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Influence of the winter phytoplankton bloom on the settled material in a temperate shallow estuary

Valeria A. Guinder^{a,*}, M. Celeste López-Abbate^a, Anabela A. Berasategui^a,
Vanesa L. Negrin^a, Georgina Zapperi^a, Paula D. Pratolongo^a,
Melisa D. Fernández Severini^a, Cecilia A. Popovich^{b,1}

^a Instituto Argentino de Oceanografía (IADO), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Bahía Blanca, Argentina

^b Laboratorio de Ficología y Micología, Universidad Nacional del Sur (UNS), Bahía Blanca, Argentina

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Summary The development of the phytoplankton winter bloom and the accumulation of particulate suspended matter (PSM) inside sediment collectors were assessed in the inner zone of the Bahía Blanca Estuary. The phytoplankton bloom (chlorophyll up to $25 \mu\text{g l}^{-1}$ and abundance up to $8 \times 10^6 \text{ cells l}^{-1}$) was related with high levels of dissolved inorganic nutrients and under-water light availability (I_m up to $355 \mu\text{E m}^{-2} \text{ s}^{-1}$) and was dominated by relatively small diatoms, e.g. *Chaetoceros* sp.1 (3–8 μm). Conversely, large planktonic diatoms, mostly *Thalassiosira* spp. 20–60 μm , were found in the accumulated material inside the collectors, together with benthic microalgae and high concentrations of chlorophyll, phaeopigments, particulate organic matter (POM between 18 and 32% of total PSM) and C:N ratios >12 . The composition of the settled material indicated vertical exportation of phytoplankton to the benthos, external loads of detritus and bottom resuspension. The present study highlights the close benthic-pelagic interactions in shallow coastal environments characterized by high productivity.

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* Corresponding author at: Instituto Argentino de Oceanografía CONICET, CC 804, B8000FWB Bahía Blanca, Argentina. Tel.: +54 291 4861112; fax: +54 291 4861112.

E-mail address: vguinder@criba.edu.ar (V.A. Guinder).

¹ Tel.: +54 291 459 5100.

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1. Introduction

Spring phytoplankton blooms represent the most important annual impulse in the pelagic food webs in temperate coastal environments (Legendre, 1990). The fate of the organic matter produced in the euphotic zone determines the role of the biological pump in the carbon cycle, and the sedimentation of phytoplankton blooms can strongly influence the benthic habitat in coastal shallow systems (Davoult and Gounin, 1995; González et al., 2009). Sink deposition of particulate matter is affected by diverse physico-chemical and biological factors such as water column structure: stratified/mixed, temperature, turbidity, phytoplankton density, aggregate formation and zooplankton grazing (Cibic et al., 2007; Kiørboe et al., 2001, Tamelander and Heiskanen, 2004). In oceans, most of the organic matter produced in the upper layers is consumed before reaching the bottom sediments (Legendre and Rassoulzadegan, 1996; Wassmann, 1998), while in coastal shallow and well mixed systems, a tight interaction between the production in the water surface and the benthic habitat is commonly observed (Botto et al., 2006; Dale and Prego, 2002). In addition, the underlying sediments may contribute to the pelagic habitat with dissolved nutrients, organic matter and microphytobenthos through resuspension induced by winds and tides (de Jonge and van Beusekom, 1995). Furthermore, high loads of allochthonous material into the pelagic environment are expected from different sources: terrestrial, littoral and river discharges (Fahl and Nöthig, 2007; Montemayor et al., 2011).

In the temperate and eutrophic Bahía Blanca Estuary, the phytoplankton seasonality and composition has been studied for decades and the winter-early spring bloom has been characterized as the most important biomass event over the annual cycle (Guinder et al., 2010 and references therein). The inner zone of the estuary is the most productive area along the main channel, as a result of high abundance and diversity of both planktonic and benthic communities (Elías, 1992; Hoffmeyer et al., 2008; Popovich and Marcovecchio, 2008). In this shallow inner zone, a tight benthic–pelagic coupling is expected. For instance, resting stages of diatoms (Guinder et al., 2012) and zooplankton resting eggs (Berasategui et al., 2013) have been found lying in the sediments and germinating in the pelagic habitat after resuspension. Conversely, a marked difference in the species composition has been found between plankton and benthos: the phytoplankton is dominated by centric diatoms while the dense microbial mats are densely formed by pennates diatoms and cyanobacterias (Pan et al., 2013; Parodi and Barría de Cao, 2003). This suggests low exportation of phytoplankton cells to the bottom either by intense grazing in the water column or high degradation processes of the organic matter. However, little is known so far on vertical transport of phytoplankton and organic matter; only short-term observations have been done during a tidal cycle (Guinder et al., 2009a). Tracking the production and fate of the organic matter produced in the surface of the water column during the blooming season will elucidate the potential benthic–pelagic interactions and the remineralization capacity of the system in the highly productive inner zone of the Bahía Blanca Estuary. In this work our goals were (1) to evaluate the evolution of the winter-early spring phytoplankton bloom

in surface waters assessing the species succession, size structure, duration and magnitude of the bloom in relation to environmental factors, and (2) to characterize the settled material inside sediment collectors in terms of accumulated particulate suspended matter (PSM) and organic matter (POM), chlorophyll and phaeopigments concentrations, and carbon-to-nitrogen ratios (C:N). Overall, we aim to obtain an approach to the modulating factors of the winter phytoplankton bloom and its potential influence in the underlying sediments.

2. Material and methods

2.1. Study area

The Bahía Blanca Estuary (38°42'–39°25'S, 61°50'–62°22'W) is located in a temperate climate region on the southwestern Atlantic, Argentina. The estuary is mesotidal (mean tidal amplitude of 3.5 m) with a semidiurnal cycle, highly turbid and eutrophic (Freije and Marcovecchio, 2004; Guinder et al., 2009b). The sampling site, Puerto Cuatrerros station (38°50'S; 62°20'W), is a shallow harbor (mean depth: 7 m) located at the head of the estuary (Fig. 1) and characterized by a restricted circulation (tidal velocities between 0.69 and 0.77 m s⁻¹), low advection and a relatively long residence time (ca. 30 days). The river runoff is low; the Sauce Chico River, the main freshwater tributary, presents a mean annual runoff of 1.9 m³ s⁻¹, with maximum of 106 m³ s⁻¹ in autumn due to rainfalls, and the Napostá Grande Creek has an annual runoff of 0.8 m³ s⁻¹ (Melo and Limbozzi, 2008).

The maximal plankton biomass of the estuary is found in the inner zone of the estuary (Barria de Cao et al., 2005; Berasategui et al., 2013; Popovich and Marcovecchio, 2008) which is highly eutrophic due to important inputs of organic matter, detritus and nutrients from anthropogenic sources (industrial, urban and agricultural activities) (Freije et al., 2008) and saltmarshes (Montemayor et al., 2011; Negrin et al., 2013). In this area, numerous interconnected channels separate small islands and vast tidal flats and saltmarshes with halophytes of the species *Sarcocornia perennis*, *Spartina alterniflora* and *S. densiflora* (Isacch et al., 2006). The extensive bare flats are mainly composed of silt-clay sediments covered with dense microbial mats (Cuadrado and Pizani, 2007; Parodi and Barría de Cao, 2003). Benthic fauna is dominated by *Laonereis acuta*, a deposit-feeder polychaete, and the burrowing crab *Neohelice granulata* (Escapa et al., 2007).

2.2. Sampling at the surface water

The sampling was carried out on a fortnightly frequency from January to December 2007 at Puerto Cuatrerros station, during midday and high tides. Mean depth of the sampling station was 7 m. Surface water temperature was measured in situ using a portable Horiba U-10 multi-probe (Horiba Ltd., Kyoto, Japan). Water samples were collected from the surface (approx. 0.5 m depth), using a van Dorn bottle (2.5 l), stored in a cooler and taken to the laboratory to estimate phytoplankton abundance, chlorophyll *a* (chl), phaeopigments (pha) and dissolved inorganic nutrient concentrations (nitrate, nitrite, phosphate and silicate) and particle size

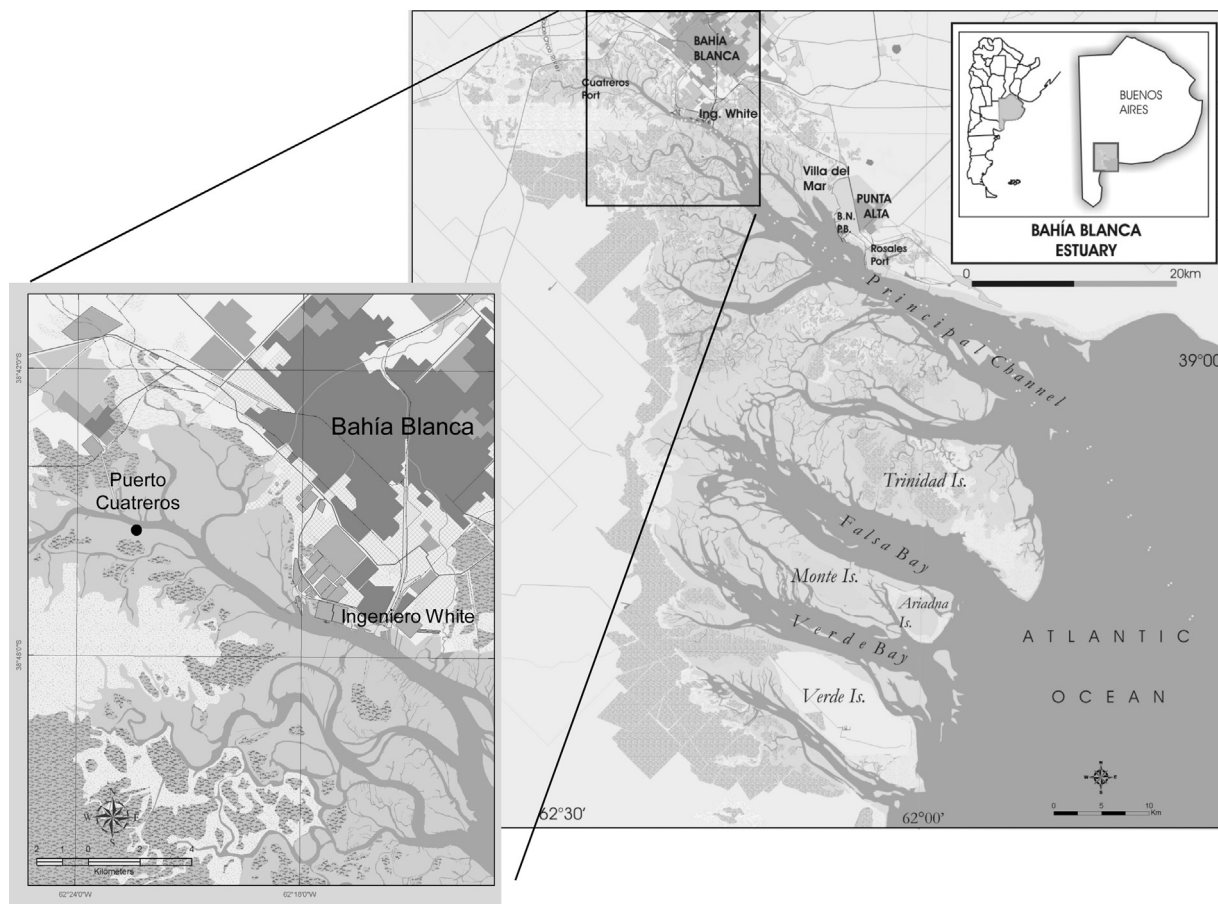


Figure 1 Map of the Bahía Blanca Estuary indicating the location of the sampling site, Puerto Cuatros station.

concentration. Samples for phytoplankton enumeration were preserved with acid Lugol's solution. For the taxonomic identification of the species, water samples were collected with a Nansen net (30 μm mesh) and preserved with formalin (final concentration 4%, v/v). For the purpose of this work, here we only present the phytoplankton species succession from May to November (winter-mid spring), which corresponds to the bloom and post-bloom periods (Guinder et al., 2009b; Popovich et al., 2008). In addition, mesozooplankton samples were collected from July to October 2007, with a plankton net (200- μm mesh) by means of subsurface horizontal tows (0.5 m depth) and were preserved in 4% buffered formalin. Abundance values were calculated taking into account the corresponding sample volume and expressed in number per cubic meter.

Vertical profiles of photosynthetically active radiation (PAR) were measured at 10 cm intervals in the vertical profile of the water column using a submersible radiometer Li-Cor LI-192SB (Lincoln, Nebraska, USA). Thereafter, light extinction coefficient (k , m^{-1}) was estimated considering that light is exponentially attenuated with depth. In addition, the mean light intensity in the mixed layer, I_m , was calculated with the equation (Riley, 1957): $I_m = I_0 (1 - e^{(-kZ_m)})^{-1}$, where I_0 (in $\mu\text{E m}^2 \text{s}^{-1}$) is the light intensity received at the water surface and Z_m is the depth of the mixed zone (in m), which corresponds to the water column depth with no vertical stratification (i.e. absence of thermocline and

halocline). The limit of the euphotic zone (Z_{eu} , m) was estimated as the depth at which irradiance is 1% of the surface value (i.e. $Z_{\text{eu}} = 4.6 k^{-1}$).

2.3. Sediment collectors' deployments during the winter-spring period

During the dates of installation and recovery of the sediment collectors (during and after the winter bloom: July–November), vertical profiles of pH, temperature, dissolved oxygen, salinity and turbidity (1 m intervals) were measured in situ with the portable Horiba U-10 multi-probe. In addition, surface water samples were collected with a van Dorn bottle (2.5 l) to assess phytoplankton abundance, chlorophyll, phaeopigments, dissolved nutrients, PSM and POM concentrations. In addition, the size of the suspended particles was analyzed from May to November in surface water.

Sediment collectors were used to assess the sinking rates of PSM and the fate of phytoplankton cells. Nor fixatives were added (Varela et al., 2004) in order to evaluate the natural physical and chemical processes that affect the accumulation of organic matter in the collectors. The cylindrical container (PVC material) had a height to diameter ratio of 8:1 and a collecting area of 0.1 m^2 ; the design was based on Lange and Boltovskoy (1995). The mooring system consisted of a 200 kg platform which was connected to a buoy by a line and a

ballast positioned at a fixed distance from the collectors. This system led to keep clear the water column above the collectors' mouth without any lines. Sampling devices were built at CCT-BB facilities, CONICET-Bahía Blanca, Argentina. The sediment collectors were moored at 300 m offshore in Puerto Cuatros station, within a relatively undisturbed area from boats and fishing. The mouths of the collectors were positioned 2 m above the bottom, where the depth fluctuated between 9.5 m in high tide and 5.5 m in low tide.

Sampling was carried out conducting a total of four deployments (D1–D4): D1 from 24 July to 7 August, 14 days; D2 from 15 to 22 August, 7 days; D3 from 22 August to 6 September, 15 days and D4 from 27 November to 30 November, 3 days. The accumulated material inside the collectors was homogenized in order to analyze PSM, POM, dissolved inorganic nutrients, chl and pha concentrations and C:N ratios. Thereafter, we estimated the pha:chl and the POM:PSM ratios to compare the composition of the particulate matter in the water surface and inside the collectors. The composition of the settled phytoplankton was qualitatively analyzed. The vertical flux or sedimentation rates ($\text{m}^{-2} \text{day}^{-1}$) of the PSM collected by the sediment containers was calculated according to Botto et al. (2006) using the equation $S = CV/At$; where C is the concentration of the sample (l^{-1}), V is the total volume (l), A is the area of the sediment collector opening (m^2) and t is the deployment time (days).

2.4. Laboratory determinations

Chl and pha (in $\mu\text{g l}^{-1}$) were measured according to Lorenzen and Jeffrey (1980) using a spectrophotometer (DU-2 UV–vis, Beckman, USA). Water samples (250 ml) were filtered through Whatman GF/C filters, which were immediately stored at -20°C . Pigment extraction was done in 90% acetone at ambient temperature overnight. Phytoplankton $>3 \mu\text{m}$ was counted with a Sedgwick–Rafter chamber (1 ml) which was a suitable volume according to the amount of suspended solids. The entire chamber was examined at $200\times$ and each algal cell was counted as a unit according to (McAlice, 1971). Phytoplankton species identification was done using a Zeiss Standard R microscope and a Nikon Eclipse microscope with $1000\times$ magnification and phase contrast.

For dissolved nutrient determinations, water samples were filtered through Whatman GF/F filters and frozen in plastic bottles until analysis. Dissolved nitrate NO_3^- , nitrite NO_2^- , phosphate PO_4^{3-} and silicate SiO_2 concentrations were determined by standardized methods (Eberlein and Kattner, 1987; Technicon, 1973; Treguer and Le Corre, 1975) using a Technicon AA-II Autoanalyzer (Technicon Instruments Corporation, USA).

PSM and POM concentrations (both in mg l^{-1}) were determined gravimetrically filtering 300–500 ml of water on pre-combusted and weighed GF/F filters. Then, the filters were dried at 60°C for 24 h and weighed for PSM estimation. Afterwards, they were combusted at 500°C for 30 min and weighed again for POM determination as the difference between both weight values.

Surface water samples (~ 500 ml) were processed in the particle size analyzer Mastersizer 2000 (Malvern®) which measures materials from $0.02 \mu\text{m}$ to $2000 \mu\text{m}$, to characterize the size structure of the suspended material during the

phytoplankton pre-bloom, bloom and post-bloom periods (May–November). The Mastersizer 2000 uses the technique of laser diffraction described by the Fraunhofer Approximation and the Mie theory. Samples were added into the dispersion unit (distilled water as the blank) until the obscuration was within an acceptable range (10–30%). The methodology followed the broad recommendations outlined in ISO13320-1. The particles are counted assuming spherical morphology and then express in % of the total volume of all particles in the sample.

In the samples of the sediment collectors, organic carbon was determined by dry combustion using a Carbon Determinator (LECO, model CR12) and total N with the Kjeldahl method by the LANAIS N-15, CONICET-UNS, Bahía Blanca. Thereafter, C:N ratios were calculated to estimate the origin of the particulate material accumulated in the sediment trap.

3. Results

3.1. Phytoplankton and physicochemical conditions in surface waters

Mean annual temperature in the water surface was $14.4 \pm 6.4^\circ\text{C}$ and in winter $6.9 \pm 1.9^\circ\text{C}$. The phytoplankton annual cycle was characterized by a winter diatom bloom (June–September), when the cellular abundance reached a maximum of $8 \times 10^6 \text{ cells l}^{-1}$ and the chlorophyll concentration was up to $25 \mu\text{g l}^{-1}$ (Fig. 2a). Small phytoflagellates ($<20 \mu\text{m}$) and some dinoflagellates (e.g. *Scropsiella trochoidea*) appeared during the blooming period, but their abundances were never over the 10% of the total phytoplankton abundance. The dominant mesozooplankton species ($>80\%$) during the period July–September was by far *Eurytemora americana*. The population of adult stages of this copepod (nauplii were not hold with the net of $200 \mu\text{m}$ pore-size) increased at the end of phytoplankton winter bloom and showed a notable peak in mid September, when it reached a maximum of $17,403 \text{ ind m}^{-3}$ (Fig. 2a).

Concerning the underwater light availability, the mixed zone Z_m was assumed equivalent to the total depth in the sampling station, as the whole water column was vertically homogeneous over the studied period. The light extinction coefficient k reached the minima annual values during the blooming period (mean value in winter: 1.5 m^{-1} , Fig. 2b), and the $Z_{\text{eu}}:Z_m$ ratios were always over the critical value of 0.2 proposed by Cloern (1987) for turbid estuaries, except for a few dates in late spring (November). Moreover, the $Z_{\text{eu}}:Z_m$ ratio was up to 1.0 in some occasions, indicating that the euphotic zone was equal to the water column depth. The light intensity in the mixed layer I_m was over the annual mean of $107 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Fig. 2b) during the period June–October, with a maximum of $355 \mu\text{E m}^{-2} \text{ s}^{-1}$. The dissolved nutrient concentrations were high over the year with a marked decrease during winter due to phytoplankton uptake (Fig. 2c).

The diatom succession during the winter bloom was mainly represented by the genera *Thalassiosira*, *Chaetoceros* and *Cyclotella*. The dominant species with more than 60% of the total phytoplankton abundance (up to $5.6 \times 10^6 \text{ cells l}^{-1}$) was *Chaetoceros* sp. 1 (diameter between 3 and $8 \mu\text{m}$)

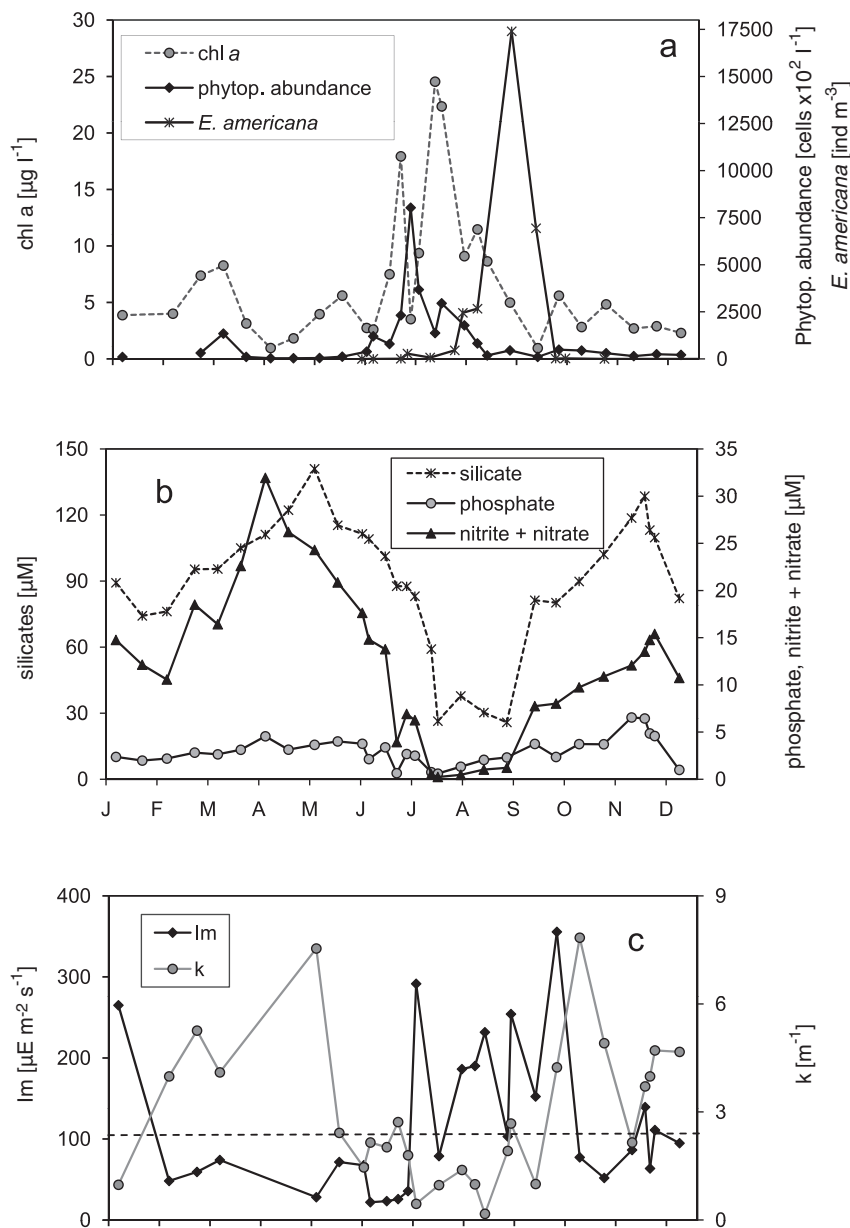


Figure 2 Annual phytoplankton dynamics and the main modulating factors in the surface water at Puerto Cuatrerros station during 2007. (a) Chlorophyll *a* concentration and the abundance of phytoplankton and the copepod *Eurytemora americana*, (b) mean light intensity in the mixed layer I_m and light extinction coefficient k , and (c) dissolved nutrient concentrations. Dashed line in (b) indicates the annual mean of I_m .

(Fig. 3a), followed by *C. debilis* (10–28 μm) with up to $2.7 \times 10^6 \text{ cells l}^{-1}$. The rest of the species did not surpass the $0.8 \times 10^6 \text{ cells l}^{-1}$, including *Cyclotella* sp. (5–12 μm) and some *Thalassiosira* species with relatively large cell size like *T. eccentrica* (25–48 μm), *T. pacifica* (22–35 μm) and *Thalassiosira* sp. (20–60 μm) (Fig. 3b and c).

3.2. Settled material during the phytoplankton bloom and post-bloom periods

The vertical profiles of water temperature, salinity, turbidity, pH and dissolved oxygen concentration showed that the

water column was vertically homogeneous during the winter-spring period (Fig. 4). Turbidity showed some variability with depth, the maximum coefficient of variation (CV) was up to 13% on 30th November.

The particle sizes were notably contrasting during bloom and post-bloom periods (Fig. 5). During bloom conditions, the range of particle size distribution was wider, from ca 1 to 1000 μm , with peaks around 10, 60 and 900 μm , while during post-bloom conditions, the range was homogenous and narrower, around a median of ca 10 μm .

The PSM and POM in the water surface in the dates of installation and removal of the sediment collectors varied in the ranges of 29–84 and 6–19 mg l^{-1} (Table 1), respectively.

Furthermore, the concentrations of PSM accumulated inside the collectors fluctuated between 350 mg l^{-1} in August–September and 80 mg l^{-1} in November, while POM varied between 26 and 65 mg l^{-1} (Table 1), although the time of deployment was not constant. Sedimentation rates of the PSM for the four deployments D1–D4 were: 75.0 , 221.4 , 116.7 and $133.3 \text{ mg m}^{-2} \text{ day}^{-1}$, respectively. The POM:PSM ratios were higher in the water surface than inside the collectors; nevertheless the POM in the settled material was likewise high, between 18 and 32% of the total PSM (Fig. 6a). POM in D2 was not measured due to technical errors.

The chl concentration found in the settled material was maximum during D1 (over 14 days), $2406 \mu\text{g l}^{-1}$, and the maximum value measured in the water surface was in July ($22.4 \mu\text{g l}^{-1}$ in July) (Table 1). Further, the pha concentrations even doubled those of chlorophyll in the settled material in some deployments (Table 1), where the pha:chl ratios

showed higher values inside the collectors (>1) than in the water surface (<1) (Fig. 6b). The phytoplankton density was conspicuously higher inside the collectors than in the water column (although quantification was not performed in the settled material) and the dominant species by far were the planktonic diatoms *Thalassiosira* sp., *T. pacifica* and *T. eccentrica*, all of them with cell diameters over $20 \mu\text{m}$ and chain forming life-styles. Benthic and tychopelagic species were also found inside the containers, such as *Navicula* sp., *Nitzschia* sp., *Paralia sulcata*, *Surirella striata* and *Cylindrotheca closterium*.

Dissolved nutrient concentrations inside the sediment collectors at the end of the deployment periods were rather higher than the levels in surface waters (Table 1), with minima during the phytoplankton bloom and maxima during the post-bloom period. The C:N ratios in the settled material were high and relatively constant over the four deployment periods (Table 1).

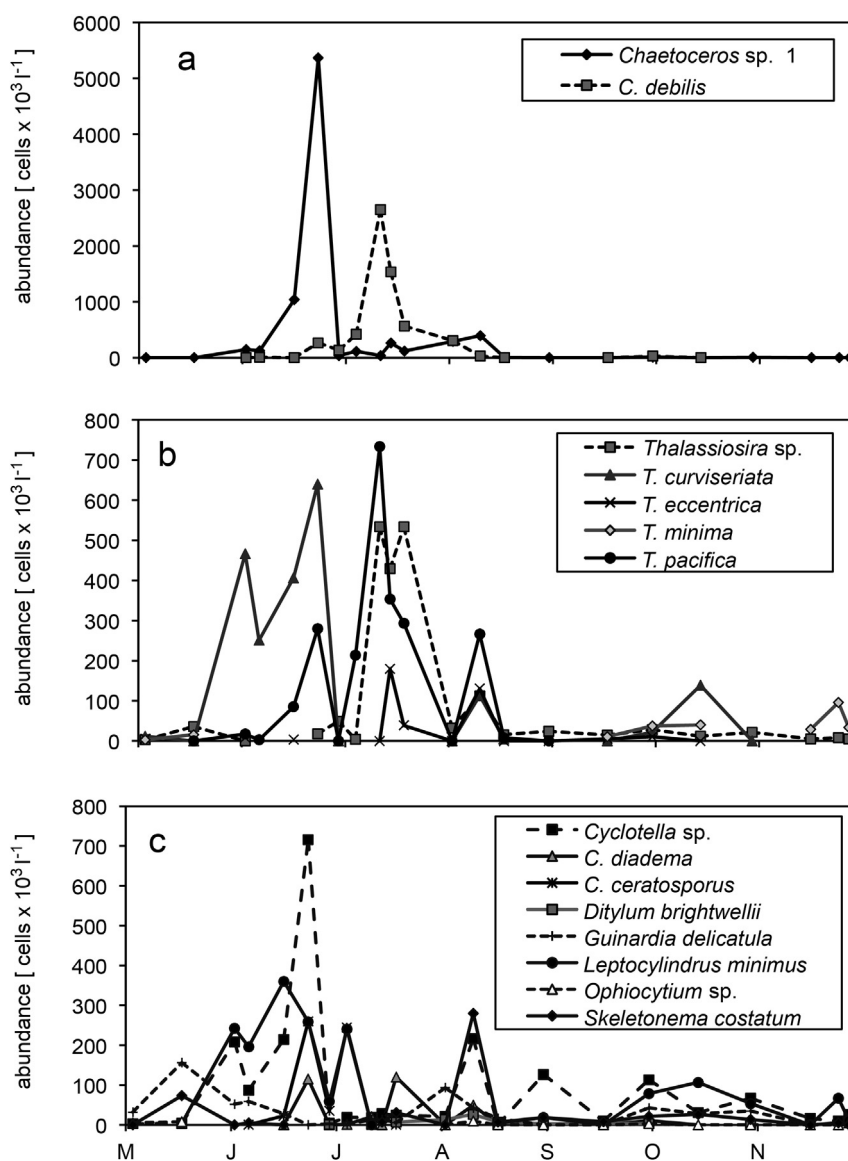


Figure 3 Phytoplankton species succession during the winter-early spring bloom (May–November) in the surface water at Puerto Cuatrerros station.

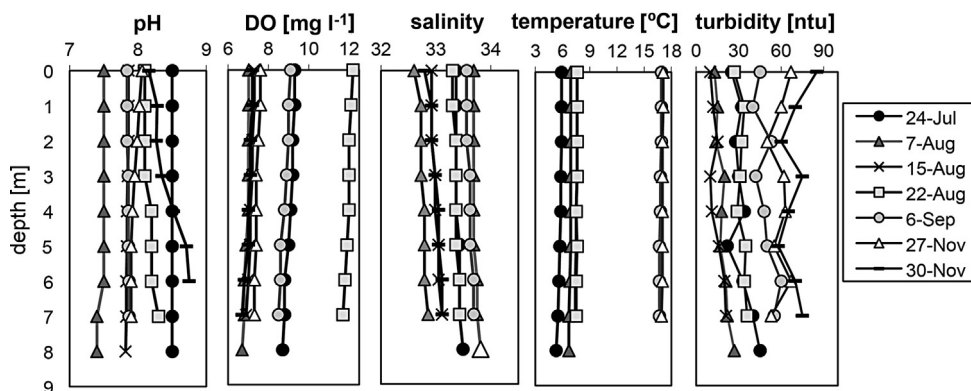


Figure 4 Water column vertical profiles of physicochemical variables measured in situ at Puerto Cuatrerros station covering the period of the sediment trap deployments (July–November).

4. Discussion

4.1. Shaping ecological mechanisms of the winter phytoplankton bloom

The findings of this work reinforce the factors that have been further recognized as triggers of the phytoplankton winter bloom initiation in the inner zone of the Bahía Blanca Estuary: high dissolved nutrient concentrations due to autumn rains (Guinder et al., 2009a; Popovich et al., 2008), increase on light penetration in the water column resultant of less suspended sediments (Guinder et al., 2009b) and low grazing pressure related to low water temperatures (Berastegui et al., 2009; Pettigrosso and Popovich, 2009). The collapse of the bloom in 2007 was likely related to nutrient depletions associated with phytoplankton uptake, and to zooplankton grazing. The copepod *Eurytemora americana* showed in this

year the maximal population abundance registered for the estuary over the last decade (Berastegui et al., 2009; Hoffmeyer and Prado Figueroa, 1997). Light availability, although may have played a significant role in bloom initiation, was not a determining factor of bloom duration as underwater light penetration remained high over the next two months after the event ended.

Dissolved nutrient concentrations were high all-year round, except during the blooming season (see Fig. 2c). This annual pattern is relatively constant in the inner zone of the Bahía Blanca Estuary, where the nutrients notably decrease in the water column during late winter-early spring in relation to microalgae consumption (Guinder et al., 2010; Popovich et al., 2008). In the present study,

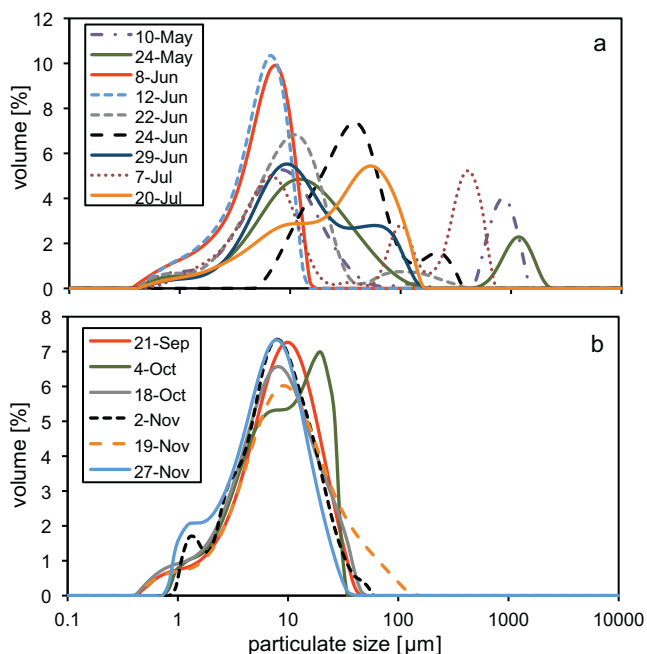


Figure 5 Particle size distribution in the surface of the water column, (a) during the winter phytoplankton bloom (May–July) and (b) during the post-bloom period (September–November).

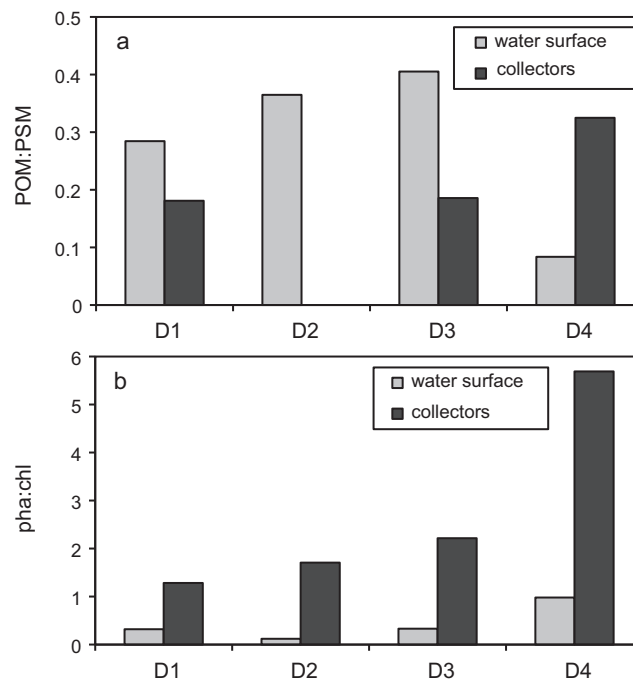


Figure 6 Ratios of (a) particulate organic matter to total particulate suspended matter (POM:PSM) and (b) phaeopigment to chlorophyll *a* (pha:chl) in the surface of the water column and inside the sediment collectors during the four deployment periods: D1–D4.

Table 1 Levels of chlorophyll (chl), phaeopigments (pha), particulate suspended matter (PSM), particulate organic matter (POM), both in $\mu\text{g l}^{-1}$, particulate suspended matter (PSM), particulate organic matter (POM), both in mg l^{-1} , phytoplankton abundance (abund, in $\text{cells} \times 10^3 \text{ l}^{-1}$) and biomass (biom, in $\mu\text{g C l}^{-1}$), dissolved inorganic nutrients (μM) and carbon:nitrogen ratios in the water surface and inside the sediment collectors over the winter phytoplankton bloom in the Bahía Blanca Estuary.

Trap deployments	Water surface													Sediment trap								
	chl	pha	PSM	POM	Cells	biom	Nitrite	Nitrate	Phos.	Silic.	C:N	chl	pha	PSM	POM	Cells	biom	Nitrite	Nitrate	Phos.	Silic.	C:N
24 Jul Installation	22.4	7.2	66.8	19.0	1785	312.4	0.0	0.2	0.6	26.4	—	2406.7	3089.9	210.0	38.0	—	—	0.1	0.6	0.7	98.6	12.5
7 Aug Recovery	9.1	1.2	48.9	18.4	824	89.2	0.1	0.4	1.3	37.9	—	—	—	—	—	—	—	—	—	—	—	—
15 Aug Installation	11.5	1.4	46.6	17.0	1749	239.2	0.2	1.4	2.2	39.2	—	—	—	—	—	—	—	—	—	—	—	—
22 Aug Recov./instal.	8.6	2.9	29.7	12.0	187	18.5	0.2	0.8	2.1	30.3	—	393.6	672.0	310.0	—	—	—	1.1	3.6	2.1	45.8	15.7
4 Sep	5.0	1.9	29.7	12.0	452	19.9	0.2	1.0	2.3	25.9	—	720.1	1595.3	350.0	65.0	—	—	1.0	3.4	1.5	87.9	12.5
6 Sep Recovery	1.8	4.6	51.4	12.6	—	—	0.4	1.4	2.5	31.0	—	—	—	—	—	—	—	—	—	—	—	—
21 Sep	1.0	5.1	99.4	8.6	108	20.8	1.1	6.7	3.7	81.3	—	—	—	—	—	—	—	—	—	—	—	—
4 Oct	5.6	1.2	85.5	13.8	491	59.0	1.2	6.8	2.4	80.2	—	—	—	—	—	—	—	—	—	—	—	—
18 Oct	2.8	4.6	118.7	12.7	445	38.9	2.0	7.7	3.7	89.9	—	—	—	—	—	—	—	—	—	—	—	—
2 Nov	4.8	4.3	276.7	9.3	303	47.6	2.6	8.3	3.7	102.1	—	—	—	—	—	—	—	—	—	—	—	—
19 Nov	2.7	4.6	181.4	6.9	149	26.7	3.0	9.1	6.6	118.6	—	—	—	—	—	—	—	—	—	—	—	—
27 Nov Installation	3.6	3.5	79.7	6.7	251	21.9	3.2	10.3	6.5	128.5	—	50.3	286.0	80.0	25.0	—	—	6.3	41.0	5.2	136.0	13.5
30 Nov Recovery	5.0	1.9	57.8	13.7	216	31.8	3.4	11.3	4.8	113.2	—	—	—	—	—	—	—	—	—	—	—	—

the estimation of nutrient ratios (data not shown) indicated a limitation (Popovich et al., 2008 and references therein) in phosphate ($\text{N:P} > 20\text{--}30$) and in nitrogen ($\text{N:P} < 10$ and $\text{Si:N} > 1$) in some dates toward the end of the blooming season.

The beginning of the winter bloom was dominated by small diatom species like *Chaetoceros* sp. ($3\text{--}8 \mu\text{m}$) and *Cyclotella* sp. ($5\text{--}12 \mu\text{m}$), which showed a peak of abundance in June–July. The abrupt population decrease of these diatoms in July–August could be related with predation by microzooplankton (Barria de Cao et al., 2005; Pettigrosso and Popovich, 2009) and nauplii of *E. americana* (Berasategui et al., 2012). Although this small-sized copepod stage was not considered in this study, as we used a net of $200\text{-}\mu\text{m}$ mesh (Berasategui et al., 2012; Grice, 1970), it is well known that in the Bahía Blanca Estuary, hatching of resting eggs of *E. americana* occurs between May–July under conditions of low temperature, high salinity and high chlorophyll levels and nauplii feed on small sized-phytoplankton (Berasategui et al., 2012, 2013). The adult stage of *E. americana* feeds preferentially on large species of the phytoplankton winter assemblage, i.e. *Thalassiosira* spp. (Hoffmeyer and Prado Figueroa, 1997). The selective grazing of the adult of *E. americana* on large cells might reduce the relative abundances of these diatoms in the mid-late winter bloom.

4.2. Accumulated matter in the collectors during the phytoplankton bloom

In this study, no fixatives were added to the containers in order to evaluate the accumulation of particulate matter near the bottom over time, embracing also natural processes of production and decomposition (Schloss et al., 1999; Varela et al., 2004). On the one hand, not using preservatives eliminates the risk of overestimating the sedimentation due to swimmer contamination (i.e. vertically migrating phototrophic micro-organisms) (Heiskanen and Leppänen, 1995; Heiskanen et al., 1998). On the other hand, when fixatives are not used, the actual sedimentation of organic matter can be slightly underestimated (e.g. 13–16% according to Tamelander and Heiskanen (2004)) due to carbon losses by decomposition, which is mainly controlled by temperature. Our findings might indicate intense production and decomposition processes in the settled material in the Bahía Blanca Estuary, even when the study was carried out in a particularly cold winter.

The high chlorophyll and phytoplankton cell density observed in the settled material could be related to a combination of (1) high phytoplankton sedimentation during the growing period, (2) low predation pressure and (3) intense in situ growth inside the collectors. First, the low river runoff and high residence time of the inner zone of the estuary (Pratolongo et al., 2010) allowed net downward flow of phytoplankton. Secondly, the phytoplankton in the pelagic habitat had to deal with high zooplankton grazing pressure, while the microalgae inside the sediment containers were released from predation by the suspension-feeder *E. americana* (Berasategui et al., 2009). Thirdly, the microenvironment inside the collectors may have benefited the phytoplankton growth compared to the water column, where the cells can be highly stressed by water mixing and fluctuating light intensities. The continuous movement of phytoplankton up and down may imply an adaptation of the

photosynthetic system to changing underwater conditions, and this might lead to an extra energy cost in contrast to the cells settled in the collectors (Villafañe et al., 2004 and references therein). In agreement, Popovich and Marcovecchio (2008) classified the phytoplankton species found in the internal zone of the Bahía Blanca Estuary as well adapted to grow under low light conditions. For instance, empirical research with the diatom *Thalassiosira curviseriata* isolated from the estuary (Popovich and Gayoso, 1999) – and one of the dominant species within the collectors in the present work – showed a growth optimum at light intensities around $32\text{--}36 \mu\text{E m}^{-2} \text{s}^{-1}$, saturation growth between 60 and $80 \mu\text{E m}^{-2} \text{s}^{-1}$ and inhibition close to $150 \mu\text{E m}^{-2} \text{s}^{-1}$. In the present study, the light intensity received at the water surface I_0 (10 cm depth) during the winter-spring period was $823 \pm 522 \mu\text{E m}^{-2} \text{s}^{-1}$ (mean value \pm standard deviation), and light intensity in the mixed layer I_m (total water column) was always over $100 \mu\text{E m}^{-2} \text{s}^{-1}$. This suggests that the further attenuated light conditions inside the sediment collectors were more suitable for *Thalassiosira* spp. growth than the light intensity received in both, the surface waters and the mixed zone.

The analysis of the particle size distribution showed that during the blooming period the size-spectrum was notably heterogeneous due to the presence of phytoplankton and zooplanktonic organisms, as well as sediment and detritus. Conversely, during the post-bloom period, the water surface appeared dominated by smaller particles (i.e. silt, clay and phytoplankton cells) likely due to aggregation and sedimentation of detritus and senescence microalgae and zooplankton clearance of large phytoplankton (Alldredge and Jackson, 1995; Kjørboe et al., 2001).

4.3. Potential sources of the settled material and benthic–pelagic interactions

The C:N ratios give an estimative idea of the origin and quality of the particulate matter (Varela et al., 2004 and reference therein). Values close to the Redfield ratio (6.7) imply flux of fresh autochthonous pelagic material, as it was observed, for instance, in the southwest Kattegat (Lund-Hansen et al., 2004) and in the Pontevedra Ria (Varela et al., 2004) during phytoplankton blooms, over trap deployments of 24 h. In our study, the C:N ratios in the settled material were on average 13.5, indicating a high proportion of decomposed material and high loads of allochthonous matter (e.g. benthic microalgae and/or decaying organic material of littoral origin) (Heiskanen and Leppänen, 1995; Olesen and Lundsgaard, 1995; Tamelander and Heiskanen, 2004). The proportion of decomposed material is in agreement with the high phaeopigments concentration measured in the collectors (higher pha:chl ratios than in the water surface) and with the fact that the particulate matter had more time to be remineralized considering the relatively long-term deployments performed in this work. Similar findings (C:N ratio closed to 11) were achieved by Fernández et al. (1995) in the Cantabrian Sea. The presence of allochthonous material in the settled material in the Bahía Blanca Estuary is in agreement with important inputs of detritus into the pelagic environment from the surrounding saltmarshes (Montemayor et al., 2011; Negrin et al., 2013), anthropogenic inputs as well as with the shallow water

column combined with high tidal and wind energies that promote resuspension of bottom sediments (Guinder et al., 2009b; Marcovecchio et al., 2009). In temperate coastal systems, sedimentation of phytodetritus after the spring bloom contributes with a significant part of the total annual sedimentary input to the bottom (de Jonge and van Beusekom, 1995; González et al., 2009). In the Bahía Blanca Estuary, the high chl levels and high density of diatoms observed inside the collectors suggest high production and accumulation of sinking phytoplankton during the winter bloom. The shallowness of the water column might allow an important number of viable cells to reach deeper layers and proliferate massively in relatively dark conditions. Moreover, the presence of viable benthic microalgae growing inside the collectors has revealed important contribution of microphytobenthos to pelagic primary production in the inner zone of the Bahía Blanca Estuary, as it has been observed in other shallow coastal environments (Cibic et al., 2007; Dale and Prego, 2002; Underwood and Kromkamp, 1999).

5. Conclusions

The preliminary approach presented here contributes to the understanding of the major processes shaping the vertical dynamics of particulate matter in the highly turbid and productive inner zone of the Bahía Blanca Estuary. Our findings show that both degradation and production can take place beyond the euphotic layer and the pelagic environment closely interacts with the underlying sediments. Further quantitative analyses of the settled material are necessary to accurately estimate the origin and fate of the suspended particulate organic carbon (POC) in this shallow and non-stratified coastal system. In addition, biomass estimation of phytoplankton and phytobenthos, together with grazing experiments, should be performed in future studies to elucidate the transfer of organic carbon through the pelagic and benthic food webs.

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