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SEASONAL VARIATION IN THE PHYTOPLANKTON OF A SALINE LOWLAND RIVER (BUENOS AIRES, ARGENTINA) THROUGHOUT AN INTENSIVE SAMPLING PERIOD

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ABSTRACT

The aim of this survey was to analyse seasonal variations in phytoplankton composition and abundance with respect to temperature and conductivity values at two sampling sites in the Salado River's lower basin: El Destino and Guerrero. Samples were taken twice a week from 9 March 2004 to 20 July 2004. A total of 145 and 143 species were identified for these two sites, respectively. Infrequent species were discarded to avoid statistical misinterpretations. Autocorrelation analyses (Ljung-Box *Q*-statistic) were performed in order to establish seasonal patterns for species abundance. Similar significant (p < 0.05) autocorrelation patterns were observed for phytoplankton species composition, temperature and conductivity, thus, illustrating correlations with seasonal behaviour. On the basis of these data, species were grouped as (1) late-summer: with 34 species well represented in warm waters (>22°C) (e.g. *Planctonema lauterbornii* and *Chroococcus* spp.); (2) winter: with 10 species that reached their highest densities in cold waters (<12°C) (e.g. *Binuclearia eriensis* and *Microcystis firma*); (3) transitional: of only four species with abundance peaks during intermediate conditions (15.5°C average) such as *Closteriopsis acicularis* and *Nodularia spumigena* and (4) independent: with 22 species of random behaviour whose autocorrelations remain within confidence limits. These four classifications pertain to species with similar presence at both sampling sites; the rest of the species evinced slightly different patterns. An apparent season-associated succession of species was detected with those adapted to the warm, stagnant water of the late summer being replaced by others acclimated to the cold water of the winter. Copyright ($^{\circ}$ 2009 John Wiley & Sons, Ltd.

KEY WORDS: seasonal succession; phytoplankton assemblages; temporal autocorrelations; lowland river; temperature; conductivity

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INTRODUCTION

Phytoplankton seasonality, in terms of changes in density and species composition, has been the subject of many studies. Since those investigations have been largely restricted to lakes, the factors regulating phytoplankton development and seasonal periodicity in rivers remain far less documented and are still poorly understood (Reynolds, 1988). Phytoplankton communities undergo significant changes within a single year that have been generally referred to as the 'seasonal succession', although this dynamic has more similarities to terrestrial succession (Padisák, 1994). Because of short generation times, many generations are involved; and therefore, plankton communities are exposed to disturbances, mostly consisting of changes in meteorological conditions (Sommer *et al.*, 1993).

Since large rivers contain native phytoplankton populations, we paid special attention to the environmental conditions to which river phytoplankton are exposed: e.g. turbulence, short residence times and hydrological connectivity with respect to backwaters – with this latter aspect being a key factor in river–floodplain systems (Reynolds, 1988; de Ruyter van Steveninck *et al.*, 1992; Ietswaart *et al.*, 1999; Gabellone *et al.*, 2001). Moreover, research in the lower Spree River indicated that seasonal differences in algal growth could be attributable to changes in mixing patterns within the regions of phytoplankton origin (i.e. the lakes), where the alterations would allow dissimilar pre-adaptations to turbulent mixing (Köhler, 1993). Nevertheless, season-dependent factors, such

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as water temperature, were found to contribute significantly to species selection in the San Joaquin River (California, USA) because of their influence on algal-growth rates (Leland, 2003). Seasonal fluctuations in river phytoplankton may reflect not only the importance of the longitudinal dynamics and lateral exchanges, but also physical and biotic interactions (Garnier *et al.*, 1995; Wehr and Descy, 1998; Izaguirre *et al.*, 2001).

River-water retention and flow-current heterogeneity are the mechanisms that increase retention time and encourage opportunities for plankton development (Reynolds and Descy, 1996). In addition, the presence of storage zones (midstream shallow zones and river arms) enhances potamoplankton populations through inoculum incorporation as a result of fluctuations in current velocities and flow discharge, an important determinant in the exchange of organisms (Reynolds, 1995; Waltz and Welker, 1998; García de Emiliani and Devercelli, 2003).

Many studies have been concerned with the phytoplankton of the Salado River lower basin, but none of them have involved intensive sampling (O'Farrell, 1993; Neschuk *et al.*, 2002). Other related reports have described the plankton dynamics of the San Miguel backwater pond, its influence of the Salado River main channel and the role of conductivity and nutrient patterns in controlling the plankton community over an entire catchment (Gabellone *et al.*, 2001, 2005; Solari *et al.*, 2002). In these latter studies, the importance of geomorphology and hydrological conditions during plankton development was also emphasized, since the dynamics and origin of the potamoplankton were considered to be linked to contributions from associated lentic bodies of water (e.g. backwaters and shallow lakes).

As Legendre (1993) pointed out, autocorrelation is a very general property of ecological variables, especially the ones observed along a time sequence (temporal autocorrelation) or over geographical distances (spatial autocorrelation). In this paper temporal autocorrelations were used as an approach to establishing season-related patterns between physicochemical parameters and variations in phytoplankton abundance. While simple correlation coefficients treat individual species as a whole, the procedure of autocorrelation has the additional advantage of distinguishing the behaviour of each species so as to produce correlograms comparing the patterns of environmental variables. This kind of statistical approach is a novel for the study of the Salado River since the present work represents the first example of an intensive sampling program that has been carried out continuously over several months, in order to allow a serial analysis with respect to time.

The main aim of this survey was to analyse seasonal variations within the phytoplankton species in order to correlate this pattern with temperature and other physical–environmental variables at two sampling sites in the Salado River lower basin. Additional physicochemical analyses, such as those of suspended solids and total phosphorous (as well as fractions), were unnecessary since they were performed by Quaíni *et al.* (2005) for the same sampling period. Other factors, such as zooplankton grazing and/or the input from benthic organisms, influences which might also alter the community structure (Chételat *et al.*, 2006) were not considered within this present context.

With an aim at performing a complete analysis of the plankton community, the objectives of the present work were (1) to determine the temporal and spatial structure and dynamics of the phytoplankton within the Salado River lower basin, (2) to analyse autocorrelations throughout regarding the seasonal behaviour of the algal species and their interdependence on environmental variables as forcing factors for these parameters, (3) to characterize the nature of the algal assemblages and the main taxonomic groups of phytoplankton to which they belong and (4) to recognize probable differences, if any, among the various sampling sites with respect to these considerations.

Study area

The Salado River is the major river within the Buenos Aires province and the southernmost tributary of La Plata River basin. The Salado is a typical lowland river 571 km in length with a low mean slope of 0.107 m km^{-1} , and its catchment is approximately $150\,000 \text{ km}^2$. Its basin is located in a dry, temperate floodplain and includes a large number of shallow lakes with different degrees of connectedness, occupying 1000 km^2 under normal conditions of river flow. The regime of the Salado River is quite variable: Its flow reaches no more than $100 \text{ m}^3 \text{ s}^{-1}$ in dry periods but increases up to as much as $1500 \text{ m}^3 \text{ s}^{-1}$ during flood periods, with consequent variations in the conductivity and transport of dissolved and particulate materials. The climate is humid, temperate, with a mean annual precipitation of 899 mm (Gabellone *et al.*, 2001, 2008; Solari *et al.*, 2002).

The studied area comprises the lower stretch of the river at two different sites, El Destino (ED) and Guerrero (G), located at 108 and 92 km from the mouth, respectively (Figure 1). This portion of the river includes a series of

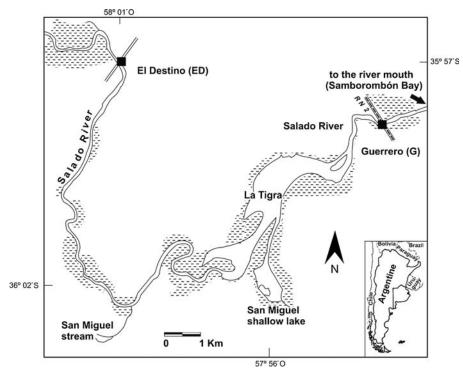


Figure 1. Map of the study area, showing the El Destino (ED) upstream site and the Guerrero (G) downstream site within the Salado River lower basin

interconnected depressions, such as the La Tigra flushing lake and the San Miguel backwater pond, which latter body is connected to the river by a short channel. The upstream site, ED ($35^{\circ}57'S$; $58^{\circ}01'W$), is located at 462 km from the source and constitutes the beginning of the river's lower basin. The other sampling site, G ($35^{\circ}59'S$; $57^{\circ}51'W$), is located downstream at the old bridge, La Postrera, whose removal and replacement were carried out during the present study. In addition to the La Tigra and San Miguel, the river also receives discharges from other connected ponds along the San Miguel stream: the Camarones Grande and Chica and the San Lorenzo shallow lakes (Solari *et al.*, 2002).

MATERIALS AND METHODS

Samples were taken twice a week from 9 March up to 20 July of 2004 and numbered 28 in all for each site, though numbers 2 and 26 were excluded from analysis because of missing data. Each integrated sample consisted of three combined 330-ml subsamples taken along the line extending from bank to bank at equal intervals. At each sampling point along the river, *in situ* measurements of physical–environmental variables (temperature, pH, conductivity, salinity, dissolved oxygen and turbidity) were obtained with a Horiba U-10 multimetre and the mean values for the data subsequently calculated. Phytoplankton samples were collected in 2-L Van-Dorn bottles, preserved in 1% (v/v) acetic Lugol's solution, and stored at room temperature until the time of analysis. The cells in 5-ml aliquots were counted under an inverted microscope according to the Utermöhl method. Phytoplanktonic algae were identified down to the lowest possible taxonomic level. Species richness (number of species) was estimated for each sampling site. The relative frequency of occurrence was calculated for each species and low-occurrence species (less than 30% of relative frequency) were discarded in order to avoid statistical misinterpretation in the autocorrelation analysis, that is, having random distributions because of scarcity rather than a simple occurrence *per se*.

In order to compare significant differences within paired sampling sites, we performed the Student's *t*-test between the various physical–environmental parameters and the different total numbers of individual species,

considering a p < 0.05 to be statistically significant throughout. We also applied Pearson's product-moment correlations in order to determine significant relations between the different pairs of physical-environmental variables and the total number of individuals (ind ml⁻¹). Data were previously log transformed in order to satisfy parametric-test assumptions, while the probability values were Bonferroni-corrected. The autocorrelation coefficients were then used to look for correspondences between species-abundance patterns and physicalenvironmental variables, especially water temperature. Autocorrelations were represented in correlograms: graphs with autocorrelation values plotted on the ordinate versus distance classes among sampling stations (or over different sampling dates) on the abscissa (Legendre, 1993). In addition, the Ljung-Box *Q*-statistic was employed as a complementary contrasting method to detect data randomness. Further smoothing techniques were applied (a 2point moving median and exponential smoothing at a = 0.2) only in cases where the data showed a weak seasonal pattern with a non-significant *Q*-statistic probability.

RESULTS

Physical-environmental variables

For most of the physical–environmental variables there were not significant differences among sampling sites with respect to pH, salinity, turbidity, temperature and conductivity (Table I). Conversely, dissolved oxygen did show significant differences between the ED and G stations, having the highest mean values. The pH values were within the alkaline range and though at a maximum at the beginning of the survey passed through a minimum in mid-April. The data for turbidity, however, displayed no specific pattern, as values shifted from 1 day to the next. Dissolved oxygen was related to the prevailing hydrologic conditions of the river; as this variable exhibited an increase corresponding to the highest river discharge during winter (June–July), with the lowest values occurring during low-flow periods (March–April). A comparable pattern was observed for the salinity since the lowest readings were registered during winter (owing to salt dilution) and highest ones at the beginning of the survey (late summer).

During the entire period studied, the water temperature and conductivity showed a constant decrease for both sampling sites. Temperature maxima were registered on 30 March at 25.8 and 27.5°C for ED and G, respectively, while the minima were observed on 1 July and 13 July at about 6°C at both sites (Figure 2a). According to the autocorrelation results, two significant periods of water temperature can be distinguished: (1) warm water, with temperatures exceeding 22°C, and occurring from the beginning of the survey up to mid-April; and (2) cold water, with temperatures below 12°C and extending from 1 June up to 20 July. Between these extremes there was a period of transitional water (3) of mean temperature 15.5°C (Figure 3a).

	El Destino	Guerrero	t-Test	p
Temperature (°C)	15.2 (6.1)	15.2 (6.7)	0.026	0.979
	25.8-6.07	27.5-6.3		
Conductivity $(mS cm^{-1})$	8.27 (2.48)	8.38 (2.41)	-0.161	0.872
	12.6-5.59	12.2-5.67		
pH	8.31 (0.28)	8.39 (0.2)	-1.07	0.291
	9.53-7.95	9.27-8.21		
Salinity $(mg L^{-1})$	0.46 (0.16)	0.46 (0.15)	-0.164	0.871
	0.72-0.3	0.70-0.3		
Dissolved oxygen $(mg L^{-1})$	6.46 (2.41)	8.87 (3.39)	-2.96	0.004^{*}
	2.82-12.0	2.75–19.1		
Turbidity (NTU)	248. (129)	221 (81.5)	0.901	0.372
	72–445	96–307		

Table I. Physicochemical parameters for both sampling sites

The first row corresponds to mean values and the standard deviation, while the second row gives the observed range. For differences between the sampling sites, the values for the Student *t*-test and the probabilities (*p*) are also shown (n = 28) *p < 0.05.

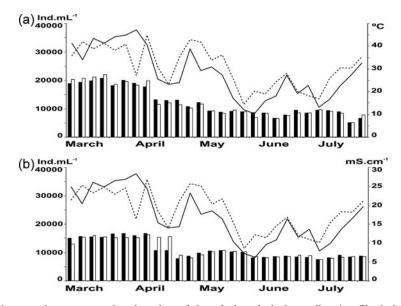


Figure 2. Physical–environmental parameters and total numbers of phytoplankton for both sampling sites. Physical–environmental variables: (a) temperature (°C) and (b) conductivity (mS cm⁻¹) for sampling sites – ED (solid bars) and G (blank bars). Total number of individuals (ind ml⁻¹) for ED (solid lines) and G (broken lines)

River conductivity is related to the prevailing hydrologic conditions and affords a similar pattern to that of temperature throughout the study at both sampling sites (Figure 3b). This conclusion stems from the observation that the autocorrelation patterns for both conductivity and temperature had the same trends and positions of significant lags. Accordingly, the highest values (up to 12 mS cm^{-1}) were recorded from the beginning of the first sampling period up to mid-April, this interval correspond fairly well to the warm-water phase. Thereafter, the conductivity values underwent a sharp decline (to 7.98 and 6.99 mS cm⁻¹ for ED and G, respectively) and then decreased gradually until their minima were reached (5.6 mS cm⁻¹) at the end of June. In this regard, the decrease in conductivity after the warm water maximum occurred a week later at sampling site G than at ED and was thus not observed there until the end of April (Figure 2b).

Positive significant correlations were found between phytoplankton density (the total number of individuals) and the physical–environmental variables at both sampling sites (n = 28): namely, for conductivity (r = 0.79, p < 0.05 for ED and r = 0.48, p < 0.05 for G); for temperature (r = 0.78, p < 0.05 for ED and r = 0.66, p < 0.05 for G) and for salinity (r = 0.79, p < 0.05 for ED and r = 0.48, p < 0.05 for ED and r = 0.48, p < 0.05 for G). A significant negative correlation was also found at ED for dissolved oxygen (r = -0.54, p < 0.05). Figure 2 shows that site G had, for most of the time, a relatively greater number of individuals than did the upstream station ED. This difference was considerably more evident from mid-April onwards, consistent with the decrease in temperature and conductivity.

Taxonomic composition of phytoplankton

During the present study, a total of 175 phytoplankton species were identified, and of these 145 were found at ED and 143 at G. The most relevant taxon was the Chlorophytes, with 55.2% and 57.3% (percentage of the total species) at ED and G, respectively. In the order of abundance, the Chlorophytes were followed by the Cyanophytes (20.7% at ED and 18.9% at G), the Diatoms (11.7% at ED and 13.3% at G) and finally by the Euglenophytes (8.3% at ED and 7% at G). Among the less representative species were the Cryptophytes (2.8% at ED and 2.1% at G) plus the Xanthophytes and the Dinoflagellates, with this latter pair being present at about the same percentage (0.7%) at both sampling stations. As regards species richness, both sampling sites had a large number per sample, with an average tally of 68–70 species at both ED and G. In general terms, the minimum number of species were registered during the cold-water period (45 and 55 species at ED and G, respectively), while the maximum values were

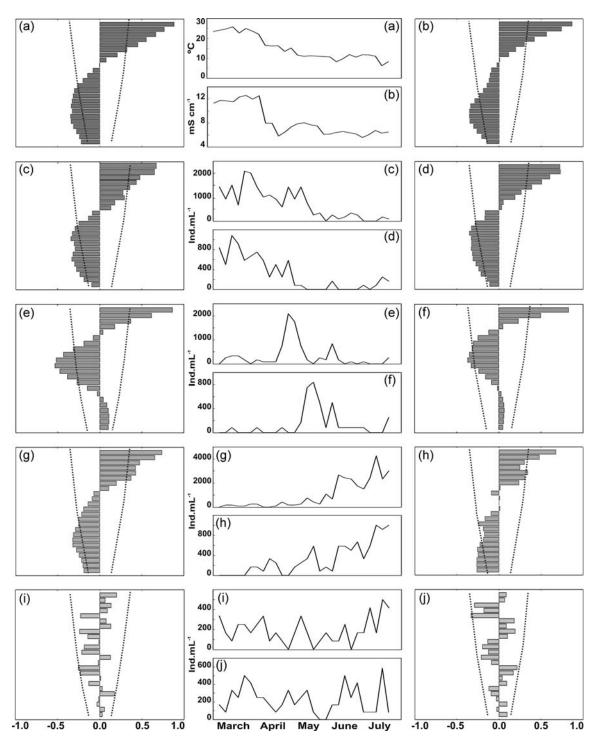


Figure 3. Autocorrelations of physical parameters and species abundances at the ED sampling site (as a representative example). Species were selected taking into account of their abundance and correspondence to the physical–environmental variables for each seasonal group. Autocorrelation plots are shown on the extreme right and left columns with confidence limits indicated by dotted lines. In the centre column are plotted the physical parameters and variation in species abundance (ind ml⁻¹) throughout the survey (March–July). (a) Temperature (°C); (b) Conductivity (mS cm⁻¹); late-summer group: (c) *Planctonema lauterbornii* and (d) *Chrooccous limneticus*; intermediate group (2-point moving median): (e) *Closteriopsis acicularis* and (f) *Nodularia spunigena*; winter group: (g) *Microcystis firma* and (h) *Binuclearia eriensis*; independent group, with random behaviour: (i) *Pseudostaurosira brevistriata* var. *inflata* and (j) *Monoraphidium griffithii*

recorded in the warm, stagnant waters (88 and 83 species for ED and G, respectively). The G sampling site appeared somewhat less variable than ED since it oscillated through a smaller range of values.

Chlorophytes dominated at both sampling sites throughout the entire survey, accounting for 67.6% and 66.5% of total individuals in ED and G, respectively. Among them, the most abundant were the Chlorococcales (*Scenedesmus* spp., *Monoraphidium* spp., *Scotelliopsis reticulata, Tetraedrum minimun, Oocystis marssonii* and Kirchneriella spp.) and some filamentous forms (*Planctonema lauterbornii* and *Geminella interrupta*). These species were followed by the Cyanophytes (21.3% at ED and 22.2% at G), with the Chroococcus being the most representative, especially with respect to members of the genus *Merismopedia, Chroococcus* and *Microcystis*. Although less frequent, some filamentous forms were also registered such as *Anabaenopsis circularis, Anabaena aphanizomenoides* and *Gleitleriana amphibium*. The remaining algal groups did not exceed 10% of the total number of individuals and, in order of importance, consisted in the Diatoms, the Cryptophytes, the Euglenophytes, the Dinoflagellates and the Xanthophytes. Among the representative Diatoms were the *Achnanthes* sp., *Achnanthes linearis, Cyclotella menenghiniana, Nitszchia fruticosa, Pseudostaurosira brevistriata* var. *inflata* and *Navicula cryptocephala*. That none of the species identified exceeded a relative frequency of 5% throughout the entire survey points to a highly diverse and heterogeneous algal community without any notably dominant species prevailing.

Phytoplankton seasonality

Taking into account the autocorrelogram for each taxon and the variation in the latter's abundance, four groups of species were identified whose presence correlated directly with temperature patterns and with the river's hydrologic conditions, as estimated by means of conductivity. According to the periods of water temperature and associated species representation cited above, most of the species were classified as (1) the late-summer group, with species that were abundant during warm-water temperatures (>22°C); (2) the winter group, comprised of species with increased development during the cold-water period (<12°C); (3) a transitional group, including few species, but with high densities only in this intermediate interval and (4) an independent group, composed of species that the species assigned to the late-summer and winter groups had the same autocorrelogram structure and position of significant lags as in the temperature and conductivity autocorrelation patterns. This conclusion is readily apparent upon comparing representation of these patterns in Figure 3.

With respect to the seasonal occurrence and distribution pattern, there are 60 species common to both sampling sites (ED and G), with about one-half (34) belonging to the warm-water period. A lesser number of species (10) were, however, associated with the cold-water group; and only 4 species seemed to be transitional, having abundance peaks during the intermediate period (Table II). The autocorrelation method has also allowed a discrimination of 22 independent species with random behaviour as a consequence of their highly significant *Q*-statistics (p < 0.05).

Late-summer group. Most of the species analysed were classified into the late-summer group and represented frequent warm-water species, having high population densities during the first part of the survey, when the water temperatures were above 22°C (Figure 3c and d). The dominant algal group was the Chlorophytes, especially the Chlorococcales; and, among these, namely: *Crucigenia rectangularis, C. quadrata, S. reticulata, Tetraedron minimum, Didimocystis bicellularis, Monoraphidium* spp., *Scenedesmus* spp., *O. marssonii, Kirchneriella* spp., along with also some filamentous forms such as *P. lauterbornii* and *G. interrupta*. Secondary in importance, we also recorded certain species of Chroococcal Cyanophytes, such as *Aphanocapsa delicatissima, Merismopedia tenuissima, M. glauca, Chroococcus limneticus, C. minutus*, and *C. dispersus*.

Transitional group. All the species categorized in this group exhibited abundance peaks during the intermediatewater period (temperature average: 15.5° C) but did not attain significant densities during most of the survey. Only four species showed this behaviour with *Closteriopsis acicularis* and *Nodularia spumigena* being the most abundant ones (Figure 3e and f).

Winter group. The cold-water period (water temperature $< 12^{\circ}$ C) was characterized by the presence of 10 species that developed progressively during the last part of the survey (June–July), coinciding with the winter season (Figure 3g and h). Of these species, the most abundant ones were: *Microcystis firma, Anabaenopsis*

Table II. List of the coincident species among the sampling sites (ED and G), according to their seasonal occurrence

Warm-water species (34)

Achnanthes sp. (Bory) Achnanthes linearis (Smith) Aphanocapsa delicatissima (W. et G. S. West) Coenochloris planconvexa (Hind.) Chondrocystis dermochroa (Näg) (An.-Kom) Crucigenia quadrata (Morren) Crucigenia rectangularis (A. Braun) (Gay) Chroococcus dispersus (Keissler) (Lemmerm.) Chroococcus limneticus (Lemmermann) Chroococcus minutus (Kützing) (Nägeli) Chroomonas coerulea (Geitler) (Skuja) Didimocystis bicellularis (Chod.) (Komárek) Dictyosphaerium ehregbergianum (Näegeli) Dictyosphaerium pulchellum (Wood) Geminella interrupta (Thurpin) (Lagerheim) Golenkinia radiata (Chodat) (Wille) Kirchneriella irregularis (Smith) (Kors) Kirchneriella obesa (West.) (Schmidle) Merismopedia glauca (Ehrenberg) (Kützing) Merismopedia minima (Beck) Merismopedia tenuissima (Lemmermann) Monoraphidium contortum (Thurpin) (Legn.) Monoraphidium convolutum (Cord) (K.-Legn) Monoraphidium minutum (Näg) (Kom.-Legn.) Oocystis marssonii (Lemmermann) Oocystis parva (West & West) Planctonema lauterbornii (Schmidle) Scenedesmus acunae (Comas) Scenedesmus intermedius acaudatus (Chodat) Scenedesmus nanus (Chodat) Scotelliopsis reticulata (Lund) (Punc. et Kal.) Spirulina platensis (Watanabe & Ischimura) Tetraedron minimum (A. Braun) (Hansgirg) Tetraedron trigonum (Näg.) (Hansgirg)

Transitional species (4)

Closteriopsis acicularis (Smith) (Bel. & Swale) Franceia droescheri (Lem.) (Smith) Kirchneriella pseudoaperta (Komárek) Nodularia spumigena (Mertens)

Cold-water species (10)

Anabaena spiroides (Klebahn) Anabaenopsis circularis (West) (Wolosz. & Miller) Binuclearia eriensis (Wittrock) Lagerheimia subsalsa (Lemmermann) Microcystis firma (Kützing) (Schmidle) Nitzschia fruticosa (Hustedt) Peridinium sp. (Ehrenberg) Pseudoanabaena limnetica (Lemm) (Komarek) Scenedesmus ecornis (Ehrenb.) (Chodat) Schroderia indica (Philipose)

Independent species (random behaviour) (22)

Actinastrum gracillimum (Lagerheim) Anabaena aphanizomenoides (Forti) Cosmarium sp. (Corda) Cryptomonas pusilla (Bachm.) Cyclotella menenghiniana (Kützing) Gleitleriana amphibium (Ag ex Gomont) (Anag) Lobocystis planctonica (Tiff. & Ahlstr.) (Fott) Monoraphidium griffithii (Berk.) (Ko.-Legn.) Monoraphidium komarkovae (Nyg.) Monoraphidium tortile (W. et G. S. West) (Kom.-Leng.) Nitzschia acicularis (W. Smith) Oocystis borgei (Snow) Oocystis solitaria (Wittrock) Oscillatoria tenuis (Agardh ex Gomont) Pseudostaurosira brevistriata var. inflata (Pan) (Edlund) Scenedesmus communis (Turp.) (de Brebisson) Scenedesmus linearis (Komárek) Scenedesmus longispina (Turp.) (Kützing) Scenedesmus obliguus (Turp.) (Kützing) Scenedesmus opoliensis (Richter) Tetrastrum triangulare (Chod.) (Komárek) Thorakochloris nygaardii (Komárek)

circularis, Anabaena spiroides, Pseudoanabaena limnetica, Nitzschia fruticosa, Schroederia indica, Binuclearia eriensis, Lagerheimia subsalsa, Scenedesmus ecornis and Peridinium sp.

Independent group. The species that belong to this category presented a random distribution and lack seasonal correspondence, therefore maintaining autocorrelogram coefficients between the confidence limits (p < 0.05; Figure 3i and j). A total of 22 species fell in this group, with the most notable being: *P. brevistriata var. inflata, Monoraphidium griffithi, M. komarkovae, M. tortile, Cryptomonas pusilla, Scenedesmus linearis, S. communis, S. opoliensis, Actinastrum gracillimum, Oscillatoria tenuis., Oocystis borgei and O. solitaria.*

With respect to the 18 species with non-coincident behaviour (Table III), some of them were present during the late summer at one station (6 and 2 for ED and G, respectively), while random associations were recorded at the other site. In contrast, other species had transitional or winter appearances at site G (2 and 1 species, respectively), whereas random associations were found at ED. The remaining species (7) exhibited random distributions at one station and a low occurrence (less than 30% frequency) at the other.

Table III. Non-coincident species (18)

	El Destino	Guerrero
Coelasphaerium sp. (Näegeli)	R	Т
Coelastrum microporum (Näegeli)	S	R
Cryptomonas erosa (Ehrenberg)	Х	R
Euglena deses (Müller)	Х	R
Melosira numuloides (Dillw.) (Agardh)	S	Х
Microcystis aeruginosa (Kützing)	S	R
Monoraphidium arcuatum (Kors.) (Hind.)	S	R
Navicula cryptocephala Kützing	R	S
Pediastrum boryanum (Turpin) (Meneghini)	R	Х
Pediastrum duplex Meyen	Х	R
Pediastrum tetras (Ehrenberg) (Ralfs)	R	х
Phacus granum (Drezepolsky)	R	S
Pseudotetraedrum sp. (Pascher)	Х	R
Raphidiopsis mediterranea (Skuja)	R	Т
Scenedesmus acutus (Meyen)	S	R
Schroderia setigera (Schroeder) (Lemmermann)	R	W
Spirulina laxissima (West)	S	R
Tetraspora sp. (Link)	S	R

Reference key: (S) late-summer group, (T) transitional group, (W) winter group, (R) species with random behaviour and (x) infrequent species discarded for that sampling site (relative frequency < 30%).

DISCUSSION

In large rivers, processes occurring at the catchment level control plankton dynamics and determine the growth and losses in that biotic community (Reynolds and Descy, 1996). Accordingly, the Salado River undergoes changes in water conductivity closely related to the particular geological characteristics of the subcatchments and to their fluctuations in discharge (Neschuk *et al.*, 2002). Moreover, as Gabellone *et al.* (2005) had pointed out earlier, taking into account the annual cycle of hydrological conditions, we can clearly see in the present work that the conductivity and temperature of the water and the changes in flow discharge are forcing factors for affecting the structure of the plankton community. Those authors also emphasized that phytoplankton composition was determined mainly by salinity, alkalinity and water trophic status. Consistent with the findings of Neschuk *et al.* (2002), we recorded seasonal variations in the composition of the phytoplankton.

In the present work, there were not significant differences between the two sampling sites with respect to an influence of physicochemical variables (e.g. temperature, conductivity, pH, turbidity and salinity); except for the parameter of dissolved oxygen, where the concentration showed higher values at site G. Nutrient limitations did not impose a primary constraint on species selection within the river's phytoplankton since the results obtained by Quaíni *et al.* (2005) during the same sampling period indicated mean values for total phosphorus of 819 and 757 μ g L⁻¹ for ED and G, respectively. As with other temperate rivers, the nutrient supply was always high enough to render limitations on algal growth improbable (Köhler, 1993; Leland, 2003).

Previous studies by several authors had cited an increasing phytoplankton abundance towards the mouth of the river, as a consequence of the geomorphological features of the river's alluvial valley, since the catchment contains lentic environments with different degrees of connectivity to the river that enabled the input of inocula (de Ruyter van Steveninck *et al.*, 1992; O'Farrell, 1993; Ietswaart *et al.*, 1999; Neschuk *et al.*, 2002; Solari *et al.*, 2002; Friedrich and Pohlmann, 2009). Moreover, local algal contributions arising from dead zones, floodplain-associated environments and the benthos could represent significant additions to the structure of the community, thus increasing the variability in taxonomic composition among rivers (García de Emiliani and Devercelli, 2003; Chételat *et al.*, 2006). Accordingly, our results showed a progressive increase in abundance downstream, since the G sampling site had relatively greater phytoplankton densities than the upstream station ED, with this difference

being especially pronounced from mid-April onwards, where increasing water flow enhanced the incorporation of inocula from the associated environments (*i. e.*, the San Miguel backwater and the La Tigra flushing lake).

As to species richness, both sampling sites had a greater number of species than did the tallies found in a previous study (Gabellone *et al.*, 2005): our average maximum and minimum species counts over both stations for warm and cold water were 86 and 50, respectively, as opposed to theirs of 55 and 23 for a single site. In terms of the general taxonomic composition of the potamoplankton, Chlorophytes completely dominated throughout the current survey, as had been observed in previous investigations on the Salado River (O'Farrell, 1993; Neschuk *et al.*, 2002; Solari *et al.*, 2002; Izaguirre *et al.*, 2004). Furthermore, nannoplanktonic coccoid green algae had been a significant component in warm-water conditions (Neschuk *et al.*, 2002); as had also been observed previously in the Seine River (Garnier *et al.*, 1995) and in Ontario and western Quebec (Canada), where small algae ($<20 \mu$ m) had dominated the phytoplankton community during the summer base flows (Chételat *et al.*, 2006). Associated Chloroccocal species and *P. lauterbornii* were also found as notable phytoplankton members during low flow periods in the Middle Paraná River (García de Emiliani and Devercelli, 2003).

Likewise, Cyanophytes were major contributors to the phytoplankton community since they were highly abundant during the late-summer stagnant-water conditions (most of these members being the colonial Chroococcals), but also present during winter (*e. g., M. firma* and certain filamentous forms); as had also been seen by Neschuk *et al.* (2002) and Solari *et al.* (2002). Although Cyanophytes are known for their inability to grow in turbulent or frequently mixed systems, large populations have been found in rivers, either under low discharges or in stagnant waters. Accordingly, in the lower Spree River Cyanophytes were able to populate only in periods with extremely low discharge, and therefore in prolonged retention times (Köhler, 1993).

Diatoms were not the dominant group; as otherwise usually occurs in temperate rivers, such as the Rhine (de Ruyter van Steveninck *et al.*, 1992; Ietswaart *et al.*, 1999; Friedrich and Pohlmann, 2009), the Seine (Garnier *et al.*, 1995), the North American rivers such as the San Joaquin (Leland *et al.*, 2001; Leland 2003) and the Canadian ones (Chételat *et al.*, 2006). At a regional scale, diatom dominances were registered for the Luján River lower basin (O'Farrell *et al.*, 2002) and for the Paraná River at the middle and lower reaches during normal flow periods (Izaguirre *et al.*, 2001; de Cabo *et al.*, 2003; García de Emiliani and Devercelli, 2003). Consistent with our results, Izaguirre *et al.* (2004) found that Diatoms were qualitatively less important, with most of them being associated with benthic and periphytic habitats. The dominance of centric Diatoms is a common characteristic of lowland rivers (Izaguirre *et al.*, 2001; de Cabo *et al.*, 2003; García de Emiliani and Devercelli, 2003; Friedrich and Pohlmann, 2009) and a species – such as *Cyclotella meneghiniana* – are considered as well adapted to turbid and turbulent systems and as part of the usual river nanoplankton fraction (Izaguirre *et al.*, 2001; Chételat *et al.*, 2006). Pennate Diatoms, like the attached members *Achnanthes* spp., *Nitzschia* spp., *N. cryptocephala* and *P. brevistriata* var. *inflata*, were well represented throughout the survey.

Cryptomonads, in which the group was generally represented by small species within the nanoplankton size range, did not represent a significant fraction of the observed phytoplankton, appearing there only occasionally; as had been reported for European rivers (Köhler, 1993; Garnier *et al.*, 1995), though this scarcity was unlike their abundance in the Canadian rivers (Chételat *et al.*, 2006) and in the Paraná River during flood periods (García de Emiliani and Devercelli, 2003). Euglenophytes were mostly minor contributors throughout the survey at both ED and G, being quite variable and scarce, in complete accordance with previous studies in the Salado River (Neschuk *et al.*, 2002).

The statistical analysis performed allowed us to determine the seasonal patterns of phytoplankton abundance with respect to variations in water temperature and conductivity. In this regard, the use of correlation coefficients established positive significant correspondences between phytoplankton density and individual physical–environmental variables for both sampling sites (e.g. conductivity and temperature), but did not indicate the distribution pattern for the species throughout the sampling, where the relationship is better reflected by means of autocorrelation plots. Since temporal autocorrelation can be a useful statistical tool for determining species abundances over time, and here according to the pattern associated with seasonal variation in physical–environmental variables, this form of analysis allowed us to confirm the precise seasonal distributions among the phytoplankton species for the Salado River lower basin.

By this means, species were classified in groups according to the resemblance of their abundance autocorrelation patterns to those of water temperature and conductivity. These physical–environmental variables underwent

changes throughout the survey, as late-summer water temperatures $(22-27.5^{\circ}C)$ dropped down to winter levels (6– $12^{\circ}C$), and increasing current flows diluted river salts, thus reducing the conductivity values (from 12 to 5.6 mS cm^{-1}). A similar water-temperature pattern was also observed in the San Joaquin River, having summer temperatures ranging from 17.5 to 28.5°C and late-autumn-to-winter ones between 6.5 and 16°C (Leland, 2003). As expected, most of the species analysed (60) had the same seasonal-abundance patterns for both sampling sites. More research should be done, however, in order to establish the probable reasons for the discrepant patterns of the remaining species between the two sampling sites.

The late-summer group was comprised of species that had prevailed and acquired their greatest development in the warm, stagnant waters with high conductivity values present during the first part of the survey. Species from this assemblage were mostly nanoplanktonic coccoid Chlorophytes and Chroococcal Cyanophytes, where the species seemed to be adapted to these low current flows and more stagnant conditions. As de Ruyter van Steveninck *et al.* (1992) suggested, the conditions for phytoplankton growth seem to improve with decreasing water flow (producing, therefore, increased retention times and less intense turbulence). Accordingly, our results indicated the highest total number of individual species during low-flow discharges and stagnant conditions. Therefore, phytoplankton members were mostly represented by nanoplanktonic Chlorophytes and Cyanophytes, whereas filamentous net plankton were of secondary importance, just as had been reported in previous studies on the Salado River (O'Farrell, 1993; Neschuk *et al.*, 2002; Solari *et al.*, 2002).

The so-called transitional period was only populated by four species that had abundance peaks during these intermediate temperature conditions (average, 15.5° C) and were also rather scarce during most of the survey. Because of their lesser members, the species of this category have no common morphological features. Thus, more research should be done in order to elucidate the possible causes of the species behaviour.

The winter assemblage involved species with increasing development during the cold-water period (6–12°C), also corresponding to lower conductivity values, with the latter parameter being a consequence of increased water flow discharge. This group was mostly represented by the dominant presence of *M. firma*, which species had likewise been found under the same conditions by Izaguirre *et al.* (2004).

The presence of a heterogeneous assemblage of species showed no clear correlation with variations in temperature and discharge so that their distribution remained random. This independent group is characterized by 22 species whose appearance lacked seasonal association and which displayed variable abundances throughout the survey without any distinct trend. This behaviour must be related to other physical and/or biological river factors, but to determine the nature of these influences more research is needed.

Previous studies on the Salado River found the various members of the phytoplankton community to have responses similar to those in our study, as they were also significantly affected by water temperature, conductivity and hydrodynamics; in which the parameters were considered by them to be the limiting factors (Neschuk *et al.*, 2002; Solari *et al.*, 2002). The same significant relationship between hydrologic conditions and plankton dynamics was reported for the Rhine River (Ietswaart *et al.*, 1999), the Baía River (Train and Rodrigues, 1998) and the Paraná River, where the composition and abundance of the phytoplankton also showed significant temporal fluctuations in response to changes in the hydrological conditions (Train and Rodrigues, 1998; Izaguirre *et al.*, 2001; de Cabo *et al.*, 2003; García de Emiliani and Devercelli, 2003).

Consistent with the general belief that hydrological and hydrodynamic factors (e.g. river discharge and water residence time) are of greater importance to planktonic development in rivers than in lakes (Chételat *et al.*, 2006), the hydrological pattern proved to be the main driving force influencing the algal communities (Train and Rodrigues, 1998). In accordance with our own results, Neschuk *et al.* (2002) pointed out that the Salado River phytoplankton showed significant seasonal variations with respect to composition and species abundance in response to physical–environmental variables such as conductivity, temperature and hydrological fluctuations. A similar circumstance was also reported for the San Joaquin River where seasonally varying factors, such as water temperature, contribute significantly to species selection because of their influence on algal-growth rates (Leland, 2003).

It has been recognized for sometime that phytoplankton communities undergo a seasonal succession, that is, significant changes in their size and structure within a single year (Padisák, 1994). Accordingly, in this study we found an evident modification in phytoplankton of the Salado River from the late summer to winter, with species substitution progressing from low-flow-, warm-water-adapted to medium-flow-, cold-water-tolerant species.

SEASONAL VARIATION OF RIVER PHYTOPLANKTON

Temporal-autocorrelation analysis allowed us to characterize the replacement of the species and their typical behaviour throughout the survey. On this basis, algal assemblages were identified according to species presence and abundance during different water-temperature periods, where the intervals would roughly correspond to progressive seasonal stages. As Sommer *et al.* (1993) pointed out the external cycle of climatic and hydrological conditions is the sole phenomenon responsible for restarting plankton succession each year. Nevertheless, biotic interactions appear to play a significant role as well in the Salado River and in other lowland rivers, though more research is needed to characterize the specific nature of these influences.

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