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Structure and Function of the Benthos in Estuarine and Coastal Ecosystems in relation to actual and future Anthropogenic Impacts

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Hyperbenthos

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Ann Dewicke, Nancy Fockedey, Jan Mees, Tom Moens,
Maaike Steyaert & Magda Vincx

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University of Gent, Zoology Institute, Marine Biology Section
K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

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SEASONAL COMPOSITION AND SPATIAL DISTRIBUTION OF HYPERBENTHIC COMMUNITIES ALONG ESTUARINE GRADIENTS IN THE WESTERSCHELDE *

JAN MEES, ANN DEWICKE and OLIVIER HAMERLYNCK

KEYWORDS: hyperbenthos; Westerschelde; estuary; community analysis.

ABSTRACT

The hyperbenthic fauna of the Westerschelde estuary was sampled in spring, summer and winter of 1990 at 14 stations along the salinity gradient. 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, belong 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. Gradients in salinity, dissolved oxygen and turbidity correlated strongly with the observed variation in community structure. The spatial patterns dominated 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 occurrence of a series of temporary hyperbenthic species in spring and summer. 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.

INTRODUCTION

The mobile hyperbenthos (*e.g* mysids, amphipods) is a little known, but potentially important part of the estuarine fauna. The hyperbenthos includes all swimming bottom-dependent animals which perform seasonal or daily vertical migrations above the bottom (BRUNEL *et al.*, 1978). This mobile upper compartment of the benthic community has rarely been studied because of the methodological problems involved in sampling. Yet, in recent studies its importance in coastal ecosystems has become well established (*e.g.* BOYSON, 1975; BUHL-JENSEN and FOSSA, 1991; HAMERLYNCK and MEES, 1991; RUDSTAM *et al.*, 1986; WOOLRIDGE, 1989).

In estuaries, density and biomass of the permanent hyperbenthos are much higher than in neighbouring coastal areas (MEES and HAMERLYNCK, 1992). Especially in the highly turbid brackish water zone of the estuary extremely high densities of mysids are noted. These mysids are an important food for fish (SORBE, 1981a; HAMERLYNCK *et al.*, 1990) and shrimp (SITTS and KNIGHT, 1979) and they are probably direct grazers of the imported organic matter (MANN, 1988). In the brackish zone, hyperbenthic animals can be considered as an important component of the detritus-based estuarine food chain joining the 'microbial loop' (detritus and its associated bacterial fauna) to higher trophic levels.

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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. In this paper 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. Such a descriptive baseline study is a first step in trying to unravel the functioning of the estuarine ecosystem. If strong correlations can be found between the environmental gradients and the hyperbenthic communities, and if the detected spatial patterns prove to be stable in time, knowledge of the fluxes involved would enable us to include the hyperbenthos in a simple mathematical model of the estuarine system.

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?

MATERIALS AND METHODS

Study area

The Westerschelde estuary 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 and STIRLING, 1976). Mixing of the water is complete (no stratification of salinity or current exists). The river drains about 19500 km^2, mainly in Flanders. The mean fresh water load is estimated at 105 m^3 s^{-1}. The total volume of the estuary ($2.5 \ast 10^9$ m^3) is large in

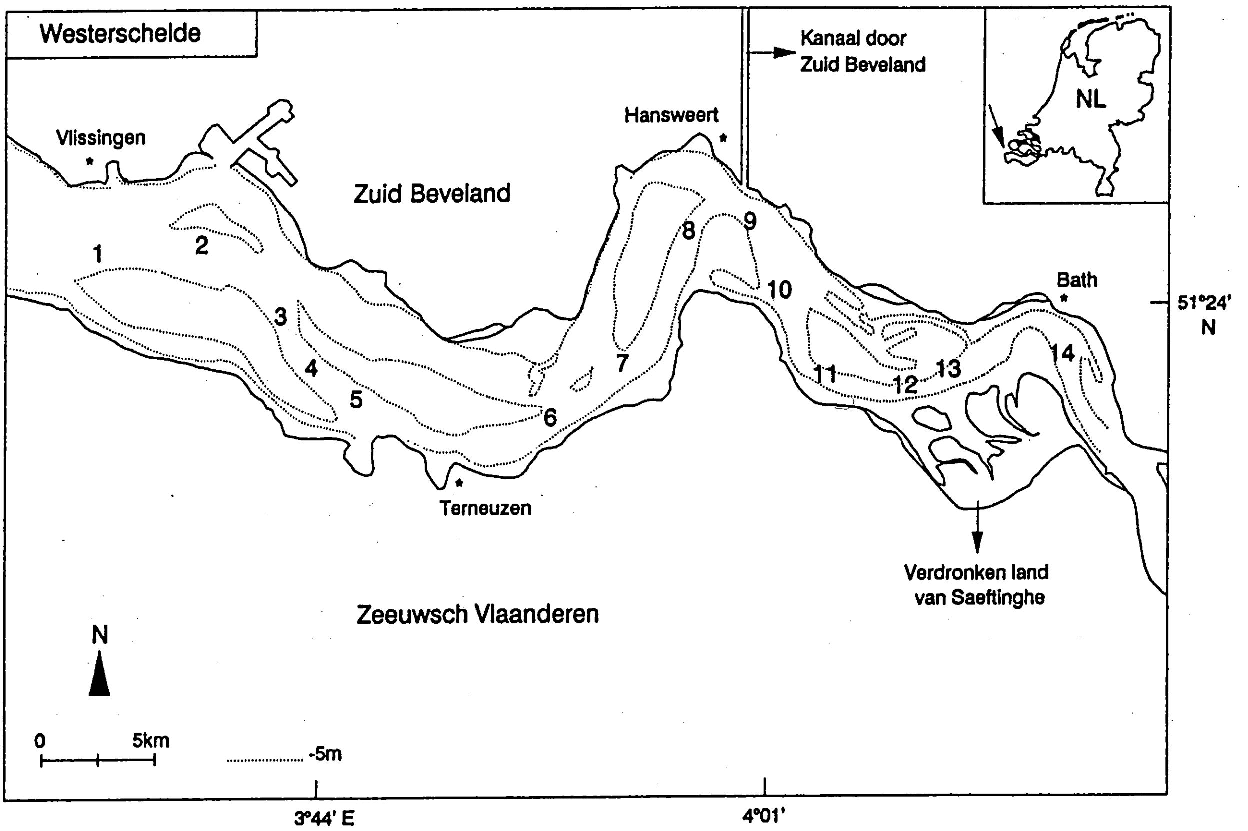

Figure 1. Westerschelde estuary (Dutch part) with location of the sampling stations.

comparison with the volume of water that enters each day from the river ($9*10^6$ m^3). Consequently, the residence time of the water is rather long: 75 days or 150 tidal cycles between the border and Vlissingen (HEIP, 1989). This duration 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^{-1} a few kilometres upstream from the Dutch-Belgian border (VAN ECK *et al.*, 1991).

Sampling

Samples were collected with a hyperbenthic sledge which consisted of a heavy metal frame equipped with two nets. The nets had 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 sampled 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 was 0.8 m^2. 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 (Fig. 1, Table 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^{-1}. Trawling was always done with the tide. This scheme was followed on three occasions (1990-April-20, 1990-August-23 and 1990-December-11) in order to cover a spring, summer and winter situation.

Temperature, salinity, conductivity, dissolved oxygen, pH and Secchi disc 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 (AFDW) per trawl (1000 m^2) or per m^2. Net efficiency was considered to be 100%; all density and biomass values should be considered as minimum estimates (MEES and HAMERLYNCK, 1992).

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 $-\infty$ to $+\infty$. 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_∞ is the reciprocal of the proportional abundance of the commonest species: the dominance index).

Table 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 following analyses were performed: a classification (clustering based on the Bray-Curtis similarity index and Group Average Sorting - GAS), an ordination (Canonical Correspondance Analysis - CCA), and a hybrid technique (Two-way Indicator Species Analysis - TWINSPAN). All multivariate techniques were applied to 4th 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 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.

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 and CURTIS, 1957) was performed on the same datamatrices.

The relationship between species composition and the environmental variables measured at each site was analyzed using the CCA option from the program package CANOCO (TER BRAAK, 1988). Conductivity data were excluded from the analysis 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.

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 kth dominant species and all more dominant species) against the logarithm of the rank k. In graphs of the species abundance distribution the number of species represented by 0, 1, 2,... individuals were plotted against logarithmic density classes.

RESULTS

Exploration of the data matrix

A total of 104 species were recorded (Table 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 were 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 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 2. The total numbers of individuals caught in the entire study area per month were in the order of 90,000 (belonging to 35 species) for April, 280,000 (48 species) for August and 18,000 (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 Fig. 2. *Neomysis integer* was absent from the western part of the Westerschelde but 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 (Fig. 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* (Fig. 3) was also restricted to the brackish zone. It occurred throughout the year in low numbers.

Table 2. List of species caught with the hyperbenthic sledge in the Westerschelde with the abbreviations used. Species marked with * were excluded from all analyses.

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

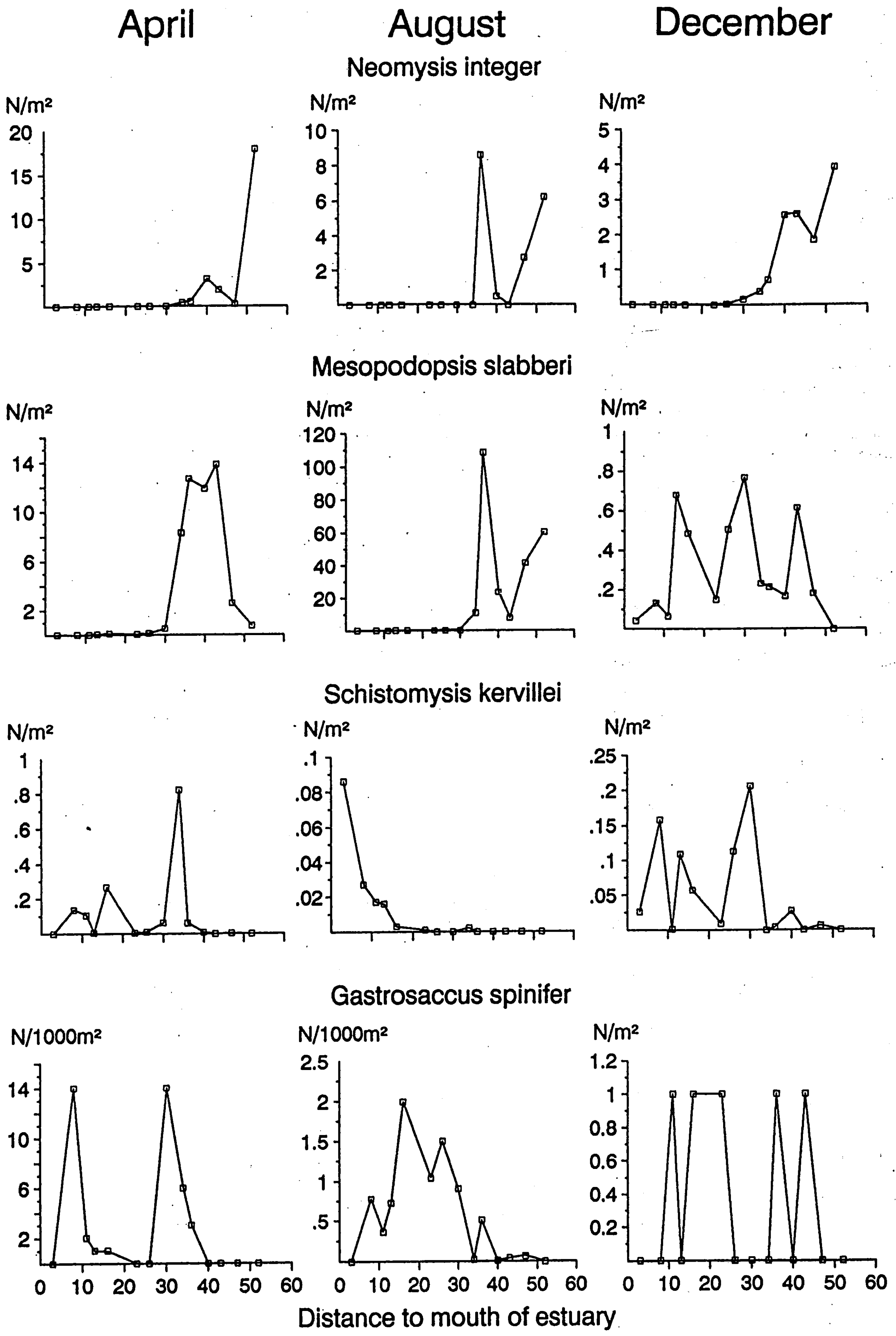

Fig. 2. Distribution of the most abundant mysid species along the axis of the estuary in April, August and December.

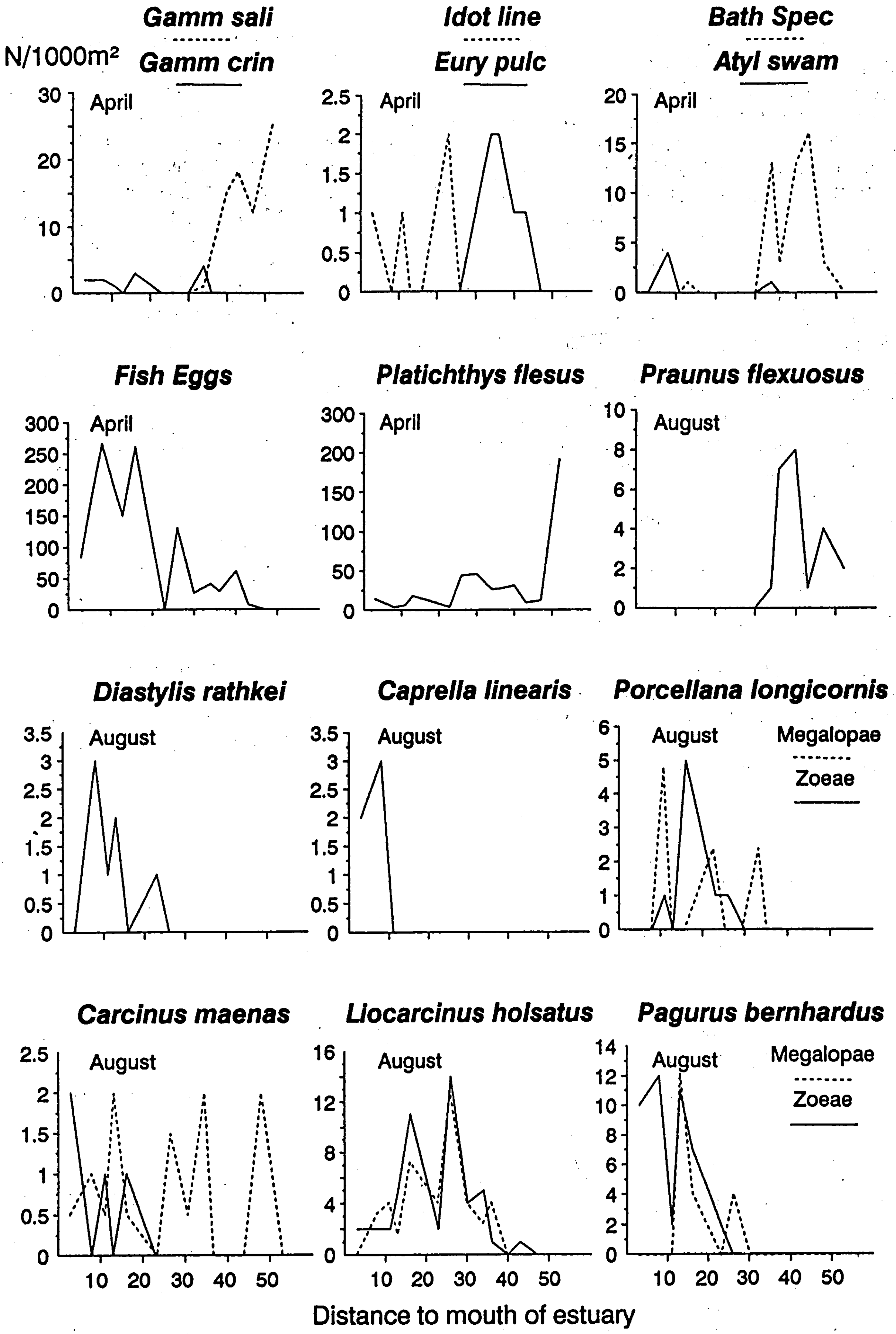

Fig. 3. Distribution of selected hyperbenthic animals along the axis of the estuary in April and August.

Schistomysis spiritus is a typical marine species which entered the estuary in winter, was still present in very low numbers in spring but completely absent in summer (not shown).

The distribution of some other hyperbenthic species characteristic for the different communities was shown in Fig. 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, *Platichthys flesus*.

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 3). The variation in diversity (N_0, N_1, N_2 and N_∞) between sites is shown in Fig. 4. The innermost sites had a clearly lower diversity for all measures: these samples are 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 were distributed more evenly among them. For the total study area, the highest number of species were 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.

Environmental variables

The main environmental gradients for each season are shown in Fig. 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 probably due to thermal enrichment from the nuclear power plant of Doel near the Dutch-Belgian border just outside the study area.

Table 3. Hill's diversity numbers N_0, N_1, N_2, and N_∞ 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	**ap1**	**ap2**	**ap3**	**ap4**	**ap5**	**ap6**	**ap7**	**ap8**	**ap9**	**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_∞	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
Aug.	**au1**	**au2**	**au3**	**au4**	**au5**	**au6**	**au7**	**au8**	**au9**	**au10**	**au11**	**au12**	**au13**	**au1**	**4 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_∞	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
Dec.	**de1**	**de2**	**de3**	**de4**	**de5**	**de6**	**de7**	**de8**	**de9**	**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_∞	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

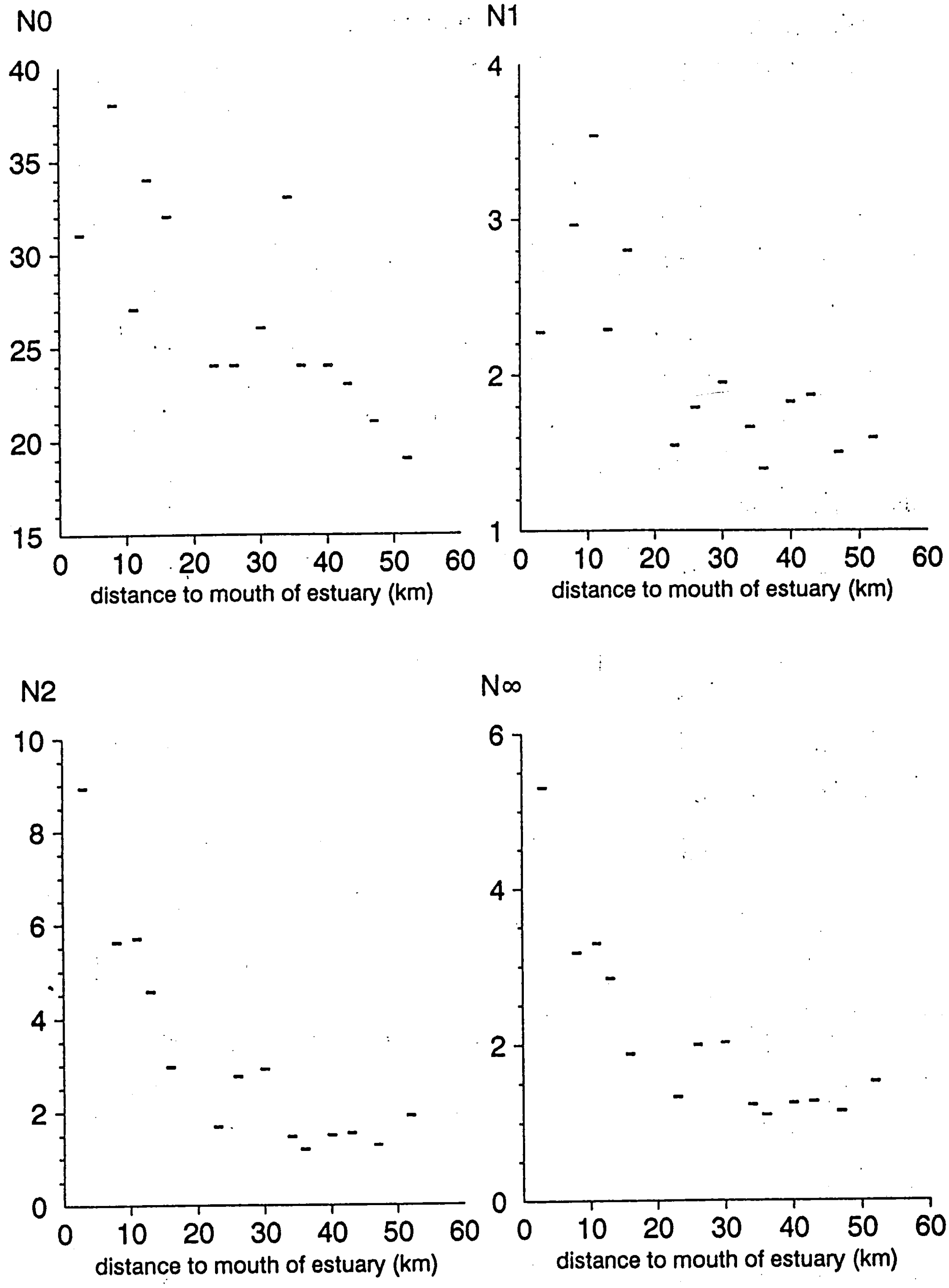

Fig. 4. Hill's diversity numbers for each station, calculated from the sum of the density data over the 3 months.

Analysis of temporal and spatial patterns (complete data set)

Identification of communities

The result of the TWINSPAN analysis performed on the (4th root transformed) density data of the three seasons taken together is presented in Fig 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*

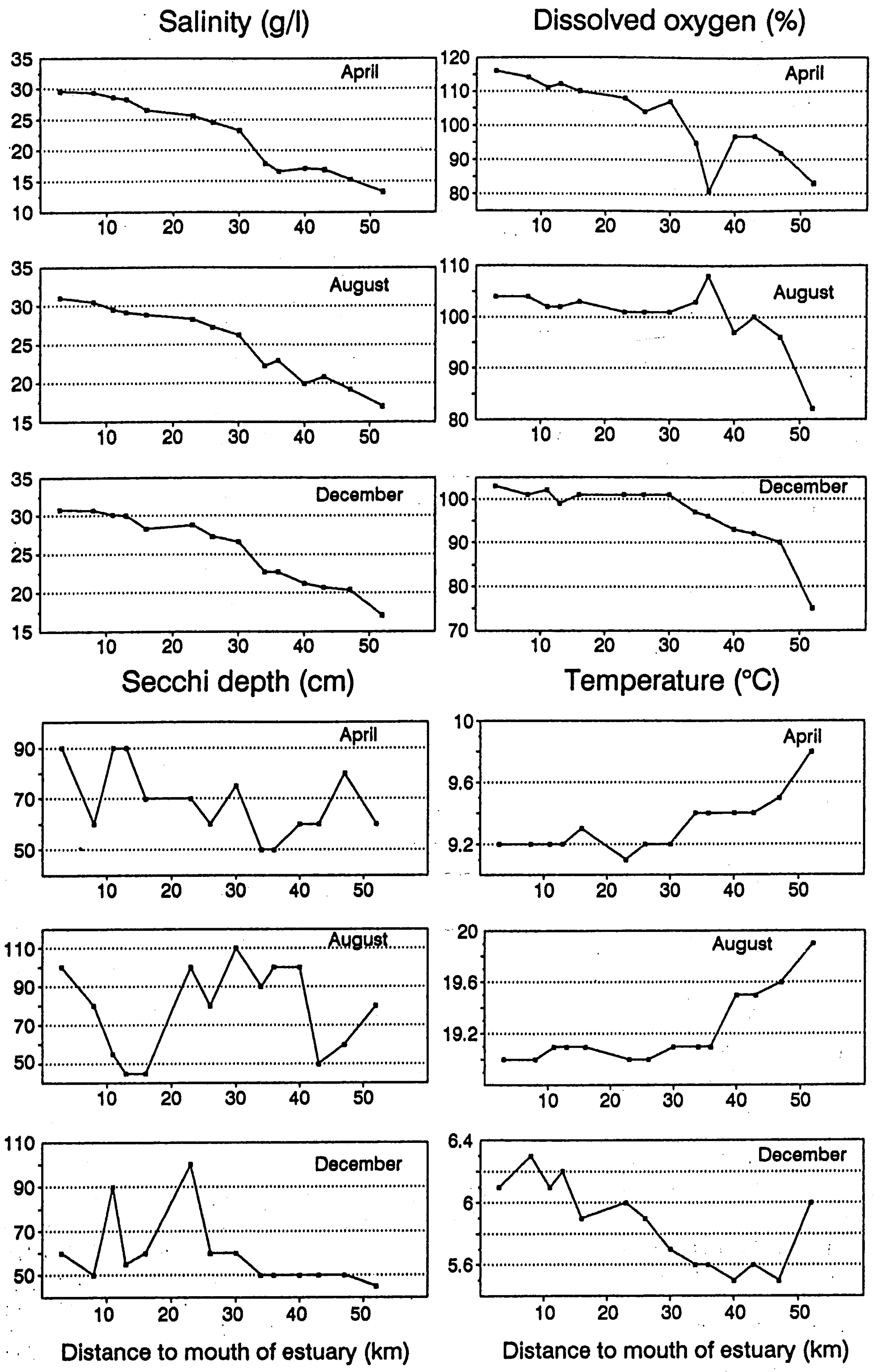

Fig. 5. Environmental variables measured at each station for the three months.

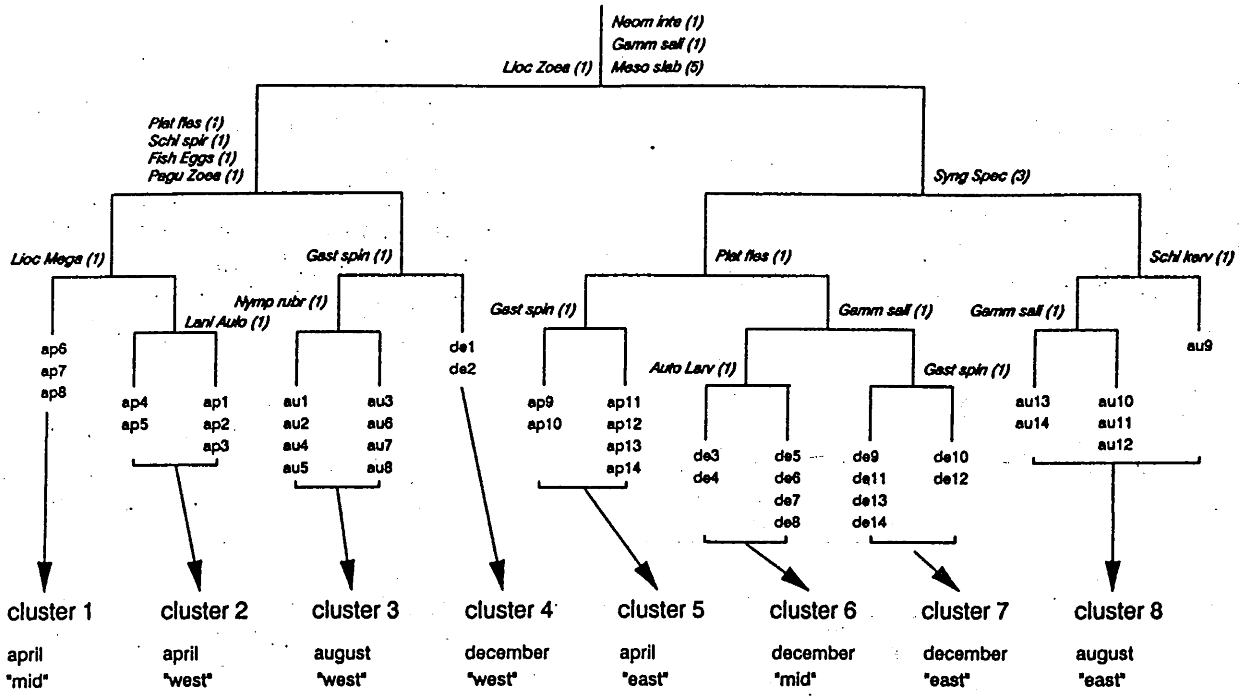

Fig. 6. TWINSPAN clusters, derived from the matrix of the (4th root transformed) density data of the three months. Indication of clusters as discussed in the text.

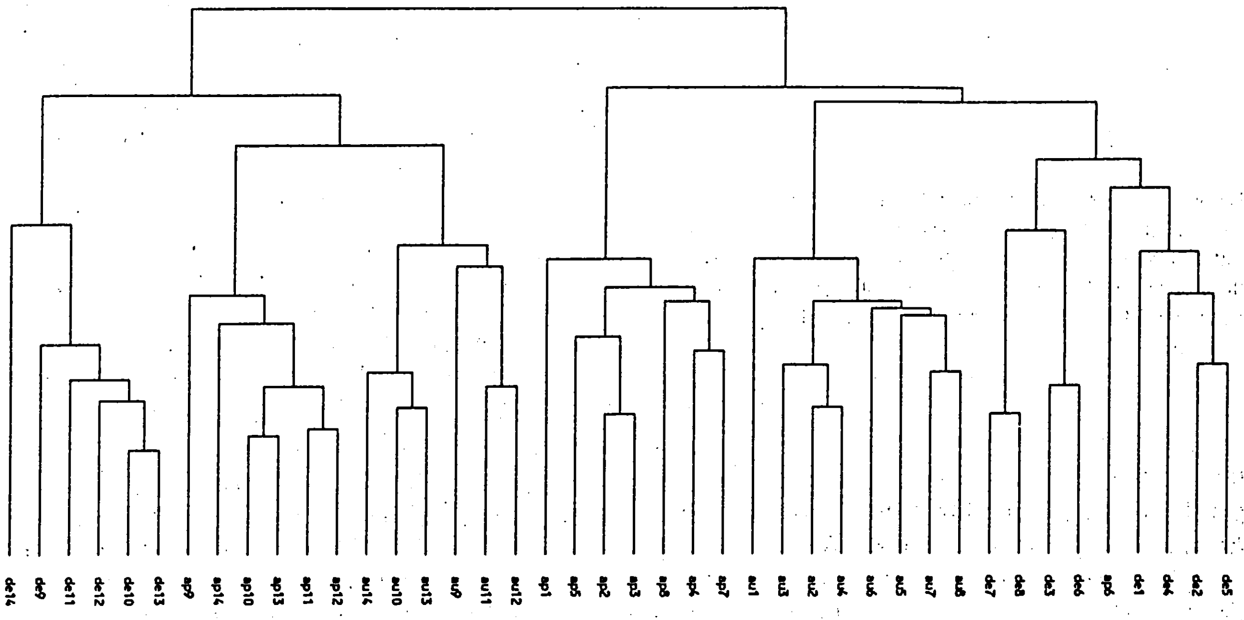

Fig. 7. Group average sorting of all density data using Bray-Curtis similarities.

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: *Platichthys 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 Fig. 6). A similar pattern appears in the Eastern group. In the first instance all summer samples are split off. In a subsequent division in

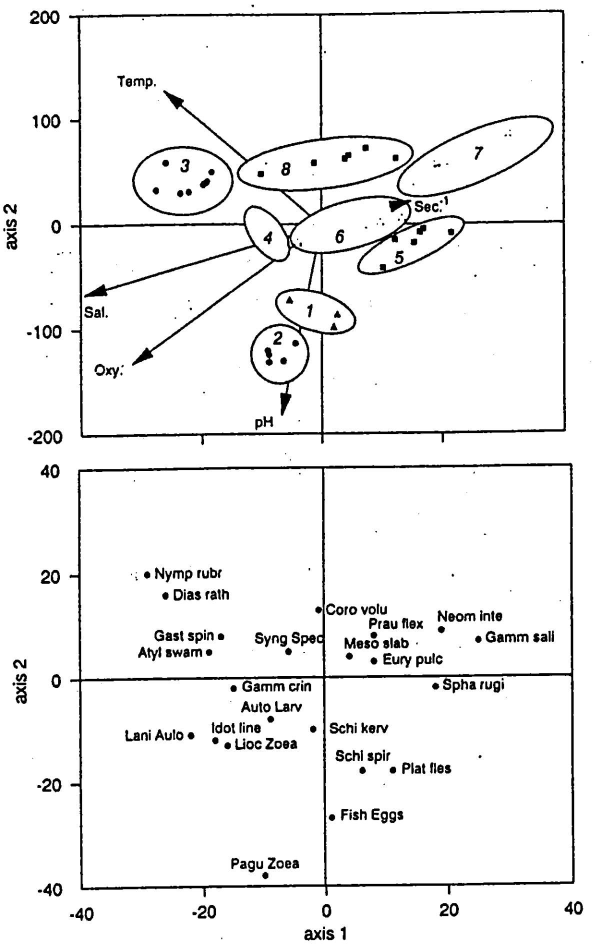

Fig. 8. Results of CANOCO analysis using the density data of the three months. Biplot of sample scores and environmental variables with indication of the communities as identified by TWINSPAN (top), and biplot of scores of the most important species (bottom). The scores of the environmental variables were divided by 4 to fit the graph.

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 yields almost the same picture (not presented). The difference is that in the very first division all April samples are isolated with *Platichthys flesus* as indicator species. The following divisions in both major groups cluster the samples in exactly the same order as indicated in Fig. 6. Only station 9, situated at the interface between the marine and the brackish parts of the estuary, occasionally shifts from one cluster to another.

Dendrograms for the cluster analyses have essentially similar configurations. The analysis with the density data (Fig. 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) were 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 (Fig. 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.

The longest arrows in the environmental biplot (Fig. 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°), 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 divided into two zones. On the left side all Western samples (characterised by high salinity, high oxygen and low turbidity) are grouped; on the right side all Eastern samples are found (characterised 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 (Fig. 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 did not penetrate far into the estuary. They are characteristic for the hyperbenthic communities of

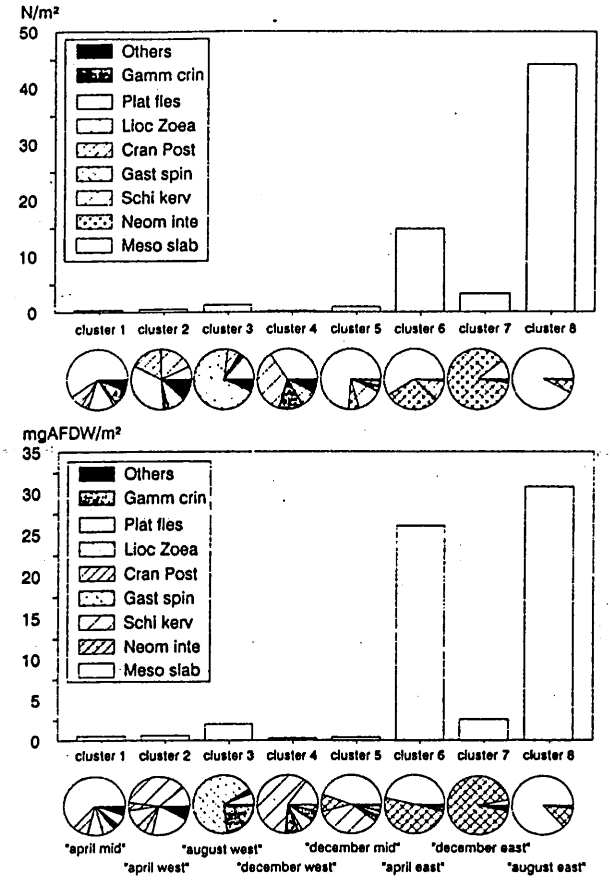

Fig. 9. Composition and average density (top) and biomass (bottom) of the communities identified by TWINSPAN of all density data.

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 were characteristic for the hyperbenthos of the Eastern part of the study area throughout the year.

In both plots the spreading of items (samples and species) along the second axis is most pronounced in the left half of the diagram. Moving towards the right, items show a tendency to converge towards the first axis. This result 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 showed a nearly identical composition in each season.

Characterisation 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 Fig. 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 characterised 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 characterised by a poor hyperbenthic fauna in terms of density and biomass, but the communities were composed of many different species.

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 *N. 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 *M. slabberi,* though this slender species did not contribute much to the total biomass of the community. The biomass pie chart showed 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 *M. slabberi* (density) and *N. 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 characterised by a mixture of the species characterising 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.

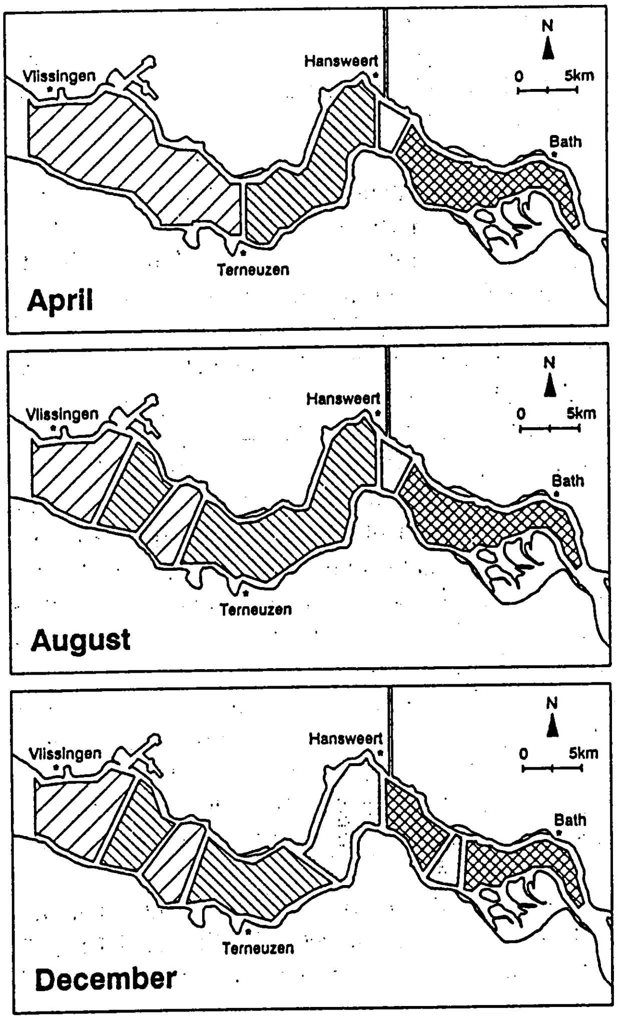

Fig. 10. Geographical location of the four different communities identified by TWINSPAN of the density data for separate months.

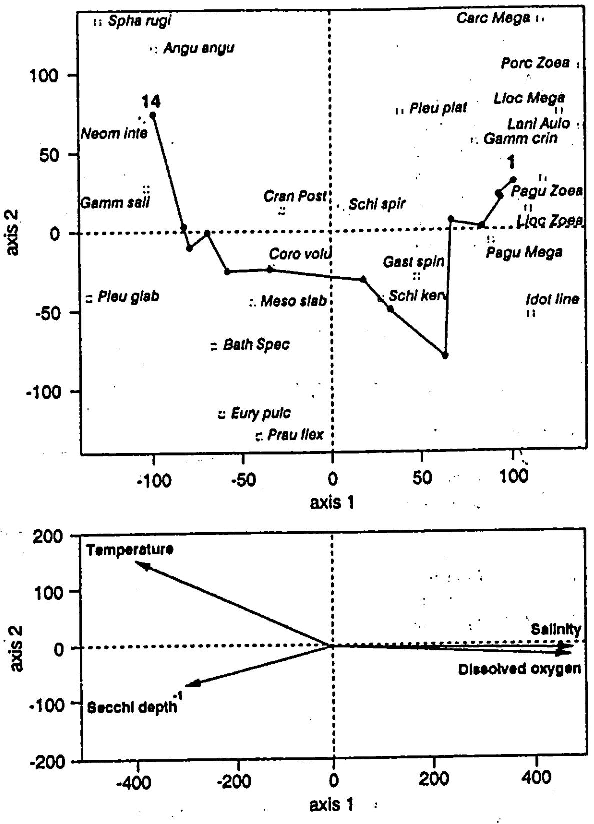

Figure 11. Results of CANOCO analysis using the density data of April. Biplot of environmental variables (bottom), and biplot of sample scores and scores of the most important species (top). The solid line in the top graph indicates the real space order of the samples.

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. Fig. 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

Fig. 11 depicts the results of the canonical correspondance analysis performed with the density data of the spring campaign and is exemplative for the 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 (Fig. 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 sali-

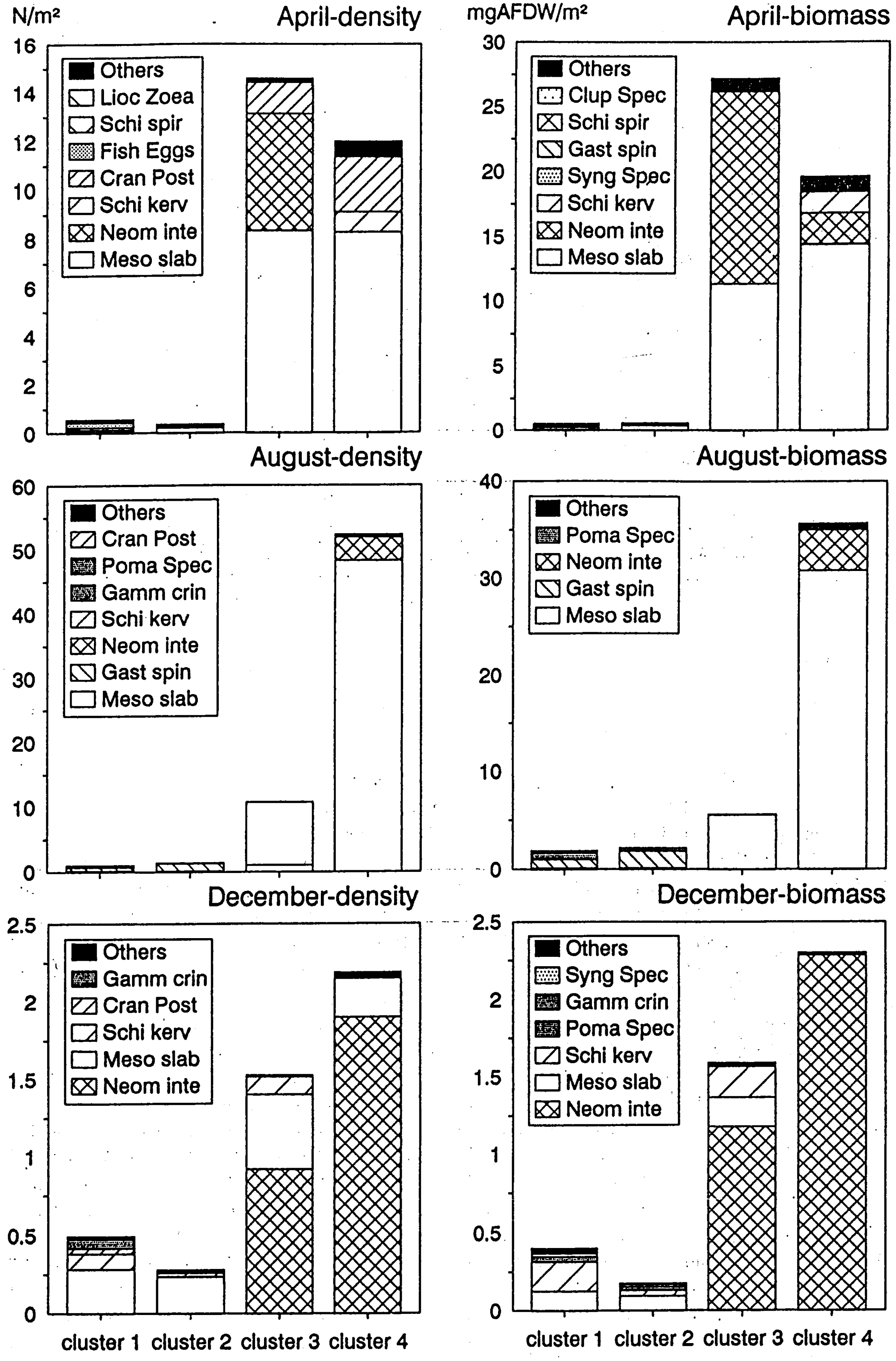

Fig. 12. Average density (left) and biomass (right) of the communities identified by the TWINSPAN analysis with the density data of the separate months.

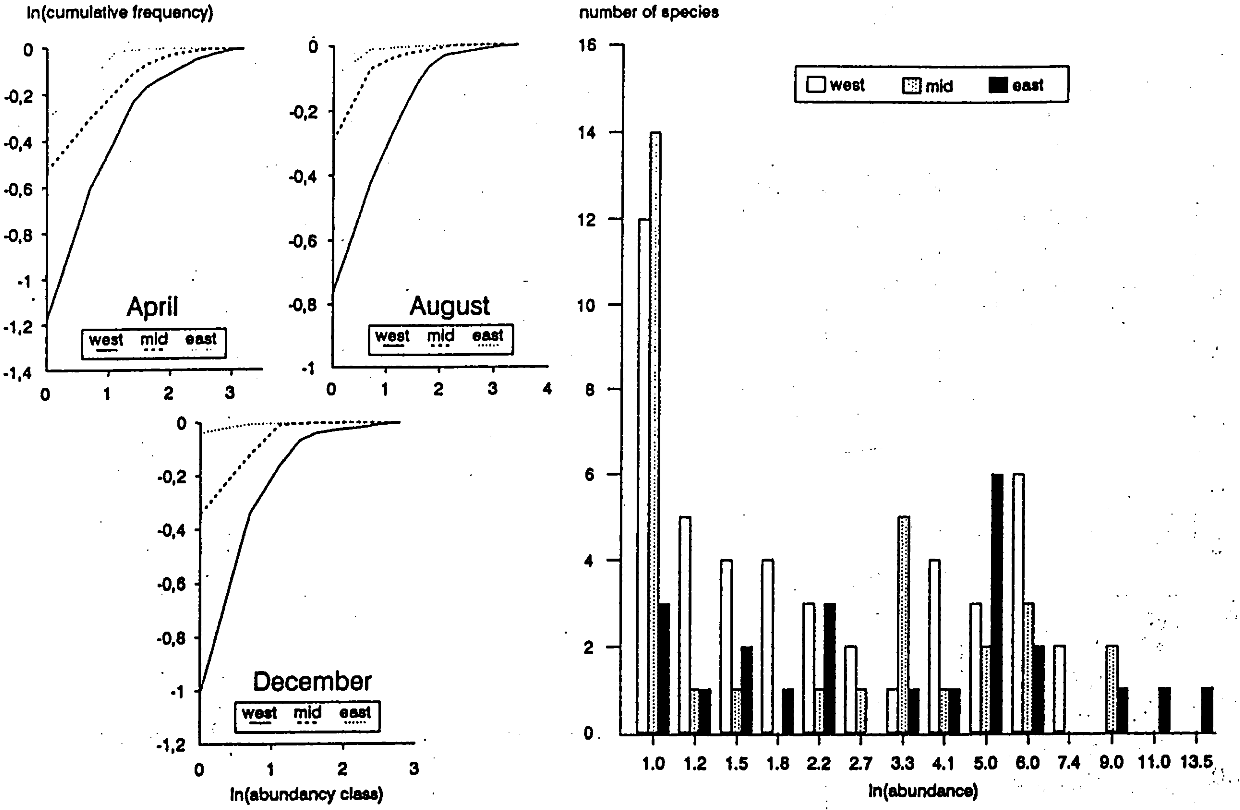

Fig. 13. K-dominance plots for three different communities in each month (left) and the species-abundance distribution for the same communities using the sum of the data over the 3 months (right).

nity 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 Figs. 2 and 3.

Characterisation of the communities

Fig. 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 characterised by a much richer hyperbenthic fauna (higher density and biomass) which was dominated by *Mesopodopsis slabberi* and *Neomysis integer*. The Western clusters (1 and 2) are characterised by lower numbers of individuals spread over a higher number of species.

For the construction of the k-dominance curves and the species-abundance plot (Fig. 13) the communities considered are not the sums of the samples of the twingroups, 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 (Fig. 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 (Fig. 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.

DISCUSSION

Ideally, a random stratified sampling scheme should be used in ecological surveys. For our sampling programme there were, however, some logistic limitations in selecting the sampling stations. First, stretches of 1000 m length had to be found which were free of 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* (TATTERSAL and TATTERSAL, 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 upstream of the Dutch-Belgian border (MEES, *et al.*, 1993). In the salinity range sampled, the species composition of the mysid fauna of the Westerschelde resembles that of other European estuaries (*e.g.* MOFFAT and 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.* CCA April). The change is not abrupt. The combination of several multivariate techniques merely gives us objective criteria to decide where one community stops and an other 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 very 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 the samples from the same location of any other month (HAMERLYNCK and 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.* Fig. 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 (Figs. 7 and 8). The main reason for this is the fact that the spatial gradient in species composition in estuaries is very 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 (Fig. 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 (Fig. 2), community structure as a whole thus remains stable throughout the year.

ACKNOWLEDGEMENTS

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Address of the authors:

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

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Comparative study of the hyperbenthos of three European estuaries

Jan Mees[1], Nancy Fockedey[1] & Olivier Hamerlynck[1,2]
[1]*Marine Biology Section, Zoology Institute, University of Ghent, K. L. Ledeganckstraat 35, B-9000 Gent, Belgium*
[2]*Centre for Estuarine and Coastal Ecology, Netherlands Institute for Ecology, Vierstraat 28, NL-4401 EA Yerseke, The Netherlands*

Key words: hyperbenthos, estuary, Mysidacea, multivariate analysis, Westerschelde, Gironde, Eems

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 g l^{-1} 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*.

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 and this volume). 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. Hartman, 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 characterised 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 (1981). No information on the hyperbenthos of the Eems estuary was available to date.

Materials and methods

Study area (Fig. 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^2, including a fresh water tidal area in the Eems of about 37 km^2 (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 12 650 km^2), which has a variable discharge ranging from 25 to 390 m^3 s^{-1}. The Westerwoldsche Aa has no well defined watershed and discharges roughly 10 % (5.1 to 31 m^3 s^{-1}) 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^{-1} (Baretta & Ruardij, 1988). Dissolved oxygen concentration in the estuary proper rarely drops 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 Antwer-

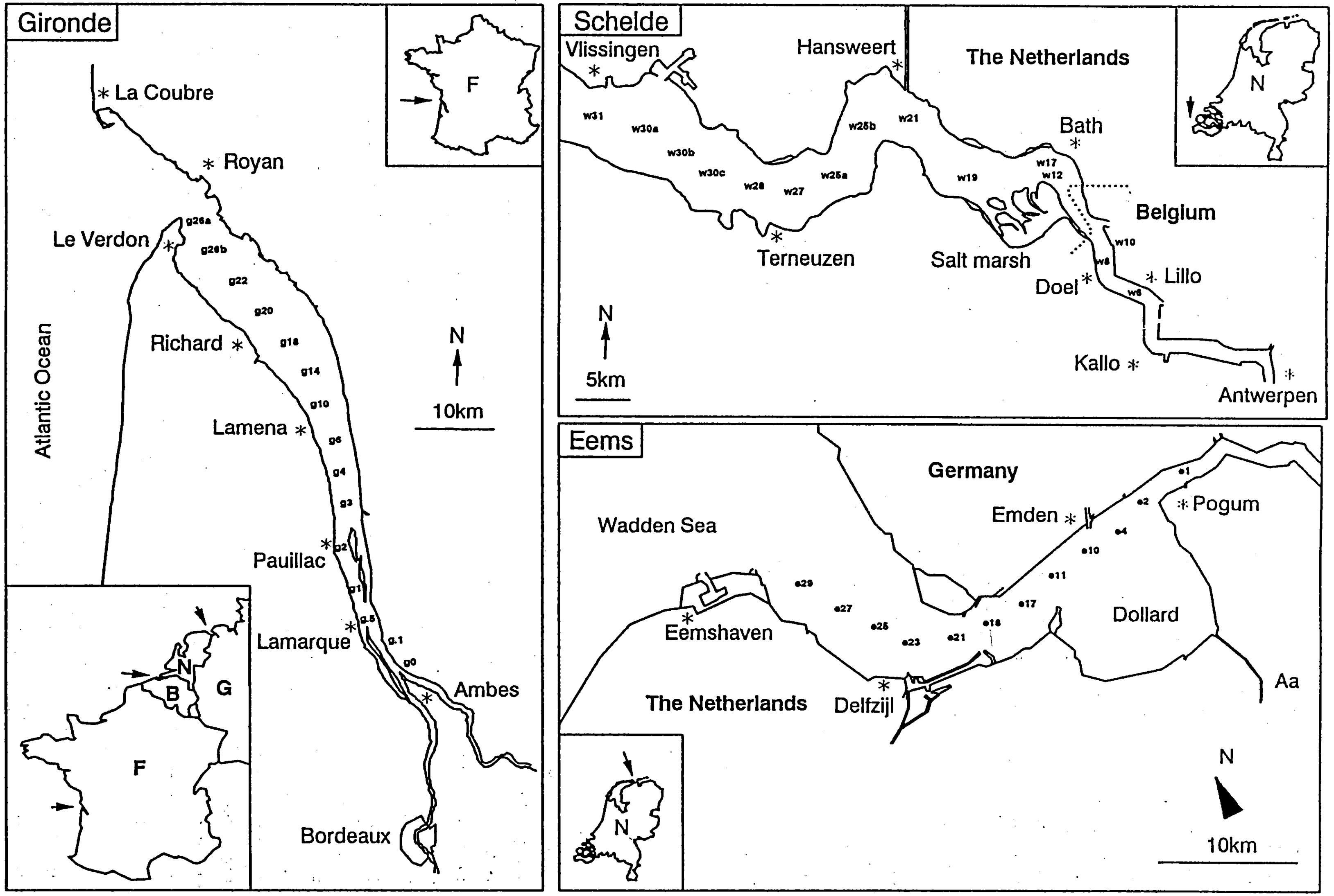

Fig. 1. Study area and sampling sites: the names of the samples are composed of a letter indicating the estuary and a number representing the salinity zone in which it was taken.

pen, 80 km inland. The estuary is rain fed, with a catchment area of some 20 000 km^2. Its surface is approximately 300 km^2. The seaward part is a well mixed region characterised 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, submitted). Consequently fresh water (average inflow 100 m^3 s^{-1}; range 30 to 500 m^3 s^{-1}) 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 g l^{-1} suggesting there is no real maximum turbidity zone in this estuary.

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 71 000 km^2 (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 characterised 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^2. 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^3 s^{-1} in summer to 1500 m^3 s^{-1} in winter (800–1000 m^3 s^{-1} 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^{-1} and values of 5 g l^{-1} and higher are regularly recorded (mainly silt and clay particles from freshwater origin).

Sampling

The location of the sampling stations in Eems, Westerschelde and Gironde is shown in Fig. 1. In the Eems 12 evenly spaced (3 km) stations were sampled in salinity zones ranging from 28.6 g l^{-1} near Eemshaven to 1.0 g l^{-1} near Pogum. In the Westerschelde 15 samples were taken from a salinity of 31.0 g l^{-1} near Vlissingen down to a salinity of 6.3 g l^{-1} 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 g l^{-1} near Le Verdon to truly freshwater (0.0 g l^{-1}) 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^2; the maximal volume of water filtered through the nets is 800 m^3. 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,

Table 1. Common species excluded from the community analyses on the basis of size, with total number caught in each estuary

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

pH, conductivity and temperature were measured near the bottom.

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 (Mees unpublished, Mees *et al.* 1994). Densities of species growing in discrete stages were converted to biomass with average AFDW values.

Statistical analysis

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

N_0 = the number of species,
$N_1 = e^H$ with $H = -\Sigma p_i \ln(p_i)$ (p_i is the relative abundance of the i dominant species),
$N_2 = \Sigma p_i^2$ and
$N_\infty = 1/p_1^{-1}$ (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 datamatrices 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.

Table 2. List of species and abbreviations used in the community analyses. Middle column: first letter of the estuary(ies) in which they occurred.

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

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 cutlevels 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.

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 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* (carapaxlength <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 accidentely caught species: *Macoma ballhica*, *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).

From a total of 101 recorded species, 58 were thus retained after data reduction (Table 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.

Environmental gradients

The environmental variables measured at each station are presented in Table 3. The most pronounced gradient in the three estuaries was salinity (see materials and methods). 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 g l^{-1} 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 characterised 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 inner-

Table 3. Environmental variables measured at the end of each trawl.

Eems	e29	e27	e25	e23	e21	e18	e17	e11	e10	e4	e2	e1
Salinity (g l^{-1})	28.63	26.54	25.34	22.87	21.00	18.47	16.65	11.44	10.03	4.45	1.96	0.94
Secchi depth (cm)	120	50	45	20	20	15	20	10	10	5	5	5
Temperature (°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
Salinity (g l^{-1})	31.00	30.30	29.50	29.50	28.00	26.60	25.40	25.00	21.10	19.30	17.00	11.90	10.30	8.10	6.30
Secchi depth (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	–

Gironde	g26a	g26b	g24	g20	g18	g14	g10	g6	g4	g3	g2	g1	g.5	g.1	g0
Salinity (g l^{-1})	26.10	26.00	24.00	20.00	18.00	14.00	10.00	6.00	4.00	3.40	2.00	1.40	0.50	0.10	0.00
Secchi depth (cm)	440	440	260	90	40	40	30	10	5	5	3	5	3	5	10
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

most 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.

General trends in density, biomass and diversity

In Westerschelde and Gironde hyperbenthic density (Fig. 2) and biomass (not figured) were lowest in the most seaward stations. They increased upstream, decreasing again towards the most riverine stations.

In comparison to the other estuaries, the Eems was characterised 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^2) but, in contrast to the other estuaries, was already high at the 27 g l^{-1} isohaline. Densities remained at about the same level (between 10 and 20 ind m^2, 10 to 47 mg AFDW per m^2) upto 17 g l^{-1}. A drop in density (again less than 5 ind m^2) was observed at the 11 g l^{-1} isohaline (mouth of the Dollard). Density and biomass then increased to a maximum of 26 individuals or 66 mg AFDW per m^2 at the 2 g l^{-1} isohaline and decreased again in the last station. Some of the density peaks reflect the appearance and disappearance of dominant species (Fig. 3): the peak around 21 g l^{-1} was mainly due to high densities of *Schistomysis kervillei*, the peak around 2 g l^{-1} reflects the abundance maximum of *N. integer*, which was of overriding importance throughout most of the estuary.

In the Westerschelde two peaks were evident (Fig. 2): a first in the 19 g l^{-1} salinity zone, a second around 10 g l^{-1}. These were an order of magnitude higher than maximal densities observed in the other estuaries (250 and 105 individuals per m^2; 555 and 208 mg AFDW per m^2). 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 g l^{-1} and in the 6 g l^{-1} 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 g l^{-1}. In the marine stations (w31 to w21) of the Westerschelde density and biomass were below 3.5 ind per m2 and 3.5 mg AFDW per m^2 respectively.

Densities in the Gironde were only substantial upstream of the 20 g l^{-1} 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

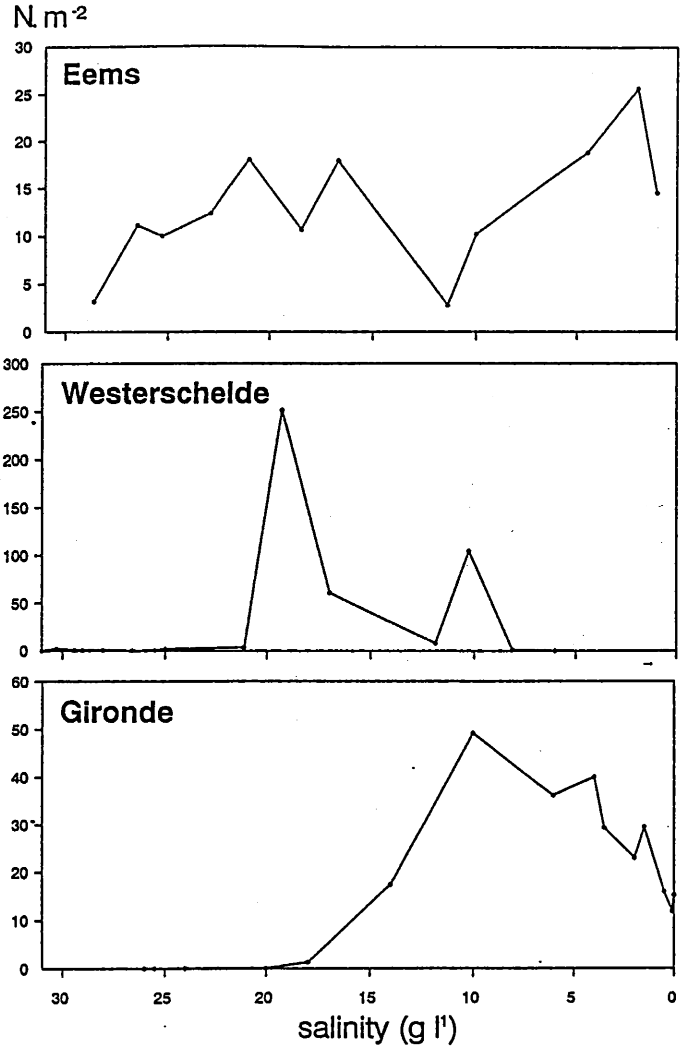

Fig. 2. Total hyperbenthic density along the salinity gradients in the three estuaries.

(50 individuals or 63 mg AFDW per m^2 at 10 g l^{-1}) coincided with the maximal abundance of *Mesopodopsis slabberi* and submaximal abundances of *N. integer* (Fig. 3), the second peak (41 individuals or 113 mg AFDW per m^2 at 4 g l^{-1}) corresponded with maximal densities of *Pomatoschistus microps* and high numbers *N. integer*, and the third peak (32 ind. m^2 or 99 mg AFDW at 1 g l^{-1}) corresponded to the abundance maximum of *N. integer* (Fig. 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 (Fig. 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 Fig. 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. L_∞ 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.

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 Fig. 5. Below, the distribution patterns are described based on the density data only (biomass data of the individual species are available on request).

Mysidacea
Gastrosaccus spinifer occurred in the three estuaries from the marine reaches upto the 10 g l^{-1} isohaline. Maximal densities amounted to 3400 ind per 1000 m^2 in the Westerschelde (at 19 g l^{-1}) and 650 ind in Gironde and Eems (at 18 and 29 g l^{-1}, 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 g l^{-1} isohaline where it reached a maximal density of 60 individuals per m^2. The same pattern was observed in the Gironde (maximal densities of 39 ind m^2 at 10 g l^{-1}), but here the species was still present in the most upstream stations (upto 0 g l^{-1}). 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 g l^{-1}) where a maximum of 20 ind m^2 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 g l^{-1} (maximum of 250 ind 1000 m^2 at 30 g l^{-1}). In the Eems the species moved much further up the estuary (upto 11 g l^{-1}) and reached maximal abundance at lower salinities (7000 ind 1000 m^2 at the 21 g l^{-1} isohaline). *S. spiritus* is also a typical coastal species which was present in the three estuaries from the mouth to 10, 21 and 14 g l^{-1} in Eems (maximal abundance of 800

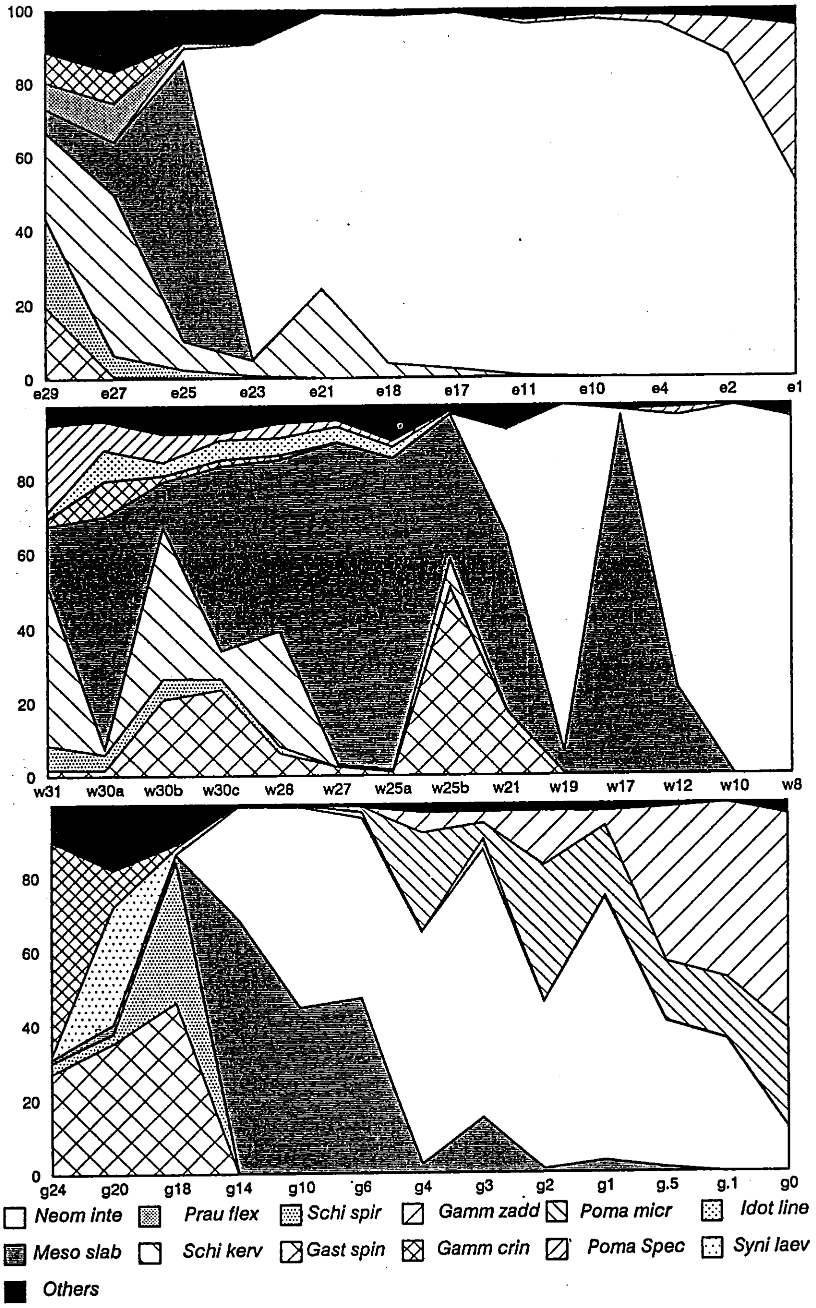

Fig. 3. Relative species composition of the hyperbenthic community along the salinity gradient in Eems (top), Westerschelde (middle) and Gironde (bottom).

individuals per 1000 m2), Westerschelde (55 ind) and Gironde (800 ind), 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 Fig. 6). In the Eems the species was present from 25 g l^{-1} upto 1 g l^{-1} (maximum of 18 ind m^2 at 4 g l^{-1}). In the Gironde it colonised the salinity zone from 18 to 0 g l^{-1} (maximum of 26 ind m^2 at 4 g l^{-1}). In the Westerschelde *N. integer* was only present from 21 to 8 g l^{-1} with much higher maximal densities of 193 and 103 ind m^2 at the 19 and 10 g l^{-1} isohaline depending on the sampling date. *Praunus flexuosus* was only recorded in Eems and Westerschelde. In the former estuary densities amounted to 284 ind m^2 at 27 g l^{-1} (range 29 to 18 g l^{-1}), in the Westerschelde density was always

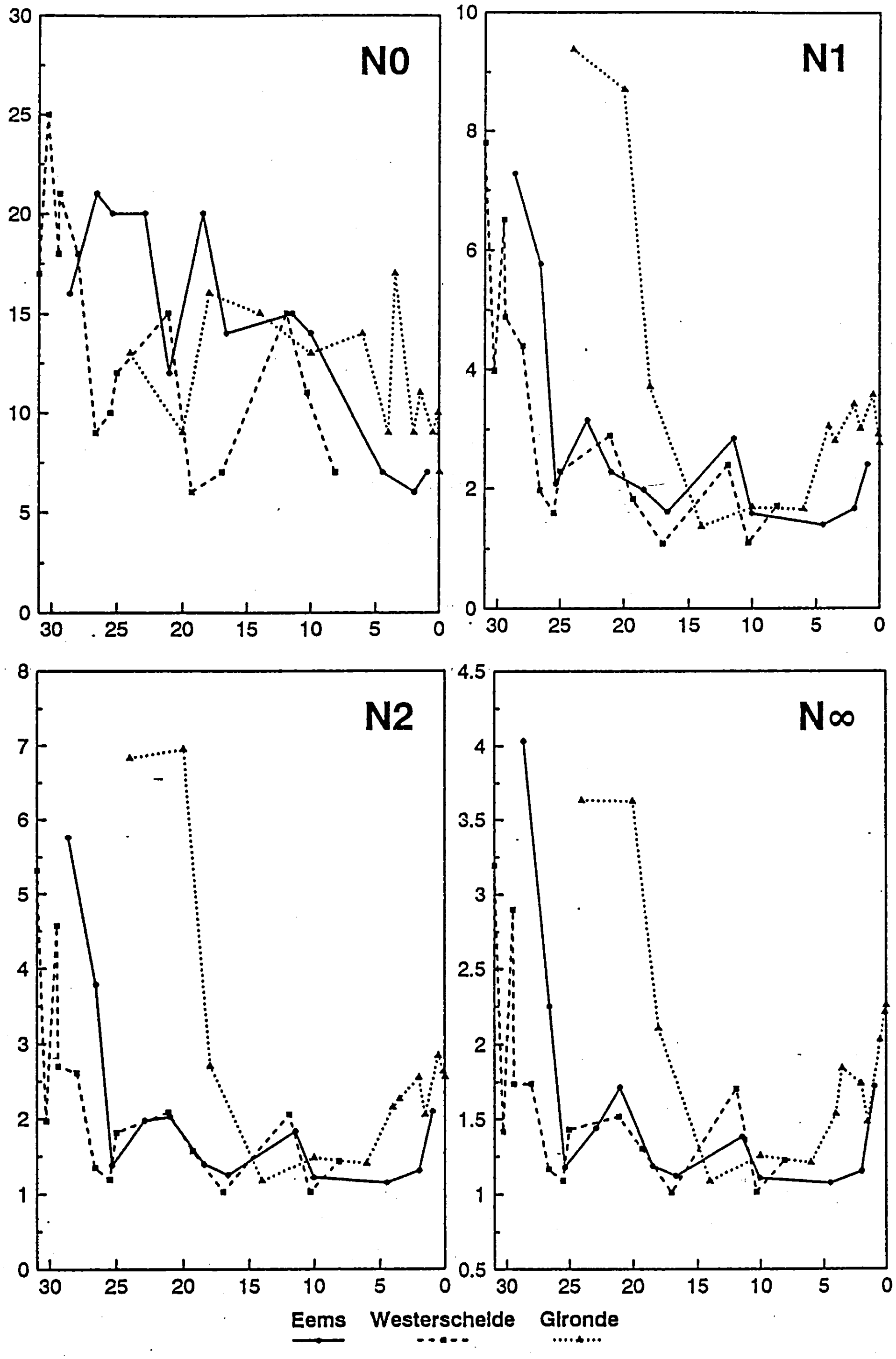

Fig. 4. Diversity numbers of Hill plotted against salinity.

low (maximum of 33 ind 1000 m^2) in the salinity zone from 25 to 17 g l^{-1}.

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 g l^{-1}), 103 (30 g l^{-1}) and 8 (24 g l^{-1}) individuals per 1000 m^2 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 g l^{-1} (maximum of 52 ind 1000 m^2 at 10 g l^{-1}) and in the Gironde between 14 and 0.5 g

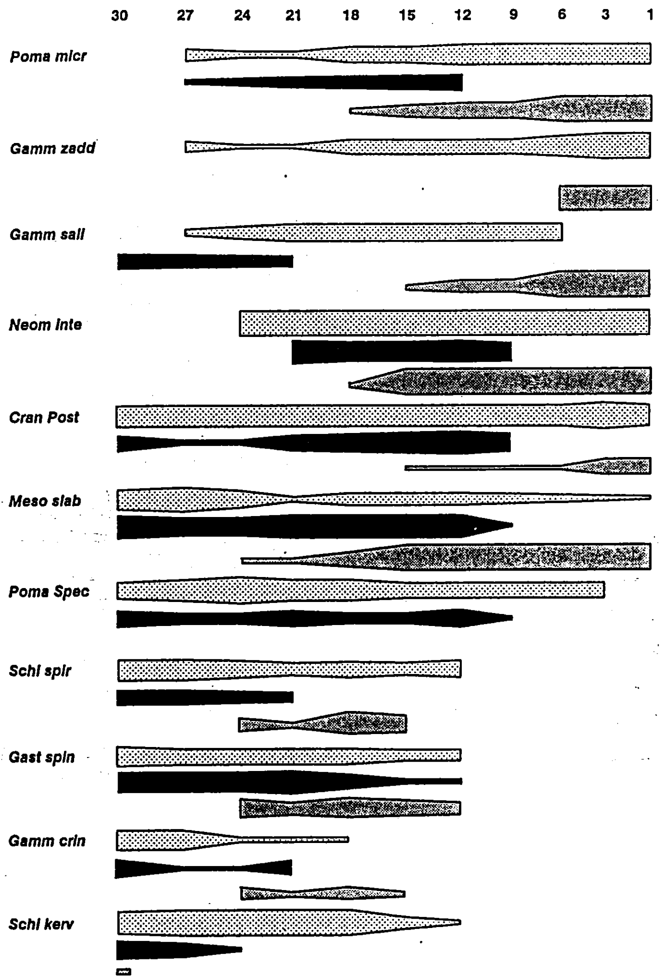

Fig. 5. Density distribution of the 11 most abundant hyperbenthic species along the salinity gradient of Eems (top), Westerschelde (middle, in black), and Gironde (bottom). Species are ordered following the two-way table of the TWINSPAN. Width of the bar gives indication of abundance reached in the salinity zone (top line).

l^{-1} (maximum of 1858 ind 1000 m^2 at 4 g l^{-1}). During this survey, *G. salinus* was only caught in low numbers (a total of 28 ind) 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 g l^{-1}: 5 and 7 ind m^2, 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 g l^{-1} station) and *G. locusta* (between 29 and 23 g l^{-1}, maximum of 160 ind 1000 m^2 at 27 g l^{-1}). *Atylus swammerdami* is a marine species. It was present in the Westerschelde from 31 to 27 g l^{-1}. In Gironde and Eems the species penetrated further into the estuary: upto 20 and 11 g l^{-1}, respectively. Densities were never higher than 30 ind 1000 m^2. 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 ind 1000 m^2). 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.

Isopoda

Eurydice pulchra was not observed in the Eems. The species was found in the Westerschelde in salinities ranging from 25 to 10 g l^{-1} with a maximal density of 26 ind 1000 m^2 at 12 g l^{-1}. In the Gironde only 4 individuals were caught between 18 and 3 g l^{-1}. *Idotea linearis* was only found in the marine parts of the Westerschelde (maximum of 85 ind 1000 m^2 at 30 g l^{-1}) and Eems (maximum of 13 ind 1000 m^2 at 29 g l^{-1}). *Synidotea laevidorsalis* was only present in the Gironde and was the only isopod which reached considerable densities and biomass (maximum of 288 ind 1000 m^2 at 3 g l^{-1}) 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 ind 1000 m^2 at 29 g l^{-1} in the Eems, 24 ind 1000 m^2 at 30 g l^{-1} in the Westerschelde, and 7 ind 1000 m^2 at 26 g l^{-1} 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 ind 1000 m^2 (1 g l^{-1}) in the Eems, 1148 ind 1000 m^2 (10 g l^{-1}) in the Westerschelde, and 39 ind 1000 m^2 (1 g l^{-1}) in the Gironde. *Palaemonetes varians* was only recorded in the Eems (zoeae and postlarvae between 23 and 10 g l^{-1}) and the Westerschelde (only postlarvae between 30 and 10 g l^{-1}). *Palaemon longirostris* is a typical species for the oligohaline reaches of estuaries. It was

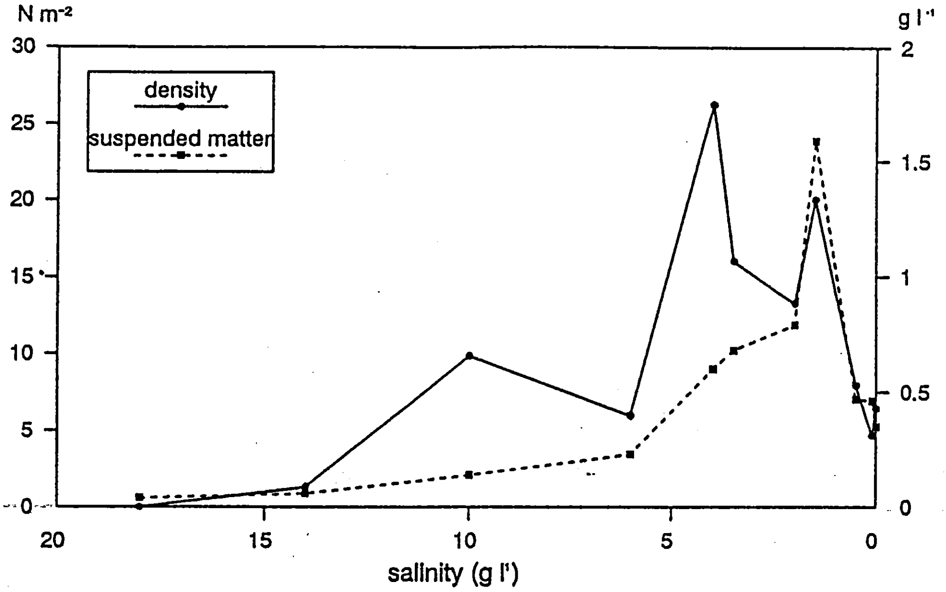

Fig. 6. Density of *Neomysis integer* (right axis) and concentration of suspended matter (left axis) plotted against the salinity gradient of the Gironde.

absent from the Westerschelde. Densities were low in the Eems (maximum of 9 zoeae, 23 postlarvae and 1 adult per 1000 m^2). In the Gironde it was the most abundant caridean: maximum of 44 zoeae (3 g l^{-1}), 324 postlarvae (2 g l^{-1}) and 224 adults (0.1 g l^{-1}) per 1000 m^2.

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 ind 1000 m^2) and megalopae (maximal densities of 861 and 17 ind 1000 m^2) were present upto the 10 g l^{-1} isohaline. *Liocarcinus holsatus* zoeae and megalopae were only common in the Westerschelde (298 zoeae and 31 megalopae per 1000 m^2 at 17 and 21 g l^{-1}, 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 ind 1000 m^2 at 1 g l^{-1}; range 27 to 1 g l^{-1}) and Gironde (maximal density of 6321 ind 1000 m^2 at 4 g l^{-1}; range 18 to 0 g l^{-1}). Densities in the Westerschelde were much lower (maximum of 5 ind 1000 m^2) and the species was only present downstream the 10 g l^{-1} isohaline. Postlarval *Pomatoschistus* species were absent from the Gironde. They were caught along the entire sampled transect of the Eems (maximum of 1260 ind 1000 m^2 at 2 g l^{-1}) and the Westerschelde (maximum of 1260 ind 1000 m^2 at 10 g l^{-1}). *Syngnathus rostellatus* was common in the marine reaches of the Eems (upto 17 g l^{-1}) and in the brackish reaches of Westerschelde (upto 12 g l^{-1}) and Gironde (upto 0.1 g l^{-1}). Larval clupeoids were always caught in low numbers (never more than 85 ind 1000 m^2) between the mouth of the estuary and 2 g l^{-1}, 19 g l^{-1} and 3 g l^{-1} 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 g l^{-1} isohaline in the Eems (300 ind 1000 m^2 as compared to less than 15 per 1000 m^2 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 *Pagu-*

rus and *Porcellana*) were recorded occasionally in the marine waters of all three estuaries.

Identification and characterisation 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 (Fig. 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 Westerschelde samples. Indicators for the Gironde group are postlarval *Palaemon longirostris*, *Syngnathus rostellatus* (second cutlevel) and *Synidotea 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 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 (Fig. 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 (Fig. 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 (Fig. 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 (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 Fig. 8): three in the Eems: a marine, western community EW from 29 to 23 g l^{-1}, a brackish community in the middle part of the estuary EM from 21 to 10 g l^{-1}, and a oligohaline, eastern community EE from 4 to 1 g l^{-1}; two in the Westerschelde: WW from 31 to 21 g l^{-1} (+w17) and WM from 19 to 8 g l^{-1}; and three in the Gironde: GW from 26 to 18 g l^{-1}, GM from 14 to 6 g l^{-1}, and GE from 4 to 0 g l^{-1}.

The biotic characteristics (species composition, density, biomass) of the 2 or 3 communities within each estuary are – per definition – distinctly different (Fig. 10). Within each estuary the marine community is characterised by many species occurring in low densities. The middle community is characterised 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 characterised by the same dominant species in each estuary.

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 ind m^3 in the zone of maximal abundance with maximal densities of 10 to 15 ind m^3 in spring and autumn and summer densities of about 3 ind m^3. This is lower than maximal density reported in this study: 33 ind m^3 at 4 g l^{-1}. Sorbe (1981) reported maximal densities of Gammarus zaddachi at 550 ind 100 m^3 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 ind 100 m^3 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 Fig. 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

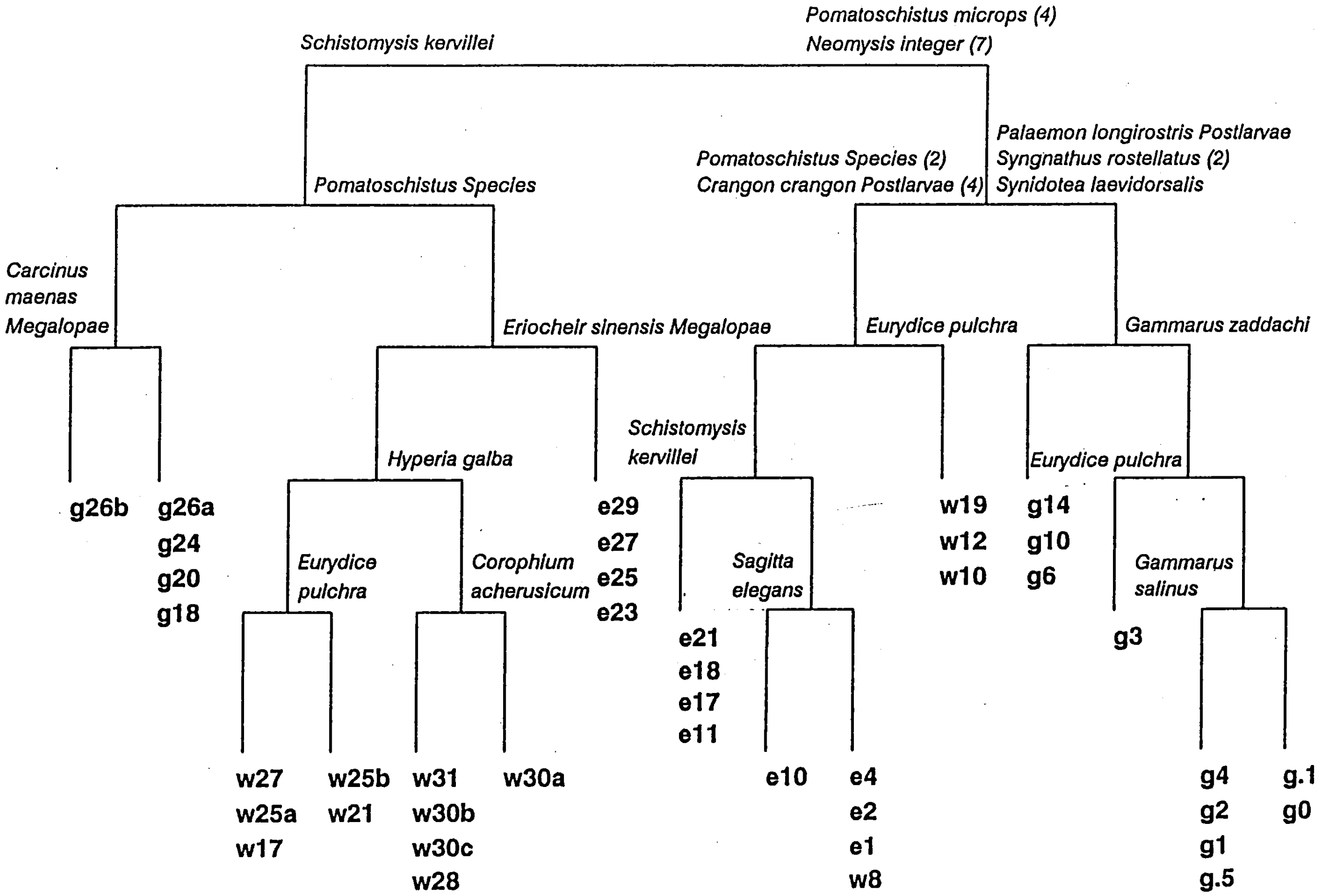

Fig. 7. TWINSPAN with the fourth root transformed biomass data of the three estuaries. Indicator species (and pseudospecies cutlevel) are given for each division.

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

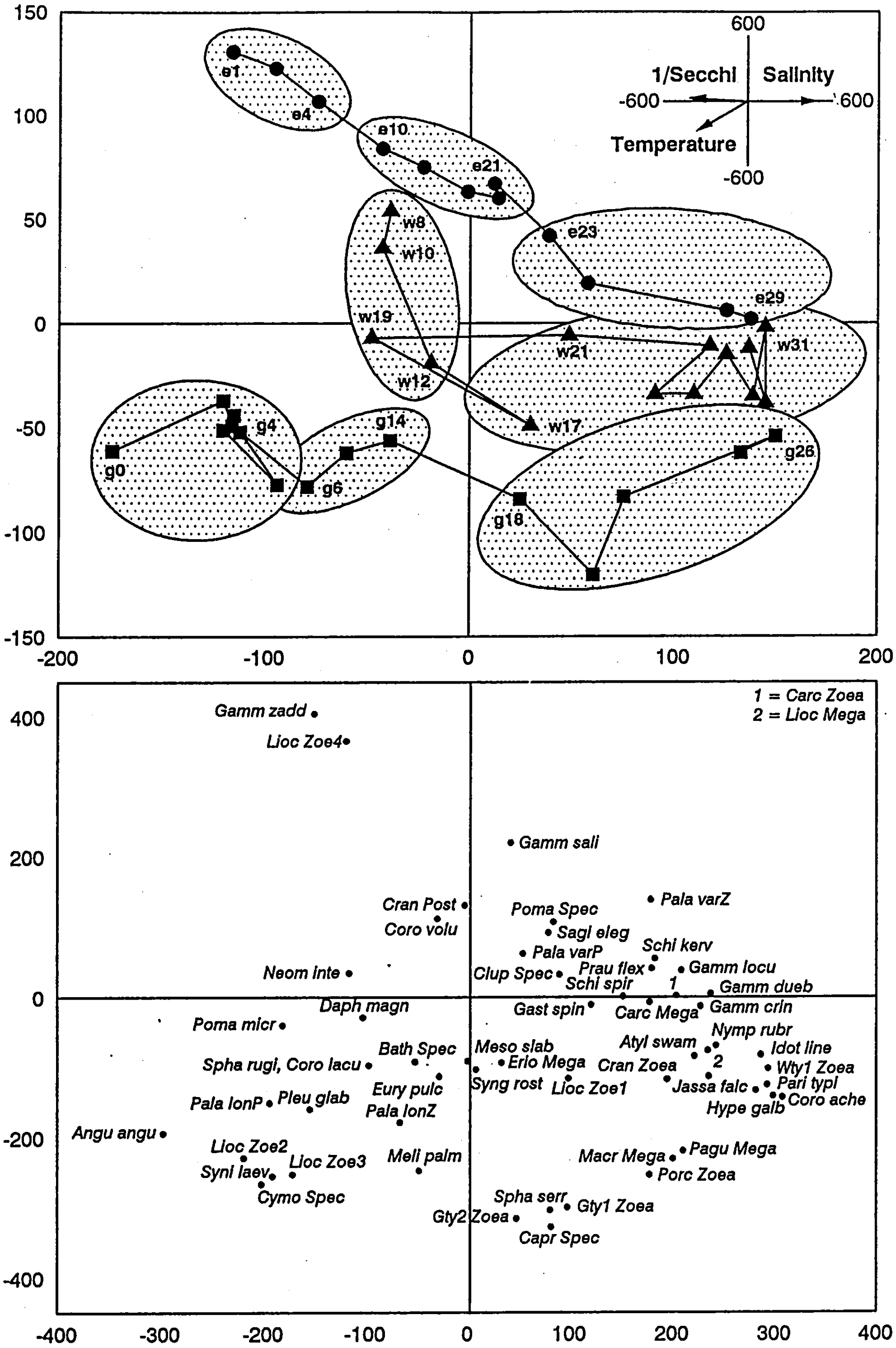

Fig. 8. Species scores (bottom), sample scores (top), and environmental biplot in the ordination plane formed by the first (horizontal) and second (vertical) canonical axes of the CCA with the fourth root transformed biomass data of the three estuaries. Samples are connected following salinity; communities as identified by TWINSPAN and GAS are circled.

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

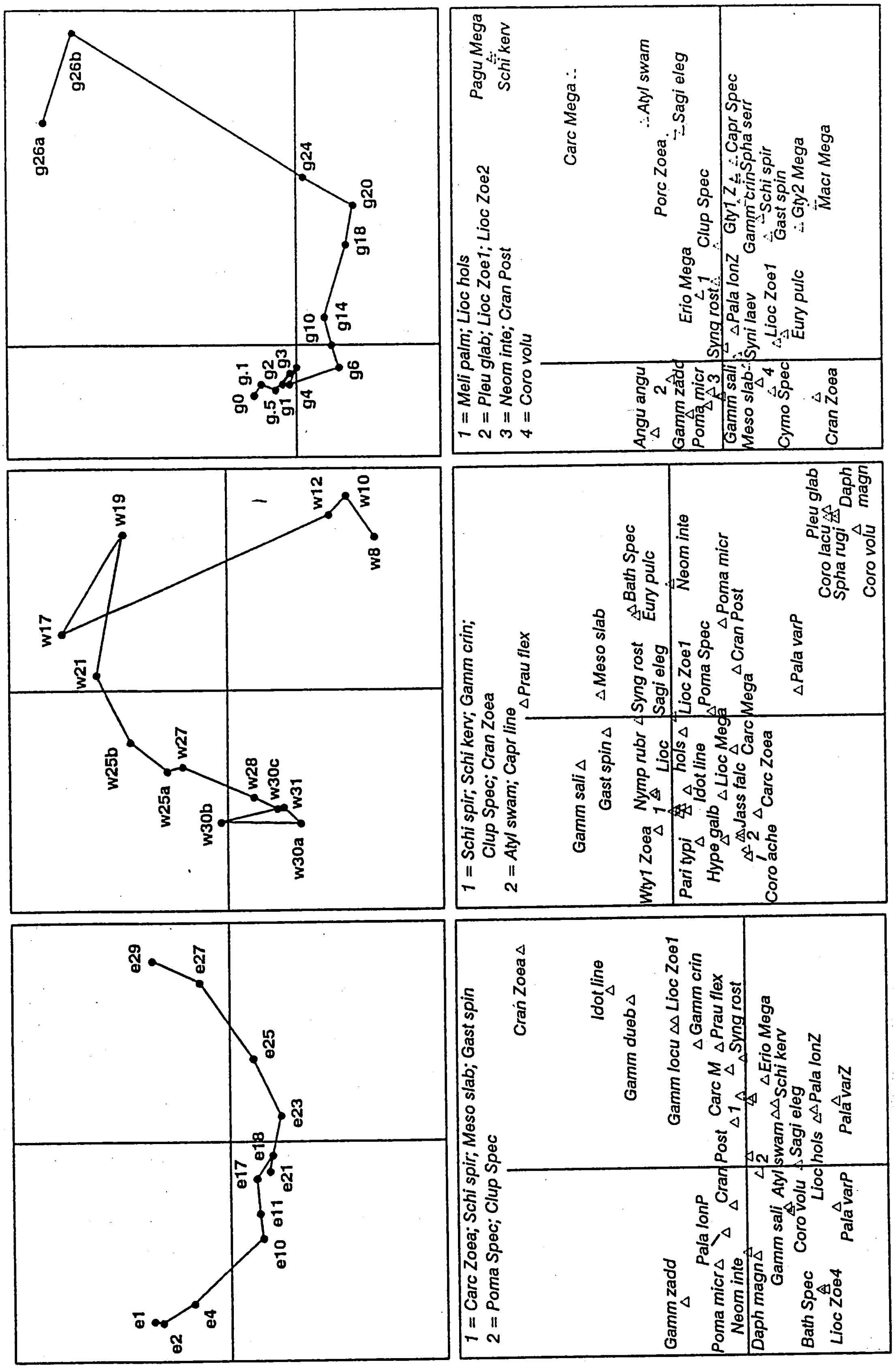

Fig. 9. Species scores (bottom) and sample scores (top) in the ordination plane formed by the first (horizontal) and second (vertical) canonical axes of the CCA with the fourth root transformed biomass data of the three estuaries separately. Samples are connected following salinity.

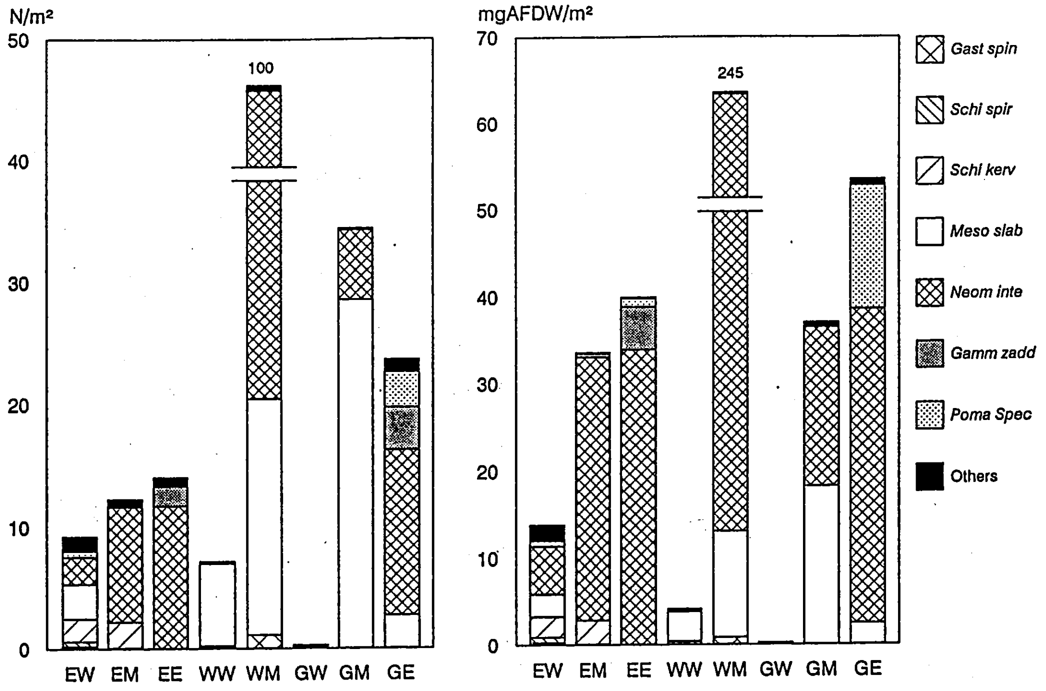

Fig. 10. Faunal composition of the 8 communities as identified by the multivariate analyses: biomass. First letter: *E*ems, *W*esterschelde, *G*ironde; second letter: *W*est, *M*iddle, *E*ast.

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 Fig. 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 g l^{-1} isohaline in the Westerschelde, whereas the density and biomass maximum was situated around the 2 to 4 g l^{-1} isohaline in Eems and Gironde. The low salinity hyperbenthic community was completely absent in the Westerschelde. Upstream of the 10 g l^{-1} 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 g l^{-1}. Averaged over the year, the abundance maximum of this species in the Westerschelde is located around the 15 g l^{-1} 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 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 g l^{-1}). 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 ind m^2 at 19 and 10 g l^{-1}) than it did in the other estuaries (30 and 33 ind m^2, for Eems and Gironde, at 4 and 2 g l^{-1} 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 *Sphaeroma 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 Vincente & 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 characterised by large amounts of peat, which may explain the higher net efficiency for larger fish and epibenthic crustaceans (Table 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 & Fockedey, 1993).

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Nursery function of an estuarine tidal marsh for the brown shrimp *Crangon crangon*

André Cattrijsse, Jan Mees & Hederick R. Dankwa

Marine Biology Section, Zoology Institute, University of Gent, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

Key words : nursery, salt marsh, *Crangon crangon*, Westerschelde estuary, feeding ground, predation refuge

Abstract

In this paper we defend the hypothesis that brown shrimp *Crangon crangon* migrate into the brackish part of the Westerschelde estuary shortly after metamorphosis and use the tidal marsh habitat as a nursery until they reach a length of about 10 mm. The importance of the marsh as a nursery was evaluated by estimating foraging activity, predation mortality and residence time. Early postlarval stages of *C. crangon* utilised the creeks of an estuarine tidal marsh from early spring (March-April) until late autumn (October-November). Postlarval shrimp leaving the marsh with the ebb tide always had significantly more food in their stomachs than shrimp entering the marsh with the incoming flood water. The predation pressure on the shrimp population was relatively low during most months, but it increased between August and October when seabass *Dicentrarchus labrax* and common goby *Pomatoschistus microps* occurred with high densities. The marsh creeks thus function both as foraging areas and as predation refugia. Depending on environmental temperature, the postlarval shrimp stayed in the marsh for a period of 2 to 3 weeks. Quantitatively, the value of the marsh as a nursery area changed drastically during a second year of sampling. Recruitment to the subtidal adult population represents an export of animals from the marsh to the estuary. This export is negligible in terms of biomass as compared to the total biomass of the estuarine population, but it may be important in terms of numbers of individuals.

Introduction

The brown shrimp *Crangon crangon* is the dominant epibenthic species in the Westerschelde estuary and it can therefore be considered to be a key species in the species-poor food web characterizing the brackish zone of the system. Throughout the year, shrimp are highly abundant in both the subtidal and intertidal areas of the estuary: annual average density is in the order of 2 ind.m^{-2} with peak densities of more than 10 ind.m^{-2} in late summer and early autumn (HAMERLYNCK *et al.* 1993, HOSTENS *in press*). The species always constitutes more than 80 % of the total epibenthic biomass in the area. *C. crangon* is an omnivore feeding on detritus, plant material and animal food (TIEWS 1967). Juvenile shrimp have been described as important predators of the meiobenthos and the microphytobenthos (PIHL & ROSENBERG 1984, MATILLA *et al.* 1990, HEDQVIST-JOHNSON & ANDRÉ 1991), while larger individuals can exert a considerable predation pressure on macrobenthic communities (PIHL & ROSENBERG 1984, REISE 1985). Juvenile fish and hyperbenthic mysids are also vulnerable to shrimp predation (PIHL & ROSENBERG 1984, VAN DER VEER & BERGMAN 1987, MEES, J. unpubl. data). On the other hand, *C. crangon* is a major prey item for all year classes of the dominant demersal fish species in the Westerschelde (HOSTENS, K. unpubl. data). This connectance between different trophic levels and the high consumption rates and secondary production of shrimp populations (REDANT 1980a) underline the important role shrimp play in the functioning of the estuarine ecosystem.

The Westerschelde estuary harbours a large population of *Crangon crangon* and is a possible nursery area for the species, but the system is presently of secondary importance for the Belgian and Dutch fisheries. The Wadden sea and, especially, the shallow coastal areas of the Southern Bight of the North Sea are of primary importance for the sustainability of the commercially exploited shrimp population (BODDEKE 1982, VAN BEEK & BODDEKE 1990). Still, there are indications that the tidal marsh of Saeftinghe, which is situated in the brackish reaches of the Westerschelde, has an important function as a nursery area for the brown shrimp (CATTRIJSSE *et al.* 1994). Almost exclusively very young individuals are known to occur in the marsh creeks. Predator densities are low (except in early autumn) and the infauna and microphytobenthos of the creeks constitute potentially rich food sources. Both food availability and the low predation pressure increase the chances of survival of the early life-history stages of shrimp that utilise the marsh habitat.

The aim of this study was to evaluate the importance of a large brackish tidal marsh as a nursery for the shrimp population in the estuary, both in terms of quality and quantity. The qualitative importance of marsh creeks as a habitat is assessed in function of two hypotheses. The hypothesis that marsh creeks are used as foraging areas is investigated by comparing the stomach fullness of incoming and outgoing shrimp. The hypothesis that they function as predator refugia is tested by measuring predation pressure of the dominant predators by means of stomach analyses. The quantification of the nursery function of the marsh habitat is done through estimates of the residence time and the numbers of individuals that recruit to the estuarine population after their stay in the salt marsh, as well as the export of biomass this represents.

Materials and methods

Study area and sampling

Samples were taken in the tidal marsh 'Het Verdronken Land van Saeftinghe', which is situated in the brackish reaches of the Westerschelde estuary (Fig. 1). With a surface area of 27.69 km^2 it is one of the largest estuarine brackish marshes left in Europe (DIJKEMA *et al.* 1984). The sampling site was located in a creek on the east side of the marsh (Fig. 1). The creek's total length and width are ca 1600 m and 36 m, respectively. It floods and drains a surface area of approximately 75 ha. The total creek volume of the tidal marsh is in the order of 10.21 x 10^6 m^3 (KRIJGER 1993). Mean tidal range at the study site is about 3 m and salinity varied between 3.4 and 16.1 PSU. Every tidal cycle the creek falls completely dry for at least 5 h. Water starts entering the system about 3 h before high tide and leaves the creek again within 4 h after. After the flooding, a narrow (< 1 m) and shallow (< 5 cm) channel with slowly running seepage water remains. For more information on the vegetation in the drainage area of the creek see HEMMINGA *et al.* (1993).

Monthly samples were taken from March 1990 through October 1991 with a fyke net (length 5 m, opening 1x1 m, mesh size 1 mm, meshed funnel and a chain in the ground rope: CATTRIJSSE *et al.* 1994). Adverse weather conditions prohibited sampling in September 1990 and February 1991. Sampling was started when water began to flood the creek. The net was placed in the centre of the creek, its mouth facing the flood current. After slack water the net was turned around to sample the ebb current. The net was hauled every hour and its contents were preserved in a 10 % formaldehyde-seawater solution. All fish used for stomach content analyses were first anaesthetized in a benzocaine (ethylamino-4-benzoate) solution in seawater to prevent regurgitation of the stomach content. Samples were taken around spring tide, generally yielding 3 flood samples and 4 ebb samples (numbered S1 through S7). During sampling, current speed and height of the water were measured every 15 min (for more details see CATTRIJSSE *et al.* 1994).

The rest water which remained in tidal pools at ebb was sampled with a drop trap (aluminium frame of 50 by 50 cm, height 20 cm). The trap was used monthly from February through October 1991. On each occasion 3 replicates were taken. All animals were removed from the trap with a small handnet (mesh size 1 mm).

Seasonal density patterns in the marsh were compared to those in the subtidal channels of the estuary proper. Epibenthos samples were taken monthly from March 1990 to October 1991 with a 3 m beam trawl (mesh size 10 mm stretched in the cod end) in 14 sampling stations between the mouth of the estuary near Vlissingen and the brackish zone a few kilometres upstream of the salt marsh near Bath (MEES *et al.* 1993, HOSTENS in press).

Treatment of samples and data analysis

Standard length (SL) is defined as the distance from the anterior end of the carapace (excluding the rostrum) to the posterior end of the last abdominal segment (excluding the telson). In the laboratory, all *Crangon crangon* larger than approximately 10 mm SL were sorted, counted and measured. Of the remaining, smaller individuals a subsample of 30 individuals was measured to the nearest 0.1 mm under a calibrated binocular microscope equipped with a drawing mirror. Thus a total of 210 postlarval shrimp were measured for each sampling date (90 for the 3 flood samples, 120 for the 4 ebb samples). In this study, an arbitrary distinction is made between early postlarval and juvenile/adult shrimps: postlarvae are all individuals smaller than or equal to 10 mm SL. For information on the associated fauna see CATTRIJSSE *et al.* (1994).

In order to quantify the catches, the volume of water filtered by the gear and the volume of water passing through the creek were estimated at intervals of 15 min. The cross-sectional area for every possible water height at the sampling point was measured. Water height, current speed and cross-section allowed for the calculation of the flow ($m^3 s^{-1}$) at the sampling point and the total volume of water for each 1 h of sampling (CATTRIJSSE *et al.* 1994).

The residence time of shrimp in the marsh was estimated by comparing the monthly length-frequency distributions with hypothetical expected distributions. These were calculated using a temperature and length dependent growth model (KUIPERS & DAPPER 1981, 1984):

$$Y = 0.1625 + 0.01025\, T - 0.00403\, L$$

where Y represents growth in mm per day, T is temperature (°C) and L is the total length (TL in cm) of the shrimp at the beginning of the considered time interval. Total length was estimated with a SL-TL regression (TL = 0.206 + 1.469 SL, R^2=0.997, n=212) established for the Westerschelde population (HOSTENS, K. & CATTRIJSSE, A. unpublished data). The overlap between the theoretical and the observed length-frequency distributions gives information about the residence time in the marsh (KUIPERS & DAPPER 1981, 1984).

Information about the foraging activity in the marsh habitat was obtained by comparing the stomach fullness of postlarval shrimp entering the creek with flood with that of individuals leaving the marsh with the outgoing water. The amount of food present in the stomachs of shrimp caught during the first 2 hours (flood samples) and the last 2 hours (ebb samples) of the sampling campaigns of May 1990, August 1990, November 1990, April 1991, May 1991 and June 1991 were compared with Mann-Withney U-tests. From each sample, some 30 individuals were selected ad random (120 per month). Stomach contents (110°C for 2 hours) and shrimp (60°C for 5 days) were dried and dry weight was determined with a microbalance to the nearest 1 µg). To assess whether a higher stomach fullness index resulted from an increased ingestion of biomass, some additional specimens were selected for qualitative diet analyses from each month.

The stomach fullness index (FI) was calculated as described by BERG (1979). The amount of food present in the stomach is expressed as a percentage of the body weight of the individual:

$$\mathrm{FI} = (S_i + s_i) / W_i$$

with S_i, s_i and W_i the dry weights of the stomach content, the stomach and the shrimp, respectively. The indices were transformed angularly prior to statistical analyses.

Predation pressure on the postlarval shrimp population in the creek was assessed in August 1990, October 1990 and November 1990. During these months the populations of potentially important predators reach their highest densities in the tidal marsh (CATTRIJSSE *et al.* 1994). No stomach analyses were done for other months since fish densities (individuals larger than 20 mm SL) were always very low. Stomach analyses were performed as described in HAMERLYNCK & CATTRIJSSE (1994). Detailed descriptions of the diet of both species will be published elsewhere. Stomach analyses of seabass *Dicentrarchus labrax* and common goby *Pomatoschistus microps* larger than 20 mm SL, yielded the average number of postlarval shrimp consumed per fish. Monthly predation mortalities were then obtained through extrapolation of these averages and the densities of seabass and gobies larger than 20 mm SL.

In calculating total emigration we assumed natural mortality of the postlarval shrimp to be negligible in the marsh creeks. Predation mortality was not taken into account since only in autumn a significant reduction of the population could be attributed to this process (see results). Furthermore, the extrapolation of predation data from August, October and November 1990 resulted in mortality estimates of > 100 % in September and October of 1991. Extrapolation of densities (ind. m^{-3}) to the total creek volume of Saeftinghe yielded the potential of postlarval shrimp that recruit to the estuarine population.

It is assumed that postlarval shrimp migrate into the marsh shortly after metamorphosis (starting length 3 mm SL, KUIPERS & DAPPER, 1981, 1984) and that they stay in the marsh for a short period of growth (upto a length of 10 mm SL) before emigrating to the estuary (see results). The amount of biomass produced by the shrimp population during their stay in the tidal marsh (and exported to the main estuarine population) was estimated by applying a standard length (SL) - ash-free dry weight (ADW) regression ($\ln ADW = -5.379 + 2.903 \ln SL$, $R^2=0.981$, $n=163$, HOSTENS, K. unpubl. data) to the monthly length-frequency distributions.

Results

The length-frequency distributions of *Crangon crangon* caught in the creek, clearly demonstrate the dominance of individuals smaller than 10 mm SL (Fig. 2). Juvenile and adult (> 20 mm SL) individuals only occurred in appreciable numbers in June and October. All larger size classes were represented by few individuals in most months and the larger individuals seem to utilise the marsh habitat erratically. The bulk of the individuals in the smaller size classes (3-20 mm SL) had a size range of 4-7 mm SL. The mode of the distributions was always located around 5-6 mm SL. The occurrence of the smallest length classes shows a clear seasonal pattern (Fig. 3). The first postlarval shrimp were observed in March 1990 (Fig. 3). Densities increased considerably during the following months, with a peak of 40 ind.m^{-3} in June. Densities dropped to levels of around 1 ind.m^{-3} in July and August, followed by an increase in October (5 ind.m^{-3}). No shrimp were observed in the marsh during winter (January-March 1991). A similar seasonal pattern was observed in 1991, but the recorded densities were much lower than during the first year. The first recruitment period was again observed in spring (April) and reached a maximum of 3 ind.m^{-3}. Densities were again higher in spring as compared to summer and an increase in abundance was again observed in October. Concurrently to the drop in density in the marsh (from June-July onwards), density in the subtidal channels of the neighbouring estuary increased. In 1990, subtidal estuarine densities were in the order of 200 ind.m^{-2} between July and September. In 1991, maximal densities were recorded in October (> 500 ind. m^{-2}).

The average growth rate of the postlarval shrimp varied seasonally between 0.25 and 0.39 mm d^{-1} (Table 1). The average residence time varied between 16 and 24 days. In spring and summer no overlap was observed between the observed and expected length-frequency distributions (Fig. 4). A small number of individuals belonging to the cohorts observed in October and November were probably still present in the creeks in November and December, respectively. The observed and expected length-frequency distributions of these months showed an overlap in the range of 8 to 13 mm SL. Since no data were available from

September, the expected distribution for October was calculated from the observations made in August. This possibly explains why the overlap between the observed and expected length-frequency distributions shows a different picture (overlap around 18 mm SL). All comparisons clearly suggest a short residence time in the marsh: the postlarval shrimp had left the creeks after a period of fourteen days to one month. The intercept between both distributions is around 10 mm SL.

Based upon (1) the densities of postlarval and juvenile-adult shrimp and their seasonal density patterns in the marsh and in the subtidal of the estuary, (2) the length-frequency distributions of individuals occurring in the marsh and (3) the comparisons between the observed and expected length-frequency distributions, we conclude that only shrimp smaller than 10 mm SL use the marsh as a habitat.

Since postlarval *Crangon crangon* utilise the creeks until reaching a length of 10 mm SL and since they stay with high densities in the restwater of tidal pools during low water (Fig. 5), a size difference was expected between individuals caught in the flood and ebb samples. The immigration of smaller individuals with flood and the emigration of somewhat larger individuals with the following ebb, could be demonstrated in March, April, July, August and October 1990 and again in May, July and October 1991 (Fig. 6). In all other months, no size difference was observed. The length difference was maximal in August 1990 (3 mm SL). In the other months the difference between flood and ebb was only 1 or 2 mm.

Upon leaving the marsh, postlarval shrimp always had significantly more food in their stomachs than upon entering (Fig. 7, Table 2). Consumption was maximal upon leaving the marsh. In May and August 1990 the fullness index increased with 1 %. In November 1990 it increased fourfold during the stay in the marsh. In 1991 the fullness indices were higher than in 1990 and the increase was in the order of 1 to 2 %. A comparison of the different flood and ebb samples with the data of 1990 yielded an identical picture (Table 3). The fullness index was always higher upon leaving the marsh (Fig. 7). All dissected stomachs contained animal prey items and, to a lesser extent, unidentifiable amorphous material. Common prey species were the amphipod *Corophium volutator* and segments of the tail end of the polychaete *Heteromastus filiformis*. Ostracoda, Nematoda and Oligochaeta were also present in the stomachs.

Both common goby *Pomatoschistus microps* and seabass *Dicentrarchus labrax* regularly preyed upon postlarval shrimp (Table 4). The number of shrimp per goby was positively correlated to the length of the fish, while no such relationship was observed for seabass. Individuals of each species consumed about 0.3 *Crangon crangon* per tidal cycle. Since *P. microps* reached much higher densities in the creeks, this species was responsible for the bulk of predation mortality. Extrapolation of the predation data to all months, yielded a total mortality reflecting the density pattern of *P. microps.* Predation mortality was maximal from August to October (Table 5), which corresponds to the time when common gobies utilise the marsh (CATTRIJSSE *et al.* 1994). In August 1990 predation mortality was almost 16 %. In October 1990 a higher number of shrimp were eaten by *P. microps* en *D. labrax*, but percentage mortality decreased since the density of postlarval shrimp increased fivefold (Table 5).

In 1990, the total number of shrimp that left the marsh monthly varied between 1 million and 400 million: during this year some 600 million shrimp spent the first few weeks of their growth period in the marsh. In 1991 the maximal monthly export was in the order of 30 million individuals and only 60 million shrimp used the marsh as a nursery. The total biomass produced in the marsh is rather low (cf. limited somatic growth and short residence time) (Table 6). Monthly export of biomass varied between 0.4 kg ADW en 1452 kg ADW. Between March and December 1990, total export was estimated around 2000 kg ADW versus only 200 kg ADW in 1991.

Discussion

Different findings in this study support the hypothesis that postlarval *Crangon crangon* utilize the marsh habitat until they reach an average length of 10 mm SL. Densities were highest in the smaller size classes and larger individuals were only recorded occasionally. As compared to their seasonal abundance in the estuary proper (HAMERLYNCK *et al.* 1993), adult shrimp are a negligible component of the nekton fauna of the marsh. The comparisons between the observed and expected length-frequency distributions also suggest that emigration to deeper areas commences upon reaching a standard length of 10 mm. Postlarval shrimp were furthermore underrepresented in the hyperbenthos of the subtidal of the Westerschelde estuary, while all other length classes regularly occurred in sledge samples (MEES *et al.* 1993). Zoea larvae only occurred in the marine reaches of the estuary (MEES *et al.* 1993). In summary, these observations support the hypothesis that postlarval shrimp migrate to the upstream brackish part of the estuary shortly after metamorphosis. They then choose the marsh creeks as a habitat before recruiting to the deeper regions of the estuary proper. The seasonal density pattern in the estuarine channels of the Westerschelde conforms with the pattern observed in the marsh. From July onwards the average density in the estuary increases (Fig. 3, HOSTENS in press). This increase can be attributed to recruitment from the reproductive wave that took place from April to June (ANONYMOUS 1993).

Postlarval shrimp probably reach the eastern basin of the Westerschelde through selective tidal migration (RIJNSDORP *et al.* 1985). *Crangon crangon* responds to increases of the hydrostatic pressure by increasing its swimming activity (DIGBY 1961). HUGHES (1969), MATHEWS *et al.* (1991) and ROGERS *et al.* (1993) suggest that there is a positive relationship between salinity and the activity of penaeid shrimp. This mechanism allows for recruitment to estuarine nursery areas. The increased salinity at flood causes the shrimp to swim around actively. During ebb, when the increasing freshwater flow decreases salinity, the animals remain inactive close to the bottom. A similar mechanism of response to hydrodynamic and/or salinity changes can allow postlarval *C. crangon* to migrate into the eastern basin of the Westerschelde estuary and the creeks of the marsh of Saeftinghe.

During a tidal cycle, no positive relationship was found between current speeds and densities of postlarval shrimp (CATTRIJSSE *et al.* 1994). This suggests that the immigration to the marsh is - at least partly - an active process. On average, highest numbers were caught when current speeds were low; shortly before and after high water, when current speeds were highest, lower numbers of shrimp migrate through the creek. Several authors assume that juvenile shrimp migrate back and forth between the subtidal and the intertidal during each tidal cycle (AL-ADHUB & NAYLOR 1975, HENDERSON & HOLMES 1987). However, according to JANSEN & KUIPERS (1980), BERGHAHN (1983) and BEUKEMA (1992) the bulk of the migrating population stays in the intertidal areas and the observed emigration results from a changing habitat choice of larger individuals. The observed behaviour of remaining in intertidal areas at ebb tide thus does not result from passive dispersion but rather reflects an active choice (BERGHAHN 1983, KNEIB 1987). CREUTZBERG *et al.* (1978) observed that early postlarval plaice *Pleuronectes platessa* increased their swimming activity after a period of starvation and remained near the bottom after saturation. The same mechanism can cause postlarval *Crangon crangon* to stay in the marsh habitat. The observed tidal pattern in the stomach fullness index and the fact that shrimp stay in the intertidal suggest that the presence of adequate food sources may well be one of the factors that terminates the selective tidal transport and triggers the temporary residence in the intertidal.

The total area of shallow tidal pools in the creek at ebb tide could not be estimated. The number of shrimp that remain in the marsh could thus not be calculated. At least part of the population is supposed to continue migrating back and forth with the tides. The advantages of staying in the intertidal at ebb include a constant food supply and the absence of predators. On the other hand, the shrimp risk to be exposed to high temperatures. Throughout the year, predation pressure is likely to be higher in the subtidal (BISHOP & KAHN 1991, RUIZ *et al.* 1993). The continuous immigration of new postlarvae, the long interval between two sampling campaigns as compared to the short residence time in the marsh and the duality between the observed tidal migrations on the one hand and the fact that at least part of the population remains in the intertidal at ebb, result in difficulties in detecting length differences between immigrating and emigrating postlarval shrimp. An evaluation of the relative risks associated with both biotopes requires the identification of factors causing mortality. Still, a cost-benefit analysis of advantages and disadvantages associated with intertidal marsh and subtidal estuarine habitats and, presumably, the limitation of space in the marsh at ebb tide, suggest that at least part of the population migrates back and forth.

The utilization of tidal marsh creeks as foraging areas for epifauna has been documented before, though not for shrimp (RYER 1987, MORTON *et al.* 1987, ROZAS & LASALLE 1990). The shrimp leaving the creek have clearly been foraging during their stay in the marsh. Since shrimp are omnivores, they do not necessarily feed exclusively on animal prey. They are also potential consumers of macrophyte detritus which is very abundant in the marsh (HUISKES 1988, CATTRIJSSE *et al.* 1994). The stomach fullness of obligatory detritivores is known to be much higher since important volumes of organic matter have to be consumed to meet their energy requirements. The higher fullness indices observed at ebb could therefore result from the intake of large amounts of detritus, which is not necessarily correlated with a higher yield of energy. However, the qualitative stomach analyses of shrimp show that the postlarvae mainly prey upon energy-rich animal food like small amphipods, ostracodes, nematodes, oligochaetes and polychaetes.

In the Wadden sea young shrimp have been reported to leave the sandflats to recruit to the subtidal population at a length of 20 mm TL (± 15 mm SL) (KUIPERS & DAPPER 1984, BEUKEMA 1992). The muddy substrates of the tidal marsh are utilised for a shorter period of time. The shrimp leave the creeks at a length of approximately 15 mm TL (± 10 mm SL). A difference in predation pressure between the tidal marsh and the estuary may explain the utilisation of the creeks during the early postlarval period. The predation pressure in the marsh is relatively low, excepting the period from August to October when seabass and gobies are present in peak densities. In the estuary predation pressure is higher in all seasons. Adult shrimp are predators of juveniles (ANONYMOUS 1993) and are abundant in the subtidal throughout the year (HAMERLYNCK *et al.* 1993). The gobies *Pomatoschistus minutus* and *P. lozanoi*, both very abundant in the Westerschelde estuary, are important predators of shrimp (REDANT 1980a, HAMERLYNCK *et al.* 1986). Further, especially whiting *Merlangius merlangus*, bib *Trisopterus luscus* and sea snail *Liparis liparis* will all contribute to the predation mortality of shrimp in the estuary (REDANT 1980b, HENDERSON & HOLMES 1989, HAMERLYNCK & HOSTENS 1993). All of these predators never or very rarely occur in the marsh creeks (CATTRIJSSE *et al.* 1994). When the postlarval shrimp migrate to the estuary, the risk of being predated upon may well have decreased significantly. The sediment is a refugium against visual predators. *Crangon crangon* is known to burry itself least efficiently in coarser sediments (PINN & ANSELL 1993). The interaction between the effects of grain size distribution and length of the shrimp results in the fact that smaller shrimp burry themselves more frequently and deeper in fine sediments (PINN & ANSELL 1993). Therefore, the predation pressure upon early postlarval shrimp is likely to be higher in the sandy subtidal than in the muddy intertidal creeks. Larger shrimp can more easily avoid predation through other escape mechanisms than burrowing. The probability of survival of penaeid shrimp has been shown to be positively related to the residence time in the marsh where they grow up (MINELLO *et al.* 1989). Furthermore, the infauna of the tidal marsh creeks probably constitutes a more suitable food source for early postlarval shrimp than the infauna of the sandflats in the estuary. Especially the abundant meio- and microphytobenthos are attractive to the smallest length-classes (PIHL & ROSENBERG 1984).

From July onwards shrimp densities in the marsh decrease. This trend has also been reported from other nursery areas (BODDEKE *et al.* 1986, KUIPERS & DAPPER 1984, BEUKEMA 1992). In the tidal marsh of Saeftinghe, this decrease can be partly explained by the appearance of juvenile shore crabs *Carcinus maenas*, common gobies and seabass (CATTRIJSSE *et al.* 1994), which results in the observed increase in predation mortality from August to October (KUIPERS & DAPPER 1984).

The development of *Crangon crangon* from egg to adult takes approximately 10 months (TIEWS 1967). Fastest growth - development from postlarva to adult in 4 months - has been reported by BODDEKE (1976). The results obtained with the model of KUIPERS & DAPPER (1981, 1984) confirm this pattern. Taking this growth rate, the interval between metamorphosis and 10 mm SL amounts to 2 or 3 weeks. This means that a new cohort was sampled during each sampling campaign. The calculated export of juveniles to the estuary is likely to be an underestimation since an important part of the shrimp that utilize the marsh as a nursery were not sampled. Since we are dealing with a continuously reproducing and migrating population, the data presented in this study do not allow for a description of growth. The transition from a planktonic to a benthic life style (hyper- to epibenthic) occurs at a length of 3 mm SL (4.6 mm TL) (KUIPERS & DAPPER 1981, 1984). These authors report an average growth rate of 0.12 to 0.35 mm d^{-1}, which results in a development time from mature egg to an adult length of 35 mm SL (50 mm TL) of approximately 8 months. The larval phase lasts for about 5 weeks. The monthly temperatures recorded by KUIPERS & DAPPER (1981) in the Wadden sea were consistently 5°C lower than those in our study area. Development is thus likely to be faster in the marsh: growth to a length of 35 mm SL will take about 3 to 4 months.

The relative importance of the tidal marsh of Saeftinghe for the estuarine shrimp population can presently not be evaluated. Such a calculation should relate the number of recruits leaving the marsh to the number of shrimp of certain length classes present in the estuary. Since monthly length-frequency data of the shrimp population in the estuary are not available, densities of specific length classes can not be estimated. In 1990, the Belgian fishing fleet landed 490 tonnes of shrimp (ANONYMOUS 1993). The wet weight of an average consumption shrimp (50 mm TL) is approximately 700 mg (HOSTENS, K. unpubl. data). If all postlarvae that used the marsh as a nursery in 1990 would have grown to this length, the resulting biomass would approximate the total yield of the Belgian shrimp fisheries (400 tonnes). Due to the high predation mortality in shrimp populations (REDANT 1980b) only a fraction of the postlarvae reach the adult stage. This factor however remains unknown, which hampers the estimation of the nursery value of the marsh

The tidal marsh of Saeftinghe is a nursery for the brown shrimp, but its relative importance seems to vary considerably between years. The observed difference in density for 1990 and 1991 remains unclear. Variability in year-class strength is a possible explanation. The densities recorded in the marsh suggest a weaker year class in 1991. Still, densities in the subtidal were much higher in autumn 1991 as compared to autumn 1990.

With the emigration of juvenile organisms that use the marsh as a nursery, part of the marsh production is exported to neighbouring ecosystems and will play a role in the local food webs (NIXON & OVIATT 1973, ODUM & HEALD 1975, WEINSTEIN *et al.* 1980). For nursery areas of *Crangon crangon* specifically this hypotheses was formulated by MÖLLER *et al.* (1985).

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Figure captions

Figure 1. Study area in the Westerschelde estuary, SW Netherlands, showing the marsh and its position in the estuary. The sampling point is circled.

Figure 2. Procentual length-frequency distribution of postlarval *Crangon crangon* in the marsh creek between March 1990 and October 1991. All distributions are plotted on the same Y-axis scale, with a maximum of 60%.

Figure 3. Density (numbers per m^3) of postlarval *Crangon crangon* in the marsh creek (dashed) and average density (numbers per $100m^2$) of subadult and adult shrimp (solid) in the subtidal of the Westerschelde estuary.

Figure 4. Comparison between the observed and expected length-frequency distributions of postlarval *Crangon crangon* in 1990.

Figure 5. Monthly densities (average ± standard error) of postlarval *Crangon crangon* remaining in tidal pools at ebb tide.

Figure 6. Cumulative length-frequency distributions of postlarval *Crangon crangon* caught during flood (solid) and ebb (dashed).

Figure 7. Stomach fullness indices of postlarval shrimp (±1se) in May, August and November 1990. S1 and S2: first two hours of flood, S6 and S7: last two hours of ebb.

Table 1. Average growth rate (mm d^{-1}) of postlarval *Crangon crangon* of 3 to 10 mm SL.

date	t° (°C)	average residence time (days)	growth rate (mm d^{-1})	date	t° (°C)	average residence time (days)	growth rate (mm d^{-1})
15/3/90	11	23	0.26	---	---	---	---
11/4/90	12	21	0.30	16/4/91	13	22	0.28
10/5/90	17	18	0.34	10/5/91	12	21	0.29
11/6/90	19	17	0.36	13/6/91	16	18	0.35
9/7/90	20	17	0.38	12/7/91	21	16	0.39
8/8/90	22	18	0.36	9/8/91	23	16	0.39
---	---	---	---	7/9/91	21	18	0.36
10/10/90	16	21	0.29	7/10/91	17	21	0.29
5/11/90	12	24	0.25	---	---	---	---
3/12/90	9	24	0.26	---	---	---	---

Table 2. Average stomach fullness indices (FI ± se) for flood and ebb with the p-values of the Mann-Withney U-tests.

Month	FI flood	FI ebb	p
May 1990	1.69 ± 0.17	2.79 ± 0.31	0.010
August 1990	1.95 ± 0.16	2.96 ± 0.28	0.008
November 1990	1.73 ± 0.17	8.30 ± 0.82	0.000
April 1991	8.53 ± 0.66	10.12 ± 0.64	0.025
May 1991	7.96 ± 0.35	8.64 ± 0.37	0.181
June 1991	8.46 ± 0.21	10.36 ± 0.42	0.000

Table 3. P-values of the Mann-Withney U-tests for the stomach fullness indices of the first 2 flood samples (S1 and S2) and the last 2 ebb samples (S6 and S7).

May 1990	S1	S2	S6
S2	0.315	---	
S6	0.040	0.008	---
S7	0.435	0.127	0.458
August 1990	S1	S2	S6
S2	0.133	---	
S6	0.009	0.238	---
S7	0.015	0.227	0.766
November 1990	S1	S2	S6
S2	0.091	---	
S6	0.000	0.000	---
S7	0.000	0.000	0.787

Table 4. Average numbers of postlarval *Crangon crangon* per predator for August, October and November 1990.

	Pomatoschistus microps			*Dicentrarchus labrax*		
	N	SL (mm)	shrimp per ind	N	SL (mm)	shrimp per ind
August 1990	94	20-26	0.12	59	27-59	0.31
October 1990	75	29-41	0.35	33	34-79	0.24
November 1990	53	31-47	0.49	18	49-76	0.39
Average			0.32			0.31

Table 5. Seasonal fluctuation in predation pressure on postlarval *Crangon crangon* in the creek, as estimated from the fish stomach analyses.

	Density (numbers m^{-3})			Predation (numbers m^{-3})		Mortality
	P. microps >20mm	*D. labrax* >20mm	*C. crangon* >10mm	*P. microps*	*D. labrax*	% population
March 1990	0.009	0.004	0.112	0.003	0.001	3.4
April	0.020	0.003	4.991	0.006	0.001	0.2
May	0.005	0.002	2.324	0.002	0.001	0.1
June	0.039	0.001	39.754	0.012	0.000	0.0
July	0.041	0.004	0.967	0.013	0.001	1.5
August	0.558	0.038	1.216	0.177	0.012	15.6
October	0.764	0.026	5.275	0.243	0.008	4.8
November	0.059	0.011	1.610	0.019	0.003	1.4
December	0.016	0.004	0.166	0.005	0.001	3.8

Table 6. Estimate of the export of postlarval *Crangon crangon* from the marsh, expressed both in numerical (number of individuals x 10^6) and in gravimetrical (mg ash-free dry weight x 10^6) terms.

month	exported numbers	exported biomass
March 1990	1.14	4.1
April 1990	50.96	182.3
May 1990	23.73	84.9
June 1990	405.89	1452.0
July 1990	9.88	35.3
August 1990	12.41	44.4
October 1990	53.86	192.7
November 1990	16.43	58.8
December 1990	1.70	6.1
April 1991	28.16	100.7
May 1991	11.02	39.4
June 1991	13.24	47.4
July 1991	5.97	21.4
August 1991	0.93	3.3
September 1991	0.10	0.4
October 1991	2.03	7.3

FIGURE 1.

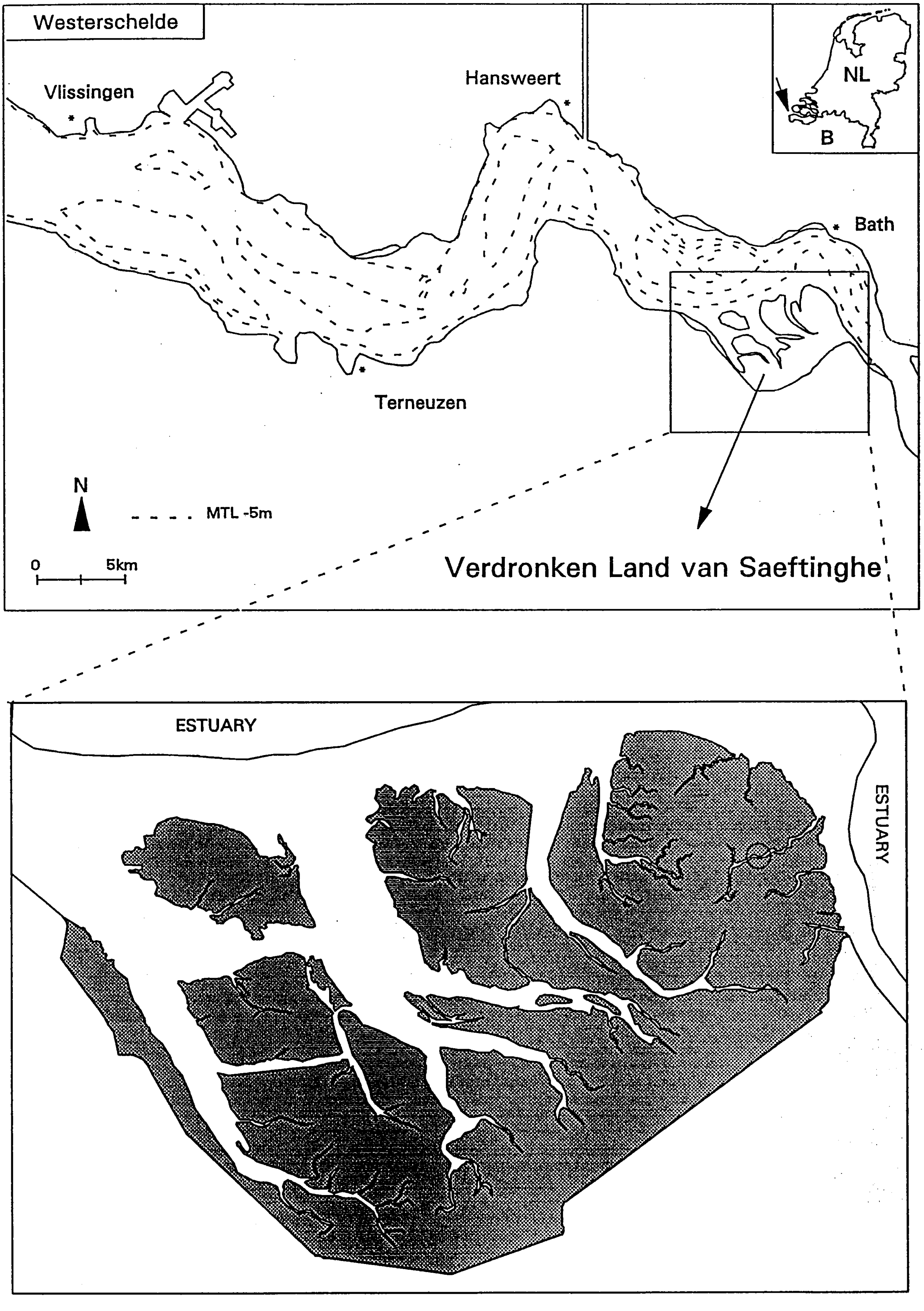

Westerschelde
Vlissingen
Hansweert
NL
B
Bath
Terneuzen
N
MTL -5m
0
5km
Verdronken Land van Saeftinghe
ESTUARY
ESTUARY

FIGURE 2.

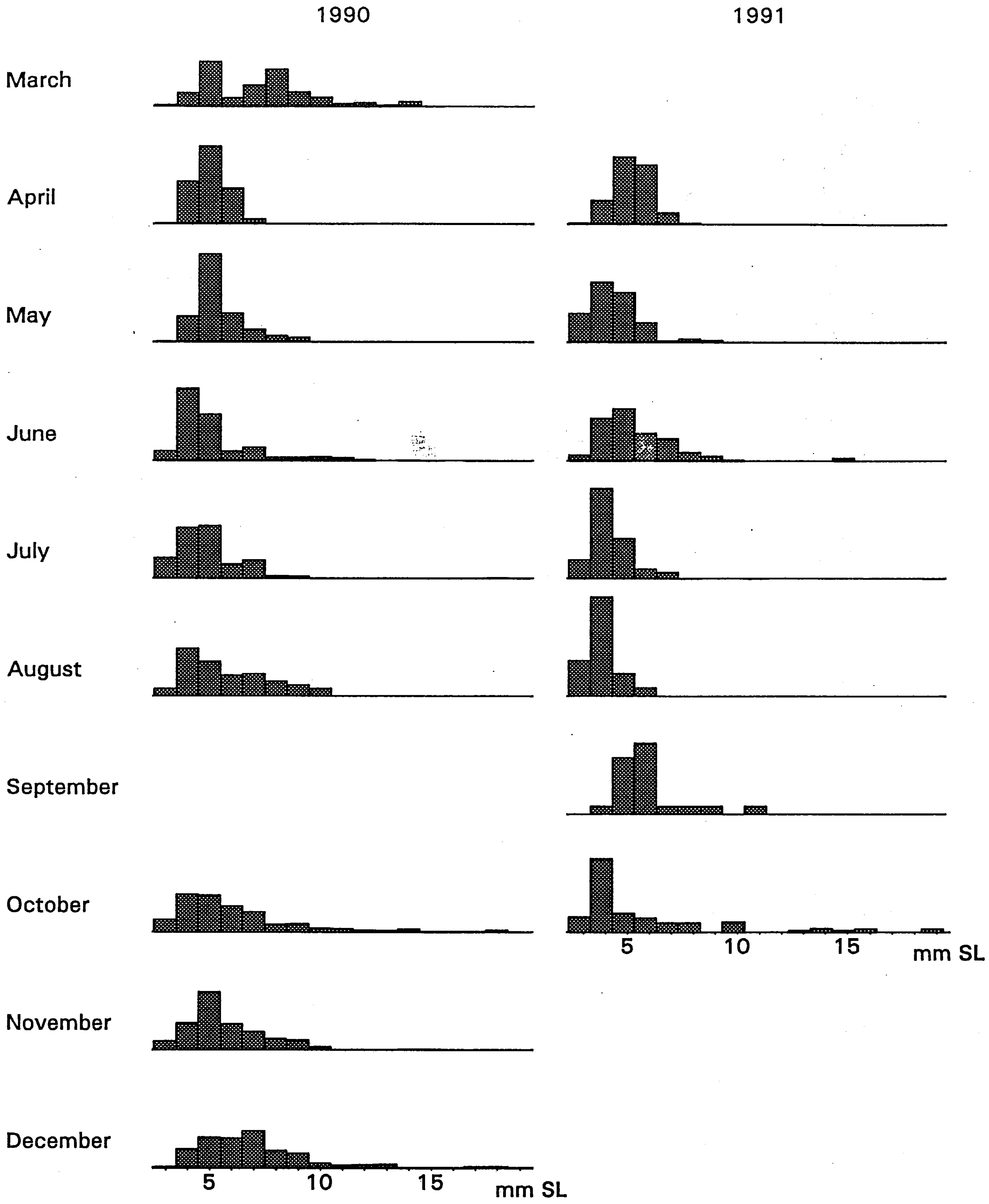

1990
1991
March
April
May
June
July
August
September
October
November
December
5
10
15
mm SL
5
10
15
mm SL

FIGURE 3.

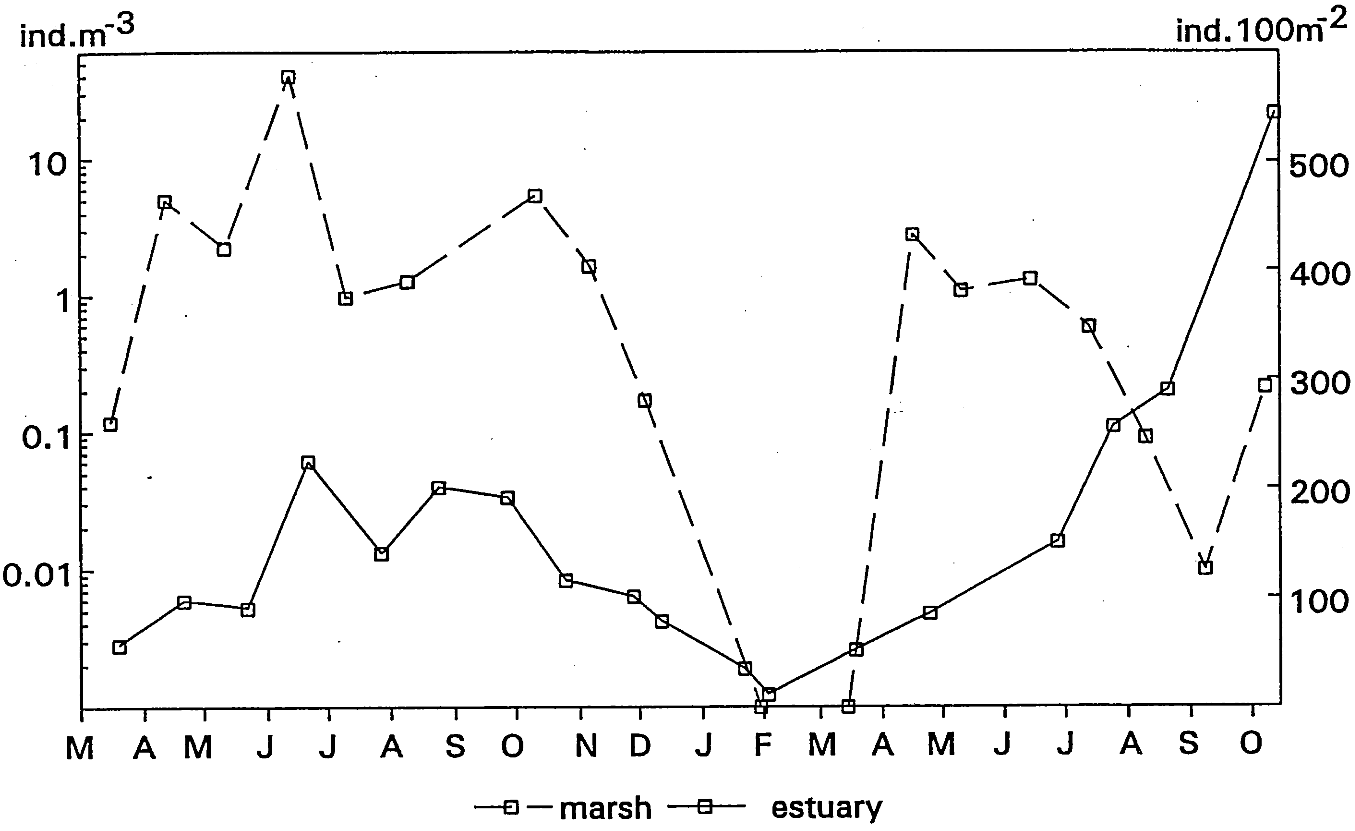
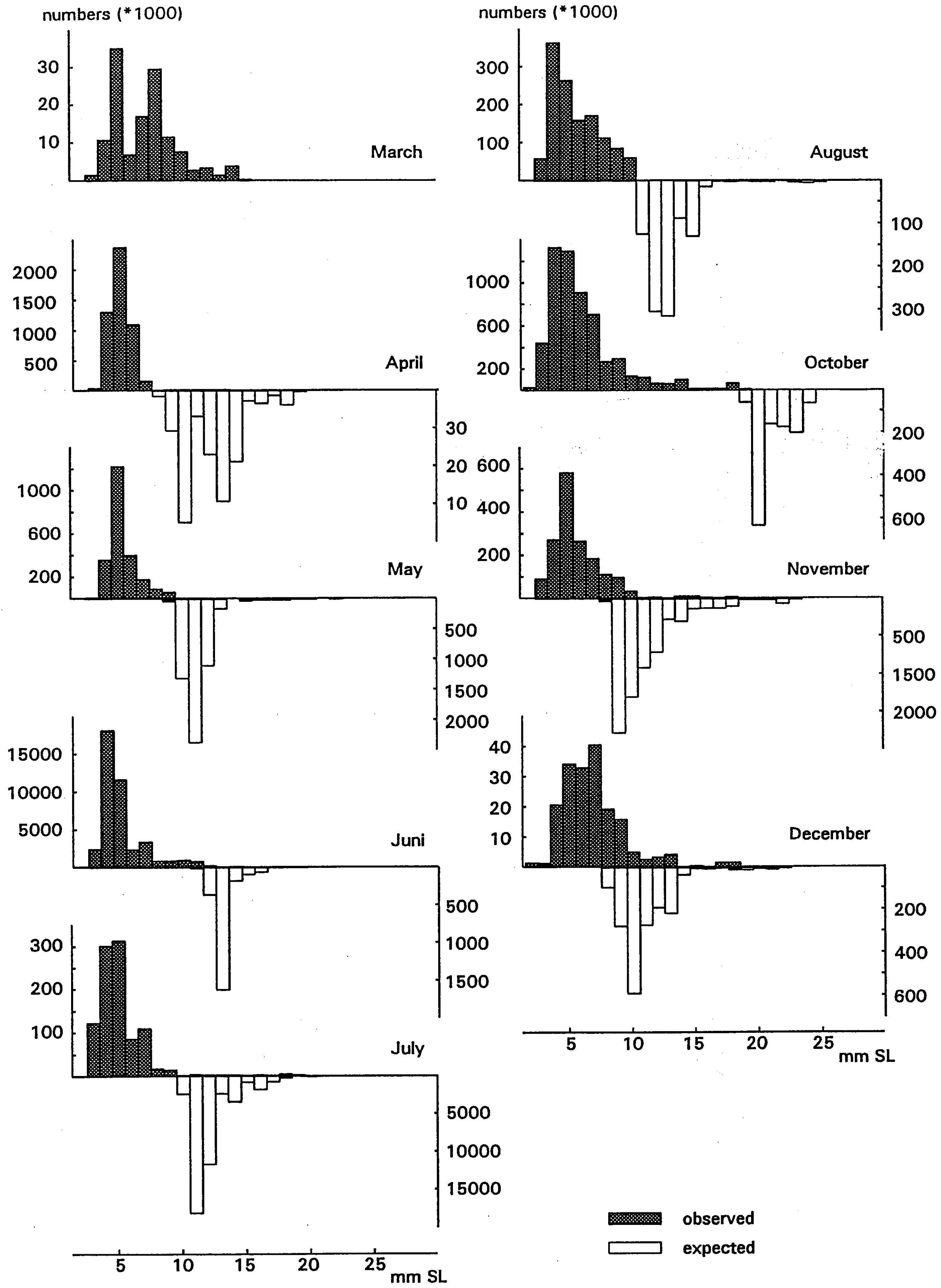

ind.m-3
ind.100m-2
10
1
0.1
0.01
500
400
300
200
100
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
marsh
estuary

FIGURE 4.


numbers (*1000)
30
20
10
March
2000
1500
1000
500
April
30
20
10
1000
600
200
May
500
1000
1500
2000
15000
10000
5000
Juni
500
1000
1500
300
200
100
July
5000
10000
15000
5
10
15
20
25
mm SL
numbers (*1000)
300
200
100
August
100
200
300
1000
600
200
October
200
400
600
600
400
200
November
500
1500
2000
40
30
20
10
December
200
400
600
5
10
15
20
25
mm SL
observed
expected

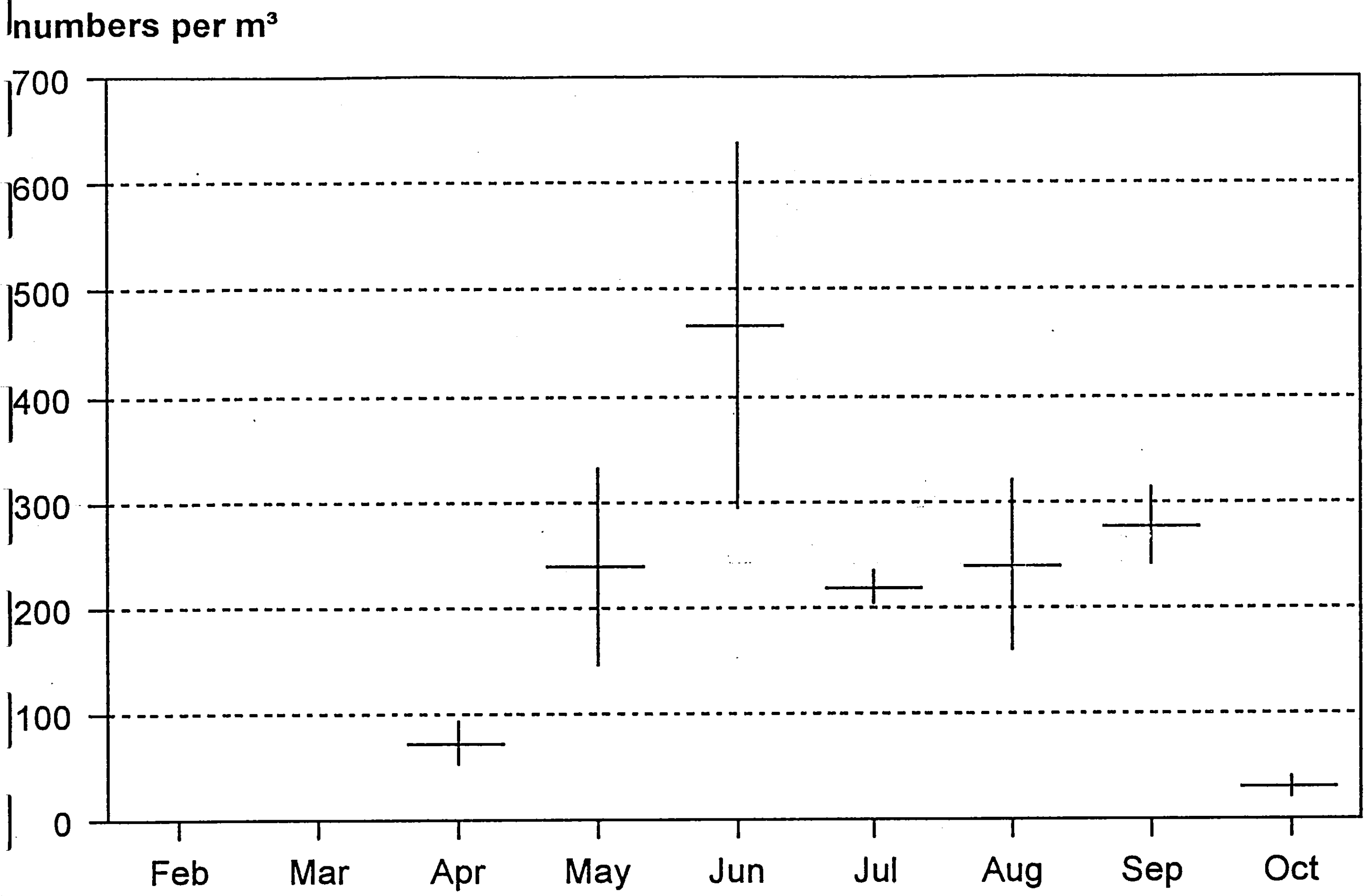

numbers per m³
700
600
500
400
300
200
100
0
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct

FIGURE 6.

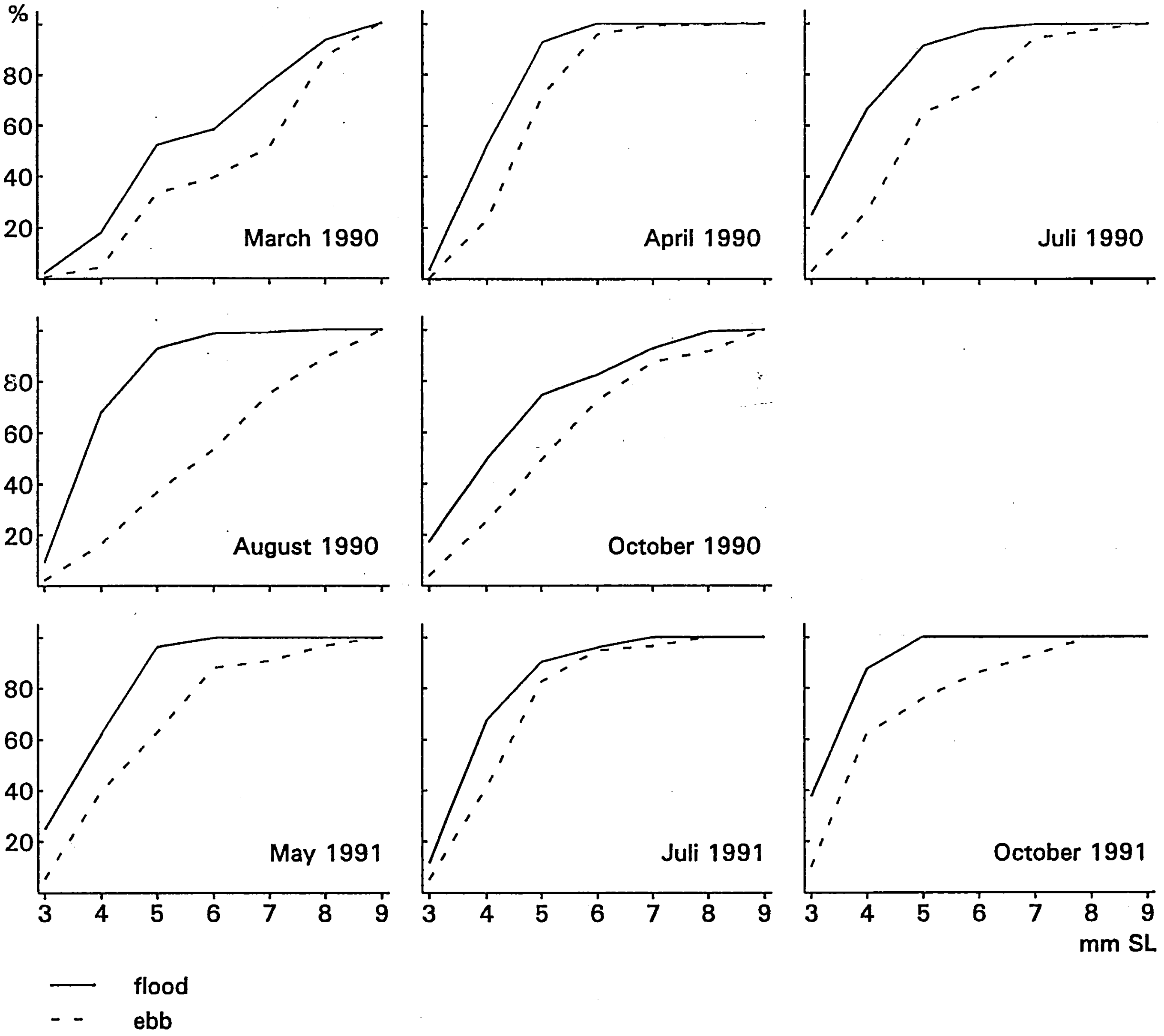
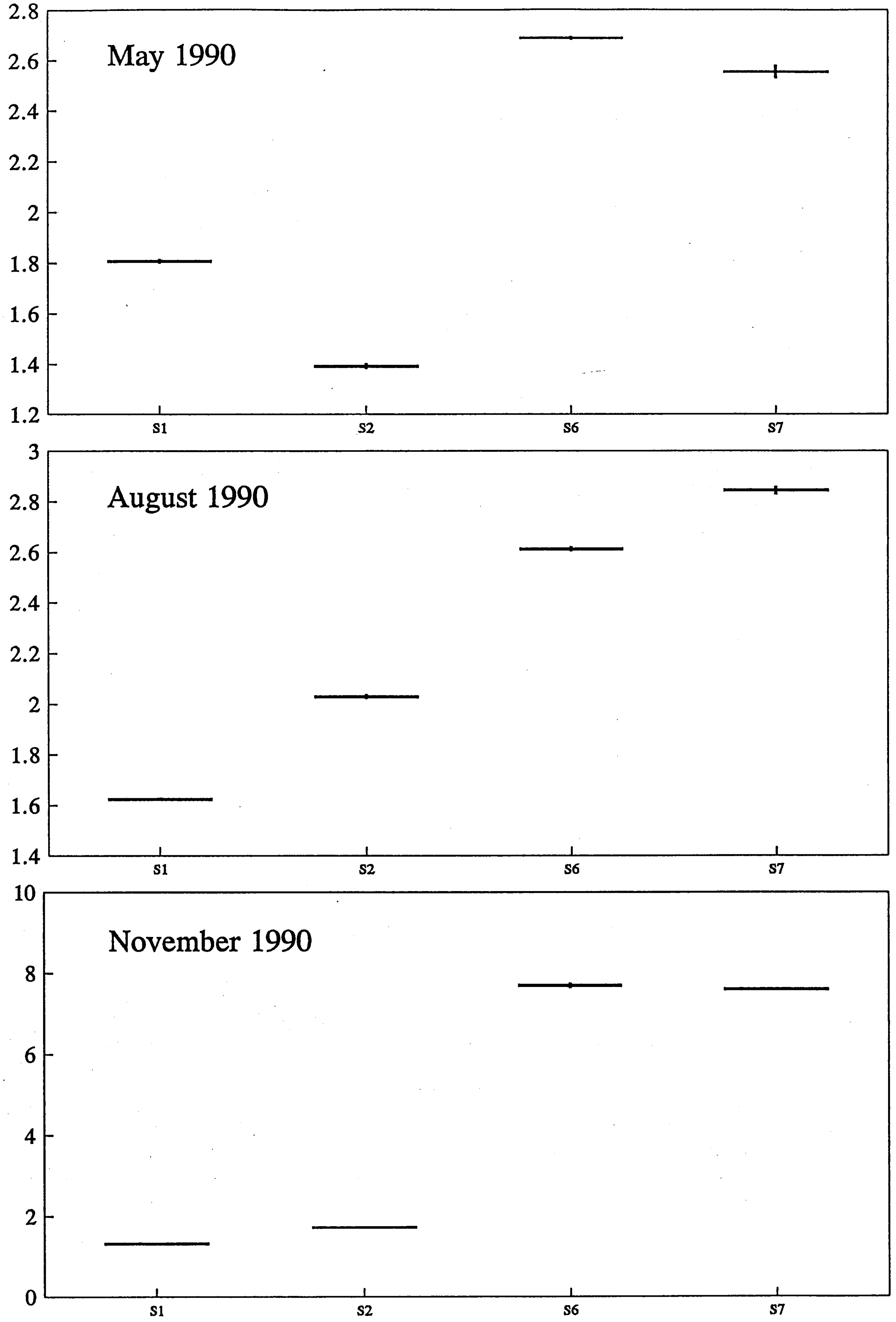

%
80
60
40
20
March 1990
April 1990
Juli 1990
August 1990
October 1990
May 1991
Juli 1991
October 1991
3
4
5
6
7
8
9
mm SL
flood
ebb

FIGURE 7.


May 1990
2.8
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
S1
S2
S6
S7
August 1990
3
2.8
2.6
2.4
2.2
2
1.8
1.6
1.4
S1
S2
S6
S7
November 1990
10
8
6
4
2
0
S1
S2
S6
S7

THE AQUATIC FAUNA OF TWO INTERTIDAL SALT MARSH CREEKS IN THE WESTERSCHELDE ESTUARY

by

ANDRE CATTRIJSSE, JAN MEES, KRIS HOSTENS and ESTHER S. MAKWAIA

University Gent, Marine Biology Section, Ledeganckstraat 35, 9000 Gent, Belgium.

SUMMARY

The natant macrofauna of two intertidal salt marsh creeks in the brackish basin of the Westerschelde estuary, was surveyed during eighteen months. Every month a stow net passively sampled the fish and the crustaceans migrating in and out of the marsh creek habitat. A complete description of the fauna of both marshes and their temporal and spatial variability is given.

During most seasons the fauna of both marshes were dominated by the mysid shrimps *Neomysis integer* and *Mesopodopsis slabberi*. In spring the communities were typified by high abundances of early juvenile brown shrimp (*Crangon crangon*), and the occurrence of postlarval flounder (*Pleuronectes flesus*) and sole (*Solea solea*). In summer the juveniles of common goby (*Pomatoschistus microps*), seabass (*Dicentrarchus labrax*) and shore crab (*Carcinus maenas*) characterized the communities. Multivariate analyses indicated that the seasonal appearance of these juvenile stages in spring and summer substantially altered the communities. In Saeftinghe, a true brackish marsh, the community appeared to be rather stable and only two different assemblages were identified: one during the winter-spring period (January until May-June) and one during the summer-autumn season (May-June until December). In the more saline marsh of Waarde seasonal changes in species composition were more pronounced, partly due to the appearance of typical marine species. In this marsh the winter-spring community could be divided into a winter-early spring (January-March) and a late spring assemblage (April-June).

Despite the difference in the salinity regime between both marshes, their nekton communities remained quite similar. The spatial difference between the two sites converged towards the winter months. Apart form the salinity factor, the position of the marshes along the estuarine channel possibly plays an important role in the species specific accessibility of the marsh habitat, and may accordingly cause a difference in species composition.

INTRODUCTION

Tidal marshes are important forage and refuge areas for some fishes and macrocrustaceans (BOESCH and TURNER, 1984). The highly productive marsh ecosystem potentially offers juvenile fish, shrimps and crabs high quality food, while the shallowness and the structural heterogeneity of the vegetated marsh surface provide protection from predators.

The studies supporting these statements have nearly all been conducted along the east coast of the United States where large areas of tidal marsh land exist. At high tide the vegetated marsh surface gets regularly flooded and is then being utilized by some species as a refuge and feeding area. European coastal marshes generally differ in this aspect from the American Atlantic tidal marshes. The vegetated surface of a European marsh is less frequently and for shorter periods flooded than a typical marsh on the American Atlantic coast. This forces the nekton to remain in the unvegetated creeks for most of the time, which reduces the refuge function of the vegetated marsh surface (CATTRIJSSE *et al.*, 1994). European marshes do however harbour high densities of juvenile fish and crustaceans (LABOURG *et al.*, 1985; DRAKE and ARIAS, 1991; COSTA *et al.*, 1994; CATTRIJSSE *et al.*, 1994).

The seasonal changes in the nekton community of a tidal creek of the brackish marsh Saeftinghe in the Westerschelde estuary, have already been described in detail by CATTRIJSSE *et al.* (1994). This paper reports on the spatial patterns in the marsh nekton assemblages of two marshes, situated along a salinity gradient in the Westerschelde estuary, SW-Netherlands. Therefore, the data of the former study were used in combination with data collected in another marsh downstream of Saeftinghe during the same period.

MATERIALS AND METHODS

Study area

Both marshes lie in the brackish reaches of the Westerschelde estuary in the southwest Netherlands (Fig. 1). The largest marsh, Het Verdronken Land van Saeftinghe, is situated close to the Dutch-Belgian border. It is one of the biggest European tidal marshes (DIJKEMA *et al.*, 1984) with a size of about 28 km² (VAN SCHAIK *et al.*, 1988). All samples were taken in one of the smaller creeks on the eastern part of the marsh. The dominant vegetation in the drainage area of the creek is composed of the following species: *Scirpus maritimus*, *Triglochin maritima*, *Puccinellia maritima*, *Elymus athericus*, *Phragmites australis* and *Atriplex hastata* (HEMMINGA *et al.*, 1993). The studied creek runs perpendicular to the main subtidal channel, which runs close by the border of the marsh (Fig. 1). The creek is about 1600 metres long, 36 metres wide, and the depth at the sampling point is about 4 metres. During every tidal cycle the creek falls completely dry for about 5 hours. The water starts to enter the system at about 3 hours before high water, after which it takes ca. 4 hours to leave the creek. After flooding only a small rivulet of seepage water and numerous shallow pools remain in the creek. The current speed is maximal just before and after high water.

The second marsh, the marsh of Waarde, is situated on the right bank of the estuary behind the large intertidal sandflat of Valkenisse (Fig. 1). It is the second largest marsh of the Westerschelde estuary with a size of about 107 ha (VAN SCHAIK *et al.*, 1988). All samples were collected in the main tidal channel of the marsh. The dominant halophytes growing in the vicinity of this creek are *Spartina anglica*, *Scirpus maritimus*, *Triglochin maritima*, *Puccinellia maritima*, *Elymus athericus*, *Aster tripolium* and *Atriplex hastata* (VAN SCHAIK *et al.*, 1988). Here, the creek runs parallel with the estuary and the border of the marsh. It opens into the large intertidal sandflat with a considerable distance from the main tidal channel of the estuary. Every tidal cycle the marsh creek falls completely dry during 7 hours, apart from a small stream of restwater and small pools. Flood brings water into the marsh about two hours before high water after which it takes on average 3 hours to leave it. In this creek the maximum currents were observed during the first hour of the incoming flood.

Sampling procedures and data analysis

A complete description of the sampling method is given in CATTRIJSSE *et al.* (1994). The net used to sample the fish and crustaceans that migrated in and out of the creeks with flood and ebb, was basically a stow net with an opening of 1 m² and a mesh size of 1 millimeter. In both marshes the gear was operated from upon a bridge. The net was placed on the bottom in the center of the creek at the moment the water started to enter. The net was hauled every hour and immediately placed back in the same position. After slack the net was turned to sample the ebb current. By means of the waterheight and the current speed, which were measured at intervals of fifteen minutes, an estimate could be given for the total volume of water that passed the sampling point and the amount of water filtered by the net for every sampling hour. The data collected during flood of one sampling date were grouped to estimate density and biomass abundances per m³ in the marsh creeks at the moment of high water. The data collected during ebb were similarly grouped to obtain a second estimate of the abundances at high water. Also the average density and biomass per sampling date were calculated. Temperature (°C), salinity (psu) and the concentration of dissolved oxygen ($mg.l^{-1}$) were measured every hour.

Between March 1990 and October 1991 both marshes were sampled monthly. In Waarde the samples were collected biweekly during April and October 1990. The marsh of Saeftinghe was sampled around spring tide while the marsh of Waarde was sampled between spring and neap tide, as spring tides flooded the bridge and most of the marsh surface. In Saeftinghe three flood samples and four ebb samples were collected and completely analysed for all sampling dates. In Waarde only two flood samples and three ebb samples could be collected, which were completely analysed for the following months: March, April and the first sampling of October of 1990 and February, April, June and August of 1991. The abundance estimates for the other months were only based upon the data collected during flood. By means of some multivariate techniques, no substantial differences in the nekton communities were detected between the flood and ebb samples. This approves a comparison between data based upon flood and ebb samples, and the data which are only based upon the flood samples.

All organisms were preserved in a 10% formalin seawater solution. Large catches were subsampled after removing all large fish, shrimp or crabs. In the laboratory all animals were determined to species level, counted and measured. The detritus in the samples was oven dried during three days at 60°C and weighed. The amount of detritus is expressed as $mgDW.m^{-3}$. Biomass was calculated through species related length - ashfreedryweigth (ADW) regressions (HAMERLYNCK *et al.*, 1990; HAMERLYNCK and CATTRIJSSE, 1994; MEES, 1994; K. HOSTENS and A. CATTRIJSSE, unpubl. data). Early postlarval brown shrimp (*Crangon crangon*) and flounder (*Pleuronectes flesus*), glasseels (*Anguilla anguilla*) and zoea and megalopa larvae of decapods were treated as separate species, because of their distinct ecology from their adult or juvenile congeners. Jellyfish (*Aurelia aurita*) and ctenophores (*Pleurobrachia pileus*), larvae of true endobenthic organisms and adult polychaetes were omitted from the analyses, as they are not regarded as a part of the actively migrating nekton.

The communities were analysed with multivariate techniques following the guidelines given by FIELD *et al.* (1982). Rare species were defined as occurring less than three times. The fourth root was taken of all data prior to analysis in order to reduce the weight of dominant species. The statistical methods employed were TWINSPAN (HILL, 1979), a cluster analysis using Bray-Curtis similarities and a CCA using CANOCO (TER BRAAK, 1988). The environmental variables that were used in the CCA analysis are the temperature and the salinity of the water, the concentration of dissolved oxygen, the amount of detritus and the waterheight attained in the creek.

A CCA was also used to compare the data set of Waarde with the data set of Saeftinghe. The measured waterheight in the creek already represents the difference in depth between both creeks. Therefore, the reciprocal value of the predicted waterlevel relative to NAP (Nieuw Amsterdams Peil, almost equal to the Mean Tidal Level) was included as an additional environmental variable, to account for the difference in tidal phase during sampling.

RESULTS AND DISCUSSION

Saeftinghe

For a detailed description and discussion of the data collected in Saeftinghe, see CATTRIJSSE *et al.* (1994). For the purpose of this paper the measurements of the environmental variables (Table 1) and the results obtained with the CCA analyses for Saeftinghe (Figure 2) are repeated. A complete species list is given as appendix.

Temperature was highest during August in both years (22°C and 23°C respectively). The salinity was equally highest during the summer with a maximum in August 1991 (16 psu) and lowest during the winter with a minimum in February 1991 (3 psu). The concentration of dissolved oxygen showed large fluctuations between 5.5 $mg.l^{-1}$ and 2.3 $mg.l^{-1}$, without clear seasonal patterns. The amount of detritus swept in and out of the creek system, was lower in spring and increased from July onwards with a maximum of 0.17 g DW.m^{-3} in January 1991. During 1991 the amount of detritus remained lower and never exceeded 0.05 g DW.m^{-3}. The waterheight in the creek at high water fluctuated between 270 cm and 390 cm.

A total number of 68 species were observed in Saeftinghe. Only 38 species were used in the analyses, as the others were only caught occasionally (see Appendix). The mysids *Neomysis integer* and *Mesopodopsis slabberi*, the shrimps *Crangon crangon* (postlarvae and adults) and *Palaemonetes varians*, the amphipods *Gammarus salinus*, *G. zaddachi*, *Corophium volutator* and *Orchestia gammarellus*, the isopods *Eurydice pulchra*, *Lekanesphaera rugicauda* and *Paragnathia formica*, the crab *Carcinus maenas*, and the fishes *Pomatoschistus microps*, *Dicentrarchus labrax*, *Pleuronectes flesus* and *Syngnathus rostellatus* were the only species which were collected during at least half of the sampling dates.

Both CCA plots showed very similar patterns. In combination with the results of the TWINSPAN and the Cluster analyses (CATTRIJSSE *et al.*, 1994), only two communities were detected: one occurring during winter and spring and one typical for the summer and autumn months. The winter situation was only apparent in the density plot. Temperature and salinity structured the communities the most, but the overall importance of these variables remained low as their vectors had a low correlation with the first canonical axis. Additionally the eigenvalues of the first and second axes were very low: 0.15 and 0.09 resp. with the density data, and 0.16 and 0.11 with the biomass data.

Waarde

The seasonal evolution of the temperature of the water flooding the marsh of Waarde was very similar to the observations made in Saeftinghe (Table 1). Maximum temperatures (21 °C) were recorded in August 1990 en 1991 and minimum values were registrated in February 1991 (2 °C). Salinity was normally twice as high as in the marsh of Saeftinghe and also strongly correlated with the seasonal pattern in the temperature. In 1990 the maximum salinity was recorded in August (25 psu) and a minimum in March (16 psu). In 1991 the maximum (25 psu) and minimum values (16 psu) were recorded in June and February respectively. The concentration of dissolved oxygen fluctuated between 7 and 10 mg.l^{-1}. In contrast with the situation in Saeftinghe the concentration of dissolved oxygen was higher and showed a positive correlation with temperature. The amount of detritus transported with the tides in the marsh of Waarde was considerably higher than in Saeftinghe, but showed the same seasonal trend. In 1991 however, the amount of detritus highly fluctuated between January and April with maximum values of 2.6 g DW.m^{-3} and minimum values of 0.09 g DW.m^{-3}. The waterheight in the creek reached values between 143 cm and 245 cm.

In the marsh of Waarde 58 species were caught with the stow net. Only 33 of these were finally used in the multivariate analysis. Almost the same abundant species as in Saeftinghe were observed in at least half of the months: *Neomysis integer*, *Mesopodopsis slabberi*, *Praunus flexuosus*, *Crangon crangon* (early postlarvae and adults), *Palaemonetes varians*, *Gammarus salinus*, *G. zaddachi*, *Corophium volutator*, *Orchestia gammarellus*, *Bathyporeia* species, *Eurydice pulchra*, *Lekanesphaera rugicauda*, *Carcinus maenas*, *Pomatoschistus microps*, *Gasterosteus aculeatus*, *Pleuronectes flesus* and *Syngnathus rostellatus*.

The species with the highest relative abundances and biomasses in Saeftinghe were as well the most important fauna elements in the marsh creek of Waarde, although the species composition was more varied. Some species alternately made high numerical contributions to the community: *Corophium volutator* (August 1990, January 1991, April 1991), *Gammarus salinus* (November 1990), *Bathyporeia* species (March 1991), *Eurydice pulchra* (December 1990, March 1991, April 1991) and *Praunus flexuosus* (April 1990). Also some substantial variations were noted in the relative biomasses (Fig. 3) of *Pleuronectes flesus* (April, July, Augustus and October 1990 and June and August 1991), *Syngnathus* *rostellatus* (May 1990, October 1990 and June 1991) and *Gasterosteus aculeatus* (December 1990 and February 1991).

The density of *Neomysis integer* in Waarde was lower, but the relative numerical and biomass abundances of this species had a similar seasonal evolution as in Saeftinghe. Its dominance decreased due to high abundances of *Crangon crangon* postlarvae in April and June, of *Mesopodopsis slabberi* in August through October and of *Corophium volutator* in January (Fig. 3). Maximum abundances of *Neomysis integer* were observed in March and June 1990: 11.5 ind. m^{-3} (61 mg ADW m^{-3}) and 9.8 ind. m^{-3} (54 mg ADW m^{-3}) respectively. The increase in abundance of *Mesopodopsis slabberi* during the autumn was apparent but less pronounced than in Saeftinghe. In Waarde the numerical dominance during that period (8 ind. m^{-3}, 2.5 mg ADW m^{-3}) was not followed by a dominance in biomass since the majority of the individuals were small juveniles. Although the population of M. slabberi reaches its density maximum in the subtidal in front of the marsh of Waarde (MEES *et al.*, 1993), the densities in the marsh creek of Waarde were always lower than in Saeftinghe.

Early postlarval brown shrimp *Crangon crangon* reached high densities between April and June. Only the maximum densities, recorded in April 1990 (26 ind. m^{-3}) and in June 1991 (5.8 ind. m^{-3}), contributed significantly to the community biomass. The much lower densities in 1991 had been observed in Saeftinghe as well. The abundance of these early juvenile shrimps in Saeftinghe and Waarde were comparable.

Densities of early postlarval flounder *Pleuronectes flesus* were also comparable with the densities found in Saeftinghe. Maximum values were observed in May 1990 (0.3 ind. m^{-3}) and in April 1991 (0.4 ind. m^{-3}). In contrast with the samples of Saeftinghe, adult flounder were regularly caught in Waarde.

Megalopa of the shore crab *Carcinus maenas* were mainly present in the marsh creek system in June 1990, and less abundant than in Saeftinghe. The juvenile shore crabs recruited simultaneously to the creek in Waarde during June (0.2 ind. m^{-3}). In 1991 these early juveniles were first caught in August (0.4 ind. m^{-3}). In comparison with the community found in Saeftinghe juvenile and adult shore crabs were less common and less important in terms of biomass.

The seasonal abundance and the observed densities of juvenile common goby *Pomatoschistus microps* are comparable with the data collected in Saeftinghe. The first recruits were caught in June, maximal densities were recorded in July 1990 (2.4 ind. m^{-3}) and in August 1991 (1.6 ind. m^{-3}), and a maximum biomass was recorded in October 1990 (20 mg ADW m^{-3}).

In contrast, the shrimp *Palaemonetes varians* was more common and more abundant in Waarde, but its abundance fluctuated strongly. In May 1990 a maximum density of 0.9 ind. m^{-3} was calculated, while the biomass of this species reached maxima of 12 mg ADW m^{-3} in May 1990 and May 1991.

TWINSPAN identified three different communities in the marsh of Waarde (Fig. 4). A winter-spring community grouping all samples between November 1990 and April 1991. The months March 1990, April 1990 and May 1991 are placed apart, indicating a more pronounced spring community. Within the summer-autumn assemblage which groups all other samples, May 1990 and June 1991 are separated and can thus be regarded as intermediate situations between the spring and summer-autumn communities. With the density data, the summer-autumn community was characterized by four indicatorspecies: *Palaemonetes varians*, *Mesopodopsis slabberi*, *Carcinus maenas*, and *Pomatoschistus microps*. By Using the biomass data, *C. maenas* and *Syngnathus rostellatus* were indicative for this community. The other clusters (winter-spring group) had *Bathyporeia* species as common indicator species. The true spring community bared *P. varians* and *Crangon crangon* as indicatorspecies for the density and biomass data respectively.

The clusteranalyses based on the biomass data confirmed the TWINSPAN results (Fig. 5). May 1990 and June 1991 now grouped within the spring community, exemplifying their transitional character. The spring and winter communities were separated in the density dendrogra spring samples.

The several communities identified by the classification methods, could also be distinguished using the CCA ordination technique (Fig. 6), but only a weak separation of the samples along the two axes was found, similar to the results of Saeftinghe. The eigenvalues of the first and second canonical axes were quite low, 0.19 and 0.13 respectively with the density data and 0.18 and 0.10 respectively for the biomass data. In the density biplot the temperature and the concentration of dissolved oxygen gave the largest vectors but only the former environmental variable, together with the salinity vector, had good correlations with the first canonical axis. The vectors for the amount of detritus and the registrated waterheight had the least influence upon structuring the communities. In the biomass biplot, the correlation of the temperature and salinity vectors with the first canonical axis was reduced while the oxygen concentration now explained more of the separation of the samples along the second axis. Waterheight and the amount of detritus had again a weak impact upon the structure of the different communities.

A comparison of the communities of Saeftinghe and Waarde

Some differences between the communities observed in both marshes have already been mentioned in the previous paragraphs. The major differences and similarities will be summarized in this section. The same dominant nekton species are found in both marshes: *Neomysis integer*, *Mesopodopsis slabberi*, *Pomatoschistus microps* and postlarvae of *Crangon crangon*. Yet, both mysids and a number of other common species showed a clear difference in occurrence between both marshes.

The most obvious feature concerned the occurrence and the abundance of some of the common species (see Appendix). *Praunus flexuosus*, *Palaemonetes varians*, *Pleuronectes flesus*, *Gasterosteus aculeatus* and *Bathyporeia* species are five common species which were collected more regularly and in larger quantities in the marsh of Waarde. All species, except *G. aculeatus* have been recorded in comparable densities in the subtidal of the Westerschelde between Waarde and Saeftinghe (CATTRIJSSE *et al.*, 1993; MEES, 1994). *G. aculeatus* rather frequents shallow areas than deep subtidals. Consequently it is an uncommon species in the subtidal demersal fish fauna (HOSTENS, this volume) but it is known to occur in saline, brackish and fresh waters. The salinity gradient can thus only partly explain the different abundances of these five species. The mysid *P. flexuosus*, the shrimp *P. varians* and flounder *P. flesus* are also typical intertidal species. The amphipod species belonging to the genus *Bathyporeia* all occur in sandy areas. In front of the marsh of Waarde the extensive intertidal sandflats and the shallow channels intersecting them, offer these species their preferred habitat. The studied creek in Saeftinghe directly opens into the main subtidal channel of the estuary. The absence of a large and partly vegetated intertidal area in that part of the estuary can explain the lower abundances of these species in the creek of Saeftinghe.

On the other hand, the isopod *Lekanesphaera rugicauda* occurred in higher abundances in Saeftinghe, which is probably a salinity effect. Also the mysid shrimps *Neomysis integer* and *Mesopodopsis slabberi* generally occurred in higher densities in Saeftinghe. *N. integer* reached its maximum distribution in the subtidal around the marsh of Saeftinghe which might explain its decreased densities in Waarde. Yet, *M. slabberi*, reached its maximum population density in the more saline parts of the estuary nearby Waarde (MEES *et al.*, 1993) but did not reach higher abundances in the marsh of Waarde. Both mysids regularly frequent shallow estuarine environments. The presence of a deeper water body in front of the creek of Saeftinghe therefore does not explain the difference in densities, nor does the salinity gradient.

The seabass *Dicentrarchus labrax* was a common species in Saeftinghe with a clear seasonal appearance, but it was only caught once in Waarde. Seabass forages on the nekton fauna in the tidal creeks (KELLEY, 1988; CATTRIJSSE unpubl. data), and juvenile fishes occur with higher densities near power plants, where they profit of the increased water temperatures (KELLEY, 1986). In the Westerschelde estuary this behaviour exists as well, as seabass was one of the common species caught in the intake screen of the Power plant of Doel, a few kilometres upstream from Saeftinghe (Vandamme *et al.*, 1994). During their life cycle seabass juveniles migrate down the estuary (KELLEY, 1988) avoiding intertidal areas. Though juvenile seabass has been observed along the sandflats in front of Waarde, they possibly do not migrate towards the creek of the marsh of Waarde.

Similarly, the more frequent occurrences and the higher abundances of juveniles of thick-lip mullet *Chelon labrosus*, thin-lip mullet *Liza ramada*, herring *Clupea harengus* and sprat *Sprattus sprattus* in Saeftinghe, can be explained by their biology: as they swim high up in the watercolumn they avoid large intertidal areas and too shallow creeks. The creek in Saeftinghe is almost twice as deep as the one in Waarde and directly connected with the subtidal, which makes it more suitable for migration of these species.

Marine species like the mysids *Schistomysis spiritus* and *S. kervillei* were more frequently observed in Waarde, while typical but rare freshwater fish species like pike-perch *Styzostedion lucioperca*, ten-spined stickleback *Pungitius pungitius* and bleak *Alburnus alburnus* were only caught in Saeftinghe. These differences can be seen as a salinity effect upon the marsh nekton community structure.

The differences between the nekton communities of the two marshes are also clear in the ordination analysis, based on the density data of both marshes together (Fig. 7). The eigenvalues of both axes were again very low in this ordination (0.16 and 0.09), which indicates that only a small part of the observed variance is explained by the variables considered. The temporal patterns as a result of the seasonal changes in temperature, were dominant and confirmed the earlier described seasonal changes in community structure in Waarde and in Saeftinghe. Both marshes are separated along the second axis, due to the spatial difference in salinity. This spatial divergence is also partly caused by the difference in moment of sampling (neap tide versus spring tide), which is illustrated by the correlation of the vector of the reciprocal value of the tabulated waterheight (1/NAP) with the second axis. Again, the amount of detritus had the lowest importance. The concentration of dissolved oxygen and the registrated waterheight in the creeks had large vectors. This can explain the separation of the samples along both axes, in contrast with the analyses on both marshes separately. In this combined analysis the recorded waterheight in the creeks is interpreted as indicative for the accessibility of the marsh creeks. Also the concentration of dissolved oxygen is considered to be a dummy variable, which expresses a spatial difference between both marshes. The oxygen concentrations were always lower in Saeftinghe but never reached lethal limits. As high densities were recorded for some very common organisms in Saeftinghe, the oxygen levels probably had no detrimental effect upon the occurrence of the different nekton species.

The estuarine assemblages that occurred in the estuarine subtidal habitats between Waarde and Saeftinghe did not differ substantially during most seasons (MEES, 1994; HOSTENS, this volume). These studies have shown that increased salinities caused true marine species to migrate up the estuary during summer, which resulted in a shift in the subtidal assemblages of the mid-estuary. The communities of both marsh creeks clearly diverged during the summer months, as some marine species appeared in the marsh of Waarde. During autumn and winter less differences were found between both marsh communities (Fig. 7).

Still, the salinity gradient cannot fully explain the observed shifts in community structure. Probably the hydrological position of the marshes is also important: the absence or presence of intertidal shallows or deep subtidals in front of a marsh creek might affect the ability for a species to reach the tidal creek. This can have an influence on the species composition and the structure of the nekton communities in the marshes.

ACKNOWLEDGEMENTS

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APPENDIX

Species list of the marshes of Waarde and Saeftinghe. ● denotes the species used in the multivariate analyses, ○ denotes species found during less than three sampling dates and not used in the final analyses.

		WAARDE	SAEFTINGHE
PISCES	*Anguilla anguilla*	○	○
	Anguilla anguilla juveniles (glasseels)	●	●
	Clupea harengus	○	●
	Sprattus sprattus		●
	Clupeidae larvae	●	●
	Atherina presbyter	●	○
	Dicentrarchus labrax	○	●
	Pomatoschistus minutus	●	●
	Pomatoschistus lozanoi	●	●
	Pomatoschistus microps	●	●
	Pomatoschistus species	●	●
	Chelon labrosus	○	●
	Liza ramada	○	○
	Ammodytes tobianus		○
	Gasterosteus aculeatus	●	●
	Syngnathus rostellatus	●	●
	Pleuronectes flesus	●	●
	Pleuronectes flesus postlarvae	●	●
	Pleuronectes platessa postlarvae		●
	Solea solea postlarvae	●	●
	Stizostedion lucioperca		○
	Alburnus alburnus		○
	Pungitius pungitius		○
	Merlangius merlangus		○
	Fish larvae indet.		●
CRUSTACEA	*Palaemonetes varians*	●	●
	Palaemonetes varians zoea		○
	Palaemonetes varians postlarvae	○	○
	Palaemon elegans		●
	Crangon crangon	●	●
	Crangon crangon postlarvae	●	●
	Crangon crangon zoea	○	
	Carcinus maenas	●	●
	Carcinus megalopae	●	●
	Carcinus zoea	○	●
	Liocarcinus megalopae		○
	Liocarcinus zoea		○
	Portumnus latipes		○
	Portumnus latipes megalopae	○	
	Pagurus pagurus megalopae	○	
	Megalopae indet.		○
	Macropodia spec.		○
	Neomysis integer	●	●
	Mesopodopsis slabberi	●	●
	Schistomysis spiritus	●	○
	Schistomysis kervillei	●	○
	Praunus flexuosus	●	●
	Gastrosaccus spinifer		●
	Corophium volutator	●	●
	Corophium lacustre	○	●
	Corophium arenarium		○
	Corophium acherusicum	○	
	Gammarus salinus	●	●
	Gammarus zaddachi	●	●
	Gammarus tigrinus		○
	Gammarus duebeni	○	○
	Gammarus crinicornis	○	
	Gammarus locusta	○	
	Gammarus spec.	●	○
	Chaetogammarus marinus	●	

	Orchestia gammarellus	●	●
	Bathyporeia spec.	●	●
	Pleusymptes glaber	●	●
	Haustorius arenarius	○	○
	Atylus swammerdami		○
	Melita palmata	○	
	Hyperia galba	○	
	Eurydice pulchra	●	●
	Lekanesphaera rugicauda	●	●
	Idotea baltica		○
	Idotea cheliceps	○	
	Jaera albifrons	○	
	Paragnathia formica	●	●
MISC.	*Nereis diversicolor*	○	○
	Lanice conchilega aulophora	○	○
	Daphnia magna		○
	Sagitta elegans	○	○
	Pleurobrachia pileus	○	○
	Aurelia aurita	○	○

TABLE 1

Environmental variables measured during the monthly sampling campagnes in both marshes.

SAEFTINGHE	15/3/90	11/4/90	10/5/90	11/6/90	9/7/90	8/8/90	10/10/90	5/11/90	3/12/90
Temperature (°C)	11	12	17	19	20	22	16	12	9
Salinity (psu)	5.6	8.5	9.9	11.5	11.9	16.1	14.3	12.1	11.9
Oxygen concentration (mg.l^{-1})	2.3	4.9	2.9	2.8	3.8	3.6	4.5	3.2	3.8
Detritus (g DW.m^{-3})	0.01	0.05	0.02	0.02	0.15	0.07	0.11	0.08	0.10
Registrated waterheight (cm)	350	388	350	323	361	356	373	388	370
Predicted waterheight (cm above NAP)	308	314	304	289	295	290	284	346	338

SAEFTINGHE	29/1/91	14/3/91	16/4/91	10/5/91	13/6/91	12/7/91	9/8/91	7/9/91	7/10/91
Temperature (°C)	6	9	13	12	16	21	23	21	17
Salinity (psu)	3.4	4.5	8.4	8.0	11.5	6.8	10.3	13.8	14.2
Oxygen concentration (mg.l^{-1})	5.5	3.7	2.7	4.0	3.4	4.3	4.5	3.8	3.6
Detritus (g DW.m^{-3})	0.17	0.01	0.01	0.004	0.001	0.04	0.02	0.03	0.04
Registrated waterheight (cm)	333	343	395	271	370	353	315	315	330
Predicted waterheight (cm above NAP)	294	285	348	242	333	320	288	278	295

WAARDE	23/3/90	5/4/90	22/4/90	19/5/90	20/6/90	3/7/90	17/8/90	1/10/90	15/10/90
Temperature (°C)	10	10	12	15	16	19	21	14	12
Salinity (psu)	15.7	19	19	19.7	21.5	21.3	25.0	23.1	23.1
Oxygen concentration (mg.l^{-1})	7.9	9.2	9.2	10.1	7.4	7.1	7.0	7.7	7.7
Detritus (g DW.m^{-3})	0.14	0.17	0.18	0.24	0.59	0.84	0.46	0.77	1.16
Registrated waterheight (cm)	214	215	245	187	215	163	185	192	243
Predicted waterheight (cm above NAP)	118	119	148	119	154	110	105	106	119

WAARDE	30/11/90	28/12/90	25/1/91	25/2/91	11/3/91	9/4/91	9/5/91	7/6/91	5/8/91
Temperature (°C)	11	6	6	2	7	12	10	13	21
Salinity (psu)	22.3	22.0	16.1	15.5	19.4	19.0	22.8	26.1	20.3
Oxygen concentration (mg.l^{-1})	7.9	8.9	9.8	8.3	7.4	8.0	9.4	8.8	6.6
Detritus (g DW.m^{-3})	0.99	0.04	1.12	2.43	0.09	2.60	0.39	0.46	0.47
Registrated waterheight (cm)	235	228	175	205	201	143	177	194	201
Predicted waterheight (cm above NAP)	154	130	201	201	137	142	183	200	201

LIST OF FIGURES

Fig. 1. - The position of both marshes within the brackish reaches of the Westerschelde estuary, and the sampling points. Note the distance to the main subtidal channel of the estuary.

Fig. 2. - CCA ordination plots based on the density and biomass data collected in the marsh of Saeftinghe. (after CATTRIJSSE *et al.*, 1994).

Fig. 3. - Relative densities and biomasses of the most important species in the marsh of Waarde. (See CATTRIJSSE *et al.* (1994) for a comparison with the marsh of Saeftinghe).

Fig. 4. - TWINSPAN dendrogrammes based on the density and biomass data of Waarde.

Fig. 5. - Results of the Cluster Analyses based on the density and biomass data of Waarde.

Fig. 6. - CCA plots obtained with the density and biomass data of Waarde.

Fig. 7. - CCA plot based on the density data collected in Saeftinghe and in Waarde.

FIGURE 1.

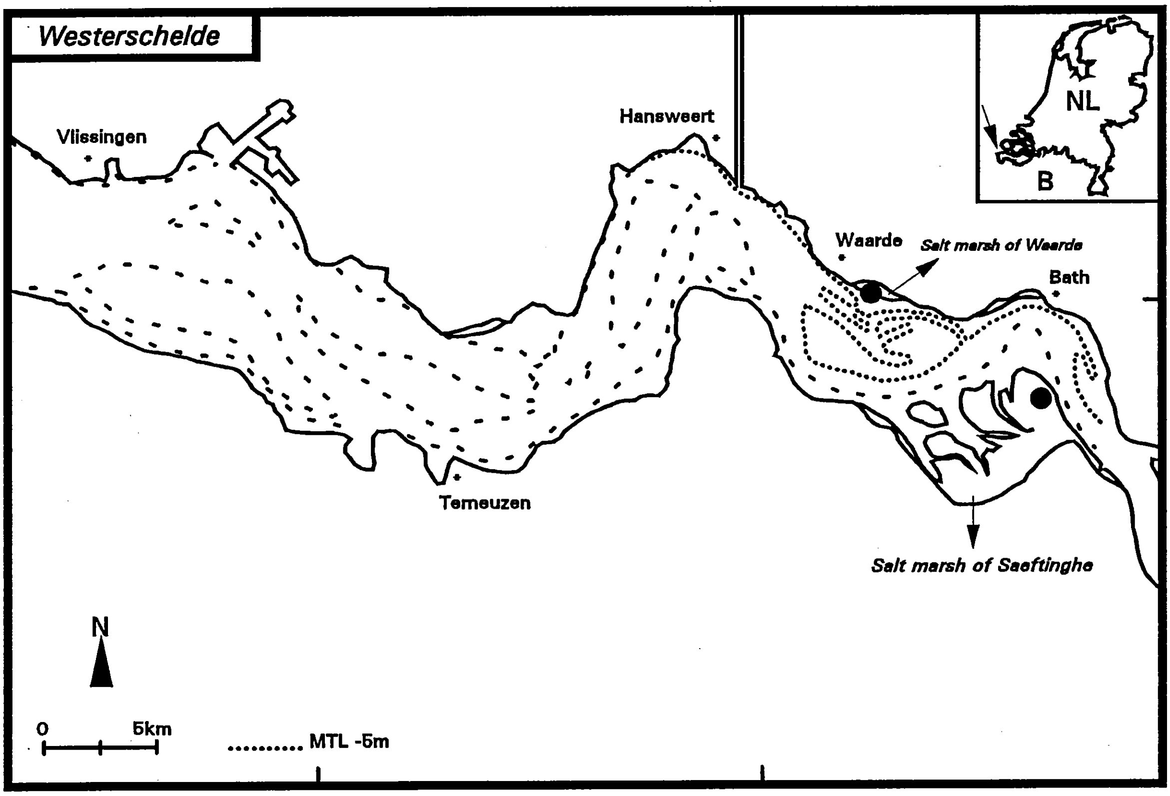

Westerschelde
Vlissingen
Hansweert
Waarde
Salt marsh of Waarde
Bath
Terneuzen
Salt marsh of Saeftinghe
NL
B
N
0
5km
.... MTL -5m

FIGURE 2.

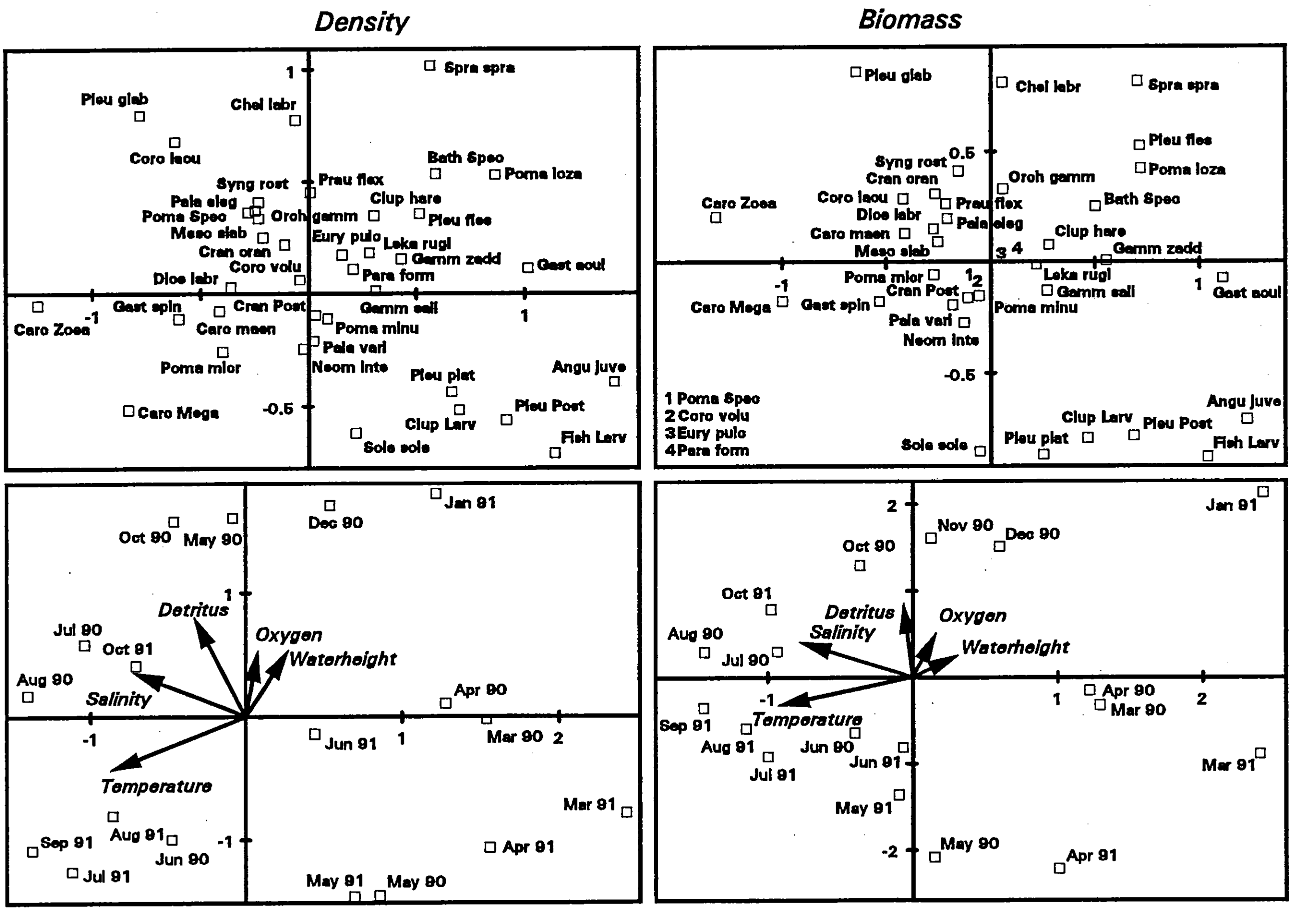

Density
Biomass
Spra spra
Pleu glab
Chel labr
Coro laou
Bath Speo
Poma loza
Syng rost
Prau flex
Clup hare
Pala eleg
Poma Speo
Oroh gemm
Pleu fles
Meso slab
Eury pulo
Leka rugi
Cran oran
Gemm zadd
Coro volu
Gast aoul
Para form
Dioe labr
Gast spin
Cran Post
Gemm sali
Caro Zoea
Caro maen
Poma minu
Pala vari
Poma mior
Neom inte
Pleu plat
Angu juve
Caro Mega
Pleu Post
Clup Larv
Fish Larv
Sole sole
1 Poma Speo
2 Coro volu
3 Eury pulo
4 Para form
1
-1
0.5
-0.5
2
-2
Oct 90
May 90
Dec 90
Jan 91
Nov 90
Oct 91
Jul 90
Aug 90
Detritus
Oxygen
Waterheight
Salinity
Temperature
Apr 90
Mar 90
Jun 91
Sep 91
Aug 91
Jun 90
Jul 91
Mar 91
Apr 91
May 91

FIGURE 3.

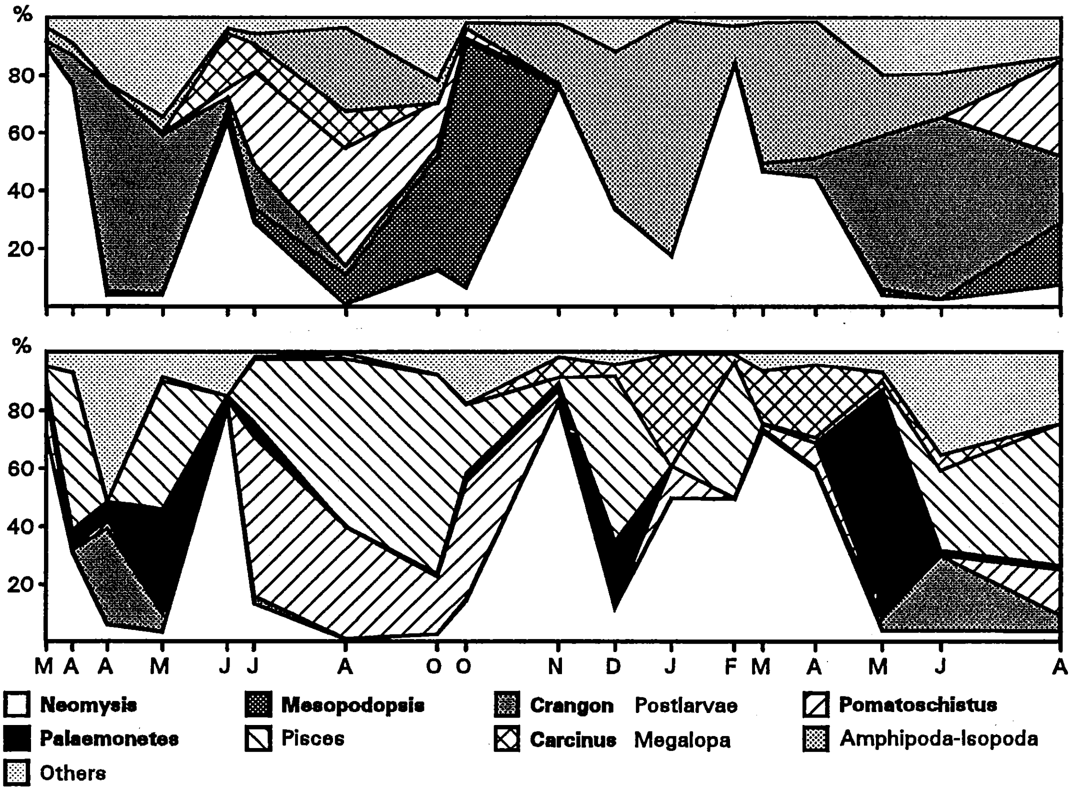

%
80
60
40
20
%
80
60
40
20
M A A M J J A O O N D J F M A M J A
Neomysis
Palaemonetes
Others
Mesopodopsis
Pisces
Crangon Postlarvae
Carcinus Megalopa
Pomatoschistus
Amphipoda-Isopoda

FIGURE 4.

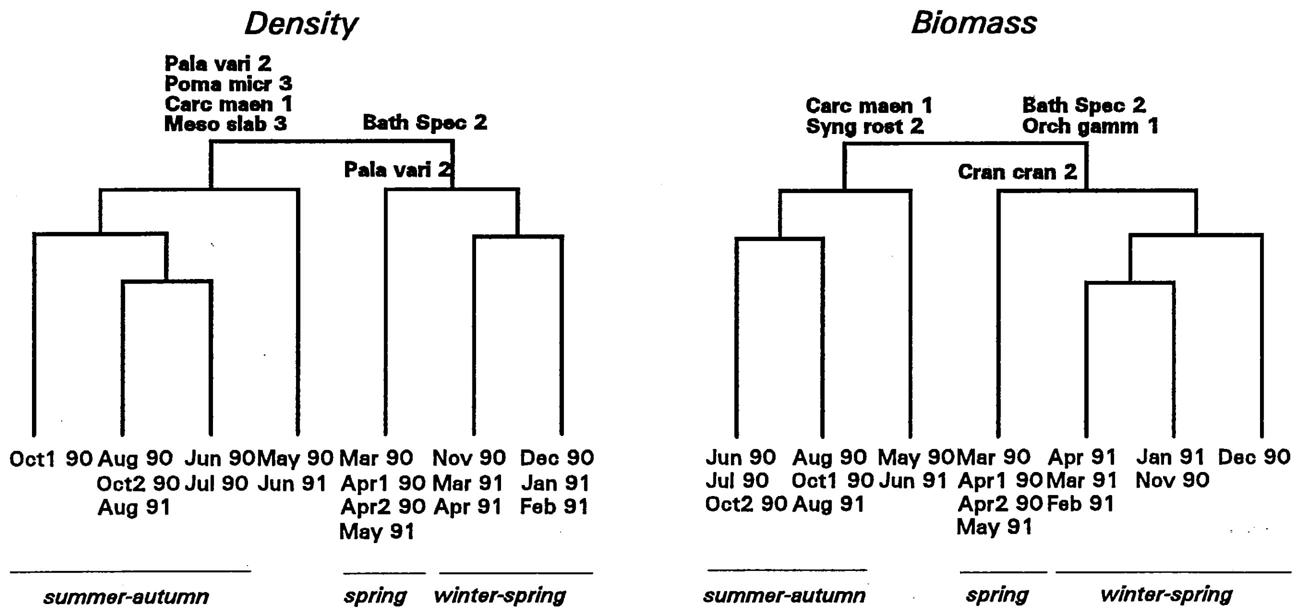

Density
Pala vari 2
Poma micr 3
Carc maen 1
Meso slab 3
Bath Spec 2
Pala vari 2
Oct1 90
Aug 90
Oct2 90
Aug 91
Jun 90
Jul 90
May 90
Jun 91
Mar 90
Apr1 90
Apr2 90
May 91
Nov 90
Mar 91
Apr 91
Dec 90
Jan 91
Feb 91
summer-autumn
spring
winter-spring
Biomass
Carc maen 1
Syng rost 2
Bath Spec 2
Orch gamm 1
Cran cran 2
Jun 90
Jul 90
Oct2 90
Aug 90
Oct1 90
Aug 91
May 90
Jun 91
Mar 90
Apr1 90
Apr2 90
May 91
Apr 91
Mar 91
Feb 91
Jan 91
Nov 90
Dec 90
summer-autumn
spring
winter-spring

FIGURE 5.

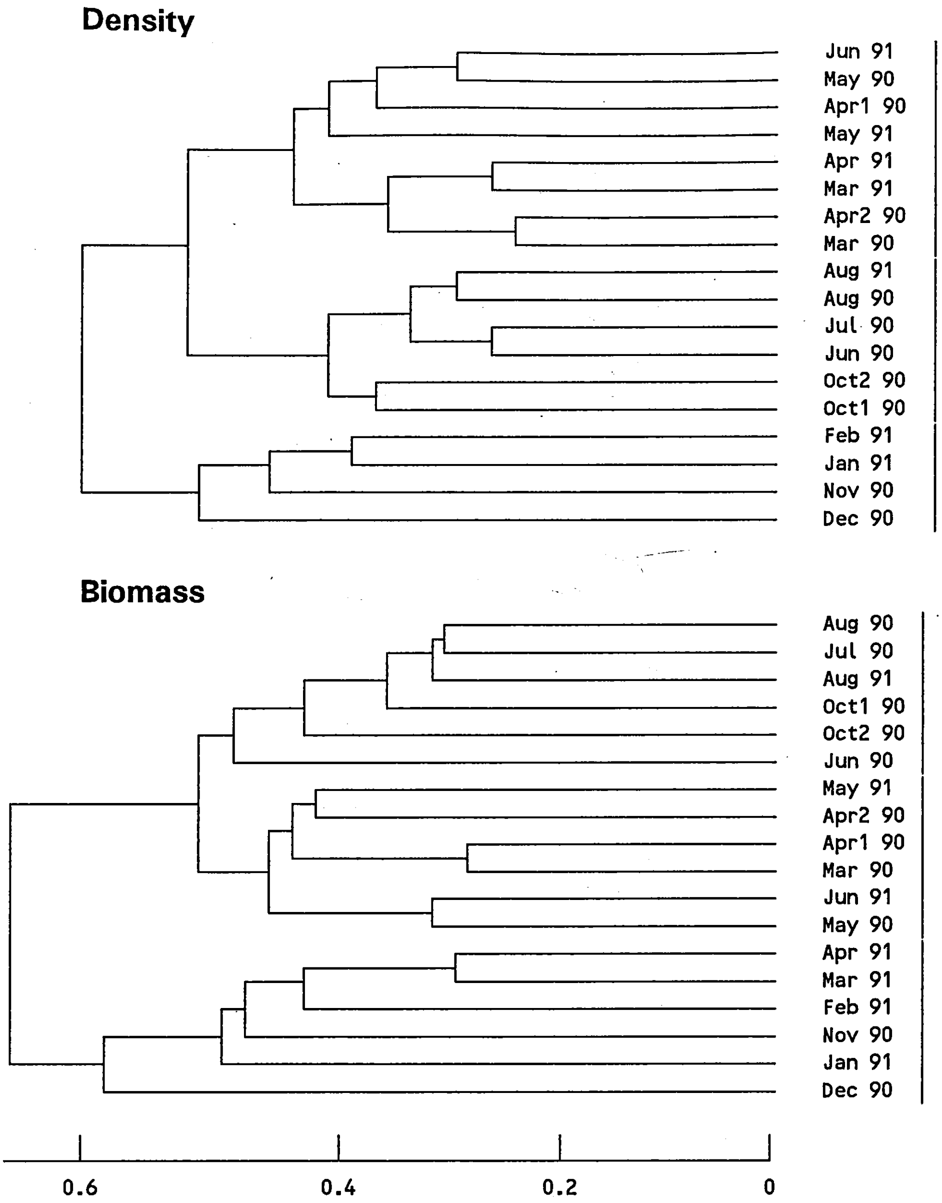
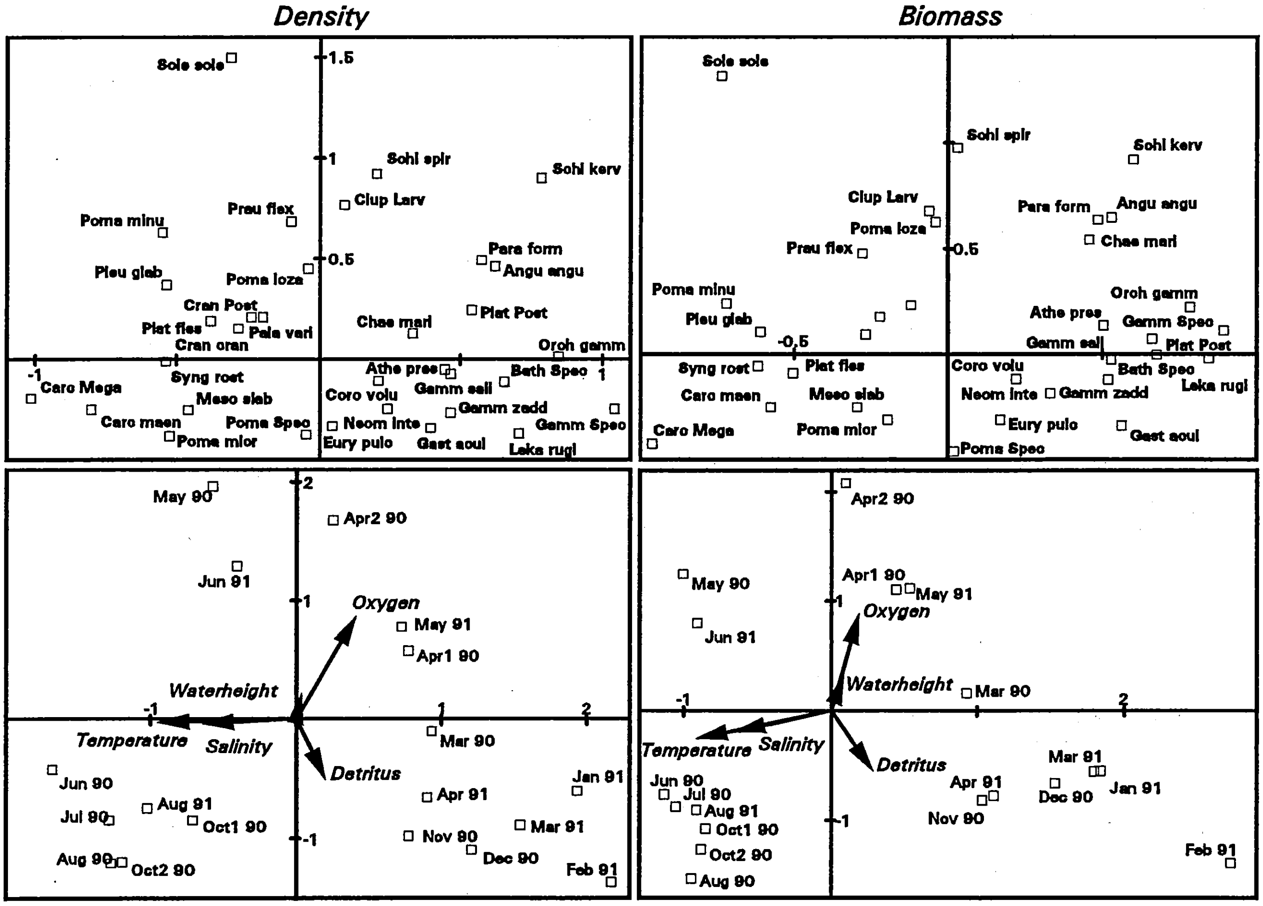

Density
Jun 91
May 90
Apr1 90
May 91
Apr 91
Mar 91
Apr2 90
Mar 90
Aug 91
Aug 90
Jul 90
Jun 90
Oct2 90
Oct1 90
Feb 91
Jan 91
Nov 90
Dec 90
Biomass
Aug 90
Jul 90
Aug 91
Oct1 90
Oct2 90
Jun 90
May 91
Apr2 90
Apr1 90
Mar 90
Jun 91
May 90
Apr 91
Mar 91
Feb 91
Nov 90
Jan 91
Dec 90
0.6
0.4
0.2
0

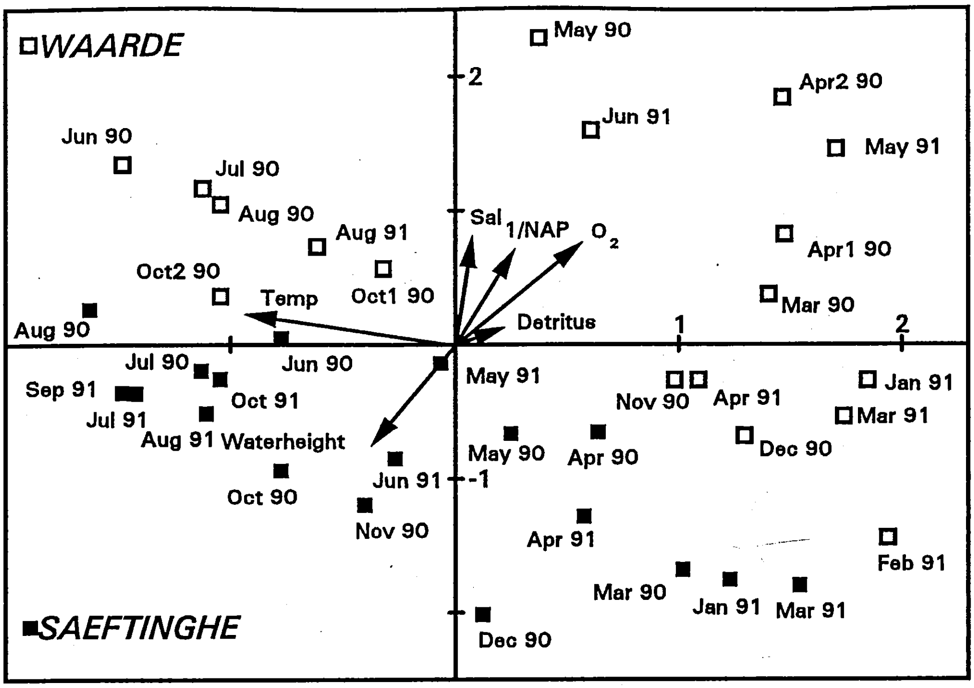
FIGURE 6.



Density

Biomass

FIGURE 7.


□WAARDE
■SAEFTINGHE
May 90
2
Apr2 90
Jun 91
Jun 90
May 91
Jul 90
Aug 90
Sal
1/NAP
O_2
Aug 91
Apr1 90
Oct2 90
Temp
Oct1 90
Mar 90
Aug 90
Detritus
1
2
Jul 90
Jun 90
May 91
Sep 91
Oct 91
Nov 90
Apr 91
Jan 91
Jul 91
Mar 91
Aug 91
Waterheight
May 90
Apr 90
Dec 90
Jun 91
-1
Oct 90
Nov 90
Apr 91
Feb 91
Mar 90
Jan 91
Mar 91
Dec 90

SEASONALITY IN THE HYPERBENTHIC COMMUNITIES OF THE WESTERSCHELDE ESTUARY

by

J. MEES, A. DEWICKE, A. CATTRIJSSE, and N. FOCKEDEY
University of Gent, Zoology Institute,
Marine Biology Section,
K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

SUMMARY

Temporal patterns in the hyperbenthos of the Westerschelde estuary are described from year cycles of monthly and forthnightly samples. 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. In each season, the brackish communities were characterized by few species occurring in high numbers, whereas the marine communities were composed of many species at lower densities. Seasonal patterns in the marine zone were quite pronounced and they were dominated by the recruitment, maximal abundance and subsequent disappearance 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 and summer by postlarval shrimp, while other seasonal differences seemed to be mainly due to reproduction and natural mortality of endemic species and to migration of marine permanent hyperbenthic species in and out of the area.

INTRODUCTION

In estuaries, a large part of the primary production and of the allochtonous detrital material can be consumed by secondary consumers, mainly the benthos and the 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 (MEES and JONES, in press). It can thus be viewed as the uppermost compartment of the benthos and it is by far the least studied. These benthic subsystems interact with each other, with other ecosystem compartments and with their abiotic environment. Studying the separate benthic units recquires specific sampling methodology and strategy. Besides endemics hyperbenthic communities contain elements suggestive of two different origins: upward movement of surface-dwelling benthic species and downward movement of planktonic species (SIBERT, 1981). Still, there is general agreement that they should be classified as a distinct benthic compartment.

To date, studies of energy fluxes through coastal and estuarine ecosystems rarely include samples taken within a few cm of the sediment and may thus seriously underestimate flux of particulate material (ODUM *et al.*, 1979). The hyperbenthos may play a significant role in the energy flow of estuarine ecosystems: animals occur in high numbers and are potentially important in nutrient recycling as grazers on zooplankton and detritus (MAUCHLINE, 1980), and as food for higher trophic levels such as larger epibenthos (SITTS and KNIGHT, 1979) and fishes (e.g. SORBE, 1981). 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.

Density and biomass of the permanent hyperbenthos in estuaries are much higher than those recorded from neighbouring coastal areas (MEES and HAMERLYNCK, 1992). Especially in the highly turbid brackish water zone hyperbenthic species (mainly mysids) occur in very high numbers (MEES *et al.*, 1993a,b). 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 paper 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.* (1993). A photo-autotrophic food chain characterizes the marine part while the web in the brackish part is predominantly heterotrophic. 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 multi-disciplinary projects on the major european tidal estuaries which aim at clarifying the role of the hyperbenthos in the estuarine ecosystem. Spatial structure along the entire salinity gradient of the Westerschelde estuary was described in MEES *et al.* (1993b). The hyperbenthos of the Westerschelde was compared with the hyperbenthic communities in neighbouring coastal waters and with those of other European estuaries in MEES and HAMERLYNCK (1992) and MEES *et al.* (1995). From these studies it was concluded that at least two distinct hyperbenthic communities are present in the system. Furthermore, their geographical location was shown to be quite stable in time: certain stations in the marine and brackish parts always clustered together and they were characterized by completely different hyperbenthic communities.

MATERIAL AND METHODS

Study area and sampling strategy

The Westerschelde estuary (Fig. 1) 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 km². Its surface is approximately 300 km². The seaward part is a well mixed region characterised 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 the 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 and HERMAN, 1995). Consequently fresh water (average inflow 100 $m^3 s^{-1}$; range 30 to 500 $m^3 s^{-1}$) 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).

Samples were collected with a small sledge (HAMERLYNCK and MEES, 1991) which consists of a metal frame equipped with two 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 with the tide 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^2 and the maximal volume of water filtered through the nets is 800 m^3. Where possible the -10 m isobath was followed. Actual sampling depths varied between 7 m and 16 m. The samples were rinsed over a 1 mm sieve and were 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.

The hyperbenthos of the Westerschelde was sampled on a monthly basis from April 1990 through March 1991. During each campaign 14 stations were sampled, covering the area from Vlissingen near the mouth of the estuary, to Bath near the Dutch-Belgian border (Figure 1, MEES *et al.*, 1993b). The two westernmost and the two easternmost 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 and HAMERLYNCK, 1992, MEES *et al.*, 1993b, MEES *et al.*, 1995).

The brackish water community was further sampled forthnightly from November 1990 through December 1991 (MEES *et al.*, 1994) in order to obtain a more detailed description of the temporal patterns in this zone of the estuary. On each occasion at least four stations were sampled and the sample containing the highest number of *Neomysis integer* - the dominant species characterizing the brackish water hyperbenthos - was selected for further analyses. The density peak was always distinctly located in one of the four samples (for more details see MEES *et al.*, 1994).

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. All density data are presented as numbers of individuals (N) per trawl (1000 m^2) or per m^2. Net efficiency was considered to be 100% for all species; all density values should therefore be considered as minimum estimates (MEES and HAMERLYNCK, 1992).

Data analysis

Three multivariate techniques, each yielding specific information, were applied to the data. The following analyses were performed: an agglomerative classification (clustering based on the Bray-Curtis similarity index and the Group Average Sorting clustering algorithm, GAS), an ordination (Principal Component Analysis, PCA, Correspondance Analysis, CA, and Canonical Correspondance Analysis, CCA), and a divisive classification (Two-way Indicator

Species Analysis, TWINSPAN). All multivariate techniques were applied to 4th root transformed abundance and biomass data.

The sampling sites were first classified into clusters according to species composition using the program TWINSPAN (HILL, 1979). TWINSPAN also yields indicator species and preferential species for each division. No downweighting of rare species was done. Pseudospecies cutlevels 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 cutlevels which contained approximately half as many observations as the other cutlevels (in this way some extra weight was given to the most abundant species). Next, a GAS clusteranalysis with Bray-Curtis similarities (BRAY and CURTIS, 1957) was performed on the same datamatrices. The outputs (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 composition and the environmental variables measured at each site was further 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 time series of marine and brackish stations. PCA was applied to the data matrix of the forthnightly samples of the brackish zone.

Once groups of samples were established using the above methods, the averages of the environmental variables of the different communities were tested for significant differences using a Kruskal-Wallis one way analysis of variance. The biological communities were further characterized using Hill's diversity numbers of the order 0, 1, 2 and ∞ (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_∞ is the reciprocal of the proportional abundance of the commonest species: the dominance index).

RESULTS AND DISCUSSION

Comparison of seasonal patterns in the marine and brackish zones

The evolution of the environmental variables in both subareas is shown in Figure 2. 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 ± 1.4 psu) than in the brackish stations (average of 16.8 ± 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 ± 66 cm, with a peak of 300 cm in June) than in the brackish stations (average of 61 ± 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 ± 6.2 %), while in the brackish stations it fluctuated around 80 % of the saturation value (77.8 ± 17.1 %). A clear minimum was observed in March (< 30 %).

For a list of the species encountered in this study and the abbreviations used see Table 1. The hyperbenthos is dominated by crustaceans, mainly mysids and amphipods. The yearly average of total hyperbenthic density and the overall species composition for both zones are presented in Figure 3 (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*, flounder *Pleuronectes flesus* and larval clupeoids) or May (megalopae of *Liocarcinus holsatus*, zoea and megalopae of *Carcinus maenas*, postlarval plaice *Pleuronectes platessa* and sole *Solea solea*,...).

The first TWINSPAN division (Figure 4) 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 5) 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.

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 6. 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 main environmental gradients structuring the communities are presented as vectors in the plot of the sample scores. The estuarine gradients in salinity, dissolved oxygen concentration and turbidity are obviously dominant along the first axis, while the temperature vector has significant components along both the first (longitudinal gradient) and second (seasonal changes) axis. The many species located on the left side of the diagram of the species scores 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).

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 7. The marine December sample was pooled with the other winter samples on the basis of the clusteranalysis. The marine and brackish April samples were not used in the calculations because of their indicisive 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*.

Detailed description of the seasonal patterns in the brackish part of the estuary

Since *Neomysis integer* was the target species of the sampling campaigns, it is not surprising that it dominated the fauna in each sample (Figure 8 top). For more information on the dynamics of the *Neomysis* population we refer to MEES *et al.* (1994). *Mesopodopsis slabberi* wasthesecond 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.

All other species together usually made up much less than 1 % of total hyperbenthic density (Figure 8 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). Temporary 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 occured from the beginning of June till the end of August. Yolk-sack larvae and postlarvae of *Pleuronectes flesus* were present in low numbers in both March samples only.

In the first TWINSPAN division the winter and early spring samples are separated from the samples from the rest of the year (Figure 9). 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 10) 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 March and April.

In Figure 11 the scores of the samples and the species are plotted in the plane formed by the first two PCA axes (eigenvalues 0.51 and 0.25, respectively). The axes of higher order did not yield additional information (eigenvalues both < 0.07).

The temperature and dissolved oxygen vectors show a strong positive correlation with the first axis and they are represented by long arrows while the long reciprocal Secchi depth vector shows a strong negative correlation with the same axis. These three variables characterize the main environmental gradient which correlates strongly with the structure of the hyperbenthic community. The temperature-oxygen-Secchi depth gradient roughly separates the winter samples (aggregated towards the left side of the diagram, above the main environmental gradient) from the summer samples, which are found scattered towards the right side beneath the gradient. The samples from spring and autumn occupy a more central position in relation to this tri-variable gradient. The second axis doesn't show strong correlation with any of the measured environmental variables. Salinity and, to a certain extent, the reciprocal of Secchi disc depth show the highest correlation with this axis. The samples from 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.

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 the results from the three methods (also these with biomass data, not presented) five more or less arbitrary seasonal groupings of samples can be established. Table 2 shows the categorization of the samples into the five groups, 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 12).

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 and WILLIAMS (1982), from their study on mysids from the Bristol Channel, classified the species as 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).

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Figure captions

Figure 1. Westerschelde estuary with location of the sampling sites. The 2 westernmost and the 2 easternmost stations were used for this study.

Figure 2. Seasonality of environmental variables measured in both subareas.

Figure 3. Composition and density of the marine (left axis) and brackish (right axis) communities, averaged over one year of monthly sampling.

Figure 4. TWINSPAN with the time series of both subareas.

Figure 5. Clusteranalyses with the time series of both subareas (mar = marine sample: bra = brackish sample. The bottom line gives the dissimilarity scale.

Figure 6. 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 species scores (bottom).

Figure 7. Time series of the marine and brackish stations. Average density and species composition of the hyperbenthic communities identified by multivariate analyses.

Figure 8. 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).

Figure 9. TWINSPAN with the time series of the brackish part.

Figure 10. Clusteranalyses with the time series of the brackish part. The bottom line gives the dissimilarity scale.

Figure 11. Output of the PCA with the density data of the forthnightly time series in the brackish part. The dotted line in the plot of the sample scores (top) indicates the sampling sequence.

Figure 12. Density and species composition of the seasonal communities in the brackish part. Stacked bars with (top) and without (bottom) the two dominant species.

Table 1. Species list, with indication of distribution (M: marine part, B: brackish part) and density (-: 1, +: 1-10, *: 10-50, **: 50-100, *: 100-500, ****: >500 ind. per 1000m^2).**

Species and stage	Abbreviation	Zone	Season	Density	Remarks
Lanice conchilega	Lani Aulo	M	May-Aug	+	
Nereis species	Nere Larv	M	Aug	-	
Sagitta elegans	Sagi eleg	M / B	all / Apr, Jul-Oct	*/*	not in B in winter
Calanus helgolandicus	Cala helg	M	May	+	
Gastrosaccus spinifer	Gast spin	M / B	Jul-Nov	**/***	peak in summer
Schistomysis spiritus	Schi spir	M	Nov-Mar	+	
Schistomysis kervillei	Schi kerv	M	all	***	peak in winter
Mesopodopsis slabberi	Meso slab	M / B	all / Apr-Nov	***/****	not in B in winter
Neomysis integer	Neom inte	B	all	****	peak in summer
Praunus flexuosus	Prau flex	M / B	Aug/ Jul-Oct	**/+	
Acanthomysis longicornis	Acan long	M	Oct	+	
Diastylis rathkei	Dias rath	M	May and Aug	+	
Diastylis bradyi	Dias brad	M	Dec	-	
Bodotria scorpioides	Bodo scor	M	May	-	
Eurydice pulchra	Eury pulc	M / B	occ / all	-/*	peak in spring (B)
Idotea linearis	Idot line	M	all	*	less in winter
Lekanesphaera rugicauda	Leka rugi	B	Apr and Sep	+	
Pariambus typicus	Pari typi	M	Oct	-	
Caprella linearis	Capr line	M	Jul-Aug	+	
Gammarus crinicornis	Gamm crin M	all		**	no clear seasonality
Gammarus salinus	Gamm sali	B	all	***	peak in spring
Atylus swammerdami	Atyl swam M / B	all / Feb		+/+	
Pleusymtes glaber	Pleu glab	M / B	Nov / Aug-Dec	-/+	
Corophium volutator	Coro volu	M / B	occ / Aug-Jan	+/*	
Bathyporeia elegans	Bath eleg	B	Jun-Oct and Feb-Mar	*	
Jassa falcata	Jass falc	M	Aug	-	
Jassa marmorata	Jass marm	M	Aug	-	
Stenothoe marina	Sten mari	M	May and Aug	-	
Pontocrates altamarinus	Pont alta	M	Dec	-	
Haustorius arenarius	Haus aren	M	Jan	-	
Melita obtusata	Meli obtu	M	Jan	-	
Crangon crangon zoeae	Cran Zoea	M	Apr-Oct	**	peak in Apr-May
Crangon crangon postlarvae	Cran Post	M / B	all / all	***/****	peak:Apr-May/ Aug
Palaemonetes varians zoeae	Pala Zoea	M	Jun-Jul	-	
Palaemonetes varians postlarvae	Pala Post	M / B	occ / Jul	+/+	in M: single records
Hypollite varians zoeae	Hypo Zoea M	May		-	
Pontophilus trispinosus postlarv.	Pont Post	M	Oct	-	
Pagurus bernhardus zoeae	Pagu Zoea	M	May-Jun	*	peak in May
Pagurus bernhardus megalopae	Pagu Mega	M	May	+	
Porcellana longicornis zoeae	Porc Zoea	M	May-Jun	*	peak in Jun
Porcellana longicornis megalopae	Porc Mega	M	May-Aug	+	peak in Jun
Carcinus maenas	Carc maen	M / B	May-Jun / Aug	-/+	
Carcinus maenas zoeae	Carc Zoea	M / B	May-Jun / Jul	***/+	peak in May
Carcinus maenas megalopae	Carc Mega	M	May-Sep	***	peak in Jun
Liocarcinus holsatus	Lioc hols	M / B	all / Jul-Aug	***/+	peak in May
Liocarcinus holsatus zoeae	Lioc Zoea	M	Apr-Sep	***	peak in Apr-Jun
Liocarcinus holsatus megalopae	Lioc Mega	M	May-Sep	*	peak in May
Portumnus latipes megalopae	Port Mega	M	Jul-Aug	-	
Corystes cassivelaunus megalop.	Cory Mega	M	May	+	
Macropodia species megalopae	Macr Mega	M	Aug	-	
Nymphon rubrum	Nymp rubr	M	occasionally	+	
Nymphon gracilis	Nymp grac	M	Jun	-	
Pelagic fish eggs	Fish Eggs	M	May	+	
Pleuronectes platessa	Pleu plat	M / B	Sep / Apr	-/*	
Pleuronectes flesus	Pleu fles	M / B	Mar-May / Mar-Apr	*/***	peak in April
Solea solea	Sole sole	M	May	*	
Clupeidae species	Clup Spec	M / B	Mar-Jun / Mar-Jul	***/***	peak in Apr (B:May)
Pomatoschistus minutus	Poma minu	M / B	May-Aug / May-Sep	*/*	peak in May-Jul
Pomatoschistus lozanoi	Poma loza	M / B	Aug-Jan / Jul-Nov	*/***	peak in Aug-Sep
Pomatoschistus microps	Poma micr	M / B	Jul-Dec / Sep-Oct	-/+	
Syngnathus species	Syng Spec	M / B	Apr-Dec / Jul-Sep	*/*	peak in Jul-Aug
Anguilla anguilla glasseels	Angu angu	B	Mar-Apr	+	
Liparis liparis	Lipa lipa	B	Jul	-	
Callyonimus lyra	Call lyra	M	May	+	

Table 2. Characterization of the seasonal communities in the brackish part of the estuary.

Season	Winter	Spring	Early summer	Late summer	Autumn
Samples	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
N_0	7	11	12	9	8
N_1	1.07	1.21	1.09	1.48	1.95
N_2	1.02	1.07	1.03	1.27	1.71
N_∞	1.01	1.04	1.01	1.14	1.40
oxygen(%)	73.6 ± 6.4	76.4 ± 9.4	86.8 ± 0.7	99.0 ± 7.8	83.0 ± 6.8
pH	7.7 ± 0.7	7.7 ± 0.1	7.7 ± 0.1	7.6 ± 0.2	7.7 ± 0.0
sal.(psu)	13.8 ± 1.2	15.0 ± 1.3	13.7 ± 1.0	18.3 ± 0.4	28.8 ± 10.6
Sec.$^{-1}$(cm^{-1})	0.020 ± 0.003	0.018 ± 0.003	0.006 ± 0.002	0.013 ± 0.004	0.020 ± 0.002
temp.(°C)	5.0 ± 1.0	9.0 ± 1.2	16.7 ± 0.9	20.5 ± 0.5	11.4 ± 1.9

FIGURE 1.

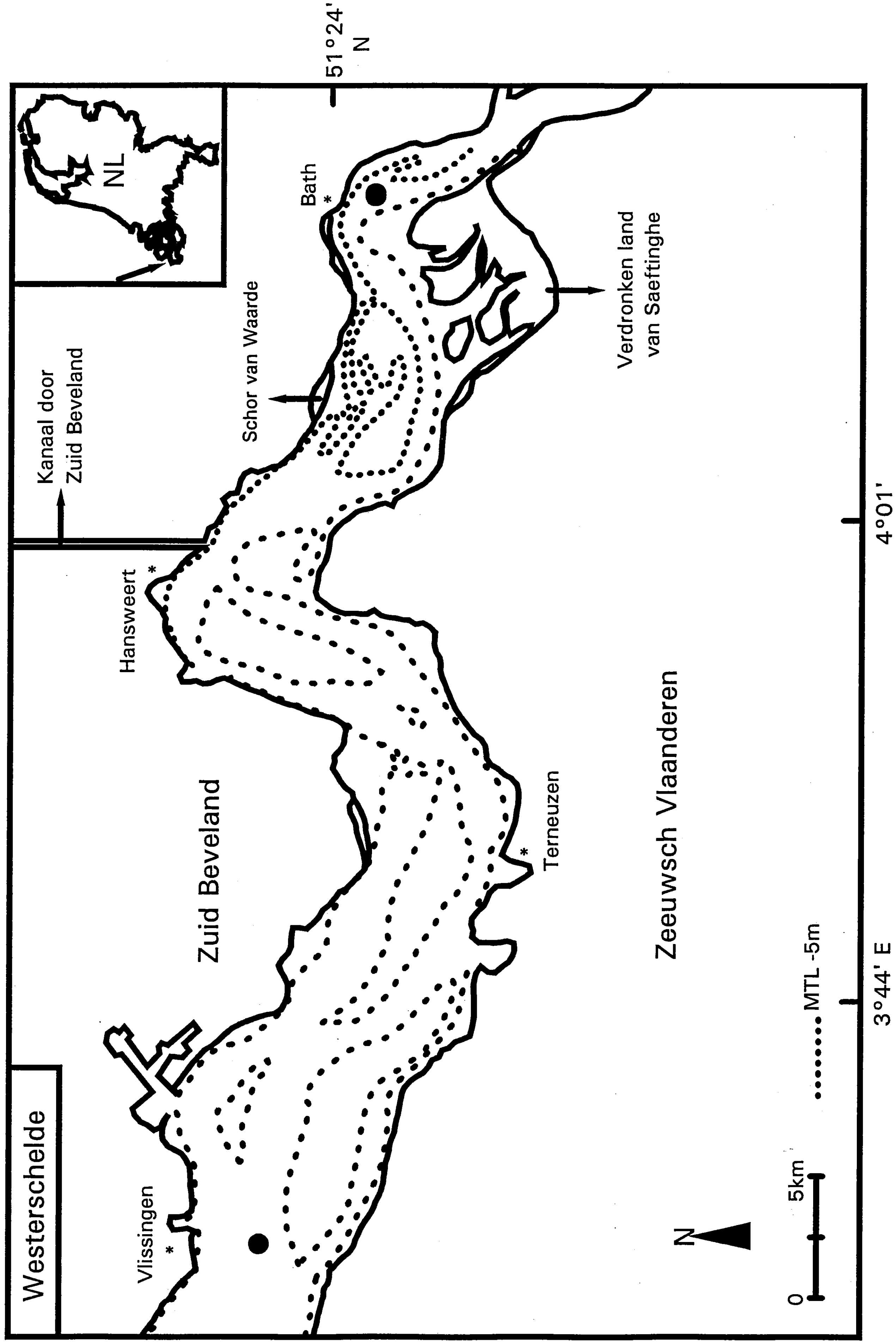

51°24' N
NL
Kanaal door Zuid Beveland
Bath
Schor van Waarde
Verdronken land van Saeftinghe
Hansweert
4°01'
Zuid Beveland
Terneuzen
Zeeuwsch Vlaanderen
Westerschelde
Vlissingen
MTL -5m
3°44' E
N
0
5km

FIGURE 2.

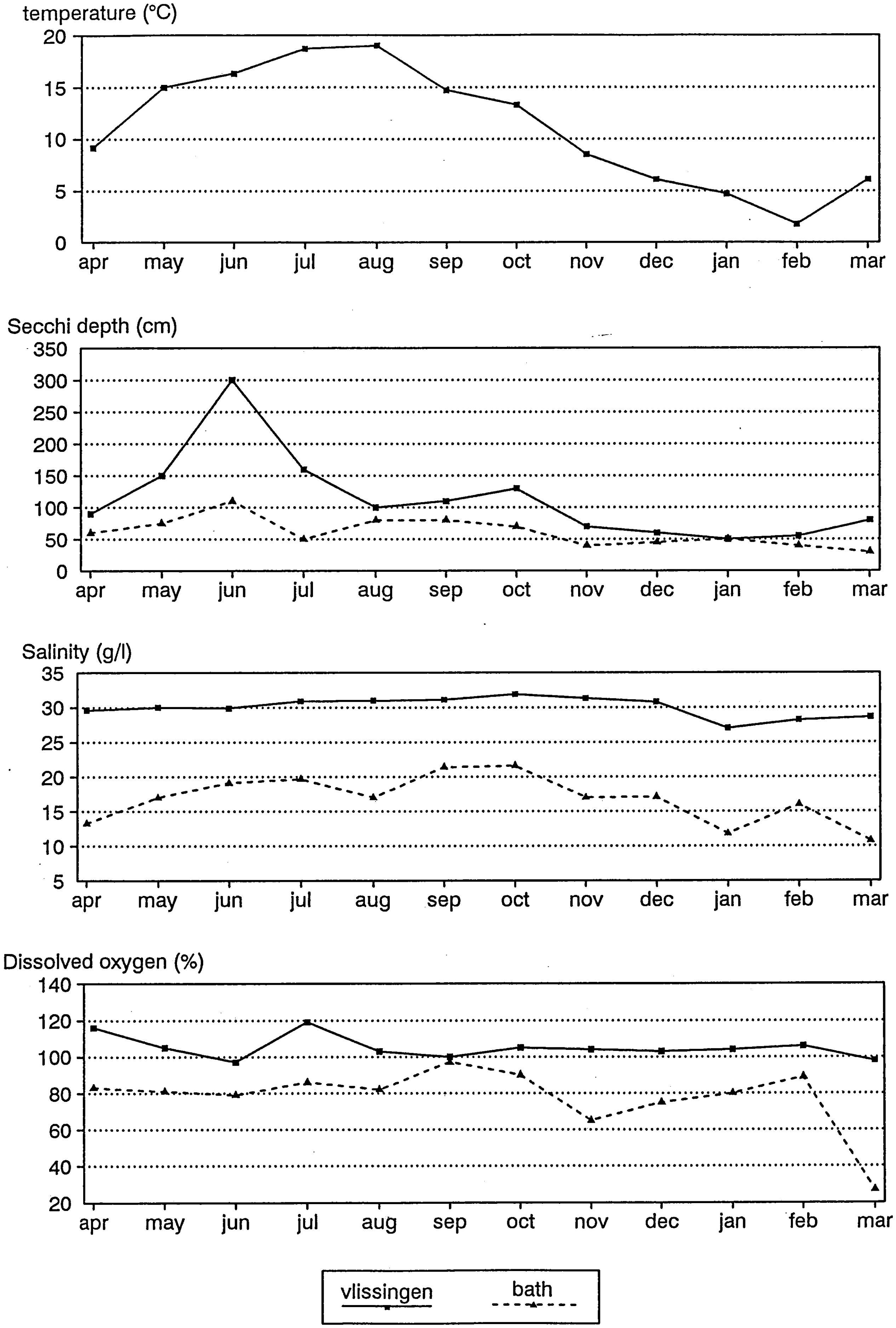

temperature (°C)
20
15
10
5
0
Secchi depth (cm)
350
300
250
200
150
100
50
0
Salinity (g/l)
35
30
25
20
15
10
5
Dissolved oxygen (%)
140
120
100
80
60
40
20
apr
may
jun
jul
aug
sep
oct
nov
dec
jan
feb
mar
vlissingen
bath

FIGURE 3.

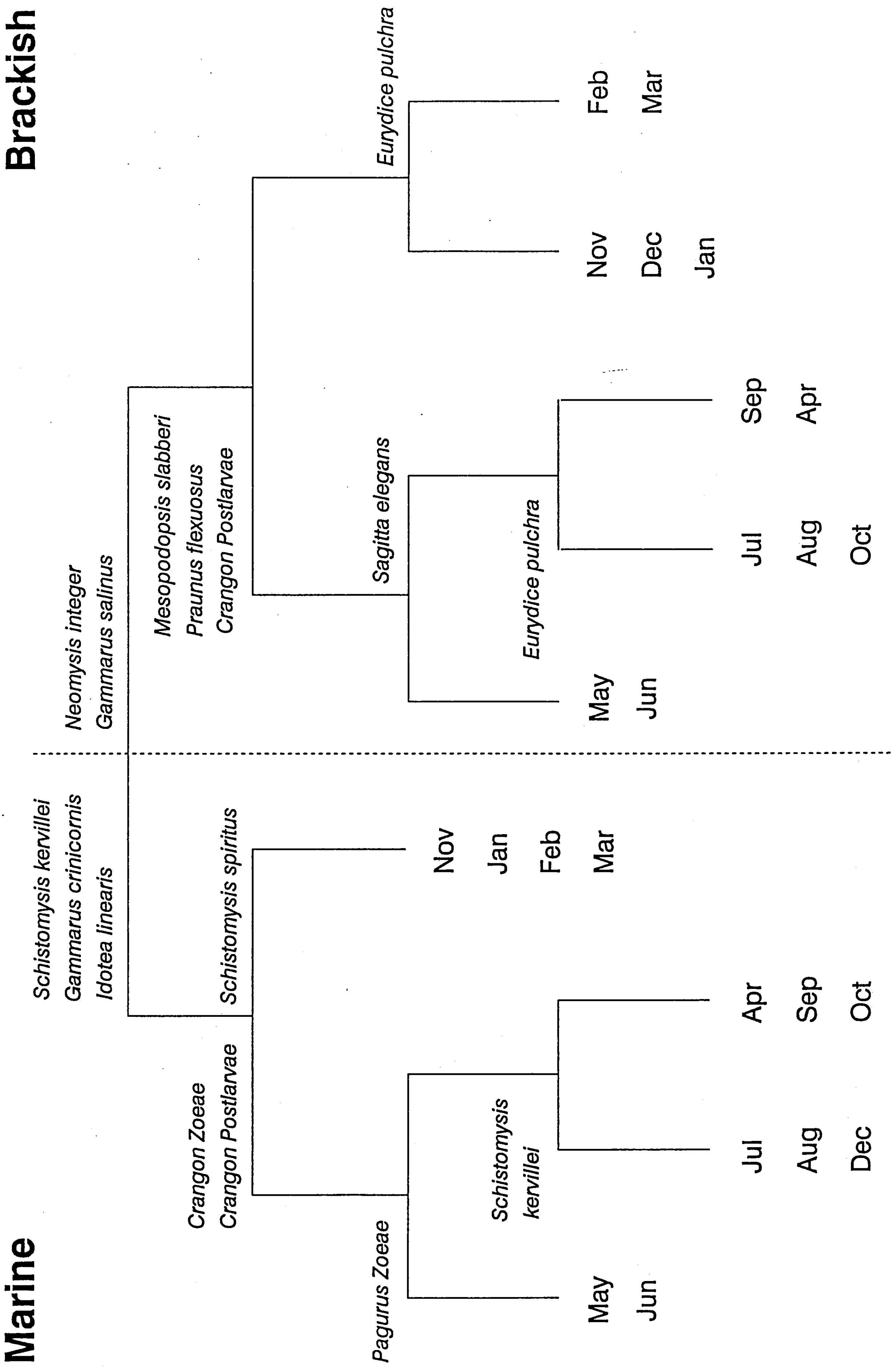

Marine
Brackish
Schistomysis kervillei
Gammarus crinicornis
Idotea linearis
Neomysis integer
Gammarus salinus
Crangon Zoeae
Crangon Postlarvae
Schistomysis spiritus
Mesopodopsis slabberi
Praunus flexuosus
Crangon Postlarvae
Pagurus Zoeae
Sagitta elegans
Eurydice pulchra
Schistomysis kervillei
Eurydice pulchra
May
Jun
Jul
Aug
Dec
Apr
Sep
Oct
Nov
Jan
Feb
Mar
May
Jun
Jul
Aug
Oct
Sep
Apr
Nov
Dec
Jan
Feb
Mar

FIGURE 4.

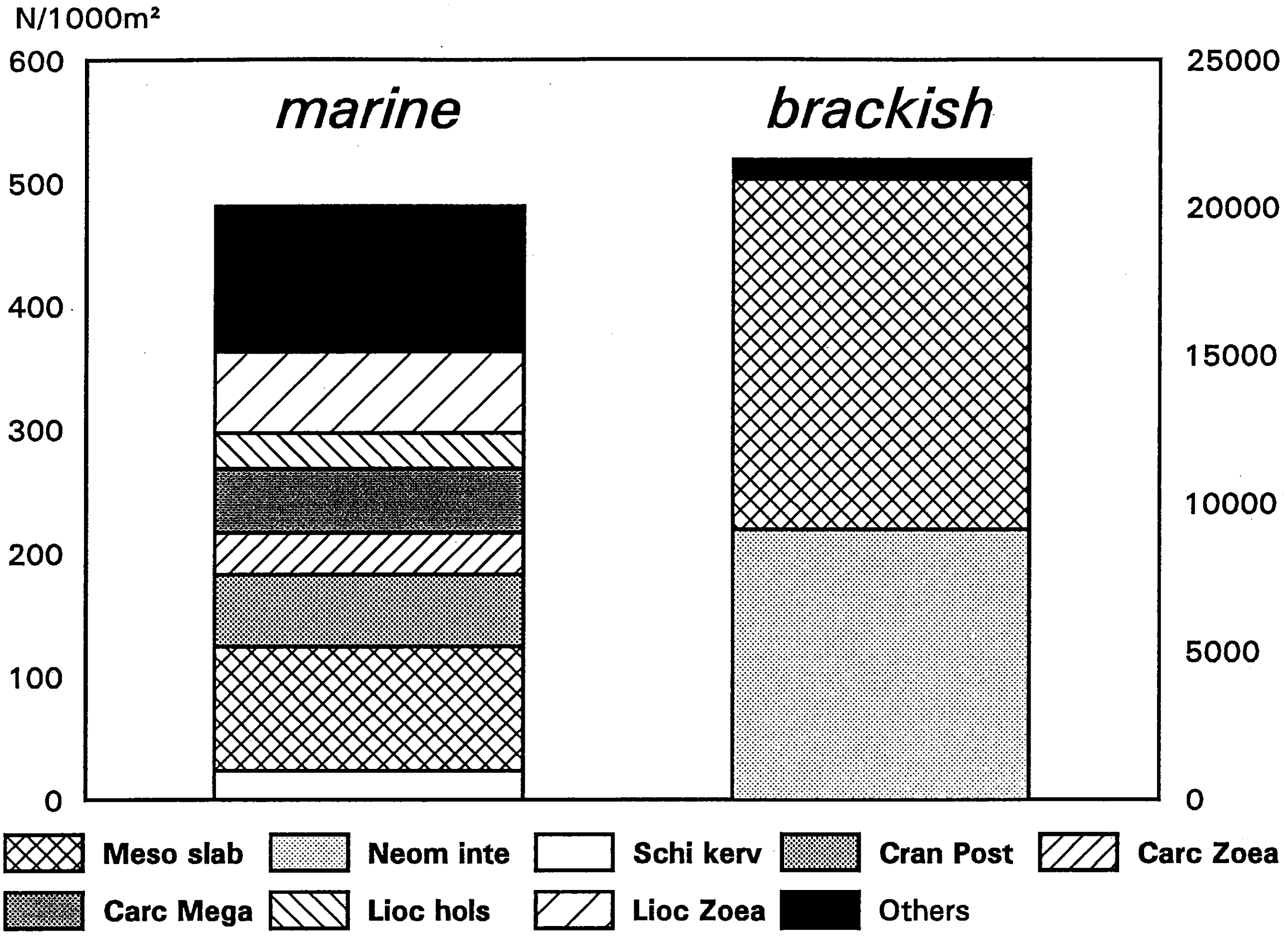
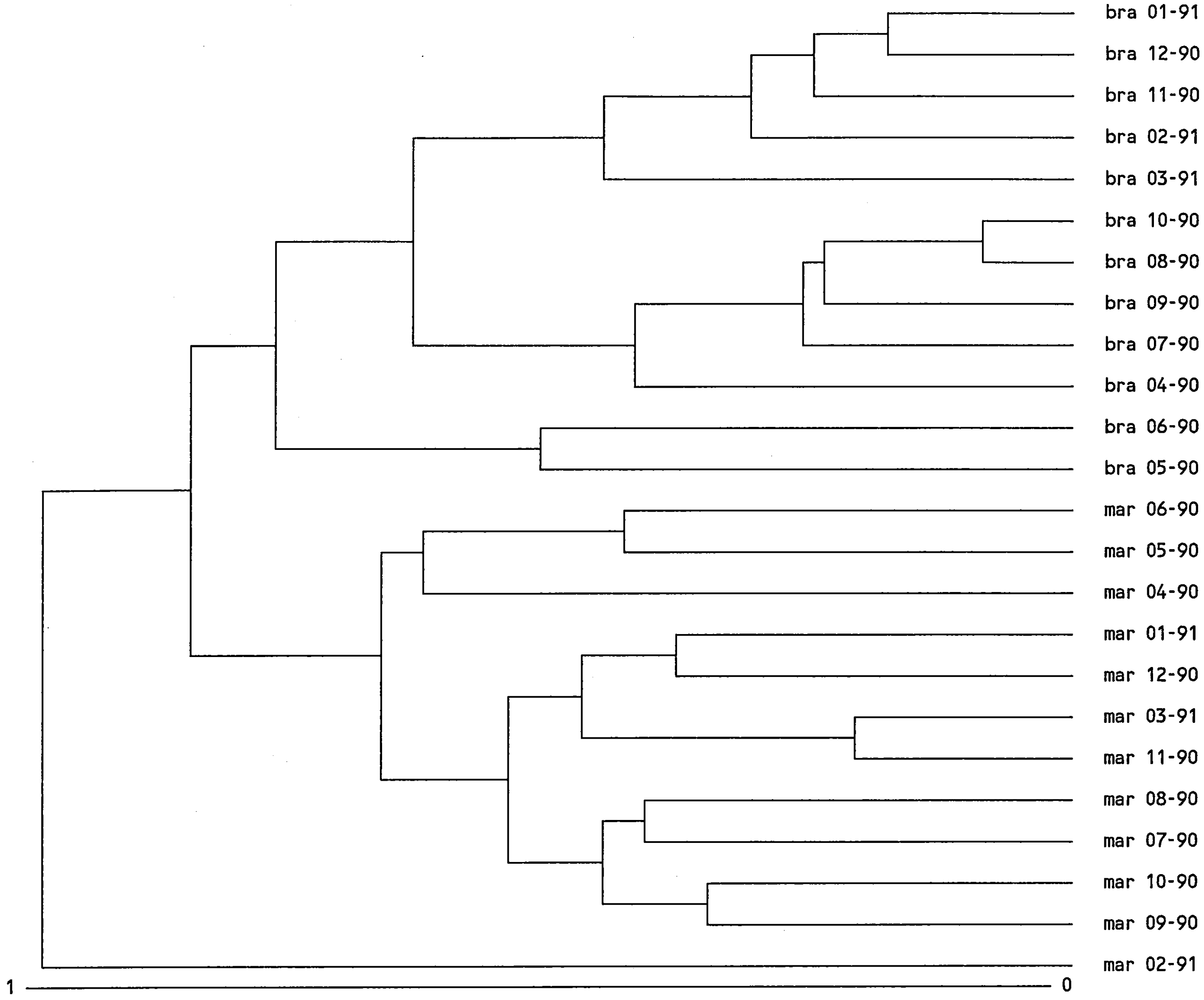

N/1000m²
600
500
400
300
200
100
0
25000
20000
15000
10000
5000
0
marine
brackish
Meso slab
Neom inte
Schi kerv
Cran Post
Carc Zoea
Carc Mega
Lioc hols
Lioc Zoea
Others

FIGURE 5.


bra 01-91
bra 12-90
bra 11-90
bra 02-91
bra 03-91
bra 10-90
bra 08-90
bra 09-90
bra 07-90
bra 04-90
bra 06-90
bra 05-90
mar 06-90
mar 05-90
mar 04-90
mar 01-91
mar 12-90
mar 03-91
mar 11-90
mar 08-90
mar 07-90
mar 10-90
mar 09-90
mar 02-91
1
0

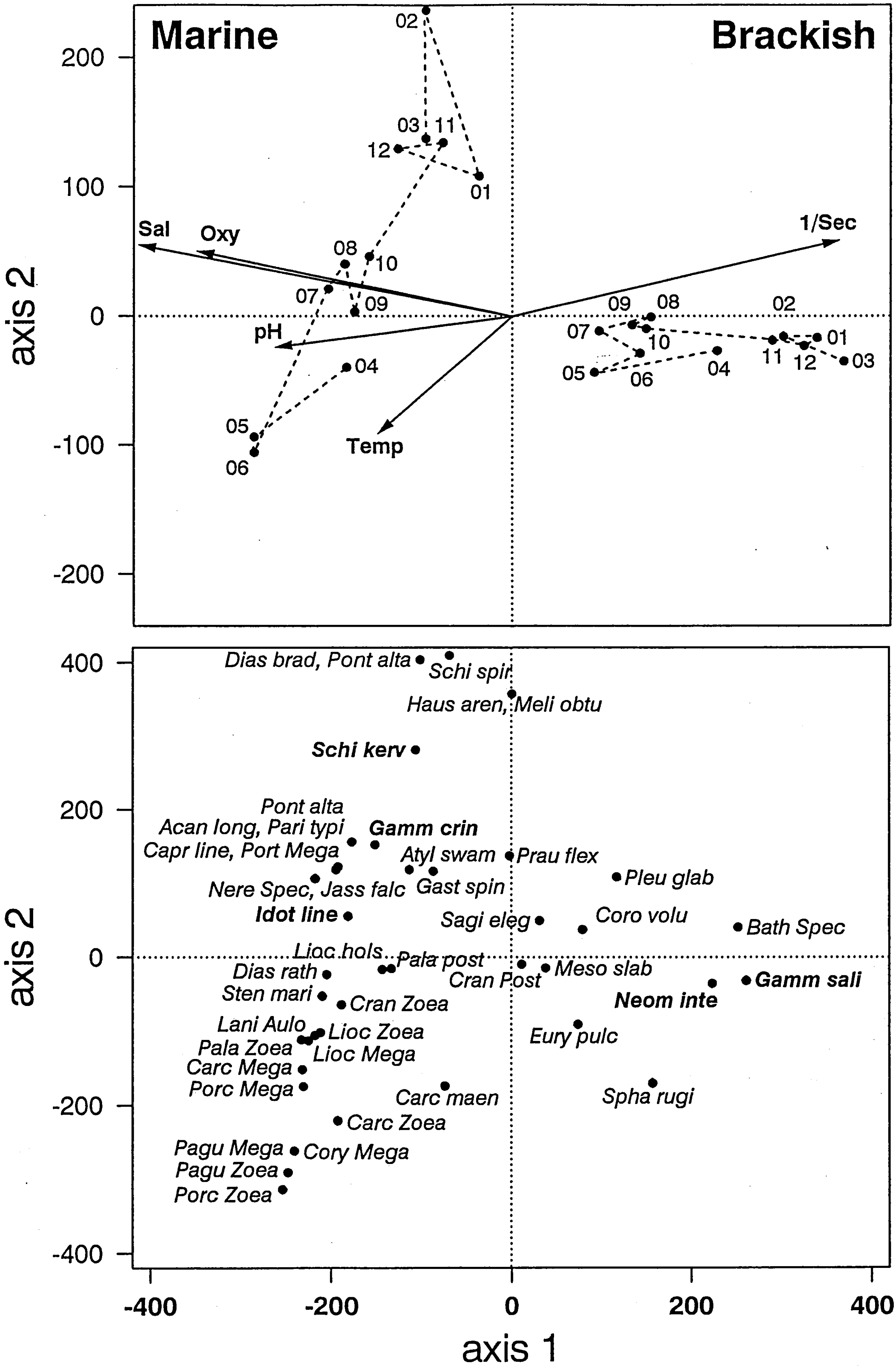

Marine
Brackish
axis 2
200
100
0
-100
-200
Sal
Oxy
pH
Temp
1/Sec
01
02
03
04
05
06
07
08
09
10
11
12
400
Dias brad, Pont alta
Schi spir
Haus aren, Meli obtu
Schi kerv
Pont alta
Acan long, Pari typi
Gamm crin
Capr line, Port Mega
Atyl swam
Prau flex
Pleu glab
Nere Spec, Jass falc
Gast spin
Idot line
Sagi eleg
Coro volu
Bath Spec
Lioc hols
Pala post
Dias rath
Cran Post
Meso slab
Gamm sali
Sten mari
Cran Zoea
Neom inte
Lani Aulo
Lioc Zoea
Eury pulc
Pala Zoea
Lioc Mega
Carc Mega
Porc Mega
Carc maen
Spha rugi
Carc Zoea
Pagu Mega
Cory Mega
Pagu Zoea
Porc Zoea
-400
-200
0
200
400
axis 1

FIGURE 7.

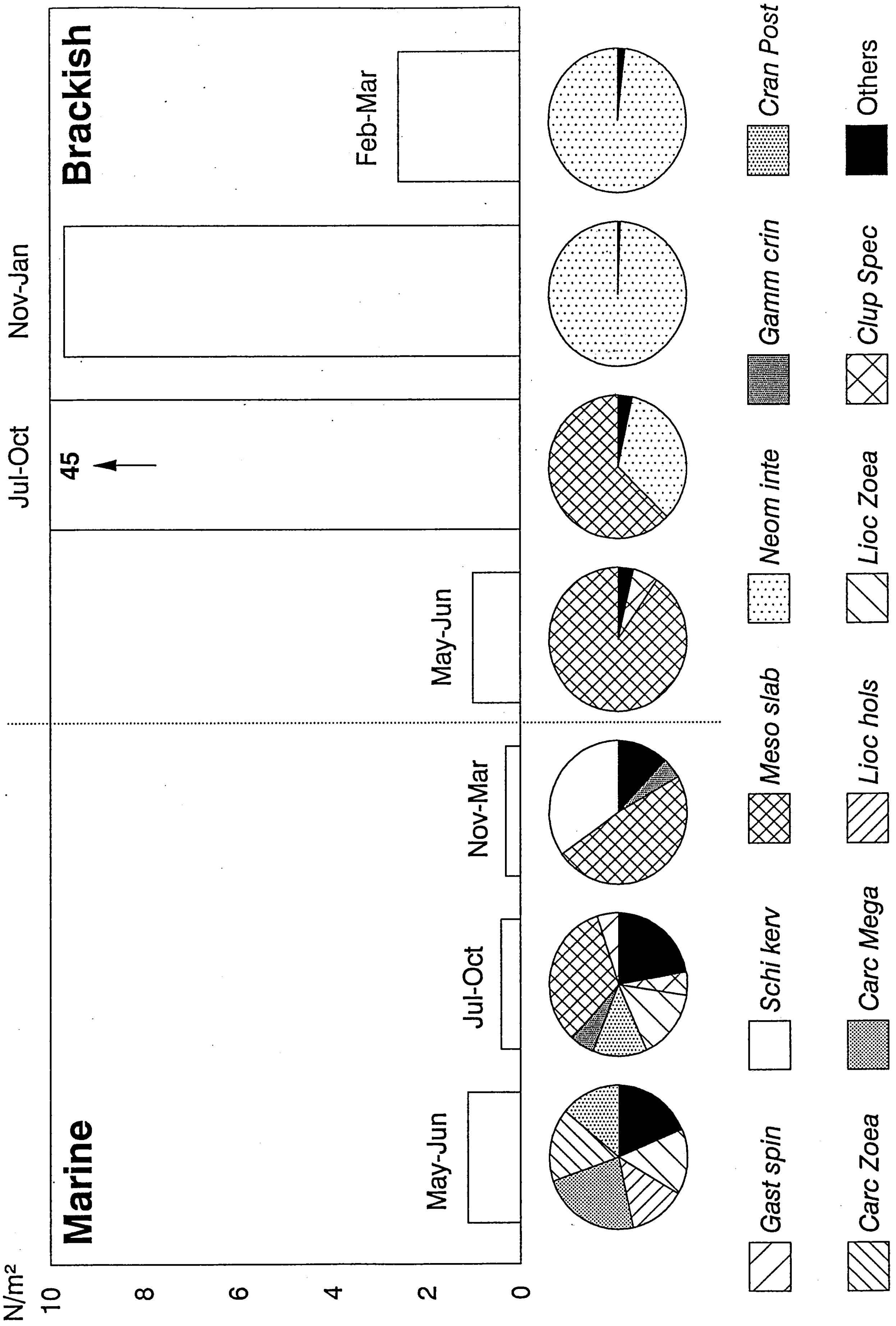

Marine
Brackish
N/m²
10
8
6
4
2
0
May-Jun
Jul-Oct
Nov-Mar
May-Jun
Jul-Oct
45
Nov-Jan
Feb-Mar
Gast spin
Schi kerv
Meso slab
Neom inte
Gamm crin
Cran Post
Carc Zoea
Carc Mega
Lioc hols
Lioc Zoea
Clup Spec
Others

FIGURE 8.

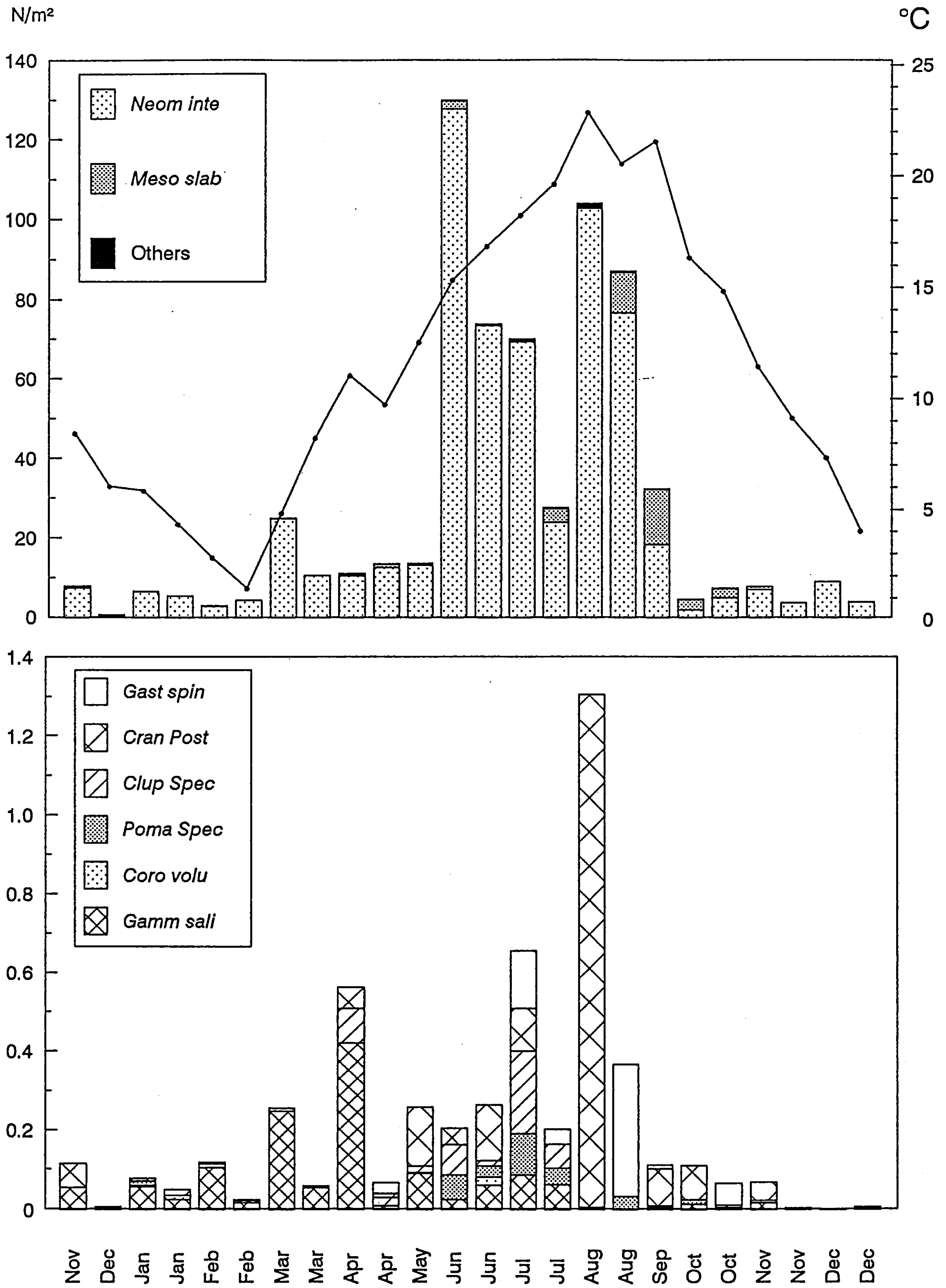

N/m²
°C
140
120
100
80
60
40
20
0
25
20
15
10
5
0
Neom inte
Meso slab
Others
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
Gast spin
Cran Post
Clup Spec
Poma Spec
Coro volu
Gamm sali
Nov
Dec
Jan
Jan
Feb
Feb
Mar
Mar
Apr
Apr
May
Jun
Jun
Jul
Jul
Aug
Aug
Sep
Oct
Oct
Nov
Nov
Dec
Dec

FIGURE 9.

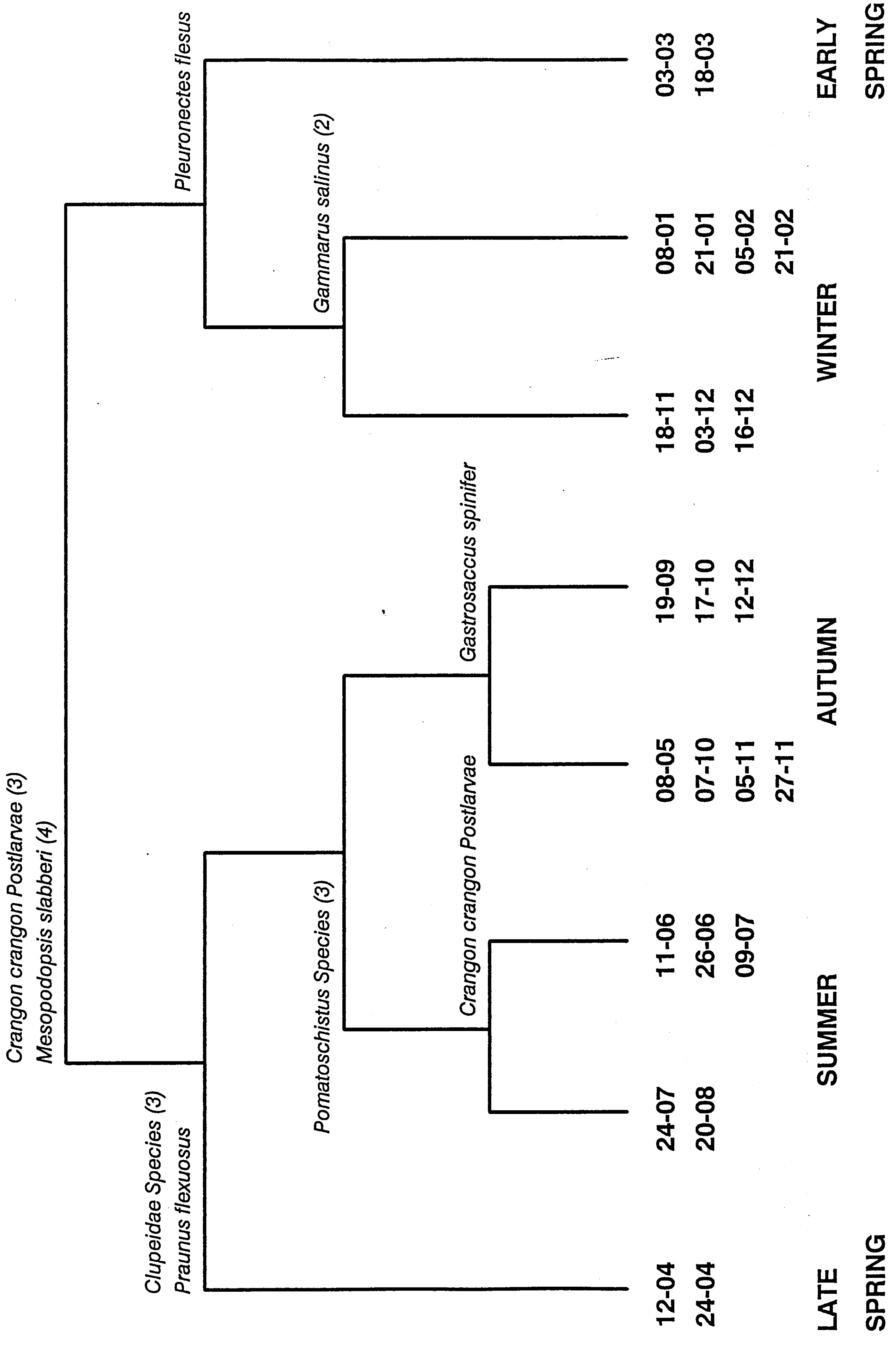

Pleuronectes flesus
Gammarus salinus (2)
Gastrosaccus spinifer
Crangon crangon Postlarvae
Pomatoschistus Species (3)
Crangon crangon Postlarvae (3)
Mesopodopsis slabberi (4)
Clupeidae Species (3)
Praunus flexuosus
03-03
18-03
08-01
21-01
05-02
21-02
18-11
03-12
16-12
19-09
17-10
12-12
08-05
07-10
05-11
27-11
11-06
26-06
09-07
24-07
20-08
12-04
24-04
EARLY SPRING
WINTER
AUTUMN
SUMMER
LATE SPRING

FIGURE 10.

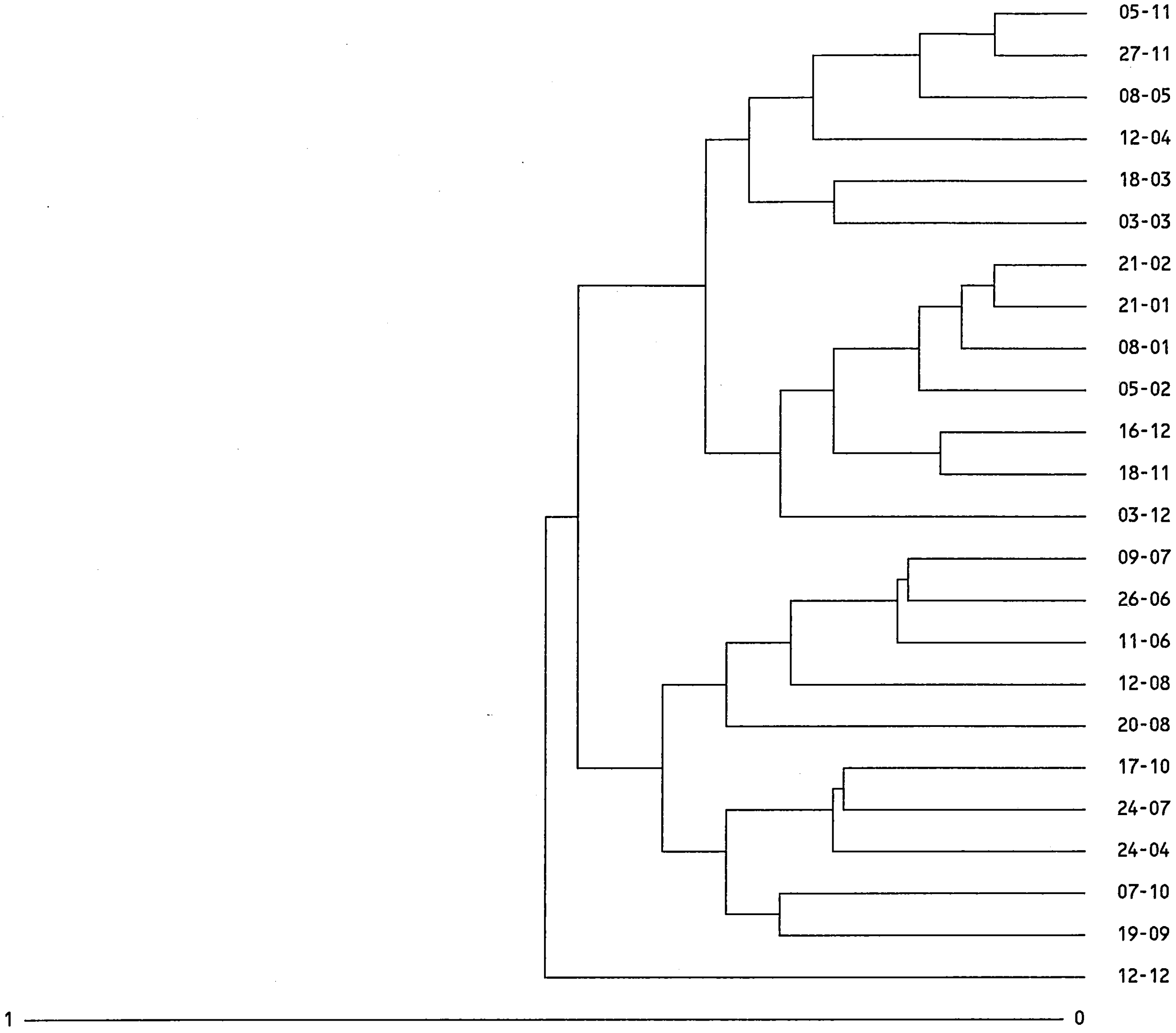
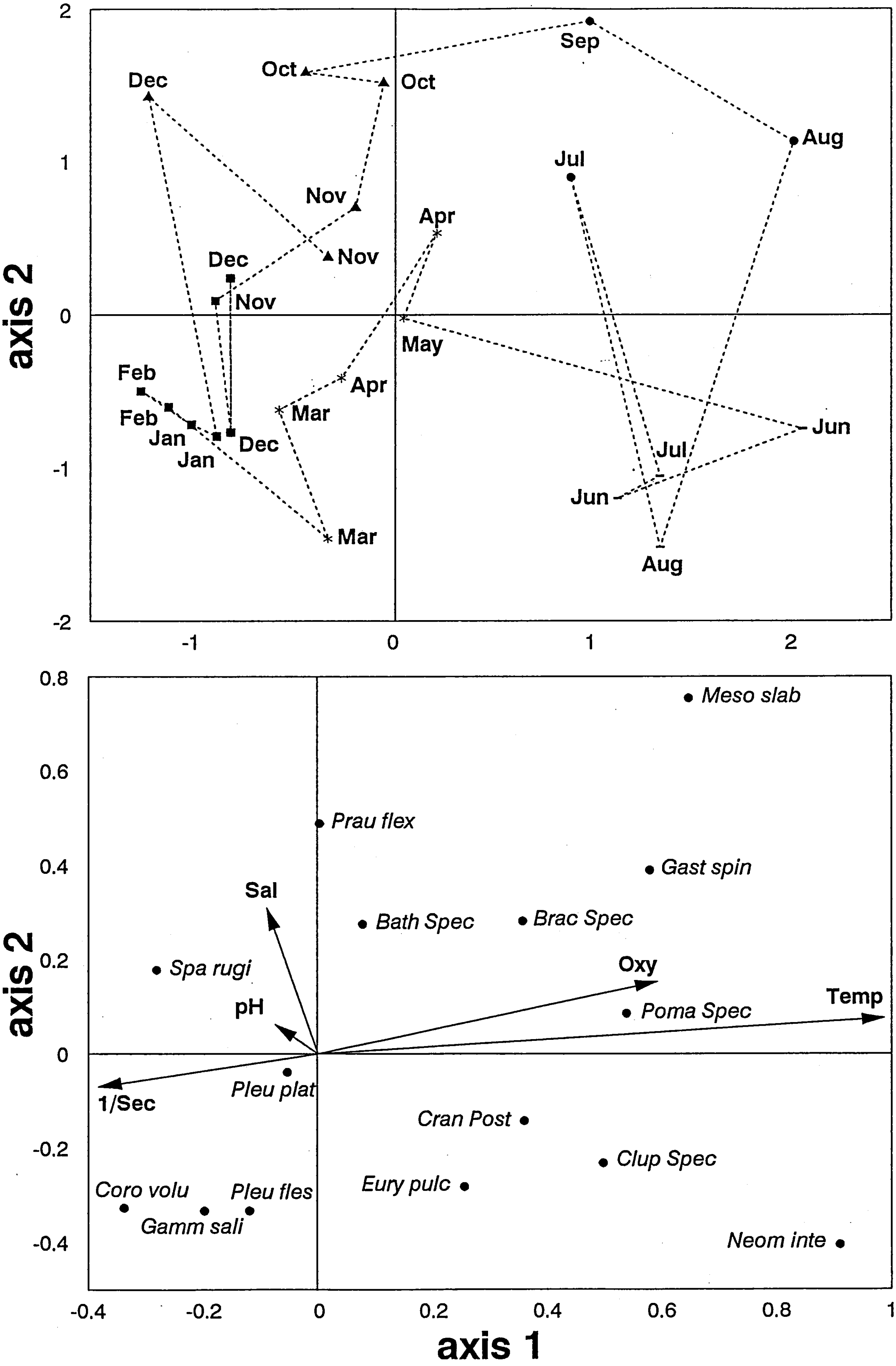
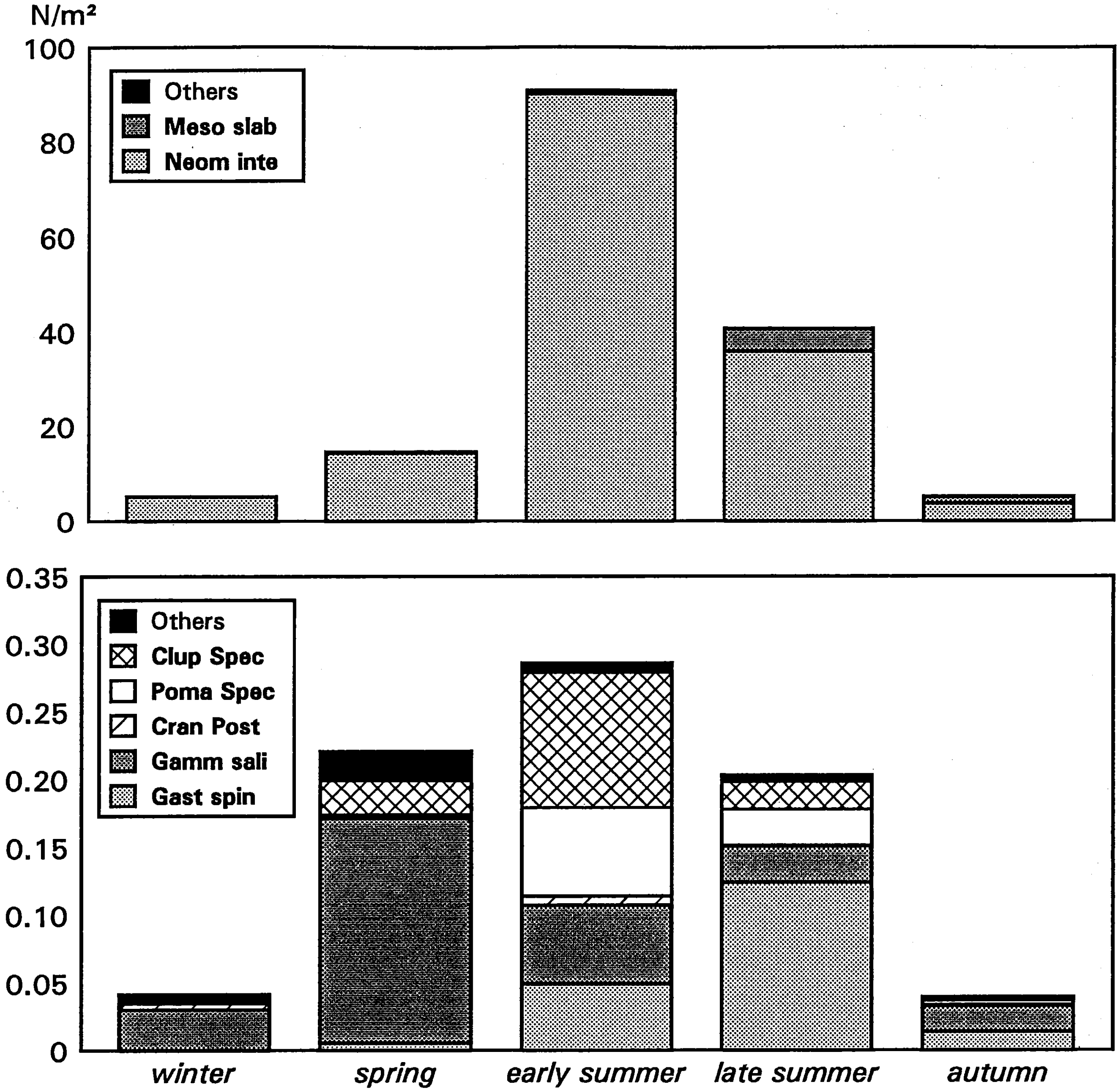

05-11
27-11
08-05
12-04
18-03
03-03
21-02
21-01
08-01
05-02
16-12
18-11
03-12
09-07
26-06
11-06
12-08
20-08
17-10
24-07
24-04
07-10
19-09
12-12
1
0

FIGURE 11.



2
1
0
-1
-2
axis 2
-1
0
1
2
Sep
Oct
Oct
Dec
Aug
Jul
Nov
Apr
Dec
Nov
Nov
May
Feb
Apr
Feb
Mar
Jan
Dec
Jan
Jun
Jul
Jun
Mar
Aug
0.8
0.6
0.4
0.2
0
-0.2
-0.4
axis 2
Meso slab
Prau flex
Gast spin
Sal
Bath Spec
Brac Spec
Spa rugi
Oxy
pH
Poma Spec
Temp
1/Sec
Pleu plat
Cran Post
Clup Spec
Eury pulc
Coro volu
Pleu fles
Gamm sali
Neom inte
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
axis 1


N/m²
100
80
60
40
20
0
Others
Meso slab
Neom inte
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0
Others
Clup Spec
Poma Spec
Cran Post
Gamm sali
Gast spin
winter
spring
early summer
late summer
autumn

THE HYPERBENTHIC FAUNA OF THE BELGIAN CONTINENTAL SHELF: SPATIAL VARIABILITY IN COMMUNITY STRUCTURE

Ann DEWICKE and Jan MEES

The hyperbenthos of the Belgian coastal waters, the Westerschelde estuary and part of the Dutch delta was sampled within a 2-week period at 41 locations in the summer of 1993 (figure 1). At each location sampling was done at two depth strata, covering all major sandbanks in the area, and the gullies separating them. Sampling depth ranged from 6 to 40 meter.

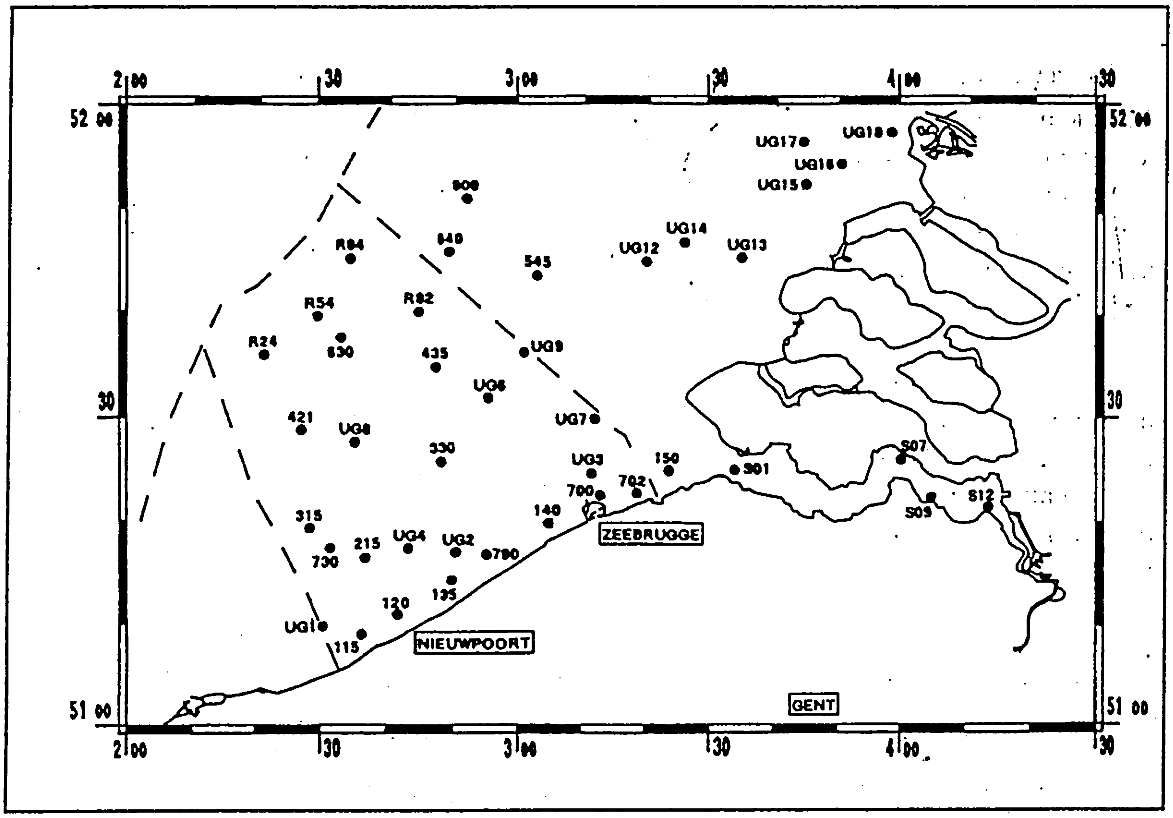


Figure 1: Location of the sampling stations on the Belgian continental shelf

Keywords: hyperbenthos, community structure, North Sea

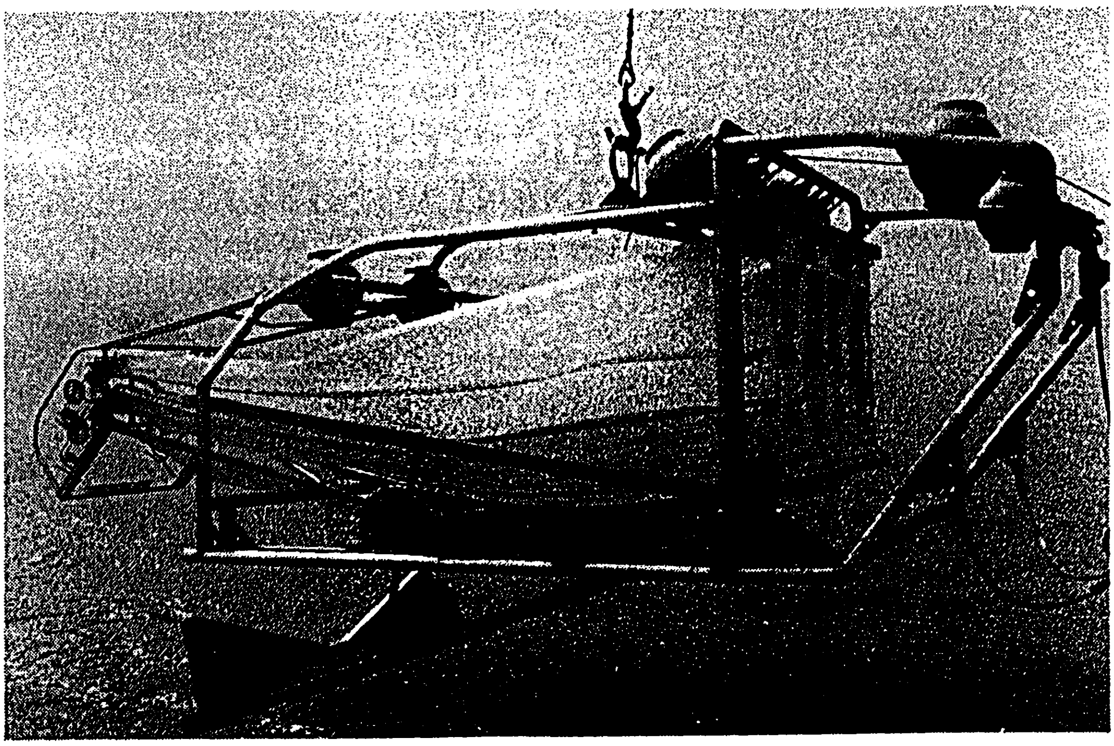


Figure 2: The hyperbenthic sledge (modified sledge described by Sorbe J.-C., 1983)

The samples were taken with a hyperbenthic sledge (figure 2) equipped with four nets (1 mm and 0.5 mm mesh size), covering two lower strata of the watercolumn: 0 to 0.5 meter and 0.5 to 1 meter above the bottom. Trawling (5 minutes at 1.5 knots: approx. 200 meter per trawl) was always done during daylight and against the tide. The sledge was equipped with an automatic opening-closing device, an odometer and a current meter. In addition, sediment and water samples were taken at each station for grain fraction analysis and pigment analysis.

In the laboratory all animals were identified, if possible to species level, counted and measured. Density was calculated and biomasses were derived from ash-free-dry-weight regressions. Density and biomass data were subjected to multivariate statistical analysis: a classification (clustering based on the Bray-Curtis similarity index and Group Average Sorting), an ordination (Canonical Correspondance Analysis) and a hybrid technique (Two-way Indicator Species Analysis).

A total of 135 species were recorded in the hyperbenthic fauna of the Belgian continental shelf. The most abundant faunistic taxa include Mysidacea (10 species), Brachyura (20 species), Amphipoda (33 species) and Caridea (14 species). Chaetognatha, Pisces, Anomura, Polychaeta, Isopoda, Copepoda and Cumacea were caught to a lesser extent. The hyperbenthos of the Belgian coastal area can be divided into 6 geographically defined communities (figure 3), characterised by their species composition, diversity, density and biomass. In the eastern part of the Westerschelde, a typical brackish water community was found ('ws'). Two communities were found onshore: 'onshore east' is located on the east coast (from Oostende to Zeebrugge) including the marine part of the

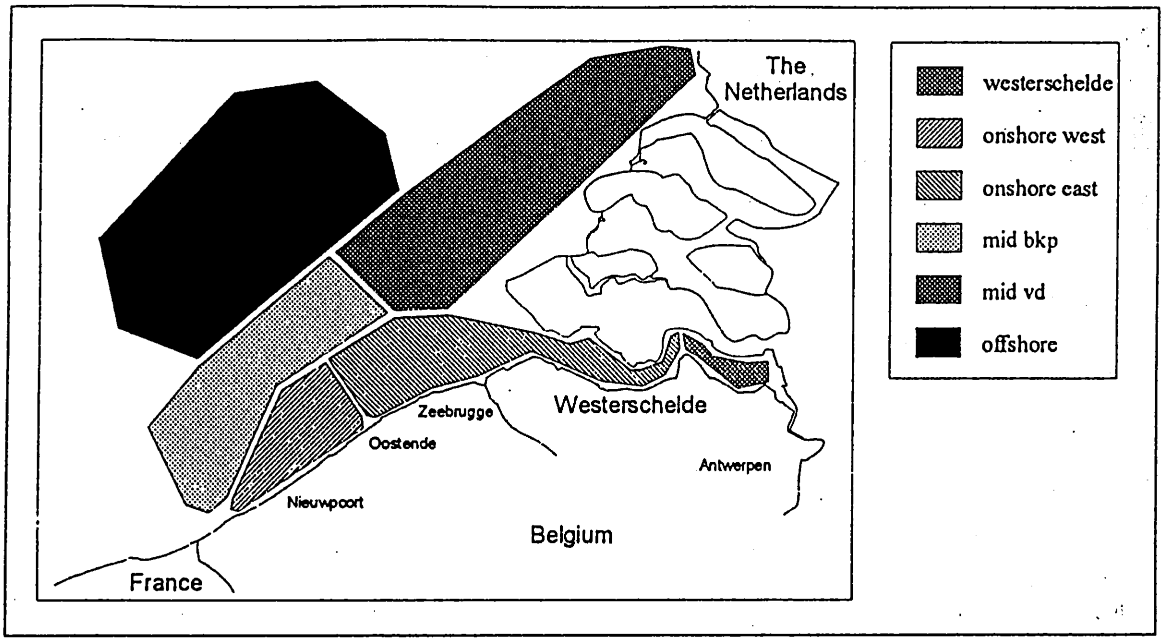


Figure 3: Geographical location of the hyperbenthic communities on the Belgian continental shelf

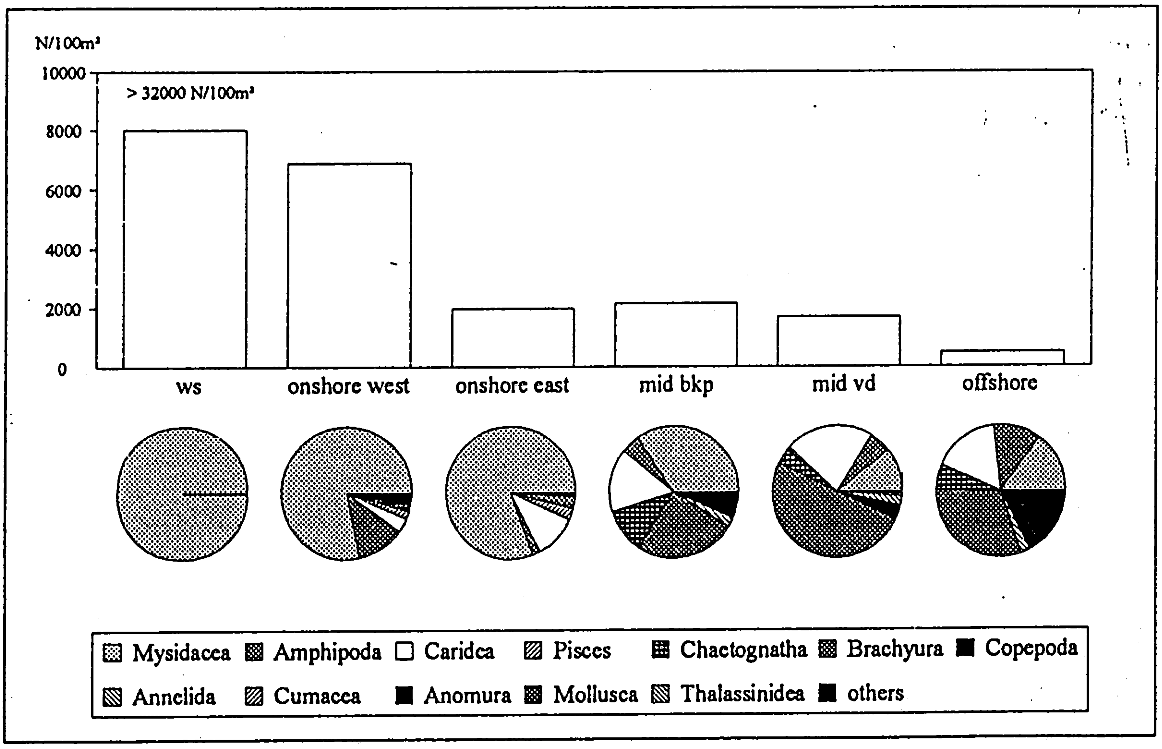


Figure 4: Average density and taxonomic composition of the hyperbenthic communities

Westerschelde; on the west coast (from Oostende to De Panne) the community 'onshore west' was found. 'Mid bkp' and 'mid vd' are the two transition communities between the onshore and more offshore area. The 'offshore' community occurs towards the open sea.

The community structure changes sharply along a gradient perpendicular to the coastline: highest densities and biomasses were recorded onshore (figure 4). The onshore communities (and the 'ws' community) were characterised by a low diversity and consist mainly of Mysidacea. Diversity increased offshore and the species composition of the hyperbenthic fauna is changed: more faunistic groups became almost equally represented, especially the Brachyura being dominant.

Acknowledgements

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University of Gent, Marine Biology Section, Institute of Zoology
K.L. Ledeganckstraat 35, B-9000 Gent, Belgium
E-mail: Ann.Dewicke@rug.ac.be / Jan.Mees@rug.ac.be

Spatial patterns in the hyperbenthos of the Belgian continental shelf.

Ann Dewicke & Jan Mees

Marine Biology Section, Zoology Institute, University of Gent
K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

Abstract

The hyperbenthos of the Belgian coastal waters, the Westerschelde estuary and part of the Dutch delta was sampled within a 2-week period at 41 locations in the summer of 1993. At each location sampling was done at two depth strata, covering all major sandbanks in the area, and the gullies separating them. Sampling depth ranged from 6 to 40 meter.

The samples were taken with a hyperbenthic sledge equipped with four nets (1 mm and 0.5 mm mesh size), covering two lower strata of the watercolumn: 0 to 0.5 meter and 0.5 to 1 meter above the bottom. Trawling (5 minutes at 1.5 knots: approx. 200 meter per trawl) was always done during daytime and against the tide. The sledge was equipped with an automatic opening-closing device, an odometer and a current meter. Several environmental variables (salinity, temperature,...) were recorded at the beginning of each trawl. In addition, sediment and water samples were taken at each station for grain size distribution, nutrient and pigment analyses.

In the laboratory, all animals were identified to species level, counted and measured. Density (numbers per 100 m^2) was calculated and biomass was derived from length-ashfree-dryweight regressions. Both density and biomass data were subjected to 3 multivariate statistical analyses: a classification (group-average sorting clustering based on the Bray-Curtis dissimilarity index), an ordination (Canonical Correspondance Analysis) and a hybrid technique (Two-way Indicator Species Analysis).

A total of 135 species were recorded in the hyperbenthic fauna of the Belgian continental shelf. The most abundant faunistic taxa included Mysidacea (10 species), Brachyura (20 species), Amphipoda (33 species) and Caridea (14 species). Chaetognatha, Pisces, Anomura, Polychaeta, Isopoda, Copepoda and Cumacea were caught to a lesser extent. The hyperbenthos of the Belgian coastal area could be divided into 6 geographically defined communities, each characterised by a specific species composition, diversity, density and biomass. In the eastern part of the Westerschelde, a typical brackish water community was found (community 'ws'). Two communities were found onshore: community 'onshore east' was located on the east coast (between Oostende and Zeebrugge) and included the marine part of the Westerschelde estuary; community 'onshore west' was found on the west coast (between Oostende and De Panne). Communities 'mid bkp' and 'mid vd' are transitional communities between the two onshore communities and more offshore area. The 'offshore' community was found towards the open sea.

The community structure changed sharply along a gradient perpendicular to the coastline: highest densities and biomasses were recorded onshore. The onshore communities (and the 'ws' community) were characterised by a low diversity and consisted mainly of Mysidacea. Diversity increased in offshore direction and the species composition of the hyperbenthic fauna changed drastically: more faunistic groups became almost equally represented.

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). To date, no information is available on this ecosystem component in Belgian coastal waters. Still, hyperbenthic animals have been shown to be an important component of coastal and estuarine foodwebs (Mees and Hamerlynck 1992). Crustaceans, especially mysids, often dominate the hyperbenthos in shallow areas (Mees et al. 1993). Mysidacea are omnivores that can feed on detritus, algae or zooplankton (Mauchline 1980) and they can contribute substantially to the diet of fish and shrimp.

For this study, the species composition of the hyperbenthic fauna of the Belgian continental shelf was investigated. Communities are identified and their geographical variation in terms of species composition, density, biomass and diversity is described. The observed patterns in community structure are related to some environmental variables, in order to gain more insight into the factors structuring the communities.

2. Materials and methods

The hyperbenthos of the Belgian continental shelf and the Dutch Voordelta was sampled in september 1993, during a two week period. Sampling strategy was systematic and depth stratified. 41 stations were investigated. The sampling sites are shown in figure 1.

All sampling was done from the R.V. Belgica with a hyperbenthic sledge which consists of a heavy metal frame equipped with four nets (1 mm and 0.5 mm mesh size), covering two lower strata of the watercolumn: 0 to 0.5 meter and 0.5 to 1 meter above the bottom. The sledge is equipped with an automatic opening-closing device, an odometer and a current meter. Trawling (5 minutes at 1.5 knots: approx. 200 meter per trawl) was always done during daytime and against the tide. Since the Belgian continental shelf is characterised by series of elongated sandbanks, two parallel tows were done in stations with a clear depth gradient: one sample was taken in the gully ('g' for gully) and one on the sandbank slope ('s' for sandbank). At the beginning of each trawl, a number of environmental variables were measured: depth, temperature, salinity and Secchi disc depth. Further, sediment samples were taken with a Reineck boxcorer for the analysis of grain size distributions, and water samples were taken near the bottom for pigment and nutrient analyses.

On board, catches were rinsed over sieves (1 or 0.5 mm mesh) and immeediately preserved in a seawater-buffered formaldehyde solution, 7 % final concentration. Only the 1 mm samples were investigated for the purpose of this study. In the laboratory, all animals were identified, if possible to species level, and counted. For the community analyses, different development stages of decapods (zoeae, megalopae, postlarvae and adults) 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 (ADW). ADW 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 ADW of batches of animals belonging to a certain stage. Density and biomass data were calculated as numbers of individuals (N) and g ADW per 100 m^2.

Non-hyperbenthic species (accidental catches of large epibenthic animals, e.g. demersal fish or adult crabs, or endobenthic species, e.g. polycheaetes) were eliminated from the density and biomass datasets. After root-root transformation, density and biomass data were subjected to multivariate statistical analyses, in order to identify biotic communities. The sampling sites were first classified into clusters according to species composition using the classification program TWINSPAN (Hill 1979). To check the stability of the TWINSPAN results and to reveal the degree of similarity between 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 analysed using the canonical correspondance analysis (CCA) option from the program package CANOCO (Ter Braak 1988). 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.

Diversity was calculated as Hill's diversity numbers (Hill 1973). Different indices (N_0, N_1, N_2 and N_∞) were calculated per station and averages (± standard errors) are reported per community.

For further characterisation 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^{th} dominant species and all more dominant species) against the logarithm of the rank k. In graphs of the species abundance distribution the number of species represented by 0, 1, 2,... individuals were plotted against logarithmic density classes.

3. Results

3.1. Exploration of the datamatrix

A total of 186 species were recorded. The complete species list with the identification levels and the developmental stages considered as separate 'functional species' is given in table 1. Accidentally caught epibenthic (e.g. demersal fish, adults of crabs, shrimps, starfish and brittlestars) and endobenthic (e.g. adult polychaetes and bivalves) organisms, as well as adult pelagic fish and true planktonic animals (Cnidaria and Ctenophora) were excluded from the dataset. After these corrections, the datamatrix was reduced to 135 species. Rare polychaete larvae, the free-living stages of the ectoparasitic Caligidae and juvenile echinoderms were not identified to species level. The amphipod species of the genus *Bathyporeia* were pooled as *Bathyporeia* species. Juveniles of the amphipod genera *Apherusa* and *Corophium* were not identified to species level and were recorded as such. The identification of larval decapods was often complicated or impossible; in several instances records had to be made on genus or family level. All zoea larvae of Brachyura that could not be identified were lumped together as 'Brachyura species zoea'. Pipefish were recorded as Syngnathidae species and were probably a mixture of *Syngnathus acus* and *S. rostellatus*. Pelagic fish eggs were not identified in more detail. A number of fish larvae were only identified to genus (e.g. *Pomatoschistus* species, probably a mixture of *P. minutus* and *P. lozanoi*) or family level (e.g. Clupeidae species, probably a mixture of *Clupea harengus* and *Sprattus sprattus*, and Ammodytidae species, probably comprising *Ammodytes tobianus* and *Hyperoplus lanceolatus*).

The most abundant taxa in the hyperbenthos of the Belgian continental shelf were (in order of decreasing density): Mysidacea (10 species), Brachyura (20 species), Amphipoda (33 species) and Caridea (14 species). Chaetognatha, Pisces, Anomura, Polychaeta, Isopoda, Copepoda and Cumacea occurred in much lower densities.

3.2. Identification of communities

Analysis of the complete dataset

In first instance, the complete datamatrices (both density and biomass) were subjected to multivariate analyses. The striking trends are discussed here, only the ordination results are shown (figure 2).

The TWINSPAN results (cutlevels 0, 1.1, 1.36, 1.75, 2.45, 3.16) for the density data showed a first division between all stations located near the coast together with the Westerschelde samples ('onshore stations') and the more offshore localities ('offshore stations'). The analysis with the biomass data yielded the same picture. Dendrograms for the clusteranalysis revealed the same major groups, with a high dissimilarity between the 'onshore stations' and the 'offshore stations'.

The ordination with the complete density and biomass datasets yields similar patterns. The three most upstream stations of the Westerschelde are spread along the first axis (eigenvalue 0.33), while all other stations are lumped together at the edge of the ordination diagram, in a plane perpendicular to this axis. Salinity and turbidity characterise the gradient along the first axis: those variables decreased in an upstream direction in the Westerschelde. After exclusion of the upstream Westerschelde stations, the division between the 'onshore stations' and the 'offshore stations' could be visualised. They are found on the right and left sides of the ordination plane (figure 2) formed by the first (eigenvalue 0.23) and second (eigenvalue 0.077) axes. The first axis has the highest eigenvalue and is most reflective for the community structure. The forward selection option of CANOCO revealed three variables that explained a significant amount of variance in the species data: 1/secchi, depth and chlorophyl a (in this sequence). The division between the 'onshore' and 'offshore' stations is mainly correlated with 1/secchi: the coastal stations are highly turbid.

For further analysis, the dataset was splitted up into an 'onshore group' and an 'offshore group', based on the TWINSPAN results.

Analysis of the onshore stations

Density and biomass data of the onshore stations were both analysed and yielded similar results. Only the output for the density data is discussed here.

The result of the TWINSPAN analysis (cutlevels 0, 1.04, 1.33, 1.7, 2.5, 3.47) is presented in figure 3. The first division separates the brackish stations from fully marine stations: the upstream stations of the Westerschelde are split off, with the mysid *Neomysis integer* as indicator species. This group is further called 'cluster ws'. A geografical distinction for the hyperbenthic fauna of the Belgian coast becomes evident at the next division. The left group contains all the stations situated along the west coast and is called cluster 'onshore west'. The remaining stations (except station UG21) are located along the east coast, they belong to the 'onshore east' cluster. The amphipod *Melita obtusata* is indicator species for 'onshore west'. Further divisions within one cluster are ecologically less relevant and are not discussed here. The clusteranalysis yields analogous results (figure 4).

The two clusters identified with the classification techniques can also be found in the ordination plane (figure 5) formed by the first (eigenvalue 0.13) and second (eigenvalue 0.09) canonical axes (note that stations 115s, UG4g and the Westerschelde stations were excluded from this analysis). The eigenvalues for the CCA analysis are quite low. The forward selection option showed that chlorophyl a concentrations could explain the underlying structure. The stations of the 'onshore east' cluster are characterised by high chlorophyl a levels, while significantly lower values were recorded for the 'onshore west' cluster.

Analysis of the offshore stations

The clearest patterns in community structure for the offshore stations were obtained with the biomass data. The analyses with the density data are not discussed further.

The TWINSPAN diagram for the biomass data is presented in figure 6 (cutlevels 0, 2.3, 3.09, 3.92, 5.27, 6.9). The most seaward stations (and also the stations UG12 and 315s) are separated from all other samples at the first division. *Galathea intermedia* megalopa is the positive indicator species for this 'offshore' cluster; negative indicator species are *Crangon crangon* postlarva and Brachyura species zoea. The remaining stations are divided into two more or less geographical coherent clusters. One group of stations (except station UG16) is situated on the Belgian continental shelf, in the transitional area between the onshore stations and the fully offshore stations. The indicator species is *Portumnus latipes* megalopa. The second group is located in the Voordelta, with *Processa modica* zoea as indicator species. The first cluster is further referred to as the 'mid bkp' community; the second as the 'mid vd' community.

The dendrogram for the clusteranalysis is not completely conforming to the TWINSPAN output. The 'mid vd' cluster and the 'offshore' cluster seemed to have a higher similarity, while the 'mid bkp' cluster is more dissimilar to these clusters (figure 7).

The CCA ordination plane formed by the first and second axes (eigenvalues 0.16 and 0.08) visualizes the described structures (figure 8). Three variables ere correlated significantly with the underlying structure: depth was the most important variable, followed by chlorophyl a and 1/Secchi disc depth. On the left side of the diagram, the offshore samples can be found together (characterised by a larger depth). The stations of both 'mid' communities are situated on the right half in the diagram and are segregated along the second axis. The eigenvalue for this axis is very low. The samples from the 'mid bkp' community are found in the upper right quadrant and are correlated with a higher turbidity. In the lower right quadrant, the 'mid vd' community is found, characterised by high chlorophyl a concentrations.

3.3. Characterisation of the communities

Based upon the output of the different multivariate analyses, six hyperbenthic communities could be identified in the area. Their geografical position is shown in figure 9. The 'ws' community is the typical brackish water community of the Westerschelde. Near the shoreline, two communities were identified: the 'onshore east' community at the eastcoast and the 'onshore west' community at the westcoast. The 'mid bkp' and 'mid vd' communities are present in the transitional area between the onshore and offshore waters. The fully offshore waters of the Belgian continental shelf harbour the 'offshore' community.

At a higher taxonomic level

The average density and biomass of the communities, and their taxonomic composition is presented in the figures 10 and 11.

One feature is very prominent: there is a distinct gradient perpendicular to the coastline, along which the composition of the hyperbenthic fauna is altered. The highest densities and biomasses are reached in the brackish water community of the Westerschelde ('ws'), this community consisted nearly exclusively of mysids. Mysids also dominated the hyperbenthos of the two coastal communities ('onshore east' and 'onshore west'). Densities and biomasses are much higher at the west coast as compared to the east coast. A number of taxa (Brachyura and Caridea) become more important in the transitional area ('mid bkp' and 'mid vd'), while the densities of Mysidacea decrease. The pie-chart also gives evidence of a gradient parellel to the coastline over which community composition changes. Brachyura are prominently present in the 'mid vd' community. Both 'mid' communities have densities comparable to the 'onshore east' community. Biomass values are however much lower, due to the high numbers of (small) larval Brachyura and Caridea. Hence, mysids are still quite important gravimetrically in both 'mid' communities. Lowest values for density and biomass were registered in the 'offshore' community. This is clearly the most diverse community at a higher taxonomic level: Brachyura, Mysidacea, Caridea, Amphipoda, Anomura and Chaetognatha are almost equally well presented. Mysids are still quite important in terms of biomass, followed by the larval Anomura.

At species level

The species composition within each taxon and the total abundance per community is presented in the figures 12 to 17.

Mysids (figure 12) reached very high densities in the brackish water area of the Westerschelde (>32000 individuals per 100 m^2) with *Mesopodopsis slabberi* as the dominant species. *Schistomysis kervillei* and *S. spiritus* are the most important species onshore ('onshore east' and 'onshore west'). Note the higher densities on the west coast (5400 individuals per 100 m^2) as compared to the east coast (1600 individuals per 100 m^2). Mysid density decreased sharply offshore (75 individuals per 100 m^2 in the 'offshore' community). Here *Gastrosaccus spinifer* was the most abundant species, followed by *Acanthomysis longicornis* and *Mysidopsis gibbosa.*

Brachyura (figure 13) reached highest densities in the transitional area between onshore and offshore waters (530 individuals per 100 m^2 for 'mid bkp' and 840 individuals per 100 m^2 for 'mid vd'). Diversity of this group was always quite high, except for the 'ws' cluster. In the latter community only *Liocarcinus holsatus* juveniles occurred in appreciable numbers. The 'onshore east' cluster was very diverse, zoeae and megalopae of *Carcinus maenas* and *Liocarcinus* species were the dominant species. Zoeae of those species were less abundant in the 'onshore west' community, while megalopae of *Carcinus maenas* and *Pilumnus hirtellus* increased in importance. The high density of larval stages of *Liocarcinus* species in the transition area is striking, especially in the 'mid vd' community.

Amphipods reached the highest densities (820 individuals per 100 m^2) in the 'onshore west' community, where diversity was very high as well (figure 14). Densities were much lower in the other communities: between 12 and 100 individuals per 100 m^2. *Microprotopus maculatus* and *Pariambus typicus* reached quite high densities in the 'onshore west' cluster, but were never found in the other communities. The 'onshore east' community consisted mainly of *Gammarus crinicornis* and *Atylus swammerdami.* The latter species also dominated the amphipod fauna in the offshore communities.

In the 'offshore' and 'ws' communities, densities of larval Caridea were low (figure 15). Denities in the other communities ranged from 210 to 370 individuals per 100 m^2. The most common Caridea for the Belgian coast were Crangonidae. Postlarvae of *Crangon crangon* were highly dominant in 'ws' and in both coastal communities, while the zoeae of Crangonidae were more important in the transitional communities ('mid bkp' and 'mid vd'). Other species gained in importance in the offshore community: the postlarvae of *Philocheras trispinosus* and *Hippolyte varians.*

Pomatoschistus species dominated the onshore larval fish fauna and reached high densities: 120 individuals per 100 m^2 for 'onshore west' (figure 16). A large number of fish eggs was recorded for the 'mid bkp' cluster. The offshore community showed the highest diversity. Postlarvae of *Arnoglossus laterna* and *Callionymus lyra* were quite abundant, yet larval gobies still reached highest densities.

Cumacea (figure 17) never reached high densities on the Belgian continental shelf (3 to 25 individuals per 100 m^2). The group was absent from the 'ws' community. *Diastylis bradyi* was the most common cumacean and it occurred in each community (except in the 'ws' community). The species composition for each cluster was quite different. In 'onshore east', *Diastylis rathkei* was also common. This species was never found in 'onshore west', where *Bodotria scorpioides* reached quite high densities. *Pseudocuma similis* became more important offshore and was even dominant in the 'offshore' community.

3.4. Diversity

Hill's diversity numbers N_1 and N_2 are presented per community in figure 18. The hyperbenthic fauna of the upstream reaches of the Westerschelde estuary was clearly the least diverse. There is a striking pattern for the other communities: the two coastal communities were characterized by a low diversity, while the offshore communities had a higher diversity. 'Onshore east' and 'onshore west' had a comparable diversity. Different results were obtained for the 'mid' communities: 'mid vd' was markedly less diverse than 'mid bkp'. The diversity of the 'offshore' community was comparable to that of the 'mid bkp' cluster.

For further characterisation of the communities, diversity was investigated along an onshore-offshore gradient. K-dominance curves were constructed (based on a same number of stations) for the onshore clusters ('onshore east' and 'onshore west' together), the 'mid bkp' cluster and the 'offshore' cluster (figure 19). The figure shows that dominance is most prononced for the onshore communities: the curve is steep and reaches the plateau first. Dominance is less pronounced for the 'offshore' community, still the plateau is reached more or less at the same time as the one for the 'mid' community. This means that both communities consist of a comparable number of species, most of which do not occur frequently.

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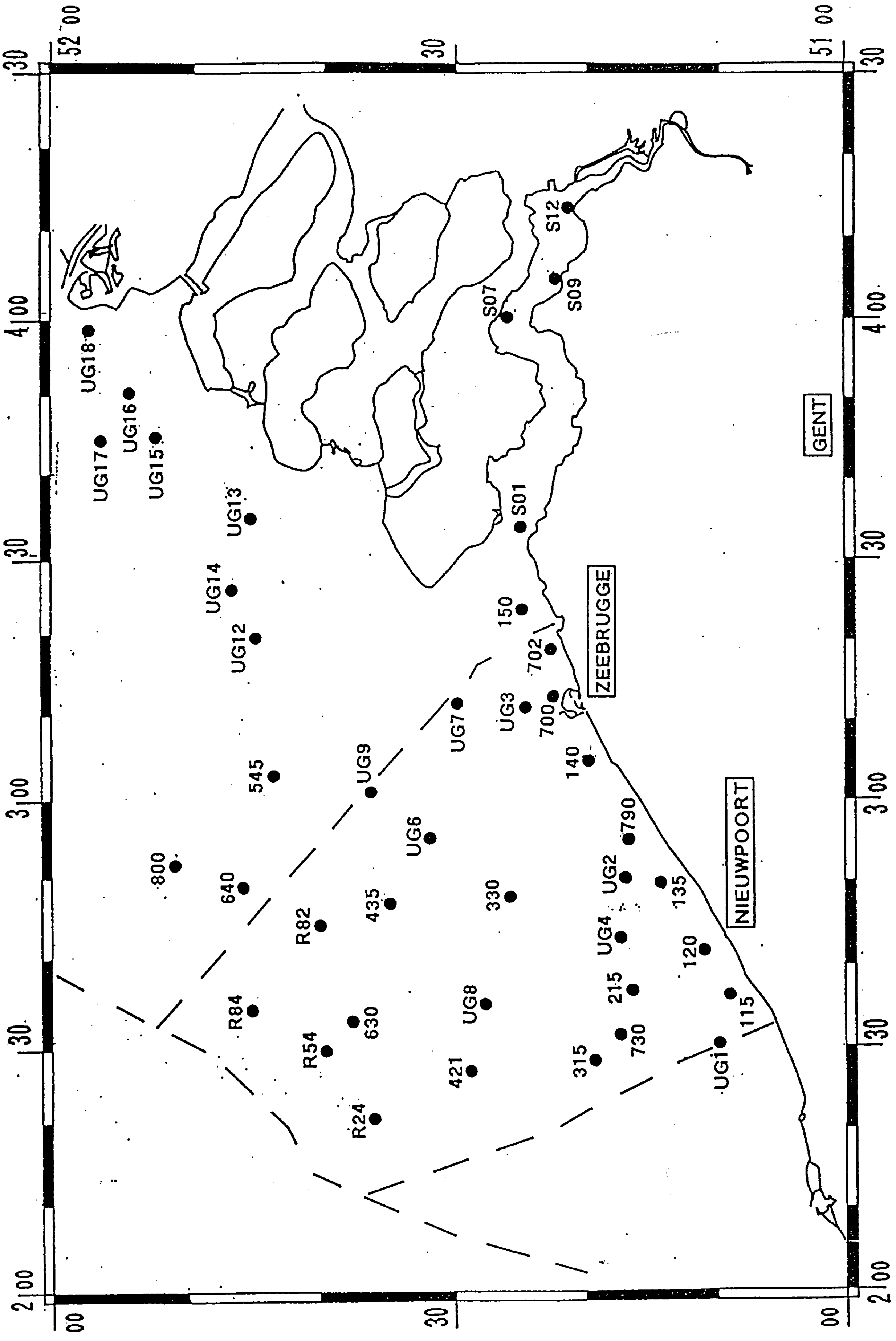
FIGURE 1.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UG9
UG6
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800
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435
330
UG2
135
R82
UG4
120
215
R84
630
UG8
115
R54
730
UG1
315
421
R24

Table 1: List of species caught with the hyperbenthic sledge on the Belgian continental shelf with the abbreviations used. Species marked with * were excluded from all analysis.

taxon	species and stage	abbreviation
Phylum Porifera		
	Porifera species	Pori Spec *
Phylum Cnidaria		
	Hydrozoa species	Hydr Spec *
	Bougainvillea britannica	Boug brit *
	Mitrocomella polydiademata	Mitr poly *
	Anthozoa species	Anth Spec *
Phylum Ctenophora		
	Pleurobrachia pileus	Pleu pile *
	Beroë cucumis	Bero cucu *
	Beroë gracile	Bero grac *
	Beroë species	Bero Spec *
Phylum Mollusca		
	Nudibranchia species	Nudi Spec *
	Patella species	Pate Spec *
	Crepidula fornicata	Crep forn *
	Gastropoda species	Gast Spec *
	Chlamys opercularis juvenile	Chla opJU
	Venerupis species	Vene Spec *
	Spisula elliptica	Spis elli *
	Macoma baltica	Maco balt *
	Abra alba	Abra alba *
	Ensis species	Ensi Spec *
	Bivalvia species	Biva Spec *
	Sepiola atlantica juvenile	Sepi atJU
Phylum Annelida		
	Lanice conchilega	Lani conc *
	Lanice conchilega auloph. larva	Lani Aulo
	Harmothoe species larva	Harm Larv
	Pectinaria koreni	Pect kore *
	Polychaeta species	Poly Spec *
	Oligochaeta species	Olig Spec *
Phylum Arthropoda		
Subphylum Chelicerata		
Class Pycnogonida		
	Nymphon rubrum	Nymp rubr
	Achelia longipes	Ache long
	Phoxichilidium femoratum	Phox femo
	Endeis laevis	Ende laev
	Pycnogonum littorale	Pycn litt
Subphylum Crustacea		
Class Copepoda		
	Centropages typicus	Cent typi
	Temora longicornis	Temo long
	Calanus helgolandicus	Cala helg
	Caligidae Species	Cali Spec
Class Malacostraca		
Order Euphausiacea		
	Nyctiphanes couchi	Nyct couc
Order Decapoda		
Infraorder Caridea		
	Palaemon elegans postlarva	Pala elPO
	Palaemonidae species zoea	Pala SpZO
	Alpheus glaber zoea	Alph glZO
	Hippolyte varians	Hipp vari *
	Hippolyte varians postlarva	Hipp vaPO
	Hippolyte varians zoea	Hipp vaZO
	Thoralus cranchii postlarva	Thor crPO
	Processa canaliculata	Proc cana *
	Processa canaliculata postlarva	Proc caPO
	Processa modica postlarva	Proc moPO
	Processa modica zoea	Proc moZO
	Pandalina brevirostris	Pand brev *
	Pandalina brevirostris postlarva	Pand brPO
	Pandalina brevirostris zoea	Pand brZO
	Crangon allmanni	Cran allm *
	Crangon crangon	Cran cran *
	Crangon crangon postlarva	Cran crPO
	Philocheras trispinosus	Phil tris *
	Philocheras trispinosus postlarva	Phil trPO
	Crangonidae species zoea	Cran SpZO
Infraorder Thalassinidea		
	Callianassa species zoea	Call SpZO
	Upogebia deltaura megalopa	Upog deME
	Upogebia species zoea	Upog SpZO
Infraorder Anomura		
	Galathea intermedia megalopa	Gala inME
	Galathea intermedia zoea	Gala inZO
	Pisidia longicornis juvenile	Pisi loJU
	Pisidia longicornis megalopa	Pisi loME
	Pisidia longicornis zoea	Pisi loZO
	Anapagurus laevis zoea	Anap laZO
	Pagurus bernhardus	Pagu bern *
	Pagurus bernhardus juvenile	Pagu beJU
	Pagurus bernhardus zoea	Pagu beZO
	Pagurus prideauxi zoea	Pagu prZO
	Paguridae species megalopa	Pagu SpME
Infraorder Brachyura		
	Inachus species megalopa	Inac SpME
	Macropodia rostrata juvenile	Macr roJU
	Macropodia species megalopa	Macr SpME
	Macropodia species zoea	Macr SpZO
	Thia scutellata juvenile	Thia scJU
	Thia scutellata megalopa	Thia scME
	Corystes cassivelaunus megalopa	Cory caME
	Liocarcinus holsatus	Lioc hols *
	Liocarcinus holsatus juvenile	Lioc hoJU
	Liocarcinus arcuatus juvenile	Lioc arJU
	Liocarcinus species megalopa	Lioc SpME
	Liocarcinus species zoea	Lioc SpZO
	Carcinus maenas megalopa	Carc maME
	Carcinus maenas zoea	Carc maZO
	Portumnus latipes juvenile	Port laJU
	Portummus latipes megalopa	Port laME
	Pilumnus hirtellus juvenile	Pilu hiJU
	Pilumnus hirtellus megalopa	Pilu hiME
	Pinnotheres pisum	Pinn pisu *
	Ebalia cranchii juvenile	Ebal crJU
	Ebalia species megalopa	Ebal SpME
	Brachyura species zoea	Zoea Spp.
Order Mysidacea		
	Siriella armata	Siri arma
	Gastrosaccus spinifer	Gast spin
	Mysidopsis gibbosa	Mysi gibb
	Paramysis arenosa	Para aren
	Schistomysis spiritus	Schi spir
	Schistomysis kervillei	Schi kerv
	Praunus flexuosus	Prau flex
	Mesopodopsis slabberi	Meso slab
	Neomysis integer	Neom inte
	Acanthomysis longicornis	Acan long
Order Cumacea		
	Bodotria scorpioides	Bodo scor
	Bodotria pulchella	Bodo pulc
	Iphinoe trispinosa	Iphi tris
	Pseudocuma longicornis	Pseu long
	Pseudocuma similis	Pseu simi
	Diastylis rathkei	Dias rath
	Diastylis bradyi	Dias brad
Order Amphipoda		
Suborder Gammaridea		
	Orchomene nana	Orch nana
	Ampelisca brevicornis	Ampe brev
	Panoploea minuta	Pano minu
	Amphilochus neapolitanus	Amph neap
	Leucothoe incisa	Leuc inci
	Stenothoe marina	Sten mari
	Gammarus crinicornis	Gamm crin
	Gammarus salinus	Gamm sali
	Melita obtusata	Meli obtu
	Bathyporeia species	Bath Spec
	Urothoe brevicornis	Urot brev
	Perioculodes longimanus	Peri long
	Pontocrates altamarinus	Pont alta
	Pontocrates arenarius	Pont aren
	Megaluropus agilis	Mega agil
	Melphidipella macra	Melp macr
	Apherusa bispinosa	Aphe bisp
	Apherusa ovalipes	Aphe oval
	Apherusa species	Aphe Spec
	Pleusymtes glaber	Pleu glab
	Atylus falcatus	Atyl falc
	Atylus swammerdami	Atyl swam
	Aora typica	Aora typi
	Microdeutopus gryllotalpa	Micr gryl
	Corophium ascherusicum	Coro asch
	Corohhium sextonae	Coro sext
	Corophium volutator	Coro volu
	Corophium species	Coro Spec
	Jassa falcata	Jass falc
	Microprotopus maculatus	Micr macu
Suborder Hyperiidea		
	Hyperia galba	Hype galb
Suborder Caprellidea		
	Phtisica marina	Phti mari
	Pariambus typicus	Pari typi
Order Isopoda		
	Eurydice pulchra	Eury pulc
	Idotea linearis	Idot line
	Idotea pelagica	Idot pela
	Prodajus ostendensis	Prod oste *
Phylum Echinodermata		
	Asterias rubens	Aste rube *
	Ophiura species	Ophi Spec *
	Ophiura juveniel	Ophi Juve
	Echinoidea species	Echi Spec *
	Echinoidea juveniel	Echi Juve
Phylum Bryozoa		
	Bryozoa species	Bryo Spec *
Phylum Chaetognatha		
	Sagitta elegans	Sagi eleg
Phylum Chordata		
Subphylum Vertebrata		
Class Osteichthyes		
	Fish Eggs	Fish Eggs
	Clupeidae species postlarva	Clup SpPO
	Trisopterus luscus	Tris lusc *
	Trisopterus luscus postlarva	Tris luPO
	Ciliata mustela	Cili must *
	Gaidropsarus vulgaris	Gaid vulg *
	Syngnathidae species	Syng Spec *
	Syngnathidae species postlarva	Syng SpPO
	Agonus cataphractus	Agon cata *
	Agonus cataphractus postlarva	Agon caPO
	Trachurus trachurus postlarva	Trac trPO
	Chelon labrosus postlarvea	Chel laPO
	Echiichthys vipera postlarva	Echi vipe *
	Echiichthys species postlarva	Echi SpPO
	Ammodytes tobianus	Ammo tobi *
	Ammodytes tobianus postlarva	Ammo toPO
	Hyperoplus lanceolatus	Hype lanc *
	Hyperoplus lanceolatus postlarva	Hype laPO
	Ammodytidae species postlarva	Ammo SpPO
	Callionymus lyra	Call lyra *
	Callionymus lyra postlarva	Call lyPO
	Callionymus reticulatus postlarva	Call rePO
	Callionymus species postlarva	Call SpPO
	Pomatoschistus minutus	Poma minu *
	Pomatoschistus lozanoi	Poma loza *
	Pomatoschistus microps postlarva	Poma miPO
	Pomatoschistus species postlarva	Poma SpPO
	Arnoglossus laterna postlarva	Arno laPO
	Pleuronectes platessa	Pleu plat *
	Limanda limanda	Lima lima *
	Solea solea	Sole sole *
	Solea solea postlarva	Sole soPO

FIGURE 2.

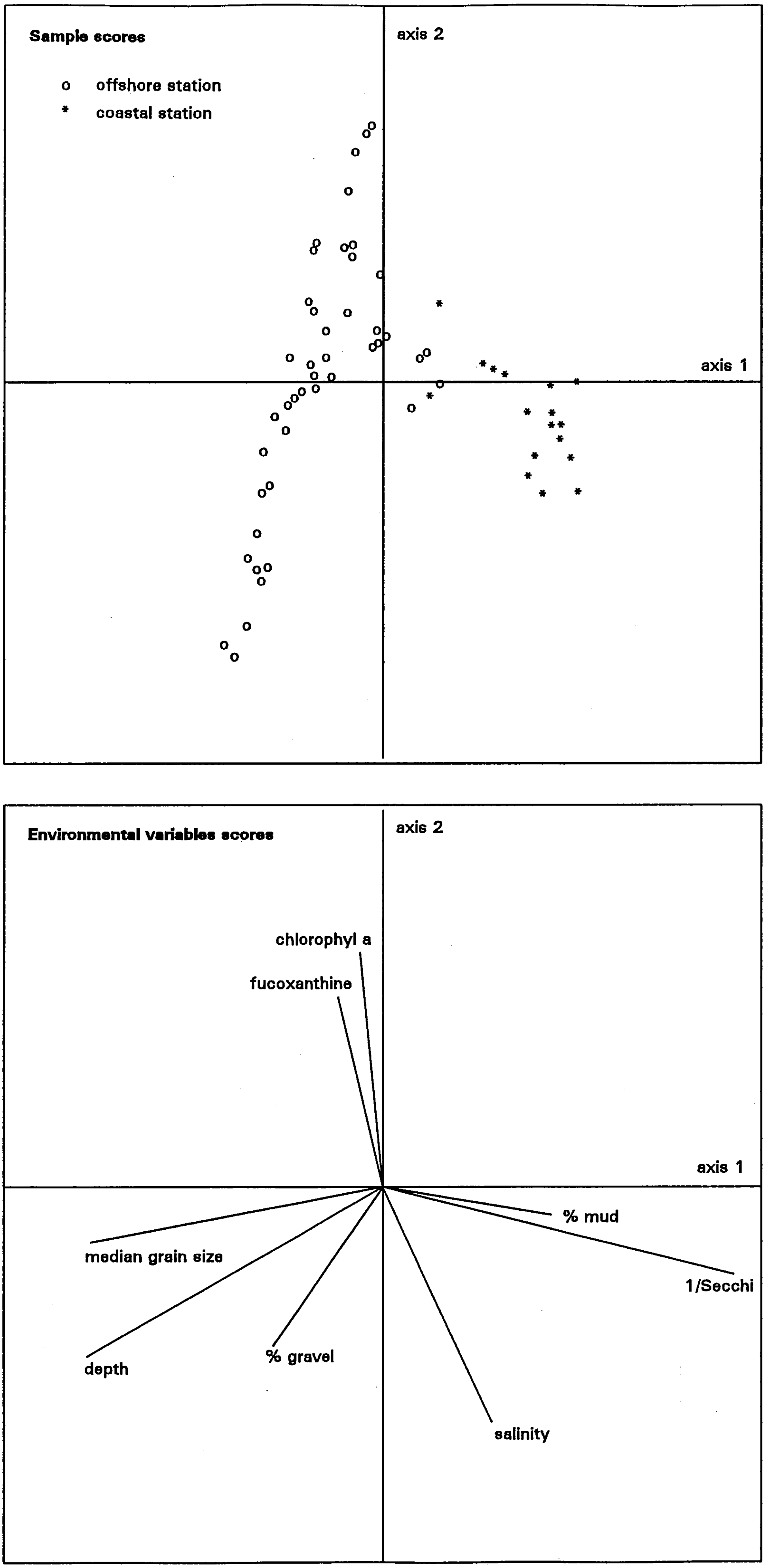

Sample scores
o offshore station
* coastal station
axis 2
axis 1
Environmental variables scores
axis 2
axis 1
chlorophyl a
fucoxanthine
median grain size
depth
% gravel
% mud
1/Secchi
salinity

FIGURE 3.

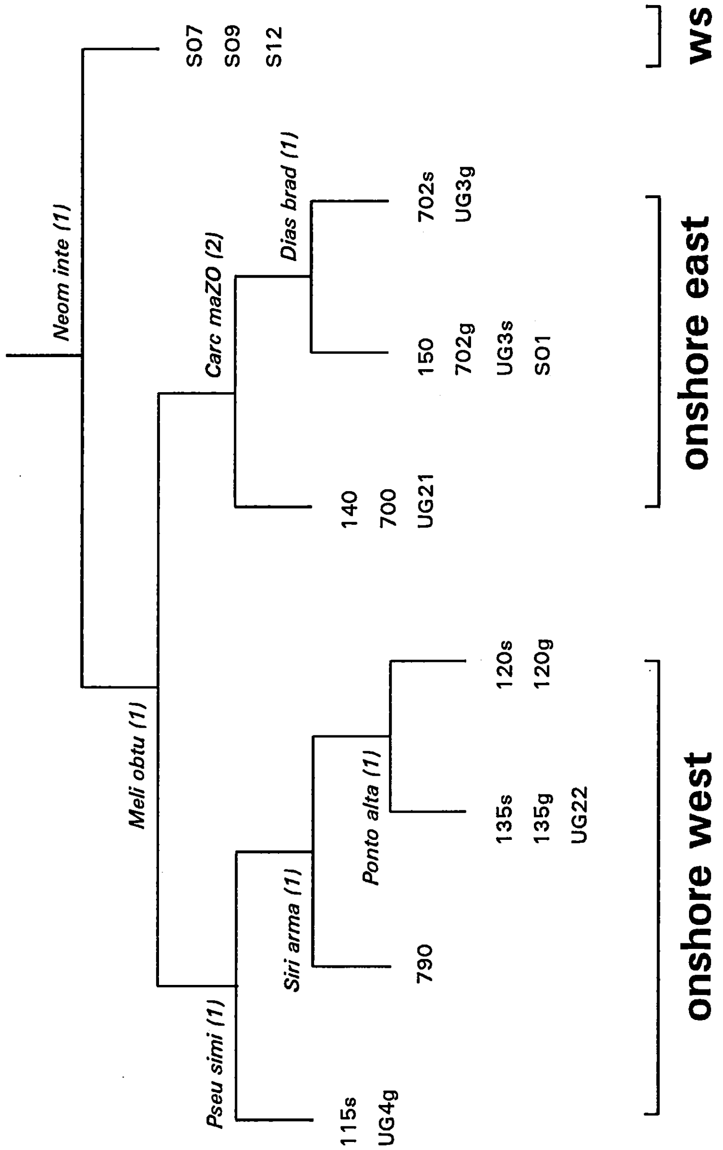

Neom inte (1)
SO7
SO9
S12
Carc maZO (2)
Dias brad (1)
702s
UG3g
150
702g
UG3s
SO1
140
700
UG21
Meli obtu (1)
Pseu simi (1)
Siri arma (1)
Ponto alta (1)
120s
120g
135s
135g
UG22
790
115s
UG4g
ws
onshore east
onshore west

FIGURE 4.

HYPERBENTHOS BCP - september 1993
density (onshore stations)
Bray-Curtis similarity, group average sorting

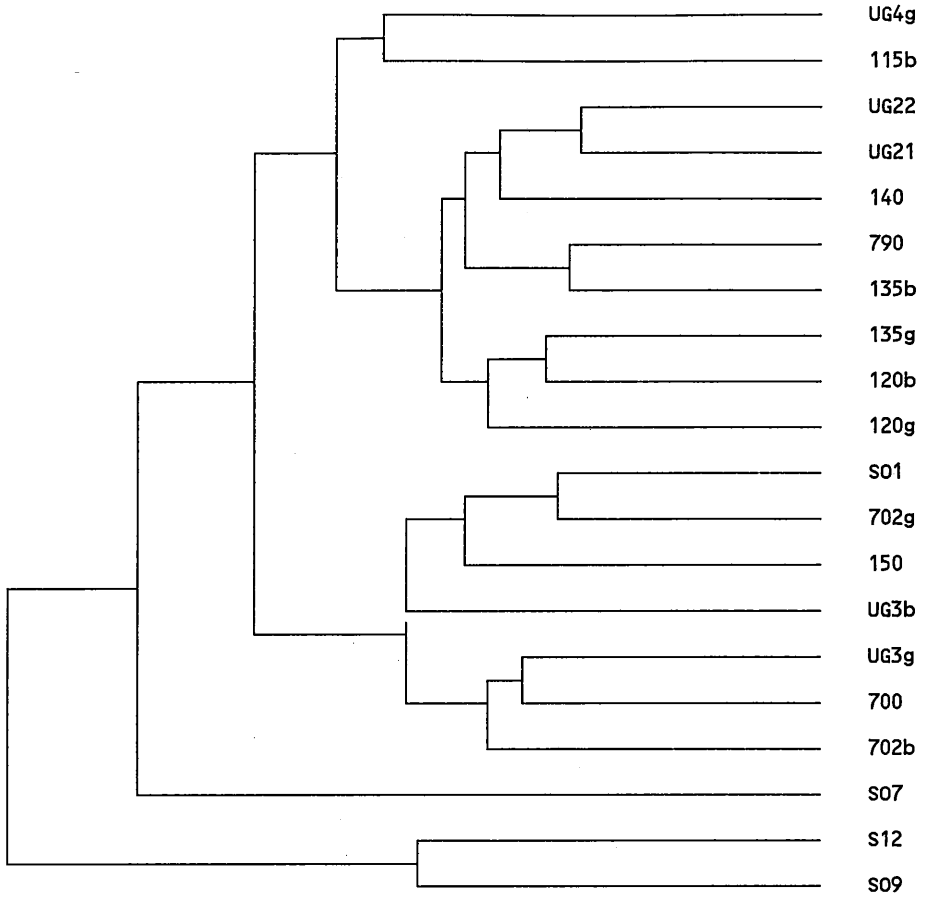
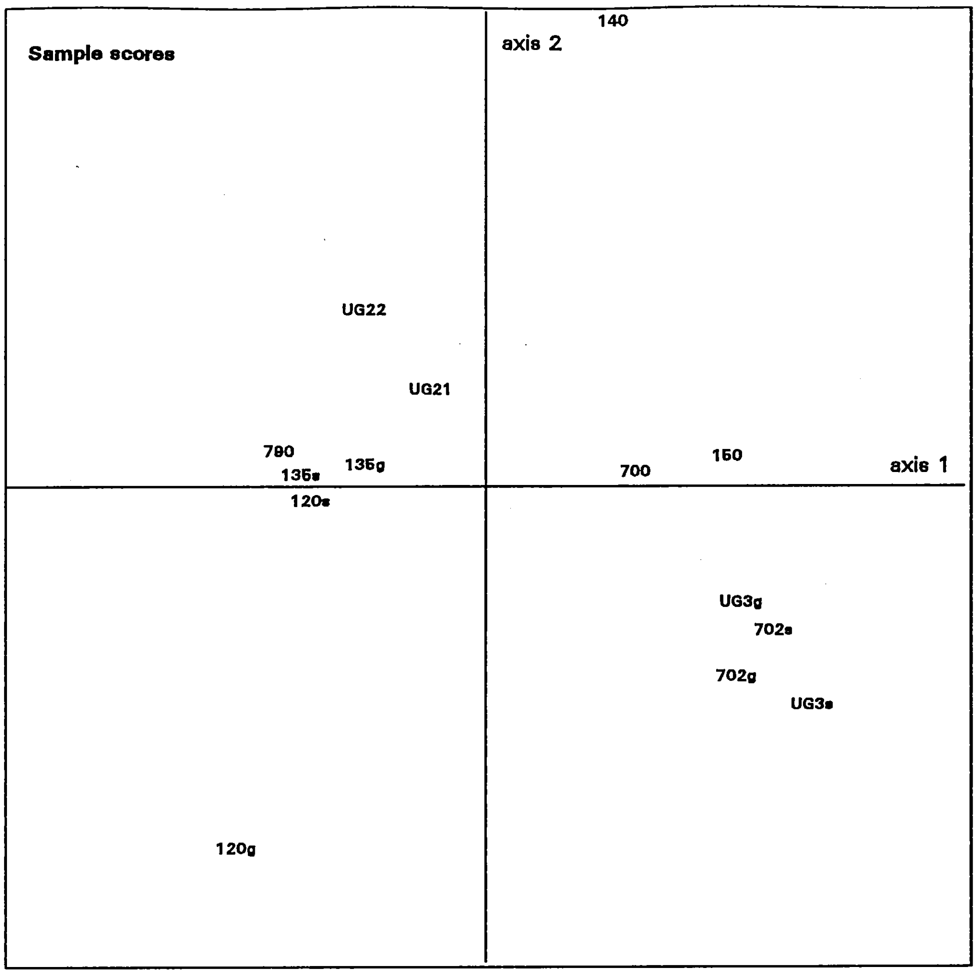
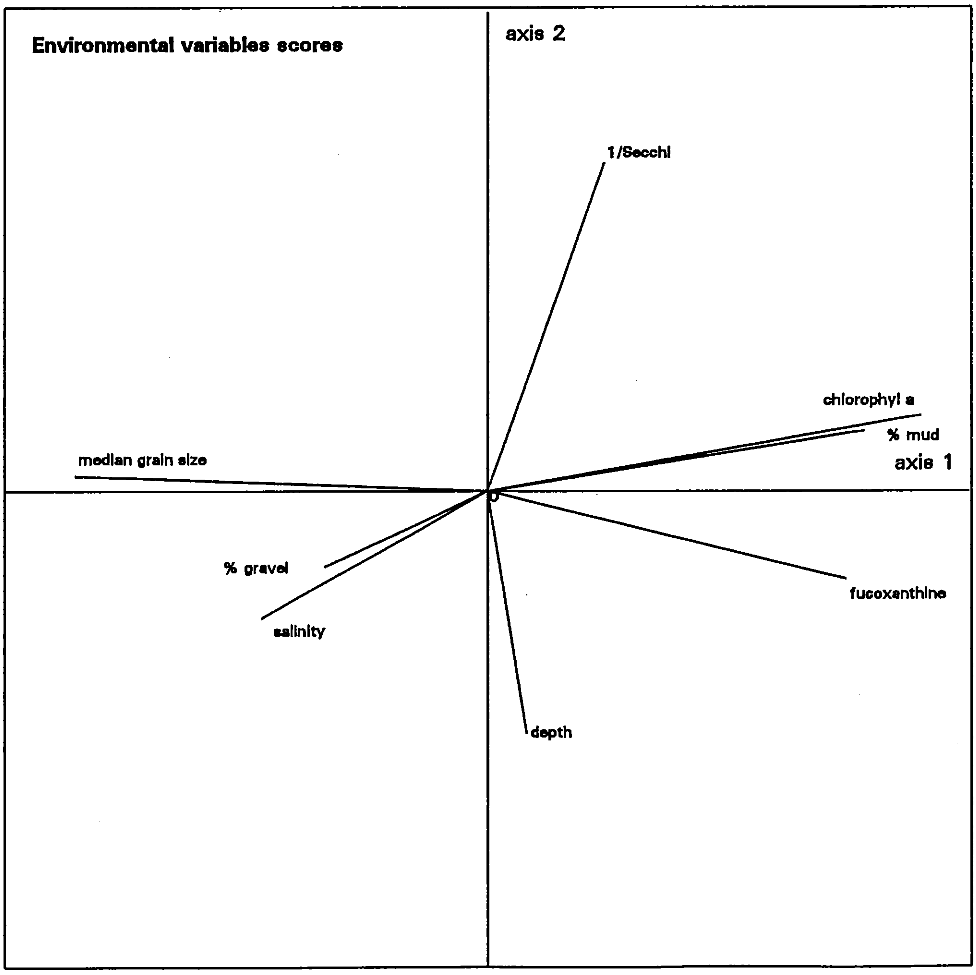


FIGURE 5.



Sample scores
axis 2
140
UG22
UG21
790
135s
135g
120s
700
150
axis 1
UG3g
702s
702g
UG3s
120g



Environmental variables scores
axis 2
1/Secchi
chlorophyl a
% mud
axis 1
median grain size
0
% gravel
salinity
fucoxanthine
depth

FIGURE 6.

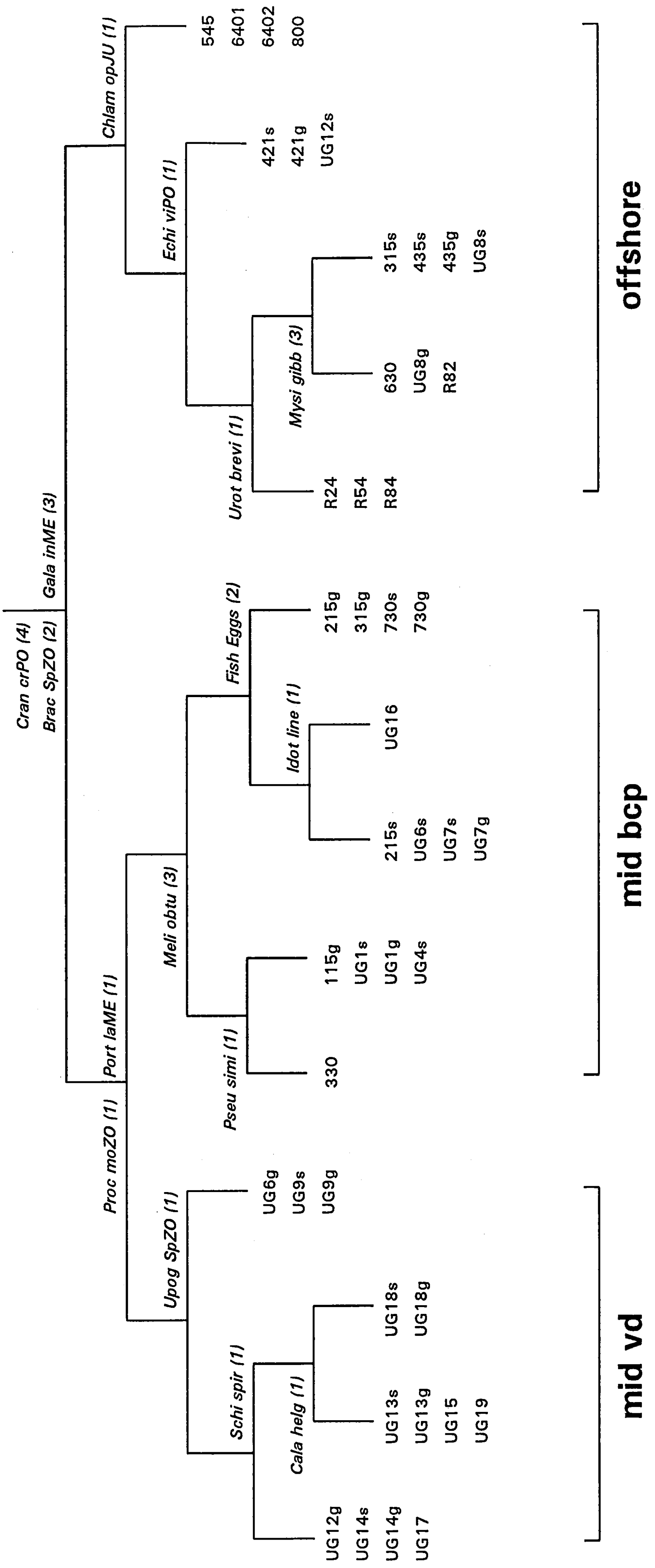

Cran crPO (4)
Brac SpZO (2)
Gala inME (3)
Chlam opJU (1)
545
6401
6402
800
Echi viPO (1)
421s
421g
UG12s
Urot brevi (1)
Mysi gibb (3)
315s
435s
435g
UG8s
630
UG8g
R82
R24
R54
R84
offshore
Port laME (1)
Meli obtu (3)
Fish Eggs (2)
215g
315g
730s
730g
Idot line (1)
UG16
215s
UG6s
UG7s
UG7g
Pseu simi (1)
115g
UG1s
UG1g
UG4s
330
mid bcp
Proc moZO (1)
Upog SpZO (1)
UG6g
UG9s
UG9g
Schi spir (1)
Cala helg (1)
UG18s
UG18g
UG13s
UG13g
UG15
UG19
UG12g
UG14s
UG14g
UG17
mid vd

FIGURE 7.

HYPERBENTHOS BCP - september 1993
biomass (offshore stations)
Bray-Curtis similarity, group average sorting

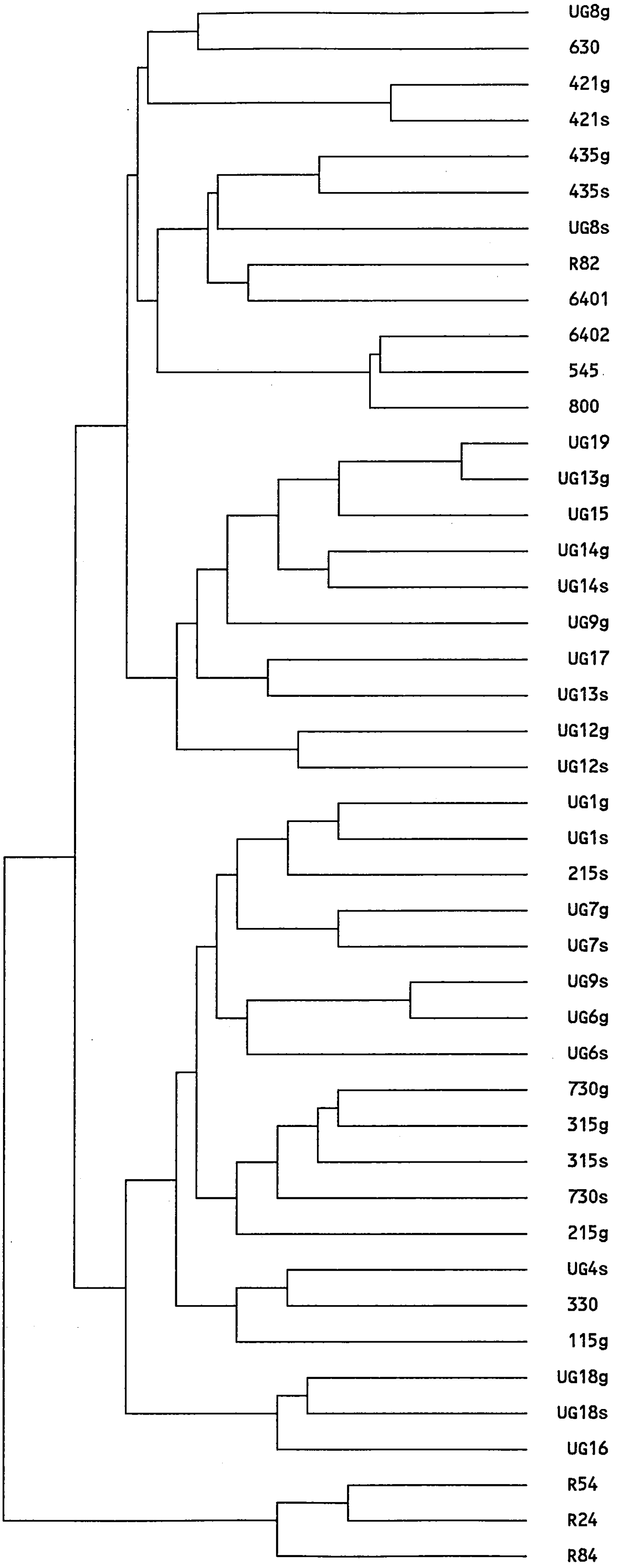
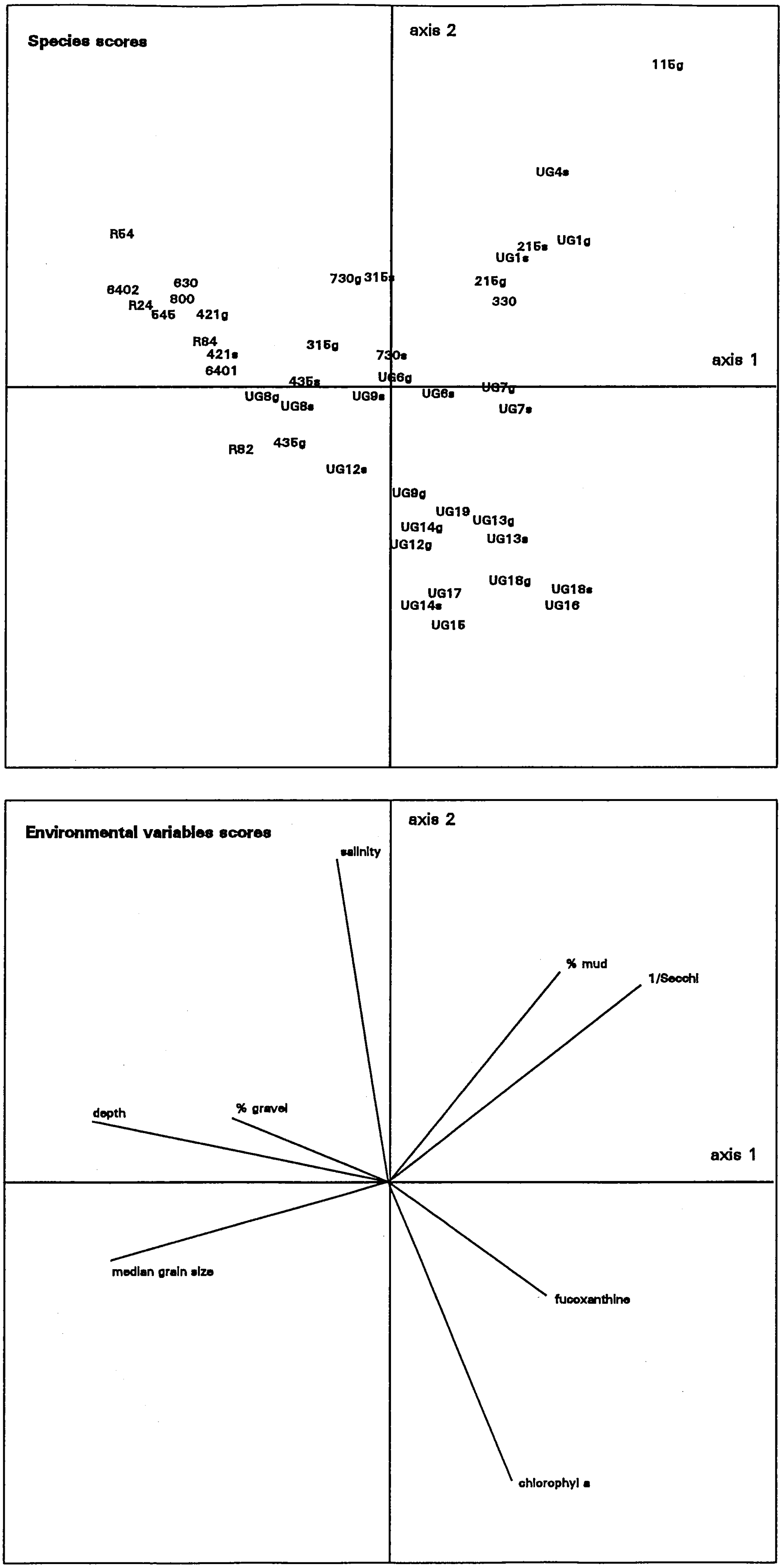


FIGURE 8.


Species scores
axis 2
axis 1
115g
UG4s
R54
215s
UG1g
UG1s
6402
630
730g
315s
215g
R24
800
330
545
421g
R84
315g
730s
421s
6401
435s
UG6g
UG6s
UG7g
UG8g
UG8s
UG9s
UG7s
R82
435g
UG12s
UG9g
UG19
UG13g
UG14g
UG12g
UG13s
UG18g
UG18s
UG17
UG14s
UG16
UG15
Environmental variables scores
axis 2
salinity
% mud
1/Secchi
depth
% gravel
axis 1
median grain size
fucoxanthine
chlorophyl a

geographical location of the hyperbenthic communities

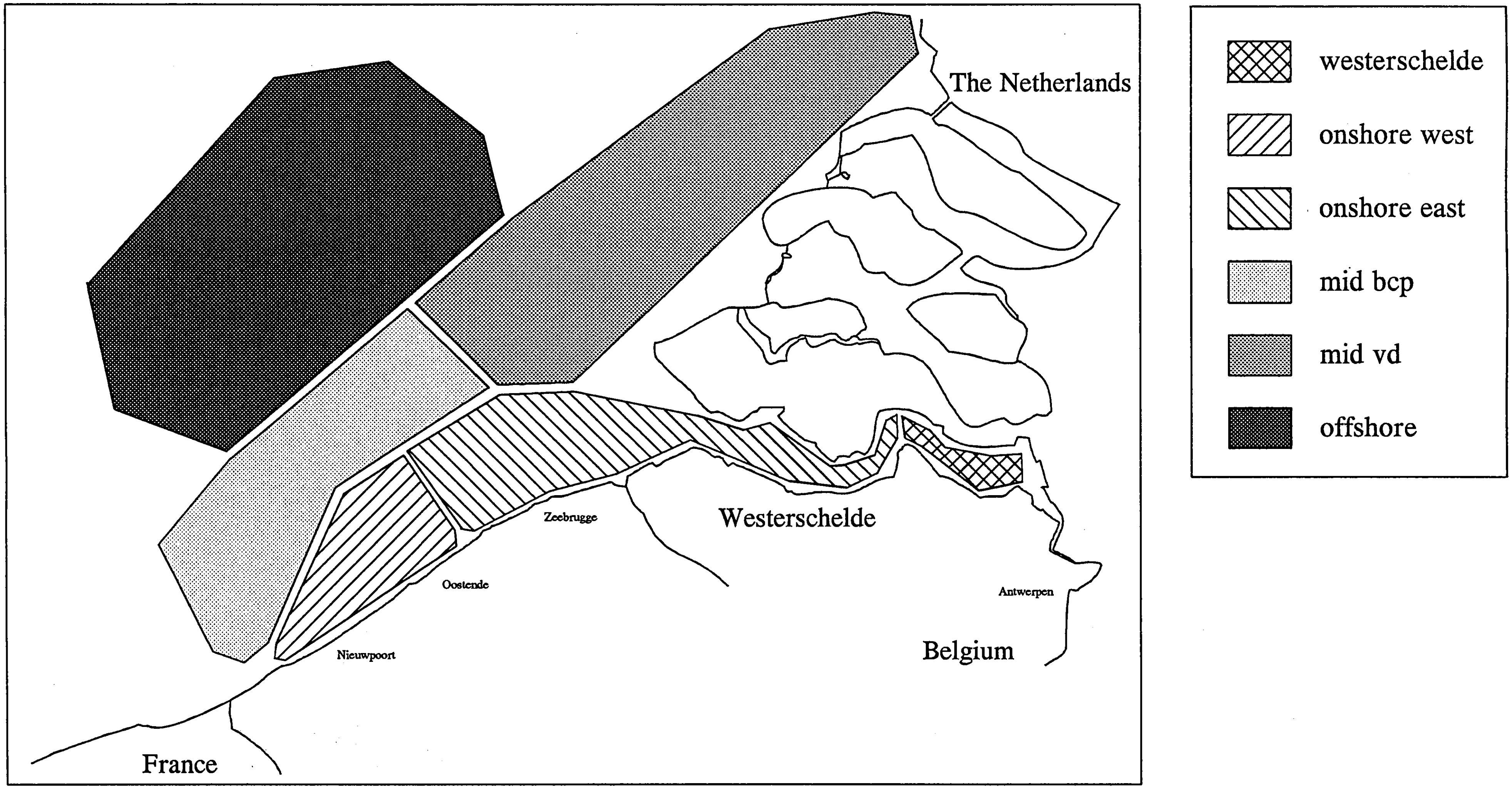


FIGURE 9.

FIGURE 10.

average density and taxonomic composition of the communities

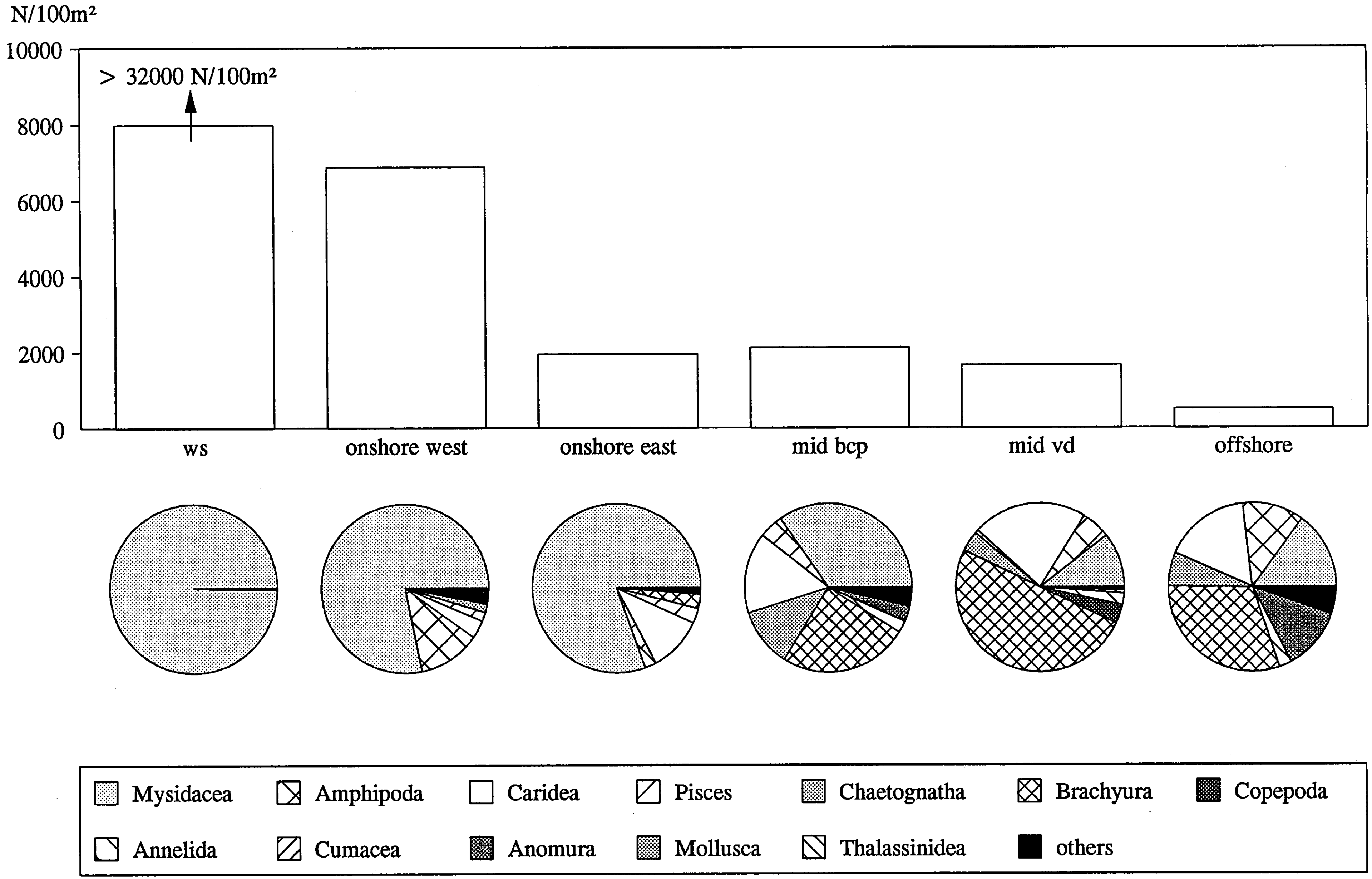


FIGURE 11.

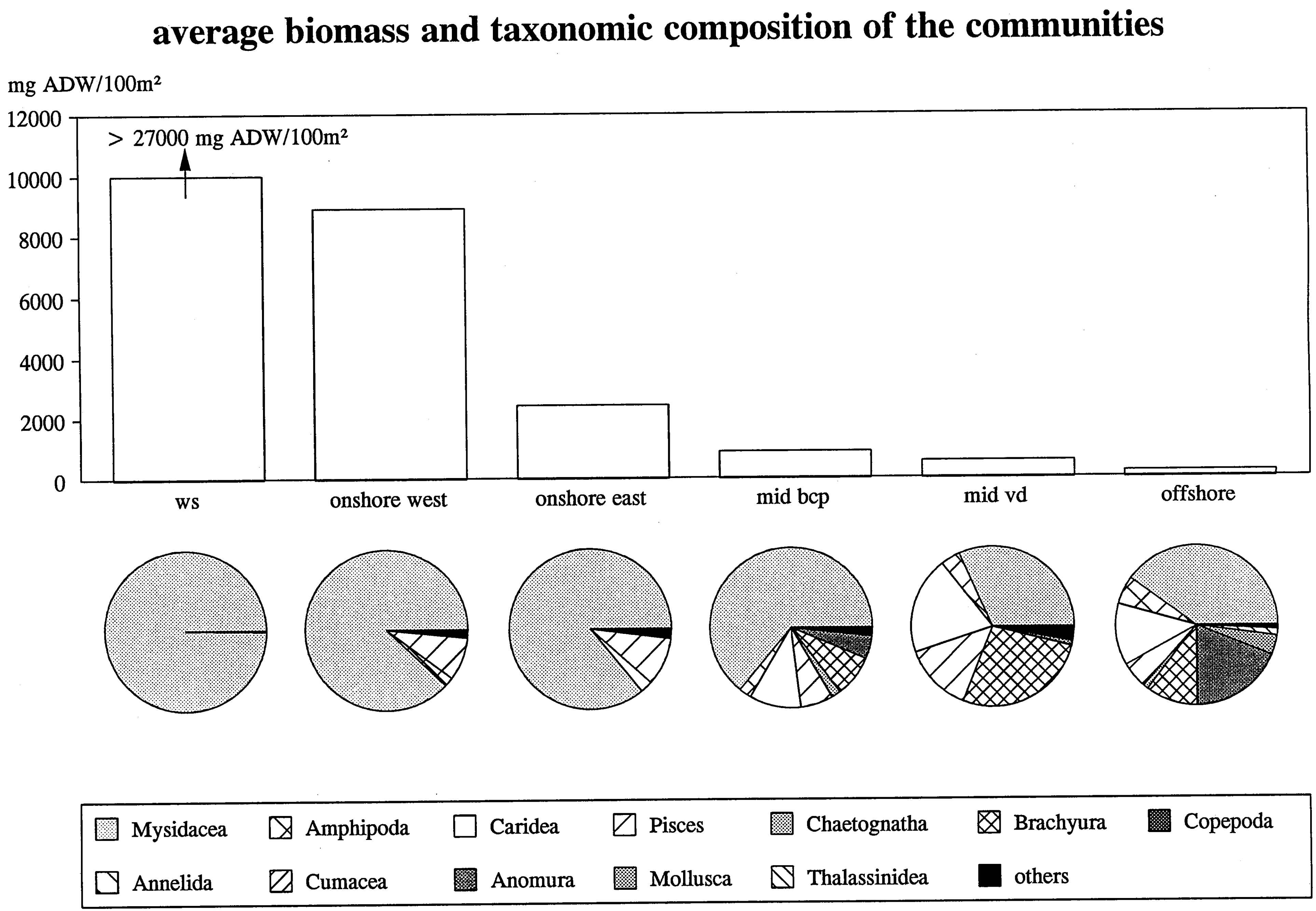

average biomass and taxonomic composition of the communities
mg ADW/100m²
12000
10000
8000
6000
4000
2000
0
> 27000 mg ADW/100m²
ws
onshore west
onshore east
mid bcp
mid vd
offshore
Mysidacea
Amphipoda
Caridea
Pisces
Chaetognatha
Brachyura
Copepoda
Annelida
Cumacea
Anomura
Mollusca
Thalassinidea
others

FIGURE 12.

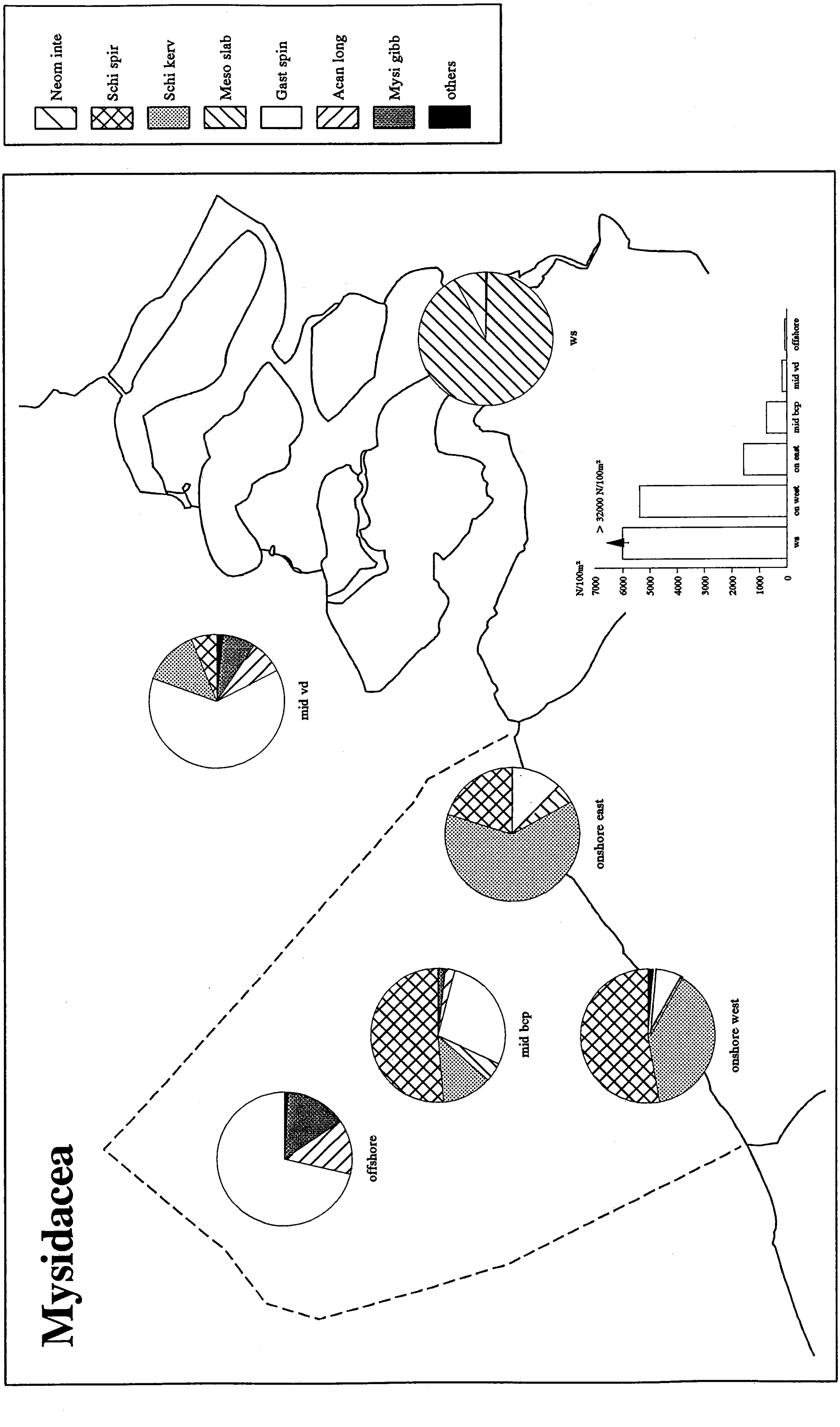

Mysidacea
Neom inte
Schi spir
Schi kerv
Meso slab
Gast spin
Acan long
Mysi gibb
others
ws
mid vd
onshore east
mid bcp
onshore west
offshore
N/100m²
7000
6000
5000
4000
3000
2000
1000
0
> 32000 N/100m²
ws
on west
on east
mid bcp
mid vd
offshore

FIGURE 13.

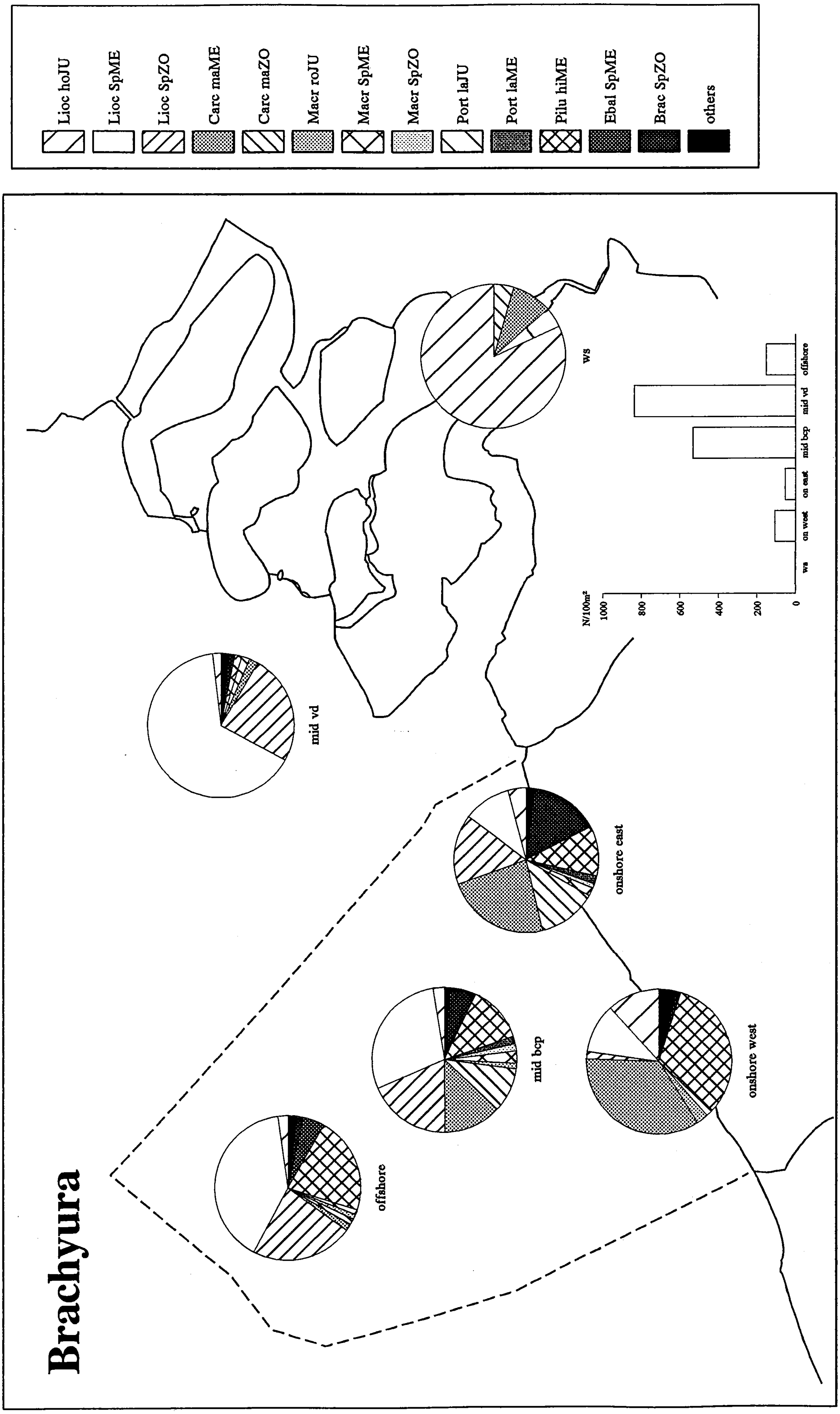

Lioc hoJU
Lioc SpME
Lioc SpZO
Carc maME
Carc maZO
Macr roJU
Macr SpME
Macr SpZO
Port laJU
Port laME
Pilu hiME
Ebal SpME
Brac SpZO
others
Brachyura
ws
mid vd
onshore east
mid bcp
onshore west
offshore
N/100m²
1000
800
600
400
200
0
ws
on west
on east
mid bcp
mid vd
offshore

FIGURE 14.

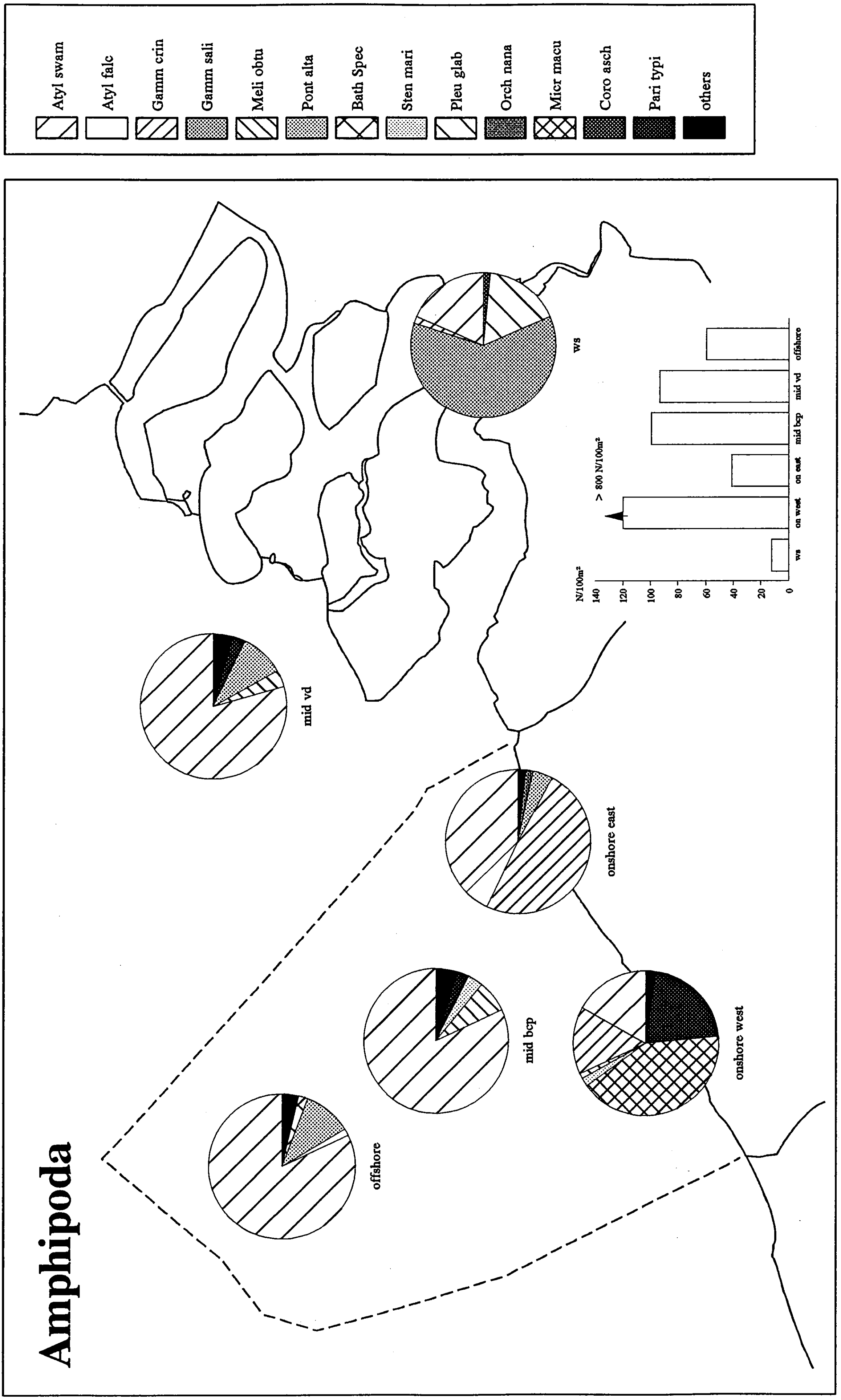

Atyl swam
Atyl falc
Gamm crin
Gamm sali
Meli obtu
Pont alta
Bath Spec
Sten mari
Pleu glab
Orch nana
Micr macu
Coro asch
Pari typi
others
Amphipoda
ws
mid vd
onshore east
mid bcp
onshore west
offshore
N/100m²
140
120
100
80
60
40
20
0
> 800 N/100m²
ws
on west
on east
mid bcp
mid vd
offshore

FIGURE 15.

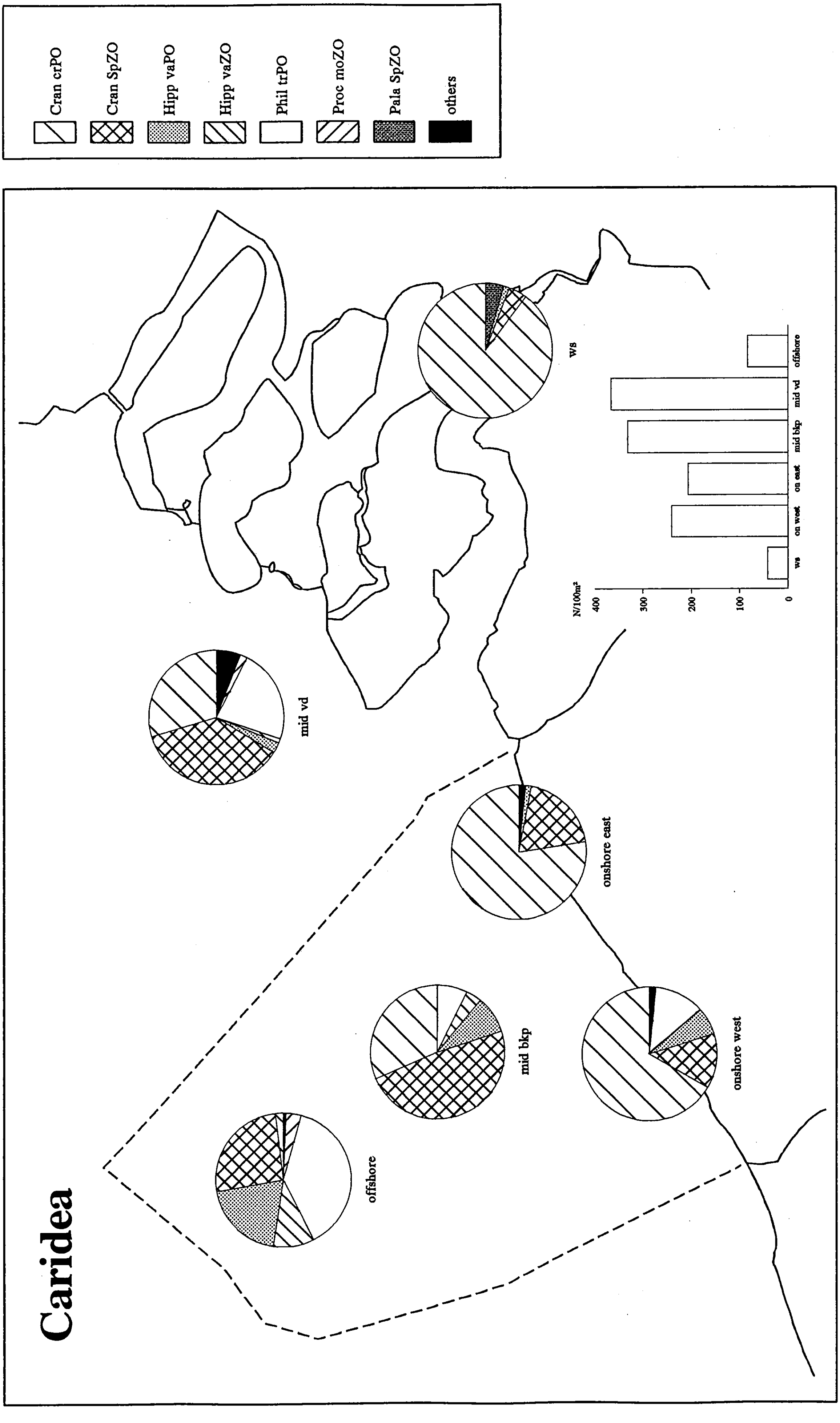

Cran crPO
Cran SpZO
Hipp vaPO
Hipp vaZO
Phil trPO
Proc moZO
Pala SpZO
others
Caridea
ws
mid vd
onshore east
mid bkp
onshore west
offshore
N/100m²
400
300
200
100
0
ws
on west
on east
mid bkp
mid vd
offshore

FIGURE 16.

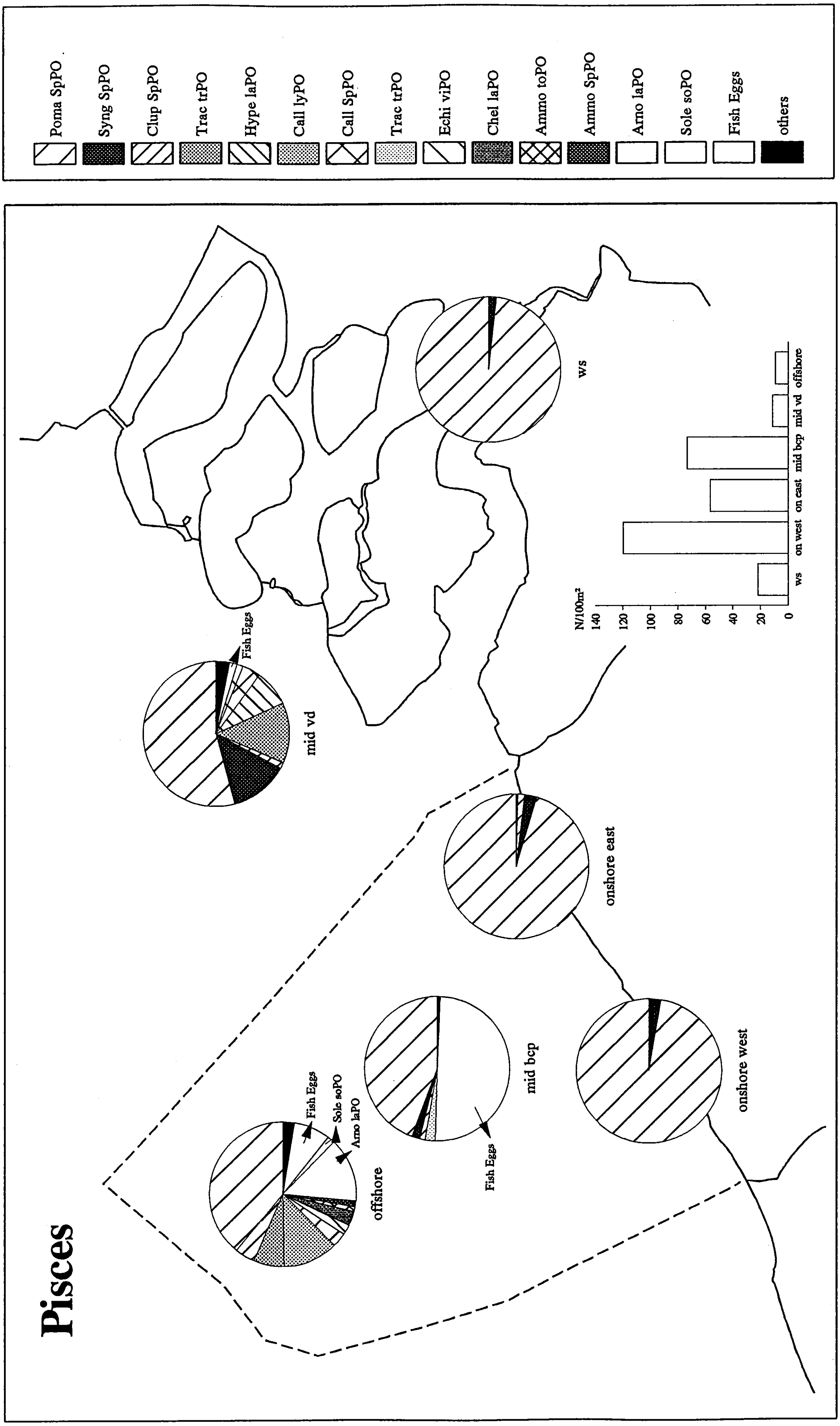

Pisces
Poma SpPO
Syng SpPO
Clup SpPO
Trac trPO
Hype laPO
Call lyPO
Call SpPO
Trac trPO
Echi viPO
Chel laPO
Ammo toPO
Ammo SpPO
Arno laPO
Sole soPO
Fish Eggs
others
ws
mid vd
Fish Eggs
onshore east
onshore west
mid bcp
Fish Eggs
offshore
Fish Eggs
Sole soPO
Arno laPO
N/100m²
140
120
100
80
60
40
20
0
ws
on west
on east
mid bcp
mid vd
offshore

FIGURE 17.

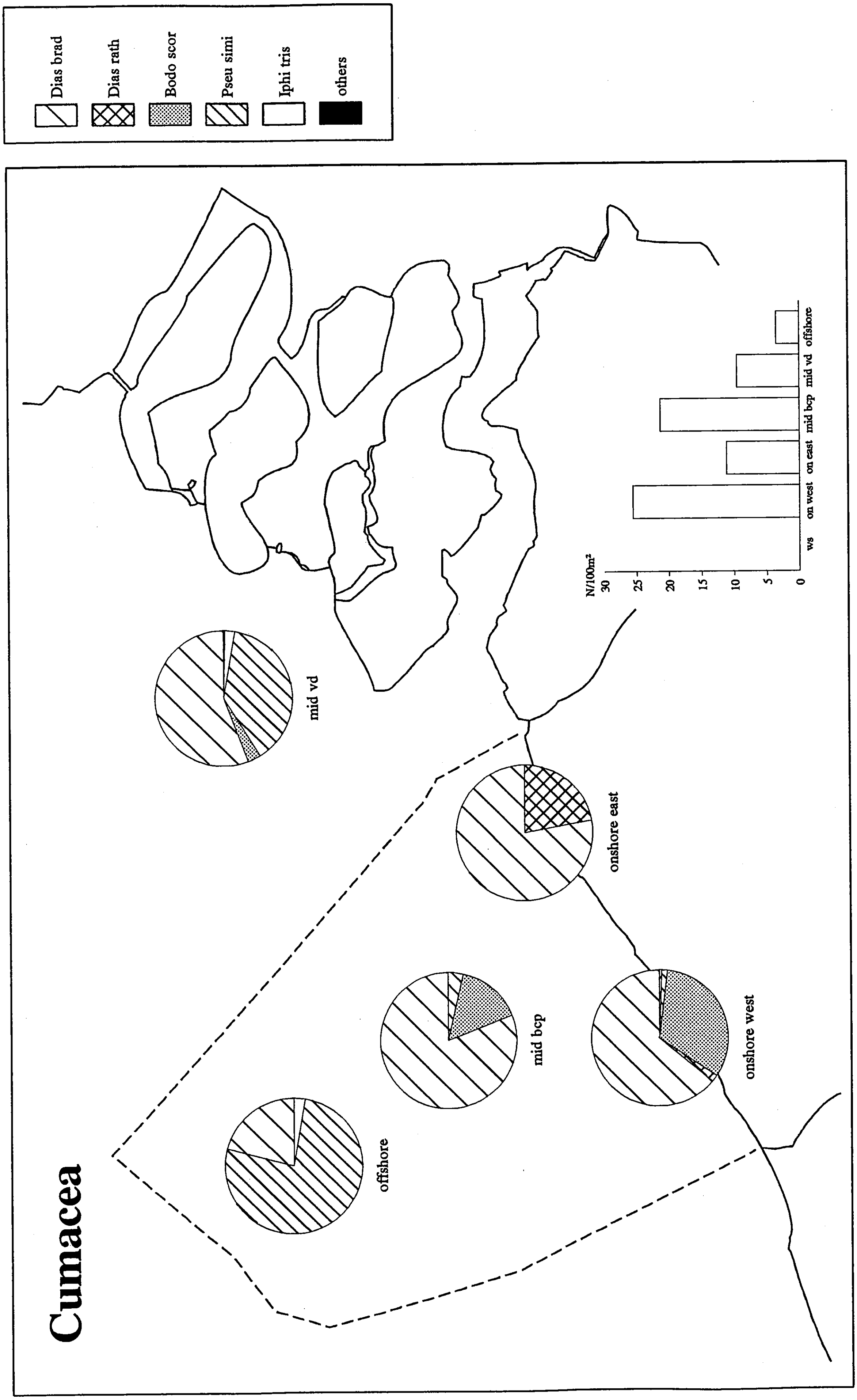

Cumacea
Dias brad
Dias rath
Bodo scor
Pseu simi
Iphi tris
others
mid vd
onshore east
mid bcp
onshore west
offshore
N/100m²
30
25
20
15
10
5
0
ws
on west
on east
mid bcp
mid vd
offshore

FIGURE 18.

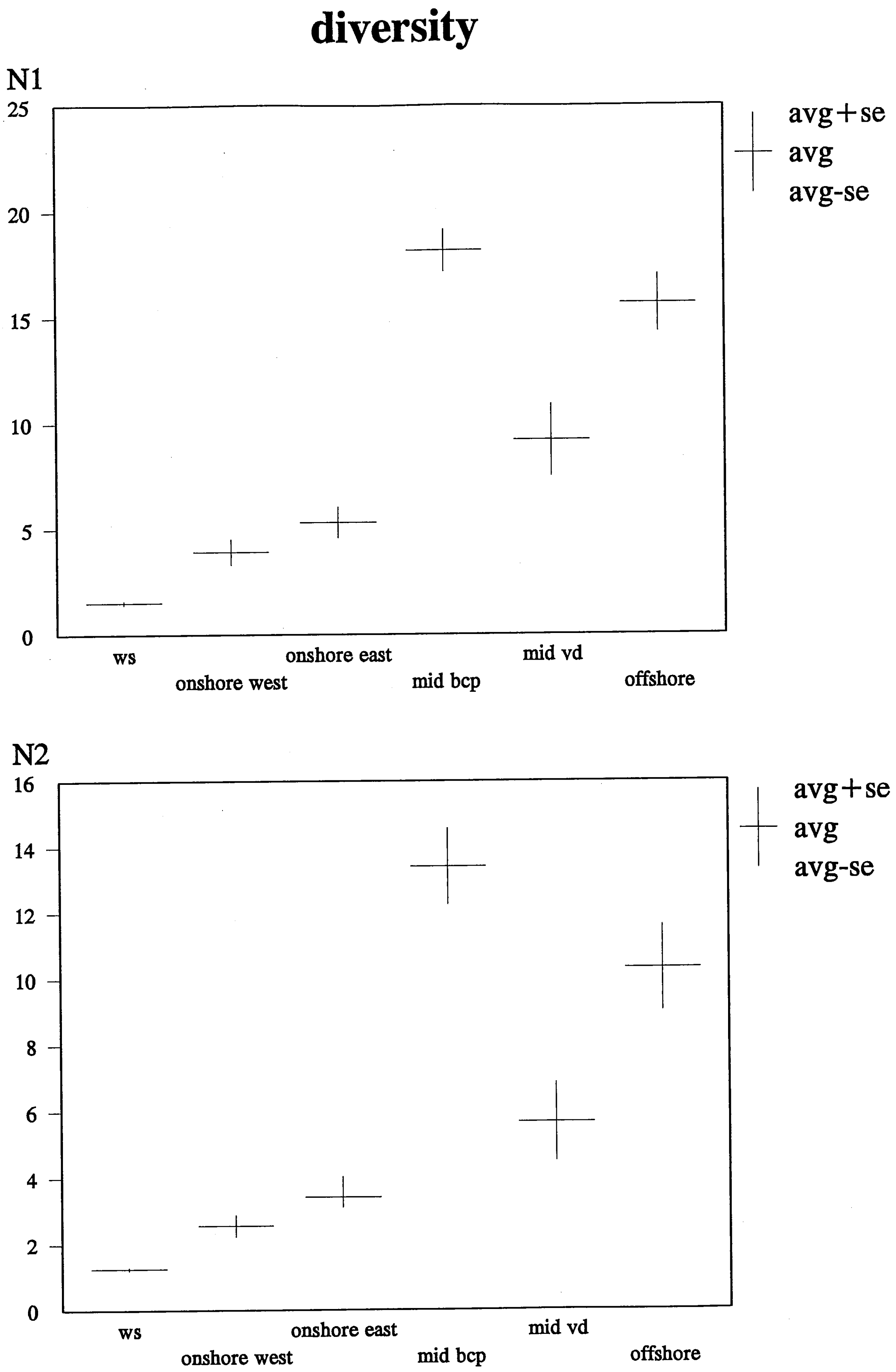
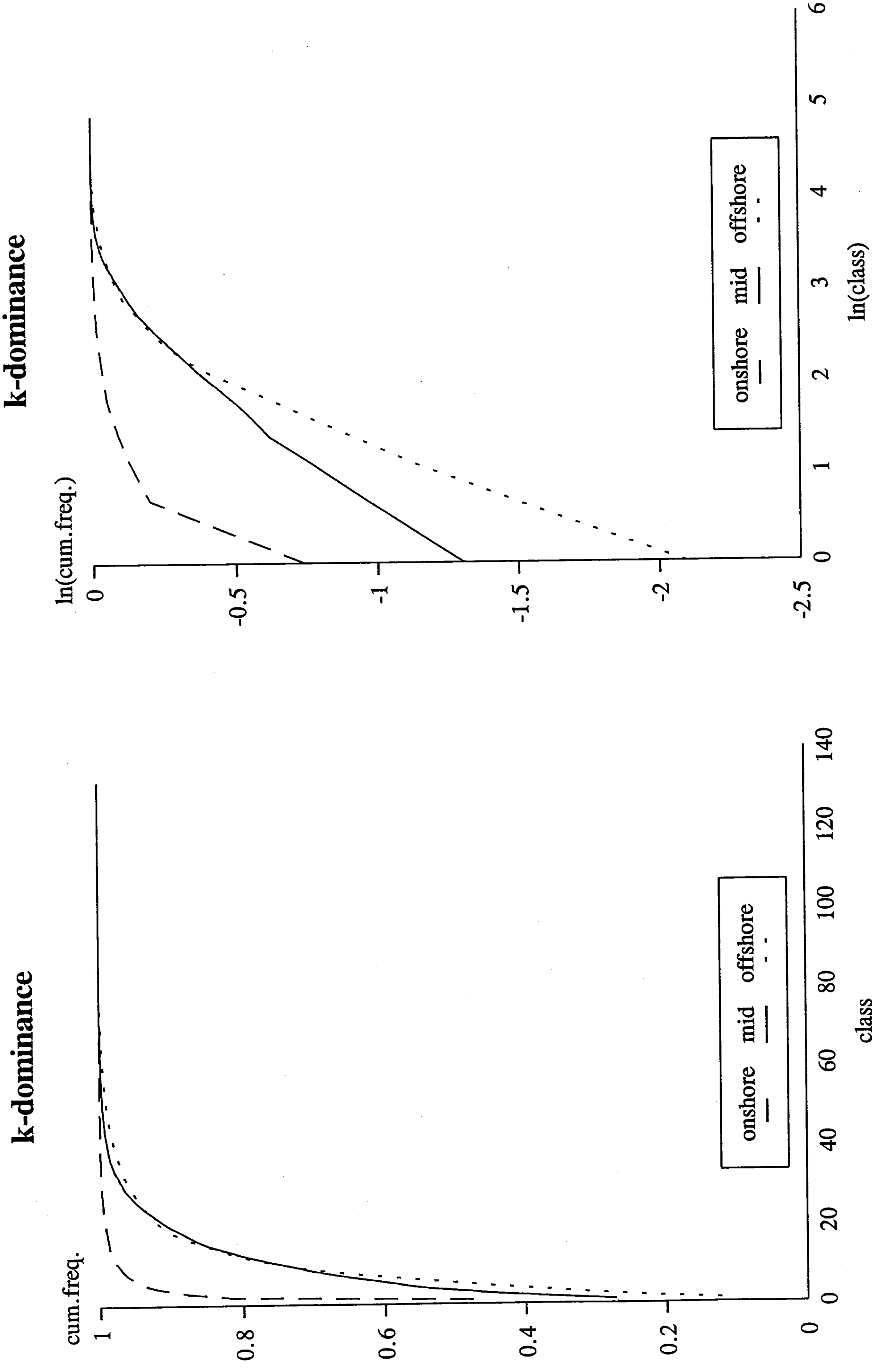

diversity
N1
25
20
15
10
5
0
avg+se
avg
avg-se
ws
onshore west
onshore east
mid bcp
mid vd
offshore
N2
16
14
12
10
8
6
4
2
0
avg+se
avg
avg-se
ws
onshore west
onshore east
mid bcp
mid vd
offshore

FIGURE 19.


k-dominance
ln(cum.freq.)
0
-0.5
-1
-1.5
-2
-2.5
0
1
2
3
4
5
6
ln(class)
onshore
mid
offshore
k-dominance
cum.freq.
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
140
class
onshore
mid
offshore

Temporal patterns in the hyperbenthos of the Belgian continental shelf.

Ann Dewicke & Jan Mees

Marine Biology Section, Zoology Institute, University of Gent
K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

Abstract

The hyperbenthos of 4 stations in the Belgian coastal waters was investigated. Three of these were rather situated onshore, spread along the coastline: station 115s on the east coast near De Panne, station 120 near Nieuwpoort and station 140 on the west coast near Zeebrugge. One site, station 330, was located more offshore.

The samples were taken with a hyperbenthic sledge equipped with four nets (1 mm and 0.5 mm mesh size), covering two lower strata of the watercolumn: 0 to 0.5 meter and 0.5 to 1 meter above the bottom. Trawling (5 minutes at 1.5 knots: approx. 200 meter per trawl) was always done during daytime and against the tide. The sledge was equipped with an automatic opening-closing device, an odometer and a current meter. Several environmental variables (salinity, temperature,...) were recorded at the beginning of each trawl. In addition, sediment and water samples were taken at each station for grain size distribution, nutrient and pigment analyses.

In the laboratory, all animals were identified to species level, counted and measured. Density (numbers per 100 m^2) was calculated and biomass was derived from length-ashfree-dryweight regressions. Density data were subjected to 3 multivariate statistical analyses: a classification (group-average sorting clustering based on the Bray-Curtis dissimilarity index), an ordination (Canonical Correspondance Analysis) and a hybrid technique (Two-way Indicator Species Analysis).

A total of 125 species were recorded in the hyperbenthic fauna of the Belgian coastal area. A strong seasonal variation in density was apparent for several species. The species composition of the hyperbenthic fauna was seasonally altered by the recruitment and disappearence of different temporary hyperbenthic species. The most important members for the permanent hyperbenthos were mysids.

Multivariate analyses yielded more insight into community structure. A discontinuity between onshore and offshore samples was obvious. Temporal patterns strongly dominated the onshore communities (stations 115s, 120 and 140). Three communities could be identified: the first one occurred during winter, the second one during spring and the other community lasted from summer until autumn. Offshore, this seasonal trend wass less pronounced: during the whole year the fauna of station 330 resembled the spring fauna of the onshore stations.

Total density was comparable for the different communities. The winter community was the least diverse and consisted mainly of permanent hyperbenthic species (mysids and amphipods) and the already fairly abundant pelagic fish eggs. A high variety of temporary representatives characterised the spring community: polychaete larvae, larval decapods, and postlarval fish appeared in high densities. Mysids were again dominant in the 'summer-autumn' community, supplemented by cconsiderable densities of temporary hyperbenthic species.

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). To date, no information is available on this ecosystem component in Belgian coastal waters. The aim of this study is to yield insight in the temporal patterns in community structure of the hyperbenthic communities of the Belgian coastal waters. The seasonal variation in density for the permanent and the temporary hyperbenthos is studied. The temporal variability of the communities is described, in terms of species composition, density, biomass and diversity. The observed patterns in community structure are related to some environmental variables, in order to gain more insight into community structure.

2. Methodology

The hyperbenthos of 4 stations in the Belgian coastal waters was investigated. Three of these were rather situated onshore, spread along the coastline: station 115s on the east coast near De Panne, station 120 near Nieuwpoort and station 140 on the west coast near Zeebrugge. One site, station 330, was located more offshore. The sampling sites are shown in figure 1.

All sampling was done from the R.V. Belgica employing a hyperbenthic sledge. This gear consists of a heavy metal frame equipped with four nets (1 mm and 0.5 mm mesh size), covering two lower strata of the watercolumn: 0 to 0.5 meter and 0.5 to 1 meter above the bottom. The sledge is equipped with an automatic opening-closing device, an odometer and a current meter. Trawling (5 minutes at 1.5 knots : approx. 200 meter per trawl) was always done during daylight and against the tide. At the beginning of each trawl, a number of environmental variables were measured: depth, temperature and salinity. A bottom sample was taken with a Reineck boxcore for grain fraction analysis. The water column just above the bottom was sampled with a niskin bottle, for nutrient and pigment analyses.

All organisms were immediately rinsed over the corresponding sieve (1 or O.5 mm) and preserved in formaldehyde, 7 % final concentration. Only the 1 mm samples were investigated for this purpose. In the laboratory all animals were identified, if possible to species level and counted. For the analysis different development stages of decapods (zoeae, megalopae, postlarvae and adults) 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 (ADW). ADW 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 ADW of batches of animals belonging to a certain stage. Density and biomass data were calculated as numbers of individuals (N) and g ADW per 100 m2. All analyses were performed on the density dataset.

Non-hyperbenthic species were eliminated from the dataset. After root-root transformation, density data were subjected to multivariate statistical analyses, in order to define biotic communities. The sampling sites were classified into clusters according to speciescomposition using the classification program TWINSPAN (Hill 1979). To check the stability of the TWINSPAN results and to reveal the degree of similarity between 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 speciescomposition and the environmental variables measured at each site was analysed using a CCA option from the program package CANOCO (Ter Braak 1988).

Diversity was investigated as Hill's diversity numbers (Hill 1973). Different indices (N_0, N_1 N_2 and N_∞) were calculated per station, their average with standard error was computed per season.

To focus on spatial differences in diversity, k-dominance curves (Lambshead *et al.* 1983) were constructed per station. The logarithm of the cumulative percentage (the percentage of total abundance made up by the kth dominant species and all more dominant species) was plotted against the logarithm of the rank k. In graphs of the species abundance distribution the number of species represented by 0, 1, 2,... individuals were plotted against logarithmic density classes.

3. Results

3.1. Exploration of the datamatrix

A total of 175 species were recorded. The complete specieslist with the identification levels and the developmental stages considered as separate 'functional species' is given in table 1. Accidentally caught epibenthic (e.g. demersal fish, adults of crabs, shrimps and echinoderms) and endobenthic (e.g. adult polychaetes and bivalves) organisms, as well as adult pelagic fish and true planktonic animals (Cnidaria and Ctenophora) were excluded from the dataset. After these corrections, the datamatrix was reduced to 125 species. Rare polychaete larvae, nudibranchs, the free-living stages of the ectoparasitic

Caligidae and Piscicolidae were not identified to species level. The amphipod species of the genus *Bathyporeia* were pooled as *Bathyporeia* species. Juveniles of the genus *Apherusa* were not further identified and recorded as such. Determination of larval decapods was often complicated, in those cases records were made on genus or family level. Two crab larvae could not be identified and were registered as 'Brachyura species zoea type 1' and 'Brachyura species megalopa type 1'. Pelagic fish eggs were not identified in more detail. If determination of pipefish wasn't possible, they were recorded as Syngnathidae species (probably a mixture of *Syngnathus acus* and *S. rostellatus*). Small postlarval fish were often difficult to identify, in those cases registration was done on genus (e.g. *Pomatoschistus* species) or family level (e.g. Clupeidae species and Ammodytidae species).

Most species showed a strong seasonal variation in density. A distinction has been made between the temporary hyperbenthos, i.e. animals that spend only part of their life cycle in the hyperbenthos, and the permanent hyperbenthos, i.e. animals that spend most of their life cycle in the hyperbenthos.

The most important members of the permanent hyperbenthos were the Mysidacea, 12 species were catched in total. Figure 2 shows the temporal variability in density of the 4 most abundant mysid species (averaged over the 3 onshore stations). *Schistomysis kervillei* and *S. spiritus* had two clear peaks in abundance: one in winter and one in summer. *Gastrosaccus spinifer* showed two abundance peaks as well. The first one felt earlier than for the former species, namely in late autumn, the second one in spring. The seasonal pattern for *Mesopodopsis slabberi* was more erratic, this species never reached high densities. In figure 3 the absolute densities for some mysid species are per month represented, as well. *Schistomysis kervillei* was the most common mysid for the Belgian coast, a maximum density of 1046N/100m^2 was reached in july. *Gastrosaccus spinifer* and *Schistomysis spiritus* could also be quite important, maximum densities were resp. 356N/100m^2 (june) and 92N/100m^2 (july). Other frequent occurring taxa belonging to the permanent hyperbenthic fauna were the cumaceans, amphipods and isopods. The seasonal variation of some common species is represented in figure 3.

Larval decapods, polychaete larvae, fish eggs and postlarval fish were the main representatives of the temporary hyperbenthos. Their appearance, high abundance and disappearance in the hyperbenthic layer was often striking, especially for fish larvae. In figure 4 the seasonal variation in abundance of some fish larvae is represented. The earliest recruitment peak for larval flatfish in the hyperbenthic layer occurred in the month april by *Pleuronectes flesus*. In may the postlarvae of *Limanda limanda* and *Solea solea* peaked, although the recruitment of the latter species was spread over a wider period. The recruitment of clupeids started already during winter (in december) and lasted till june, peak densities were recorded in may. Postlarval gobies were found the whole year, although the highest abundances were recorded from may until july. The seasonal occurrence of different development stages of larval decapods is illustrated in figure 5 and is not further discussed here.

3.2. Environmental variables

The temporal fluctuation of the main environmental variables is presented in the figures 6 and 7 .

Temperature ranged from 8°C in february and march, to 20°C in july. Station 140 is situated close to the mouth of the Westerschelde estuary and was still influenced by tidal rhytm as can be derived from the salinity curve. Median grain size and % mud showed a yearly variation, but during the whole year the coarsest sand was present at station 330. Two periods of higher chlorophyl a content could be found during the year: a first peak in autumn, and a second higher peak in spring. There were no marking differences for the 4 stations, except station 330 behaved somewhat different. The following nutrients were extracted: NO_3-N, PO_4-P and SiO_3-Si. Their yearly variation gives a similar picture: nutrient concentrations were much higher in autumn and early winter than during the rest of the year. A difference between onshore (stations 115s, 120, 140) and offshore (station 330) waters can be noticed here, much lower values were reached in the latter area. Nitrate and Phosphate content was slightly higher for station 140 in comparison to the stations 115s and 120.

3.3. Community analysis

Multivariate analyses were performed on the densities of the onshore (stations 115s, 120 and 140) and offshore samples together (station 330). Since there is a sharp discontinuity in community structure between onshore and offshore waters (see task G), more detailed analysis were done on the onshore samples only (with elimination of station 330).

onshore and offshore samples

The result of the TWINSPAN analysis (cutlevels 0, 0.94, 1.18, 1.53, 2.2, 2.8) performed on the density data of the integral dataset is presented in figure 8. The first division is both spatial and temporal. At the left arm of the dendrogram most of the samples of station 330 are found (except dec 330), together with the spring samples (apr, may, jun) for the stations 115s, 120 and 140 (except jun 120). The second division for this cluster 'offshore + spring onshore' is temporal: all spring samples group together (except jun 330) and the remaining samples of 330 form one group. At the right arm of the dendrogram all the samples of the stations 115s, 120 and 140, for the months july till march (except jul 115s) are located. Further temporal patterns become evident at the next division and the winter samples (dec, feb, mar) are separated from the summer-autumn samples (jul, sep, oct, nov).

The dendrogram for the cluster analysis is comparable with the TWINSPAN output (figure 9). The fauna of station 330 is the whole year highly similar to the fauna of the spring samples of the other stations. For the onshore stations, the strong temporal dominance is apparent.

The ordination plane formed by the first (eigenvalue 0.193) and second canonical axis (eigenvalue 0.168) is presented in figure 10. Both axes are of equal importance, since they have comparible eigenvalues. The spread along the first axis reveals temporal patterns. In the left half of the diagram the samples from june to december are found, the samples from february to may are plotted in the right half. A spatial division between onshore and offshore samples becomes clear along the second axis: all samples of station 330 are plotted at the bottom half. The forward selection option of CANOCO revealed three variables that explained a significant amount of variance in the species data: temperature, silicate and median grain size (in this sequence). Temperature shows the highest correlation with the first axis and characterises the temporal structure. Silicate and median grain size give some information about the spatial pattern: the offshore stations are characterised by lower silicate concentrations and a coarser sand fraction.

onshore samples

The result of the TWINSPAN analysis (cutlevels 0, 0.92, 1.1, 1.43, 2.2, 2.85) for the onshore samples is presented in figure 11. The first division is a temporal one: the spring samples are separated from the other samples. At the second division level one can identify a winter cluster and a summer-autumn cluster. Temporal patterns seem to be very dominant onshore, even at further divisions no clear spatial patterns emerge.

The dendrogram yield by the KLUS analysis (figure 12) is not completely conform with the above result. Here the fauna of the winter samples shows the highest dissimilarity with the other samples. Still, the strong dominance of the temporal patterns over the spatial ones is clear.

This strong temporal effect is also visualised by the ordination plot (figure 13) formed by the first (eigenvalue 0.2095) and the second axis (eigenvalue 0.1570). The subsequent months are spread anticlockwise over the ordination plane. With the forward selection option is showed that temperature, silicate and salinity could explain the underlying structure significantly. There is no clear correlation of the higher defined clusters and a single environmental variable. Therefore the effect of temperature was eliminated to reveal other patterns. A second CCA analysis was performed on the same dataset, with temperature as covariable.

The CCA ordination plane formed by the first (eigenvalue 0.188) and second axis (eigenvalue 0.132) is presented in figure 14. Two variables were significant in declaring the underlying structure: silicate and salinity. A marking trend appears: all the samples of station 140 are plotted at the top half of the diagram and coincide with a high silicate concentration and a low salinity.

3.4. Characterisation of the communities (onshore samples)

Since the fauna of station 330 differed distinctly in community structure with the onshore stations, those samples were eliminated here. Attention was focused on the temporal trends of the faunistic composition in onshore waters. Three clusters could be identified based on the TWINSPAN output (for the onshore stations). The core of the 'summer-autumn' community were the autumn samples (sep, oct, nov) and the samples of july, the only sampled month during summer. Samples of the months december, february and march constituted the 'winter' community. The spring community consisted of the april, may and june samples.

The faunistic composition and density is per community presented in figure 15 at taxonomic level and in figure 16 at specieslevel.

For the 'summer-autumn' community the Mysidacea, Amphipoda and Caridea dominated the hyperbenthic fauna. The most common species were *Schistomysis kervillei* (29N/100m2), *Gammarus crinicornis* (21 N/100m^2) and postlarvae of *Crangon crangon* (16N/100m^2).

Fish eggs were highly abundant in the 'winter' community. Those members of the temporary hyperbenthos appeared early in the year, in high numbers. Since their consideration as hyperbenthos can be discussed, this group can also be excluded from the hyperbenthos. Other characteristics will be revealed then and permanent hyperbenthic species would constitute the 'winter' community nearly exclusively. Mysids will then clearly be dominating, again with *Schistomysis kervillei* (30N/100m^2) as most important species.

The 'spring' community was characterised by a strong presence of temporal hyperbenthic species. The aulophora larvae of *Lanice conchilega* reached the highest densities here (33N/100m^2). Mysids' density decreased in comparison with the other communities. The postlarvae of *Crangon crangon*, some postlarval flatfish and crab larvae gained in importance.

3.5. Diversity

Hill's diversity numbers N_1 and N_2 were calculated per station and averaged per community (figure 17). There was a striking seasonal pattern for all the stations: the hyperbenthic fauna was the least divers during winter. No sharp spatial discontinuity in diversity could be found, except for the spring samples. They showed a wider variation in diversity between the different stations.

K-dominance curves were constructed per station, for all monthly samples together. They are represented in figure 17 . Station 330 behaves different than the onshore stations: the intersection of the curve with the y-axis is much higher. This means that over the whole year, the highest number of species occurred at the onshore stations (stations 115s, 120 and 140), probably caused by the recruitment and disappearance of different temporary hyperbenthic species. The feature of the strong seasonal dominance in community structure in onshore waters is here again emphasized.

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FIGURE 1.

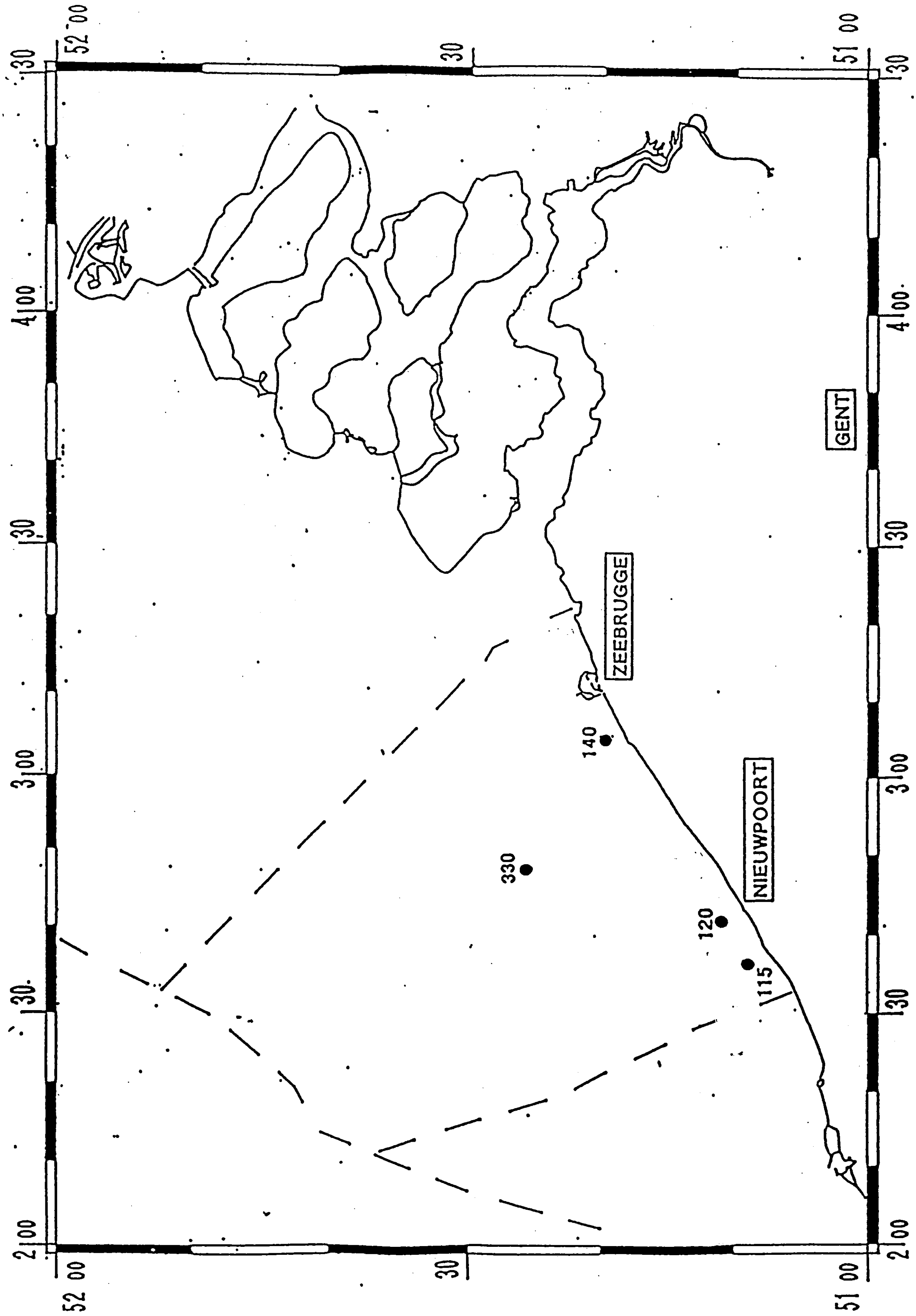

52 00
30
51 00
2 00
30
3 00
30
4 00
30
ZEEBRUGGE
NIEUWPOORT
GENT
140
330
120
115

Table 1: List of species caught with the hyperbenthic sledge on the Belgian continental shelf with the abbreviations used. Species marked with * were excluded from all analysis.

taxon	species and stage	abbreviation
Phylum Porifera		
	Porifera species	Pori Spec*
Phylum Cnidaria		
Class Hydrozoa		
	Sarsia species medusa	Sars SpME*
	Bougainvillia species medusa	Boug SpME*
	Mitrocomella species medusa	Mitr SpME
	Eutima gracilis medusa ?	Euti grME*
	Eutonina indicans medusa ?	Euto inME*
	Hydrozoa species polyp	Hydr SpPO *
Class Scyphozoa		
	Chrysaora hysoscella medusa	Chry hyME*
Class Anthozoa		
	Anthozoa species	Anth Spec *
Phylum Ctenophora		
Class Tentaculata		
Order Cydippida		
	Pleurobrachia pileus	Pleu pile*
Class Nuda		
Order Beroida		
	Beroë species	Bero Spec*
Phylum Nematoda		
	Nematoda species	Nema Spec*
Phylum Mollusca		
Class Gastropoda		
Subclass Prosobranchia		
	Patella species	Pate Spec*
	Prosobranchia species	Pros Spec *
Subclass Opisthobranchia		
Order Nudibranchia		
	Nudibranchia species	Nudi Spec
Class Bivalvia		
	Bivalvia species	Biva Spec*
Class Cephalopoda		
Subclass Coleoidea		
	Sepiola atlantica juvenile	Sepi atJU
	Loligo vulgaris juvenile	Loli vuJU
Phylum Annelida		
Class Polychaeta		
	Harmothoë species larva	Harm SpLA
	Lanice conchilega	Lani conc*
	Lanice conchilega aulophora larva	Lani coLA
	Polychaeta species	Poly Spec*
	Polychaeta species larva	Poly SpLA
Class Hirudia		
	Piscicolidae species	Pisc Spec
Phylum Arthropoda		
Subphylum Chelicerata		
Class Pycnogonida		
	Anoplodactylus petiolatus	Anop peti
Subphylum Crustacea		
Class Copepoda		
Order Calanoida		
	Calanus helgolandicus	Cala helg
	Temora longicornis	Temo long
	Centropages typicus	Cent typi
	Centropages hamatus	Cent hama
	Candacia armata	Cand arma
	Labidocera wollastoni	Labi woll
Order Siphonostomatoida		
	Caligus species	Cali Spec
Class Malacostraca		
Order Euphausiacea		
	Nyctiphanes couchi	Nyct couc
Order Decapoda		
Infraorder Caridea		
	Palaemonidae species zoea	Pala SpZO
	Hippolyte varians	Hipp vari*
	Hippolyte varians postlarva	Hipp vaPO
	Hippolyte varians zoea	Hipp vaZO
	Thoralus cranchii	Thor cran*
	Thoralus cranchii postlarva	Thor crPO
	Processa edulis crassipes	Proc edul*
	Processa species zoea	Proc SpZO
	Pandalina brevirostris postlarva	Pand brPO
	Pandalus propinquus postlarva	Pand prPO
	Crangon allmanni	Cran allm*
	Crangon crangon	Cran cran*
	Crangon crangon postlarva	Cran crPO
	Philocheras trispinosus	Phil trisp*
	Philocheras trispinosus postlarva	Phil trPO
	Crangonidae species zoea	Cran SpZO
Infraorder Thalassinidea		
	Upogebia species postlarva	Upog SpPO
	Upogebia species zoea	Upog SpZO
Infraorder Anomura		
	Galathea intermedia postlarva	Gala inPO
	Galathea species zoea ?	Gala spZO
	Pisidia longicornis juvenile	Pisi loJU
	Pisidia longicornis postlarva	Pisi loPO
	Pisidia longicornis zoea	Pisi loZO
	Pagurus bernhardus zoea	Pagu beZO
	Pagurus prideauxi zoea	Pagu prZO
	Paguridae species	Pagu Spec*
	Paguridae species juvenile	Pagu SpJU
	Paguridae species postlarva	Pagu SpPO
Infraorder Brachyura		
	Hyas coarctatus megalopa	Hyas coME
	Hyas species juvenile	Hyas SpJU
	Macropodia species	Macr Spec
	Macropodia species juvenile	Macr SpJU
	Macropodia species megalopa	Macr SpME
	Macropodia species zoea	Macr SpZO
	Cancer pagurus megalopa	Canc paME
	Corystes cassivelaunus	Cory cass*
	Corystes cassivelaunus juvenile	Cory caJU
	Corystes cassivelaunus megalopa	Cory caME
	Liocarcinus holsatus	Lioc hols*
	Liocarcinus holsatus juvenile	Lioc hoJU
	Liocarcinus arcuatus	Lioc arcu*
	Liocarcinus arcuatus juvenile	Lioc arJU
	Liocarcinus species megalopa	Lioc SpME
	Liocarcinus species zoea	Lioc SpZO
	Carcinus maenas megalopa	Carc maME
	Carcinus maenas zoea	Carc maZO
	Portumnus latipes juvenile	Port la JU
	Portumnus latipes megalopa	Port laME
	Pilumnus hirtellus juvenile	Pilu hiJU
	Pilumnus hirtellus megalopa	Pilu hiME
	Pinnotheres pisum	Pino pisu*
	Ebalia cranchii	Ebal cran*
	Ebalia species megalopa	Ebal SpME
	Brachyura species zoea type1	Brac S1ZO
	Brachyura species megalopa type1	Brac S1ME
Superorder Peracarida		
Order Mysidacea		
	Siriella armata	Siri arma
	Siriella clausii	Siri clau
	Gastrosaccus spinifer	Gast spin
	Anchialina agilis	Anch agil
	Leptomysis lingvura	Lept ling
	Mysidopsis gibbosa	Mysi gibb
	Schistomysis spiritus	Schi spir
	Schistomysis kervillei	Schi kerv
	Paramysis arenosa	Para aren
	Mesopodopsis slabberi	Meso slab
	Neomysis integer	Neom inte
	Acanthomysis longicornis	Acan long
Order Cumacea		
	Cumopsis species	Cumo Spec
	Bodotria scorpioides	Bodo scor
	Bodotria species	Bodo Spec
	Pseudocuma longicornis	Pseu long
	Pseudocuma similis	Pseu simi
	Hemilamprops rosea	Hemi rose
	Diastylis bradyi	Dias brad
	Diastylis rathkei	Dias rath
Order Amphipoda		
Suborder Gammaridea		
	Orchomene nana	Orch nana
	Ampelisca brevicornis	Ampe brev
	Amphilochus neapolitanus	Amph neap
	Leucothoe incisa	Leuc inci
	Stenothoe marina	Sten mari
	Gammarus crinicornis	Gamm crin
	Gammarus locusta	Gamm locu
	Melita obtusata	Meli obtu
	Melita palmata	Meli palm
	Bathyporeia species	Bath spec
	Urothoe poseidonis	Urot pose
	Perioculodes longimanus	Peri long
	Pontocrates altamarinus	Pont alta
	Megaluropus agilis	Mega agil
	Melphidipella macra	Melp macr
	Apherusa ovalipes	Aphe oval
	Apherusa species	Aph Spec
	Atylus falcatus	Atyl falc
	Atylus swammerdami	Atyl swam
	Aora typica	Aora typi
	Microprotopus maculatus	Micr macu
	Corophium ascherusicum	Coro asch
	Corophium volutator	Coro volu
	Jassa falcata	Jass falc
	Dyopedos monacanthus	Dyop mona
Suborder Hyperiidea		
	Hyperia galba	Hype galb
Suborder Caprellidea		
	Phtisica marina	Phti mari
	Pariambus typicus	Pari typi
	Caprella linearis	Capr line
Order Isopoda		
Suborder Flabellifera		
	Eurydice pulchra	Eury pulc
Suborder Valvifera		
	Idotea linearis	Idot line
	Idotea pelagica	Idot pela
Phylum Chaetognatha		
	Sagitta elegans	Sagi eleg
Phylum Echinodermata		
Subphylum Asterozoa		
Class Asteroidea		
	Asterias rubens	Aste rube*
Class Ophiuroidea		
	Ophiuroidea species	Ophi Spec*
Subphylum Echinozoa		
Class Echininoidea		
	Echinoidea species	Echi Spec*
Phylum Chordata		
Subphylum Vertebrata		
Class Osteichthyes		
	Pisces species egg	Pisc SpEG
	Clupea harengus	Clup hare*
	Sprattus sprattus	Spra spra*
	Clupeidae species postlarva	Clup SpPO
	Merlangius merlangus postlarva	Merl mePO
	Trisopterus luscus	Tris lusc*
	Trisopterus luscus postlarva	Tris luPO
	Syngnathus acus	Syng acus*
	Syngnathus rostellatus	Syng rost*
	Syngnathidae species	Syng Spec*
	Syngnathidae species postlarva	Syng SpPO
	Agonus cataphractus	Agon cata*
	Trachurus trachurus postlarva	Trac trPO
	Ammodytes tobianus	Ammo tobi*
	Hyperoplus lanceolatus	Hype lanc*
	Ammodytidae species postlarva	Ammo SpPO
	Callionymus lyra	Call lyra*
	Callionymus lyra postlarva	Call lyPO
	Pomatoschistus minutus	Poma minu*
	Pomatoschistus lozanoi	Poma loza*
	Pomatoschistus pictus	Poma pict*
	Pomatoschistus species postlarva	Poma SpPO
	Pleuronectes platessa	Pleu plat*
	Pleuronectes platessa postlarva	Pleu plPO
	Limanda limanda	Lima lima*
	Limanda limanda postlarva	Lima liPO
	Pleuronectes flesus postlarva	Pleu flPO
	Solea solea	Sole sole*
	Solea solea postlarva	Sole soPO
	Buglossidium luteum	Bugl lute*
	Diplecogaster bimaculata postlarva	Dipl biPO
Miscellaneous		
	Miscellaneous	Misc ella*

Permanent hyperbenthos

Seasonal variation of the density of mysids

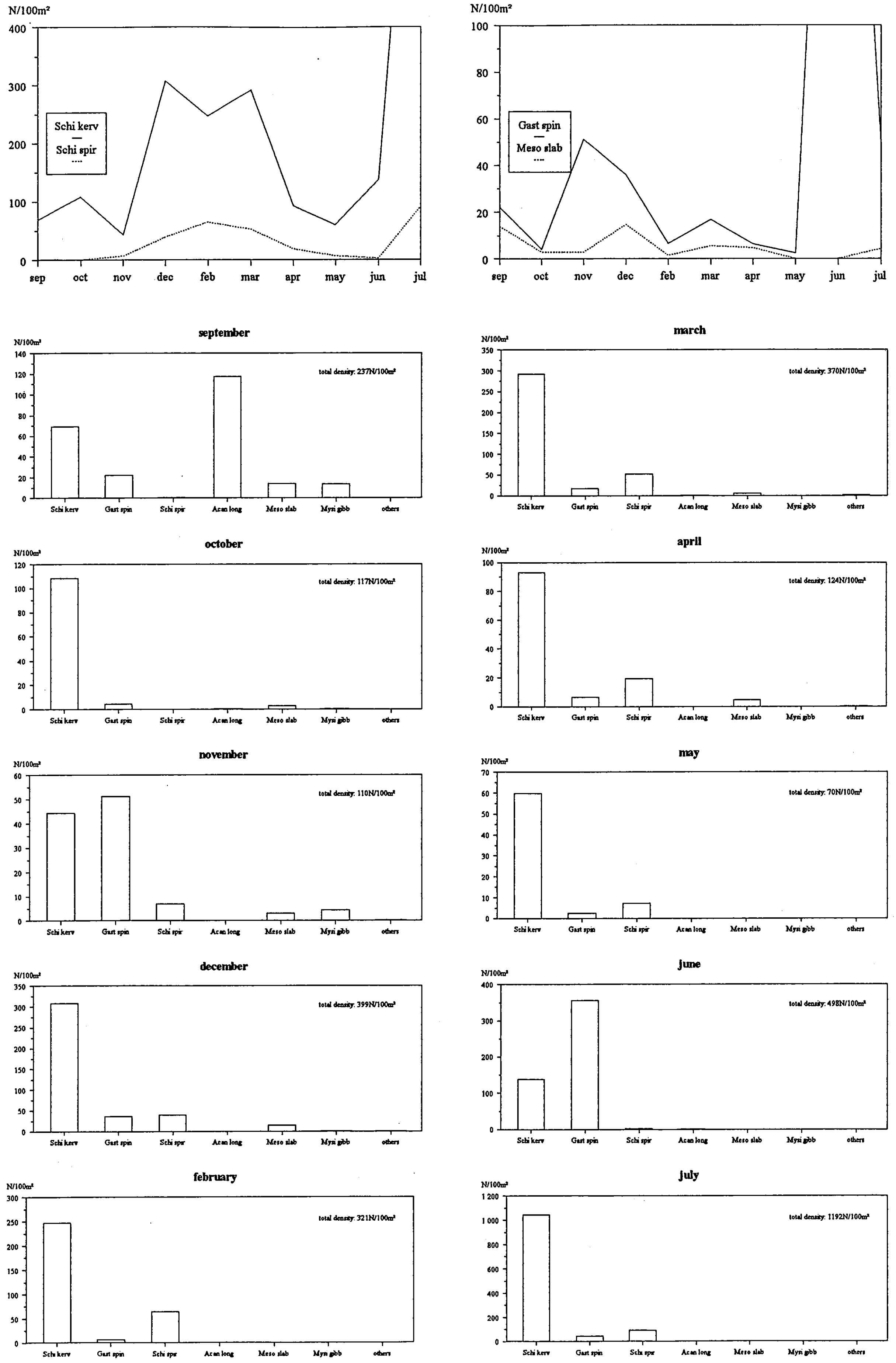
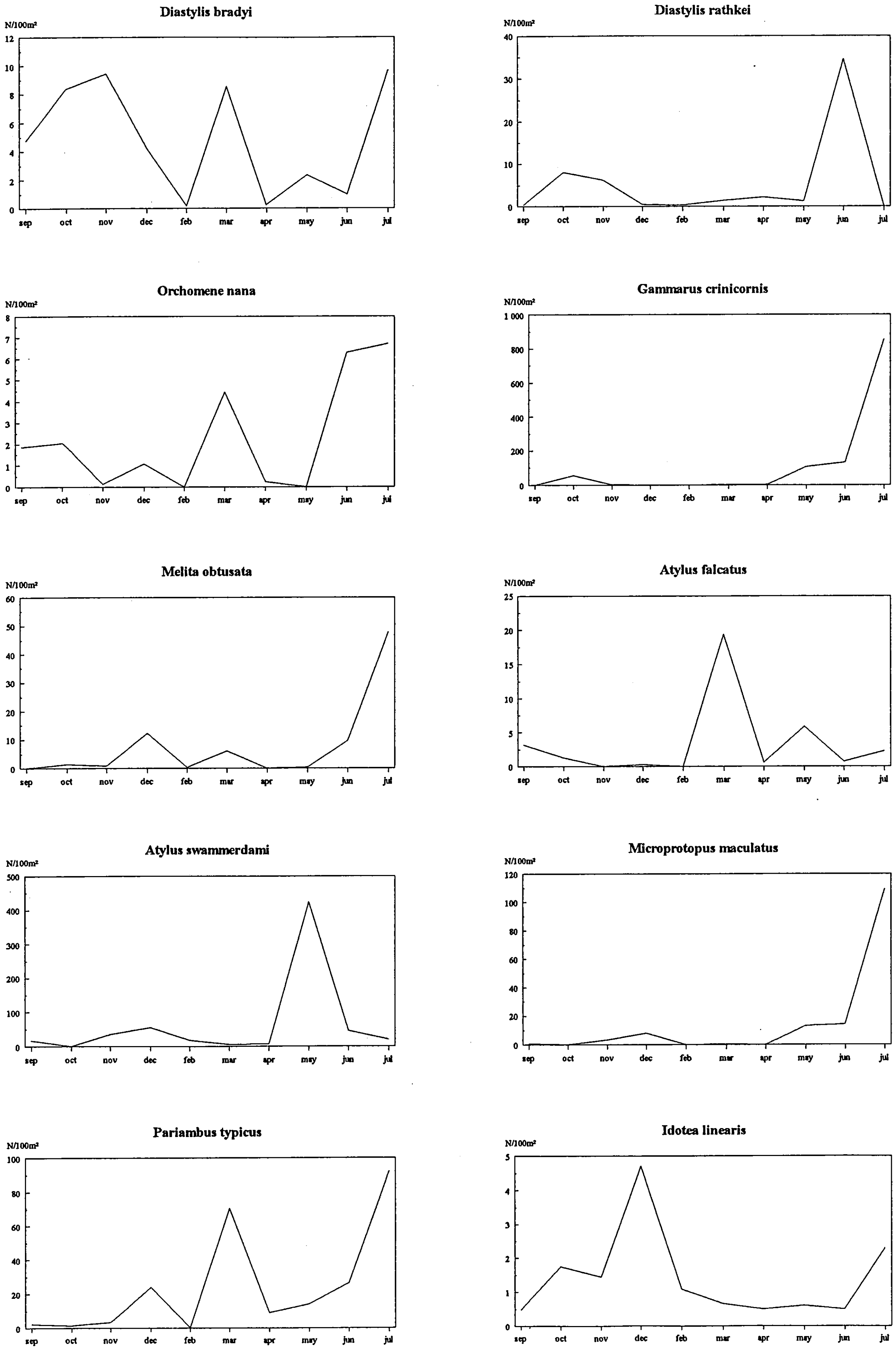


FIGURE 3.

Permanent hyperbenthos

Seasonal variation of the density of cumaceans, amphipods and isopods



Temporary hyperbenthos

Seasonal variation of the density of postlarval fish

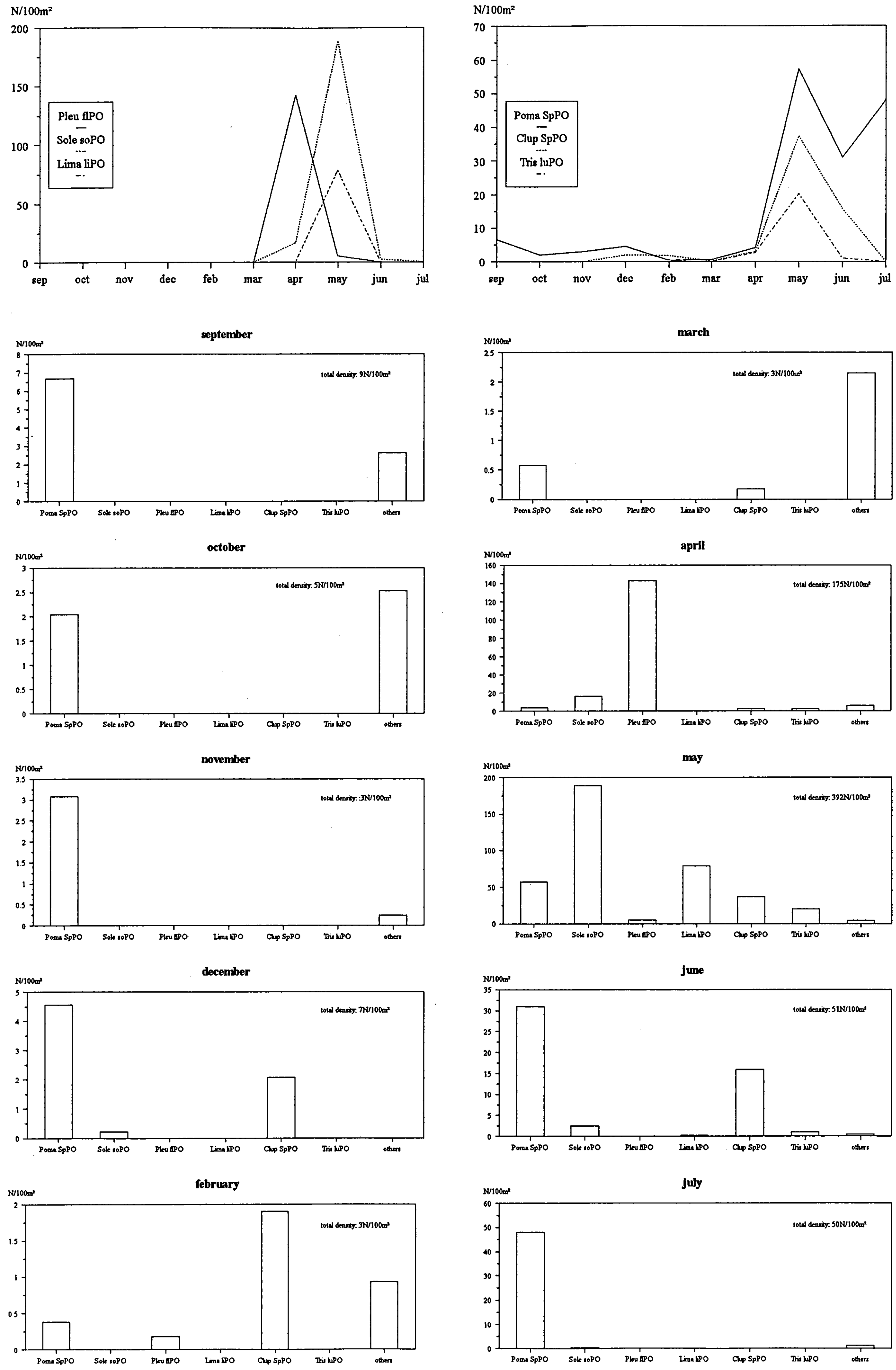
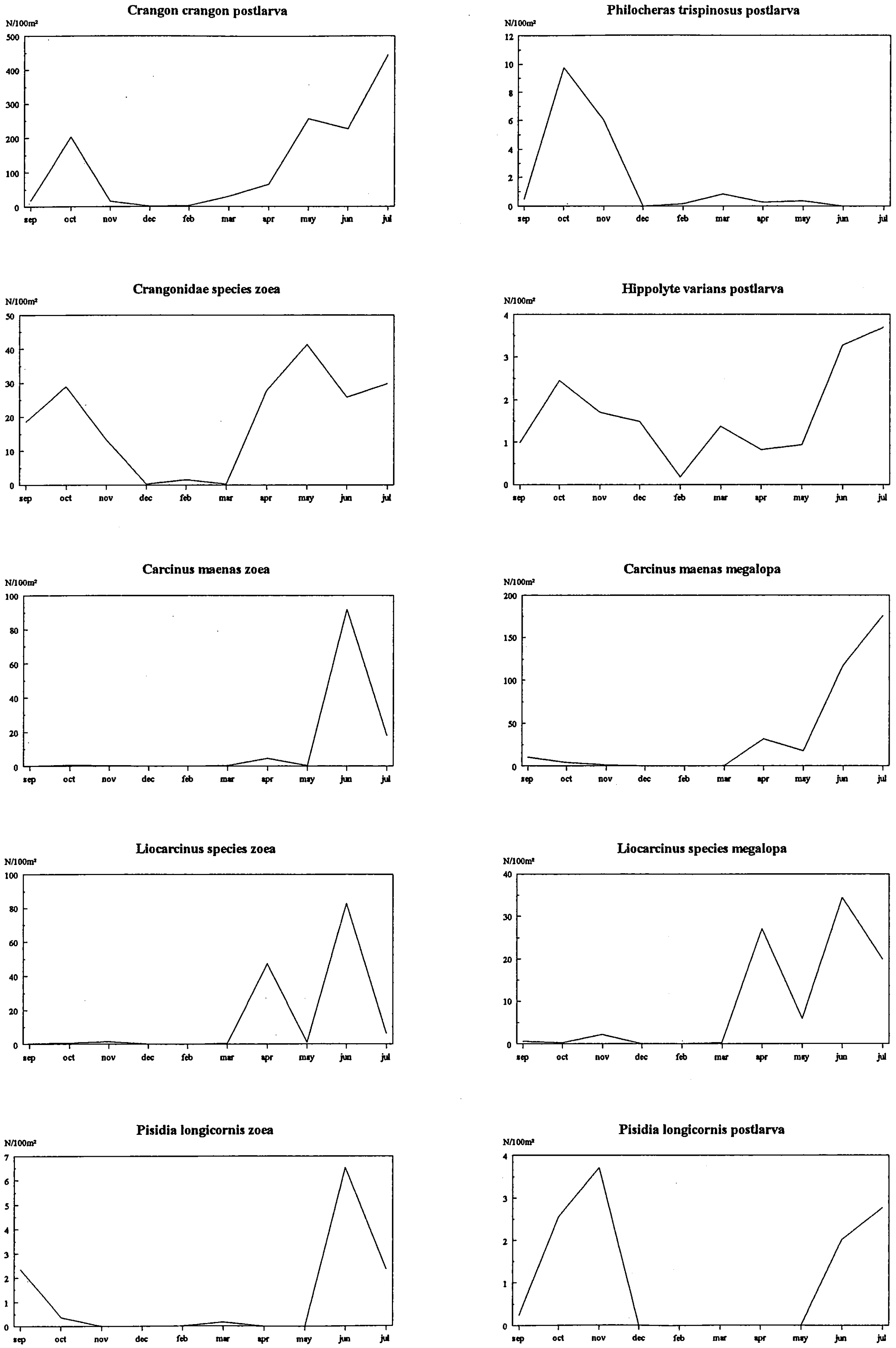


FIGURE 5.

Temporary hyperbenthos

Seasonal variation of the density of decapod larvae



Crangon crangon postlarva

Philocheras trispinosus postlarva

Crangonidae species zoea

Hippolyte varians postlarva

Carcinus maenas zoea

Carcinus maenas megalopa

Liocarcinus species zoea

Liocarcinus species megalopa

Pisidia longicornis zoea

Pisidia longicornis postlarva

FIGURE 6.

Temporal fluctuation of some measured environmental variables

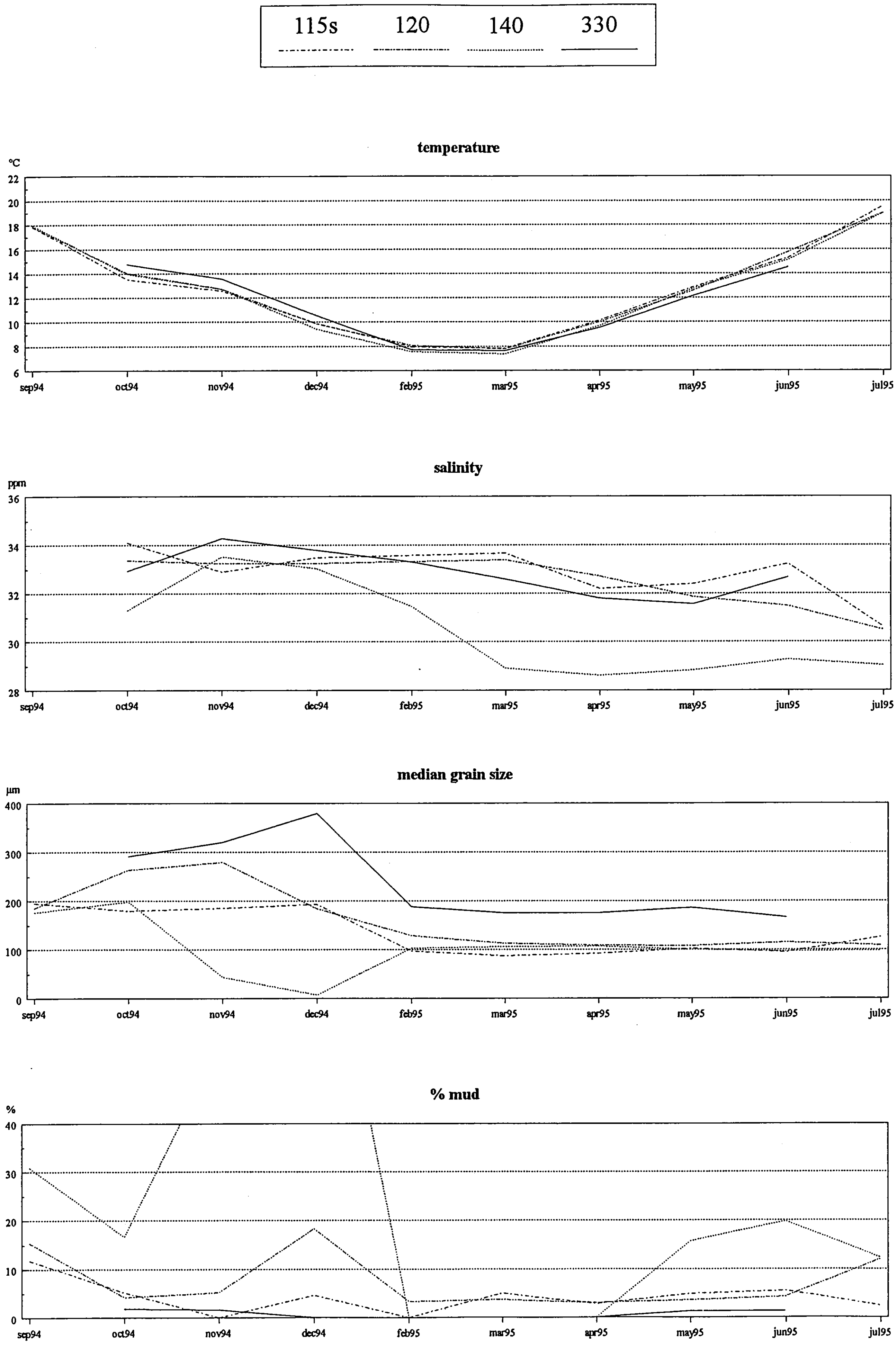


FIGURE 7.

Temporal fluctuation of some measured environmental variables

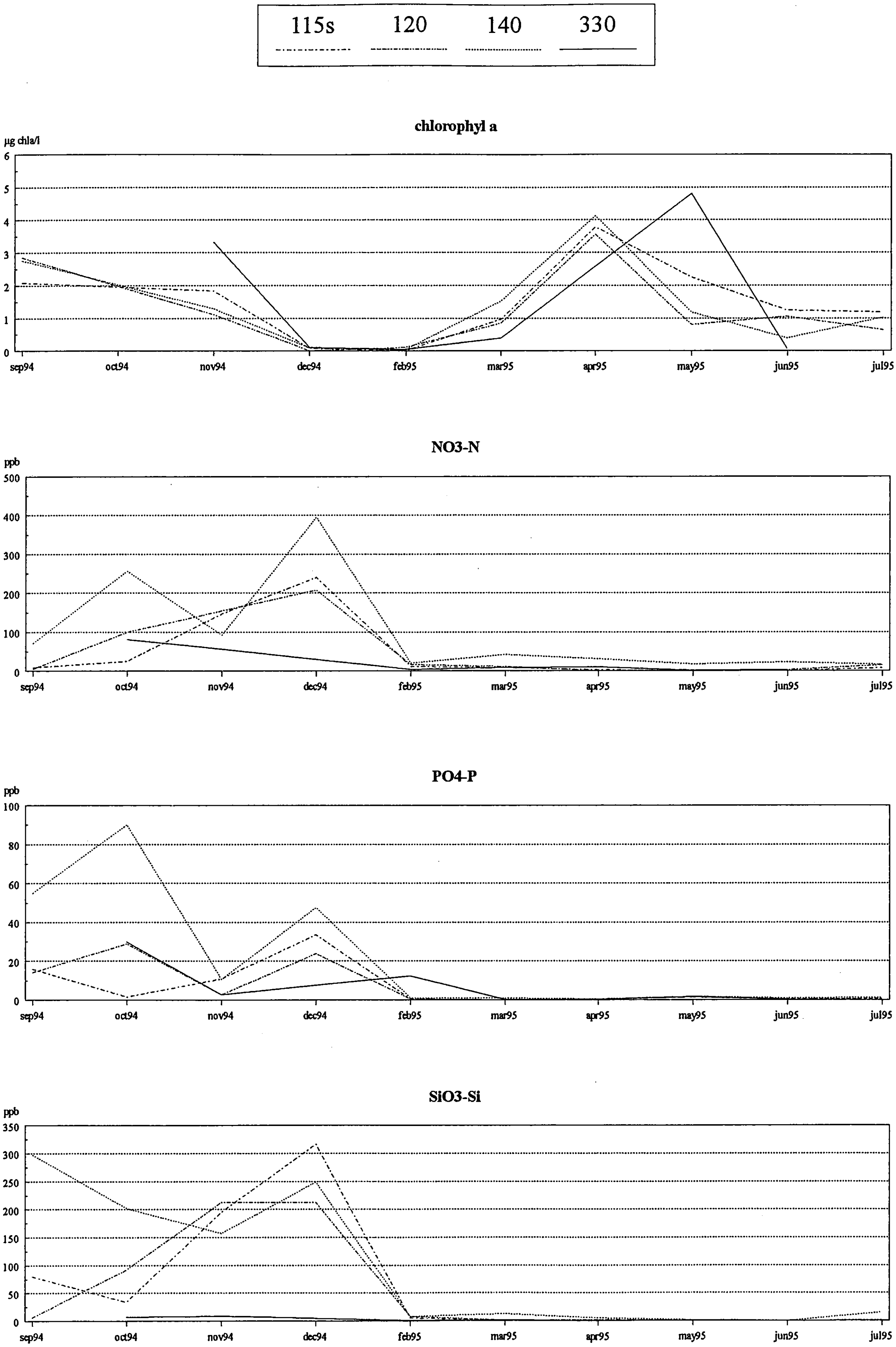


FIGURE 8.

ONSHORE STATIONS (density data)

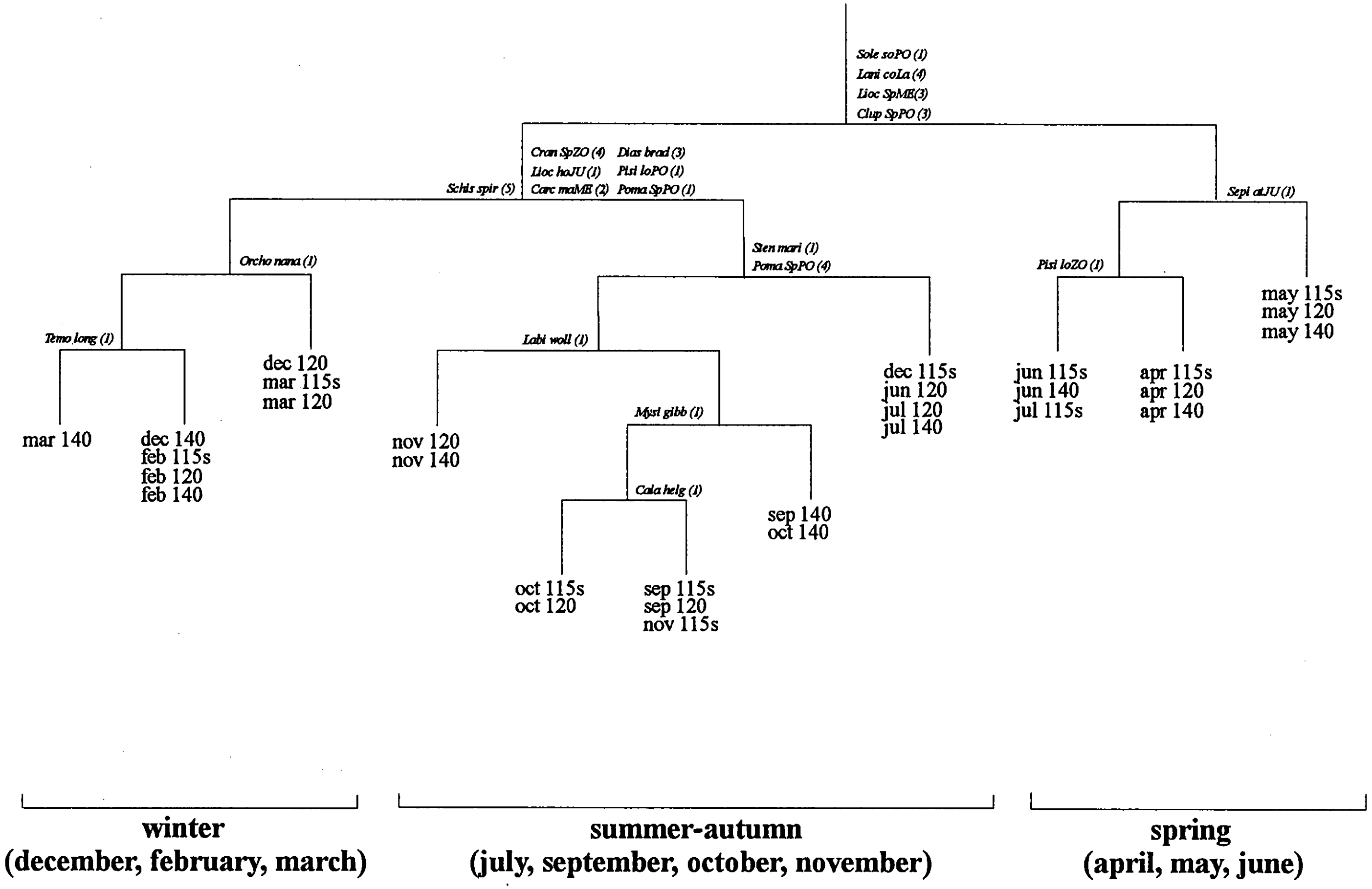


FIGURE 9.

HYPERBENTHOS BCP - yearcycle 1994-1995
density (onshore + offshore stations)
Bray-Curtis similarity, group average sorting

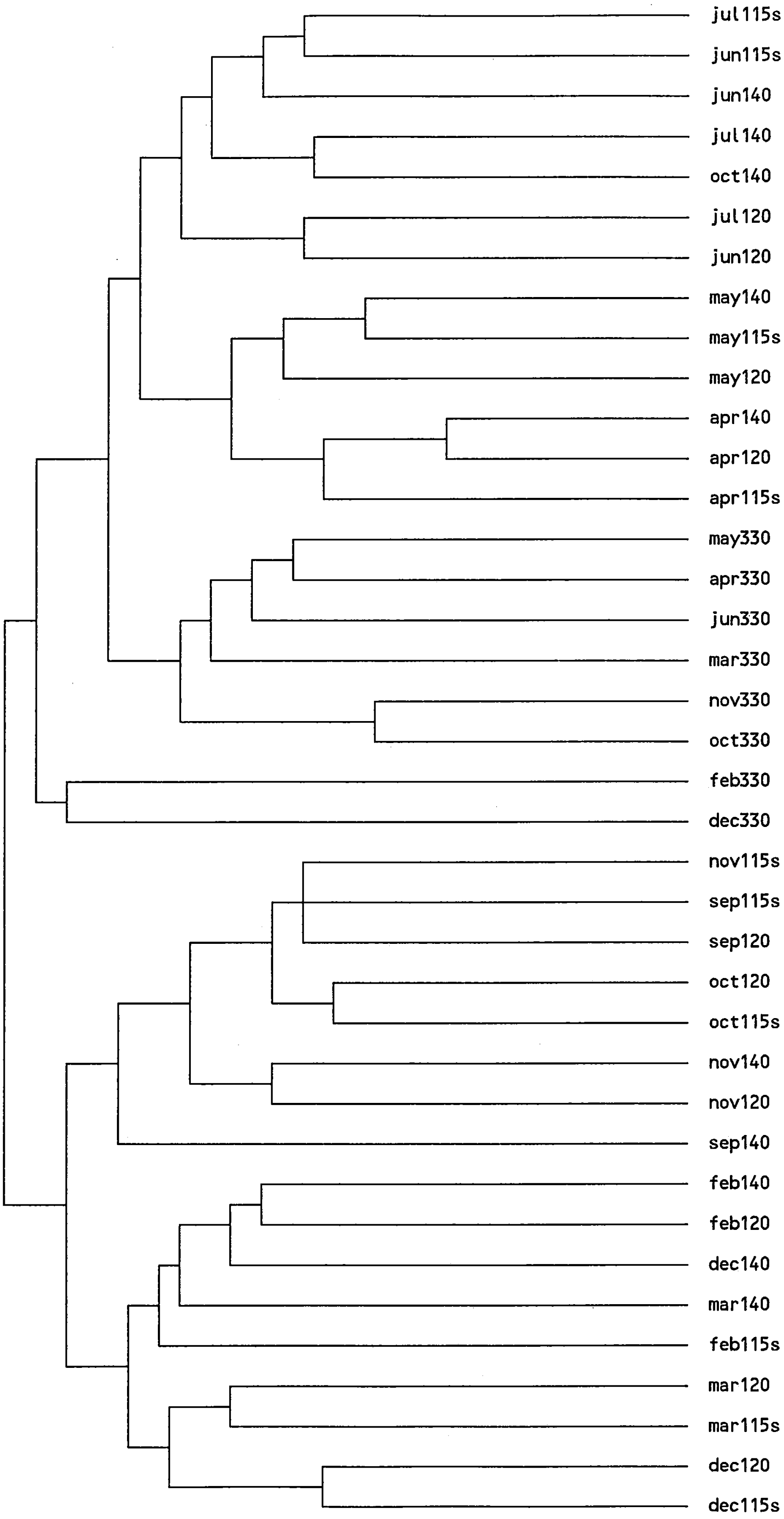


FIGURE 10.

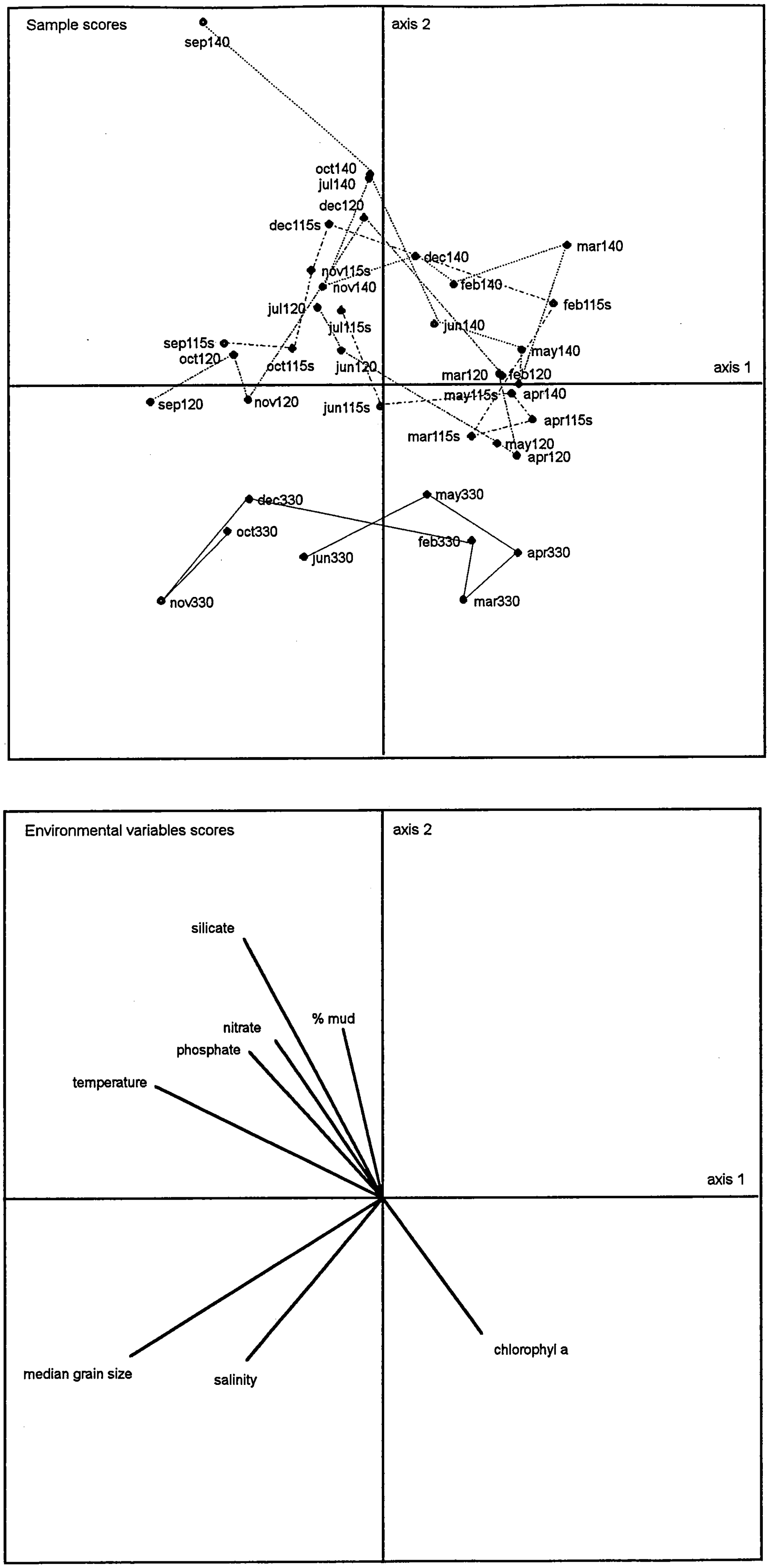

Sample scores
axis 2
axis 1
sep140
oct140
jul140
dec120
dec115s
dec140
mar140
nov115s
nov140
feb140
feb115s
jul120
jul115s
jun140
sep115s
oct120
oct115s
jun120
may140
mar120
feb120
axis 1
sep120
nov120
jun115s
may115s
apr140
apr115s
mar115s
may120
apr120
dec330
may330
oct330
feb330
apr330
jun330
nov330
mar330
Environmental variables scores
axis 2
silicate
% mud
nitrate
phosphate
temperature
axis 1
chlorophyl a
median grain size
salinity

FIGURE 11.

ONSHORE + OFFSHORE STATIONS (density data)

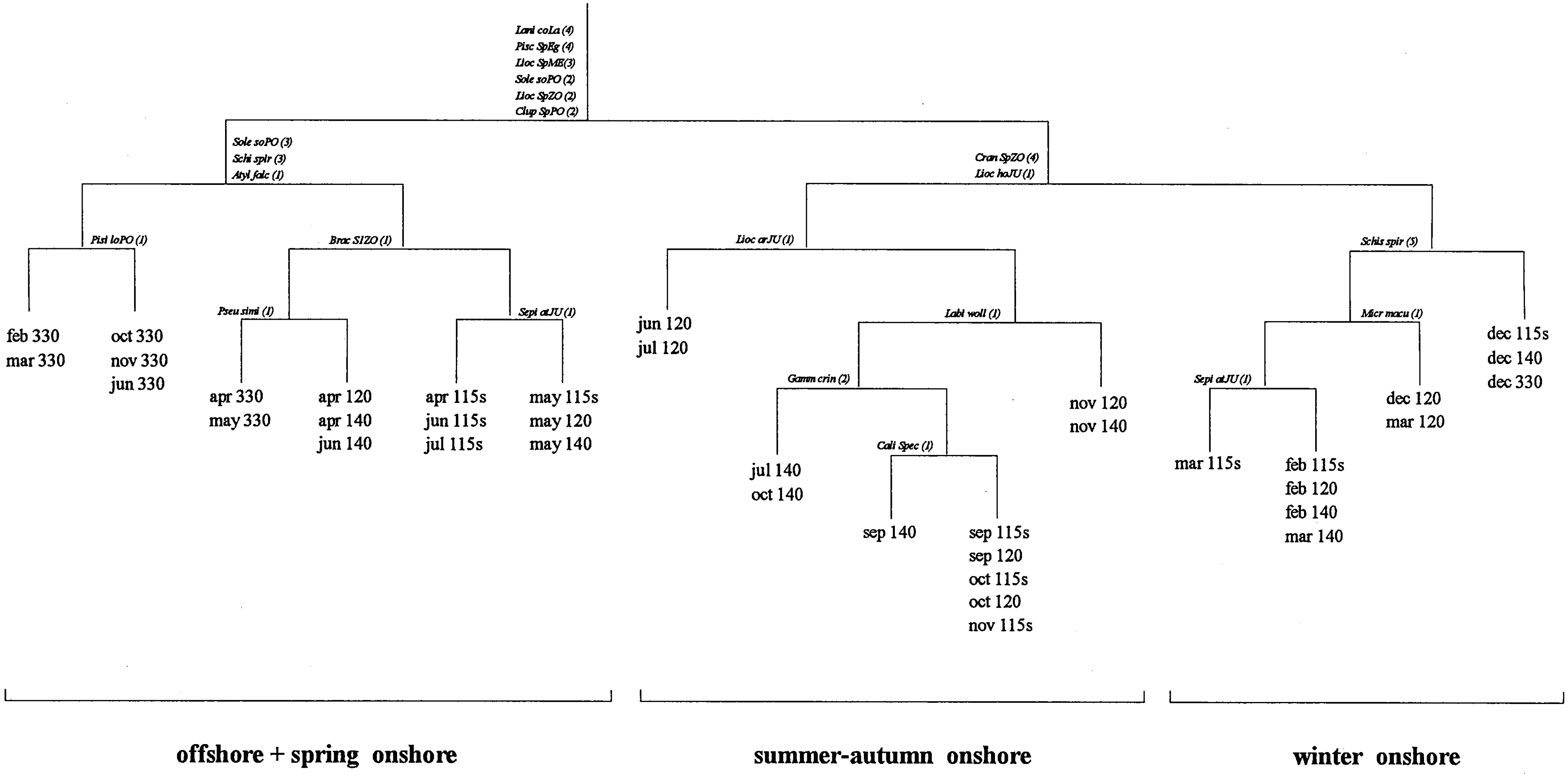


FIGURE 12.

HYPERBENTHOS BCP - yearcycle 1994-1995
density (onshore stations)
Bray-Curtis similarity, group average sorting

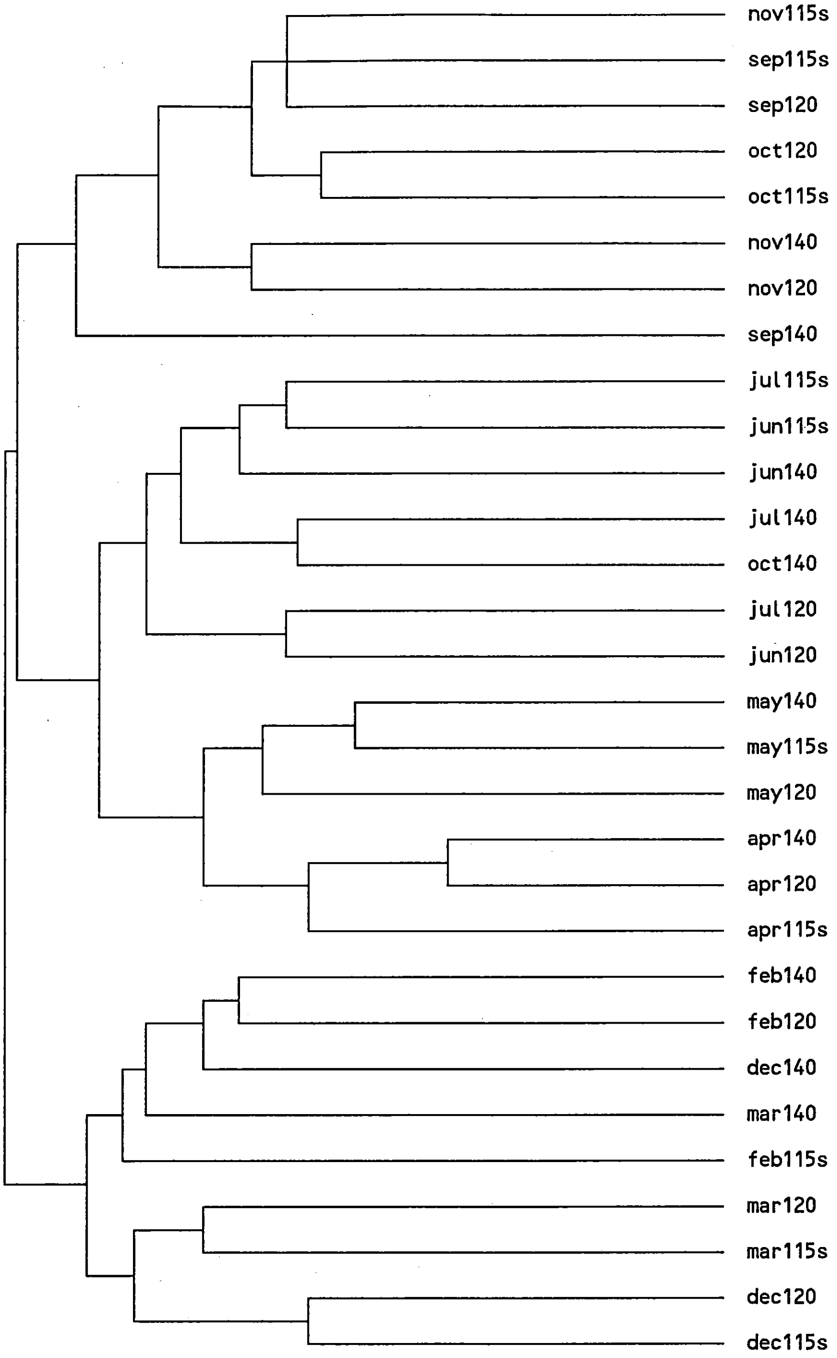


FIGURE 13.

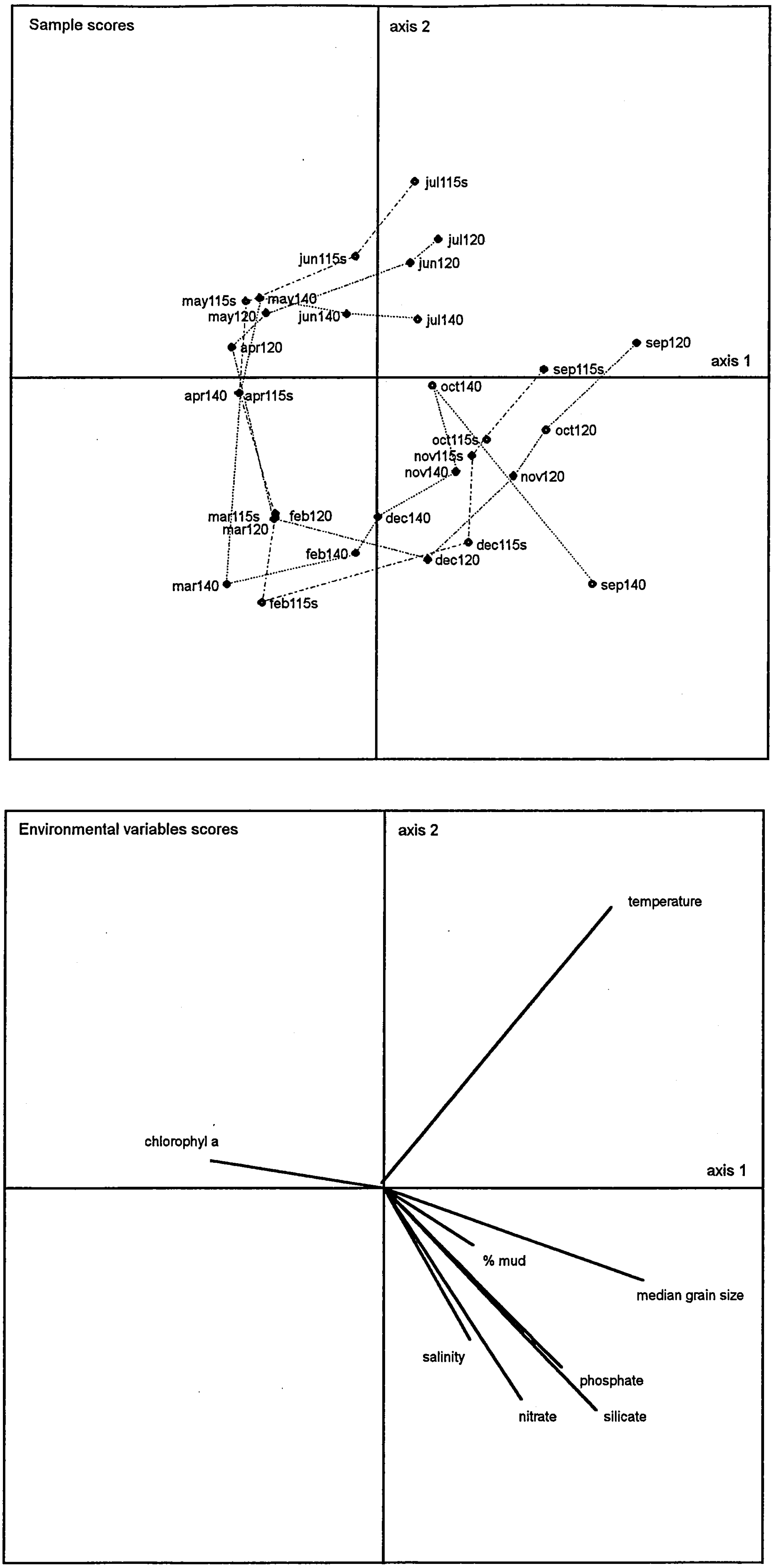
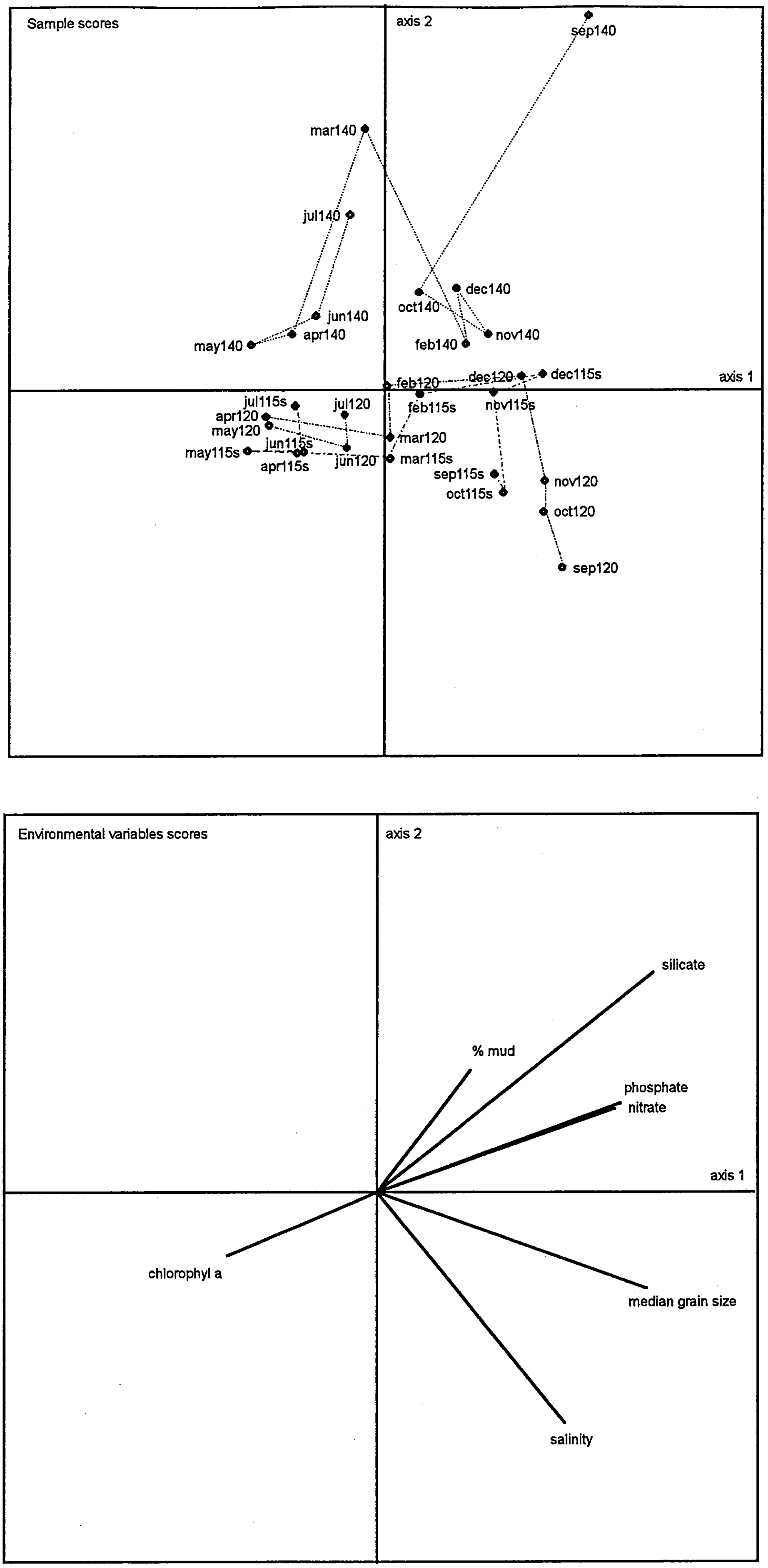

Sample scores
axis 2
axis 1
jul115s
jul120
jun115s
jun120
may115s
may140
may120
jun140
jul140
apr120
sep120
sep115s
oct140
apr140
apr115s
oct120
oct115s
nov115s
nov140
nov120
mar115s
feb120
mar120
dec140
dec115s
feb140
dec120
mar140
sep140
feb115s
Environmental variables scores
axis 2
temperature
chlorophyl a
axis 1
% mud
median grain size
salinity
phosphate
nitrate
silicate

FIGURE 14.


Sample scores
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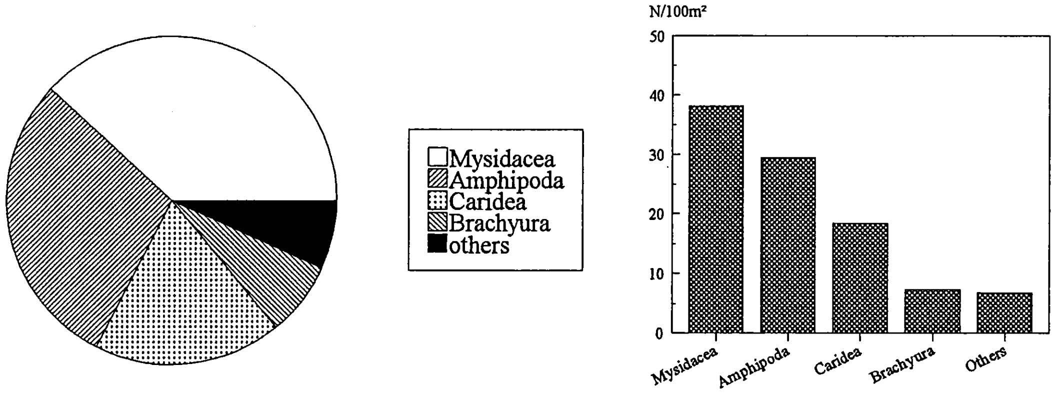
sep140
mar140
jul140
dec140
oct140
jun140
nov140
apr140
may140
feb140
feb120
dec120
dec115s
axis 1
jul115s
jul120
feb115s
nov115s
apr120
may120
mar120
jun115s
may115s
jun120
mar115s
apr115s
sep115s
oct115s
nov120
oct120
sep120
Environmental variables scores
axis 2
silicate
% mud
phosphate
nitrate
axis 1
chlorophyl a
median grain size
salinity

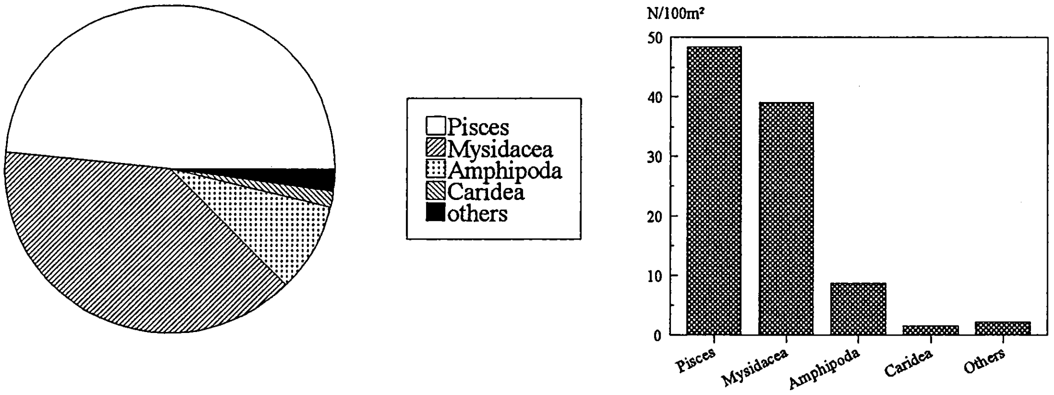
FIGURE 15.

taxonomic composition of the communities

summer-autumn community



winter community



spring community

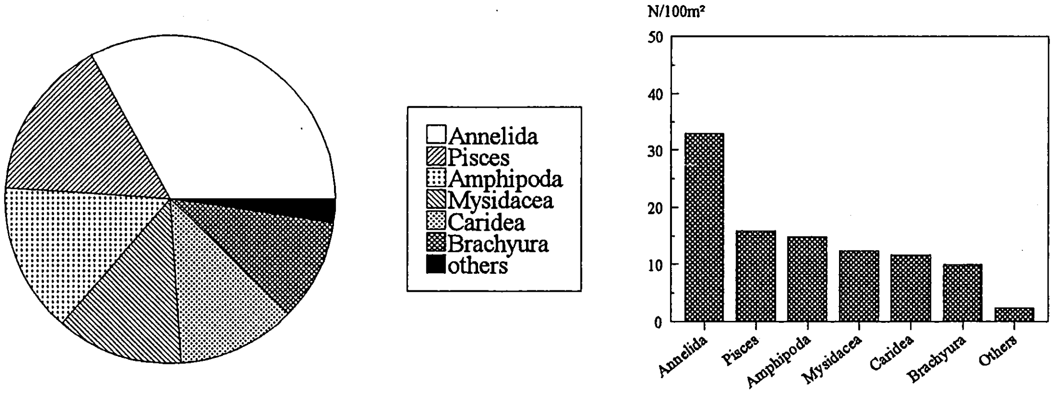
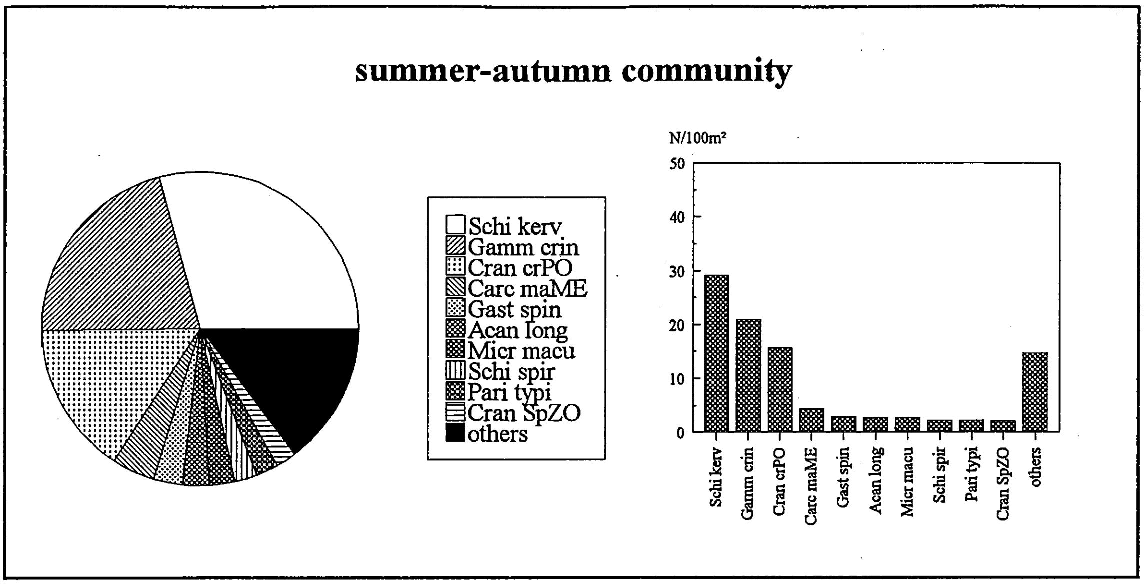
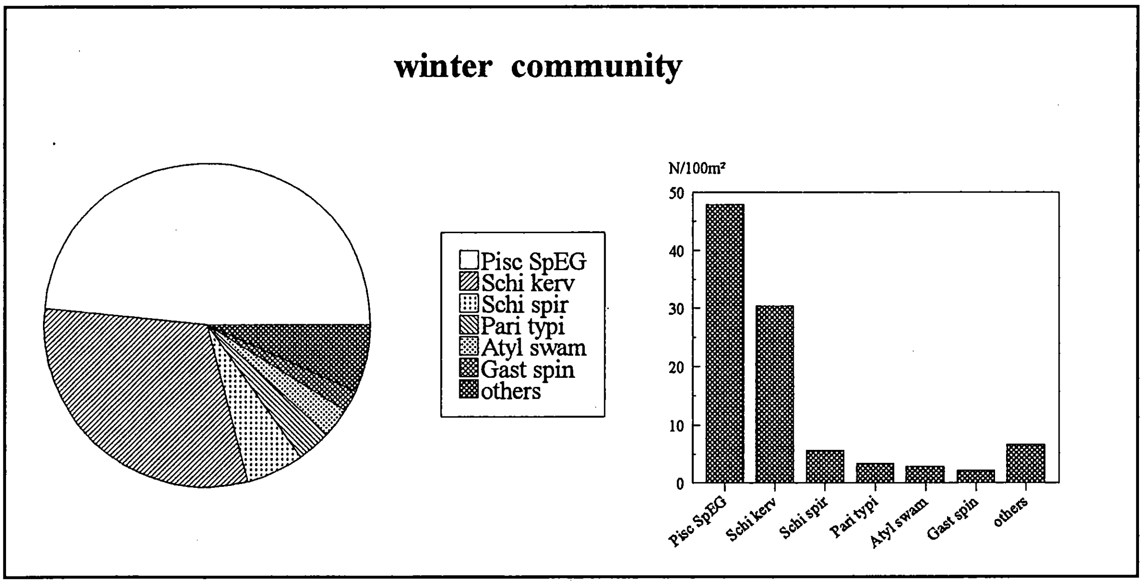


FIGURE 16.

species composition of the communities


summer-autumn community


winter community

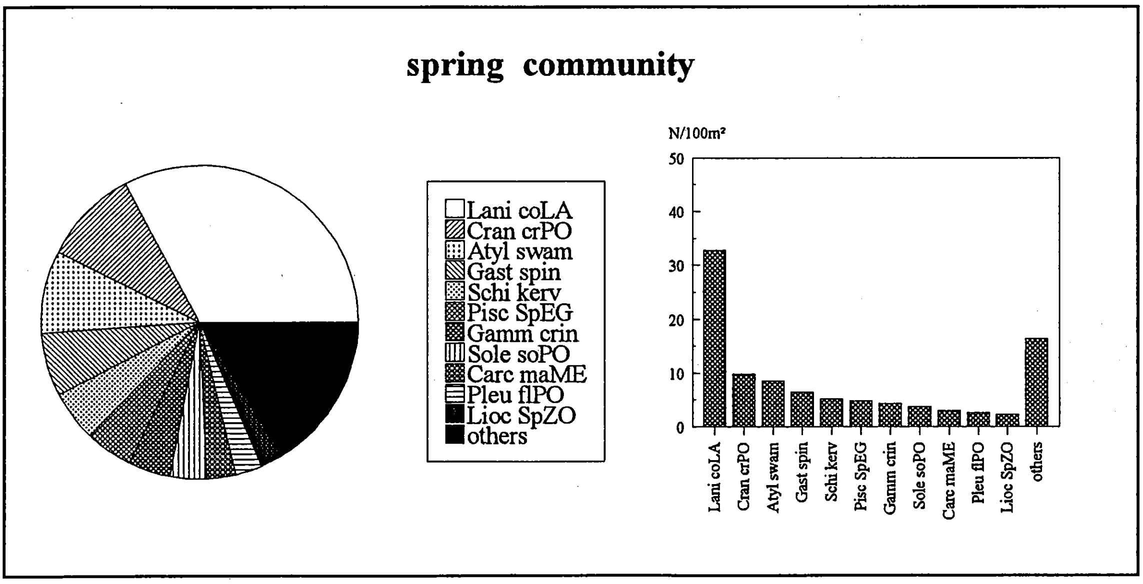
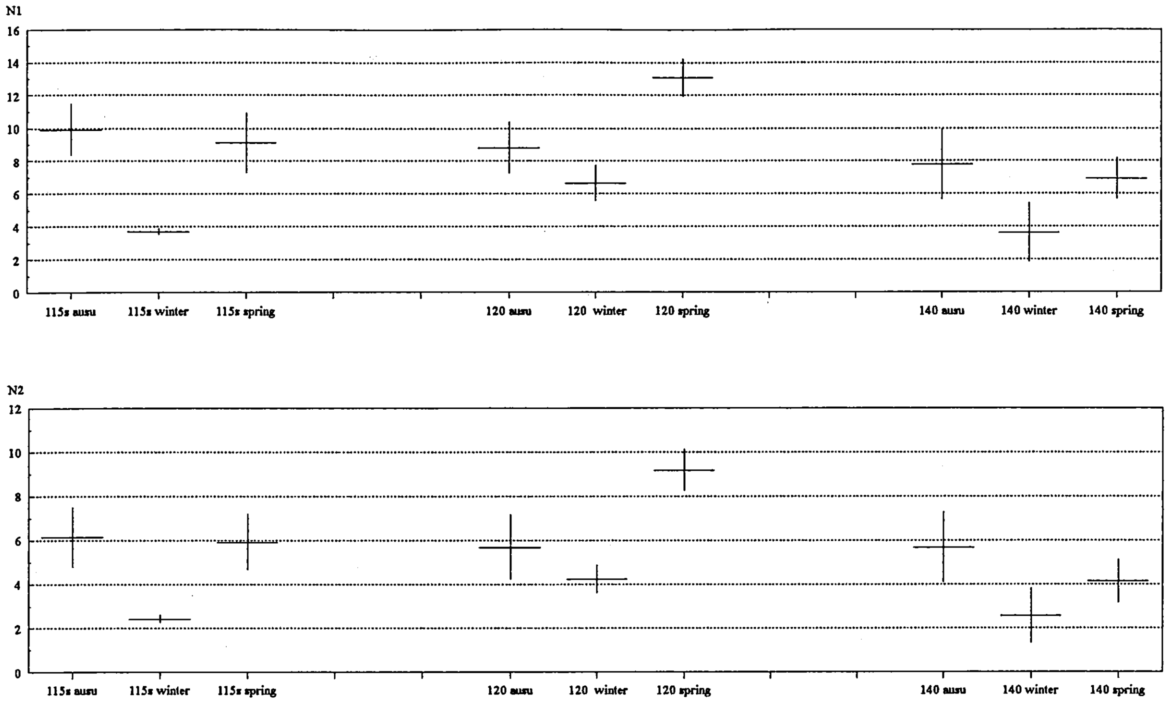

spring community

FIGURE 17.

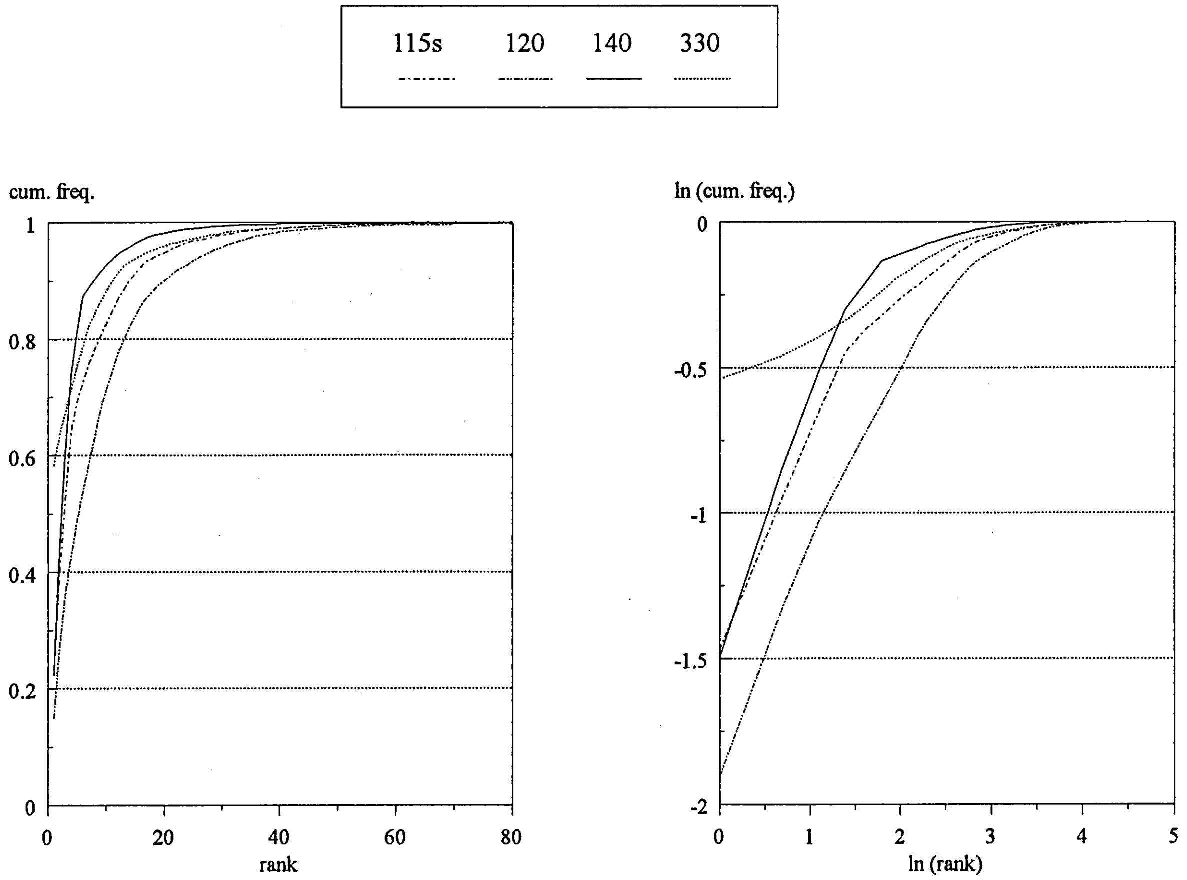
Hill's diversity numbers

(average value calculated per station, per season)



K-dominance

(calculated per station, based on all the samples from one month)



THE DIET OF *NEOMYSIS INTEGER* (CRUSTACEA, MYSIDACEA) IN THE MAXIMUM TURBIDITY ZONE OF ESTUARIES

Nancy FOCKEDEY and Jan MEES

Most European estuaries are characterised by high organic loads. When the riverine water reaches the incoming marine water in the estuary (at salinities of 1-5 psu), the suspended organic matter and sediment particles flocculate. This process and other hydrodynamical events (baroclinic circulation and tidal pumping) lead to a prominent turbidity in that zone (the maximum turbidity zone or MTZ) (Wolanski, 1995). The flocs are sites of high heterotrophic bacterial activity resulting in a high degree of remineralisation. On the other hand, the bacteria on the flocs attract other Protozoa (flagellates, ciliates, ...). These organisms can form a link to higher trophic levels (figure 1).

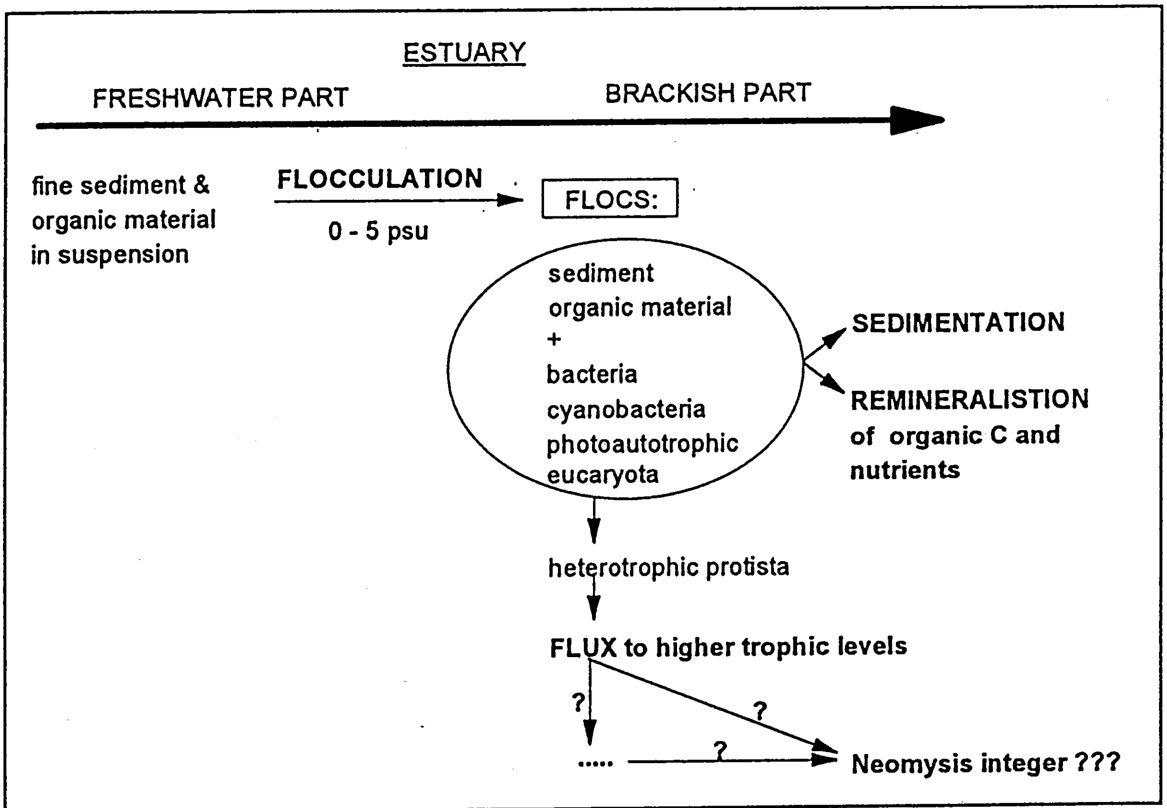
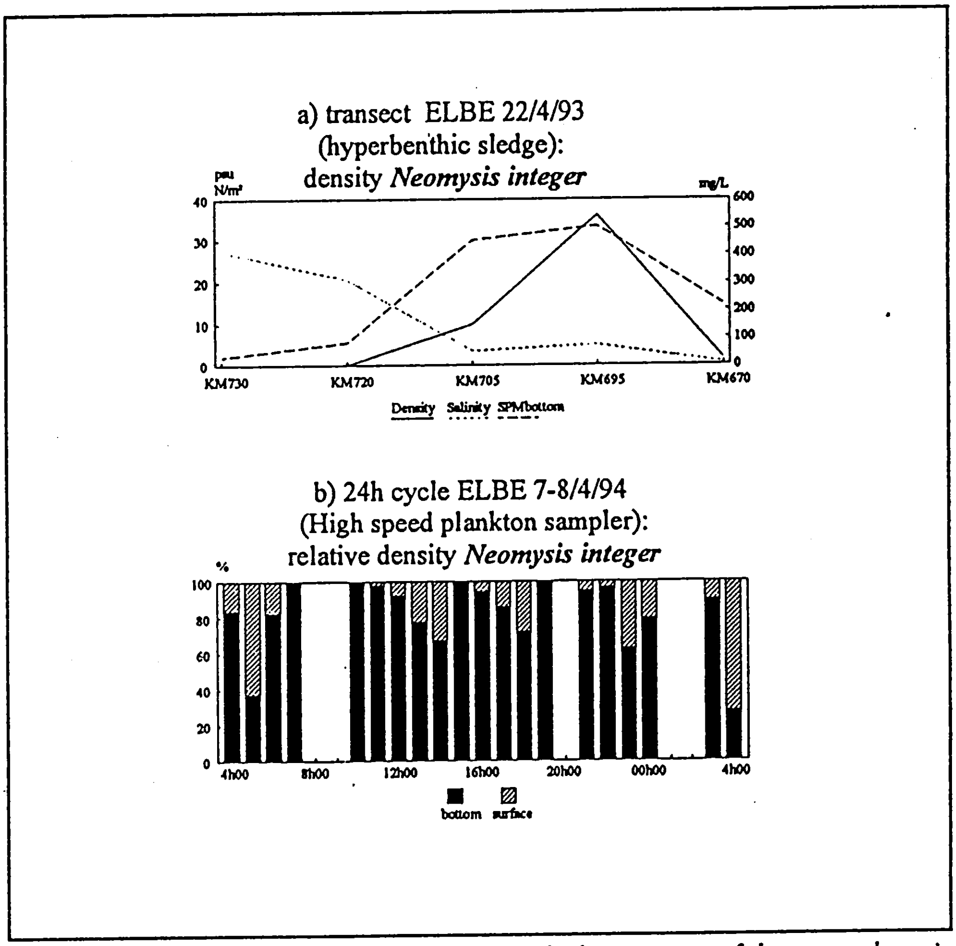


Figure 1: Salt flocculation in the MTZ of estuaries leads to the formation of flocs which might be, directly or indirectly (via the zooplankton), important to the diet and energy balance of *Neomysis integer*.

Keywords: hyperbenthos, estuaries, turbidity, feeding ecology

In the MTZ of Western-European estuaries the hyperbenthic community is dominated by the brackish water mysid *Neomysis integer*. It is a key species in the brackish ecosystem, since *N. integer* is an important prey item for demersal fishes and epibenthic crustaceans (estuarine residents and temporary users of the estuarine nursery). The *N. integer* population is concentrated in the vicinity of the MTZ and most individuals occur near the bottom (the hyperbenthal) throughout the day (figure 2). This suggests that the mysids feed in the lower layers of the watercolumn or at the water-sediment interface and that they may constitute an important component in the benthic-pelagic coupling in estuaries and coastal systems.



a) transect ELBE 22/4/93
(hyperbenthic sledge):
density *Neomysis integer*

b) 24h cycle ELBE 7-8/4/94
(High speed plankton sampler):
relative density *Neomysis integer*

Figure 2(a): Distribution of Neomysis integer in the lowest meter of the watercolumn in relation to salinity and suspended matter concentration (SPM) as exemplified for a transect in the Elbe. 2(b): Relative densities of Neomysis integer caught in bottom and surface waterlayers during a 24 hour sampling campaign in the Elbe. (Fockedey, unpublished)

The degree to which lower trophic levels (phytoplankton, zooplankton, detritus and flocs) are consumed by *Neomysis integer* in the MTZ of three European estuaries (Elbe, Westerschelde and Gironde) was investigated in the spring of 1993. The diet of the species was studied by means of qualitative techniques (microscopy and EDAX) and quantitative stomach analysis (dry weight of the stomach contents and image analysis).

Neomysis integer was found to be an omnivore which mainly utilizes mesozooplankton and detritus carbon pools (figure 3). The quality of the diet did not differ between the sexes. In all three estuaries the diet was dominated by calanoid copepods (5-10 *Eurytemora affinis* ind^{-1}) and was supplemented with Rotifera (genera *Keratella* and *Brachyonus*) and Cladocera (*Bosmina spec.*). Nauplii of calanoids were only found in low numbers. Benthic organisms (Harpacticoida, Halacaridae and microphytobenthic diatoms), though present in the stomachs, were negligible to the diet of *N. integer*. Phytoplankton (solitairy cells and filamental strands) and pollen had a high frequency of occurrence, but were only present in low numbers.

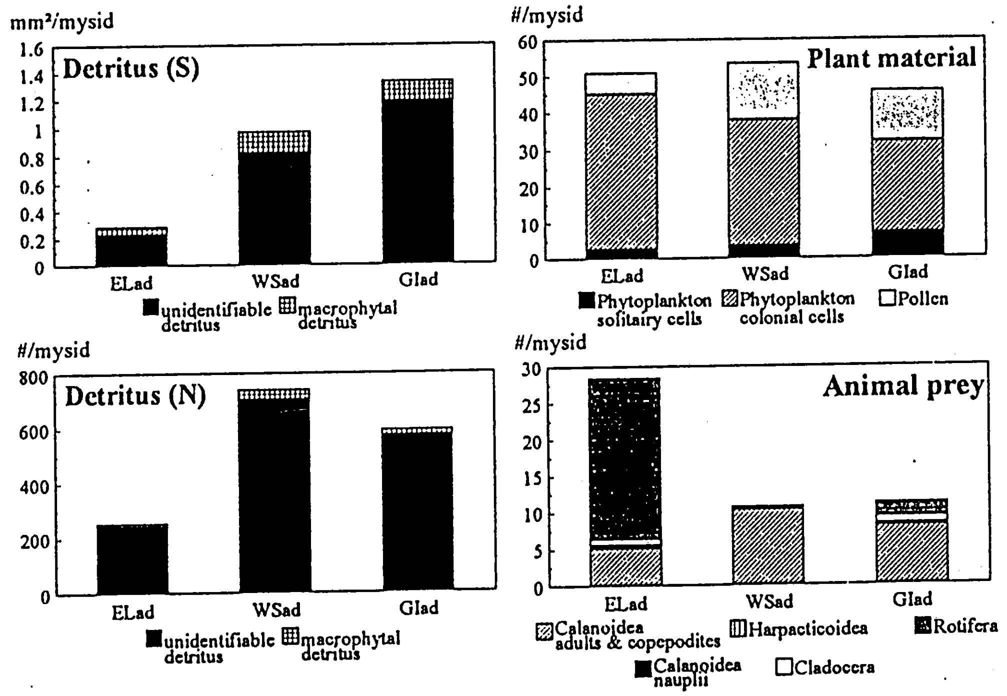


Figure 3: Absolute composition of the diet (in numbers per individual, for detritus surface (S) in mm² per individual) of adult Neomysis integer of the Elbe (EL), Westerschelde (WS) and Gironde (GI).

Special attention was paid to the contribution of detritus to the diet of *Neomysis integer*. Macrophytal detritus accounted for less than 5 % of the total number of detritus particles in the stomachs. This detritus can serve as an energy source to mysids, especially in periods of low availability of other nutritionally more important food items. Amorphous material, unidentifiable under the light microscope, was very abundant as a food item (242 particles in the Elbe, 704 in the Westerschelde and 572 in the Gironde). The amorphous detritus was found to originate from the suspended sediment flocs which are characteristic for the MTZ. In all three estuaries these mainly consisted of clay minerals, as shown by an elemental composition of Si and Al with Mg, K and Fe (EDAX analysis) (Fockedey and Mees, submitted). The size frequency distributions of the unidentifiable fraction of the detritus showed the same pattern in all estuaries: the modes of the size distributions were located around 30-35 µm, consistent with measurements of (micro)flocs in estuaries (Eisma, 1986). The energetic value of the flocs for *N. integer* remains unclear.

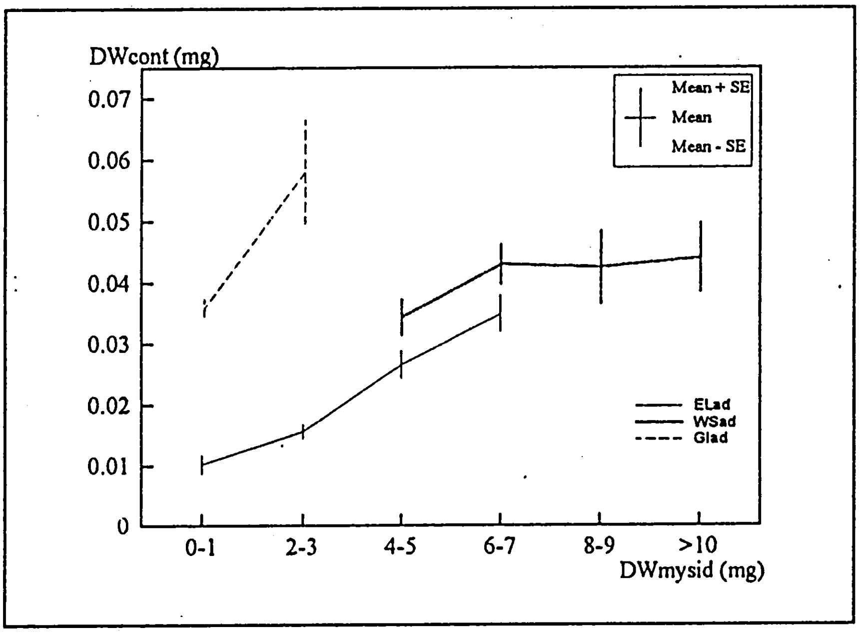


Figure 4: The mean dry weight of the stomach content for different size classes of adult Neomysis integer in Elbe, Westerschelde and Gironde.

The mean dry weight of the stomach contents of *Neomysis integer* from the three estuaries were, for each 2 mm size class, smallest in the Elbe, intermediate in the Westerschelde and highest in the Gironde (Figure 4). No sexual differences were found.

Future research will include field studies on ontogenic, diurnal and seasonal shifts in the diet of *Neomysis integer* in the Westerschelde.

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University of Gent, Marine Biology Section, Institute of Zoology
K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

Feeding of the hyperbenthic mysid *Neomysis integer* in the maximum turbidity zone of the Elbe, Westerschelde and Gironde estuaries

Fockedey, N. and Mees, J.
Marine Biology Section, Institute of Zoology, University of Gent, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium
E-mail: Nancy.Fockedey@rug.ac.be / Jan.Mees@rug.ac.be

ABSTRACT

The diet of the mysid *Neomysis integer* in the maximum turbidity zone (MTZ) of three European estuaries (Elbe, Westerschelde and Gironde) was investigated in spring 1993. The quality and quantity of the diet were assessed through measurement of the stomach fullness and microscopical analysis of the stomach content combined with image analyses. *N. integer* was found to be an omnivore which mainly utilizes mesozooplankton and detritus carbon pools. The quality of the diet did not differ between the sexes nor between different developmental stages, although smaller individuals consumed fewer items. In all three estuaries the diet was dominated by Copepoda Calanoida (5-10 *Eurytemora affinis* ind^{-1} for adults; 2-5 ind^{-1} and 2-3 ind^{-1} for subadults and juveniles, respectively) and was supplemented with Rotifera and Cladocera. Phytoplankton and benthic organisms, though present in the stomachs, were negligible. Macrophytal detritus and amorphous material, the latter unidentifiable under the light microscope, were very abundant food items. The amorphous detritus was found to originate from the suspended sediment flocs which are characteristic for the MTZ. These mainly consist of clay minerals, as shown by EDAX-analysis. The energetic value of the flocs for *N. integer* remains unclear.

INTRODUCTION

The turbidity of a water mass is the measure to which the water contains particles that cause backscattering and extinction of light (Barretta-Bekker *et al.*, 1992). It reflects the degree to which light penetrates in the watercolumn and is determined by the concentration of suspended material (seston). Seston consists of living matter (bacteria, fungi, phytoplankton, zooplankton, ...), detritus and anorganic sediment particles. The amount of seston present in the watercolumn of an estuary depends on (1) local primary and secondary production in the estuary proper and in adjacent intertidal areas, (2) the import of marine and fluvial materials and (3) the amount of sediment resuspended *in situ* (Mc Lusky, 1981; Ketchum, 1983).

In the brackish zone of estuaries the suspended matter flocculates into larger particles, which increases turbidity (*e.g.* Eisma, 1986; Wolanski, 1995). This phenomenon typically occurs in salinities of 1 to 5 psu, and the area is called the Maximum Turbidity Zone or MTZ. The axial position of the MTZ depends on freshwater drainage and varies seasonally depending on the river flow. In the Westerschelde estuary (NW-Netherlands) 250000 tons of detritus and organic matter are imported to the brackish zone per year (Peters & Sterling, 1976; Duursma *et al.*, 1988; Heip, 1988; Van Eck *et al.*, 1991), 46 % of which flocculate and precipitate in the MTZ (Wollast, 1976). In the Westerschelde the concentration of suspended matter (SPM) is on average around 0.05 g l^{-1}. In the Gironde (SW-France) the suspended flocs mainly consist of silt and clay from freshwater origin (Castel, 1992) and are generally present in the MTZ with concentrations higher than 1 g l^{-1}. The mean SPM concentration in the MTZ of the Elbe (NW-Germany) varies between 0.1 and 0.2 g l^{-1} (Brockmann, 1992).

Recently, an increased research interest has focused on processes concerning the production and fate of particles in the MTZ. In the brackish zone of estuaries a detritus based foodweb has been described (Hummel *et al.*, 1988; Smith *et al.*, 1989; Findlay *et al.*, 1991; Hamerlynck *et al.*, 1993).

Heterotrophic bacteria, responsible for the remineralisation of the nutrients (Herman *et al.*, 1991; Goossen *et al.*, 1992), form the basis of the foodweb for higher trophic levels (Azam *et al.*, 1983; Cole *et al.*, 1988; Billen *et al.*, 1990). Bacteria are consumed, directly or indirectly, by the microzooplankton (Fenchel, 1988), mesozooplankton, hyperbenthos (described as the fauna living in the lowest part of the watercolumn) and epibenthos (Hamerlynck *et al.*, 1993). Fish and epibenthic macro-invertebrates can then feed at this 'secondary energy level'.

The structure of the hyperbenthic community of the brackish zone has been investigated for many Western European estuaries (Mees & Jones, submitted). However, studies on the functional impact of the hyperbenthos on other particles in the MTZ are lacking. Their impact on suspended particles can be twofold: the hyperbenthos may be described as a higher trophic level feeding on particles present in the MTZ. On the other hand, the hyperbenthic fauna can be a source of particles (*e.g.* through the production of faecal pellets or fragmentation of larger particles). Only the feeding aspect is treated in this study.

In the MTZ of West-European estuaries the hyperbenthic community is dominated, both in terms of density and biomass, by the brackish water mysid *Neomysis integer* (Mees & Hamerlynck, 1992; Mees *et al.*, 1993b; Mees *et al.*, 1995). This species probably has an important function in the energy transfer to higher trophic levels in the ecosystem (Mees *et al.*, 1994). Therefore, *N. integer* was chosen as a model to assess the impact of the feeding of the hyperbenthic community on particles in the MTZ of the Elbe, Westerschelde and Gironde.

Mysidacea are generally described as omnivores, feeding on detritus, algae and zooplankton (*e.g.* Mauchline, 1980). They can feed selectively on different zooplankton species and size groups (*e.g.* Cooper & Goldman, 1980; Murtaugh, 1981a), and thus have the potential of structuring zooplankton communities (Fulton, 1982a; 1982b; Rudstam *et al.*, 1989). The phytoplankton (Kost & Knight, 1975; Siegfried & Kopache, 1980) and tychoplankton (Webb *et al.*, 1987; Wooldridge, 1989; Webb & Wooldridge, 1990) are possibly also influenced through selective grazing by mysids. Mysid predation has even been reported as a possible control on meiofaunal densities (Parker, 1979; Siegfried & Kopache, 1980; Grossnickle, 1982; Johnston & Lasenby, 1982). Most mysids utilize organic detritus to a considerable extent and can be responsible for the remineralisation of a substantial proportion of the refractile detritus (Raymont *et al.*, 1964; Kost & Knight, 1975; Pechen'-Finenko & Pavlovskaya, 1975; Jansen, 1985). Detrivory may be especially important during periods when zooplanktonic food sources are scarce (Zagursky & Feller, 1985).

Literature on the description of the diet of *Neomysis integer* is scarce, and mainly qualitative information is available. According to Lucas (1936) and Tattersall & Tattersall (1951) the species is an efficient filter feeder, grazing on organic detritus and/or planktonic diatoms. According to these authors it only feeds on zooplankton when concentrations of suspended food are too low. More recent studies describe *N. integer* as an omnivore consuming detritus, algae, diatoms, rotifers, copepods, amphipods, and other crustaceans, carrion, fragments of leaves and of macroalgae, spores and seeds, terrigenous materials and insect larvae (Kinne, 1955; Mauchline, 1971; 1980). In the German Ostsee the impact of *N. integer* on the phytoplankton is negligible, while up to 16 % of the zooplankton production is consumed by the species (Jansen, 1985). Chitinases and cellulases have been found in the gut of *N. integer* (Zagursky & Feller, 1985). It can be assumed that they are capable of digesting refractile macrophyte detritus, as is the case in *Neomysis americana* (Zagursky & Feller, 1985) and *Mysis stenolepis* (Foulds & Mann, 1978; Wainwright & Mann, 1982). Still, the growth efficiency of *N. integer* has been shown to be highest (27%) with animal food (dead mysids) and lowest (7.5%) with detritus (Zagursky & Feller, 1985).

In this paper a methodology is described for quantitative and qualitative diet analyses of mysids by means of stomach fullness measurements and microscopical stomach analyses. These techniques are applied for a comparison of the diet of *Neomysis integer* in the MTZ of 3 West-European estuaries. Sexual and ontogenic shifts in the diet are also investigated.

METHODS

Samples

The *Neomysis integer* populations of the maximum turbidity zones of the Elbe (NW-Germany), Westerschelde (SW-Netherlands and Belgium) and Gironde (SW-France) estuaries were sampled in spring 1993. All samples were collected in a one month period. In each estuary, a station in the MTZ was sampled during daytime with a hyperbenthic sledge in the main estuarine channel (for a description of the sampling gear and the sampling strategy see Hamerlynck & Mees, 1991).

In the Elbe a station near Brunsbüttel was sampled on April 22, 1993. In the Westerschelde the sampling point was located near Bath (May 6, 1993). Since upstream of Bath dissolved oxygen concentrations are to low for hyperbenthic life (Herman *et al.*, 1991; Hamerlynck & Mees, 1991; Mees *et al.*, 1993a; 1993b; 1994; 1995), this station was chosen because it was characterized by highest mean *Neomysis integer* densities in previous studies. For this reason the sampling point was not at the height of the MTZ. In the Gironde estuary a station near Pauillac was sampled on May 23, 1993. The salinity at the time of sampling was 4.84, 11.60 and 1.20 psu, in Elbe, Westerschelde and Gironde respectively. Information on other environmental variables are available in the Mature-database.

Catches were immediately fixed in a 7 % neutral formaldehyde solution. In the laboratory, the samples were rinsed over a 1 mm sieve. Adults, subadults and juveniles of *Neomysis integer* were picked out for quantitative and qualitative diet analyses. Sexes and developmental stages were identified according to Mauchline (1980) and Mees *et al.* (1994). No gravid females were used for the diet analysis. Individual *Neomysis integer* were rinsed in distilled water to remove salts, formaldehyde crystals and other impurities. Additionally, the standard length (distance from the basis of the eyestalk to the last abdominal segment) was measured for around 100 individuals per stage and sex.

In order to obtain valuable information on the diet of a species it is advisable to combine several (objective) methods of stomach analysis: at least one method measuring the amounts of the different food items (here named qualitative analysis) and one measuring the bulk of the food material present (quantitative analysis). Ideally, the latter must be linked with the size of the individual (Hyslop, 1980).

Qualitative diet analyses

Information on the diet composition of *Neomysis integer* was obtained by light microscopic analysis of the stomach contents, in combination with image-analysis techniques. Additionally, EDAX-analyses were performed to identify the detritus particles.

To obtain semi-permanent microscopic slides of the stomach contents, each mysid was first dehydrated (Seinhorst, 1959). A gradual dehydration series from a formaldehyde solution to glycerin causes no risk for abrupt shrinkage of the stomach or intestine: no ingested particles are pushed from the stomach to the intestine nor does digested material return from the intestine into the stomach.

The carapax was removed and the gut was cut just after the round stomach. The stomach (oesophagus included) was dissected out and pulled open in a drop of glycerine on a microscopic slide.

Analysis of the slides was performed by light microscope (magnification 250 times) connected to an Image Analyzer (Leica Quantimet 500+). For each estuary 15 individuals were processed per sex and stage (30 juveniles).

The identification and processing of the different prey categories present in the stomach of *Neomysis integer* was done according to the following procedure:

The chitinous body of adult and copepodite stages of calanoid copepods were usually found to be fragmented (figure 1.b), depending on the degree of digestion. Mandibles (figure 1.a) were found to be the most persisting parts. The number of ingested copepods and copepodites was estimated by counting the mandibles and dividing this figure by 2. Uneven counts were rounded off upwards. The width of the mandible's cutting edge was measured with the image analyzer to investigate possible size selectivity of the different ontogenic stages. Significant differences were sought for with ANOVA and subsequent contrast analysis. The copepods were identified to genus level based on other recognisable parts: the caudal rami (figure 1.b), the antennae and the fifth pleopods.

Rotifera (figure 1.c and 1.f), Cladocera (figure 1.d), Harpacticoida (figure 1.e) and nauplii of Copepoda were usually found intact. Most specimens present could be identified to genus level and counted. Nauplii were noted as such. Halacaridae (figure 1.g) and insect larvae were found occasionally, but were not used in further analyses.

Phytoplankton cells were usually found intact and were counted as such. Based on size and shape, a distinction between different types was made: solitary phytoplankton cells (figure 1.k and l) and colonial cells or filamentous algae (figure 1.h, i and j) were counted separately. Only a minority of the specimens found could be identified to genus level. Still a distinction could be made between species originating from intertidal areas, freshwater or brackish water in most cases (Muylaert & Sabbe, submitted).

Pollen were common in the stomachs of *Neomysis integer*. They were counted and divided into round formes (figure 1. m and o) and pollen of gymnosperms (figure 1.n).

Large particles with a plant cell structure were denoted as 'macrophytal detritus' (figure 1.p and q). Particles with no regular cell structure were classified as 'unidentifiable detritus' (figure 1.r). All the detritus particles present in the stomach were counted by means of an image analyzer and the surface areas and maximal lengths of the particles were measured.

The numerical abundance of each dietary item present in the stomachs was tested for differences between estuaries, ontogenic stages and sexes by means of Kruskall-Wallis tests and subsequent Mann-Whitney U-tests. For macrophytal and unidentifiable detritus, the surface areas and length-frequency distributions of the particles were compared. The frequency of occurrence of all the food items present in the stomachs was calculated as the proportion of stomachs containing a certain prey item (Hyslop, 1980). No attempt was made to determine the relative importance of the various food items to the total energy intake of the mysid population.

Further characterisation of the 'unidentifiable detritus' was done by EDAX analysis, using a JEOL JSM-6400 scanning electron microscope with a Voyager II 2100/2110 microanalysis system (Noran Instruments). The stomachs of 10 adult animals per estuary were dissected out. The content was rinsed out in a drop of distilled water, placed on specimen mounts and dried in an oven (40°C) for 30 minutes. The mounted samples were subsequently coated with carbon. The elemental composition of the detritus flocs was determined, recalculated for the eight most abundant elements (excluding C and O), and compared between estuaries.

Quantitative diet analyses

The stomach of each mysid was carefully dissected out after removing the carapax. The stomach (and its content) and the mysid were dried separately in small aluminium weighing pans for 4 days at 60°C, after which the dry weight of both was determined with a microbalance to the nearest 1 µg. For the comparison of the three estuaries, 20 adult females and 20 adult males from each estuary were processed. For the ontogenic diet comparison 5 times 3 subadult and 5 times 5 juvenile individuals were pooled.

Additionally, the empty stomachs of 30 adults per estuary were weighed after carefully emptying the dissected stomach. A linear regression analysis was done on the dry weight of the mysids and the dry weights of the corresponding empty stomachs. This regression was used to correct the total stomach dry weights to calculate the dry weight of the stomach content itself:

$$DW_{content} \quad DW_{stomach} \quad DW_{empty}$$

where:

$$DW_{empty} \quad a \quad b\ DW_{mysid}$$

with $DW_{content}$: the dry weight of the stomach content
$DW_{stomach}$: the dry weight of the stomach with its content
DW_{empty}: the dry weight of the empty stomach derived by a regression from DW_{mysid} - the dry weight of the mysid (without its stomach).

A fullness index (FI) was calculated with these data. This relative measure is frequently used in fisheries research for the comparison of stomach contents of fish taken from different size classes (e.g. Hyslop, 1980). The amount of food present in the stomach of *Neomysis integer* at a given time *t* is then expressed as the fullness index FI_t:

$$FI_t \quad \frac{DW_{stomach} \quad DW_{empty}}{DW_{mysid}} \quad 100$$

Although the fullness index is used as a measure for the stomach content which is ideally not depending on the size of the mysid, FI's were found to covary with the DW_{mysid} in this study. For this reason, the dry weights of the stomach contents ($DW_{content}$) were used as such. Latitudinal, ontogenic and sexual differences were assessed with ANalyses of COVAriance (ANCOVA), in which DW $_{ysid}$ was used as a covariable. For comparative purposes, the mean dry weights of the stomach contents were adjusted for the covariable (Sokal & Rohlf, 1981). Prior to statistical testing, the dry weights were transformed logarithmically; fullness indices were transformed angularly.

RESULTS

Neomysis integer occurred with densities of 36.0, 9.4 and 10.8 individuals per m^2 and biomasses of 184.6, 39.0 and 21.5 mg per m^2 in the MTZ stations of the Elbe, Westerschelde and Gironde, respectively. The absolute and relative density and biomass of all sexes and stages of *N. integer* present in the MTZ in the three estuaries (spring 1993) is shown in table 2.

Qualitative diet analysis

Comparison between estuaries

In all three estuaries, the diet of all ontogenic stages of *Neomysis integer* was composed of zooplankton, phytoplankton and detritus (figure 2; table 3). In the Westerschelde and the Gironde the diet of *N. integer* was numerically dominated by adult and copepodite stages of the calanoid *Eurytemora affinis* (figure 1.a and 1.b) with respectively 10.27 and 8.00 copepods consumed per adult, 4.20 and 5.72 per subadult and 2.20 and 2.90 per juvenile mysid. In the Elbe rotifers were the most abundant animal prey items for the three ontogenic stages. Here, 5.07 copepods were consumed per adult and 2.43 per subadult mysid. Only the juvenile mysids in the Elbe showed minor differences in number of copepods consumed (1.77 ind^{-1}) with those of the Westerschelde and Gironde. Nauplii of calanoids were present in low numbers in the stomachs from the Elbe (0.03-0.23 ind^{-1}) and the Gironde (0.10-0.15 ind^{-1}); they were not consumed in the Westerschelde. Their frequency of occurrence was low (3-20 % in adults and subadults of the Elbe and 10-15 % in the Gironde), except for the juveniles in the Elbe (70%). Adult harpacticoids (figure 1.e) were also rare in the stomachs. They were only encountered in 7 % of the adult individuals of the Westerschelde and 3-7 % of the juveniles and adults in the Gironde. In the Elbe they occurred in 20-33 % of the individuals, though always in low numbers. Cladocera of the genus *Bosmina* (figure 1.d) were encountered in 33-70 % of the stomachs of Elbe and Gironde, but rarely in those of the Westerschelde (max. 7 %). Rotifers of the genera *Keratella* (figure 1.c) and *Brachyonus* (figure 1.f) were the most abundant prey items for *N. integer* in the MTZ of the Elbe (16.10-22.17 ind^{-1}). In Gironde and Westerschelde they were consumed in lesser numbers (1.38-1.93 ind^{-1} and 0.17-0.40 ind^{-1} respectively). The frequency of occurrence of the rotifers decreased from 100 % in the Elbe, to 67-83 % in the Gironde and 17-27 % in the Westerschelde. Other zooplanktonic prey were excluded for further analyses. Halacaridae (figure 1.g) were infrequently encountered in the Westerschelde and the Gironde (a total of 6 observations) and one larval Homoptera (Insecta) was found in the Gironde.

For each prey, the average numbers per stomach were tested for significant differences between the three estuaries for the three ontogenic stages (table 4A) by Mann-Whitney U-tests. Except for copopod nauplii and harpacticoids in all ontogenic stages and calanoids in juveniles, most of the differences were significant.

Also some phytoplankton was consumed by *Neomysis integer* in the three estuaries. Solitary (figure 1.k and l) and colonial phytoplankton (1.h, i and j) species could be recognized in the stomachs with a mean frequency of occurrence of 82 %. Colonial and filamental algal strands were the most abundant (table 3). For adults *e.g.* 42.50, 34.40 and 24.89 cells (4.56, 5.08 and 4.80 strands) were found per mysid in the Elbe, Westerschelde and Gironde respectively, while solitary cells only amounted to 2.5, 3.4 and 6.9 counts per adult. Still, most of these differences were not significant (table 4A). Similar trends were found in the subadults and juveniles in the Westerschelde and Gironde. Only in the Elbe, juveniles had consumed significant higher amounts of solitary phytoplankton cells (table 4A) compared to other estuaries.

Pollen were found in 90 to 100 % of the stomachs. Average numbers per stomach were 4.9, 11.6 and 13.8 in Elbe, Westerschelde and Gironde, respectively. Two general types were distinguished. The round forms (figure 1.m and o) could not be identified. Pollen with an air sac on either side (figure 1.n) were recognized as originating from gymnosperms. These were especially abundant in the Gironde (62.53 %) and Westerschelde (37.3 %), while in the Elbe only 6.3% of the pollen originated from gymnosperms.

The frequency with which macrophytal detritus was consumed in the three estuaries was always higher than 60 %. Although macrophyte detritus accounted for less than 5 % of the total number of detritus particles consumed. The size distributions of the macrophytal detritus in the stomachs (*e.g.* for adults in the Gironde: figure 4.a and b) were comparable over the estuaries: the majority (> 90 %) was smaller than 0.020 mm² for adults, 0.013 mm² for subadults and 0.015 mm² for juveniles. Maximal particle sizes of 0.039 mm², 0.061 mm² and 0.064 mm² were recorded in the Elbe, Westerschelde and Gironde, respectively. Highest number of macrophyte detritus were consumed by adults in the Westerschelde (36.50 ind^{-1}), while subadults and juveniles in the Gironde consumed significant higher numbers (12.62 and 6.57 ind^{-1} respectively) compared to the other estuaries.

The size frequency distributions of the unidentifiable fraction of the detritus (figure 4 c and d for adults in the Gironde) showed the same patterns in all estuaries. The bulk (90 %) of the particles found in adult stomachs were smaller than 85 μm (Elbe), 90μm (Westerschelde) and 125 μm (Gironde). In subadults and juveniles the bulk of the particles had smaller sizes. Particles with a maximal length up to 300 (Elbe), 500 μm (Westerschelde) and 600 μm (Gironde) were regularly found in the stomachs. In the three estuaries, the modes of the size frequency distributions were located around 30-35 μm. Adult *Neomysis integer* of the Westerschelde consumed the highest number of unidentifiable detrital particles (704 particles ind^{-1}), while for subadults and juveniles highest numbers were found in the Gironde (496 and 308 ind^{-1} respectively). Mean total numbers of detritus particles consumed by the three ontogenic stages were 158.82, 378.46 and 472.06 ind^{-1} in the Elbe, Westerschelde and Gironde.

Microscopic analysis of the 'unidentifiable fraction' of the detritus, using a petrographic optical microscope, revealed a high mineral content. The elemental composition of the detritus was assessed by EDAX analysis. In back-scattered electron (BSE) images of the samples, the flocs were easily identified as aggregates with much lighter grey values, indicating a major difference in composition between the flocs and other components (figure 5). For EDAX analyses, only flocs with lengths of 150-300 μm were used. The composition of the flocs was very similar in Elbe, Westerschelde and Gironde (figure 5 and table 5). The elemental composition, dominated by silicon and aluminium (around 60 % by weight) and with subordinate amounts of magnesium, potassium and iron, demonstrate that the flocs mainly consist of clay minerals. Part of the iron occurs in the form of pyrite (FeS_2), whose presence as individual crystals or grains, was often directly observed. Because a carbon coating was used, the carbon content of the flocs could not be quantified, but the EDAX spectra and BSE images show that their carbon content is not high. No diatoms or other unicellular organisms could be found attached to the flocs.

Comparison of developmental stages

The diet of subadults and juveniles consisted of the same prey categories as that of adults (figure 2; tables 3 and 4B), but generally a lower number of particles was consumed by the smaller mysids. Stomachs of juveniles in Westerschelde and Gironde contained significantly less detritus, calanoid copepods and colonial phytoplankton cells, compared to adults and subadults. In the Elbe the diet of juveniles was not that significantly different from the subadults, whereas in the Gironde the diet of adults resembled that of the subadults. The numbers of nauplii, harpacticoids and rotifers did not differ significantly between developmental stages. Ontogenic differences in number of solitairy phytoplankton consumed where only found in the Elbe. The number of pollen differed only in Elbe and Westerschelde, and Cladocera only in Elbe and Gironde. Adults and copepodites of *Eurytemora affinis* were the most important zooplankters consumed by all the mysid stages, except in the Elbe where rotifers are the most abundant zooplankters in the diet. In the Westerschelde and Gironde the smaller mysids selected significantly smaller copepods, whereas in the Elbe no significant difference in copepod size selection could be noted along the ontogenic stages (figure 3; table 4B). In the latter, the number of mandibles measured was significantly lower compared to the other estuaries.

The total number of detritus particles consumed was comparable for adults and subadults in the Gironde (593 and 509 particles ind^{-1}), while the stomachs of juveniles contained significantly less (315 ind^{-1}). In the Westerschelde the three ontogenic stages consumed different amounts of detritus: 741, 236 and 158 particles ind^{-1} for adults, subadults and juveniles. In the Elbe adults consumed significantly higher numbers of detritus (254.10 ind^{-1}) than subadults and juveniles (116.90 and 105.47 ind^{-1}). Macrophytal particles only accounted for a minor part of the total detrital fraction in the diet (3-5 % for adults, 2-3 % for subadults and juveniles). The mean size of the macrophyte detritus particles was independent with the size of the mysid: for all ontogenic stages the mean surface area per macrophyte particle lied around 0.004 mm² in Elbe and Westerschelde and 0.007 mm² in the Gironde. The size range of the unidentifiable detritus was comparable for the different mysid stages in the Gironde: all stages preferably consumed particles with a surface area smaller than 0.005 mm² (modus length 35 μm). In the Elbe and Westerschelde the size of the unidentifiable detritus particles found in the stomach decreased with the size of the mysid: modal length of 30 μm in adults, 15 μm in subadults and 10 μm in juveniles.

Comparison of sexes

For most dietary items no sexual difference was found. One exception is that the number of macrophytal detritus particles was higher in the stomachs of adult females (a factor of 2.3, 3.4 and 1.5 in the Elbe, Westerschelde and Gironde, respectively) and subadult females in the Elbe (factor 3.91). Another is that adult males in the Elbe consumed only 3.0 calanoid copepods per individual, whereas females contained 7.1.

Quantitative diet analysis

The dry weight of the empty stomachs could be derived from the following regression equation, after which the dry weight of the stomach content could be calculated by substraction.

$$\ln DW_{empty} \quad 5.04722 \;\; 0.513386 \ln DW_{mysid}$$
$$(N \; 89; \; r \;\; .672; \; p \;\; .000)$$

Although the fullness index (FI) should theoretically be independent to the weight of the mysid, a relationship between the 2 variables could be demonstrated (figure 6). This relation was comparable for the Elbe and Westerschelde. In the Gironde no correlation could be found between FI and DW_{mysid}. Adult individuals in the Gironde were much smaller than those in the Elbe and the Westerschelde (tables 2 and 3), which can partly explain the higher FI's in the Gironde. Furthermore, adult males were always smaller than females, which can explain their higher FI.

Because of the size dependence of the fullness indices, they could not simply be compared in time or space with ANOVA or Kruskall-Wallis tests. Differences between the dry weights of the stomach content ($DW_{content}$) in the three estuaries were therefore tested as such with ANCOVA, using DW_{mysid} as covariable and revealing differences as shown in table 6. Table 7 shows the adjusted values where the analyses are based on. The mean $DW_{content}$ of *Neomysis integer* from the three estuaries is shown in figure 7, for each weight class of 2 mg. Stomach contents are, for every size class, highest in the Gironde. For adult mysids stomach contents are lowest in the Elbe, for subadults and juveniles lowest in the Westerschelde. The stomach weights of adults, subadults and juveniles differed significantly. These differences where only significant for adults and juveniles. Smaller mysids had a smaller stomach content weight within each estuary. Adjusted for the weight of the mysid significant differences could be found between all ontogenic stages in the Westerschelde, between adults and subadults in the Elbe, and between adults on the one hand and subadults on the other in the Gironde. In non of the estuaries significant differences could be found between adult males and females.

DISCUSSION

A relative large size range of adult *Neomysis integer* was used for the stomach analyses (tables 3 and 4). This is not surprising, since the three populations were sampled in different stages of the annual population dynamical cycle. The different length-frequency distributions and population compositions found in the three estuaries can be explained by a seasonal temperature effect. The average temperatures in the MTZ's of the Elbe, Westerschelde and Gironde on the sampling campaign were 9°C, 15°C and 17°C, respectively. Studies on the population dynamics of *N. integer* in the Westerschelde (Mees *et al.*, 1994) and the Gironde (Mees & Sorbe, in preparation) have shown that the adults of the overwintering cohort are larger than those belonging to the summer generations and that the species does not reproduce when water temperature is lower than 10°C. In the Elbe, little juveniles were found and a considerable part of the females were gravid. The population was still in a 'late winter phase': individuals belonging to the spring generation were not born yet. The relative higher abundance of juveniles in the Westerschelde (12.8 % of the total density) and Gironde (14.8 %) was due to the fact that reproduction by the overwintering cohort took place before the time of sampling. The populations of *N. integer* in the latter two estuaries were sampled during the 'spring phase'. Although the sampling campaigns in the three estuaries were executed within a one month period, the latitudinal temperature effect was amplified by the North to South sequence of sampling. Also, the length at maturity has been found to increase with increasing latitude (Mees *et al.*, in preparation).

For the preparation of the microscopic slides the mysids were dehydrated from a formaldehyde solution to glycerin, in which the stomach content was subsequently embedded. This procedure yields semi-permanent slides in which artifacts are avoided. The stomach and oesophagus, together forming the foregut, were dissected. The oesophagus of *Neomysis integer* is short and muscular, and has spines and setae that tend to point towards the stomach. The stomach itself is internally armed with heavy spines and setae (Mauchline, 1980) used to macerate the food. Both parts are lined with chitin and do not play an important role in the digestive processes which take place in the midgut and its associated glands and diverticula (Brunet *et al.*, 1994). Generally, the gut passage time of mysids is recorded in the range of 30-90 minutes (Zagursky & Feller, 1985), so the particles present in the stomach will give a good idea about the recently ingested food. The microscopic slides contained parts of the stomach and oesophagus tissue. The cell structure and armature were easily distinguished from parts of zooplanktonic prey categories.

The frequencies of occurrence (table 3) of the ingested prey items were usually higher than 60 %, except for calanoid nauplii, harpacticoids and cladocerans. Therefore, the within variation of a sample is low and the analysis of 30 animals per sample sufficed to describe the diet of *Neomysis integer* (Hyslop, 1980).

Neomysis integer mainly fed upon mesozooplankton. It consumed 5.07, 10.27 and 8.00 copepods per adult mysid in the MTZ's of Elbe, Westerschelde and Gironde, respectively. Subadults and juveniles consumed subsequently less copepods (table 3).

Although the gut passage time of mysids is in the order of one hour, it is known that rigid zooplankton parts (*e.g.* mandibles) can stay in the stomachs for more than 12 hours (Rudstam *et al.*, 1989). The counting of the number of mandibles present in the stomach can therefore result in an overestimation of the actual number of copepods consumed. Late copepodite stages and adults of *Eurytemora affinis* contain 4-7 µg C per individual (MATURE database: Castel *et al.*). They are making up the most important prey item in the energy uptake of *N. integer* in the MTZ of estuaries. Siegfried and Kopache (1980) quantified the relative importance of carnivory up to 90% of the total nutritional uptake of *Neomysis mercedis*. 90-100 % of the diet of *Mysis mixta* consisted of copepods and cladocera (Rudstam *et al.*, 1989). However in both studies, the detritus was not included in the calculation, thus overestimating the importance of carnivory.

During the same sampling campaigns in spring 1993, the densities of adult and copepodite stages of *Eurytemora affinis* in the MTZ of the Elbe and Westerschelde were in the order of 10000 and 40000 individuals per m^3, respectively (MATURE database: Castel *et al.*). No data were available on copepod densities in the MTZ of the Gironde for spring 1993, although in the MTZ of the Gironde a density between 5000 and 15000 individuals per m^3 can be expected in March-April (Castel & Veiga, 1990). The results of the qualitative analysis indicate a positive correlation between the densities and the predation by *Neomysis integer* on *E. affinis*. Similar results are found for other mysid species: the predation rate was found to increase with the copepod densities (*e.g.* Siegfried & Kopache, 1980; Bowers & Vanderploeg, 1982; Folt *et al.*, 1982). No other calanoid copepod species were found in the stomachs of *N. integer*, although some were recorded in the watercolumn in low densities: in the MTZ of the Elbe *Diaptomus* species were present with 25 ind m^{-3} and in the Westerschelde species of the genus *Acartia* and *Temora* were recorded with densities of 400 ind m^{-3}. In the three estuaries cyclopoid copepods were abundant in the MTZ: 1000, 800 and 300 (the latter in 1994) individuals per m^3 were recorded in Elbe, Westerschelde and Gironde, respectively. Nevertheless they were never encountered in the stomachs of *N. integer*, probably due to a higher escape response of the cyclopoids, as compared to *E. affinis* (Tackx, pers. comm.).

In spring 1993 high densities of calanoid nauplii were recorded in the watercolumn (79000 and 23000 individuals per m^3 in Elbe and Westerschelde, respectively). *Neomysis integer* seems to show a negative selection for nauplii. Also *Neomysis mercedis* (Murtaugh, 1981b; Siegfried & Kopache, 1980) and *Mysis relicta* (Siegfried & Kopache, 1980; Bowers & Vanderploeg, 1982) do not consume nauplii in large amounts. Nauplii can be less represented in the diet of the mysid because adult and copepodite stages of calanoids, which are energetically more valuable, are positively selected. Or they might be more successful in avoiding the mysid feeding current than are the later life stages. Another explanation can be the high digestion rate of these soft prey items (Rudstam *et al.*, 1989), which can result in an underestimation of the predation on this prey by means of stomach analysis.

Although Harpacticoida were very abundant in the meiobenthos communities of the subtidal sediments in the MTZ of Elbe (4500 ind m^{-2}), Westerschelde (2000 ind m^{-2}) and Gironde (9000 ind m^{-2}) (MATURE database: Vincx *et al.*), they were hardly consumed by *Neomysis integer*. Other meiobenthic animals and microphytobenthic diatoms were very rarely encountered in the stomachs. This indicates that the mysids feed in the hyperbenthic layer of the watercolumn and do not scrape the bottom while foraging. Low densities of harpacticoid copepods were found in the watercolumn in Elbe (25 ind m^{-3}) and Westerschelde (800 ind m^{-3}) (MATURE database: Castel *et al.*) and it might be possible these free swimming individuals were caught.

The numbers of Cladocera and Rotifera consumed by *Neomysis integer* in the three estuaries could not be related to the availability in the watercolumn.

Neomysis integer consumed filamental algae rather than solitary phytoplankton cells. Siegfried & Kopache (1980) reported already for *Neomysis mercedis* a higher selectivity for larger algae and filamental cells, while small phytoplankters were not consumed in high numbers although very abundant in the environment. Some ten algal cells per individual (figure 2, table 3) were consumed by *N. integer* in Elbe, Westerschelde and Gironde. Still, the importance in the diet of the mysids is negligible: the most abundant phytoplankton species found in the MTZ of the three estuaries have a carbon content between 1-13 pg C per cell (Muylaert & Sabbe, pers. comm).

Moreover one has to keep in mind that in the turbid zone of estuaries, where peak densities of *N. integer* are encountered, phytoplankton concentrations generally are low (Muylaert & Sabbe, submitted in same volume). In most cases, it was impossible to identify the phytoplankton up to genus or species level. Still, a distinction could be made between specimens from fresh, brackish or marine origin. In the three estuaries mainly algae from the brackish and freshwater parts of the system were consumed: *Thalassiosira proschkinae*, *Nannochloris coccoides*, *Paralia sulcata*, *Pediastrum species* and colonial chlorophyta (figure 1.h) were the most common. Phytoplankton from the more marine reaches of the estuary (*e.g. Skeletonema species*) were rarely encountered in the stomachs. Filamental phytobenthic strands from the brackish zone (*Vaucheria species*: figure 1.j) could be recognised in the stomachs from the three estuaries. The samples of *Neomysis integer* were all taken in the subtidal channels of the estuaries. The presence of intertidal algal strands in the stomachs of subtidally caught mysids could indicate on horizontal migration of *N. integer* to intertidal areas for feeding, although the possibility that the strands were teared off and drifting in the subtidal water can not be eliminated.

Pollen of gymnosperms were mainly found in the stomachs in Westerschelde and Gironde. The rivers Schelde and Garonne run through extensive pine forests. It is not known if the pollen are selectively ingested, nor if they can be digested by *Neomysis integer*. Pine pollen were also found in the stomachs of the euryhaline mysid *Mysis mixta* from the Baltic Sea (Rudstam *et al.*, 1989) and were supposed to be digested (individual carbon content of 5 ng).

3-5 % of the total number of detrital particles consumed by *Neomysis integer* in the three estuaries was clearly from macrophytal origin. It is possible that the mysid fragments larger macrophyte detritus particles to a size between 1000 and 20000 μm^2 before ingestion. *Neomysis integer* possesses cellulase enzymes (Zagursky and Feller, 1985), so the species can theoretically digest the macrophytal detritus. It is not known if they are capable of deriving substantial nutrition directly from macrophyte detritus either via digestion with its own cellulases or by an associated gut microflora. *Mysis stenolepis* has an assimilation efficiency of 30-50 % on sterile cellulose (Foulds & Mann, 1978; Wainwright & Mann, 1982). Artificially made macrophytal detritus of *Spartina alterniflora* (Zagursky & Feller, 1985) contains 42.7% C and 2.4% N of the total dry weight. This detritus can serve as a nutritionally significant food item for *Neomysis americana*, especially in periods of low availability of other nutritionally more valuable food items. Hence mysids can be an important link between (march-) macrophyte production and higher trophic levels.

However the bulk of the 'unidentifiable detritus' originated from sediment flocs present in the watercolumn, some of the particles counted as unidentifiable detritus probably were partly digested zooplankton and phytoplankton or originated from the stomach contents of ingested prey species (Kinne, 1955; Siegfried & Kopache, 1980; Mauchline, 1980; Jansen, 1985). According to Eisma (1987) two size groups of flocs can be found suspended in the watercolumn. Microflocs are firmly held together and have lengths between 1 and 125 µm. Together with single mineral particles these microflocs are the basic units of the more loosely bound, fragile macroflocs. The latter can reach sizes of 3-4 mm in turbid water. The 'unidentifiable detritus' particles in the stomachs of *Neomysis integer* were within the range of 10 to 500 µm length and the fraction smaller than 125 µm was dominant.

By EDAX technique it was impossible to quantify the relative concentration of carbon in the flocs, because of the carbon coating. Analysis of the particles with diffracted electronic beams showed a general low concentration of carbon present in the flocs. The particulate organic carbon (POC) of the river suspended matter is on average between 1 and 5% (Eisma, 1985). If the carbon content of the unidentifiable detritus is assumed to be of the same order, the importance in the energy balance of *N. integer* is negligible. The reason why so many flocs are present in the stomach can not be explained. The uptake might occur accidentally when feeding on other prey items. No associated bacteria, fungi, nanoflagelates, Protozoa or diatoms were found on the detritus flocs in the stomachs, but this can be due to the conservation method used.

No clear ontogenetic shifts in the diet composition were observed, though a smaller number of particles was consumed by smaller mysids. The size of a freshly hatched *Neomysis integer* is 2-3 mm (Fockedey, unpublished).

Due to the sampling gear it was not possible to collect the smallest juveniles of 2 to 4 mm (Mees *et al.*, 1994), hence no investigations could be made on this size range of mysids. Studies on *Neomysis mercedis* revealed an ontogenic shift in diet composition during the individuals growth (Kost & Knight, 1975; Siegfried & Kopache, 1980). Main changes were found for the small juveniles (2-3 mm). Differences in feeding by various life stages can allow for an efficient partitioning of food resources, reducing intraspecific competition (Siegfried & Kopache, 1980).

The mandible widths of the calanoids consumed decreased with the size of the mysid in the Gironde and Westerschelde. Although juvenile *Neomysis integer* consume the smallest calanoid copepodite stages, still spermatophores were frequently found in their stomachs. Since these are attached to the gonopores of adult females only, it suggests that juvenile mysids at least hunt adult calanoid copepods. In the Elbe *Neomysis integer* did not show a size selectivity for *Eurytemora affinis*.

Female mysids were significantly larger than males. Nevertheless, no significant differences were found in the diet composition, nor in the number of items consumed. One can conclude that male individuals ate relatively more than the females.

In this study a description of the diet of *Neomysis integer* is made for a spring situation in the MTZ's of three European estuaries, but one has to keep in mind that the diet can be vary considerably with the tides, the day/night cycle and seasonally (*e.g.* Zagursky & Feller, 1985).

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Abbreviation	
EL	Elbe individuals
WS	Westerschelde individuals
GI	Gironde individuals
ad	adults
sub	subadults
juv	juveniles
mal	males separately
fem	females separately

Table 1: Abbreviations used in the following figures and tables

	Elbe		**Westerschelde**		**Gironde**	
	N/m^2 (%)	mg/m^2 (%)	N/m^2 (%)	mg/m^2 (%)	N/m^2 (%)	mg/m^2 (%)
ad fem	9.4 (26.1)	70.5 (38.2)	2.0 (21.3)	16.9 (43.3)	0.7 (6.5)	2.3 (10.7)
ad fem (gravid)	5.0 (13.9)	41.7 (22.6)	0.9 (9.6)	7.8 (20.0)	0.3 (2.8)	0.9 (4.2)
ad mal	3.6 (10.0)	13.6 (7.4)	1.6 (17.0)	7.7 (19.7)	0.1 (0.9)	0.2 (0.9)
sub fem	12.7 (35.3)	44.6 (24.2)	1.8 (19.1)	3.0 (7.7)	6.3 (58.3)	13.1 (60.9)
sub mal	5.1 (14.2)	13.8 (7.5)	1.9 (20.2)	2.9 (7.4)	1.8 (16.7)	3.2 (14.9)
juv	0.2 (0.6)	0.4 (0.2)	1.2 (12.8)	0.7 (1.8)	1.6 (14.8)	1.8 (8.4)
TOTAL	36.0	184.6	9.4	39.0	10.8	21.5

Table 2: Absolute and relative density (in N/m^2 and %) and biomass (in mg/m^2 and %) of *Neomysis integer* in the MTZ of Elbe, Westerschelde, and Gironde.

	ELad	ELsub	ELjuv	WSad	WSsub	WSjuv	GIad	GIsub	GIjuv
Standard length (mm)	12.53±0.27 (90)	9.70±0.13 (89)	7.27±0.20 (22)	13.44±0.26 (90)	7.16±0.12 (89)	4.69±0.10 (45)	9.42±0.09 (90)	7.95±0.11 (75)	6.26±0.10 (45)
Unidentifiable detritus Surface (mm^2)	0.224±0.038 100% (15)	0.052±0.009 100% (15)	0.030±0.007 100% (15)	0.821±0.125 100% (15)	0.192±0.026 100% (15)	0.079±0.013 100% (15)	1.184±0.126 100% (15)	1.369±0.149 100% (14)	0.634±0.052 100% (15)
Unidentifiable detritus Number	241.53±54.83 100% (15)	113.47±13.37 100% (15)	103.87±11.62 100% (15)	704.13±140.98 100% (15)	229.93±23.13 100% (15)	155.20±13.06 100% (15)	572.20±61.50 100% (15)	496.36±34.57 100% (14)	308.13±32.88 100% (15)
Macrophyte detritus Surface (mm^2)	0.061±0.020 93% (15)	0.016±0.006 77% (30)	0.007±0.003 60% (30)	0.152±0.048 100% (15)	027±0.06 93% (30)	0.013±0.003 73% (30)	0.152±0.035 100% (15)	0.084±0.014 100% (14)	0.047±0.011 93% (15)
Macrophyte detritus Number	12.57±1.89 97% (30)	3.43±1.02 77% (30)	1.60±0.41 60% (30)	36.50±7.04 100% (30)	6.40±1.12 93% (30)	3.23±0.77 73% (30)	20.30±2.05 100% (27)	12.62±1.99 100% (29)	6.57±0.91 93% (30)
Calanoidea Adult & copepodite	5.07±0.62 100% (30)	2.43±0.32 97% (30)	1.77±0.18 93% (30)	10.27±0.68 100% (30)	4.20±0.32 100% (30)	2.20±0.21 100% (30)	8.00±0.73 100% (27)	5.72±0.31 100% (29)	2.90±0.32 97% (30)
Calanoidea Mandible width (μm)	33.46±0.93 (206)	35.82±1.71 (85)	36.94±2.04 (53)	43.47±0.66 (407)	39.38±0.84 (204)	38.04±1.34 (84)	36.79±0.58 (320)	35.08±0.68 (271)	32.45±0.90 (137)
Calanoidea Nauplii	0.03±0.03 3% (30)	0.23±0.09 20% (30)	0.07±0.05 70% (30)	0.00±0.00 0% (30)	0.00±0.00 0% (30)	0.00±0.00 0% (30)	0.15±0.07 15% (27)	0.00±0.00 0% (29)	0.10±0.06 10% (30)
Harpacticoidea	0.40±0.12 33% (30)	0.40±0.11 33% (30)	0.20±0.07 20% (30)	0.07±0.05 7% (30)	0.00±0.00 0% (30)	0.00±0.00 0% (30)	0.07±0.05 7% (27)	0.00±0.00 0% (29)	0.03±0.03 3% (30)
Cladocera	0.80±0.11 70% (30)	0.37±0.10 33% (30)	0.40±0.09 40% (30)	0.07±0.05 7% (30)	0.00±0.00 0% (30)	0.03±0.03 0.03% (30)	0.96±0.16 70% (27)	1.03±0.14 76% (29)	0.40±0.12 33% (30)
Rotifera	22.17±2.50 100% (30)	21.83±2.05 100% (30)	16.10±1.43 100% (30)	0.27±0.10 23% (30)	0.17±0.07 17% (30)	0.40±0.14 27% (30)	1.93±0.38 67% (27)	1.38±0.22 79% (29)	1.87±0.29 83% (30)
Phytoplankton solitary	2.53±0.42 77% (30)	33.73±6.72 100% (30)	22.63±6.03 97% (30)	3.40±0.50 87% (30)	4.30±0.78 93% (30)	2.67±0.39 90% (30)	6.93±2.35 85% (27)	7.45±3.86 66% (29)	3.40±0.47 93% (30)
Phytoplankton colonial	42.50±17.63 77% (30)	10.80±4.85 47% (30)	26.90±8.69 63% (30)	34.40±12.75 83% (30)	19.57±9.27 57% (30)	35.20±7.23 97% (30)	24.89±6.52 96% (27)	28.24±5.40 97% (29)	11.83±3.33 73% (30)
Pollen	5.93±0.53 97% (30)	4.50±0.51 97% (30)	3.47±0.44 90% (30)	15.80±1.41 100% (30)	9.80±1.05 100% (30)	9.07±0.92 100% (30)	14.00±1.02 100% (27)	13.31±0.79 100% (29)	14.20±1.18 100% (30)

Table 3: Means and standard errors for the different dietary items in Neomysis integer of Elbe, Westerschelde and Gironde. Second line: frequency of occurence (%) and between brackets, the number analyzed.

	LATITUDE								
	ELad vs WSad	ELad vs GIad	WSad vs GIad	ELsub vs WSsub	ELsub vs GIsub	WSsub vs GIsub	ELjuv vs WSjuv	ELjuv vs GIjuv	WSjuv vs GIjuv
Standard length (mm)	**	***	***	***	***	***	***	***	***
Unidentifiable detritus Surface area (µm^2)	***	***	*	***	***	***	***	***	***
Unidentifiable detritus Number	***	***	NS	***	***	***	*	***	***
Macrophyte detritus Surface area (µm^2)	NS	**	NS	*	***	***	NS	***	**
Macrophyte detritus Number	**	**	NS	**	***	**	NS	***	**
Calanoidea Adult & copepodite	***	**	*	***	***	**	NS	*	NS
Calanoidea (*) Mandible width (µm)	***	***	***	**	NS	***	NS	*	***
Calanoidea Nauplii	NS	NS	NS	NS	NS	NS	NS	NS	NS
Harpacticoidea	NS	NS	NS	*	*	NS	NS	NS	NS
Cladocera	***	NS	***	*	**	***	*	NS	*
Rotifera	***	***	***	***	***	***	***	***	***
Phytoplankton solitary	NS	*	NS	***	***	NS	***	***	NS
Phytoplankton colonial	NS	NS	NS	NS	***	***	**	NS	***
Pollen	***	***	NS	***	***	**	***	***	***

Table 4A: Results of the Mann-Whitney U-tests for the different dietary items for adult, subadult, and juvenile Neomysis integer of Elbe, Westerschelde and Gironde (latitudinal effect). [(*): contrast analysis]
(with *: $p < .05$; **: $p < .01$; ***: $p < .001$; NS: $p > .05$)

	ONTOGENY								
	ELad vs ELsub	ELad vs ELJuv	ELsub vs ELjuv	WSad vs WSsub	WSad vs WSjuv	WSsub vs WSjuv	GIad vs GIsub	GIad vs GIjuv	GIsub vs GIjuv
Standard length (mm)	***	***	***	***	***	***	***	***	***
Unidentifiable detritus Surface area (µm²)	***	***	*	***	***	**	NS	**	***
Unidentifiable detritus Number	*	**	NS	***	***	*	NS	**	***
Macrophyte detritus Surface area (µm²)	**	***	NS	***	***	*	NS	**	*
Macrophyte detritus Number	***	***	NS	***	***	**	**	***	**
Calanoidea Adult & copepodite	***	***	NS	***	***	***	*	***	***
Calanoidea (*) Mandible width (µm)	NS	NS	NS	***	***	NS	*	***	*
Calanoidea Nauplii	NS	NS	NS	NS	NS	NS	NS	NS	NS
Harpacticoidea	NS	NS	NS	NS	NS	NS	NS	NS	NS
Cladocera	*	*	NS	NS	NS	NS	NS	**	**
Rotifera	NS	NS	*	NS	NS	NS	NS	NS	NS
Phytoplankton solitary	***	***	NS	NS	NS	NS	NS	NS	NS
Phytoplankton colonial	**	NS	NS	*	NS	***	NS	*	**
Pollen	*	***	NS	**	***	NS	NS	NS	NS

Table 4B: Results of the Mann-Whitney U-tests for the different dietary items for adult, subadult, and juvenile Neomysis integer of Elbe, Westerschelde and Gironde (ontogenic effect). [(*): Contrast analysis] (with *: $p < .05$; **: $p < .01$; ***: $p < .001$; NS: $p > .05$)

	SEX					
	ELad mal vs ELad fem	ELsub mal vs ELsub fem	WSad mal vs WSad fem	WSsub mal vs WSsub fem	GIad mal vs GIad fem	GIsub mal vs GIsub fem
Standard length (mm)	***	***	***	NS	***	**
Unidentifiable detritus Surface area (µm²)	no data	no data	no data	no data	no data	no data
Unidentifiable detritus Number	no data	no data	no data	no data	no data	no data
Macrophyte detritus Surface area (µm²)	no data	*	no data	NS	no data	no data
Macrophyte detritus Number	**	*	***	NS	**	NS
Calanoidea Adult & copepodite	***	NS	NS	NS	NS	NS
Calanoidea (*) Mandible width (µm)	NS	NS	NS	NS	NS	NS
Calanoidea Nauplii	NS	NS	NS	NS	NS	NS
Harpacticoidea	NS	NS	NS	NS	NS	NS
Cladocera	NS	NS	NS	NS	NS	NS
Rotifera	NS	*	NS	NS	NS	NS
Phytoplankton solitary	NS	NS	NS	NS	NS	NS
Phytoplankton colonial	NS	NS	NS	NS	NS	NS
Pollen	NS	NS	NS	NS	NS	NS

Table 4C: Results of the Mann-Whitney U-tests for the different dietary items for adult and subadult male and female Neomysis integer of Elbe, Westerschelde and Gironde (sexual effect). [(*): t-test]
(with *: $p < .05$; **: $p < .01$; ***: $p < .001$; NS: $p > .05$)

Element	ELad	WSad	GIad
Mg	2.65 ± 0.51	1.30 ± 0.48	2.09 ± 0.35
Al	15.56 ± 0.82	13.52 ± 0.85	20.56 ± 0.70
Si	41.87 ± 1.16	43.61 ± 1.28	44.71 ± 0.99
P	4.87 ± 1.21	5.57 ± 1.38	1.45 ± 0.89
S	5.05 ± 0.82	1.78 ± 0.90	1.71 ± 0.59
K	5.59 ± 0.73	5.85 ± 0.93	6.76 ± 0.67
Ca	6.10 ± 0.86	13.24 ± 1.20	11.13 ± 0.85
Fe	18.20 ± 1.91	15.13 ± 2.36	11.58 ± 1.60

Table 5: Relative elemental composition (weight percent ± S.E.) of the flocs found in the stomachs of adult Neomysis integer from Elbe, Westerschelde and Gironde. Note that the relative abundance was calculated with the eight most abundant elements, excluding C and O.

LATITUDE: ***		ONTOGENY: ***		SEX: *	
EL vs. WS	NS	AD vs. SUB	NS	Mal vs. Fem	*
EL vs. GI	***	AD vs. JUV	***		
WS vs. GI	***	SUB vs. JUV	**		
LATITUDE & ONTOGENY: ***				LATITUDE & SEX: NS	
ELad vs. WSad	NS	ELad vs. ELsub	*	ELad mal vs. ELad fem	NS
ELad vs. GIad	***	ELad vs. EL juv	*	WSad mal vs. WSad fem	NS
WSad vs. GIad	***	ELsub vs. ELjuv	NS	GIad mal vs. GIad fem	NS
ELsub vs. WSsub	NS	WSad vs. WSsub	**	ELad mal vs. WSad mal	NS
ELsub vs. GIsub	**	WSad vs. WS juv	**	ELad mal vs. GIad mal	***
WSsub vs. GIsub	*	WSsub vs. WSjuv	NS	WSad mal vs. GIad mal	***
ELjuv vs. WSjuv	NS	GIad vs. GIsub	**	ELad fem vs. WSad fem	NS
ELjuv vs. GIjuv	***	GIad vs. GI juv	***	ELad fem vs. GIad fem	***
WSjuv vs. GIjuv	***	GIsub vs. GIjuv	***	WSad fem vs. GIad fem	***

Table 6: Result of the two-way ANOVA's on the dry weights of the fullness index (FI) for the latitudinal-ontogenic and latitudinal-sexual effects.
(with *: $p < .05$; **: $p < .01$; ***: $p < .001$; NS: $p > .05$)

	LATITUDE		
	Mean DWcontent	Mean DWmysid	Adjusted mean DWcontent
ELad	0.01994	3.24299	0.01989
WSad	0.03920	6.76119	0.02625
GIad	0.03836	1.54319	0.05135
ELsub	0.00900	1.10816	0.00893
WSsub	0.00797	0.74748	0.00804
GIsub	0.01462	0.96071	0.01460
ELjuv	0.00413	0.43887	0.00305
WSjuv	0.00281	0.25225	0.00292
GIjuv	0.00616	0.17320	0.00804

	ONTOGENY		
	Mean DWcontent	Mean DWmysid	Adjusted mean DWcontent
ELad	0.01705	3.24299	0.00665
ELsub	0.00900	1.10816	0.00941
ELjuv	0.00413	0.43887	0.01013
WSad	0.03721	6.76119	0.02170
WSsub	0.00797	0.74748	0.00890
WSjuv	0.00281	0.25225	0.00432
GIad	0.03630	1.54319	0.02494
GIsub	0.01462	0.96071	0.01228
GIjuv	0.00616	0.17320	0.01067

	SEX		
	Mean DWcontent	Mean DWmysid	Adjusted mean DWcontent
ELad mal	0.01114	2.02897	0.01718
ELad fem	0.02610	5.18340	0.01692
WSad mal	0.03497	5.54258	0.03689
WSad fem	0.03971	8.33445	0.03765
GIad mal	0.03239	1.32990	0.03521
GIad fem	0.04069	1.89240	0.03743

Table 7: Mean DWcontent, mean DWmysid and adjusted mean DWcontent (backtransformed) used in the one-way ANCOVA's on the dry weight of the stomach contents (DWcontent in mg) with the dry weight of the mysid (DWmysid in mg) as covariable covariable for the latitudinal, ontogenic and sexual effects.
(with *: $p < .05$; **: $p < .01$; ***: $p < .001$; NS: $p > .05$)

FIGURE CAPTIONS

Figure 1: The dominant prey items found in the stomachs of *Neomysis integer* in the Elbe, Westerschelde and Gironde. **Zooplankton**: (a) mandible of *Eurytemora affinis*; (b) part of the calanoid copepod *Eurytemora affinis*; in the bottom left corner the caudal rami are recognisable; (c) *Keratella species*; (d) *Bosmina species;* (e) caudal part of a harpacticoid copepod; (f) *Brachyonus species*; (g) Halacaridea species. **Algae**: (h) Filamental Chlorophyta; (i) filamental centricate diatom; (j) the intertidal benthic *Vaucheria species*; centricate diatom in frontal (k) and lateral (l) view. **Pollen**: (m and o) round forms and (n) pollen of gymnosperms. **Detritus**: (p and q) macrophytal and (r) unidentifiable detritus particles.

Figure 2: Absolute composition of the diet (in number per individual) of adult, subadult and juvenile *Neomysis integer* for the Elbe, Westerschelde and Gironde.

Figure 3: Mean mandible width (and standard error) of the calanoid copepods (*Eurytemora affinis*) consumed by adult, subadult and juvenile *Neomysis integer* in Elbe, Westerschelde and Gironde.

Figure 4: Length- (left) and surface area (right) frequency distribution of macrophyte detritus (top) and 'unidentifiable' detritus (bottom) present in the stomach of adult *Neomysis integer* in the MTZ of the Gironde.

Figure 5: Output of an EDAX analysis on 'unidentifiable' detritus particles from the stomach contents of adult *Neomysis integer* in the Elbe (a), Westerschelde (b) and Gironde (c). The X-axis was cut off short of the primary Fe-peaks (located around 6.4 and 7.1 keV). Upper right corner: back-scattered electron (BSE) image of an analyzed floc.

Figure 6: Relationship between the fullness index (FI) and the dry weights of the mysids (DW_{mysid}) for adult male and female *Neomysis integer* in Elbe, Westerschelde and Gironde.

Figure 7: The mean dry weight of the stomach content for different size classes of adult, subadult and juvenile *Neomysis integer* in Elbe, Westerschelde and Gironde.

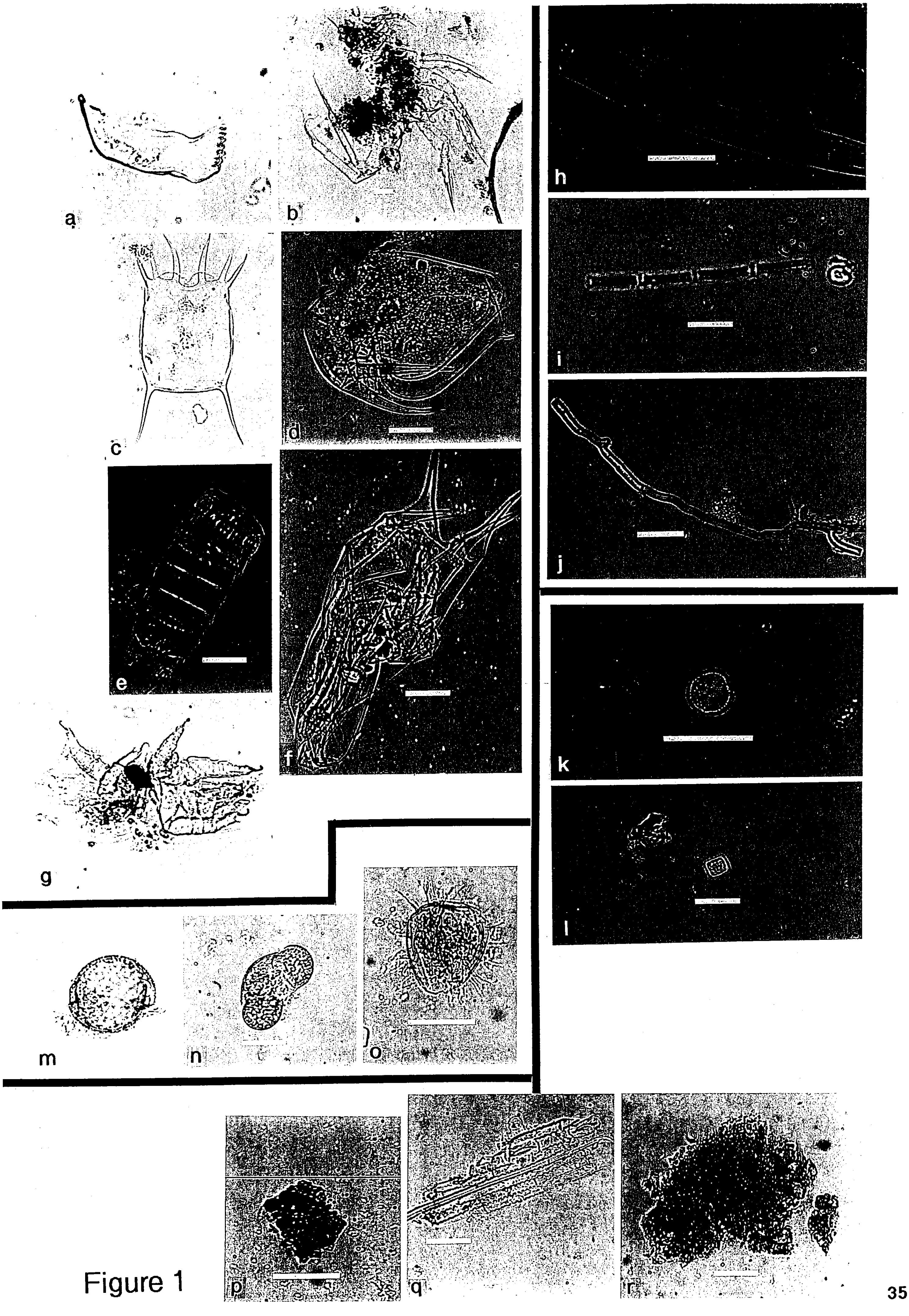


Figure 1

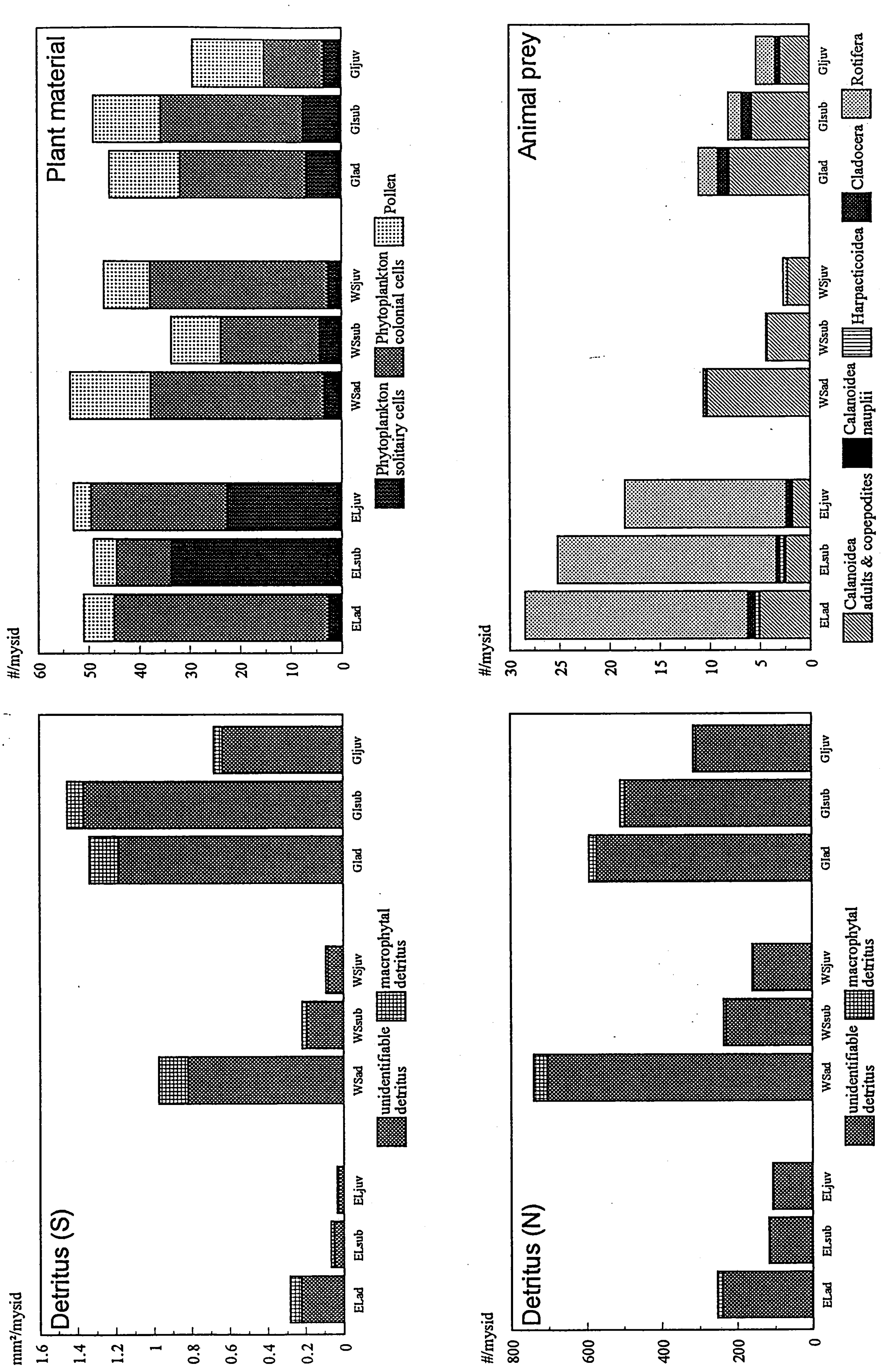

Detritus (S)
mm²/mysid
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
unidentifiable detritus
macrophytal detritus
Plant material
#/mysid
60
50
40
30
20
10
0
Phytoplankton solitary cells
Phytoplankton colonial cells
Pollen
Detritus (N)
#/mysid
800
600
400
200
0
unidentifiable detritus
macrophytal detritus
Animal prey
#/mysid
30
25
20
15
10
5
0
Calanoidea adults & copepodites
Calanoidea nauplii
Harpacticoidea
Cladocera
Rotifera
ELad
ELsub
ELjuv
WSad
WSsub
WSjuv
Glad
Glsub
Gljuv

Figure 2

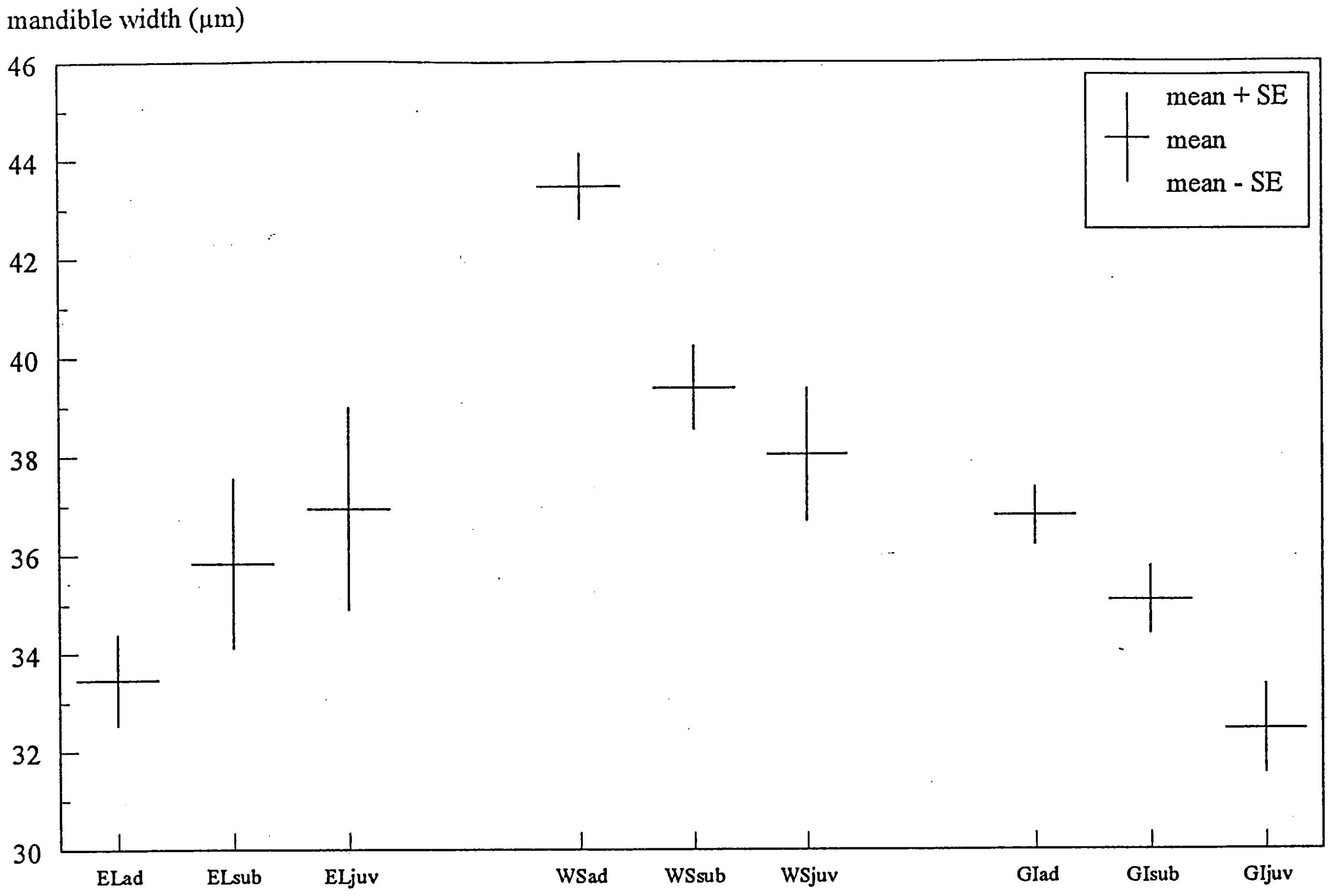
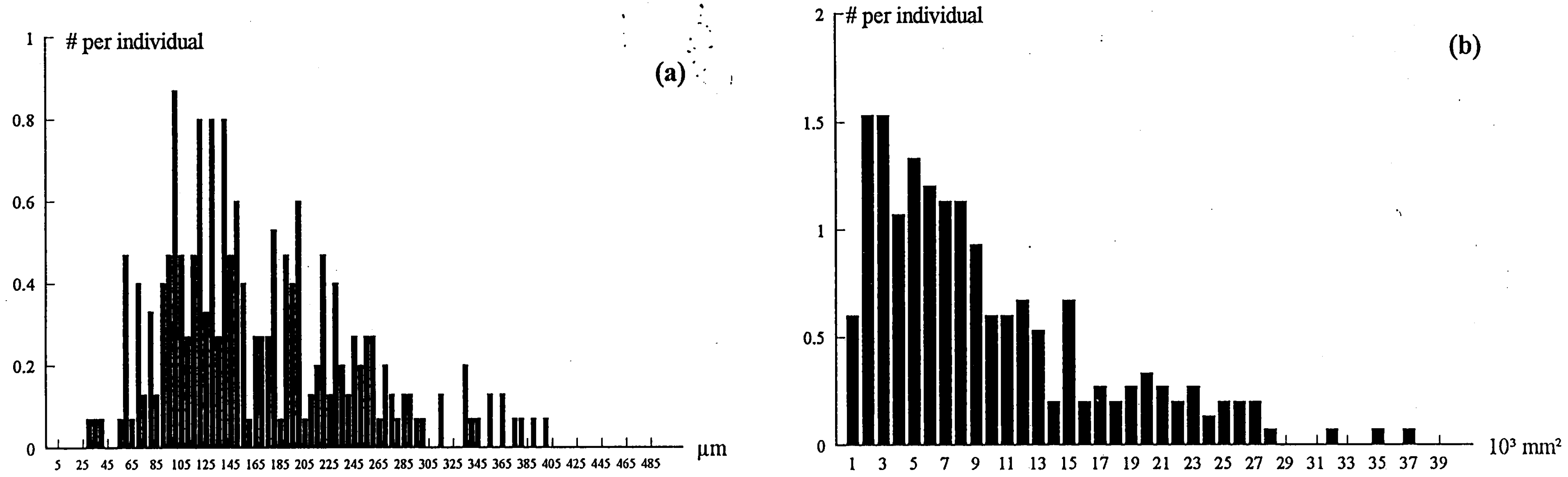

mandible width (μm)
46
44
42
40
38
36
34
32
30
mean + SE
mean
mean - SE
ELad
ELsub
ELjuv
WSad
WSsub
WSjuv
GIad
GIsub
GIjuv

Figure 3

MACROPHYTE DETRITUS



UNIDENTIFIABLE DETRITUS

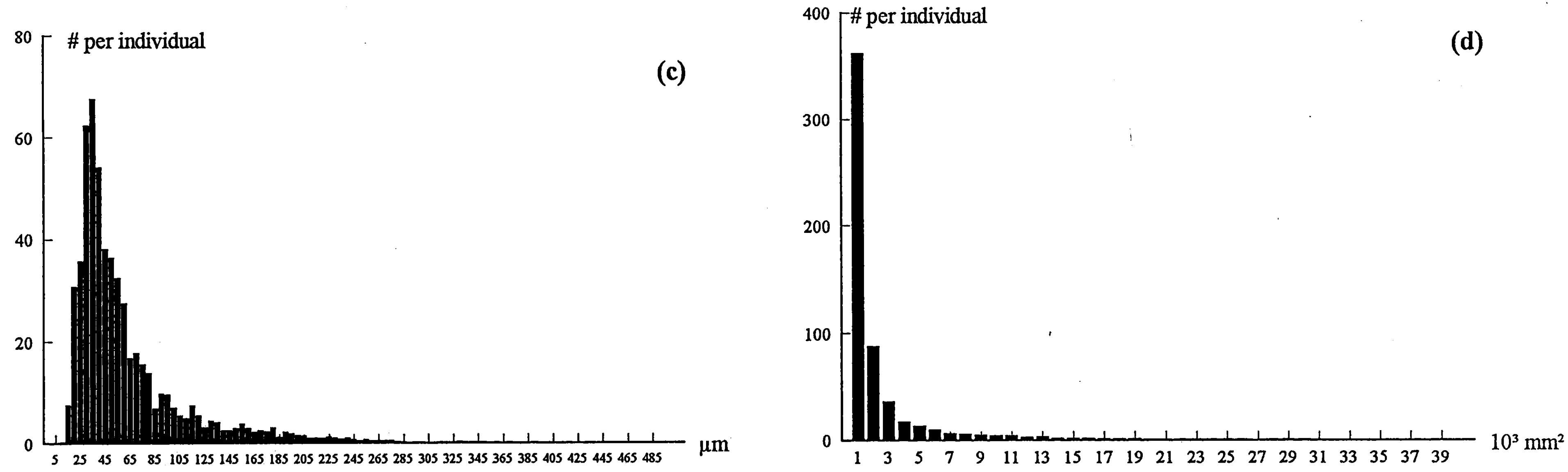


Figure 4

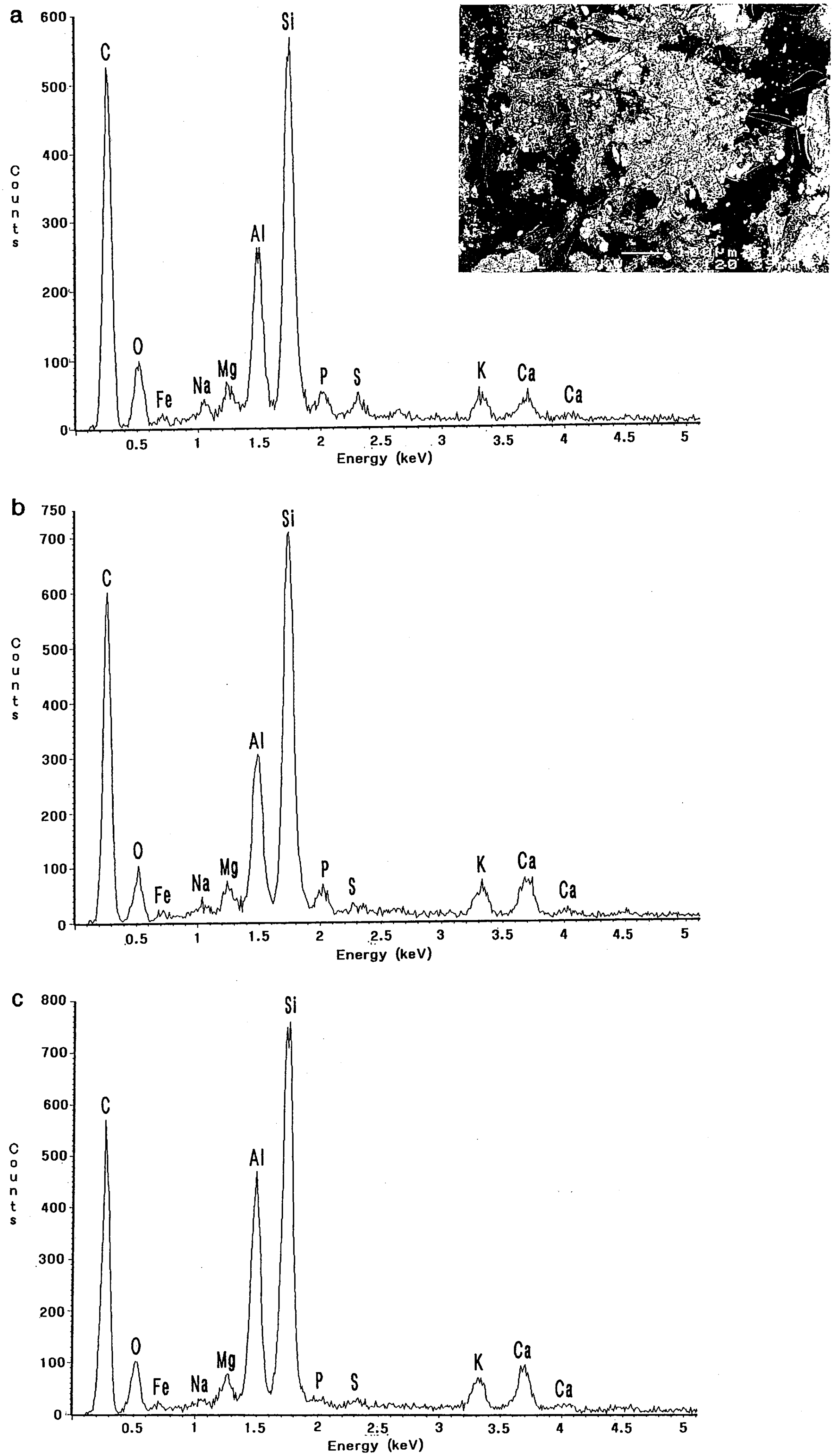

a
b
c
Counts
Energy (keV)
0
100
200
300
400
500
600
700
750
800
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
C
O
Fe
Na
Mg
Al
Si
P
S
K
Ca
Ca

Figure 5

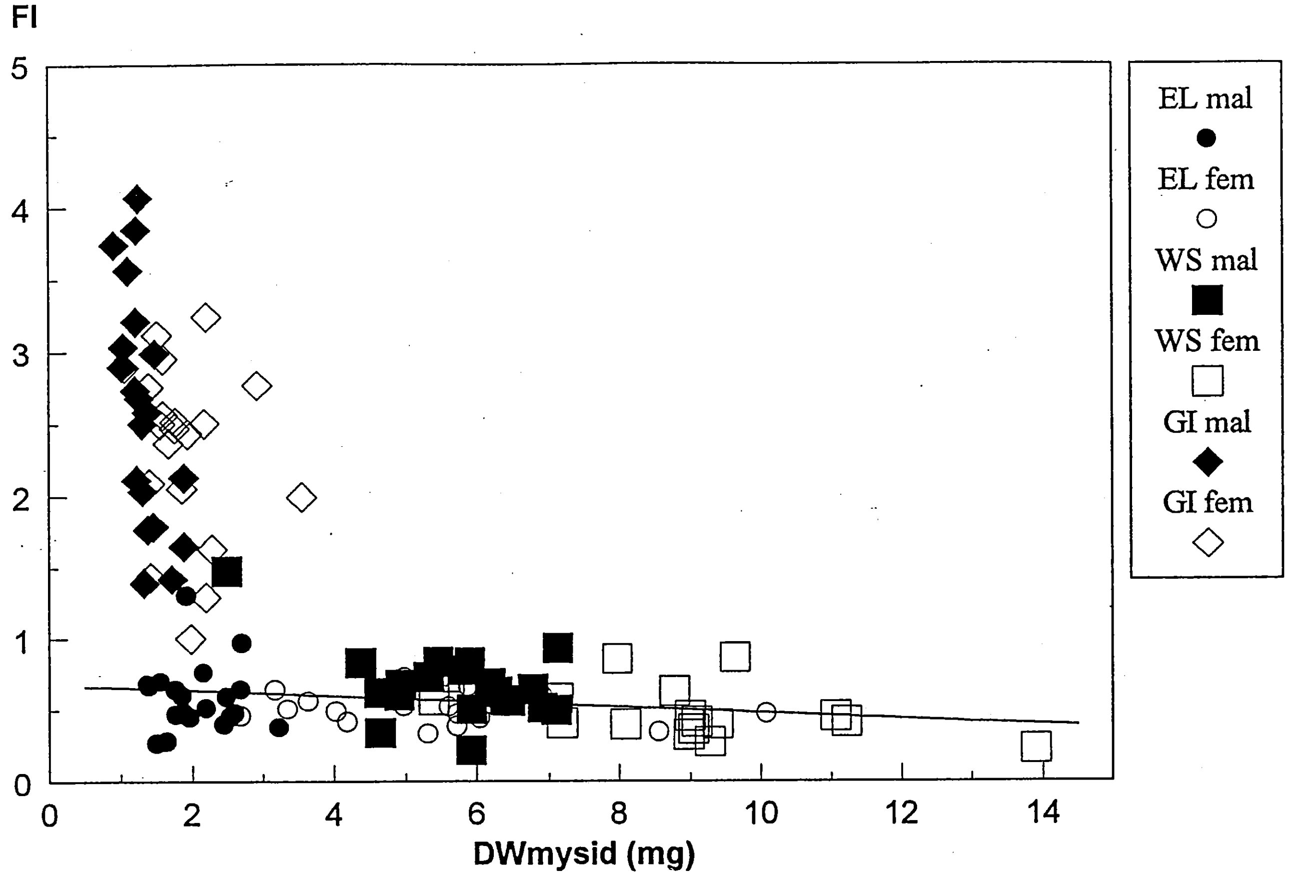


Figure 6

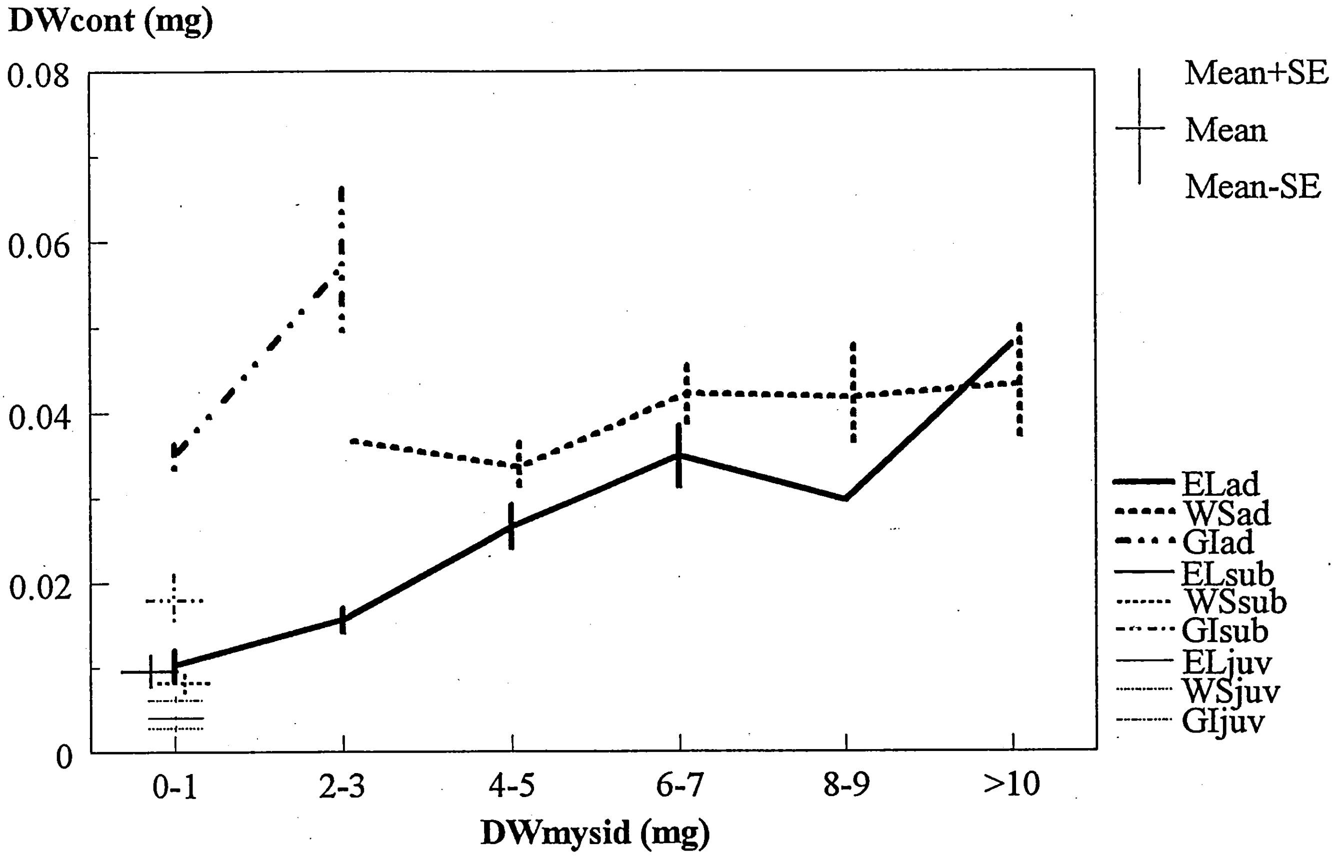


Figure 7

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

Jan Mees, Zekeria Abdulkerim, Olivier Hamerlynck

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

ABSTRACT: 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 4 approaches. The seasonal pattern in density and biomass showed 3 peaks: a relatively small, yet distinct, peak in early March (30 ind. m^{-2}, 60 mg AFDW m^{-2}) and 2 main peaks in late spring (160 ind. m^{-2}, 225 mg AFDW m^{-2}) and in summer (140 ind. m^{-2}, 125 mg AFDW m^{-2}). Throughout winter, *N. integer* density remained well below 30 ind. m^{-2}. Three periods of increased reproductive activity and subsequent input of juveniles were found. This suggests that 3 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 3 mo, while the summer generation lived from summer until early winter. The 3 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 2 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: females generally lived longer, grew faster and consequently became larger than males. The size-frequency, growth summation and removal summation methods yielded comparable production estimates. The annual production was 0.3 g AFDW m^{-2} 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 3 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 2 cohorts was overestimated.

KEY WORDS: *Neomysis integer* · Mysidacea · Estuary · Westerschelde · Life history · Growth · Production

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 occurs especially in 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 characterised 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. 1993, 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 freshwater bodies which in 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 1971), an Irish lough (Parker & West 1979) and in the coastal waters of 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 1981) 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, b). These studies indicated *Neomysis 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 (Fig. 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 & 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. 1993). It is therefore believed to be a key species in the ecosystem of the brackish part of the Westerschelde.

MATERIALS AND METHODS

Study area. The Westerschelde estuary (Fig. 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 this delta area and is characterised by a marked salinity gradient. The water is completely mixed and the residence time is rather high (about 70 d or 150 tidal cycles). Consequently, freshwater (average inflow 100 $m^3 s^{-1}$) 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).

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 1). Each sampling day 4 stations (OV, SA, BA and LI) were covered (Fig. 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 (Hamerlynck & Mees 1991), 1 m wide, consisting of a heavy metal frame equipped with 2 nets, one above the other. The catch in both nets was pooled for this study. The nets were 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^2 and sampled the hyperbenthos from 20 to

Table 1. Sampling sites where the peak abundances of *Neomysis integer* were recorded

Date	Station	Salinity (PSU)	Temp. (°C)	Oxygen (%)	Secchi (cm)	pH	Conductivity (µS cm^{-1})
27 Nov 1990	BA	17.0	8.4	65	40	7.65	28.1
11 Dec 1990	OV	17.1	6.0	75	45	7.60	28.3
08 Jan 1991	SA	9.0	5.8	79	40	7.88	15.2
21 Jan 1991	OV	14.6	4.3	90	45	7.85	25.2
05 Feb 1991	SA	11.8	2.8	64	25	7.63	19.8
22 Feb 1991	OV	18.2	1.4	95	40	7.88	29.9
05 Mar 1991	BA	12.3	4.8	67	40	7.54	19.8
18 Mar 1991	SA	13.3	8.2	47	40	7.42	21.6
12 Apr 1991	BA	13.1	11.0	75	60	7.64	20.8
24 Apr 1991	SA	18.7	9.7	98	100	7.86	26.5
08 May 1991	LI	–	–	–	–	–	–
11 Jun 1991	BA	15.0	15.3	88	55	7.88	24.3
26 Jun 1991	BA	14.4	16.8	–	45	7.68	23.5
09 Jul 1991	SA	11.7	–	–	70	7.42	16.1
24 Jul 1991	OV	17.5	19.6	84	50	7.61	28.8
12 Aug 1991	LI	10.3	22.8	49	50	7.45	17.6
20 Aug 1991	SA	18.6	20.5	110	100	7.22	30.6
19 Sep 1991	OV	18.9	21.5	103	125	7.84	34.9
07 Oct 1991	BA	16.8	16.3	83	45	7.68	28.0
17 Oct 1991	SA	21.4	14.8	106	80	7.85	35.1
05 Nov 1991	BA	17.7	11.4	86	50	7.81	29.5
18 Nov 1991	BA	13.3	9.1	70	50	7.70	22.1
03 Dec 1991	SA	12.6	7.3	44	45	7.41	21.4
16 Dec 1991	SA	17.3	4.0	73	55	7.67	28.9
Average		15.2		79	56	7.66	25.0
SD		3.1		18	23	0.18	5.4

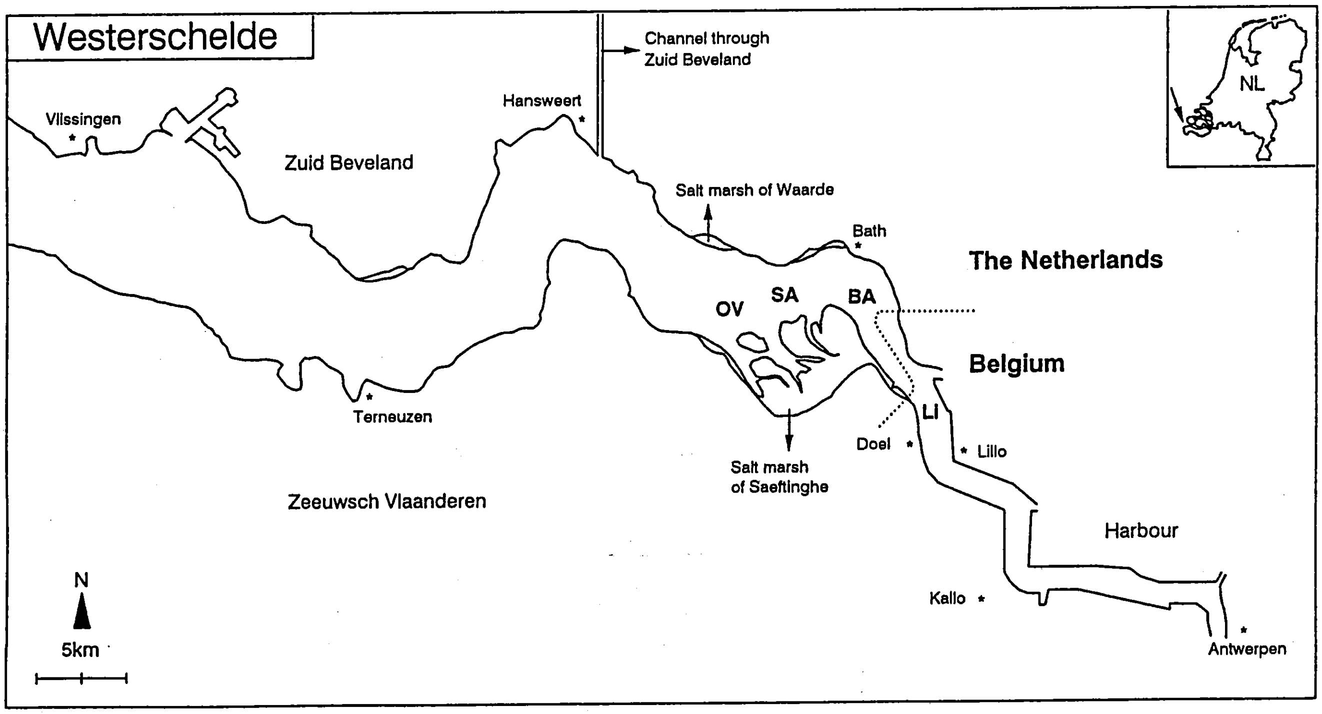

Fig. 1. Study area and the 4 sampling sites, Westerschelde estuary, SW Netherlands

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^2. 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 1).

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 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 1000 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 6 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 characterised 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 characteristics. 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 criterion 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 60 females with complete broods per sample. Bisexual individuals, i.e. individuals which have elongated 4th pleopods and a marsupium, were rare (less than 30 individuals encountered in the study) and were excluded from further analyses.

In each sample, the standard lengths (the distance from the base of the eye stalk to the end of the last abdominal segment) of 60 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 (10 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 5 d. The dry weight of the mysids was determined to the nearest microgram. The ash weight of the individuals was later measured after inceneration at 550 °C for 2 h. The ash-free dry weight (AFDW) 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 individuals 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 2 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).

Data analysis. Density of the population is expressed as number of individuals (n) per m^2, biomass as mg AFDW per m^2.

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 2 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 SL and 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 analyzed 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 generalized von Bertalanffy growth function (Gayanilo et al. 1989):

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

where L_t is the predicted standard length at age t, L_∞ is the asymptotic length, K is a growth constant, C is the amplitude of the seasonal growth oscillation, t_s is the starting point of that oscillation with respect to t_0 [within ELEFAN t_s is replaced by the winter point WP corresponding to the time of the year with the slowest growth ($\mathrm{WP} = t_s + 0.5$)], and 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_∞ 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 dates (27 November and 12 December 1990) were not used in the calculations. The year over which production was calculated thus started on 8 January 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 (Waters 1977, Menzie 1980, Crisp 1984).

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:

$$P = \sum N \Delta \overline{W}$$

where N = the number of individuals at time t, and $\Delta \overline{W}$ = 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:

$$P = \sum \overline{W} \Delta N$$

where $\overline{W}$ is the weight of the average individual during the sampling interval, and ΔN is the change in number of individuals 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:

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

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 jth size category, and 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 1 yr 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 3 cohorts differed in their life span. Hence an average CPI was calculated from the CPIs of the 3 cohorts. Since the 3 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 3 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).

RESULTS

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 at Stns SA and BA (9 and 8 times, respectively). Only twice was the maximum located upstream of the Dutch-Belgian border (at Stn LI) and only 4 times in the most downstream station (OV).

Most environmental variables measured (Table 1) did not display clear seasonal patterns. Salinity varied between 9 and 21.4 PSU with an average of 15.2 ± 3.12 (conductivity 15.2 to 35.1 $\mu S\ cm^{-1}$, average 25 ± 5.42 $\mu S\ cm^{-1}$). Average pH was 7.66 ± 0.18. Dissolved oxygen concentration averaged 78.6 ± 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 water column 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.

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:

$$TL = 1.165\ SL - 0.080 \quad (N = 112,\ r = 0.997,\ p < 0.001)$$
$$CL = 0.266\ SL + 0.439 \quad (N = 112,\ r = 0.908,\ p < 0.001)$$

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

$$\ln(AFDW) = 2.267 \ln(SL) - 5.539 \quad (N = 100,\ r = 0.997)$$

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

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

In autumn and winter (October to the end of February), densities were low (less than 25 ind. 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 ind. m^{-2} in June and August (Fig. 2).

In the observed length-frequency distributions by date several bimodalities (Fig. 3a) indicate recurring

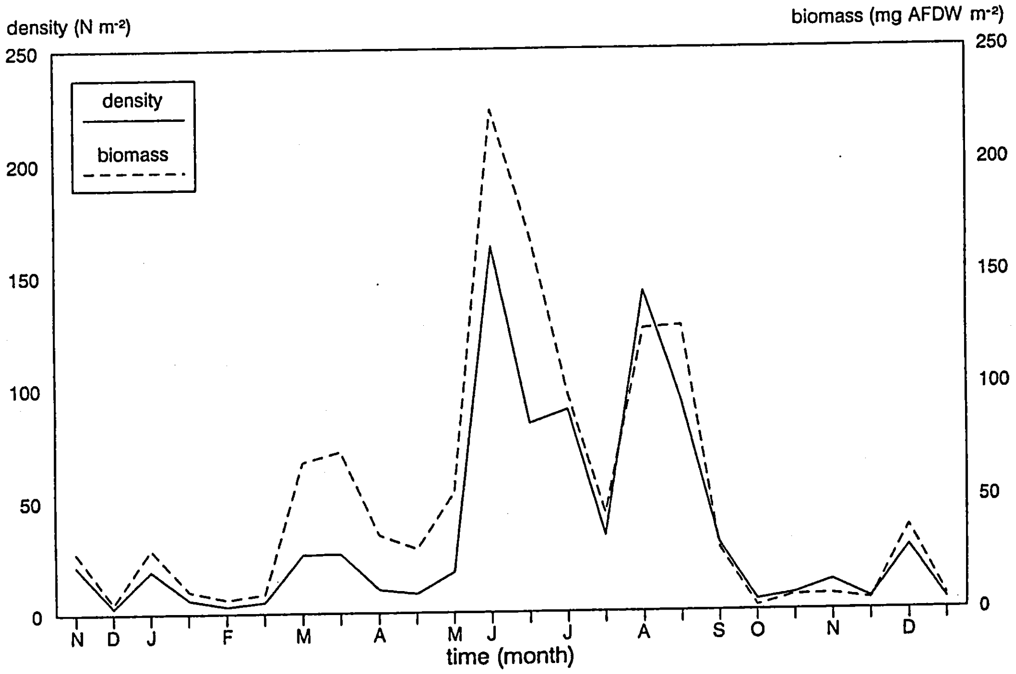

Fig. 2. *Neomysis integer.* Density and biomass for each sampling date

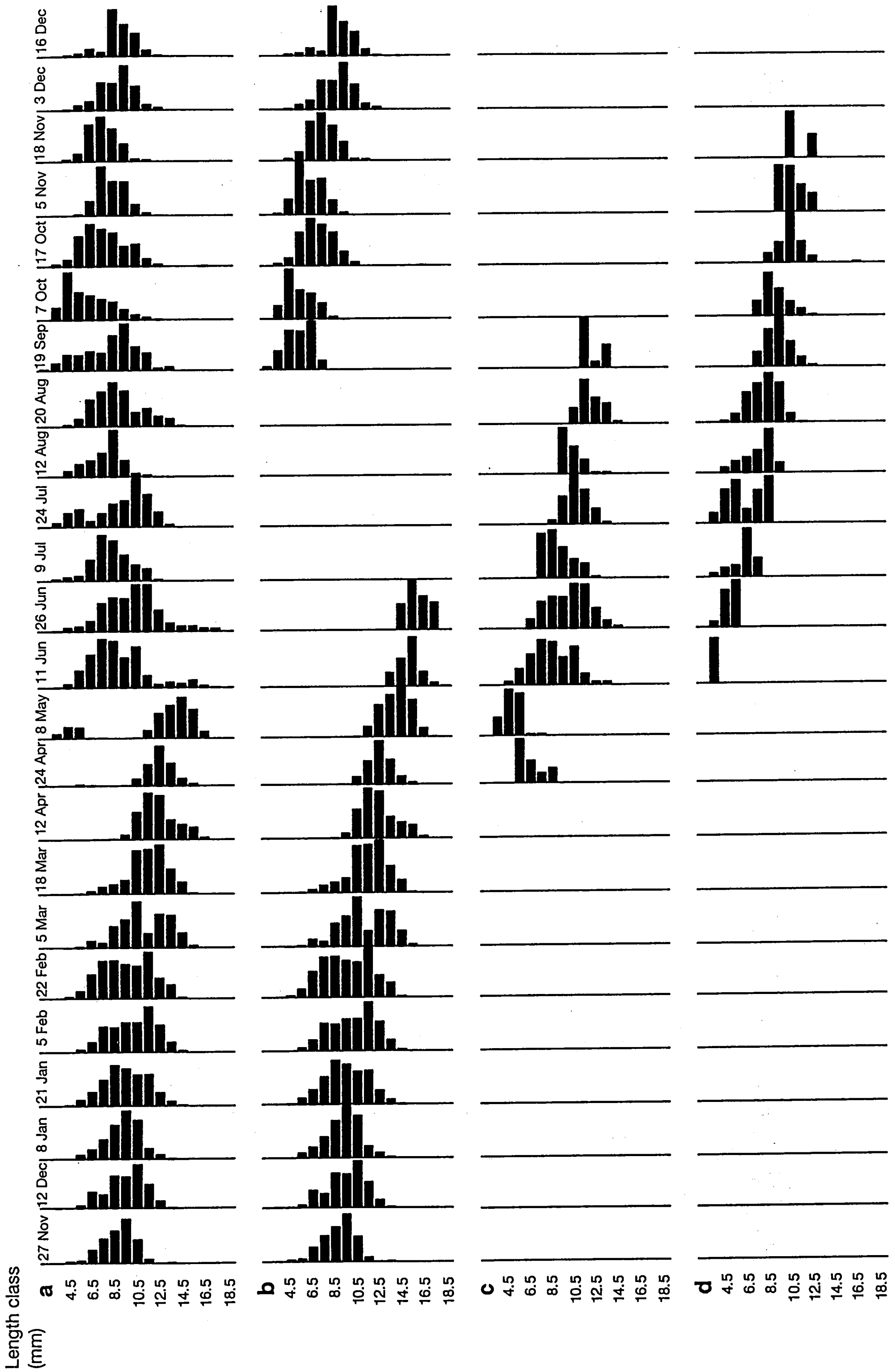

Fig. 3. *Neomysis integer*. Relative length-frequency distribution per sampling, 1990–1991. The *x*-axes are percentage scales; the *y*-axes are 1 mm classes with class marks of 2.5 to 18.5 mm and practical limits of 2.0–2.9 mm, 3.0–3.9 mm, etc. (a) All *Neomysis*; (b) cohort I; (c) cohort II; (d) cohort III

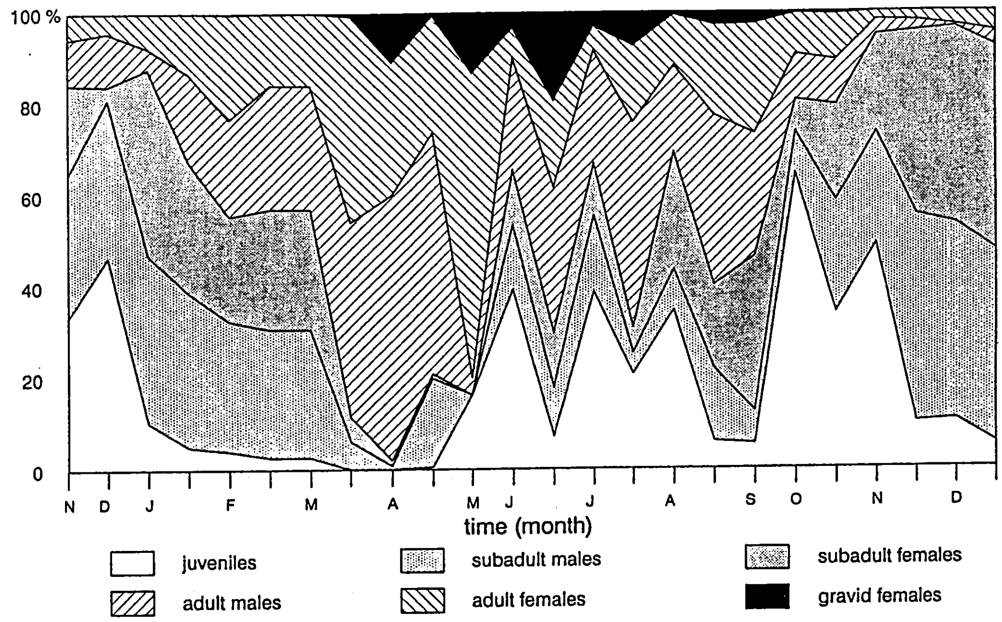

Fig. 4. *Neomysis integer.* Observed population structure on each sampling date

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 through 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 Fig. 4. In November and December 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, 3 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.

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 individuals were born before the start of the sampling period. 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 sampling 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.

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 (Fig. 5). 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

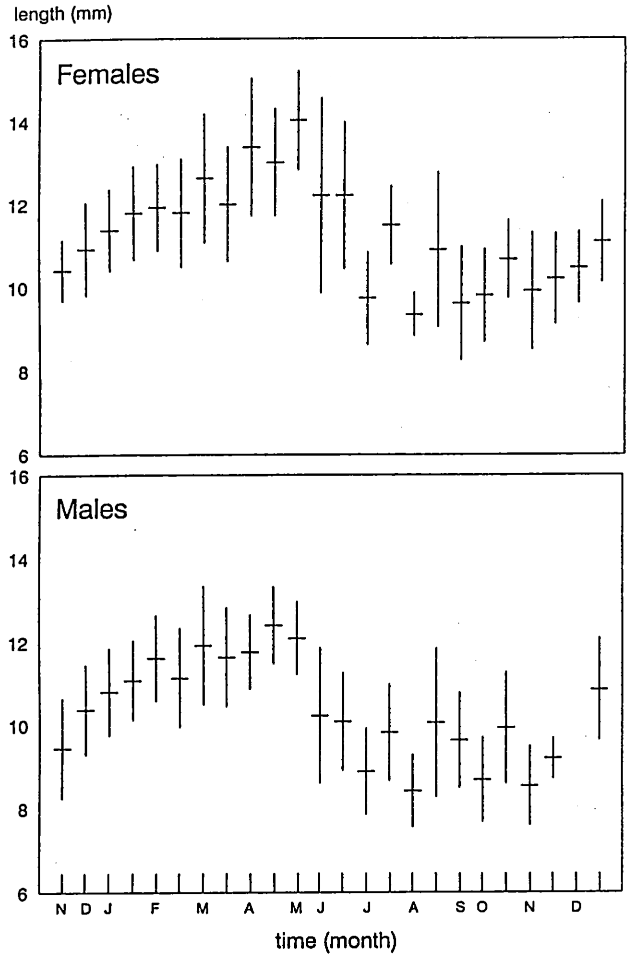

Fig. 5. *Neomysis integer.* Temporal variation in mean length (± SD) of adult males and females

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.

Length-frequency distributions and population structure of the 3 cohorts are presented in Figs. 3b, c, d & 6, respectively. The autumn samples contained only recently released individuals 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 individuals died in November. No difference in mortality between the sexes was observed for the summer cohorts.

Growth

The growth parameters of the von Bertalanffy growth curves of the 3 separate cohorts are presented in Table 2. In Fig. 7 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 mysids grew at a rate of 3 to 4 mm mo^{-1}. 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

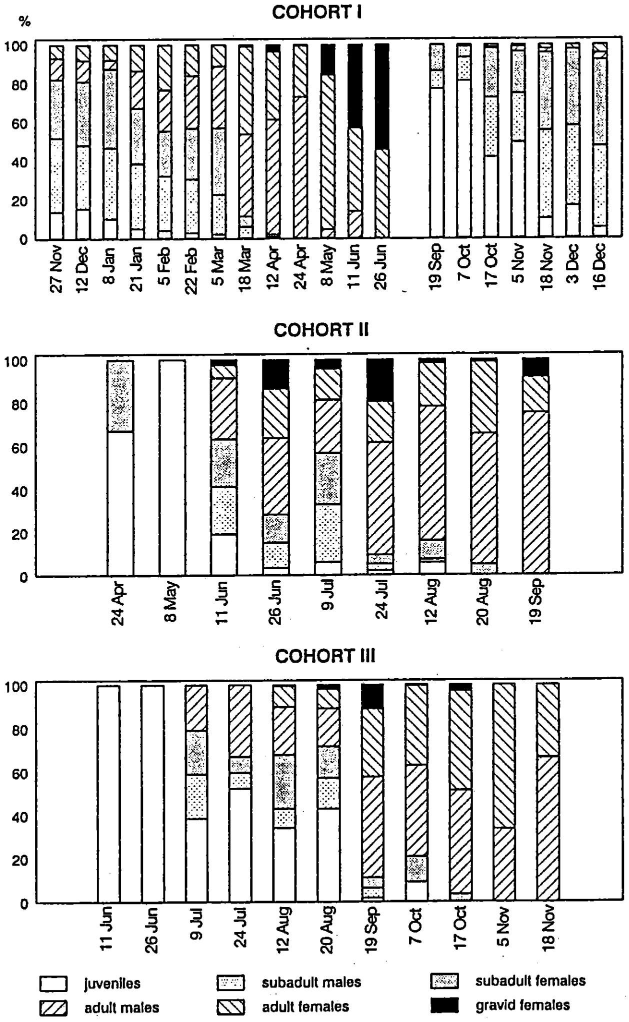

Fig. 6. *Neomysis integer.* Population structure of the 3 cohorts

Table 2. *Neomysis integer.* Growth parameters of the von Bertalanffy growth curves of the 3 cohorts and both sexes separately. L_∞: asymptotic length; K: growth constant; C: amplitude of seasonal growth oscillation; t_s: starting point of oscillation; t_0: age at zero length; Rn: a measure of goodness of fit

Sex/Cohort	L_∞	K	C	t_s	t_0	Rn
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

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 mo^{-1}); the larger mysids (mainly adults) grew less (1 to 2 mm mo^{-1}).

Individuals of the overwintering generation attained a larger size than spring or summer individuals (higher L_∞ for both sexes). Marked differences in growth patterns of the 2 sexes were evident in all cohorts: the females always had a higher L_∞ 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).

Brood size

The number of larvae in the marsupium, i.e. the brood size (b), showed a strong positive correlation with female length (l) (Fig. 8):

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

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 3 cohorts:

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.

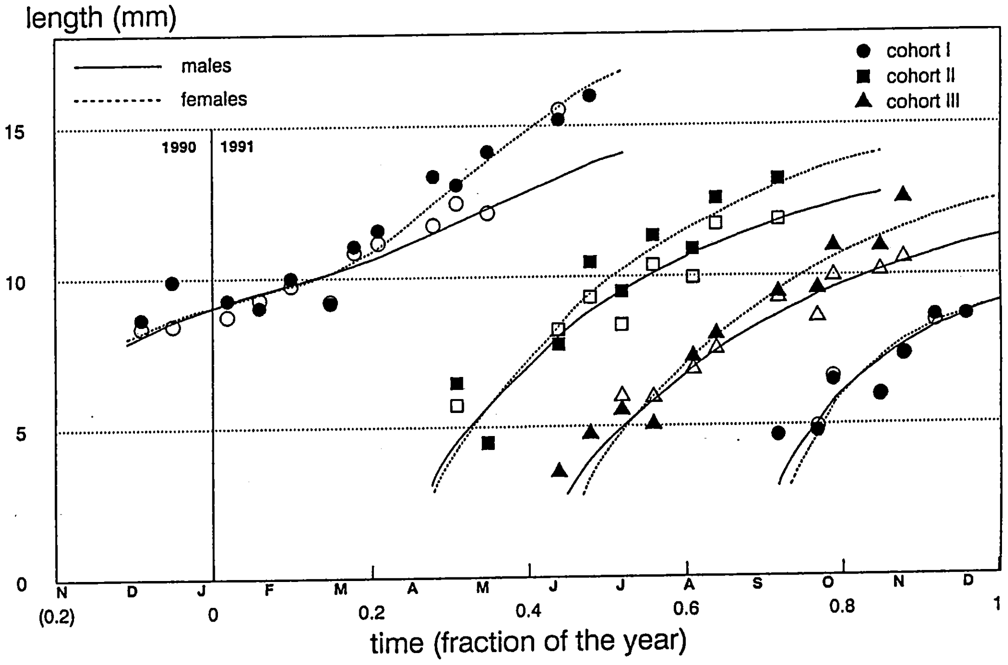

Fig. 7. *Neomysis integer.* Growth curves of the 3 cohorts and both sexes separately. Open symbols: males; solid symbols: females

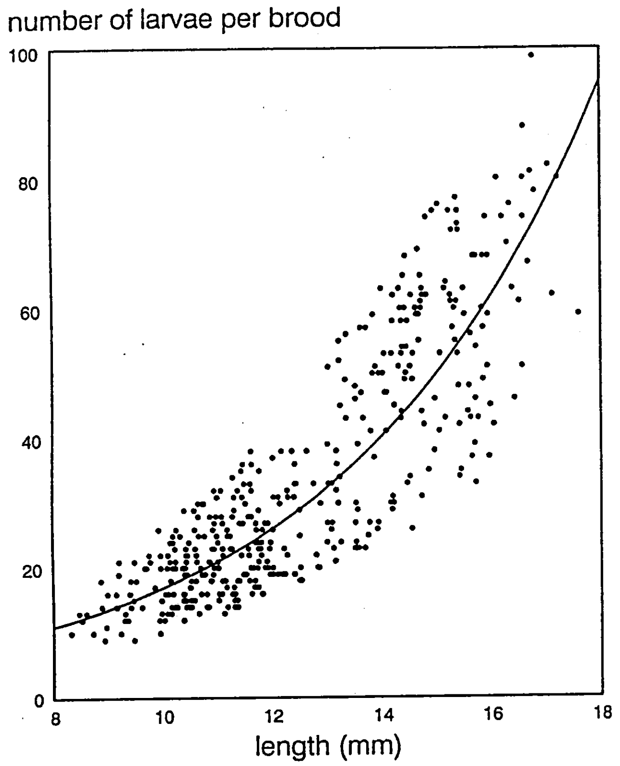

Fig. 8. *Neomysis integer.* Relation between female length and brood size (all data)

Table 3. *Neomysis integer.* Summary of the production estimates (mg AFDW m^{-2} yr^{-1}) obtained with different methods

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

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 3 & 4. The annual production estimates obtained with the growth summation and removal summation methods are almost identical (322 mg AFDW m^{-2} yr^{-1}). The result of the size-frequency method is very close (2% difference) to that of the 2 former methods only when the calculations were performed for the 3 cohorts and both sexes separately. Calculations on pooled length-frequency distributions of the 2 sexes per cohort and of the 3 cohorts (average CPI of 202 d) 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.

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 distribu-

Table 4. *Neomysis integer.* 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)
Cohort I				
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
Cohort II				
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
Cohort III				
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
Annual production			398.66	329.06

tions 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.

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 and is therefore found at a much higher salinity than in other, less polluted, estuaries. In the Gironde, the Eems (The Netherlands), the Elbe (Germany) and the Shannon (Ireland), for example, the population maximum was found at 3.5 and typically a differential distribution of the developmental stages and sexes along the salinity gradient is observed (Sorbe 1981, 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.

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 (1971), Borghouts (1978), Parker & West (1979) and Bremer & Vijverberg (1982) all concluded that *N. integer* produced 3 generations per year in the IJsselmeer (former Zuiderzee), the west coast lochs of Scotland, Lake Veere (southwest 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 1981).

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 mysids 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 up to 5 consecutive broods (C. R. Janssen unpubl.). The physiological background and/or ecological adaptiveness of these different reproductive strategies remain unclear.

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 characterised 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.

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 microphthalma* from the Japan Sea (Ikeda 1992) and the hyperbenthic *Antarctomysis maxima* and *Mysidetes posthon* from Antarctic waters (Siegel & Mühlenhardt-Siegel 1988).

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 4 mo prior to analysis and the weight loss associated with formalin preservation, estimated to be about 10% by Bremer & Vijverberg (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^{-2} yr^{-1}. This is much higher than the estimate by Bremer & Vijverberg (1982) for a lacustrine population (10 mg DW m^{-2} yr^{-1} with a P/B of 4.0). However, our estimate is remarkably close to the production values reported for *N. 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).

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 mo, 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^{-2} yr^{-1}. The size-frequency method only resulted in values 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. In spite of its longer lifespan, the overwintering cohort accounted for barely half of the total annual production.

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ABERRANT INDIVIDUALS OF *NEOMYSIS INTEGER* AND OTHER MYSIDACEA: INTERSEXUALITY AND VARIABLE TELSON MORPHOLOGY

JAN MEES[1], NANCY FOCKEDEY[1], ANN DEWICKE[1], COLIN R. JANSSEN[2] and JEAN-CLAUDE SORBE[3]

KEYWORDS: mysid; estuary; morphology; regeneration.

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 telson, rather than a typically truncated one, were also recorded from the four populations studied. A culture experiment with damaged specimens revealed that all types 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 common 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 and 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). Adult males of this species are characterized by elongated fourth pleopods which reach well beyond the base of the uropods, whereas adult females have uniformly short pleopods and oostegites forming a brood pouch or marsupium between the thoracic legs. In addition, the males are 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 species of 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, thence the species name (Fig. 1 a, b). A pair of long outer and short inner terminal spines can be distinguished. CHOJNACKI and 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).

MATERIALS AND METHODS

Samples

The Mysidacea of the Westerschelde (south-west Netherlands) estuary were sampled monthly or fortnightly between April 1990 and April 1991.

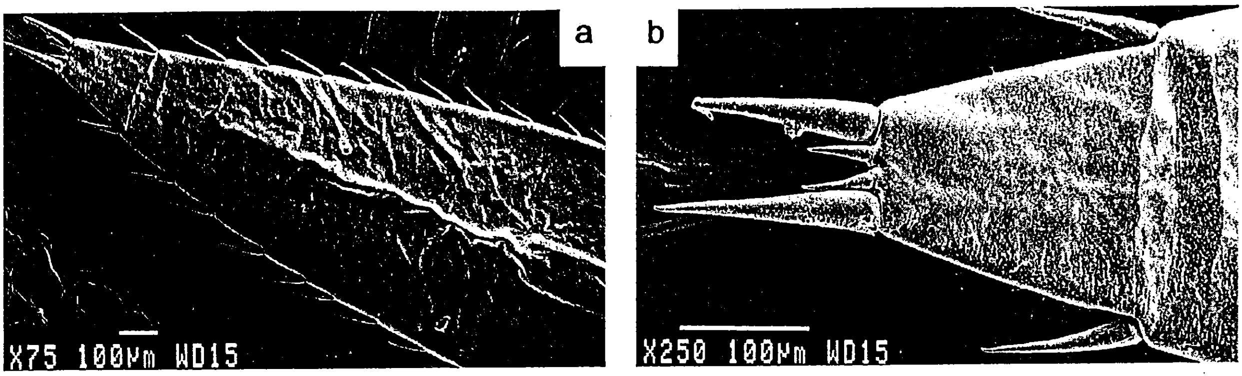

Fig. 1. (a) and (b): Normally truncated telson of *Neomysis integer*.

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 and 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.*, 1995). 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 and 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 and 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, 1995).

Specimens for scanning electron microscope (SEM, JEOL840) were washed, dehydrated, and then critical point dried from liquid CO_2 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 Antwerp. The telsons of 5 subadult specimens (7–8 mm standard length) were carefully mutilated with a scalpel under a binocular microscope. The tip of the telson was removed by a transverse cut at about mid-length. 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. Of all specimens examined, 36.4% also had a setose *appendix masculinus* as a 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 1. 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 (<<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 (Fig. 2, a to l). The number and the position of the terminal and subterminal lateral spines were particularly 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. This species typically has a cleft telson.

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 2). As can be seen from Fig. 3 (mysids A and B), the regeneration was asymmetrical at first (Chojnacki and Ciupinski's class B) but the telson became more or less symmetrically rounded in the fourth moult (Chojnacki and 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.

Table 1. Percentage of the *Neomysis integer* populations with aberrant telson morphology (* = <1% of the population; - = no aberrant individuals found; n.d. = no data).

Sampling date	Westerschelde	Gironde	Eems	Elbe
1990-Apr	2.9			
1990-May	–			
1990-Jun	–			
1990-Jul	*			
1990-Aug	–			
1990-Sep	*			
1990-Oct	*			
1990-Nov	1.5			
1990-Dec	4.0			
1991-Jan	1.1			
1991-Feb	1.5			
1991-Mar	2.2			
1991-Apr	5.7			
1991-Aug	–	*	*	n.d.
1993-Apr	5.3	1.5	n.d.	9.1

Table 2. 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 and CIUPINSKI (1986) reported altered telson morphology in *Neomysis* from the Baltic. They found that in some months 1 to 5% of

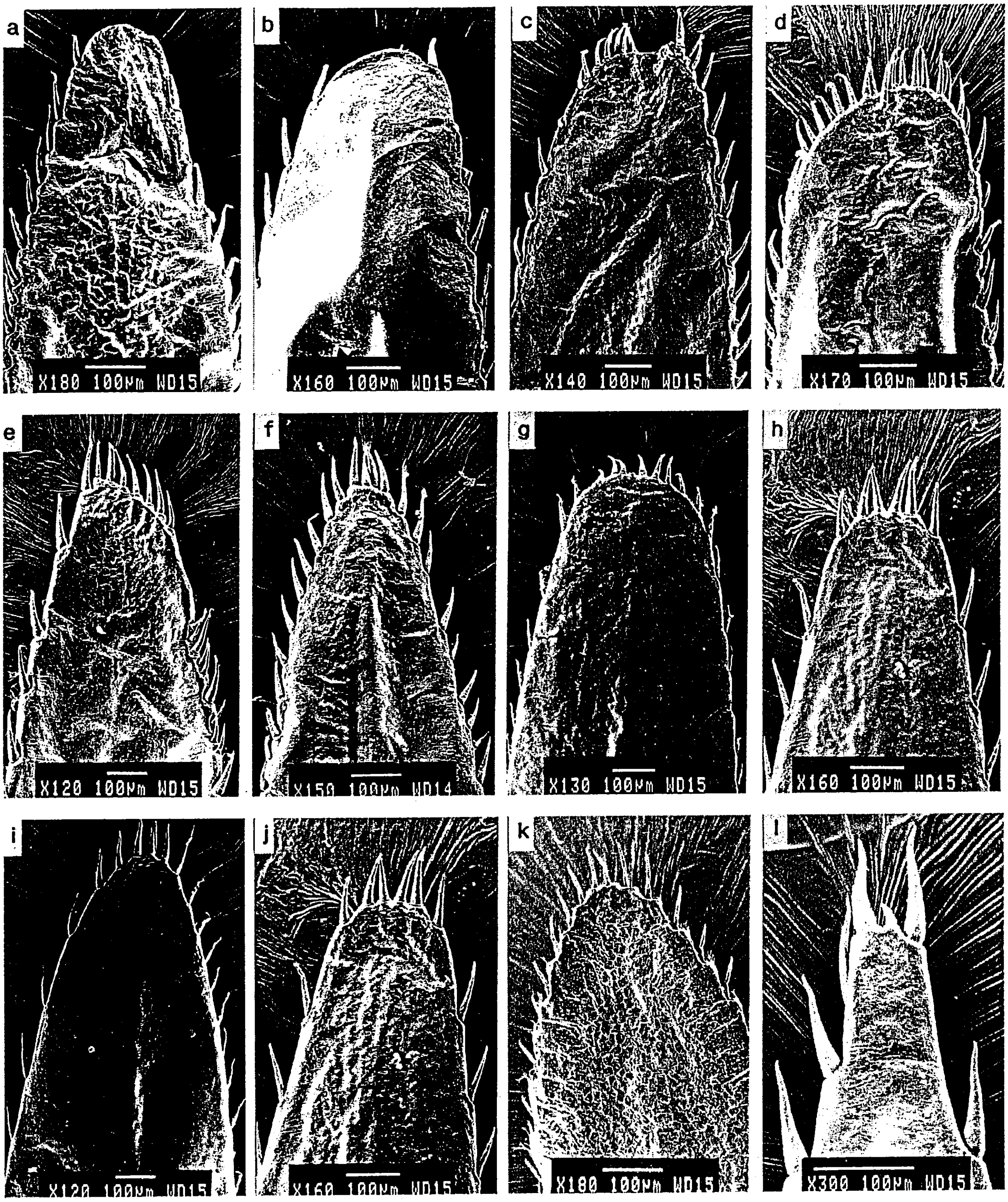

Fig. 2. (a) to (l): Aberrant telson morphology of *Neomysis integer* collected in the field.

the adult individuals in the population displayed aberrant telson structure and hypothesized 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

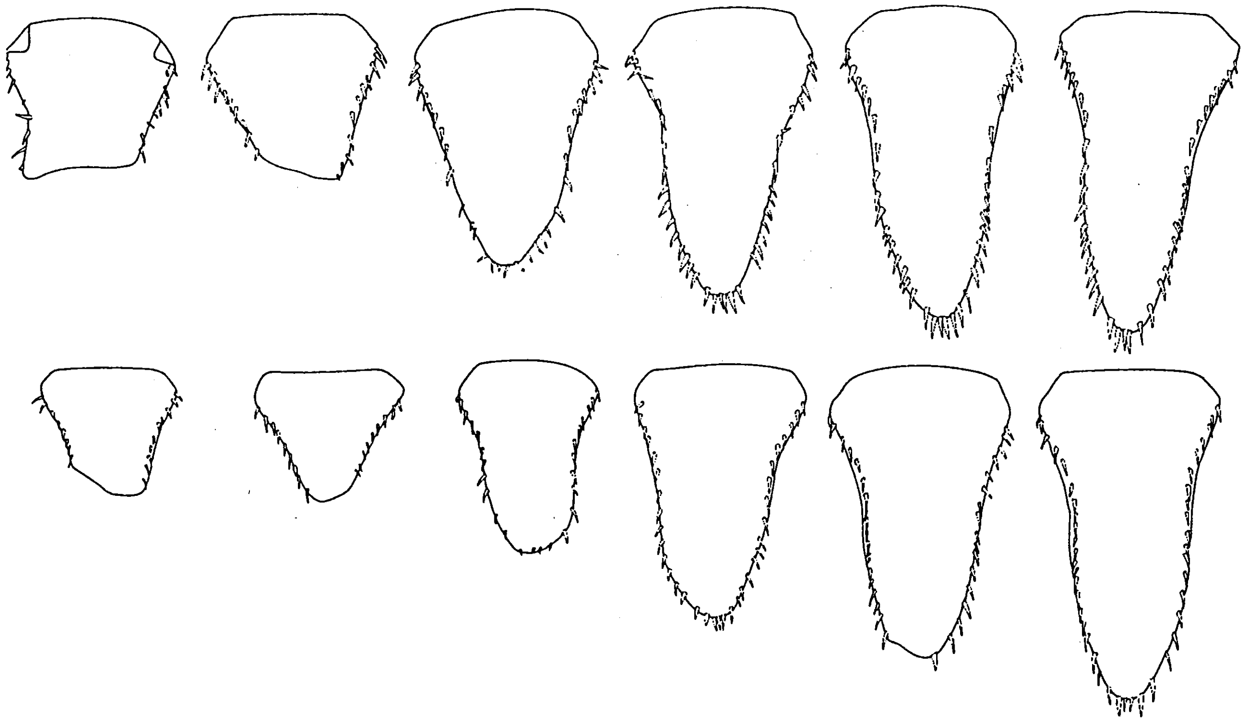

Fig. 3. Regeneration of the telson of *Neomysis integer*. Schematic drawing of 6 consecutive moults (from left to right) from the experiment (individuals A and B, see Table 2).

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 genetical reason 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 aber rant 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 and Kils, unpubl.). 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 µg 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°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 detectable for longer 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 (temperatures of 14.6 and 8.6°C, respectively), animals belonging to the overwintering generation were still present in high numbers, while the Gironde population (temperature 17.5°C) 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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Addresses of the authors:

[1] Marine Biology Section, Zoology Institute, University of Ghent, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium.
[2] Laboratory for Biological Research in Aquatic Pollution, University of Ghent, J. Plateaustraat 22, B-9000 Gent, Belgium.
[3] Laboratoire d'Océanographie Biologique, Université de Bordeaux I, 2 rue Jolyet, F-33120 Arcachon, France.

LABORATORY STUDIES ON GROWTH AND DEVELOPMENT OF THE BRACKISH WATER MYSID *Neomysis integer*

Fockedey Nancy and Mees Jan

ABSTRACT

The life history characteristics of a species depend to a certain extent on the characteristics of its habitat. The combined effects of temperature, salinity, and quality and quantity of available food are likely to influence the growth parameters of brackish water species. The aim of this study was to determine the influence of a broad range of salinity-temperature combinations on growth parameters, moulting frequency and sexual development of the mysid *Neomysis integer*. *N. integer* was cultured in the laboratory and the offspring of the cultured animals was used in 'longterm' growth experiments. Individual *N. integer* were followed from birth (immediately after hatching from the marsupium) until they reached asymptotic length (maximum duration of the experiments was 4 months). They were kept at several constant temperature-salinity conditions: at 15 °C salinity was 1, 5, 15 and 30 psu; at 8, 20 and 25 °C salinity was 5 psu. They were fed freshly hatched *Artemia* nauplii *ad libidum.*

Growth was studied by collecting and measuring the moults. The total length of the exuvia could not be measured (too elastic). Hard appendages (antennal scale, uropod, telson) were measured and converted to standard length with allometric linear regressions.

The growth of *Neomysis integer* was described by logistic functions. Within each treatment individual variability was small. Absolute or incremental growth rates ($\Delta L/\Delta t$) fluctuated nonlinearly with size and age, and were maximal around the inflection point (t_0). The developmental time before reaching the inflection point increased with increasing salinity and decreased with increasing temperature.

INTRODUCTION

To date, growth curves and other population dynamical parameters of the brackish water mysid *Neomysis integer* were mainly derived from field studies. Populations of brackish water ponds in the Dutch Delta area were studied by Borghouts (1978) and Platenkamp (1983) and information on the biology of *N. integer* populations in Frisian lakes was made available by Vorstman (1951), Beattie & Kruijf (1978), and Bremer & Vijverberg (1982). Information is also available on *N. integer* populations of Scottish (Mauchline, 1971) and Irish lakes (Parker & West, 1983) and from coastal waters of the Baltic sea (Jansen *et al.*, 1980; Rudstam *et al.*, 1986; Wiktor, 1961). Estuarine populations of *N. integer* were studied in the Ythan (Astthorson & Ralph, 1984), Eider-Ring (Kinne, 1955), Gironde (Sorbe, 1981) and Westerschelde (Mees *et al.*, 1994).

The life history of a species depends on the characteristics of its habitat. The combined effect of temperature, salinity, and food quality and quantity is likely to influence the growth parameters of estuarine endemics. For further research on the biology of *Neomysis integer* it is essential to investigate the impact of these environmental variables on growth and development. The objectives of this study were to determine the influence of a broad range of salinity-temperature combinations on the growth of *N. integer* throughout its life and to identify differential sensitivity to the environmental variables in growth patterns over time.

First, techniques to maintain a laboratory stock culture of *Neomysis integer* were refined (methods adapted from Clutter & Theilacker, 1971, Toda *et al.*, 1984, Assthorson & Ralph, 1984, Lussier *et al.*, 1988, Greenwood *et al.*, 1989). This part of the research was done in close cooperation with Dr. C.R. Janssen and Drs. M. Vangheluwe (University Gent, Laboratory for biological research of water pollution). The offspring of the cultured animals was used in 'longterm' growth experiments. Growth, moulting frequency and sexual development of individual *N. integer* were followed from birth (immediately after hatching from the marsupium) until senescence or death. They were kept at constant temperature-salinity conditions and were fed freshly hatched *Artemia* nauplii *ad libidum*. Preliminary results are reported here.

MATERIALS AND METHODS

Sampling site and sampling method

Non-quantitative samples of *Neomysis integer* were taken in the brackish water pond 'Galgenweel' near Antwerpen. The pond is located in the vicinity of the brackish water zone of the Westerschelde estuary with which it was connected until the mid seventies. Salinity in the pond is relatively stable over the year (3.58 ± 0.54 psu). Density, biomass and population dynamics of the Galgenweel population were studied for basic background information (Fockedey unpublished). *N. integer* is highly abundant in the Galgenweel: densities of 100-1000 individuals per m^2 and biomasses of 100-1300 mg AFDW per m^2 were recorded over a one year period.

Samples were taken with a handnet (mesh size 0.5 mm). The animals were transported to the laboratory in plastic containers with water from the sampling site within 2 hours after sampling.

Laboratory stock culture

The stock culture was kept in a flow-through system: a tank of 200 litres equipped with an 'under gravel filter'. The filter consisted of 4 layers: from bottom to top the layers were filtering cotton wool, sand, filtering cotton wool and broken oyster shells. The water in the tank was continuously aerated. The aeration tubes were placed at the height of the water surface thus causing a continuous current in the tank. Filtered sea water diluted to a final salinity of 5 psu was used as a culture medium. The system required minimal maintenance: every 2 weeks 50% of the culture medium was replaced, while the filter needed replacing only once every 6 months. The stock culture was kept in a climate room at a constant temperature of 20 ± 2 °C and at a 12 hours light and 12 hours dark cycle. The density of *Neomysis integer* in the tank was approximately 5 individuals per litre. The mysids were fed twice a day *ad libidum* with 1 - 2 days old *Artemia salina* nauplii.

Gravid females from the stock culture were kept separately in smaller aquaria. They were checked daily for newly released juveniles. These freshly hatched individuals (max. 1 day old) were used in the growth experiments.

Experiments on influence of temperature and salinity on growth

The juveniles were kept individually in small glass containers (400 ml) under different temperature and salinity conditions. At 15 °C individuals were kept at 4 salinities: 1, 5, 15 and 30 psu. Additionally, individuals were kept at 8, 20 and 25 °C at a salinity of 5 psu. The culture media were made of artificial sea salt (INSTANT OCEAN) in distilled water. The artificial seawater was aerated for at least 24 hours before use in the experiments. The experimental glass containers were kept in water baths placed in climate cabinets of 8 and 15°C. Temperatures of 20 and 25 °C were achieved by heating of the water baths (± 1°C).

The growth of crustaceans is generally characterised by continuous moulting during their entire lifespan. Length therefore increases gradually when ecdysis occurs. In this experiment, the growth of *N. integer* was followed by recording length increases of the moulted exuvia.

This method causes least stress for the animals. The experimental containers were checked daily for exuvia or dead individuals. If present, they were collected and preserved in a 4 % formaldehyde solution.

Every day, half of the culture medium was replaced with new aerated water. Faecal strings and dead food items were collected from the bottom of the containers with a pipet. The animals were fed *ad libidum* with 1 or 2 days old *Artemia salina* nauplii (250-1500 nauplii per day, depending on the individual's age).

Standard length of the exuvia could not be measured: during ecdysis the moult often breaks in 2 parts and the moults are very elastic. By measuring hard appendages (antennal scale, uropod, telson) of the exuvia, standard lengths can be derived with allometric regressions. For this report the mean length of both endopods of the uropod of the moult was used to calculate the standard length of the mysid. Note that this procedure yields the standard length of the animal before the specific moulting.

The experiments lasted for maximally 4 months. After this period, the surviving animals were killed and formalised. Individuals which had moulted less than 5 times and/or did not become subadult were not used for further analyses.

Allometric regressions

Allometric linear regressions were calculated for several appendages of the mysid and its standard length. Standard length (SL), telson length (TELL), telson width (TELB), length of the exopod (EXO) and endopod (ENDO) of the uropod, length of the antennal scale (ATOT) and its anterior (AVOOR) and posterior (APOST) parts were measured for 100 individuals (Figure 1). Standard length is defined as the distance from the base of the eye stalk to the end of the last abdominal segment. The full length range of the population was covered by measuring 10 juveniles, 10 subadult males, 10 sudadult females, 10 adult males and 10 adult females from both the summer and the overwintering generations (June and December samples of the Galgenweel population). The appendages were drawn by means of a drawing tube mounted on a microscope and their length was measured by means of a digitiser.

Growth parameters and growth model

The absolute or incremental growth rate (of a mysid of the age n) was calculated as:

$$\Delta L/\Delta t = L_n - L_{n-1} / t \qquad \text{(in mm per day)}$$

where $L_n - L_{n-1}$ is the increase in length in a certain time interval [n-1; n]; and t is the number of days between age n and age n-1. The length increase from birth to old age is described with the logistic function:

$$L_t = L_{max} / [1 + e^{-g(t-t0)}]$$

where L_{max} is the final, asymptotic length; g is the overall growth constant (the instantaneous growth rate when $L \rightarrow 0$; t_0 is the inflection point of the curve (reflecting the time when the absolute rate of increase in length ($\Delta L/\Delta t$) begins to decrease); and t is the time in days after birth (Pöckl, 1995). This model was fitted to the data of the different treatments. In this report sexual differences in growth are not considered.

According to Mauchline (1976) the growth of Mysidacea can be described by using two parameters: the period between two successive moults (the intermoult period or IMP) and the growth factor (GF) expressing the relative growth between two moults (in %). These parameters were not yet calculated for this report, but the basic data are available.

RESULTS

Allometric regressions

The parameters of the allometric linear regressions between standard length and the different appendages are presented in table 1. All regressions were highly significant ($p < .0000$) and had a good fit. Thus, either part can be used to get an appropriate estimate of the standard length. In this report the mean length of the endopods of the uropod is used, since this part was almost always collected in the experiments. Fixation of animals and exuvia in a formaldehyde solution could have caused shrinking. This is not taken into account. It is assumed that shrinking, if present, affects both dead animals and exuvia equally.

Experiments on influence of temperature and salinity on growth

28 to 52 animals were used per treatment, of which 15 to 28 moulted at least 6 times and will be processed further. The preliminary results presented in this report are based on the 5 or 6 longest living individuals per treatment. The increase in standard length (in mm; Y axis) over time (in days; X axis) for each individual is presented in figures 2a and 2b. For each treatment, individual variability is small. The treatments 15°C/0psu and 25°C/5psu showed the highest individual variability. This may be caused by high stress (salinity too low, temperature too high). This was also reflected in a higher mortality in the treatments 15°C/0psu and 25°C/5psu. Growth is obviously stepwise, standard length increasing after moulting. The intermoult period clearly increases with age. Juveniles originating from the stock-culture all had a standard length between 2 and 3 mm. The growth presented here is the post-marsupial growth. Growth within the marsupium remains unknown.

A final asymptotic length was reached in all treatments and the length/age data conformed to a sigmoid or 'S-shaped' curve. The observed growth can be approximated by the logistic curve (figures 3a, 3b and 4). This emphasizes the fact that after leaving the marsupium the absolute length increments per unit time progressively increased to a maximum at a point in the life cycle beyond which the length increments progressively decreased (figure 5). On both sides of this inflection point (t_0) there is a period where incremental growth appears to be approximately linear. This point is located at half the asymptotic length $L_{max}/2$ (figure 6). The parameter estimates of the logistic functions are given in table 2. The correlation coefficients r^2 were high, indicating that most of the variation was attributed to variation in age.

Individuals of all treatments reached the subadult stage, but only in 15°C/5psu, 15°C/15psu and 20°C/5psu they reached sexual maturity (table 3). At 15°C, the animals became adult earlier at 5 psu (63 days) than at 15 psu (93 days). At 5 psu, adulthood was reached sooner at 20°C, as compared to 15°C (not included in table).

At 15°C, the asymptotic length (L_{max}) was highest at 15 psu (11.96 mm), but these individuals showed a delay in their sexual development. At 5 psu, L_{max} was somewhat lower (11.37 mm), but adulthood was reached faster. In these two treatments the growth constants were identical (0.0436). At 30 psu, the growth constant was comparable (0.0431), but a smaller asymptotic length was reached (10.58 mm). Animals reared at 1 psu (treatment 15°C/0psu) showed the highest growth constant (0.0457) and the lowest maximal length (8.12 mm). The inflection point of the curve was reached first by individuals at 1 psu (25 days), subsequently by individuals at 5 psu (31 days), 15 psu (34 days) and 30 psu (36 days): t_0 is located at higher age with increasing salinity. At 5 psu, *Neomysis integer* reached highest asymptotic length (11.37 mm) at 15°C, as compared to individuals reared at 20°C (9.73 mm), 25°C (8.82 mm) and 8°C (7.45 mm). The growth constant decreased from 0.0529, to 0.0500, 0.0435 and 0.0321 for individuals in the treatments 20°C/5psu, 25°C/5psu, 15°C/5psu and 8°C/5psu respectively. The times when the inflection points occurred decreased with increasing temperature. Animals reared at 8°C reached the inflection point of the curve after 35 days, at 15°C after 31 days and at 20°C and 25°C after 19-20 days.

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Figure captions

Figure 1: Appendages (and their codes) measured for the allometric linear regressions.

Figure 2a: Increase in standard length (in mm; Y axis) over time (in days; X axis) for each individual reared at 15 °C and salinities of 1 psu (15/0), 5 psu (15/5), 15 psu (15/15) and 30 psu (15/30).

Figure 2b: Increase in standard length (in mm; Y axis) over time (in days; X axis) for each individual reared at 5 psu and temperatures of 8°C (8/5), 15°C (15/5), 20°C (20/5) and 25°C (25/5).

Figure 3a: Logistic growth curve fitted to the data of the treatments at 15 °C and salinities of 1 psu (15/0), 5 psu (15/5), 15 psu (15/15) and 30 psu (15/30).

Figure 3b: Logistic growth curve fitted to the data of the treatments at 5 psu and temperatures of 8°C (8/5), 15°C (15/5), 20°C (20/5) and 25°C (25/5).

Figure 4: Logistic growth curve for all treatments.

Figure 5: Absolute or incremental growth $\Delta L/\Delta t$ (in mm.day^{-1}; Y axis) over time (in days; X axis).

Figure 6: Absolute or incremental growth $\Delta L/\Delta t$ (in mm.day^{-1}; Y axis) over mean standard length (in mm; X axis).

$SL = a + b X$

	X	N	a	b	r	R^2	p
Carapax length	CL	99	0.0801	2.9282	.9741	0.9489	<.0000
Telson length	TELL	94	0.591	5.6298	.9782	0.9596	<.0000
Telson width	TELB	99	-0.082	11.727	.9759	0.9524	<.0000
Exopod length	EXO	97	1.0856	4.0818	.9784	0.9573	<.0000
Endopod length	ENDO	99	-0.346	6.4698	.9795	0.9595	<.0000
Antennale scale length (total)	ATOT	100	0.836	3.37	.9770	0.955	<.0000
Antennale scale length (anterior)	AVOOR	97	-1.42	23.98	.9223	0.851	<.0000
Antennale scale length (posterior)	APOST	98	1.428	3.822	.9732	0.947	<.0000

Table 1: Allometric linear regression values for the standard length (SL in mm) and different appendages X (in mm) for individuals of the field population (Galgenweel).

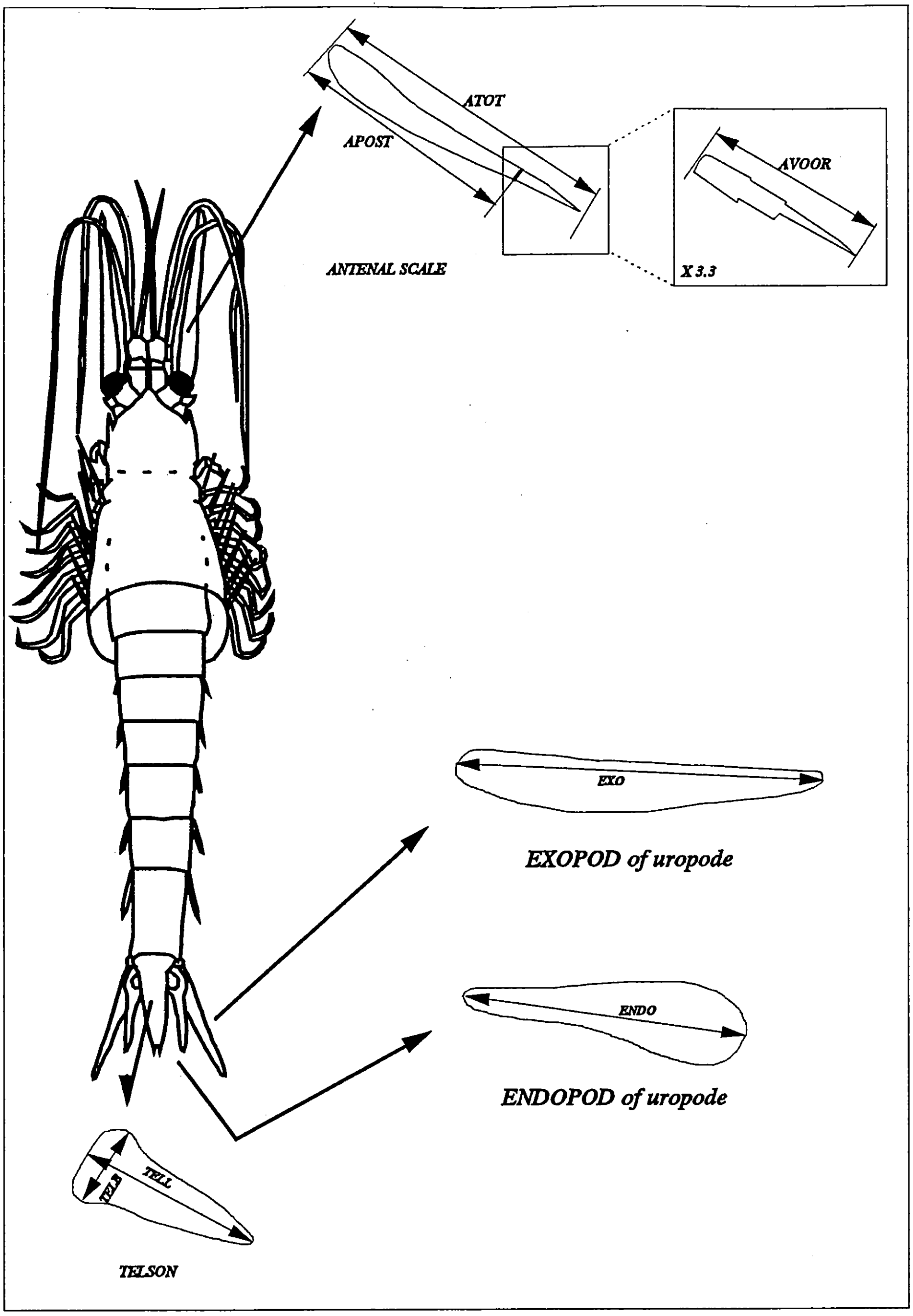
$L_t = L_{max} / [1 + e^{-g(t-t0)}]$

Treat-ment	Temp (°C)	Sal (psu)	N	L_{max}	g	t0	r^2
15/0	15	1	273	8.1223	.045716	24.5563	.8808
15/5	15	5	546	11.3733	.043554	31.2183	.9838
15/15	15	15	491	11.9584	.043623	33.6650	.9694
15/30	15	30	479	10.5782	.043052	35.7696	.9198
8/5	8	5	513	7.45153	.032113	35.3945	.9418
15/5	15	5	546	11.3733	.043554	31.2183	.9838
20/5	20	5	484	9.73146	.052933	19.1237	.9542
25/5	25	5	149	8.82339	.050098	20.2571	.8530

Table 2: Logistic growth functions values for the different experimental treatments

	15/0	15/5	15/15	15/30	8/5
SUB	28.20 (0.84)	15.60 (0.57)	19.60 (1.34)	23.40 (1.34)	39.00 (2.55)
AD	------------	63.20 (2.17)	92.75 (7.41)	------------	------------
DEAD	62.40 (23.10)	112.40 (0.89)	113.20 (17.11)	113.60 (4.72)	115.00 (4.95)

Table 3: Mean (± standard deviation) numbers of days to become subadult (SUB) or adult (AD), and numbers (± standard deviation) of days individuals live at the different treatments.


ATOT
APOST
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EXOPOD of uropode
ENDO
ENDOPOD of uropode
TELL
TELB
TELSON

Figure 1

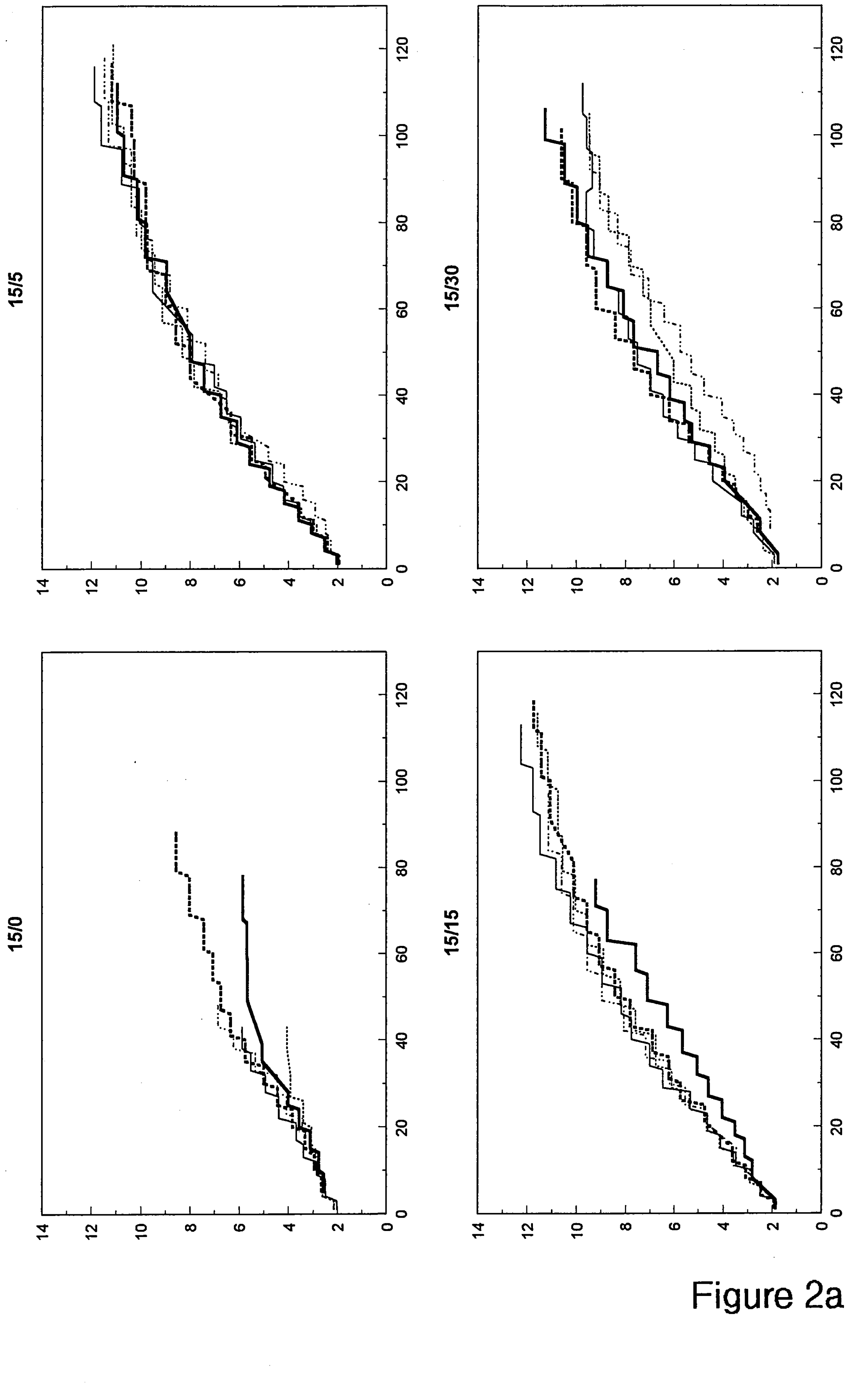


Figure 2a

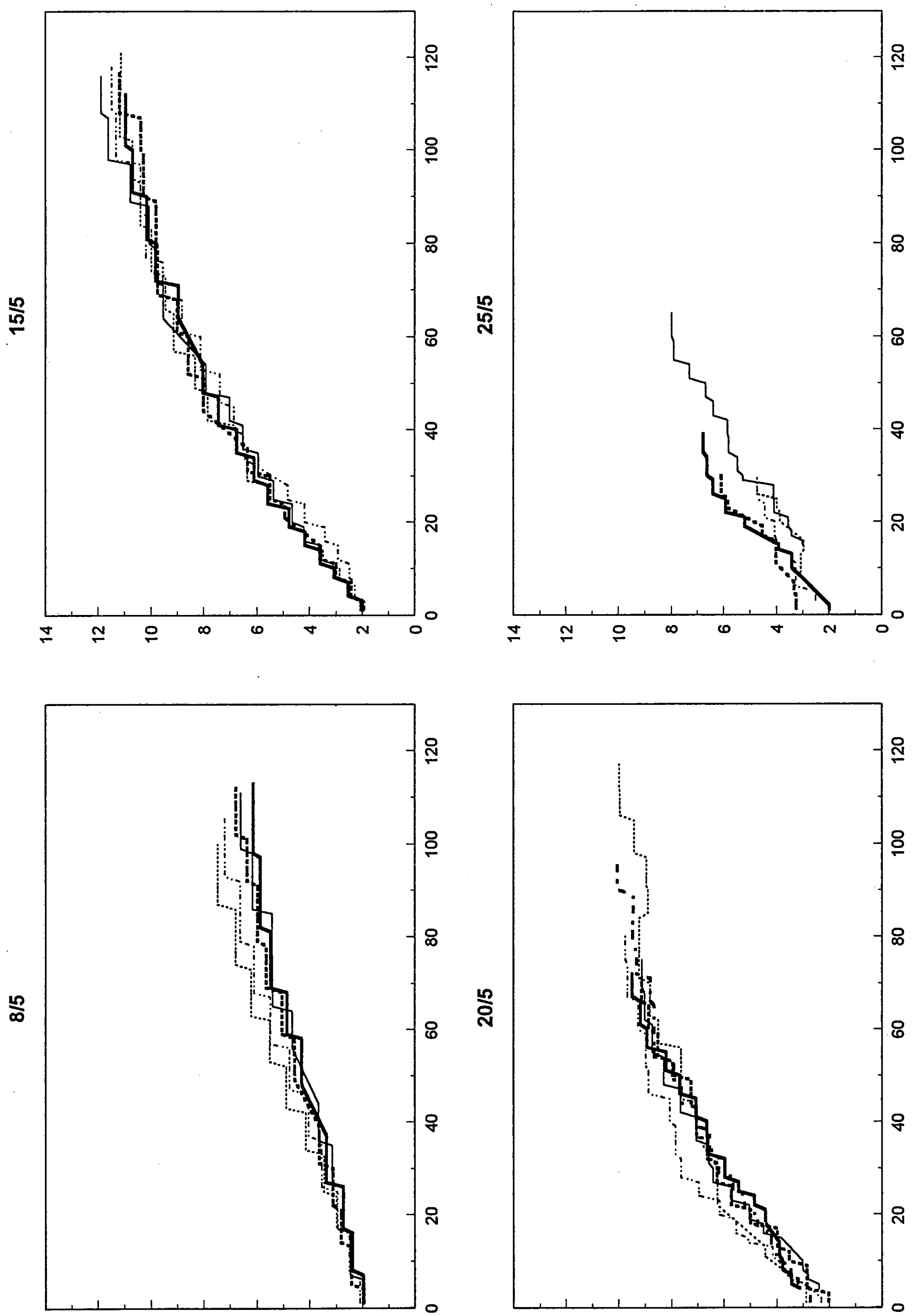
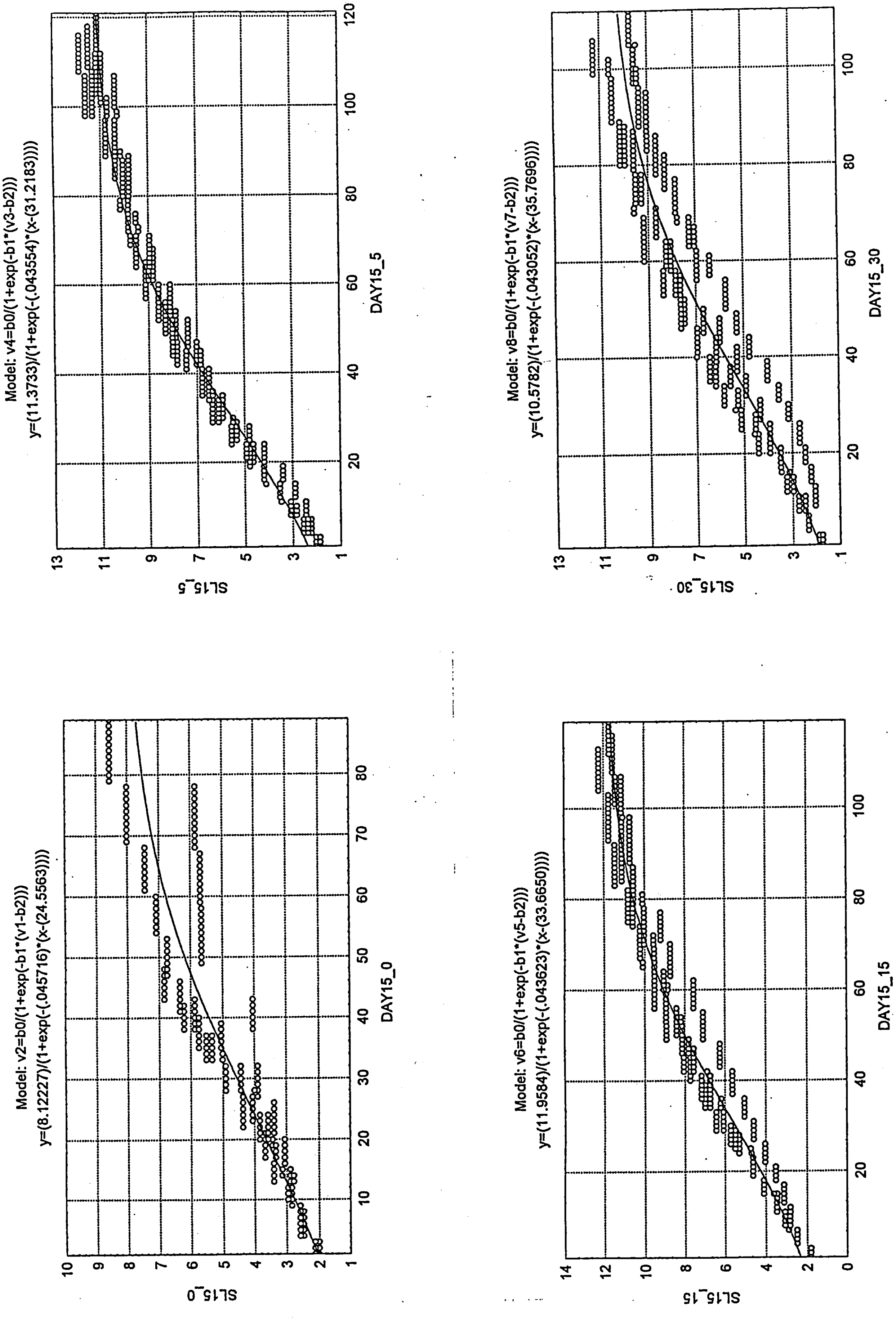


Figure 2b



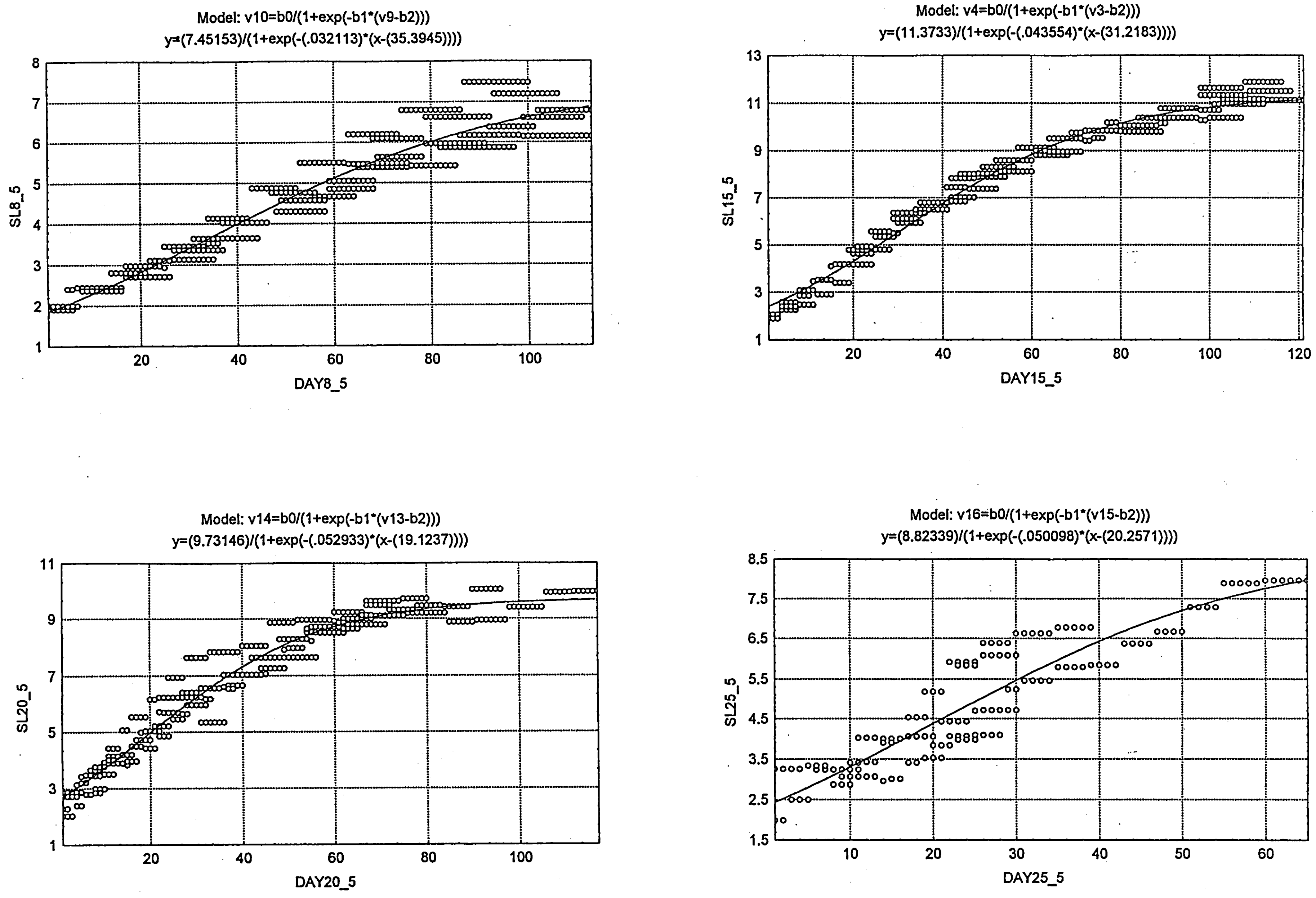
Model: v2=b0/(1+exp(-b1*(v1-b2)))
y=(8.12227)/(1+exp(-(.045716)*(x-(24.5563))))

Model: v4=b0/(1+exp(-b1*(v3-b2)))
y=(11.3733)/(1+exp(-(.043554)*(x-(31.2183))))

Model: v6=b0/(1+exp(-b1*(v5-b2)))
y=(11.9584)/(1+exp(-(.043623)*(x-(33.6650))))

Model: v8=b0/(1+exp(-b1*(v7-b2)))
y=(10.5782)/(1+exp(-(.043052)*(x-(35.7696))))

Figure 3a

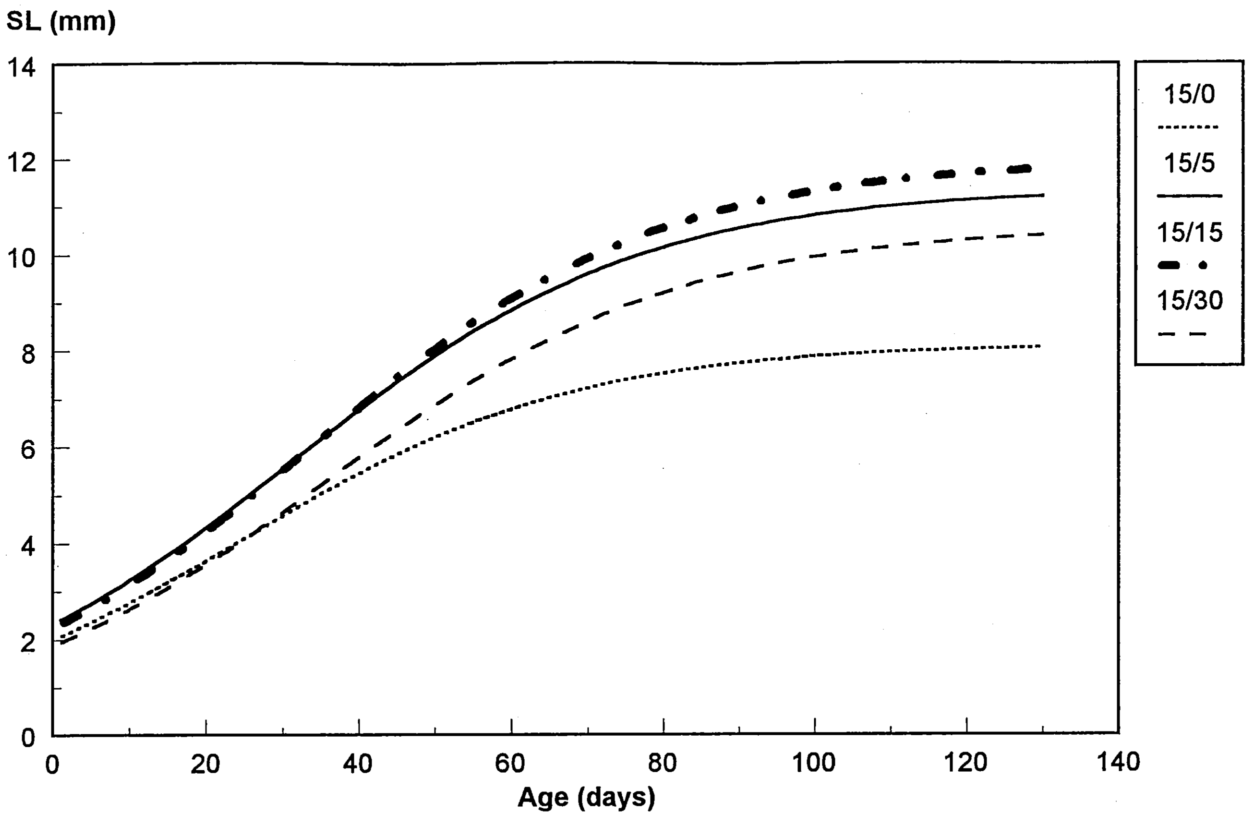

Model: v10=b0/(1+exp(-b1*(v9-b2)))
y=(7.45153)/(1+exp(-(.032113)*(x-(35.3945))))

Model: v4=b0/(1+exp(-b1*(v3-b2)))
y=(11.3733)/(1+exp(-(.043554)*(x-(31.2183))))

Model: v14=b0/(1+exp(-b1*(v13-b2)))
y=(9.73146)/(1+exp(-(.052933)*(x-(19.1237))))

Model: v16=b0/(1+exp(-b1*(v15-b2)))
y=(8.82339)/(1+exp(-(.050098)*(x-(20.2571))))

Figure 3b


SL (mm)
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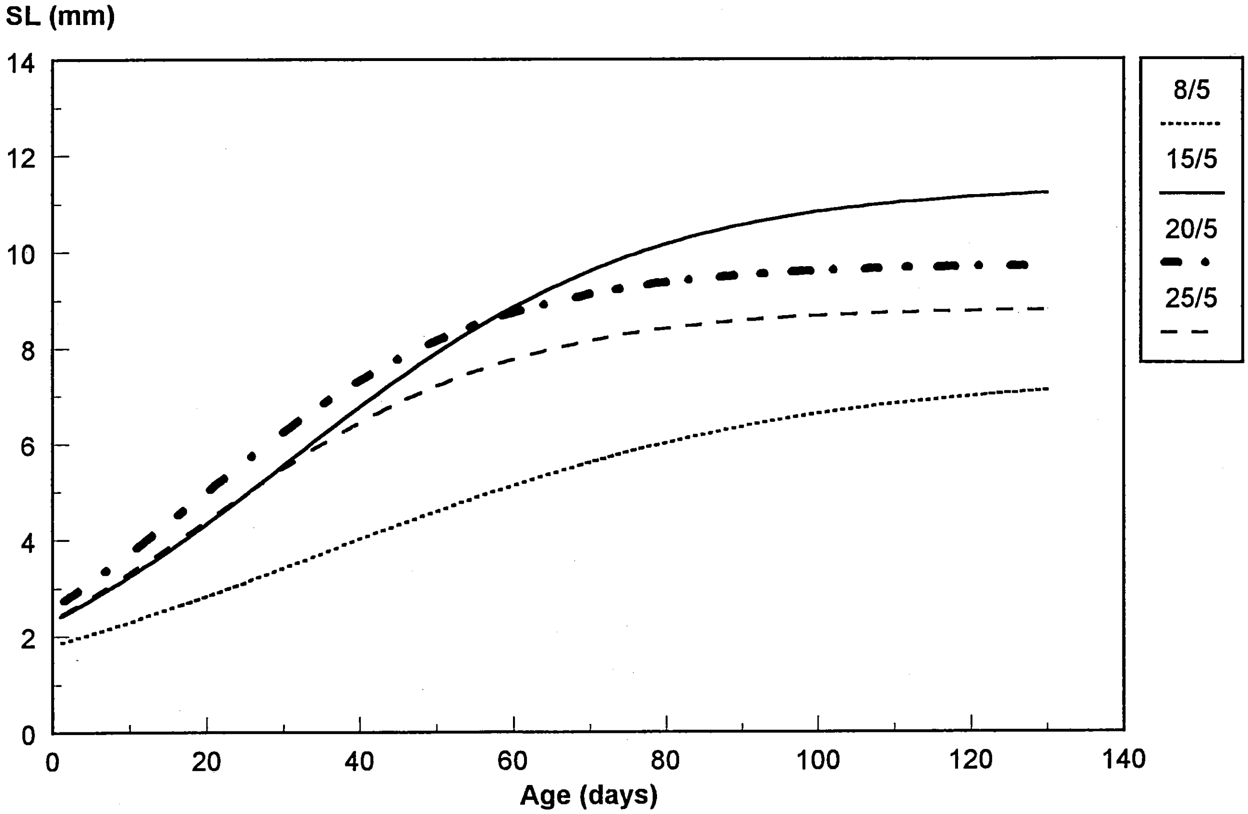
120
140
Age (days)
15/0
15/5
15/15
15/30


SL (mm)
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Age (days)
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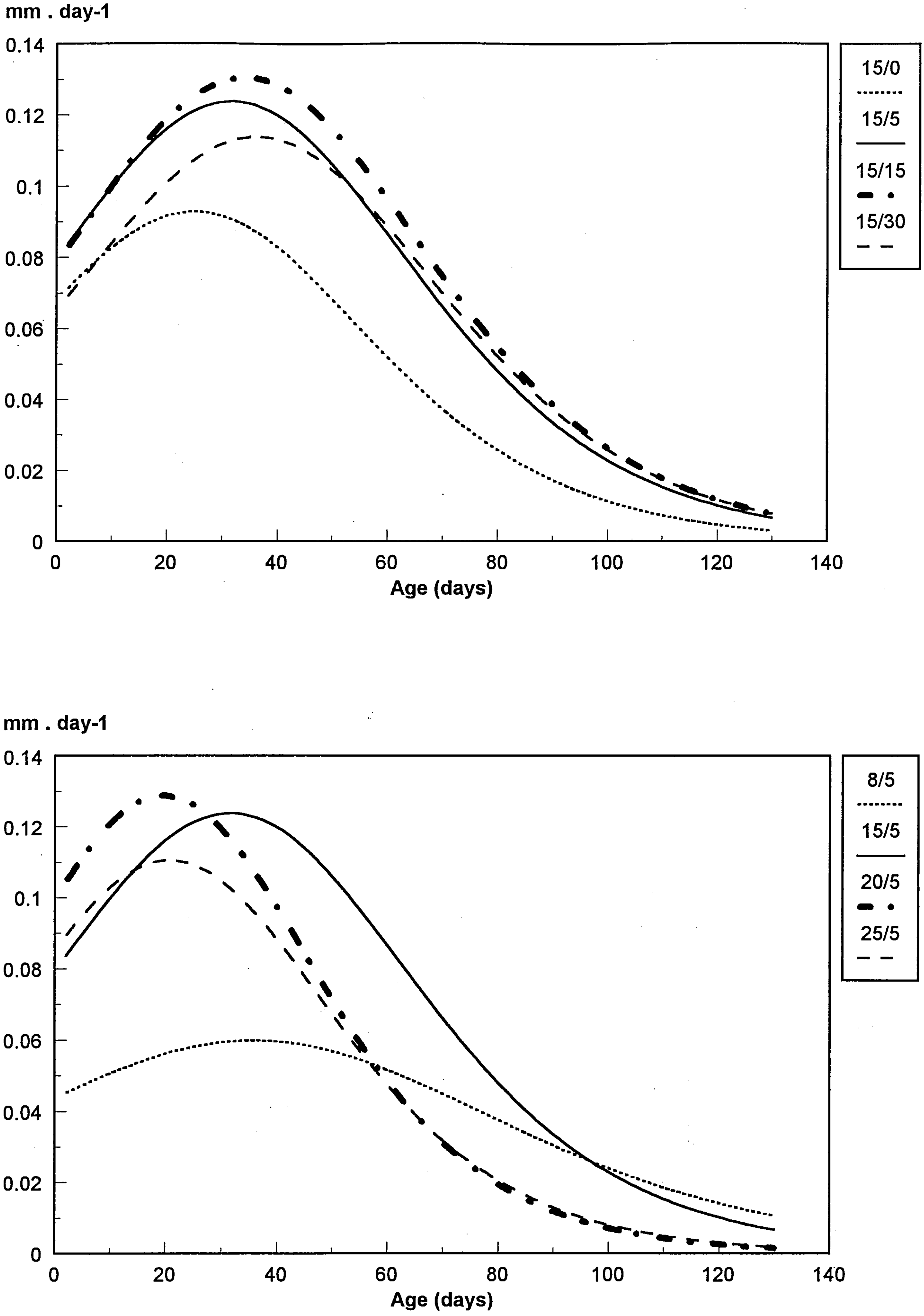
15/5
20/5
25/5

Figure 4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Age (days)
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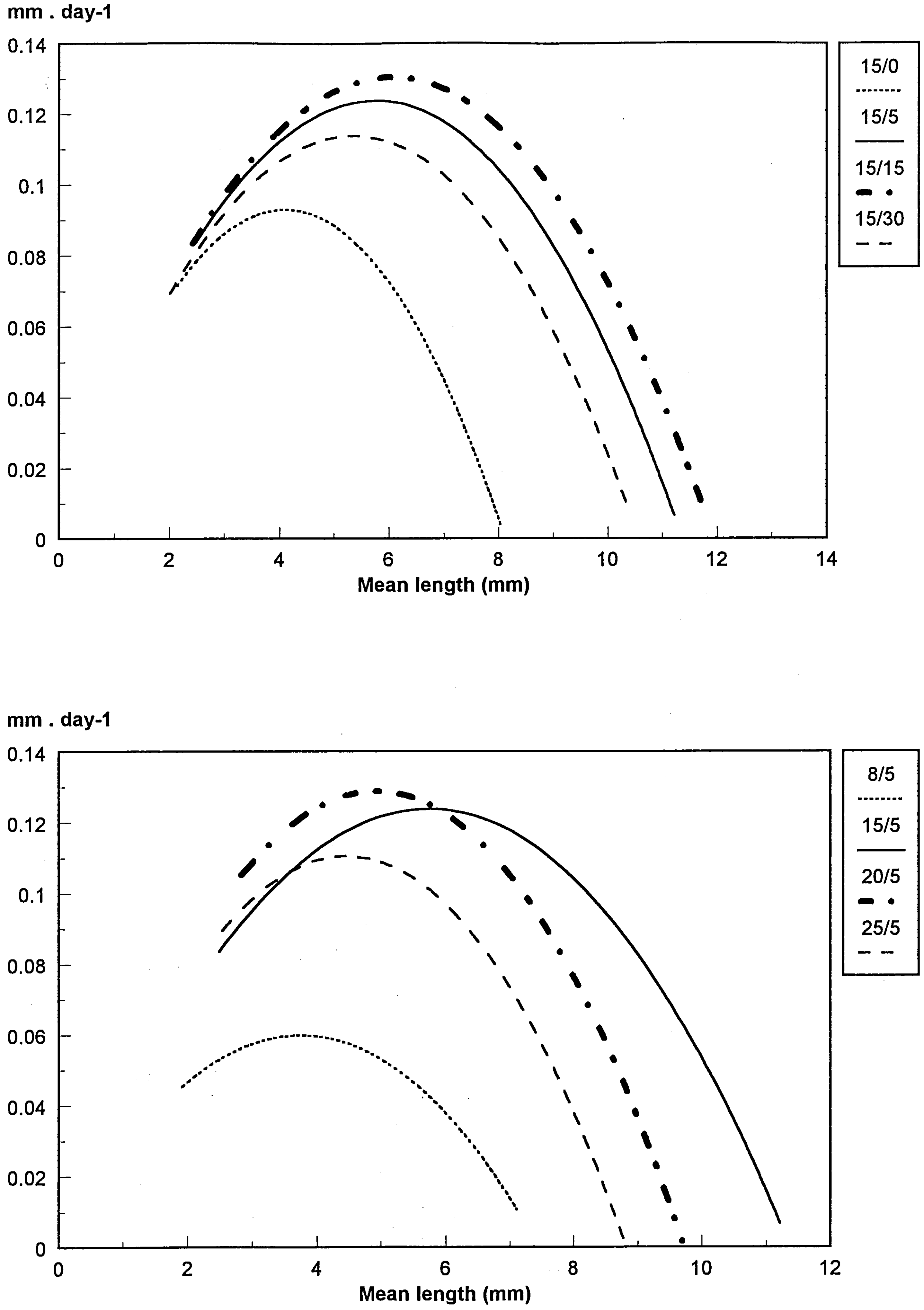
15/5
20/5
25/5

Figure 5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Mean length (mm)
8/5
15/5
20/5
25/5

Figure 6