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Comparative study of the hyperbenthos of three European estuaries

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Abstract

The hyperbenthic fauna of the subtidal channels of the Eems (N. Netherlands), Westerschelde (S.W. Netherlands), and Gironde (S.W. France) estuaries was sampled within a 15-day period in summer 1991. In each estuary, quantitative samples were taken at regularly spaced stations covering the entire salinity gradient from marine conditions at the mouth to nearly freshwater conditions upstream. The diversity of the samples and the distribution of the species along the main estuarine gradients were assessed. Hyperbenthic communities were identified using different multivariate statistical techniques. The species composition and the density and biomass of the dominant species of each community were compared among communities.

Spatial patterns in density, biomass and diversity of the hyperbenthos were similar in the three estuaries: diversity was highest in the marine zone where density and biomass were lowest. Diversity decreased upstream and was lowest in the brackish part where density and biomass reached maximal values. In Eems and Gironde there was a slight increase in diversity towards the freshwater zone. Within each estuary two (Westerschelde) or three (Eems and Gironde) communities could be distinguished and their position along the unidirectional salinity-turbidity-temperature gradient was similar: a marine community in the high salinity zone, a brackish water community in the middle reaches and a third community (absent in the Westerschelde) in the stations with the lowest salinities. Qualitative and quantitative differences in the corresponding hyperbenthic communities among estuaries were evident. Some species were restricted to one or two of the estuaries studied, while others, especially the abundant species in the brackish part, were common to all three. Still, these differences were marginal compared to the overriding similarity of the hyperbenthos in the three estuaries. The distribution of single species in the estuaries varied to some extent but the among estuary differences in density and biomass in comparable salinity zones rarely exceeded an order of magnitude.

In the Westerschelde, the low salinity hyperbenthic community was completely absent. Upstream of the 10 g l^{-1} isohaline the dissolved oxygen concentration dropped to a critical threshold value for hyperbenthic life. The populations of a number of species, which in Gironde and Eems reached highest density and biomass in this zone, seem to have (almost) disappeared from the Westerschelde (e.g. *Gammarus zaddachi* and *Palaemon longirostris*). Other brackish water species did not occur in their 'normal' salinity range and their populations have shifted to higher, atypical salinity zones (e.g. *Neomysis integer*, *Mesopodopsis slabberi*, *Pomatoschistus microps* and *Gammarus salinus*.

Introduction

Estuaries are located at the interface between sea and land. As ecosystems they perform several vital functions, e.g. as nursery areas for juvenile fish and shrimp, migration routes for anadromous and catadromous fish, habitats for estuarine residents and spawners, etc.

(Ketchum, 1983). They are highly productive systems around which many human activities are concentrated (shipping, cities, industry). Correlated with this is a high anthropogenic stress (e.g. dredging, eutrophication, pollution,...) which may have important negative effects on the biota and thus the ecological structure of the system. Though interest in the functioning of estuaries has sharply increased in the last decades, thorough baseline studies on several of the food web compartments are still lacking, even for the relatively well studied northwestern European estuaries. Historical data are scanty and virtually no long time series are available on the different functional compartments of estuarine ecosystems (but see Castel 1993 and this volume). For an understanding of pollution impact only extensive sampling campaigns permit comparisons of estuaries subjected to high pollution loads with relatively pristine estuaries. The influence of zoogeographical differences (i.e. latitudinal effects) can be accommodated by choosing estuaries situated both north and south of the estuary under consideration. To date few synoptic studies have been conducted using the same methodology in different estuaries. This is especially true for the hyperbenthos since sampling methodology for this compartment is far from standardised and recognition of the importance of the hyperbenthos is relatively recent. Research on the hyperbenthos has only started in the last few decades (the term was defined by Beyer in 1958) and very few studies have been conducted in European estuaries. For purposes of comparison, scanty records of accidentally caught hyperbenthic animals in zooplankton and macrobenthos surveys are virtually the only source of information. Hyperbenthic animals (mainly mysids, but also amphipods, juvenile shrimp, ...) successfully exploit a diversity of food resources and are an important link in the detritus based food chains. Their size is intermediate between zooplankton and fish and nearly all estuarine fish species are found to feed to some extent on *Neomysis integer* and *Crangon crangon* (e.g. Hartman, 1940, review in Mauchline 1980). Any threats to the estuarine system which affect this fauna will consequently endanger its nursery function for commercially important crustaceans and fish.

For this study three major European estuaries were sampled quasi-synoptically along the longitudinal salinity gradient ranging from marine waters near the mouth to nearly fresh water upstream: the Eems (north Netherlands), the Westerschelde (southwest Netherlands) and the Gironde (southwest France). All samples were taken with a single gear and processed by the same research team. Sampling was concentrated within a short time interval (15 days) to minimise seasonal effects on hyperbenthic community structure. Indeed, seasonal patterns can dominate hyperbenthic community structure due to the presence of temporary hyperbenthic species (Hamerlynck & Mees, 1991). The hyperbenthos of the Westerschelde estuary, which is characterised by a high degree of industrialisation and urbanisation making it one of the most polluted rivers of Europe, has been intensively studied in recent years (Mees & Hamerlynck, 1992, Cattrijsse *et al.*, 1993, Mees *et al.* 1993a, Mees *et al.* 1993b). The hyperbenthos of the Gironde has been studied by Sorbe (1981). No information on the hyperbenthos of the Eems estuary was available to date.

Materials and methods

Study area (Fig. 1)

The Eems-Dollard estuary is situated in the northeast of the Netherlands on the border with Germany. The system is about 33 km long from Eemshaven to Pogum. The surface area of the estuary (excluding the part extending to the Wadden Sea islands downstream Eemshaven) is approximately 255 km^2, including a fresh water tidal area in the Eems of about 37 km^2 (de Jonge, 1988). The tidal influence is artificially stopped upstream of Leer (Germany). In the marine part two major gullies are separated by sandbanks; further upstream (past the mouth of the Dollard) only one channel remains. The major source of freshwater inflow is the river Eems (catchment area of about 12 650 km^2), which has a variable discharge ranging from 25 to 390 m^3 s^{-1}. The Westerwoldsche Aa has no well defined watershed and discharges roughly 10 % (5.1 to 31 m^3 s^{-1}) of the discharge of the river Eems in the southeast corner of the Dollard. Variable (and still smaller) amounts of fresh water enter the estuary from some channels near Delfzijl. The tidal excursion is approximately 15 km. There is no stratification and water turnover is 18 to 36 days. Suspended matter concentrations in the maximum turbidity zone rarely exceed 0.4 g l^{-1} (Baretta & Ruardij, 1988). Dissolved oxygen concentration in the estuary proper rarely drops below 70% of the saturation value, even in the maximum turbidity zone.

The Westerschelde estuary is the lower part of the river Schelde. The estuarine zone of the tidal system extends from the North Sea (Vlissingen) to Antwer-

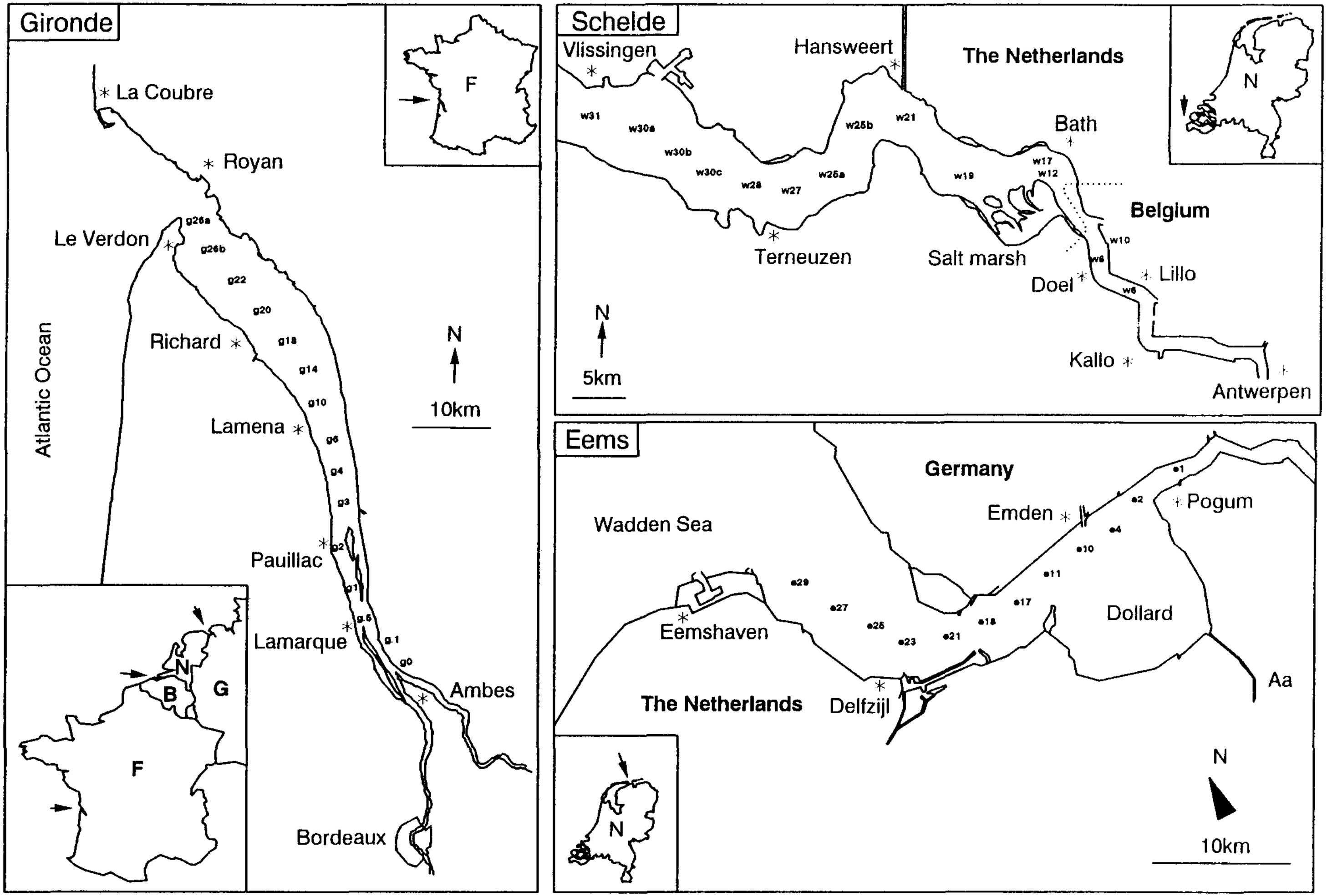

Fig. 1. Study area and sampling sites: the names of the samples are composed of a letter indicating the estuary and a number representing the salinity zone in which it was taken.

pen, 80 km inland. The estuary is rain fed, with a catchment area of some 20 000 km^2. Its surface is approximately 300 km^2. The seaward part is a well mixed region characterised by a complex system of channels. There are two major gullies in the marine part and only one main channel in the weakly stratified region more upstream. Tidal influence extends to Gent (160 km from mouth) were it is artificially stopped. The residence time in the brackish part is rather high: about 60 days or 120 tidal cycles in summer (Soetaert & Herman, submitted). Consequently fresh water (average inflow 100 m^3 s^{-1}; range 30 to 500 m^3 s^{-1}) dilution is gradual and downstream transport is relatively slow. Shifts in salinity zone distribution occur in accordance with seasonal variations in the freshwater inflow. The physical, chemical and biological characteristics are discussed in Heip (1989), Herman *et al.* (1991) and Van Eck *et al.* (1991). The estuary is subject to a large anthropogenic stress, e.g. dredging (Belmans, 1988), and carries high pollution loads, both in anorganic and organic contaminants (Duursma *et al.* 1988). Dissolved oxygen concentration decreases sharply upstream the Dutch–Belgian border and the riverine part of the system is anoxic throughout most of the year (Herman *et al.*, 1991). Suspended matter concentrations are never higher than 0.05 g l^{-1} suggesting there is no real maximum turbidity zone in this estuary.

The Gironde estuary on the atlantic coast of France is the estuarine part of the rivers Garonne and Dordogne, which together have a catchment area of about 71 000 km^2 (Jouanneau & Latouche, 1981). The estuary is 70 km long from the inlet near Le Verdon to Bec d'Ambès where both rivers meet. The upstream part is characterised by the presence of numerous islands and sandbanks separating a network of channels. The downstream part consists of two main channels separated by shallower areas and sandbanks. The surface area at flood tide is 625 km^2. In summer tidal influence extends 160 km upstream Pointe de Grave. The water is well mixed: especially in summer there is virtually no stratification. Seasonal variations in salinity are related to freshwater discharge. River flow of the Garonne and Dordogne varies between 200 m^3 s^{-1} in summer to 1500 m^3 s^{-1} in winter (800–1000 m^3 s^{-1} on average). The residence time of a water particle is on average 20 tidal cycles in winter and 140 tidal cycles in summer. Dissolved oxygen concentrations in summer are never lower than 70% of the saturation value. One of the main features of the Gironde is the high turbidity of the water: suspended matter concentrations in the maximum turbidity zone generally exceed 1 g l^{-1} and values of 5 g l^{-1} and higher are regularly recorded (mainly silt and clay particles from freshwater origin).

Sampling

The location of the sampling stations in Eems, Westerschelde and Gironde is shown in Fig. 1. In the Eems 12 evenly spaced (3 km) stations were sampled in salinity zones ranging from 28.6 g l^{-1} near Eemshaven to 1.0 g l^{-1} near Pogum. In the Westerschelde 15 samples were taken from a salinity of 31.0 g l^{-1} near Vlissingen down to a salinity of 6.3 g l^{-1} near Lillo. The stations were selected according to the sampling grid used in Mees *et al.* (1993b). Since no animals were caught in the last station, no further attempts were made to sample more upstream. In the Gironde 15 stations (evenly spaced at 5 km) were selected covering salinity zones ranging from 26.1 g l^{-1} near Le Verdon to truly freshwater (0.0 g l^{-1}) near Bec d'Ambès.

Both Gironde and Eems were sampled in 2 consecutive days (5–6 August and 14–15 August, respectively). In the Westerschelde stations w31 upto w17 were sampled on the 12th of August; stations w12 upto w6 one week later on the 20th of the same month.

The samples were collected with a sledge (Hamerlynck & Mees, 1991) which consists of a heavy metal frame with two mounted monofilament nets. The nets are 4 m long and 1 m wide with a mesh size of 2 × 2 mm in the first 3 m and 1 × 1 mm in the last 1 m. The sledge glides over the bottom and samples the water column from 20 to 100 cm above the sediment. On each occasion it was trawled over a distance of 1000 m (radar readings from fixed points) at an average ship speed of 4.5 knots relative to the bottom. All samples were taken during daytime when hyperbenthic animals are known to be concentrated near the bottom. The contents of both nets were pooled for the present study. Thus the recorded densities are numbers of individuals (N) per 1000 m^2; the maximal volume of water filtered through the nets is 800 m^3. Where possible the 10 m isobath was followed. Actual sampling depths varied between 10.5 m and 7.5 m in the Eems, between 6.1 m and 15.8 m in the Westerschelde, and between 6 m and 15 m in the Gironde. The samples were rinsed over a 1 mm sieve and immediately preserved in a buffered formaldehyde solution, 7% final concentration.

At the end of each trawl Secchi disc depth was recorded and salinity, dissolved oxygen concentration,

Table 1. Common species excluded from the community analyses on the basis of size, with total number caught in each estuary

	Eems	Westerschelde	Gironde
Adult Caridea			
Crangon crangon	6268	474	850
Palaemonetes varians	4	1	
Palaemon longirostris	3		887
Adult Brachyura			
Carcinus maenas	39	37	
Liocarcinus holsatus	77	87	5
Liocarcinus pusillus			16
Portumnus latipes	6	1	
Macropodia species		1	
Rhithropanopeus harrisii	4		
Pinnotheres pisum			1
Adult Pisces			
Anguilla anguilla			9
Clupea harengus	19	3	
Sprattus sprattus	2	2	1
Osmerus eperlanus	335		3
Trisopterus luscus	1		
Gasterosteus aculeatus		4	3
Liparis liparis	3		
Gymnocephalus cernuus	9		
Zoarces viviparus	2		
Pomatoschistus microps	453	3	335
Pomatoschistus minutus	141	442	189
Pomatoschistus lozanoi	15	92	1
Limanda limanda	1		
Pleuronectes platessa	4		
Solea solea	24		1

pH, conductivity and temperature were measured near the bottom.

Laboratory procedures

After sorting, all animals present in the samples were identified, if possible to species level, and counted. Different developmental stages of some crustacean groups were considered as different functional species (zoeae, postlarvae and adults for caridean shrimp; zoeae, megalopae and adults for anomuran and brachyuran crabs). For gobies of the genus *Pomatoschistus* only *P. microps* could always be identified to species level. Small individuals (less than 25 mm standard length) of *P. minutus* and *P. lozanoi* were pooled as *Pomatoschistus* species. Other identification problems concerned postlarval clupeoids (probably a mixture of *Clupea harengus* and *Sprattus sprattus*) and amphipods of the genus Bathyporeia (pooled as Clupeidae species and *Bathyporeia* species, respectively). Possibly the counts of zoeae and megalopae of *Liocarcinus holsatus* also include larvae of other crabs of the same genus (e.g. *L. pusillus* in the Gironde). Several rare larval stages of brachyuran crabs could not be identified at all. Single records of a caprellid (*Caprella*) and an isopod (*Cymothoa*) in the Gironde could only be identified to genus level, though the former probably is *C. aequilibra* (Sorbe, 1978). For animals with more or less continuous growth, a maximum of 60 individuals per species and per sample (30 from each net) were measured to the nearest 0.1 mm using a binocular microscope and drawing mirror. Except for crabs (carapace width) standard lengths (from the tip of the rostrum to the last abdominal segment) were used. Biomass was then derived from the length-frequency distributions and length-ashfree dry weight (AFDW) regressions obtained from Westerschelde and Voordelta populations (Mees unpublished, Mees *et al.* 1994). Densities of species growing in discrete stages were converted to biomass with average AFDW values.

Statistical analysis

Diversity of each sample was calculated as Hill's diversity numbers of the order 0, 1, 2 and ∞ (Hill, 1973), with

N_0 = the number of species,
$N_1 = e^H$ with $H = -\Sigma p_i \ln(p_i)$ (p_i is the relative abundance of the i dominant species),
$N_2 = \Sigma p_i^2$ and
$N_\infty = 1/p_1^{-1}$ (the reciprocal of the relative abundance of the most abundant species).

Diversity calculations were not considered meaningful if less than 10 animals were caught (station g26).

All multivariate analyses were performed on both density and biomass matrices. First, in order to assess differences between estuaries, the datamatrices combining the samples of the 3 estuaries were analysed. Then, to refine the identification of communities within each estuary, the analyses were repeated on smaller data matrices comprising only the samples of a single estuary.

Table 2. List of species and abbreviations used in the community analyses. Middle column: first letter of the estuary(ies) in which they occurred.

Sagitta elegans	E	W	G	Sagi eleg
Gastrosaccus spinifer	E	W	G	Gast spin
Schistomysis spiritus	E	W	G	Schi spir
Schistomysis kervillei	E	W	G	Schi kerv
Mesopodopsis slabberi	E	W	G	Meso slab
Neomysis integer	E	W	G	Neom inte
Praunus flexuosus	E	W		Prau flex
Eurydice pulchra		W	G	Eury pulc
Idotea linearis	E	W		Idot line
Synidotea laevidorsalis			G	Syni Spec
Sphaeroma rugicauda		W		Spha rugi
Sphaeroma serratum			G	Spha serr
Cymothoa species			G	Cymo Spec
Daphnia magna	E	W		Daph magn
Caprella linearis	W			Capr line
Caprella species			G	Capr Spec
Pariambus typicus	W			Pari typi
Gammarus crinicornis	E	W	G	Gamm crin
Gammarus salinus	E	W	G	Gamm zali
Gammarus zaddachi	E		G	Gamm zadd
Gammarus duebeni	E			Gamm dueb
Gammarus locusta	E			Gamm locu
Melita palmata			G	Meli palm
Atylus swammerdami	E	W	G	Atyl swam
Pleusymtes glaber		W	G	Pleu glab
Corophium volutator	E	W	G	Coro volu
Corophium acherusicum		W		Coro ache
Corophium lacustre		W		Coro lacu
Bathyporeia species	E	W		Bath Spec
Jassa falcata		W		Jass falc
Hyperia galba		W		Hype galb
Crangon crangon postlarva	E	W	G	Cran Post
Crangon crangon zoea	E	W	G	Cran zoea
Palaemonetes varians postlarva	E	W		Pala varP
Palaemonetes varians zoea	E			Pala varZ
Palaemon longirostris postlarva	E		G	Pala lonP
Palaemon longirostris zoea	E		G	Pala lonZ
Pagurus species megalopa			G	Pagu Mega
Porcellana species zoea		W	G	Porc Zoea
Carcinus maenas megalopa	E	W	G	Carc Mega
Carcinus maenas zoea	E	W		Carc Zoea
Liocarcinus holsatus small adults	E	W	G	Lioc hols
Liocarcinus holsatus megalopa		W		Lioc Mega
Liocarcinus holsatus zoea	E	W	G	Lioc Zoel
Liocarcinus species zoea type 2			G	Lioc Zoe2
Liocarcinus species zoea type 3			G	Lioc Zoe3
Liocarcinus species zoea type 4	E			Lioc Zoe4
Macropodia species megalopa		W	G	Macr Mega
Eriocheir sinensis megalopa	E		G	Erio Mega
Unidentified zoea Westerschelde		W		Wtyl Zoea
Unidentified zoea Gironde type 1			G	Gtyl Zoea
Unidentified zoea Gironde type 2			G	Gty2 Zoea
Nymphon rubrum		W		Nymp rubr
Anguilla anguilla glass eels			G	Angu angu
Clupeidae species postlarva	E	W	G	Clup Spec
Syngnathus rostellatus	E	W	G	Syng rost
Pomatoschistus microps postlarva	E	W	G	Poma micr
Pomatoschistus species postlarva	E	W		Poma Spec

Density and biomass data were subjected to fourth root transformation prior to analysis. Three multivariate techniques, each yielding specific information, were applied to the data (Field *et al.*, 1982). The sampling sites were classified into clusters according to species composition using the classification technique TWINSPAN (Hill, 1979). This is a hybrid (the first step involves a reciprocal averaging ordination) divisive clustering technique which also gives indicator species and preferential species for each division. Pseudospecies cutlevels (7 in each case) were chosen to equalise the number of observations within each cutlevel, except for the lowest cutlevel which contained all the zero observations and the two highest cutlevels which contained approximately half as many observations as the other levels (in this way some extra weight was given to the most abundant species). The minimum group size for division was set to 5 and the analysis was stopped at the fifth division. An agglomerative clustering method (group average sorting or GAS of Bray-Curtis dissimilarities) was also applied to the data. The output (dendrograms) of these analyses were compared with the TWINSPAN results and the degree of similarity between clusters, and (within clusters) between samples could be assessed. The relationship between species, stations and environmental variables was investigated by means of a Canonical

Correspondence Analysis or CCA (Jongman *et al.*, 1987; Ter Braak, 1988), a technique performing regression and ordination of the data concurrently. Preliminary analyses showed that pH did not correlate well with any axis and that conductivity was strongly and positively correlated with salinity. Thus both parameters were not used in further analyses. Secchi disc depth was transformed reciprocally and thus becomes a light extinction measure, correlated with turbidity of the water. Whereas the first two techniques emphasised discontinuities in the data, the CCA emphasised continuities along the estuarine gradients. Plotting of the TWINSPAN/GAS clusters on the CCA ordination planes aided in evaluating the divisions imposed.

Results

Accidentally caught individuals one or several orders of magnitude larger than an 'average' hyperbenthic animal can seriously distort analyses with biomass data. Adult individuals of epibenthic shrimp and crab species and adult demersal or pelagic fish species, although often very abundant in the samples (Table 1), were excluded from the community analyses. Though these animals apparently make use of the hyperbenthal as a habitat they are inefficiently sampled with the sledge and are normally studied using beam trawls. Only small adults of *Liocarcinus holsatus* (carapaxlength <10 mm) and postlarval gobies (S.L.<25 mm), clupeoids (not yet displaying adult pigmentation nor habitus, S.L.<25 mm), pipefish (S.L.<60 mm) and glass eels were considered to be representative residents of the hyperbenthal. Other species eliminated from the data matrices are: Porifera species (epibenthic freshwater sponges in Eems and Gironde), Hydrozoa species (epibenthic, in every sample of Eems and Westerschelde, rarely in the Gironde), *Aurelia aurita* (planktonic, high densities in Eems and Westerschelde), Cyanea species (planktonic, high densities in Gironde), Anthozoa species (epibenthic, rare), *Pleurobrachia pileus* (planktonic, high densities in Eems, Westerschelde and Gironde), Nematoda species (benthic, mainly among peat in the brackish Eems samples), *Lanice conchilega* aulophore larvae (planktonic, 9 and 3 individuals in Westerschelde and Gironde, respectively), *Nereis* species (benthic, rarely caught in all three estuaries), and a variety of rarely and accidentely caught species: *Macoma ballhica*, *Cerastoderma edule*, *Mytilus edulis*, *Hydrobia ulvae*, *Sepiola* species, Bryozoa species, *Asterias rubens* and Cirripedia species. Also excluded were regularly encountered groups originating from land, air or fresh water: Aranea species, Diptera species, Lepidoptera species and Coleoptera species (adults and larvae).

From a total of 101 recorded species, 58 were thus retained after data reduction (Table 2). Eighteen were recorded from all three estuaries and most of these were very abundant. Four species were only encountered in the Eems, eleven only in the Gironde and ten only in the Westerschelde. Most of these species were rare and have previously also been recorded from the other estuaries in other studies. Exceptions are *Synidotea laevidorsalis* in the Gironde and *Gammarus locusta* in the Eems, which were quite common constituents of the hyperbenthos and have never been recorded from one of the other estuaries. Four species occurred both in Gironde and Eems but were absent from the Westerschelde. Four were only absent from the Eems and seven from the Gironde.

Environmental gradients

The environmental variables measured at each station are presented in Table 3. The most pronounced gradient in the three estuaries was salinity (see materials and methods). The three estuaries displayed the characteristic summer temperature gradient with lowest values near the mouth gradually increasing upstream. Geographical differences between the estuaries are obvious, with temperature increasing with decreasing latitude from Eems over Westerschelde to Gironde. The temperature difference between the mouth of the estuary and the 8 g l^{-1} isohaline in the Westerschelde (maximal difference of 3.0 °C) is high in comparison to that in Gironde and Eems (difference of 3.4 and 1.3 °C over a longer gradient). This may reflect the one week gap in the sampling scheme. An alternative explanation may be thermal pollution by the nuclear power plant of Doel. Secchi disc visibility decreased with increasing distance from the mouth. The marine reaches of the Gironde were characterised by very high light penetration. Upstream of the maximum turbidity zone in the Gironde there was a slight increase in light penetration. The maximum turbidity zone was not reached in Westerschelde (supposedly situated around Antwerpen) and in the Eems its upstream border was not reached. Dissolved oxygen concentrations of the water ranged from oversaturation in the marine part to about 80% of the saturation value in the 17 to 12 salinity zone of the Westerschelde. Then a rapid decline in the oxygen content was observed in the three inner-

Table 3. Environmental variables measured at the end of each trawl.

Eems	e29	e27	e25	e23	e21	e18	e17	e11	e10	e4	e2	e1
Salinity (g l^{-1})	28.63	26.54	25.34	22.87	21.00	18.47	16.65	11.44	10.03	4.45	1.96	0.94
Secchi depth (cm)	120	50	45	20	20	15	20	10	10	5	5	5
Temperature (°C)	19.8	19.6	19.4	19.2	19.6	19.7	19.8	20.1	20.1	20.3	20.4	20.5

Westerschelde	w31	w30a	w30b	w30c	w28	w27	w25a	w25b	w21	w19	w17	w12	w10	w8	w6
Salinity (g l^{-1})	31.00	30.30	29.50	29.50	28.00	26.60	25.40	25.00	21.10	19.30	17.00	11.90	10.30	8.10	6.30
Secchi depth (cm)	125	120	125	125	100	100	140	140	80	90	100	40	50	60	–
Temperature (°C)	20.0	20.0	19.8	20.1	20.2	20.2	20.1	20.1	20.3	20.5	20.6	22.3	22.8	22.7	–

Gironde	g26a	g26b	g24	g20	g18	g14	g10	g6	g4	g3	g2	g1	g.5	g.1	g0
Salinity (g l^{-1})	26.10	26.00	24.00	20.00	18.00	14.00	10.00	6.00	4.00	3.40	2.00	1.40	0.50	0.10	0.00
Secchi depth (cm)	440	440	260	90	40	40	30	10	5	5	3	5	3	5	10
Temperature (°C)	21.0	21.2	21.6	22.4	22.6	22.8	23.5	24.0	24.2	24.1	24.4	24.4	24.4	24.4	24.4

most stations: 49% in w10, over 38% in w8 down to 22% in w6. In the other two estuaries dissolved oxygen concentration never dropped below 70% saturation.

General trends in density, biomass and diversity

In Westerschelde and Gironde hyperbenthic density (Fig. 2) and biomass (not figured) were lowest in the most seaward stations. They increased upstream, decreasing again towards the most riverine stations.

In comparison to the other estuaries, the Eems was characterised by a rather uniform density over a wide salinity range: density was low in the outermost station (<5 individuals or 5 mg AFDW per m^2) but, in contrast to the other estuaries, was already high at the 27 g l^{-1} isohaline. Densities remained at about the same level (between 10 and 20 ind m^2, 10 to 47 mg AFDW per m^2) upto 17 g l^{-1}. A drop in density (again less than 5 ind m^2) was observed at the 11 g l^{-1} isohaline (mouth of the Dollard). Density and biomass then increased to a maximum of 26 individuals or 66 mg AFDW per m^2 at the 2 g l^{-1} isohaline and decreased again in the last station. Some of the density peaks reflect the appearance and disappearance of dominant species (Fig. 3): the peak around 21 g l^{-1} was mainly due to high densities of *Schistomysis kervillei*, the peak around 2 g l^{-1} reflects the abundance maximum of *N. integer*, which was of overriding importance throughout most of the estuary.

In the Westerschelde two peaks were evident (Fig. 2): a first in the 19 g l^{-1} salinity zone, a second around 10 g l^{-1}. These were an order of magnitude higher than maximal densities observed in the other estuaries (250 and 105 individuals per m^2; 555 and 208 mg AFDW per m^2). The two peaks probably do not represent two distinct zones of higher density but are an artefact of the discontinuous sampling scheme. Both peaks correspond to the maximum abundance of *N. integer* and, depending on the geographical location of the oxygen depletion zone, the population maximum can be found in different salinity zones on different sampling days. In the Westerschelde *N. integer* are always concentrated near the limit of viable oxygen concentrations (about 40% of the saturation value) regardless of salinity (Mees *et al.*, 1993a; Mees *et al.*, 1993b). Density became very low at 8 g l^{-1} and in the 6 g l^{-1} sample no hyperbenthic animals were found. In Gironde and Eems the abundance maximum of *N. integer* was correlated with the tidally shifting salinity zone around 2–4 g l^{-1}. In the marine stations (w31 to w21) of the Westerschelde density and biomass were below 3.5 ind per m2 and 3.5 mg AFDW per m^2 respectively.

Densities in the Gironde were only substantial upstream of the 20 g l^{-1} isohaline. Very few animals were caught in the most seaward Gironde samples g26a, g26b, g24 and g20 (7, 7, 69 and 29 individuals, respectively). Three peaks were evident: the first peak

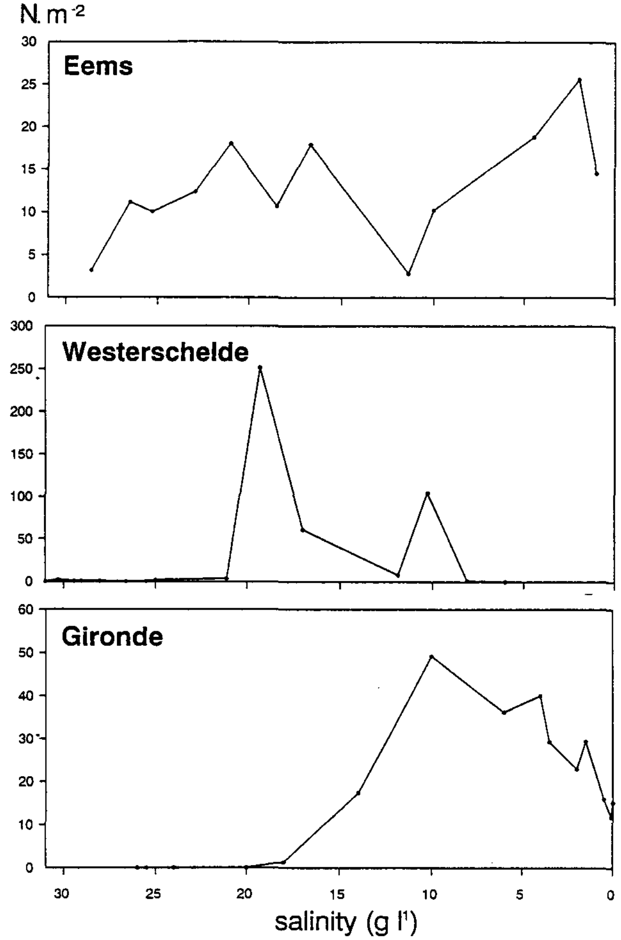

Fig. 2. Total hyperbenthic density along the salinity gradients in the three estuaries.

(50 individuals or 63 mg AFDW per m^2 at 10 g l^{-1}) coincided with the maximal abundance of *Mesopodopsis slabberi* and submaximal abundances of *N. integer* (Fig. 3), the second peak (41 individuals or 113 mg AFDW per m^2 at 4 g l^{-1}) corresponded with maximal densities of *Pomatoschistus microps* and high numbers *N. integer*, and the third peak (32 ind. m^2 or 99 mg AFDW at 1 g l^{-1}) corresponded to the abundance maximum of *N. integer* (Fig. 3). Since *M. slabberi* is a very slender species, the first peak became lower than the other two in terms of biomass.

All diversity measures (Fig. 4) were highest in the marine part of the estuaries. In the high salinity zone many species were present, with no species clearly dominating the fauna. This is also evident from Fig. 3 where the 'others' section accounted for a higher percentage of the community than in the brackish part. Diversity decreased towards the brackish reaches where fewer species occurred in higher numbers (cf. L_∞ approaches a value of 1 in the stations with maximal abundance of *N. integer*). In Eems and Gironde diversity increased slightly towards the fresh water.

The species

The hyperbenthos was dominated by crustaceans, especially mysids. Other important groups were gammaridean amphipods, isopods (in the Gironde), caridean shrimp, larval stages of brachyuran crabs and postlarval fish. Chaetognaths, daphnids, pycnogonids, caprellid and hyperiid amphipods and larval stages of anomurans were observed occasionally. The distribution of the 11 most abundant species along the salinity gradients of the three estuaries is depicted in Fig. 5. Below, the distribution patterns are described based on the density data only (biomass data of the individual species are available on request).

Mysidacea

Gastrosaccus spinifer occurred in the three estuaries from the marine reaches upto the 10 g l^{-1} isohaline. Maximal densities amounted to 3400 ind per 1000 m^2 in the Westerschelde (at 19 g l^{-1}) and 650 ind in Gironde and Eems (at 18 and 29 g l^{-1}, respectively). One adult female from the Eems was infested with the parasitic isopod *Prodajus ostendensis*. *Mesopodopsis slabberi* was abundant throughout the Westerschelde from the mouth upto the 10 g l^{-1} isohaline where it reached a maximal density of 60 individuals per m^2. The same pattern was observed in the Gironde (maximal densities of 39 ind m^2 at 10 g l^{-1}), but here the species was still present in the most upstream stations (upto 0 g l^{-1}). In the Eems *M. slabberi* also occurred over the entire transect but it only reached important densities in a narrower salinity band (between 29 and 10 g l^{-1}) where a maximum of 20 ind m^2 was recorded. In the Gironde only one individual of *Schistomysis kervillei* was caught in the most downstream station. This essentially coastal species was present in the Westerschelde from the mouth upto 21 g l^{-1} (maximum of 250 ind 1000 m^2 at 30 g l^{-1}). In the Eems the species moved much further up the estuary (upto 11 g l^{-1}) and reached maximal abundance at lower salinities (7000 ind 1000 m^2 at the 21 g l^{-1} isohaline). *S. spiritus* is also a typical coastal species which was present in the three estuaries from the mouth to 10, 21 and 14 g l^{-1} in Eems (maximal abundance of 800

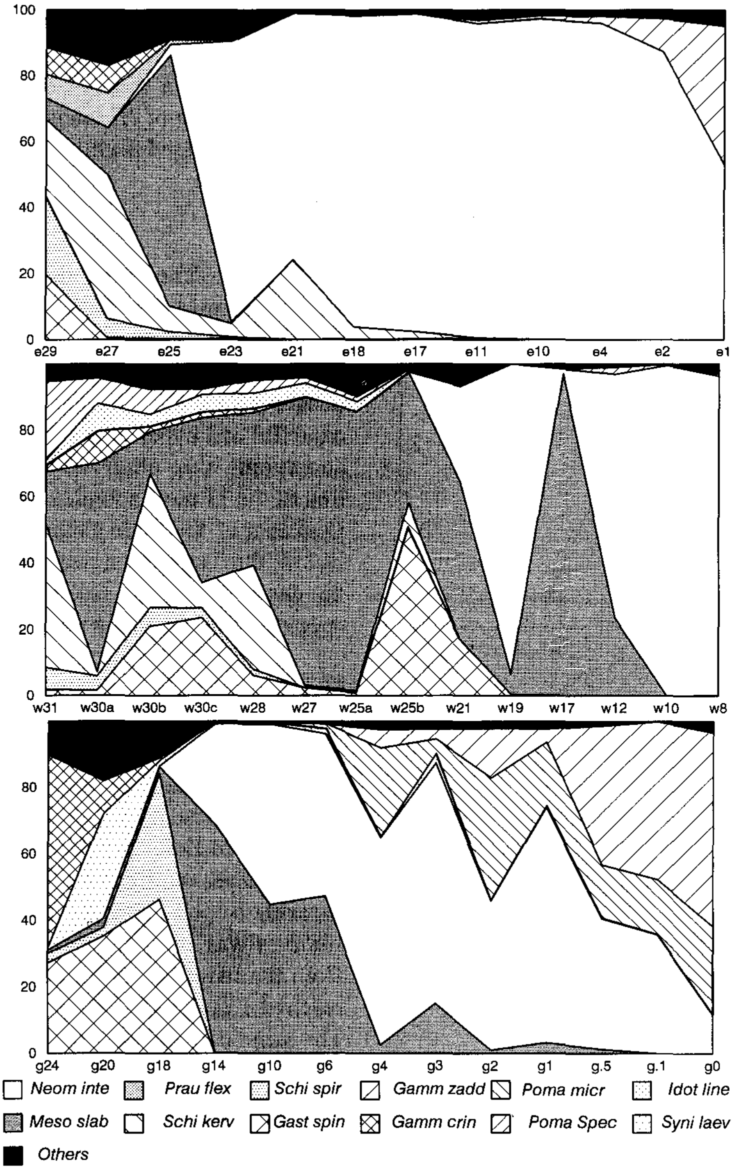

Fig. 3. Relative species composition of the hyperbenthic community along the salinity gradient in Eems (top), Westerschelde (middle) and Gironde (bottom).

individuals per 1000 m2), Westerschelde (55 ind) and Gironde (800 ind), respectively. The estuarine endemic *Neomysis integer* was, especially in biomass terms, the most important constituent of the hyperbenthos in the three estuaries. It was restricted to the brackish reaches, never being caught in fully marine conditions. The zone of maximal abundance in Eems and Gironde was situated in the vicinity of the maximum turbidity zone (as exemplified for the Gironde in Fig. 6). In the Eems the species was present from 25 g l^{-1} upto 1 g l^{-1} (maximum of 18 ind m^2 at 4 g l^{-1}). In the Gironde it colonised the salinity zone from 18 to 0 g l^{-1} (maximum of 26 ind m^2 at 4 g l^{-1}). In the Westerschelde *N. integer* was only present from 21 to 8 g l^{-1} with much higher maximal densities of 193 and 103 ind m^2 at the 19 and 10 g l^{-1} isohaline depending on the sampling date. *Praunus flexuosus* was only recorded in Eems and Westerschelde. In the former estuary densities amounted to 284 ind m^2 at 27 g l^{-1} (range 29 to 18 g l^{-1}), in the Westerschelde density was always

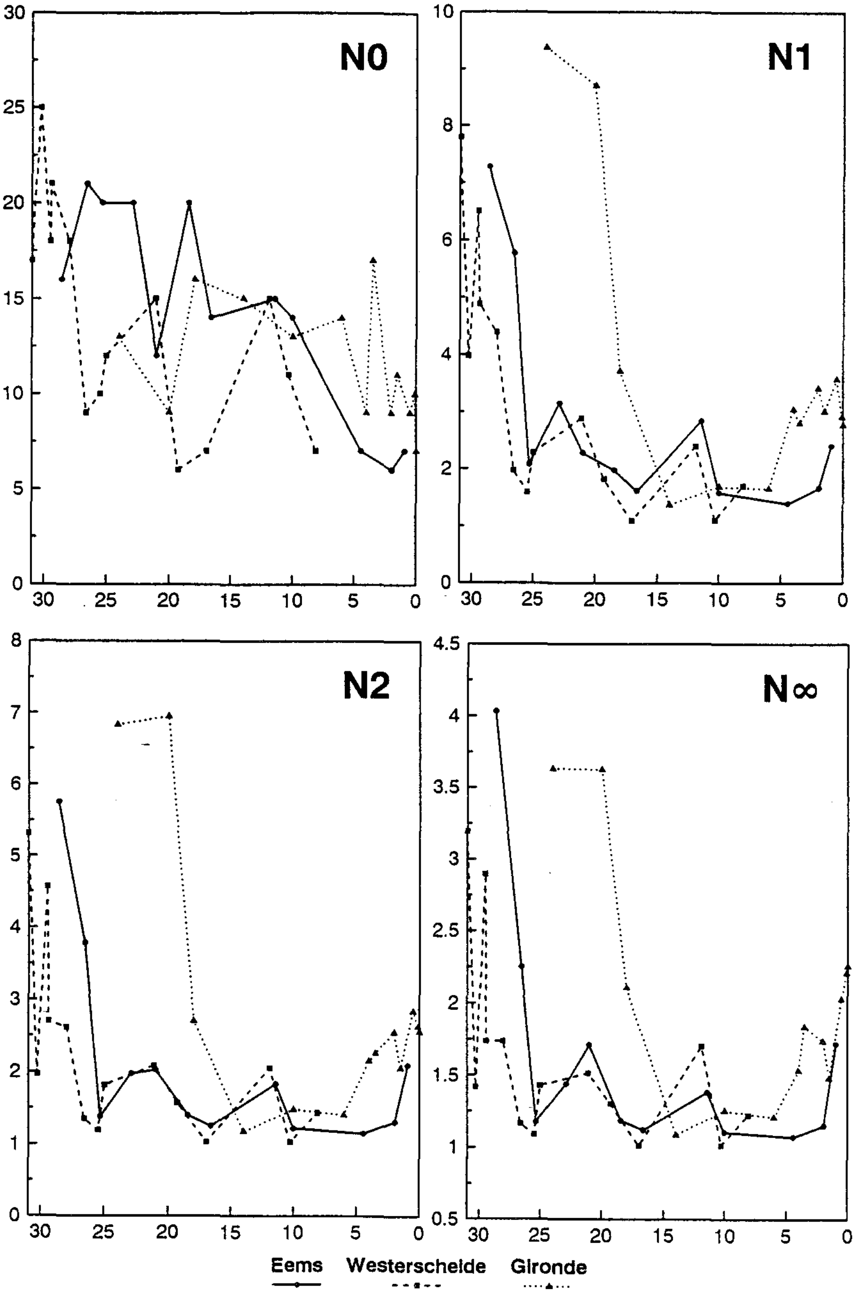

Fig. 4. Diversity numbers of Hill plotted against salinity.

low (maximum of 33 ind 1000 m^2) in the salinity zone from 25 to 17 g l^{-1}.

Amphipoda Gammaridea

Gammarus crinicornis is a marine species which does not penetrate the estuarine system very far. It occurred in all three estuaries with maximal densities of 646 (at 27 g l^{-1}), 103 (30 g l^{-1}) and 8 (24 g l^{-1}) individuals per 1000 m^2 in Eems, Westerschelde and Gironde respectively. *Gammarus salinus* is a brackish water species which in all three estuaries replaced *G. crinicornis* upstream. The species occurred in the Eems between 25 and 4 g l^{-1} (maximum of 52 ind 1000 m^2 at 10 g l^{-1}) and in the Gironde between 14 and 0.5 g

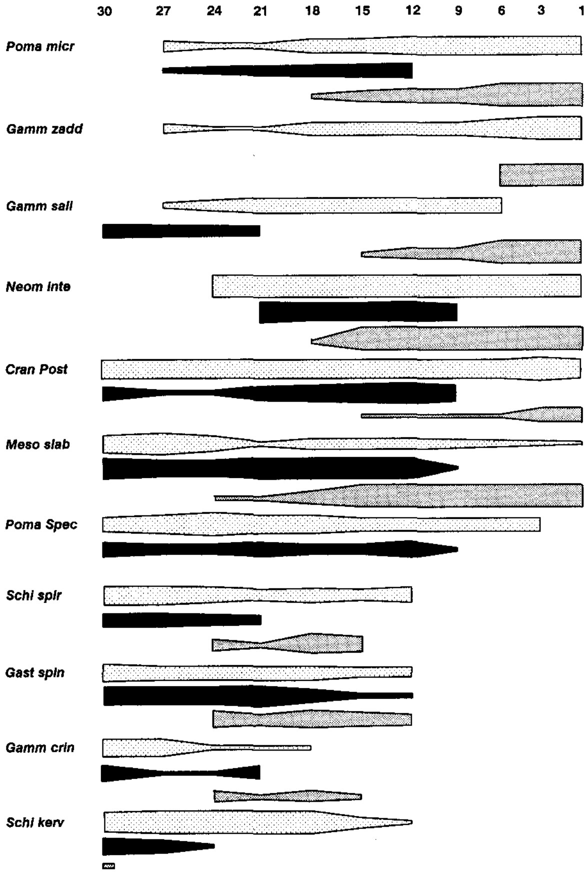

Fig. 5. Density distribution of the 11 most abundant hyperbenthic species along the salinity gradient of Eems (top), Westerschelde (middle, in black), and Gironde (bottom). Species are ordered following the two-way table of the TWINSPAN. Width of the bar gives indication of abundance reached in the salinity zone (top line).

l^{-1} (maximum of 1858 ind 1000 m^2 at 4 g l^{-1}). During this survey, *G. salinus* was only caught in low numbers (a total of 28 ind) in the Westerschelde although the species is known to be the most common amphipod in the hyperbenthos of the brackish part of this estuary (Cattrijsse *et al.*, 1993; Mees *et al.*, 1993b). *Gammarus zaddachi* replaced *G. salinus* in the oligohaline reaches of Eems and Gironde. Densities were very high in the salinity zone between 2 and 0 g l^{-1}: 5 and 7 ind m^2, respectively. The species was not caught in the Westerschelde. Two other *Gammarus* species were only caught in the Eems: *G. duebeni* (only a few individuals in the 27 g l^{-1} station) and *G. locusta* (between 29 and 23 g l^{-1}, maximum of 160 ind 1000 m^2 at 27 g l^{-1}). *Atylus swammerdami* is a marine species. It was present in the Westerschelde from 31 to 27 g l^{-1}. In Gironde and Eems the species penetrated further into the estuary: upto 20 and 11 g l^{-1}, respectively. Densities were never higher than 30 ind 1000 m^2. Individuals of *Melita palmata* (in marine waters) and *Pleusymtes glaber* (in brackish stations) were only caught in the Gironde, although they are also known to occur in the Westerschelde (Mees *et al.*, 1993b). *Corophium volutator* is a euryhaline, tube building species regularly encountered in the hyperbenthos of the three estuaries (density was never higher than 50 ind 1000 m^2). In the Westerschelde three other species were found in very low numbers: *C. acherusicum*, *C. lacustre*, and *Jassa falcata*. *Bathyporeia* species were only found in Eems and Westerschelde.

Isopoda

Eurydice pulchra was not observed in the Eems. The species was found in the Westerschelde in salinities ranging from 25 to 10 g l^{-1} with a maximal density of 26 ind 1000 m^2 at 12 g l^{-1}. In the Gironde only 4 individuals were caught between 18 and 3 g l^{-1}. *Idotea linearis* was only found in the marine parts of the Westerschelde (maximum of 85 ind 1000 m^2 at 30 g l^{-1}) and Eems (maximum of 13 ind 1000 m^2 at 29 g l^{-1}). *Synidotea laevidorsalis* was only present in the Gironde and was the only isopod which reached considerable densities and biomass (maximum of 288 ind 1000 m^2 at 3 g l^{-1}) in the brackish part of this estuary. Details on its distribution have been published elsewhere (Mees & Fockedey, 1993). *Sphaeroma rugicauda*, *Sphaeroma serratum*, and *Cymothoa* species were rare constituents of the hyperbenthos.

Caridean shrimp

Crangon crangon was very abundant in the three estuaries. The developmental stages were found to be segregated along the salinity gradient: zoeae did not penetrate the estuary as far as postlarvae. Maximal densities for the zoeae were 12 ind 1000 m^2 at 29 g l^{-1} in the Eems, 24 ind 1000 m^2 at 30 g l^{-1} in the Westerschelde, and 7 ind 1000 m^2 at 26 g l^{-1} in the Gironde. Postlarvae (and adults) were present over the entire sampled salinity range but were most abundant in the brackish part: maximal densities of 976 ind 1000 m^2 (1 g l^{-1}) in the Eems, 1148 ind 1000 m^2 (10 g l^{-1}) in the Westerschelde, and 39 ind 1000 m^2 (1 g l^{-1}) in the Gironde. *Palaemonetes varians* was only recorded in the Eems (zoeae and postlarvae between 23 and 10 g l^{-1}) and the Westerschelde (only postlarvae between 30 and 10 g l^{-1}). *Palaemon longirostris* is a typical species for the oligohaline reaches of estuaries. It was

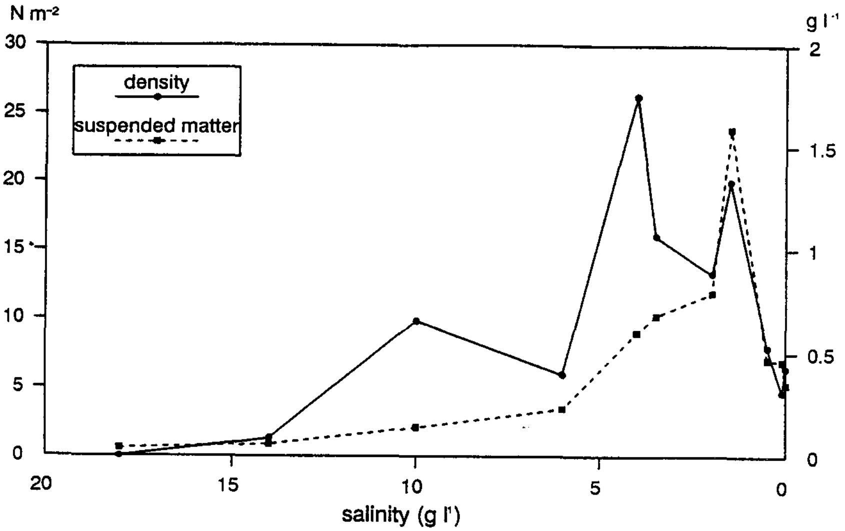

Fig. 6. Density of *Neomysis integer* (right axis) and concentration of suspended matter (left axis) plotted against the salinity gradient of the Gironde.

absent from the Westerschelde. Densities were low in the Eems (maximum of 9 zoeae, 23 postlarvae and 1 adult per 1000 m^2). In the Gironde it was the most abundant caridean: maximum of 44 zoeae (3 g l^{-1}), 324 postlarvae (2 g l^{-1}) and 224 adults (0.1 g l^{-1}) per 1000 m^2.

Larval Brachyura

Larval stages of the shore crab *Carcinus maenas* were rare in the Gironde (only 3 megalopae). In Eems and Westerschelde both zoeae (maximal densities of 15 and 34 ind 1000 m^2) and megalopae (maximal densities of 861 and 17 ind 1000 m^2) were present upto the 10 g l^{-1} isohaline. *Liocarcinus holsatus* zoeae and megalopae were only common in the Westerschelde (298 zoeae and 31 megalopae per 1000 m^2 at 17 and 21 g l^{-1}, respectively). Both stages were present but rare in Eems and Gironde. *Eriocheir sinensis* megalopae were only caught in Eems and Gironde, all other crab larvae were rare and mostly restricted to a single estuary.

Postlarval fish

Pomatoschistus microps was very abundant in the oligohaline reaches of Eems (maximal density of 435 ind 1000 m^2 at 1 g l^{-1}; range 27 to 1 g l^{-1}) and Gironde (maximal density of 6321 ind 1000 m^2 at 4 g l^{-1}; range 18 to 0 g l^{-1}). Densities in the Westerschelde were much lower (maximum of 5 ind 1000 m^2) and the species was only present downstream the 10 g l^{-1} isohaline. Postlarval *Pomatoschistus* species were absent from the Gironde. They were caught along the entire sampled transect of the Eems (maximum of 1260 ind 1000 m^2 at 2 g l^{-1}) and the Westerschelde (maximum of 1260 ind 1000 m^2 at 10 g l^{-1}). *Syngnathus rostellatus* was common in the marine reaches of the Eems (upto 17 g l^{-1}) and in the brackish reaches of Westerschelde (upto 12 g l^{-1}) and Gironde (upto 0.1 g l^{-1}). Larval clupeoids were always caught in low numbers (never more than 85 ind 1000 m^2) between the mouth of the estuary and 2 g l^{-1}, 19 g l^{-1} and 3 g l^{-1} in Eems, Westerschelde and Gironde, respectively. Glass eels *Anguilla anguilla* were only encountered (a total of 7 individuals) in the three lowest salinity samples of the Gironde.

Other taxa

Highest densities of the marine chaetognath *Sagitta elegans* were recorded around the 10 g l^{-1} isohaline in the Eems (300 ind 1000 m^2 as compared to less than 15 per 1000 m^2 in Westerschelde and Gironde). *Daphnia magna* is the only cladoceran large enough to be caught with a 1 mm mesh. The species was found in the brackish stations of Westerschelde and Eems, always in low numbers. Caprellid amphipods and pycnogonids are typical 'aufwuchs' species, rarely encountered in the estuarine hyperbenthos. Hyperiid amphipods (*Hyperia galba*) are commensals on coelenterates and were only encountered in the marine part of the Westerschelde, often in association with their host *Aurelia aurita*. Larvae of anomuran decapods (genera *Pagu-*

rus and *Porcellana*) were recorded occasionally in the marine waters of all three estuaries.

Identification and characterisation of communities

Multivariate analysis with density and biomass data permitted the identification of 8 geographically separated communities. The general pattern in the data is illustrated with the TWINSPAN result using the biomass data (Fig. 7). The first division groups the high salinity samples of the three estuaries on the positive side and all low salinity samples on the negative side. Indicator species for the latter group are the mysid *Neomysis integer* at the 7th and the common goby *Pomatoschistus microps* at the 4th cutlevel; the mysid *Schistomysis kervillei* is indicator for the former group. In the second and third divisions geographical groupings per estuary become prominent in both main clusters: in each group one or two Gironde, Eems and Westerschelde communities can be identified. Stations w8 and e21 are indicated by the program as misclassified and borderline negative respectively. The marine cluster (left side) is divided in three groups, one for each estuary: Gironde West (GW: g26b to g18), Westerschelde West (WW: w31 to w21 and w17) and Eems West (EW: e29 to e23). In the brackish cluster (right side) the Gironde samples are first split from the Eems and Westerschelde samples. Indicators for the Gironde group are postlarval *Palaemon longirostris*, *Syngnathus rostellatus* (second cutlevel) and *Synidotea laevidorsalis*. Within this group the lowest salinity samples (Gironde East, GE: g4 to g0) are further split from the rest (Gironde Mid, GM: g14 to g6) on the basis of *Gammarus zaddachi*. Indicators for the Eems-Westerschelde group are postlarval *Crangon crangon* (fourth cutlevel) and *Pomatoschistus* species (second cutlevel). The third division divides this cluster in an Eems group and a Westerschelde group (Westerschelde Mid, WM with indicator *Eurydice pulchra*). The Eems samples are further divided in an Eems Mid group (e21 to e11) with indicator species *Schistomysis kervillei* and an Eems East group (e10 to e1 plus w8). Further divisions in these 8 clusters are not considered to be ecologically meaningful: the groupings they yield are not consistently found with the other multivariate analyses and their indicator species have limited significance. The TWINSPAN with the density data (not figured) yielded nearly the same picture. Differences only apply to transitional stations showing indecisive behaviour in all analyses and indicated by the program either as misclassified samples or borderline positives or negatives (e.g. w8 rather clustering with the w10 to w19 stations than with the Eems samples, and e21 clustering with the e23 to e29 cluster rather than with the e11 to e18 cluster). The TWINSPAN divisions were confirmed by group average sorting clusteranalyses (not figured): the two main low and high salinity clusters could always be distinguished with high dissimilarity. Groupings of samples with high similarities yielded the same 8 clusters (again with some stations shifting between geographically adjacent clusters). G26b and g26a were found to be highly dissimilar from the rest of the samples, reflecting the fact that few individuals were caught in these stations. The same applies to w8 which, though it invariably clustered with the brackish main group, was always found in an isolated position with lower similarity to the other stations. In the CCA only the first (eigenvalue 0.44) and second (eigenvalue 0.23) axes are important and the ordination plane they form suffices to visualise the structure in the data (Fig. 8). The axes of higher order (eigenvalues lower than 0.10) do not yield additional information and are not discussed. The first axis correlates strongly with the main estuarine gradients: salinity, Secchi disc depth and, to a lesser extent, temperature. The largest vector, which, per definition, explains most of the variance, nearly parallels the first axis and represents the salinity gradient. It is strongly and negatively correlated with the 1/Secchi vector. Projection of the temperature vector on the first axis reflects its correlation with the estuarine temperature gradient. The second axis also has an important temperature component, now being a covariable of latitude. The first axis (with its correlated salinity-turbidity-temperature gradient) thus reflects within-estuary variation, whereas the second axis (with its latitudinal temperature component) rather reflects among-estuary differences. All marine samples are located on the positive side of the first axis. The three western clusters can be found segregated along the second axis, with the EW cluster in the upper right quadrant, the GW cluster in the lower right quadrant and the WW cluster situated upon the first axis in between EW and GW. The mid estuary clusters are located close to the second axis with WM near the centre of the diagram, again in between EM (top) and GM (bottom). The clusters grouping the eastern Eems and Gironde samples are situated in the upper and lower left quadrants respectively. Interestingly, corresponding salinity zones in the three estuaries have the same position along the first axis. The gap along the second axis between the EE and GE clusters suggests the position where we might expect the WE cluster. The position of the species in the ordination plane reveals groups of hyperbenthic species characteristic for the sample clusters identified (Fig. 8 bottom). The analyses with the data of the single estuaries emphasise the continuous, gradual aspect of community replacement. Only the ordination planes formed by the first two canonical axes of the CCA with the density data (Fig. 9) are presented. First axis eigenvalues are 0.38, 0.41 and 0.58 for Eems, Westerschelde, and Gironde, respectively. The three variables are always represented by long vectors lying close to the first axis, temperature and 1/Secchi pointing towards the brackish samples, salinity towards the marine samples (not figured). The horse-shoe effect could readily be removed by detrending after which all stations were located in the same order close to the first axis (results not figured), implying these are truly single-axis ordinations. There are no real gaps between any two stations but within each estuary an eastern, middle and western group (sometimes forming tight clusters) can be delineated confirming the ecological significance of the classifications.

Combining the three techniques, in each estuary two (Westerschelde) or three (Eems and Gironde) communities could be distinguished. The species composition of these communities can differ, but their position along the gradient is similar: a marine or western community in the high salinity zone (GW, EW and WW), a brackish water community in the middle reaches (GM, EM and WM) and a third community in the stations with the lowest salinities (eastern communities GE and EE). As shown by CCA (and also by the progressive agglomerative clustering of the stations along the salinity gradient, not figured) the classification of the gradients into distinct clusters is somewhat artificial: some stations show indecisive behaviour, clustering with one community in one analysis and with another, neighbouring community in the next. Still, despite the fact that in each estuary one or two stations represent a transitional situation where two neighbouring communities meet, the communities are distinct and for practical purposes an objective division can be made.

In summary, it was decided to consider the following 8 communities (see also Fig. 8): three in the Eems: a marine, western community EW from 29 to 23 g l^{-1}, a brackish community in the middle part of the estuary EM from 21 to 10 g l^{-1}, and a oligohaline, eastern community EE from 4 to 1 g l^{-1}; two in the Westerschelde: WW from 31 to 21 g l^{-1} (+w17) and WM from 19 to 8 g l^{-1}; and three in the Gironde: GW from 26 to 18 g l^{-1}, GM from 14 to 6 g l^{-1}, and GE from 4 to 0 g l^{-1}.

The biotic characteristics (species composition, density, biomass) of the 2 or 3 communities within each estuary are – per definition – distinctly different (Fig. 10). Within each estuary the marine community is characterised by many species occurring in low densities. The middle community is characterised by few species reaching very high densities and biomass. The eastern communities of Eems and Gironde have still higher biomass (though somewhat lower density in the Gironde) and again more species contribute. Differences between estuaries especially concern GW which is very poor and WM which is very rich in comparison to the corresponding communities in the other estuaries. The eastern and middle communities are characterised by the same dominant species in each estuary.

Discussion

Though no data on net efficiency of the sledge are available, the sampling gear deployed seems to be suitable for quantitative sampling of the hyperbenthos. Densities reported for the Gironde from previous studies are either lower than, or comparable to, densities reported in this study. Mees & Sorbe (in preparation) using a passive fishing technique with a rectangular plankton net (0.5 mm mesh), estimated average annual density for *Neomysis integer* at 6 ind m^3 in the zone of maximal abundance with maximal densities of 10 to 15 ind m^3 in spring and autumn and summer densities of about 3 ind m^3. This is lower than maximal density reported in this study: 33 ind m^3 at 4 g l^{-1}. Sorbe (1981) reported maximal densities of Gammarus zaddachi at 550 ind 100 m^3 in summer, which is about the same density as found in this study. The same author estimated maximal density of *G. salinus* at 20–30 ind 100 m^3 water which is about 10 times lower than maximal densities reported in this study. The sampling strategy seems to have a sufficiently narrow grid for studying the replacement of hyperbenthic communities along the estuarine gradients (e.g. the continuous aspect of the CCA sample score biplots in Fig. 9).

The three estuaries are remarkably similar qua species composition (especially in the brackish reaches) and general trends in diversity, density and biomass. The following within-estuary patterns were consistently found: diversity was highest in the marine zone, where density and biomass were lowest. Diversity then

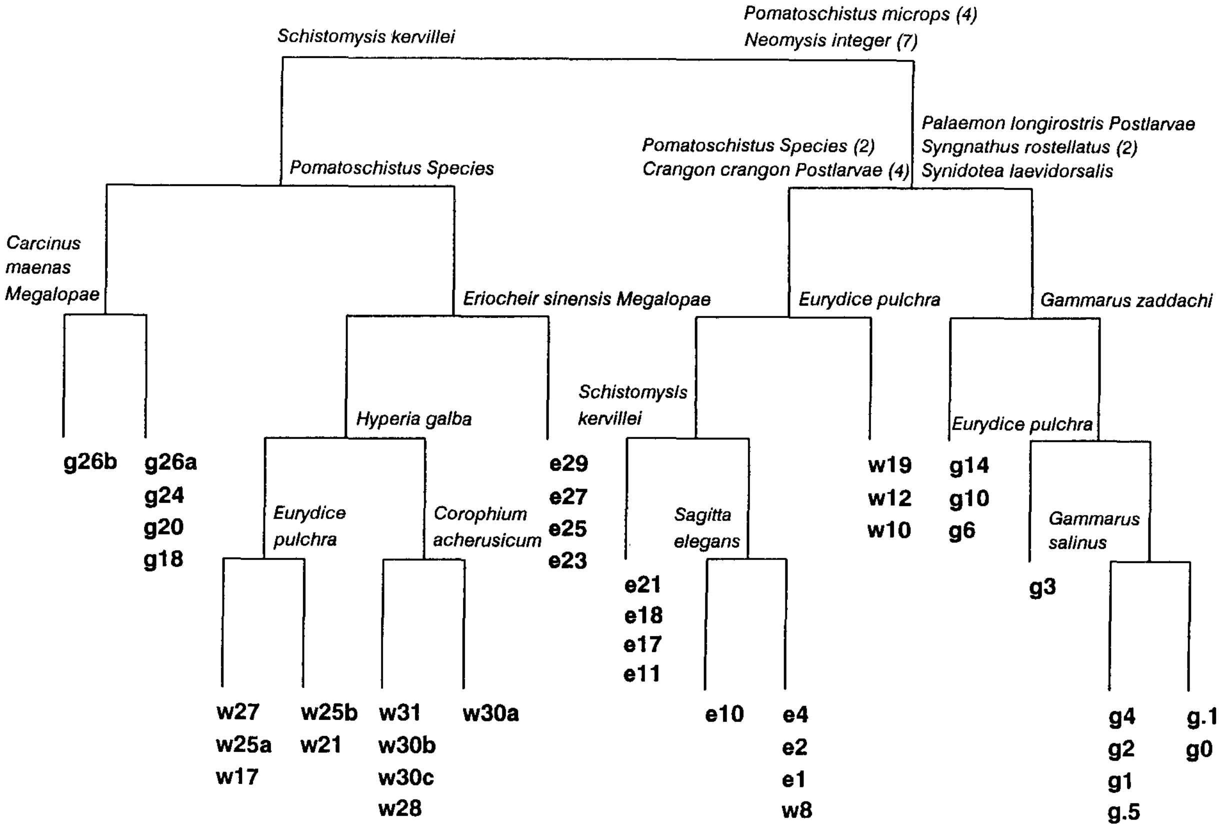

Fig. 7. TWINSPAN with the fourth root transformed biomass data of the three estuaries. Indicator species (and pseudospecies cutlevel) are given for each division.

decreased in an upstream direction and became minimal in the brackish part, where density and biomass reached maximal values. In Eems and Gironde diversity then increased slightly towards the freshwater zone. The poorness of the most seaward Gironde samples is exceptional. The capture of very few animals in these stations coincided with very high Secchi disc values. Possibly net avoidance contributed to the low densities. Other explanations may include the elimination of hyperbenthic populations by visual predators or lower food availability in this area. The overall higher densities reported for the marine part of the Eems as compared to Westerschelde and Gironde are probably related to the adjacent Wadden Sea system. The Wadden Sea itself is highly productive and has estuarine characteristics. No comparable system borders the mouths of the other estuaries, which open onto a typical coastal area. The low density found in the station located in front of the mouth of the shallow Dollard area of the Eems can not be explained.

Each estuary contained distinct communities along the unidirectional salinity-turbidity-temperature gradient. The position of these communities was similar in each estuary: a marine community in the high salinity zone, a brackish water community in the middle reaches and a third community (absent from the Westerschelde) in the stations with the lowest salinities. The similarity of the brackish water faunas among estuaries is high, higher than the within-estuary similarity of brackish and marine fauna. Brackish water species are few and the dominant residents occurred in all three estuaries at about the same density. In his extensive literature review Wolff (1973) concluded that the macrobenthic faunas of the brackish estuaries of N.W. Europe (including the Eems, the Delta area and the Arcachon Bay) were very similar to one another. This similarity can be extended to the hyperbenthic brackish water fauna and can be traced back to a common ancestral area on the western coast of France during the last Pleistocene glaciation, some 18 000–20 000 years ago. As for the macrobenthos, the low

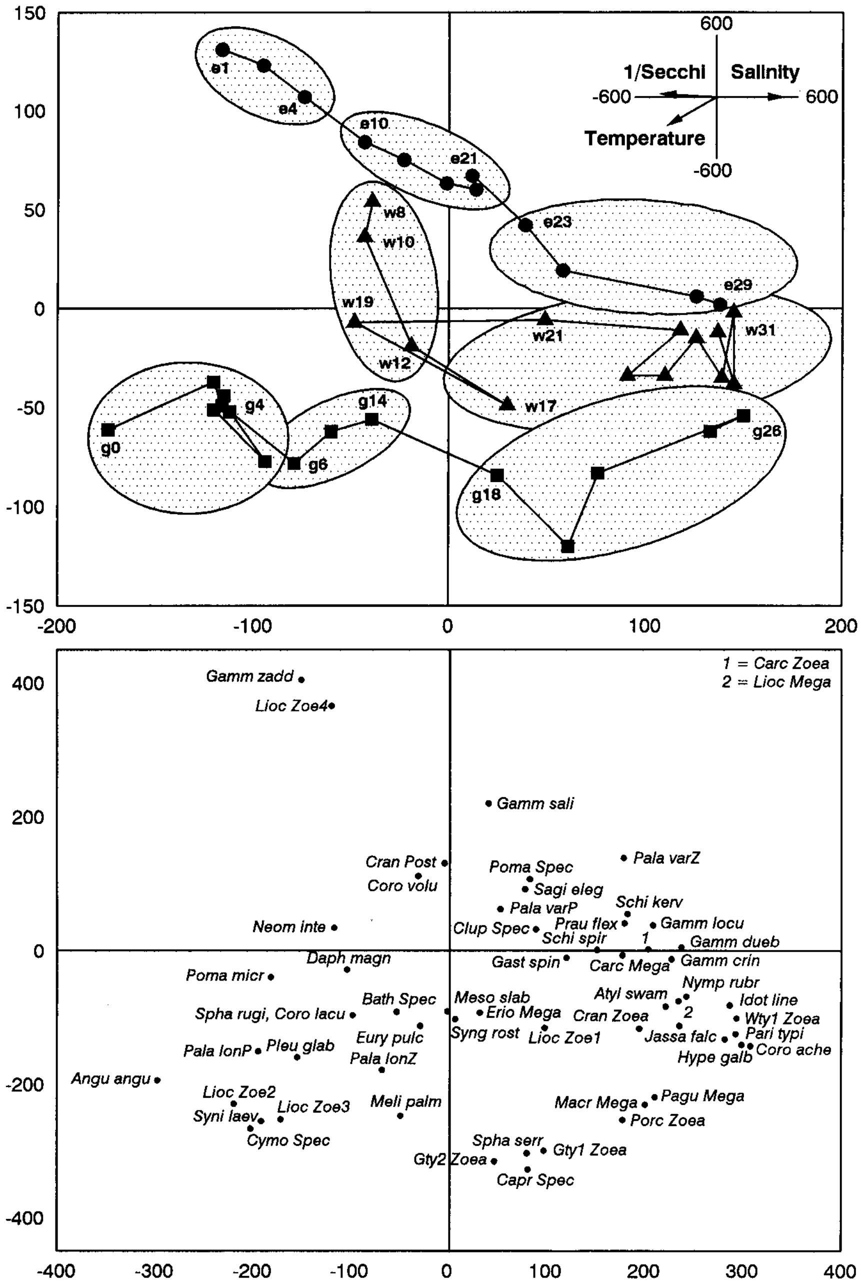

Fig. 8. Species scores (bottom), sample scores (top), and environmental biplot in the ordination plane formed by the first (horizontal) and second (vertical) canonical axes of the CCA with the fourth root transformed biomass data of the three estuaries. Samples are connected following salinity; communities as identified by TWINSPAN and GAS are circled.

number of hyperbenthic brackish water species can be explained by the low predictability of the environment and the geological history of northwestern Europe, and by the physiological stress which confronts the animals colonizing them (McLusky, 1981).

The classical pattern in species succession within *Gammarus*, already described for many European tidal estuaries (Lincoln, 1979; Sorbe, 1978, 1979; Meurs & Zauke, 1988), was confirmed in the present study. *G. crinicornis* is a marine species which penetrates estuaries, *G. salinus* is a brackish water species and

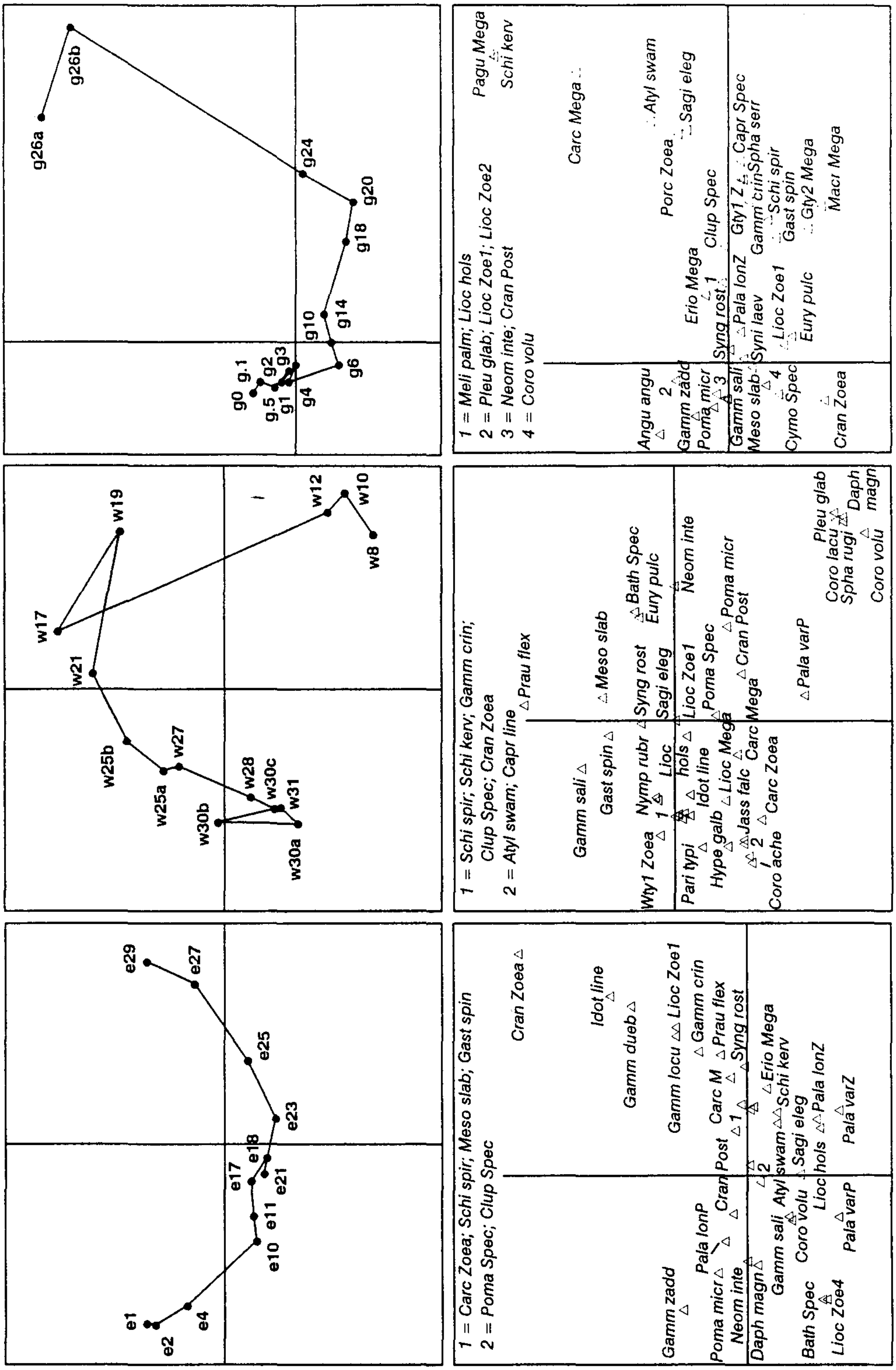

Fig. 9. Species scores (bottom) and sample scores (top) in the ordination plane formed by the first (horizontal) and second (vertical) canonical axes of the CCA with the fourth root transformed biomass data of the three estuaries separately. Samples are connected following salinity.

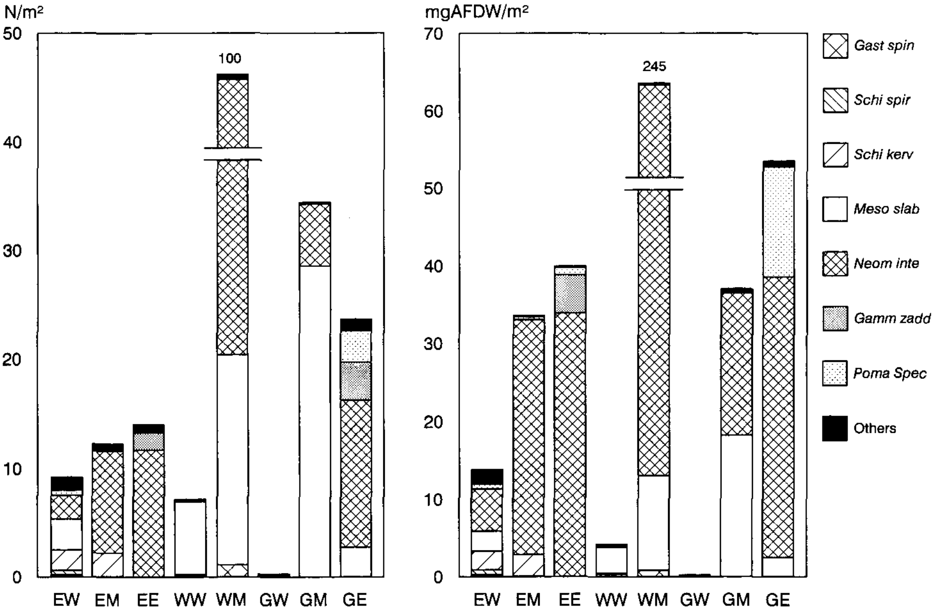

Fig. 10. Faunal composition of the 8 communities as identified by the multivariate analyses: biomass. First letter: *E*ems, *W*esterschelde, *G*ironde; second letter: *W*est, *M*iddle, *E*ast.

G. zaddachi prefers the areas of very low salinity. In contrast to the findings of Meurs & Zauke (1988) an overlap was recorded in the distribution of *G. salinus* and *G. zaddachi* in the Eems and the Gironde.

Still, qualitative and quantitative differences in the corresponding hyperbenthic communities of the three estuaries were obvious. Some species were restricted to one or two of the estuaries studied, while others, especially in the brackish part, were common to all three. The distribution of these common species along the salinity gradient – and the density and biomass they reach in the corresponding salinity zones – varied to some extent between estuaries (for examples see Fig. 5).

The most prominent difference between the estuaries was caused by the oxygen deficiency in the Westerschelde: there was no hyperbenthos present upstream of the 8 g l^{-1} isohaline in the Westerschelde, whereas the density and biomass maximum was situated around the 2 to 4 g l^{-1} isohaline in Eems and Gironde. The low salinity hyperbenthic community was completely absent in the Westerschelde. Upstream of the 10 g l^{-1} isohaline the dissolved oxygen concentration dropped below 40% of the saturation value, which seems to be a critical threshold for hyperbenthic life. The oxygen depletion zone was probably located around even higher salinities on the first sampling day when the *Neomysis* peak was situated around 19 g l^{-1}. Averaged over the year, the abundance maximum of this species in the Westerschelde is located around the 15 g l^{-1} isohaline (Mees *et al.*, 1994). Whereas the distribution of hyperbenthic species in Gironde and Eems seemed to be primarily determined by salinity, the location of the Westerschelde populations was governed by dissolved oxygen concentration. The populations of a number of species, which in Gironde and Eems reached highest density and biomass in the oligohaline zone, seem to have almost disappeared from the Westerschelde (e.g. *Gammarus zaddachi* and *Palaemon longirostris*). Other species did not occur in their 'normal' salinity range and their populations have shifted to higher, atypical salinity zones (e.g. *Neomysis integer*, *Mesopodopsis slabberi*, *Pomatoschistus microps*, *Gammarus salinus*). In the case of *P. microps* and *G. salinus* this is probably accompanied by a considerable decrease in numbers. Most 'marine' species did not penetrate as far into the Westerschelde as they did in Gironde and Eems and had a more limited upstream distribution (e.g. *Schistomysis spiritus*, *S. kervillei*, *Pomatoschistus* species).

Absence of a species from the samples does not necessarily mean it is not present in the estuary. This is certainly true for the rare species and for animals not efficiently caught with the sledge e.g. *Pleusymtes glaber* and *Melita palmata* (Mees *et al.*, 1993b), and *Rhithropanopeus harrisii* (Wolff & Sandee, 1971; Van

Damme *et al.*, 1992) were previously recorded from the Westerschelde and *Sphaeroma rugicauda* is known to be present in the Eems (Michaelis *et al.*, 1992). Still, especially for the abundant species of Eems and Gironde (e.g. Table 1), the low number of individuals (if any) caught in the Westerschelde can give an indication of significantly reduced population sizes in the impoverished Westerschelde. *Gammarus zaddachi* was not recorded from the Westerschelde in this study although occasionally an individual is caught in the tidal marsh of Saeftinghe (Cattrijsse *et al.*, 1993). Den Hartog (1964) discussed the Gammaridea of the Westerschelde and reported *G. zaddachi* from several locations in the Delta area. The species disappeared from the Rhine before 1958 and from all other estuarine waters in the area in 1960, probably due to pollution or an epidemic. The estuarine populations had not recovered by 1963. *Palaemon longirostris* was formerly common in the oligohaline parts of the estuaries of the Delta area (Holthuis, 1950). During intensive sampling in the early seventies only 1 individual was found in the Westerschelde near Bath (Heerebout, 1974) and the disappearance was attributed to pollution. *P. longirostris* is very common in European estuaries of the geographical area covered (e.g. Heerebout, 1974; Marchand, 1981; Sorbe, 1983). It occurs along the entire estuarine gradient (0 to 28 g l^{-1}). It is reasonable to conclude that these species should normally also occur in the Westerschelde and that their absence from the system has to do with pollution.

Neomysis integer occurred in much higher densities in the Westerschelde (242 and 129 ind m^2 at 19 and 10 g l^{-1}) than it did in the other estuaries (30 and 33 ind m^2, for Eems and Gironde, at 4 and 2 g l^{-1} respectively). This suggests a spatial compression of the population between critically low oxygen concentrations on the freshwater side and perhaps species better adapted to higher salinities on the seaward side. The population was concentrated in the immediate vicinity of the edge of the oxygen depletion zone, probably in order to be as close as possible to the large amounts of high quality food (organic detritus with associated bacteria) entering the oxygenated part of the system. The high biomass in this narrow zone indicates *N. integer* is capable of successfully exploiting this detrital material, either directly or through the second trophic level (e.g. the copepod *Eurytemora affinis*). Like most brackish water species *N. integer* is euryhaline and eurythermic. There are no indications that the species' growth or reproduction are hampered by the higher salinities at which it occurs in the Westerschelde (Mees *et al.*, 1994; Mees & Sorbe, in preparation).

Other differences among the estuaries are related to latitude. Some species probably reached their northern or southern distribution limits in one of the systems studied (e.g. the absence of *Idotea linearis* from the Gironde; the occurrence of *Sphaeroma serratum* and the several crab larvae only found in the Gironde). *Schistomysis kervillei* has its southern distribution limit in the north of Spain and, though quite common in the coastal waters adjacent to the Gironde (San Vincente & Sorbe, 1990), the species probably avoids the high summer temperatures in the estuary. Also, the smaller salinity range and lower densities of *Mesopodopsis slabberi* in the Eems may be linked to the lower temperature: possibly its summer migration into the brackish reaches (Mees *et al.*, 1993a) occurs later in the year. The absence of juveniles of coastal *Pomatoschistus* species from the Gironde can not be explained. Both *P. lozanoi* and *P. minutus* are distributed south to the Portuguese coasts (Miller, 1986). *P. lozanoi* seems to avoid estuaries in southern Europe (Hamerlynck, 1990), but *P. minutus* is very common even in the Tagus (Moreira *et al.*, 1991).

Differences among the estuaries in the reproductive state of populations may also be related to temperature. Populations of the same species are liable to have been sampled in a different life cycle phase at each latitude, which may explain the presence/absence and relative densities of certain developmental stages – i.e. functional species or temporary hyperbenthic species (Hamerlynck & Mees, 1991) – in the estuaries (e.g. the lower density of *Crangon crangon* zoeae and *Palaemon longirostris* zoeae in the Eems, the presence of *Pagurus*, *Porcellana* and *Macropodia* megalopae in the Gironde). Other differences may relate to the physical characteristics of the estuaries. Sorbe (1983) found *Palaemonetes varians* to be common in less dynamic areas close to the Gironde, but thinks it doesn't tolerate the high current velocities in the estuary proper. The Eems samples were characterised by large amounts of peat, which may explain the higher net efficiency for larger fish and epibenthic crustaceans (Table 1). Other differences result from recent introductions of brackish water species. Whereas the crabs *Eriocheir sinensis* and *Rhithropanopeus harrisii* were both successful in colonising the three estuaries, the isopod *Synidotea laevidorsalis* is only present in the Gironde (Mees & Fockedey, 1993).

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