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# Structure and dynamics of a benthic invertebrate community in an intertidal area of the Tagus estuary, western Portugal: a six year data series

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## Abstract

The intertidal benthic invertebrate community adjacent to "Parque das Nações", Tagus estuary, western Portugal, was studied at seven sites between October of 1996 and 2002. Grain size analysis revealed that the area was essentially muddy with total organic matter ranging from 5.4 to 11.4%. Annelida represented more than 85% of the total abundance. The dominant taxa were Oligochaeta, *Streblospio shrubsolii*, *Scrobicularia plana*, *Hediste diversicolor*, *Hydrobia ulvae* and Cirratulidae. Analysis of abundance revealed high seasonal and interannual heterogeneity, although clear aggregations between winter/spring and summer/autumn sampling periods were detected by multivariate techniques. *Paragnathia formica* and Dolichopodidae were closely related to winter/spring cluster while *S. shrubsolii, Cossura* sp., *S. plana* and *Corbula gibba* were associated to the summer/autumn aggregation. Although other taxa were abundant in several seasons, constancy in their numbers throughout the year could be observed. Temperature, rainfall and daylight hours were the environmental variables best related to the biological data. Temperature and daylight hours were important for the establishment of the two seasonal aggregations. Rainfall has also shown to be an essential factor on the structuring of this intertidal community, closely related to the abundance increase of Cirratulidade and decrease of *Polydora* sp., *Nephtys* spp., *Cerastoderma glaucum, Corophium* spp. and other Gammaridea. Sediment composition seems to play an important role in changing the community characteristics during the year since some species abundance appear to be favoured by coarser particles and many by fine sediments.

## Introduction

Benthic invertebrates are relatively sedentary and play an important role in cycling nutrients and inorganic compounds between sediments and water column. These facts, associated with their importance as food sources for economically or recreationally important fish species and the ability to react to natural or human induced disturbances allow these communities to exhibit great potential for integrating long-term environmental conditions (Bilyard, 1987; Herman et al., 1999).

The study of temporal and spatial variability of benthic communities is essential to understand their structure and dynamics. Some studies have been done on the relations between the temporal and spatial variation of several environmental variables and the biological patterns and processes in macrobenthic assemblages of soft-sediments (e.g. Ysebaert & Herman, 2002; Bazaïri et al., 2003; Ysebaert et al., 2003). In muddy sediments of temperate intertidal habitats, such as lagoons and salt marshes, marked seasonal fluctuation in density of macrofaunal assemblages in which deposit feeders dominate has been observed (Marsh & Tenore, 1990). Physical variables fluctuate with greater amplitude in intertidal areas, thus subjecting organisms inhabiting this environment to great physical stress (Woodin, 1974).

Long-term data studies consist on the assessment of temporal changes in macrofaunal composition based on a regular sampling period or on the comparison at selected sites after a long time interval (Grémare et al., 1998). Long-term data series are common in many marine areas: Wadden Sea (e.g. Reise, 1982), western English Channel (e.g. Ibanez & Dauvin, 1988), French Mediterranean coast (e.g. Salen-Piccard & Arlhac, 2002), Chesapeake Bay (e.g. Dauer & Alden, 1995) and southern California (e.g. Desmond et al., 2002). However, few long-term studies have been published from the Iberian Peninsula (e.g. López-Jamar et al., 1995).

In Portugal, studies involving soft-sediments macrofaunal assemblages have taken place in several estuaries (e.g. Calvário, 1982; Quintino & Rodrigues, 1989; Rodrigues & Quintino, 1993; Mucha & Costa, 1999; Marques et al., 2002; Mucha et al., 2003) and have also investigated the ecology of several species (e.g. Guerreiro, 1998; Abrantes et al., 1999; Lillebø et al., 1999; Cunha et al., 2000). In the Tagus estuary the studies on the benthic communities were either dedicated to the study of spatial patterns (Calvário, 1982; Rodrigues et al., this volume) or involved monitoring assessment works (Pereira et al., 1997; Costa et al., 1999). Long-term series of benthic macrofauna communities of the Tagus estuary exist but were not published. Therefore, the present study, which began in October 1996, becomes an important data asset.

The aim of this research was to assess the structure of the benthic invertebrate community of an intertidal soft-sediment area in the Tagus estuary and evaluate the relationship between several environmental factors and the dynamics of this community.

## Materials and methods

### *Sampling*

The study area was located in the right bank of the Tagus estuary, in a 5 km long intertidal zone in front of "Parque das Nações", Lisbon (Fig. 1), being all sampling sites located at the same relative shore height. Salinity values ranged usually from 15 to 20 (Cabral, 1998). Until 1995 this area was polluted due to the nearby existence of several industries. The closing of these units and the rehabilitation of the area for the EXPO'98 World Exhibition and consequent implementation of the "Parque das Nações" changed this situation. Between 1995 and 1998 several dredging operations associated to the construction works of the "Parque das Nações" and the Vasco da Gama Bridge took place in this area. Benthic macrofauna samples were taken seasonally (although not always done in the same months for the different years), during high tide from a boat, in seven sites using a 0.05 $m^2$ Van Veen grab Sousa-Reis/LMG model, from autumn of 1996 until autumn of 2002. However, during this period, four seasons were not sampled (autumn of 1997, winter of 1998, spring and summer of 1999). At each site of the 21 sampling moments, six replicates were collected for macrofauna analysis (total area sampled = 0.30 $m^2$ per site) and another grab was taken for sediment analysis, which included grain size and total organic matter (TOM) determination.

### *Sediment analysis*

Grain size analysis was carried out according to Gaudêncio et al. (1991). Sediments were classified as gravel (particles diameter above ≥2.000 mm), coarse sand (0.500–2.000 mm), medium sand (0.250–0.500 mm), fine sand (0.250–0.063 mm) and mud ($<$0.063 mm). TOM was determined by loss of weight on ignition at 500 °C (adapted from Pereira et al., 1997).

### *Other environmental variables*

In order to evaluate the relationship between other environmental variables and the benthic invertebrate community, daylight hours (*D*) of each sampling date (Anonymous, 1992), mean monthly air

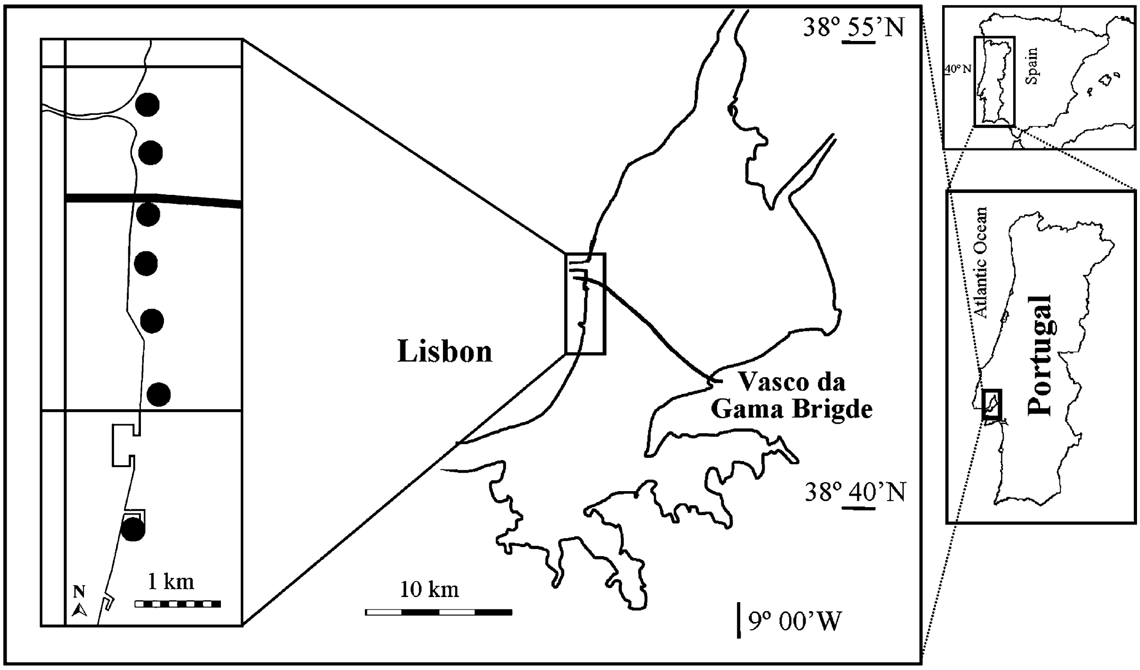

*Figure 1.* Map showing the location of the study area in the Tagus estuary and the sampling sites (●)

temperature ($T$) in °C, total monthly rainfall ($R$) in mm and river flow ($F$) data, presented as monthly mean discharge in $m^3$ $s^{-1}$, for the River Tagus were analysed. These three last sets of data were obtained from the Ministry of Environment (DSM-DRAOT/LVT). Besides using the values of the sampling month for the air temperature, rainfall and river flow, community lagged response to these variables was also assessed when considering the values for the previous month (1 month) and for the cumulative previous 3 months since community responses may have lagged behind environmental conditions (Desmond et al., 2002). Due to the significant variations caused by the tides during the day, salinity was not considered in this study.

### *Macrofauna analysis*

Benthic invertebrate samples were fixed in 5% neutralized formalin, washed through a 0.5 mm mesh sieve and preserved in 70% ethyl alcohol. Samples were sorted and organisms identified to the lowest taxonomic level possible. Each identified taxon was counted and density (number of individuals per 0.05 $m^2$) was determined. To evaluate mean individual biomass (milligrams per individual), dry weight was determined according to Rumohr (1999).

### *Statistical analysis*

In total 41 invertebrate taxa were identified in 21 sampling occasions, but in subsequent statistical analyses only the 17 taxa corresponding to more than 0.05% of the total individuals captured were included in order to improve the robustness of the non-parametric tests applied to the data (avoiding the uncertainty of the reliability of the relative abundance of rare species) (Sokal & Rohlf, 1995) and the readability of the diagrams of the mutivariate technique used (ter Braak & Šmilauer, 2002). Altogether, these taxa accounted for 99.77% of total abundance. For these analyses several organisms had to be associated in higher taxonomic groups, either because specific identification was difficult, or the organisms were damaged to an extent that the identification of those individuals could not be possible.

To determine if the differences observed throughout the study period between the densities of the most abundant taxa were significant, Friedman test (Siegel & Castellan, 1988) was performed for that set of 17 taxa, using the 21 samplings as replicates. Spearman rank-order correlation coefficient (Siegel & Castellan, 1988) was applied to assess the level of similitude of the community structure along the study period, i.e. which fraction of the 210 crossed comparisons between the 21 samplings revealed high ($p < 0.001$), moderate ($0.001 \le p < 0.01$), low ($0.01 \le p < 0.05$) or absence ($p \ge 0.05$) of correlation when the abundances of those 17 taxa were considered (Sokal & Rohlf, 1995). However, due to the lack of independence of pairwise correlation values (Anonymous, 1997), special care was taken in the interpretation of these results. The same correlation coefficient was used to analyse the degree of correlation between the environmental variables. Both these non-parametric univariate statistical procedures were performed in SPSS statistical package (Anonymous, 1997).

Patterns of variation in community structure were investigated by means of canonical correspondence analysis (CCA) (ter Braak & Šmilauer, 2002): (i) performed considering all studied environmental variables; and also (ii) only those associated with sediment characterization, since the high correlation of these variables with the climatic variables might have obscured in the first CCA any specific relationship between the sediment variables and the biological data (ter Braak & Šmilauer, 2002). These analyses allowed the evaluation of the relationship between different abiotic factors and the structure of this soft-sediment intertidal community. For both situations a global Monte Carlo permutation test was used to evaluate the significance ($p < 0.05$) of the first ordination axis and the sum of all canonical axes (ter Braak & Šmilauer, 2002). In the first CCA the number of environmental variables had to be reduced by means of manual forward selection using a Monte Carlo permutation test ($p < 0.05$) (ter Braak & Šmilauer, 2002), since the proximity in the number of samples and environmental variables originated a non-significant relationship between species and environmental variables when the whole set of those environmental variables was considered (ter Braak & Verdonschot, 1995). However, since all non-selected environmental variables in that CCA were correlated to one of the explanatory variables, its addition as supplementary variables was performed and represented in the ordination diagram (ter Braak & Šmilauer, 2002). In the case of the CCA performed considering only the environmental variables associated with sediment, such constrain was not observed and therefore all were included as explanatory variables. Multivariate analyses were carried out using the package CANOCO 4.5 (ter Braak & Šmilauer, 2002).

## Results

### *Sediment analysis*

During the sampling period few variations in the sediment grain-size were registered (Fig. 2). In all sampling occasions, mud was the predominant fraction and its percentage was always above 80%. However, a slight increase of coarse particles was observed in the beginning of the study. TOM values were high throughout the study (Fig. 2), ranging from 5.04% (summer 2001) to 11.40% (winter 1999).

### *Other environmental variables*

The mean monthly air temperature and total monthly rainfall values (Fig. 3) were characteristic of temperate zones. Mean air temperature values ranged between 7.50 and 24.30 °C and the lowest values were always registered in the winter months. Total monthly rainfall values ranged between 0.00 and 358.40 mm. The highest values of this parameter were registered in the winter months of 1996, 1997, 1998 and 2001 and were considerably lower in the remaining winters. Total monthly rainfall showed a variable pattern from year to year while mean air temperature revealed a more constant pattern.

### *Macrofauna analysis*

A total of 18,140 individuals belonging to 41 taxa were collected between autumn of 1996 and 2002 in the study area (Table 1). Polychaeta accounted for 45% of the total abundance and Oligochaeta for 42%. Friedman test showed significant differences between the densities of the 17 considered taxa throughout the study ($\chi^2 = 220.95$; df = 16; $p < 0.001$). The benthic community of the study area was characterized by high abundances of six

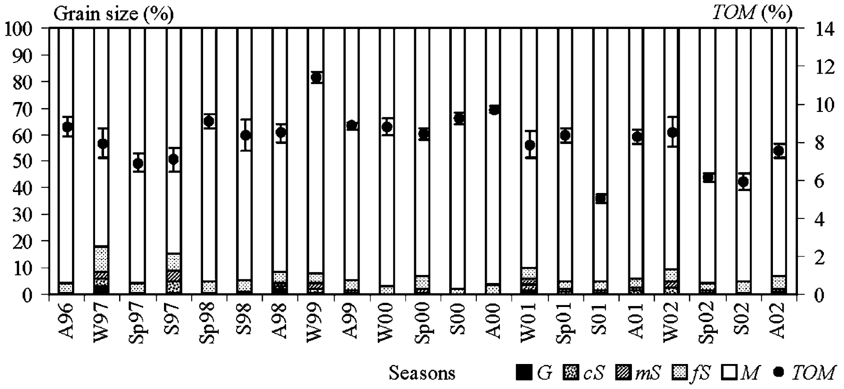

*Figure 2.* Variation of grain size defined as gravel (*G*), coarse sand (*cS*), medium sand (*mS*), fine sand (*fS*) and mud (*M*), and total organic matter (TOM - mean ± SE) in the sampled seasons (W – winter; Sp – spring; S – summer; A – autumn).

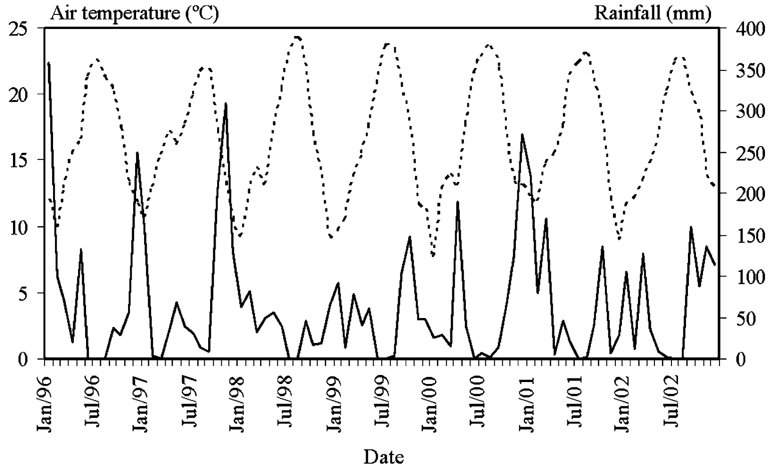

*Figure 3.* Monthly mean air temperature (discontinuous line) and total rainfall (continuous line) between January of 1996 and December 2002.

taxa. Oligochaeta, *Streblospio shrubsolii* (Buchanan, 1890) and *Scrobicularia plana* (da Costa, 1778) dominated the community and *Hediste diversicolor* (O.F. Müller, 1776), *Hydrobia ulvae* (Pennant, 1777) and Cirratulidae were also abundant in this area. All other taxa were less represented (Table 2).

Considering the abundance in each sampled season, Oligochaeta showed two density peaks (spring of 1998 and winter of 2001) with more than 50 ind. 0.05 m$^{-2}$. In the remaining seasons values of this parameter for this taxon were considerably lower (<15 ind. 0.05 m$^{-2}$). Two other species, *Streblospio shrubsolii* and *Scrobicularia plana*, although always present, never revealed such high abundances, except in the autumn of 2000, when *S. shrubsolii* registered 47.5 ind. 0.05 m$^{-2}$. In general, densities obtained for these two species were always below 10 ind. 0.05 m$^{-2}$ presenting less variability than Oligochaeta.

In spite of the dominant taxa remaining the same throughout the sampled period, high degree of variation was observed in the community structure. In fact, using the Spearman correlation coefficient to compare the numerical relative importance of the most abundant taxa on different sampling moments (210 comparisons) only 26% of the comparisons revealed a high degree of association ($p < 0.001$; $N = 17$) and 15% of the correlations were found not significant ($p > 0.05$; $N = 17$).

To assess the influence of recruitment on the community structure changes, density and mean

*Table 1*. Taxa identified in the intertidal zone of the studied area by Calvário (1982) (◇), Pereira et al. (1997) (‡) and in the present study (Δ)

| Taxa | | |
|---|---|---|
| Anthozoa | *Actinia equina* (Linnaeus, 1768) | ‡ Δ |
| Hydrozoa | Hydrozoa unid. | Δ |
| Nematoda | Nematoda unid. | ‡ Δ |
| Nemertea | Nemertea unid. | Δ |
| Polychaeta | Aphroditidae unid. | ‡ |
| | *Autolytus* sp. | Δ |
| | Syllidae unid. | Δ |
| | *Hediste diversicolor* (O.F. Müller, 1776) | ◇ ‡ Δ |
| | *Nephtys hombergii* (Savigni, 1818) | ‡ Δ |
| | *Nephtys cirrosa* Ehlers, 1868 | Δ |
| | *Marphysa sanguinea* (Montagu, 1815) | Δ |
| | *Ophryotrocha puerilis* (McIntosh, 1885) | Δ |
| | *Cossura* sp. | Δ |
| | *Polydora* sp. | ‡ Δ |
| | *Pygospio elegans* Claparède, 1863 | ‡ Δ |
| | *Prionospio* sp. | ‡ |
| | *Streblospio shrubsolii* (Buchanan, 1890) | ‡ Δ |
| | *Cirratulus cirratus* (Müller, 1776) | Δ |
| | *Tharyx marioni* (Saint-Joseph, 1894) | ‡ Δ |
| | *Caulleriella* sp. | ‡ |
| | Capitellidae unid. | ‡ Δ |
| | *Sabellaria spinulosa* Gravier, 1906 | ‡ |
| Oligochaeta | Oligochaeta unid. | ◇ ‡ Δ |
| Gastropoda | *Hinia reticulata* (Linnaeus, 1758) | ‡ |
| | *Hydrobia ulvae* (Pennant, 1777) | ◇ ‡ Δ |
| Bivalvia | *Anomia ephippium* (Linnaeus, 1758) | ‡ |
| | *Cerastoderma edule* (Linnaeus, 1758) | ‡ |
| | *Cerastoderma glaucum* (Poiret, 1789) | Δ |
| | *Abra alba* (Wood, 1802) | Δ |
| | *Scrobicularia plana* (da Costa, 1778) | ◇ ‡ Δ |
| | *Corbula gibba* (Olivi, 1792) | Δ |
| Isopoda | *Paragnathia formica* (Hesse, 1864) | ◇ Δ |
| | *Cyathura carinata* (Krøyer, 1847) | Δ |
| | *Idotea negleta* Sars, 1899 | Δ |
| | *Lekanesphaera monodi* (Arcangeli, 1934) | Δ |
| | *Lekanesphaera rugicauda* (Leach, 1814) | ◇ |
| | *Porcellio pruinosus* Brandt, 1833 | ◇ |
| Amphipoda | *Corophium multisetosum* Stock, 1952 | Δ |
| | *Corophium sextonae* Crawford, 1937 | ‡ |
| | *Jassa pusilla* (O. Sars, 1894) | ‡ |
| | *Melita palmata* (Montagu, 1804) | Δ |
| | *Orchestia kosswigi* Ruffo, 1949 | ◇ |
| | *Orchestia mediterranea* Costa, 1857 | ◇ |
| | *Orchestia stephenseni* Cecchini, 1928 | ◇ |
| | *Stenothoe marina* (Bate, 1856) | ‡ |
| Sessilia | *Balanus improvisus* Darwin, 1854 | ‡ |
| | *Elminius modestus* Darwin, 1854 | ‡ |
| Decapoda | *Carcinus maenas* (Linnaeus, 1758) | ◇ ‡ Δ |
| Diptera | Ceratopogonidae unid. | Δ |
| | Chironomidae unid. | Δ |
| | Dolichopodidae unid. | ‡ Δ |
| | Tabanidae unid. | Δ |
| | Tipulidae unid. | Δ |
| | Psycodidae unid. | Δ |
| | Diptera unid. | ◇ Δ |
| Lepidoptera | *Nymphula* sp. | Δ |
| | Bryozoa unid. | Δ |
| Ascidiacea | Molgulidae unid. | ‡ |

individual biomass for every bimonthly period were computed for some selected taxa (Fig. 4). In all seasons recruitment peaks could be observed in these taxa: winter (Oligochaeta); spring (*Paragnathia formica* (Hesse, 1864)); late summer (*Streblospio shrubsolii* and *Cossura* sp.); and late summer/autumn (*Scrobicularia plana*). Three taxa revealed separated recruitment peaks: *Hediste diversicolor* in early spring and late summer; *Hydrobia ulvae* in early spring and late autumn and Dolichopodidae in winter and spring.

### *Relationships between environmental and biological variables*

CCA revealed that the 3-month lagged rainfall, 3-month lagged air temperature and daylight hours were the environmental variables most related to the benthic community (Fig. 5). The first two CCA ordination axes explained 40.40% of taxa temporal variability and 96.30% of the relationship between abundance and the three selected environmental variables. The relative high correlation between taxa and environmental data for the first two axes (Table 3) suggests that the environmental variables explain the variability associated with taxa. The global permutation test showed that, for the first canonical axis ($F$-ratio $= 7.07$) as well as for the sum of all canonical axes ($F$-ratio $= 4.10$), relations between taxa abundance and those environmental variables were statistically significant ($p < 0.01$).

*Table 2.* Density (ind. 0.05 $m^2$) (median and interquartile range) and frequency of occurrence (FO) of the 17 most important taxa in the studied area and respective taxa codes

| Taxa | Codes | Median | Interquartile range | FO (%) |
|---|---|---|---|---|
| Oligochaeta | Oli | 2.40 | 1.43–1.43 | 100.00 |
| *Streblospio shrubsolii* | Ssr | 1.48 | 1.08–4.05 | 100.00 |
| *Scrobicularia plana* | Spl | 1.00 | 0.35–1.73 | 100.00 |
| *Hediste diversicolor* | Hdv | 0.34 | 0.25–0.85 | 95.24 |
| *Hydrobia ulvae* | Hul | 0.30 | 0.03–1.45 | 80.95 |
| Cirratulidae | Crr | 0.28 | 0.05–1.15 | 95.24 |
| Dolichopodidae | Dch | 0.05 | 0.05–0.13 | 71.43 |
| *Polydora* sp. | Ply | 0.03 | 0.00–0.10 | 57.14 |
| *Corophium* spp. | Crp | 0.03 | 0.00–0.08 | 61.90 |
| *Cerastoderma glaucum* | Cgl | 0.03 | 0.00–0.03 | 52.38 |
| Gammaridea | Gmm | 0.00 | 0.00–0.03 | 42.86 |
| *Nephtys* spp. | Npt | 0.00 | 0.00–0.05 | 38.10 |
| *Cyathura carinata* | Cct | 0.00 | 0.00–0.03 | 38.10 |
| *Cossura* sp. | Css | 0.00 | 0.00–0.00 | 23.80 |
| *Paragnathia formica* | Pfm | 0.00 | 0.00–0.00 | 14.29 |
| Capitellidae | Cap | 0.00 | 0.00–0.00 | 9.52 |
| *Corbula gibba* | Cgb | 0.00 | 0.00–0.00 | 9.52 |

CCA shows that the biological community mainly aggregated in four different taxa groups and two seasonal clusters (Fig. 5a). Group I (GI) is composed by the isopod *Paragnathia formica* and larval forms of the Dolichopodidae insect family. Group II (GII) comprises the polychaetes *Streblospio shrubsolii* and *Cossura* sp. and the bivalves *Scrobicularia plana* and *Corbula gibba* (Olivi, 1792). Group III (GIII) assembles the annelids *Hediste diversicolor* and Oligochaeta, the gastropod *Hydrobia ulvae* and the isopod *Cyathura carinata* (Krøyer, 1847). Group IV (GIV) gathers the polychaetes *Polydora* sp. and *Nephtys* spp., the bivalve *Cerastoderma glaucum* (Poiret, 1789) and the amphipods *Corophium* spp. and other Gammaridea.

The two main seasonal aggregations, winter/spring and summer/autumn, were associated to two of the taxa groups. Species group GI was related to winter/spring and GII with summer/autumn. These two main seasonal trends were linked with the increase of some of the aforementioned environmental variables, daylight hours and 3-month lagged air temperature, respectively (Fig. 5). GIII positioning indicated different taxa behaviour. In spite of being abundant all year, Oligochaeta showed an affinity towards winter/spring cluster and *Hydrobia ulvae* to summer/autumn grouping. With relatively constant abundances throughout the year *Hediste diversicolor* and *Cyathura carinata* appeared in different to any seasonal association. Almost all taxa included in these three groups did not seem particularly affected by a rainfall gradient. Conversely, taxa from GIV appeared in all seasons and seem inversely related to a precipitation gradient, such as *H. diversicolor* to a less extent. Whereas for Cirratulidae, this was the most important and directly related factor (Fig. 5). Therefore, this community presented two distinct assemblages associated to winter/spring and summer/autumn periods. The first one was composed by taxa of GI and GIII and the second by taxa of GII and GIII. However, *Corbula gibba* and *Cossura* sp. were only present in summer/autumn of warmer years as it can be inferred from the CCA diagram (Fig. 5). Cirratulidae and taxa from GIV can also be present in both assemblages, by association to heavy rainfalls for the first one and inversely for the latter group. Capitellidade showed the same trend as taxa of GIV, but was only present in those years of lesser rainfall (Fig. 5).

The other environmental variables were added as supplementary variables to the CCA (Fig. 5b)

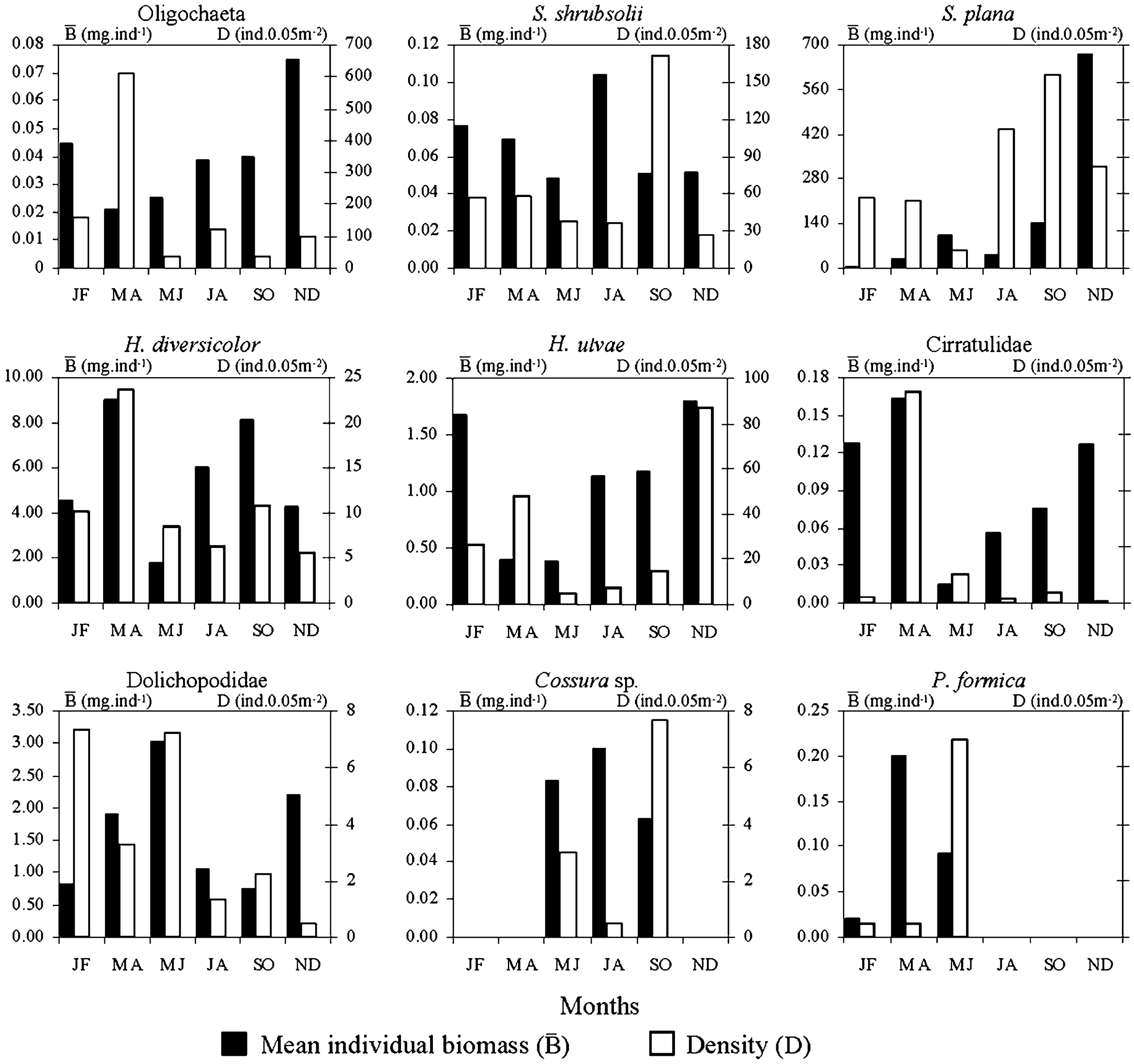

*Figure 4.* Mean individual biomass and density of several taxa during the studied period on a bimonthly periodicity (JF – January and February; MA – March and April; MJ – May and June; JA –July and August; SO – September and October; ND – November and December). The remaining taxa were not represented due to the reduced number of individuals in most seasons.

and revealed that river flow, rainfall and the larger grain size particles (gravel, coarse and medium sand) showed the same trend as 3-month lagged rainfall. Also, all temperature variables demonstrated the same tendency. Regarding muddy sediments and TOM it was obvious the association with the decrease of rainfall, since larger particles tend to appear when higher values of this parameter were registered. All these trends were confirmed statistically by means of Spearman rank-order correlation test ($p < 0.05$). Finally, fine sand increases with moderate rainfall levels, as it can be observed by the relationship between that sediment fraction and winter/spring samplings collected in lesser precipitation years (Fig. 5).

Figure 6 shows the CCA performed to analyse the 17 most abundant taxa distribution in function of sediment variables only, in order to reveal any existing relationships between them that might have been overlooked in the previous analysis. The first two ordination axes explained 6.50% of taxa abundance variability and 72.70% of the relation-

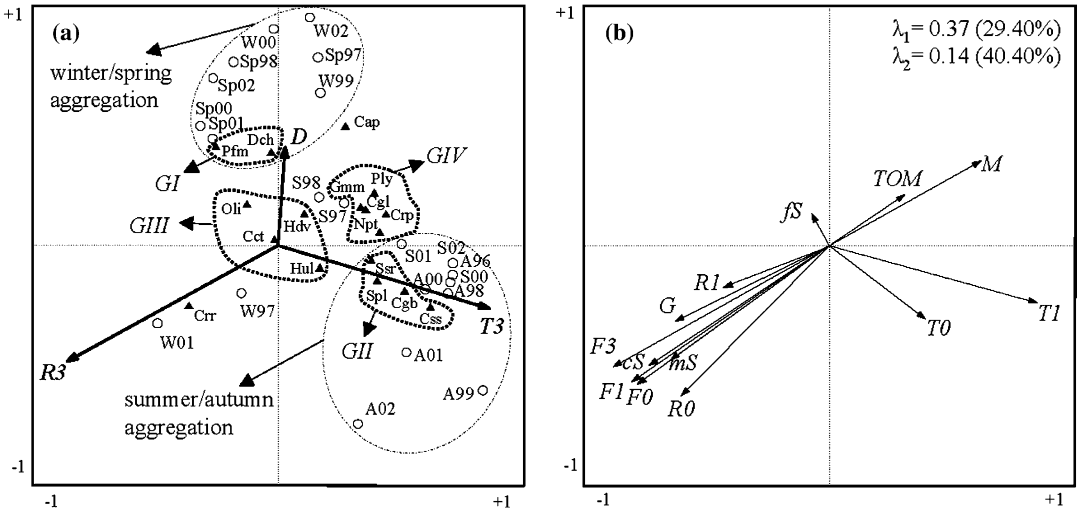

*Figure 5.* CCA ordination diagram with the 17 most abundant taxa and all environmental variables. Explanatory variables are represented apart (a) from the supplementary variables (b). Eigenvalues ($\lambda_i$) and cumulative percentage explained (between brakets) are also given. Taxa represented by triangles (for codes see Table 2), sampled seasons by circles (for codes see Fig. 2 caption) and environmental variables indicated by arrows (*D* – daylight hours, *F0* – sampling month river flow, *F1* – 1-month lagged river flow, *F3* – 3-month lagged river flow, *T0* – sampling month air temperature, *T1* – 1-month lagged air temperature, *T3* – 3-month lagged air temperature, *R0* – sampling month rainfall, *R1* – 1-month lagged rainfall, *R3* – 3-month lagged rainfall, *G* – gravel, *Cs* – coarse sand, *mS* – medium sand, *fS* – fine sand, *M* – mud, TOM-total organic matter).

*Table 3.* Results of the ordination by CCA performed for the 17 most abundant taxa considering all environmental variables

| | Axis I | Axis II |
|---|---|---|
| Eigenvalues | 0.37 | 0.14 |
| Taxa/environment correlations | 0.92 | 0.84 |
| Intraset correlations of variables | | |
| 3-mo lagged rainfall | −0.79 | −0.42 |
| 3-mo lagged air temperature | 0.79 | −0.22 |
| Daylight hours | 0.03 | 0.34 |

ship between abundance and sediment variables. The correlation between taxa and environmental variance obtained for the first two axes suggests that these variables still explain an important part of the variability associated to taxa abundance (Table 4). The global permutation test showed that the relations between taxa abundance and sediment variables were statistically significant ($p < 0.05$) for the first canonical axis ($F$-ratio = 6.34) as well as for the sum of all canonical axes ($F$-ratio = 2.54).

As previously mentioned the study area was typically muddy, however this analysis revealed that slight variations on sediment composition also played an important role on this biological community structure. Cirratulidae, *Cyathura carinata* and *Paragnathia formica* showed preference for coarser particles. *P. formica* simultaneously tended to be greatly related to fine sand sediments. Oligochaeta, *Cerastoderma glaucum* and Dolichopodidae also seemed slightly associated with fine sand grains and in contrast, abundance of Gammaridea and *Cossura* sp. were chiefly related to the decrease of this particular sediment. The remaining taxa (*Hediste diversicolor*, *Nephtys* spp., *Polydora* sp., *Streblospio shrubsolii*, Capitellidae, *Hydrobia ulvae*, *Corbula gibba*, *Scrobicularia plana*, *Corophium* spp.) seem closely associated with muddy sediments and the consequent increase of the TOM.

## Discussion

In the study area sediment composition revealed that substrate was essentially muddy as previously observed in other studies (Calvário, 1982; Gaudêncio et al., 1991; Pereira et al., 1997). TOM contents were high and very similar to those mentioned by Pereira et al. (1997) for the same area. The registered values of this parameter reflect

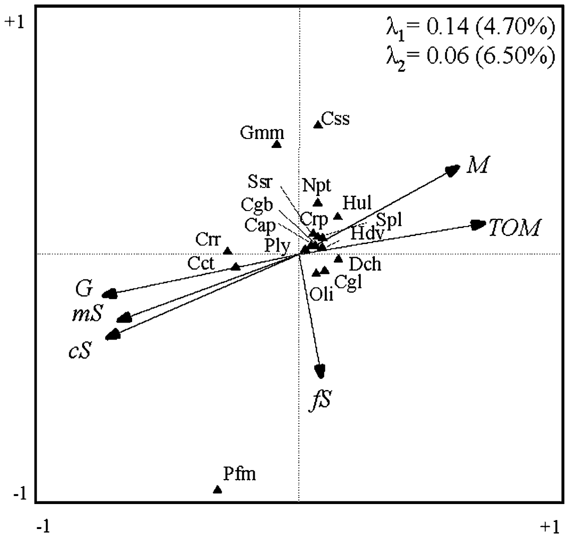

*Figure 6.* Ordination diagram of the CCA performed for the 17 most abundant taxa and sediment variables. Eigenvalues ($\lambda_i$) and cumulative percentage explained (between brakets) are also given. Taxa represented by triangles (for codes see Table 2) and sediment variables indicated by arrows (for codes see Fig. 5 caption).

*Table 4.* Results of the ordination by CCA performed for the 17 most abundant taxa considering only the sediments variables

| | Axis I | Axis II |
|---|---|---|
| Eigenvalues | 0.14 | 0.06 |
| Taxa/sediment correlations | 0.53 | 0.36 |
| Intraset correlations of variables | | |
| TOM | 0.37 | 0.05 |
| Mud | 0.32 | 0.13 |
| Fine sand | 0.05 | −0.18 |
| Medium sand | −0.36 | −0.10 |
| Coarse sand | −0.38 | −0.12 |
| Gravel | −0.39 | −0.06 |

that higher mud contents are directly related to the increase of organic matter (Creutzberg et al., 1984) since sediments with smaller grain size have reduced interstitial space thus meaning a decrease in permeability (Wolff, 1973).

Twenty-four new taxa were identified for this area and in the case of *Cossura* sp. it is the first reference for the Tagus estuary, together with Rodrigues et al. (this volume). In comparison to other studies done in the same area (Calvário, 1982; Pereira et al., 1997) it can be observed that the number of identified taxa was higher, which could be related to the increase in total area sampled. Only five taxa were common to all three studies: *Hediste diversicolor*, Oligochaeta, *Hydrobia ulvae*, *Scrobicularia plana* and *Carcinus maenas* (Linnaeus, 1758). This latter species, though very common, was not quantified due to the sampling method used.

This community seems to be typical of the inner middle part of the estuaries found normally in muddy sand flat bottoms and well oxygenated waters (Borja et al., 2004). Initially described as "*Macoma balthica* community" (Petersen, 1913, 1918) was classified in the coast of Portugal as the "*Scrobicularia plana – Cerastoderma edule* community" (Thorson, 1957). However, in this case it seems that *Cerastoderma edule* (Linnaeus, 1758) was replaced by *Cerastoderma glaucum*, a species with Mediterranean affinities and preferences for higher temperatures (Russell, 1971). As described for the Basque Country (Borja et al., 2004) the main taxa associated with this community are the Oligochaeta group, the polychaetes *Streblospio shrubsolii* and *Hediste diversicolor*, the gastropod *Hydrobia ulvae* and the crustaceans *Corophium* spp., *Cyathura carinata* and *Carcinus maenas*. The family Cirratulidae was one of the most important taxa in this intertidal community of the Tagus estuary but was not mentioned for other places (Junoy & Viétiez, 1990; Bazaïri et al., 2003; Borja et al., 2004). On the other hand, as for the Basque Country the spionid *Pygospio elegans* Claparède, 1863 was not found to be an important species, although characteristic of this type of community in other estuaries of the Cantabrian Sea (Junoy & Viétiez, 1990). This community also includes other, more or less abundant, polychaetes (*Polydora* sp.) or insect larvae, due to salinity decreases (e.g. Dolichopodidae) (Borja et al., 2004).

Polychaeta were the most important group in this intertidal area, which concurs with Fauchald's (1977) statement that polychaetes dominate macrofauna communities within fine sediments. The benthic community of this intertidal area was characterized by high number of individuals belonging to only six taxa: Oligochaeta, *Streblospio shrubsolii*, *Scrobicularia plana*, *Hydrobia ulvae*, *Hediste diversicolor* and Cirratulidae. These are often found in intertidal areas, particularly in muddy sediments (Dales, 1951; Wolff, 1973; Robineau, 1987; Guerreiro, 1998). Oligochaeta abundance showed higher variability in comparison to the others, probably related to rapid local increases in that population size after disturbances (Cowie et al., 2000).

In spite of the constant dominance of few abundant taxa, high variability of the community structure throughout the studied period was observed. Although two major human interventions took place in the area in the beginning of the study, it seems that the effects caused on community structure were considerably lesser than those due to natural events, otherwise aggregations of sampling seasons closer in time to the interventions (1996–1998) would be expected. Some of the existing variations may be a consequence of cyclic seasonal patterns (originated by air temperature and daylight hours variations) while others were related to isolated events (heavy rainfall). Irregular disturbances in some invertebrate assemblages appear to be more important than predictable seasonal cues, a conclusion supported by the density of more opportunistic species (Desmond et al., 2002). Several taxa in this study, including some of the most abundant, are considered to be opportunistic, such as Oligochaeta, *Streblospio shrubsolii*, Cirratulidae, Capitellidae and others tolerant to excess of organic matter, namely *Hediste diversicolor*, *Corophium* spp. and *Cyathura carinata* (Pearson & Rosenberg, 1978; Hily et al., 1986; Grall & Glémarec, 1997; Borja et al., 2000). Even without the occurrence of human induced disturbances these tolerant and opportunistic taxa are usually abundant in this area (Silva et al., 1999) and in many other intertidal areas of the estuary (Calvário, 1982; Rodrigues et al., this volume). Most likely natural instability of estuaries, due to the transition from marine to freshwater environment, as well as being an interface between aquatic and terrestrial habitats causes the fluctuations in this intertidal area.

CCA showed the existence of distinct assemblages associated to winter/spring and summer/autumn periods as a result of the increase of daylight hours and air temperature, respectively. These factors influencing the structure and dynamics of this community may be related to recruitment and mortality particularly of the most relevant taxa. In temperate latitudes, most coastal soft-bottom benthic communities exhibit variability in intrannual population density due to seasonal patterns of reproduction (López-Jamar et al., 1986; Desmond et al., 2002; Ysebaert et al., 2003).

The association between *Paragnathia formica* and Dolichopodidae and winter/spring aggregation was essentially a result of high abundances of those taxa between the months of January and June. Furthermore, for this isopod there were clear indications that in late spring post-feeding stages of larvae (praniza) occurred here, which like the adults live burrowed in the sediment (Upton, 1987). For the Dolichopodidae, all individuals were larval forms, and although present throughout the year seemed to register two different recruitment peaks, probably due to different species.

*Corbula gibba* and *Cossura* sp. were only present in summer/autumn of warmer years revealing the existence of certain thermal constraint for their settlement in the area. In the case of *C. gibba* this might be related to the fact that reproduction and settlement is thought to occur in that period (Jensen, 1990). *Scrobicularia plana* is a very common species in the Tagus estuary. Recruitment peak of this species took place in late summer/early autumn as also noted by Guerreiro (1998) in a previous study of this species in the Tagus estuary. *Streblospio shrubsolii* recruitment seemed to occur in early autumn as recorded for the western Mediterranean by Lardicci et al. (1997). However, this spionid might have constant recruitment throughout the year as detected in Alfacs Bay by Sardá & Martin (1993), a fact that should not be excluded in the Tagus estuary.

Oligochaeta, the most abundant taxon, tends to be related to winter/spring aggregation mainly because of the high number of individuals observed in late winter and early spring. This also appeared to be a recruitment period, because the highest abundance and the lowest mean individual biomass were registered in this season. *Hydrobia ulvae* associated to summer/autumn aggregation, chiefly because of the high abundances observed in autumn, although a recruitment peak could also be observed in the spring. Planas & Mora (1987) also observed high abundances in those periods at sites with considerable organic content. Lillebø et al. (1999) observed high percentage of individuals carrying egg masses in the spring and summer, and

September was one of the settlement periods detected.

Rainfall also seemed to be an important environmental factor affecting the structure and dynamics of this community. It was clear that some taxonomic entities, more than being associated to any seasonal aggregations observed in the CCA, were related to the rainfall gradient. This was the case of Amphipoda, *Polydora* sp., *Nephtys* sp. and *Cerastoderma glaucum* that even without revealing high abundances throughout the year were relatively constant showing significant decreases after heavy rainfalls. However, Cirratulidae abundance benefit from elevated values of this parameter showing high number of individuals towards the end of winter, especially in those years of intense precipitation. As in other studies (Desmond et al., 2002; Salen-Picard & Arlhac, 2002) freshwater inputs revealed to be important factors in structuring the macrobenthic communities, especially when lagged effects were considered.

Nevertheless, besides the direct impact of rainfall in the organisms' metabolism there should be also an indirect effect on the benthic community structure by promoting changes in sediments. In fact, after intense precipitation the fraction of coarser grains increased and therefore the fraction of smaller particles and TOM diminished. These seemed to be a consequence of coarse terrestrial sediments being transported to this intertidal area and/or of muddy and organic particles being washed away to adjacent subtidal zones. In years of lesser precipitation there was only a slight increase of the fine sand fraction in winter and spring.

Several species of the Capitellidae family are typical of muddy areas with high organic content, and usually are dominant taxa in polluted environments (Pearson & Rosenberg, 1978; Hily et al., 1986; Grall & Glémarec, 1997). Therefore, the appearance of this taxon in years of lesser rainfall was probably related to the increase of TOM and mud fraction in those situations.

Several studies have considered sediment variations as an important factor in the distribution of benthic assemblages in intertidal soft-sediments (Junoy & Viétiez, 1990; Ysebaert & Herman, 2002; Bazaïri et al., 2003; Ysebaert et al., 2003). However, in our study sediment variations were small and the majority of taxa seem to have a preference for sediments common to the seasons in which they were most abundant. For this reason it was impossible to isolate the cause for that preference and an association between those factors seems to be the probable explanation for the observed patterns. The only exceptions were *Cerastoderma glaucum*, Gammaridea and *Cyathura carinata* that seemed to have their sediment preference less influenced by temporal variations. In the latter species abundance was favoured by the increase of coarse sediments while Gammaridea preferred fine grain sizes avoiding even sediments with small fraction of fine sand.

## Conclusion

This estuarine intertidal community revealed a high degree of natural instability through major structural temporal variations and the presence of opportunistic and tolerant taxa. Nevertheless, it showed a tendency for the occurrence of annual cycles, with typical assemblages of winter/spring and summer/autumn periods that were closely related to temperature and daylight hours. On the other hand, the main source of non-cyclic variations was rainfall, either by directly influencing the biological community or by inducing changes in sediments. In fact, sediment characteristics appear to play an important role in changing the community throughout the year, since in this predominantly muddy area some species abundance seemed favoured by coarser particles and many by fine sediments. This study proved that long-term data series are an essential tool to assess the structure and dynamics of benthic communities allowing the detection of inter- and intrannual fluctuations and their relationship with environmental factors.

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