Using trait-based approaches to study phytoplankton seasonal succession in a subtropical reservoir in arid central western Argentina

S. G. Beamud · J. G. León · C. Kruk · F. Pedrozo · M. Diaz

Abstract The application of trait-based approaches has become a widely applied tool to analyse community assembly processes and dynamics in phytoplankton communities. Its advantages include summarizing information of many species without losing essentials of the main driving processes. Here, we used trait-based approaches to study phytoplankton temporal succession in a subtropical reservoir. We applied a combined approach including morphological traits (i.e. volume, surface) and functional clustering of species (morphology-based functional groups (MBFG) and Reynolds' groups) and related the clustering of species with the environment. We found that this reservoir is characterized by a low richness and a bimodal distribution of phytoplankton biomass. Taxonomic and functional classifications were coincident, and the dominant species and groups biomasses were explained by the same group of variables. For instance, group X_2, MBFG V and *Carteria* sp. biomasses were explained by: pH, Secchi disk depth, N-NH$_4$; while group B, MBFG VI and *Cyclotella ocellata* biomasses were explained by stability of the water column, incident solar radiation, Secchi disk depth and N-NH$_4$. From our results, we state that functional and taxonomic classifications are complementary rather than opposed approaches, and their specific uses depend exclusively on the aim of the study and the characteristics of the environment under evaluation. Our work is the first description of phytoplankton dynamics in a reservoir in the arid central western Argentina (Cuyo region).

Keywords Functional groups · Morphological traits · Reservoirs · Argentina

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Introduction

Trait-based approaches have become a widely applied tool for understanding, explaining and predicting community assembly (Lavorel et al. 1997; Follows et al. 2007; McGill 2010). Functional traits include physiological, morphological and phenological features that govern ecological performance (Violle et al. 2007; McGill 2010) and reflect the ability to acquire resources, to grow and to avoid mortality (Reynolds 1984; Naselli-Flores et al. 2007). Trait-based approaches are applicable measuring individual traits and clustering species into functional groups. Simple integrating functions can be used to scale up from individual organisms to

the community and ecosystem processes (Violle et al. 2007). This can be done by combining in different manners community-level properties (i.e. biovolume per unit of water volume) and information at the individual level (i.e. morphological traits) and analysing the temporal change of these variables and their relation to environmental gradients.

Functional groups classifications cluster species with common traits and similar responses to environmental changes and have been proposed for phytoplankton by several authors (i.e. Reynolds 1998; Reynolds et al. 2002; Salmaso and Padisák 2007). Functional classifications are based on the combination of physiological, ecological and morphological attributes—which are powerful predictors of optimum dynamic performance (Reynolds and Irish 1997). A particularly influential functional classification is the one proposed by Reynolds et al. (2002) based on individual functional traits, on the ranges of environmental conditions over which the species are found to occur, as well as on their co-occurrence patterns. An alternative, simpler classification has been proposed based exclusively on morphological aspects such as individual volume, surface area, maximum length and presence or otherwise of categorical traits such as mucilage (Kruk et al. 2010; Reynolds et al. 2014).

Functional groups classifications have been applied to different aquatic ecosystems such as estuaries, lakes and reservoirs (Huszar et al. 2003; Borges et al. 2008; Crossetti and Bicudo 2008; Mieleitner et al. 2008; Becker et al. 2009, 2010; Costa et al. 2009; Pacheco et al. 2010; Gallego et al. 2012; Segura et al. 2013). However, most times the problem addressed is to determine if one or other approach is better suited to solve a specific question in a particular location or aquatic ecosystem. Here, we foresee a combined application of analysis of individual traits and different functional classifications. We argue that different phytoplankton ecological classification might serve to different objectives and be complementary when solving a specific problem. Some classifications have the advantage of being more refined and enabling the dissection of specific combinations of species (Reynolds et al. 2002; Salmaso and Padisák 2007; Mieleitner et al. 2008), while others might be easy to use and to apply to any organism to predict coarse patterns (Reynolds 1998; Kruk et al. 2010; Reynolds et al. 2014). The combination of both approaches with the analysis of individual traits seems prolific.

In arid central western Argentina, water resources are scarce and highly variable at inter-annual scale. Water bodies in this area are warm temperate and subtropical (Quirós and Drago 1999). Moreover, basic limnological studies are scarce (Peralta and Claps 2001, 2002; Peralta and Fuentes 2005; Scheibler and Debandi 2008). Particularly, El Carrizal Reservoir is characterized by the dominance of diatoms throughout the year and chlorophytes during summer and autumn (Peralta and León 2006; León 2013). Mechanisms that explain temporal community changes and the potential effects of changing environmental conditions derived from land use, urban increase or climate changes are partially explained and not yet clear.

Here, we used a combined trait-based approach (community morphological traits and functional groupings) to analyse the succession of the phytoplankton community and its relation to the environmental variables in El Carrizal Reservoir. We compared the results with the use of individual species.

Methods

Study area

The reservoir El Carrizal is located at 33°17′52″S 68°43′25″W (Fig. 1) in the Tunuyán River basin. This water course originates in the eastern slopes of the South Central Andes, and it flows along 370 km from the mountain range (−3800 m asl) to Desaguadero River (−430 m asl) which is a tributary of the Colorado River which in turn drains to the Atlantic Ocean. The basin area upstream the dam can be divided into two different subunits considering topography, lithology and human activities: (i) the river headwater in the mountain region (>1200 m asl) is characterized by steep slopes (−30 %), high content of sedimentary rocks and scarce human presence (León and Pedrozo 2014) and (ii) an irrigation oasis downstream (1200–780 m asl) where the human activities are settled (100,000 inhabitants) in a 1500 km^2 cultivated area with vines, fruit, vegetables and aspen (*Populus* sp.). The reservoir is fed almost entirely by snow and glacier melting in the mountain range, and it was built in 1972 to store water for hydropower and irrigation use during low-flow periods. The main reservoir tributaries are the Tunuyán River (−1100 hm^3 year^{-1}) and the Carrizal Stream (−28 hm^3 year^{-1}). The reservoir area ranges between 11.8 and 30.3 km^2; its

Fig. 1 Location of El Carrizal Reservoir and the sampling sites: Presa, Centro and Cola
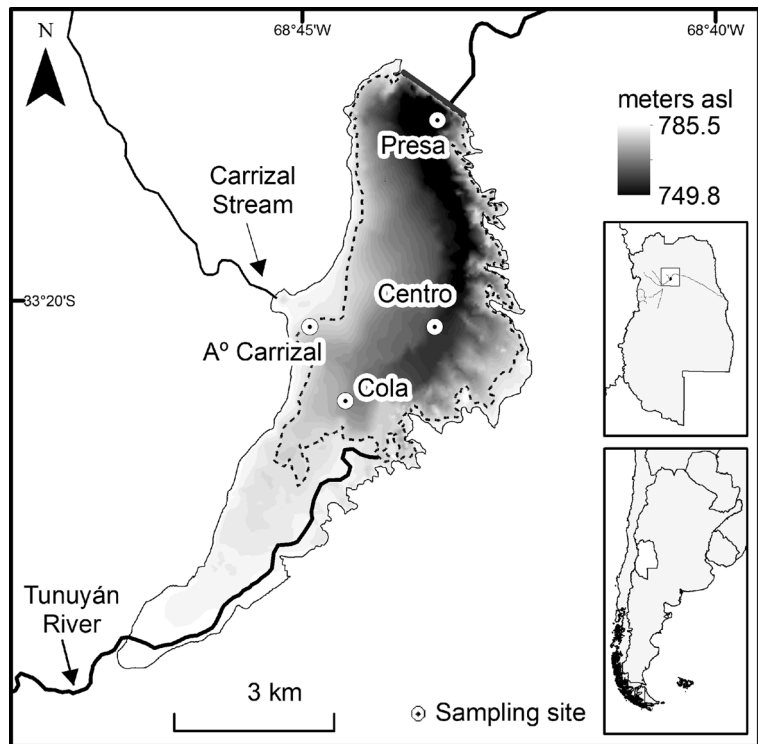
maximum length is 9.4 km and its maximum width is 4.7 km. It has a maximum volume of 289.9 hm^3 at 785.5 m asl, with an average depth of 9 m and a maximum of 41 m (DGI 2006). The climate in the Köppen classification is cold desert (Peel et al. 2007). Daily average air temperature ranges from −30 °C to just above 0 °C. Rainfall concentrates in summer averaging 150 mm year^{-1}.

Sampling

Water samples were taken at monthly intervals from March 2009 to February 2011 in El Carrizal Reservoir (Fig. 1). Samples were collected in 4 sites of the lake to assess the water body vertical and horizontal homogeneity. The site Presa, representative of the limnetic environment, was selected for the study of the functional groups. Temperature profile was determined. In situ dissolved oxygen (DO), pH and electrical conductivity (EC) were measured with a multiparameter probe HORIBA W-23XD. Water transparency was measured in metres with a Secchi disk. Light irradiance (PAR) was measured by using a LI-COR radiometer equipped with a submersible quantum sensor LI-192SB. Daily average

incident solar irradiance Rad (300–3000 nm) was measured with a thermoelectric transducer (SIAP+ MICROS t055) at Junin meteorological station located at −20 km NE from the reservoir (DACC 2012). Samples for analyses of inorganic nutrients, chlorophyll *a* and phytoplankton were collected right below the surface (0.5 m), with a Van Dorn bottle (3 l). Phytoplankton samples were fixed with neutral Lugol's solution.

Sample analysis

Dissolved inorganic nutrients were analysed in filtered samples (membrane cellulose-acetate filters; 0.45 μm) in compliance with APHA (1998): soluble reactive phosphorus (SRP) was measured spectrophotometrically by the ascorbic acid method, nitrate (N-NO$_3$) analysis by using the cadmium reduction method, ammonium (N-NH$_4$) by the indophenol spectrophotometric method and soluble reactive silicate (Si) by the molybdate method. Dissolved inorganic nitrogen (DIN) was considered as the sum of N-NH$_4$ and N-NO$_3$). Total phosphorus (TP) (the potassium persulphate acid oxidation

method) and total nitrogen (TN) (the potassium persulphate basic oxidation method) were determined on unfiltered samples.

Chlorophyll *a* concentration was determined spectrophotometrically from acetone (90 %) extracts (GF/F filters) in compliance with APHA (1998). Phytoplankton was quantitatively analysed under a Hydro-Bios inverted microscope following Utermöhl (1958) method, until at least 100 organisms were counted in random fields.

Data analysis

The dimensionless parameter relative water column stability (RWCS) was calculated according to Padisák et al. (2003): RWCS=$(D_b–D_s)/(D_4–D_5)$, where D_b is the water density at the bottom, D_s is the water density at the surface and D_4 and D_5 are the water density at 4 and 5 °C, respectively. Water density was estimated from temperature and total dissolved solids (Ji 2008). The vertical attenuation coefficient (K_d) for PAR was calculated according to Kirk (2011). Water residence time Tw (Vol/Q) was estimated (Xu et al. 2010) by using the inflow discharge ($Q=1100$ hm^3 year^{-1}) and the reservoir Volume (Vol=290 hm^3).

The organism dimensions of at least 30 specimens of each species were measured in order to determine the individual volume (v, μm^3) and surface (s, μm^2) according to Hillebrand et al. (1999) under an Olympus BX40 microscope. Fresh weight biomass (μg ml^{-1}) was estimated according to Wetzel and Likens (1991). Morphological traits of phytoplankton species such as maximum linear dimension (MLD, Reynolds 2006) and the presence of heterocytes, akinetes, mucilage, vacuoles, flagella and silica walls were determined in order to group the species in morphology-based functional groups (MBFG) (Kruk et al. 2010). Phytoplankton organisms were also taxonomically identified and classified according to the functional classifications proposed by Reynolds et al. (2002). Species and functional groups were classified as dominant when they contributed at least 10 % of the relative abundance in each sample.

The weighted averages of v, s/v and MLD were estimated for the whole community (i.e. WA of volume) in each sample (Eq. 1). This was done by weighting species individual traits by their

individual contribution to the total phytoplankton community biovolume in a specific sample.

$$WA_jT = \frac{\sum_1^i spT_i spPB_i}{\sum_1^i PB_i} \tag{1}$$

WA_iT is the weighted average of the morphological trait of interest (T_i) at station j (stations 1 to 11), sp is the species (from 1 to i at a particular station), and PB_i is the biovolume of the species at the particular station.

Data ordinations were performed by using CANOCO 5.0 for Windows (ter Braak and Smilauer 2002). Detrended correspondence analysis (DCA) for the species data was employed to decide whether linear or unimodal ordination methods should be applied. Redundancy analysis (RDA), which is a constrained linear ordination method, was applied to examine the relationships between the environmental variables and phytoplankton biomass, chlorophyll *a*, dominant functional groups (FG) and morphologically based functional groups (MBFG) and species, and to choose the best variables describing phytoplankton dynamics. Monte Carlo simulations with 499 permutations were used to test the significance of the environmental variables to explain the functional groups data in the RDA. The environmental variables involved in the RDA analysis were DO, pH, transparency of the Secchi disk (SD), RWCS, EC, Tw, Rad and dissolved nutrients (N-NO$_3$, N-NH$_4$, SRP, Si).

We additionally used multiple linear regression models to evaluate the reliability of the environmental variables determined in predicting the seasonal variation in the phytoplankton estimated as chlorophyll *a*, total biomass and the dominant biomass of FG, MBFG and species. A stepwise procedure was used to minimize co-linearity and to select the significant continuous variables. The independent variables (predictors) and the dependent variables were log$_{10}$ transformed. Pearson's (r_p) and Spearman's (r_s) correlation coefficients were used to determine the degree of association between environmental and biological variables.

All correlation and regression analyses were performed with the statistical package Infostat (Di Rienzo et al. 2011).

Results

Phytoplankton temporal succession

A total of 14 species were observed during the whole study period (Table 1). Two of them were dominant most of the time: *Carteria* sp. and *Cyclotella ocellata*, while *Aulacoseira granulata* was a co-dominant species in few occasions. Accompanying species never represented more than 15 % of the total biomass. Total biomass showed maximum values in summer (January) and minimum values in winter (June and August) (Fig. 2a) ranging between 0.2 and 2.7 µg ml^{-1}. In contrast, chlorophyll a contents were high in summer and winter (10.1–14.7 mg m^{-3}) and low in autumn and spring (2.1–2.4 mg m^{-3}) (Fig. 2a). *Carteria* sp. and *C. ocellata* (hereafter dominant species) alternated in their dominance along the period (Fig. 2b). The sequence was similar for both years: *Carteria* sp. showed maximum biovolume in autumn (1.45 µg ml^{-1}) and end of summer (2.69 µg ml^{-1}), medium values in spring and early summer, and the lowest values in winter (0.02 µg ml^{-1}). *C. ocellata* showed the highest values in spring-summer (2.30 µg ml^{-1}), intermediate values in autumn and the lowest biovolume in winter (0.07 µg ml^{-1}). *A. granulata* presented maximum values in summer-autumn March 2011 (1.41 µg ml^{-1}). Concerning the biomass of the species related to the total biomass, *Carteria*

dominates the community during autumn and *C. ocellata* during spring. During the winter of 2009, *A. granulata* and *C. ocellata* were the dominant species, and *C. ocellata* dominates during the summer of 2009–2010. In the winter of 2010, the most abundant species was *Carteria* as much as during the summer of 2010–2011.

Four MBFG were observed: V (medium size flagellates), VI (non-flagellated organisms with siliceous exoskeletons), I (small organisms with high s/v) and IV (organisms of medium size lacking specialized traits). Groups V (*Carteria* sp.) and VI (*C. ocellata* and *A. granulata*) were dominant accounting up to 89 and 96 % of the total biomass, respectively, while I and IV clustered the low biovolume species (Table 1, Fig. 2c). V and VI showed clear alternating dominance along the period. MBFG V presented maximum values during autumn and MBFG group VI showed high biomass values at spring (with the exception of one sampling in 2009) and winter. MBFG VI also dominated summer of 2009–2010 and during the summer of 2010–2011 groups VI and V co-dominated the phytoplankton community.

The species into Reynolds' functional groups resulted in 11 groups (Table 1). Similarly to the MBFG, only two groups were dominant; *Carteria* sp. (V) and *C. ocellata* (VI) were classified into X_2 and B, respectively, reaching up to the 89 and 97 % of the total biomass. The co-dominant species *A. granulata* (VI)

Table 1 List of observed species and genus and their classification into MBFG (Kruk et al. 2010) and Reynolds' groups (Reynolds 2006; Padisák et al. 2009)

| Observed morphotypes	Dominant vs. rare species	Taxonomic group	MBFG	Reynolds' group
Chlorella-like species	Rare	Chlorophyta	I	X_1
Closterium sp.	Rare	Charophyta	I	P
Monoraphidium sp.	Rare	Chlorophyta	I	X_1
Scenedesmus sp.	Rare	Chlorophyta	I	J
Small flagellates	Rare	Chlorophyta	I	X_2
Oocystis sp.	Rare	Chlorophyta	IV	F
Carteria sp.	Dominant	Chlorophyta	V	$X2$
Cryptomonas sp.	Rare	Cryptophyta	V	Y
Gymnodinium sp.	Rare	Dinophyta	V	L_O
Peridinium sp.	Rare	Dinophyta	V	L_O
Aulacoseira granulata	Dominant	Bacillariophyta	VI	P
Cyclotella ocellata	Dominant	Bacillariophyta	VI	B
Navicula spp	Rare	Bacillariophyta	VI	MP
Nitzschia spp	Rare	Bacillariophyta	VI	D
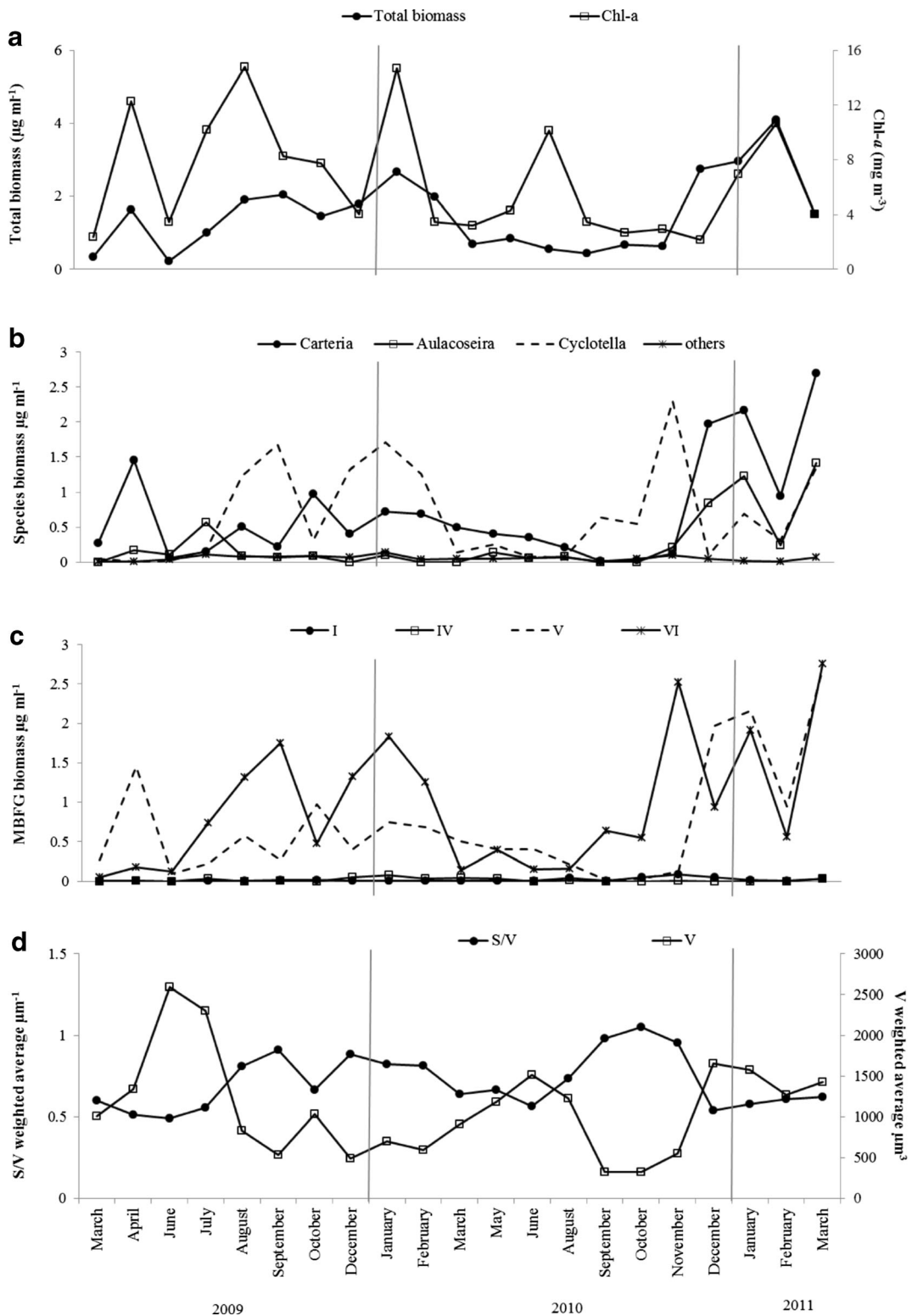
Fig. 2 Temporal succession of the phytoplankton community structure from 2009 to 2011, represented by **a** total biomass and chlorophyll *a* contents, **b** dominant species and others, **c** by grouping organisms into MBFG and **d** by the community weighted average of two morphological traits—*s* and *s/v*

was the only species clustered in the P group representing between 0 and 57 % of the total biomass. The remainder species were included into the X_1, F, J, Y, L_O, MP and D groups. The temporal pattern observed was similar independently of the approaches applied (FG, taxonomic and MBFG).

Finally, we compared the community organisms weighted average of volume (v) to surface to volume (s/v) ratio (Fig. 2d). It was observed that a pattern of larger volume in winter was followed by a decrease in summer-autumn and a further increment in s/v at the end of the year (spring-summer) for both years.

When examining the relative dominance of the main species (% in biovolume), we saw that there was a linear and opposed relation (Fig. 3) ($r_p=v0.80$, $p<0.05$). When the same relation is analysed comparing dominant MBFG (V and VI), a better correlation is observed along the whole studied period ($r_p=0.99$; $p<0.05$). The cases below the adjusted line in the Fig. 3a correspond to *A. granulata*, which is included as member of the VI group in the MBFG figure (Fig. 3b).

Environmental variables and phytoplankton

Incident solar radiation (Rad) is shown in Fig. 4a. The RWCS (Fig. 4b) showed a variation according to that seasonality with maximum values during summer (13.7–20.1) and the lowest ones in winter (0.1–0.2). pH and EC values remained almost constant through seasons with an average value of 8.4 for the pH and a range of EC values of 744 (particularly low value found in January 2010) and 1521 µS cm^{-1} (Fig. 4c). DO (Fig. 4d) also showed a seasonal variation with lower values in summer and higher values in winter (average DO=7.5–12 mg l^{-1}). Tw had maximum values in winter

(203.1–328.1 days^{-1}) (Fig. 4e). SD depth was higher during autumn and spring (1.2–2.5 m) (Fig. 4f).

Nutrient concentrations showed seasonal differences between years (Fig. 5). Si, SRP, N-NH$_4$ and N-NO$_3$ showed a similar seasonal change: with the highest contents in winter and spring and the lowest values during the end of summer-autumn (Fig. 6a–d). The seasonal patterns observed in the biological and environmental variables were supported by the correlations found between them, in this sense, total phytoplankton biomass (Fig. 2a) variability was associated to Rad ($r_s=0.66$; $p<0.05$) and RWCS ($r_s=0.45$; $p<0.05$) (Fig. 4a, b). Chlorophyll *a* content (Fig. 2a) increased with DO ($r_s=0.47$; $p<0.05$) and decreased with Secchi Disk depth ($r_s=-0.71$; $p<0.05$) (Fig. 4d–f).

Individual volume weighted average (v) decreased with SD depth ($r_s=-0.47$; $p<0.05$) and RWCS ($r_s=-0.46$; $p<0.05$). s/v ratio was positively associated with SD depth ($r_s=0.50$; $p<0.05$) and MBFG VI biomass ($r_s=0.47$; $p<0.05$) (Figs. 2d and 4b, f). Water temperature and Rad increased together ($r_s=0.87$; $p<0.05$) (Fig. 4a). This temperature increase favoured by RWCS ($r_s=0.73$; $p<0.05$) was associated to lower Tw ($r_s=-0.52$; $p<0.05$), DO ($r_s=-0.75$; $p<0.05$) (Fig. 4b, d, f) and a lower N-NO$_3$ concentration ($r_s=-0.61$; $p<0.05$) (Fig. 5d). EC was positively associated with Si ($r_s=0.78$; $p<0.05$), SD depth ($r_s=0.44$; $p<0.05$), Tw ($r_s=0.57$; $p<0.05$) and SRP ($r_s=0.51$; $p<0.05$) (Figs. 4e, f and 5a, b). RWCS was negatively related to DO ($r_s=-0.66$; $p<0.05$), while DO was negatively related to Rad ($r_s=-0.64$; $p<0.05$) and positively to Tw ($r_s=0.60$; $p<0.05$) (Fig. 4a, b, e, f).

Three different RDA were performed with the environmental variables (excluding water temperature because of a high collinearity when fitting this variable in
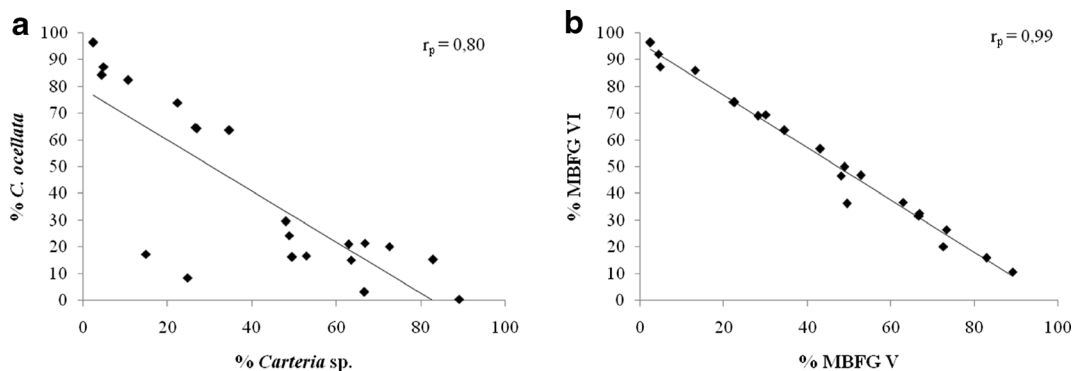

Fig. 3 Relation between percentage of **a** dominant species (*Carteria* sp. and *C. ocellata*) and **b** dominant MBFG (V and VI), during the studied temporal succession in El Carrizal Reservoir. *r*=Pearson's linear correlation coefficient

Fig. 4 Seasonal variations in environmental variables from 2009 to 2011. **a** *Rad*: incident solar radiation and *Temp*: water temperature; **b** *RCWS/10*: relative water column stability; **c** *pH* and *EC*: electrical conductivity; **d** *DO*: dissolved oxygen concentration; **e** *TW*: water residence time and **f** Secchi disk transparency
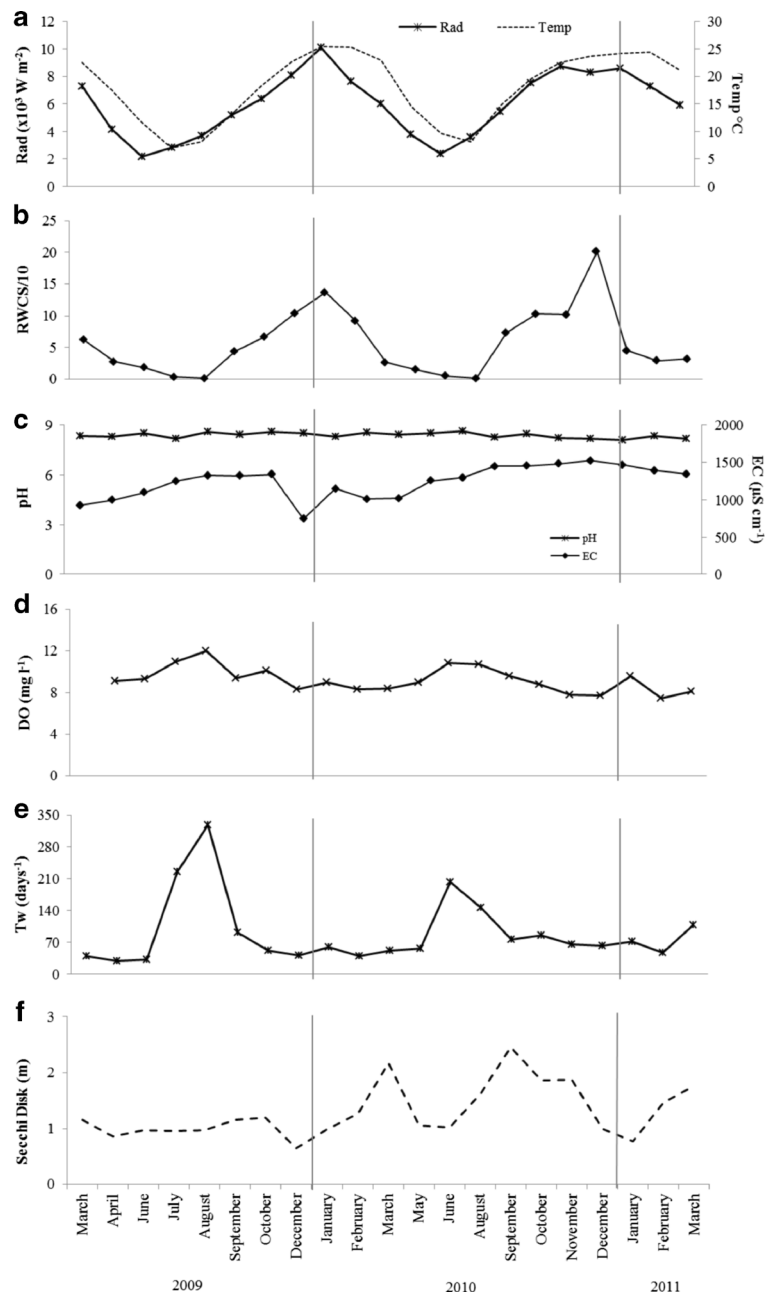
the analysis), and the biomass of the dominant MBFG, FG and species, separately (Fig. 6). The statistics details of these analyses are summarized in Table 2.

The results of RDA analyses indicated that the biomass of the phytoplankton groups corresponding to the three classification approaches can be well predicted from the same environmental variables: Secchi disk depth, N-NH$_4$ concentration, incident solar radiation and the stability of the water column RWCS. The application of FG or dominant species results in almost identical conclusions.

Particularly, in the RDA with MBFG (Fig. 6a), the first axis was mainly correlated with SD depth, Rad and N-NH$_4$ (intra-set correlation coefficients: 0.57, −0.55 and 0.44, respectively), and the second axis was mainly defined by N-NH$_4$, Rad and RWCS (intra-set correlation
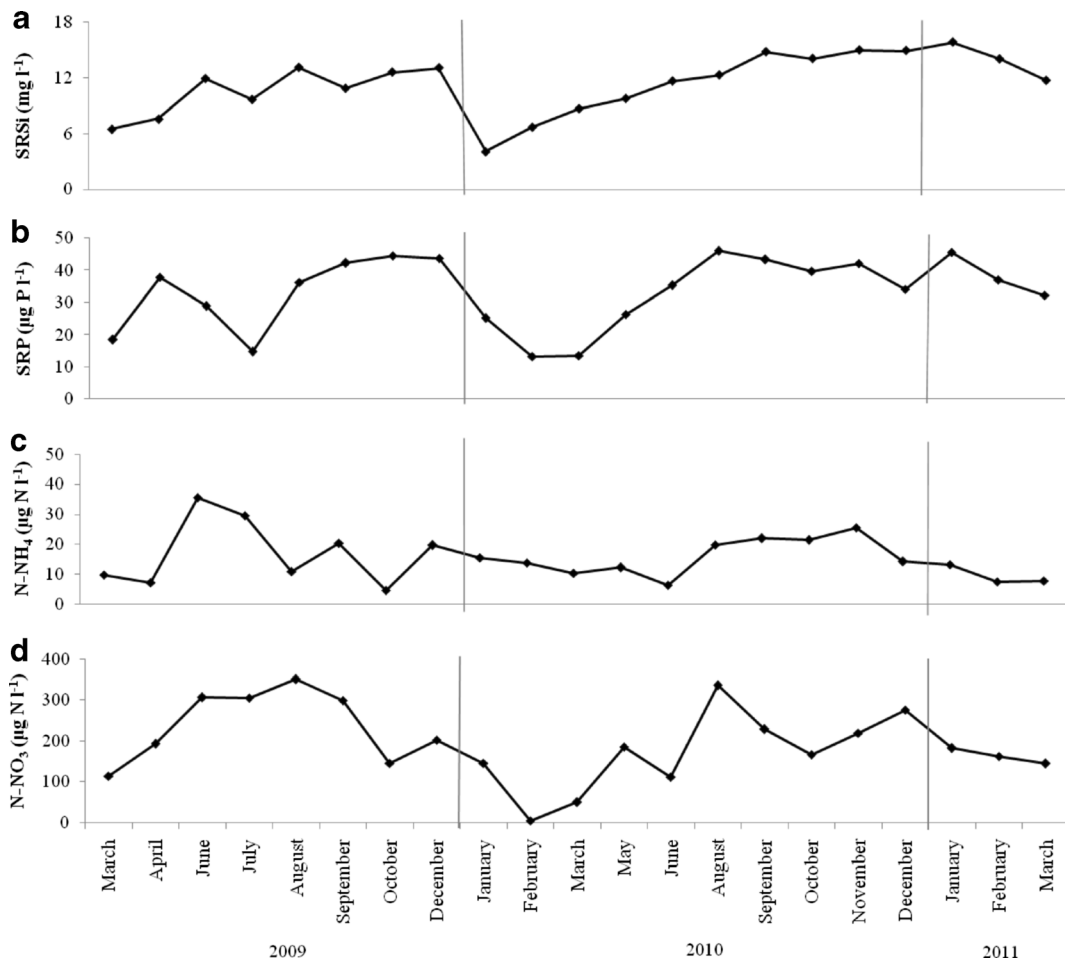
Fig. 5 Seasonal variations in dissolved nutrients contents from 2009 to 2011. **a** *SRSi*: soluble reactive silica; **b** *SRP*: soluble reactive phosphorus; **c** *N-NH₄*: ammonium and **d** *N-NO₃*: nitrates

coefficients: −0.48, −0.43 and −0.38, respectively). In the RDA with Reynolds' FG (Fig. 6b), the first axis was mainly correlated with SD depth and N-NH$_4$ (intra-set correlation coefficients: 0.66 and 0.42, respectively), and the second axis was mainly defined by Rad, RWCS and N-NH$_4$ (intra-set correlation coefficients: 0.68, 0.37 and −0.25, respectively). And finally, in the RDA with species biomasses (Fig. 6c), the first axis was mainly correlated with SD depth and N-NH$_4$ (intra-set correlation coefficients: 0.61 and 0.40, respectively), and the second axis was mainly defined by Rad, RWCS and N-NH$_4$ (intra-set correlation coefficients: 0.68, 0.36 and −0.31, respectively).

The temporal dynamics of phytoplankton in El Carrizal Reservoir were well described by the distributions of samples in the RDA ordination diagram (Fig. 6). The samplings were grouped according to warmer and colder dates in different quadrants for all the classification approaches. The warmer seasons showed high values of relative water column stability RWCS and incident solar radiation Rad whereas the colder seasons showed high values of dissolved oxygen DO, N-NO$_3$, N-NH4 concentrations and water transparency. High values of Rad along with a stable water column enabled high development of phytoplankton biomass. Particularly, ordination of the biomasses of MBFG (V and VI), FG (X_2 and B) and taxonomic species (*Cyclotella ocellata* and *Carteria* sp.) distributed mostly in the Rad and RWCS direction.

We used multiple lineal regressions to create predictive models to explain phytoplankton biomass (total and from dominant MBFG classification), chlorophyll *a* from all the environmental variables determined during our study (Table 3). The total variation (R^2 adjusted)
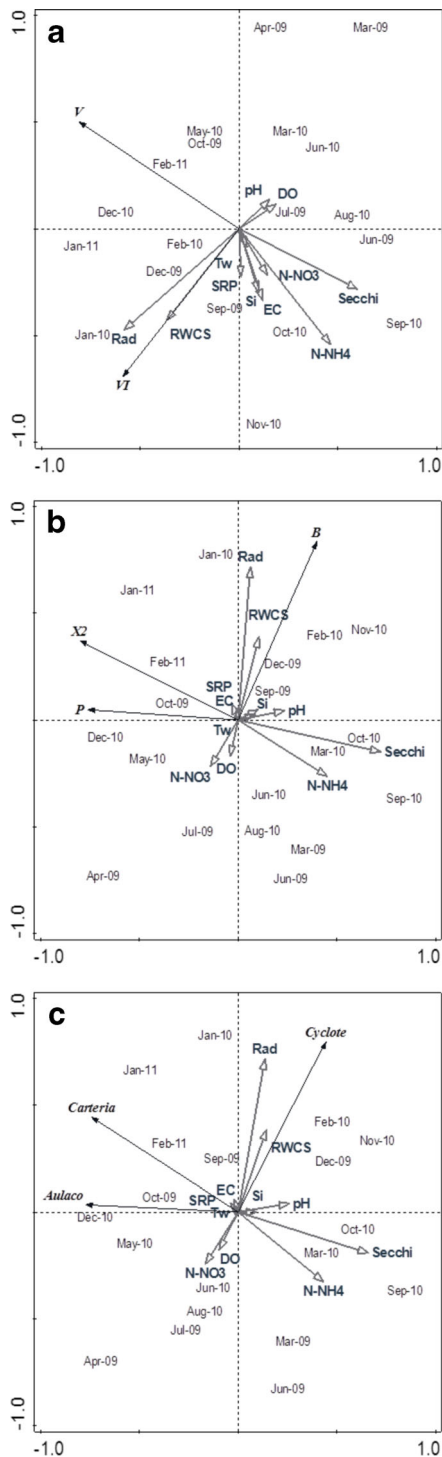
◀ **Fig. 6** RDA triplots of sampling dates, environmental variables and phytoplankton data. *DO* dissolved oxygen, *pH*, *Secchi* Secchi disk transparency, *RWCS* relative water column stability, *EC* electrical conductivity, *Tw* water residence time, *Rad* incident solar radiation, *N-NO₃* nitrates, *N-NH₄* ammonium, *SRP* soluble reactive phosphorus and *Si* soluble reactive silica. **a** MBFG classification (Kruk et al. 2010): *VI*: MBFG VI biomass, *V*: MBFG V biomass; **b** FG classification (Reynolds et al. 2002): *X2*: FG X_2 biomass, *B*: FG B, *P*: FG P biomass; **c** species taxonomic classification: *Cyclotel*: *Cyclotella ocellata* biomass, *Carteria*: *Carteria* sp. biomass, *Aulaco*: *Aulacoseira granulata* biomass

were also the SD depth, as well as Si concentrations, pH and RWCS.

Discussion

Here, we used different trait-based approaches to study the environmental processes affecting phytoplankton temporal succession in a subtropical reservoir. We found similar results independently of the approach applied. Water stability, temperature variation, and light and dissolved nutrients availability were the main driving mechanisms of the phytoplankton structure dynamics. Probably, the simplicity of the community studied partially explains the similarity observed. However, similar results might well be obtained in other more complex circumstances (Kruk et al. 2002, 2011; Reynolds et al. 2014). We think this work might encourage others to use functional approaches in a complementary way when solving a specific problem. Furthermore, we provide new evidence to disentangle the mechanisms explaining temporal community changes and the potential effects of changing environmental conditions in aquatic ecosystems of the understudied arid area of Cuyo.

Main driving processes of phytoplankton

Temporal dynamics of phytoplankton biomass and chlorophyll *a* in El Carrizal Reservoir were influenced principally by incident solar radiation, water transparency and ammonium contents. Relative stability of the water column, pH, dissolved oxygen and Si concentrations were also significant. Phytoplankton biomass increased with solar incident radiation and water column stability (higher residence time), having a negative relation to ammonium availability and water transparency, due to phytoplankton growth. According to Reynolds (1999), the most important variables in determining

explained by the significant models ranged from 0.71 to 0.85. The significant major predictors ($p < 0.05$) of phytoplankton biomass were the SD depth, N-NH₄ and Rad; and the predictors for chlorophyll *a* concentration

Table 2 Summary of the RDA detailed statistics showing the explained variation of the data, and the significance of the analysis (significance level 5 %)

Classification approach	Total adjusted explained variation (adjusted) in %	Test on all axes[a]	
		Pseudo-F	p
MBFG	60.1	4.2	0.004
FG	64	3.9	0.004
Species	70.2	4.9	0.002

[a] Test for significance of all canonical axes by Monte Carlo simulation

phytoplankton biomass and assemblages are the availability of nutrients and solar energy flux all of which may be strongly constrained by water movements, morphometrics characteristics and hydrology.

In man-made lakes and reservoirs characterized by conspicuous water level fluctuations, the variability in abundance and composition of phytoplankton is strongly influenced by the hydraulic regimes rather than by nutrient availability (Naselli-Flores 2000; Wilk-Woźniak and Pociecha 2007). Our results confirm that physical constraints in reservoirs have strong effects in shaping the structure of phytoplankton assemblages, but light and nutrients availability are also very important (Naselli-Flores 2000; Naselli-Flores and Barone 2005). Ammonium was the most important and significant

nutrient for predicting phytoplankton biomass and chlorophyll a concentration. The importance of ammonium was in accordance with the low ratios of DIN: SRP observed in this study (ranging from 1.3 to 24.1), which suggests that phytoplankton growth was most likely limited by nitrogen, diminishing the ammonium available as a source of inorganic nitrogen.

A strong seasonal variability was observed. Water column mixing during periods of isothermy and low incident solar radiation are indicative of light limitation in winter and early spring. When light availability was high, it led to the development of high biomass in the epilimnion, mainly in summer. During late summer and spring, chlorophyll a concentration underwent an obvious decrease along with a shortening in retention time. Seasonal variation was also observed for nutrients with the lowest contents in summer-autumn and in relation to concentration/dilution processes acting on the river's dissolved solids during low (winter) and high (summer) discharges controlled by snowmelt inputs (León and Pedrozo 2014).

Phytoplankton community composition and seasonal dynamics

Phytoplankton seasonal or temporal succession refers to changes in total biomass and structure along an annual cycle as a result of autogenic and allogenic drivers. This

Table 3 Results of the multiple linear regressions for total biomass (TB, $\mu g \, ml^{-1}$), chlorophyll a (Chlo a, mg m^{-3}), MBFG V and VI biomasses ($\mu g \, ml^{-1}$) and environmental variables, *p<0.05

Dependent variables	n	R^2 adj	Significant lineal regression model	Predictors with significant coefficients
Total biomass	19	0.71*	TB=$-1.5\beta_0$+1.4Rad -0.9Secchi+0.3Tw	Rad Secchi
Chlorophyll a	19	0.85*	Chlo a=$7.1\beta_0-0.9$Secchi+2.3DO -0.5 N-NH$_4$−7.1pH −0.7Si+0.2RCWS+ 0.3Tw+0.1 N-NO$_3$	Secchi N-NH$_4$ Si RWCS
MBFG V biomass	19	0.76*	MBFG V=$26.2\beta_0-1.3$ N-NH$_4-$ 2.3Secchi-26.1pH -0.3 N-NO3	N-NH$_4$ Secchi pH
MBFG VI biomass	19	0.74*	MBFG VI=$-20.8\beta_0+2.1$Rad -1.2Secchi+ 0.7 N-NH$_4$+14.0pH+1.4EC+0.5Tw	Rad N-NH$_4$ Secchi

The environmental variables involved in the analysis were: DO dissolved oxygen, pH, transparency of the Secchi disk, RWCS relative water column stability, EC electrical conductivity, Tw water residence time, Rad incident solar radiation, N-NO$_3$ nitrates, N-NH$_4$ ammonium, SRP soluble reactive phosphorus and Si soluble reactive silica

reservoir was characterized by a low richness and a bimodal distribution of phytoplankton biomass. These biomass peaks occurred during a 'stratification period' with RWCS>50 and a temperature difference between surface and bottom waters of 8 °C. The seasonal succession observed in El Carrizal conformed an alternative dominance of two species *Carteria* sp. (MLD<20 μm) and *C. ocellata* (MLD<10 μm). In accordance with a general successional trend (Margalef 1978), small organisms (lower v, higher s/v) with high growth rates (colonizers, r-strategies) were dominant in summer and larger species (higher v, lower s/v) with low growth rates (K-strategies) were dominant in winter (Reynolds 1998), thus following the general seasonal patterns observed in the abiotic measured variables.

Despite few exceptions, the significant predictor variables of phytoplankton biomass were similar independently of the different classifications used, the statistical approaches applied and the patterns of environmental variables.

Using the dominant species to explain the main driving processes, we were able to identify the environmental conditions that favoured their change in biovolume. The peaks of *C. ocellata* occurred when the reservoir presented high water column stability with large temperature differences between surface and bottom waters. *Cyclotella* species are commonly found in reservoirs and are a reference of primary productivity in oligo-mesotrophic water bodies (Gurbuz et al. 2003; Hu et al. 2013) being particularly adapted to low light availability (Reynolds 1997). The diatom *Aulacoseira granulata* also showed high biomass values under similar conditions to *Cyclotella* but as co-dominant. Diatoms such as *A. granulata* are strongly dependent on mixing, and nutrient-rich waters (Wang et al. 2011) and its maximum value were found during the summer of 2011, when the water column was stratified. Considering the phylogenetic origin of the observed species and according to Tilman et al. (1982), diatoms might dominate when Si:P ratios in lakes are high, such is the case in El Carrizal Reservoir with a Si:P ratio of 150 for the studied period (2009–2011). Although diatoms have higher affinity for P compared to cyanobacteria or chlorophytes, we expected the presence of some species of cyanobacteria such as *Microcystis aeruginosa* and *Anabaena* spp., typically found in reservoirs (Wang et al. 2011; Xiao et al. 2011). One of the possible reasons for the absence of cyanobacteria species during our study could be the high

abundance of cations; the basin of the Tunuyán river is dominated by Ca^{2+}-SO_4^{2-} (León and Pedrozo 2014).

By using Reynolds' FG, we were able to link community structure with trophic state. El Carrizal Reservoir is a mesotrophic water body, and because of its trophic state, the dominant phytoplankton functional groups were X_2, B, P and Lo (Reynolds et al. 2002). Species of Group B are indicative of calcareous, often very phosphorus-rich environments (Reynolds et al. 2002). The preferred habitat of this group is small and medium-sized lakes to large shallow lakes grouping species sensitive to the onset of stratification. The biomass of X_2 group (mostly *Carteria* sp.) in the studied period reached its maximum when the values of Secchi disk depth and the concentrations of ammonium and total phosphorus were low. These results disagree with what was expected from the characteristics of X_2 group: nutrient-rich waters with non-positive effects of nitrogen concentrations below 14 μg l^{-1} (Reynolds et al. 2002).

Based on the description of the traits of the MBFG, we were able to relate their potential ecological performance to the environmental conditions in El Carrizal. Group V includes unicellular flagellates of medium to large size and moderate s/v ratio, which together with the possession of flagella have reduced sinking losses. Motility also allows effective nutrient foraging that, in conjunction with the production of cysts, might have increased tolerance to low nutrient conditions. In addition, the capacity of some species to benefit from mixotrophy and phagotrophy implies a means of tolerating conditions of low dissolved nutrients availability (Graham and Wilcox 2000). Accordingly, group V was observed under lower nutrients and light conditions. Group VI includes non-flagellated organisms with siliceous exoskeletons mainly diatoms. Here, it included species ranging from the small r-selected *Cyclotella* to large, more K-selected *A. granulata*. The presence of a siliceous wall is the main constraining trait of these species, large representatives sink rapidly and are excluded from waters. According to Kruk and Segura (2012), it is as follows: group VI (*C. ocellata*, B group and *A. granulata*, P group) is important in lakes with high light (Kd<3.9 m^{-1}), temperature below 24 °C and Si lower than 1730 μg l^{-1}. Lakes dominated by group V (*Carteria* sp., X_2 group) show low light (Kd>3.9 m^{-1}), TN lower than 2800 μg l^{-1} and temperatures below 20 °C. In our study, the nutrient conditions (Si and TN) were similar to those described for groups VI and V; although particularly for group V, the threshold

values for light and temperature were not always coincident. For instance, group V biovolume was higher when sampling under high light (Kd=0.56 m^{-1}, León 2013) and temperatures occasionally above 20 °C.

Similar dynamics of the phytoplankton community structure (FG, dominant species and MBFG) were found in China reservoirs: Liuxihe (Xiao et al. 2011), ZhuXianDong and NanPing reservoirs (Hu et al. 2013). Liuxihe Reservoir is a deep, monomictic, oligo-mesotrophic canyon reservoir in the subtropical monsoon climate region. However, it shares some similar characteristics with El Carrizal regarding area, volume, depth and nitrogen contents, but phosphorus and chlorophyll *a* contents are much lower (TN:TP>10). On the other hand, the reservoirs studied by Hu et al. (2013) are much richer in nitrogen and chlorophyll *a* contents but phosphorus concentration is lower, as well as their area and depth. The mechanisms driving phytoplankton composition and succession in these environments were similar to those we found in our study. For instance, Xiao et al. (2011) showed that monsoonal hydrology, water residence time, mixing regime, light and nutrient availability were important factors; whereas Hu et al. (2013) found that physical factors such as water residence time, inflow, mixing, temperature and conductivity were important while nutrient availability was not.

Application of trait-based approaches to study reservoirs

The use of different approaches did not bring about opposed results but increased the understanding of the main driving processes. The same group of environmental variables was significant predictors of the biomass of the dominant functional groups or species, enabling to choose the most comfortable classification to pursuit a long-term study of phytoplankton dynamics. For instance, group X_2, MBFG V and *Carteria* sp. biomasses were explained by: pH, Secchi disk transparency, N-NH$_4$, while group B, MBFG VI and *Cyclotella ocellata* biomasses were explained by: stability of the water column, incident solar radiation, Secchi disk and N-NH$_4$. El Carrizal Reservoir was a suitable environment to compare different approaches because of its low species diversity. Between-method differences were only of emphasis and detail. Therefore, if classifications are circumscribed within the limits of ecological questions and hypotheses (Salmaso et al. 2014), conclusions should be analogous in more complex successions or with a great variety of critical drivers.

If we compare the application of the same approaches with more complex communities, we might think of two main situations. A more taxonomically diverse community based on new but functionally redundant species. In this situation, we would expect similar conclusions in relation with the functional groupings approaches. However, as the information of individual species might be less accessible, their use to explain community dynamics might have been more difficult (Huisman and Weissing 2001). On the other hand, a more functionally diverse community with species belonging to different functional groups, and potentially a great variety of drivers, might cause some differences in the main conclusions when comparing functional classifications. Reynolds classification has the advantage of being more refined and enable the dissection of specific combinations of species (Reynolds et al. 2002) while the application of average morphologies and MBFG might be easy to use if the objective is to predict coarse patterns (Reynolds 1998; Kruk et al. 2010). Therefore, we might think of using both approaches or selecting one of them depending on our main objective (Salmaso et al. 2014).

FG classification allows separating a group of species into oligotrophic, mesotrophic, eutrophic or even hypertrophic lakes according to resources availability, thus facilitating an adjustment in the interpretation of environmental conditions (Hu et al. 2013). One of the disadvantages of this classification is that the criteria for allocating coda to species are not clear at all, and there is need to acquire a deeper knowledge of species (Izaguirre et al. 2012).

MBFG are simple, easy to use and proved to be predictable (Kruk et al. 2011; Reynolds et al. 2014). However, they might have low sensitivity when studying particularly narrow environmental gradients (Izaguirre et al. 2012) and are not adequate to analyse the spatial ordering of lakes (Machado et al. 2015).

Morphological traits are the most accessible descriptors because of their ease to be measured (Weithoff 2003) and, although they do not all reflect the ecological properties, they could be representatives of the physiological traits (Fraisse et al. 2013) and of the main driving processes when averaging all community members (Kruk et al. 2015).

Studies analysing phytoplankton main driving processes are especially scarce for latitudes in the Southern Hemisphere (Jeppesen et al. 2005; Meerhoff et al. 2012). Our work is the first description of the dynamics of phytoplankton in an environment of the Cuyo region

in Argentina. Particularly, El Carrizal should meet basic water quality requirements as it belongs to a region where water is a limiting resource, and therefore, its ecological and environmental status should be appropriately monitored. The results presented here will contribute to forecast the effects of environmental changes on the temporal dynamic of El Carrizal phytoplankton with potential application to management strategies.

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