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# Dissolved Nutrient Availability during Winter Diatom Bloom in a Turbid and Shallow Estuary (Bahía Blanca, Argentina)

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## ABSTRACT

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The inner zone of Bahía Blanca Estuary is a shallow, well-mixed, highly turbid, and nutrient-rich temperate ecosystem. The phytoplankton annual cycle is characterized by a recurrent winter/early-spring diatom bloom. From May to August 2002 a research program aimed to describe the potential relations between the dynamics of phytoplankton and nutrients was carried out. Phytoplankton composition, abundance, chlorophyll *a* (Chl *a*), and dissolved inorganic nutrients (nitrate, nitrite, ammonium, phosphate, and silicate) were measured. The species involved were classified in blooming (including *Thalassiosira* spp. and *Chaetoceros* spp.) and nonblooming species (including other diatoms and dinoflagellates).

The results show: (1) a prebloom period, which includes low biomass values and a strong decrease of NO<sub>3</sub><sup>-</sup>; (2) an initial bloom period characterized by high diatom abundance and Chl *a*, a marked dominance of *Thalassiosira curviseriata*, and a strong decrease of NH<sub>4</sub><sup>+</sup>; (3) an intermediate bloom period of high abundance, codominance of blooming species, and a strong decrease of PO<sub>4</sub><sup>3-</sup>; and (4) a final bloom period with a decrease in abundance of blooming species and a general nutrient recovery. *Thalassiosira curviseriata* seems to be a species associated with high nutrient stock and low light intensity. Its growth, mainly concurrent with DIN decrease, was related to new production in this area. The obtained data suggest that low phosphate concentrations, more than DIN and silicates, contributed to the diatom bloom collapse. According to our results, this high production during winter can be explained as a net growth of phytoplankton because of a successful low light- and temperature-acclimated species, possibly favored by low predation and high nutrient availability.

**ADDITIONAL INDEX WORDS:** *Estuarine ecosystem, winter, phytoplankton bloom, dissolved nutrients, Argentina.*

## INTRODUCTION

The nutrient stock in aquatic ecosystems significantly decreases when a phytoplankton bloom occurs, being transformed into biomass. In the same way, nutrient availability usually limits species growth at the end of the bloom (HOWARTH, 1988; ROELKE, ELDRIDGE, and CIFUENTES, 1999). A general functioning model of a temperate coastal environment usually includes a nutrient cycle, with the highest levels during winter, followed by phytoplankton blooms primarily during spring and summer and secondarily in early autumn (HALLEGRAEFF and JEFFREY, 1993; SMAYDA, 1980).

The inner zone of Bahía Blanca Estuary is a shallow, well-mixed, highly turbid and temperate ecosystem. Its margins include a large tidal plain, mud-dominated and partially vegetated with halophyte species (*i.e.*, *Spartina alterniflora*, *Sar-*

*cocornia perennis*). This region is considered to be highly eutrophic because of maximum nutrient concentration reached in autumn (FREIJE and MARCOVECCHIO, 2004). Its phytoplankton annual cycle is characterized by a winter/early-spring diatom bloom, which includes very recurrent blooming species, with *Thalassiosira curviseriata* as the dominant one (POPOVICH, 2004; POPOVICH and GAYOSO, 1999). Historical (1978–1991) biomass values have reached up to 12 × 10<sup>6</sup> cells L<sup>-1</sup>, chlorophyll *a* (Chl *a*) concentrations up to 54 μg L<sup>-1</sup> (GAYOSO, 1999), and levels of primary production up to 300 mg m<sup>-3</sup> h<sup>-1</sup> C within the Bahía Blanca Estuary bloom (FREIJE and GAYOSO, 1988; FREIJE and MARCOVECCHIO, 2004).

This mentioned diatom bloom seems to be the most important event of the phytoplankton cycle within Bahía Blanca Estuary, not only due to its magnitude but also for its early start time. When a multispecific bloom occurs (as in the Bahía Blanca Estuary case) the comprehension of the existing relations and processes is extremely difficult. The main goal of this study is to settle the relations between nutrient avail-

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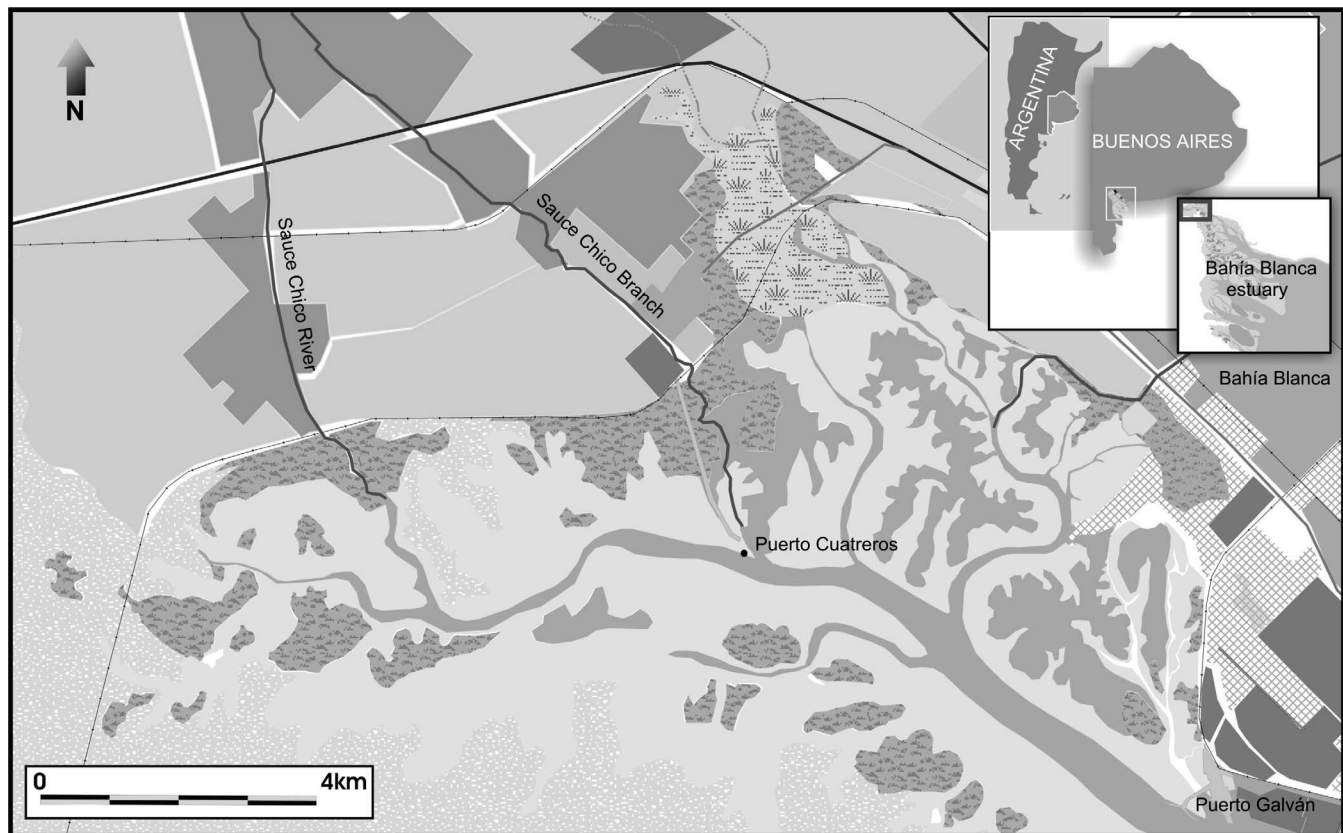


Figure 1. Map of the Bahía Blanca Estuary, indicating the localization of Puerto Cuatrerros (sampling station) in the inner zone of the estuary.

ability and phytoplankton assemblage development within Bahía Blanca Estuary.

The rates and pathways through which blooms act as agents of geochemical change are highly dependent on the species abundance and composition of the bloom communities (CLOERN, 1996). In the present study the bloom was defined as a period where a deviation of a population had occurred, *i.e.*, an increase of abundance or biomass, from its average (SMAYDA, 1997). The analysis was focused on dominant species, even though nonbloom stages and relations between composition and relative dominance of both blooming and nonblooming species were used.

## MATERIALS AND METHODS

### Study Area

The area of study involves the inner part of the Bahía Blanca Estuary ( $38^{\circ}45'–39^{\circ}40' S$ ,  $61^{\circ}45'–62^{\circ}30' W$ ), in Buenos Aires Province, Argentina (Figure 1). The sampling station Puerto Cuatrerros, which is considered to be representative of this part of the estuary (FRELJE and MARCOVECCHIO, 2004), is located within this region. The inner zone has a mean depth of 7 m; the water column is vertically homogeneous and highly turbid as a result of the combined effect of winds and tide currents, which maintain large amounts of suspended matter (PERILLO and PICCOLO, 1999). Water exchange with-

in the estuary is regulated by a semidiurnal tidal wave. The Sauce Chico River discharges in the innermost region of the estuary (Figure 1), with a mean annual runoff of  $1.9 \text{ m}^3 \text{ s}^{-1}$ , although autumnal rainfalls can increase to flows up to  $106 \text{ m}^3 \text{ s}^{-1}$  (PICCOLO, PERILLO, and ARANGO, 1990). A branch of this river discharges near the sampling station (Figure 1). In addition, freshwater input from other smaller tributaries into the estuary is intermittent and only significant during periods of high local rainfall.

### Sampling

From May 3. until August 26. 2002, on a twice-a-week basis, water samples were collected at Puerto Cuatrerros during high tide and daylight hours. Water samples were collected near the surface (approximately 0.50 m depth) with a 2.5-L Van Dorn bottle to analyse nutrients, Chl *a*, phaeopigments, and phytoplankton. Temperature, conductivity/salinity, pH, turbidity, and dissolved oxygen (DO) were *in situ* measured using a Horiba U-10 multisensor probe. Photosynthetically active radiation (PAR) in the sampling layer was measured by a submersible Li-Cor 192SB. Data of daily precipitation and historical (10 years) total monthly precipitation at Bahía Blanca City were obtained from the Argentine National Meteorological Service.

Water samples for the study of dissolved inorganic nutrients

were filtered through Whatman GF/C and were frozen in plastic bottles until analysed. Nitrate ( $\text{NO}_3^-$ ), nitrite ( $\text{NO}_2^-$ ), ammonium ( $\text{NH}_4^+$ ), phosphate ( $\text{PO}_4^{3-}$ ), and silicates were determined following the methods of TREGUER and LE CORRE (1975), GRASSHOF, ERHARDT, and KREMLING, (1983), RICHARDS and KLETSCHE (1964), EBERLEIN and KATTNER (1987), and TECHNICON® (1973), respectively. Dissolved inorganic nitrogen concentrations were calculated as the sum of  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ , and  $\text{NH}_4^+$ . A Technicon AA-II Autoanalyzer expanded to five channels was used to perform the nutrient analyses.

Chlorophyll *a* and phaeopigment concentrations were measured according to the method of the American Public Health Association (APHA), AWWA, WEF (1998).

Samples for quantitative analysis of phytoplankton were preserved with acid Lugol's solution. Abundance of phytoplankton species was determined by enumeration of cells in a Sedgwick-Rafter chamber (MCALICE, 1971) using an inverted light microscope (Nikon, Eclipse RE 300). For identification purposes bottle sampling was complemented by surface samples taken with a Nansen 30- $\mu\text{m}$  net, preserved in 4% formaldehyde and examined under a Zeiss Standard R microscope in phase contrast mode. Identified taxa were classified according to GAYOSO (1999) in blooming and nonblooming species.

Samples were also grouped in bloom and nonbloom samples according to composition, abundance, and dominance degree of the main species for each sampling date (IGNATIADIS, 1994). Dominance was assessed using a dominance index (DI), that is, percentage of the total standing crop contributed by the two most important species and calculated as

$$DI = 100(N_1 + N_2)/N,$$

where  $N_1$  and  $N_2$  are the number of individuals of the two most abundant species and  $N$  is the total number of individuals. The relative dominances of the first (dominant species) and the second (subordinate species) main species ( $RD_1$  and  $RD_2$ ) were calculated as  $100(N_1/N)$  and  $100(N_2/N)$ , respectively.

## RESULTS

### Environmental Variables

During the considered period subsurface water temperature decreased from 11.9°C to 5.4°C (on July 12), and then increased to 10.7°C (Figure 2a). Salinity did not show significant fluctuations (30.4–32.8 psu), with only one minimum value of 28.1 psu on Aug 23 (Figure 2a). Total daily precipitation was generally scarce and ranged between 0.0 and 39.9 mm (National Meteorological Service). Dissolved oxygen concentration and pH showed values between 6.8 and 10.54 mg  $\text{L}^{-1}$  and 8 and 9.55, respectively. In addition, from June 19 to July 19 both percentage of oxygen saturation and pH had values of 93–108% and 8.6–9.55, respectively (Figure 2b).

Turbidity was extremely high and varied between 13 and 147 ntu (nephelometric turbidity units) (Figure 2c). Consequently, light intensity was very low and varied between 14.85 and 128.71  $\mu\text{E m}^{-2} \text{s}^{-1}$ .

### Phytoplankton Abundance, Chl *a*, and Dominant Species

Both total phytoplankton abundance and Chl *a* concentrations (Figure 3) showed a winter diatom bloom (June to Au-

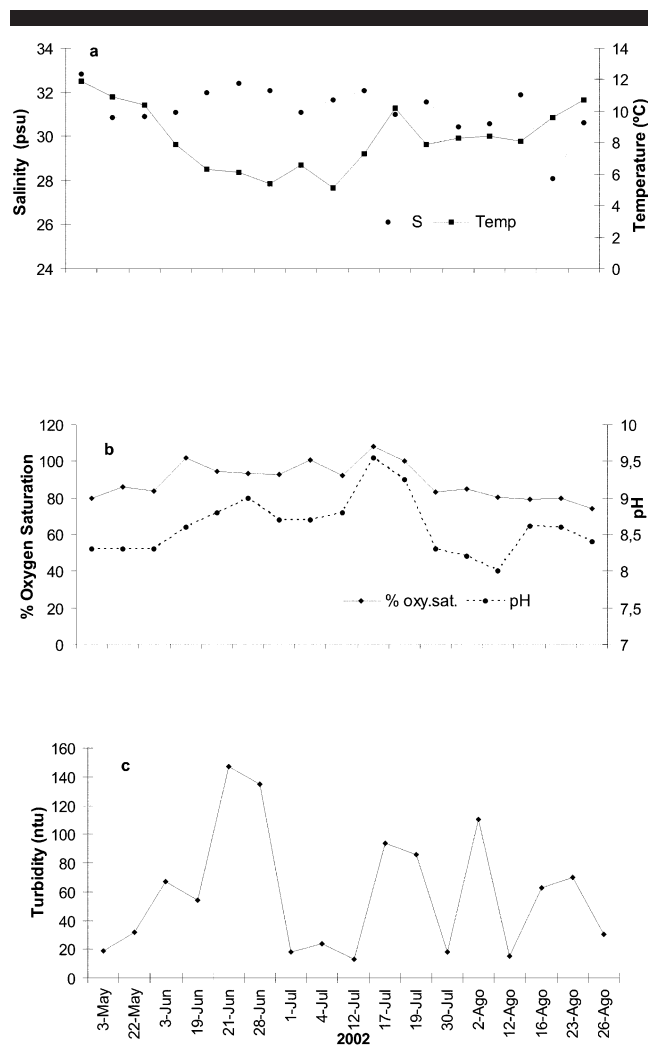


Figure 2. Temperature and salinity (a), dissolved oxygen percentage and pH (b), and turbidity (c) at Puerto Cuatros during the sampling period (May–August 2002).

gust) in the inner zone of Bahía Blanca Estuary; the phytoplankton community was dominated by an assemblage of blooming species (*Thalassiosira* spp. and *Chaetoceros* spp.) together with nonblooming species (other diatoms and dinoflagellates) (Table 1).

From June 19 to July 1, *Thalassiosira curviseriata* was the dominant species (Table 2). During this period Chl *a* concentrations reached two peaks, 44  $\mu\text{g L}^{-1}$  and 30.4  $\mu\text{g L}^{-1}$  (Figure 3a), in correspondence with maximum in diatom numbers ( $4 \times 10^6$  cells  $\text{L}^{-1}$  on June 19 and  $3.5 \times 10^6$  cells  $\text{L}^{-1}$  on June 28) (Figure 3b). During this period dinoflagellate abundance was low ( $10 \times 10^3$  cells  $\text{L}^{-1}$ ) (Figure 3b).

The samples associated with these data had high values of DI (73.39–96.2 %) (Table 2). Of blooming species, 90%, including *Thalassiosira* spp. and *Chaetoceros* spp., were recorded during this period, but *T. curviseriata* was always the dominant one (relative dominance  $RD_1 > 64.5\%$ ) (Table 2). In each sample the total cell abundance surpassed  $1 \times 10^6$  cells

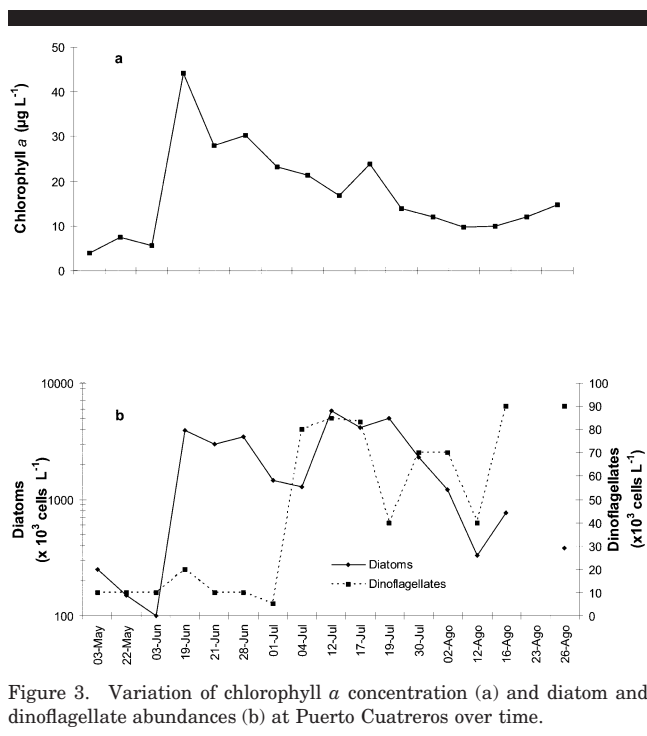


Figure 3. Variation of chlorophyll *a* concentration (a) and diatom and dinoflagellate abundances (b) at Puerto Cuatrerros over time.

$L^{-1}$ , and 64.5–81.89% of this increase was due to *T. curviseriata*, 6.75–31.7% to the subordinate one (*T. hibernalis* or *T. eccentrica*) (Table 2), and the rest to all the other species in the assemblage (Figure 4). *Thalassiosira curviseriata* was the only blooming species that occurred during May (in the pre-bloom period), appearing in all the analysed samples, and also increasing its abundance.

On July 4 the composition of dominant species changed and until July 19 the phytoplankton community was codominated by several blooming species, mainly by *Chaetoceros* spp and bigger species of *Thalassiosira* (Table 2). The maximum Chl *a* value was  $23.9 \mu g L^{-1}$ , while the diatom abundance reached  $5 \times 10^6$  cells  $L^{-1}$  (July 12) (Figures 3a, 3b). Moreover, dinoflagellate abundance increased up to  $80 \times 10^3$  cells  $L^{-1}$  (Figure 3b).

This period has been characterized by the occurrence of smaller DI values (36–48%) and smaller and homogeneous values of relative dominance ( $RD < 31.51\%$ ) in comparison with first period (June 19 to July 1) (Table 2). The total cell abundance has surpassed  $1 \times 10^6$  cells  $L^{-1}$  in each sample; however, 19.6–31.5% of this increase was due to the first dominant species (*Chaetoceros* spp., *T. curviseriata* or *T. hibernalis*), 16.4–19.59% to the subordinate one (*Chaetoceros* spp., *T. eccentrica*, or *T. curviseriata*), and the rest to all the other species in the assemblage (Figure 4). Among the non-blooming species *Guinardia delicatula* was the most outstanding, reaching values of  $4.7 \times 10^5$  cells  $L^{-1}$  while the dinoflagellate *Scropsiella trochoidea* rapidly increased up to values close to  $80 \times 10^3$  cells  $L^{-1}$ .

A different dominance pattern was observed from July 30 to August 12. The occurrence of a dominant blooming species was always linked to a nonblooming one (like *Cyclotella meneghiniana* or *Leptocylindrus minimus*) (Table 2). The bio-

Table 1. Assemblage of blooming species and nonblooming species and their maximal abundance observed during the sampling period (May–August 2002).

Assemblage	Maximum Abundance cells $L^{-1} \times 10^3$	Codes
<b>Blooming species</b>		
<i>Thalassiosira curviseriata</i>	2850	T.cur
<i>T. rotula</i>	320	T.rot
<i>T. hibernalis</i>	820	T.hib
<i>T. anguste-lineata</i>	260	T.ang
<i>T. eccentrica</i>	620	T.ecc
<i>T. pacifica</i>	900	T.pac
<i>Chaetoceros similis</i>	1580	C.sim
<i>C. ceratosporus</i>	160	C.cer
<i>C. diadema</i>	960	C.dia
<i>C. sp</i>	680	C.sp
<b>Nonblooming species</b>		
<i>Thalassiosira hendeyi</i>	40	T.hen
<i>Guinardia delicatula</i>	470	G.del
<i>Leptocylindrus minimus</i>	360	L.min
<i>Paralia sulcata</i>	100	P.sul
<i>Skeletonema costatum</i>	120	S.cos
<i>Cyclotella</i> sp.	460	Cy.sp
<i>Asterionellopsis glacialis</i>	460	A.gla
<i>Cylindrotheca closterium</i>	44	Cyl.clo
<i>Ditylum brightwellii</i>	140	D.bri
<i>Cerataulina pelagica</i>	180	Ce.pel
<i>Scropsiella trochoidea</i>	80	Sc.tro
Unidentified dinoflagellate	80	

Codes of taxa are used in the figures.

mass decreased down to minimum values of  $9.7 \mu g L^{-1}$  Chl *a* and  $3.3 \times 10^5$  cells  $L^{-1}$  (Figures 3a, 3b) and only 45% of blooming species appeared. The dinoflagellate *S. trochoidea* remained present in the samples up to August 2, when it was replaced by an unidentified dinoflagellate (length  $27 \mu m$ ) that reached up to  $90 \times 10^3$  cells  $L^{-1}$  (Figure 3b). The contribution of both the blooming species and the nonblooming species to the total phytoplankton abundance ranged between 40% and 50% (Figure 4). Finally, August 12 was the last day of bloom, taking in consideration that from August 16 both dominant species were nonblooming ones (*G. delicatula*, *L. minimus*, and *Cerataulina pelagica*) (Table 2).

### Nutrient Availability

The highest nutrient concentrations determined during the prebloom period (May) have been considered as the available nutrient stock (Figure 5). Thus, the maximum concentrations that were observed were  $NO_3^-$  ( $10.8 \mu M$ ),  $NO_2^-$  ( $1.6 \mu M$ ),  $NH_4^+$  ( $102.82 \mu M$ ),  $PO_4^{3-}$  ( $1.6 \mu M$ ), and silicates ( $121.28 \mu M$ ). Nitrite and nitrate showed an abrupt fall in coincidence with the first biomass peak (June 19) (Figure 5a).  $NO_2^-$  decreased down to values of  $0.24 \mu M$  and  $NO_3^-$  down to nondetectable values (n.d.  $\mu M$ ) (Figure 5a); after this, a  $NO_3^-$  partial recovery ( $3.08 \mu M$ ) was observed.  $NH_4^+$  was the dominant form of DIN and its concentration quickly decreased to  $14.28 \mu M$  just before the occurrence of the second biomass peak (June 28), after which the concentration remained stable and close to  $15 \mu M$  (Figure 5b). This ammonium decreasing process occurred 6 weeks after the starting point of the decrease of

Table 2. Dominant species composition, relative dominance (RD<sub>1</sub> and RD<sub>2</sub>), and dominance index (DI) during the sampling period.

Date	Dominant Taxa	RD (%)	DI (%)
Jun 19	<i>Thalassiosira curviseriata</i>	71.9	78.67
	<i>T. hibernalis</i>	6.75	
Jun 21	<i>T. curviseriata</i>	64.4	73.39
	<i>T. hibernalis</i>	9.02	
Jun 28	<i>T. curviseriata</i>	81.89	91.94
	<i>T. eccentrica</i>	10.05	
Jul 1	<i>T. curviseriata</i>	64.48	96.2
	<i>T. eccentrica</i>	31.72	
Jul 4	<i>T. eccentrica</i>	17.18	
	<i>T. hibernalis</i>	24.22	41.4
Jul 12	<i>T. curviseriata</i>	17.18	
	<i>T. curviseriata</i>	23.13	39.8
Jul 17	<i>Chaetoceros diadema</i>	16.69	
	<i>Chaetoceros</i> sp.	19.59	36.17
Jul 19	<i>C. similis</i>	16.58	
	<i>C. similis</i>	31.51	47.86
Jul 30	<i>T. curviseriata</i>	16.35	
	<i>T. pacifica</i>	39.13	59
Aug 2	<i>Cyclotella</i> sp.	20	
	<i>Leptocylindrus minimus</i>	30.2	48.3
Aug 12	<i>Thalassiosira pacifica</i>	18.1	
	<i>T. curviseriata</i>	42	70
Aug 16*	<i>L. minimus</i>	30	
	<i>Guinarida delicatula</i>	42	73
Aug 26*	<i>L. minimus</i>	31	
	<i>Cerataulina pelagica</i>	47	75
	<i>Asterionellopsis glacialis</i>	32	

\* Example of postbloom samples dominated by two nonblooming species.

nitrate and nitrite.  $\text{PO}_4^{3-}$  concentration rapidly decreased to  $0.95 \mu\text{M}$  (Figure 5c) at the first biomass peak, and then progressively increased ( $1.36 \mu\text{M}$ ). The silicate concentrations showed a steady decrease to  $85.95 \mu\text{M}$  (Figure 5c).

Following this trend, the DIN/  $\text{PO}_4^{3-}$  ratio (Figure 5d) increased from 60 (before bloom) to 100, concurring with the first biomass peak and showing a strong use of P with respect to N. However, among N sources, it must be mentioned that while a strong  $\text{NO}_3^-$  and  $\text{NO}_2^-$  decrease occurred, both the high  $\text{NH}_4^+$  concentration and the  $\text{PO}_4^{3-}$  concentration decrease contributed to the DIN/ $\text{PO}_4^{3-}$  increase. Thus, these high N/P values, as when they were related to those of REDFIELD (1958), together with  $\text{PO}_4^{3-}$  concentrations close to  $1 \mu\text{M}$ , should not be interpreted as evidence of P limitation. Before the second biomass peak, the strong  $\text{NH}_4^+$  decrease, the low  $\text{NO}_3^-$  and  $\text{NO}_2^-$  values, and the partial  $\text{PO}_4^{3-}$  recovery contributed to the sharp decrease of the DIN/ $\text{PO}_4^{3-}$  ratio down to 14.3 (Figure 5d).

From July 4 to July 19 and in correspondence with peaks of codominant blooming species, all of the analysed nutrients reached their minimum values (Figures 5a–d); however, ammonium concentrations were never less than  $14.6 \mu\text{M}$ . The DIN/ $\text{PO}_4^{3-}$  ratio increase (13 to 77) (Figure 5d), concurring with the abundance of peaks of codominant blooming species, indicated high P consumption. Finally, August 12 was the starting point of all the nutrient recovery within the system (Figure 5).

## DISCUSSION

High levels of phytoplankton biomass were associated with depletion of  $\text{NO}_3^-$  (nondetectable values), minimum values of

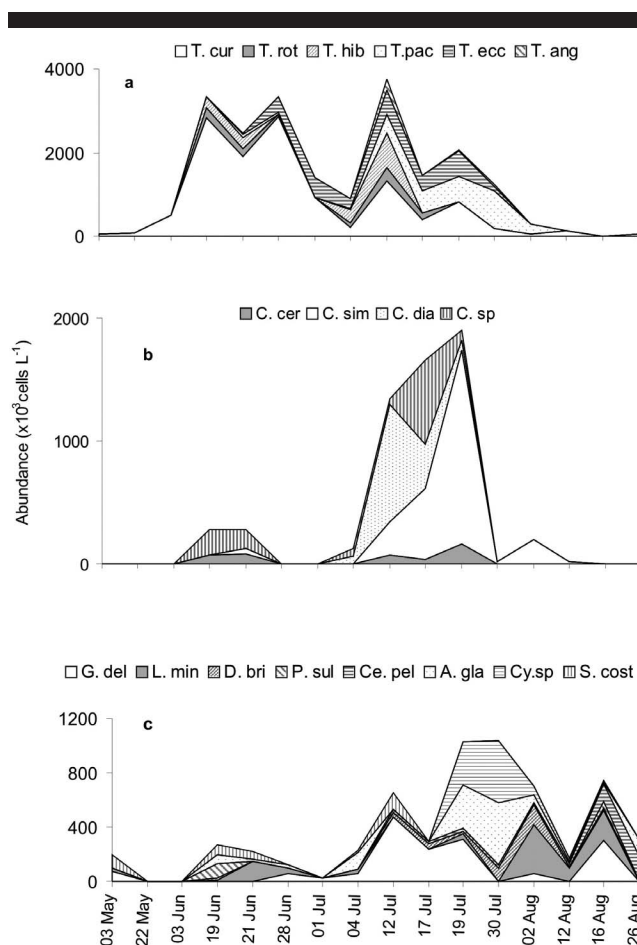


Figure 4. Abundance of *Thalassiosira* spp. (a), *Chaetoceros* spp. (b), and nonblooming species (c) in the sampling station over time. Denomination of taxa as in Table 1.

$\text{PO}_4^{3-}$  (around  $0.2 \mu\text{M}$ ), and silicates (around  $35 \mu\text{M}$ ); oxygen saturation percentage (up to 108%); and increase of pH (up to 9.5) during the sampling period. These variations have been observed in many other temperate bays and estuaries during bloom periods (CABEÇADAS, NOGUEIRA, and BROGUEIRA, 1999; CLOERN, 1996 and cites therein; TOWNSEND and THOMAS, 2002), and have been associated with phytoplankton productivity. CLOERN (1996) has pointed out that these large fluctuations in the water indicate a net autotrophic ecosystem. The increase of biomass (Chl *a* up  $44.3 \mu\text{g L}^{-1}$ ), which characterized the beginning of the bloom within the inner zone of Bahía Blanca Estuary, was almost (64.5–81.89%) because of *T. curviseriata* growth, while the subsequent increases of abundance were the result of a community 50% codominated by different blooming species.

The highest nutrient concentrations at the sampling site were observed in autumn (prebloom period), in accord with the general pattern of nutrients within the inner zone of Bahía Blanca Estuary (FREJE and MARCOVECCHIO, 2004). These values were relatively higher than those reported for Río de la Plata Estuary, which is the Argentina's largest one

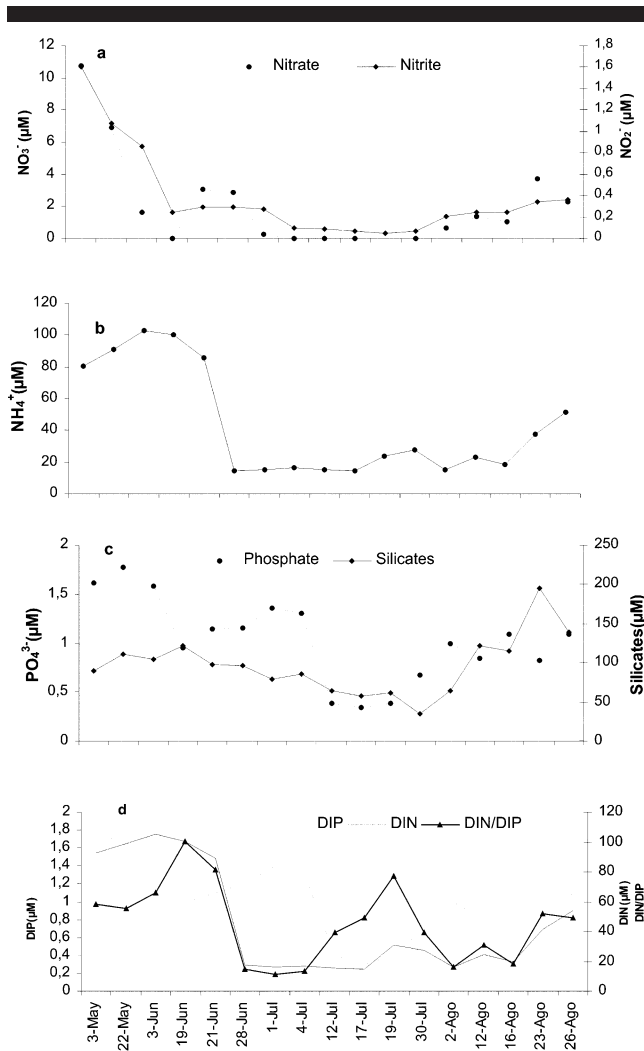


Figure 5. Dissolved nutrients concentrations: nitrite and nitrate (a), ammonium (b), phosphate, and silicates (c), and DIN, DIP concentrations and  $\text{DIN}/\text{PO}_4^{3-}$  ratio (d) at Puerto Cuatros during the sampling period (May–August 2002).

and which is strongly dominated by riverine input (CALLIARI, GÓMEZ, and GÓMEZ, 2005). In the case of  $\text{NH}_4^+$ , our values were even similar to the highly eutrophic Colne Estuary (at the seaward end), which is influenced by anthropogenic inputs (KOCUM, UNDERWOOD, and NEDWELL, 2002). Bahía Blanca Estuary shows low influence of riverine input; however, Sauce Chico River discharge at the inner area of this estuary, with high load of DIN, has been shown to be an important source of dissolved nutrients to this system, mainly during autumn (prebloom period) and spring (postbloom period) when its flow increases because of high precipitation within the region (PICCOLO, PERILLO, and ARANGO, 1990) (Figure 6). In particular, inflow from Sauce Chico River supplied up to 220.5  $\mu\text{M}$  of nitrate and 118.6  $\mu\text{M}$  of ammonium (R.H. FREIJE, personal communication). These high concentrations of N may be partially explained by considering that the studied catchments cross over a region with intense farm-

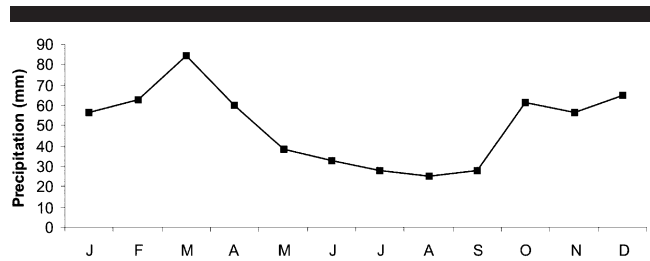


Figure 6. Variation of historical monthly precipitation at the Bahía Blanca City (Argentine National Meteorological Service)

ing and cattle-raising activities. In addition, the occurrence of both the nutrient regeneration process within the water–sediment interface as well as the zooplankton activity increase during the postbloom period within these shallow waters must be considered (BARRÍA DE CAO, BEIGHT, and PICCOLO, 2005; HOFFMEYER, FROST, and CASTRO, 2000), together with other sources (e.g., adjacent salt marshes, anthropogenic inputs) that may contribute to nutrient increase during spring and summer. Thus, the river runoff appears to be a potential important source of N for new production (*sensu*, DUGDALE and GOERING, 1967) in the inner zone of Bahía Blanca Estuary.

The decrease in concentration of maximum dissolved nutrient stock started close to a month before the bloom regardless of corresponding sources. A lag in response of phytoplankton blooms to nutrient availability has been associated with mechanism of uptake by phytoplankton (GENTILHOMME and LIZON, 1998). Our results show that mainly the use of nitrate, even at high  $\text{NH}_4^+$  concentrations (around 100  $\mu\text{M}$ ), agrees with *T. curviseriata* growth. When  $\text{NO}_3^-$  decreased close to 1.6  $\mu\text{M}$  (but not depleted from the water column),  $\text{NH}_4^+$  appeared to be the main source of N that supported the second abundance peak of this species. These maximum population points were strongly linked with highest Chl *a* concentrations, suggesting that DIN—unlike P and Si—was responsible for the highest primary production in this area. Nevertheless, and bearing in mind the observed trends of the N sources, this type of use could occur gradually, alternating the utilization of  $\text{NO}_3^-$  to  $\text{NH}_4^+$ . Our observation must be correlated with many studies about uptake of  $\text{NO}_3^-$  by phytoplankton, especially from coastal and estuarine environments, at high  $\text{NH}_4^+$  levels (COMIN and VALELA, 1993; KUDELA and DUGDALE, 2000). Even this mechanism up to the present has not been fully understood; both cultivated and natural phytoplankton communities have evidenced an optimum nitrate uptake under low light conditions (LEONARDOS and GEIDER, 2004; MARTINEZ, 1991; NEEDOBA and HARRISON, 2004). *Thalassiosira curviseriata*, isolated from this environment, showed high  $\alpha$  values (slope of light-limited growth) and maximum growth rate at low light intensities (saturation intensity 70–80  $\mu\text{E m}^{-2} \text{s}^{-1}$ ) (POPOVICH and GAYOSO, 1999). So, the potential ability of *T. curviseriata* to play a significant role as a colonist species (equivalent to C-strategies of REYNOLDS and SMAYDA, 1998) in environments with high nutrient stock (especially DIN availability) and low

irradiance must be fully assessed in future studies, mainly in experimental ones.

The increase in abundance of populations that codominated the phytoplankton assemblage during the intermediate period of the bloom agree with lower Chl *a* concentrations as well as with a lower stock of available nutrients.  $\text{NH}_4^+$  was the main source of N, showing stable values (around 15  $\mu\text{M}$ ) up to the end of the bloom, irrespective of phytoplankton abundance increase. During this dry winter period, both the relatively constant values of  $\text{NH}_4^+$  and undetectable values of nitrate suggest alternative sources of N relative to riverine input ones. Zooplankton grazing as studied during winter bloom in this environment showed a coupling of aloricate ciliates (microzooplankton) and diatom populations, particularly on the phytoplankton cells <25  $\mu\text{m}$  (PETTIGROSSO, BARRIA DE CAO, and POPOVICH, 1997). Ciliates with *T. curviseriata* (valve diameter 6–21.5  $\mu\text{m}$ ) in their food vacuoles have frequently been observed (PETTIGROSSO, 2003). Bacterially mediated degradation of organic matter from sediments and regeneration through grazing and excretion by microheterotrophs (“regenerated nitrogen”) were recognized as an important source of  $\text{NH}_4^+$  to sustain algal growth in shallow coastal environments when tributary inputs were low (BODE *et al.*, 2005; SHOSTELL and BUKAVECKAS, 2004). In our environment, the occurrence of a trophic coupling between diatom bloom and aloricate ciliate could play a double role: on the one hand, they could represent a potential source of  $\text{NH}_4^+$  to “regenerated production” (*sensu*, DUGDALE and GOERING, 1967). On the other hand, they could favor the growth of blooming species of larger size (*Thalassiosira pacifica*, *T. rotula*, *T. anguste-lineata*, *etc.*) and *Chaetoceros* spp., as those found in advanced stages of bloom. The *Chaetoceros* dominance within other environments has been explained, considering that it is not an optimal food source for many ciliates (HAIGH *et al.*, 1992).

Moreover, during the intermediate period the increase of DIN/ $\text{PO}_4^{3-}$  values (20 to 80), in correspondence with peaks of abundance of codominant blooming species, suggests that mainly phosphate (more than N) was removed from water by the growing phytoplankton, reaching values around 0.2  $\mu\text{M}$ . After this, the biomass decreased, and bloom finished in early August. DORTCH and WHITLEDGE (1992) indicated limitation of P if  $\text{N/P} > 30$  and  $\text{PO}_4^{3-} < 0.2 \mu\text{M}$ . So, P appeared to be the main potential limiting nutrient for this blooming diatom community. This effect was clearer than that of silicate (>35  $\mu\text{M}$ ) and DIN (around 15  $\mu\text{M}$  of  $\text{NH}_4^+$ ). Phosphate limitation had already been reported in many coastal and estuarine systems (BENITEZ-NELSON, 2000; FISHER *et al.*, 1999; FLYNN, 2002) and its largest effect was linked to limitation of winter and spring production (CONLEY, 2000 and references therein). Additionally, diatoms are poor competitors for phosphate compared with other groups (flagellates), although silicate is in excess (EGGE, 1998). Dinoflagellate abundance increase at a later stage of bloom in Bahía Blanca Estuary may be indicating some competitive strategies of this phytoplankton community. Additionally, the significant increase of the autochthonous copepod *Acartia tonsa* (omnivorous) and *Eurytemora americana* (herbivorous) in August and September occurring within Bahía Blanca Estuary (HOFFMEYER, FROST, and CASTRO, 2000) could help to explain the mentioned diatom bloom collapse.

Both nutrients and phytoplankton biomass data recorded

along a longitudinal transect within Bahía Blanca Estuary showed a negative gradient toward the outer zone of the estuary (POPOVICH, 1997), indicating that the inner estuary performs as the original area of the bloom as well as a source of inorganic nutrients. Under this context, our results suggested that the successful development of an autochthonous diatom community within the inner zone of the Bahía Blanca Estuary during winter may represent an important mechanism of eutrophication regulation within coastal waters. In the inner Bahía Blanca Estuary the tidal velocity is 0.69–0.77  $\text{m s}^{-1}$  (PÉREZ and PERILLO, 1998) and the water residence time is near 28 days (G.M.E. PERILLO, personal communication), conditions under which a strong utilization of nutrients in the inner zone might be expected. In estuaries, the dynamics of nutrients and hence primary productivity are strongly dependent upon their external supply and regeneration. Our results indicate that during the early stage of winter bloom, the dominance of *T. curviseriata* (“new production”) will be favored by autumnal nutrient freshwater input, in combination with other environmental factors (*i.e.*, low light intensities, shallow mixing, low predation, and low temperatures). During later stage ones, *in situ* nutrient regeneration will sustain the production of other blooming species (“regenerated production”), in comparison to tributary loadings. From these considerations emerge the hypothesis that in this extremely turbid environment, different mechanisms of nutrient production (inputs, regenerations) could act in the inception, magnitude, and duration of winter diatom bloom. The solutions to this hypothesis emphasize our need for a better understanding of mechanisms of nutrient cycling estuaries (reservoir and turnover). As a first step, studies conducted to investigate the nutrient dynamics for different compartments within the system (surface estuarine water, pore-water, and sediments) will be published.

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