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Scientific Editors

Aquatic Ecology of the Mondego River Basin Global Importance of Local Experience



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CHARACTERISATION OF THE MACROINVERTEBRATE BENTHIC COMMUNITIES IN THE MONDEGO ESTUARY

Abstract

The Mondego estuary is under severe environmental stress, but despite the increasing pressure, until 1985 there was no reference data on the Mondego estuary on which further studies on the impact of human activities over the structure and functioning of the ecosystem could be based. From 1985 to 1990 a reference study on the benthic communities was carried out, regarding both the intertidal and subtidal zones, aiming to characterise the macrobenthic communities structure in relation to physicochemical environmental factors and identify the most important species, which could play a key role in the ecosystem functioning. The intertidal communities were surveyed in December 1986 and July 1987, while the subtidal communities were seasonally studied from December 1989 to September 1990.

With regard to the intertidal area, the community's structure revealed differences between the two arms of the estuary for populations densities and diversity, which was consistent with results from the analysis of physicochemical data. The south arm appears to be less affected by human activities, presenting more favourable conditions for the development of abundant populations of typical estuarine species. Salinity was the most important factor controlling the distribution of hard substrates organisms, while particles size and organic matter contents of sediments, salinity, and dissolved oxygen are the most important factors for soft substrates organisms. *Spartina maritima* and *Zostera noltii* marshes, mainly located in the middle section of the south arm, exhibited the richest macrofaunal composition with regard to abundance and diversity.

The subtidal macrofauna in the Mondego estuary appears to be clearly impoverished. In the south arm, the macrobenthic community consists mainly of infaunal species and appears to be more stable and structured, presenting higher macrofauna abundance. On the contrary, sparse mobile epibenthic species populations mainly characterise the north arm community, exhibiting a lower biodiversity and an impoverished macrofauna, compared to the south arm. The subtidal communities appear to be physically controlled, with emphasis on the type of sediment, salinity, and currents, and biologically, due to their distinct physicochemical characteristics. The two

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arms of the estuary can be considered different sub-systems. Due to harbour facilities dredging takes place regularly along the north arm, and time intervals between dredging operations appear to be inadequate to allow macrofauna recovery.

As a whole, the south arm community appears to be structurally more stable, but due to the feeble water circulation may be more exposed to environmental changes. Monitoring of the Mondego estuary biological communities was considered clearly necessary to assess temporal trends and to establish if the ongoing environmental changes are reversible.

Results from these studies were published in two previous papers (Marques et al. 1993 a, 1993 b).

Introduction

The Mondego, due to a set factors previously described, may be considered under a severe increase of environmental stress. But despite the increasing pressure, until 1985 there was no reference data on the Mondego estuary on which further studies on the impact of human activities over the structure and functioning of the ecosystem could be based.

From 1985 to 1990 reference studies on the benthic communities were carried out, regarding the intertidal area, in December 1986 and July 1987, and the subtidal zone, from December 1989 to September 1990. The aim of these studies was:

- a) To characterise the macrobenthic communities structure in relation to physicochemical environmental factors;
- b) To identify the most important species, which could play a key role in the ecosystem functioning;
- c) To provide reference information to assess afterwards the impact of human activities on the communities structure and functioning.

The results of these studies were previously published in two independent papers, regarding respectively the intertidal (Marques et al. 1993 a) and the subtidal communities (Marques et al. 1993 b).

Material and methods

Intertidal sampling programme

In December 1986 and July 1987 quantitative samples were carried out at 19 sampling stations (figure 1) to characterise the structure of the intertidal communities in winter and summer situations. Each time, sampling took place during five consecutive days, always in the morning and during a 3 hours period in low water. This allowed samples to be carried out in approximately uniform conditions.

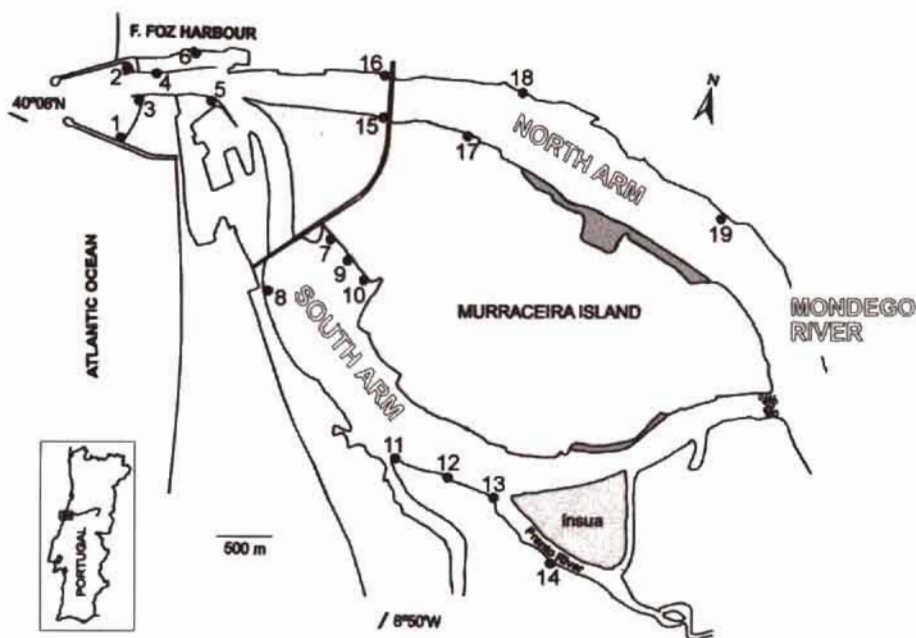


Figure 1. The Mondego estuary. Localization of the intertidal sampling stations.

Both hard and soft substrates were frequently found at the same sampling station, and depending on slope the area of the intertidal zone was quite variable. On soft substrates, *Spartina maritima* and *Zostera noltii* marshes could be present or not.

In order to establish a uniform sampling criterion, at each station the intertidal zone was stratified, taking into consideration different eulittoral levels, and the type of macroalgae or macrophytes covered areas. This criterion allowed considering three approximately equidistant levels between high water and low water levels. On hard substrates, depending on the sampling site, the two upper levels corresponded approximately to *Enteromorpha* spp. and *Fucus* spp. algal belts, whereas the lower level in stations located near the mouth of the estuary presented also a significant population of *Mytilus galloprovincialis* (mussels). On soft substrates with vegetal covered areas the two upper levels frequently corresponded respectively to the marsh-grass *Spartina maritima* belt and to the eelgrass *Zostera noltii* meadows, while the lower level corresponded mainly to sandy or muddy substrates without macrophytes.

Two different sampling techniques were used as a function of the type of substrate. On hard substrates three replicates of 625 cm² were randomly sampled in each level by scratching out organisms with a chisel. On soft substrates we adapted the technique described by Dexter (1979, 1983) for sandy beaches, and eight replicates were randomly sampled in each level by using a manual corer (each core corresponding to 141 cm² and approximately 3 litres of sediment).

All biological samples were sieved in situ using a 1 mm mesh size sieve, and then fixed in 4% neutralised formaldehyde. This mesh size was considered suitable for this study, regarding the types of sediment we expected to find along the estuary.

Each time and for each station, several physicochemical factors were determined, respectively salinity, temperature, pH, dissolved oxygen (measured *in situ*), nitrites, nitrates, and phosphates (analysed in the laboratory). The analysis of water samples followed the methods described in Strickland and Parsons (1968). Sediment samples were also collected and subsequently analysed for particles size, organic matter and carbonate contents.

For each sediment sample, particles were ranked into eight size categories (table I):

TABLE I Particle – size categories used to classify sediment types in the present study

Size class	Diameter (mm)	Sediment classification
1	> 2	Gravel
2	1 to 2	Coarse sand
3	0.5 to 1	Medium sand
4	0.250 to 0.5	
5	0.125 to 0.250	Fine sand
6	0.063 to 0.125	Silt
7	0.002 to 0.063	
8	< 0.002	Clay

The organic matter content in the sediments was calculated after destruction in a muffle furnace (8 hours at 500 °C).

In the laboratory the organisms were separated, preserved in 70% ethanol or in 4% neutralised formaldehyde, according to the presence or absence of calcareous parts, and identified and counted.

Subtidal sampling programme

In December 1989 and March, June, and September 1990 quantitative samples were taken at 13 sampling stations (A to M) (figure 2), to allow a seasonal characterisation of the subtidal macrobenthic communities. Each time samples were taken over a two days period, during high water of spring tides. At each station six replicates were sampled randomly, using a small Van Veen grab, capable of collecting up to 5 L of sediment, operated from a boat. The number of replicates per sample was settled by using the rank-frequency diagram method (Frontier 1983) for stabilising variability. Although the sampled area was approximately constant (496 cm²), the amount of sediment collected was not, depending on bottom compactness. A certain degree of bias was therefore introduced into the sampling strategy.

The biological samples, both in the field and the laboratory, were treated the same way as indicated above, and physicochemical factors were also determined each time and for each station, following the same methodology.

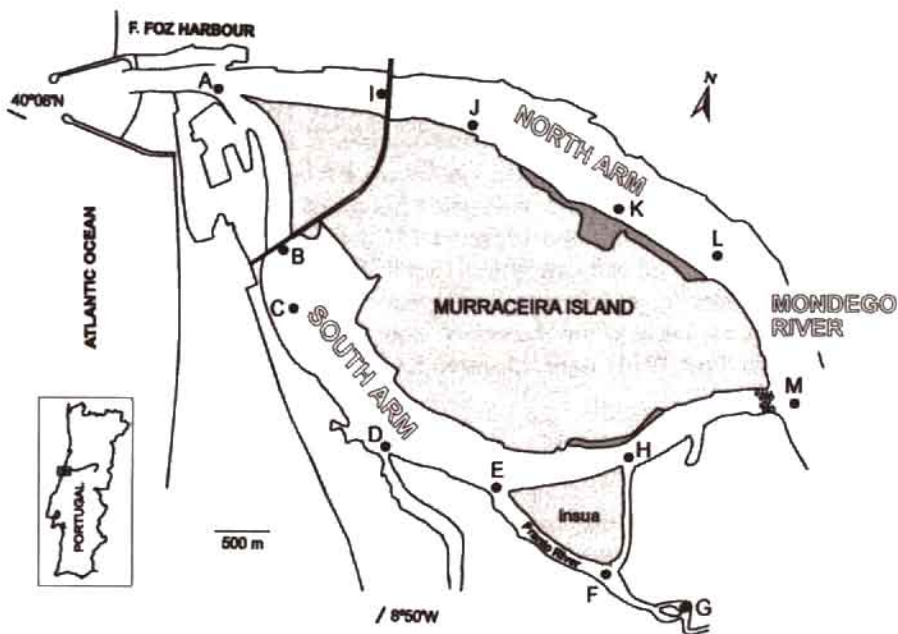


Figure 2. The Mondego estuary; Location of the subtidal sampling stations.

Data analysis

Intertidal communities

Data on both hard and soft substrates and on winter and summer situations were assumed to correspond to different ecological conditions, and therefore were analysed separately.

With regard to biological data, species X stations matrices were analysed, considering data on each sampling site as a whole. The goal of the analysis was to study the horizontal distributional ecology of the species along the estuary and to reveal differences between the two estuarine arms with regard to community's structure. A first analysis was achieved taking into consideration all the species, and a second one overlooking the species found only once (Legendre and Legendre 1984).

On hard substrates, since it was not possible to collect water in each sampling level, water samples for determination of physicochemical factors were always taken from the water column (one sample per station). On soft substrates, because of water retention in pools during low tide, it was always possible to get water and sediment samples in each sampling level. Consequently, in the first case, we analysed factors X stations matrices, while in the second case the analysis was based upon factors X samples matrices.

Data underwent principal component analysis (PCA), using the sampling stations or the samples as operational units in the space of biological or physicochemical

variables. Sediment particles size fractions (expressed in %) and dissolved oxygen (% of saturation) were both submitted to angular transformation. Eigenvalues and eigenvectors of correlation matrices between variables were computed after centering and reduction to unit variance (Legendre and Legendre 1984). Correlation matrices were computed using the Pearson's correlation index. In addition, biological data was submitted to cluster analysis, using the Chi-Square distance coefficient (Lebart et al. 1984) (Q mode analysis) and the unweighted pair group mean of analysis (UPGMA) clustering method (Legendre and Legendre 1984). Data treatment was effectuated with the NTSYS-PC 1.60 software system (Rohlf 1990).

Finally, in order to get information on species richness and evenness in different estuarine areas, the values of the Shannon-Wiener heterogeneity index (Legendre and Legendre 1984, Peet 1974) were calculated for each sampling station in winter and summer situations.

Subtidal community

It was also assumed that data for each season should correspond to distinct ecological conditions, and were therefore analysed separately.

With regard to the biological data, seasonal matrices of taxa X stations were analysed, considering data from each station (a series of six replicates) as a whole. In this case, biological data underwent Correspondence Analysis (CA). The Chi-Square Distance coefficient (Lebart et al. 1984) was used to calculate the association matrices for the column (stations) variables. The eigenvalues and eigenvectors for the columns were then computed, followed by the computation of the row (taxa) vectors by projection.

Like before, the Shannon-Wiener heterogeneity index was used to assess biological diversity. Moreover, and as described above, physicochemical data on water and sediments underwent principal component analysis (PCA). The same software was used to perform multivariate data analysis.

Results

A – Intertidal zone

We identified 90 macrofaunal species from samples carried out in winter and summer situations (table II). A first look to data confirmed our primary assumptions for data analysis, showing that 34 taxa (38%) were found only in the winter, while 19 (21%) were found exclusively in the summer, reflecting a seasonal variation in the species composition. Moreover, 36 taxa (40%) were found exclusively on hard substrates, while 24 (27%) occurred only in soft substrates, exhibiting a different species composition as a function of the type of substrate.

Table II – List of the taxa identified in winter and summer situations, and on both hard and soft substrates. For each taxa, the average density (number of individuals.m⁻²) is given.

Taxa	Winter		Summer	
	Hard substrates	Soft substrates	Hard substrates	Soft substrates
TURBELLARIA				
<i>Convoluta</i> sp		0.7	0.4	0.6
NEMERTINI				
<i>Lineus</i> sp	4.2			
<i>Oerstedia</i> sp		2.8	0.4	
<i>Tetrastemma</i> sp		3.5	2	0.6
<i>Palaenemertea</i>				0.6
OLIGOCHAETA		0.7		
POLYCHAETA				
<i>Eteone picta</i>		6.3		
<i>Glycera convoluta</i>		4.2		
<i>Lepidanotus clava</i>			0.4	
<i>Nephtys cirrosa</i>		0.7		
<i>Hediste diversicolor</i>	10.8	661	13.2	890
<i>Neanthes irrorata</i>		2.8	0.4	
<i>Phyllodoce</i> sp	1.4			
<i>Polydora</i> sp			2.9	
<i>Amage adspersa</i>		34.6	2	128
<i>Amphicteis gunneri</i>		17		
<i>Capitella capitata</i>		4.8	0.8	30.3
<i>Cirratulus cirratus</i>	0.5			
<i>Heteromastus filiformis</i>		72.9		
<i>Lagis koreni</i>		2.8		
<i>Mercierella enigmatica</i>			4.4	
<i>Pomatocerus triqueter</i>	9.4	0.7		
<i>Pseudomalacocerus cantabra</i>		8.4		
<i>Pygospio elegans</i>		0.7		
<i>Sabellaria alveolata</i>	2.4			
<i>Spio filicornis</i>		3.5		3.7
<i>Streblospio dekhuyzeni</i>		24.5	2.4	23.9
Sabellidae			0.4	
POLYPLACOPHORA	0.5			
<i>Lepidochitona cinereus</i>	0.5			
GASTROPODA				
<i>Bittium reticulatum</i>				0.6
<i>Cerithium vulgatum</i>				0.6
<i>Gibbula umbilicalis</i>				0.6
<i>Haminea hydatis</i>	30	200		0.6
<i>Hydrobia ulvae</i>	52.2	1980	181	859
<i>Littorina littorea</i>	0.5	15.4		10
<i>Littorina nertoides</i>	2.8			
<i>Littorina saxatilis</i>				0.6
<i>Murex trunculus</i>	0.9			
<i>Nassarius reticulatus</i>				5

<i>Nucella lapillus</i>			0.4	
<i>Odostomia unidentata</i>	0.9			
<i>Patella aspera</i>	0.5			
<i>Patella lusitanica</i>	1.4			
<i>Rissoa membranacea</i>	0.5			
<i>Rissoa parva</i>	0.9			1.3
<i>Cerastoderma edule</i>		66.6	2.8	36
<i>Montacuta ferruginosa</i>	32.9	0.7		
<i>Mytilus galloprovincialis</i>	5790	4.9	1390	
<i>Scrobicularia plana</i>	1.9	283	4.8	103
ANOSTRACA				
<i>Artemia salina</i>		0.7		
CIRRIPEDIA				
<i>Ballanus perforatus</i>	11.8			
<i>Chthamalus stellatus</i>	764		1470	
ISOPODA				
<i>Cyathura carinata</i>	0.9	322	11.2	128
<i>Dynamene bidentata</i>	0.5		2.4	
<i>Gnathia vorax</i>	0.5			
<i>Eurydice pulchra</i>				0.6
<i>Eurydice spinigera</i>				0.6
<i>Idotea chelipes</i>	3.8	0.7		
<i>Idotea granulosa</i>	3.3		1.6	0.6
<i>Idotea pelagica</i>	64.9	0.7	37.6	
<i>Jaera forsmanni</i>	9.9		63.6	
<i>Sphaeroma hookeri</i>	24.4	0.7	10.4	1.8
AMPHIPODA				
<i>Amphithoe valida</i>	1.4			
<i>Amphithoe ramondi</i>	3.3			
<i>Amphithoe rubricata</i>	3.4			
<i>Bathyporeia sarsi</i>		1.4		1.3
<i>Corophium insidiosum</i>	33.1		2.8	
<i>Corophium multisetosum</i>		3.4		5.7
<i>Echinogammarus marinus</i>	196	12.6	951	3.1
<i>Echinogammarus stoerensis</i>			68.4	
<i>Gammarus chevreuxi</i>	1.4	1.4		
<i>Gammarus locusta</i>	2.6		6.4	
<i>Haustorius arenarius</i>		0.7		
<i>Hyale crassipes</i>	3.3			
<i>Hyale perieri</i>	2.8			
<i>Hyale stebbingi</i>	184		117	
<i>Jassa marmorata</i>			0.4	
<i>Leptocheirus pilosus</i>	44.7		88.4	
<i>Melita palmata</i>	88.9	19.1	66.8	11.9
<i>Talorchestia sp</i>			8.4	
MYSIDACEA				
<i>Paramysis helleri</i>				1.9
DECAPODA				

<i>Carcinus maenas</i>	13.2	13.3	80	15
<i>Crangon crangon</i>		2	7.6	11.3
<i>Pachygrapsus marmoratus</i>	6.6		1.2	
<i>Palaemonetes varians</i>	0.9	0.7	2.8	1.8
INSECTA				
<i>Diptera larvae</i>	4.2	9.1	86.4	3.7
<i>Lepidoptera larvae</i>				1.6
PISCES				
<i>Blennius sp 1</i>	0.5			
<i>Blennius sp 2</i>	0.5			
<i>Pomatoschistus sp</i>	0.5	0.7		1.9

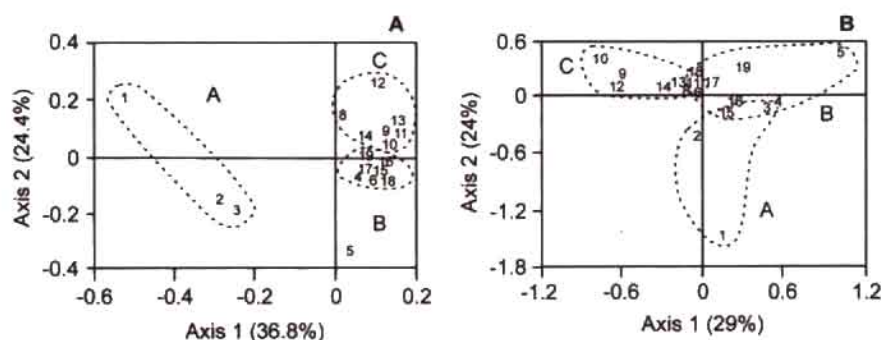


Figure 3. Analysis of hard substrates community structure from PCA of species X stations matrices overlooking species found only once. A - winter situation: Projection of stations against the first two axis, $r = 0.88934$. B - summer situation: Projection of stations against the first two axis, $r = 0.85206$. The percentage of variability explained by the principal axis is given. Groups of stations pointed out are discussed in the text.

Hard substrates community

Winter situation

PCA of species X stations data (figure 3-A) shows a clear separation between stations located near the mouth (group A) and stations located inside the estuary (groups B and C) along the first axis. A separation between stations from the south arm (group C) and stations from the north arm, together with a few stations located near the mouth (group B), is evident along the second axis. Near the mouth, sessile marine species like *Chthamalus stellatus* and *Mytilus galloprovincialis* are very abundant, and significant populations of *Montacuta ferruginosa*, *Idotea pelagica*, and *Hyale stebbingi*, all marine species, together with less important populations of *Littorina neritoides*, *Balanus perforatus*, *Idotea chelipes*, *I. granulosa*, *Jaera forsmanni*, *Amphithoe ramondi*, *A. rubricata*, and *Pachygrapsus marmoratus* are also found. In the inner areas of the estuary, *Mytilus galloprovincialis* and *Chthamalus stellatus* populations become much less

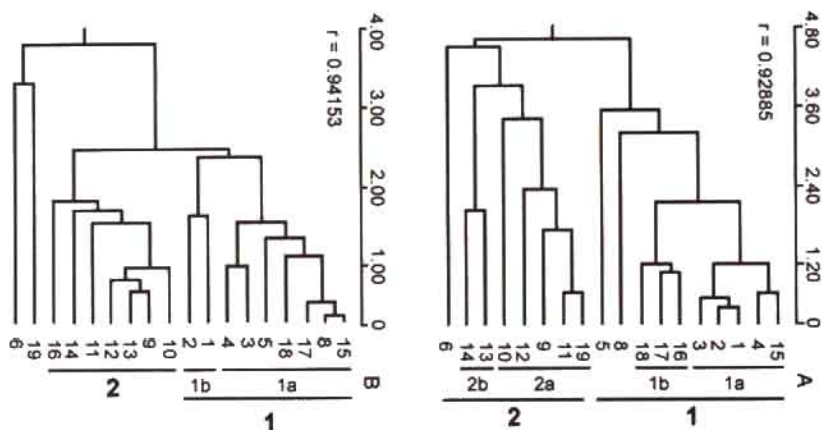


Figure 4. Hard substrates community structure: Cluster analysis of species X stations matrices overlooking species found only once. Data analysed using the Chi-Square distance coefficient (Q mode analysis) and the UPGMA clustering method. A - winter situation; B - summer situation. Values of cophenetic correlation coefficients are indicated.

abundant, and the presence of other marine species is inconspicuous. Station 1, which exhibits the strongest marine influence, (typical estuarine species are represented only by sparse populations of *Echinogammarus marinus* and *Carcinus maenas*), presents dense populations of *Mytilus galloprovincialis*, *Chthamalus stellatus*, and *Hyale stebbingi*. The separation of stations from both estuarine arms along the second axis is mainly due to the preferential occurrence of *Leptocheirus pilosus* and *Melita palmata*, followed by *Sabellaria alveolata*, in stations from the north arm, and of *Echinogammarus marinus*, *Sphaeroma hookeri*, and *Hediste diversicolor* (frequently found in sediment deposits over rock), followed by *Idotea chelipes*, *I. pelagica*, *Amphithoe ramondi*, *A. rubricata*, and *Carcinus maenas*, in stations from the south arm.

Station 5, located near the connection of the two arms, appears to be peculiar, exhibiting significant densities of *Melita palmata* (704 individuals/m²) and *Leptocheirus pilosus* (437 individuals/m²) populations. Typical estuarine species like *Hydrobia ulvae*, *Echinogammarus marinus*, *Sphaeroma hookeri*, and *Carcinus maenas* show higher abundances in the south arm, while *Mytilus galloprovincialis* and *Chthamalus stellatus* populations are significant in the north arm (although less abundant than in stations located near the mouth) and very scarce in the south arm.

Cluster analysis of species X stations data (figure 4-A) allows to recognise a structural discontinuity in the communities from both arms and near the mouth, corroborating therefore the results from ordination. Group 1 consists of stations located near the mouth (basically sub-group 1a) and inside the north arm (sub-group 1b), together with stations 8 and 5, located in the downstream section of the south arm. Group 2 consists primarily of stations from inner areas of the south arm, despite station 19 (upstream section of the north arm) being included in sub-group 2a, and station 6 (near the mouth) is still comprised in the group.

Summer situation

PCA of species X stations data (figure 3-B), show an opposition between stations located in the north arm and near the mouth (group B), and stations located in the inner areas of the south arm (group A) along the first axis. Stations from group B are characterised by the presence of several marine species, with a clear dominance of *Mytilus galloprovincialis* and *Chthamalus stellatus*, followed by significant populations of *Echinogammarus stoerensis*, *Leptocheirus pilosus*, and *Melita palmata*. Stations located in the south arm present *Hydrobia ulvae* and *Echinogammarus marinus* dense populations, exhibiting also a typical estuarine fauna with regard to other species.

The opposition between stations 1 and 2 (more exposed to marine influence), and the other stations is evident along the second axis. These two stations are characterised by a very strong abundance of *Mytilus galloprovincialis* and by the occurrence of typical marine species like *Hyale stebbingi*, *Dynamene bidentata*, *Idotea pelagica*, and *Jaera forsmanni*. Station 5, like in the winter situation, is found to be peculiar, presenting relatively abundant populations of *Leptocheirus pilosus* (901 individuals /m²) and *Melita palmata* (267 individuals /m²). It must be emphasised that *Echinogammarus marinus* shows a quite abundant population all over the estuary in the summer situation.

Cluster analysis of species X stations data (figure 4-B) shows again a discontinuity within the hard substrates community structure in both arms and near the mouth. Group 1 consists basically of stations located in the north arm and near the mouth despite station 8 (downstream area of the south arm) being comprised in sub-group 1a. Stations 1 and 2 (sub-group 1b), located very close to the mouth appear to be distinct from stations inside the north arm (sub-group 1a). Group 2 consists of all stations from the inner areas of the south arm and station 16 (north arm). Stations 19 and 6 appear as outsiders.

Diversity

In the winter situation, the Shannon-Wiener index values calculated for each station (table III) demonstrate that the distance relatively to the mouth is not related with a diversity gradient. However, stations from the south arm show higher diversity values than stations located in the north arm and near the mouth, which may be due to the combined effects of tides and stronger freshwater discharge along the north arm, creating a significant daily environmental stress for environmental organisms.

Table III Values of the Shannon-Wiener index calculated for each station in winter and summer situations and for hard and soft substrates communities

		SAMPLING STATIONS																		
		Hard substrates																		
		Near the mouth						South arm						North arm						
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Winter		0.98	0.61	0.81	1.24	2.54	1.23	-	0.99	1.07	1.21	1.26	2.31	1.16	1.94	1.11	2.27	0.35	0.62	1.2
Summer		1.55	2.09	2.22	2.12	1.58	2.2	-	0.41	0.78	1.21	1.4	0.73	1.12	1.07	0.78	0.99	0.97	1.5	3.0

Soft substrates

	Near the mouth						South arm								North arm				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Winter	1.0	1.39	-	-	-	1.52	2.32	1.5	2.69	2.19	1.96	1.43	1.91	1.71	2.13	3.08	1.6	2.01	1.52
Summer	0.92	0.76	-	-	-	-	2.65	1.83	2.3	1.6	2.08	1.36	1.19	1.62	1.51	1.45	0.66	1.38	0.54

On the other hand, in the summer situation, the Shannon-Wiener index values calculated for each station (table III) revealed several differences as compared to the winter situation. In the summer, the highest values for diversity are found near the mouth of the estuary, while the lowest values are found inside the south arm.

With regard to hard substrates community, a decrease in diversity was observed in the south arm from winter to summer, while an increase occurred in the north arm and near the mouth. The decrease in diversity observed in the south arm may be explained by the change in biological activity of *Echinogammarus marinus*, which becomes extremely abundant in the summer situation (average about 3000 individuals /m² in the south arm on the *Fucus* sp. covered areas), affecting species evenness.

Soft substrates community

Winter situation

PCA of species X stations data (figure 5-A) shows the opposition between stations 7, 9, 10, and 11 (group A), located in the south arm, corresponding to *Spartina maritima* and *Zostera noltii* marshes, and stations without vegetal covered areas (groups B and C) along the first axis. These stations differ from the others by the fact that several species (e. g. *Amage adspersa*, *Heteromastus filiformis*, *Hediste diversicolor*, *Hydrobia ulvae*, *Cerastoderma edule*, *Scrobicularia plana*, and *Cyathura carinata*) present considerably higher population abundances. Along the second axis we can distinguish

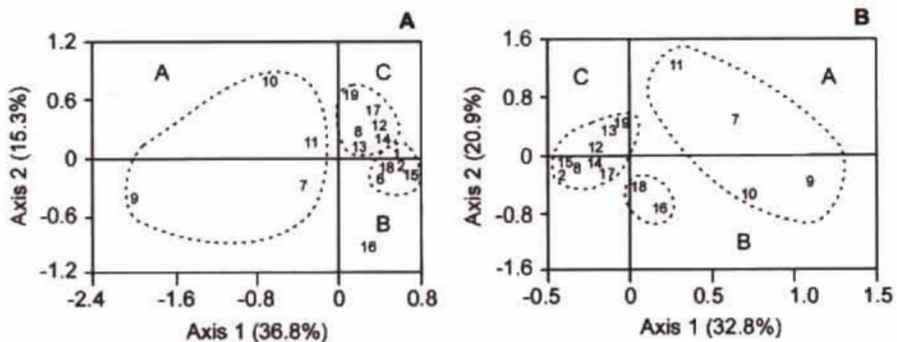


Figure 5. Analysis of soft substrates community structure from PCA of species X stations matrices overlooking species found only once. A - winter situation: Projection of stations against the first two axis, $r = 0.80878$. B - summer situation: Projection of stations against the first two axis, $r = 0.87681$. The percentage of variability explained by the principal axis is given. Groups of stations pointed out are discussed in the text.

between stations located in the south arm (8, 12, 13, and 14), followed by stations 17 and 19 (north arm) (group C), and stations located in the north arm and near the mouth of the estuary (group B). Stations from the south arm, even those located in areas without vegetal cover, present higher population abundances than stations from the north arm, namely with regard to common species like *Hediste diversicolor*, *Hydrobia ulvae*, *Scrobicularia plana*, and *Cyathura carinata*. Station 16, located in the north arm, is clearly separated along the second axis, which is explained by the sporadic occurrence of several rare species in the estuary like *Eteone picta*, *Glycera convoluta*, and *Spio filicornis*.

Cluster analysis of species X stations data (figure 6-A) does not reveal a clear discontinuity within the soft substrates community. Actually, a single main group of stations is recognisable (group 1), consisting of stations from both estuarine arms, while stations 1, 2, and 6, located near the mouth appear as outsiders. Nevertheless, stations 9, 11, 10, and 7, located in *Spartina maritima* and *Zostera noltii* marshes, are clearly assembled (sub-group 1b), which agrees with results from ordination.

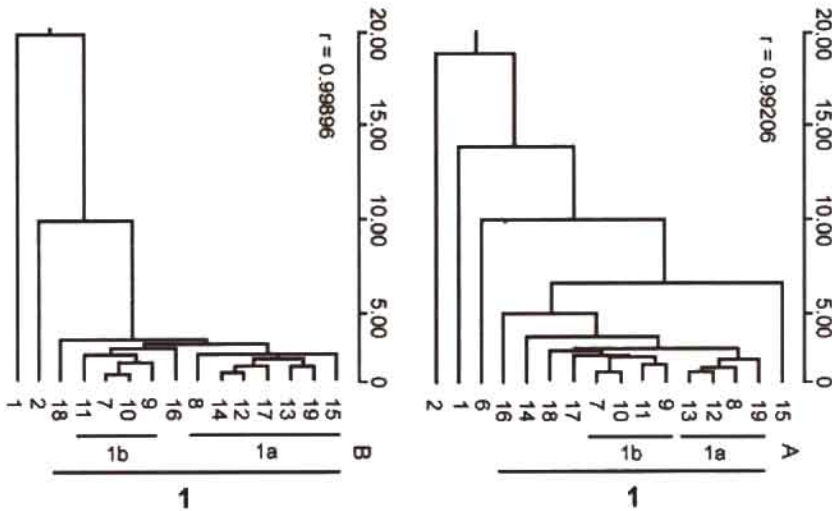


Figure 6. Soft substrates community structure: Cluster analysis of species X stations matrices overlooking species found only once. Data analysed using the Chi-Square distance coefficient (Q mode analysis) and the UPGMA clustering method. A - winter situation; B - summer situation. Values of cophenetic correlation coefficients are indicated.

Summer situation

PCA of species X stations data (figure 5-B) shows once more the opposition between stations corresponding to *Spartina maritima* and *Zostera noltii* marshes (group A) and stations without vegetal covered areas (groups B and C) along the first axis. Like in the winter situation, the most important species contributing to the observed variability are *Amage adspersa*, *Heteromastus filiformis*, *Hediste diversicolor*, *Hydrobia ulvae*, *Cerastoderma edule*, *Scrobicularia plana* and *Cyathura carinata* (positive side of

factor 1), which populations are much more abundant in stations from group A as compared to other areas. Contrarily to the winter situation, differences between stations located in the south arm and stations located in the north arm are not evident. This may be due to the increase of marine influence inside the estuary in the summer, determining the occurrence of more uniform conditions.

Cluster analysis of species X stations data (figure 6-B), like in the winter situation, does not bare a discontinuity within the soft substrates community, and again a single group of stations is recognisable (group 1), consisting of stations from both estuarine arms, Stations 1 and 2 located very close to the mouth appear as outsiders. Again like in the winter situation, stations 9, 10, 7, and 11, located in *Spartina maritima* and *Zostera noltii* marshes, are assembled (sub-group 1b), corroborating results from ordination.

Diversity

The Shannon-Wiener index values calculated for each station in both winter and summer situations (table III) are consistently higher in stations located in *Spartina maritima* and *Zostera noltii* marshes, which emphasises their favourable conditions for the development of abundant populations and higher biodiversity. However, differences between other estuarine areas and seasonal variations in diversity are not outstanding.

Physical and chemical parameters

With regard to the winter situation, PCA of water physicochemical factors X stations matrices (figure 7-A) reveals a clear separation between stations from the north and south arms (groups A and B respectively) along the first axis, and a gradient from the mouth (group C) to inner areas of the estuary along the second axis. The variability along the first axis is mainly explained by the distribution pattern of dissolved oxygen and nitrates concentration values (negative side of factor 1), and of salinity and temperature values (positive side of factor 1). Along the second axis, variability is mainly explained by the distribution of salinity, temperature and nitrites values (negative side of factor 2), and of pH (positive side of factor 2). Actually, it is very clear the opposition along the first axis between stations from the north arm, presenting lower salinities (20.8 ± 6.8 ‰) (average \pm standard deviation), more stable temperatures (12 ± 0.5 °C), higher concentrations of dissolved oxygen (76.5 ± 11.6 % of saturation) and nitrates (0.32 ± 0.18 mg.l⁻¹) during low tide, and stations from the south arm, presenting higher salinities (22.9 ± 6.7 ‰), more variable temperatures (12.9 ± 2.4 °C), lower dissolved oxygen (70.6 ± 7.1 %) and nitrates concentrations (0.16 ± 0.09 mg.l⁻¹).

These results can be explained taking into consideration the hydraulic circulation in the estuary. In the north arm, the water circulation depends on tides and on the freshwater discharge, determining a faster renewal of the water mass, and consequently higher values of dissolved oxygen. Moreover, since samples were taken during low tide, the river discharge (transporting nutrients from agricultural areas) determined the occurrence of lower salinities and higher nitrate concentrations in the north arm and areas near the mouth. The smaller depth may explain larger

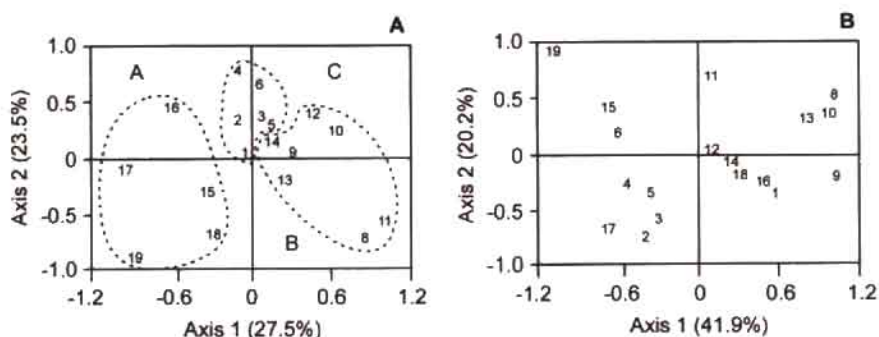


Figure 7. Analysis of physicochemical factors of the water from PCA of factors X stations matrices. A - winter situation: Projection of stations against the first two axis, $r = 0.94057$. B - summer situation: Projection of stations against the first two axis, $r = 0.93314$. The percentage of variability explained by the principal axis is given. Groups of stations pointed out are discussed in the text.

temperature ranges found in the south arm. Finally, the lower concentration of nitrates in the south arm may be a function of the smaller freshwater discharge.

Due to marine influence, temperature and pH values (7.4 ± 0.4) seem to be more uniform near the mouth of the estuary, and nitrite concentration to be low ($0.006 \pm 0.002 \text{ mg.l}^{-1}$) (probably as a function of stronger oxygenation of the water column).

In the summer situation, the analysis of physicochemical factors of the water does not show conspicuous differences between stations located in both estuarine arms and near the mouth (figure 7-B). Stations 2, 3, 4, 5, 6, 15, 17, and 19 (in the north arm and near the mouth) are opposed to stations 1, 8, 9, 10, 11, 12, 13, 14, 16, and 18 (in the north arm, south arm, and near the mouth) along the first axis. The variability along the first axis is mainly explained by lower salinities ($25 \pm 2.1 \text{ ‰}$), higher values of dissolved oxygen ($92.8 \pm 6.1 \text{ ‰}$), pH (7.8 ± 0.3) and nitrites ($0.01 \pm 0.002 \text{ mg.liter}^{-1}$) found in stations from the negative side of factor 1, and by higher salinities ($27.3 \pm 2.4 \text{ ‰}$) found in stations from the positive side of factor 1.

Along the second axis, stations from the inner areas of both arms (8, 10, 11, 12, 13, 15, and 19) are partially separated from stations located in the downstream section of the north arm and near the mouth. Temperature is the factor that contributed the most for this partial separation. Actually, the smaller depth as compared to areas near the mouth may explain higher temperatures of the water found in estuarine inner areas.

PCA of water and sediments physicochemical factors X samples matrices shows similar results with regard to winter (figure 8-A) and summer (figure 8-B) situations. In both cases, projection of samples against the first two axis of variability allows to consider three distinct equivalent groups. Groups A1 and A2 correspond mainly to samples obtained on fine or medium sand bottoms with small organic matter contents (0 to 1.5%), proceeding from the lower limits of the eulittoral zone (low water level) in the downstream sections of both arms and near the mouth (sand pole). Groups B1, B2, C1, and C2 correspond to samples from bottoms with large fractions of fine

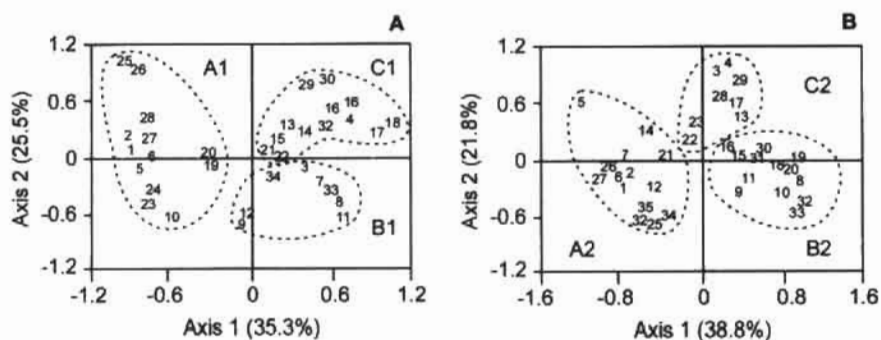


Figure 8. Analysis of physicochemical factors of water and sediments from PCA of factors X samples matrices. A - winter situation: Projection of samples against the first two axis, $r = 0.91314$; B - summer situation: Projection of samples against the first two axis, $r = 0.94261$. The percentage of variability explained by the axis is given. Groups of samples pointed out are discussed in the text.

particles (clay or silt) and higher organic matter contents (2 to 4.5%), proceeding from the inner areas of both estuarine arms. Groups B1 and B2 consist of samples from *Spartina maritima* and *Zostera noltii* covered areas in the south arm, characterised by fine sandy mud sediments with high organic matter contents (3.5 to 4.5%). Groups C1 and C2 consist essentially of samples from muddy bottoms with no vegetal cover, mainly characterised by clay and silty sediments mixed with medium to coarse sand (10 to 40%) (originated mainly by dredging activities), and significant organic matter contents (2 to 4%). Additionally, in the summer situation (figure 8-B) oxygen dissolved levels and salinities are higher in samples from group C2 as compared with samples from group B2.

B – Subtidal zone

52 samples, corresponding to 306 replicates distributed over the year, provided 7554 macrofaunal individuals and allowed the identification of 58 taxa (Table IV).

The relative frequencies of taxa and the average population densities (Table IV) show that only a few species appear consistently well represented through the year. The most frequent and abundant are *Amage adspersa*, *Scrobicularia plana*, and *Cyathura carinata* but other species are also well represented over the year: *Hediste diversicolor*, *Streblospio shrubsolei*, *Cerastoderma edule*, *Hydrobia ulvae*, *Saduniella losadai*, *Neomysis integer*, and *Carcinus maenas*.

Higher abundances of *Amage adspersa*, *Scrobicularia plana*, and *Cyathura carinata* populations (although values are expressed in number of individuals and not biomass, which may introduce a significant bias), suggest that these species play a key role in the ecosystem. However, *Scrobicularia plana* is primarily represented by juveniles (adults are typical of the intertidal zone), which is probably related to the planktonic larvae colonisation process.

Table IV List of taxa identified. The number assigned to each taxa correspond to numbers plotted in figures 9 – 12. The relative frequencies (F: number of replicates in which the taxa was found/total number of replicates) and average population density (AD: individuals.m⁻² for the total surface of all the samples) found in the Mondego estuary each season are given.

Taxa	December		March		June		September	
	F(%)	AD	F(%)	AD	F(%)	AD	F(%)	AD
1 <i>Turbellaria</i> sp	2.7	0.5	0	0	0	0	0	0
Nemertini								
2 <i>Oerstedtia</i> sp	4.1	1.3	0	0	7.7	2.1	0	0
3 <i>Tetrorstemma</i> sp	1.4	0.3	1.3	0.3	5.1	1.6	4	0.9
4 sp 1	1.4	0.3	0	0	0	0	0	0
Oligochaeta								
5 sp 1	6.8	1.2	0	0	2.6	0.5	2.7	0.8
Polychaeta								
6 <i>Amoqe adspersa</i>	24.7	22.6	32.9	88.2	42.3	565	37.3	138
7 <i>Capitella capitata</i>	1.4	0.5	2.6	0.5	11.5	4.9	6.7	1.6
8 <i>Chaetozone setosa</i>	1.4	0.3	1.3	0.3	1.3	0.5	0	0
9 <i>Chane collaris</i>	0	0	0	0	1.3	5.4	2.7	0.8
10 <i>Eteone picta</i>	2.7	0.5	0	0	0	0	1.3	0.3
11 <i>Eulalia</i> sp	1.4	0.2	0	0	0	0	0	0
12 <i>Glycera convoluta</i>	0	0	0	0	0	0	4	0.8
13 <i>Hediste diversicolor</i>	13.7	3.4	6.6	2.1	7.7	4.7	10.7	30.3
14 <i>Heteromastus filiformis</i>	1.4	0.9	5.3	1	3.8	1.6	4	0.8
15 <i>Lagus koreni</i>	0	0	0	0	0	0	1.3	0.3
16 <i>Neanthes succinea</i>	0	0	1.3	0.3	0	0	0	0
17 <i>Nephtys cirrosa</i>	2.7	1.3	0	0	1.3	0.3	5.3	1.5
18 <i>Nephtys hombergii</i>	1.4	0.3	0	0	0	0	1.3	0.3
19 <i>Nephtys longisetosa</i>	1.4	0.3	0	0	0	0	0	0
20 <i>Nephtys paradoxa</i>	2.7	1.0	0	0	1.3	0.3	0	0
21 <i>Pemmeris cultrifera</i>	0	0	0	0	0	0	1.3	0.3
22 <i>Polydora ciliata</i>	4.1	0.9	1.3	1.8	34.6	55.0	8	2.3
23 <i>Oniopis</i> sp <i>Spio decoratus</i>	0	0	0	0	1.3	0.3	0	0
24 <i>Spio decoratus</i>	0	0	0	0	3.8	1.3	6.7	2.6
25 <i>Streblospio shrubsolii</i>	1.1	12.9	25	31.8	35.9	19.5	38.7	38.9
Mollusca								
Bivalvia								
26 <i>Abra nitida</i>	0	0	0	0	0	0	2.7	1
27 <i>Cerastoderma edule</i>	5.5	1.5	0	0	16.7	5.4	33.3	50.2
28 <i>Scrobicularia plana</i>	42.5	147	34.2	103	24.4	10.3	5.2	88.9
29 <i>Solen marginatus</i>	0	0	0	0	0	0	2.7	0.5
30 <i>Spisula subtruncata</i>	0	0	0	0	1.3	1.6	1.3	0.3
31 <i>Spisula elliptica</i>	1.4	0.5	0	0	0	0	0	0
32 <i>Tellina tenuis</i>	6.8	2.1	0	0	0	0	6.7	4.4
Gastropoda								
33 <i>Hydrobia ulvae</i>	8.2	2.7	11.8	7.8	43.6	37.2	33.3	14.3
34 <i>Nassarius reticulatus</i>	1.4	0.2	0	0	0	0	0	0
Isopoda								
35 <i>Cyathura caninata</i>	41.6	55.6	39.5	41.4	33.3	35.9	49.3	59.1
36 <i>Eurydice pulchra</i>	1.2	0.2	0	0	0	0	0	0
37 <i>Idotea chelipes</i>	0	0	0	0	1.3	0.3	1.3	0.3
38 <i>Paragnathia formica</i>	0	0	0	0	0	0	1.3	0.3
39 <i>Sodunella lasada</i>	6.8	1.8	1.3	0.3	9	5.4	6.7	4.3
40 <i>Sphaeroma hookeri</i>	5.5	2.7	0	0	6.4	1.3	10.7	3.2
Amphipoda								
41 <i>Bathyporeia sarsi</i>	4.1	3.1	0	0	7.7	2.3	2.7	1.3
42 <i>Corophium multisetosum</i>	2.7	0.6	0	0	1.3	0.3	2.7	1.6
43 <i>Haustorium arenarius</i>	0	0	1.3	0.3	0	0	0	0

44	<i>Melita palmata</i>	1.4	0.2	0	0	7.7	5.6	10.7	2.6
Cumacea									
45	<i>Eocuma dollfus</i>	0	0	0	0	1.3	0.3	0	0
Mysidacea									
46	<i>Mesopodopsis slabberi</i>	0	0	0	0	1.3	0.3	0	0
47	<i>Neomysis integer</i>	16.4	4.3	11.8	17.2	2.6	0.5	1.3	0.3
Decapoda									
48	<i>Carcinus maenas</i>	5.5	1	3.9	0.8	6.4	1.3	6.7	1.7
49	<i>Crangon crangon</i>	0	0	0	0	10.3	2.6	13.3	3.8
50	<i>Palaeomonetes varians</i>	0	0	0	0	1.3	0.5	0	0
Echinodermata									
51	<i>Marthasterias glacialis</i>	1.4	0.2	0	0	0	0	0	0
52	<i>Ophiuroidea sp.</i>	1.4	0.2	0	0	0	0	0	0
Insecta									
53	<i>Chironominae larvae</i>	2.7	0.5	0	0	3.8	2.6	1.3	1
54	<i>Diptera larvae</i>	0	0	0	0	0	0	4	1
	<i>Gomphus pulchellus</i>	1.4	0.3	0	0	0	0	0	0
Pisces									
55	<i>Ammodytes tobianus</i>	0	0	1.3	0.3	0	0	0	0
56	<i>Engraulis encrasicolus</i>	1.4	0.3	0	0	0	0	0	0
57	<i>Platichthys flesus</i>	0	0	0	0	0	0	1.3	0.3

Seasonal variation of community structure

A seasonal variation of the total macrofaunal abundance was observed, with the lowest values for total macrofaunal abundance being found in December (972 individuals of 38 species were collected). Until March, although total macrofaunal abundance increased (1556 individuals were collected), the number of species found was much lower (only 17), probably as a repercussion of the effects of winter. From March to June, the spring influence was clearly discernible in the increase of total macrofaunal abundance and number of species (2981 individuals of 33 species were collected). Finally, from June to September, a small decrease in total macrofaunal abundance was observed (2045 individuals collected), although the number of species collected (37) was slightly higher.

The analysis of matrices of taxa X stations revealed clear differences between the macrofaunal community structure of the two arms of the estuary. Projection against the first and second axis of variability, based on December, March, June, and September data (figures 9: A, 10: A, 11: A, and 12: A), and despite seasonal variations, show a consistent pattern of structural discontinuity between stations D, E, F, G, and H, located in the inner areas of the south arm, and stations J, K, L, and M, located in the middle and upstream sections of the north arm.

Station A, located close to the mouth of the estuary, stations B and C, located in the downstream area of the south arm, and station I, located in the downstream section of the north arm, appear to be structurally more similar to each other, although seasonal variability in the macrofauna composition seems to be stronger, which can explain their irregular pattern of assemblage through the year. On the other hand, stations located in the upstream section of the north arm (L and M) appear to be relatively different from other stations in the north arm with regard to macrofauna, which is particularly evident in March situation (figure 10:A), where these two stations are clearly separated from the rest.

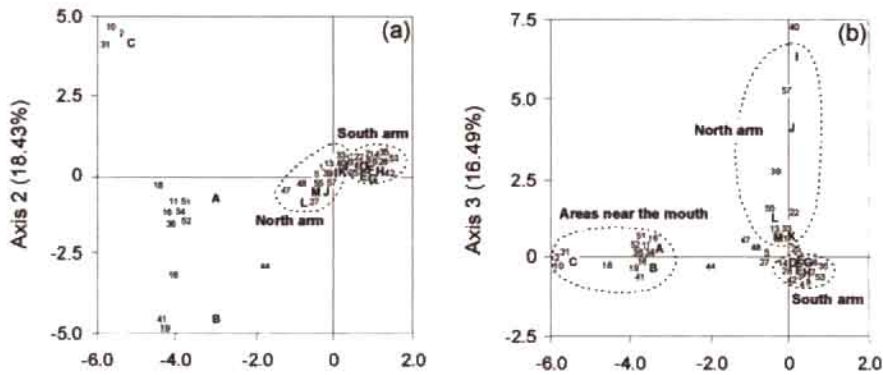


Figure 9. December situation: Results from Correspondence Analysis of benthic macrofaunal data. Projection of stations (A to M) and taxa (corresponding to numbers assigned in table 2) against the first and second (A) and first and third (B) axis of variability. The percentage of variability associated with each axis is indicated in parentheses.

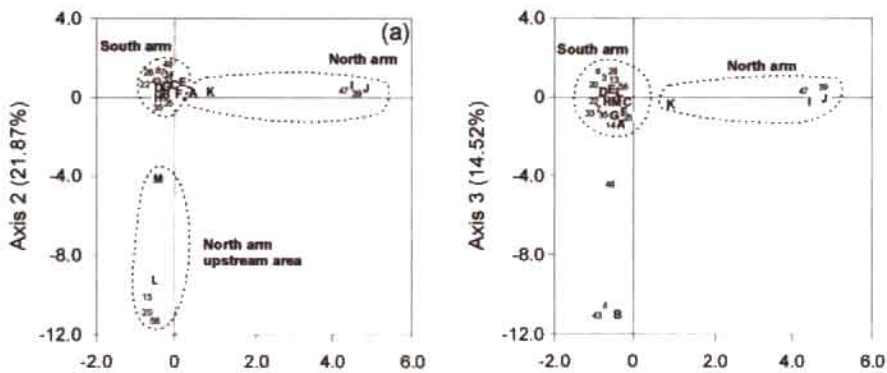


Figure 10. March situation: Results from Correspondence Analysis of benthic macrofaunal data. Projection of stations (A to M) and taxa (corresponding to numbers assigned in table 2) against the first and second (A) and first and third (B) axis of variability. The percentage of variability associated with each axis is indicated in parentheses.

Projection against the first and third axis of variability (figures 9: B, 10: B, 11: B, and 12: B) reveals a roughly comparable structural organisation, showing nevertheless more clearly the higher similarity between stations located closer to the mouth, with the exceptions of station I in December and station B in March.

Stations from the inner areas of the south arm (D, E, F, G, and H) are mainly characterised by the occurrence of abundant populations of *Amage adpersa*, *Scrobicularia plana*, and *Cyathura cannata*, true estuarine species, followed by more sparse populations of *Capitella capitata*, *Heteromastus filiformis*, and *Polydora ciliata*, and depending on the time of the year, by the less frequent or occasional occurrence of

other species, like *Tetrastemma* sp. and other nemertines, oligochaetes, *Chaetozone setosa*, *Chone collaris*, *Oriopsis* sp., *Spio decoratus*, *Streblospio shrubsolii*, *Hydrobia ulvae*, *Idotea chelipes*, *Corophium multisetosum*, *Haustorius arenarius*, and tolerant Chironominae and Diptera larvae.

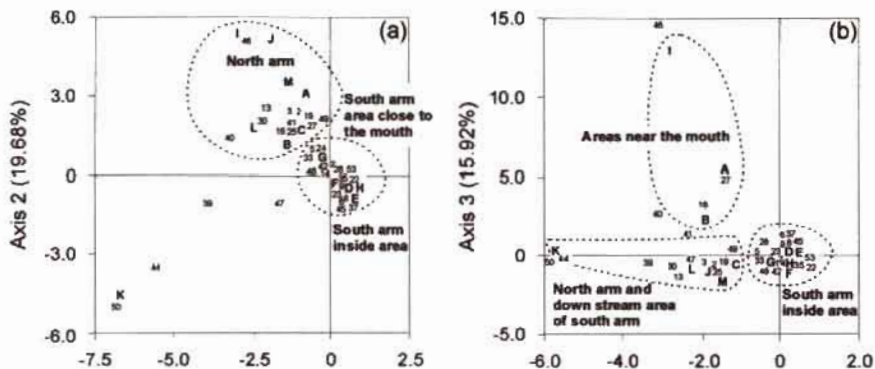


Figure 11. June situation: Results from Correspondence Analysis of benthic macrofaunal data. Projection of stations (A to M) and taxa (corresponding to numbers assigned in table 2) against the first and second (A) and first and third (B) axis of variability. The percentage of variability associated with each axis is indicated in parentheses.

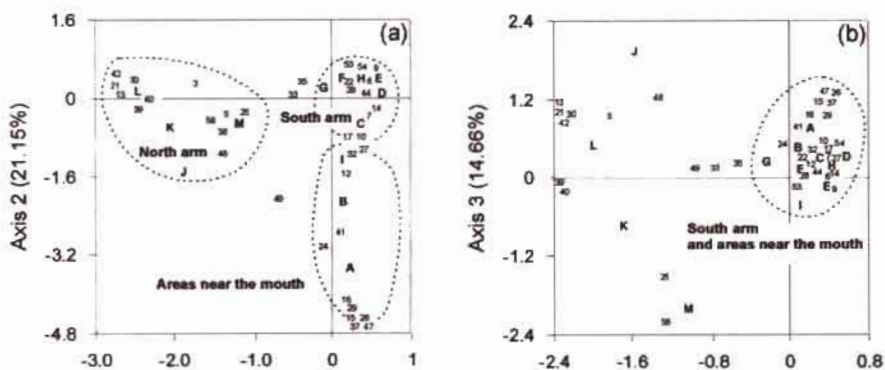


Figure 12. September situation: Results from Correspondence Analysis of benthic macrofaunal data. Projection of stations (A to M) and taxa (corresponding to numbers assigned in table 2) against the first and second (A) and first and third (B) axis of variability. The percentage of variability associated with each axis is indicated in parentheses.

Stations located along the north arm (J, K, L, and M), which present an impoverishment of the benthic populations, are mainly characterised by the presence of sparse populations of *Hediste diversicolor*, *Saduniella losadai*, *Sphaeroma hookeri*, and *Neomysis integer*. Through the year other species can be found more or less sporadically in these stations, like turbellarians, *Oerstedtia* sp., *Tetrastemma* sp., oligochaetes, *Nephtys paradoxa*, *Perinereis cultrifera*, *Streblospio shrubsolii*, *Cerastoderma edule*, *Hydrobia ulvae*, *Spisula subtruncata*, *Paragnathia formica*, *Bathyporeia sarsi*,

Corophium multisetosum, *Melita palmata*, *Mesopodopsis slabberi*, *Carcinus maenas*, *Crangon crangon*, *Palaemonetes varians*, *Gomphus pulchellus*, *Ammodytes tobianus*, and *Platichthys flesus*. The presence of infaunal species, like *Hediste diversicolor* or *Streblospio shrubsolii* is nevertheless almost limited to stations L and M, located in the upstream section of the north arm. On the other hand, the occurrence of *Gomphus pulchellus* (a freshwater insect) in station M in December was surely related to the river freshwater discharge.

Finally, stations located closer to the mouth (A, B, C, and I), despite strong seasonal variations in macrofaunal composition, can be primarily characterised by the presence of sparse populations of *Cerastoderma edule* and *Bathyporeia sarsi*, followed by the irregular or sporadic occurrence of *Oerstedtia* sp., *Eteone picta*, *Eulalia* sp., *Glycera convoluta*, *Lagis koreni*, *Nephtys* spp., *Nereis succinea*, *Spio decoratus*, *Streblospio shrubsolii*, *Abra nitida*, *Nassarius reticulatus*, *Solen marginatus*, *Spisula elliptica*, *Tellina tenuis*, *Eurydice pulchra*, *Idotea chelipes*, *Saduriella losadai*, *Sphaeroma hookeri*, *Neomysis integer*, *Marthasterias glacialis*, and ophiuroids, which obviously reflects a stronger marine influence.

Influence of environmental factors on biodiversity and total macrofauna abundance

In order to understand the influence of physicochemical factors on the macrofauna distribution it was firstly necessary to characterise the estuary with regard to these factors.

PCA of matrices of physicochemical factors X sampling stations (figure 13) also reveal a consistent pattern over the year. From the projection against the first two axis of variability, stations appear distributed along a physical and chemical gradient, with stations located in the downstream areas of the north arm in one of the edges, stations located in the upstream section of the north arm and downstream areas of the south one in the middle, and stations located in the inner areas of the south arm in the other edge. This is clearly the situation in December (figure 13: A) and June (figure 13: C), while in March and September (figure 13: B and 13: D) station A, located near the mouth, appears to be separated.

Stations from inner areas of the south arm (D, E, F, G, and H) and stations from the downstream areas of the south arm, north arm and from near the mouth (A, B, C, I, J, K, L, and M) are almost always opposed along the first axis of variability. Stations located in the inner area of the south arm are mainly characterised by more fine sediments, with larger fractions of fine sand to clay, higher organic matter (from 3.2% in station D to 9% in station G) and carbonate contents (from 3.3% in station D to 8.7% in station G) and, in December, higher nitrite concentrations in the water column (from 1.28 mg.l⁻¹ in station D to 2.07 mg.l⁻¹ in station F). Stations located in downstream areas of the south arm, along the north arm, and near the mouth are mainly characterised by more coarse sediments, which tend to present larger fractions of gravel and coarse to medium sand, while the water column tends to present higher salinities (during high water), higher dissolved oxygen levels (the minimum observed was 86% of saturation in station A in March) and, in December, higher pH (from 6.7 in station A to 8 in station M).

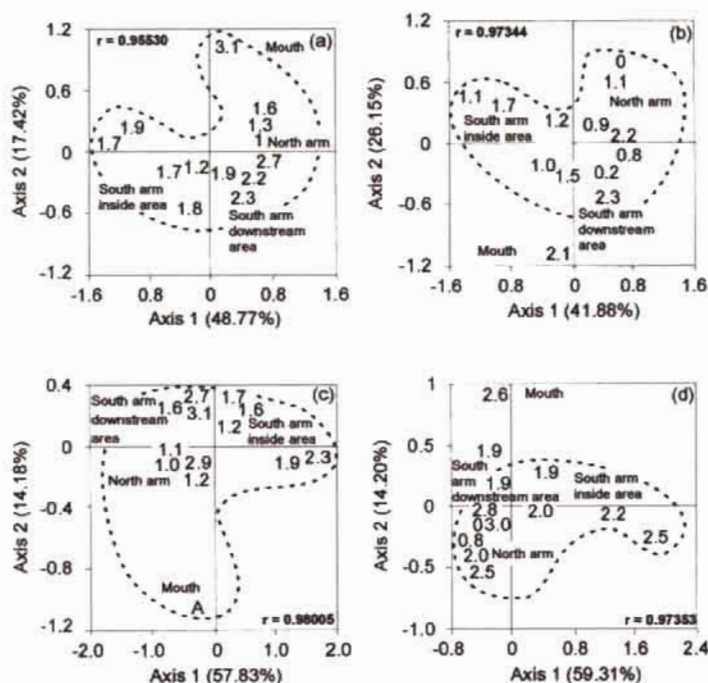


Figure 13. Results from PCA of physicochemical data of water and sediments. Projection of stations against the first two axis of variability: A - December; B - March; C - June; D - September. The percentage of variability associated with each axis is indicated in parentheses.

Along the second axis of variability station A, located near the mouth of the estuary, is opposed to the other stations, especially as a function of the characteristics of the water column, reflecting also the seasonal variations. In relation to water factors, resemblance between stations located inside both estuarine arms and station A, located close to the mouth, clearly changes through the year. It is nevertheless impossible to go further in the analysis of the seasonal variation of water factors, because it depends on changes in the river freshwater discharge and on water circulation. Since the available data are prompt measures, they cannot be considered very significant. Nevertheless, closer to the mouth of the estuary salinity tends to be higher, which is normal, as well as dissolved oxygen levels, while in the inner areas temperature tends to be higher, as well as nitrogen concentrations.

The projection of the Shannon-Wiener index values, seasonally calculated for each station, over the ordination obtained from PCA of matrices of physicochemical factors X stations (figure 14), show a roughly regular pattern for the distribution of diversity values through the year. Despite seasonal variations, biodiversity tends to reach the highest values near the mouth and in the downstream area of the south arm, remaining approximately stable with relatively high values in the inner areas of the south arm. On the contrary, strong seasonal changes in biodiversity are evident in the north arm, although there is a certain pattern over the year. Diversity values tend to

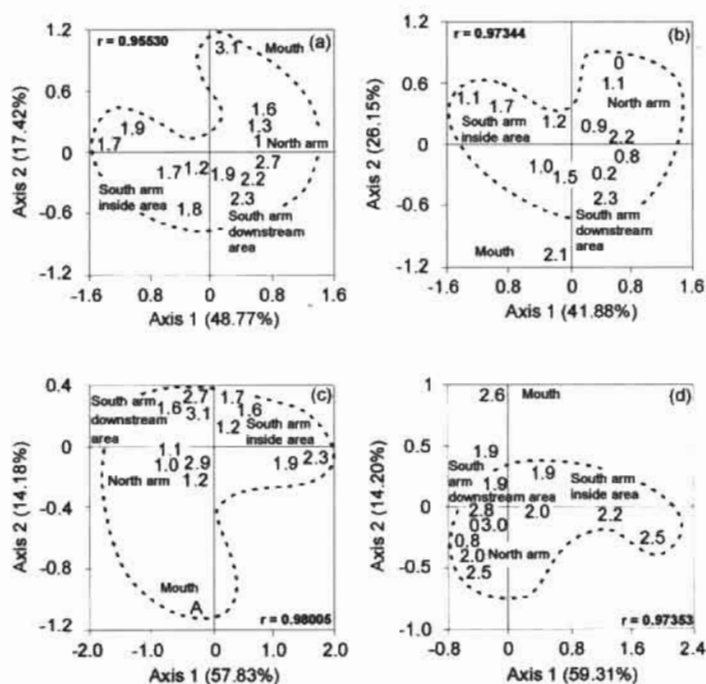


Figure 14. Plot of the Shannon-Wiener index values, calculated for each station in each time of the year, over the projection of stations against the first two axis of variability, obtained from PCA of physicochemical data of water and sediments: A - December; B - March; C - June; D - September. The percentage of variability associated with each axis is indicated in parentheses.

be higher closer to the mouth, decreases in the middle section of the north arm, and increases again in the upstream section.

With regard to total macrofauna abundance (individuals.m²), despite seasonal variations and the bias introduced by the sampling method, a pattern of distribution through the year is also recognisable (figure 15). Macrofauna is consistently more abundant in the inner areas of the south arm, although in the Pranto river values are comparatively lower (figure 15), and also significantly elevated in the downstream area of the south arm and upstream section of the north arm. In the north arm, there is a clear rarefaction of macrofauna from the upstream areas to the mouth, which is particularly evident in the middle section.

Summarising, it is possible to distinguish several areas in the estuary with regard to biodiversity and total macrofauna abundance:

Stations from the inner areas of the south arm, characterised by fine sediments, richer in organic matter and carbonate contents, and by higher concentrations of nitrogen in the water column, present a relatively stable and high biodiversity and by far the highest macrofauna abundances.

Comparatively, the downstream area of the south arm, characterised by sediments with significant fractions of coarse to medium sand, more poor in organic

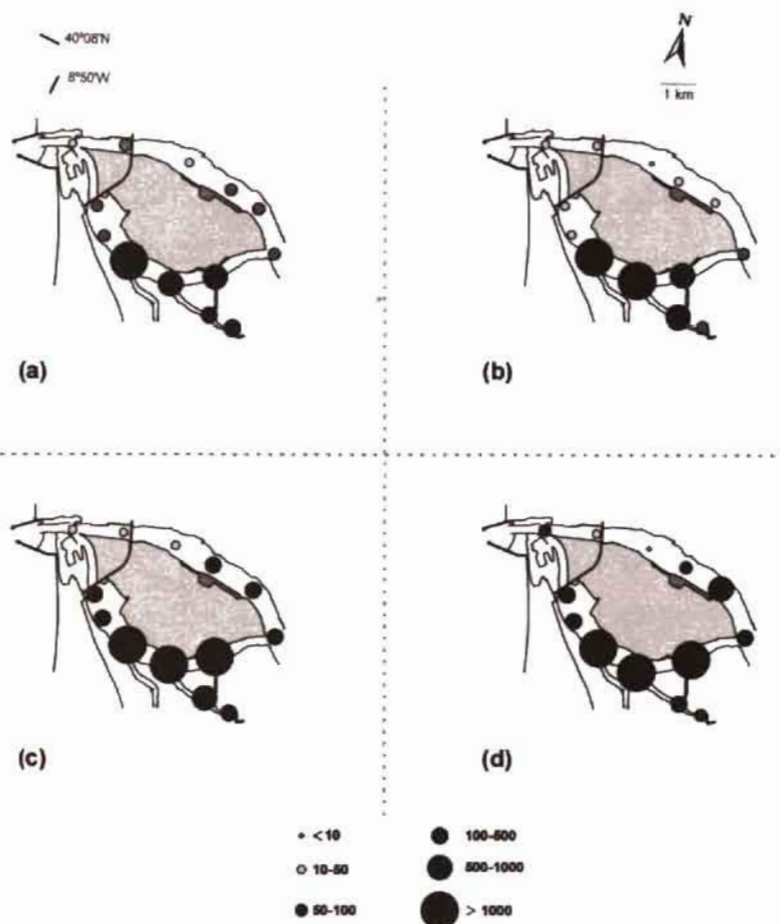


Figure 15. Spatial and temporal variation of total macrofauna abundance (individuals.m⁻²) in the Mondego estuary: A - December; B - March; C - June; D - September.

matter and carbonate contents, and by higher salinities and dissolved oxygen levels, presents an higher biodiversity but a lower macrofauna abundance.

Areas near the mouth and along the north arm are characterised by sandy bottoms, poor in organic matter and carbonate contents, although the fine sand fraction is more important near the mouth and in the upstream section, while the gravel to medium sand fractions are predominant in the middle section. Salinities and dissolved oxygen levels are also consistently higher along the north arm, although salinity tends to decrease from the mouth to the upstream areas. However, due to tidal currents and freshwater discharge, daily salinity fluctuations are by far more significant

in the north arm (Marques 1989), especially in rainy periods. Near the mouth, biodiversity presents regularly the highest values found in the estuary, while the lowest ones and the strongest changes over the year occur in the north arm, particularly in the middle section. Total macrofaunal abundance is low along the north arm, with the exception of its upstream section, and therefore the middle section of the north arm constitutes the poorest area in the estuary for both biodiversity and macrofaunal abundance.

Discussion

Intertidal zone

The analysis of both hard and soft substrates communities structure showed clear differences between the two arms of the Mondego estuary, namely with regard to populations abundance and biodiversity. In both cases a good agreement was found between results from the analysis of biological and physicochemical data.

The observed differences are most probably due to very dissimilar hydrographic characteristics of the two arms. The south arm is still less affected by human activities and presents more favourable environmental conditions for the development of enhanced populations of true estuarine species. Nevertheless, the south arm is also shallower than the north arm, and water circulation depends widely on tides, especially in the summer. For these reasons, we consider that the south arm appears potentially much more exposed to environmental changes.

Salinity appears to be the most important factor controlling the hard substrates community structure, while sediments granulometry is the most important factor controlling the distributional ecology of soft substrates macrofauna, followed by organic matter contents, salinity, and dissolved oxygen. Other studied factors seem to play a less important role with regard to macrofauna distribution.

Spartina maritima and *Zostera noltii* marshes appear to be the richest areas with regard to macrofauna abundance and biodiversity. However, occasional blooms of *Enteromorpha spp.* have been observed in the south arm, probably as a function of excessive nutrients release into the estuary. Since macrophytes have roots and are only able to take up nutrients from the sediments, it seems possible that macroalgae like *Enteromorpha*, which is able to take up nutrients directly from the water, can take advantage from this situation. Therefore, it seems also likely that an eutrophication process might take place in the south arm, and in such a case a shift in the benthic primary producers could occur, affecting the structure and functioning of the trophic chain and ultimately the species composition in the community.

Subtidal zone

The subtidal benthic macrofauna of the Mondego estuary appears to be clearly impoverished. The Mira estuary, located in the Portuguese southwest coast, which is

approximately identical to the Mondego in size, have been considered as relatively unaffected by human impacts, and can therefore provide a reasonable basis for comparison. Moreover, data on the Mira estuary (Andrade 1986) was collected according to a relatively similar sampling strategy and using identical sampling devices. With regard to subtidal benthic organisms, 151 taxa were identified for the Mira, while only 58 (about 38%) were identified for the Mondego. Furthermore, only 21 species were found in both estuaries, which appear to indicate a considerable contrast in the species composition. Differences observed with regard to total macrofaunal abundance were not so important (an average of 624 individuals.m⁻² per sample in the Mira, and 466 individuals.m⁻² per sample in the Mondego). Despite any conceivable bias in sampling, the observed differences must be considered highly significant.

The analysis of benthic macrofauna community structure through the year shows that, biologically, the two arms of the Mondego estuary constitute different sub-systems. This structural discontinuity is quite obvious between the inside areas of both arms, although closer to the mouth, due to the marine influence, differences become less apparent. This fits well with results from the independent analysis of environmental factors, and additionally the present results are consistent with those from the study on the intertidal communities. With regard to the community structure, biodiversity, and total macrofaunal abundance it is therefore possible to recognise different estuarine areas in relation to physicochemical environmental factors, respectively the inner areas of the south arm, the mouth of the estuary and downstream areas of both arms, and the middle and upstream sections of the north arm.

Since the water circulation in the south arm is mostly dependent on tides, current velocities are inferior and conditions are more favourable to fine particles and organic matter deposition (McLusky 1989). This tends to bring about a biological improvement, since subtidal fauna usually depends on sediments stability and organic matter contents (Gould et al. 1987). This can explain the relatively high and stable biodiversity values found through the year, and the higher abundances for total macrofauna, as observed in the inner areas of the south arm.

On the contrary, current velocities are higher along the north arm, due to both the river discharge (during low water) and a fast tidal penetration. This can explain the change in bottom characteristics, and although the species-sediment relationship is not always a simple linear function of grain size and organic matter contents (Jones et al. 1986), this bottom change is certainly one of the most important reasons for biological differences observed between both estuarine arms. Additionally, due to the river discharge and strong tidal current, daily salinity fluctuations in the north arm are higher than in the south arm (Marques 1989), which is probably a second major cause of faunal impoverishment (Barr et al. 1990). This agrees with the direct relationship between faunal type and tidal stress, as observed by Warwick and Uncles (1980).

The granulometric structure of the inhabitat and salinity fluctuations seems therefore to be the most important factors conditioning the subtidal macrofauna distribution in the Mondego estuary.

On the other hand, infaunal species are dominant in the south arm, especially in the inner areas (e. g. *Amage adspersa*, *Capitella capitata*, *Heteromastus filiformis*, *Polydora*

ciliata, and *Scrobicularia plana*), while a clear dominance of epifaunal species (e. g. *Saduriella losadai*, *Sphaeroma hookeri*, *Neomysis integer*, and *Carcinus maenas*) is evident in the north one. This is probably related with shifting sediments, caused by a faster water circulation, which tend to prevent the colonisation and long-term establishment of a permanent infauna, determining the occurrence of typically sparse benthic communities, mainly constituted by mobile epibenthic species (Barr et al. 1990). Nevertheless, in the upstream section of the north arm, where dredging operations do not take place, infaunal species (e. g. *Hediste diversicolor* and *Streblospio shrubsolii*) can be found through the year. It appears therefore that the strong changes in biodiversity and the extreme macrofaunal impoverishment in the middle section of the north arm are also a function of regular dredging. Actually, dominant species decimation following disturbance of the bottom as been observed in other case studies. In Long Island Sound, for instance, polychaete populations of *Nephtys* strongly decreased at or near the disturbance site, although little or no effects on the populations were detected at more than 400 m from the impacted area (Zajac and Whitlatch 1988).

It has been observed that the recovery of dredged zones in number of species is practically obtained six months after the completion of dredging operations, although biomass takes longer to reach values similar to those found in unaffected areas (López-Jamar and Mejuto 1988). In the Mondego estuary, time intervals between dredgings (approximately twice a year) are likely to be too short, and do not allow macrofauna recovery, which surely contributes to the obvious instability of the north arm community. However, there are no other indications on the effects of dredging besides the absence of infaunal species and macrofaunal impoverishment.

Conclusions

The Mondego estuary is under severe environmental stress, and it is difficult to establish the benthic community temporal trends and if the ongoing changes are reversible. The benthic communities in estuarine environments are generally characterised by wide fluctuations in the abundance of constituent species, although they present a more persistent qualitative composition (Boesch et al. 1976). Moreover, benthic organisms, namely infauna, are especially important components in estuarine ecosystems, because most of them have limited mobility and respond to environmental stress (Bilyard 1987). It seems therefore necessary to monitor the Mondego estuary communities, probably with emphasis on benthic macrofauna, although such studies need labour-intensive sample sorting and taxonomy. This monitoring study should take all species into consideration, once using only the most abundant ones for characterising communities, or as indicators of physicochemical conditions, may be unreliable because of variation in both time and space in dominant species, and the lack of stress-response knowledge for local species (Jones 1990). It will provide valuable information that cannot otherwise be obtained, since the dynamics of estuarine benthos is very complex and strongly limits the usefulness of short-term baseline and impact studies.

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