Rapp. P.-v. Réun. Cons. int. Explor. Mer, 183: 101–110. 1984.

Distribution and density of the benthic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditions

F. Creutzberg, P. Wapenaar, G. Duineveld, and N. Lopez Lopez

Netherlands Institute for Sea Research
P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

The eastern part of the southern North Sea, west and north of the Dutch coast, is characterized from south to north by a gradual increase in depth and a decrease in tidal-current velocity. This may have contributed to the gradual transition from coarse to fine sediment from south to north and to the occurrence of muddy areas in the north.

At a certain latitude (ca. 53°30′N) the tidal-current velocity drops to a critical value at which deposition of silt can take place. North of this boundary there is a very rich mud fauna with a biomass comparable to that of the fauna of the tidal flats of the Wadden Sea. This enrichment may be attributed to the deposition of organic matter from primary production, not only from the overlying water masses, but also from adjacent sandy areas where water turbulence prevents deposition of detritus. Farther north the biomass of the benthic fauna seems to decrease. Alternatively, the enriched zone may be related to the presence of a tidally induced front between a well-mixed area in the south and a seasonally stratified area in the north in which primary production is enhanced.

At the transition from sand to mud a succession of feeding types has been observed in the bottom fauna, the significance of which is discussed.

Introduction

The present paper deals with investigations on the ecology of soft-bottom, macro-infaunal communities, carried out in the southern part of the North Sea west and north of the Dutch coast. To explain the distribution of this fauna much attention has been paid to the sedimentary characteristics of the area. Since 1975, therefore, sediment samples have been collected at all stations for the determination of the "mud" content (particles < 50 μm) and the median grain size.

The Dutch offshore shelf – roughly between 3° and 5·5°E – offers a promising area for investigations of this type. From south to north there is an increasing depth (20–50 m) and a decreasing velocity of tidal streams (1·8–0·7 knots). These factors, which both determine the rate of turbulence, may have contributed to the formation of a remarkable gradual transition from coarse to fine sediment, from south to north (Jarke, 1956; Schüttenhelm, 1980) and to the occurrence of mud in the northern part of the area (Borley, 1923; Creutzberg and Postma, 1979).

For the study of marine ecosystems in terms of energy flow, such transitions from sand to mud may be important. Areas where mud can settle receive potential productivity, not only from primary production in the overlying water masses, but also from adjacent sandy areas where water turbulence prevents deposition of detritus (Rees *et al.*, 1976; Gerlach, 1978).

This type of transition is also important for the question of the availability of food which – depending on hydrographic conditions – may, for the major part, occur in either of three feeding zones: a) suspended in the water column, b) deposited on the surface of the sediment, or c) reworked into the sediment. These three feeding zones are exploited differently by the various species which, accordingly, can be divided into a) suspension feeders, b) surface deposit feeders, and c) subsurface deposit feeders or deposit swallowers (Pearson, 1971).

The present study is an attempt to explain the occurrence of certain macro-faunal communities and their sediment relationships.

Material and methods

Bottom samples were taken with a 0·2 m² van Veen bottom grab. As soon as the grab was on board, the water was poured off carefully and a vertical cylindrical sample (10 cm deep) was taken from the content of the grab. For transport and storage the sample was deepfro-

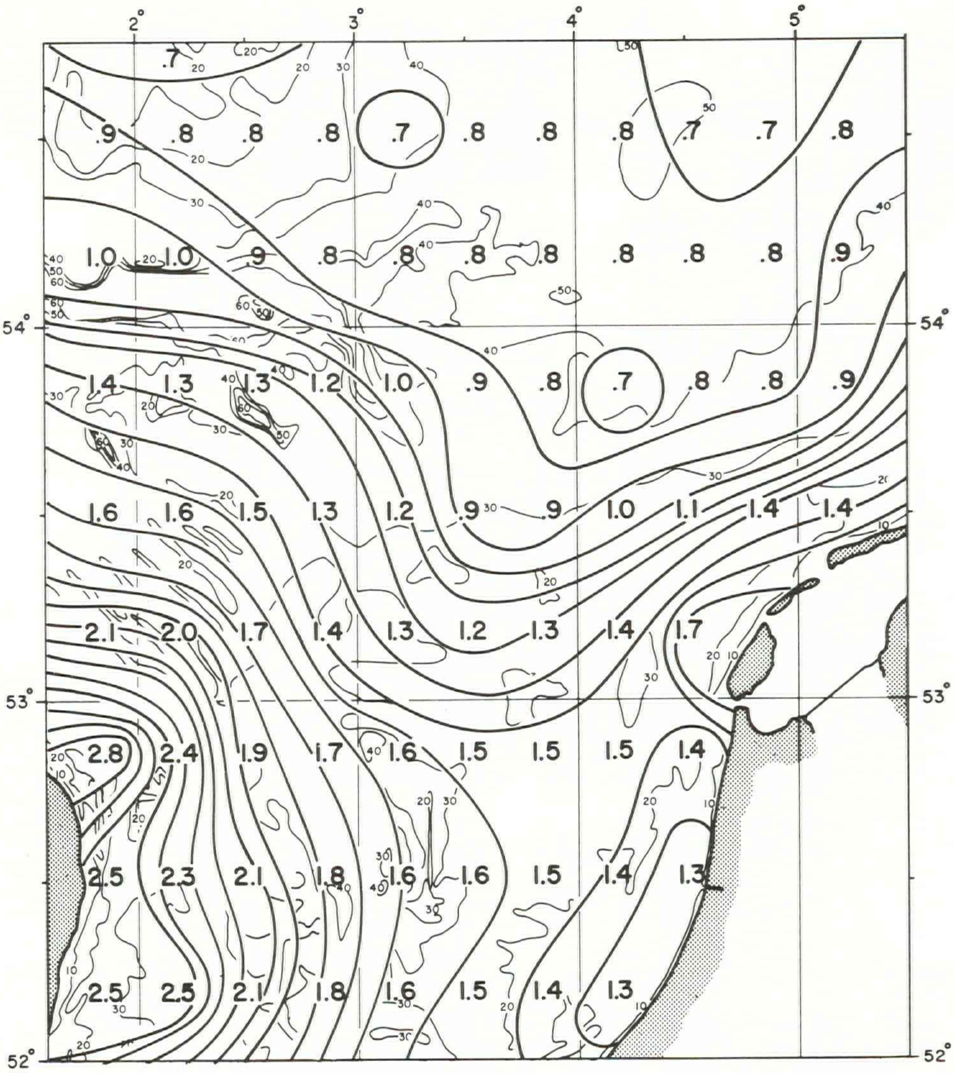

Figure 1. Maximum tidal velocities (mean spring tide) in knots, and lines of equal velocity as deduced from the atlas of tidal streams published by the Deutsches Hydrographisches Institut, Hamburg (1963).

zen (−20°C). In the laboratory the mud content (all material smaller than about 50 μm equivalent grain size) was determined by the decantation method as used by Eisma (1966) and described by Creutzberg and Postma (1979).

Median grain size, derived from the grain-size frequency distribution including the fraction smaller than 50 μm, was determined by dry sieving in an EML sieve analysis shaker.

In a number of samples the content of particulate organic carbon (POC) of the sediment was measured with the wet oxidation method of Menzel and Vaccaro (1964).

For the determination of the faunal composition, the rest of the content of the van Veen grab was washed through a 2 mm sieve. For more specific macrobenthic studies 5 grab samples were taken at each station and washed through a 1 mm sieve. All species were identified and counted. For each sample ash-free dry weight (AFDW) of all species was determined by desiccation during 2 days at 80°C and combustion during 2 hours at 560°C, in order to obtain an estimate of the biomass of the macro-infauna.

Description of the area investigated

Water movements

The character of the bottom, the granular composition of the sediment, and the deposition or resuspension of inorganic and organic particles are mainly controlled by the strength of the water movements.

The most important among the water movements are the tidal currents with a maximum velocity varying by more than a factor of 2 in the area investigated (Fig. 1). The maximum velocities of the tidal currents (mean

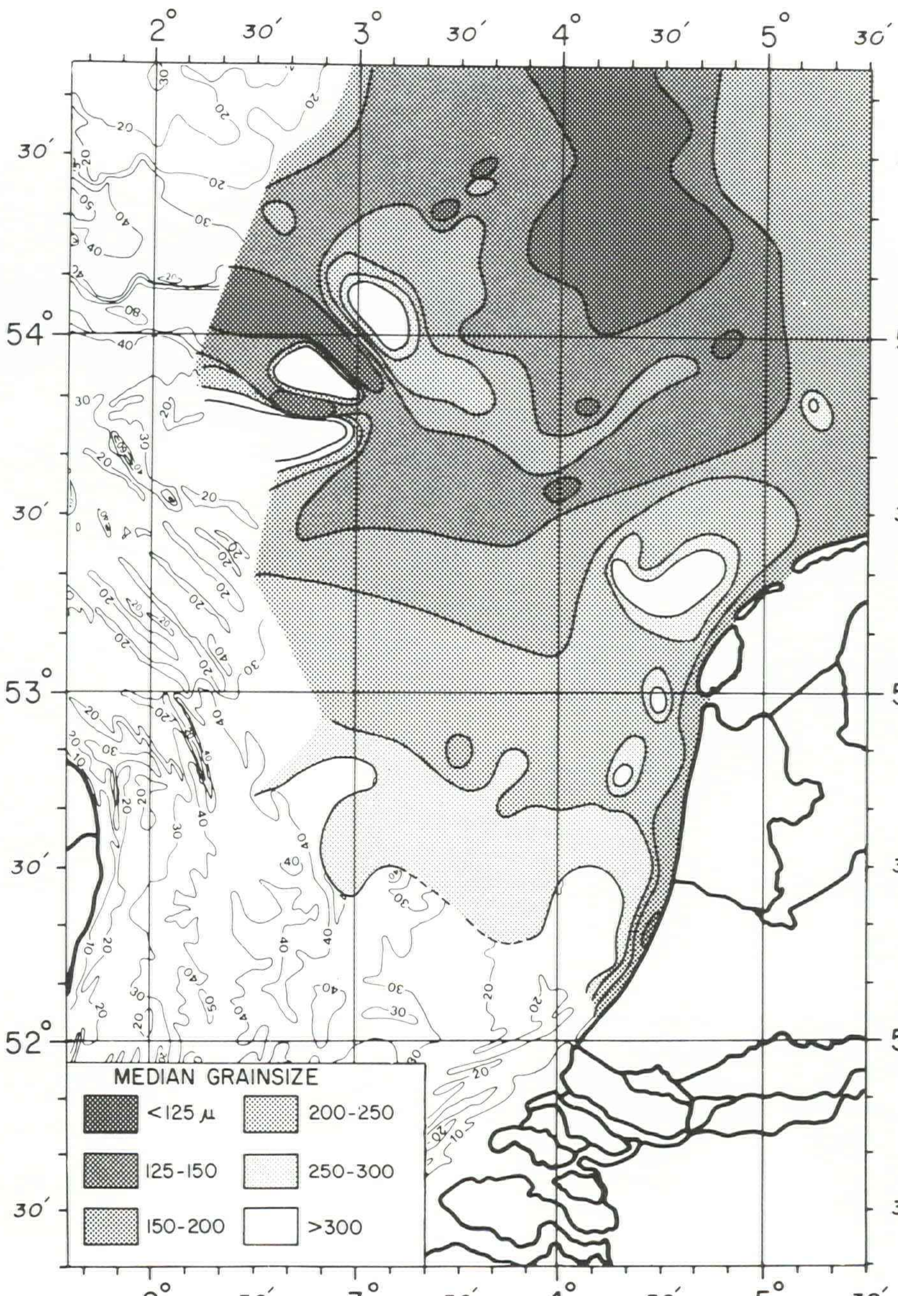

Figure 2. Distribution of sediments according to median grain size.

spring tide), plotted in this chart in knots, are derived from the atlas of tidal streams edited by the Deutsches Hydrographisches Institut, Hamburg (1963).

In addition to tidal currents, waves will promote erosion of fine sediments through the action of near-bottom oscillatory water movements. The effectiveness of waves – even of storm waves – generated in the southern North Sea, is, however, supposed to be small below depths of 30 m (McCave, 1971).

Grain-size distribution

The particle-size distribution, expressed as median grain size, is summarized in Figure 2, in which contours have been drawn tentatively. A comparison with the current chart (Fig. 1) indicates a clear relationship between the particle-size distribution and the distribution of maximum surface current velocities. The grain-size distribution of the southern North Sea bottom sedi-

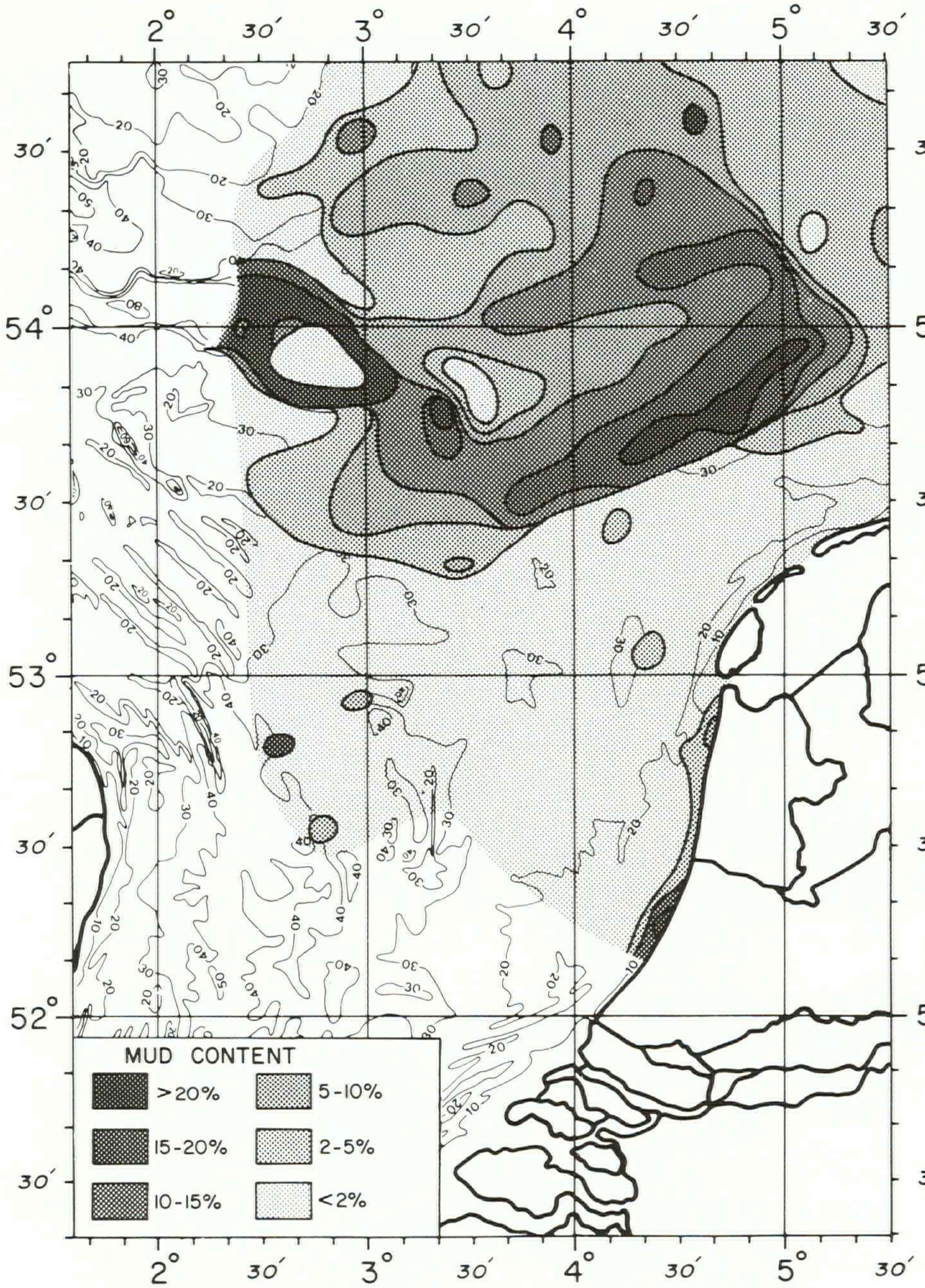

Figure 3. Distribution of sediments according to mud content (particles < 50 μm).

ments will not, however, exclusively be the result of the present environmental, especially hydrolic, regime. There are for instance ancient glacial deposits of sands, gravels, and stones. In the area of the Oyster ground, on the other hand, an earlier "Wadden Sea" existed about 9000 years B.P. and must partly be responsible for the presence of silt and clay in that area. But if the local median grain sizes are plotted against the current velocities, a highly significant linear regression is found (Fig. 4). The maximum surface current velocities shown in Figure 1 are here converted into currents at 15 cm above the bottom in cm per sec, with the formula of van Veen (1936) for tidal velocity profiles (see Creutzberg and Postma, 1979). The positions chosen for this comparison are located in the most intensively studied area between 3°10′ and 5°10′E and between 52°30′ and 54°30′N.

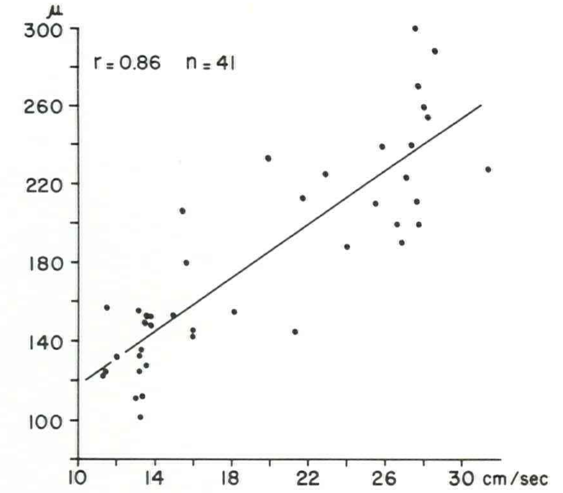

Figure 4. Median grain size as a function of current velocity 15 cm above the sea bed.

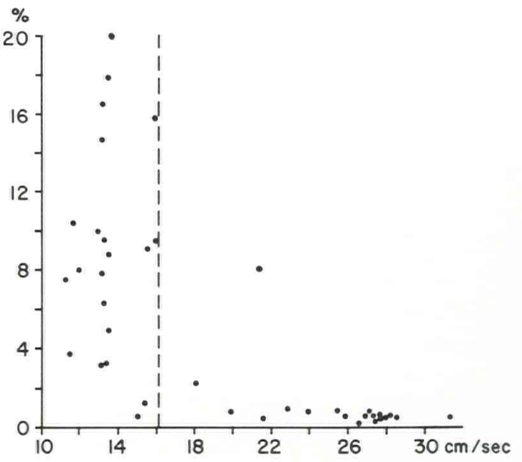

Figure 5. Mud content as a function of current velocity 15 cm above the sea bed.

Distribution of mud

The distribution of mud expressed as dry weight percentage of the sediment is shown in Figure 3 and, similar to Figure 2, tentative contours are drawn. A comparison with the current-velocity chart (Fig. 1) strongly suggests that the occurrence of mud is restricted to areas where maximum surface current velocities do not exceed 0·9 knots, or more accurately, 16 cm per second at 15 cm above the bottom. If mud-content percentages are plotted against current velocities (Fig. 5), the critical velocity of 16 cm per sec at 15 cm above the sea bed is clearly indicated. Below this critical velocity, however, there is, apparently, no clear relation between current velocity and mud content of the sediment. The variability of the mud content below this velocity will undoubtedly be controlled by other factors, such as e.g. the amount of suspended matter present in the overlying water masses. In the northern part of the area investigated (north of 54°10′N) the water is generally very clear, as appears from Secchi-disk readings, ranging from 15 to 20 m.

Distribution of organic matter

Unfortunately there are only few data available on the organic-matter content of the sediment in the area investigated. Only during one cruise in 1981 was particulate organic carbon (POC) content of the sediment (43 samples) measured. If plotted against mud content, a very significant linear regression is obtained (Fig. 6). It is clear that deposition of very fine particles is accompanied by the introduction of organic matter into the sediment.

The macrobenthic fauna

Distribution of biomass

To compare the biomass figures in different localities, the area is provisionally divided into three sectors (Fig. 7):

(a) A homogeneous sandy sector in the south of the area with median grain sizes varying from 150 to 250 µm, mud contents below 2 %, and maximum surface current velocities ranging from 1·0 to 1·6 knots. In this sector the mean biomass of the infauna has been estimated at 3·6 g AFDW m^{-2} (s.d. = 3·9; n = 20).

(b) A zone of muddy sands, sharply delimited from the southerly sandy area. The mud content is high, varying

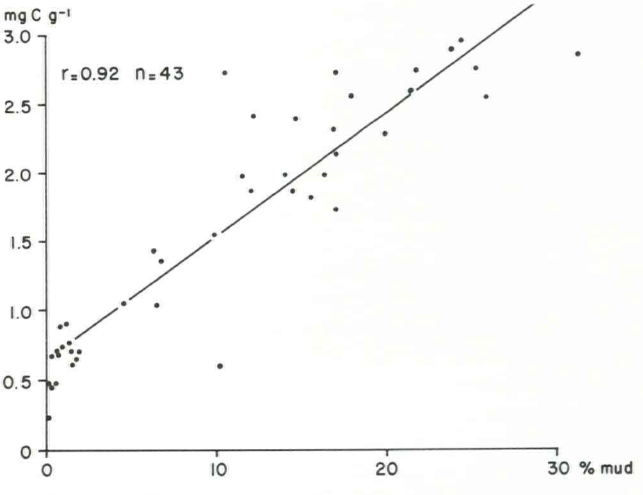

Figure 6. Particulate organic carbon (POC) content of the sediment as a function of the mud content. The samples were collected along the transects of Figure 8.

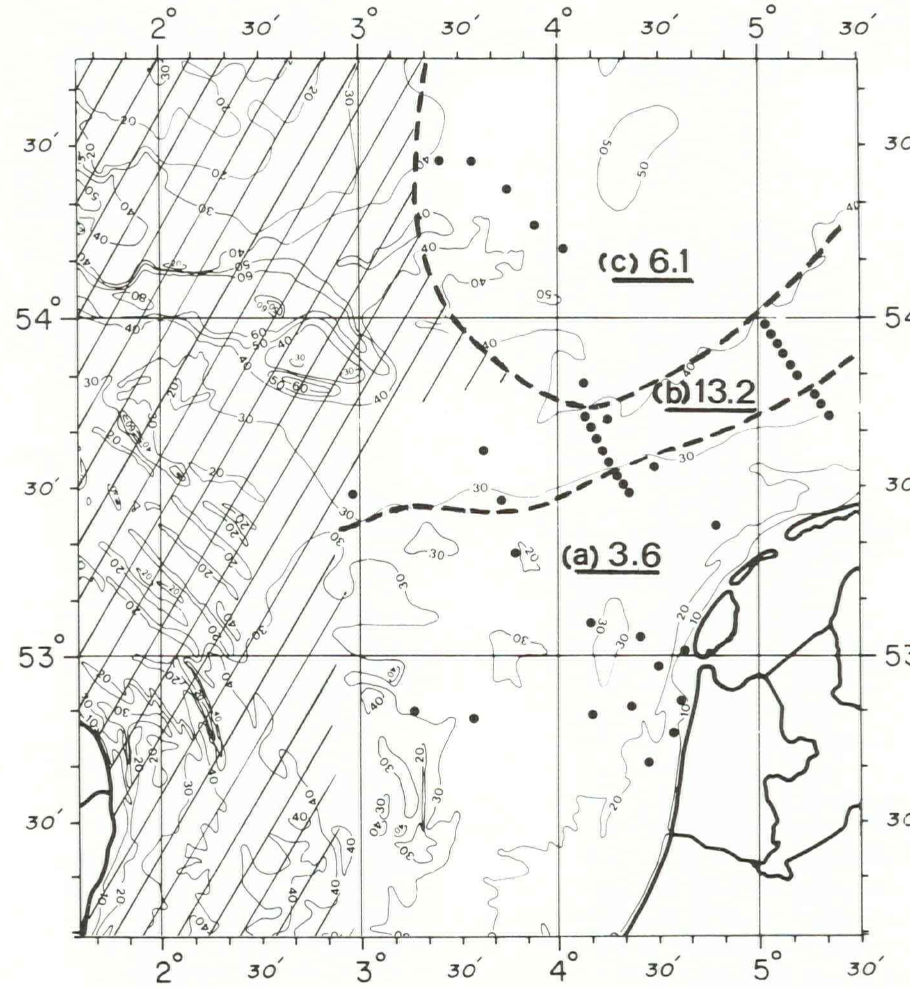

Figure 7. Mean biomass (g AFDW m^{-2}) of the benthic macrofauna in three different sectors (a), (b), and (c). The dots are sample stations.

from 10 to 25 %. The median grain size shows little variation, with values between 125 and 150 μm. Maximum current velocities are in the order of 0·8–0·9 knots. In the classic terms of communities, here an *Echinocardium cordatum – Amphiura filiformis* community (Petersen, 1918) can be recognized. In this sector the biomass is estimated at 13·2 g AFDW m^{-2} (s.d. = 6·8; n = 15).

(c) A sector with fine to very fine sands (100–150 μm) and moderate mud contents (5–15 %). The maximum surface current velocities are relatively low (0·7–0·8 knots). The area is characterized by the occurrence of a thermocline during the summer, and high Secchi-disk readings (15–20 m). A characteristic inhabitant is the suspension-feeding polychaete *Chaetopterus variopedatus*. On the basis of a few data available the mean biomass of the benthic fauna might provisionally be estimated at 6·1 AFDW m^{-2} (s.d. = 3·2; n = 6).

If the non-parametric Mann-Whitney U-test (Elliott, 1973) is applied it appears that the estimated biomass values of the macrobenthos in sectors (a) and (b) are significantly different ($P < 0\cdot001$), whereas the differences between sectors (b) and (c) are also significant ($P = 0\cdot01$). It should be borne in mind, however, that the biomass figures presented here are derived from van Veen bottom-grab samples. The main problem of this traditional type of grab is that the depth of penetration varies greatly with the sediment type. In general the van Veen grab is satisfactorily reliable for estimating the biomass of animals living near the surface of the sediment such as most echinoderms and bivalves, but regarding deep-burrowing animals (*Nephtys, Lanice, Upogebia, Mya truncata*), serious underestimates may occur (Beukema, 1974). There is, therefore, a great need for more accurate observations with a box sampler.

Distribution of various trophic groups

The situation described here, of a declining turbulence in the benthic layer from south to north, and its

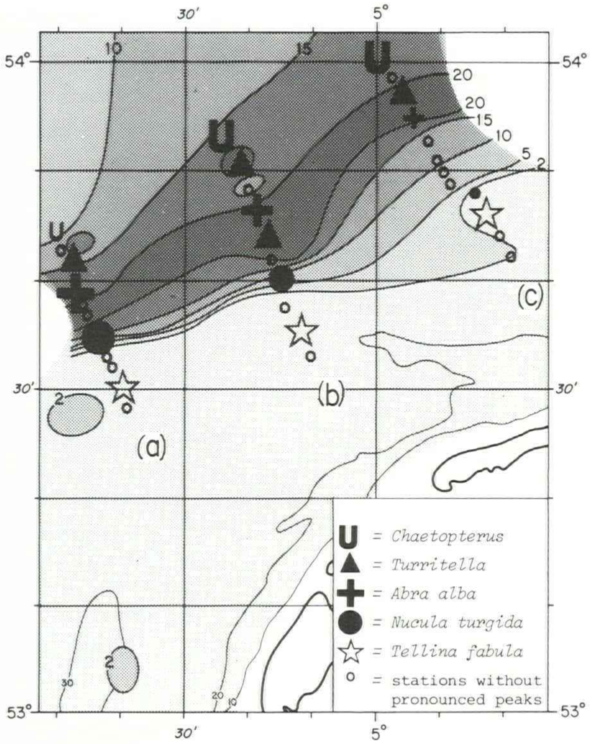

Figure 8. The topographical position of the peaks of some dominant species along three transects in relation to mud content of the sediment (in percentage; see shading). Size of symbols denotes relative abundance.

sedimentary consequences, has given rise to a more detailed examination of the critical boundary between sandy and silty sediments in a specially selected area (Fig. 8). In 1981 three transects, with closely spaced sample stations (2–3 miles apart) positioned across the area of large changes in the sediments, were investigated for faunal changes in relation to the local hydrographic and sedimentary characteristics. In the present context results on the distribution of some dominant species will be given. Following the three transects from southeast to northwest (Fig. 9) a number of species show clear peaks in their abundance. These peaks are topographically shown in Figure 8.

Coming from the southeast the first species showing a peak is *Tellina fabula,* occurring in the sandy area in front of the muddy zone. This species is known as a surface deposit feeder, but also as a suspension feeder of sandy bottoms (Salzwedel, 1979).

Some miles to the north just at the transition from sand to mud, *Nucula turgida* shows peaks on the western and central transect, and a slight peak on the eastern one. *Nucula* is a sub-surface deposit feeder and according to Picard (1965) an indicator of unstable sediments. In the western and central transects *Echinocardium cordatum* also shows very marked peaks, coinciding with the *Nucula* peaks, whereas in the eastern transect *E. cordatum* does not show a clear maximum. According to Buchanan (1966) *E. cordatum* is a facultative sub-surface deposit feeder as well as a surface deposit feeder. *Echinocardium* and *Nucula* (Rachor, 1976) both have the ability to move forward through the sediment.

Still farther north *Abra alba* (a primary surface deposit-feeding bivalve) is dominant on the western and central transect (450 and 100 indiv. m^{-2}), whereas on the eastern transect *A. alba* does not reach high densities and has only a small, insignificant peak. *Pectinaria koreni,* a sub-surface deposit feeder, has a distribution largely corresponding with that of *A. alba.*

North of the *A. alba* zone *Turritella communis* reaches maxima with densities of 25–45 indiv. m^{-2} (an exception is the occurrence of an additional peak between the *Nucula* zone and the *A. alba* zone in the central transect). *Turritella* is a sedentary suspension feeder, living just beneath the surface of muddy sediments. With its mantle cavity open at the surface of the sediment, it generates a separate inhalant and exhalant water current through the mantle cavity and a large

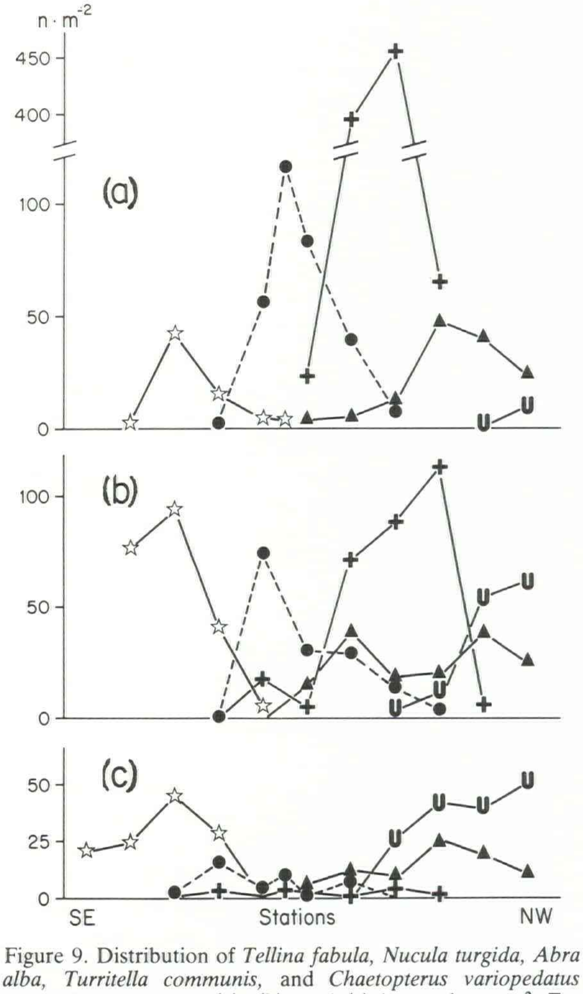

Figure 9. Distribution of *Tellina fabula, Nucula turgida, Abra alba, Turritella communis,* and *Chaetopterus variopedatus* along three transects (a), (b), and (c) in numbers m^{-2}. For symbols, see Figure 8.

ctenidium. This species is reported to be very sensitive to disturbances of the surrounding sediment (Yonge, 1946). It has some adaptations, such as a veil of tentacles around the inhalant opening, preventing the ingress of excessive silt (Fretter and Graham, 1962).

The most northerly stations of all three transects show the highest density of the suspension-feeding polychaete *Chaetopterus variopedatus* (western transect: 10, central transect: 62, and eastern transect: 52 indiv. m^{-2}). This large worm, with its leathery, U-shaped tubes of mucus, is a common inhabitant of sector (c) (Fig. 7).

By far the most abundant species of the transects (except on the southern sandy stations) is *Amphiura filiformis*. At the stations with a mud content below 2 % the species is absent. In the *Nucula* zone moderate numbers (about 20 per m^2) are found. A dramatic increase in numbers is found just north of the *Nucula* zone, with densities ranging from 400 to 2000 indiv. m^{-2} up to the most northerly stations, but there is no specific peak. *A. filiformis* is a suspension feeder as well as a surface deposit feeder (Buchanan, 1964; Ockelmann and Muus, 1978).

According to Ockelmann and Muus (1978) the small bivalve *Mysella bidentata* is associated with *Amphiura filiformis*, living in its burrows. However, in our transects its distribution shows clear maxima, not following the distribution of its host, but more or less coinciding with the maxima of the surface deposit feeding bivalve *Abra alba*. On the northern stations, where the suspension-feeding *Turritella* and *Chaetopterus* show their highest densities, *Mysella* occurs in much lower densities. This holds both for the western and central transects. In the eastern transect *Mysella* shows very low densities, just as *A. alba* does. Ockelmann and Muus (1978) have studied the feeding habits of *M. bidentata* and suggest that this species is dependent for its food on deposited detritus, descending into the burrows, whereas its host, *A. filiformis*, also acts as a suspension feeder with its arms above the sediment.

Discussion

This paper reports on an attempt to explain the distribution of the benthic macrofauna on the basis of sedimentary characteristics and the pattern of water movements in the area north and west of the Dutch coast.

The amount of solar energy introduced through primary production into the ecosystem of the southern North Sea shows a spatial and dynamic distribution that is controlled by the geographic and seasonal distribution of nutrients and the rate of penetration of solar energy into the water column (Gieskes and Kraay, 1975, 1977). The quantitative distribution of pelagic consumers (herbivores as well as carnivores) is not substantially different from this distribution (Fransz, 1976, 1977; Fransz *et al.*, 1978). For the benthic fauna, on the other hand, the supply of food will largely be determined by conditions that allow sinking and deposition of organic particles. It will be clear that for the benthic system (as the result of differential current velocities, diverse effectiveness of wave action, and the direction of residual currents) a redistribution of potential productivity should be taken into account.

As suggested earlier, there is – in terms of water movements – an extensive gradient from a turbulent to a calm area, covering about 120 miles from south to north (Fig. 1). Apart from locally occurring relict sediments, this is clearly reflected in a gradual transition from coarse to fine sediments, from south to north (Fig. 2). The distribution of mud (Fig. 3) strongly suggests that there is a critical current velocity of about 0·9 knots, below which the smallest particles can settle.

Sedimentation of mud will not necessarily always take place at low current velocities at the same rate. There may be, for instance, a shortage of suspended particles in the overlying water masses. This might be the case in the northern part of the silty area (north of 54°N) where the sea water is very clear (Secchi-disk readings of 15–20 m) and mud contents of the sediment show moderate values (5–15 %), despite low current velocities.

On the basis of the distribution of mud, the area is provisionally divided into three sectors (Fig. 7), in which the following processes are supposed to take place.

In the southern sector (a) tidal currents (and wave action) prevent the settlement of the smallest particles. Organic as well as inorganic particles will remain in suspension.

In the second sector (b), where current velocities are below the critical value (0·9 knots), inorganic and organic particles will both settle and cause an accumulation of silt, clay, and organic matter. The supply of organic matter to the benthic system will not only depend on local primary production, but will also originate from adjacent – more turbulent – areas (sector (a), for example).

In the third sector (c), farther north, suspended silt and clay particles will be present in smaller amounts because they were already deposited. Suspended organic particles, on the other hand, are still available through local primary production and will, owing to low tidal current velocities, partly sink to the sediment.

There is no doubt that these processes controlling the distribution of food resources will result in a differentiated productivity of the benthic macrofauna. The distribution of biomass figures of the macrobenthic infauna, collected hitherto and presented as mean values in Figure 7, supports this view.

There is, however, another possible explanation for the presence of the highest faunal abundance in the muddy zone (b) (Fig. 7). This rich zone is located between a well-mixed area in the south, sector (a), and an area in the north where during spring and summer a thermocline is formed, sector (c). In comparable frontal regions in the Celtic Sea and in the western English Channel, Pingree (1978) demonstrated a continued and probably enhanced phytoplankton growth throughout the summer, so that the local primary production might be responsible for the observed high faunal abundance. Whether this is a significant contribution to the food supply of the benthic fauna as compared with the horizontal supply from more turbulent adjacent areas needs further analysis.

Regarding the different patterns of exploitation of primary food resources by the secondary producers, an attempt has been made to understand the succession of various feeding types in a selected area with a pronounced transition from clean sand to muddy sand (Fig. 8).

From south to north, the first habitat of fine sand, close to the mud boundary, is occupied by *Tellina fabula,* a surface deposit feeder as well as a suspension feeder (Salzwedel, 1979). Its occurrence there may be explained by a possible intermittent deposition and re-suspension of detritus with the tidal rhythm, or with the neap and spring tide rhythm.

The boundary between the sandy and the muddy area is occupied by the sub-surface-feeding species *Nucula turgida* (Ansell, 1974 b) and the sub-surface and surface deposit feeder *Echinocardium cordatum* (Buchanan, 1966). Primary surface deposit feeders and suspension feeders are scarce in this zone. The processes taking place at this sand–mud boundary are not known, but the presence of *Nucula* suggests instability of the sediment (Picard, 1965; Rhoads and Young, 1970).

Some miles to the north of the *Nucula* zone, surface deposit feeders such as *Abra alba* (Ansell, 1974 a) show maxima. Here, apparently, conditions for species dependent on the settlement of detritus are most favourable.

Farther north, at the boundary of sectors (b) and (c) (Fig. 7), conditions for suspension feeders, sensitive to disturbances of the sediment, seem to become favourable. There is a *Turritella communis* zone, followed in the north by an increase in numbers of *Chaetopterus variopedatus.* The latter is a common inhabitant of sector (c), where, according to the hypothesis advanced here, there is a rain of fine, mainly organic, particles. Striking are the low densities of surface deposit feeders in this area.

In this context, the differences in distribution between *Mysella bidentata* and its host *Amphiura filiformis* are most remarkable. *A. filiformis,* a surface deposit feeder as well as a suspension feeder, is by far the most abundant species north of the *Nucula* zone (400–2000 indiv. m^{-2}). It occurs in the *Abra alba* zone, as well as in the area of *Turritella* and *Chaetopterus,* without specific peaks along the transects of Figure 8. *Mysella bidentata,* according to Ockelmann and Muus (1978) dependent on deposited detritus, shows, however, a maximum more or less coinciding with that of the surface deposit-feeding *A. alba.*

These speculations, whether justified or not, emphasize the need for a much fuller analysis of the processes taking place in the mini-environment of the benthic animals, a few centimetres above and beneath the surface of the sediment. They further demonstrate the need for very detailed knowledge on the autecology of a large number of species.

Acknowledgements

We are grateful to G. J. van Noort for his wide-ranging assistance, to R. Dapper for the extensive grain-size and mud-content determinations, and to J. Hegeman for the organic carbon measurements. We wish to thank the crew of the research vessel "Aurelia" as well as Mrs L. Everhardus for typing the manuscript, and B. Aggenbach, B. Verschuur, and H. Hobbelink for the drawings. We are also indebted to our colleagues M. Fonds and B. Kuipers for reading and commenting on the manuscript.

References

Ansell, A. D. 1974 a. Seasonal changes in biochemical composition of the bivalve *Abra alba* from the Clyde Sea area. Mar. Biol., 25: 13–20.

Ansell, A. D. 1974 b. Seasonal changes in biochemical composition of the bivalve *Nucula sulcata* from the Clyde Sea area. Mar. Biol., 25: 101–108.

Beukema, J. J. 1974. The efficiency of the Van Veen grab compared with the Reineck box sampler. J. Cons. int. Explor. Mer, 35 (3): 319–327.

Borley, J. O. 1923. The marine deposits of the southern North Sea. Fishery Invest., (2) 4 (6): 1–73.

Buchanan, J. B. 1964. A comparative study of some features of the biology of *Amphiura filiformis* and *Amphiura chiajei* (Ophiuroidea) considered in relation to their distribution. J. mar. biol. Ass. U.K., 44: 565–576.

Buchanan, J. B. 1966. The biology of *Echinocardium cordatum* (Echinodermata:Spatangoidea) from different habitats. J. mar. biol. Ass. U.K., 46: 97–114.

Creutzberg, F., and Postma, H. 1979. An experimental approach to the distribution of mud in the southern North Sea. Neth. J. Sea Res., 13 (1): 99–116.

Eisma, D. 1966. The distribution of benthic marine molluscs off the main Dutch coast. Neth. J. Sea Res., 3 (1): 107–163.

Elliott, J. M. 1973. Some methods for the statistical analysis of samples of benthic invertebrates. Scientific publications, Freshwater Biological Association No. 25, 148 pp.

Fransz, H. G. 1976. The spring development of calanoid copepod populations in the Dutch coastal waters as related to primary production. 10th Eur. Symp. Mar. Biol., Ostend, Belgium, 2: 247–269.

Fransz, H. G. 1977. Produktiviteit van zoöplankton in de zuidelijke bocht van de Noordzee. Vakbl. Biol., 57 (17): 288–291.

Fransz, H. G., Ottema, M., and Seip, P. A. 1978. Abundance and growth of fish larvae during the summer decline of copepod populations in Dutch coastal waters of the North Sea and possible interactions with jellyfish and ctenophores. ICES CM 1978/L:19, 9 pp. (mimeo).

Fretter, V., and Graham, A. 1962. British prosobranch molluscs, their functional anatomy and ecology. Ray Society, London, No. 144, 755 pp.

Gerlach, S. A. 1978. Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. Oecologia, Berlin, 33: 55–69.

Gieskes, W. W. C., and Kraay, G. W. 1975. The phytoplankton spring bloom in Dutch coastal waters of the North Sea. Neth. J. Sea Res., 9 (2): 166–196.

Gieskes, W. W. C., and Kraay, G. W. 1977. Primary production and consumption of organic matter in the southern North Sea during the spring bloom of 1975. Neth. J. Sea Res., 11 (2): 146–167.

Jarke, J. 1956. Eine neue Bodenkarte der südlichen Nordsee. Dt. hydrogr. Z., 9: 1–9.

McCave, I. N. 1971. Wave effectiveness at the sea bed and its relationship to bedforms and deposition of mud. J. sedim. Petrol., 41: 89–96.

Menzel, D. W., and Vaccaro, R. F. 1964. The measurement of dissolved and particulate carbon in sea water. Limnol. Oceanogr., 9: 138–142.

Ockelmann, K. W., and Muus, K. 1978. The biology, ecology and behaviour of the bivalve *Mysella bidentata* (Montagu). Ophelia, 17: 1–93.

Pearson, T. H. 1971. Studies on the ecology of the macrobenthic fauna of Lochs Linnhe and Eil, west coast of Scotland. II. Analysis of the macrobenthic fauna by comparison of feeding groups. Vie Milieu, Suppl. No. 22: 53–91.

Petersen, C. G. J. 1918. The sea-bottom and its production of fish-food. A survey of the work done in connection with the valuation of the Danish waters from 1883–1917. Rep. Dan. biol. Stn, 25: 1–62.

Picard, J. 1965. Recherches qualitatives sur les biocoenoses marines des substrates meubles dragables de la région Marseillaise. Rec. Trav. Station Marine d'Endoume, Fasc. 52, Bull. 36: 1–160.

Pingree, R. D. 1978. Mixing and stabilization of phytoplankton distribution on the northwest European continental shelf. *In* Spatial patterns in plankton communities, pp. 181–220. Ed. by J. H. Steele. Plenum Press, London.

Rachor, E. 1976. Structure, dynamics and productivity of a population of *Nucula nitidosa* (Bivalvia, Protobranchiata) in the German Bight. Ber. dt. wiss. Kommn Meeresforsch., 24: 296–331.

Rees, E. I., Eagle, R. A., and Walker, A. J. M. 1976. Trophic and other influences on macrobenthos population fluctuations in Liverpool Bay. Proceedings 10th Eur. Symp. Mar. Biol., Vol. 2, pp. 589–599. Ed. by G. Persoone and E. Jaspers. Universa Press, Wetteren, Belgium.

Rhoads, D. C., and Young, D. K. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. mar. Res., 28: 150–178.

Salzwedel, H. 1979. Reproduction, growth, mortality, and variations in abundance and biomass of *Tellina fabula* (Bivalvia) in the German Bight in 1975/76. Veröff. Inst. Meeresforsch. Bremerh., 18: 111–202.

Schüttenhelm, R. T. E. 1980. The superficial geology of the Dutch sector of the North Sea. Marine Geology, 34 (1/2): M27–M37.

Veen, J. van 1936. Onderzoekingen in de Hoofden in verband met de gesteldheid der Nederlandsche kust. Thesis, University of Leiden, 1–252.

Yonge, C. M. 1946. On the habits of *Turitella communis* Risso. J. mar. biol. Ass. U.K., 26: 377–380.