

Meiobenthic distribution and nematode community structure in five European estuaries

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Abstract

Meiofauna from the intertidal zone of five European estuaries (Ems, Westerschelde, Somme, Gironde, Tagus) was investigated. Samples represented a cross section of various benthic habitats from near-freshwater to marine, from pure silts to fine-sandy bottoms. The meiobenthic community comprised everywhere a fauna strongly dominated by nematodes, with meiobenthic density increasing with increasing salinity. The Ems differed from the other estuaries due to the presence of a well developed community of Copepods, Gastrotrichs, large Ciliates and/or soft-shelled Foraminiferans in some sites. The Westerschelde stood out due to the near-absence of harpacticoid copepods and, as in the Tagus, the lower meiobenthic densities in the marine part of the estuary. For nematode community analysis, we also included data from the Tamar which were obtained from the literature (Warwick & Gee, 1984). This resulted in the enumeration of 220 species, belonging to 102 genera, each with a characteristic distribution along the salinity, sedimentary and latitudinal gradients. Using the multivariate technique CANOCO, a zonation along these different physicochemical determinants was observed as well although salinity and sediment characteristics (scale of hundreds of meters to kilometers) proved to be more important in explaining community structure than latitudinal differences (scale of hundreds of kilometers). Nematode diversity was nearly entirely determined on the genus level and was positively related to salinity. Deviations from this general trend in the Gironde and the Tamar were attributed to sedimentary characteristics or to low macrobenthic predation. The presence of a typical opportunistic colonizing nematode species *Pareurodiplogaster pararmatus* in the low-salinity region of the Gironde could indicate (organic?) pollution or disturbance of the intertidal mud-flats.

Introduction

Meiobenthic communities in European estuaries have only been studied in the U.K. (Capstick, 1959; Warwick, 1971; Warwick & Price, 1979; Warwick & Gee, 1984; Moore, 1987; Austen & Warwick, 1989), Germany (Gerlach, 1953; Riemann, 1966; Skoolmun & Gerlach, 1971), the Netherlands (Van Damme *et al.*, 1980; Bouwman, 1983; Smol *et al.*, 1994) and northern France (Gourbault, 1981). No data exist on more southern estuaries. Moreover, intercomparison between estuaries is complicated by taxonomic difficulties. Especially in the past, the chaotic taxonomy of *e.g.* the nematodes made this taxon only accessi-

ble to the specialist (Gerlach, 1980). Thanks to the publication of pictorial keys (Platt & Warwick, 1983; 1988) nematode identification is now much easier – at least to the genus level. However, the identity of many species remains problematic. If different estuaries are investigated by the same researcher, as in this study, it becomes more easy to distinguish within-species variability from between-species variability and, although determinations may not always be exact, this will introduce more consistency into the results.

This study is part of a general research program, which aims at the understanding of major biological processes in European tidal estuaries (MAST CEC project, JEEP92). As part of this programme, a base-

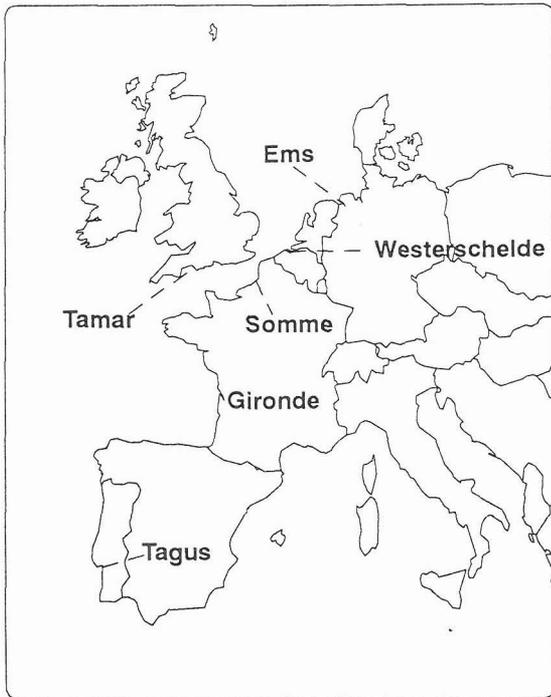


Fig. 1. Location of the various estuaries under study.

line study of the meiobenthos in five European estuaries was made, with emphasis on the nematode species composition. For this purpose, data on the Tamar estuary, as provided in Warwick & Gee (1984) were included. The distribution of the most important species and the influence of large-scale spatial structure on the community level are reported.

Material and methods

Samples were taken from intertidal areas of the Ems, the Tagus, the Gironde, the Somme (April 1992), and the Westerschelde (April 1990) along a salinity gradient (Fig. 1). A total of twenty five sites were sampled, and at least two replicates (10 cm²) per station were taken with plastic cores for meiofauna and an additional one for sediment analysis. Samples from the Gironde were taken from the mean tidal level and subdivided into 0–1 and 1–5 cm slices. Samples from the Westerschelde were also vertically subdivided. However, information on the vertical distribution was not retained in this study. Vertical distribution of nematodes in the Westerschelde is discussed in Soetaert *et al.* (1994).

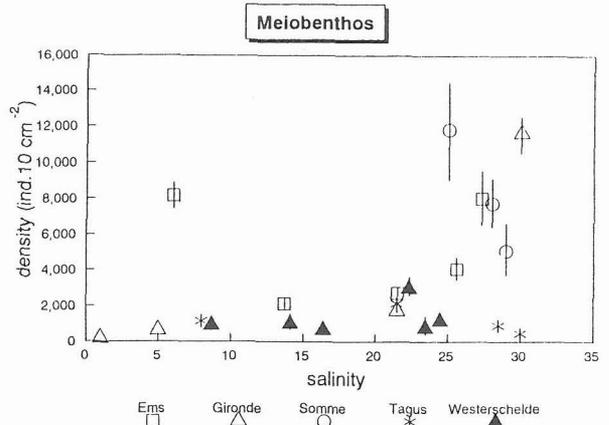


Fig. 2. Mean meiobenthos density and total range (ind. 10 cm⁻²) for the five European estuaries under study.

Salinity was measured in the water column. All sediment and meiofauna samples were treated in the same laboratory (Ghent). Sediment particle size distribution was determined using Coulter LS particle size analysis equipment.

The meiofauna was extracted using LUDOX TM as described in Heip *et al.* (1985). After colouring with Rose Bengal the meiofaunal taxa (i.e. those animals retained on a 38 μ m sieve) of two replicates were enumerated after which at least 200 randomly chosen nematodes per replicate were mounted into slides for further identification. If total nematode density was less than 200 individuals, all were processed. Identification to genus – and in some cases species – level was done using the pictorial keys in Platt & Warwick (1983, 1988) and Bongers (1988). For many species further identification required consultation of the relevant literature.

The species-abundance matrix was analysed using the multivariate technique CANOCO (CANONICAL CORRESPONDENCE analysis; Jongman *et al.*, 1987; Ter Braak, 1989). This method was used to relate the observed trends to the major environmental gradients. Diversity was measured as Hill's diversity numbers of order 0 (i.e. N0, the number of species present), 1 (i.e. N1, the exponential of the Shannon Wiener index), 2 and ∞ (i.e. N ∞ , the reciprocal of the dominance of the most common species) as suggested by Heip *et al.* (1988). This spectrum of diversity indices gives a clear representation of the influence of rare (lower order indices) and more common (higher order indices) species on diversity. In order to correct for the size-dependency of diversity indices (Soetaert &

Heip, 1990) and as a means of comparing with other studies, the indices were calibrated on 100 randomly chosen individuals as described in Soetaert & Heip (1990). The life-history traits of the communities were summarized into the 'maturity index' as described in Bongers (1990) and Bongers *et al.* (1991). In short, a higher value of this index indicates a higher degree of persistence, a lower value a more opportunistic community.

The different estuarine environments

The estuaries under investigation are situated along a north-south gradient (Fig. 1). The climate changes from temperate (mild winters, relatively cool summers) in the North of the Netherlands, with a well pronounced variation in temperature and a relatively smooth precipitation curve, to warmer in Portugal, where precipitation is very variable.

The Ems estuary (the Netherlands, Germany) connects the north-eastern part of the Netherlands and the north-western part of Germany with the North Sea. It is an important shipping route with three harbours along its side. Sediments are dredged from the estuarine channels and dumped in other parts (de Jonge, 1992). The major freshwater input to the Ems estuary, the river Ems and the Westerwoldsche AA are also important sources of nutrient enrichment (de Jonge & Essink, 1992). In its upper reaches, the Ems estuary has a vast intertidal mudflat: the Dollard. The total average annual discharge varies from 80 to 180 m³ s⁻¹ with seasonal variation; tidal currents are moderate.

The Westerschelde estuary (the Netherlands) provides the link from the harbour of Antwerp towards the North Sea. It has busy shipping lanes and concurrent dredging and dumping activities of polluted sediments. Large cities on the river banks, and the high degree of industrialization stand for a high input of organics, inorganics and nutrient wastes. The high load of organic matter in the turbidity maximum zone causes strong anoxic conditions in summer (Heip, 1989). The average freshwater flow is about 100 m³ s⁻¹ and it fluctuates in a seasonal manner.

The Somme (North of France) is an embayment of the Somme and Maye river system and opens to the west in the English Channel; the northern half of the bay is subjected to strong waves from the Channel (Ducrottoy & Sylvand, 1989). The Somme is characterized by a low freshwater output (30 m³ s⁻¹) and is thus primarily under marine influence. It consists of

large intertidal areas with high biomasses of cockles (Rybarczyk *et al.*, 1992).

The Gironde estuary (South of France) is fed by the rivers Garonne and Dordogne and has the city of Bordeaux along its banks. The mean river discharge is high, varying from 600 to 1000 m³ s⁻¹ and is subjected to seasonal variations. It is a highly turbid estuary but with a distinct turbidity maximum (Castel & Feurtet, 1989).

The Tagus (Portugal, Spain) is the largest river of the Iberic peninsula and is characterized by an extensive intertidal area (>30%) (Moreira *et al.*, 1992). It is flanked by the city of Lisbon which disposes its untreated wastes into the estuary. The port of Lisbon is also an important source of industrial waste in the marine part of the estuary (Gaudencio *et al.*, 1991). Another centre of industrialization causes heavy pollution along a narrow channel in the brackish part (R. Neves, pers. comm.). The freshwater outflow of the Tagus is very variable, both annually and interannually; it varies from 30 to 18 000 m³ s⁻¹ and the salinity varies concurrently.

The Tamar estuary is situated in South-West England and is characterized by extensive tidal flats and mud banks. River discharge varies in a seasonal way from about 2 to 150 m³ s⁻¹ (Morris *et al.*, 1985). A turbidity maximum in the upper estuary acts as a trap for particles of marine, estuarine and fluvial origin (Bale *et al.*, 1985).

Results

Sediments

The majority of intertidal stations had fine-grained sediments although some stations in the three most northerly estuaries were more coarse. Grain characteristics, salinity and name of the stations are presented in Table 1.

Meiobenthos

Meiobenthic taxa observed included Nematoda, Copepoda, Gastrotricha, Plathelminthes, soft-shelled Foraminifera, Ciliata, Polychaeta, Oligochaeta, Ostracoda, Halacarida, Cnidaria, Priapulida and Tardigrada.

Meiobenthos densities (Fig. 2) varied from 130 to 14 500 ind 10 cm⁻² and were highest in the Somme and the marine part of the Gironde and Ems. Low meioben-

Table 1. Salinity, silt content and median grain size of the intertidal samples.

Estuary	Station	Salinity (‰)	Silt (%)	Median (μm)
Ems	E 6	6	78	18
Ems	E 5	14	16	124
Ems	E 4	22	23	107
Erns	E 2	26	45	73
Ems	E 1	27	6	136
Westerschelde	WS 1	9	0	187
Westerschelde	WS 22	14	6	133
Westerschelde	WS 32	16	1	238
Westerschelde	WS 42	22	3	167
Westerschelde	WS 61	28	40	77
Westerschelde	WS 53	29	84	15
Somme	HH	25	17	165
Somme	LC	28	17	169
Somme	LM	29	15	181
Tamar	Clifton (*)	9	94	11
Tamar	Neal point (*)	23	94	15
Tamar	West mud (*)	31	87	34
Gironde	Lamarque	2	96	9
Gironde	St Estephe	5	85	23
Gironde	Richard	22	58	60
Gironde	Le Verdon	30	92	9
Tagus	Cala do Norte	8	95	9
Tagus	Banco do Ladeiro	22	36	148
Tagus	Banco dos Cavalos	30	77	11
Tagus	Banco do Destroi	29	72	13

(*) = data from Warwick and Gee (1984).

thic densities were observed all along the transect in the Westerschelde and the Tagus and in the brackish part of the Gironde. In general, meiobenthic density increased with increasing salinity (Fig. 2).

Nematodes were always the most abundant taxon (Fig. 3) and their dominance was in the order of 81 to 99%, except for the Ems. The Ems seemed to be the only estuary where other groups were of some significance: the most upstream station had fairly large numbers of soft-shelled Foraminiferans and Copepods, the most marine station had a large Gastrotrich community (30% of all meiobenthic animals), while Turbellarians, Ciliates and soft-shelled Foraminiferans were numerous in the two most marine stations (Fig. 3).

Apart from the Ems, turbellarians and large ciliates were also present in low quantities (at most 20, resp. 75 ind 10 cm^{-2}) in the Westerschelde, while virtually absent in other estuaries. Gastrotrichs were observed

in high densities in the Ems and the Somme only, while soft-shelled Foraminiferans were also numerous in the most marine station of the Gironde. Harpacticoids were present in low quantities in most estuaries; in the Westerschelde (maximum 6 ind 10 cm^{-2}) and the Somme (7 ind 10 cm^{-2}) harpacticoid densities were very low (Fig. 3).

Nematodes

A total of 220 species, belonging to 102 genera and 35 families, were recorded in the intertidal of the investigated estuaries. The majority of these species were confined to only one estuary, some were found in two or three estuaries (Appendix). Only three species were common to all estuaries: *Dichromadora cephalata*, *Halalaimus gracilis* and *Viscosia viscosa*. Another thirteen species were observed in all but one estuary: *Daptonema normanicum*, *Chromadorita tentaculata*, *Anoplostoma viviparum*, *Calyptronema maxweberi*, *Metalinhomoeus aff biformis*, *Daptonema setosa*, *Sabatieria punctata* group, *Dichromadora geophila*, *Ptycholaimellus ponticus*, *Praeacanthochus punctatus*, *Axonolaimus paraspinosus*, *Metachromadora remanei* and *Chromadora macrolaima*.

As salinity and sediment characteristics were fairly evenly distributed (Table 1), the distribution characteristics of the most important species and genera (defined as making up at least 15% of the total community in at least one station and observed in more than two stations) were computed with respect to their salinity and sediment grain size preferences. The median distribution (50%) and the 10% and 90% occurrences as well as the total range along which the species were observed were calculated and represented as box-whisker plots (Figs 4–5). By comparing the specific distribution with the repartition of all nematodes combined (total DENSITY), the degree of selectivity for any one parameter can be evaluated. Some species exhibit broad ecological tolerances to both factors and have a distribution along the sedimentary and salinity axis that is not noteworthy different from the total nematode density: *Viscosia viscosa* and *Dichromadora cephalata*. These two species were also observed in all estuaries (see above). Most species or genera have more clear preferences.

A Canonical correspondence analysis based on species, genera or families yielded – after permutation of the X-axis in the genus and family level – very similar results. The CANOCO plot of species (or genera) and environmental variables (Fig. 6) yields

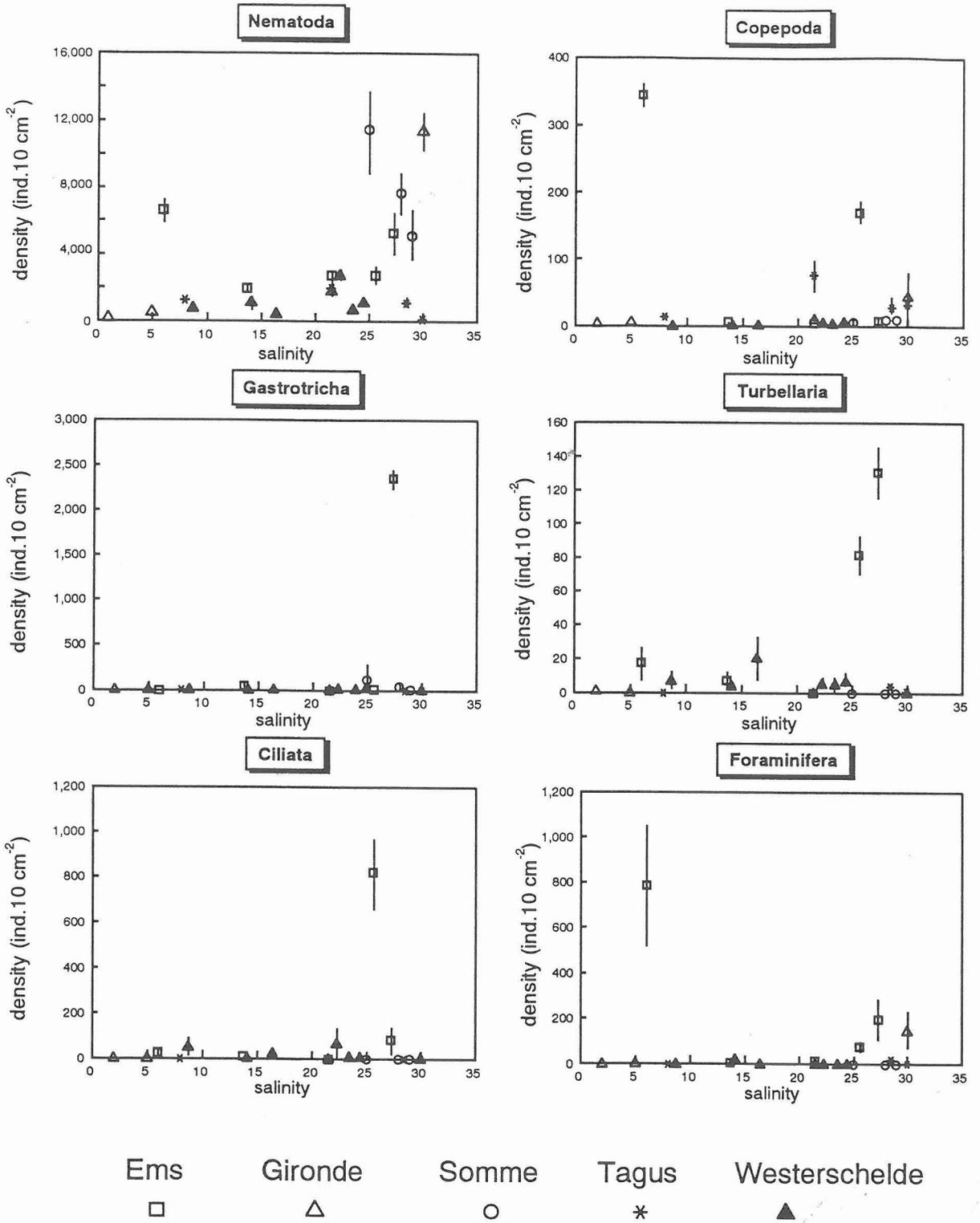


Fig. 3. Mean densities and total range (ind 10 cm⁻²) of nematodes, copepods, gastrotrichs, turbellarians, ciliates and softshelled foraminiferans in the five European estuaries under study.

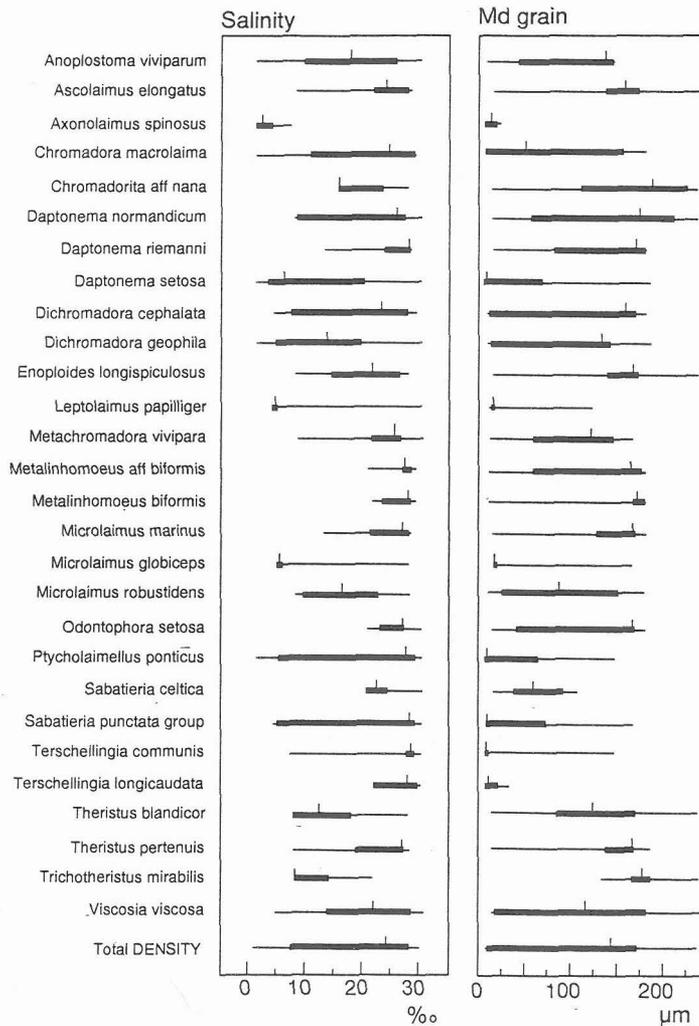


Fig. 4. Distributional characteristics of the most important species along the salinity and sediment grain gradient (all studied estuaries combined). Indicated are the total range (horizontal line), the median occurrence (vertical dash) and the 10 to 90% occurrence (horizontal bar).

similar information with respect to the figures (4–5) and (appendix): specific preferences for any variable can be ‘appreciated’ by orthogonally projecting the species position on the environmental axis. The positions of the species (Fig. 6) can aid in the interpretation of the station position in the same graph as they are weighted averages of the species positions. The length of the environmental arrows indicates their relative importance in explaining community structure. The relative position of the arrows reflects the relationship of the environmental variables, with orthogonality indicating no correlation, parallelism indicating positive (same direction) or negative (opposite) correlation. Thus salinity and grain characteristics (order of kilometres) were about equally important and independent

factors, while latitudinal differences (correlated with grain size), although on the scale of hundreds to thousands of kilometres were much less pronounced.

The positions of the stations in the CANOCO plot with the same axes are represented in Fig. 7 for the species level. Results were very similar for genus or even family level (not depicted). There was a great overlap between stations of different estuaries. Within estuaries, the community gradually changed along the salinity gradient (arrows in Fig. 7) rather than along the sediment gradient (not depicted). This could indicate that the predictive ability of the type of sediment was overemphasized by the analysis, due to its relationship with latitude.

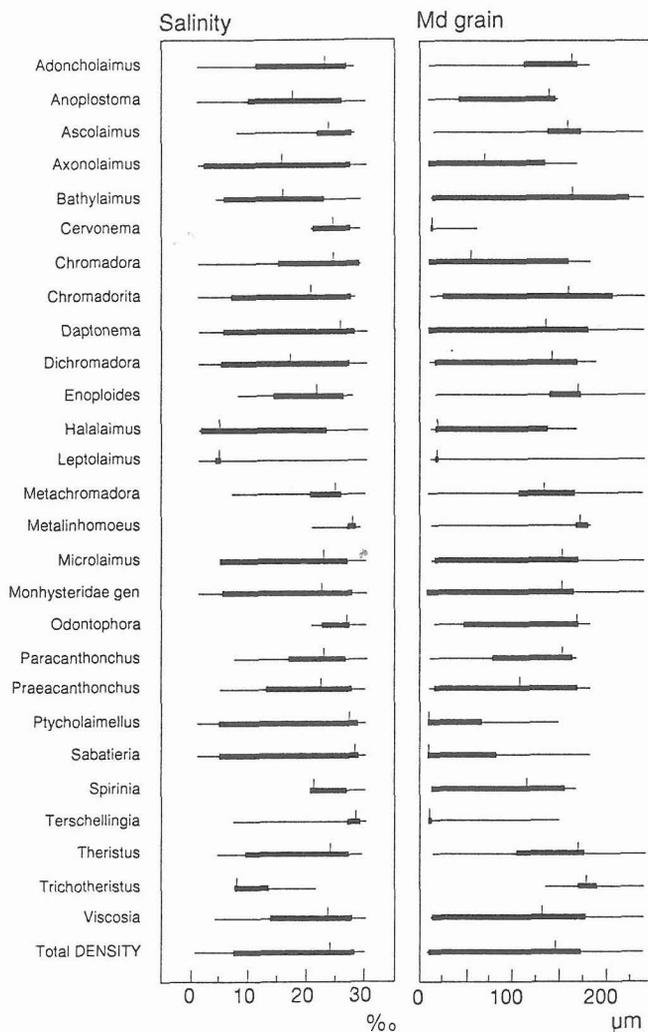


Fig. 5. Distributional characteristics of the most important genera along the salinity and sediment grain gradient. For an explanation, we refer to Fig. 4.

Nematode distributions (Figs 4–6, appendix)

The most important nematode families in terms of total density were the Xyalidae, the Axonolaimidae, the Comesomatidae, the Microlaimidae, the Linhomoeidae and the Chromadoridae.

The Comesomatidae were predominantly observed in silty sediments and preferred to some extent a more saline environment. There are two important members of this group. Species which have been described in the literature as *Sabatieria punctata*, *S. pulchra* and *S. breviseta* were present in this study both in their typical morphology as well as in all kinds of intermediate forms. This makes their systematic identity rather problematic and they were consequently grouped as

one species which we called the '*Sabatieria punctata* group'. They were more strongly bound to silty sediments than the other member of the genus, *S. celtica*. Whereas the genus *Sabatieria* seemed to be more indifferent with respect to salinity and latitude, the genus *Cervonema* is a clear representative of the more saline and silty bottoms of estuaries at the lower latitudes (Gironde, Tagus).

The Xyalidae were a very abundant family encompassing three important genera: *Daptonema*, *Theristus* and *Trichotheristus*. *Trichotheristus mirabilis* and *Theristus blandicor* were only present in the most northerly estuaries (WS, resp. Ems and WS) and both prefer brackish waters. *Daptonema setosa* was found in the brackish part of all but one estuaries in silty sed-

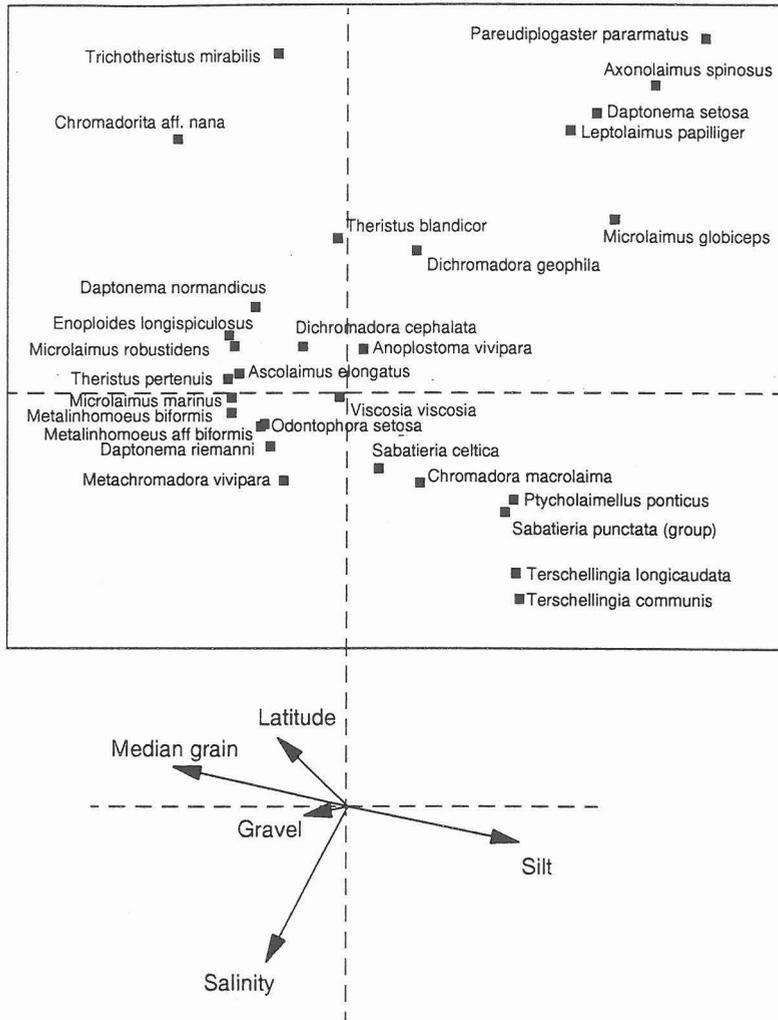


Fig. 6. Upper part: position of the most important species in two-dimensional CANOCO space (first two axes). Lower part: environmental arrows in the same CANOCO space.

iments (in the Somme the brackish area was not sampled). *Daptonema riemanni* was a common species in more marine and sandy bottoms of the northern estuaries. *Daptonema normandicum* and *Theristus pertenuis* are more northerly species with an affinity for coarser-grained and saline sediments.

The Linhomoeidae were represented by *Terschellingia longicaudata* and *Terschellingia communis* which co-occur in the silty sediments of the marine part in the Tagus, the Gironde and the Tamar and by two closely related species of the genus *Metalinhomoeus* (called *Metalinhomoeus typicus* and *M. biformis* in Bouwman, 1981, but referred to as *Metalinhomoeus biformis* resp. *M. aff. biformis* in this

study), which had greater preference for sandy sediments in the marine part.

The Chromadoridae were a very diverse group with important species as *Chromadora macrolaima* and *Ptycholaimellus ponticus* which are more common in silty sediments and the genus *Chromadorita* (*C. aff. nana*, *C. tentabunda*) which was more frequently observed in coarser sediments and/or higher latitudes. Within the genus *Dichromadora*, we note the predominance of *D. geophila* in brackish water and the more neutral position of *D. cephalata*.

The Axonolaimidae encompassed amongst others *Ascolaimus elongatus* and *Odontophora setosa*, two northerly species which had an affinity for somewhat coarser sediments in the marine area. The

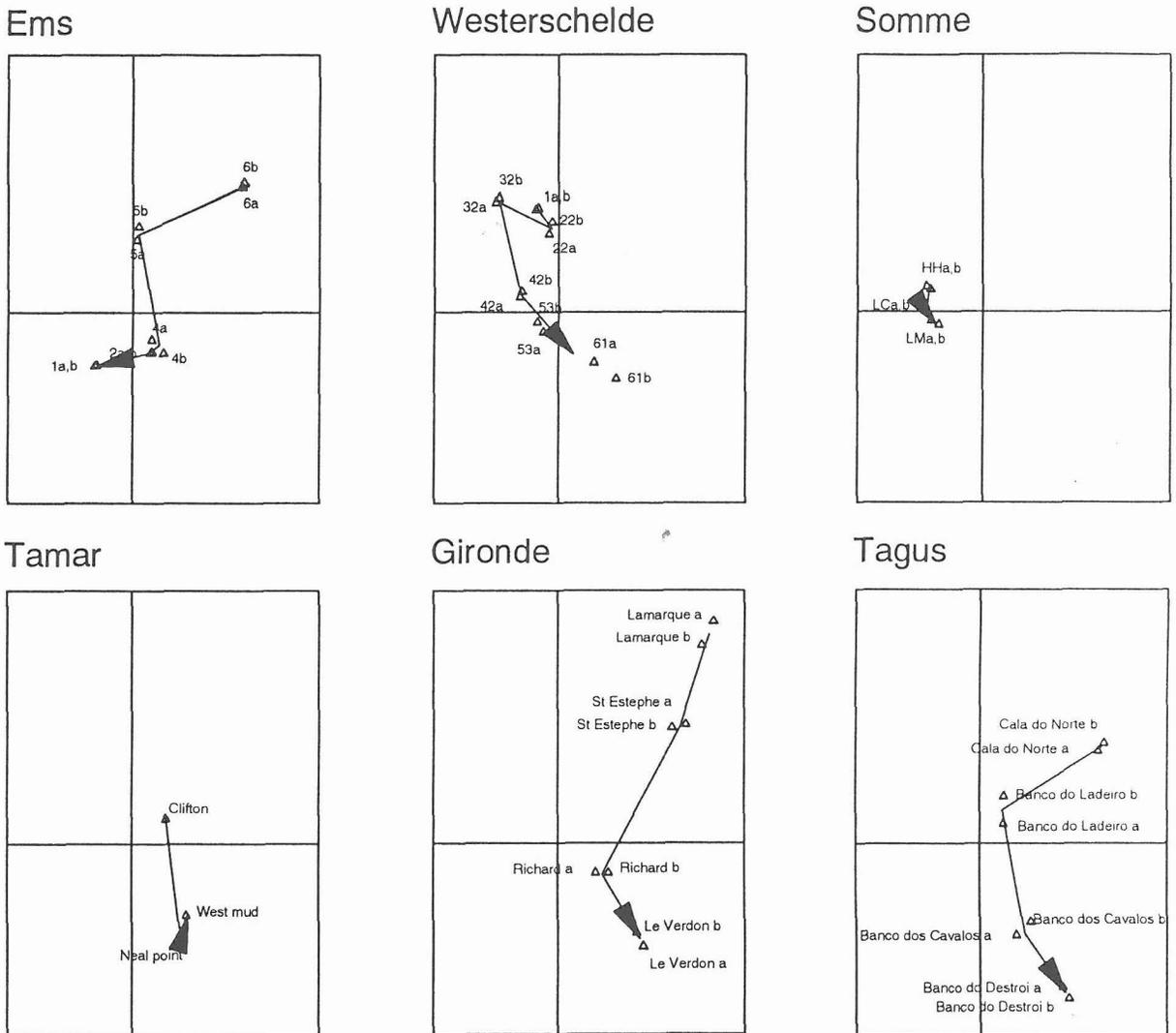


Fig. 7. Station plot of the various European estuaries in two-dimensional CANOCO space (first two axes). For convenience, the stations of one estuary were depicted separately. All plots have the same scale. The salinity gradient is depicted by the arrows.

genus *Axonolaimus* was represented by *A. spinosus*, a southern species in silty brackish-water bottoms, and *A. paraspinosus* having a broader distribution.

The Desmodoridae had as most common representatives *Metachromadora vivipara* and *Spirinia parasitifera*, which are marine species.

Amongst the Microlaimidae *Microlaimus marinus* and *M. robustidens* were more common in coarser sediment, while *M. globiceps* peaked clearly in the more freshwater part of the estuaries.

The Neodiplogasteridae – with their only representative *Pareudiplogaster pararmatus* – were only

observed in a freshwater station of the Gironde, together with *Tobrilus diversipapillatus*.

Amongst the important species we also note *Anoplostoma viviparum* and *Viscosia viscosa* which had a very broad distributional range.

Nematode diversity and life-history traits

When randomly drawing 100 nematodes from the samples, a total of 8 to 29 species was found (N_0 , Fig. 8). Hill's diversity number of the first order (N_1) varied from 3 to 22 equivalent species (Fig. 8), while N_2 varied from 2 to 21, N_∞ from 1 to 9.

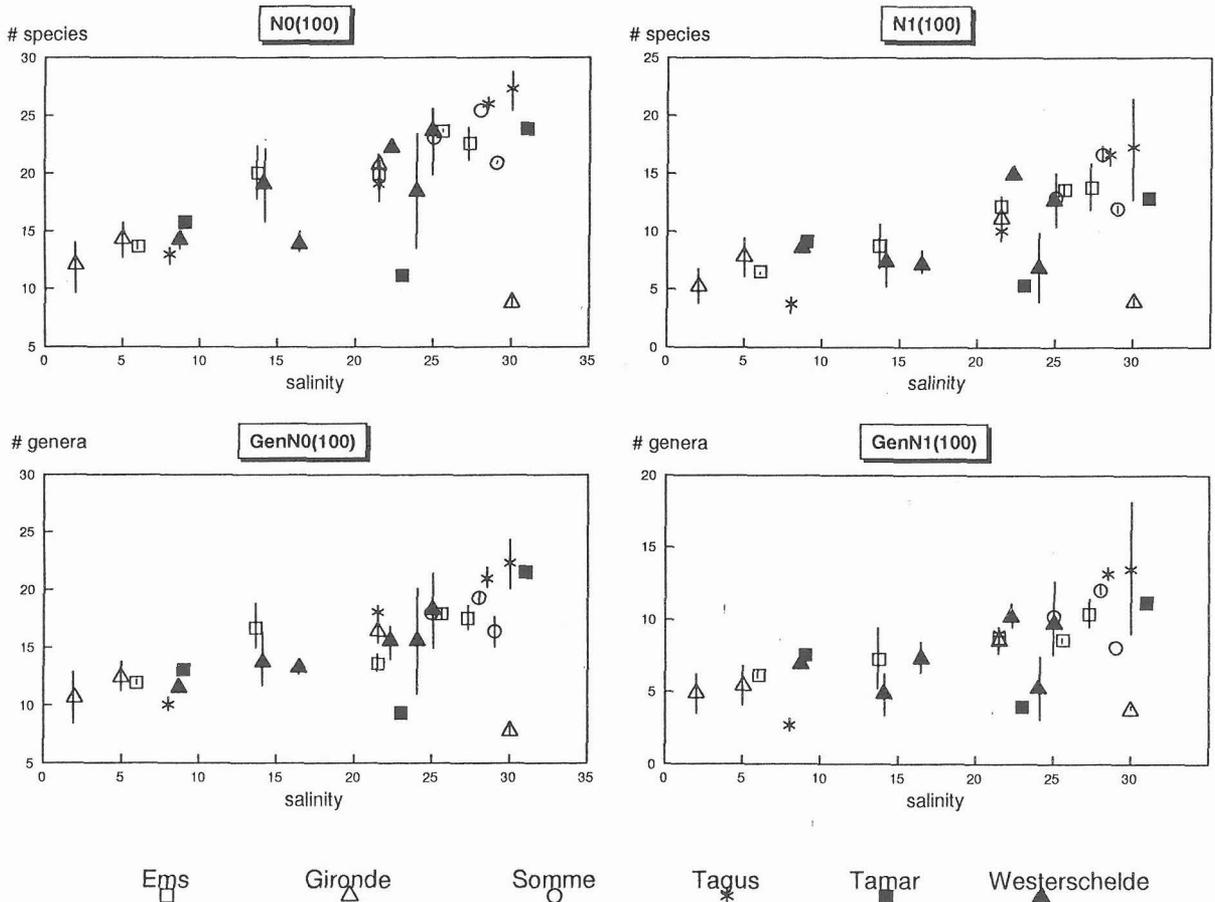


Fig. 8. Hill's diversity numbers of order 1 and 2, calibrated on 100 randomly picked nematodes for the six European estuaries, along the salinity gradient. Upper half: diversity on the species level, lower half: diversity on the genus level.

All estuaries combined, diversity increased with increasing salinity and there was no relationship with granulometry nor with latitude. No estuary could be clearly separated from the others on the basis of diversity although the Gironde and the Tamar had one station that scored relatively low.

Nematode diversity was nearly entirely expressed at the generic level: the diversity at the genus level was about 80 percent of total diversity (all Hill's numbers) and also increased with increasing salinity. On average only 1.2 species per genus were present in any one station and the vast majority were monospecific genera, even on the scale of the entire estuary. Considering the entire study area, many genera were represented by very few species (Addendum). Genera which are successful, both in number of species and density, are *Dichromadora* (5 species), *Microlaimus* (7 species), *Theristus* (9 species) and *Daptonema* (14 species).

The maturity index revealed no real trend (Fig. 9), but the fresh-water station in the Gironde had a much lower index than the other stations, which should indicate a low quality environment. This low value is caused by the relatively high concentrations of *Pareudiplogaster pararmatus* in this station, a species which has a great colonizing ability (Bongers, 1990).

Discussion

The estuarine environment shows large fluctuations of e.g. salinity, temperature and oxygen over different time scales, from a tidal cycle to a year (and longer). Meiobenthic organisms, being bound to the sediment, have to adapt to a range of these conditions and their present occurrence is based on a past set of environ-

mental conditions. How far back one should consider the environmental history for explaining a specific distribution and abundance depends on the life-history characteristics of the species: fast-reproducing and fast-growing species will show a quick response to favourable conditions, while slow-growing and slow-reproducing nematodes have experienced much larger fluctuations. How to translate this into the values of abiotic factors (i.c. salinity) is uncertain, particularly since extreme events (ice cover, storm, desiccation) could possibly be more important. We therefore chose to relate meiobenthic distributions to the abiotic parameters measured at the time of sampling.

Whereas the use of the *in situ* salinity as environmental determinant can cause concern, one could also be sceptical about the scale of this study, encompassing five (resp. 6) estuaries separated up to a thousand kilometres one from another. Moreover, only a few sites in each estuary were sampled. It has for instance been shown that the nematode and copepod fauna can be significantly different at sites as close as several metres to kilometres apart (Eskin & Coull, 1984, Phillips & Fleeger, 1985) and nematodes generally have aggregated distributions on the scale of centimetres (Heip *et al.*, 1985). Moreover, in the intertidal area some zonation along the tidal elevation gradient exists (Warwick, 1971) and for this study, samples were taken at a random spot along this gradient. Even when discarding the temporal variation, it is clear that in this study, in which we had to compromise between spatial coverage and labour intensity, a large degree of intertidal variability within any one of the estuaries has been missed. In view of all these restraints it is remarkable to find a high consistency in the nematode structure along the different estuaries. Mesoscale variability (in the order of kilometres) due to salinity changes or grain-size differences are more important than 'huge'-scale variability (hundreds of kilometres) among estuaries. Microscale variability (centimetres) seemed negligible in view of the great resemblance between subsamples. Of course the importance of such factors as salinity or grain size characteristics on nematode community structure is well documented (e.g. Ward, 1975; Warwick & Gee, 1984; Austen & Warwick, 1989; Vanreusel, 1990; Vincx *et al.*, 1990) but as this is the first study to consistently include among-estuarine variability, the similarity of these gradients in the various estuaries has been clearly demonstrated. Likewise there is nothing innovating in the salinity and sedimentary preferences reported for the species in this study, as they greatly confirm what has been

observed in other areas. However, the species distributions form the basis for sophisticated multivariate techniques like CANOCO and as such they may contribute to our appreciation of and help in understanding the results from these multivariate techniques.

A striking feature of nematode assemblages is the large number of species present in any one habitat – usually an order of magnitude higher than for any other taxon (Heip *et al.*, 1985). The highest known species diversity values for nematode communities were reported from the deep sea (Soetaert *et al.*, 1991), while the lowest nematode diversity was observed in the polluted subtidal muds off the Belgian East coast (Vincx, 1990) where at some sites only one species was present. The diversity values reported here fall well in between these extremes. Diversity in the marine part of the estuaries can be compared to the ones observed in the sublittoral coastal North Sea as reported by Vincx (1990) and Vanreusel (1990).

According to Bouwman (1983) and Heip *et al.* (1985), the estuarine environment was invaded by marine species which have adapted to reduced salinities in varying degrees and these species vanish with decreasing salinity. On its upstream boundary, penetration of freshwater species (up to a salinity of about 10‰) or even of species of terrestrial origin (Bouwman, 1983) add up to those of marine origin. Hence nematode diversity usually increases from about 5‰ salinity towards both the marine and the freshwater zone (Heip *et al.*, 1985). This general trend has been confirmed in this study except for the freshwater part that was not sampled. If such a clear trend can be demonstrated, deviations from this pattern become interesting. Why was the diversity in the most marine station of the Gironde and in the mid-saline station of the Tamar (Neal point) lower than one would expect? Diversity patterns in the Tamar were discussed by Warwick & Gee (1984) and by Austen & Warwick (1989). They argue – in agreement with Huston's dynamic equilibrium hypothesis – that the lower diversity at mid-salinity could be related to the lower degree of disturbance by macrofauna, which is far less numerous here. The nematode community in the marine station of the Gironde (Le Verdon) was very similar to the low-diversity site of the Tamar: it was largely dominated by *Sabatieria punctata* (group) and *Terschellingia communis*, whereas *T. communis*, *T. longicaudata*, *Metachromadora vivipara* and *S. punctata* (group) were co-dominant in Neal point. All these species are conservative with low respiration rates and long generation times. They are typical for tidal mud

flats with rather anoxic sediments (Vincx *et al.*, 1990) and this might also be the case for the sediments at Le Verdon (Castel, pers. comm.). Although the low diversity in these stations could be due to a lower degree of disturbance, as invoked by the dynamic equilibrium hypothesis, the macrofauna cannot be the cause of this at Le Verdon where macrofaunal biomass is highest (Castel, 1992) and, remarkably enough, the macrofaunal diversity is also reasonably high in this station. It may be that the low oxygen concentrations in some of the mud flats do not allow the establishment of the higher-diversity assemblage one could expect according to salinity, as only a few species have physiological tolerances suited for persisting in such a harsh environment.

Nematodes have been shown to be possible indicators of pollution or other kinds of disturbances (Heip *et al.*, 1985) and especially the influence of perturbations on diversity has been well documented (Lambhead *et al.*, 1983; Platt *et al.*, 1984) and debated (Hodda & Nicholas, 1986). Amongst the estuaries studied, organic and inorganic pollution have the highest levels in the Westerschelde, and one would expect to find significant differences in diversity in this estuary, as compared to the other estuaries. This was shown to be the case for intertidal copepods (Van Damme *et al.*, 1984), when compared to the Ems. However, the deviation of nematode diversity from the general trend in the Westerschelde is only suggestive at most and not consistent enough to establish a possible effect of pollution on nematode diversity. As for the study of copepods in Van Damme *et al.* (1984), the diversity differences between the Ems and the Westerschelde could be reflections of the density differences, because of the large dependence of diversity indices on the number of individuals (Soetaert & Heip, 1990).

Perhaps the most striking result of this study lies in the distribution of higher meiofaunal groups in the various estuaries. Whereas nematodes were overall the most abundant organisms in the intertidal zone, their dominance was much lower in the Ems compared to the other estuaries. Only in the Ems have we observed important populations of harpacticoids, turbellarians, ciliates and gastrotrichs in some stations. Although the occurrence of these high densities could very well be short-term events, this does not explain their absence in other estuaries and the causes of this are uncertain.

The paucity of harpacticoid copepods in the Westerschelde, when compared to the Ems, was already noted by Van Damme *et al.* (1984) and ascribed to pollution effects in the Westerschelde. From our study, the West-

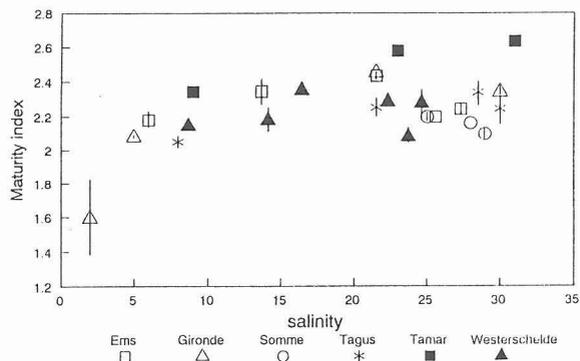


Fig. 9. Maturity index of the various stations along the salinity gradient.

erschelde indeed appeared to be nearly devoid of intertidal populations of harpacticoids, whereas the other estuaries had, albeit weakly developed, populations in at least some of their stations. However, harpacticoids were shown to be more abundant in the subtidal area of the Westerschelde (max. 27 ind 10 cm⁻², Soetaert *et al.*, 1994) compared to the intertidal and it would be interesting to see whether these subtidal abundances are also consistently lower when compared to the other estuaries. Subtidal samples analyzed from the Tagus indeed suggest that Westerschelde abundances are lower since mean densities of more than 1500 ind 10 cm⁻² were observed in one Tagus station (own unpublished data).

Total meiobenthic densities tended to increase exponentially with increasing salinities but were low in the most saline range of the Tagus and to a smaller extent of the Westerschelde. The lack of low-salinity tolerance of species of marine origin is usually invoked to explain the decreasing densities in the low salinity ranges of an estuary (e.g. Coull, 1988; Montagna & Kalke, 1992). However, whereas this could very well explain the presence or absence of species (and hence diversity), it is unclear why species that have adapted to brackish situations cannot attain large densities. Moreover, large densities were observed in the salt marshes of the brackish area of the Westerschelde (Van Damme *et al.*, 1980) and this seems to contradict the thesis of salinity tolerance.

Other explanations could be linked with food availability and both the supply and reactivity of the organic matter in the bottom is important. In the turbid regions of the estuaries primary production in the water is lowest (Kromkamp *et al.*, 1992; Soetaert *et al.*, 1994b) and this may result in a lower food supply for the benthos. Bacterial mineralization in this turbid area

is high (Goosen *et al.*, 1992; Soetaert & Herman, 1995) and hence the residual organic matter of fluvial descent, downstream from this region, will be more refractory (Soetaert & Herman, 1995) and thus less suitable as a food source. On the other hand primary pelagic productivity increases downstream as turbidity decreases (Soetaert *et al.*, 1994b). The closer to the marine zone, the more important the input of organics from marine origin will become (Soetaert & Herman, 1995) and this higher quality food source could allow the benthos to increase in abundance. Also of possible importance in explaining meiobenthic density is macrofaunal predation (e.g. Warwick & Gee, 1984). However, the magnitude of macrofaunal interaction with the meiofauna along the salinity gradient is difficult to assess. In the Westerschelde for instance, macrofaunal biomass increases with increasing salinities but the trophic structure of the macrofauna changes concurrently from detritus-feeding (and thus meiofauna consuming) in the brackish part to filter feeding in the marine part (Meire *et al.*, 1991). Van Damme *et al.* (1980) even invoked pollution effects to explain the lower densities of the Westerschelde meiobenthos compared to the Ems. However, as may be apparent from this study, meiobenthic densities of the Westerschelde are not consistently lower, except perhaps in the marine part. Moreover, the Ems was not so well chosen as a reference estuary as from our study it appears to be the only estuary where large densities in the brackish part were observed. Nevertheless, in many instances pollution decreases in parallel with increasing salinity and thus cannot be ruled out as a possible cause of benthic depauperation. Another factor which could be of possible importance is the degree of environmental fluctuation, with brackish areas that are usually more unpredictable (varying current velocities, steeper gradients of several solutes and particulates), while the human impact (dredging) usually is more intense in this region.

Pollution is expected to be high in the Tagus, which receives high amounts of untreated waste from the city of Lisbon, and many industrial effluents are pumped into the estuary. This estuary has low numbers of meiobenthic animals all along its banks, and one could be tempted to conclude that this is a pollution effect. But seasonal environmental fluctuations in the Tagus are much more pronounced than in the other estuaries and this too could cause low densities. However, too little is known about the abiotic and biotic factors from this area to be conclusive about the causes of meiobenthic distributions.

Another way of looking for anomalies among stations is by comparing the life-history traits of nematodes: are they predominantly *r* or *K* strategists? Very recently, an index has been proposed that summarizes this information into one number: the maturity index (Bongers, 1990; Bongers *et al.*, 1991). On the whole, not much information could be extracted from this measure and it appeared to be unable to reveal gradients. However, it did point to a spuriously low 'maturity' of the station located in the most freshwater part of the Gironde (Lamarque). This muddy intertidal flat was also very poor in macrobenthos, which was dominated by oligochaetes (Castel, 1992) and it is situated at about 30–40 km from the city of Bordeaux.

The low maturity of the nematode community could nearly entirely be accounted for by the dominance of the freshwater nematode *Pareudiplogaster pararmatus*. This nematode is known to be successful in waste-water exposed intertidal mud flats in the low-salinity range of estuaries (Romeyn *et al.*, 1983) and belongs to a family which has high colonization capabilities (Bongers, 1990). Being ovoviviparous, it can survive under extreme conditions and become dominant due to the disappearance of less resistant competitors. Its dominance at Lamarque could thus be indicative for some kind of organic enrichment in this area although the total densities were relatively low. Another possibility is that we have observed a pioneer community after some kind of 'catastrophic event' (e.g. storm) has taken place.

In 1980 *Pareudiplogaster pararmatus* was the most important member of the nematode fauna in an area exposed to organic pollution in the Ems (Bouwman *et al.*, 1983). The fact that it was not observed in the Ems during this study could indicate the improved conditions in this part of the estuary as was shown from the macrobenthos (Esselink *et al.*, 1989).

Although ecological interpretations are difficult to make without an extensive background environmental data set, this study has provided some insight in the structure of estuarine meiobenthic communities. The results of this work could serve as a base-line for a more intensive study where smaller spatial scales and temporal variation should be taken into account and a more extensive environmental data set should be procured. If one wants to spot pollution or produce conclusive evidence for the causes of benthic distributions, a global research project as this one is not appropriate. Yet it can provide a reference frame against which other results can be put into perspective.

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Appendix. Species list, indicating the maximum density (10 cm^{-2}) of each species in the five estuaries of the current study and the Tamar (data derived from Warwick & Gee, 1984).

	Ems	Wester- schelde	Somme	Tamar	Gironde	Tagus
Enoplida						
Enoplidae						
Enoplus brevis	—	—	**	—	—	—
Enoplus sp	*	*	—	—	—	—
Thoracostomopsidae						
Enoploides longispiculosus	**	***	***	—	—	—
Enoplolaimus litoralis	—	—	**	—	—	—
Enoplolaimus propinquus	—	**	—	—	—	—
Anoplostomatidae						
Anoplostoma viviparum	***	**	—	**	**	***
Chaetonema riemanni	**	—	—	—	—	—
Ironidae						
Syringolaimus sp	—	*	—	—	*	*
Leptosomatidae						
Leptosomatidae T1	—	—	—	—	—	**
Oxystominidae						
Halalaimus gracilis	***	**	**	*	**	**
Halalaimus sp	—	—	—	*	**	—
Halalaimus T1	—	—	—	—	—	**
Halalaimus T2	—	—	—	—	—	**
Halalaimus T3	—	—	—	—	—	*
Nemanema cylindricaudatum	**	—	—	*	—	—
Oxystomina elongata	—	—	**	*	—	—
Oxystomina sp	**	—	—	—	—	—
Thalassoalaimus septentrionalis	**	*	—	—	—	**
Oncholaimidae						
Adoncholaimus fuscus	***	***	***	—	—	—
Adoncholaimus thalassophygas	—	—	—	—	*	—
Oncholaimellus mediterraneus	—	*	—	—	—	—
Oncholaimidae sp	—	—	—	—	—	**
Oncholaimus oxyuris	—	*	***	—	—	—
Oncholaimus sp	**	—	—	—	*	—
Viscosia abyssorum	—	—	—	*	—	—
Viscosia aff rustica	***	**	—	—	—	—
Viscosia glabra	**	—	—	—	—	—
Viscosia viscosa	***	***	***	**	***	***
Enchelidiidae						
Calyptronema maxweberi	**	**	***	*	**	—
Eurystomina sp	—	—	—	—	—	**

Appendix (Continued).

	Ems	Wester- schelde	Somme	Tamar	Gironde	Tagus
Tripyloidea						
Bathylaimus australis	—	**	—	—	—	—
Bathylaimus sp	—	—	—	—	*	**
Bathylaimus stenolaimus	—	*	—	—	—	—
Tripyloides gracilis	—	**	***	*	**	—
Tobrilidae						
Tobrilus diversipapillatus	—	—	—	—	*	—
Trefusiida						
Trefusiidae						
Trefusia Longicaudata	—	***	—	—	—	—
Trefusia multipapillatus	***	—	—	—	—	—
Trefusia S1	—	—	***	—	—	—
Trefusia S2	—	—	**	—	—	—
Trefusia W2	—	*	—	—	—	—
Chromadorida						
Chromadoridae						
Atrochromadora microlaima	*	*	—	**	—	—
Chromadora aff nudicapitata	—	—	—	—	—	**
Chromadora axi	—	*	—	—	—	**
Chromadora macrolaima	***	**	***	—	****	***
Chromadorida sp	**	—	—	—	*	**
Chromadorina germanica	—	—	—	—	*	—
Chromadorita aff nana	**	***	—	—	—	—
Chromadorita tentabunda	**	***	***	—	**	**
Dichromadora cephalata	**	*	***	**	**	**
Dichromadora cucullata	—	*	—	—	—	—
Dichromadora geophila	***	**	—	**	**	***
Dichromadora hyalocheile	—	—	***	—	—	—
Dichromadora sp	—	—	**	—	—	**
Dichromadora T3	—	—	—	—	—	*
Hypodontolaimus balticus	—	—	—	*	—	—
Hypodontolaimus W1	—	**	—	—	—	—
Neochromadora sp	—	—	—	*	—	—
Prochromadorella ditlevseni	—	**	***	—	—	—
Ptycholaimellus ponticus	***	*	—	**	****	**
Spilophorella candida	—	*	—	—	—	*
Spilophorella paradoxa	—	*	**	*	—	*

Appendix (Continued).

	Ems	Wester- schelde	Somme	Tamar	Gironde	Tagus
<i>Comesomatidae</i>						
<i>Cervonema</i> G1	—	—	—	—	**	—
<i>Cervonema</i> T1	—	—	—	—	—	***
<i>Paracomesoma</i> sp	—	—	—	*	—	—
<i>Sabatieria celtica</i>	***	*	—	*	—	—
<i>Sabatieria longisetosa</i>	—	—	—	—	—	**
<i>Sabatieria longispinosa</i>	***	—	—	—	—	—
<i>Sabatieria punctata</i> group	****	***	—	**	****	***
<i>Sabatieria</i> sp	**	—	**	—	*	**
<i>Setosabatieria hilarula</i>	—	—	—	*	—	**
<i>Ethmolaimidae</i>						
<i>Neotonchus</i> aff <i>cupulatus</i>	—	*	—	—	—	—
<i>Neotonchus</i> sp	—	—	—	*	—	—
<i>Cyatholaimidae</i>						
<i>Cyatholaimidae</i> sp	—	—	***	—	—	—
<i>Paracanthochus</i> aff <i>caecus</i>	—	—	—	*	—	—
<i>Paracanthochus</i> aff <i>heterodontus</i>	—	—	—	—	—	***
<i>Paracanthochus</i> aff <i>thausiasius</i>	—	—	****	—	—	—
<i>Paracanthochus caecus</i>	**	—	—	—	—	—
<i>Paracanthochus heterodontus</i>	***	—	—	—	—	**
<i>Paracanthochus thausiasius</i>	—	**	—	—	—	—
<i>Paracyatholaimoides</i> W1	—	*	—	—	—	—
<i>Paracyatholaimus</i> W1	—	**	—	—	—	—
<i>Praeacanthochus punctatus</i>	***	*	***	*	**	—
<i>Selachinematidae</i>						
<i>Halichoanolaimus robustus</i>	**	—	—	—	—	*
<i>Desmodoridae</i>						
<i>Desmodora</i> A	—	—	—	*	—	—
<i>Desmodora</i> B	—	—	—	*	—	—
<i>Leptonemella</i> sp	—	—	**	—	—	—
<i>Metachromadora</i> aff <i>suecica</i>	***	**	—	—	—	—
<i>Metachromadora remanei</i>	**	***	***	—	**	**
<i>Metachromadora</i> sp	—	—	**	—	—	—
<i>Metachromadora vivipara</i>	****	***	—	***	—	—
<i>Molgolaimus cuanensis</i>	***	—	—	—	—	—
<i>Molgolaimus</i> S1	—	—	***	—	—	—
<i>Molgolaimus</i> S2	—	—	**	—	—	—
<i>Molgolaimus</i> sp	—	—	***	—	—	*
<i>Molgolaimus tenuispiculum</i>	—	—	—	*	—	—
<i>Molgolaimus turgofrons</i>	—	*	—	—	—	—
<i>Onyx sagittarius</i>	—	*	—	—	—	—
<i>Sigmaphoranema</i> aff <i>rufus</i>	—	**	—	—	—	—
<i>Spirinia parasitifera</i>	**	***	—	*	—	—

Appendix (Continued).

	Ems	Wester- schelde	Somme	Tamar	Gironde	Tagus
<i>Microlaimidae</i>						
<i>Aponema torosa</i>	—	—	—	*	—	—
<i>Calomicrolaimus S1</i>	—	—	****	—	—	—
<i>Calomicrolaimus S3</i>	—	—	****	—	—	—
<i>Microlaimus arenicola</i>	—	**	***	—	—	—
<i>Microlaimus globiceps</i>	****	**	***	—	—	—
<i>Microlaimus marinus</i>	***	***	****	—	—	—
<i>Microlaimus parahonestus</i>	***	***	—	**	—	—
<i>Microlaimus robustidens</i>	—	—	ph ****	*	—	—
<i>Microlaimus sp</i>	**	—	—	—	—	—
<i>Microlaimus W1</i>	—	**	—	—	—	—
<i>Microlaimus W4</i>	—	*	—	—	—	—
<i>Monoposthiidae</i>						
<i>Monoposthia mirabilis</i>	—	**	—	—	—	—
<i>Monoposthia sp</i>	**	—	—	—	—	—
<i>Nudora bipapillata</i>	—	—	—	**	—	—
<i>Leptolaimidae</i>						
<i>Antomicron elegans</i>	**	—	**	—	*	*
<i>Camacolaimus tardus</i>	—	**	***	—	—	—
<i>Dagda bipapillata</i>	—	*	—	—	—	—
<i>Deontolaimus papillatus</i>	—	*	—	—	—	—
<i>Leptolaimus acicula</i>	—	*	—	—	—	—
<i>Leptolaimus ampullaceus</i>	—	*	—	—	—	—
<i>Leptolaimus elegans</i>	—	**	—	—	—	—
<i>Leptolaimus luridus</i>	—	—	—	—	—	*
<i>Leptolaimus papilliger</i>	****	—	—	*	**	—
<i>Leptolaimus S1</i>	—	—	***	—	—	—
<i>Leptolaimus sp</i>	—	*	—	—	*	*
<i>Stephanolaimus aff spartinae</i>	—	—	***	—	—	—
<i>Haliplectidae</i>						
<i>Haliplectus wheeleri</i>	—	—	—	—	—	**
<i>Aegialoalaimidae</i>						
<i>Aegialoalaimus aff tenuicaudatus</i>	—	—	—	—	—	**
<i>Aegialoalaimus elegans</i>	**	—	—	—	**	*
<i>Cyarthonema E1</i>	**	—	—	—	—	—
<i>Cyarthonema germanica</i>	***	—	—	—	**	—
<i>Cyarthonema W1</i>	—	*	—	—	—	—
<i>Southernia zosteræ</i>	**	**	—	—	—	—

Appendix (Continued).

	Ems	Wester- schelde	Somme	Tamar	Gironde	Tagus
Tubolaimoididae						
Chitwoodia warwicki	—	**	—	—	—	—
Meyliidae						
Meyliidae T1	—	—	—	—	—	**
Desmoscolecidae						
Calligyus sp	—	—	—	*	—	—
Desmoscolex falcatus	—	—	—	**	—	—
Tricoma sp	—	—	—	*	—	—
Monhysterida						
Monhysteridae						
Diplolaimella sp	—	—	***	—	*	*
Monhysteridae sp	**	**	***	*	**	**
Monhysteridae T1	—	—	—	—	—	**
Xyalidae						
Daptonema acc Bouwman	***	*	***	—	—	—
Daptonema cfr biggi	—	—	—	—	**	—
Daptonema G1	—	—	—	—	***	—
Daptonema kornoense	—	—	—	—	—	**
Daptonema normandicum	**	***	***	*	**	—
Daptonema oxycerca	***	—	—	*	***	*
Daptonema procera	—	—	—	*	—	—
Daptonema riemanni	****	***	****	—	—	—
Daptonema setosa	***	**	—	*	***	***
Daptonema sp	**	**	***	—	***	***
Daptonema T1	—	—	—	—	—	**
Daptonema T2	—	—	—	—	—	*
Daptonema tenuispiculum	—	**	—	—	—	—
Daptonema W1	—	**	—	—	—	—
Daptonema xyaliforme	**	—	—	—	**	**
Metadesmolaimus 2	—	*	—	—	—	—
Metadesmolaimus E1	**	—	—	—	—	—
Metadesmolaimus gaelicus	—	*	—	—	—	—
Paramonohystera E1	***	—	—	—	**	**
Paramonohystera sp	—	*	—	—	—	—
Pseudothieristus furcatus	—	—	—	—	—	*
Theristus 1	—	**	—	—	—	—
Theristus acer	**	—	***	*	—	**
Theristus aff profundus	—	*	—	—	—	—
Theristus blandicor	****	***	—	—	—	—
Theristus cfr subcurvatus	**	**	—	—	—	—

Appendix (Continued).

	Ems	Wester- schelde	Somme	Tamar	Gironde	Tagus
<i>Theristus ensifer</i>	—	*	***	—	—	—
<i>Theristus G1</i>	—	—	—	—	*	—
<i>Theristus longus</i>	***	**	***	—	—	—
<i>Theristus pertenuis</i>	***	**	****	—	—	—
<i>Theristus sp</i>	**	—	***	—	—	—
<i>Trichotheristus mirabilis</i>	—	***	—	—	—	—
<i>Xyala striata</i>	—	*	—	—	—	—
Sphaerolaimidae						
<i>Sphaerolaimus balticus</i>	—	—	—	*	—	—
<i>Sphaerolaimus gracilis</i>	—	—	—	*	**	**
<i>Sphaerolaimus hirsutus</i>	**	—	—	*	**	*
<i>Sphaerolaimus sp</i>	—	**	—	—	—	—
Siphonolaimidae						
<i>Siphonolaimus sp</i>	—	*	—	—	—	—
Linhomoeidae						
<i>Desmolaimus S1</i>	—	—	***	—	—	—
<i>Desmolaimus T1</i>	—	—	—	—	—	*
<i>Desmolaimus zeelandicus</i>	***	—	—	**	—	—
<i>Eleutherolaimus aff stenosoma</i>	—	—	—	—	—	**
<i>Eleutherolaimus amasi</i>	**	—	—	—	—	—
<i>Eleutherolaimus sp</i>	**	—	—	—	—	—
<i>Eleutherolaimus stenosoma</i>	**	**	—	*	—	—
<i>Linhomoeidae T1</i>	—	—	—	—	—	**
<i>Linhomoeidae sp</i>	**	*	***	—	**	*
<i>Linhomoeidae W1</i>	—	*	—	—	—	—
<i>Linhomoeidae W2</i>	—	*	—	—	—	—
<i>Linhomoeidae W4</i>	—	*	—	—	—	—
<i>Linhomoeidae W5</i>	—	**	—	—	—	—
<i>Linhomoeus S1</i>	—	—	***	—	—	—
<i>Megadesmolaimus W1</i>	—	**	—	—	—	—
<i>Metalinhomoeus aff biformis</i>	**	**	****	—	**	***
<i>Metalinhomoeus biformis</i>	—	**	****	—	—	**
<i>Paralinhomoeus ilensis</i>	**	—	—	—	—	—
<i>Paralinhomoeus sp</i>	**	—	—	—	—	**
<i>Paralinhomoeus T1</i>	—	—	—	—	—	**
<i>Terschellingia communis</i>	—	*	—	**	****	**
<i>Terschellingia longicaudata</i>	—	—	—	***	**	**

Appendix (Continued).

	Ems	Wester- schelde	Somme	Tamar	Gironde	Tagus
<i>Axonolaimidae</i>						
<i>Ascolaimus elongatus</i>	***	***	****	—	—	—
<i>Axonolaimus</i> cfr <i>orus</i>	—	—	—	—	—	**
<i>Axonolaimus paraspinosus</i>	***	*	—	**	**	**
<i>Axonolaimus spinosus</i>	—	—	—	—	**	*
<i>Odontophora</i> aff. <i>paravilloti</i>	—	*	—	—	—	—
<i>Odontophora rectangula</i>	***	***	—	—	—	—
<i>Odontophora setosa</i>	***	***	****	*	—	—
<i>Odontophora</i> sp	**	—	***	—	—	—
<i>Odontophora</i> W4	—	**	—	—	—	—
<i>Pseudolella granulifera</i>	—	—	—	—	***	***
<i>Diplopeltidae</i>						
<i>Campylaimus gerlachi</i>	—	—	—	—	—	**
<i>Diplopeltis incisus</i>	—	—	—	*	—	—
<i>Diplopeltula asetosa</i>	**	—	—	—	—	—
<i>Rhabditida</i>						
<i>Diploscapteridae</i>						
<i>Diploscapter</i> sp	**	*	—	—	—	—
<i>Neodiplogasteridae</i>						
<i>Pareudiplogaster pararmatus</i>	—	—	—	—	***	—
<i>Dorylaimida</i>						
<i>Dorylaimida</i>						
<i>Dorylaimida</i> W2	—	*	—	—	—	—

(—) absent, (*) 0–10 ind, (**) 10–100, (***) 100–1000, (****) >1.000