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Wind effect as forcing factor controlling distribution and diversity of copepods in a shallow temperate estuary (Solis Grande, Uruguay)*

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SUMMARY: Spatial and temporal variations of planktonic copepods were investigated in relation to environmental conditions in the Solís Grande estuary (34°22'S, 55°33'W), Uruguay. Over a period of fifteen days, samples were taken daily at three stations along the main axis of the estuary, and the species composition and abundance were determined. The Solís Grande is a shallow estuary (2.0 m) with no vertical discontinuities. Comparisons of surface *versus* bottom hydrographic values indicated no vertical stratification of temperature and salinity during the studied period. The species-environmental relationships explain 63.6% of the system's variability considering the two first axes from Redundance Analysis (RA). Copepods showed strong differences in distribution and abundance between stations and successive days. In the region the winds quickly rotate from sectors S-SE (frontal period) to E-NE (post-frontal period). Changes in abundance were significantly related to the inflow and outflow of water produced by the rotation of winds. At smaller space and time scales, the differences highlighted by the RA were the result of wind-forced hydrodynamics after the frontal period. In this situation hydrographic features were dominant (factor one of RA) and wind effects were of secondary importance (factor two of RA). Six species were identified and the estuary was clearly dominated by *Acartia tonsa*. The results showed two negatively correlated groups: one was integrated by *Oithona nana*, *O. simplex*, *Paracalanus parvus* and *P. crassirostris* while the second group was integrated by *A. tonsa* and *Euterpina acutifrons*. Environmental variability may be responsible for the low diversity.

Key words: zooplankton, copepod diversity, environmental factor, wind.

INTRODUCTION

Temporal changes in the distribution and abundance of zooplankton may be caused by variations of many abiotic and biotic factors. Especially in estuaries the distribution of zooplankton depends largely upon the physical and dynamic characteristics of the water. Relations between plankton and environment in estuarine areas have been studied by several authors, by analyzing the distribution of species in relation to horizontal and vertical environmental gradients (Maurer *et al.*, 1978; Collins and Williams, 1982; Stearns *et al.*, 1989; Hough and Naylor, 1991; Madariaga *et al.*, 1992; Laprise and Dodson, 1993, 1994). More recently the effect of wind on fish larvae (Govoni and Pietrafesa, 1994) and on dispersal dynamics of postlarval macrofauna of benthic systems (Commito, 1995) was introduced in models as an explanatory variable.

In the Río de la Plata, meteorological factors (rotation of winds) play an important role in the dynamic of its coastal systems (Balay, 1961; Ottman

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and Urien 1965; Nagy *et al.,* 1987; Norbis, 1995; Guerrero *et al.,* 1997). The effect of the astronomical tides along the coast is minimal. This is due to the dynamics of the estuary, to its shallow depth and mainly to the wind action that hides its effect (Balay, 1961; Ottman and Urien, 1965). At Cassino Beach in Southern Brazil, Odebrecht *et al.* (1995) gave evidence that the mesoscale variability of chlorophyll *a* and accumulation of patches is primarily controlled by meteorological factors. In Uruguayan estuaries, the zooplankton has received little attention. Milstein (1983) and Milstein and Juanicó (1985) published results on spatial and temporal distribution of plankton communities in Maldonado Bay. These studies demonstrated that copepods dominate the larger members of the zooplankton, and that variations at different spatial and temporal scales overlap, involving different main factors in each scale.

The aim of this study was to investigate spatial and temporal small-scale variations in planktonic copepods in relation to environmental conditions in the Solís Grande estuary.

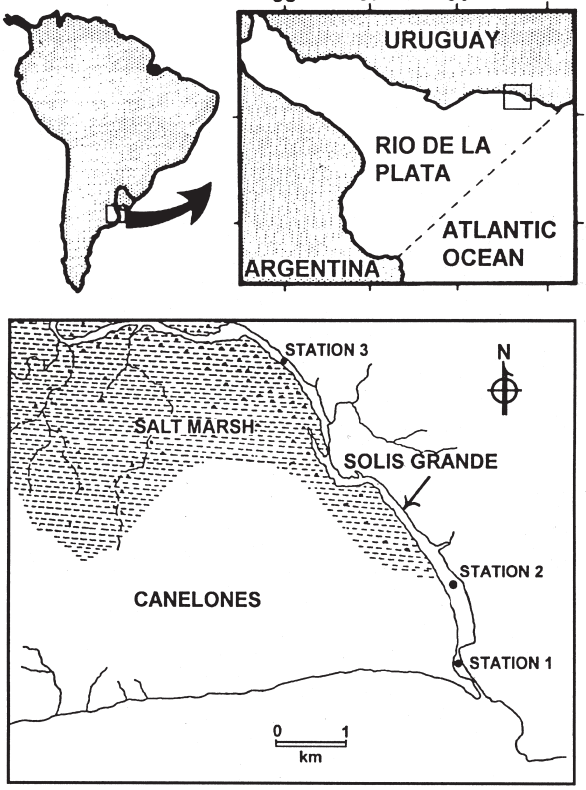

FIG. 1. – Study area and locations of the three stations sampled from November 16 to 30, 1982.

MATERIALS AND METHODS

Sampling area

The Solís Grande river (Fig. 1) situated in the Department of Canelones about 80 km off Montevideo (34°22'S, 55°33' W, Uruguay), is the second largest estuary on the Uruguayan coast. It covers an area of 1.409 Km^2 with an average depth of 2.0 m and a mean annual discharge of 145 m^3 s^{-1}. No data exist on astronomical tides for Solis Grande estuary, but the adjacent area (Río de la Plata) have a small tidal amplitude (0.3 m) (MTOP-PNUD, 1979; Mazio and Martínez, 1989). The lower estuary has a gentle slope and its communication with the Río de la Plata is permanent, causing an important inward water flow from the latter. The characteristics and rotations of predominant winds (north and south sectors) over the year generate strong upstream coastal water currents from the Río de la Plata (MTOP-PNUD, 1979).

Sampling and field measurements

Zooplankton and hydrographical data were obtained daily from November 16 to 30, 1982 between 0700 and 0900 h (local time). Three stations were sampled on a roughly north to south transect across the Solís Grande estuary (Fig.1). The location of the stations was selected to cover the entire salinity gradient from the upstream of Solís Grande to its mouth. Depths at the stations 1, 2 and 3 were 2.5 m, 1.8 m and 2.4 m respectively. Water temperature and salinity were measured (YSI model 33 SCT) at each station at the surface and bottom, and transparency was determined with a Secchi disk. Hourly data of wind direction and speed, were provided by the Oceanographic, Meteorological and Hydrographical Service of the Army (SOHMA, Montevideo) at Laguna del Sauce weather station, situated 40 km from the study area.

The sampling strategy was oriented to detect zooplankton and environmental variability at a small scale (days). On days 23 and 29, only station 2 was sampled, and at day 27 no samples were taken. The zooplankton samples corresponding to station 3 at day 16 were lost. At each station, zooplankton samples were collected from a standard net (158 μm) with a flowmeter fitted in its mouth. Five-minute horizontal tows were carried out at approximately 1 m s^{-1}, sampling water of the upper meter of the column ("surface") and of the lower meter ("bottom").

Sample treatment and data analysis

Each sample was first described by the abundance of species of copepods. Samples for counting of species were brought to a constant volume (100 ml) and subsampled with a 10 ml Stempel pipette. At least two aliquots, containing a minimum of 500 zooplankters, were counted using a Wild M5 stereoscopic microscope. The resulting abundances were expressed as the mean number per cubic meter.

In order to describe characteristics and distribution patterns of zooplankton species in the sampling period, the Shannon-Weaver Diversity Index (Shannon and Weaver, 1949) was used. To test differences between species collected in surface and bottom water, the non-parametric Mann-Whitney test (Sokal and Rohlf, 1981) was applied. Differences between surface and bottom temperature and salinity were tested by Student-test (Sokal and Rohlf, 1981).

Abundance species data were log (x+1) transformed. Two "stations-day-by-variables" matrices (species and environmental) were constructed. Species were classified hierarchically, for cluster analysis choosing the correlation coefficient as a measure of associations (Sokal and Rohlf, 1962) and the unweighted pair group method using arithmetic averages (UPGMA; Sokal and Michener, 1958) as aggregation algorithm. The distortion of the relationships was measured by cophenetic correlation coefficient (Cunningham and Ogilvie, 1972). Relationships between abundance of zooplankton species and environmental variations were analyzed using Redundancy Analysis (RA) (ter Braak, 1987). It is used when responses of the species are expected to be related to their habitat conditions, as is the case in short segments of ecological gradients (Jongman *et al.,* 1987). We used the computer program CANOCO (Canonical Community Ordination) (ter Braak, 1988; 1990) that includes RA. The "stations-day-environmental" matrix was constructed taking into account the following variables: temperature (TEM), salinity (SAL), depth of Sechii disk (SEC), occurrence of calms (C), daily average wind speed (Avs), daily maximum speed (Maxs), and persistence of winds (total number of occurrences per sector during a period of 18 hours: from 0600 to 2400) in sectors north (N), north-east (NE), north-west (NW), south (S), south-west (SW), south-east (SE), east (E) and west (W).

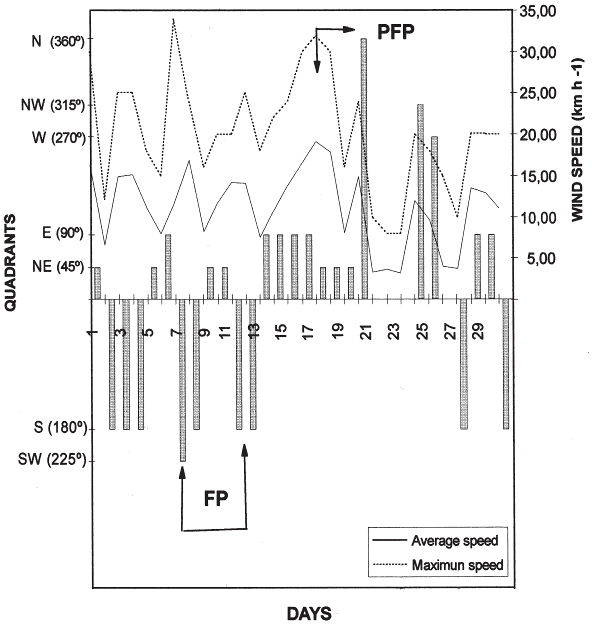

FIG. 2. – Daily average and maximum speed and dominant persistence of winds during November, 1982. The bars indicates the direction of wind; FP: Frontal Period and PFP: Post Frontal Period.

RESULTS

Environmental variables

Figure 2 shows that from November 6 to 8, 1982, roughly ten days before the start of our study, the winds blew from the quadrant E to SW-S reaching velocities up to 34 km h^{-1}. Strong E to NE winds (20-32 Km h^{-1}) prevailed during days 14 to 18, and relatively weak variable winds during days 21 to 23. Calm periods predominated after the passage of fronts.

There were no significant differences (p>0.05) between temperature and salinity data from surface and bottom samples (Table 1), so average values were used for later analysis. From days 19 to 21 colder and saltier water entering from the Rio de la Plata was registered (Figs. 3a and 3b). Subsequently, salinity declined and temperature increased with a similar trend at the three stations. There was an inversion of the salinity gradient from days 25 to 31 (Fig. 3b).

At the three stations, the water transparency increased in a similar manner during days 18 to 21, differed during days 22 to 24 and tended to remain stable up to the end of the sampling period (Fig. 3c).

Zooplankton composition

The mesozooplankton of the Solís Grande estuary was clearly dominated by copepods. No signifi-

TABLE 1. – Environmental variables registered along the studied period at the 3 stations and results of Student t-test for testing the differences between surface and bottom (STD: standard deviation; ns: p>0.05).

Environmental variable	Surface Mean	Surface STD	Surface N	Bottom Mean	Bottom STD	Bottom N	t-value
Station 1							
Temperature	17.17	3.343	13	15.71	3.389	13	1.106ns
Salinity	16.74	6.649	13	18.92	7.997	13	0.757ns
Station 2							
Temperature	17.757	2.467	14	16.757	2.314	14	1.105ns
Salinity	15.771	5.335	14	16.455	5.285	14	0.382ns
Station 3							
Temperature	19.031	2.7376	13	17.931	2.785	13	1.105ns
Salinity	13.001	5.7853	13	13.301	5.617	13	0.134ns

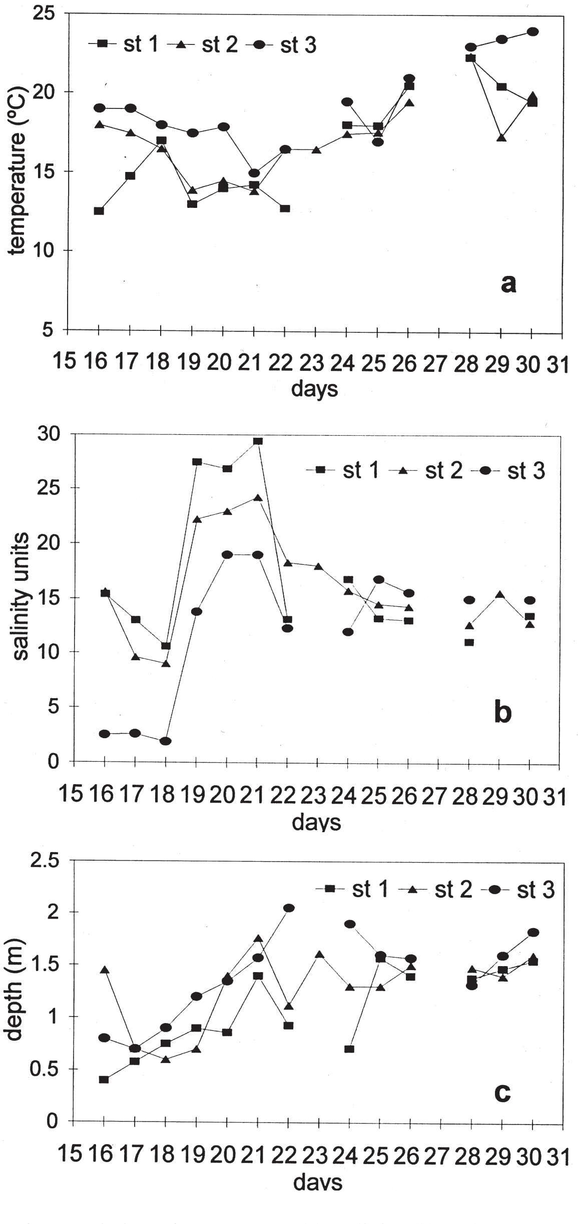

FIG. 3. – Variation of temperature (a), salinity (b) and water transparency (c) during the study period at the three sampling stations.

TABLE 2. – Results for species Mann-Whitney test (MW) for testing the differences between surface and bottom sampling (in all cases p>0.05).

Species	MW test	Sig. level
Acartia tonsa	0.0024	0.9604
Paracalanus parvus	1.1115	0.2918
Parvocalanus crassirostris	3.9878	0.0658
Oithona nana	1.5702	0.2102
Oithona simplex	1.3611	0.2433
Euterpina acutifrons	2.1005	0.1472

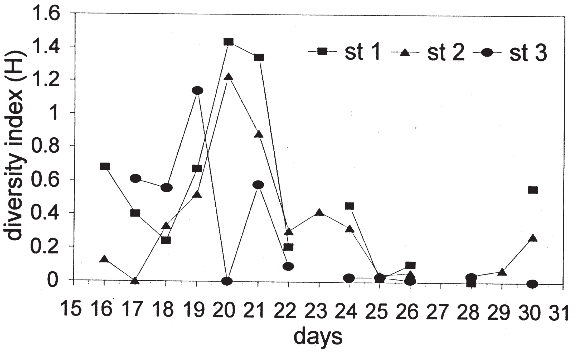

FIG. 4. – Changes of the diversity H by sampling stations.

cant differences of composition (p>0.05) were registered between surface and bottom samples (Table 2). Six species were identified, and *Acartia tonsa* was the dominant species throughout the sampling period and at the three stations analyzed (Tabla 3).

At the three sampling stations, the species diversity increased on day 19, decreased on day 21, and the values were relatively stable from day 22 until the end of the sampling period (Fig. 4).

Cluster analysis (Fig. 5) showed two groups negatively correlated (r = -0.10), of which one group included *Oithona nana*, *Oithona simplex*, *Paracalanus parvus* and *Parvocalanus crassirostris*

TABLE 3. – Species (%) and total copepod abundance (N m^{-3}) by station along the sampling period in the Solis Grande river (Aton = *Acartia tonsa*, Ppar = *Paracalanus parvus*, Pcra = *Parvocalanus crassirostris*, Onan = *Oithona nana*, Osim = *Oithona simplex*, Eacu = *Euterpina acutifrons*).

Station	Day	Aton	Ppar	Pcra	Onan	Osim	Eacu
1	16	389	9	9	69	9	0
1	17	224	2	2	25	2	0
1	18	129	0	0	9	0	0
1	19	89	0	59	0	0	0
1	20	156	8	166	137	143	0
1	21	4	23	46	74	18	0
1	22	1305	3	19	34	0	0
1	23						
1	24	1791	9	132	84	2	2
1	25	1103	0	3	0	0	0
1	26	3864	13	59	0	0	2
1	27						
1	28	1509	0	0	0	0	0
1	29						
1	30	1203	35	3	176	16	0
	total	11767	103	499	607	190	4
	percentage	89.34	0.78	3.79	4.61	1.44	0.03
2	16	4591	3	71	6	27	0
2	17	681	0	0	0	0	0
2	18	211	0	9	9	0	0
2	19	484	0	41	36	0	2
2	20	95	16	17	13	10	2
2	21	6	0	83	72	2	0
2	22	847	0	44	21	0	0
2	23	1096	0	105	31	0	2
2	24	3980	0	299	59	0	0
2	25	5242	4	13	13	0	0
2	26	12136	0	104	9	0	0
2	27						
2	28	10907	2	45	0	0	23
2	29	5089	3	13	44	0	0
2	30	4202	13	9	248	16	2
	total	49571	43	853	563	56	32
	percentage	96.97	0.08	1.67	1.10	0.11	0.06
3	16						
3	17	119	9	0	19	0	0
3	18	59	0	0	19	0	0
3	19	349	9	89	49	29	19
3	20	9	0	0	0	0	0
3	21	1079	0	59	49	79	0
3	22	2039	0	0	39	0	0
3	23						
3	24	2199	0	0	0	9	0
3	25	23079	9	79	9	0	0
3	26	19549	0	29	0	0	0
3	27						
3	28	16749	0	0	0	0	99
3	29						
3	30	2479	0	0	0	0	0
	total	67709	27	256	184	117	118
	percentage	98.97	0.04	0.37	0.27	0.17	0.17

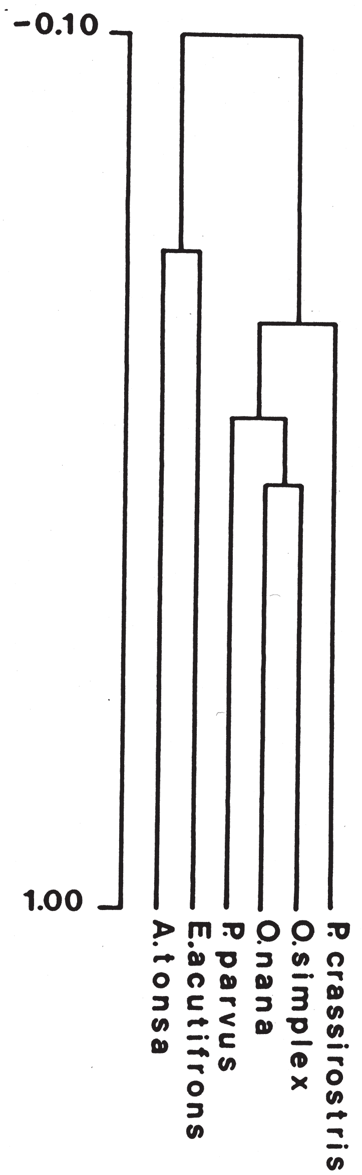

FIG. 5. – Classification of species according to cluster analysis. Ordinate shows coefficient of correlation. Cophenetic correlation coefficient: 0.88.

while the second group included *Acartia tonsa* and *Euterpina acutifrons*.

Table 4 gives the correlations matrix of RA for the 14 environmental variables, the three species axes and the three environmental axes. The correlation between the first species axis and the first environmental axis was 0.85 and the correlation between the second axis was 0.71. The eigenvalues and their cumulative percentage for ordination axes indicate that the first two axes represent 63.6%. In the following, results and discussion therefore relate to axes 1 and 2.

The species-environment biplot ordination (Fig. 6) displays the results for the fourteen environmental variables and the six species, without showing stations days samplings. The first axis separates *A. tonsa* and *E. acutifrons* from the rest of species. Positive scores on axis 1 were associated with maximum temperature, northern winds and east winds.

TABLE 4. – Correlation coefficients among environmental variables, species axes and environmental axes, and ordination results estimated by redundancy analysis.

	SPEC AX1	SPEC AX2	SPEC AX3	ENVI AX1	ENVI AX2	ENVI AX3
SPEC AX2	0.1876					
SPEC AX3	-0.0305	-0.2277				
ENVI AX1	0.8536	0.0001	-0.0002			
ENVI AX2		0.7129				
ENVI AX3			0.5910			
SEC	0.1704	-0.1225	-0.0038	0.1997	-0.1718	-0.0047
TEM	0.6582	0.0334	0.0537	0.7712	0.0467	0.0682
SAL	-0.4454	-0.2456	0.3310	-0.5217	-0.3445	0.3183
Avs	0.1127	0.3574	-0.0670	0.1319	0.5012	-0.0846
Maxs	-0.0179	0.3648	-0.1066	-0.0212	0.5115	-0.1347
C	-0.3076	-0.1787	0.0618	-0.3602	-0.2504	0.0779
N	0.3109	-0.2235	-0.2823	0.3643	-0.3136	-0.2568
NE	0.1459	0.4817	-0.2189	0.1708	0.6757	-0.2767
E	0.2473	-0.0362	0.1439	0.2896	-0.0510	0.1821
SE	-0.1374	-0.0384	0.3570	-0.1608	-0.0538	0.3512
S	-0.2756	-0.0089	0.1791	-0.3227	-0.0126	0.2263
SW	0.0285	-0.1016	-0.3118	0.0333	-0.1424	-0.2941
W	0.0937	-0.2730	-0.1086	0.1097	-0.3830	-0.1372
NW	0.1595	-0.2930	-0.2212	0.1868	-0.4110	-0.2796

	AXES		
	1	2	3
Eigenvalues	0.241	0.111	0.087
Species - environment correlations	0.854	0.713	0.591
Cumulative percentage variance			
of species data	24.1	35.2	43.9
of species environment relation	43.5	63.6	79.4

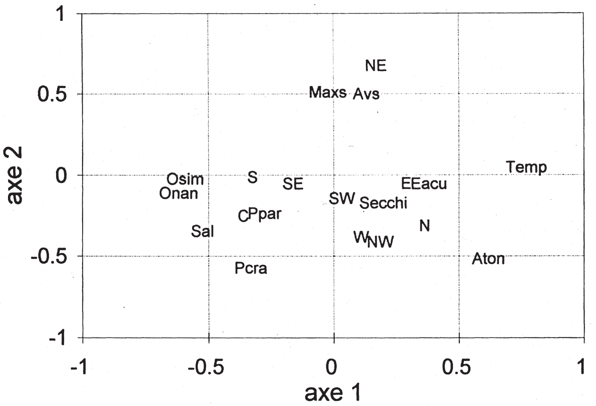

FIG. 6. – Ordination results from RA of copepods species and environmental conditions. The environmental variables are: temperature (TEM), salinity (SAL), depth of Sechii disk (SEC), occurrence of calms (C), daily average speed (Avs) and daily maximum speed (Maxs), and persistence of winds in sectors north (N), north-east (NE), north-west (NW), south (S), south-west (SW), south-east (SE), east (E), and west (W). The species represented are: *O. simplex* (Osim), *O. nana* (Onan), *P. parvus* (Ppar), *P. crassirostris* (Pcra), *E. acutiforns* (Eacu), and *A. tonsa* (Aton).

Negative scores on axis 1 were associated with higher salinities, south winds and calms. Positive scores on axis 2 were associated with NE winds and with maximum and mean velocity. Negative scores were associated with NW winds and W winds (Table 4).

DISCUSSION

Results of this study show that the topography of the estuary, the orientation of its mouth, and the rotation and speed of winds is responsible for inflow and outflow of coastal marine water which in turn determines changes in the distribution and abundance of copepods. Wind stress generally causes vertical mixing and results in the sinking of the mixed upper layer (Farmer, 1972; Denman and Powell, 1984). In various shallow estuaries, Geyer (1997) demonstrated the influence of wind forcing on the salinity structure and flushing characteristics. The Solís Grande, a shallow estuary with no vertical discontinuities, can be considered the vertically mixed type (Pickard and Emery, 1990) during this situation. Its shallow depth and the effects of winds are responsible for strong vertical mixing and inflow and outflow of coastal marine water. The inversion of the salinity gradient between days 25 and 30 could be a consequence of the dynamic of the Río de la Plata. The Solís Grande estuary flows into the fluviomarine zone of the Río de la Plata, and there is frequent fluvial discharge along the Uruguayan coast (Lopez and Nagy, 1999; Framiñan *et al*., 1999). Thus stations 1 and 2, close to the mouth, could receive the influence of fluvial discharge. The decrease of the Río de la Plata northern coast salinity was a consequence of extraordinary increase in fluvial discharge (Nagy *et al*, 1997), and the influence of wind direction from days 25-26 (NW-W) to day 28 (S).

Environmental variability is the principal factor influencing distribution and low diversity in the Solís Grande estuary. In the Río de la Plata region, winds rotate quickly from sectors S-SE to E-NE and the weather tends to be stable. The cycles have a duration that may vary between one and fifty days (Balay, 1961; MTOP-PNUD, 1979). Between days 7 and 18, an atmospheric front originated from the South (frontal period , Balay. 1961) caused a rotation of winds from S to E-NE and the maximum velocity of wind increased from 20 to 32 km h $^{-1}$. Days with rotation and persistence wind from the E-NE and high velocity (post-frontal period; Balay, 1961) generated strong inflow of colder and saltier water from Río de la Plata. This phenomenon produced an increase in species diversity and is the principal mechanism of transport for zooplankton species, playing a significant role in controlling community dynamics. Towards the end of the sampling period, when velocity and rotation of winds were variable and calm periods prevailed, salinity decreased while temperature increased. At the Uruguayan coast, it is common to find calm situations associated with winds blowing daily from S to N during day and from N to S during night. This produced a decrease in diversity together with an increase of dominance of *A. tonsa*. At smaller space and time scales, the differences highlighted by the RA were the result of wind-forced hydrodynamics after the frontal period. In this situation hydrographic features have been dominant (factor one of RA) and wind effects have had secondary importance (factor two of RA).

Various authors discuss the use of diversity indices to characterize the community (Wolda, 1981; Magurran, 1988; Washington, 1984). According to Peet (1974), the Shannon index is more sensitive to changes of rare species in community samples. Therefore, the Shannon index could reflect changes in species composition of a determined station when the move of saline water into the estuary was provoked by the rotation of winds.

Plankton species assemblages are not simply the result of the salinity or temperature tolerance of the organisms. Two distinct associations of zooplankton species were detected at the Solís Grande estuary: (1) One group, composed of *P. parvus*, *P. crassirostris*, *O. nana* and *O. simplex,* was associated with the inflow of Río de la Plata coastal waters (saline waters). These are subtropical species common in coastal waters with marine influence (Björnberg, 1963; Ramírez, 1977). Their entry into the Solís Grande was produced after the post-frontal period led to an increase in diversity. (2) The second group, composed of *A. tonsa* and *E. acutifrons,* could be associated with lower salinity and higher temperature. *A. tonsa,* which is generally related to coastal waters (Björnberg, 1963; Ramírez, 1981; Montú, 1980), was the most abundant species throughout the study period. Its abundance showed a clear downward trend upon entering saltier water and an upward trend towards the end of the sampling period (Bastreri, 1991). In the summer, *A. tonsa* usually dominates in estuarine zooplankton and warm to temperate coastal areas (Uye and Fleminger, 1976). Contrastingly, *E. acutifrons* can be defined as a rare species with a wide distribution range. It is particularly common in neritic and estuarine waters, tolerating sudden decreases of salinity (Björnberg, 1963; González and Bowman, 1965; Ramírez, 1981, Viñas and Gaudy 1996). Considering an annual sampling strategy, seasonal changes in species composition and abundance could be due to changes in thermal preference for the resident species (Kimmerer, 1993). In our study, the alteration in abundance and diversity, related to changes in salinity and temperature, was forced by influence of external factors. The applied sampling strategy produced information about variations at small temporal and spatial scales, and proved to be useful for studying zooplankton assemblages particularly in this fluctuating environment. According to Milstein and Juanicó (1985), fluctuations at reduced spatial and temporal scales can be equal or of greater magnitude than at large scales, and thus constitute important indicators of the characteristics of the system. The employed sampling strategy unveiled phenomena that had not been perceived at a larger temporary scale. Changes of abundance and composition at a determined station as a function of time reflect the position and mixing of coastal and estuarine water bodies, as we show associating species composition to temperature and salinity. Whether the movements of the estuarine water bodies inside and outside the estuary affect the populations (retention, losses, etc.) can only be checked by following the evolution in time of the population in the same estuarine water body. Along the Uruguayan coast, temperature and salinity combined with wind-driven currents potentially provide transport mechanisms, helping zooplankton and other species to reach new habitats for development.

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