Spatial patterns and seasonality in the epibenthic communities of the Westerschelde (Southern Bight of the North Sea)

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Beamtrawl samples were taken monthly between January 1988 and December 1989 in 14 subtidal stations along the longitudinal axis of the Westerschelde Estuary. The estuary harboured high densities of epibenthic species (total average of 2250 ind 1000 m^{-2}). Only 37 fish species were recorded and three mobile macroinvertebrate species were quantified. Seventeen epibenthic species were common, only eight of which were very abundant. An overall dominance of the brown shrimp *Crangon crangon* was noted. The near absence of anadromous and freshwater species was correlated with the low oxygen concentrations upstream the Dutch–Belgian border. The epibenthic species could be divided into a polyhaline and a mesohaline community along the main salinity–oxygen–turbidity gradients of the estuary. The mesohaline zone was characterized by higher densities and biomasses for shrimps, gobies and flatfish. The spatial structure in the epibenthic community of the polyhaline zone was more influenced by the watermasses from the sea and inflowing channels, and was correlated with the degree of exposure (current velocities and tides). A classification is proposed, based on the season in which the epibenthic species occur in the estuary, and on their life stages and abundances during that period. The monthly data demonstrate that while the eight abundant epibenthic species were generally present throughout the year (summer or winter resident), the majority tended to appear in the Westerschelde at varying times (summer, winter or bimodal) and often remained in large numbers (nine common species) for only a short time. The fact that mainly juveniles were recorded in the higher density-classes, suggests that the Westerschelde Estuary still acts as a nursery area for many epibenthic species.

INTRODUCTION

The Westerschelde Estuary is the maritime zone of the River Schelde in the Delta area of the Netherlands. It stretches from Vlissingen near the mouth to the Dutch–Belgian border (Figure 1). This part of the estuary is characterized by large intertidal sandflats and two main subtidal channels (mud percentage lower than 2%), and it is bordered by mudflats and saltmarshes (Van Maldegem et al., 1993). The tidal zone upstream the border is called the Zeeschelde. The Schelde is a highly polluted system, both with industrial and domestic waste. It is especially threatened by huge organic loads, but it also suffers from strong anthropogenic perturbations such as dredging, dumping, sand extraction, land reclamation, and—to a lesser extent—recreation and industrial fisheries.

De Veen et al. (1979) reported on a ten year survey on some economically important epibenthic species in the Westerschelde. These authors compared the system with the Wadden Sea and the Dutch coastal zone, and emphasized its importance as a nursery area. Hamerlynck et al. (1993) compared the fish fauna of the Westerschelde with that of the neighbouring Oosterschelde. Data on the fish fauna of the lower Zeeschelde were presented by Van Damme et al. (1994). The present study focuses on the abundance and distribution of the demersal fish and mobile macro-invertebrates, which together constitute the epibenthic community. Fish distribution and abundance in estuarine and coastal environments are determined by physical and chemical factors (e.g. salinity, temperature, water transparency, tidal cycles, wave action and wind), and biotic factors (e.g. migration, reproduction, feeding and habitat selection) (Morin et al., 1992). The spatial and seasonal distribution patterns of the epibenthic species are described by means of multivariate statistical techniques, and are correlated with some environmental variables. A classification of the epibenthic species is proposed in accordance with their presence in the estuary.

MATERIALS AND METHODS

Between January 1988 and December 1989 monthly samples were taken at 14 subtidal stations, following the 10 m depth contour along the longitudinal axis of the Westerschelde. The stations were more or less evenly distributed between 3 and 52 km upstream from Vlissingen (Figure 1). The epibenthos was always sampled during daytime with a 3 m beamtrawl, which was towed over a distance of 1000 m from the RV 'Luctor' (34 m, 500 pK). The beamtrawl was equipped with a small-meshed net (10 mm stretched in the codend), one tickler chain and a chain in the groundrope. After sampling, four environmental variables were measured: temperature
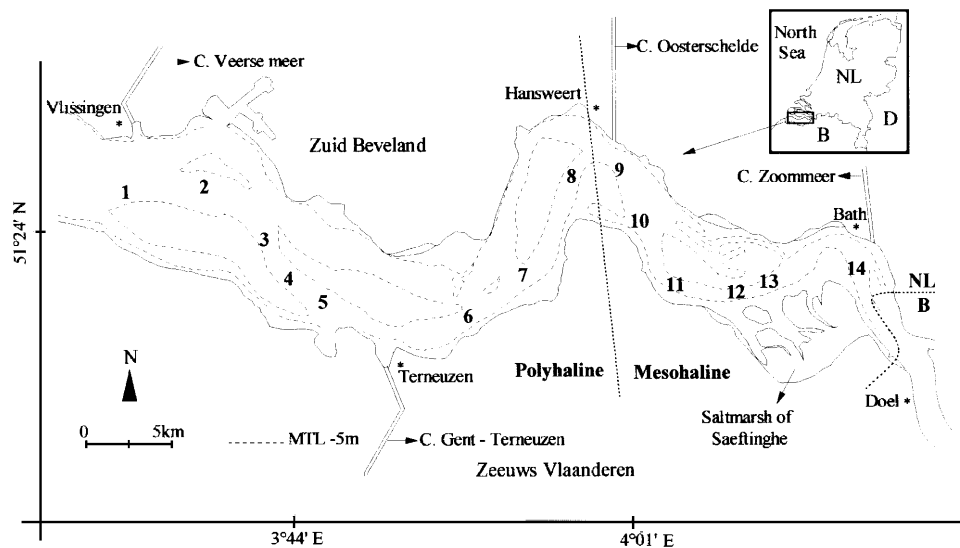
Figure 1. Map of the study area with location of the 14 sampled stations in the subtidal of the Westerschelde. Note the division between the 'polyhaline' and 'mesohaline' epibenthic communities around Hansweert.

(°C), salinity (psu), dissolved oxygen content (mg l^{-1}) and Secchi disc depth (cm). The latter was reciprocally transformed, thus becoming a measure of turbidity (light extinction, cm^{-1}).

All fish were identified to species level and measured to total length on board, except for the gobies which were identified and measured to standard length in the laboratory. Only the most abundant and conspicuous mobile macroinvertebrates (*Crangon crangon* and two crab species) were counted and/or weighed in bulk. A number of rare invertebrate species could not be quantified. From hyperbenthic studies in the subtidal zone of the Westerschelde (Mees et al., 1993b), we know that the prawn species *Palaemonetes varians* and *Palaemon elegans*, the crabs *Portumnus latipes* and *Eriocheir sinensis*, and the hermit crab *Pagurus bernhardus* are sometimes present in low numbers. Density values are expressed in numbers of individuals per 1000 m^2, assuming a net efficiency of 20% for the 0- and 1-groups of all fish and invertebrates (Hostens & Hamerlynck, 1994). The biomass was calculated from the

length–frequency tables, by means of length–weight regressions which were based on measurements in the Oosterschelde and the Voordelta area (K. Hostens, unpublished data). Biomass is expressed in grams ashfree dry weight (ADW) per 1000 m^2.

Different multivariate techniques were used to describe the spatial and seasonal community structure of the epibenthos, based on the average density and biomass per station and per month over the period 1988–89. Prior to the multivariate analyses, the data were fourth-root transformed. Different data reductions were based on average density and biomass levels for the whole study period, excluding the rare species. Also the environmental variables were averaged per station and per month. Two-Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979) and Group Average Sorting cluster analysis based on the Bray–Curtis dissimilarities (Bray & Curtis, 1957), were used as classification techniques. The ordination techniques used were Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) (Jongman et

Table 1. *Average density (ind 1000 m^{-2}) and biomass (g ADW 1000 m^{-2}) over the period January 1988–December 1989, for the whole epibenthic community (fish and invertebrates) and for the fish alone, per station (25 campaigns) and per month (28 locations).*

Station	Polyhaline								Mesohaline					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Km from mouth	3	8	11	13	16	23	26	30	34	36	40	43	47	52
Total density	1900	2220	1370	1490	1000	1390	1250	1650	2390	4440	4130	2810	1950	3310
Fish density	170	320	90	200	150	160	250	300	450	1070	750	330	220	770
Total biomass	1000	610	500	580	480	480	430	500	970	2430	1880	940	790	1860
Fish biomass	320	130	120	220	200	160	180	180	500	1630	1080	340	370	1280

| Month	Winter			Summer						Winter		
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Fish density	700	210	130	270	130	120	470	440	840	510	320	320
Total biomass	2110	560	440	660	510	570	1050	860	1430	1200	1200	1110
Fish biomass	1810	450	320	520	180	140	170	170	420	530	480	760
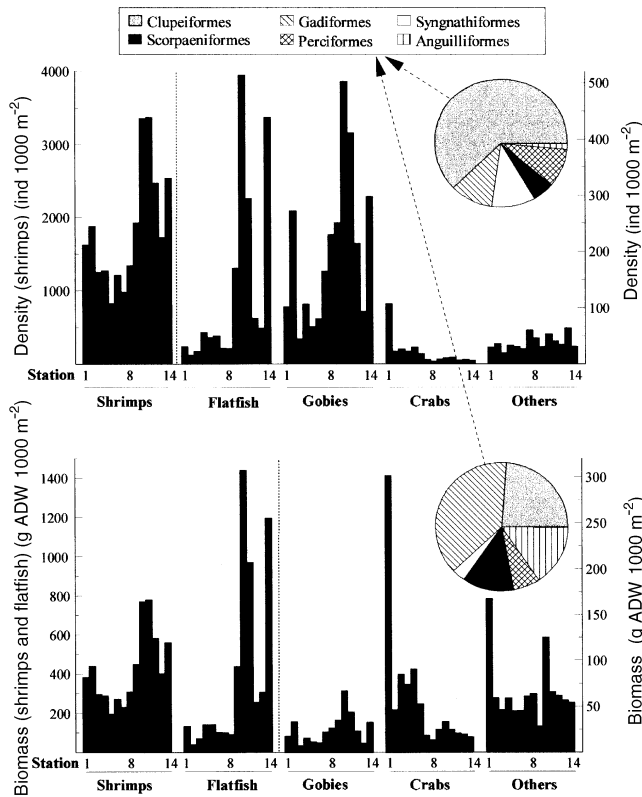
Figure 2. Average density (ind 1000 m^{-2}) and average biomass (g ADW 1000 m^{-2}) per station for the main epibenthic groups. The insets show the relative composition (averaged over all samples) of the 'Others' group. Note that the left axis only refers to 'shrimps' in the density plot and to 'shrimps' and 'flatfish' in the biomass plot.
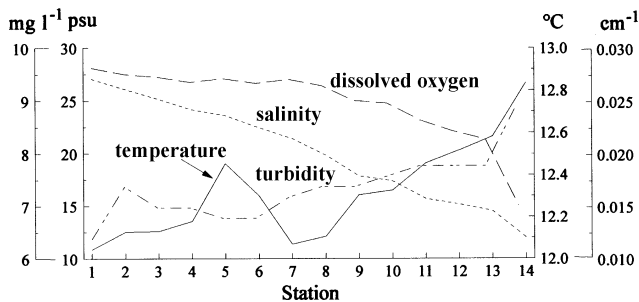
Figure 3. Average values for the four environmental variables per station: dissolved oxygen (mg l^{-1}), salinity (psu), temperature (°C) and turbidity (cm^{-1}).

al., 1987). As the different techniques applied to both density and biomass data yielded similar results, only the cluster analysis and the CCA with the average biomass data per station (criterion: total average density >0.1 ind 1000 m^{-2}) and the CCA with the average biomass data per month (criterion: total average density >0.01 ind 1000 m^{-2}), are presented.

Seasonality in the data was further analysed by means of some aspects of the biology of the epibenthic species. The period of maximum abundance and the modal length class during this period were extracted from the average density data and the length–frequency distributions per month. For *C. crangon* the patterns are based on biomass data, since this species was only weighed in bulk.
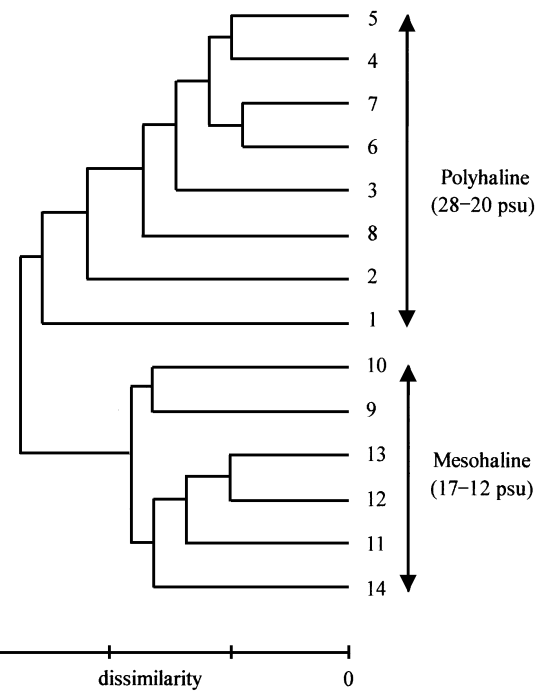
Figure 4. Dendrogram of the cluster analysis, with an indication of the two zones and the degree of dissimilarity on a scale of 0–1.

No data on the densities of the different life stages of the invertebrate species were available. The epibenthic species were divided into different density-classes and categories, depending on their seasonal occurrence and the time they spent in the estuary.

RESULTS

Spatial patterns

During the study period a total of 37 fish and three invertebrate species were recorded: on average eight and 11 species were caught per month and per station, respectively. The total average density for all stations over the period 1988–89 was 2250 ind 1000 m^{-2} and the total average biomass amounted to 970 g ADW 1000 m^{-2}. The brown shrimp *Crangon crangon* constituted some 80% of the total density (Table 1). Moreover, this species dominated the fauna along the entire salinity gradient sampled. Only in the more brackish stations (upstream of Hansweert) did the larger flatfish attain some higher biomass values (1440 g ADW 1000 m^{-2} at station 10) (Figure 2). The third important group were the gobiid fish. In terms of density they were equally important as the flatfish (on average 200 ind 1000 m^{-2}). All three groups showed similar density patterns along the salinity gradient: densities stayed uniformly low in the marine part (except for station 2) up till Hansweert; they then gradually increased in the brackish reaches and decreased again, but peaking again with very high densities in the last station around Bath (Figure 2).

Two other groups did not follow this pattern: brachyuran crabs had higher biomasses in the marine part, and the group of all other fish species together had
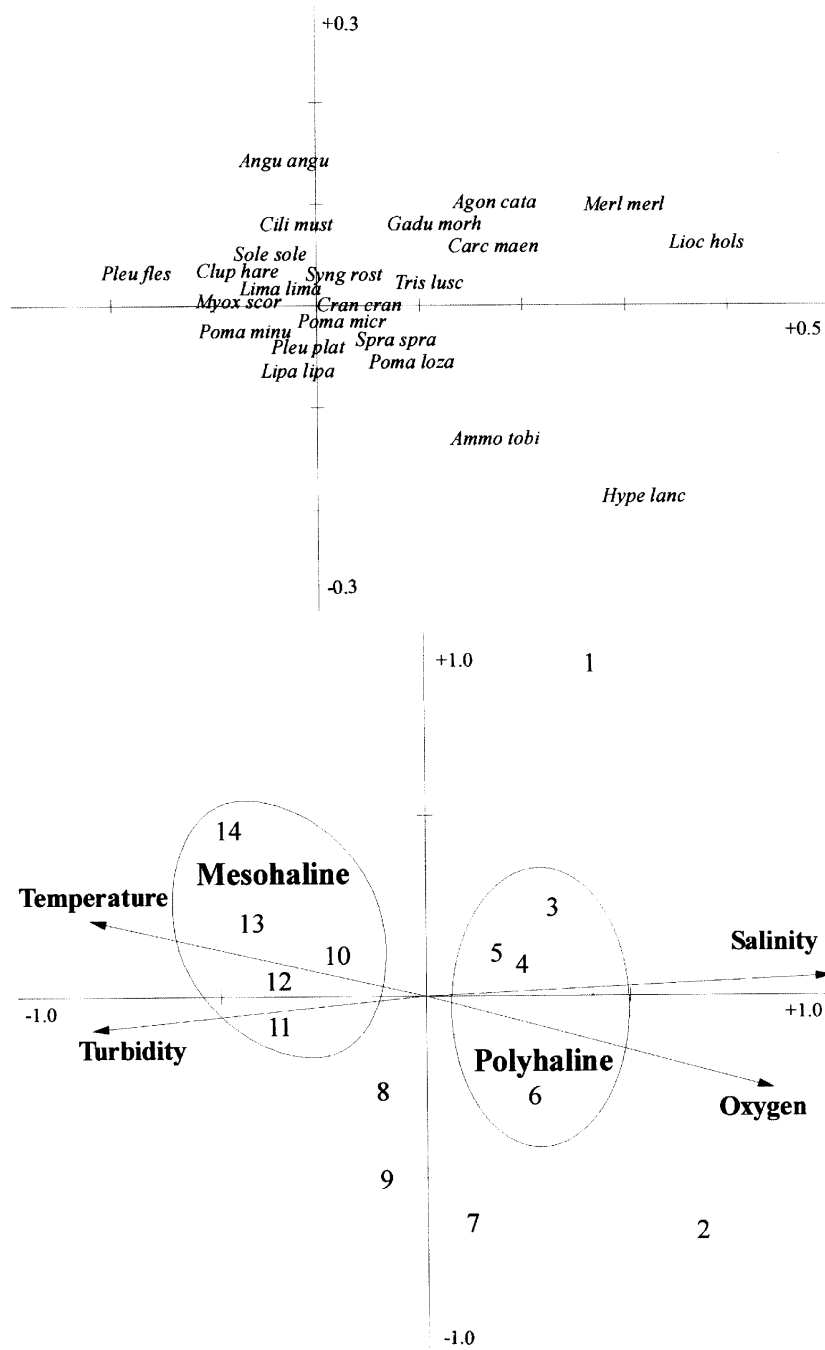
Figure 5. CCA ordination plots (first two axes), based on a reduced set of the average biomass data and on the environmental variables per station, with a projection of the two main clusters. See Table 2 for full species names (abbreviated to first four letters of genus and species names).

comparable values in all stations. The relative composition of this last group is given in the insets of Figure 2. The clupeoids were most important in terms of density, while gadoids, Scorpaeniformes and eels had comparable biomass values.
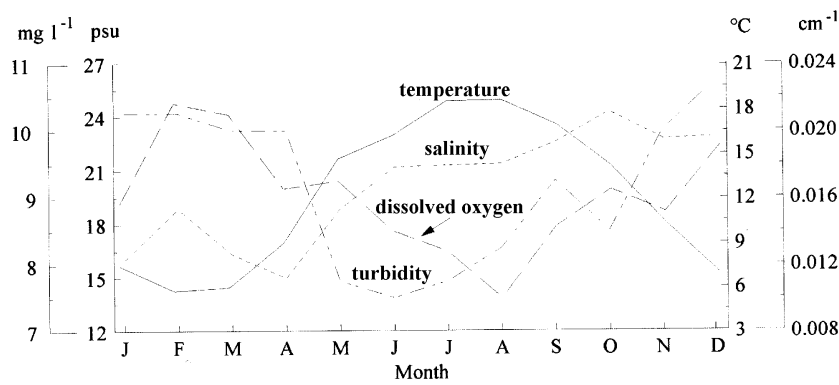
The average values of the four environmental variables are presented in Figure 3. Salinity gradually decreased from 28 to 12 psu upstream. The dissolved oxygen concentration remained above the saturation level downstream of Hansweert, decreasing to $8.2 \, mg \, l^{-1}$ with a decline to $7 \, mg \, l^{-1}$ at Bath. Turbidity showed the inverse pattern of the oxygen content. Temperature gradually increased in upstream direction from 12 to 13°C, with somewhat higher values around stations 5 and 6.

Cluster analysis classified the 14 stations in two main groups, one upstream and the other downstream of Hansweert (Figure 4). All stations were rather similar, with a maximum dissimilarity of 0.3 on a scale from 0 to 1. The CCA on the reduced biomass matrix visualizes the major gradients in the estuary and the environmental preferences of the main species. The four variables explain 73% of the variance along the first axis (eigenvalue 0.09) (Figure 5). The projection of the cluster groups on the CCA plot shows that the more saline stations are separated from the more brackish (and turbid) stations. Two smaller clusters are suggested: stations 3–5, with the shore crab *Carcinus maenas* and whiting *Merlangius merlangus* as characteristic species; and stations 10–13, characterized by high biomass

Table 2. *Some biological aspects of the 40 epibenthic species caught in the Westerschelde, based on the monthly average densities over the period January 1988–December 1989, with an indication of the proposed classifications.*

Abundancy class	Species	Systematic group	Density†	Period max. abundance	Month of, and max. abundance†	Seasonal class	Modal length class during period of max.‡	Main life stage	Life history
	Crangon crangon	Caridea	416.9	Jul–Nov	Sep, 939	Summer-resident		Independent	Marine
	Pomatoschistus lozanoi	Gobiidae	110.5	Aug–Oct	Sep, 529	Summer-resident	30–40	Juvenile	Brackish
	Limanda limanda	Pleuronectiformes	84.4	Oct–Jan, Jan	Jan, 385	Winter	60–90, 140–160	Juvenile	Marine
Abundant	*Pomatoschistus minutus*	Gobiidae	76.7	Jul–Sep	Jul, 344	Summer-resident	25–45	Juvenile	Brackish
	Solea solea	Pleuronectiformes	33.4	Jan–Apr	Apr, 215	Winter-resident	90–110	Juvenile	Brackish
	Sprattus sprattus	Clupeiformes	17.2	Dec–Jan, Jul	Jan, 53	Bimodal	65–80, 45	Juvenile	Marine
	Pleuronectes platessa	Pleuronectiformes	16.9	Sep–Feb	Jan, 70	Winter	70–100	Juvenile	Marine
	Carcinus maenas	Brachyura	16.6	May–Aug	May, 28	Summer-resident		Independent	Brackish
	Clupea harengus	Clupeiformes	7.7	Jan–Feb, Jul–Aug	Jan, 32	Bimodal	90–100, 45–55	Juvenile	Marine
	Pomatoschistus microps	Gobiidae	6.5	Nov–Mar	Jan, 24	Winter	30–40	Elder	Brackish
	Liocarcinus holsatus	Brachyura	4.1	May–Sep	May, 12	Summer		Independent	Marine
	Syngnathus rostellatus	Syngnathiformes	3.9	Aug–Sep, Jun	Aug, 10	Summer	90–100, 110–120	Juvenile	Marine
Common	*Ammodytes tobianus*	Perciformes	3.5	Feb–Apr	Apr, 9	Winter-resident	80–90	Junveile	Marine
	Pleuronectes flesus	Pleuronectiformes	2.7	Dec–Mar	Mar, 5.8	Winter-resident	200–400, 100–120	Independent	Catadromous
	Trisopterus luscus	Gadiformes	2.0	Jun–Aug	Jun, 9	Summer	70–75, (50–130ʃ)	Juvenile	Marine
	Merlangius merlangus	Gadiformes	1.3	Jun–Jul	Jun, 9	Summer	70–90	Juvenile	Marine
	Agonus cataphractus	Scorpaeniformes	1.0	Dec–Feb*	Jan, 2.6	Winter-resident	65–75	Juvenile	Marine
	Liparis liparis	Scorpaeniformes	0.8	May–Jul, Sep–Dec	Jun, 2.2	Bimodal	60–70, 110–120	Independent	Brackish
	Gadus morhua	Gadiformes	0.4	Sep–Nov*	Sep, 1.2	Summer	160–220	Elder	Marine
	Anguilla anguilla	Anguilliformes	0.3	May–Jul	Jul, 1	Summer	300–400	Elder	Catadromous
	Myoxocephalus scorpius	Scorpaeniformes	0.3	Feb–Mar	Feb, 1	Winter	160–200	Elder	Marine
	Hyperoplus lanceolatus	Perciformes	0.2	Jun–Sep	Jun, 0.7	Summer	150–180	Juvenile	Marine
	Ciliata mustela	Gadiformes	0.2	Sep–Nov	Oct, 1.3	Winter	100–120	Juvenile	Marine
	Gasterosteus aculeatus	Gasterosteiformes	0.2	Dec–Mar	Mar, 0.7	Winter	45–55	Juvenile	Brackish
	Zoarces viviparus	Perciformes	0.08	—	May, 0.2	Summer-resident	150–155	Juvenile	Brackish
	Trigla lucerna	Scorpaeniformes	0.06	May, Oct	Oct, 0.3	Bimodal	150–170, 45–60	Independent	Marine
	Mugilidae sp.	Perciformes	0.05	Oct–Dec	Oct, 0.3	Winter	40–45	Juvenile	Catadromous
	Engraulis encrasicolus	Clupeiformes	0.04	Sep–Oct	Oct, 0.3	Winter	65–75	Juvenile	Brackish
Occasional	*Syngnathus acus*	Syngnathiformes	0.04	Jun–Jul	Jul, 0.1	Summer	320–380	Elder	Marine
	Dicentrarchus labrax	Perciformes	0.04	Dec–Mar	Dec, 0.4	Winter	70–75	Juvenile	Brackish
	Pungitius pungitius	Gasterosteiformes	0.03	Mar*	Mar, 0.3	Winter	40–45	Juvenile	Fresh
	Alosa fallax	Clupeiformes	0.02	Nov**	Nov, 0.2	Winter	95–100	Juvenile	Anadromous
	Aphia minuta	Gobiidae	0.02	Apr–Jul	Oct, 0.06	Summer	40–50	Elder	Marine
	Scophthalmus rhombus	Pleuronectiformes	0.02	Jan–Apr	Sep, 0.07	Winter	200–300	Elder	Marine
	Lampetra fluviatilis	Petromyzontiformes	0.01	Jun**	Jun, 0.1	Summer	170–175	Elder	Anadromous
	Atherina presbyter	Atheriniformes	0.01	Sep–Oct**	Oct, 0.07	Winter	85–90	Elder	Marine
	Trachurus trachurus	Perciformes	0.01	Aug–Sep	Sep, 0.07	Summer	60–70	Juvenile	Marine
	Buglossidium luteum	Pleuronectiformes	0.006	May*	May, 0.07	Summer	55–60	Juvenile	Marine
	Pomatoschistus pictus	Gobiidae	0.006	Oct**	Oct, 0.07	Winter	30–35	Juvenile	Marine
	Solea lascaris	Pleuronectiformes	0.006	Jul**	Jul, 0.07	Summer	100–105	Juvenile	Marine

*, mainly 1988; **, mainly 1989; †, average density (ind 1000 m^{-2}) except for *Crangon crangon*, biomass (g ADW 1000 m^{-2}); ‡, total length (mm) except for Gobiidae, standard length (mm); ʃ, range over the three months.

Figure 6. Average values for the four environmental variables per month: dissolved oxygen (mg l^{-1}), salinity (psu), temperature (°C) and turbidity (cm^{-1}).
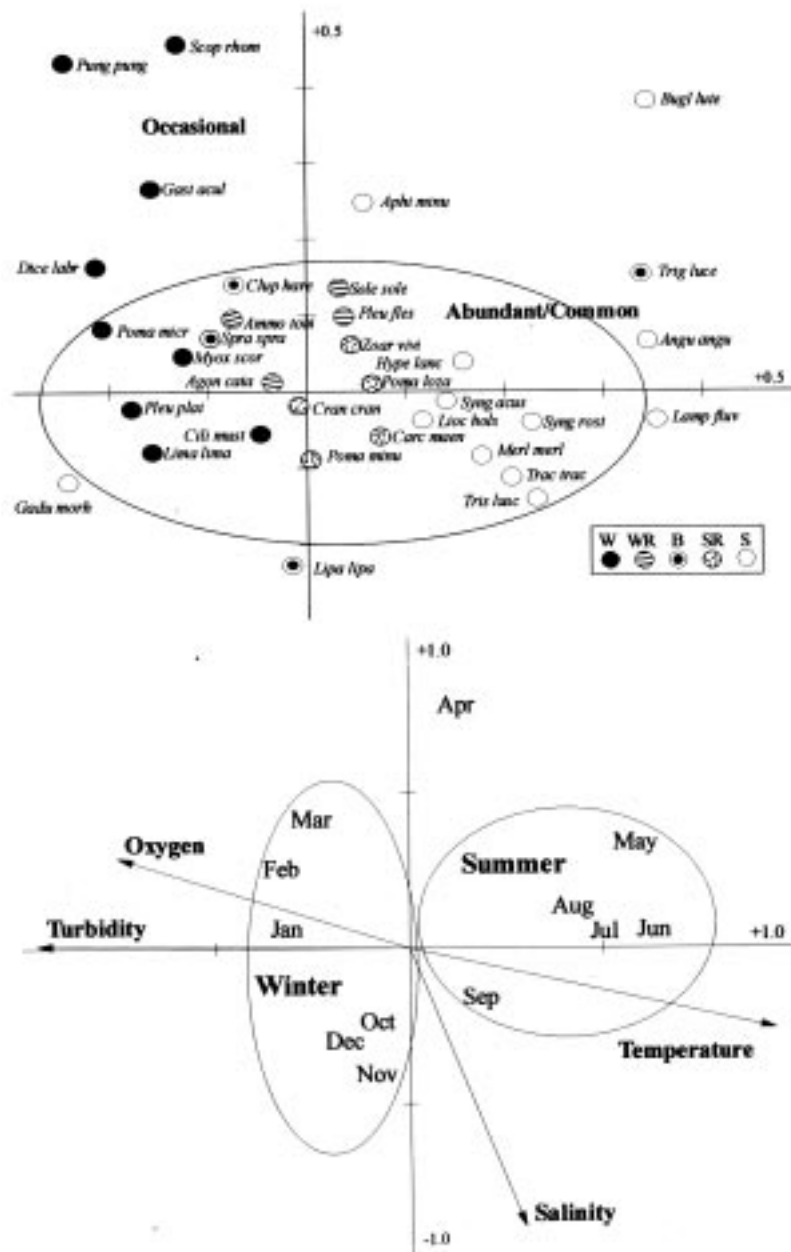
Figure 7. CCA ordination plots based on the average biomass data and on the four environmental variables per month, with a projection of the proposed classification of the epibenthic species. See Table 2 for full species names (abbreviated to first four letters of genus and species names). W, winter; WR, winter-resident; B, bimodal; SR, summer-resident; S, summer species.

values for the sand goby *Pomatoschistus minutus*, the flatfish *Limanda limanda* and *Solea solea*, and herring *Clupea harengus*. Stations 6, 8 and 9 take up a position between these two groups; the dominant species are lozano's goby *Pomatoschistus lozanoi* and sea snail *Liparis liparis*. Along the second axis (eigenvalue 0.02) stations 1, 2 and 7 are plotted near the edges. Stations 2 and 7 are characterized by the Ammodytidae (*Ammodytes tobianus* and *Hyperoplus lanceolatus*).

Seasonality

Although most epibenthic species were caught throughout the year, their densities and biomasses displayed seasonal trends. Based on the period(s) of maximum abundance, the epibenthos could be divided into five categories. The 'resident species' were present in the estuary throughout the year (though not necessarily during their whole life history), and showed peak densities either in summer (summer-resident, SR) or in winter (winter-resident, WR). The 'bimodal species' (B) clearly showed two density peaks, while other species were almost exclusively present in the estuary during summer (summer species, S) or during winter (winter species, W). 'Summer' is defined as the period from May to September; 'winter' as October to April. Based on the average density over the period 1988–89 and on the modal length-classes, the epibenthos could further be divided into six density–life history groups. The species were classified as either occasional (O), common (C) or abundant (A), and as juvenile (J), elder (E) or life stage independent (I).

A total of 25 juvenile, nine elder and six independent species were found (Table 2). In the 'abundant' (eight species) and 'common' (nine species) density-classes, mainly 'juveniles' were registered, while 'juvenile' and 'elder' species were more or less equally distributed over the 'occasional' density-classes with less than 1 ind 1000 m^{-2} (23 species). The numbers of 'summer' and 'winter' species were almost equal, namely 5 SR, 13 S, 4 WR and 14 W, but the distribution of the main life stages was different: 7 J, 5 E and 1 I in summer vs 10 J and 4 E in winter, and 6 J and 3 I in the group of resident species. The four 'bimodal' species were either 'juveniles' or the two peaks were found to belong to two different cohorts, with the highest densities being recorded in the winter period (Table 2).

The seasonal patterns for the four environmental variables are presented in Figure 6. The dissolved oxygen concentration gradually decreased from 10.5 mg l^{-1} in February to 7.5 mg l^{-1} in August. Temperature showed the inverse pattern with a minimum of 6°C in February and a maximum of 19°C in August. Turbidity was highest during the winter months (0.02 cm^{-1} from November to April), and dropped to a value of 0.01 cm^{-1} between May and July. Salinity increased from 16 psu in January to 23 psu in December, with an exception for March and April when low salinities of 15 psu were recorded.

The classification of the epibenthic species is reflected in the CCA plot of average biomasses per month (Figure 7). The species–environment relations of the first two axes explain 92% of the variance in the data. The 'winter' and 'summer' periods (as defined above), were separated along

the first axis (eigenvalue 0.16). The 'winter' period could further be divided in 'early winter' (September–December) and 'late winter' (January–March) along the second axis (eigenvalue 0.07). The division in winter and summer species is in agreement with the plot of the months. Resident (R) species and common juvenile (C, J) and independent (C, I) species are mostly located near the centre of the species plot. Occasional juvenile (O, J) and elder (O, E) species are plotted near the edges.

DISCUSSION

Spatial distribution

The most abundant fish in estuaries are benthic or demersal species. The average densities for the most common species are comparable with those recorded by De Veen et al. (1979) for the period 1969–1978 in Zeeland, and with those recorded for the Oosterschelde in 1988 (Hostens & Hamerlynck, 1994). In the Forth estuary maximum abundances for dab and plaice were lower, while these for whiting, clupeoids and eelpout were higher (Elliott et al., 1990). A beamtrawl with a small-meshed net is very efficient for catching mobile macro-invertebrates, such as shrimps, crabs and echinoderms. These invertebrates generally are the main component of the demersal epibenthic communities in estuaries (80% shrimp) and coastal zones (50% starfish, 30% shrimp) (Hamerlynck et al., 1993). Unfortunately, only the three most common macroinvertebrate species could be quantified. This has no implications for the structural patterns described: all other invertebrates were undoubtedly rare, and the multivariate analyses were done on reduced data-sets, excluding the rare species.

In the Westerschelde 17 species were common and only eight species could be considered to be really abundant. This holds true for all salinity zones. Also in other European estuaries few species have been reported to dominate the epibenthic communities (e.g. Nash & Gibson, 1982; Henderson, 1989; Elliott & Dewailly, 1995). Still, two groups of stations always clustered together in the different multivariate analyses: stations 3–5 and stations 10–13. The higher salinity and oxygen saturation for the first group of stations was correlated with the presence of a variety of species which mainly occurred in the polyhaline zone at low densities and biomasses. For example, the shore crab *Carcinus maenas* is known to avoid low salinities during most of the year (De Veen et al., 1979). On the other hand a higher turbidity and—to a lesser extent—higher temperature characterized stations 10–13 with high densities and biomasses for only a few species.

Four main factors can explain the higher densities of shrimps, gobies and flatfish in the mesohaline zone: (1) in the subtidal area of the Westerschelde mysids are very abundant (Mees et al., 1993a). This offers a high food supply for fish species which prey upon the hyperbenthos and zooplankton, such as gadoids and gobies (Hostens & Mees, 1999). In the Loire Estuary, fish were mainly concentrated in areas with large trophic resources (Marchand, 1993). (2) Large sandflats and sheltered mudflats are found in this part of the Westerschelde (Oenema et al., 1988). These intertidal areas harbour high macro-

benthic biomasses (Ysebaert et al., 1993), which are preyed upon by epibenthic species such as flatfish during high tide (Hostens & Mees, 1999). (3) Mainly juvenile epibenthic life history stages (O- and I-group) are abundant in the Westerschelde. These can profit from the mesohaline conditions in turbidity, salinity and temperature, to escape from larger predators which are probably less adapted to this environment (Potter et al., 1986). (4) The brackish tidal marshes, such as the marsh of Saeftinge, act as adjacent nursery areas for postlarval individuals of shrimps, gobies and flatfish (Cattrijsse et al., 1994).

The innermost brackish station (14) had a comparable epibenthic community as the group of stations 10–13. Probably, the high turbidity and muddy sediment in station 14 (K. Hostens, personal observation) provide favourable conditions for flatfish (mainly *Limanda limanda* and *Pleuronectes flesus*). The spatial separation for the other stations was not so clear, which also explains the low eigenvalues for both the first ordination axes. This could be due to the fact that the species in the 'other fish' group didn't show a clear preference for a specific salinity zone. The high number of species recorded at station 9 could be influenced through the connecting channel between the Oosterschelde and the Westerschelde. Indeed, some species mainly found at station 9, such as *Trigla lucerna*, *Zoarces viviparus* and *Engraulis encrasicolus*, were typical in the Oosterschelde during the 1980s (Hamerlynck & Hostens, 1994; Hostens & Hamerlynck, 1994).

Patterns in current velocity, current direction and waves, can affect the distribution, growth and survival of benthic species in shallow water communities (Barry & Dayton, 1991). The most marine station off Vlissingen, characterized by a high transparency of the water, was separated in all analyses. The current velocities in the Westerschelde stay high up till Antwerp with an average of 70 cm s^{-1} (Claessens, 1988), but probably the maximum current velocities at the mouth of the estuary were too high for the 'settling' of demersal species. Station 2 was located near a point where reflection of the tidal waves has to occur, while station 7 was located at the head of a sandflat which is mainly influenced by the flood tides (Vroon et al., 1997). Both stations 2 and 7 were characterized by sandeel, a typical species for exposed areas (Hostens & Hamerlynck, 1994). Station 6 was probably subject to the high tidal movement of the ebb tides, but in some analyses it was classified together with station 5. Both stations are characterized by somewhat higher average temperatures. The epibenthic community at these stations could deviate from that of other stations due to the water from the Canal Gent-Terneuzen that enters the Westerschelde between station 5 and 6.

Seasonality

In the Forth Estuary 42 fish species were classified as marine (20), resident (12), fresh (4) and diadromous (5) (Pomfret et al., 1991). If the same classification were followed, the 37 fish species in the Westerschelde should be classified as 24 marine, eight resident and five diadromous species. This kind of classification is based on the life history and abundance of the epibenthic species, and whether the marine species are juveniles or not (Elliott & Taylor, 1989; Elliott & Dewailly, 1995). The time of the

year they appear in the estuary is not included in this classification. In the present study, the classification is based on the main season the epibenthic species are present in the estuary, and their main life stage and abundance during that period. As already noted, the abundant (A) and common (C) classes are mainly constituted of shrimps, gobies and flatfish, followed by clupeoids, crabs, gadoids, pipefish and sandeels (Table 2).

A fourth classification criterion, which takes into account the life history of the species, was not used. In this study 'resident' means that the species is present in the estuary during the whole year, but not necessarily during all life history stages. *Solea solea*, for example, were mainly found as juveniles (J) in the estuary during the whole year. Therefore they were classified as winter-resident (WR), which also specifies in what season they were most abundant. The invertebrate species *Crangon crangon* and *Carcinus maenas* were classified as summer-resident (SR). Most of the species classified as SR and WR, can also be placed in a group of 'estuarine' resident species. But these species also occur in marine coastal systems (Hamerlynck et al., 1993) and in other neighbouring systems like the marine embayment of the Oosterschelde (Hostens & Hamerlynck, 1994) or the brackish lake Grevelingen (Doornbos, 1982). Perhaps a term 'brackish' species would be more appropriate. *Pomatoschistus microps* has been classified in most studies as an estuarine resident. During the early summer months this gobiid species was rarely found in the subtidal of the Westerschelde. It is known that in this period *P. microps* grows up in the adjacent salt marshes (Cattrijsse et al., 1994). The species then recruits to the subtidal of the estuary, which makes it an estuarine resident. But, based on the subtidal density data and on the modal length-class, *P. microps* has been classified as a winter elder (W, E) species. On the other hand, *Syngnathus rostellatus* (also classified as estuarine resident in other studies) was placed in the summer group (S) since it was nearly absent from the Westerschelde between December and April.

Most juvenile and some of the elder species in the Westerschelde can be classified as 'marine' species. In this study, it is specified in which period they have entered the estuary. *Trisopterus luscus*, for example, is a typical juvenile summer (J, S) species. During a short period of three months they grow from 50 to 130 mm in the estuary (modal length-class 70 mm). A typical juvenile winter (J, W) species is *Limanda limanda*: from September onwards only O+ individuals were found. In January two clear cohorts (0 and 1) could be detected. This is in accordance with observations in the estuaries on the west coast of Scotland as well as in the Wadden Sea (Elliott et al., 1990).

New in this study is the class of bimodal (B) species, mainly formed by the clupeid species. The individuals of both *Clupea harengus* and *Sprattus sprattus* in summer are small (modal length 50 mm), these of the winter cohort are larger (Table 2). The winter cohorts of both species are more abundant, but both abundance peaks for *C. harengus* are one month later. According to Elliott et al. (1990) the winter usage of estuaries by clupeoids is correlated with the higher turbidity, which protects these species from visual predators. Another bimodal species

(normally classified as estuarine resident) is *Liparis liparis*, with small individuals (65 mm) occurring between May and July and larger ones (115 mm) in September to December. *Liparis liparis* was rare in January and absent from the estuary between February and April. This is in contrast with the findings of Potter et al. (1986) who noted a peak abundance in December–January in the Severn Estuary.

Pleuronectes flesus is a catadromous species, but in contrast to other catadromous species elder individuals were recorded during the whole year, while from December to March 1+ juveniles were also found. It is therefore classified as a winter-resident (WR) species in this study. *Anguilla anguilla* on the other hand, was classified as elder summer (E, S) species, caught at the moment they pass through the estuary to spawn at sea. They were found in the mesohaline zone in May, while in September they were mainly caught in the polyhaline zone of the estuary.

Other studies state that estuarine environments are important nursery areas not only for juvenile marine fishes but also for anadromous species (Morin et al., 1992). In the Westerschelde, only two anadromous species (*Alosa fallax* and *Lampetra fluviatilis*) and one freshwater species (*Pungitius pungitius*) were recorded a few times. *Gasterosteus aculeatus* is a rather brackish species and was mainly found as winter elder (W, E) individuals. Van Damme et al. (1994) recorded six freshwater and one anadromous species in the lower Zeeschelde. Three of these were only caught once. In comparison with some 50 years ago, the total number of fish species in the Wester-schelde Estuary has been reduced from 67 to 37, although it is not always clear where exactly the species were recorded in the study by Poll (1945). Man-made structures such as sluices in the upper and middle reaches of the River Schelde, can form migration barriers. Still, the striking absence of freshwater and anadromous species is almost exclusively correlated with the low oxygen concentrations upstream the Dutch–Belgian border. Most probably a regulated and slow sanation of the Schelde basin would be appropriate to enlarge and ensure the diversity of epibenthic communities. Large-scale and internationally coordinated reintroduction programmes will probably be necessary to bring back typical anadromous species such as sturgeon *Acipenser sturio*, sea lamprey *Petromyzon marinus* or salmon *Salmo salar*.

Although estuaries are used by many marine fish as nursery areas, only few species reproduce in the system (Wootton, 1992). The clockwise arrangement of the monthly sample scores in the CCA illustrate the cyclical changes in abundance and species composition in the fish communities of the Westerschelde. In contrast with the findings of Potter et al. (1986), these seasonal changes can be largely explained by the four environmental variables that were measured. The plot of the species scores in the plane of the first two canonical axes was somewhat distorted by the high number of occasional species. Still, it mainly reflects the different periods of maximal densities, which can be brought back to the periods of immigration of the different species. Between July and October most summer juveniles and elder species from marine origin enter the estuary, and the resident species reach maximal densities through reproduction. September was plotted near most summer species in the CCA, but it is also the period when some of the overwintering species joined the summer community. Between October and December most of the occasional winter species reached a maximum density, while in January densities were highest for five of the ten abundant species. Potter et al. (1986) also found more estuarine dependent species between late summer and early winter. These data are in agreement with Elliott et al. (1990) who noted that marine juveniles and overwintering species are the most important epibenthic species in most estuaries.

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