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## **The hyperbenthos of shallow coastal waters and estuaries: community structure and biology of the dominant species**

**Het hyperbenthos van ondiepe kustgebieden en estuaria:  
gemeenschapsstructuur en biologie van de dominante soorten**

Jan Mees



Promotor: Prof. Dr. M. Vincx  
Copromotor: Dr. O. Hamerlynck

Verhandeling voorgelegd tot  
het behalen van de graad van  
Doctor in de Wetenschappen,  
Groep Biologie

Universiteit Gent  
Faculteit der Wetenschappen  
Vakgroep morfologie, systematiek en ecologie  
Instituut voor Dierkunde

Academiejaar 1993-1994

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*We see the ancient spirit of speculation revived and a desire manifestly shown to cut, rather than patiently to untie, the Gordian Knot.*

*Charles Lyell, 1833*

*Few honest passions are not based upon some valid perception of unity or some anomaly worthy of note.*

*Stephen Jay Gould, 1980*

*Dirigeons donc notre vue vers ce fluide qui couvre une si grande partie de la terre...  
Lacépède*

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## Voorwoord.

*This Dutch text is a translation of the English 'Preface' and 'Summary' presented on pages v to x.*

Het hyperbenthos is de fauna die in de onderste lagen van de waterkolom leeft, en nog afhankelijk is van de nabijheid van de bodem. Hyperbenthische gemeenschappen worden nu algemeen als normale componenten van kust- en estuariene ecosystemen beschouwd. Recent onderzoek heeft aangetoond dat het hyperbenthos hoge densiteiten bereikt. De rol van hyperbenthische organismen in het voedselweb is ook genoegzaam gekend: enerzijds vormen ze een belangrijke voedselbron voor talrijke vissoorten, anderzijds zijn het potentieel belangrijke predatoren van zooplankton en consumenten van detritus. Ondanks de erkenning van het belang in de energiedoorstroming van lagere naar hogere trofische niveaus, blijft het hyperbenthos onderbestudeerd. Zelfs in druk bemonsterde gebieden, waar andere componenten van het ecosysteem sinds lang grondig bestudeerd worden, is de basisinformatie over soortensamenstelling, densiteiten en biomassa's van het hyperbenthos tot op heden niet beschikbaar.

In deze thesis wordt het hyperbenthos van een ondiep kustgebied en enkele estuaria in detail beschreven. De meeste stalen werden genomen in het zogenaamde Delta gebied in het zuidwesten van Nederland (Zuidelijke Bocht van de Noordzee). De Voordelta en de Westerschelde werden grondig bestudeerd. Twee andere Europese estuaria werden éénmalig bemonsterd.

In een eerste hoofdstuk wordt een overzicht gegeven van alle literatuur die over het hyperbenthos verschenen is. Dit hoofdstuk wordt gevolgd door een aparte referentielijst, omdat de inhoud ervan sterk verschilt van die van de rest van de thesis. Hoofdstuk 2 geeft een beschrijving van de ruimtelijke en temporele patronen in de structuur van de hyperbenthische gemeenschap van de Voordelta, een ondiep kustgebied. In hoofdstuk 3 wordt het hyperbenthos van de Voordelta vergeleken met dat van een aanpalende mariene baai, de Oosterschelde, en dat van een echt estuarium in hetzelfde gebied, de Westerschelde. In hoofdstuk 4 worden dan de ruimtelijke en temporele patronen in het hyperbenthos van de Westerschelde in detail beschreven. Hoofdstuk 5 geeft een overzicht van de seizoensaliteit, densiteit en verspreiding van de dominante diergroep van het hyperbenthos in beide deelgebieden, namelijk de aasgarnalen (Mysidacea). In hoofdstuk 6 wordt het hyperbenthos van de Westerschelde vergeleken met dat van 2 andere estuaria: de Eems (Noord-Nederland) en de Gironde (Zuid-Frankrijk). Dit hoofdstuk wordt gevolgd door een kort addendum, waarin over het voorkomen van een grote soort zeepissebed, nieuw voor de Europese fauna, wordt gerapporteerd. In hoofdstuk 7 tenslotte, wordt de populatiedynamica van de belangrijkste estuariene soort, de aasgarnaal *Neomysis integer*, in detail beschreven. Ook dit hoofdstuk wordt gevolgd door een addendum, waarin enkele aberrante vormen van deze soort worden besproken. Na de referenties van hoofdstukken 2 tot 7 volgt een uitgebreide verzameling appendices. Hierin worden naast de regressies gebruikt

voor het berekenen van de biomassa's en een geïntegreerde soortenlijst, ook alle ruwe dichtheids- en biomassagegevens getabelleerd.

De meeste hoofdstukken van deze thesis zijn gepubliceerd in de internationale literatuur. Een nadeel van deze benadering is dat, door beperking van plaats in de tijdschriften, de resultaten van een aanzienlijk aantal analyses niet zijn afgebeeld. Ik heb dit trachten te compenseren door in sommige hoofdstukken bijkomende figuren in te lassen, en door de ruwe data van elk hoofdstuk op te nemen in de appendices.

Afgezien van enkele kleine veranderingen in de figuren, zijn *hoofdstukken 2 en 3* als dusdanig gepubliceerd:

*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.*

*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. 29: 357-370.*

Een deel van *hoofdstuk 4* is ook gepubliceerd (de analyses met de transecten van lente, zomer en winter) als

*Mees, J., A. Dewicke & O. Hamerlynck, 1993. Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde. Neth. J. Aquat. Ecol. 27: 359-376.*

maar dit hoofdstuk is aanzienlijk uitgebreid met jaarcycli van zowel het mariene als het brakwaterdeel van de Westerschelde.

*Hoofdstuk 5* is ook in zijn huidige vorm gepubliceerd. Een parallel artikel dat handelt over de Amphipoda en de Isopoda van dezelfde stalen werd niet in deze thesis opgenomen:

*Mees, J., A. Cattrijsse & O. Hamerlynck, 1993. Distribution and abundance of shallow-water hyperbenthic mysids (Crustacea, Mysidacea) and euphausiids (Crustacea, Euphausiacea) in the Voordelta and the Westerschelde, south-west Netherlands. Cah. Biol. Mar. 34: 165-186.*

*Cattrijsse, A., J. Mees & O. Hamerlynck, 1993. The hyperbenthic Amphipoda and Isopoda of the Voordelta and the Westerschelde estuary. Cah. Biol. Mar. 34: 187-200.*

*Hoofdstuk 6* is in druk in Hydrobiologia en het addendum is gepubliceerd in hetzelfde tijdschrift:

*Mees, J., N. Fockedey & O. Hamerlynck, in press. Comparative study of the hyperbenthos of three European estuaries. Hydrobiologia.*

*Mees, J. & N. Fockedey, 1993. First record of *Synidotea laevidorsalis* (Miers, 1881) (Crustacea: Isopoda) in Europe (Gironde estuary, France). Hydrobiologia 264: 61-63.*

**Hoofdstuk 7** verschijnt binnenkort in een gewijzigde vorm in Marine Ecology-Progress Series: in de thesis zijn 2 bijkomende figuren opgenomen.

*Mees, J., Z. Abdulkerim & O. Hamerlynck, 1994. Life history, growth and production of *Neomysis integer* (Leach, 1814) in the Westerschelde estuary (S.W. Netherlands). Mar. Ecol. Prog. Ser.: in press.*

## Preface.

The hyperbenthos is the fauna living in the lower layers of the watercolumn, close to the sediment. Hyperbenthic communities are now recognized as normal features of marine and estuarine ecosystems. In spite of recent reports of high densities, the well-known importance as food for fish, and its possible role in the energy fluxes from detritus and zooplankton to higher trophic levels, the hyperbenthos remains unstudied in vast geographical regions. Even in most areas close to old biological stations, where other ecosystem compartments have historically been intensely studied, basic data on species composition, density and biomass of the hyperbenthos are generally lacking.

This thesis presents a descriptive baseline study of the hyperbenthos in shallow coastal and estuarine areas. Sampling was mainly conducted in the Delta area in the southwest Netherlands (Southern Bight of the North Sea). The Voordelta area and the Westerschelde estuary were studied in detail. Point measurements in two other European estuaries, the Eems and the Gironde, were also performed.

In Chapter 1 all existing literature on hyperbenthos is summarized and reviewed. The chapter takes a separate reference list because its contents differ from the remainder of the thesis. In Chapter 2 spatial and temporal patterns in the structure of the hyperbenthic community of a shallow coastal area, the Dutch Voordelta, are described. In Chapter 3 the hyperbenthic community of the Voordelta is compared with that of an adjacent bay, the Oosterschelde, and that of a true estuary, the Westerschelde. In Chapter 4 the spatial and temporal patterns in the hyperbenthos of the Westerschelde are described in detail. Chapter 5 summarizes seasonality, density and distribution of the Mysidacea, the dominant components of the hyperbenthos in both subareas. In Chapter 6 the hyperbenthos of the Westerschelde is compared with that of two other estuaries: the Eems (North Netherlands) and the Gironde (South France). This chapter is followed by a short addendum reporting a large isopod species which is new for the European fauna. In Chapter 7 the population dynamics of the dominant estuarine species, the mysid *Neomysis integer*, is described in detail. In an addendum to this chapter some aberrant morphologies of this species are reported to be more widespread than previously thought. After the References from chapters 2 to 7, an extensive collection of Appendices follows. The regressions used to calculate biomass, a species list, and all matrices with raw density and biomass data and environmental variables measured in the field are presented.

The bulk of this thesis has been published in international literature. This has some negative consequences: due to the limitation of space in the journals, the output of a lot of analyses is not depicted. I have tried to compensate this by including additional graphs in some chapters and by providing appendices with all the raw data discussed in the individual chapters. Furthermore, though most journals have very capable language editors, it will be obvious that English is not my mother tongue.

Besides some minor changes in the graphs, *Chapters 2 and 3* have been published as such:

*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.*

*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. 29: 357-370.*

Part of *Chapter 4* has been published (the analyses with the spring, summer and winter transects) in the proceedings of the ECSA-21 symposium as

*Mees, J., A. Dewicke & O. Hamerlynck, 1993. Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde. Neth. J. Aquat. Ecol. 27: 359-376.*

but this chapter has been largely extended to include time series of the brackish and marine parts of the Westerschelde.

*Chapter 5* has also been published as such. Its 'twin-paper' dealing with the amphipods and isopods from the same samples is not included in this thesis:

*Mees, J., A. Cattrijsse & O. Hamerlynck, 1993. Distribution and abundance of shallow-water hyperbenthic mysids (Crustacea, Mysidacea) and euphausiids (Crustacea, Euphausiacea) in the Voordelta and the Westerschelde, south-west Netherlands. Cah. Biol. Mar. 34: 165-186.*

*Cattrijsse, A., J. Mees & O. Hamerlynck, 1993. The hyperbenthic Amphipoda and Isopoda of the Voordelta and the Westerschelde estuary. Cah. Biol. Mar. 34: 187-200.*

*Chapter 6* is in press in *Hydrobiologia* and the addendum has been published in the same journal:

*Mees, J., N. Fockedey & O. Hamerlynck, in press. Comparative study of the hyperbenthos of three European estuaries. Hydrobiologia.*

*Mees, J. & N. Fockedey, 1993. First record of *Synidotea laevidorsalis* (Miers, 1881) (Crustacea: Isopoda) in Europe (Gironde estuary, France). Hydrobiologia 264: 61-63.*

*Chapter 7* will shortly appear in *Marine Ecology-Progress Series*, though in a slightly different form: in the thesis two additional figures have been included.

*Mees, J., Z. Abdulkarim & O. Hamerlynck, 1994. Life history, growth and production of *Neomysis integer* (Leach, 1814) in the Westerschelde estuary (S.W. Netherlands). Mar. Ecol. Prog. Ser.: in press.*

## Summary.

**Chapter 1** provides, I believe, a quasi-complete overview of the existing literature on the hyperbenthos. It thus serves as a general introduction to the work presented in this thesis. Studies are situated in space and time and the main structural characteristics of hyperbenthic communities are summarised. Quite some effort is paid to resolve the overriding semantic disagreement which seems to slow down progress in the field. Sampling methodology and the history of hyperbenthic research are reviewed. The role of hyperbenthic animals in marine food webs is briefly touched upon.

**Chapter 2** describes the hyperbenthic communities of the Voordelta. Twelve locations were sampled monthly at two depths between August 1988 and July 1989. Three subareas were covered: the ebb-tidal deltas of the Oosterschelde and the Grevelingen, and the more seaward Banjaard area in between. High densities of a variety of animals were found to be present in the lower metre of the water column. Hyperbenthic community structure was strongly dominated by seasonal fluctuations due to the sequential appearance, high abundance and disappearance of the different species of temporary hyperbenthic species. In winter and early spring, when the community was dominated by its permanent residents, spatial patterns emerged. Averaged over the year these spatial patterns were consistent with the hydrodynamical regime in the system. The geomorphological changes, following the closure of the Grevelingen estuary, in its ebb-tidal delta seem to have created a sheltered area with low current velocities. The hydrodynamical properties of the area are favourable towards the sedimentation of silt and detritus and possibly concentrate fish eggs. Decapod larvae, probably from offshore origin, occur in high densities in the area and macrobenthic larvae find favourable conditions for settlement. This richness and a high primary productivity probably attracts mobile animals (e.g. mysids and fish). In comparison, the equally sheltered ebb-tidal delta of the Oosterschelde is much poorer. Most probably higher current velocities there do not allow sedimentation of silt and detritus and are not conducive to the entrapment of neutrally buoyant animals.

**Chapter 3** gives the results of a pilot study on estuarine hyperbenthos conducted in December 1988. 41 stations in the Westerschelde and Oosterschelde estuaries, and in part of the neighbouring shallow coastal area, the Voordelta, were sampled quasi-simultaneously. Winter was chosen as the sampling period to avoid the presence of temporary hyperbenthic species. The dominant components of the hyperbenthic communities were identified. Their spatial distribution, the geographical variation in species composition, density and biomass were described and the observed patterns were related to some environmental variables. Using multivariate analysis all sites sampled could be grouped into 7 geographically coherent clusters corresponding to 7 species assemblages. Mysids dominated the winter hyperbenthos in all communities. Species distributions in the Westerschelde seemed to be primarily determined by a salinity-turbidity-dissolved oxygen gradient. Hyperbenthic animals, mainly the mysid *Neomysis integer*, reached high densities in the brackish part whereas the more seaward stations were characterized by lower densities but a higher number of species.

In the benthic filter-feeder dominated Oosterschelde, the total density of the hyperbenthos was very low. The shallow coastal area was characterized by intermediate densities.

**Chapter 4** describes the hyperbenthos of the Westerschelde, both in space and time. Samples were taken in spring, summer and winter of 1990 at 14 stations along the salinity gradient. Temporal patterns are further described from year cycles of monthly and fortnightly samples taken from April 1990 to December 1991. Mysids dominated the hyperbenthos in each season. Other important species, either permanently (e.g. amphipods and isopods) or temporarily (e.g. fish larvae and decapod larvae) hyperbenthic, belonged to a variety of faunistic groups. Spatial structure was stable through time: the estuary could be divided in the same geographically defined zones in each season. Each zone had a characteristic fauna. Throughout the year, the hyperbenthic community of the mouth region of the estuary was markedly different from that of the upstream brackish area, both in terms of density and species composition. Gradients in salinity, dissolved oxygen and turbidity correlate strongly with the observed variation in community structure. The spatial patterns dominate over the temporal patterns, especially in the brackish part of the estuary. In the marine part, seasonal differences in the communities were more pronounced due to the recruitment, maximal abundance and subsequent disappearance of a series of temporary hyperbenthic species. In the brackish zone seasonal patterns were less obvious. Still, spring was characterized by the presence of postlarval flounder and clupeoids, while other seasonal differences seemed to be mainly due to natural mortality and to migration of permanent hyperbenthic species in and out of the area. In each season, the upstream (brackish) communities were characterized by few species occurring in very high numbers, whereas the downstream (marine) communities were composed of many species but at lower densities.

**Chapter 5** gives a detailed account on the species of Mysidacea and the one species of Euphausiacea encountered in the preceding chapters. The hyperbenthic mysids and euphausiids of the shallow coastal waters and the Westerschelde were regularly sampled between 1988 and 1991 (see above). These data were supplemented with monthly samples from two salt marshes in the brackish part of the estuary. Eight mysid species and one euphausiid species were identified. The spatial and seasonal distribution patterns of all species were described. The most abundant species in the coastal area was *Schistomysis spiritus*, followed by *Mesopodopsis slabberi*, *Schistomysis kervillei*, and *Gastrosaccus spinifer*. In the marine part of the Westerschelde the same four species were dominant but densities were generally higher than in the coastal area. Only *Siriella armata* and the euphausiid *Nyctiphanes couchi* never entered the estuary. Highest mysid densities, mainly *M. slabberi* and the estuarine endemic *Neomysis integer*, were 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.



**Chapter 6** compares the hyperbenthos of the Westerschelde with that of two other, less polluted European estuaries: the Eems (north of the Westerschelde) and the Gironde (south of the Westerschelde). The three estuaries were sampled at regularly spaced stations covering the entire salinity gradient from marine conditions at the mouth to nearly freshwater conditions upstream within a 15 day period in summer 1991. The diversity of the samples and the distribution of the species along the main estuarine gradients were assessed. Again, hyperbenthic communities were identified using different multivariate statistical techniques. The species composition and the density and biomass of the dominant species of each community were compared among communities. Spatial patterns in density, biomass and diversity of the hyperbenthos were similar in the three estuaries: diversity was highest in the marine zone where density and biomass were lowest. Diversity decreased upstream and was lowest in the brackish part where density and biomass reached maximal values. In the Eems and the Gironde there was a slight increase in diversity towards the freshwater zone. Within each estuary two (Westerschelde) or three (Eems and Gironde) communities could be distinguished and their position along the unidirectional salinity-turbidity-temperature gradient was similar: a marine community in the high salinity zone, a brackish water community in the middle reaches and a third community (absent in the Westerschelde) in the stations with the lowest salinities. Qualitative and quantitative differences in the corresponding hyperbenthic communities among estuaries were evident. Some species were restricted to one or two of the estuaries studied, while others, especially the abundant species in the brackish part, were common to all three. Still, these differences were marginal compared to the overriding similarity of the hyperbenthos in the three estuaries. The distribution of single species in the estuaries varied to some extent but the among estuary differences in density and biomass in comparable salinity zones rarely exceeded an order of magnitude. In the Westerschelde, the low salinity hyperbenthic community was completely absent. Upstream of the 10 psu isohaline the dissolved oxygen concentration dropped to a critical threshold value for hyperbenthic life. The populations of a number of species, which in Gironde and Eems reached highest density and biomass in this zone, seem to have (almost) disappeared from the Westerschelde (e.g. *Gammarus zaddachi* and *Palaemon longirostris*). Other brackish water species did not occur in their "normal" salinity range and their populations have shifted to higher, atypical salinity zones (e.g. *Neomysis integer*, *Mesopodopsis slabberi*, *Pomatoschistus microps* and *Gammarus salinus*). The **addendum** to this chapter concerns an oddity, namely the discovery of a hitherto unreported isopod species in the Gironde estuary. *Synidotea laevidorsalis*, new for the European fauna, is a nonendemic shallow-water species which was probably introduced into the Gironde from Asia. In the salinity range of 1 to 10 psu of the Gironde the species constitutes an important component of the brackish-water hyperbenthic community.

**Chapter 7** concerns the population dynamics of the key species of the Westerschelde hyperbenthos: the mysid *Neomysis integer*. The population was sampled on a fortnightly basis from November 1990 to December 1991. Density, biomass,

population structure and brood size were recorded. The Bhattacharya method was applied to the length-frequency data for the detection and separation of cohorts. Growth is described both by a generalised von Bertalanffy function and by a von Bertalanffy function incorporating seasonal oscillations in growth. Secondary production was estimated for each cohort using four approaches. The seasonal pattern in density and biomass showed three peaks: a relatively small, yet distinct, peak in early March and two main peaks in late spring and in summer. Throughout winter, *Neomysis* density remained low. Three periods of increased reproductive activity and subsequent input of juveniles were found. This suggests that three cohorts were produced per year. The overwintering generation lived from autumn until the following spring. The spring generation was born in early spring and lived for about three months, while the summer generation lived from summer until early winter. The three cohorts showed marked differences in their biology. The overwintering generation showed seasonal growth oscillations, larger brood size, and a larger size at maturity. Individuals belonging to the other two cohorts generally grew faster, produced less young per female, and attained maturity at a smaller size. Within each cohort, both sexes exhibited different growth characteristics: the females generally lived longer, grew faster and consequently became larger than the males. The size-frequency, growth summation and removal summation methods yielded comparable production estimates. The annual production was  $0.3 \text{ g AFDW m}^{-2} \text{ yr}^{-1}$  with an annual P/B ratio of 6. The average cohort P/B was 3. The size-frequency method gave similar results only when applied to the three cohorts and to both sexes separately. The spring cohort accounted for almost half of the annual production. Despite the longer life span of the overwintering generation, it generated only a quarter of the annual production. An independent estimate of production using the mortality rate of the different cohorts, resulted in values comparable to those obtained by the other methods for the overwintering cohort, while the production of the other two cohorts was overestimated. The *addendum* to this chapter reports on intersexuality in the mysid *Neomysis integer* collected in the 3 estuaries mentioned above, supplemented with samples from the Elbe (Germany). Individuals which had an irregularly shaped or nearly symmetrically rounded, rather than a typically truncated, telson were also recorded from the four populations studied. A culture experiment with damaged specimens revealed that every type of abnormal telson morphology found in the field can result from regeneration of damaged parts. It is concluded that both intersexuality and aberrant telson morphology are widespread phenomena among estuarine *Neomysis* populations. Both abnormalities were found to be rare in the other dominant mysid species in the study area.

## **Samenvatting.**

**Hoofdstuk 1** geeft naar ik meen een nagenoeg volledig overzicht van de bestaande literatuur over het hyperbenthos. Het kan bijgevolg worden beschouwd als een algemene inleiding tot het onderwerp van deze thesis. Het onderzoek is gesitueerd in ruimte en tijd en de belangrijkste structurele kenmerken van hyperbenthische gemeenschappen worden samengevat. Er is veel aandacht besteed aan de terminologie, daar de vooruitgang in dit studiegebied belemmerd wordt door semantische onenigheid tussen auteurs. De staalname methodologie en de geschiedenis van hyperbenthisch onderzoek worden uitvoerig behandeld. De rol van hyperbenthische organismen in mariene voedselwebben wordt kort besproken.

**Hoofdstuk 2** beschrijft de hyperbenthische gemeenschappen van 12 lokaties in de Voordelta. Deze werden maandelijks bemonsterd op 2 dieptes tussen augustus 1988 en juli 1989. Hierbij werden 3 deelgebieden bestreken: de delta's van de Oosterschelde en de Grevelingen, en het meer zeewaarts gelegen Banjaard gebied. In de onderste meter van de waterkolom werden hoge densiteiten van een grote verscheidenheid aan organismen gevonden. De hyperbenthische gemeenschapsstructuur was sterk onderhevig aan seizoenale veranderingen. Dit was te wijten aan het opeenvolgend verschijnen, bloeien en verdwijnen van verschillende tijdelijk hyperbenthische soorten. 's Winters en in de vroege lente, wanneer de gemeenschap gedomineerd was door permanent hyperbenthische soorten, werden ruimtelijke patronen aantoonbaar. Uitgemiddeld over het ganse jaar waren deze patronen consistent met het hydrodynamische regime van het gebied. De geomorfologische veranderingen die gepaard gingen met het sluiten van de Grevelingen, leiden in de nabijgelegen kustzone tot een beschut gebied met lage stroomsnelheden. De hydrodynamische eigenschappen van het gebied begunstigen de sedimentatie van slib en detritus. Waarschijnlijk worden er ook viseieren geconcentreerd. Larvale stadia van Decapoda komen er met hoge densiteiten voor en ook larven van macrobenthische organismen vinden er gunstige omstandigheden om te settelen. Deze voedselrijkheid, en een hoge lokale primaire produktie, trekt waarschijnlijk talrijke mobiele dieren (bvb. aasgarnalen en vissen) aan. De delta van de Oosterschelde is veel armer. Waarschijnlijk laten de hoge stroomsnelheden geen sedimentatie van slib en detritus toe, en worden er geen neutraal drijvende organismen geaccumuleerd.

**Hoofdstuk 3** geeft de resultaten weer van een pilootstudie over estuarien hyperbenthos die werd uitgevoerd in december 1988. In de Westerschelde, de Oosterschelde en de Voordelta werden 41 stations vrijwel gelijktijdig bemonsterd. De staalname was in de winter gesitueerd om de aanwezigheid van tijdelijk hyperbenthische soorten te vermijden. De dominante componenten van de hyperbenthische gemeenschappen werden geïdentificeerd. Hun ruimtelijke verspreiding, de geografische variatie in soortensamenstelling, densiteit en biomassa werden beschreven. De waargenomen patronen werden gerelateerd tot een aantal omgevingsvariabelen. Met multivariate statistische technieken konden de stations op basis van hun soortensamenstelling in 7 geografisch coherente clusters opgedeeld

worden. Mysidacea domineerden het winter hyperbenthos in alle gemeenschappen. De verspreiding van de soorten in de Westerschelde werd voornamelijk bepaald door parallelle gradiënten in saliniteit, troebelheid en opgeloste zuurstof. Hyperbenthische organismen, vooral de aasgarnaal *Neomysis integer*, bereikten hoge densiteiten in het brakwater deel. Het meer zeewaarts gelegen deel werd gekenmerkt door lagere densiteiten maar een groter aantal soorten. In de door benthische filtervoeders gedomineerde Oosterschelde, was de totale densiteit van het hyperbenthos zeer laag. Het ondiepe kustgebied was gekenmerkt door tussenliggende densiteiten.

**Hoofdstuk 4** beschrijft het hyperbenthos van de Westerschelde, zowel in ruimte als in tijd. In lente, zomer en winter van 1990 werden 14 stations langs de saliniteitsgradiënt bemonsterd. Temporele patronen werden verder beschreven aan de hand van tijdsreeksen van maandelijke en veertiendaagse stalen genomen van april 1990 tot december 1991. Mysidacea domineerden het hyperbenthos in elk seizoen. Andere belangrijke soorten, zowel permanent (bvb. Amphipoda en Isopoda) als tijdelijk (bvb. vislarven en larvale Decapoda) hyperbenthische, behoorden tot een grote verscheidenheid van taxa. De ruimtelijke structuur was stabiel in de tijd: het estuarium kon in elk seizoen in dezelfde geografisch gedefinieerde zones verdeeld worden. Elke zone had een karakteristieke fauna. De hyperbenthische gemeenschap van het mondingsgebied was gedurende het ganse jaar sterk verschillend van deze in het stroomopwaartse brakwater gebied, zowel qua soortensamenstelling als qua densiteit. De gradiënten in saliniteit, opgeloste zuurstof en troebelheid waren sterk gecorreleerd met de variatie in gemeenschapsstructuur. De ruimtelijke patronen domineerden over de temporele patronen, vooral in het brakke deel van het estuarium. In het mariene deel waren seizoenale verschillen meer uitgesproken ten gevolge van de rekrutering, maximale abundantie en verdwijning van een reeks tijdelijk hyperbenthische soorten. In het brakwater deel was de seizoenaliteit minder opvallend. Toch werd de lente gekenmerkt door de aanwezigheid van postlarvale bot en haringachtigen, terwijl andere seizoenale verschillen vooral te wijten waren aan natuurlijke mortaliteit en migratiepatronen van permanent hyperbenthische soorten. De brakwater gemeenschap werd in elk seizoen gekenmerkt door weinig soorten die in grote aantallen voorkwamen; het mariene deel was gekenmerkt door een groter aantal soorten maar lagere densiteiten.

**Hoofdstuk 5** geeft een gedetailleerde beschrijving van de soorten Mysidacea en de enige soort Euphausiacea die tijdens de voorgaande studies werden aangetroffen. De hyperbenthische aasgarnalen en krill van de Voordelta en de Westerschelde werden regelmatig bemonsterd tussen 1988 en 1991 (zie hoger). Deze gegevens werden aangevuld met maandelijke stalen van 2 schorren in het brakwaterdeel van het estuarium. Acht soorten aasgarnalen en één krill soort werden geïdentificeerd. De ruimtelijke en seizoenale verspreidingspatronen van de soorten werd beschreven. De meest abundante soort in het kustgebied was *Schistomysis spiritus*, gevolgd door *Mesopodopsis slabberi*, *Schistomysis kervillei*, en *Gastrosaccus spinifer*. In het mariene deel van de Westerschelde werden dezelfde 4 soorten aangetroffen, over het algemeen in hogere densiteiten. De aasgarnaal *Siriella armata* en de krill soort *Nyctiphanes couchi*

werden nooit in het estuarium gevangen. De hoogste densiteiten aan aasgarnalen, voornamelijk *M. slabberi* en de estuariene endem *Neomysis integer*, werden genoteerd in het brakwater deel van de Westerschelde. *Praunus flexuosus* is een euryhaliene soort met een voorkeur voor intertidale gebieden. De estuariene populaties van *N. integer*, *M. slabberi*, *P. flexuosus*, en in mindere mate *S. spiritus* lijken de schorren te gebruiken in periodes van voortplanting.

In **hoofdstuk 6** wordt het hyperbenthos van de Westerschelde vergeleken met dat van twee andere, minder vervuilde Europese estuaria: de Eems (ten noorden van de Westerschelde) en de Gironde (ten zuiden ervan). In elk estuarium werden, binnen een periode van 15 dagen in de zomer van 1991, een vijftiental stations bemonsterd langsheen de volledige saliniteitsgradiënt van de mariene zone aan de monding tot het nagenoeg zoete water stroomopwaarts. De diversiteit van de stalen en de verspreiding van de soorten langs de belangrijkste estuariene gradiënten werden onderzocht. Hyperbenthische gemeenschappen werden geïdentificeerd met verschillende multivariate statistische technieken en hun soortensamenstelling, densiteit en biomassa werden vergeleken. De 3 estuaria hadden vergelijkbare patronen in densiteit, biomassa en diversiteit: de diversiteit was het hoogst, en densiteit en biomassa waren het laagst, in de mariene zone. De diversiteit daalde stroomopwaarts en was minimaal in het brakwater deel, waar densiteit en biomassa maximale waarden bereikten. In de Eems en de Gironde werd verder stroomopwaarts nog een lichte stijging van de diversiteit waargenomen. In elk estuarium werden 2 (Westerschelde) of 3 (Eems en Gironde) gemeenschappen gevonden. Hun voorkomen langsheen de gradiënt van saliniteit-turbiteit-temperatuur was vergelijkbaar: een mariene gemeenschap in de zone van hoge saliniteit, een brakwater gemeenschap in het middendeel en een derde gemeenschap (afwezig in de Westerschelde) in de oligohaliene zone. De overeenkomstige gemeenschappen van de 3 estuaria waren zowel kwalitatief als kwantitatief verschillend. Sommige soorten kwamen slechts in één of twee estuaria voor, terwijl andere soorten (vooral de zeer abundante soorten van het brakwater deel) overal aanwezig waren. Toch waren deze verschillen marginaal in vergelijking tot de overheersende similariteit van het hyperbenthos in de 3 systemen. De verdeling van individuele soorten verschilde wel een beetje in elk estuarium, maar de densiteiten en biomassa's die in overeenkomstige saliniteitszones werden bereikt, waren zelden een grootte-orde verschillend. De oligohaliene hyperbenthische gemeenschap is totaal afwezig in de Westerschelde. Stroomopwaarts van de isohaliene 10, daalde de concentratie aan opgeloste zuurstof onder een waarde die kritisch is voor het voorkomen van hyperbenthisch leven. Een aantal soorten die in de Eems en de Gironde juist in deze zone hun hoogste densiteiten en biomassa's bereiken, lijken (bijna) uitgestorven te zijn in de Westerschelde (bvb. *Gammarus zaddachi* en *Palaemon longirostris*). Andere brakwatersoorten kwamen niet in hun 'normaal' saliniteitsbereik voor: hun populaties waren opgeschoven naar hogere, atypische saliniteiten (bvb. *Neomysis integer*, *Mesopodopsis slabberi*, *Pomatoschistus microps* en *Gammarus salinus*). Het **addendum** bij dit hoofdstuk betreft de ontdekking van een tot hier toe onbekende soort in de Gironde. De zeepissebed *Synidotea laevidorsalis*, nieuw voor de

europese fauna, is een grote, niet-endemische soort van ondiep water die waarschijnlijk in de Gironde werd geïntroduceerd vanuit Azië. In de saliniteitszone van 1 tot 10 ‰ vertegenwoordigt de soort een belangrijke component van de hyperbenthische gemeenschap.

**Hoofdstuk 7** handelt over de populatiedynamica van de belangrijkste hyperbenthische soort van de Westerschelde: de aasgarnaal *Neomysis integer*. De populatie werd om de 14 dagen bemonsterd van november 1990 tot december 1991. De densiteit, biomassa, populatie structuur en grootte van het broed werden genoteerd. Voor het detecteren en scheiden van de cohorten, werd de Bhattacharya methode toegepast op de lengte-frequentie gegevens. De groei werd beschreven met de algemene von Bertalanffy vergelijking en met een aangepaste vorm daarvan die rekening houdt met seizoensale oscillaties in de groei. De secundaire produktie werd met 4 verschillende methodes geschat voor elke cohorte. Het seizoenaal verloop van densiteit en biomassa vertoonde 3 pieken: een relatief kleine, doch duidelijke piek in begin maart en 2 grote pieken in de late lente en in de zomer. 's Winters bleef de *Neomysis* densiteit laag. Er werden 3 periodes van verhoogde reproductieve activiteit gevonden, elk gevolgd door een input van juvenielen. Dit betekent dat er 3 cohorten per jaar geproduceerd worden. De overwinterende generatie leefde van de herfst tot de volgende lente. De lente generatie werd geboren in de vroege lente en leefde gedurende 3 maanden; de zomer generatie leefde van de zomer tot de vroege winter. De biologie van de 3 cohorten was duidelijk verschillend. De overwinterende generatie vertoonde seizoenale oscillaties in de groei, meer larven per wijfje en een grotere lengte bij geslachtsrijpheid. Individuen van de andere cohorten groeiden sneller, produceerden minder jongen per wijfje en waren kleiner bij geslachtsrijpheid. Sex-gerelateerde groeiverschillen werden in elke cohorte gevonden: de wijfjes leefden langer, groeiden sneller en werden groter dan de mannetjes. De vier methodes voor het schatten van de produktie gaven vergelijkbare resultaten. De jaarlijkse produktie was  $0.3 \text{ g AVDW m}^{-2} \text{ yr}^{-1}$  met een jaarlijkse P/B ratio van 6. De gemiddelde P/B per cohorte was 3. De lengte-frequentie methode gaf enkel vergelijkbare resultaten als ze werd toegepast op de 3 cohorten en beide geslachten afzonderlijk. De lente-cohorte vertegenwoordigde bijna de helft van de jaarlijkse produktie. Ondanks de langere levenstijd, genereerde de winter-generatie amper een kwart van de jaarlijkse produktie. Een afzonderlijke produktie-schatting gebaseerd op de totale mortaliteit van de cohorten, resulteerde in vergelijkbare produktieschattingen voor de overwinterende generatie, terwijl de produktie van de andere cohorten overschat werd. Het **addendum** bij dit hoofdstuk handelt over aberrante morfologische vormen in 4 populaties van *N. integer*. Zowel intersexualiteit als onregelmatige of afgeronde (i.p.v. de typische afgeknotte) telsons werden gevonden. Een kweekexperiment met beschadigde individuen leert dat elk abnormaal telson-type het gevolg kan zijn van regeneratie van beschadigde delen. Zowel intersexualiteit als aberrante telsonvormen zijn algemeen in estuariene *Neomysis* populaties.

## CHAPTER 1.

### Hyperbenthos: a review.

*Au moindre obstacle qu'il trouve sur son chemin, le mysis se jette de côté avec la rapidité de l'éclair, et continue ensuite tranquillement sa course ... Cette espèce, considérée pendant si longtemps comme rare, vit en abondance dans nos huîtreries, à Ostende, et le nombre en est souvent si grand qu'en pêchant au petit filet, l'eau en devient comme gélatineuse: on pourrait en remplir un sac en peu de temps.*

*(P.-J. Van Beneden, 1860)*

*Les pilotes me signalent ... des bancs d'êtres blanchâtres ... si nombreux qu'on dirait 'que la mer est pleine d'une soupe de vermicelles fins'. Cette expression des matelots donne une idée juste de l'aspect et de l'importance de cette 'bouillie' de petits êtres.*

*(A.-F. Marion, 1894)*

*(both about the mysid Mesopodopsis slabberi)*

#### Abstract

The hyperbenthos is the association of animals living in the water layer close to the sea bed. It includes all bottom-dependent species and life history stages (mainly crustaceans) which perform, with varying amplitude, intensity and regularity, seasonal or daily vertical migrations above the sea-floor. As functional members of the bottom animal community, they thus constitute the uppermost component of the benthos. The hyperbenthos differs from other ecosystem compartments, both in quantity and quality. In nearly all marine subsystems that have been investigated to date, a general increase in biomass at the benthic boundary layer relative to the water column immediately above it, has been observed. Furthermore, the species composition of the hyperbenthos is distinctly different from that of other benthic and planktonic strata. Besides endemic species that are resident in the near-bottom environment, it also contains elements suggestive of two different origins: (1) species derived from downward extensions, often seasonal in nature, of pelagic planktonic populations, and (2) endo- or epibenthic species emerging into the water column, often in diel cycles.

The existence and importance of hyperbenthic communities is now well established, but as hyperbenthic research is still a young discipline, the zone and its fauna remain relatively poorly studied. This is mainly due to methodological difficulties: the often highly mobile animals are not sampled efficiently by either conventional benthic or pelagic samplers. A plethora of devices has now been constructed and used with varying success. Soft bottom communities are usually sampled with sledges,

whereas hard substrates and coral reefs are usually sampled with traps. In recent years, considerable progress in hyperbenthos research has been achieved in tropical areas (mostly coral reef lagoons), in temperate to cold-water coastal and shelf regions, and in deep sea environments. Unfortunately, there is little or no mutual acknowledgement of results. This lack of exchange seems to be partly due to differences in terminology. 'Hyperbenthos' and 'suprabenthos' are mainly used in temperate and northern areas, while 'demersal zooplankton' and 'benthopelagic plankton' are preferred to designate the same fauna in tropical areas and in the deep-sea, respectively. Semantic agreement would certainly speed up progress. It is concluded that the lack of interest for this fauna seems no longer justified on both methodological and ecological grounds.

### 1.1. Introduction

Through the ages, the water layer adjacent to the bottom of the sea has been a major field for commercial exploitation by various kinds of fishing gear. This sharply contrasts with the lack of attention that is paid by marine ecologists to the associations of smaller animals inhabiting the same biotope, i.e. to the potential prey species of the exploited stocks or their pre-recruits. Technical difficulties were at least partly responsible for the discrepancy, as most hyperbenthic animals are small and notoriously difficult to sample quantitatively. Consequently, with a variety of other compartments available for study, researchers have relegated hyperbenthic communities to minor roles in most marine studies, regardless of their true importance in the marine ecosystem. A considerable variety of sampling methods has now been described, and in recent decennia an increased scientific activity relating to the hyperbenthic region became evident. This seems to be mainly due to the recognition of the importance of interactions with fishes (as observed from stomach content analyses) and to a growing interest in benthic-pelagic coupling (for the development of carbon-flux models). The importance of hyperbenthic research for fisheries biologists is evident: the hyperbenthic is the zone where many demersal fish and epibenthic crustaceans feed for at least part of their life. Furthermore, there is also a renewed interest in pre-recruit studies (e.g. Simard *et al.* 1990); many larval and postlarval fish and crustaceans that are considered in these studies have a hyperbenthic life style. Studies of energy fluxes through marine environments rarely include samples that are taken within a few centimetres of the sediment and may therefore seriously underestimate the flux of particulate material (Odum *et al.* 1979). Other disciplines have recently been attracted to hyperbenthos research: mysids are increasingly used in aquaculture, ecotoxicology and pollution studies (e.g. Laughlin & Linden 1983, Brandt *et al.* 1993).

Parallel progress, achieved entirely independent of each other, has been made by workers in tropical, temperate to cold-water and deep sea environments. As rightfully noticed by Sainte-Marie & Brunel (1985), there is little or no mutual acknowledgement of their respective efforts. This is partly attributable to differences in terminology: 'demersal zooplankton' is used by tropical researchers, whereas 'hyperbenthos' or 'suprabenthos' is used in temperate and northern areas. Deep-sea



researchers usually prefer the term 'benthopelagic plankton' or refer to the zone as the 'benthic boundary layer'. In all, the zone and its fauna remain relatively unstudied. Vast geographical regions and habitats where hyperbenthic animals are expected to occur abundantly, and thus to play an important role in benthic-pelagic coupling, have not been sampled to date.

In this introductory chapter, I have tried to enumerate and evaluate all studies concerned with the main structural features of hyperbenthic communities. The literature on hyperbenthos has not yet been reviewed and had therefore to be collected from widely divergent sources. Semantic disagreement further complicated the reviewing process. Attention is mainly focused on the history of hyperbenthic research, on sampling methodology and on literature dealing with hyper- and suprabenthos and its less common synonyms. Since most information pertains to temperate and cold water environments, these sections unavoidably reflect this bias. Links to tropical and deep sea research are briefly discussed, but those parts are mainly restricted to selected recent key-studies. More information about earlier research, sampling methodology and the structure of the communities in these environments can be found in papers cited therein. Functional relationships are also briefly touched upon. No attempt was made to review the extensive literature on the biology of the constituting taxa and no unpublished theses and reports are included in the review. For ease of comparison, all reported densities are, where possible, expressed as numbers of individuals per 100m<sup>3</sup>. The densities presented in chapters 2 through 7 of this thesis are expressed per 1000m<sup>2</sup>. Since trawling in our studies was always done with the tide, and since the surface area of the sledge was 0.8m<sup>2</sup>, the maximum amount of water that is filtered was 800m<sup>3</sup> per trawl. Thus, densities were divided by 8 to obtain numbers per 100m<sup>3</sup>. This is likely to contribute to actual densities being underestimated, especially in estuaries where high current velocities prevail.

## 1.2. Terminology and definitions

Standardized operational definitions are essential if different workers are to make comparable measurements of similar entities. A recurrent problem in operationalization for ecologists is the isolation of distinct classes that are convenient to use during further study. This especially adheres to community ecology, a discipline which may be unique amongst the branches of science in lacking a consensus definition of the entity with which it is principally concerned (Giller & Gee 1987). Many authors have expressed concern that communities rarely exist as naturally definable units.

Still, a number of terms have been introduced in order to facilitate ecological surveys of the marine fauna. Most classifications divide the marine environment, and the fauna occurring in the different zones, on the basis of depth, light regime and/or size of the organisms. The term benthos (< Gk *bénthos* depth (of the sea)) is generally intended to include the entire bottom community and its immediate physical environment, which, as a whole, has been named the benthic boundary layer (McCave 1976). Traditionally, studies of the marine benthos arbitrarily divide the fauna into macro-,

meio-, and microbenthos, and further classify organisms as either endobenthic (< Gk *éndon* within) or epibenthic (< Gk *epi* upon) (Pearson & Rosenberg 1987). Subdivisions are thus based on the size of the organisms, and on their position relative to the sediment-water interface. In accordance with the principles behind this common terminology, the uppermost benthic layer should be called the hyperbenthos (< Gk *hypér* over, above). It is not possible to draw sharp dividing lines between the various types of distribution and behaviour. Many animals move from one level to the other. Such shifts occur erratically or regularly, at specific times of the day or year, or at certain life history stages. Animals that are normally considered to be endobenthic are known to emerge from the sediment for varying lengths of time. Epibenthic animals swim regularly: their behaviour ranges from haptic (referring to organisms which are normally continuously moving, but which attach themselves to the substrate when scared) to hemisessile (referring to the opposite behaviour). In analogy to the fact that many organisms are so flexible in their diet that trophic relations and levels change seasonally, ontogenetically and geographically, the benthic sub-communities are subject to fluctuations and to the occurrence of borderline members. Still, the hyperbenthos can be considered to be a real community (locationally defined, i.e. referring to all organisms within the stratum or habitat) as 'a group of organisms occurring together, many of which will interact within a framework of horizontal and vertical linkages' (Giller & Gee 1987). Like other benthic or pelagic ecosystem compartments, the hyperbenthos comprises a broad assemblage of diverse forms that are only related by their distribution in space, rather than by phylogeny or by exclusively functional attributes (Day *et al.* 1989). Nevertheless, the fact that they spend part or all of their lives in association with the bottom results in unifying consequences. The benthic fauna can thus be divided into *three* compartments depending on the location of the animals in relation to the water-sediment interface: the endobenthic fauna, the epibenthic fauna and the hyperbenthic fauna. Some sub-communities or components of these three main compartments, including the hyperbenthos, are also often studied; they are mostly defined taxonomically.

As for other compartments of marine ecosystems, the current definitions for the hyperbenthos are also far from standardized. We rather deal with a concept cluster *sensu* Peters (1991), i.e. a group of similar, but not identical, definitions. Most authors use a working definition: they study the animals caught by the sampling gear that was deployed, although more often than not certain taxa or organisms are arbitrarily excluded from the sampled fauna. There is a general need for a closer link of terminology to current knowledge and for better agreement between authors. Existing discrepancies in the selection and definitions of terms in various textbooks and articles have an obvious negative influence on the progress of science and on the process of education (Beyer 1986).

Traditionally, Greek and Latin are used to coin technical terms. Plankton, derived from the Greek word *plagtos* ('wandering'), is defined as all the passively floating or weakly swimming organisms carried by the water as opposed to animals living on the ocean floor or capable of active locomotion. By analogy, the name of the

fauna associated with the bottom of the sea should preferably also be derived from Greek, introducing the use of the Greek noun *benthos*. Terms referring to the spatial occurrence in relation to the bottom should be derived from this word, analogous to, for example, the terms hyperpelos, epipelos and endopelos characterizing organisms living over, on and in the mud, respectively (Beyer 1986). In deciding between employing the term hyperbenthos or the frequently used suprabenthos, two strong arguments in favor of the former term can be put forward. The first argument is etymological: a noun derived from Greek (*benthos*) should be preceded by a Greek prefix (*hyper-*) rather than by its Latin equivalents (*supra-*, *super-*). Unfortunately, the prefix *hyper-* is often used with the meaning of excessive, undue, unusual or abnormal. This might be especially the case for its use in the French language (pers. comm. by different colleagues). This is, however, not a valid reason for not using the linguistically correct Greek form, and the term *suprabenthos* should therefore preferably be abandoned. The second argument is historical: the term *hyperbenthos* was coined by Frederic Beyer in 1958 (see below), several years before any of its synonyms that are currently in use.

A wide variety of names has been used to designate what we refer to as the hyperbenthos. Animals that occupy the lower layers of the water column during different periods of their life or at different times of the day, when they are in some way related to the substratum, were first called *hyperbenthos* by Beyer (1958). He made a further distinction between *tychobenthos* and *hekobenthos* (see below). Boysen (1975a) referred to the hyperbenthos as the transitional zone between the sections that are occupied by the benthos and the plankton. He added that it is not clearly delimited in space, but that it rather represents a water layer near the bottom in which animals from two neighbouring 'Lebensräume' meet: the plankton reaches the sea bed during its diurnal migration and the benthos rises to this or an even higher level in the water column. The term *hyperbenthos* was later used by several other research groups (e.g. Hesthagen 1973, Sibert 1981, Mees & Hamerlynck 1992). Planktonic organisms (mostly mysids) that live within one metre of the bottom were referred to as *hypoplankton* by Fager *et al.* (1966), a term that was later adopted by several other authors (e.g. Mauchline 1972, Gros 1977). The term *suprabenthos* was probably introduced by Friedrich (1969). Brunel *et al.* (1978) define the hyperbenthos (their *suprabenthos*) as including all swimming bottom-dependent animals (mainly crustaceans) which perform, with varying amplitude, intensity and regularity, seasonal or daily vertical migrations above the sea-floor. They give preference to the term *suprabenthos*, because *hyperbenthos* would imply 'more than benthic' rather than 'above the benthos'. Since they also cite a number of unpublished reports and theses (12 in total, not checked by the author, and spanning a period of 1969 to 1976) in whose titles the term *hyperbenthos* is consistently used, it seems that the term *suprabenthos* only came to be widely used around that time. It has, in any case, been adopted by many later authors (e.g. Sorbe 1984, Kaartvedt 1989). **Benthopelagic plankton** and **benthic boundary layer macrofauna** have mainly been used in reports on deep-sea studies (e.g. Marshall & Merrett 1977, Wishner 1980a, 1980c), and only

exceptionally in studies of shallower areas (Wildish *et al.* 1992). **Resident, swarming or demersal zooplankton** have mainly been used in tropical areas (e.g. Emery 1968, Hamner & Carleton 1979, Alldredge & King 1985). The mobile component of the hyperbenthos, especially mysids, has often been referred to as **micronekton** (e.g. Andersen & Sardou 1992) or **nektobenthos** (Greze 1951, Salemaa *et al.* 1990, Simm & Kotta 1992) and fish larvae are sometimes indicated as **ichthyoplankton**. Wang & Dauvin (1994) and Wang *et al.* (1994) make a distinction between the **permanent hyperbenthos** (mysids, cumaceans, decapods, amphipods, isopods and pycnogonids) and **near-bottom zooplankton** (subdivided into mesozooplankton: copepods, crustacean larvae, chaetognaths, polychaete larvae, and macrozooplankton: ctenophores and postlarval fish). Other terms that are used for the same assemblage include **semiplanktonic animals** (Sentz-Braconnot 1967) and **motile epibenthos** (Kritzler & Eide-miller 1972). The distinction between **merohyperbenthos** (animals that spend only part of their early life history in the hyperbenthos and recruit to the nekton, epibenthos or endobenthos) and **holohyperbenthos** (animals that spend variable periods of their adult life in the hyperbenthos) seems also to be useful (Hamerlynck & Mees 1991). A further classification, based on size, dividing the fauna in **macro- and meiohyperbenthos**, is also recommended (new terms).

### 1.3. Methodology

Studies of the distribution and abundance of marine medium-sized fauna have been performed mainly by sampling gear constructed to catch either planktonic or benthic animals (reviews in Unesco 1968 and Eleftheriou & Holme 1984). The often highly mobile animals that live immediately above the bottom are caught only occasionally by such ordinary sampling gear. In order to sample the hyperbenthos, specific sampling devices have to be used. The choice of the equipment will largely depend on local (logistical and physical) conditions, e.g. size of the ship, power and capabilities of the lifting gear, degree of exposure, depth of the water column, bottom conditions and the type of sample that is required for the specific research topics that are investigated (Eleftheriou & Holme 1984). Each of the many and various sledges and traps which have been produced are undoubtedly well suited to local conditions. Because of this critical dependence on local conditions, there is at present no real need to attempt standardizing sampling gear, nor is it appropriate to discuss the universal merit of individual existing samplers.

#### *Sampling soft bottom communities*

##### Intertidal collections

Littoral and estuarine areas can be sampled quite satisfactorily by a variety of hand dipnets or push-nets. Several handnets have been described (e.g. Jansen 1983). Small sledges operated at a standard speed and for a fixed length of time can also

produce replicable data (Mauchline 1980). Colman & Segrove (1955) designed a light, man-hauled, two-level sledge. Mauchline's hand-pulled D-net (Mauchline 1980) or modifications thereof (e.g. Miller 1973) can catch mysids efficiently. Standing nets have been used to sample tidal marsh creeks (Cattrijsse *et al.* 1994).

#### Remote collections

Heavier and more robust equipment is required to sample the neritic habitats. Normally, sledges are deployed, consisting of towed plankton nets mounted in frames which slide over the surface of the sediment. The sledges are preferably designed in a way that at least the lower one metre of the water column is sampled and that no contamination of the sample with sediment occurs. A disadvantage of such towed sledges is that they can only be used when the bottom is relatively even.

Many types of sledges have been designed. An extensive summary of the early epi- and hyperbenthic sledges is given by Bhaud (1979). The most primitive design, used successfully by several researchers, consists of small-meshed nets which are fixed to Agassiz trawls (Russell 1928) or otter trawls (Brunel 1979). Several lines of development may be traced in the later, more quantitative devices. These mainly consist of the addition of extensions with opening and closing mechanisms and multiple nets.

For operation in shallow areas no closing mechanism is required as the error that is introduced by pelagic sampling during recovery is assumed to be small (Oug 1977). There are many examples of such small, simple sledges (Isaac & Kidds 1953, Lacroix & Bergeron 1962, Sentz-Braconnot 1967, Hamerlynck & Mees 1991). Sledges with an opening and closing mechanism are to be preferred for sampling at greater depths since they assure that the samples exclusively represent the targeted fauna (Bossanyi 1951, Greze 1951, Wickstead 1953, Beyer 1958, Frolander & Pratt 1962, Clutter 1965, Macer 1967, Bieri & Tokioka 1968, Omori 1969, Poirier *et al.* 1969, Bhaud 1979, Sorbe 1983). Opening is usually triggered mechanically on first contact with the bottom or by a messenger (Beyer's sledge). Acoustically operated mechanisms have also been described (Aldred *et al.* 1976). A modified Rothlisberg & Percy (1977) sledge, used by Buhl-Jensen (1986), was later equipped with a pneumatic opening and closing device by Fossa *et al.* (1988). Beyer's epibenthic sledge is illustrated in Holme (1964). It was modified by Oug (1977) to sample at different levels in the water column. The light-weight Macer sledge (1967) has not often been used as such (except, e.g. by Williams & Collins 1984). It was enlarged and modified as the Macer-GIROQ sledge (Brunel *et al.* 1978) and later again by Dauvin & Lorgeré (1989). After these alterations, it has been quite popular and successful. Presently, multilevel nets are most commonly used (Fager *et al.* 1966, Dragonet II of Bieri & Tokioka 1968, the modified Beyer sledge of Oug 1977, Macer-GIROQ sledge of Brunel *et al.* 1978, Sorbe 1983, Mees & Hamerlynck 1991). Diver pushed nets have also been described (Fager *et al.* 1966, Kritzler & Eidemiller 1972, Potts 1976). Passive fishing with fixed nets can be used where strong water currents prevail (Falconetti 1975, Vaissiere &

Falconetti 1975, Falconetti & Seguin 1977, Sorbe 1981b). Finally, modified sledges with stimulation devices like a tickler chain (Ockelmann 1964), and those based on water-jet or electric currents (Turnbull & Watson 1992), can be used to include the epibenthos and the fauna of the upper millimetres of the sediment.

### *Sampling over hard substrates*

Hard substrates are logistically difficult to sample and most of the conventional sampling gear that has been used to capture demersal zooplankton or hyperbenthos in the open ocean is ineffective for collecting zooplankton living on coral reefs. Deploying boat-towed devices is extremely difficult. A host of unique alternative sampling devices have been developed, including anchored swivel nets (Johannes *et al.* 1970, Vaissiere & Seguin 1984), diver pushed nets (Emery 1968, Hobson & Chess 1978, Hamner & Carleton 1979), nets pushed by underwater vehicles (Schroeder 1974, Potts 1976), suction samplers and airlifts (Emery 1968, Rützler *et al.* 1980), light traps (Emery 1968, Sale *et al.* 1976, 1978, Kawagushi *et al.* 1986), photographic sampling techniques (Hamner & Carleton 1979), emergence traps (Youngbluth 1982), re-entry traps (Alldredge & King 1980, Stretch 1985) and baited traps (e.g. Christiansen *et al.* 1990). Recently, Setran (1992) described a promising intertidal plankton trap. A remotely operated bottom-closing drop net to capture mysids over uneven bottom terrains was described by Lasenby & Sherman (1991). A very efficient diver operated device utilizing the escape response of motile animals that live upto 1 metre above the bottom was used by Carleton & Hamner (1987).

### *Other methods of sampling, and supporting techniques*

Direct observation during SCUBA diving can be interesting for behaviour studies and for assessing the efficiency of sampling gear. The use of an underwater camera has proven useful as an adjunct to sledge sampling (Aldred *et al.* 1976, Rice *et al.* 1982), providing the opportunity for quantitative comparisons between estimates of population density by photography and actual catches in the net. However, fast moving animals are seldom seen in photographs (Holme 1984) and its main use seems to be the assessment of the fishing behaviour of the gear. Television cameras mounted on sledges could also prove to be useful (Holme 1984). Indirect methods, such as information obtained from stomach content analyses of fish, may show the presence of otherwise unreported species and has frequently been used to describe the bathymetric distribution of deep-living hyperbenthic mysids (Mauchline 1982, 1986, Astthorsson 1984, 1985). High volume pumps (Sibert 1981, Jahn & Lavenberg 1986) or cooling intakes of nuclear power stations (Moore *et al.* 1979) can yield interesting information at fixed locations. High-speed plankton samplers or WP2 plankton nets with a large mesh have been used to sample mysids in estuaries (Sorbe 1981b, Williams & Collins 1984). Wheeled Bongo nets are efficient for catching fish larvae (Brewer & Kleppel 1986). Cages that are lowered to the bottom (Van Clevé *et al.* 1966), or smaller throw,

drop or pull-up traps can also be applied (Holme 1984). High-frequency sonars can be used to locate near-bottom scattering layers, both in the deep sea (Wishner 1980b) and in shallower areas (Mees unpublished).

### *Efficiency and selectivity of samplers*

As already mentioned, most of the hyperbenthic samplers were designed for specific objectives and for sampling in specific areas. They have met with varying degrees of success and acceptance. A device that can sample hyperbenthic animals quantitatively has yet to be constructed. Satisfactory samples can be taken at some distance from the bottom with plankton nets mounted on sledges. As for samplers for other ecosystem compartments, general use of a gear is usually based on convenience and on the premise that 'it appears to do a better job than others' (Unesco 1968). Until much more data on their field performance are available, a rating for the samplers cannot be given. However, some general recommendations can anyway be put forward. It is advisable to install an opening-closing mechanism, especially when operating in deeper waters. The sledge is preferably equipped with both an odometer and a current meter, so that densities can be reported per volume of water that is filtered and per surface area of sea bottom that is trawled. Mesh sizes of 0.5 mm are the rule. In areas where risk for clogging is high a mesh size of 1 mm is acceptable. Towing speed should always be as low as possible.

Unfortunately, not much is known about gear efficiency. Most sledges are at best semi-quantitative. The efficiency, judged by its ability to capture all the animals within its sweep, is usually low. For epifauna dredges, and when total fauna is considered, a value near 10% is thought to be realistic (Eleftheriou & Holme 1984). Mysids have been observed to avoid capture by swimming in front of trawls (Lasenby & Sherman 1991).

A general flaw of most sledges is that they do not sample the lowermost centimetres of the watercolumn. By a combination of sledge sampling and aquarium observations, Fossa (1985, 1986) showed that species of mysids may have the highest abundance at or just a few centimeters above the bottom. Huberdeau & Brunel (1982) showed that the Macer-GIROQ hyperbenthic sledge sampled a specific fauna but added that no information is obtained on the lower 28 cm of water column, which may be very rich.

The replicability of Beyer's sledge was assessed by Hesthagen & Gjermundsen (1978). They concluded that, although some difficulties may arise when deciding which organism belongs where, the sledge provides replicable samples. Schnack (1978), using the same data, concluded that for many groups of animals the replicability of the results that are obtained by this method was satisfactory and that density estimates had a similar precision as for net tow samples in plankton studies. Huberdeau & Brunel (1982) compared the performance, efficiency and selectivity of the Macer-GIROQ sledge with endo- and epibenthic samplers. The sampled fauna was found to be very distinct. The replicability of a modified Rothlisberg & Percy sledge was tested by

Brattegard & Fossa (1991). An acceptable level of replicability for number of individuals and of spread of individuals over species was observed. Thus, if time and money are limited and only one haul is taken at a given station, it is highly probable that the sample will be representative.

Three traps for sampling demersal zooplankton were compared by Youngbluth (1982). The Alldredge & King trap gave the best results with  $238 \pm 13$  individuals per  $m^2$  per hour, followed by the Hobson & Chess trap ( $138 \pm 23$ ) and the Porter & Porter trap ( $70 \pm 8$ ). Density and species composition depended on the distance between the bottom and the base of the trap, and on the porosity of the trap walls. Madhupratap *et al.* (1992) found that direct sampling of demersal zooplankton with a corer yielded densities that were about 25 times higher than those estimated with emergence traps. They reported emergence rates of up to 80% of all organisms present in the sediment.

Carleton & Hamner (1987) designed a diver-operated trap for mysids which utilizes the escape response of the animals. Near-absolute density estimates seem to be possible with this apparatus as over 90% of all mysids could be taken with only two sweeps. Testing several other sampling methods in a coral reef lagoon, they found that their density estimates were several orders of magnitude higher than these obtained with towed devices. In a first trial, their trap took 786 individuals per  $m^3$ , a sledge took 11.7 and a towed plankton net 0.7. In a second trial 109 individuals were caught with the trap versus 22, 6.2 and 1.3 with a sledge, a towed net and a diver pushed net, respectively.

#### *Treatment and sorting of samples*

Unlike other benthos samples, a hyperbenthos sample does not consist of a large volume of sediment from which the animals must be extracted. No initial reduction of sample volume is carried out in the field. Preservation is satisfactory with 4 to 10% buffered formalin (formaldehyde in seawater, with a concentration depending on the water volume of the sampled material).

Sorting is a very time consuming task which may severely restrict the extent of the sampling program. Especially in areas where a lot of detritus is suspended in the lower part of the water column, bulk staining of samples with vital stains (usually rose bengal) can be used to facilitate sorting. Different groups of animals can be stained to different extents by adding an aqueous solution of phenol to the rose bengal (Hesthagen 1970). A counterstaining technique for samples containing large quantities of detritus was described by Williams & Williams (1974): the primary stain, rose bengal, is counterstained with chlorazol black E, yielding a high color contrast. Staining with rhodamin B causes the animals to fluoresce when examined under longwave ultra violet light (Hamilton 1969). Eosin or Lugol's iodine can also be used (Eleftheriou & Holme 1984).



#### 1.4. Hyperbenthic communities

In this section, a more or less chronological history of hyperbenthic research is presented. Marine hyperbenthic research is a young discipline, unlike, for example macrobenthic or zooplanktonic research, whose roots can be traced back to the late 18th century. Hyperbenthic studies did not commence until the presence of high concentrations of specific animals near the bottom was recognized. These animal assemblages were reported by naturalists before the beginning of this century, but the first speculations on their ecological significance and their recognition as a research topic in its own right, appears not to have occurred until the late fifties (Bossanyi 1957, Beyer 1958).

##### 1.4.1. Bottom plankton: the roots of hyperbenthic research

The ineffectiveness of the commonly used grabs, dredges and trawls to catch small and agile animals had been noted by several researchers by the end of the 19th century (Sars 1870, 1895, 1903, Hjort & Dahl 1900). These authors suspected that not even the combined use of all types of ordinary equipment allowed an adequate assessment of the composition of the fauna on soft bottoms. Sars (1870, 1895, 1903) made use of a variety of alternative sampling methods. Besides using baited traps, he attached 'surface nets' or 'fine hand-nets' to the dredge rope at a short distance from the dredge. Elsewhere, he mentioned the use of 'a very light dredge, by which only a small portion of the superficial bottom-material is taken up'. The apparatus (probably the very first hyperbenthic sledge) was not described in detail, but he did mention that the light dredge which he had been using with great success was of a peculiar design, supplied with a bag of fine gauze, and preferably mounted on a pair of runners (Sars 1870). Hjort & Dahl (1900) applied an exterior bag of embroidery net to the terminal part of the cod end of an otter trawl. These early collections were mainly made by naturalists for taxonomical purposes, i.e. for the purpose of collecting and describing new species. Other collecting gear, mostly light dredges or sled nets without closing devices, was made and used for qualitative studies by a number of other workers (Reighart 1894, Hensen 1895). The animals that generally escaped were found to be mainly crustaceans (ostracods, copepods, isopods, amphipods, mysids, male cumaceans and larval and postlarval decapods).

In the first half of this century a number of scientists explicitly recognized and investigated what they called the 'bottom plankton'. Collections were first made with fine nets mounted on or inside trawl nets (e.g. Russell 1928). This type of sampling was performed off the coasts of Ireland (Holt & Tattersall 1905, Calman 1906, Tattersall 1906), in the English Channel (Russell 1928, 1931, 1933, Tattersall 1938) and off New England (Wilson 1932). The first biologist to recognize the importance of the hyperbenthos through such work - although he did not coin a specific term for the zone or the fauna - was probably Russell (1925, 1926). In the course of his extensive research on the vertical distribution of plankton in the Plymouth area (English Channel),

he found that daytime plankton samples from different depths differed both in quantity and quality: with increasing depth a sudden increase in plankton abundance was observed 'which existed nearly to the bottom', and in deeper layers species appeared in the catches that were not represented in the collections from the layers above. It became evident that the layers that are very close to the sea bottom had to be properly sampled. This led him to the construction of the first semi-quantitative hyperbenthic sampler that is described in the literature: a fine meshed tow net which could fish inside an Agassiz trawl as it was dragged along the bottom, in a way to only catch animals that swim just above the bottom. Mysids, postlarval fish, chaetognaths and copepods were found to be living very close to the bottom in daytime and he predicted that 'it is quite to be expected that in course of time many young stages of animals that have been rarely caught will appear in greater quantity in such collections' (Russell 1928). The same net was used by Tattersall (1938) to study the mysid fauna of the same area. He concluded that species-specific diurnal, seasonal and ontogenic migrations were common and that 'idly swimming just above the bottom' was a normal feature of these animals' lives. Early intertidal collections of the bottom plankton were made with tow nets around the same time (Elmhirst 1932, Watkin 1939, 1941: see below).

In a next stage, some simple sledges with or without closing mechanism were constructed (Beauchamp 1932, Elster 1933, Walford 1938, Werner 1938). In the early fifties, more elaborate plankton trawls were devised, which were fitted with opening and closing devices to obtain uncontaminated samples from the bottom layers in deeper waters and intertidal areas (Bossanyi 1951, Greze 1951, Wickstead 1953, Colman & Segrove 1955). Around this time the 'small natant fauna immediately above the sea floor' was seen as an ecological entity (Bossanyi 1957). Their importance in the diet of fish was explicitly recognized, which led to an increased interest. The fauna was found to be diverse and to reach high densities, and it was stated that it 'undoubtedly plays an important role in the economy of the sea' (Bossanyi 1957). Although, until that time, the fauna was usually included in the plankton, Smidt (1951) distinguished between 'true benthos' which lives permanently on the bottom, and 'nekto-benthos', comprising species that occur both along the bottom and higher in the water column.

#### 1.4.2. The hyperbenthos as defined by Beyer

Beyer (1958) designed and used a sledge (described in Holme 1964) to study the bottom plankton populations in the Oslofjord (Norway). Besides a preponderance of a new species of Trachymedusae, otherwise rarely encountered calanoid copepods were discovered. Species that were generally known as plankton were found in much higher concentrations in the vicinity of the bottom. His study led him to conclude that 'whatever the reason for the remarkable proximity of the bottom plankters to the sea bed, they should, in accordance by the view held (at that time by Shelford & Boesel 1942, Jones 1950), be considered functional members of the soft bottom animal community whilst they remain in the vicinity of the soft bottom' (Beyer 1958). He continued that they 'thus constitute, together with members of the nekton, the

uppermost, *hyperbenthonic* subdivision of the biocoenosis'. He also introduced the term hyperpelos to designate those organisms that live just above the mud, by analogy with the terms endopelos and epipelos, referring to animals living in and on the mud, respectively (terms introduced by Remane in 1940). A further distinction was made between tychobenthonic (< Gk *tycho* accident) and hekobenthonic (< GK *hekon* voluntary) components of the hyperbenthos. The former are basically pelagic species (plankton or nekton), which, due to negative phototropism, are 'accidentally' found in the hyperbenthos (depth-loving animals that are found in the vicinity of the bottom because the bottom happens to be there), while the latter are the true members of the benthonic community or those animals that join it on purpose (animals that are in some way related to the bottom).

#### 1.4.3. Later quantitative field studies

Since the work of Beyer (1958), quite a number of studies dealing with hyperbenthic communities have been published. A comparison of the results of these studies is not straightforward, for a number of different reasons. A first problem is the arbitrary elimination of species from the species lists. Secondly, densities are either expressed per unit of volume of water that is filtered or per unit of area of the surface that is trawled. Finally, the composition of the species lists depends on the methods that are used for collecting. In the following sections, emphasis is placed on the gross taxonomic composition, on reported densities and on general patterns in vertical distribution and seasonality.

##### *Shallow coastal and shelf areas*

Bieri & Tokioka (1968) sampled the hyperbenthos quantitatively down to a depth of 100m in Tanabe Bay (Japan) with a two-level sledge. Gammaridean amphipods occurred with densities of up to 80000 individuals per 100m<sup>3</sup> in the water layer from 0 to 20cm above the bottom, while the layer from 20 to 40cm never contained more than 500 individuals per 100m<sup>3</sup>. The same trend was also observed for subdominant groups like mysids (3300 versus 50), copepods (7600 versus 150), cumaceans (1900 versus 0) and decapod larvae (4300 versus 100).

Hesthagen (1970) used Beyer's sledge over the Great Meteor (8 samples) and Josephine seamounts (7 samples) down to a depth of 300m. Recorded densities ranged from 81 to 3400 individuals per 100m<sup>3</sup>. Copepods were found to dominate the fauna. A variety of other taxonomic groups (mainly polychaetes, ostracods, decapods and mysids) were also found to be abundant. The same author made the first extensive study on diurnal and seasonal patterns in the hyperbenthic community of the deeper channels (-30m) of the Kiel Bight (Hesthagen 1973). Cumaceans generally dominated the fauna with densities ranging from 300 to 26000 individuals per 100m<sup>3</sup> in winter and summer, respectively. Subdominant groups were mysids (including a lot of rare and new species), copepods and chaetognaths. Densities of the latter taxa rarely exceeded

1000 individuals per 100m<sup>3</sup>. Representatives of a variety of rarer taxa were also collected, a.o. coelenterates, cladocerans, isopods, pycnogonids, postlarval fish, amphipods, euphausiids and decapods. Seasonal variations in the hyperbenthos of the Kiel Bight were further investigated by Boysen (1975a, 1975b, 1976). A yearly average of monthly samples in 8 stations (-8 to -25m) yielded hyperbenthic densities of 1600 individuals per 100 m<sup>3</sup>. A marked seasonality was observed for several groups with maximal densities in February-May and again in September, and with minimal densities in December. Regional differences in the composition of the fauna were observed to be correlated with (1) sediment type (amphipods were dominant over sand, while cumaceans and polychaetes were rather found over mud), (2) depth (isopods and fish larvae tended to occur in the shallower stations, mysid species were found to be segregated bathymetrically) and (3) dissolved oxygen concentration (especially important for mysid distribution). Diurnal variations in a 30m deep station were later studied by Hesthagen & Gjermundsen (1979). The summer fauna was dominated by one polychaete species (400 to 1500 individuals per 100m<sup>3</sup>), one cumacean (1000 to 4000 individuals per m<sup>3</sup>) and one chaetognath (100 to 700 individuals per 100m<sup>3</sup>). Day-night differences mainly consisted of changes in density patterns of cumaceans, mysids, caridean and paguroid larvae. The former group was mainly present in night catches while all other groups were largely restricted to day catches. The existence of the hyperbenthic community in the area was briefly disputed by Anger & Valentin (1976), whose criticism was based on doubts concerning the adequacy of the sampling methodology. Their arguments were later convincingly refuted by several authors (e.g. Hesthagen & Gjermundsen 1978, Schnack 1978, Huberdeau & Brunel 1982).

Oug (1977) used a modified Beyer sledge to study the hyperbenthos in a shallow (22 to 24m) land locked fjord on the west coast of Norway. The sledge was fitted with three nets, in a manner to obtain simultaneous, overlapping samples of the hyperbenthos. She concluded that the hyperbenthos was a fauna with its own characteristic species distribution, different from that obtained by simply adding zooplankton and vagile benthic forms in a fixed proportion. From January to March a pronounced seasonal change in quantity and quality was observed. The most common taxa (with maximal recorded densities) were chaetognaths (8900 per 100m<sup>3</sup>), coelenterates (1700 per 100m<sup>3</sup>), cumaceans (1430 per 100m<sup>3</sup>), cirriped larvae, decapods, calanoids, cladocerans and fish eggs (all latter groups with densities between 500 and 1000 individuals per 100m<sup>3</sup>). Hesthagen & Gjermundsen (1978) took deep (115m) daytime samples in Oslofjord (Norway). The dominant taxa were calanoids (around 1000 per 100m<sup>3</sup>), mysids, cumaceans, polychaetes, coelenterates and chaetognaths (each around 500 per 100m<sup>3</sup>), amphipods and carideans (between 50 and 100 per 100m<sup>3</sup>) and euphausiids (less than 10 per 100m<sup>3</sup>). The modified Beyer sledge was later used by Fossa (1985) and Kaartvedt (1985) in their detailed studies on the small-scale vertical distribution of hyperbenthic mysids in deep Norwegian fjords (150 to 220m). A modified Rothlisberg & Percy (1977) sledge was used by Buhl-Jensen (1986) and Fossa & Brattegard (1990) to examine the bathymetric distribution of mysids in Norwegian fjords. Buhl-Jensen & Fossa (1991) further studied the hyperbenthic crustaceans

along a transect from the Skaggerak to the inner Gullmarfjord, in Sweden. Hyperbenthic amphipods of the Norwegian continental shelf were compared with the fauna of 5 adjacent fjords by Buhl-Jensen (1986). Deep shelf localities (-247 to -520m), shallow shelf localities (-147 to -272m) and fjords were characterized by distinct amphipod communities. A change in the amphipod fauna was observed at -200 to -300m depth. Bathymetric isolation, depth and median grain size of the sediment were found to be significantly correlated with diversity which, as a result, was higher in shelf sites than in the fjords. Oedocerotidae was the dominant family, especially over mud substrates, which was also observed by Sainte-Marie & Brunel (1985) in the Gulf of St Lawrence.

Seasonal changes and diurnal vertical migrations of the hyperbenthos of the gulf and estuary of St Lawrence were studied extensively at depths between 10 to 400m (Brunel *et al.* 1978, Brunel 1979). Huberdeau & Brunel (1982) used the two-level Macer-GIROQ sledge in a deep station (-350m) in the same area. The lower net (sampling the section between 28 and 64cm above the bottom) contained 680 to 1065 individuals per 100m<sup>3</sup> representing 87 species, while the upper net (sampling the section between 106 and 142cm above the bottom) only caught 1 to 169 individuals per 100m<sup>3</sup>, representing 21 species. The same trend was observed in a shallow station (-20m): the lower net caught 1600 individuals per 100m<sup>3</sup> (54 species), the upper net 45 individuals per 100m<sup>3</sup> (5 species). Thus, at both localities, the lower one metre was shown to be the most important stratum by far. Using a slightly modified model, Chevrier *et al.* (1991) compared the structure of hyperbenthic gammaridean amphipod communities in the Bay of Fundy, Baie des Chaleurs and the Gulf of St Lawrence. They reported average densities of 450, 1300 and 120 to 300 individuals per 100m<sup>3</sup> in the 3 subareas, respectively. Densities in the lower net were consistently higher than those in the upper net. The same sledge was also used by Wildish *et al.* (1992) over the Browns Bank. They sampled down to a depth of 240m in different seasons, over hard bottoms and in some places over rocky sands or gravel (34 stations). In this study, daytime densities in the upper and lower nets were not significantly different ( $3300 \pm 1100$  and  $3850 \pm 1690$  individuals per 100m<sup>3</sup>, respectively). Copepods dominated the fauna, with only about 75 individuals per 100m<sup>3</sup> of other taxa (mainly amphipods). Some amphipod and cumacean species had significantly higher densities in the lower net. Marked seasonal differences were also observed in selected stations.

Following the construction of a new two-level sledge (Sorbe 1983), the continental shelf of the Gulf of Gascogne was studied in detail (Cornet *et al.* 1983, Sorbe 1984, 1989). Twelve stations were sampled along a bathymetric transect from 25 to 237m depth. Important qualitative depth-related and day-night differences were noted. The upper net (sampling the section between 50 and 100cm above the bottom) contained 1.1 and 13.8% of the fauna in the lower net (which sampled between 0 and 50cm above the bottom) during day and night, respectively. Stations at -31 and -91m depth were characterized by two distinct communities, with fewer species (56 versus 104), lower diversity and more pronounced seasonal density fluctuations in the shallower station. Average annual densities were 8730 individuals per 100m<sup>3</sup> at 31m, and 3620 (day) and 2060 (night) at 91m. In the shallow station, amphipods (68%) and

mysids (29%) dominated the fauna, with a minor presence of cumaceans (1.4%), euphausiids and Natantia (both less than 1%). In the deeper station, mysids (44%) and amphipods (27%) still predominated, but ranking in reverse order, while Natantia (11.9%), euphausiids (9.9%) and cumaceans (5.5%) occurred in more sizeable quantities. During the night, the dominance of mysids decreased (17%), while that of amphipods and cumaceans increased to 42 and 16%, respectively. Elizalde *et al.* (1991) used a modified Macer-GIROQ sledge to study the hyperbenthos at great depths in the Cap-Ferret canyon (see below).

The hyperbenthos of the shallow (-5 to -10m) coastal zone in the Dutch delta area was studied at 24 stations, during one year, and with a simple sledge (Hamerlynck & Mees 1991, Mees & Hamerlynck 1992, Cattrijsse *et al.* 1993, Mees *et al.* 1993a). The yearly average density was 160 individuals per 100m<sup>3</sup>, with monthly averages ranging from 10 in February to 660 in June. Mysids dominated the fauna (with a maximum of 150 individuals per 100m<sup>3</sup>); the other more important permanent members of the hyperbenthos were amphipods, cumaceans and isopods, while temporary hyperbenthic taxa included larval and postlarval stages of polychaetes, carideans, brachyurans and fish. Seasonal patterns strongly influenced the hyperbenthic community structure.

The hyperbenthos of a shallow (-10m) station in the Bay of Seine (eastern English Channel) was studied in two 24-hour sampling campaigns in June (Wang & Dauvin 1994, Wang *et al.* 1994), using a modified Macer-GIROQ sledge that sampled at 4 levels (Dauvin & Lorgeté 1989). Mysids and cumaceans dominated the permanent hyperbenthic fauna. Average density was 220 individuals per 100m<sup>3</sup>. Average daytime density was 120 individuals per 100m<sup>3</sup>, with 56% of the animals caught in the lower net. Average night density was 480 individuals per 100m<sup>3</sup>, with a more even distribution of the animals over the four nets. Other groups (mainly ctenophores, copepods and crustacean larvae) reached average densities of 21600 individuals per 100m<sup>3</sup> (16600 during day, 33700 at night). In a 75 m deep station in the western English Channel densities of 30 to 1720 individuals were reported, with an average of 240 for six campaigns). Over this coarse sand substrate, mysids (22%) and amphipods (74%) predominated (Dauvin *et al.* 1994), and animals were mainly concentrated in the lower net.

### *Deep-sea*

Hyperbenthic associations of animals are also known to inhabit the near-bottom environment of the deep-sea. This fauna is usually termed benthopelagic plankton (Marshall & Merrett 1977), and the zone in which they occur is referred to as the benthopelagic or benthic boundary layer (Wishner 1980a, 1980c, Childress *et al.* 1989, Mauchline & Gordon 1991, Hudon *et al.* 1993, Dauvin *et al.* submitted). In the deep ocean, the sea bed can be viewed as a sediment sink, halting the downward drift of particles. Resuspension and biological and geochemical processes within the benthic boundary layer lead to an enrichment of the waters above the sediment. In parallel with

this enrichment, a probably related increase of the pelagic biomass occurs, at least to a distance of up to 100m from the bottom (Wishner 1980a). This hyperbenthic zone seems to be inhabited by a distinct community of nektonic and planktonic species. As in coastal and shelf waters, a higher biomass is generally observed at the boundary layer, relative to the water column immediately above it (Wishner 1980a). Besides an enrichment in biomass, the abyssal benthopelagic zone also contains a higher number of species relative to the overlying water column (Angel 1990). It is inhabited by (1) pelagic species whose ranges are truncated by the sea bed, (2) benthic species that use the zone as a refuge for dispersal or for locating their food, and (3) a specialized fauna which includes many novel species (Angel 1990). Deep-sea hyperbenthic communities were also referred to as demersal zooplankton by a.o. Grice (1972).

Samples are usually taken with specially designed plankton nets or benthic trawls, or by mounting nets on submeribles (Grice 1972, Wishner & Meise-Munns 1984). A hyperbenthic net which opens and closes simultaneously with benthic nets was added to a sophisticated epibenthic sledge designed to sample the deep-sea megafauna, thus sampling the section from 0.6 to 1.2 m above the sea floor (Rice *et al.* 1982).

Most early collections from deep-sea environments were made to describe new species. New hyperbenthic copepods were described from -1200 to -1700m off New Zealand (Bradford 1969) and from -1200 to -1700m in the Atlantic (Grice & Hulsemann, 1970, Grice 1972). The hyperbenthic community on the slopes of the Porcupine Seabight (S.W. Ireland) has been sampled with a rectangular mid-water trawl. The decapods and mysids are described by Hargreaves (1984, 1985), the ostracod fauna by Ellis (1985).

The first community analysis of deep-sea hyperbenthos was presented by Wishner (1980c). Samples were taken in the San Diego Trough, the eastern tropical Pacific and the northeast Atlantic. The water layers from 10 to 100 m above the bottom were sampled at depths of -1100 to -3200m with an opening-closing net with 183 $\mu$  mesh size. 80% of the animals that were collected were copepods. Other abundant groups were isopods, ostracods and chaetognaths. Representatives of larger taxa were found to be rare, but this may have been due to net avoidance. In contrast to shallower areas, day samples were found to be similar to night samples. Densities ranged from 2 to 230 individuals per 100m<sup>3</sup>. Another difference with shallower areas, was the near-absence of larvae of benthic animals. Still, larval and juvenile stages of many benthic species were reported to occur between 1 and 5m above deep-sea hydrothermal vents (Berg & Van Dover 1987). These waters are enriched in terms of biomass and abundance with respect to non-vent areas, but they are depleted in biomass relative to the surface zooplankton.

Recently, the structure and species composition of the hyperbenthic communities of the Arcachon plateau and the Cap Ferret canyon (Bay of Biscay) have been described (Elizalde *et al.* 1991, 1993, Dauvin *et al.* submitted). Samples were taken from depths of -346 down to -3070m with a modified Macer-GIROQ sledge (Dauvin & Lorgeté 1989). Asselote isopods and gammaridean amphipods dominated the fauna,

with mysids becoming less important with increasing depth. Three depth intervals, each characterized by a specific hyperbenthic fauna, could be identified. The hyperbenthos of the upper part of the plateau (muddy sand substrate between -350 and -500m) was characterized by high densities, and mainly consisted of asellote isopods. At intermediate depths (mud substrate between -600 and -1100m) amphipods dominated the fauna, sometimes accompanied by cumaceans. In the canyon proper, isopods predominated again, with significant numbers of pycnogonids and tanaidaceans. Densities in the lower net were about 2700 individuals per 100m<sup>3</sup> at -430m, 4500 at -710m, 600 at -1030m and 700 at -3060m. Densities in the other 3 nets were always much lower.

The Catalan sea (western Mediterranean) was sampled qualitatively at 10 stations between -552 and -1808m, using a small plankton net attached to a beam trawl (Cartes & Sorbe 1993). This study yielded 9 new records of pericarid crustaceans for the Mediterranean. On the upper slope amphipods predominated; cumaceans became progressively more abundant with increasing depth, and they dominated on the lower slope.

### *Estuaries*

Like other benthic compartments, brackish water hyperbenthic communities also have fewer species than their marine counterparts. The St Lawrence estuary was studied in detail (Dauvin & Dodson 1990, Dodson *et al.* 1990), and several European estuaries have also been well investigated, like the Gironde (France), the Westerschelde (The Netherlands) and the Eems (The Netherlands) (Sorbe 1981b, Mees *et al.* in press). Sorbe (1981b) reported very high hyperbenthic densities for the Gironde estuary. Different salinity zones were characterized by a specific fauna. Besides estuarine endemics, a variety of animals of freshwater and marine origin were present (Sorbe 1981b). Densities of over 300 mysids per m<sup>3</sup> were recorded in summer. Williams & Collins (1984) studied the mysid fauna of the Bristol Channel and Severn estuary with a high speed plankton sampler and a Macer sledge. *Schistomysis spiritus* peaked in September with 14 per m<sup>3</sup> (250 per m<sup>2</sup>), which constituted 76% of the omnivore biomass. Over one year, the species was found to contribute 43% of the total integrated omnivore standing stock. Abundance was mainly correlated with temperature and salinity, which are subjected to seasonal change. Species occurred in well-defined salinity zones. Jones *et al.* (1989) sampled the mysids close to the bottom of the Avon-Heathcote estuary (New Zealand) with a weighed plankton net. They reported mysid densities ranging from 20 to more than 1500 individuals per 100m<sup>3</sup> and also found species to be separated along the salinity gradient. The same conclusion was reached by Mees *et al.* (1993a, 1993b, in press) in studies in the Eems, Westerschelde and Gironde estuaries. In the marine reaches generally fewer than 600 individuals per 100m<sup>3</sup> were recorded, while in the oligohaline part densities were an order of magnitude higher. A summer peak of 31250 individuals per 100m<sup>3</sup> was recorded in the Westerschelde (Mees *et al.* in press). Yearly averages for 2 stations in this estuary



amounted to 60 individuals per 100m<sup>3</sup> in the marine part (ranging from 2 in winter, 190 in spring), and 3000 individuals per 100m<sup>3</sup> in the brackish part (ranging from 30 in May to 8450 in April). In the Tamar, densities of *Mesopodopsis slabberi* shifted from less than 5000 individuals per 100m<sup>3</sup> in spring to more than 100000 in summer, while *Neomysis integer* reached 20000 individuals per 100m<sup>3</sup> (Moffat & Jones 1992).

### *Intertidal areas*

Data on intertidal hyperbenthic communities are very scarce. Some papers report on vertical movements in intertidal waters. Early plankton collections with tow nets at the edge of sandy beaches (Elmhirst 1932, Watkin 1939, 1941) showed that certain species of amphipods swim to the surf zone during the night. A distinction can be made between local endobenthic species that actively perform nocturnal vertical migrations and tidal migrants carried in from sublittoral habitats by the tide. A light, man-hauled two-level bottom sledge for intertidal collections was later developed by Colman & Seagrove (1955). Studying the water's edge of a sandy beach in summer they found that amphipods, mysids and decapods dominated the fauna. Other taxa included isopods, cumaceans, copepods, pycnogonids, polychaetes and gastropods. Few endobenthic species that are known to occur in the same area were found. Species which were previously thought to inhabit the sand were found to swim for 2<sup>-1</sup> to 283<sup>-1</sup> of the time that the beach was covered with water; the same range was reported by Watkin (1939, 1941). Sex ratio's differed in and above the sand for some species, and species-specific small scale vertical zonation were noted. An improved version of this sledge was later used to study amphipods in the surf plankton (Fincham 1970). Clear seasonal variations in numbers were also reported, with spring (Elmhirst 1931) or summer (Fincham 1970) maxima. Wooldridge (1983, 1989) used sledges to sample the surf zone of sandy shores in South Africa. Densities of the dominant mysid species often exceeded 15 individuals per m<sup>2</sup>. Migrations of various crustacean groups have also been reported over rocky shores (Jansson & Källander 1968) and seagrass beds (Ledoyer 1964). Marked day-night differences were evident. The most detailed study on intertidal hyperbenthos was performed by Sibert (1981) in the Nanaimo estuary. Two pumps, sampling at 5 and 30cm above the bottom, were deployed to study the meiohyperbenthos (>100µm) in spring. Total densities ranged from 400 to 14000 individuals per m<sup>3</sup>. The dominant taxa were harpacticoid, calanoid and cyclopoid copepods in several life history stages, various categories of meroplankton, and nematodes. Isopods (50 to 9600 per 100m<sup>3</sup>), mysids (0 to 2300 per 100m<sup>3</sup>), amphipods (200 to 2000 per 100m<sup>3</sup>) and cumaceans (40 to 2600 per 100m<sup>3</sup>) were also represented, but in smaller numbers. This is comparable with densities reported for macrohyperbenthos communities in subtidal areas. Consistently large differences in population density were observed between the two levels. Densities in the bottom samples always exceeded those in the top samples by a factor between 2 and 20. Cat-trijse *et al.* (1994) studied the hyperbenthos that visits a creek in a brackish tidal marsh (Westerschelde estuary). A stow net, modified after McIvor & Odum (1986),

was used to passively sample the fauna entering and leaving the creek with the tide, monthly during 2 years. Total hyperbenthic density ranged from 10 (winter) to 30000 (summer) individuals per 100m<sup>3</sup>. Mysids, amphipods, isopods, and postlarval fish, shrimp and crabs dominated the fauna. The mysids, amphipods and isopods are discussed in detail in Mees *et al.* (1993) and Cattrijsse *et al.* (1993). Peak densities of the mysids *Neomysis integer* (24000 individuals per 100m<sup>3</sup>) and *Mesopodopsis slabberi* (20200) were observed in early summer and autumn, respectively.

### *Tropical areas*

Most studies in subtropical and tropical environments deal with sandy lagoons in reef areas. Usually traps are deployed, with mesh sizes varying from 63 to 333 $\mu$ . This makes comparisons of reported densities and species lists quite difficult (Youngbluth 1982). Comparisons are further complicated by the fact that most studies are restricted in time. Only some general features and recent key-studies are discussed here (more references can be found therein).

Coral reefs have been shown to harbour a unique and abundant hyperbenthic fauna, that is not found in the surrounding waters (Sale *et al.* 1976, 1978, Goswami 1979). Constituents of this reef habitat assemblage are usually referred to as resident, swarming or demersal zooplankters (Emery 1968, Hamner & Carleton 1979). The most common taxa are copepods, amphipods, cumaceans, mysids, ostracods, tanaids, caridean and anomuran larvae, polychaetes, chaetognaths, larvaceans, fish larvae and mollusc veligers. Alldredge & King (1985) studied a subtidal sand flat in the Gulf of California. Copepods, amphipods and isopods predominated the fauna, followed by ostracods, cumaceans, tanaids and polychaetes. Carideans, mysids, cephalochordates and decapod larvae were only occasionally caught. All these animals remain closely associated with the substratum during daytime (Jacoby & Greenwood 1988). There is some discussion as to the extent of their upward migration into the water column. Smaller animals have been reported to remain within 0.3m of the bottom, while larger individuals were found to migrate throughout the watercolumn (Alldredge & King 1985). Jacoby & Greenwood (1988) found that all animals, independent of size, moved to at least 0.5m from the bottom. Studies with emergence traps have indicated that the distribution, abundance and behaviour of these animals varied with location on the reef, season, substratum type, lunar period, and daylight and that these effects varied for different taxa (Alldredge & King 1977, 1980, 1985, Porter *et al.* 1977, Porter & Porter 1977, Feeley *et al.* 1979, Hobson & Chess 1979, McWilliam *et al.* 1981, Ohlhorst 1982, Jacoby & Greenwood 1988). Lewis & Boers (1991) reported marked temporal variability and patchiness, in a study based on weekly sampling over one year. Re-entry trapping in a shallow bay in North Carolina showed that demersal zooplankton is taxonomically distinct from the holozooplankton, and that high densities typically occur (Cahoon & Tronzo 1992). Densities reported with emergence trapping range from less than 50 to nearly 500 individuals per m<sup>2</sup> per hour (references and study areas in Youngbluth *et al.* 1982) or 160 to 8000 individuals per m<sup>2</sup> per night (Jacoby &

Greenwood 1988, and references therein).

The majority of these studies has concentrated on demersal zooplankton, referring to organisms that burrow or hide within the reef substrate during the day, rise up into the water column at dusk and return before dawn (Carleton & Hamner 1989). Mysids usually constitute only a very small portion of the samples that are collected by emergence or re-entry trapping. Carleton & Hamner (1989) monitored the seasonal and diel variations in community structure of mysids in the Davies reef lagoon (Great Barrier reef) during one year. Densities were higher during the day than during the night. The epibenthic mysid community differed from that of the overlying section of the water column. They found marked seasonality and diel groupings. Densities ranged from 110 to 790 individuals per  $m^3$ . Schooling species occurred at local densities of up to 500000 per  $m^3$ .

### *Rocky substrates*

Hardly any information is available on hard substrates other than coral reefs. The very few papers found report on the performance of new sampling gear. Potts (1976) described a diver-controlled plankton net. Lasenby & Sherman (1991) tested a bottom-closing drop net at depths ranging from -7 to -27m in lake Ontario and caught 50 to 300 mysids per  $m^2$ . The same apparatus was used in a shallow (-0.1 to -2m) lake in New Zealand, where densities up to 800 mysids per  $m^2$  were reported close to the shore (Lasenby & Sherman 1991). Setran (1992) made preliminary intertidal collections with a new trap on the California coast. He mainly recorded calanoid and harpacticoid copepods, gammarid and caprellid amphipods, mysids and larval crabs.

#### 1.4.4. Selected topics of hyperbenthos research

##### *Taxonomic interest and diversity*

A common feature of papers reporting hyperbenthic research is the overwhelming evidence that most species encountered in the hyperbenthos either (1) are endemic, i.e. are not found elsewhere, (2) are present in much higher densities there than in the overlying water layers or in the adjacent sediment, and (3) are not there accidentally. Beyer (1958) already discussed species that are found in abundance in the hyperbenthos which were rare or absent elsewhere. More recent studies have led to the recognition of a distinction between truly hyperbenthic species and a variety of 'visiting' animals that can either be classified as meiobenthic or macrobenthic species. Many of the areas investigated to date are near to old marine biological stations, allowing a comparison between sampling methods to be made. Huberdeau & Brunel (1982) compared the selectivity of endo-, epi- and hyperbenthic samplers. They were able to show that the Macer-GIROQ hyperbenthic sledge sampled a specific fauna. A higher diversity in the hyperbenthos, compared to the macrobenthos of the same area was demonstrated by Cornet *et al.* (1983). With the modern gear, to give only a few

examples, a new species of *Trachymedusa* was discovered in the Oslofjord (Beyer 1958), Carleton & Hamner (1989) recorded 6 new mysid species for the Great Barrier Reef, Mees & Fockedey (1993) found a hitherto undiscovered isopod species in the Gironde estuary and 15% of the 69 gammaridean species collected by Dauvin *et al.* (1994) were new for the Roscoff fauna. The latter authors also compared their hyperbenthic catches with macrobenthos samples from the same area, concluding that they comprised different kinds of species.

Early studies already demonstrated the taxonomic interest of the hyperbenthos. As mentioned above, Beyer (1958) found a new, bottom-living *Trachymedusa*. Using the same gear, Matthews (1961) reported a new calanoid copepod. Fosshagen (1968) and Brattegard (1973) described several new copepod and mysid species collected off the Bahamas and Colombia with a modified Ockelmann detritus-sledge (Ockelmann 1964). Omori (1969) also found many new species and high abundances of species which were scarcely collected by ordinary plankton townets. The recognition of the hyperbenthos as a specific habitat has increased in recent years. Many species of a variety of taxonomic groups are now explicitly referred to as hyperbenthic. Besides mysids, probably the most typical hyperbenthic taxon (Mauchline 1980), several new species, genera and even a family of Copepoda Calanoidea (Grice & Hulsemann 1970, Grice 1972, Ohtsuka & Mitsuzumi 1990, Ohtsuka *et al.* 1991, Ohtsuka *et al.* 1992, Ohtsuka *et al.* 1993), a variety of new benthoplanktonic chaetognaths (Casanova 1992), and an entirely novel hyperbenthic ostracod fauna (Angel & Baker 1982, Ellis 1985) have recently been described.

Many taxa which were previously thought to be exclusively endobenthic, epibenthic or pelagic, are now found to have hyperbenthic representatives. Benthopelagic medusae are more numerous and diverse than previously believed with densities up to 80 individuals per m<sup>2</sup> on or near the bottom (Larson *et al.* 1992). Hydromedusae concentrate in the hyperbenthos during the day (Arkett 1984) and the same applies to sea cucumbers (Pawson & Foell 1986). Swimming holothurians were also recorded in high densities from abyssal depths (e.g. Childress *et al.* 1989). Concentrations of chaetognaths near the bottom were already noted by Russell (1928). A much greater diversity in habitat utilization by different groups of chaetognaths is now recognized (Bieri 1991). Decapod larvae have been shown to be more common along the bottom during the day than during the night (Bossanyi 1957, Hesthagen & Gjermundsen 1979) and some stages of larval polychaetes are reported to swim close to the bottom (Qian & Chia 1989). Since body size of marine invertebrate larvae can impose restrictions on the mode of locomotion, differences in ways of propulsion between life history stages occur, and this affects their choice of habitat (Chia *et al.* 1984). Antarctic krill change their habitat from the pelagic zone to the hyperbenthos as a strategy to survive the winter under the coastal fast ice (Kawaguchi *et al.* 1986). Hyperbenthic or semi-hyperbenthic fish microhabitat guilds (mainly small-sized fish like gobies) have been described (e.g. Costello 1992, Wilkins & Myers 1992).

An important taxonomic group among temporary members of the hyperbenthos is late-stage larval fish. Especially the larger fish larvae are most abundant in the near-

bottom layers. The distribution of larval fish is controlled by both active behaviour and passive transport mechanisms. These mechanisms result from a combination of biotic and abiotic factors (Norcross & Shaw 1984). Biotic factors include seasonal abundances of adults and larvae, environmental preferences, availability of suitable food, potential predators, and behaviour of the larvae. Physical-chemical factors are the oceanography or hydrological and climatological parameters of the area, including temperature, salinity, stratification, turbidity, riverine discharges, weather patterns and water-flow patterns, rates, directions, and anomalies. Reproduction and spawning occur in a selected portion of the species' total range. The relative importance of passive and behaviourally mediated transport is still under discussion. The depth distribution of fish larvae is also discussed by Brewer & Kleppel (1986) and Jahn & Lavenberg (1986).

### *Small-scale zonation*

Population assessment and sampling problems relating to vertically and horizontally unevenly distributed species and patchiness are discussed by Omori & Hamner (1982). Several authors have investigated vertical distribution patterns of species residing close to the bottom, with nets mounted at different levels on sledges (Oug 1977, Hesthagen & Gjermundsen 1978, Brunel 1979, Sainte-Marie & Brunel 1983, 1985, Fossa 1985, Kaartvedt 1985, Elizalde *et al.* 1991, Dauvin *et al.* 1994, Wang & Dauvin 1994). Swimming activity and preferred height above the bottom were found to differ between sexes and between developmental stages, both in shallow (Clutter 1967, 1969, Wittmann 1977) and deeper areas (Fossa 1985, Kaartvedt 1985). A valuable tool for measuring swimming activity and classifying species are the coefficients used by e.g. Elizalde *et al.* (1991) and Dauvin *et al.* (1994), especially when a four-level net is used. These investigations have shown that both plankton and vagile benthic species differ in their vertical zonation in the near-bottom area. Generally, the highest number of species is found in the lowermost layers sampled (Dauvin *et al.* 1994). In a deep-sea environment, Dauvin *et al.* (submitted) recognized an overall vertically increasing density gradient; some species occurred preferentially in the upper layers, while others were equally represented in both depth strata that were sampled.

Diel activity patterns close to the sediment have been documented for several groups. Generally, deep living hyperbenthic cumaceans and amphipods are living in association with the sediment during the day. Swimming activity increases during darkness, with a variety of migration patterns within the lower metres of the water column (Brunel 1979, Sainte-Marie & Brunel 1983, 1985, Kaartvedt 1986). Although occasional planktonic catches have been reported, the amplitude of the vertical migrations is usually small (Kaartvedt 1989). Direct observations of hyperbenthic mysids show that different species display varying degrees of affinity to the substratum (O'Brien 1988, O'Brien & Ritz 1988). Clutter (1969) studied the swarming and schooling of pelagic invertebrates in hawaiian waters. Mysid species occurred in well defined layers near the sea floor, usually tied to specific sediment types and in well

defined bathymetric zones. Mauchline (1980) also provides evidence that some hyperbenthic species of mysids prefer certain types of substrates. In the intertidal zone, at the edge of sandy beaches, small scale vertical zonation can also be observed (Colman & Segrove 1955, Sibert 1981).

#### *Day-night rhythms and vertical migrations*

Many hyperbenthic species show diel and tidal changes in their distribution. These are mainly in the form of nocturnal (especially in marine and lacustrine environments) or tidally-phased (especially in estuaries) vertical migrations (Hough & Naylor 1992). Many authors have noted the nocturnal vertical movement of benthic organisms into the water column, including amphipods, isopods, cumaceans, copepods and decapods (Macquart-Moulin 1976, 1984, 1985, 1991), crab larvae (Sulkin 1984) and polychaetes (Evans 1971). Kaartvedt (1985), using sledges at 150 m depth in Fanafjorden (Norway), found a great number of mysid species near the bottom during the day, living in, at or close to the sediment. Many of these undertook vertical migrations at night, but a significant proportion of the total population of each species remained in the hyperbenthic layer during darkness. The hypotheses put forward to explain vertical migrations refer to availability of food in superficial layers, advantage of lower metabolism at deeper layers, avoidance of visual predation, horizontal dispersion and breeding migrations. Vertical movements in intertidal waters are well documented (e.g. Russell 1925, Elmhirst 1931, Watkin 1939, 1941, Coleman & Seagrove 1955). Over rocky shores, a variety of taxa are also known to perform vertical migrations into the surf at night (Jansson & Källader 1968, Setran 1992).

#### *Meiohyperbenthos*

Studies of meiofaunal recolonization after sediment disturbance indicate that partial recovery occurs within a few tidal cycles (Sherman & Coull 1980). Recruitment for this rapid recovery may occur through hyperbenthic populations. Recent investigations revealed a partially hyperbenthic occurrence of meiofauna which was regularly caught in sediment traps high above the ground (Palmer 1988, Armonies 1988). By analogy to the meiobenthos *sensu stricto*, the term meiohyperbenthos could be introduced, as opposed to macrohyperbenthos (animals larger than 0.5 or 1 mm). Periodical hyperbenthic behaviour has been reported from harpacticoids (mainly diatom eaters), encompassing both passive suspension and active emergence for rapid dispersion and recolonization (Armonies 1988, 1989a, 1990, Bell & Sherman 1980, Palmer 1988). A considerable amount of turbellarian species regularly enters the overlying water column (Armonies 1989b, Giere 1993). After distribution through water currents they can colonize new areas in a short while. This hyperbenthic behaviour is preferably nocturnal (Armonies 1989a, 1989b, 1990). Meiobenthic copepods were also reported from water layers over seagrass beds by Bell *et al.* (1988).

## 1.5. Role in marine food webs

For most hyperbenthic taxa, much of the basic information on relationships between length, weight and chemical composition is generally not available in sufficient detail for the study of energy fluxes through food webs. Secondary production estimates are scattered and, with few exceptions, not detailed for any one species. Naturally, for broad ecological studies, in contrast to experimental studies, this kind of information may not need to be precise, as it is pointless carrying out analyses and calculations to a greater accuracy than the sampling methodologies themselves allow. For a review on the productivity of epi- and hyperbenthic species we refer to Redant (1989). Some recent detailed studies giving production estimates for mysids are Rudstam *et al.* (1986) for baltic populations of *Mysis mixta* ( $0.6 \text{ g carbon m}^{-2} \text{ yr}^{-1}$ ), Sorbe (1991) and San Vicente & Sorbe (1990) for littoral populations of *Schistomysis ornata* ( $23 \text{ mg ashfree dry-weight m}^{-3} \text{ yr}^{-1}$ ) and *S. kervillei* ( $130 \text{ mg ashfree dry-weight m}^{-3} \text{ yr}^{-1}$ ) and Mees *et al.* (1994) for an estuarine population of *Neomysis integer* ( $300 \text{ mg ashfree dry-weight per m}^{-2} \text{ yr}^{-1}$ ).

It is not clear from the available literature where the hyperbenthos can be expected to be most important. Whether high hyperbenthic densities are accompanied by decreasing densities of other benthic compartments is also not clear to date. The highest hyperbenthic densities have been reported from the brackish reaches of estuaries, eutrophic shallow coastal areas and medium to deep areas of continental slopes. In very turbid areas, where the hyperbenthos tends to peak, clogging of feeding mechanisms and the risk of burial generally causes sessile guilds to diminish (Pearson & Rosenberg 1987). Alternatively, below certain a certain threshold of food availability, mobility may become necessary to acquire sufficient food. Mobility may be a further advantage to anticipate stochastic events in highly unpredictable environments like estuaries, e.g. to flee adverse oxygen conditions or high concentrations of pollutants (Mees *et al.* 1993a).

The hyperbenthos plays an important role in coupling of benthic and pelagic food webs. Perissinotto & McQuaid (1990) found that in sub-antarctic waters the population of a shrimp species forms a 5 to 10m thick hyperbenthic layer. The larvae utilize the phytoplankton biomass that sinks to the sea floor and constitute, through daily vertical migrations, a link to higher trophic levels.

### 1.5.1. Food and feeding

Most mysids are omnivores feeding on detritus, algae and zooplankton (e.g. Mauchline 1980). Since they probably feed selectively on different zooplankton species and size groups (e.g. Cooper & Goldman 1980, Murthaugh 1981) they have the potential of structuring zooplankton communities (Fulton 1982a, 1982b). The community structure of phytoplankton (Webb *et al.* 1987) and diatoms (Wooldridge 1989, Webb & Wooldridge 1990) is possibly also influenced by selective grazing by mysids. Mysid predation has even been reported as a possible important control on

meiofaunal densities (Johnston & Lasenby 1982). Most mysids utilize organic detritus to a considerable extent and can be responsible for remineralization of a substantial proportion of the refractile detritus. Mysids also play an important role as macrophages, carnivores and detritivores in coral reef trophodynamics (Gottfried & Roman 1983, Mullin & Roman 1986, Carleton & Hamner 1989). In the same biotope, demersal zooplankton has been reported to graze on heterotrophic particulate matter and nanophytoplankton (Roman *et al.* 1990). Gowing & Wishner (1992) found a preponderance of gram-positive bacteria in the guts of deep-living copepods, mysids and amphipods.

### 1.5.2. Predators

**Coelenterates** may play a significant role as predators in the hyperbenthal (Bossanyi 1957, Möller 1979). The annual average of the standing stock of the metazoan plankton in the Kiel Bight includes 1% hyperbenthic crustaceans (mysids and cumaceans) versus 51% coelenterates (Möller 1979). These results might be biased, as the result of the sampling method that was used (Van Veen grab).

The study of the hyperbenthic fauna was recommended by many authors in its role as a constituent of the diet of fish (e.g. Blegvad 1917), and some of the earliest studies were specifically conducted for that purpose (Greze 1951). A review of the occurrence of mysids in the diet of fish is presented in Mauchline (1980). Although their importance as fish food is widely recognized, the prey communities are rarely termed hyperbenthic. Some recent exceptions are Zander & Hartwig (1988) and Mason & Clugston (1993) who explicitly mention hyperbenthic feeding habits. Hyperbenthic micro-habitat feeding guilds were recognized in the gobiid assemblage in Lough Hyne, Ireland (e.g. Wilkins & Myers 1992) and mysid-feeding guilds were distinguished in several demersal fish assemblages (Blaber & Bulman 1987, Gibson & Ezzi 1987, Moreira *et al.* 1992).

As a food source for demersal fish, mysids progressively replace copepods in the diet during growth (Sorbe 1981a). Such ontogenic shifts have been observed in several species, for example in cod by Mattson (1990). The hyperbenthos often predominates in the diet of 0-group individuals of commercially important fish, and it also sustains high densities of non-commercial demersal fish, e.g. gobies, which are an important prey for the larger size classes of the same species. Deep-sea fish have recently also been reported to forage in the benthic boundary layer (e.g. Zander & Hartwig 1982, Mauchline & Gordon 1991, Stefanescu & Cartes 1992).

Availability for fish is higher when individuals occur in the hyperbenthal than when they are buried in the sediment (Sorbe 1981a). Though a very small fraction of the populations of essentially endobenthic species can be present in the hyperbenthal, this quantity is not necessarily negligible, since this hyperbenthic fraction is obviously bound to be more readily available for predators. An example is the amphipod *Corophium volutator*. Although less than 0.1% of the population of this species is present in the hyperbenthal, it constitutes a significant part of the diet of demersal and



even pelagic fish species (Essink *et al.* 1989, Hughes 1988).

Birds (Schneider 1981, Johnson 1984, Cairns 1987, Steele & Montevecchi 1994) and marine mammals (Murison *et al.* 1984) are also possible predators. The analysis of faecal matter of grey whales has, for example, revealed a preponderance of hyperbenthic mysid exoskeleton fragments. Direct consumption by man is rare, although some mysid species are fished commercially for this purpose in Asia (Tattersall & Tattersall 1951, Omori 1978).

In recent years numerous invertebrates have been reported to feed on hyperbenthic prey. Juveniles of sepiolid squid *Sepietta oweniana* forage day and night in the hyperbenthos of nordic waters, preferentially catching free-swimming mysids (Bergstrom 1985). The diet of *Sepia officinalis* evolves as a function of its size, with the smallest animals feeding on mysids (Le Mao 1985). The diet of deep-sea cephalopods (Octopoda) also consists to a large extent of hyperbenthic material (Villanueva & Guerra 1991). Predatory crustaceans, often in commercially exploited stocks, include caridean shrimp (Chong & Sasekumar 1981, Siegfried 1982) and rock lobsters (Barkai & Branch 1988).

#### 1.6. Concluding remarks

The simple benthic-planktonic dichotomy, although still fundamental, is no longer entirely adequate when attention is focused on the region where both environments meet. Special types of equipment are needed to sample this significantly different habitat and species which now seem rare may prove to be very abundant when proper collecting apparatus is used.

Until much more information about the individual species and life stages that are caught becomes available, it seems advisable to use a working definition. The hyperbenthos is thus said to comprise all the animals that are caught by the gear that is deployed, except for those animals which manifestly belong to other communities or which are not sampled efficiently. At the present state of our knowledge of, for example, mysid and copepod behaviour it is recommended to report density and biomass data both per volume and per surface area. Indeed, mysids are known to be concentrated near the bottom and to maintain their position even in strong currents (Hough & Naylor 1992). In the same context, the best strategy seems to be not to exclude animals from the samples. Large fish and epibenthic crustaceans, though they feed in the hyperbenthos and are thus an integral part of the community, can be considered as accidental catches because they are not efficiently sampled by sledges and they will seriously bias biomass estimates. The position of polychaetes and molluscs is more difficult to decide upon, since, although they have the ability to swim, their presence is sometimes correlated with the amount of sediment in the sledge.

Although the intensity of hyperbenthic research has increased in recent years, a lot of descriptive baseline studies are still needed. Even the North Sea is relatively poorly studied. Studies on the hyperbenthos of tropical areas are generally lacking. Special attention should be paid to areas where commercial fishing activity is high and

to the nursery areas for the commercially important species. Although studies of the fluxes from the hyperbenthos to higher trophic levels are available from several areas, there is still a general need for studies on the fluxes from lower trophic levels to the hyperbenthos, including production and consumption estimates for the dominant species.

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## CHAPTER 2.

### **Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables.**

#### **Abstract**

Monthly sampling with a sledge type gear at 24 stations in the shallow coastal area in front of the Dutch Delta (Southern Bight of the North Sea) shows that high densities of a variety of animals are present in the lower 1 metre of the water column: the hyperbenthos. Hyperbenthic community structure is strongly dominated by seasonal fluctuations due to the sequential appearance, high abundance and disappearance of the different species of temporary hyperbenthos. In winter and early spring, when the community is dominated by its permanent residents, spatial patterns emerge. Averaged over the year these spatial patterns are consistent with the hydrodynamical regime in the system. Sedimentation of silt occurs in the same sheltered areas where the highest biomass of hyperbenthic animals is encountered. Low current velocities and protection from wave action thus create an environment suitable for settlement of macrobenthic larvae and for sedimentation of the phytoplankton bloom. This rich area attracts mobile invertebrates and juvenile fish.

#### **2.1. Introduction**

The hyperbenthos is the fauna element living in the lower part of the water column and dependent on the proximity of the bottom (Beyer 1958). Because of the difficulty of quantitative sampling, the importance of hyperbenthic animals is usually underestimated, or not even considered, in marine studies (Hesthagen 1973). Nevertheless, hyperbenthic animals can structure zooplankton communities by predation (Dodson 1974, Fulton 1982) and they are an important part of the diet of demersal fish (Mauchline 1980, Sorbe 1981a, Hamerlynck *et al.* 1990). Thus the hyperbenthos is an important link in the marine food web. The study of the hyperbenthic fauna is relatively new in marine studies and there is, as yet, no standardisation of definitions or sampling gear. The hyperbenthos goes under a variety of names, e.g. suprabenthos (Brunel *et al.* 1978) or nektobenthos (Sorbe 1972), and is caught with a plethora of sampling devices (review in Mauchline 1980). In this study the working definition used is that: the hyperbenthos is the fauna caught with the hyperbenthic sledge we deployed.

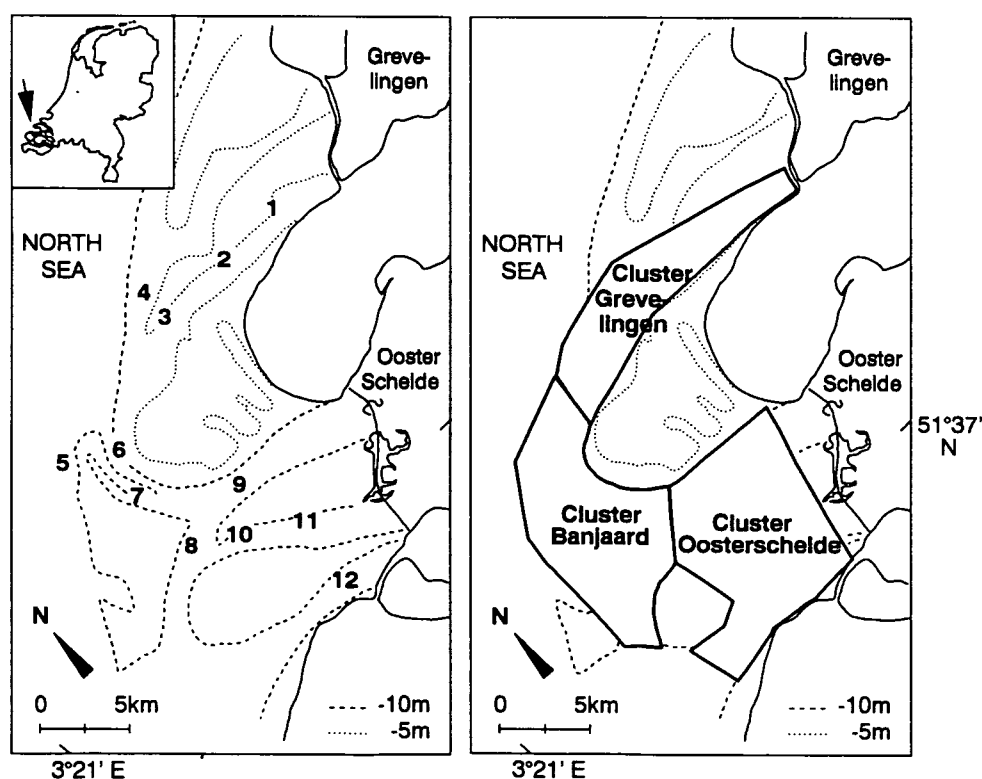
This study is part of a major program sponsored by Rijkswaterstaat (Dutch Ministry of Transport), Tidal Waters Division, to evaluate the effects of the engineering works in the Dutch delta on the biota. To predict the changes on the marine side of the storm surge barrier in the mouth of the Oosterschelde (completed in 1986), a comparative study of macrobenthos, meiobenthos, hyperbenthos, epibenthos and fish was undertaken between the geomorphologically stabilised ebb-tidal delta of the

Grevelingen (closed off in 1971) and the more dynamic ebb-tidal delta of the Oosterschelde. If strong correlations exist between the abiotic environment and the biota we should be able to predict future animal communities in the ebb-tidal delta of the Oosterschelde on the basis of hydrodynamic and geomorphological forecasts. This study reports only on the community structure of the hyperbenthos. Other aspects of the hyperbenthos and results on the other benthic compartments investigated will be published elsewhere.

## 2.2. Material and methods

### 2.2.1. Study area and sampling design

The Voordelta is the shallow coastal area at the mouth of the delta of the rivers Rhine, Meuse and Scheldt in the Southern Bight of the North Sea (Figure 2.1). It stretches from the Belgian-Dutch border in the south to the Hoek van Holland in the north. Its marine boundary is arbitrarily defined by the 15 m depth contour. River outflow, tidal currents and wave action have created a complex pattern of gullies and sandbanks. Due to major engineering works hydrodynamics and bottom morphology are still changing (Elgershuizen 1981, Van den Bergh 1984). The mean tidal amplitude is ca. 3 metres. For a detailed description we refer to Kohsiek & Mulder (1988).



*Figure 2.1. Map of the study area with the sampling localities and the 5 and 10 m depth contours (left) and the three subareas found by cluster analysis using the annual means per station (right).*

Monthly sampling was undertaken from 10 August 1988 to 27 June 1989 in 12 localities covering the ebb-tidal deltas of the Oosterschelde and the Grevelingen, as well as the more seaward Banjaard area in between (Figure 2.1). At each locality two trawls of approximately 1 km length were done, one at 10 m below mean sea level in the gullies and one at 5 m below mean sea level on the sandbank slope. In September only the 10 m stratum could be sampled. Because of bad weather no samples were taken in October 1988. In January, March, April and late June 1989 only part of the area could be sampled for similar reasons. A total of 210 trawls were taken (Table 2.1). In June 1989 the area was sampled twice. The sample taken on 27 June is called the "July" sample. Trawling was always done with the tide, the average speed relative to the bottom was 4.5 knots.

*Table 2.1. Sampling dates with the number of trawls and the localities sampled.*

Date	# trawls	Localities
10-08-88	23	all except 1 (10 m)
20-09-88	11	all 10 m, except 6
15-11-88	24	all
01-12-89	24	all
16-01-89	9	1, 2, 3 (10 m), 4, 12
13-02-89	24	all
17-03-89	12	2, 3, 4, 5, 6, 7
11-04-89	17	1, 2, 3, 4, 7 (5 m), 8, 9, 10, 11
10-05-89	23	all except 3 (10 m)
08-06-89	24	all
26-06-89	19	1, 2, 3, 4, 7 (5 m), 8, 9, 10, 11, 12

### 2.2.2. Sampling gear

Sampling was done from the R.V. Luctor (34 m, 500 hp) using a hyperbenthic sledge (Figure 2.2). The sledge weighs about 250 kg and has two nets mounted one above the other. The lower net samples from 0.2 to 0.5 m, the upper net from 0.5 to 1.0 m above the bottom. Each net is 4 m long with a 2\*2 mm mesh in the first 3 metres and a 1\*1 mm mesh in the last 1 m. For the data reported here the animals in both nets taken together are treated as one sample. There is no closing mechanism provided as pelagic sampling is minimal at shallow depths (Oug 1977).

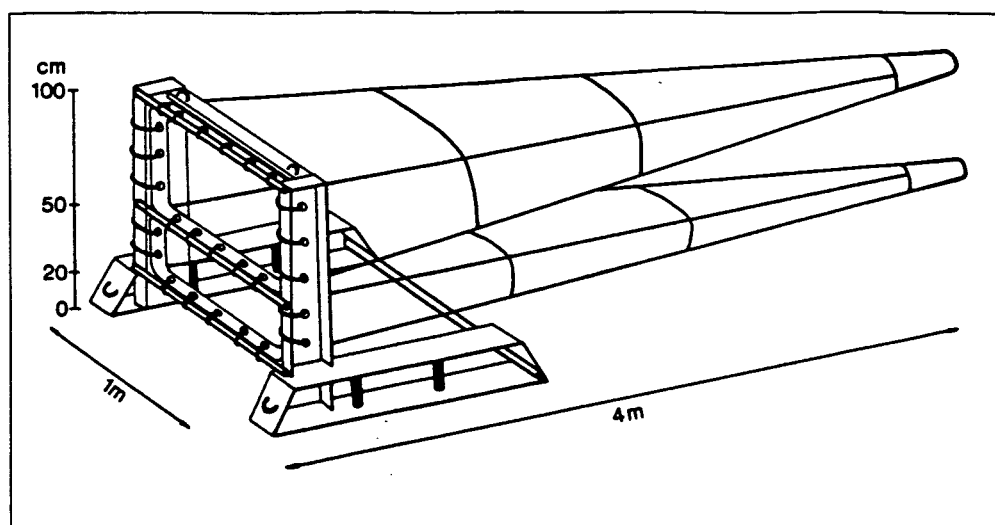


Figure 2.2. Sketch of the hyperbenthic sled used.

### 2.2.3. Analysis

All samples were immediately preserved in neutralised formaldehyde 7% final concentration. In the laboratory all animals were identified, if possible to species level, and counted. Accidentally caught epibenthic species, e.g. large fish or adult crabs, and endobenthic species, e.g. sedentary polychaetes or bivalves, were eliminated from the analysis. A maximum of one hundred animals per species per sample were measured for biomass calculation. Length - ash free dry weight regressions (2 hours at 110 °C for dry weight, 2 hours at 550 °C for ash weight) were determined for all the common species with continuous growth. For species with discrete stages e.g. zoeae and megalopae of crabs, ash free dry weights of batches of animals were determined per species. Densities and biomasses were calculated using a hypothetical net efficiency of 20 % for all animals. For the analysis 'functional species' were used: zoeae, megalopae and postlarvae of decapods and eggs and larvae of fish were considered as separate 'species' as they have different floating and swimming characteristics, different feeding modes etc...

Statistical analysis was performed according to Field *et al.* (1982): first the biotic data were analysed using classification techniques to yield groups of biotically similar samples, then we tested the environmental variables associated with these groups for statistical differences. First the density and biomass data per species of the 210 separate trawls were used as input for a Two Way Indicator Species Analysis - Twinspan (Hill 1979). Data were root-root transformed prior to Twinspan. Next, group-average sorting with Bray-Curtis similarities (Bray & Curtis 1957), after logarithmic transformation of the data, was used on the annual mean density and biomass for each species per station to define communities spatially. Afterwards an additional Twinspan was performed on the same annual means, after root-root transformation, to yield indicator species.

Kruskal-Wallis H test (Siegel 1956) was performed on a number of variables, measured at the stations of each community, to look for significant differences between environmental conditions in the different communities. The variables measured were of three different kinds (details in Van Dijke & Buijs 1987):

1. hydrodynamic variables: depth, significant wave height (= the wave height that is reached 1% of the time in one year), orbital velocity at the bottom (= the horizontal component of the orbital movement of the wave action), maximal current velocity ( $v_{\max}$ ), minimal current velocity ( $v_{\min}$ ) and maximum velocity difference ( $v_{\text{diff}} = v_{\max} - v_{\min}$ ).

2. sediment characteristics: percentage mud (fine elements  $< 60 \mu$ ), median grain size of the sand fraction and sorting coefficient.

3. water quality: salinity, chlorophyll a content and seston.

### 2.3. Results

A total of 120 'functional species' from 107 biological species were recorded (Table 2.2).

#### 2.3.1. Temporal pattern

Twinspan analysis of the 210 separate trawls shows a strong dominance of temporal structure, i.e. most samples of a single month resemble one another more closely than samples from the same station in any other month, except during winter (Figure 2.3).

#### *Density*

A first split divides the year in a cluster from April through September and a cluster from November through February (Figure 2.3). Indicator species for the spring and summer samples are *Lanice conchilega* aulophorus larvae, *Crangon crangon* zoeae, *Liocarcinus holsatus* zoeae and megalopae, *Carcinus maenas* megalopae and *Pagurus bernhardus* zoeae.

In the next division in the spring-summer cluster June and July are separated from the rest with indicator species *Callionymus lyra*, *Pomatoschistus minutus* and *Carcinus maenas* megalopae. The next split within this cluster isolates the June samples from the July samples. The June group also contains the July samples from the Grevelingen area. These separate in the subsequent division. From the fourth division onward spatial patterns begin to emerge in the July samples. The June samples stay together as a group. The next split in the other main cluster of the spring-summer group divides the samples in an August-September group (indicator species *Syrngnathus* spec. and *Carcinus maenas* zoeae) and an April-May group (indicator species Clupeidae spec. and fish eggs). Next both these clusters split into the separate months. The April cluster also contains the Banjaard samples of March. Spatial patterns begin to emerge

from the fifth split onward and are most obvious in the April and May samples. In the autumn-winter cluster the situation is more complex. A first split separates all remaining March samples and the main body of January and February samples from the rest (indicator species *Nyctiphanes couchi* and *Calanus helgolandicus*). Next, March (samples from the Grevelingen and Oosterschelde areas) splits off. In the remaining cluster of January and February samples the spatial pattern emerges at the next division. The second main cluster of the first division in the autumn-winter group is a rather heterogeneous mixture of the November and December samples with the remaining January and February samples. The next split here separates most of the November and December samples from those of the remaining two months. Subsequent divisions in these groups show spatial patterns rather than a temporal structure.

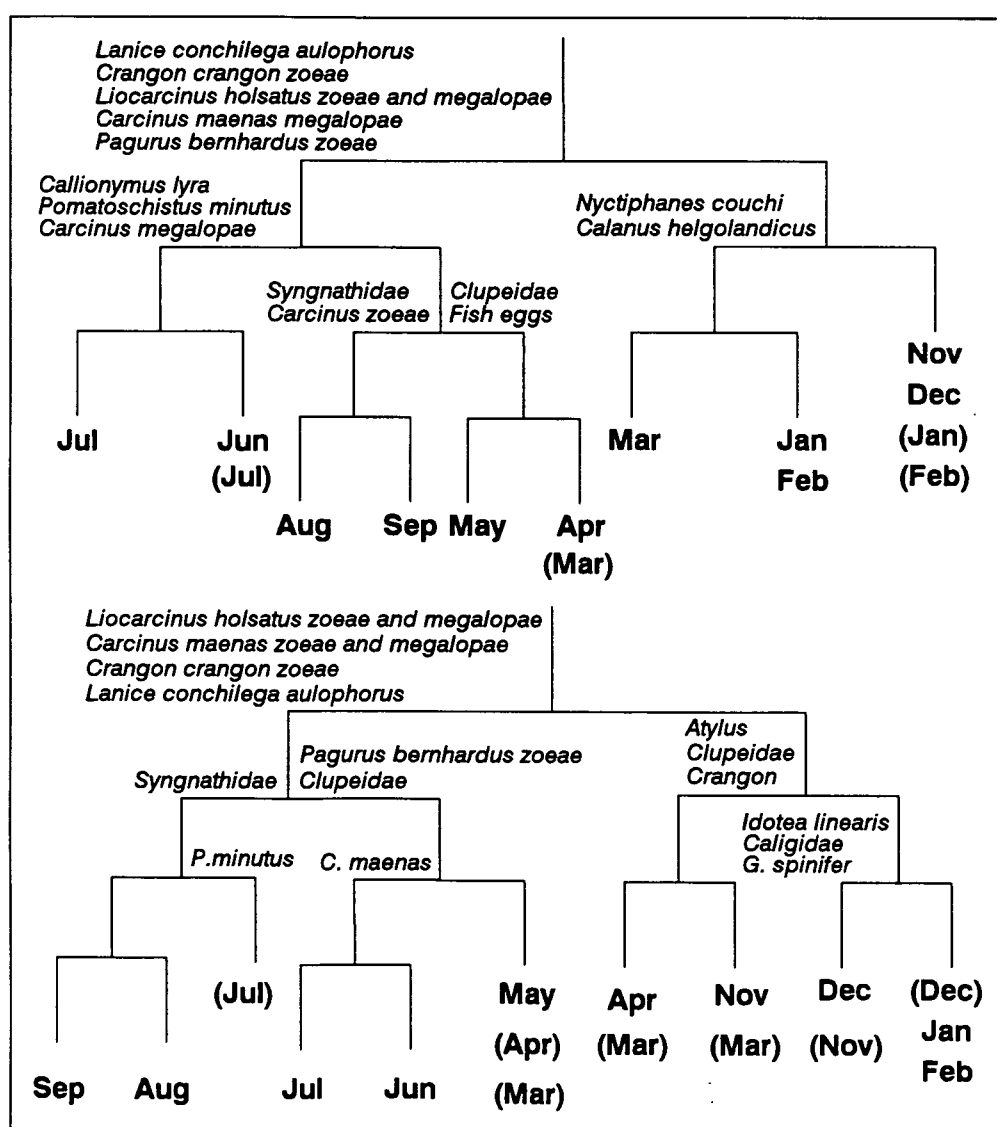


Figure 2.3. Dendrograms showing temporal community structure and indicator species for the density (top) and biomass (bottom) data of the separate trawls.

Table 2.2. List of the hyperbenthic species recorded during the study.

<b>Annelida, Polychaeta</b>		<b>Crustacea, Isopoda</b>	
<i>Lanice conchilega</i> aulophorus		<i>Eurydice pulchra</i>	
<i>Harmothoe</i> species larva		<i>Idotea emarginata</i>	
<i>Pectinaria koreni</i> larva		<i>Idotea baltica</i>	
<b>Chelicerata, Pycnogonida</b>		<i>Idotea linearis</i>	
<i>Callipallene brevirostris</i>		<b>Crustacea, Copepoda</b>	
<i>Picnognonum littorale</i>		<i>Centropages typicus</i>	
<i>Anoplodactylus pygmaeus</i>		<i>Centropages hamatus</i>	
<i>Phoxichilidium femoratum</i>		<i>Temora longicornis</i>	
<i>Nymphon rubrum</i>		<i>Calanus helgolandicus</i>	
<b>Crustacea</b>		<i>Euterpina acutifrons</i>	
<b>Crustacea, Decapoda</b>		Caligidae species	
<i>Crangon crangon</i> postlarva		<b>Crustacea, Cumacea</b>	
<i>Crangon crangon</i> zoaea		<i>Pseudocuma longicornis</i>	
<i>Pontophilus trispinosus</i> postlarva		<i>Pseudocuma similis</i>	
<i>Pontophilus trispinosus</i> zoaea		<i>Lamprops fasciata</i>	
<i>Hippolyte</i> species postlarva		<i>Bodotria scorpoides</i>	
<i>Hippolyte</i> species zoaea		<i>Diastylis bradyi</i>	
<i>Palaemon</i> species postlarva		<i>Diastylis rugosa</i>	
<i>Palaemon</i> species zoaea		<i>Diastylis rathkei</i>	
<i>Processa modica</i> postlarva		<i>Diastylis laevis</i>	
<i>Processa modica</i> zoaea		<i>Diastylis lucifera</i>	
<i>Pagurus bernhardus</i> megalopa		<i>Iphinoe tenella</i>	
<i>Pagurus bernhardus</i> zoaea		<b>Crustacea, Euphausiacea</b>	
<i>Porcellana longicornis</i> megalopa		<i>Nyctiphanes couchi</i>	
<i>Porcellana longicornis</i> zoaea		<b>Crustacea, Mysidacea</b>	
<i>Macropodia</i> species megalopa		<i>Gastrosaccus spinifer</i>	
<i>Macropodia</i> species zoaea		<i>Gastrosaccus</i> species	
<i>Portunus latipes</i> megalopa		<i>Mesopodopsis slabberi</i>	
<i>Carcinus maenas</i> megalopa		<i>Schistomysis spiritus</i>	
<i>Carcinus maenas</i> zoaea		<i>Schistomysis kervillei</i>	
<i>Liocarcinus holsatus</i> megalopa		<i>Praunus flexuosus</i>	
<i>Liocarcinus holsatus</i> zoaea		<i>Siriella armata</i>	
<i>Liocarcinus</i> species zoaea		<b>Chaetognatha</b>	
<i>Corystes cassivelaunus</i> megalopa		<i>Sagitta elegans</i>	
<b>Crustacea, Amphipoda</b>		<b>Pisces</b>	
<i>Pariambus typicus</i>		Fish eggs	
<i>Phtisica marina</i>		<i>Anguilla anguilla</i>	
<i>Caprella linearis</i>		Clupeidae species	
<i>Gammarus crinicornis</i>		<i>Merlangius merlangius</i>	
<i>Gammarus salinus</i>		<i>Trisopterus luscus</i>	
<i>Gammarus locusta</i>		<i>Ciliata mustela</i>	
<i>Gammarus oceanicus</i>		<i>Atherina presbyter</i>	
<i>Gammaropsis nitida</i>		<i>Gasterosteus aculeatus</i>	
<i>Atylus swammerdami</i>		<i>Syngnathidae</i> species	
<i>Atylus falcatus</i>		<i>Myoxocephalus scorpius</i>	
<i>Apherusa ovalipes</i>		<i>Agonus cataphractus</i>	
<i>Parajassa pelagica</i>		<i>Liparis liparis</i>	
<i>Jassa pusilla</i>		<i>Trachurus trachurus</i>	
<i>Jassa falcata</i>		<i>Trachinus vipera</i>	
<i>Jassa marmorata</i>		<i>Pholis gunellus</i>	
<i>Bathyporeia elegans</i>		<i>Ammodytes tobianus</i>	
<i>Bathyporeia sarsi</i>		<i>Callionymus lyra</i>	
<i>Bathyporeia guilliamsoniana</i>		<i>Pomatoschistus minutus</i>	
<i>Bathyporeia tenuipes</i>		<i>Pomatoschistus lozanoi</i>	
<i>Haustorius arenarius</i>		<i>Aphia minuta</i>	
<i>Orchomene nana</i>		<i>Scophthalmus rhombus</i>	
<i>Melita palmata</i>		<i>Pleuronectes platessa</i>	
<i>Melita obtusata</i>		<i>Limanda limanda</i>	
<i>Melita hergensis</i>		<i>Solea solea</i>	
<i>Stenothoe marina</i>			
<i>Stenothoe valida</i>			
<i>Metope pusilla</i>			
<i>Metopa alderi</i>			
<i>Maera grossimana</i>			
<i>Pontocrates arenarius</i>	<i>Pontocrates altamarinus</i>		
<i>Ampelisca brevicornis</i>	<i>Monoculodes carinatus</i>		
<i>Dyopodos porrectus</i>	<i>Hyperia galba</i>		
<i>Urothoe brevicornis</i>	<i>Urothoe poseidonis</i>		

### Biomass

The Twinspan analysis using the biomass data of the 210 separate trawls, largely shows the same structure (Figure 2.3). A first split separates May through September (indicator species *Liocarcinus holsatus* zoeae and megalopae, *Carcinus maenas* zoeae and megalopae, *Crangon crangon* zoeae and *Lanice conchilega* aulophorus larvae) from November through April.

In the spring-summer cluster an August-September group (including the July samples from the Grevelingen area) is first separated from the rest (indicator *Syngnathus* spec.). The July samples split off in the next division (indicator *Pomatoschistus minutus*). Next August and September are separated, showing a clear spatial pattern in subsequent divisions.

The other main group of the spring-summer cluster (indicator species *Pagurus bernhardus* zoeae and Clupeidae spec.) splits into the separate months in the next two divisions. First a June-July group (indicator species *Carcinus maenas* zoeae and megalopae) is separated from a group containing all May samples, the April samples from the Grevelingen area and the March samples from the Banjaard area. Following the next division all samples are grouped per month. A further spatial separation only appears in the May group. The June samples again stay together as one group.

In the autumn-winter cluster most November samples and the remaining March and April samples are first separated from the rest (indicator species *Atylus swammerdami*, Clupeidae spec. and *Crangon crangon* postlarvae). In subsequent divisions the April samples split from the March samples from the Banjaard area in one cluster, and the November samples split from the March samples from the Grevelingen area in the other cluster. In the next division the spatial pattern emerges clearly again in November.

In the other main group of the autumn-winter cluster the bulk of the December samples and the November samples from the Oosterschelde area are first separated from the rest (indicator species *Idotea linearis*, *Crangon crangon* postlarvae, Caligidae spec. and *Gastrosaccus spinifer*). The next split separates both months. The January, February and December samples in the other cluster are separated roughly but considerable overlap remains.

#### 2.3.2. Spatial pattern

Both classification techniques, group-average sorting and Twinspan, using the annual means for each species per station, split up the samples into three geographically defined communities (Figure 2.1): ebb-tidal delta of the Grevelingen (stations 1-4), Banjaard area (stations 5-8) and ebb-tidal delta of the Oosterschelde (stations 9-12). The boundaries of these community-defined areas are identical for the density data using both techniques. There is a slight difference between the group-average sorting and the Twinspan using the biomass data: station 5 is classified within the Grevelingen cluster instead of within the Banjaard cluster using the first technique



(Figure 2.4). The stations in the ebb-tidal delta of the Grevelingen are more similar to those of the Banjaard area than to the stations of the ebb-tidal delta of the Oosterschelde. In the analysis on the basis of density indicator species for the Grevelingen-Banjaard stations are *Crangon crangon* zoeae, *Limanda limanda*, *Solea solea* and *Orchomene nana*. Indicator species for the ebb-tidal Grevelingen is *Carcinus maenas* zoeae. Indicator species for the Banjaard area are *Nyctiphanes couchi*, *Hippolyte* species zoeae and *Diastylis rathkei*. In the analysis based on biomass indicator species for the Grevelingen-Banjaard stations are again *Limanda limanda* and the mysids *Mesopodopsis slabberi* and *Schistomysis spiritus*. Indicator species for the ebb-tidal Grevelingen is *Pseudocuma longicornis*. Indicator species for the Banjaard area are *Nymphon rubrum*, *Trachurus trachurus*, *Pagurus bernhardus* zoeae and *Liocarcinus holsatus* zoeae.

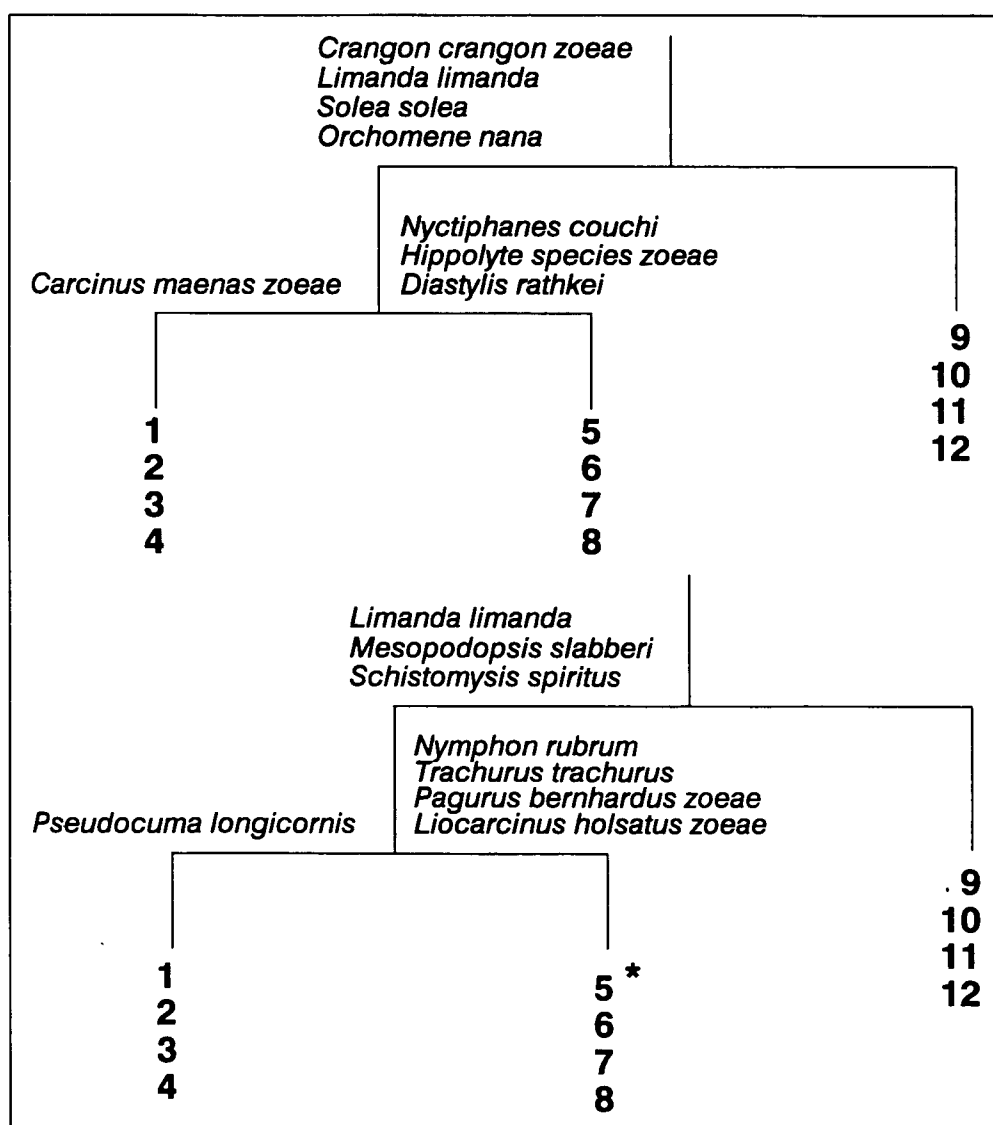


Figure 2.4. Dendrograms showing spatial community structure and indicator species for the annual mean density (top) and biomass (bottom) per station.

The composition of the biological communities in the three areas differs substantially, though the main groups are similar in all three areas: decapod larvae, mysids, macrobenthic larvae and fish eggs and fish larvae (Figure 2.5). The ebb-tidal delta of the Grevelingen has the highest total biomass, the highest density and biomass of macrobenthic larvae, mysids and fish eggs and larvae. The Banjaard area has the highest total densities, mainly due to the high densities of decapod larvae. The ebb-tidal delta of the Oosterschelde is clearly the poorest area with densities only half as high as in the other areas.

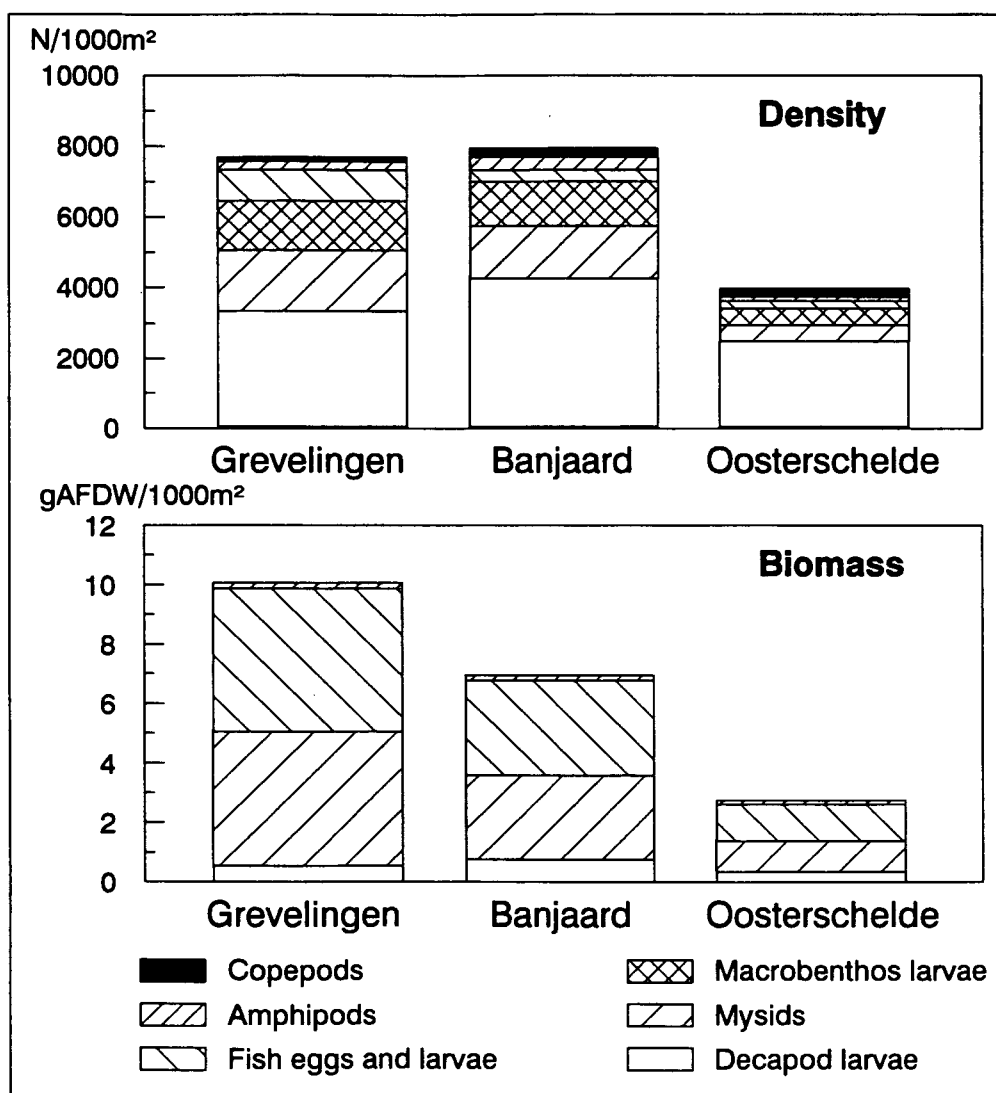


Figure 2.5. Faunal composition for the main groups using the annual mean density and biomass for the three subareas.

### 2.3.3. Relations with the environment

Kruskal-Wallis H test, using the measured variables for the separate stations in the biologically defined communities, shows significant differences ( $p < 0.05$ ) between

these sets for  $v_{\max}$ ,  $v_{\min}$ ,  $v_{\text{diff}}$  and 1% wave, chlorophyll and seston (Table 2.3 and Figure 2.6). The ebb-tidal delta of the Grevelingen has the lowest  $v_{\max}$ ,  $v_{\min}$  and  $v_{\text{diff}}$ , a low 1% wave and the lowest seston. It also has the highest chlorophyll a content. The Banjaard area has the highest  $v_{\min}$ , the highest 1% wave and the lowest chlorophyll a. The ebb-tidal delta of the Oosterschelde has the highest  $v_{\max}$  and  $v_{\text{diff}}$ , the lowest 1% wave and the highest seston.

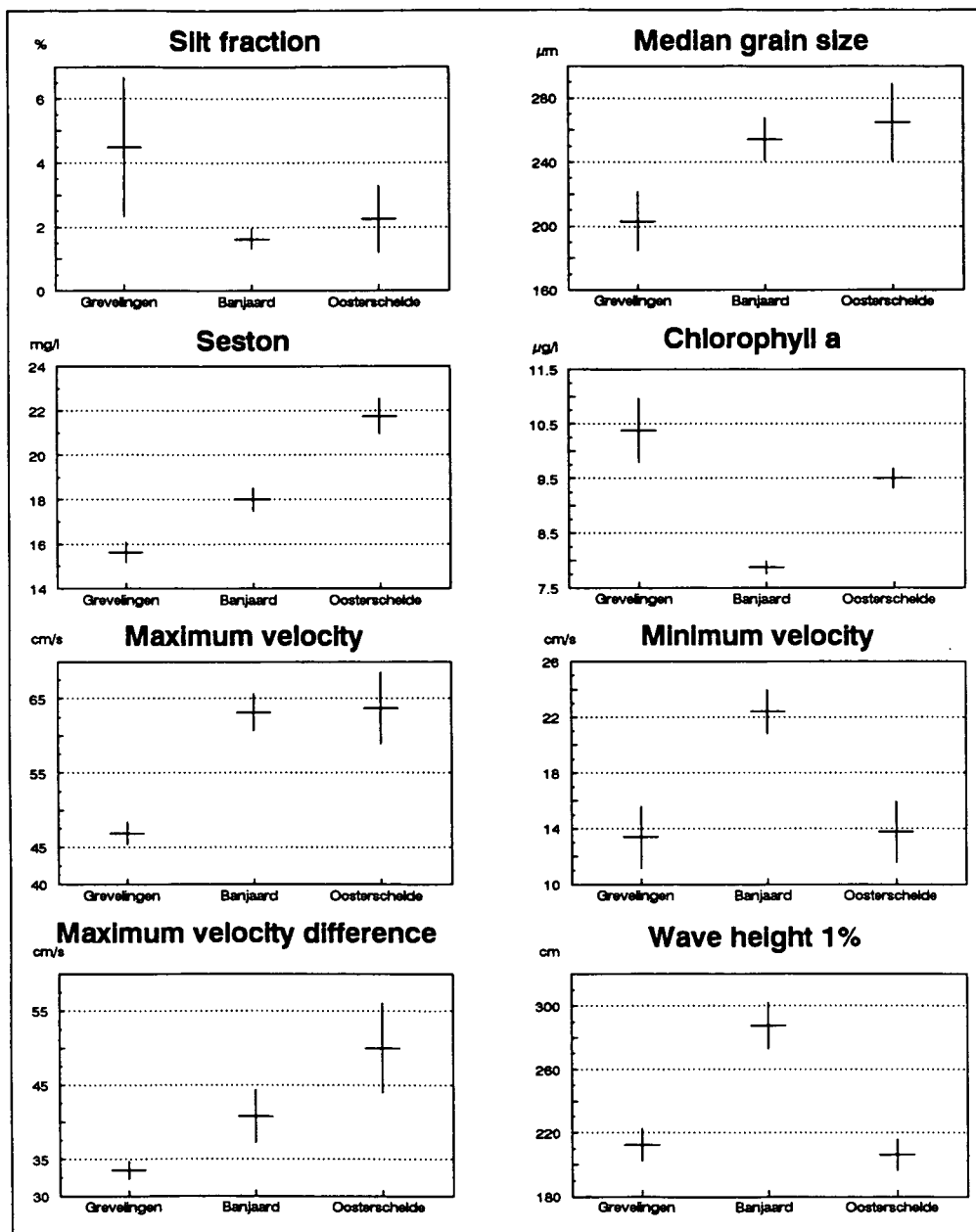


Figure 2.6. Environmental variables with their standard errors for the three subareas.

## 2.4. Discussion

We can distinguish a temporary hyperbenthos (merohyperbenthos), i.e. animals that spend only part of their life cycle in the hyperbenthos, and a permanent hyperbenthos (holohyperbenthos), i.e. animals that spend most of their life in the hyperbenthos. The main representatives of the temporary hyperbenthos are larval and post-larval decapods, larval stages of macrobenthic animals and eggs, larvae and early post-larvae of several fish species. The main representatives of the permanent hyperbenthos are mysids and amphipods. From March through September the sequential appearance, high abundance and disappearance of the different species of the temporary hyperbenthos strongly dominate the community structure. In the rest of the year temporal patterns remain important, but spatial patterns begin to emerge. Still, there is little diagonal structure in the Twinspan table, which means spatial structure is rather weak, i.e. the common species are common everywhere. Yet the same spatial patterns are clearly demonstrated by the analysis of the annual means per station.

*Table 2.3. List of the environmental variables tested for differences between the three subareas by Kruskal-Wallis H test and their significance levels.*

Hydrodynamical variables	
depth	NS
significant wave height	$p < .005$
orbital velocity bottom	NS
maximal current velocity	$p < .005$
minimal current velocity	$p < .05$
maximum velocity difference	$p < .005$
Sediment characteristics	
percentage mud	NS
median grain size	NS
sorting coefficient	NS
Water quality	
salinity	NS
chlorophyll a content	$p < .001$
seston	$p < .001$

From the studies in the Bristol Channel and Severn estuary it is known that salinity is a major factor determining the distribution of "planktonic" animals (Williams 1984). With high river outflows in winter and northwesterly winds, Rhine water can

significantly lower the salinity, especially in the ebb-tidal delta of the Grevelingen (Van Dijke & Buijs 1987). Such instances were not recorded during sampling. Salinities were always more or less homogeneous over the whole area studied.

The three different areas corresponding to the biological communities differ in a number of characteristics. The ebb-tidal delta of the Grevelingen is the least dynamic area. Co-occurrence of a certain community and a set of, not strictly independent, environmental variables is no proof of any causal relation. However, the hydrodynamic characteristics of the ebb-tidal delta of the Grevelingen clearly suit a number of animals.

High densities of macrobenthic larvae may be associated with high local production by adult populations. The Grevelingen area, dominated by *Spisula subtruncata*, has the highest benthic biomass of the entire Voordelta (Craeymeersch, pers. comm.). Macrobenthic communities with a high biomass, e.g. *Venus* communities, preferably settle in areas with intermediate bed stress (Warwick 1984). The ebb-tidal delta of the Grevelingen is such an area.

Judging from the chlorophyll a content, the ebb-tidal delta of the Grevelingen probably has the highest primary production. The sediment in the area also has the highest concentrations of phaeopigment, indicating sedimentation of dead phytal material (Craeymeersch, pers. comm.). Mysids are known to migrate actively to areas of high primary productivity (Wooldridge 1989). Mysids also feed on concentrated detritus (Mauchline 1980). Fish larvae and postlarvae may also actively migrate to the area to profit from the high abundance of invertebrate food (Creutzberg *et al.* 1978).

Most fish eggs caught are *Solea solea* eggs. As *Solea solea* is not a spawner in the area we must conclude that the eggs either undergo selective passive transport from the spawning ground to the area or else they are selectively trapped from a more or less homogeneous distribution in the coastal water. Although mud content does not differ significantly between the three areas (yet?), the ebb-tidal delta of the Grevelingen has the highest mud percentages (Figure 2.6). In this area the old tidal gullies are silting up rapidly (Kohsiek & Mulder 1988). Thus the ebb-tidal delta of the Grevelingen may act as a sink for various sorts of passively transported material i.e. silt, decaying phytoplankton, macrobenthic larvae and fish eggs with near neutral buoyancy. This creates a rich and varied benthic life that sustains the high densities of demersal fish, shrimp, crabs and sea stars found in the ebb-tidal delta of the Grevelingen (Hamerlynck & Craeymeersch 1990). Although the Banjaard area has a rich hyperbenthic fauna, wave conditions there prevent sedimentation, as attested by the low mud content of the bottom, and preclude settlement of rich macrobenthic communities. Despite being sheltered from the wave action the ebb-tidal delta of the Oosterschelde is poor. The richer water masses of the Banjaard (and offshore) do not reach the area because they are flushed outward at every low tide by the relatively oligotrophic water from the Oosterschelde. Moreover the high current velocities, attested by high seston loads, prevent sedimentation and settlement in the ebb-tidal delta of the Oosterschelde.

## 2.5. Conclusion

The closure of the Grevelingen estuary in 1971 and the subsequent geomorphological changes in its ebb-tidal delta have created a sheltered area with low current velocities. The hydrodynamical properties of the area are favourable towards the sedimentation of silt and detritus and possibly concentrate fish eggs. Decapod larvae, probably from offshore origin, occur in high densities in the area and macrobenthic larvae find favourable conditions for settlement. This richness and a high primary productivity attract mobile animals.

In comparison, the equally sheltered ebb-tidal delta of the Oosterschelde is much poorer. Most probably high current velocities there do not allow sedimentation of silt and detritus and are not conducive to the entrapment of neutrally buoyant animals.

## CHAPTER 3.

### **Spatial community structure of the winter hyperbenthos of the Schelde-estuary, The Netherlands, and the adjacent coastal waters.**

#### **Abstract**

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

#### **3.1. Introduction**

The hyperbenthal is the transition zone between the benthos and the plankton (Boysen 1975). The hyperbenthos, often termed suprabenthos or demersal zooplankton, is defined as the fauna living in the water column but more or less dependent on the proximity of the bottom (Beyer 1958). Numerous animals belonging to a variety of taxonomic groups occupy the hyperbenthal. Permanent hyperbenthic animals spend their whole life in the hyperbenthal (e.g. mysids, amphipods, and isopods). Animals that spend only part of their life cycle in the hyperbenthal (e.g. larvae of decapods and fishes) make up the temporary hyperbenthos (Hamerlynck & Mees 1991). Since it is not possible to sample mobile hyperbenthic animals quantitatively with conventional techniques used in zooplankton or macrobenthos research, the study of the hyperbenthos is often neglected even in comprehensive ecological studies. Still hyperbenthic animals, especially mysids, are an important component of the biomass of estuarine and coastal regions (e.g. Williams & Collins 1984). They contribute substantially to the diet of fish (e.g. Mauchline 1982, Hamerlynck *et al.* 1990) and

shrimps (Sitts & Knight 1979). They can be significant predators structuring zooplankton populations (Fulton 1982, Hansson *et al.* 1990) and can be important grazers of organic matter (Johnston & Lasenby 1982, Zagursky & Feller 1985). The few papers dealing with the hyperbenthos of estuaries (e.g. Hulburt 1957, Siegfried *et al.* 1979, Sorbe 1981b, Williams & Collins 1984, Jones *et al.* 1989) and shallow coastal areas (e.g. Clutter 1966, Hesthagen 1973, Boysen 1975, Rudstam *et al.* 1986) focus almost exclusively on the mysid component. A community approach, though often used in macrobenthos and phytoplankton studies, has not yet been applied to this compartment of the marine ecosystem.

In the so-called Delta area of the south-west Netherlands (Figure 3.1) hyperbenthos studies were started on a monthly basis in the Voordelta in 1988 (Hamerlynck & Mees 1991). After a pilot study covering the Voordelta, Oosterschelde and Westerschelde, which is reported here, further studies were concentrated in the Westerschelde (Mees *et al.* 1993b).

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

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

## 3.2. Material and methods

### 3.2.1. Study area

Three major European rivers: the Rhine, Meuse and Schelde, enter the North Sea in the so-called Dutch Delta in the south-western part of the Netherlands. Most of the former estuaries in this area have been altered by man (review in Heip 1989). The study area proper covers only three parts of the Dutch Delta: the Westerschelde, the Oosterschelde and the central part of the Voordelta (Figure 3.1).

The lower part of the river Schelde is generally known as the Westerschelde estuary. It is the last true estuary of the Delta area in the south-west of the Netherlands with a marked salinity gradient. The sampled part of the estuarine system is about 70 km long from the North Sea (Vlissingen) to the Dutch-Belgian border. The mean fresh water load is  $105 \text{ m}^3 \text{ s}^{-1}$ . The input from organic and inorganic pollutants is very high, especially in the brackish part (Duursma *et al.* 1988). The organic pollution results in lowered oxygen saturation levels in the brackish part (Table 3.1).

The Oosterschelde estuary is a tidal inlet of the Southern Bight of the North



Sea. After the construction of a storm-surge barrier in 1986, the hydrodynamics of the system changed substantially. The tidal amplitude and tidal velocities decreased and the transparency of the water increased. The construction of secondary dams in the landward part, completed by mid-1987, led to a reduced fresh water inflow, which amounts to  $10 \text{ m}^3 \text{ s}^{-1}$  (Nienhuis & Smaal in press). There is no salinity gradient, and turbidity and pollution are low.

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

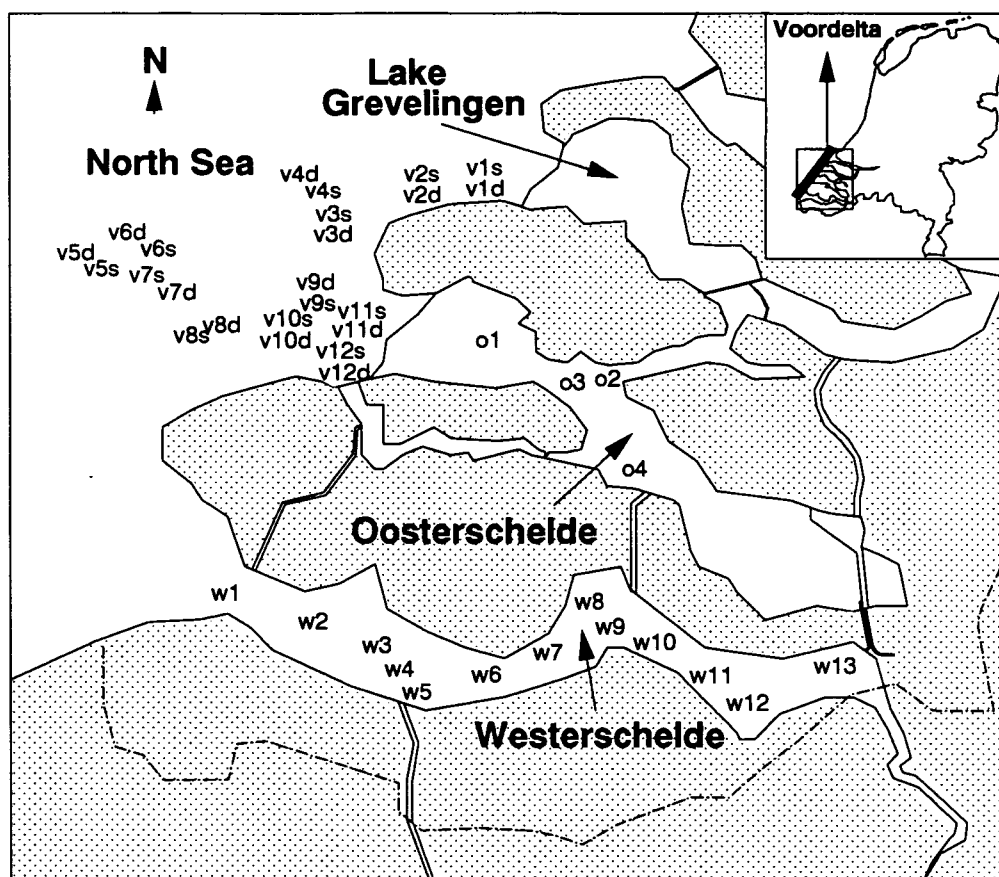


Figure 3.1. Map of the Delta area with the sampling sites.

### 3.2.2. Sampling

The 41 sampling stations are shown in Figure 3.1. Thirteen stations were located in the Westerschelde and four in the Oosterschelde (only in the western and central parts). Twenty-four stations were located in the Voordelta: ten in the ebb-tidal delta of the Oosterschelde (v8-v12), eight in the ebb tidal delta of the former

Grevelingen estuary (v1-v4) and six in the more seaward Banjaard area (v5-v7). These 24 Voordelta stations were really two depth strata of 12 localities. At each locality two parallel tows were done in proximity to one another: one at a depth of MTL minus 10 m (e.g. v4d, 'd' for deep) in the gully and one at MTL minus 5 m (e.g. v4s, 's' for shallow) on the sandbank slope.

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

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

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

### 3.2.3. Multivariate analysis of community structure

The sampling sites were classified into clusters according to species composition using the classification program TWINSpan (Hill 1979), which is a dichotomous divisive technique. In order to reduce the weight of the dominant species, the density and biomass data were subjected to a fourth root transformation prior to the TWINSpan analysis (Clarke & Green 1988). TWINSpan allows the user to define a number of 'cutlevels' which will split the data for a species into different 'pseudospecies', one for each chosen abundance level. The cutlevels used in the analysis were 0, 1, 2, 5, 10, 20, and 30 for the density data and 0, 0.1, 0.5, 1, 2, 3 and 5 for the biomass data. TWINSpan yields indicator species characterizing the

various groups. The TWINSPAN classification was stopped at the 4th or 5th division, as further groupings ceased to be ecologically meaningful. As advocated by Field *et al.* (1982) the consistency of the TWINSPAN results was assessed by comparing it to the result of an agglomerative type of analysis: a group-average sorting (GAS) cluster analysis with Bray-Curtis similarities (Bray & Curtis 1957), also performed on the fourth root transformed density data.

At each site, depth was recorded and the following environmental variables were measured at 1 m from the bottom: temperature, salinity, conductivity, dissolved oxygen, pH and Secchi disk depth. A Van Veen grab was used to take bottom samples to measure mud content and median grain of the sand fraction. The ranges of the environmental variables measured are summarized in Table 3.1.

*Table 3.1. Ranges of the environmental variables measured, with (between brackets) the stations at which the extremes were recorded, the mean for all stations and the standard deviation of that mean.*

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

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

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

### 3.3. Results

A total of 39 'species' were identified (Table 3.2). Mysids were the dominant faunistic group at each station. Only seven mysid species were recorded. Four of them are relatively abundant in at least part of the study area: *Schistomysis spiritus*, *Schisto-*

are relatively abundant in at least part of the study area: *Schistomysis spiritus*, *Schistomysis kervillei*, *Mesopodopsis slabberi* and *Neomysis integer*. The species *Gastrosaccus spinifer* and *Praunus flexuosus* occurred in low densities almost throughout the study area. *Siriella armata* was only recorded from one locality in the Voordelta (v11d). Besides mysids, postlarvae of the brown shrimp *Crangon crangon* and a few amphipod species made up the bulk of the hyperbenthos.

**Table 3.2.** List of species: permanent and temporary hyperbenthic species are marked P and T respectively. Species marked Z are truly zooplanktonic species; species marked A are 'aufwuchs' species.

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

All *Gammarus* were lumped as *Gammarus* species but this category referred mainly to *G. crinicornis* in the Voordelta and the marine part of the Westerschelde and predominantly *G. salinus* in the brackish part of the Westerschelde (Cattrijsse *et al.* 1993, Mees *et al.* 1993b). Two other common amphipods were *Atylus swammerdami* (mainly in the Voordelta), and *Corophium volutator* (mainly in the brackish part of the Westerschelde). A detailed description of the distribution of the individual species is published elsewhere (Cattrijsse *et al.* 1993, Mees *et al.* 1993a).

The result of the TWINSpan for both density and biomass can be seen in Figure 3.2. Figure 3.3 shows the geographical location of the clusters identified by TWINSpan.

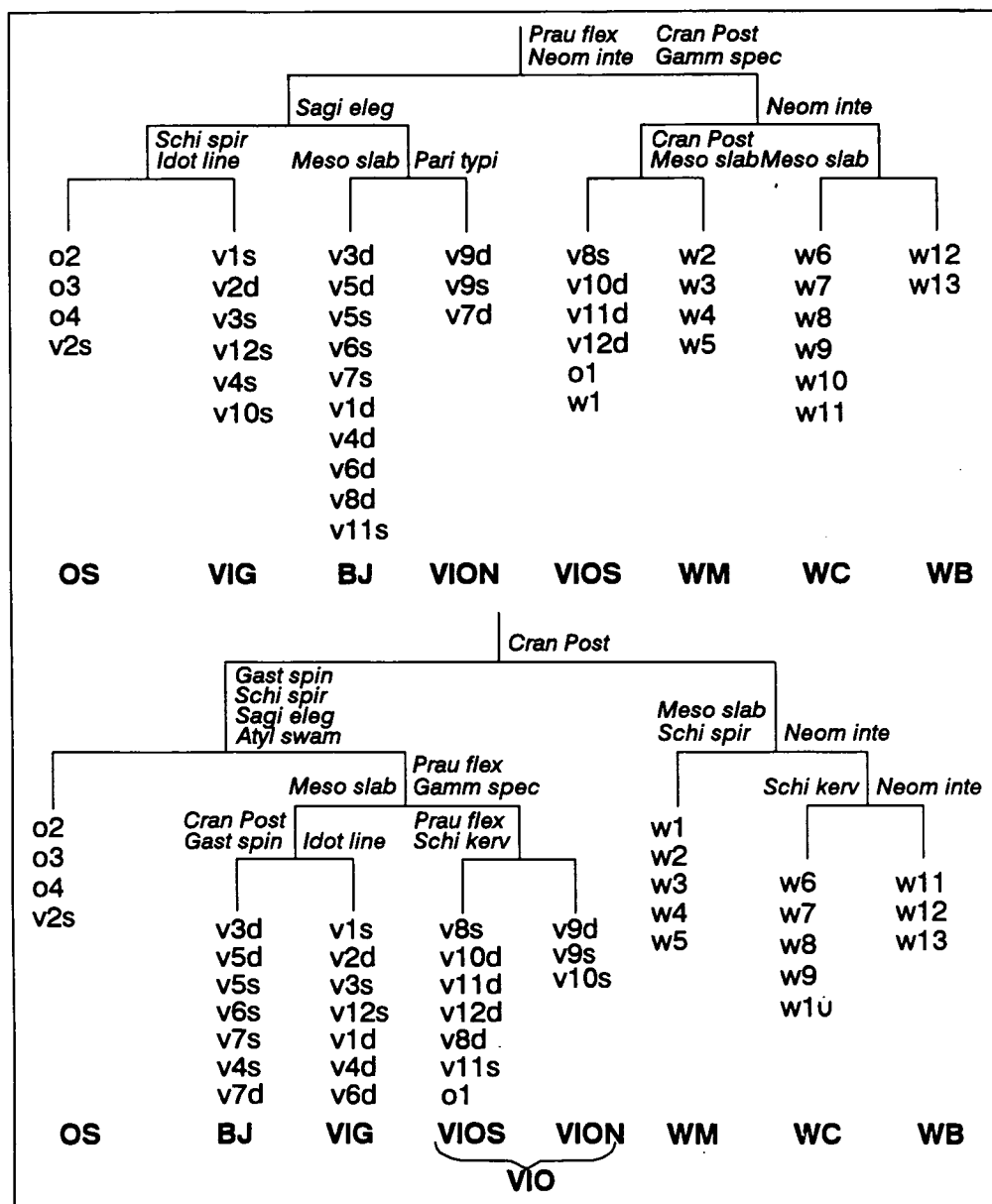
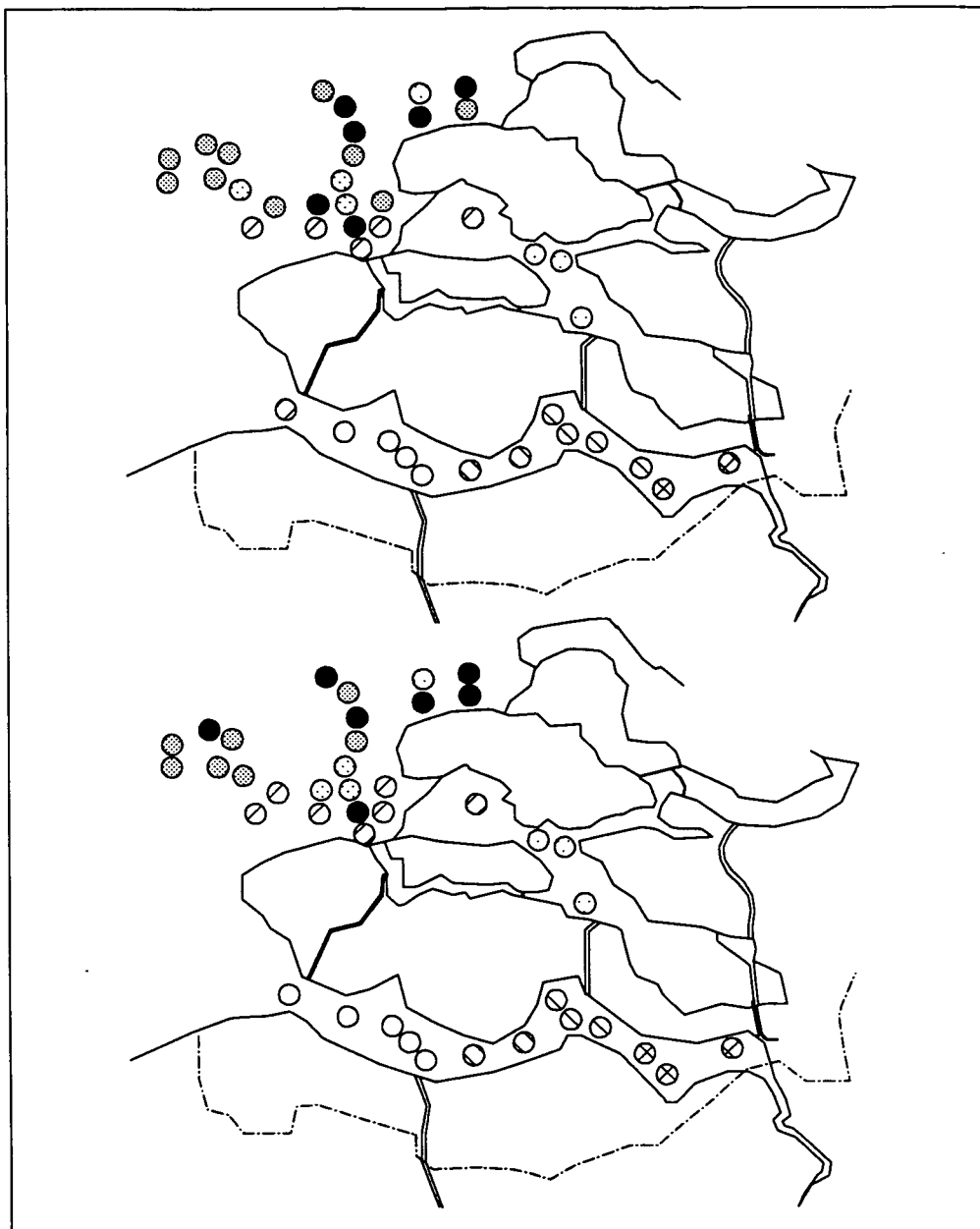


Figure 3.2. The TWINSpan analysis of the samples based on the transformed density (top) and biomass (bottom) data with the indicator species for each division indicated.



**Figure 3.3.** *The location of the TWINSpan clusters based on density data (top) and biomass data (bottom).*

When the clusters of stations resulting from the analysis of the density (Figures 3.2 and 3.3 top) and biomass data (Figures 3.2 and 3.3 bottom) are compared, a number of strong resemblances is apparent: the Oosterschelde (OS) cluster which includes the station v2s from the ebb tidal delta of the Grevelingen, the cluster corresponding to the marine part of the Westerschelde (WM) covering the stations w2 through w5, the cluster corresponding to the central part of the Westerschelde (WC) covering the stations w6 through w10 and the two inner stations in the brackish part of the Westerschelde (WB).

In the Voordelta the situation is more complex but some associations of stations in the four clusters occur in both dendrograms: a group of stations from the 'offshore' Banjaard area (v5s, v5d, v6s, v7s) and a station from the outer part of the ebb tidal delta of the Grevelingen (v3d) are the core of the Banjaard (BJ) cluster, a group of stations from the ebb tidal delta of the Grevelingen (v1s, v2d, v3s) and a station from the ebb tidal delta of the Oosterschelde (v12s) are the core of the Voordelta inshore Grevelingen cluster (VIG), a group of stations from the southern part of the ebb tidal delta of the Oosterschelde (v8s, v10d, v11d, v12d) and the westernmost station of the Oosterschelde (o1) are the core of the Voordelta inshore Oosterschelde cluster (VIOS), and finally two stations in the northern part of the ebb tidal delta of the Oosterschelde (v9d and v9s) form the VION (N for north) cluster. Many of the stations on the 'edges' between these clusters switched from one cluster to another: station w11 moved to the WB cluster in the biomass data, w1 moved to the VIOS cluster in the density data, station v4s moved between the VIG and BJ clusters, etc. In the TWINSPAN of the biomass data the VION and VIOS clusters are closely tied and can be grouped into a more comprehensive VIO cluster containing all the stations in the ebb tidal delta of the Oosterschelde (except for v12s), the two v8 stations intermediate between this area and the Banjaard area and the westernmost station of the Oosterschelde.

When the TWINSPAN (Figure 3.2) and the GAS result (not figured) for the density data are compared, the three Westerschelde clusters (WM, WC and WB) can be distinguished. For the other groupings there is less similarity though most of the stations of the BJ and VIG clusters occur in one large cluster (supplemented by both v11 stations). Some parts of other TWINSPAN clusters can also be recognized. There is a mixed cluster of shallow stations (plus v9d) associated to the Oosterschelde stations.

In the species plot of the plane formed by the first (eigenvalue 0.52) and second (eigenvalue 0.18) canonical axes of the ordination analysis (CCA) (Figure 3.4 centre) two main strings of stations can be distinguished: a first string stretching from the upper right to the lower left along which the three WS clusters can be seen and a second string from the upper left to the lower centre. In this second string the Banjaard stations are plotted in the upper left corner, then come the stations from the ebb tidal delta of the Grevelingen (first the outer and then the inner stations, with stations o2, v8d and v9s in between) and finally the string merges with the lower left part of the first string in a mixture of stations from the Oosterschelde proper and stations from the ebb tidal delta of the Oosterschelde. In the plot of the species scores (Figure 3.4 top) the species corresponding to these strings can be found: *Neomysis integer*, *Corophium volutator*, *Eurydice pulchra* and *Crangon crangon* postlarvae towards the right, corresponding to the WB and WC clusters in the Westerschelde string; *Gammarus* species, *Praunus flexuosus*, *Schistomysis kervillei*, and *Mesopodopsis slabberi* (close to the origin of the diagram) corresponding to the WM and VIO clusters. The species assemblage typical for the diverse marine fauna of the Banjaard area is located in the upper left corner. The biplot diagram of the environmental data (Figure 3.4 bottom) reveals a main gradient connecting the salinity vector on the left with the 1/secchi

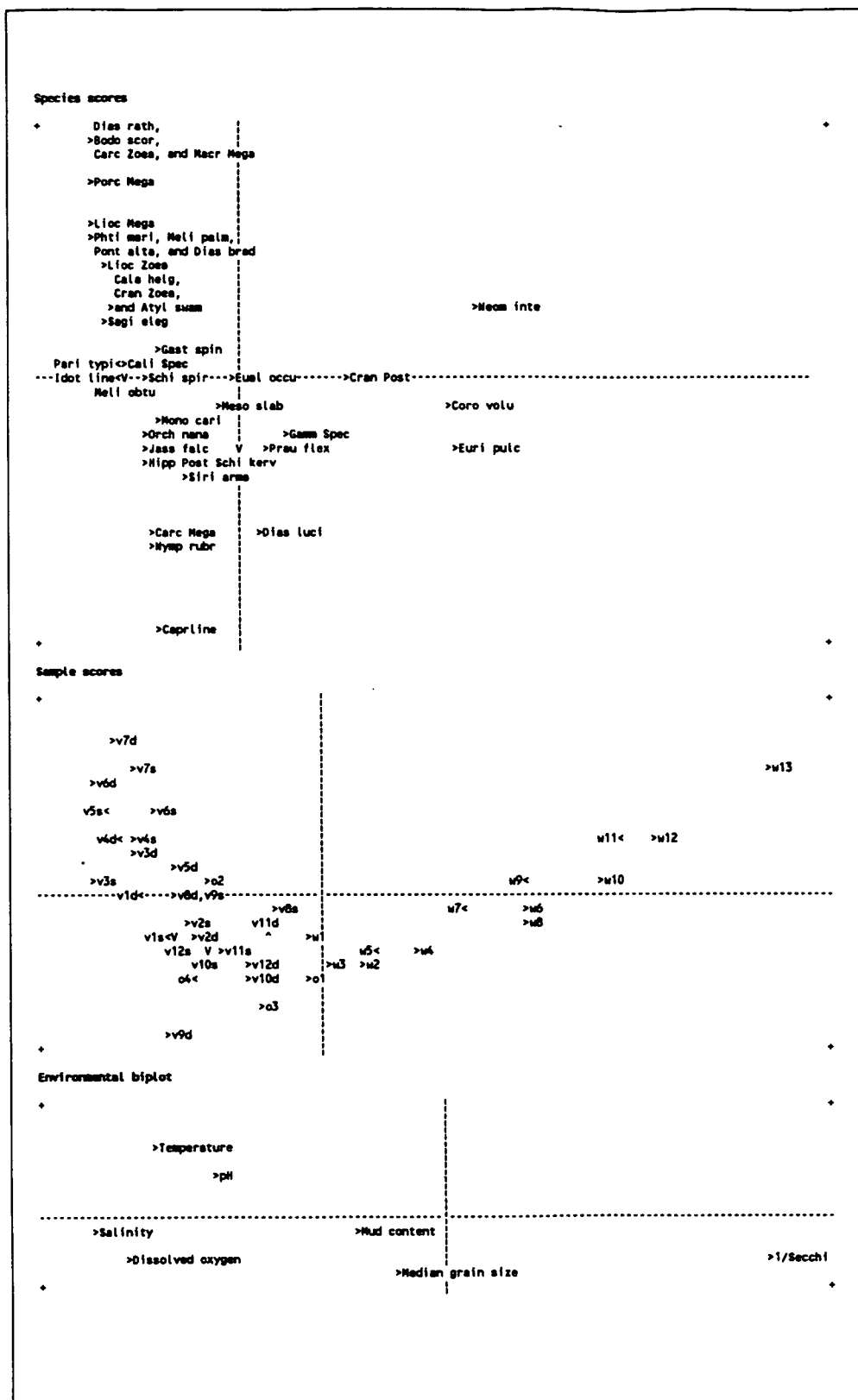
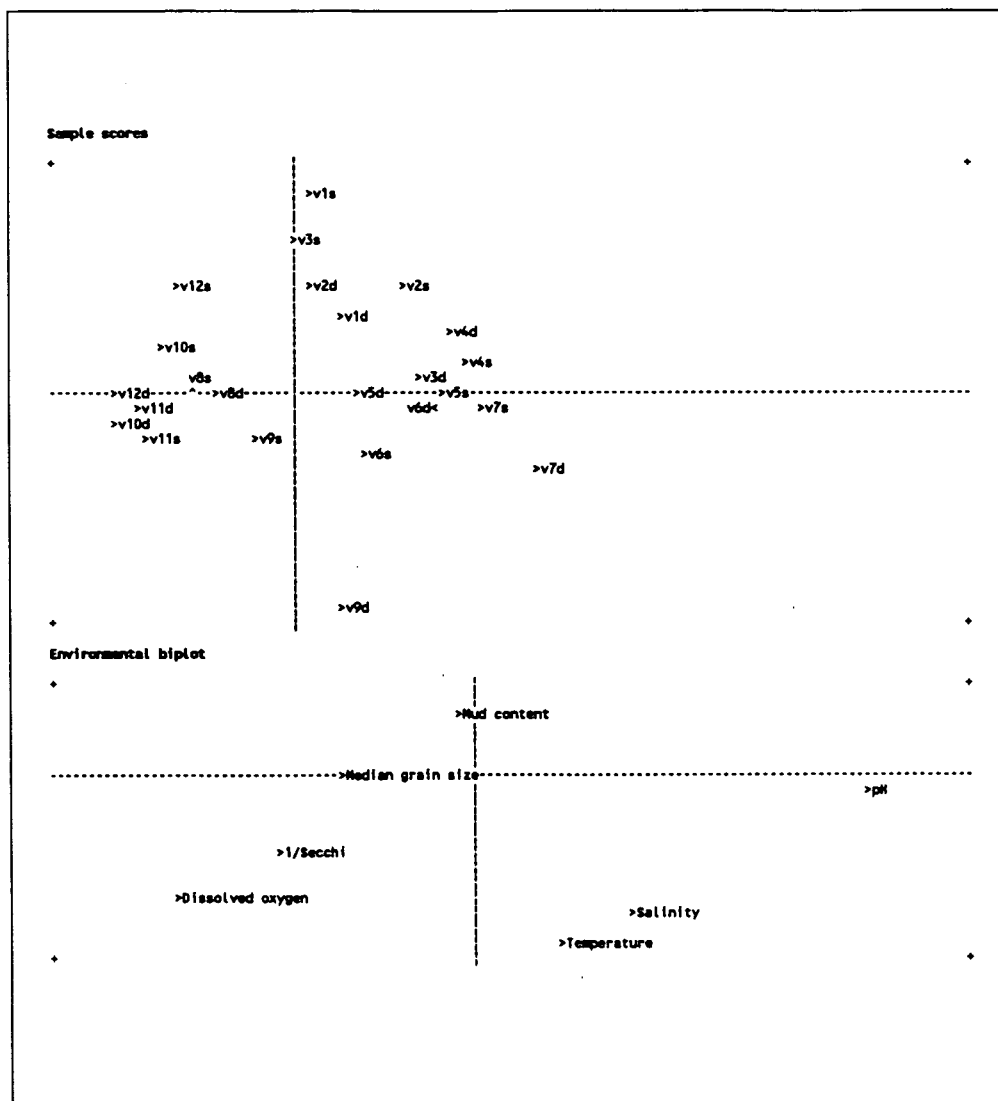


Figure 3.4. Canonical Correspondence Analysis (density data for all samples): scores of species, samples and environmental variables in the plane of the first two canonical axes.



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



**Figure 3.5.** Canonical Correspondence Analysis (biomass data of the Voordelta samples only): scores of samples and environmental variables in the plane of the first two canonical axes.

The plot of the sample scores for the first and third (eigenvalue 0.16) canonical axes (not depicted) is more difficult to interpret. There is a segregation of the Oosterschelde and Voordelta clusters with the species-poor Oosterschelde cluster near the top of the diagram, followed by the majority of VIG stations, a mixture of the BJ and remaining VIG stations and finally the VIO cluster near the centre and towards the bottom. The third axis does not correlate strongly with any of the environmental variables measured. A CCA on the biomass data of the Voordelta sites only (Figure 3.5) reveals the spatial structure in this area more clearly. The first (eigenvalue 0.26) and second (eigenvalue 0.12) axes suffice to interpret the data. All VIO stations (v8 to v12) of the dynamic ebb tidal delta of the Oosterschelde are located on the left side of the plot and are characterised by low values for Secchi disk depth, and high values for dissolved oxygen concentration and median grain size of the sand fraction. The VIG stations (v1 to v4) in the upper right quadrant have a higher mud content and Secchi disk depth, and lower dissolved oxygen concentrations. All seaward BJ stations (v5 to v7) are situated in the lower right quadrant of the plot. These are characterised by higher temperature and salinity values.

On the basis of the clusterings, giving precedence to the TWINSpan biomass result, and confirmed by the CCA, seven more or less coherent geographical subareas can be distinguished on the basis of their species-abundance composition: OS: 02-4(+v2s), WB: w11-w13, WC: w6-w10, WM: w1-w5, BJ: v3-v7, VIG: v1-v2, and VIO: v8-v12 and o1.

Figure 3.6 shows the average density (left) and biomass (right) values of the most important species in each subarea. The composition of the species assemblages in the seven clusters differed substantially, but mysids were always dominant. The subareas also differed in total density and biomass. The subarea with by far the highest hyperbenthic density and biomass (35 g AFDW per 1000 m<sup>2</sup> on average with peaks exceeding 50 g) was the brackish part of the Westerschelde (cluster WB). Here *Neomysis integer* reaches densities of more than 12 animals per m<sup>2</sup>. The upper estuarine fauna mainly comprised *Neomysis integer*, *Gammarus* species, *Corophium volutator*, *Eurydice pulchra*, and *Crangon crangon* postlarvae. Density and biomass declined markedly towards the mouth of the estuary. The WM stations were characterized by a higher number of species represented by a lower number of individuals than the upper estuarine stations. Consequently, diversity was highest in the western part and lowest in the eastern part of the estuary (Table 3.3). *Schistomysis kervillei* and *Mesopodopsis slabberi* were the dominant mysids in the western part, the latter species penetrating further into the estuary. *Schistomysis spiritus* was only present in the westernmost stations and was the most important species in the Voordelta. The seaward decline of total density and biomass of the hyperbenthos in the Westerschelde, as well as the distribution of the most important mysid species is illustrated in Figure 3.7. Note that though *Mesopodopsis slabberi* could be numerically important, this slender species did not contribute much to the total biomass of the hyperbenthic community. Still, even the poorest Westerschelde clusters (about 5 g AFDW per 1000 m<sup>2</sup>) had hyperbenthic densities and biomass values that were,

respectively, more than 5 and 3 times higher than the richest cluster in the rest of the study area. The fauna of the coastal area was more diverse (Table 3.3), especially in the ebb-tidal delta of the Oosterschelde towards the outer Banjaard, and the highest biomass was found in the Grevelingen area (1.5 g AFDW per 1000 m<sup>2</sup>). The Voordelta clusters near the storm surge barrier and the one of the Banjaard area were poor (both less than 0.5 g AFDW per 1000 m<sup>2</sup>). In the samples of the Oosterschelde cluster hardly any hyperbenthos was present (0.004 g AFDW per 1000 m<sup>2</sup>).

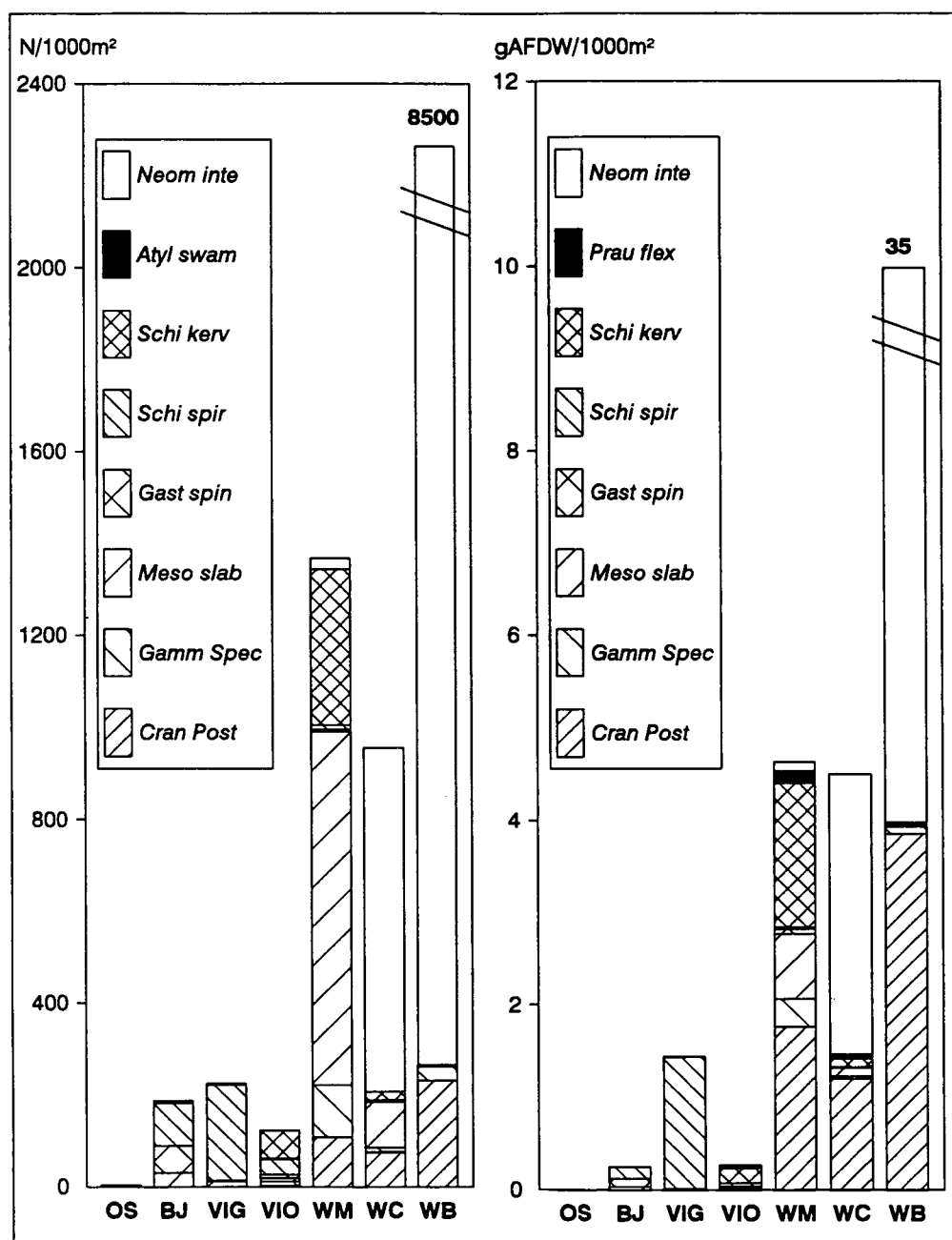


Figure 3.6. Average density (left), biomass (right) and species composition in the subareas.

Table 3.3. Hill's  $N_1$ : mean and standard deviation for the samples in the 7 TWINSpan clusters.

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

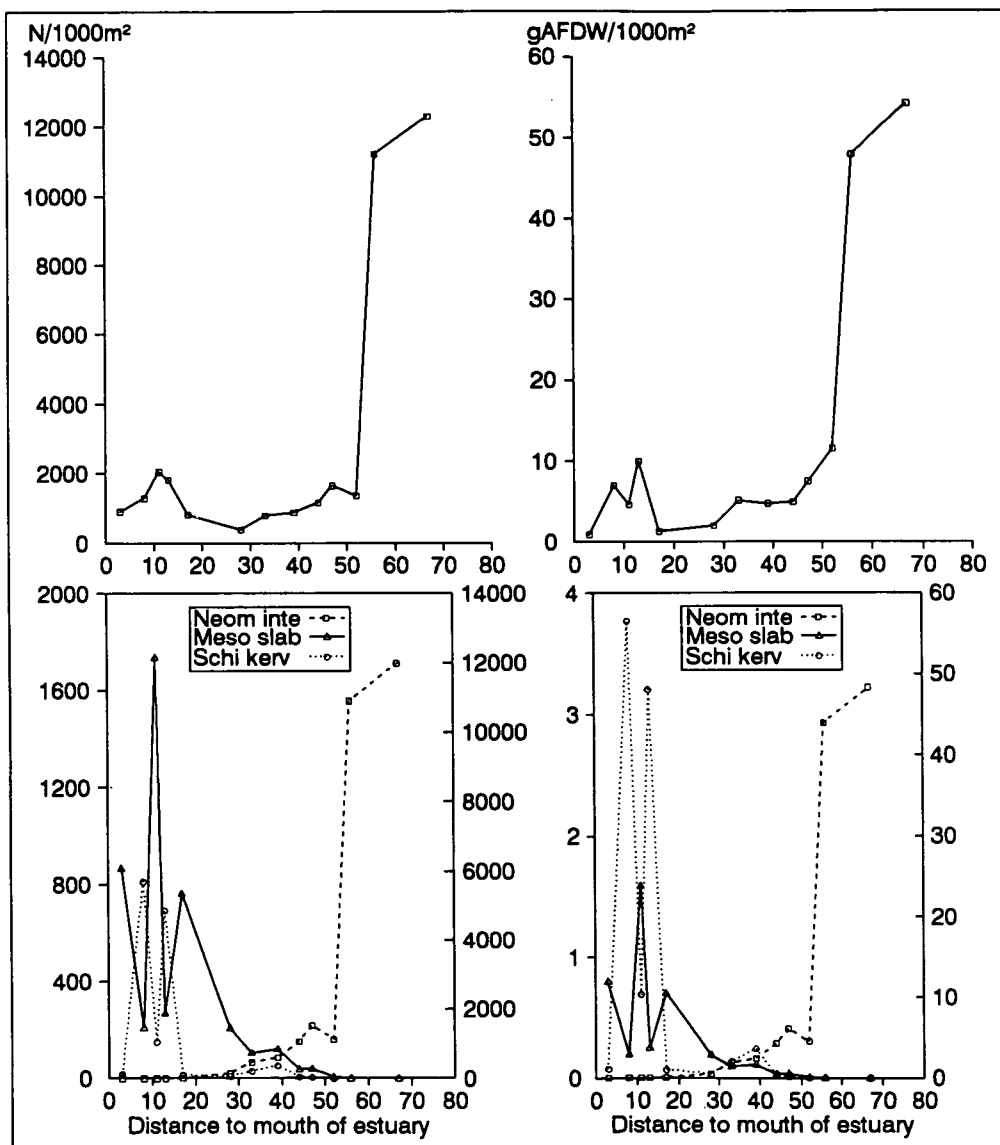


Figure 3.7. Density (left) and biomass (right) of the entire hyperbenthic community (top) and the most important mysid species (bottom) along the salinity gradient in the Westerschelde. Note that for *Neomysis integer* a different scale is used (right Y-axis).

### 3.4. Discussion

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

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

Multivariate analysis is a useful descriptive tool for an exploratory analysis of the data in a pilot study such as this. The use of different techniques, which are then compared, enhances one's perception of the underlying structure in the data. However, it also introduces a certain subjectivity by allowing one to select the most aesthetically pleasing result, which is not necessarily the most meaningful from an ecological perspective. The result of the GAS, though similar to the results of the other techniques in a broad sense, differs quite substantially in the details. This is perhaps because this technique is quite sensitive to rare species, which could not be omitted from the data set owing to the relative species poverty of the hyperbenthos in

comparison to e.g. meiobenthic (Heip *et al.* 1990) or macrobenthic (Craeymeersch *et al.* 1990) communities in the same area. Multivariate analysis neatly summarizes the structure in complex data sets and can help us to formulate hypotheses that may take years to prove or disprove (review in James & McCulloch 1990).

The spatial pattern observed in the Voordelta is brought out more clearly by the annual means per station (Hamerlynck & Mees 1991). The possible causes for this pattern are discussed in that paper. In summary: the hydrodynamical regime leads to a high primary production and an accumulation of passively transported particles in the ebb-tidal delta of the Grevelingen (Louters *et al.* 1991, Hamerlynck *et al.* 1993). This concentration of food probably attracts mobile animals (e.g. mysids) to this subarea and accounts for the presence of a relatively abundant hyperbenthic fauna. In the Banjaard area and the ebb-tidal delta of the Oosterschelde, where wave action and high current velocities prevent the sedimentation of detritus, densities are lower.

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

In a comparison of the hyperbenthic fauna of the Oosterschelde and the Westerschelde, the difference in food supply may be structurally important. The Oosterschelde has a much poorer hyperbenthic fauna than neighbouring areas. Due to the construction of the barrier and the other engineering projects in the Oosterschelde, average seston concentrations and nutrient loadings are very low (Bakker *et al.* 1990). Benthic suspension feeders dominate in the western and central parts of the embayment, used as a culture area for mussels. The two key species in the trophodynamics of the system are the mussel, *Mytilus edulis*, and the cockle, *Cerastoderma edule*. Mean mussel biomass reaches 456 g AFDW per m<sup>2</sup> on the culture plots. The cockle *Cerastoderma edule* mainly occupies the intertidal flats with a mean biomass as high as 63 g AFDW per m<sup>2</sup> on the cockle banks (Prins & Smaal 1990). The volume of the western part of the Oosterschelde can be filtered by the bivalves every four days (Smaal *et al.* 1986). Thus most of the organic matter is grazed by the benthos. This dominance of filter feeders in the Oosterschelde results in a stable ecosystem (Herman & Scholten 1990) where hyperbenthic animals may lose the competition for food. Other factors, such as a high predation pressure (linked to the high water transparency) probably also contribute to the absence of substantial mysid populations in the area. Because of logistical limitations only the western and central part of the Oosterschelde were sampled. In the eastern part, where turbidity is higher

and filter-feeder biomass lower, the situation may be different and mysids may be more abundant. In summer, schools of *Praunus flexuosus* can be seen swimming over vegetated stony ground in this area (P.H. Nienhuis, pers. comm.). Unfortunately, this type of substrate is inaccessible to the sampling gear used.

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

### 3.5. Recommendations

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

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



## **CHAPTER 4.**

### **Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde.**

#### **Abstract**

The hyperbenthic fauna of the Westerschelde estuary was sampled in spring, summer and winter of 1990 at 14 stations along the salinity gradient. Temporal patterns in the hyperbenthos of the Westerschelde are further described from year cycles of monthly and fortnightly samples. Mysids dominate the hyperbenthos in each season. Other important species, either permanently (e.g. amphipods and isopods) or temporarily (e.g. fish larvae and decapod larvae) hyperbenthic, belong to a variety of faunistic groups. Spatial structure is stable through time: the estuary can be divided in the same geographically defined zones in each season. Each zone has a characteristic fauna. Throughout the year, the hyperbenthic community of the mouth region of the estuary is markedly different from that of the upstream brackish area, both in terms of density and species composition. Gradients in salinity, dissolved oxygen and turbidity correlate strongly with the observed variation in community structure. The spatial patterns dominate over the temporal patterns, especially in the brackish part of the estuary. In the marine part, seasonal differences in the communities are more pronounced due to the recruitment, maximal abundance and subsequent disappearance of a series of temporary hyperbenthic species. In the brackish zone seasonal patterns are less obvious. Still, spring is characterized by the presence of postlarval flounder and clupeoids, while other seasonal differences seem to be mainly due to natural mortality and to migration of permanent hyperbenthic species in and out of the area. In each season, the upstream (brackish) communities are characterized by few species occurring in very high numbers, whereas the downstream (marine) communities are composed of many species but at lower densities.

#### **4.1. Introduction**

A successful understanding of the structure and functioning of marine ecosystems requires detailed knowledge of the spatial and temporal distribution of communities and of their constituting species. In estuaries and shallow coastal areas a major part of the primary production and of the allochthonous detrital material can be removed by secondary consumers, mainly benthos and plankton. The benthos can be divided into three functional units depending on their position relative to the substratum. The endobenthos lives in the bottom and is further composed of distinct macrobenthic and meiobenthic communities. The epibenthos comprises the animals living on - or in very close contact with - the substratum. The hyperbenthos is defined as the fauna living in the lower part of the water column, and still dependent on the

proximity of the bottom. It includes all swimming bottom-dependent animals which perform seasonal or daily vertical migrations above the bottom (Brunel *et al.* 1978) and can thus be viewed as the uppermost compartment of the benthos. It has been shown that hyperbenthic communities are real phenomena and that they are of considerable importance in trophodynamics. The hyperbenthos may play a significant role in the energy flow of marine ecosystems: animals occur in high numbers and are potentially important in nutrient recycling as grazers on zooplankton and detritus (Mann 1988), and as food for higher trophic levels such as larger epibenthos (Sitts & Knight 1979) and fishes (Sorbe 1981a, Hamerlynck *et al.* 1990). The exact position of the hyperbenthos in food webs can only be derived after knowledge of the species' spatial and temporal variability and by the investigation of the energy flow through the system.

In recent studies, the potential importance of the hyperbenthos in coastal ecosystems became well established (e.g. Boysen 1975, Rudstam *et al.* 1986, Wooldridge 1989, Buhl-Jensen & Fossa 1991, Hamerlynck & Mees 1991). In estuaries, density and biomass of the permanent hyperbenthos are much higher than in neighbouring coastal areas (Mees & Hamerlynck 1992). Especially in the highly turbid brackish water zone very high densities of mysids are noted. For the Westerschelde (as for most European estuaries) no detailed information on the composition and the spatial and temporal characteristics of the hyperbenthic communities is available to date. In this chapter the distribution of the hyperbenthos in the Westerschelde estuary is studied both in space and time, and correlations with some major environmental gradients are sought. Community parameters like species richness, abundance, biomass, and diversity are calculated. The concomitant existence of two separate food chains in the Westerschelde estuary has been hypothesised and validated by Hummel *et al.* (1988) and Hamerlynck *et al.* (1993b). A photo-autotrophic food chain characterizes the marine part while the web in the brackish part is predominantly heterotrophic. In the second part of this study the communities inhabiting the brackish and marine waters of the Westerschelde estuary are compared by means of monthly samples taken over a whole year in fixed stations, two from each subarea. Seasonal changes in the brackish water community are further analysed from a year of fortnightly samples in which the density peak of the dominant species *Neomysis integer* was followed.

This study is part of a multi-disciplinary project on major european tidal estuaries and aims at clarifying the role of the hyperbenthos in the estuarine ecosystem. The following questions are addressed in this paper: (1) what are the dominant species in the hyperbenthic communities, what densities do they reach, what is their biomass? (2) what is the spatial distribution of the most important hyperbenthic species along the salinity gradient? (3) is there an important seasonal variability in densities and hyperbenthic community structure in the Westerschelde? (4) which environmental variables correlate with the presence and structure of these communities?

## 4.2. Materials and methods

### 4.2.1. Study area

The Westerschelde estuary (Figure 4.1) is the lower part of the river Schelde. It is the last true estuary remaining in the delta area in the south-west of the Netherlands that is characterized by an important salinity gradient (Heip 1989). The maritime zone of the tidal system is about 70 km long from the North Sea (Vlissingen) to the Dutch-Belgian border. In this zone deep and large flood and ebb channels are separated by large sandbanks (Peters & Stirling 1976). Mixing of the water is complete (no stratification of salinity or current exists). The river drains about 19500 km<sup>2</sup>, mainly in Flanders. The mean fresh water load is estimated at 105 m<sup>3</sup> s<sup>-1</sup>. The total volume of the estuary (2.5 10<sup>9</sup> m<sup>3</sup>) is large in comparison with the volume of water that enters each day from the river (9 10<sup>6</sup> m<sup>3</sup>). Consequently, the residence time of the water is rather long: 75 days or 150 tidal cycles between the border and Vlissingen (Heip 1989). This results in a gradual dilution of the seawater and relatively stable salinity zones, which are maintained in more or less the same position throughout a tidal cycle. Seasonal shifts can be more important depending on the freshwater inflow. The input of organic and inorganic pollutants is very high, especially in the brackish part (Duursma *et al.* 1988). The important organic load results in intense bacterial activity which rapidly exhausts the oxygen in the river. The annual mean oxygen content drops to less than 2 mg l<sup>-1</sup> a few kilometres upstream from the Dutch-Belgian border (Van Eck *et al.* 1991).

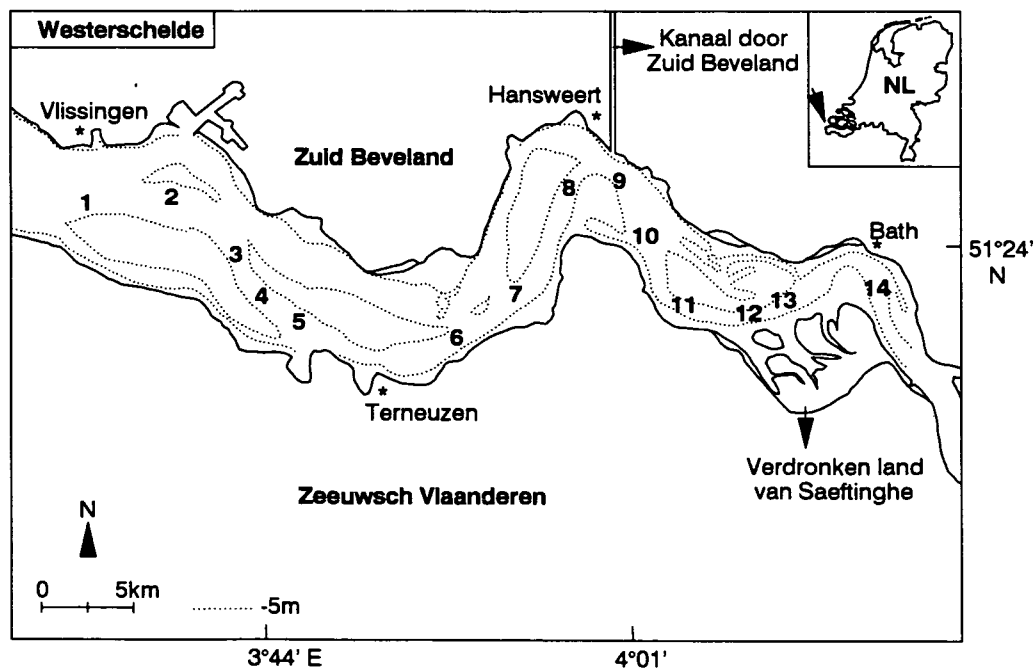


Figure 4.1. Westerschelde estuary with location of the sampling stations.

#### 4.2.2. Sampling

Samples were collected with a hyperbenthic sledge which consists of a heavy metal frame equipped with two nets. The nets have a length of 4 m, with a mesh size of 2\*2 mm in the first 3 m and 1\*1 mm in the last 1 m. The lower net samples the water column from 20 to 50 cm, the upper net from 50 to 100 cm above the bottom. For the purpose of this paper the contents of both nets were pooled and treated as one sample. The total area of the net's mouth is 0.8 m<sup>2</sup>. The samples were immediately rinsed over a 1 mm sieve and preserved in a buffered formaldehyde solution, 7% final concentration.

Fourteen stations were selected along the salinity gradient of the Westerschelde, covering the area from Vlissingen near the mouth of the estuary, to Bath near the Dutch-Belgian border (Figure 4.1, Table 4.1). All samples were taken in the subtidal channels of the Westerschelde. Where possible the 10 m depth contour was followed. All samples were taken during daytime. The sledge was towed over a distance of 1000 m at an average ship speed of 8 km h<sup>-1</sup>. Trawling was always done with the tide. This scheme was followed on three occasions (20 April 1990, 23 August 1990 and 11 December 1990) in order to cover a spring, summer and winter situation.

*Table 4.1. Names and codes of the sampling stations. The distances (from mouth of estuary) give the position of the starting point of the trawl.*

Name station	Code	Distance (km)
Vlissingen	1	3
Schaar van de Spijkerplaat	2	8
Hoge Springer	3	11
Springergeul	4	13
Geul van de Spijkerplaat	5	16
Margarethapolder	6	23
Pas van Baarland	7	26
Platen van Ossenisse	8	30
Hansweert	9	34
Schaar van Waarde	10	36
Zuidergat	11	40
Overloop van Valkenisse	12	43
Saeftinghe	13	47
Bath	14	52

The same transect was sampled on a monthly basis from April 1990 through March 1991. The two westernmost (1 and 2) and the two easternmost (13 and 14) stations were selected for further analysis. In exploratory cluster analyses, these pairs of samples consistently clustered together and they have been proven to be representative for the hyperbenthic communities of the marine and brackish zones of the system, respectively (Mees & Hamerlynck 1992, Mees *et al.* 1993b, Mees *et al.* in press).

The brackish water zone was further sampled fortnightly from November 1990 through December 1991 (Mees *et al.* 1994). On each occasion at least four stations were sampled (11, 12, 13 and 14) and the sample containing the highest number of *Neomysis integer* - the dominant species characterizing the brackish water hyperbenthos - was selected for further analyses (for more details we refer to Mees *et al.* 1994 and to Chapter 7 of this study).

Temperature, salinity, conductivity, dissolved oxygen, pH and Secchi disk depth were recorded at the end of each trawl.

In the laboratory all animals were identified, if possible to species level, and counted. For the analyses, different developmental stages of decapods (zoeae, megalopae, postlarvae and adults) were treated as separate species. Animals with continuous growth were measured (standard length: from the rostral tip to the end of the last abdominal segment for crustaceans, from the tip of the nose to the base of the caudal fin for fish) and their biomass was derived from length - ash-free dry weight regressions. Discrete developmental stages were given a mean biomass value (Mees, unpubl. data). All density and biomass data are presented as numbers of individuals (N) and grams ash-free dry weight (g AFDW) per trawl (1000 m<sup>2</sup>) or per m<sup>2</sup>. Net efficiency was considered to be 100%; all density and biomass values should be considered as minimum estimates (Mees & Hamerlynck 1992).

#### 4.2.3. Data analysis

Diversity was calculated as Hill's diversity numbers (Hill 1973). This set of indices incorporates the most widely used diversity measures in a continuum of indices of the order  $-\infty$  upto  $+\infty$ . The indices differ in their tendency to include or to ignore the relatively rarer species: the impact of dominance increases and the influence of species richness decreases with increasing order of the diversity numbers. When characterizing a community it is advisable to give diversity numbers of different order (Heip *et al.* 1988). Of particular interest are the numbers of the order 0 ( $N_0$  is equal to the number of species present in the sample), 1 ( $N_1$  is the inversed natural logarithm of the Shannon-Wiener diversity index), 2 ( $N_2$  is the reciprocal of Simpson's dominance index and gives more weight to the abundance of common species), and  $+\infty$  ( $N_\infty$  is the reciprocal of the proportional abundance of the commonest species: the dominance index).

The following analyses were performed: a classification (clustering based on the Bray-Curtis similarity index and Group Average Sorting, GAS), an ordination (Principal Component Analysis, PCA, Correspondance Analysis, CA, and Canonical

Correspondance Analysis, CCA), and a hybrid technique (Two-way Indicator Species Analysis, TWINSpan). All multivariate techniques were applied to 4<sup>th</sup> root transformed abundance and biomass data.

The sampling sites were classified into clusters according to species composition using the classification program TWINSpan (Hill 1979). TWINSpan also yields indicator species characterizing the various communities. No downweighting of rare species was done. The cutlevels used in the analyses of the data from the spring, summer and winter campaigns were 0, 0.1, 0.5, 1, 2, 3 and 5 for the biomass data and 0, 1, 2, 5, 10, 20, and 30 for the density data. Within a wide range of values, the choice of these cutlevels did not influence the output of the analyses. For the analyses with the data from the brackish part, pseudospecies cutlevels were chosen as to equalise the number of observations within each cutlevel, except for the lowest cutlevel which contained all the zero observations and the two highest cutlevel which contained approximately half as many observations as the other levels (in this way some extra weight was given to the most abundant species).

To check the stability of the TWINSpan results and to reveal the degree of similarity between and within the detected clusters of samples, a group-average sorting clusteranalysis with Bray-Curtis similarities (Bray & Curtis 1957) was performed on the same datamatrices.

The relationship between species composition and the environmental variables measured at each site was analyzed with the CA, PCA and CCA options from the program package CANOCO (Ter Braak 1988). Conductivity data were excluded from the analyses since they proved to covary strongly with salinity values. Secchi depth values, a measure for light penetration in the water, were transformed reciprocally before use in the analysis. In this way the variable becomes a light extinction measure and reflects the turbidity of the water. The datamatrices were first subjected to an exploratory CA to assess total community variability and to compare the scales of the species scores and the sample scores. It was then decided whether a linear or unimodal response model was to be preferred (Jongman *et al.* 1987, Ter Braak 1988). CCA, a technique performing regression and ordination of the data concurrently, was done on the data from the spring, summer and winter transects, and on the time series of marine and brackish stations. Principal Component Analysis (PCA) was applied to the data matrix of the fortnightly samples of the brackish zone.

Once groups of samples were established, the averages of the environmental variables of the different communities were tested for significant differences with a Kruskal-Wallis one way analysis of variance.

For further characterization and comparison of the communities k-dominance curves (Lambshead *et al.* 1983) were constructed, plotting the logarithm of the cumulative percentage (the percentage of total abundance made up by the k<sup>th</sup> dominant species and all more dominant species) against the logarithm of the rank k. In graphs of the species abundance distribution the numbers of species represented by 0, 1, 2,... individuals were plotted against logarithmic density classes.

### 4.3. Results of the spring, summer and winter campaigns

#### 4.3.1. Exploration of the data matrix

A total of 104 species were recorded (Table 4.2). Accidentally caught epibenthic (e.g. demersal fish, adult crabs, adult shrimp) and endobenthic (e.g. adult polychaetes and bivalves) organisms, as well as adult pelagic fish and true planktonic animals (e.g. coelenterates) were excluded from the analysis. The amphipod species of the genus *Bathyporeia* (probably a mixture of *B. elegans*, *B. sarsi* and *B. pilosa*) were pooled as *Bathyporeia* species. Small postlarval gobies (*Pomatoschistus minutus*, *P. lozanoi*, and *P. microps*) and larvae of the Clupeidae (*Clupea harengus* and *Sprattus sprattus*) were not identified to species level and were pooled as *Pomatoschistus* species and Clupeidae species respectively. Pipefish were recorded as Syngnathidae species, but are probably exclusively *Syngnathus rostellatus*. The pelagic eggs of fish and the free-living stages of the ectoparasitic Caligidae were recorded as such and were not identified in more detail. Rare polychaete larvae and some rare decapod larvae were only identified to genus level (Table 4.2). Two crab larvae and one amphipod could not be identified and are registered as "Zoea indet. type 1 and type 2", and "Amphipod indet. type 1".

After these corrections of the datamatrix, the hyperbenthic fauna was reduced to 66 species. The complete species list with the identification levels and the developmental stages considered as separate "functional species" can be found in Table 4.2. The total numbers of individuals caught in the entire study area per month were in the order of 90000 (belonging to 35 species) for April, 280000 (48 species) for August and 18000 (30 species) for December. Only 19 species (mainly chaetognaths, mysids, isopods and amphipods) were present in every season, 6 species only occurred in the April samples (all temporary hyperbenthic species), 17 species were restricted to the August campaign (8 temporary and 9 permanent hyperbenthic species) and 5 species were only found in December (2 temporary and 3 permanent hyperbenthic species).

Mysids dominated the hyperbenthos in each station. The distribution of the 4 most abundant mysid species along the estuary is illustrated in Figure 4.2. *Neomysis integer* was absent from the Western part of the Westerschelde but was always present in high numbers in the Eastern part. *Mesopodopsis slabberi* is a euryhaline species which occurred throughout the estuary, highest numbers being reached in the Eastern part (Figure 4.2). In winter numbers were low in every station along the gradient. *Schistomysis kervillei* and *Gastrosaccus spinifer* were the dominant mysids in the marine part of the study area. Both species tended to penetrate further into the estuary during winter. *Praunus flexuosus* (Figure 4.3) was also restricted to the brackish zone. It occurred throughout the year in low numbers. *Schistomysis spiritus* is a typical marine species which entered the estuary in winter, was still present in very low numbers in spring but was completely absent in summer (not figured).

Table 4.2. List of species. Species marked \* were excluded from all analyses.

Name and stage	Abbreviation	Name and stage	Abbreviation
Porifera species	Pori Spec *	<i>Crangon crangon</i>	Cran cran *
Hydrozoa species	Hydr Spec *	<i>Crangon crangon</i> postlarva	Cran Post
<i>Aurelia aurita</i>	Aure auri *	<i>Crangon crangon</i> zoea	Cran Zoea
Anthozoa species	Anth Spec *	<i>Palaemonetes varians</i>	Pala vari *
<i>Pleurobrachia pileus</i>	Pleu pile *	<i>Palaemonetes varians</i> postlarva	Pala Post
Nematoda species	Nema Spec *	<i>Palaemonetes varians</i> zoea	Pala Zoea
Oligochaeta species	Olig Spec *	<i>Processa modica</i> postlarva	Proc Post
<i>Lanice conchilega</i>	Lani conc *	<i>Pagurus bernhardus</i> megalopa	Pagu Mega
<i>Lanice conchilega</i> autophorelarva	Lani Aulo	<i>Pagurus bernhardus</i> zoea	Pagu Zoea
<i>Nereis</i> species	Nere Spec *	<i>Porcellana longicornis</i> megalopa	Porc Mega
<i>Nereis</i> species larva	Nere Larv	<i>Porcellana longicornis</i> zoea	Porc Zoea
<i>Harmothoë</i> species	Harm Spec *	<i>Carcinus maenas</i>	Carc maen *
<i>Harmothoë</i> species larva	Harm Larv	<i>Carcinus maenas</i> megalopa	Carc Mega
<i>Pectinaria</i> species	Pect Spec *	<i>Carcinus maenas</i> zoea	Carc Zoea
Terrellidae species	Terr Spec *	<i>Liocarcinus holsatus</i>	Lioc hols *
<i>Autolytus</i> species larva	Auto Larv	<i>Liocarcinus holsatus</i> megalopa	Lioc Mega
<i>Macoma baltica</i> spat	Maco balt *	<i>Liocarcinus holsatus</i> zoea	Lioc Zoea
<i>Cerastoderma edule</i> spat	Cera edul *	<i>Liocarcinus arcuatus</i>	Lioc arcu *
<i>Mytilus edulis</i> spat	Myti edul *	<i>Portumnus latipes</i>	Port lati *
<i>Ensis</i> species spat	Ensi Spec *	<i>Portumnus latipes</i> megalopa	Port Mega
Bryozoa species	Bryo Spec *	<i>Portumnus latipes</i> zoea	Port Zoea
<i>Sagitta elegans</i>	Sagi eleg	<i>Corystes cassivelaunus</i> megalopa	Cory Mega
<i>Asterias rubens</i>	Aste rube *	<i>Macropodia</i> species megalopa	Macr Mega
<i>Calanus helgolandicus</i>	Cala helg	Zoea indet. type 1	Zoea typ1
Caligidae species	Cali Spec	Zoea indet. type 2	Zoea typ2
Cirripedia species	Cirr Spec *	Araneae species	Arac Spec *
<i>Gastrosaccus spinifer</i>	Gast spin	<i>Nymphon rubrum</i>	Nymp rubr
<i>Schistomysis spiritus</i>	Schi spir	<i>Pycnogonum littorale</i>	Pycn litt
<i>Schistomysis kervillei</i>	Schi kerv	<i>Phoxochilidium femoratum</i>	Phox femo
<i>Neomysis integer</i>	Neom inte	Diptera species	Dipt Spec *
<i>Mesopodopsis slabberi</i>	Meso elab	Coleoptera species	Cole Spec *
<i>Praunus flexuosus</i>	Prau flex	<i>Lampetra fluviatilis</i>	Lamp fluv *
<i>Diastylis rathkei</i>	Dias rath	Pelagic eggs of fish	Fish eggs
<i>Diastylis bradyi</i>	Dias brad	<i>Anguilla anguilla</i> glass eels	Angu angu
<i>Bodotria scorpioides</i>	Bodo scor	<i>Clupea harengus</i>	Clup hare *
<i>Eurydice pulchra</i>	Eury pulc	<i>Sprattus sprattus</i>	Spra spra *
<i>Idotea linearis</i>	Idot line	Clupeidae species larvae	Clup Spec
<i>Sphaeroma rugicauda</i>	Spha rugi	<i>Trisopterus luscus</i>	Tris lusc *
<i>Pariambus typicus</i>	Pari typi	Syngnathidae species	Syng Spec
<i>Caprella linearis</i>	Capr line	<i>Dicentrarchus labrax</i>	Dice labr *
<i>Gammarus crinicornis</i>	Gamm crin	<i>Ammodytes tobianus</i>	Ammo tobi *
<i>Gammarus salinus</i>	Gamm sali	<i>Liza ramada</i>	Liza rama *
<i>Atylus swammerdami</i>	Atyl swam	<i>Pomatoschistus minutus</i>	Poma minu *
<i>Pleusymtes glaber</i>	Pleu glab	<i>Pomatoschistus lozanoi</i>	Poma loza *
<i>Corophium volutator</i>	Coro volu	<i>Pomatoschistus microps</i>	Poma micr *
<i>Corophium arenarium</i>	Coro aren	<i>Pomatoschistus</i> spec. postlarvae	Poma Spec
<i>Bathyporeia</i> species	Bath Spec	<i>Pleuronectes platessa</i> postlarvae	Pleu plat
<i>Jassa falcata</i>	Jass falc	<i>Pleuronectes flesus</i> postlarvae	Pleu fles
<i>Jassa marmorata</i>	Jass marm	<i>Solea solea</i> postlarvae	Sole sole
<i>Ischyrocerus anguipes</i>	Isch angu	<i>Limanda limanda</i> postlarvae	Lima lima
<i>Stanothoë marina</i>	Sten mari		
<i>Pontocrates altamarinus</i>	Pont alta		
Amphipode indet. type 1	Amph typ1		
<i>Hyperia galba</i>	Hype galb		



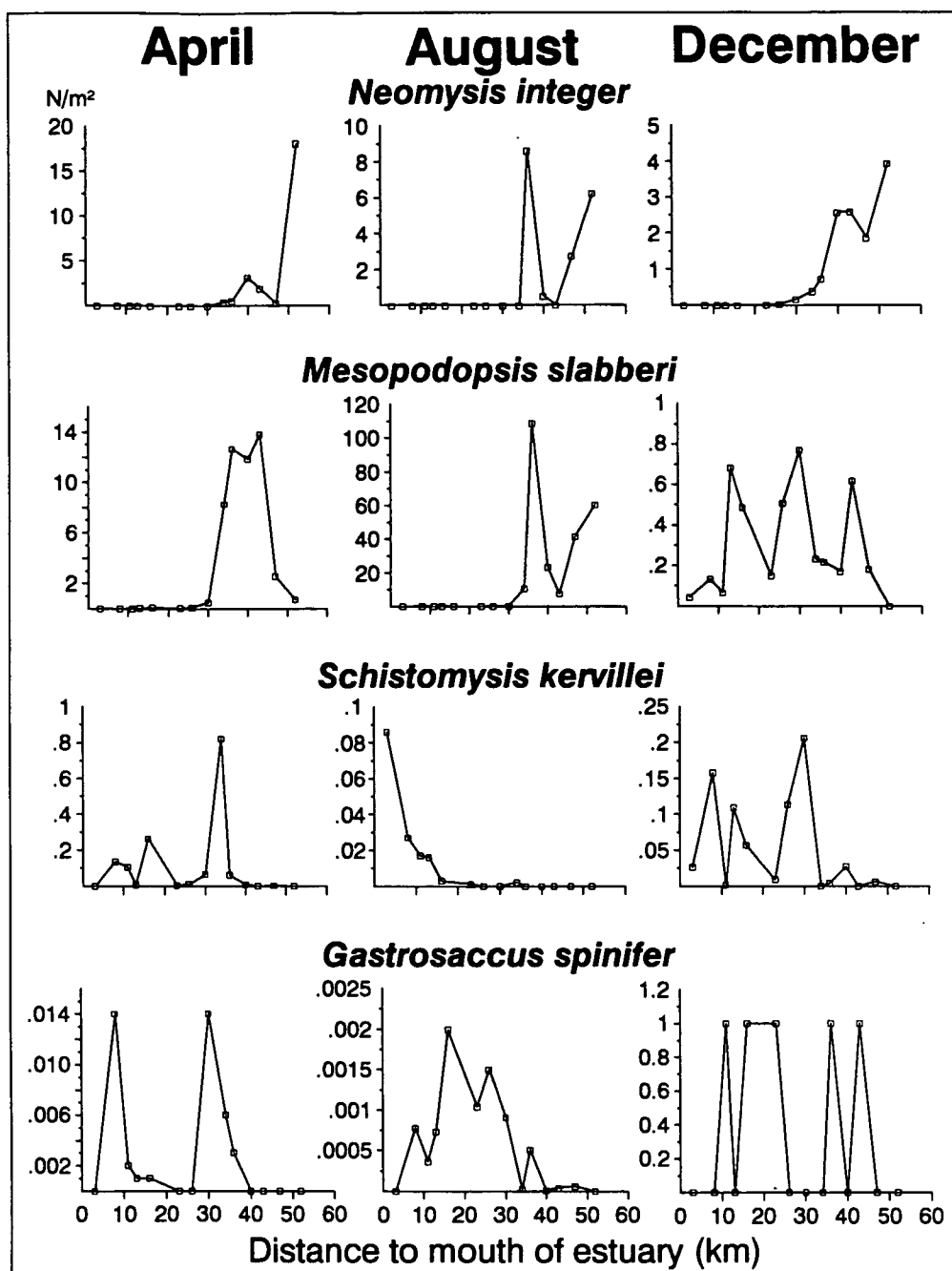


Figure 4.2. Distribution of the most abundant mysid species along the axis of the estuary in April, August and December.

The distribution of some other hyperbenthic species characteristic for the different communities is shown in Figure 4.3. The most common amphipod species in the marine part of the estuary was *Gammarus crinicornis*. Upstream, this species was gradually replaced by *Gammarus salinus* which reached much higher densities. *Atylus swammerdami* was also restricted to the marine zone, whereas *Bathyporeia* species were much more common in the brackish waters. Other typically marine species that did not penetrate far into the estuary included the isopod *Idotea linearis*, the amphipod

*Caprella linearis*, all cumacean species encountered in the study (e.g. *Diastylis rathkei*) and a high variety of temporary hyperbenthic species (e.g. fish eggs and decapod larvae). Note that the megalopa stages of the shore crab *Carcinus maenas* penetrated further into the estuary than the zoeal stages. The only temporary hyperbenthic species reaching highest densities in the brackish part of the estuary was postlarval flounder, *Pleuronectes flesus*.

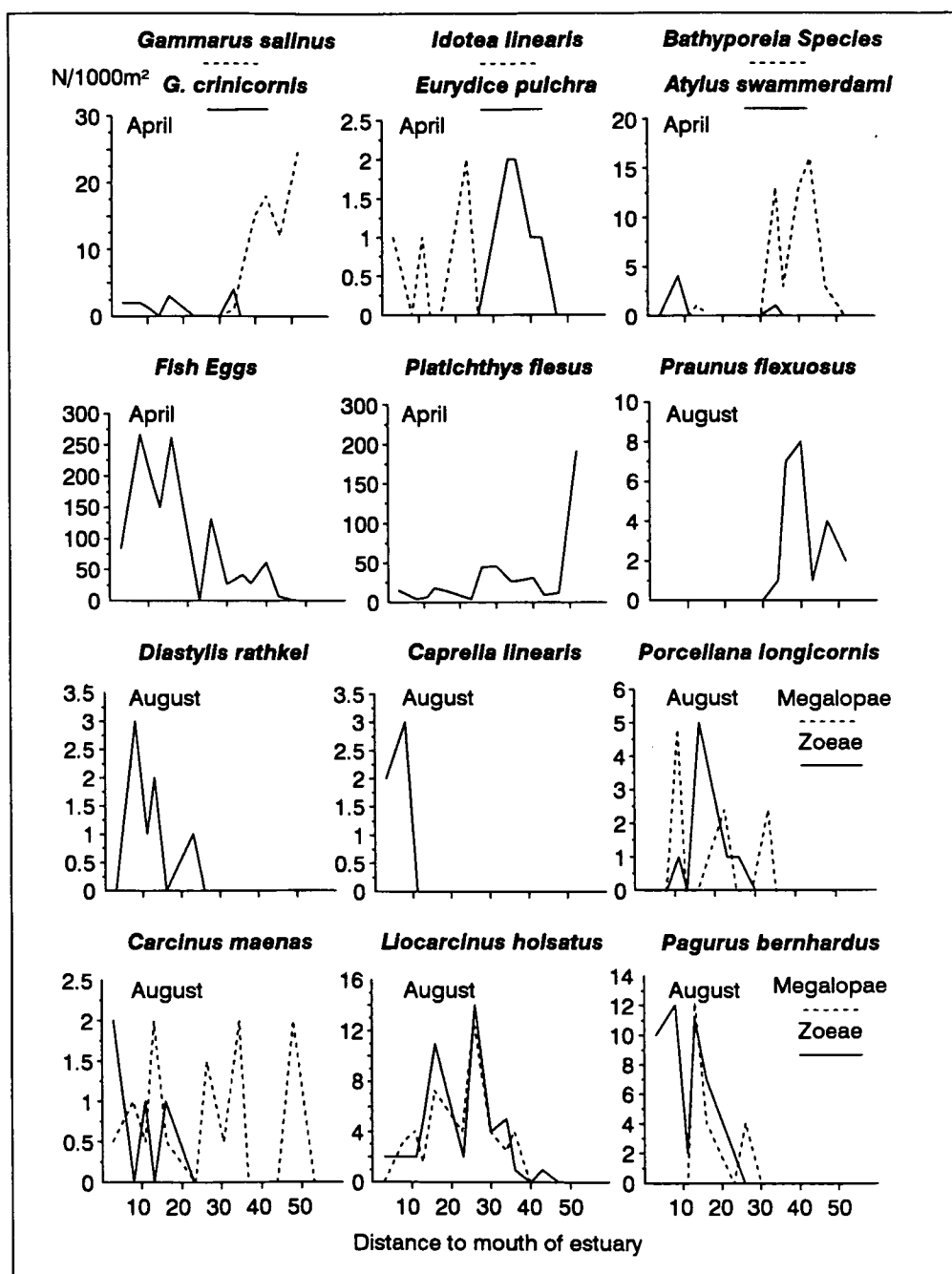


Figure 4.3. Distribution of selected hyperbenthic animals along the axis of the estuary in April and August.

Hill's diversity numbers were calculated for each station in each season and for the stationwise sum of all density data over the three sampling periods (Table 4.3). The variation in diversity ( $N_0$ ,  $N_1$ ,  $N_2$  and  $N_\infty$ ) between sites is shown in Figure 4.4. The innermost sites had a clearly lower diversity for all measures: these samples were characterized by a low number of species with one or two species dominating the community numerically. The most downstream stations had the highest diversities: here a high number of species were present and the individuals are distributed more evenly among them. For the total study area, the highest number of species was present in summer (cf. highest  $N_0$ ). However, a lot of these species were rare (only 1 or 2 individuals caught): for all other diversity numbers the spring and winter samples show higher values, the spring samples being by far the most diverse.

**Table 4.3.** Hill's diversity numbers  $N_0$ ,  $N_1$ ,  $N_2$  and  $N_\infty$  for each sample and for the whole month. The month in which the sample was taken is indicated by two letters preceding the code (ap for April, au for August and de for December).

April	ap01	ap02	ap03	ap04	ap05	ap06	ap07	ap08	ap09	ap10	ap11	ap12	ap13	ap14	Total
$N_0$	20	20	20	17	17	9	15	14	20	15	18	14	10	12	35
$N_1$	7.149	5.882	6.535	6.619	5.472	3.709	4.950	3.118	2.679	1.555	2.422	1.868	2.090	1.804	3.191
$N_2$	5.070	4.041	4.440	4.187	4.217	2.174	3.558	1.915	1.929	1.229	1.911	1.453	1.574	1.393	2.419
$N_\infty$	3.051	2.930	2.630	2.370	3.140	1.500	2.710	1.410	1.450	1.110	1.450	0.820	1.275	1.191	1.749
August	au01	au02	au03	au04	au05	au06	au07	au08	au09	au10	au11	au12	au13	au14	Total
$N_0$	21	26	16	22	23	18	12	15	20	14	11	12	13	12	48
$N_1$	3.010	3.301	3.054	2.841	1.539	1.284	1.730	2.044	1.051	1.342	1.149	1.077	1.329	1.411	1.571
$N_2$	6.031	2.599	2.493	2.866	1.357	1.194	1.647	1.758	1.027	1.171	1.056	1.031	1.165	1.226	1.239
$N_\infty$	4.590	1.714	1.703	1.860	1.170	1.894	1.316	1.385	1.013	1.085	1.028	1.015	1.082	1.113	1.117
December	de01	de02	de03	de04	de05	de06	de07	de08	de09	de10	de11	de12	de13	de14	Total
$N_0$	6	15	7	14	12	7	6	8	6	14	7	12	14	5	30
$N_1$	2.317	3.964	1.866	2.021	1.731	1.510	1.696	1.826	2.481	1.960	1.375	1.802	1.435	1.013	2.466
$N_2$	3.285	3.497	1.414	1.920	1.433	1.346	1.563	1.999	2.191	1.650	1.169	1.518	1.231	1.007	1.886
$N_\infty$	2.400	2.540	1.190	1.420	1.206	1.160	1.280	1.490	1.740	1.340	1.080	1.266	1.114	1.003	1.457

#### 4.3.2. Environmental variables

The main environmental gradients for each season are shown in Figure 4.5. Salinity and dissolved oxygen always showed a continuous decline from the mouth towards the inner reaches of the estuary. The Secchi depth gradient was less regular but the Eastern half of the study area was on average characterized by a higher turbidity of the water. In spring and summer temperature increased towards the inner part of the estuary; in winter this trend was reversed but still the innermost station had a higher temperature than the neighbouring stations downstream. This was possibly due to thermal enrichment from the nuclear power plant of Doel near the Dutch-Belgian border just outside the study area.

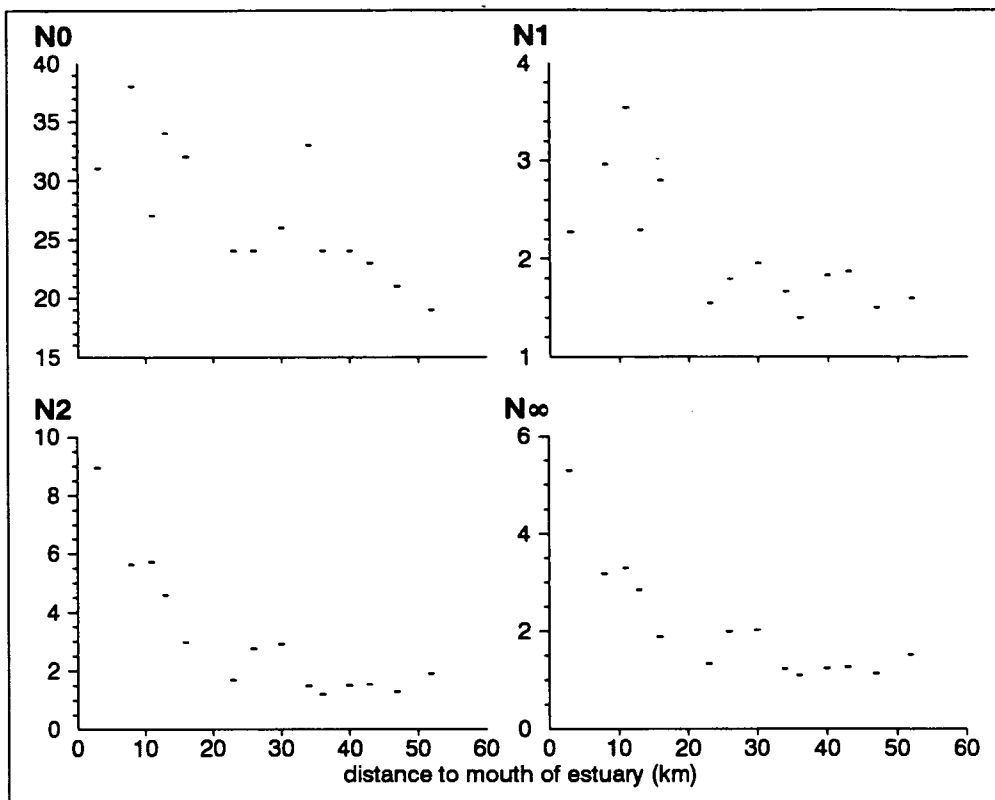


Figure 4.4. Hill's diversity numbers for each station, calculated from the sum of the density data over the 3 months.

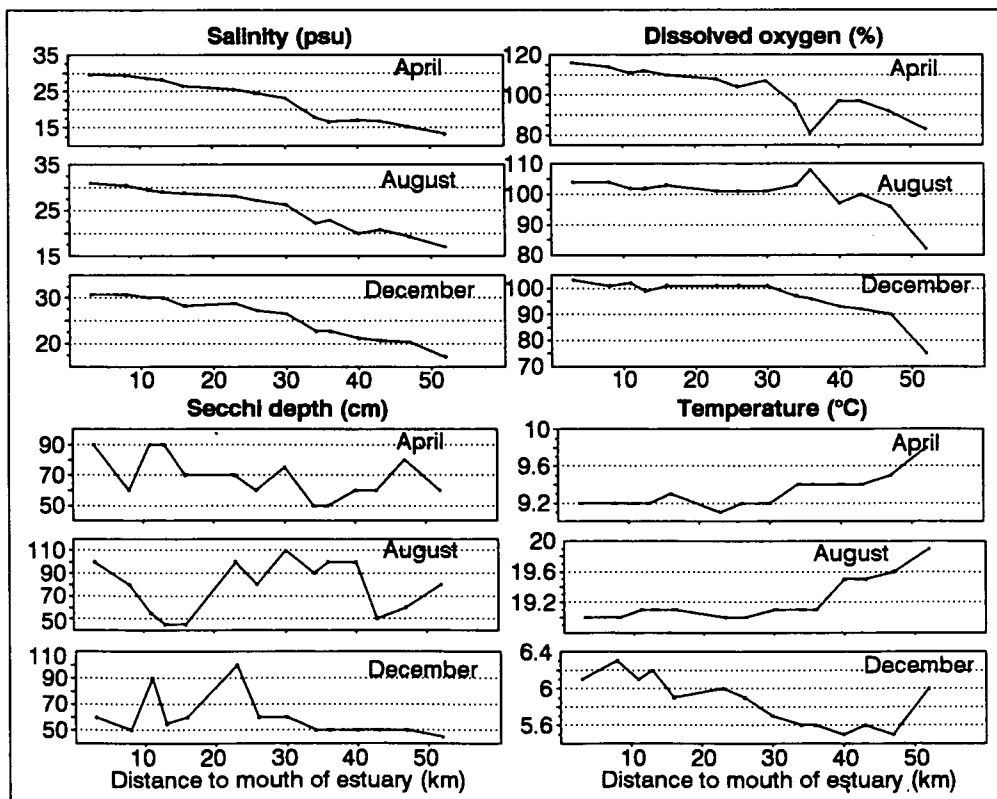


Figure 4.5. Environmental variables measured at each station for the 3 months.

### 4.3.3. Analyses with the complete set of data: temporal and spatial patterns

#### Identification of communities

The result of the TWINSpan analysis performed on the (4<sup>th</sup> root transformed) density data of the three seasons taken together is presented in Figure 4.6. The first division is a spatial one: all downstream (Western or 'marine') samples of the three seasons are separated from the upstream (Eastern or 'brackish') samples. Indicator species for the Western group are zoea larvae of the swimming crab, *Liocarcinus holsatus*. The indicators for the Eastern group are the amphipod *Gammarus salinus* and the mysids *Neomysis integer* and *Mesopodopsis slabberi*, the latter species at high densities (cutlevel 5). The subsequent divisions reveal seasonal patterns in both major clusters. In the Western group the 8 outermost spring samples first split off from a group comprising the 8 outermost summer samples and the 2 most downstream winter samples. Indicator species for the spring samples are all temporary hyperbenthic species: *Pleuronectes flesus* (larvae of flounder), fish eggs and the zoea larvae of the hermit crab *Pagurus bernhardus*. An additional indicator is the marine mysid *Schistomysis spiritus*. Further divisions yield 4 ecologically meaningful clusters, each grouping a number of spatially and seasonally segregated samples (see Figure 4.6). A similar pattern appears in the Eastern group. In the first instance all summer samples are split off. In a subsequent division in the remaining group the spring samples are completely separated from the winter samples (indicator species again larval flounder). A third division, grouping the winter samples into two clusters ('mid' and 'east') is also considered to be meaningful. In total 8 clusters are distinguished.

The analysis with the biomass data yielded almost the same picture (not presented). The difference is that in the very first division all April samples were isolated with *Pleuronectes flesus* as indicator species. The following divisions in both major groups clustered the samples in exactly the same order as indicated in Figure 4.6. Only station 9, situated at the interface between the marine and the brackish parts of the estuary, occasionally shifted from one cluster to another.

Dendrograms for the clusteranalyses have essentially similar configurations. The analysis with the density data (Figure 4.7) as well as with the biomass data (not presented) show that the samples from the Western part of the estuary (roughly stations 1 to 8) are faunistically very different from the samples from the Eastern part (samples 10 to 14, with station 9 again showing an indecisive behaviour). Then again the same temporal and spatial patterns emerge dividing the estuary in 2 or 3 geographically isolated areas in each season.

#### Relation to environmental gradients

The ordination is in general agreement with the divisive cluster analyses. The 8 clusters identified by TWINSpan can also be identified in the ordination plane formed by the first (eigenvalue 0.34) and second (eigenvalue 0.22) canonical axes (Figure 4.8

top). The eigenvalues for the third and fourth canonical axes are much lower (0.12 and 0.05 respectively) and yield no additional information.

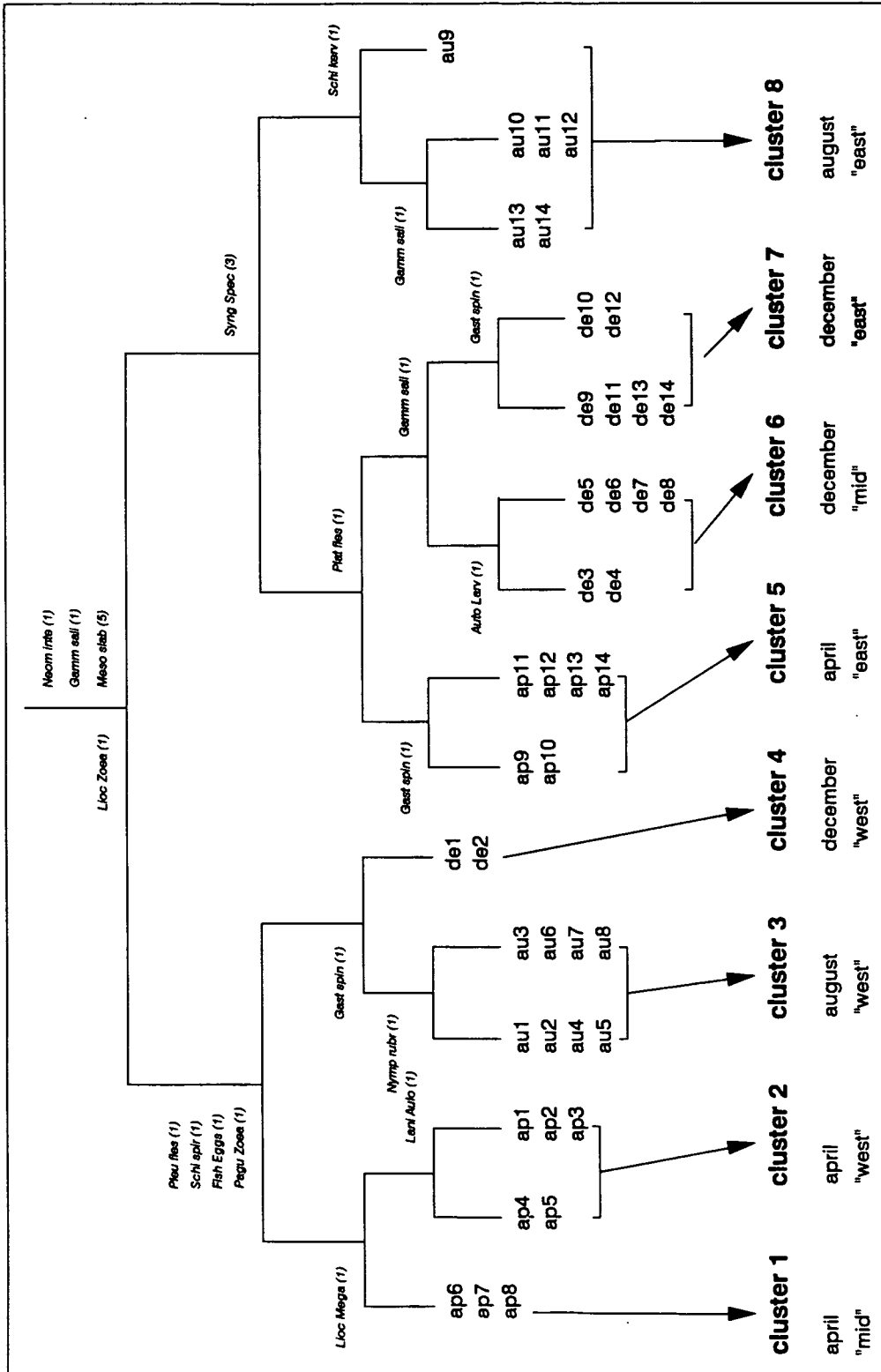
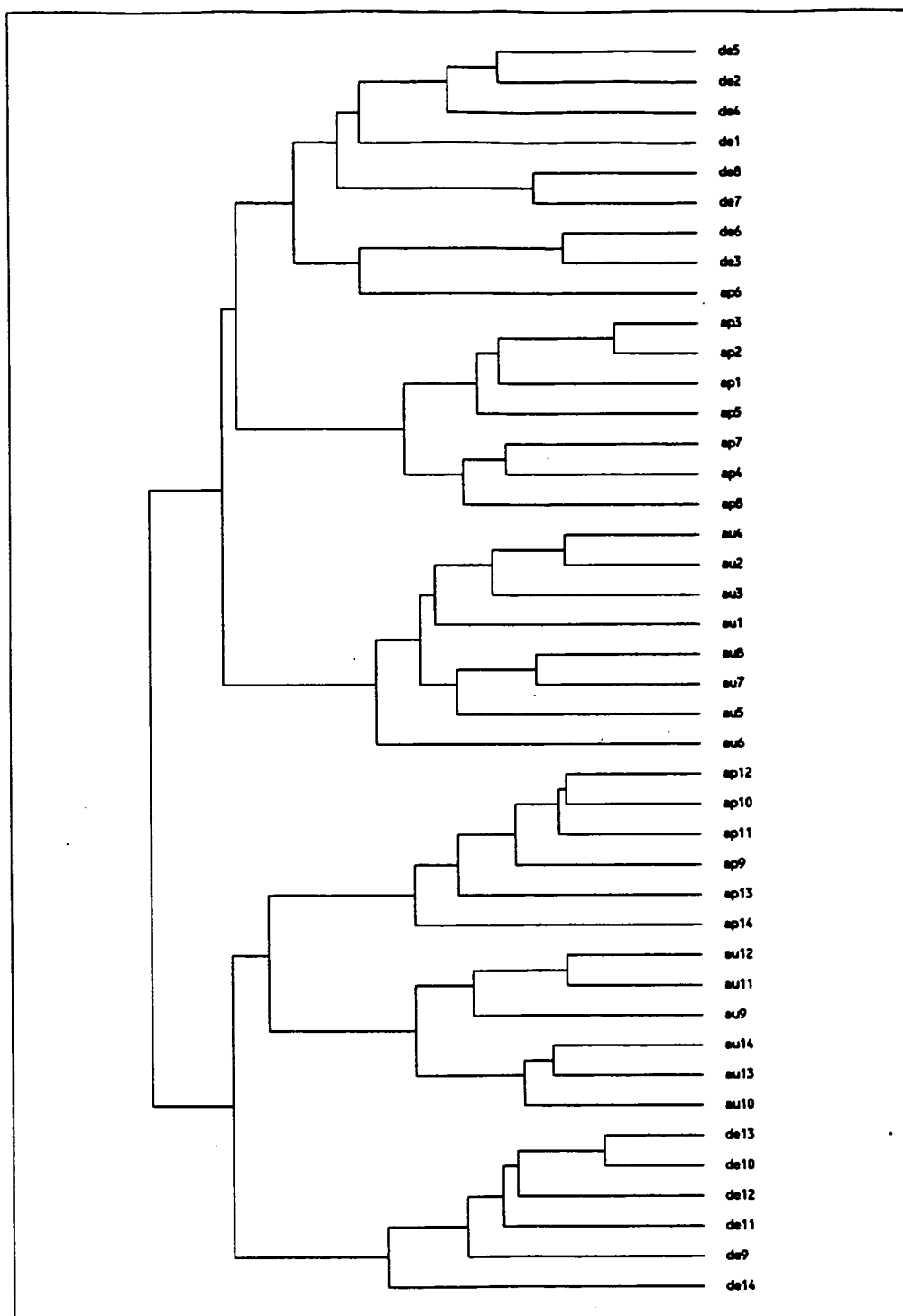
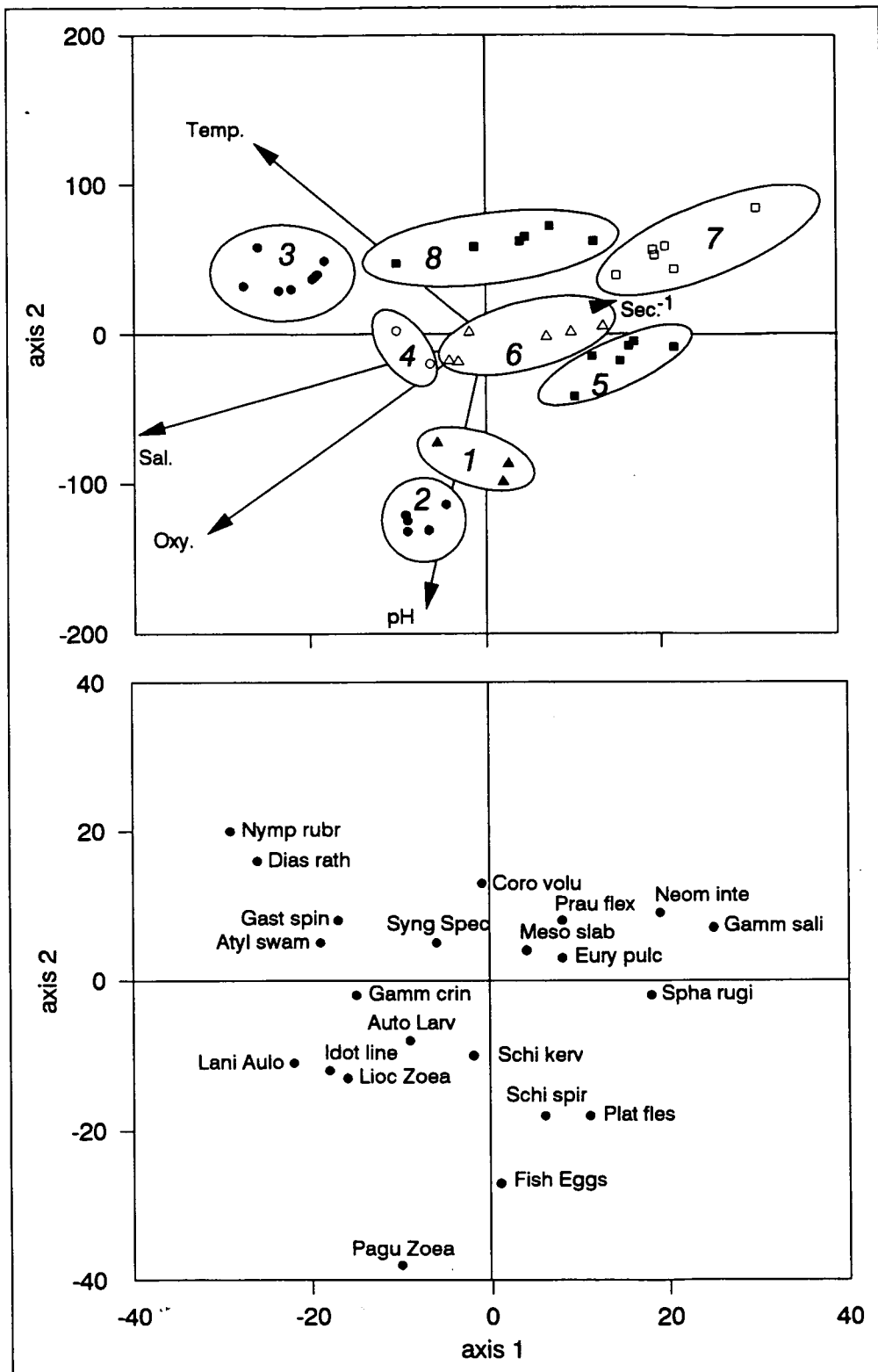


Figure 4.6. TWINSPLAN clusters, derived from the matrix of the (4th root transformed) density data of the three months. Indication of clusters as discussed in the text.



*Figure 4.7. Group average sorting of all density data using Bray-Curtis similarities.*

The longest arrows in the environmental biplot (Figure 4.8 top) are salinity and dissolved oxygen. Both variables show a strong positive correlation. Together with the arrow of the reciprocal of Secchi depth, which is negatively correlated with salinity (angle of  $180^\circ$ ), these two variables characterize the main environmental gradient correlated with the structure of the hyperbenthic communities. Along this gradient, which lies close to the first (and most important) canonical axis, the ordination plane is



*Figure 4.8. Results of CANOCO analysis using the density data of the three months. Biplot of sample scores and environmental variables with indication of the communities as identified by TWINSpan (top), and biplot of scores of the most important species (bottom). The scores of the environmental variables were divided by 4 to fit the graph.*



divided into two zones. On the left side all Western samples (characterized by high salinity, high oxygen and low turbidity) are grouped; on the right side all Eastern samples are found (characterized by low salinity, low oxygen and high turbidity). The samples of the middle part of the estuary are located in the middle of the diagram. The second canonical axis is correlated with temperature and pH. The temperature arrow is almost orthogonal to the main structuring gradient, indicating no correlation between the values of this variable and the main gradient mentioned above. Along this axis a temporal segregation of the communities can be seen. The summer samples are situated in the higher half of the diagram (clusters 3 and 8). In the bottom half of the diagram the spring samples produce tight clusters (2, 1 and 5). Located between the summer and spring samples the winter clusters (4, 6 and 7) are found.

In the plot of the species scores (Figure 4.8 bottom) the most important discriminating species are shown. Roughly, the species in the left half of the plot are 'marine' species which prefer high salinities and do not penetrate far into the estuary. They are characteristic for the hyperbenthic communities of the Western part of the Westerschelde in summer (upper left quadrant) and spring (lower left quadrant). Note the temporary hyperbenthic species which had their peak abundance in spring in the lower left quadrant and were mostly restricted to the marine part. Fish eggs (only just) and flounder larvae are the only temporary hyperbenthic species found in the lower right quadrant. In the right half of the graph the typical brackish water species are found which are characteristic for the hyperbenthos of the Eastern part of the study area throughout the year.

In both plots the spread of the items (samples and species) along the second axis is most pronounced in the left half of the diagram. Moving towards the right items, items show a tendency to converge towards the first axis. This suggests that temperature (seasonal) effects are most decisive in structuring the hyperbenthic community in the marine and, to a lesser extent, in the middle part of the estuary. In the brackish zone the hyperbenthic fauna shows a nearly identical composition in each season.

#### Characterization of the communities

The average abundance and biomass of the different communities, as identified by TWINSpan and confirmed by the other multivariate techniques, are shown in Figure 4.9. In the pie charts the faunistic composition of each cluster is roughly presented (only species that make up 4% or more of the total hyperbenthic community are considered). Mysids dominated the hyperbenthos of every subarea in each season. In the clusters from the brackish part of the estuary densities and biomass are consistently higher than in the clusters from the middle and marine parts. They are furthermore characterized by a more monotonous fauna: throughout the year few species occurred in this area but they reached very high numbers. The Western stations on the other hand were characterized by a poor hyperbenthic fauna in terms of density and biomass, but the communities were composed of many different species.

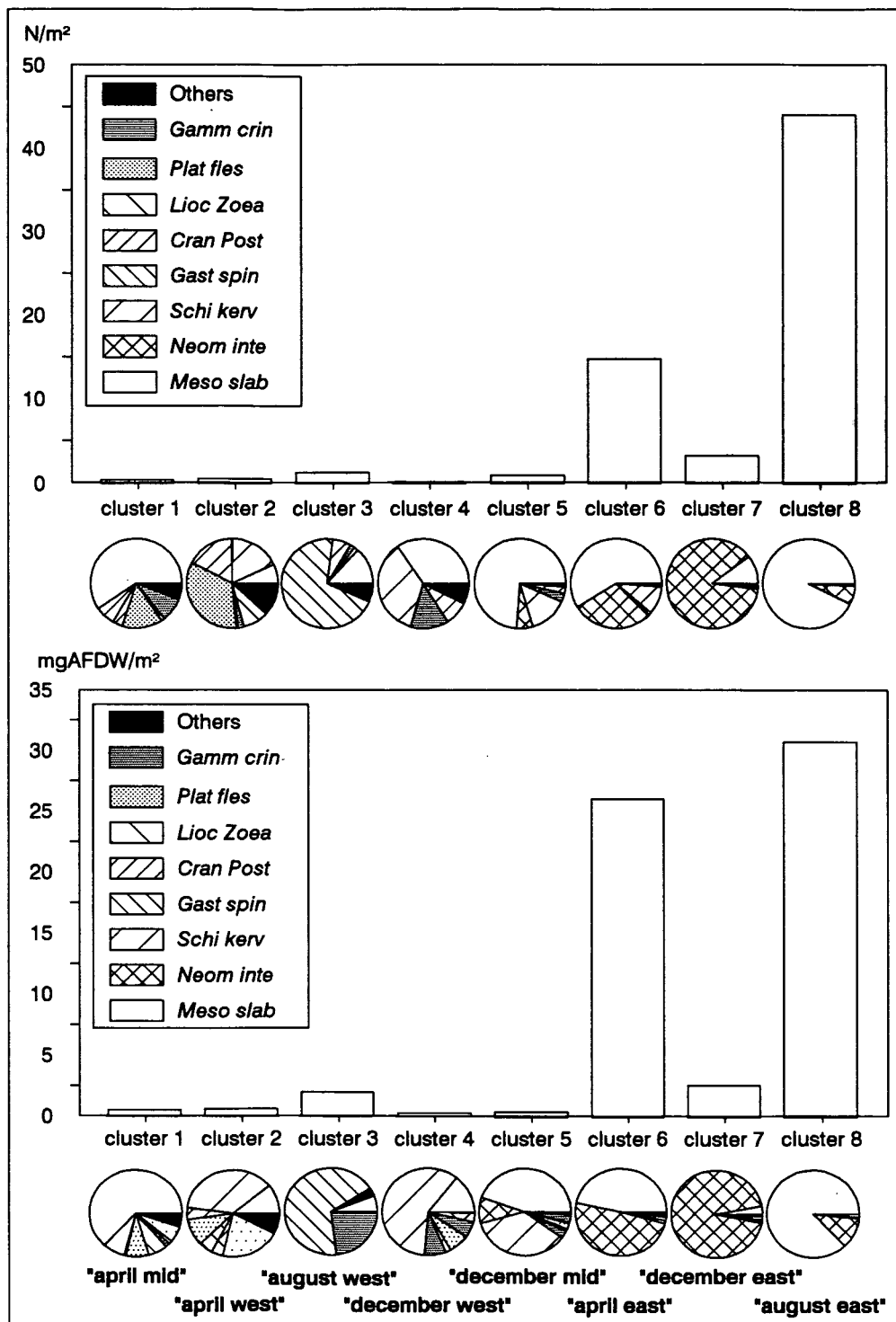


Figure 4.9. Composition and average density (top) and biomass (bottom) of the communities identified by TWINSpan of all density data.

The hyperbenthic fauna reached highest numbers in summer in both marine and brackish parts. The Eastern community was dominated by *Mesopodopsis slabberi* and, to a lesser extent, by *Neomysis integer*; the Western part by *Gastrosaccus spinifer*.

Winter is the poorest season: density, biomass and diversity were lowest. In the Eastern part the fauna was almost exclusively composed of *Neomysis integer*; the hyperbenthos of the Western part was again more diverse and the most important species were *Schistomysis kervillei* (especially in biomass terms), *Mesopodopsis slabberi*, and a variety of other permanent hyperbenthic species. The middle part of the estuary was dominated numerically by *Mesopodopsis slabberi*, though this slender species did not contribute much to the total biomass of the community. The biomass pie chart shows that representatives from both Eastern and Western communities were equally well represented in this area.

In spring total densities were high, yet lower than in summer. The dominant species in the April-East community were *Mesopodopsis slabberi* (density) and *Neomysis integer* (biomass). The April-West community was the most diverse of all, due to the presence of a variety of equally important mysid and temporary hyperbenthic species. The middle part was again characterized by a mixture of the species characterizing the other communities of the same month, *M. slabberi* being the dominant species. Due to the larger body size of the individual mysids in the spring generation (Mees, unpubl.) their biomass value was proportionally a lot higher than in the other seasons.

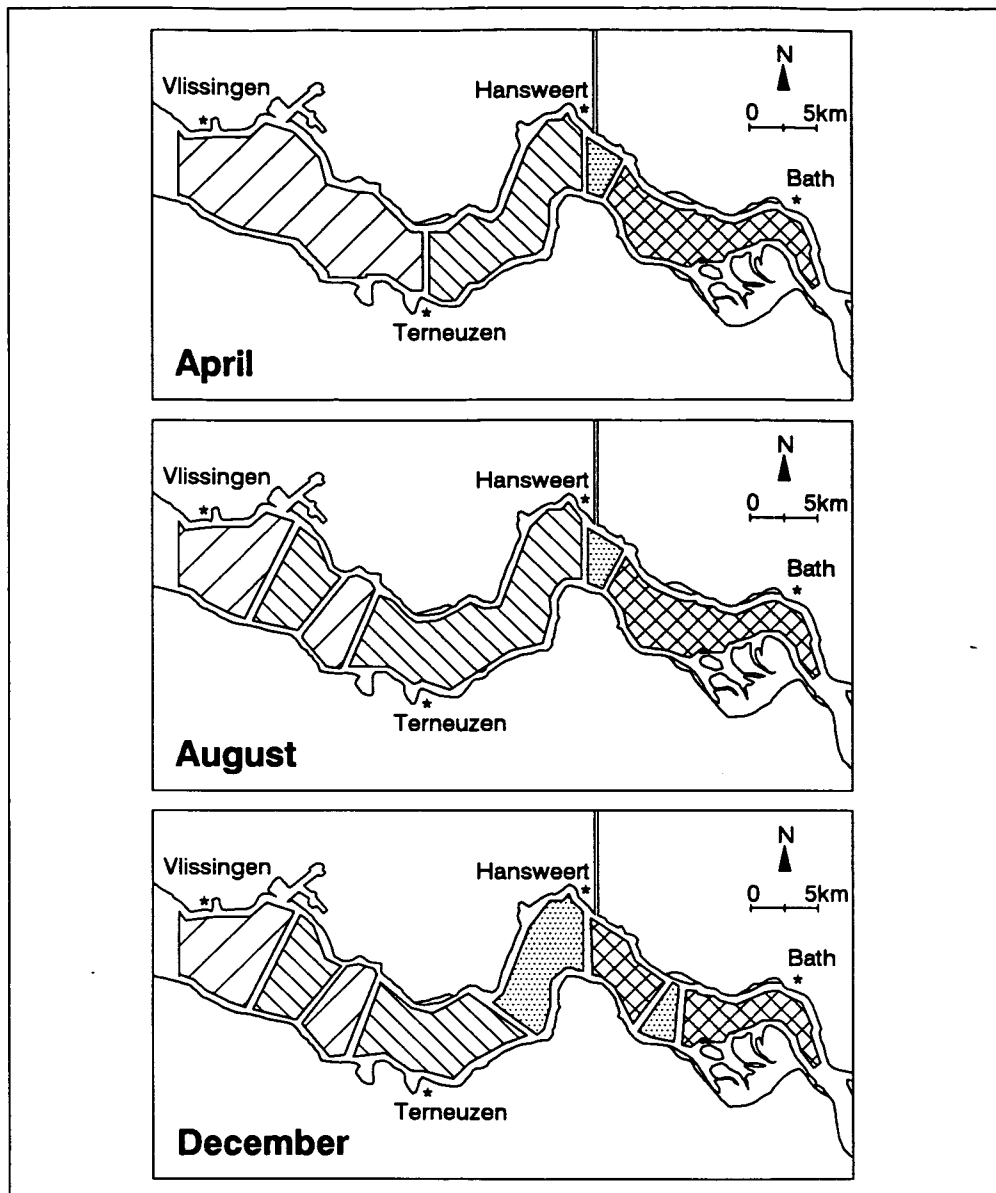
#### 4.3.4. Analyses with data per season

##### Identification of communities

The dendrograms of the TWINSPAN analyses using density and biomass data of the separate months are not presented as such. Figure 4.10 shows the geographical location in real space of the clusters yielded after the second division in the analysis of the density data. The analyses with the biomass data give exactly the same picture except for some minor shifts of marginal stations in the middle part of the estuary to the neighbouring clusters (one station in summer and one in winter). The general spatial pattern is the same for each month. Four different communities were present in the study area: two were located in the Western part of the estuary (clusters 1 and 2) and two in the Eastern part (clusters 3 and 4). Cluster 3 of April and August consists of only one station (station 9). The group average sorting cluster analysis yields the same groups of samples. These analyses further show that the communities of clusters 1 and 2 are always highly similar and that the stations in cluster 4 have a highly dissimilar faunistic composition in comparison with the other groups. The small cluster 3 shows an unstable behaviour: in one analysis it clusters closer to the Western stations, closer to the Eastern stations in the next.

##### Relation to environmental gradients

Figure 4.11 depicts the results of the canonical correspondance analysis performed with the density data of the spring campaign and is exemplary for the



*Figure 4.10. Geographical location of the four different communities identified by TWINSpan of the density data for separate months.*

output yielded by this technique for the other seasons too. Only the ordination plane formed by the first two axes (eigenvalues 0.35 and 0.09) is considered; the eigenvalues of the higher axes are always negligible (never more than 0.05). The plot of the scores of the environmental variables (Figure 4.11 bottom) shows a clear gradient with highest salinities, dissolved oxygen concentrations and light penetration values and lower temperatures on the right side of the ordination plane. The salinity and dissolved oxygen arrows are long and have a strong positive correlation. They nearly coincide with the first axis and are thus most important in explaining the observed variation. In the top half of the same figure the scores of the samples and the most important species are plotted together. The consecutive stations of the sampling

scheme are connected by a line, with the most downstream station (1) situated on the right and the innermost station (14) on the left. All species located in the left part of the diagram are typical for the brackish water zone, the species on the right for the marine zone of the estuary. The spatial distributions of the most important species in each season are presented in more detail in Figures 4.2 and 4.3.

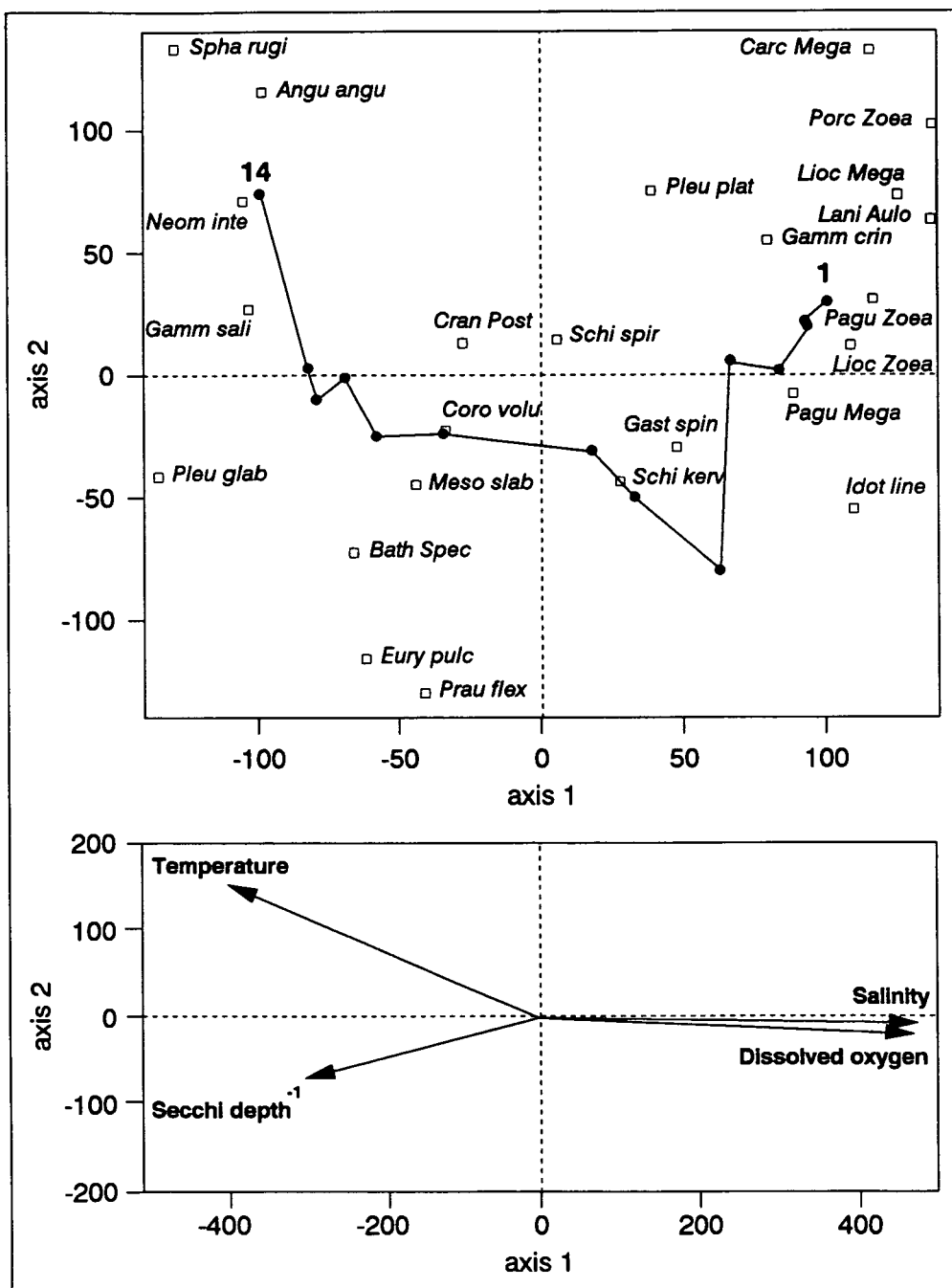


Figure 4.11. Results of CANOCO analysis using the density data of April. Biplot of environmental variables (bottom), and biplot of sample scores and scores of the most important species (top). The solid line in the top graph indicates the real space order of the samples.

## Characterization of the communities

Figure 4.12 shows the average density and biomass and the composition of the hyperbenthic fauna in each cluster identified by TWINSpan for each season. It is immediately obvious that the eastern clusters (3 and 4) are always characterized by a much richer hyperbenthic fauna (higher density and biomass) which is dominated by *Mesopodopsis slabberi* and *Neomysis integer*. The Western clusters (1 and 2) are characterized by lower numbers of individuals spread over a higher number of species.

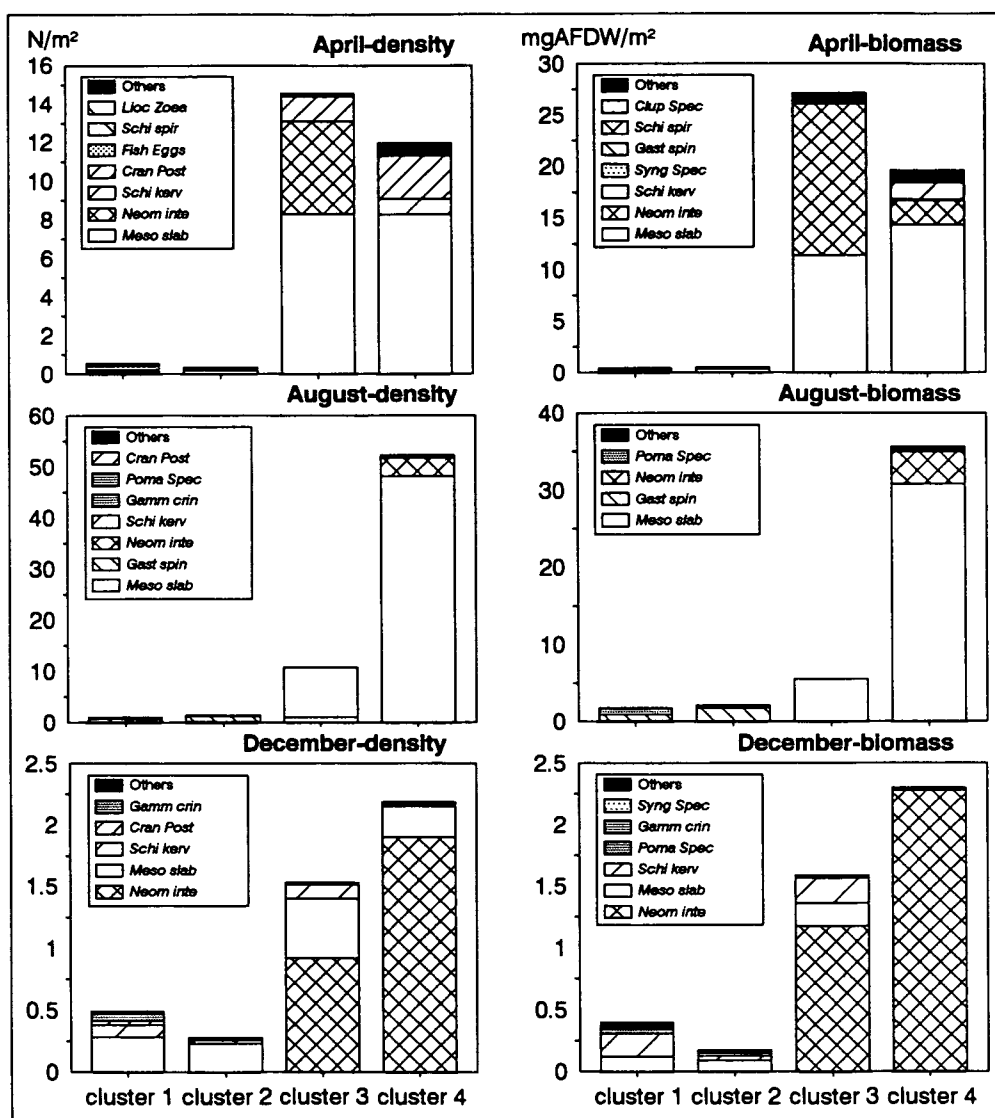
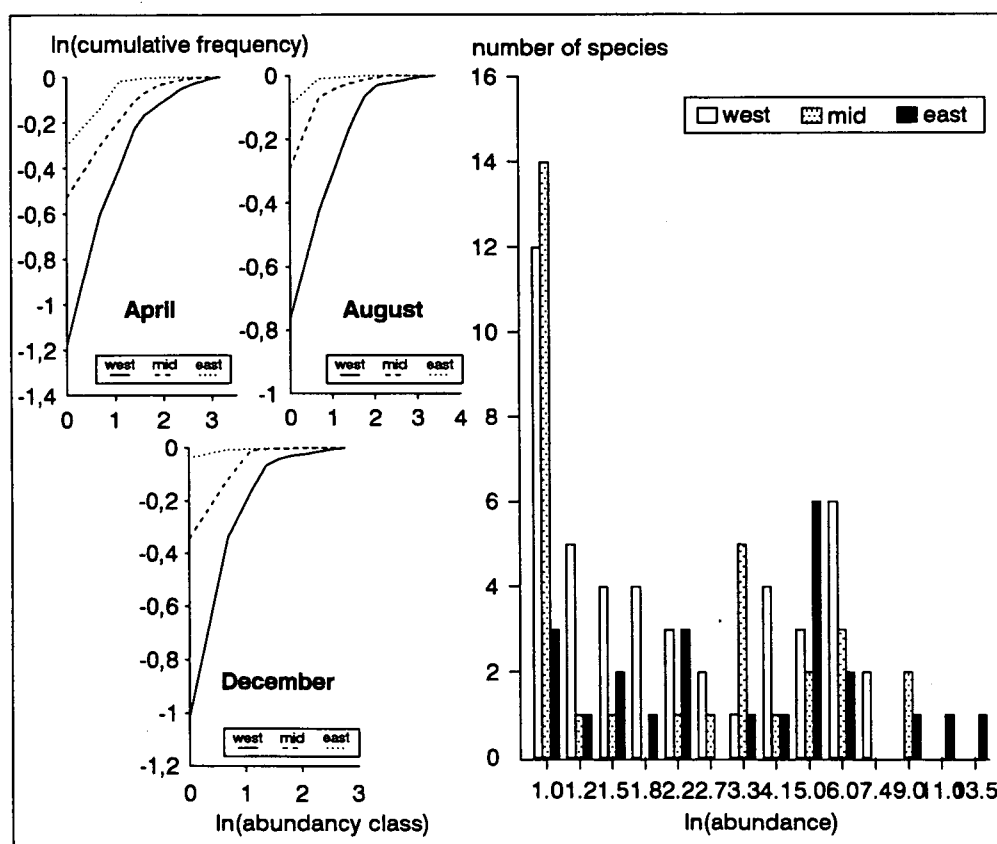


Figure 4.12. Average density (left) and biomass (right) of the communities identified by the TWINSpan with the density data of the separate months.

For the construction of the k-dominance curves and the species-abundance plot (Figure 4.13) the communities considered are not the sums of the samples of the twin-groups, since different clusters contain different numbers of samples and the sampling effort is thus not the same for each community. Instead, 2 stations per subarea were

selected which consistently clustered together throughout the study period: stations 1 and 2 are representative for the Western part, stations 7 and 8 for the middle part and stations 13 and 14 for the Eastern part of the estuary. For the three seasons, the k-dominance plots (Figure 4.13 left) show essentially the same picture: the curves of the Eastern communities are very steep and reach the plateau first, the curves for the Western communities are least steep and the curves of the communities of the middle reaches of the study area take an intermediate position. In the spring situation, species are most equally distributed over the different abundance classes; dominance effects are most pronounced in the winter situation. The species-abundance plot (Figure 4.13 right) shows species belonging to lower abundance classes to be best represented in the Western part of the estuary. The highest abundance classes are only occupied by species occurring in the Eastern part of the estuary. The community of the middle part again takes an intermediate position except for the very lowest abundance class. This is not surprising since in this area several species belonging to the marine and brackish communities meet and are subsequently caught in low numbers.



**Figure 4.13.** K-dominance plots for three different communities in each month (left) and the species-abundance distribution for the same communities using the sum of the data over the three months (right).

#### 4.4. Comparison of seasonal patterns in the marine and brackish zones

The evolution of the environmental variables in both subareas is shown in Figure 4.14. Temperature of the Westerschelde water was just below 10°C at the start of sampling in April. It gradually increased to about 20°C in July-August after which it started to decrease, dropping below 10°C in November and reaching a minimum of about 2°C in February of the next year. Salinity naturally was consistently higher in the marine stations (average of  $30.0 \pm 1.4$  psu) than in the brackish stations (average of  $16.8 \pm 3.3$  psu). Salinity in the brackish zone tended to fluctuate seasonally: lowest values were recorded in winter and spring when freshwater runoff was highest; the highest values were recorded in the summer months (the 'dry season'). Secchi disc depths were nearly always higher in the marine stations (average of  $113 \pm 66$  cm, with a peak of 300 cm in June) than in the brackish stations (average of  $61 \pm 22$  cm). In both zones values tended to be lower in winter. The water in the marine stations was saturated with oxygen throughout the year ( $105.0 \pm 6.2$  %), while in the brackish stations it fluctuated around 80 % of the saturation value ( $77.8 \pm 17.1$  %). A clear minimum was observed in March ( $< 30$  %).

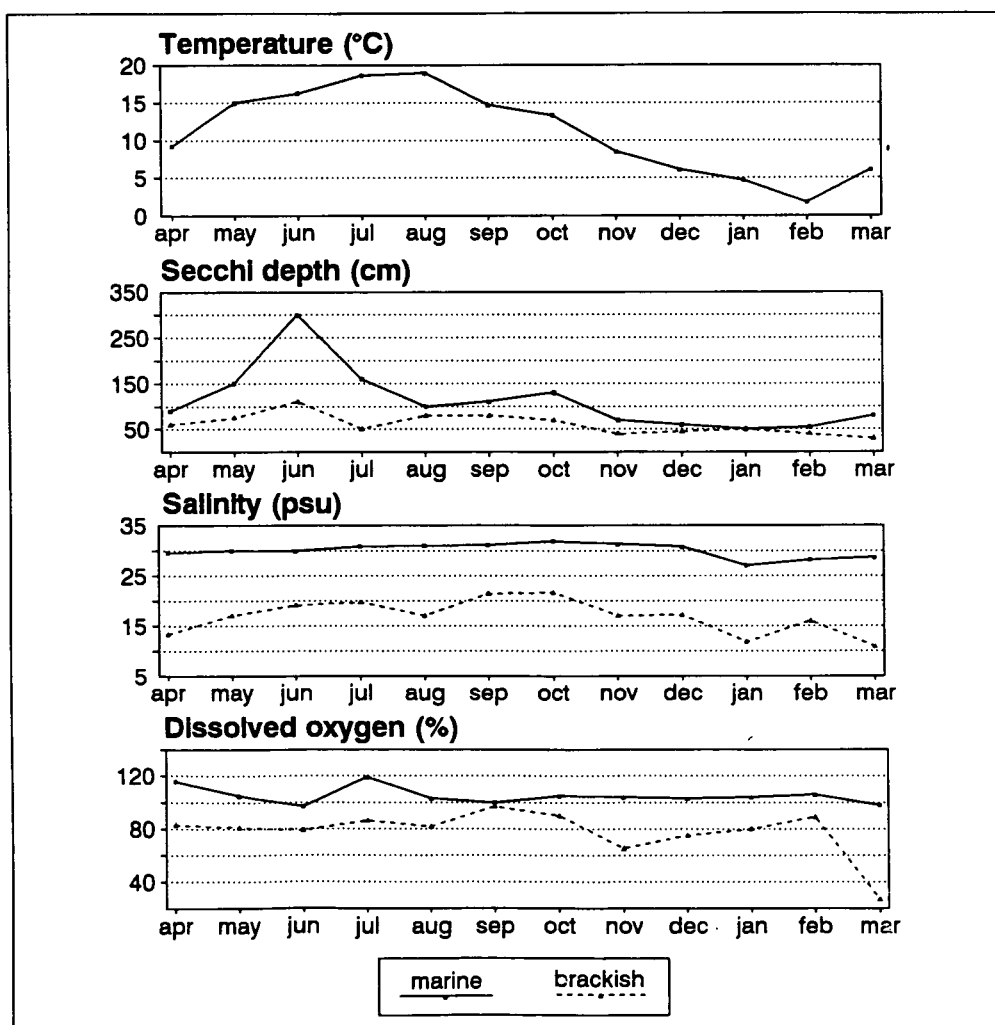


Figure 4.14. Seasonality of environmental variables measured in both subareas.



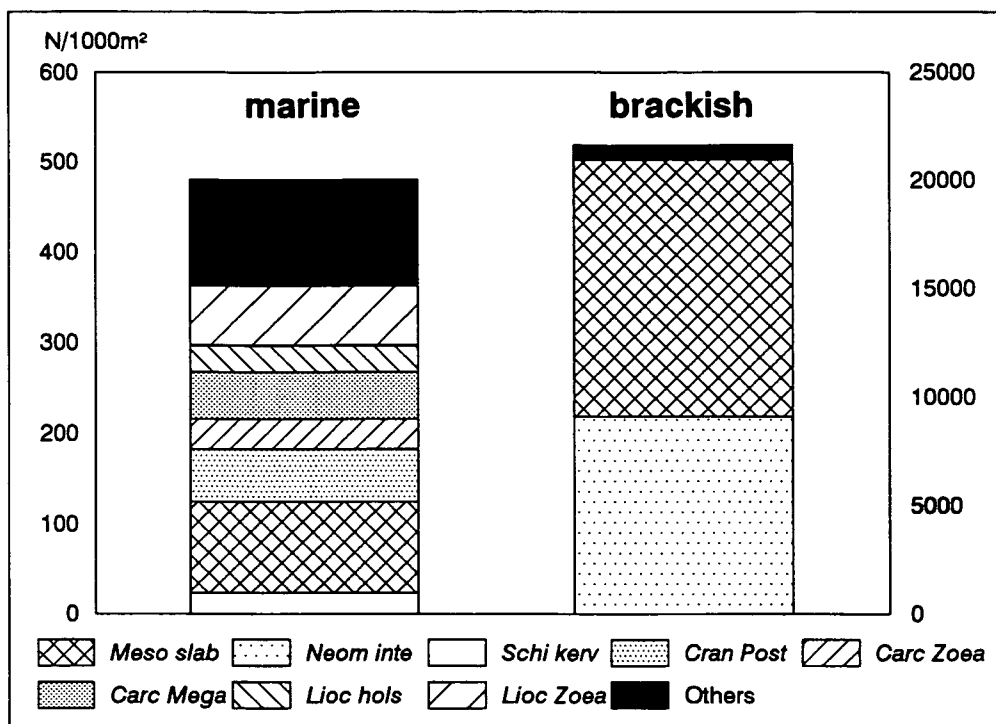


Figure 4.15. Composition and density of the marine (left axis) and brackish (right axis) communities, averaged over one year of monthly sampling.

The yearly average of total hyperbenthic density and the overall species composition for both zones are presented in Figure 4.15 (only species constituting more than 4% of total density are shown; the remainder is grouped as 'others'). Average density is more than 4 times higher in the brackish stations. In the brackish zone the fauna is strongly dominated by only 2 species: the mysids *Neomysis integer* and *Mesopodopsis slabberi*. In the marine zone 7 species are about equally well represented: the mysids *Mesopodopsis slabberi* and *Schistomysis kervillei*, postlarval shrimp *Crangon crangon*, and larval and postlarval stages of the shore crab *Carcinus maenas* (zoeae and megalopae) and the swimming crab *Liocarcinus holsatus* (zoeae and small post-metamorphosis juveniles). Also note the important 'others' section in the marine hyperbenthos which is mainly composed of the mysids *Gastrosaccus spinifer* and *Praunus flexuosus* (2.6 and 1.2 %, respectively), the amphipod *Gammarus crinicornis* (3.9 %), zoeae of *Crangon crangon* (2.5 %) and the postlarvae of gobies and clupeoids (3.5 and 3.2 %, respectively), together with many rarer species belonging to a variety of taxonomic groups. This is also reflected in the total number of species recorded in both zones (58 in the marine zone vs. 27 in the brackish zone).

For a detailed description of the seasonal occurrence and migrations of the mysid, amphipod and isopod species the reader is referred to Cattrijsse *et al.* (1993) and Mees *et al.* (1993a). Most of the temporary hyperbenthic species in the marine stations appear in April (*Crangon crangon*, zoeae of *Liocarcinus holsatus*, *Pleuronectes flesus* and larval clupeoids) or May (megalopae of *Liocarcinus holsatus*, zoea and megalopae of *Carcinus maenas*, postlarval *Pleuronectes platessa* and *Solea solea*,...).

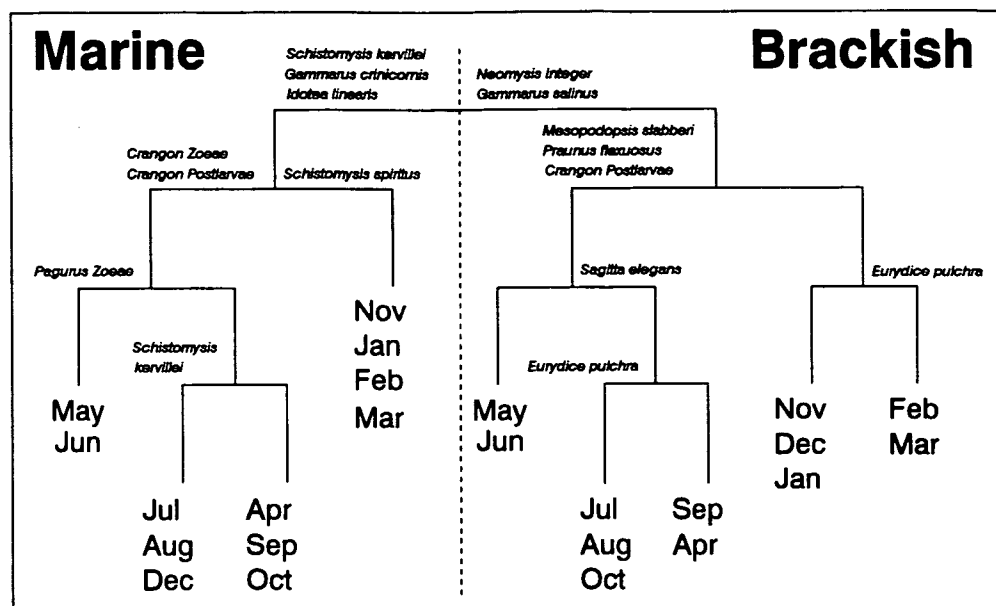
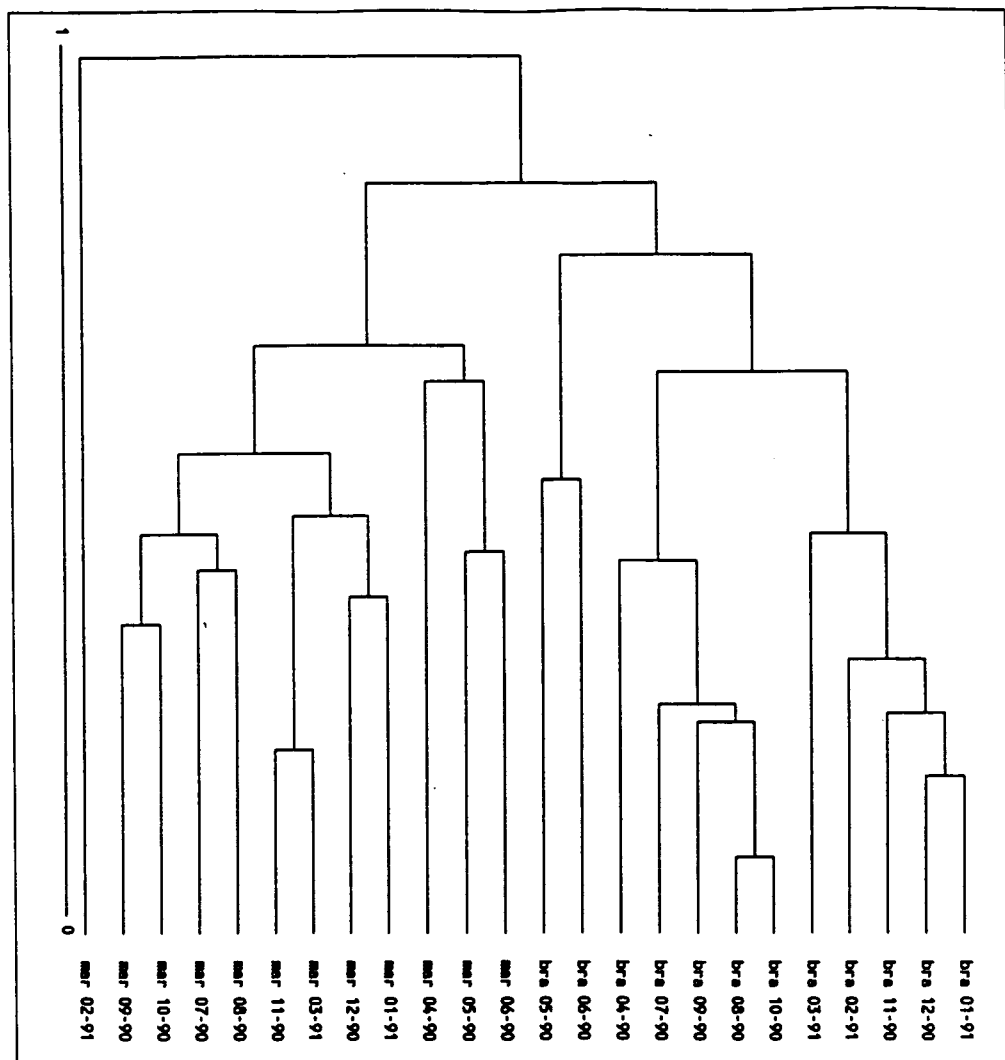


Figure 4.16. TWINSpan with the time series (density) of both subareas.

The first TWINSpan division (Figure 4.16) clusters all marine stations in the positive group (indicator species are the mysid *Schistomysis kervillei*, the amphipod *Gammarus crinicornis* and the isopod *Idotea linearis*) and all brackish stations in the negative group (indicator species are the mysid *Neomysis integer* and the amphipod *Gammarus salinus*). From the second division onwards temporal patterns emerge in both main groups. In the marine and brackish clusters respectively four and five subgroups can be distinguished after the 4th division. The second division separates the winter samples (November through March) from the rest. The only exception is the marine December sample, which the program identified as a borderline positive. For both subareas postlarval shrimp *Crangon crangon* are indicative for the April-October group. In the marine part zoea larvae of the same species are also indicators, while the mysid *Schistomysis spiritus* is indicator species for the winter cluster. In the brackish part the mysids *Praunus flexuosus* and *Mesopodopsis slabberi* are additional indicator species for the April-October cluster. In both zones, the third division splits the May and June samples from a July-October group. In the marine zone zoeae of the hermit crab *Pagurus bernhardus* are indicator species for the May-June group; the chaetognath *Sagitta elegans* is indicator species for the brackish July through October group. The winter group is only further divided in the brackish zone: February and March are separated from November through January (indicator species is the isopod *Eurydice pulchra*). Based on the results of the other multivariate analyses (see below), the fourth division was considered not to be ecologically meaningful.

The result of clusteranalysis (Figure 4.17) strongly resembles the TWINSpan result. The marine February sample is highly dissimilar from all other samples, but the further dichotomies allow for the identification of the same clusters of samples: two highly dissimilar clusters grouping all marine and brackish samples can be seen to be composed of seasonal groupings of samples at decreasing dissimilarity levels.



*Figure 4.17. Clusteranalysis with the time series (density) of both subareas (mar = marine sample; bra = brackish sample). The bottom line gives the dissimilarity scale.*

The scores of the species, samples and environmental variables in the CCA ordination plane formed by the first and second axes (eigenvalues 0.58 and 0.25 respectively) is presented in Figure 4.18. The marine and brackish stations are segregated along the first axis. On the left side the marine stations are further segregated along the second axis: the May and June samples can be found together in the lower left quadrant, the samples from November through February form a tight cluster in the upper left quadrant, while the samples from July through October cluster together in the middle. The intermediate position of the April sample between the spring and autumn groups is evident from this graph. On the right side the brackish stations are all situated close to the first axis. Though seasonal patterns are less obvious here, a May-October group can still be distinguished from a November-March group, April again taking an intermediate position. No further seasonal segregation of the brackish samples could be visualised along the third (eigenvalue 0.12) or fourth (eigenvalue 0.06) canonical axis. The seasonal gradient in the brackish part becomes

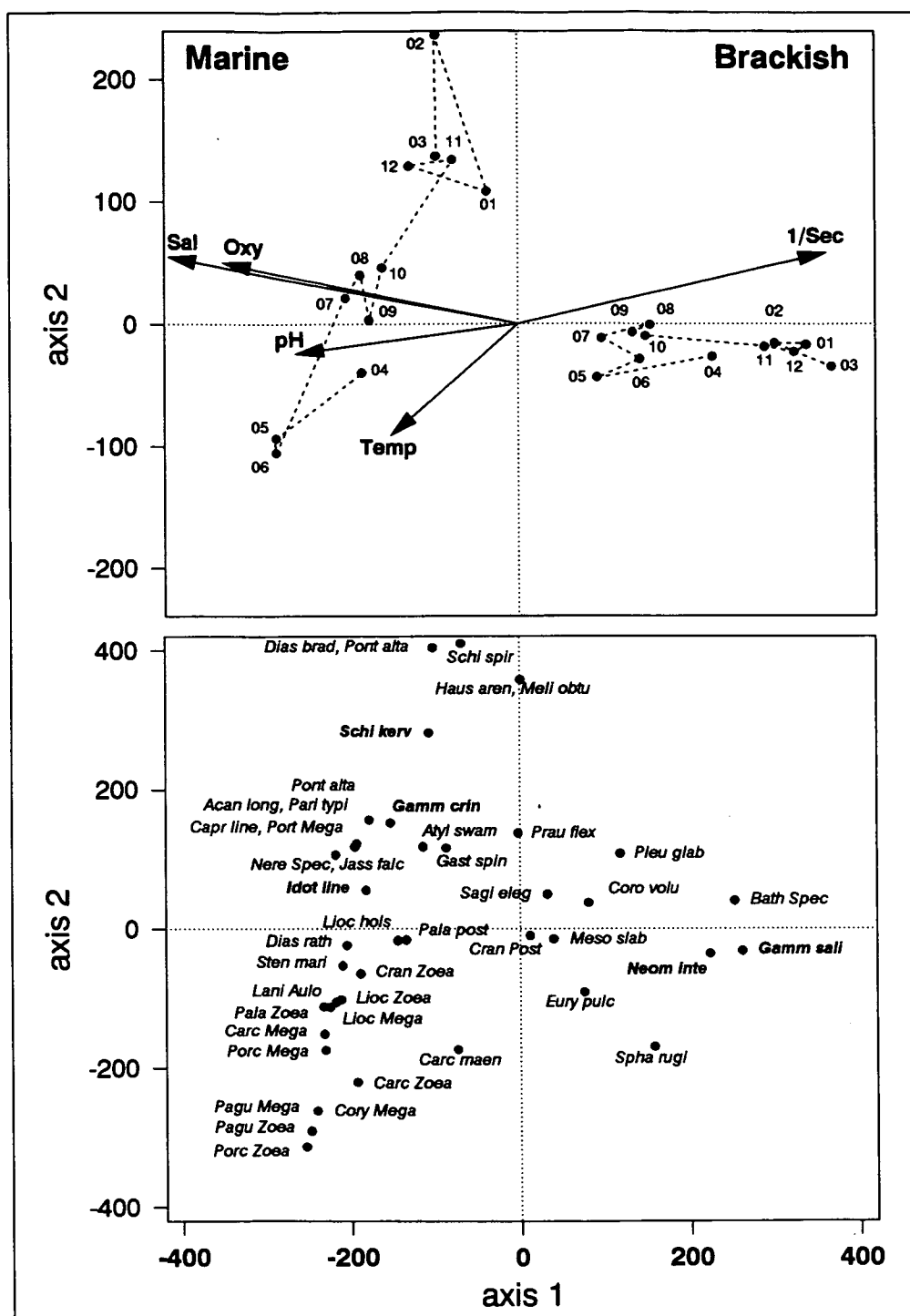


Figure 4.18. Plane formed by the first two axes of the CCA with the density data from the time series of the marine and brackish stations. In the plot of the scores of samples and environmental variables (top), dotted lines indicate monthly sampling sequence in each subarea. TWINSPAN indicator species are printed bold in the plot of the species scores (bottom).

more obvious in the PCA with the fortnightly samples of the *Neomysis* community (see section 4.6). The main environmental gradients structuring the communities are presented as vectors in the plot of the sample scores. The estuarine gradient in salinity,

dissolved oxygen concentration and turbidity are obviously dominant along the first axis. The many species located on the left side of the diagram are characteristic for the communities found in the marine part of the estuary. The spring and summer communities are further characterized by the presence of a high number of temporary hyperbenthic species (larval crustaceans, fish, polychaetes) while winter is mainly characterized by permanently hyperbenthic species (mysids, amphipods, isopods and cumaceans). The fewer species characteristic for the communities of the brackish part are located on the right side of the diagram (all permanent hyperbenthic).

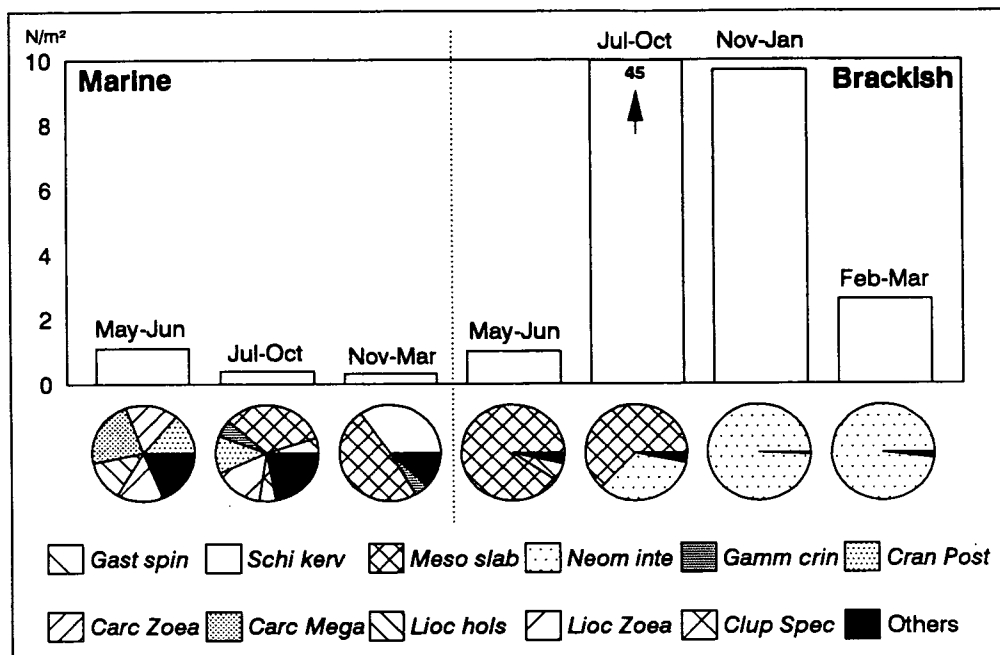


Figure 4.19. Time series of the marine and brackish stations. Average density and species composition of the hyperbenthic communities identified by multivariate analyses.

A summary of the output of the multivariate analyses, i.e. the composition of the communities as identified by TWINSpan after 3 divisions, is presented in Figure 4.19. The marine December sample was pooled with the other winter samples on the basis of the cluster analysis. The marine and brackish April samples were not used in the calculations because of their indistinctive behaviour in the different analyses. The graph is again based on the species constituting at least 4 % of total density in any of the samples in the cluster.

Throughout the year the hyperbenthos of the brackish part is dominated by the two mysid species *Mesopodopsis slabberi* (spring and summer) and *Neomysis integer* (summer through winter). Only in spring larval clupeoids also reach significant densities. In the marine part diversity is much higher: the communities are characterized by many species which are equally represented. Many of these are temporary hyperbenthic species: mainly crab larvae in spring and shrimp and fish in summer-autumn. Only in winter the community is composed almost exclusively of the permanent hyperbenthic species *Mesopodopsis slabberi*, *Schistomysis kervillei* and *Gammarus crinicornis*.

#### 4.5. Detailed description of the seasonal patterns in the brackish part

Since *Neomysis integer* was the target species of the sampling campaigns, it is not surprising that it dominated the fauna in each sample (Figure 4.20 top). For more information on the dynamics of the *Neomysis* population we refer to Mees *et al.* (1994). *Mesopodopsis slabberi* was the second most important species. This mysid started migrating into the estuary in late spring (Mees *et al.* 1993a). Only in summer and autumn (from late June through October) did it co-occur with *Neomysis* in appreciable numbers.

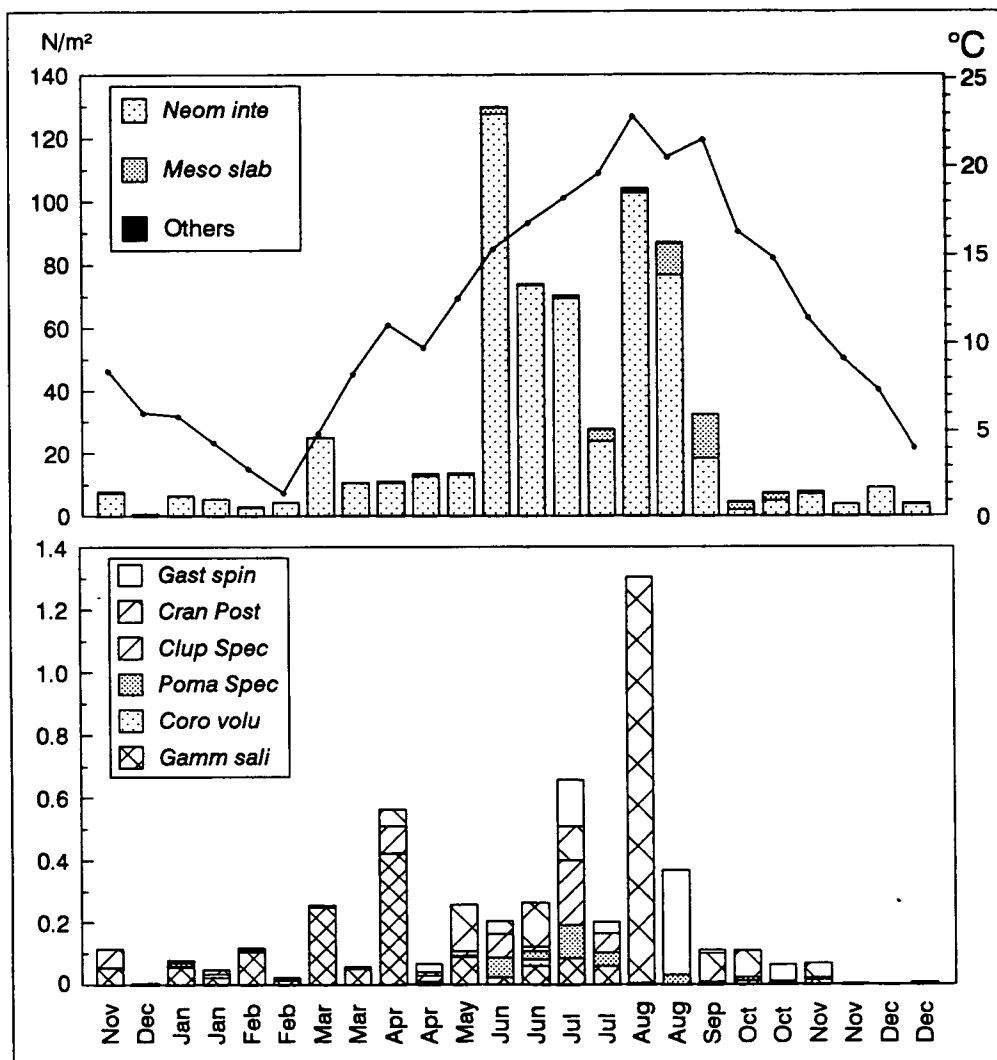


Figure 4.20. Hyperbenthic density in the brackish part of the Westerschelde, including (top) and excluding (bottom) *Neomysis integer* and *Mesopodopsis slabberi*. Evolution of water temperature is also shown (solid line, top right Y axis).

All other species together usually made up much less than 1 % of total hyperbenthic density (Figure 4.20 bottom). The most common of these were *Gammarus salinus* (January through November) and *Gastrosaccus spinifer* (mainly in summer and autumn) which was sometimes accompanied by *Corophium volutator* (always in very low numbers). Temporal hyperbenthic species were few in this zone. Postlarval

*Crangon crangon* were present from April through November with a clear maximum in August. Larval clupeoids also appeared in April. They had disappeared again from the hyperbenthos by the beginning of August. Juvenile gobies occurred from the beginning of June till the end of August. Yolk-sack larvae and postlarvae of flounder *Pleuronectes flesus* were present in low numbers in both March samples only.

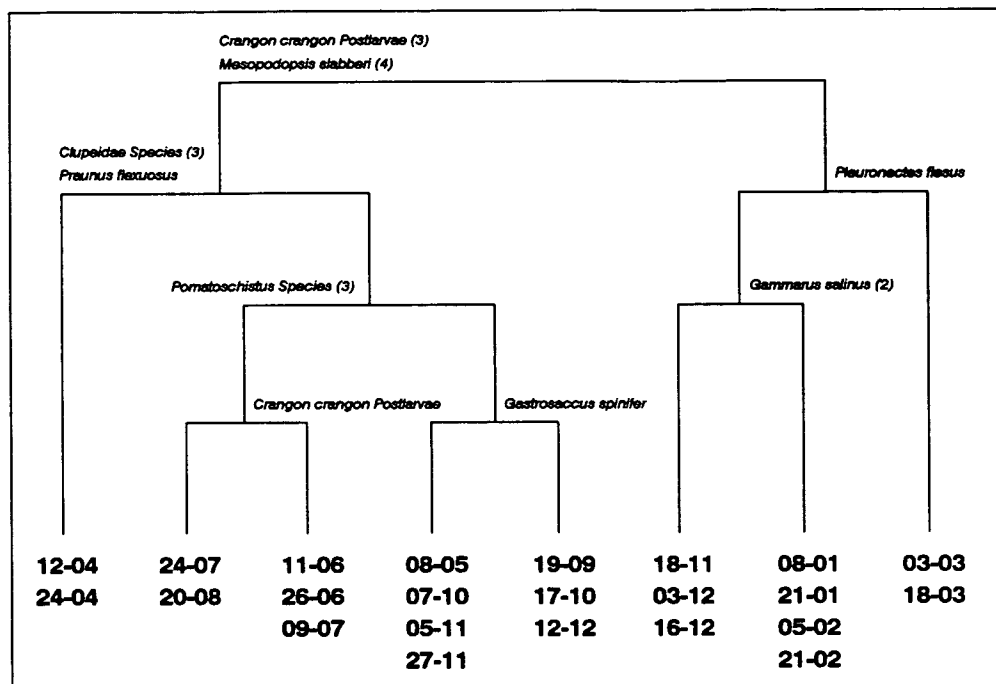


Figure 4.21. TWINSpan with the time series of the brackish part (density).

In the first TWINSpan division the winter and early spring samples are separated from the samples from the rest of the year (Figure 4.21). Indicators for the latter group are the mysid *Mesopodopsis slabberi* and postlarval shrimp *Crangon crangon*, both in high pseudospecies cutlevels. Indicator species for the early spring samples (March) is postlarval flounder *Pleuronectes flesus*, while the community in winter (January and February, plus the second November sample and the December samples of 1991) is characterized by the amphipod *Gammarus salinus* in the second cutlevel. In the other main group late spring (April) first splits from the summer and autumn samples. Indicator species are the mysid *Praunus flexuosus* and larval clupeoids, the latter in high densities. A summer group (June through August) is then separated from an autumn group (September through early November 1991, plus November and December 1990). Juvenile gobies are indicator species for the former cluster (third cutlevel). The May 08 sample is indicated by the programme as a borderline negative in the second division. A comparison with the output of the clusteranalysis (Figure 4.22) shows that the observed patterns are not as stable and clearcut as these demonstrated in the previous dataset. Indeed, dissimilarity between any pair of samples or clusters was always quite low. The sample of May 08, which was mixed with the autumn samples in the previous analysis now appears close to the samples from April.





autumn are scattered near the end of the salinity vector. From the spring samples the March samples are found on the opposite side of the salinity vector while April and May samples hold the central position with regard to both the first and second axes.

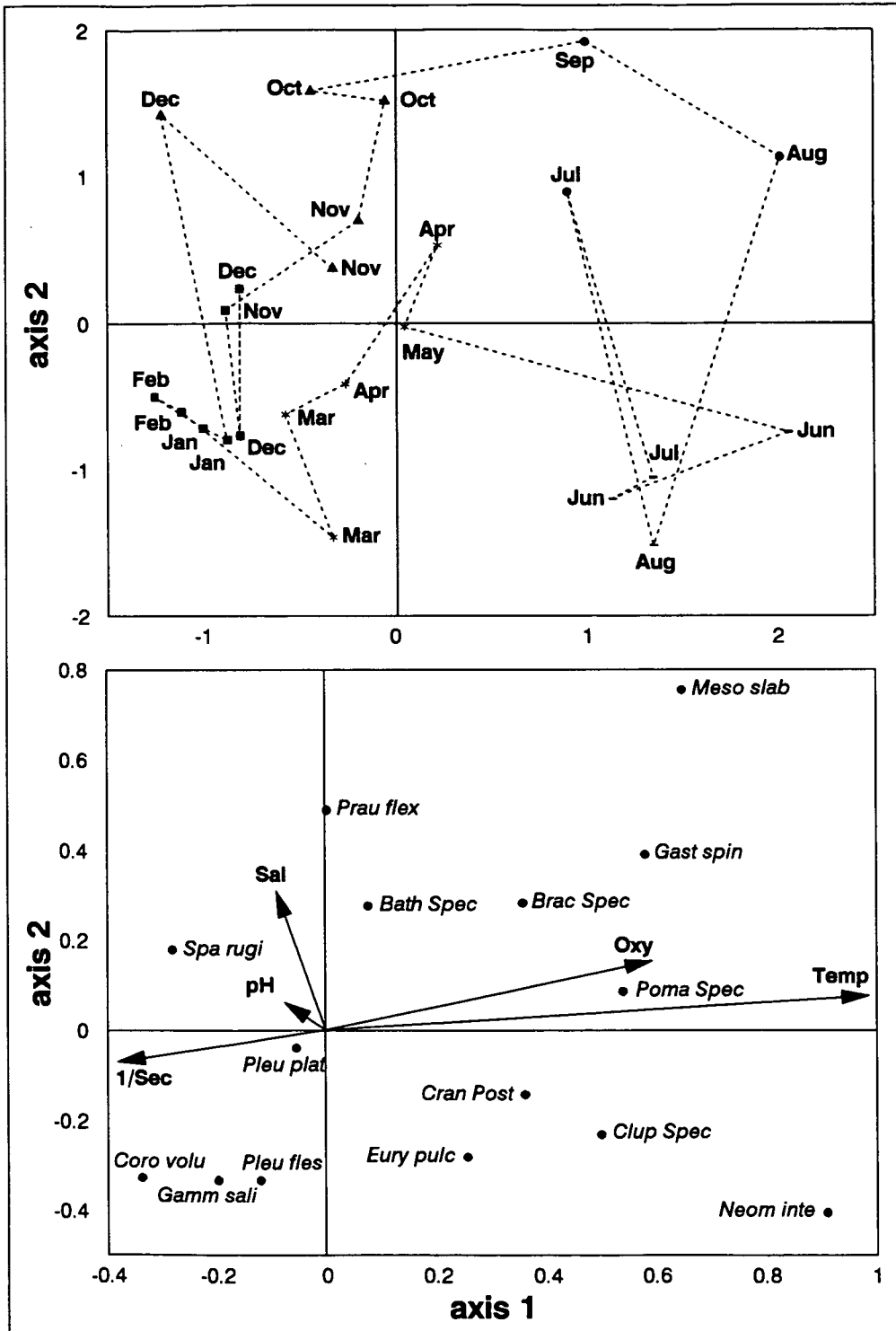


Figure 4.23. Output of the PCA with the density data of the fortnightly time series in the brackish part. The dotted line in the plot of the sample scores (top) indicates the sampling sequence.

In the plot of the species scores the late summer - early autumn species *Mesopodopsis slabberi*, *Gastrosaccus spinifer*, crab larvae and postlarval *Crangon crangon* are located near the temperature-oxygen end of the environmental biplot, while the amphipods *Corophium volutator* and *Gammarus salinus* appear on the opposite end of the gradient, indicating their occurrence in colder seasons. The position of the postlarvae of both flatfish species (*Pleurnectes flesus* and *P. platessa*) corresponds to the position taken by the spring samples. The position corresponding to the autumn samples is taken by less dominant species (*Praunus flexuosus*, *Lekanosphaera rugicauda* and *Bathyporeia* species) in the species plot. *Neomysis integer*, and *Pomatoschistus* species and *Clupeidae* species, appear near the bottom right corner of the plot. This is the position occupied by samples from summer when both *Neomysis* and the fish species occurred with maximal abundances.

There is general agreement among the results from the classification and ordination techniques. Based on these results from the three methods (also these with the biomass data, not presented) five more or less arbitrary seasonal groupings of samples can be established. Table 4.4 shows the categorization of the samples into the five groups, their characteristic species, the Hill numbers for each seasonal group and the mean and standard error of the measured environmental variables. *Neomysis integer* is the dominant species throughout the year; *Mesopodopsis slabberi* becomes visible in early summer (Figure 4.24).

Table 4.4. Characterization of the seasonal communities in the brackish part of the estuary.

Season	Winter	Spring	Early summer	Late summer	Autumn
<b>Samples</b>	08 & 21-01-91 05 & 21-02-91 18-11-91 03 & 16-12-91	03 & 18-03-91 12 & 24-04-91 08-05-91	11 & 26-06-91 09-07-91 12-08-91	24-07-91 20-08-91 19-09-91	27-11-90 12-12-90 07 & 17-10-91 05-11-91
<b>Charact. species</b>	<i>Coro volu</i> <i>Gamm sali</i>	<i>Pleu plat</i> <i>Prau flex</i> <i>Eury pulc</i>	<i>Poma spec</i> <i>Clup spec</i>	<i>Gast spin</i> <i>Crab larv</i>	<i>Prau flex</i> <i>Bath spec</i> <i>Spha rugi</i>
<b>N<sub>0</sub></b>	7	11	12	9	8
<b>N<sub>1</sub></b>	1.07	1.21	1.09	1.48	1.95
<b>N<sub>2</sub></b>	1.02	1.07	1.03	1.27	1.71
<b>N<sub>∞</sub></b>	1.01	1.04	1.01	1.14	1.4
<b>oxygen(%)</b>	73.6 ± 6.4	76.4 ± 9.4	86.8 ± 0.7	99.0 ± 7.8	83.0 ± 6.8
<b>pH</b>	7.7 ± 0.7	7.7 ± 0.1	7.7 ± 0.1	7.6 ± 0.2	7.7 ± 0.0
<b>sal.(psu)</b>	13.8 ± 1.2	15.0 ± 1.3	13.7 ± 1.0	18.3 ± 0.4	28.8 ± 10.6
<b>Sec.<sup>-1</sup>(cm<sup>-1</sup>)</b>	0.02 ± 0.003	0.018 ± 0.003	0.006 ± 0.002	0.013 ± 0.004	0.02 ± 0.002
<b>temp.(°C)</b>	5.0 ± 1.0	9.0 ± 1.2	16.7 ± 0.9	20.5 ± 0.5	11.4 ± 1.9

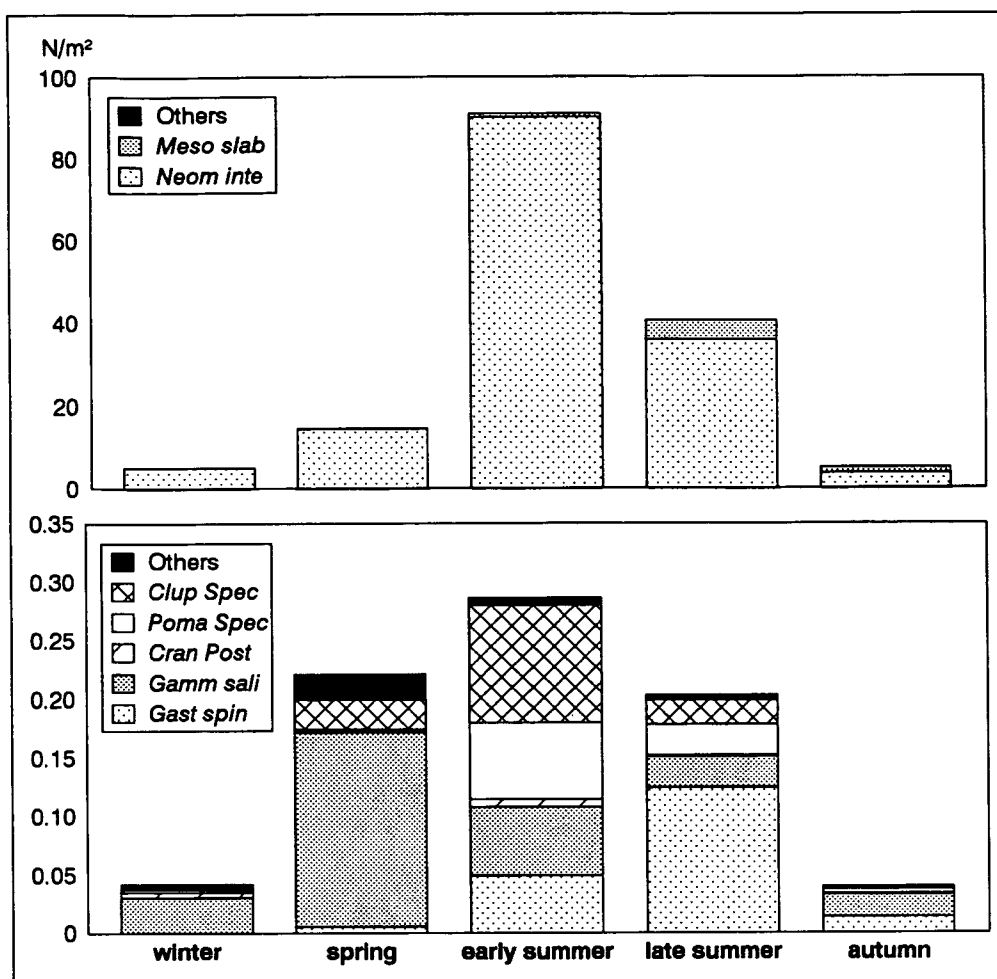


Figure 4.24. Density and species composition of the seasonal communities in the brackish part. Stacked bars with (top) and without (bottom) the two dominant species.

The values of the environmental variables from the different communities were tested for significant differences using a Kruskal-Wallis analysis of variance. Out of the five variables measured only temperature showed a significant difference ( $p < 0.05$ ). The relatively high number of rare species in spring and early summer is not reflected in higher values in the Hill's numbers of higher order. Instead, the autumn group, despite its poorer species composition, has greater values. This is due to the decline in the abundance of *Neomysis integer* and a simultaneous increase of the densities of *Mesopodopsis slabberi*. As the calculation of the values is based on the proportionate abundance of the species (except for  $N_0$ ) the influence of the rare species remained very low even during spring and summer. Because the two mysid species strongly dominated the community, the Hill's numbers did not reflect the dynamics of the rare species. The winter months showed lower species diversity than the other months. During these months the community was mainly composed of permanent hyperbenthic fauna. In spring and summer some temporary hyperbenthic species, mainly postlarvae and larvae of fish and decapods joined the community. These months coincided with the breeding season of these organisms. The number of *Mesopodopsis slabberi* in the study area started increasing in June and July and reached a maximum value in

September. This was the time when the species migrates from the maritime to the brackish zone of the estuary (Mees *et al.* 1993a). Mauchline (1980) also noted that marine populations of *M. slabberi* may undergo an offshore/inshore migration. Collins & Williams (1982), from their study on mysids from the Bristol Channel, classified the species as a more estuarine in summer (April and August) and rather marine in winter (January). Such apparent seasonal inshore/offshore movements may have underlying salinity-related reproductive significance (Greenwood *et al.* 1989).

#### 4.6. Discussion

Ideally, a random stratified sampling scheme should be designed for ecological surveys. For our sampling programme there were, however, some logistical limitations in selecting the sampling stations. First, stretches of 1000 m length had to be found which were free from obstacles. Further, we had to take into account the draught of the ship, the distance that can be taken in one day, etc. The result was a more or less systematic sampling at fixed locations in the subtidal channels of the estuary. These limitations did not necessarily lead to an important loss of information, since an estuary can be considered as a fairly linear system dominated by unidirectional linear environmental gradients. However, the impossibility to sample shallow areas and the fact that the sampling methodology is not flexible enough to adapt to the tidal situation, can lead to an incomplete picture and to gaps in the knowledge of the hyperbenthic compartment of the ecosystem. This is certainly the case for species like *Praunus flexuosus* (Tattersall & Tattersall 1951) and *Palaemonetes varians* (Smaldon 1979) which are known to prefer shallow intertidal parts of estuaries. No samples were taken upstream from Bath because of problematic bottom conditions and busy shipping. This did not lead to much loss of information because hyperbenthic life ceases shortly after the Dutch-Belgian border (Mees *et al.* 1993a). In the salinity range sampled, the species composition of the mysid fauna of the Westerschelde resembled that of other European estuaries (e.g. Moffat & Jones 1993, Sorbe 1981b).

Results from the various types of multivariate analysis performed on the data differed only in small details, confirming the stability of the patterns described. The transition in space from one community to the next should of course be considered to be a gradual process (cf. figure 4.11). The change is not abrupt. The combination of several multivariate techniques merely gives us objective criteria to decide where one community stops and another one begins. The division of an estuary into several zones on the base of changes in community structure can never be absolute, because the constituting species do not respond in exactly the same way to environmental variables, each having e.g. a specific salinity range and optimum. A division like the one presented here can however be useful for modelling purposes. The number of estuarine species is quite low and their distribution seems to be highly predictable in relation to the reigning physical and chemical conditions.

In the hyperbenthic community of a shallow coastal area seasonal patterns dominated over the spatial structure, i.e. a sample resembled any other sample of the

same month more than it did the samples from the same location of any other month (Hamerlynck & Mees 1991). This was mainly due to the sequential appearance, high abundance and disappearance of temporary hyperbenthic species (e.g. larval Decapoda and Polychaeta, larval and postlarval fish). An important difference with the hyperbenthic community structure in the estuarine habitat is that here the spatial patterns are more important than the temporal ones (e.g. Figure 4.6). This is the case especially in the brackish part of the system, where the similarities between the clusters grouping the samples of the different months are high (e.g. Figures 4.17 and 4.22). The main reason for this is the fact that the spatial gradient in species composition in the estuary is quite steep: the communities of the marine and brackish parts are composed mostly of different species. Furthermore, most temporary and migratory hyperbenthic species are not able to penetrate far into the estuary (Figure 4.3) resulting in a species-poor community upstream, which is always dominated by the same few species. Despite the fact that strong temporal variations in abundances are observed for the main brackish water populations community structure as a whole thus remains stable throughout the year.

## CHAPTER 5.

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

#### Abstract

The hyperbenthic mysids and euphausiids of the subtidal shallow coastal waters (the Voordelta) and the Westerschelde estuary in the Delta area (south-west 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.

#### 5.1. Introduction

In comparison to other groups of marine invertebrates, e.g. zooplankton (De Pauw 1975, Soetaert & Van Rijswijk 1993), 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 south-west 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 hyperbenthic), 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 (1886) 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.* 1993b) 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.

## 5.2. 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 (Figure 5.1) 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 (Figure 5.1) 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 discussed 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 Figure

5.1) 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 (2760 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 5.1.

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<sup>2</sup> and it samples the hyperbenthos from 20 to 100 cm above the bottom. The sampler was towed for approximately 1000 m (radar readings from fixed points) at an average ship speed of 4.5 knots relative to the bottom. The total area sampled was 1000 m<sup>2</sup>. Trawling was always done with the tide. Thus, the maximal amount of water filtered in one trawl was 800 m<sup>3</sup>.

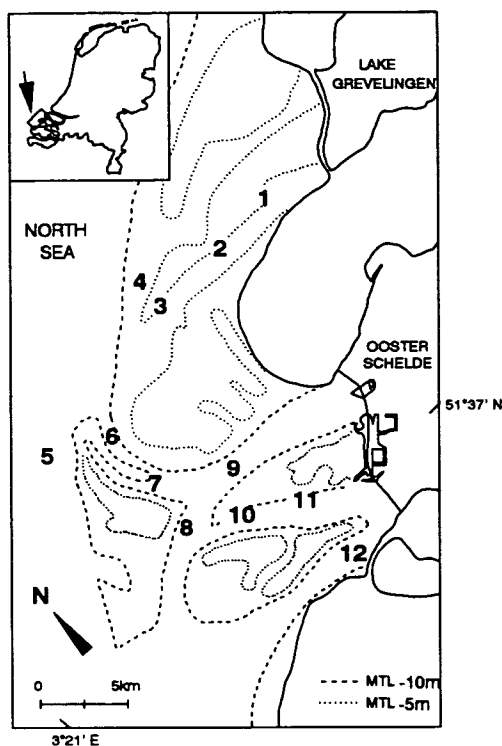
The salt-marsh samples were taken passively with a fyke net modified after McIvor & Odum (1986). The net is 5 m long with a 1\*1 mm mesh and has a weir at the end. The mouth area of the net is 1\*1 m. It was mounted on an iron frame and two heavy weights were attached at the lower end in order to keep 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.

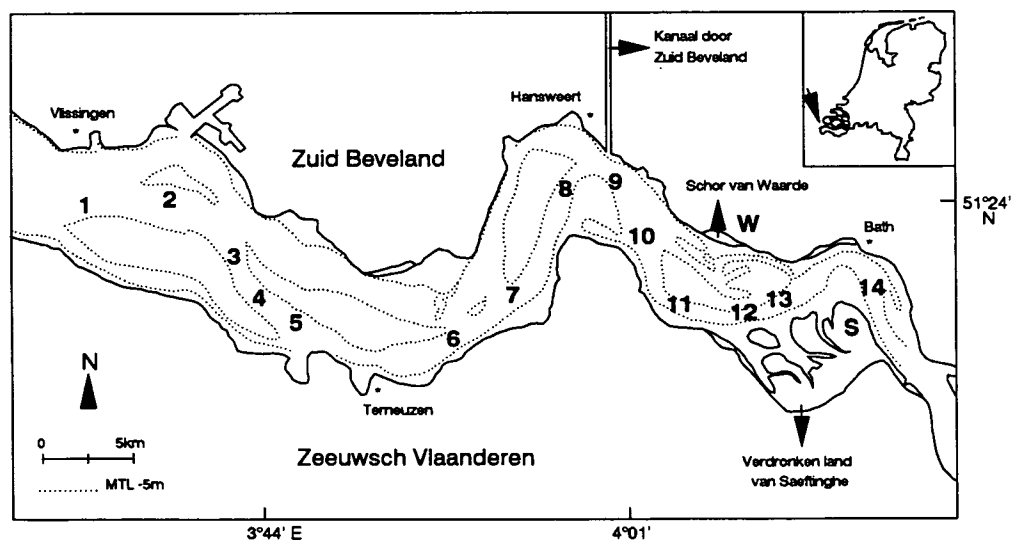
The samples were preserved in a buffered formaldehyde solution, 7% final concentration. In the laboratory all mysids and euphausiids were sorted out, identified to species level and counted. Special attention was paid to the presence of juvenile animals in the samples. These are defined as animals with 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 per 1000 m<sup>2</sup>), averaged over the whole study period. Densities of the intertidal samples are numbers per 1000 m<sup>3</sup> of water filtered through the net.





**Figure 5.1.** Maps of the Voordelta and the Westerschelde estuary with the subtidal (1-12 and 1-14, respectively) and intertidal (W and S) sampling localities.



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.* 1993b). 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.* (1993b).

**Table 5.1.** 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

### 5.3. Results

In total only eight species of mysid and one euphausiid were recorded (Table 5.2). Total mysid densities often exceeded 5000 and 50000 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.

#### 5.3.1. Spatial distribution

The geographical distribution and abundance of all mysid species and the single euphausiid are presented separately for the Voordelta and the Westerschelde (Figures 5.2 & 5.3).

**Table 5.2.** 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.

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

### Voordelta

In the Voordelta (Figure 5.2), average densities were never higher than 1000 individuals. *Schistomysis spiritus* was the most abundant species in the area, followed by *Schistomysis kervillei*, *Mesopodopsis slabberi* and *Gastrosaccus spinifer*. The four species had overlapping geographical distributions. Densities were 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 were characterized by intermediate densities and are dominated by *S. spiritus*. *S. kervillei* was never found in the most seaward Banjaard stations.

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

### Westerschelde

In the Westerschelde, the two most abundant mysid species were *Neomysis integer* and *Mesopodopsis slabberi*. Both species reached average densities of more than 1000 individuals in the upstream stations (Figure 5.3). *Neomysis integer* is confined to the brackish zone of the estuary. The species was recorded in salinities ranging from 25 to 8 psu and was 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

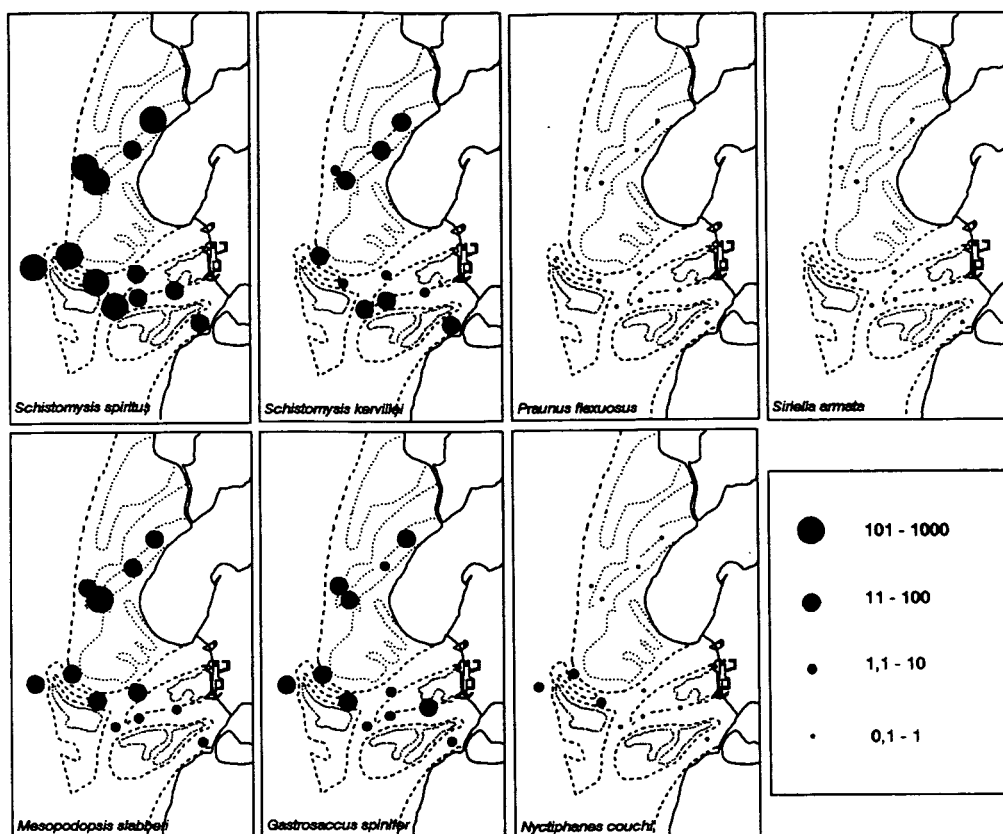


Figure 5.2. Distribution of all species caught in the Voordelta. Densities are yearly averages of the numbers of individuals caught per trawl (N per 1000 m<sup>2</sup>).

exemplified by the results of the campaign from April 1991 (Figure 5.4). 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* was common throughout the estuary. As for *N.integer*, densities were 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 was generally more abundant than in the Voordelta.

Both *Schistomysis* species also penetrated into the estuary but they were never found at the innermost stations. In the marine part of the estuary densities of *S. kervillei* were 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* was far less abundant in the Westerschelde than in the Voordelta and seems to be the more marine species of the two. It entered the saltmarshes only occasionally.

*Gastrosaccus spinifer* occurred in higher densities in the downstream stations of the Westerschelde than in the Voordelta. Densities decreased 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

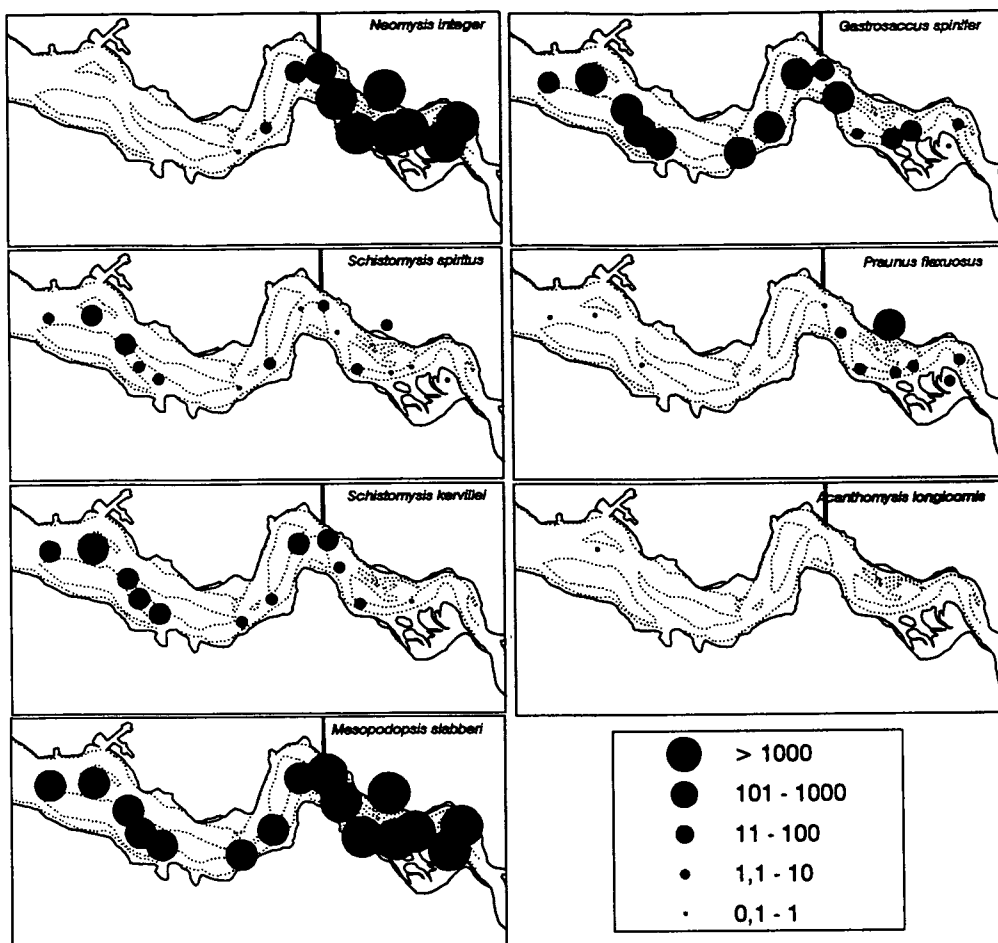


Figure 5.3. Distribution of all species caught in the Westerschelde and its salt marshes. Densities are yearly averages of the numbers of individuals caught per trawl (1000 m<sup>2</sup>) for the subtidal samples and N per 1000 m<sup>3</sup> for the salt marsh samples.

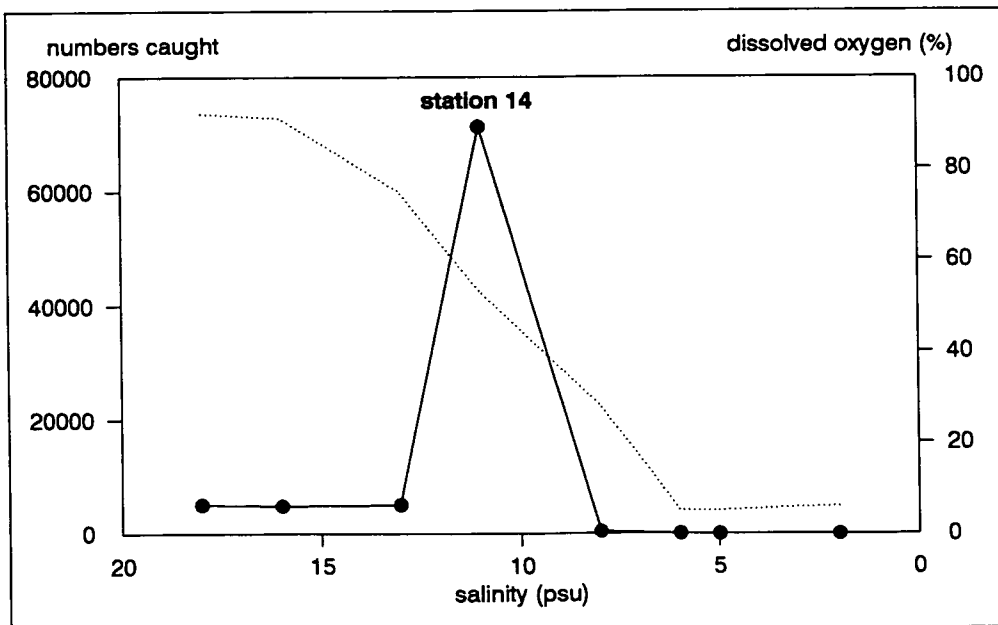


Figure 5.4. Density of *Neomysis integer* along the salinity gradient from station 11 upto Antwerp in April 1991. Dissolved oxygen concentration is presented by the dotted line.

for the salt marsh areas (especially the salt marsh of Waarde). In the main channel of the estuary, it was only abundant in the 6 most brackish stations.

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

### 5.3.2. Temporal patterns

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

#### Voordelta

In the Voordelta (Figure 5.5), *Schistomysis spiritus*, *Mesopodopsis slabberi* and *Schistomysis kervillei* had two clear peaks in abundance: one in autumn and one in spring. These maxima coincided with periods of higher reproductive activity, with a lot of juveniles recruiting into the catch. In the two former species there was a strong peak in abundance during spring (March-April) and a smaller one in autumn (September-November). For *S. kervillei* the autumn peak was observed somewhat later (November) and it was more pronounced than the spring peak. For all three species lowest numbers were found in winter (January-February) and in summer (June-August).

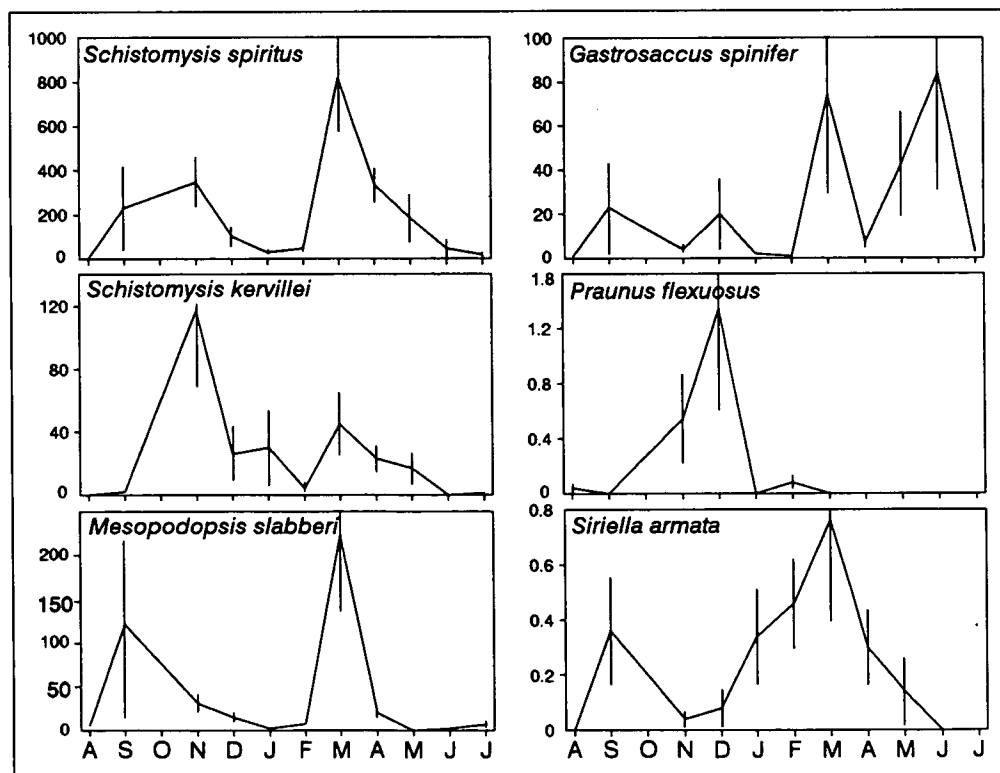


Figure 5.5. Seasonal variation of the number of individuals for the mysid species in the Voordelta (with standard errors). Densities are numbers caught per trawl averaged over all stations per sampling date (N per 1000 m<sup>2</sup>).

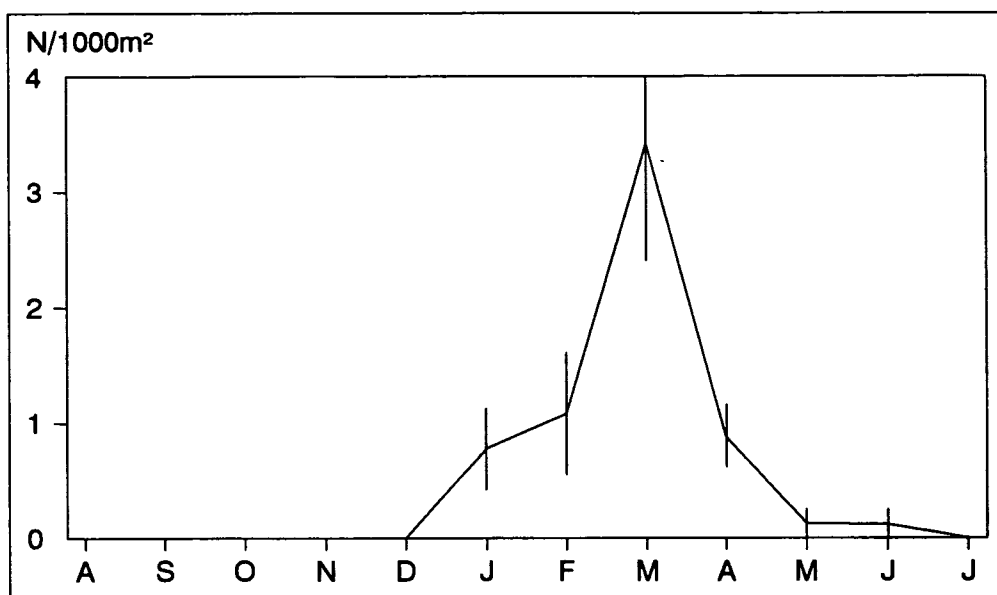


Figure 5.6. Seasonal variation in the number of individuals of *Nyctiphanes couchi* in the Voordelta, with standard errors.

*Gastrosaccus spinifer* showed 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 showed a bimodal abundance pattern. A small autumn maximum was observed in September. Densities were low in November and December, but increased 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* (Figure 5.5) and *Nyctiphanes couchi* (Figure 5.6) are the only species which had maximal abundances during the winter months: *P. flexuosus* was only caught in late autumn and winter, *N. couchi* was present in the area from January to early June with peak densities from February to April.

### Westerschelde

*Schistomysis spiritus* (Figure 5.7) seems to be a typically marine species. It was absent from the estuary from late spring (June) until autumn (September). It entered the marine part of the estuary in low numbers in late autumn and winter. Here, the species reached 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* penetrated into the brackish part of the estuary and even entered the salt marshes. In the salt marsh of Waarde a small reproductive peak was recorded: all animals caught in April were juveniles.

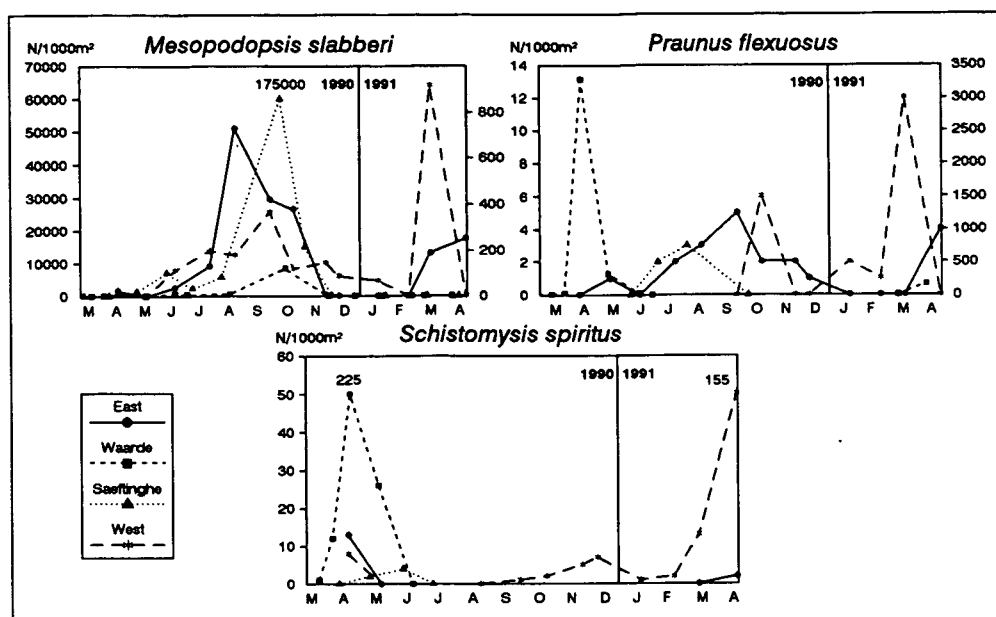


Figure 5.7. Seasonal variation of the number of individuals of the mysid species in the Westerschelde. Densities are numbers caught per trawl averaged over all stations per sampling date ( $N$  per 1000  $m^2$  for the subtidal samples and  $N$  per 1000  $m^3$  for the salt marshes). Note that *Mesopodopsis slabberi* West and *Praunus flexuosus* Waarde follow the right Y-axis.

*Schistomysis kervillei* and *Gastrosaccus spinifer* (not figured) were present in the western part of the estuary throughout the year. Average numbers were generally lower than 100 individuals per 1000  $m^2$ . *S. kervillei* was most abundant from November through April, with peak abundances of 650 individuals per 1000  $m^2$  in January and early March. The *G. spinifer* population showed reproductive peaks in the marine part of the estuary in March and April (maximum of 100 individuals per 1000  $m^2$  in April) and again from July through September (maximum of 450 individuals per 1000  $m^2$  in August). At the time of peak abundance a small part of both populations also migrated to the brackish stations (densities never higher than 10 and 50 individuals per 1000  $m^2$  for *S. kervillei* and *G. spinifer*, respectively).

*Praunus flexuosus* (Figure 5.7) was 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 was restricted to certain periods of the year: in spring (April to June), an important reproductive peak was 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 seemed 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* (Figure 5.7) was virtually absent from the estuary in winter: from November through February it was only present in low numbers in the



downstream stations. It entered the marine part of the estuary in important numbers in early spring where it remained abundant throughout summer and autumn. The abundance of *M. slabberi* resembled 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 moved into the eastern part of the estuary. Migration into the eastern part was completed by August when very high densities were observed in the subtidal stations of the main channel. *M. slabberi* made extensive use of the saltmarshes only in autumn: maximal density recorded was 176 individuals per m<sup>3</sup> (mainly juveniles) in October in Saeftinghe. By November the species had left the brackish waters.

*Neomysis integer* (Figure 5.8) was confined to the brackish part of the estuary. Numbers were high throughout the year. Three maxima in abundance were 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 are published elsewhere (Mees *et al.* 1994). The species also utilised the salt marshes (mainly the salt marsh of Waarde in spring and the salt marsh of Saeftinghe in summer and autumn), where the density maxima were always observed 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.

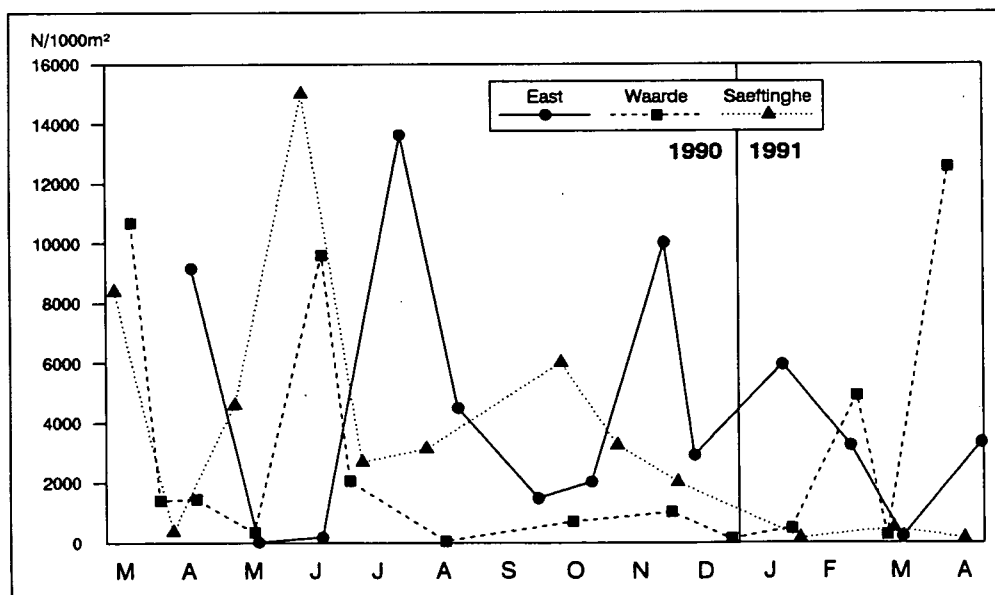


Figure 5.8. Seasonal variation of the number of individuals of *Neomysis integer* in the different subareas of the Westerschelde.

#### 5.4. 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.

#### 5.4.1. Euphausiids

*Nyctiphanes couchi* is the only euphausiid species encountered in the study area. It is also the only euphausiid which is 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. 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. *N. couchi* is absent from the southern North Sea from May to August (Tesch 1911, Glover 1952).

#### 5.4.2. Mysids

##### *General remarks*

As can be seen from Figure 5.5, the variabilities in the densities reported for the mysid species in the Voordelta were 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). It 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. 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 (1911) reports it to be common in the Delta area in salinities ranging from 2.6 to 30 psu. It occurs from Norway to western Africa. It is also found in the Mediterranean and the Black Sea. Records from southern Africa are thought to concern a different species (Wooldridge pers. comm.).

The only *Gastrosaccus* species found during the study period was *G. spinifer*. It is common in the whole southern North Sea (Tesch 1911). 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. It 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). This stratum 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 psu isohaline, there is

a rapid extinction of all hyperbenthic life (Figure 5.4). 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 psu 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 records of *Praunus flexuosus* in the Voordelta and the marine part of the Westerschelde are probably a 'washout' phenomena linked to the winter state of the river Schelde. The species' retention mechanisms seems 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 caused by a combination of natural mortality and migration to deeper waters.

The summer minima in the Voordelta are more difficult to explain, but they 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 hyperbenthos 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 and which is virtually exclusively dependent on mysids for most of the year (Hamerlynck *et al.* 1990), switches to feeding on 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 that if they occur in offshore environments the seasonal maxima of occurrence tend to be in 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.

## CHAPTER 6.

### Comparative study of the hyperbenthos of three European estuaries.

#### Abstract

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

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

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

## 6.1. Introduction

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

For this study three major European estuaries were sampled quasi-synoptically along the longitudinal salinity gradient ranging from marine waters near the mouth to nearly fresh water upstream: the Eems (north Netherlands), the Westerschelde (southwest Netherlands) and the Gironde (southwest France). All samples were taken with a single gear and processed by the same research team. Sampling was concentrated within a short time interval (15 days) to minimise seasonal effects on hyperbenthic community structure. Indeed, seasonal patterns can dominate hyperbenthic community structure due to the presence of temporary hyperbenthic species (Hamerlynck & Mees 1991). The hyperbenthos of the Westerschelde estuary, which is characterized by a high degree of industrialisation and urbanisation making it

one of the most polluted rivers of Europe, has been intensively studied in recent years (Mees & Hamerlynck 1992, Cattrijsse *et al.* 1993, Mees *et al.* 1993a, Mees *et al.* 1993b). The hyperbenthos of the Gironde has been studied by Sorbe (1981b). No information on the hyperbenthos of the Eems estuary was available to date.

## 6.2. Materials and methods

### 6.2.1. Study area (Figure 6.1)

The Eems-Dollard estuary is situated in the northeast of the Netherlands on the border with Germany. The system is about 33 km long from Eemshaven to Pogum. The surface area of the estuary (excluding the part extending to the Wadden Sea islands downstream Eemshaven) is approximately 255 km<sup>2</sup>, including a fresh water tidal area in the Eems of about 37 km<sup>2</sup> (de Jonge 1988). The tidal influence is artificially stopped upstream of Leer (Germany). In the marine part two major gullies are separated by sandbanks; further upstream (past the mouth of the Dollard) only one channel remains. The major source of freshwater inflow is the river Eems (catchment area of about 12650 km<sup>2</sup>), which has a variable discharge ranging from 25 to 390 m<sup>3</sup> s<sup>-1</sup>. The Westerwoldsche Aa has no well defined watershed and discharges roughly 10 % (5.1 to 31 m<sup>3</sup> s<sup>-1</sup>) of the discharge of the river Eems in the southeast corner of the Dollard. Variable (and still smaller) amounts of fresh water enter the estuary from some channels near Delfzijl. The tidal excursion is approximately 15 km. There is no stratification and water turnover is 18 to 36 days. Suspended matter concentrations in the maximum turbidity zone rarely exceed 0.4 g l<sup>-1</sup> (Baretta & Ruardij 1988). Dissolved oxygen concentration in the estuary proper rarely drop below 70 % of the saturation value, even in the maximum turbidity zone.

The Westerschelde estuary is the lower part of the river Schelde. The estuarine zone of the tidal system extends from the North Sea (Vlissingen) to Antwerpen, 80 km inland. The estuary is rain fed, with a catchment area of some 20000 km<sup>2</sup>. Its surface is approximately 300 km<sup>2</sup>. The seaward part is a well mixed region characterized by a complex system of channels. There are two major gullies in the marine part and only one main channel in the weakly stratified region more upstream. Tidal influence extends to Gent (160 km from mouth) were it is artificially stopped. The residence time in the brackish part is rather high: about 60 days or 120 tidal cycles in summer (Soetaert & Herman in press). Consequently fresh water (average inflow 100 m<sup>3</sup> s<sup>-1</sup>; range 30 to 500 m<sup>3</sup> s<sup>-1</sup>) dilution is gradual and downstream transport is relatively slow. Shifts in salinity zone distribution occur in accordance with seasonal variations in the freshwater inflow. The physical, chemical and biological characteristics are discussed in Heip (1989), Herman *et al.* (1991) and Van Eck *et al.* (1991). The estuary is subject to a large anthropogenic stress, e.g. dredging (Belmans 1988), and carries high pollution loads, both in anorganic and organic contaminants (Duursma *et al.* 1988). Dissolved oxygen concentration decreases sharply upstream the Dutch-Belgian border and the riverine part of the system is anoxic throughout most of the year (Herman *et al.* 1991).



Suspended matter concentrations are never higher than  $0.05 \text{ g l}^{-1}$  suggesting there is no real maximum turbidity zone in this estuary.

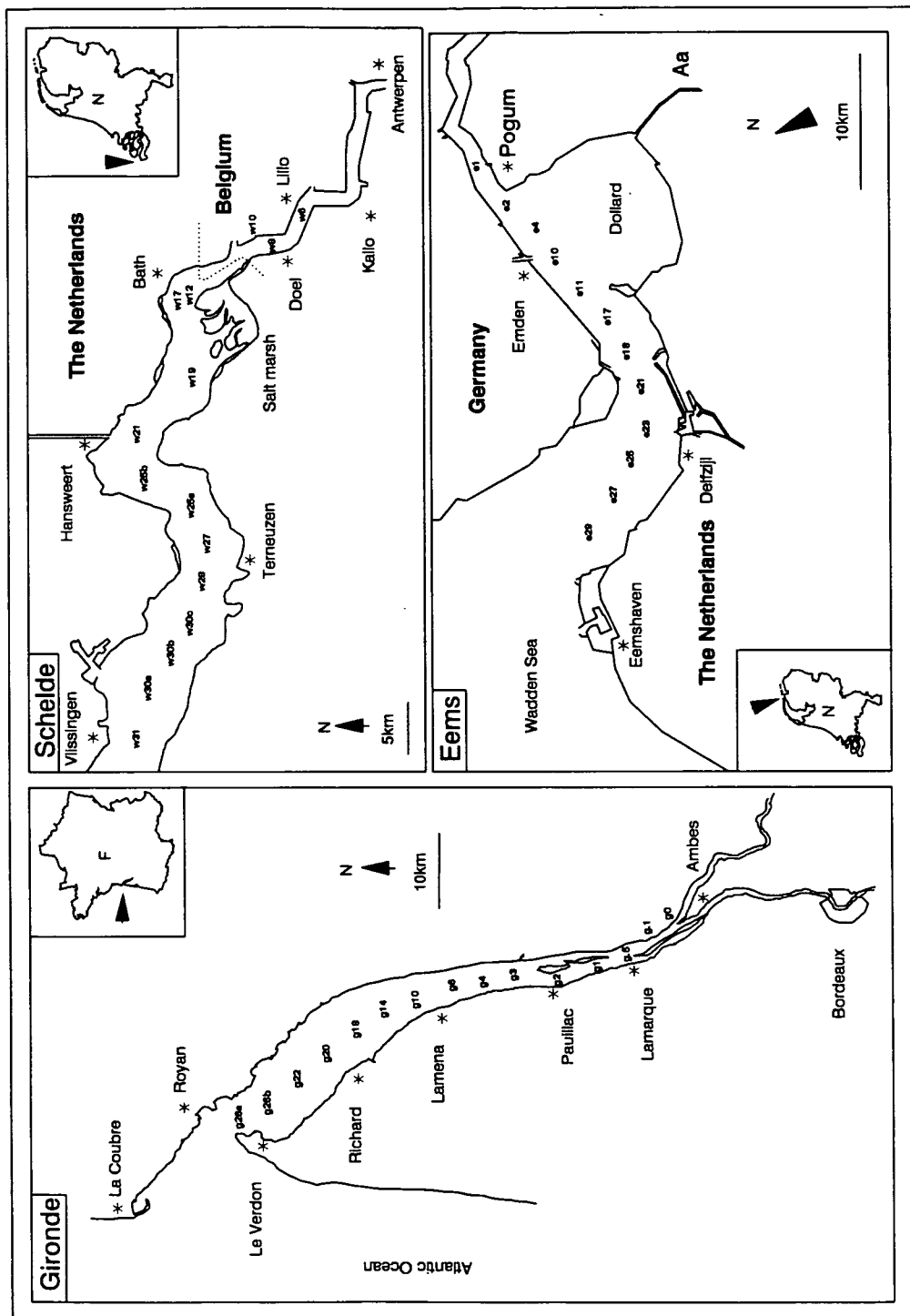


Figure 6.1. Study area and sampling sites: the names of the samples are composed of a letter indicating the estuary and a number representing the salinity zone in which it was taken.

The Gironde estuary on the atlantic coast of France is the estuarine part of the rivers Garonne and Dordogne, which together have a catchment area of about 71000 km<sup>2</sup> (Jouanneau & Latouche 1981). The estuary is 70 km long from the inlet near Le Verdon to Bec d'Ambès where both rivers meet. The upstream part is characterized by the presence of numerous islands and sandbanks separating a network of channels. The downstream part consists of two main channels separated by shallower areas and sandbanks. The surface area at flood tide is 625 km<sup>2</sup>. In summer tidal influence extends 160 km upstream Pointe de Grave. The water is well mixed: especially in summer there is virtually no stratification. Seasonal variations in salinity are related to freshwater discharge. River flow of the Garonne and Dordogne varies between 200 m<sup>3</sup> s<sup>-1</sup> in summer to 1500 m<sup>3</sup> s<sup>-1</sup> in winter (800-1000 m<sup>3</sup> s<sup>-1</sup> on average). The residence time of a water particle is on average 20 tidal cycles in winter and 140 tidal cycles in summer. Dissolved oxygen concentrations in summer are never lower than 70 % of the saturation value. One of the main features of the Gironde is the high turbidity of the water: suspended matter concentrations in the maximum turbidity zone generally exceed 1 g l<sup>-1</sup> and values of 5 g l<sup>-1</sup> and higher are regularly recorded (mainly silt and clay particles from freshwater origin).

### 6.2.2. Sampling

The location of the sampling stations in Eems, Westerschelde and Gironde is shown in Figure 6.1. In the Eems 12 evenly spaced (3 km) stations were sampled in salinity zones ranging from 28.6 psu near Eemshaven to 1.0 psu near Pogum. In the Westerschelde 15 samples were taken from a salinity of 31.0 psu near Vlissingen down to a salinity of 6.3 psu near Lillo. The stations were selected according to the sampling grid used in Mees *et al.* (1993b). Since no animals were caught in the last station, no further attempts were made to sample more upstream. In the Gironde 15 stations (evenly spaced at 5 km) were selected covering salinity zones ranging from 26.1 psu near Le Verdon to truly freshwater (0.0 psu) near Bec d'Ambès.

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

The samples were collected with a sledge (Hamerlynck & Mees 1991) which consists of a heavy metal frame with two mounted monofilament nets. The nets are 4 m long and 1 m wide with a mesh size of 2\*2 mm in the first 3 m and 1\*1 mm in the last 1 m. The sledge glides over the bottom and samples the water column from 20 to 100 cm above the sediment. On each occasion it was trawled over a distance of 1000 m (radar readings from fixed points) at an average ship speed of 4.5 knots relative to the bottom. All samples were taken during daytime when hyperbenthic animals are known to be concentrated near the bottom. The contents of both nets were pooled for the present study. Thus the recorded densities are numbers of individuals (N) per 1000 m<sup>2</sup>; the maximal volume of water filtered through the nets is 800 m<sup>3</sup>. Where possible

the 10 m isobath was followed. Actual sampling depths varied between 10.5 m and 7.5 m in the Eems, between 6.1 m and 15.8 m in the Westerschelde, and between 6 m and 15 m in the Gironde. The samples were rinsed over a 1 mm sieve and immediately preserved in a buffered formaldehyde solution, 7% final concentration.

At the end of each trawl Secchi disc depth was recorded and salinity, dissolved oxygen concentration, pH, conductivity and temperature were measured near the bottom.

### 6.2.3. Laboratory procedures

After sorting, all animals present in the samples were identified, if possible to species level, and counted. Different developmental stages of some crustacean groups were considered as different functional species (zoeae, postlarvae and adults for caridean shrimp; zoeae, megalopae and adults for anomuran and brachyuran crabs). For gobies of the genus *Pomatoschistus* only *P. microps* could always be identified to species level. Small individuals (less than 25 mm standard length) of *P. minutus* and *P. lozanoi* were pooled as *Pomatoschistus* species. Other identification problems concerned postlarval clupeoids (probably a mixture of *Clupea harengus* and *Sprattus sprattus*) and amphipods of the genus *Bathyporeia* (pooled as Clupeidae species and *Bathyporeia* species, respectively). Possibly the counts of zoeae and megalopae of *Liocarcinus holsatus* also include larvae of other crabs of the same genus (e.g. *L. pusillus* in the Gironde). Several rare larval stages of brachyuran crabs could not be identified at all. Single records of a caprellid (*Caprella*) and an isopod (*Cymothoa*) in the Gironde could only be identified to genus level, though the former probably is *C. aequilibra* (Sorbe 1978). For animals with more or less continuous growth, a maximum of 60 individuals per species and per sample (30 from each net) were measured to the nearest 0.1 mm using a binocular microscope and drawing mirror. Except for crabs (carapace width) standard lengths (from the tip of the rostrum to the last abdominal segment) were used. Biomass was then derived from the length-frequency distributions and length-ashfree dry weight (AFDW) regressions obtained from Westerschelde and Voordelta populations (see appendix 1, Mees *et al.* 1994). Densities of species growing in discrete stages were converted to biomass with average AFDW values.

### 6.2.4. Statistical analysis

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

$N_0$  = the number of species,

$N_1 = e^H$  with  $H = -\sum p_i \ln(p_i)$  ( $p_i$  is the relative abundance of the  $i$  dominant species),

$N_2 = \sum p_i^2$ , and

$N_\infty = p_1^{-1}$  (the reciprocal of the relative abundance of the most abundant species).

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

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

Density and biomass data were subjected to fourth root transformation prior to analysis. Three multivariate techniques, each yielding specific information, were applied to the data (Field *et al.* 1982). The sampling sites were classified into clusters according to species composition using the classification technique TWINSpan (Hill 1979). This is a hybrid (the first step involves a reciprocal averaging ordination) divisive clustering technique which also gives indicator species and preferential species for each division. Pseudospecies cutlevels (7 in each case) were chosen to equalise the number of observations within each cutlevel, except for the lowest cutlevel which contained all the zero observations and the two highest cutlevel which contained approximately half as many observations as the other levels (in this way some extra weight was given to the most abundant species). The minimum group size for division was set to 5 and the analysis was stopped at the fifth division. An agglomerative clustering method (group average sorting or GAS of Bray-Curtis dissimilarities) was also applied to the data. The output (dendrograms) of these analyses were compared with the TWINSpan results and the degree of similarity between clusters, and (within clusters) between samples could be assessed. The relationship between species, stations and environmental variables was investigated by means of a Canonical Correspondence Analysis or CCA (Jongman *et al.* 1987, Ter Braak 1988), a technique performing regression and ordination of the data concurrently. Preliminary analyses showed that pH did not correlate well with any axis and that conductivity was strongly and positively correlated with salinity. Thus both parameters were not used in further analyses. Secchi disc depth was transformed reciprocally and thus becomes a light extinction measure, correlated with turbidity of the water. Whereas the first two techniques emphasised discontinuities in the data, the CCA emphasised continuities along the estuarine gradients. Plotting of the TWINSpan/GAS clusters on the CCA ordination planes aided in evaluating the divisions imposed.

### 6.3. Results

Accidentally caught individuals one or several orders of magnitude larger than an "average" hyperbenthic animal can seriously distort analyses with biomass data. Adult individuals of epibenthic shrimp and crab species and adult demersal or pelagic fish species, although often very abundant in the samples (Table 6.1), were excluded from the community analyses. Though these animals apparently make use of the hyperbenthal as a habitat they are inefficiently sampled with the sledge and are normally studied using beam trawls. Only small adults of *Liocarcinus holsatus* (carapax length < 10 mm) and postlarval gobies (S.L. < 25 mm), clupeoids (not yet displaying adult pigmentation nor habitus, S.L. < 25 mm), pipefish (S.L. < 60 mm)

and glass eels were considered to be representative residents of the hyperbenthal. Other species eliminated from the data matrices are: Porifera species (epibenthic freshwater sponges in Eems and Gironde), Hydrozoa species (epibenthic, in every sample of Eems and Westerschelde, rarely in the Gironde), *Aurelia aurita* (planktonic, high densities in Eems and Westerschelde), Cyanea species (planktonic, high densities in Gironde), Anthozoa species (epibenthic, rare), *Pleurobrachia pileus* (planktonic, high densities in Eems, Westerschelde and Gironde), Nematoda species (benthic, mainly among peat in the brackish Eems samples), *Lanice conchilega* aulophore larvae (planktonic, 9 and 3 individuals in Westerschelde and Gironde, respectively), *Nereis* species (benthic, rarely caught in all three estuaries), and a variety of rarely and accidentally caught species: *Macoma balthica*, *Cerastoderma edule*, *Mytilus edulis*, *Hydrobia ulvae*, *Sepiola* species, Bryozoa species, *Asterias rubens* and Cirripedia species. Also excluded were regularly encountered groups originating from land, air or fresh water: Aranea species, Diptera species, Lepidoptera species and Coleoptera species (adults and larvae).

**Table 6.1.** Common species excluded from the community analyses on the basis of size, with total number caught in each estuary.

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

Table 6.2. List of species and abbreviations used in the community analyses. Middle column: first letter of the estuary(ies) in which they occurred.

<i>Sagitta elegans</i>	E W G	Sagi eleg
<i>Gastrosaccus spinifer</i>	E W G	Gast spin
<i>Schistomysis spiritus</i>	E W G	Schi spir
<i>Schistomysis kervillei</i>	E W G	Schi kerv
<i>Mesopodopsis slabberi</i>	E W G	Meso slab
<i>Neomysis integer</i>	E W G	Neom inte
<i>Praunus flexuosus</i>	E W	Prau flex
<i>Eurydice pulchra</i>	W G	Eury pulc
<i>Idotea linearis</i>	E W	Idot line
<i>Synidotea laevidorsalis</i>	W G	Syni Spec
<i>Sphaeroma rugicauda</i>	W	Spha rugi
<i>Sphaeroma serratum</i>	G	Spha serr
<i>Cymothoa species</i>	G	Cymo Spec
<i>Daphnia magna</i>	E W	Daph magn
<i>Caprella linearis</i>	W	Capr line
<i>Caprella species</i>	G	Capr Spec
<i>Pariambus typicus</i>	W	Pari typi
<i>Gammarus crinicornis</i>	E W G	Gamm crin
<i>Gammarus salinus</i>	E W G	Gamm sali
<i>Gammarus zaddachi</i>	E G	Gamm zadd
<i>Gammarus duebeni</i>	E	Gamm dueb
<i>Gammarus locusta</i>	E	Gamm locu
<i>Melita palmata</i>	G	Meli palm
<i>Atylus swammerdami</i>	E W G	Atyl swam
<i>Pleusymtes glaber</i>	W G	Pleu glab
<i>Corophium volutator</i>	E W G	Coro volu
<i>Corophium acherusicum</i>	W	Coro ache
<i>Corophium lacustre</i>	W	Coro lacu
<i>Bathyporeia species</i>	E W	Bath Spec
<i>Jassa falcata</i>	W	Jass falc
<i>Hyperia galba</i>	W	Hype galb
<i>Crangon crangon postlarva</i>	E W G	Cran Post
<i>Crangon crangon zoea</i>	E W G	Cran zoea
<i>Palaemonetes varians postlarva</i>	E W	Pala varP
<i>Palaemonetes varians zoea</i>	E	Pala varZ
<i>Palaemon longirostris postlarva</i>	E G	Pala lonP
<i>Palaemon longirostris zoea</i>	E G	Pala lonZ
<i>Pagurus species megalopa</i>	G	Pagu Mega
<i>Porcellana species zoea</i>	W G	Porc Zoea
<i>Carcinus maenas megalopa</i>	E W G	Carc Mega
<i>Carcinus maenas zoea</i>	E W	Carc Zoea
<i>Liocarcinus holsatus small adults</i>	E W G	Lioc hols
<i>Liocarcinus holsatus megalopa</i>	W	Lioc Mega
<i>Liocarcinus holsatus zoea</i>	E W G	Lioc Zoe1
<i>Liocarcinus species zoea type 2</i>	G	Lioc Zoe2
<i>Liocarcinus species zoea type 3</i>	G	Lioc Zoe3
<i>Liocarcinus species zoea type 4</i>	E	Lioc Zoe4
<i>Macropodia species megalopa</i>	W G	Macr Mega
<i>Eriocheir sinensis megalopa</i>	E G	Erio Mega
Unidentified zoea Westerschelde	W	Wty1 Zoea
Unidentified zoea Gironde type 1	G	Gty1 Zoea
Unidentified zoea Gironde type 2	G	Gty2 Zoea
<i>Nymphon rubrum</i>	W	Nymp rubr
<i>Anguilla anguilla glass eels</i>	G	Angu angu
<i>Clupeidae species postlarva</i>	E W G	Clup Spec
<i>Syngnathus rostellatus</i>	E W G	Syng rost
<i>Pomatoschistus microps postlarva</i>	E W G	Poma micr
<i>Pomatoschistus species postlarva</i>	E W	Poma Spec

From a total of 101 recorded species, 58 were thus retained after data reduction (Table 6.2). Eighteen were recorded from all three estuaries and most of these were very abundant. Four species were only encountered in the Eems, eleven only in the Gironde and ten only in the Westerschelde. Most of these species were rare and have previously also been recorded from the other estuaries in other studies. Exceptions are *Synidotea laevidorsalis* in the Gironde and *Gammarus locusta* in the Eems, which were quite common constituents of the hyperbenthos and have never been recorded from one of the other estuaries. Four species occurred both in Gironde and Eems but were absent from the Westerschelde. Four were only absent from the Eems and seven from the Gironde.

### 6.3.1. Environmental gradients

The environmental variables measured at each station are presented in Table 6.3. The most pronounced gradient in the three estuaries was salinity (see materials and methods).

**Table 6.3. Environmental variables measured at the end of each trawl.**

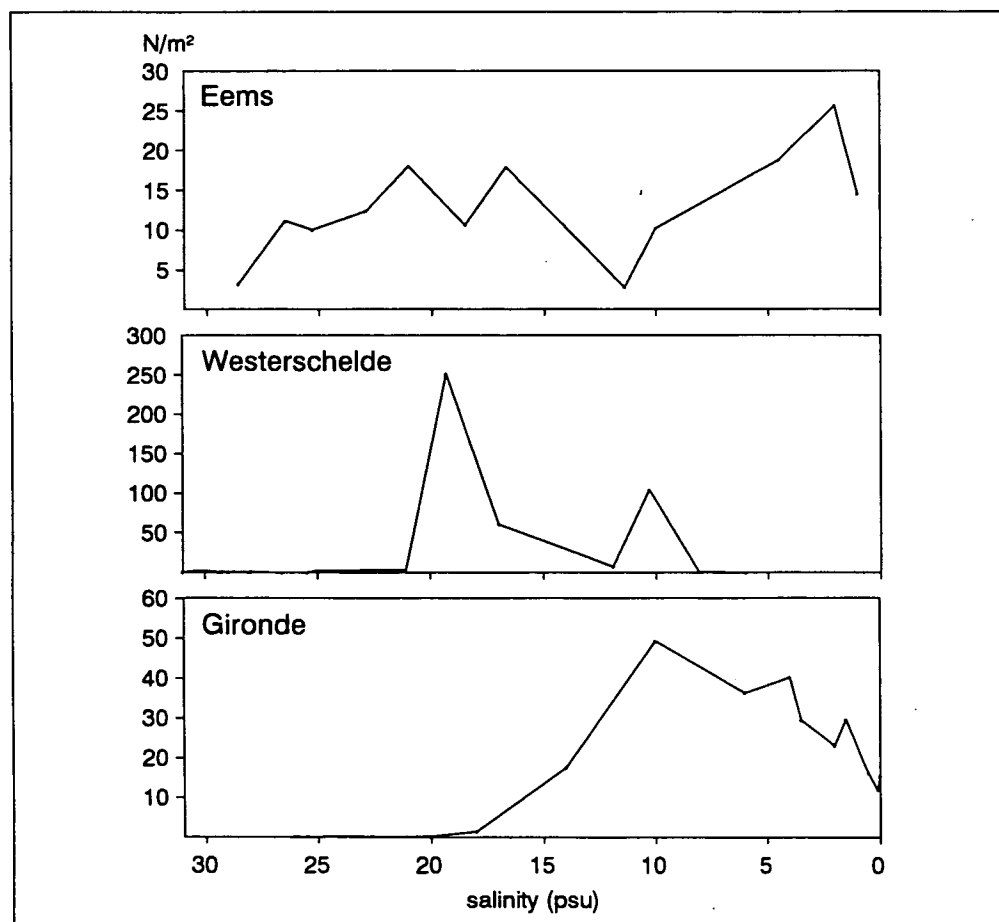
Eems															
	e29	e27	e25	e23	e21	e18	e17	e11	e10	e4	e2	e1			
Sal. (psu)	28.6	26.5	25.3	22.9	21.0	18.5	16.7	11.4	10.0	4.5	2.0	0.9			
Sec. (cm)	120	50	45	20	20	15	20	10	10	5	5	5			
Tem. (°C)	19.8	19.6	19.4	19.2	19.6	19.7	19.8	20.1	20.1	20.3	20.4	20.5			
Westerschelde															
	w31	w30a	w30b	w30c	w28	w27	w25a	w25b	w21	w19	w17	w12	w10	w8	w6
Sal. (psu)	31.0	30.3	29.5	29.5	28.0	26.6	25.4	25.0	21.1	19.3	17.0	11.9	10.3	8.1	6.3
Sec. (cm)	125	120	125	125	100	100	140	140	80	90	100	40	50	60	-
Tem. (°C)	20.0	20.0	19.8	20.1	20.2	20.2	20.1	20.1	20.3	20.5	20.6	22.3	22.8	22.7	-
Gironde															
	g26a	g26b	g24	g20	g18	g14	g10	g6	g4	g3	g2	g1	g.5	g.1	g0
Sal. (psu)	26.1	26.0	24.0	20.0	18.0	14.0	10.0	6.0	4.0	3.4	2.0	1.4	0.5	0.1	0.0
Sec. (cm)	440	440	260	90	40	40	30	10	5	5	3	5	3	5	10
Tem. (°C)	21.0	21.2	21.6	22.4	22.6	22.8	23.5	24.0	24.2	24.1	24.4	24.4	24.4	24.4	24.4

The three estuaries displayed the characteristic summer temperature gradient with lowest values near the mouth gradually increasing upstream. Geographical differences between the estuaries are obvious, with temperature increasing with decreasing latitude from Eems over Westerschelde to Gironde. The temperature difference between the mouth of the estuary and the 8 psu isohaline in the Westerschelde (maximal difference of 3.0 °C) is high in comparison to that in Gironde and Eems (difference of 3.4 and 1.3 °C over a longer gradient). This may reflect the one week gap in the sampling scheme. An alternative explanation may be thermal pollution by the nuclear power plant of Doel. Secchi disc visibility decreased with

increasing distance from the mouth. The marine reaches of the Gironde were characterized by very high light penetration. Upstream of the maximum turbidity zone in the Gironde there was a slight increase in light penetration. The maximum turbidity zone was not reached in Westerschelde (supposedly situated around Antwerpen) and in the Eems its upstream border was not reached. Dissolved oxygen concentrations of the water ranged from oversaturation in the marine part to about 80% of the saturation value in the 17 to 12 salinity zone of the Westerschelde. Then a rapid decline in the oxygen content was observed in the three innermost stations: 49% in w10, over 38% in w8 down to 22% in w6. In the other two estuaries dissolved oxygen concentration never dropped below 70% saturation.

### 6.3.2. General trends in density, biomass and diversity

In Westerschelde and Gironde hyperbenthic density (Figure 6.2) and biomass (not figured) were lowest in the most seaward stations. They increased upstream, decreasing again towards the most riverine stations.



**Figure 6.2.** Total hyperbenthic density along the salinity gradients in the 3 estuaries.

In comparison to the other estuaries, the Eems was characterized by a rather uniform density over a wide salinity range: density was low in the outermost station (<



5 individuals or 5 mg AFDW per m<sup>2</sup>) but, in contrast to the other estuaries, was already high at the 27 psu isohaline. Densities remained at about the same level (between 10 and 20 individuals per m<sup>2</sup>, 10 to 47 mg AFDW per m<sup>2</sup>) upto 17 psu. A drop in density (again less than 5 individuals per m<sup>2</sup>) was observed at the 11 psu isohaline (mouth of the Dollard). Density and biomass then increased to a maximum of 26 individuals or 66 mg AFDW per m<sup>2</sup> at the 2 psu isohaline and decreased again in the last station. Some of the density peaks reflect the appearance and disappearance of dominant species (Figure 6.3): the peak around 21 psu was mainly due to high densities of *Schistomysis kervillei*, the peak around 2 psu reflects the abundance maximum of *N. integer*, which was of overriding importance throughout most of the estuary.

In the Westerschelde two peaks were evident (Figure 6.2): a first in the 19 psu salinity zone, a second around 10 psu. These were an order of magnitude higher than maximal densities observed in the other estuaries (250 and 105 individuals per m<sup>2</sup>; 555 and 208 mg AFDW per m<sup>2</sup>). The two peaks probably do not represent two distinct zones of higher density but are an artefact of the discontinuous sampling scheme. Both peaks correspond to the maximum abundance of *N. integer* and, depending on the geographical location of the oxygen depletion zone, the population maximum can be found in different salinity zones on different sampling days. In the Westerschelde *N. integer* are always concentrated near the limit of viable oxygen concentrations (about 40% of the saturation value) regardless of salinity (Mees *et al.* 1993a, Mees *et al.* 1993b). Density became very low at 8 psu and in the 6 psu sample no hyperbenthic animals were found. In Gironde and Eems the abundance maximum of *N. integer* was correlated with the tidally shifting salinity zone around 2-4 psu. In the marine stations (w31 to w21) of the Westerschelde density and biomass were below 3.5 individuals per m<sup>2</sup> and 3.5 mg AFDW per m<sup>2</sup> respectively.

Densities in the Gironde were only substantial upstream of the 20 psu isohaline. Very few animals were caught in the most seaward Gironde samples g26a, g26b, g24 and g20 (7, 7, 69 and 29 individuals, respectively). Three peaks were evident: the first peak (50 individuals or 63 mg AFDW per m<sup>2</sup> at 10 psu) coincided with the maximal abundance of *Mesopodopsis slabberi* and submaximal abundances of *N. integer* (Figure 6.3), the second peak (41 individuals or 113 mg AFDW per m<sup>2</sup> at 4 psu) corresponded with maximal densities of *Pomatoschistus microps* and high numbers *N. integer*, and the third peak (32 individuals per m<sup>2</sup> or 99 mg AFDW at 1 psu) corresponded to the abundance maximum of *N. integer* (Figure 6.3). Since *M. slabberi* is a very slender species, the first peak became lower than the other two in terms of biomass.

All diversity measures (Figure 6.4) were highest in the marine part of the estuaries. In the high salinity zone many species were present, with no species clearly dominating the fauna. This is also evident from Figure 6.3 where the "others" section accounted for a higher percentage of the community than in the brackish part. Diversity decreased towards the brackish reaches where fewer species occurred in higher numbers (cf.  $N_{\infty}$  approaches a value of 1 in the stations with maximal abundance of *N. integer*). In Eems and Gironde diversity increased slightly towards the fresh water.

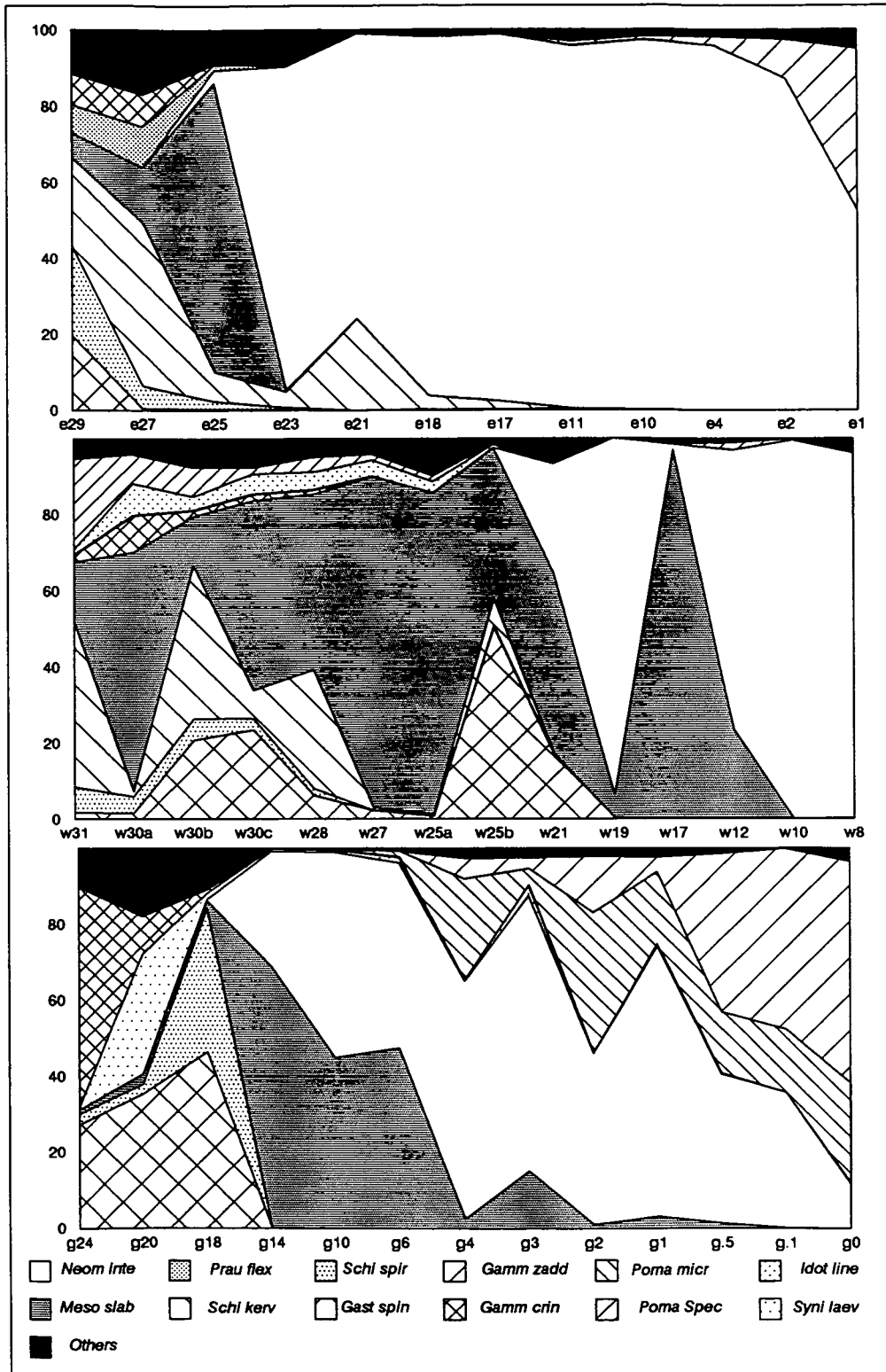


Figure 6.3. Relative species composition of the hyperbenthic community along the salinity gradient in Eems (top), Westerschelde (middle) and Gironde (bottom).

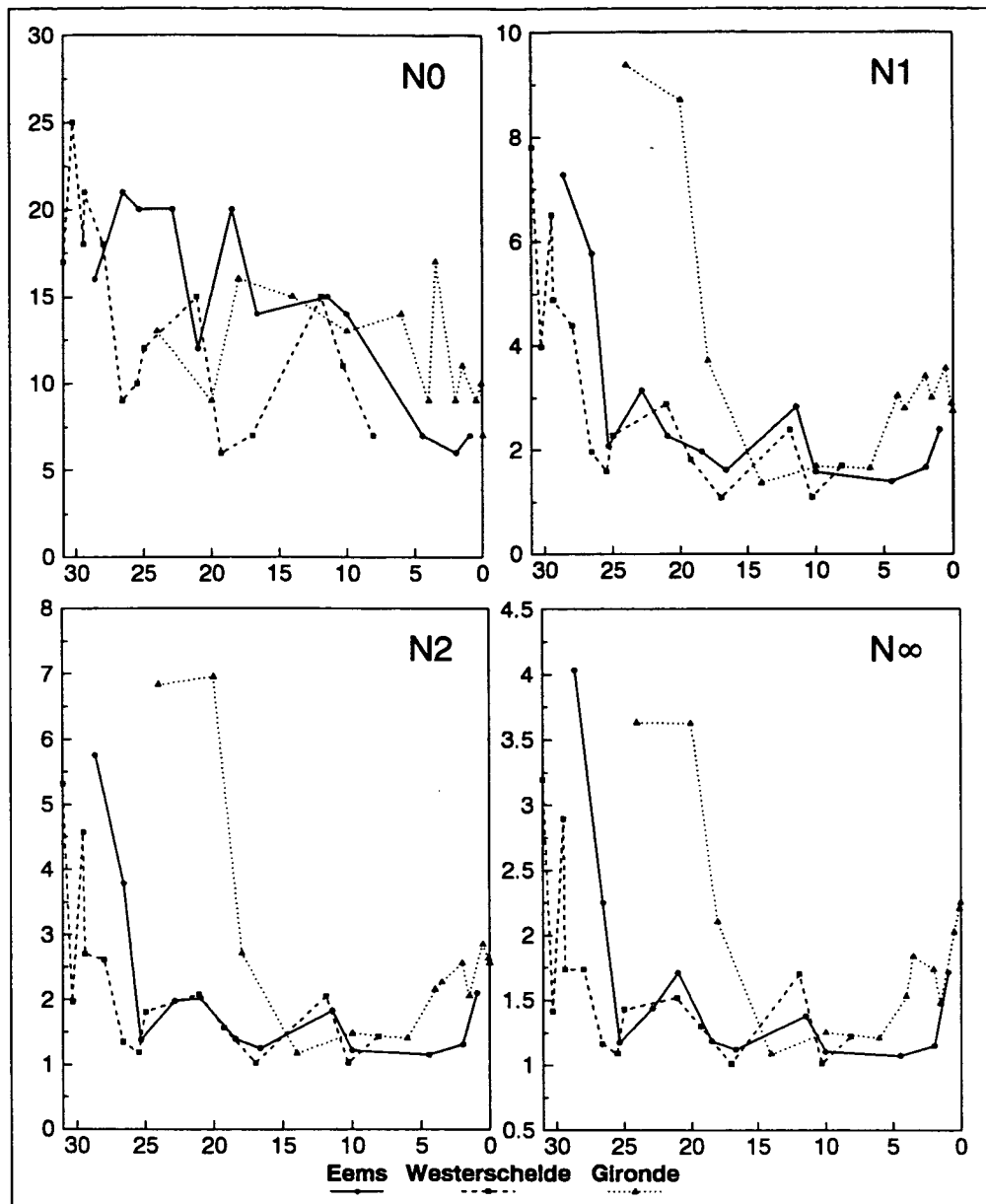
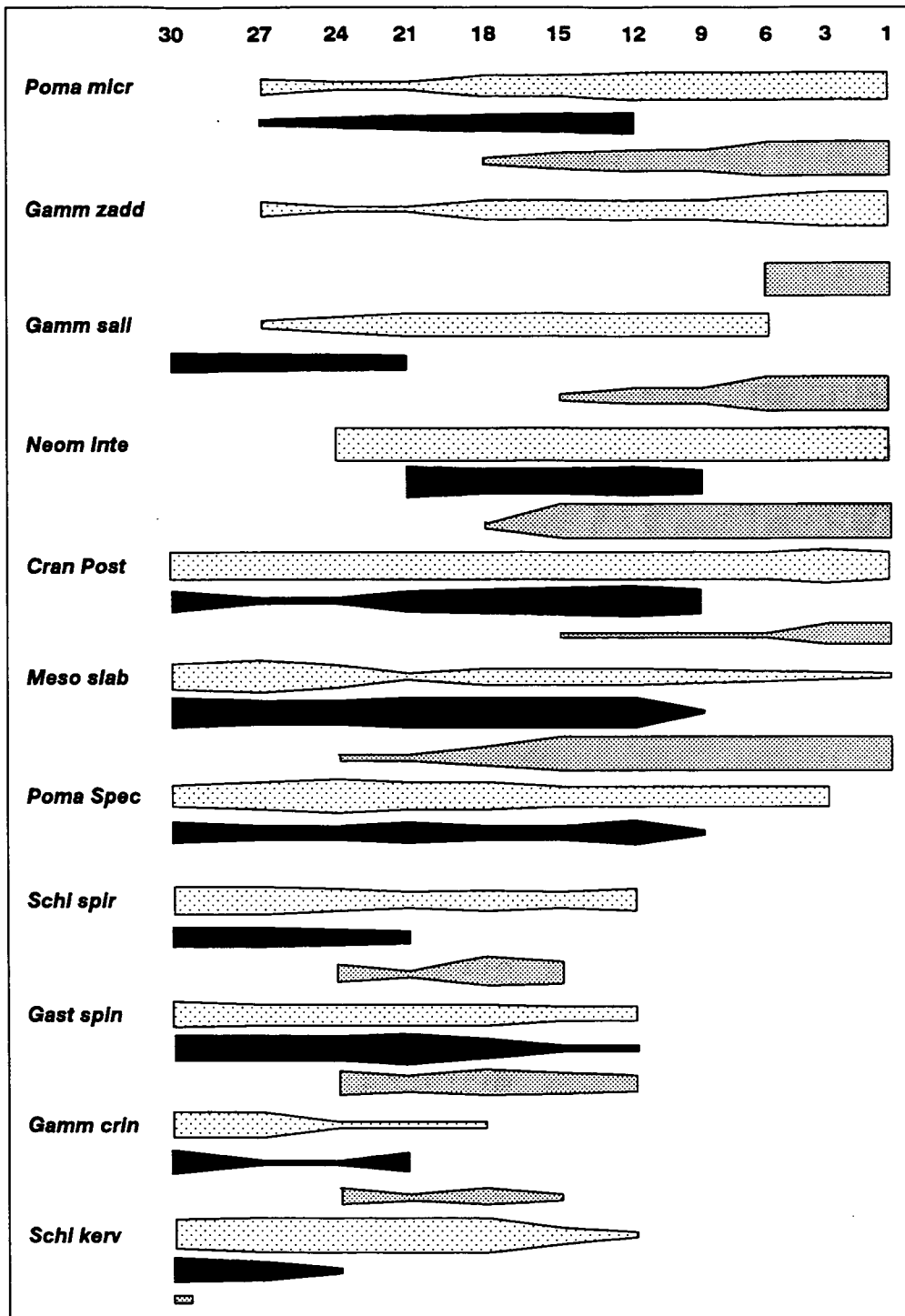


Figure 6.4. Diversity numbers of Hill plotted against salinity.

### 6.3.3. The species

The hyperbenthos was dominated by crustaceans, especially mysids. Other important groups were gammaridean amphipods, isopods (in the Gironde), caridean shrimp, larval stages of brachyuran crabs and postlarval fish. Chaetognaths, daphnids, pycnogonids, caprellid and hyperiid amphipods and larval stages of anomurans were observed occasionally. The distribution of the 11 most abundant species along the salinity gradients of the three estuaries is depicted in Figure 6.5. Below, the distribution patterns are described based on the density data only (biomass data of the individual species are available on request).



**Figure 6.5.** Density distribution of the 11 most abundant hyperbenthic species along the salinity gradient of Eems (top), Westerschelde (middle, in black), and Gironde (bottom). Species are ordered following the two-way table of the TWINSPAN. Width of the bar gives indication of abundance reached in the salinity zone (top line).

### *Mysidacea*

*Gastrosaccus spinifer* occurred in the three estuaries from the marine reaches upto the 10 psu isohaline. Maximal densities amounted to 3400 individuals per 1000 m<sup>2</sup> in the Westerschelde (at 19 psu) and 650 individuals in Gironde and Eems (at 18 and 29 psu, respectively). One adult female from the Eems was infested with the parasitic isopod *Prodajus ostendensis*. *Mesopodopsis slabberi* was abundant throughout the Westerschelde from the mouth upto the 10 psu isohaline where it reached a maximal density of 60 individuals per m<sup>2</sup>. The same pattern was observed in the Gironde (maximal densities of 39 individuals per m<sup>2</sup> at 10 psu), but here the species was still present in the most upstream stations (upto 0 psu). In the Eems *M. slabberi* also occurred over the entire transect but it only reached important densities in a narrower salinity band (between 29 and 10 psu) where a maximum of 20 individuals per m<sup>2</sup> was recorded. In the Gironde only one individual of *Schistomysis kervillei* was caught in the most downstream station. This essentially coastal species was present in the Westerschelde from the mouth upto 21 psu (maximum of 250 individual per 1000 m<sup>2</sup> at 30 psu). In the Eems the species moved much further up the estuary (upto 11 psu) and reached maximal abundance at lower salinities (7000 individuals per 1000 m<sup>2</sup> at the 21 psu isohaline). *S. spiritus* is also a typical coastal species which was present in the three estuaries from the mouth to 10, 21 and 14 psu in Eems (maximal abundance of 800 individuals per 1000 m<sup>2</sup>), Westerschelde (55 individuals) and Gironde (800 individuals), respectively. The estuarine endemic *Neomysis integer* was, especially in biomass terms, the most important constituent of the hyperbenthos in the three estuaries. It was restricted to the brackish reaches, never being caught in fully marine conditions. The zone of maximal abundance in Eems and Gironde was situated in the vicinity of the maximum turbidity zone (as exemplified for the Gironde in Figure 6.6). In the Eems the species was present from 25 psu upto 1 psu (maximum of 18 individuals per m<sup>2</sup> at 4 psu). In the Gironde it colonised the salinity zone from 18 to 0 psu (maximum of 26 individuals per m<sup>2</sup> at 4 psu). In the Westerschelde *N. integer* was only present from 21 to 8 psu with much higher maximal densities of 193 and 103 individuals per m<sup>2</sup> at the 19 and 10 psu isohaline depending on the sampling date. *Praunus flexuosus* was only recorded in Eems and Westerschelde. In the former estuary densities amounted to 284 individuals per 1000 m<sup>2</sup> at 27 psu (range 29 to 18 psu), in the Westerschelde density was always low (maximum of 33 individuals per 1000 m<sup>2</sup>) in the salinity zone from 25 to 17 psu.

### *Amphipoda Gammaridea*

*Gammarus crinicornis* is a marine species which does not penetrate the estuarine system very far. It occurred in all three estuaries with maximal densities of 646 (at 27 psu), 103 (30 psu) and 8 (24 psu) individuals per 1000 m<sup>2</sup> in Eems, Westerschelde and Gironde respectively. *Gammarus salinus* is a brackish water species which in all three estuaries replaced *G. crinicornis* upstream. The species occurred in

the Eems between 25 and 4 psu (maximum of 52 individuals per 1000 m<sup>2</sup> at 10 psu) and in the Gironde between 14 and 0.5 psu (maximum of 1858 individuals per 1000 m<sup>2</sup> at 4 psu). During this survey, *G. salinus* was only caught in low numbers (a total of 28 individuals) in the Westerschelde although the species is known to be the most common amphipod in the hyperbenthos of the brackish part of this estuary (Cattrijsse *et al.* 1993, Mees *et al.* 1993b). *Gammarus zaddachi* replaced *G. salinus* in the oligohaline reaches of Eems and Gironde. Densities were very high in the salinity zone between 2 and 0 psu: 5 and 7 individuals per m<sup>2</sup>, respectively. The species was not caught in the Westerschelde. Two other *Gammarus* species were only caught in the Eems: *G. duebeni* (only a few individuals in the 27 psu station) and *G. locusta* (between 29 and 23 psu, maximum of 160 individuals per 1000 m<sup>2</sup> at 27 psu). *Atylus swammerdami* is a marine species. It was present in the Westerschelde from 31 to 27 psu. In Gironde and Eems the species penetrated further into the estuary: upto 20 and 11 psu, respectively. Densities were never higher than 30 individuals per 1000 m<sup>2</sup>. Individuals of *Melita palmata* (in marine waters) and *Pleusymtes glaber* (in brackish stations) were only caught in the Gironde, although they are also known to occur in the Westerschelde (Mees *et al.* 1993b). *Corophium volutator* is a euryhaline, tube building species regularly encountered in the hyperbenthos of the three estuaries (density was never higher than 50 individuals per 1000 m<sup>2</sup>). In the Westerschelde three other species were found in very low numbers: *C. acherusicum*, *C. lacustre*, and *Jassa falcata*. *Bathyporeia* species were only found in Eems and Westerschelde.

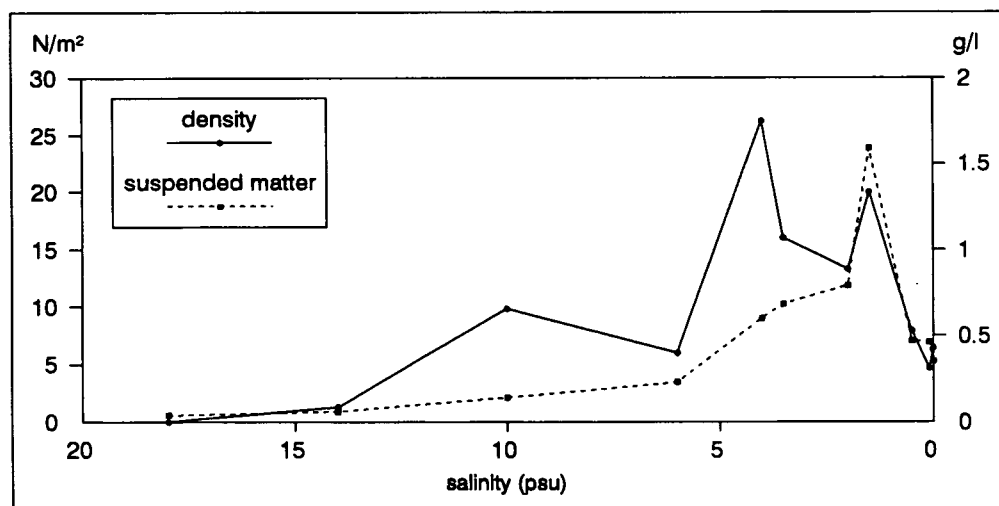


Figure 6.6. Density of *Neomysis integer* (right axis) and concentration of suspended matter (left axis) plotted against the salinity gradient of the Gironde.

### Isopoda

*Eurydice pulchra* was not observed in the Eems. The species was found in the Westerschelde in salinities ranging from 25 to 10 psu with a maximal density of 26 individuals per 1000 m<sup>2</sup> at 12 psu. In the Gironde only 4 individuals were caught

between 18 and 3 psu. *Idotea linearis* was only found in the marine parts of the Westerschelde (maximum of 85 individuals per 1000 m<sup>2</sup> at 30 psu) and Eems (maximum of 13 individuals per 1000 m<sup>2</sup> at 29 psu). *Synidotea laevidorsalis* was only present in the Gironde and was the only isopod which reached considerable densities and biomass (maximum of 288 individuals per 1000 m<sup>2</sup> at 3 psu) in the brackish part of this estuary. Details on its distribution have been published elsewhere (Mees & Fockedey 1993). *Sphaeroma rugicauda*, *Sphaeroma serratum*, and *Cymothoa* species were rare constituents of the hyperbenthos.

#### *Caridean shrimp*

*Crangon crangon* was very abundant in the three estuaries. The developmental stages were found to be segregated along the salinity gradient: zoeae did not penetrate the estuary as far as postlarvae. Maximal densities for the zoeae were 12 individuals per 1000 m<sup>2</sup> at 29 psu in the Eems, 24 individuals per 1000 m<sup>2</sup> at 30 psu in the Westerschelde, and 7 individuals per 1000 m<sup>2</sup> at 26 psu in the Gironde. Postlarvae (and adults) were present over the entire sampled salinity range but were most abundant in the brackish part: maximal densities of 976 individuals per 1000 m<sup>2</sup> (1 psu) in the Eems, 1148 individuals per 1000 m<sup>2</sup> (10 psu) in the Westerschelde, and 39 individuals per 1000 m<sup>2</sup> (1 psu) in the Gironde. *Palaemonetes varians* was only recorded in the Eems (zoeae and postlarvae between 23 and 10 psu) and the Westerschelde (only postlarvae between 30 and 10 psu). *Palaemon longirostris* is a typical species for the oligohaline reaches of estuaries. It was absent from the Westerschelde. Densities were low in the Eems (maximum of 9 zoeae, 23 postlarvae and 1 adult per 1000 m<sup>2</sup>). In the Gironde it was the most abundant caridean: maximum of 44 zoeae (3 psu), 324 postlarvae (2 psu) and 224 adults (0.1 psu) per 1000 m<sup>2</sup>.

#### *Larval Brachyura*

Larval stages of the shore crab *Carcinus maenas* were rare in the Gironde (only 3 megalopae). In Eems and Westerschelde both zoeae (maximal densities of 15 and 34 individuals per 1000 m<sup>2</sup>) and megalopae (maximal densities of 861 and 17 individuals per 1000 m<sup>2</sup>) were present up to the 10 psu isohaline. *Liocarcinus holsatus* zoeae and megalopae were only common in the Westerschelde (298 zoeae and 31 megalopae per 1000 m<sup>2</sup> at 17 and 21 psu, respectively). Both stages were present but rare in Eems and Gironde. *Eriocheir sinensis* megalopae were only caught in Eems and Gironde, all other crab larvae were rare and mostly restricted to a single estuary.

#### *Postlarval fish*

*Pomatoschistus microps* was very abundant in the oligohaline reaches of Eems (maximal density of 435 individuals per 1000 m<sup>2</sup> at 1 psu; range 27 to 1 psu) and Gironde (maximal density of 6321 individuals per 1000 m<sup>2</sup> at 4 psu; range 18 to 0

psu). Densities in the Westerschelde were much lower (maximum of 5 individuals per 1000 m<sup>2</sup>) and the species was only present downstream the 10 psu isohaline. Postlarval *Pomatoschistus* species were absent from the Gironde. They were caught along the entire sampled transect of the Eems (maximum of 1260 individuals per 1000 m<sup>2</sup> at 2 psu) and the Westerschelde (maximum of 1260 individuals per 1000 m<sup>2</sup> at 10 psu). *Syngnathus rostellatus* was common in the marine reaches of the Eems (upto 17 psu) and in the brackish reaches of Westerschelde (upto 12 psu) and Gironde (upto 0.1 psu). Larval clupeoids were always caught in low numbers (never more than 85 individuals per 1000 m<sup>2</sup>) between the mouth of the estuary and 2 psu, 19 psu and 3 psu in Eems, Westerschelde and Gironde, respectively. Glass eels *Anguilla anguilla* were only encountered (a total of 7 individuals) in the three lowest salinity samples of the Gironde.

#### *Other taxa*

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

#### 6.3.4. Identification and characterization of communities

Multivariate analysis with density and biomass data permitted the identification of 8 geographically separated communities. The general pattern in the data is illustrated with the TWINSpan result using the biomass data (Figure 6.7). The first division groups the high salinity samples of the three estuaries on the positive side and all low salinity samples on the negative side. Indicator species for the latter group are the mysid *Neomysis integer* at the 7th and the common goby *Pomatoschistus microps* at the 4th cutlevel; the mysid *Schistomysis kervillei* is indicator for the former group. In the second and third divisions geographical groupings per estuary become prominent in both main clusters: in each group one or two Gironde, Eems and Westerschelde communities can be identified. Stations w8 and e21 are indicated by the program as misclassified and borderline negative respectively. The marine cluster (left side) is divided in three groups, one for each estuary: Gironde West (GW: g26b to g18), Westerschelde West (WW: w31 to w21 and w17) and Eems West (EW: e29 to e23). In the brackish cluster (right side) the Gironde samples are first split from the Eems and



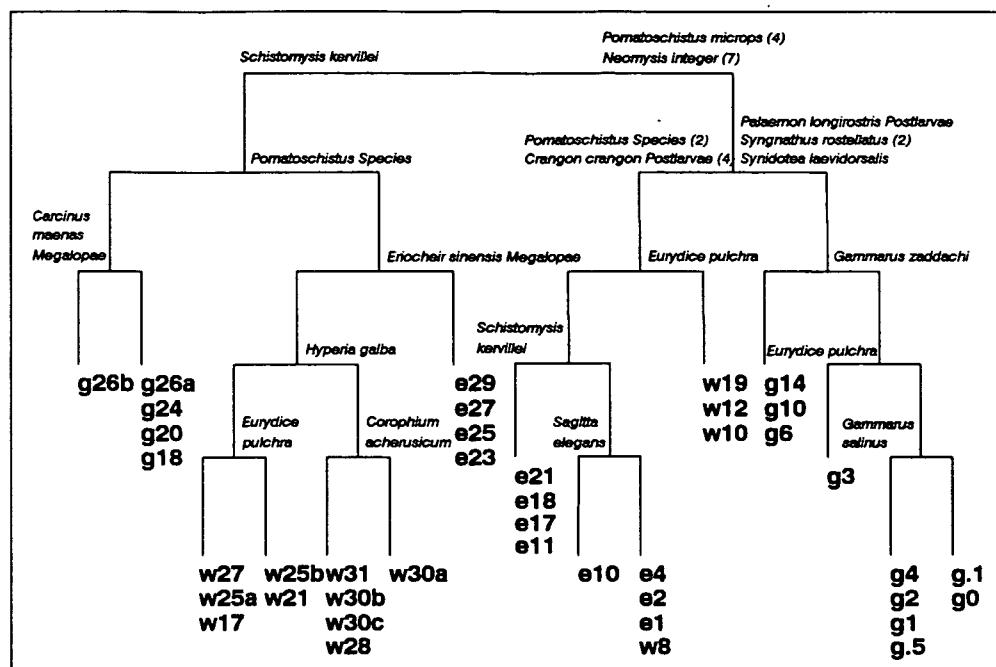


Figure 6.7. TWINSpan with the fourth root transformed biomass data of the three estuaries. Indicator species (and pseudospecies cutlevel) are given for each division.

Westerschelde samples. Indicators for the Gironde group are postlarval *Palaemon longirostris*, *Syngnathus rostellatus* (second cutlevel) and *Syndotea laevidorsalis*. Within this group the lowest salinity samples (Gironde East, GE: g4 to g0) are further split from the rest (Gironde Mid, GM: g14 to g6) on the basis of *Gammarus zaddachi*. Indicators for the Eems-Westerschelde group are postlarval *Crangon crangon* (fourth cutlevel) and *Pomatoschistus* species (second cutlevel). The third division divides this cluster in an Eems group and a Westerschelde group (Westerschelde Mid, WM with indicator *Eurydice pulchra*). The Eems samples are further divided in an Eems Mid group (e21 to e11) with indicator species *Schistomysis kervillei* and an Eems East group (e10 to e1 plus w8). Further divisions in these 8 clusters are not considered to be ecologically meaningful: the groupings they yield are not consistently found with the other multivariate analyses and their indicator species have limited significance. The TWINSpan with the density data (not figured) yielded nearly the same picture. Differences only apply to transitional stations showing indecisive behaviour in all analyses and indicated by the program either as misclassified samples or borderline-positives or negatives (e.g. w8 rather clustering with the w10 to w19 stations than with the Eems samples, and e21 clustering with the e23 to e29 cluster rather than with the e11 to e18 cluster). The TWINSpan divisions were confirmed by group average sorting clusteranalyses (not figured): the two main low and high salinity clusters could always be distinguished with high dissimilarity. Groupings of samples with high similarities yielded the same 8 clusters (again with some stations shifting between geographically adjacent clusters). G26b and g26a were found to be highly dissimilar from the rest of the samples, reflecting the fact that few individuals were

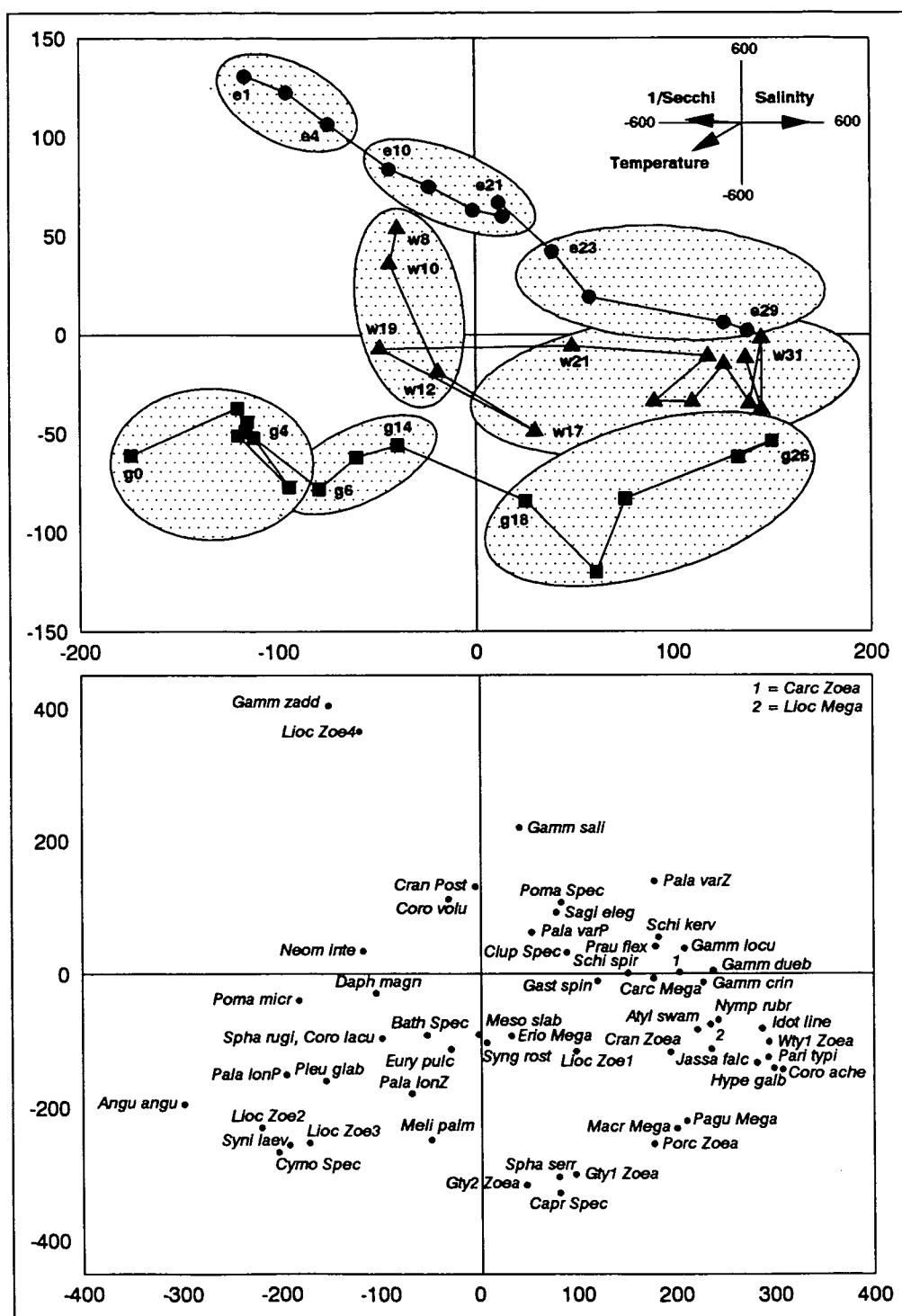


Figure 6.8. Species scores (bottom), sample scores (top), and environmental biplot (upper right corner) in the ordination plane formed by the first (horizontal) and second (vertical) canonical axes of the CCA with the fourth root transformed biomass data of the three estuaries. Samples are connected following salinity; communities as identified by TWINSPLAN and GAS are circled.

caught in these stations. The same applies to w8 which, though it invariably clustered with the brackish main group, was always found in an isolated position with lower

similarity to the other stations. In the CCA only the first (eigenvalue 0.44) and second (eigenvalue 0.23) axes are important and the ordination plane they form suffices to visualise the structure in the data (Figure 6.8). The axes of higher order (eigenvalues lower than 0.10) do not yield additional information and are not discussed. The first axis correlates strongly with the main estuarine gradients: salinity, Secchi disc depth and, to a lesser extent, temperature. The largest vector, which, per definition, explains most of the variance, nearly parallels the first axis and represents the salinity gradient. It is strongly and negatively correlated with the 1/Secchi vector. Projection of the temperature vector on the first axis reflects its correlation with the estuarine temperature gradient. The second axis also has an important temperature component, now being a covariable of latitude. The first axis (with its correlated salinity-turbidity-temperature gradient) thus reflects within-estuary variation, whereas the second axis (with its latitudinal temperature component) rather reflects among-estuary differences. All marine samples are located on the positive side of the first axis. The three western clusters can be found segregated along the second axis, with the EW cluster in the upper right quadrant, the GW cluster in the lower right quadrant and the WW cluster situated upon the first axis in between EW and GW. The mid estuary clusters are located close to the second axis with WM near the centre of the diagram, again in between EM (top) and GM (bottom). The clusters grouping the eastern Eems and Gironde samples are situated in the upper and lower left quadrants respectively. Interestingly, corresponding salinity zones in the three estuaries have the same position along the first axis. The gap along the second axis between the EE and GE clusters suggests the position where we might expect the WE cluster. The position of the species in the ordination plane reveals groups of hyperbenthic species characteristic for the sample clusters identified (Figure 6.8 bottom). The analyses with the data of the single estuaries emphasise the continuous, gradual aspect of community replacement. Only the ordination planes formed by the first two canonical axes of the CCA with the density data (Figure 6.9) are presented. First axis eigenvalues are 0.38, 0.41 and 0.58 for Eems, Westerschelde, and Gironde, respectively. The three variables are always represented by long vectors lying close to the first axis, temperature and 1/Secchi pointing towards the brackish samples, salinity towards the marine samples (not figured). The horse-shoe effect could readily be removed by detrending after which all stations were located in the same order close to the first axis (results not figured), implying these are truly single-axis ordinations. There are no real gaps between any two stations but within each estuary an eastern, middle and western group (sometimes forming tight clusters) can be delineated confirming the ecological significance of the classifications.

Combining the three techniques, in each estuary two (Westerschelde) or three (Eems and Gironde) communities could be distinguished. The species composition of these communities can differ, but their position along the gradient is similar: a marine or western community in the high salinity zone (GW, EW and WW), a brackish water community in the middle reaches (GM, EM and WM) and a third community in the stations with the lowest salinities (eastern communities GE and EE). As shown by CCA

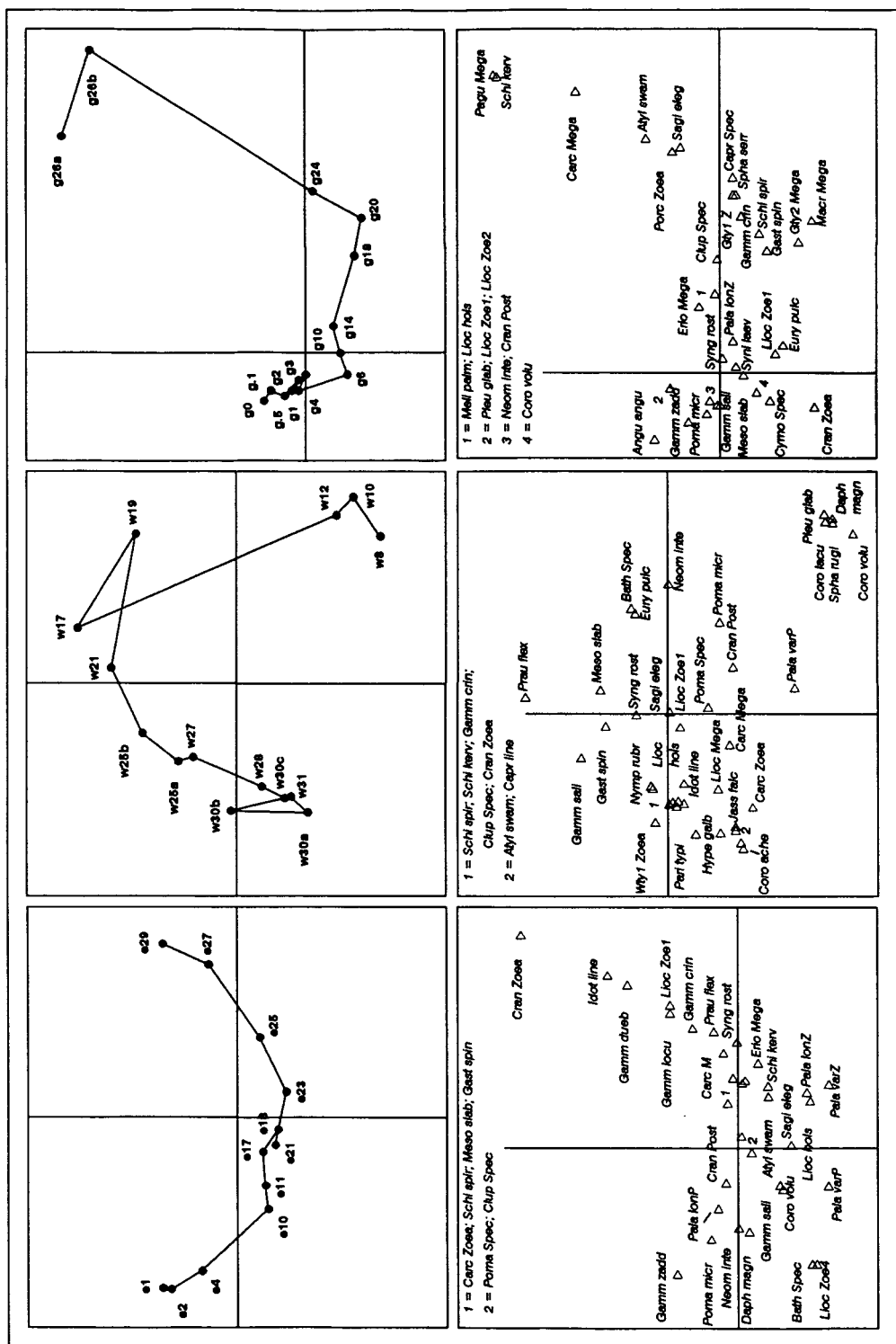


Figure 6.9. Species scores (bottom) and sample scores (top) in the ordination plane formed by the first (horizontal) and second (vertical) canonical axes of the CCA with the fourth root transformed biomass data of the three estuaries separately. Samples are connected following salinity.

(and also by the progressive agglomerative clustering of the stations along the salinity gradient, not figured) the classification of the gradients into distinct clusters is

somewhat artificial: some stations show indecisive behaviour, clustering with one community in one analysis and with another, neighbouring community in the next. Still, despite the fact that in each estuary one or two stations represent a transitional situation where two neighbouring communities meet, the communities are distinct and for practical purposes an objective division can be made.

In summary, it was decided to consider the following 8 communities (see also Figure 6.8): three in the Eems: a marine, western community EW from 29 to 23 psu, a brackish community in the middle part of the estuary EM from 21 to 10 psu, and a oligohaline, eastern community EE from 4 to 1 psu; two in the Westerschelde: WW from 31 to 21 psu (+ w17) and WM from 19 to 8 psu; and three in the Gironde: GW from 26 to 18 psu, GM from 14 to 6 psu, and GE from 4 to 0 psu.

The biotic characteristics (species composition, density, biomass) of the 2 or 3 communities within each estuary are - per definition - distinctly different (Figure 6.10). Within each estuary the marine community is characterized by many species occurring in low densities. The middle community is characterized by few species reaching very high densities and biomass. The eastern communities of Eems and Gironde have still higher biomass (though somewhat lower density in the Gironde) and again more species contribute. Differences between estuaries especially concern GW which is very poor and WM which is very rich in comparison to the corresponding communities in the other estuaries. The eastern and middle communities are characterized by the same dominant species in each estuary.

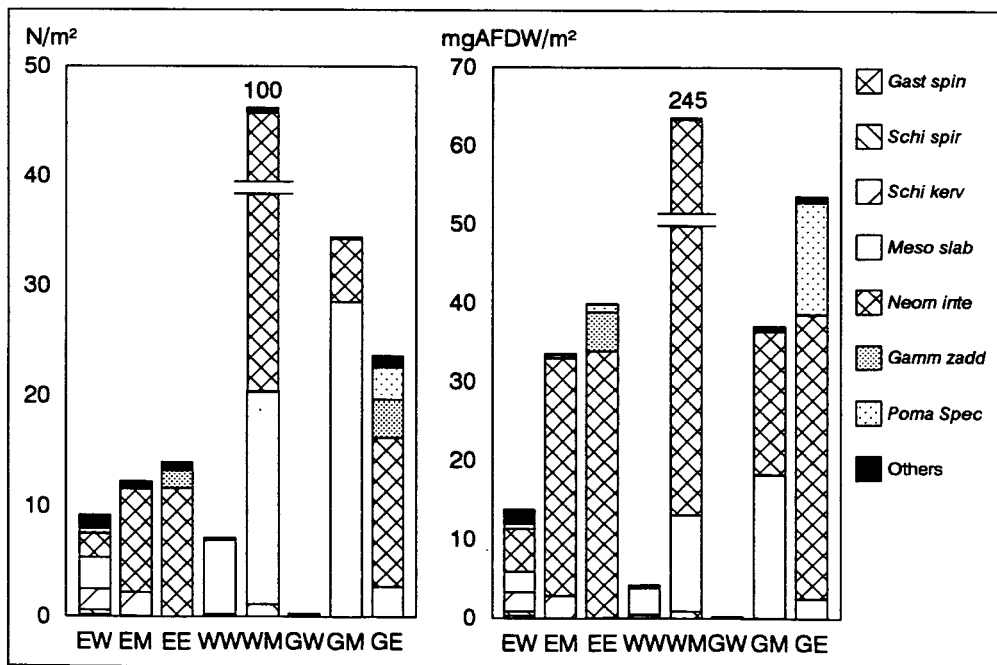


Figure 6.10. Faunal composition of the 8 communities as identified by the multivariate analyses: density (left) and biomass (right). First letter: Eems, Westerschelde, Gironde; second letter: West, Middle, East.

#### 6.4. Discussion

Though no data on net efficiency of the sledge are available, the sampling gear deployed seems to be suitable for quantitative sampling of the hyperbenthos. Densities reported for the Gironde from previous studies are either lower than, or comparable to, densities reported in this study. Mees & Sorbe (in preparation) using a passive fishing technique with a rectangular plankton net (0.5 mm mesh), estimated average annual density for *Neomysis integer* at 6 individuals per m<sup>3</sup> in the zone of maximal abundance with maximal densities of 10 to 15 individuals per m<sup>3</sup> in spring and autumn and summer densities of about 3 individuals per m<sup>3</sup>. This is lower than maximal density reported in this study: 33 individuals per m<sup>3</sup> at 4 psu. Sorbe (1981b) reported maximal densities of *Gammarus zaddachi* at 550 individuals per 100 m<sup>3</sup> in summer, which is about the same density as found in this study. The same author estimated maximal density of *G. salinus* at 20-30 individuals per 100 m<sup>3</sup> water which is about 10 times lower than maximal densities reported in this study. The sampling strategy seems to have a sufficiently narrow grid for studying the replacement of hyperbenthic communities along the estuarine gradients (e.g. the continuous aspect of the CCA sample score biplots in Figure 6.9).

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

Each estuary contained distinct communities along the unidirectional salinity-turbidity-temperature gradient. The position of these communities was similar in each estuary: a marine community in the high salinity zone, a brackish water community in the middle reaches and a third community (absent from the Westerschelde) in the stations with the lowest salinities. The similarity of the brackish water faunas among estuaries is high, higher than the within-estuary similarity of brackish and marine fauna. Brackish water species are few and the dominant residents occurred in all three estuaries at about the same density. In his extensive literature review Wolff (1973)

concluded that the macrobenthic faunas of the brackish estuaries of N.W. Europe (including the Eems, the Delta area and the Arcachon Bay) were very similar to one another. This similarity can be extended to the hyperbenthic brackish water fauna and can be traced back to a common ancestral area on the western coast of France during the last Pleistocene glaciation, some 18000-20000 years ago. As for the macrobenthos, the low number of hyperbenthic brackish water species can be explained by the low predictability of the environment and the geological history of northwestern Europe, and by the physiological stress which confronts the animals colonizing them (McLusky 1981).

The classical pattern in species succession within *Gammarus*, already described for many European tidal estuaries (Lincoln 1979; Sorbe 1978, 1979; Meurs & Zauke 1988), was confirmed in the present study. *G. crinicornis* is a marine species which penetrates estuaries, *G. salinus* is a brackish water species and *G. zaddachi* prefers the areas of very low salinity. In contrast to the findings of Meurs & Zauke (1988) an overlap was recorded in the distribution of *G. salinus* and *G. zaddachi* in the Eems and the Gironde.

Still, qualitative and quantitative differences in the corresponding hyperbenthic communities of the three estuaries were obvious. Some species were restricted to one or two of the estuaries studied, while others, especially in the brackish part, were common to all three. The distribution of these common species along the salinity gradient - and the density and biomass they reach in the corresponding salinity zones - varied to some extent between estuaries (for examples see Figure 6.5).

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

did in Gironde and Eems and had a more limited upstream distribution (e.g. *Schistomysis spiritus*, *S. kervillei*, *Pomatoschistus* species).

Absence of a species from the samples does not necessarily mean it is not present in the estuary. This is certainly true for the rare species and for animals not efficiently caught with the sledge e.g. *Pleusymtes glaber* and *Melita palmata* (Mees *et al.* 1993b), and *Rhithropanopeus harrisii* (Wolff & Sandee 1971, Van Damme *et al.* 1992) were previously recorded from the Westerschelde and *Sphaeroma rugicauda* is known to be present in the Eems (Michaelis *et al.* 1992). Still, especially for the abundant species of Eems and Gironde (e.g. Table 6.1), the low number of individuals (if any) caught in the Westerschelde can give an indication of significantly reduced population sizes in the impoverished Westerschelde. *Gammarus zaddachi* was not recorded from the Westerschelde in this study although occasionally an individual is caught in the tidal marsh of Saeftinghe (Cattrijsse *et al.* 1993). Den Hartog (1964) discussed the Gammaridea of the Westerschelde and reported *G. zaddachi* from several locations in the Delta area. The species disappeared from the Rhine before 1958 and from all other estuarine waters in the area in 1960, probably due to pollution or an epidemic. The estuarine populations had not recovered by 1963. *Palaemon longirostris* was formerly common in the oligohaline parts of the estuaries of the Delta area (Holthuis 1950). During intensive sampling in the early seventies only 1 individual was found in the Westerschelde near Bath (Heerebout 1974) and the disappearance was attributed to pollution. *P. longirostris* is very common in European estuaries of the geographical area covered (e.g. Heerebout 1974, Marchand 1981, Sorbe 1983). It occurs along the entire estuarine gradient (0 to 28 psu). It is reasonable to conclude that these species should normally also occur in the Westerschelde and that their absence from the system has to do with pollution.

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

Other differences among the estuaries are related to latitude. Some species probably reached their northern or southern distribution limits in one of the systems studied (e.g. the absence of *Idotea linearis* from the Gironde; the occurrence of *Sphae-*



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

Differences among the estuaries in the reproductive state of populations may also be related to temperature. Populations of the same species are liable to have been sampled in a different life cycle phase at each latitude, which may explain the presence/absence and relative densities of certain developmental stages - i.e. functional species or temporary hyperbenthic species (Hamerlynck & Mees 1991) - in the estuaries (e.g. the lower density of *Crangon crangon* zoeae and *Palaemon longirostris* zoeae in the Eems, the presence of *Pagurus*, *Porcellana* and *Macropodia* megalopae in the Gironde). Other differences may relate to the physical characteristics of the estuaries. Sorbe (1983) found *Palaemonetes varians* to be common in less dynamic areas close to the Gironde, but thinks it doesn't tolerate the high current velocities in the estuary proper. The Eems samples were characterized by large amounts of peat, which may explain the higher net efficiency for larger fish and epibenthic crustaceans (Table 6.1). Other differences result from recent introductions of brackish water species. Whereas the crabs *Eriocheir sinensis* and *Rhithropanopeus harrisii* were both successful in colonising the three estuaries, the isopod *Synidotea laevidorsalis* is only present in the Gironde (Mees & Fockede 1993).

## CHAPTER 6: addendum.

### First record of *Synidotea laevidorsalis* (Miers, 1881) (Crustacea: Isopoda) in Europe (Gironde estuary, France).

#### Abstract

This note reports on the presence of a well established population of the isopod *Synidotea laevidorsalis* (Miers) in the Gironde estuary (southwestern France). This species is new for the European fauna. *S. laevidorsalis* is a nonendemic cool-temperate to subtropical, shallow-water species which was probably introduced into the study area from Asia. In the salinity range of 1 to 10 psu of the Gironde the species constitutes an important component of the brackish-water hyperbenthic community. The population was already present in 1975 when it was misidentified as the native species *Idotea emarginata* (Fabricius).

#### Introduction

Isopods belonging to the genus *Synidotea* Harger have not yet been recorded from European waters. *Synidotea laevidorsalis* (Miers) is a nonendemic species for the study area. This large isopod (body length upto 30 mm) is an oriental species which in the past 100 years has undergone a human-borne global invasion (Chapman & Carlton 1991). According to these authors it is common in shallow temperate estuaries of East Asia (from Shanghai, China to Hokodate, Japan) from where it was introduced into the northeastern Pacific (records from San Francisco Bay, California and Willapa Bay, Washington) and into the South Atlantic (records from northern Argentina and southern and central Brazil). Chapman & Carlton (1991) further predicted that "many new records of introduced populations of *Synidotea* remain to be discovered".

#### Material and methods

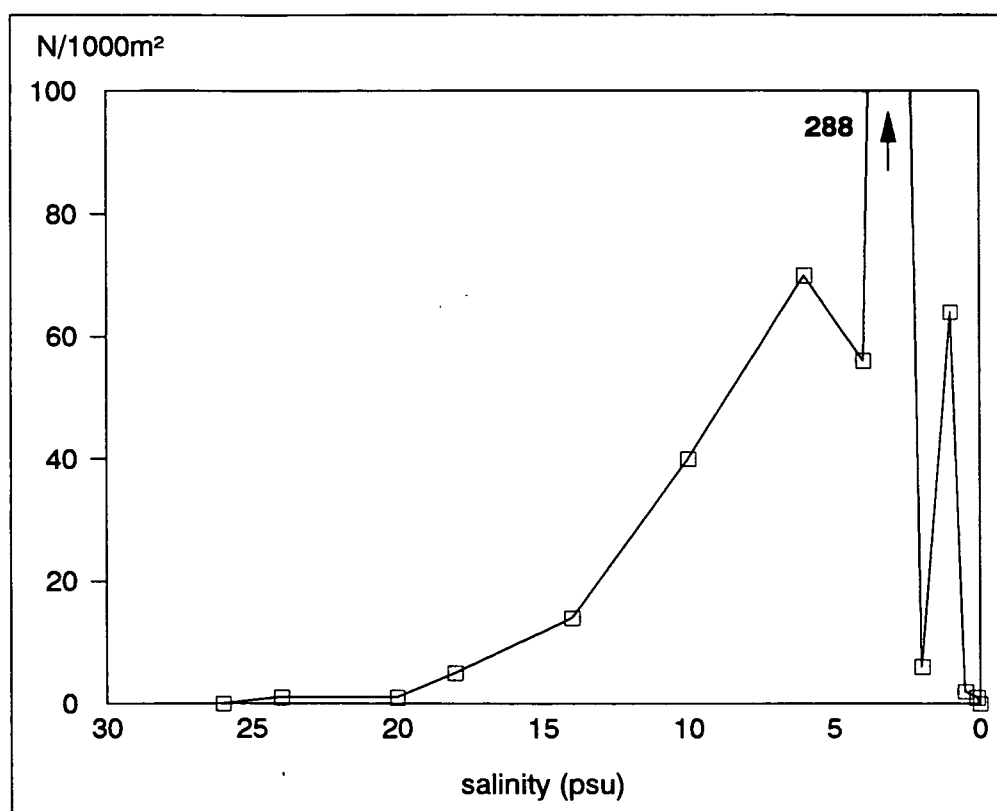
The Gironde (latitude 45°20'N, longitude 0°45'W) is the largest French estuary (625 km<sup>2</sup> at flood tide). It is 70 km long from the inlet to the point where the rivers Dordogne and Garonne join. A detailed description of the study area is given by Castel & Veiga (1990). The estuary was sampled on two consecutive days in Summer of 1991 (5 and 6 August). Fifteen more or less equally spaced stations were sampled along the salinity gradient ranging from 26 psu (Port Bloc - 45°34'N/1°02'W) to 0 psu (Bec d' Ambès - 45°02'N/0°37'W).

Sampling was done from the Côte d'Aquitaine using a hyperbenthic sledge (Hamerlynck & Mees 1991) which samples the lower one metre of the watercolumn. Trawling was done with the tide at an average ship speed of 4.5 knots relative to the bottom. All samples were taken during daytime in the main subtidal channel. At each

locality a trawl of approximately 1000 m was done. Where possible the 10 m isobath was followed; actual sampling depth varied between 6 and 14 m. The temperature of the water increased from 21.6 to 24.4 °C in upstream direction. Salinity was measured one metre above the bottom at the end of each trawl. The samples were immediately preserved in neutralized formaldehyde 7% final concentration.

For descriptions and illustrations of *S. laevidorsalis* we refer to the papers of Miers (1881), Menzies & Miller (1972) (as *Synidotea laticauda* Benedict) and Pires & Moreira (1975) (as *Synidotea brunnea* Pires & Moreira).

## Results



**Figure 6.11.** Distribution of *Synidotea laevidorsalis* along the Gironde estuary salinity gradient. All points represent the number of individuals caught in one trawl of 1000 m.

More than 500 individuals of *Synidotea laevidorsalis* were collected during the survey. The species was present in 12 of the 15 stations sampled, only being absent in the 2 most downstream stations (salinities of 27 and 26 psu) and the innermost station (fresh water: salinity 0 psu). They were caught in water with salinities ranging from 0.1 to 24 psu (Figure 6.11). *S. laevidorsalis* was present with more than 50 individuals per trawl (i.e. per 1000 m<sup>2</sup>) in the zone from 1 to 10 psu with a maximum of 288 individuals in the trawl around the 3 psu isohaline. In the population sampled subadults, males and females (most of which were gravid) were equally represented.

Associated species in the brackish water hyperbenthic community were the mysids *Neomysis integer* (Leach) and *Mesopodopsis slabberi* (van Beneden), the amphipods *Gammarus salinus* Spooner and *Gammarus zaddachi* Sexton, postlarvae of the caridean shrimp species *Crangon crangon* (L.) and *Palaemon longirostris* (Milne Edwards), and of the fish species *Syngnathus rostellatus* Nilsson and *Pomatoschistus microps* (Kroyer).

## Discussion

Although this is the first study in the Gironde in which *Synidotea laevidorsalis* is identified as such, we know that a well established population of the species has been present in the study area for at least 20 years. Monthly samples of the hyperbenthos of the Gironde in 1975 revealed *S. laevidorsalis* to be the dominant isopod in the brackish water zone (Sorbe 1981b). The species was wrongly reported as *Idotea emarginata* (Fabricius) (Sorbe 1981b and pers. comm.). According to this author the species is an estuarine endemic, never being caught in neighbouring waters with fully marine conditions (Sorbe pers. comm.). Their hyperbenthic distribution along the salinity gradient depends on the tides. Reproduction occurs in September-October (Sorbe 1981b).

Except for the collections of Sorbe (1981b) no historical information is available on the origin and age of the population. However, following the arguments of Chapman & Carlton (1991) about its oriental origin, it is probable that the species arrived on the hulls of nineteenth-century sailing ships or that it has been transported with importations of Japanese oysters.

Chapman & Carlton (1991) state that most records of *S. laevidorsalis* are from "intertidal pilings, and rock jetties or floats and buoys among dense masses of hydroids or bryozoans in shallow brackish and marine waters". No hand collections of the species were made for this study. Still, the species was never encountered in the extensive macrobenthos surveys conducted in the area (e.g. Bachelet 1985 and references therein) and Hydrozoa and Bryozoa have not been reported to occur in important numbers in the brackish part of the estuary. This suggests that the animals crawl over the bottom and that at least part of the Gironde population migrates into the water column, even during daytime. This observation can be due to the sampling methodology used in this study: specifically sampling the hyperbenthos in the areas where the species is known to occur may yield additional information on the ecology of other populations of *S. laevidorsalis*.

## CHAPTER 7.

### Life history, growth and production of *Neomysis integer* in the Westerschelde estuary (SW Netherlands).

#### Abstract

The *Neomysis integer* (Leach, 1814) (Crustacea, Mysidacea) population of the brackish part of the Westerschelde estuary was sampled on a fortnightly basis from November 1990 to December 1991. Density, biomass, population structure and brood size were recorded. The Bhattacharya method was applied to the length-frequency data for the detection and separation of cohorts. Growth is described both by a generalised von Bertalanffy function and by a von Bertalanffy function incorporating seasonal oscillations in growth. Secondary production was estimated for each cohort using four approaches.

The seasonal pattern in density and biomass showed three peaks: a relatively small, yet distinct, peak in early March (30 individuals per m<sup>2</sup>, 60 mg AFDW per m<sup>2</sup>) and two main peaks in late spring (160 individuals per m<sup>2</sup>, 225 mg AFDW per m<sup>2</sup>) and in summer (140 individuals per m<sup>2</sup>, 125 mg AFDW per m<sup>2</sup>). Throughout winter, *N. integer* density remained well below 30 individuals per m<sup>2</sup>. Three periods of increased reproductive activity and subsequent input of juveniles were found. This suggests that three cohorts were produced per year. The overwintering generation lived from autumn until the following spring. The spring generation was born in early spring and lived for about three months, while the summer generation lived from summer until early winter. The three cohorts showed marked differences in their biology. The overwintering generation showed seasonal growth oscillations, larger brood size, and a larger size at maturity. Individuals belonging to the other two cohorts generally grew faster, produced less young per female, and attained maturity at a smaller size. Within each cohort, both sexes exhibited different growth characteristics: the females generally lived longer, grew faster and consequently became larger than the males.

The size-frequency, growth summation and removal summation methods yielded comparable production estimates. The annual production was 0.3 g AFDW m<sup>-2</sup> yr<sup>-1</sup> with an annual P/B ratio of 6. The average cohort P/B was 3. The size-frequency method gave similar results only when applied to the three cohorts and to both sexes separately. The spring cohort accounted for almost half of the annual production. Despite the longer life span of the overwintering generation, it generated only a quarter of the annual production. An independent estimate of production using the mortality rate of the different cohorts, resulted in values comparable to those obtained by the other methods for the overwintering cohort, while the production of the other two cohorts was overestimated.

## 7.1. Introduction

Generally the lack of reliable estimates of secondary production due to poorly documented life history data for key species constitutes a major problem in understanding the functioning of aquatic ecosystems. This problem especially adheres to studies of energy flows through food webs in estuaries.

Estuaries are highly productive ecosystems. They are widely recognised as important nurseries for fish and epibenthic crustaceans. Especially the low salinity zone around the typical estuarine turbidity maximum is characterized by high amounts of organic detritus, high densities of zooplankton (Soetaert & van Rijswijk 1993), epi- and hyperbenthos and both demersal and pelagic fish (Hamerlynck *et al.* 1993a, Mees *et al.* 1993b).

The genus *Neomysis* Czerniavsky has representatives on and around each continent and detailed studies exist on the biology of several species (e.g. Ishikawa & Oshima 1951, Heubach 1969, Pezzack & Corey 1979, Toda *et al.* 1982, Cooper *et al.* 1992 and references therein). *Neomysis integer* (Leach, 1814) is one of the most common mysids around the coasts of Europe. It is a hyperbenthic, euryhaline and eurythermic species, typically occurring in high numbers in estuarine, brackish water environments (Tattersall & Tattersall 1951). It also occurs in oligohaline to fresh water bodies which, in their recent geological history, were connected to the sea (Bremer & Vijverberg 1982). Tesch (1911) reported the species to be common in and characteristic for low salinity waters in the Delta area in the southwest of the Netherlands.

This study, which is part of an integrated study on major food chains in European tidal estuaries, focuses on the estimation of the production of *Neomysis integer*.

The life history of lacustrine *Neomysis integer* populations in the Dutch delta was previously studied by Borghouts (1978) and Platenkamp (1983). The biology of *N. integer* in lakes and pools in the Netherlands was studied by Vorstman (1951), Beattie & de Kruijf (1978) and Bremer & Vijverberg (1982). Other valuable information is available on populations in a Scottish loch (Mauchline 1971a), an Irish lough (Parker & West 1979) and in the coastal waters in the Baltic (Wiktor 1961, Jansen *et al.* 1980, Rudstam *et al.* 1986). Life cycle studies in the Ythan, Scotland (Astthorsson & Ralph 1984), the Eider-Ring, Germany (Kinne 1955) and the Gironde, France (Sorbe 1981b) are the only estuarine studies to date, but these do not give any production estimates of *N. integer*.

Baseline studies on spatial and temporal patterns in the hyperbenthic component of the Westerschelde have been published (Mees & Hamerlynck 1992, Mees *et al.* 1993a, 1993b). These studies indicated *N. integer* as the dominant species in the brackish part of the estuary, both in the main channel and adjacent tidal marshes. The mysid was recorded in salinities ranging from 8 to 25 psu, but it was never found downstream of Hansweert (Figure 7.1). The lacustrine limit of the population lies a few kilometres upstream of the Dutch-Belgian border (Mees *et al.*

1993a). Data on the horizontal distribution of the Westerschelde population are described in Mees *et al.* (1993b). As life history characteristics of a species can vary considerably from one habitat to another, local knowledge of the biology of *N. integer* in the Westerschelde is essential for further use in ecosystem modelling, energy-flow studies and experimental work (e.g. von Oertzen *et al.* 1988).

*Neomysis integer* is an omnivorous species. As a predator on zooplankton (e.g. Bremer & Vijverberg 1982) it can structure zooplankton populations and as a detritivore it can also, to a certain extent, affect the detrital food chain. The species is also an important prey for demersal and pelagic fish and larger epibenthic crustaceans (e.g. Mauchline 1980). In the Westerschelde *N. integer* is known to be a major food source for sand goby *Pomatoschistus minutus*, Lozano's goby *P. lozanoi*, common goby *P. microps*, seabass *Dicentrarchus labrax*, bib *Trisopterus luscus*, sea snail *Liparis liparis*, pipefish *Syngnathus rostellatus* and the brown shrimp *Crangon crangon* (A. Cattrijsse and K. Hostens pers. comm.). Other potential (and commercially important) predators on *N. integer* include sprat *Sprattus sprattus*, herring *Clupea harengus*, flounder *Pleuronectes flesus*, dab *Limanda limanda* and plaice *Pleuronectes platessa* (Mauchline 1980), all of which are common in the study area (Hamerlynck *et al.* 1993a). It is therefore believed to be a key species in the ecosystem of the brackish part of the Westerschelde.

## 7.2. Materials and Methods

### 7.2.1. Study area

The Westerschelde estuary (Figure 7.1) 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 characterized by a marked salinity gradient. The water is completely mixed and the residence time is rather high (about 70 days or 150 tidal cycles). Consequently fresh water (average inflow  $100 \text{ m}^3 \text{ s}^{-1}$ ) dilution is gradual and this results in relatively stable salinity zones which are maintained in more or less the same position throughout a tidal cycle. The most important shifts occur in accordance with seasonal variations in the freshwater inflow. The abiotic environment is discussed in Heip (1988) and Van Eck *et al.* (1991).

### 7.2.2. Sampling

Samples were taken on a more or less fortnightly basis from 27 November 1990 to 16 December 1991. In December 1990, May 1991 and September 1991 the estuary could only be sampled once (Table 7.1). Each sampling day 4 stations (OV, SA, BA and LI) were covered (Figure 7.1). Sampling was done from the RV 'Luctor'. All samples were taken during daytime when hyperbenthic mysids are known to concentrate near the bottom. The samples were collected with a hyperbenthic sledge

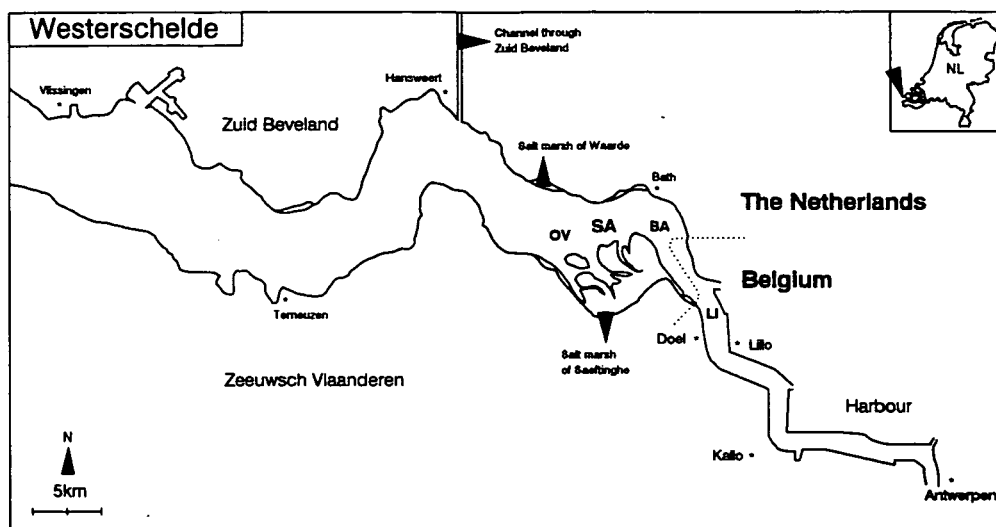


Figure 7.1. Study area and the 4 sampling sites.

(Hamerlynck & Mees 1991), 1 m wide, consisting of a heavy metal frame equipped with two nets one above the other. The catch in both nets was pooled for this study. The nets are 4 m long with a mesh size of 2\*2 mm in the first 3 m and 1\*1 mm in the last 1 m. The mouth of each net had a total area of 0.8 m<sup>2</sup> and sampled the hyperbenthos from 20 to 100 cm above the bottom. The sledge was towed for 1000 m at an average ship speed of 4.5 knots relative to the bottom. Positioning was done by radar readings from fixed points. The total area sampled on each occasion was thus approximately 1000 m<sup>2</sup>. Trawling was always done with the tide. The samples were taken in the main ebb-tidal channel of the estuary (where possible, the 10 m depth isobath was followed). The samples were immediately preserved in a buffered formaldehyde solution, 7% final concentration. Salinity, conductivity, pH, dissolved oxygen concentration, temperature (all measured at 1 m above the bottom) and Secchi disc depth were recorded at the end of each haul (Table 7.1).

### 7.2.3. Laboratory procedures

Samples were sorted and the number of specimens per sample was counted. Each sampling date, the sample with the highest number was selected for further analysis (Table 7.1). After picking out all *Neomysis integer* specimens in each catch these were emptied on a white tray divided into 48 squares. Subsamples, each containing 500 specimens, were then obtained by picking from randomly selected squares. About one thousand individuals of *N. integer* were thus obtained for each sample (500 from the upper net and 500 from the lower net). These were sexed and categorized in six life cycle stages according to Mauchline (1980): adult males, adult females, subadult males, subadult females, juveniles and gravid females. Mauchline's 7th stage, post-gravid females, was not distinguished in this study. Adult males are distinguished by their elongated 4th pleopods which reach beyond the posterior edge of the last abdominal segment. They are further characterized by a well developed and



setose *lobus masculinus* between the flagellae of the antennal peduncle. Adult females all have a fully developed marsupium between their thoracic legs. Juveniles lack secondary sexual characters. A further distinction between adult and subadult (immature) males and females is often more subjective. For subadult males the following criteria were used: the 4th pleopods stop short of reaching the end of the last abdominal segment and/or the *lobus masculinus* is present but it is much smaller than in adult males and it is not yet setose. The latter criterium is the most reliable one to distinguish the immature males from the juveniles. Females were categorized as adults when their marsupia were large enough to be seen from the lateral side. In contrast, the oostegites between the thoracopods in subadult females are only visible when the ventral side of the animal is carefully examined. Adult females were further divided into females without larvae (fully developed but empty marsupia) and 'gravid' or ovigerous females (larvae present in the marsupium). When such gravid females were present, larval counts were made on sixty females with complete broods per sample. Bisexual individuals, i.e. animals which have elongated 4th pleopods and a marsupium, were rare (less than 30 individuals encountered in the study) and were excluded from further analyses.

Table 7.1. Sampling sites where the peak abundances of *Neomysis integer* were recorded.

Date	Station	Sal. (pss)	Temp. (°C)	Oxyg. (%)	Secc. (cm)	pH	Cond. ( $\mu\text{S}\cdot\text{cm}^{-1}$ )
27-11-90	BA	17.0	8.4	65	40	7.65	28.1
11-12-90	OV	17.1	6.0	75	45	7.60	28.3
08-01-91	SA	9.0	5.8	79	40	7.88	15.2
21-01-91	OV	14.6	4.3	90	45	7.85	25.2
05-02-91	SA	11.8	2.8	64	25	7.63	19.8
22-02-91	OV	18.2	1.4	95	40	7.88	29.9
05-03-91	BA	12.3	4.8	67	40	7.54	19.8
18-03-91	SA	13.3	8.2	47	40	7.42	21.6
12-04-91	BA	13.1	11.0	75	60	7.64	20.8
24-04-91	SA	18.7	9.7	98	100	7.86	26.5
08-05-91	LI	-	-	-	-	-	-
11-06-91	BA	15.0	15.3	88	55	7.88	24.3
26-06-91	BA	14.4	16.8	-	45	7.68	23.5
09-07-91	SA	11.7	-	-	70	7.42	16.1
24-07-91	OV	17.5	19.6	84	50	7.61	28.8
12-08-91	LI	10.3	22.8	49	50	7.45	17.6
20-08-91	SA	18.6	20.5	110	100	7.22	30.6
19-09-91	OV	18.9	21.5	103	125	7.84	34.9
07-10-91	BA	16.8	16.3	83	45	7.68	28.0
17-10-91	SA	21.4	14.8	106	80	7.85	35.1
05-11-91	BA	17.7	11.4	86	50	7.81	29.5
18-11-91	BA	13.3	9.1	70	50	7.70	22.1
03-12-91	SA	12.6	7.3	44	45	7.41	21.4
16-12-91	SA	17.3	4.0	73	55	7.67	28.9
Average		15.2		79	56	7.66	25.0
Standard deviation		3.1		18	23	0.18	5.4

In each sample, the standard lengths (the distance from the base of the eye stalk to the end of the last abdominal segment) of sixty individuals of *Neomysis integer* per sex and per developmental stage were measured to the nearest 0.1 mm using a calibrated binocular microscope with drawing mirror and a digitizer (subsamples taken in a similar way as described above).

Fifty specimens (ten individuals from each stage and sex, excluding gravid females) from the April and October samples were used for weight measurements. Specimens covering the entire representative size range for each stage were selected for this analysis. They were dried in an oven at 60°C for five days. The dry weight of the animals was determined to the nearest microgram. The ash weight of the individuals was later measured after incineration at 550°C for two hours. The ash-free dry weight of the mysids was then calculated as the difference between the dry weight and ash weight. Length-weight regressions were linearised through double logarithmic transformation. Possible differences between spring and autumn animals were assessed by analysis of covariance of the corresponding linear regressions. The same 100 specimens were also used to determine regressions between standard length (SL) and two other length measures frequently used in mysid research: carapace length (CL, the distance from the tip of the rostrum to the mediodorsal margin of the carapace) and total length (TL, the distance from the base of the eye stalk to the posterior end of the uropods excluding the setae).

#### 7.2.4. Data analysis

Density of the population is expressed as number of individuals (N) per m<sup>2</sup>, biomass as mg ash-free dry weight (AFDW) per m<sup>2</sup>.

On each sampling date the mysids were pooled in 1 mm length classes. Because preliminary examination of the data revealed length and growth differences between males and females, length-frequency data of the two sexes were analysed separately, unless otherwise stated. Juveniles were divided equally over the male and female data matrices. To facilitate calculations of biomass, a regression between standard length (SL) and ash-free dry weight (AFDW) was determined by the least-squares-method. Biomass was then derived from the length-frequency distributions and the SL-AFDW regression.

In order to detect and separate cohorts the length-frequency distributions were analysed with the Bhattacharya method (Bhattacharya 1967, implemented in Pauly & Caddy 1985). It splits composite length-frequency distributions into separate normal distributions (Sparre 1985). The means of the normal distributions for all sampling dates are then linked to trace the modal length progression of the cohorts.

After cohort separation, the resulting mean sizes by age for each cohort and sex were submitted to ELEFAN I (Pauly & David 1981) in order to determine cohort and sex specific growth curve parameters.

The growth model used in ELEFAN I is a seasonally oscillating version of the generalised von Bertalanffy growth function (Gayaniilo *et al.* 1989):

$$L_t = L_\infty \left[ 1 - e^{(-K(t-t_0) - \frac{CK}{2\pi} (\sin 2\pi(t-t_g) - \sin 2\pi(t_0-t_g)))} \right]$$

Where

- $L_t$  is the predicted standard length at age  $t$
- $L_\infty$  is the asymptotic length
- $K$  is a growth constant
- $C$  is the amplitude of the seasonal growth oscillation
- $t_g$  is the starting point of that oscillation with respect to  $t_0$ ; within ELEFAN  $t_g$  is replaced by the winter point WP corresponding to the time of the year with the slowest growth ( $WP = t_g + 0.5$ )
- $t_0$  is the age at zero length

A detailed explanation of the different parameters is given in Pauly (1987).

An independent estimate of  $L_\infty$  was obtained with the Wetherall method as modified by Pauly (1986) (also available in the ELEFAN package).

Production estimates of *Neomysis integer* were obtained from the basic length-frequency data, and the length-weight regression. The first 2 sampling campaigns (27 November 1990 and 12 December 1990) were not used in the calculations. The year over which production was calculated thus started on 8 January 1991 and ended on 16 December 1991.

Three commonly used methods were applied to estimate annual production: the growth summation method, the removal summation method, and the size-frequency method (Crisp 1984, Waters 1977, Menzie 1980).

In the growth summation method (Crisp 1984) production ( $P$ ) is calculated as the increment of biomass from one sampling time to the next throughout the cohort's life span. In mathematical terms this can be expressed as:

$$P = \sum N \times \Delta \bar{W}$$

where

- $N$  is the number of individuals at time  $t$
- $\Delta \bar{W}$  is the increase in weight of an average individual during the time interval

The removal summation method (Crisp 1984) sums the loss (instead of growth) in weight between consecutive samples for the whole life span of the cohort and is given as:

$$P = \sum \bar{W} \times \Delta N$$

where

- $\bar{W}$  is the weight of the average animal during the sampling interval
- $\Delta N$  is the change in number of animals during the interval

The size-frequency method used here (Menzie 1980) involves the calculation of an average length-frequency distribution from quantitative samples taken at evenly spaced intervals throughout the year. Production is estimated as the sum of the losses of individuals from one size class to the next and the biomass loss this represents, compensated by the increase in mean individual weight with increasing age. The following expression was used:

$$P = \left[ i \times \sum_{j=1}^i (\bar{n}_j - \bar{n}_{j+1}) \times (W_j \times W_{j+1})^{1/2} \right] \times 365 / CPI$$

where

- P is annual production
- i is the number of size classes
- $\bar{n}_j$  is the number of individuals that have developed into a particular size category (j) during the year
- $W_j$  is the mean weight of an individual in the (j) size category
- CPI is the cohort production interval (the number of days from the date of birth of the cohort to the attainment of the largest size).

The size-frequency method was originally designed to estimate production in mixed populations of univoltine species (Hynes & Coleman 1968). However, it has usually been applied in single species production studies. In species with life spans different from one year the cohort production is multiplied by the ratio of 365 to the cohort production interval, CPI, in days (365/CPI) to obtain annual production. In the present study the three cohorts differed in their life span. Hence an average CPI was calculated from the CPIs of the three cohorts. Since the three cohorts overlapped in time, the use of this average CPI may not yield a good estimate of production. To check on this another estimate of annual production was obtained by considering each cohort separately. Annual production according to this treatment is then the sum of the production of each of the three cohorts. Waters & Crawford (1973) suggested that separate production estimates are needed in species which show sex-related length differences. As this was clearly the case for *Neomysis integer* in the study area, production estimates were also made for the males and females separately.

Furthermore, an independent estimate of production was obtained from the mortality rate. Under certain conditions (in case of a steady state model and if individual growth is described by a von Bertalanffy function) the total mortality of a population is equal to the P/B ratio of the population (Allen 1971). If the average annual biomass of the population is known, the production can be determined as the product of the biomass and the P/B obtained from the mortality rate. Total mortality (Z) for these calculations was obtained from a length converted catch curve (e.g. Gulland 1983).

### 7.3. Results

#### 7.3.1. Location of the abundance maximum and environmental variables

The density peaks of the *Neomysis integer* population were always distinctively located in one station. The abundance maxima were usually found in stations SA and BA (9 and 8 times, respectively). Only twice was the maximum located upstream of the Dutch-Belgian border (at station LI) and only four times in the most downstream station (OV).

Most environmental variables measured (Table 7.1) did not display clear seasonal patterns. Salinity varied between 9 and 21.4 psu with an average of  $15.2 \pm 3.12$  (conductivity 15.2 to 35.1  $\mu\text{S cm}^{-1}$ , average  $25 \pm 5.42 \mu\text{S cm}^{-1}$ ). Average pH was  $7.66 \pm 0.18$ . Dissolved oxygen concentration averaged  $78.6 \pm 18.3$  % of the saturation value and only reached saturation values on 3 occasions, but dropped below 50 % twice. Peaks of 100 cm Secchi disc depth and more were observed in April and August-September while the annual average was about 60 cm. The temperature in the watercolumn was 8.4°C at the start of sampling in November. It decreased to a minimal value of 1.4°C in February and then gradually increased to a maximum of 22.8°C in August. From September onwards it decreased again to winter values of 4°C by the end of sampling in December.

#### 7.3.2. Seasonal changes in density, biomass, length composition and stage distribution

The allometric relationships between total length (TL), carapace length (CL) and standard length (SL) were found to be:

$$\begin{aligned} \text{TL} &= 1.165 \text{ SL} - 0.080 & (\text{N} = 112, r = 0.997, p < 0.001) \\ \text{CL} &= 0.266 \text{ SL} + 0.439 & (\text{N} = 112, r = 0.908, p < 0.001) \end{aligned}$$

The following SL-AFDW regression, significant at the  $p < 0.001$  level, was used for the calculation of biomass:

$$\ln(\text{AFDW}) = 2.267 \ln(\text{SL}) - 5.539 \quad (\text{N} = 100; r = 0.997)$$

No significant differences ( $p > 0.5$ ) were found between SL-AFDW regressions of spring and autumn animals, nor between males and females.

The seasonal pattern in density and biomass is shown in Figure 7.2. Mean density for the study period was 28 individuals  $\text{m}^{-2}$  with a minimum of 2.5  $\text{m}^{-2}$  in December 1990 and a maximum of 128  $\text{m}^{-2}$  in June. Mean annual biomass was 54 mg AFDW  $\text{m}^{-2}$ .

In autumn and winter (October to the end of February), densities were low (less than 25 individuals  $\text{m}^{-2}$ ). In spring (March, April and May) densities remained low but biomass increased due to growth. From late spring onwards high densities and

biomass of *Neomysis integer* were recorded, with peak densities of more than 100 individuals  $m^{-2}$  in June and August (Figure 7.2).

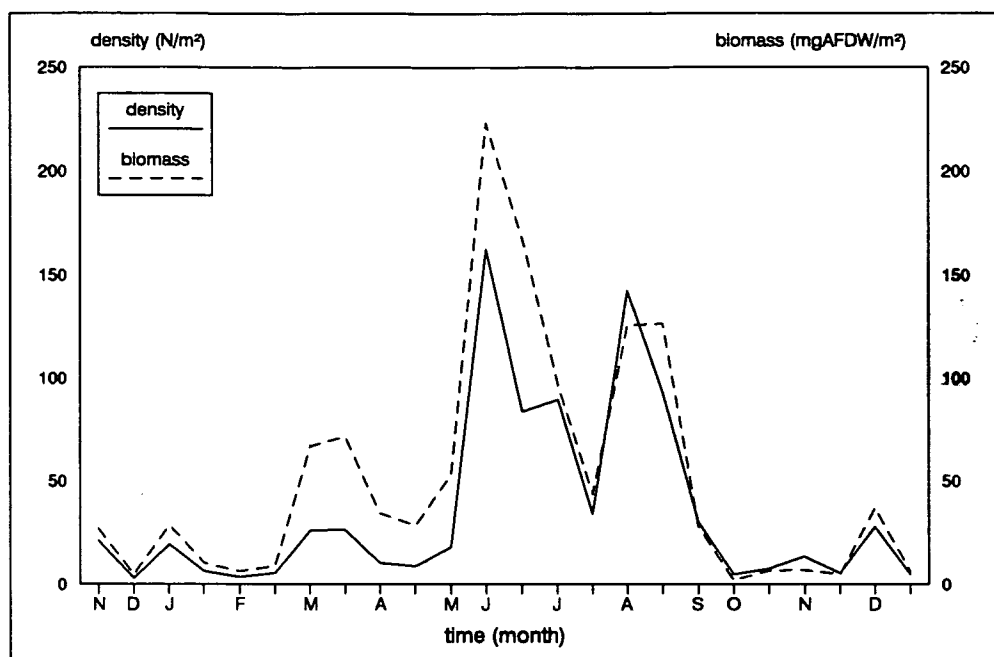
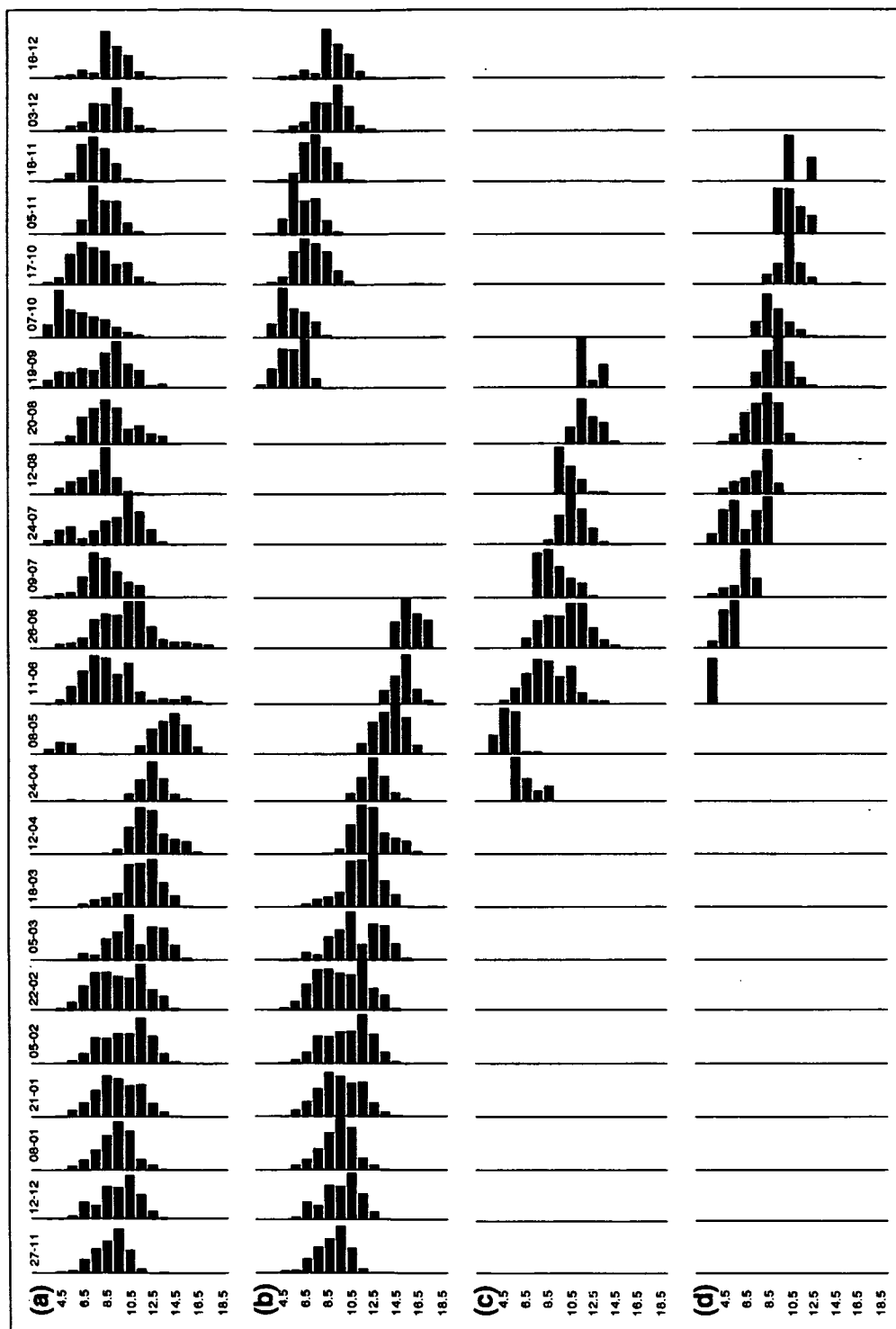


Figure 7.2. *Neomysis integer*. Density and biomass for each sampling date.

In the observed length-frequency distributions by date several bimodalities (Figure 7.3a) indicate recurring recruitment of cohorts. The larvae of mysids develop in the marsupium of the females and are released as miniature mysids at a length of about 2 mm (Mauchline 1980). Recruitment of a spring cohort in April-May was obvious as well as the presence of an overwintering generation that grew from November 1990 to May 1991 and from October 1991 to December 1991, respectively. The summer situation was generally more complex. Maximum observed length was 18.7 mm for a female in June.

The stage composition of the population on each sampling date is presented in Figure 7.4. In November and December of 1990, about 40% of the population were (large) juveniles. Immature males and females together accounted for another 40% of the population. Less than 20% of the population were adults. Throughout winter and in early spring juveniles appeared to be growing gradually into subadult stages, and the subadults simultaneously became adult males and females. In early March the number of adults increased sharply and some of the females were gravid. In early April nearly all mysids were adult and a substantial number of gravid females was observed. Throughout late spring and summer changes of the population structure were more difficult to follow. Still, three periods of juvenile-subadult recruitment, each preceded by an increase in the percentage of gravid females, were evident: May-June, July-August and September-November. Stage composition from November 1991 onwards was similar to the observations in the year before with a dominance of subadults.



**Figure 7.3.** Relative length-frequency distribution per sampling date, 1990-1991. The X-axes are percentage scales; the Y-axes are 1 mm classes with class marks of 2.5 to 18.5 mm and practical limits of 2.0-2.9 mm, 3.0-3.9 mm, etc. (a) All *Neomysis*, (b) cohort I, (c) cohort II, (d) cohort III.

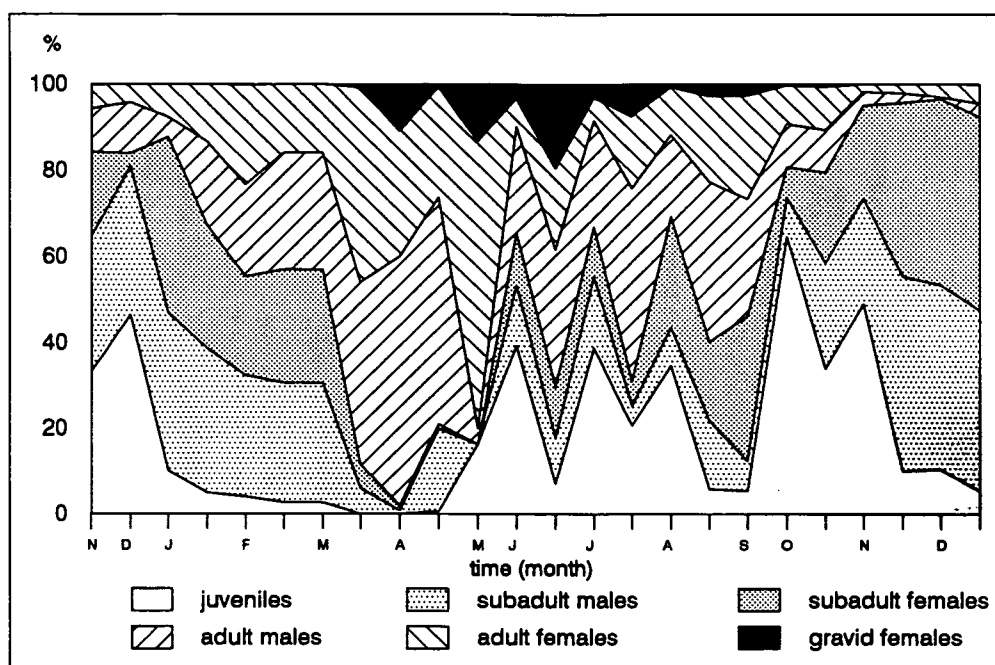


Figure 7.4. Observed population structure on each sampling date.

### 7.3.3. Cohort separation

Three different cohorts were identified in the length-frequency distribution. The overwintering cohort (cohort I) was first detectable in November 1990 at a mean length of 8 mm indicating that these animals were born before the start of the sampling period (Figure 7.5). The mean length of this cohort increased to 14 mm by May-June. This cohort died out by the end of June. A corresponding cohort for the next year was first visible in September 1991 having a mean length of 4 mm. These mysids had attained a mean length of 9 mm by the end of the sampling program in December. The spring cohort (cohort II) was detected in late April-May at a mean length of 3 mm. By the end of June cohort II had an average length of about 10 mm. This cohort was not detectable in early August. The summer cohort (cohort III) showed a similar increase in average size from its recruitment in July to the death of the last mysids in the first half of October (Figure 7.5).

Data on adult length also contributed to a reliable separation of the cohorts. The mean length of the adults of both sexes varied considerably during the course of the year (Figure 7.6). Mean length of overwintering adult males increased steadily from about 9 mm in November to more than 12 mm in April. The decrease in mean size and the high standard deviations in June, August and November indicate co-occurrence of adult males belonging to different generations. Adult females showed similar patterns of variation in mean length: the average increase in length was from 10 to 14 mm. As in case of the males the occasional decrease in mean size and standard deviations indicate co-occurrence of individuals belonging to 2 generations.



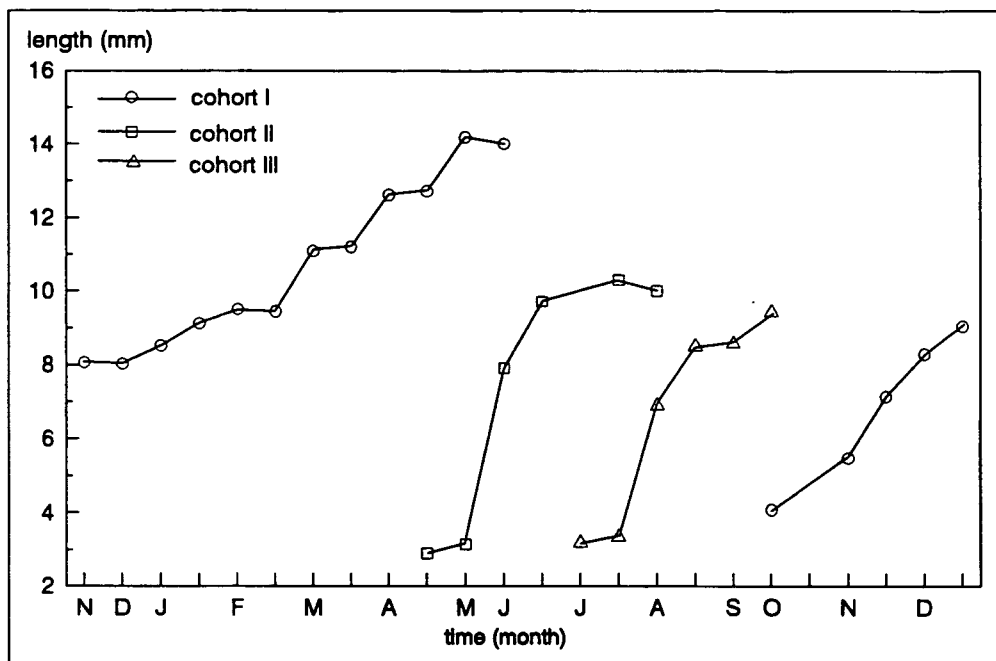


Figure 7.5. Output of the Bhattacharya method.

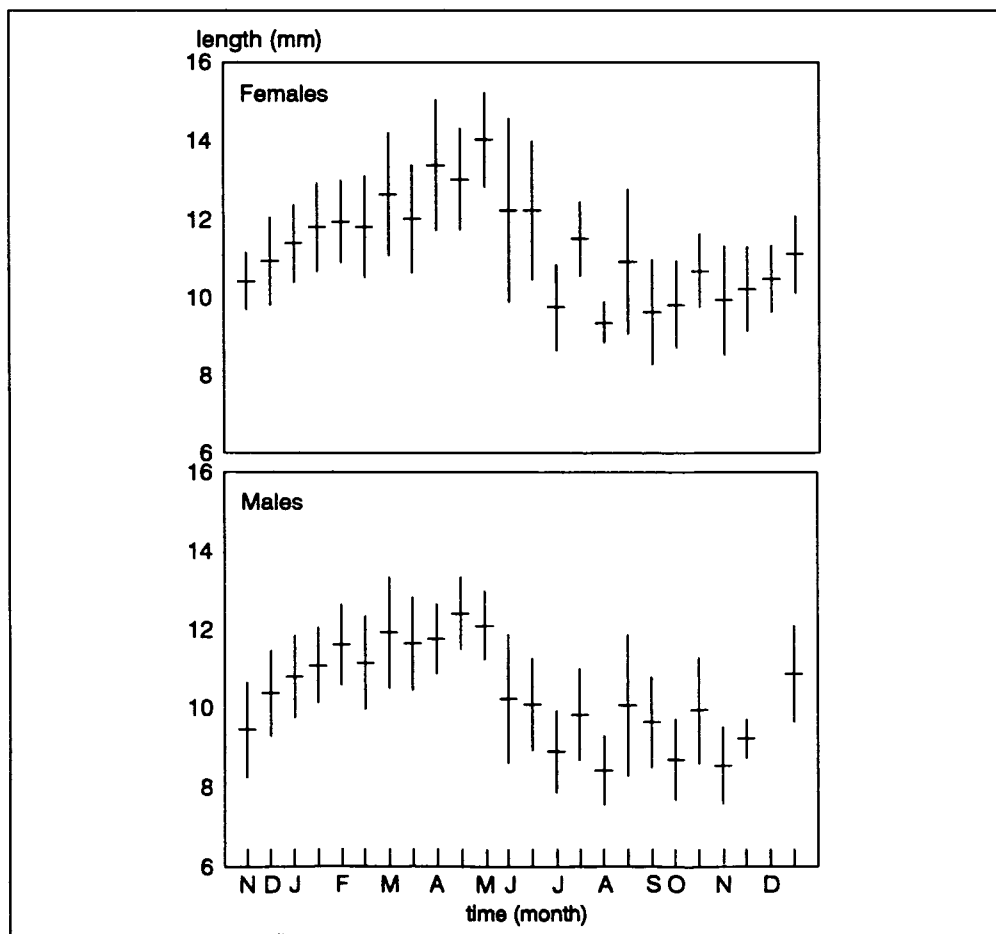


Figure 7.6. Temporal variation in mean length (+ standard deviation) of adult males and females.

Length-frequency distributions and population structure of the three cohorts are presented in Figures 7.3b, c, d and Figure 7.7, respectively. The autumn samples contained only recently released animals from cohort I, the majority of which overwintered as subadults and matured in March. Gravid females were present from April until June. From May onwards cohort I consisted to a very high extent of adult females, suggesting that the males died soon after mating. The cohort I females released the young of cohort II which caused the density peak in early May. Individuals of cohort II matured very rapidly: the first gravid females were already observed in June. The last juveniles were observed in August and breeding continued until the disappearance of the cohort in September. Cohort III juveniles appeared in the June samples and continued to recruit until October. This cohort also matured rapidly and bred from August until October, yielding the juveniles of the new overwintering generation. The last cohort III animals died in November. No difference in mortality between the sexes was observed for the summer cohorts.

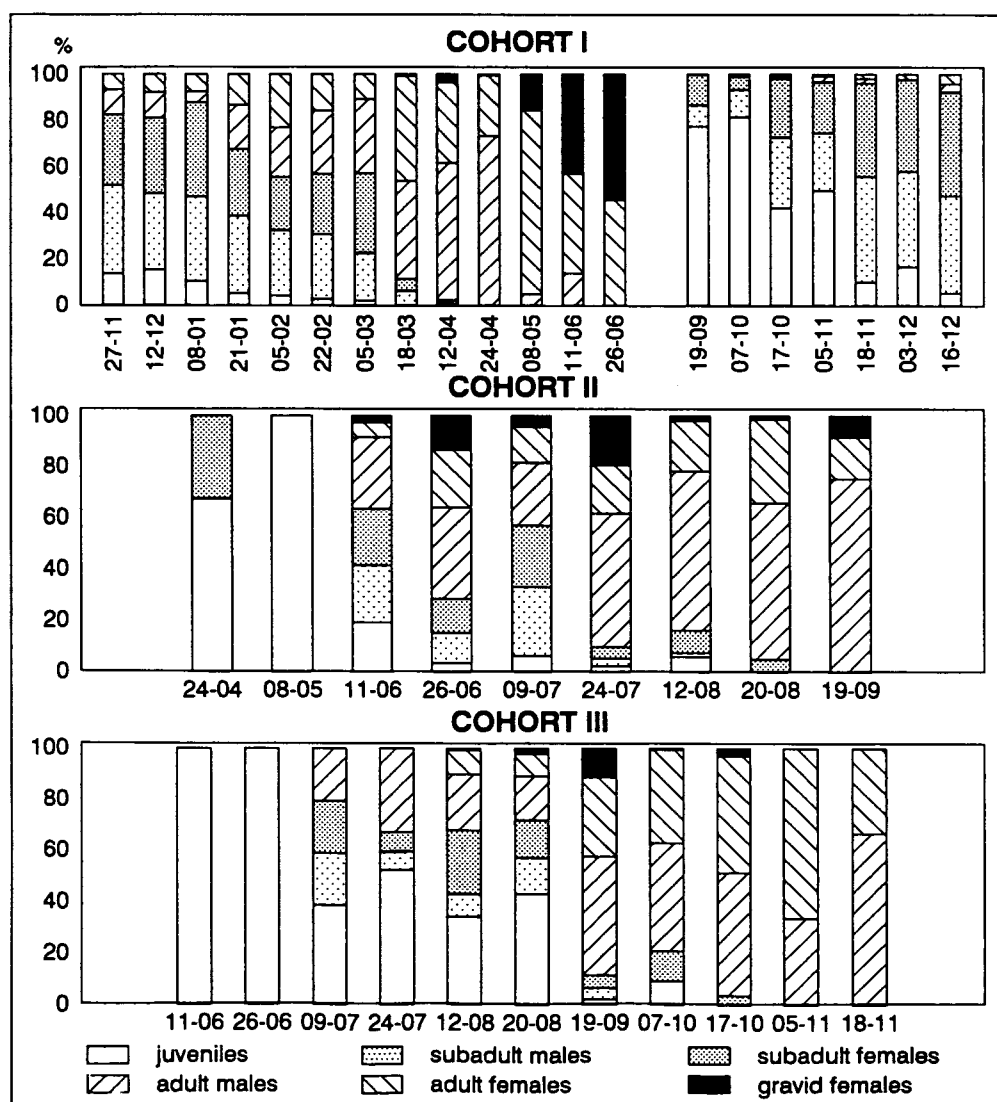


Figure 7.7. Population structure of the three cohorts.

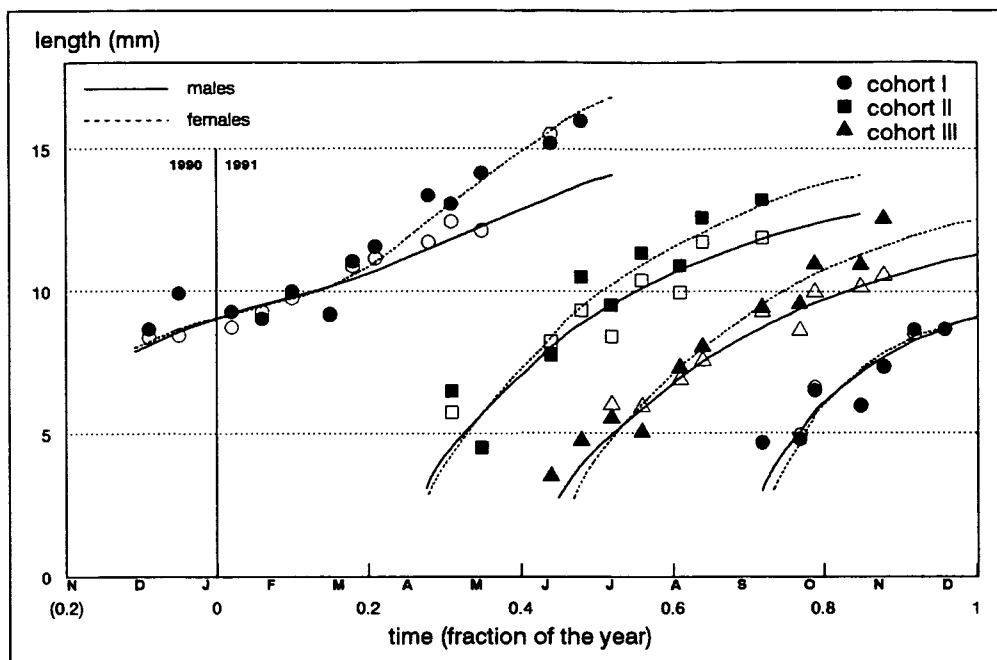
### 7.3.4. Growth

The growth parameters of the von Bertalanffy growth curves of the three separate cohorts are presented in Table 7.2. In Figure 7.8 these growth curves are plotted together with the corresponding modal length of the observed length-frequency distributions. Only the overwintering generation showed seasonally oscillating growth ( $C > 0.5$ ). From September through November the animals grew at a rate of 3 to 4 mm per month. In December growth slowed down and ceased almost completely during the winter months ( $WP = t_s - 0.5 = 0$ ). In spring, the mysids regained their fast growth rate. There was no seasonal oscillation detected in the growth of the mysids of the spring and summer generations ( $C = 0$ ). In these cohorts the smaller mysids (mainly juveniles and subadults) grew fastest (3 to 4 mm per month); the larger mysids (mainly adults) grew less (1 to 2 mm per month).

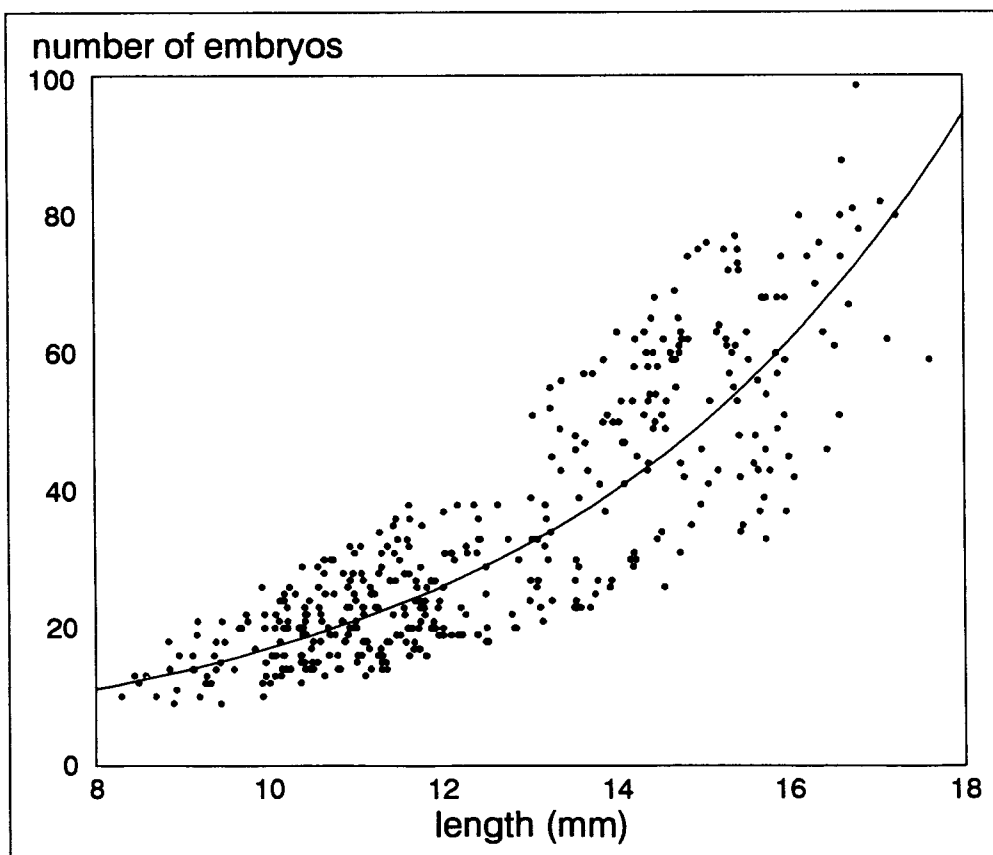
*Table 7.2. Growth parameters of the von Bertalanffy growth curves of the 3 cohorts and both sexes separately.  $L_\infty$ : asymptotic length,  $K$ : growth constant,  $C$ : amplitude of seasonal growth oscillation,  $t_s$ : starting point of the oscillation,  $t_0$ : age at zero length,  $R_n$ : a measure of goodness of fit.*

Sex/Cohort	$L_\infty$	$K$	$C$	$t_s$	$t_0$	$R_n$
Males I	16.0	2.70	0.66	0.50	0.72	0.75
Females I	19.0	3.00	0.80	0.52	0.78	0.69
Males II	14.3	3.43	0.00	0.00	0.20	0.61
Females II	16.0	3.35	0.00	0.00	0.25	0.48
Males III	13.1	3.01	0.00	0.00	0.33	0.50
Females III	14.3	3.37	0.00	0.00	0.41	0.76

Individuals of the overwintering generation attained a larger size than spring or summer animals (higher  $L_\infty$  for both sexes). Marked differences in growth patterns of the two sexes were evident in all cohorts: the females always had a higher  $L_\infty$  than the males. The average size at maturity for females (14 mm) and males (10 mm) of the overwintering generation was larger than for the spring and summer generations at 10 mm (females) and less than 9.5 mm (males).



*Figure 7.8. Growth curves of the three cohorts and both sexes separately. Open symbols: males, solid symbols: females.*



*Figure 7.9. Relation between female length and brood size (all data).*

### 7.3.5. Brood size

The number of larvae in the marsupium, i.e. the brood size ( $b$ ) showed a strong positive correlation with female length ( $l$ ) (Figure 7.9):

$$\ln(b) = -3.349 + 2.676 \ln(l)$$

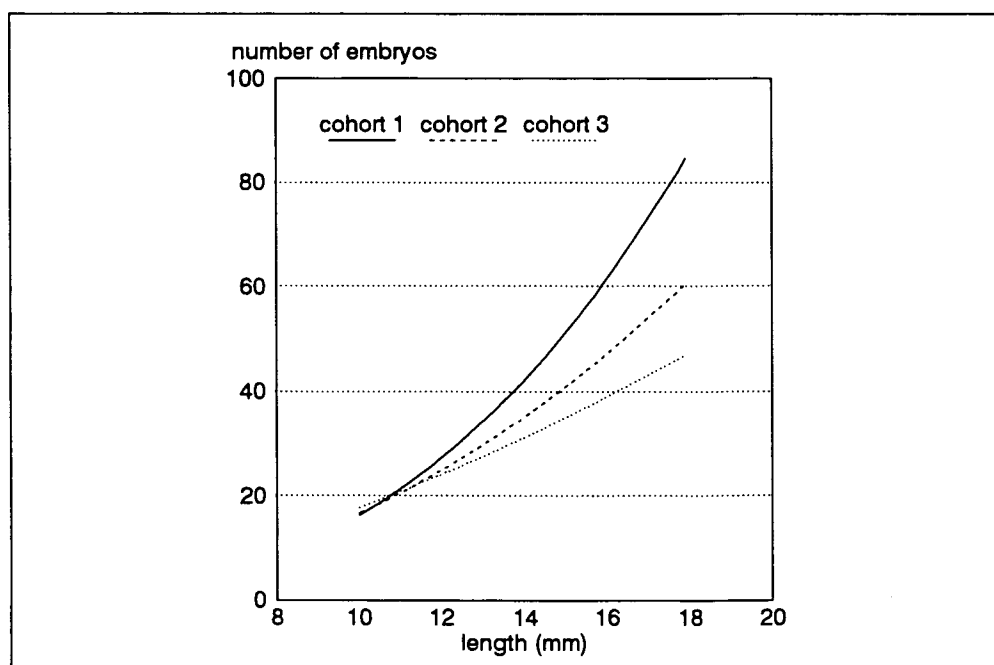
$$\text{or } b = 0.0365 l^{2.656}$$

( $n = 420$ ;  $r = 0.866$ ;  $p < 0.001$ )

Analysis of covariance showed that females in the overwintering generation had significantly larger broods than females in the spring and summer generations ( $p < 0.05$ ). The difference in brood size between the spring and summer generations was marginally significant at  $p = 0.067$ . The following equations were found to apply to the three cohorts (Figure 7.10):

Cohort I	$\ln(b) = -3.720 + 2.828 \ln(l)$	( $n = 167$ ; $r = 0.655$ ; $p < 0.01$ )
Cohort II	$\ln(b) = -2.307 + 2.223 \ln(l)$	( $n = 149$ ; $r = 0.562$ ; $p < 0.01$ )
Cohort III	$\ln(b) = -0.974 + 1.673 \ln(l)$	( $n = 104$ ; $r = 0.615$ ; $p < 0.01$ )

Thus, at the same body size, a female of the overwintering generation on average produces a higher number of larvae per brood than a female of the spring or summer generations.



**Figure 7.10.** Brood size vs. standard length for the three cohorts.

## 7.3.6. Production

The production estimates for *Neomysis integer* obtained with the different methods and at different levels of pooling of sexes and cohorts are summarised in Tables 7.3 and 7.4. The annual production estimates obtained with the growth summation and removal summation methods are almost identical (322 mg AFDW m<sup>-2</sup> yr<sup>-1</sup>). The result of the size-frequency method is very close (2% difference) to that of the two former methods only when the calculations were performed for the three cohorts and both sexes separately. Calculations on pooled length-frequency distributions of the two sexes per cohort and of the three cohorts (average CPI of 202 days) gave estimates that were 9% and 39% higher, respectively. Annual production as estimated from the mortality rate of each cohort was 24% higher than the estimates using the growth summation, the removal summation or the maximally disaggregated size-frequency methods. Only the values for the first cohort are comparable to the ones obtained with the other methods.

Table 7.3. Summary of the production estimates (mg AFDW m<sup>-2</sup> yr<sup>-1</sup>) obtained with different methods.

	Production	Biomass	P/B ratio
<b>Growth summation</b>			
CohortI	81.65	24.20	3.4
CohortII	164.51	51.28	3.2
CohortIII	76.54	19.48	3.9
Total	322.69	94.97	6.0
<b>Removal summation</b>			
CohortI	81.82	24.20	3.4
CohortII	163.82	51.28	3.2
CohortIII	76.78	19.48	3.9
Total	322.43	94.97	6.0
<b>Size-frequency</b>			
<b>Sexes separated</b>			
CohortI	91.70	25.34	3.6
CohortII	175.41	55.93	3.1
CohortIII	61.95	21.15	2.9
Total	329.06	102.42	6.1
<b>Sexes not separated</b>			
CohortI	96.94	25.34	3.8
CohortII	183.54	55.93	3.3
CohortIII	65.63	21.15	3.1
Total	351.82	101.85	6.5
All Cohorts	448.52	53.73	8.3

**Table 7.4.** Production estimates ( $P$ , in mg AFDW  $m^{-2} yr^{-1}$ ) obtained from the mortality rate ( $Z$ ) as compared to the estimates from the disaggregated size-frequency method ( $s-f$ ).

	Z	Biomass	P (Z)	P (s-f)
<b>Cohort I</b>				
males	3.15	10.10	31.82	35.65
females	4.27	15.24	65.07	56.05
total		25.34	96.89	91.70
<b>Cohort II</b>				
males	3.27	29.37	96.04	91.31
females	4.41	26.56	117.13	84.09
total		55.93	213.17	175.41
<b>Cohort III</b>				
males	4.49	10.37	46.56	29.49
females	3.90	10.78	42.04	32.46
total		21.16	88.60	61.95
<b>Annual production</b>			398.66	329.06

#### 7.4. Discussion

A more or less standard method is presented for studying the life history and population dynamics of mysids from field data. It was successfully applied to the Westerschelde population: samples were taken at regular intervals and the temporal evolution of the population structure was assessed by dividing the animals in a number of distinct sexual and developmental stages (Mauchline 1980). Length-frequency distributions per stage and per sampling date then allowed an estimate of the number of generations produced in a year. Seasonally oscillating (for the overwintering generation) or generalised (for the spring and summer generations) von Bertalanffy growth models could be fitted to the data, provided males and females were treated separately.

##### 7.4.1. Distribution

Salinity zones in the Westerschelde are relatively stable (Heip 1988). In the Westerschelde, in contrast to other European estuaries, the *Neomysis integer* population is concentrated in a narrow zone of approximately 20 km throughout the year (Mees *et al.* 1993b). This is attributed to the adverse oxygen conditions upstream of the Dutch-Belgian border (Mees *et al.* 1993a). The maximum population density is found around the isohaline of 15 psu and is therefore found at a much higher salinity than in other, less polluted, estuaries. In the Gironde (France), the Eems (The Netherlands), the Elbe (Germany) and the Shannon (Ireland), for example, the population maximum was found at 3.5 psu and typically a differential distribution of the

developmental stages and sexes along the salinity gradient is observed (Sorbe 1981b, Hough & Naylor 1992). The restricted distribution of the species in the Westerschelde results in a homogenous mix of developmental stages. This facilitates the study of *N. integer* population dynamics and justifies the selection of a single 1000 m sample in the zone of maximal abundance for the production estimates.

#### 7.4.2. Reproduction

The life cycle of *Neomysis integer* in the Westerschelde is similar to the life cycle previously described for this species occurring in other localities. Vorstman (1951), Mauchline (1971a), Borghouts (1978), Bremer & Vijverberg (1982) and Parker & West (1979) all concluded that *N. integer* produced 3 generations per year in the IJsselmeer (former Zuiderzee), the west coast lochs of Scotland, lake Veere (south-west Netherlands), in the Frisian lakes (north Netherlands) and in a lough in western Ireland, respectively. Two generations per year were found in the Ythan (Astthorsson & Ralph 1984) and Eider-Ring estuaries (Kinne 1955) and in the coastal waters in the Baltic Sea (Kinne 1955, Wiktor 1961, Jansen *et al.* 1980, Rudstam *et al.* 1986). At lower latitudes life cycles are more complex, breeding being almost continuous throughout the year (Sorbe 1981b).

In the Westerschelde, reproduction of *Neomysis integer* halted completely in winter. It restarted in April when the water temperature rose to 10°C and stopped again in October when the temperature dropped below the same value. Females of the overwintering generation had larger brood sizes for animals of the same length than females in the other generations. Whether this was correlated with a higher fecundity can not be derived from the field data. Smaller brood sizes may be compensated by the production of several broods per female in the spring and summer generations. Indeed, in culture experiments conducted at 20°C individual females were found to produce upto 5 consecutive broods (C.R. Janssen, unpublished). The physiological background and/or ecological adaptiveness of these different reproductive strategies remain unclear.

#### 7.4.3. Brood size

The results of the present study seem to corroborate the hypothesis of Bremer & Vijverberg (1982) that brood size is positively correlated with salinity: the Westerschelde population lives at a higher salinity than other studied populations and is characterized by the largest average brood sizes reported to date. However, the reason for this and why most populations of *Neomysis integer* are found at salinity ranges that result in relatively small brood sizes remains unclear. Possible explanations may include a trade-off for suboptimal brood sizes with competitive advantages of living in low-salinity waters which in estuaries coincides with the zone of maximum turbidity: lower (visual) predation pressure, more available food, less competition with other mysids (e.g. *Mesopodopsis slabberi*) or benthic filter feeders.



#### 7.4.4. Growth

The most frequently used method for determining growth in crustaceans involves the identification and tracing of modes (cohorts which are generated by seasonal reproduction) in the length-frequency distributions. As a result of the asynchrony of moulting between individual mysids the lengths within a cohort are assumed to be normally distributed. Growth curves are then fitted to the mean lengths of the traced cohorts in relation to their age. For the analysis of growth the complete ELEFAN program package (Pauly & David 1981) proved to be very useful. The Bhattacharya method is a powerful tool for identifying cohorts, but a careful examination of the population structure and length-frequency distributions of the different developmental stages was still necessary. The growth model used was a von Bertalanffy equation which incorporates seasonal variation in growth. In the absence of seasonal growth variations this function is reduced to the generalized von Bertalanffy growth equation. We were able to show that differences in growth between the sexual stages had to be taken into account. Seasonally oscillating von Bertalanffy growth equations have previously only been applied to the mesopelagic mysids *Meterythrops microphthalmus* from the Japan Sea (Ikeda 1992) and the hyperbenthic *Antarctomysis maxima* and *Mysidetes posthon* from Antarctic waters (Siegel & Mühlenhardt-Siegel 1988).

#### 7.4.5. Production

Production estimates of *Neomysis integer* are difficult to make because of sampling methodological problems. No correction was made for net efficiency which is unlikely to be 100 % as mysids are known to avoid nets to a considerable extent (Mauchline 1980). The abundance of the smallest size classes was certainly underestimated due to mesh selection. Only the water column between 0.2 m and 1 m above the bottom was sampled and, though there are indications that a large part of the population is concentrated in this zone throughout the day, some *N. integer* can be found in zooplankton samples taken at intermediate depths. Moreover, only the subtidal channel was sampled and *N. integer* makes extensive use of the salt marshes (Mees *et al.* 1993a) and possibly of other shallow areas. Samples were preserved for at least four months prior to analysis and the weight loss associated with formalin preservation, estimated to be about 10% by Beattie (1982), was not taken into account. Nor was a correction made for the underestimate of weight which results from backtransformation of the linearised length-weight relationship (Baskerville 1972). Organic matter is also lost during moulting. Holmquist (1959) found that *Mysis relicta* lost 5 to 10% of its dry weight due to ecdysis. This bias is not necessarily relevant since use of this refractory chitinous material in the food web is probably limited. Finally, no attempt was made to include intra-marsupial production in the calculations. Against this background, the production estimates presented in this study are likely to be too low.

*Neomysis integer* produced about 0.3 g AFDW m<sup>-2</sup> yr<sup>-1</sup>. This is much higher than the estimate by Bremer & Vijverberg for a lacustrine population (10 mg DW m<sup>-2</sup> yr<sup>-1</sup> with a P/B of 4.0). However, our estimate is remarkably close to the production values reported for *Neomysis mercedis* in lakes that support similar population densities (summarised in Cooper *et al.* 1992).

The growth summation and removal summation methods yielded approximately the same production estimates. The use of the size-frequency method is only recommended for populations that can easily be disaggregated into cohorts and/or sexes with more uniform life-history characteristics. Pooling of data leads to an overestimation of production. Indeed, one of the basic assumptions of the size-frequency method is that all species or, as in the case of this study, all sexes and cohorts must have the capability of growing to the same maximum size (Hamilton 1969). Waters & Crawford (1973) already noted that the method yielded estimates 15 to 26% higher than the removal summation method and postulated that this could be due to the size difference between the sexes. Although identification of cohorts is not required to obtain a production value with the size-frequency method, not doing so will thus lead to overestimates. The same conclusions apply to the method which uses the total mortality within the population to estimate production. Though not frequently used, the effort required to calculate production with this method is very low, as no abundance and mean individual weight per sampling date is necessary. Only a length-frequency distribution at each sampling date and an estimate of mean annual biomass is required (Brey 1986).

## 7.5. Conclusions

The *Neomysis integer* population of the Westerschelde produced 3 generations per year. The overwintering generation lived from autumn until spring of the following year. The spring generation was born in April and lived for around 3 months, while the summer generation lived from July until early winter of the same year. The spring generation produced the highest number of mysids and accounted for almost half of the annual biomass. The overwintering generation contributed least to the biomass. The biology of the mysids in the latter generation was markedly different from that of individuals belonging to the spring and summer generations: they had a lower growth rate, larger size at maturity and a larger brood size. Within any one cohort both sexes showed different growth characteristics, with the females generally living longer, growing faster and attaining a larger size than the males. Biomass production of *Neomysis integer* was found to be quite high in the brackish zone of the Westerschelde. The 3 methods for estimating secondary production yielded comparable results. Annual production amounted to 0.3 g AFDW m<sup>-2</sup> yr<sup>-1</sup>. The size-frequency method only resulted in figures similar to those obtained with the growth summation and removal summation methods when it was applied to the 3 cohorts and both sexes separately. The spring cohort produced nearly half of the total annual production, the overwintering cohort accounted for barely half of the total annual production.

## CHAPTER 7. Addendum.

### Aberrant individuals of *Neomysis integer* and other Mysidacea: intersexuality and variable telson morphology.

#### Abstract

Intersexuality in the mysid *Neomysis integer* is described from samples collected in the Elbe (north Germany), Eems-Dollard (north Netherlands), Westerschelde (south-west Netherlands) and Gironde (south-west France) estuaries. Individuals which had an irregularly shaped or nearly symmetrically rounded, rather than a typically truncated, telson were also recorded from the four populations studied. A culture experiment with damaged specimens revealed that every type of abnormal telson morphology found in the field can result from regeneration of damaged parts. It is concluded that both intersexuality and aberrant telson morphology are widespread phenomena among estuarine *N. integer* populations. Both abnormalities seem to be rare in the other dominant mysid species in the study area: only one intersexual *Gastrosaccus spinifer* and one *Schistomysis kervillei* with an aberrant telson were recorded.

#### Introduction

*Neomysis integer* (Leach) is one of the most common mysids around the coasts of Europe. It is a hyperbenthic, euryhaline and eurythermic species, typically occurring in high numbers in estuarine, brackish water environments (Tattersall & Tattersall 1951). Hough *et al.* (1992) reported intersexual individuals of this species, i.e. animals which display both male and female secondary sexual traits, from the Conwy estuary (North Wales) and claim that theirs is the first record of this phenomenon among the Mysidacea. Adult males of this species are characterized by elongated fourth pleopods which reach well beyond the base of the uropods (Plate 7.1 a), whereas adult females have uniformly short pleopods and oostegites forming a brood pouch or marsupium between the thoracic legs (Plate 7.1 b). The males are further characterized by an *appendix masculinus*, setose in adult individuals, which is located between the flagellae of the antennal peduncle. Intersexuality is a common phenomenon among other orders of peracaridan crustaceans. It has previously also been reported in representatives of the Isopoda, the Tanaidacea, and the Amphipoda (Hough *et al.* 1992).

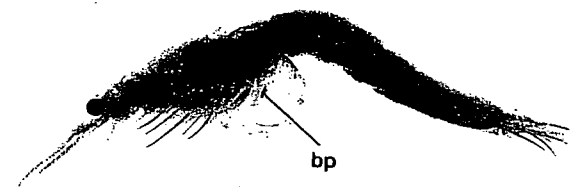
*Neomysis integer* typically has an entire truncated telson, whence the species name (Plate 7.1 d, e). A pair of long outer and short inner terminal spines can be distinguished. Chojnacki & Ciupinski (1986) reported altered telson morphology in *N. integer* from the Baltic coastal waters and considered this to be a result of predation and subsequent regeneration of the damaged parts (for the irregularly shaped telsons, their group B) or of mutations resulting from environmental pollution (for the telsons with a smoothed or rounded terminal margin, their group A).

Plate 7.1. *Neomysis integer*. (a) adult male; (b) adult female; (c) intersexual individual; (d) and (e) normal truncated telson. The elongated fourth pleopods (ep) and brood plates (bp) are marked.

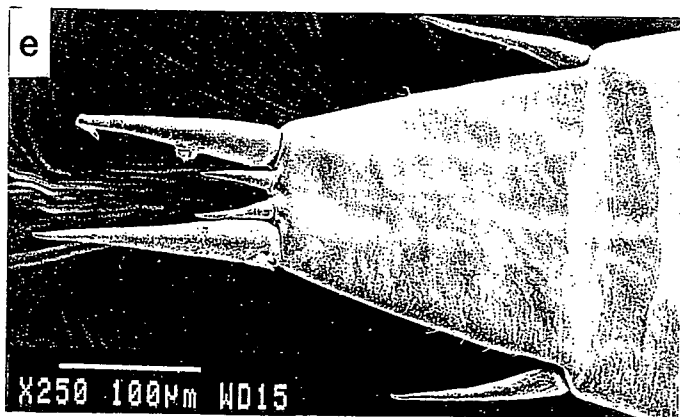
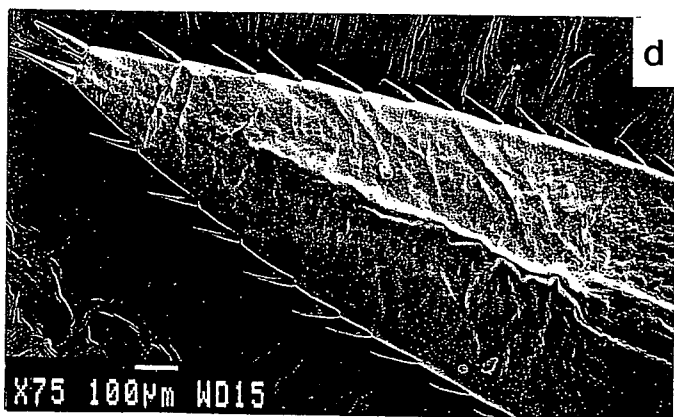
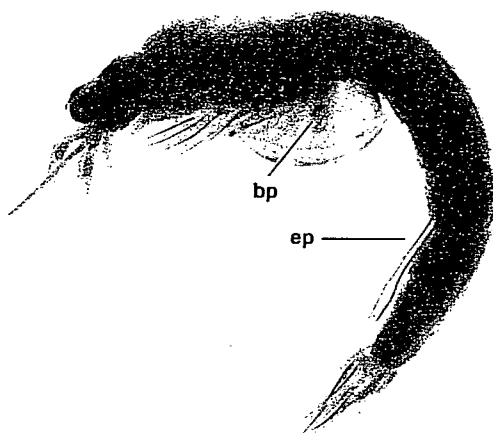
a



b



c



## Materials and methods

### *Samples*

The Mysidacea of the Westerschelde (southwest Netherlands) estuary were sampled monthly or fortnightly between April 1990 to April 1991. Each survey comprised several stations along the salinity gradient (Mees *et al.* 1993a, 1993b, 1994). All samples were collected subtidally with a towed sledge (Hamerlynck & Mees 1991). Where possible, the mean tidal level -10 m isobath was followed. In August 1991 the mysids of the Eems (north Netherlands), Westerschelde and Gironde (France) estuaries were sampled within a 2 week period (Mees *et al.* in press). In each estuary, some 15 evenly spaced stations were covered along the entire salinity gradient (from 0 to 30 psu). In April 1993 a similar sampling campaign was conducted in the Elbe (Germany) and, again, in the Westerschelde and the Gironde. The samples were preserved in a buffered formaldehyde solution, 7% final concentration.

### *Treatment of samples*

The samples were processed according to the methodology described in Mees & Hamerlynck (1992) and Mees *et al.* (1994). In the laboratory, all mysids (the dominant component of the sampled fauna) were sorted out and identified to species level with the key of Tattersall & Tattersall (1951). Per sampling date, a minimum of 1000 individuals per species were sexed and categorized into six life cycle stages according to Mauchline (1980). The same animals were examined for aberrant telson morphology. The dominant species in the brackish water zones of all 4 study areas was *Neomysis integer*, an estuarine endemic. In the Westerschelde, it was present throughout the year in high densities (Mees *et al.* 1994). In the more marine reaches of the estuaries, *Mesopodopsis slabberi*, *Schistomysis spiritus*, *S. kervillei*, and *Gastrosaccus spinifer* were most common. For more details on the distribution of these species see Mees *et al.* (1993a, 1993b, and in press).

Specimens for scanning electron microscope (SEM, JEOL840) were washed, dehydrated, and then critical point dried from liquid CO<sub>2</sub> and coated with gold before examination.

### *Experiment*

Live *Neomysis integer* were collected from the Galgenweel, a brackish water pond close to the Westerschelde near the harbour of Antwerpen. The telsons of 5 subadult specimens (7-8 mm standard length) were carefully damaged with a scalpel under a binocular microscope. The tip of the telson was removed by a transverse cut at about midlength. Care was taken not to damage the uropods. The operation only took a few seconds, and the animals seemed not to be stressed after manipulation. They were then individually cultured in 400 ml artificial seawater (salinity 5 psu) at 20°C and were

fed 500 freshly hatched *Artemia* nauplii each day. The containers were checked daily for moults. When present, these were collected and preserved in 4 % formalin. The telsons of the moults were examined and schematically drawn under a microscope with drawing tube, with special attention for their shape and the position and numbers of spines.

## Results

### *Intersexuality*

Intersexual individuals were found in the four estuaries studied. Each intersex was characterized by the presence of oostegites and elongated fourth pleopods (Plate 7.1 c). 36.4 % of all specimens examined also had a setose *appendix masculinus* as male secondary characteristic. In the Westerschelde, a total of 27 intersexual individuals was recorded throughout the study period. Three of these were subadults. Ten of the adults were gravid (larvae present in the marsupium). An additional adult specimen was recorded from the brackish tidal marsh of Saeftinghe (A. Cattrijsse, unpublished). In August 1991, 7 (6 adults, 3 of which were gravid, and one subadult) and 5 (all adults, 2 of which were gravid) individuals were found in Gironde and Eems, respectively. In the samples from the April 1993 campaign, additional adult specimens were found in the Gironde and in the Elbe (both single records). Most adult individuals appeared to have reproduced as normal females; several (30%) had larvae in the marsupium. Besides 1 subadult *Gastrosaccus spinifer*, no intersexual individuals of other mysid species were encountered in the samples.

### *Telson morphology*

#### Field data

The results are summarised in Table 7.5. In August 1991, incidence of aberrant telson shapes was very low in the three populations studied. Only 1, 0 and 4 individuals with an abnormal telson shape were recorded from Eems, Westerschelde and Gironde, respectively ( $\ll 1$  % of the population). In April 1993, the percentage of the populations displaying aberrant telsons was much higher: 9.1, 5.3 and 1.5 % in Elbe, Westerschelde and Gironde, respectively. In the Westerschelde, the percentage of aberrant individuals in the population varied seasonally. Incidence was low from May through October ( $< 1$  %). From November through April incidence was much higher, with a peak of nearly 6 % in April 1990.

Some telsons were asymmetrically shaped, while others were more or less symmetrically rounded or nearly truncated (Plate 7.2). Especially the number and the position of the terminal and subterminal lateral spines were quite variable.

In all other mysid species, aberrant telsons morphologies were not observed.

Only one *Schistomysis kervillei* collected from the Eems estuary had an irregularly shaped telson (Plate 7.3 b). This species typically has a cleft telson (Plate 7.3 a).

**Table 7.5.** Percentage of the *Neomysis integer* populations with aberrant telson morphology (\* = < 1 % of the population and - = no aberrant individuals found).

Sampling date	Westerschelde	Gironde	Eems	Elbe
04-90	2.9			
05-90	-			
06-90	-			
07-90	*			
08-90	-			
09-90	*			
10-90	*			
11-90	1.5			
12-90	4.0			
01-91	1.1			
02-91	1.5			
03-91	2.2			
04-91	5.7			
08-91	-	*	*	no data
04-93	5.3	1.5	no data	9.1

#### Culture experiment

The experiment lasted 48 days. Two individuals with a damaged telson were followed through 6 moults, two through 4 moults, while one died after the first moult (Table 7.6). As can be seen from Figure 7.11 (mysids A and B), the regeneration was asymmetrical at first (Chojnacki & Ciupinski's class B) but the telson became more or less symmetrically rounded in the fourth moult (Chojnacki & Ciupinski's class A). Though every individual died before the regeneration was complete, the telsons obviously resemble the 'normal' telson more after each moult. The other 2 individuals displayed a similar regeneration pattern.

Plate 7.2. Aberrant telson morphology of *Neomysis integer* collected in the field.

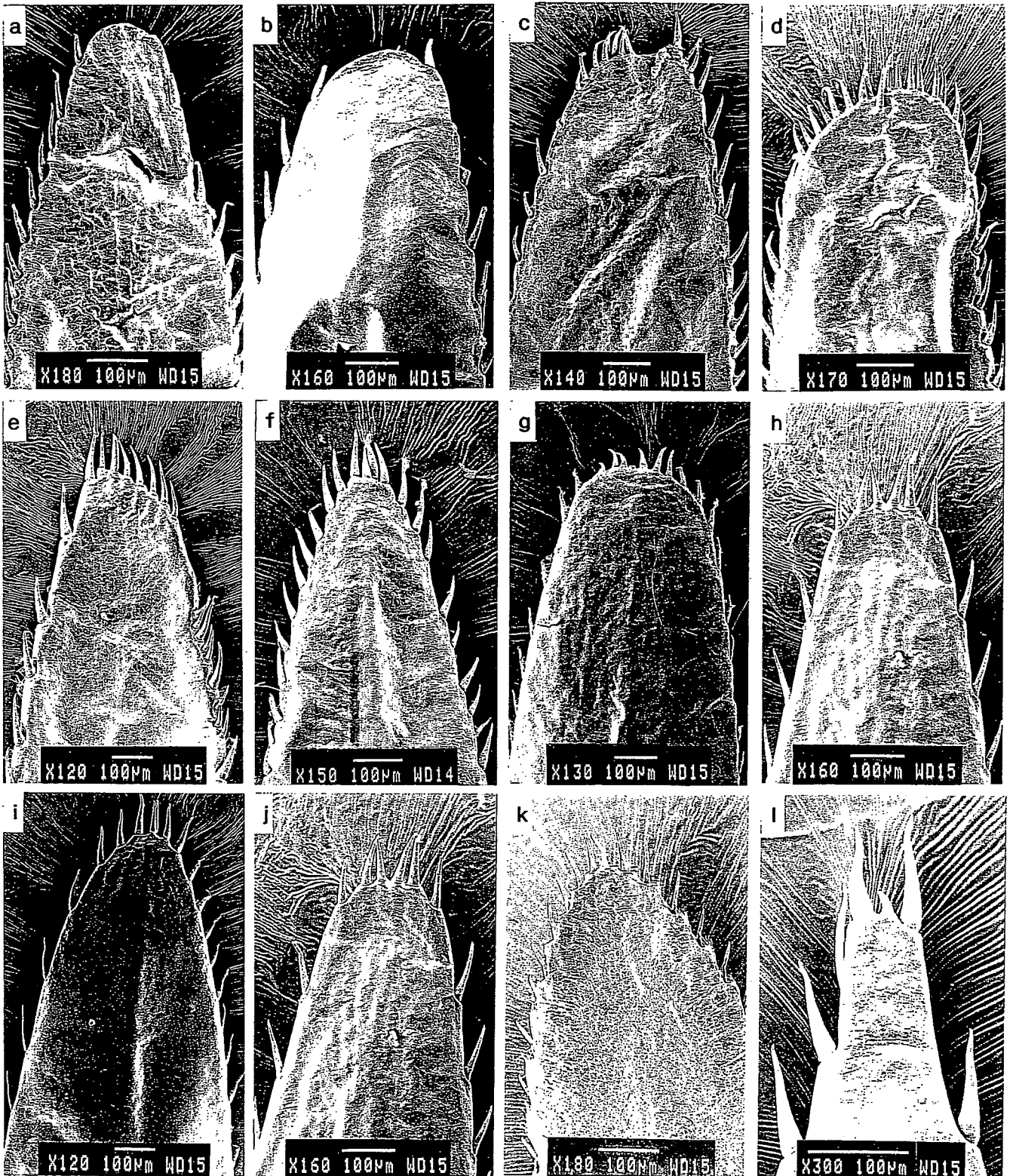




Plate 7.3. Normal (a) and aberrant (b) telson of *Schistomysis kervillei*.

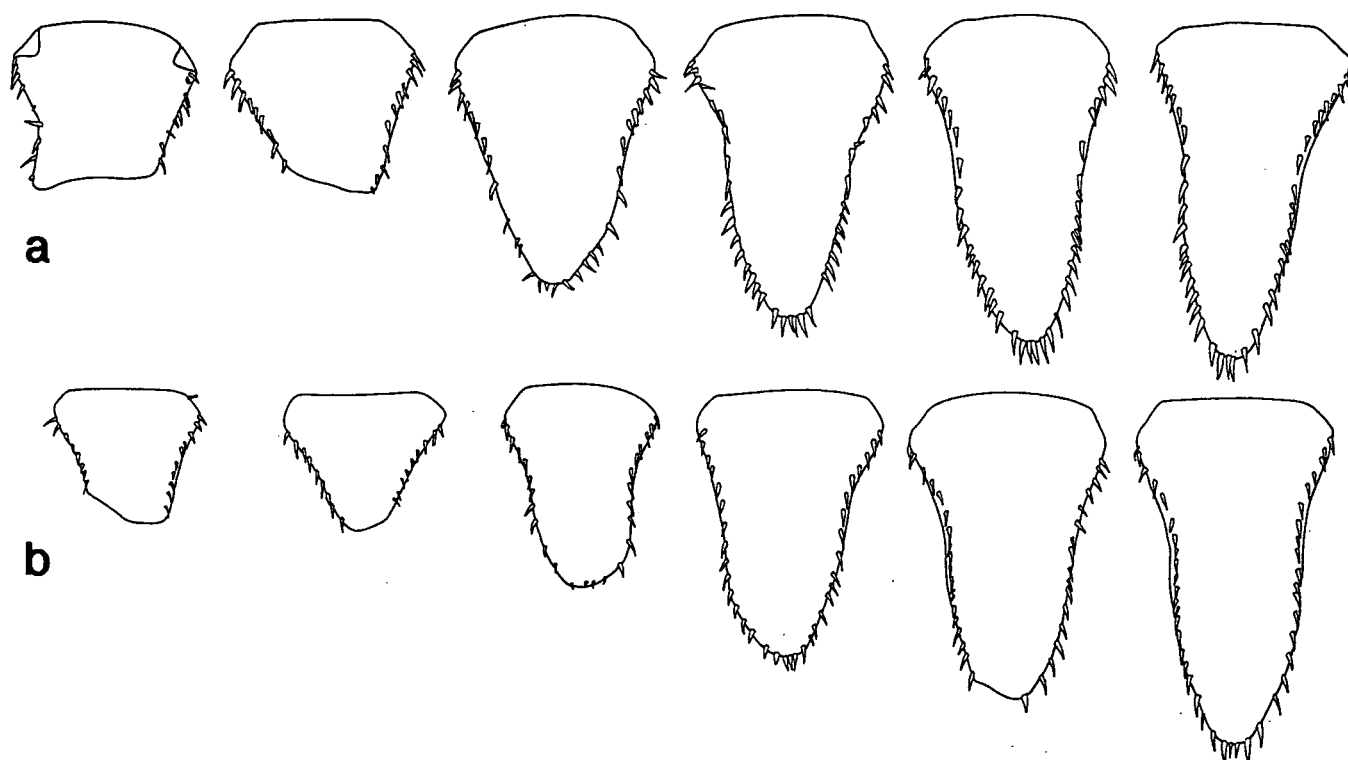
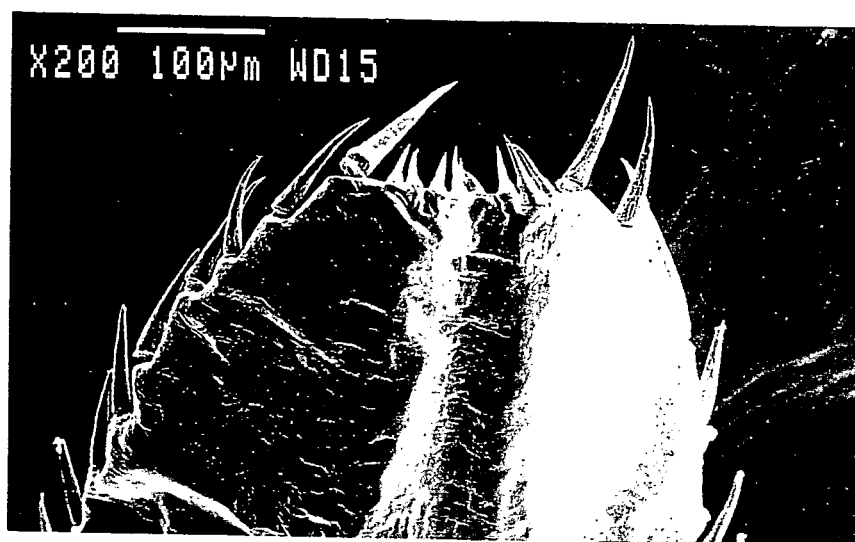
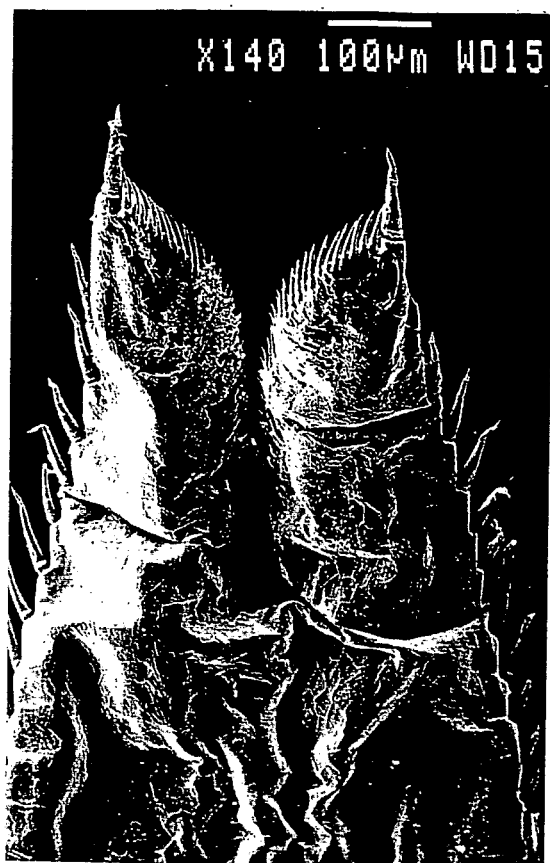


Figure 7.11. Regeneration of the telson of *Neomysis integer*. Schematic drawing of 6 consecutive moults from the experiment (individuals A and B, see table 7.6).

Table 7.6. Results of the culture experiment with 5 *Neomysis integer*: day of moulting for each individual (0 = start of experiment; † = day of death).

mysid	moult						†	total number of moults
	1	2	3	4	5	6		
A	6	12	19	26	33	41	48	6
B	3	7	12	19	26	34	48	6
C	4	15	28	34			39	4
D	1	8	17	26	34		42	4
E	3						7	1

## Discussion

Hough *et al.* (1992) claim that their records of intersexual individuals of *Neomysis integer* in the Conwy estuary are the first occurrences among the Mysidacea. This is not the case. Sexual intermediates (masculinized females) of this species were previously reported by Kinne (1955) and Holmquist (1957), both cited in Mauchlines standard work on Mysidacea (Mauchline 1980, p. 10). Kinne (1955) found three individuals in the Eider-Ring estuary (Germany). Holmquist (1957) found three individuals in Norwegian and Swedish waters. One of the latter seemed to be a feminized male. The present study reports intersexual individuals from 4 more estuarine populations. We conclude that intersexuality is a common phenomenon in *Neomysis* populations, though frequency is always low. As indicated by Hough *et al.* (1992), it is probably a rare genetic abnormality.

Chojnacki & Ciupinski (1986) reported altered telson morphology in *Neomysis* from the Baltic. They found that in some months 1 to 5 % of the adult individuals in the population displayed aberrant telson structure and hypothesised that this was caused (1) by mechanical damage by predators and subsequent regeneration of the damaged part or (2) by mutations resulting from environmental pollution. According to these authors, the former mechanism yields asymmetrical telsons (often oblique) with numerous long spines on the distal part (their group B). Pollution is supposed to lead to a symmetrical telson shape with a smooth or rounded terminal margin and an increased number of spines in the distal part (their group A). Holmquist (1957) and Nouvel (1964) also reported aberrant telson morphology in individuals of a number of mysid species (the latter reference was not checked by the author). Holmquist (1957) mainly discussed *Praunus flexuosus*. In one land-locked locality more than 30 % of the specimens examined had an aberrant rostrum, antennal scale, telson or uropod. Abnormalities were less frequent in *P. inermis*, *P. neglectus*, *Mysis oculata* and *Boreomysis rostrata*. Only 2 *Neomysis integer* with irregularly inserted spines on the lateral margins near the apex were found. Holmquist (1957) suggested an industrial chemical

effluent as the cause of these abnormalities, but she also considered a general source to be genetical and related to the isolation of the populations studied. Nouvel (1964) considered abnormalities to be the result of regeneration after injury (damage inflicted by predators). This hypothesis was supported by personal observations on *Praunus flexuosus* by Mauchline (1980). The present study strongly supports the hypothesis that every type of aberrant telson morphology results from regeneration of parts damaged by predation. Chojnacki & Ciupinski's groups A and B seem to be nothing more than different intermediate moult stages in the regeneration process.

Mysids are heavily preyed upon by fish and caridean shrimp, and they probably also interact with, e.g. epibenthic amphipods. *Neomysis integer* is one of the fastest swimmers among the zooplankton. Its high-speed escape response by tail flipping seems to be very effective: only 25 % of its predator's attacks are successful under laboratory conditions (Rademacher & Kils submitted). The tail flip itself seems to expose the telson to the bite of the predator, making it quite vulnerable for mechanical damage, even when the attack is not effective. Still, a genetic or epigenetic basis can not be ruled out completely. Gentile *et al.* (1982) reported morphological aberrations at the onset of sexual maturity in *Mysidopsis bahia* and *M. bigelowi* exposed to  $10\mu\text{g l}^{-1}$  Cd. But, although the Westerschelde is heavily polluted (Duursma *et al.* 1988, Van Eck *et al.* 1991), incidence of aberrant telsons was not higher there than in the other systems studied.

Aberrant telson morphologies are rare (< 1 % of the population) from May through October. They occur predominantly in large, adult individuals belonging to the overwintering generation. This is possibly correlated with the slower growth in winter. Growth stops when temperature drops below  $10^{\circ}\text{C}$  (Mees *et al.* 1994). This logically results in an accumulation of individuals displaying an aberrant telson because frequency of moulting is lower and the regeneration rate will be slower. In colder months, individuals displaying an aberrant telson thus remain longer detectable in the population. This can also explain why, in April 1993, incidence in the Gironde was lower than in the other estuaries: in Westerschelde and Elbe, animals belonging to the overwintering generation were still present in high numbers, while the Gironde population was almost exclusively composed of individuals belonging to the first (and even second) summer generations (Fockedey, unpublished data). An alternative (partial) explanation may also include a higher predation pressure on mysids in winter. The winter period coincides with the time when the diet of postlarval fish shifts from mainly calanoid copepods to mysids. This shift is partly size-related as by the end of autumn most predators have sufficiently grown to feed on larger hyperbenthic animals. Also, the copepod *Eurytemora affinis* is present in much lower densities at that time, making overwintering mysids the only attractive available prey. Possibly, the colder water temperatures also weaken the escape response of the mysids, making them more susceptible to damage by predation.

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# Appendices

## Appendix 1.

- L-AFDW regressions and assigned values used to calculate biomass (1 page)
- integrated species list with abbreviations (2 pages)

## Appendix 2.

all data from the time series of the Voordelta (chapter 2):

- environmental variables (2 pages)
- density: yearly average (2 pages) and data per month (2 pages per month)
- biomass: yearly average (2 pages) and data per month (2 pages per month)

composition of sample names: month-station-depth

e.g. 08sr05 = August sample of station 'sr' shallow (-5m)

sample names correspond to the numbers used in chapter 2 as follows: sr=1, bh=2, bz=3, oo=4, nb=5, os=6, gb=7, wg=8, nl=9, o2=10, o6=11, rp=12

## Appendix 3.

data from the pilot study in Voordelta, Oosterschelde and Westerschelde in winter 1988 (chapter 3):  
density and environmental variables per subarea (2 pages), biomass per subarea (2 pages).

## Appendix 4.

data from the transects and time series of the Westerschelde (chapter 4):

- density and environmental variables, biomass April 1990 (2 pages)
- density and environmental variables, biomass August 1990 (2 pages)
- density and environmental variables, biomass December 1990 (2 pages)
- density and environmental variables marine part (1 page)
- density and environmental variables brackish part (1 page)

for time series fortnightly samples brackish part see appendix 6

## Appendix 5.

data from the summer campaign in the three estuaries (chapter 6):

- density, biomass, environmental variables Westerschelde (1 page)
- density, biomass, environmental variables Gironde (1 page)
- density, biomass, environmental variables Eems (1 page)

## Appendix 6.

raw data time series targeting *Neomysis integer* (chapter 7):

- density data and env. variables of the hyperbenthic community (first page, top)
- length-frequency data (page 1 bottom, page 2, page 3)

## **Appendix 1, General**

List of the assigned values and the Length-AshFree dry Weight (AFDW) regressions of most hyperbenthic species. All lengths (L), standardlengths (SL), total lengths (TL) and carapax widths (CB) are in millimeter, all weights (AFDW) and assigned values are in milligram AFDW.

**Nematoda:** 0.003

**Annelida**

**Polychaeta - Errantia**

*Anaitides* species (& others): In AFDW =  $-5.882 + 1.674 \ln L$   
*Harmothoe* Larvae: 0.1

**Polychaeta - Sedentaria**

*Capitella* species: In AFDW =  $-6.354 + 2.051 \ln L$   
*Pectinaria koreni*: In AFDW =  $-6.918 + 2.689 \ln L$   
*Lanice conchilega* (& others): In AFDW =  $-6.918 + 2.181 \ln L$   
*Lanice* Aulophora larvae: 0.03

**Oligochaeta:** In AFDW =  $-6.030 + 1.831 \ln L$

**Mollusca**

**Bivalvia** spat: In AFDW =  $-4.052 + 2.817 \ln L$

**Chaetognatha** *Sagitta elegans*: 0.5

**Crustacea**

**Cladocera** *Daphnia* species: 0.1

**Copepoda**

Calanoidea adult: 0.016  
Harpacticoidea small: 0.002

**Cirripedia** larvae: 0.014

**Peracarida**

**Cumacea:** In AFDW =  $-6.078 + 2.525 \ln TL$

**Mysidacea:**

*Gastrosaccus spinifer*: In AFDW =  $-5.896 + 2.876 \ln SL$   
*Schistomysis spiritus*: In AFDW =  $-5.237 + 2.601 \ln SL$   
*Schistomysis kervillei*: In AFDW =  $-5.898 + 2.931 \ln SL$   
*Neomysis integer*: In AFDW =  $-4.103 + 2.294 \ln SL$   
*Mesopodopsis slabberi*: In AFDW =  $-6.107 + 2.867 \ln SL$

Other Mysidacea: In AFDW =  $-6.120 + 2.994 SL$

**Isopoda:** see Amphipoda

**Amphipoda:** In AFDW =  $-5.857 + 2.863 \ln TL$

**Eucarida - Decapoda**

**Caridea**

*Crangon crangon*: In AFDW =  $-7.684 + 3.321 \ln TL$   
Postlarvae: 0.238  
Zoeae: 0.175

**Anomura**

Megalopae: 0.669  
Zoeae: 0.619

**Brachyura**

*Carcinus maenas*: In AFDW =  $-3.967 + 3.164 \ln CB$   
*Carcinus* Megalopae: 0.081  
*Carcinus* Zoeae: 0.050

*Liocarcinus holsatus*: In AFDW =  $-4.489 + 3.247 \ln CB$   
*Liocarcinus* Megalopae: 0.189  
*Liocarcinus* Zoeae: 0.152

Other Brachyura: see *Carcinus*

**Chelicerata - Pycnogonida** *Nymphon rubrum*: 0.1

**Pisces**

Fish eggs: 0.025  
Other Pisces: see *Pomatoschistus*

**Clupeiformes** Larvae: In AFDW =  $-10.2 + 3.816 \ln SL$   
**Syngnathiformes** Larvae: In AFDW =  $-10.42 + 3.139 \ln SL$   
**Perciformes** *Pomatoschistus* species: In AFDW =  $-7.851 + 3.460 \ln SL$

SYSTEMATIC PLACE	SPECIES NAME (& STAGE)	ABBREVIATION	SYSTEMATIC PLACE	SPECIES NAME (& STAGE)	ABBREVIATION
Porifera	<i>Porifera species</i>	Pori Spec	Copepoda (continued)		
Cnidaria	<i>Hydrozoa species</i> <i>Aurelia aurita</i> <i>Anthozoa species</i> <i>Cyanea species</i>	Hydr Spec Aure auri Anth Spec Cyan Spec	Harpacticoida	<i>Euterpina acutifrons</i>	Eute acut
Ctenophora	<i>Pleurobrachia pileus</i>	Pleu pile	Siphonostomatoidea	<i>Caligidae species</i>	Cali Spec
Nematoda	<i>Nematoda species</i>	Nema Spec	Cirripedia	<i>Cirripedia species</i>	Cirr Spec
Annelida			Peracarida		
Polychaeta	<i>Polychaeta species</i> <i>Polychaeta larvae</i> <i>Harmothoe species</i> <i>Harmothoe larvae</i> <i>Anaitides species</i> <i>Eulalia pusilla</i> <i>Autolytus larvae</i> <i>Nereis species</i> <i>Nereis larvae</i>	Poly Spec Poly Larv Harm Spec Harm larv Anai Spec Eula pusi Auto Larv Nere Spec Nere Larv	Cumacea	<i>Iphinoe tenella</i> <i>Bodotria scorpioides</i> <i>Pseudocuma longicornis</i> <i>Pseudocuma similis</i> <i>Lamprops fasciata</i> <i>Diastylis rathkei</i> <i>Diastylis bradyi</i> <i>Diastylis lucifera</i> <i>Diastylis rugosa</i> <i>Diastylis laevis</i>	Iphi tene Bodo scor Pseu long Pseu simi Lamp fasc Dias rath Dias brad Dias luci Dias rugo Dias laev
Errantia			Mysidacea	<i>Siriella armata</i> <i>Gastrosaccus spinifer</i> <i>Gastrosaccus species</i> <i>Schistomysis spiritus</i> <i>Schistomysis kervillei</i> <i>Neomysis integer</i> <i>Mesopodopsis slabberi</i> <i>Acanthomysis longicornis</i> <i>Praunus flexuosus</i>	Siri arma Gast spin Gast Spec Schi spir Schi kerv Neom inte Meso slab Acan long Prau flex
Sedentaria	<i>Ophelia borealis</i> <i>Capitella species</i> <i>Pectinaria species</i> <i>Pectinaria larvae</i> <i>Terrebellida species</i> <i>Lanice conchilega</i> <i>Lanice Aulophora larvae</i>	Ophe bore Capi Spec Pect Spec Pect Larv Terr Spec Lani conc Lani Aulo	Isopoda	<i>Eurydice pulchra</i> <i>Idotea emarginata</i> <i>Idotea linearis</i> <i>Idotea pelagica</i> <i>Idotea baltica</i> <i>Synidotea laevidorsalis</i> <i>Lekanesphaera rugicauda</i> <i>Sphaeroma serratum</i> <i>Cymothoa species</i>	Eury pulc Idot emar Idot line Idot pela Idot balt Syni laev Leka rugi Spha serr Cymo Spec
Oligochaeta	<i>Oligochaeta species</i>	Olig Spec	Amphipoda		
Mollusca			Caprellidea	<i>Phtisica marina</i> <i>Pariambus typicus</i> <i>Caprella species</i> <i>Caprella linearis</i>	Phti mari Pari typi Capr Spec Capr line
Gastropoda	<i>Gastropoda species</i> <i>Patella species</i> <i>Littorina species</i> <i>Hydrobia ulvae</i>	Gast Spec Pate Spec Litt Spec Hydr ulva	Gammaridea	<i>Amphipoda type 1</i> <i>Orchomene nana</i> <i>Ampelisca brevicornis</i> <i>Metopa alderi</i> <i>Metopa pusilla</i> <i>Stenothoe marina</i> <i>Stenothoe valida</i> <i>Gammarus crinicornis</i> <i>Gammarus duebeni</i> <i>Gammarus locusta</i> <i>Gammarus oceanicus</i> <i>Gammarus salinus</i> <i>Gammarus zaddachi</i> <i>Maera grossimana</i> <i>Melita hergensis</i> <i>Melita obtusata</i> <i>Melita palmata</i> <i>Bathyporeia species</i> <i>Bathyporeia elegans</i> <i>Bathyporeia guillamsoniana</i> <i>Bathyporeia sarsi</i> <i>Bathyporeia tenuipes</i> <i>Haustorius arena rius</i> <i>Urothoe brevicornis</i> <i>Urothoe poseidonis</i> <i>Monoculodes carinatus</i>	Amph Typ1 Orch nana Ampe brev Meto alde Meto pusi Sten mari Sten vali Gamm crin Gamm dueb Gamm locu Gamm ocea Gamm sali Gamm zadd Maer gros Meli herg Meli obtu Meli palm Bath Spec Bath eleg Bath guil Bath sars Bath tenu Haus aren Urot brev Urot pose Mono cari
Bivalvia (spat)	<i>Bivalvia species</i> <i>Mytilus edulis</i> <i>Cerastoderma edule</i> <i>Macoma baltica</i> <i>Ensis species</i>	Biva Spec Myti edul Cera edul Maco balt Ensi Spec			
Cephalopoda	<i>Sepiolo species</i> <i>Sepiolo atlantica</i> <i>Loligo vulgaris</i>	Sepi Spec Sepi atla Loli vulg			
Bryozoa	<i>Bryozoa species</i>	Bryo Spec			
Chaetognatha	<i>Sagitta elegans</i>	Sagi eleg			
Echinodermata	<i>Asterias rubens</i> <i>Ophiura species</i> <i>Echinoidea species</i>	Aste rube Ophi Spec Echi Spec			
Crustacea					
Cladocera	<i>Daphnia magna</i> <i>Daphnia species</i>	Daph magn Daph Spec			
Copepoda	<i>Copepoda species</i>	Cope Spec			
Calanoidea	<i>Centropages typicus</i> <i>Centropages hamatus</i> <i>Temora longicornis</i> <i>Calanus helgolandicus</i>	Cent typi Cent hama Temo long Cala helg			

SYSTEMATIC PLACE	SPECIES NAME (& STAGE)	ABBREVIATION	SYSTEMATIC PLACE	SPECIES NAME (& STAGE)	ABBREVIATION
<b>Gammaridea (continued)</b>	<i>Pontocrates altamarinus</i>	Pont alta	<b>Chelicerata</b>		
	<i>Pontocrates arenarius</i>	Pont aren	<b>Arachnida</b>	<i>Aranea species</i>	Aran Spec
	<i>Apherusa ovalipes</i>	Aphe oval			
	<i>Pleusymtes glaber</i>	Pleu glab	<b>Pycnogonida</b>	<i>Nymphon rubrum</i>	Nymp rubr
	<i>Atylus falcatus</i>	Atyl falc		<i>Nymphon gracile</i>	Nymp grac
	<i>Atylus swammerdami</i>	Atyl swam		<i>Phoxochilidium femoratum</i>	Phox femo
	<i>Gammaropsis nitida</i>	Gamm niti		<i>Pycnogonum littorale</i>	Pycn litt
	<i>Corophium arenarium</i>	Coro aren		<i>Callipallene brevirostris</i>	Call brev
	<i>Corophium ascherusicum</i>	Coro asch		<i>Anoplodactylus pygmaeus</i>	Anop pygm
	<i>Corophium lacustre</i>	Coro lacu	<b>Insecta</b>		
	<i>Corophium volutator</i>	Coro volu	<b>Lepidoptera</b>	<i>Lepidoptera species</i>	Lepi Spec
	<i>Ischyrocerus anguipes</i>	Isch angu			
	<i>Jassa falcata</i>	Jass falc	<b>Diptera</b>	<i>Diptera species</i>	Dipt Spec
	<i>Jassa marmorata</i>	Jass marm			
	<i>Jassa pusilla</i>	Jass pusi	<b>Coleoptera</b>	<i>Coleoptera species</i>	Cole Spec
	<i>Parajassa pelagica</i>	Para pela		<i>Coleoptera species larvae</i>	Cole Larv
	<i>Dyopodos porrectus</i>	Dyop porr			
<b>Hyperideia</b>	<i>Hyperia galba</i>	Hype galb	<b>Pisces</b>	<i>Pelagic fish eggs</i>	Fish Eggs
<b>Eucarida</b>			<b>Petromyzontiformes</b>	<i>Lampetra fluviatilis</i>	Lamp fluv
<b>Euphausiacea</b>	<i>Nyctiphanes couchi</i>	Nyct couc	<b>Anguilliformes</b>	<i>Anguilla anguilla glasseels</i>	Angu angu
<b>Decapoda</b>			<b>Clupeiformes</b>	<i>Clupeidae species larvae</i>	Clup Spec
<b>Caridea</b>	<i>Palaemon longirostris</i>	Pala long		<i>Clupea harengus</i>	Clup hare
	<i>Palaemon longirostris postlarvae</i>	Pala lonP		<i>Sprattus sprattus</i>	Spra spra
	<i>Palaemon species zoeae</i>	Pala lonZ	<b>Salmoniformes</b>	<i>Osmerus eperlanus</i>	Osme eper
	<i>Palaemon serratus</i>	Pala serr			
	<i>Palaemonetes varians</i>	Pala vari	<b>Gadiformes</b>	<i>Merlangius merlangus</i>	Merl merl
	<i>Palaemonetes varians postlarvae</i>	Pala varP		<i>Trisopterus luscus</i>	Tris lusc
	<i>Palaemonetes varians zoeae</i>	Pala varZ		<i>Ciliata mustela</i>	Cili must
	<i>Eualus occultus</i>	Eual occu	<b>Atheriniformes</b>	<i>Atherina presbyter</i>	Athe pres
	<i>Hippolyte longirostris</i>	Hipp long	<b>Gasterosteiformes</b>	<i>Gasterosteus aculeatus</i>	Gast acul
	<i>Hippolyte varians</i>	Hipp vari	<b>Syngnathiformes</b>	<i>Syngnathidae species</i>	Syng Spec
	<i>Hippolyte varians postlarvae</i>	Hipp Post	<b>Scorpaeniformes</b>	<i>Myoxocephalus scorpius</i>	Myox scor
	<i>Hippolyte varians zoeae</i>	Hipp Zoea		<i>Agonus cataphractus</i>	Agon cata
	<i>Processa modica</i>	Proc modi		<i>Liparis liparis</i>	Lipa lipa
	<i>Processa modica postlarvae</i>	Proc Post	<b>Perciformes</b>	<i>Dicentrarchus labrax</i>	Dice labr
	<i>Processa modica zoeae</i>	Proc Zoea		<i>Gymnocephalus cernuus</i>	Gymn cern
	<i>Pandalus montagui</i>	Pand mont		<i>Trachurus trachurus</i>	Trac trac
	<i>Crangon allmanni</i>	Cran allm		<i>Liza ramada</i>	Liza rama
	<i>Crangon crangon</i>	Cran cran		<i>Zoarces viviparus</i>	Zoar vivi
	<i>Crangon crangon postlarvae</i>	Cran Post		<i>Pholis gunnellus</i>	Phol gunn
	<i>Crangon crangon zoeae</i>	Cran Zoea		<i>Ammodytes tobianus</i>	Ammo tobi
	<i>Pontophilus trispinosus</i>	Pont tris		<i>Callionymus lyra</i>	Call lyra
	<i>Pontophilus trispinosus postlarvae</i>	Pont Post		<i>Pomatoschistus species larvae</i>	Poma Spec
	<i>Pontophilus trispinosus zoeae</i>	Pont Zoea		<i>Pomatoschistus microps</i>	Poma micr
				<i>Pomatoschistus minutus</i>	Poma minu
				<i>Pomatoschistus lozanoi</i>	Poma loza
<b>Anomura</b>	<i>Galathea species megalopae</i>	Gala Mega	<b>Pleuronectiformes</b>	<i>Scophthalmus rhombus</i>	Scop rhom
	<i>Pagurus bernhardus</i>	Pagu bern		<i>Pleuronectes platessa</i>	Pleu plat
	<i>Pagurus bernhardus megalopae</i>	Pagu Mega		<i>Limanda limanda</i>	Lima lima
	<i>Pagurus bernhardus zoeae</i>	Pagu Zoea		<i>Pleuronectes flesus</i>	Pleu fles
	<i>Porcellana longicornis</i>	Porc long		<i>Solea solea</i>	Sole sole
	<i>Porcellana longicornis megalopae</i>	Porc Mega			
	<i>Porcellana longicornis zoeae</i>	Porc Zoea			
<b>Brachyura</b>	<i>Macropodia species</i>	Macr Spec			
	<i>Macropodia species megalopae</i>	Macr Mega			
	<i>Macropodia species zoeae</i>	Macr Zoea			
	<i>Corystes cassivelaunus megalopae</i>	Cory Mega			
	<i>Portunus latipes</i>	Port lati			
	<i>Portunus latipes megalopae</i>	Port Mega			
	<i>Portunus latipes zoeae</i>	Port Zoea			
	<i>Carcinus maenas</i>	Carc maen			
	<i>Carcinus maenas megalopae</i>	Carc Mega			
	<i>Carcinus maenas zoeae</i>	Carc Zoea			
	<i>Liocarcinus arcuatus</i>	Lioc arcu			
	<i>Liocarcinus pusillus</i>	Lioc pusi			
	<i>Liocarcinus holsatus</i>	Lioc hols			
	<i>Liocarcinus holsatus megalopae</i>	Lioc Mega			
	<i>Liocarcinus holsatus zoeae</i>	Lioc Zoea			
	<i>Liocarcinus species zoeae 2</i>	Lioc Zoe2			
	<i>Liocarcinus species zoeae 3</i>	Lioc Zoe3			
	<i>Liocarcinus species zoeae 4</i>	Lioc Zoe4			
	<i>Rhithropanopeus harrisi</i>	Rhit harr			
	<i>Pinnotheres pisum</i>	Pinn pisu			
	<i>Eriocheir sinensis megalopae</i>	Erio Mega			
	<i>Zoeae Westerschelde type 1</i>	Wty1 Zoea			
	<i>Zoeae Gironde type 1</i>	Gty1 Zoea			
	<i>Zoeae Gironde type 2</i>	Gty2 Zoea			

## **Appendix 2, Voordelta**





**VOORDELTA, ENVIRONMENTAL VARIABLES**

<b>SALINITY (psu)</b>	<b>sr10</b>	<b>bh10</b>	<b>bz10</b>	<b>oo10</b>	<b>nb10</b>	<b>gb10</b>	<b>os10</b>	<b>wg10</b>	<b>nl10</b>	<b>o210</b>	<b>o610</b>	<b>rp10</b>
August 1988		31.3	31.5	31.6	32.3	32.3	32.2		31.2	31.9	31.4	31.1
September 1988	29.4	29.6	30.7	31.3		31.6		31.2	31.0	31.0	31.2	31.3
November 1988	30.4	30.4	30.4	31.3	32.6	32.3	31.2	32.1	32.2	32.2	32.2	32.4
December 1988	31.2	31.5	32.4	31.6	32.9	32.7	32.7	32.3	32.1	31.8	31.9	32.0
January 1989	31.6	31.6	31.6	31.6								31.4
February 1989	31.7	31.7	32.1	31.9			32.2		32.0	32.0	31.9	31.5
March 1989		32.1	32.2	32.4	33.0	32.9	32.8					
April 1989	32.6	32.5	32.6			33.1		32.8	32.7	32.6		
May 1989		29.0	28.6	29.6	31.0	31.5	31.3	31.2	30.8	31.1	30.6	30.8
June 1989	29.9	29.9	30.2		31.6	31.7		31.7		31.7	31.0	30.9
July 1989	31.0	31.0	31.6	31.5	32.1				32.1	32.2	31.9	31.6
<b>TEMPERATURE (°C)</b>	<b>sr10</b>	<b>bh10</b>	<b>bz10</b>	<b>oo10</b>	<b>nb10</b>	<b>gb10</b>	<b>os10</b>	<b>wg10</b>	<b>nl10</b>	<b>o210</b>	<b>o610</b>	<b>rp10</b>
August 1988		18.4	18.3	18.3	17.9	18.1	18.0		18.8	18.6	18.7	18.9
September 1988	16.7	16.6	16.7	16.7		16.7		16.2	16.2	16.2	16.1	16.1
November 1988	10.4	10.3	10.5	10.8	11.2	11.1	10.5	10.7	10.7	10.5	10.5	10.6
December 1988	8.0	8.2	8.5	8.5	9.3	9.1	9.1	8.9	8.8	8.8	8.8	8.8
January 1989	7.1	7.2	7.2	7.2								7.0
February 1989	6.1	6.0	6.1	6.1			6.3		5.9	5.9	5.7	5.7
March 1989		7.2	7.3	7.3	7.5	7.5	7.4					
April 1989	6.4	6.5	6.4			6.3		6.3	6.3	6.3		
May 1989		10.7	11.0	10.6	10.7	10.8	10.7	11.0	11.2	11.1	11.5	11.5
June 1989	13.5	13.5	13.6		14.5	14.5		14.5		14.5	14.7	14.7
July 1989	17.9	18.2	17.5	17.0	16.8				16.9	16.7	17.2	17.8
<b>pH</b>	<b>sr10</b>	<b>bh10</b>	<b>bz10</b>	<b>oo10</b>	<b>nb10</b>	<b>gb10</b>	<b>os10</b>	<b>wg10</b>	<b>nl10</b>	<b>o210</b>	<b>o610</b>	<b>rp10</b>
August 1988		8.4	8.4	8.3	8.3	8.3	8.3		8.3	8.3	8.3	8.3
September 1988	8.0	8.0	8.0	8.1		8.0		8.0	8.0	8.0	8.0	8.0
November 1988	8.1	8.1	8.1	8.1	8.1	8.1	8.1	8.1	8.1	8.1	8.1	8.1
December 1988	8.1	8.1	8.1	8.1	8.1	8.1	8.1	8.1	8.1	8.0	8.0	8.0
January 1989	8.1	8.1	8.1	8.1								8.1
February 1989	8.0	8.1	8.0	8.0			8.0		8.2	8.2	8.2	8.1
March 1989		8.2	8.2	8.1	8.2	8.2	8.2					
April 1989	8.4	8.4	8.4			8.4		8.3	8.3	8.3		
May 1989		8.3	8.3	8.3	8.3	8.3	8.3	8.3	8.4	8.3	8.4	8.3
June 1989	8.3	8.3	8.3		8.3	8.3		8.3	8.3	8.3	8.2	8.2
July 1989	8.4	8.4	8.4	8.4	8.4				8.4	8.4	8.4	8.4
<b>OXYGEN (mg/l)</b>	<b>sr10</b>	<b>bh10</b>	<b>bz10</b>	<b>oo10</b>	<b>nb10</b>	<b>gb10</b>	<b>os10</b>	<b>wg10</b>	<b>nl10</b>	<b>o210</b>	<b>o610</b>	<b>rp10</b>
August 1988		11.0	11.8	10.8	11.6	11.5	11.7		9.6	9.4	9.3	10.0
September 1988	8.8	8.8	8.9	9.0		9.3		9.2	9.1	9.4	9.0	9.0
November 1988	10.0	10.1	9.8	9.8	9.6	9.6	10.0	9.7	9.5	9.7	9.8	9.5
December 1988	10.0	9.8	9.8	10.0	9.8	10.3	9.9	10.4	10.4	10.3	10.5	10.3
January 1989	10.8	10.9	10.9	11.0								10.8
February 1989	10.9	10.7	10.8	10.8			10.8		10.8	10.8	10.9	10.8
March 1989		9.8	9.7	9.7	9.8	9.9	9.9					
April 1989	12.3	12.5	11.9			11.4		11.0	11.0	10.9		
May 1989		9.1	9.6	9.2	9.6	9.6	9.6	9.7	9.9	9.7	10.0	9.3
June 1989	9.9	10.6	10.4		9.2	9.0		8.7		9.0	7.8	8.1
July 1989	12.5	13.1	12.2	12.7	11.6				11.6	11.3	10.9	10.0
<b>SECCHI (cm)</b>	<b>sr10</b>	<b>bh10</b>	<b>bz10</b>	<b>oo10</b>	<b>nb10</b>	<b>gb10</b>	<b>os10</b>	<b>wg10</b>	<b>nl10</b>	<b>o210</b>	<b>o610</b>	<b>rp10</b>
August 1988		200.0	250.0	250.0	400.0	300.0	400.0		225.0	225.0	200.0	250.0
September 1988	90.0	90.0	110.0	300.0		175.0		110.0	150.0	150.0	140.0	
November 1988	40.0	60.0	45.0	150.0			30.0	140.0	140.0	120.0	110.0	110.0
December 1988	110.0	90.0	100.0	90.0	140.0	140.0	140.0	110.0	90.0	90.0	80.0	110.0
January 1989	100.0	100.0	60.0	100.0								
February 1989	60.0			100.0			130.0		90.0	90.0	90.0	150.0
March 1989		45.0	50.0	50.0	125.0	100.0	100.0					
April 1989	110.0	125.0				80.0		80.0	80.0	80.0		
May 1989		160.0			250.0	250.0	275.0	140.0	125.0	175.0	125.0	175.0
June 1989	400.0					550.0		550.0		450.0	400.0	400.0
July 1989	150.0	250.0	250.0		250.0				250.0	300.0		170.0

































VOORDELTA, DENSITY MARCH 1988 per 1000 m<sup>2</sup>  
 maas89 A

	03bh10	03bh05	03bz10	03bz05	03oo10	03oo05	03mb10	03mb05	03oo10	03oo05	03pb10	03pb05
Lari Amno	0	1	0	0	0	0	0	13	5	14	1	4
Harm Larv	0	0	0	0	0	0	0	2	0	0	0	0
Pect Larv	0	0	0	0	0	0	0	0	0	0	0	0
Callibrev	0	0	0	0	0	0	0	0	0	0	0	0
Plicn litt	0	0	0	0	0	0	0	0	0	1	0	0
Anop pygfm	0	0	0	0	0	0	0	0	0	0	0	0
Phox femo	0	0	0	0	0	0	0	0	0	0	0	0
Nymp rubr	0	0	0	0	0	0	0	1	0	0	0	0
Cran Post	67	11	35	34	82	38	0	1	2	0	1	0
Cran Zoel	42	11	21	112	0	40	0	22	15	23	13	30
Pont Post	0	0	0	0	0	0	0	0	0	0	0	0
Pont Zoel	0	0	0	0	0	0	0	0	0	0	0	0
Hipp Post	0	0	0	5	0	1	0	0	0	0	0	0
Hipp Zoel	0	0	0	0	0	0	6	0	0	0	0	0
Pala Post	0	0	0	0	0	2	0	0	0	0	0	0
Pala Zoel	0	0	0	0	0	0	0	0	0	0	0	0
Proc Post	0	0	0	0	0	0	0	0	0	0	0	0
Proc Zoel	0	0	0	0	0	0	0	0	0	0	0	0
Pegu Mega	0	0	1	1	0	0	15	1	0	2	0	4
Pagu Zoel	0	0	7	8	0	8	330	521	488	426	182	264
Porc Mega	0	0	0	0	0	0	0	0	0	0	0	0
Porc Zoel	0	0	0	0	0	0	0	0	0	2	0	1
Macr Mega	0	0	0	0	0	0	0	0	0	0	0	0
Macr Zoel	0	0	0	0	0	0	0	0	0	0	0	0
Port Mega	0	0	0	0	0	0	0	0	0	0	0	0
Carc Mega	0	0	0	1	0	0	0	0	0	0	0	0
Carc Zoel	0	0	0	0	0	0	0	0	0	0	0	0
Lloc Mega	0	0	0	0	0	0	3	0	0	0	0	0
Lloc Zoel	2	0	0	1	0	0	15	1	8	6	0	2
Lloc RZoe	0	0	0	0	0	0	0	0	0	0	0	0
Cory Mega	0	0	0	0	0	0	0	0	0	0	0	0
Part typ1	0	0	0	0	0	0	0	0	0	0	0	0
Phd mari	0	0	0	0	0	0	0	0	0	0	0	0
Capr line	0	1	0	0	0	0	0	0	0	0	0	0
Capr line	12	5	17	65	34	60	0	2	1	0	0	3
Gamm crin	0	0	0	0	0	0	0	0	0	0	0	0
Gamm eall	0	0	0	0	0	0	0	0	0	0	0	0
Gamm locu	0	0	0	7	0	2	0	0	1	0	0	0
Gamm ocea	0	0	0	0	0	0	0	0	0	0	0	0
Gamm nhl	0	0	0	0	0	0	0	0	0	0	0	0
Alyl swam	2	1	5	82	17	38	27	14	5	10	16	35
Alyl falc	0	0	0	0	0	0	0	0	0	0	0	0
Aphe oval	0	0	0	0	0	0	0	0	0	0	0	0
Para puss	0	0	0	0	0	0	0	0	0	0	0	0
Jass pusi	0	0	0	0	0	0	0	0	0	0	0	0
Jass falc	0	0	0	0	1	0	0	0	0	0	0	0
Jass marm	0	0	0	0	0	2	0	0	1	0	0	0
Bath eleg	0	0	0	1	2	0	0	1	0	0	0	0
Bath ears	0	0	0	0	0	0	0	0	0	0	0	0
Bath tenu	0	0	0	0	0	0	0	0	0	0	0	0
Haus aren	0	0	0	0	0	1	0	0	0	0	0	0
Orch nana	2	0	0	1	0	1	3	1	0	0	0	0
Meli palm	0	1	0	0	0	0	0	0	0	0	0	0
Meli obtu	0	0	1	2	0	1	0	0	0	0	0	0
Meli herg	0	0	0	0	1	1	0	0	0	0	0	0
Sten mari	0	0	0	0	0	0	0	0	0	0	0	0
Sten vali	0	0	0	0	0	0	0	0	0	0	0	0
Meto puss	0	0	0	0	0	0	0	0	0	0	0	0
Meto alde	0	0	0	0	0	0	0	0	0	0	0	0
Maer gros	0	0	0	0	0	0	0	0	0	0	0	0
Mono carl	0	0	0	0	0	0	0	0	0	0	0	0





















VOORDELITA, AVERAGE BIOMASS, mg AFDW per 1000 m<sup>2</sup>  
all A

	Aar10	Aar05	Abh10	Abh05	Abz10	Abz05	Aoo10	Aoo05	Anb10	Anb05	Aos10	Aos05	Agb10	Agb05	Awg10	Awg05	Anl10	Anl05	Ar210	Ar205	Ar610	Ar605	Arp10	Arp05
Lani Aulo	5.0	2.8	20.1	4.1	8.8	6.3	10.8	11.3	3.7	8.9	13.5	17.8	7.8	4.7	3.7	2.0	6.4	2.5	2.5	2.3	1.1	1.9	3.1	3.8
Harm Larv	0.3	0.0	0.1	0.0	0.8	0.1	0.3	0.1	0.2	0.0	0.0	0.0	0.0	0.2	0.2	0.1	0.2	0.5	1.0	0.3	0.2	0.7	0.1	0.0
Pect Larv	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calli brev	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Picn litt	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anop Pygm	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phox femo	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nymp rubr	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cran Post	6.3	1.0	5.5	1.8	8.7	2.8	5.1	5.1	2.8	0.3	8.8	5.1	1.8	1.5	3.2	1.8	0.8	2.0	2.5	1.8	3.1	3.1	1.8	0.8
Cran Zoel	18.6	8.4	29.1	11.3	15.1	8.8	12.6	13.1	9.2	3.1	17.2	8.8	23.7	5.9	10.8	6.7	3.1	6.2	4.1	3.7	3.5	3.2	4.9	3.2
Pont Post	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pont Zoel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hipp Post	0.7	0.0	0.1	0.0	0.3	0.3	0.0	0.1	0.1	0.0	0.1	0.0	0.0	0.3	0.1	0.1	0.0	0.1	0.1	0.3	0.0	0.1	0.4	0.0
Hipp Zoel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pala Post	0.2	0.1	0.1	0.1	0.0	0.0	0.1	0.0	0.2	0.5	0.5	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Pala Zoel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Proc Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Proc Zoel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pagu Mega	51.7	15.8	41.8	13.6	10.8	11.5	19.9	20.0	14.8	5.0	13.2	15.7	4.9	8.5	2.0	3.6	6.7	8.8	7.0	11.0	14.5	7.4	11.9	4.3
Pagu Zoel	44.5	6.1	9.1	3.5	4.8	12.4	28.8	9.3	39.9	56.6	50.5	53.7	21.0	72.8	21.3	27.7	27.2	30.2	21.4	24.0	14.0	31.3	5.3	6.0
Porc Mega	0.4	0.2	0.3	0.6	0.1	0.7	0.2	1.0	0.1	0.3	0.3	0.0	0.6	1.1	1.8	0.8	0.4	0.7	0.7	0.4	0.1	0.3	0.2	0.2
Porc Zoel	0.0	0.0	0.0	0.0	0.3	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.2	0.1	0.0	0.1	0.1
Macr Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macr Zoel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Port Mega	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Port Zoel	39.8	11.3	13.0	4.8	28.0	14.1	19.9	9.4	10.8	8.1	5.3	9.9	16.4	8.4	47.4	33.4	19.8	25.8	14.6	18.0	17.3	27.5	16.0	20.5
Carc Mega	4.1	2.7	3.1	3.7	1.1	1.7	3.4	7.2	0.7	0.7	0.8	2.9	1.3	0.6	2.2	1.9	5.0	2.5	2.0	2.7	2.1	2.8	2.4	1.1
Carc Zoel	19.0	8.3	18.2	6.7	70.4	23.8	30.4	39.5	4.5	2.5	27.6	41.3	5.5	17.7	152.6	38.2	3.3	2.9	3.9	6.5	6.9	3.2	13.1	6.5
Loc Mega	7.4	4.9	8.0	12.8	4.7	8.0	9.1	28.6	16.5	18.4	18.9	28.4	38.9	19.3	87.6	74.4	31.2	6.3	21.5	13.8	8.1	4.7	5.3	2.5
Loc Zoel	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.2	0.0	0.0
Loc RZoe	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cory Mega	0.1	0.0	0.1	0.1	0.1	0.0	0.2	0.0	0.2	0.2	0.0	0.0	0.5	0.2	0.1	0.0	0.1	0.0	0.1	0.2	0.0	0.1	0.0	0.0
Cory Zoel	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Part typ1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Part mar1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Capr line	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm crfn	3.1	12.4	23.9	10.1	22.6	53.8	15.8	26.7	0.1	3.0	1.5	2.4	12.6	7.9	48.1	3.3	15.1	32.0	62.8	37.4	13.6	13.4	3.3	8.5
Gamm sal1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Gamm locu	0.0	0.0	1.8	1.6	0.0	0.0	0.0	3.5	0.0	0.8	3.4	0.0	13.2	0.0	2.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm ocea	0.0	0.1	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm nit1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ayl1 awam	19.3	3.1	5.1	3.4	40.3	15.9	11.6	8.5	23.2	24.8	37.0	40.5	31.5	7.5	7.0	4.9	4.0	5.7	3.1	5.7	3.3	2.4	1.7	2.0
Ayl1 falc	2.8	0.8	0.4	0.0	1.8	0.1	0.4	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.8	0.2	0.7	0.6	0.0	0.3	0.0	0.0
Aphe oval	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Para pela	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jass pusi	0.5	0.0	0.3	0.0	0.2	0.1	0.0	0.1	0.1	0.0	0.1	0.0	0.3	0.1	0.3	0.8	0.9	0.5	0.2	0.8	0.7	0.9	0.1	0.2
Jass mar1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bath eleg	3.1	0.1	0.2	0.2	1.3	0.1	0.2	0.1	0.0	0.2	0.1	0.0	0.2	0.4	0.4	0.0	0.1	0.0	0.2	0.0	0.1	0.2	0.2	0.0
Bath sars	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bath tenu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Haus aren	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orch nana	0.1	0.0	0.2	0.0	0.1	0.1	0.1	0.1	0.0	0.0	0.1	0.2	0.1	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Mell pal1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mell obtu	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Mell herg	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sten mar1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sten vall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meto pusa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meto alce	0.0	0.0	0																					













































VOORDELTA, BIOMASS JUNE 1989, mg AFDW per 1000 m<sup>2</sup> (Continued)

Jun89 B	08sr10	08sr05	08bh10	08bh05	08bz10	08bz05	08oo10	08oo05	08nb10	08nb05	08os10	08os05	08gb10	08gb05	08wg10	08wg05	08n110	08n105	08r210	08r205	08r810	08r805	08rp10	08rp05
Pont aren	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Pont alta	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Ampe brev	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dyop porr	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Uret brev	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Uret pose	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hype gas'b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eul pulc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Idot emar	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Idot bait	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Idot line	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cent typ1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cent hama	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Temo long	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eute acut	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calu helg	0.1	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calli Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseu long	0.0	0.0	0.1	0.0	0.2	0.0	0.9	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseu alim1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lamp fasc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bodo scor	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias brad	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias rigo	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias rath	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias luc1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias luc2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nict couc	0.0	0.0	0.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gas. spin	3.0	1.9	18.6	7.2	1850.5	34.3	0.0	12.4	0.0	0.0	408.9	19.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	23.5	36.0
Gas. sanc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gas. scic	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mies> slab	0.9	0.0	0.2	5.9	2687.9	30.9	7.9	0.0	0.0	0.0	31.0	6.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	12.0	26.2
Schl spir	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	66.0
Schl kern	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prau flex	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sifi arma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagl elog	48.5	4.0	3.5	0.5	111.0	6.0	6.5	1.5	7.5	7.5	0.0	1.5	23.5	1.5	0.0	0.0	3.0	1.5	24.0	3.0	1.5	1.5	18.5	3.0
Plac Eggs	0.4	0.2	0.0	0.0	0.2	0.3	0.1	0.0	0.2	0.2	0.4	0.5	0.1	0.0	0.0	0.3	0.1	0.1	0.1	0.0	0.0	0.0	0.4	0.0
Poma minu	61.5	15.7	30.5	12.4	230.4	22.2	26.2	63.2	28.6	66.9	48.2	121.2	10.0	55.4	0.0	34.6	8.6	22.2	58.6	17.2	14.2	15.6	93.3	52.4
Poma loza	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lpsa lipa	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clup spec	554.1	212.2	336.1	290.3	1345.6	406.6	907.3	164.4	10.1	25.8	625.8	97.7	14.3	15.1	22.8	36.5	291.8	66.1	173.7	89.2	68.1	103.3	143.2	60.3
Syng Spec	0.0	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amno tobi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sole sole	11.4	1.8	8.2	13.2	118.9	54.3	56.0	15.7	1.0	1.7	37.2	7.3	0.5	0.6	1.6	3.5	0.3	0.2	0.7	0.4	0.0	0.0	3.1	3.2
Trac trac	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meri meri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calli lya	5.0	1.0	3.2	1.0	4.3	5.4	12.3	4.0	0.6	1.3	6.8	3.6	1.4	0.5	0.8	1.3	0.4	0.6	0.2	0.2	0.7	1.9	0.0	0.7
Scop rhom	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pleu plat	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gas. acul	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lima lima	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trac vips	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cill must	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aphi minu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phol gune	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Angu angu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Myox scor	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tris luc	0.7	1.2	1.2	0.0	8.9	2.5	4.8	1.5	0.0	2.3	0.0	3.3	3.2	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	3.1	







## **Appendix 3, Winter**

WINTER HYPERBENTHOS, DENSITY per 1000 m<sup>2</sup> (DECEMBER 1988)

VOORDELTA	v1d	v1s	v2d	v2s	v3d	v3s	v4d	v4s	v5d	v5s	v6d	v6s	v7d	v7s	v8d	v8s	v9d	v9s	v10d	v10s	v11d	v11s	v12d	v12s
Cran Post	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0	0	0	2	0	14	12	0	0
Cran Zoeta	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eual occu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hipp Post	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Porc Mega	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Carc Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carc Zoeta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lloc Mega	0	0	0	0	0	0	0	0	2	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0
Lloc Zoeta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macr Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capr line	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parl typ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pht marl	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pht marl	1	0	0	0	0	0	1	0	1	5	2	4	13	3	0	0	0	0	0	0	4	4	1	1
Ayl swam	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coro volu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gamm Spec	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jass falc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mell palm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mell obtu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mono carl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Port alta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orch nana	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eury pulc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Idet line	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	4	0	1
Cala helg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Call Spec	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bodo scor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dias brad	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dias luc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dias rath	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gast spin	1	0	0	0	3	0	0	0	345	1	7	52	2	0	0	0	0	0	17	0	0	0	0	0
Meso slab	14	18	11	1	16	0	28	2	88	12	18	17	38	40	5	11	3	0	2	4	5	12	21	1
Neom lnte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prau flex	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siri arma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schl spir	1130	188	15	3	69	8	9	5	385	19	112	58	89	30	13	12	1	9	80	5	30	188	17	2
Schl kew	5	0	1	0	0	0	0	0	5	0	4	0	0	0	5	0	0	0	263	0	10	20	315	5
Nymp rubr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagl eleg	2	0	0	0	5	0	1	0	1	12	20	12	6	2	1	0	1	1	1	0	0	4	0	0

WINTER HYPERBENTHOS, ENVIRONMENTAL VARIABLES (DECEMBER 1988)

VOORDELTA	v1d	v1s	v2d	v2s	v3d	v3s	v4d	v4s	v5d	v5s	v6d	v6s	v7d	v7s	v8d	v8s	v9d	v9s	v10d	v10s	v11d	v11s	v12d	v12s
Salinity (psu)		31.2		31.5		32.4		31.8		32.9		32.7		32.7		32.3		32.0		31.8		31.9		32.0
Oxygen (mg/l)		103		103		103		106		104		103		108		111		110		108		111		110
pH		8.1		8.1		8.1		8.1		8.1		8.1		8.1		8.1		8.0		8.0		8.0		8.0
Temperature (°C)		8.0		8.2		8.5		8.5		9.3		9.1		9.1		8.8		8.8		8.8		8.8		8.8
Secchi (cm)		110		90		100		90		140		140		140		110		90		90		80		110
Median grain size (µm)	300	125	250	180	180	160	200	230	245	200	240	240	260	240	340	270	200	290	340	290	240	230	400	220
Mud content (%)	5.0	20.0	1.0	4.0	1.0	4.0	1.0	0.0	1.0	3.0	1.0	1.0	1.0	3.0	1.0	2.0	1.0	10.0	1.0	10.0	1.0	1.0	1.0	1.0

WINTER HYPERBENTHOS, DENSITY per 1000 m<sup>2</sup> (DECEMBER 1988)

WESTERSCHELDE	w1	w2	w3	w4	w5	w6	w7	w8	w9	w10	w11	w12	w13	o1	o2	o3	o4
Cran Post	14	161	104	236	26	29	156	83	41	69	188	209	296	0	0	0	1
Cran Zoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eual occu	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hipp Post	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porc Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carc Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carc Zoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lic Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lic Zoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macr Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capr line	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Par typ1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phi marl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phi swam	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ayl swam	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coro volu	0	0	0	0	1	0	0	2	0	0	0	4	0	0	0	0	0
Gamm Spec	3	68	15	469	14	7	11	14	7	9	12	80	0	0	0	0	0
Jass falc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meil palm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meil obtu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mono carl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pont alia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orch nana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eury pulc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Idot line	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cala helg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Call Spec	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bodo scor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dias brad	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dias luci	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Dias rath	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dias slab	0	0	0	11	0	0	0	0	0	0	0	4	0	0	0	0	1
Gast spin	0	7	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meso slab	887	209	1736	268	764	205	103	119	35	38	6	0	0	1	8	6	8
Neom inte	0	1	0	109	9	127	481	589	1063	1520	1122	10859	11992	0	0	0	0
Prau flex	0	1	12	15	0	0	2	6	1	2	0	4	0	0	0	0	5
Siri arma	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Schl spir	0	17	23	7	2	0	13	4	0	0	0	0	0	0	0	0	3
Schl kern	16	815	148	693	14	7	28	52	6	3	0	0	0	0	0	0	1
Nymp rubr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagi eleg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

WINTER HYPERBENTHOS, DENSITY per 1000 m<sup>2</sup> (DECEMBER 1988)

OOSTERSCHELDE	o1	o2	o3	o4
Cran Post	0	0	0	1
Cran Zoa	0	0	0	0
Eual occu	0	0	0	0
Hipp Post	0	0	0	0
Porc Mega	0	0	0	0
Carc Mega	0	0	0	0
Carc Zoa	0	0	0	0
Lic Mega	0	0	0	0
Lic Zoa	0	0	0	0
Macr Mega	0	0	0	0
Capr line	0	0	0	0
Par typ1	0	0	0	0
Phi marl	0	0	0	0
Phi swam	0	0	0	0
Ayl swam	0	0	0	0
Coro volu	0	0	0	0
Gamm Spec	0	0	0	0
Jass falc	0	0	0	0
Meil palm	0	0	0	0
Meil obtu	0	0	0	0
Mono carl	0	0	0	0
Pont alia	0	0	0	0
Orch nana	0	0	0	0
Eury pulc	0	0	0	0
Idot line	0	0	0	0
Cala helg	0	0	0	0
Call Spec	0	0	0	0
Bodo scor	0	0	0	0
Dias brad	0	0	0	0
Dias luci	0	0	0	0
Dias rath	0	0	0	0
Dias slab	0	0	0	0
Gast spin	0	0	0	0
Meso slab	0	0	0	0
Neom inte	0	0	0	0
Prau flex	0	0	0	0
Siri arma	0	0	0	0
Schl spir	0	0	0	0
Schl kern	0	0	0	0
Nymp rubr	0	0	0	0
Sagi eleg	0	0	0	0

WINTER HYPERBENTHOS, ENVIRONMENTAL VARIABLES (DECEMBER 1988)

WESTERSCHELDE	w1	w2	w3	w4	w5	w6	w7	w8	w9	w10	w11	w12	w13
Salinity (psu)	27.4	26.0	25.3	24.5	22.6	21.4	18.5	18.6	16.2	12.5			
Oxygen (mg/l)	96	89	83	97	98	85	80	80	87	73			
pH	7.9	7.1	7.9	7.9	7.8	7.8	7.8	7.7	7.7	7.6			
Temperature (°C)	7.5	7.5	7.5	7.4	7.3	7.3	7.3	7.4	7.4	7.5			
Secchi (cm)	90	70	45	60	50	45	45	45	45	40			
Median grain size (µm)	303	357	209	186	234	283	195	244	127	208			
Mud content (%)	0.8	1.5	0.3	2.2	0.0	2.0	2.6	1.1	0.0	1.3			

WINTER HYPERBENTHOS, ENVIRONMENTAL VARIABLES (DECEMBER 1988)

OOSTERSCHELDE	o1	o2	o3	o4
Salinity (psu)	30.6	30.7	30.8	30.8
Oxygen (mg/l)	108	108	109	109
pH	8.0	8.0	8.0	8.0
Temperature (°C)	7.0	7.2	7.3	7.4
Secchi (cm)	250	250	150	160
Median grain size (µm)	155	189	255	275
Mud content (%)	0.6	8.5	0.4	7.4

WINTER HYPERBENTHOS, BIOMASS mg AFDW per 1000 m<sup>2</sup> (DECEMBER 1988)

VOORDELTA	v1d	v1s	v2d	v2s	v3d	v3s	v4d	v4s	v5d	v5s	v6d	v6s	v7d	v7s	v8d	v8s	v8d	v8s	v9d	v9s	v10d	v10s	v11d	v11s	v12d	v12s
Cran Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.2	0.2	0.2	0.2	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.5	0.0	3.3	2.9	0.0	0.0
Cran Zoec	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eual occu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hipp Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Porc Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carc Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carc Zoec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lloc Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lloc Zoec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Miscr Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Capr line	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parl typ	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phit marl	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phit marl	0.5	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Alyl swam	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coro volu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jass falc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mell palm	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mell obtu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Mono carl	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pontalta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orch nana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eury pulc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Idot line	1.1	0.9	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eute acut	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calli Spec	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bode scor	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias brad	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias luci	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias rath	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gast spin	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meso slab	28.5	24.7	12.8	0.9	15.0	0.0	25.0	2.2	80.8	10.0	17.6	17.9	52.4	48.5	4.8	7.8	4.8	4.8	1.4	0.0	2.8	2.7	5.3	6.1	16.3	0.9
Neom inte	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prau flex	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Schl arma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Schl spir	8318.2	4077.7	27.5	3.8	188.0	7.5	9.1	8.9	452.1	21.7	163.8	65.5	152.0	37.8	16.1	14.2	0.7	15.8	0.0	0.0	128.8	5.4	48.7	127.8	28.3	4.0
Schl kern	13.2	0.0	1.5	0.0	0.0	0.0	0.0	0.0	8.2	0.0	8.1	0.0	0.0	0.0	11.9	0.0	0.0	0.0	0.0	0.0	733.8	0.0	18.0	12.8	792.0	8.5
Nymp rubr	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagl eleg	1.0	0.0	0.0	0.0	2.5	0.0	0.5	0.0	0.5	6.0	10.0	6.0	3.0	1.0	0.5	0.0	0.5	0.0	0.5	0.0	0.5	0.0	0.0	2.0	0.0	0.0

WINTER HYPERBENTHOS, BIOMASS mg AFDW per 1000 m<sup>2</sup> (DECEMBER 1988)

WESTERSCHELDE

	w1	w2	w3	w4	w5	w6	w7	w8	w9	w10	w11	w12	w13	o1	o2	o3	o4
Cran Post	23.8	2683.1	1730.2	3936.8	441.0	476.4	2607.8	1378.1	389.8	1153.5	3134.4	3485.5	4939.8	0.0	0.0	0.0	0.1
Cran Zoa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eual occu	29.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hipp Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Porc Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Porc Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carc Zoa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lloc Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lloc Zoa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macr Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Capr line	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Part typ1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phi mari	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ayl swam	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coro volu	6.9	181.2	38.3	1249.5	37.3	21.2	26.0	37.3	18.8	22.1	32.0	213.1	0.0	0.0	0.0	0.0	0.1
Gamm Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jass falc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mell palm	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mell obtu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mono carl	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pont alba	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orch nana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eury pulc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Idot line	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cala heig	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Call Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bodo scor	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias brad	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias luci	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias rath	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gast spin	0.0	66.2	114.5	110.5	0.0	0.0	0.0	0.0	7.1	0.0	0.0	34.0	0.0	0.0	0.0	0.0	4.0
Meso slab	793.2	181.2	1588.3	245.2	899.0	187.8	94.2	108.9	32.0	34.8	5.5	0.0	0.0	0.4	6.7	4.3	6.2
Neom lnte	0.0	10.8	0.0	439.4	28.8	512.0	1858.4	2414.7	4285.1	6127.4	4523.0	43935.7	48341.8	0.0	0.0	0.0	68.0
Prau flex	0.0	22.3	265.2	369.9	0.0	42.7	42.7	134.9	22.3	44.0	0.0	90.1	0.0	0.0	0.0	2.9	0.0
Siri arma	0.0	0.0	0.0	0.0	10.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	3.9
Schi spir	0.0	0.0	0.0	0.0	4.2	0.0	27.0	8.5	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0
Schi kerv	74.0	3768.0	688.9	3203.9	64.7	32.4	134.1	240.4	27.7	13.9	0.0	0.0	0.0	0.0	0.0	0.0	1.8
Nymp rubr	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagi eleg	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

OOSTERSCHELDE

## **Appendix 4, Westerschelde**



WESTERSCHELDE TRANSECT SEASONALLY 1990, DENSITY per 1000 m<sup>2</sup>

APRIL 1990	vi040	ss040	hs040	sg040	gs040	mp040	pb040	po040	hw040	sw040	zg040	ov040	sa040	ba040
Lani Aulo	1	2	1	0	0	0	0	0	0	0	0	0	0	0
Nere Larv	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harm Larv	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Auto Larv	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagi eleg	2	4	2	18	0	4	6	0	4	1	8	5	0	4
Cala helg	4	0	0	0	0	0	1	2	10	0	0	2	0	0
Calli Spec	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gast spin	0	14	2	1	1	0	0	14	6	3	0	0	0	0
Schi spir	2	14	28	3	10	0	12	9	26	2	19	7	4	22
Schi kern	0	136	105	6	264	4	9	63	821	61	8	0	1	0
Meso slab	27	2	14	49	105	48	126	482	8278	12662	11852	13806	2574	728
Neom inte	0	0	0	0	0	0	0	0	424	566	3163	1901	267	18026
Prau flex	0	0	0	0	0	0	1	0	23	1	0	0	0	0
Dias rath	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dias brad	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bodo scor	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eury pulc	0	0	0	0	0	0	0	1	2	2	1	1	0	0
Idot line	1	0	1	0	0	2	0	0	0	0	0	0	0	0
Spha rugi	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hype galb	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parl typi	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capr line	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gamm crin	2	2	1	0	3	0	0	0	4	0	0	0	0	0
Gamm sali	0	0	0	0	0	0	0	0	1	8	15	18	12	25
Atyl swam	0	4	0	0	0	0	0	0	1	0	0	0	0	0
Pleu glab	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Coro volu	0	0	0	0	1	0	0	0	0	0	1	1	0	0
Coro aren	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bath Spec	0	0	0	1	0	0	0	0	13	3	13	16	3	0
Jass falc	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jass marm	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isch angu	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sten mari	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pont alta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amph typ1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cran Zoa	5	18	18	3	2	0	1	0	0	0	1	0	0	0
Cran Post	31	244	89	10	113	2	12	25	2233	687	1986	1028	394	2381
Pala Zoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pala Post	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proc Post	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pagu Zoa	10	12	2	11	7	2	0	0	0	0	0	0	0	0
Pagu Mega	0	0	0	3	1	0	1	0	0	0	0	0	0	0
Porc Zoa	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Porc Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carc Zoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carc Mega	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Lioc Zoa	118	26	29	66	17	4	3	1	0	0	0	0	0	0
Lioc Mega	1	6	4	5	1	0	0	0	0	0	0	0	0	0
Port Zoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Port Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cory Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macr Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zoa typ1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zoa typ2	1	6	1	6	0	0	0	0	0	0	0	0	0	0
Nymp rubr	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pycn litt	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phox femo	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fish Eggs	84	286	194	150	261	0	131	26	41	28	61	7	0	0
Lima lima	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleu plat	0	8	4	0	0	0	0	1	1	0	0	0	0	1
Plat flies	15	4	6	18	15	4	44	46	26	27	31	9	12	191
Sole sole	1	2	0	0	1	0	0	0	53	0	2	0	0	0
Clup Spec	50	10	7	2	26	0	4	6	10	18	12	38	14	91
Poma Spec	0	0	0	0	0	2	1	0	0	0	0	0	0	0
Syng Spec	3	2	4	4	0	0	3	1	0	4	2	4	3	4
Angu angu	0	0	0	0	0	0	0	0	1	0	1	0	0	1

WESTERSCHELDE TRANSECT SEASONALLY 1990, ENVIRONMENTAL VARIABLES

APRIL 1990	vi040	ss040	hs040	sg040	gs040	mp040	pb040	po040	hw040	sw040	zg040	ov040	sa040	ba040
Salinity (psu)	29.6	29.4	28.6	28.3	26.5	25.6	24.5	23.2	17.9	16.6	17.1	16.9	15.3	13.3
Oxygen (%)	118	114	111	112	110	108	104	107	95	81	97	97	92	83
Secchi (cm)	80	60	90	90	70	70	60	75	50	50	60	60	80	60
Conductivity (µS/cm)	47.0	46.6	45.5	45.1	42.5	41.0	39.6	37.5	29.4	27.5	28.3	28.0	25.4	22.6
pH	8.2	8.2	8.2	8.2	8.1	8.1	8.1	8.1	7.9	8.0	7.9	7.8	7.8	7.8
Temperature (°C)	9.2	9.2	9.2	9.2	9.3	9.1	9.2	9.2	9.4	9.4	9.4	9.4	9.5	9.8
Depth (m)	13	9	14	13	8	13	7	15	0	0	12	12	9	10

WESTERSCHELDE TRANSECT SEASONALLY 1990, BIOMASS mg AFDW per 1000 m<sup>2</sup>

APRIL 1990	vl040	ss040	hs040	sg040	gs040	mp040	pb040	po040	hw040	sw040	zg040	ov040	sa040	ba040
Lari Aulo	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nere Larv	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Harm Larv	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Auto Larv	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagi eieg	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cala helg	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Cali Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gast spin	0.0	108.9	8.9	3.5	6.6	0.0	0.0	118.4	41.2	21.1	0.0	0.0	0.0	0.0
Schi spir	0.5	25.2	53.0	5.5	26.8	0.0	10.4	10.7	55.6	6.9	17.6	8.5	5.5	55.9
Schl kerv	0.0	188.2	172.3	12.8	592.8	11.8	3.9	122.7	1624.2	105.3	19.4	0.0	5.1	0.0
Meso siab	42.0	4.3	22.7	72.2	144.9	73.9	188.9	825.8	14422.9	8851.3	20541.1	21615.7	4886.8	1214.2
Neom inte	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2383.3	2979.8	10244.3	8863.3	1253.3	50342.0
Prau flex	0.0	0.0	0.0	0.0	0.0	0.0	11.3	0.0	312.0	15.0	0.0	0.0	0.0	0.0
Dias rath	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dias brad	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bodo scor	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eury pulc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.7	0.8	0.0	0.0	0.0
Idot line	11.2	0.0	36.2	0.0	0.0	27.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spha rugi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
Hype gaib	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pari typi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Capr line	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm crin	1.3	1.5	2.7	0.0	0.7	0.0	0.0	0.0	8.2	0.0	0.0	0.0	0.0	0.0
Gamm sail	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	3.5	37.1	14.8	22.6	51.9
Atyl swam	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pleu glab	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Coro volu	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.5	0.8	0.0	0.0
Coro aren	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bath Spec	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	2.2	0.7	2.5	3.1	0.7	0.0
Jass falc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jass marm	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isch angu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sten mari	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pont alta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amph typ1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cran Zoea	0.9	2.8	2.8	0.5	0.4	0.0	0.2	0.2	0.0	0.0	0.2	0.0	0.0	0.0
Cran Post	7.4	58.1	21.2	2.4	26.9	0.5	2.9	6.0	531.5	163.5	472.7	244.7	93.8	566.7
Pala Zoea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pala Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Proc Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pagu Zoea	6.2	7.4	1.2	6.8	4.3	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pagu Mega	0.0	0.0	0.0	2.0	0.7	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Porc Zoea	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Porc Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carc Zoea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carc Mega	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lioc Zoea	5.9	1.3	1.5	3.3	0.9	0.2	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Lioc Mega	0.1	0.5	0.3	0.4	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Port Zoea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Port Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cory Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macr Mega	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Zoea typ1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Zoea typ2	0.1	0.3	0.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nymp rubr	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pycn litt	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phox femo	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fish Eggs	2.1	6.7	4.9	3.8	6.5	0.0	3.3	0.7	1.0	0.7	1.5	0.2	0.0	0.0
Lima lima	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pleu plat	0.0	23.9	6.6	0.0	0.0	0.0	0.0	2.1	2.1	0.0	0.0	0.0	0.0	2.8
Plat fles	6.3	23.9	4.0	9.4	2.5	2.1	17.8	24.9	15.5	15.0	15.1	3.7	4.6	74.4
Sole sole	1.1	1.6	0.0	0.0	0.0	0.0	0.0	0.0	118.2	0.0	1.1	0.0	0.0	0.0
Clup Spec	339.2	44.6	36.6	26.9	100.2	0.0	52.4	51.0	96.5	122.9	83.0	296.2	83.0	545.4
Poma Spec	0.0	0.0	0.0	0.0	0.0	14.1	12.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syng Spec	47.5	38.6	82.6	79.6	0.0	0.0	122.8	13.9	0.0	111.9	54.1	81.9	148.9	166.4
Angu angu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	942.7	0.0	691.4	0.0	0.0	691.4

WESTERSCHELDE TRANSECT SEASONALLY 1990, DENSITY per 1000 m<sup>2</sup>

AUGUST 1990	vi080	ss080	hs080	sg080	gs080	mp080	pb080	po080	hw080	sw080	zg080	ov080	sa080	ba080
Lani Aulo	1	1	0	0	2	0	0	0	0	0	0	0	0	0
Nere Larv	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Harm Larv	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Auto Larv	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagi eleg	1	0	0	0	6	0	6	2	38	8	36	16	12	18
Cala helg	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calli Spec	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gast spin	96	780	364	730	1892	1042	1500	907	22	507	11	39	65	0
Schi spir	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schi kern	86	27	17	16	3	1	0	0	2	0	0	0	0	0
Meso siab	119	236	40	212	160	50	335	272	10740	108705	23464	7604	41392	60288
Neom inte	0	0	0	0	0	0	0	1	0	8602	516	9	2746	6217
Prau flex	0	0	0	0	0	0	0	0	1	7	8	1	4	2
Dias rath	0	3	1	2	0	1	0	0	0	0	0	0	0	0
Dias brad	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Bodo scor	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Eury pulc	1	0	0	0	1	1	0	0	0	0	0	0	0	1
Idot line	6	0	0	0	1	0	0	0	0	0	0	0	0	0
Spha rugi	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Hype galb	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pari typi	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capr line	2	3	0	0	0	0	0	0	0	0	0	0	0	0
Gamm crin	118	32	7	16	2	2	0	0	1	0	0	0	0	0
Gamm sali	0	0	0	0	0	0	0	0	0	0	0	0	28	3
Atyl swam	11	17	3	3	0	1	0	1	0	0	0	0	0	0
Pleu glab	0	0	0	0	0	0	0	0	1	3	0	0	100	7
Coro volu	1	3	0	5	2	0	2	5	19	85	10	17	88	6
Coro aren	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Bath Spec	0	0	0	2	1	0	0	0	0	0	0	0	0	3
Jass falc	0	2	0	0	0	0	0	0	1	0	0	0	0	0
Jass marm	0	1	1	1	0	0	1	0	0	0	0	0	0	0
Isch angu	0	0	0	0	2	1	0	0	0	0	0	0	0	0
Sten mari	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pont alta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amph typ 1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cran Zoa	1	2	3	1	0	0	0	0	0	0	0	0	0	0
Cran Post	63	136	137	224	17	13	52	43	2	21	8	7	244	255
Pala Zoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pala Post	0	2	0	1	1	0	0	0	1	2	0	0	0	0
Proc Post	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pagu Zoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pagu Mega	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Porc Zoa	0	0	1	0	5	1	1	0	0	0	0	0	0	0
Porc Mega	0	2	0	0	1	0	0	1	0	0	0	0	0	0
Carc Zoa	2	0	1	0	1	0	0	0	0	0	0	0	0	0
Carc Mega	1	2	1	4	1	0	3	1	4	0	0	0	4	0
Lioc Zoa	2	2	2	5	11	2	14	4	5	1	0	1	0	0
Lioc Mega	0	4	5	2	9	5	16	5	3	5	0	0	0	0
Port Zoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Port Mega	0	1	0	1	0	0	0	0	4	0	0	0	0	0
Cory Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macr Mega	0	1	0	1	0	0	0	0	2	0	0	0	0	0
Zoa typ1	0	0	0	0	0	0	0	0	1	1	1	2	4	0
Zoa typ2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymp rubr	1	4	0	3	2	0	0	0	0	0	0	0	0	0
Pycn litt	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoxfemo	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fish Eggs	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lima lima	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleu plat	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Plat flies	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sole sole	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clup Spec	0	1	0	0	2	0	0	0	0	0	0	0	0	0
Poma Spec	22	50	30	122	100	11	30	10	7	13	13	2	40	278
Syng Spec	10	23	7	5	8	5	14	3	27	26	55	24	52	31
Angu angu	0	0	0	0	0	0	0	0	0	0	0	0	0	0

WESTERSCHELDE TRANSECT SEASONALLY 1990, ENVIRONMENTAL VARIABLES

AUGUST 1990	vi080	ss080	hs080	sg080	gs080	mp080	pb080	po080	hw080	sw080	zg080	ov080	sa080	ba080
Salinity (psu)	31.0	30.5	29.5	29.1	28.6	28.2	27.2	26.2	22.2	22.9	19.9	20.8	19.2	17.0
Oxygen (‰)	104	104	102	102	103	101	101	101	103	100	97	100	96	82
Secchi (cm)	100	80	55	45	45	100	80	110	90	100	100	50	60	80
Conductivity (µS/cm)	48.2	47.4	46.1	45.5	45.2	44.2	42.2	41.0	36.6	36.6	32.2	33.6	31.3	27.9
pH	7.5	7.5	7.6	7.6	7.8	8.1	7.9	7.9	7.9	7.7	7.8	7.5	7.5	6.9
Temperature (°C)	19.0	19.0	19.1	19.1	19.1	19.0	19.0	19.1	19.1	18.1	18.5	18.5	19.6	19.9
Depth (m)	8	8	10	10	6	12	10	14	6	6	7	8	10	6



WESTERSCHELDE TRANSECT SEASONALLY 1990, DENSITY per 1000 m<sup>2</sup>

DECEMBER 1990	vl120	ss120	hs120	sg120	gs120	mp120	pb120	po120	hw120	sw120	zg120	ov120	sa120	ba120
Lani Aulo	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nere Larv	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harm Larv	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Auto Larv	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Sagi eleg	0	2	7	5	7	1	0	4	0	1	0	0	2	0
Cala helg	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cali Spec	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Gast spin	0	0	1	0	1	1	0	0	0	1	0	1	0	0
Schi spir	0	13	1	3	1	1	0	1	0	0	0	0	0	0
Schi kern	26	158	1	108	57	9	113	206	0	4	27	0	6	0
Meso slab	44	133	66	685	489	152	511	773	234	217	170	618	183	0
Neom inte	0	0	0	0	3	8	25	165	382	724	2568	2597	1863	3935
Prau flex	0	0	0	1	0	0	0	0	0	1	0	4	1	0
Dias rath	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dias brad	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Bodo scor	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eury pulc	0	0	0	1	0	0	0	0	4	1	0	0	1	0
ldot line	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spha rugi	0	0	0	0	0	0	1	1	0	1	2	4	2	0
Hype galb	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pari typi	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capr line	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gamm crin	28	42	0	110	2	0	1	0	0	0	0	0	0	0
Gamm sali	0	0	0	0	0	0	0	0	2	3	5	10	10	2
Atyl swam	2	0	0	4	0	0	0	0	0	0	0	0	0	0
Pleu glab	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Coro volu	0	0	0	0	0	0	0	0	0	1	0	11	2	6
Coro aren	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bath Spec	0	0	0	0	0	0	0	0	0	1	0	3	1	0
Jass falc	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jass marm	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isch angu	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sten mari	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pont alta	0	2	0	0	2	0	0	0	0	0	0	0	0	0
Amph typ1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cran Zoea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cran Post	4	40	2	53	23	5	4	4	42	9	8	32	1	3
Pala Zoea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pala Post	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Proc Post	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pagu Zoea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pagu Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porc Zoea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porc Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carc Zoea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carc Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lioc Zoea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lioc Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Port Zoea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Port Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cory Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macr Mega	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zoea typ1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zoea typ2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymp rubr	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pycn litt	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Phox femo	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fish Eggs	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lima lima	0	2	0	0	0	0	0	0	0	0	0	0	2	3
Pleu plat	0	0	0	0	0	0	0	0	0	0	0	5	0	0
Piat files	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sole sole	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Clup Spec	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Poma Spec	2	2	0	1	3	0	0	0	2	6	3	3	2	0
Syng Spec	0	2	0	1	1	0	0	0	0	0	0	0	0	0
Angu angu	0	0	0	0	0	0	0	0	0	0	0	0	0	0

WESTERSCHELDE TRANSECT SEASONALLY 1990, ENVIRONMENTAL VARIABLES

DECEMBER 1990	vl120	ss120	hs120	sg120	gs120	mp120	pb120	po120	hw120	sw120	zg120	ov120	sa120	ba120
Salinity (psu)	30.8	30.7	30.1	30.0	28.3	28.8	27.3	26.6	22.7	22.7	21.2	20.7	20.4	17.1
Oxygen (%)	103	101	102	99	101	101	101	101	97	96	93	82	90	75
Secchi (cm)	60	50	80	55	60	100	60	60	50	50	50	50	50	45
Conductivity (µS/cm)	48.8	48.6	47.7	47.6	45.2	45.8	43.8	42.6	36.7	36.8	34.6	33.8	33.4	28.3
pH	8.0	8.0	8.0	8.0	7.9	7.9	7.9	7.8	7.8	7.8	7.7	7.7	7.7	7.6
Temperature (°C)	6.1	6.3	6.1	6.2	5.9	6.0	5.9	5.7	5.8	5.6	5.5	5.6	5.5	6.0
Depth (m)	11	9	14	12	12	14	13	13	9	10	10	6	12	8



WESTERSCHELDE, DENSITY MARINE and BRACKISH part per 1000 m<sup>2</sup> (APRIL 1990 – MARCH 1991)

MARINE	vi0490	vi0590	vi0690	vi0790	vi0890	vi0990	vi1090	vi1190	vi1290	vi0191	vi0291	vi0391
Lani Aulo	0	8	0	0	1	0	0	0	0	0	0	0
Nere Larv	0	0	0	0	1	0	0	0	0	0	0	0
Sagi eleg	0	3	0	0	1	0	0	6	0	7	0	7
Cala helg	0	6	0	0	0	0	0	0	0	0	0	0
Gast spin	0	0	0	3	96	19	8	13	0	0	0	14
Schi spir	0	0	0	0	0	0	0	9	0	0	3	12
Schi kern	0	7	0	24	25	0	0	130	26	39	10	267
Meso slab	86	4	1	187	119	282	86	177	44	103	0	338
Neom inte	0	0	0	0	0	0	0	0	0	0	0	0
Prau flex	0	0	0	0	61	0	0	0	0	0	1	7
Acan long	0	0	0	0	0	0	6	0	0	0	0	0
Dias rath	0	1	0	0	2	0	0	0	0	0	0	0
Dias brad	0	0	0	0	0	0	0	0	1	0	0	0
Bodo scor	0	1	0	0	0	0	0	0	0	0	0	0
Eury pulc	0	1	1	0	1	0	1	0	0	1	0	0
Idot line	8	1	12	0	3	2	4	2	0	0	0	4
Spha rugi	0	0	0	0	0	0	0	0	0	0	0	0
Pari typi	0	0	0	0	0	0	1	0	0	0	0	0
Capri line	0	0	0	2	3	0	0	0	0	0	0	0
Gamm crin	0	39	3	5	75	4	21	5	35	21	0	34
Gamm sall	0	0	0	0	0	0	0	0	0	0	0	0
Atyl swam	0	14	0	1	14	2	6	0	1	1	0	0
Pleu glab	0	0	0	0	0	0	0	1	0	0	0	1
Coro volu	0	0	2	0	3	0	1	0	0	1	0	0
Bath eleg	0	0	0	0	0	0	0	0	0	0	0	0
Jass falc	0	0	0	0	1	0	0	0	0	0	0	0
Jass marm	0	0	0	0	1	0	0	0	0	0	0	0
Sten mari	0	1	0	0	1	0	0	0	0	0	0	0
Pont alta	0	0	0	0	0	0	0	0	1	0	0	0
Haust aren	0	0	0	0	0	0	0	0	0	1	0	0
Meli obtu	0	0	0	0	0	0	0	0	0	1	0	0
Cran Zoea	40	61	11	0	2	15	3	0	0	0	0	0
Cran Post	88	297	17	38	114	14	37	2	27	7	1	0
Pala Zoea	0	0	1	1	0	0	0	0	0	0	0	0
Pala Post	0	1	1	0	1	2	0	0	1	0	0	0
Hypo Zoea	0	1	0	0	0	0	0	0	0	0	0	0
Pont Post	0	0	0	0	0	0	1	0	0	0	0	0
Pagu Zoea	0	40	3	0	0	0	0	0	0	0	0	0
Pagu Mega	0	7	0	0	0	0	0	0	0	0	0	0
Porc Zoea	0	5	30	0	0	0	0	0	0	0	0	0
Porc Mega	0	2	4	0	1	0	0	0	0	0	0	0
Carc maen	0	1	1	0	0	0	0	0	0	0	0	0
Carc Zoea	0	318	51	0	1	0	0	0	0	0	0	0
Carc Mega	0	213	304	52	2	2	0	0	0	0	0	0
Lioc hols	0	291	6	9	7	3	5	0	1	0	0	1
Lioc Zoea	384	80	250	5	2	1	0	0	0	0	0	0
Lioc Mega	0	32	6	2	2	1	0	0	0	0	0	0
Port Mega	0	0	0	1	1	0	0	0	0	0	0	0
Cory Mega	0	17	0	0	0	0	0	0	0	0	0	0
Macr Mega	0	0	0	0	1	0	0	0	0	0	0	0
Nymp rubr	0	1	0	0	3	0	1	0	1	1	0	0
Nymp grac	0	0	1	0	0	0	0	0	0	0	0	0
Fish Eggs	0	3	0	0	0	0	0	0	0	0	0	1
Pleu plat	0	0	0	0	0	1	0	0	0	0	0	0
Plat fles	24	8	0	0	0	0	0	0	0	0	0	12
Sole sole	0	12	0	0	0	0	0	0	0	0	0	0
Clup Spec	128	35	3	0	1	0	0	0	1	1	1	6
Poma minu	0	21	4	49	3	0	1	1	2	1	0	0
Poma loza	0	0	0	0	37	20	19	18	6	11	0	3
Poma micr	0	0	0	1	1	1	1	0	1	0	0	0
Syng Spec	8	5	2	2	17	5	0	1	1	0	0	0
Angu angu	0	0	0	0	0	0	0	0	0	0	0	0
Lipa lipa	0	0	0	0	0	0	0	0	0	0	0	0
Call lyra	0	5	0	0	0	0	0	0	0	0	0	0

WESTERSCHELDE, ENVIRONMENTAL VARIABLES (APRIL 1990 – MARCH 1991)

MARINE	vi0490	vi0590	vi0690	vi0790	vi0890	vi0990	vi1090	vi1190	vi1290	vi0191	vi0291	vi0391
Depth (m)	13.0	10.0	16.0	11.0	8.0	9.0	14.0	9.0	11.0	9.0	15.0	12.0
Temperature (°C)	9.2	15.0	16.3	18.7	19.0	14.7	13.3	8.5	6.1	4.7	1.8	6.1
Secchi (cm)	90.0	150.0	300.0	160.0	100.0	110.0	130.0	70.0	60.0	50.0	55.0	80.0
Salinity (psu)	29.8	30.0	29.9	30.9	31.0	31.1	31.9	31.3	30.8	27.0	28.2	28.6
Conductivity (mS/cm)	47.0	48.5	48.8	47.9	48.2	48.7	49.8	49.4	48.8	43.3	41.8	41.8
Oxygen (%)	116.0	105.0	97.0	119.0	103.0	100.0	105.0	104.0	103.0	104.0	106.0	98.0
pH	8.2	8.2	8.2	7.7	7.5	7.9	8.0	8.0	8.0	8.0	8.1	7.9

WESTERSCHELDE, DENSITY MARINE and BRACKISH part per 1000 m<sup>3</sup> (APRIL 1990 – MARCH 1991)

BRACKISH	ba0490	ba0590	ba0690	ba0790	ba0890	ba0990	ba1090	ba1190	ba1290	ba0191	ba0291	ba0391
Lani Aulo	0	0	0	0	0	0	0	0	0	0	0	0
Nere Larv	0	0	0	0	0	0	0	0	0	0	0	0
Sagi eleg	12	0	0	8	18	9	22	0	0	0	0	0
Caia helg	0	0	0	0	0	0	0	0	0	0	0	0
Gast spin	0	0	0	42	0	7	1	0	0	0	0	0
Schi spir	0	0	0	0	0	0	0	0	0	0	0	0
Schi kern	0	0	0	0	0	0	0	0	0	0	0	0
Meso slab	2416	59	1780	11010	61062	17341	48251	111	0	0	0	0
Neom inte	58440	0	16	6644	6217	1572	2549	18097	3935	6856	4713	413
Prau flex	0	0	0	2	2	6	3	0	0	0	0	0
Acan long	0	0	0	0	0	0	0	0	0	0	0	0
Dias rath	0	0	0	0	0	0	0	0	0	0	0	0
Dias brad	0	0	0	0	0	0	0	0	0	0	0	0
Bodo scor	0	0	0	0	0	0	0	0	0	0	0	0
Eury pulc	0	8	2	2	1	0	2	0	0	0	1	12
Idot line	0	0	0	0	0	0	0	0	0	0	0	0
Spha rugi	4	0	0	0	0	3	0	0	0	0	0	0
Pari typi	0	0	0	0	0	0	0	0	0	0	0	0
Capr line	0	0	0	0	0	0	0	0	0	0	0	0
Gamm crin	0	0	0	0	0	0	0	0	0	0	0	0
Gamm sali	76	0	0	0	3	6	4	10	2	37	8	53
Atyl swam	0	0	0	0	0	0	0	0	0	0	4	0
Pleu glab	0	0	0	0	7	0	2	1	0	1	0	0
Coro volu	0	0	0	0	6	5	1	2	6	6	0	0
Bath eleg	0	0	0	0	3	0	3	0	0	0	2	4
Jass falc	0	0	0	0	0	0	0	0	0	0	0	0
Jass marm	0	0	0	0	0	0	0	0	0	0	0	0
Sten mari	0	0	0	0	0	0	0	0	0	0	0	0
Pont alta	0	0	0	0	0	0	0	0	0	0	0	0
Haut aren	0	0	0	0	0	0	0	0	0	0	0	0
Meli obtu	0	0	0	0	0	0	0	0	0	0	0	0
Cran Zoea	0	0	0	0	0	1	0	0	0	0	0	0
Cran Post	6120	0	0	16	255	32	117	12	3	1	1	0
Pala Zoea	0	0	0	0	0	0	0	0	0	0	0	0
Pala Post	0	0	0	2	0	0	0	0	0	0	0	0
Hypo Zoea	0	0	0	0	0	0	0	0	0	0	0	0
Pont Post	0	0	0	0	0	0	0	0	0	0	0	0
Pagu Zoea	0	0	0	0	0	0	0	0	0	0	0	0
Pagu Mega	0	0	0	0	0	0	0	0	0	0	0	0
Porc Zoea	0	0	0	0	0	0	0	0	0	0	0	0
Porc Mega	0	0	0	0	0	0	0	0	0	0	0	0
Carc maen	0	0	0	0	2	0	0	0	0	0	0	0
Carc Mega	0	0	0	2	0	0	0	0	0	0	0	0
Carc Mega	0	0	0	0	0	0	0	0	0	0	0	0
Lioc hols	0	0	0	4	2	0	0	0	0	0	0	0
Lioc Zoea	0	0	0	0	0	0	0	0	0	0	0	0
Lioc Mega	0	0	0	0	0	0	0	0	0	0	0	0
Port Mega	0	0	0	0	0	0	0	0	0	0	0	0
Cory Mega	0	0	0	0	0	0	0	0	0	0	0	0
Macr Mega	0	0	0	0	0	0	0	0	0	0	0	0
Nymp rubr	0	0	0	0	0	0	0	0	0	0	0	0
Nymp grac	0	0	0	0	0	0	0	0	0	0	0	0
Fish Eggs	0	0	0	0	0	0	0	0	0	0	0	0
Pleu plat	0	0	0	0	0	0	0	0	0	0	2	0
Plat fles	440	0	0	0	0	0	0	0	0	0	0	4
Sole sole	0	0	0	0	0	0	0	0	0	0	0	0
Clup Spec	0	113	8	2	0	1	0	0	0	0	0	2
Poma minu	0	48	1	20	16	6	1	0	0	1	0	0
Poma loza	8	0	0	2	283	32	2	11	0	1	0	0
Poma micr	0	0	0	0	0	3	1	0	0	0	1	0
Syng Spec	4	0	0	42	31	6	0	0	0	0	0	0
Angu angu	4	0	0	0	0	0	0	0	0	1	0	4
Lipa lipa	0	0	0	1	0	0	0	0	0	0	0	0
Call lyra	0	0	0	0	0	0	0	0	0	0	0	0

WESTERSCHELDE, ENVIRONMENTAL VARIABLES (APRIL 1990 – MARCH 1991)

BRACKISH	ba0490	ba0590	ba0690	ba0790	ba0890	ba0990	ba1090	ba1190	ba1290	ba0191	ba0291	ba0391
Depth (m)	10.0	10.0	12.0	10.0	6.0	11.0	6.0	6.0	6.0	13.0	12.0	7.0
Temperature (°C)	9.8	15.0	17.5	18.7	19.9	14.5	13.1	8.4	6.0	4.4	1.6	8.7
Secchi (cm)	60.0	75.0	110.0	50.0	80.0	80.0	70.0	40.0	45.0	50.0	40.0	30.0
Salinity (psu)	13.3	17.0	19.1	19.7	17.0	21.4	21.6	17.0	17.1	11.8	16.0	10.8
Conductivity (mS/cm)	22.6	29.0	31.3	32.0	27.9	34.6	35.1	28.1	28.3	19.8	26.4	18.1
Oxygen (%)	83.0	81.0	79.0	86.0	82.0	97.0	80.0	65.0	75.0	80.0	89.0	27.0
pH	7.8	7.8	7.8	7.3	6.9	7.6	7.7	7.7	7.6	7.7	7.7	7.4



## **Appendix 5, 3 estuaries**

THREE ESTUARIES, DENSITY per 1000 m<sup>3</sup> (AUGUST 1991) along SALINITY GRADIENT

WESTERSCHELDE	w31	w30a	w30b	w30c	w28	w27	w25a	w25b	w21	w19	w17	w12	w10	w8	w6
Sagi eleg	1	11	0	0	0	0	0	0	1	0	1	3	0	0	0
Gast spin	11	49	133	117	26	1	7	526	560	3361	18	3	1	0	0
Schi spir	21	54	52	12	7	0	2	10	6	0	0	0	0	0	0
Schi kern	109	11	254	47	135	1	3	70	1	0	0	0	0	0	0
Meso slab	81	1598	178	383	367	134	456	1485	2302	54814	60095	2855	66	2	0
Neom inte	0	0	0	0	0	0	0	0	493	183212	393	4476	102840	891	0
Prau flex	0	0	0	0	1	0	0	4	33	0	3	0	0	0	0
Eury pulc	0	0	0	0	0	0	0	1	11	15	0	26	1	0	0
Idot line	4	81	9	13	4	3	4	6	0	0	1	0	0	1	0
Spha rugi	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Daph Spec	0	0	0	0	0	0	0	0	0	0	0	93	2	0	0
Capr line	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0
Pari typi	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0
Gamm crin	3	103	6	7	7	0	0	4	12	0	0	0	0	0	0
Gamm sali	0	0	21	0	0	0	0	0	7	0	0	0	0	0	0
Atyl swam	4	30	0	3	5	1	0	0	0	0	0	0	0	0	0
Pleu glab	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Coro volu	0	0	0	0	0	0	0	0	0	0	0	7	7	2	0
Coro ache	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
Coro lacu	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Bath Spec	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0
Jass falc	0	1	0	1	3	0	0	0	0	0	0	0	0	0	0
Hype galb	3	2	18	9	3	0	0	0	0	0	0	0	0	0	0
Cran Zoa	2	24	0	4	4	0	1	0	3	0	0	0	0	0	0
Cran Post	7	23	2	6	21	0	0	5	11	77	0	18	1148	187	0
Pala varP	0	2	0	3	0	0	0	0	0	0	0	0	32	0	0
Porc zoe	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Carc zoe	11	34	1	4	2	0	0	0	0	0	0	0	0	1	0
Carc Mega	6	19	3	8	4	0	3	1	0	0	0	17	4	0	0
Lioc zoe1	22	110	18	24	1	7	0	0	0	0	298	10	13	0	0
Lioc Mega	2	18	3	2	0	0	0	1	0	0	0	1	0	0	0
Macr Mega	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Wty1 Zoa	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Nymp rubr	0	1	1	2	0	1	0	0	3	0	0	0	0	0	0
Clup Spec	3	8	7	7	3	2	6	0	0	1	0	0	0	0	0
Syng rost	1	5	0	4	0	1	4	0	3	0	28	8	0	0	0
Poma micr	0	0	0	0	2	0	0	0	0	5	0	0	0	0	0
Poma Spec	55	43	22	6	16	5	8	8	13	0	6	92	184	5	0

THREE ESTUARIES, BIOMASS mg AFDW per 1000 m<sup>2</sup> (AUGUST 1991) along SALINITY GRADIENT

WESTERSCHELDE	w31	w30a	w30b	w30c	w28	w27	w25a	w25b	w21	w19	w17	w12	w10	w8	w6
Sagi eleg	0.1	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.3	0.0	0.0	0.0
Gast spin	7.7	24.6	228.1	124.9	39.5	3.1	4.4	1780.2	860.0	2513.4	12.8	4.6	1.3	0.0	0.0
Schi spir	29.3	65.7	62.0	15.3	11.5	0.0	2.1	14.0	8.5	0.0	0.0	0.0	0.0	0.0	0.0
Schi kern	190.9	18.7	442.2	40.1	200.1	1.0	1.0	255.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meso slab	69.0	962.4	140.7	264.0	295.5	114.9	433.5	1404.3	2381.6	33225.3	27495.6	3318.1	66.8	2.1	0.0
Neom inte	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1444.7	518013.8	403.7	10343.1	206368.8	1427.3	0.0
Prau flex	0.0	0.0	0.0	0.0	8.1	0.0	0.0	41.8	225.7	0.0	36.3	0.0	0.0	0.0	0.0
Eury pulc	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	9.2	19.6	0.0	27.6	0.9	0.0	0.0
Idot line	8.3	127.5	39.9	28.1	29.8	5.5	15.3	27.7	0.0	0.0	6.0	0.0	0.0	0.0	0.0
Spha rugi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
Daph Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.3	0.2	0.0	0.0
Capr line	0.0	1.2	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pari typi	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm crin	7.9	146.4	16.1	8.9	6.9	0.0	0.0	4.8	19.8	0.0	0.0	0.0	0.0	0.0	0.0
Gamm sali	0.0	0.0	18.7	0.0	0.0	0.0	0.0	0.0	6.6	0.0	0.0	0.0	0.0	0.0	0.0
Atyl swam	0.9	7.4	0.0	0.7	1.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pleu glab	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0
Coro volu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.9	2.1	0.5	0.0
Coro ache	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coro lacu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Bath Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.4	0.0	0.0	0.0
Jass falc	0.0	0.4	0.0	0.1	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hype galb	6.1	1.0	24.2	9.8	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cran Zoa	0.4	4.2	0.0	0.7	0.7	0.0	0.2	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Cran Post	1.7	5.5	0.5	1.4	5.0	0.0	0.0	1.2	2.8	18.3	0.0	3.8	273.2	44.5	0.0
Pala varP	0.0	0.5	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.6	0.0	0.0
Porc Zoa	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carc Zoa	0.6	1.7	0.1	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Carc Mega	0.5	1.5	0.2	0.6	0.3	0.0	0.2	0.1	0.0	0.0	0.0	1.4	0.3	0.0	0.0
Lioc zoe1	3.3	16.7	2.4	3.6	0.2	1.1	0.0	0.0	0.0	0.0	45.3	1.5	2.0	0.0	0.0
Lioc Mega	0.4	3.4	0.6	0.4	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Macr Mega	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wty1 Zoa	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nymp rubr	0.0	0.1	0.1	0.2	0.0	0.1	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Clup Spec	8.0	12.9	37.0	4.5	4.7	4.1	17.4	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0
Syng rost	1.7	6.5	0.0	17.2	0.0	0.0	32.9	0.0	49.4	0.0	352.5	98.5	0.0	0.0	0.0
Poma micr	0.0	0.0	0.0	0.0	7.8	0.0	0.0	0.0	0.0	15.1	0.0	0.0	0.0	0.0	0.0
Poma Spec	104.5	116.5	81.9	8.5	24.8	2.1	7.9	11.4	24.1	0.0	4.9	290.7	707.8	10.1	0.0

THREE ESTUARIES, ENVIRONMENTAL VARIABLES (AUGUST 1991) along SALINITY GRADIENT

WESTERSCHELDE	w31	w30a	w30b	w30c	w28	w27	w25a	w25b	w21	w19	w17	w12	w10	w8	w6
Salinity (psu)	31.0	30.3	29.4	29.4	28.0	26.6	25.5	25.0	21.1	19.3	17.0	11.9	10.3	8.1	6.0
Secchi (cm)	125	120	125	125	100	100	140	140	80	90	100	40	50	60	-
Temperature (°C)	20.0	20.0	19.8	20.1	20.2	20.2	20.1	20.1	20.3	20.5	20.6	22.3	22.8	22.7	23.0

THREE ESTUARIES, DENSITY per 1000 m<sup>3</sup> (AUGUST 1991) along SALINITY GRADIENT

GIRONDE	g26a	g26b	g24	g20	g18	g14	g10	g6	g4	g3	g2	g1	g.5	g.1	g0
Sagi eleg	0	1	13	2	0	0	0	0	0	0	0	0	0	0	0
Gast spin	0	0	19	8	642	24	10	0	0	0	0	0	0	0	0
Schi spir	0	0	6	2	504	14	0	0	0	0	0	0	0	0	0
Schi kerv	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meso slab	0	0	4	3	79	18131	39352	30060	3540	11160	640	3333	512	28	10
Neom inte	0	0	0	0	1	1310	9829	5963	26250	16020	13261	20004	7910	4670	6403
Eury pulc	0	0	0	0	4	0	2	1	0	1	0	0	0	0	0
Syni spec1	0	0	1	1	5	12	39	62	56	282	6	64	2	1	0
Syni spec2	0	0	0	0	0	2	1	8	0	8	0	0	0	0	0
Spha serr	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0
Cymo Spec	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0
Capr Spec	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Gamm crin	0	0	8	2	5	2	0	0	0	0	0	0	0	0	0
Gamm sali	0	0	0	0	0	1	5	52	1858	597	1057	1284	519	0	0
Gamm zadd	0	0	0	0	0	0	0	3	1922	568	3453	1138	4821	5400	6778
Meli palm	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Atyl swam	2	0	5	1	0	0	0	0	0	0	0	0	0	0	0
Pleu glab	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Coro volu	0	0	0	0	0	0	1	2	0	6	0	0	0	0	0
Cran Zoa	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0
Cran Post	0	0	0	0	0	1	0	3	0	18	0	39	0	2	0
Pala IonZ	0	0	2	0	22	0	4	0	0	44	10	5	0	0	0
Pala IonP	0	0	0	0	18	1	1	3	39	84	324	59	300	72	19
Pagu Mega	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porc zoe	0	3	3	0	2	0	0	0	0	0	0	0	0	0	0
Carc Mega	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Lioc zoe1	0	0	0	2	0	0	2	7	0	8	0	0	0	0	0
Macr Mega	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Gty1 Zoa	0	0	2	0	5	0	0	0	0	0	0	0	0	0	0
Erio Mega	1	0	2	0	10	3	2	0	0	0	0	4	0	4	1
Gty2 Mega	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lioc zoe2	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0
Lioc zoe3	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0
Angu angu	0	0	0	0	0	0	0	0	0	0	0	0	1	1	5
Clup Spec	1	0	1	0	36	4	3	0	0	2	0	0	0	0	0
Syng rost	1	0	1	5	17	18	20	25	174	69	18	263	17	10	0
Poma micr	0	0	0	0	1	6	18	78	6321	522	4238	3374	1834	1743	2069

THREE ESTUARIES, BIOMASS mg AFDW per 1000 m<sup>3</sup> (AUGUST 1991) along SALINITY GRADIENT

GIRONDE	g26a	g26b	g24	g20	g18	g14	g10	g6	g4	g3	g2	g1	g.5	g.1	g0
Sagi eleg	0.0	0.1	1.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gast spin	0.0	0.0	14.0	5.5	545.9	11.4	12.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Schi spir	0.0	0.0	1.5	0.4	445.2	24.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Schi kerv	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meso slab	0.0	0.0	0.5	0.4	24.2	11959.0	28105.0	14614.6	2820.4	10221.3	622.0	3153.8	576.4	23.1	5.7
Neom inte	0.0	0.0	0.0	0.0	3.6	5269.9	34105.8	15083.8	70180.9	49280.6	26121.0	69822.3	17567.1	13577.8	5497.1
Eury pulc	0.0	0.0	0.0	0.0	3.7	0.0	0.8	0.9	0.0	0.6	0.0	0.0	0.0	0.0	0.0
Syni spec1	0.0	0.0	0.4	4.9	18.2	99.6	285.9	478.4	169.2	1872.1	27.1	405.3	16.4	8.7	0.0
Syni spec2	0.0	0.0	0.0	0.0	0.0	0.0	3.1	28.1	0.0	21.4	0.0	0.0	0.0	0.0	0.0
Spha serr	0.0	0.0	0.1	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cymo Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Capr Spec	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm crin	0.0	0.0	30.1	1.5	10.3	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm sali	0.0	0.0	0.0	0.0	0.0	0.9	17.1	94.6	2489.4	1030.0	1147.9	2304.1	481.9	0.0	0.0
Gamm zadd	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.6	6214.3	2002.4	8688.8	3979.4	18839.0	18268.8	27671.3
Meli palm	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Atyl swam	0.8	0.0	1.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pleu glab	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
Coro volu	0.0	0.0	0.0	0.0	0.0	0.0	0.6	1.5	0.0	0.6	0.0	0.0	0.0	0.0	0.0
Cran Zoa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cran Post	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.7	0.0	3.8	0.0	9.3	0.0	0.5	0.0
Pala IonZ	0.0	0.0	0.4	0.0	3.9	0.0	0.7	0.0	0.0	7.7	1.8	0.9	0.0	0.0	0.0
Pala IonP	0.0	0.0	0.0	0.0	3.8	0.2	0.2	0.7	9.3	20.0	77.1	14.0	71.4	17.1	4.5
Pagu Mega	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Porc Zoa	0.0	0.2	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carc Mega	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lioc zoe1	0.0	0.0	0.0	0.3	0.0	0.0	0.3	1.1	0.0	0.9	0.0	0.0	0.0	0.0	0.0
Macr Mega	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gty1 Zoa	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Erio Mega	0.1	0.0	0.2	0.0	0.8	0.2	0.2	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.1
Gty2 Mega	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lioc zoe2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0
Lioc zoe3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0
Angu angu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1662.6
Clup Spec	2.1	0.0	2.1	0.0	75.7	13.4	12.8	0.0	0.0	7.4	0.0	0.0	0.0	0.0	0.0
Syng rost	0.2	0.0	0.0	0.8	37.3	5.4	160.1	138.1	397.3	601.2	83.1	0.0	84.9	16.6	0.0
Poma micr	0.0	0.0	0.0	0.0	2.4	23.4	95.9	436.1	30203.6	2985.8	21393.3	18822.8	7166.7	6314.5	12393.6

THREE ESTUARIES, ENVIRONMENTAL VARIABLES (AUGUST 1991) along SALINITY GRADIENT

GIRONDE	g26a	g26b	g24	g20	g18	g14	g10	g6	g4	g3	g2	g1	g.5	g.1	g0
Salinity (psu)	26.0	26.0	24.0	20.0	18.0	14.0	10.0	6.0	4.0	3.5	2.0	1.5	0.5	0.1	0.0
Secchi (cm)	440	440	260	90	40	40	30	10	5	5	3	5	3	5	8
Temperature (°C)	21.0	21.2	21.6	22.4	22.6	22.8	23.5	24.0	24.2	24.1	24.4	24.4	24.4	24.4	24.4

THREE ESTUARIES, DENSITY per 1000 m<sup>3</sup> (AUGUST 1991) along SALINITY GRADIENT

EEMS	e29	e27	e25	e23	e21	e18	e17	e11	e10	e4	e2	e1
Sagi eleg	2	38	38	68	19	178	65	153	298	0	0	0
Gast spin	655	34	31	42	31	17	10	4	6	0	0	8
Schi spir	789	605	143	92	4	21	67	14	12	0	0	0
Schi kern	719	4944	621	1278	7017	680	1023	3	0	0	0	0
Meso slab	280	2485	8520	100	0	5	5	2	11	0	0	4
Neom inte	0	0	143	8622	10536	8960	15982	2023	9237	17520	22320	8461
Prau flex	51	294	28	11	0	1	0	0	0	0	0	0
Idot line	4	14	0	0	0	0	0	0	0	0	0	0
Daph Spec	0	0	0	0	0	0	0	1	0	0	0	0
Gamm crin	171	646	6	2	4	3	0	0	0	0	0	0
Gamm sali	0	0	3	9	16	25	18	52	28	16	0	0
Gamm zadd	0	0	13	1	4	14	14	54	65	392	2076	5353
Gamm dueb	1	37	0	0	0	0	0	0	0	0	0	0
Gamm locu	35	180	1	0	0	0	1	0	0	0	0	0
Atyl swam	0	17	1	1	0	1	0	1	0	0	0	0
Coro volu	0	1	0	47	27	3	5	4	1	0	0	28
Bath Spec	0	0	0	0	0	0	0	0	1	0	0	0
Cran Zoa	12	0	0	0	0	0	0	0	0	0	0	0
Cran Post	103	649	107	557	224	569	683	359	442	677	978	207
Pala lonZ	0	0	9	0	0	1	0	0	0	0	0	0
Pala lonP	0	0	0	0	23	1	0	0	0	0	0	11
Pala varZ	0	1	0	9	0	0	0	0	0	0	0	0
Pala varP	0	0	0	8	0	1	0	2	1	0	0	0
Carc Zoe	2	2	15	0	0	5	0	0	1	0	0	0
Carc Mega	241	881	38	168	0	0	0	1	2	0	0	0
Lioc zoe1	0	1	0	0	0	0	0	0	0	0	0	0
Erio Mega	4	5	5	18	0	6	0	0	0	0	0	0
Lioc zoe4	0	0	0	0	0	0	0	0	2	0	0	0
Clup Spec	1	18	39	84	0	3	2	4	6	16	1	0
Syng rost	16	46	32	4	0	0	1	0	0	0	0	0
Poma micr	0	3	5	6	3	8	24	84	104	94	188	435
Poma Spec	95	270	203	1260	107	127	35	29	0	85	100	0

THREE ESTUARIES, BIOMASS mg AFDW per 1000 m<sup>3</sup> (AUGUST 1991) along SALINITY GRADIENT

EEMS	e29	e27	e25	e23	e21	e18	e17	e11	e10	e4	e2	e1
Sagi eleg	0.2	3.8	3.8	6.8	1.9	17.8	6.5	15.3	29.8	0.0	0.0	0.0
Gast spin	839.7	81.2	27.8	71.3	26.4	34.4	7.5	26.2	14.4	0.0	0.0	7.5
Schi spir	1132.0	914.7	214.2	132.7	1.8	38.4	110.0	63.7	23.6	0.0	0.0	0.0
Schi kern	1112.7	8709.3	781.7	1037.1	9026.1	1064.2	1025.7	2.5	0.0	0.0	0.0	0.0
Meso slab	307.8	2257.4	7694.0	103.2	0.0	6.4	7.1	10.2	11.9	0.0	0.0	1.2
Neom inte	0.0	0.0	330.5	21519.4	28070.1	27538.0	45468.1	19340.3	32198.3	57746.4	57268.8	20579.0
Prau flex	341.4	1642.3	143.7	79.3	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Idot line	21.3	71.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Daph Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Gamm crin	394.3	1281.7	12.1	2.7	5.2	3.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm sali	0.0	0.0	6.4	33.9	48.0	47.1	23.5	49.9	35.7	24.1	0.0	0.0
Gamm zadd	0.0	0.0	31.7	0.6	12.5	53.7	50.4	186.3	308.5	1297.6	6599.5	16455.5
Gamm dueb	6.0	278.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gamm locu	251.8	697.5	4.9	0.0	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0
Atyl swam	0.0	5.7	0.4	0.2	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Coro volu	0.0	0.9	0.0	26.4	29.0	1.9	6.5	2.5	0.6	0.0	0.0	1.8
Bath Spec	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Cran Zoa	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cran Post	24.5	154.5	25.5	132.6	53.3	135.4	157.8	85.4	105.2	161.1	232.3	49.3
Pala lonZ	0.0	0.0	1.6	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Pala lonP	0.0	0.0	0.0	0.0	5.5	0.2	0.0	0.0	0.0	0.0	0.0	2.6
Pala varZ	0.0	0.2	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pala varP	0.0	0.0	0.0	1.9	0.0	0.2	0.0	0.5	0.2	0.0	0.0	0.0
Carc Zoe	0.1	0.1	0.8	0.0	0.0	0.3	0.0	0.0	0.1	0.0	0.0	0.0
Carc Mega	19.5	69.7	3.1	13.4	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0
Lioc zoe1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Erio Mega	0.3	0.4	0.4	1.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Lioc zoe4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Clup Spec	2.1	77.8	195.7	301.3	0.0	9.5	10.7	56.1	25.6	65.6	2.1	0.0
Syng rost	170.8	967.8	395.0	83.1	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0
Poma micr	0.0	18.0	17.5	70.1	18.0	41.4	180.1	396.0	408.4	590.8	1235.7	1912.6
Poma Spec	52.2	302.5	229.9	1685.0	212.1	246.0	156.0	58.4	0.0	342.1	335.2	0.0

THREE ESTUARIES, ENVIRONMENTAL VARIABLES (AUGUST 1991) along SALINITY GRADIENT

EEMS	e29	e27	e25	e23	e21	e18	e17	e11	e10	e4	e2	e1
Salinity (psu)	28.8	26.5	25.3	22.9	21.0	18.5	16.7	11.4	10.0	4.5	2.0	0.8
Secchi (cm)	120	50	45	20	20	15	20	10	10	5	5	5
Temperature (°C)	19.8	19.6	19.4	19.2	18.6	19.7	19.8	20.1	20.1	20.3	20.4	20.5

## **Appendix 6, *Neomysis integer***









