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Spring phytoplankton of Río de la Plata: a temperate estuary of South America

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Abstract

Phytoplankton community composition, structure and biomass, spatial distribution patterns in relation to abiotic factors and life-form strategies were assessed in spring 2001 in the Río de la Plata estuary. A total of 224 taxa were identified, with a mean total density of 110 cells ml^{-1}. Although cell numbers were of the same order of magnitude in the upper freshwater tidal zone and in the mouth of the estuary, the maximum carbon contents of phytoplankton were observed in the latter, due to the presence of large dinoflagellate cells. Diversity values ranged between 0.3 and 3.2 bits $ind.^{-1}$. Chlorophytes and cyanophytes were dominant upstream; diatoms were the most important downstream (in the maximum turbidity front). In the outer, mixohaline zone, diatoms and pyrrophytes were dominant. The phytoplankton of 48% of the Río de la Plata estuary is dominated by riverine specimens. The dominant phytoplankton morphologies in the Río de la Plata were filaments (*Planctonema lauterbornii*, *Ulothrix* cf. *subconstricta*) or chains (*Aulacoseira* spp., *Skeletonema costatum*), which provide extensive light absorbing surfaces. Canonical correspondence analysis allowed identification of two species assemblages, one containing freshwater taxa and one with brackish-marine species. In the first group it was recognised that there was a secondary grouping due to the light gradient. Along the fluvial-mixohaline axis it was recognised that the dominant R-strategy species were replaced by S-strategists in the outer sector of the estuary.

Keywords: phytoplankton; species composition; structure; biomass; distribution; morphology; life-strategies; Río de la Plata

1. Introduction

The Río de la Plata is an extensive, shallow, coastal plain estuary on the eastern coast of South America. It receives freshwater from South America's second largest watershed (about 3.2 million km^2). The watershed is impacted by both subsistence and highly productive agriculture and cattle rearing. Industrial and urban areas around the estuary, principally Buenos Aires and Montevideo with about 13 million inhabitants, also affect the aquatic habitats and conflict with management of water quality. In addition, the Río de la Plata provides access to ports upstream along the Paraná, Paraguay, and Uruguay rivers. The regional importance of the estuary has been the subject of many research programs attempting to understand different aspects of its environment and ecosystem (Framiñan et al., 1999; Mianzan et al., 2001).

Despite the socio-economic importance of the freshwater tidal zone of the Río de la Plata, major efforts to understand biological aspects of the estuary have been carried out mainly in the mixohaline zone (Boschi, 1988; CARP-SIHN-SOHMA, 1989; Méndez et al., 1996; EcoPlata Team, 1996; Gómez and Bauer, 2000; Mianzan et al., 2001). The ecology of the phytoplankton, in particular, of the freshwater tidal zone has scarcely been explored, and existing studies refer mainly to coastal areas (Guarrera, 1950; Roggiero, 1988; CARP-SIHN-SOHMA, 1989; Gómez and Bauer, 1998a,b, 2000; Gómez et al., 2002).

According to Schuchardt and Schirmer (1991) the tidal freshwater reaches of estuaries have, in general, received little attention in ecological research, which may be partly due to their intermediate position between limnological and estuarine (marine) research. Nevertheless, for a better understanding of the ecological

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functioning of estuaries it is essential to include studies of these reaches. The objectives of our investigation were to investigate: (1) the composition and biomass of the phytoplankton; (2) its spatial distribution patterns; (3) the principal abiotic factors which influence the phytoplankton composition and distribution; and (4) the life-form strategies of the algae in the Río de la Plata. This study of the phytoplankton is the first to analyse both the freshwater tidal and mixohaline zones of this extensive estuary in southern South America.

2. Study area

The Río de la Plata is located between 34° 00′ and 36° 20′S and 55° 00′ and 58° 30′W. It is 320 km long and its width varies from 38 km in the upper region to 230 km at the mouth. The estuary can be separated into the upper and lower based on its morphology and dynamics (CARP-SIHN-SOHMA, 1989) by a submerged shoal, the Barra del Indio (Fig. 1). The inner, fluvial system is under strong tidal influence, with depths between 1 and 5 m, and is about 180 km long and up to 80 km wide, extending over 13,000 km^2. The outer, mixohaline system has an area of about 22,000 km^2, depths between 5 and 25 m and vertical stratification (Framiñan et al., 1999; Mianzan et al., 2001).

The freshwater discharge (annual mean 22,000 $m^3 s^{-1}$) from the Paraná and Uruguay rivers into the estuary exhibits minimal seasonality, with a mean maximum of 26,000 $m^3 s^{-1}$ in winter and a mean minimum of 19,000 $m^3 s^{-1}$ in summer. The tidal wave originates on the outer shelf and enters the estuary from the southeast, with amplitudes ranging from 30 to 100 cm. Tidal currents are typically below 45 cm s^{-1} and residence time is 46.6 days in the fluvial-mixohaline zone. The dynamics of the Río de la Plata estuary is controlled by tides and wind-driven waves and the continental runoff but are modified by topography and Coriolis force. The equilibrium between these forces is highly variable, depending largely on the intensity of wind stress and the freshwater discharge (Guerrero et al., 1997).

3. Material and methods

3.1. Sampling and laboratory analysis

Two replicate subsurface water samples were collected for quantitative analysis of phytoplankton at 29 sampling sites during spring 2001 (November 5th to December 1st) in the Río de la Plata (Fig. 1). The samples were fixed with formalin (2%). Qualitative samples were also taken with a 32 μm plankton net and fixed with Lugol's iodine and formalin. Temperature and salinity (Horiba multiparameter), dissolved oxygen (YSI sensor), and pH (Barnat Model 30 sensor) were measured at each site. Salinity was measured using the Practical Salinity Scale and Turbidity was expressed as

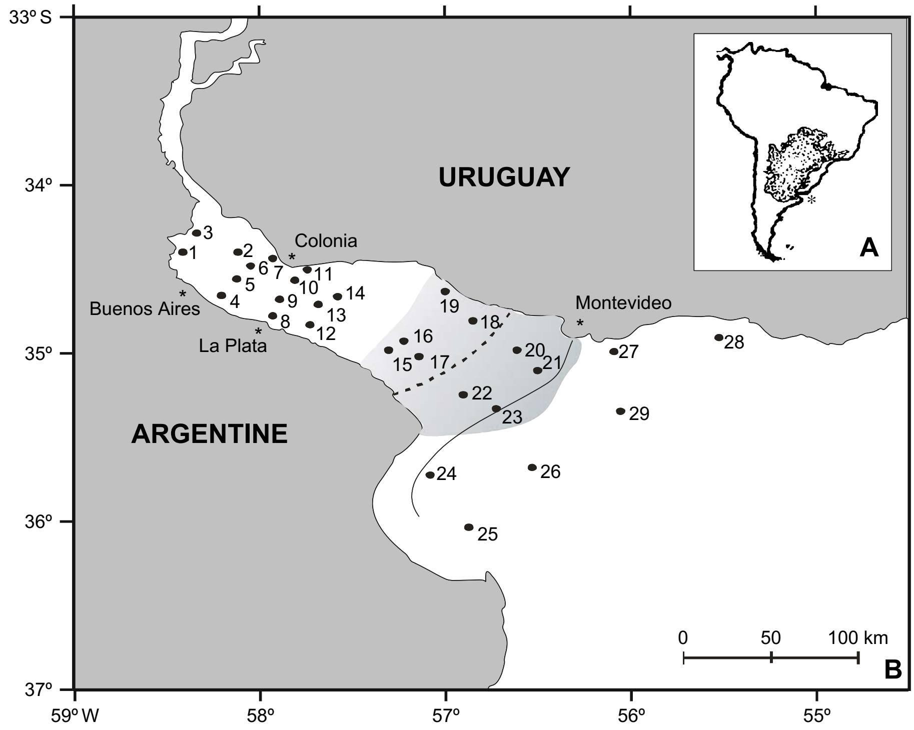

Fig. 1. Map showing (A) the Plata drainage basin and (B) Río de la Plata and sampling sites. The shaded area shows the turbidity front and the solid line indicates Barra del Indio, a submerged shoal. The dashed line shows the isohaline of 0.5 psu.

% of reflectance. Water samples were analysed for dissolved inorganic nutrients (Si, NH_4^+-N, NO_3^--N, PO_4^{3-}-P) and suspended solids (PNUD/GEF RLA/99/631 database, 2002) (Table 1).

Phytoplankton species from the qualitative samples were identified using an optical microscope, an Olympus BX 50 with magnification of ×1000, phase and interferential contrast. Diatoms were cleaned with H_2O_2, washed thoroughly using distilled water and mounted on microscope slides with Naphrax®. The following keys were used for species identification: Balech (1987), Bourrely (1966, 1968, 1970), Desikachary (1950), Ferrario (1984a,b), Frenguelli (1941), Guarrera et al. (1968, 1972), Harris and Fryxell (1974), Hustedt (1930), Jensen and Moestrup (1998), Kiselev (1969), Komarek and Anagnostidis (1999), Komarek and Fott (1983), Krammer and Lange-Bertalot (1986, 1988, 1991a,b), Patrick and Reimer (1966, 1975), Ramanathan (1964), Roggiero (1988), Tell and Conforti (1986), West and West (1904–1912), and Yacubson (1960, 1965).

Phytoplankton counts were done according to Lund et al. (1958), with an inverted microscope, an Olympus CK2 at 400×, using 5 ml sedimentation chambers which were a suitable size according to the amount of suspended solids. The entire chamber was examined, and each algal cell was counted as a unit. The two replicates were averaged. The identified taxa were measured at 600× to calculate cell volumes (Hillebrand et al., 1999), which were converted to carbon content (Menden-Deuer and Lessard, 2000; Gosselain et al., 2000). The algae were classified according to their morphology as: motile unicellular, non-motile unicellular, coenobial or colonial, filamentous and chains (Reynolds, 1984; Stevenson et al., 1996). Species diversity was calculated using the Shannon and Winer index (H') according to Ludwig and Reynolds (1988).

3.2. Statistical analysis

The degree of relationship between major taxonomic groups of phytoplankton was assessed using a cluster analysis, employing Euclidean distance and complete linkage procedure (Crisci and López Armengol, 1983). Canonical Correspondence Analysis (CCA) was employed to explore the relationship between species composition and the environmental variables measured. According to Muylaert et al. (2000), when the gradient length in standard deviation units, in a preliminary detrended correspondence analysis, exceeds 2 units, unimodal species response curves could be expected and, subsequently, ordination techniques based on weighted averaging are recommended. In this analysis those species that contributed more than 1% of total density in the quantitative samples and had a frequency above 15% were included, as well as species that accounted for more than 50% of the abundance in a single sample (Table 2).

Species abundance data were $\log(x+1)$ transformed. Environmental data which were not normally distributed were normalised; temperature, pH and DO were ln transformed; NO_3^--N was square root transformed and NH_4^+-N and PO_4^{3-}-P were $\ln(x+1)$ transformed. Only the environmental variables with a variance inflation factor <10 were retained in the analysis, because a greater value would indicate multicolinearity among variables (ter Braak and Verdonschot, 1995). The overall significance of the ordination and the significance of the first axis were tested with a Monte Carlo permutation test ($P < 0.01$) using restricted permutations.

Table 1
Values of physico-chemical variables, mean values (SD) for the freshwater and mixohaline zones of the Río de la Plata estuary

	Freshwater zone	Mixohaline zone
Depth (m)	4.9 (2.3)	9.9 (3.5)
Temperature (°C)	21.0 (1.4)	19.3 (0.5)
Turbidity (reflectance %)	8.1 (1.8)	6.1 (3.8)
Suspended solids (mg l^{-1})	57.5 (20.9)	47.0 (60.2)
Salinity (psu)	0.10 (0.05)	10.67 (6.08)
pH	7.5 (0.2)	8.1 (0.2)
Dissolved oxygen (mg l^{-1})	6.5 (1.1)	7.9 (0.5)
Si (μmol l^{-1})	208.4 (9.5)	163.4 (28.9)
NO_3^--N (μmol l^{-1})	8.1 (8.4)	4.8 (5.8)
NH_4^+-N (μmol l^{-1})	3.9 (3.4)	3.1 (2.0)
PO_4^{3-}P (μmol l^{-1})	2.5 (1.3)	1.5 (0.7)

4. Results

4.1. Physico-chemical characteristics

A freshwater tidal area with salinity lower than 0.5 psu (sites 1–19) was distinguished from the mixohaline area with values between >0.5 and 18.3 psu (sites 20–29) (Table 1). The sites located in the freshwater area had higher temperatures and nutrient concentrations. Salinity, pH and dissolved oxygen increased downstream. The maximum turbidity front (9–11% reflectance) was located among sites 15–23.

4.2. Distribution patterns of major taxonomic groups

A total of 224 taxa were identified, distributed among the following taxonomic groups: chlorophytes (105), diatoms (99), cyanophytes (10), pyrrophytes (5), euglenophytes (2), silicoflagellates (2) and cryptophytes (1). Despite the great number of taxa identified, only 38 were abundant (Table 2).

Six groups of samples were defined in the cluster analysis (Fig. 2). Chlorophytes and cyanophytes were dominant upstream (groups 2, 5 and 1) in the shallower waters (depths less than 5 m); downstream (in the maximum turbidity front) diatoms were the dominant

Table 2
List of the species that contributed with more than 1% of total density and had a frequency above 15%, as well as species that accounted for more than 50% of the abundance in a single sample

Acronym	Species	Carbon content (pg cell^{-1})
ANMN	*Actinocyclus normanii* (Ehr.) Simon.	1540
AUAM	*Aulacoseira ambigua* (Grun.) Simon.	66
AUDI	*A. distans* (Ehren.) Simon.	19
AUGR	*A. granulata* (Her.) Simon.	123
AUGA	*A. granulata* var. *angustissima* (O. Müller) Simon.	28
AUGC	*A. granulata* var. *curvata* Grun.	67
AUGS	*A. granulata* var. *angustissima* f. *spiralis* (Hust.) Czarneki & Reinke	66
CHSP	*Chaetoceros* spp. Ehr.	212
CMEN	*Cyclotella meneghiniana* Kütz.	212
CSTR	*C. striata* Kütz.	138
SKCO	*Skeletonema costatum* (Grev.) Clev.	24
EMON	*Eunotia monodon* Ehr.	230
FHEI	*Fragilaria heideni* Öest.	24
GSPE	*Gyrosigma spencerii* (W. Smith) Clev.	245
NHUN	*Nitzschia hungarica* Grunow	123
AHAN	*Actinastrum hantzschii* Lagerh.	13
CLAV	*Closterium acutum* var. *variabile* Lemm.	48
CLCY	*C. cynthia* De Not.	1000
CLJE	*C. jenneri* Ralfs.	199
CLLO	*Closteriopsis longissima* (Lemm.) Lemm.	144
EUFO	*Eutetramorus fottii* (Hind.) Kom.	4
MOAR	*Monoraphidium arcuatum* (Kors.) Hind.	27
MOMI	*M. mirabile* (W. & G.S. West.) Pankow	56
MOTO	*M. tortile* (W. & G.S. West.) Kom.-Legn.	19
PLAU	*Planctonema lauterbornii* Schmidle	12
SCAC	*Scenedesmus acuminatus* (Lagerh.) Chod.	12
SCEC	*S. ecornis* (Ehr.) Chod.	10
SCIN	*S. intermedius* var. *acaudatus* Hortob.	6
SCQU	*S. quadricauda* (Turp.) Bréb.	15
SCAN	*Schroederia antillanum* Kom.	35
SCSE	*S. setigera* (Schröd.) Lemm.	17
ULSU	*Ulothrix* cf. *subconstricta* G.S. West	29
MIAE	*Microcystis aeruginosa* Kütz.	14
PSCO	*Pseudoanabaena constricta* (Szafer) Lauterb.	6
CETR	*Ceratium tripos* (Müller) Nitzsch	48013
PRSC	*Prorocentrum scutellum* Schröder	341
PTOB	*Protoperidinium obtusum* (Karsten) nov. comb.	500
PTSP	*P.* spp.	703

Acronyms are shown next to the species names. The cell carbon content (pg cell^{-1}) is given for each species.

algae (group 3). In the outer, mixohaline zone, diatoms and pyrrophytes were predominant (groups 4 and 6) (Fig. 3A).

4.3. Phytoplankton morphology, density, biomass and diversity

The predominant morphology of the phytoplankton was cells arranged in filaments or chains forming elongated cylinders in shape. Upstream of the tidal freshwater zone the filaments of *Planctonema lauterbornii* and *Ulothrix* cf. *subconstricta* were as much as 59% of the total abundance; downstream, in the maximum turbidity zone, these species were replaced by chains of centric diatoms such as *Aulacoseira* spp. (49%) and, in the mixohaline zone, by *Skeletonema costatum* (78%) and flagellated forms of pyrrophytes forming a subdominant group in the mouth of the estuary (Fig. 3B).

More than 87% of the phytoplankton was dominated by nanoplankton (5–50 μm, according to Margalef, 1955), up to a mean total density of 110 cells ml^{-1}. Densities below 50 cells ml^{-1} were found toward the Uruguayan side of the estuary and in the maximum turbidity zone. Phytoplankton values above 100 cells ml^{-1} were located upstream toward the Argentinian side and in the lower part of the estuary (Fig. 4A).

The carbon content of the phytoplankton was as much as 56 ng C ml^{-1} in the freshwater tidal zone, consisting principally of *Aulacoseira* spp. (50%). In the mixohaline zone, the carbon content was 231 ng C ml^{-1} being predominantly *Protoperidinium* spp., which made up 73% of the total (Fig. 4B).

Diversity values ranged between 0.3 and 3.2 bits ind.$^{-1}$, decreasing in the mixohaline zone (Fig. 4C). The most frequent values were between 1 and 3 bits ind.$^{-1}$.

4.4. Phytoplankton and environmental variables

According to the canonical correspondence analysis, the first axis explained 65% and the second 14% of the sum of all canonical eigenvalues. These axes were selected for the graphical representation (Fig. 5). Considering the variance in the species data, the first axis explained 39% and the second 9%.

The direct ordination allowed us to distinguish two species assemblages in the Río de la Plata, differentiated mainly by salinity and pH gradients ($P < 0.001$ with the first axis, in both cases). One of these assemblages was associated with the sampling sites located in the mixohaline zone of the estuary, with salinity >0.5 psu and pH >8. This assemblage was mainly made up of *Skeletonema costatum*, with other centric diatoms such as *Chaetoceros* spp. The pyrrophytes *Ceratium tripos*, *Prorocentrum scutellum*, *Protoperidinium obtusum*, *Protoperidinium* spp., and the chlorophytes *Schroederia*

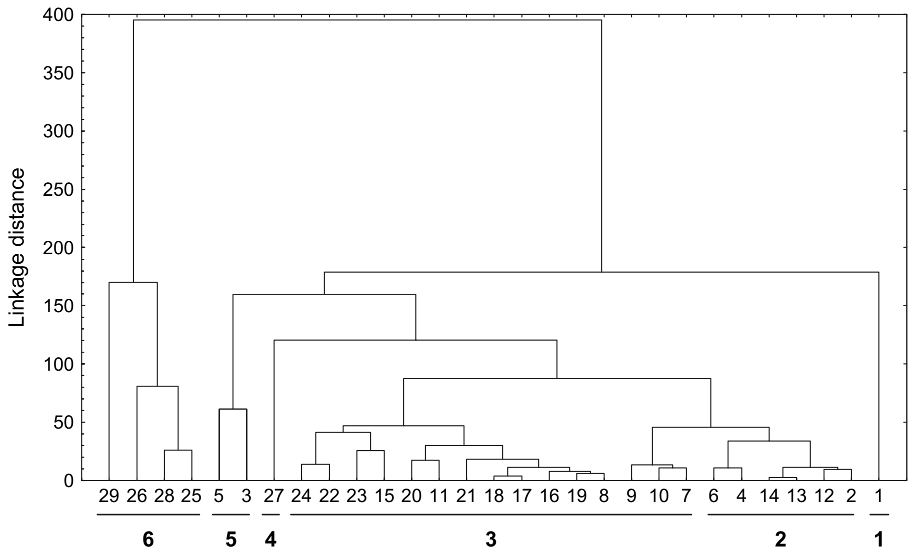

Fig. 2. Dendrogram from a cluster analysis of samples based on the abundance of the major taxonomic groups found in the Río de la Plata.

setigera and *Schroederia antillanum* were also present in this assemblage. The second assemblage was related to the sampling sites with salinity <0.5 psu and pH <8. Two groups of taxa could be distinguished within this assemblage, according to the second axis where the turbidity was the main gradient in the ordination ($P < 0.01$). One group of species was associated with sampling sites where turbidity ranged between a reflectance of 5 and 7% (average suspended solids: 58 mg l^{-1}) including *Pseudoanabaena constricta*, *Planctonema lauterbornii*, *Ulothrix* cf. *subconstricta*, *Eutetramorus fotti*, *Eunotia monodon*, *Nitzschia hungarica*, *Scenedesmus acuminatus* and *Scenedesmus quadricauda*. The other group was associated with a poorer light regime where turbidity ranged between a reflectance of 9 and 11% (average suspended solids: 75 mg l^{-1}). This group was dominated by centric diatoms such as *Aulacoseira granulata*, *Aulacoseira granulata* var. *angustissima*, *Aulacoseira granulata* var. *angustissima* f. *spiralis*, *Aulacoseira distans* and *Aulacoseira ambigua*. The pointed form of clorococcalean species such as *Monoraphidium arcuatum*, *Monoraphidium mirabile*, *Monoraphidium tortile* and *Actinastrum hantzschi* was also represented.

5. Discussion

The species composition found in the freshwater tidal zone, in the Río de la Plata, was similar to the assemblages observed in the lower basin of the Uruguay and Paraná rivers (O'Farrell, 1994; O'Farrell et al., 1998; Izaguirre et al., 2001; Unrein, 2002).

Planctonema lauterbornii and *Ulothrix* cf. *subconstricta* were not abundant in the main tributaries of the estuary (O'Farrell, 1992) and in general in the phytoplankton typical of large rivers (Rojo et al., 1994; Reynolds and Descy, 1996). Because of their abundance and frequency in the upper freshwater tidal zone of the Río de la Plata, these species could be considered autochthonous. According to Schuchardt and Schirmer (1991) and De Sève (1993), some freshwater reaches of estuaries are mainly influenced by riverine phytoplankton whereas others are dominated by autochthonous species. The ability of an autochthonous planktonic population to maintain itself within an estuarine segment is determined mainly by its rate of growth relative to the proportion of population biomass lost through flushing from the segment during each tidal cycle (Schuchardt and Schirmer, 1991). Reynolds and Descy (1996) explained that with a mean velocity of 0.5 m sec^{-1} an algae dividing once every day would be expected to double its mass over 43 km. In the Río de la Plata velocity is low and the residence time is more than 40 days, conditions under which an autochthonous phytoplankton might be expected.

Chlorophytes and cyanophytes were dominant in the upper freshwater tidal zone; downstream, in the maximum turbidity zone, the abundance of these groups decreased and diatoms dominated the phytoplankton (several species and varieties of the genus *Aulacoseira*). In the mixohaline zone diatoms such as *Skeletonema costatum*, which are frequent in spring phytoplankton assemblages of several estuaries (Rijstenbil et al., 1993; Mallin, 1994; Muylaert and Sabbe, 1999), predominated. Dinoflagellates were more abundant near the mouth of the estuary. These results differ from those reported by various authors (Schuchardt and Schirmer, 1991; Mallin, 1994; Muylaert and Sabbe, 1999) in studies of the spring phytoplankton assemblages in temperate estuaries of the Northern Hemisphere where

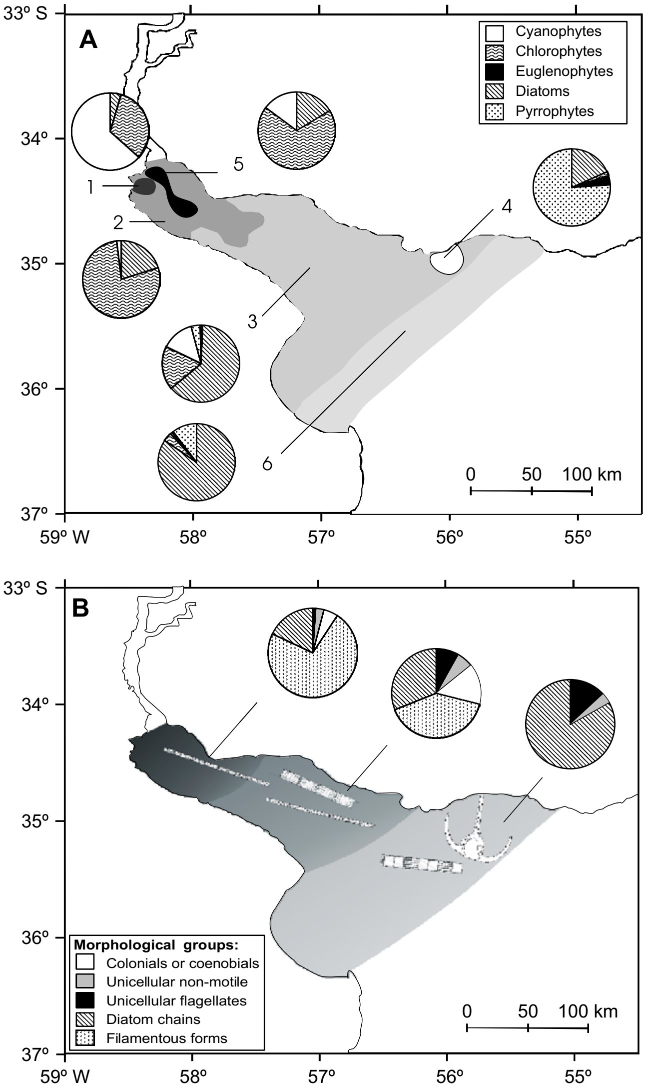

Fig. 3. Distribution of (A) major taxonomic groups of the phytoplankton according to the grouping of the cluster analysis and (B) relative abundance of morphological groups observed along the fluvial-mixohaline axis in the Río de la Plata.

the phytoplankton community was mainly dominated by diatoms.

The phytoplankton of 48% of the Río de la Plata surface is dominated by riverine specimens whose distribution is influenced by the discharges of the main tributaries and by reduced salinity tolerance from the input of brackish water from the sea.

In terms of size, nanoplankton were the dominant fraction of the phytoplankton analysed. The minimum density was located in the maximum turbidity zone while the maximum was observed in the upper freshwater tidal zone, and in the lower part of the mixohaline zone. Thirty-four percent of the samples showed density values above 100 cells ml^{-1}, which according to Margalef (1974, 1983) are common in eutrophic environments. Despite the fact that the highest quantities of nutrients were located in the upper zone of the Río de la Plata, the phytoplankton density reached such values only in four sampling sites of the freshwater zone. The input of suspended solids from the Paraná river reduces the light

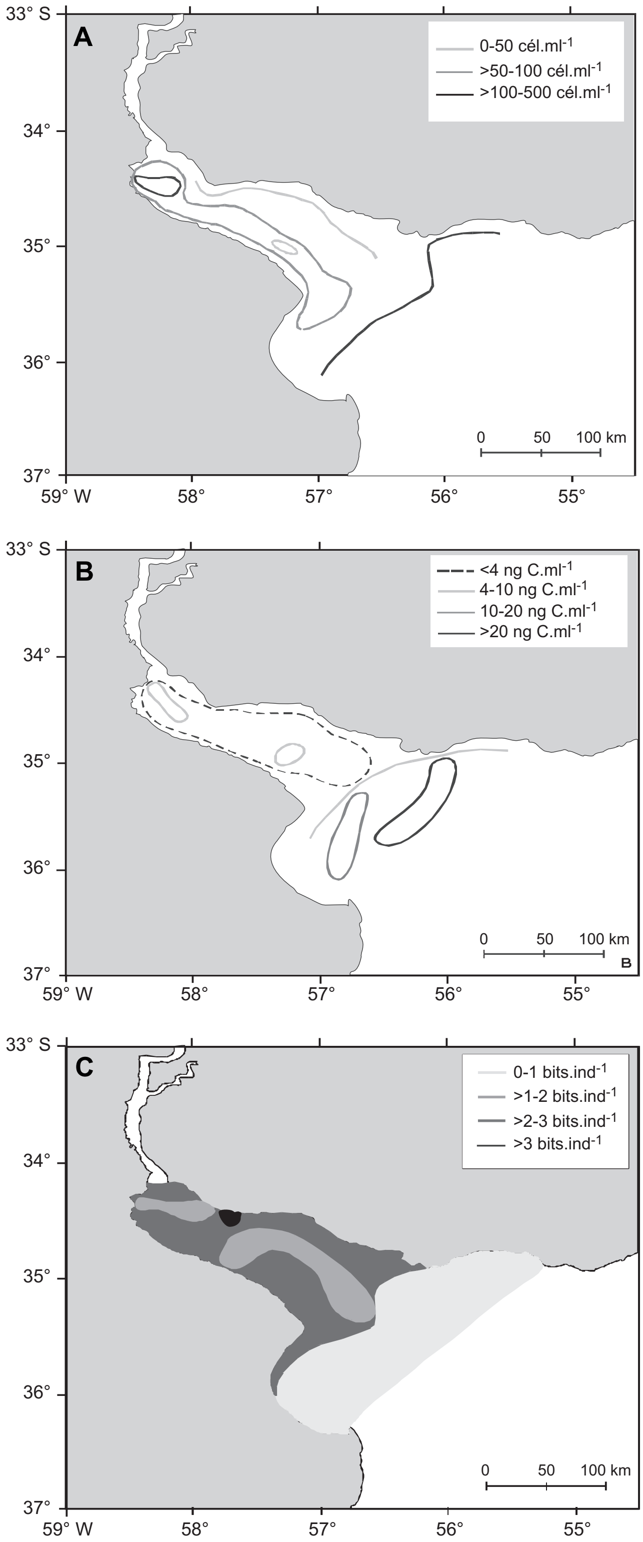

Fig. 4. Distribution of (A) phytoplankton abundance, (B) total carbon content, and (C) phytoplankton diversity (H') in the Río de la Plata.

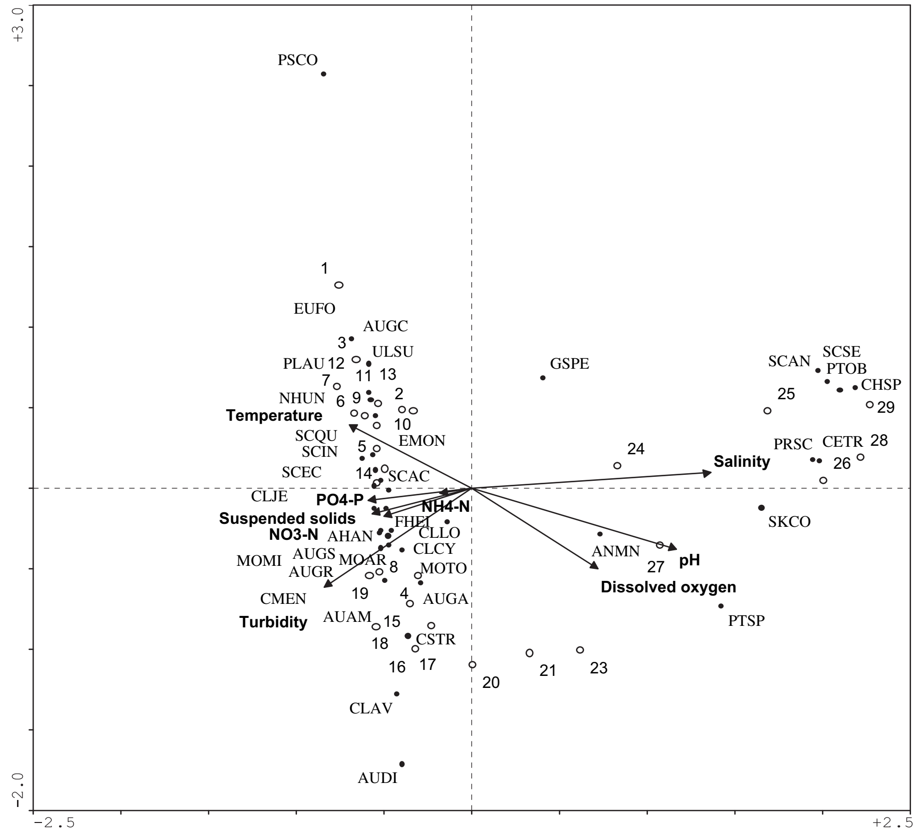

Fig. 5. Ordination diagram displaying the first two axes of the CCA constrained with environmental variables. For abbreviations of the species names, see Table 2. Numbers represents samples sites.

penetration (average Kd (light extinction coefficient) 6.47 m^{-1}) in the freshwater zone of the Río de la Plata, and this is the factor mainly responsible for the restricted development of the phytoplankton. Mallin et al. (1991) and Mallin and Paerl (1992, 1994) in studies of North Carolina estuaries reported higher density values.

Despite the fact that cell numbers were of the same order of magnitude in the upper freshwater tidal zone and in the mouth of the estuary, the maximum carbon contents of the phytoplankton were observed in the latter, due to the presence of large dinoflagellate cells. The values of carbon measured in the Río de la Plata were similar to those reported in other estuaries with high turbidity (e.g. Westerchelde in Belgium and Gironde in France) by Rijstenbil et al. (1993) and Muylaert and Sabbe (1999).

The dominant phytoplankton morphology in the Río de la Plata was filaments or chains, which provide extensive light absorbing surfaces (Reynolds, 1992) and are an advantage in environments with a high concentration of suspended solids as in the Río de la Plata.

Along the fluvial-mixohaline axis it was recognised that the dominant R-strategy species were replaced by S-strategists in the outer sector of this estuary. According to Reynolds (1987) R-strategists are of intermediate to large size but with morphologies that preserve a high surface/volume ratio, high metabolic activity, and potential rapid growth rates. They therefore generally depend on high coefficients of turbulent mixing to offset losses due to passive sinking. S-Strategists are able to regulate their vertical position in the stratified water column. These species are large, with low surface/volume ratios. Their low rates of growth in situ are compensated for by enhanced resistance to sinking and grazing losses, high nutrient-storage capacity, and the potential ability to augment growing populations with recruitment from stocks of resting propagules.

Despite the fact that the relationship between phytoplankton and zooplankton was not analysed in this investigation, we recognise that grazing pressure could be important in the phytoplankton dynamics of the Río de la Plata. A number of researchers have concluded that centric diatoms provide a preferred food source for zooplankton in estuaries (Ryther and Sanders, 1980; Willen, 1991; Mallin and Paerl, 1994).

The diversity index values obtained for the freshwater tidal zone of the Río de la Plata were similar to those observed in the Paraná River in spring (O'Farrell et al., 1996). De Sève (1993) also reported similar diversity values in Rupert Bay (Canada). In our case the greater diversity values of the freshwater zone would be influenced by (1) the shallow depth of this area of the

Río de la Plata that favours the incorporation of ticoplanktonic species in the water column and (2) the contribution of species proceeding from the main tributaries and other small rivers. The low values observed in the mixohaline zone due to the instability of this part of the ecosystem are in agreement with those reported by Margalef (1974) for estuaries.

Finally, the spring phytoplankton analysed was arranged in two assemblages along a progressive change in the salinity gradient. The light regime was a further factor (acting at a different scale) that influenced the species distribution along the principal gradient. The distribution analysed in our study would fit the two ecocline model proposed by Attrill and Rundle (2002), one in the direction of the freshwater-mixohaline zone and the other in the direction of the marine-mixohaline zone. However, more spatial and temporal studies over the whole salinity gradient are needed for a better understanding of the ecological functioning of the Río de la Plata.

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