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Benthic foraminiferal distributions on the Uruguayan continental margin (South-western Atlantic) and controlling environmental factors

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ABSTRACT

The data on benthic foraminifera analysed from 110 box-core samples collected on the Uruguayan continental margin (outer shelf and upper and middle slope, between 36.54–34.64°S and 51.66–53.71°W) were used to evaluate the distribution of the benthic foraminiferal fauna and its relationship with selected abiotic parameters. Primary productivity (PP) and the organic flux (Jz) reaching the sea floor were also estimated for comparison with the foraminiferal distributions. The study area was characterised by elevated PP and Jz values, mainly in the southernmost region, which were associated with thermohaline fronts due to the presence of the Subtropical Shelf Front. The dominant identified taxa were *Rhumblerella sepetibaensis* (this is the first study recording the ecology of this species) and the opportunistic species *Epistominella exigua*, *Bulimina* spp. and *Reophax fusiformis*, which displayed maximal densities at the southernmost stations, concurrent with the highest Jz levels. The dominant species and vertical foraminiferal distributions responded to the different environmental conditions impacting the area (e.g. PP, grain size, nutrient content), which were most likely related to the hydrodynamic conditions. Hydrodynamic conditions cause differences in PP according to the locations of water masses and their fronts at the surface, according to the depth and current intensity; they determined energetic differences across the benthic environment, controlling organic matter sedimentation as well as grain size, which influenced oxygen availability within sediments.

1. Introduction

The organic particle flux generated by surface waters with high primary productivity produces a layer of phytodetritus on the sea floor, which serves as food for benthic organisms (Lochte and Turley, 1988; Graf, 1989; Pfannkuche and Lochte, 1993). In situ data show that there may be up to a 4-week delay between a phytoplankton bloom and phytodetritus deposition over sediments (Fontanier et al., 2003, 2005; Sun et al., 2006; Murray, 2006).

Foraminifera respond to pulses in the organic particle flux by increasing their biomass. A quantitative relationship between the benthic foraminiferal density and ocean surface productivity has been recognised, which constitutes one of the best trophic proxies for the organic carbon flux to the seafloor (Altenbach, 1985, 1988, 1992; Altenbach and Sarnthein, 1989; Herguera and Berger, 1991; Linke et al., 1995; Loubere, 1996; Fariduddin and Loubere, 1997; Martins et al., 2007; Burone et al., 2011). The usefulness of foraminifera in reconstructions of productivity and oxygen availability in bottom waters has become evident in paleoceanographic studies (Kaiho, 1991; Sjoerdsma and Van der Zwaan, 1992; Moodley et al., 1998; Fontanier et al., 2003). This group provides some of the most numerous and easily collectable fossils on which such studies can be based. However, the accurate interpretation of these microfossils to reconstruct past changes depends on knowledge of the recent ecological features of living foraminifera.

To describe the vertical distribution of benthic foraminifera within sediments, these taxa are classified according to their microhabitats as epifaunal taxa (found in the first centimetre of the sediment), shallow infaunal taxa (found in the uppermost 2 cm), intermediate infaunal taxa (from 1 to 4 cm) (Jorissen et al., 1995), and deep infaunal taxa (found deeper than 4 cm). However, most species are able to modify their microhabitat in response to changes in environmental conditions, even temporarily at the same place responding e.g., to increases in organic carbon due to seasonal upwelling (Jorissen et al., 1995; Schmiedl et al., 2000).

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According to Schönfeld (2002a, 2002b), active microhabitat selection is pursued as a basic strategy of foraminifers to optimise their food acquisition, and this better access to food sources consequently stimulates reproduction.

In recent decades, several authors have highlighted the importance of organic carbon fluxes and oxygen concentrations as the main controlling factors explaining the deep sea vertical distribution of benthic foraminifera within sediments (Jorissen et al., 1995; Jorissen, 1999; Fontanier et al., 2002). In this regard, a conceptual model explaining the vertical foraminiferal distribution as a function of the relationship between the main controlling factors stands out (TROX model; Jorissen et al., 1995).

According to this model, in oligotrophic environments, food availability is the factor limiting the vertical distribution of species. In such environments it is expected that low diversities and densities of organisms will be found, limited to the topmost sediment layer, where the scarce food that arrives is rapidly consumed. In contrast, in eutrophic environments, the oxygen concentration acts as the limiting factor, with interstitial oxygen being consumed due to the high aerobic organic matter degradation rate in the first millimetres of the sedimentary column. Although there may be high contents of organic matter available in deep layers, the lack of oxygen limits the penetration of most fauna, resulting in a low-diversity fauna, but with high individual densities that are limited to the upper sediment strata. Under these conditions, typical infaunal taxa are found in surface sediments. Finally, the maximum penetration within sediments is expected to be found in mesotrophic environments, where organic matter and oxygen availability is observed deep within the sediment column. In these environments, organic particles are introduced within the sediment by bioturbation. The predictions of this model have been fully confirmed by Fontanier et al. (2002).

Finally, it is important to note that the trophic state and other environmental conditions (e.g., energy and nutrient contents) are reflected in benthic foraminiferal assemblages (e.g., in their density, specific composition, diversity and vertical distribution). Thus, knowledge of the foraminiferal community structure makes it possible to infer environmental conditions (Jorissen et al., 2007).

The aim of this report is to contribute to the understanding of trophic processes based on living benthic foraminiferal assemblages and oceanographic conditions on the Uruguayan continental margin (outer shelf and upper and middle slope). Thus, the relationships between this fauna and primary productivity, carbon fluxes and sediment variables are analysed (nutrient content and grain size). Finally, the identification of marker species to organic carbon flux in the area is also expected.

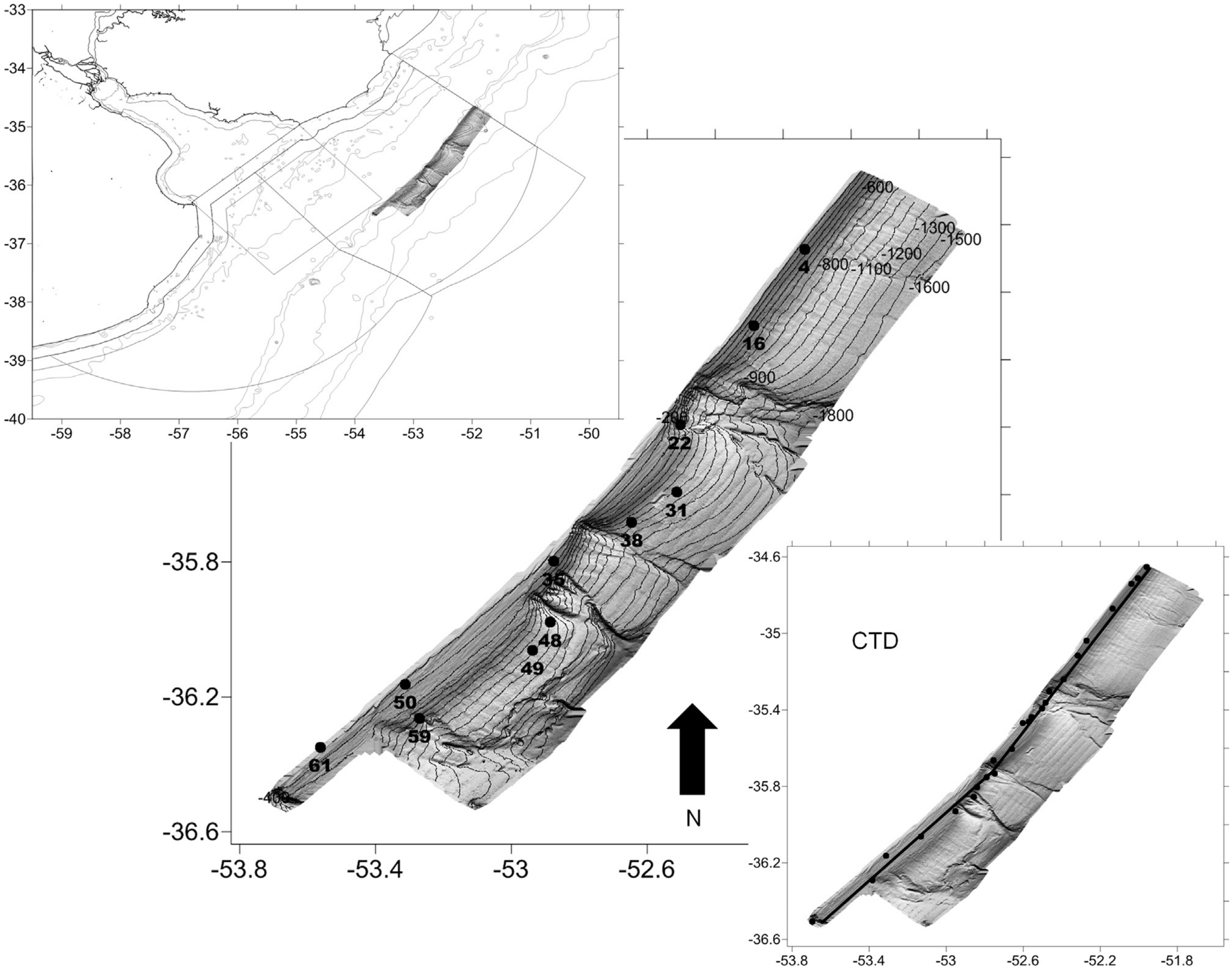

Fig. 1. Study area, bathymetric characteristics and canyons present in the area, sedimentological and microfaunal stations are shown as well as the CTD transect are analysed.

2. Study area

The study area is located on the Uruguayan continental margin (outer shelf, upper and middle slope) between 36.54–34.64°S and 51.66–53.71°W (Fig. 1).

2.1. Physiographic and sedimentary characteristics

The southwestern Atlantic continental margin is a passive margin composed of an extensive continental shelf, a steep slope and an extensive continental rise. The shelf break zone occurs at water depths between 160 and 220 m (Urien and Ewing, 1974). The shelf break and slope are characterised by the presence of four submarine canyons (Fig. 1). There are also many submarine mounds at depths lower than 327 m (de Mello and López, 2011; Franco-Fraguas et al., 2014).

The bottom sediments of the Uruguayan shelf and slope are dominated by sands and silty sands with variable percentages of clay (c.a. 4%, graded from sandy silt to clayey silt sediments with up to 25% clay). In general, carbonate values in the area range from 3.6% to 32% (Franco-Fraguas et al., 2014), classifying the sediments as lithoclastic ($<30\%$, Larssoneur et al., 1982). An important Contouritic Depositional System that controls sedimentary processes on the Argentinean margin reaches the Uruguayan continental margin, influencing sedimentation (Preu et al., 2010; Hernández-Molina et al., 2009; Krastel et al., 2011; Preu et al., 2013; Franco-Fraguas et al., 2014).

2.2. Hydrography

The Uruguayan continental margin is characterised by encountering water masses with contrasting thermohaline characteristics, advected by the warm poleward-flowing Brazil Current (BC) and the cold equatorward-flowing Malvinas (Falkland) Current (MC). The two currents converge at approximately 38°S, forming the Brazil–Malvinas Confluence (BMC) (Peterson and Stramma, 1991; Stramma and England, 1999).

The BC is a boundary current that originates at c.a. 10°S and flows southward along South America's continental margin until reaching the BMC zone. The transport of the BC increases towards the south, with different transport values being estimated: 17.5 Sv ($1\ \mathrm{Sv}=10^6\ \mathrm{m}^3\ \mathrm{s}^{-1}$) at 33°S, by Stramma (1989), and 68 Sv at 38°S, by Peterson (1992). On the other hand, the MC is an Antarctic Circumpolar Current meander flowing to the north, which achieves transport of 76 Sv at 42°S (Peterson, 1992).

The flux of the BC is associated with the movement of two water masses, Tropical Water (TW; Emilsson, 1961; Thomsen, 1962) and South Atlantic Central Water (SACW; Sverdrup et al., 1942), also known as Subtropical Water (STW; Emilsson, 1961; Thomsen, 1962). TW flows in the first 200 m and is generated due to the negative precipitation–evaporation balance as well as the intense solar radiation typical of the equatorial South Atlantic. In contrast, SACW is formed at the Confluence Zone as the result of mixing of the BC and MC, occupying the first 500 m of the water column. The MC carries cold, fresh and nutrient-rich Subantarctic Water (SAW, Sverdrup et al., 1942; Thomsen, 1962). Additionally, Coastal Water (CW, Guerrero and Piola, 1997) may be present at the surface over the area during periods of high freshwater discharges (mainly from the Río de la Plata estuary, RdlP). Finally, under the surface water masses, Antarctic Intermediate Water (AAIW, Sverdrup et al., 1942) is observed over the area at depths roughly between 500 and 1000 m (Table 1).

The oceanic BMC extends to the continental shelf, generating the Subtropical Shelf Front (STSF), which is formed by the convergence of BC and MC waters diluted at the surface by CW (Fig. 2) (Piola et al., 2000, 2008). The convergence of these water masses with contrasting thermohaline characteristics over the Uruguayan continental margin determines the existence of pronounced horizontal gradients. These frontal zones are related to vertical water movements, enabling nutrients located near the bottom to reach the surface (Froneman and Perissinotto Pakhomov, 1997; Brandini et al., 2000; Olson, 2000; Conkright et al., 2002). These processes, combined with the presence of canyons and shelf break upwelling, resulting in high concentrations of chlorophyll *a* and high productivity over the area (Ciotti et al., 1995; Longhurst, 1998; Brandini et al., 2000; Saraceno et al., 2005; Pimenta et al., 2008).

Table 1
Temperature and salinity values characteristic of Southwestern Atlantic water masses and used for their identification. TW: Tropical Water (Emilsson, 1961; Thomsen, 1962): SACW: South Atlantic Central Water (Emilsson, 1961; Thomsen, 1962); SAW: Subantartic Water (Sverdrup et al., 1942; Thomsen, 1962); AAIW: Antartic Intermediate Water (Sverdrup et al., 1942); CW: Coastal Water (Guerrero and Piola, 1997).

Water mass	T (°C)	S
CW		<33.2
TW	>20	>36
SACW	$6<T<20$	$34.2<S<36$
SAW	$4<T<15$	$33.7<S<34.2$
AAIW	$3.0<T<6$	$34.2<S<34.6$

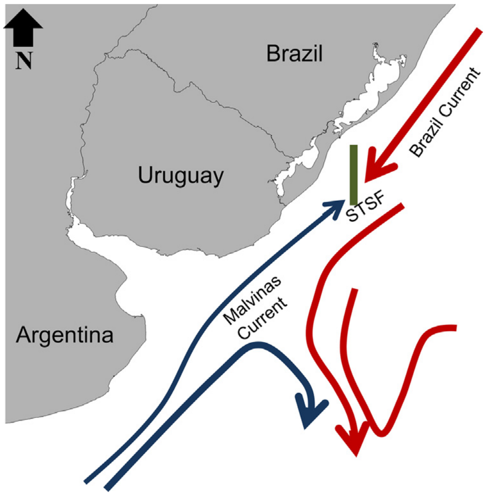

Fig. 2. Scheme of the regional circulation of the Southwestern Atlantic continental shelf and slope, re-drawn from Ref. Matano et al. (2010). STSF: Subtropical Shelf Front, BMC: Brazil Malvinas Confluence.

3. Materials and methods

During January and February of 2010, a high-resolution, large-scale sampling campaign was performed on the Uruguayan outer continental shelf and slope on board the R/V Miguel Oliver by the Uruguayan (*Dirección Nacional de Recursos Acuáticos*, DINARA) and Spanish governments (*Secretaría General del Mar* and *Instituto Español de Oceanografía*). During the cruise, geophysical, bathymetric, sedimentological, biological and hydrological data were obtained. Bathymetric data were acquired using a hull-mounted Kongsberg-Simrad EM 302 multi-beam swath-bathymetry system. Swath data were processed at DINARA, through the removal of anomalous pings and gridded at a cell size of 50 m using MB-System software.

To obtain sedimentological, geochemical and microfaunal characteristics, 11 stations were selected across the area (Fig. 1) and

Table 2
Analysed stations, their positions and depth.

N°BC	Latitude (°S)	Longitude (°W)	Depth (m)
4	34.87	52.14	313
16	35.10	52.29	436
22	35.39	52.50	759
31	35.59	52.51	919
35	35.80	52.88	271
38	35.68	52.65	923
48	35.98	52.89	908
49	36.06	52.94	879
50	36.16	53.31	239
59	36.26	53.27	669
61	36.35	53.56	174

sampled using a mega box-corer. Samples were collected between water depths of 174 and 923 m, between latitudes of 36.35°S and 34.87°S and longitudes of 53.56°W and 52.14°W. In order to select different environments, one station (BC22) was located inside a submarine canyon (Table 2 and Fig. 1).

At each station, two sub-sample cores (15 cm deep) were obtained from the mega box-corer, one to be used for live microfaunal analysis and the other to obtain sedimentological and geochemical data. Each core was visually described and sliced into 10 sub-samples (1 cm thick), starting at the surface.

Temperature (T) and salinity (S) profiles were recorded using a SBE 25 SEALOGGER CTD along a transect to characterise the area, as shown in Fig. 1. Water masses were classified based on their T–S values (Table 1). The vertical and horizontal distribution contours of temperature and salinity were constructed via krigging spatial interpolation across the study area; limits between water masses were approximately established. Surface and bottom T and S values from each of the 11 selected stations were also obtained.

Primary production was estimated for the euphotic zone ($\mathrm{g\,Cm^{-2}\,year^{-1}}$) over the study area during periods of 8 days for the three months before sampling, using a light-dependent, depth-resolved model developed by Behrenfeld and Falkowski (1997)

$$\mathrm{pp} = 0.66125\ \times \mathrm{pbopt} \times \left(\frac{\mathrm{PAR}}{\mathrm{PAR}+4.1}\right) \times \mathrm{Euz}\ \times \mathrm{Clo}\ \times \mathrm{dl}$$

where pbopt was estimated using a temperature-dependent model developed by Behrenfeld and Falkowski (1997).

$$\begin{aligned}\mathrm{pbopt} = & -3.27\mathrm{e}^{-8}\mathrm{SST}^7 + 3.4132\mathrm{e}^{-6}\mathrm{SST}^6 - 1.348\mathrm{e}^{-4}\mathrm{SST}^5 \\ & + 2.462\mathrm{e}^{-3}\mathrm{SST}^4 - 2.05\mathrm{e}^{-2}\mathrm{SST}^3 + 6.17\mathrm{e}^{-2}\mathrm{SST}^2 \\ & + 0.2749\ \mathrm{SST} + 1.2956\end{aligned}$$

and dl = day length; PAR = photosynthetic active radiance; Chl = chlorophyll *a* concentration ($\mathrm{mg_{Clo}\,m^{-3}}$); Euz = euphotic zone depth; and SST = sea surface temperature.

Chl, SST and PAR were derived from global 4 × 4 km^2-resolution images obtained from MODIS/Aqua satellite available on http://oceancolor.gsfc.nasa.gov/, after applying current SeaWiFS Data Analysis System (SeaDAS) processing tools, and the dl data are available at http://www.sohma.armada.mil.uy/almanaq.htm. Finally, Euz data were estimated using the following two equations, proposed by Morel and Berthon, 1989 and Morel and Maritorena (2001), respectively

$$\mathrm{Ctot} = 40.6\mathrm{Clo}^{0.459}$$

$$\mathrm{Euz} = 10^{(2.1236 + (0.932468\ \log\ 10(\mathrm{Ctot})) - 1.4264(\log\ 10(\mathrm{Ctot}))^2 + 0.52776(\log\ 10(\mathrm{Ctot}))^3 - 0.07617(\log\ 10(\mathrm{Ctot}))^4}$$

At each point, median values were taken as primary productivity values characterising the conditions during the three months prior to the sampling. Calculation of the organic carbon flux to the sea floor was based on Ref. Betzer et al. (1984):

$$\mathrm{Jz} = \frac{a\mathrm{PP}^q}{Z^m}$$

where Jz is the organic carbon flux reaching the sea floor at a given water depth, z (in metres), and PP is the primary productivity in surface waters (expressed at $\mathrm{g\,Cm^{-2}\,year^{-1}}$). The constants a, q and m should be determined by adjusting the function to the data for the local area. However, these data are not available for the study area or adjacent areas; thus, we decided to employ the same values used by Betzer et al. (1984), following Burone et al. (2011), namely $a = 0.4$, $q = 1.4$ and $m = 0.6$.

To study sedimentological (grain size) and geochemical (organic carbon, C_{org} and total nitrogen, N_t) characteristics, samples were collected from each slice from every station. The grain size distribution was determined using a low-angle laser light scattering apparatus (LALLS type Malvern 2000), and the size intervals were classified using the Wentworth scale (Wentworth, 1922 in Suguio (1973)).

C_{org}, N_t and calcium carbonate ($CaCO_3$) values were determined using 500 mg of freeze-dried sediment. Each sample was decarbonated with 1 M HCl, washed 3 times with deionised water, freeze-dried again and then analysed using a Finnigan Delta VPlus coupled with a Costech Elemental Analyser. The carbon/nitrogen ratio (C/N) was calculated as a first approach for determining the origin of organic matter. The $CaCO_3$ percentage in each sample was obtained by leaching the sample with 1 M HCl and weighing the sample before and after leaching.

To study the living benthic foraminiferal fauna, approximately 50 cm^3 of sediment was extracted from each layer. Each sample was stained with buffered Rose Bengal dye (1 g of Rose Bengal in 1 L of alcohol, see Walton (1952)) to distinguish between living and dead organisms. Wet samples were carefully washed through 0.125 mm and 0.063 mm sieves. After drying at 40 °C, the samples were subjected to flotation with a KI solution (density = 1.59 g cm^{-3}). The floated material was then washed again, transferred to filter paper and air-dried. After flotation, the residues were washed and examined, and all of the living specimens (>0.063 mm) in each sample were picked. We considered as live specimens only those showing all except the last chamber stained, thus avoiding the problem of dead stained specimens (Corliss, 1991). The tests were identified based on specific literature, such as Boltovskoy et al. (1980) and Loeblich and Tappan (1988) for gender identification and regional thesis and papers for species identification.

Parameters of the foraminiferal assemblages, such as richness (R), total density (D_t, number of individuals in the core, 500 cm^{-3}) and weighted average density ($\overline{H}$), were calculated for each core. $\overline{H}$ was obtained by Burone and Pires-Vanin (2006) as follows:

$$\overline{H} = \sum_{k=1}^{X} \frac{H_k R_k}{n}$$

where H_k is the Shannon–Wiener index for k strata; R_k is the richness of k strata; n is the total number of species at the station.

The average living depth (ALD_x) was calculated for each station according to Jorissen et al. (1995), as follows:

$$\mathrm{ALD}_x = \sum_{k=1}^{X} \frac{Z_k D_k}{N}$$

where X is the lower boundary of the deepest sample included in calculation; D_k is the number of specimens in each interval; Z_k is the midpoint of the sample interval; N is the total number of individuals in all levels. Because each core was sliced into 10 subsamples, $X = 10$ for all cores.

The Benthic Foraminifera High Productivity index (BFHP) was calculated (considering species abundance in the entire core) in order to identify high-productivity zones according to the availability of labile organic matter, applying a modification of the index described in Martins et al. (2007). Thus, the total percentage of indicators of high productivity calcareous foraminifera in each core was used. Therefore, the percentages of Bolivinids, Buliminids, *Stainforthia complanata*, *Uvigerina* spp., *Nonionella* spp. (Martins et al., 2007), *Epistominella exigua* and *Alabaminella wedellensis* (Sun et al., 2006) were considered.

Vertical foraminiferal density distribution profiles were obtained. Two mathematical functions, a Boltzmann function and a pure exponential function, were sufficient to fit most of the vertical foraminiferal distributions within sediments.

$$\text{Boltzmann function}: y(Z)=\frac{A1-A2}{1+e^{z-z0/dz}}+A2$$

$$\text{Exponential function}: y(Z)=A1e^{-z/t1}+y0$$

In these equations, $y(z)$ stands for the density at a depth of z within the sediments, and all of the constants ($A1$, $A2$, w, $t1$, $z0$, b, dz and $y0$) were estimated adjusting the functions to the data. Constants A_1 and A_2 in the Boltzmann function correspond to the surface and deepest assemblage levels, respectively; dz measures how rapidly the assemblage density changes; and $z0$ indicates the position where the change occurs. The constant $A1$ in the exponential function represents the density in the uppermost level, and $t1$ is the decay constant.

For ordination of the sampling locations in relation to trophic conditions, a principal component analysis (PCA) was carried out. A previously normalised and centred matrix was constructed using the following parameters: PP, Jz and surface sediment data on % C_{org}, % N_t, % $CaCO_3$ and C/N. Data normality was verified before conducting the analysis.

Classifications of species (*R* Mode) and of stations (*Q* Mode) were obtained using Ward's linkage method and the Euclidean distance. A data matrix was generated based on the relative abundance of species with a total abundance higher than 1%.

Finally, the biological parameters D_t, ALD_{10}, $\overline{H}$, BFHP and the densities of dominant species (*Bulimina* spp., *Reophax* spp., *Epistominella exigua* and *Rhumblerella sepetibaensis*) were correlated (Spearman correlation) with PP, Jz and the surface sediment percentages of C_{org} and the C/N relationships, considering $p < 0.05$ as the level of significance.

4. Results

4.1. Water column

According to the *T*–*S* values, the influence of CW was restricted to surface waters (from surface to approximate 15 m). The water masses that dominated below the surface (i.e., from approximate 15 m to 500–600 m) were SAW and SACW, developing a steep frontal zone at the shelf, the Subtropical Shelf Front. Finally, below 500–600 m, AAIW was found to dominate (Fig. 3).

PP values were higher in the southern portion of the area, mainly close to the shelf break, ranging between 365 g Cm^{-2} $year^{-1}$ (station BC31) and 1362 g Cm^{-2} $year^{-1}$ (station BC61). The same behaviour was observed in the estimated Jz values, with the lowest value being obtained at station BC31 (26 g Cm^{-2} $year^{-1}$) and the highest value at station BC61 (331 g Cm^{-2} $year^{-1}$). However, the Jz values were negatively related to water depth (Fig. 4 and Table 3).

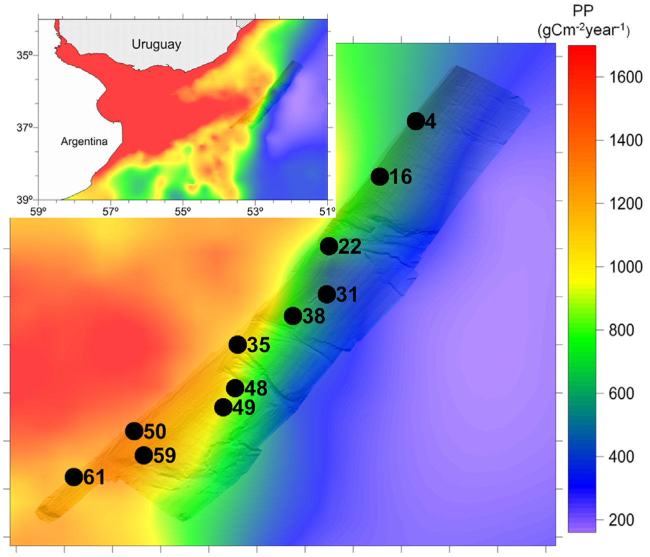

Fig. 4. Primary productivity values estimated (g Cm^{-2} $year^{-1}$) over the studied area.

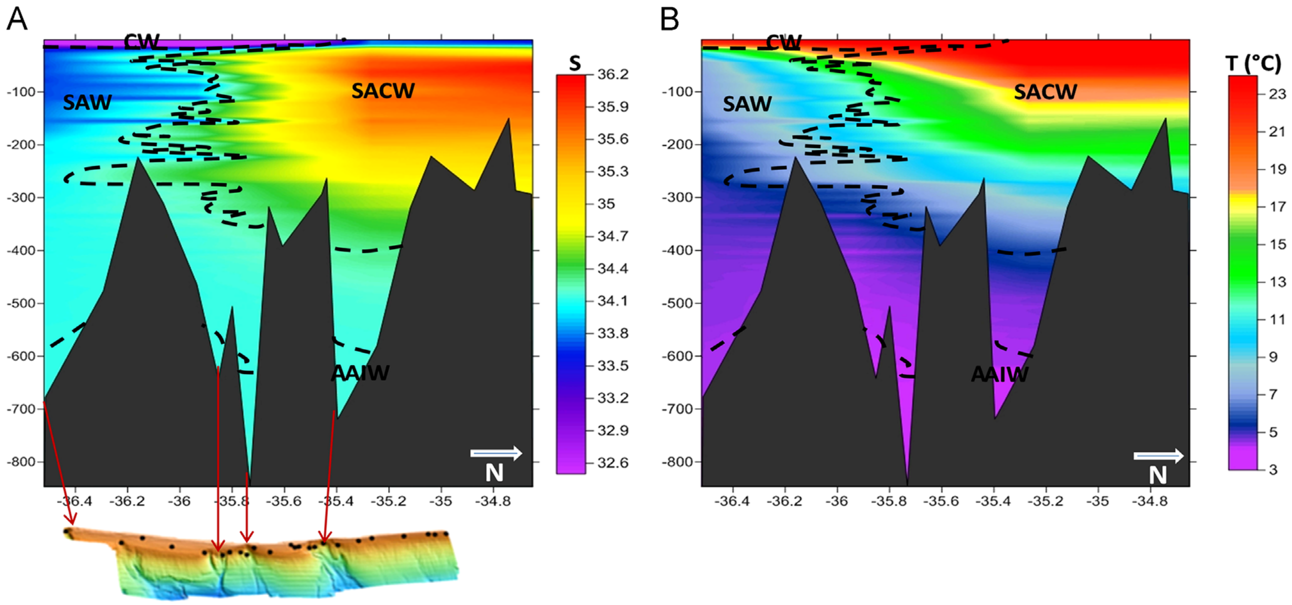

Fig. 3. Salinity (A) and temperature (B) distributions according to latitude over the study area. Water masses were identified according *T* and *S* values, CW (Coastal Waters), SACW (South Atlantic Central Water), SAW (Subantarctic Water) and AAIW (Antarctic Intermediate Water). Limits between masses were approximately determined and are marked as dashed lines.

4.2. Sedimentary and geochemical data

The grain size distribution was dominated by sand ($>54\%$) at stations BC4, BC16, BC35, BC49, BC50 and BC61. The highest sandy contents (between 91 and 100%) were found at station BC61, which was the only station located at the continental shelf (174 m depth). Sandy silt sediments were found at stations BC22 and BC31. Finally, cores BC38, BC48 and BC59 showed high proportions of silt and clay (Fig. 5).

The obtained C_{org} values ranged from 0.32 to 5.59%. Cores BC22, BC31, BC38 and BC50 showed high C_{org} contents ($>1.24\%$) along the sedimentary column, with stations BC22 and BC38, showing the highest values (Fig. 6). In general, the stations were depleted in $CaCO_3$, showing values between 3.18% and 24.76%. The C/N values ranged from 1.79 in the station BC49 to 11.79 in the station BC31 (C/N and $CaCO_3$ distributions are presented in Section 1 of the Supplementary data).

Table 3
Primary productivity (PP) and organic carbon flux (Jz) estimated over the analysed stations.

BC	PP ($g\ C\,m^{-2}\,year^{-1}$)	Jz ($g\ C\,m^{-2}\,year^{-1}$)
4	447	65
16	431	51
22	573	54
31	365	26
35	906	192
38	629	55
48	826	81
49	979	105
50	1072	261
59	1053	137
61	1362	442

The PCA grouped the stations according to their trophic conditions (Fig. 7). The first and second component together explained 79.1% of the total variance in the data. Axis 1 was positively correlated with $\%\ C_{org}$, $\%\ N_t$, C/N and $\%\ CaCO_3$. Axis 2 was negatively correlated with all of the variables, especially PP and Jz. It was possible to distinguish three groups of stations. The first group (G1) was formed by cores BC4 and BC16, from the northern portion of the study area. It was positively correlated with axis 2 and showed the lowest values of all parameters. The second group (G2) was composed of the samples from the centre of the study area (BC22, BC31 and BC38) and was positively correlated with axis 1. It was characterised by the highest percentages of C_{org}, $CaCO_3$ and N_t and the highest C/N ratios. Finally, the third group (G3) consisted of stations located in the southern region of the study area and was characterised by the highest values of PP and Jz. Within this group, 2 subgroups could be observed. The first was formed by stations BC48, BC49, BC35 and BC61 and was characterised by lower C_{org} levels, while the second was composed of stations BC50 and BC59 and showed higher C_{org} levels along the sedimentary column.

4.3. Species and ecological indicators

The highest total density was found at station BC50 (5182 individuals), while the lowest was registered at BC38 (257 individuals), with a tendency for the density to decrease with water depth being observed. The maximum R value was registered in core BC4 (39 species), whereas the minimum value was found in core BC22 (14 species). $\overline{H}$ showed values between 1.56 (core BC16) and 12.7 (core BC35). The values of ALD_{10} were greater than 2 cm, except in cores BC16 and BC59, where the fauna was concentrated at the surface. Finally, the behaviour of BFHP was similar to that of Jz, as at the stations displaying high Jz values, high BFHP values were also observed (Fig. 8). Additionally, The D_t, R, $\overline{H}$, ALD_{10} and

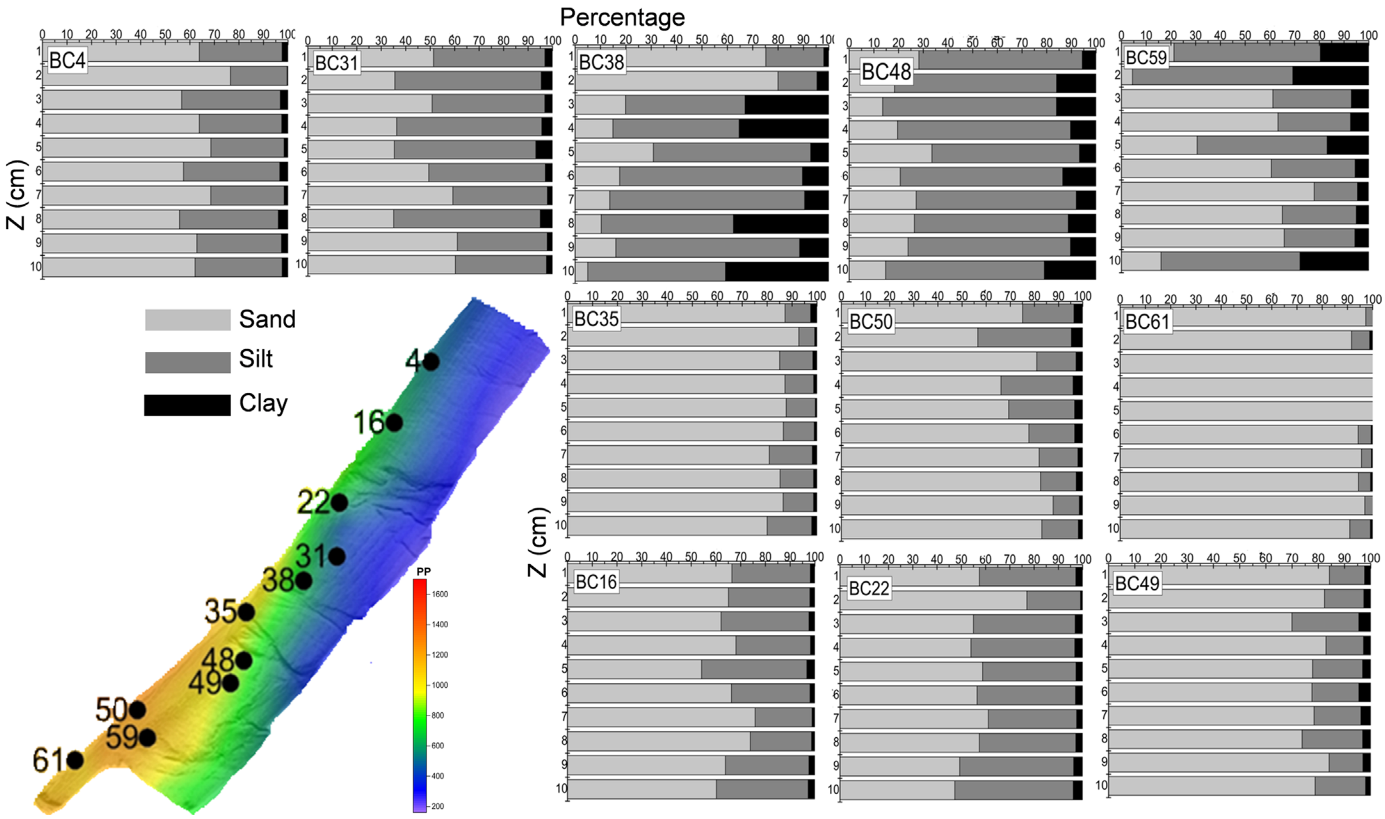

Fig. 5. Sediment fractions in the studied cores. Stations location and primary productivity over the studied area are also shown.

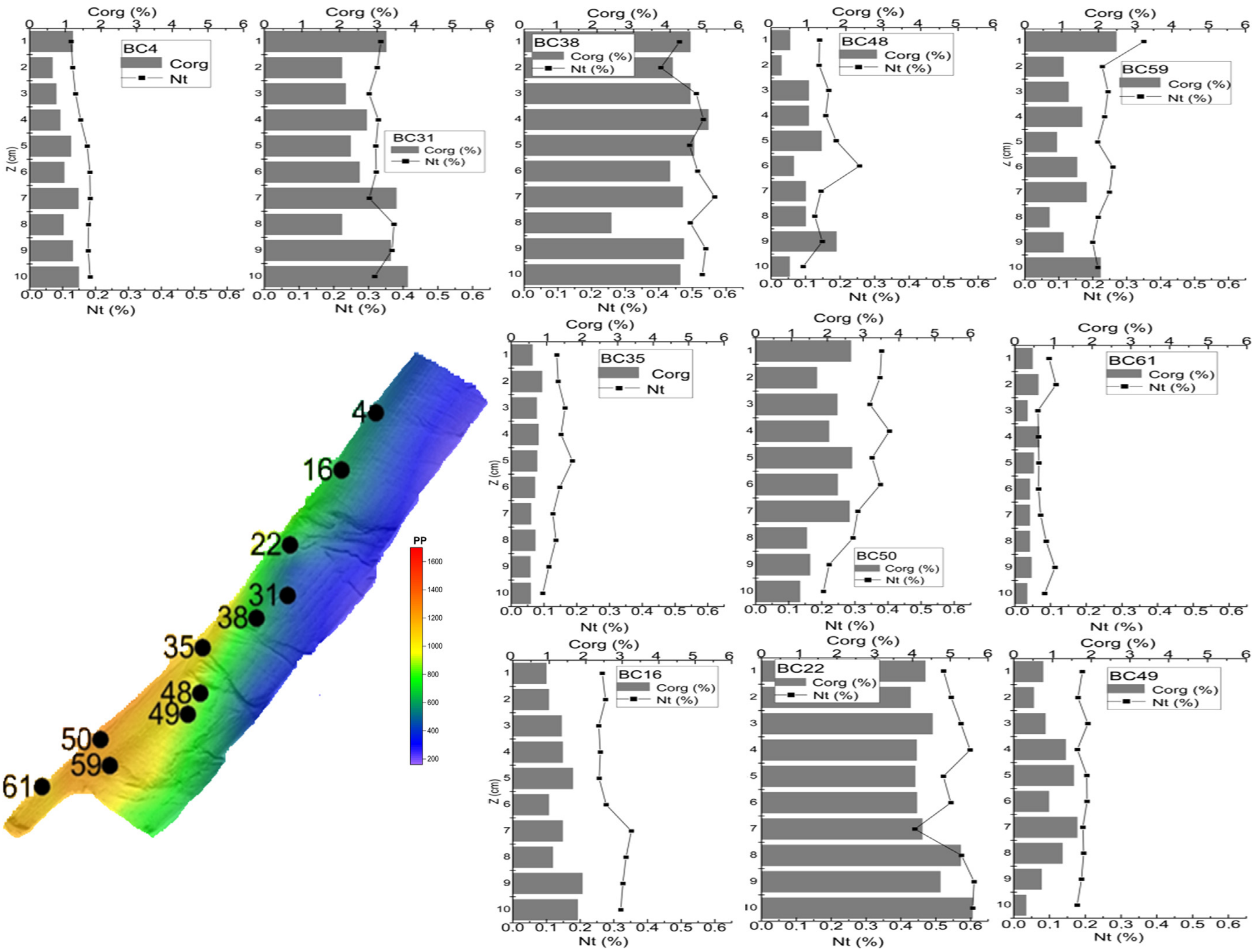

Fig. 6. Percentages of (C_{org}) and total nitrogen (N_t) in the studied cores. Stations location and primary productivity over the studied area are also shown.

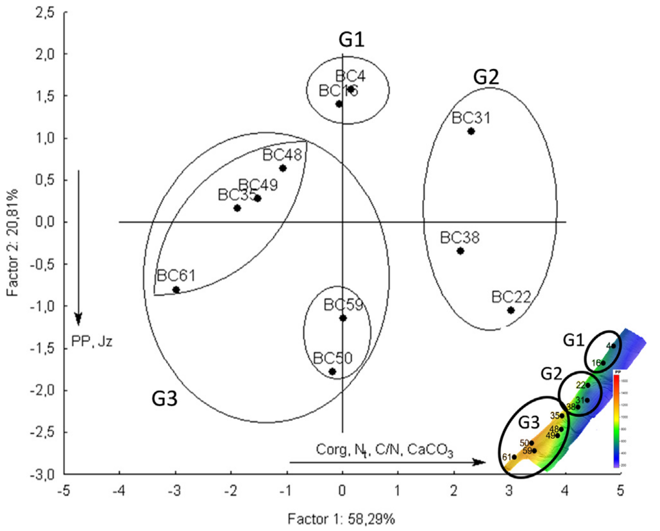

Fig. 7. Principal Component Analysis (PCA) ordination diagram of samples based on abiotic variables. Three principal groups found are shown (G1, G2, and G3). PP=Primary productivity, Jz=Organic carbon flux, N_t=percentage of nitrogen, C_{org}=percentage of organic carbon and $CaCO_3$=percentage or calcium carbonate.

BFHP values for each station are shown in Section 2 of the Supplementary data.

A total of 79 species were recorded (54 calcareous and 25 agglutinated). Stations located in the southern portion of the 7area and close to the shelf break (BC35, BC50 and BC61) showed dominance of calcareous foraminifera, while in the northern portion of the area (BC16, BC22, BC31 and BC38), higher densities of agglutinated foraminifera were found. The agglutinated species *R. sepetibaensis* was the species that presented the highest density (4370 individuals registered for all the study area) and widest distribution; it was found at all stations except BC61. The species that was second in terms of its density (4270 individuals registered for all the study area) and spatial distribution was *E. exigua*, which displayed elevated densities at stations located in the southern region of the study area (BC35, BC48, BC49, BC50, BC59 and BC61). High densities of individuals belonging to the *Bulimina* and *Reophax* genera were also observed in this portion of the area. A list of the species with their abundance found at each station and plates for some of the species are presented in the Appendix I and II respectively, in the Supplementary data.

The cluster analysis allowed 3 groups of stations to be differentiated based on foraminiferal assemblages. The first group (GI) was formed by those stations where the vertical species distribution

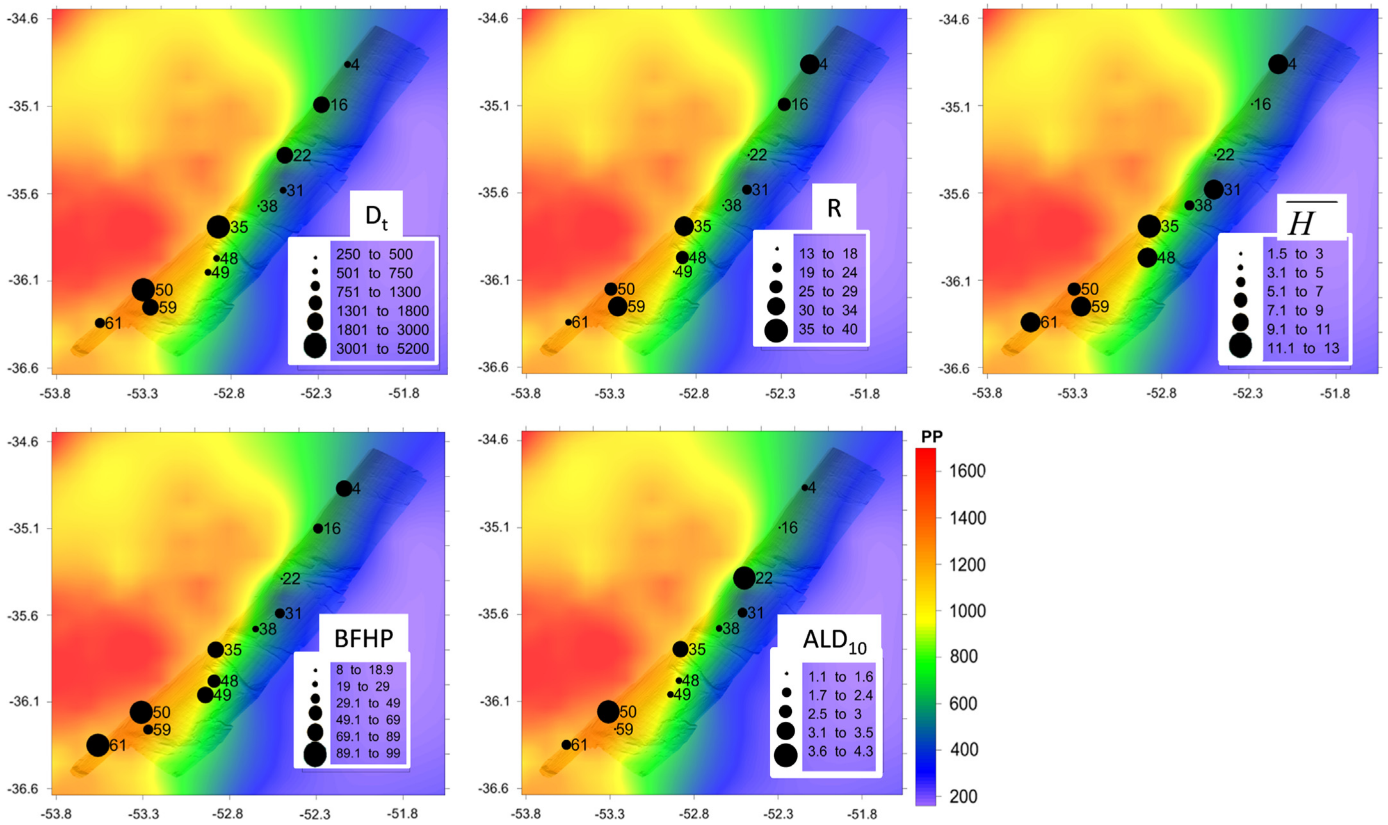

Fig. 8. Biological parameters distribution for the analysed stations, D_t=total density, R=richness, $\overline{H}$=weighted average density, BFHP=benthic foraminifera high productivity index, ALD_{10}=average living depth. Productivity distributions over the studied area is also shown.

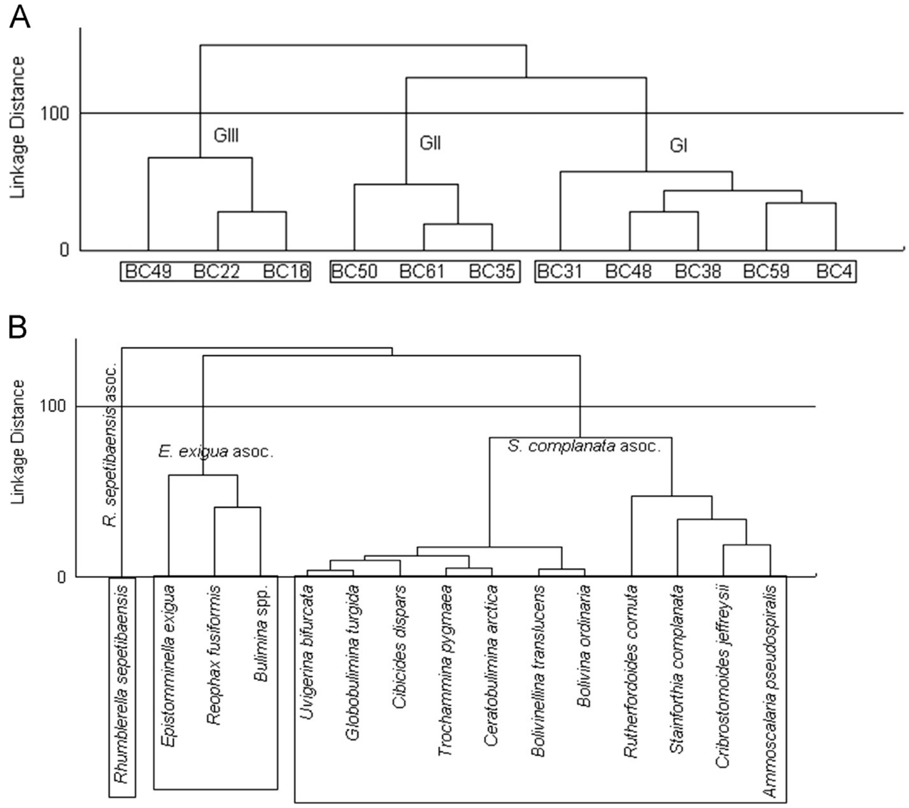

Fig. 9. Cluster analysis diagram of stations based on the relative abundance of species (>1%). (A) Q mode, the three principal stations association (GI, GII and GIII) are shown. (B) *R* mode, the three principal species association are shown (*R. sepetibaensis. E. exigua* and *S. complanata*).

suggested exponential decay (BC4, BC31, BC35, BC48 and BC59) and corresponded to the *S. complanata* assemblage. In this group BC4 was an exception because *Stainforthia complanta* was not dominant there; however the station still belongs to GI. The second group (GII) clustered the stations located in southern portion of the study area at the shallowest depths (BC50, BC35 and BC61). These stations were dominated by the species *E. exigua*, *Bulimina* spp. and *Reophax fusiformis*. The third group (GIII) include the stations BC49, BC22 and BC16 and corresponded to the *R. sepetibaensis* assemblage (Fig. 9A and B).

4.4. Vertical foraminiferal distribution

In all cases except for BC16, living foraminifera were registered until the tenth centimetre of the sedimentary column. It was found that the exponential and Boltzmann's functions fit most of the observed vertical foraminiferal distributions. The Boltzmann function was significantly adjusted at stations BC4 and BC16 ($r^2 > 0.95$); these stations showed a clear population maximum in the first 2 cm, followed by decay. The calcareous species *Bulimina* spp., *Bolivina ordinaria* and *Bolivinellina translucens* were dominant at station BC4, followed by the agglutinant species *R. sepetibaensis*. In contrast, station BC16 was dominated by *R. sepetibaensis*, and after the fifth centimetre, no living foraminifera were found (Fig. 10).

The exponential function was significantly adjusted ($r^2 > 0.95$) at stations BC38, BC48 and BC59. An exponential adjustment was also observed for BC31 until the sixth centimetre, after which an increase of density occurred in the 7th and 8th centimetres. This station was dominated by the agglutinated species *Cribrostomoides jeffreysii* and *Ammoscalaria pseudospiralis*. At BC48, there were a total of 714 living foraminifera recorded (458 at the surface). The dominant species was *S. complanata*, and its maximum density was also observed in the first centimetre. Finally, among the 1802 individuals found at BC59, 1326 were found at the surface. This station displayed many species with elevated densities (*Rutherfordoides* spp. *E. exigua* and *Trochammina pygmaea* were dominant) (Fig. 10).

At BC35, an increase of density with increasing depth was observed until the third centimetre, after which the density decreased exponentially (Fig. 10). The maximum density occurred between depths of 2 and 5 cm. Molluscs (gastropods and bivalves), polychaetes and ostracods were also recorded in the first 2 cm of this core.

Finally, at stations BC22, BC49, BC50 and BC61, no significant adjustment of the analysed functions was observed. Station BC22 (located inside a submarine canyon) was dominated by the

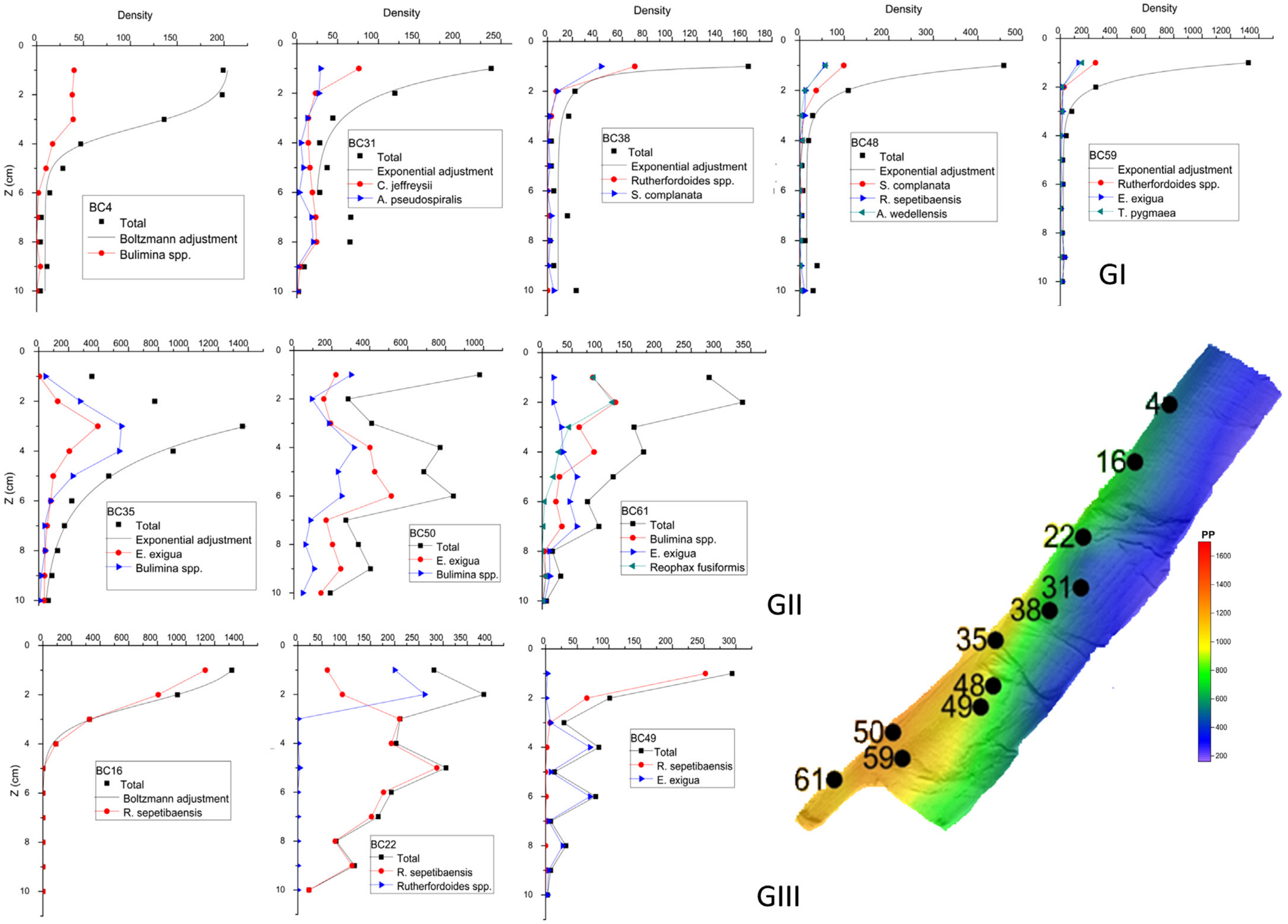

Fig. 10. Vertical distributions of total foraminifera and of the main species density for all cores analysed. The coordinate *z* represents the sediment depth. The dots represent density. BC4: Boltzmann adjustment. $A1=206$ $A2=9.06$ $z0=3.32$ $dz=0.51$. BC16: Boltzmann adjustment. $A1=1437$ $A2=-0.155$ $z0=2.34$ $dz=0.52$. BC22: no function was adjusted. BC31: Exponential adjustment: $y0=23.31$ $A1=158$ $t1=1.076$. BC35: Exponential adjustment $y0=19.15$ $A1=6886$ $t1=1.86$. BC38: Exponential adjustment $y0=8.94$ $A1=1634$ $t1=0.42$. BC48: Exponential adjustment. $y0=15.75$ $A1=2160$ $t1=0.631$. BC59: Exponential adjustment. $y0=21.97$ $A1=9165$ $t1=0.526$. Stations BC49, BC50 and BC61 did not adjust to the functions analysed. Stations are organised in the figure according to the cluster groups of stations identified (GI, GII and GIII).

agglutinant species *Rutherfordoides* spp. in the first two centimetres and from the third centimetre onward by the species *R. sepetibaensis*, which showed density maxima in the 2nd, 5th and 9th centimetres. At BC49, the density decreased with depth but showed three intermediate maxima related to the species *E. exigua*. At BC50, high densities were found (> 190 individuals) in all of the analysed layers. The maximum density was observed at the surface and was represented by 31 species. Then, from the second centimetre onward, *E. exigua* followed by *Bulimina* spp. became dominant, together representing more than 95% of the individuals at each level. These species reached their maximum density in the sixth centimetre. Finally, although the density profile obtained for BC61 did not fit to the analysed functions, it decreased from the second centimetre onward. Species segregation was also observed in this core; in the first layer, *Reophax* spp. and *Bulimina* spp. were the dominant *taxa*, while *E. exigua* became dominant at increasing water depth (Fig. 10). This station presented signs of bioturbation, polychaetes and ostracods were found at depths of 7 and 9 cm, respectively.

4.5. Spearman correlations

The correlations between the biotic and abiotic parameters are shown in Section 3 of the Supplementary data. Surface C_{org} was negatively related to the Jz, D_t, $\overline{H}$ and BFHP values and the densities of the dominant taxa. *Bulimina* spp., *Epistominella exigua* and *Reophax* spp. were positively correlated with PP and Jz. Finally, ALD_{10} was not significantly correlated with either Jz or to % C_{org}.

5. Discussion

5.1. Environmental conditions

The presence of the STSF over the southernmost and shallowest region of the area explains the recorded distributions of chlorophyll and, consequently, PP, which were higher in this area. It is also important to note that despite finding different trophic conditions in the surface water across the area, during the study period, all of the registered PP values were typical of a high-productivity region (e.g., Estrada and Marrasé, 1987; Negri, 1993; Iriarte and González, 2004). In this sense, 188 g Cm^{-2} $year^{-1}$ were estimated in the Cabo Frio upwelling region (Burone et al., 2011), between 219 and 588 g Cm^{-2} $year^{-1}$ were estimated in the Mauritanian upwelling region (Steinhoff et al., 2012) and finally values up to 3394 g Cm^{-2} $year^{-1}$ were estimated off the Antofagasta upwelling system (Danieri et al., 2000).

The presence of CW demonstrates the influence of the RdlP discharge in the study region. The period in which primary productivity was estimated coincided with the maximum magnitude of an El Niño event, which began in June–August 2009 (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.html). An increase in precipitation is seen over the Uruguayan territory (in spring) during El Niño events (Pisciottano et al., 1994, Díaz et al., 1998; Cazes-Boezio et al., 2003). This causes an increase in RdlP discharge (up to 70%), resulting in a greater nutrient input to the ocean, with a consequent increment in the phytoplanktonic biomass (Depetris et al., 1996; Guerrero et al., 1996).

Within the sedimentary column, the C_{org}, N_t and $CaCO_3$ contents did not reflect the differences observed in surface water productivity. However, it is important to note that the three-month temporal series used to estimate PP was examined with the aim of evaluating the foraminiferal response and not the possible input of organic matter to the sediments and also not the organic matter accumulation within the sediments. Additionally, the lack of age-depth models for each station means that any inference is simply hypothetical. Thus, this data may have some limitations regarding the identification of oceanographic processes that display seasonal variability, such as oceanic productivity.

The sediments in the shallowest zones, between depths of 175–500 m (BC4, BC16, BC35, BC50 and BC61) were characterised by high percentages of sand and low contents of C_{org} (Figs. 5 and 6). This finding is in agreement with previous sedimentological studies carried out in the area (Urien et al., 1980; Ayup-Zouain et al., 2001; Mahiques et al., 2009; Franco-Fraguas et al., 2014). It is known that at the convergence of BC and MC, offshore migration of currents occurs with sufficient energy to allow off-shelf sediment transport (Bender, 2012; Franco-Fraguas et al., 2014). It is also known that both the Brazil and Malvinas currents exhibit elevated volume transport in the study region (Gordon and Greengrove, 1986; Stramma, 1989; Peterson, 1992; Garzoli, 1992; Cirano et al., 2006), reaching velocities of up to 30 cms^{-1} for MC and 20 cms^{-1} for BC (Gwilliam, 1996). Notably, the highest percentages of sand were registered at the stations showing the highest PP and Jz values (Fig. 5 and Table 3). Thus the current's intensity and the elevated energy produced by the fronts would have hindered organic carbon deposition. Additionally, the high percentages of sand facilitated oxygen diffusion in the sediments.

On the other hand, in the southern portion of the study area, on the middle slope (500–1000 m) there is an erosive terrace caused by the action of AAIW (Franco-Fraguas et al., 2014) explaining the high contents of sand found in the station BC49, located there. This terrace disappears north of the study area as a consequence of the decrease of the AAIW flux due to the BC–MC convergence (Franco-Fraguas et al., 2014). Accordingly, stations located on the middle slope over the central part of the area (BC31 and BC38) registered high percentages of fine grain sediments, indicating that there was less energy affecting the area and more organic matter deposition. According to Frenz et al. (2003), there is a corridor located between longitudes of 52°W and 54°W at water depths between 500 and 3500 m that shows high organic carbon concentrations (> 2.5%). This corridor is assumed to be caused by elevated rates of surface PP due to the BC–MC convergence and RdlP discharge. Hence, the elevated C_{org} and N_t values found in the central zone of the area could be due to the presence of this corridor.

The stations located close to and inside of canyons (BC48, BC59 and BC22, respectively), showed the dominance of fine grain sediments. In this regard, submarine canyons differ from the open ocean in terms of the sedimentary processes determining an increase in organic matter deposition. In the open ocean, the main organic flux corresponds to fresh phytodetritus exported from surface waters (Newton et al., 1994). In contrast, canyons are highly dynamic environments, where material may be trapped or transported from the slope to the abyssal plain by different hydrodynamic processes, e.g., suspension and re-suspension events and gravity flows (e.g., Rowe et al., 1982; Soetaert et al., 1991; Maurer et al., 1994; Soetaert and Heip, 1995; Vetter and Dayton, 1998; Heussner et al., 1999; Duineveld et al., 2001; Durrieu de Madron et al., 2005; Hess et al., 2005; Gaudin et al., 2006; Hsu et al., 2008; Khripounoff et al., 2009; Pusceddu et al., 2010a). Thus, the organic components found inside canyons are a complex mixture of phytodetritus material that is reworked to varying degrees, associated with different proportions of terrigenous material (e.g., Van Weering et al., 2002; Tesi et al., 2010).

Finally, considering all abiotic parameters together, based on the PCA results, it was possible to identify three main groups of stations that showed different trophic conditions. The southern zone, formed by the stations belonging to G3 (BC35, BC48, BC49, BC50, BC59 and BC61), and the central zone, formed by the stations belonging to G2 (BC22, BC31 and BC38), displayed the most eutrophic conditions, at least for the studied period. In the southern zone, the elevated trophic state was a consequence of the elevated surface primary productivity, while the middle zone showed lower surface productivity levels, but the highest C_{org} contents in its sediments. On the other hand, stations belonging to G1, located in the northern zone (BC4 and BC16), were characterised by the lowest trophic levels. These stations were affected by the BC, whose oligotrophic waters accounted for the lowest PP and Jz values registered. Additionally, the G1 stations were located on the upper slope, which is recognised as an erosive region (Franco-Fraguas et al., 2014). As a result, sedimentation could be inhibited by the elevated environmental energy, explaining the low C_{org} and N_t values recorded.

5.2. Foraminiferal responses

Foraminiferal assemblages, vertical distributions and ALD_{10} values reflect organisms' responses to different environmental conditions in the benthic environment, such as Jz, the quality and quantity of organic matter, the sediment composition, hydrodynamic conditions, bioturbation and trophic interactions (Gooday, 1988, 1993; Gooday and Turley, 1990; Kitazato et al., 2000, 2003). Thus, microfaunal data (e.g. biodiversity, richness, species, assemblages) are relevant because they reflect recent processes occurring in the area.

Organic matter reaching the sea floor influences the composition of foraminiferal assemblages, both quantitatively and qualitatively (Gooday, 1993; Jorissen et al., 1998; Fontanier et al., 2002). Three foraminiferal assemblages were found in the area (*S. complanata*, *E. exigua* and *R. sepetibaensis* assemblage), showing different responses to environmental conditions (Fig. 7).

The *S. complanata* assemblage was composed of most of the species found in the area, which were typically infaunal taxa, characteristic of hypoxic conditions (such as *S. complanata*, *Bolivina* spp. and *Globobulimina turgida*) (Kaiho, 1994; Fariduddin and Loubere, 1997; Fontanier et al., 2005; Murray, 2006; Silva et al., 1996). This assemblage was found in the GI group of stations (BC4, BC31, BC48, BC38 and BC59), which showed the lowest ALD_{10} values (Fig. 8), exponential decreasing abundance foraminiferal distribution profiles (Fig. 10) and the dominance of fine grain size sediments (limiting oxygen diffusion in the sediments), together with elevated C_{org} and N_t values (except at BC4, which will be discussed later) (Figs. 5 and 6).

According to the TROX model (Jorissen et al., 1995), in areas subjected to high trophic conditions, the main redox front is expected to be found near the surface of the sedimentary column. Consequently, deep infaunal taxa would be located close to the surface. Thus, the species assemblages as well as their vertical distribution profiles would be indicative of an environment limited by oxygen because of both the high rate of oxygen consumption and the difficulty of the oxygen penetration of muddy sediments by interstitial water. Therefore, the low ALD_{10} values observed in GI stations should reflect a vertical distribution of foraminifera that is limited by oxygen availability. On the other hand, in oligotrophic environments, organic matter would be rapidly consumed in the upper sediment layers, and the scarcity of food would determine the concentration of the fauna in surface sediment layers (Jorissen et al., 1995; Jorissen, 1999). Hence, similar profiles would be expected at the two extremes of food availability, though they would differ in the total density of individuals.

Because of the elevated PP and Jz values observed throughout the study the area, the exponential profiles were not considered to be limited by food and were all considered to be limited by oxygen availability. However, a distinction could be made between the exponential profiles from the stations belonging to GI stations that were subjected to some of the lowest Jz levels in the area (BC31 and BC38) and those subjected to some of the highest Jz values registered (BC59). Differences between these stations were found in terms of the total foraminiferal density and, particularly, in the surface sediment layer density, which was higher at BC59 (located in the southern part of the area) than at BC31 and BC38 (Fig. 8). Those 2 stations, in addition to being subjected to some of the lowest PP and Jz values found in the area, showed high percentages of C_{org} ($>2.06\%$). It is likely that this type of organic matter had undergone transport and would be more refractory, showing less nutritional values. That hypothesis is supported by the C/N values registered, which was higher in stations BC31 and BC38 than in BC59.

The exponential function parameters also reflected differences between the stations displaying higher and lower PP and Jz values. For example, BC31 and BC38 presented lower $A1$ values than station BC59. The decay constant ($t1$) also exhibited differences indicating different consumption responses within the sedimentary column. The $t1$ value obtained at B59 was higher than that obtained at BC38, showing faster decay probably because of a more rapid consumption of organic matter and a likely decline in oxygen concentrations, limiting the penetration depth of the fauna.

In the northern portion of the area, station BC4 was also found to belong to GI because of the elevated number of species at this station, most of which are recognised as proxies for hypoxic conditions (Fontanier et al., 2003; Sun et al., 2006; Murray, 2006). However, unlike the other GI stations, BC4 did not present a typical exponential decreasing profile, and its sediment was dominated by sands, indicating a minor importance of oxygen as a limiting factor for the vertical faunal distribution (Figs. 4 and 8). The presence of sandy sediments at this station could have influenced the species diversity, favouring the habitat heterogeneity and contributing to explaining the elevated richness found there. In sediments with high grain size variability, the coexistence of a large number of species adapted to different conditions (inhabiting different niches) that are able to consume the organic matter that reaches the floor is common (Levin et al., 2001).

The *E. exigua* assemblage was dominated by the opportunistic species *E. exigua*, *Bulimina* spp. and *Reophax* spp. (Fontanier et al., 2003; Sun et al., 2006; Murray, 2006) and belonged to the GII group of stations (BC35, BC50 and BC61). In GII, we also identified juveniles of *Bulimina* spp. Elevated phytoplanktonic production is known to be followed by an increase in *E. exigua* and *Bulimina* spp. biomass after a few weeks' delay (Fontanier et al., 2003, 2005), and *E. exigua* and *Reophax* spp. have been documented as the first taxa showing a response following deposition of phytodetritus (Fontanier et al., 2003). In this sense, the identification of those opportunistic species reacting to the elevated productivity conditions in the study area is a new and significant finding with application in paleoceanographic studies.

This group (*E. exigua* assemblage) also exhibited elevated densities, BFHP, $\overline{H}$ and ALD_{10} values (Fig. 8) as well as the highest infaunal percentages ($>75\%$), together with the maximum percentages of sand (which facilitates oxygen penetration in sediments) and maximum PP and Jz values (Fig. 5 and Table 3). This deep faunal distribution is in agreement with the TROX model (Jorissen et al., 1995), which considers the foraminiferal microhabitat to show depth maxima when both oxygen and food are available within the sedimentary column. Thus, the *E. exigua* assemblage appears to represent a proxy of fresh phytodetritus and a marker of the presence of labile organic matter (Fontanier et al., 2003; Sun et al., 2006; Murray, 2006), and its vertical distribution could be used as a proxy of oxygen availability (Jorissen et al., 1995). Additionally, the presence of juveniles demonstrated the faunal response to the favourable trophic conditions at the time of sampling.

The GII stations were also characterised by vertical distribution profiles showing subsurface maxima (Fig. 10). Competition for better access to food particles with elevated nutritional value is an important factor causing differences in the microhabitat occupied by foraminiferal species (Van der Zwaan and Jorissen, 1991). Thus, the profiles obtained for the GII group most likely represent microfaunal strategies to avoid competition and or predation in organic matter-rich environments. Moreover, the GII stations presented signs of bioturbation. Through the disturbance of sediments, macrofaunal organisms (e.g., polychaetes and bivalves) favour the penetration and diffusion of oxygen within the sedimentary column and facilitate foraminiferal transport. Consequently, typical epifaunal species (such as *Cibicides* spp.) can be found at deeper depths in these environments (Murray, 2006). Another factor influencing the microhabitats occupied by benthic foraminifera and affecting the faunal composition are sedimentary conditions (Kaminski, 1985; Kaminski and Schroeder, 1987; Murray, 2006; Fontanier et al., 2008). For example, *Reophax* spp. is found in sandy regions, where the sediment surface is periodically disturbed by contour currents (Fontanier et al., 2008).

The profile obtained for BC35, showing the maximum density in the third centimetre (Fig. 10), may represent a strategy for avoiding predation and competition with the macrofaunal species observed at surface at this station. At BC50 and BC61, we found high foraminiferal densities in the surface sediments involving various species, while the subsurface maxima were mainly related to the densities of only 2 species, *Bulimina* spp. and *E. exigua*, revealing habitat segregation. A possible explanation for the vertical profiles observed could be that under the different processes co-occurring together (elevated primary productivity, high energetic conditions, bioturbation, competition and predation), *Bulimina* spp. and *E. exigua* were able to migrate and tolerate the conditions present deep within the sediments, decreasing competition with surface species.

Finally, it is important to note that at BC35 and BC61, rapid consumption of organic matter is another factor (beyond the elevated energy levels discussed above) that would explain why the lowest C_{org} values were found at these stations. This phenomenon was previously suggested by Burone et al. (2011) and Yamashita (2011).

The *R. sepetibaensis* assemblage was found in the GIII group of stations (BC16, BC22 and BC49). *R. sepetibaensis* was the most abundant and widely distributed species throughout the study area. The ecological information on this species available in the literature is insufficient, though it has been found to show an affinity for carbon sources that are commonly associated with upwelling areas at Campos Basin, Brazil (Disaró, *personal communication*). Each of the station belonging to GIII corresponded to a different PCA group (BC16 corresponded to G1, BC22 to G2 and BC49 to G3), indicating that the observed *R. sepetibaensis* distribution was influenced by various environmental conditions. Hence, *R. sepetibaensis* was registered under a wide range of environmental conditions, at different depths, in different types of sediments and under different conditions of productivity, characterising it as a species that is tolerant of different environmental conditions.

The vertical profiles obtained at station BC16 adjusted to a Boltzmann function, while BC49 showed a decay of density with depth with 3 intermediate maxima. Both of these stations are located in erosive areas (Franco-Fraguas et al., 2014), which could have affected the distribution of the fauna and, consequently, their profiles. Meanwhile, the vertical density distribution recorded at BC22 was probably related to its location inside a canyon. In this sense, it is important to note that bottom morphology plays an important role in the distribution and structure of communities. The influence of canyons over microfauna was demonstrated by Schmiedl et al. (2000), who detected differences in foraminiferal densities and diversity between the open ocean and canyons.

BC22 was the only station showing an elevated percentage of silt and clay (which suggests limited oxygen availability) that also presented a vertical distribution profile with surface and subsurface density maxima, without any bioturbation sign. At the surface, *Rutherfordoides* spp. dominated, which is a typical infaunal taxon that serves as a proxy of hypoxic environments (Kaiho, 1994). This finding is in agreement with the hypothesis that oxygen would have acted as a limiting factor for the vertical foraminiferal distribution. The subsurface maxima corresponded to *R. sepetibaensis*, indicating its tolerance to hypoxic conditions. BC22 also showed one of the highest C_{org} concentrations, together with one of the lowest organic fluxes and some contribution of terrigenous material (according to the elevated C/N ratio registered), indicating that *R. sepetibaensis* would be able to consume refractory organic carbon.

6. Final considerations

Based on the faunal characteristics and their relationships with environmental parameters observed in this work, it was possible to infer that the main parameters controlling the specific composition, density and vertical distribution of foraminifera in the study area are hydrodynamic conditions.

At the surface, the hydrodynamic conditions resulted in elevated PP values throughout the study area, and the PP distribution was related to the position of the STSF. Close to the bottom, hydrodynamics directly affect the benthic environment, controlling organic matter sedimentation as well as the grain size distribution, which influence oxygen availability through the sedimentary column.

The observed foraminiferal responses to varying environmental conditions reinforce the importance of these species as proxies in environmental and paleoenvironmental studies. In this regard, the elevated foraminiferal densities, elevated opportunistic species densities and vertical foraminiferal distributions were in accord with the PP values estimated throughout the area. These results were indicative of an environment with elevated trophic conditions in the whole area that is limited by oxygen at those stations dominated by fine grain sediments.

Lateral transport processes were demonstrated in this study. Elevated C_{org} values and low foraminiferal densities were found to be associated with the lowest organic fluxes and viceversa. Low carbon values found in stations with elevated PP were associated to sandy sediments, evidencing elevated current strengths and lateral sediment and carbon transports. This finding is in accordance with the current strengths (BC and MC), water masses and sedimentary contouritic processes in the study region.

In the study area, ALD_{10} was not a good trophic estimator. It was not related to Jz or to C_{org} in the sediments. High ALD_{10} values indicate food and oxygen availability. However, lower values do not necessarily indicate lower food availability; in the study region, low values may indicate an oxygen-depleted environment. The species *R. sepetibaensis* appeared to be a tolerant taxon to low oxygen conditions that is able to live deep within the sedimentary column and, likely, also in oxygen-depleted environments.

Finally, the obtained results represent the first assessment on the Uruguayan continental margin based on foraminiferal distribution and its relationship with environmental parameters. These findings reinforce the potential to utilise benthic foraminiferal distributions to reconstruct environmental conditions at the ocean surface and on ocean floors.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.csr.2014.08.006.

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