

Drivers shaping phytoplankton diversity and composition in a humid Pampean floodplain lake (Natural Reserve)

Paula de Tezanos Pinto · Rubén Lombardo ·
Inés O'Farrell · Irina Izaguirre

Received: 11 April 2014 / Revised: 30 June 2014 / Accepted: 9 August 2014
© Springer International Publishing Switzerland 2014

Abstract We aimed to identify the driver/s of phytoplankton diversity (gamma, beta, alpha) and community composition in a Pampean floodplain wetland (Otamendi), using species and functional groups. We performed a seasonal regional survey (2004–2006, phytoplankton regime) across the different aquatic systems in the wetland. Gamma diversity was 254 species. Beta diversity was 2.53 in late spring, 2.49 in winter, and was lowest in summer (2.05) when the wetland was over flooded. Alpha diversity (mean richness) ranged between 29 and 50 species. Multiple regressions showed that phytoplankton alpha diversity (richness, Shannon–Wiener, evenness, and Simpson diversity index) responded to dissolved inorganic nitrogen, suspended solids, light attenuation, and pH. Nutrients also explained well the distribution of phytoplankton functional groups. Dissolved inorganic nitrogen concentrations were usually limiting in the shallow lakes, whereas phosphate concentration was always high. Light attenuation was mostly caused by

high suspended solids and high humic substances. We also re-analyzed data from a survey performed during a free-floating plant regime (1998–2000); the dense macrophyte cover attenuates most incoming light into the water column. Compared with the phytoplankton regime, the free-floating plant regime had markedly lower chlorophyll, lower alpha, higher beta (high heterogeneity among habitats with and without macrophytes), and similar gamma diversity.

Keywords Phytoplankton · Diversity · Functional groups · Wetland · Free-floating plants

Introduction

Wetlands of the Pampa region were included in different zones by Gómez & Toresani (1998), mainly according to the basins they belong. Considering this characterization, the Otamendi floodplain wetland is located in the Parano-Platense zone. The Otamendi wetland is a RAMSAR site (Convention on Wetlands of International Importance), which includes very productive systems characterized by high aquatic and terrestrial diversity (Revenga & Mock, 2000).

In floodplain wetland ecosystems, the hydrological pulse is usually a major shaping axis, including floods seasonality and water level variability (Junk et al., 1989). The Otamendi wetland has a complex hydrological regime, its aquatic systems are affected by

Guest editors: I. Izaguirre, L. A. Miranda, G. M. E. Perillo, M. C. Piccolo & H. E. Zagarese / Shallow Lakes from the Central Plains of Argentina

P. de Tezanos Pinto (✉) · R. Lombardo ·
I. O'Farrell · I. Izaguirre
Departamento de Ecología, Genética y Evolución,
Facultad de Ciencias Exactas y Naturales, Universidad de
Buenos Aires, IEGEBA (CONICET-UBA),
C1428EHA Buenos Aires, Argentina
e-mail: paulatezanos@ege.fcen.uba.ar

rains, *sudestadas* (strong southern winds typical in the region), the tides of the estuary of the Río de la Plata, and by sub-superficial connection with the Luján and Paraná rivers (Atlas Ambiental de Buenos Aires, 2010). Strong hydrological changes have occurred in the last decade in this wetland, related to cyclic climatologic phenomena (O'Farrell et al., 2011).

Water bodies in this wetland shift between a free-floating plant and a phytoplankton regime sensu Scheffer (2009), both in time (O'Farrell et al., 2011) and space (O'Farrell et al., 2003; Izaguirre et al., 2004; Chaparro et al., 2014). Field experiments show that dense free-floating plants mats (>75% cover) generate a strong decrease in light penetration (>90% attenuation), low oxygen levels, and affect phytoplankton composition (de Tezanos Pinto et al., 2007). Also, field experiments mimicking the shading caused by free-floating plants showed that phytoplankton diversity decreased because of persistent low light (O'Farrell et al., 2009).

The Otamendi wetland is characterized by colored waters, because of a high humic content (Rodríguez & Pizarro, 2007). This causes strong attenuation of the incoming light (ca. 60–70% attenuation, de Tezanos Pinto et al. (2007)), and the prevalence of red wavelengths (Kirk, 1994). Hence, light availability in the Otamendi wetland is markedly affected by patchiness of free-floating plants mats and/or by a high humic content (Izaguirre et al., 2004). Also nitrogen may be a limiting nutrient for phytoplankton development in this wetland (Unrein, 2001), whereas phosphorus levels are usually high. Phytoplankton diversity and composition in this wetland may be either affected by water level fluctuations, light, and/or nitrogen availability.

Diversity measures are informative and easy to interpret when comparing similar environments, and when applied to a well-defined taxonomical group (Magurran, 2008). Diversity can be measured at different scales, providing information at a local scale (alpha diversity), across communities (beta diversity), and at regional scale (gamma diversity). Alpha diversity focuses either on rare species (e.g. richness and Shannon–Wiener diversity index) or on abundant species (e.g. Simpson index) (Magurran, 2008). Beta diversity measures how different or similar communities are along a gradient or between habitats. The fewer the species shared among communities, the higher the beta diversity (Wilson & Mohler, 1983).

Finally, gamma diversity includes all species encountered in a region (Magurran, 2008).

The assessment of phytoplankton diversity is usually based on the number of species (e.g., richness) (e.g., Vyverman, 1996; García de Emiliani, 1997; Rodrigues Ibañez, 1998) and abundance (e.g., Shannon–Wiener and Simpson) (e.g., Zalocar de Domitrovic, 1990; de Melo & Huszar, 2000; Devercelli et al., 2014). Phytoplankton diversity can also be calculated in terms of species biomass (García de Emiliani, 1997; Huszar & Reynolds, 1997; Paidere et al., 2007; Borics et al., 2012). Very few studies have calculated diversity using both density and biomass (O'Farrell et al., 2009). It is unclear if calculating alpha diversity based on species abundance or biomass results in similar outcomes.

Another approach to study phytoplankton diversity is to classify phytoplankton into functional groups sensu Reynolds et al. (2002), pooling taxa which respond in similar way to a suite of ecological conditions into up to 40 groups (coda) (updated by Padisák et al., 2009). Functional approaches reduce system complexity by aggregating species with some shared role they play in a particular ecosystem (Simberloff & Dayan, 1991). The functional group approach sensu Reynolds et al. (2002) has been widely used as a tool for studying phytoplankton ecology in lakes, reservoirs, and rivers in multiple geographical regions (Huszar et al., 2003; Devercelli, 2006; Sarmiento et al., 2006; Abonyi et al., 2012; Izaguirre et al., 2012).

Although the functional approach has become popular in phytoplankton ecology, the diversity of functional groups is rarely analyzed (e.g., Borics et al., 2012; Pálffy et al., 2013). There is increasing evidence that using diversity measures based on the role of species in a community can yield a better understanding of community patterns than traditional taxonomic analyses (Pálffy et al., 2013 and cites therein). The relationship between species richness and functional group richness can be linear or logarithmic. The latter would indicate that there is redundancy in function at high species richness. As the complementarity of the species increases, the value of functional diversity becomes more strongly associated with species richness (Magurran, 2008).

The aim of this study is to identify, in the Otamendi floodplain wetland, the driver/s of phytoplankton diversity (alpha, beta, and gamma) and community

composition of species and functional groups, at spatial and temporal scales. We also aimed to study the relationship between (a) species and functional group richness, (b) each diversity index calculated using density or biovolume, and species or functional groups.

Our hypothesis and predictions are:

- (i) Extreme environmental conditions result in a decline of species and functional diversities. We expect lower alpha species and functional diversities associated with the free-floating plant regime or very low water levels.
- (ii) A high connectivity among aquatic systems constrains diversity by flood washing. We expect lower beta diversities during over-flow periods.

Materials and methods

Study site

The Natural Reserve of Otamendi (34°10′–34°17′S; 58°48′–58°53′O) is a RAMSAR site (Convention on Wetlands of International Importance), located in the Province of Buenos Aires, Argentina. It is delimited by the rivers Paraná de las Palmas and Luján. The climate in the region is humid temperate (Juliarena de Moretti, 1982). Winter and summer mean temperatures are 9.5 and 22°C, respectively (Chichizola, 1993). Precipitation occurs throughout the year, with annual means of 950 mm. The aquatic environments in this wetland include two shallow lakes (Laguna and Pescado), two relictual oxbow lakes, and a canal. The shallow Lake Grande is the largest water body (ca. 156 hectares, average depth is usually <1 m), the shallow Lake Pescado has a surface of about 39 ha, and the largest relictual oxbow lake has ca. 17 ha, with average depth of 0.3–1 m.

The development of free-floating plants can be very dense, mostly by duckweeds (*Lemna* L., *Azolla* Lam., *Wolffiella* Horkerl ex Schleid, *Salvinia* Seguiet and *Ricciocarpus natans* L.) and occasionally by water lettuce (*Pistia stratiotes* L.). The free-floating plant cover is variable, as these can be moved by wind action or killed by freezing temperatures in winter. Also emergent plants (*Schoenoplectus californicus* (C.A. Mey.) Palla, *Typha latifolia* L., *Scirpus*

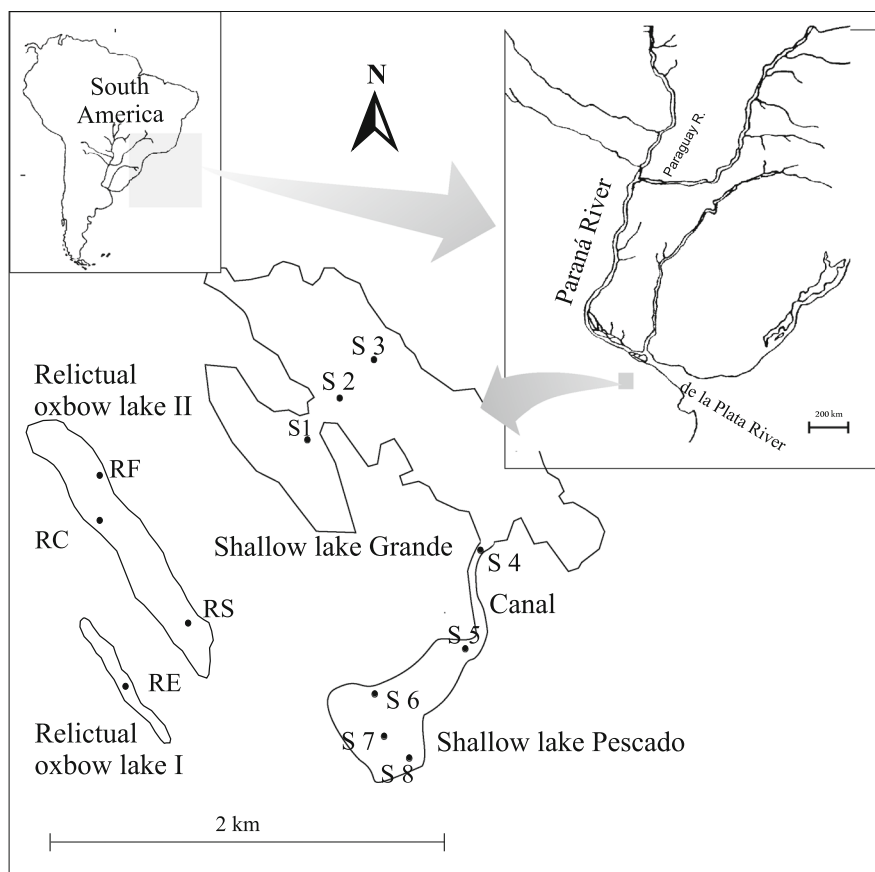
giganteus Kunth, *Sagittaria montividentis* Cham. & Schltdl. and *Zizaniopsis bonariensis* (Balansa & Poitr.) Speg.) grow in patches. In accordance to the descriptions of Williamson et al. (1999), the Otamendi floodplain wetland is an ecosystem of mixotrophic shallow lakes, characterized by high dissolved organic carbon and high total phosphorus concentrations.

Field sampling

We performed three regional surveys encompassing periods with different water levels: late spring (6 December 2004), winter (13 July 2005) and summer (24 January 2006) in 12 sites across the five aquatic environments in the wetland (Fig. 1). The sites chosen were RE in the small relictual oxbow lake (ROL I); RC, RS and RF in the big oxbow lake (ROL II); S1, S2, S3 in the shallow Lake Grande (SG); S4 and S5 in the canal (C) that connects the two shallow lakes in the wetland; and S6, S7, S8 in the shallow Lake Pescado (SP). Sites had different dominant vegetations. Throughout the surveys, RE was completely covered by emergent plants (*S. californicus*) while S1, S2, S5, S6, and S8 had few emergent plants. At the onset of the study, RC and RS had duckweed cover (*Lemna* spp.) of 100% and 50%, respectively, whereas in the following samplings duckweed became scarce or disappeared. Sites S3, S4, and S7 lacked macrophytes (emergent and free-floating plants) throughout the survey.

In the field we measured, conductivity, pH, and temperature (HI 991301 Hanna), dissolved oxygen concentration (HI 9143 Hanna) and photosynthetic active radiation (LI-193SA, Li-Cor, Lincoln, Neb., USA). We also collected samples for assessing nutrients, suspended solids and humic substances, and for quantifying phytoplankton chlorophyll *a*, density and biomass. In the laboratory, we analyzed reactive soluble phosphorus following Mackereth et al. (1978) and ammonium following APHA (2005). Nitrate concentrations were analyzed with HACH® reagents using the cadmium reduction method. For suspended solids, we first filtered the sample through dried and pre-weighted Whatman GF/C filter, then dried sediments until constant weight, and estimated its concentration by subtracting the weight of the filter with material to the filter without material. We quantified humic substances from the absorbance of the sample at 250 nm (Williamson et al., 1999).

Fig. 1 Map of the study area showing the twelve sampling sites in the five aquatic ecosystems in the Otamendi wetland during the phytoplankton regime (2004–2006). Sites RT, RC, S1, and S3 were also sampled in the free-floating plant regime (1998–2000)



For phytoplankton chlorophyll assessment, we first filtered the samples through fiberglass filters (Whatman GF/F) and stored them in the freezer. Next, we extracted pigments using hot ethanol (60–70°C) and measured chlorophyll with a spectrophotometer following Marker et al. (1980). We assessed phytoplankton density using an inverted microscope, following Utermöhl (1958), and then estimated biovolume using the formulas of Hillebrand et al. (1999) and Jun & Dongyan (2003). Phytoplankton species were identified to species and then sorted into functional groups sensu Reynolds et al. (2002).

We calculated phytoplankton gamma diversity as the total amount of species encountered in all surveys, following Magurran (2008) and beta diversity (β) following Whittaker (1960) ($\beta_w = (S/\alpha) - 1$, S = total number of the species in the system, α = average species richness). We measured alpha diversity (α) as richness, Shannon–Wiener index ($H = -\sum p_i \ln p_i$, p_i is the relative abundance of

the species $i = n_i/N$), Evenness (Shannon–Wiener/log (richness)), and reciprocal Simpson diversity index ($1/D = 1/\{\sum (n_i * (n_i - 1))/(N(N - 1))\}$, n_i is the density of the species i , N is the total number of organisms). A high reciprocal Simpson diversity index value reflects a higher diversity. We calculated all alpha diversity metrics for species and for functional groups, in density and biovolume.

We compared the data obtained in the current survey (2004–2006) with data from a period where the Otamendi wetland was characterized by a free-floating plant regime (1998–2000) (Izaguirre et al., 2001; ÓFarrell et al., 2003; Izaguirre et al., 2004). The sites compared were RT, RC, S1, and S3 (Fig. 1), which in 1998–2000 formed an ecotone from dense free-floating plants mats (100% cover) to complete absence of macrophytes. In 2004–2006, however, these four sites generally remained without free-floating plant cover. The seasons compared were late spring (18 December 1998), summer (22 January 1999), and winter (23 July 1999).

Statistical analyses

Phytoplankton regime (2004–2006)

We used analysis of variance to test for differences in the alpha diversity indexes among sites (Magurran, 2008) and the Tukey test for multiple pairwise comparisons. We tested normality and homoscedasticity. In cases of heteroscedasticity, we used the tests of Welch, Brown–Forsythe, and Games–Howell. Bootstrap re-sampling was also performed. We used the Pearson’s correlation coefficient (r) to estimate the correlation between phytoplankton richness of species and of functional groups ($n = 12$ sites \times 3 samplings = 36). We assessed bivariate normality using the Shapiro–Wilk test. We applied model II regression to estimate linear and nonlinear relationships—log, exponential, potential—(Sokal & Rohlf, 1995). We also used the Pearson’s correlation coefficient to estimate the correlation between diversity indexes calculated: (i) on densities and biovolume and (ii) on species and functional group basis.

We run multiple regression models to assess the relationships between the different alpha diversity indices and the environmental variables. For this, we performed stepwise forward selection, and the significantly important predictor variables were only incorporated in the model. A linear response model was selected analyzing the length of gradient in a detrended correspondence analysis (DCA) (ter Braak & Smilauer, 2002). Hence, we used Redundancy analysis (RDA) to find the relationships between functional groups composition and the environmental variables. The effects of water level (high/low) and of floating plants (presence/absence) were introduced into the models as additional dummy variables (Zar, 2010). We performed forward selection of the environmental variables to extract synthetic gradients that explain the variation in functional group composition. Significance of the canonical axes was tested using Monte Carlo permutation of samples (Leps & Smilauer, 2003). For the multivariate analyses, rare functional groups occurring in less than 5% in all samples were removed without much influence in the analysis.

Free-floating plant regime (1998–2000)

We re-analyzed the phytoplankton data of a survey run during 1998–2000 when the wetland was dominated by free-floating plants. We sorted species into functional groups, and calculated gamma, beta and alpha (richness,

Shannon–Wiener, Evenness and Simpson) for species and functional group diversity. We run one-way ANOVA to compare the mean of the variables between the free-floating plant and the phytoplankton regimes.

Results*Phytoplankton regime (2004–2006)**Environmental variables*

The accumulated rains of the month previous to each sampling date were 66 mm in late spring, 108 mm in winter, and 255 mm in summer. In summer the water level was about 10 cm higher than in all other periods, and the aquatic systems in the floodplain were connected by superficial water (flood). The shallowest environments were the relictual oxbow lakes I and II, and the shallow Lake Pescado; the deepest sites were the shallow Lake Grande and the canal (Table 1). The water temperature was above 22°C in both warm periods and was approximately 10°C lower in winter. Mean pH ranged from neutral to basic, and was similar across environments and sampling periods (Table 1).

Conductivity was high (means between 2347 and 4,297 $\mu\text{S cm}^{-1}$) and markedly changed across sampling periods; the relictual oxbow lake II had the highest conductivities (Table 1). Dissolved oxygen ranged from suboxic to anoxic in both relictual oxbow lakes, and the shallow Lake Grande, but was higher in the canal and shallow Lake Pescado (Table 1). The concentration of humic substances was approximately twice higher in the relictual oxbow lakes than in the shallow lakes system (Table 1); humic substances were positively correlated with conductivity ($r = 0.86$, $P = 0.0001$). Suspended solids were about twice higher in the relictual oxbow lake II and shallow Lake Grande, than in the other systems (Table 1).

The attenuation of incoming light was higher in the relictual oxbow lakes than in the shallow lakes system and markedly changed across samplings (Table 1). In the relictual oxbow lake I, which was completely and persistently covered with emergent plants, the sub-superficial light was at least ten times lower than in the other environments (mean 37.14 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) (Table 1).

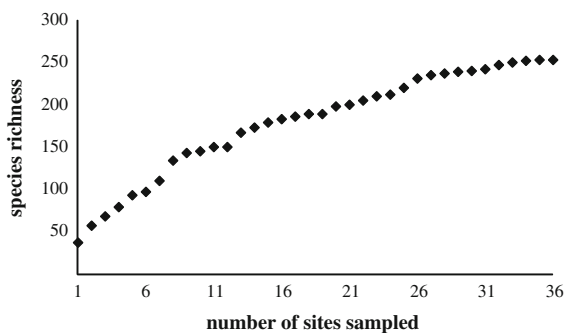
Phosphate concentrations were always very high (mean range 864–3,857 $\mu\text{g l}^{-1}$) and markedly

Table 1 Main environmental characteristics in the five environments studied in the Otamendi floodplain wetland (sorted by spatial distribution)

Variables	ROL I	ROL II	SL Grande	Canal	SL Pescado
Depth (cm)	24.5 ± 0.7	30.7 ± 8.6	50.3 ± 21	64.0 ± 13.8	31.6 ± 7.5
pH	7.8 ± 0.8	8.1 ± 0.6	8.3 ± 0.3	8.2 ± 0.1	8.2 ± 0.2
Conductivity ($\mu\text{S cm}^{-1}$)	2,803 ± 2,511	4,297 ± 2,106	2,347 ± 1,164	2,468 ± 1,224	2,500 ± 1,216
Dissolved oxygen (mg l^{-1})	3.5 ± 3.4	6.0 ± 4.5	4.8 ± 3.2	7.2 ± 0.6	6.4 ± 2.2
Humic substances (Abs.)	3.1 ± 1.8	3.3 ± 1.4	1.7 ± 0.4	1.5 ± 0.3	1.5 ± 0.3
Suspended solids (mg l^{-1})	38.3 ± 16.8	62.4 ± 37.7	69.2 ± 105.1	38.8 ± 21.8	39.8 ± 29.1
Light attenuation (%)	62 ± 68	76 ± 89	59 ± 77	50 ± 86	55 ± 81
Phosphate ($\mu\text{g l}^{-1}$)	3,857 ± 4,431	1,031 ± 1,148	1,107 ± 1,276	694 ± 170	864 ± 757
Dissolved inorganic N ($\mu\text{g l}^{-1}$)	242 ± 132	246 ± 174	162 ± 142	296 ± 364	202 ± 223
Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	94.0 ± 81.1	89.3 ± 38.1	72.2 ± 46.5	36.1 ± 33	36.3 ± 28.1

Values represent the mean and standard deviation for the studied period, in each environment. Sites within each system: ROL I = RE, ROL II = RC, RS and RF, SL Grande = S1, S2, S3, Canal = S4 and S5, SL Pescado = S6, S7, S8

ROL relictual oxbow lake, SL shallow lake

**Fig. 2** Cumulative gamma diversity in the Otamendi wetland during the phytoplankton regime (2004–2006)

changed across samplings (Table 1). Dissolved inorganic nitrogen (ammonium + nitrate) was usually low, particularly in the shallow lakes system (mean of 162–296 $\mu\text{g l}^{-1}$), and markedly changed across samplings (Table 1). Mean phytoplankton chlorophyll *a* ranged between 36 and 94 $\mu\text{g l}^{-1}$; its concentration markedly changed across samplings (Table 1). Free-floating plants occurred only in late spring (RC, S1 and S8 >75% cover, and RS <50% cover) and winter (S1 >75% cover, and RC, S5 and S7 <50% cover), accounting for 8 of the 36 sampled sites.

Phytoplankton diversity

Gamma diversity for the whole study was 254 phytoplankton species (in 20 functional groups). It increased with the area and samplings up to sampling

number 33, after which it leveled off (Fig. 2). Green algae presented the highest species richness (63), followed by diatoms (42), cyanobacteria (34), and euglenoids (22); chrysophytes, cryptophytes, and xanthophytes had 4 species each, and dinoflagellates only one species.

Beta diversity was similar in late spring and winter (2.53 and 2.49, respectively), but was lower in summer when the wetland was flooded (2.05). Regarding alpha diversity, mean richness ranged between 29–50 species and 13–15 functional groups (Table 2). The average Shannon–Wiener and Simpson indexes calculated on species—in density and biovolume—were similar; values were lower when calculated using functional groups (Table 2). Evenness, however, was similar for species and functional groups, both in density and biovolume (Table 2). We found absence of correlation between diversity indexes calculated on density and biovolume basis (e.g., Shannon–Wiener index calculated on species densities and biovolume), but positive and significant correlations for all indexes calculated on species and functional groups (either on density or biovolume basis) ($r = 0.76$ – 0.86 , $P < 0.0001$), except for Shannon–Wiener index based on density ($r = 0.34$). The shallow lakes system (Grande, Canal, and Pescado) had higher Shannon–Wiener index (in density of species) than both relictual oxbow lakes ($P = 0.022$).

The linear model was the best fit to the relationship between phytoplankton species and functional group

Table 2 Range of phytoplankton mean alpha diversity in the five aquatic systems of the Otamendi floodplain wetland measured in species and functional group basis

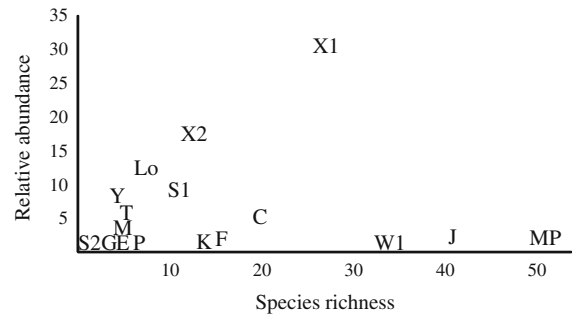
Diversity	Species	Functional group
Richness	29–50	13–15
Shannon–Wiener	Density: 2.0–3.8	Density: 2.1–2.5
	Biovolume: 2.8–3.6	Biovolume: 2.2–2.7
Evenness	Density: 0.6–0.7	Density: 0.6–0.6
	Biovolume: 0.5–0.7	Biovolume: 0.6–0.7
Simpson	Density: 5.3–8.1	Density: 3.1–4.2
	Biovolume: 5.5–7.7	Biovolume: 3.4–5.3

Table 3 Results of the stepwise multiple regression analysis for the phytoplankton alpha diversity indexes, in terms of species and functional groups

Diversity	Species	Functional group
Richness (<i>S</i>)	$S = -\text{NO}_3 + \text{SS}$ (0.55)	$S = -\text{NO}_3$ (0.34)
Shannon–Wiener (<i>H</i>)	H density = pH (0.42)	H density = $-\text{NO}_3$ (0.42)
	H biovolume = $-\text{SS} - \text{light attenuation}$ (0.50)	H biovolume = $-\text{SS} - \text{pH}$ (0.50)
Evenness (<i>J</i>)		$J = \text{DIN}$ (0.38)
	$J = -\text{SS} - \text{light attenuation}$ (0.47)	$J = -\text{SS}$ (0.39)
Simpson (<i>D</i>)		$D = -\text{NO}_3$ (0.41)
		$D = -\text{SS}$ (0.41)

Only significant ($P < 0.05$) predictor variables are included. Pearson correlation coefficients (r) are given in brackets. Evenness is calculated using the Shannon–Wiener index SS suspended solids, DIN dissolved inorganic nitrogen

richness (the greatest $r = 0.58$ and lowest ANOVAs residual mean square, $P = 0.0001$); the slope of the functional regression was $b = 0.11$ (95% confidence limits: 0.05–0.16). The multiple regression analysis shows that the drivers shaping phytoplankton functional group alpha diversity were dissolved inorganic nitrogen (DIN), suspended solids, and pH (Table 3). For phytoplankton species, also light attenuation drove the diversity response (Table 3). The drivers shaping phytoplankton diversity (either species or functional groups) differed depending if phytoplankton was estimated by density or by biovolume (Table 3). For example, when functional groups were

**Fig. 3** Phytoplankton functional group richness and relative cumulative abundance (36 samplings) of the 20 functional groups recorded in the Otamendi wetland during the phytoplankton regime (2004–2006). Note that $S2 = SN$ and $E = H = W2$

quantified on density, low nitrate was the main driver for richness, Shannon–Wiener, Evenness, and Simpson indexes. Conversely, when functional groups were quantified on biovolume, the main drivers of Shannon–Wiener, evenness and Simpson indexes was (generally) decreased suspended solids (and pH to a lesser extent) (Table 3).

Phytoplankton composition

Functional groups with intermediate species richness displayed higher relative accumulated density (throughout the study period, 36 samples) than functional groups with or low or high species richness (Fig. 3). The most important variables explaining the distribution of the dominant phytoplankton functional groups densities were related to nutrient (DIN and phosphate) or light availability (% attenuation of incoming light, concentration of humic substances and of suspended solids) (Fig. 4a, b). The functional group–environment correlation—with the first axis was 0.8. A high percentage of the functional group environment relation (66.4%), was explained by the first two canonical axes. Monte Carlo permutation tests on the first eigenvalue indicated significant ($P = 0.006$) relations between the species and the environmental variables included in the model by forward selection (Fig. 4a, b).

Functional groups **S1** (filamentous non-fixing cyanobacteria with thin diameter), **SN** (filamentous fixing and non-fixing cyanobacteria with thin diameter), **X2** (chrysophytes, small sized, flagellated mixotrophs), and **Y** (cryptophytes, unicellular-flagellated mixotrophs) were related to high phosphate and low DIN

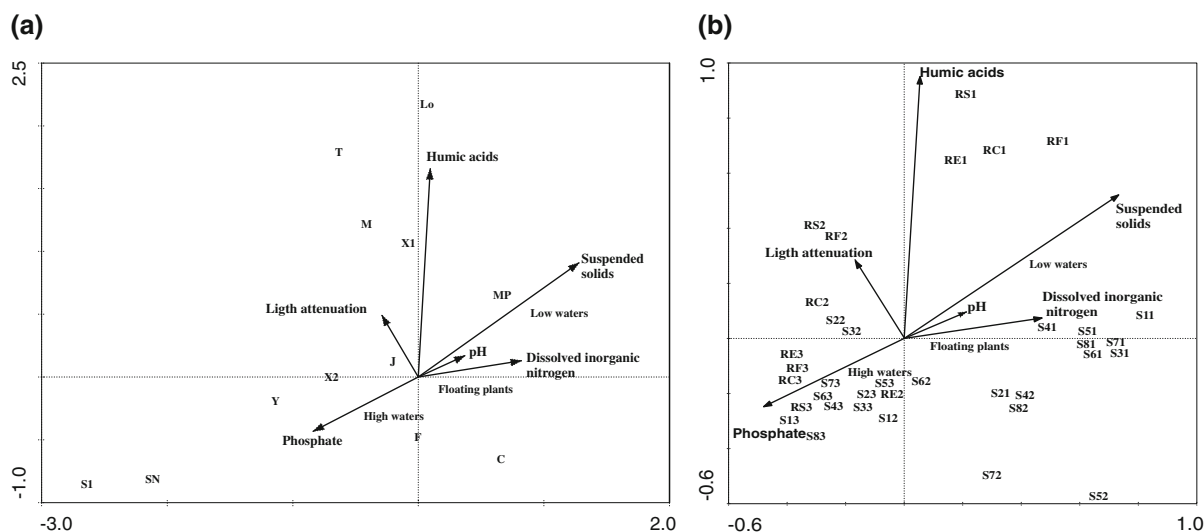


Fig. 4 Ordination biplot based on redundancy analysis (RDA) of the dominant phytoplankton functional groups density during the phytoplankton regime (2004–2006). **a** Functional groups ordination. Quantitative environmental variables are indicated by arrows. High waters, low waters, and free-floating plants

concentrations (Fig. 4a). Conversely, functional groups **C** (planktonic diatoms) and **MP** (benthic diatoms found in the plankton) were related to high suspended solids and high DIN, but low phosphate concentrations. Functional groups **M** (large cyanobacteria colonies with gas vesicles), **L_o** (small cyanobacteria colonies without gas vesicles), **X₁** (unicellular and small organisms, without flagella), and **T** (unicellular and elongated organisms) were related to high humic substances concentrations and high attenuation of the incoming light, while **F** (colonial green algae) showed the opposite pattern. Light attenuation in the water column seemed mostly caused by high suspended solids and high humic substances concentrations (Fig. 4a).

The centroids of high and low water level separate well the samplings, but not the centroid of free-floating plants (Fig. 4b). At low water levels (sampling 1) sites were related to DIN, suspended solids, and humic substances content. Also, spatial heterogeneity was high, with the relictual oxbow lakes separated from the shallow lakes system (Grande, Canal and Pescado) mostly because of high humic substances concentration. At higher waters, (samplings 2 and 3) phosphate characterized the studied sites. During the summer with high waters—flood—(sampling 3), sites were similar across the wetland, characterized by high phosphate and low humic substances concentration. In

represent the centroid of the points for sites in which they occur. **b** Samples ordination. RE = Relictual oxbow lake I; RC, RS, and RF = Relictual oxbow lake II; S1, S2, S3 = Shallow Lake Laguna Grande; S4 and S5 = Canal; S6, S7, S8 = Shallow lake Pescado; *de* December, *jl* July, *ja* January

winter (sampling 2), despite high waters, there was high spatial heterogeneity, which reflected the actual spatial ordination of the aquatic ecosystems in the wetland. The relictual oxbow lakes (in samplings 1 and 2) separated from the shallow lakes system mostly because of humic substances content and attenuation of incoming light (Fig. 4b).

Comparison between free-floating plant (1998–2000) and phytoplankton (2004–2006) regimes

Gamma diversity in the free-floating plant (1998–2000) and phytoplankton (2004–2006) regimes was similar (Table 4), but the free-floating plant regime was characterized by more diatoms and less green algae species (72 diatoms, 36 green algae) than the phytoplankton regime (36 diatoms, 63 green algae). All other groups of phytoplankton had similar contributions among regimes. Beta diversity was higher in the free-floating plant regime than in the phytoplankton regime (Table 4), and the opposite happened for alpha diversity (which was 12–29% lower for species, and 6–32% lower for functional groups) (Table 4).

During the free-floating plant regime, mean phytoplankton functional group composition markedly

Table 4 Comparison of phytoplankton gamma, beta, and mean alpha diversity between the free-floating plant (1998–2000) and a phytoplankton regime (2004–2006) in the Otamendi floodplain wetland

	Free-floating plant	Phytoplankton
Gamma	166	174
Beta		
Late spring	1.9	1.2
Winter	1.6	1.3
Summer	1.5	1.1
Alpha		
Late spring	31 (12)	35 (13)
Winter	34 (12)	47 (14)
Summer	38 (12)	49 (16)

The sites compared (which coincide in both surveys) are RT, RC, S1, and S3. During the free-floating plant regime, sites RT and RC were covered with 100% free-floating plants during the whole sampling period, whereas S1 was sometimes covered and S3 never had free-floating plants. All indexes were calculated using species richness. For alpha diversity, we also provide—in brackets—the functional group richness

differed in sites with contrasting free-floating plants cover (Fig. 5). The relictual oxbow lakes (RT and RC), which were completely covered by free-floating plants, were dominated by cyanobacteria functional groups, **S₂** (thin filaments of non-fixing cyanobacteria), **Z** (prokaryotic picoplankton), and **K** (small cell-sized cyanobacteria colonies, and co-dominated by diatoms in functional group **C** (plankton diatoms). The shallow lake Grande (sites S1 and S3), which generally remained without free-floating plants, was dominated by **X₁** (small non-flagellated green algae) and sub-dominated by **Y** (cryptophytes). During the phytoplankton regime functional group composition was similar in all sampled sites, with dominance of functional groups containing green algae (**X₁** and **X₂**) and sub-dominated by functional groups containing cyanobacteria (**S₁** and **L_o**). Comparing among regimes, the functional composition in the phytoplankton regime was rather similar to the composition found in the shallow Lake Grande (usually without free-floating plants) during the free-floating regime (Fig. 5).

The one-way ANOVA showed that nitrate was higher ($P = 0.001$) and chlorophyll *a* lower ($P = 0.037$) in the free-floating plant regime (means: 304 $\mu\text{g l}^{-1}$ N and 40.9 $\mu\text{g l}^{-1}$ chlorophyll *a*) than in the phytoplankton regime (means: 114 $\mu\text{g l}^{-1}$ N and 85 $\mu\text{g l}^{-1}$ chlorophyll *a*).

Discussion

Phytoplankton regime (2004–2006)

Compared to other similar floodplain ecosystems, the phytoplankton gamma diversity in the Otamendi wetland was relatively high (254 species in 36 samples). In the River Paraná floodplain (shallow Lake El Tigre, Argentina), García de Emiliani (1997) found similar high gamma diversity (218 taxa in 36 samplings). In the Upper Paraná River floodplain (Brazil), Borges & Train (2009) found a gamma diversity of 366 taxa (112 more species than in our study), but they sampled more habitats (33 instead of 12 habitats) with a higher sampling frequency (132 instead of 36 samplings). In an Amazonian floodplain lake (Lake Camaleão, Brazil), Rodrigues Ibañez (1998) found a similar gamma diversity (262 taxa) but in 84 samples. In three floodplain lakes from the Rivers Paraná and Paraguay, Zalocar de Domitrovic (1990) found much lower gamma diversity than in our study (88 in Los Pájaros, 78 in Turbia, and 136 in Catay lakes, in 48 samplings). Finally, in the Sepik-Ramu floodplain, in Papua New Guinea, the phytoplankton gamma diversity was 296 taxa across 26 lakes (Vyverman, 1996) while in our study we found a comparable diversity in 5 aquatic ecosystems. The relatively high diversity found in Otamendi floodplain wetland probably results from a high regional species “pool,” high disturbance (e.g., changes in nutrient and light availability and water level fluctuations) and a high habitat heterogeneity, including connected and disconnected aquatic environments, and vegetated (free-floating and emergent) and open water environments.

Our seasonal surveys captured the regional diversity pool during the studied period. Phytoplankton species gamma diversity resulted in 20 functional groups. This value represents 50% of all the phytoplankton functional groups (reviewed by Padisák et al., 2009). Functional groups, by definition, contain different numbers of species; for example, codon **J** can encompass 100 species while codon **SN** has a maximum of two species (Borics et al., 2012). In our study, functional groups with very high and low richness (>30 species in **W₁**, **J**, and **MP** or <3 species in **SN** and **H₁**) contributed little to the cumulative relative density. In particular, the high richness in group **MP**—benthic species found in the plankton—may occur due

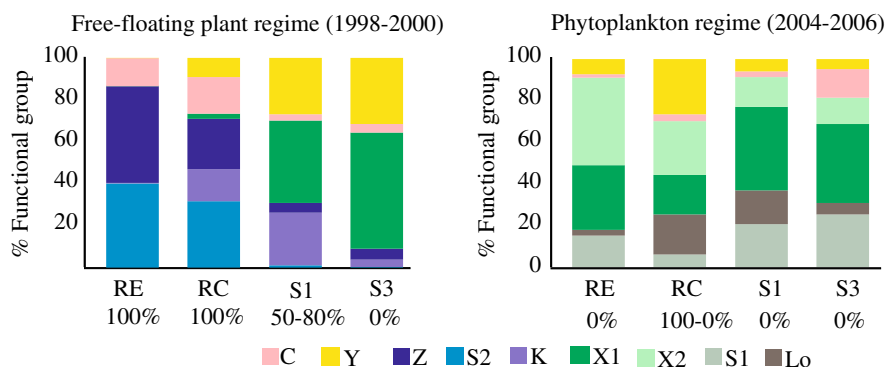


Fig. 5 Comparison of the mean phytoplankton functional groups relative abundance during the free-floating plant (1998–2000) versus the phytoplankton regime (2004–2006). RT and RC = relictual oxbow lakes, S1 and S3 = shallow Lake

Grande. We only depict functional groups with at least $\geq 10\%$ relative abundance in one (out of 12) sample. The percentages on the x axis represent the free-floating plant cover during samplings

to the frequent sediment re-suspension in the shallow Otamendi wetland. Group **J** frequently dominates phytoplankton in enriched ponds (Reynolds et al., 2002), but in our study it achieved low relative densities despite having a high number of species. Functional groups **X1** and **X2** were the most dominant, with 25 and 12 species, respectively. The high diversity of green algae (sorted in groups **X1**, **X2**, **J**, **F**, or **G**) compared to other phytoplankton groups probably responds to good light and high nutrient availabilities in the Otamendi wetland.

The changes in the water level in the wetland were mostly explained by the accumulated rains (in the 30 days previous to sampling). The period of low waters evidenced the isolation of habitats across the wetland (high suspended solids, high dissolved inorganic nitrogen, and high humic substances) and heterogeneity in the phytoplankton assemblages (high beta diversity). Conversely, in summer the overflow caused high connectivity across the wetland's environments. Waters were characterized by high phosphate (suggesting its input from land runoff), dilution (low suspended solids, low dissolved inorganic nitrogen, and low humic substances), and similar phytoplankton assemblages (lower beta diversity). Our results agree with those obtained by Borges & Train (2009) who found the highest values of phytoplankton beta diversity (higher heterogeneity) in floodplain lakes of the Upper-Paraná during a dry period (La Niña), coinciding with low hydrometric levels which isolated the aquatic environments. The events of high connectivity—which cause a decrease in beta

diversity (“homogenization effect”)—are key to keep long-term high species richness of floodplains (gamma diversity) (Thomaz et al., 2007).

Alpha diversity was higher in the shallow lakes system than in the relictual oxbow lakes, likely because the latter have higher light attenuation (mostly due to high humic substances content). Alpha diversity indexes calculated in terms of species or functional groups rendered high and positive correlations, probably because there was a linear fit among these richness classifications. The linear relationship among these phytoplankton richness classifications suggests lack of redundancy in the species function for the Otamendi wetland. The positive relationship between ecosystem functioning and species richness is often attributed to the greater number of functional groups found in richer assemblages (Magurran, 2008). Also, we found an absence of correlation between diversity indexes calculated in terms of density or biovolume, suggesting that species size may play an important role in the diversity assessment.

The multiple regressions showed in most cases that low nitrate availability alone, or in combination with high suspended solid concentration, resulted in higher phytoplankton functional group diversity. Dissolved inorganic nitrogen was usually sufficient in the oxbow lakes, but was potentially limiting phytoplankton growth in both the shallow lakes ($<100 \mu\text{g l}^{-1} \text{N}$, Reynolds, 2006). Phosphate concentration was always within the range of hypereutrophic systems (OECD, 1982) and showed an inverse relationship with nitrate concentration. This may explain why low dissolved

inorganic nitrogen (but no phosphate) enhanced phytoplankton diversity in this wetland. Attenuation of the incoming light, which occurred mostly due to high suspended solids and humic substances concentrations, also affected phytoplankton diversity in this wetland. Because free-floating plant development was scarce during the phytoplankton regime, they contributed little to light attenuation.

Comparison between the free-floating plant and phytoplankton regime

In the free-floating plant regime we found more diatoms (30 more) and less green algae species (23 less) than in the phytoplankton regime. Schwaderer et al. (2011) showed that diatoms are low light adapted organisms while green algae are high light adapted. Hence, low light availability during the free-floating plant regime may explain the prevalence of diatoms over green algae. Despite differences in taxonomic composition across regimes, the gamma diversity was surprisingly similar. Beta diversity, however, was higher in the free-floating plant regime than in the phytoplankton regime. The higher spatial heterogeneity was probably caused by differences in free-floating plant cover (e.g., differences in light and dissolved nutrient availability).

Though phytoplankton diversity at regional scale (gamma diversity) was similar across regimes, local phytoplankton richness (alpha diversity) was markedly lower in the free-floating plant than in the phytoplankton regime. The lower alpha diversity probably reflects the negative effect of the extreme low light engineered by dense free-floating plant cover. Indeed, O'Farrell et al. (2009) recorded, in a field experiment run in the Otamendi wetland, the loss of 30 phytoplankton species in mesocosms exposed to permanently low irradiances, compared to better illuminated mesocosms. In cold temperate ecosystems, Pasztaleniec & Poniewozik (2013) also found lower alpha diversity (richness and Shannon–Wiener) in lakes dominated by free-floating plant compared to lakes without these macrophytes.

During the free-floating plant regime, phytoplankton chlorophyll *a* was significantly lower than in the phytoplankton regime. Also, in the free-floating regime, phytoplankton community composition in the oxbow lakes (covered by dense mats of free-floating plants) was characterized by cyanobacteria

and diatoms, which are well adapted to low light (Schwaderer et al., 2011). Phytoplankton community composition in the shallow Lake Grande (without free-floating plants) was mostly composed by green algae and cryptophytes, and by cyanobacteria of large dimensions including colonial and filamentous forms. Green algae show good performance at high light (Schwaderer et al., 2011) and cryptophytes are capable of persisting in a wide range of scenarios (Naselli-Flores & Barone, 2000).

Meerhoff (2006) and Abdel-Tawwab (2006) suggested that the effect caused by free-floating plants on the ecosystem depends upon the proportion of the water body covered by them. The free-floating plant regime was linked to high water levels whereas phytoplankton dominated in low waters (O'Farrell et al., 2011) with a poor ability of zooplankton to control phytoplankton abundance (Chaparro et al., 2014). Free-floating plant dominance exerts strong controls on phytoplankton ecology, including biomass, decreases in alpha diversity, prevalence of low light adapted species within cyanobacteria and diatoms, and lower zooplankton biomass (de Tezanos Pinto & ÓFarrell, 2014). Global climate change scenarios predict extreme droughts and rain events, which would increase the frequency of regime shifts between phytoplankton and free-floating plants in this wetland. Such regime shifts would promote changes in phytoplankton alpha and beta diversity, with less influence on gamma diversity.

Concluding remarks

Phytoplankton gamma, beta, and alpha diversity were relatively high in the Otamendi wetland throughout the studied period. In the absence of free-floating plants, enhanced phytoplankton diversity occurred at low nitrate availability; water connectivity also enhanced beta diversity. In the free-floating plants regime, alpha diversity was lower and beta diversity higher than the phytoplankton regime (probably because of the extreme environment engineered by plants), though gamma diversity was similar in both periods.

Acknowledgments Financial support for this project was provided by UBACYT X195 and PICT 01-12332 ANCYPT. We are grateful to the Otamendi Natural Reserve (Parques

Nacionales) staff for their collaboration and to Dr. Jarad Mellard for linguistic assistance. We would like to thank the Managing and Subject Editor, and reviewers for their comments; they have improved our manuscript.

References

- Abdel-Tawwab, M., 2006. Effect of free-floating macrophyte, *Azolla pinnata*, on water physico-chemistry, primary productivity, and the production of Nile Tilapia, *Oreochromis niloticus* (L.), and common carp, *Cyprinus carpio* L., in fertilized earthen ponds. *Journal of Applied Aquaculture* 18: 21–41.
- Abonyi, A., M. Leitão, A. M. Lançon & J. Padišák, 2012. Phytoplankton functional groups as indicators of human impacts along the River Loire (France). *Hydrobiologia*. doi:10.1007/s10750-012-1130-0.
- APHA, 2005. Standard Methods for the Examination of Water and Wastewaters, 21st edn. American Public Health Association APHA, AWWA, WEF, Washington, DC: 1368 pp.
- Atlas Ambiental de Buenos Aires, 2010. [<http://atlasdebuenaaires.gov.ar>].
- Borges, P. A. F. & S. Train, 2009. Phytoplankton diversity in the Upper Paraná River floodplain during two years of drought (2000 and 2001). *Brazilian Journal of Biology* 69: 637–647.
- Borics, G., B. Tóthmérész, B. A. Lukács & G. Várbíró, 2012. Functional groups of phytoplankton shaping diversity of shallow lake ecosystems. *Hydrobiologia* 698: 251–262.
- Chaparro, G., M. S. Fontanarrosa, M. R. Schiaffino, P. de Tezanos Pinto & I. O'Farrell, 2014. Seasonal-dependence of the responses of biological communities to flood pulses in warm temperate floodplain lakes: implications for the “alternative stable states” model. *Aquatic Sciences*. doi:10.1007/s00027-014-0356-5.
- Chichizola, S. E., 1993. Las comunidades vegetales de la Reserva Natural Estricta de Otamendi y sus relaciones con el ambiente. *Parodiana* 8: 227–263.
- de Melo, S. & V. L. M. Huszar, 2000. Phytoplankton in an Amazonian flood-plain lake (Lago Batata, Brasil): diel variation and species strategies. *Journal of Plankton Research* 22: 63–76.
- de Tezanos, Pinto P & I. O'Farrell, 2014. Regime shifts between free-floating plants and phytoplankton: a review. *Hydrobiologia*. doi:10.1007/s10750-014-1943-0.
- de Tezanos Pinto, P., L. Allende & I. O'Farrell, 2007. Influence of free-floating plants on the structure of a natural phytoplankton assemblage: an experimental approach. *Journal of Plankton Research* 29: 47–56.
- Devercelli, M., 2006. Phytoplankton of the middle Paraná River during an anomalous hydrological period: a morphological and functional approach. *Hydrobiologia* 563: 465–478.
- Devercelli M., Y. Zalocar de Domitrovic, M. E. Forastier & N. Meichtry de Zaburlín, 2014. Phytoplankton of the Paraná River Basin. *Advances in Limnology* 65: 39–65.
- García de Emiliani, M. O., 1997. Effects of water level fluctuations on phytoplankton in a river-floodplain lake system (Paraná River, Argentina). *Hydrobiologia* 357: 1–15.
- Gómez, S. E. & N. I. Toresani, 1998. Pampas, pp. 97–114. In Canevari, P., D. E. Blanco, E. Bucher, G. Castro & I. Davidson (eds), *Los humedales de la Argentina: Clasificación, situación actual, conservación y legislación*, Vol 46. Wetlands International Publication, Buenos Aires: 208 pp.
- Hillebrand, H., C.-D. Durselen, D. Kirshtel, U. Pollinger & T. Zohary, 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35: 403–424.
- Huszar, V. & C. Reynolds, 1997. Phytoplankton periodicity and sequences of dominance in an Amazonian flood-plain lake (Lago Batata, Pará, Brazil): responses to gradual environmental change. *Hydrobiologia* 346: 169–181.
- Huszar, V., C. Kruk & N. Caraco, 2003. Steady-state assemblages of phytoplankton in four temperate lakes (NE USA). *Hydrobiologia* 502: 97–109.
- Izaguirre, L., R. Sinistro, I. O'Farrell, F. Unrein & G. Tell, 2001. Algal assemblages in anoxic relictual oxbow lakes from the Lower Paraná floodplain (Argentina). *Nova Hedwigia* 123: 95–106.
- Izaguirre, I., I. O'Farrell, F. Unrein, R. Sinistro, M. dos Santos Afonso & G. Tell, 2004. Algal assemblages across a wetland, from a shallow lake to relictual oxbow lakes (Lower Paraná River, South America). *Hydrobiologia* 511: 25–36.
- Izaguirre, I., L. Allende, R. Escaray, J. Bustingorry, G. Pérez & G. Tell, 2012. Comparison of morpho-functional phytoplankton classifications in human-impacted shallow lakes with different stable states. *Hydrobiologia* 698: 203–216.
- Juliarena de Moretti C. E., 1982. La vida silvestre en el área de Otamendi. Serie Cuadernos de Ecología I. Facultad de Filosofía y letras. Instituto de Geografía “Romualdo Ardissonne”.
- Jun, S. & L. Dongyan, 2003. Geometric models for calculating cell biovolume and surface area for phytoplankton. *Journal of Plankton Research* 25: 1331–1346.
- Junk, W. J., P. B. Bayley & R. Esparks, 1989. The flood pulse concept in river floodplain systems. In Podge, J. P. (ed.), *Proceedings of the International Large River Symposium*. Canadians Special Publication of Fisheries and Aquatic Sciences, Ottawa: 110–127.
- Kirk, J. T. O., 1994. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Melbourne.
- Leps J. & P. Smilauer, 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, New York: 269 pp.
- Mackereth, F. J. H., J. Heron & J. F. Talling, 1978. Water analysis: some revised methods for limnologists. *Scientific Publications of the Freshwater Biological Association* 36: 1–120.
- Magurran, A. E., 2008. *Measuring Biological Diversity*. Blackwell Science, Malden.
- Marker, A. F. H., A. Nusch, H. Rai & B. Riemann, 1980. The measurement of photosynthetic pigments in freshwater and standardization of methods: conclusions and recommendations. *Archiv fur Hydrobiologie Beihandlung Ergebnisse der Limnologie* 14: 91–106.
- Meerhoff M., 2006. The structuring role of macrophytes on trophic dynamics in shallow lakes under a climate warming scenario. PhD Thesis.
- Naselli-Flores, L. & R. Barone, 2000. Phytoplankton dynamics and structure: a comparative analysis in natural and man-made water bodies of different trophic state. *Hydrobiologia* 438: 65–74.

- OECD, 1982. Eutrophication of Waters, Monitoring, Assessment and Control. Organisation for Economic Cooperation and Development, Paris.
- O'Farrell, I., R. Sinistro, I. Izaguirre & F. Unrein, 2003. Do steady state assemblages occur in shallow lentic environments from wetlands? *Hydrobiologia* 502: 197–209.
- O'Farrell, I., P. de Tezanos Pinto, P. Rodríguez, G. Chaparro & H. Pizarro, 2009. Experimental evidence of the dynamic effect of free-floating plants on phytoplankton ecology. *Freshwater Biology* 54: 363–375.
- O'Farrell, I., I. Izaguirre, G. Chaparro, F. Unrein, R. Sinistro, H. Pizarro, P. L. Rodríguez, P. de Tezanos Pinto, R. Lombardo & G. Tell, 2011. Water level variation as the main driver of the alternation between a free-floating plant and a phytoplankton dominated state: a long term study in a floodplain lake. *Aquatic Science* 73: 275–287.
- Padisák, J., L. Crossetti & L. Naselli-Flores, 2009. Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. *Hydrobiologia* 621: 1–19.
- Paidere, J., D. Gruberts, A. Škute & I. Druvietis, 2007. Impact of two different flood pulses on planktonic communities of the largest floodplain lakes of the Daugava River (Latvia). *Hydrobiologia* 592: 303–314.
- Pálffy, K., M. Présing & L. Vörös, 2013. Diversity patterns of trait-based phytoplankton functional groups in two basins of a large, shallow lake (Lake Balaton, Hungary) with different trophic state. *Aquatic Ecology* 47: 195–210.
- Pasztaleniec, A. & M. Poniewozik, 2013. The impact of free-floating plant cover on phytoplankton assemblages of oxbow lakes (The Bug River Valley, Poland). *Biologia* 68: 18–29.
- Revenga C. & G. Mock, 2000. Freshwater biodiversity in crisis. In *Earth Trends*. World Resources Institute, Washington, DC.
- Reynolds, C. S., 2006. *Ecology of Phytoplankton*. Cambridge University Press, Cambridge.
- Reynolds, C. S., V. Huszar, C. Kruk, L. Naselli-Flores & S. Melo, 2002. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research* 24: 417–428.
- Rodrigues Ibañez, M. do S., 1998. Phytoplankton composition and abundance of a central Amazonian floodplain lake. *Hydrobiologia* 362: 79–83.
- Rodríguez, P. & H. Pizarro, 2007. Phytoplankton productivity in a highly colored shallow lake of a South American floodplain. *Wetlands* 27: 1152–1159.
- Sarmiento, H., M. Isumbisho & J. P. Descy, 2006. Phytoplankton ecology of Lake Kivu (Eastern Africa). *Journal of Plankton Research* 28: 815–829.
- Scheffer, M., 2009. *Critical Transitions in Nature and Society*. Princeton University Press, Princeton.
- Schwaderer, A., K. Yoshiyama, P. de Tezanos Pinto, N. G. Swenson, C. A. Klausmeier & E. Litchman, 2011. Eco-evolutionary differences in light utilization traits and distributions of freshwater phytoplankton. *Limnology and Oceanography* 56: 589–598.
- Simberloff, D. & T. Dayan, 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22: 115–143.
- Sokal, R. R. & F. J. Rohlf, 1995. *Biometry: The principles and Practice of Statistics in Biological Research*, 3rd edn. W. H. Freeman, San Francisco.
- ter Braak, C. J. F. & P. Smilauer, 2002. *CANOCO Reference Manual and CanoDraw for Windows Users Guide: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power, New York.
- Thomaz, S. M., L. M. Bini & R. L. Bozelli, 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579: 1–13.
- Unrein F. 2001. Efecto de los nutrientes y el pH sobre el crecimiento y la estructura del fitoplancton en ambientes de la llanura aluvial del Paraná inferior. PhD Thesis. Universidad de Buenos Aires, Buenos Aires.
- Utermöhl, M., 1958. Zur Vervollkommnung der quantitativen Phytoplankton Methodik, MIH. *Verhandlungen des Internationalen Verein Limnologie* 9: 1–38.
- Vyverman, W., 1996. Phytoplankton diversity and abundance along environmental gradients in tropical floodplain lakes (Sepik-Ramu floodplain, Papua New Guinea). In *Perspectives in Tropical Limnology*. SPB Academic Publishing, Amsterdam: 277–294.
- Whittaker, R. H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279–338.
- Williamson, C. E., D. P. Morris & M. L. Pace, 1999. Dissolved organic carbon and nutrients as regulators of lake ecosystems: resurrection of a more integrated paradigm. *Limnology and Oceanography* 44: 795–803.
- Wilson, M. V. & C. L. Mohler, 1983. Measuring compositional change along gradients. *Vegetatio* 54: 129–141.
- Zalocar de Domitrovic, Y., 1990. Efecto de las fluctuaciones del nivel hidrométrico sobre el fitoplancton en tres lagunas isleñas en el area de la confluencia de los ríos Paraná y Paraguay. *Ecosur* 16: 13–29.
- Zar, J. H., 2010. *Biostatistical Analysis*, 5th ed. Pearson Prentice Hall, Upper Saddle River.