

# Short-term variability on mesozooplankton community in a shallow mixed estuary (Bahía Blanca, Argentina): Influence of tidal cycles and local winds

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## ABSTRACT

The short-term dynamics of zooplankton in coastal ecosystems are strongly influenced by physical processes such as tides, riverine runoff and winds. In this study, we investigated the short-term changes of the representative taxa within mesozooplankton in relation to the semidiurnal tidal cycles. Also, we evaluated the influence of local winds on this short-term variability. Sampling was carried out bimonthly from December 2004 to April 2006 in a fixed point located in the inner zone of the Bahía Blanca Estuary, Argentina. Mesozooplankton samples were taken by pumps during 14-h tidal cycles at 3-h intervals, from surface and bottom. Vertical profiles of temperature and salinity as well as water samples to determine suspended particulate matter were acquired at each sampling date. All data concerning winds were obtained from a meteorological station and water level was recorded with a tide gauge. Holoplankton dominated numerically on meroplankton and adventitious fraction. Concerning holoplankton abundance, the highest values were attained by the calanoid copepods *Acartia tonsa* and *Eurytemora americana*. Meroplankton occurred mainly as barnacle larvae while benthic harpacticoids and *Corophium* sp. dominated the adventitious component. Semidiurnal tide was the main influence on the *A. tonsa* variability. However, noticeable differences in the abundance pattern as function of wind intensity were detected. Meroplankton abundance did not show a clear variation along the tidal cycle. Distributional pattern of harpacticoids seemed to be mainly modulated by velocity asymmetries in the tidal currents, in the same way as suspended particulate matter. However, the *Corophium* sp. distribution indicated probable behavioural responses associated with tides. The obtained results show how variable the mesozooplankton community structure can be over short-term time scales in mesotidal temperate estuaries. This variability should be taken into account for any zooplankton monitoring program conducted in temperate systems with a high-tidal regime but also to register changes in zooplankton community at a fine temporal scale.

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## 1. Introduction

In coastal ecosystems, biotic and abiotic factors that affect plankton communities fluctuate markedly at different time scales, i.e. tidal, diurnal, seasonal and year to year (Devreker et al., 2010). Tides, winds and riverine runoff are well known phenomena that induce major environmental changes which in turn determine the spatio-temporal dynamics of zooplankton (Villate, 1997). Several studies have emphasized the importance of tidal dynamic inducing spatial (vertical and horizontal) and short-term temporal variability in zooplankton within estuaries (Morgan et al., 1997; Roman et al., 2001; Hampel et al., 2003; Devreker et al., 2008, 2010; Hsieh et al., 2010).

However, the effect of wind on zooplankton variability has received less attention, even though wind has been regarded as a major forcing factor on plankton distribution (Villate, 1994; Gómez Erache et al., 2000). Variable environmental factors, in particular salinity, also act controlling the spatial distribution of zooplankton in estuaries (Devreker et al., 2010). However, in a homogeneous, well-mixed environment these do not constrain zooplankton distribution. In estuaries that are not subject to high salinity variation, tides have a major influence on the structure and density of the zooplankton communities (Robertson et al., 1988). The effect of tidal cycles in regulating estuarine zooplankton may be especially relevant in systems where there is a low river discharge and the tidal energy and circulation figure among the primary factors underlying the estuarine productivity.

Biological mechanisms may also play a role in the spatio-temporal zooplankton variability (Marques et al., 2009). Some

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estuarine species have developed evolutionary strategies to adapt to a highly variable environment (Devreker et al., 2010), resulting in recurrent distributional patterns (Houser and Allen, 1996). Holoplanktonic copepods can migrate vertically in response to the tidal cycles and maintain their horizontal position into the estuaries by avoiding or using tidal currents of different flow rates and salinities (Hough and Naylor, 1991, 1992a,b; Morgan et al., 1997; Devreker et al., 2008). However, the abundance of *Coullana canadensis* in the Columbia River Estuary (Morgan et al., 1997) as well as *Eurytemora affinis* in the Gironde Estuary and Chesapeake Bay (Castel and Veiga, 1990; Roman et al., 2001) is highly correlated with temporal and spatial patterns of turbidity, suggesting that the same physical processes trap and concentrate both, sediments and zooplankton. A recent study has showed that weaker swimmers act more like passive particles while stronger swimmers, such as some meroplanktonic larvae and copepods, may respond to flow conditions to some extent (Hsieh et al., 2010). Several studies have documented how meroplanktonic larvae and meiofauna are also subject to hydrodynamic constraints under which they act as passive particles (Walters and Bell, 1986; Villate, 1997; Shanks et al., 2003). However, they are also reported to be capable of actively dispersing with flows, particularly those organisms with efficient swimming abilities (Walters and Bell, 1986; Cattrijse et al., 1997; Villate, 1997; Hampel et al., 2003; Cardoso et al., 2010).

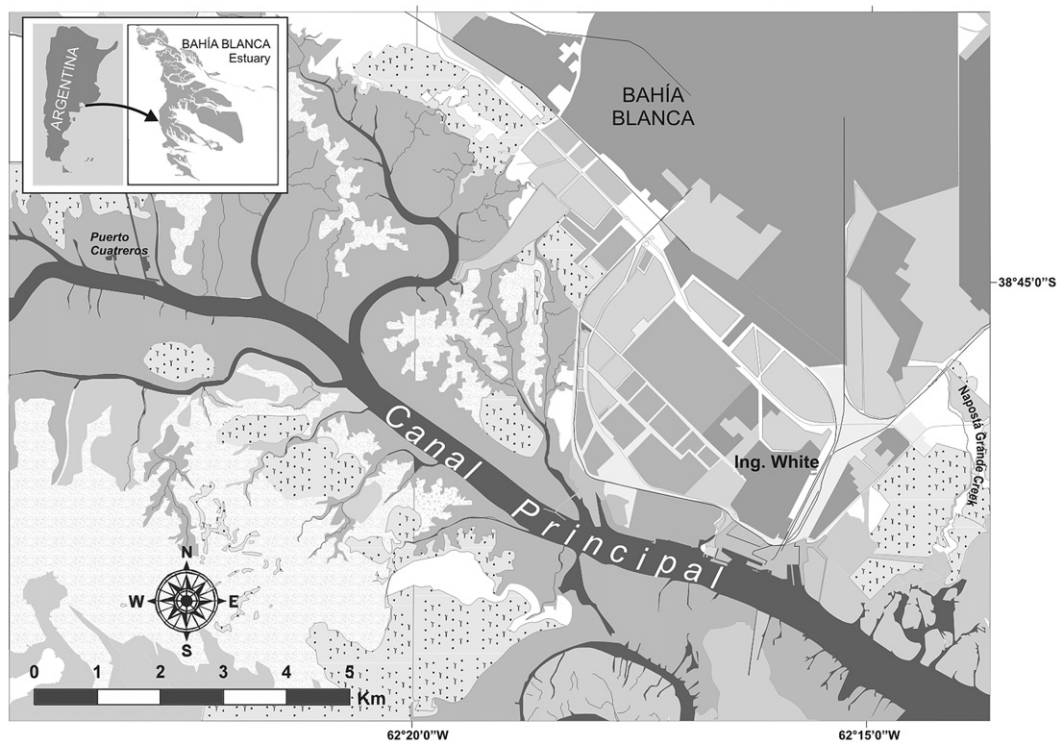
The Bahía Blanca Estuary, located on the southwestern Atlantic coast in Argentina, is a mesotidal, highly turbid system characterized by a eutrophic inner zone (Guinder et al., 2009). The shallow and well-mixed water column is strongly influenced by semidiurnal tides and local winds and to a lesser extent by river inflow (Perillo and Piccolo, 1991). Several authors have pointed that the dominant energy source for mixing and circulation in the estuary is produced by the standing, semidiurnal tidal wave (Piccolo and Perillo, 1990; Perillo and Piccolo, 1991; Perillo et al., 2004). Winds also play an important role in the dynamic of this coastal ecosystem. They are

persistent all year round in the estuary, with an annual mean velocity of  $22 \text{ km h}^{-1}$  (Perillo and Piccolo, 1991). Strong wind days with velocities consistently higher than  $43 \text{ km h}^{-1}$  are frequent in more than half of the year (Perillo and Piccolo, 1991). Consequently, winds have a great influence on wave height and tidal amplitude in the estuary, especially in the inner zone (Perillo et al., 2004). The temporal and spatial dynamics of the mesozooplankton in the estuary have been extensively studied (e.g. Hoffmeyer, 1994, 2004; Hoffmeyer et al., 2009) but none of these works have considered the short-term variability associated with tidal cycles. In this study we examine the short-term temporal and spatial (vertical) variability of the mesozooplankton community in the inner zone of the Bahía Blanca Estuary. In highly dynamic areas dominated by tides, there is also a tidal control of zooplankton community, and thus we predict that vertical and short-term temporal distribution of many organisms might change accordingly. Additionally, considering that winds have important effects on tidal dynamics in the estuary, they will have indirect effects on mesozooplankton distribution. The specific aims were (1) to evaluate the short-term changes of the main taxa within zooplankton community in relation to the semi-diurnal tidal cycles and (2) to analyse the influence of winds on this short-term variability.

## 2. Materials and methods

### 2.1. Study site

The Bahía Blanca Estuary is a mesotidal coastal plain system ( $38^{\circ}45'S$ ;  $62^{\circ}22'W$ ) located on the Atlantic coast of Argentina (Fig. 1). This temperate estuary covers an area close to  $2300 \text{ km}^2$  and it 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, Principal Channel, has a funnel shape and it extends over 80 km length in a NW-SE



**Fig. 1.** Inner zone of the Bahía Blanca Estuary, Argentina, and location of the fixed sampling site: Puerto Cuatros. In the upper right corner: general location of the Bahía Blanca Estuary in Argentina.

direction (Perillo et al., 2004) (Fig. 1). Tides and winds are the main factors controlling the water turbulence processes, especially in the inner zone where the tidal height is maximal (tidal range of up to 3.6 m) (Piccolo and Perillo, 1990). Tidal currents are reversible with maximum surface velocities of about  $1.3 \text{ m s}^{-1}$  and maximum vertical averaged values of 1.2 and  $1.05 \text{ m s}^{-1}$  for ebb and flood, respectively (Cuadrado et al., 2005). Both, the occurrence of dominant NW winds parallel to the main channel as well as the oscillation of the semidiurnal tidal wave, lead to vertical mixing and homogeneous distribution of the main oceanographic parameters (Piccolo and Perillo, 1990). However, the inner zone of the estuary could eventually function as a partially stratified system during rainfall periods (Piccolo and Perillo, 1990). Freshwater inflow is low and mainly contributed by the Sauce Chico River and the Napostá Grande Creek, which provide an annual mean runoff of 1.9 and  $0.8 \text{ m}^3 \text{ s}^{-1}$ , respectively (Perillo et al., 2004) (Fig. 1). Puerto Cuatreceros station, the fixed sampling site, is representative of the inner zone of the estuary (Fig. 1). It is relatively shallow (4–7 m in the channel margin and a mean depth of 10 m in the central zone of the main channel), well-mixed and highly turbid as a result of the combined effect of winds, tidal currents and river discharges (Perillo and Piccolo, 1991). The dominant winds are from NW–NNW and the mean tidal range is 3.6 m (Cuadrado et al., 2005).

## 2.2. Field methods

Sampling was carried out bimonthly between December 2004 and April 2006, and a total of nine 14-h tidal cycles were sampled. The fixed sampling site coincides with the northern margin of the Principal Channel (Fig. 1). The sampling dates were selected to coincide with the transition from spring to neap tides. Zooplankton samples were collected during the daytime every 3-h, beginning at flood tide. Two submersible pumps were used to obtain simultaneous surface (within the upper 1 m layer) and bottom water samples (1 m above the bottom). A reinforced PVC hose (15 m long, 5 cm wide) linked the pumps to 200  $\mu\text{m}$  pore size plankton nets which were placed on the pier. Water was filtered through the nets for 10–20 min, covering a total volume between 1.5 and  $2.9 \text{ m}^3$ . To estimate the precise water volume sampled, flow rate of the pumps was calculated before and after each sampling time by recording the time taken to fill a known volume of water. Immediately after the collection, the samples were preserved in a buffered formaldehyde solution at a final concentration of  $\sim 4\%$ .

Vertical profiles of temperature and salinity (intervals: 1 m) were obtained with a digital multisensor Horiba U-10 at the same time as the zooplankton sampling. Additionally, samples of surface and bottom water were taken through pumping water for the determination of suspended particulate matter (SPM). Tidal height was continuously measured by means of a tidal gauge and all data concerning winds (velocity and direction) were obtained every 30 min by a meteorological base settled on the pier. Precipitation data (mm) was also obtained. No field data for the entire tidal cycle of February and June 2005 are available due to equipment problems.

## 2.3. Laboratory procedures

Zooplankton samples were firstly analysed under a Wild M5 stereoscopic microscope to identify the organisms to the lowest possible taxonomic level using appropriate identification keys and descriptions (e.g. Boltovskoy, 1981, 1999; Young, 2002). Samples with high abundances were further sub-sampled (1/10), and all taxa present were counted. In the case of samples with low abundances, the entire sample was examined. Abundance of each taxon was calculated as the number of individuals per cubic metre of

filtered water ( $\text{ind. m}^{-3}$ ). The SPM water content ( $\text{mg L}^{-1}$ ) was determined as dry weight ( $60^\circ\text{C}$ , 24 h) after filtration of 250 ml of estuarine water through previously dried and weighed Whatman GF/C filters (pore diameter  $0.45 \mu\text{m}$ ).

## 2.4. Data analysis

### 2.4.1. Univariate analysis

In order to overcome the uncertainty of normality and equality of variance, non-parametric statistics were performed for a univariate analysis of variance (ANOVA), following the procedures described by Hsieh et al. (2010). The abundance of the dominant taxa within zooplanktonic fractions (holoplankton, meroplankton and adventitious plankton) were analysed using Mann–Whitney *U*-test and Kruskal–Wallis test, to see whether there were distributional differences among two sample settings: (1) two depths and (2) five tidal phases (flood, high tide, ebb, low tide, flood) (Hsieh et al., 2010). When significant results were found, a multiple-means comparison using Dunn's test were performed (Hollander and Wolfe, 1999). Because of we wanted to evaluate wind effect on mesozooplankton distribution, sampling dates were analysed based on their registered wind condition (see multivariate analysis section). Above mentioned tests were applied on taxa abundances of low wind sampling days, and each date was taken as replicates. In order to detect patterns given by wind effect, dates characterized by high wind velocities were considered individually. Statistical analyses were limited to the most abundant taxa, since relationships with rare or occasional species may be strongly biased and/or independent from tidal cycles. The taxa considered were *Acartia tonsa* (Copepoda), *Eurytemora americana* (Copepoda), cirripeds larvae (Cirripedia), benthic harpacticoids (Copepoda) and *Corophium* sp. (Amphipoda).

### 2.4.2. Multivariate analysis

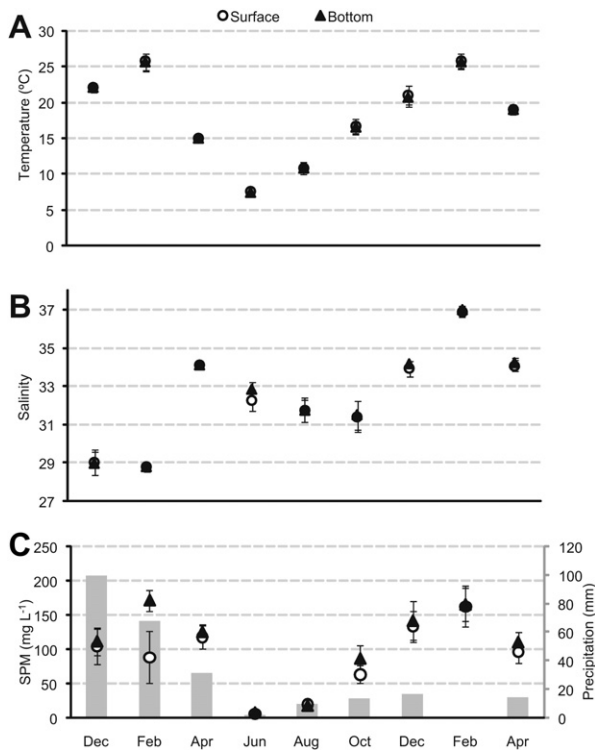
Hierarchical agglomerative clustering coupled with group average linkage was used to represent wind velocity patterns. This technique was based on a Euclidean matrix of wind velocity data (Clarke and Warwick, 1994) and it allows to obtain an optimal division at any degree of grouping of the sampling days according to wind velocity information. Tidal patterns of taxa were analysed using the previously aggregated sampling dates according to clustering technique. Abundances of sampling days with low wind velocities were grouped and separated from each one corresponding to days with high velocities.

A Principal Component Analysis (PCA) by Spearman's rank correlation matrix was applied to arrange and visualise the data, to detect relationships among variables, and to identify the major sources of variation. We used the following data as inputs: temperature, wind velocity, SPM, tidal height, precipitations and abundance of the main taxa (*Acartia tonsa*, *Eurytemora americana*, cirripeds larvae, *Corophium* sp. and benthic harpacticoids). Sampling dates were included as supplementary variables in order to find their spatial arrangement according to the data input. Salinity was extracted from the analysis due to its very low contribution to the first two axes. The first two principal components (PC1 and PC2) were retained as they explained a significant part of the total variation. Plotted variables showed a reconstruction percentage higher than 50% in the two dimensional plot.

## 3. Results

### 3.1. Environmental variables

Water temperature varied from  $7.4 \pm 0.1^\circ\text{C}$  in June 2005 to  $25.7 \pm 0.7^\circ\text{C}$  in February 2005–06 (Fig. 2A). Vertical gradients were always lower than  $0.1^\circ\text{C m}^{-1}$ , suggesting thermal homogenization



**Fig. 2.** Variation of mean ( $\pm$ standard deviation) surface (open circle) and bottom (closed triangle) water temperature (A), salinity (B) and suspended particulate matter (C) in Puerto Cuatros station, from December 2004 to April 2006. In figure C, the closed bars stand for precipitation.

of the water column (Fig. 2A). At a short-term time scale, the highest temperature was reached during the ebb or low tide and the lowest one during the floods (range: 0.6–3.5 °C) (Table 1). Annual salinity changes were mainly related to local precipitations (Fig. 2B). The lowest values were registered in December 2004 and February 2005 (surface:  $29 \pm 0.67$  and  $28.8 \pm 0.17$ ; bottom:  $28.9 \pm 0.61$  and  $28.7 \pm 0.21$ , respectively) and the highest ones in February 2006 (surface:  $36.8 \pm 0.2$ , bottom:  $37 \pm 0.2$ ) (Fig. 2B). Salinity presented a mean vertical gradient of  $0.15 \text{ m}^{-1}$ , indicating homogeneous conditions of the water column (Fig. 2B). At the tidal

scale, salinity generally increased at high tide and decreased at low tide (range: 0.3–4.8) (Table 1). An opposite trend was observed in December 2005 and February 2006, mainly attributed to hypersalinity (Table 1). The SPM showed a clear seasonal pattern, with minimum values in winter ( $2\text{--}34.8 \text{ mg L}^{-1}$ ) and maximum ones in summer ( $50.7\text{--}275.2 \text{ mg L}^{-1}$ ) (Fig. 2C). The seasonal variation of the SPM showed a strong relationship to both, precipitations and water temperature (Fig. 2A and C). The SPM dynamics over the tidal cycle evidenced maximum concentrations during ebb tide near the bottom (Fig. 3). High values were also registered during flood conditions and generally, the SPM concentrations were slightly greater near the bottom than at the surface (Fig. 3).

### 3.1.1. Wind data

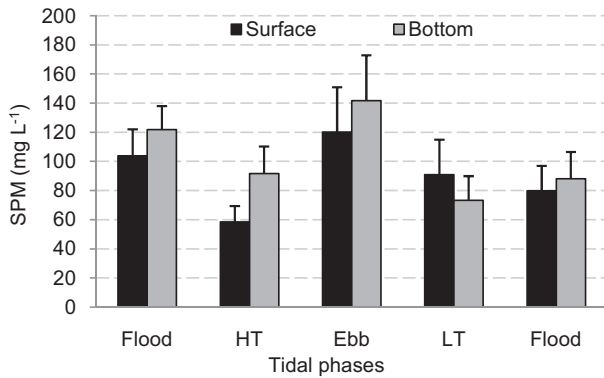
NW-NNW winds dominated most of the study period (33.4%) but some events of SE (14.1%) and N (12.8%) winds were also observed. Fig. 4 shows wind velocity patterns for each sampling date. In February 2005, April 2005, June 2005, October 2005, December 2005 and April 2006, mean velocities were low and fluctuated between 9 and  $25 \text{ km h}^{-1}$  (Fig. 4). The lowest values ( $0\text{--}3.4 \text{ km h}^{-1}$ ) were registered during June 2005 and April 2006 (Fig. 4). Three sampling days were characterized by high wind velocities (December 2004, August 2005 and February 2006), with mean values over  $35 \text{ km h}^{-1}$  (Fig. 4). In December 2004, wind direction was predominantly from the SE with gusts up to  $60 \text{ km h}^{-1}$  (Fig. 4). Strong NW-NNW winds prevailed during August 2005 and February 2006 and in both cases, maximum velocities ( $45$  and  $54.7 \text{ km h}^{-1}$ , respectively) were observed during the flood and high tide (Fig. 4). The comparison between the predicted astronomical tide and the actual tide records showed substantial differences predominantly in tidal height, which was more pronounced in days with high wind velocities. Strong SE winds produced an increase of the tidal height prediction whereas NW-NNW winds caused the opposite effect.

Cluster analysis clearly separated the three sampling dates with higher wind velocities (December 2004, August 2005, and February 2006) from the rest of the days (Fig. 5). At the next hierarchical level, one group including June 2005 and April 2006 was separated from the second one comprising April 2005, October 2005, February 2005, and December 2005 (Fig. 5). The latter is formed by two sub-groups: April 2005 and October 2005 and other including February 2005 and December 2005 (Fig. 5).

**Table 1**  
Tidal variation of water temperature (°C) and salinity at surface (S) and bottom (B). Bold numbers indicate the highest and lowest (only for salinity) values of the measured variables. HT: high tide; LT: low tide.

Date	Depth	Temperature (°C)					Salinity				
		Flood	HT	Ebb	LT	Flood	Flood	HT	Ebb	LT	Flood
20-12-2004	S	21.5	22.1	<b>22.8</b>	22.1	22.3	29.41	<b>30.75</b>	29.09	<b>26.60</b>	29.30
	B	21.1	21.8	<b>22.9</b>	22.2	22.5	28.45	<b>30.88</b>	28.77	<b>27.18</b>	29.60
18-02-2005	S	25.1	25.2	<b>27</b>	—	—	28.65	<b>29.16</b>	28.65	—	—
	B	25.2	24.7	<b>27</b>	—	—	28.71	<b>29.16</b>	28.45	—	—
19-04-2005	S	14.7	15.2	<b>15.3</b>	14.9	14.7	34.07	34.13	34.20	34.13	33.88
	B	14.7	15.2	<b>15.3</b>	14.9	14.8	34.07	34.2	34.2	34.07	34.07
23-06-2005	S	—	7.5	7.2	<b>7.7</b>	7.6	—	<b>32.92</b>	32.35	<b>30.11</b>	32.67
	B	—	7.3	7.1	<b>7.5</b>	7.3	—	<b>33.24</b>	32.54	<b>31.58</b>	33.11
26-08-2005	S	9.9	9.9	11.4	<b>11.6</b>	11.3	32.16	<b>33.05</b>	32.35	<b>29.28</b>	31.96
	B	10	9.8	11.4	<b>11.6</b>	11.2	32.28	<b>32.98</b>	32.03	<b>29.6</b>	31.77
11-10-2005	S	16	15.4	17.3	<b>17.8</b>	17.1	32.35	<b>32.98</b>	31.77	<b>28.39</b>	31.58
	B	15.8	15.2	17.3	<b>17.5</b>	17.1	32.35	<b>32.73</b>	31.84	<b>28.84</b>	31.84
21-12-2005	S	19.2	19.9	21.7	<b>22.6</b>	21.4	33.88	<b>33.43</b>	34.07	<b>34.26</b>	34.32
	B	19.1	19.4	21.6	<b>21.9</b>	21.3	34.07	<b>33.81</b>	34.01	<b>34.32</b>	34.45
20-02-2006	S	24.7	24.6	<b>26.9</b>	26.4	26.4	37.07	<b>36.17</b>	37.07	<b>37.64</b>	36.37
	B	24.7	24.5	<b>26.8</b>	26.4	26.2	37.20	<b>36.37</b>	37.26	<b>37.45</b>	36.75
05-04-2006	S	18.3	18.5	<b>20</b>	19.2	19.2	33.94	<b>34.58</b>	34.39	<b>32.98</b>	34.39
	B	18.2	18.6	<b>20</b>	19.2	19.2	34.39	<b>34.71</b>	34.32	<b>33.24</b>	34.52





**Fig. 3.** Tidal variation in surface (closed black bars) and bottom (closed grey bars) mean ( $\pm$ standard deviation) suspended particulate matter, during 14-h series in Puerto Cuatreros station. HT: high tide. LT: low tide.

### 3.2. Mesozooplankton composition and abundance

The mesozooplankton community consisted of 33 identifiable taxa, including species, genera and in some cases higher taxa. Holoplankton represented 48.48% of the total taxa observed whereas the remaining percentage corresponded to meroplankton (30.3%) and adventitious fraction (21.21%). The calanoid copepod *Acartia tonsa* dominated the community largely, reaching abundances of up to 5000 ind.  $m^{-3}$  in December 2004. These high densities constituted between 40 and 97% of the total mesozooplankton abundance. On the other hand, *Eurytemora americana* was the dominant taxa in August 2005, accounting for more than 90% of the total abundance. Lower densities of *Paracalanus parvus* (mean value: 7.45 ind.  $m^{-3}$ ), *Euterpina acutifrons* (4.25 ind.  $m^{-3}$ ) and the mysid *Neomysis americana* (2.05 ind.  $m^{-3}$ ) were also registered in the samples but their contribution to the holoplankton fraction was very small. Other copepod species as *Calanoides carinatus* and *Labidocera fluviatilis* occurred sporadically. Meroplankton, which made up 4–35% of total zooplankton abundance, was mostly represented by barnacle larvae (mean abundance: 87.9 ind.  $m^{-3}$ ). Other taxa that occurred regularly but in low

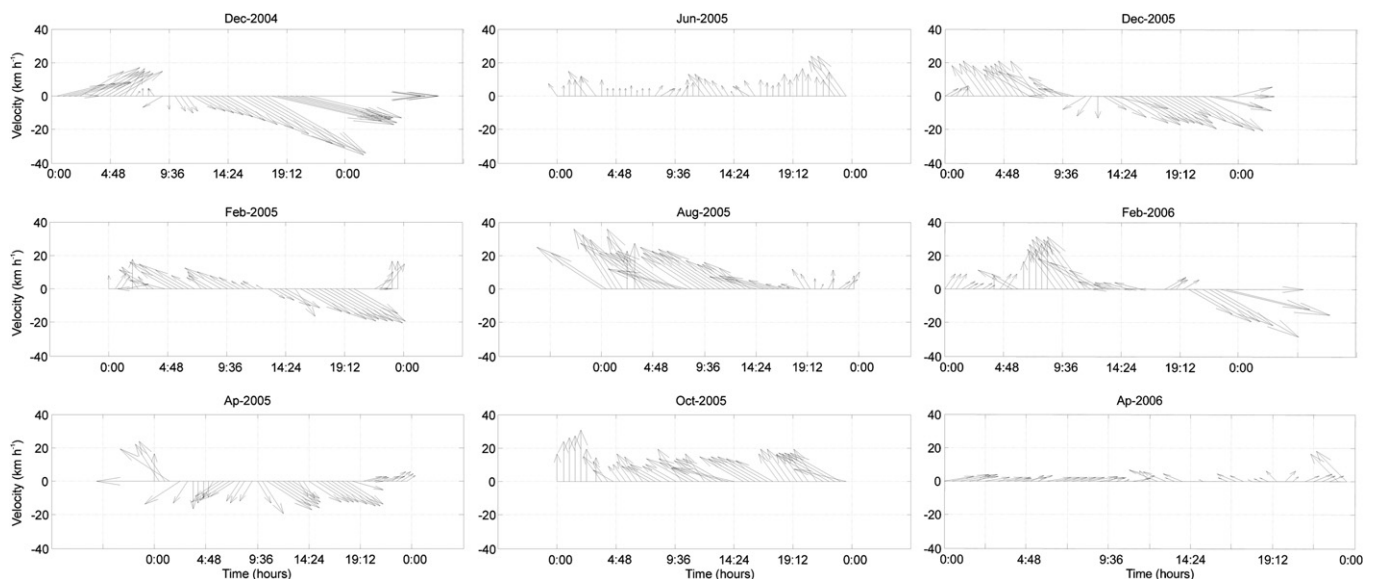
numbers were Spionidae (24.71 ind.  $m^{-3}$ ), Varunidae (21.68 ind.  $m^{-3}$ ), bivalves (20.83 ind.  $m^{-3}$ ) and gastropod larvae (26.09 ind.  $m^{-3}$ ). Concerning adventitious plankton, the highest abundances were attained by two taxa: the amphipod *Corophium* sp. (mean value: 24.19 ind.  $m^{-3}$ ) and non-identified benthic harpacticoids (mean value: 18.14 ind.  $m^{-3}$ ).

### 3.3. Principal Component Analysis (PCA): relationships among variables

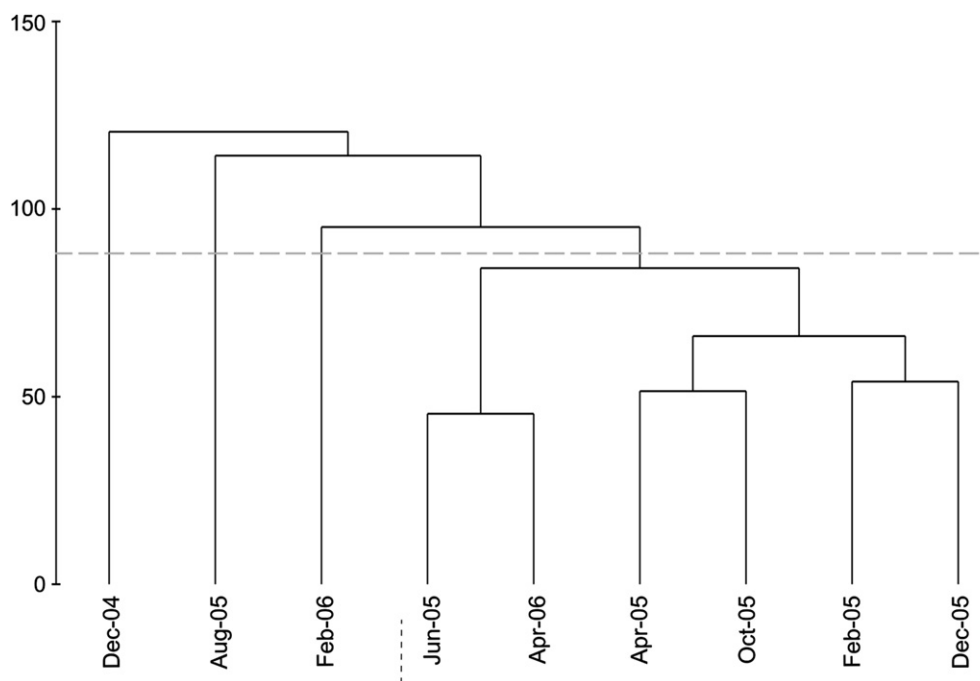
The first two components of the PCA explained respectively 39.68 and 16.92% of the total variance (Fig. 6). The first axis (PC1) was positively correlated to temperature, *Acartia tonsa* abundance, wind velocities and SPM concentration (contributions of 21.8, 18.4, 16.2 and 15.4% to PC1); and negatively with *Eurytemora americana* abundance (contribution of 16.3% to PC1) (Fig. 6). These variables displayed significant correlations with one another (Table 2) and were spatially linked with sampling dates (supplementary variables) (Fig. 6). As a whole, the spatial arrangement in the first two axes of variability of the sampling dates made it possible to recognize a temporal gradient, with winter and summer samples discriminate on the axis ends (Fig. 6). Two sampling dates with high wind velocities, December 2004 and February 2006, were arranged on the right side of the plot (Fig. 6). However, August 2005 was separated of them by the strong seasonal influence. The second axis (PC2) of the PCA was positively correlated to tidal height and precipitations (contribution of 28.9 and 21.5% to PC2), and negatively with the abundance of cirripeds larvae, benthic harpacticoids and *Corophium* sp. (contribution of 16.5, 12.9 and 12.4% to PC2) (Fig. 6).

### 3.4. Holoplankton fraction: dynamics with tidal cycles

In sampling days with low wind velocities, *Acartia tonsa* mean abundance was markedly higher during ebb tide near the surface (Fig. 7A). The lowest values were registered during low and high tide, especially during high tide near the surface (Fig. 7A). Kruskal–Wallis test determined significant statistical differences ( $Z = 13.62$ ,  $p < 0.01$ ) in the *A. tonsa* mean abundance between tidal phases (Fig. 7A). In contrast, no statistical differences were detected



**Fig. 4.** Wind direction and intensity (represented by the length of the arrows) during each sampling date in Puerto Cuatreros station, Bahía Blanca Estuary, Argentina. Wind direction is indicated according to the meteorological convention (i.e. the direction from which the wind is blowing). Dec: December, Feb: February, Ap: April, Jun: June, Aug: August, Oct: October.



**Fig. 5.** Classification of the sampling dates according to wind velocity data in the inner zone of the Bahía Blanca Estuary (Puerto Cuatros). Cluster analysis was based on a Euclidean matrix of wind velocity and average linkage. Dotted line indicates reference value used to separate groups.

between depths (Mann–Whitney test,  $Z = 711$ ,  $p = 0.91$ ). Different trends were observed with high wind velocities (Fig. 7B–D). In December 2004 (winds mainly from the SE sector), the abundances were generally greater near the bottom and the highest values were observed during high and low tide (Fig. 7B). In February 2006 (NW–NNW winds), the abundances were similar between depths and did not show a noticeable increase during the ebb (Fig. 7C). The highest value was registered during the second flood (Fig. 7C). A similar

pattern was detected for *Eurytemora americana* in August 2005 (NW–NNW winds) but in this case, the highest abundance was detected during the first flood (Fig. 7D).

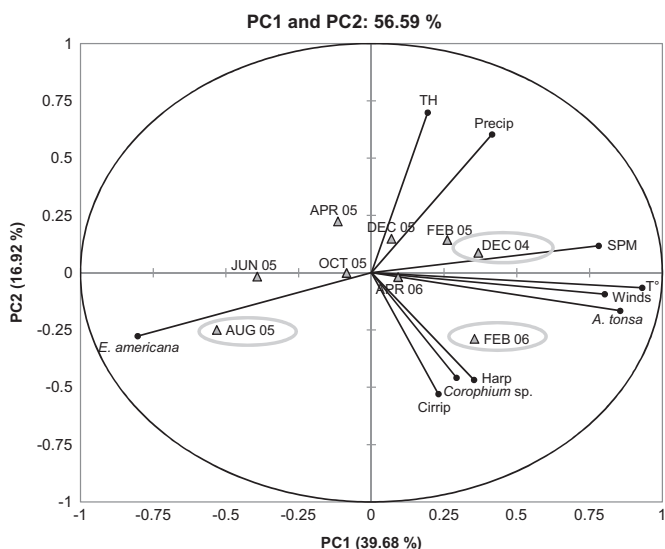
### 3.5. Meroplankton and adventitious plankton: dynamics with tidal cycles

An inconsistent pattern was observed during the tidal cycles for cirripeds larvae (Fig. 8A–D). Cirriped larvae abundances were highly variable not only between depths but also among tidal phases (Fig. 8A–D). Accordingly, no statistical differences in the mean abundance were detected among tidal phases (Kruskal–Wallis test,  $Z = 3.146$ ,  $p = 0.534$ ) and between depths (Mann–Whitney test,  $Z = 2.610$ ,  $p = 0.106$ ). In addition, we did not find a clear pattern comparing days with low and high wind velocities (Fig. 8A–D).

Examining their concurrence with tidal cycles, both benthic harpacticoids and *Corophium* sp. abundances changed with the tidal setting, but the trends differed from each other (Kruskal–Wallis test,  $F = 12.74$ ,  $p < 0.05$  for harpacticoids;  $Z = 13.88$ ,  $p < 0.01$  for *Corophium* sp.; Fig. 9A and F). Benthic harpacticoids showed similar patterns in days with low and high wind velocities (Fig. 9A–D). The highest abundances were generally observed during the floods and ebb tide, especially during the ebb near the bottom (Fig. 9A–D). *Corophium* sp. also showed a similar pattern during all sampled tidal cycles (Fig. 9F–I). Generally, its abundance was higher during the first flood and ebb tide near the bottom (Fig. 9F–I). Surface abundances were very low during most of the tidal cycle but they increased at low tide (Fig. 9F–I). Both taxa exhibited significant depth gradients, showing higher densities near the bottom (Mann–Whitney test,  $Z = 8.016$ ,  $p < 0.01$  for harpacticoids;  $Z = 20.91$ ,  $p < 0.001$  for *Corophium* sp.).

## 4. Discussion

Previous research in the Bahía Blanca Estuary has been motivated mainly by seasonal zooplankton dynamics (Hoffmeyer, 1994, 2004) and their environmental regulation (Hoffmeyer et al., 2009).



**Fig. 6.** Results of the Principal Components Analysis (PCA) considering environmental variables and abundance of the main taxa. Principal components 1 and 2 (PC1 and PC2) are plotted for variables with the correlation circle. Sampling dates are represented as supplementary variables. Dates with grey circles indicate sampling occasion with high wind velocities. T°: temperature; SPM: suspended particulate matter concentration; Winds: wind velocity; TH: tidal height; Precip: precipitations; Harp: benthic harpacticoids; Cirrip: cirripeds larvae; Dec: December, Feb: February, Apr: April, Jun: June, Aug: August, Oct: October.

**Table 2**Spearman's correlation matrix corresponded to Principal Component Analysis. In bold letters, significant correlation values ( $p < 0.001$ ).

Variables	T°	SPM	Precip.	TH	Winds	<i>A. tonsa</i>	Cirrip	Harp	<i>Corophium</i> sp.	<i>E. americana</i>
T°	–									
SPM	<b>0.657</b>	–								
Precip.	0.265	0.262	–							
TH	0.099	0.104	<b>0.475</b>	–						
Winds	<b>0.899</b>	<b>0.499</b>	0.145	0.088	–					
<i>A. tonsa</i>	<b>0.722</b>	<b>0.649</b>	0.280	0.073	<b>0.553</b>	–				
Cirrip	0.249	–0.094	–0.019	–0.150	0.177	<b>0.305</b>	–			
Harp	0.211	0.226	–0.040	0.044	0.123	<b>0.486</b>	<b>0.290</b>	–		
<i>Corophium</i> sp.	0.252	0.161	0.031	–0.219	0.265	0.197	0.070	0.236	–	
<i>E. americana</i>	<b>–0.716</b>	<b>–0.645</b>	<b>–0.425</b>	–0.190	<b>–0.550</b>	<b>–0.604</b>	–0.046	–0.039	–0.070	–

However, little information is still known about the short-term temporal mesozooplankton dynamics. Most of the environmental (biotic and abiotic) variability has been attributed to a strong regional seasonality, where temperature is the main variable determining monthly zooplankton species composition and abundance (Hoffmeyer et al., 2009). The well-defined temporal gradient revealed by the PCA is a common feature of this and other temperate estuaries (Leandro et al., 2007; Hoffmeyer et al., 2009; Marques et al., 2009; Modéran et al., 2010). The main copepod species in the estuary, *Acartia tonsa* and *Eurytemora americana*, reflected quite well the strong seasonal influence. *A. tonsa* was the dominant species in warm months and its density decreased in the cold season, in which *E. americana* reached the highest abundances. Although the strong seasonality mainly driven by temperature, velocity winds and tidal height appeared to contribute significantly to the variability of the data, especially considering copepod main species distributions. The present study, by emphasizing the importance of local sources of variation, also reveals the complex response of zooplanktonic organisms to a variable environment.

#### 4.1. *Acartia tonsa* tidal patterns: low wind velocities

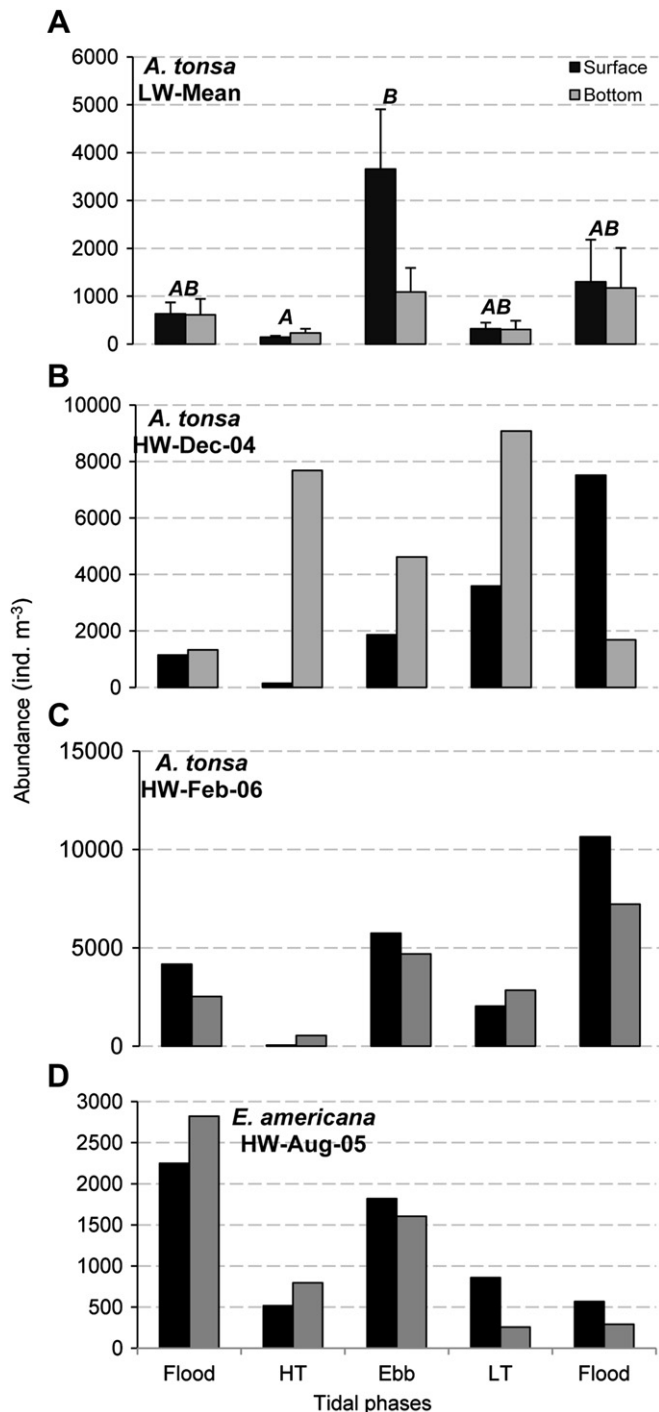
The results of this study showed a daytime situation in which the short-term temporal variability of the *Acartia tonsa* was strongly affected by the tidal rhythm, especially by the ebb conditions. Additionally, significant variations in the abundance pattern as function of wind intensity can be highlighted as additional conclusions of this work. In sampling days with low wind velocities, most of the variability in the population abundance could be explained by tidal dynamics. The highest abundances coincided with the time of peak current velocities usually reported for the inner zone of the estuary (Perillo and Piccolo, 1991; Perillo et al., 2004). Similar results were reported for *Eurytemora affinis* by Morgan et al. (1997) in the Columbia River Estuary, where greater densities were found around the time of maximum ebb velocities. In the Tanshui River system, Hsieh et al. (2010) observed a high correlation between copepod abundance, increasing flow velocity and decreasing particulate organic carbon content. These correlations seemed to be a concomitant event with the nature of seawater-dominated ebb tide water rather than with the organisms' selection for or against these gradients (Hsieh et al., 2010). Likewise, Devreker et al. (2008) reported that *E. affinis* population structure in the Seine Estuary varies accordingly to hydrodynamic properties including water velocity but also, salinity and temperature.

##### 4.1.1. *Acartia tonsa* maintenance in the inner zone of the Bahía Blanca Estuary

Zooplankton organisms may employ active and passive mechanisms to enhance retention in particular estuarine regions (Roman et al., 2001). According to Naylor (2006), the strategy employed by zooplankton, particularly crustaceans, varies accordingly to the

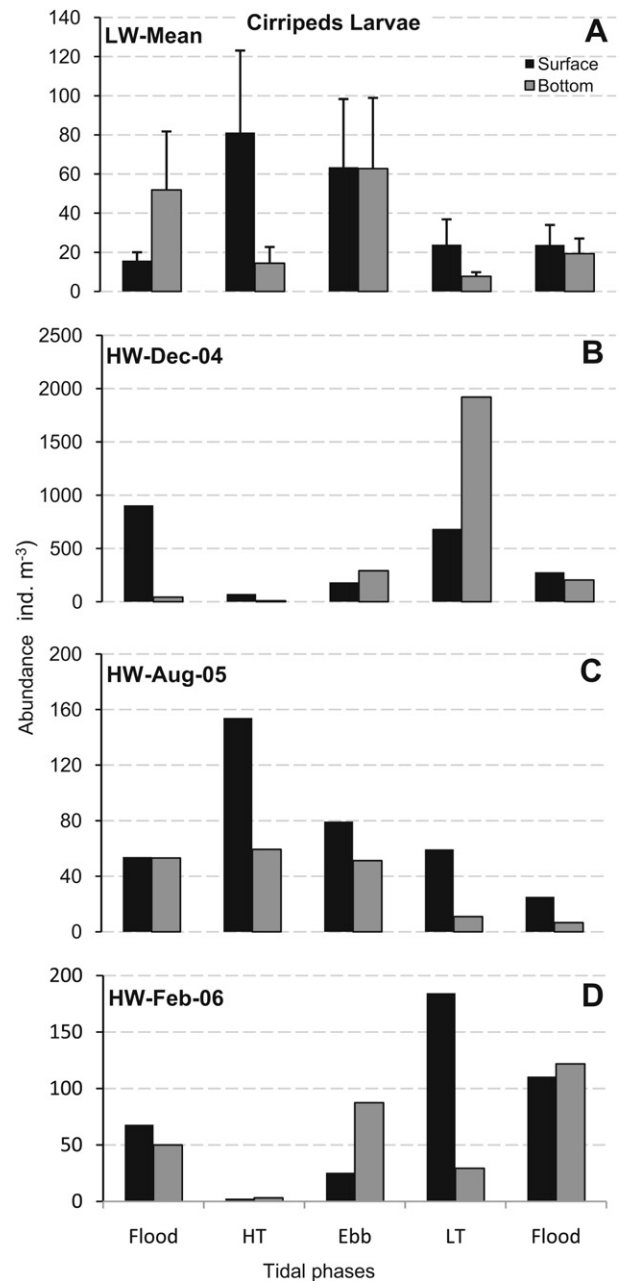
tidal nature of the estuary: whether it is markedly stratified or tidally mixed. A two-layered estuarine circulation is considered the most likely mechanism for retaining zooplankton considering that organisms could theoretically control their distribution and horizontal transport by migrating vertically between the two layers (Wooldridge and Erasmus, 1980; Castel and Veiga, 1990; Hill, 1991; Morgan et al., 1997; Dauvin et al., 1998; Roman et al., 2001). However, selective tidal stream transport in layers of different salinities is unlikely to occur in a well-mixed system like the Bahía Blanca Estuary. For well-mixed estuaries, the behavioural basis of the *Eurytemora affinis* population stability has been attributed to an avoidance of adverse currents when in its preferred salinity zone (De Pauw, 1973), active anadromous migration against prevailing water movement (Heckman, 1986) and tide-related vertical migrations (Hough and Naylor, 1991, 1992a; Devreker et al., 2008) (see Table 3). Additionally, Morgan et al. (1997) observed greater densities of *E. affinis* higher in the water column during the flood and lower during the ebb in the Columbia River Estuary, suggesting that settling or swimming to a lower position in the water column could occur prior to the ebb in order to avoid advective losses (Table 3). In this study, we did not find a tide-related migration pattern for *Acartia tonsa*. Although dispersal of this species occurred into the water column during flood tides, the highest population densities were registered during ebb tide near the surface. The alternative of passive transport for different copepod species was reported by several authors (Castel and Veiga, 1990; Morgan et al., 1997; Roman et al., 2001). Castel and Veiga (1990) suggested that *E. affinis* population in the Gironde Estuary is maintained through the same hydrological processes that resuspend, advect, trap and concentrate suspended particles (Table 3). In our study, the abundance pattern of *A. tonsa* did not match exactly that of SPM, suggesting that additional mechanisms to hydrodynamic process would maintain *A. tonsa* population in the inner zone of the estuary. Even though both, *A. tonsa* abundances and SPM concentration appeared to be strongly influenced by tidal currents, the short-term temporal dynamics differed from one another.

The interdependence of planktonic organisms' exchanges with water circulation in order to control the seaward transport arises mainly from differences in the density between flood and ebb tides (Morgado et al., 2003). Thus, the recurrent distributional pattern observed for *Acartia tonsa* on calm wind days could be related to a retention mechanism of this species in the inner zone of the Bahía Blanca Estuary. It is well known that most *A. tonsa* population remains within the innermost zone of the estuary, and that densities of this copepod decrease towards the mouth of the estuary (A. Berasategui, personal communication). Considering that our fixed sampling site coincides with the northern margin of the Principal Channel, the increase of the abundance during the ebb may be associated with a lateral movement of this species to areas of decreased flushing such as channel margins. This option has



**Fig. 7.** Tidal variation in surface (closed black bars) and bottom (closed grey bars) abundance of *Acartia tonsa* (A–C) and *Eurytemora americana* (D) in Puerto Cuatreceros station. A: mean abundance (± standard deviation) corresponding to sampling days with low wind velocities. B–D: abundance pattern in days with high wind velocities. LW-Mean: mean abundance in days with low wind velocities. HW: high wind velocity. Dec-04: December 2004. Aug-05: August 2005. Feb-06: February 2006. HT: high tide. LT: low tide. Abundances with the same italicized letters do not significantly differ using Dunn's test.

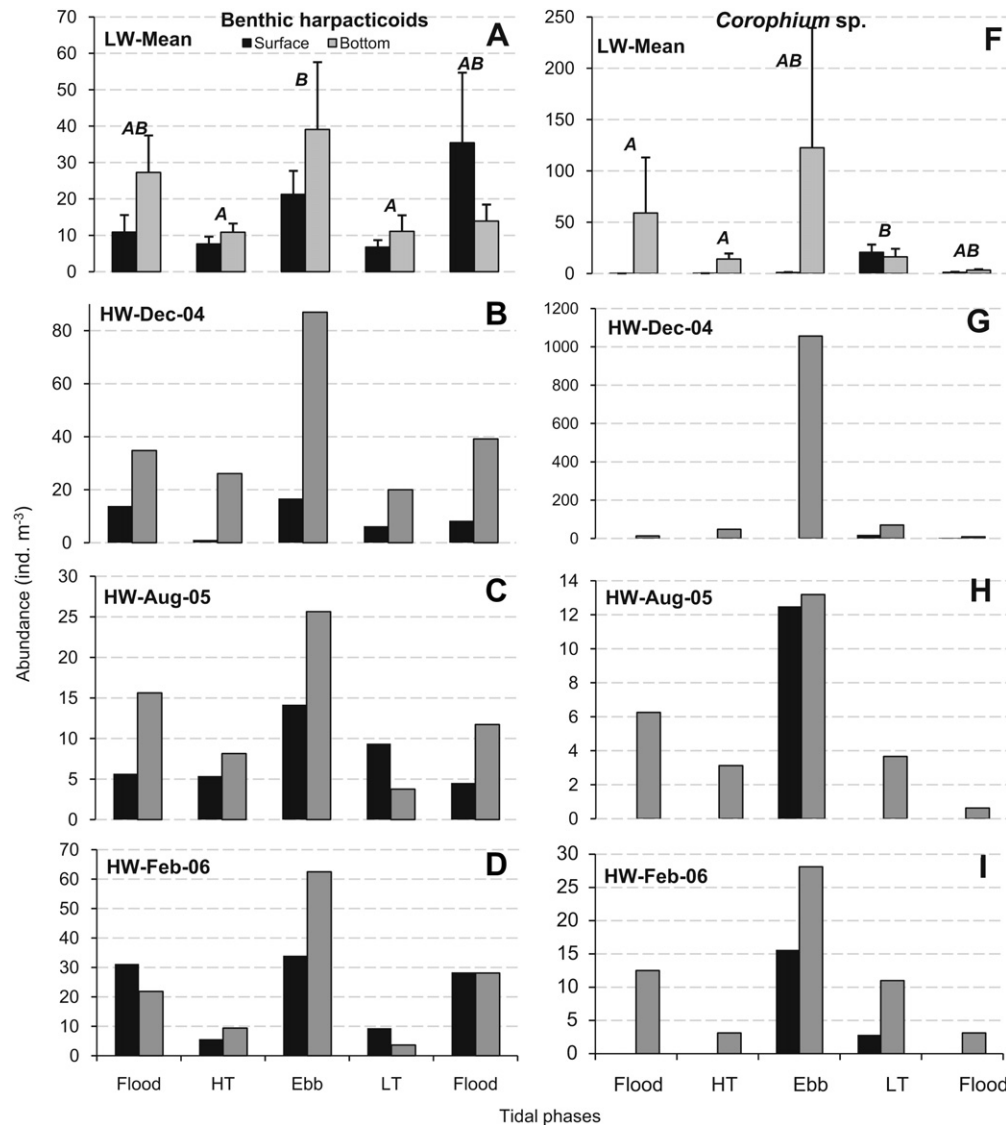
been suggested for different copepod species in order to resist the seaward net flow during the ebb (Cronin et al., 1962; De Pauw, 1973; Roddie et al., 1984; Castel and Veiga, 1990; Menéndez et al., 2011), but there are few data illustrating this. In a study closely related to this, Menéndez et al. (2011) compared the mesozooplankton



**Fig. 8.** Tidal variation in surface (closed black bars) and bottom (closed grey bars) abundance of cirripeds larvae in Puerto Cuatreceros station. A: mean abundance (± standard deviation) corresponding to sampling days with low wind velocities. B–D: abundance pattern in days with high wind velocities. LW-Mean: mean abundance in days with low wind velocities. HW: high wind velocity. Dec-04: December 2004. Aug-05: August 2005. Feb-06: February 2006. HT: high tide. LT: low tide.

distribution between two zones: the northern margin, which coincide exactly with our fixed station, and the deeper central zone of the main channel (approximately 200 m away from our fixed sampling site). In coincidence with our results, the abundance in the channel margin was markedly higher during ebb tide than during flood, low or high tide events (Menéndez et al., 2011). Interestingly, *A. tonsa* abundances in the central zone of the main channel were of similar magnitude throughout the tidal cycle and they did not report an increase during the ebb (Menéndez et al., 2011). Thus, the increase of the abundance during the ebb only in the channel margin may be associated with a lateral movement of





**Fig. 9.** Tidal variation in surface (closed black bars) and bottom (closed grey bars) abundance of benthic harpacticoids (A–D) and *Corophium* sp. (F–I) in Puerto Cuatrerros station. A and F: mean abundance ( $\pm$ standard deviation) corresponding to sampling days with low wind velocities. B–D and G–I: abundance pattern in days with high wind velocities. LW-Mean: mean abundance in days with low wind velocities. HW: high wind velocity. Dec-04: December 2004. Aug-05: August 2005. Feb-06: February 2006. HT: high tide. LT: low tide. Abundances with the same italicized letters do not significantly differ using Dunn's test.

this species to avoid the net outflow at this time (Menéndez et al., 2011). Determination of whether such a retention mechanism operates for *A. tonsa* in the Bahía Blanca Estuary awaits further studies not only considering another sampling stations but also

complementary observations related to behaviour of individual copepods species.

Taking into account our results as well as those published by Menéndez et al. (2011), the highest *Acartia tonsa* abundances in the

**Table 3**

Retention mechanisms for different copepod species in well-mixed (Scheldt, Elbe, and Conway River Estuary and Seine Estuary) and/or partially mixed estuaries (Columbia River Estuary, Chesapeake Bay, Gironde River Estuary). ETM: estuarine turbidity maxima region.

Site	Copepod species	Retention mechanism	Source
Scheldt Estuary, Belgium	<i>E. affinis</i>	Sinking, actively or passively, out of the water column on encountering high salinities	De Pauw (1973)
Elbe Estuary, Germany	<i>E. affinis</i>	Active: anadromous migration against prevailing water movement	Heckman (1986)
Gironde River Estuary, France	<i>E. affinis</i>	Passive: hydrodynamics processes	Castel and Veiga (1990)
Conway River Estuary, USA	<i>E. affinis</i>	Active: tidal vertical migrations	Hough and Naylor (1991, 1992a,b)
Columbia River ETM, USA	<i>E. affinis</i>	Active: tidal vertical migrations	Morgan et al. (1997)
Columbia River ETM, USA	<i>C. canadensis</i>	Passive: physical trapping	Morgan et al. (1997)
Chesapeake Bay TM, USA	<i>E. affinis</i>	Passive: physical trapping	Roman et al. (2001)
Seine Estuary, France	<i>E. affinis</i>	Active: variation in vertical dispersion	Devreker et al. (2008)
Mondego Estuary, Portugal	<i>A. tonsa</i>	Tidal vertical migration (active), Diapause eggs, Life history traits	Marques et al. (2009)

inner zone of the Bahía Blanca Estuary were consistently observed in a zone of net residual landward flow. This may be interpreted as a mechanism that prevents individuals from being washed out of the estuary considering that landward residual currents help to maintain the populations into the estuaries (Castel and Veiga, 1990). Considering the net transport completely landward on shallower parts (Perillo and Piccolo, 1991), the organisms situated near the margin of the channel would increase the chance to remain into the estuary. In the deeper parts of the main channel, the flow reverses with depth, being mouthward in the upper third of the water column and landward near the bottom (Perillo and Piccolo, 1991). Menéndez et al. (2011) reported that in the central part of the main channel, *A. tonsa* abundances were higher near the bottom during the entire tidal cycle. Thus, the greater proportion of the population lower in the water column in this zone would reduce the advective losses and may be associated with a mechanism or strategy developed by the species to avoid outward advection by surface currents during the receding tide.

#### 4.2. *Acartia tonsa* and *Eurytemora americana* tidal patterns: high wind velocities

In days with high wind velocities, the spatial (vertical) and short-term temporal arrangement of *Acartia tonsa* was not as clear as in low wind days. Concerning *Eurytemora americana*, we did not have the possibility to compare low and high wind days due to this species was registered in a sampling date characterized by high winds. However, it is clear that its pattern was different to that observed on calm days. Both, velocity and direction of local winds seemed to influence the observed distributional patterns. The topography of the estuary (funnel shape), the orientation of the main channel (NW to SE) and the velocity and direction of predominant local winds appeared to be responsible for the inflow and outflow of water in the inner zone which in turn determined changes in the distribution and abundance of copepods. It is well known that in the Bahía Blanca Estuary, strong NW winds produce a set down on the water level by pushing the surface water out preventing the tidal penetration (Perillo and Piccolo, 1991). The opposite effect is generally observed with SE winds (Perillo and Piccolo, 1991). Thus, winds from the NW-NNW (blowing mainly during the flood) could have prevented the accumulation of the organisms in the inner zone of the estuary during flood tide. However, under SE winds, most of the organisms were probably retained in the innermost zone of the estuary. Studies considering the effect of winds on zooplankton dynamics mentioned that vertical mixing of the water column may also produce a lack of vertical segregation pattern of the organisms (Villate, 1994). This does not coincide exactly with our results, in which with NW winds we observed a great homogeneity of the water column but with SE winds, the abundances were higher near the bottom. Gómez-Erache et al. (2000) also observed changes in zooplankton abundances related to wind-forced hydrodynamic in the Solís Grande Estuary, Uruguay. However, they observed that winds occasioned an increase of species diversity, situation that was not evident during the present study. These findings could have significant effects on the distribution and interaction of planktonic biota in the inner zone of the Bahía Blanca Estuary. Turbulent processes have relevant effects on processes such as metabolic rates, predator-prey encounter rates, grazing rates, egg production, swimming behaviour and population dynamics (Saiz and Alcaraz, 1992; Kiorbøe and Saiz, 1995; Kiorbøe, 1997; Seuront et al., 2004). Numerous results suggest that the swimming abilities of zooplankton allow them to overcome turbulent fluctuations (Yamazaki and Squires, 1996; Schmitt and Seuront, 2001; Seuront et al., 2004), making them independent of local turbulent fluctuations. Due to turbulence induced by winds is

a ubiquitous feature of the marine environment, a better understanding of the zooplankton responses to changes in turbulence is needed to predict and interpret the distributional patterns and their biological consequences on the ecosystem.

#### 4.3. Cirripeds larvae, benthic harpacticoids and *Corophium* sp. tidal patterns

Within meroplankton and adventitious fraction, only benthic harpacticoids and *Corophium* sp. exhibited considerable variations with semidiurnal tidal cycles. Additionally, prevailing local winds did not seem to have an evident influence on their abundance distributional patterns at a short-term time scale.

The occurrence of benthic harpacticoids into the water column appears to be mainly modulated by velocity asymmetries in the tidal currents (Piccolo and Perillo, 1990), in a similar way to that described for the SPM. The highest abundances were registered during flood and ebb tides, especially near the bottom. According to Walters and Bell (1986), the pelagic occurrence of these sediment-associated organisms may result from passive resuspension (current mediated erosion), active migration (behaviourally directed emergence), or a combination of both. We suggest that the observed pattern is likely to be due to resuspension of the organisms from sediments into the water column when tidal currents were stronger (ebb and flood tides) (Piccolo and Perillo, 1990), such that copepod densities were lower during slack time at high and low tide. Care was taken to ensure that low and high tide samples were collected at slack tide, when water currents and thus resuspension were minimal. Our results corroborate the observed findings in other shallow systems where meiobenthos is found to contribute largely to the zooplankton biomass over the entire tidal cycles (Bell and Sherman, 1980; Palmer and Brandt, 1981; Palmer and Gust, 1985; Armonies, 1988; Villate, 1994; Cardoso et al., 2010). The cyclic inputs of meiofauna into the water column might be relevant in the feeding ecology of predator species (Villate, 1994; Cardoso et al., 2010) and it may have important consequences for increasing nutritive values of resuspended material (Rhoads et al., 1975; Tenore, 1976; Roman and Tenore, 1978), survival of benthos (Rhoads and Young, 1970) and meiofauna dispersion (Bell and Sherman, 1980; Cardoso et al., 2010).

In this study, *Corophium* sp. occurred relatively close to the bottom during most of the tidal cycles. *Corophium* was described as a benthic species, but with a capability to swim (Hughes, 1988). Under laboratory conditions, *Corophium volutator* rarely swam higher than about 25 cm from the bottom of a chamber (Meadows and Reid, 1966). Here, *Corophium* sp. seemed to evidence a tide-related pattern, with higher abundances during the first flood and ebb tide. Morgan (1965) and Holmstrom and Morgan (1983) demonstrated endogenous circatidal swimming rhythms in *C. volutator*, that were possibly cued by hydrostatic pressure changes associated with tidal movements. Additionally, Hough and Naylor (1992b) showed that migration of *Gammarus zaddachi* along estuaries was controlled by endogenous swimming rhythms and salinity preference behaviour. Alldredge and King (1980) proposed the short-term swimming activity of meiobenthos as a means of dispersal over short distances. Other causes might be endobenthic and epibenthic predator avoidance, disturbance (Armonies, 1988) or decreased food availability (Montagna et al., 1983). On the other hand, each tide may bring organisms to the marsh habitats, which may offer refuge and foraging opportunities (Kneib, 1997). Selective tidal transport is a well documented mechanism by which small organisms reach upstream habitats (Hampel et al., 2003). With rising water levels, the intertidal habitat becomes available and migrations onto and out of the intertidal are fully synchronised with tides (Cattrijsse et al., 1997). While some organisms are adapted to remain within the marsh proper, most return to the subtidal on ebbing tides (Cattrijsse et al., 1997).

Accordingly, we found the highest abundances of *Corophium* sp. during the ebb. Finally, the low *Corophium* sp. abundances registered during the second flood may be explained taking into account the diel activity patterns. Holmstrom and Morgan (1983) and Hampel et al. (2003) demonstrated that swimming activity of *C. volutator* was present in daylight but more abundant in darkness. Hughes (1988) observed that swimming of benthic amphipods is a nocturnal activity and Cattrijsse et al. (1997) and Hampel et al. (2003) reported that *C. volutator* were caught mostly at night in the marsh, which can be attributed to higher night activity.

## 5. Conclusion

Our results demonstrate that short-term variation of meso-zooplankton community in the inner zone of the Bahía Blanca Estuary is strongly influenced by semidiurnal tidal cycles. The present findings also reflect different adaptation patterns of the organisms to a highly variable environment, mainly dominated by tidal energy. The dominant species *Acartia tonsa* was strongly affected by the tidal rhythm, especially by the ebb conditions. Its highest abundances were observed during ebb tide, coinciding with the time of peak current velocity reported for the estuary. This recurrent pattern seemed to be associated to low wind velocities considering that it was quite different under high wind velocities. Cirripeds larvae did not show an influence of tidal cycle on their spatial (vertical) and short-term temporal distribution. Pattern of benthic harpacticoids seemed to be modulating mainly by velocity asymmetries in the tidal currents, in the same way as SPM. These organisms were suspended into the water column by tidal currents, such that greatest abundances were found during ebb and flood tides, when friction velocity increased. However, the short-term temporal distribution of *Corophium* sp. may also indicate some behavioural responses associated with tidal cycles. Local winds did not seem to have an evident influence on the distributional pattern of the main taxa within meroplankton and adventitious fraction. These results show how variable the zooplankton community structure can be over short-term time scales in meso-tidal temperate estuaries. This variability should be taken into account for any zooplankton monitoring program conducted in temperate systems with a high-tidal regime but also to register changes in zooplankton community at a fine temporal scale.

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