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Spatial and temporal variability of phytoplankton and environmental factors in a temperate estuary of South America (Atlantic coast, Argentina)

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Abstract

A spatial and temporal study on data collected along the longitudinal gradient of the Principal Channel of Bahía Blanca estuary, Argentina, was carried out during 1992-1993. At nine stations, phytoplankton abundance, chlorophyll a (Chl-a) concentration, inorganic nutrient levels, Secchi disk depth, euphotic depth:mixing depth ratio (Z_{eu} : Z_m), salinity and temperature were recorded. Phytoplankton abundance, Chl-a concentration and nutrient levels decreased towards the outer zone of the estuary. The inner zone (stations 1 and 2), which was characterized by high turbidity, high nutrient concentrations and high $Z_{eu}:Z_m$ (>0.16, [critical mixing ratio]), registered the highest phytoplankton abundance and Chl-a concentrations. Temporal variability of data was also noteworthy in this zone. The highest biomass values thus corresponded to June, July, August and the beginning of spring (18 μ g Chl-a L⁻¹ and 9×10^{6} cells L⁻¹) concomitantly with a diatom bloom. In the middle zone (stations 3–6), a strong phytoplankton biomass decrease was observed and it coincided with both deep-mixed depths and low Z_{eu} : Z_m (<0.16). The outer zone (stations 7–9), which was characterized by low phytoplankton biomass values and low nutrient levels all along the year, was the area mostly influenced by waters from the adjacent continental shelf. In view of the above, it can be concluded that the most important primary production in the Bahía Blanca would be produced in the shallow inner zone during winter, being the spatial reach of the phytoplankton biomass principally limited to estuarine waters. Presumably, less than 5% of such biomass may reach the coastal area of the estuary. © 2007 Elsevier Ltd. All rights reserved.

Keywords: Phytoplankton; Chlorophyll a; Winter diatom bloom; Nutrients; Euphotic depth: Mixing depth ratio; Estuary; Argentina

1. Introduction

Estuaries are distinctive environments where continental runoff interacts with adjacent continental shelf waters (Cloern and Nichols, 1985; Verity et al., 1993). Their usually complex and strong circulation as well as their typically shallow depths characterize these kinds of systems, generating highly variable gradients in physical

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and chemical properties, which influence the phytoplankton dynamics (including productivity and spatial/temporal changes in biomass) (Smayda, 1983). Light availability plays a key role in the control of biomass-specific productivity in turbid and nutrient-rich estuaries (Cloern, 1987; Cole et al., 1992). A primary production decrease in the landward direction, where turbidity is usually high, has therefore been extensively observed. In spite of the fact that these zones are nutrient-rich areas, high concentrations of suspended particulate matter (SPM) are commonly found in them, thus limiting both light for photosynthesis and phytoplankton growth rate (McMahon et al., 1992; Kocum et al., 2002).

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Bahía Blanca estuary is a temperate mesotidal coastal plain estuary (Perillo, 1995) and is located at 38°42'-39°25'S and 61°50'-62°22'W on the eastern coast of Argentina in South America. It covers an area that is approximately 2300 km² with a hydrographic basin of 19,000 km² (Melo, 2004). Due to tidal flats and mesotidal conditions and circulation mechanisms in the estuary, in general, and in the Principal Channel, in particular, Bahía Blanca estuary displays a very complex configuration. In addition, Bahía Blanca estuary includes the largest deepwater harbour system in Argentina, a fact which makes it economically important. This area gathers important urban centres as well as large industrial enterprises (such as a petrochemical industrial park, a thermoelectric plant, fertilizer plants and a commercial duty-free zone between Bahía Blanca and Punta Alta cities) on its northern coast.

Both phytoplankton and the physical-chemical environmental characteristics in Bahía Blanca estuary have been thoroughly and systematically studied during the last 20 years (Freije et al., 1981; Gayoso, 1983, 1988; Popovich and Gayoso, 1999; Popovich, 2004; Popovich et al., 2006). These studies have presumably generated the largest database regarding South America coastal systems (Gayoso, 1998, 1999). Particularly, the sampling station located at Puerto Cuatreros, which Freije et al. (1981) reported as representative of the innermost area of the estuary, has been the main source of information on account of the fact that it has been systematically monitored since 1975 (Freije and Marcovecchio, 2004). These studies indicate that waters in the inner zone of the estuary are shallow, turbid, nutrient-rich and vertically mixed by tides and winds. In addition, the phytoplankton annual cycle in this area is characterized by a winter/early spring diatom bloom, which includes very recurrent blooming species (Gayoso, 1999) of which Thalassiosira curviseriata is the dominant one (Popovich and Gayoso, 1999). Historical (1978-1991) biomass values have reached up to 12×10^6 cell L⁻¹, chlorophyll *a* concentrations up to $54 \,\mu g \, L^{-1}$ and levels of primary production up to $300 \text{ mg Cm}^{-3} \text{h}^{-1}$ within the Bahía Blanca estuary bloom (Freije and Gayoso, 1988; Freije and Marcovecchio, 2004).

Literature on the ecology and dynamics of phytoplankton along the estuary is rather poor, especially toward the outer part of the estuary and the neighbouring coastal system. The absence of studies of these aspects in Bahía Blanca estuary is critical in view of the importance of this zone not only as a nursery area for several fish species (Lopez Cazorla, 2000) but also as a natural reserve area, which is used as a multiple-use zone, mainly Bahía Blanca, Bahía Falsa and Bahía Verde (Fig. 1).

The present study provides information on the seasonal and spatial variation in physical-chemical characteristics and phytoplankton biomass along the estuary. Considering the occurrence of a diatom bloom at the innermost zone of the estuary, the aims of the present study are to analyse the mechanisms involved in the regulation of phytoplankton biomass distribution at temporal mesoscale within the estuary, and to determine both the quantitative (biomass) and qualitative nature (occurrence of blooming species) of the spatial reach of winter/early spring diatom bloom.

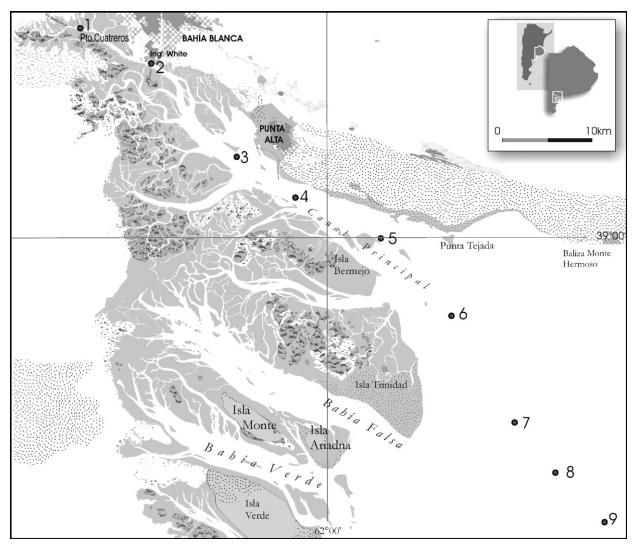
2. Materials and methods

2.1. Study site

Bahía Blanca estuary (Fig. 1) is formed by a series of NW–SE tidal channels separated by extensive intertidal flats, low marshes and islands. The northern area is geomorphologically dominated by the Principal Channel (Main Navigation Channel) while the southern area is dominated by Bahía Falsa and Bahía Verde, the largest channels within the estuary (Perillo and Piccolo, 1991). The Principal Channel, which includes our study area, covers a total length of 61 km and a width varying from about 3–4 km at the mouth (22 m depth) to 200 m at the head (3 m depth). The Principal Channel is partly closed by a modified ebb delta (Cuadrado and Perillo, 1997).

The principal energy input to Bahía Blanca estuary comes from a standing semidiurnal tidal wave (Perillo and Piccolo, 1991). Strong NW and N winds dominate the typical weather pattern of the region, with a mean velocity of 24 km h^{-1} and gusts of over 100 km h^{-1} (Piccolo and Perillo, 1990). Freshwater input is low on the northern coast towards Sauce Chico River (drainage area of 1600 km²) in the inner area and the Napostá Grande Stream (drainage area of 920 km²) in the middle zone of the estuary (Fig. 1), both with an annual mean discharge of 1.9 and 0.8 m³ s⁻¹, respectively. However, Sauce Chico River may reach higher runoffs during autumn, with peaks of up to $106 \text{ m}^3 \text{ s}^{-1}$ in coincidence with the high autumnal rainfall in the study area (Piccolo et al., 1990). The basin also includes small streams of discontinuous flow. In addition, the inner zone is highly turbid as a result of the combined effect of winds and tide currents containing large amounts of suspended matter (Piccolo and Perillo, 1990; Gelós et al., 2004).

The thermal vertical structure of the estuary is homogeneous with variations less than 2 °C (Piccolo et al., 1990). Mean annual (13 °C), summer (21.6 °C), and winter (8.5 °C) surface water temperatures in the Principal Channel are always slightly higher at the head of the estuary (Piccolo et al., 1987), while mean surface salinity increases exponentially from the head to mid-reaches of the estuary. The water column is vertically homogeneous all throughout the estuary although it may be partially mixed in the inner zone depending on freshwater runoff conditions (Piccolo et al., 1990). Salinity varies between 17.29 and 41.89 at the inner zone of the estuary (Freije and Marcovecchio, 2004). Dissolved oxygen values are usually close to saturation level values, which stimulates both oxidation and re-mineralization of organic matter within the system. During the typical winter/early spring phytoplankton bloom within the estuary, it is therefore common to register supersaturating oxygen levels of up to 130%



C.A. Popovich, J.E. Marcovecchio / Continental Shelf Research 28 (2008) 236–244

Fig. 1. Location of Bahía Blanca estuary and sampling stations (station 1 to station 9).

(Freije and Marcovecchio, 2004). Nutrient concentrations are also high except during the bloom period when they undergo a notorious decrease as a result of phytoplankton consumption (Freije and Marcovecchio, 2004; Popovich et al., 2006).

2.2. Sampling and analysis

Sampling was carried out between August 1992 and August 1993 along seven sampling stations (stations 3–9) (Fig. 1) within the Principal Channel (depth > 13 m) in Bahía Blanca estuary, on monthly cruises on board of *Prefectura Naval Argentina* ships. In addition, samples from shallower areas (ca. 5 m depth) were collected both from Puerto Cuatreros dock (station 1) and Puerto Ing. White dock (station 2) (Fig. 1) either on the same day of the cruise or, on certain occasions, 1 day before the cruise. This sampling design facilitated the assessment of the whole longitudinal spatial range within the estuary.

Water samples were collected near the surface (approximately 0.50 m depth) using a 2.5 L Van Dorn bottle sampler, and they were subsequently used for the determination of salinity, dissolved inorganic nutrients, chlorophyll a (Chl-a), phaeopigments and phytoplankton abundance. Water temperature and salinity were determined by means of a surface thermometer and a Beckman salinometer.

Measurements of water column depth with an ecosonde and Secchi disk depth (D_s , m) were recorded at every sampling station and light attenuation coefficient (K, m⁻¹) was estimated according to Holmes (1970) as $K = 1.44/D_s$ and $K = 1.7/D_s$ equations for highly turbid and transparent waters (euphotic zone > 5 m), respectively.

Euphotic zone depth (Z_{eu} , m) was calculated as 4.61/K assuming that irradiance at the bottom was 1% of surface irradiance (Cloern, 1987). On the other hand, and taking into account that the water column within Bahía Estuary is vertically homogenous, the mixed zone depth (Z_m , m) was calculated as the depth of water column *in situ* measured for each sampling station. The euphotic depth:mixing depth ratio (Z_{eu} : Z_m) was calculated as proposed by Cloern (1987).

Water samples were filtered through Whatman GF/C for the study of dissolved inorganic nutrients, and frozen until they were analysed. Nitrate (NO₃⁻), nitrite (NO₂⁻), phosphate (PO₄³⁻) and silicate were determined by standardized methods (Treguer and Le Corre, 1975; Eberlein and Kattner, 1987; Technicon[®], 1973) using a Technicon AA-II autoanalyser. Nitrate + nitrite was expressed as μM N, phosphate as μM P and silicate as μM Si.

Chl-*a* and phaeopigments were determined spectrophotometrically according to Lorenzen and Jeffrey (1980) from 250 mL sample aliquots filtered through Whatman GF/C membranes, which were stored at -20 °C until they were used for analytical treatment.

Samples were preserved in acid Lugol's solution for the quantitative analysis of phytoplankton. Abundance of phytoplankton species was determined by enumeration of cells in a Sedgwick-Rafter chamber (McAlice, 1971) using a Zeiss Standard R microscope at $200 \times$ equipped with phase-contrast objectives. Strongly diluted samples were placed in settling chambers (10 mL) and counted under a Wild inverted microscope at $400 \times$ following Utermöhl method (Hasle, 1978). The entire chamber was examined and each cell was counted as a unit in both cases. Bottle sampling was complemented by surface sampling, which was carried out with a Nansen 30 µm net for identification purposes. Samples were preserved in 4% formaldehyde and examined under a Zeiss Standard R microscope in phase-contrast mode.

Temperature, salinity, dissolved inorganic nutrients: nitrate + nitrite (N), phosphate (P), silicate (Si), phytoplankton abundance and Chl-*a* concentration for each sampling stations were averaged over 10 months. The mean values of these variables among stations were compared using an analysis of variance (ANOVA) and multiple comparisons LSD test (Sokal and Rohlf, 1995). Phytoplankton abundance was ln transformed in order to obtain normal distribution within the data. Statistical analyses were performed using a software package (Statistical Area, Mathematical Department, Universidad Nacional del Sur, 2005).

3. Results

3.1. Physical-chemical variables

Variations in temperature, salinity and inorganic nutrient concentrations in Bahía Blanca estuary during an annual cycle are shown in Fig. 2, Table 1. These variables were plotted for each station using the annual average values. Water temperature showed a regular seasonal cycle, with a minimum of 7.3 °C in July and a maximum of 24.6 °C in February. There were no significant differences in mean temperature values among stations along the estuary (ANOVA, F = 0.4, n = 84, p > 0.05) (Fig. 2a). Salinity showed the highest annual variation at stations 1 and 2, with a minimum of 28.64 and a maximum of 35.11. Minimum values were registered in autumn after a period

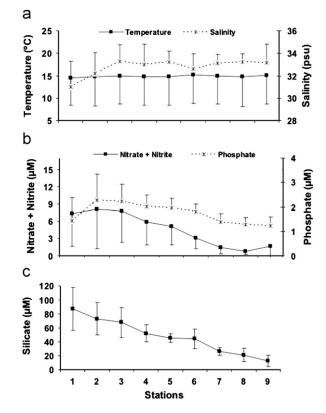


Fig. 2. Variation of (a) temperature and salinity, (b) nitrate + nitrite and phosphate and (c) silicate at nine sampling stations along Bahía Blanca estuary averaged over 10 months from August 1992 to August 1993.

Table 1

Average values and standard deviations (in brackets) of environmental variables, Chl-*a* concentrations and phytoplankton abundance recorded at three zones of Bahía Blanca estuary during 1992–1993

	Inner zone	Middle zone	Outer zone
Sampling stations	1 and 2	3, 4, 5 and 6	7, 8 and 9
Temperature (°C)	14.67 (6.14)	14.91 (6.04)	14.94 (6.16)
$NO_{3}^{-} + NO_{2}^{-} (\mu M)$	7.73 (6.13)	5.41 (3.91)	1.36 (1.61)
$PO_4^{3-}(\mu M)$	1.85 (1.07)	1.79 (0.47)	1.30 (0.32)
Silicate (µM)	80.22 (27.53)	51.29 (15.82)	20.22 (9.62)
Salinity	31.61 (2.10)	32.80 (1.84)	32.91 (1.59)
Secchi depth (m)	0.55 (0.17)	0.65 (0.22)	2.04 (1.57)
$Z_{\rm eu}:Z_{\rm mix}$	0.35 (0.03)	0.13 (0.05)	0.43 (0.15)
Chl- a (µg L ⁻¹)	10.77 (4.97)	6.14 (2.98)	3.19 (1.74)
Abundance ($\times 10^3$ cells L ⁻¹)	1577 (2517)	117 (121)	50 (62)

of very high rainfall while maximum values were registered in February in coincidence with high temperature and low rainfall in the region. Annual mean salinity was significantly different among stations (ANOVA, F = 2.1, n = 77, p < 0.05). Mean salinity tended to increase from station 1 to station 3 and after there this variable showed relatively constant values (ca. 33) from station 3 to station 9 (LSD test, p < 0.05).

The mean concentrations of all nutrients (N, P and Si) showed significant differences among stations (ANOVA, p < 0.01, F = 2.1 and n = 78 for N; F = 3.55 and n = 78 for

P; F = 18.3 and n = 79 for Si). A general spatial pattern for nutrients was to decrease from the inner zone to the outer zone (Fig. 2b and 2c, Table 1), however we only found significant differences for mean nutrient values between the inner (stations 1 and 2) and the outer zones (stations 7-9) (LSD test, p < 0.05). In addition, all sampling stations, particularly stations 1 and 2, revealed an inorganic nutrient seasonal pattern with maximum values during summer and autumn and minimum values during winter in agreement with the occurrence of the phytoplankton bloom. The highest concentrations were recorded at station 1, with values of 16 µM N, 3.4 µM P and 131 µM Si in autumn. During winter, station 1 showed the lowest N and P values with respect to those at the other sampling stations, with values close to the analytical detection limits of N and $0.39 \,\mu\text{M}$ P. Mean values were thus slightly lower than those at station 2 (Fig. 2b). Silicate concentrations were always highest at station 1, regardless of the season. All the nutrients at the outer zone showed maximum concentrations falling below 2.05 µM N, 1.94 µM P (Fig. 2b) and 36.54 µM Si (Fig. 2c). In this zone, nutrient levels showed no clear time-trend.

Secchi depth values ranged from 0.25 to 6.5 m, with mean values higher at outer zone than in the inner and middle zones (Fig. 3a, Table 1). The light attenuation coefficients (K, m⁻¹) varied from 0.26 to 5.76, with a general increase up the estuary (Fig. 3a, Table 1). Stations 1 and 2 evidenced the lowest depth of water column (Z_{mix}) within the Principal Channel, while stations 4–6 were the deepest (15–20 m). Consequently, Z_{eu} : Z_{mix} ratio varied from 0.08 to 0.60, with the lowest values in the middle zone (stations 4–6) (Fig. 3b).

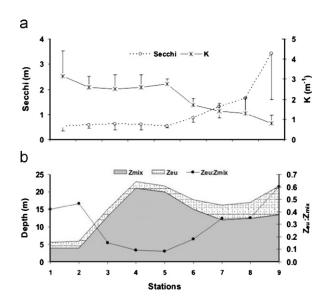


Fig. 3. Spatial variation (average of 10 months) of (a) Secchi depth and light extinction coefficient (K, m⁻¹) and (b) euphotic zone depth (Z_{eu} , m), mixed layer depth (Z_{mix} , m) and Z_{eu} : Z_{mix} ratio along Bahía Blanca estuary.

3.2. Chl-a concentration and phytoplankton abundance

Both mean Chl-a concentration and mean phytoplankton abundance (In abundance) presented significant differences among stations (ANOVA, p < 0.01, F = 5.7 and n = 58 for Chl-a; F = 6.4 and n = 66 for ln abundance). These variables tended to decrease from the inner to the outer zone (Fig. 4a, Table 1), but showed significant differences between the inner and outer zones (LSD test, p < 0.05). The inner and middle zones exhibited a clear phytoplankton biomass seasonal pattern (Fig. 4c). In winter (July-early September) a diatom bloom was observed, with maximum values of $18 \mu g \text{ Chl-} a \text{ L}^{-1}$ and 9×10^6 cells L⁻¹ at station 1. Diatom community was dominated by Thalassiosira curviseriata, Thalassiosira anguste-lineata, Thalassiosira pacifica, Thalassiosira rotula, Thalassiosira hibernalis, Thalassiosira eccentrica, Chaetoceros ceratosporus, Chaetoceros diadema, Chaetoceros debilis and Skeletonema costatum. During summer and autumn phytoplankton biomass was low (<10 µg Chl $a L^{-1}$ and $< 2 \times 10^5$ cells L^{-1}), being Cerataulina pelagica, Guinardia delicatula, Cylindrotheca closterium and phytoflagellates the most important taxa. In the outer zone, biomass values were usually low during the whole studied annual cycle (biomass values lower than $4.35 \,\mu g \,\mathrm{Chl} \cdot a \,\mathrm{L}^{-1}$ and 235×10^3 cells L⁻¹) (Fig. 4).

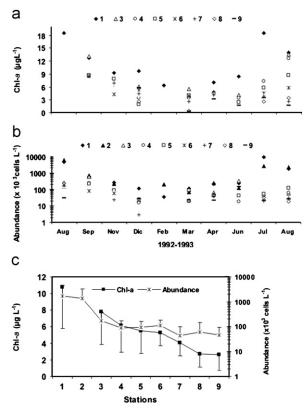


Fig. 4. Variation of (a) Chl-*a* concentrations (b) phytoplankton abundance at nine sampling stations all along Bahía Blanca estuary during 1992–1993 and (c) Chl-*a* and phytoplankton abundance averaged over all period for each sampling station.

During winter, *T. curviseriata* was the species with most spatial reach (from station 1 to station 9), covering > 50% of the total phytoplankton abundance at stations 1 and 2, from 41.4% to 11.5% at the stations 3–6, and from 2.6% to 0.5% at the stations 7–9. From station 5 to station 9, phytoplankton composition differed with respect to what it was observed in the inner zone. Several species which were not usually found at stations 1 and 2, such as *Corethron cryophylum* and several *Coscinodiscus* and *Actinoptychus* species, among others, were recorded at the outer stations on the same sampling date.

4. Discussion

Chl-*a* concentrations, phytoplankton abundance and nutrient levels showed a marked trend to decrease from the head to the mouth of the Bahía Blanca estuary. The main feature of such variation was manifested by a contrast between a rich inner zone (stations 1 and 2) and relatively poor waters in the outer zone (station 7 to station 9) of the estuary. In addition, important temporal variability of both phytoplankton biomass concentrations and nutrients levels was observed in the inner zone, and in a lesser extent in the middle zone (station 3 to station 6). The inner zone also showed the highest biomass values (usually diatom-dominated) throughout the whole year with respect to those of the other zones, with maximum levels during a diatom winter–early spring bloom, in agreement with antecedents in this zone (Gayoso, 1998, 1999).

The influence of basin tributaries (such as Sauce Chico River) within the head of the estuary—with large loads of dissolved inorganic nutrients (Freije, personal communication)-proved to be an important source of nutrients in the inner zone, particularly during autumn and spring when the flow of Sauce Chico River increases due to high rainfall in the area (Piccolo and Perillo, 1990). In addition, nutrient regeneration processes resulting from water-sediment interactions, the increase of zooplankton activity during post-bloom period (Hoffmeyer, 1994; Pettigrosso et al., 1997), and presumably other factors (such as adjacent salt marshes) may contribute to the nutrient increase that occurs during spring and summer. According to nutrient levels, the inner zone is representative of an eutrophic environment with respect to other estuaries (Domingues et al., 2005, Calliari et al., 2005), however, this peculiarity showed a temporal component strongly related to the annual phytoplankton cycle, reaching limiting values after winter phytoplankton bloom. Therefore, phytoplankton biomass in the inner zone of the estuary could be stimulated by new nutrients coming in from rivers, creeks, re-mineralization processes and probably other complementary sources.

On the other hand, the high nutrient levels as recorded within the middle zone could not be only explained through point land-inputs, as in the inner one. An alternative explanation to be considered is that the inner nutrient enriched mass water can be transported from the inner area mouthward. The residual circulation shows a marked difference in the direction of the mass transport at the inner and middle reaches of the Bahía Blanca estuary (Piccolo and Perillo, 1990). The net transport is completely landward on the shallower parts, while in the deeper parts of the sections (northern flank) the flow reverses with depth, being headward near the bottom. This fact could minimize the nutrient losses due to advection processes to coastal zones, as well as to allow nutrients retention within the middle one.

The outer zone (stations 7-9) showed both low phytoplankton biomass and low nutrient concentrations throughout the year suggesting a region strongly influenced by marine waters. Similar nutrient levels were reported on the seaward side of the frontal zone of Georgia (Yoder et al., 1993) and within the outer zone of Colne estuary (Kocum et al., 2002) as well as on the neighbouring continental shelf area (Perillo, 1994; Perillo et al., 2006). Nitrogen has been reported to be the main limiting nutrient to primary production in a variety of offshore ecosystems (Yoder et al., 1993; Nixon et al., 1996; Gentilhomme and Lizon, 1998). In addition, in estuarine systems, a spatial trend with P-limitation at the freshwater-influenced area and N-limitation at the seaward area has been reported (Pennock and Sharp, 1994; Conley, 2000). Therefore, of all nutrients registered the low concentrations of nitrogen $(NO_3 + NO_2 always < 1.5 \mu M)$ in the outer zone could be a possible reason for the general low levels of biomass observed within this zone.

Phytoplankton biomass was higher in the mixohaline inner zone of the estuary than in the euhaline middle and outer zones. A marked succession of species has been observed along the salinity gradient in other estuaries (Schuchardt and Schirmer, 1991; Gómez et al., 2004), where continental species are important for estuarine production. In contrast, the phytoplankton species observed in Bahía Blanca estuary were typically estuarine taxa. In this respect, it was observed that diatoms were the dominant group along the estuary and that the highest biomass values within the inner zone were associated with a winter diatom bloom, in which T. curviseriata was the dominant species (>50%), decreasing down to <3% at station 7. This species showed the widest spatial distribution within the estuary with respect to the other blooming species (Thalassiosira spp. and Chaetoceros spp.). Colonies of T. curviseriata with high amounts of sediment adhered to cells were observed up to station 9. Both euryhaline and eurythermic behaviour of T. curviseriata have been experimentally studied (Popovich and Gayoso, 1999), in this respect the variation of temperature and salinity recorded along the whole estuary would not represent a stress condition to the growth of this dominant species.

Other blooming species observed within the inner zone of the estuary, such as *T. pacifica*, *T. anguste-lineata*, *T. rotula*, *T. hibernalis*, *T. eccentrica*, *C. diadema*, *C. ceratosporus*, *Ditylum brightwellii* and *S. costatum* have also been found in mixohaline–euhaline areas from other estuaries (Muylaert et al., 2000). The abundance of Cyclotella meneghiniana at stations 1 and 2, which has been reported in oligohaline areas from other estuarine environments (Muylaert and Sabbe, 1999; Gómez et al., 2004), revealed a higher influence of freshwater on these stations with respect to the other sampling stations. On the other hand, the occurrence of several marine species such as *C. cryophylum, Odontella mobiliensis, Coscinodiscus* spp. and *Actinoptychus* spp. at stations 5, 6, 7, 8 and 9 indicated a higher influence of euhaline offshore waters on this zone of the estuary. This phytoplanktonic composition requires further analysis, which, on this instance, goes beyond the aims of the present study.

In estuarine systems characterized by high nutrient concentrations and turbidity levels, such as Bahía Blanca estuary, light availability seems to play a key role in the control of biomass-specific productivity (Mallin and Paerl, 1992; Cloern, 1999; Underwood and Kromkamp, 1999). Thus, in other turbid estuaries, such as Río de la Plata (Calliari et al., 2005), phytoplankton biomass generally decreases in the landward direction, where the turbidity is usually highest. However, in the present study it was observed that a phytoplankton biomass peak occurred only in the inner zone, which showed SPM levels of $10-33 \text{ mg L}^{-1}$ at the surface of the water column and 65 mg L^{-1} near the bottom (Pérez and Perillo, 1998; Perillo et al., 2001). These conditions may be indicative of an increase in light limitation on phytoplankton productivity.

Euphotic zone to mixed zone ratios $(Z_{eu}:Z_{mix})$ have been reported to play a key role in phytoplanktonic primary production in turbid and nutrient-rich estuaries (McMahon et al., 1992; Kocum, et al., 2002). In these environments, a $Z_{eu}:Z_{mix}$ ratio > ca. 0.16–0.2 (which equals 5-6 times that of euphotic depth) is indicative of conditions suitable for net primary production under light limiting conditions (Alpine and Cloern, 1988; Cole et al., 1992). Our results show that under similar conditions of turbidity in the inner and middle zones, the ratio only reached favourable values for phytoplankton growth (mean $Z_{eu}:Z_{mix}$ ca. 0.28–0.3) in the inner zone. At the middle zone, a deeper mixing depth $(Z_{mix}: 13-21 \text{ m})$ effectively reduced the ratio (Z_{eu} : Z_{mix} was always <0.16) and could explain, among other factors (i.e. water circulation, velocity and direction of current), the outstanding decrease in phytoplanktonic biomass values. This interpretation is also consistent with other turbid and wellmixed environments (Fichez et al., 1992; Irigoien and Castel, 1997).

The outer zone showed relatively transparent waters $(Z_{eu} = 4-9 \text{ m})$ throughout the whole year. This is in agreement with data from a hydrographic study conducted within the inner shelf offshore Bahía Blanca estuary (Cuadrado et al., 2002), which reported low SMP values (21.6 mg L⁻¹) all over the water column. Thus, in these relatively clear waters, there is no obvious indication of light limitation.

According to our results, indirect evidences supporting the idea that the most important primary production occurs within the inner zone during the winter diatom bloom (i.e. higher biomass levels, favourable growth conditions as represented by euphotic to mixing depths ratio and nutrient levels) have been obtained. However, the observed biomass is the resultant of competing growth (primary production) and loss processes (grazing rates, advection). In this zone and during winter, the mesozooplanktonic grazing impact is usually lower than in other periods of year (Hoffmeyer, 1994). In addition, restricted circulation (tidal velocity is $0.69-0.77 \,\mathrm{m \, s^{-1}}$) (Pérez and Perillo, 1998), with a residence time close to 28 days (Perillo, personal communication), indicate suitable conditions for the development and persistence of autochthonous estuarine populations within the inner zone. On the other hand, the biomass at the middle zone seems to be strongly related to production processes of the inner zone, as well as to seawater intrusion mechanisms. Finally, and taking into account both the physical-chemical characteristics and phytoplankton behaviour within Bahía Blanca estuary, it can be concluded that the outer zone of the studied area seems to belong to the continental shelf.

Thus, and even though the boundaries corresponding to the zones identified in the present study are susceptible to variations resulting from the environmental dynamics (such as tidal stage, both velocity and direction of winds, storms, etc.), the behaviour of these zones may be differently interpreted in the light of the primary production perspective. This constitutes a significantly important requirement for the planning of future studies on the modelling of productivity and the trophic structures of both Bahía Blanca estuary and its neighbouring coastal area.

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C.A. Popovich, J.E. Marcovecchio / Continental Shelf Research 28 (2008) 236-244

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