Hydrobiologia (2007) 587:225–239
DOI 10.1007/s10750-007-0685-7

ECSA39

Spatial and temporal distribution patterns of the macrozoobenthos assemblage in the salt marshes of Tejo estuary (Portugal)

João P. Salgado · H. N. Cabral · M. J. Costa

Abstract The present study focuses on the spatial and temporal distribution of the macroinvertebrate community of the salt marsh areas of the Tejo estuary, based on surveys conducted from autumn 1998 to summer 2000. Samples were collected quarterly in five different intertidal areas along an elevation gradient in: mudflats, creek mouths, creeks, pioneer salt marsh areas and middle marsh areas. A total of 36 benthic invertebrate taxa were identified. Insect larvae were the most well represented group, with 10 taxa identified. Oligochaetes and ostracods were the most numerically abundant taxa, whereas bivalves dominated in biomass. Benthic macroinvertebrate assemblages were dominated, both in number and biomass, by deposit feeders. Three distinct macroinvertebrate assemblages were distinguished along the elevation gradient, based on species presence, density and biomass: the unvegetated muddy areas with a macrobenthic assemblage composed mostly by infauna; the salt marsh pioneer areas of *Spartina maritima* in which several epibenthic taxa were found, as well as endobenthic taxa characteristic of muddy sediment; and the creek margins, with epifauna taxa such as insect larvae and crustaceans and a low abundance of benthic infauna. Total biomass in the unvegetated and *Spartina* areas was higher during spring and summer mainly due to the increase in biomass of *Scrobicularia plana* and *Hydrobia ulvae*. No decreases in the salt marsh macroinvertebrate biomass values were observed during the highest densities of their potential nektonic predators (summer). This fact might indicate that macroinvertebrates are not a limiting resource for the nektonic species, and that the natural biomass increment of these invertebrate species could be masking the predation/disturbance caused by the nektonic species.

Keywords Benthic invertebrates · Distribution patterns · Salt marsh · Tejo estuary

Introduction

Benthic invertebrates take a central role within estuarine food webs, being one of the most important primary consumers. On the other hand, macrobenthos is the main food item of many estuarine fish and bird species, and may also be consumed by man (Ysebaert et al., 1998).

Guest editors: M. J. Costa, H. Cabral & J. L. Costa
Towards an integrated knowledge and management of estuarine systems

J. P. Salgado (✉) · H. N. Cabral · M. J. Costa
Universidade de Lisboa, Faculdade de Ciências,
Instituto de Oceanografia, Campo Grande, 1749-016
Lisbon, Portugal
e-mail: jp.salgado@sapo.pt

H. N. Cabral · M. J. Costa
Universidade de Lisboa, Faculdade de Ciências,
Departamento de Biologia Animal, Campo Grande,
1749-016 Lisbon, Portugal

In salt marsh systems, macrobenthic fauna is subjected to a wide range of structuring biotic and abiotic factors along and within the intertidal elevation gradient. Invertebrates inhabiting salt marsh sediments are generally eurecious species that tolerate strong daily and seasonal fluctuations of environmental conditions (Kneib, 1984).

Most of what is known about benthic invertebrate communities in salt marshes is due to studies conducted on the West coast of the Atlantic (see review by Levin and Talley, 2000). Along the East Atlantic coast, benthic assemblages of salt marsh areas have rarely been studied, although the important role of these habitats as feeding areas had already been emphasized by several studies focused on nekton assemblages (Cattrijsse et al., 1994; Laffaile et al., 1998, 1999; Mathieson et al., 2000) and bird communities (Moreira, 1995). Studies concerning salt marsh benthic invertebrates in Europe include Jackson (1985) and Frid and James (1989), for the East coast of England. The majority of the other studies focused on few species or only described the species composition of benthic assemblages (e.g. Wolff, 1973; Calvário, 1982; Marques et al., 1993).

In the Tejo Estuary, the marsh macrozoobenthos communities assume a particular importance sustaining large populations of fishes and birds, whose preferential areas are located in areas adjacent to the salt marsh (Moreira, 1995, Costa & Cabral, 1999). However, information concerning the structure and dynamic of intertidal macrobenthos is scarce.

The present study, based on 2 years of surveys, focused on the spatial and temporal distribution of the macroinvertebrate community on the salt marsh areas of the Tejo estuary, in order to determine abundance and biomass distribution patterns at different salt marsh sites and to evaluate their availability as prey for higher trophic levels of the estuarine food web.

Materials and methods

Study area

The Tejo Estuary (Portugal), with an area of 320 km^2 (Fig. 1), is the largest estuary in Western Europe. It is a semi-diurnal mesotidal system with almost 4 m of tidal range during spring tides. The intertidal zone covers 113 km^2, of which 100 km^2 are mud flats and 13 km^2 are salt marshes (Catarino et al., 1985). Samplings were performed at two areas, Hortas (H) and Ponta da Erva (E), both located in the upper part of the estuary and included in the Tejo Estuary Natural Reserve, at ca. 30 km from the coastline. At each area 5 sites were sampled following an increasing elevation gradient, from the lower intertidal to the salt marshes areas: mudflats (A) daily flooded being located at an elevation ranging from –0.8 m to –0.1 m (mean sea level); creeks mouth (B) and creeks (C) daily flooded and with an elevation between –0.1 m and 0.2 m; pioneer site (S) which is covered by *Spartina maritima* (Curtis) Fernald, 1916 and has an elevation around 0.6 m being flooded daily except during neap tides; and the middle marsh site (M) which includes the creek margins, covered mainly by two species of salt marsh plants: *Halimione portulacoides* (Linnaeus) Allen, 1938 and *Arthrocnemum perenne* (Miller) Moss, 1948. This latter site presents an elevation higher than 1.2 m, being only submersed during spring tides.

Sampling procedures and data analysis

Samples were collected quarterly between autumn 1998 and summer 2000 (October—autumn; January—winter; April—spring; July—summer), at tides of similar tidal amplitude (spring tides), using a 0.12 m diameter core. The number of cores collected varied according to the extension and variability of each site and were based on preliminary surveys performed in the same study sites. Nine cores were randomly taken at each of the creek mouths, pioneer and middle marsh sites, while 18 were collected at the mudflat and creek sites.

For each sampling site and season, temperature (°C) and salinity were determined in low-water pools, whereas the water content (H_2O), total organic matter (TOM) and the grain size distribution of the sediment were determined in the laboratory. Water content (%) was assessed by drying the samples at 60°C for 24 h, while TOM (%) was determined after ignition at 450°C.

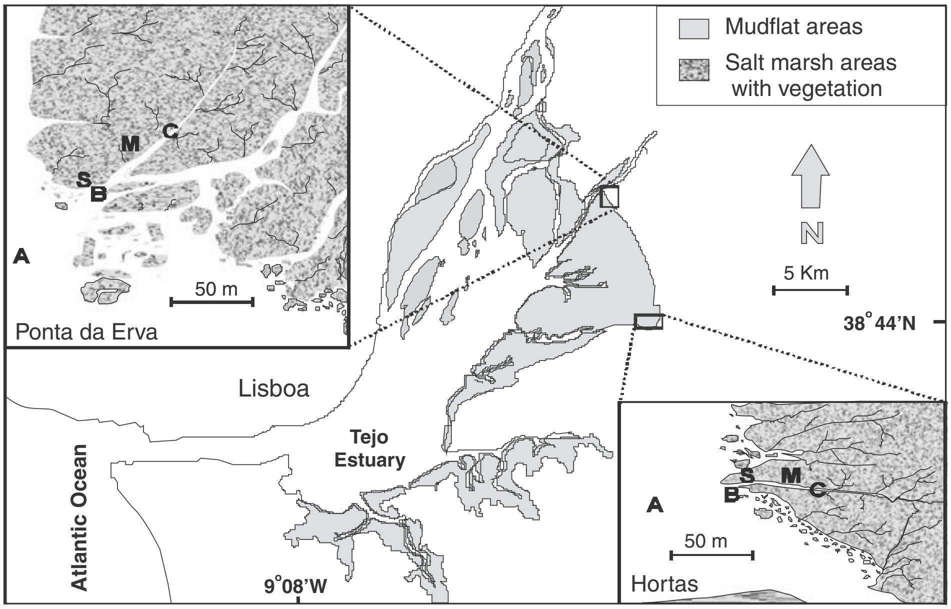

Fig. 1 Location of the sampling sites and areas within the Tejo estuary

Sediment grain size composition was determined using an AFNOR type sieve battery (0.063 mm, 0.125 mm, 0.250 mm and 0.500 mm) after drying the sediment (60°C) for a period of 48 h (Gaudêncio et al., 1991).

At the laboratory, sediment samples for macrofauna identification were washed through a 500 μm mesh size sieve. The benthic invertebrates were then identified to the lowest possible taxonomic level, counted and ash free dry weight (AFDW) was estimated per taxa for each site according to Rees et al. (1990).

Benthic macroinvertebrate assemblages were analyzed through the evaluation of the frequency of occurrence (FO), density (D, ind m^{-2}) and biomass (B, g of AFDW m^{-2}). Mysids, shrimps and crabs were excluded from the analysis due to the unsuitable sampling procedures for these crustaceans. The classification proposed by Wolff (1973) was followed, in order to establish trophic guilds. Four trophic guilds were considered: suspension feeders (SF), deposit feeders (DF), which includes selective and non-selective deposit-feeders, carnivores (C) and omnivores (O). The classification into each group was based on the information given by several authors (e.g. Wolff, 1973; Robineau, 1987; Rodrigues, 1992; Gaston et al., 1998; Lillebø et al., 1999).

The G-test (Sokal & Rohlf, 1981) was performed in order to understand whether the numeric abundance of different taxa varied according to each site.

A cluster analysis, using Bray-Curtis similarities and WPGMA, was performed based on presence/absence data of sampled sites, using the PRIMER software package (Clarke & Warwick, 1994).

Taxa richness (S), Pielou's evenness (J) and Shannon-Wiener's (H') diversity indices were calculated for each sampling site and season (Ludwig & Reynolds, 1988). Spearman's correlation coefficient was used to compare the Shannon-Wiener's index values (Zar, 1996) of the 2 years in the different sites.

The Wilcoxon paired-test was applied in order to compare the taxa abundance between the 2 years of sampling considering the two areas, Ponta da Erva and Hortas, together and separately.

The macroinvertebrate benthic assemblage structure was also evaluated using a correspondence analysis (CA). In order to evaluate both spatial and temporal variation, in each sampling year, species density and biomass data were averaged by sampled site and season. Since results of the CA are affected by the presence of rare species (Ter Braak, 1995), species with frequencies of occurrence lower than 10% were excluded from the analysis. Diptera larvae were considered as one group. Elevation, salinity, temperature, % of mud (<64 μm) in the sediment, TOM and water content data were also included in the analysis as a co-variable data matrix.

Results

Sediment conditions

The granulometric analysis (Table 1) revealed a high homogeneity in all sites with the predominance of mud, always higher than 98%. For both areas the percentage of TOM was higher in sites with vegetation cover, pioneer (S) and middle marsh (M) sites. On the contrary, the water content of the sediment was lower in sites with the highest elevation and, thus, shorter flooded periods. Mean salinity values were similar among areas following an increased gradient towards the mudflat areas.

Species composition

A total of 36 benthic invertebrate taxa (Table 2), 35 in Ponta da Erva and 32 in Hortas, were identified during the 2 years of sampling. Insect larvae were the better represented group accounting for almost one third of the total number of taxa. Oligochaetes and ostracods accounted for 57.7% of the total number of individuals collected, while bivalves dominated biomass values with 77.2%. Only six of the 36 taxa identified occurred with frequencies higher than 50% in the studied area, i.e. *Scrobicularia plana* (Da Costa, 1778), *Hydrobia ulvae* (Pennant, 1777), *Streblospio shrubsolii* (Buchanan, 1890), *Hediste diversicolor* (O. F. Müller, 1776), oligochaetes and *Cyathura carinata* (Kröyer, 1847).

Regarding trophic guilds, 80% of the taxa were deposit-feeders, which dominated also in number and biomass in both areas (Table 2). Omnivores and carnivores represented a small proportion of the taxa sampled in the studied areas both in density and biomass. Insect families were not included into the trophic guilds analysis since their trophic habits differ within each insect family.

Spatial and temporal analysis

The total number of species was, in general, higher in the Hortas sampling areas compared to Ponta da Erva. In both sites unvegetated areas presented the highest average number of species (Fig. 2a). Although presenting a high total number of taxa, the middle marsh (M) benthic macrofauna was quite different from the fauna observed in the remaining sampling areas. The main differences were associated with the abundance presence of different insect larvae families and epibenthic macrofauna and the practical absence of endobenthic macrofauna, which were dominant in the remaining areas (Table 2). These results are illustrated by the cluster analysis based on taxa presence/absence when applied to the

Table 1 Average values ± standard deviation of the % of water content (% H_2O), % of total organic matter (TOM) and % of fine grains (< 0.063 mm) of sampled sediments, salinity and temperature of the interstitial water of the sediment for each sampled area

Sampling sites	H_2O (%)	TOM (%)	% Fine grains	Salinity	Temperature (°C)
HA	52.90 ± 2.52	8.35 ± 1.07	98.76 ± 0.66	27.11 ± 4.76	14.89 ± 4.70
HB	54.76 ± 2.38	8.14 ± 0.66	99.38 ± 0.13	25.39 ± 4.67	14.75 ± 5.23
HC	55.07 ± 2.39	9.18 ± 0.49	99.77 ± 0.03	24.89 ± 4.57	14.63 ± 5.32
HS	49.78 ± 1.94	9.09 ± 0.60	99.09 ± 0.17	25.23 ± 4.55	15.00 ± 6.41
HM	43.52 ± 2.09	10.68 ± 0.72	98.48 ± 0.40	24.00 ± 5.36	15.63 ± 7.25
EA	49.46 ± 2.68	8.99 ± 0.43	98.83 ± 0.57	27.36 ± 3.94	15.25 ± 4.50
EB	48.99 ± 2.15	9.40 ± 0.46	98.71 ± 0.72	25.82 ± 3.68	15.00 ± 4.70
EC	50.42 ± 2.87	8.80 ± 0.87	98.67 ± 0.52	25.36 ± 3.47	14.88 ± 4.82
ES	48.71 ± 3.14	9.71 ± 1.74	98.14 ± 0.07	25.41 ± 3.86	15.50 ± 5.45
EM	44.52 ± 1.31	10.28 ± 0.69	98.88 ± 0.59	24.48 ± 4.85	15.63 ± 6.16

Table 2 Occurrence, density and biomass (in percentage) of benthic invertebrate *taxa* in each area, Hortas and Ponta da Erva (P. Erva)

Taxa	Code	FT	Sites	% Occurrence		% Density		% Biomass	
				Hortas	P. Erva	Hortas	P. Erva	Hortas	P. Erva
Phylum Protozoa									
Class Sarcodina									
Forameniferida n.i.			AB	5.0	2.5	0.03	0.02	<0.01	<0.01
Phylum Nematoda									
Nematoda n.i.	Nema		ASM	10.0	7.5	0.31	0.47	<0.01	<0.01
Phylum Annelida									
Class Polychaeta									
Hediste diversicolor	Hdiv	O	ABCS	57.5	57.5	3.08	1.18	9.41	2.09
Nephtys hombergii	–	C	AC	5.0	2.5	0.02	0.02	0.01	0.04
Pygospio elegans	Pele	DF	AC	7.5	7.5	0.02	0.10	<0.01	<0.01
Polydora sp.	Poly	DF	ABC	15.0	5.0	0.08	0.05	<0.01	<0.01
Streblospio shrubsolii	Sshr	DF	ABCS	67.5	67.5	7.96	8.41	0.13	0.13
Spionidae n.i.	spio	DF	ABC	7.5	10.0	0.05	0.25	<0.01	<0.01
Cirratulidae n.i.	–	DF	ABS	10.0	0	0.08	–	<0.01	–
Capitella capitata	Ccap	DF	ABCS	37.5	5.0	4.04	0.05	0.24	<0.01
Class Oligochaeta									
Oligochaeta n.i.	Olig	DF	ABCS	75.0	77.5	21.39	67.49	0.29	1.16
Phylum Mollusca									
Class Bivalvia									
Scrobicularia plana	Spla	DF	ABCS	62.5	52.5	8.42	2.11	67.65	89.65
Abra tenuis	Aten	DF	ABS	22.5	2.5	0.29	0.02	1.14	0.01
Class Gastropoda									
Hydrobia ulvae	Hulv	DF	ABCSM	90.0	75.0	15.70	4.44	18.92	2.04
Ovatella myosotis	Omyo	DF	CSM	15.0	12.5	0.57	0.67	0.56	0.42
Phylum Arthropoda									
Class Arachnidae									
Araneae n.i.	–	–	M	2.5	2.5	0.01	0.17	<0.01	<0.01
Acari n.i.	–	–	CSM	2.5	7.5	0.03	0.08	<0.01	<0.01
Class Ostracoda									
Ostracoda n.i.	Ostr	DF	ABC	50.0	20.0	30.38	0.48	0.59	<0.01
Class Crustacea									
Paragnathia formica	Pfor	C	CSM	10.0	2.5	3.37	2.78	0.30	0.18
Cyathura carinata	Ccar	O	ABCSM	35.0	65.0	0.71	2.54	0.12	0.60
Lekansphaera monodi	Lmon	DF	ACSM	15.0	20.0	1.00	1.13	0.24	0.33
Orchestia gammarellus	Ogam	DF	M	7.5	7.5	0.10	0.84	0.04	0.49
Melita palmata	Mpal	DF	CSM	10.0	7.5	0.08	0.07	0.02	0.82
Corophium volutator	Cvol	DF	BCS	10.0	5.0	0.07	0.05	0.01	<0.01
Amphipoda n.i.	–	–	M	2.5	5.0	0.01	<0.01	<0.01	0.01
Class Insecta									
Dolichopodidae	Ldip	–	ABCSM	37.5	50.0	0.66	1.79	0.07	0.28
Rhajionidae	Ldip	–	ABCSM	17.5	25.0	0.53	1.41	0.06	0.23
Limonidae	Ldip	–	CSM	10.0	15.0	0.77	2.18	0.09	0.37
Chironomidae	Ldip	–	SM	0	12.5	–	0.68		<0.01
Ceratopogonidae	Ldip	–	M	2.5	0	0.01	–	<0.01	–
Tipulidae	Ldip	–	M	0	2.5	0	0.05	–	<0.01
Tabanidae	Ldip	–	AM	2.5	2.5	0.01	0.01	<0.01	0.01
Lepidoptera	–	–	M	0	2.5	0	0.02	–	<0.01
Coleoptera	–	–	SM	5.0	2.5	0.06	0.12	<0.01	<0.01
Homoptera	–	–	A	0	2.5	0	0.01	–	<0.01
Insecta n.i.	–	–	ACM	15.0	15.0	0.16	0.31	0.10	1.13
					Total	2588.8 ind.m^{-2}	1484.8	6.78 g of AFDW m^{-2}	4.58

Code—abbreviation codes used in the CA analysis; FT—Feeding type (O—omnivore; C—carnivore; DF—deposit feeder; SF—suspension feeders); Areas—Presence in the different salt marsh sites studied (A—mudflats; B—creeks mouth; C—creeks; S—pioneer marsh areas; M—middle marsh areas) different sampling sites (Fig. 2b). The first division (40% similarity level) segregates the middle marsh (M) sites of both areas from the sites with a higher flooded period. On a further division (61% similarity level) the unvegetated sites, which were grouped together, were separated from the *Spartina* ones (S).

Total average densities were 1484.6 ind m^{-2} and 2588.8 ind m^{-2} in Ponta da Erva and Hortas, respectively. These differences were specially marked in the mudflat (A), creek mouth (B) and pioneer sites (S), especially due to significant higher densities of four taxa in Hortas area: *S. plana* (G test; Gw = 267.9, df = 3, $P < 0.05$), *H. ulvae* (Gw = 423.0, df = 3, $P < 0.05$), *Capitella capitata* (O. Fabricius, 1780) (Gw = 271.7, df = 3, $P < 0.05$) and Ostracoda (Gw = 2837.3, df = 3, $P < 0.05$). Oligochaeta (Gw = 3220.0, df = 3, $P < 0.05$) and *Orchestia gammarellus* Pallas, 1766 (Gw = 41.6, df = 3, $P < 0.05$) were the only taxa with significant higher densities in Ponta da Erva area. Bearing in mind the occurrence, density and biomass values, special attention was given to the six main taxa in the density and biomass analysis (Figs. 3 and 4). Higher densities were obtained during summer seasons (maximum of 15667.9 ind m^{-2} in B area of Hortas) (Fig. 3) mainly due to the higher contribution of ostracods (more than 75% of the other-taxa-group). The lowest densities were observed in the creek (C) sites of both areas. Oligochaetes were mainly present in the sites of Ponta da Erva and in the *Spartina* (S) site of Hortas area, with a highest value of 7787.6 ind m^{-2} during winter in the *Spartina* (S) site of the former area. Highest densities of *H. diversicolor* were registered during winter and spring in the *Spartina* sites of both areas (maximum of 1563.4 ind m^{-2} in S area of Hortas). Densities of *S. plana* were higher during spring and summer seasons in sites A and B of Hortas. Densities of this species were higher during the second sampling year.

Regarding biomass, total average values were higher in Hortas (6.78 g AFDW m^{-2}) than in Ponta da Erva sites (4.58 g AFDW m^{-2}). A similar trend was observed for both areas (Fig. 4), with decreasing values towards sites with a lower flood period. The higher biomass values in the *Spartina* sites of Hortas were the exception. Compared to the same sites in Ponta da Erva, the difference was mostly associated with the higher contribution to the biomass values of three species: the bivalve *S. plana*, the gastropod *H. ulvae* and the polychaete *H. diversicolor*. Biomass values of the former species were higher in sites A and B of both areas, with a maximum of 71.1 g AFDW m^{-2} during spring in site A of Hortas. Highest biomass values of *H. diversicolor* were registered during the winter seasons (maximum of 17.7 g AFDWm^{-2} in the *Spartina* site of Hortas).

Analysis of the diversity indices for the 2 years of study (Fig. 5) showed that all values were lower than 2. Diversity values at Ponta da Erva sites were, in most of the cases, lower than at Hortas sites. This seemed to be related with the reduced values of evenness in that area, caused by the higher dominance of one taxon (oligochaeta).

In general, the vegetated sites were the ones with the lowest diversity values. These values were mainly explained by the reduced presence of

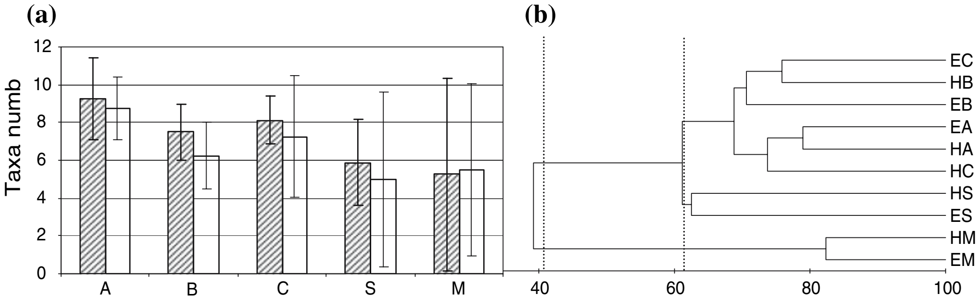

Fig. 2 Total number of taxa in each sampled site (Ponta da Erva (□) and Hortas (▨)) (**a**) and group average cluster of Bray-Curtis similarities based on taxa presence/absence applied to the different sampling sites (**b**)

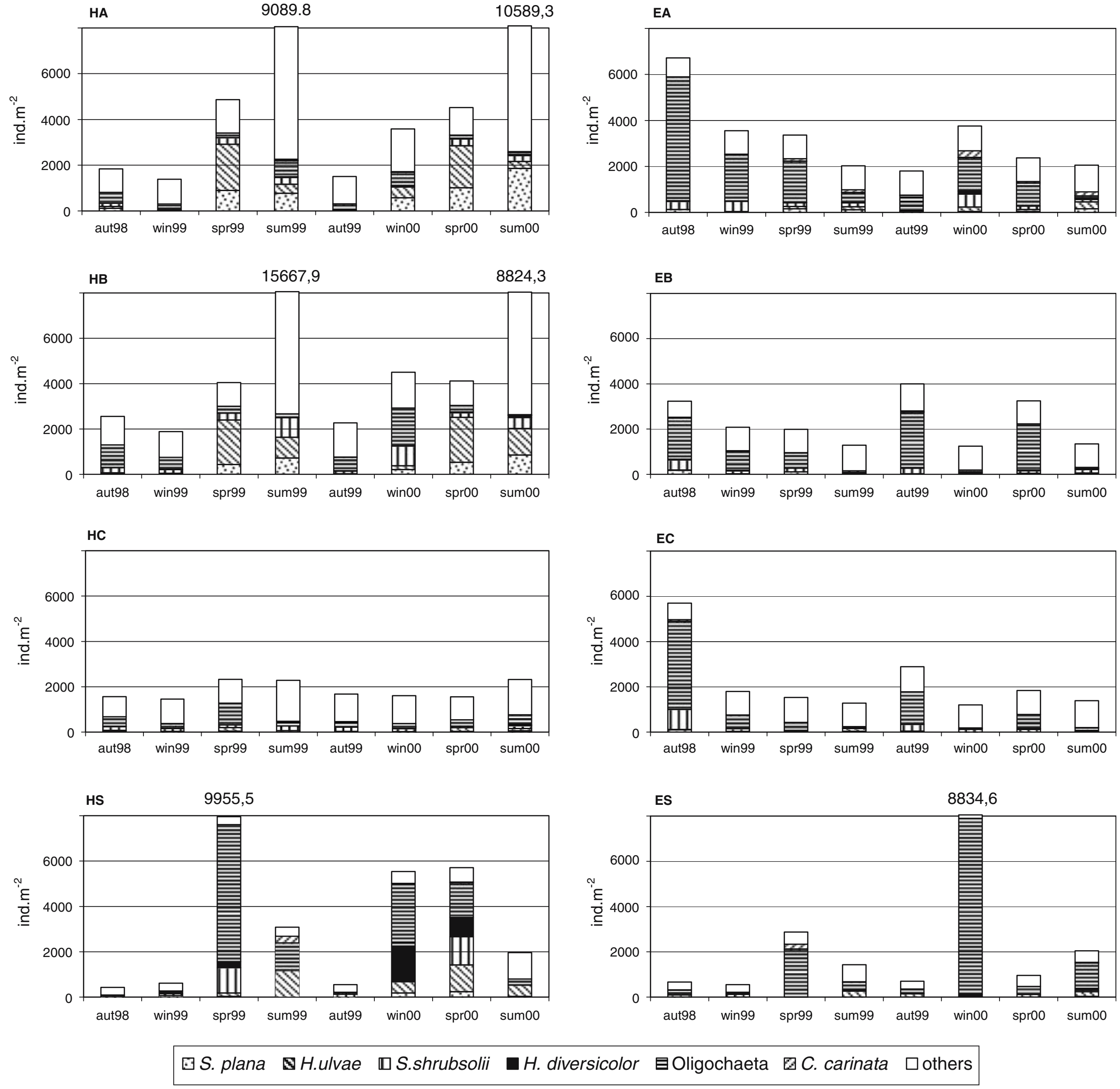

Fig. 3 Density (ind m^{-2}) in each sampled site and season. Middle marsh areas were not included in the figure since the main species are absent from these sites

taxa, which was especially observed in the middle marsh sites where during autumn and winter a maximum of two taxa were recorded. However, these sites registered some of the highest diversity values during spring and summer due to the increase of the specific richness and the absence of numerically dominating taxa. Mudflats, creek mouths and creek sites of each area exhibited resembling trends for the different indices within each season, only with reduced oscillations. In Ponta da Erva sites, the higher diversity values during summer were mainly due to the reduction in relative importance of Oligochaeta, and thus the increase of the evenness values.

In spite of the temporal variation observed in the diversity indices of each site, there was a

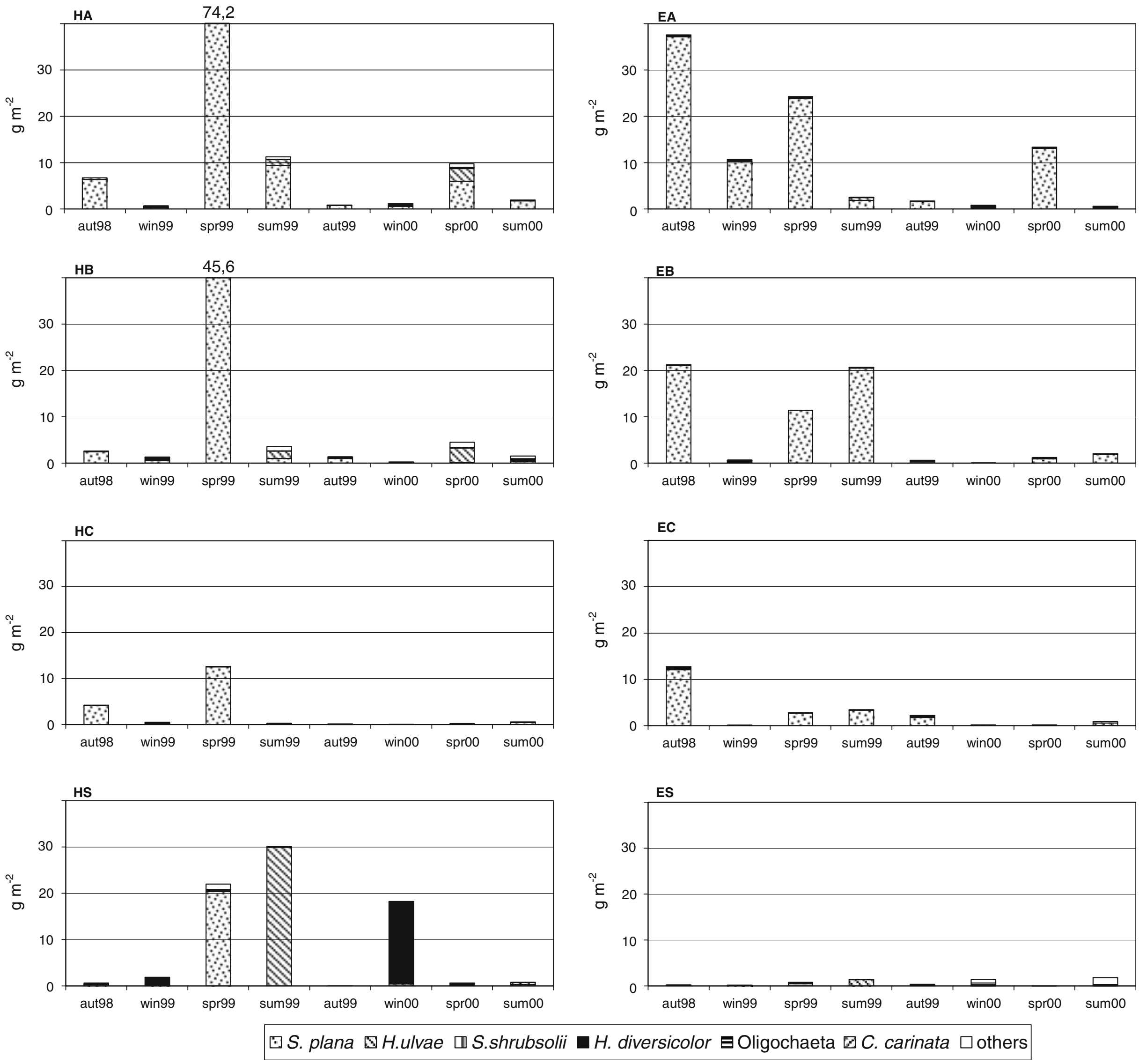

Fig. 4 Biomass (g of ash free dry weight) in each sampled site and season. Middle marsh sites were not included in the figure since the main species are absent from these sites

correlation between the ranked diversity values of all sites in the first and the second years of sampling ($r_s = 0.72$; $n = 10$; $P > 0.05$).

Comparing the taxa abundance between the 2 years of sampling using the Wilcoxon paired-sample test, no significant differences were found considering the two areas, together (t = 100; $n = 23$; $P > 0.05$) or separately for Ponta da Erva (t = 88.5; $n = 23$; $P > 0.05$) and for Hortas (t = 125.5; $n = 23$; $P > 0.05$).

The first two axes of the correspondence analysis performed on the species density (Fig. 6) and biomass (Fig. 7) data for the first and second sampling years explained about 50% of the total variance. The ordination diagrams show the main variation pattern of the macroinvertebrate assemblages, representing the centers of the species distribution in relation to sampling areas and seasons and their relation to environmental variables. The projections along the first axis of the ordination diagrams on species densities (Fig. 6) discriminate mostly the middle marsh sites, which are located on the right side of the diagrams, from the remaining sampled sites,

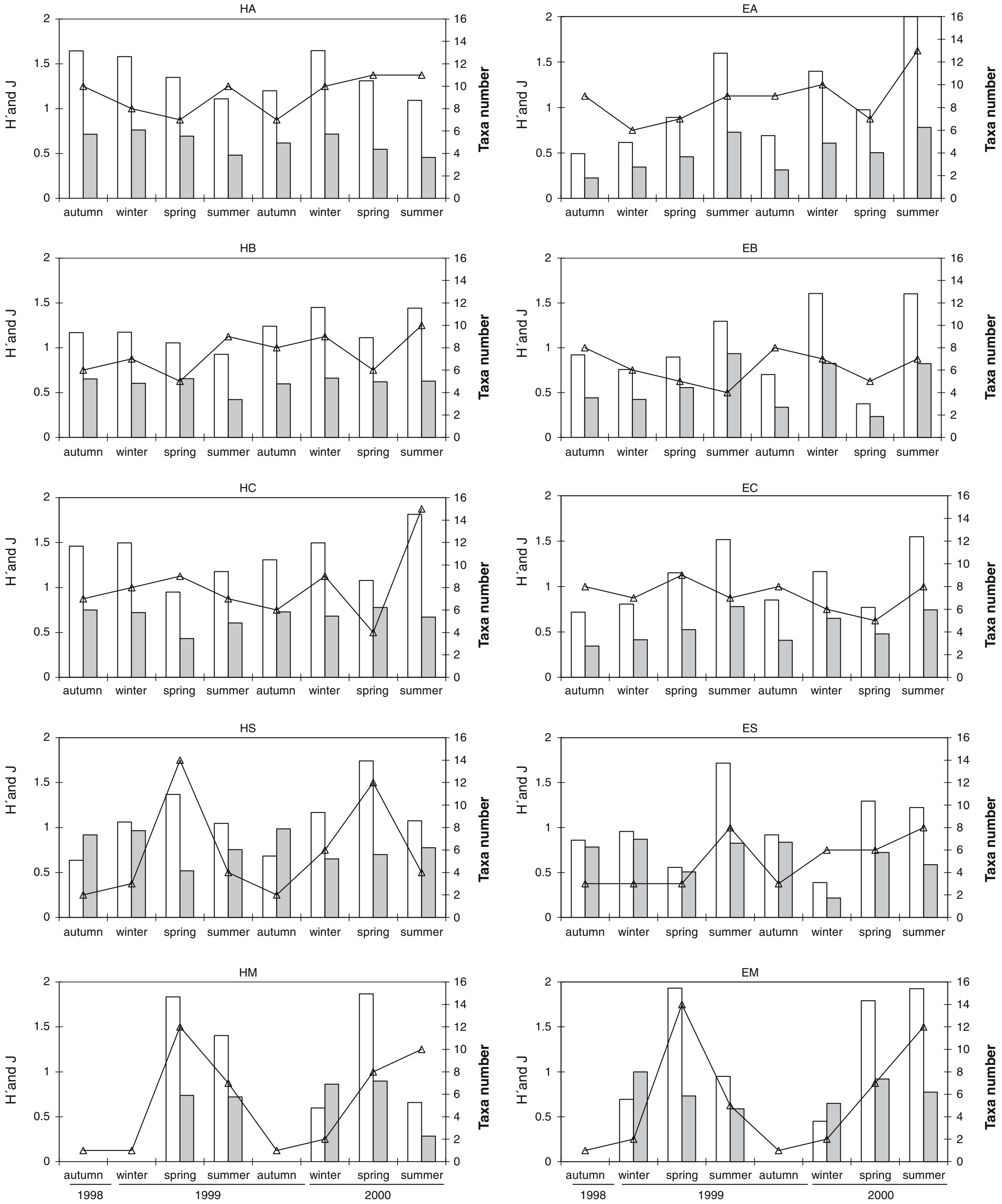

Fig. 5 Seasonal values of the taxa richness (N) (line), Pielou's evenness (J) (white bar) and Shannon-Wiener's (H') (grey bar) diversity indices for each sampling site

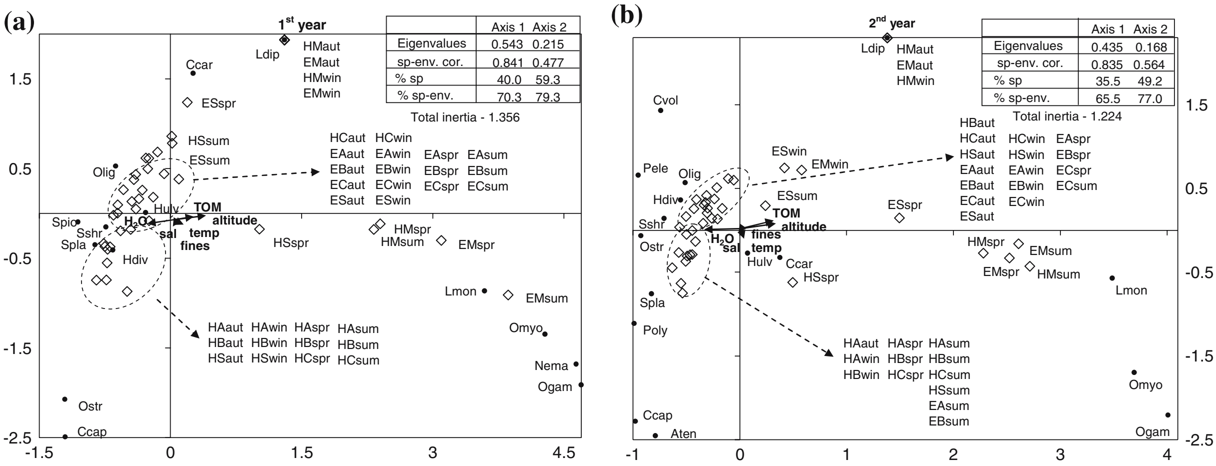

Fig. 6 Ordination diagrams of the first two axes of the correspondence analysis performed on the species abundance data for 1998/1999 (**a**) and 1999/2000 (**b**) (seasons: aut—autumn, win—winter, spr—spring, sum—summer; areas: H—Hortas, E—Ponta da Erva; sampled sites: A—mudflat, B—creeks mouth, C—creeks, S—pioneer area, M—middle marsh; environmental parameters (solid arrows): sal—salinity, temp—temperature, H_2O—water content of the sediment, TOM—total organic matter content of the sediment, fines—fine particles content of the sediment, elevation—elevation of the sampling areas in relation to the hydrographic zero). See Table 2 for taxa (black circles) abbreviation code

closer to the origin. The former sites were separated by seasons along the second axis. Spring and summer periods were projected in the lower part of the ordination diagrams, associated with the presence of the isopod *Lekanesphaera monodi* (Arcangeli, 1934), the amphipod *O. gammarellus* and the pulmonate gastropod *Ovatella myosotis* (Draparnaud, 1801), while winter and autumn periods were located in the upper part of the diagram, associated with insect larvae, almost the only taxa collected during these sampling periods. The second axis also reflected a separation between the two sampling areas, except for the middle marsh sites. Most of the sites of the Hortas area are located below the first axis associated to taxa such as ostracodes and *C. capitata*, which were particularly abundant in these sites. Ponta da Erva sites were mainly projected on the upper side associated with the oligochaetes.

The projections along the first axis on the ordination diagram related with the species biomass (Fig. 7) showed a pattern of discrimination similar to the density diagram. The projections in the second ordination axis show the most marked difference, which suggests a distinction between summer, and autumn and winter sampling seasons. Summer was mainly linked with taxa such as *H. ulvae*, ostracods, *S. shrubsolii* and *C. capitata*, while autumn and winter were associated with oligochaetes and *H. diversicolor*. Concerning the environmental data, TOM and altitude were positively related, whereas water content of the sediment was negatively related to the first axis, both for density and biomass in the two studied years.

Discussion

Species composition

The presence of a low number of macroinvertebrate taxa in the upper Tejo salt marsh areas is in agreement with the findings from other authors for different salt marshes worldwide (Kneib, 1984; Frid & James, 1989; Levin & Talley, 2000) and adjacent mudflats (Jackson, 1985; Hampel, 2003).

Intertidal areas are subject to strong physical and biological gradients related to the frequency and duration of tidal submergence. In such unstable and often extreme environments few species may be expected to thrive, and those

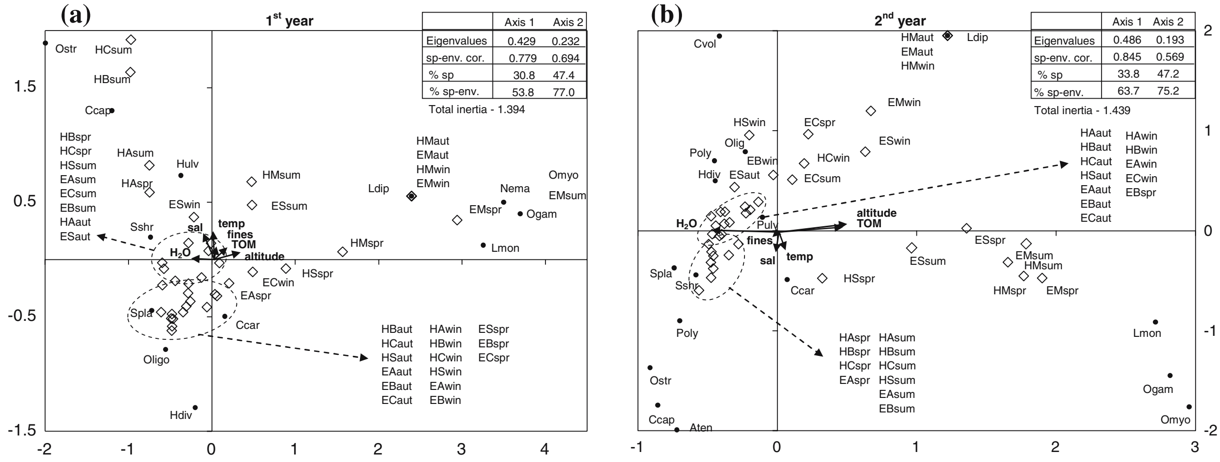

Fig. 7 Ordination diagrams of the first two axes of the correspondence analysis performed on the species biomass data for 1998/1999 (**a**) and 1999/2000 (**b**) (seasons: aut—autumn, win—winter, spr—spring, sum—summer; areas: H—Hortas, E—Ponta da Erva; sampled sites: A—mudflat, B—creeks mouth, C—creeks, S—pioneer area, M—middle marsh; environmental parameters (solid arrows): sal—salinity, temp—temperature, H_2O—water content of the sediment, TOM—total organic matter content of the sediment, fines—fine particles content of the sediment, elevation—elevation of the sampling areas in relation to the hydrographic zero). See Table 2 for taxa (black circles) abbreviation code

species must be very ubiquitous (Eagle, 1975; Beukema, 1976; Kneib, 1984).

Benthic macroinvertebrate assemblages present in the Tejo salt marsh areas were dominated by deposit feeders, both in number and biomass. High values of TOM were registered in the sediment samples, which corroborates the findings from several authors outlining that benthic deposit feeders' densities are generally correlated with the organic content of the sediment (Pearson & Rosenberg, 1978; Whitlatch, 1981; Ieno & Bastida, 1998).

The most common taxa present in the study areas (*S. plana*, *H. ulvae*, oligochaeta, *S. shrubsolii*, *H. diversicolor*), are known to exhibit higher tolerances to high organic matter enrichment of sediments (Wolff, 1973; Pearson & Rosenberg, 1978). The only exception was the isopod *C. carinata*, for which Marques et al. (1994) found a negative effect of organic enrichment on its densities.

Spatial and temporal analysis

The two studied areas revealed similar compositions of their benthic macroinvertebrate assemblages. Nevertheless, differences were found in their density and biomass values, which were significantly higher in Hortas for most taxa, especially in mudflat and creek mouth sites. These differences could not be attributed to the measured abiotic variables, since these variables did not differ considerably between areas and the taxa found in the studied areas are known to be tolerant to their wide fluctuations (Wolff, 1973; Kneib, 1984). These facts are probably associated with the relatively higher hydrodynamism in the Ponta da Erva area, promoted by the confluence of three tidal creeks and by the higher exposure to predominant winds. This higher sediment disturbance, which is well documented by the deeper ripple marks present between the *Spartina* stems of this area (personal observation), may displace organisms that live on or just under the sediment surface or complicate larvae settlement (Beukema, 1976). Another factor affecting density and biomass values of *S. plana*, which represents more than 75% of total biomass, is its intense commercial exploitation in Hortas. Densities of this species in Hortas area are seven times higher than in Ponta da Erva, while biomass values are similar between both areas. Thus, the *S. plana* population in Hortas is dominated by small size individuals, whereas in Ponta da Erva larger size individuals are present in higher abundances. Commercial exploitation affects mainly larger size individuals promoting disequilibrium in the population structure (Guerreiro, 1998).

Three distinct macroinvertebrate assemblages based on species presence, density and biomass were distinguished in the studied sites along the elevation gradient: the creek margins, covered by dense vegetation dominated by *Halimione portulacoides* and *Arthrocnemum perene*; the salt marsh pioneer sites of *S. maritima*; and the unvegetated muddy sites, which included the salt marsh creeks, the creek mouths and the mudflats adjacent to the salt marsh.

Similar patterns of macroinvertebrate distribution were observed in other salt marsh areas; however most of those studies were performed in marshes which do not comprise each habitat type in the same proportion, and included others such as pools and salt pans which did not occur in the present one (Jackson, 1985; Frid & James, 1989; Levin et al., 1998). Most of them reported on salt marshes dominated by a single plant genus, *Spartina*, and were located in the North American Atlantic coast (Levin et al., 1998). In Europe, vegetation does not occur lower than mean high water neap tide (Beeftink, 1977), while in most of the North American Atlantic salt marshes mean tide level borders the low marsh (Reimold, 1977), thus these latter sites are more frequently flooded in comparison to vegetated sites in European salt marshes, allowing the abundant presence of benthic invertebrate marine taxa.

In the Tejo estuary, the creek margins may act as a transition zone between terrestrial and marine biotopes. Invertebrate assemblages in these sites were dominated by insect larvae and epibenthic crustaceans, presenting a reduced density and biomass values. Moy & Levin (1991) also found decreasing total macrofauna densities with increasing tidal height. Invertebrates inhabiting these upper areas of salt marshes exhibit physiological or behavioral adaptations, which allow them to survive in an environment that is occasionally more terrestrial than aquatic (Kneib, 1984). The lower percentage of water in the sediment caused by short submergence periods and the dense vegetation cover may difficult the burrowing and survival of benthic infauna in the compact sediments of these sites. Calvário (1982), in a qualitative study of the intertidal benthic populations of the Tejo estuary, also reported for the Arthrocnemum/Halimione sites the presence of amphipods of the *Orchestia* genera, *Lekanesphaera monodi* (Arcangeli, 1934) and the gastropods *H. ulvae* and *O. myosotis* together with different species of insects, all epibenthic taxa. Kneib (1984) also registered higher relative abundance of Diptera larvae and amphipods in the upper marsh sites. In North American marshes, Rader (1984) observed a significant effect of tidal level on the abundance of most of the taxa present, Diptera larvae were mostly abundant in the upper marsh sites, while polychaetes and oligochaetes followed an opposite pattern, as observed in the present study.

Higher total density and biomass values were registered in the lower marsh sites covered by *Spartina*. The structure of the macroinvertebrate assemblage observed in these areas during the present study was in agreement with the results of Calvário (1982), which described the presence of several of the epibenthic invertebrates such as insect families and isopods species as in the middle marsh sites but also benthic infauna characteristic of muddy sediments such as *S. plana*, *H. diversicolor* and oligochaetes. Marques et al. (1993) also observed high abundances of *H. diversicolor*, *H. ulvae*, *S. plana* and *C. carinata* in *Spartina* sites in the Mondego estuary. Similar assemblages were observed in the *Spartina anglica* C. E. Hubbard marshes of East England, where Frid & James (1989) reported oligochaetes and *H. ulvae* as dominant taxa, while Jackson et al. (1985) registered the presence of insect larvae and arachnids and the dominance of *Corophium volutator* (Pallas, 1766), *H. ulvae*, oligochaetes and *H. diversicolor*. In the present study, this site in the Hortas area registered one of the highest total biomass values, being *H. ulvae*, *H. diversicolor* and *S. plana* the main contributors. Differences in density and biomass in both areas may be explained by the referred relatively higher hydrodinamism in Ponta da Erva.

In the unvegetated sites there was a marked reduction in the presence of insects larvae and amphipods and a higher abundance of ostracods, bivalves and polychaetes. In the Tejo estuary, Saldanha (1980) and Calvário (1982) described *H. diversicolor*, *C. carinata*, *H. ulvae* and *S. plana* as the most common species in these muddy sediments, as found in the present study. These species were also referred to as dominants in number and biomass in the muddy areas of the Mondego estuary (Marques et al., 1993) and the Ria Formosa (Sprung, 1994). Cabral (1998), observed a similar macroinvertebrate composition, for mudflats near Hortas, but with lower densities of oligochaetes (1158.2 ind m^{-2}) and higher densities of *S. plana* (1122.9 ind m^{-2}) in relation to those registered in this study. One general pattern from most studies dealing with macroinvertebrates in salt marshes, also observed for the Tejo estuary salt marsh areas, is that oligochaetes form a larger fraction of the total infauna in vegetated than unvegetated sediments (Levin & Talley 2000; Hampel 2003).

Although with lower biomass values of *H. diversicolor* and *H. ulvae* than in *Spartina* sites, the highest total biomass values were registered in the mudflat sites, mostly due to the greater contribution of *S. plana*. This species represented more than 90% of the total biomass in these sites, although with lower average values than those registered by Guerreiro (1998) for nearby areas (28.42 g AFDW m^{-2}).

Although presenting a similar macroinvertebrate assemblage in the present study, a decreasing density and biomass trend was noted from the unvegetated muddy sites, towards sites with shorter periods of submergence. The creek sites exhibit lower densities and biomass values especially for taxa with larger individuals, such as *H. diversicolor*, *S. plana*, *H. ulvae* and *C. carinata*. This fact may result from higher predation pressure by the nektonic fauna concentrated inside the salt marsh creeks, which would be mainly focused on larger individuals (Wiltse et al., 1984; Sarda et al., 1998) and also from the higher instability of the surface sediments in these sites (Kneib, 1984).

The studied salt marsh areas support an invertebrate community of low diversity with higher values towards the unvegetated sites as has already been reported for other salt marsh studies (Jackson, 1985; Frid & James, 1989; Levin & Talley, 2000). Few taxa were found in middle marsh sites during autumn and winter, however, during spring and summer taxa diversity increased, supported by several insect larvae and by epibenthic crustaceans, which may use the high amount of plant detritus deposited on the sediment surface during these seasons to prevent desiccation (personal observation).

Total biomass in the unvegetated and *Spartina* sites was higher during spring and summer, mostly due to the increment of *S. plana* and *H. ulvae*. Higher biomass values during spring and summer are consistent with the results from other authors for *S. plana* (Guerreiro, 1998) and *H. ulvae* (Curras & Mora, 1990).

In the studied salt marsh sites higher abundances of fish and decapod taxa preying on benthic invertebrates occur precisely during this year's seasons (Salgado et al., 2004a). In fact, Salgado et al. (Unpublished data), within the same salt marsh areas, found high abundances of the goby *Pomatoschistus microps* (Krøyer, 1838), which were feeding inside the creeks preying mainly on oligochaetes and small polychaetes, such as *S. shrubsolii*. Several authors have reported a decreased in the salt marsh macroinvertebrates biomass values during summer due to predation by nektonic species (Kneib, 1984; Wiltse et al., 1984; Sarda et al., 1998). In the present study this biomass reduction trend was only observed for *S. plana*, but was not directly caused by predation. Since predation on this species by fishes (Costa, 1988; Cabral, 1998; Salgado et al., 2004b) and by birds (Moreira, 1995) is focused on their siphons, which have the capability of regenerating, it does not kill the affected individuals (Begon et al., 1986). These facts might indicate that macroinvertebrates are not a limiting resource for the nektonic species and that the natural biomass increment of these invertebrate species could be masking the predation/disturbance promoted by the nektonic species.

Another predation pressure for the macroinvertebrate assemblage arrives from the bird community, for which the Tejo estuary is an important winter and breeding area, being the large mudflat areas adjacent to the salt marsh areas their preferential areas for feeding (Moreira, 1995). According to the same author, during winter it is possible to find the highest abundances of most species, which have a great feeding dependence on *S. plana*, but also on *H. ulvae* and *H. diversicolor*. However, *H. diversicolor* is mainly preyed on birds during the summer (Moreira, 1995) due to its higher availability in this season related to higher sediment temperatures and thus, higher superficial activity of this species (Esselink & Zwarts, 1989). No reduction in the density and biomass values of this species was noted during that season.

The present study reinforces the general idea that estuaries and salt marsh areas support an important macroinvertebrate community of low diversity, but with high abundance and biomass values, which plays a key role in the food web of the ecosystem sustaining large fish and bird populations. Which amount of the macroinfaunal secondary production is consumed and how structure composition is altered by predation are questions that should be addressed in future studies.

Acknowledgements This work was possible due to the financial support of the EU through the project EUROSAM (contract ENV4-CT97-0436) and of the Fundação para a Ciência e Tecnologia through the project FESTA (PRAXIS 2/2.1/MAR/1715/95) and the grant PRAXIS XXI BD/3541/97. We would also like to thank Paula Chainho and Luisa Chaves for their precious comments on the final draft of this manuscript.

References

Beeftink, W. G., 1977. The coastal salt marshes of Western and Northern Europe: an ecological and phytosociological approach. In Chapman, V. J. (eds), Wet Coastal Ecosystems. Elsevier, Amsterdam, 93–121.

Begon, M., J. L. Harper & C. R. Townsend, 1986. Ecology. Individuals, Populations and Communities. Blackwell Scientific Publications, Oxford.

Beukema, J. J., 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. Netherlands Journal of Sea Research 10: 236–261.

Cabral, H. N., 1998. Utilização do estuário do Tejo como área de viveiro pelos linguados, *Solea solea* (Linnaeus, 1758) e *Solea senegalensis* Kaup, 1858, e robalo, *Dicentrarchus labrax* (Linnaeus, 1758). [Ph.D Thesis]. Universidade de Lisboa, Lisbon.

Calvário, J., 1982. Estudo Ambiental do Estuário do Tejo. Povoamentos Bentónicos Intertidais (substratos móveis). Comissão Nacional do Ambiente, Lisbon.

Catarino, F., J. D. Tenhunen, V. Brotas & O. Llange, 1985. Application of CO_2-porometer methods to assessment of components of photosynthetic production in estuarine ecosystems. Marine Biology 89: 37–43.

Cattrijsse, A., E. S. Makwaia, H. R. Dankwa, O. Hamerlynck & M. A. Hemminga, 1994. Nekton communities of an intertidal creek of an European estuarine brackish marsh. Marine Ecology Progress Series 109: 195–208.

Clarke, K. R. & R. M. Warwick, 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Natural Environmental Research Council, Plymouth Marine Laboratory, Plymouth.

Costa, M. J., 1988. Écologie alimentaire des poissons de l'estuaire du Tage. Cymbium 12: 301–320.

Costa, M. J. & H. N. Cabral, 1999. Changes in the Tejo nursery function for commercial fish species: some perspectives for management. Aquatic Ecology 33: 287–292.

Curras, A. & J. Mora, 1991. Comunidades bentonicas de la ria del Eo (Galicia-Asturias: NW España). Cahiers de Biologie Marine 32: 57–81.

Eagle, R. A., 1975. Natural fluctuations in a soft bottom benthic community. Journal of the Marine Biological Association of the United Kingdom 55: 865–878.

Esselink, P. & L. Zwarts, 1989. Seasonal trend in the burrow depth and tidal variation in feeding activity of *Hediste diversicolor*. Marine Ecology Progress Series 56: 243–254.

Frid, C. L. J. & R. James, 1989. The marine invertebrate fauna of a British coastal salt marsh. Holarctic Ecology 12: 9–15.

Gaston, G. R., C. Rakocinski, S. S. Brown & C. M. Cleveland, 1998. Trophic structure in estuaries: response of macrobenthos to natural and contaminant gradients. Marine and Freshwater Research 49: 833–846.

Gaudêncio, M. J., M. T. Guerra & M. Glémarec, 1991. Recherches biosedimentaires sur la zone maritime de l'estuaire du Tage, Portugal: données sédimentaires préliminaires. In Elliot, M. & J.-P. Ducrotoy (eds), Estuaries and Coasts: Spatial and Temporal Intercomparisons. Olsen & Olsen, Fredenberg.

Guerreiro, J., 1998. Growth and production of the bivalve *Scrobicularia plana* in two Southern European estuaries. Vie et Milieu 48: 121–131.

Hampel, H., 2003. Factors influencing the habitat value of tidal marshes for nekton in the Westerschelde estuary. [Ph.D Thesis]. University of Gent, Gent.

Ieno, E. N. & R. O. Bastida, 1998. Spatial and temporal patterns in coastal macrobenthos of Samborombo bay, Argentina: a case study of very low diversity. Estuaries 21: 690–699.

Jackson, D., 1985. Invertebrate population associated with *Spartina anglica* salt-marsh and adjacent intertidal mud flats. Estuarine and Brackish-Water Sciences Association Bulletin 40: 8–14.

Jackson, D., C. F. Mason & S. P. Long, 1985. Macroinvertebrate populations and production on a saltmarsh in East England dominated by *Spartina anglica*. Oecologia 65: 406–411.

Kneib, R. T., 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries 7: 392–412.

Laffaille, P., S. Brosse, E. Feunteun, A. Baisez & J.-C. Lefeuvre, 1998. Role of fish communities in particulate organic matter fluxes between salt marshes and coastal marine waters in the Mont Saint-Michel Bay. Hydrobiologia 373–374: 121–133.

Laffaille, P., E. Feunteun & J.-C. Lefeuvre, 1999. Compétition alimentaire entre deux espèces de gobies, *Pomatoschistus lozanoi* (de Buen) et *P. minutus* (Pallas), dans un marais salé macrotidal. Compte Rendu de l'Académie des Sciences de la Vie 322: 897–906.

Levin, L. A. & T. S. Talley, 2000. Influences of vegetation and abiotic environmental factors on salt marsh invertebrates. In Weinstein, M. P. & D. A. Kreeger (eds), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishing, Amsterdam, 661–708.

Levin, L. A., T. S. Talley & J. Hewitt, 1998. Macrobenthos of *Spartina foliosa* (Pacific cordgrass) salt marshes in Southern California: community structure and comparison to a Pacific mudflat and a *Spartina alterniflora* (Atlantic smooth cordgrass) marsh. Estuaries 21: 129–144.

Lillebø, A. I., M. A. Pardal & J. C. Marques, 1999. Population structure, dynamics and production of *Hydrobia ulvae* (Pennant) (Mollusca: Prosobranchia) along an eutrophication gradient in the Mondego estuary (Portugal). Acta Oceanologica 20: 289–304.

Ludwig, J. A. & J. F Reynolds, 1988. Statistical Ecology. A Primer on Methods and Computing. John Wiley, New York.

Marques, J. C., I. Martins, C. Teles-Ferreira & C. Cruz, 1994. Population dynamics, life history, and production of *Cyathura carinata* (Krøyer) (Isopoda: Anthuridae) in the Mondego estuary, Portugal. Journal of Crustacean Biology 14: 258–272.

Marques, J. C., L. B. Rodrigues & A. J. A. Nogueira, 1993. Intertidal macrobenthic communities structure in the Mondego estuary (Western Portugal): reference situation. Vie et Milieu 43: 177–187.

Mathieson, S., A. Cattrijsse, M. J. Costa, P. Drake, M. Elliott, J. Gardner & J. Marchand, 2000. Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. Marine Ecology Progress Series 204: 225–242.

Moreira, F. M., 1995. A utilização das zonas entre-marés do estuário do Tejo por aves aquáticas e suas implicações para os fluxos de energia na teia trófica estuarina. [Ph.D Thesis]. Universidade de Lisboa, Lisbon.

Moy, L. D. & L. A. Levin, 1991. Are *Spartina* marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. Estuaries 14: 1–16.

Pearson, T. H. & R. Rosenberg, 1978. Macrobenthic succession in relation to organic enrichment and pollution of marine environment. Oceanography and Marine Biology: an Annual Review 16: 229–311.

Rader, D. N., 1984. Salt marsh benthic invertebrates: small-scale patterns of distribution and abundance. Estuaries 7: 413–420.

Rees, H. L., D. C. Moore, T. Pearson, M. Elliott, M. Service, J. Pomfret, & D. Johnson, 1990. Procedures for the monitoring of marine benthic communities at UK sewage sludge disposal sites. Department of Agriculture & Fisheries for Scotland. Fisheries Information Pamphlet 18.

Reimold, R. J., 1977. Mangals and salt marshes of the Eastern United States. In Chapman, V. J. (ed.), Wet Coastal Ecosystems. Elsevier, Amsterdam, 157–166.

Robineau, B., 1987. Caratérisation des peuplements macrozoobenthiques de l'estuaire de la Loire. Vie et Milieu 37: 67–76.

Rodrigues, A. M., 1992. Environmental status of a multiple use estuary, through the analysis of benthic communities: the Sado estuary, Portugal. [Ph.D Thesis]. Department of Biological and Molecular Sciences, University of Sterling, Sterling.

Saldanha, L., 1980. Estudo Ambiental do Estuário do Tejo. Povoamentos Bentónicos. Peixes e Ictioplâncton do Estuário do Tejo. Comissão Nacional do Ambiente, Lisbon.

Salgado, J. P., H. N. Cabral & M. J. Costa, 2004a. Comparison of the fish assemblages in tidal salt marsh creeks and in adjoining mudflat areas in the Tejo estuary (Portugal). Cahiers de Biologie Marine 45: 213–224.

Salgado, J. P., H. N. Cabral & M. J. Costa, 2004b. Feeding ecology of the gobies *Pomatoschistus minutus* (Pallas, 1770) and *Pomatoschistus microps* (Krøyer, 1838) in the upper Tagus estuary, Portugal. Scientia Marina 68: 425–434.

Sardá, R., K. Foreman, C. E. Werme & J. Valiela, 1998. The impact of epifaunal predation on the structure of macroinfaunal invertebrate communities of tidal saltmarsh creeks. Estuarine, Coastal and Shelf Science 46: 657–669.

Sokal, R. R. & F. J. Rohlf, 1981. Biometry. 2nd edn. W. H. Freeman, New York.

Sprung, M., 1994. Macrobenthic secondary production in the intertidal zone of the Ria Formosa lagoon in the Southern Portugal. Estuarine, Coastal and Shelf Science 38: 539–558.

Ter Braak, C. J. F., 1995. CANOCO—a Fortran program for canonical community ordination by partial detrended canonical correspondence analysis, principal components and redundancy analysis. Agricultural and Mathematical Group, Ministry of Agriculture and Fisheries, ITI-TNO, Wageningen.

Whitlatch, R., 1981. Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. Journal of Experimental Marine Biology and Ecology 53: 31–45.

Wiltse, W. I., K. H. Foreman, J. M. Teal & I. Valiela, 1984. Effects of predators and food resources on the macrobenthos of salt marsh creeks. Journal of Marine Science 42: 923–942.

Wolff, W. J., 1973. The estuary as an habitat. An analysis of data on the soft bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Zoologische Verhandelingen 126: 1–242.

Ysebaert, T. P., P. Meire, J. Coosen & K. Essink, 1998. Zonation of intertidal macrobenthos in the estuaries of Schelde and Ems. Aquatic Ecology 32: 53–71.

Zar, J. H., 1996. Biostatistical Analysis. 3rd edn. Prentice Hall, New Jersey.