Netherlands Journal of Sea Research
29 (4): 357-370 (1992)

SPATIAL COMMUNITY STRUCTURE OF THE WINTER HYPERBENTHOS OF THE SCHELDE ESTUARY, THE NETHERLANDS, AND THE ADJACENT COASTAL WATERS

J. MEES and O. HAMERLYNCK

Marine Biology Section, Zoology Institute, University of Gent, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium and Centre for Estuarine and Coastal Ecology, Vierstraat 28, 4401 EA Yerseke, The Netherlands

ABSTRACT

A first assessment of the ecological importance of the hyperbenthic fauna in coastal and estuarine systems was made in December 1988 in a pilot study (41 stations) covering the Westerschelde and Oosterschelde estuaries, and part of the neighbouring shallow coastal area, the Voordelta. Multivariate analysis revealed three major gradients which could be divided into seven spatially defined hyperbenthic communities. Canonical Correspondence Analysis was applied to correlate these species assemblages with a number of environmental variables measured at each station. Species distributions in the Westerschelde appear to be primarily determined by a gradient involving salinity, turbidity and dissolved oxygen. Hyperbenthic animals, mainly the mysid *Neomysis integer*, reached high densities in the brackish part (>12 ind·m^{-2}), whereas the more seaward stations had lower densities but a higher number of species. In the benthic filter-feeder dominated Oosterschelde, the total density of the hyperbenthos was very low (<0.05 ind·m^{-2}). The shallow coastal area had intermediate densities. There was a clear gradient from offshore to inshore but the environmental variables measured did not correlate well with this gradient. Though there were substantial overlaps between the clusters, as defined by the different multivariate techniques used, the Voordelta area can be divided into three main subareas.

1. INTRODUCTION

The hyperbenthal is the transition zone between the benthos and the plankton (BOYSON, 1975). The hyperbenthos, often termed suprabenthos or demersal zooplankton, is defined as the fauna living in the water column but more or less dependent on the proximity of the bottom (BEYER, 1958). Numerous animals belonging to a variety of taxonomic groups occupy the hyperbenthal. Permanent hyperbenthic animals spend their whole life in the hyperbenthal (*e.g.* mysids, amphipods, and isopods). Animals that spend only part of their life cycle in the hyperbenthal (*e.g.* larvae of decapods and fishes) make up the temporary hyperbenthos (HAMERLYNCK & MEES, 1991). Since it is not possible to sample mobile hyperbenthic animals quantitatively with conventional techniques used in zooplankton or macrobenthos research, the study of the hyperbenthos is often neglected even in comprehensive ecological studies. Still hyperbenthic animals, especially mysids, are an important component of the biomass of estuarine and coastal regions (*e.g.* WILLIAMS & COLLINS, 1984). They contribute substantially to the diet of fish (*e.g.* MAUCHLINE, 1982; HAMERLYNCK *et al.*, 1990) and shrimps (SITTS & KNIGHT, 1979). They can be significant predators structuring zooplankton populations (FULTON, 1982; HANSSON *et al.*, 1990) and can be important grazers of organic matter (JOHNSTON & LASENBY, 1982; ZAGURSKY & FELLER, 1985). The few papers dealing with the hyperbenthos of estuaries (*e.g.* HULBURT, 1957; SIEGFRIED *et al.*, 1979; SORBE, 1981; WILLIAMS & COLLINS, 1984; JONES *et al.*, 1989) and shallow coastal areas (*e.g.* CLUTTER, 1966; HESTHAGEN, 1973; BOYSON, 1975; RUDSTAM *et al.*, 1986) focus almost exclusively on the mysid component. A community approach, though often used in macrobenthos and phytoplankton studies, has not yet been applied to this compartment of the marine ecosystem.

In the so-called Delta area of the southwest Netherlands (Fig. 1), hyperbenthos studies were started on a monthly basis in the Voordelta in 1988 (HAMERLYNCK & MEES, 1991). After a pilot study covering the Voordelta, Oosterschelde and Westerschelde, which is reported here, further studies were concentrated in the Westerschelde (MEES *et al.*, 1993).

The pilot study was a first assessment of the ecological importance of the hyperbenthos. Sampling was carried out in winter (December 1988) to avoid the presence of temporary hyperbenthic species: the sequential appearance, ephemeral density peak and subsequent rapid disappearance of temporary hyperbenthic animals can strongly influence community structure if sampling is not perfectly synoptic (HAMERLYNCK & MEES, 1991). The presumably low winter densities will also preclude overestimating the importance of the hyperbenthos.

The objectives were (a) to identify the dominant components of the hyperbenthic community, (b) to describe their spatial distribution, (c) to investigate the geographical variation in species composition, density and biomass, and (d) to try to relate the observed patterns to some environmental variables.

Acknowledgements.—This study was supported by the EEC Marine Science and Technology Program (MAST-0024-C(A)), by Rijkswaterstaat Dienst Getijdewateren and by FKFO grant 2.0086.88. Contribution nr. 581 of the Centre for Estuarine and Coastal Ecology.

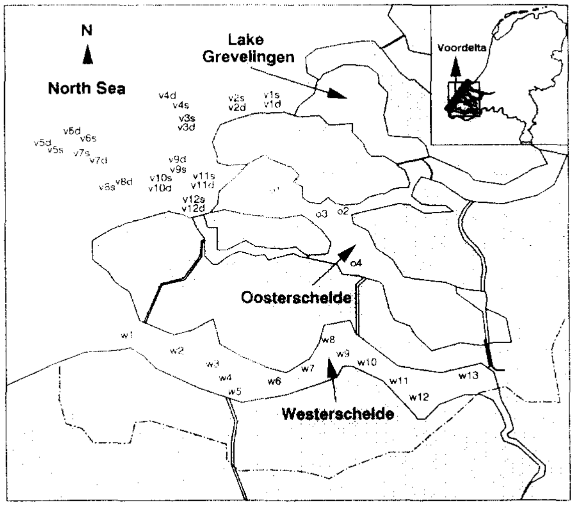

Fig. 1. Map of the Delta area with the sampling sites.

2. MATERIAL AND METHODS

2.1. STUDY AREA

Three major European rivers: the Rhine, Meuse and Schelde, enter the North Sea in the so-called Dutch Delta in the southwestern part of the Netherlands. Most of the former estuaries in this area have been altered by man (review in HEIP, 1989). The study area proper covers only three parts of the Dutch Delta: the Westerschelde, the Oosterschelde and the central part of the Voordelta (Fig. 1).

The lower part of the river Schelde is generally known as the Westerschelde estuary. It is the last true estuary of the Delta area in the southwest of the Netherlands with a marked salinity gradient. The sampled part of the estuarine system is about 70 km long from the North Sea (Vlissingen) to the Dutch-Belgian border. The mean freshwater load is 105 $m^3 \cdot s^{-1}$. The input from organic and inorganic pollutants is very high, especially in the brackish part (DUURSMA *et al.*, 1988). The organic pollution results in lowered oxygen saturation levels in the brackish part (Table 1).

The Oosterschelde estuary is a tidal inlet of the Southern Bight of the North Sea. After the construction of a storm-surge barrier in 1986, the hydrodynamics of the system changed substantially. The tidal amplitude and tidal velocities decreased and the transparency of the water increased. The construction of secondary dams in the landward part, completed by mid-1987, led to a reduced freshwater inflow of 10 $m^3 \cdot s^{-1}$ (NIENHUIS & SMAAL, 1993). There is no salinity gradient, and turbidity and pollution are low.

The Voordelta is the shallow coastal area formed by the interlinked ebb-tidal deltas at the mouth of the rivers Schelde, Meuse and Rhine. It stretches from the Belgian-Dutch border in the south to Hoek van Holland in the north. Its marine boundary is arbitrarily defined by the isobath of 15 m below Mean Tidal Level (MTL). More details on the abiotic environment and the recent geomorphological changes in the Voordelta are given in LOUTERS *et al.* (1991).

TABLE 1

Ranges of the environmental variables measured with (between brackets) teh stations at which the extremes were recorded, the mean for all stations and the standard deviation of that mean.

variable (unit)	*min*		*max*		*mean*	S.D.
salinity (ppt)	12.5	(w13)	32.9	(v5)	28.57	5.51
dissolved oxygen (%)	73	(w13)	111	(v8,v9,v11)	102.2	8.4
pH	7.1	(w13)	8.1	(v5,v6,v7)	7.95	0.19
temperature (°C)	7.0	(o4)	9.3	(v5,v7)	8.17	0.75
Secchi depth (cm)	40	(w13)	250	(o2,o4)	98.0	49.8
median grain size (μm)	125	(v1d)	400	(v12s)	236.9	60.1
mud content (%)	0.0	(v4d,w11)	20.0	(v1d)	2.43	3.53

2.2. SAMPLING

The 41 sampling stations are shown in Fig. 1. Thirteen stations were located in the Westerschelde and four in the Oosterschelde (only in the western and central parts). Twenty-four stations were located in the Voordelta: ten in the ebb-tidal delta of the Oosterschelde (v8-v12), eight in the ebb-tidal delta of the former Grevelingen estuary (v1-v4) and six in the more seaward Banjaard area (v5-v7). These 24 Voordelta stations were really two depth strata of 12 localities. At each locality two parallel tows were done in proximity to one another: one at a depth of MTL minus 10 m (*e.g.* v4d, 'd' for deep) in the gully and one at MTL minus 5 m (*e.g.* v4s, 's' for shallow) on the sandbank slope.

Samples were collected with a hyperbenthic sledge which consists of a heavy metal frame with two mounted monofilament nets. The nets are 4 m long with a mesh size of 2×2 mm in the first 3 m and 1×1 mm in the last metre. The lower net samples the water column from 20 to 50 cm, the upper net from 50 to 100 cm above the bottom. For this paper the contents of both nets were combined and treated as one sample. The sledge was towed over a distance of approximately 1000 m (starting from a buoy or other fixed marker, the distance covered was read from the radar screen) at an average ship speed of 4.5 knots relative to the bottom. All samples were taken during daytime on four days within a two-week period. Trawling was always done with the tide. The samples were immediately rinsed over a 1 mm sieve and preserved in a buffered formaldehyde solution, 7% final concentration.

In the lab all animals were identified, if possible to species level, and counted. For the analysis different developmental stages of decapods (zoeae, megalopae, and postlarvae) were treated as separate 'species', since they have a different ecology. Animals with continuous growth were measured (standard length from the rostral tip to the last abdominal segment) and their biomass was derived from regressions relating length to ash-free dry weight (AFDW). AFDW was determined as the difference between dry weight (60°C for 5 days) and ashed weight (650°C for 2 hours) for representative size distributions of the various species. For animals growing in discrete stages an average biomass value was assigned per stage. This value was determined by measuring the AFDW of batches of animals belonging to a certain stage (Mees, unpubl. data).

Pelagic fish, epibenthic (demersal fish and adult crabs) and infaunal (adult polychaetes and bivalves) organisms were excluded from the analysis. All density and biomass data are presented as numbers of individuals (N) and grammes ash-free dry weight (gAFDW) per trawl (1000 m^2).

2.3. MULTIVARIATE ANALYSIS OF COMMUNITY STRUCTURE

The sampling sites were classified into clusters according to species composition using the classification program TWINSPAN (HILL, 1979), which is a dichotomous divisive technique. In order to reduce the weight of the dominant species, the density and biomass data were subjected to a fourth root transformation prior to the TWINSPAN analysis (CLARKE & GREEN, 1988). TWINSPAN allows the user to define a number of 'cutlevels' which will split the data for a species into different 'pseudospecies', one for each chosen abundance level. The cutlevels used in the analysis were 0, 1, 2, 5, 10, 20, and 30 for the density data and 0, 0.1, 0.5, 1, 2, 3 and 5 for the biomass data. TWINSPAN yields indicator species characterizing the various groups. The TWINSPAN classification was stopped at the 4th or 5th division, as further groupings ceased to be ecologically meaningful. As advocated by FIELD *et al.* (1982) the consistency of the TWINSPAN results was assessed by comparing it to the result of an agglomerative type of analysis: a group-average sorting (GAS) cluster analysis with the Bray-Curtis similarities (BRAY & CURTIS, 1957), also performed on the fourth root transformed density data.

At each site, depth was recorded and the following environmental variables were measured at 1 m from the bottom: temperature, salinity, conductivity, dissolved oxygen, pH and secchi disk depth. A Van Veen grab was used to take bottom samples to measure mud content and median grain of the sand fraction. The ranges of the environmental variables measured are summarized in Table 1.

The relationship between species composition and these environmental variables was analysed using the Canonical Correspondence Analysis (CCA) option from the program package CANOCO (TER BRAAK, 1988) on the fourth root transformed density data. Because of the hyperbolic relationship between secchi depth and the first CCA axis this variable was transformed reciprocally. This variable thus becomes a light extinction measure correlated to the turbidity of the water.

Diversity of the communities was calculated as the mean of Hill's diversity number N_1 (HILL, 1973) for each station in the TWINSPAN clusters. N_1 is defined as exp(H), with H the Shannon-Wiener diversity index.

3. RESULTS

A total of 39 'species' were identified (Table 2). Mysids were the dominant faunistic group at each station. Only seven mysid species were recorded. Four of them were relatively abundant in at least part

TABLE 2

List of species: permanent and temporary hyperbenthic species are marked P and T respectively. Species marked Z are truly zooplanktonic species; species marked A are 'aufwuchs' species.

taxonomic group *name and stage*	*abbreviation*	
Crustacea		
Decapoda		
Caridea		
Crangon crangon postlarvae	Cran Post	T
Crangon crangon zoea	Cran Zoea	T
Eualus occultus postlarvae	Eual occu	T
Hippolyte varians postlarvae	Hipp Post	T
Anomura		
Porcellana longicornis megalopa	Porc Mega	T
Brachyura		
Carcinus maenas megalopa	Carc Mega	T
Carcinus maenas zoea	Carc Zoea	T
Liocarcinus holsatus megalopa	Lioc Mega	T
Liocarcinus holsatus zoea	Lioc Zoea	T
Macropodia species megalopa	Macr Mega	T
Amphipoda		
Caprellidea		
Caprella linearis	Capr line	A
Pariambus typicus	Pari typi	A
Phtisica marina	Phti mari	A
Gammaridea		
Atylus swammerdami	Atyl swam	P
Corophium volutator	Coro volu	P
Gammarus species	Gamm spec	P
Jassa falcata	Jass falc	P
Melita palmata	Meli palm	P
Melita obtusata	Meli obtu	P
Monoculodes carinatus	Mono cari	P
Pontocrates altamarinus	Pont alta	P
Orchomene nana	Orch nana	P
Isopoda		
Eurydice pulchra	Eury pulc	P
Idotea linearis	Idot line	P
Copepoda		
Calanus helgolandicus	Cala helg	Z
Caligidae species	Cali spec	Z
Cumacea		
Bodotria scorpioides	Bodo scor	P
Diastylis bradyi	Dias brad	P
Diastylis lucifera	Dias luci	P
Diastylis rathkei	Dias rath	P
Mysidacea		
Gastrosaccus spinifer	Gast spin	P
Mesopodopsis slabberi	Meso slab	P
Neomysis integer	Neom inte	P
Praunus flexuosus	Prau flex	P
Siriella armata	Siri arma	P
Schistomysis spiritus	Schi spir	P
Schistomysis kervillei	Schi kerv	P
Chelicerata		
Pycnogonida		
Nymphon rubrum	Nymph rubr	A
Chaetognatha		
Sagitta elegans	Sagi eleg	Z

of the study area: *Schistomysis spiritus, Schistomysis kervillei, Mesopodopsis slabberi* and *Neomysis integer*. The species *Gastrosaccus spinifer* and *Praunus flexuosus* occurred in low densities almost throughout the study area. *Siriella armata* was only recorded from one locality in the Voordelta (v11d). Besides mysids, postlarvae of the brown shrimp *Crangon crangon* and a few amphipod species made up the bulk of the hyperbenthos. All *Gammarus* were lumped as *Gammarus* species but this category referred mainly to *G. crinicornis* in the Voordelta and the marine part of the Westerschelde and predominantly *G. salinus* in the brackish part of the Westerschelde (Mees *et al.*, 1993). Two other common amphipods were *Atylus swammerdami* (mainly in the Voordelta), and *Corophium volutator* (mainly in the brackish part of the Westerschelde). A detailed description of the distribution of the individual species will be published elsewhere.

The result of the TWINSPAN for both density and biomass can be seen in Fig. 2. Fig. 3 shows the geographical location of the clusters identified by TWINSPAN. When the clusters of stations resulting from the analysis of the density (Figs 2 and 3 top) and biomass data (Figs 2 and 3 bottom) are compared, a number of strong resemblances are apparent: the Oosterschelde (OS) cluster which includes the station v2s from the ebb tidal delta of the Grevelingen, the cluster corresponding to the marine part of the Westerschelde (WM) covering the stations w2 through w5, the cluster corresponding to the central part of the Westerschelde (WC) covering the stations w6 through w10 and the two inner stations in the brackish part of the Westerschelde (WB).

In the Voordelta the situation is more complex but some associations of stations in the four clusters occur in both dendrograms: a group of stations from the 'offshore' Banjaard area (v5s, v5d, v6s, v7s) and a station from the outer part of the ebb tidal delta of the Grevelingen (v3d) are the core of the Banjaard (BJ) cluster, a group of stations from the ebb tidal delta of the Grevelingen (v1s, v2d, v3s) and a station from the ebb tidal delta of the Oosterschelde (v12s) are the core of the Voordelta inshore Grevelingen cluster (VIG), a group of stations from the southern part of the ebb tidal delta of the Oosterschelde (v8s, v10d, v11d, v12d) and the westernmost station of the Oosterschelde (o1) are the core of the Voordelta inshore Oosterschelde cluster (VIOS), and finally two stations in the northern part of the ebb tidal delta of the Oosterschelde (v9d and v9s) form the VION (N for north) cluster. Many of the stations on the 'edges' between these clusters switched from one cluster to another: station w11 moved to the WB cluster in the biomass data, w1 moved to the VIOS cluster in the density data, station v4s moved between the VIG and BJ clusters, *etc*. In the TWINSPAN of the biomass

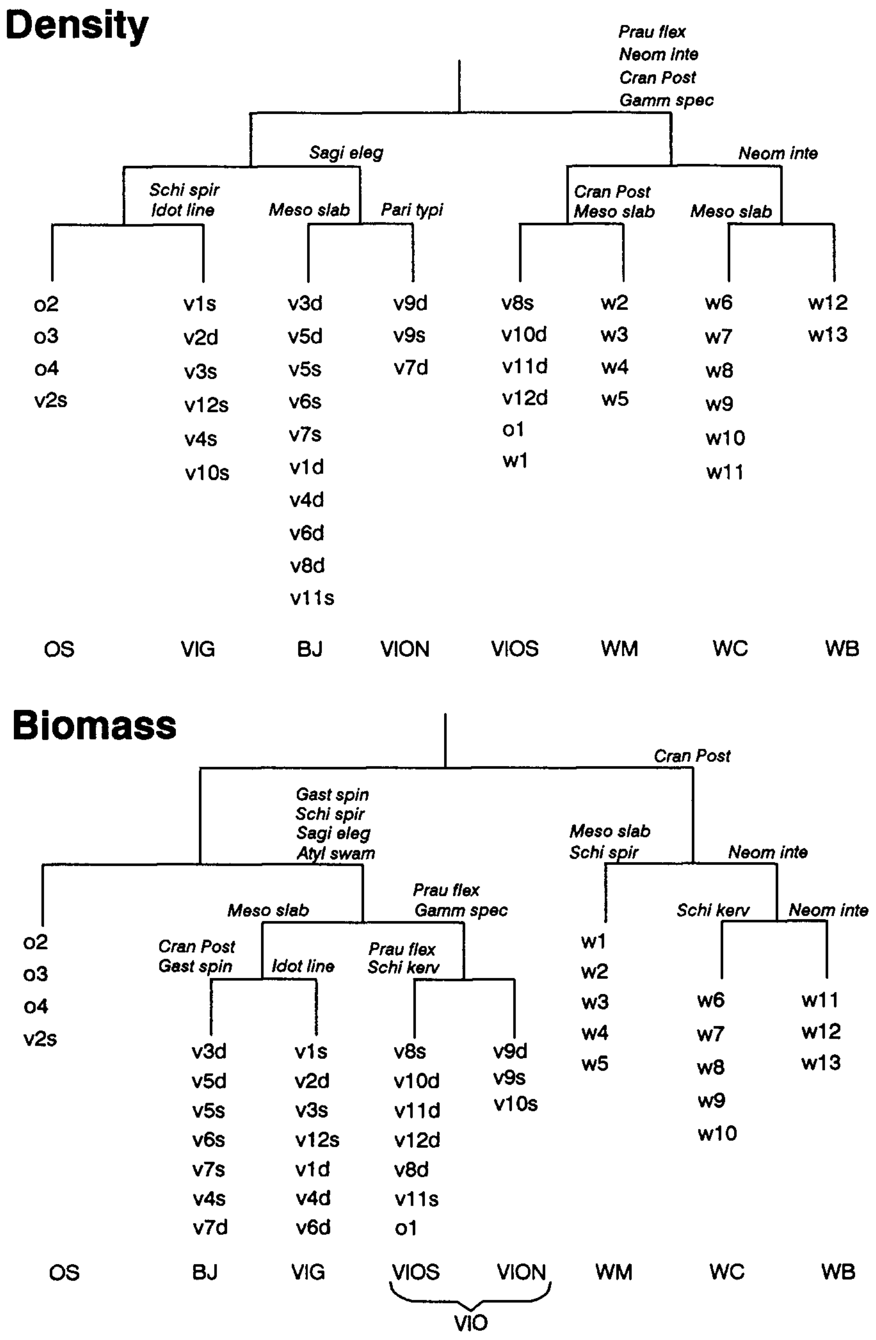

Fig. 2. The TWINSPAN analysis of the samples based on the transformed density (top) and biomass (bottom) data with the indicator species for each division indicated. Abbreviations are explained in Table 2.

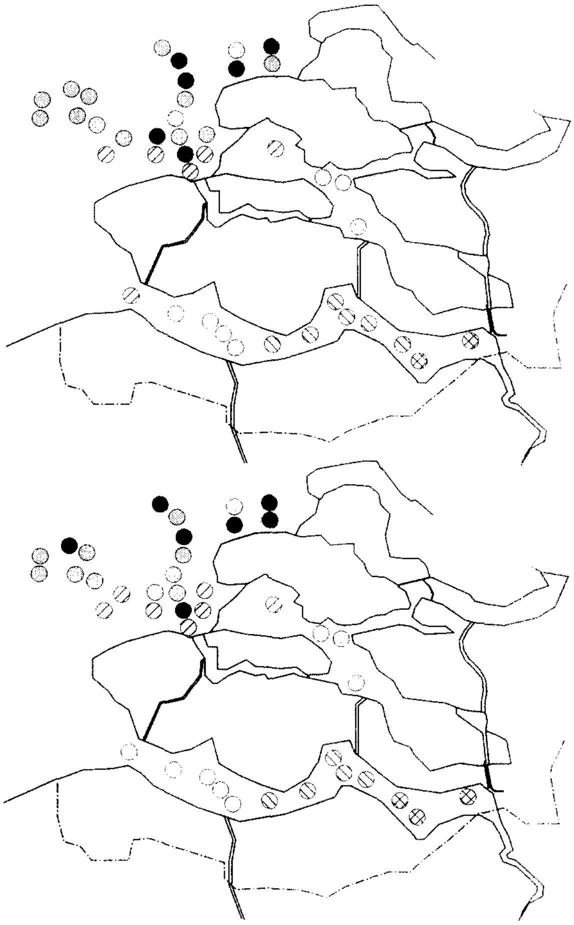

Fig. 3. The location of the TWINSPAN clusters based on density data (top) and biomass data (bottom).

data the VION and VIOS clusters are closely tied and can be grouped into a more comprehensive VIO cluster containing all the stations in the ebb tidal delta of the Oosterschelde (except for v12s), the two v8 stations intermediate between this area and the Banjaard area and the westernmost station of the Oosterschelde.

When the TWINSPAN (Fig. 2) and the GAS result (not depicted) for the density data are compared, the three Westerschelde clusters (WM, WC and WB) can be distinguished. For the other groupings there is less similarity though most of the stations of the BJ and VIG clusters occur in one large cluster (supplemented by both v11 stations). Some parts of other TWINSPAN clusters can also be recognized. There is a mixed cluster of shallow stations (plus v9d) associated with the Oosterschelde stations.

In the species plot of the plane formed by the first (eigenvalue 0.52) and second (eigenvalue 0.18) canonical axes of the ordination analysis (CCA) (Fig. 4 centre) two main strings of stations can be distinguished: a first string stretching from the upper right to the lower left along which the three WS clusters can be seen and a second string from the upper left to the lower centre. In this second string the Banjaard stations are plotted in the upper left corner, then come the stations from the ebb tidal delta of the Grevelingen (first the outer and then the inner stations, with stations o2, v8d and v9s in between) and finally the string merges with the lower left part of the first string in a mixture of stations from the Oosterschelde proper and stations from the ebb tidal delta of the Oosterschelde. In the plot of the species scores (Fig. 4 top) the species corresponding to these strings can be found: *Neomysis integer, Corophium volutator, Eurydice pulchra* and *Crangon crangon* postlarvae towards the right, corresponding to the WB and WC clusters in the Westerschelde string; *Gammarus species, Praunus flexuosus, Schistomysis kervillei*, and *Mesopodopsis slabberi* (close to the origin of the diagram) corresponding to the WM and VIO clusters. The species assemblage typical of the diverse ma-

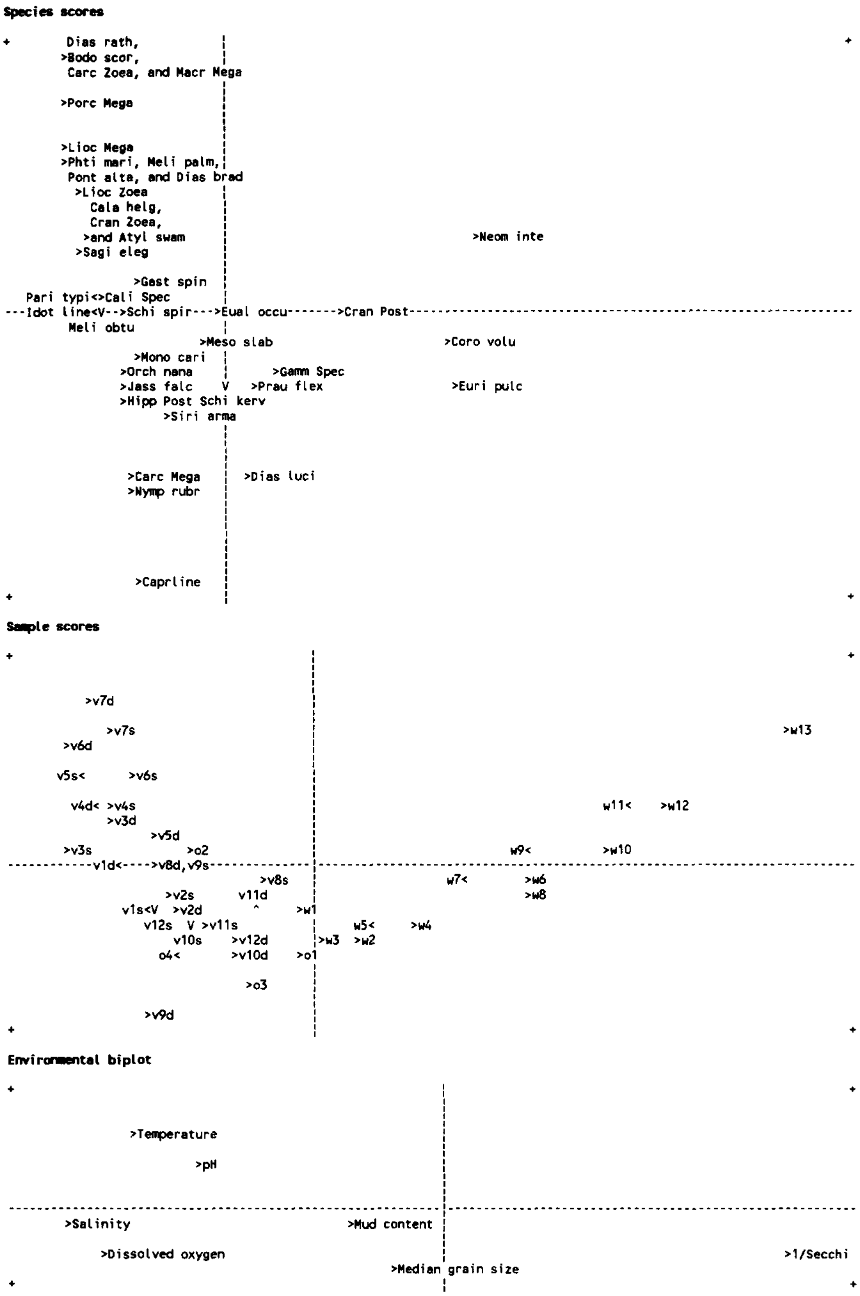

Fig. 4. Canonical Correspondence Analysis (density data for all samples): scores of species, samples and environmental variables in the plane of the first two canonical axes. Abbreviations are explained in Table 2.

rine fauna of the Banjaard area is located in the upper left corner. The biplot diagram of the environmental data (Fig. 4 bottom) reveals a main gradient connecting the salinity vector on the left with the 1/secchi depth vector on the right. This gradient nearly coincides with the first canonical axis. Both vectors are quite long, which indicates that these variables are highly correlated with the ordination plane. In CCA the ordination axes are, by definition, derived as linear functions of the environmental variables. Thus salinity and 1/secchi (together with dissolved oxygen concentration) are very important in determining the first canonical axis, and seem to define the main gradient structuring the communities. There is a gradient from the left part of the biplot diagrams with high salinity, transparent and oxygen saturated ('marine') conditions to the right part with brackish, turbid and low oxygen ('estuarine') conditions. The correlations of the second axis are less obvious, though the relatively small vector of median grain size lies close to it. This environmental variable is correlated to the hydrodynamics of an area, mainly current speed and wave action.

The plot of the sample scores for the first and third (eigenvalue 0.16) canonical axes (not depicted) is more difficult to interpret. There is a segregation of the Oosterschelde and Voordelta clusters with the species-poor Oosterschelde cluster near the top of the diagram, followed by the majority of VIG stations, a mixture of the BJ and remaining VIG stations and finally the VIO cluster near the centre and towards the bottom. The third axis does not correlate strongly with any of the environmental variables measured. A CCA on the biomass data of the Voordelta sites only (Fig. 5) reveals the spatial structure in this area more clearly. The first (eigenvalue 0.26) and second (eigenvalue 0.12) axes suffice to interpret the data. All VIO stations (v8 to v12) of the dynamic ebb tidal delta of the Oosterschelde are located on the left side of the plot and are characterized by low values for Secchi disk depth, and high values for dissolved oxygen concentration and median grain size of the sand fraction. The VIG stations (v1 to v4) in the upper right quadrant have a higher mud content and Secchi disk depth, and lower dissolved oxygen concentrations. All seaward BJ stations (v5 to v7) are situated in the lower right quadrant of the plot. These are characterized by higher temperature and salinity values.

On the basis of the clusterings, giving precedence to the TWINSPAN biomass result, and confirmed by the CCA, seven more or less coherent geographical subareas can be distinguished by their species-abundance composition: OS: o2-4(+v2s), WB: w11-w13, WC: w6-w10, WM: w1-w5, BJ: v3-v7, VIG: v1-v2, and VIO: v8-v12 and o1.

Figs 6 and 7 show the average density and biomass values of the most important species in each subarea. The composition of the species assemblages in the seven clusters differed substantially, but mysids were always dominant. The subareas also

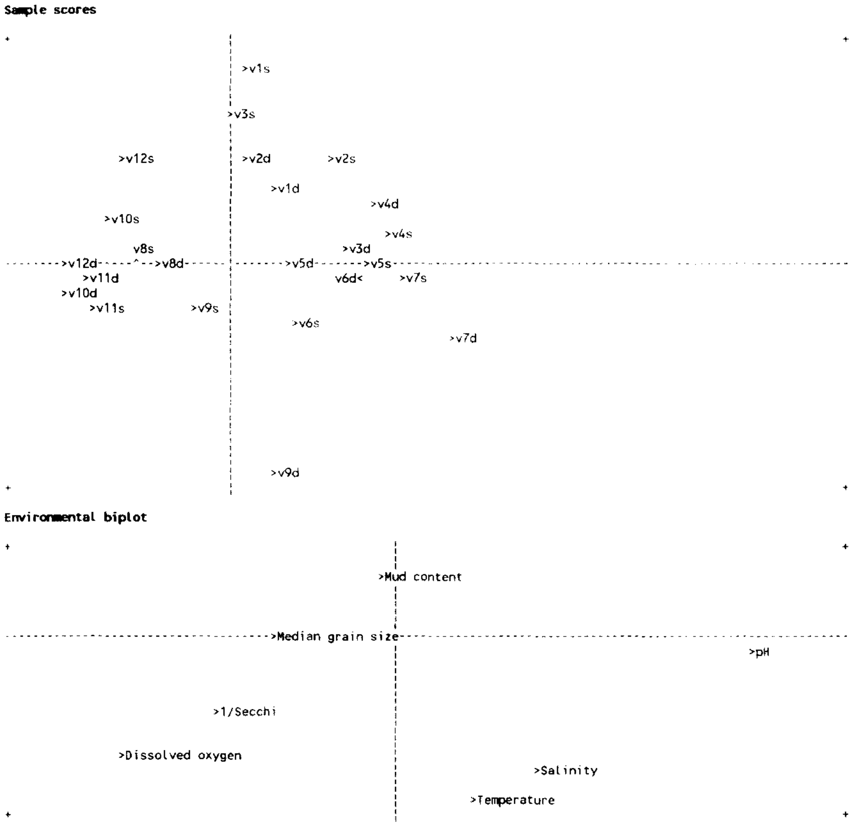

Fig. 5. Canonical Correspondence Analysis (biomass data of the Voordelta samples only): scores of samples and environmental variables in the plane of the first two canonical axes.

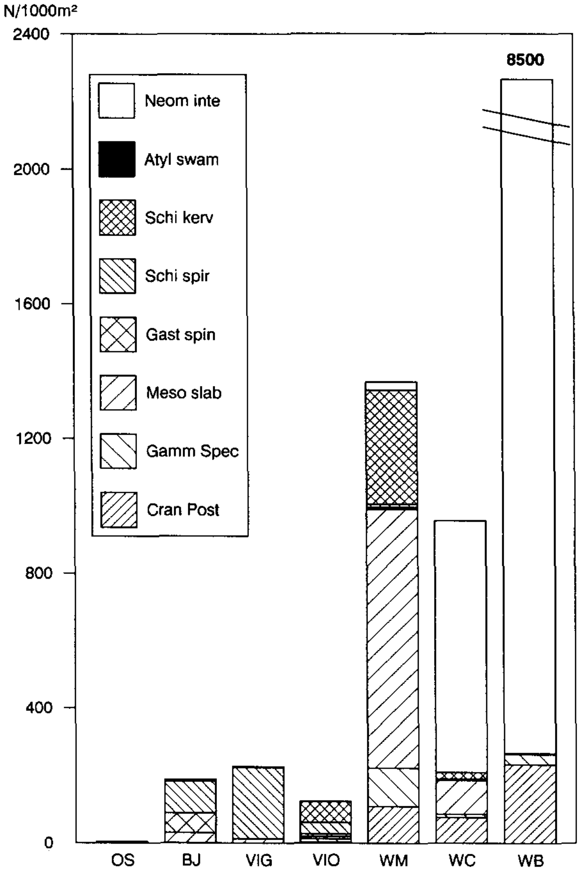

Fig. 6. Average density and species composition in the subareas. Abbreviations are explained in Table 2.

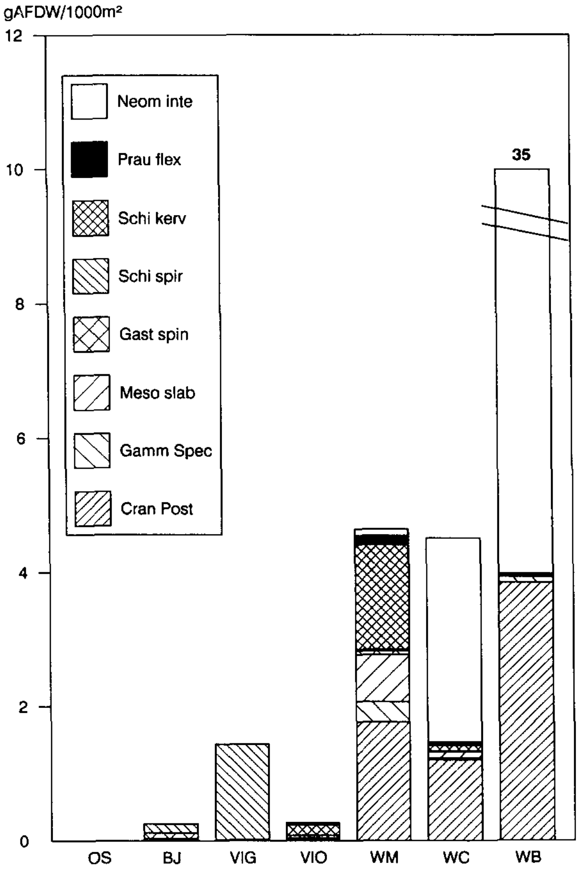

Fig. 7. Average biomass and species composition in the subareas. Abbreviations are explained in Table 2.

differed in total density and biomass. The subarea with by far the highest hyperbenthic density and biomass (35 g AFDW per 1000 m^2 on average with peaks exceeding 50 g) was the brackish part of the Westerschelde (cluster WB). Here *Neomysis integer* reached densities of more than 12 animals per m^2. The upper estuarine fauna mainly comprised *Neomysis integer, Gammarus* species, *Corophium volutator, Eurydice pulchra*, and *Crangon crangon* postlarvae. Density and biomass declined markedly towards the mouth of the estuary. The WM stations were characterized by a higher number of species represented by a lower number of individuals than the upper estuarine stations. Consequently, diversity was highest in the western part and lowest in the eastern part of the estuary (Table 3). *Schistomysis kervillei* and *Mesopodopsis slabberi* were the dominant mysids in the western part, the latter species penetrating further into the estuary. *Schistomysis spiritus* was only present at the westernmost stations and was the most important species in the Voordelta. The seaward decline of total density and biomass of the hyperbenthos in the Westerschelde, as well as the distribution of the most important mysid species, is illustrated in Fig. 8. Note that though *Mesopodopsis slabberi* could be numerically important, this slender species did not contribute much to the total biomass of the hyperbenthic community. Still, even the poorest Westerschelde clusters (about 5 g AFDW per 1000 m^2) had hyperbenthic densities and biomass values that were,

TABLE 3

Hill's N_1: mean and standard deviation for the samples in the 7 TWINSPAN clusters.

cluster	*mean*	*S.D.*
OS	1.739	0.595
BJ	3.709	0.772
VIG	2.691	1.123
VIO	4.429	1.988
WM	2.444	1.239
WC	2.379	0.779
WB	1.301	0.231

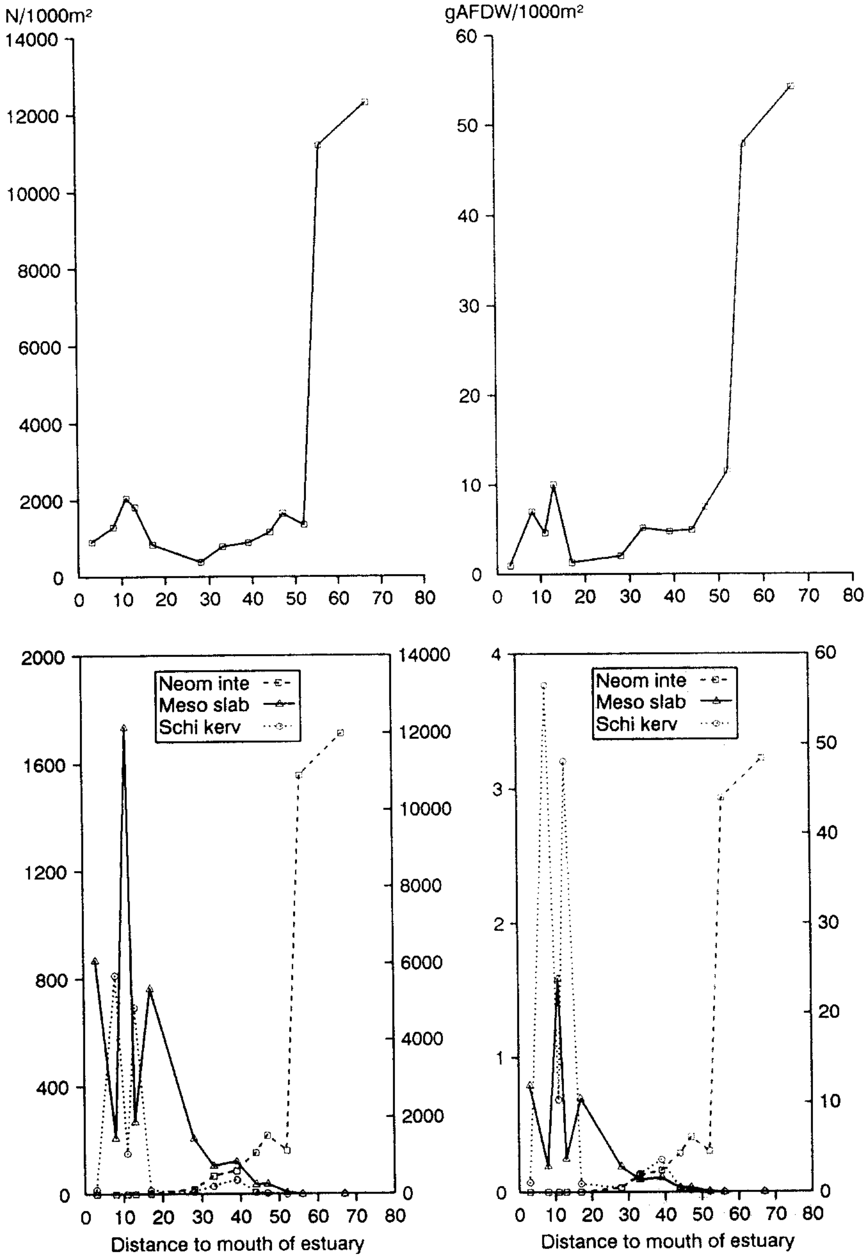

Fig. 8. Density (left) and biomass (right) of the entire hyperbenthic community (top) and the most important mysid species (bottom) along the salinity gradient in the Westerschelde. Note that for *Neomysis integer* a different scale is used (Y-axis on the right).

respectively, more than 5 and 3 times higher than the richest cluster in the rest of the study area. The fauna of the coastal area was more diverse (Table 3), especially in the ebb-tidal delta of the Oosterschelde towards the outer Banjaard, and the highest biomass was found in the Grevelingen area (1.5 g AFDW per 1000 m^2). The Voordelta clusters near the storm surge barrier and the one of the Banjaard area were poor (both less than 0.5 g AFDW per 1000 m^2). In the samples of the Oosterschelde cluster hardly any hyperbenthos was present (0.004 gAFDW per 1000 m^2).

4. DISCUSSION

Mysids dominated the winter hyperbenthos in all communities. The recorded densities are subject to several possible sources of bias. Net efficiency was assumed to be 100%. However, mysids are good swimmers which are known actively to avoid nets (MAUCHLINE, 1980). Thus, the reported densities may be a gross underestimate of the actual number of mysids present in the area. Net avoidance may be more pronounced in areas with high water transparencies (Oosterschelde, Banjaard) than in highly turbid situations (Westerschelde) and this difference may contribute to the high densities recorded in the Westerschelde. Most mysid species encountered in this study are known to concentrate near the bottom during the day (HEUBACH, 1969; HESTHAGEN, 1973; MAUCHLINE, 1980), but in a highly turbid estuary with little light penetration, such as the Westerschelde, the animals probably occupy the entire depth range throughout the day (J.-C. Sorbe, pers. comm.). As only the lower metre of the water column was sampled this would lead to an underestimate of density. Mysids are also known to aggregate in dense shoals in very shallow areas (less than 5 m deep) not sampled in this study (CLUTTER, 1966; MAUCHLINE, 1980). The species *Gastrosaccus spinifer* spends most of the daytime buried in the sand (TATTERSALL & TATTERSALL, 1951) and was most certainly underestimated. On the whole, the reported mysid density and biomass are therefore likely to be minimum estimates. Moreover, a winter situation was recorded and hyperbenthic and mysid biomass are known to increase substantially in spring and summer, both in the Voordelta (HAMERLYNCK & MEES, 1991) and the Westerschelde (MEES *et al.*, 1993).

All sites sampled could be grouped into 7 geographically coherent clusters corresponding to 7 species assemblages. Note that the underlying structure is a continuum and that some stations such as v3 and v4 are really intermediate between the VIG and BJ clusters. Other stations are in a sense 'misclassified', *e.g.* station v2s which clusters with the three inner Oosterschelde stations in the TWINSPAN. In a year of monthly sampling at all Voordelta sites the catch composition at this site was always similar to that of the neighbouring sites (v1 and v2), both qualitatively and quantitatively (Mees, unpublished data). The extremely low number of animals caught at this station in December 1988 is therefore most probably of an aleatory nature. Note also that, because of migrations, species distributions may be different in other seasons.

Multivariate analysis is a useful descriptive tool for an exploratory analysis of the data in a pilot study such as this. The use of different techniques, which are then compared, enhances one's perception of the underlying structure in the data. However, it also introduces a certain subjectivity by allowing one to select the most aesthetically pleasing result, which is not necessarily the most meaningful from an ecological perspective. The result of the GAS, though similar to the results of the other techniques in a broad sense, differs quite substantially in the details. This is perhaps because this technique is quite sensitive to rare species, which could not be omitted from the data set owing to the relative species poverty of the hyperbenthos in comparison to *e.g.* meiobentic (HEIP *et al.*, 1990) or macrobenthic (CRAEYMEERSCH *et al.*, 1990) communities in the same area. Multivariate analysis neatly summarizes the structure in complex data sets and can help us to formulate hypotheses that may take years to prove or disprove (review in JAMES & MCCULLOCH, 1990).

The spatial pattern observed in the Voordelta is brought out more clearly by the annual means per station (HAMERLYNCK & MEES, 1991). The possible causes for this pattern are discussed in that paper. In summary: the hydrodynamical regime leads to a high primary production and an accumulation of passively transported particles in the ebb tidal delta of the Grevelingen (LOUTERS *et al.*, 1991; HAMERLYNCK *et al.*, 1992). This concentration of food probably attracts mobile animals (*e.g.* mysids) to this subarea and accounts for the presence of a relatively abundant hyperbenthic fauna. In the Banjaard area and the ebb-tidal delta of the Oosterschelde, where wave action and high current velocities prevent the sedimentation of detritus, densities are lower.

The Westerschelde is the only true estuary in the Delta area and is characterized by a distinct hyperbenthic fauna. Apparently the environmental variables measured suffice to explain the structure of the hyperbenthic communities in the estuary. Salinity, dissolved oxygen and turbidity explain the main variation in species distributions. Naturally, in a causal sense, the structure may be determined by other covariables, both biotic or abiotic, which were not measured. Density and biomass are very high, especially in the brackish high turbidity zone, and the faunal assemblages recorded from the three Westerschelde subareas show a seaward replacement of brackish water species by marine species. Salinity is almost certainly the most important environmental variable restricting access to the brackish part for stenohaline marine species.

In a comparison of the hyperbenthic fauna of the Oosterschelde and the Westerschelde, the difference in food supply may be structurally important. The Oosterschelde has a much poorer hyperbenthic fauna than neighbouring areas. Due to the construction of the barrier and the other engineering projects in the Oosterschelde, average seston concentrations and nutrient loadings are very low (BAKKER *et al.*, 1990). Benthic suspension feeders dominate in the western and central parts of the embayment, used as a culture area for mussels. The two key species in the trophodynamics of the system are the mussel, *Myti-*

lus edulis, and the cockle, *Cerastoderma edule*. Mean mussel biomass reaches 456 g AFDW per m^2 on the culture plots. The cockle *Cerastoderma edule* mainly occupies the intertidal flats with a mean biomass as high as 63 g AFDW per m^2 on the cockle banks (PRINS & SMAAL, 1990). The volume of the western part of the Oosterschelde can be filtered by the bivalves every four days (SMAAL *et al.*, 1986). Thus most of the organic matter is grazed by the benthos. This dominance of filter feeders in the Oosterschelde results in a stable ecosystem (HERMAN & SCHOLTEN, 1990) where hyperbenthic animals may lose the competition for food. Other factors, such as a high predation pressure (linked with the high water transparency) probably also contribute to the absence of substantial mysid populations in the area. Because of logistical limitations only the western and central parts of the Oosterschelde were sampled. In the eastern part, where turbidity is higher and filter-feeder biomass lower, the situation may be different and mysids may be more abundant. In summer, schools of *Praunus flexuosus* can be seen swimming over vegetated stony ground in this area (P.H. Nienhuis, pers. comm.). Unfortunately this type of substrate is inaccessible to the sampling gear used.

Benthic biomass is much lower in the Westerschelde than in the Oosterschelde. MEIRE *et al.* (1991) report a shift from a filter feeder dominated macrobenthic community in the Oosterschelde and the marine part of the Westerschelde to a deposit feeder dominated community in the inner Westerschelde. Average biomass in the Oosterschelde is estimated at 50 g AFDW per m^2, in the Westerschelde a gradient is found from a relatively low benthic biomass in the brackish part (9 g AFDW per m^2) to a higher biomass in the marine part (33 g AFDW per m^2) (VAN DER MEER *et al.*, 1989). This gradient corresponds with the existence of two different types of food chain in the Westerschelde (HUMMEL *et al.*, 1988): a detritus based food chain in the brackish part and a coastal phytoplankton based food chain in the seaward part. In the brackish part there is a continuous supply of large quantities of detrital material from the river (VAN ECK *et al.*, 1991) and in this typical estuarine turbidity zone the hyperbenthos reaches its maximum abundance. The few species that can resist the harsh conditions in the brackish part can benefit from the abundant and potentially high quality food (aggregations of detritus and bacteria). Most mysid species are omnivores and consume a variety of items, often indiscriminately (MAUCHLINE, 1980). Species of the genus *Neomysis* are known to feed on organic matter and detritus on or near the sediments (MAUCHLINE, 1971; SIEGFRIED & KOPACHE, 1980; JOHNSTON & LASENBY, 1982; ZAGURSKY & FELLER, 1985). KOST & KNIGHT (1975) showed that detritus is the principal dietary item of *N. mercedis* in a North American estuary. There are indications of adaptations in mysids that may render a high efficiency of detritus use possible (FRIESEN *et al.*, 1986). In the brackish high turbidity zone the sedentary benthic fauna is probably highly stressed because of unstable sediments (high current velocities), considerable dredging activities, high loads of pollutants and, especially in summer, oxygen depletion due to the intense heterotrophic bacterial activity (VAN ECK *et al.*, 1991). In summary, in sharp contrast to the situation in the Oosterschelde, the infaunal benthos in the Westerschelde may not be able to compete successfully with the mysids for the available food. The mobile mysids have a further advantage over macrobenthic animals in being able to flee from the occasional bouts of oxygen depletion or pollutant stress in the brackish area.

5. RECOMMENDATIONS

This study describes the hyperbenthos in quantity and quality. In the brackish part of the Westerschelde mysids are abundant. They are probably also important because they play an important role in the detrital food chain, as suggested by MANN (1988). Detrital food webs are still poorly understood, but may support valuable fisheries. An assessment of the trophodynamics of the mysid component seems necessary for an understanding of the energy and material fluxes in such areas.

In shallow coastal areas such as the Voordelta the hyperbenthos is also an important component of the ecosystem. A study of the productivity of the dominant species is recommended. In a description of the functioning of the Oosterschelde ecosystem, the hyperbenthos can be neglected because this ecocystem is dominated by filter feeders.

6. REFERENCES

BAKKER, C., P.M.J. HERMAN & M. VINK, 1990. Changes in seasonal succession of phytoplankton induced by the storm surge barrier in the Oosterschelde (S.W. Netherlands).—J. Plankton Res. **12:** 947-972.

BEYER, F., 1958. A new bottom-living *Trachymedusa* from the Oslofjord.—Nytt Mag. Zool. **6:** 121-143.

BOYSON, H.O., 1975. Seasonal variations in abundance of hyperbenthic animals in the Kiel Bight.—Merentutkimuslait. Julk. **239:** 206-212.

BRAAK, C.J.F. TER, 1988. CANOCO - a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Agricultural Mat. Group, Ministry of Agriculture and Fisheries: 1-95.

BRAY, J.R. & J.T. CURTIS, 1957. An ordination of the upland forest communities of Southern Wisconsin.—Ecol. Monogr. **27:** 325-349.

CLARKE, K.R. & R.H. GREEN, 1988. Statistical design for a 'biological effects' study.—Mar. Ecol. Prog. Ser. **46:** 213-226.

CLUTTER, R.I., 1966. Zonation of nearshore mysids.—Ecology **48:** 200-208.

CRAEYMEERSCH, J.A., O. HAMERLYNCK, K. HOSTENS, A. VANREUSEL & M. VINCX, 1990. De ekologische ontwikkeling van de Voordelta. Deelrapport 1. De huidige ekologische situatie. Internal Rep. Delta Inst. Hydrobiol. Res. - Univ. Gent: 1-92.

DUURSMA, E.K., A.G.A. MERKS & J. NIEUWENHUIZE, 1988. Exchange processes in estuaries such as the Westerschelde, an overview.—Hydrobiol. Bull. **22:** 7-20.

ECK, G.T.M. VAN, N. DE PAUW, M. VAN DEN LANGENBERGH & G. VERREET, 1991. Emissies, gehalten, gedrag en effecten van (micro)verontreinigingen in het stroomgebied van de Schelde en het Schelde-estuarium.—Water **60:** 164-181.

FIELD, J.G., K.R. CLARKE & R.M. WARWICK, 1982. A practical strategy for analysing multispecies distribution patterns.—Mar. Ecol. Prog. Ser. **8:** 37-52.

FRIESEN, J.A., K.H. MANN & J.A. NOVITSKY, 1986. *Mysis* digests cellulose in the absence of a gut microflora.—Can. J. Zool. **64:** 442-446.

FULTON, R.S., 1982. Preliminary results of an experimental study of the effects of mysid predation on estuarine zooplankton community structure.—Hydrobiologia **93:** 79-84.

HAMERLYNCK, O. & J. MEES, 1991. Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables.—Oceanologica Acta Vol. sp. **11:** 205-212.

HAMERLYNCK, O., P. VAN DE VYVER & C.R. JANSSEN, 1990. The trophic position of *Pomatoschistus lozanoi* (Pisces: Gobiidae) in the Southern Bight. In: M. BARNES & R.N. GIBSON. Trophic Relationships in the Marine Environment. Proc. 24th Europ. Mar. Biol. Symp. Aberdeen University Press, Aberdeen: 183-190.

HAMERLYNCK, O., K. HOSTENS, J. MEES, R.V. ARELLANO, A. CATTRIJSSE, P. VAN DE VYVER & J.A. CRAEYMEERSCH, 1992. The ebb tidal delta of the Grevelingen: a man-made nursery for flatfish?—Neth. J. Sea Res. **30:** in press.

HANSSON, S., U. LARSSON & S. JOHANSSON, 1990. Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area.—J. Plankton Res. **12:** 1099-1116.

HEIP, C., 1989. The ecology of the estuaries of Rhine, Meuse and Scheldt in the Netherlands. In: J.D. ROSS. Topics in marine biology.—Scient. Mar. **53:** 457-463.

HEIP, C., R. HUYS, M. VINCX, A. VANREUSEL, N. SMOL, R. HERMAN & P.M.J. HERMAN, 1990. Composition, distribution, biomass and production of North Sea meiofauna.—Neth. J. Sea Res. **26:** 333-342.

HERMAN, P.M.J. & H. SCHOLTEN, 1990. Can suspension-feeders stabilise estuarine ecosystems? In: M. BARNES & R.N. GIBSON. Trophic Relationships in the Marine Environment. Proc. 24th Europ. Mar. Biol. Symp., Aberdeen University Press, Aberdeen: 104-116.

HESTHAGEN, I.H., 1973. Diurnal and seasonal variations in the near-bottom fauna - the hyperbenthos - in one of the deeper channels of the Kieler Bucht (Western Baltic).—Kieler Meeresforsch. **29:** 116-140.

HEUBACH, W., 1969. *Neomysis awatschensis* in the Sacramento-San Joaquin river estuary.—Limnol. Oceanogr. **14:** 533-546.

HILL, M.O., 1973. Diversity and evenness: a unifying notation and its consequences.—Ecology **54:** 427-432.

——, 1979. TWINSPAN - a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University, Ithaca, New York: 1-60.

HULBURT, E.M., 1957. The distribution of *Neomysis americana* in the estuary of the Delaware river.—Limnol. Oceanogr. **2:** 1-11.

HUMMEL, H., G. MOERLAND & C. BAKKER, 1988. The concomitant existence of a typical coastal and a detritus food chain in the Westerschelde estuary.—Hydrobiol. Bull. **22:** 35-41.

JAMES, F.C. & C.E. MCCULLOCH, 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box.—Annu. Rev. Ecol. Syst. **21:** 129-166.

JOHNSTON, N.T. & D.C. LASENBY, 1982. Diet and feeding of *Neomysis mercedis* Holmes (Crustacea, Mysidacea) from the Fraser River estuary, British Columbia.—Can. J. Zool. **60:** 813-824.

JONES, M.B., J.G. GREENWOOD & J. GREENWOOD, 1989. Distribution, body size, and brood characteristics of four species of mysids (Crustacea: Peracarida) in the Avon-Heathcote Estuary, New Zealand.—New Zealand J. mar. Freshw. Res. **23:** 195-199.

KOST, A.L.B. & A.W. KNIGHT, 1975. The food of *Neomysis mercedis* Holmes in the Sacramento-San Joaquin estuary.—Calif. Fish Game **61:** 35-46.

LOUTERS, T., J.P.M. MULDER, R. POSTMA & F.P. HALLIE, 1991. Changes in coastal morphological processes due to the closure of tidal inlets in the SW Netherlands.—J. coast. Res. **7:** 635-652.

MANN, K.H., 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems.—Limnol. Oceanogr. **33:** 910-930.

MAUCHLINE, J., 1971. The biology of *Neomysis integer*.—J. mar. biol. Ass. U.K. **51:** 347-354.

——, 1980. The biology of mysids and euphausiids. In: J.H.S. BLAXTER, F.S. RUSSELL & M. YONGE. Advances in marine biology **18**. Academic Press, London: 1-681.

——, 1982. The predation of mysids by fish of the Rockall Trough, northeastern Atlantic Ocean.—Hydrobiologia **93:** 85-99.

MEER, J. VAN DER, A. VAN DEN DOOL, A. ENGELBERTS, D.J. DE JONG, R.H.D. LAMBECK & J.M. POLDERMAN, 1989. Het macrozoöbenthos van enkele intergetijdegebieden in de Oosterschelde. Resultaten van een inventarisatie in de nazomer van 1985. Rijkswaterstaat-Dienst Getijdewateren, Notitie GWAO-89.307: 1-6.

MEES, J., A. DEWICKE & O. HAMERLYNCK, 1993. Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde.—Neth. J. aquatic Ecol. (in press).

MEIRE, P.M., J.J. SEYS, T.J. YSEBAERT & J. COOSEN, 1991. Comparing macrobenthic distribution and community structure between two estuaries in SW-Netherlands. In: M. ELLIOT & J.-P. DUCROTOY. Estuaries and Coasts: Spatial and Temporal Intercomparisons. Int. Symp. Series. Proc. ECSA 19th symposium. Olsen & Olsen, Fredensborg: 221-230.

NIENHUIS, P.H. & A.C. SMAAL, 1993. The Oosterschelde estuary, a case study of a changing ecosystem: an introduction.—Hydrobiologia (in press).

PRINS, T.C. & A.C. SMAAL, 1990. Benthic-pelagic coupling: the release of inorganic nutrients by an intertidal bed of *Mytilus edulis*. In: M. BARNES & R.N. GIBSON. Trophic Relationships in the Marine Environment. Proc. 24th Europ. Mar. Biol. Symp., Aberdeen University Press, Aberdeen: 89-103.

RUDSTAM, L.G., S. HANSSON & U. LARSSON, 1986. Abundance, species composition and production of mysid shrimps in a coastal area of the Northern Baltic Proper.—Ophelia, Suppl. **4:** 225-238.

SIEGFRIED, C.A. & M.E. KOPACHE, 1980. Feeding of *Neomysis mercedis* (Holmes).—Biol. Bull., Woods Hole **159:** 193-205.

SIEGFRIED, C.A., M.E. KOPACHE & A.W. KNIGHT, 1979. The distribution and abundance of *Neomysis mercedis* in relation to the entrapment zone in the western Sacramento-San Joaquin Delta.—Trans. Am. Fish. Soc. **108:** 262-270.

SITTS, R.M. & A.W. KNIGHT, 1979. Predation by the estuarine shrimps *Crangon fransiscorum* Stimpson and *Palaemon macrodactylus* Rathbun.—Biol. Bull. **156:** 356-368.

SMAAL, A.C., J.H.G. VERHAGEN, J. COOSEN & H.A. HAAS, 1986. Interaction between seston quantity and quality and benthic suspension feeders in the Oosterschelde, The Netherlands.—Ophelia **26:** 385-399.

SORBE, J.-C., 1981. La macrofaune vagile de l'estuaire de la Gironde: distribution et migration des espèces, modes de reproduction, régimes alimentaires.—Oceanis **6:** 579-592.

TATTERSALL, W.M. & O.S. TATTERSALL, 1951. The British Mysidacea. Ray Society, London: 1-460.

WILLIAMS, R. & N.R. COLLINS, 1984. Distribution and variability in abundance of *Schistomysis spiritus* (Crustacea: Mysidacea) in the Bristol Channel in relation to environmental variables, with comments on other mysids.—Mar. Biol. **80:** 197-206.

ZAGURSKY, G. & R.J. FELLER, 1985. Macrophyte detritus in the winter diet of the estuarine mysid, *Neomysis americana*.—Estuaries **8:** 355-362.

(received 30 September 1991; revised 14 July 1992)