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Modern diatoms from a temperate river in South America: the Colorado River (North Patagonia, Argentina)

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Diatom assemblage composition and distribution from surface sediment samples of the Colorado River, Patagonia were analysed in relation to environmental variables using multivariate techniques. The aim of this study was to determine the ecological preferences of the taxa and provide analogues for paleoenvironmental reconstructions in estuarine and fluvial environments of southern South America. Cluster analysis identified two main diatom assemblages, one grouping sites with a marine influence, and another group influenced by typical riverine conditions. Canonical correspondence analysis indicated that major ion concentrations contribute significantly to explain the variation in the composition of diatom assemblages. A total of 208 taxa belonging to 56 genera were recorded. In estuarine sites, the assemblages were characterized by marine-brackish tychoplankton, such as *Cymatosira belgica*, *Rhaphoneis amphiceros*, *Delphineis minutissima*, *Paralia sulcata* and *Paralia sulcata* var. *coronota*. Diatom communities in riverine sites were dominated by freshwater taxa such as *Staurosira venter*, *Pseudostaurosira brevistriata*, *Punctastriata glubokoensis* and *Punctastriata lancettula*. Two *Punctastriata* species that were difficult to distinguish with LM were examined in detail with SEM, and the value of detailed LM and SEM analysis for distinguishing *Punctastriata* spp. and other small fragilarioids is discussed. Based on their autoecological affinities, it is likely that the dominance of small fragilarioids is related to the increase in ionic concentration in the basin, as a consequence of both precipitation decrease, and an increase in urban, industrial and agricultural activities. The construction of a flood-control structure in the northern branch of the delta modified the diatom community so that marine taxa were replaced by brackish-freshwater taxa in response to changes in salinity, substrata and water depth.

Keywords: *diatoms, rivers, estuaries, paleoecology, Patagonia, Argentina*

Introduction

Rivers, streams and transitional environments are heterogeneous and dynamic ecosystems in which geomorphological and hydrological characteristics vary on different spatial and temporal scales to form environmental gradients, along which different types of biological communities are found (Wetzel 2001). Among the algae, benthic diatoms contribute significantly to primary production and are considered an important component of biodiversity and ecological resources of lotic and coastal environments (Battarbee et al. 2001). In these ecosystems, they respond quickly to recent environmental changes and reflect accurately both the physical and chemical characteristics of the water. They are biological indicators commonly used in the assessment of ecological status and for monitoring anthropogenic impacts in freshwater and estuarine environments (Stevenson et al. 2010, Trobajo & Sullivan 2010). The reliability of these techniques requires a thorough knowledge of the diatom assemblages and their relationships with measured water-quality variables (Birks 2010).

On a global scale, changes in climate, geology, topography, land use and other landscape characteristics affect the ionic strength, nutrient concentrations, pH, availability of substrata, current velocity and light across the watershed, as well as controlling the composition and distribution of diatom communities (Potapova & Charles 2002, Soininen 2007).

The distribution and composition of diatom communities have been well studied in North America and Europe, but not in South America, where both the absence of ecological information and the assumed cosmopolitan distribution of most taxa have historically favoured the use of autecological data gathered from other regions of the world. Although the study of freshwater and coastal/marine diatoms in relation to environmental parameters has intensified in Argentina over the last 10 years (Espinosa et al. 2006, Hassan et al. 2006, Licursi et al. 2006, Hassan et al. 2007, Gómez et al. 2009, Licursi et al. 2010, Hassan et al. 2013, Espinosa & Isla 2015), the existing information on diatom ecology

is still scattered and fragmentary and often restricted to taxonomical studies. Even fewer works have employed robust statistical methods to explore diatom-environment relationships.

In the Patagonia region, Argentina, several studies have been performed on the middle and lower basins of the Negro and Chubut rivers to analyse the seasonal relationships between phytoplankton and environmental factors (Santinelli et al. 1990, Sastre et al. 1990, Villafañe et al. 1991, Sastre et al. 1994, Pucci et al. 1996), inferring paleoenvironmental change using semi-quantitative methods (Escandell et al. 2009, Escandell & Espinosa 2012). Nevertheless, the knowledge of ecological preferences of modern diatoms along freshwater and coastal environments from north Patagonia remains largely unstudied.

Traditionally, Frenguelli's research on surface water and sediments from Bahía San Blas, the San Jorge and San Matías Gulfs, constituted the basis of diatom taxonomy in this region (Espinosa 2008). Recently, Espinosa & Isla (2015) studied the diatom composition of surface sediments from the estuaries of the Negro and Chubut Rivers, San Julián Bay and the Santa Cruz River. Biasotti et al. (2013, 2014) and Galea et al. (2014) analysed the seasonal changes of phytoplankton in the middle basin of the Colorado River, while Vouilloud & Leonardi (2001) studied the diatom floras from five brackish water drainage channels of the CORFO (Corporación de Fomento del Valle Bonaerense del Río Colorado) within the lower basin. Seasonal variability in the phytoplankton composition, especially diatoms, in Anegada Bay was studied by Garibotti et al. (2011).

In this context, studies of the diatom composition and distribution along the Colorado River, a fluvial system located in the northern region of Patagonia, were undertaken. The principal aims of our investigation were to determine: (1) the specific composition of diatom assemblages from surface sediments, (2) their spatial distribution patterns and (3) the principal environmental factors that constrain diatom composition and distribution. In addition, because the taxonomy of fragilarioid taxa remains largely understudied in South America, a brief discussion of the morphological features (light and scanning electron microscopy (SEM)) of two araphid diatoms from sediment samples is provided. These taxa share features with species currently included in *Punctastriata* Williams & Round.

Regional setting

The original Colorado basin spanned north-western Argentina to Patagonia, comprising the watersheds of the Vinchina, Bermejo, Mendoza, Tunuyán, Diamante, Atuel, Desaguadero, Salado, Chadileuvú and Curacó rivers (Tapia 1935, Isla & Toldo 2013). The Colorado River is formed by the junction of the Barrancas River ($35.8 \, \text{m}^3 \, \text{s}^{-1}$ average) and Grande River ($34.8 \, \text{m}^3 \, \text{s}^{-1}$ average) on the eastern slope of the Central Andes, at approximately 36°52′19″S and 69°45′34″W (Alcalde 2014). After flowing about 920 km in a NW-SE direction, the Colorado River reaches the South Atlantic Ocean where it discharges through several channels as an extended deltaic plain (Fig. 1) (Spalletti & Isla 2003).

Given the extent of its basin and the west-east orientation, the climate of the Colorado River valley is marked by a rainfall gradient which increases toward the east. The average annual precipitation between 2002 and 2014 was 163 mm in the upper basin (Buta Ranquil), and 235 mm in the middle basin (Casa de Piedra) (COIRCO 2016). A dry to semi-arid climate with an average annual precipitation of 465 mm near to E06 characterizes the lower basin and river mouth, while the air temperatures vary from 22.2°C in January to 7.5°C in July.

This river represents a pluvio-nival regime, and according to records from the Buta Ranquil station since 1940, the annual mean discharge is $148 \, \text{m}^3 \, \text{s}^{-1}$, with the highest values in spring, lowest in summer (Alcalde 2014). In the middle basin (near to Casa de Piedra dam), the mean current velocity is approximately $0.53 \, \text{m} \, \text{s}^{-1}$, with the highest values in winter ($0.69 \, \text{m} \, \text{s}^{-1}$) and the lowest in autumn ($0.35 \, \text{m} \, \text{s}^{-1}$) (Biasotti et al. 2014, Galea et al. 2014). Although there is no precise information on the amount of sediment transported, the Colorado River is a patagonian fluvial system with high-suspended sediment load (Spalletti & Isla 2003).

The Colorado River delta extends from the Verde Peninsula to Otero Island in southern Buenos Aires Province, and is one of two deltas along the Argentinian coast (the northern one is the Paraná Delta at the Río de La Plata estuary). It is a highly sinuous and destructive delta, formed of active and abandoned channels, and is exposed to strong littoral drift, low sediment, high wave energy and low offshore slope conditions (Codignotto & Marcomini 1993). The area of the deltaic plain experiences semi-diurnal to mixed tides, with a meso-tidal regime, and a mean tidal amplitude of about 2.5 m near the E01, E02 and E03 sites (Isla & Bertola 2003). According to Codignotto &Marcomini (1993), the tidal action can penetrate up to 16 km inland.

The basin morphology, water and sediment load discharges have changed substantially as result of the construction of channels and the Casa de Piedra dam in 1996. This dam is located 340 km from the coast (Piccolo & Perillo 1999, Spalletti & Isla 2003). In addition, the discharges of chemical pollutants resulting from human activities, such as water treatment works, sewage plants and petrochemical industries, increase downstream (Spalletti & Isla 2003, Brunet et al. 2005, Ashcroft 2009), further modifying the structure and functioning of aquatic ecosystems.
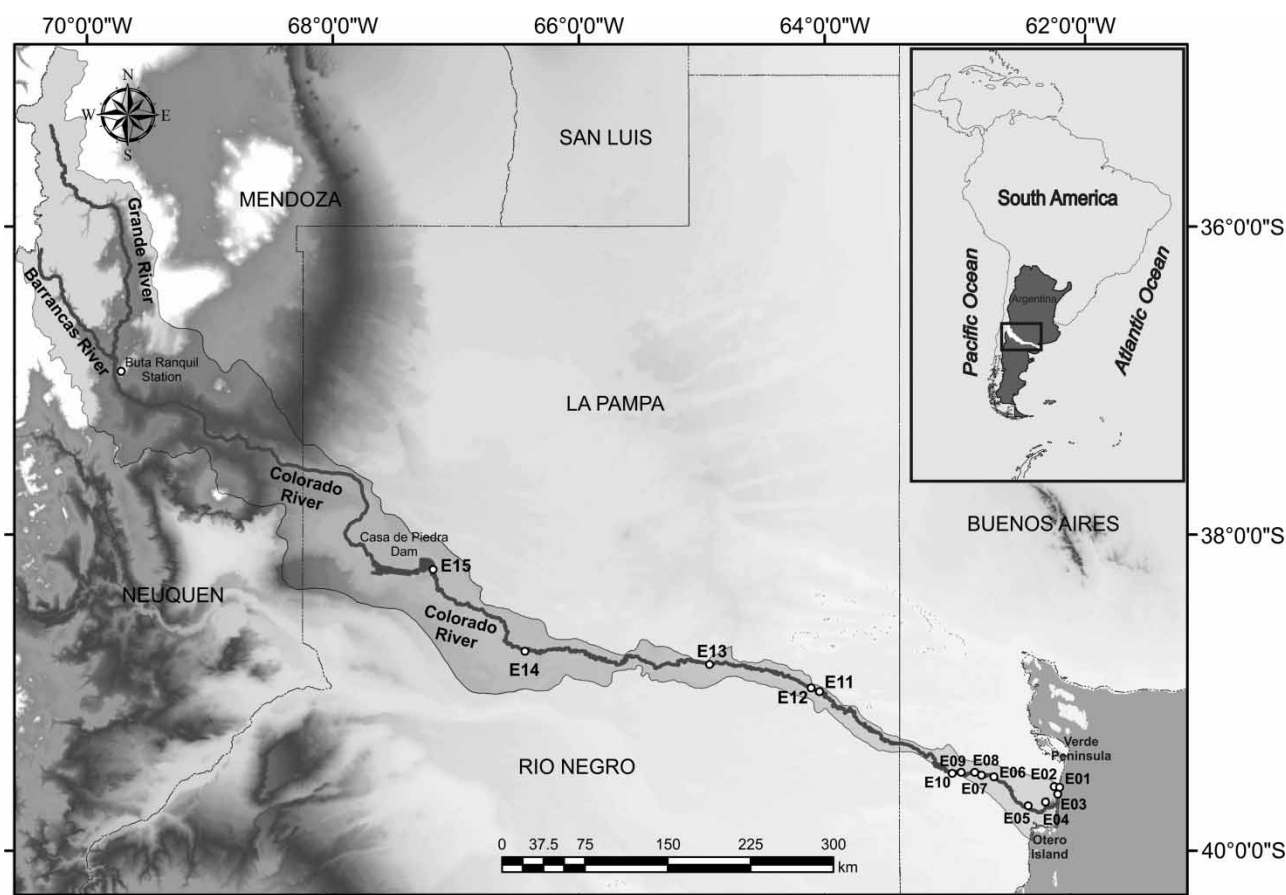
Figure 1.   Location map showing the sample sites.

Materials and methods

Field and laboratory methods

Fifteen sampling sites were selected from the middle and lower basins, representing the maximum heterogeneity along the aquatic environment. Surface sediment samples for diatom and sedimentological analyses were collected along the Colorado River in February 2014 (summer) while environmental variables were measured in February 2014 and August 2015 (winter). It was not possible to measure environmental variables at sampling sites along the northern branch of the delta (E01, E02, E03 and E04) during winter (August 2015) because these sites became inaccessible due to rains and waterlogged roads. In addition, the recent construction of a flood-control structure close to the inlet caused a decrease in water inflow, and led to surface water drying out. Nevertheless, a surface sediment sample was collected from E01 in winter 2015 and environmental variables were measured. These data were not used in the ordination analysis and distribution diagram, but were used to compare winter diatom composition with those taken in the summer before the gate was built.

At each site, the salinity, conductivity, water temperature and pH were measured from the subsurface water using a Horiba U-10 water-quality analyser. In addition,

Table 1.   Salinity and water depth in La Chiquita Beach (near to E03).

Hours	Salinity (‰)	Depth (cm)
10:45	8.5	16.5
13:05	5.8	12.5
13:55	5.7	11.0
14:50	5.8	12.0
15:20	6.9	29.0
15:45	8.9	36.0
16:15	29.7	NA

water samples were taken for nutrient and major ion analysis using standard methods. The summer environmental variables at the estuarine sites (E01, E02 and E03) were measured at low tide. At E03 (located 1.18 km from the coast), salinity and water depth were repeatedly measured over six hours in summer (03/02/2014) to determine the effects of tides into the estuary (Table 1).

The top of the surficial sediment layer (ca. 500 g) was scraped with a spatula and placed into airtight plastic bags for sedimentological analysis. In the laboratory, a subsample (ca. 100 g) was taken to quantify the proportion of gravel (> 2 mm in diameter), sand (2 mm–62 μm)

and mud ($< 62\,\mu m$) using the dry-sieving technique (Folk 1980). The total organic carbon (TOC) content of surface sediments was estimated according to the Walkley & Black (1934) method, using potassium dichromate as an oxidizing agent.

Diatom samples were collected with plastic tubes (20 mm × 100 mm) from surface sediments of the littoral zone. At each site, three samples were taken and the top 1 cm of sediment of each was then carefully extracted and combined for cleaning and analysis. For estuarine sites (E01, E02 and E03), they were collected from the foreshore (part of the shore between high and low tides) at low tide.

Sediment samples were oven dried at 105°C and 5 g of dry sediment were oxidized with hydrogen peroxide (30%) and hydrochloric acid (10%) to remove organic matter and carbonates, then washed five or six times with distilled water until the pH was neutral. Permanent diatom slides were prepared with Zrax®, and a minimum of 500 diatom valves were identified and counted along random transects for each slide under oil immersion using a Zeiss Axiostar plus light microscope. A scanning electron microscope (SEM; Jeol JSM-6460 LV) operated at 15 kV was used to confirm identifications. Diatom species were identified to the lowest taxonomic level according to the standard literature.

Data Analysis

Several studies found that the diatom thanatocoenoses (dead diatoms, both autochthonous and allochthonous remains present in sediments) of the littoral zone of streams, lakes, tidal wetland and estuaries have a direct relationship with environmental variables and, hence, can be used for specific assessments (Sawai 2001, Hassan et al. 2008, Gillett et al. 2009). The statistical analysis to assess the response of diatom assemblages to environmental factors measured in the Colorado River was performed only with the summer data, due to the absence of winter measurements at sampling sites E01, E02, E03 and E04. Exploratory data analysis and multivariate ordination techniques were used to analyse the spatial variation of diatoms and environmental factors. All analyses were conducted with the statistical software R version 3.2.2 (R Development Core Team 2015), using the packages 'rioja' version 0.9-5 (Juggins 2015), 'vegan' version 2.3-0 (Oksanen et al. 2015), 'mvnormtest' version 0.1-9 (Jarek 2015) and 'ggtern' version 1.0.6.1 (Hamilton 2015).

Diatom counts were expressed as percentages; only those taxa with an occurrence above 2% of the total sample dataset were included for further statistical analysis. Species data were log $(x + 1)$ transformed and all environmental variables were standardized by the Z-score method ($Z_i = (x_i - \mu_i)/\sigma_i$) prior to analysis to obtain normal distributions and equalize variances. Diatom zones were defined using constrained hierarchical clustering based on Bray–Curtis distances, and their statistical significance was assessed using the broken stick model. Unconstrained and constrained ordinations (see below) were applied to summer data, including all 15 sampling sites along the river; the same ordinations were also performed on the summer data subset excluding the sites near the coast (E01, E02 and E03) to observe the effect of the environmental variables on riverine sites. Since the Shapiro–Wilk test showed multivariate normality ($p = .523$), Pearson correlations were applied to explore the statistical dependence between explanatory variables, and the sampling site ordination was explored through a principal components analysis (PCA). A ternary diagram considering relative abundance, salinity requirements and life form was carried out to compare diatom composition between samples taken before and after flood-control structure construction at E01.

In order to determine the gradient length of the first canonical axis, and thus to define whether a unimodal or linear ordination model was the most appropriate for the dataset, a detrended correspondence analysis (DCA) was applied to all biological variables. Since the DCA shows a first-gradient standard deviation (SD) length of 3.27, a canonical correspondence analysis (CCA) was carried out to explore the relationship between species composition and environmental variables. The statistical significance was assessed by analysis of variance (ANOVA) permutation tests. In addition, diatom species richness and Shannon's (H) indices were calculated, while the ecological optima and tolerances of *Punctastriata glubokoensis* Williams, Chudaev & Gololobova and *Punctastriata lancettula* (Schumann) Hamilton & Siver were estimated by a weighted average (WA) and weighted standard deviation (WSD), respectively (Oksanen et al. 1988, Potapova & Charles 2003).

Results

Environmental variables

Spatial and temporal variations in the environmental data are summarized in Table 2. The Colorado River tends to be slightly alkaline to alkaline (pH = 8.35 ± 0.58), with a surface temperature between 20°C and 27.4°C in summer, between 5.1°C and 10.5°C in winter. Sediment composition is mainly sandy, with the exception of some sites near to Pedro Luro (E06, E07, E08, E09 and E10), where fractions of silt and clay are dominant and TOC is highest. Salinity and conductivity increase significantly in those sampling sites with marine influence (E01, E02 and E03), where hardness and ionic values are highest. It is relevant to point out that upstream salinity is slightly higher in winter (average 0.84 ± 0.13‰) than in summer (average 0.56 ± 0.06‰) (Table 2). With regard to this variable, the riverine sites of the Colorado River have the highest salinity values among the Patagonian rivers, whose waters always have negligible salinity (Espinosa & Isla 2015).

Table 2. Environmental variables of the 15 sampling sites.

Sample sites	Location	Season	pH	Cond	T	Sal	Hard	HCO_3^-	Cl^-	SO_4^{2-}	NO_3^-
E01. La Chiquita 6	39°36′2″S-62°06′7″W	Summer	8.29	20.10	22.15	12.10	2110.00	227.00	5065.00	1770.00	0.30
		Winter	–	–	–	–	–	–	–	–	–
E02. La Chiquita 4	39°36′11.1″S-62°06′23.9″W	Summer	8.24	16.60	20.45	9.80	2005.00	386.00	5021.00	1590.00	10.40
		Winter*	9.70	5.63	8.2	2.8	334.00	268.00	1609.00	64.00	4.50
E03. La Chiquita 1	39°35′52.62″S-62°6′43.14″W	Summer	8.85	11.30	21.55	6.40	1814.00	387.00	2554.00	1220.00	4.30
		Winter	–	–	–	–	–	–	–	–	–
E04. Las Isletas	39°43.06′5″S-62°20.49′4″W	Summer	7.95	1.51	20.60	0.65	681.00	235.00	194.00	480.00	4.60
		Winter	–	–	–	–	–	–	–	–	–
E05. Estancia San Pedro	39°39′51.9″S-62°10′56.1″W	Summer	7.36	1.26	25.70	0.50	777.00	205.00	174.00	260.00	1.50
		Winter	7.57	2.07	8.40	0.90	1000.00	129.00	326.00	670.00	4.80
E06. El Cencerro	39°32′13″S-62°37′15,5″W	Summer	9.39	1.33	22.60	0.60	565.00	194.00	238.00	315.00	1.00
		Winter	8.54	2.07	7.85	0.90	790.00	136.00	297.00	530.00	8.10
E07. Pedro Luro	39°31′38,9″S-62°43′20,1″W	Summer	9.36	0.13	22.50	0.60	487.00	161.00	204.00	230.00	1.00
		Winter	8.43	2.08	6.55	0.90	756.00	136.00	326.00	410.00	0.50
E08. La Carreta	39°30′34,8″S-62°46′40,8″W	Summer	7.79	1.41	24.05	0.60	395.00	380.00	156.00	390.00	0.50
		Winter	8.49	2.09	5.95	0.90	417.00	151.00	286.00	560.00	0.50
E09. El Micelio	39°30′32,8″S-62°53′13,5″W	Summer	9.29	1.27	20.00	0.50	534.00	118.00	223.00	240.00	0.50
		Winter	8.51	2.09	5.65	0.90	546.00	189.00	337.00	570.00	4.10
E10. Presa del Colorado	39°30′57.7″S-62°57′41.7″W	Summer	7.93	1.40	22.35	0.60	576.00	113.60	222.00	320.00	1.10
		Winter	8.90	2.05	5.55	0.90	500.00	136.00	268.00	470.00	4.40
E11. El Meandro	39°0′04,6″S-64°02′27,6″W	Summer	9.05	1.33	27.45	0.60	467.00	174.00	256.00	225.00	2.70
		Winter	8.08	2.04	7.90	0.90	477.00	220.00	320.00	410.00	1.90
E12. Balneario	38°58′37.2″S-64°6′30.1″W	Summer	8.60	1.42	24.20	0.60	476.00	227.00	152.00	440.00	3.40
		Winter	8.18	2.00	9.35	0.90	842.00	106.00	307.00	530.00	8.50
E13. Pichi Mahuida	38°49′44.5″S-64°56′1.6″W	Summer	7.62	1.31	21.40	0.50	508.00	227.00	148.00	290.00	0.30
		Winter	–	–	–	–	–	–	–	–	–
E14. Gob. Duval	38°44′41.1″S-66°26′8.8″W	Summer	7.83	1.25	24.05	0.50	474.00	219.00	148.00	270.00	0.30
		Winter	8.45	1.49	5.10	0.60	447.00	122.00	200.00	228.00	6.20
E15. Casa de Piedra	38°13′30.1″S-67°10′57.4″W	Summer	7.97	1.24	21.20	0.50	470.00	250.00	156.00	350.00	5.40
		Winter	8.88	1.40	10.75	0.60	452.00	189.00	183.00	240.00	1.20

(*Continued*)

Table 2. Continued.

Sample sites	Season	SiO_2	Na^+	K^+	Ca^{2+}	Mg^{2+}	TOC	Gravel	Sand	Mud
E01. La Chiquita 6	Summer	13.40	2650.00	50.00	780.00	38.40	0.31	0.00	99.91	0.09
	Winter	–	–	–	–	–				
E02. La Chiquita 4	Summer	17.80	2600.00	140.00	230.00	343.00	0.19	0.00	96.68	3.32
	Winter*	8.20	915.00	40.00	42.00	55.00				
E03. La Chiquita 1	Summer	23.20	1350.00	600.00	400.00	196.00	0.28	0.00	98.74	1.26
	Winter	–	–	–	–	–				
E04. Las Isletas	Summer	7.88	160.00	8.00	97.00	106.00	0.36	0.00	95.06	4.94
	Winter	–	–	–	–	–				
E05. Estancia San Pedro	Summer	7.58	90.00	5.00	89.00	133.00	0.27	0.00	96.12	3.88
	Winter	7.05	160.00	3.00	132.00	160.80				
E06. El Cencerro	Summer	17.00	95.00	1.60	91.00	81.00	0.79	1.05	64.22	34.73
	Winter	9.67	140.00	4.00	96.00	132.00				
E07. Pedro Luro	Summer	12.90	87.00	3.30	75.00	71.80	0.68	0.03	75.94	24.02
	Winter	8.92	160.00	3.00	80.00	133.40				
E08. La Carreta	Summer	7.88	190.00	5.00	89.00	41.40	0.64	20.76	61.85	17.40
	Winter	10.00	280.00	6.00	70.00	58.10				
E09. El Micelio	Summer	15.70	90.00	1.60	79.00	80.70	0.23	0.53	96.26	3.21
	Winter	3.04	370.00	3.50	182.00	22.00				
E10. Presa del Colorado	Summer	9.70	90.00	3.00	85.00	87.40	0.46	0.17	77.94	21.89
	Winter	2.55	180.00	5.50	112.00	53.00				
E11. El Meandro	Summer	12.50	92.00	3.20	120.00	40.08	0.29	0.04	98.68	1.28
	Winter	5.50	230.00	8.50	142.00	29.30				
E12. Balneario	Summer	8.04	160.00	4.00	100.00	54.20	0.33	0.00	90.50	9.50
	Winter	6.62	140.00	3.00	111.00	136.00				
E13. Pichi Mahuida	Summer	6.74	90.00	2.00	90.00	68.00	0.30	0.00	84.63	15.37
	Winter	–	–	–	–	–				
E14. Gob. Duval	Summer	6.61	160.00	4.00	86.00	62.10	0.34	7.49	84.64	7.88
	Winter	4.02	50.00	8.00	100.00	47.30				
E15. Casa de Piedra	Summer	7.07	150.00	1.00	84.00	62.40	0.30	11.15	84.91	3.94
	Winter	5.62	68.00	2.80	134.00	28.08				

*Measurements after the construction of flood-control structure

Notes: Cond, conductivity (mS cm^{-1}); T, water temperature (°C); Sal, salinity (‰); Hard, total hardness (mg L^{-1} of CaCO$_3$). Categories of grain size (gravel, sand and mud) and total organic carbon (TOC) are expressed in percentage (%). Concentrations of ions are expressed in mg L^{-1}.

According to the Kaiser–Guttman criterion (a factor selection method based on the average of the eigenvalue output), three components of the PCA ordination contribute to 75% of the variation in the summer environmental data, although the first two axes explain most of the variance in the data set (Table 3, Fig. 2A). The first axis explains 51% of the total variation and describes a gradient of ionic strength that is highly correlated with conductivity, salinity, hardness, chloride (Cl^-), sulphates (SO_4^{2-}), sodium (Na^+), calcium (Ca^{2+}), manganese (Mg^{2+}) and potassium (K^+).

The second axis explains 14% of the total variation and exhibits a positive correlation between TOC and mud, but negative correlation with percentage of sand (Table 3).

Considering only the sampling sites away from the inlet, the PCA ordination shows that the bi-dimensional plot describes 50% of the total variation in summer data (Table 4, Fig. 2B). The first axis explains 28% of the variation and shows a positive correlation with bicarbonate (HCO_3^-), sulphate (SO_4^{2-}) and sodium (Na^+), but negative correlation with pH, chloride (Cl^-) and silicon dioxide (SiO_2). The second component explains 22% variation and shows negative correlation with mud and TOC, but positive correlation with sand and hardness.

Therefore, the original matrix of 18 environmental variables (measured in summer) was reduced to five (pH, temperature, salinity, mud, HCO_3^- and NO_3^-). The original summer data set (excluding sites near the mouth) was reduced to eight variables (conductivity, temperature, SiO_2, NO_3^-, K^+, Ca^{2+}, Mg^{2+} and mud).

Distribution patterns of major taxa

Most of the surface sediment samples contain abundant well-preserved diatom valves. A total of 208 taxa belonging to 56 genera were recorded in 16 samples, of which only 28 taxa contributed more than 2% in at least two samples (Figs 3, 4–21). The genera with the greatest number of species are *Nitzschia* Hassall (29), *Navicula* Bory (24), *Amphora* Ehrenberg ex Kützing (7) and *Diploneis* Ehrenberg ex Cleve (6).

The broken stick model shows three main groups in the constrained cluster analysis. The distribution pattern changes significantly between estuarine (zone I) and riverine (zone II and III) sites. Diatom composition of zone I, where tidal effects are important, is dominated by marine/brackish tychoplankton: *Cymatosira belgica* Grunow, *Rhaphoneis amphiceros* (Ehrenberg) Ehrenberg, *Delphineis minutissima* (Hustedt) Simonsen, *Paralia sulcata* (Ehrenberg) Cleve, *Paralia sulcata* var. *coronota* (Ehrenberg) Andrews and *Delphineis surirella* (Ehrenberg) G.W. Andrews.

Zones II and III have well-developed populations of fragilarioid diatoms considered as brackish/freshwater tychoplankton. *Staurosira venter* (Ehrenberg) Cleve & Möller is the most abundant species (> 50% of the total in zone II) accompanied by *Pseudostaurosira brevistriata* (Grunow) Williams & Round, *P. glubokoensis* and *P. lancettula*, which are also abundant in this section of the river.

Freshwater planktonic taxa such as *Stephanodiscus agassizensis* Håkansson & Kling and *Cyclotella ocellata*

Table 3. Principal components analysis (PCA) results of summer environmental variables including all sampling sites.

|	PC1	PC2	PC3	PC4
Eigenvalues of the correlation matrix				
Eigenvalue	9.15	2.43	1.99	1.77
Percentage explained	51	14	11	10
Cumulative Percentage	51	64	75	85
Eigenvectors associated with the principal components				
pH	0.03	0.53	− 0.61	− 0.16
Conductivity	0.90	0.09	0.05	0.23
Temperature	− 0.33	− 0.20	− 0.01	0.27
Salinity	0.89	0.11	0.04	0.24
Hardness	0.92	0.09	0.00	0.10
Bicarbonates (HCO_3^-)	0.52	0.11	0.64	− 0.25
Chloride (Cl^-)	0.90	0.11	0.06	0.17
Sulphates (SO_4^{2-})	0.91	0.11	0.10	0.17
Nitrates (NO_3^-)	0.53	− 0.15	0.19	− 0.60
Silicon dioxide (SiO_2)	0.58	0.49	− 0.36	− 0.28
Sodium (Na^+)	0.90	0.10	0.09	0.18
Potassium (K^+)	0.59	0.18	− 0.03	− 0.32
Calcium (Ca^{2+})	0.74	0.10	− 0.08	0.53
Manganese (Mg^{2+})	0.63	0.03	0.11	− 0.59
Total carbon organic (TOC)	− 0.47	0.76	0.12	0.12
Gravel	− 0.28	0.09	0.76	0.11
Sand	0.57	− 0.62	− 0.40	− 0.04
Mud	− 0.52	0.69	0.04	− 0.01
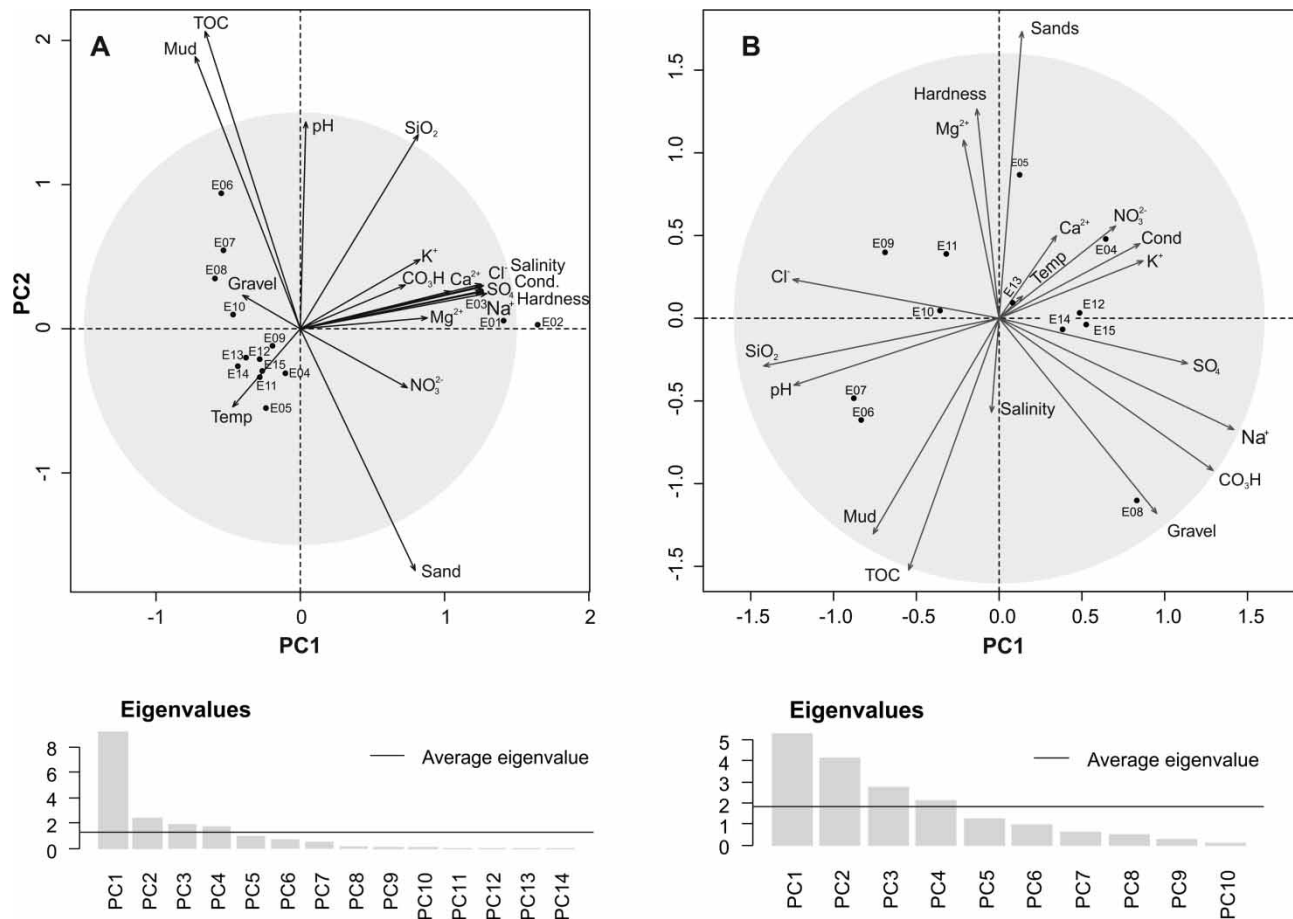
Figure 2. Principal component analysis and Kaiser–Guttman plot of summer environmental data from the Colorado River. (A) Two-dimensional plot including all sampling sites. (B) Two-dimensional plot without sampling sites near the coast.

Pantocsek, as well as the brackish/freshwater tychoplanktonic species, *Pseudostaurosira* sp. 1, *Cocconeis placentula* Ehrenberg, *Cocconeis pediculus* Ehrenberg, *Cocconeis euglypta* Ehrenberg, *Epithemia sorex* Kützing and *Staurosira construens* Ehrenberg, increased in zone III while *S. venter* decreased slightly.

Species richness along the river ranges between 20 and 73, and the Shannon diversity index (H') fluctuates between 1.19 and 2.98. In zone I, species richness and Shannon index are highest (E01:67 species and $H' = 2.45$; E02:68 species and $H' = 2.98$; E03:73 species and $H' = 2.93$). Sampling sites in zone III also have high diversity (E15: $H' = 2.60$, E14: $H' = 2.30$), while sites in zone II show the lowest values (E12: $H' = 1.28$, E10: $H' = 1.19$, E09: $H' = 1.88$, E08: $H' = 1.47$, E07: $H' = 1.58$, E06: $H' = 1.59$) (Fig. 3).

The diatom assemblage changed significantly after the construction of the flood-control structure upstream of E01. At this sampling site marine taxa are replaced by brackish-freshwater taxa (Fig. 22) and the assemblage is dominated by *Nitzschia fontifuga* Cholnoky, *Tryblionella apiculata* Gregory, *Halamphora veneta* (Kützing) Levkov and *Nitzschia fonticola* (Grunow) Grunow. Species

richness and Shannon diversity index (H') are 38 and 2.28, respectively; these values are lower than those recorded when the river course was active.

Diatom assemblages and environmental variables

The first two CCA axes for summer data (considering all sampling sites) explain 89% of the total variation, and identify two diatom assemblages differentiated mainly by salinity gradients, grain size and concentration of bicarbonates (Fig. 23A). The variation explained for the first two CCA axes is 79% and 9.2%, respectively. Species on the right hand side of the diagram are dominant in areas of higher salinity, bicarbonates and sandy substrata, while those species that are on the left hand side are most abundant in sampling sites of fresher water. The ANOVA permutation test is highly significant in all canonical axes ($p = .002$), while the test of the CCA axis 1 ($p = .003$) and 2 ($p = .031$) are also significant. On the other hand, removing sampling sites near the coast the test indicates that environmental variables did not explain significant portions of the assemblage variances in summer (Fig. 23B).

Table 4. Principal components analysis (PCA) results of summer environmental variables without sampling sites E01, E02 and E03.

	PC1	PC2	PC3	PC4
Eigenvalues of the correlation matrix				
Eigenvalue	5.06	4.01	2.61	2.33
Percentage explained	28	22	15	13
Cumulative percentage	28	50	65	78
Eigenvectors associated with the principal components				
pH	−0.66	−0.19	0.31	−0.23
Conductivity	0.45	0.21	0.22	−0.06
Temperature	0.08	0.06	0.27	−0.41
Salinity	−0.02	−0.27	0.78	0.20
Hardness	−0.07	0.60	0.08	0.58
Bicarbonates (HCO_3^-)	0.69	−0.43	0.02	−0.01
Chloride (Cl^-)	−0.66	0.11	0.46	−0.08
Sulphates (SO_4^{2-})	0.60	−0.13	0.39	0.33
Nitrates (NO_3^-)	0.37	0.26	0.36	−0.03
Silicon dioxide (SiO_2)	−0.75	−0.14	0.24	−0.06
Sodium (Na^+)	0.75	−0.32	0.12	−0.02
Potassium (K^+)	0.46	0.16	0.41	0.37
Calcium (Ca^{2+})	0.18	0.24	0.62	−0.45
Manganese (Mg^{2+})	−0.11	0.51	−0.08	0.67
Total carbon organic (TOC)	−0.29	−0.72	0.22	0.31
Gravel	0.50	−0.56	−0.20	−0.14
Sand	0.07	0.82	0.05	−0.23
Mud	−0.40	−0.62	0.06	0.36
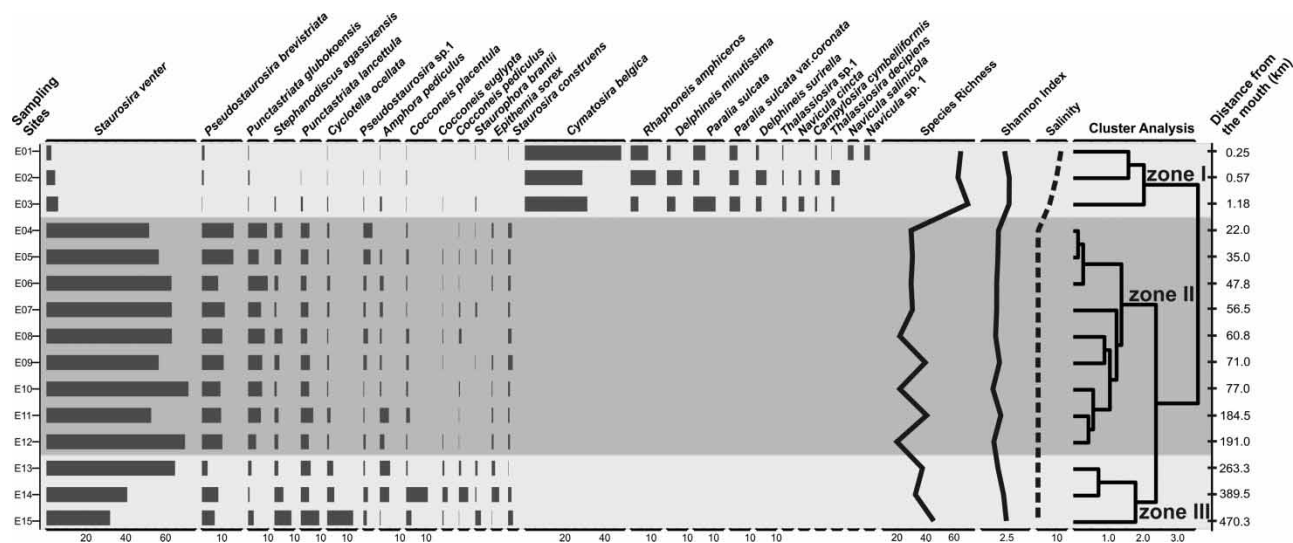
Figure 3. Relative percent of the most common (> 2%) diatom taxa in surface sediment. Species richness, Shannon index, salinity and cluster analysis from the Colorado River are also included.

The taxa associated with the highest salinity and sandy composition are *C. belgica*, *R. amphiceros*, *D. minutissima*, *P. sulcata*, *P. sulcata* var. *coronata*, *D. surirella*, *Campylosira cymbelliformis* (A. Schmidt) Grunow ex Van Heurck, *Thalassiosira decipiens* (Grunow ex Van Heurck) Jørgensen and *Navicula cincta* (Ehrenberg) Ralfs. Freshwater sites are characterized by species such as *S. venter*, *P. brevistriata*, *P. glubokoensis*, *P. lancettula*, *S. agassizensis*, *C. ocellata*, *A. pediculus*, *C. placentula*, *C. pediculus* and *S. construens*.

Diatom taxonomic notes

The araphid species *P. glubokoensis* and *P. lancettula* are abundant in the lower and middle basins and represent new records for Argentina. The morphological features and ecological requirements of these taxa are described below.

Punctastriata glubokoensis Williams, Chudaev & Gololobova (Figs 24–28)

Description: Frustules rectangular in girdle view. Valves elliptical, slightly heteropolar with rounded apices, length:
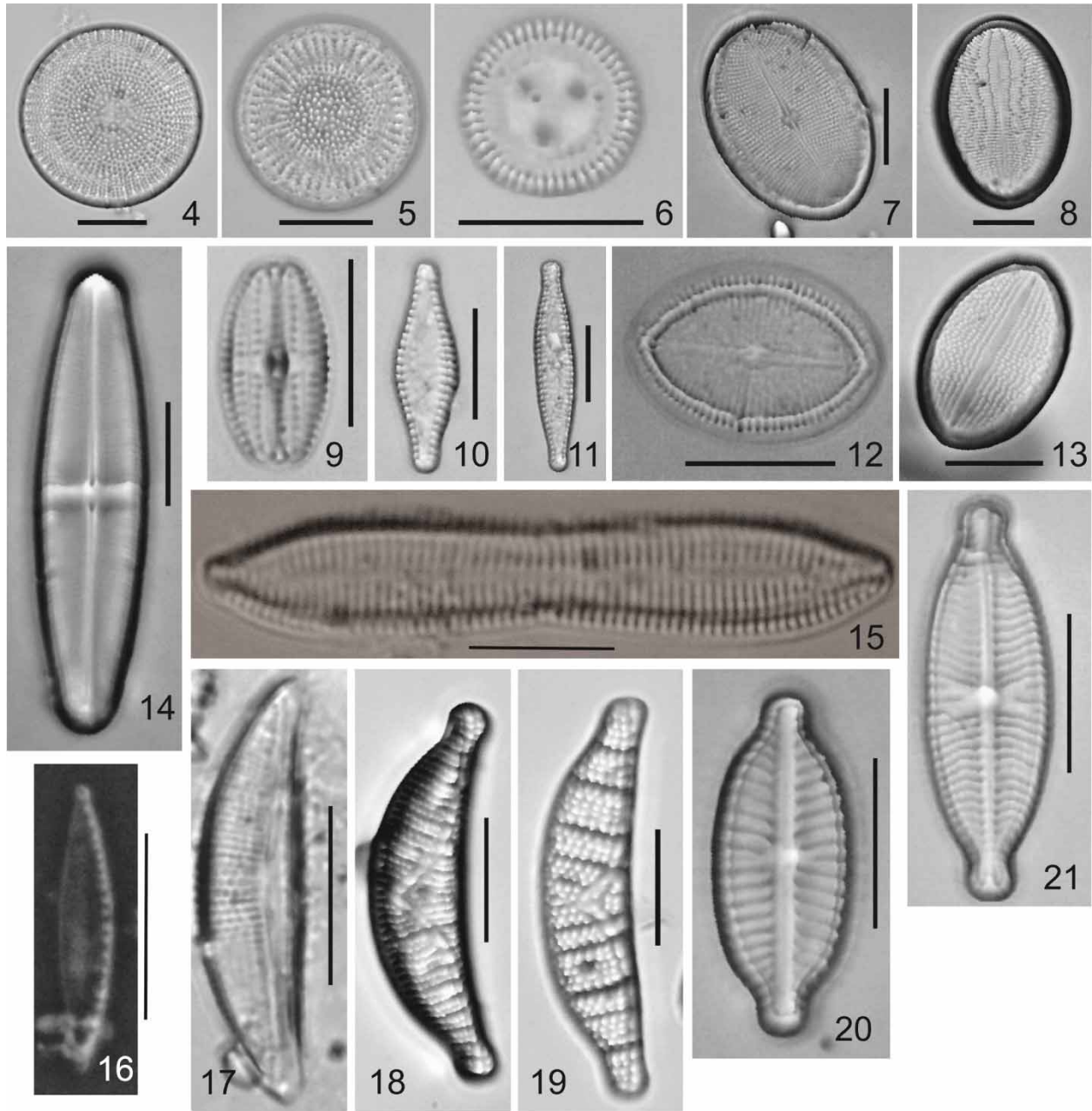
Figures 4–21. Predominant diatoms from sediments in the Colorado River under LM. **Figs 4–5**. *Stephanodiscus agassizensis*. **Fig. 6.** *Cyclotella ocellata*. **Fig. 7.** *Cocconeis pediculus* (rapheless valve). **Fig. 8.** *Cocconeis pediculus* (raphe valve). **Fig. 9.** *Amphora pediculus*. **Fig. 10.** *Pseudostaurosira brevistriata*. **Fig. 11.** *Pseudostaurosira* sp 1. **Fig. 12.** *Cocconeis placentula* (raphe valve). **Fig. 13.** *Cocconeis placentula* (rapheless valve). **Fig. 14.** *Staurophora brantii*. **Fig. 15.** *Tryblionella apiculata*. **Fig. 16.** *Nitzschia fontifuga*. **Fig. 17.** *Halamphora veneta*. **Fig. 18.** *Epithemia sorex*. **Fig. 19.** *Epithemia adnata*. **Fig. 20.** *Placoneis pseudanglica*. **Fig. 21.** *Geissleria decussis.* Scale bar: 10 µm

5.5–7 µm; width: 4–4.5 µm; striae 8–10 (12) per 10 µm. Axial area narrow, linear to lanceolate. Striae extending to mantle, parallel in the centre of the valve to slightly radiate toward the apices, composed of four to five rows of areolae at valve face margin and one to two areolae near the axial area. A single apical pore field composed of a few round poroids is present at the foot pole.

Autoecology: pH: 8.48 ± 0.73 (7.75–9.21). Temp: 22.9 ± 2.2°C (20.7–25.1 °C). Salinity: 0.77 ± 1.33‰ (0.0–2.1‰). : 352.6 ± 198 mg L^{-1} (154.6–550.6 mg L^{-1}). NO$_3^-$: 1.98 ± 1.8 mg L^{-1} (0.18–3.78 mg L^{-1}).

Punctastriata lancettula (Schumann) Hamilton & Siver (Figs 33–38)

Description: Frustules rectangular in girdle view. Valves slightly heteropolar, cruciform to rhomboid with rounded (smaller specimens) to subcapitate ends (large specimens),
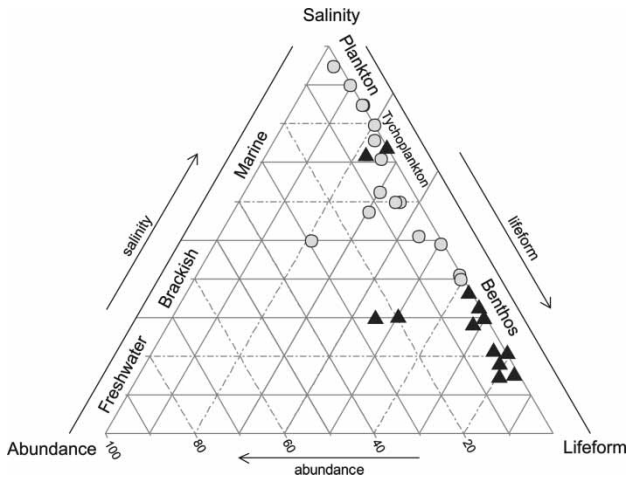
Figure 22. Ternary plot comparing the diatom assemblages between two sediment samples collected from E01, before (circles) and after (triangles) the contruction of flood-control structure. Each symbol represents a diatom species found at > 2% relative abundance. Ecological preferences (salinity and life form) were taken from Denys (1991/1992).

Autoecology: pH: 8.32 ± 0.67 (7.65–9.0). Temp: 22.89 ± 2.2°C (20.67–25.12 °C). Salinity: 0.70 ± 0.98‰ (0.0–1.68‰). SO_4^{2-}: 338.46 ± 165.14 mg L^{-1} (173.32–503.60 mg L^{-1}). NO_3^-: 2.31 ± 1.95 mg L^{-1} (0.36–4.27 mg L^{-1}).

Table 5. List of diatom species and codes with relative abundances higher than 2% of the total sample.

Acronym	Diatom taxa
APED	*Amphora pediculus*
CCYM	*Campylosira cymbelliformis*
CEUG	*Cocconeis euglypta*
CPED	*Cocconeis pediculus*
CPLA	*Cocconeis placentula*
COCE	*Cyclotella ocellata*
CBEL	*Cymatosira belgica*
DMIN	*Delphineis minutissima*
DSUR	*Delphineis surirella*
DTEN	*Diatoma tenuis*
ESOR	*Epithemia sorex*
NCIN	*Navicula cincta*
NSAL	*Navicula salinicola*
NAV1	*Navicula sp 1*
PSUL	*Paralia sulcata*
PSCOR	*Paralia sulcata var coronata*
PBRE	*Pseudostaurosira brevistriata*
PSE1	*Pseudostaurosira sp 1*
PGLU	*Punctastriata glubokoensis*
PLAN	*Punctastriata lancettula*
RAMP	*Rhaphoneis amphiceros*
SBRA	*Staurophora brantii*
SCON	*Staurosira construens*
SVEN	*Staurosira venter*
STEP	*Stephanodisccus agassizensis*
TDEC	*Thalassiosira decipiens*
THAL1	*Thalassiosira sp 1*

length: 13–16 μm; width: 5–6 μm; striae 8–12 per 10 μm. The axial area is narrow, varying from linear to slightly lanceolate. Striae are wide, extend continuously onto the mantle, parallel in the centre of the valve to slightly radiate toward the valve ends. Under SEM the striae are composed of circular to elliptical areolae, with three to four rows of areolae at the junction of the mantle and valve face, decreasing to one to two areolae near the axial area and on the valve mantle. Virgae thickened, bearing spines externally, and internally raised above the areola openings. Apical pore fields present at both valve apices.
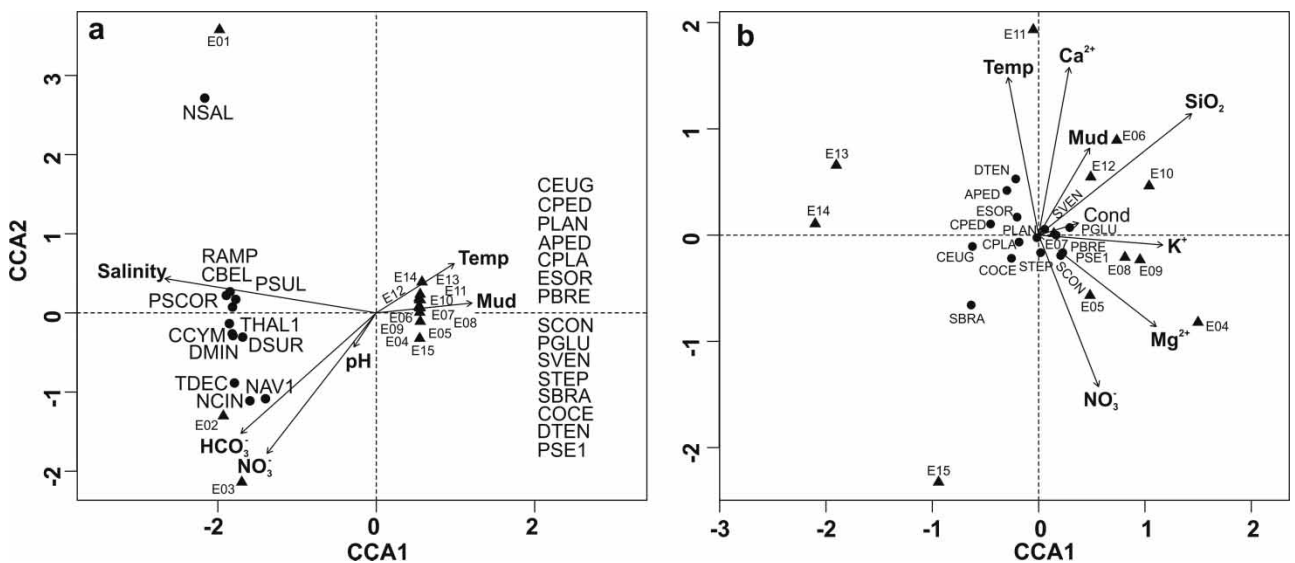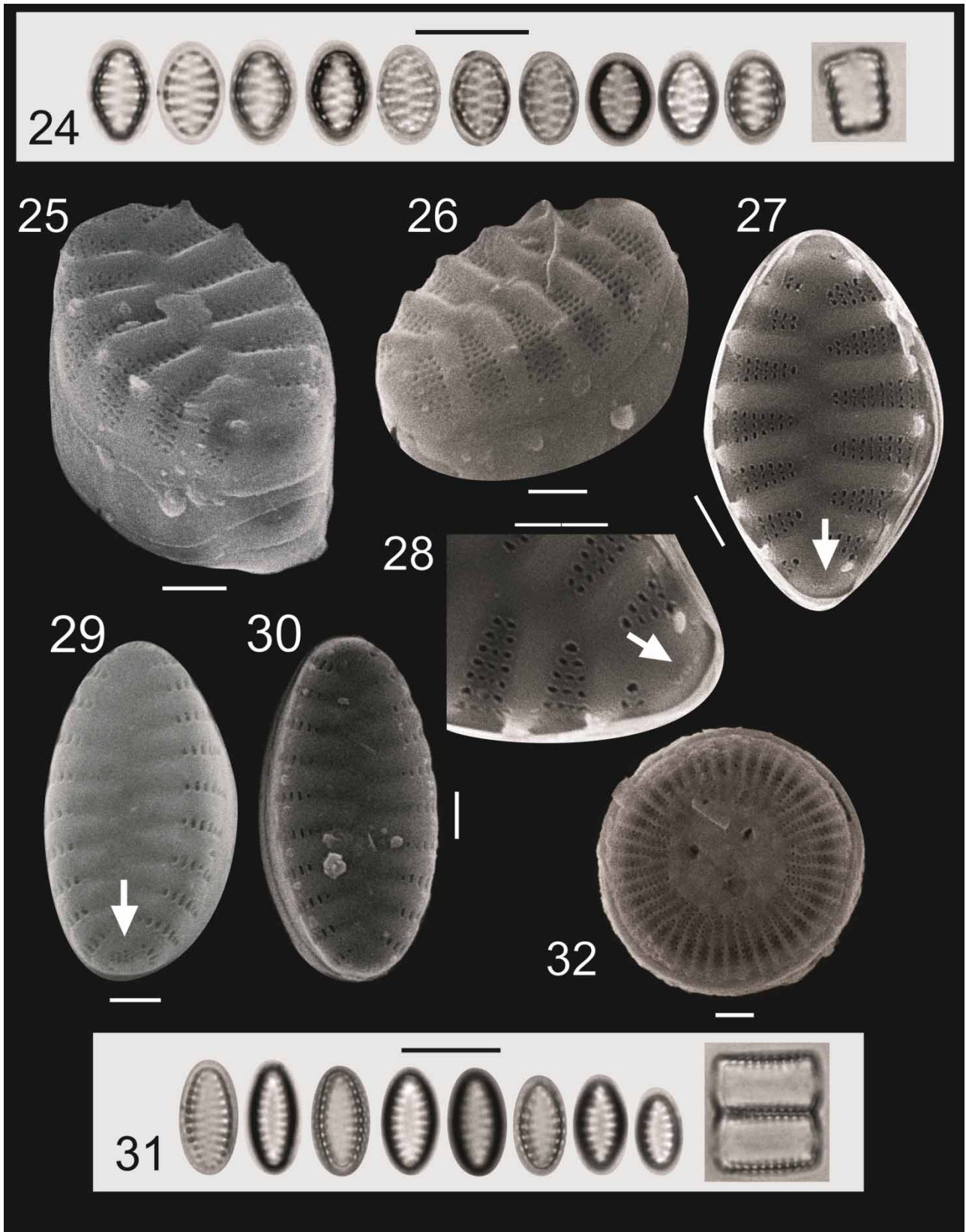

Figure 23. Canonical correspondence analysis plot showing the relationship between summer environmental variables and diatom species. (A) Two-dimensional biplot including all sampling sites. (B) Two-dimensional biplot without sampling sites near the coast. For acronyms of the species names, see Table 5.

Figures 24–32. **Fig. 24.** Morphological variability of *Punctastriata glubokoensis* in LM. **Figs 25–26.** SEM external view of *P. globokoensis*, note the presence of multiseriate striae. **Figs 27–28.** SEM external view of *P. glubokoensis*, note the apical pore field (arrows) and spines located between striae. **Figs 29–30.** SEM external view of *Staurosira venter*, note the apical pore field. **Fig. 31.** Morphological variability of *S. venter* in LM. **Fig. 32.** SEM external view of *Cyclotella ocellata*. Scale bar = 1 μm.

Discussion

Composition and distribution of diatom assemblages

Most of the diatom assemblages identified in the Colorado River are similar to those in rivers, streams and estuaries in other areas of Argentina (Licursi & Gómez 2002, Hassan 2010, Garibotti et al. 2011, Espinosa & Isla 2015).

The analysis of surface sediment samples collected in the middle and lower basins of the Colorado River shows important differences in diatom composition and distribution between estuarine and riverine sites. With decreasing tidal effects, freshwater diatom assemblages become dominant. CCA shows a clear response of these microalgae to local water chemistry: conductivity, salinity, hardness and major ions are the principal environmental predictors. Our results are in agreement with regional and global studies where species turnover is mainly driven by the gradient in major ion concentrations along rivers, streams and estuaries (Villafañe et al. 1991, Pucci et al. 1996, Potapova & Charles 2003, Soininen 2004, Laut et al. 2011, Rovira et al. 2012, Nodine & Gaiser 2014, Espinosa & Isla 2015).

Experimental data offer evidence that diatom assemblage response is associated with conductivity or specific ion concentrations, due not only to osmotic stress on the organisms, but also because osmotic pressure may play a direct role in the availability, cellular requirements and uptake rate of nutrients (Tuchman et al. 1984, Saros & Fritz 2000, 2002).

According to Soininen (2007), ion concentration and trophic status are the major environmental drivers of diatom distribution in streams and rivers. In the Colorado River, nitrates and silicon dioxide concentrations do not show a clear effect on the diatom community, but ion concentration does. Grain size is also important for defining the sedimentological characteristics of the sites, but has less importance on species turnover in our study.

Even though salinity fluctuates in the deltaic plain, the dominance of marine/brackish species remains similar at each site, indicating that most of the species are euryhaline, adapted to environments with fluctuating salinity regimes. Salinity changes are related to tidal effects that extend 1.8 km from the mouth (E03). The presence of tychoplankton, such as *C. belgica*, *R. amphiceros*, *D. minutissima*, *D. surirella* and *P. sulcata*, in the sites near to the coast is distinctive of typical estuarine environments. These taxa have been reported from plankton and surface sediments of estuarine and shallow coastal environments of Buenos Aires province and Patagonia (Sar et al. 2007, Hassan et al. 2009, Garibotti et al. 2011, Espinosa & Isla 2015).

Estuarine and marine tychoplanktonic species are used in paleoenvironmental reconstructions of coastal environments due to their abundance in sediments, wide distribution and resistant frustules (McQuoid & Nordberg 2003, Ryu et al. 2005, Cremer et al. 2007). Since they are exposed to high-energy coastal processes such as tide currents, waves, wind-induced turbulence or sudden freshwater inflow, they can be easily detached from different substrata and may be distributed along a wide salinity gradient, so they have been used to reconstruct both salinity and depth changes in relation to Holocene sea level fluctuation (Escandell et al. 2009, Espinosa & Isla 2011).

Data from our study show that the small tychoplanktonic taxa, *S. venter*, *P. brevistriata*, *P. glubokoensis* and *P. lancettula*, are dominant in riverine sites, together contributing between 50.6% and 92.1% relative abundance (Figs 24–31 and 33–41). These small fragilarioids usually develop very large populations that can mask the distribution patterns of other taxa. Although some attempts have been made to relate the occurrence of these taxa to environmental variables and habitat preferences, clear relationships about their ecological affinities have not been established. Some studies indicate that they prefer shallow habitats with high light levels, in the littoral and sublittoral of lakes, rivers and streams. However, they are poor indicators of water quality due to their wide tolerance of nutrient concentrations (Bennion et al. 2001, Sayer 2001, Schmidt et al. 2004). Although the permutation test is not statistically significant ($p > .05$), the CCA results from summer (without sampling sites near the coast) show a slight response of some fragilarioids to conductivity (Fig. 23B).

Several studies performed in coastal and lacustrine environments from Argentina have shown that the brackish-freshwater tychoplanktonic taxa, *S. venter* and *P. brevistriata*, are very common diatoms, recorded in modern and Holocene sediments from the Buenos Aires province, Patagonia and Tierra del Fuego (Espinosa 2008, Hassan et al. 2009, 2011, Espinosa et al. 2012). These species have also been reported from sediment cores from North American estuaries, such as the Chesapeake Bay, the Pamlico and Neuse estuaries (North Carolina), as well as in the Charlotte Harbor estuary (Florida), where *S. venter* was one of the most abundant species at salinities between 1.2‰ and 1.4‰ (Cooper 1995, 2000, Nodine & Gaiser 2014). In a large-scale investigation of benthic diatoms in the United States, Potapova & Charles (2003) found that *S. venter* had a conductivity optimum of 300 μS/cm (about 0.2‰ of salinity) and tolerances of 109–822 μS/cm (about 0.07‰ and 0.5‰ of salinity), respectively. Unfortunately, as a result of taxonomic uncertainty around *P. glubokoensis* and *P. lancetulla*, comparisons with other areas are limited.

Cocconeis placentula, *C. euglypta* and *C. pediculus* appear in higher proportions in zone III than zones II and I. These are the most common taxa in freshwater bodies and are reported as good indicators of moderately alkaline and slightly to strongly polluted conditions (Sylvestre et al. 2001, Jahn et al. 2009, Thomas & John 2010), as well as high to middle conductivity and ionic concentrations (Bona et al. 2007). *Cocconeis euglypta* is abundant in mesotrophic water and tolerates different pollution levels (Romero & Jahn 2013). Differences in the distribution of
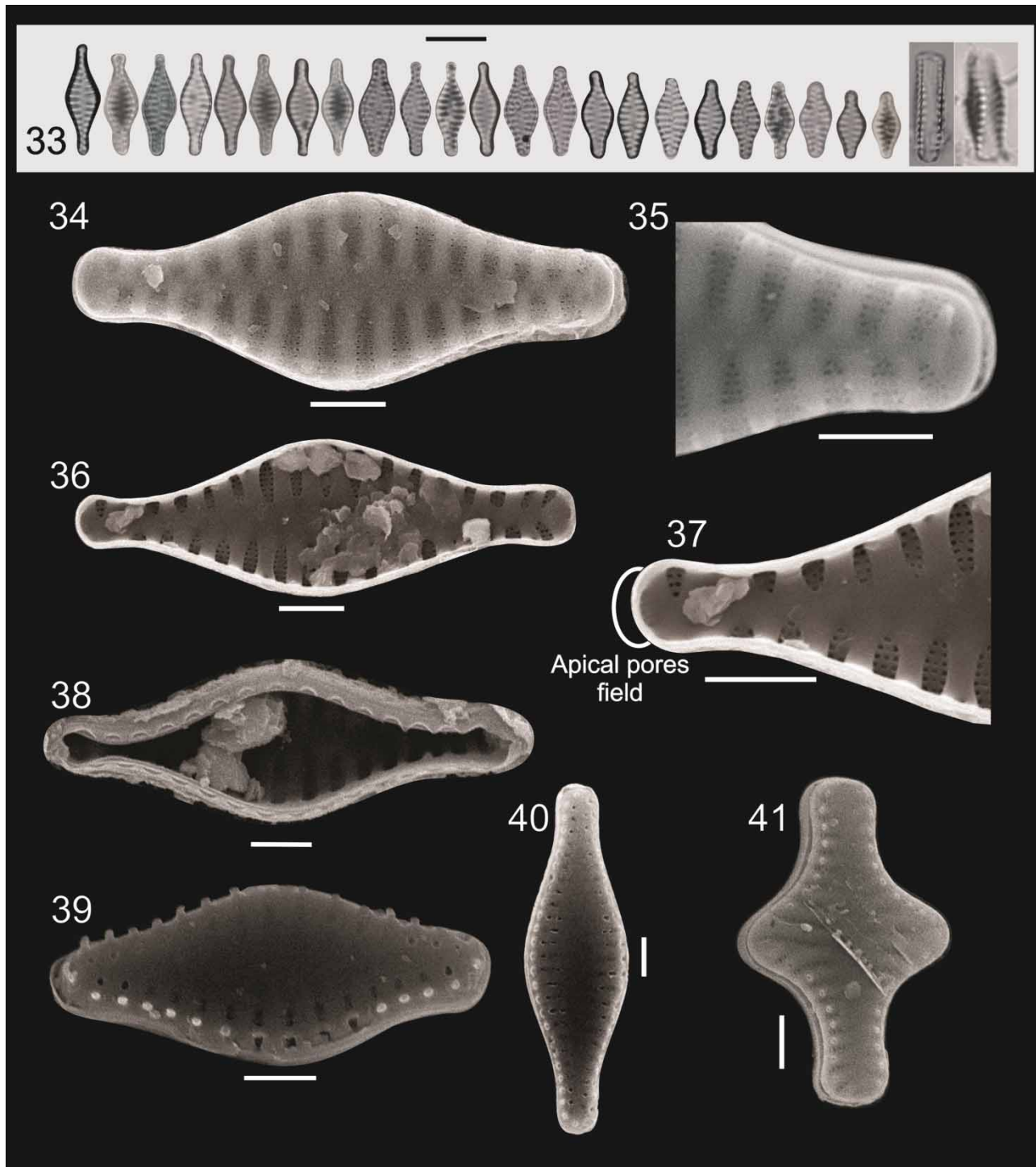
Figures 33–41.   **Fig. 33.** Morphological variability of *Punctastriata lancettula* in LM. **Figs 34–35.** SEM external view of *P. lancettula*, note the presence of multiseriate striae. **Figs 36–38.** SEM internal view of *P. lancettula*, note the apical pore field (**Fig. 37**). Girdle bands seem to be closed and they lack perforations (**Fig. 38**). **Figs 39–40.** SEM external view of *Pseudostaurosira brevistriata*. **Fig. 41.** SEM external view of *Staurosira construens*. Scale bar = 2 μm.

C. placentula and *C. euglypta* in surface sediments from the Negro and Chubut Rivers are also reported (Espinosa & Isla 2015). Overall, the highest abundance of *C. euglypta* is found in the upper valley of the Negro River, while *C. placentula* is dominant in the middle valley.

Cocconeis euglypta is not recorded at the Chubut River. The explanation for this pattern is not clear, but some previous research suggests that *C. euglypta* is more tolerant than *C. placentula* to organic pollution (Kelly et al. 2005).

The contribution of centric taxa, those euplanktonic diatoms associated with lentic systems, is lower in abundance than the tychoplankton, epiphyton and epipelon. The abundance of *S. agassizensis* and *C. ocellata* in freshwater sites is favoured at the Casa Piedra dam where there is less turbulence (Figs 4–6, 32).

Another important species is *Staurophora brantii* Bahls, an epipelic taxon frequently occurring in fresh alkaline waters with slightly higher concentrations of electrolytes, particularly sodium and sulphate, co-existing with others that prefer environments with elevated concentrations of dissolved solids (Bahls 2012). In spite of their low abundance, it is important to point out that 12 species of *Navicula* were identified at riverine sites. Among them, *Navicula antonii* Lange-Bertalot, *N. capitatoradiata* Germain, *N. cryptotenella* Lange-Bertalot and *N. cryptocephala* Kützing show broad ranges of conductivity tolerance and are considered good indicators of alkaline, electrolytic-rich, organic matter and mesotrophic to eutrophic water (Gómez & Licursi 2001, Segura-García et al. 2010). These taxa together with *A. pediculus*, *Achnanthidium minutissimum* (Kützing) Czarnecki and *C. euglypta* are considered as accurate indicator species of riverine conditions in the Ebro estuary (Rovira et al. 2012).

Vouilloud & Leonardi (2001), Biasotti et al. (2014) and Galea et al. (2014) analysed diatom assemblages, obtained using plankton nets, from five, one and two selected sites, respectively, along the middle and lower basins of the Colorado River. Comparison of these studies with the present research is not suitable, because diatoms have different life forms in riverine and estuarine environments, differ in their taxonomic composition and are subject to different taphonomic biases. Fragilarioids are not important in these net samples. It is necessary to take into account that, in the present study, sediment samples include all the taxa accumulated during the year. In addition, it is likely that fragilarioid abundances are probably underestimated in previous studies because of the small size of their frustules and the sampling methods.

In the present study, spatial differences in species richness and diversity index are found between the middle and lower valley. Sampling sites with lower diversity are near urban places (E12, E11, E10 and E07) or agricultural areas (E09, E08, E06, E05 and E04), whereas diversity is higher in less disturbed areas. A similar pattern was observed in three streams systems of São Carlos, Brazil (Bere & Tundisi 2010). Although there are no significant differences among sites, they show a general trend of higher species richness and diversity indices in less-polluted sites compared to polluted sites. Pollution-intolerant species, such as *Aulacoseira granulata* (Ehrenberg) Simonsen, are replaced by pollution-tolerant taxa as *Gomphonema parvulum* (Kützing) Kützing and *Nitzschia palea* (Kützing) W.Smith.

Fayó et al. (2016) analysed a surface-sediment sample obtained near E05 in 2007 in which they observed lower abundance of *S. venter*, *P. brevistriata*, *P. glubokoensis* and *P. lancettula* and high abundance of *A. granulata*. Recent changes in the major ion concentrations in the water, due to natural and anthropogenic processes and potential interspecific competition, could explain these changes.

Like many estuarine and deltaic systems around the world, the Colorado delta is subject to changes in response to natural processes and anthropogenic impacts, which can significantly alter the delta's water quality, habitats and biotic communities. The Colorado River configuration has high sinuosity and a high load of suspended solids in its final stretches. Water inflow has decreased in recent times as a result of climate change, channel infill due to eolian deposition, irrigation projects and construction of flood-control structures (Spalletti & Isla 2003).

The construction of a flood-control structure upstream of E01 modified the salinity, substratum and water depth, and the diatom assemblages responded to these changes (Figs 4–21). The replacement of marine taxa by brackish-freshwater taxa (e.g. *N. fontifuga*, *T. apiculata* and *H. veneta*) and the dominance of brackish epipelon, correspond to a very shallow, brackish environment, with 2.8‰ salinity (Table 2).

As a consequence of their high runoff, Patagonian rivers developed broad valleys during the Holocene. However, decrease in precipitation and dam construction along the tributaries has reduced the river discharge (Piccolo & Perillo 1999). Over the last century, the Colorado River has been significantly affected by El Niño Southern Oscillation-ENSO-triggered floods. The amount of water delivered by the reactivation of the Desaguadero-Curacó system in the 1983 flood may explain the slight increase in salinity in the Colorado River (Isla & Toldo 2013). Further investigations show that, since 2010, the Colorado River basin has a water crisis as a result of decreased precipitation increasing the ion concentration (Alcalde 2014). Particularly in the middle and lower river basins, chemical releases from water treatment processes and sewage discharges from urban, industrial and agricultural activities likely cause increases in the conductivity and the concentration of certain ions, with consequent ecological impact on diatom communities (Carpenter & Waite 2000, Potapova & Charles 2003, Alcalde 2014).

Taxonomic remarks

Better characterization of the diagnostic features of numerous taxa from the use of SEM has led to new identifications and the study of type material on diatoms, particularly fragilarioids (Cejudo-Figueiras et al. 2011). However, these studies have focused on material collected in the northern Hemisphere, while similar taxonomic studies are still developing in South America (Flower et al. 1996, Morales 2001, Morales et al. 2014).

On the basis of their ultrastructure, two taxa in our samples, *P. glubokoensis* and *P. lancettula*, share

morphological features consistent with their placement in *Punctastriata*. Since the description of this genus, six new species have been recognized: *P. linearis* Williams & Round (1987); *P. ovalis* Williams & Round (1987); *P. discoidea* Flower (2005); *P. mimetica* Morales (2005); *P. lancettula* Hamilton & Siver (2008) and *P. glubokoensis* Williams et al. (2009). Some morphological similarities, such as raised and strongly silicified virgae, the absence of rimoportulae, open, not perforated, valvocopulae and under-developed or absent apical pore fields, suggest a closer relationship between *Punctastriata* and *Staurosira* Ehrenberg, *Staurosirella* Williams & Round, *Pseudostaurosiropsis* Morales, *Pseudostaurosira* Williams & Round and *Sarcophagodes* Morales, rather than with *Fragilaria* sensu lato (Williams & Round 1987, Williams et al. 2009).

The presence of multiseriate striae and the unique morphology of their spines are the most distinctive features among this group of araphid diatoms, features that can only be observed with electron microscopy. As a result of this, it is very likely that some species of *Punctastriata* have been incorrectly identified as *Fragilaria pinnata* Ehrenberg, *Fragilaria pinnata* var. *lancettula* (Schumann) Hustedt, *Staurosirella pinnata* (Ehrenberg) Williams & Round or as a species of *Opephora* Petit (Williams et al. 2009).

Variability in valve outline, morphometric parameters, apical pore fields and the position and shape of the spines differentiate these six *Punctastriata* species. Available information indicates that *P. glubokoensis* shares many morphological features with *P. discoidea* and *P. ovalis* (valve outline and shape of the striae). However, the position and some details of the spines differentiate them. In *P. ovalis*, the bifurcate hollow spines are situated along the valve face/mantle junction across the striae, while in *P. glubokoensis* and *P. discoidea*, the spines are located on the virgae. The narrow axial area and the presence of horizontal projections on the spines of *P. discoidea* differentiate this species from *P. globokoensis*, which in turn has a slightly lanceolate axial area and flaps at the base of the spines. In addition, *P. glubokoensis* has an apical depression that is lacking in *P. discoidea* (Williams & Round 1987, Flower 2005, Williams et al. 2009).

Punctastriata lancettula and *P. mimetica* have cruciform to lanceolate valves and can be confused with light microscopy. Three characters could help their differentiation: (1) *P. mimetica* is larger than *P. lancettula*, (2) *P. mimetica* has two apical pore fields (one more developed than the other), whereas *P. lancettula* has only one pore field, and (3) although both have solid spines located on the virgae, in *P. lancettula* the spines are spathulate, but thinner and forked in *P. mimetica* (Morales 2001, Hamilton & Siver 2008).

Some taxonomic, ecological and paleoecological studies in Argentina reported the presence of *Staurosirella* (= *Fragilaria*) *pinnata* and *S. venter* in different environmental samples (sediment surface samples, surface water,

sediments from cores and outcrops) (Vouilloud 2003, Hassan 2010). However, these studies were not supported by descriptions or electron microscopy. Therefore, it is likely that *P. glubokoensis* and *P. lancettula* were incorrectly identified as *S. pinnata* or *S. venter*, or their varieties (Morales 2001). It is worth noting that some LM features, such as elliptical, slightly heteropolar valves with rounded apices, a single apical depression, lanceolate central sternum and narrower virgae than striae, allow specimens of *P. glubokoensis* to be distinguished from other small fragilarioids, particularly *S. venter*. From a practical perspective, especially in future water-quality assessments and paleoecological studies, clear identification of these features will favour rapid comparison between araphid diatoms that share similar autoecological preferences (Figs 24, 31, 33).

Conclusions

Multivariate analysis allowed the assessment of the spatial patterns of environmental variables and the identification of ecological preferences of diatom taxa along the Colorado River. The gradient of major ion concentration (conductivity, salinity, hardness, chloride, sulphates, sodium, calcium, manganese and potassium) was the main factor affecting diatom distribution. The recent increase in salt concentration at non-marine sites has probably altered the diatom composition along the middle and lower basins of the Colorado River. On the basis of their ultrastructure, it was possible to identify *P. glubokoensis* and *P. lancettula*, the first records of these species in the region.

Given the scarcity of local ecological and taxonomic information, these results support additional environmental/ecological/taxonomic assessments of this watershed and provide a basis for future paleoenvironmental studies. The integration of the present data set with data from other estuarine/fluvial systems may lead to the development of diatom-based calibration models, allowing reliable quantitative reconstructions of environmental parameters related to Holocene changes in southern South America.

Disclosure statement

No potential conflict of interest was reported by the authors.

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