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CHAPTER 2 - ADDENDUM 2 THE MOBILE EPIBENTHIC FAUNA OF SOFT BOTTOMS IN THE DUTCH DELTA (SOUTH-WEST NETHERLANDS): SPATIAL STRUCTURE

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Abstract. During 1989 monthly beam trawl samples were collected at 48 stations in the Dutch Delta. The annual mean densities of the demersal fishes and mobile epibenthic invertebrates at these stations were calculated. These data were then subjected to multivariate statistical techniques for an analysis of the spatial structure of the communities found and to study the relationship between these communities and their environment. The present study confirms the results of Henderson (1989) that, given a fairly limited number of environmental variables, mainly salinity and exposure/substratum type, quite accurate predictions of the type of community expected at a certain site can be made. The explicit inclusion of epibenthic invertebrates, a dominant group in most assemblages, in studies mainly targeted at demersal fishes, is strongly recommended. In the Dutch Delta rich and varied communities exist in the Voordelta. A number of groups, such as salmonids, anadromous species and starfish, expected in the Westerschelde are absent or extremely rare probably as a consequence of pollution stress. The Oosterschelde is relatively poor in density terms but has a highly diverse epibenthic fauna dominated by fishes.

2.1 Introduction

Most studies reporting on fishes and larger epibenthic invertebrates (e.g. shrimps, crabs) are heavily biased towards the exploited life stages of commercial species. Despite general agreement on the qualitative notion that estuaries and shallow coastal areas are important nurseries for marine fishes (Haedrich 1983) there is still a need for quantitative studies. In comparison to macrobenthic studies there are relatively few studies describing the structure of estuarine fish communities and these have been mainly restricted to British estuaries (Claridge *et al.* 1986, Henderson 1989, Elliott *et al.* 1990). Some comparative exercises have been done (Costa & Elliott 1991,

Pomfret *et al.* 1991) and functional studies are beginning to emerge (Elliott & Taylor 1989, Chapter 3). Process studies have as yet been restricted to single species of commercial importance (e.g. van der Veer 1986).

The development of multivariate statistical techniques has created the possibility of summarising the structure in large multispecies data sets. These techniques are very popular in many ecological fields (review in James & McCulloch 1990) but have rarely been used in studies of marine fishes of the North Sea. Henderson (1989) used Principle Component Analysis to analyse the structure of the fish communities as recorded from the intake screens of power stations in England and Wales. Daan *et al.* (1990) applied an unspecified type of cluster analysis to the fifty most abundant fish species recorded in the Eng-

lish Groundfish Surveys 1982-1985. Though the sampling gears deployed to sample fish catch a number of mobile epibenthic invertebrates, these animals are rarely integrated into the results.

In this study a multivariate analysis of the spatial structure of the mobile epifauna of the Dutch Delta, on the basis of annual mean density and biomass, is presented. The study is restricted to soft bottoms. An attempt is made to assess the correlation between the occurrence of a certain species assemblage and its environment. A lot of detail is provided on the practical strategy for the multivariate analysis. These details are not often reported in papers but may be important to judge if the choice of the technique and the way in which it was applied were adequate (James & McCulloch 1990).

The purpose of this study is to provide a baseline for future functional and process studies of the mobile epifauna of the Delta area and of the Westerschelde in particular. These will have to be based on spatial units coinciding with the biological communities. To comply with international standards a massive reduction of the pollution load of the Westerschelde will have to be achieved in the (near?) future and the impact assessment of these changes will hopefully be monitored. A baseline study is a prerequisite for such a monitoring programme.

2.2 Materials and methods

2.2.1 Study area (Fig. 2.10)

The Rhine, Meuse and Schelde, the three main European rivers, enter the North Sea in the Dutch Delta region in the south-western part of The Netherlands. Most of the former estuaries in this area have been altered by man (review in Heip 1989b). The study area covers only three parts of the Dutch Delta: the Westerschelde, the Oosterschelde and the central part

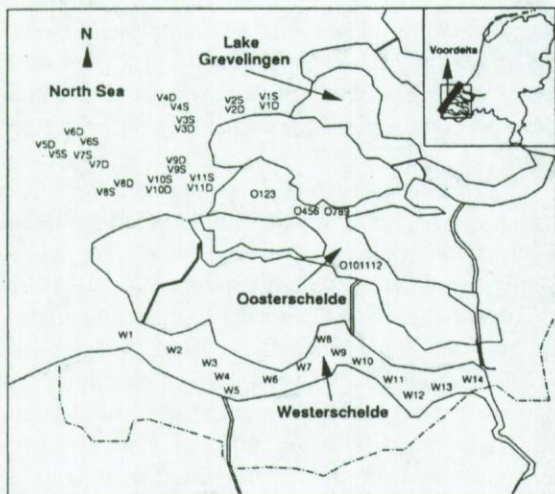


Fig. 2.10 Map of the study area with the sampling stations

of the Voordelta.

The lower part of the river Schelde is generally known as the Westerschelde estuary. It is the last remaining true estuary in the Dutch Delta and exhibits marked gradients in salinity, oxygen and turbidity. The mean fresh water load is $105 \text{ m}^3 \cdot \text{s}^{-1}$ (Herman *et al.* 1991). The input of organic and inorganic pollutants is very high, especially in the brackish part (Duursma *et al.* 1988, Van Eck *et al.* 1991). The division between the marine and the brackish part is situated between stations W8 and W9 (Fig. 2.10) (Hummel *et al.* 1988b).

The former Oosterschelde estuary is now a tidal inlet of the Southern Bight of the North Sea. By the construction of a number of dams in the landward part, the fresh water inflow was reduced to $55 \text{ m}^3 \cdot \text{s}^{-1}$ and in 1986 a storm-surge barrier was completed at the mouth. This caused substantial changes in the functional characteristics of the ecosystem (Bakker *et al.* 1990). Some impact could also be detected on the fishes and epibenthic invertebrates (Chapter 3-Add., Chapter 3).

The Voordelta is the shallow coastal area formed by the interlinked ebb-tidal deltas of the (former) estuaries of the Dutch Delta. It extends from the Belgian-Dutch border in the South to the Hoek van Holland in the North. Its marine boundary is arbitrarily defined by the Mean Tidal Level (MTL) -10 m isobath. The closure of the former estuaries has had an important impact on the geomorphology (Louters *et al.* 1991) and ecology (Chapter 4-Add.) of the area. Only the central part of the Voordelta, the ebb-tidal delta of the former Grevelingen estuary and the ebb-tidal delta of the Oosterschelde, have been investigated in this study.

2.2.2 Sampling

During 1989 monthly samples were taken at 22 stations in the Voordelta, 12 stations in the Oosterschelde, and 14 stations in the Westerschelde (Fig. 2.10). In the Voordelta the 22 stations cover two depth strata (MTL -5 m and MTL -10 m) at eleven localities. In the Oosterschelde the 12 stations correspond to three parallel tows at four localities. In the Westerschelde the stations are located at the edges of the ebb-tidal channel from the mouth to the Dutch-Belgian border. Several trials were made to sample further upstream but, due to the inordinate amount of rubbish covering these grounds, gear loss was so frequent that no results can be reported (see also Pomfret *et al.* 1991).

In January and August the six most seaward stations of the Voordelta could not be sampled because of adverse weather conditions. Five other Voordelta samples and 5 Westerschelde samples were lost because the net was torn or the beam trawl hit an obstacle.

Samples were taken from the R.V. Luctor (34 m, 500 Hp) using a 3-m beam trawl, equipped with a 6-m long net with a 5 x 5 mm mesh in the cod end, a tickler chain and a chain in the groundrope. Hauls were 1 km in length. Ship speed relative to the bottom when trawling was on average 4.5 knots. All fishes, with the exception of the gobies, were identified to species level on board. Gobies of the genus *Pomatoschistus* were preserved for identification in the laboratory (Hamerlynck 1990). As the invertebrates were treated more or less in bulk, a number of rare species were overlooked: the shrimps *Crangon allmani*, *Pontophilus trispinosus*, *Processa modica modica* and *Pandalus montagui*, the crabs *Portunus latipes*, *Liocarcinus arcuatus* and *Macropodia rostrata*. Specimens of these species were occasionally observed in the Voordelta but were not quantified. *C. allmani*, *P. montagui* and the three crab species mentioned were sometimes also noted in the Oosterschelde catches. In the Westerschelde *Palaemonetes varians* was seen occasionally. Although the hermit crab *Pagurus bernhardus* occurs commonly, this crab was not quantified. Sometimes Cephalopoda and Echinodermata Crinoidea were caught but not quantified.

Standard length was recorded for all fish specimens. Biomass was calculated from length - Ashfree Dry Weight (ADW) regressions compiled for the Dutch Delta (see Tables 4.2 and 5.2). Invertebrates were counted and (wet)weighed. Net efficiency was assumed to be 20 % for all size classes of fish and invertebrates. This assumption is based on the work of Kuipers (1975) on plaice. For the relatively immobile starfish efficiency was assumed to be 40 %. Efficiency adjusted densities are given as N per 1000 m², biomass as gADW per 1000 m².

2.2.3 Environmental variables

At each site salinity (ppt), water temperature (°C), water depth (m), Secchi disk depth (m) and oxygen content (mg l⁻¹) were measured. Salinity, temperature and oxygen content were measured at about 1 m above the bottom. For these variables means were calculated per station. These averages are not true annual means because they were only calculated for those months in which all stations were sampled. The measurements in January and August were therefore not included in the calculations. In November no measurements could be taken because of a technical failure of the probe.

In December 1988 hyperbenthos samples were taken with a hyperbenthic sledge at all the stations according to the methodology described in Mees & Hamerlynck (1992). The hyperbenthic biomass data (mgADW m⁻²) were taken from that study. At each sampling station of the Westerschelde and Oosterschelde three Van Veen grabs were taken and sieved over a 1-mm mesh. Macrobenthic biomass

Table 2.3 Ranges of the environmental variables measured, with (between brackets) the station at which the extremes were recorded, the mean for all stations and the standard deviation of that mean

VARIABLE (unit)	MINIMUM	MAXIMUM	MEAN	S.D.
Salinity (ppt)	13.4 (W14)	32.1 (V7)	28.5	5.0
Temperature (°C)	11.5 (V2)	13.2 (W14)	12.0	0.4
Depth (m)	5.3 (V1S)	21.7 (OR2)	10.4	3.7
Secchi depth (m)	0.5 (W14)	3.3 (OW)	1.9	0.9
Oxygen (mg.l ⁻¹)	7.4 (W14)	10.6 (V2)	10.0	0.5
Hyperbenthos (mg ADW.m ⁻²)	0.02 (OW)	242 (W14)	19.4	56
Macrobenthos (g ADW.m ⁻²)	0 (W12-W14)	90 (V1D)	7.2	18
Mud content (%)	0 (V4D,W6,W11)	20 (V1D)	2.8	3.7
Median grain size (µm)	125 (V1D)	357 (W3)	230	56
1% significant wave (m)	1 (OW,W11-W14)	3.5 (V5)	1.8	0.7

(gADW m⁻²), mud content (%) and median grain size of the sand fraction (mm) were measured. Macrobenthic biomass data for the Voordelta stations were taken from Craeymeersch *et al.* (1990). The sediment composition data for the Voordelta and the 1% wave height (the wave height exceeded for 1 % of the year) were taken from van Dijke & Buijs (1987). Benthic biomass data were collected to investigate possible correlations between epifauna and their main food. Wave height is used as a measure of exposure.

Table 2.3 summarises the range of the environmental variables recorded. It should be noted that only the means per station are shown and that in some months more extreme values have been recorded, *e.g.* 4 mg l⁻¹ of oxygen in April at station W14.

2.2.4 Multivariate analysis of community structure

Density and biomass data from each haul were subjected to a fourth root transformation prior to further analysis (Clarke & Green 1988). This transformation partly compensates for the deviation from normality typical for species abundance data. The transformed data set then still contains an inordinate amount of zero observations. Eliminating rare species (Field *et al.* 1982, Henderson 1989, Daan *et al.* 1990) may alleviate this, but it entails a loss of information. In the present, relatively species-poor data set, no *a priori* reduction of the number of species was accomplished.

All hauls at a sampling station were considered to be replicates and the annual means of (the transformed) density and biomass were calculated.

The data were subjected to a Two Way Indicator Species Analysis (TWINSPAN) (Hill 1979) and a Group Average Sorting (GAS) using the Bray Curtis similarities (Bray & Curtis 1957). The clusters of stations distinguished by both techniques were then compared. The choice of the cut levels in the TWINSPAN was based on the simple rule of thumb that the number of observations (*e.g.* density values) within each cut level should be approximately equal, except for the lowest cut level which contains all the zero observations and the two highest cut levels which contain approximately half as many observations as the other levels. In this way some extra weight was given to the most common species. Cut levels chosen for the density data were 0, 0.11, 0.2, 0.4, 0.7, 1.2, 2.1 and 3. For the biomass data these were 0, 0.15, 0.36, 0.81, 1.59, 2.3 and 4.2. All other settings in the TWINSPAN are default, with the exception of the maximum number of divisions, which was set to four instead of six.

The data were then subjected to ordination techniques from the CANOCO package (Ter Braak 1987). A Correspondence Analysis (CA) was done to assess total community variability and to compare the scales of the species scores and the sample scores (Ter Braak & Prentice 1988, Jongman *et al.* 1987). Next, a Principal Component Analysis (PCA) was performed, combining the biotic data with the environmental variables.

In the PCA euclidean distances were calculated from the correlation matrix (James & McCulloch 1990). Environmental variables were centred, *i.e.* replaced by the deviation from the mean for all stations (Jongman *et al.* 1987). As the underlying response model of PCA is linear, the hyperbolic relationship which was found between Secchi disk depth and the first ordination axis was linearised by a reciprocal transformation of this variable.

When characterizing a community, Hill's diversity numbers (Hill 1973) of the order 0, 1, 2 and $+\infty$ are of particular interest (Heip *et al.* 1988). For each of these Hill numbers the means and standard deviations were calculated per assemblage. With increasing order of the Hill number, the influence of dominant species increases and the influence of species richness decreases (see also Mees *et al.* 1993b).

2.2.5 Terminology

All Voordelta samples were taken in inshore waters but to simplify the description of the results the most seaward stations (V5 to V7) are labelled 'offshore' stations in comparison to the stations V1 to V3 and V9 to V11 which are labelled 'inshore'. The V4 and V8 stations are labelled 'intermediate'. The word 'locality' refers to a broader site including two sta-

tions in the Voordelta (*e.g.* locality V1 is composed of stations V1S and V1D) and three stations in the Oosterschelde. In the figures species names were shortened to the first four letters of the genus and the first four of the species name.

2.3 Results

2.3.1 Species composition

Fiftythree species were quantified (Table 2.4). These species are classified into six ecological types according to the use they make of estuarine areas (Elliott & Taylor 1989, Costa & Elliott 1991). Eighteen species are truly marine and do not depend on estuaries for any part of their life-cycle (MO in Table 2.4), sixteen species are estuarine resident species (ER), ten marine species make use of the estuary as a nursery ground (MJ), five species are catadromous or anadromous (CA), three marine species spend part of the year in the estuarine environment as adults (MS). The three-spined stickleback *Gasterosteus aculeatus* is difficult to classify. It is partly a freshwater species, partly an estuarine resident (FW/ER).

2.3.2 Spatial structure

The results of the analyses with the biomass data were very similar to those of the corresponding analyses using the density data. Therefore, except for the TWINSPAN, only the density results are reported.

2.3.3 Classification

The result of the TWINSPAN (first division, eigenvalue 0.13) using the density data is shown in Fig. 2.11 (top). The first division separates the Westerschelde stations from the rest. Within this last group the next division separates a cluster mainly composed of offshore and intermediate Voordelta stations (VX). In the Westerschelde cluster the next division splits the stations in the brackish part (WB) from the stations in the marine part (WM).

Further divisions in the central cluster first separate the Oosterschelde stations from the inshore Voordelta and then split each of these into two smaller groupings. Thus four clusters are created:

- the deep inshore stations in the ebb-tidal delta of the Oosterschelde (VIO)
- the inshore stations in the ebb-tidal delta of the Grevelingen (VIG)
- the stations in the most landward part of the Oosterschelde (OI)
- the more seaward stations of the Oosterschelde (OO)

Table 2.4 List of the species quantified with their abundance (N per 1000 m²) in the different assemblages and their ecological type (for abbreviations see text)

Species name	Assemblage							
	VX	VIO	VIG	OI	OO	WM	WB	
<i>Lampetra fluviatilis</i>						<0.1		CA
<i>Anguilla anguilla</i>	<0.1	0.5	0.1	0.1	0.9	0.3	0.6	CA
<i>Clupea harengus</i>	11	20	62	3	10	3	6	MJ
<i>Sprattus sprattus</i>	22	7	29	18	3	24	18	MJ
<i>Alosa fallax</i>							0.1	CA
<i>Engraulis encrasicolus</i>	<0.1		<0.1	<0.1	0.1	0.1	0.1	ER
<i>Gadus morhua</i>	0.2	1	1		0.2	0.2	0.2	MJ
<i>Merlangius merlangus</i>	3	23	54	2	7	3	<0.1	MJ
<i>Trisopterus luscus</i>	0.8	7	10	7	11	1	2	MJ
<i>Trisopterus minutus</i>				<0.1	0.1			MO
<i>Ciliata mustela</i>	<0.1	0.4	2	0.1	0.1	0.2	0.6	MS
<i>Zoarcetes viviparus</i>	<0.1		0.3	3	0.6		0.2	ER
<i>Atherina presbyter</i>	0.1	0.7	0.6	1	0.1	<0.1	<0.1	ER
<i>Gasterosteus aculeatus</i>	0.2				0.3		0.3	FW/ER
<i>Syngnathus acus</i>	0.1		0.1	0.4	0.1		<0.1	ER
<i>Syngnathus rostellatus</i>	4	6	12	15	3	4	7	ER
<i>Entelurus aequoreus</i>	<0.1		<0.1	0.1	<0.1			MO
<i>Trigla lucerna</i>	0.3	0.4	0.8	0.4	0.1	0.1	<0.1	MJ
<i>Myoxocephalus scorpius</i>	0.1	1	0.5	1	0.2	0.1	0.3	ER
<i>Taurulus bubalis</i>				0.1	<0.1			MO
<i>Agonus cataphractus</i>	0.2	4	9	0.8	0.1	0.3	0.4	ER
<i>Liparis liparis</i>	0.1	2	1		<0.1	0.7	0.6	ER
<i>Dicentrarchus labrax</i>		0.1		<0.1			0.1	MJ
<i>Trachurus trachurus</i>	<0.1			3		0.4	<0.1	MO
<i>Mullus surmuletus</i>	0.3	0.6	0.3	<0.1				MO
Mugilidae species			0.5	0.1	0.2	0.1	0.1	CA
<i>Trachinus vipera</i>	0.2							MO
<i>Pholis gunnellus</i>			0.6	0.4	<0.1			ER
<i>Ammodytes tobianus</i>	26	0.7	2	0.1	0.5	4	2	ER
<i>Hyperoplus lanceolatus</i>	2		0.1			0.7	<0.1	MO
<i>Callionymus lyra</i>	10	42	25	15	0.7			MO
<i>Pomatoschistus microps</i>	<0.1			0.7	0.3	3	3	ER
<i>Pomatoschistus pictus</i>	4	4	5	0.3	0.2	<0.1		MO
<i>Pomatoschistus minutus</i>	50	64	506	161	37	39	118	MS
<i>Pomatoschistus lozanoi</i>	105	38	221	3	2	143	192	MS
<i>Aphia minuta</i>	0.2	1	2		0.1			MO
<i>Gobius niger</i>				<0.1				ER
<i>Scophthalmus rhombus</i>	0.1		0.1	0.2	0.2	<0.1		MO
<i>Scophthalmus maximus</i>	0.1		0.1					MO
<i>Pleuronectes platessa</i>	3	48	19	63	25	3	13	MJ
<i>Limanda limanda</i>	14	67	133	43	8	11	44	MJ
<i>Pleuronectes flesus</i>	0.1	1	2	0.2	<0.1	0.4	5	CA
<i>Solea solea</i>	0.2	12	9	2	0.7	4	8	MJ
<i>Buglossidium luteum</i>		0.1	0.2					MO
<i>Microstomus kitt</i>				0.3				MO
<i>Arnoglossus laterna</i>	<0.1							MO
<i>Crangon crangon</i>	697	1224	3071	446	460	1358	2467	ER
<i>Liocarcinus holsatus</i>	44	122	572	16	10	9	2	MO
<i>Carcinus maenas</i>	1	15	42	73	7	21	12	ER
<i>Cancer pagurus</i>	0.1	0.9			0.1			MO
<i>Eriocheir sinensis</i>							<0.1	ER
<i>Homarus gammarus</i>				<0.1				MO
<i>Asterias rubens</i>	175	1226	5426	106	132			ER

The TWINSpan result (first division eigenvalue 0.14) for the biomass data (Fig. 2.11, bottom) resembles the result for the density data, though the order in which the groupings are separated and the indicator species may differ. Some stations are in a different cluster when comparing both results. Station

W1, in the mouth of the Westerschelde is found in the WB cluster of the biomass result. Station V3D from the ebb-tidal delta of the Grevelingen is classified into the VIO cluster in the density result.

In the GAS the same four major clusters WS, OS, VI (this time without V10D) and VX, can be recognized as separate entities (Fig. 2.12). Within the

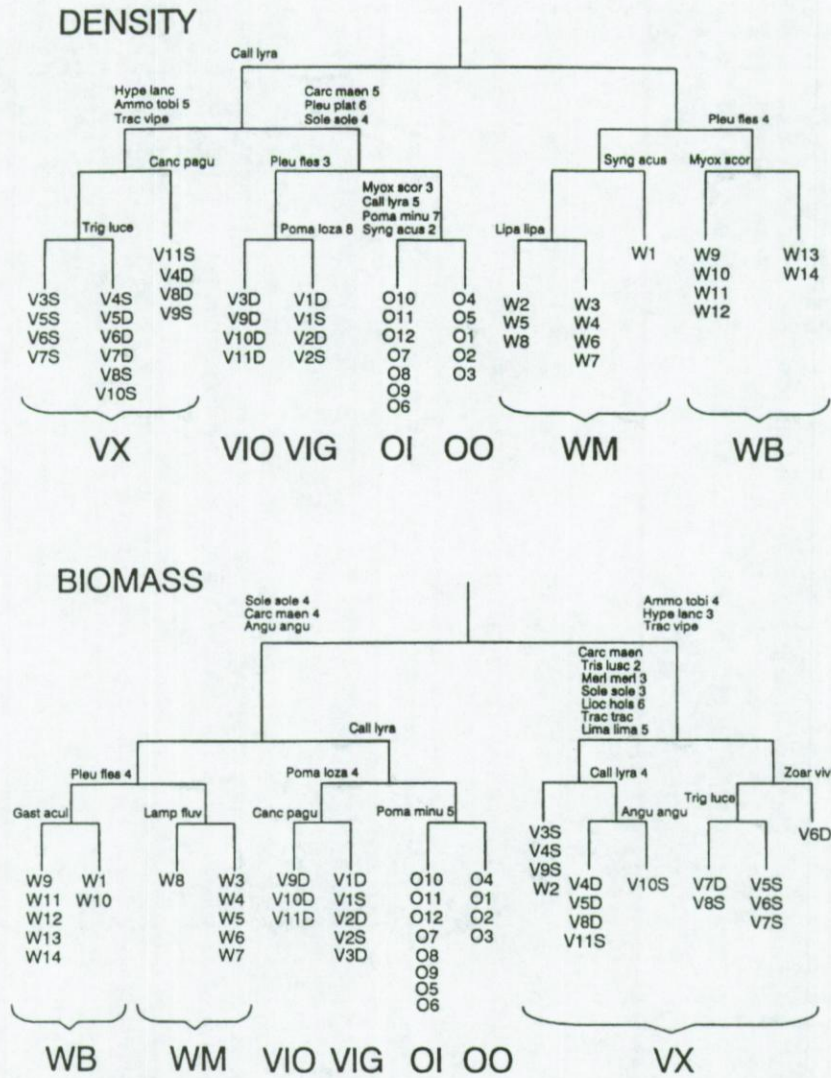


Fig. 2.11 Results of the TWINSpan for density (top) and biomass (bottom). Indicator species are indicated with their cut level (level 1 is not indicated)

WS cluster the WB cluster lacks the stations W9 and W12. In the VX cluster (which now includes V10D) there is a subcluster grouping the shallow offshore stations and V8S. In the OS cluster the three stations from each of the four localities form tight clusters. In the VI cluster the VIG stations are found in close association. Station V3D is again closely associated to the VIO stations V9D and V11D.

2.3.4 Characterization of the species assemblages

From the results of the classification techniques it is clear that seven different clusters of stations can be defined comprising two in the Westerschelde (WM and WB), two in the Oosterschelde (OW and OE) and three in the Voordelta (VX, VIG and VIO). Station W1 was included in the WM cluster on the basis of the TWINSpan using the density data and the GAS results. Station V3D was included in the VIG

cluster on the basis of the TWINSpan using the biomass data.

The densities of the various species in the assemblages corresponding to the different clusters are given in detail in Table 2.4 and are summarized in Fig. 2.13. Only fourteen species account for more than 1 % of the density in any of the communities thus defined. These species are starfish (*Asterias rubens*), brown shrimp (*Crangon Crangon*), swimming crab (*Liocarcinus holsatus*) shore crab (*Carcinus maenas*), sand goby (*Pomatoschistus minutus*), lozano's goby (*Pomatoschistus lozanoi*), plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), sprat (*Sprattus Sprattus*), herring (*Clupea harengus*), sandeel (*Ammodytes tobianus*), dragonet (*Callionymus lyra*) and bib (*Trisopterus luscus*).

The VX assemblage has the lowest total abundance among the Voordelta clusters (Fig. 2.13). It has few starfish and very few flatfish. It has the highest densities of its indicator species *A. tobianus* and greater sandeel (*Hyperoplus lanceolatus*) and is

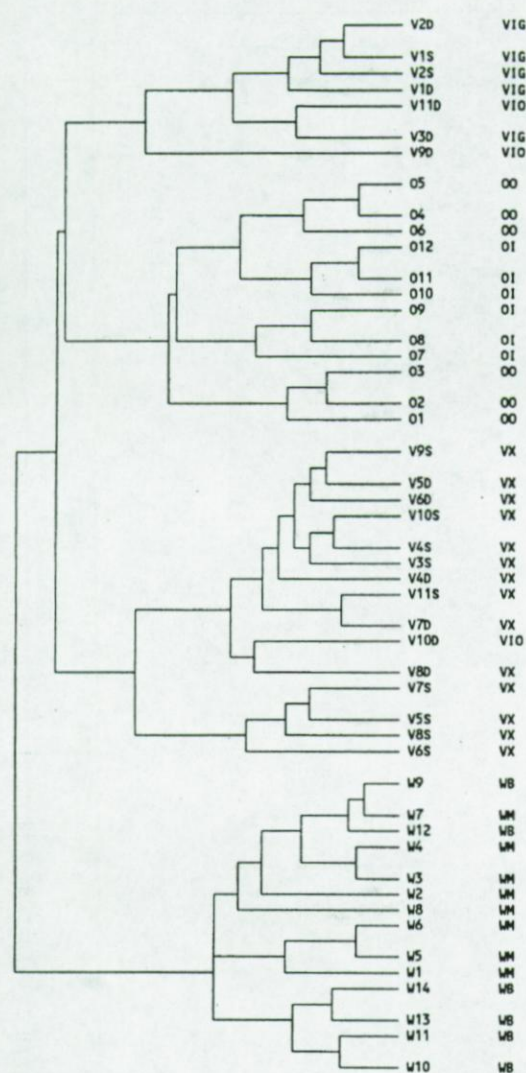


Fig. 2.12 Results of the Group Average Sorting using the Bray-Curtis similarities. Station names are followed by their classification into assemblages on the basis of the TWINSpan results

the only group of stations in which the lesser weever *Trachinus vipera* and the scaldfish *Arnoglossus laterna* were recorded (Table 2.4).

The VIO assemblage has an intermediate total abundance. It is poorer than the VIG assemblage for almost all species except for *C. lyra*, *P. platessa*, sole (*Solea solea*) and its indicator species edible crab (*Cancer pagurus*).

The VIG assemblage has the highest total abundance being more than three times higher than in any other assemblage. *C. harengus*, *S. Sprattus*, whiting (*Merlangius merlangus*), *P. minutus*, *P. lozanoi*, *L. limanda*, *C. Crangon*, *L. holsatus* and *A. rubens* plus a host of less abundant species all reach their peak densities in this assemblage.

The OI assemblage has a low total abundance. It has, however, the highest *P. platessa* densities and also the peak densities of a number of species that are rare in the study area as a whole. The latter species are eelpout (*Zoarces viviparus*), sands

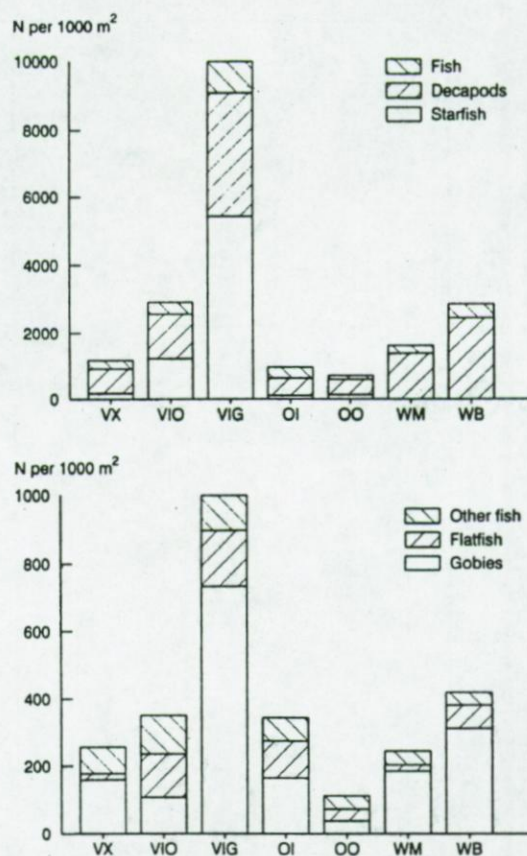


Fig. 2.13 Total density and composition of the different species assemblages for the three main taxonomic groups (top) and the three main fish groups (bottom)

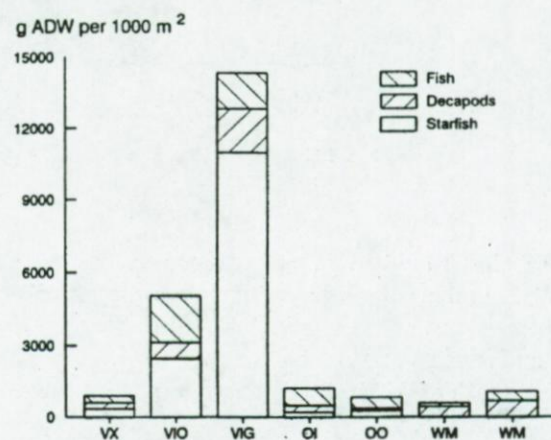


Fig. 2.14 Total biomass and composition of the different species assemblages for the three main taxonomic groups

melt (*Atherina presbyter*), scad (*Trachurus trachurus*) and three pipefish species (*Syngnathus acus*, *S. rostellatus* and *Entelurus aequoreus*). It is also the only assemblage in which the black goby (*Gobius niger*), the lemon sole (*Microstomus kitt*) and the lobster (*Homarus gammarus*) were recorded.

The OO assemblage has the lowest total abundance. Only the poor cod (*Trisopterus minutus*) has its peak abundance in this assemblage. Both Oosterschelde communities have exceptionally low abundances of *P. lozanoi*. The Oosterschelde is the

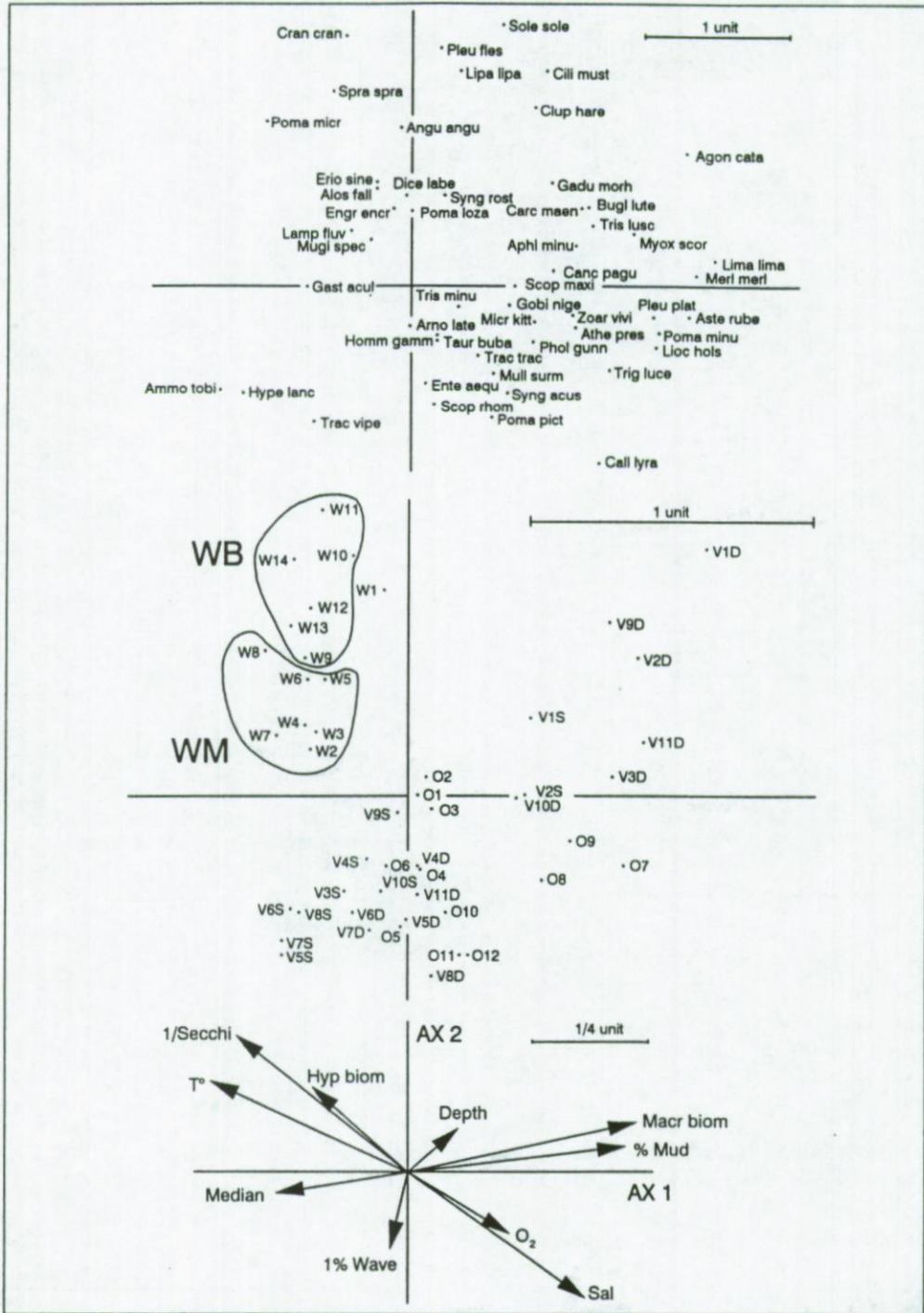


Fig. 2.15 Result of the Principal Component Analysis for the first two axes. The species scores (top), the sample scores (centre) and the environmental biplot (bottom) have different scales

only area were *T. minutus* and the sea scorpion (*Taurulus bubalis*), a rocky shore species, were recorded.

The WM assemblage has an intermediate abundance. Except for the only record of lampern (*Lampetra fluviatilis*) there are no typical species.

The WB assemblage has a somewhat higher total abundance than the WM assemblage. It has the highest densities of its indicator species flounder (*Pleuronectes flesus*). Notable but rare species are twaite shad (*Alosa fallax*) and mitten crab (*Eriocheir*

sinensis), both only recorded in this assemblage. The absence of starfish in the Westerschelde is a distinguishing feature. The common goby (*Pomatoschistus microps*) reaches its highest densities in the Westerschelde.

Biomass composition for the three main groups fish, decapods and starfish is shown in Fig. 2.14. It can be seen that the dominance of the invertebrate groups in the Voordelta clusters is even

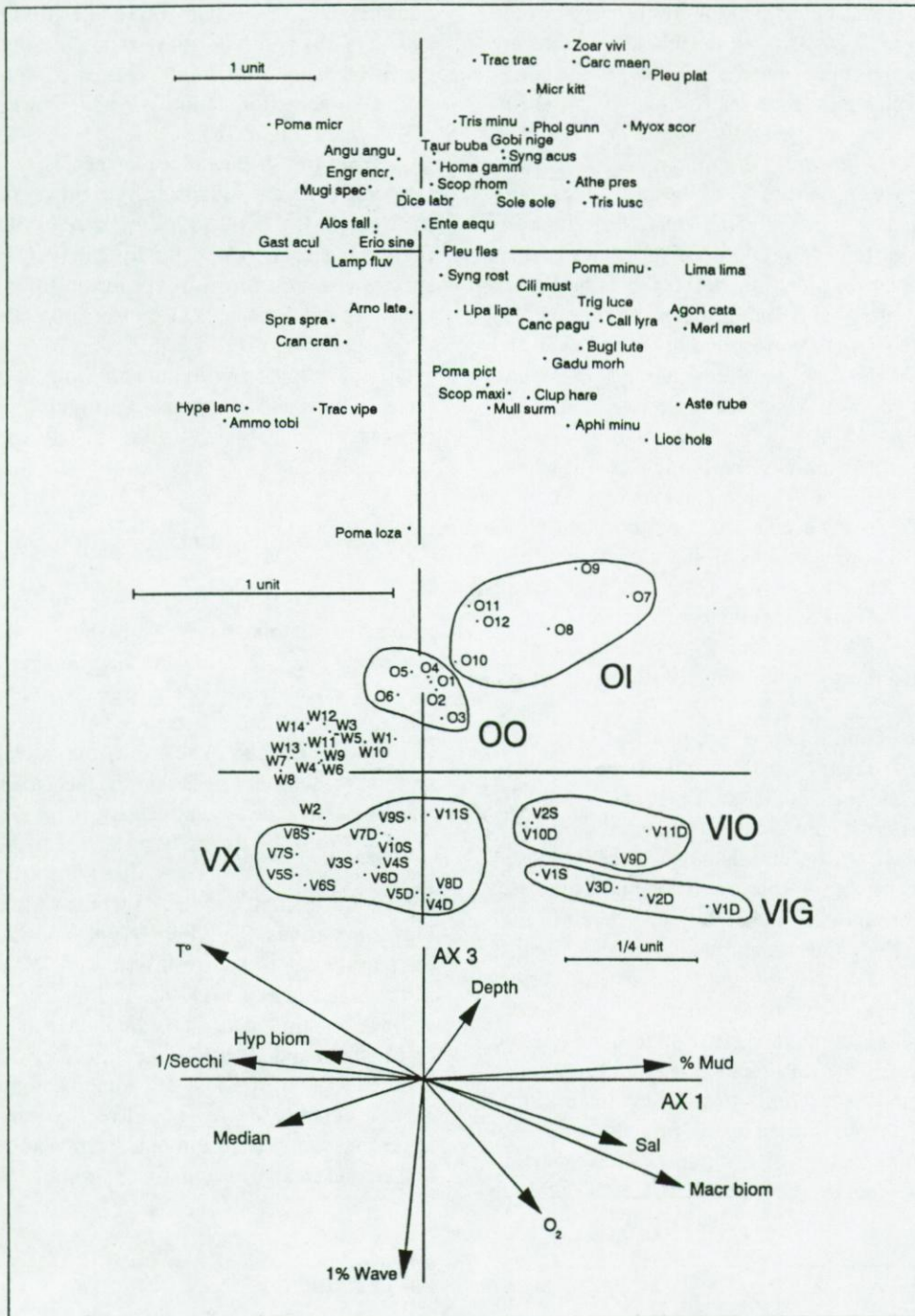


Fig. 2.16 Result of the Principal Component Analysis for the first and third axes. The species scores (top), the sample scores (centre) and the environmental biplot (bottom) have different scales

stronger than in density terms. Fish are the dominant group only in the Oosterschelde.

2.3.5 Relation to the environmental variables

The total community variability, which corresponds to the distance between the two most extreme stations along the first axis, as measured in units of scale (1 unit scale equals 1 unit standard deviation by definition) in the CA (not depicted) is only 1.2 units. This result means that a linear response model is

most appropriate for the data. Moreover, most species have their optima outside of the range covered by the sampling because the scale of the species scores in the CA is 7.3 times smaller than the scale of the sample scores. Therefore, we choose PCA for the ordination with the environmental variables (Ter Braak & Prentice 1988, Jongman *et al.* 1987).

The first PCA axis has an eigenvalue of 0.16, both the second and third axes have eigenvalues of 0.13. In the plain formed by the first and the second PCA axis the sample scores clearly separate the

totality of Westerschelde stations from the rest of the Delta area (Fig. 2.15). All Westerschelde stations are located in the left upper quadrant which, in the corresponding species plot, contains *C. Crangon*, *S. Sprattus*, *P. microps*, eel (*Anguilla anguilla*), sea bass (*Dicentrarchus labrax*), *A. fallax*, *L. fluviatilis*, Mugilidae species, anchovy (*Engraulis encrasicolus*), *Eriocheir sinensis* and *G. aculeatus*. Interestingly, these species do not necessarily have their highest abundances in these stations but they are a constant and prominent feature of the Westerschelde stations. The stations corresponding to the WB and WM assemblages are separated along the second axis, except for W1 which associates with the WB cluster.

The other stations are plotted as a diagonal string with, at the left lower extreme, the shallow stations at the marine edge of the Voordelta (V3S through V8S), corresponding to the indicator species of the VX assemblage in the lower left quadrant of the species plot. This assemblage, characterized by *A. tobiamus*, *H. lanceolatus* and *T. vipera*, has a clear preference for the dynamic sands at the edge of the ebb-tidal delta.

In the central part of the plot there is a mixture of Voordelta and Oosterschelde stations. In the right upper quadrant one finds the stations of the VIG and VIO clusters. From the environmental biplot it is clear that the first axis correlates strongly with mud content and its covariable macrobenthic biomass. These two variables are negatively correlated to median grain size. The second axis correlates most strongly with the estuarine gradient in the Westerschelde with low water transparency (high 1/Secchi disk depth), high temperature and high hyperbenthic biomass towards the left upper corner and high oxygen content and high salinity towards the lower right.

In the plain formed by the first and third axes of the PCA the stations divide into an Oosterschelde cluster which can be separated into the OO and OI

clusters, the VI cluster where the VIO (now with station V2S) and VIG clusters can be distinguished, the VX cluster and a tight cluster of Westerschelde stations (except for station W2 which lies close to the VX cluster) (Fig. 2.16).

In the species plot the species typical for the Oosterschelde are found in the right upper quadrant. In the right lower quadrant the species closest to the first axis are characteristic for the VIO cluster, the species towards the extreme lower right corner are those typical for the VIG cluster, notably *A. rubens* and *L. holsatus*.

From the environmental biplot it is clear that the third axis shows a strong correlation with the 1% significant wave, which itself is negatively correlated with depth.

2.3.6 Diversity (Fig. 2.17)

The average number of species recorded per station in each assemblage (N_0) is highest in the inshore Voordelta and Oosterschelde assemblages and lowest in the Westerschelde assemblages. Note that, though the highest number of species (41) was recorded in the VX assemblage (Table 2.4) the average number per station (N_0) is lower than in the other Voordelta and Oosterschelde assemblages.

From the diversity measures of higher order the exceptional character of the OI cluster is apparent. In this assemblage forty species were recorded at only six stations. The high N_1 , N_2 and $N_{+\infty}$ measures are mainly due to the locality in the Northern branch of the Oosterschelde (O7,8,9 in Fig. 2.10). The three stations at this locality are dominated by *A. rubens*, *C. Crangon* and *P. minutus* and have low densities of a host of other species. The other communities exhibit a steadily decreasing diversity for all higher order measures when moving from seaward to landlocked and finally to estuarine conditions.

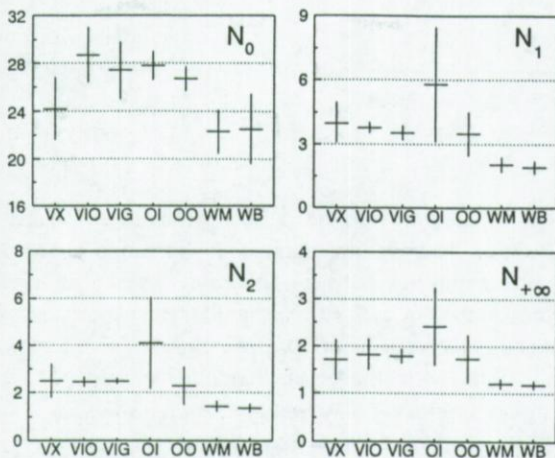


Fig. 2.17 Means of the Hill diversity numbers N_0 , N_1 , N_2 and $N_{+\infty}$ for the different species assemblages with their standard deviations

2.4 Discussion

The typical beam trawl surveys designed for monitoring of fishes are also very efficient for catching mobile epibenthic invertebrates. These invertebrates are a dominant component in each assemblage and the information inherent in the occurrence of these animals should therefore be used. The present study also suffers partially from this interference, at least for some of the less abundant species. Though each fish was examined in detail, the invertebrates were treated in bulk and only occasionally, e.g. in small catches, the rarer invertebrates were noticed. It seems likely for instance that *Pontophilus trispinosus* and *Portunus latipes*, though rare, are typical members of the VX community. The exceptionally high diversity of the Oosterschelde, especially as measured by N_1

would also be even more spectacular if all invertebrates found had been quantified. Community structure is, at least partly, determined by species interactions such as competition and predation. These interactions are not limited to either fish-fish or crab-crab but go across taxonomic boundaries. Some of these predatory interactions are structurally important, e.g. shrimp-plaice (van der Veer 1986), whiting-shrimp (Henderson & Holmes 1989). Evidence on competitive interactions is less conclusive, but many species are known to share the same food (Costa & Elliott 1991, Le Mao 1986). Therefore, it is recommended that future studies reporting primarily on demersal fish include data on the mobile epibenthic invertebrates.

As most fish and epibenthic crustaceans are highly mobile and perform seasonal migrations, obscured by the use of annual means, it is not surprising that the spatial structure found is relatively weak (low eigenvalues). Still, there is a remarkably strong similarity between the species assemblages found in the present study and those defined by Henderson (1989). This is even more amazing if one considers the fact that Henderson's data were collected from the intake screens of power stations, whilst ours were collected by beam trawl. It is also evident that many of the environmental variables that correlate strongly with the structure of the respective communities are related to 'exposure' in a broad sense. Sediment structure (median grain size and mud content, macrobenthic biomass and wave height either directly or indirectly reflect the hydrodynamics of the overlying water (Pearson & Rosenberg 1987) and have been shown to affect settlement of postlarval fish (Pihl & van der Veer 1992, Chapter 4-Add.) and the efficiency of antipredator behaviour (Tallmark & Evans 1986). Henderson's 'exposed estuarine' assemblage consists of three species associations that can be found in virtually the same configuration in the plot of the first two principal components (Fig. 2.15). Some species can be found in close association in both studies, e.g. hooknose (*Agonus cataphractus*), cod (*Gadus morhua*) and *T. luscus*. Similarly Henderson's 'sheltered estuarine' assemblage, characterized by *D. labrax*, Mugilidae species and sea snail (*Liparis liparis*) corresponds to the WS cluster. Two of the species in Henderson's 'sheltered marine' assemblage: *Atherina boyeri* and *G. niger* are typical for the Oosterschelde cluster (considering that the present study classifies all sandmelts as *A. presbyter*, but see Creech 1991). Within the 'exposed marine' assemblage of Henderson there is some disagreement between the two studies. Whilst *A. tobianus* and *T. vipera* are common to both Henderson's 'exposed marine' assemblage and the VX cluster, his assemblage contains a host of other species typical for the VIO and VIG clusters. According to P. Henderson (pers. comm.) this is probably due to the fact that no power stations have been built at truly ex-

posed marine sites of the kind occurring in the seaward part of the Voordelta. The highly dynamic, low macrobenthic biomass sands in VX are ideal for burrowing fishes that do not depend on macrobenthos for their food. The planktivorous sandeels need well oxygenated sands in which rapid burrowing is possible to avoid predators (Macer 1966). *T. vipera* is a sit-and-wait predator that burrows to avoid detection by its preferred prey *Pomatoschistus* species (Creutzberg & Witte 1989) which are quite abundant in that area. The close association of *P. lozanoi* to the negative side of the third axis is not due to a clear preference for the exposed sites but is mainly caused by its conspicuous rarity in the Oosterschelde. In contrast to its close relative *P. minutus* it does not seem to be able to establish itself in the Oosterschelde. In summer, when the small juvenile *P. lozanoi* enter the Oosterschelde, water transparencies are at their maximum (often over 4 m Secchi disk depth), they are presumably very effectively eliminated by visual predators such as *T. luscus* (Chapter 7-Add.) and *P. minutus* (O. Hamerlynck, unpublished data).

From both studies it appears that inshore marine and estuarine fish communities are strongly structured by their environment. When more data will become available it seems likely that, given a number of important characteristics such as latitude, sediment type, current velocities, wave impact and salinity, quite accurate predictions could be made on the type of fish assemblage expected at a certain site. It is therefore recommended that such environmental variables be recorded when sampling demersal fishes and mobile epifaunal invertebrates. Deviations from the expected assemblage could therefore be indicators of special circumstances either in the positive or in the negative sense.

In the positive sense the richness of the VIG assemblage is probably a result of recent changes in the ebb-tidal delta of the former Grevelingen estuary. Since the closure of that estuary in 1971, changes in the current patterns have turned the area into a sink which traps mud, detritus and larvae of fishes, decapods and macrobenthic animals (Chapter 4-Add.). It does not necessarily follow that there is a causal relationship between macrobenthic biomass, or any of its covariables, and the occurrence of a certain species assemblage. Still, it is likely that some of the species occurring towards the right end of the species plot, e.g. *L. limanda*, *P. minutus* and *A. rubens*, because of their food preferences, seek actively for localities with a high macrobenthic biomass. The VIO assemblage resembles the VIG assemblage but is less rich. The stations of the VIO assemblage correspond to those parts of the ebb-tidal delta of the Oosterschelde where mud has started to accumulate as a consequence of the reduction in current velocities since the completion of the storm-surge barrier in 1986.

A typical example of a deviation in the negative sense can be seen in the Westerschelde which is completely devoid of the freshwater species that, in other areas, occasionally venture into waters of higher salinity. Other notable absents are the Salmonidae, and especially the smelt *Osmerus eperlanus*, which is very abundant in estuaries with sufficient oxygen (Wharfe *et al.* 1984). Though a beam trawl is not the most efficient device to catch such fishes, a number of anadromous fish species should be much more common than at present. Thus *L. fluviatilis* was only recorded once, of *A. fallax* three individuals were caught in a single haul and in total less than ten Mugilidae were caught. This result is in sharp contrast to their abundance in the Severn (Claridge *et al.* 1986) and two British east coast estuaries (Pomfret *et al.* 1991). In 1989, the annual mean oxygen content measured at the Dutch-Belgian border, only a few kilometres upstream from W14, was below 2.5 mg l⁻¹ (Van Eck *et al.* 1991). Marine fishes become severely stressed at oxygen levels of less than 4.5 mg l⁻¹ (Poxton & Allouse 1982, Marchand 1993). It is therefore unlikely that important fish concentrations occur upstream of W14. The low oxygen levels in the freshwater part of the Schelde are presumably the prime cause for the near absence of the freshwater and anadromous species. Two other absents are the starfish *A. rubens* and the eelpout *Z. viviparus*. The first species used to be common in the Westerschelde but has virtually disappeared (Van Eck *et al.* 1991). The polychlorobiphenyl- and cadmium-contents of starfish from the Westerschelde which are six times higher than the levels in starfish from the Oosterschelde, seem to affect their reproduction (den Besten 1991). The eelpout, a typical estuarine resident which is common in the Tyne and the Forth (Pomfret *et al.* 1991) is very rare in the Westerschelde. Fry survival in this species is known to be negatively affected by mercury (Jacobsson *et al.* 1986, Essink 1989). Though mercury concentrations in the suspended particulate matter of the Westerschelde have decreased to about one third of their former value over the last decade (Van Eck *et al.* 1991) concentrations in the sediments are still four to twentyfive times higher than North Sea background levels. Similar tests as those performed for starfish could be done with eelpout to prove or disprove this hypothesis.

The second axis in the PCA is clearly influenced by the estuarine gradients in a series of co-variables but none of the variables measured has a particularly strong correlation with this second component of the PCA. There are certainly conflicting cost-benefit aspects for fishes inhabiting the brackish part. For species such as *S. sprattus*, *P. minutus* and *P. lozanoi*, which are abundant in the brackish part and are known to feed predominantly on mysids there (Hamerlynck *et al.* 1990 and unpublished data), the important mysid concentrations must be attrac-

tive. Avoidance of visual predators in the very turbid inner estuary (Blaber & Blaber 1980) is another bonus for those species. The brown shrimp *C. Crangon* may profit both from the high turbidity and the large supply of detritus from the river. On the other hand, slow moving fish and invertebrates may be subjected to oxygen stress. For flatfish the situation is certainly less than optimal because of the low macrobenthic biomass.

The third axis is very important in the sense that it neatly separates the assemblages defined, except for the subdivision WM-WB. However, except for the stronger correlation with wave height, there is little difference between the environmental biplots for the second and third axes. Some hidden variable e.g. current velocity may be structurally important.

2.5 Conclusions

As seen from the results of this study, multivariate statistical techniques have a great potential as a tool for an increased understanding of the structure of natural communities, even of mobile species. Most studies of fishes and fisheries are either based on areas of convenience, e.g. the nearest estuary or on statistical rectangles, and these do not necessarily correspond to the extent of natural communities. It would make great biological sense to base functional and process studies on entities which can be distinguished clearly on the basis of their species-abundance composition.

Datasets which can be used for these exploratory studies exist but they often lie idle in the fisheries research institutes. Most often they are only used for the extraction of data on the stock size or on the imminent recruitment of commercially important species. An exception to this rule is the study by Daan *et al.* (1990) which defines three different types of fish community in the North Sea on the basis of a multivariate analysis of the English groundfish survey data. There are many other datasets, covering vastly greater areas than the present study, e.g. the ICES Demersal Young Fish Surveys (DYFS) or the 'Aurelia' cruises dataset (Creutzberg 1985) whose spatial and temporal structure could be analysed to great benefit.

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