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Distribution and abundance of shallow-water hyperbenthic mysids (Crustacea, Mysidacea) and euphausiids (Crustacea, Euphausiacea) in the Voordelta and the Westerschelde, southwest Netherlands.

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Abstract : The hyperbenthic mysids and euphausiids of the subtidal shallow coastal waters (the Voordelta) and the Westerschelde estuary in the Delta area (SW Netherlands) were regularly sampled between 1988 and 1991. Two salt marshes in the brackish part of the estuary were studied in the same period. Eight mysid species and one euphausiid species were identified. The spatial and seasonal distribution patterns of all species are described. The most abundant species in the coastal area is *Schistomysis spiritus,* followed by *Mesopodopsis slabberi, Schistomysis kervillei,* and *Gastrosaccus spinifer.* In the marine part of the Westerschelde the same four species are dominant but densities are generally higher than in the coastal area. Only *Siriella armata* and the euphausiid *Nyctiphanes couchi* never enter the estuary. Highest mysid densities, mainly *M. slabberi* and the estuarine endemic *Neomysis integer,* are found in the brackish part of the Westerschelde. *Praunus flexuosus* is a euryhaline species with a preference for the intertidal areas. The estuarine populations of *N. integer, M. slabberi, P. flexuosus,* and - to a lesser extent - S. *spiritus* seem to utilise the salt marshes during periods of reproduction.

Résumé : Les mysidacés et euphausiacés suprabenthiques d'une zone côtière sous-tidale peu profonde (le Voordelta) et l'estuaire de l'Escaut occidental, dans la région du Delta (SW des Pays-Bas) ont été échantillonnés à partir à intervalles réguliers entre 1988 et 1991. Deux marais maritimes situés dans la partie saumâtre de l'estuaire ont été étudiés pendant la même période. Huit espèces de mysidacés et une espèce d'euphausiacé ont été identifiées. La distribution spatiale et temporelle de toutes les espèces est décrite. L'espèce la plus abondante dans la zone côtière est *Schistomysis spiritus*, suivie par *Mesopodopsis slabberi, Schistomysis kervillei* et *Gastrosaccus spinifer*. Dans la partie marine de l'Escaut les quatre mêmes espèces sont dominantes mais leur densité sont généralement plus élevées que dans la zone côtière. Seuls *Siriella armata* et l'euphausiacé *Nyctiphanes couchi* n'entrent jamais dans l'estuaire. Les plus fortes densités en mysidacés, surtout *M. slabberi* et l'espèce estuarienne endémique *Neomysis integer*, sont observés dans la partie saumâtre de l'Escaut. *Praunus flexuosus* est une espèce euryhaline, avec une préférence pour les zones intertidales. Les populations estuariennes de *N. integer, M. slabberi, P. flexuosus* et, dans une moindre mesure, *S. spiritus* semblent utiliser les marais maritimes pendant les périodes de reproduction.

INTRODUCTION

In comparison to other groups of marine invertebrates, e.g. zooplankton (De Pauw, 1975 ; Soetaert & Van Rijswijk, in press), macrobenthic animals (Wolff, 1973, Craeymeersch *et al.*, 1990 ; Meire *et al.*, 1991) and meiobenthic animals (Heip *et al.*, 1990 ; Vanreusel, 1990, 1991), the mysids and euphausiids of the Delta area in the southwest Netherlands (and in Dutch waters in general) have hardly been studied. This is probably mainly due to the problems involved in sampling the lower part of the watercolumn (the hyperbenthal), where most shallow water mysids concentrate during the day (review in Mauchline, 1980). This lack of studies contrasts with the recognized importance of mysids in coastal and estuarine food webs : they are reported to be omnivorous feeders and they constitute an important part of the diet of fish and shrimps (review in Mauchline, 1980).

Information on the mysid fauna of the area is scattered in rather dated and often 'grey' literature. Hoek (1887) gives a list of the mysids of Dutch waters including the Delta area and Tesch (1910) covers the mysids and euphausiids of the surface waters of the Southern Bight of the North Sea. Van Beneden (1860), Kramp (1913) and Zimmer (1932) provide some information on the mysid fauna of the Belgian coast. Occasional records of mysids can be found in the extensive studies of the macrozoobenthos of the Delta area (Wolff, 1973) and in a study of the zooplankton of the Westerschelde estuary (De Pauw, 1975). Data are available on the distribution and population biology of *Praunus flexuosus* and *Neomysis integer* in the saline Lake Grevelingen (Borghouts, 1978 ; Fortuin, 1980 ; Platenkamp, 1983). In studies of the hyperbenthos of the Voordelta (Hamerlynck & Mees, 1991) and the Westerschelde (Mees & Hamerlynck, 1992 ; Mees *et al.*, in press) mysids are the dominant component. Data also exist on the neritic mysid and euphausiid fauna in the surface plankton near the Texel lightship, situated some 200 km north of the area under consideration (Van der Baan & Holthuis, 1969, 1971).

This study focuses on the distribution and abundance of the mysids of the shallow coastal area in front of the mouth of the rivers Rhine, Meuse and Schelde (the Voordelta) and of the Westerschelde. In order to assess horizontal seasonal migrations the temporal variability in the distributional patterns is also investigated. Studies on the population biology and the trophodynamics of the different species will be published elsewhere.

MATERIAL AND METHODS

The Voordelta stretches from the Dutch-Belgian border in the south to the Hoek van Holland in the north. Offshore, the area is arbitrarily defined by the Mean Tidal Level (MTL) - 15 m depth contour. The study covers only the central part of the Voordelta (Fig. 1) at the mouth of the former Grevelingen and Oosterschelde estuaries. The abiotic environment is discussed in Louters *et al.* (1991). Between August 1988 and July 1989 ten surveys were conducted at approximately monthly intervals in 12 localities : stations 1-4 in the ebb-tidal delta of the Grevelingen, stations 8-12 in the ebb-tidal delta of the Oosterschelde and stations 5-7 in the more seaward Banjaard area between both ebb-tidal deltas. In each station 2 samples were taken : one in the gully at a depth of about MTL - 10 m and one on the sandbank slope at a depth of about MTL - 5 m. As no consistent differences were found between these two depth strata, the number of individuals caught in both samples were pooled and divided by 2 for the purpose of this paper.

The Westerschelde estuary (Fig. 2) is the lower part of the river Schelde. The maritime zone of the tidal system is about 70 km long from the North Sea (Vlissingen) to the Dutch-Belgian border near Bath. The Westerschelde is the last remaining true estuary of the Delta area and is characterised by a marked salinity gradient. The abiotic environment is discus-

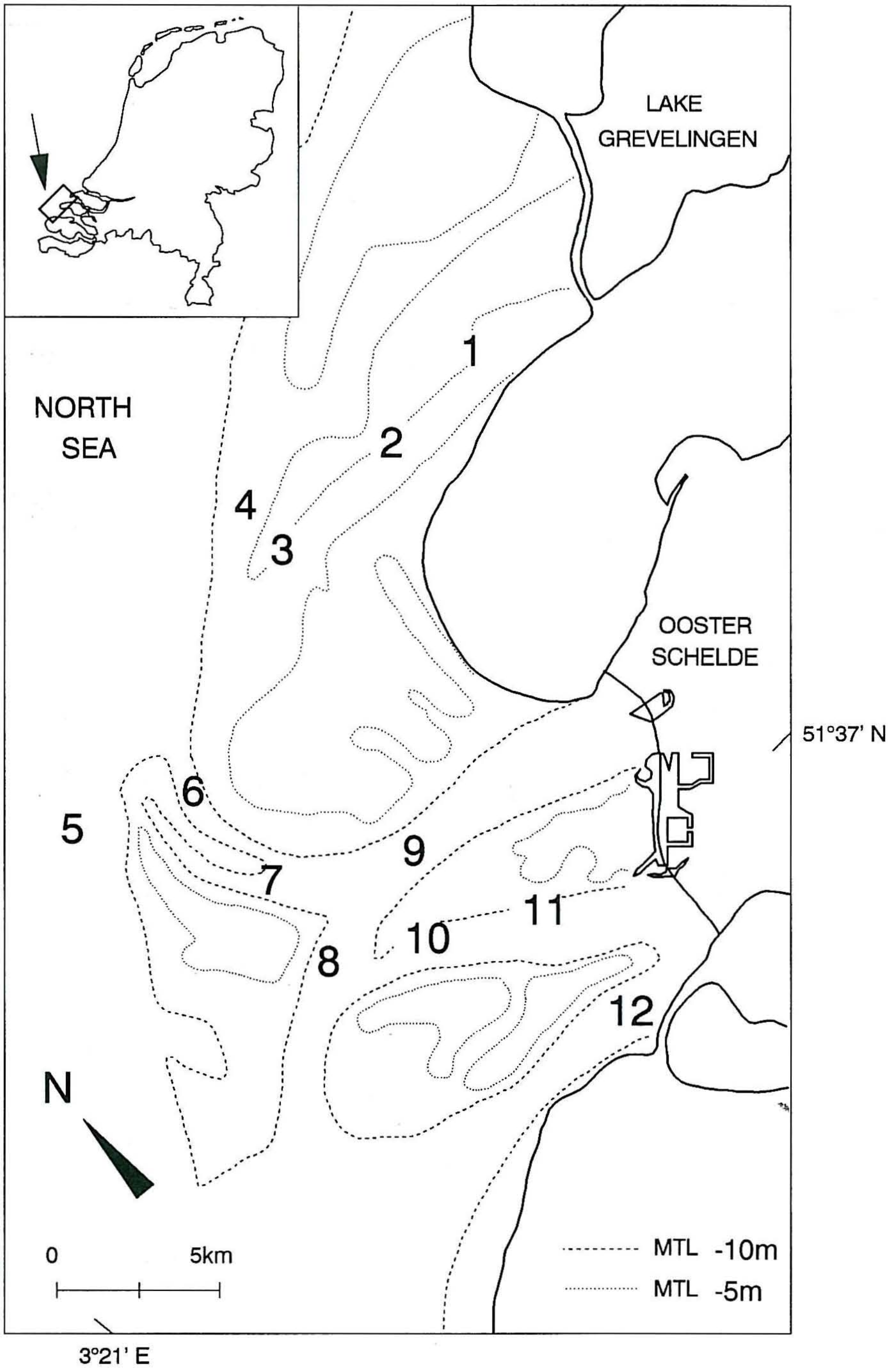


Fig. 1 : Map of the Voordelta with the sampling localities.

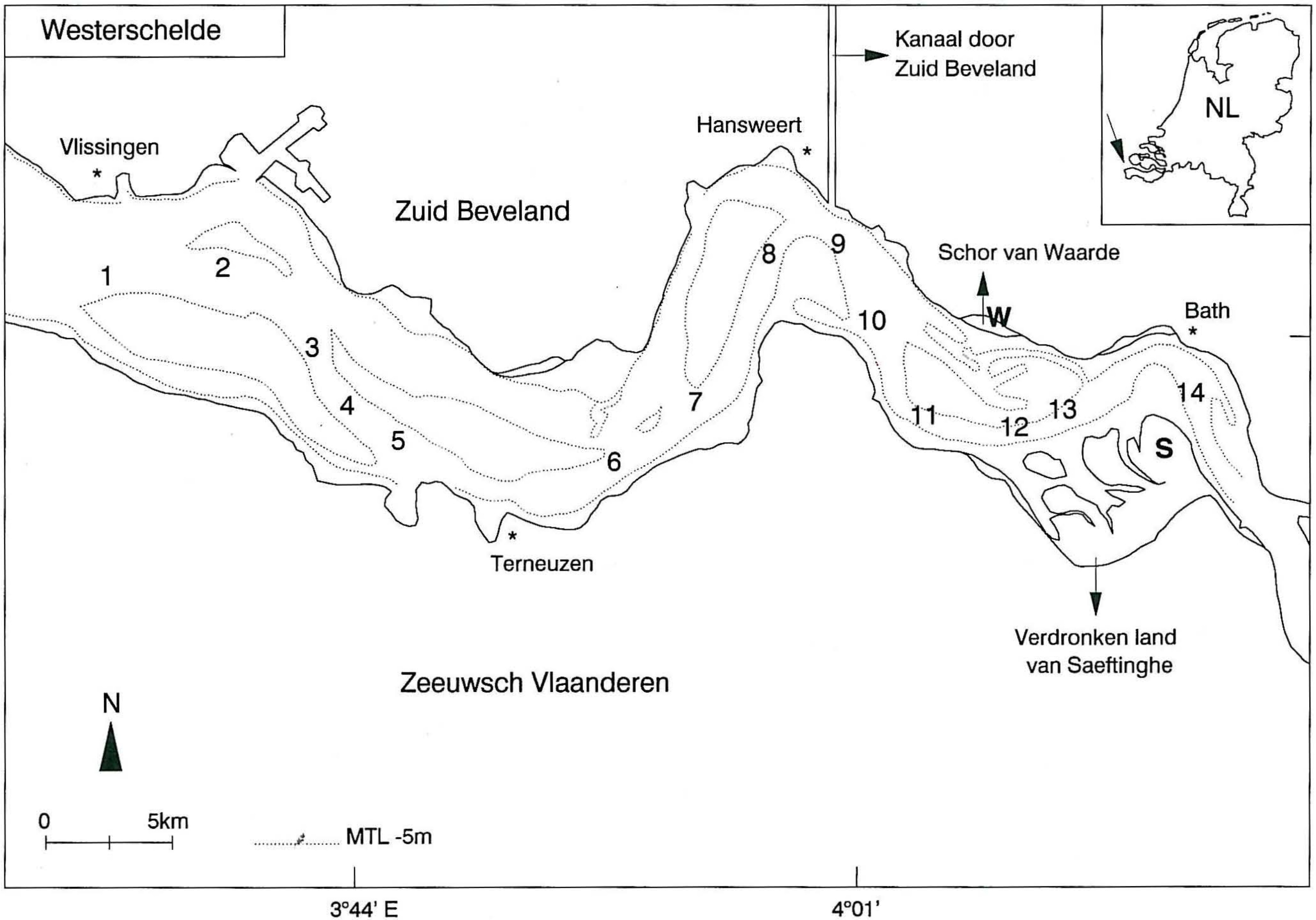


Fig. 2 : Map of the Weserschelde with the subtidal (1 to 14) and intertidal (W and S) sampling localities.

sed in Van Eck *et al.* (1991) and Heip (1988, 1989). Between April 1990 to April 1991 thirteen surveys were conducted. Each survey comprised 14 stations along the salinity gradient. On 3 occasions (March, April and May 1991) 5 additional samples were taken upstream from Bath to the city of Antwerp. All samples were taken in the subtidal channels. Where possible, the MTL - 10 m isobath was followed. Besides the subtidal surveys, monthly samples were taken at two intertidal stations in the salt marshes of Saeftinghe and Waarde (S and W in Fig. 2) from March 1990 to November 1990. The salt marsh of Waarde (107 ha) is a long-drawn marsh situated on the right bank of the estuary. It is drained by one major creek which runs parallel to the main channel of the estuary. The salt marsh of Saeftinghe (2 760 ha), situated on the left bank north of the harbour of Antwerp, is one of the largest of western Europe. It is drained by several large creeks which run perpendicular to the main estuarine channel. An overview of all sampling dates is presented in Table I.

TABLE I

Sampling dates for the different subareas (S is the salt marsh of Saeftinghe, W the salt marsh of Waarde).

Voordelta	Westerschelde	Salt marshes
10-08-1988	24-04-1990	15-03-1990 S
20-09-1988	21-05-1990	23-03-1990 W
15-11-1988	20-06-1990	05-04-1990 W
01-12-1988	26-07-1990	11-04-1990 S
16-01-1989	23-08-1990	22-04-1990 W
13-02-1989	29-09-1990	10-05-1990 S
17-03-1989	24-10-1990	11-06-1990 S
11-04-1989	27-11-1990	20-06-1990 W
10-05-1989	12-12-1990	03-07-1990 W
08-06-1989	21-01-1991	09-07-1990 S
26-06-1989	22-02-1991	08-08-1990 S
	18-03-1991	17-08-1990 W
	24-04-1991	10-10-1990 S
		15-10-1990 W
		05-11-1990 S
		30-11-1990 W

All subtidal samples were taken during daytime when hyperbenthic mysids are known to concentrate near the bottom. The samples were collected with a hyperbenthic sledge (Hamerlynck & Mees, 1991) which consists of a heavy metal frame equipped with two nets one above the other. The sledge is one meter wide. Both nets are 4 m long and have a mesh size of 2*2 mm in the first 3 m and 1*1 mm in the last 1 m. The contents of both nets were pooled for this study. The total area of the nets' mouth is 0.8 m^2 and it samples the hyperbenthal from 20 to 100 cm above the bottom. The sampler was towed for approximately 1 000 m (radar readings from fixed points) at an average ship speed of 4.5 knots relative to the bottom. The total area sampled was 1 000 m^2. Trawling was always done with the tide. Thus, the maximal amount of water filtered in one trawl was 800 m^3.

The salt-marsh samples were taken passively with a fyke net modified after McIvor & Odum (1986). The net is 5 m long with a 1*1 mm mesh and has a weir at the end. The mouth area of the net is 1*1 m. It was mounted on an iron frame and two heavy weights were attached at the lower end in order to keep the frame on the bottom of the creek. Ropes attached to the frame prevented lateral movement of the gear. The net was installed in the creek at low water, its mouth facing the current. Sampling covered a whole tidal cycle, the orientation of the gear evidently being changed at high tide. The net was emptied every 1 hour. Simultaneous measurements (every 15') of water height and current velocity in the creek allowed calculation of the volume of water filtered by the net.

During sampling temperature, salinity and dissolved oxygen content of the water were measured near the bottom.

The samples were preserved in a buffered formaldehyde solution, 7 % final concentration. In the laboratory all mysids and euphausiids were sorted out, identified to species level and counted. Special attention was payed to the presence of juvenile animals in the samples. These are defined as animals with no distinguishable secondary sexual characteristics. In female mysids a marsupium (or at least the oostegites) are visible and males are characterized by elongated fourth pleopods and a lobus masculinus between the flagellae of the antennal peduncle. The identification keys of Tattersall & Tattersall (1951) and Mauchline (1984) were used for mysids and euphausiids, respectively.

The reported densities in each station are the mean number of individuals per sample taken in that station (N/1 000 m^2), averaged over the whole study period. Densities of the intertidal samples are numbers per 1 000 m^3 of water filtered through the net.

The temporal patterns in the densities of the mysid and euphausiid populations are presented as the variation of average densities over all stations per subarea (Voordelta, Westerschelde) per sampling campaign. In order to describe the migrations and seasonal patterns in the Westerschelde, the main channel of the estuary is divided into a western and eastern part on the basis of community analyses in previous work (Mees & Hamerlynck, 1992 ; Mees *et al.*, in press). The marine part of the estuary (west) comprises the 8 downstream stations and the brackish part (east) comprises stations 10 to 14. Station 9 represents a transitional situation between the two communities and was eliminated for the purpose of this analysis. The seasonal variations in abundance in the salt marshes of Waarde and Saeftinghe are also presented separately.

Other faunal components of the hyperbenthos included amphipods, larval decapods, fish eggs, larval and postlarval fish, isopods, cumaceans, chaetognaths and a variety of other, less abundant groups. For full species lists we refer to Hamerlynck & Mees (1991) and Mees *et al.* (in press).

RESULTS

In total only eight species of mysid and one euphausiid were recorded (Tabl. II). Total mysid densities often exceeded 5 000 and 50 000 individuals per sample in the Voordelta and the Westerschelde, respectively. The Euphausiid *Nyctiphanes couchi* was only recorded in the Voordelta and always in low numbers with a maximum of 12 individuals per sample.

Most mysid species occur in both subareas, though not necessarily throughout the year. *Siriella armata* is restricted to the Voordelta. *Neomysis integer* and *Acanthomysis longicornis* were only recorded in the estuary, though for the latter species this concerns a single record (twelve specimens) in the mouth of the estuary.

TABLE II

Mysid and euphausiid species found in the Voordelta (V) and in the brackish (WB) and marine (WM) parts of the Westerschelde estuary and in the tidal creeks of the salt marshes (S). Capital letters indicate main distribution subarea.

Mysidacea	
Siriella armata (Milne-Edwards, 1837)	V
Gastrosaccus spinifer (Göes, 1864)	V, WM (wb)
Schistomysis spiritus (Norman, 1860)	V, WM (wb, s)
Schistomysis kervillei (Sars, 1885)	V, WM (wb, s)
Praunus flexuosus (Müller, 1776)	WB, S (v, wm)
Mesopodopsis slabberi (van Beneden, 1861)	V, WM,WB, S
Neomysis integer (Leach, 1814)	WB, S
Acanthomysis longicornis (Milne-Edwards, 1837)	WM
Euphausiacea	
Nyctiphanes couchi Bell, 1853	V

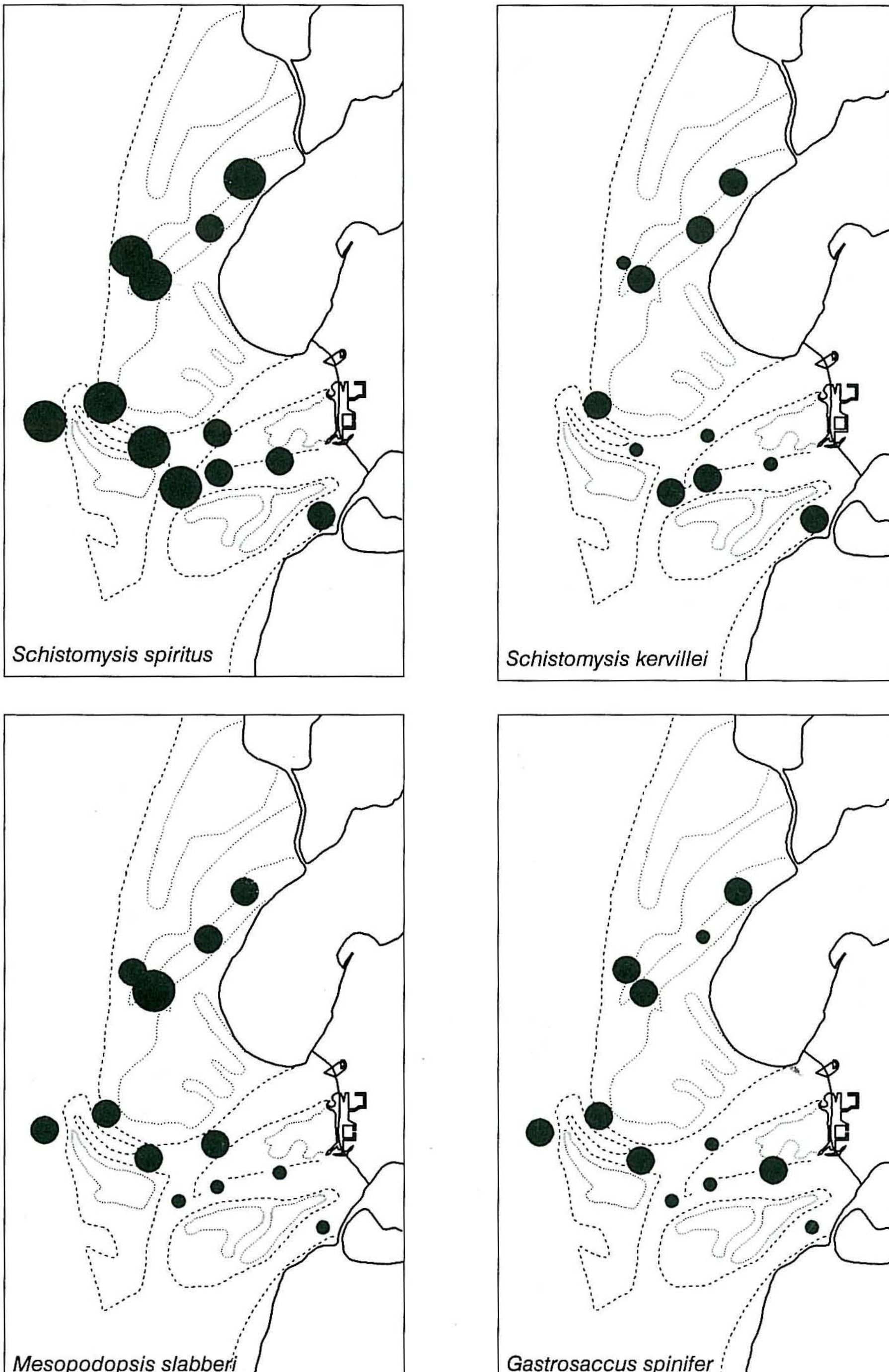
Spatial distribution

The geographical distribution and abundance of all mysid species and the single euphausiid are presented separately for the Voordelta and the Westerschelde (Figs. 3 & 4).

Voordelta

In the Voordelta (Fig. 3), average densities are never higher than 1 000 individuals. *Schistomysis spiritus* is the most abundant species in the area, followed by *Schistomysis kervillei, Mesopodopsis slabberi* and *Gastrosaccus spinifer*. The four species have overlapping geographical distributions. Densities are on average higher in the more sheltered area (see Louters *et al.*, 1991) of the ebb-tidal delta of the Grevelingen, and lower in the more dynamic ebb tidal delta of the Oosterschelde. The Banjaard stations are characterized by intermediate densities and are dominated by *S. spiritus*. *S. kervillei* is never found in the most seaward Banjaard stations.

Siriella armata and *Praunus flexuosus* are both large, shallow water species (Tattersall & Tattersall, 1951). They occur in low densities in the more inshore stations of the Voordelta, never in the Banjaard area. *Nyctiphanes couchi*, the euphausiid, is restricted to the marine waters of the Voordelta and is most common in the more seaward Banjaard stations.


Schistomysis spiritus
Schistomysis kervillei
Mesopodopsis slabberi
Gastrosaccus spinifer

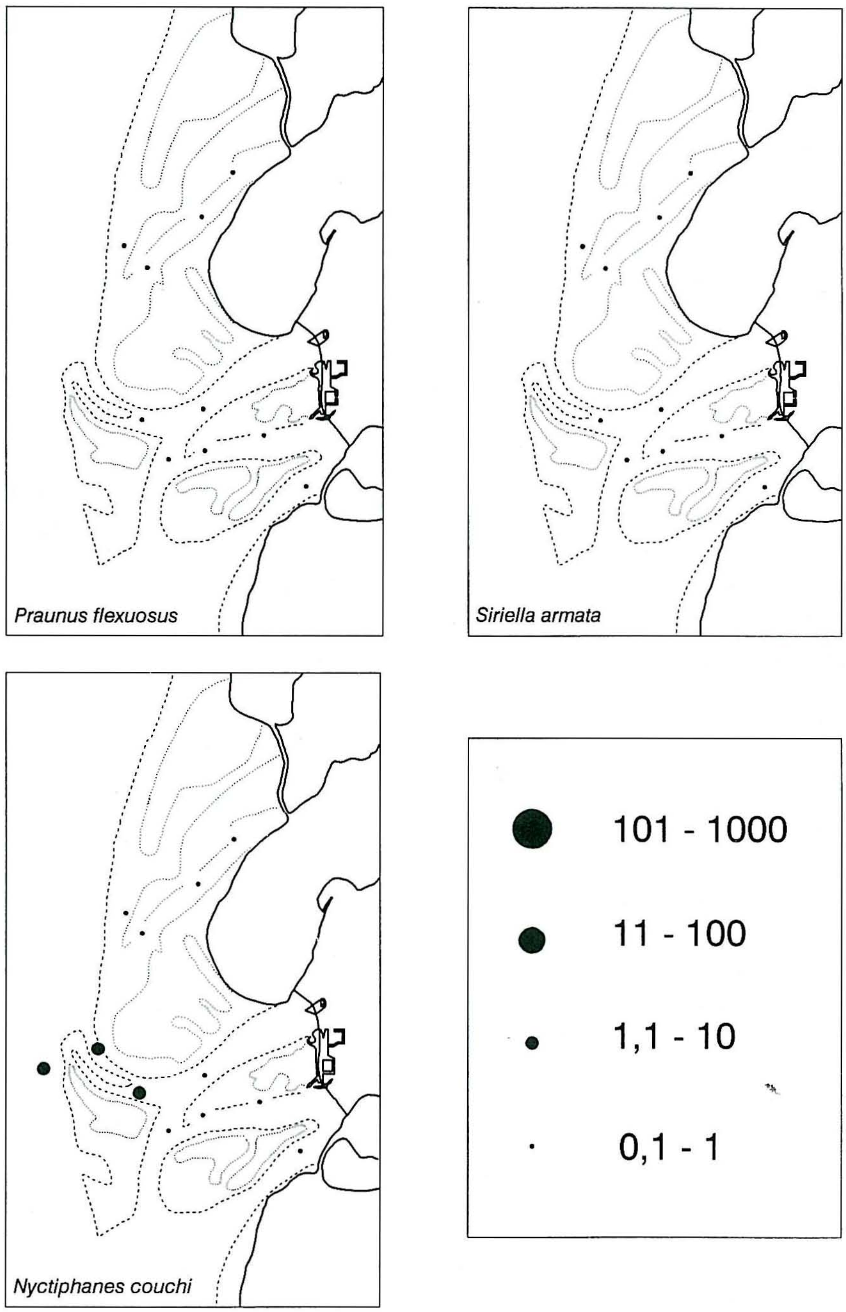


Fig. 3 : Distribution of all species caught in the Voordelta. Densities are yearly averages of the numbers of individuals caught per trawl (N/1 000 m²).

Westerschelde

In the Westerschelde, the two most abundant mysid species are *Neomysis integer* and *Mesopodopsis slabberi*. Both species reach average densities of more than 1 000 individuals in the upstream stations (Fig. 4). *Neomysis integer* is confined to the brackish zone of the estuary. The species is recorded in salinities ranging from 25 to 8 g/l and is very abundant in the main channel as well as in both salt marshes. It was never caught downstream from station 6, nor in the Voordelta. The lacustrine limit of the population lies a few kilometres upstream of station 14 as exemplified by the results of the campaign from April 1991 (Fig. 5). This result is typical for all three surveys conducted upstream of the Dutch-Belgian border : a very rapid decline in abundance where oxygen saturation becomes less than 40 %.

Mesopodopsis slabberi is common throughout the estuary.

As for *N. integer*, densities are highest in the brackish part, with the upstream limit defined by the oxygen depletion zone. In the western, marine part of the estuary the species is generally more abundant than in the Voordelta.

Both *Schistomysis* species also penetrate into the estuary but they were never found at the innermost stations. In the marine part of the estuary densities of *S. kervillei* are comparable to those in the Voordelta. It is the only common mysid of the estuary which was never found in the salt marshes. *S. spiritus* is far less abundant in the Westerschelde than in the Voordelta and seems to be the more marine species of the two. It enters the saltmarshes only occasionally.

Gastrosaccus spinifer occurs in higher densities in the downstream stations of the Westerschelde than in the Voordelta. Densities decrease towards the upstream part. This species has only rarely been caught in the salt marsh of Saeftinghe, never in the salt marsh of Waarde.

Praunus flexuosus is a shore species which is common in brackish waters and in tidal zones around the coasts (Tattersall & Tattersall, 1951). It has a clear preference for the salt marsh areas (especially the salt marsh of Waarde). In the main channel of the estuary, it is only abundant in the 6 most brackish stations.

Acanthomysis longicornis is a rare occurrence in the area. The only record is a single catch of twelve individuals at station 2 in October 1990.

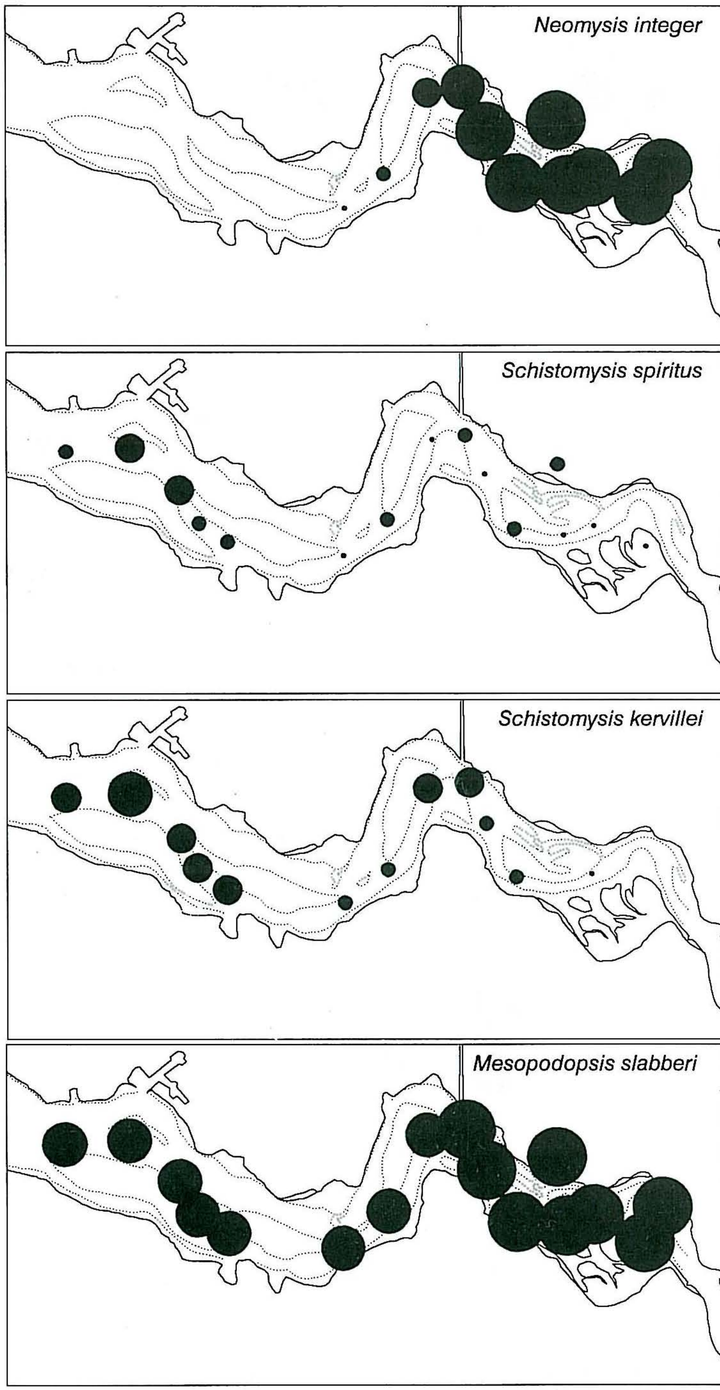
Temporal patterns

Marked seasonal variations are noted in the catches of the regularly occurring species.

Voordelta

In the Voordelta (Fig. 6), *Schistomysis spiritus, Mesopodopsis slabberi* and *Schistomysis kervillei* have two clear peaks in abundance : one in autumn and one in spring. These maxima coincide with periods of higher reproductive activity, with a lot of juveniles recruiting into the catch.

In the two former species there is a strong peak in abundance during spring (March-April) and a smaller one in autumn (September-November). For *S. kervillei* the autumn


Neomysis integer
Schistomysis spiritus
Schistomysis kervillei
Mesopodopsis slabberi

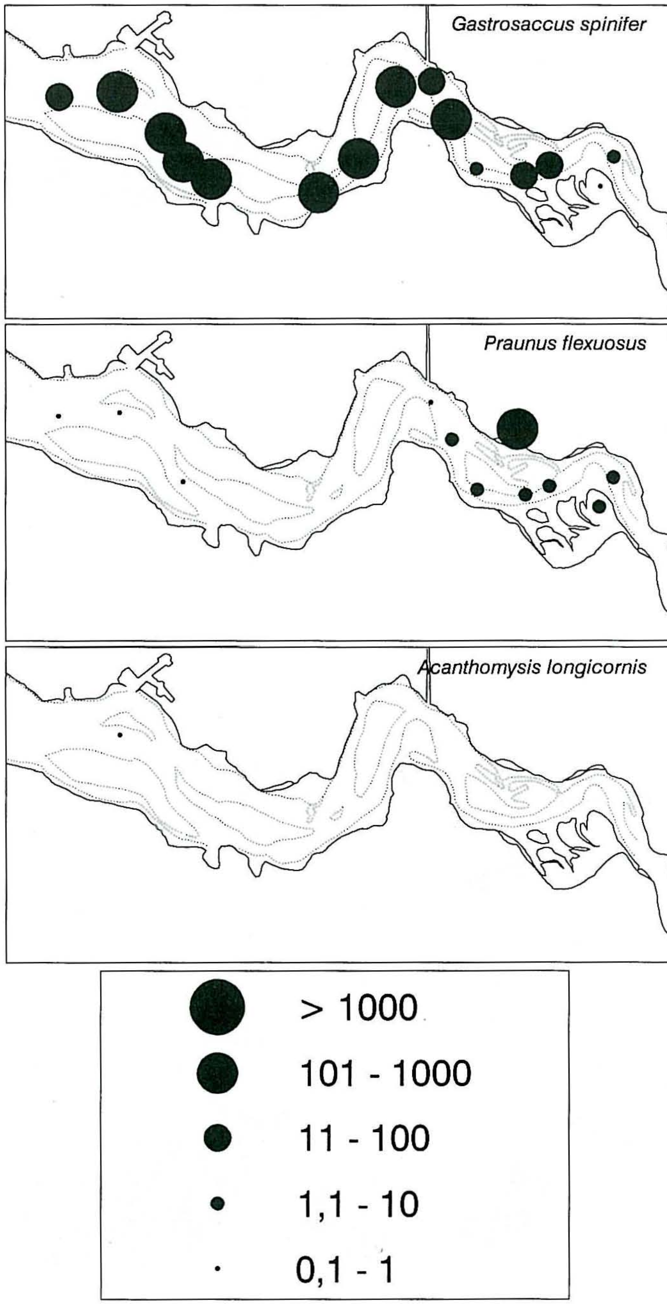


Fig. 4 : Distribution of all species caught in the Westerschelde and the salt marshes. Densities are yearly averages of the numbers of individuals caught per trawl (N/1 000 m²) for the sledge samples and N/1 000 m³ for the salt marsh samples.

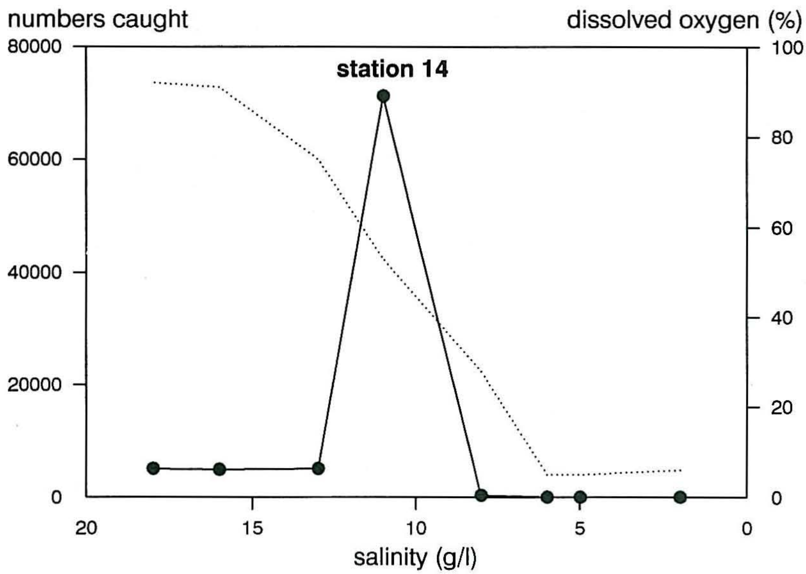


Fig. 5 : Densities of *Neomysis integer* along the salinity gradient from station 11 upto Antwerp in April 1991. Dissolved oxygen concentration is presented by the dotted line.

peak is observed somewhat later (November) and it is more pronounced than the spring peak. For all three species lowest numbers were found in winter (January-February) and in summer (June-August).

Gastrosaccus spinifer shows a more erratic seasonal pattern. This is a burrowing species (Mauchline, 1980) and catches are probably influenced by many factors such as wind, wave action, sediment characteristics, etc. Still, spring and autumn reproduction periods were observed and the same winter and summer minima as for the other species were evident.

Siriella armata also shows a bimodal abundance pattern. A small autumn maximum is observed in September. Densities are low in November and December, but increase again from January onwards to reach a spring maximum in March. The species was not recorded in the area from June through August. Neither of the two small abundance peaks were linked to recruitment of juveniles. Throughout the study period catches consisted solely of adults.

Praunus flexuosus (Fig. 6) and *Nyctiphanes couchi* (Fig. 7) are the only species which have maximal abundances during the winter months : *P. flexuosus* is only caught in late autumn and winter, *N. couchi* is present in the area from January to early June with peak densities from February to April.

Westerschelde

Schistomysis spiritus (Fig. 8) seems to be a typically marine species. It is absent from the estuary from late spring (June) until autumn (September). It enters the marine part of the

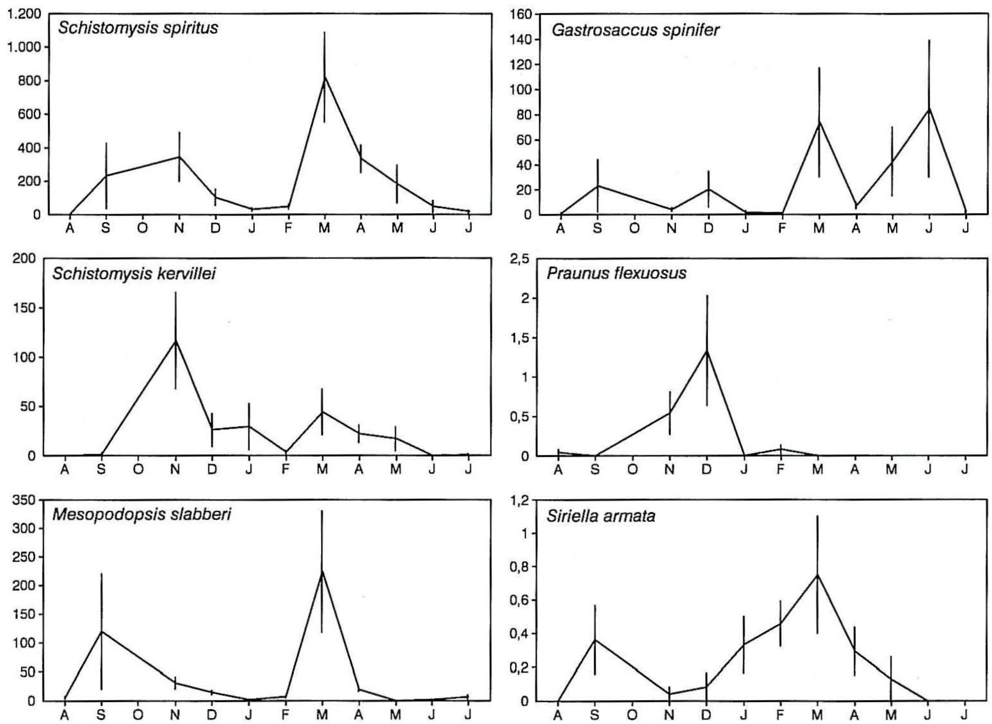


Fig. 6 : Seasonal variation of the number of individuals for the mysid species in the Voordelta (with standard errors). Densities are numbers caught per trawl averaged over all stations per sampling date (N/1 000 m²).

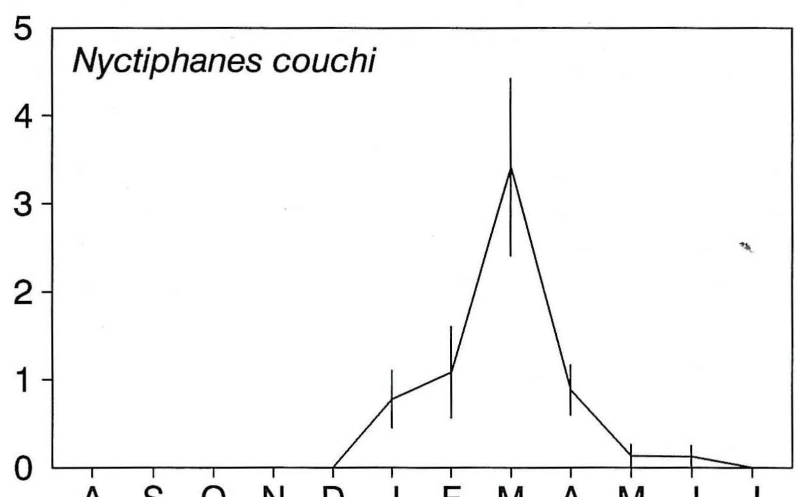


Fig. 7 : Seasonal variation of the number of individuals of *Nyctiphanes couchi* in the Voordelta, with standard errors.

estuary in low numbers in late autumn and winter. Here, the species reaches maximal abundance in spring (March to May, with a peak in April). At the time of this spring peak a small number of *S. spiritus* penetrate into the brackish part of the estuary and even enter the salt marshes. In the salt marsh of Waarde a small reproductive peak was recorded : all animals caught in April were juveniles.

Schistomysis kervillei and *Gastrosaccus spinifer* (not figured) are present in the western part of the estuary throughout the year. Average numbers are generally lower than 100 individuals per 1 000 m^2. *S. kervillei* is most abundant from November through April, with peak abundances of 650 individuals per 1 000 m^2 in January and early March. The *G. spinifer* population shows reproductive peaks in the marine part of the estuary in March and April (maximum of 100 individuals per 1 000 m^2 in April) and again from July through September (maximum of 450 individuals per 1 000 m^2 in August). At the time of peak abundance a small part of both populations also migrates to the brackish stations (densities never higher than 10 and 50 individuals per 1 000 m^2 for *S. kervillei* and *G. spinifer*, respectively).

Praunus flexuosus (Fig. 8) is only observed in the marine part of the estuary (and in the Voordelta) in late autumn, winter and early spring (October through March). During winter (January to early March) it seemed to be absent from the eastern part of the estuary. Its occurrence in the salt marshes is restricted to certain periods of the year : in spring (April to June), an important reproductive peak is observed in the saltmarsh of Waarde, followed by a less intense peak in the larger saltmarsh of Saeftinghe during the summer months (June to August). After reproduction the adults seem to migrate to the main channel of the estuary where the species is most abundant during autumn. Juveniles were only rarely observed in the upstream subtidal stations.

Mesopodopsis slabberi (Fig. 8) is virtually absent from the estuary in winter : from November through February it is only present in low numbers in the downstream stations. It enters the marine part of the estuary in important numbers in early spring where it remains abundant throughout summer and autumn. The abundance of *M. slabberi* resembles the two-peaked pattern observed in the Voordelta : a spring maximum (March) and an extended summer-autumn maximum (June-October). In late spring, the bulk of the population moves into the eastern part of the estuary. Migration into the eastern part is completed by August when very high densities are observed in the subtidal stations of the main channel. *M. slabberi* makes extensive use of the saltmarshes only in autumn : maximal densities recorded were of 176 individuals per m^3 (mainly juveniles) in October in Saeftinghe. By November the species has left the brackish waters.

Neomysis integer (Fig. 9) is confined to the brackish part of the estuary. Numbers are high throughout the year. Three maxima in abundance are observed, all of which correspond to reproductive peaks : one in spring (March-April), a large one in summer (July-August) and one in autumn (October-November). Details on the population biology of this species will be published elsewhere (Mees *et al.*, submitted). The species also utilises the salt marshes (mainly the salt marsh of Waarde in spring and the salt marsh of Saeftinghe in

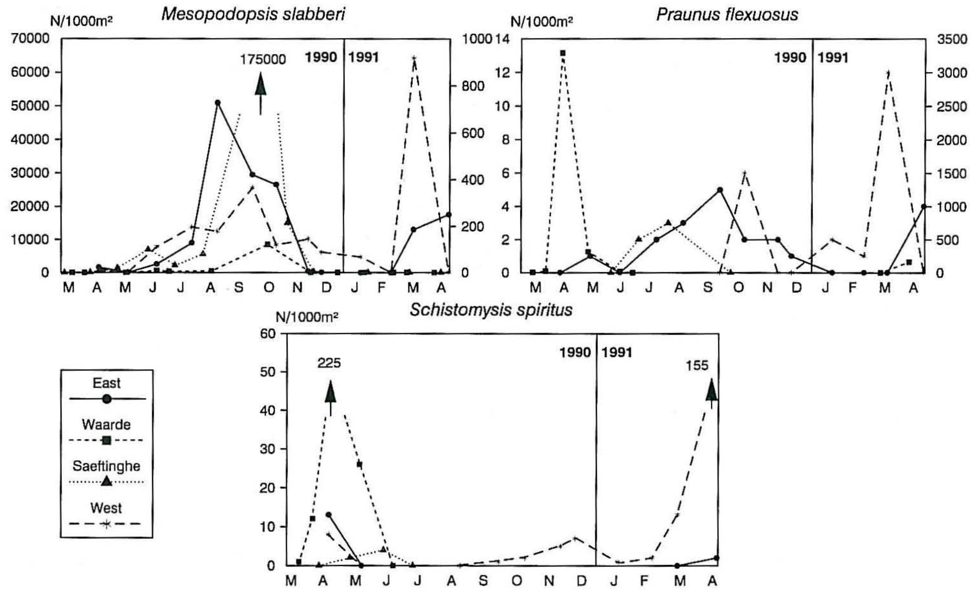


Fig. 8 : Seasonal variation of the number of individuals for the mysid species in the Westerschelde. Densities are numbers caught per trawl averaged over all stations per sampling date (N/1 000 m² for the subtidal samples and N/1 000 m³ for the salt marshes). Note *Mesopodopsis slabberi* West and *Praunus flexuosus* Waarde follow the right Y-axis.

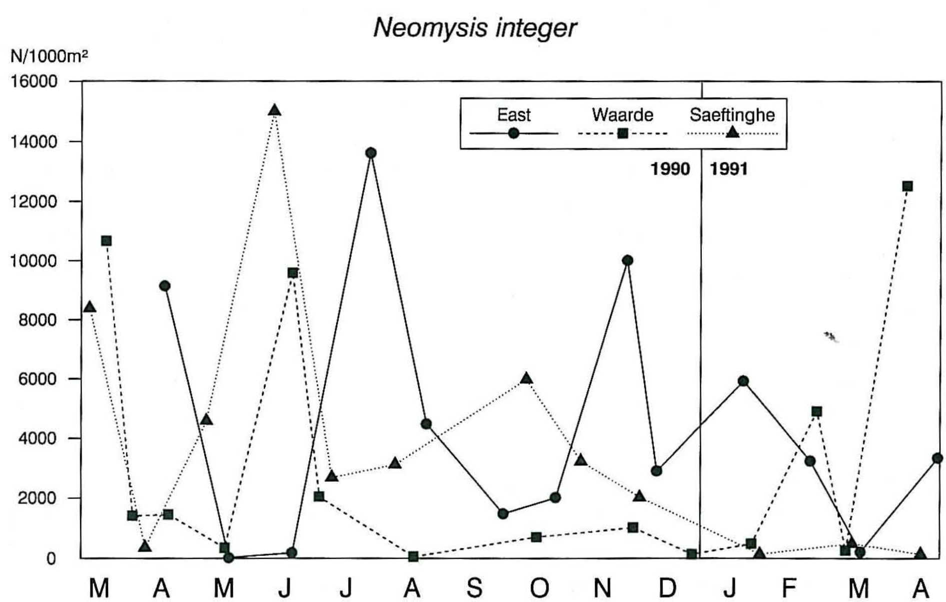


Fig. 9 : Seasonal variation of the number of individuals of *Neomysis integer* in the different subareas of the Westerschelde.

summer and autumn), where the density maxima are always earlier than in the main estuary. The data suggest that the animals enter the shallow, sheltered marshes for reproduction, as the young are found earlier here than in the main estuarine channels.

DISCUSSION

Most of the information available on the mysid fauna of the Delta area comes from the bycatch in zooplankton studies (e.g. De Pauw, 1975) or from macrobenthos samples taken with grabs (e.g. Wolff, 1973). It is therefore not surprising that new species are found and that densities of the common species were previously underestimated. The mysid *Acanthomysis longicornis* and the euphausiid *Nyctiphanes couchi* are new to the Delta region. The former species is new to the Dutch fauna. All other species are found to be far more abundant and widespread in the area than previously reported.

Euphausiids

Nyctiphanes couchi is the only euphausiid species encountered in the study area. It is the only euphausiid common in the southern North Sea. The species is restricted to temperate latitudes of the northeastern Atlantic. It is present in the North Sea, around Britain, southwards to the Bay of Biscay and northwest Africa and in the Mediterranean (Mauchline, 1984). It is thought to be indicative for the inflow of Atlantic water through the Channel (Van der Baan & Holthuis, 1969). All euphausiids are strictly marine organisms which do not occur in brackish or fresh waters (Mauchline, 1984). They do not occur commonly in regions shallower than about 100 m. Consequently, they live at some distance from the shore. Euphausiids are not restricted to the hyperbenthal. They have a pelagic way of life, probably colonising the whole water column. They are known to form seasonal breeding aggregations in the late winter to facilitate mating. Those that survive the breeding season disperse. This dispersal often involves shallower regions than were occupied by the breeding aggregations. *N. couchi* is absent from the southern North Sea from May to August (Tesch, 1911 ; Glover, 1952). Our results compare well to these general remarks and to the observations of Van der Baan & Holthuis (1969) in the surface waters near the Texel light ship : numbers are never high and greatest density is recorded in winter and early spring in the most offshore stations.

Mysids

General remarks

As can be seen from Figure 6 the variability in the densities reported for the mysid species in the Voordelta are rather high. This is not the case for the variability in the Westerschelde, and especially in the eastern part. This is probably due to the swarming behaviour of most of these species which seems to be far less pronounced in estuarine habitats.

Spatial patterns of the individual species

Only 12 individuals of *A. longicornis* were caught. These were all taken in one haul, suggesting that this species too forms aggregations. Mauchline (1971c) thought the species to be a possible exception to this widespread social behaviour.

Schistomysis spiritus was already reported by Hoek (1886) from the Voordelta in the mouth of the Oosterschelde estuary. Tesch (1911) reported it from several locations along the Dutch coast. It is a euryhaline, littoral and neritic species (Tattersall & Tattersall, 1951) which occurs from the west coast of Norway to the west coast of France.

Schistomysis kervillei was found by Hoek (1886) in the Oosterschelde and Tesch (1911) reported it from various places in the Delta area. It is also a euryhaline species (Tattersall & Tattersall, 1951) distributed from the British Isles to southern France. It is often recorded from estuaries (e.g. Sorbe, 1981 ; Williams & Collins, 1984). Another species of the same genus, *Schistomysis ornata*, was previously recorded from the Westerschelde by De Pauw (1975). It was not found in the present study. *S. ornata* generally lives in deeper waters from 30 to 100 m and only in fully marine conditions (Mauchline, 1970 ; Fossa & Brattegard, 1990 ; Sorbe, 1991). Since *S. ornata* and *S. kervillei* are morphologically quite similar it is suggested the individuals found by De Pauw belong to the latter species.

Hoek (1886) reports *Praunus flexuosus* as the most common mysid species of the Dutch fauna, being especially abundant in the Westerschelde and Oosterschelde estuaries. Hoek's (1886) observation probably relates to the conspicuousness of the species due to its large size and its habit to aggregate in dense shoals near the low water mark. The same author found only 2 individuals of *Neomysis integer* in the brackish part of the Westerschelde estuary, though the present study reveals it to be much more abundant than *Praunus flexuosus*. Both species are also very abundant in the Delta Area's saline and brackish lakes such as Lake Grevelingen (Platenkamp, 1978 ; Fortuin, 1980) and Lake Veere (Borghouts, 1978).

Mesopodopsis slabberi was reported by Hoek (1886) from the Oosterschelde. Tesch (1910) reports it to be common in the Delta area in salinities ranging from 2.6 to 30 g/l. It occurs from Norway to western Africa. It is also found in the Mediterranean and the Black Sea. Records from southern and western Africa are thought to concern different species (Wittmann, 1992).

The only *Gastrosaccus* species found during the study period was *G. spinifer.* It is common in the whole southern North Sea (Tesch, 1910). It is distributed from the west coast of Norway south to West Africa and the Black Sea. De Pauw (1975) found it in the western part of the Westerschelde. This is the most common mysid species in grab samples from the Delta area and has a preference for sandy sediments (Wolff, 1973). This explains why the species is more variable in its distribution than other species (see also Williams & Collins, 1984). *Gastrosaccus sanctus* was not recorded in this study although it is reported to be common in the Voordelta as well as in the marine part of the westerschelde (Hoek, 1886). This species essentially lives in shallower waters of less than a few metres depth (Tattersall & Tattersall, 1951), a stratum which was not covered in this study.

Neomysis integer was never caught in the Voordelta nor in the marine part of the Westerschelde, suggesting an efficient retention mechanism. Tesch (1911) reports it to be common and characteristic for low salinity waters in the Delta area. Upstream of the Dutch-Belgian border, which nearly coincides with the 10 g/l isohaline, there is a rapid extinction of all hyperbenthic life (Fig. 5). The high input of organic matter in this part of the estuary results in an intense bacterial activity which rapidly exhausts the dissolved oxygen. The location of this zone of oxygen depletion (oxygen saturation values lower than 40 %) is stable in space and time (Mees, unpubl. data ; Van Eck *et al.*, 1991). In normal situations estuarine populations of *Mesopodopsis slabberi* and *Neomysis integer* are present upto the 5 g/l isohaline and nearly freshwater, respectively. Wolff (1973) found *N. integer* elsewhere in the Delta area in nearly fresh water. De Pauw (1975) already pointed to the absence of these species from lower salinity waters (with the same upstream distribution limit at Bath) and suggested a relation to the heavy pollution in the area. It is interesting to note that in the early 1950's both *M. slabberi* and *N. integer* still occurred some 20 km upstream of Bath (Leloup & Konietzko, 1956). The data presented here are the first evidence that dissolved oxygen concentrations can act as primary controlling factors in the distribution and behaviour of a mysid species.

Temporal patterns

The seasonal maxima and minima in the observed population densities can be real or apparent (Mauchline, 1971c). Real maxima are those caused by increases in the size of the population owing to active breeding and production of young. Apparent seasonal maxima can be caused by a disaggregated population aggregating in an area so that they are sampled more effectively than previously or by migration into the area from elsewhere. In the Voordelta, *Schistomysis spiritus*, *Schistomysis kervillei*, *Mesopodopsis slabberi*, and *Gastrosaccus spinifer* have two periods of real population increase which largely explain the spring and autumn maxima. The low numbers in winter and summer can be due to natural mortality and/or to active migration either to deeper or to shallower waters and/or to active migration into the estuaries and marine bays bordering on the area.

The observations of *Praunus flexuosus* in the Voordelta and the marine part of the Westerschelde are probably a 'washout' phenomenon linked to the winter state of the river Schelde. The species' retention mechanisms seem less strong than in *N. integer*.

The lower numbers of mysids found in winter are often attributed to a migration from shallow coastal to deeper offshore waters in winter (e.g. Hesthagen, 1973). Van der Baan & Holthuis (1971) already suggested this behaviour for *Gastrosaccus spinifer*, *Schistomysis kervillei* and *Mesopodopsis slabberi* since these species displayed winter maxima in their offshore sampling station. The same migration pattern probably applies for *Schistomysis spiritus*. Populations of *S. spiritus* tend to occur deeper during winter (Mauchline, 1967) and Van der Baan & Holthuis (1971) also observed a winter peak. For all these species, the winter maximum is probably a combination of natural mortality and migration to deeper waters.

The summer minima in the Voordelta are more difficult to explain, but are possibly also partly real and partly apparent. Predation may be an important factor in determining the seasonal abundance of species. The sudden decrease of nearly all mysid populations in early summer in the Voordelta is preceded by a bloom of the ctenophore *Pleurobrachia pileus* and the cnidarian *Aurelia aurita*. Other potential predators in the hyperbenthal include chaetognaths and demersal fish. In early summer the 0-group gadoids *Merlangius merlangus* and *Trisopterus luscus* are strongly dependent on mysids for their food supply (Hamerlynck & Hostens, 1993). Interestingly in the adjacent Belgian coastal area the goby *Pomatoschistus lozanoi,* which is very abundant in the area (Hamerlynck *et al.*, in press) and which is virtually exclusively dependent on mysids for most of the year (Hamerlynck *et al.*, 1990), switches to feeding on to macrobenthic animals in August. As these fish also make extensive use of intertidal areas this suggests there are truly very few mysids available in the coastal area at that time. Therefore the summer minimum of most species is unlikely to be explained by a mass migration into shallower areas. An exception may be *Mesopodopsis slabberi* whose summer decline in the Voordelta is accompanied by a great increase of the population in the Westerschelde estuary.

The seasonal patterns of population maxima and minima in the marine part of the Westerschelde are analogous to those observed for the Voordelta, though the autumn peak tends to occur earlier. This is conform to the findings of Mauchline (1984) who observed that estuarine and littoral species tend to occur maximally during the warmer months of the year but if they occur in offshore environments the seasonal maxima of occurrence tend to occur in the autumn and winter.

The highly seasonal pattern of *N. integer* in the brackish part of the estuary parallels that of other European populations (e.g. Mauchline, 1971a). *P. flexuosus* is a shallow water, littoral species (Tattersall & Tattersall, 1951 ; Mauchline, 1971b) which agrees with the higher densities found in the intertidal samples. Its apparent absence from the brackish waters in the coldest months may reflect the lack of salt marsh samples from that period. It is well possible that the population overwinters in the salt marshes. The summer-autumn maximum of *Mesopodopsis slabberi* in the eastern part of the estuary is a combined effect of active migration and reproduction. A population decrease caused by a combination of natural mortality and active migration out of the brackish waters probably explains the winter minimum.

The estuarine populations of *Neomysis integer*, *Mesopodopsis slabberi*, *Praunus flexuosus*, and - to a lesser extent - *Schistomysis spiritus* (only in the salt marsh of Waarde) seem to utilise the salt marshes during periods of reproduction. Peak densities of the juveniles of these species are first observed in the intertidal samples. Only later do they migrate into the main channel.

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REFERENCES

Borghouts, C.H., 1978. Population structure and life-cycle of *Neomysis integer* (Leach) (Crustacea, Mysidacea) in two types of inland waters. *Verh. Internat. Verein. Limnol.*, Vol. 20 : 2561-2565.

Craeymeersch, J.A., O. Hamerlynck, K. Hostens, A. Vanreusel & M. Vincx, 1990. De ekologische ontwikkeling van de Voordelta. Deelrapport 1 : de huidige ekologische situatie van de Voordelta. Rijkswaterstaat Direktie Noordzee. 92 p.

De Pauw, C., 1975. Bijdrage tot de kennis van milieu en plankton in het Westerschelde-estuarium. Thesis University of Gent : 380 p.

Fortuin, A.W., 1980. Life history of *Praunus flexuosus* (Müller) (Crustacea, Mysidacea) in lake Grevelingen, 1981. *DIHO Progress Report* 1980 : 23-25.

Fossa, J.H. & T. Brattegard, 1990. Bathymetric distribution of Mysidacea in fjords of western Norway. *Mar. Ecol. Prog. Ser.*, Vol. 67 : 7-18.

Glover, R.S., 1952. Continuous zooplankton records : the Euphausiacea of the northeastern Atlantic and the North Sea, 1946-8. *Hull. Bull. mar. Ecol.*, Vol. 3 : 185-214.

Hamerlynck, O. & K. Hostens, 1993. Growth, feeding, production and consumption in O-group bib *Trisopterus luscus* L. and whiting *Merlangius merlangus* L. in a shallow coastal area of the SW Netherlands. ICES *J. mar. Sci.*, Vol. 50.

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 : Barnes, M. & Gibson, R. (eds.). Proceedings of the 24th EMBS. Aberdeen University Press : 183-190.

Hamerlynck, O., K. Hostens, R.V. Arellano, J. Mees & P.A. Van Damme, in press. The mobile epibenthic fauna of soft bottoms in the Dutch Delta (south-west Netherlands) : spatial structure. *Neth. J. Aquat. Ecol.*

Heip, C., 1988. Biota and abiotic environment in the Westerschelde estuary. *Hydrobiol. Bull.*, Vol. 22 : 31-34.

Heip, C., 1989. The ecology of the estuaries Rhine, Meuse and Scheldt in the Netherlands. In : Ross, J.D. (ed.) : Topics in Marine Biology. *Scient. Mar.*, Vol. 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.*, Vol. 26 : 333-342.

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

Hoek, P.P.C., 1886. Crustacea Neerlandica. *Tijdschr.* ned. dierk. Ver., Vol. 2 (1) : 93-105.

Kramp, P.L., 1913. Schizopoda. *Bull. trimest. Résult. Crois. périod. Cons. perm. int. Explor. Mer*, 1913 : 539-556.

Leloup, E. & B. Konietzko, 1956. Recherches biologiques sur les eaux saumâtres du Bas-Escaut. *Mém. Inst. r. Sci. nat. Belg.*, Vol. 132 : 1-100.

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.*, Vol. 7 : 635-652.

Mauchline, J., 1967. The biology of *Schistomysis spiritus* (Crustacea, Mysidacea). *J. Mar. Biol. Ass. U.K.*, Vol. 47 : 383-396.

Mauchline, J., 1970. The biology of *Schistomysis ornata* (Crustacea, Mysidacea). *J. Mar. Biol. Ass. U.K.*, Vol. 50 : 169-175.

Mauchline, J., 1971a. The biology of *Neomysis integer* (Crustacea, Mysidacea). *J. Mar. Biol. Ass. U.K.*, Vol. 51 : 347-354.

Mauchline, J., 1971b. The biology of *Praunus flexuosus* and *P. neglectus* (Crustacea, Mysidacea). *J. Mar. Biol. Ass. U.K.*, Vol. 51 : 641-652.

MAUCHLINE, J., 1971c. Seasonal occurrence of mysids (Crustacea) and evidence of social behaviour. *J. Mar. Biol. Ass. U.K*, Vol. 51 : 809-825.

MAUCHLINE, J., 1980. The biology of mysids and euphausiids. *Adv. Mar. Biol.*, Vol. 18 : 681 p.

MAUCHLINE, J., 1984. Euphausiid, stomatopod and leptostracan crustaceans. *Synopses of the British Fauna (New Series)*, n° 30 : 91 p.

McIVOR, C.C. & W.E. ODUM, 1986. The flume net : a quantitative method for sampling fishes and macrocrustaceans on tidal march surfaces. *Estuaries*, Vol. 9 : 219-224.

MEES, J., A. DEWICKE & O. HAMERLYNCK, in press. Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde. *Neth. J. Aquat. Ecol.*

MEES, J. & O. HAMERLYNCK, 1992. Spatial community structure of the winter hyperbenthos of the Schelde estuary, the Netherlands, and the adjacent coastal waters. *Neth. J. Sea Res.*, Vol. 29 : 357-370.

MEES, J., Z. ABDULKERIM & O. HAMERLYNCK, in press. Life history, growth and production of *Neomysis integer* (Leach, 1814) in the Westerschelde estuary (S.W. Netherlands).

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 : ELLIOT, M. & J.P. DUCROTOY (eds.) : Estuaries and Coasts-Spatial and Temporal intercomparisons, Olsen & Olsen Int. Symp. Series. Proc. ECSA 19^{th} symposium 1 : 221-230.

PLATENKAMP, G.A.J., 1983. Verspreiding, biomassa en groei van epi- en hyperbenthische macrocrustaceeën in het Grevelingen-meer. *DIHO student report*, D6 1983 : 94 p.

SOETAERT, K. & P. VAN RIJSWIJK, in press. Spatial and temporal patterns of the zooplankton in the Westerschelde estuary.

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

SORBE, J.-C., 1991. Biologia del misidaceo suprabentonico *Schistomysis ornata* (Sars, 1864) en la plataforma continental aquitana (suroeste de Francia). *Actas V Simp. Ibér. Estud. Bentos Mar.*, Vol. 1 : 273-298.

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

TESCH, J.J., 1911. Bijdragen tot de fauna der zuidelijke Noordzee. VI. Schizopoden, verzameld met de "Wodan". *Jaarboek Rijksinst. Onderz. Zee. Helder*, 1910 : 35-83.

VAN BENEDEN, P.J., 1860. Recherches sur les crustacés du littoral de Belgique. *Mém. Acad. R. Belg.*, Vol. 33.

VAN DER BAAN, S.M. & L.B. HOLTHUIS, 1969. On the occurrence of Euphausiacea in the surface plankton near the lightship "Texel" in the southern North Sea. *Neth. J. Sea Res.*, Vol. 4 : 364-371.

VAN DER BAAN, S.M. & L.B. HOLTHUIS, 1971. Seasonal occurrence of Mysidacea in the surface plankton of the Southern North Sea near the "Texel" lightship. *Neth. J. Sea Res.*, Vol. 5 : 227-239.

VAN ECK, G.T.M., 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*, Vol. 60 : 164-181.

VANREUSEL, A., 1990. Ecology of the free-living marine nematodes from the Voordelta (Southern Bight of the North Sea). I. Species composition and structure of the nematode communities. *Cah. Biol. Mar.*, Vol. 31 : 439-462.

VANREUSEL, A., 1991. Ecology of the free-living marine nematodes from the Voordelta (Southern Bight of the North Sea). II. Habitat preferences of the dominant species. *Nematologica*, Vol. 37 : 343-359.

WOLFF, W.J., 1973. The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse, and Scheldt. *Zool. Verh. Leiden*, Vol. 126.

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.*, Vol. 80 : 197-206.

WITTMANN, K.J., 1992. Morphogeographic variations in the genus *Mesopodopsis* Czerniavsky with description of 3 new species (Crustacea, Mysidacea). *Hydrobiologia*, Vol. 241 : 71-89.

ZIMMER, C., 1932. Ueber einige mysidaceen des Musée Royal d'histoire naturelle in Bruessel. *Bull. Mus. R. hist. nat. Belg.*, Vol. 8 (21) : 1-12.