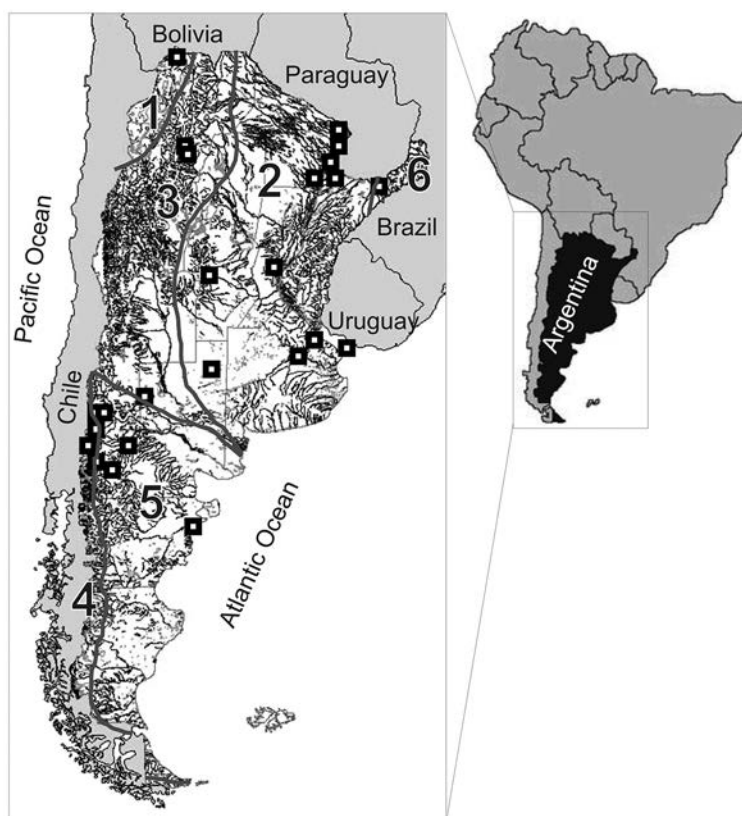
Fig. 1. Hydrographic basin of Argentina, including lakes, reservoirs and rivers. The lines indicate the limits of the six geographical regions as defined by Quirós & Drago (1999): 1) Puna; 2) Chaco-Pampa Plain; 3) Peri-Pampean Sierras; 4) Andean Patagonia; 5) Patagonia Plateau; 6) Misiones Plateau. The symbols indicate the sites were PPP studies have been done.

diluted lakes in the central and northwestern portions of the Corrientes Province, through the shallow lakes of central Pampa, to the high saline lakes in Buenos Aires, La Pampa and Córdoba (Quirós & Drago 1999).

Information on PPP in the Paraná – Paraguay – de la Plata basin is, surprisingly, very scarce in spite that it is the second in importance in South America (with large cities and industrial development in their coasts) after that of the Amazonas River. The early studies carried out in the Paraná River have reported high variability in integrated PPP along its main axis, ranging 10 to 990 mg C m^{-2} d^{-1} (Bonetto 1982, Bonetto et al. 1983, Perotti de Jorda 1984). The rates of PPP varied from 0.195 to 0.041 mg C m^{-3} h^{-1} (Perotti de Jorda 1980a, b) depending on the time of the year (in turn associated to factors such as amount of precipitation, turbidity conditions and taxonomic composition). Additionally, several studies have been conducted in lakes of the Lower Paraná River floodplain, which are generally shallow, and with high amounts of dissolved and organic materials (Rodríguez & Pizarro 2007) and with extensive mats of free floating plants (Caro 1983, O´Farrell et al. 2009). In spite of the prevailing limited light conditions Rodríguez

& Pizarro (2007) determined the highest P_{max} value (7.8 µg C (µg chl a)$^{-1}$ h^{-1}) when the water color was the highest, indicating that PPP was not limited as the different communities (mostly alternating between cryptophytes and cyanophytes) were well adapted to low solar radiation. Furthermore, in experiments devoted to understand the role of free floating plants in affecting the radiation climate and PPP and diversity in Laguna Grande, O'Farrell et al. (2009) found that even when the density of free floating plants was high, PPP was maintained, although biomass was low. However, when free floating plants density was low, nitrogen rather than solar radiation appeared to be limiting PPP. Additionally, recent extensive studies of P vs. E curves were carried out in this area, finding important seasonal variability in their parameters (Rodríguez et al. 2012a). Some studies have been also carried out in other lakes of the Paraná River basin i.e., Lake El Tigre, in the Middle Paraná River, where García de Emiliani (1993) determined the temporal variations in PPP as a result of the hydrological characteristics, with the highest values during the drainage/isolation and through-flow phases and the low ones during the filling phase, mainly due to replacement of species that occurred throughout the seasonal succession. In another study evaluating PPP in relation to the taxonomic composition in Lake Barranqueras (Chaco Province) Caro (1983) determined relatively high integrated PPP values i.e., 834 mg C m^{-2} d^{-1} during a cyanophyte pulse, whereas the values were much lower (< 100 mg C m^{-2} d^{-1}) during the rest of the study period. Very few studies were carried out in the Paraguay River i.e., those carried out by Bonetto et al. (1981) and Bonetto (1982) and later reviewed by Neiff (1990). As in the Paraná River, important spatial variability has been observed, with the integrated PPP ranging from 4 to 1250 mg C m^{-2} d^{-1} (Bonetto et al. 1981, Bonetto 1982) mostly related to phytoplankton concentration and water transparency, but independent of nutrient conditions (Bonetto et al. 1981).

As a result of the confluence of the Paraná and Uruguay rivers, the estuary of the Río de la Plata is formed. The Río de la Plata is considered one of the widest rivers of the World, and it constitutes a natural frontier between Argentina and Uruguay. The capital cities of both countries (Buenos Aires and Montevideo, respectively) lie on the opposite banks of the river. The Río de la Plata also hosts other important cities and large industrial facilities in its coasts, and its waters are used for several purposes, from drinking to waste sink, and shipping and recreation, among others. Because the Río de la Plata ends in the Atlantic Ocean, a salinity gradient in the NW-SE direction from < 1 (freshwater) to > 36 (seawater) is observed and thus PPP is highly variable along the main axis; for example, Gómez-Erache et al. (2002) gave values of integrated PPP of 4–14 g C m^{-2} month^{-1} for salinities < 4, and of 10–100 g C m^{-2} month^{-1} in the outer zone with high salinities. Calliari et al. (2009) carried out an extensive biological and physical sampling along the main axis of the river and they found that the rate of PPP was maximum in shallow, turbid waters with strong river influence (i.e., 64.2 mg C m^{-3} h^{-1} in the innermost station) but assimilation numbers peaked at the outer shelf in fronts or in upwelled Sub-Antarctic waters (i.e., 12–15 µg C (µg chl a)$^{-1}$ h^{-1}). Modeling of PPP in the area has been done by Huret et al. (2005) who coupled a biogeochemical to a hydrodynamic model of the estuary and the shelf. The model simulated well the low integrated PPP in the light-limited highly turbid tidal river (20 g C m^{-2} yr^{-1}), the high production area in the frontal zone where it can reach values up to 500 g C m^{-2} yr^{-1}, and the nutrient-limited production in the outer estuary and inner shelf (300 g C m^{-2} yr^{-1}).

Other studies were done in lakes of this geographical area, as those carried out in the shallow lakes of the Salado River (Buenos Aires Province). These lakes belong to one of

the following three categories: a) Clear with submerged macrophytes; b) Turbid dominated by phytoplankton and, c) Inorganic turbid, with high contents of suspended material, with low phytoplankton and absence of macrophytes. In particular, an extensive survey of phytoplankton taxonomic composition and PPP has been carried out by Allende et al. (2009) in these lakes characterized by different light conditions. The authors found that clear-vegetated lakes had relatively low PPP and photosynthetic efficiency (e.g., Lake Kakel Huincul: P_{max} = 0.641 mg C (mg chl a)$^{-1}$ h^{-1}), in contrast to turbid lakes that presented relatively high PPP (e.g., Lake San Jorge: P_{max} = 8.644 mg C (mg chl a)$^{-1}$ h^{-1}); obviously, not only the light climate but also taxonomic composition played a significant role in PPP, but other factors, in particular hydrology seemed to be important as well. Particular interest has received the eutrophic Lake Chascomús, which is one of the largest chained-lakes (i.e., interconnected by streams) of the Salado River. Early studies carried out by Conzonno & Claverie (1987) determined highly variable values of integrated PPP (37.9–981.6 mg C m^{-2} d^{-1}) and P_{max} ranging from 104.2 and 307 mg C m^{-3} h^{-1} throughout the annual cycle, mainly due to the influence of suspended particulate matter and hydrological changes. Subsequently, Romero & Arenas (1990) determined that phytoplankton with size < 10 μm contributed for the bulk of PPP in this lake. In recent studies carried out by Torremorell et al. (2007, 2009) the authors found that this lake was permanently light-limited due to the amount of suspended solids. These light-limitation conditions were further corroborated by the fact that the mean irradiance in the epilimnion was lower than the E_k; additional evidence of light limitation was provided by analyses of P vs E curves. However, and even under these light-limited conditions, annual PPP was as high as 2835.2 g C m^{-2} yr^{-1} (Torremorell et al. 2009). The high productivity of Lake Chascomús was also confirmed during mesocosms experiments carried out by Llames et al. (2009).

At the Embalse de Río Tercero, an artificial eutrophic reservoir (maximum depth = 40 m) located in the central Córdoba Province, several studies about PPP have been conducted in the 70´s and 80´s. In studies carried during 1977–1979 (Mariazzi & Conzonno 1980) the authors reported a range of values of gross PPP between 94 and 1279 mg O$_2$ m^{-2} h^{-1} for the winter and summer seasons. Further investigations were carried out during 1980–1981 by Nakanishi et al. (1985) who determined a range of PPP values between 0.4–2.1 g C m^{-2} d^{-1}. Finally, in the eutrophic, urban Lake Don Tomás in La Pampa, Fiorda Giordanino et al. (unpubl. data) carried out long-term studies throughout the annual cycle devoted to determine the photosynthetic performance of natural populations. The general response was of important daily inhibition of yield, with almost complete recovery in the afternoon, and with little variation throughout the duration of each experiment.

c) Peri-Pampean Sierras: This region comprises the whole "arid corridor" (except for the Puna) and it includes high and low mountain ranges, valleys and the so called "bolsones" (Quirós & Drago 1999). In the Tucumán Province it is located the Lake La Angostura, a protected reservoir that was created for watering, regulation of floods, fishery and touristic purposes. In this lake, Helbling et al. (2006) determined assimilation numbers as high as ~ 3 μg C (μg chl a)$^{-1}$ h^{-1} during early summer. However, in situ experiments carried out in winter in both Lakes El Cadillal and La Angostura showed surface phytoplankton photosynthetic inhibition due to PAR by as much as 16% and 20% respectively, as compared to samples incubated at 1 m depth (Helbling et al., unpubl. data; Helbling et al. 2006). Measure-

ments of chl *a* fluorescence also indicated a strong inhibition of PSII at noon (due to PAR) and only a partial recovery when the samples were under dim light; chronic inhibition of ~ 50% was still observed after the samples from both lakes were taken out from radiation stress for 15 hs. Other measurements conducted in parallel supported the idea that the combination of low solar radiation levels, together with deep mixing during winter, resulted in high inhibition rates due to the low-light history of cells in these environments.

d) Andean Patagonia: This area contains the largest and deepest glacial lakes in South America (Quirós & Drago 1999) as well as other small lakes. Patagonian rivers also originate in this area, feed the Patagonian Plateau and ultimately end in the Atlantic Ocean. An early review of PPP in lakes and reservoirs of the Andean region was done by Montecino (1991) who, based on measurements of P_{max} (INALI 1972, Maglianesi et al. 1973) calculated annual carbon fixation of 43.1, 35.2 and 63 g C m^{-2} yr^{-1} for lakes Mascardi, Guillelmo and Hess, respectively. In a comparative study among lakes with different optical characteristics Villafañe et al. (2004) determined higher carbon fixation rates in the opaque Lake El Trébol (~ 11 µg C l^{-1} h^{-1}) as compared with the clear Lake Moreno (~ 4 µg C l^{-1} h^{-1}) due to differences in their previous light history as well as in the taxonomic composition and size structure of the community. Studies carried out in shallow lakes of this area showed that the contribution of picophytoplankton to total PPP was, in general, very high, exceeding 50%. Furthermore, it was found that picophytoplankton (0.2–2 µm) were photosynthetically more efficient than the larger autotrophs (> 2 µm) although there was important photoinhibition in surface waters (Bastidas Navarro et al. 2009b). Similarly, a study evaluating PPP in picophytoplankton and larger autotrophs in deep oligotrophic lakes of the region – Mascardi, Moreno, Gutiérrez, Espejo, Correntoso and Nahuel Huapi (Callieri et al. 2007) found important photoinhibition in surface waters due to PAR resulting in high chl *a* and PPP in deep waters; moreover, photosynthetic efficiency increased with depth although it was higher in picophytoplankton, hinting for a higher fitness of this group to low light levels. In particular, PPP in the picophytoplankton fraction ranged between 44.7 and 95.2 mg C m^{-2} d^{-1} (Lakes Moreno and Gutiérrez, respectively). Additionally, the authors reported an inverse relationship between PPP in picophytoplankton and total dissolved phosphorus, demonstrating the competitive advantage of this size fraction under the prevailing low phosphorus conditions characteristic of these lakes (Callieri et al. 2007). It is interesting to note that in these deep oligotrophic lakes an important share of primary production is due to the presence of mixotrophic ciliates e.g., *Ophrydium* and *Stentor* containing endosymbiotic algae such as *Chlorella* (Modenutti et al. 2003, 2004; Modenutti 2014).

e) Patagonian Plateau: This is an arid region with artificial and natural lakes. Towards the west, and in close proximity to the Andean mountains region, it is located the Ezequiel Ramos Mexía Reservoir, in the border of the Río Negro and Neuquén Provinces. The reservoir was formed by damming of the Limay River during 1972. Studies carried out in this clear reservoir have described the PPP during the period 1981–1982, having the highest values during summer – 106.9 mg C m^{-2} h^{-1} whereas during the rest of the year PPP was ~ 25 mg C m^{-2} h^{-1} (Mariazzi et al. 1991). Another survey in this reservoir reported slightly high maximum values i.e., 173 mg C m^{-2} h^{-1} also during summer time (Di Siervi et al. 1995a, b). Depth profiles of PPP were characterized by important photoinhibition in surface waters, with the optimum PPP occurring around 25% of incident light (Mariazzi et al. 1991). In proximity

of the Ezequiel Ramos Mexía Reservoir it is located the Lake Pellegrini, another artificial reservoir in the Río Negro Province. For this site, Conzonno et al. (1981) reported P_{max} values of 5.8 mg C m^{-3} h^{-1} and, based on these data, Montecino (1991) determined an annual carbon fixation of 77.9 g C m^{-2} y^{-1}.

In the coastal side of the Chubut Province, studies have been done to evaluate diverse photosynthesis parameters of phytoplankton, i.e. the impact of solar radiation on the photochemical quantum yield (Y), as well as its potential recovery (i.e., when cells were no longer exposed to solar radiation). In the eutrophic urban Lake Chiquichano, the photosynthesis dynamics throughout the year was evaluated by Gonçalves et al. (2011) and Fiorda Giordanino et al. (unpubl. data) using PAM techniques. The authors determined important fluctuations in the taxonomic composition of phytoplankton communities, with cyanobacteria and diatoms alternating during the year. In particular, it was found that the ecological succession of phytoplankton is dependent on zooplankton abundance and on solar radiation, so that their temporal variations in turn influence photosynthetic parameters. In long-term studies it was seen, on daily basis, the typical pattern of yield decrease at noon, and recovery in the afternoon; however, and especially when cyanobacteria dominated, there was a trend of acclimation to solar radiation conditions towards the end of the experiments (Fiorda Giordanino et al., unpubl. data). Finally, and in studies carried out in the Chubut River estuary, Helbling et al. (2010) evaluated the effects of the tidal dynamics and physical forcing on phytoplankton distribution and photosynthesis dynamics. The authors found strong stratification during the flood and almost complete mixing during the period high tide–ebb–low tide. Strong stratification resulted in significant inhibition of photosynthesis of mostly nanoplankton cells at the surface, while microplankton sank out of this upper layer and thus, they were less inhibited. Mixing conditions during the ebb, together with relatively high concentration of dissolved organic matter and particulate material, resulted in partial protection for phytoplankton against solar radiation stress and, therefore, relatively high maximum ETR values were determined under this condition. However, the lowest photoinhibition and P_{max} values occurred at depth during stratified conditions, probably due to relatively low solar radiation in this condition.

Concluding remarks

The data set available, mainly through published articles, highlight for several difficulties at the time to get a global picture of PPP from a country that has many water resources. First of all, sampling seemed to respond to local interests and / or politics, rather than to provide an overall view of the country. This is observed not only in the cluster of sampling points in some areas (Fig. 1) but also in the lack of continuity in these studies. Therefore, it has been almost impossible to detect or control the impact of local events of anthropogenic origin on the water resources, or global problems such as climate change. Furthermore, most of the PPP studies have been carried out in lakes and lagoons, but we virtually lack of this information in several rivers and streams. In addition, different methodologies were used, therefore in many cases it was not possible to compare the data available or use them to obtain a more detailed or integrated information.

On the other hand, by highlighting in this article the present knowledge and the existing data on PPP in Argentina, we tried to focus not only on the limitations of the database, but also on the potential of future studies. By continuing with monitoring in sites where studies were already done in the past, and by starting in those where no data are currently available, we will be able to obtain a very important database that could be used not only for future studies but also to monitor our water resources.

Acknowledgments

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