

Community structure of benthic macroinvertebrates inhabiting a highly stratified Mediterranean estuary

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SUMMARY: The community composition and spatial distribution of benthic macroinvertebrates were studied along the Ebro estuary, a highly stratified estuary located in the NE Iberian Peninsula. During the last decade the oligotrophication process occurring in the lower Ebro River and its estuary has allowed a complex benthic macroinvertebrate community to become established; these results contrast with the poor community found there in the early nineties. A total of 214 taxa were identified, and polychaetes dominated the community both in abundance and species richness. The results showed spatial differences in the structure and composition of macroinvertebrates, which suggests that there are two distinct communities along the estuary. Each community was found in a specific stretch (upper and lower estuary) in function of the presence of the salt wedge. The macrobenthos of the upper estuary was dominated by freshwater taxa, but some euryhaline species were also found. The lower estuary showed a marine community typical of shallow Mediterranean environments. The transition between these two communities fits an ecotone model. The highest abundances, richness and diversities were recorded at the lower estuarine stations, especially those closer to the river mouth, whereas the lowest values corresponded to the stations adjacent to the tip of the salt wedge.

Keywords: benthic macroinvertebrates, community structure, distribution patterns, salt wedge, highly stratified estuary, Ebro estuary.

RESUMEN: ESTRUCTURA DE LA COMUNIDAD DE MACROINVERTEBRADOS BENTÓNICOS EN UN ESTUARIO MEDITERRÁNEO ALTAMENTE ESTRATIFICADO. – La composición de la comunidad y la distribución espacial de los macroinvertebrados bentónicos ha sido estudiada a lo largo del estuario del Río Ebro, un estuario altamente estratificado localizado al NE de la Península Ibérica. El proceso de oligotrofización ocurrido durante la última década en el tramo bajo del río Ebro y su estuario, ha permitido el establecimiento de una compleja comunidad de macroinvertebrados, contrastando con la comunidad encontrada a principios de los noventa. Un total de 214 taxones fueron identificados; los poliquetos constituyeron el grupo dominante en términos de riqueza y abundancia. Los resultados mostraron diferencias espaciales en la estructura y composición de macroinvertebrados, sugiriendo la existencia de dos comunidades diferentes a lo largo del estuario. Cada una de estas comunidades fue encontrada en un tramo específico (alto y bajo estuario) en función de la presencia de la cuña salina. El macrobentos del tramo alto del estuario estaba integrado mayoritariamente por taxones de agua dulce y algunos taxones eurihalinos. Por el contrario, el tramo bajo presentó una comunidad marina típica de ambientes mediterráneos someros. La transición entre estas dos comunidades encajó con un modelo ecotonal. Las abundancias, riquezas y diversidades más elevadas fueron registradas en las estaciones del tramo bajo, especialmente en aquellas cercanas a la desembocadura; en cambio, los valores más bajos correspondieron a las estaciones adyacentes al extremo de la cuña salina.

Palabras clave: macroinvertebrados bentónicos, estructura de la comunidad, patrones de distribución, cuña salina, estuario altamente estratificado, estuario del Ebro.

INTRODUCTION

The Ebro estuary (NE, Iberian Peninsula) is a salt wedge or highly stratified estuary (Hansen and Rattray, 1966; Ibáñez *et al.*, 1997). The specific characteristics

of salt wedge estuaries are: (i) the river discharge controls the marine intrusion mainly due to the low tidal range (usually with an amplitude less than 2 meters); (ii) weak mixing effects cause the water column to be strongly stratified; (iii) the vertical profile of density

and salinity shows a marked change with a narrow interface between layers called haloclines; and (iv) the isohalines are arranged horizontally. Although this kind of estuary is well represented along microtidal coasts worldwide (e.g. the Mediterranean Sea and the Gulf of Mexico), there is little research on the macroinvertebrate communities that inhabit them. The Ebro estuary has been extensively studied in relation to its hydrology and salt wedge dynamics (e.g. Ibáñez *et al.*, 1997, 1999; Sierra *et al.*, 2002, 2004), and some benthic communities of adjacent areas have also been studied (Capaccioni-Azzati and Martín, 1992; Martín *et al.*, 2000). A few studies have focused on the biota of the estuary (e.g. Rovira *et al.*, 2009), but only one includes a brief description of its macroinvertebrate community (Ibáñez *et al.*, 1995). Furthermore, this study was performed when the lower Ebro River and its estuary were under severe eutrophic conditions, very different from the present situation. Highly fluctuating estuarine systems produce strong environmental gradients, which leads to a patchy distribution of organisms that must cope with a wide variety of stresses (Morrisey *et al.*, 1992; Gray and Elliott, 2009) due to both natural and anthropogenic factors (McLusky, 1999; Dauer *et al.*, 2000; Dauvin, 2007; Elliott and Quintino, 2007). Therefore, the benthic invertebrate communities, often used as indicators of the health of an ecosystem, can be very similar in both impacted and non-disturbed estuarine systems. This therefore increases the difficulty of distinguishing natural from anthropogenic stresses. The *Estuarine Quality Paradox* concept (Dauvin, 2007; Elliott and Quintino, 2007) refers to the challenge of detecting anthropogenic impacts in naturally stressed systems using biological assessment methods. In Mediterranean regions and particularly in the Iberian Peninsula, besides the spatial fluctuation there is strong temporal environmental variability in the aquatic systems due to limited water availability during part of the year (Caiola *et al.*, 2001; Ferreira *et al.*, 2007a). This variability is exacerbated by a long history of human-induced pressures that have led to serious changes in the natural ecological cycles of estuarine systems from this region (Ferreira *et al.*, 2007b). Therefore, identifying the factors that structure the benthic macroinvertebrate community of the Ebro estuary will provide a clearer understanding of the ecological functioning of the system both at the spatial and temporal scales. Moreover, it will help to interpret the recent changes in the estuarine system observed during the last two decades (Ibáñez *et al.*, 2008). Therefore, this study establishes a robust basis so that macroinvertebrates can be used as indicators of the ecological status of the Ebro estuary.

The purpose of this study was to examine the macroinvertebrate community of the Ebro estuary with regard to species composition, community structure and distribution patterns along spatial and temporal scales and to describe the main abiotic factors affecting benthic communities in this type of estuary.

MATERIALS AND METHODS

Study area

The study was conducted in the Ebro estuary (40°43'10''N, 0°40'30''E) located in the NE of the Iberian Peninsula (Catalonia, Spain) (Fig. 1). The Ebro is 910 km long and has a drainage area of 85362 km²; it is the Spanish river with the highest mean annual flow and one of the most important tributaries to the Mediterranean Sea. The main land use in the basin is agriculture with more than 10000 km² of irrigation, corresponding to approximately 90% of the water usage in the basin (Ibáñez *et al.*, 2008). The whole basin is strongly regulated by nearly 190 dams (Batalla *et al.*, 2004). These affect the mean annual flow, which has decreased greatly since the beginning of the century to the present (Ibáñez *et al.*, 1996). The Ebro estuary is highly stratified (30 km long, 240 m mean width and 6-8 m mean depth) and the microtidal amplitude of the Mediterranean Sea, about 20 cm (Cacchione *et al.*, 1990), promotes the formation of a salt wedge. The river discharge controls the salt wedge dynamic (advance, retreat and permanence): when the flow exceeds 350-400 m³ s⁻¹ the salt wedge is pushed from the river channel, and the salt wedge reaches its maximum distance upstream (30-32 km from the river mouth) with flows lower than 100 m³ s⁻¹ (Ibáñez *et al.*, 1997).

Sampling design and laboratory procedures

Nine sampling stations were established in order to cover the whole estuarine stretch of the Ebro River (Fig. 1). Each station was sampled seasonally (summer 2007 to spring 2008). On each sampling occasion, three sediment samples were collected using a Ponar grab (0.046 m²). The samples were washed in situ through a 0.5-mm mesh sieve to separate macroinvertebrates from sediment, and the organisms retained were immediately fixed with buffered 10% formalin. Later in the laboratory, all macroinvertebrates were sorted, counted and identified under a stereomicroscope to the lowest possible taxonomic level. Two sediment aliquots of 30 g and 200 g were taken from each grab and stored at -20°C to estimate the total organic matter (TOM) with the loss on ignition method following Kristensen and Andersen (1987), and grain-size characterization according to Holme and McIntyre (1984). Bottom water samples were collected at each station with a water pump, preserved on ice in the absence of light, transported to the laboratory and stored at -20°C until analysis. Posterior processing included estimating the total chlorophyll and pheophytin concentration using the colorimetric method (Jeffrey and Humphrey, 1975), the dissolved and total nutrient concentration (PO₄, P_T, NH₄, NO₂, NO₃, N_T and SiO₄) following Koroleff (1977) and the suspended solid concentration (Total suspended solids (TSS, mg l⁻¹) and organic suspended solids (OSS, mg l⁻¹)) in compliance with the UNE-EN 872 norm (AENOR, 1996). In addi-

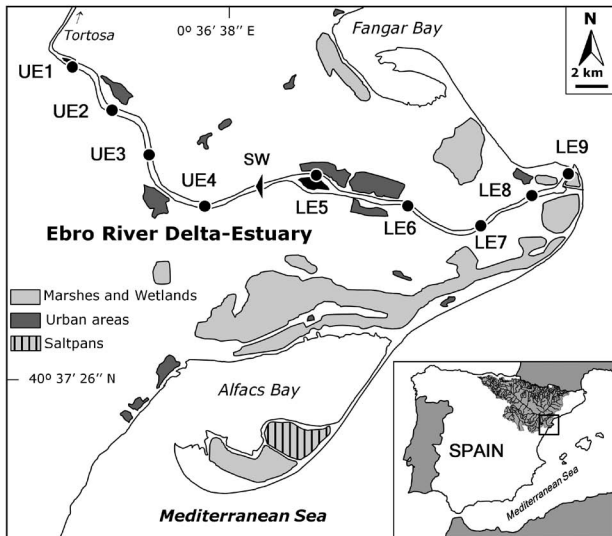


FIG. 1. – Location of the Ebro estuary and its deltaic plain showing the nine sampling stations. UE, upper estuary stations; LE, lower estuary stations; SW, position of the salt wedge tip.

tion, physicochemical and hydromorphological characteristics were recorded on each sampling occasion. A YSI 556 multi-parameter probe was used to measure water temperature ($^{\circ}\text{C}$), dissolved oxygen (mg l^{-1}), oxygen saturation (%), pH, salinity and conductivity (mS cm^{-1}). Water depth (m) was measured using a Speedtech SM-5 depth-meter sounder. Water flow velocity (m s^{-1}) was recorded with a Valeport m.001 current-meter, and water transparency was estimated using a Secchi disc. The accumulated permanence time (in days) of the salt wedge was calculated using daily mean flow values measured 40 km upstream from the river mouth (Tortosa) by counting the accumulated days before each sampling occasion with mean flow values lower than $350 \text{ m}^3 \text{ s}^{-1}$. This data is available at the Ebro Water Authority (CHE) web site (<http://www.chebro.es/>).

Data analysis

The following community descriptive parameters were calculated for each station and season ($n=36$): total abundance (N), density (D, ind m^{-2}), richness (S), Shannon-Wiener's diversity index (H' , as \log_2), Margalef index (d), Simpson dominance index ($1-\lambda'$) and Pielou's evenness index (J'). In addition, species were classified with the constancy index (Dajoz, 1971) into five categories according to the number of stations in which any given taxa was found in relation to the total number of stations: constant ($>76\%$), very common (51-75%), common (26-50%), uncommon (13-25%) and rare ($<12\%$). Each species was classified into feeding guilds based on the available literature. The feeding guilds included deposit feeders (DF), grazers (G), omnivores (O), parasites (Pa), predators (Pr) and suspension feeders (SF). Appendix 1 provides a list of the taxa, together with their feeding guild, that are mentioned in the text. Non-parametric multivari-

ate techniques were used as described by Field *et al.* (1982) to identify the possible macroinvertebrate communities. A similarity matrix was computed using the Bray-Curtis coefficient (Legendre and Legendre, 1998) after the four root transformation was applied to the abundance data to downweight the contribution of the most abundant taxa to the similarity (Clarke and Warwick, 2001). All the other statistical analyses were performed using the different routines available in the Multivariate Ecological Research software package PRIMER V6 (Clarke and Gorley, 2006). The stations and taxa were ordered using non-metrical multidimensional scaling (MDS) (Clarke and Warwick, 2001). A similarity percentage analysis (SIMPER) that examines the contribution of each variable to the average resemblances between sample groups was performed. This analysis was also used to identify taxa that contributed to dissimilarity among stations and estuary domains that were pre-determined by ordination analysis. Differences in the community composition were identified using the 1-way analysis of similarities test (ANOSIM) that hypothesizes for differences between groups of samples (defined a priori) through randomization methods on a resemblance matrix. Finally, the relationship between the community structure and environmental variables was investigated with the BIOENV routine, which maximizes a rank correlation (Spearman's coefficient) between resemblance matrices derived from biotic and environmental data, iterating for all possible combinations of environmental variables (Clarke and Warwick, 2001). A Spearman's coefficient value close to 0 indicates a weak relation between the community and environmental variables, whereas a value close to 1 indicates that the environmental variables selected explain the community structure.

RESULTS

Water and sediment features

The Ebro estuary has a sand dominated bottom and a relatively low TOM percentage in both the upper (UE) and lower (LE) parts and throughout the entire year (Table 1). During the study period the salt wedge was only found in the lower estuary stations. At these stations, the accumulated permanence time was different in each season: 55, 143, 257 and 344 days respectively for summer, autumn, winter and spring. The null point (the tip of the salt wedge) was located between UE4 and LE5 in all sampling periods. Nutrient concentrations were higher in the upper estuary stretch (Table 1) except for the ammonia, nitrite, phosphate and silicate concentrations in spring and total phosphorous in summer. The chlorophyll concentrations showed marked differences between the upper and lower estuary; the UE stretch had the highest values during winter and spring, whereas the maximum values in the LE stretch were in summer/autumn. Levels of total pheophytin were lower in the UE stretch except for during the two

TABLE 1. – Sediment characteristics and water physicochemical parameters (seasonal mean±standard deviation, n=4) in the two different stretches. TOM, total organic matter in sediment; Transp., transparency; DO, dissolved oxygen; Cond., conductivity; Sal., salinity; TDS, total dissolved salts; TSS, total suspended solids; OSS, organic suspended solids.

	Upper Estuary				Lower Estuary			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Mud (%)	11.31±14.59	11.31±14.59	21.08±28.43	1.53±2.08	15.89±10.90	15.89±10.90	25.27±20.78	6.51±5.75
Sand (%)	73.35±23.41	73.35±23.41	57.93±33.30	88.78±16.81	79.84±13.01	79.84±13.01	74.32±21.06	85.36±18.10
Gravel (%)	15.34±27.22	15.34±27.22	20.99±36.79	9.69±17.68	4.27±6.26	4.27±6.26	0.41±0.29	8.13±12.52
TOM (%)	2.67±1.03	2.67±1.03	2.89±1.11	2.45±1.88	4.03±1.22	4.03±1.22	4.36±1.59	3.70±2.21
Depth (m)	3.50±1.73	4.25±1.89	3.75±2.22	4.25±2.06	6.00±1.41	6.80±1.48	6.00±1.58	6.00±1.58
Velocity (m s ⁻¹)	0.13±0.06	0.17±0.05	0.14±0.05	0.42±0.10	0.06±0.04	0.10±0.09	0.05±0.05	0.25±0.21
Transp. (m)	2.40±0.71	2.68±0.78	1.98±0.73	2.21±0.22	2.37±0.27	1.89±0.23	1.88±0.13	1.60±0.22
T (°C)	24.26±0.40	22.80±0.07	11.12±0.36	16.32±0.14	22.07±0.19	22.30±0.83	13.27±0.04	15.30±0.51
DO (mg l ⁻¹)	7.85±0.47	7.89±1.22	13.82±0.69	7.94±0.69	5.25±1.22	6.00±2.4	10.32±0.83	6.72±2.11
DO (%)	94.00±6.26	92.00±14.25	126.28±7.02	81.30±7.24	74.10±17.64	84.78±33.61	123.90±10.11	74.36±16.52
Cond.(mS cm ⁻¹)	0.95±0.01	1.37±0.00	1.12±0.03	1.04±0.00	51.27±0.53	51.51±0.71	43.21±0.50	25.00±19.78
Sal.	0.47±0.01	0.72±0.00	0.77±0.02	0.62±0.00	35.97±0.31	35.98±0.40	36.89±0.45	20.02±16.27
TDS (g l ⁻¹)	0.62±0.01	0.93±0.00	0.99±0.02	0.81±0.00	35.30±0.27	35.30±0.34	36.19±0.39	20.09±15.95
Chlorophyll (µg l ⁻¹)	0.09±0.06	1.16±0.24	1.07±0.91	2.83±2.82	1.01±0.80	2.83±1.06	0.79±0.23	0.69±0.41
Pheophytin (µg l ⁻¹)	0.05±0.02	1.06±0.10	1.00±0.55	3.43±2.28	0.31±0.18	1.38±0.32	0.66±0.26	0.87±0.50
pH	8.20±0.06	8.25±0.05	7.89±0.09	8.00±0.02	7.98±0.06	8.28±0.15	7.94±0.05	7.83±0.11
PO4 (mg l ⁻¹)	0.02±0.00	0.03±0.00	0.03±0.01	0.03±0.01	0.01±0.01	0.01±0.02	0.01±0.01	0.03±0.01
P _T (mg l ⁻¹)	0.08±0.01	0.06±0.01	0.05±0.01	0.05±0.00	0.11±0.02	0.05±0.02	0.02±0.02	0.04±0.02
NH ₄ (mg l ⁻¹)	0.02±0.02	0.04±0.03	0.02±0.02	0.19±0.14	0.05±0.02	0.09±0.12	0.05±0.02	0.20±0.30
NO ₂ (mg l ⁻¹)	0.01±0.00	0.01±0.00	0.02±0.00	0.04±0.01	0.00±0.01	0.00±0.01	0.01±0.00	0.04±0.01
NO ₃ (mg l ⁻¹)	2.08±0.16	1.85±0.34	3.52±0.05	4.45±0.15	0.04±0.03	0.04±0.02	0.10±0.02	3.26±0.89
N _T (mg l ⁻¹)	2.42±0.08	2.43±0.04	3.52±0.05	5.37±0.08	0.28±0.07	0.20±0.12	0.10±0.02	4.39±1.13
SiO ₄ (mg l ⁻¹)	1.89±0.06	0.85±0.17	1.01±0.15	1.21±0.13	0.42±0.48	0.47±0.33	0.17±0.16	1.28±0.31
TSS (mg l ⁻¹)	3.05±0.98	3.56±2.68	2.91±1.66	14.69±11.25	20.60±2.17	24.99±3.78	16.91±32.53	5.84±3.51
OSS (mg l ⁻¹)	1.94±0.52	1.47±0.81	0.99±0.21	3.20±2.31	4.75±1.11	4.71±1.02	1.76±2.27	1.52±0.75
OSS (%)	66.49±18.14	46.07±8.76	43.07±21.78	23.19±2.59	22.92±3.70	18.72±1.53	27.34±12.39	27.04±2.95

last seasons. The UE stretch always had seasonal mean water flow velocities higher than the LE stretch. The values of TSS and OSS were higher in the LE stretch in summer, autumn and winter, whereas in spring the UE stretch showed the maximum values.

Macroinvertebrate abundance, taxa richness and diversity

During one year of seasonal sampling in the Ebro estuary a total of 21805 individuals were collected belonging to 214 different taxa that comprised 151 species, 115 families, 57 orders, 20 classes and 9 phyla (Supplementary material Appendix 1). Annelida was the dominant phylum and accounted for 71.07% of the total abundance. Polychaeta and Oligochaeta contributed with 49.64% and 21.42% respectively. Spionidae was the most abundant family (28.56%) due to the contribution of the most dominant species *Streblospio benedicti* (24.10% of the total abundance). Another dominant phylum was Arthropoda, which contributed 15.56% of the total abundance, with Malacostraca accounting for 10.37% of the total abundance. Mollusca was the third most abundant phylum with 12.09% of the total abundance, and Bivalvia contributed 10.61% of the total abundance. In terms of species richness, Polychaeta contributed with 49 different taxa (40 species) and Bivalvia with 37 taxa (32 sp), followed by Gastropoda with 29 taxa (18 sp) and Euentomata with 24 taxa (14 sp). Applying Dajoz's constancy index (considering the 9 stations), 1% of the taxa were found constant, 8% very common, 27% common, 20% uncommon and 44%

were rare. Applying the constancy index to UE stations revealed that 9% of the taxa were constant, 14% very common, 19% common, 58% were uncommon and no taxa were rare; whereas in the LE stretch 22% of the taxa were constant, 16% very common, 20% common and 42% were uncommon.

Total density values throughout seasons ranged from 216 to 20022 ind m⁻² (Table 2). The highest densities were found at the mouth (station LE9) due to the high abundance of the polychaete *S. benedicti*. Intermediate densities were found in the uppermost stations UE1 and UE2 with a large contribution of Tubificidae and the introduced bivalve *Corbicula fluminea*. The lowest densities corresponded to stations UE3, UE4 and LE5 in the middle part of the estuary. Station LE9 had the highest richness values with a maximum of 69 taxa and an annual mean value of 48 taxa; other stations located near the river mouth (LE8 and LE7) also reached high values of richness, whereas stations UE3, UE4 and LE5 showed the lowest richness values (Table 2). Diversity indices showed the same tendency as density and richness, with low values at stations located near the limit of the salt wedge (Table 2). In terms of the trophic structure, the deposit feeders (32%), suspension feeders (29%) and predators (17%) were the dominant feeding guilds in the entire estuary. The contribution of the different feeding guilds in the UE stretch was: deposit feeders (38%), predators (22%), grazers (19%), suspension feeders (14%), omnivores (5%) and parasites (3%). The trophic structure of the LE stretch was dominated by suspension feeders (35%) and deposit feeders (30%).

TABLE 2. – Community descriptive parameters for each sampling station and season. N, total abundance per 0.14 m²; D, density (ind m⁻²); S, richness; H' (log₂), Shannon-Wiener diversity index; d, Margalef index; 1-λ', Simpson's index; J', Pielou's evenness; DF (%), deposit feeders; G (%), grazers; O (%), omnivores; Pa (%), parasites; Pr (%), predators; SF (%), suspension feeders. See Figure 1 for sampling station codes.

Station	Season	Density	Community indices					Trophic structure					
			S	H' (log ₂)	d	1-λ'	J'	DF	G	O	Pa	Pr	SF
UE1	Summer	2792	11	1.96	1.68	0.67	0.57	54.55	0.00	9.09	9.09	9.09	18.18
UE2	Summer	4820	25	2.16	3.69	0.59	0.47	44.00	16.00	4.00	8.00	12.00	16.00
UE3	Summer	830	6	2.02	1.05	0.72	0.78	33.33	0.00	16.67	16.67	0.00	33.33
UE4	Summer	491	3	1.45	0.47	0.61	0.91	0.00	0.00	33.33	0.00	0.00	66.67
LE5	Summer	216	4	0.63	0.88	0.19	0.31	50.00	25.00	25.00	0.00	0.00	0.00
LE6	Summer	1457	7	1.03	1.13	0.32	0.37	57.14	0.00	14.29	0.00	0.00	28.57
LE7	Summer	2670	23	2.52	3.72	0.67	0.56	47.83	4.35	8.70	0.00	4.35	34.78
LE8	Summer	2583	23	3.18	3.74	0.82	0.70	56.52	0.00	8.70	0.00	8.70	26.09
LE9	Summer	11212	32	0.48	4.22	0.09	0.10	25.00	3.13	15.63	0.00	18.75	37.50
UE1	Autumn	491	13	2.79	2.84	0.80	0.75	30.77	23.08	7.69	0.00	23.08	15.38
UE2	Autumn	2403	23	3.15	3.79	0.80	0.70	34.78	13.04	4.35	0.00	34.78	13.04
UE3	Autumn	1335	8	1.29	1.34	0.42	0.43	62.50	0.00	0.00	0.00	25.00	12.50
UE4	Autumn	505	12	2.57	2.59	0.78	0.72	58.33	0.00	16.67	0.00	16.67	8.33
LE5	Autumn	2020	11	2.00	1.77	0.60	0.58	54.55	0.00	0.00	0.00	0.00	45.45
LE6	Autumn	599	21	3.94	4.53	0.93	0.90	52.38	0.00	4.76	4.76	23.81	14.29
LE7	Autumn	2316	31	3.19	5.20	0.75	0.64	35.48	0.00	6.45	3.23	16.13	38.71
LE8	Autumn	2648	36	2.84	5.93	0.66	0.55	30.56	5.56	5.56	2.78	8.33	47.22
LE9	Autumn	13485	69	2.84	9.03	0.68	0.47	31.88	1.45	7.25	7.25	17.39	34.78
UE1	Winter	9632	21	0.79	2.78	0.18	0.18	33.33	19.05	0.00	4.76	23.81	19.05
UE2	Winter	4906	17	1.57	2.45	0.41	0.38	47.06	17.65	11.76	5.88	5.88	11.76
UE3	Winter	981	4	1.05	0.61	0.48	0.53	50.00	0.00	0.00	0.00	25.00	25.00
UE4	Winter	1522	6	0.99	0.93	0.34	0.38	66.67	0.00	0.00	0.00	16.67	16.67
LE5	Winter	2756	19	2.64	3.03	0.78	0.62	47.37	5.26	0.00	5.26	5.26	36.84
LE6	Winter	4278	27	3.30	4.07	0.86	0.69	51.85	3.70	7.41	3.70	14.81	18.52
LE7	Winter	6934	62	3.81	8.88	0.83	0.64	46.77	3.23	4.84	3.23	16.13	25.81
LE8	Winter	3413	48	4.04	7.63	0.87	0.72	50.00	0.00	8.33	2.08	14.58	25.00
LE9	Winter	20022	58	1.66	7.19	0.35	0.28	37.93	1.72	6.90	5.17	18.97	29.31
UE1	Spring	18319	21	0.98	2.55	0.27	0.22	44.44	22.22	0.00	5.56	11.11	16.67
UE2	Spring	5368	24	1.74	3.48	0.46	0.38	41.67	20.83	8.33	0.00	16.67	12.50
UE3	Spring	1198	9	2.42	1.56	0.78	0.76	55.56	0.00	0.00	0.00	22.22	22.22
UE4	Spring	3802	8	0.34	1.12	0.08	0.11	50.00	12.50	12.50	0.00	12.50	12.50
LE5	Spring	3629	7	0.91	0.96	0.33	0.32	42.86	0.00	14.29	14.29	0.00	28.57
LE6	Spring	1941	28	3.14	4.83	0.80	0.65	46.43	0.00	10.71	0.00	21.43	21.43
LE7	Spring	6486	59	4.15	8.53	0.88	0.71	47.46	1.69	11.86	3.39	15.25	20.34
LE8	Spring	7417	63	4.62	8.94	0.93	0.77	41.27	1.59	12.70	3.17	17.46	23.81
LE9	Spring	1876	33	3.30	5.75	0.81	0.65	48.48	0.00	6.06	3.03	21.21	21.21

Analysis of benthic macroinvertebrate communities

Two different communities were determined according to the ordination of stations and taxa of the MDS analysis based on macroinvertebrate abundance. The ordination showed two definite groups of sampling stations: those corresponding to the upper estuary (UE) and lower estuary (LE) respectively (Fig. 2). The UE group (UE1-UE4) included stations located in the upper estuary stretch and corresponded to a freshwater community, whereas the second group comprised the lower estuary stations (LE5-LE9) and had a community with a large marine influence. In addition, we also applied the MDS analysis considering lower taxonomic categories e.g. genus and family; the results obtained showed the same grouping of stations regardless of the taxonomic level employed in the ordinations. Significant differences in community composition were found between these two groups (ANOSIM r : 0.891, $p < 0.001$). Significant differences were also found among stations (ANOSIM global r : 0.694, $p < 0.001$) except for the following pairs: UE1-UE3, UE3-UE4, UE4-LE5, LE5-LE6, LE6-LE7, LE6-LE8, LE7-LE8, LE7-LE9 and LE8-LE9, $p > 0.05$ (Table 3).

The SIMPER analysis showed that the mean community similarity within the UE group was 32.30%. The taxa that most contributed to the high similarity among stations were *C. fluminea* (27.26%), Tubificidae (18.34%), Naididae (12.02%) and Chironomidae (17.00%). The mean similarity of the LE group was 29.67% with a high contribution from *S. benedicti* (10.44%), *Corophium orientale* (8.56%) and *Caulleriella zetlandica* (6.01%). The similarity contribution of taxa within this group was more balanced than in the UE group, since a total of 35 taxa was necessary to accumulate 90% of the similarity. The mean dissimilarity between these two groups was 96.58% with *C. fluminea*, *S. benedicti*, Tubificidae, *C. orientale*, Naididae, *C. zetlandica*, *Pseudopolydora antennata* and *Armandia cirrhosa* as the taxa with the highest contributions to dissimilarity.

The BIOENV analysis showed that the combination of salinity, dissolved phosphate, total phosphorous, ammonia and the distance from the mouth have a large influence on the structure of the macroinvertebrate communities ($\rho = 0.741$). The combination of salinity, dissolved phosphate, ammonia and nitrate explained the differences in taxa abundance in the upper estuary ($\rho = 0.308$). However, within the community of the lower estuary, the combination of ammonia, total chlorophyll, sand percentage,

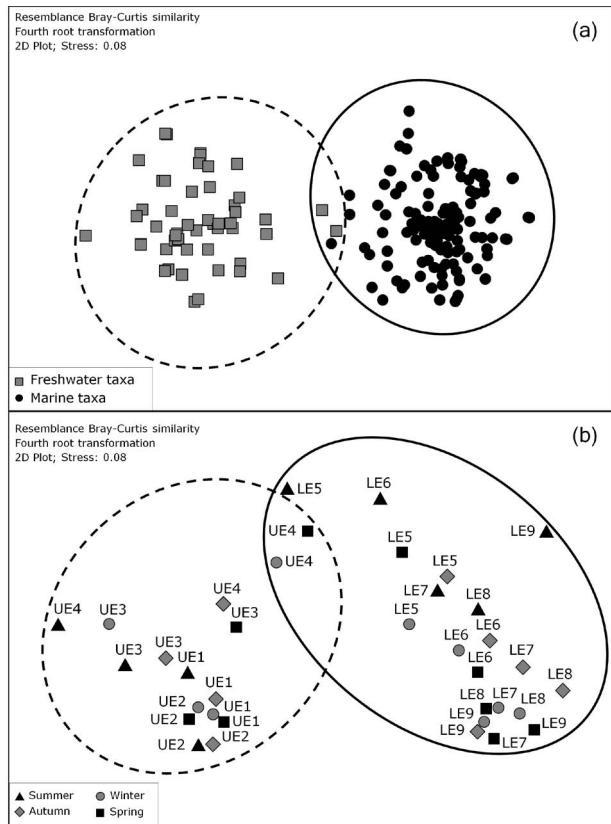


FIG. 2. – Two dimensional MDS plots based on Bray-Curtis similarities of fourth-root transformed macroinvertebrate abundance data: (a) ordination using inter-species resemblance matrix of nine stations; (b) ordination of the nine stations sampled in the Ebro estuary. The dashed line and the solid line encircle the freshwater and marine communities respectively. See Figure 1 for sampling station codes.

TABLE 3. – One-way ANOSIM test to compare the macroinvertebrate communities at different sampling stations. The test results are shown in the lower diagonal of the table. Significant differences between stations ($P < 0.05$) are indicated (*). The R values are shown in bold letters in the upper diagonal of the table. See Figure 1 for sampling station codes.

	UE1	UE2	UE3	UE4	LE5	LE6	LE7	LE8	LE9
UE1		0.708	0.458	0.552	1.000	1.000	1.000	1.000	1.000
UE2	0.029*		0.719	0.635	1.000	1.000	1.000	1.000	1.000
UE3	0.057	0.029*		0.219	0.917	0.990	1.000	1.000	1.000
UE4	0.029*	0.029*	0.143		0.302	0.688	0.849	0.885	0.880
LE5	0.029*	0.029*	0.029*	0.114		0.219	0.542	0.667	0.604
LE6	0.029*	0.029*	0.029*	0.029*	0.143		0.167	0.115	0.448
LE7	0.029*	0.029*	0.029*	0.029*	0.029*	0.171		0.000	0.240
LE8	0.029*	0.029*	0.029*	0.029*	0.029*	0.200	1.000		0.083
LE9	0.029*	0.029*	0.029*	0.029*	0.029*	0.029*	0.086	0.229	

TOM and the permanence time of the salt wedge showed the highest correlation and explained the main differences in the macroinvertebrate abundance data ($\rho = 0.681$)

DISCUSSION

The whole Ebro estuary is dominated by sand; however, the percentage of fine deposits such as clay or mud was higher in the lower stretch due to flocculation and settling processes and low velocities recorded at the salt

wedge (Sierra *et al.*, 2002). During the study period the bottom water layer of the estuary showed important differences in physicochemical features between the lower and upper estuary stretches. We found freshwater stations (UE1-UE4) that were not exposed to marine intrusions, and saltwater stations (LE5-LE9) that were permanently exposed to marine intrusions and had a well stratified water column. At LE stations, salinity in the salt wedge decreased upstream with small fluctuations but with values always higher than 30, which evidences the weak mixing between water layers. In highly stratified estuaries the salt wedge dynamics are complex and can be explained by a combination of hydromorphological factors, such as the tide amplitude, river channel cross section and flow, and the freshwater runoff is one of the main factors determining the salt wedge regime (Ibáñez *et al.*, 1997). Nevertheless, in the lower estuary the salt wedge was present on all sampling occasions and the permanence time almost reached a complete year. Although other long periods of marine intrusion in the Ebro estuary have been recorded before (Ibáñez *et al.*, 1995), under natural conditions this period should be approximately 6 months per year (Ibáñez *et al.*, 1997). These conditions of the quasi permanent presence of the salt wedge in the lower estuary stretch are exacerbated by the strong flow regulation and the almost total absence of peak flows, which leads to reduced turbulence and therefore to highly stable density-thermal stratification (Ibáñez *et al.*, 1995, 1996).

The present conditions of nutrient loading of the Ebro estuary are quite different from the past situation of eutrophication (Ibáñez *et al.*, 1995). Under eutrophic conditions, and with long periods of permanence of the salt wedge in the lower estuary at the same time, the water quality was worse below the wedge than above it due to organic matter deposition and low water renewal. This organic enrichment caused oxygen depletion through microbial consumption (Ibáñez *et al.*, 1995; Casamayor *et al.*, 2001). Recent changes in the nutrient content of the river, especially the reduction of phosphates, have reduced the primary production in the upper layer, whereas in the lower layer it has increased due to higher light penetration (Falco *et al.*, 2010); thus, the hypoxic conditions in the lower layer have decreased (Casamayor *et al.*, 2001; Ibáñez *et al.*, 2008).

Under the present oligotrophication process, the long periods of salt wedge permanence ensure the stability of the water column, which allows the complexity of the benthic communities to increase, as suggested by Sousa *et al.* (2006a). The present situation is very different to that of the early nineties, when a survey conducted in October 1992 showed an impoverished macroinvertebrate community (only seven different taxa were found) due to eutrophication, which caused severe anoxic episodes below the halocline (Ibáñez *et al.*, 1995).

The benthic macroinvertebrate community in the Ebro estuary shows considerable spatial and temporal differences, with a complex structure and composition. The multivariate analysis defined two different communities: one from the lower and one from the upper

estuary stretch. In contrast, the pattern described in more mixed estuaries (Rundle *et al.*, 1998; Ysebaert *et al.*, 1998; Sousa *et al.*, 2008) supports the idea that these systems work as a continuum of overlapping communities along the salinity gradient, which fits with the ecocline boundary model suggested by Attrill and Rundle (2002). However, the weak longitudinal salinity gradient and the narrow transition zone between fresh and marine water suggest that the Ebro estuary fits much better into an ecotone model, when ecotone is defined as an area of relatively rapid change that produces a narrow ecological zone between two different and homogeneous community types (Van der Maarel, 1990).

The upper stretch of the Ebro estuary was characterized by an impoverished macroinvertebrate community dominated by the non-indigenous bivalve *C. fluminea*, which tends to acquire an invasive pattern (Sousa *et al.*, 2006b), together with tolerant taxa such as Tubificidae, Naididae (Oligochaeta) and abundant Chironomidae. The amphipod *C. orientale* was well-represented in number of individuals but its presence was restricted to stations UE3 and UE4 located close to the salt wedge tip due to its euryhaline nature. The salt wedge community was dominated in terms of abundance by the Polychaeta and Malacostraca classes, followed by the phylum Mollusca. Nevertheless, in terms of richness it was dominated by molluscs, polychaetes and crustaceans in this order. This pattern was slightly different from those found in other temperate intertidal areas, where polychaetes are the most diverse group, followed by molluscs and crustaceans (Ysebaert *et al.*, 1998; Rodrigues *et al.*, 2006). Comparing our results with those from other European estuarine ecosystems we found that the Ebro estuary was colonized in its mouth area by typical marine species associated with the *Abra alba-Lagis koreni* community (colonizing fine sediments rich in organic matter) and with the *Nephtys* spp. community (colonizing sandy sediments). These two communities are widely distributed throughout European estuarine and coastal areas (Dauvin, 2000, 2007; Martín *et al.*, 2000; Van Hoey *et al.*, 2004; Puente *et al.*, 2008). In addition to these communities, we also found tolerant groups dominated by Capitellidae and Spionidae (Polychaeta), together with *Corbula gibba*, which usually colonizes disturbed areas; whereas in the upper stations close to the null point the community was dominated by eurybiontic taxa like *Hediste diversicolor*, *Perinereis cultrifera*, *Heteromastus filiformis*, *C. orientale* and *Cyathura carinata*. These species are also very common in other European estuaries and coastal areas (Marques *et al.*, 1993; Ysebaert *et al.*, 1998, 2003; Martín *et al.*, 2000; Chainho *et al.*, 2006; Rodrigues *et al.*, 2006; Sousa *et al.*, 2006a, 2008).

Currently, the Ebro estuary shows high levels of richness compared with other European estuaries (Rodrigues *et al.*, 2006). The trophic structure is well represented with six different trophic guilds. Deposit feeders, suspension feeders and predators are dominant, which suggests that different resources are available (Brown *et al.*, 2000). In the upper stretch the diversity

and richness decreased seawards, with minimum values found close to the null point because the salinity fluctuation is a physiological barrier for stenohaline freshwater and marine taxa (Mannino and Montagna, 1997). However, diversity and richness at the salt wedge stations declined with increasing distance from the sea, which is a recurring tendency in mixed estuaries (Remane and Schleiper, 1971; Schlacher and Woolbridge, 1996). In the Ebro estuary this impoverishment tendency could be explained by the increase in organic matter, ammonia and total phosphorous towards the tip of the salt wedge in combination with the salinity fluctuations in the same area.

The present study provides baseline data that can be used in future ecological studies on this important Mediterranean estuarine ecosystem, as well as in comparisons with other highly stratified estuaries. Complementary studies are necessary to improve our understanding of the spatial and temporal variability of the macrozoobenthic estuarine community. This knowledge could be an important tool for conserving the biodiversity in the Ebro estuary and could be used to develop biological indices for assessing its ecological status according to the Water Framework Directive of the European Union.

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SUPPLEMENTARY MATERIAL

The following Appendix is available through the web page <http://www.icm.csic.es/scimar/supplm/sm75n3577sm.pdf>

APPENDIX 1. – List of the identified taxa that were found at all the stations over the entire study period.

Community structure of benthic macroinvertebrates inhabiting a highly stratified Mediterranean estuary

ALFONSO NEBRA, NUNO CAIOLA and CARLES IBÁÑEZ

Supplementary material

APPENDIX 1. – List of the identified taxa that were found at all the stations over the entire study period. The stations where each taxon was found are also listed. See Figure 1 for sampling station codes; FG, feeding guild (see Table 2 for feeding guild codes); CI, Constancy index; Ct, constant; VC, very common; C, common; UC, uncommon; R, rare.

Taxa	Summer	Autumn	Winter	Spring	FG	CI	CI UE	CI LE
PHYLUM CNIDARIA								
Class Anthozoa								
<i>Diadumene</i> sp.	LE9				Pr	R		UC
PHYLUM PLATYHELMINTHES								
Class Turbellaria								
<i>Dugesia</i> sp.	UE2	UE2		UE2	Pr	R	UC	
Turbellaria indet.		UE2	UE1		Pr	UC	C	
PHYLUM NEMERTINA								
Class Enopla								
Nemertina indet.		LE6,7,9	LE5,6,7,8,9	LE6,7,8,9	Pr	VC		Ct
<i>Prostoma graecense</i> (Böhmgig, 1892)		UE2	UE1,2,4	UE2	Pr	C	VC	
PHYLUM NEMATODA								
Nematoda indet.	UE1,2,3	LE9	UE1,2; LE9	UE1	Pa	C	VC	UC
PHYLUM MOLLUSCA								
Class Gastropoda								
Aplysiidae indet.	LE9	LE8			G	UC		C
<i>Bittium reticulatum</i> (da Costa, 1778)		LE8,9	LE7,8,9	LE7,8,9	DF	C		VC
<i>Buccinum</i> sp.	LE9				O	R		UC
<i>Chrysallida</i> sp.		LE6,7,8,9	LE5,6,7,8,9	LE5,7,8,9	Pa	VC		Ct
<i>Eulimella polita</i> (Verrill, 1872)		LE9			Pa	R		UC
<i>Ferrissia clessiniana</i> (Jickeli, 1882)	UE2	UE2		UE2	G	R	UC	
<i>Gyraulus albus</i> (Müller, 1774)				UE1,2,4	G	C	VC	
<i>Haminoea navicula</i> (da Costa, 1778)			LE6,7		G	UC		C
<i>Hinia limata</i> (Chemnitz, 1795)	LE9	LE9		LE9	Pr	R		UC
<i>Hydrobia</i> sp.	LE7		LE5	LE7	G	UC		C
<i>Hydrobia ulvae</i> (Pennant, 1777)			LE7		O	R		UC
<i>Mangelia</i> sp.		LE9			G	R		UC
<i>Melanella polita</i> (Linnaeus, 1758)			LE9		Pa	R		UC
<i>Nassarius mutabilis</i> (Linnaeus, 1758)		LE9	LE9		O	R		UC
<i>Nassarius pygmaeus</i> (Lamarck, 1822)	LE7,8,9	LE9			O	C		VC
<i>Nassarius</i> sp.		LE7,9			O	UC		C
<i>Neverita josephina</i> Risso, 1826	LE9	LE9			Pr	R		UC
<i>Odostomia conoidea</i> (Brocchi, 1814)				LE8	Pa	R		UC
<i>Odostomia</i> sp.		LE9			Pa	R		UC
<i>Physella acuta</i> (Draparnaud, 1805)	UE2	UE1,2	UE1,2	UE1,2	G	UC	C	
<i>Radix auricularia</i> (Linnaeus, 1758)			UE2		G	R	UC	
<i>Radix peregra</i> (Müller, 1774)	UE2		UE1	UE2	G	UC	C	
<i>Retusa truncatula</i> (Bruguère, 1792)	LE8	LE9	LE7	LE6,7,8	Pr	C		Ct
<i>Rissoa</i> sp.		LE9	LE9		G	R		UC
<i>Rissoa ventricosa</i> Desmarest, 1814				LE8	G	R		UC
<i>Tricolia</i> sp.		LE8			G	R		UC
<i>Turbonilla lactea</i> (Linnaeus, 1758)		LE9	LE7	LE7	Pa	UC		C
<i>Turritella</i> sp.		LE9			SF	R		UC
Class Bivalvia								
<i>Abra alba</i> (Wood, 1802)	LE9	LE5,7,8,9	LE7,8,9	LE7,8,9	SF	C		Ct
<i>Abra nitida</i> (Müller, 1776)		LE9	LE9	LE8	SF	UC		C
<i>Acanthocardia echinata</i> (Linnaeus, 1758)		LE7,8,9			SF	C		VC
<i>Acanthocardia paucicostata</i> (Sowerby, 1841)	LE8	LE6,7	LE7,8,9	LE7,8	SF	C		Ct
<i>Acanthocardia tuberculata</i> (Linnaeus, 1758)				LE9	SF	R		UC
<i>Cerastoderma edule</i> (Linnaeus, 1758)				LE8	SF	R		UC
<i>Cerastoderma glaucum</i> (Poiret, 1789)		LE8	LE5,7		SF	C		VC
<i>Circomphalus casina</i> (Linnaeus, 1758)	LE7	LE8	LE8		SF	UC		C
<i>Corbicula fluminea</i> (Müller, 1774)	UE1,2,3,4	UE1,2,3,4	UE1,2,3,4	UE1,2,3	SF	C	Ct	
<i>Corbula gibba</i> (Olivi, 1792)	LE7,9	LE5,6,7,8,9	LE5,6,7,8,9	LE5,6,7,8	SF	VC		Ct
<i>Donax semistriatus</i> Poli, 1795	LE9	LE9			SF	R		UC
<i>Donax</i> sp.		LE9			SF	R		UC
<i>Donax trunculus</i> Linnaeus, 1758	LE7				SF	R		UC
<i>Donax venustus</i> Poli, 1795		LE8			SF	R		UC
<i>Dosinia lupinus</i> (Linnaeus, 1758)		LE8,9	LE7,8,9	LE8,9	SF	C		VC
<i>Gari fervensis</i> (Gmelin, 1791)		LE9			SF	R		UC
<i>Gastrana fragilis</i> (Linnaeus, 1758)			LE9		SF	R		UC
<i>Glycymeris glycymeris</i> (Linnaeus, 1758)		LE9			SF	R		UC
<i>Laevicardium crassum</i> (Gmelin, 1791)		LE8			SF	R		UC
<i>Lutraria lutraria</i> (Linnaeus, 1758)	LE9				SF	R		UC
<i>Mactra corallina</i> (Linnaeus, 1758)	LE7,9	LE7,8			SF	C		VC
<i>Mactra</i> sp.		LE9	LE9		SF	R		UC
<i>Musculus discors</i> (Linnaeus, 1767)	LE7,8	LE7,9	LE5,7	LE6,7,8	SF	VC		Ct
<i>Mytilus galloprovincialis</i> Lamarck, 1819				LE8	SF	R		UC
<i>Pandora inaequalis</i> (Linnaeus, 1758)	LE7,8	LE7,8,9	LE8,9	LE7	SF	C		VC
<i>Pharus legumen</i> (Linnaeus, 1758)		LE9		LE9	SF	R		UC

APPENDIX 1 (cont.). – List of the identified taxa that were found at all the stations over the entire study period. The stations where each taxon was found are also listed. See Figure 1 for sampling station codes; FG, feeding guild (see Table 2 for feeding guild codes); CI, Constancy index; Ct, constant; VC, very common; C, common; UC, uncommon; R, rare.

Taxa	Summer	Autumn	Winter	Spring	FG	CI	CI UE	CI LE
<i>Pitar rudis</i> (Poli, 1795)		LE8	LE8		SF	R		UC
<i>Scrobicularia plana</i> (da Costa, 1778)	LE9			LE8	SF	UC		C
<i>Solemya togata</i> (Poli, 1795)			LE9		SF	R		UC
<i>Solen</i> sp.		LE9	LE5		SF	UC		C
<i>Spisula subtruncata</i> (da Costa, 1778)	LE8,9	LE9	LE7	LE7,8,9	SF	C		VC
<i>Tapes philippinarum</i> (Adams and Reeve, 1850)			LE7	LE7	SF	R		UC
<i>Tapes pullastra</i> (Unspecified)	LE7	LE7,8			SF	UC		C
<i>Tapes</i> sp.		LE8,9	LE6,7,8,9	LE7,8,9	SF	C		Ct
<i>Tellina albicans</i> (Gmelin, 1791)		LE8,9	LE7,9	LE7	SF	C		VC
<i>Tellina</i> sp.		LE8,9	LE7,9	LE6,9	SF	C		Ct
<i>Tellina tenuis</i> da Costa, 1778		LE9	LE5,8,9	LE7	SF	C		Ct
Class Scaphopoda								
<i>Antalis novemcostata</i> (Lamarck, 1818)				LE8	Pr	R		UC
<i>Antalis</i> sp.		LE8,9	LE9	LE7,8	Pr	C		VC
PHYLUM ANNELIDA								
Class Hirudinea								
<i>Helobdella stagnalis</i> (Linnaeus, 1758)	UE2				Pr	R	UC	
<i>Piscicola geometra</i> (Linnaeus, 1758)	UE2				Pa	R	UC	
Class Oligochaeta								
Haplotaxidae indet.			UE3		DF	R	UC	
Lumbricidae indet.	UE2			UE1	DF	UC	C	
Naididae indet.	UE1,2	UE1,2,3	UE1,2,4; LE5	UE1,2,3,4	DF	VC	Ct	UC
Tubificidae indet.	UE1,2,3; LE5	UE1,2,3,4	UE1,2,3	UE1,2,3	DF	VC	Ct	UC
Class Polychaeta								
<i>Ampharete grubei</i> Malmgren, 1865	LE6,7,8	LE6,7,8,9	LE6,7,8,9	LE6,7,8	DF	C		Ct
<i>Aricidea</i> sp.	LE8,9	LE6,7,8,9	LE7,8,9	LE6,7,8,9	DF	VC		Ct
<i>Armandia cirrhosa</i> Filippi, 1861	LE6,7,8	LE5,6,7,9	LE5,6,7,9	LE7,8	DF	VC		Ct
<i>Capitella capitata</i> (Fabricius, 1780)	LE6		LE5,6,7,8,9	LE6,8,9	DF	VC		Ct
Capitellidae indet.	LE8	LE7			DF	UC		C
<i>Cauterella zetlandica</i> (McIntosh, 1911)	LE8	LE6,7,8,9	LE6,7,8,9	LE6,7,8,9	DF	C		Ct
<i>Cirratulus cirratus</i> (Müller, 1776)			LE7,8,9	LE7,9	DF	C		VC
<i>Clymenura clypeata</i> (Saint-Joseph, 1894)			LE7	LE7,8	DF	UC		C
<i>Diopatra neapolitana</i> Delle Chiaje, 1841			LE8,9	LE7,9	DF	C		VC
<i>Eteone picta</i> Quatrefagues, 1865		LE6,7,9	LE7,9	LE7	Pr	C		VC
<i>Euclymene oerstedii</i> (Claparède, 1863)			LE7,8,9	LE6,7,8	DF	C		Ct
<i>Eunice harassii</i> Audouin & Edwards, 1834		LE8,9	LE7		DF	C		VC
<i>Ficopomatus enigmaticus</i> (Fauvel, 1923)	LE6				SF	R		UC
<i>Glycera</i> sp.		LE6,9	LE6,7,8,9	LE6,7,8,9	Pr	C		Ct
<i>Glycera tessellata</i> Grube, 1840				LE9	Pr	R		UC
<i>Glycera tridactyla</i> Schmarda, 1861	LE8,9	LE6,7			Pr	C		Ct
<i>Harmothoe</i> sp.		LE6,9	LE7,8,9		Pr	C		Ct
<i>Hediste diversicolor</i> (Müller, 1776)	LE7,8	LE6,7,8	LE7,8	LE5,6,7,8	O	C		Ct
<i>Heteromastus filiformis</i> (Claparède, 1864)		LE5,6	LE7,8,9	LE6,7,8,9	DF	VC		Ct
<i>Hydroides norvegicus</i> Gunnerus, 1768		LE7			SF	R		UC
<i>Lagis koreni</i> Malmgren, 1866	LE9		LE6,9		DF	UC		C
<i>Laonice cirrata</i> (Sars, 1851)			LE8,9		DF	UC		C
<i>Lepidonotus squamatus</i> (Linnaeus, 1758)			LE7,9	LE8	Pr	C		VC
<i>Lumbrineris</i> sp.		LE7,8,9	LE6,7,8	LE7,8	Pr	C		Ct
<i>Magelona papillicornis</i> Müller, 1858		LE9		LE7,9	DF	UC		C
<i>Melinna palmata</i> Grube, 1870		LE6,7,8,9	LE5,7,8,9	LE6,7,8	DF	VC		Ct
<i>Micronephthys maryae</i> San Martín, 1982	LE7	LE7,8,9	LE7,8,9	LE6,7,8,9	Pr	C		Ct
<i>Neosabellides oceanica</i> (Fauvel, 1909)			LE6,7,8	LE7	DF	C		VC
<i>Nephtys assimilis</i> Örsted, 1843				LE9	Pr	R		UC
<i>Nephtys cirrosa</i> (Ehlers, 1868)	LE9				Pr	R		UC
<i>Nephtys hombergii</i> Lamarck, 1818			LE9		Pr	R		UC
<i>Nephtys</i> sp.				LE6,8	Pr	UC		C
Nereididae indet.			UE4; LE6,7	UE4	DF	C	UC	C
<i>Notomastus</i> sp.		LE9	LE7,8,9		DF	C		VC
<i>Oriopsis armandi</i> (Claparède, 1864)	LE7,8,9	LE5,7,9	LE5,6,9	UE4; LE5,8	SF	VC	UC	Ct
<i>Paradoneis lyra</i> (Southern, 1914)		LE7,9	LE6,7,8,9	LE7,8,9	DF	C		Ct
<i>Perinereis cultrifera</i> (Grube, 1840)	LE5,6	UE4	LE6	UE4; LE8	O	VC	UC	VC
<i>Phyllodoce mucosa</i> Örsted, 1843	LE9	LE9	LE9		Pr	R		UC
<i>Phylo foetida</i> (Claparède, 1869)			LE8	LE7	DF	UC		C
<i>Pista cristata</i> (Müller, 1776)	LE7,8	LE6,7,8,9	LE7,8,9	LE7,8	DF	C		Ct
<i>Prionospio malmgreni</i> Claparède, 1869		LE7,8,9	LE7,8,9	LE7,8,9	DF	C		VC
<i>Pseudopolydora antennata</i> (Claparède, 1869)	LE7,8	LE5,6,9	LE5,6,7,8,9	LE6,7,8,9	DF	VC		Ct
<i>Sabella pavonina</i> Savigny, 1822			LE8	LE7,8	SF	UC		C
Sabellidae indet.	LE6		LE8,9	LE6	SF	C		VC
<i>Serpula vermicularis</i> Linnaeus, 1767		LE5,6,7,8	LE7		SF	C		Ct
<i>Sigambra parva</i> (Day, 1963)		LE9	LE7,8,9	LE7,8	Pr	C		VC

APPENDIX 1 (cont.). – List of the identified taxa that were found at all the stations over the entire study period. The stations where each taxon was found are also listed. See Figure 1 for sampling station codes; FG, feeding guild (see Table 2 for feeding guild codes); CI, Constancy index; Ct, constant; VC, very common; C, common; UC, uncommon; R, rare.

Taxa	Summer	Autumn	Winter	Spring	FG	CI	CI UE	CI LE
<i>Spio filicornis</i> (Müller, 1776)	LE8	LE5,6,7,9	LE5,6,7,8,9	LE6,7,8,9	DF	VC		Ct
<i>Streblospio benedicti</i> Webster, 1879	LE7,8,9	LE5,6,7,8,9	LE5,6,7,8,9	LE5,6,8,9	DF	VC		Ct
<i>Syllidia armata</i> Quatrefages, 1866			LE6,7,8,9	LE6,7,8,9	Pr	C		Ct
PHYLUM ARTHROPODA								
Class Arachnida								
Acaridida indet.			UE1		Pr	R	UC	
Halacaridae indet.				UE3	Pr	R	UC	
<i>Hydrozetes</i> sp.		UE2			Pr	R	UC	
<i>Lebertia</i> sp.	UE2	UE2,4			Pr	UC	C	
<i>Sperchon</i> sp.		UE2		UE2	Pr	R	UC	
<i>Torrenticola</i> sp.		UE2,3	UE3		Pr	UC	C	
Class Pantopoda								
<i>Nymphon gracile</i> Leach, 1814				LE7	O	R		UC
Class Branchiopoda								
<i>Daphnia longispina</i> (Müller, 1776)	LE5				G	R		UC
<i>Eurycerus lamellatus</i> (Müller, 1776)				UE1	G	R	UC	
<i>Ilyocypris sordidus</i> (Liévin, 1848)			UE1		G	R	UC	
<i>Simocephalus exspinosus</i> (Koch, 1841)		UE1			G	R	UC	
<i>Simocephalus vetulus</i> (Müller, 1776)				UE1	G	R	UC	
Class Ostracoda								
<i>Cyprideis torosa</i> (Jones, 1850)			LE7	LE8	DF	UC		C
<i>Fabaeformiscandona fabaeformis</i> (Fischer, 1851)		UE2	UE1,2	UE1,4	DF	C	VC	
<i>Herpetocypris brevicaudata</i> (Kaufmann, 1900)		UE3			DF	R	UC	
<i>Herpetocypris</i> sp.		UE4			DF	R	UC	
Class Copepoda								
<i>Acanthocyclops latipes</i> (Lowndes, 1927)			UE1		SF	R	UC	
<i>Canuella furcigera</i> Sars, 1903			LE7		SF	R		UC
<i>Centropages chierchae</i> Giesbrecht, 1889			LE6		SF	R		UC
<i>Cyclops</i> sp.				UE1,3	SF	UC	C	
<i>Eucyclops serrulatus</i> (Fischer, 1851)			UE1		SF	R	UC	
<i>Macrocyclus albidus</i> (Jurine, 1820)		UE1,2	UE1	UE1	SF	UC	C	
Class Malacostraca								
<i>Ampelisca brevicornis</i> (Costa, 1853)			LE9		SF	R		UC
<i>Ampelisca</i> sp.			LE7		SF	R		UC
<i>Ampelisca typica</i> (Bate, 1856)	LE8,9	LE9	LE9		SF	UC		C
<i>Apeudes latreillii</i> (Milne-Edwards, 1828)	LE9	LE8,9			DF	UC		C
<i>Bathyporeia</i> sp.				LE9	DF	R		UC
<i>Bodotria arenosa</i> Goodsir, 1843				LE9	DF	R		UC
<i>Corophium orientale</i> Schellenberg, 1928	LE5,6,7,8,9	UE4; LE5,6,9	UE4; LE5,6	UE3,4; LE5,6	DF	Ct	C	Ct
<i>Corophium rotundirostre</i> Stephensen, 1915			LE7,8,9	LE7,8,9	DF	C		VC
<i>Cumopsis goodsir</i> (Van Beneden, 1861)		LE9			DF	R		UC
<i>Cyathura carinata</i> (Krøyer, 1847)	LE7		LE7,8	LE7,8	DF	UC		C
Decapoda indet.	LE9			LE7,9	O	UC		C
<i>Diastylis</i> sp.		LE8	LE8	LE6,7,8	DF	UC		C
<i>Echinogammarus longisetosus</i> Pinkster, 1973	UE1,3,4	UE4	UE2	UE2	O	C	Ct	
<i>Gammarus aequicauda</i> (Martyinov, 1931)				LE8	O	R		UC
<i>Iphinoe</i> sp.	LE9	LE9		LE7,8	DF	UC		UC
<i>Lembos</i> sp.					DF	R		UC
<i>Lembos spiniventris</i> (Stebbing, 1895)				LE7	DF	R		UC
<i>Leptocheirus pilosus</i> Zaddach, 1844	LE9		LE7	LE8	SF	C		VC
<i>Leucothoe incisa</i> (Robertson, 1892)	LE9		LE7,8	LE7,8	O	C		VC
<i>Liocarcinus corrugatus</i> (Pennant, 1777)			LE9		O	R		UC
<i>Medorippe lanata</i> (Linnaeus, 1767)			LE9		O	R		UC
<i>Microprotopus</i> sp.		LE9			O	R		UC
<i>Monoculodes acutipes</i> Ledoyer, 1983	LE9		LE8	LE6,7,8,9	O	C		Ct
<i>Pariambus typicus</i> (Krøyer, 1844)		LE8	LE8,9	LE6,7,8	O	C		Ct
<i>Perioculodes longimanus</i> (Bate & Westwood, 1868)				LE7,8	DF	UC		C
<i>Phtisica marina</i> Slabber, 1769			LE6,7	LE7,8	O	C		VC
<i>Praunus flexuosus</i> (Müller, 1776)	LE9				SF	R		UC
<i>Pseudocuma longicorne</i> (Bate, 1858)	LE8	LE9			DF	UC		C
<i>Sphaeroma serratum</i> (Fabricius, 1787)				LE8	O	R		UC
<i>Synchelidium haplocheles</i> (Grube, 1864)	LE7	UE4			DF	UC	UC	UC
<i>Synchelidium</i> sp.	LE8				DF	R		UC
<i>Upogebia pusilla</i> (Petagna, 1792)	LE9				SF	R		UC
<i>Upogebia</i> sp.		LE9			SF	R		UC
Class Euentomata								
<i>Baetis fuscatus</i> (Linnaeus, 1761)	UE2	UE2,3		UE2	DF	UC	C	
<i>Baetis pavidus</i> Grandi, 1949	LE7		LE6,7		DF	UC		C
<i>Caenis luctuosa</i> (Burmeister, 1839)	UE1,2,3	UE1,2	UE1,2	UE1,2	DF	C	VC	

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Taxa	Summer	Autumn	Winter	Spring	FG	CI	CI UE	CI LE
<i>Ceraclea dissimilis</i> (Stephens, 1836)				UE2	DF	R	UC	
<i>Ceraclea sobradieli</i> (Navás, 1917)	UE2			UE2	DF	R	UC	
Chironomus sp.	LE7,8	UE4	UE1	UE1,3; LE6	DF	VC	VC	VC
<i>Choroterpes picteti</i> (Eaton, 1871)	UE2				DF	R	UC	
<i>Coenagrion pulchellum</i> (Van der Linden, 1825)				UE1	Pr	R	UC	
Coenagrionidae indet.			UE1		Pr	R	UC	
<i>Drypos</i> sp.		UE1	UE1		G	R	UC	
<i>Enomus tenellus</i> (Rambur, 1842)	UE2	UE1,2	UE2	UE2	O	UC	C	
<i>Ephoron virgo</i> (Olivier, 1791)	UE1,2,3,4			UE2	SF	C	Ct	
<i>Hydropsyche exocellata</i> Dufour, 1841	UE2	UE2	LE5	UE2	SF	UC	UC	UC
<i>Hydroptila</i> sp.	UE2	UE2		UE2	G	R	UC	
<i>Mystacides azurea</i> (Linnaeus, 1761)	UE2				DF	R	UC	
<i>Orthotrichia angustella</i> (McLachlan, 1865)			UE2		G	R	UC	
<i>Pseudocloeon atrebatinus</i> Eaton, 1870	UE2	UE2	UE2		DF	R	UC	
<i>Psychomyia pusilla</i> (Fabricius, 1781)				UE2	DF	R	UC	
Sf. Orthoclaadiinae indet.	UE1,2; LE7	UE1,2,4	UE1,2,4; LE5,6,7	UE1,2; LE5,7,8	DF	Ct	VC	Ct
Sf. Tanypodinae indet.	UE1	UE1,2,3,4	UE1	UE1,2,3,4	Pr	C	Ct	
<i>Simulium erithrocephalum</i> (De Geer, 1776)	UE2		UE2		SF	R	UC	
Tr. Chironomini indet.	UE1	UE4	UE2	UE2	DF	C	VC	
Tr. Tanytarsini indet.	UE1,2	UE2,3	UE1,2	UE1,2,3	DF	C	VC	
<i>Trithemis annulata</i> (Palisot de Beauvois, 1807)		UE1			Pr	R	UC	
PHYLUM PHORONIDA								
Class Phoronida								
<i>Phoronis ovalis</i> Wright, 1856				LE6	SF	R		UC
<i>Phoronis psammophila</i> Cori, 1889		LE5,7,8,9	LE6,7,8	LE6,7,8	SF	VC		Ct
PHYLUM ECHINODERMATA								
Class Holothuroidea								
<i>Thyone</i> sp.			LE7	LE7,8	DF	UC		C
Class Ophiuroidea								
<i>Amphipholis squamata</i> (Delle Chiaje, 1828)	LE9	LE9	LE7,8	LE8	DF	C		VC
<i>Amphiura chiajei</i> Forbes, 1843			LE9	LE7	DF	UC		C
Class Echinoidea								
Fibulariidae indet.	LE9				DF	R		UC
<i>Echinocardium</i> sp.		LE9			DF	R		UC