

## Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring

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**ABSTRACT:** Macrobenthic and meiobenthic communities of an area off the Belgian coast of the North Sea were studied from 1970 until 1975 at 74 stations. On the basis of both macro- and meiobenthos, three zones can be distinguished in the area. The coastal zone is characterized by the macrobenthic *Abra alba* community, corresponding to the meiobenthic *Microarthridion littorale* - *Halectinosoma herdmanni* community, and the open sea zone by the macrobenthic *Venus gallina* community and the meiobenthic *Leptastacus laticaudatus* - *Paramesochra helgolandica* community. In between is a transient zone where elements of both other zones mix. The distribution of these zones is governed by the hydrodynamical regime of the region, especially by the residual and tidal current system of the Southern Bight. Within the coastal zone, the composition of the community is influenced by pollution which especially affects the epibenthic detritus-feeders of the meiobenthos. The spatial stability of parameters describing community structure can be used for monitoring changes. Temporal characteristics of these parameters could not be investigated properly, but diversity seems to be much stabler than biomass.

### INTRODUCTION

Much of the considerable research effort for measuring the biological impact of pollution is directed to its effect on the individual organism, mainly because non-specific effects of pollution can generally be diagnosed by physiological, pathological and biochemical responses which enable quantitative assessment of animal health (Bayne, 1979). The merit of such studies on individuals is the early warning that can be signalled, because the effect of sub-lethal stressors will become visible in individual response long before it is apparent in the population or community (Bayne, 1979). Moreover it is possible to establish causal and quantitative relationships in laboratory experiments.

However, in most natural situations pollution is not of a single type and the simultaneous and often synergistic action of many different kinds of pollutants is very difficult to deduce from laboratory experiments only. Furthermore, it is questionable whether sublethal effects on individuals will provide sufficient motivation for action in decision-making processes; only spectacular effects on populations or communities are likely to result in political concern. These effects are hardly predictable from laboratory experiments on single species; whereas it is probably true that ecological monitoring will provide neither an early warning nor the possibility of establishing irrefutably causal relationships, it is the only way to measure changes in communities directly.

Management must involve monitoring of marine systems. The present state of ecological theory with its emphasis on interactions between populations as the main structuring force in community organisation does not allow prediction of future states of the system and in fact has never been intended to do so. However, understanding the dynamics of a process is not necessary for prediction and it is not the case that the biological interactions underlying population fluctuations have to be understood before these fluctuations can be predicted. Prediction can be based on regularity as well as on its explanation, and statistical models, based on sufficiently long time series, are to be preferred at present (Poole, 1978).

Moreover, even if ecological understanding were possible, there would remain uncertainty introduced by the environment; this would make it impossible to use the traditional mechanistic solutions to optimization problems as used in the physical and engineering sciences. Optimal control of systems in which uncertainty is the only thing that is certain can only be based on options in which the optimal control of the system at some future time will depend on the state of the system at that time, and this requires frequent monitoring of the system.

Once the necessity of monitoring is accepted it is necessary to decide which parameters are suitable to be monitored. The choice of parameters depends on many things but must always involve statistical considerations; the marine environment is heterogeneous and therefore information about the nature of a phenomenon must come from samples which are distributed in space and time so that they cover all significant scales on which variability characterizing the phenomenon exists. The Nyquist criterion of time series analysis states that sampling frequency must be at least twice the highest frequency of the phenomenon studied, and therefore it is clear that when a large part of the variance in a parameter is found in the high frequencies of space and/or time, that parameter is in general unfit for monitoring.

This paper summarizes results of a study of benthic communities of the Southern Bight of the North Sea; details will be published separately. In this paper attention is focused on a description of these communities using structural parameters such as density, biomass and diversity, and their possible use in ecological monitoring. Some of the spatial characteristics of these parameters are discussed, and the possibility of describing large areas and the changes occurring in them in terms of the structure of the communities inhabiting them are examined.

## MATERIAL AND METHODS

### Description of the study area

The sampling stations (Figs 2, 4) cover a quadrangle with a length of about 170 km running parallel to the Belgian coast and a width of 63 km in the southwest and 95 km in the northeast. Along the Belgian coast the nearest stations lie about 1 km off-shore; along the Dutch coast all stations are more than 5 km off-shore, except for three within the three-mile zone of the Dutch coastal waters.

The sediments in this investigated area are heterogeneous. The area near the Belgian coast acts as a sediment sink where the highly turbid and polluted waters of the

western Scheldt enter the North Sea and turn in a huge gyre between the mouth of the estuary and Ostend, depositing most of their load of mud above the fine grained sands (median grain size:  $< 200 \mu\text{m}$ ).

To the south, polluted muds and detritus enter the coastal zone partly from the IJzer river and partly from currents running along the northwestern French coast, with its two large agglomerations Dunkirk and Calais. The mud cover however is not as extensive in this part of the area, and the patches of fine materials are not fixed but seem to be resuspended and displaced periodically.

To the north of the gyre, the runoff from the Rhine is swept by the currents along a narrow strip close to the Dutch coast (McCave, 1973). The fine materials remain in suspension and only under certain conditions (slack water) are temporary mud layers formed (Moens, 1974).

The mud along the Belgian coast contains more than 0.5 % organic matter and the highest concentrations of heavy metals have also been found in this area: Zn  $> 200$  ppm; Cu  $> 30$  ppm; Mn  $> 500$  ppm;  $\text{Fe}_2\text{O}_3 > 2500$  ppm (see Wollast, 1977; Elskens, 1974 for a description of methods). However, most of the sediment in the area studied consists of pure sands with a low clay-silt fraction (1 to 0.1 %) and accordingly a low amount of organic material ( $< 0.15$  %). The median grain size of this sand is not homogeneous but varies according to the declining velocity of the tidal currents: coarser than  $350 \mu\text{m}$  south of  $52^\circ 00' \text{ N}$ ,  $350\text{--}275 \mu\text{m}$  south of  $52^\circ 12' \text{ N}$  and  $275\text{--}200 \mu\text{m}$  south of  $52^\circ 25' \text{ N}$  (Gullentops, 1974). Since the silt-clay fraction is low, the concentrations of heavy metals and pesticides are equally low (maximum concentrations found are 100 ppm Mn, 10 ppm Cu, 100 ppm Zn, 0.17 ppm Hg and  $1.5 \text{ } \text{‰}$   $\text{Fe}_2\text{O}_3$ ).

Between the near-shore predominantly muddy bottoms and the off-shore pure sands is an intermediary zone where sediments are heterogeneous both in space and in time. This heterogeneity is enhanced by a ripple-like sandbar complex.

### Sampling

From 1971 until 1975 a total of 2337 samples were collected from the area. About 250 samples covering 60 stations were analysed for macrobenthos and about 350 samples from 74 stations for meiobenthos. All samples were taken with a  $0.1\text{-m}^2$  Van Veen grab (weight: 50 kg). The material was collected in a bucket and fixed in 7 % neutralised formalin on board the ship. Macrobenthic samples were sorted using a rust-free 0.87-mm sieve (the only sieve available at the time). Meiobenthos samples were taken from the bucket, prior to sieving out the macrobenthos. The use of a bucket reduces the influence of small-scale spatial variability on the estimates (Heip et al., 1977), but the Van Veen grab greatly underestimates meiofauna abundance and biomass. In order to correct for this, density in the grab was compared with density in cores simultaneously collected by SCUBA diving; correction factors of 1.5 for nematodes and 1.2 for other meiobenthic groups were applied for sandy sediments. Nevertheless, sampling with a Van Veen grab always introduces bias which cannot be completely eliminated in the way described. Meiofauna samples were either washed by decantation through a 0.038-mm sieve (sandy samples), or a sugar-flotation-extraction technique was used (in the case of sandy muds or pure muds) (see Heip et al., 1974, for a description of the method and an evaluation of its efficiency). A Mettler ME22/BA 25 microbalance, accurate to  $1 \mu\text{g}$ , was used for

estimating the dry weight of the representatives of the meiofaunal groups, measured after drying in an oven at 110° for 2 h. The ash-free dry weight of the macrofauna was measured after drying for 3–4 h at 550 °C.

The species occurring in more than 5 % of the stations were used for cluster analysis. In the *Q*-mode the analyses were based on matrices of similarity between all possible pairs of stations and in the *R*-mode between all possible pairs of species. The indices used were, in the *Q*-mode: the Canberra metric (Lance & Williams, 1967) and the Czekanowski quantitative similarity coefficient (Sneath & Sokal, 1973); in the *R*-mode: the product-moment correlation coefficient. The matrices of similarity thus obtained were subjected to group-average sorting (Sokal & Sneath, 1963) and flexible sorting (Lance & Williams, 1967), with the cluster intensity coefficient  $\beta$  set at  $-0.25$ .

For macrobenthos, after inspection of the dendrograms resulting from this analysis of 60 stations, 18 station groups were formed to filter out noise caused by small-scale spatial variability. The total number of species in these 18 groups was again subjected to cluster analysis in the *Q*- and *R*-mode.

As a measure of diversity the Shannon-Wiener index was used:  $H' = - \sum_{i=1}^n p_i \log_2 p_i$  (Pielou, 1966).

## RESULTS

### Macrobenthos of the Southern Bight

Using cluster analysis, two species groups can be established (Govaere, 1978). The first corresponds roughly to the "boreal off-shore sand association" of Jones (1950) or the "*Venus gallina* community" of Petersen (1914) and is characterized by *Spisula elliptica*, *Ophiura affinis*, *Echinocyamus pusillus* and a number of interstitial polychaetes. The second group corresponds to the "boreal shallow muddy sand association" (Jones, 1950) or the "*Abra alba* community" (Petersen, 1914). Characteristic species are *Abra alba*, *Tellina fabula* and *Nephtys hombergii*.

The normal analysis (*Q*-mode) of the 18 station groups revealed three major clusters corresponding to: (1) open sea zone (2) a coastal zone and (3) a transition zone (Fig. 1). Numerical dominant species in the open sea zone – which cannot be considered homogeneous on the basis of hierarchical clustering – are, in descending order, *Spiophanes bombyx* (more than 50 % of total numbers), *Hesionura augeneri*, *Ophiura affinis*, *Nephtys cirrosa*, *Eteone longa*, *Bathyporeia guilliamsoniana*, *Echinocardium cordatum*, *Scolecopsis bonnieri*, *Glycera capitata*, *Anaitides subulifera*, *Spisula elliptica* and *Echinocyamus pusillus*. In terms of biomass the dominant species are: *Nephtys cirrosa*, *Ophiura affinis*, *Spisula elliptica*, *Spiophanes bombyx*, *Echinocardium cordatum*, *Scolecopsis bonnieri*, *Echinocyamus pusillus* and *Glycera capitata*, which make up more than 50 % of the total biomass. A number of species occur exclusively in this zone: e. g. *Anaitides subulifera*, *Ophiura affinis*, *Tellina pygmaea*, *Echinocyamus pusillus*, *Branchiostoma lanceolatum* and many interstitial polychaetes such as *Exogone hebes*, *Macrochaeta helgolandica*, *Streptosyllis arenae* and *Opisthodonta pterochaeta*.

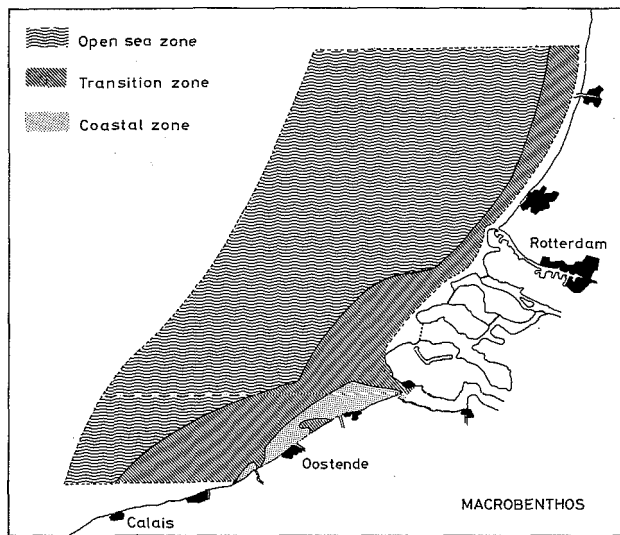


Fig. 1. Map of the Southern Bight with the investigated area, showing the three zones delimited on the basis of macrobenthic associations

The coastal zone is a very heterogeneous collection of species-poor stations. Number and biomass are dominated by *Cistena cylindraria*, *Macoma balthica*, *Nephtys hombergii* and *Albra alba*. Capitellid polychaetes are frequent and relatively abundant.

Between the open sea and the coastal zone there is a transition zone where the following species are numerically dominant: *Lanice conchilega*, *Nephtys cirrosa*, *Spiophanes bombyx*, *Magelona papillicornis*, *Cistena cylindraria*, *Anaitides mucosa*, *Tellina fabula*, *Eumida sanguinea*, *Ophelia limacina*, *Nephtys hombergii*, *Abra alba* and *Mysella bidentata*, which account for nearly 40 % of total numbers. In terms of biomass the dominant species are *Abra alba* (50 % of total biomass), *Tellina fabula*, *Nephtys hombergii* and *Nephtys cirrosa*, which together account for more than 60 % of total biomass. Neither in this nor in the coastal zone are there species which are exclusive to the zone.

Six station groups were recognized in each of the three zones. Table 1 gives the biomass and diversity of the three zones (as means of 6 station groups in each zone). From this table, it can be seen that there is a clear gradient in diversity from the coast towards the open sea (Fig. 2), a gradient that can be detected quite easily as the standard error on diversity values is small. There is much more variability in the biomass data, and this variability is larger in the coastal zone: the coefficient of variation  $s/\bar{x}$  varies from 0.47 in the open sea over 0.71 in the transition zone to 1.71 in the coastal zone for the Polychaeta. For diversity the respective figures are only 0.04, 0.36 and 0.40. For macrobenthos as a whole, biomass variability shows the same pattern, varying from 0.43 over 1.30 to 1.31, whereas diversity varies from 0.08 over 0.24 to 0.39. This clearly demonstrates the much more heterogeneous nature of the near-shore stations.

Table 1. Mean biomass and diversity of macrobenthos in three zones of the Southern Bight (B: g ash-free dry weight; H : bits per ind.). Mean and standard error (n = 6)

Zone		Polychaeta	Mollusca	Total
Open sea zone	B	0.94 ± 0.18	0.27 ± 0.99	2.12 ± 0.37
	H	2.59 ± 0.04	0.69 ± 0.13	3.28 ± 0.11
Transition zone	B	0.83 ± 0.24	1.72 ± 1.24	2.74 ± 1.45
	H	1.98 ± 0.29	0.92 ± 0.23	2.58 ± 0.25
Coastal zone	B	0.40 ± 0.28	0.97 ± 0.75	1.46 ± 0.78
	H	0.62 ± 0.10	0.35 ± 0.03	1.18 ± 0.19

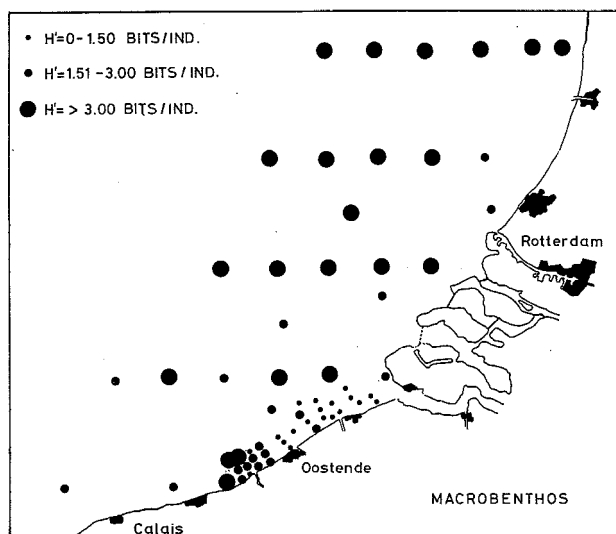


Fig. 2. Species diversity (Shannon-Wiener index) of macrobenthos on 60 stations during the 1971-1972 survey

### Meiobenthos of the Southern Bight

Van Damme & Heip (1977) classified three zones according to their harpacticoid copepod composition. These zones coincide more or less with those based on macrobenthos. Again there are two clearly distinguishable communities with a transition zone in between (Fig. 3).

Close to the coast an assemblage of species designated as the *Microarthridion littorale* - *Halectinosoma herdmani* community is found; this is an iso-community of the very widespread *H. herdmani* - *Harpacticus flexus* community (Soyer, 1970). *M. littorale* is very dominant, followed in descending order by *H. herdmani*, *H. sarsi* and *Canuella perplexa*. All these species are large epibenthic or endobenthic forms. Interstitial species are extremely scarce in this region (only two individuals were found). Only 30 out of 53

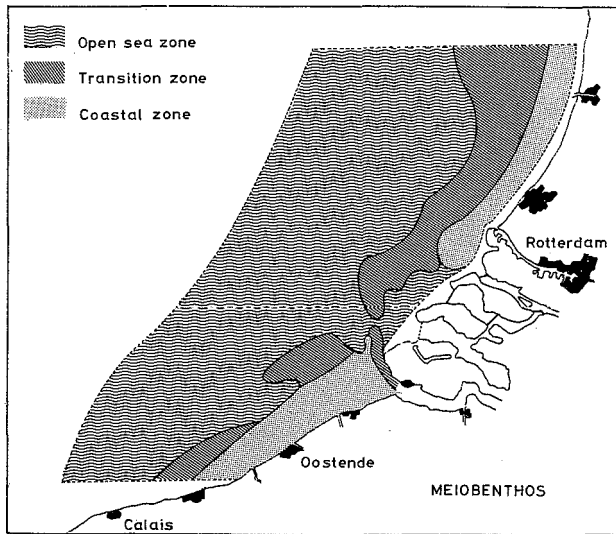


Fig. 3. Map of the Southern Bight with the investigated area, showing the three zones delimited on the base of the associations of harpacticoid copepods

coastal stations yielded harpacticoid copepods. The total number of species was extremely low (ten). The average number of species per station was 0.90, average diversity  $H' = 0.18$  bits/ind. The initial results (June 1979) of an ongoing survey in the same area (18 stations) are strikingly similar: the average number of species per station was 0.89 and the average diversity of  $H' = 0.20$  bits/ind. (Table 2; Fig. 4).

The nematode fauna of the coastal zone is dominated by the genera *Sabatieria* and *Theristus* and other non-selective deposit-feeders such as *Tubolaimoides tenuicaudatus*, *Daptonema normandicum*, *Odontophora armata*, *Daptonema tenuispiculum* and *Viscosia viscosa*.

The transition zone is characterized by a *Leptastacus laticaudatus* – *Halectinosoma herdmani* community, i. e. an association where both epibenthic and interstitial harpacticoids occur. In the 1972 survey 31 species were found at 8 stations; the most common species in descending order of dominance were *Leptastacus laticaudatus*, *Halectinosoma herdmani*, *Paraleptastacus espinulatus*, *Kliopsyllus holsaticus*, *Arenocaris bifida*, *Intermediopsyllus intermedius* and *Halectinosoma sarsi*. The average number of species per station was 8.9 and the average diversity  $H' = 1.98$  bits/ind.

The nematode fauna of stations in the transition zone close to the coastal region bears a close resemblance to the fauna of that region, with *Sabatieria*, *Richtersia inaequalis* and *Theristus* spp. comprising more than half the individuals (Jensen, 1974).

The open sea is characterized by a *Leptastacus laticaudatus* – *Paramesochra helgolandica* community in which the large epibenthic or endobenthic species are nearly absent. In the 14 stations in the 1972 survey 54 species were found; the most common were (in descending order of dominance) *Leptastacus laticaudatus*, *Paramesochra helgolandica*, *Arenosetella germanica*, *Kliopsyllus paraholsaticus*, *Psammotopa phyllose-tosa*, *Intermediopsyllus intermedius* and *Evansula incerta*. All these species are small

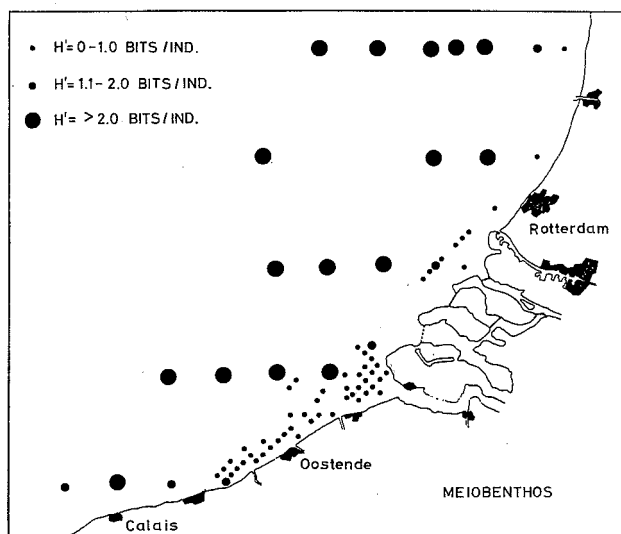


Fig. 4. Species diversity (Shannon-Wiener index) of the harpacticoid copepods (meiobenthos) on 74 stations during the 1971-1972 survey

Table 2. Harpacticoid species in the coastal zone of the Southern Bight. Cumulative number and frequency in n stations

Species	1972 (25 stations)		1977-78 (14 stations)	
	N	f	N	f
<i>Halectinosoma herdmani</i>	39	9	5	4
<i>Halectinosoma sarsi</i>	11	9	9	3
<i>Halectinosoma gothiceps</i>	0	0	6	2
<i>Halectinosoma propinquus</i>	0	0	1	1
<i>Pseudobradya tenella</i>	0	0	2	1
<i>Pseudobradya beduina</i>	1	1	0	0
<i>Pseudobradya spec.</i>	1	1	0	0
<i>Canuella perplexa</i>	6	2	8	1
<i>Thompsonula hyaenae</i>	0	0	3	1
<i>Microarthridion littorale</i>	130	11	76	12
<i>Ameira parvuloides</i>	1	1	1	1
<i>Altheuta interrupta</i>	0	0	1	1
<i>Robertsonia propinqua</i>	1	1	0	0
<i>Kliopsyllus holsaticus</i>	1	1	0	0
<i>Cylindropsyllus laevis</i>	1	1	0	0
Mean number of species per station	1.5		2.0	
Total diversity: (bits/ind)	1.35		1.63	
Total number of species	10		10	



interstitial forms. The average number of species per station was 13.7 and the average diversity 2.73 bits/ind.

Most nematodes from this area are epistratum feeders with dominant genera such as *Chromadorita*, *Neochromadora*, *Hypodontolaimus* and *Dichromadora* (Jensen, 1974). Other meiofauna groups such as Hydrozoa (*Halammohydra*), Gastrotricha, Archiannelida, Echinodermata (*Leptosynapta minuta*), Kinorhyncha, Oligochaeta and Halacarida are all present in this zone but absent from the coastal zone.

Mean density and biomass of meiofauna from all stations in the three different zones are given in Table 3. In terms of both density and biomass there is a slight decrease over the five years. However, it is impossible to evaluate the significance of this decrease as sampling was extremely erratic during this period. We wish to draw attention to the similarity of these data, mainly due to the overwhelming dominance of nematodes, which make up more than 99 % of total meiobenthic biomass in the coastal zone and 74 % in the open sea zone.

The average weight of an individual nematode was  $1.26 \pm 0.11 \mu\text{g}$  dwt (mean of 26 determinations on 100 individuals each), with insignificant differences between the zones:  $1.37 \pm 0.35 \mu\text{g}$  (coastal zone, 4 stations),  $1.24 \pm 0.18 \mu\text{g}$  (transition zone, 13 stations) and  $1.24 \pm 0.18 \mu\text{g}$  (open sea zone, 9 stations). However, later measurements of coastal stations by Bisschop (1977) yielded lower values in most cases and an average of  $0.59 \pm 0.09 \mu\text{g}$  ( $n = 11$ ) was found. Bisschop's data are from very polluted stations close to the Belgian coast, where total nematode biomass goes as low as 40 mg dwt/m<sup>2</sup>. Surkyn (1977) found values closer to ours:  $0.92 \pm 0.24 \mu\text{g}$  in the eastern Scheldt (8 stations) and  $1.19 \pm 0.15 \mu\text{g}$  dwt in Lake Grevelingen (7 stations). Claeys (1979) found an average of 2.60  $\mu\text{g}$  dwt on a sandbar in the transition zone, with a nematode fauna related to what was found in the open sea zone (Vincx, personal communication).

Table 3. Total density and biomass of meiobenthos in three zones of the Southern Bight. N: ind./10 cm<sup>2</sup> · B: g dwt/m<sup>2</sup>

Year	Coastal zone		Transition zone		Open sea zone	
	N	B	N	B	N	B
1971 (summer)	934	1.21	1739	2.44	1640	2.24
1972	1182	1.51	2735	1.81	1340	1.75
1973	1261	1.60	774	1.02	852	1.24
1974	1092	1.39	761	1.04	803	1.02
1975 (winter)	1129	1.43	623	0.84	757	0.97

## DISCUSSION

Comparing the pattern of residual currents (Fig. 5), material in suspension (Fig. 6) and turbidity (Fig. 7) with the distribution of the macro- and meiofauna reveals a striking similarity. There seems to be a very close relation between velocity and direction of tidal and residual currents and the distribution of the macrobenthic communities.

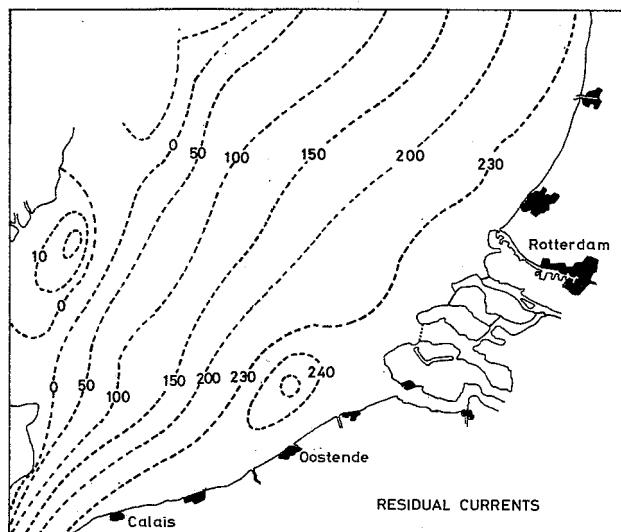


Fig. 5. Residual currents in the Southern Bight, taking into account the tidal stress, but not the wind stress. The friction coefficient on the bottom is considered equal to  $K = 1.25 \cdot 10^{-3} \text{ m/s}$ . The isocurrent lines are expressed in  $10^3 \text{ m}^3/\text{s}$  (modified after Rondan, 1976)

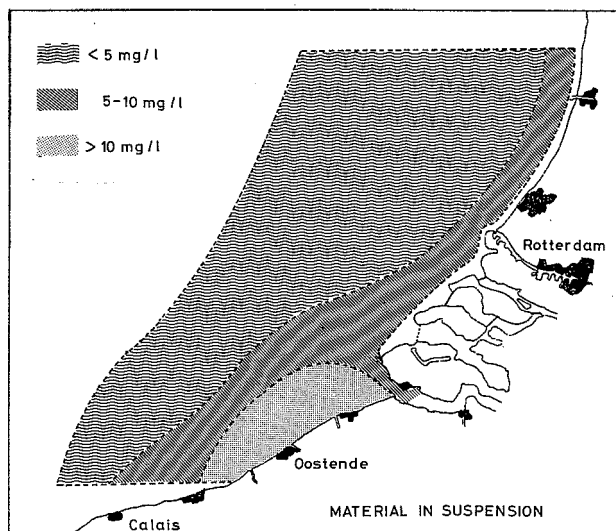


Fig. 6. Distribution of average concentrations of material in suspension (mg/l) along the Belgian and Dutch coast (1970–1979) (modified after Gullentops et al., 1977)

The macrobenthic coastal community coincides with the area covered by the residual gyre (Fig. 5), where highly polluted muds derived from the western Scheldt and from coastal effluents are trapped and deposited in an extensive layer of mud. The smaller southern part of the macrobenthic coastal zone near the IJzer estuary is not

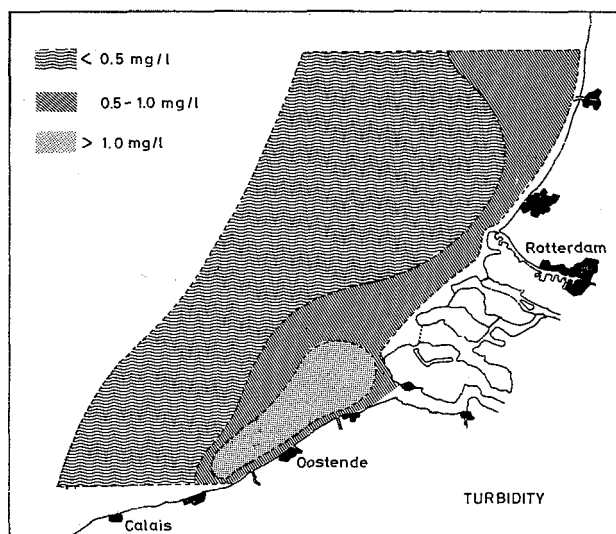


Fig. 7. Distribution of turbidity (mg/l) along the Belgian and Dutch coast in 1971 (modified after Wollast, 1972)

related to residual currents: a small muddy patch persists here because the output of mud from the river exceeds the amount which can be removed by turbulence and currents (Gullentops et al., 1977). In Dutch coastal waters a similar situation is found near the Rhine estuary and the Noordzeekanaal. Impoverished *Abra alba* communities also occur here, but they were not sampled during our survey.

The macrobenthic transitional zone coincides with the region swept by residual currents with an intensity between  $230 \times 10^3 \text{ m}^3/\text{s}$  and  $240 \times 10^3 \text{ m}^3/\text{s}$  (Fig. 5). In this area continental coastal water transports a relatively high load of material in suspension (5 to 10 mg/l). In the south this material is from French coastal effluents and submarine deposits, and in the north from the Rhine and the Noordzeekanaal. However, the suspended material in the transitional zone is not deposited but only temporarily and periodically decanted (Gullentops et al., 1977). It thus appears that this combination of features – i. e. sandy sediments and suspension-loaded waters – allows the existence of a mixed community.

Further west the residual currents carry the English Channel waters, which are practically suspension-free and nutrient-poor (Wolff, 1973). This zone coincides with the macrobenthic "open sea" zone.

In comparison with the macrobenthic zones, the following differences may be noted in the distribution of the meiobenthic zones: (a) The meiobenthic coastal zone extends over a much larger area and continues along the Dutch coast. The northern area coincides with the macrobenthic transitional zone. (b) The meiobenthic transitional zone is discontinuous along the Belgian coast, but broadens significantly towards the north.

Unlike the macrobenthic coastal area, the meiobenthic zone seems to cover the maximal area influenced by the gyre, i. e. the whole of the coastal region. This region is shielded by sandbars stretching out in a southwest-northeast direction, so that the

hydrodynamic conditions are those of an outer lagoon. Pure mud patches cover only a relatively minor part of the bottom but – due to water turbulence – the remaining sandy areas seem to be permanently mixed with mud (2 % to 36 % mud). Although the mud content of the sands is usually relatively low (5 % to 6 %) (Gullentops et al., 1977), the interstitial bacteria-feeders have disappeared and the detritus-feeders are drastically reduced (with the exception of nematodes). This marked impoverishment of the fauna cannot be explained exclusively by hydrodynamic forces, which affect the interstitial fauna; it must also be caused by the severe pollution in this area, which affects the epibenthic detritus-feeders. Along the Dutch coast the polluted runoff from the Rhine and Noordzeekanaal similarly affects the meiobenthos along the narrow stretch where these waters are carried by the tidal and residual currents.

The discontinuity in the meiobenthic transition zone as mapped in the 1972 survey is probably erroneous; it may be due to the small number of sampling stations and the topography of the area. Further study in the region of the Flemish Banks (Claeys, 1979) showed that a transitional type of fauna does indeed occur, probably over the entire area of the banks. The true shape of the meiobenthic transitional zone along the Belgian coast must therefore resemble that of the macrobenthos. At the northeastern edge of the grid the meiobenthic transitional zone broadens distinctly and is similar to the distribution of turbidity. Again hydrodynamics are involved but no single hypothesis has yet been generally accepted to account for the turbidity pattern. The curving of the turbid area to the northwest seems related to the fact that the tidal currents turn northwest during the incoming tide, while when the tide goes out the currents descend from the nutrient-rich Wadden Sea. It appears that the existence of a mixed macrobenthic community is determined on the one hand by the velocity and direction of currents (either tidal or residual) which transport a certain amount of material in suspension but do not allow it to settle, and on the other hand by water turbulence which mixes the suspended materials with the sandy surface. The fact that the meiobenthic transitional zone shifts more to the northwest than the corresponding macrobenthic zone only indicates that a smaller amount of suspended materials must reach the sediment for smaller meiobenthic detritus-feeders to exist.

As with the macrobenthic zone, the meiobenthic "open sea" zone corresponds to the region where waters of the English Channel are transported by the residual currents and the amount of suspended material is minimal; this results in harpacticoid fauna dominated by interstitial bacteria-feeders.

From the foregoing considerations it must be concluded that hydrodynamic and related forces regulate and determine the distribution of finer sediments, suspended materials and nutrients, and hence the benthic communities. Pollution seems to greatly affect the smaller meiobenthic groups. The boundaries of the macrobenthic coastal zone are determined by the extension of the muddy sediments and not by pollution, although this factor influences the quality of macrobenthic life inside the zone.

Since the dynamics of the benthic system are a reflection of the distribution of residual and tidal currents and the load of suspended materials, we may expect that the basic composition and occurrence of the respective communities and their distribution in space will remain stable as long as the currents and the amount of suspended material carried will not drastically change. If changes in the dimensions of the zones do occur, they should be predictable and trend-like. Since mud precipitation in the gyre is

Our North Sea data are too irregularly spaced in time to allow the study of temporal characteristics of the communities. However, diversity seems to be one of the most stable

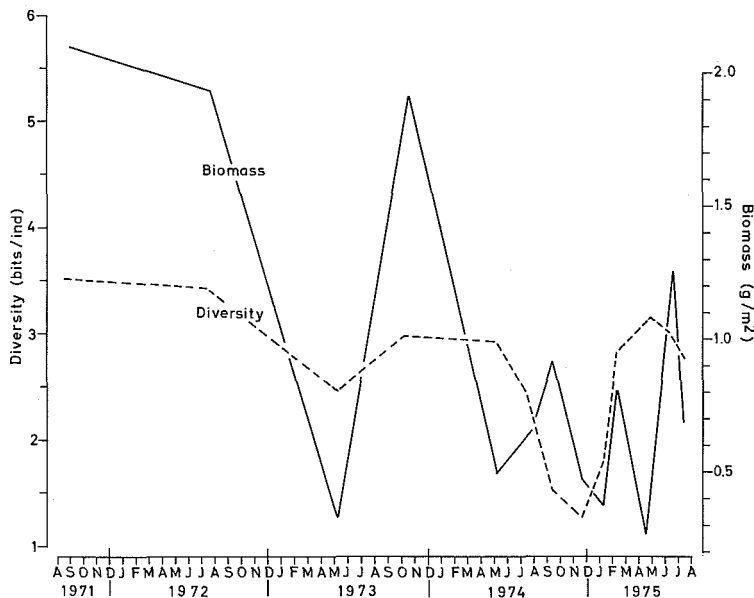


Fig. 8. Fluctuations of macrobenthic biomass (g/m<sup>2</sup> ash-free dry weight) and diversity ( $H'$  in bits/ind.) at a station in the open sea zone. Diversity remaining stable during the period 1971–1973, reestablished in 1975 after a sharp decrease in 1974

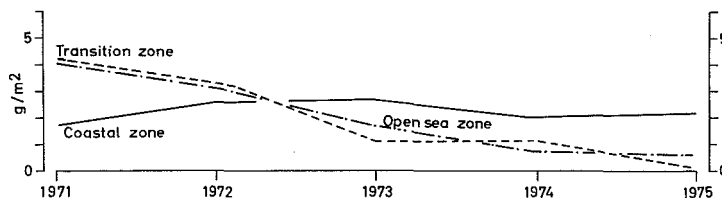


Fig. 9. Fluctuations of total meiobenthic biomass ( $\text{g/m}^2$  dry weight) in the three faunal zones

parameters, both for the macrobenthos (Fig. 8) and the meiobenthos (Table 2). Biomass proved to be very variable for macrobenthos (Fig. 8) but less so for meiobenthos (Fig. 9). The stability of meiobenthic biomass is caused entirely by that of the nematode biomass. Without nematodes, the meiobenthic biomass would be much more variable. Whether these parameters are suitable for describing the temporal behaviour of the system cannot be judged from our data. Heip (unpublished), using spectral analysis on data from a brackish-water meiobenthic community, found both biomass and diversity predominantly low-frequency parameters, thus making them suitable for monitoring even at sea.

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