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Seasonal and Tidal Dynamics of Water Temperature, Salinity, Chlorophyll-*a*, Suspended Particulate Matter, Particulate Organic Matter, and Zooplankton Abundance in a Shallow, Mixed Estuary (Bahía Blanca, Argentina)

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ABSTRACT

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Estuaries are characterized by a variety of interrelated, abiotic and biotic, structural components and intensive physical, chemical, and biological processes. The aim of this study was to investigate the seasonal- and tidal-mediated variability in water temperature, salinity, suspended particulate matter (SPM), particulate organic matter (POM), chlorophyll-*a* (Chl-*a*), and zooplankton abundance in the Bahía Blanca estuary, Argentina. The underlying mechanisms responsible for the observed variability are also discussed. Sampling was carried out every two months (December 2004–April 2006) during 14-h tidal cycles in a fixed station located in the inner zone of the estuary. Vertical profiles of temperature and salinity and water samples were obtained at the surface and the bottom to determine SPM, POM, Chl-*a*, and zooplankton. SPM (97.3 ± 6.9 mg L^{-1}) showed a strong seasonality, mainly attributed to biological activity. POM concentration (1539 ± 107.6 mgC m^{-1}) was high, possibly derived from vascular plants and benthic microalgae. Chl-*a* (6.91 ± 0.73 mg m^{-3}) and zooplankton (2024.23 ± 9.16 individuals m^{-3}) also showed a seasonal pattern, with higher concentrations in the summer. During the tidal cycle, the highest amounts of the measured variables were observed during the ebb tide. The results highlight the strong variability in the physicochemical and biological variables at different time scales in mesotidal, temperate estuaries. It is essential to take into account this variability in any monitoring program performed in a temperate system dominated by such a tidal regime.

ADDITIONAL INDEX WORDS: *Temporal dynamics, physicochemical variables, biological variables, estuarine system*

INTRODUCTION

Estuarine systems are transition areas between land and open sea, characterized by a variety of interrelated, abiotic and biotic, structural components and intensive physical, chemical, and biological processes (Marques *et al.*, 2006). Tides, winds, and riverine runoff are well-known phenomena that induce important environmental changes and lead to variability at various temporal scales (Chen *et al.*, 2010). Marine and freshwater influxes into the estuaries are especially involved in these regular environmental fluctuations, producing changes in the physicochemical and biological water properties. Whereas marine tidal cycles are generally predictable and reproducible, fluvial contributions are difficult to forecast because they respond to seasons and the variability of the precipitation regime throughout the watershed (Lam-Hoai, Guiral, and Rougier, 2006).

Short-term variability of water properties in estuaries is strongly influenced by the effect of tidal cycles. On a time scale of a few hours, ebb advection of freshwater and salt-water intrusion during the flood can be responsible for major changes in water temperature and salinity, suspended particulate matter (SPM), particulate organic matter (POM), and chlorophyll-*a* (Chl-*a*) concentrations (*e.g.,* Cloern, Powell, and Huzzey, 1989; De Jonge and van Beusekom, 1995; Grossart *et al.*, 2004; Magni, Montani, and Tada, 2002; McCandliss *et al.*, 2002; van Leussen, 1996; Velegrakis *et al.*, 1997). Moreover, these changes fluctuate according to spring-neap tidal state or amplitude, current velocities, winds, and precipitation rates (Magni, Montani, and Tada, 2002). In addition, the physicochemical variability is also reflected in the dynamics of the biological populations, particularly in the planktonic populations. The effect of tidal cycles in regulating estuarine zooplankton may be especially relevant in systems where the river discharge is relatively low (Menéndez, Piccolo, and Hoffmeyer, 2012).

The Bahía Blanca Estuary (BBE), located on the southwestern Atlantic Ocean in Argentina, is a mesotidal estuary, highly turbid, and characterized by an eutrophic inner zone (Marcovecchio *et al.*, 2009). The temporal and spatial dynamics of physicochemical (temperature, salinity, photosynthetic pigments, dissolved nutrients) and biological variables (phytoplankton, zooplankton) have been studied extensively (*e.g.,* Guinder, Popovich, and Perillo, 2009a; Perillo and Piccolo,

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1991; Perillo *et al.*, 2004; Piccolo and Perillo, 1990; Popovich *et al.*, 2008; Spetter *et al.*, 2013). However, few of these works have considered the short-term variability associated with tidal cycles. The aim of the present study was to investigate the seasonal- and tidal-mediated variability in water temperature, salinity, SPM, POM, Chl-*a*, and zooplankton in the inner zone of the BBE. This work is also a contribution to understanding not only the mechanisms responsible for this variability but also the interrelationship among variables. Future studies will be hampered by uncertainties at short-term time scales until the tidal variability of SPM, POM, Chl-*a*, and zooplankton are established. The results will enhance our understanding of the ecosystem as a whole and may be useful for future monitoring programs performed in similar, shallow, well-mixed, and tidal-dominated systems.

METHODS

In this section, the general characteristics of the study area, the data sources (collection of samples), and a comprehensive description of the applied methodological approach are described. The methodology consisted of analytical methods and statistical analysis.

Study Area

The BBE (38°45′–30°40′ S, 61°45′–62°30′ W) is located in a temperate region in the south of Buenos Aires Province, Argentina, on the southwestern Atlantic Coast (Figure 1). This temperate estuary covers an area close to 2300 km^2, which is formed by a series of NW–SE tidal channels separated by extensive intertidal flats, low marshes, and islands (Piccolo and Perillo, 1990). The main navigation channel of the estuary, Principal Channel, has a funnel shape, and it extends more than 80 km in a NW–SE direction, with depths between 3 and 20 m and a width varying from 200 m to 3–4 km (Perillo *et al.*, 2004; Piccolo and Perillo 1990) (Figure 1). The estuary has been reported to be a turbid, shallow, and homogeneous system, where semidiurnal tide and winds are the main factors controlling the water-turbulence processes (Piccolo and Perillo, 1990).

The primary energy inputs into the system are quasistationary and semidiurnal tidal waves (Piccolo and Perillo, 1990). The mean tidal range increases from the mouth of the estuary to the head (2.2 and 3.6 m, respectively) (Perillo *et al.*, 2004). Tidal currents are reversible with maximum velocities measured at the surface of about 1.3 m s^{-1} and maximum vertically averaged values of 1.2 and 1.05 m s^{-1} for ebb and flood conditions, respectively (Cuadrado, Gomez, and Ginsberg, 2005). The mean wind speed fluctuates between 22 and 24 km h^{-1} with prevailing wind directions from the NW, N, and NE. The strongest wind speeds come from the SE, especially in spring and summer. Winter is the season of the year that presents the lowest wind speeds and also more calm days (SMN, 1992). It is well known that when winds blow parallel to the main channel of the estuary, they interact with the tidal wave, generating leads, lags, and variations in the final tidal height in comparison with the forecasted one (Perillo *et al.*, 2004). In addition, winds affect the estuarine circulation, generating wind waves and interaction waves, which are produced at the interface of the winds and tides (Perillo and Piccolo, 1999).

Based on the salinity distribution, the inner zone of the BBE can be classified as a vertically mixed estuary during normal runoff conditions, but with a strong tendency to become partially mixed during rainfall periods (Perillo *et al.*, 2004). The annual mean precipitation of the region is 588 mm, occurring mainly in summer months (Gabella, Zapperi, and Campo, 2010). The study area is highly influenced by El Niño-Southern Oscillation (ENSO) events, being a key factor in the interannual climate variability by affecting the total amounts of precipitations (Aceituno, 1988; Grimm, Barros, and Doyle, 2000). Freshwater inflow into the estuary is low and is mainly contributed by the Sauce Chico River and the Napostá Grande Creek, which provide an annual mean runoff of 1.9 and 0.8 m^3 s^{-1}, respectively (Perillo *et al.*, 2004). There are also a series of small tributaries that may input minor quantities of runoff activated by local rainfalls (Perillo and Piccolo, 1999).

Collection of Samples

Sampling was carried out every 2-months between December 2004 and April 2006 in a fixed station located in the inner zone of the estuary (Puerto Cuatreros, Figure 1). All sampling was performed during the day, every 3 h for a period of 14 h, beginning approximately at the midflood stage. The sampling dates were selected to coincide with the transition from spring to neap tides. Vertical profiles of water temperature and salinity (interval: 1 m) were obtained using a digital multisensor Horiba U-10. However, given the homogeneity of the water column, only surface and bottom data were used. SPM, POM, Chl-*a*, and phaeopigment concentrations were determined with water samples collected near the surface (about 0.50 m depth) and 1 m above the bottom with two submersible pumps. A reinforced polyvinyl chloride (PVC) hose linked the pumps to 200-μm pore-size plankton nets, which were used to obtain zooplankton samples. A detailed description of the procedure can be found in Menéndez *et al.* (2012) and Menéndez, Piccolo, and Hoffmeyer (2012). No field data for the entire tidal cycle of February and June 2005 are available because of equipment problems.

Tidal height was continuously measured with a tidal gauge located *in situ* at Puerto Cuatreros during all sampling period. Continuous measurements of meteorological variables (*i.e.* air temperature, wind speed, and direction) were recorded with an automatic weather station (Weather Monitor II Station). This station, placed at Puerto Cuatreros, was equipped with a temperature sensor developed at the Instituto Argentino de Oceanografía. All sensors have a measuring frequency of 10 minutes.

Analytical Methods

The SPM water content (in milligrams per liter) was determined as dry weight (60°C, 24 h) after filtration of 250 mL of water through previously dried and weighed Whatman GF/C filters (pore diameter: 0.45 μm). Water samples for POM analysis were filtered (250 mL) through muffled (450–500°C, 1 h) Whatman GF/C membranes (1.2 mm), and the filters with the retained material were frozen (–20°C) (Clesceri, Greenberg, and Eaton, 1998). POM concentration was measured following the Strickland and Parsons (1968) protocols (range of 10–4000

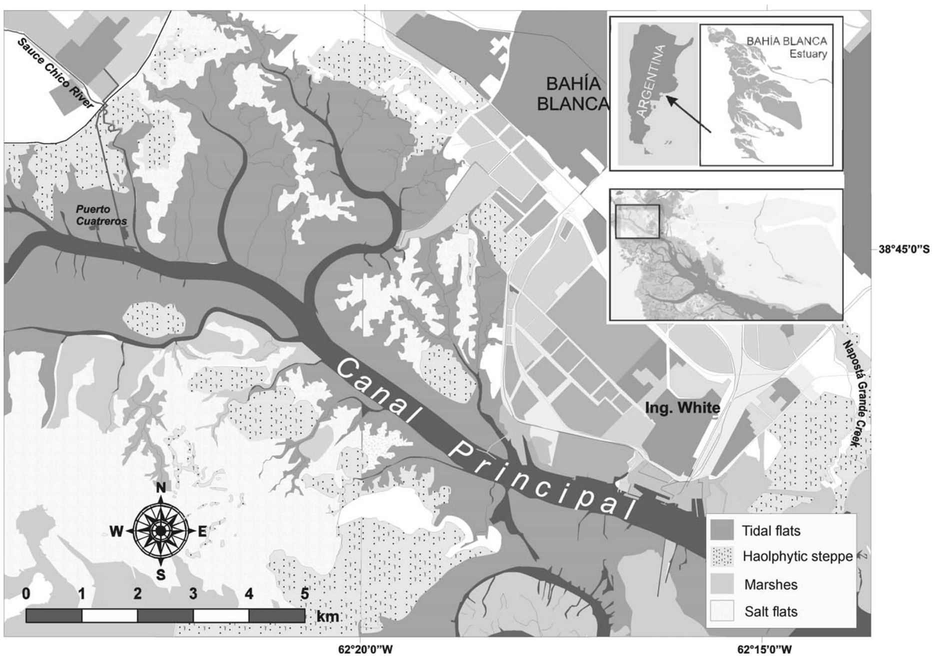

Figure 1. General map of the inner zone of the Bahía Blanca estuary (BBE) and location of the fixed sampling site, Puerto Cuatreros. In the upper right corner: general location of the BBE in Argentina.

mgC m^{-3}), using a Beckman DU-II ultraviolet-visible spectrophotometer.

Chl-a and phaeopigments concentrations (milligrams per cubic meter) were measured spectrophotometrically following the methods described in APHA (1998). Water samples (250 mL) were filtered through Whatman GF/C filters, which were immediately frozen and stored at –20°C. Pigment extraction was done in 90% acetone for 20 minutes at environmental temperatures. Zooplankton samples with high abundances were further subsampled (1/10). In the case of samples with low abundances, the entire sample was examined. Abundance was calculated as the number of individuals per cubic meter of water filtered through the nets.

Statistical Analysis

Most of the variables (SPM, POM, Chl-a, phaeopigments, and zooplankton) were analyzed using nonparametric analysis of variance (ANOVA) because of the rejection of the normality assumption (Kolmogorov-Smirnov test). Data were tested for homogeneity of variance using the Levene's test. The Kruskal-Wallis and the Mann-Whitney U test were used to determine whether there were distributional differences among three sampling settings: (1) four seasons, (2) five tidal phases (flood, high tide, ebb, low tide, and flood), and (3) two depths. When ANOVA results were significant, a multiple means comparison, using Dunn's test, was carried out (Hollander and Wolfe, 1999). Multivariate statistical analyses were performed using the PRIMER-E software package (Clarke and Warwick, 1994). A Principal Component Analysis (PCA) using Spearman's rank-correlation matrix was performed on the environmental data set to (1) explore relationships between variables, and (2) identify the major sources of variation. The first two components were retained because they explained a significant part of the total variation. Plotted variables showed a reconstruction percentage higher than 50% in the two-dimensional plot.

RESULTS

The following paragraphs describe the seasonal and tidal dynamics of temperature, salinity, SPM, POM, Chl-a, phaeopigments, and zooplankton abundance in Puerto Cuatreros. The results are divided into three subsections: the physical environment comprises the description of the meteorological and hydrological data, whereas seasonal and tidal analyses describe the dynamics of SPM, POM, Chl-a, phaeopigments, and zooplankton at these particular time scales.

Physical Environment: Meteorological and Hydrographical Data

Meteorological conditions during the sampling days are showed in Figure 2. Maximum air temperatures were observed in February 2005 and 2006 (26.7°C and 25.2°C, respectively) followed by December 2005 (22.9°C). In December 2004, relative low-temperatures were observed for typical summer conditions because of strong winds blowing from the sea (SE). The lowest air temperatures were registered in June 2005 (8.3°C).

The NW continental winds dominated most of the study period (33.4%). Mean daily wind speed varied between 5.6 (April 2006) and 23.7 km h^{-1} (December 2004) (Figure 2B). The lowest velocities ($<$10 km h^{-1}) were registered in June 2005 (N) and April 2006 (NNE). The strongest wind speeds occurred in December 2004 (SE) and August 2005 (NW), with mean values

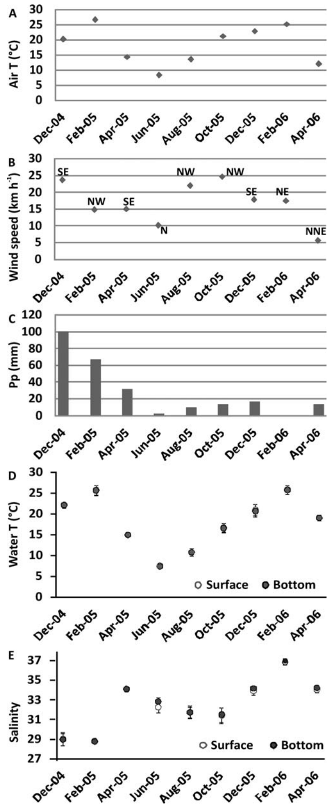

Figure 2. (A–C) Meteorological and (D and E) hydrographical conditions on the days measurements were taken. (A) Daily mean air temperature (°C). (B) Daily mean wind speed (km h^{-1}) and predominant direction. (C) 30 d precipitation (mm) before the day measurements were taken. (D) Daily mean water temperature (°C) of the bottom and surface waters. (E) Daily mean salinity at the bottom and surface. Abbreviations: T = temperature, Pp = precipitation.

of 23.7 and 22 km h^{-1} and gusts up to 60 and 48 km h^{-1}, respectively. Substantial differences were detected between the predicted astronomical tide and the measured tide records, which were more pronounced in days with high wind velocities. Strong SE winds produced a height increase over the tidal prediction, whereas NW winds caused the opposite effect.

During the study period, precipitation was characterized by a strong interannual and seasonal variability (Figure 2C). Maximum records were detected in December 2004 and February 2005, reaching 100 and 65 mm, respectively. On the other hand, in the following summer, low amounts were registered (17 mm in December 2005, and no precipitations in February 2006). Winter was the driest period, with a total precipitation of 4 mm in June 2005 and 8 mm in August 2005.

Water temperature throughout the sampling period varied between 7.1°C and 27.1°C. The highest mean ± SE values were recorded in February 2005–06 (25.7 ± 0.6°C and 25.7 ± 0.4°C, respectively), and the lowest temperatures were in June 2005 (7.5 ± 0.12°C) (Figure 2D). Vertical profiles of water temperature did not indicate stratification, and they were homogeneous throughout the year, with differences between surface and bottom less than 0.1°C m^{-1}. Maximum daily temperature amplitude was observed in summer, reaching a range of 3.5°C (Figure 2D).

Annual and seasonal salinity changes were strongly related to local precipitation (Figure 2E). The lowest values were measured in December 2004 and February 2005 (surface: 29 ± 0.67 and 28.8 ± 0.17; bottom: 28.9 ± 0.61 and 28.7 ± 0.21, respectively), and the highest ones were in February 2006 (surface: 36.8 ± 0.2; bottom: 37 ± 0.2) (Figure 2E). Mean vertical gradients were less than 0.15 m^{-1}, indicating homogeneous conditions in the water column. At the tidal time scale, salinity generally increased during high tide and decreased during low tide (range: 0.3–4.8). An opposite trend was observed in December 2005 and February 2006. The mean salinity gradient between high and low water ranged up to 4.8 at both depths.

Seasonal Analysis

SPM showed strong seasonality, with minimum values in winter (2–34.8 mg L^{-1}) and maximum in the summer months (50.7–275.2 mg L^{-1}) (Kruskal-Wallis test, $Z = 52.87$, $p < 0.001$; Figure 3A). The highest concentration was registered in February 2005, near the bottom, being almost twofold greater than the annual mean (96.9 mg L^{-1}). However, no statistical differences among depths were detected during the study period (Mann-Whitney U test, $Z = 823$, $p = 0.385$). The SPM decreased during winter, and low levels persisted during that season, being considerably less than the annual mean (Figure 3A). The Spearman rank-correlation test revealed that SPM was significantly correlated with water temperature, salinity, Chl-*a*, phaeopigments, POM, and zooplankton abundance (in all cases, with $p < 0.01$) (Table 1).

POM concentrations ranged from 172 to 3441 mgC m^{-1}. The highest amounts were registered in December 2004–05, February 2006 and April 2006, in all cases near the bottom (Figure 3B). The lowest concentrations were recorded in June 2005. Kruskal Wallis test determined significant differences in POM values between seasons ($Z = 16.5$, $p < 0.05$; Figure 3B) but no statistical differences were detected among depths (Mann Whitney U-test, $Z = 561$, $p = 0.185$). POM was significantly correlated with water temperature, salinity, SPM, and zooplankton ($p < 0.01$) (Table 1).

Mean Chl-*a* values fluctuated between 1.38 ± 0.2 mg m^{-3} in June 2005 and 27.53 ± 4.5 mg m^{-3} in February 2005 (Kruskal-Wallis test, $Z = 34.51$, $p < 0.001$; Figure 3C). The Chl-*a* seasonal pattern was characterized by a marked late-summer peak (February 2005–06). However, Chl-*a* concentrations in February 2005 were about twice as high as they were in 2006. Two lower peaks occurred in December 2004 and April 2006. The Mann-Whitney U test did not reveal significant differences between depths ($Z = 922$, $p = 0.867$). In the Spearman correlation analysis, Chl-*a* appeared to be significantly correlated with water temperature, phaeopigments, SPM, and zooplankton ($p < 0.01$) (Table 1).

Mean phaeopigments varied between 0.43 ± 0.19 and 14.22 ± 4.87 mg m^{-3} (Figure 3D). The highest amounts were also recorded in late summer (February 2005–06), with the lowest ones during winter months (Kruskal-Wallis test, $Z = 19.02$, $p < 0.001$; Figure 3D). Nevertheless, high values were also detected in April 2005 and October 2005. The Mann-Whitney U test did

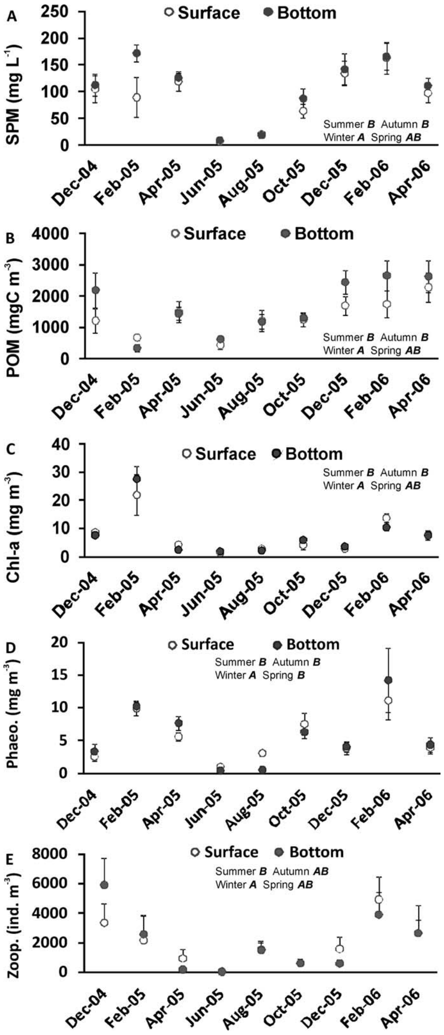

Figure 3. Daily mean values of physicochemical and biological variables between December 2004 and April 2006 in the study area. (A) SPM (mg L^{-1}), (B), POM (mgC m^{-3}), (C) chlorophyll-*a* (mg m^{-1}), (D) Phaeopigments (mg m^{-3}), and (E) zooplankton abundance (individuals m^{-3}). Concentrations/abundances with the same bold, italicized letters do not significantly differ using Dunn's test. Abbreviations: SPM = suspended particulate matter, POM = particulate organic matter, Chl-*a* = chlorophyll-*a*, Phaeo = phaeopigments, Zoop = zooplankton abundance.

not find significant differences between depths ($Z = 544$, $p = 0.437$). Phaeopigments were significantly correlated with water temperature, Chl-*a*, SPM, and zooplankton ($p < 0.01$) (Table 1).

Zooplankton abundance ranged between 20.2 ± 8.5 and 5923.4 ± 1805.8 individuals m^{-3}, evidencing strong temporal variation (Figure 3E). The highest values were observed during summer to early autumn (December 2004, February 2005–06, and April 2006), whereas the lowest ones were in June 2005. Seasons were a significant source of variation (Kruskal-Wallis test, $Z = 16.37$, $p < 0.001$; Figure 3E); moreover, no significant differences were detected between depths (Mann-Whitney U test, $Z = 0.37$, $p = 0.356$). Zooplankton abundance was significantly correlated with water temperature, Chl-*a*, SPM, and POM ($p < 0.01$) (Table 1).

PCA: Relationships Among Variables

The PCA highlighted the temporal dynamics of the physicochemical and biological variables and the correlations among them (precipitations, water temperature, salinity, SPM, POM, Chl-*a*, phaeopigments, and zooplankton) (Figure 4A). The first two components explained, respectively, 49.58% and 24.68% of the total variance. The first axis (F1) was positively related to water temperature, Chl-*a*, SPM, zooplankton abundance, and phaeopigments (contributions of 21.1%, 19.16%, 18.52%, 15.52%, and 13.81% to F1). These variables displayed strong correlations with one another (Table 1). The second axis (F2) was positively related to salinity and POM (contributions of 45.45 and 18.6%, respectively) (Figure 4A). On the other hand, precipitation was strongly correlated with the negative axis of F2. The sampling dates were also clearly separated along F1 (Figure 4B), plotting the summer months on the right side of the plot (positive axis) and the winter months on the left side (negative axis). The first group displayed the highest water temperatures and zooplankton abundances, and elevated SPM, Chl-*a*, and phaeopigments concentrations. The second group, which comprised mainly winter samples, exhibited the opposite characteristics. Two other groups could be identified on both sides of the F2 axis. The first one included autumn and summer months (December 2005, February 2006) and was characterized by high salinity and POM concentration, and low precipitations. The second group comprised summer months with low salinities (high precipitations) and POM concentrations.

Tidal Analysis

During the tidal cycle, the general pattern of SPM appeared to be controlled mainly by current velocities, because the

Table 1. *Spearman's correlation matrix. In bold type are significant correlation values (p < 0.001).*

Variables	T (°)	Salinity	SPM	POM	Chl-*a*	Phaeopigments	Zooplankton Abundance
T°	–						
Salinity	0.088	–					
SPM	**0.754**	**0.313**	–				
POM	**0.308**	**0.382**	**0.5**	–			
Chl-*a*	**0.744**	−0.133	**0.532**	0.043	–		
Phaeopigments	**0.51**	**0.258**	**0.451**	0.151	**0.359**	–	
Zooplankton abundance	**0.62**	0.013	**0.503**	**0.413**	**0.485**	**0.293**	–

Abbreviations: T = water temperature, SPM = suspended particulate matter, POM = particulate organic matter, Chl-a = chlorophyll-a.

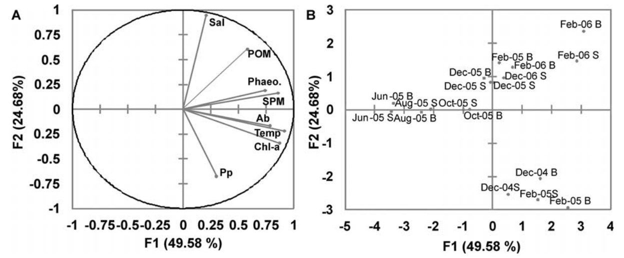

Figure 4. Results of the principal components analysis. Principal components 1 and 2 (F1, F2) are plotted with the correlation circle (A) and for the samples (B). Abbreviations: Temp = water temperature, Sal = salinity, Chl-*a* = chlorophyll-*a*, Phaeo = phaeopigments, POM = particulate organic matter, SPM = suspended particulate matter, Pp = precipitations, S = surface, B = bottom.

highest concentrations occurred during the ebb tide (134–158 mg L^{-1}) and the flood tide (90–121 mg L^{-1}) (Figure 5A). The lowest concentrations were registered near the high tide (65–102 mg L^{-1}). However, no statistical differences were detected between tidal stages (Kruskal-Wallis test, $Z = 8.12$, $p = 0.087$). A different pattern was observed in June 2005, with the maximum SPM concentrations during high tide (bottom) and low tide (surface). SPM spatial distribution indicated that maximum values were generally detected near the bottom with the exception of low tide, when maximum values were observed at the surface (Figure 5A). The range between both layers oscillated between 9 and 36 mg L^{-1}.

Similar to SPM, POM showed maximum values during the ebb (2146–2411 mgC m^{-3}) and flood (1409–2226 mgC m^{-3}) tides (Figure 6A). However, the Kruskal-Wallis test did not detect significant differences between tidal stages ($Z = 4.73$, $p = 0.316$). On the other hand, the POM greatest concentration was reached during high tide in April 2005 and June 2005, whereas lower values were observed during the other tidal stages (Figures 6B and C). In general, higher concentrations of POM were recorded near the bottom, reaching maximum differences between both layers during the low tide (867 mg Cm^{-3}) (Figure 6).

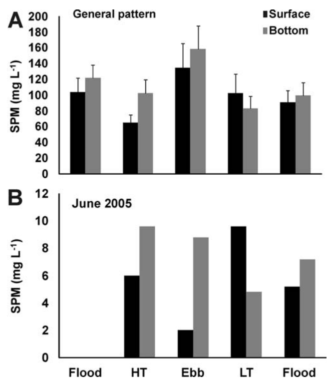

Figure 5. Suspended particulate matter (SPM) tidal cycle dynamics. (A) General pattern (means ± SE).(B) SPM concentration during June 2005. Abbreviations: HT = high tide, LT = low tide, SE = standard error.

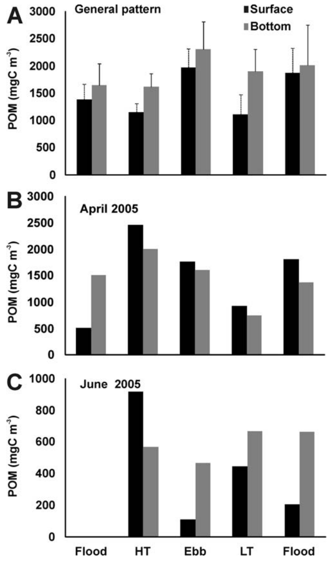

Figure 6. Particulate organic matter (POM) tidal cycle dynamics. (A) General pattern (means ± SE). (B) POM concentration during April 2005. (C) POM concentration during June 2005. Abbreviations: HT = high tide, LT = low tide, SE = standard error.

Short-term Chl-*a* behavior was characterized by a strong gradient along the tidal cycle. The highest amounts were detected during the ebb tide, reaching mean values of 11.53 and 10.64 mg m^{-3} at the surface and bottom, respectively (Figure 7). Nevertheless, Kruskal-Wallis test failed to detect significant differences among tidal phases ($Z = 6.32$, $p = 0.176$). The general variation in phaeopigments was not considerable because differences in total amounts were less than 2 mg m^{-3} between tidal stages (Figure 8). Maximum vertical differences were observed during the ebb (2.3 mg m^{-3}) and floods (1.3–4.3 mg m^{-3}) tides, with higher concentrations near the bottom. However, during high and low tides, slightly higher amounts were detected at the surface.

Zooplankton abundance was markedly greater at the surface during the ebb tide (4013.03 ± 1298.15 individuals m^{-3}) (Figure 9). Lower values were recorded during high (309.25 ± 78.52 individuals m^{-3}) and low (379.11 ± 178.3 individuals m^{-3}) tides (Figure 9). The Kruskal-Wallis test revealed

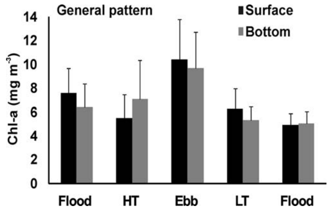

Figure 7. General pattern (means ± SE) of chlorophyll-*a* (Chl-*a*) concentration during the tidal cycle. Abbreviations: HT = high tide, LT = low tide, SE = standard error.

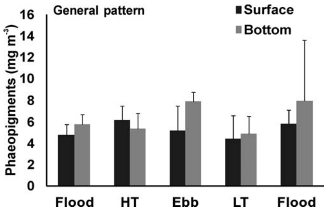

Figure 8. General pattern (means ± SE) of phaeopigments concentration during the tidal cycle. Abbreviations: HT = high tide, LT = low tide, SE = standard error.

significant differences in mean abundance between tidal phases ($Z = 12.89$, $p < 0.05$; Figure 9).

DISCUSSION

In this section, we discuss the main results related to water temperature and salinity dynamics and the seasonal and tidal-scale variability of SPM, POM, Chl-*a*, and zooplankton abundance.

Water Temperature and Salinity

The BBE is a turbid, shallow, and homogeneous system, in which the semidiurnal tide and atmospheric conditions are the major forces controlling the physicochemical and biological processes. Air temperature was highly coupled with water temperature on a seasonal and tidal scale, reaching maximum values in February 2005 and minimum ones in June 2005. Variability of the tidal-water temperature depended mainly on atmospheric heat transfer during the day; therefore, maximum temperatures were reached between 1700 and 1900 hours as a result of heat accumulation during daylight hours. Furthermore, maximum daily amplitudes occurred in spring and summer, when the net radiation budget was higher (Beigt, Piccolo, and Perillo, 2008).

According to Piccolo and Perillo (1990), the restricted water circulation, as well as the evaporation processes, increases the salt concentration levels in the inner zone of the BBE, producing greater salinities than in the adjacent open sea. Moreover, the high temperatures and low precipitation contribute greatly to this scenario. In this study, salinity showed high seasonal amplitude (~9), tightly related to local precipitation. The lowest value was registered in summer 2005, when maximum precipitation was observed. On the other hand, salinity values in summer 2006 reached 37 (hypersaline), when minimum precipitation occurred. The high interannual variability of the amounts of precipitation and the anomalous extreme rainfall events took place mainly in spring and summer (*e.g.,* Scian, 2002), which is considered a key factor in determining the expected salinity in the BBE system. On a tidal scale, salinity was related to the tidal height, showing the lowest values at low tide because of the advection of riverine runoff in the inner zone of the estuary. Thus, salinity ranges were positively related with tidal ranges. An opposite trend was observed in December 2005 and February 2006 (hypersaline summer), when salinity values were higher in the inner zone than those described for the adjacent continental shelf sea (Martos and Piccolo, 1988).

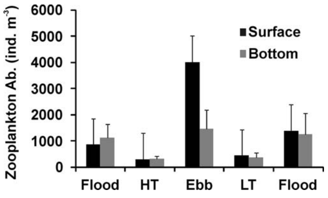

Figure 9. General pattern (mean values ± standard error) of zooplankton abundance during the tidal cycle. Abundances with the same bold, italicized letters do not significantly differ using Dunn's test. Abbreviations: HT = high tide, LT = low tide, Ab = abundance.

Seasonal Analysis: SPM, POM, Chl-*a*, and Zooplankton Abundance

As discussed by others (*e.g.*, Gardner *et al.*, 1989; Hutchinson, Sklar, and Roberts, 1995; Kim, Kim, and Noh, 2011; Murphy and Voulgaris, 2006; Wolaver *et al.*, 1988), SPM varied in response to the season, with maximum concentrations in the summer and minimum levels during winter months. In other similar coastal ecosystems, the SPM dynamics are essentially driven by river discharge (Postma, 1967); nonetheless, the freshwater inflow is generally low in the BBE, so river runoff has not been considered a significant source of SPM. On the other hand, and in contrast to earlier findings in the study area (Guinder, Popovich, and Perillo, 2009a), no relationship between precipitation and SPM seasonal dynamics was found because high SPM concentrations were registered in a dry summer (2005–06). The seasonal variability of the SPM could, in part, be attributed to biological activity because maximum SPM amounts coincided with peaks of Chl-*a* and zooplankton. Summer conditions in the BBE enhance biological productivity, and planktonic community abundance increases (Hoffmeyer *et al.*, 2009). Additionally, the influence of microphytobenthic community can be considered. This community is responsible of the secretion of large amounts of extracellular polymeric substances, which build a biofilm that stabilizes the sediment (Pan *et al.*, 2013; Stal, 2010). In the estuary, the biovolume of this community by total biomass is considerably less in the summer (Pan *et al.*, 2013); thus, the biofilm is thinner, allowing the bed to remobilize and higher amounts of SPM in the water column.

On the other hand, macrofaunal bioturbation can desestabilize cohesive sediments, which directly affect sediment porosity and permeability (Widdows *et al.*, 1998) and indirectly affect sediment transport (Escapa, Perillo, and Iribarne, 2008; Wood and Widdows, 2002). The burrowing activity of the crab *Neohelice granulata* (the most important bioturbator in the BBE), which is high in summer months, would expose sediments to water flows, mainly by the generation of biogenic mounds (Escapa, Perillo, and Iribarne, 2008). The burrow density and intensity vary seasonally, enhancing sediment trapping in winter and favoring sediment transport in summer (Escapa, Perillo, and Iribarne, 2008). In addition, the disaggregation of the marsh surface by *Spartina alterniflora*, with maximum activity also occurring in the summer months (Gonzales Trilla *et al.*, 2009), could contribute to the increase in sediment concentration in the water column. Finally, because the strong SE and NW winds, typical of spring and summer, affect the estuarine circulation of waves, storm surges, and sea-level variations (Perillo and Piccolo, 1999), the winds may collaborate with the erosion of the tidal flats and salt marshes by bed remobilization. It is, therefore, possible to hypothesize that the BBE in summer is a source of SPM, and it exports sediment offshore. Meanwhile in winter, the SPM source could be the open sea, and the estuary may act as a sink for sediments.

In the inner zone of the BBE, POM concentrations were relatively high in comparison with other similar ecosystems (*e.g.,* Calliari *et al*., 2005; Goosen *et al*., 1999; Hemminga *et al*., 1993). This estuary is highly eutrophic because of the external inputs of nutrients and organic matter from diverse anthropogenic sources: petrochemical industries, oil refineries, silos and cereal mills, fertilizers from agricultural activities, and urban wastewaters (Marcovecchio *et al*., 2009). However, the estuary is also productive because of the presence of extensive tidal flats and islands partially covered by halophytes such as *Sarcocornia perennis* and *S. alterniflora*, which are responsible of large contributions of organic matter into the system (Marcovecchio *et al*., 2009). The low phytoplankton biomass reported in the inner zone (Guinder, Popovich, and Perillo, 2009a), support that vascular plants and possibly benthic microalgae are alternative sources that keep the high levels of organic matter into the estuary. Also, because bottom resuspension is substantial because of the intense water turbulence induced by tides and winds, the close benthic–pelagic interaction may have an important role in nutrient regeneration and carbon cycling, as has been observed in other shallow coastal ecosystems with high microphytobenthos production (de Jonge and van Beusekom, 1992; Kromkamp *et al*., 1995).

Phytoplankton community in the BBE has been characterized by a marked, recurrent pattern, with a single winter–early spring diatom bloom (*e.g.,* Guinder, Popovich, and Perillo, 2009a; Popovich *et al.,* 2008; Spetter *et al*., 2013). The bloom has been attributed to a high nutrient concentration and the relaxation of zooplankton grazing pressure because of the low water temperatures (Popovich *et al*., 2008). Recently, Popovich, Guinder, and Petigrosso (2009) referred to changes in the seasonal succession pattern of phytoplankton from 2003 to 2007. The main discrepancy in the annual pattern was the decrease or absence of the winter–early spring bloom, the decreasing or disappearance of typical blooming species, the occurrence of short biomass peaks throughout the year, and the presence of a few uncommon diatom species in the system that became most abundant in summer and autumn (Popovich, Guinder, and Petigrosso, 2009). In this study, maximum values of Chl-*a* were observed in summer (February 2004–05) rather than in winter, supporting the tendency of the winter bloom to be absent or to diminish. Even though sampling had a frequency of every 2 months, Chl-*a* values in August 2005 were also low compared with summer levels.

Zooplankton showed a clear seasonal pattern with higher abundance in warmer months, a condition that is well known in this and some other temperate estuaries (*e.g.,* Leandro *et al*., 2007; Marques *et al*., 2009; Menéndez, Piccolo, and Hoffmeyer, 2012; Vieira *et al*., 2003). Because of tight physicobiological coupling, temperate coastal ecosystems often exhibit strong spatiotemporal gradients in both environmental variables and zooplankton assemblages (Marques *et al*., 2007). In this study, water temperature seemed to be the most important factor in determining the seasonality of zooplankton abundance. This is in agreement with the results of other studies in similar areas (Vieira *et al*., 2003; Villate, 1994), which demonstrated that water temperature enhances metabolic processes (Leandro *et al*., 2007; Marques *et al*., 2009). Phaeopigment concentration in this study showed peaks during spring and summer, which could indicate high zooplankton grazing pressure or more-intense resuspension of bottom sediments, rich in degraded chlorophyll derived from the senescence of phytoplankton, microphytobenthos, and macrophytes.

Tidal Time-Scale Analysis: SPM, POM, Chl-*a*, and Zooplankton Abundance

In tidally dominated estuaries, the spatial and short-term temporal variations in SPM concentrations mainly depend on two mechanisms, the horizontal advection and the resuspension (Velegrakis *et al*., 1997). In the present study, maximum SPM values were generally observed in association with the time of high current velocities, mainly during the ebb, thus tidal currents are considered to be the main hydrodynamic factor controlling SPM dynamics (horizontal advection). The variation in SPM concentration reached up to twofold between ebb and flood tides and high and low tides. The increasing current velocity controlled by tides and winds (van Leussen, 1996), leads to stronger shear forces, resulting in resuspension of sediments, which could explain the observed changes in SPM at this fine temporal scale. Furthermore, the maximum abundance of SPM was observed near the bottom, indicating the recent resuspension of the sediment matter. These results agree with those reported by Cloern, Powell, and Huzzey (1989) and Velegrakis *et al*. (1997) for the San Francisco Bay (USA) and the English Channel (United Kingdom), which recorded the highest concentrations of SPM during the peak energy of the tidal cycle. In the Wadden Sea (Germany), Grossart *et al*. (2004) also addressed that maximum sediment matter was observed during the ebb tide and near the bottom when maximum shear rates occurred. In the present study, the opposite tendency occurred in June 2005, when maximum concentrations of sediment matter were registered during the high tide. As explained in the previous section, winter season presents the lowest abundance of SPM, mainly because of the stabilization of the sediment caused by the biofilm buildup, the low borrowing activity of crabs, and the lower wind conditions, which diminish the strength of the shear forces (waves and tides). Consequently, during winter, the source of sediment for the system is the open sea instead of the inner zone of the estuary; therefore, the highest concentrations are reached during high tide and probably deposited on the tidal flat during the inundation.

Similar to SPM short-term dynamics, the variability of POM was strongly affected by the tidal rhythm, especially by the ebb conditions. In most sampling dates, maximum POM concentrations were detected in association with maximum current velocity, with greater amounts near the bottom. Similar tidal-driven POM dynamics have been observed in other estuaries (*e.g.,* Grossart *et al*., 2004; McCandliss *et al*., 2002; Roman and

Daiber, 1989). The increasing quantity of POM during the ebb tide can be attributed to a resuspension of the organic matter–rich benthic layer, as reported by McCandliss *et al*. (2002) for the coastal North Sea in The Netherlands. Moreover, the transport of marsh-derived organic matter toward adjacent estuarine water systems could be an alternative source of POM (Hemminga, Cattrijsse, and Wielemaker, 1996). Detritus may be washed out efficiently from the marsh because of its longer exposure to the tidal energy (Bouchard and Lefeuvre, 2000), one of the most important factors regulating material fluxes from marshes to adjacent waters (Minchinton, 2006; Odum, 2000). Accordingly, Negrin *et al*. (2011) reported an efficient exchange between pore water and the overlying water in a lower marsh of the BBE, with a consequent greater export of POM from the marsh sediments over each tidal cycle (Hemminga, Cattrijsse, and Wielemaker, 1996). During the sampling dates corresponding to April and June 2005, we did not observe a tide-related distributional pattern of POM. In these cases, resuspension of the benthic-layer appeared to be of minor relevance, probably because the surface of the benthic layer is firmer during the growing season of epibenthic microalgae (Grossart *et al*., 2004; Noffke *et al*., 2001).

Chl-*a* varied also periodically with tidal dynamics (increasing on ebbing currents), suggesting that the short-term variability may result from the tidal advection (Cloern, Powell, and Huzzey, 1989). Several mechanisms are related to the short-term variations of phytoplankton in estuaries, including tide- and wind-driven resuspension, diel growth, synthesis and grazing cycles, and vertical migrations (Cloern, Powell, and Huzzey, 1989). However, the cyclic pattern of Chl-*a* observed in this study suggests that the redistribution of phytoplankton biomass by tidal currents is the most important mechanism in the inner zone of the estuary. Because the phytoplankton community of the BBE is mainly represented by diatoms species (Guinder, Popovich, and Perillo, 2009; Popovich *et al*., 2008), which behave as relatively passive particles, their concentration and distribution depend mainly on water displacements. Thus, resuspension may also be an important driver of local variability because Chl-*a* concentrations were also high near the bottom during the ebb tide. Accordingly, Guinder, Popovich, and Perillo (2009b) addressed the presence of benthic diatoms as *Gyrosigma* sp., *Fragilaria* spp., *Nitzschia* spp. and *Surirella* sp. in bottom samples of the BBE during the tidal cycle. This is common in other shallow coastal systems, such as the SE English Channel, where benthic species are released into the water column because of resuspension processes induced by tides (Brunet and Lizon, 2003). Tidally driven resuspension is presumed to be a primary mechanism of Chl-*a* variability not only in shallow estuaries but also in shallower parts of deeper estuaries (such as tidal flats) (Desmit *et al*., 2005). De Jonge and van Beusekom (1992) observed that, in tidal flats of the Ems estuary (Netherlands/Germany), the fluxes of microphytobenthos between sediment and water from tidal and wind effects had a crucial role in the system. A clear difference with this study is that, in the Ems estuary, tidal currents were of minor importance compared with wind speeds (De Jonge and van Beusekom, 1992). In opposition to what happened with SPM and POM dynamics, Chl-*a* in the BBE was slightly higher near the surface, suggesting that advection could be the principal mechanism involved in Chl-*a* short-term variability.

Zooplankton abundance in the inner zone of the BBE seemed to be strongly affected by semidiurnal tidal cycles, as was discussed by Menéndez, Piccolo, and Hoffmeyer (2012) and Menéndez *et al*. (2012) in two previous studies closely related to this one. Similar to what was observed for SPM, POM, and Chl-*a*, the greatest abundances of planktonic organisms coincided with the time of peak current velocities. However, the patterns of SPM and POM did not match exactly with the Chl-*a* and zooplankton behavior. Contrary to what occurs with SPM and POM, Chl-*a* concentration and zooplankton abundance were always greater near the surface during the ebb tide. For zooplankton, this pattern suggests the occurrence of an additional mechanism to the hydrodynamic processes that would maintain populations in the inner zone of the BBE. As was discussed by Menéndez, Piccolo, and Hoffmeyer (2012) and Menéndez *et al*. (2012), the highest zooplankton abundance was observed in a zone of net residual landward flow. This has been interpreted as a feature that prevents individuals from being washed out of the estuary, considering that landward residual currents help to maintain populations within the estuaries (Castel and Veiga, 1990; Menéndez, Piccolo, and Hoffmeyer, 2012; Menéndez *et al*., 2012). Additionally, Menéndez *et al*. (2012) associated the increment in abundance during the ebb tide with a lateral movement of organisms to areas of decreased flushing, such as channel margins, where the fixed sampling site coincides with a margin of the main channel. The greater proportion of zooplankton near the surface would reduce the advective losses and may be associated with a mechanism or strategy to avoid outward advection by bottom currents during the receding tide. This option has been suggested for some copepod species to resist the seaward net flow during the ebb (Castel and Veiga, 1990; Cronin, Daiber, and Hulbert, 1962; Menéndez *et al*., 2011; Roddie, Leakey, and Berry, 1984).

CONCLUSIONS

This study presents for the first time, to our knowledge, a comprehensive analysis of the seasonal and tidal-time variations of some abiotic and biotic variables in the inner zone of the BBE. The results demonstrated that water temperature, salinity, SPM, POM, Chl-*a*, and zooplankton abundance exhibited not only pronounced seasonal differences but also significant variations at a short-term time scale. Certain local environmental conditions of the estuarine system, such as a relatively low fluvial contribution, may be helpful in other similar estuaries of the world to explain the behavior of the physicobiological variables. For example, SPM and POM seasonal distribution were highly related to biological community activity, but not to the expected fluvial regime.

The variables were strongly influenced by semidiurnal tidal cycles, especially by the ebb conditions. The highest concentrations of SPM, POM, Chl-*a*, and zooplankton were detected during the ebb tide, suggesting that local hydrological conditions are responsible for the spatial (vertical) variations. These results highlight the major role of the tidal cycle in estuaries with low riverine input. To summarize, this study emphasized the strong variability that the physicochemical and biological parameters can present over different time scales in mesotidal, temperate estuaries. This variability must be accounted for in any monitoring program performed in a temperate system dominated by such a tidal regime.

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