



The role of the seasonal and semi-diurnal tidal cycle on mesozooplankton variability in a shallow mixed estuary (Bahía Blanca, Argentina)

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The role of the seasonal and semi-diurnal tidal cycle on mesozooplankton dynamics was investigated in the inner zone of the Bahía Blanca Estuary (BBE), Argentina. Hydrological data and mesozooplankton samples were obtained bimonthly from December 2004 to April 2006, during 14 h tidal cycles. The mesozooplankton community was represented by 33 taxa. Taxa richness was greater near the bottom, where the contribution of benthic forms was notable. Abundances were greatest during summer (>5500 ind. m^{-3}) and lowest during winter (<70 ind. m^{-3}). The mesozooplankton community was dominated by *Acartia tonsa* and *Eurytemora americana*. Multivariate analyses revealed significant seasonal differences in community structure, especially in terms of density. Seasonal differences in community structure are well explained by the natural change of abiotic and biotic conditions, but temperature played a key role in structuring the mesozooplankton community. The zooplankton was significantly more abundant during the ebb, suggesting that local hydrological conditions are responsible for the spatial variations. The results demonstrate how variable the mesozooplankton community structure can be over different time-scales and provide a better understanding of zooplankton variability in the BBE and other temperate, turbid, mixed systems.

Keywords: estuary, mesozooplankton, seasonal dynamics, tidal cycle.

Introduction

Estuaries are among the most productive natural ecosystems in the world, supporting a great variety of marine resources, many of which have economic potential (Leandro *et al.*, 2007). The high levels of productivity are related to characteristics such as the regular environmental fluctuations that result from marine and freshwater influxes (Garboza da Costa *et al.*, 2008) and the abundance and fast regeneration of nutrients (run-off, rivers; Leandro *et al.*, 2007). The resultant mixtures from marine and freshwater flows, and their persistence within the estuarine zone, are the products of interference between hydrodynamic cycles that have independent, different periodicities (Lam-Hoai *et al.*, 2006). Whereas marine tidal cycles are predictable and reproducible, fluvial contributions are variable because they reflect the seasons as well as the instability of the precipitation regime throughout the watershed (Lam-Hoai *et al.*, 2006). Planktonic organisms are subject to strong tidal, diurnal, and seasonal environmental variability in estuaries (Marques *et al.*, 2009), and knowledge of zooplankton dynamics at different spatial and temporal scales is

important for understanding the ecosystem dynamics (Marques *et al.*, 2009).

The inner zone of the Bahía Blanca Estuary (BBE) is characterized by turbidity, with fine suspended sediments (silt and clay), and has been regarded as eutrophic (Freije and Marcovecchio, 2004). Because of limited freshwater discharge into the BBE (Perillo and Piccolo, 1991), tides have a strong influence on the structure and density of the zooplankton community. The mesozooplankton is dominated by the calanoid copepods *Acartia tonsa* and *Eurytemora americana* (Hoffmeyer, 1994, 2004). The former is found year-round in the plankton, with peak abundance in spring, summer, and autumn, and the latter, an exotic species possibly introduced into the estuary in ballast water (Hoffmeyer, 2004), is found during the cooler months of June–October. The mesozooplankton of the BBE has been documented in terms of composition and abundance (Hoffmeyer 1994, 2004; Hoffmeyer *et al.*, 2008), but the results were based on monthly samples and did not address short-term variation. Therefore, the current study focuses on seasonal and tidal effects on the

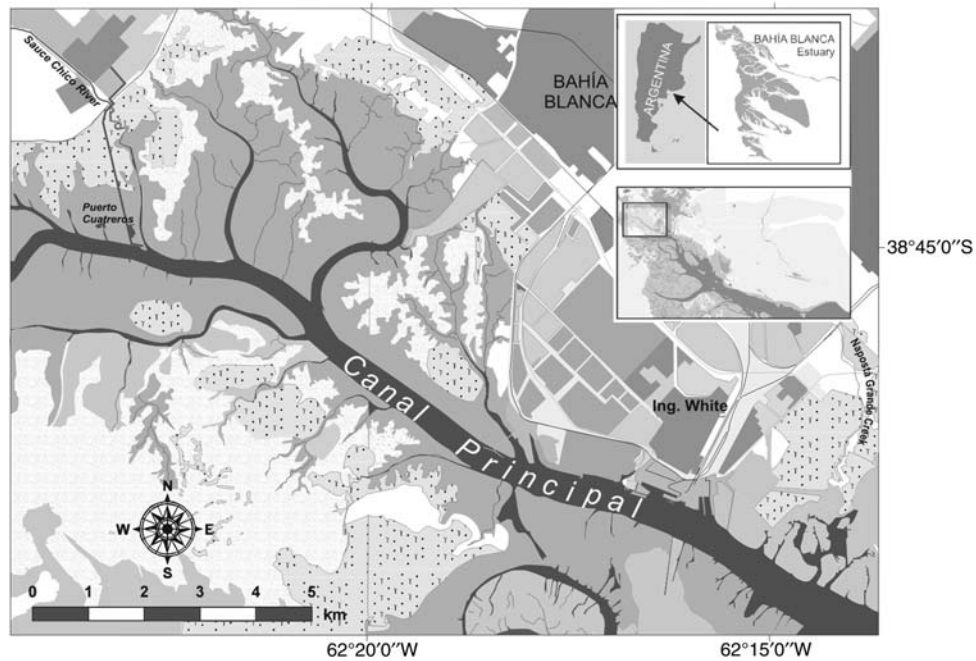


Figure 1. Map of the inner zone of the BBE, Argentina, showing the fixed sampling station at Puerto Cuatreros.

mesozooplankton dynamics in the inner zone of the BBE. The specific aims were (i) to describe the taxonomic composition and abundance pattern at a seasonal scale, and (ii) to evaluate short-term changes in the community in relation to semi-diurnal tidal cycles.

Material and methods

The BBE is located between $38^{\circ}45'$ and $39^{\circ}40'S$ and between $61^{\circ}45'$ and $62^{\circ}30'W$ in southeast Buenos Aires Province, Argentina (Figure 1). It is a mesotidal coastal plain estuary, formed by a series of northwest–southeast tidal channels separated by extensive intertidal flats, low marshes, and islands (Perillo and Piccolo, 1991). The main navigation channel, Canal Principal, is some 68 km long in a northwest–southeast direction, with depths between 3 and 20 m, and the width varies between 200 m and 3–4 km (Piccolo and Perillo, 1990). The principal energy input into the system is produced by a standing, semi-diurnal tidal wave (Perillo and Piccolo, 1991). Mean tidal amplitude varies from 3.5 m at the head of the estuary to 2.2 m at its mouth. Strong north and northwest winds dominate the typical weather pattern of the region, with a mean velocity of 24 km h^{-1} and gusting to $>100 \text{ km h}^{-1}$ (Piccolo and Perillo, 1990). The northwesterly winds parallel to the axis of the main channel, along with the oscillation of the semi-diurnal tidal wave, lead to vertical mixing and a homogeneous distribution of the main oceanographic parameters (Piccolo and Perillo, 1990). However, in the inner zone during the periods of high rainfall, the system can become partially stratified. Freshwater inflow is limited and dominated by the Sauce Chico River and Napostá Grande Creek (mean annual run-off 1.9 and $0.8 \text{ m}^3 \text{ s}^{-1}$, respectively). Puerto Cuatreros station, the fixed sampling site (Figure 1), is representative of the inner zone of the estuary (Guinder et al., 2009). It is relatively shallow (mean depth 7 m), well mixed, and turbid as a result of the combined effect of

winds and tidal currents, which sustain the large quantities of matter in suspension (Perillo and Piccolo, 1991).

Field methods and sample processing

Sampling was conducted bimonthly at Puerto Cuatreros from December 2004 to April 2006 (23 December 2004, 18 February 2005, 19 April 2005, 23 June 2005, 26 August 2005, 11 October 2005, 23 December 2005, 20 February 2006, and 5 April 2006). On each sampling date, zooplankton samples were collected during daylight at intervals of 3 h during multiple 14-h periods. Two submersible pumps were used to obtain simultaneous subsurface (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- μm -mesh plankton nets located on the pier. Water was filtered through the nets for 10–20 min, for a total sample volume of $1.5\text{--}2.9 \text{ m}^3$. To estimate the precise water volume sampled, the flow rate of the pumps was calculated before and after each sampling by recording the time taken to fill a known-volume water container. Immediately after collection, the samples were preserved in 4% buffered formaldehyde.

For zooplankton analysis, samples were first examined under a Wild M5 stereoscopic microscope to identify the organisms to the lowest possible taxon level. Most holoplanktonic forms were identified to species level, and meroplanktonic larvae and benthic or littoral forms to family, order, or class. Samples containing abundant plankton organisms were subsampled (1/10) and all individuals were then identified and counted, but for those with few plankton organisms, the entire sample was analysed and the constituents enumerated. Zooplankton abundances were expressed as number of individuals per m^3 (ind. m^{-3}).

In addition to zooplankton sampling, vertical profiles of water temperature and salinity were obtained *in situ*, employing a digital multisensor Horiba U-10. Additionally, water samples for determining chlorophyll *a* and suspended particulate matter (SPM) were collected from subsurface and just above the bottom.

Precipitation and wind data were acquired from a meteorological station located at the sampling site. Chlorophyll *a* concentration (mg m^{-3}) was measured spectrophotometrically according to the methods described in APHA-AWWA-WEF (1998). The SPM water content (mg l^{-1}) was measured gravimetrically, filtering 250 ml of water on previously dried and weighed Whatman GF/F filters (pore diameter $0.45 \mu\text{m}$). Filters were then dried at 60°C for 24 h and weighed for SPM estimation.

Statistical analysis

To overcome the uncertainty of normality and equality of variance, non-parametric statistics were used. The number of taxa and zooplankton densities (total zooplankton, holoplankton, meroplankton, adventitious plankton) were analysed using non-parametric analysis of variance (ANOVA) with a Mann–Whitney *U*-test and a Kruskal–Wallis test, to determine whether there were distributional differences among three sample settings: (i) two depths, (ii) four seasons, and (iii) five tidal phases (flood, high tide, ebb, low tide, flood). 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). Non-metric multidimensional scaling (MDS) ordination (Kruskal and Wish, 1978) and a clustering method with average linkage were used to detect and determine groups within the mesozooplankton community, on a temporal scale. These analyses were based on triangular matrices of the Bray–Curtis similarities on fourth-root-transformed abundance data to downweight the influence of very abundant organisms, using taxa that represented $>0.1\%$ of the zooplankton community (Marques *et al.*, 2009). The final stress was examined in relation to ordination dimensionality, to help select the fewest dimensions necessary to describe the data adequately. The groups determined by cluster analysis were superimposed on the MDS plot. According to Clarke and Warwick (1994), the two techniques (cluster and MDS) should be thought of as complementary when stress values are between 0.1 and 0.2, as was the case in this study. The contribution of each taxon to the average Bray–Curtis similarity within each group was analysed using the similarity percentage (SIMPER) procedure. A one-way analysis of similarity (ANOSIM) was then used to test whether the community structure differed significantly among groups. Finally, the BIOENV procedure (using the Spearman's rank correlation method) was used to determine which set of abiotic variables (water temperature, salinity, chlorophyll *a*, SPM, similarity calculated with a Euclidean distance coefficient) best explained the biological matrix (abundance data, using the Bray–Curtis similarity measure; Clarke and Ainsworth, 1993).

Results

Environmental variables

Water temperature varied seasonally, from $7.1 \pm 0.1^\circ\text{C}$ in June 2005 to $27.1 \pm 0.6^\circ\text{C}$ in February of 2005 and 2006 (Figure 2). Differences in temperature between surface and bottom samples were not large, always $<0.1^\circ\text{C m}^{-1}$. Salinity varied from 28.7 ± 0.21 to 37 ± 0.2 , and as expected, was lower when precipitation levels were high (Figure 2). Mean vertical gradients were $<0.15 \text{ m}^{-1}$, indicating homogeneity of the water column (Figure 2). The mean salinity gradient between high and low

water ranged up to 4.8 at both depths and was more pronounced in winter and spring. Chlorophyll *a* concentrations fluctuated between $1.38 \pm 0.2 \text{ mg m}^{-3}$ in June 2005 and $27.53 \pm 4.5 \text{ mg m}^{-3}$ in February 2005 (Figure 2). In terms of the tidal scale, chlorophyll *a* values were generally higher during the ebb (Figure 3). The seasonal cycle of SPM was marked, with minimum values in winter ($2\text{--}34.8 \text{ mg l}^{-1}$) and maximum in summer ($50.7\text{--}275.2 \text{ mg l}^{-1}$; Figure 2), clearly related to both precipitation and water temperature (Figure 2). Secchi disc visibility varied inversely with SPM concentration (Figure 2). Over the short term, it peaked during the ebb near the bottom (Figure 3), but was also high during the flood near the bottom (Figure 3).

Mesozooplankton composition and abundance

In all, 33 mesozooplanktonic taxa were identified during the study (Table 1). Nevertheless, overall specific richness was underestimated, because some organisms were only identified to genus or higher level (most of the meroplankton and the adventitious component). Taxa were few in winter (11–16), but increased during spring and summer (14–25; Figure 4). Differences in the number of taxa among seasons were statistically significant (Kruskal–Wallis, $Z = 29.31$, $p < 0.001$; Figure 4). Moreover, taxon richness seemed to be significantly higher near the bottom, where the contribution of benthic forms was more relevant (Mann–Whitney *U*-test, $Z = 3.46$, $p < 0.001$; Figure 4).

Total mesozooplankton abundance exhibited strong temporal variation during the study period, ranging from 20.2 ± 8.5 to $5923.4 \pm 1805.8 \text{ ind. m}^{-3}$ (Figure 4). Season was a significant source of the variation, explaining the fluctuations in abundance for total mesozooplankton (Kruskal–Wallis, $Z = 16.37$, $p < 0.001$; Figure 4). However, the differences between depths were not significant (Mann–Whitney *U*-test, $Z = 0.37$, $p = 0.356$; Figure 4). Zooplankton abundance peaked during summer and early autumn (December 2004, February 2005 and 2006, and April 2006) and was lowest during winter (June 2005; Figure 4). Abundance was up to $1354.33 \pm 563 \text{ ind. m}^{-3}$ during August 2005 (Figure 4). Holoplanktonic zooplankton were the best represented fraction and copepods the main group (Table 1). The dominant species were calanoids, predominantly the estuarine species *A. tonsa* and *E. americana*. The former dominated throughout the study, with abundances of up to 5900 ind. m^{-3} and was present year-round, but with abundance greater during summer and early autumn (40–97% of total mesozooplankton abundance). In August 2005, however, *E. americana* was the dominant taxon, accounting for $>90\%$ of the total zooplankton. Lower densities of *Paracalanus parvus* (mean 7.45 ind. m^{-3}), *Euterpina acutifrons* (4.25 ind. m^{-3}), and the mysid *Neomysis americana* (2.05 ind. m^{-3}) were also recorded, but the contribution of those species to the holoplankton fraction was very small (Table 1). Other copepod species, such as *Calanoides carinatus* and *Labidocera fluviatilis*, were found sporadically (Table 1). Meroplankton organisms, which constituted just 4–35% of total zooplankton abundance, were mainly barnacle larvae (mean abundance 87.9 ind. m^{-3} ; Table 1). Other taxa found regularly but in small numbers were spionids ($24.71 \text{ ind. m}^{-3}$), varunids ($21.68 \text{ ind. m}^{-3}$), bivalves ($20.83 \text{ ind. m}^{-3}$), and gastropod larvae ($26.09 \text{ ind. m}^{-3}$; Table 1). Of the adventitious plankton, the most common were the amphipod *Corophium* sp. (mean $24.19 \text{ ind. m}^{-3}$) and unidentified benthic harpacticoids (mean $18.14 \text{ ind. m}^{-3}$; Table 1).

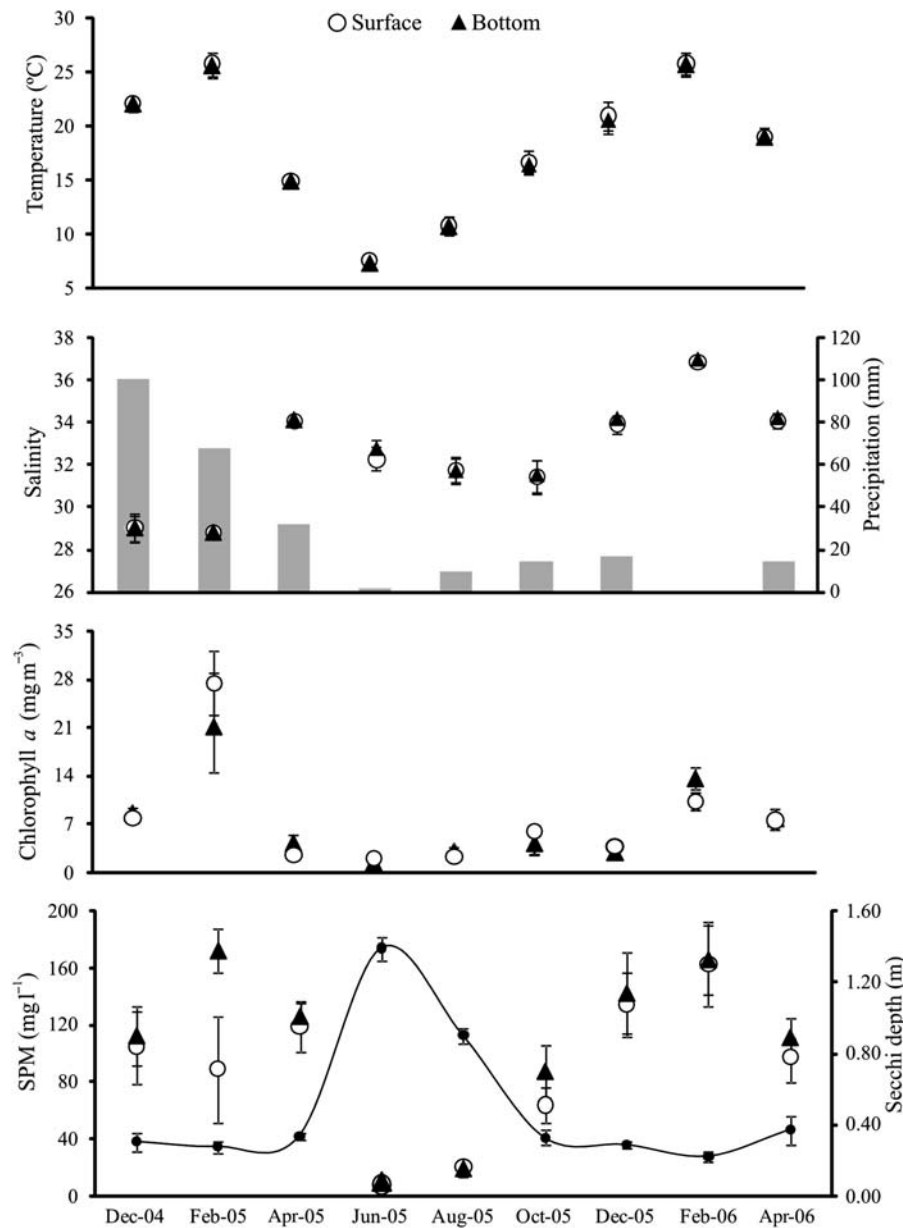


Figure 2. Seasonal variations in water temperature, salinity, precipitation, chlorophyll *a*, SPM, and Secchi depth in the inner zone of the BBE. Open circles, surface samples; closed triangles, bottom samples; Bars, precipitation; dots and line, Secchi depth.

Over a short time-scale, the zooplankton community was affected mainly by the tidal phase, especially in terms of abundance (Figure 5). Mean abundance was markedly greater during ebb tide near the surface ($4013.03 \pm 1298.15 \text{ ind. m}^{-3}$; Figure 5). Values were lowest during high ($309.25 \pm 78.52 \text{ ind. m}^{-3}$) and low tide ($379.11 \pm 178.3 \text{ ind. m}^{-3}$; Figure 5). A Kruskal–Wallis test on zooplankton density revealed significant differences in mean abundance among tidal phases ($Z = 12.79$, $p < 0.05$; Figure 5), and a similar pattern was observed for holoplankton abundance, which was dominated by *A. tonsa* (Kruskal–Wallis, $Z = 12.89$, $p > 0.05$; Figure 5). However, an inconsistent pattern was observed among tidal cycles for meroplankton (Figure 5). Abundance was greatest during ebb and low tide near the surface and at the bottom and near the surface at first flood (Figure 5). However, no statistical differences were detected for

this fraction among tidal phases (Kruskal–Wallis, $Z = 3.59$, $p = 0.464$) or sampling depths (Mann–Whitney *U*-test, $Z = 968$, $p = 0.710$). Adventitious plankton abundance seemed to be greater during flood and ebb tide near the bottom (Figure 5), but a Kruskal–Wallis test failed to detect significant differences among tidal phases ($Z = 5.05$, $p = 0.282$; Figure 5). This fraction showed a significant depth gradient, with density greatest near the bottom (Mann–Whitney *U*-test, $Z = 628$, $p < 0.05$; Figure 5).

Multivariate analysis: seasonal patterns in mesozooplankton

Classification and ordination analysis separated samples into three main groups, corresponding mainly to season (Figure 6). Based on those two plots, group 1 included 54 samples, and groups 2 and 3,

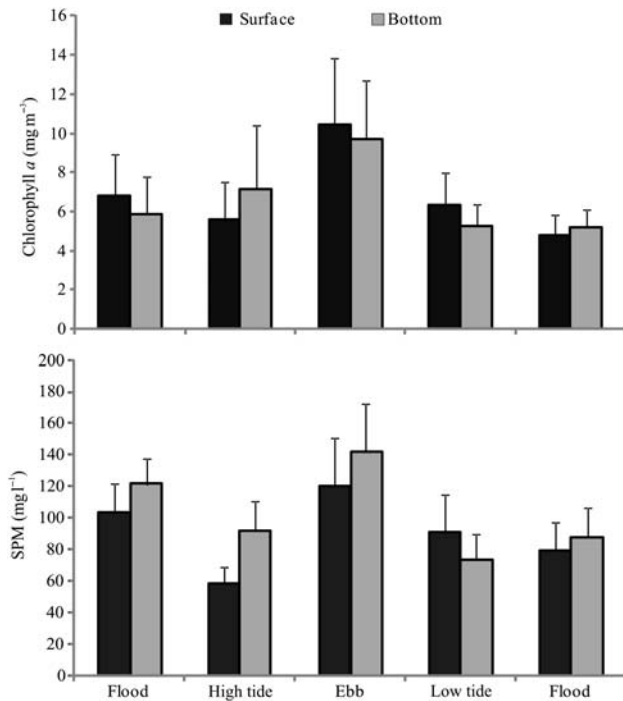


Figure 3. Chlorophyll *a* and SPM concentration (mean \pm s.d.) during the tidal cycle at Puerto Cuatreros station.

respectively, 6 and 20 samples. Figure 6 shows the two-dimensional MDS ordination of samples clustered at a similarity of 60%. Group 1 represented the austral summer/autumn samples, which were in warmer water. Group 2 included austral winter samples, taken from cooler water, and group 3 austral late-winter and spring samples. The taxa that typified group 1 were the copepod *A. tonsa*, cirripede larvae, and benthic harpacticoids (SIMPER analysis; Table 2). Gastropod larvae and decapods (Varunidae) were also common (Table 2). Group 2 consisted of *A. tonsa*, cirripedes and harpacticoids, but also of spionid larvae and the copepod *E. americana* (Table 2). The native species *A. tonsa* was typical in all groups, but densities were highest in groups 1 and 2 (Table 2). The exotic species *E. americana* was typical in groups 2 and 3, but its abundance was greater in group 3 (Table 2); it was absent from group 1 (Table 2). Considering that most of the species were found in all seasons/groups, differences among groups appeared to be mainly the result of variations in relative abundance. However, there were marked differences between summer/autumn (group 1) and winter/spring (groups 2 and 3), driven by a distinct zooplankton composition attributable to the presence of *E. americana*. Seasonal groups obtained by MDS were significantly different (ANOSIM global $R = 0.655$, $p < 0.001$, for all paired comparisons test).

BIOENV analysis revealed that water temperature was the main single physical variable closely correlated with the zooplankton community patterns ($\rho = 0.62$). A combination of temperature and salinity also revealed a high level of correlation ($\rho = 0.62$). Temperature was the dominant factor and was the single variable retained in most of the better results. SPM in combination with the above parameters and chlorophyll *a* were also closely correlated with zooplankton community structure ($\rho = 0.51$), although correlation without salinity was nearly as great ($\rho = 0.50$).

Discussion

The results presented here suggest a seasonal pattern of high abundance and taxon richness in warmer months, a condition well known in some other temperate estuaries (Vieira *et al.*, 2003; Leandro *et al.*, 2007; Marques *et al.*, 2009). Total mesozooplankton abundance mirrored the seasonal variations in copepod populations, especially those of *A. tonsa* and *E. americana*, the dominant species in the estuary. Copepods dominated in all seasons and constituted 40–98% of the total zooplankton, which is common in estuarine areas throughout the world (David *et al.*, 2005; Leandro *et al.*, 2007; Garboza da Costa *et al.*, 2008; Marques *et al.*, 2009). The most abundant taxon was *A. tonsa*, which is also typical for estuarine environments (Mouny and Dauvin, 2002; David *et al.*, 2005); it is known to be abundant in water containing a high concentration of particulate organic matter (Marques *et al.*, 2007). It peaked during summer and autumn (December 2004 and February and April 2006) and was at its minimum abundance in winter (June–August 2005). In August 2005, *E. americana* was the dominant taxon, accounting for >90% of total zooplankton abundance. According to Berasategui *et al.* (2009), *E. americana* peaks between June and October in the inner zone of the estuary, during which time it coexists with *A. tonsa* and maintains a competitive relationship (Hoffmeyer, 1994, 2004). Thereafter, it disappears from the water column but persists in its resting stage in bottom sediments (Berasategui *et al.*, 2009). During the past 20 years, the species has become the most abundant calanoid copepod in the BBE from August to October, excluding the dominant native species, *A. tonsa* (Hoffmeyer, 2004).

There was seasonal succession of the dominant taxa of meroplankton and the adventitious fraction over the study period. Cirripede larvae were the most important contributors. In the BBE, there are only two barnacle species: *Balanus glandula* (winter) and *Balanus amphitrite* (summer; Hoffmeyer, 2004). Hence, the maximum values found in August 2005 would have been *B. glandula* and the maximum in summer would have corresponded to *B. amphitrite*. Decapod larvae (mostly varunids) were also abundant, especially during summer; this is not surprising because the local benthic community at that time of year contains common decapod populations (mainly the crabs *Neohelice granulata* and *Cyrtograpsus altimanus*; Spivak, 1997). In winter and spring, those larvae are replaced by the nauplii of other crustaceans, such as copepods and barnacles (Hoffmeyer, 2004). Although they were not taxonomically examined in detail, a high abundance of benthic harpacticoid copepods was found in the samples. These organisms were relatively common year-round, but with higher values in spring and summer. Accounting for the shallowness of the water column and the influence of tides and winds as mixing agents, this phenomenon might be indicative of the existence of benthic-pelagic coupling in the inner zone of the estuary. If so, it would support the findings in other similar shallow systems, where the meiobenthos contributes extensively to mesozooplankton biomass (Bell and Sherman, 1980; Palmer and Brandt, 1981; Armonies, 1988; Villate, 1997), perhaps with a significant inference in terms of the functioning of coastal systems. Cyclic inputs of meiofauna into the water column might be relevant in the diets of pelagic planktophages and filter-feeding benthic populations (Villate, 1997), and it may have consequences for increasing the nutritional value of resuspended

Table 1. Mean abundance (ind. m⁻³) by season of each taxon registered during the sampling period, with horizontal lines separating holoplankton (top), meroplankton (centre), and the adventitious fraction (bottom).

Taxon	Summer		Autumn		Winter		Spring	
	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
<i>Acartia tonsa</i>	1 014.15	956.79	116.53	1 076.01	3 293.4	1 777.27	903.71	1 217.10
<i>Eurytemora americana</i>	153.55	359.57	60.58	97.22	329.71	312.75	236.68	139.84
<i>Paracalanus parvus</i>	16.72	1.90	7.62	3.92	6.96	2.56	3.09	4.05
<i>Labidocera fluviatilis</i>	0.10	0.06	0.47	0.52	0	0	0	0
<i>Calanoides carinatus</i>	0	0.39	0.06	0	0	0.35	0	0.06
<i>Oithona nana</i>	0.90	0.51	2.96	0.52	0.63	0.73	0.16	0.11
<i>Euterpina acutifrons</i>	4.06	1.84	12.50	3.58	6.93	3.89	1.17	0.89
<i>Neomysis americana</i>	0.10	3.41	0.31	8.11	0.94	3.80	0.04	1.57
<i>Bosmina longirostris</i>	0	0.06	0	0.35	0	0	0	0
Anostraca larvae	0.06	0	0.03	0	0	0	0	0
<i>Penella</i> sp.	0	0	0	0	0	0	0.27	0.16
<i>Monstrilla</i> spp.	0.41	0.39	0.03	0.45	0	0.75	0	0.04
<i>Longipedia</i> sp. larvae	0.94	0	0	0	2.52	0	0.43	0.22
<i>Ciona intestinalis</i>	0	0.06	0.03	0.49	0	0.03	0	0
<i>Botryllus</i> sp.	0	0	0	0	0	0	0.04	0.02
Cirripedia larvae	123.04	50.75	79.75	17.53	75.28	85.70	130.98	179.20
Spionidae larvae	12.81	15.23	11.02	3.92	35.89	32.41	56.99	36.61
Aphroditidae larvae	0.35	1.60	1.10	0.45	0.63	0.96	0.82	0.59
<i>Tubularia</i> sp. larvae	0.97	1.01	4.25	3.35	0.63	0.93	3.01	3.02
Gastropoda larvae	20.09	71.02	5.38	8.45	39.02	46.58	13	11.17
Bivalvia larvae	3.21	42.71	4.16	6.04	34.32	52.43	3.125	2.78
Ceriantharia larvae	0.85	5.74	0.31	2.25	5.98	7.65	1.9	1.98
Bryozoa larvae	0	0	0	0	0	0	0.04	0.02
Varunidae larvae	22.37	32.30	7.65	42.16	34.13	25.60	11.64	14.23
Decapoda larvae	0.35	0.39	0	0.73	0.63	0.73	0.04	0.62
Teleostei eggs	0	0	0	0	0	0.48	0	0
Harpacticoida	12.44	29.77	6.90	13.66	23.58	41.82	7.30	7.71
<i>Corophium</i> sp.	0.09	58.98	0.22	14.03	0.98	122.76	20.74	18.65
<i>Caprella</i> sp.	0	8.20	0	0.76	0	2.24	0.08	1.43
Gammaridae	0	0	0	0.97	0.31	0.38	0.39	0.26
Ostracoda	0.23	15.57	0.13	1.97	7.24	13.49	0.08	0.09
Isopoda	0	0	0.03	0	0	0	0	0
Foraminifera	0.09	14.07	2.68	0.19	28.31	21.74	1.29	0.95

material (Rhoads *et al.*, 1975; Tenore, 1976), the survival of benthos (Rhoads and Young, 1970), and meiofauna dispersion (Bell and Sherman, 1980).

Coastal ecosystems in temperate zones often exhibit spatio-temporal gradients, in both environmental variables and zooplankton assemblages, because of their tight physico-biological coupling (Marques *et al.*, 2007). Here, temperature was the most important single factor in determining the seasonality of zooplankton composition and abundance, agreeing with the results of other studies in similar areas (Villate, 1994; Vieira *et al.*, 2003) that demonstrated that the metabolic processes of zooplankton are related to water temperature (Leandro *et al.*, 2007; Marques *et al.*, 2009). However, it is known that the factors that determine taxa distribution generally interact in complex ways (Marques *et al.*, 2009). In fact, earlier studies in the same estuary revealed the *A. tonsa* population to be positively influenced by temperature increase (Sabatini, 1989; Hoffmeyer *et al.*, 2008) and also by enhanced photoperiod and radiation and decreases in salinity (Hoffmeyer *et al.*, 2008). The influence of salinity on the *A. tonsa* population can also be supported by the results here.

The hypersalinity observed during summer 2005/2006 could have influenced the dynamics of *A. tonsa*, delaying the peak to February rather than December. Calliari *et al.* (2006) showed that increases in salinity negatively influence the fecundity of this species (hatching success, egg production, development of nauplii larvae), affecting population growth dynamics.

For *E. americana*, Berasategui *et al.* (2009) reported that a combination of low temperature, high salinity, and good food availability modulates the planktonic pulse observed each year in the BBE. These conditions stimulate the hatching of the diapause eggs in the bottom sediments, supporting the onset of the *E. americana* pulse. This species is classified as herbivorous based on its oral field and cephalic appendices (Hoffmeyer and Prado Figueroa, 1997), so has several advantages in the winter/spring phytoplankton bloom. This scenario, coupled with the low temperatures, appears to provide optimal conditions for the development of this invasive species. Therefore, the partial exclusion of the indigenous *A. tonsa* during this period could be attributed to the fact that the exotic *E. americana* utilizes the phytoplankton bloom more efficiently than *A. tonsa*. Such other

biotic factors as selective predation by fish larvae and ctenophores (Hoffmeyer *et al.*, 2008) seem also to contribute to the *A. tonsa* decline during winter and spring. The gradients of the main environmental factors seem to have given rise to niche separation, facilitating the coexistence of the two copepod populations in the estuary.

Zooplankton abundance in estuaries is potentially limited by two main characteristics: turbidity and tidal currents (McLusky

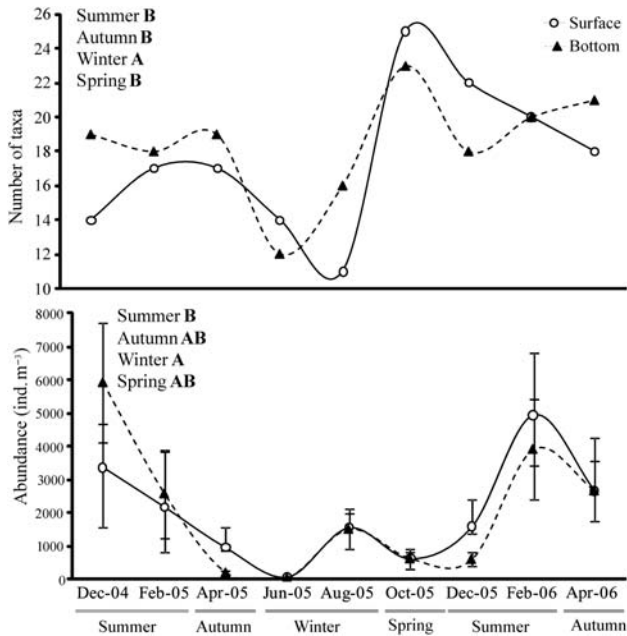


Figure 4. Number of taxa and mesozooplankton abundance (mean \pm s.d.) during the study period. Seasons with the same emboldened letters do not differ significantly according to the Dunn's test.

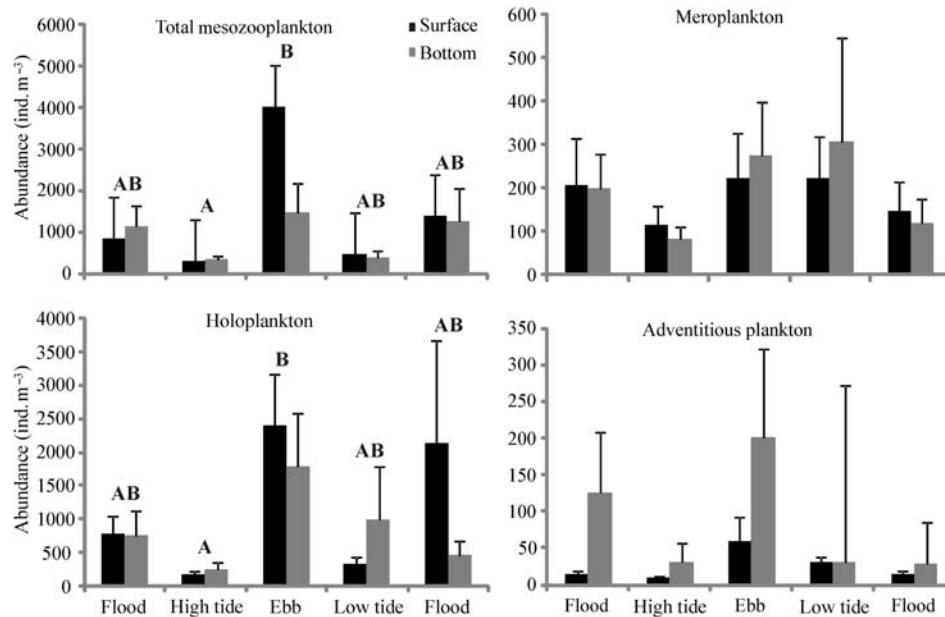


Figure 5. Mean abundance (mean \pm s.d.) of mesozooplankton, holoplankton, meroplankton, and the adventitious fraction. Abundances with the same emboldened letters do not differ significantly according to the Dunn's test.

and Elliot, 2004; Marques *et al.*, 2009). SPM reduces the penetration of irradiance into the water column, affecting phytoplankton growth (Colijn, 1982). Therefore, reduced primary production can indirectly control the temporal variation in planktonic organisms (Marques *et al.*, 2009). In this work, SPM in combination with other variables were also clearly closely correlated with mesozooplankton community structure. Suspended sediments and detritus are a good food source for copepods (Roman, 1984; Irigoien and Castel, 1995; Diodato and Hoffmeyer, 2008). Roman (1984) showed that the ingestion rate of *A. tonsa* on detritus (alone and mixed with algae) increased over the range of concentrations tested. Further, Roman *et al.* (2001) suggested that the ability of some copepod species to ingest suspended sediments and detritus allows them to prosper in areas of maximum turbidity. In the BBE, the SPM concentration varies from 30 to 400 mg l⁻¹ in the inner zone and is derived from the erosion of tidal flats and island shores (Piccolo and Perillo, 1990). During certain periods, phytoplankton and microzooplankton are scarce in the estuary, so suspended particles and detritus become the main food of plankton and benthos filter-feeding consumers. Detritus does indeed constitute a supplementary diet to algae for *A. tonsa* (Diodato and Hoffmeyer, 2008).

Mesozooplankton abundance in the BBE seemed to be influenced largely by semi-diurnal tidal cycles, especially during ebb conditions. Greatest abundance coincided with peak current velocities in the inner zone of the estuary (Perillo and Piccolo, 1991). Similar results were given by Morgan *et al.* (1997) for the Columbia River Estuary, where greater densities of the planktonic copepod *E. affinis* were found near the bottom around the time of maximum ebb velocities. Hsieh *et al.* (2010) reported that the distribution of the dominant taxa in the Tanshui River system was affected by the ebb through the increasing of flow velocity. Likewise, Devreker *et al.* (2008) observed that in the Seine Estuary, France, copepod population structure varies according to the main hydrodynamic properties of the water masses. Zooplankton organisms can employ active and passive

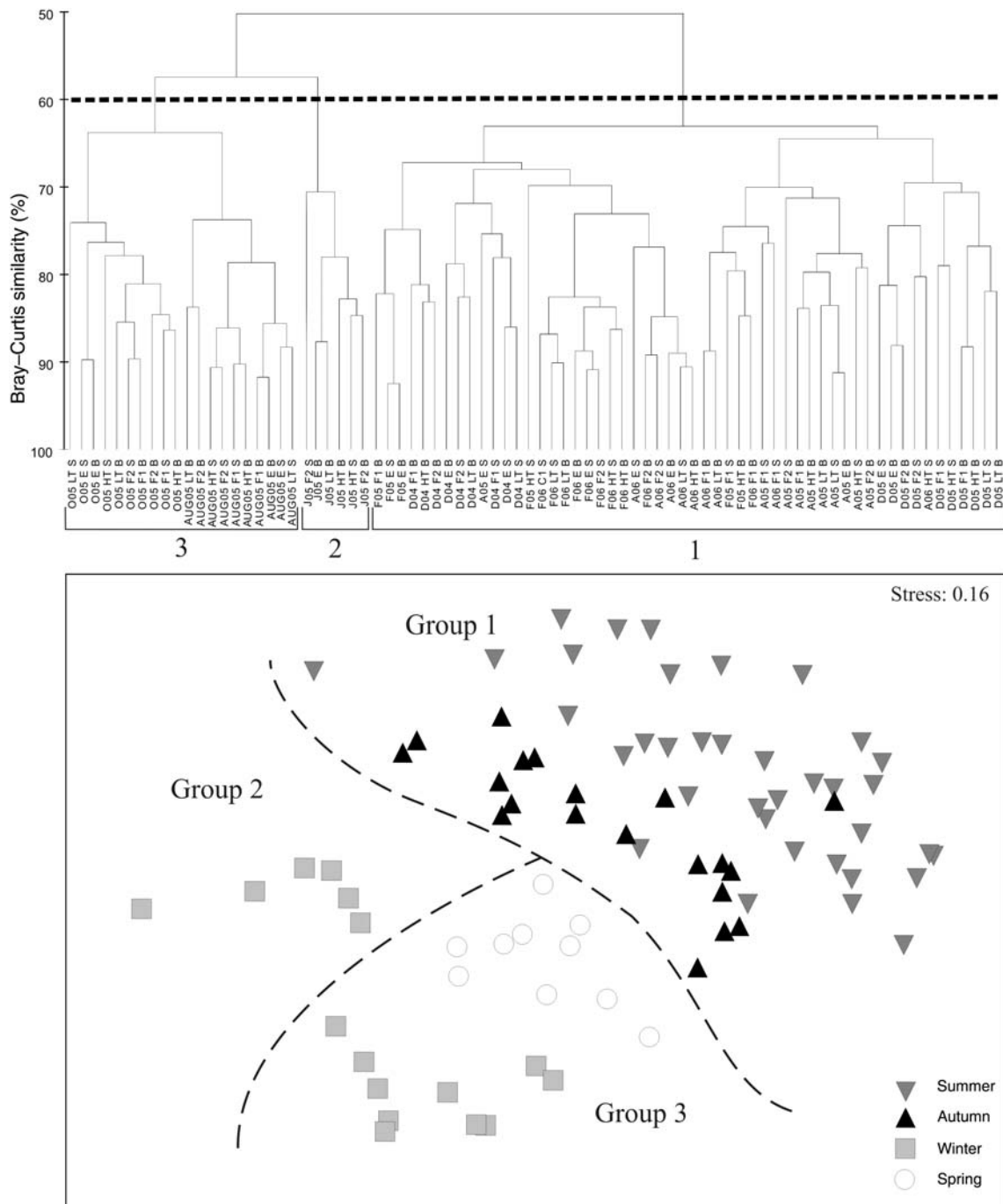


Figure 6. Cluster and MDS plots, showing the sample groups observed in the inner zone of the BBE. Cluster groups obtained at a similarity level of 60% (dashed line) were superimposed on the MDS plot. The main groups shown in the MDS are separated by dashed lines. D, December; F, February; A, April; J, June; AUG, August; O, October; F1 and F2, floods; HT, high tide; E, ebb; LT, low tide; S, surface; B, bottom.

mechanisms to enhance retention in particular estuarine regions. [Castel and Veiga \(1990\)](#) suggested that the copepod *E. affinis* in the Gironde Estuary is maintained through the same hydrological processes that trap and concentrate suspended particles. Similar results were mentioned by [Morgan et al. \(1997\)](#) for a benthic harpacticoid in the Columbia River Estuary, where the distribution and abundance mirror that of SPM.

In our study, the patterns of abundance and distribution of mesozooplankton did not match those of the SPM, suggesting that mechanisms additional to hydrodynamic processes would

maintain the populations in the inner zone of the estuary. Additionally, there was no evidence of a tide-related migration pattern, which is common in other estuaries ([Hough and Naylor, 1991, 1992](#); [Morgan et al., 1997](#); [Devreker et al., 2008, 2010](#)). Although the species disperse into the water column during flood tides, population densities were greatest during the ebb tide near the surface. Tidal migration has been reported in estuarine systems with high river outflows ([Morgan et al., 1997](#)), and this pattern could be the adaptive result of organisms to the net outflow conditions. Variation in vertical dispersion may lead to

Table 2. SIMPER procedure (cut-off 50%) for zooplankton abundances per group determined with MDS, showing taxon percentage contribution to the average similarity within groups 1, 2, and 3.

Taxon	Group 1 (64.52)	Group 2 (72.66)	Group 3 (70.98)
<i>Acartia tonsa</i>	34.15	31.46	20.07
Cirripede larvae	13.06	18.08	16.17
Harpacticoida	11.74	15.66	13.83
Gastropod larvae	9.58	–	0.48
Varunid larvae	7.25	–	2.17
Spionid larvae	6.01	12.14	9.00
<i>Corophium</i> sp.	5.07	1.73	4.57
Ceriantharia larvae	4.72	–	0.61
<i>Paracalanus parvus</i>	2.79	1.37	0.09
<i>Euterpina acutifrons</i>	2.46	7.07	4.69
Bivalve larvae	1.42	–	–
<i>Eurytemora americana</i>	–	10.90	27.08
Total	98.25	98.41	98.15

Total refers to the percentage contribution to similarity accumulated for each group.

avoidance of surface water during the flood by the organisms swimming into deeper water moving faster upstream (Devreker *et al.*, 2008). However, in low-flow habitats, this is probably not necessary and it may be better for the organisms to stay at the surface in areas of high concentration of food. In addition, phytoplankton growth in the BBE is limited by light penetration (Guinder *et al.*, 2009), so is concentrated in the upper layer. Taking into account the fact that the fixed sampling site coincided with the margin of the main channel, the increase in abundance during the ebb may be associated also with a lateral movement of the species to areas of decreased flushing, such as the channel margins. This option has been suggested for other copepod species to resist the seaward net flow during the ebb (Cronin *et al.*, 1962; Roddie *et al.*, 1984; Castel and Veiga, 1990; Menéndez *et al.*, 2011).

In this study, the abundance of adventitious plankton peaked during the ebb near the bottom, but also during floods at the same depth. Hence, the presence of benthic forms in the water column appears to be modulated mainly by velocity asymmetries in the tidal currents (Piccolo and Perillo, 1990) in a similar way to that described for the SPM. According to Walters and Bell (1986), the pelagic occurrence of 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 pattern observed was attributable to resuspension of the organisms from sediments into the water column when tidal currents were stronger, i.e. during ebb and flood tides (Piccolo and Perillo, 1990). Our results support the findings in other shallow systems where meiobenthos contributes extensively to mesozooplankton biomass over the whole tidal cycle (Bell and Sherman, 1980; Palmer and Brandt, 1981; Armonies, 1988; Villate, 1994).

This study has analysed the seasonal and tidal variation in mesozooplankton composition and abundance in the inner zone of the BBE. The conclusions are that, although the main difference among seasons was revealed through variations in abundance, changes in the composition (mainly variations in *E. americana* population dynamics) were also relevant at the time-scale studied. On the other hand, abundance was the variable that

best explained the differences among tidal phases. Seasonal differences are well explained by the natural change of abiotic and biotic conditions, but temperature played a key role in structuring the mesozooplankton community. At a tidal scale, the zooplankton was significantly more abundant during the ebb tide, suggesting that local hydrological conditions are responsible for the spatial variations. Note that this short-term variability in mesozooplankton abundance was relevant and in some cases, of equal or greater magnitude to that arising at longer time-scales.

To conclude, our results confirm how variable the mesozooplankton community structure can be over different time-scales in mesotidal temperate estuaries. This variability needs to be taken into account in any zooplankton monitoring programme conducted in a temperate system dominated by such a tidal regime.

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