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

Hydrodynamics
Hyperbenthos
Community structure
North Sea

Hydrodynamique
Hyperbenthos
Structure de la communauté
Mer du Nord

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ABSTRACT

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

*Oceanologica Acta*, **1991**. Proceedings of the International Colloquium on the environment of epicontinental seas, Lille, 20-22 March, 1990, **vol. sp. n° 11**, 205-212.

RÉSUMÉ

Structure temporelle et spatiale au sein d'une communauté hyperbenthique d'une zone côtière peu profonde. Relations avec les variables de l'environnement

Un chalutage mensuel utilisant un traîneau en 24 stations de la zone côtière peu profonde face au delta zéelandais (Mer du Nord) a montré qu'une faune diverse et très abondante est présente dans la couche d'eau avoisinant le fond : l'hyperbenthos. La structure de la communauté hyperbenthique est fortement dominée par des fluctuations saisonnières, qui sont dues à l'apparition, puis à l'abondance, et finalement à la disparition de différentes espèces de l'hyperbenthos temporaire. En hiver et au printemps, quand la communauté est dominée par ses résidents permanents, une structure spatiale apparaît. En utilisant la moyenne par station sur toute l'année, la structure spatiale reflète le régime hydrodynamique du système. Les éléments fins se sédimentent aux mêmes endroits protégés où la biomasse des animaux hyperbenthiques est maximale. Des vitesses réduites du courant et la protection de l'action des vagues créent ainsi un environnement favorable à l'installation des larves d'animaux macrobenthiques et à la sédimentation du bloom phytoplanctonique. Ce secteur riche attire ainsi des invertébrés mobiles et des poissons juvéniles.

*Oceanologica Acta*, **1991**. Actes du Colloque International sur l'environnement des mers épicontinentales, Lille, 20-22 mars 1990, **vol. sp. n° 11**, 205-212.

## INTRODUCTION

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

This study forms part of a major programme sponsored by Rijkswaterstaat (Dutch Ministry of Transport), Tidal Waters Division, to evaluate the effects on the biota of the engineering works in the Dutch delta. To predict the changes on the marine side of the storm surge barrier at the mouth of the Oosterschelde (completed in 1986), a comparative study of macrobenthos, meiobenthos, hyperbenthos, epibenthos and fish was undertaken between the geomorphologically stabilized ebb-tidal delta of the Grevelingen (closed off in 1971) and the more dynamic ebb-tidal delta of the Oosterschelde. If strong correlations exist between the abiotic environment and the biota we should be able to predict future animal communities in the ebb-tidal delta of the Oosterschelde on the basis of hydrodynamic and geomorphological forecasts. This study reports only on the community structure of the hyperbenthos. Other aspects of the hyperbenthos and results on the other benthic compartments investigated will be published elsewhere.

## MATERIAL AND METHODS

### Study area and sampling design

The Voordelta is the shallow coastal area at the mouth of the delta of the rivers Rhine, Meuse and Scheldt in the southern bight of the North Sea (Fig. 1). It stretches from the Belgian-Dutch border in the south to the Hoek van Holland in the north. Its marine boundary is arbitrarily defined by the 15 m depth contour. River outflow, tidal currents and wave action have created a complex pattern of gullies and sandbanks. Due to major engineering works, hydrodynamics and bottom morphology are still changing (Elgershuizen, 1981; Bergh, 1984). The mean tidal amplitude is ca. 3 m. For a detailed description of the area we refer to Kohsiek and Mulder (1988).

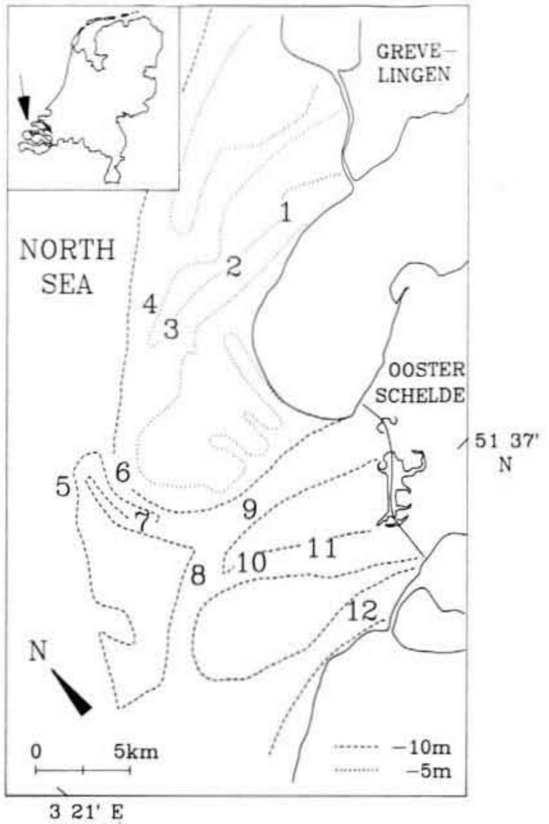


Figure 1

*Map of the study area with the sampling localities and the 5 and 10 m depth contours.*

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

### Sampling gear

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

**Analysis**

All samples were immediately preserved in neutralized formaldehyde 7 % final concentration. In the laboratory all animals were identified, if possible to species level, and counted. Accidentally caught epibenthic species, *e.g.* large fish or adult crabs, and endobenthic species, *e.g.* sedentary polychaetes or bivalves, were eliminated from the analysis. A maximum of one hundred animals per species per sample were measured for biomass calculation. Length-ash free dry weight regressions (2 hours at 110 °C for dry weight, 2 hours at 550 °C for ash weight) were determined for all the common species with continuous growth. For species with discrete stages, *e.g.* zoeae and megalopae of crabs, ash free dry weights of batches of animals were determined per species. Densities and biomasses were calculated using a hypothetical net efficiency of 20 % for all animals.

For the analysis "functional species" were used: zoeae, megalopae and postlarvae of decapods and eggs and larvae of fish were considered as separate "species" as they have different floating and swimming characteristics, different feeding modes, *etc*.

Statistical analysis was performed according to Field *et al.* (1982): first the biotic data were analysed using classification techniques to yield groups of biotically similar samples, then we tested the environmental variables associated with these groups for statistical differences.

First, the density and biomass data per species of the 210 separate trawls were used as input for a Two-Way Indicator Species Analysis-Twinspan (Hill, 1979). Data were root-root transformed prior to Twinspan. Next, group-average sorting with Bray-Curtis similarities (Bray and Curtis, 1957), after logarithmic transformation of the data, was used on the annual mean density and biomass for each species per station to define communities spatially. Afterwards an additional Twinspan was performed on the same annual means, after root-root transformation, to yield indicator species.

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

*Hydrodynamic variables*

Depth; significant wave height (= the wave height that is reached 1 % of the time in one year); orbital velocity at the bottom (= the horizontal component of the orbital movement of the wave action); maximal current velocity ($v_{max}$ ); minimal current velocity ($v_{min}$) and maximum velocity difference ($v_{dif} = v_{max} - v_{min}$);

*Sediment characteristics*

Percentage mud (fine elements < 60 μ); median grain size of the sand fraction; and sorting coefficient.

*Water quality*

Salinity; chlorophyll *a* content; and seston.

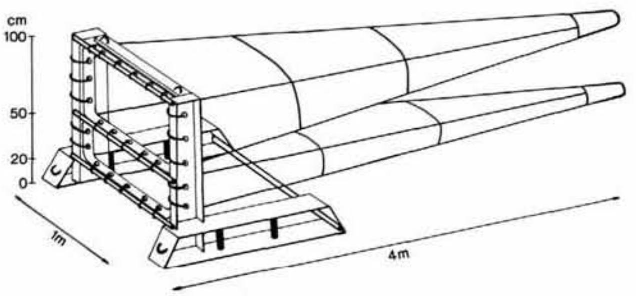


Figure 2

*Sketch of the hyperbenthic sledge used.*

Table 1

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

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

RESULTS

A total of 120 "functional species" from 107 biological species were recorded (Tab. 2).

**Temporal pattern**

Twinspan analysis of the 210 separate trawls shows a strong dominance of temporal structure, *i.e.* most samples of a single month resemble one another more closely than samples from the same station in any other month, except during winter (Fig. 3).

**Density**

A first split divides the year in a cluster from April through September and a cluster from November through February (Fig. 3). Indicator species for the spring and summer samples are *Lanice conchilega* aulophorus larvae, *Crangon crangon* zoeae, *Liocarcinus holsatus* zoeae and megalopae, *Carcinus maenas* megalopae and *Pagurus bernhardus* zoeae.

Table 2

*List of the hyperbenthic species recorded during the study.*

Annelida, Polychaeta
- *Lanice conchilega* aulophorus
- *Harmothoe* species larva
- *Pectinaria koreni* larva

Chelicerata, Pycnogonida
- *Callipallene brevirostris*
- *Picnogonum littorale*
- *Anoplodactylus pygmaeus*
- *Phoxichilidium femoratum*
- *Nymphon rubrum*

Crustacea

Decapoda
- *Crangon crangon* postlarva
- *Crangon crangon* zoaea
- *Pontophilus trispinosus* zoaea
- *Hippolyte* species postlarva
- *Hippolyte* species zoaea
- *Palaemon* species postlarva
- *Palaemon* species zoaea
- *Processa modica* postlarva
- *Processa modica* zoaea
- *Pagurus bernhardus* megalopa
- *Pagurus bernhardus* zoaea
- *Porcellana longicornis* megalopa
- *Porcellana longicornis* zoaea
- *Macropodia* species megalopa
- *Macropodia* species zoaea
- *Portumnus latipes* megalopa
- *Carcinus maenas* megalopa
- *Carcinus maenas* zoaea
- *Liocarcinus holsatus* megalopa
- *Liocarcinus holsatus* zoaea
- *Liocarcinus* species zoaea
- *Corystes cassivelaunus* megalopa

Amphipoda
- *Pariambus typicus*
- *Phtisica marina*
- *Caprella linearis*
- *Gammarus crinicornis*
- *Gammarus salinus*
- *Gammarus locusta*
- *Gammarus oceanicus*
- *Gammaropsis nitida*
- *Atylus swammerdami*
- *Atylus falcatus*
- *Apherusa ovalipes*
- *Parajassa pelagica*
- *Jassa pusilla*
- *Jassa falcata*
- *Jassa marmorata*
- *Bathyporeia elegans*
- *Bathyporeia sarsi*
- *Bathyporeia guilliamsoniana*
- *Bathyporeia tenuipes*
- *Haustorius arenarius*
- *Orchomene nana*
- *Melita palma*
- *Melita obtusata*
- *Melita hergensis*
- *Stenothoe marina*
- *Stenothoe valida*
- *Metopa pusilla*
- *Metopa alderi*
- *Maera grossimana*
- *Monoculodes carinatus*
- *Pontocrates arenarius*
- *Pontocrates altamarinus*
- *Ampelisca brevicornis*
- *Dyopedos porrectus*
- *Urothoe brevicornis*
- *Urothoe poseidonis*

Isopoda
- *Eurydice pulchra*
- *Idotea emarginata*
- *Idotea baltica*
- *Idotea linearis*

Copepoda
- *Centropages typicus*
- *Centropages hamatus*
- *Temora longicornis*
- *Calanus helgolandicus*
- *Euterpina acutifrons*
- Caligidae species

Cumacea
- *Pseudocuma longicornis*
- *Lamprops fasciata*
- *Bodotria scorpioides*
- *Diastylis bradyi*
- *Diastylis rugosa*
- *Diastylis rathkei*
- *Diastylis laevis*
- *Diastylis lucifera*
- *Iphinoe tenella*

Euphausiacea
- *Nyctiphanes couchi*

Mysidacea
- *Gastrosaccus spinifer*
- *Gastrosaccus sanctus*
- *Mesopodopsis slabberi*
- *Schistomysis spiritus*
- *Schistomysis kervillei*
- *Praunus flexuosus*
- *Siriella armata*

Chaetognatha
- *Sagitta elegans*

Pisces
- Fish eggs
- *Anguilla anguilla*
- Clupeidae species
- *Merlangius merlangus*
- *Trisopterus luscus*
- *Ciliata mustela*
- *Atherina presbyter*
- *Gasterosteus aculeatus*
- Syngnathidae species
- *Myoxocephalus scorpius*
- *Agonus cataphractus*
- *Liparis liparis*
- *Trachurus trachurus*
- *Trachinus vipera*
- *Pholis gunnellus*
- *Ammodytes tobianus*
- *Callionymus lyra*
- *Pomatoschistus minutus*
- *Pomatoschistus lozanoi*
- *Aphia minuta*
- *Scophthalmus rhombus*
- *Pleuronectes platessa*
- *Limanda limanda*
- *Solea solea*

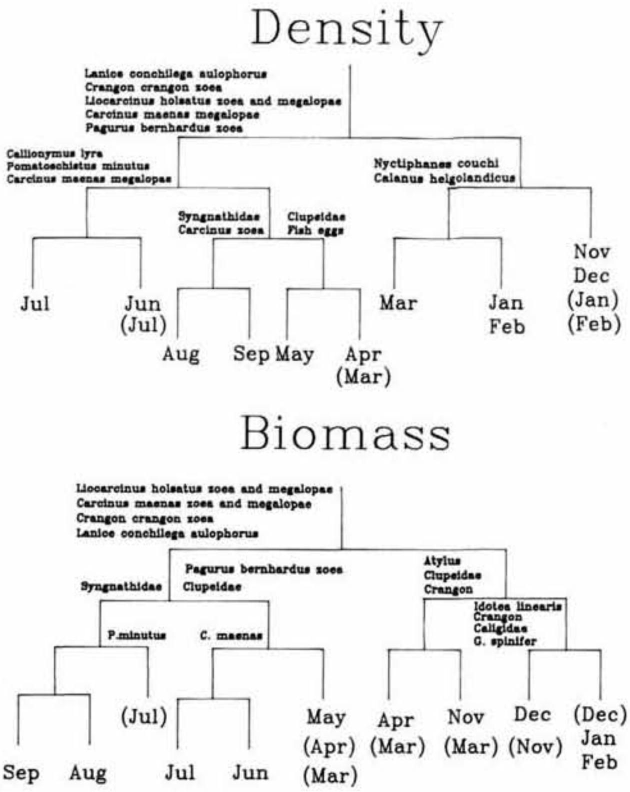


Figure 3

*Dendrogram showing temporal community structure and indicator species for the density and biomass data of the separate trawls.*

In the next division, in the spring-summer cluster June and July are separated from the rest with indicator species *Callionymus lyra*, *Pomatoschistus minutus* and *Carcinus maenas* megalopae. The next split within this cluster isolates the June samples from the July samples. The June group also contains the July samples from the Grevelingen area. These separate in the subsequent division. From the fourth division onward, spatial patterns begin to emerge in the July samples. The June samples stay together as a group.

The next split in the other main cluster of the spring-summer group divides the samples in an August-September group (indicator species *Syngnathus* sp. and *Carcinus maenas* zoeae) and an April-May group (indicator species Clupeidae sp. and fish eggs). Next, both these clusters split into the separate months. The April cluster also contains the Banjaard samples of March. Spatial patterns begin to emerge from the fifth split onward and are most obvious in the April and May samples.

In the autumn-winter cluster, the situation is more complex. A first split separates all remaining March samples and the main body of January and February samples from the rest (indicator species *Nyctiphanes couchi* and *Calanus helgolandicus*). Next, March (samples from the Grevelingen and Oosterschelde areas) splits off. In the remaining cluster of January and February samples the spatial pattern emerges at the next division.

The second main cluster of the first division in the autumn-winter group is a rather heterogeneous mixture of the November and December samples with the remaining January and February samples. The next split here separates most of the November and December samples from those of the remaining two months. Subsequent divisions in these groups show spatial patterns rather than a temporal structure.

### Biomass

The Twinspan analysis, using the biomass data of the 210 separate trawls, largely shows the same structure (Fig. 3). A first split separates May through September (indicator species *Liocarcinus holsatus* zoeae and megalopae, *Carcinus maenas* zoeae and megalopae, *Crangon crangon* zoeae and *Lanice conchilega* aulophorus larvae) from November through April.

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

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

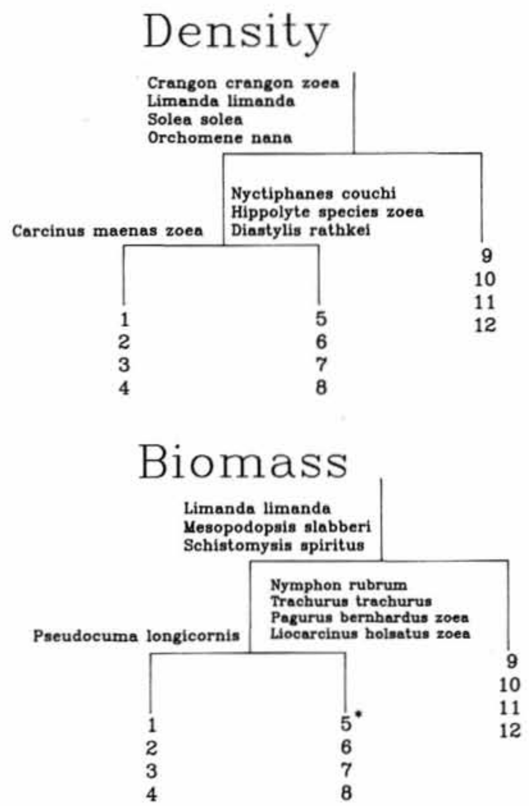


Figure 5

*Dendrogram showing spatial community structure and indicator species for the annual mean density and biomass per station.*

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

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


Figure 4

*Map of the study area showing the three subareas found by cluster analysis using the annual means per station.*

### Spatial pattern

Both classification techniques, group-average sorting and Twinspan, using the annual means for each species per station, split up the samples into three geographically defined communities (Fig. 4): ebb-tidal delta of the Grevelingen (stations 1-4), Banjaard area (stations 5-8) and ebb-tidal delta of the Oosterschelde (stations 9-12). The boundaries of these community-defined areas are identical for the density data using both techniques. There is a slight difference between the group-average sorting and the Twinspan using the biomass data: station 5 is classified within the Grevelingen cluster instead of within the Banjaard cluster using the first technique (Fig. 5). The stations in the ebb-tidal delta of the Grevelingen are more similar to those of the Banjaard area than to the stations of the ebb-tidal delta of the Oosterschelde. In the analysis on the basis of density, indicator species for the Grevelingen-Banjaard stations are *Crangon crangon* zoeae, *Limanda limanda*, *Solea solea* and *Orchomene nana*. Indicator species for the ebb-tidal Grevelingen is *Carcinus maenas* zoeae. Indicator species for the Banjaard area are *Nyctiphanes couchi*, Hippolyte species zoeae and *Diastylis rathkei*. In the analysis based on biomass, indicator species for the Grevelingen-Banjaard stations are again *Limanda limanda* and the mysids *Mesopodopsis slabberi* and *Schistomysis spiritus*. Indicator species for the ebb-tidal Grevelingen is *Pseudocuma longicornis*. Indicator species for the Banjaard area are *Nymphon rubrum*, *Trachurus trachurus*, *Pagurus bernhardus* zoeae and *Liocarcinus holsatus* zoeae.

The composition of the biological communities in the three areas differs substantially, though the main groups are similar in all three areas: decapod larvae, mysids, macrobenthic larvae and fish eggs and fish larvae (Fig. 6). The ebb-tidal delta of the Grevelingen has the highest total biomass, the highest density and biomass of macrobenthic larvae, mysids and fish eggs and larvae.

The Banjaard area has the highest total densities, mainly due to the high densities of decapod larvae. The ebb-tidal delta of the Oosterschelde is clearly the poorest area, with densities only half as high as in the other areas.

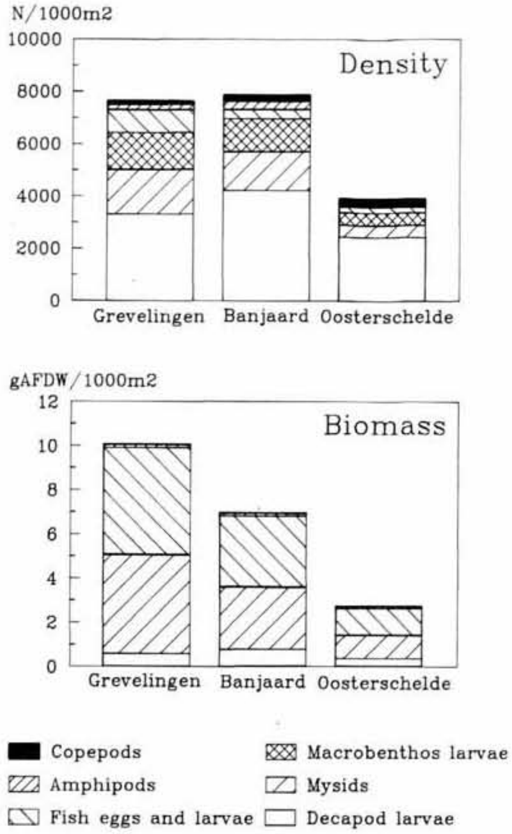


Figure 6

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

**Relations with the environment**

The Kruskal-Wallis H test, using the measured variables for the separate stations in the biologically defined communities, shows significant differences ($p < 0.05$) between these sets for $v_{max}$, $v_{min}$, $v_{dif}$ and 1 % wave, chlorophyll and seston (Tab. 3 and Fig. 7). The ebb-tidal delta of the Grevelingen has the lowest $v_{max}$, $v_{min}$ and $v_{dif}$, a low 1 % wave and the lowest seston. It also has the highest chlorophyll *a* content. The Banjaard area has the highest $v_{min}$, the highest 1 % wave and the lowest chlorophyll *a*. The ebb-tidal delta of the Oosterschelde has the highest $v_{max}$ and $v_{dif}$, the lowest 1 % wave and the highest seston.

DISCUSSION

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

From studies in the Bristol Channel and Severn estuary it is known that salinity is a major factor determining the distribution of "planktonic" animals (Williams, 1984). With high river outflows in winter and northwesterly winds, Rhine water can significantly lower the salinity, especially in the ebb-tidal delta of the Grevelingen (Dijke and Buijs, 1987). Such instances were not recorded during sampling. Salinities were always more or less homogeneous over the whole area studied.

The three different areas corresponding to the biological communities differ in a number of characteristics. The

Table 3

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

| | |
|---|---|
| **Hydrodynamic variables** | |
| Depth | NS |
| Significant wave height | p < .005 |
| Orbital velocity bottom | NS |
| Maximal current velocity | p < .005 |
| Minimal current velocity | p < .05 |
| Maximum velocity difference | p < .005 |
| **Sediment characteristics** | |
| Percentage mud | NS |
| Median grain size | NS |
| Sorting coefficient | NS |
| **Water quality** | |
| Salinity | NS |
| Chlorophyll *a* content | p < .001 |
| Seston | p < .001 |

ebb-tidal delta of the Grevelingen is the least dynamic area. Co-occurrence of a certain community and a set of, not strictly independent, environmental variables is no proof of any causal relation. However, the hydrodynamic characteristics of the ebb-tidal delta of the Grevelingen clearly suit a number of animals.

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

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

Most fish eggs caught are *Solea solea* eggs. As *Solea solea* is not a spawner in the area, we must conclude that the eggs either undergo selective passive transport from the spawning ground to the area or else they are selectively trapped from a more or less homogeneous distribution in the coastal water. Although mud content does not differ significantly between the three areas (yet ?), the ebb-tidal delta of the Grevelingen has the highest mud percentages (Fig. 7). In this area the old tidal gullies are silting up rapidly (Kohsiek and Mulder, 1987). Thus the ebb-tidal delta of the Grevelingen may act as a sink for various sorts of passively transported material *i. e.* silt, decaying phytoplankton, macrobenthic larvae and fish eggs with near neutral buoyancy. This creates a rich and varied benthic life that sustains the high densities of demersal fish, shrimp, crabs and starfish found in the ebb-tidal delta of the Grevelingen (Hamerlynck and Craeymeersch, 1990). Although the Banjaard area has a rich hyperbenthic fauna, wave conditions there prevent sedimentation, as attested by the low mud content of the bottom, and preclude settlement of rich macrobenthic communities. Despite being sheltered from the wave action the ebb-tidal delta of the Oosterschelde is poor. The richer water masses of the Banjaard (and offshore) do not reach the area because they are flushed outward at every low tide by the relatively oligotrophic water from the Oosterschelde. Moreover the high current velocities, attested by high seston loads,

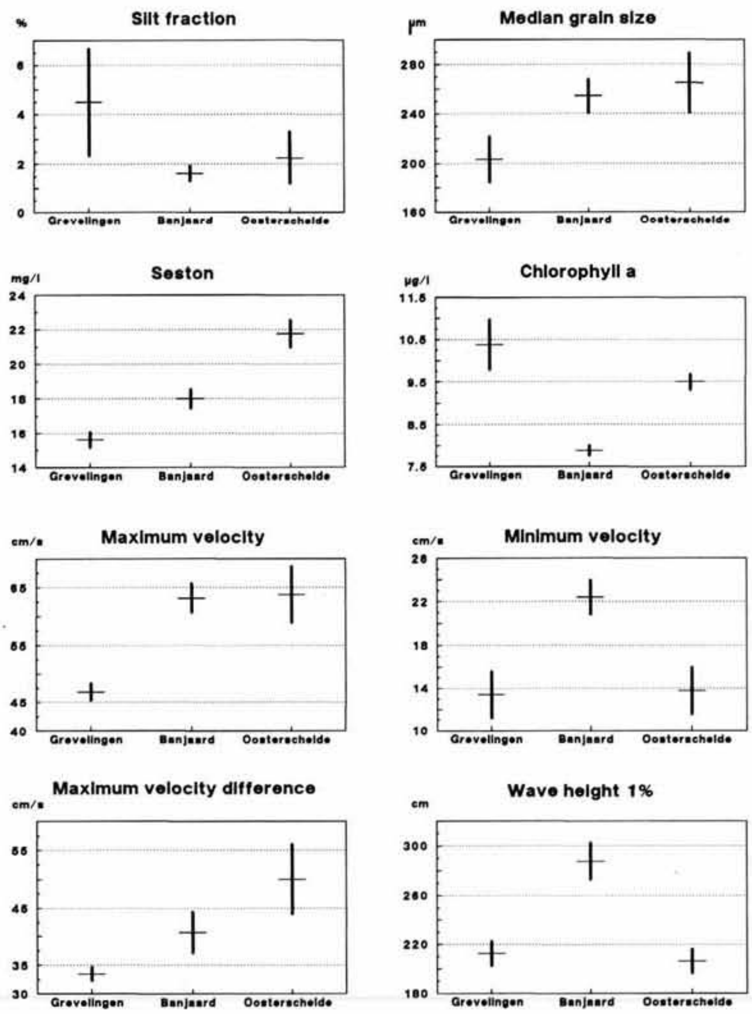


Figure 7

*Environmental variables with their standard errors for the three subareas.*

prevent sedimentation and settlement in the ebb-tidal delta of the Oosterschelde.

## CONCLUSION

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

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

## Acknowledgements

This study was sponsored by Rijkswaterstaat (Dutch Ministry of Transport), Tidal Waters Division, Middelburg. It is registered as publication n° 504 of the Delta Institute for Hydrobiological Research, Yerseke.

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