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SEDIMENTARY CHARACTERISTICS, MACROINFAUNA AND TYPES AND ABUNDANCES OF BIVALVES IN A TIDAL FLAT OF THE NORD-PATAGONIC ARCHIPELAGO, CHILE

E. JARAMILLO^{1*}, J. LÓPEZ², M. INCERA², M. LASTRA², H. CONTRERAS¹, C. DUARTE¹

¹Instituto de Zoología, Universidad Austral de Chile, Valdivia, Chile

²Departamento de Ecología y Biología Animal, Facultad de Ciencias del Mar, Universidad de Vigo, 36310 Vigo, Spain

*Corresponding author: ejaramillo@uach.cl

BIVALVES
MACROINFAUNA
SEDIMENTARY ORGANIC MATTER
SEDIMENT BIOCHEMICAL COMPOSITION
TIDAL FLAT
SOUTHERN CHILE

ABSTRACT. – The physico-chemical characteristics of the sediment, the nutritional value and the biochemical composition of the sedimentary organic matter and the structure of macroinfaunal assemblages were studied in three sites of the low intertidal of Pelluco, a tidal flat located on the inland coast of the Nord-Patagonic archipelago, southern Chile. The Site 1 was dominated by the razor clam *Tagelus dombeii*; Site 2 was dominated by the razor clam *Tagelus dombeii* and the bivalves *Diplodonta inconspicua* and *Semele solida*; while Site 3 had no bivalves at all. The site without bivalves showed a stronger decrease in depth of the redox potential than the sites with bivalves. This result was probably related to the process of bivalve reworking which redistributes reduced compounds from deeper layers to the sediment surface. Sedimentological differences and differences in the macroinfauna structure among sites were noticed. Thus the sediment characteristics of deeper strata were more different at the site without bivalves as compared to deeper strata of sites 1 and 2. The total number and the total abundance of the macroinfauna were higher at site 1 and 2. The results of BIO-ENV routine showed that the highest fit between the macroinfauna structure and sedimentological variables, was reached with two and four variables (total carbon and redox, $p_w = 0.391$ and carbohydrates, total nitrogen, total carbon and redox, $p_w = 0.385$, respectively), suggesting that that pattern was closely related to the presence of bivalves which would promote macroinfaunal assemblages throughout biogenic reworking of sediments.

INTRODUCTION

The physico-chemical characteristics of marine sediments, such as, grain size, porosity, water content, amount of organic matter and chemical properties, have major influences on benthic macroinfauna (e.g. Sanders 1958, Rhoads & Young 1970, Gray 1974, 1981, Rhoads & Boyer 1982, Thiyagarajan *et al.* 2005). It is also widely accepted that the activity of benthic organisms also influences the surrounding sediments and consequently its own community structure. Thus, even when earlier studies primarily related species richness and abundances of the macroinfauna with grain size and organic matter content of sediments (e.g. Rhoads & Young 1970), today it is widely accepted that by virtue of their feeding, burrowing and ventilation activities (bioturbation), benthic organisms have profound influences on their surrounding sediments (see Cadée 2001 for a review).

Studies of bioturbation, i.e. macroinfauna particle reworking of sediments, started quite early; just to mention two examples: Darwin (1837, 1881) was able to demonstrate that earthworms were able to modify the land surface of England, while Davidson (1891) studied the sediment reworking on a tidal flat of Northumberland by measuring the production of casts produced by the polychaete *Arenicola marina*. Thus, macroinfaunal organisms affect both rates and spatial distribution of sediment pro-

cesses by bioturbation (Aller & Yingst 1985, Andersen & Kristensen 1991). Their sediment reworking activity leads to the transport of newly deposited and labile organic matter to the deeper layers of the substrate (Gerino 1990), thereby increasing the depth interval over which rapid decomposition activities take place (Aller & Yingst 1980). Bioturbation also leads to the redistribution of reduced compounds from deeper layers to the sediment surface, thus stimulating their reoxidation rates (Fenchel & Riedl 1970, Rhoads 1974).

Bivalves usually dominate the biomass of infaunal communities inhabiting tidal flats around the world (Peterson 1977, Legendre *et al.* 1997, Lardies *et al.* 2001, Stead *et al.* 2002); these invertebrates are one of the most common bioturbators on those coastal habitats (e.g. Rhoads & Young 1970, Aller 1982, Rhoads & Boyer 1982, Reise 1983). One of the most general ways in which bivalves affect the sediment processes is by burrowing, including foot anchoring and hydraulic effect by ejection of water through the sediment (Trueman & Ansell 1969, Checa & Cadée 1997). This bio reworking of the sediment directly affects its fabric, changing vertical distribution of sedimentary components, water content and sediment stability (Rhoads & Young 1970, Nowell *et al.* 1981, Hall 1994). Apart from that, the mechanisms of burrowing also releases nutrients from the sediment to the water column (Davis 1993, Vaughn & Hakenkamp 2001) and

increases oxygen availability in the interstitial environment, allowing that a rich and varied infauna penetrate in the sediment and survive deeper than they could otherwise (Gutiérrez *et al.* 2000, Little 2000). Moreover, suspension and deposit feeding of bivalves produce faeces and pseudo-faeces that increase organic content of the sediments and, in turn, make easier the penetration of macrofauna into the sediment column (Gutiérrez *et al.* 2000, Vaughn & Hakenkamp 2001). All these processes suggest that sedimentary bivalves promote species richness and population abundances of the infaunal organisms occupying the surrounding sediments. As a matter of fact, Reise (1983) used the word amelioration to describe the facilitation process that *Macoma balthica* produces on the abundances of the surrounding meiofaunal assemblages of a tidal flat of the North Sea.

The coexistence of several species of bivalves in the intertidal zone of sedimentary habitats of the inland coast (i.e. not exposed to the breaking waves of Pacific Ocean) of the Nord-Patagonic archipelagos of Chile, provides the opportunity to examine relationships between types and abundances of bivalves and sedimentary characteristics and community structure of the surrounding macroinfaunal assemblages. Such coexisting bivalves are the razor clam *Tagelus dombeii* (Lamarck) and the clams *Venus antiqua* King & Broderip, *Semele solida* (Gray), *Gari solida* (Gray) and *Diplodonta inconspicua* Philippi (e.g. Lardies *et al.* 2001, Stead *et al.* 2002). While the burial depths of *T. dombeii* may go down to nearly 30 cm into the sediment, that of the other species are restricted to the upper 5 cm of the sediment. The effect of macroinfaunal assemblages on sediment characteristics have been intensively studied (Hansen & Kristensen 1997, Widdicombe *et al.* 2000, Norkko *et al.* 2002, Karlson *et al.* 2005). However, little is known about the role of bioturbation on the nutritional quality of the surrounding organic matter and its eventual effect to benthic organisms. Based upon the fact that physico-chemical characteristics of sediments are affected by the bioturbation produced by bivalves, we aimed to examine the spatial variability in sediment characteristics, quality of the organic matter and structure of the macroinfaunal assemblages in sediments differing in abundance and burial depth of bivalves in a tidal flat of the inland coast of the Nord-Patagonic archipelago (ca. 41°S). Thus, the objective of this study was to analyze the community structure of the macroinfauna and sediment characteristics at three different scenarios: i) a site dominated by the razor clam *Tagelus dombeii*, but also having some clams, ii) a site with lower abundances of bivalves, namely razor clams and clams in similar proportions, and iii) a site with no bivalves at all. Based upon the biomass and sizes of the most common infaunal bivalves (shell lengths of *T. dombeii*, *V. antiqua* and *S. solida* are close to 60 mm, that of *D. inconspicua* is close to 30 mm) as compared to other infaunal organisms of the study site, we assumed a

gradient of decreasing bioturbation by bivalves from scenario i to iii, and thus, a probable change in sedimentary characteristics and structure of macroinfaunal assemblages across that gradient.

METHODS

Study area: This study was done on the tidal flat of Pelluco (41°29'S, 72°54'W), on the inland coast of the Nord-Patagonic archipelago, south of Chile, during February 2004 (Fig. 1a). This flat corresponds to the western side of an intertidal sedimentary habitat roughly 23 km² in surface (Stead *et al.* 2002) (Fig. 1b) and affected by tidal ranges close to 6 meters during spring tides (Viviani 1979). Three sites (hereafter referred to as sites 1, 2 and 3), about 20 meters apart, were chosen. Site 1, was dominated by the razor clam *Tagelus dombeii* but also had some clams, site 2 had a lower abundances of bivalves being razor clams and clams in similar proportions, while site 3 had no bivalves at all. These sites were on swash areas located near a tidal shallow channel perpendicularly located to the low tide level of the whole flat (Fig. 1c).

Sampling and preliminary treatment of samples: At each site, five patches, about 100 x 50 cm and at least 2 m apart, were randomly selected. At each patch, sediment samples for macroinfaunal, biochemical and sedimentological analyses were collected with a plastic cylinder of 7.5 cm in diameter and 15 cm long. After that, sediment samples were divided into five strata of 3 cm (i.e. 0-3, 3-6, 6-9, 9-12 and 12-15 cm). Right after that, each patch was excavated to a depth of about 30 cm to collect all macroscopically visible bivalves. Those samplings were carried out during spring low tides. Samples for sedimentological and biochemical analyses were frozen at -30°C until further processing, while samples for faunistical analyses were sieved through a 500 micron mesh and preserved in 10% formalin-sea water solution. All organisms were sorted and determined to the lowest taxonomic level possible (usually species). Sediment redox potential (Eh) was measured *in situ* at 1.5, 4.5, 7.5, 10.5 and 13.5 cm depth (i.e. mid depth of each stratum) using an Eh-electrode (Metrohm 740) connected to an mV meter.

Textural and granulometric analyses of sediments: Textural analyses were carried out to determine percentages of gravel (particles > 2000 microns), sand (63-2000 microns), mud (< 63 microns), biogenic aggregates and total organic matter (Anderson *et al.* 1981). Mean grain size of the sand fraction was determined with a settling tube (Emery 1938) and the moment's computational method (Seward - Thompson & Hails 1973).

Biochemical analyses: All biochemical analyses were carried out on sediment samples previously oven dried at 60°C until constant weight and finely powdered with a pestle (Pulverisette 2, FRITSCH). Depending on the organic content or nature of sediments, 0.5 to 2.0 grams of sediment were used for each biochemical analysis. After a previous extraction with 5% trichlo-

racetric acid (TCA), total carbohydrates were analysed according to Dubois *et al.* (1956) and expressed as glucose equivalents. Total protein analyses were carried out following an extraction with NaOH and were determined according to Lowry & Rosebrough (1951) as modified by Markwell *et al.* (1978). Protein concentrations were given as bovine serum albumin (BSA) equivalents. Total lipids were extracted from dried sediment samples by direct elution with a chloroform-methanol solution (2:1, v/v) and analysed according to Zöllner & Kirsch (1962). Data were normalised to sediment dry weight. Sediment samples combusted at 500°C for 6 hours and processed as described above were used as blanks for all biochemical analyses.

Total sediment carbon and nitrogen were determined on sediment subsamples (approximately 15-20 mg) by gaschromatography using a CHNS Fisons Elemental Analyser (mod. EA1108). Sulphanilamide was used as standard.

The nutritional value of the sediment was evaluated by combining the three main biochemical classes of sedimentary organic matter. Carbohydrate (CHO), protein (PRT) and lipid (LIP) concentrations were converted to carbon equivalents assuming a conversion factor of 0.45, 0.50, and 0.70 respectively (Fabiano *et al.* 1995). The sum of lipid, protein and carbohydrate carbon is reported as the biopolymeric carbon (BPC *sensu* Mayer 1989, Fabiano & Danovaro 1994, Fabiano *et al.* 1995). The BPC was assumed as an estimate of the labile fraction of total sediment organic matter, i.e. the fraction that was potentially available to

deposit feeders. The protein to carbohydrates ratio was also calculated to assess the age of the organic material (Cauwet 1978, Fabiano *et al.* 1997). The food index was calculated as the ratio of the biopolymeric carbon (as the sum of lipid, protein and carbohydrate carbon) to total carbon and expressed as a percentage.

Data analyses: Variability in textural, granulometric, biochemical and faunistic data among sites and depths (strata) were analysed by a two-way ANOVA with site and strata as fixed factors (Sokal & Rohlf 1995). When necessary, transformations were used to achieve the assumptions of homogeneity of variances and normality (Sokal & Rohlf 1995). When appropriate, Tukey's tests were used for multiple comparisons of the means ($\alpha = 0.05$) (Zar 1984). All univariate analyses were done using SPSS program (Nie *et al.* 1975). Analysis of Non Metric Multidimensional Scaling (NMMDS) was carried out to explore similarity in sedimentological and faunistic characteristics of sites and depths. The ordination analyses of sedimentological data were based upon a similarity matrix calculated through Normalised Euclidian Distance on square root transformation of data, while the analysis of faunistic data was run with the Bray-Curtis similarity coefficient with fourth root transformation (Clarke & Warwick 1994). The usefulness of the NMMDS analyses (i.e. display of relationships between sites and depths) was evaluated with the stress statistics: val-

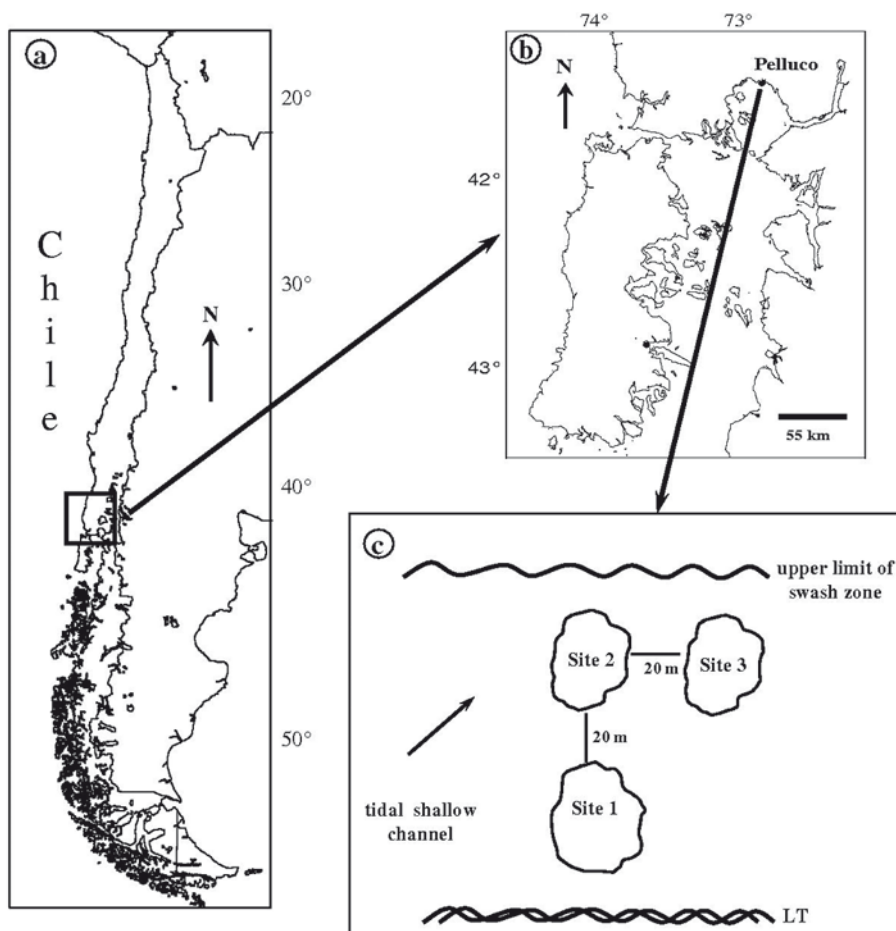


Fig. 1. – Location of the tidal flat of Pelluco on the inland coast of the northern coast of the Nord-Patagonic archipelago, south of Chile (a). The location of the flat on that coast is shown in inset b, while the location of sampling sites 1 (dominated by razor clams), 2 (with razor clams and clams) and 3 (without clams) are shown in inset c; LT = low tide level.

ues < 0.1 indicates that the depiction of relationships is good, while if stress values are > 0.2 the depiction is poor (Clarke 1993). The routine two-way ANOSIM (Clarke & Warwick 1994) of the statistical package PRIMER was used to evaluate if significant differences were present among the sedimentological and faunistical composition of sites and depths. The routine BIO-ENV of PRIMER (see Clarke & Ainsworth 1993), was used to explore which physical variables had a significant role in explaining the spatial variability of the macroinfauna. Physical variables were successively added to the predicted model BIO-ENV to improve the coefficient of correlations. To evaluate if any physical variables were colinear ($r > 0.95$), the Pearson correlation analysis was performed, before running the BIO-ENV routine.

RESULTS

Bivalve assemblages

Bivalves exhibited total mean densities close to 122 and 54 ind.m⁻² at sites 1 and 2, respectively; thus, bivalves were nearly two times more abundant at site 1, dominated by razor clams, than at site 2 dominated by both razor clams and clams. While at site 1, the mean density of *Tagelus dombeii* (ca. 88 ind.m⁻²) represented nearly 72% of the total population of bivalves, the abundances of razor clams at site 2 (ca. 22 ind.m⁻²) represented a percentage close to 41%. Clams were mostly represented by the small *Diplodonta inconspicua* at site 1 and *Semele*

solida at site 2 (mean densities close to 18 ind.m⁻² for both species).

Redox potential, texture and granulometry of sediments

Redox potential values showed a stronger decrease with depth at site 3 (from a mean close to 220 mV at the stratum 0-3 cm to a mean close to -158 mV at the deepest sediments), than at sites 1 and 2 (from a mean close to 211 and 246 mV at the strata 0-3 cm to a mean close to -36 and 97 mV at the strata 12-15 cm, respectively, Fig. 2). Redox potential values varied significantly with sites depending on the depth (Table I). Results of Tukey's tests showed that the lowest values of redox potential occurred at sites 3 and 1 and that the deepest strata had the lowest values of redox potential (less oxygenated sediments) (Table I).

Sand particles were the dominant fraction at all studied sites representing more than 80 % by weight (Fig. 2). However, the percentage of sand at site 3 (site without bivalves) was significantly higher than at sites 1 and 2 (Table I). Mean grain size of sands showed significant differences among sites but not among depths or strata (Table I, Fig. 2). Thus, site 1 showed medium size sands (250-500 microns, Folk 1980), whereas site 2 and 3 showed coarse grain sands (500-1000 microns, Folk 1980). Percentages of mud were lower than 2.5% at all sites and varied significantly with sites, but not with depth (Table I, Fig. 2). Thus, site 1 had higher content of mud particles (1.6-2.2%) than sites 2 (1.4-1.7%) and 3

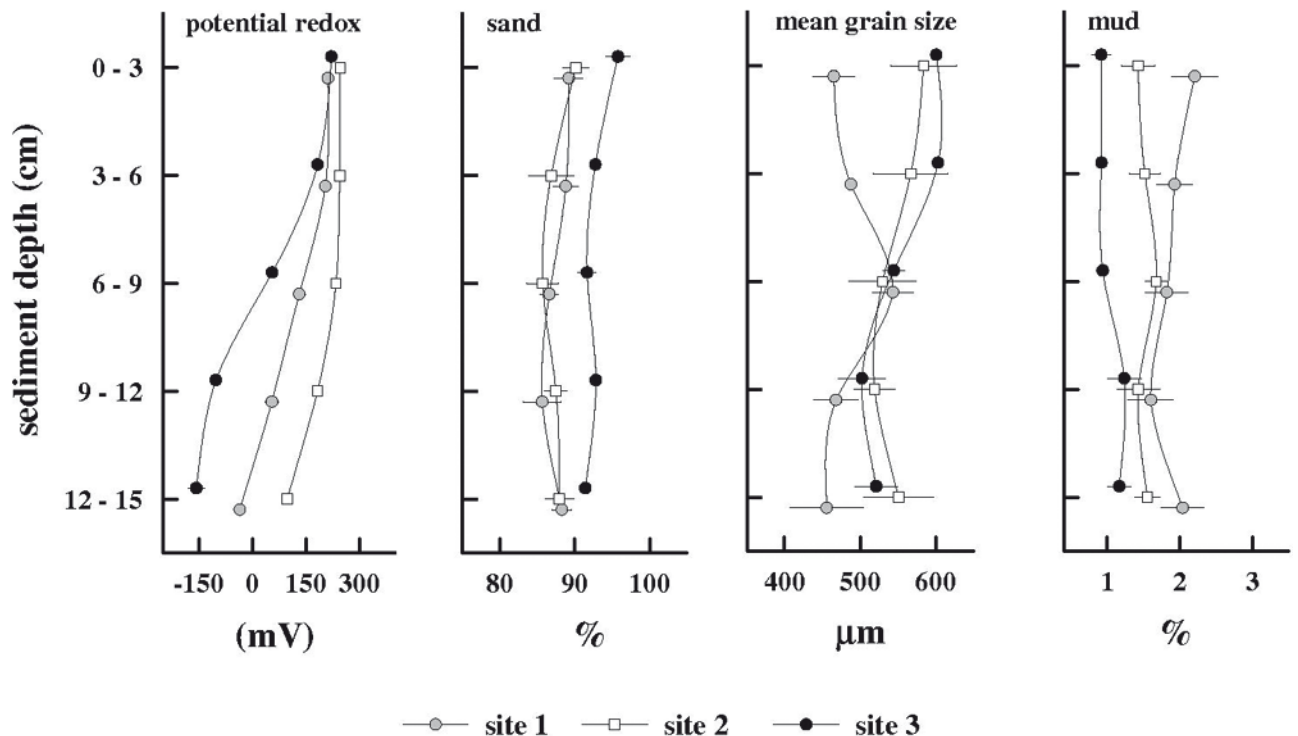


Fig. 2. – Vertical profiles of redox potential, percentage of sand, percentage of mud and mean grain size of sand. Plotted data are means (± 1 standard error) of 5 replicates.

Table I. – Results of the effects of site and depth on redox potential, percentage of sand, mean grain size of sand, and percentages of mud, biogenic aggregates and total organic matter in sediments. df = degrees of freedom, S = sampling sites, D = depths or strata (1 = 0-3 cm, 2 = 3-6 cm, 3 = 6-9 cm, 4 = 9-12 cm and 5 = 12-15 cm).

Source of variation	df	Redox potential (mV)		Sand (%)		Mean grain size (microns)		Mud (%)		Biogenic aggregates (%)		Total organic matter (%)	
		F	p	F	p	F	p	F	p	F	p	F	P
Site (S)	2	250.01	< 0.001	14.63	< 0.001	6.63	< 0.01	18.80	< 0.001	9.45	< 0.001	18.36	< 0.001
Depth (D)	4	280.03	< 0.001	1.73	0.15	1.89	0.12	0.22	0.92	3.71	< 0.01	1.61	0.18
S x D	8	25.83	< 0.001	0.430	0.89	1.15	0.34	0.70	0.69	3.71	0.24	1.71	0.11
Residual	60												
Tukey's test		S ₃ < S ₁ < S ₂		S ₁ = S ₂ < S ₃		S ₁ < S ₂ = S ₃		S ₃ < S ₂ < S ₁		S ₃ = S ₂ < S ₁		S ₃ = S ₂ < S ₁	
		D ₃ < D ₄ < D ₃ > D ₂ > D ₁								D ₃ < D ₄ = D ₃ = D ₂ = D ₁			

(0.9-1.2%). Percentages of biogenic aggregates and total organic matter were significantly higher at site 1 (0.3-0.5 and 1.0-1.4%, respectively), than at sites 2 and 3 (Table I). There were significant differences among depths in the percentage of biogenic aggregates, with minimum values at the deepest strata (Table I).

Elemental and biochemical composition of sedimentary organic matter

Proteins were the dominant biochemical component at the three sites (60.2, 77.9 and 81.7% at sites 1, 2 and 3, respectively), followed by carbohydrates (31.5, 13.8 and 11.1%, respectively) and lipids (8.2, 8.2 and 7.2%, respectively). The highest and lowest concentrations of carbohydrates occurred at the 0-3 cm strata of sites 1 and 3 (188.32 and 38.22 $\mu\text{g g}^{-1}$ sediment dry weight, respectively) (Fig. 3a). The highest concentration of proteins was determined in the stratum 9-12 cm of site 2 (752.25 $\mu\text{g g}^{-1}$ sediment dry weight) and the lowest in the stratum 6-9 cm of site 1 (213.26 $\mu\text{g g}^{-1}$ sediment dry weight) (Fig. 3). The highest concentration of lipids was determined in the stratum 0-3 cm of site 2 (104.03 $\mu\text{g g}^{-1}$ sediment dry weight), while the lowest occurred at the stratum 6-9 cm of site 3 (21.44 $\mu\text{g g}^{-1}$ sediment dry weight) (Fig. 3). The highest concentration of biopolymeric carbon (BPC) occurred at the stratum 0-3 cm of site 2 (508.85 $\mu\text{g g}^{-1}$ sediment dry weight) while the lowest was estimated for the same stratum but in site 3 (199.49 $\mu\text{g g}^{-1}$ sediment dry weight) (Fig. 3). There were significant differences among sites in concentrations of proteins, carbohydrates, lipids and BPC (Table II). Moreover, lipids also varied with depths. No significant effects of the interaction between site and depth were found (Table II). Results of Tukey's tests showed that proteins, lipids and BPC had significant higher concentrations at site 2 as compared with sites 1 and 3, which did not differ significantly among themselves. Carbohydrate concentrations decreased significantly from site 1 to site 2 and from there to site 3 (Table II).

The highest and lowest concentrations of total carbon were estimated for the stratum 0-3 cm of site 1 and the stratum 3-6 cm of site 3 (3.08 mg g^{-1} and 1.14 mg g^{-1} sediment dry weight, respectively) (Fig. 3). Total nitrogen peaked at the stratum 0-3 cm of site 2 (0.57 mg g^{-1} sediment dry weight) while the lowest value occurred at the 0-3 and 3-6 cm strata of site 3 (0.13 mg g^{-1} sediment dry weight) (Fig. 3). Results of Tukey's test showed that concentrations of total carbon and total nitrogen were significantly higher at sites 1 and 2 as compared with site 3 (Table II).

The highest value of protein:carbohydrate ratio was found at the stratum 0-3 cm of site 3 (8.03) and the lowest at the stratum 6-9 cm of site 1 (1.57). The biopolymeric carbon: total carbon ratio peaked at different strata of sites 2 and 3 (0.20). The highest value of total carbon:total nitrogen (9.59) was found at the stratum 12-15 cm of site 3. All these ratios varied significantly with sites ($p < 0.001$) but not with depth ($p > 0.05$). Thus, protein:carbohydrate ratio decreased significantly from site 3 to site 2 and site 1. The ratio of biopolymeric carbon:total carbon was significantly higher at sites 2 and 3 which did not differ significantly among themselves, while total carbon:total nitrogen ratio decreased significantly from site 3 to site 1 and 2.

Multivariate analyses of sediments

The graphic results of NMMDS show that samples of each site separated quite clear, with samples representing depths being more separated at site 3 (without bivalves) as compared to sites 1 and 2 (Fig. 4). The stress value of this analysis (0.14) indicates that the depiction of relationships among sites and depths is quite good (cf. Clarke 1993). Results of SIMPER and the two way ANOSIM test showed that the physico chemical compositions of sediments differed among sites: site 1 was around 6-7 % significantly dissimilar from sites 2 and 3, respectively, while the percentage dissimilarity of sites 2 and 3 was nearly 7% (Table III). Comparisons among depths showed

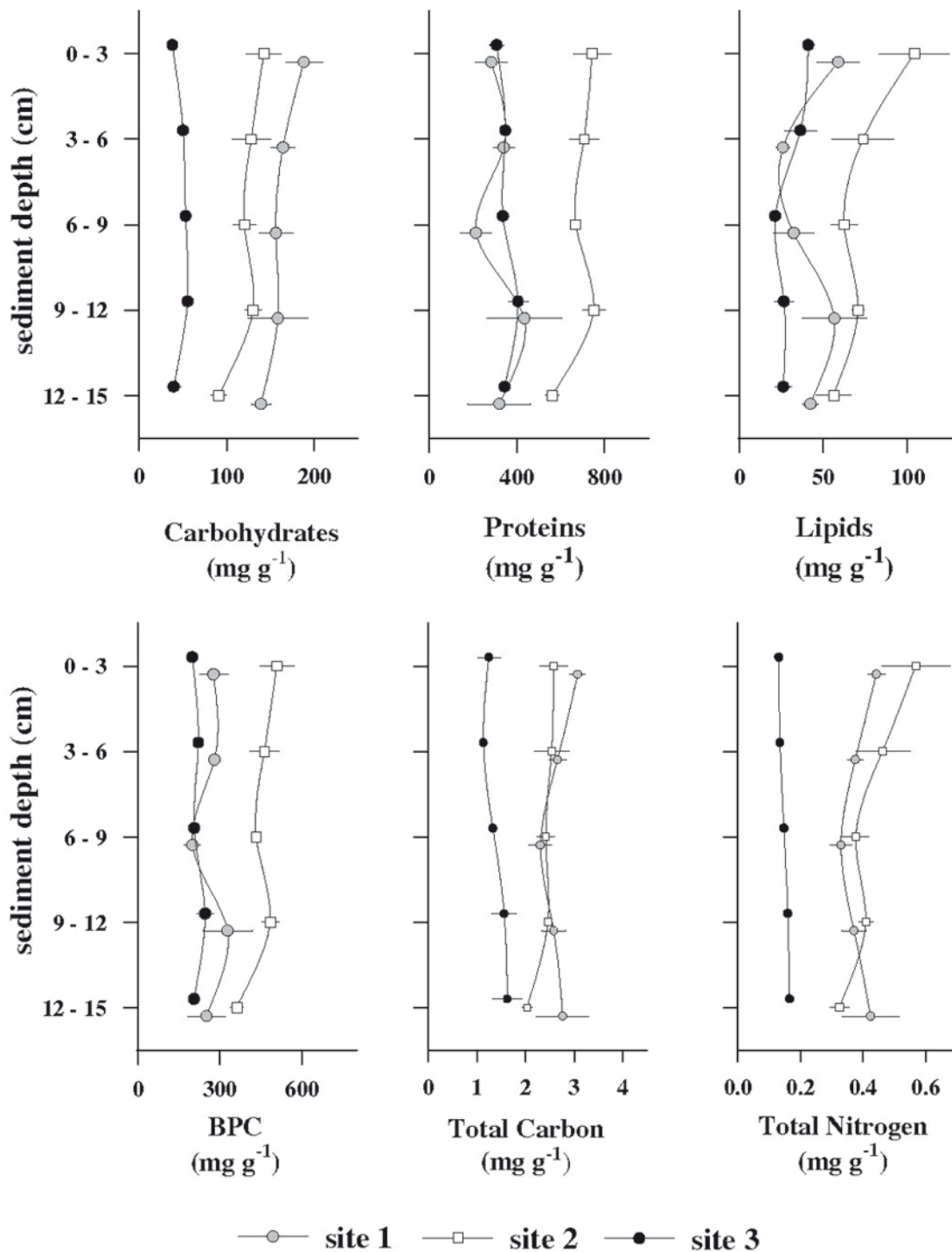


Fig. 3. – Vertical profiles of carbohydrates, proteins, lipids, biopolymeric carbon (BPC), total carbon and total nitrogen concentrations. Plotted data are means (± 1 S.E.) of 5 replicates.

that the two shallowest and the two deepest strata (0-3 and 3-6 cm and 9-12 and 12-15 cm, respectively) were similar among themselves but different to the other ones (Table III).

The macroinfauna

The total number of species and abundance of the total

macroinfauna were higher at sites 1 and 2, as compared to site 3 (Fig. 5, Table IV). The abundances of the three most common species of the macroinfauna (the archiannelid *Polygordius* sp., the amphipod *Corophium* sp. and the small gastropod *Caecum chilense*), followed a similar trend to that shown by the total macroinfauna, i.e. higher population abundances at sites 1 and 2 than at site 3 (Fig 5, Table IV). The highest mean abundances of *Poly-*

Table II. – Results of the effects of site and depth on the concentrations of proteins, carbohydrates, lipids, biopolymeric carbon (BPC), total carbon and total nitrogen. df = degrees of freedom. S = sampling sites, D = depths or strata (1 = 0-3 cm, 2 = 3-6 cm, 3 = 6-9 cm, 4 = 9-12 cm and 5 = 12-15 cm).

Source of variation	df	Proteins (µg g ⁻¹)		Carbohydrates (µg g ⁻¹)		Lipids (µg g ⁻¹)		BPC (µg g ⁻¹)		Total Carbon (mg g ⁻¹)		Total Nitrogen (mg g ⁻¹)	
		F	p	F	p	F	p	F	p	F	p	F	p
Site (S)	2	40.71	<0.001	64.65	<0.001	19.75	<0.001	42.74	<0.001	36.00	<0.001	45.44	<0.001
Depth (D)	4	1.52	0.21	1.67	0.17	3.28	0.017	1.90	0.12	0.48	0.93	1.60	0.18
S x D	8	0.57	0.80	0.56	0.80	0.86	0.55	0.65	0.73	1.03	0.19	1.42	0.20
Residual	60												
Tukey's test		S ₁ = S ₃ < S ₂		S ₃ < S ₂ < S ₁		S ₁ = S ₃ < S ₂		S ₁ = S ₃ < S ₂		S ₃ < S ₁ = S ₂		S ₃ < S ₁ = S ₂	
				D ₁ = D ₂ > D ₃ = D ₄ = D ₅									

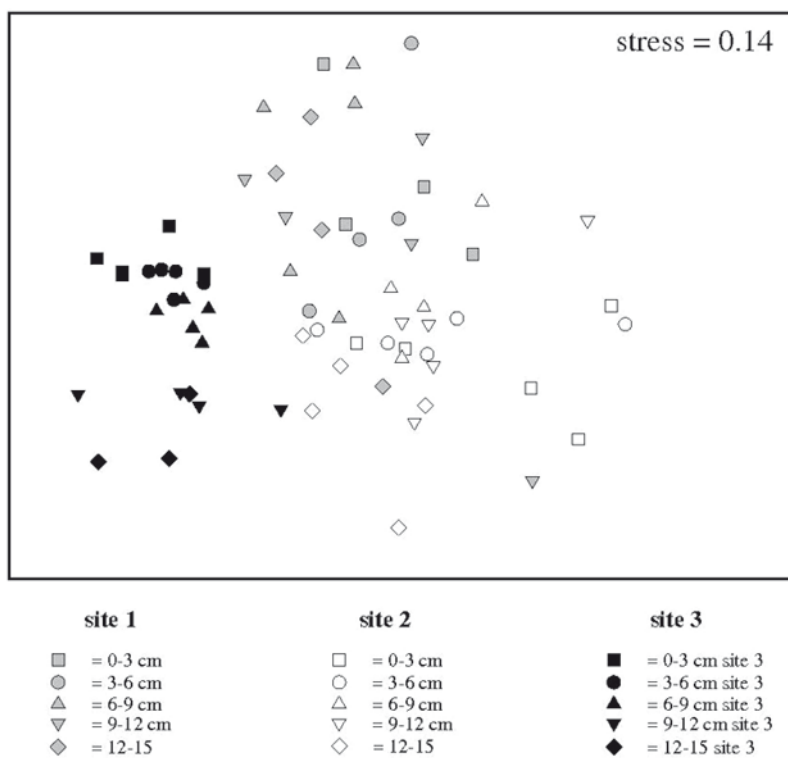


Fig. 4. – Graphic display of the Non Metric Multi Dimensional Scaling (NMMDS) analysis carried out with the sedimentological data (see Material and methods for details).

Table III. – Dissimilarity in percentage among sites and depths: results of SIMPER analysis based on the sedimentological characteristics. * = p < 0.05 according the results of the two way ANOSIM test (see Material and methods for details).

sites	1	2	3
1			
2	5.89*		
3	6.59*	7.29*	

depths (strata)	0-3 cm	3-6 cm	6-9 cm	9-12 cm
0-3 cm				
3-6 cm	5.52			
6-9 cm	6.02*	4.99*		
9-12 cm	6.24*	5.51*	5.99*	
12-15 cm	6.03*	5.27*	5.56*	5.98

gordius sp. and *Corophium* sp. were found at the stratum 0-3 cm of site 1 (11750 and 24050 ind.m⁻², respectively), while *Caecum chilense* occurred at the same stratum of site 2 (7100 ind.m⁻²). The abundance of the total macroinfauna and that of the most common species varied significantly with sites and depth with no significant interactions among these factors (Table IV).

Multivariate analyses of the macroinfauna

The graphic results of NMMDS show that samples of sites 1 and 2 were close together and more separated from site 3 and its depths (Fig. 6). However, the value of the stress statistics (0.20) indicates that the depiction of macroinfaunal relationships is close to the limit to be

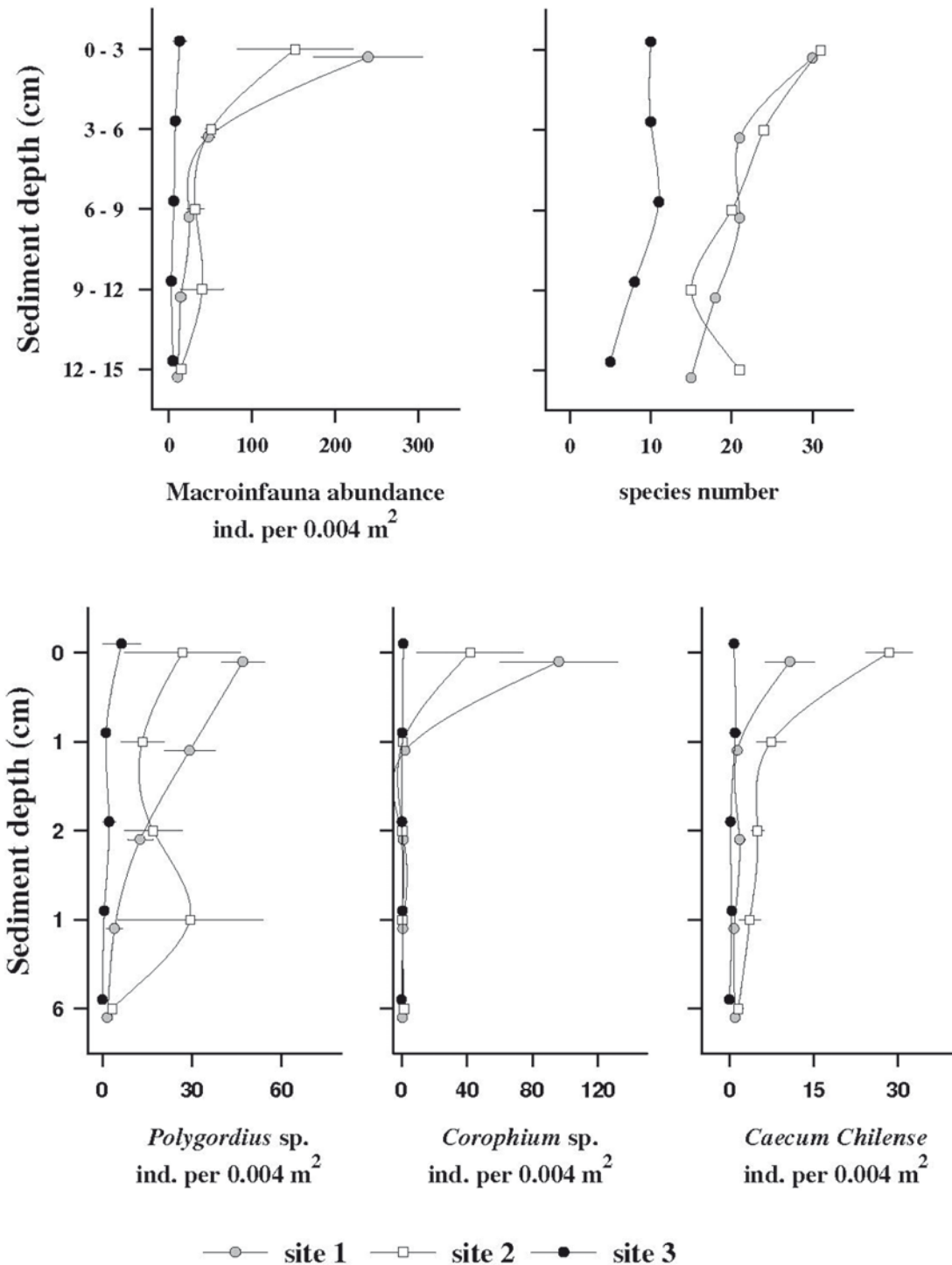


Fig. 5. – Vertical profiles of total macrofaunal abundances, species number and abundances of the three most common species. Plotted data are means (± 1 S.E.) of 5 replicates.

considered appropriate (cf. Clarke 1993). Results of SIMPER and the two way ANOSIM test showed that the macrofaunal assemblage differed among sites: site 1 was around 66–86% significantly dissimilar from sites 2 and 3, respectively, while the percentage dissimilarity of sites 2 and 3 was nearly 87% (Table V). *Polygordius* sp. and *Corophium* sp. were the species that contributed more to the differences between sites 1 and 2 (7.5 and

6.5%, respectively), while annelid and *Caecum chilense* were the top contributors to the macrofaunal differences between sites 1 and 3 (11.9 and 9.5% dissimilarity, respectively). Finally, *Polygordius* sp. and one species of Sillidae contributed more to the percentage dissimilarity between sites 2 and 3 (810.8 and 7.4%, respectively) (Table V). From stratum 6–9 cm till stratum 12–15 cm, no significant differences were found in the macrofaunal

Table IV. – Results of the effects of site and depth on abundance of total macroinfauna, *Polygordius* sp., *Corophium* sp. and *Caecum chilense* (ind.m⁻²). df = degrees of freedom. S = sampling sites, D = depths or strata (1 = 0-3 cm, 2 = 3-6 cm, 3 = 6-9 cm, 4 = 9-12 cm and 5 = 12-15 cm).

Source of variation	df	Total Macroinfauna		<i>Polygordius</i> sp.		<i>Corophium</i> sp.		<i>Caecum chilense</i>	
		F	p	F	p	F	p	F	p
Site (S)	2	32.40	< 0.001	30.95	< 0.001	7.93	0.001	18.46	< 0.001
Depth (D)	4	9.33	< 0.001	4.29	< 0.01	5.49	0.001	5.14	0.001
S x D	8	0.70	0.68	1.31	0.25	0.95	0.48	0.29	0.96
Residual	60								
Tukey's test		S ₃ < S ₁ = S ₂		S ₃ < S ₁ = S ₂		S ₃ < S ₁ = S ₂		S ₃ < S ₁ = S ₂	
		D ₁ = D ₂ > D ₃ = D ₄ = D ₅		D ₁ = D ₂ = D ₃ = D ₄ > D ₅		D ₁ > D ₂ = D ₃ = D ₄ = D ₅		D ₁ > D ₂ = D ₃ = D ₄ = D ₅	

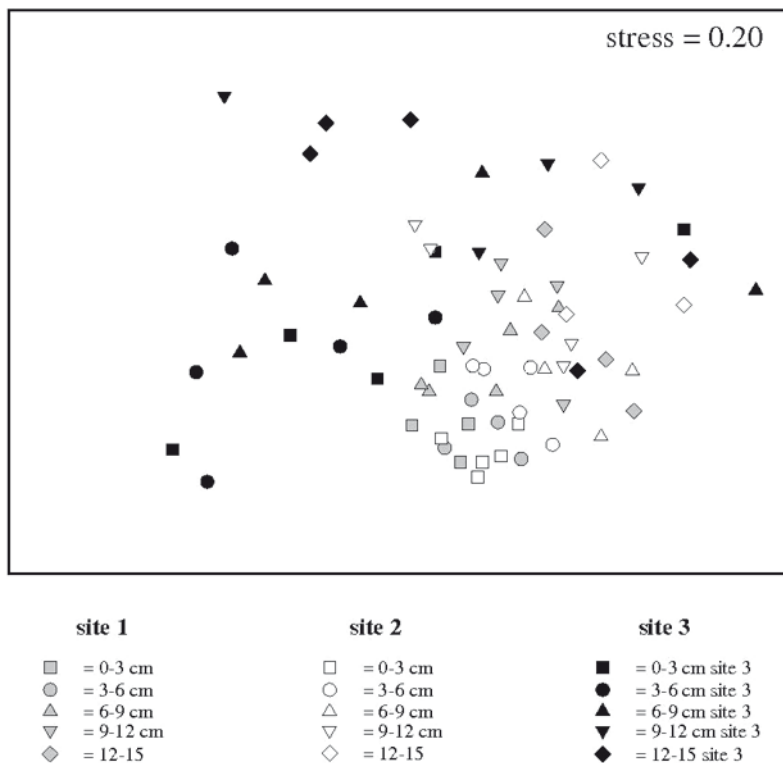


Fig. 6. – Graphic display of the Non Metric Multi Dimensional Scaling (NMMDS) analysis carried out with the macroinfaunal data (see Material and methods for details).

Table V. – Dissimilarity in percentage among sampling sites and depths: results of SIMPER analysis based on the abundances of the macroinfaunal species. * = p < 0.05 according to the results of the two way ANOSIM test (see Material and methods for details).

sites	1	2	3
1			
2	65.91*		
3	85.77*	86.59*	

depths (strata)	0-3 cm	3-6 cm	6-9 cm	9-12 cm
0-3 cm				
3-6 cm	71.03*			
6-9 cm	76.23*	72.71		
9-12 cm	79.04*	76.20*	73.66	
12-15 cm	83.82*	82.91*	78.65	75.96

assemblage, the same situation for stratum 3-6 cm and stratum 6-9 cm (Table V). The shallowest stratum (0-3 cm) differed significantly from all other strata (i.e. higher population abundances and species richness).

Relationships between macroinfauna and sediment characteristics

The results of BIO-ENV routine show that the best fit between the taxonomic composition of the macroinfauna and sedimentological variables, was reached with two variables ($p_w = 0.391$): total carbon and potential redox (Table VI). However, the combination of three and four variables (carbohydrates, total carbon and potential redox and carbohydrates, total nitrogen, total carbon and redox)

Table VI. – Results of the BIO-ENV routine: only the highest correlations between the matrices of biotic and abiotic similarity are given (see Material and methods for details).

n° of variables	Variable combination	Spearman rank correlation (p_w)
2	total carbon, redox	0.391
2	total nitrogen, redox	0.358
2	carbohydrates, redox	0.354
3	carbohydrates, total carbon, redox	0.390
3	total nitrogen, total carbon, redox	0.385
3	carbohydrates, total nitrogen, redox	0.366
4	carbohydrates, total nitrogen, total carbon, redox	0.385
4	carbohydrates, total carbon, redox, mud	0.359
4	total nitrogen, total carbon, redox, mud	0.353
5	carbohydrates, total nitrogen, total carbon, redox, mud	0.366

resulted in similar values of p_w (0.390 and 0.385).

DISCUSSION

This study shows that sediment characteristics and community structure of macroinfauna differ between sediments occupied by burrowing bivalves and sediments without bivalves. Macroinfaunal abundances were higher at the sediments of sites with burrowing bivalves (sites 1 and 2) and lower at the sediments without bivalves, the opposite pattern found in other tidal flats where abundance of infaunal invertebrates, such as amphipods, was negatively correlated with abundances of infaunal bivalves (Jensen 1985, Flach 1992). Having in mind that relationships and that positive relationships between abundance of infaunal bivalves and macroinvertebrate assemblages, have been also found in freshwater sedimentary habitats (e.g. Vaughn & Spooner 2006), it can be concluded that infaunal bivalves influence the distribution of co-occurring benthic macroinvertebrates.

The sediments occupied by burrowing bivalves showed a less marked decline of redox potential values, suggesting that the burrowing and subsequent bioturbation by bivalves is an important factor in the redistribution of reduced compounds from deeper layers to the sediment surface (Fenchel & Riedl 1970). It is noteworthy, that higher decreases in redox potential from shallow to deeper strata occurred at site 3 which had the coarsest sands. This could be probably explained by the absence of processes of bioturbation by bivalves as mentioned above. Although sites 1 and 2 had lower percentages of sands and finer particles than site 3, i.e. more favourable conditions for lower redox potential values, these sites showed higher redox values than site 3 probably due to the influence of bivalve's sediment reworking activities. However, the effect of bioturbation by bivalves probably decreases with depth due to the negative values of redox potential detected in the deepest strata (12-15 cm). On the other

hand, the deepest stratum of site 2, which had coarser sand grains than site 1 and lower densities of bivalves, presented positive values of redox potential. Thus, this site, dominated by both razor clams and clams, probably has more oxygenated conditions than the site dominated by razor clams and the site without bivalves. In this case, grain size seems to be the overriding factor of the observed pattern of redox potential.

The relative contribution of biochemical compounds to the total organic matter was dominated by proteins, followed by carbohydrates and lipids. This was also observed in other studies conducted on coastal sediments rich in organic matter (Sargent *et al.* 1983, Incera *et al.* 2003a, b), but it is in contrast with the biochemical composition reported from open ocean sediments which generally show carbohydrate dominance (Danovaro *et al.* 1993). The highest relative contribution of proteins was found in sediments of site 3 (ca. 82%), which was located on an upper ridge of the study area, probably more affected by hydrodynamic processes such as flooding and ebbing tides. That relative protein contribution was similar to that found for exposed sandy beaches with low organic matter located on the West coast of Spain (ca. 84%; Incera *et al.* 2003a). The relative protein contribution found in sediments dominated by razor clams (site 1) was similar to that found on tidal flats of Spain (ca. 61%; Cividanes *et al.* 2002), while that found in sediments dominated by razor clams and clams was a bit higher to that reported for sheltered fine sandy beaches of the same coast (ca. 71%; Incera *et al.* 2003a). The similarity in relative contribution of proteins to the total organic matter, between site 3 and exposed beaches and between site 2 and tidal flats suggests that relative contribution of proteins on sedimentary habitats could gradate according to exposure and hydrodynamic conditions.

The highest concentrations of proteins and biopolymeric carbon were found in the sediments of site 2 (nearly twice as much as compared to that in sites 1 and 3), indicating that the sedimentary organic matter of site 2 is

more readily available for consumers than at site 1 and 3. The specific location of site 2, in a shallow through with low hydrodynamic conditions and the presence of turf forming algae (which probably act as biological traps of organic matter transported in the water column; Scoffin 1970, Stewart 1983, Airoidi *et al.* 1996), could explain the higher food availability of this site.

The organic matter content in marine sediments is represented by labile and refractory compounds; while the first ones are easily remineralized, the last ones have low degradation rates (Fabiano & Danovaro 1994). Within the labile fraction of the organic matter, proteins are more readily utilized by bacteria than carbohydrates (Williams & Carlucci 1976, Newell & Field 1983). Thus, a high ratio protein:carbohydrate suggests the presence of organic matter recently generated and vice versa (Danovaro *et al.* 1993). Protein: carbohydrate ratios increased significantly from site 1 to site 2 and 3, suggesting that the sediments of sites 2 and 3 had a higher amount of new aged organic detritus than site 1 (Danovaro *et al.* 2003, Incera *et al.* 2003a, b). That differences may well be related to the fact that sediments of site 3 had macroinfaunal abundances significantly lower than that of the other sites and that the population abundances of *Tagelus dombeii* (a facultative deposit feeder bivalve) were nearly twice as lower than that at site 1. Thus, consumption of new aged organic detritus would be lower at sites 2 and 3 and in turn protein: carbohydrate ratio would be higher. Although we do not have comparative data for similar intertidal habitats as that studied here, some comparisons can be still carried out. The protein: carbohydrate ratios observed in this study (7.30-8.03 in site 3) were lower than that estimated for exposed sandy beaches of the Iberian Peninsula (up to 12.3; Incera *et al.* 2003a). On the other hand, the ratios estimated for site 2 (5.32-6.28) were quite similar to that calculated for sheltered sandy beaches of that same area (up to 5.24; Incera *et al.* 2003a). The highest protein: carbohydrate ratios estimated for site 3 suggests that due to its location (exposed to hydrodynamic conditions) the accumulation of organic matter is lower than in the other two sites which were located in an intertidal through, and consequently more prone to act as a natural trap of falling organic matter. That lead us to hypothesize that the high protein: carbohydrate ratio of site 3 is the result of organic matter primarily represented by the macroinfaunal organisms with scarce presence of old aged organic matter. On the other hand, the lowest protein: carbohydrate ratio calculated for site 1, suggests that apart from its more sheltered location, the high abundances of bivalves also has an important explanatory role in the accumulation of old aged organic matter, via the production of faecal pellets (as a fact of the matter, biogenic aggregates peaked at this site), primarily represented by vegetable matter. The last assertion is supported by the highest concentration of carbohydrates found at site 1 and also by the low proportion of biopolymeric carbon: total carbon (9-12%), lower than

the proportions estimated for sheltered sandy beaches (ca. 25%) (Cividanes *et al.* 2002). But, lacking the experimental evidence, our results pinpoint to a mixture of bivalve bioturbation and location of that sites, to account for the observed differences.

CONCLUSIONS

The results of this study show that significant differences in sediment characteristics, do indeed occur at small spatial scales (i.e. tens of meters) in the sedimentary intertidal of the inland coast of the Nord-Patagonic archipelagos. The multivariate analyzes aimed to examine the relationships between macroinfaunal assemblages and sediment characteristics, showed that redox and nutritional value of sediments were more important to explain spatial variability of that macroinfauna than textural characteristics of substrate.

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