Ministry of Transport, Public Works and Water Management

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Physical Processes and Dynamics of Microphytobenthos in the Ems Estuary
(The Netherlands)

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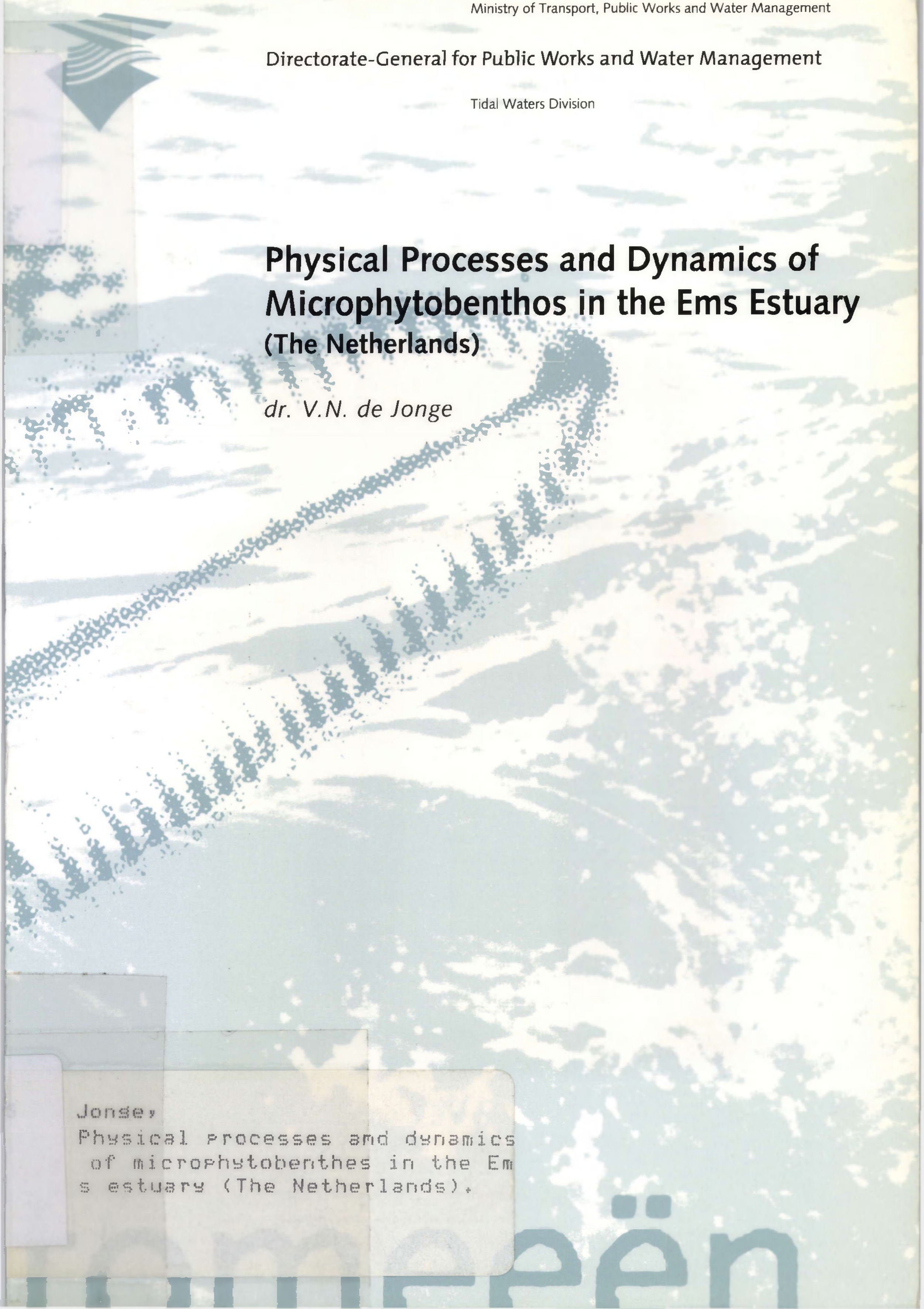

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PHYSICAL PROCESSES AND DYNAMICS OF MICROPHYTOBENTHOS IN THE EMS ESTUARY (THE NETHERLANDS)

1. INTRODUCTION AND SUMMARY

2. PHYSICS

3. BIOLOGY

4. PHYSICS AND BIOLOGY

5. APPLICATION OF KNOWLEDGE AND DISCUSSION

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1. INTRODUCTION AND SUMMARY

INTRODUCTION

Justification of the research

Sediment-dwelling microalgae varying in size between several µm to over 100 µm are found on the intertidal flats of estuaries. Benthic diatoms are the most important representatives of this microphytobenthos. In the early seventies some ecological research was done on these benthic diatoms, largely by German and British scientists. They studied the distribution of these diatoms within estuaries, their movement under experimental conditions, their adhesive ability and their migratory behaviour.

In 1973 an multidisciplinary study began on the influence of discharges of waste water into the Ems estuary from factories making cardboard from straw and starch from potatoes. The aims of the research included quantifying various aspects of the many species that comprise the microphytobenthos: their properties, their activities and their importance as food for herbivores.

Various studies were done to estimate the role of microphytobenthos as a link in the food chain under various circumstances. The primary production of the microphytobenthos was studied (Colijn, 1983), as were the physiological characteristics and behaviour of representative benthic diatoms (Admiraal, 1980). In addition, extensive attention was paid to sediment nematodes, a group of organisms which together with copepods, were generally assumed to be the most important grazers of microphytobenthos (Bouwman, 1983). My task was to quantify the biomass of the microphytobenthos in space and time. These data were needed to arrive at reliable figures on the grazing of microphytobenthos.

To enable these figures to be calculated I first had to solve some methodological problems. Furthermore, it soon became clear that in a system dominated by tides and wind the variation in the biomass of the microphytobenthos is not determined solely by the primary production and the grazers. Therefore, as well as quantifying the biomass, I also devoted much time to studying the effects of currents and wind-induced waves on the suspension of silt and microphytobenthos, in an attempt to find a satisfactory explanation for the enormous variations I had found in the biomass of the microphytobenthos. And it was in this context that the chemical, physical and sedimentological parameters, the tide-driven water transports and the variations in mud regimes under the influence of dredging and wind were studied.

Establishing the biomasses of the microphytobenthos in space and in time, unravelling the importance of various physical processes in the distribution of the biomasses and their transport, and the repercussions of this on our understanding of the functioning of the ecosystem in the Ems estuary are among the important issues dealt with in this thesis.

Overview

Estuaries are extraordinary areas. Geographically, they form the transition between river and sea, where the often funnel-shaped river mouth widens seaward. This funnel shape is produced by the discharge of the fresh river water and the powerful flow of salt water twice daily under the influence of the tide. Together with wind-induced waves this flowing water produces fanciful geomorphological structures via erosion and sedimentation. Within these morphological structures there are areas floored with coarse sand and others floored with very fine mud.

The discharging river water and the invading sea water intermix. This mixing is intense, partly because of the tides and partly because of the area's complex morphology. It results in longitudinal gradients of dissolved substances (such as nutrients and salt) and of fine particulate matter (e.g. mud). Examples are given in the first part of chapter 2. Aspects of abiotic processes are also dealt with in that chapter.

The organisms that live in estuarine areas are often adapted to the extraordinary environmental conditions: the latter are particularly apparent in the rapid displacements of gradients of dissolved and particulate matter. As a result, the organisms living in and on the sediment are continuously exposed to rapidly changing environmental conditions. Some aspects that are associated with these rapid changes are discussed in chapter 3, in relation to the microphytobenthos. The latter mainly comprises the sediment-dwelling diatoms or siliceous algae.

If the organisms are small (like the sediment-dwelling diatoms), sooner or later they risk being swept along or churned up by the flowing water. Chapter 4 describes the interactions between tidal currents and waves on the one hand and the transport of sediment-dwelling diatoms - and of the substrate (mainly mud aggregates) on and in which they live - from flats to channels.

The significance and possible applications of the results of these studies are discussed in chapter 5.

SUMMARY

General

Geographically, the Ems estuary (situated on the border between the Netherlands and the Federal Republic of Germany) forms the transition between the river Ems and the North Sea. In this area fresh water and sea water meet. Apart from the river Ems also other relatively small freshwater discharge points are present. The most important one being the river Westerwoldsche Aa.

The moderate tides in the estuary are responsible for a gradual transition between fresh water and sea water. However, the tides also play a role in processes as resuspension and sedimentation. In this shallow area wind-induced waves cause sediments to be resuspended while absence of waves result in sedimentation. This process occurs on the tidal flats during high tide.

In this very dynamic area abundant populations of organisms are available. In their life-style these are adapted to the rapidly changing life conditions. A very special group of organisms is formed by the sediment-dwelling micro algae or microphytobenthos. This group mainly consists of siliceous algae called benthic diatoms. These organisms mainly live on and in the sediments of the intertidal flats. However, they also occur in the water of the main channels apparently be suspended from the tidal flats. As all algae they need light energy, carbon dioxide, oxygen and nutrients to grow.

Physics

Various general estuarine processes that are responsible for the estuarine distribution of nutrients, salt and mud are discussed in the first part of chapter 2, using data obtained by sampling water for several years (de Jonge, 1988). The resulting data series were later used as input for the BOEDE ecosystem model (Baretta & Ruardij, 1988). The second part of the chapter (de Jonge, 1991) deals with some characteristics of the mass of water moving backwards and forwards in the Ems estuary. Given is a more detailed description of the water movement, in which Euler measurements show that residual currents form throughout the estuary, at very different scales, between and within channels. This residual water transport varies between 1% and 43% of the total local transport and has an overall mean value of ca. 11%. The residual currents range from 0.01 to 0.33 m s^{-1} with an overall mean value of 0.06 m s^{-1}. It is hypothesized that residual flood currents and ebb currents whose distribution over a cross section corresponds very well with the local bathymetry indicate stable hydraulic conditions. Consequently, distributions of residuals that show poor correpondence with the local bathymetry indicate unstable hydraulic conditions, i.e. a changing local morphology.

The influence of dredging in the Ems estuary on the concentrations of suspended matter in that estuary is also highlighted (de Jonge, 1983). In the Ems estuary the mean annual concentrations of suspended matter correlate very well with the distance dredged and not with the volume dredged. It is demonstrated that during the same period the tidal amplitudes increased with distance dredged. From this it is concluded that the increase in concentrations of suspended matter with increased distance dredged could be the result of a temporary intensification of the cycle of erosion and sedimentation that is initiated after the local equilibrium between channel morphology and current pattern has been disturbed.

Biology

Sediment-dwelling diatoms have some properties that make them ideally suited to survive in dynamic environments (see above and chapter 2). The first property is that they are small (micro-organisms) and that they generally reproduce directly, by cell division. This means that these organisms may grow, even at very low densities. The second is their mobility; this enables them to move in the sediment, away from and towards the light. Their third property is that most species can adhere to the substrate and hence are not swept away by the slightest of currents. The fourth is that they can survive for long periods in hostile (anoxic, dark) conditions. Most of these properties determine not only their chances of survival under natural conditions, but also the problems that arise when studying these sorts of organisms. The handicaps include the minuteness of the individuals, the large differences in their dimensions (3 to 150 μm) and the varying ability of the different species to adhere to diverse substrates (plants, rocks, grains of sand and aggregates of mud). This means that it is difficult to collect individuals free from sediment and in a quantitatively reliable way. This is discussed in chapter 3. A method was available to isolate sediment-dwelling diatoms from the sediment (Eaton & Moss, 1966), but it proved to be quantitatively unreliable. Therefore the first step was to develop a method to separate sediment diatoms quantitatively from the inorganic fractions of sediment. The successful formula was found to be density centrifugation, using step-gradients of the silica-sol Ludox-TM as a medium (de Jonge, 1979). Sand, clay and other minerals were quantitatively separated from detritus, meiofauna and sediment diatoms. Unlike the other methods, the recovery of the method was large - around 80%, measured on the basis of chlorophyll-*a*.

To quantify the organisms and their activity organic carbon has been chosen as the measure of biomass. Therefore the second method developed was to determine the ratio of carbon to chlorophyll-*a* for sediment diatoms, so that the corresponding amount of organic carbon could be calculated from the chlorophyll-*a* concentrations. This method was based on a modification of the lens-tissue technique developed by Eaton & Moss (see above). This relation has to be determined because it is impossible to directly determine how much diatom carbon is present in field material, because of the presence of large amounts of carbon from dead organisms (detritus). The procedure followed is to determine the amount of chlorophyll-*a* from field samples and also to determine the ratio of carbon to chlorophyll-*a* (C/Chl-*a*) in a pure field population of diatoms. These two values are multiplied together to give an estimate of the amount of carbon in the sediment diatoms. The analyses indicated that the C/Chl-*a* ratio varies seasonally, with minima below 10 and maxima above 100. The annual mean values varied between 42 and 70. The neglect of this variation may result in errors of 34 - 50% whereas the use of C/Chl-*a* ratios from a previous year may increase the error by another 50%.

Both the techniques described above were used to determine the fluctuations of the biomass expressed as organic carbon of sediment diatoms and other algae, such as the Cyanobacteria *Merismopedia glauca*. There appeared to be clear differences in the seasonal variation of the diatom biomass expressed in chlorophyll-*a* and in organic carbon. The total biomass (expressed in Chl-*a* or organic carbon) in the uppermost 2 cm of sediment largely agreed with the amount estimated by the BOEDE ecosystem model (Admiraal *et al.*, 1988). The distribution in the model appeared not to deviate strongly from the vertical distribution under field conditions, even though those field data were not available to calculate this vertical distribution at that time. The biomass of these sediment algae appeared to be relatively large, partly because other researchers have generally not measured chlorophyll-*a* below a depth of 1 cm in the sediment to determine the biomass. The mean annual biomass of the total microphytobenthos varied between about 3 and 16.5 g C m^{-2}, or from 0.06 to 0.4 g chlorophyll-*a* m^{-2} (de Jonge & Colijn, this thesis). It is also striking that, on average, the percentage of biomass in the uppermost 0.5 cm *vis-à-vis* the uppermost 2 cm increased gradually from 40% in the most seaward part of the estuary to 60% in the south-eastern part of the Dollard.

The primary production (i.e. the growth) of these benthic algae as measured on intertidal flats is also described in chapter 3. This growth varied from ca. 60 to 250 g C m^{-2} a^{-1} (Colijn & de Jonge, 1984) and is closely related to the elevation of the tidal flat station. The primary production values in this estuary very well correspond with those for other estuaries.

At world scale estuaries are productive areas. This is related to the fact that rivers supply estuaries with a varying amount of nutrients. Finally, it is interesting that this fluctuating supply of nutrients also leads to a fluctuating growth in such areas (de Jonge, 1990; de Jonge & Essink, 1991; Schaub & Gieskes, 1991).

Relation between physics and biology

It has already been mentioned that estuaries are very dynamic environments where important displacements of sediment occur. These displacements are accompanied by resuspension of sediment and suspension of microphytobenthos. Material is displaced across the estuary floor and also higher in the water column. One of the results of these transports is a variation in the biomass of the microphytobenthos (see chapter 3). Chapter 4 examines the role of tidal currents and wind-induced waves on the suspension and transport of microphytobenthos and mud.

A study of the occurrence of benthic diatoms in or on various types of particles in the water (de Jonge, 1985) indicated that 80% of the sediment diatoms occurring in water are found on or in aggregates of mud which may be adhering to sand grains. Furthermore, 7% of all the sand grains suspended in the water appeared to be occupied by one or more sediment diatoms: the percentage was 13% for the flats, indicating that there must be an intensive sediment exchange between the flats and the channels. This hypothesis was supported by the great similarity between the species composition of the sediment diatoms found in the water and that on the flats in the various parts of the estuary. However, per species there were differences in relative numbers between water and flats. *Navicula aequora*, *Navicula salinicola*, *Catenula adhaerens* and *Achnanthes hauckiana* were very rarely found in the water. This led to the hypothesis that in relation to tidal currents and wind-induced waves the diatoms have two properties that determine the dynamics of the species composition: in the first place, the capacity of the various species to adhere to a substrate, and in the second place the potential of water to sort sediment as this water flows over the flats at high tide.

The hypotheses were further corroborated by performing an experimental study (de Jonge & van den Bergs, 1987) and a field study (de Jonge & van Beusekom, this thesis.) on how flowing water affects the suspension of bottom sediment and of sediment diatoms. The experiments indicated that the suspension of sediment and sediment diatoms becomes quantitatively important especially when the thickness of the current velocity boundary layer approaches zero (the water in the upper layer of the sediment then begins to flow too). This is an indication of the moment at which the water becomes very turbulent. Furthermore, it was established that the sediment diatoms largely go into suspension together with the sediment, and that, at the species level, there were further indications that there is a differential suspension of diatoms - i.e., not all diatom species go into suspension simultaneously.

When these hypotheses were tested under field conditions (de Jonge & van Beusekom, this thesis), it appeared that the tide-induced current velocity had less impact than the wind-induced waves on the suspension of mud and diatoms on intertidal flats. The effect of the wind-induced waves can be attributed to the shallowness of the water (only a few metres deep) above these flats at high tide. The tidal currents are largely responsible for transporting these materials from the flats to the channels and, depending on the weather, back again. Unexpectedly, the concentrations of mud (fraction < 55 μm) in the middle of the channels could be described as a linear function of the 'effective wind speed', that is the mean wind speed during the three periods of high water preceding sampling. This relation held for the area between Eemshaven and the islands of Rottumeroog and Borkum, and for the Dollard - though with a different regression coefficient. The fraction of the total mass of microphytobenthos-derived chlorophyll-*a* present in the water of a given part of the estuary and in the uppermost 0.5 cm of sediment in that part of the estuary also seemed to be linearly correlated with this 'effective wind speed'. The finding that the suspension of benthic diatoms can be calculated without taking into account the behaviour of mud was most unexpected. It enables fluxes in diatom carbon between flats and channels to be calculated much more easily than previously imagined.

The results of this thesis indicate the resuspension and redistribution of mud to be regulated by at least three processes. These are:

a. A wind-induced process in which wave-induced oscillating currents cause sediment resuspension. Increase of wave energy than results in resuspension while decrease in it results in sedimentation.

b. A tide-induced process mainly causing the (re)distribution of suspended mud. The time scale of this process is estimated to be ca. 3 tidal cycles. Moreover, also the tidal currents above the tidal flats cause sediment resuspension the effect of it being much smaller than the effect of the waves.

c. An anthropogenically induced process in which changes in estuarine bathymetry and thus hydraulics, e.g. resulting from dredging, lead to changes in background concentrations of suspended matter in the main channels.

Only the first two processes are relevant for the suspension of microphytobenthos because it is assumed the effects of dredging to be mainly restricted to the sublittoral area.
Apart from the three above mentioned processes also the tidal cycle itself and the lunar cycle affect the concentrations of mud in the channels. Also the effect of these cycles is thought to be restricted to the sublittoral, thus not significantly affecting the microphytobenthos directly.
These last two aspects (tidal cycle and lunar cycle) were not studied for this thesis.

The knowledge accumulated in the studies described above can be applied to do calculations on the transport of microphytobenthos and mud. They have been done for the Dollard and the area between Eemshaven and the islands of Borkum (in Germany) and Rottumeroog (the outer reaches); a few estimates were made for the middle reaches. In chapter 5 results are presented on the amounts of algae and mud that were transported between flats and channels in 1977 under the influence of wind and tides.

Some of the calculations needed to quantify the fluxes can also be used to estimate the variation in the mud concentrations in the water for the same year (1977). These values are important because they determine the light extinction and hence the primary production of the algae in the water column. A second aspect is that the presence of much mud in the water may lead to more dredging in the harbours.

The calculation method is also used to estimate the amount of microphytobenthos that shifts with the tide from the uppermost 0.5 cm of sediment to the underlying 1.5 cm layer. For that purpose also the data on the changes in the vertical distribution of the microphytobenthos chlorophyll-*a* on the tidal flats were needed.

Finally, it is now possible to estimate the contribution of suspended microphytobenthos to the chlorophyll-*a* concentrations in the water in the channels too. This figure is very important because it enables the contribution of suspended microphytobenthos to total primary production in the water column to be quantified. Laboratory experiments have shown that microphytobenthos grows just as efficiently in suspension as in a batch culture (H. Peletier, personal communication).

Gross fluxes

The calculations, done for the year 1977, show that in the area between Eemshaven and the islands of Rottumeroog and Borkum (lower reaches) the gross lateral fluxes of mud under the influence of wind alone are about 12 x 10^6 tonnes a^{-1}; in the Dollard they are about 7.5 x 10^6 tonnes a^{-1}. In terms of microphytobenthos biomass, the annual fluxes between the intertidal flats and the water in the lower reaches contribute about 20 x 10^3 tonnes organic carbon; the corresponding figure for the Dollard is 10 x 10^3 tonnes organic carbon. The annual fluxes of microphytobenthos biomass between the uppermost 0.5 cm sediment of the intertidal flats and the underlying 1.5 cm of sediment contribute about 12.5 x 10^3 tonnes organic carbon in the lower reaches; the figure for the Dollard is about 5 x 10^3 tonnes organic carbon.

The average mud concentration in 1977 (calculated from the earlier mentioned relation between the 'effective wind speed' and the concentration of suspended matter) is 46.9 g m^{-3} for the lower reaches and 178.2 g m.$^{-3}$ for the Dollard. Both values are close to the concentrations actually measured.

Suspended microphytobenthos accounts for 2.3 mg Chl-*a* m^{-3} of the mean annual chlorophyll-*a* concentration in the water of the lower reaches. When these two values are compared with the mean annual concentrations actually measured over the period 1975 - 1980 (de Jonge, this thesis), the figures for chlorophyll-*a* in the outer reaches indicate that almost 30% of the phytoplankton consists of microphytobenthos. Interestingly, this means that 30% of the annual production of the phytoplankton (i.e. 76 gC m^{-2}) can also be attributed to suspended microphytobenthos. The picture is even clearer for the Dollard: here, almost all the chlorophyll-*a* (6.1 mg m^{-3} or 92% of the total) originates from the microphytobenthos. Accordingly, 92% of the primary production (i.e. 24 gC m^{-2}) can also be attributed to microphytobenthos.

Net fluxes

Mud. Van Heuvel's recent (1991) large inventory of the sediment composition of flats and channels in the Ems estuary enabled the total sediment input to this estuary to be calculated. This was done using the accretion rate of 0.008 m a^{-1} that Reenders & van der Meulen (1972) established for the Dollard, and assuming that this figure is valid for the rest of the estuary. The resulting figure for total annual sediment input to the Ems estuary is 5.6 million tonnes. The total annual input of mud (fraction < 55 µm) to the various reaches of the estuary is estimated at 1.5 x 10^6 tonnes on the basis of the average sediment composition (van Heuvel, 1991); this is one and a half times the estimate given in Baretta & Ruardij (1988). Only a very small part (about 0.1 x 10^6 tonnes) of this 1.5 x 10^6 tonnes is supplied by the river Ems (Hinrich, 1974) and of this, less than half is supplied by the Westerwoldsche Aa.

Organic carbon. The allochthonous particulate organic carbon largely comes from the coastal zone (69 x 10^3 tonnes *versus* 13 x 10^3 tonnes from the Ems and Westerwoldsche Aa combined). The total annual production of organic matter by algae within the area itself is almost double the input from elsewhere and comprises 110 x 10^3 tonnes particulate organic carbon.

Comparison of gross fluxes, net fluxes and amounts of silt

The mean annual amount of suspended mud in the Ems estuary is 61 x 10^3 tonnes in the outer reaches, 49 x 10^3 tonnes in the middle reaches and 39 x 10^3 tonnes in the Dollard. Comparing these amounts with the wind-driven lateral transport of mud (see the gross fluxes) in these areas reveals that the wind-driven fluxes in the lower reaches and the Dollard are nearly 200 times greater than the mean amount of mud present. Comparing the lateral fluxes with the net input from elsewhere reveals that these fluxes are also much more important than the net input: by a factor of ten for the lower reaches and a factor of 20 for the Dollard alone. These comparisons clearly show the dominating character of the wind-driven fluxes. These fluxes are so large that the net input of mud from the North Sea and from the adjacent tidal basins (via tidal water sheds) cannot be quantified with conventional techniques.

Comparison of gross fluxes, net fluxes and amounts of algal biomass present

The input of particulate organic matter from the North Sea is estimated to be 69 x 10^3 tonnes C per annum and is calculated from the mud transport and the percentage of organic carbon that transport contains. The carbon input from the Ems is appreciably less: about 11 x 10^3 tonnes C per annum (Baretta & Ruardij, 1988). The input of particulate carbon from the Westerwoldsche Aa is small: about 2 x 10^3 tonnes C per annum (Baretta & Ruardij, 1988).

As in the case of mud, the lateral fluxes of organic carbon are nearly 200 times greater than the mean amount of suspended particulate carbon in the lower reaches: the same holds for the Dollard. This is not surprising, given that most of the particulate organic carbon consists of detritus. The relation between lateral fluxes and net input from the coastal zone is of the same magnitude as that of the mud.

In this case too, it is impossible to measure the net transport of particulate organic matter. Notwithstanding, the situation is more complex for organic carbon than for mud, because there is an appreciable local supply in the form of primary production, as well as an input via the gross lateral fluxes and the net input. This makes it even more difficult to quantify the transport than was the case for mud (see above). Therefore it must be concluded that it is unlikely that the net input of particulate organic matter from the coastal zone to the Ems estuary can be reliably estimated using currently available methods.

Applying the findings of this research

The magnitude of the lateral mud fluxes in the total dynamics illustrates that these fluxes are probably mainly responsible for the seasonal variations in the concentrations of suspended matter and hence also the variations in light penetration of the water. Thus, in addition to nutrient supply from freshwater sources (de Jonge, 1990; de Jonge & Essink, 1991) the dynamics of mud are also one of the most important factors that determine the primary production in the water column.

The high lateral fluxes of microphytobenthos also have important implications. In the lower reaches ca. 40% of the total microalgal chlorophyll-*a* biomass is present in the water. In the Dollard this amount is much smaller (c. 10%); the remainder is present on the extensive intertidal flats.

On average resuspended microphytobenthos account for c. 30% of the total amount of chlorophyll-*a* biomass present in the water of the lower reaches of the estuary. In the Dollard this value is much higher: c. 85%. Consequently, the microphytobenthos is assumed to contribute the same percentages to the annual primary production of the water column too.

For the period of investigation approximately 25% of the annual primary production in the entire estuary of the river Ems is caused by resuspended microphytobenthos, 53% by real phytoplankton and c. 22% by microphytobenthos living on the tidal flats.

The total algal biomass and its concentration in the uppermost 2 cm of the tidal flats exceeds the total biomass and concentration in the water. Therefore, it may be argued that the tidal flats are more important than the water column in terms of providing food for grazers.

The magnitude of the fluxes of particulate organic carbon (from microphytobenthos and detritus) by comparison with the estimated input of this material from elsewhere also suggest that an important part of the pelagial in the Ems estuary is fed by the intertidal flats. In this context it is important to note that a further deterioration of the flats cannot be permitted, even if this increases the area of saltmarsh. Saltmarshes do contribute to the character of the estuary and are used by breeding birds on a large scale as high-water refuges and nesting sites, but in terms of primary production these salt marshes contribute little to the direct feeding of the ecosystem (Dankers *et al.*, 1984).

The relation found between effective wind speed and suspended matter concentrations and between 'effective wind speed' and the suspension of microphytobenthos can be applied in transport models (e.g. models of mud transport). It can also be used to calibrate such models.

The findings to do with the resuspension of mud from the extensive mudflats have important implications for the management of coastal waters. It is not yet sufficiently clear precisely which factors are responsible for the mud concentrations in the water. Yet it is vitally important to know this, so that detailed relations can be established between natural (wind and current) and anthropogenic (dredging, sand extraction, shellfish harvesting, fishery) activities and the resulting enhanced mud concentrations that are responsible for turbidity.

The findings about the magnitude of residual currents can be applied in transport models, to elucidate the processes that determine the distribution of the dissolved matter and the mud.

An aspect not dealt with in this research but nonetheless possibly of importance for the algae is the nutrient supply in the water and with special reference to phosphorus. The water contains dissolved phosphate but phosphate is also present adsorbed to various minerals that make up the suspended matter (de Jonge & Villerius, 1989). When dissolved phosphate is taken up from the water a certain amount comes from this suspended matter. When there are large wind-driven fluxes the nutrients in the water can be appreciably supplemented in this way by nutrients from the floor of intertidal flats (de Jonge & Engelkes, in prep.).

The importance of the findings presented in this thesis transcends the study area. They are applicable to other shallow tidal systems i.e. other parts of the Wadden Sea.

POSTSCRIPT

This multidisciplinary study illustrates the need to draw on biology as well as physics when endeavouring to unravel the complex interactions in natural systems. It is also important to draw on chemistry, although that was not an essential part of this thesis.

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2. PHYSICS

THE ABIOTIC ENVIRONMENT

V.N. de Jonge

INTRODUCTION

Estuaries can be defined in many ways. A generally accepted and biologically useful definition of an estuary is a "semi-enclosed and coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage" (Cameron & Pritchard, 1963).

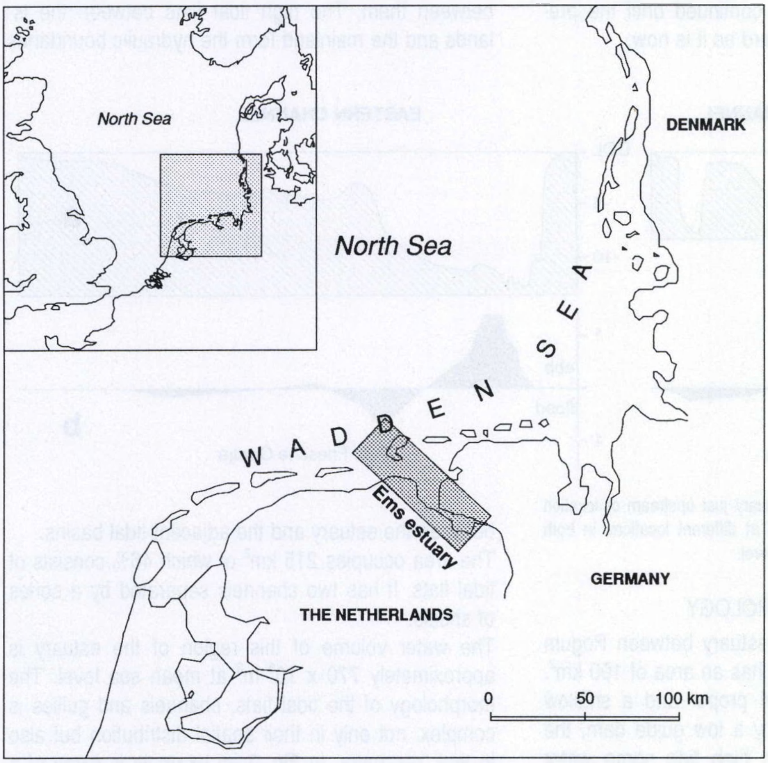

Fig. 1. Map of the North Sea, Wadden Sea, and the Ems estuary.

The Ems estuary is part of the 600-km-long European Wadden Sea (Fig. 1). This shallow sea consists of a series of tidal basins protected from direct North Sea wave action by a string of barrier islands. The islands are separated by tidal inlets. The tidal basins are partly separated from each other by high tidal flats allowing water exchange only during high tide. A number of rivers drain into the Wadden Sea, the river Ems being one of them.

The surface of the Ems estuary (Fig. 1) is approximately 500 km^2, including a fresh water tidal area in the Ems of about 37 km^2.

HISTORY

The Wadden Sea and its estuaries originate from the last two glaciations. River valleys were formed during the glacial periods, while in the interglacial periods the sea transgressed and the river valleys became inundated. When large quantities of sediment were supplied and the tidal range was small, the valleys could completely fill in so that deltas developed.

However, when sediment supply was less the river valleys drowned, giving rise to so-called coastal plain estuaries, which widen in a seaward direction.

The final shape of the Ems estuary was formed during the Pleistocene (Jelgersma, 1960; de Smet, 1960; Voorthuijsen, 1960) by the combined effects of sediment supply, a high tidal range and presumably storm surges (Russell, 1967). Originally the estuary had a funnel shape, with the river Ems more or less in its present place. A number of storm floods in the 14th and 15th century changed the original shape drastically and enlarged the estuary considerably (Stratingh & Venema, 1855). At the same time accretion began in the Dollard area (Wiggers, 1960; de Smet & Wiggers, 1960), followed by land reclamation from the sea. This process continued until the present day resulting in the Dollard as it is now.

TOPOGRAPHY AND MORPHOLOGY

The upper part of the Ems estuary between Pogum and the mouth of the Dollard has an area of 100 km^2. It consists of the upper part proper and a shallow bay, the Dollard separated by a low guide dam, the Geisedamm (Fig. 1). During high tide some water exchange is possible by a number of perforations in the dam. The main channel is canalized and heavily dredged but it has tidal-flat embankments. Tidal flats also cover 85% of the Dollard area. Consequently, the mean water depth in the Dollard is low (1.2 m). The volume of water in the upper estuary at mean sea level is approximately 120 x 10^6 m^3.

The middle part of the estuary, downstream of the Dollard (Fig. 1) has a funnel shape. This region extends to Eemshaven where the estuary joins the Wadden Sea. Most flats lie along the shore, but a large tidal flat divides the estuary longitudinally into two parts creating two channels. The main channel is on the east side. The total surface of this section is 155 km^2 of which 36% comprises tidal flats. The mean depth of this section increases gradually in a seaward direction, with the average water depth being 3.5 m. The water volume of this area at mean sea level is approximately 550 x 10^6 m^3.

The most seaward region of the estuary is the Wadden Sea part of the estuary. This region is situated between Eemshaven and the islands Rottumeroog and Borkum (Fig. 1). The boundary with the North Sea is formed by these two islands and the tidal inlet between them. The high tidal flats between the islands and the mainland form the hydraulic boundaries between the estuary and the adjacent tidal basins.

The area occupies 215 km^2 of which 46% consists of tidal flats. It has two channels separated by a series of shoals.

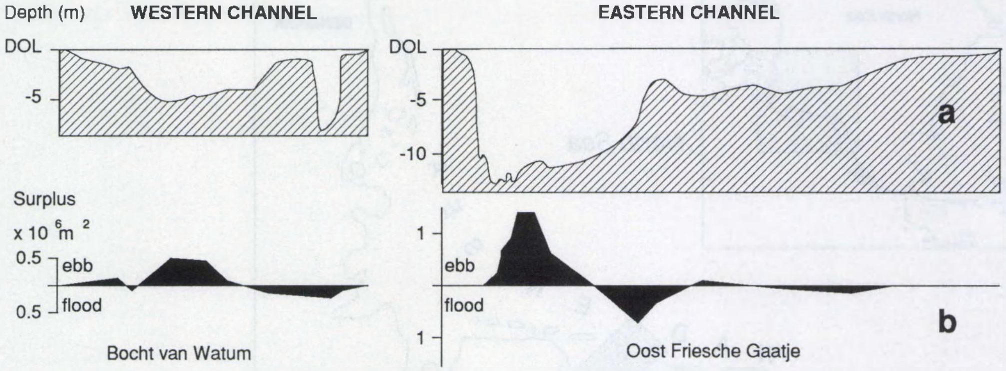

Fig. 2. (a) Cross section of the estuary just upstream of location Eemshaven. (b) the residual flows at different locations in both channels. DOL = Dutch Ordnance Level.

The water volume of this region of the estuary is approximately 770 x 10^6 m^3 at mean sea level. The morphology of the tidal flats, channels and gullies is complex, not only in their spatial distribution but also in their geometry. In Fig. 2 an example is given of a cross-section of the middle part of the estuary. The bottom profile shows two channels separated by a shoal, with considerable differences in the residual flow profiles.

The morphology of the Ems estuary is not static. Slow changes are not only induced by natural processes such as sedimentation, meandering of channels and gullies, but also by human activities such as land reclamation, building of harbours, dredging and sand mining. An example of natural morphological changes near the tidal inlet is given in Fig. 3 (Samu, 1979). Samu concluded that these morphological changes were cyclic and occurred with a periodicity of some 25 years.

Similar morphological changes were initiated by dredging activities and sand mining (in Randzelgat). The effects of these activities were noticeable within 1 year (de Jonge, 1983).

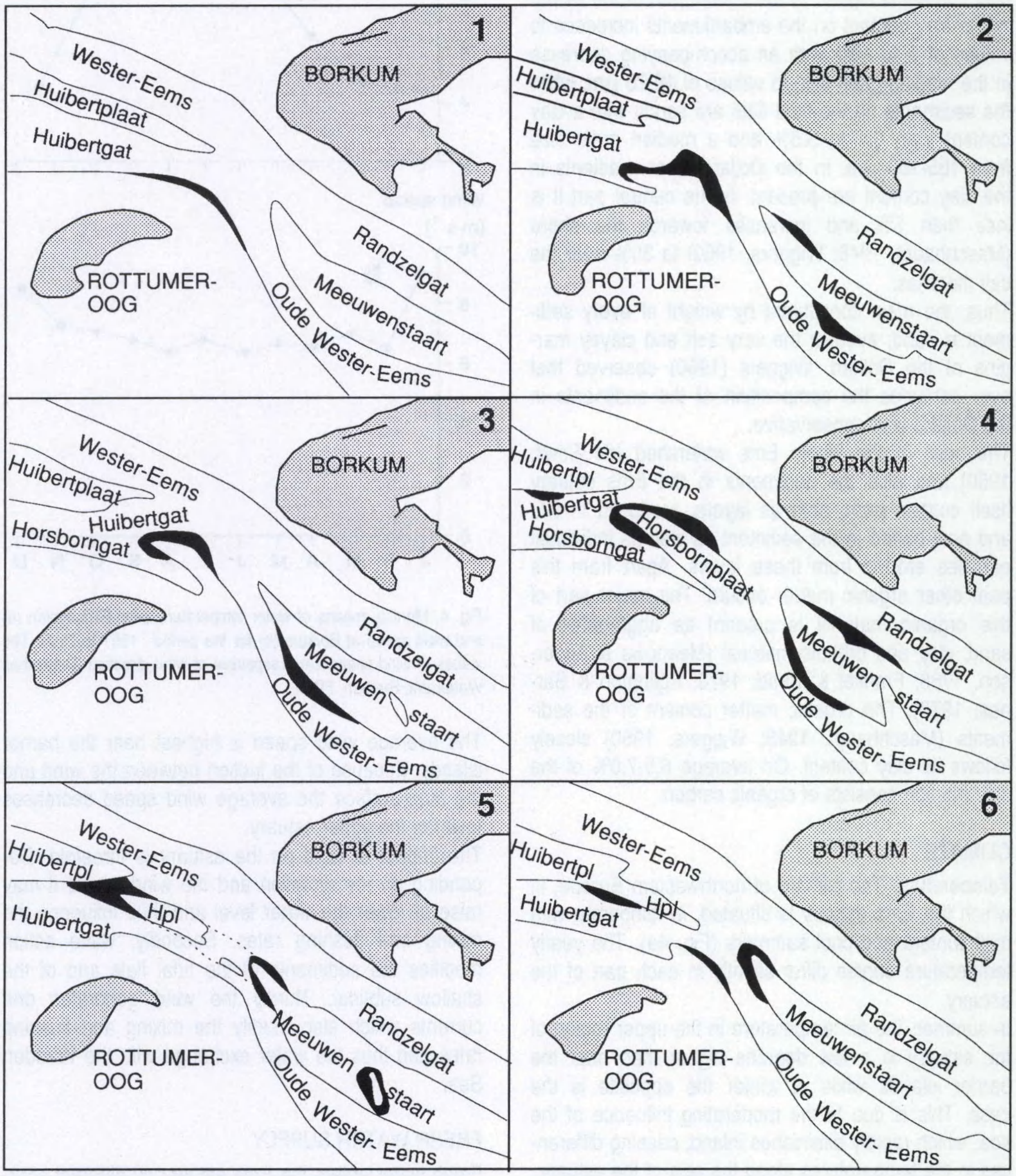

Fig. 3. Periodic changes in the morphology of the Ems estuary in the reaches upstream of the tidal inlet. The cycle of the changes is known for over a century and determined to be approx. 25 years (after Samu, 1979).

SEDIMENT COMPOSITION

The sediments in the outer estuary are mainly composed of sand with median grain sizes between 95 and 155 µm. The clay content (grain size <2 µm) varies, depending on the degree of exposure to currents and waves, between 0.3 to 3.5%; nearshore the clay content is higher. In the middle part of the estuary the clay content on the embankments increases to values of 9 to 18% with an accompanying decrease in the median grain size to values of 16-75 µm, while the sediments on the tidal flats are sandy with a clay content from 0.1 to 5.5% and a median grain size from 105-150 µm. In the Dollard clear gradients in the clay content are present. In the central part it is less than 5% and increases towards the shore (Maschhaupt, 1948; Wiggers, 1960) to 35% near the salt marshes.

Thus, the main constituent by weight of every sediment is sand, even at the very soft and clayey margins of the Dollard. Wiggers (1960) observed that over centuries the composition of the sediments in the Dollard was conservative.

The soils of the whole Ems watershed (de Smet, 1960) and also the sediments in the Ems estuary itself contain peat, both as layers, produced in situ and now buried in the sediment as well as individual particles eroded from these layers. Apart from this peat other organic matter occurs. The major part of this organic material is present as aggregates of sand, clay and organic material (Meadows & Anderson, 1968; Frankel & Mead, 1973; Eglington & Barnes, 1978). The organic matter content of the sediments (Maschhaupt, 1948; Wiggers, 1960) closely follows its clay content. On average 6.5-7.0% of the clay fraction consists of organic carbon.

CLIMATE

Temperature. The climate of northwestern Europe, in which the Ems estuary is situated, is temperate with mild winters and cool summers (Fig. 4a). The yearly temperature curves differ slightly in each part of the estuary.

In summer, the air temperature in the upper region of the estuary is a few degrees higher than near the barrier islands while in winter the opposite is the case. This is due to the moderating influence of the sea, which rapidly diminishes inland, causing differences in the temperatures along the axis of the estuary.

Wind. There is a clear seasonal cycle in wind speed (Fig. 4b), with lowest monthly averages in summer and highest values in winter. The wind is predominantly westerly, especially the high winds.

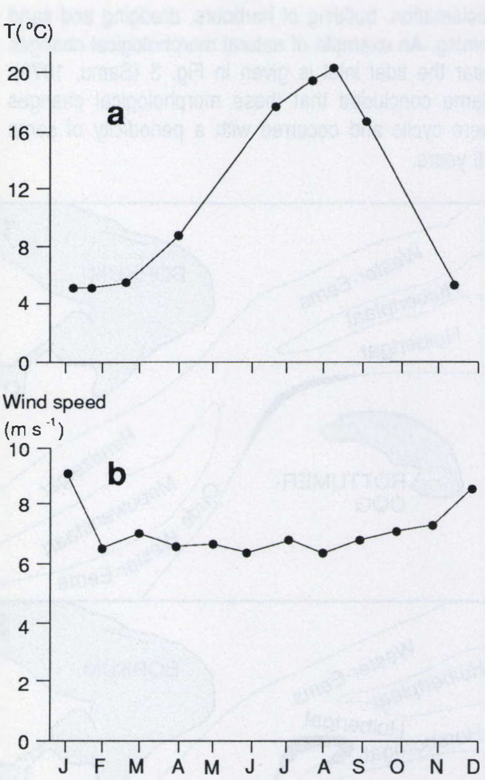

Fig. 4. Monthly means of water temperature near Eemshaven (a) and wind speed at Borkum (b) for the period 1951 to 1960. The values of wind speed are irrespective of wind direction (Deutsches Wetteramt, Bremen, FRG).

The average wind speed is highest near the barrier islands. Because of the friction between the wind and the land surface the average wind speed decreases towards the upper estuary.

The impact of wind on the estuary is threefold. Depending on the direction and the wind speed it may raise or lower the water level and thus influence the mixing and flushing rates. Secondly, wave action modifies the sediments of the tidal flats and of the shallow subtidal. Thirdly the wind generates drift currents which also modify the mixing and flushing rates and thus the water exchange with the Wadden Sea.

FRESH WATER SUPPLY

Fresh water enters the Ems estuary by different sources of which the most important is the river Ems with a watershed of 12,650 km^2 (Hinrich, 1974). The discharge is very variable, ranging from a high of 390 $m^3 s^{-1}$ to a low of 25 $m^3 s^{-1}$.

The second fresh water source is the Westerwoldsche Aa. Being part of the canal system of the northern provinces, the Westerwoldsche Aa has no well-defined watershed. The water discharge is roughly 10% of that of the river Ems (Fig. 5).

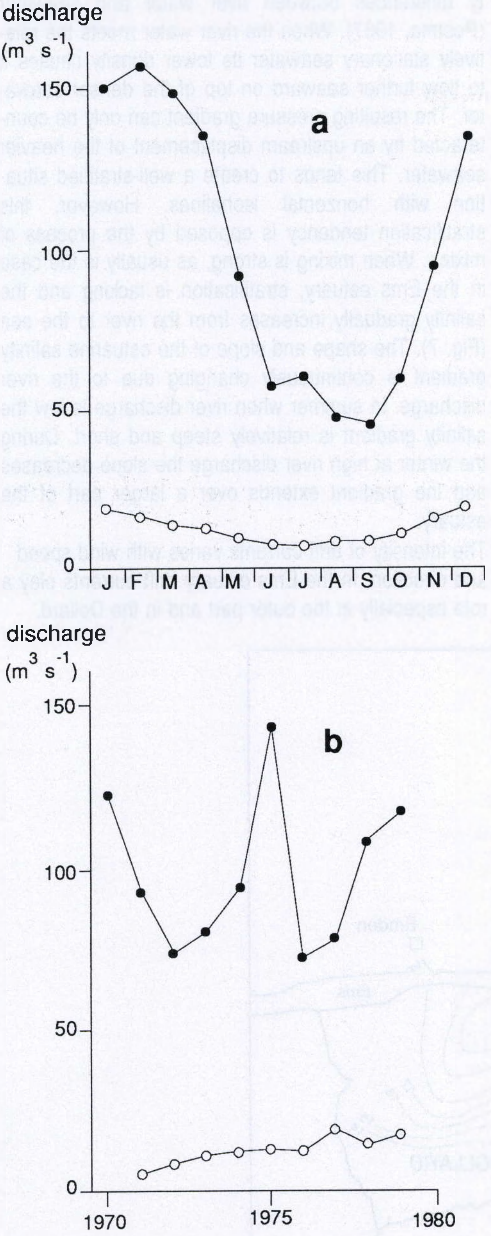

Fig. 5. Monthly mean (a) and annual mean (b) discharge of the River Ems (●) and Westerwoldsche Aa (O) for the period 1970 - 1979.

Another fresh water source is the precipitation in the estuary. The annual precipitation is 72.5 cm near the barrier islands and 74 cm at Emden (Dorrestein, 1960). The precipitation in the estuary is approximately balanced by evaporation (KNMI, 1972). Precipitation on the tidal flats during emergence can temporarily lower the salinity of the interstitial water and may act as a stress factor on the benthic communities.

TIDE

The tide in the Ems estuary is dominated by the semi-diurnal lunar tide and has a mean period of 12 h 25'. The tidal curve is asymmetric. At Delfzijl, the mean period of the flood is 5 h 45', which is 55 min shorter than the ebb period. Hence, the flood currents are stronger than the ebb currents (Fig. 6).

In addition, there is a significant diurnal inequality in the tidal amplitude.

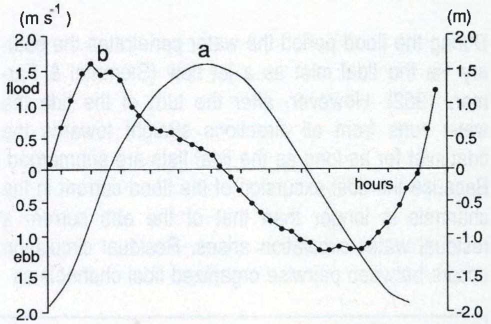

Fig. 6. (a) Water level in metres at Delfzijl (Dutch tide tables, Staatsuitgeverij, 's-Gravenhage, The Netherlands). (b) Tidal variation in current velocity in m s^{-1} in the middle reaches of the Ems estuary (9.5.1978). DOL = Dutch Ordnance Level.

The tidal range along the axis of the estuary increases upstream. In 1971 the mean annual tidal range was 2.20 m near Borkum, 2.79 m in Delfzijl and 3.03 m at Emden. In the southeastern part of the Dollard the mean tidal range is somewhat higher than at Emden.

The annual average tidal range is not constant but has increased by c. 5% in the period from 1960-1980. Part of this increase is possibly caused by heavy dredging over the last 2 decades (de Jonge, 1983) while another part corresponds with an increase which is observed on the east side as well as the west side of the Atlantic Ocean (Führböter, 1989).

WATER MOVEMENT AND MIXING

The rise and fall of the water level in the North Sea, caused by the passing tidal wave (vertical tide), generates the horizontal tidal currents (horizontal tide) in the Ems estuary. This horizontal water movement is the dominant feature of the tide and it can be expressed in terms of the tidal prism (the water volume passing through a cross-section twice each tidal period). The tidal prism at the tidal inlet is approximately 900 x 10^6 m^3. At the entrance of the Dollard the tidal prism is reduced to approximately 115 x 10^6 m^3. The tidal excursion (the distance a water parcel is displaced during half a tidal period) also varies over the estuary, although less than the tidal prism. Near the tidal inlet the tidal excursion is approximately 17 km and in the Dollard it amounts to 12 km.

The water movements lead to typical circulation patterns and to mixing. In the Ems estuary the following mixing mechanisms are present:

1. Tide-induced water circulation
2. River-induced water circulation
3. Wind-driven water circulation or drift currents.

During the flood period the water penetrates the estuary via the tidal inlet as a jet flow (Stommel & Farmer, 1952). However, after the turn of the tide the water runs from all directions straight towards the tidal inlet for as long as the tidal flats are submerged. Because the tidal excursion of the flood current in the channels is longer than that of the ebb current a residual water circulation arises. Residual circulation occurs between pairwise organized tidal channels as well as within one channel (cf. Fig. 2).

They are caused by cross-sectional pressure gradients in the water and the Coriolis force (Zimmerman, 1976 a, b). Mean volumes of the residual circulations amount to 4-15% of the tidal volumes.

The river-induced water circulation is based on density differences between river water and seawater (Postma, 1967). When the river water meets the relatively stationary seawater its lower density causes it to flow further seaward on top of the denser seawater. The resulting pressure gradient can only be counteracted by an upstream displacement of the heavier seawater. This tends to create a well-stratified situation with horizontal isohalines. However, this stratification tendency is opposed by the process of mixing. When mixing is strong, as usually is the case in the Ems estuary, stratification is lacking and the salinity gradually increases from the river to the sea (Fig. 7). The shape and slope of the estuarine salinity gradient is continuously changing due to the river discharge. In summer when river discharge is low the salinity gradient is relatively steep and short. During the winter at high river discharge the slope decreases and the gradient extends over a larger part of the estuary.

The intensity of drift currents varies with wind speed and direction. In the Ems estuary drift currents play a role especially in the outer part and in the Dollard.

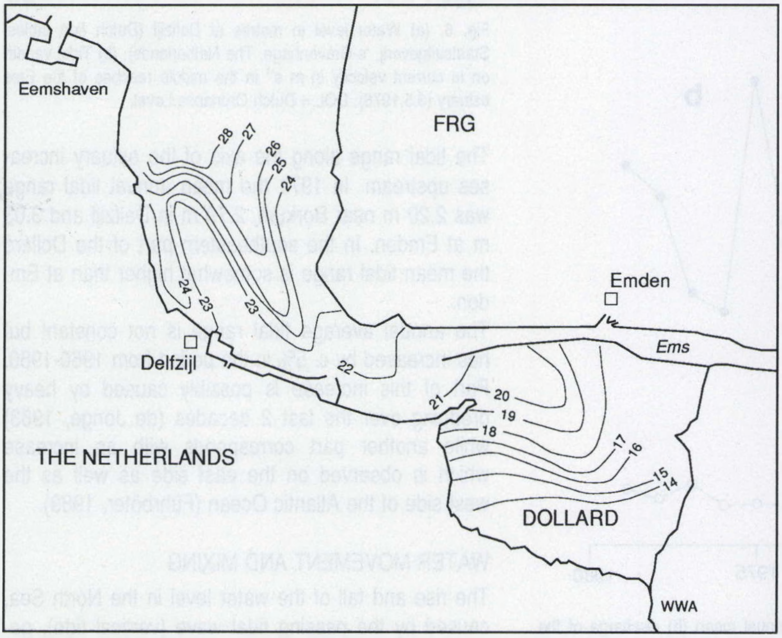

Fig. 7. Example of salinity distribution in the Ems estuary at high tide.

Table 1. Characteristics of water transport (in days) at high discharge (351 $m^3 s^{-1}$) and low discharge (34.1 $m^3 s^{-1}$) of fresh water for the Ems estuary as a whole and in the Dollard separately at high discharge (31.0 $m^3 s^{-1}$) and low discharge (5.1 $m^3 s^{-1}$) of Westerwoldsche Aa water. (Helder & Ruardij, 1982)

	time scale (days)	
	High discharge	Low discharge
EMS ESTUARY		
Seawater:		
mean age	14.0	36.3
Ems water:		
mean age	19.3	64.7
flushing time	12.1	72.1
WWA water:		
mean age	12.9	32.4
Turnover time of basin:	17.7	35.7
DOLLARD		
Water entering at mouth:		
mean age	5.9	17.9
WWA water:		
mean age	8.5	27.1
flushing time	8.7	31.2
Turnover time of basin:	10.0	21.0

The various circulation processes are very complex, necessitating simplification to formulate model calculations. Dorrestein & Otto (1960) presented a simple one-dimensional transport model for the Ems estuary which was improved by Helder & Ruardij (1982). Some data on the mean age, flushing time and turnover time of the water mass in the estuary, derived from Helder & Ruardij (1982) are given in Table 2. Here, the mean age is the time that water parcels located in a certain region are present in the estuary since arrival from their source (viz. sea, Ems, Westerwoldsche Aa).

The flushing time is the ratio between the total fresh water volume in the estuary and the discharge rate of fresh water. The turnover time is the time needed to decrease the volume of water or mass of dissolved constituent present at $t = 0$ in a region of the estuary to a fraction e^{-1}. Another characteristic often used is the residence time which is the average time a parcel of water needs to pass through a region.

SEDIMENT TRANSPORT AND ACCUMULATION

The concentration gradient of suspended matter in the Ems estuary is typical for most coastal plain estuaries (Fig. 8), with low concentrations near the tidal inlet and high values in the inner part of the estuary.

The importance of the tide-induced sediment transport was first recognized by Postma (1954). Later, this was analyzed experimentally (Postma, 1961) as well as theoretically (van Straaten & Kuenen, 1958; Groen, 1967; Postma, 1982).

Two factors contribute to this process. The first is the asymmetry of the tidal curve. The higher maximal current velocities during flood erode more bottom sediment than the ebb currents and therefore effectuate a net upstream transport of suspended matter. This is illustrated by the tidal fluctuations for the coarser fraction (>55 µm) in Fig. 9. The finer suspended matter fraction (<55 µm) does not show this phenomenon as clearly because of its lower settling velocity. Consequently, the net transport of sand is larger than that of the finer fractions and larger close to the bottom (bed-load transport) than near the surface.

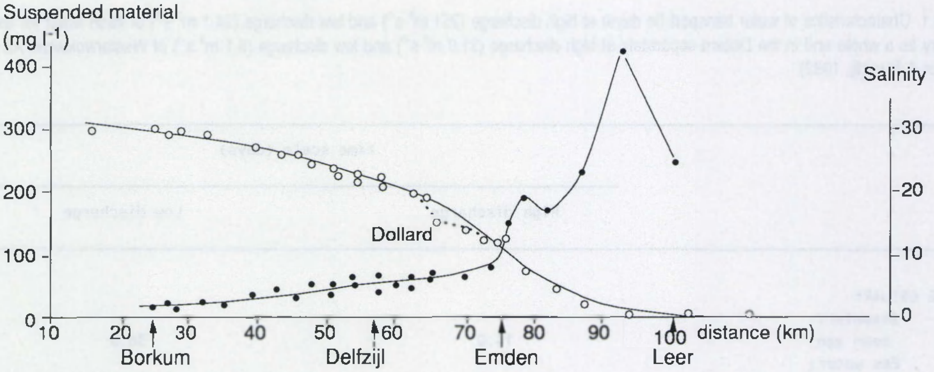

Fig. 8. Concentration gradient of suspended matter (●) and salinity (O) in the main channels of the Ems estuary. Values are averages for the period 1975-1976.

The second factor contributing to a net upstream transport of suspended matter is that the critical current velocity for erosion is higher than that for deposition of the same material (Postma, 1967). Thus particles deposited at a certain current velocity during flood are resuspended again during ebb at a later phase in the tidal cycle.

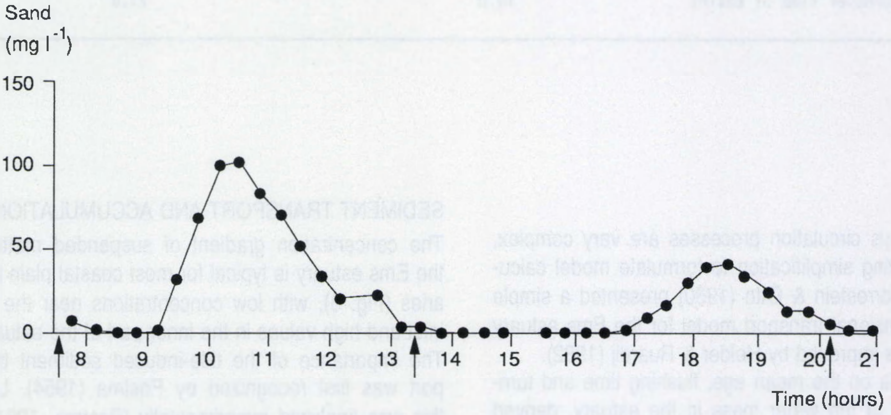

Fig. 9. Tidal variation in concentrations of suspended sand (fraction > 55 μm), in the middle reaches of the Ems estuary (9.5.1978). The arrows indicate the time of slack water.

So far, only the net transport of suspended material has been considered. However, the net amount of transported material is extremely low in comparison to the amount that is deposited and resuspended. During each tidal period a considerable exchange of suspended material and sediment occurs between the tidal flats and the channels. The physical properties of particles also play a significant role in the transport process. Particles with a low density (e.g. colloids) behave approximately like water and hence can be exported to the sea while for heavier particles a net import can occur. Similarly the exchange rate of the relatively light mud aggregates is higher than that of the heavy sand grains.

Together with the sediments, also small organisms and organic matter are exchanged between the sediments and the water. This was observed by de Jonge (1985), who found a resemblance between the species composition of benthic diatoms on the tidal-flat sediments and those suspended in the water.

Deposition and resuspension of sediments is also affected by drift currents, wind waves and biological activity. Drift currents and wind waves increase the resuspension of sediments and lessen deposition.

The higher the wind speed, the higher the wave energy, which results in an increased suspended matter concentration in the water and a higher degree of sorting (less fine fractions) of the sediments on the tidal flats. In high winds the highest values of suspended matter are found during high water near the margins of the tidal flats where resuspension is highest.

The effects of biological activity on resuspension and deposition of sediment and suspended matter are many and various. Organisms filtering water with suspended matter and producing faecal pellets or pseudofaeces can substantially contribute to the deposition of particles and aggregates (Verwey, 1952). Micro-organisms such as benthic diatoms, bacteria, fungi, etcetera can consolidate the sediment surface by forming a mat structure, which is often cemented to the heavier sand particles by adhesive excretion products (e.g. mucus). On the other hand, benthos and epibenthos (bottom fishes, shrimps and crabs) can increase the resuspension of sediment because they may actively suspend sediment or disturb surface mat structures. The latter generally leads to irregularities at the sediment surface increasing turbulent flow conditions (Jumars & Nowell, 1984) and consequently erosion.The import of suspended matter by the two rivers is considerable and contributes to an accretion in the Dollard (and presumably also the rest of the estuary) of c. 0.008 m a^{-1} (Reenders & van der Meulen, 1972). Nevertheless, the suspended matter in the water and the material-deposited in the sediment of the estuary is of predominantly marine origin (Favejee, 1960; Salomons, 1975). This is in agreement with the theory (Postma 1982) that the import and sedimentation of marine particulate material predominates in the Ems estuary.

NUTRIENTS

The rivers Ems, Westerwoldsche Aa and some small canals bring large amounts of nutrients into the estuary. These are partly in dissolved and partly in particulate form. Rainfall contributes only a small amount of nutrients to the estuary. Furthermore, large amounts of particulate nitrogen and phosphorus are transported from the Wadden Sea and the North Sea into the estuary. At present the particulate nitrogen from these sources cannot be quantified. The annual particulate phosphorus supply, calculated from data on particulate phosphorus in suspended matter, the accretion rate of the estuary and the mineral composition of the sediments, amounts to some 3.5 x 10^3 tonnes P.

This value agrees well with the estimate of de Jonge & Postma (1974) for the western part of the Dutch Wadden Sea. Calculated and estimated fresh water discharges of different forms of nitrogen, phosphorus and silicon are given in Table 2.

After arrival in the estuary the dissolved components are mixed and flushed in the same way as the water. This results in a concentration gradient (Fig. 10) with generally high values in the river water and low values near the tidal inlet. The particulate nutrients, however, are distributed according to the transport processes described for the suspended material.

Table 2. Annual supply and concentration ranges of nutrients from the River Ems, the Westerwoldsche Aa and other sources

Source	Metric tonnes a^{-1}	Data from	Nutrient component	Concentration range	
				Minimum (μmol l^{-1})	Maximum (μmol l^{-1})
RIVER EMS					
Total nitrogen	18500	a,b,c	Inorganic nitrogen	70	460
Total phosphorus	2190	a,b	Orthophosphate	3	20
Reactive silicate	13700	a,b	Reactive silicate	40	240
WESTERWOLDSCHE AA					
Total nitrogen	6550	d,f	Inorganic nitrogen	430	5000
Total phosphorus	890	d,f	Orthophosphate	3	100
Reactive silicate	1625	a,d,e	Reactive silicate	80	315
OTHER SOURCES					
Total nitrogen	2780	d,f,g,h			
Total phosphorus	430	d,f,g,h,			
Reactive silicate	>2400	a,d,g			

a. BOEDE measurements. b. River discharges (Wasser und Schiffahrtsamt Emden). c. Preston (1978). d. River discharges (Rijkswaterstaat). e. Helder *et al.* (1983). f. Measurements Rijkswaterstaat. g. Dankers *et al.* (1984). h. Precipitation (KNMI, 1972).

Biologically, the most important areas are those where the dissolved nutrients reach low concentration levels so that nutrient limitation of primary production might occur, which is in the outer part of the estuary. On their way through the estuary dissolved nutrients are taken up by phytoplankton or are regenerated by mineralization. Particulate nutrients can pass into solution or dissolved nutrients can become particulate due to biological as well as physico-chemical processes. These processes together show a strong seasonal cycle. In the Dollard nutrient limitation is unlikely to occur as the concentrations are high throughout the year. However, in the outer regions seasonally low levels are reached. Dissolved silicate is often depleted in spring, indicating silicate limitation for diatoms. The role of nitrogen and phosphate is less evident because of rather large year to year variation. Occasionally nitrogen depletion occurs in early summer together with continuously high phosphate concentrations, but in more recent data sets phosphate depletion predominates. It seems unlikely that nitrogenous nutrients often become limiting to primary production in the Ems estuary. As a considerable part of the total organic carbon production occurs by benthic diatoms, the nutrient levels in the pore water of the surface layers of the, tidal flats are important.

During low tide the concentration of reactive phosphate and reactive silicate in the thin water layer on the sediment and in the pore water of the surface layer of the tidal flats are usually higher than 1 μmol.l^{-1}. Only in the outer region do the reactive silicate values drop below 1 μmol.l^{-1} during the phytobenthos bloom in spring. This indicates that growth limitation due to low nutrient values in this area can occur. In the other areas growth limitation due to low nutrient values probably never occurs.

The nitrogen cycle in the estuary was studied by Rutgers van der Loeff *et al.* (1981) and Helder (1983). Their data as well as the BOEDE data indicate that this nutrient does not regulate the benthic diatom growth through nutrient limitation. On the contrary, there are indications (Admiraal, 1977c) that ammonia concentrations higher than 500 μmol.$^{-1}$, which occur in parts of the Dollard, inhibit diatom growth. There were only scant indications that nutrient levels in the sediment might become limiting to phytobenthos production.

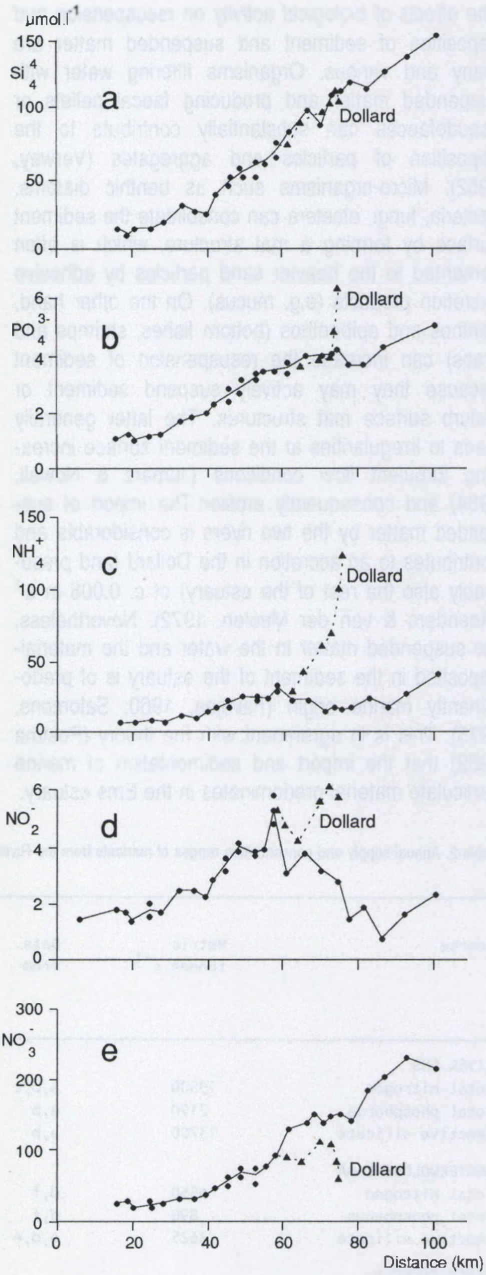

Fig. 10. Annual means of reactive silicate (a), phosphate (b), ammonia (c), nitrite (d), and nitrate (e) in the main channels of the Ems estuary. For meaning of distance see Fig. 8.

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TIDAL FLOW AND RESIDUAL FLOW IN THE EMS ESTUARY

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29477

ABSTRACT

Tidal water flow and residual tidal flow between and within channels was ascertained for 20 cross sections in the Ems estuary (The Netherlands). The tidal prism of the estuary is approximately 1×10^9 m^3. In the middle reaches the residual ebb and flood transports over the cross sections varied between 1-18% of the tidal water transport, increasing to 43% near the river proper and near the tidal watersheds. The overall mean is c. 11%. Tidally averaged residual current velocities in the cross sections varied from less than 0.01 to 0.33 m s^{-1} with an overall mean of 0.06 m s^{-1}. The distribution of the tidally averaged residual currents along and over the cross sections studied corresponds very well with the results of a horizontally two-dimensional water transport simulation model.

The data from this study show that the distribution of large-scale (between channels) and small scale (within channels) residual currents is reflected in the local cross-sectional bathymetry. It is hypothesized that deviations from a good correspondence between the location of residuals and bathymetry indicate a hydraulically unstable situation, which implies a changing local morphology.

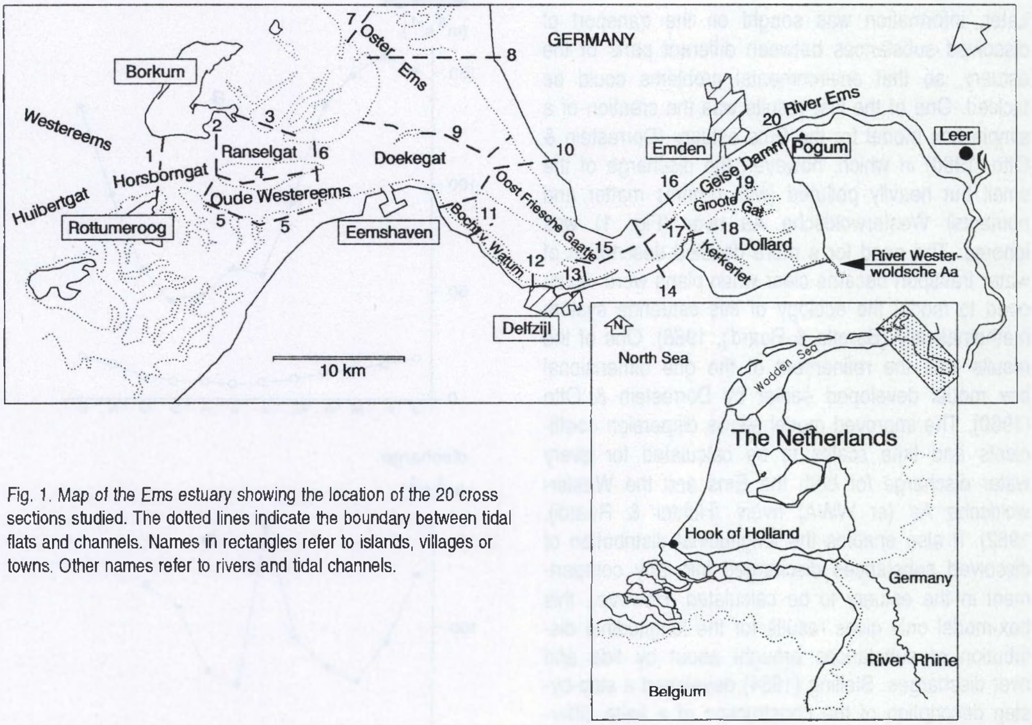

Fig. 1. Map of the Ems estuary showing the location of the 20 cross sections studied. The dotted lines indicate the boundary between tidal flats and channels. Names in rectangles refer to islands, villages or towns. Other names refer to rivers and tidal channels.

INTRODUCTION

In common with most coastal plain estuaries, the Ems estuary (Fig. 1) consists of a complicated system of channels and tidal flats. There are several discharge points, from which the tidal distribution of natural and xenobiotic substances must be calculated. Further, sediments dredged from estuarine channels and harbours are dumped in certain parts of the estuary, and some of these deposits and the dissolved substances they contain are subsequently dispersed. The longitudinal transports of these substances cannot be calculated adequately without the use of models.

Various studies have been done on the water movement in the Ems estuary. Initially, work was focused on the preparation of tide tables and current charts for safe navigation.

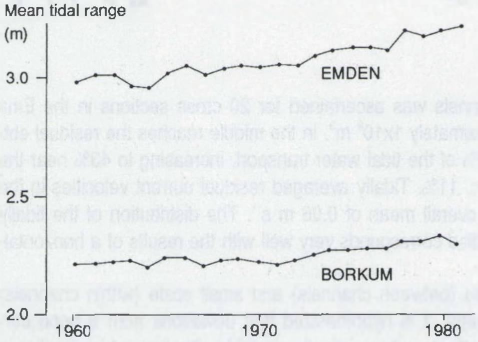

Fig. 2. The mean annual tidal range for stations Emden and Borkum for the period 1960-80.

Later, information was sought on the transport of dissolved substances between different parts of the estuary, so that environmental problems could be tackled. One of the first results was the creation of a simple box model for the Ems estuary (Dorrestein & Otto, 1960) in which, however, the discharge of the small but heavily polluted (with organic matter and nutrients) Westerwoldsche Aa river (Fig. 1) was ignored. The need for a more detailed description of water transport became clear when plans were developed to model the ecology of this estuarine system mathematically (Baretta & Ruardij, 1988). One of the results was the refinement of the one dimensional box model developed earlier by Dorrestein & Otto (1960). The improved model allows dispersion coefficients and time scales to be calculated for every water discharge for both the Ems and the Westerwoldsche Aa (or WWA) rivers (Helder & Ruardij, 1982). It also enables the longitudinal distribution of dissolved substances discharged into any compartment in the estuary to be calculated. However, this box-model only gives results for the longitudinal distribution of substances brought about by tide and river discharges. Stelling (1984) developed a step-by-step description of the construction of a finite difference method for approximating of shallow water equations. This method was used to construct a new horizontally two-dimensional water transport model for the Ems estuary which describes water flow and residual flow in that estuary.

However, no detailed field observations were available for calibration, even though this information is necessary for various reasons. This paper therefore aims to present tidal water transport, residual tidal water transport and mean residual current velocities for different channel cross sections and parts of cross sections in the Ems estuary. Moreover, the magnitude of the tidal water transports will be compared with river discharge, and the influence of the wind on these will be discussed. The possible relation between morphology, sediment composition and the location of residuals within the channel bathymetry is given.

MATERIALS AND METHODS

Hydrographical features of the estuary

The Ems estuary is situated in the northeast of The Netherlands on the border with Germany (Fig. 1). Its total area, including the tidal river but excluding the outer delta, is ca. 500 km^2. The area of the outer delta is ca. 100 km^2.

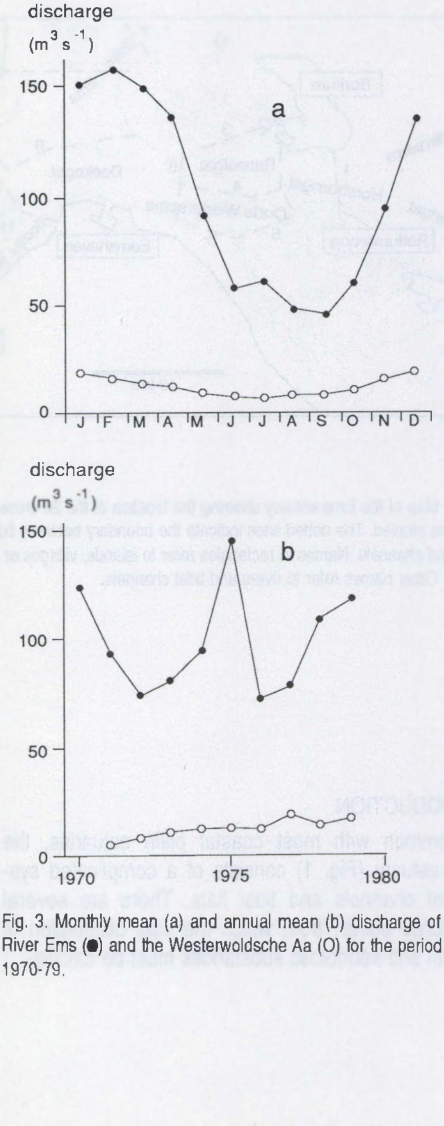

Fig. 3. Monthly mean (a) and annual mean (b) discharge of the River Ems (●) and the Westerwoldsche Aa (O) for the period 1970-79.

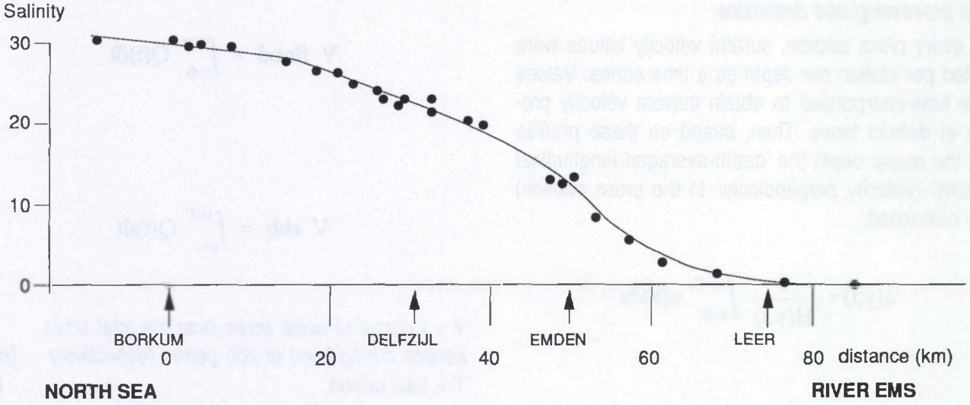

Fig. 4. Gradient of the mean salinity measured in the main channels of the estuary. Dots represent sampling stations. Values are averages for the period 1975/76.

From the tidal inlet to the town of Leer the estuary is approximately 75 km long. The tidal range is not stable in time; mean annual values for the tidal inlet (island of Borkum) and the town of Emden plotted as a time series revealed a significant increase over the period 1960-80 (Emden) and since 1970 (Borkum) (see Fig. 2). For an explanation of the phenomenon, see de Jonge (1983).

The estuary receives water from the river Ems (100 $m^3 s^{-1}$ on average) and the small canalized river Westerwoldsche Aa (12.5 $m^3 s^{-1}$ on average). These discharges vary strongly within and between years. For the monthly means and the annual means for both during the period of investigation, see Fig. 3.

The result of the interaction between fresh water discharge and sea water brought in by the tide is a salinity gradient, as shown in Fig. 4.

Field measurements

Between 1971 and 1979 data were collected from 20 cross sections in the Ems estuary (Fig. 1) to determine the local tidal currents and water transport. These locations were chosen to be representative of the morphological units of the estuarine system and to represent dredged areas, areas where harbour sludge is dumped and areas affected by the construction of the Eemshaven harbour (cf. Fig. 1) or likely to be affected by other planned engineering works like terminals and harbours. All the measurements were carried out by the "Meet en Adviesdienst, Delfzijl" (Rijkswaterstaat, Dutch Ministry of Transport and Public Works) and the "Wasser und Schiffahrtsamt Emden" (local authorities, Germany).

Before every water transport measurement the cross-sectional depth profile was determined so that the measuring boats could be postioned appropriately (see Fig. 7). The number of boats required depended on the cross-sectional depth profile. During the actual measurements, the survey boats were moored within 5 metres of the designated point, using the Hi-Fix system (Decca, Racal, England). The current velocity profiles, which were obtained using Ott current meters (Ott, type 10.002, Kempten, Germany), were determined at intervals of 20 minutes. If the current velocity was 0.5 m s^{-1} or less, the measurements were done for 1 minute; at faster current velocities the measuring period was reduced to 30 seconds. This measuring time was used to obtain a reliable velocity value in the turbulent estuarine flow. The strategy was to determine the vertical current velocity least at 4 fixed points: two just below the water surface, at depths of 0.2 m and 0.7 m, and two close to the bottom, at 0.3 m and 0.8 m above the channel bed. The number of intermediate measurements depended on the local water depth. Two additional determinations were done in channels up to 3 m deep, 3 additional determinations in channels between 3 and 5 m deep, 4 in channels between 5 and 14 m deep, 6 in channels between 14 and 27 m deep and, finally, 7 in channels deeper than 27 m. Thus, the actual depths at which measurements were obtained varied. They were scaled according to the variation in water depth resulting from the tidal range. Per profile, the measurements were done consecutively because only one current meter was available for each boat. Measurements always started approximately one hour before low water slack tide and were stopped the next low tide after the current had turned at all stations and all depths.

Data processing and definitions

For every cross section, current velocity values were plotted per station per depth as a time series. Values were time-interpolated to obtain current velocity profiles at distinct times. Then, based on these profiles and the actual depth the 'depth-averaged longitudinal velocity' (velocity perpendicular to the cross section) was calculated:

$$\overline{u}(y,t) = \frac{1}{H(y,t)} \int_{z=0}^{z=H} u(z)dz$$

u = current velocity perpendicular to the cross section at vertical position z (m s^{-1})

$\overline{u}$ = average current velocity (m s^{-1})

z = vertical position in the water column (m)

H = height of the water column at time t (m)

y = lateral position along the cross section (m)

t = time (s)

The depth-averaged longitudinal current velocity was multiplied by the actual water depth of the profile at that station, resulting in a 'local line flux', being the area of a vertical plane of a body of water passing a certain location (y) per unit of time (t):

$$q(y,t) = \overline{u}(y,t)H(y,t)$$

q = local water flux per metre channel width (m^3 s^{-1} m^{-1})

Integration of the local line fluxes over the entire cross section (B) gives the water transport rate:

$$Q(t) = \int_{y=0}^{y=B} q(y,t)dy$$

Q = water transport rate over the total cross section (m^3 s^{-1})

B = channel width at the surface (m)

The integration over the ebb period or flood period then results in a cross-sectional semi-tidal water transport.

$$V\ flood = \int_{t=0}^{t=\tau} Q(t)dt$$

$$V\ ebb = \int_{t=\tau}^{t=T} Q(t)dt$$

V = Volume of water prism over the total cross section during flood or ebb period respectively (m^3)

T = tidal period (s)

t = 0, t=τ and t=T represent slack tide (s)

The residual water transport per total cross section or per channel per cross section (V res) is defined as V flood - V ebb. The local water fluxes per metre width per station (q) can be integrated over the flood period and ebb period respectively, resulting in:

$$V\ flood(y) = \int_{t=0}^{t=\tau} q(y,t)dt$$

$$V\ ebb(y) = \int_{t=\tau}^{t=T} q(y,t)dt$$

in which:

V flood (y) or V ebb (y) = water prism during flood or ebb period per metre width (m^3 m^{-1})

The plots of the semi-tidal (ebb and flood respectively) integrated water prisms (V flood and V ebb) and the semi-tidal integrated local water fluxes per metre width [V flood (y) and V ebb (y)] were the data available for the present study.

Data were also available on the duration (s) in seconds of the ebb and the flood periods, the cross-sectional depth profile, the precise variation in water depth over the tide, and the mean wind speed and wind direction.

These data enabled several characteristics to be calculated. The residual transport between channels was calculated, using the semi-tidal water transports per channel (V flood and V ebb).

The semi-tidal integrated local water fluxes per metrechannel width per station enabled of Eulerian residual currents within the channels to be calculated.

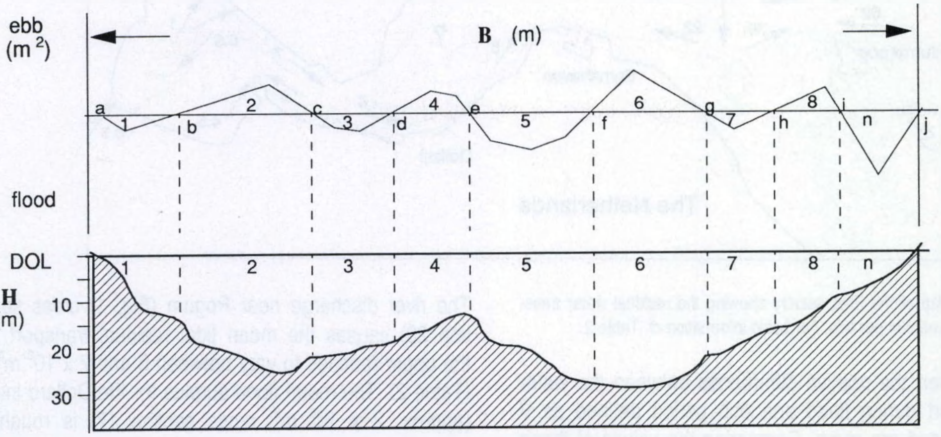

Fig. 5. A hypothetical situation of residual currents at a cross section with given bathymetry. Numbers refer to the different residual currents while the letters (except n) refer to the position of the residuals in the cross section. In Table 3 the flood and ebb residuals are numbered independently of each other, for reasons of space. DOL = Dutch Ordnance Level.

Thus, V flood (y) - V ebb (y) = V residual (y) in which flood or ebb refers to the direction (landward or seaward respectively) of the residual flow. All the values 1 to n (number of residual flows) are numbered from west to east along the cross sections (Fig. 5). The V residual flood (y) and V residual ebb (y) were integrated over the appropriate channel width (i.e. the width of the flood or ebb residual), per cross section. This resulted in local residual flood transports and residual ebb transports per channel per cross section. This can be written as

$$V(n)\ res = \int_{y=i}^{y=j} V\ res(y)dy$$

in which:

V(n)res = the local flood or ebb directed residual water transport over part n of the cross section that belongs to this residual. (m^3)

It must thus be realized that more than one residual cell can be present within one channel (cf. Fig. 5).

The mean residual current velocity per flood or ebb cell was calculated by dividing these residual transports by both the actual tidal period (T) and the area of the cross-section over which this flood or ebb residual had been determined (in the bottom part of Fig. 5, the surface of one of the numbered parts of the total cross section). Thus:

$$\bar{v}(n)\ res = \frac{V(n)\ res}{\bar{A}(n)T}$$

in which: v(n)res is the mean residual mass transport velocity of residual n in the total cross section (Fig. 5), and A(n) is the mean surface area of cross sectional part n in the total cross section

$$A(t) = \frac{1}{T}\int_{t=0}^{t=T} B(t)H(t)dt$$

RESULTS

Tidal water transport

Tables 1 and 2 give values for water transport over the 20 cross sections (for their location see Fig. 1). In Table 1 the total water transport (V flood and V ebb), mean wind speed and mean wind direction are given separately per channel for the flood and ebb periods.

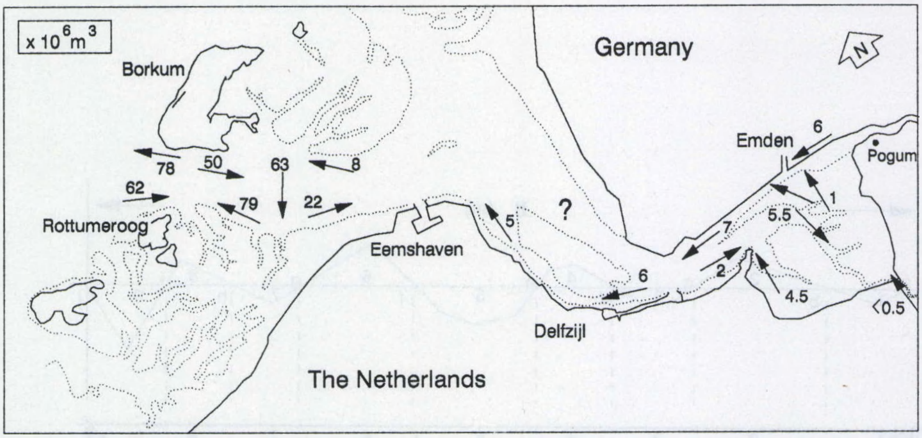

Fig. 6. Map of the Ems estuary showing the residual water transport per channel per tide. For basic information cf. Table 2.

Moreover, the relative differences between the water transport during flood and ebb period defined as V res/V flood are given. Comparing the values of these relative differences with the values of the wind speed indicates that considerable differences may occur between flood and ebb transport at wind speeds above 7.5 m s^{-1}, especially in the shallow reaches where the advective contribution of the river is small (cf. Table 1, cross sections 8, 9, 14, 17 and 19). This data set was too small to be able to detect any systematic differences between flood and ebb transport that could be attributed to wind speed coupled with wind direction. At cross sections where the advective transport due to river discharge contributes significantly to the tidal water transport, systematic differences between flood and ebb usually occur (cf. Table 1 cross section 16 and 20).

Residual water transport

Between channels - Estuaries often contain double channels. Consequently, most cross sections contain two channels separated by a tidal flat or a shoal (cf. Fig. 1). The half tidal water transports of the individual channels (V) and the (mean) residual water transports $[V\ res = \sum_{1}^{n} V(n)res]$ between double channels, (measured during moderate wind conditions only) are given in Table 2. Usually, one channel shows a flood surplus whereas the other shows an ebb surplus, illustrating the major residual circulation of water known from these "flood and ebb channels" (Fig. 6).

The river discharge near Pogum (Fig. 1, cross section 20) causes the mean tidal residual transport in the upper reaches to vary between 5 and 7 x 10^6 m^3 (Table 2). The mean flood surplus for the Dollard inlet (approx. 2 x 10^6 m^3; cross section 17) is roughly balanced by a residual transport over the Geise Damm which separates the Dollard from the River Ems. This results in that the residual ebb transport in the lower Ems (cross section 16) being greater (approx. 0.5 to 2.5 x 10^6 m^3) than at cross section 20 (Fig. 6).

Water exchange between the Dollard area proper and the lowest reach of the River Ems between cross sections 16 and 20 occurs through a perforated dam, the "Geise Damm" (Fig. 1). The data available in Fig. 6 (cf. also data in Table 2) illustrate the presence of a large scale residual circulation of water within the Dollard, where the main channel (Groote Gat, cross section 19) shows a flood surplus of ca. 5.5 x 10^6 m^3 which is counterbalanced by the discharge of the small WWA river (<0.5 x 10^6 m^3), a considerable ebb surplus via the Kerkeriet channel (cross section 18) and an ebb surplus of the lowest reach of the river Ems (cross section 16).

Remarkably, nearly all the measurements in the middle part of the estuary confirm the presence of a variable ebb surplus in that area (Table 2 cross sections 10, 11, 12 and 13) which cannot be explained solely by river discharge. In the Bocht van Watum channel (cross sections 11, 12 and 13) the mean surplus values fluctuate between 0 and 6.5 x 10^6 m^3, whereas for the lower part, cross section 10 (where the channel bifurcates a residual ebb surplus of 11 x 10^6 m^3 was measured in the same channel. In the Oost Friesche Gaatje channel (cross section 10), previously recognized as a flood channel,

Table 1. Basic data on tidal water transport over the different cross sections.

Number of cross section	date	water transport V flood $(\times 10^6 m^3)$	water transport V ebb $(\times 10^6 m^3)$	total residual transport V res. flood $(\times 10^6 m^3)$	total residual transport V res. ebb $(\times 10^6 m^3)$	$\frac{V\ res}{V\ flood} \times 100$ (%)	mean wind speed $(m.s^{-1})$ and wind direction flood	mean wind speed $(m.s^{-1})$ and wind direction ebb
1	13-06-1979	1253	1268	-	15	1	2.5 E	2.5 E
2	27,28-05-1975	954	961	-	7	<1	7.5 NE	5 NE
	12-06-1979	1201	1231	-	30	2.5	7 NW	4 NW
3	20-08-1974	38	39	-	1	2.5	2.5 E	6 NE
	21-08-1974	39	40	-	1	2.5	2.5 E	6 NE
4	27-05-1975	261	190	71	-	27	12.5 ENE	13 ENE
	27-05-1975	255	189	66	-	26	7.5 ENE	5.5 ENE
	12-06-1979	300	263	37	-	12	7 NW	7 NW
5	20-08-1974	44.9	40.4	4.5	-	10	2.5 E	5 NE
	21-08-1974	35.2	38.5	-	3.3	9	3 SE/NE	6 NE
6	27,28-05-1975	729	720	9	-	1	7.5 NE	5 NE
	12-06-1979	852	866	14	-	1.5	7	7 NW
7	19-04-1977	100	91	9	-	9	6 NW	5 NNW
	20,21-04-1977	22	33	-	11	50	8 SW	9.5 SW
8	27-04-1976	21 SW	25 SW	-	46	219	12 NW	12 NNE
	19-04-1977	32 SW	20 NE	-	12	38	6 NW	6 NW
	20-04-1977	17 SW	19 NE	2	-	12	7.5 SW	10 SW
	21-04-1977	10 SW	23.5 NE	13.5	-	135	9 WSW	9 WSW
9	27-04-1976	251	238	13	-	5	12 NW	12 NNE
	20,21-04-1977	218	188	30	-	14	9 WSW	9 WSW
10	22-09-1971	428	457	-	29	7	2.5 SE/N	4 NNE
	10-05-1978	480	491.5	-	11.5	2.5	7.5 N	10 NE
11	11-05-1978	66	71	-	5	8	3.5 N	5 N
12	11-05-1978	40	40	0	0	0	3.5 N	5 N
13	01-06-1972	37	45	-	8	22	5 NW	5 NW
	12-10-1976	21	33	-	12	57	5 Z	10 SW
	05-04-1977	25	34	-	9	36	7.5 W	10 W
	11-05-1978	17	22	-	5	29	3.5 N	5 N
14	10-06-1975	261	259	2	-	<1	5 NE	6 NE
	01-09-1976	245	252	-	7	3	10 WSW	7.5 W/NE
	30-08-1977	280	282	-	2	<1	1 E	2 N
	25-04-1978	230	259	-	29	13	3 NE	3 NE
	10-04-1979	185	182	3	-	2	7.5 E	7.5 E
15	23-06-1971	123	155	-	32	26	3 S	2 SW
	24-06-1971	131	159.5	-	28.5	22	N.M.	
16	21-09-1971	59	65	-	6	10	0	1.5 E
	22-09-1971	65	73	-	8	12	0	3 E
	23-09-1971	56	61	-	5	9	3 SSE	2 SW
	10-08-1972	68	79	-	11	16	6 SW	3 N
	23-04-1974	82	83	-	1	1	12.5 W/NW	10 NW
	10-06-1975	79	90	-	11	14	5 NE	6 NE
	01-09-1976	80	79	1	-	1	10 WSW	7.5 W/NE
	30-08-1977	87.5	95.5	-	8	9	1 O	2 N
	25-04-1978	74	79	-	5	7	3 NE	3 NE

Number of cross section	date	water transport V flood	water transport V ebb	total residual transport V res. flood	total residual transport V res. ebb	V res / V flood x 100	mean wind speed ($m.s^{-1}$) and wind direction flood		mean wind speed ($m.s^{-1}$) and wind direction ebb	
		($x10^6 m^3$)		($x10^6 m^3$)		(%)				
17	23-09-1971	123	124	-	1	1	3	SSE	2	SW
	10-08-1972	153	162	-	9	6	6	SW	3	N
	23-04-1974	158	165	-	7	4	12.5	W/NW	10	NW
	10-06-1975	169	169	0	0	0	5	NE	6	NE
	02-09-1976	144	134	10	-	7	7.5	NW	7.5	NW
	31-08-1977	149	142	7	-	5	3.5	SW	1	E
	26-04-1978	107	107	0	-	0	12	E	12	E
18	24-08-1976	10	14.3	-	4.3	43	2.5	SE	2.5	SE
	25-08-1976	12	-	-	-	-	2	SE	-	
19	23-04-1974	68	79	-	11	16	12.5	NW	10	NW
	29-05-1975	65	60	5	-	8	N.M.			
	02-09-1976	62	55	7	-	11	7.5	NW	7.5	NW
	31-08-1977	64	60	4	-	6	3.5	SW	1	E
	26-04-1978	51	42	9	-	18	12	E	12	E
20	23-04-1974	48	53	-	5	10	12.5	W/NW	10	NW
	01-09-1977	49	56	-	7	14	2	SSE	1.5	NW
	27-04-1978	41	47	-	6	15	12	E	9	E

Table 2. Tidal water transport (V) per channel per cross section and residual values (V res) per pair of channels. Transport values during wind speeds higher than 7.5 m s^{-1} were not used except for the River Ems where wind effect is small. The deviating value for cross section 14 (10.04.1979) was also omitted from further calculations.

number of cross section	channel	date	water transport V flood	V ebb	(mean) water transport $\bar{V}$ flood	$\bar{V}$ ebb	(mean) residual transport (V res) flood directed	ebb directed
			($\times 10^6 m^3$)		($\times 10^6 m^3$)		($\times 10^6 m^3$)	
1	Horsborngat	13-06-1979	1253	1268	-	-	62.5	-
	Westereems	13-06-1979					-	77.5
2	Oude Westereems	27,28-05-1975	332	390	370	438	-	68
		12-06-1979	407	486				
	Ranselgat	27,28-05-1975	622	571	708	658	50	-
		12-06-1979	794	745				
3	Fischer Balje	20-08-1974	0.14	0.18	0.14	0.18	-	0.04
		21-08-1974	0.14	0.18				
	Blinde Ranselgat	20-08-1974	38.2	38.8	38.4	39.2	-	0.85
		21-08-1974	38.6	39.7				
4	Meeuwenstaart	27-05-1975	255	189	278	226	52	-
		12-06-1979	300	263				
5	Eemsrand	20-08-1974	44.9	40.4	40	39.5	0.5	-
		21-08-1974	35.2	38.5				
6	Oude Westereems	27,28-05-1979	491	490	534	522	12	-
		12-06-1979	576	554				
	Ranselgat	27,28-05-1975	238	230	264	264	0	
		12-06-1979	290	298				
7	Wester Balje	19-04-1977	100	91	-	-	9	-
8	Schuiten Sand					very variable due to drift currents		
9	Eems Horn					very variable due to drift currents		
10	Oostfriesche Gaatje	22-09-1971	336	354	-	-	-	18
	Bocht van Watum	22-09-1971	92	103	-	-	-	11
11	Bocht van Watum	11-05-1978	66	71	-	-	-	5
12	Bocht van Watum	11-05-1978	40	40	-	-	0	0
13	Bocht van Watum	01-06-1972	37	45	27	33.5	-	6.5
		11-05-1978	17	22				
14	Gaatje Bocht	10-06-1975	261	259	257	267	-	10
		30-08-1977	280	282				
		24-04-1978	230	259				
15	Paap-Geisesteert	23-06-1971	123	155	127	157	-	30 (NE)
		24-06-1971	131	159.5				
16	Emder Vaarwater	21-09-1971	59	65	70	77.5	-	7.5
		22-09-1971	65	73				
		23-09-1971	56	61				
		10-08-1972	68	79				
		10-06-1975	79	90				
		30-08-1977	87.5	95.5				
		25-04-1978	74	79				
17	Mond Dollard	23-09-1971	123	124	147.5	146	1.5	
		10-08-1972	153	162				
		10-06-1975	169	169				
18	Kerkeriet	24-08-1976	10	14.3	-	-	-	4.3
19	Groote Gat	29-05-1975	65	60	63.5	58.5	5.0	-
		02-09-1976	62	55				
		31-08-1977	64	60				
20	River Ems	23-04-1974	48	53	46.0	52.0	-	6.0
		01-09-1977	49	56				
		27-04-1978	41	47				

(Anonymous (1963), Gerritsen (1955) and van Straaten (1960)) none of the measurements available shows a flood surplus. The total ebb surplus determined for the Oost Friesche Gaatje channel, a part of cross section 10, was relatively high: 18 x 10^6 m^3. The ebb surplus of the total cross section was 29 x 10^6 m^3 (Table 2).

An estimate of the deviations that may occur as the result of measurement errors can be derived from the data from cross sections 11, 12 and 13 measured on 11-5-1978 (Table 1). On that date in cross section 11 and 13 an ebb surplus of 5 x 10^6 m^3 was measured per tide while in cross section 12 the ebb and flood volume were in equilibrium. This indicates that deviations of over 10% are quite realistic under field conditions.

In the various channels of the lower reaches the absolute amount of the residual water transports increases markedly, concomitantly with that of the total water transport (Table 2). The residual ebb transport downstream of Eemshaven is especially pronounced. This could be a result of water transport between the Ems estuary and adjacent tidal basins (see below), the accuracy of measurements and daily tidal inequality. The residual water transport between the main channels at cross section 1 is ca. 70 x 10^6 m^3 per tidal cycle or ca. 5.5% of the mean tidal water transport (Table 2).

Within channels - The phenomenon of residual water transports, described above between channels, also exists within individual channels. This is illustrated by the local residual flood or ebb directed transports V(n)res for a number of cross sections whose local bathymetry and residuals are given in Fig. 7.

The ebb and flood residuals within the channels are organized in pairs reflecting the presence of residual cells. Within the channels different residual cells can be present, as can be seen from the parts of the cross section where a flood or an ebb surplus was measured. In the present paper no attempt was made to estimate the dimensions and other characteristics of these cells. Only the mean residual water transport rate (V(n)res / T) and the mean residual current velocity $\overline{v}$(n)res were calculated for each of the n parts in the total cross section where surpluses were found. All these values are listed in Table 3. The data available on water transport (V flood and V ebb cf. also Table 1) illustrate the relation between the magnitude of the tidal water transport and the residual transport (V res). Except for the water divides between the Ems estuary and the adjacent tidal basins and the reaches where the river discharge is a predominant factor, the residual water transports amount to between 1% and 43% of the local volume of the tidal water prism during the flood (V flood).

Effects of wind

As well as the tide, the wind also plays a role in the horizontal circulation of water. Significant transports of water may occur over the shallows between the tidal basin of the Oster Ems (Fg. 1) and the Ems estuary (cf. cross sections 7, 8 and 9 in Table 1). Wind-driven water circulations also occur in the shallow Dollard area. At cross section 19 a residual flood water transport is usually found. It is compensated for by an ebb surplus via cross sections 16 and 18.

At increasing wind speed the residual transport over cross section 19 also increases. At certain wind directions and high wind speed (here above 10 m s^{-1}) the direction of the residual water transport can even be reversed (cf. Table 1, cross section 19 d.d. 23.04.1974) as a result of an increased flood transport over cross section 16 (cf. Table 1, cross section 16 d.d. 23.04.1974) penetrating the Dollard area indirectly, that is via the perforated Geise Damm. This surplus is counterbalanced by a high ebb surplus over cross sections 17 and 19.

In Fig. 8 all available curves on residual water transports for cross sections 16, 17 and 20 are given, per measuring date. It can be seen that the shape of the curves for cross sections 16 and 20, that is in the lower River Ems is similar, even during different weather conditions (Fig. 8 a to d and e to f). This indicates that the residuals are relatively independent of external factors such as changes in tidal range, river discharge and wind. Thus, the residual currents given in Fig. 7 are not ephemeral but can be considered to represent more persistent phenomena (cf. Zimmerman, 1976). However, this does not hold for cross section 17 in the inlet of the shallow Dollard area. This may be because in this very shallow area predominant but varying fields of drift currents are induced, resulting in varying residuals (cf. Fig. 8 g with h and i).

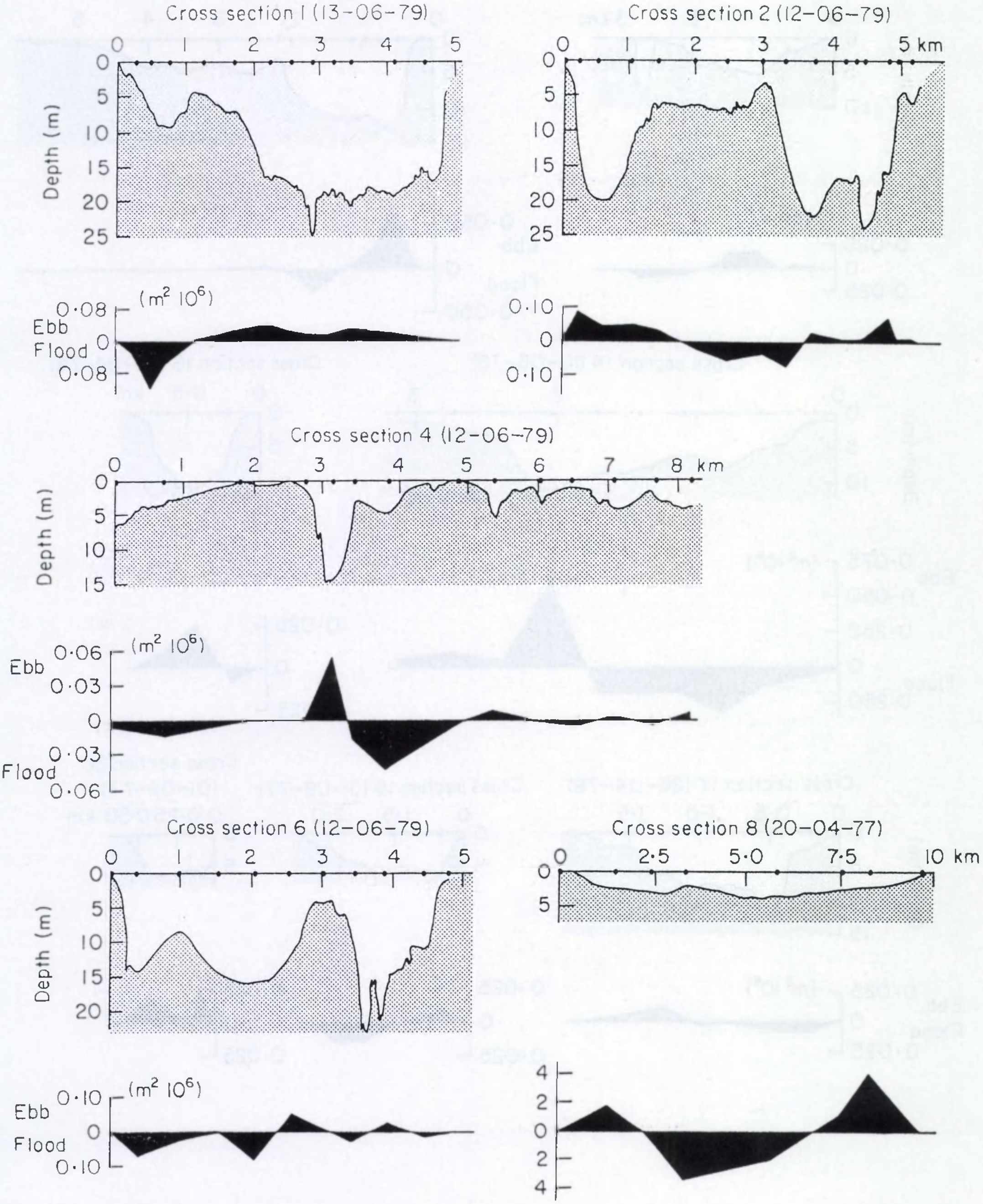

Fig. 7. Bathymetry of a selection of cross sections and corresponding local flood or ebb directed residual water transports V (n) res perpendicular to the cross sections. The cross sections are viewed looking seawards. The dots in the cross sections represent the stations where current velocity profiles were measured.

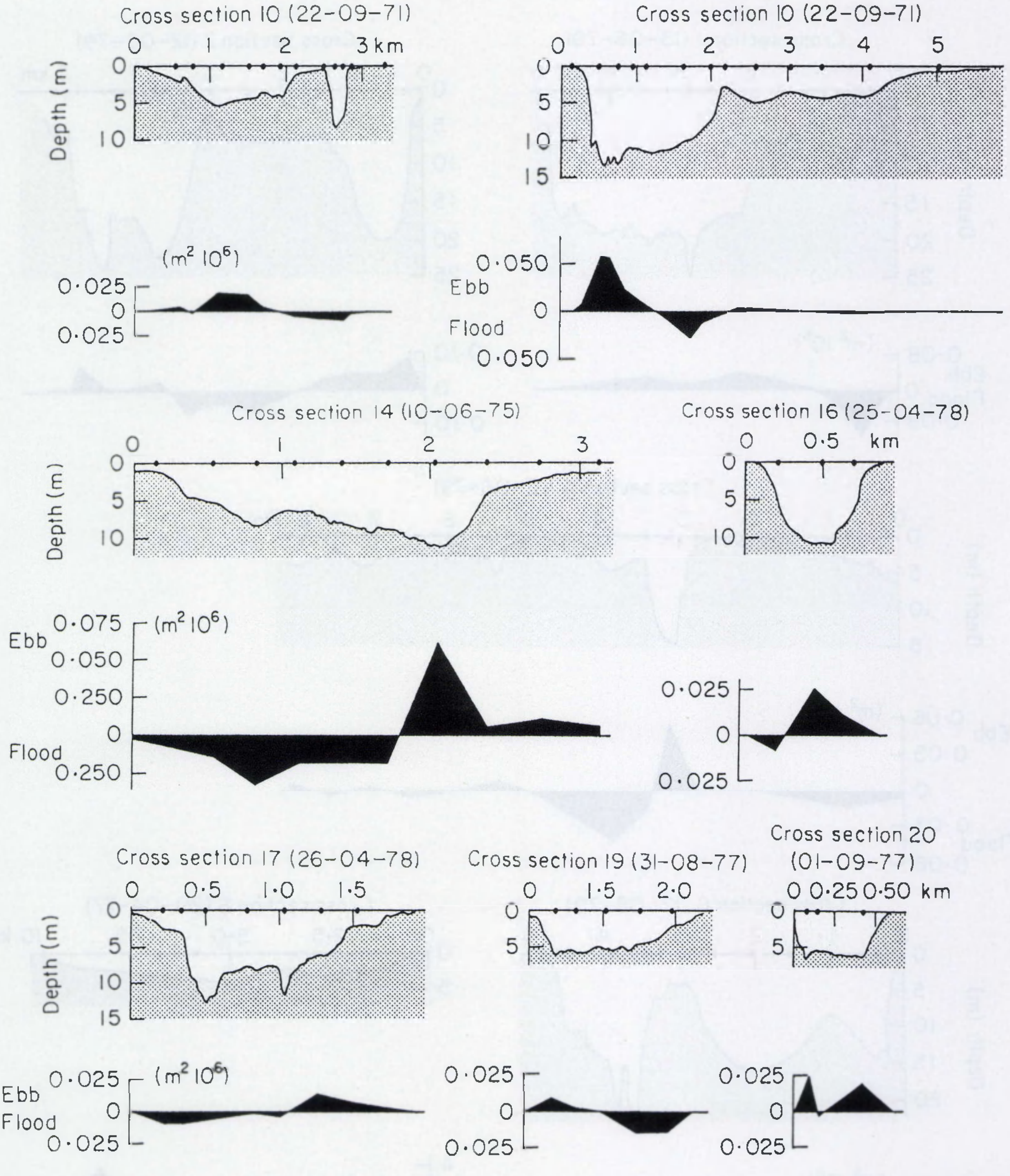
Cross section 10 (22-09-71)
0 1 2 3 km
Depth (m)
0
5
10
(m² 10⁶)
0·025
0
0·025
Cross section 10 (22-09-71)
0 1 2 3 4 5
0
5
10
15
0·050
Ebb
0
Flood
0·050
Cross section 14 (10-06-75)
0 1 2 3
Depth (m)
0
5
10
Ebb
0·075
(m² 10⁶)
0·050
0·250
0
Flood
0·250
Cross section 16 (25-04-78)
0 0·5 km
0
5
10
0·025
0
0·025
Cross section 17 (26-04-78)
0 0·5 1·0 1·5
Depth (m)
0
5
10
15
Ebb
0·025
(m² 10⁶)
Flood
0
0·025
Cross section 19 (31-08-77)
0 1·5 2·0
0
5
0·025
0
0·025
Cross section 20
(01-09-77)
0 0·25 0·50 km
0
5
0·025
0
0·025

Table 3. Tidally averaged local flood-or ebb-directed residual transport rate [V(n)res/T; $m^3\ s^{-1}$] and velocity of mean residual mass transport [v(n)res; $m\ s^{-1}$]. In the "flood" column no. 1 refers to the first residual flood flow while the second is indicated by 2, etc. The same notation holds for the "ebb" column (cf.also Fig. 5). *Moreover, the mean fresh water discharges of the River Ems* (Q_r) *during the various measuring* periods are given. Note that the numbering of the residuals does not correspond with the example in Fig. 5 but that the numbering for the flood as well as the ebb period starts from 1. This was done to keep the table a manageable size.

Number of residual flow			1		2		3		4	
FLOOD		Q_r	$\frac{V(n)res}{T}$	$\overline{V}(n)res$	$\frac{V(n)res}{T}$	$\overline{V}(n)res$	$\frac{V(n)res}{T}$	$\overline{V}(n)res$	$\frac{V(n)res}{T}$	$\overline{V}(n)res$
	date	$(m^3.s^{-1})$	$(m^3.s^{-1})$	$(m.s^{-1})$	$(m^3.s^{-1})$	$(m.s^{-1})$	$(m^3.s^{-1})$	$(m.s^{-1})$	$(m^3.s^{-1})$	$(m.s^{-1})$
1	13-06-1979	82	1550	0.20						
2	12-06-1979	82	1976	0.15						
4	12-06-1979	82	433	0.08	1044	0.33	112	0.06	109	0.10
6	12-06-1979	82	352	0.02	178	0.02	94	0.02	26	0.01
8	20-04-1977	135	170	0.02						
10	22-09-1971	27	11	0.05	262	0.10	388	0.07	84	0.03
13	05-04-1977	135	-							
14	10-06-1975	62	729	0.06						
	25-04-1978	117	162	0.03						
16	22-09-1971	27	30	0.07						
	10-08-1972	74	117	0.11						
	01-09-1976	27	135	0.04						
	25-04-1978	117	59	0.08						
17	23-09-1971	27	97	0.20	60	0.03				
	02-09-1976	27	12	0.14	24	0.02				
	26-04-1978	117	144	0.02						
19	31-08-1977	64	147	0.06						
20	01-09-1977	63	3	0.01						
	27-04-1978	177								
EBB										
1	13-06-1979	82	1542	0.03						
2	12-06-1979	82	1566	0.08	186	0.01	435	0.03		
4	12-06-1979	82	362	0.06	194	0.10	31	0.02	63	0.05
6	12-06-1979	82	175	0.02	70	0.01				
8	20-04-1977	135	68	0.02	144	0.04				
10	22-09-1971	27	44	0.07	397	0.09	695	0.06	46	0.01
13	05-04-1977	135	166	0.05						
14	10-06-1975	62	577	0.08						
	25-04-1978	117	39	0.03	685	0.06				
16	22-09-1971	27	7	0.04	164	0.07				
	10-08-1972	74	294	0.07						
	01-09-1976	27	82	0.03						
	25-04-1978	117	125	0.03						
17	23-09-1971	27	117	0.04	60	0.02				
	02-09-1976	27	124	0.02						
	26-04-1978	117	121	0.05						
19	31-08-1977	64	52	0.02						
20	01-09-1977	63	57	0.07	75	0.04				
	27-04-1978	177	111	0.04						

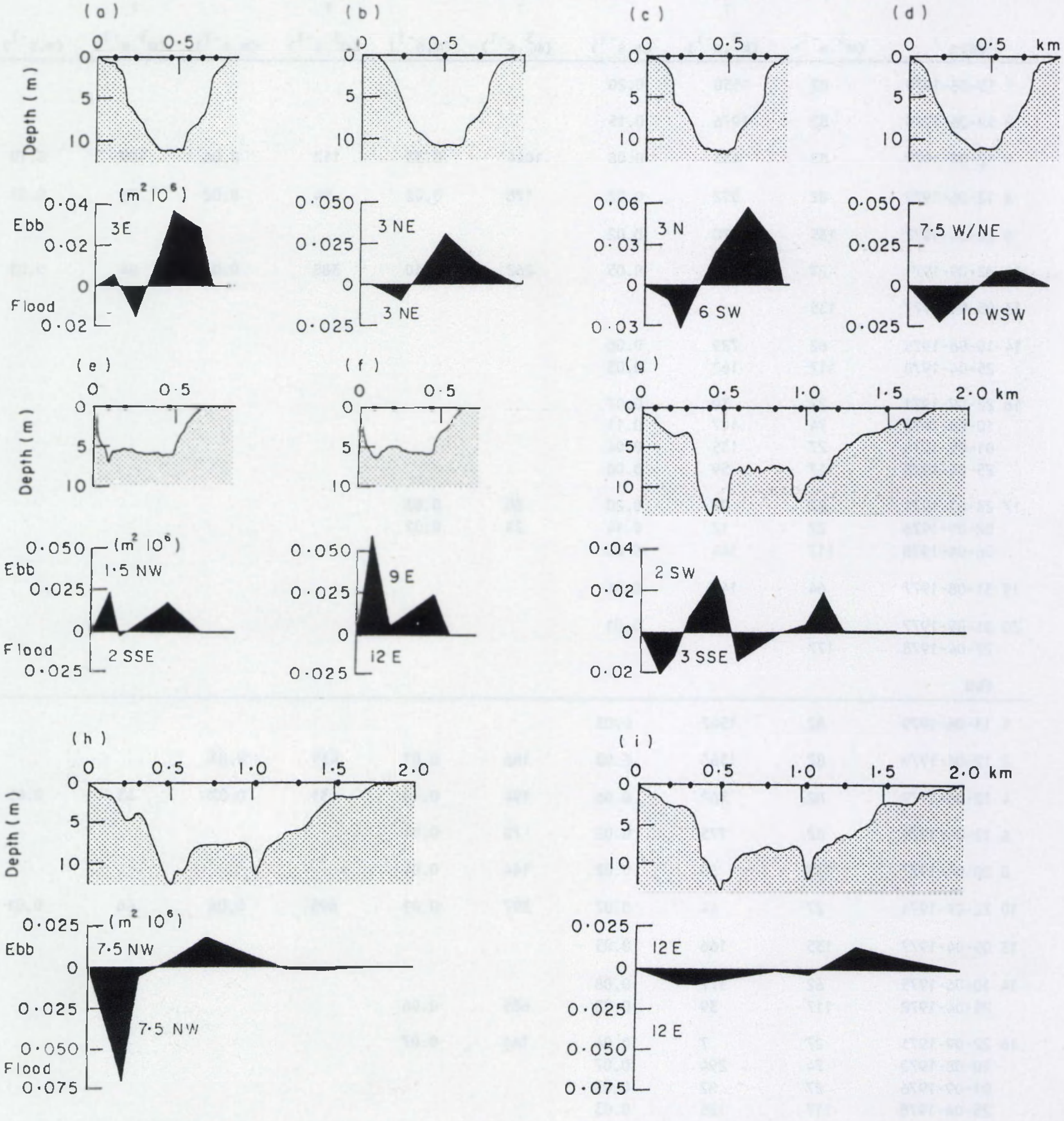

Fig. 8. Bathymetry and local flood-or ebb-directed residual water transports V (n) res at cross sections 16, 17 and 20 under different wind conditions. The dots in the cross section represent the stations where current velocity profiles were measured.
(a) Cross section 16 (22-09-71), (b) cross section 16 (25-04-78, (c) cross section 16 (10-08-72), (d) cross section 16 (01-09-76), (e) cross section 20 (01-09-77), (f) cross section 20 (27-04-78), (g) cross section 17 (23-09-71), (h) cross section 17 (02-09-76), (i) cross section 17 (26-04-78).

Residual currents

The mean residual mass transport velocities ($\bar{v}$(n)res) in Fig. 9 were used to calculate the distribution of the residual currents within the different channels of the estuary (for values see Table 3). The distribution of the residual mass transport velocities and knowledge of the large-scale distribution of residual cells in estuaries (Zimmerman, 1976; Ridderinkhof & Zimmerman, 1990) were used to indicate the distribution of residual eddies (see larger arrows in Fig. 9) and residual currents (small arrows). The distribution of the residual currents over the cross sections clearly shows the complexity of the horizontal distribution of the smaller and weaker residual cells in the channels of this estuary.

DISCUSSION

Water transport

Water transport in estuaries may vary as a result of several natural factors (Fisher *et al.*, 1979). Changes in water transport may be caused by changes in tidal range that occur at sea (Führböter, 1989), in the estuary as a result of dredging (de Jonge, 1983), and in the shallow Dutch Wadden Sea as a result of the closure of the former Zuiderzee (Thijsse, 1972) and sea level rise (Misdorp *et al.*, 1990).

The few available data for the 10-year period in Table 2 indicate that the water transport may have increased temporarily. Records of mean annual tidal range at the tidal inlet (Borkum) and at Emden (de Jonge, 1983) indicate that between 1970 and 1980, i.e. during the study period, the tidal range in the inlet increased by c. 12 cm and at Emden by c. 18 cm (Fig. 2). This value is much greater than the calculated mean annual increase of 0.4 cm which is based on Führböter's (1989) figures for coastal stations over a period of 50 to 80 years. The observed increase in tidal range in the inlet of the Ems estuary may have resulted in an increase of c. 5% in the tidal prism. Given the variation in these water transport measurements such an increase is hardly detectable under field conditions. The increase in tidal range near the entrance of the Dollard is responsible for an increase of c. 12% in water transport. This relative increase in water transport is also difficult to determine reliably in the field from only a few measurements. Thus, the expected effects of the increased tidal range on the water transport cannot yet be confirmed by field measurements, not even when older data on water transport (Anonymous, 1963) are added to the available data set. This certainly does not mean that the recorded changes in tidal range are insignificant. It has been shown (de Jonge, 1983) that changes in tidal range occur concomitantly with changes in the estuarine gradient of suspended matter. This was explained in terms of dredging intensity and in the extension of the dredged navigation route in the estuary. At present, it can only be hypothesized that the changes in tidal range have also triggered hydraulic changes. Comparison of the residual water transport and river discharge stresses the importance of the former factor in the estuarine transports. For the period 1970 - 1979 the mean monthly discharges of the River Ems varied between 23 and 382 $m^3\ s^{-1}$ whereas the residual water transport (Table 2) varied between 5.5 and 3754 $m^3\ s^{-1}$. Thus, the lowest river discharges and lowest observed residual transports differ by no more than a factor of 4, whereas the highest residual transports (V res) are ten times the maximum river discharge. Thus, these residual cells may represent an effective mechanism of water exchange within the estuary as well as between the estuary and the North Sea coastal zone (Zimmerman, 1986).

Residual currents

The shape and distribution of the large scale residual eddies near the tidal inlet (Fig. 9: larger arrows) and the very complicated pattern in the other estuary parts roughly agrees with the results of computer simulations of the distribution of tidally averaged residual transport velocities in the western Dutch Wadden Sea (Ridderinkhof, 1988) and the Ems estuary (Robaczewska, 1990). The large scale quadrupole-like eddies near the tidal inlet found under natural conditions (Fig. 9) also occur in the simulation models and apparently represent a very persistent phenomenon (cf. also Zimmerman, 1986).

Clear deviations are observed when the field results for cross sections 4, 5 and 6 are compared with the results of the computer simulations. The field measurements give no evidence of persistent clockwise macroscale circulations of residual water around the Möwesteert shoal (cf. Fig 1). Moreover, the small scale eddies within the Ranselgat channel were not indicated by the computer model, possibly because a relatively large (300 m) grid was used for the model calculations. The complicated small scale residual circulation above the Möwesteert is evident from both the field measurements and the simulation model. The residual circulation predicted by the model in the middle reaches (cross sections 10 to 15) of the Ems estuary agrees well with the field measurements. However, the residual circulation near cross sections

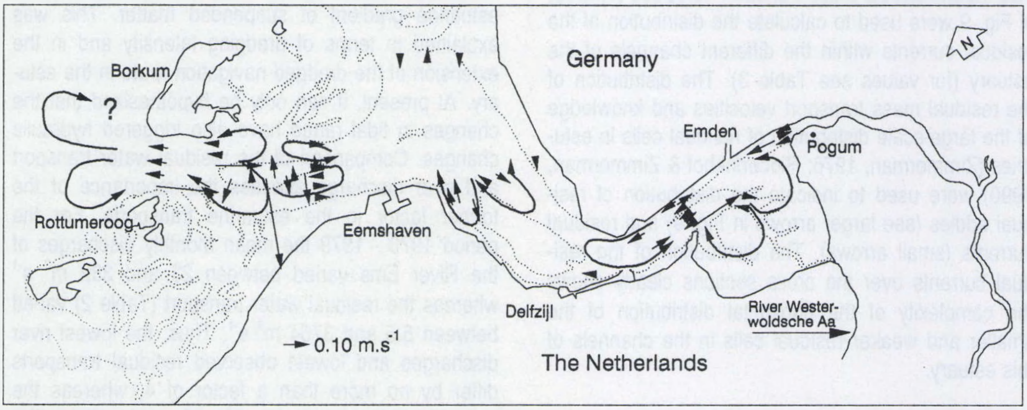

Fig. 9. Indication of the distribution of residual currents that represent part of the tidal residual cells in the estuary. Large arrows represent assumed large scale residual water circulation, small arrows represent location of flood or ebb directed mean residual mass transport velocities obtained from Eulerian measurements.

13 and 15 found in the field does not agree with the model predictions. Interestingly, the residual circulations in the Dollard and the lower reaches of the River Ems calculated from the field measurements do correspond very well with the model results.

The variability in form and number of the residual cells under certain conditions was clearly indicated in Fig. 8. Thus at certain locations and under certain conditions, the presence of the residual cells seems less persistent, as suggested by Fig. 9 and as stated above in the Results. One of these conditions is certainly caused by drift currents (cf. Fig. 8, cross section 17) where, for instance, a possible return current in the deeper parts of the channels is concealed by averaging values over depth (Dronkers & Zimmerman, 1982). The strongly fluctuating river discharges (23-382 $m^3 s^{-1}$) mentioned earlier might be another cause of variation in residual cells.

It is well known (Uncles & Jordan, 1979; Al-Ramadhan, 1988) that relative to the depth-averaged values used in the present study vertical variations can also occur in the tidally averaged residual mass transport values acting at the different depths. The possible effect of this vertical variation in values was not taken into account in the present study.

A study done by Uncles and Jordan (1980) has shown the Eulerian residual current velocity to be c. 0.05 $m s^{-1}$. This value holds for the middle reaches of the Severn estuary and was found to vary more than twofold over a spring - neap cycle. These figures suggest that the residual velocities presented here are no more than a fair indication of the actual velocities. The residual values presented by Uncles and Jordan (1980) are of the same order of magnitude (in the order of centimetres per second) as the values presented here. The mean residual velocities determined for the Bay of Fundy (Tee, 1976; Holloway, 1981) are also roughly in the range of the values presented in Table 3.

Residual currents and bathymetry

The basis for the large-scale interactions between currents and coastal morphology was given by van Veen (1936, 1937, 1938). He was one of the first to recognize the presence of ebb channels and flood channels in estuaries (van Veen, 1950), by their net water transport and their characteristic morphological features (cf. also van Straaten, 1960).

Comparison of the bathymetry and ebb and flood surpluses in Fig. 7 shows the similarity in the organization of ebb channels and flood channels and bathymetry between for instance the North Inlet estuary (Kjerve, 1978) and the Ems estuary. The shallower part of the channel (cf. cross sections 1, 2, 6 and 10) contains the flood-directed net current and the other part contains the ebb-directed net current. Interestingly, the two channels are separated by a shoal.

There is not only a relation between bathymetry and ebb and flood channels but also between bathymetry and tidal residual cells within individual channels. A nice relation between both characteristics can be observed, e.g. between the local bathymetry and the location of ebb or flood surpluses of cross sections 1, 2, 10 and 20 (Fig. 7). This is less clear for cross section 6 and the lowest reach of the small Bocht van

Watum channel (cross section 10, western part). The first examples are representative of the hydraulically stable parts of the estuarine system, whereas the second two (cross sections 6 and part of 10) are not. This can easily be deduced from the morphological development of the lower reaches during the last decades. The Oude Westereems (Fig. 1) channel used to be dredged and maintained as a navigation route, but since 1976 the other channel, the Ransel Gat, has been dredged and maintained as the main navigation route. Since that time the Oude Westereems channel has undergone drastic morphological changes which were still in progress in 1979 when the current measurements were carried out (cf. changes of morphology in this area, de Jonge, 1983, 1988). The Bocht van Watum channel has also been subject to natural continuous siltation for years, and to the dumping of harbour spoil, and hence the hydraulic situation there may be unstable. The reason for the natural local long-term siltation is unclear.

The distribution of tidal residual cells is not only reflected by the channel bathymetry but also by the sediment composition of the channel bed. An interesting relation between these two parameters can be deduced from data on grain size distribution published back in 1957 by Postma. As expected, the median grain size in the deeper parts of the channel was higher than in shallow parts. However, depth changes of only one or two metres in the deeper parts of a 10 m deep channel showed a significant shift in the median of the 100-200 µm grain size fraction. For the morphologically unstable outer delta of the Marsdiep tidal basin (western Dutch Wadden Sea) the grain size distribution did not correlate well with the channel bathymetry, but it did correlate well in several tidal channels within the tidal basin itself (Postma, 1957). The same may be true for the Ems estuary, where relatively unstable parts of the estuary can be distinguished from more stable parts by a "disharmonic" distribution of residual flows over the bathymetry. It is of interest to investigate the assumption adopted here that under stable conditions relative elevations in the channel bed correspond with the change between a flood residual and an ebb residual and a decrease in median grain size. Thus, in addition to integrating tidal and residual currents and morphology (cf. Zimmerman, 1981; Ridderinkhof, 1988, Ridderinkhof & Zimmerman 1990), research to elucidate the fine-scale processes of the formation and destruction of morphological structures by transport processes in the complex morphology of estuaries and tidal inland seas should also incorporate the study of grain size distribution. Hence the relation between the bathymetry, sediment composition of the channel bed and net currents deserves continuing attention (cf. Postma, 1950; Abraham *et al.*, 1987).

CONCLUSIONS

1. The Ems estuary has a tidal prism of c. 1 x10^9 m^3. It shows a large scale residual watercirculation in which the River Ems contributes c. 5 x 10^6 m^3 of advective water transport per tidal cycle. The residual water transport increases markedly in seaward direction up to values of 65 x10^6 m^3 per tidal cycle.
2. Available data on current velocity over the period 1970 to 1979 indicate that there are some large-scale residual cells within the Ems estuary. Six large cells are present near the tidal inlet, two cells are indicated in the middle reaches and one large cell seems to be present at the lower end of the River Ems. Within the Dollard there are two major cells that appear to be connected with the lower reaches of the River Ems proper. The presence of numerous smaller and weaker cells is also indicated.
3. The residual water transport during calm wind amounts to between 1% and 43% of the local tidal water transport and has an overall mean value of c. 11%. The residual currents range from 0.01 to 0.33 m s^{-1} with an overall mean value of 0.06 m s^{-1}.
4. Residual flood currents and ebb currents whose distribution over a cross section corresponds well with the local bathymetry, are hypothesized to indicate stable hydraulic conditions.

   Consequently, distributions of residuals that show poor correspondence with the local bathymetry indicate unstable hydraulic conditions. This implies a changing local morphology.

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RELATIONS BETWEEN ANNUAL DREDGING ACTIVITIES, SUSPENDED MATTER CONCENTRATIONS, AND THE DEVELOPMENT OF THE TIDAL REGIME IN THE EMS ESTUARY

V.N. de Jonge

ABSTRACT

This paper challenges Kühl and Mann's suggestion (1973) that an increase in organic matter in the Ems estuary between 1950 and 1970 caused a five- to tenfold increase in the turbidity in that period. Their hypothesis is refuted because: (a) during that period the discharge of organic matter via both the River Ems and the River Westerwoldsche Aa did not change significantly; (b) the increase in particulate organic carbon in the western Dutch Wadden Sea and possibly also in the Ems estuary resulting from eutrophication of the North Sea by the River Rhine during 1950-70 is unlikely to have been more than twofold; and (c) Secchi-disc data do not support the five- to tenfold increase in turbidity. It is suggested that dredging is probably responsible for the increase in turbidity because the volume of material dredged annually increased fourfold between 1950 and 1970. The mean annual concentration of suspended matter increased by a factor ranging from 1.3 to 2.1 between 1954 and the period 1970 to 1979. The fluctuations in concentrations of suspended matter showed a statistically significant correlation with the distance dredged annually and not with the volume dredged annually. This indicated that the relation depended more on how "extensive" rather than on how "intensive" the dredging was.

The fluctuations in concentrations of suspended matter are caused by the intensified erosion and sedimentation cycle that is initiated after the local natural equilibrium between channel morphology and current pattern is disturbed. This explanation is supported by the morphological changes that occurred in part of the study area between 1975 and 1979. Further support for this hypothesis was found in the changes of the tidal regime in the estuary. It is postulated that the complete cessation of dredging would probably be accompanied by the concentrations of suspended solids falling from the 1979 levels to values nearer those obtained in 1954. The biological implications of the processes described are discussed.

INTRODUCTION

The Wadden Sea in northwestern Europe is a shallow coastal sea separated from the North Sea by barrier islands. It is aproximately 600 km long and extends from north Denmark to the northwestern part of the Netherlands.

A number of rivers enter the North Sea via the Wadden Sea, one of them being the River Ems (Fig. 1) whose estuary forms the border between the Federal Republic of Germany and the Netherlands.

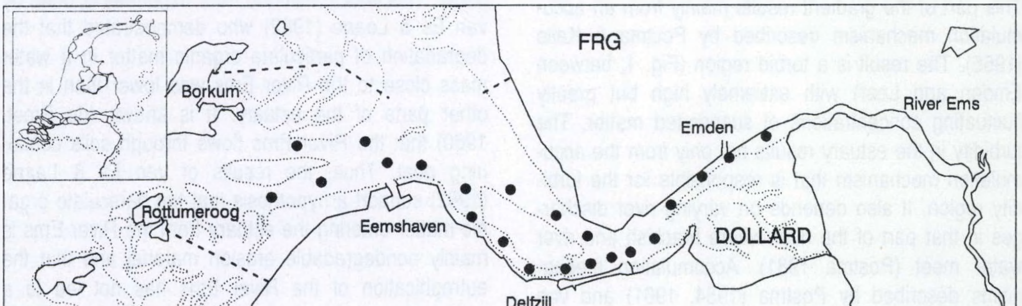

Fig. 1. Ems estuary showing sampling stations and the divides (---) between the estuary and other tidal basins of the Wadden Sea formed by high tidal flats. Dotted lines represent mean low water.

The estuary is approximately 100 km long and its area is approximately 600 x 10^6 m^2 (including the outer delta). The tide is semidiurnal with a diurnal inequality and the tidal prism in the inlet near Borkum is approximately 1250 x 10^6 m^3 over the flood or ebb, respectively. At the cross section near Knock (Fig. 1) the tidal prism is reduced to approximately 280 x 10^6 m^3. The mean tidal range near Borkum is 2.25 m and near Knock it is 2.87 m. In the estuary the gradient of suspended matter, and consequently of turbidity, rises steeply upstream of Knock (Fig. 2).

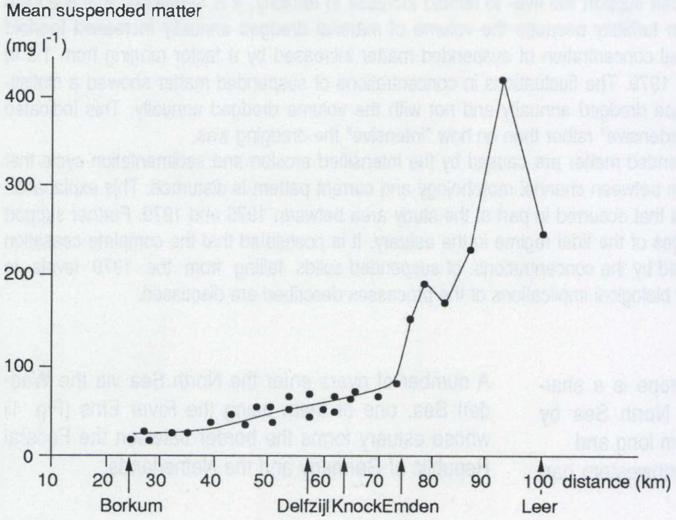

Fig. 2. Surface values of mean suspended matter for the Ems estuary between the barrier islands and the River Ems, excluding the Dollard.

This part of the gradient results mainly from an accumulation mechanism described by Postma & Kalle (1955). The result is a turbid region (Fig. 1, between Emden and Leer) with extremely high but greatly fluctuating concentrations of suspended matter. The turbidity in the estuary results not only from the accumulation mechanism that is responsible for the turbidity region. It also depends on varying river discharges in that part of the river where brackish and river water meet (Postma 1981). Accumulation mechanisms described by Postma (1954, 1961) and van Straaten & Kuenen (1957) also builds up a gradient in suspended matter between the deeper tidal inlet and the shallower water on the high tidal flats (Fig. 1). In this estuary, this gradient is well developed between the tidal inlet and the Dollard area (Fig. 1). It partly interferes with the gradient formed by the estuarine circulation. In the Dollard area the concentrations of suspended matter near the water surface reach high values ranging from 50 to 200 mg l^{-1}. Strong tidal and seasonal fluctuations also occur here. In 1973 Kühl & Mann reported a five- to tenfold increase in the turbidity of the Ems estuary between approximately 1950 and 1970, which they attributed to an increase in organic matter. They used a photometer to assess turbidity. i.e. they measured the combined values of the amounts of dissolved compounds and of inorganic and organic suspended materials. Consequently, changes in any of these components or combinations of components could be responsible for the observed increase in turbidity.

In this paper some processes that could have had particular influence on changing the concentrations of organic and/or inorganic suspended matter in the area will be briefly discussed. Extensive morphological changes can lead to a change in the salinity gradient and consequently to a change in the gradient of fine suspended matter(Postma, 1967). Bathymetric charts show that this did not occur between 1950 and 1970. Increased eutrophication of natural fresh waters such as the River Ems could also have led to an increase in the particulate organic carbon entering the estuary. However, the particulate organic carbon entering the Ems estuary seems to be barely degradable. This was concluded from experiments done by van Es & Laane (1982) who demonstrated that the degradation of particulate organic matter in a water mass close to the River Ems was lower than in the other parts of the estuary. It is known (de Smet, 1960) that the River Ems flows through soils containing peat. Thus, the results of van Es & Laane (1982) support a hypothesis that the particulate organic matter entering the estuary from the River Ems is mainly nondegradable erosion material and that the eutrophication of the River Ems has not led to a strong increase in the degradable particulate organic carbon. We can assume that the amount of the erosion material entering the Ems annually did not change between 1950 and 1970 because the Ems is a rainfed river and the land use of the river-basin did not change during that period.

An increase in eutrophication of the North Sea, and consequently an increase in the content of suspended organic carbon in the estuary, is possible. Although the organic matter content was not determined in the early 1950s, this parameter can be roughly estimated, enabling the recent situation in the Ems estuary to be compared with the recent and former situations in the western Dutch Wadden Sea. Data from the surface water collected by Manuels & Postma (1974) in 1970 and 1971 showed that the mean annual content of particulate organic carbon in the part of the estuary lying roughly between Borkum and the mouth of the River Ems (Fig. 1) was 2.2 mg l^{-1}. This was in the same order of magnitude as the mean value they calculated for the western Dutch Wadden Sea (1.5 mg l^{-1} particulate organic carbon). The difference in mean carbon content between the Ems estuary and the Wadden Sea may have been caused by the input of the barely degradable organic matter from the River Ems and the large discharge of organic matter in the southeastern part of the Dollard. The discharge in the Dollard is mainly from the potato-flour industry, and, to a lesser extent, strawboard factories as well as domestic sewage (de Wolf, 1978). On the basis of the phosphorus cycle in the eastern Dutch Wadden Sea, de Jonge & Postma (1974) calculated that between 1950 and 1970 the particulate organic carbon could have doubled. They attributed this development to an increasing eutrophication of the North Sea, mainly by the River Rhine, resulting in an increase in the transport of organic carbon from the North Sea into the Wadden Sea. The eutrophication of the North Sea may also have influenced the transport of particulate organic carbon to the Ems estuary during the same period. Consequently, it is feasible to attribute a doubling of the mean particulate organic carbon to an increased input of carbon into the Ems estuary. This increase, however, does not even roughly correspond with the increase in turbidity reported by Kühl & Mann (1973). Published (Anon., 1965) and unpublished data of the RIZA showed that the large annual waste water discharge of organic matter in the southeastern part of the Dollard did not change greatly between 1960 and the period 1970-79. Although no values are available for 1950, it is assumed here that the waste discharges also remained fairly constant between 1950 and 1960.

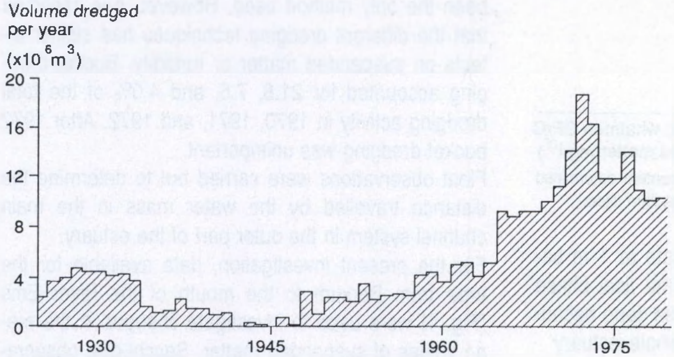

Fig. 3. Development of the combined German and Dutch dredging activities and sand extraction in the Ems estuary between 1925 and 1979.

Figure 3 shows the changes in total annual dredging activities, including sand extraction, carried out by The Netherlands and Germany in the Ems estuary. It can be seen that the total volume of removed and/or replaced sediment increased between 1950 and 1970 from approximately 2.3 to 9.2 x 10^6 m^3 per year. This is an approximately fourfold increase and therefore seems to be a likely explanation for the five- to tenfold increase in turbidity observed by Kühl & Mann (1973). The possibilities outlined above indicate that the turbidity changes observed by Kühl & Mann (1973) cannot merely be attributed to an increase in organic matter alone but might also have arisen from an increase in total suspended material resulting from dredging. The increase in turbidity reported by Kühl & Mann was, however, not supported by the increase in suspended matter calculated from data published by Manuels & Rommets (1972) and unpublished Secchi-disc data from NIOZ (Netherlands Institute for Sea Research). This inspired a new, detailed study on changes in turbidity and concentrations of total suspended matter in relation to dredging activities, the results of which are reported in this paper.

MATERIALS AND METHODS

Collection of data

The primary data used were the concentrations of suspended matter, turbidity (Secchi-disc visibility values) and chlorophyll-*a* concentrations, collected during 1975-79. In addition, concentrations of suspended matter reported by Manuels & Rommets (1972) for the period 1970-72 were used. Chlorophyll-*a* concentrations for 1972 were obtained from Cadée (NIOZ) who discussed standing stock and primary production of the estuary of the River Ems in Cadée

& Hegeman (1974). Unpublished Secchi-disc observations for the period 1970-72 were obtained from the NIOZ data file. Data on concentrations of suspended matter and chlorophyll-*a* concentrations for 1954 were obtained from Postma (1960), and data on Secchi-disc visibilities for 1954 and 1956 were obtained from Dorrestein (1960).

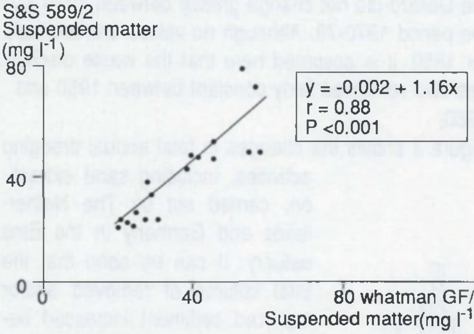

Fig. 4. Comparison of the suspended matter content determined using S&S 589/2 filters and Whatman GF/C glass fibre filters.

Samples were usually taken in duplicate at 1 m below the water surface irrespective of the tidal phase or spring tide - neap tide cycle. This was done because it was impossible to sample the whole estuary between Leer and Borkum (Fig. 1) at the same tidal phase. No data from surveys carried out during high wind were used for this study. Some high values (outliers) for suspended matter resulting from resuspension of sand from the bottom of the channels were omitted.

The authorities in The Netherlands (Rijkswaterstaat, Delfzijl) and the Federal Republic of Germany (Wasser und Schiffahrtsamt, Emden) provided values on mean annual tidal ranges for the period 1960-80. The Rijkswaterstaat supplied bathymetric data for the outer part of the estuary of the River Ems and data on changes in time lag between high water and slack high water. Data on dredging activities and sand extraction were obtained from the Rijkswaterstaat and the Wasser- und Schiffahrtsamt. Over the years the technique of dredging has changed. Before 1960 all dredging was done by a bucket dredge. In 1965 suction dredging was introduced and since 1973 has been the only method used. However, it is assumed that the different dredging techniques had similar effects on suspended matter or turbidity. Bucket dredging accounted for 21.8, 7.5, and 4.0% of the total dredging activity in 1970, 1971, and 1972. After 1972 bucket dredging was unimportant.

Float observations were carried out to determine the distance travelled by the water mass in the main channel system in the outer part of the estuary.

For the present investigation, data available for the area from Borkum to the mouth of the River Ems (Fig. 1) were used to investigate changes in the mean values of suspended matter, Secchi-disc observations and concentrations of chlorophyll-*a*. The choice of this area was primarily based on the geographical distribution of available data. Furthermore, the values for suspended matter in the Dollard and in the Ems are very high and variable because of the influence of the accumulation mechanisms described in the introduction. Moreover, these areas lay outside the region that had been dredged.

Table 1. Mean annual content of suspended matter in the Ems estuary between the barrier islands and the River Ems.

	Suspended matter (mg.l^{-1})	Data available for following quarters	Total number of stations	Total no. of observations	Correlation coefficient (r)	Significance level (P) using correlation test[b]
1954	45.8[a]	3	9	16	0.69	0.06
1970	61.3[a]	3, 4	9	29	0.92	0.02
1971	60.4	1-4	11	104		
1972	90.4[a]	1-3	11	51	0.83	0.01
1975	58.2	1-4	21	178		
1976	57.6	1-4	19	140		
1977	68.3[a]	3, 4	15	57	0.92	0.02
1978	96.6	1-4	10	50		
1979	76.5	1-4	13	90		

[a] mean annual content estimated by regression analysis.

[b] Correlation test was only applied to the data from which some annual means were estimated

Analytical Procedures

Concentrations of suspended matter were determined gravimetrically using Whatman GF/C glass fibre filters. In 1954, suspended matter was determined using S&S 589/2 paper filters (Postma 1960). Therefore, a comparison between these filters was made for the suspended matter retained.

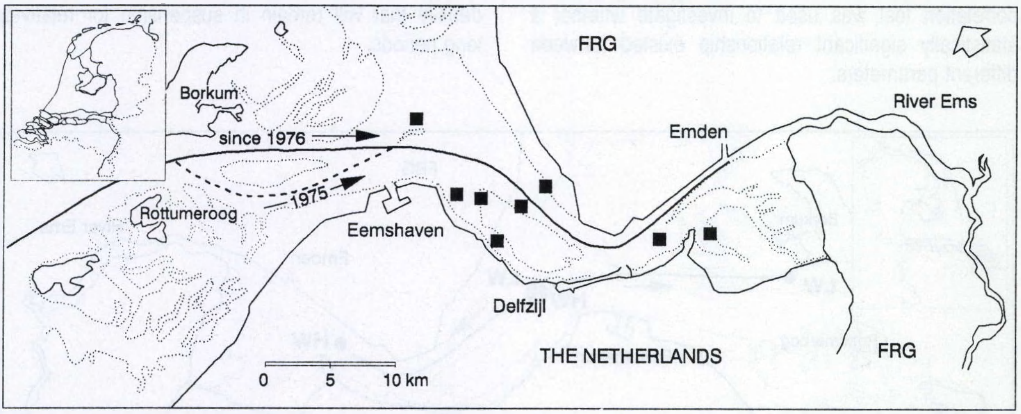

Fig. 5. The navigation route dredged until 1975 and from 1976 to the present. Locations of spoil (mainly sand) dumps are indicated.

Figure 4 shows that only a slight difference exists between both series of observations.

The results show that the S&S 589/2 filters used in 1954 gave, on average, a 13% higher dry weight than the Whatman GF/C filters that were used subsequently. This relatively slight difference was not taken into account in the calculations, because the annual mean for 1954 given in Table 1 was an estimate obtained by calculations using a linear regression equation. Secchi-disc visibilities were obtained using a 30 cm diameter white disc. Chlorophyll-*a* content was determined according to the method described in Lorenzen (1967). The volumes dredged were calculated to be the net volume of wet sediment transported by the ships. Dredged distances were expressed per annum and calculated to be the total length of the main channel where any operation (dredging or sand extraction) was carried out, irrespective of the depth to which or the breadth over which sediment was removed. The fine-grained sediment obtained from the area between Knock and Emden (Fig. 1) was usually brought on land while most of the coarse-grained sediment was either deposited at one of the localities indicated in Fig. 5 or, if it was derived from sand mining, was also brought on land. Only small amounts of dredged material were dumped at the localities indicated on Fig. 5. Usually, the dredging along the navigation route (Fig. 5) was done round the clock. The sand mining involved different numbers of ships at different localities. The mean annual content of suspended matter in the study area was calculated by averaging the annual station means.

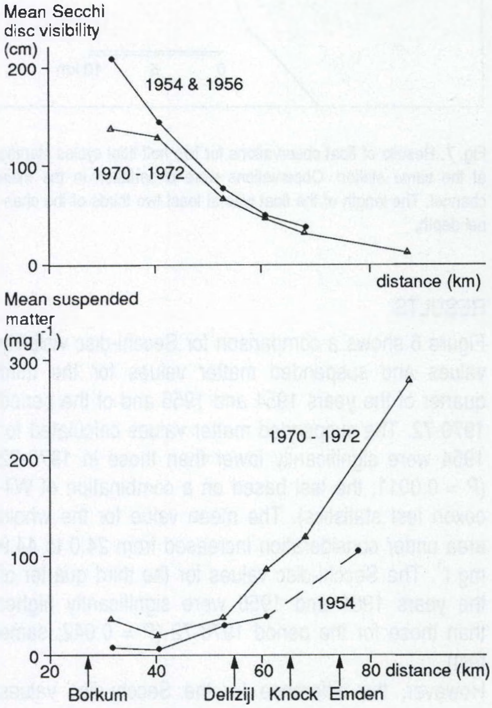

Fig. 6. Comparison between 1954 and 1970-72 for the mean concentrations of suspended matter and between 1954 and 1956 and 1970-72 for the mean Secchi-disc visibilities.

For sampling surveys that had been carried out over less than four quarters per year, the annual area mean was estimated using linear regression analysis. A correlation test was used to ascertain statistical significance. A test based on a linear combination of Wilcoxon test statistics (van Elteren, 1960) was applied to compare changes in the suspended matter and Secchi-disc visibilities for the third quarter of the year, based on the combined 1954 and 1956 data and on the combined 1970-72 data. Spearman's rank correlation test was used to investigate whether a statistically significant relationship existed between different parameters.

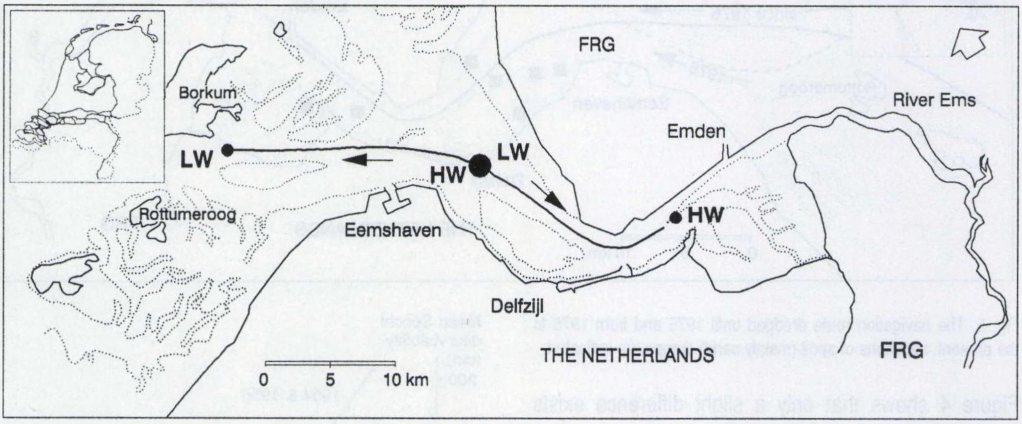

Fig. 7. Results of float observations for two half tidal cycles starting at the same station. Observations were undertaken in the main channel. The length of the float was at least two thirds of the channel depth.

RESULTS

Figure 6 shows a comparison for Secchi-disc visibility values and suspended matter values for the third quarter of the years 1954 and 1956 and of the period 1970-72. The suspended matter values calculated for 1954 were significantly lower than those in 1970-72 ($P = 0.0011$; the test based on a combination of Wilcoxon test statistics). The mean value for the whole area under consideration increased from 24.0 to 44.9 mg l^{-1}. The Secchi-disc values for the third quarter of the years 1954 and 1956 were significantly higher than those for the period 1970-72 ($P = 0.042$; same test).

However, the difference for the Secchi-disc values was less significant than for suspended matter, because of a smaller decrease in mean value (from 101 to 83 cm). Note that for both parameters, the values in the outer region deteriorated relatively sharply (Fig. 6). Results of float experiments undertaken in the outer region of the estuary are presented in Fig. 7. If dredging at a certain site increases the concentrations of suspended matter, then this effect should be spread out by tidal water movements over a long distance in the main channel.

Such an effect should, of course, only be seen from the fine material and/or suspended material of low density that will remain in suspension for relatively long periods.

The float observations indicated that the maximum distance over which effects should be measurable was approximately 35 km within one full tidal cycle, i.e. approximately 75% of the area under consideration.

Table 1 gives the results of the mean values for suspended matter per annum. The asterisked annual values were estimated using regression analysis between annual mean values and means calculated for single quarters or combinations of quarters.

Figure 8 gives the relation between volume dredged per year including sand extraction and the mean suspended matter values for the area under consideration. It can be concluded that the mean content of suspended matter increased after 1954 and fluctuated clearly from year to year. These fluctuations were not similar to the fluctuations in dredging operations. The same picture was obtained if spoil (mainly sand) partly dumped into the estuary was also taken into account. The Spearman rank correlation test carried out on the values given in Fig. 8 showed that the rank correlation coefficient between volume dredged

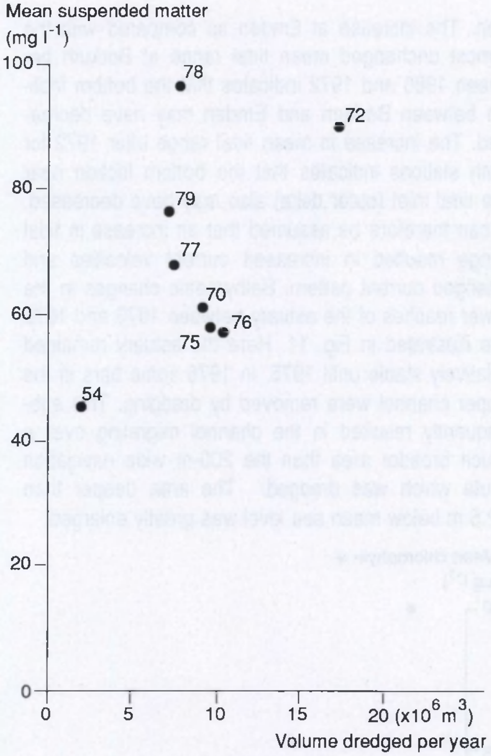

Fig. 8. Relation between volume dredged per year (including sand extraction) and mean annual concentrations of suspended matter.

and mean suspended matter concentrations was low (r = 0.08) and statistically not significant (P > 0.10). Figure 9 gives the relation between the total distance dredged and the mean values for suspended matter. The total distance dredged represents approximately the total length of bars removed and widened or deepened channels. Here, a consistent picture emerges. Depending on a dredging distance that increased from 8 km in 1954 to approximately 53 km in 1972 and 1978, suspended matter increased from approximately 45 to 95 mg l^{-1}. However, after 1975 the values seem to show a somewhat different relationship than those for the period 1954-75. A Spearman's rank correlation test using all the annual values resulted in a high (r = 0.83) rank correlation coefficient between distance dredged and mean suspended matter concentrations, which was statistically significant (P = 0.01). To ascertain why the relationship between distance and suspended matter provided a better correlation than the relationship between volume dredged and suspended matter, changes in tidal characteristics were examined near Borkum, Knock, and Emden (Fig. 1) for the period 1960-80. It was found (Fig. 10) that the time lag between high

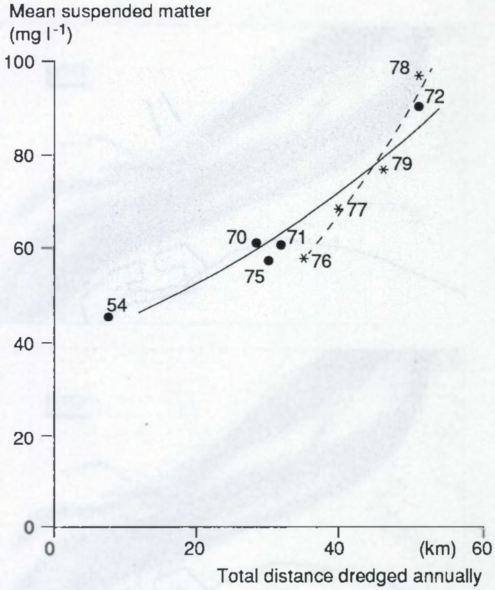

Fig. 9. Relation between total length of bars removed and channels widened or deepened and mean annual concentrations of suspended matter.

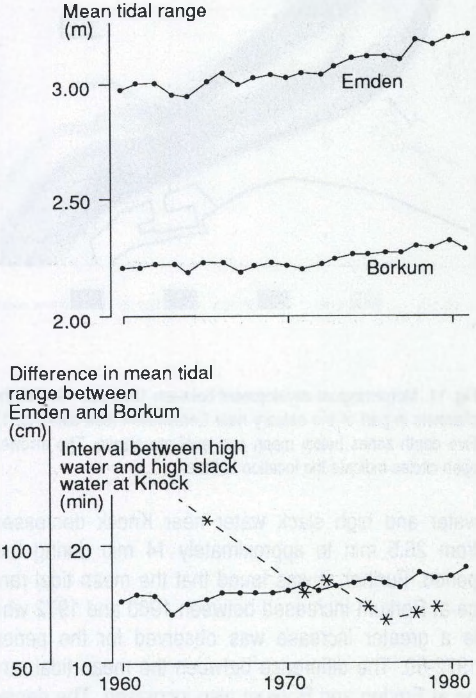

Fig. 10. Changes in time lag between high water and high slack water (asterisk), mean annual tidal ranges and difference between mean annual tidal ranges for stations Emden and Borkum for the time period 1960-80.

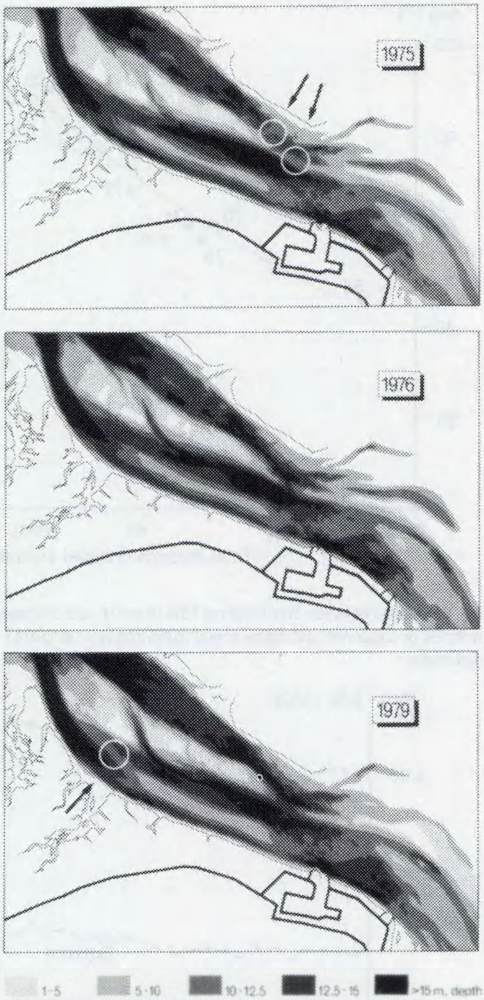

Fig. 11. Morphological development between 1970 and 1979 of the channels in part of the estuary near Eemshaven (see also Fig. 1). Five depth zones below mean sea level are shown. The arrowed open circles indicate the location of bars.

water and high slack water near Knock decreased from 25.5 min to approximately 14 min during this period. Further, it was found that the mean tidal range at Borkum increased between 1960 and 1972 while a greater increase was observed for the period 1972-80. The difference between the mean tidal range at Emden and Borkum also increased. The decrease in time lag between 1960 and 1980 indicates that the bottom friction within the estuary decreased progressively during that period. This is confirmed by the increases in mean tidal ranges near Borkum and Emden. The increase at Emden as compared with the almost unchanged mean tidal range at Borkum between 1960 and 1972 indicates that the bottom friction between Borkum and Emden may have decreased. The increase in mean tidal range after 1972 for both stations indicates that the bottom friction near the tidal inlet (outer delta) also may have decreased. It can therefore be assumed that an increase in tidal range resulted in increased current velocities and changed current pattern. Bathymetric changes in the lower reaches of the estuary between 1970 and 1979 are illustrated in Fig. 11. Here the estuary remained relatively stable until 1975. In 1976 some bars in the upper channel were removed by dredging. This subsequently resulted in the channel migrating over a much broader area than the 200-m wide navigation route which was dredged. The area deeper than 12.5 m below mean sea level was greatly enlarged.

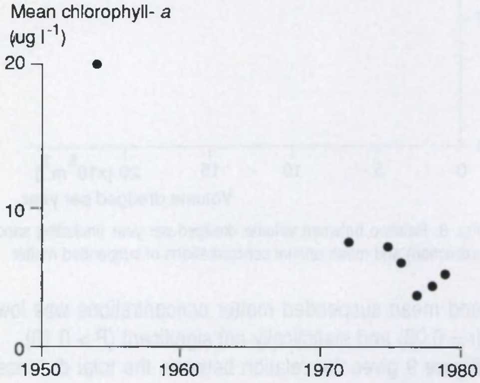

Fig. 12. Mean concentrations of chlorophyll-*a* in the study area in the third quarter of certain years.

The changes in phytoplankton standing stock expressed as chlorophyll-*a* concentrations over the study period are given in Fig. 12. For 1954 data were only available for the third quarter. Therefore, phytoplankton standing stock is represented per year for only the third quarter. The chlorophyll-*a* values declined between 1954 and 1972. Furthermore, there seems to be a continuing decline in chlorophyll-*a* for the period 1972 to 1979. However, no clear relationship could be found between suspended matter and chlorophyll-*a*.

DISCUSSION

Turbidity

The reasons for challenging Kühl & Mann's (1973) assertion that the five- to tenfold increase in turbidity in the estuary of the River Ems between 1950 and

1970 was due to an increase in organic matter and for proposing that dredging was more likely to have been responsible for these changes were stated in the introduction. They were that: (a) the increase in transport of particulate organic carbon from the North Sea to the estuary of the River Ems during the period would be unlikely to have been more than twofold, (b) the discharge of organic matter via both the River Ems and the River Westerwoldsche Aa did not change significantly, (c) Secchi-disc data did not support the five- to tenfold increase in turbidity, and (d) the annual volume of material dredged increased fourfold between 1950 and 1970.

The statistical analyses of levels of suspended matter and degree of turbidity (Secchi-disc visibility values) between the years 1954 and 1956 and the period 1970-72 showed that both parameters differed significantly over the time periods reviewed. However, the mean increase in the suspended matter in certain stretches of the estuary (Fig. 6) ranged from 120 to 590% and the decrease in Secchi-disc values ranged from 8.3 to 31.5%. The increase in turbidity reported by Kühl & Mann (1973) for approximately the same period was not of the same magnitude. To ascertain that this discrepancy was not caused by differences in the method of calculation, I used the original data collected by Kühl & Mann (1954, 1972) in 1951-53 and 1968-70 to recalculate the turbidity in the part of the Ems estuary I studied using the procedure described in Materials and Methods. I found a fivefold increase in turbidity for the period 1950-70. Although Kühl & Mann's reported increase in turbidity seems reasonable, it is not in accordance with the 20% decrease of the light penetration calculated using the Secchi-disc data (Fig. 6). These differences cannot satisfactorily be explained: although the methods used were different, it is unlikely that this led to the observed discrepancy. The most probable reason could be the limited number of surveys carried out by Kühl & Mann (1973), mainly in one season.

The five- to tenfold increase in turbidity found by Kühl & Mann (1973) also disagrees with the increase in suspended matter (1.3 - 2.1 times higher) found in the present study. Because the dry weight content of the suspended material can be determined more accurately than the Secchi-disc values, only the former will be considered in discussing the mechanism thought to be responsible for increases in suspended matter (turbidity).

In the introduction it was suggested that the changes in dredging activities, including sand extraction, could be responsible for the observed temporal changes in the suspended matter content. However, Postma (1981) showed that a good inverse correlation was present between the mean monthly river discharges of the Ems and the maximum values of concentrations of suspended matter in the turbid zone. This suggested that, for the present, a relationship between river discharge and concentrations of suspended matter in the more seaward part of the estuary should not be overruled. Although not reported here, statistical analysis of the available data sets for the period 1954-79 showed no significant relationship between both parameters and consequently did not show that river discharges also influenced concentrations of suspended matter in the more seaward parts of the estuary.

Dredging

Much effort was spent to obtain a detailed picture of the possible relation between changes in concentrations of suspended matter and dredging activity. The estuary was divided into seven sections and possible relations between mean annual suspended matter, volumes dredged, spoil disposed, and distance dredged were investigated. This was done per section and per combination of sections. Not all these attempts shed new light on the relation between dredging and suspended material.

Windom (1976) reviewed the effects of dredging on turbidity and concluded that they have temporal and spatial restrictions. The total annual dredging activity in the estuary of the River Ems, about 17.6 x 10^6 m^3, is high compared with, for example, the total activity in the USA (approximately 300 x 10^6 m^3 a^{-1}; Windom 1976), particularly considering that the part of the Ems that is dredged is only 0.2% of the total length of waterways maintained by dredging in the USA (approximately 35000 km). Although the dredging expressed in m^3 in the estuary of the River Ems is relatively intensive, its effects can be restricted, as discussed by Windom (1976).

The float observations described earlier indicated that an increase in suspended material resulting from dredging operations should be measurable over a long distance. Baretta *et al.* (1980) showed that an increase in suspended matter content resulting from spoil dumping was only measurable over a distance of a few kilometres. But if dredging is carried out at one site for a longer time period, which is usually the case, then a cumulative increase in suspended matter concentrations cannot be dismissed. Various processes could have influenced the suspended matter content: the possible positive contribution of dredging on concentrations of suspended matter; the long distance travelled by the water mass; the unknown magnitude of the interaction between the increase in suspended matter brought about by dredging and the decrease caused by the suspended matter accumulation mechanisms described; and the continuous dredging operations varying in intensity from place to place. In view of this, and the limited number of observations available, a less detailed comparison of the available data was undertaken. The most realistic approach seemed to be to compare data obtained over longer time periods and over relatively long distances, to ascertain the relation between changes in the concentrations of suspended matter and dredging activity. The mean concentrations of suspended matter, total annual distances dredged, and total annual volumes dredged were calculated as described in Materials and Methods. A Spearman rank correlation test on the data for annual suspended matter and dredging (Figs. 8 and 9) confirmed my supposition: the rank correlation coefficient between the mean annual concentrations of suspended matter and the annual volumes dredged was low and statistically not significant, whereas the rank correlation coefficient between the mean annual concentrations of suspended matter and the total annual distance dredged was high and statistically significant.

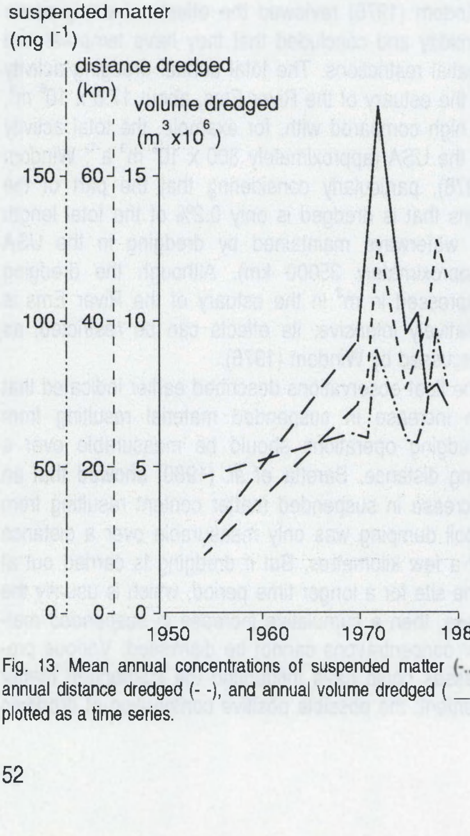

Fig. 13. Mean annual concentrations of suspended matter (-..-), annual distance dredged (- -), and annual volume dredged (__), plotted as a time series.

To interpret these results, the values given in Figs. 8 and 9 were replotted as a time series (Fig. 13). It is clear that the mean annual concentrations of suspended matter for the 45 km long channel between Borkum and Emden were more dependent on the length of the channel dredged than on the volume of material removed, i.e. on how "extensive" rather than on how "intensive" the dredging was. For the time period 1970-75 both dredging parameters (volume and distance) clearly varied concomitantly, while after 1975 only suspended matter varied concomitantly with distance dredged. The transition between both time periods coincided with the dredging of another channel near the tidal inlet in 1976 as before (Fig. 5). This suggested that dredging activity influenced concentrations of suspended matter mainly indirectly by disturbing the equilibrium between morphology and current pattern when sediment is removed, and that the longer the distance over which sediment was removed the greater this disturbance. This explanation also satisfies the contention (Windom, 1976; Baretta *et al.*, 1980) that the direct effects of spoil dumping on suspended matter are usually restricted. The relation between suspended matter and distance dredged seems to be different for the time period 1970-75 as compared with the subsequent period (Fig. 9). It seems that after 1975, the estuary was more sensitive to dredging operations than before that year. This observed difference in trend is not unexpected, because different estuarine channels were modified over both periods. The relation between distance dredged and suspended matter became more evident when only the mean annual suspended matter content was plotted against the distance of channel improvements in the outer estuary (seaward of Eemshaven, Fig. 1) (Fig. 14). This suggests that channel modifications near the tidal inlet of the estuary were especially important in determining the levels of suspended matter over the whole estuary.

The hypothesis that dredging activity influences the estuarine sediment cycle by disturbing the existing equilibrium between morphology and current pattern and that operations near the tidal inlet have a particularly strong influence on the whole suspended matter gradient between Borkum and Emden, can be supported by the changes observed in certain tidal characteristics (Fig. 10). The progressive change in tidal propagation (i.e. diminishing of the bottom friction within the system) that accompanied dredging in the 1960s-76 is demonstrated by the decrease in the time lag between high water and slack high water. It is interesting that this change in time lag is related to the increase in the channel length that was dredged. Between 1960 and 1968 the area between Eemshaven and the island of Borkum (Fig. 1) was modified, and after 1968 the Huibertgat channel between the island of Borkum and the North Sea was also included in the area modified to meet changing navigational requirements. In 1976, another estuarine channel was dredged, possibly resulting in minimal bottom friction and consequently a minimal time lag (Fig. 10), maybe because no natural bars were present in either the southern or northern estuarine channels in the outer part of the estuary (Fig. 11, 1976). The slightly increased time lag after 1976 could have resulted from a readjustment of the morphology of the channel bed in the southern channel.

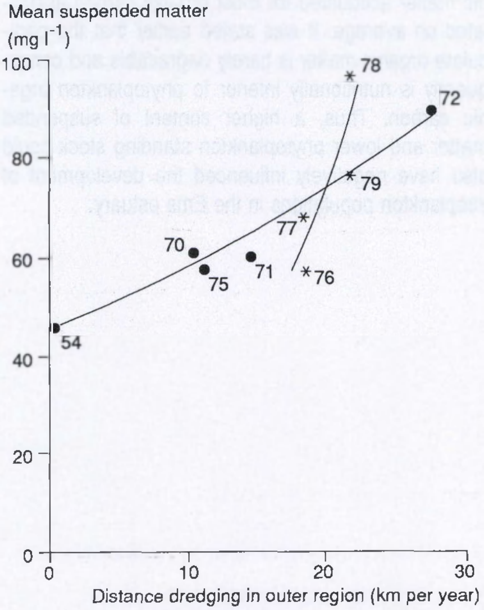

Fig. 14. Relation between length of bars removed and channels widened of deepened seaward from Eemshaven and the mean annual concentrations of suspended matter for the whole study area.

The progressive change in tidal propagation is also apparent from the development of the mean tidal ranges between 1960 and 1980 near Borkum and Emden (Fig. 10). The tidal ranges near Borkum remained virtually constant between 1960 and 1972. After that year, a clear increase was observed. The development of the tidal ranges near Emden was different from that of Borkum: between 1960 and 1972 a slight increase in the mean tidal range was calculated, probably mainly the result of the extension of dredging activities between Eemshaven and Borkum. After 1972 the tidal ranges near Emden increased further, but more in accordance with the changes in the tidal ranges near Borkum. This was probably mainly the result of the further improvements made to the Huibertgat navigation route seaward from Borkum. Because the tidal ranges near Emden are a complex function of those near Borkum, the increase near Emden was more pronounced than that near Borkum. The differences in tidal propagation and tidal range may also have resulted in changes in the complex current patterns (Zimmerman, 1976) within the estuarine channels. Thus, after the channels were deepened, there was a decrease in the bottom friction and an increase in the tidal propagation, a shortening of the time lag between high water and slack high water, an increase in tidal range and, consequently, increased current velocities with new local current patterns. This means that the bed is continuously adjusting to the new regime. For this to happen erosion must occur elsewhere and an increase in fine suspended sediment would be expected as a result of sorting (because coarse-grained material will mainly settle in the channels whereas fine sediment remains in suspension for a longer time). This supposition is confirmed by the morphological development of the area near Eemshaven between 1975 and 1979. The morphology of the area between Borkum and Eemshaven remained relatively stationary between 1965 and 1975 (Fig. 11; 1975). After 1976, when a new channel was adapted to navigation requirements, the initial channel improvements (Fig. 11; 1976 arrows) within the navigation route led to much greater changes in the total channel morphology (note the changes in the - 12.5 m isobath). This strongly suggests the interference of local changes in channel morphology and changes in current patterns, leading to an intensified cycle of erosion and sedimentation followed by a further widening of the main channels (Fig. 11; 1979) until a new bed equilibrium has been reached. A complicating factor is that after 1976 (Fig. 10; 1979 arrow), the bed levels in the southern formerly dredged channel readjusted. This could also have had a positive influence on the concentrations of suspended matter (see high 1978 values in Figs. 9 and 14). However, the reasonable correspondence between distance dredged (Figs. 9 and 14) and mean suspended matter suggests that the increase in suspended matter was mainly caused by the improvements carried out annually in the northern channel and not by the relatively slow readjustment of the southern channel over the period 1975-79 (Fig. 11). The morphological development clearly confirms that readjustment occurs. Therefore, it would not be unreasonable to postulate from this that, all things being equal, the complete cessation of dredging and sand-mining would probably be accompanied by the concentrations of suspended matter falling to values nearer those in 1954 than those measured in 1979.

Productivity

Unfortunately, no values for primary production were available for 1954. However, it is clear that the decrease in chlorophyll-*a* values between 1954 and 1972-79 (Fig. 12) is of approximately the same order of magnitude as the increase in suspended matter (Table 1). Because chlorophyll-*a* is the most important photo pigment this must also have led to a decrease in primary production. This means less food for the total ecosystem. This conclusion seems to be of importance, because van Es & Laane (1982) have shown by experiments that only a small part of the particulate organic matter is degradable within one month. This clearly indicates that the organic matter from the North Sea is of relatively low nutritional quality. However, it is not certain that the chlorophyll-*a* decrease was entirely caused by the increase in mean concentrations of suspended matter and that turbidity increased as a result: this can be demonstrated by the fact that the chlorophyll-*a* values did not vary inversely with dredging activities or concentrations of suspended matter. Furthermore, it is well known that the chlorophyll-*a* concentrations are not solely determined by the light regime but reflect a number of factors (de Jonge, 1980).

The increase in suspended matter and decrease in algal standing stock has consequences for the fauna. From transplantation experiments, Vrins (1978) concluded that in the Ems estuary the bivalve *Cerastoderma edule* grows poorly compared with specimens taken to the western Dutch Wadden Sea. She attributed this to the lower organic carbon content of the suspended matter in the Ems estuary as compared with the reference station in the western Wadden Sea. However, her determinations of the particulate organic carbon content in the Ems estuary and in the western Dutch Wadden Sea were based on relatively few observations. In the introduction, it was indicated that during 1970-71 the content of particulate organic carbon in the Ems estuary was somewhat higher than that in the Wadden Sea area, partly because of the peaty soils through which the Ems flows. As a result, the organic matter in the Ems estuary mineralizes very slowly. It is not unlikely that bivalves are unable to use the remains of phanerogams because even freshly prepared detritus derived from *Spartina foliosa* and *Salicornia viriginica* appear to have low food value for *Mytilus edulis* (Williams 1981). Thus, it seems that the unselective suspension feeders must invest so much energy in filtering large quantities of suspended matter that they cannot grow very well in the more inner parts of the estuary. Today these populations must filter approximately four times as much suspended matter as in 1954 to obtain the same amount of usable organic carbon, e.g. in the form of phytoplankton and phytobenthos (compare Table 1 and Fig. 12).

Chervin *et al.* (1981) maintained that copepod production was directly dependent on the assimilation of phytoplankton, even though nonphytoplankton organic matter accounted for most organic carbon assimilated on average. It was stated earlier that the particulate organic matter is barely degradable and consequently is nutritionally inferior to phytoplankton organic carbon. Thus, a higher content of suspended matter and lower phytoplankton standing stock could also have negatively influenced the development of zooplankton populations in the Ems estuary.

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3. BIOLOGY

QUANTITATIVE SEPARATION OF BENTHIC DIATOMS FROM SEDIMENTS USING DENSITY GRADIENT CENTRIFUGATION IN THE COLLOIDAL SILICA LUDOX-TM

V.N. de Jonge

ABSTRACT

A quantitative density separation method for benthic diatoms is described in detail. Both epipelic and epipsammic diatoms have been separated from inorganic sediment components including empty diatom frustules. The method is based on differences in specific weight, using medium speed centrifugation on a step gradient of the colloidal silica Ludox-TM. Results obtained with this new method have been compared with those obtained by the lens tissue method. For the density method, applied to samples preserved with a mixture of acrolein, glutaraldehyde and tannic acid, a mean recovery of 82.3% chlorophyll-*a* was found. In the lens tissue harvest experiments, mean chlorophyll-*a* harvests ranged from 29.1 to 53.2%. Moreover, the standard deviation was several times larger for the lens tissue harvest experiments than for the acrolein series processed by the density method. With the density method, sand fractions were removed entirely, while the clay fractions were removed almost completely. The remaining organic carbon (detritus), with a mean value of 42.3% of the original sample, does not interfere with diatom identification and counting, since all organic matter can be fully oxidized. The density method was found to be applicable to widely different kinds of estuarine sediment and varying quantities of benthic diatom biomass present in the samples. The method can also be used for some other algal groups such as Euglenophyceae and Cyanophyceae.

INTRODUCTION

Until recently, ecological investigations on benthic diatom populations living on the unstable sediments of tidal flats have posed great problems. Direct quantitative microscopic observations on the amount of sediment suspended in water are almost impossible, as sediment components hamper the detection of organisms on and between the sediment particles. Therefore, quantitative isolation of benthic diatoms from their inorganic substrates seemed desirable.

Reinicke (1858) developed a trap technique to harvest positively phototactic benthic diatoms on fabric. Williams (1963), however, demonstrated that only about 50% of the sediment-inhabiting diatom populations could be harvested in this way. Eaton & Moss (1966) improved the method by the introduction of Green's Grade 105 lens tissue instead of fabric. They established that nearly 90% of the total epipelic diatom fraction could be harvested by the lens tissue method. However, in the present study, for intertidal sediments the yield of harvesting with this method was usually low and very variable.

Bowen *et al.* (1972) introduced density gradient centrifugation by Ludox-AM to marine research. Price *et al.* (1974) studied differences in specific weight of some planktonic algae and determined the recovery of density centrifugation using Ludox-AM in a zonal rotor. Onge & Price (1975) added organic and inorganic compounds to silica gradients with the aim of influencing banding densities of different zooplankton organisms. Price *et al.* (1977) showed that automatic sorting of some groups of net zooplankton is possible by isopycnic sedimentation in silica gradients.

For all the above mentioned studies based on the use of density gradients for sorting of plankton organisms, samples were used which contained no or only a little detritus and inorganic sediment. Yet all authors suggested that the technique would be more widely applicable. However, they did not apply the method to raw field samples containing a great amount of detritus and inorganic sediment and only a relatively low content of organisms. The suitability of Ludox-TM for the quantitative isolation of meiobenthic organisms from various sediments has already been demonstrated by de Jonge & Bouwman (1977). New experiments with Ludox-TM showed that benthic diatoms have a relatively high density. The density range however is restricted.

In the present paper, based on these initial results, a new method is presented for the separation of benthic diatoms from inorganic sediment, empty diatom frustules and from a large part of the organic detritus. The method is based on density gradient centrifugation in Ludox-TM.

The method will be described in detail because small deviations in the procedure can greatly influence the results.

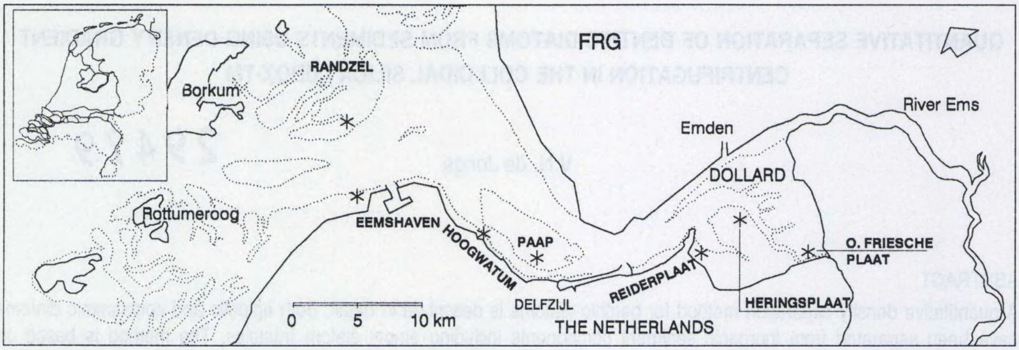


Fig. 1. Map of Ems estuary, with sampling stations Randzel, Eemshaven, Hoogwatum, Paap, Reiderplaat, Heringsplaat and Oost Friesche Plaat. Dotted line refer to mean low water.

The results of the method will be compared with those of the lens tissue method. Comparison will be based only on chlorophyll-*a* determinations.

MATERIALS END METHODS

Lens tissue method

Surface sediment samples of 1 cm thickness were collected from sandy and muddy tidal flats at the Stations Randzel and Heringsplaat in the Ems estuary (Fig. 1). These samples were divided into 4 series per station and incubated under 4°, 8°, 12°, and 16 °C, respectively, under identical light conditions (55 μE m^{-2} s^{-1}) and a light dark cycle of 8 h light: 16 h dark.

Diatoms were trapped 5 times in succession by means of Green's Grade 105 lens tissues, and harvested once a day. Harvested tissues were air-dried in the dark, and the chlorophyll-*a* content determined according to Lorenzen (1967).

Density separation technique

Differences in specific weight between intact benthic diatoms and other sediment components were used to separate these fractions with Ludox-TM. Ludox is the trade name of a series of colloidal silica polymers (Du Pont, 1973). The specific weight of the undiluted Ludox-TM is about 1.39 g cm^{-3}, and is here assumed to be 100%. Ludox-TM is toxic to all living organisms, and may contain insoluble floccules in the gel-form. These floccules can be removed by filtering the Ludox over a combination of a thick layer of gauze bandages and paper filters (Schleicher & Schüll, No. 520 b II). Furthermore, Ludox-TM cannot be diluted with sea water, since it is very sensitive to the addition of positively charged ions (Du Pont, 1973) such as Ca^{2+} and Mg^{2+}.

Linear gradients

Eight uni-algal strains of benthic diatoms from laboratory cultures and 1 raw field sample were used to determine the range of specific weight of diatom cells in Ludox-TM. Linear gradients were made in 15 ml calibrated centrifuge tubes with a LKB 11300 Ultrograd Gradient Mixer and LKB 12000 Vario Perpex pumps (LKB Produkter AB, Stockholm, Sweden), using 100% Ludox-TM and distilled water. About 1 ml of the diatom suspensions was placed on top of the gradients with a pipette. The tubes, including one reference, were centrifuged for 1 h at 1660 x *g* on top of the tubes. The gradually increasing density in the tubes was measured by duplicate weighing of 0.1 ml of the Ludox-water mixture from the reference tube. The presence of the diatom cells over the gradients was examined under the microscope, by sampling the various layers of the tube with a pipette.

STEP GRADIENTS

Preparation of gradients.

Distilled water was used to prepare 0, 20, 70 and 90% (v/v) Ludox-TM. To prevent desiccation and consequently gelation, the diluted Ludox was immediately stored in closed jars. The Ludox dilutions of various densities were layered on a piston in a Perspex tube, 13 x 9.7 cm in diameter ("D" in Fig. 4). Step gradients were built up using a plastic syringe (50 ml) or a peristaltic pump with a capacity of 25 ml min^{-1}. The layers measured between 1.5 and 2 cm, corresponding to about 90 to 120 ml. The tubes were suitable for use in an IEC centrifuge (Type PR-6000, Rotor No. 981 and Bucket No. 408; International Equipment Company, Needham Height, Massachusetts, USA).

Preparation of field samples.

Sediment samples from the top 0.5 cm were collected from tidal flats at the Stations Eemshaven, Hoogwatum, Paap, Reiderplaat, Heringsplaat and Oost Friesche Plaat in the Ems estuary (Fig. 1). Samples were put into plastic beakers and diluted by 15 to 20% (v/v) Ca, Mg-free artificial sea water (30.77 g NaCl, 0.88 g KCl, 1.10 g Na_2SO_4 and 0.20 g $NaHCO_3$ per litre distilled water being isotonic with sea water of a salinity of 35) until a slurry was obtained. The artificial sea water was isotonic (within 5 salinity units) with the salinity of the water at the sampling station. The slurry was homogenized by a variable-speed IKA-Werk stirring machine with a propeller (Janke & Kunkel K.G., Staufen, Breisgau, FRG). A propeller size of 65% of the beaker diameter proved to be effective. The number of revs min^{-1} was adjusted to 800 to 1200 to achieve thorough mixing. To prevent settling of sand grains, a T-piece was attached to the lower side of the propeller. This T-piece was rotating just above the bottom of the beaker. After stirring for 5 min, subsamples of about 1.2 cm^3 of diluted sediment, corresponding to 1.0 cm^3 of undiluted sediment, were taken with a plastic syringe (2.5 cm^3) from which the conical top had been cut off. During the subsampling stirring was continued. Five subsamples were taken, 3 for determination of chlorophyll-*a* and 2 for the diatom separation procedure.

The 3 former subsamples were centrifuged for 5 min at 760 x *g* on top of the tubes. The greater part of the supernatant was carefully sucked off by a pipette connected with a vacuum pump. Residues were stored at -20 °C, freeze-dried, and the chlorophyll-*a* content determined and used as a reference to estimate the recovery of the separation procedure.

For the diatom separation procedure, each of the 2 subsamples was transferred by syringe into a 6 ml tube with stopper for storage. For direct processing, each subsample was transferred from the syringe to a 70 ml glass bottle of a Braun cell homogenizer MSK (Braun, Melsungen, FRG) containing 5 ml 80% Ludox-TM, to achieve a final concentration of 70% Ludox-TM. The syringe was rinsed with 70% Ludox-TM, which was also added to the bottle. The bottle was then filled with 70% Ludox-TM to a final volume of 25 ml, using a plastic syringe without a needle. The bottle was shaken in the cell homogenizer for 60 sec at high speed. After shaking, sand grains were allowed to settle for about 15 sec and the supernatant was sucked into a 50 ml plastic syringe with a long stainless steel tube (3 x 2 mm diameter) instead of a needle. The bottle was rinsed three times with about 7 ml 70% Ludox-TM, and carefully whirled by hand to resuspend the retained diatom fraction; after 15 sec settling of sand grains, the supernatant was also sucked into the 50 ml syringe. The glass bottle of the homogenizer was then half-filled with distilled water to prevent desiccation of the Ludox, and stoppered until further processing during the loading procedure.

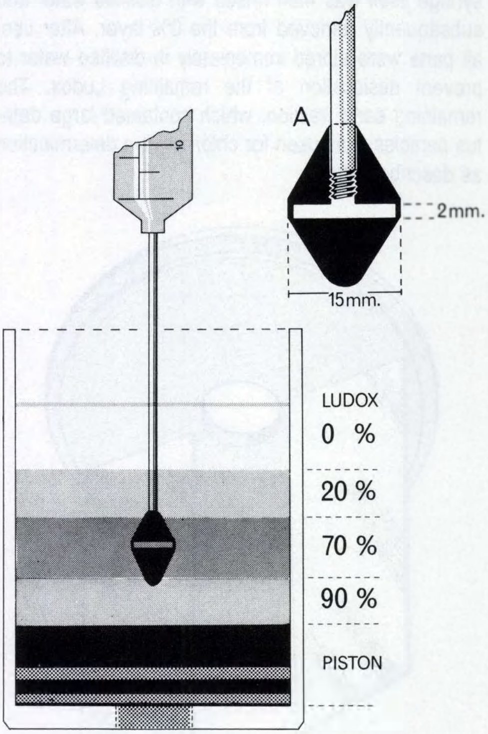


Fig. 2. Arrangement for loading a Ludox step gradient. Sample is suspended in 70% Ludox; it is introduced by means of a 50 ml plastic syringe with stainless steel needle, on top of which a conical head of PVC is adjusted by screw thread. A: Detail of conical head through which suspended sample is introduced horizontally into the 70% Ludox layer to prevent disturbing gradient during loading procedure.

Loading of the gradients.

A small PVC head with apertures on all sides (Fig. 2) was mounted to the end of the stainless steel tube of the 50 ml syringe. This PVC head was introduced into the 70% Ludox layer into which the content of the syringe was injected. To mix the 70% layer with the sample, part of it was sucked into the syringe and subsequently re-injected. The syringe end was taken out of the gradient, the piston was removed from the syringe, and the PVC head on the tube end was brought into the 0% Ludox layer.

The piston was rinsed above the syringe with distilled water so that the rinsing water was added, via the syringe, to the 0% layer. Then the homogenizer glass bottle was whirled by hand, sand grains were allowed to settle for 15 sec, and the supernatant was finally decanted into the syringe. To remove all retained diatoms, the glass bottle was rinsed three times. The syringe itself was then rinsed with distilled water and subsequently removed from the 0% layer. After use, all parts were stored immediately in distilled water to prevent desiccation of the remaining Ludox. The remaining sand fraction, which contained large detritus particles, was used for chlorophyll-*a* determination as described above.

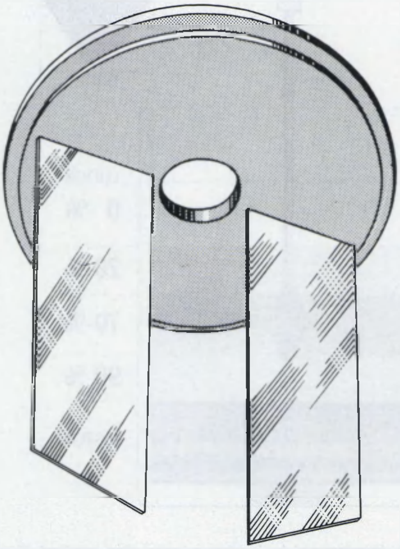


Fig. 3. Antiwhirl apparatus, consisting of two 0.5 mm thick stainless steel plates hanging from a PVC lid. The stainless steel plates are pushed through grooves in the lid, and are secured by bending back over the upper side of the lid. The apparatus is put on the centrifuge tube with loaded gradient after the tube has been introduced into the centrifuge.

Centrifugation.

The centrifuge tubes containing the step gradients were put into the centrifuge and fitted with two 0.5 mm thick stainless steel plates which were mounted on a PVC lid (Fig. 3). The plates prevented rotation of the tube content and consequently disturbance of the gradients at the start and the end of the run. Centrifugation was carried out for 2 h at 940 x *g* on top of the tubes. The centrifuge was adjusted in such a way that the number of revs min^{-1} slowly increased from 0 to 500.

Harvesting of the fractions.

After centrifugation, the stainless steel plates were removed carefully. The separated fractions were collected by suction with the apparatus illustrated in Fig. 4. To this end, a Perspex ring and lid ("C" in Fig. 4) were placed on the centrifuge tube (D), and the combination was fastened to the table. A vacuum pump with a capacity of 5 N m^3 h^{-1} air was connected with the vacuum flask (A) via Tube 1. The Perspex ring was connected with the vacuum flask (A) via Tube 2 by opening Valve I. Then Valve II was opened. This resulted in a very small but continuous flow of distilled water from the flask (B) via Tube 3, the Perspex ring (C), and Tube 2 to the vacuum flask (A), which prevented desiccation of the Ludox. The vacuum flask (A) was filled with about 100 ml of distilled water. While the waterflow continued, the piston ("D" in Fig. 4) in the centrifuge tube was pushed up at a rate of 2.5 cm min^{-1} by means of Apparatus E, built into the table. Thus, during this procedure, the fractions were diluted with distilled water and captured in the vacuum flask. The harvesting procedure was always continued until the next band was almost reached, and distilled water was then added to the vacuum flask up to a final volume of about 1 l to dilute the Ludox about 10 times.

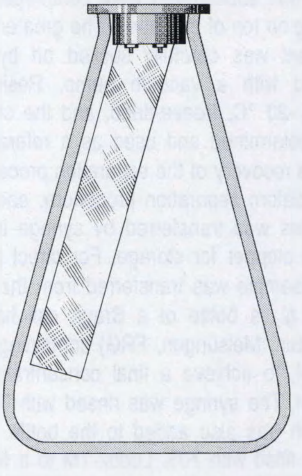
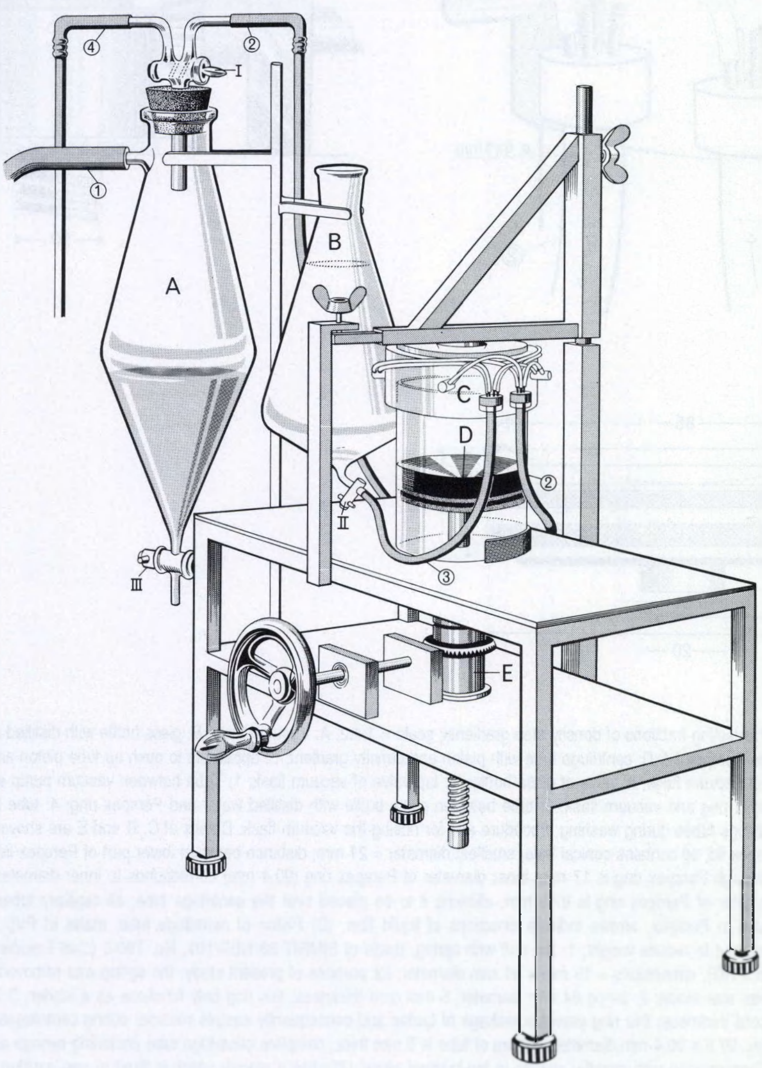


Fig. 5. Polyethylene flask, used as centrifuge tube. Flask contains an antiwhirl apparatus, consisting of one 0.5 mm thick stainless steel plate hanging on a PVC lid. Plate is mounted by means of bolts.

To wash out all Ludox, the harvested fractions were poured by Valve III into 15 x 9.7 cm diameter polyethylene vacuum flasks (Fig. 5), which were used as centrifuge tubes. The vacuum flask (A) was rinsed by admitting some distilled water through Tube 4

(Fig. 4) to the vacuum flask. This procedure was repeated three times. Centrifuge tubes (the above mentioned polyethylene vacuum flasks) were provided with a PVC lid with one stainless steel plate. The tubes were centrifuged for 20 min at 1120 x *g* on top of the tubes. Most of the supernatant was carefully removed under suction by the apparatus shown in Fig. 6A. This apparatus was connected with the vacuum flask by Tube 4 (Fig. 4).

The resultant pellet was resuspended in about 400 ml distilled water, and the centrifugation procedure was repeated twice. Subsequently, the pellets with the remaining water were transferred to 250 ml tubes with a conical bottom, and the washing procedure by centrifugation continued until the opaque colour disappeared and consequently all Ludox had been removed.



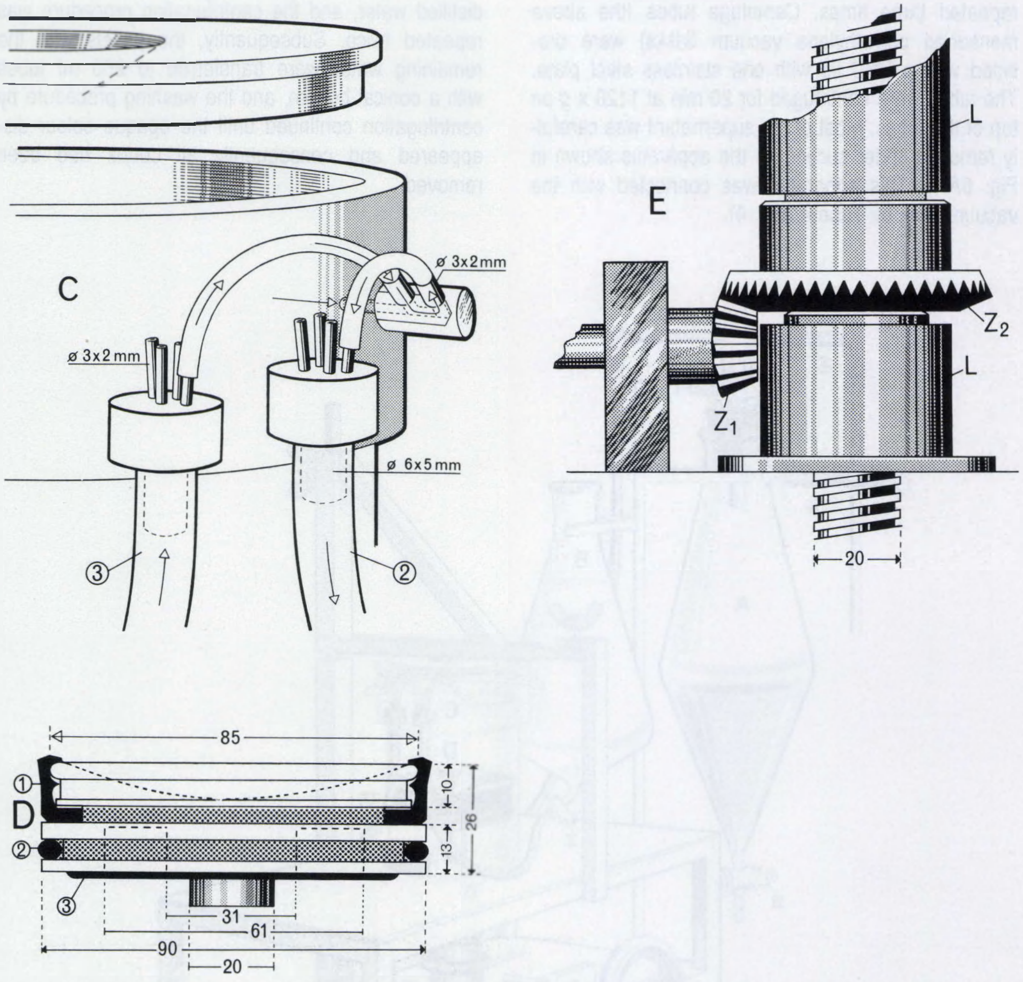


Fig. 4. Apparatus for harvesting fractions of density step gradients; scale = 1:4.2. A: Vacuum flask; B: glass bottle with distilled water; C: Perspex ring with loose Perspex lid; D: centrifuge tube with piston and density gradient; E: apparatus to push up tube piston and density gradient. I: Valve on top of vacuum flask; II: valve of glass bottle; III: tap valve of vacuum flask; 1: Tube between vacuum pump and apparatus; 2: tube between Perspex ring and vacuum flask; 3: tube between glass bottle with distilled water and Perspex ring; 4: tube for sucking off supernatant from centrifuge tubes during washing procedure and for rinsing the vacuum flask. Details of C, D and E are shown on right - (C) Perspex ring and Perspex lid, lid contains conical hole, smallest diameter = 21 mm; distance between lower part of Perspex lid and stainless steel tubes inserted through Perspex ring is 17 mm; inner diameter of Perspex ring (90.4 mm) corresponds to inner diameter of the centrifuge tube; bottom diameter of Perspex ring is 97.5 mm, allowing it to be placed over the centrifuge tube; all capillary tubes are made of stainless steel, mounted in Perspex; arrows indicate directions of liquid flow. (D) Piston of centrifuge tube, made of PVC, top concave; excess piston PVC was cut to reduce weight; 1: top cuff with spring, made of SIMRIT 88 NBR/101, No. T90-5 (Carl Freudenberg SIMRIT-Werk, 6940 Weinheim, FRG); dimensions = 15 mm x 91 mm diameter; for purpose of present study, the spring was removed and a central hole of 70 mm diameter was made; 2: 0-ring 84 mm diameter, 5 mm cord thickness; this ring only functions as a leader; 3: 0-ring, 78 mm diameter and 4 mm cord thickness; this ring prevents leakage of Ludox and consequently sample material during centrifugation. Centrifuge tube itself is of Perspex, 97.5 x 90.4 mm diameter; bottom of tube is 8 mm thick; complete centrifuge tube (including syringe and gradient) is shown in Fig. 2. (E) Transmission with spindle; spindle in big-toothed wheel (Z2) has a groove which is fixed in one position by a spline in one of the leaders (L); with the transmission the spindle can be moved up and down; the big-toothed wheel is fixed between the two leaders by axial bearings to decrease friction resistance and thereby facilitate rotation of the big-toothed wheels. The module of the toothed wheels (Z1 and Z2) is 1.5 and the proportion between the teeth of both wheels 1:3. All dimensions in "D" and "E" are in mm.

Centrifugation was continued for 20 min at 630 x *g*. Usually one run proved sufficient. The supernatant in the 250 ml tubes was removed with the apparatus shown in Fig. 6B, a simplified form of that illustrated in Fig. 6A. The fraction pelleted onto the PVC piston in the Perspex tube was transferred directly into a polyethylene vacuum flask by rinsing the piston carefully with distilled water.

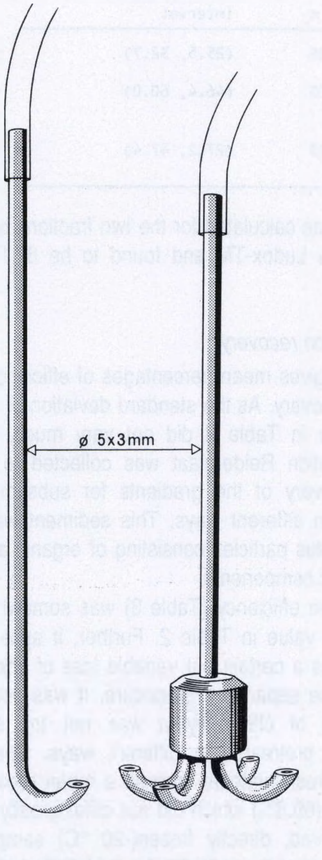


Fig. 6. Two types of an apparatus designed to suck off supernatant from centrifuge tubes during washing procedure.

The washed fractions in the 250 ml tubes were stored at -20 °C, freeze-dried, and the chlorophyll-*a* content determined. The chlorophyll-*a* content of the fractions was used to determine the efficiency and the recovery of the procedures used. For a number of experiments, the organic carbon content as well as the dry weight of the harvested fractions was determined. Organic carbon content was determined using a Coleman C and H analyzer, model 33 (Coleman Instruments Inc., Maywood, Illinois, USA). Dry weight was determined by weighing at room temperature (c. 20 °C), after the samples had been dried at 105 °C for 1 h.

Loss of chlorophyll-a.

To determine the loss of chlorophyll-*a* during the above described procedure, the removed supernatant per harvested fraction per washing procedure was filtered over glassfibre filters (Whatman GF/C) and the chlorophyll-*a* content determined.

Storage of field samples.

The influence of preservation and storage upon efficiency of the gradient type and density levels (expressed as recovery percentages) was investigated. Samples from the upper 0.5 cm of the surface sediment were collected from Station Reiderplaat. Samples were prepared as usual and stored in 6 ml stoppered glass tubes. One series of subsamples was used for chlorophyll-*a* determination, one series was directly used for the separation procedure, one series was stored without further treatment at -20 °C, one series was preserved with 4% formaldehyde in sea water and stored at -20 °C, while the last series was preserved with an acrolein mixture and also stored at -20 °C. The acrolein mixture was prepared according to the formula of J. van der Veer (1982) and consisted of 2% (w/v) tannic acid, 4% (v/v) acrolein, 4% (v/v) glutaraldehyde added to an equal volume of the sample.

RESULTS

Lens tissue method

Two-way and one-way analyses of variance were applied to the lens tissue harvesting data. The results of the first harvest proved to be dependent on sediment type, incubation temperature and sampling station. The results are summarized in Table 1 for the 3 remaining series, the results which were not affected by incubation temperature reveal very different mean harvest percentages as well as standard deviations.

DENSITY SEPARATION TECHNIQUE

Linear gradients

The results of the separation procedure with linear density gradients are given in Fig. 7. Density ranges measured in Ludox displayed great differences for specimens belonging to the same species as well as for different species. The total range for the diatom cells under consideration was 1.06 to 1.29 g cm^{-3} (15.4 to 74.4% Ludox-TM). This result was the same

Table 1. Mean first-harvest percentages (mean chlorophyll-a) with 95% confidence intervals, using lens tissue technique, for stations which displayed no significant incubation temperature effect. 95% confidence intervals were calculated using the formula

$$[\bar{x} \pm (\frac{S}{\sqrt{n}})]\ t_{n-1\,;0.975}$$

from Student's t distribution for small sampling, in which S is standard deviation, t is test statistic, and n-1(= υ) is number of degrees of freedom.

Station	Sediment	$\bar{x}$	S	n	95% confidence interval
Randzel	Sandy	29.1	7.6	20	(25.5, 32.7)
Hering-splaat	Sandy	53.2	14.6	20	(46.4, 60.0)
Hering-splaat	Muddy	37.3	21.6	20	(27.2, 47.4)

as for a field sample. The observations show that it is not likely that mixtures of different diatoms will band between narrow-density levels.

Step gradients

The use of the density separation technique leads to a certain loss of diatom biomass. Therefore, two definitions are introduced. The first is the efficiency, defined as the separated diatom biomass compared with the sum of the values of all fractions. Thus, efficiency can be expressed as

$$\frac{\text{chl-}a\text{ content of fractions 0 to 70\% Ludox-TM}}{\text{chl-}a\text{ content of all fraction}} \times 100\%.$$

The second is the recovery, defined as the separated diatom biomass, compared with a reference. Thus, the recovery can be expressed as

$$\frac{\text{chl-}a\text{ content of fractions 0 to 70\% Ludox-TM}}{\text{mean reference chl-}a\text{ content}} \times 100\%.$$

Separation efficiency.

Table 2 gives mean separation results of a number of samples taken from 6 stations with very different sediment composition. The fractions 0 to 70% Ludox-TM contained the greater part of the chlorophyll-*a*.

Furthermore, the removal of organic detritus (organic carbon) was on an average 57.7%, the removal of material 94.3 % (expressed as dry weight), and the removal of material excluding the sand fraction was 76.9% (expressed as dry weight).

As diatom identification requires oxidation of organic material and removal of inorganic components, only a relatively small amount of inorganic material can be present if valid results are to be obtained. Thus, efficiency was calculated for the two fractions between 0 and 70% Ludox-TM and found to be 87.1% on an average.

Separation recovery.

Table 3 gives mean percentages of efficiency as well as of recovery. As the standard deviation of the mean efficiency in Table 2 did not vary much, sediment from Station Reiderplaat was collected to estimate the recovery of the gradients for subsamples pretreated in different ways. This sediment was rich in fine detritus particles consisting of organic as well as inorganic components.

The mean efficiency (Table 3) was somewhat higher than the value in Table 2. Further, it appeared that there was a certain but variable loss of chlorophyll-*a* during the separation procedure. It was notable that the loss of chlorophyll-*a* was not the same for samples pretreated in different ways. Directly processed fresh material showed a mean recovery percentage (69.8%) which did not differ greatly from the unpreserved, directly frozen(-20 °C) samples (64.0%). Preservation with 4% formaldehyde in sea water decreased the mean recovery by 15.3%, while preservation with the acrolein mixture increased the mean recovery by 12.5% compared with the unpreserved samples.

Thus, the best results were obtained with samples preserved using the acrolein mixture. For these series of preserved samples the total chlorophyll-*a* loss was 17.7%, of which 5.6% was lost from the fraction with a density higher than 70% Ludox-TM. On an average, 12.1% of the chlorophyll-*a* content in the 0 to 70% Ludox-TM fractions disappeared or was retained during some step of the procedure.

Table 2. Harvest percentages (as chlorophyll-*a*), efficiency percentages, percentages of dry weight, and organic carbon content per fraction obtained using density method on samples from Stations Eemshaven, Hoogwatum, Paap, Reiderplaat, Heringsplaat and Oost-Friesche Plaat (Fig. 1). Sediment composition ranged from coarse to very fine-grained sand, the latter with a high detritus content. Total number of observations = 8.

	Mean percentages			
	Chlorophyll-a	Dry weight including sand fraction	Dry weight excluding sand fraction	Organic carbon
Sand fraction	1.7	75.4		36.2
Fractions banded between Ludox-TM concentrations				
0-20%	6.8 }	5.7	23.0	42.3
20-70%	80.3 }			
70-90%	5.9	0.7	2.9	6.2
>90%	5.4	18.2	74.0	15.3
0-70% (efficiency)	87.1 ± 2.8 (95% confidence limits)			
Percentage dry weight of sand fraction and fractions >70%		94.3		
Percentage dry carbon of sand fraction and fractions >70%				57.7

Table 3. Harvest percentages (mean chlorophyll-*a*), efficiency percentages and recovery percentages using density method on samples from Station Reiderplaat pretreated in different ways.

	Unpreserved, direct-processed	Unpreserved stored at -20°C	Formaldehyde-preserved, stored at -20°C	Acrolein-preserved, stored at -20°C
Fractions banded between Ludox-TM concentrations				
0-20%	16.8	11.5	18.2	17.5
20-70%	76.6	77.7	71.5	75.0
70-90%	1.0	3.0	3.2	2.2
>90%	5.6	7.9	7.2	5.3
Mean efficiency (%)	93.4	89.2	89.7	92.5
Mean recovery (%)	69.8	64.0	54.5	82.3
Numbers of observations	2	3	3	4

Loss of material.

From the results given in Table 4 it is clear that loss of material was mainly due to the washing procedure and not to decomposition of pigments. The total loss was 11.8% (40.0 µg). The sum of the total loss and harvest was 347.4 µg chlorophyll-*a*, i.e., 7.4 µg chlorophyll-*a* more than in the reference; this was probably caused by determination inaccuracy.

Table 4. Harvest and losses of chlorophyll-*a* (chl-*a*) during density separation procedure. All values are means of 2 observations. Samples were from Station Reiderplaat.

	Harvested and washed chl-a (µg)	Total loss of chl-a over 3 washings (µg)
Fractions banded between Ludox-TM concentrations		
0-20%	92.0	12.0
20-70%	173.2	12.8
70-90%	13.1	6.1
>90%	29.1	6.4
Antiwhirl plates		2.7
Total harvest	307.4	
Total loss		40.0
Reference µg chl-a	340.0	
Efficiency (%)	86.3	
Recovery (%)	78.0	
Numbers of observations	2	

Discussion

Chlorophyll-*a* measurements were used as a rapid estimate for diatom biomass. The use of chlorophyll-*a* content as indication of biomass may have introduced a certain overestimation for the samples separated by the density gradient method, due to the presence of dead diatom cells or to the presence of chlorophyll-*a* in detritus floccules (Moss & Round, 1967). With the density method it is possible to discriminate between intact and damaged diatom cells. However, discrimination between live and dead cells is not possible.

To enable comparison between the isolation methods investigated, the standard deviations were calculated for the 3 lens tissue series results in Table 1 and the acrolein-preserved density series results in Table 3. From Table 5 it is obvious that, despite the 20 replicates, the lens tissue method gives rather unreliable results. For the density method, with only 4 replicates, the standard deviation was much smaller.
This means that for the lens tissue method very large numbers of replicates are necessary to provide a reliable harvest percentage. Also, the mean recovery percentage of the density method is much better than the harvest percentage of the lens tissue method. Moreover, no epipsammic diatoms can be trapped using lens tissues, while this is partially possible with the density method.
The very constant percentages of efficiency (Tables 2 and 3) indicate that the values obtained with the density method are independent of sediment composition as well as the total diatom biomass present in the sediment samples, despite the wide range of chlorophyll-*a* contents with a factor of about 17.5. The density method described is, therefore, generally applicable to all kinds of estuarine sediment and to all quantities of benthic diatom biomass present in the sediment.

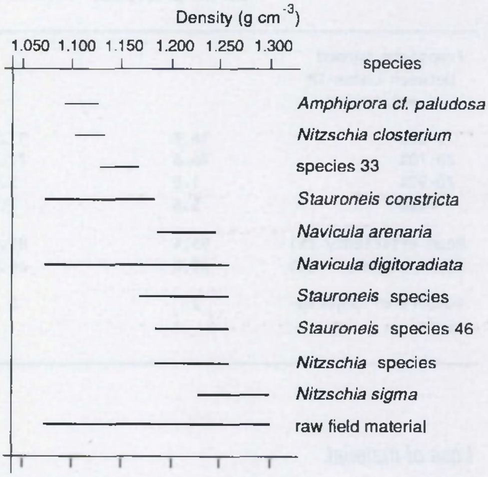


Fig. 7. Density ranges of some benthic diatom strains and a raw field sample, as measured in linear gradients of Ludox-TM. Density values were determined by weighing.

Table 5. Recovery percentages with standard deviations (SD) for 20 replicates, calculated for the 3 lens-tissue harvest-series not affected by temperature and for replicates from the acrolein-preserved series of the density method.

Lens tissue		Density method	
Mean harvest (%)	SD	Mean recovery (%)	SD
29.1	7.6	82.3	5.8
53.2	14.6		
37.3	21.6		

The relatively low chlorophyll-*a* values measured for the sand fraction (Table 2) indicate that most of the epipsammic diatoms were removed from their substrate. This was confirmed by microscopial observation. Residual chlorophyll-*a* content can also have been derived from small Cyanophyceae, which are often attached to sand grains.

As direct processing of field samples is impracticable and often not possible, experiments were carried out to investigate the effects caused by storage and preservation. Acrolein-preserved samples always gave the highest recovery. It is thought that this phenomenon results from a better fixation of phospholipids by acrolein and glutaraldehyde (Jones, 1976), which possibly also reduces chlorophyll-*a* loss.

The results in Fig. 7 in combination with microscopical observations indicated that sometimes a relatively large part of a dominant species can be lost if only the fractions between 0 and 70% Ludox-TM are used for species identification and counting. For this reason, when checking that part of the fractions with a density higher than 70% Ludox-TM microscopically for intact diatoms, it is also important to use acrolein-preserved samples. Microscopical observations showed that in the fractions 0 to 70% Ludox, only a few empty diatom frustules occurred. At present, the fate of very fragile species submitted to the density method is not known.

Preliminary experiments have indicated that the isolation method presented here is also applicable to algal groups such as Euglenophyceae and Cyanophyceae (e.g. *Merismopedia* species). The method is probably also applicable to other benthic and planktonic algal groups.

In this paper, density values (g cm^{-3}) are given as measured in Ludox-TM because the effect of the positively charged colloidal particles upon the banding level of the diatom cells is not known. Onge & Price (1975) established that additions of organics as well as inorganics to silica sols may lead to a shift in the sedimentation level of the organisms. They found that such a shift also occurs if untreated Ludox-AM is used. This shifting, caused by the exchange of ions and water between organisms and Ludox-TM, is presumed to cease within a very short time for small diatom cells, and should, therefore, have been negligible in the present case.

Moreover, the density method described in this paper is based on step gradients with very great density differences between the Ludox layers, while Onge & Price used linear gradients.

It also has been found necessary to apply middle- and not top-loading for the gradients. When samples suspended in water were brought on top of the gradients large floccules immediately formed (see also Price *et al.*, 1977) which considerably descreased the efficiency of separation. By middle loading, formation of large floccules is prevented since Ludox-TM has a higher viscosity than water. A second advantage is that during centrifugation the interaction between particles will be low, because one part of the material moves up to a lower density level while another part sinks to a higher density level. The volume of 1 ml undiluted sediment is the maximum which can be separated without markedly affecting efficiency. The use of 20 as well as 70% Ludox-TM is necessary to prevent loss of the light organisms during the first washing procedure.

The use of conical polyethylene vacuum flasks as centrifuge tubes is necessary to prevent settling op particles against the tube wall during centrifugation. Dimensions of the Perspex ring and lid, as given, are important with regard to the air capacity of the vacuum pump.

During harvesting of fractions, the gentle air flow through the hole in the lid, combined with the strong air-flow through the pores in the Perspex ring, drives all the floating material to the pores ("C" in Fig. 4). A smaller hole in the lid would result in a stronger and more turbulent air flow, which would disturb the gradient and consequently decrease recovery percentages.

Small modifications in the processing procedure of the density method may decrease the recovery percentage by even more than 25%.

Current investigations confirm the suitability of the application of a modified density method for research on raw phytoplankton and suspended matter samples.

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FLUCTUATIONS IN THE ORGANIC CARBON TO CHLOROPHYLL-*A* RATIOS FOR ESTUARINE BENTHIC DIATOM POPULATIONS

V.N. de Jonge

ABSTRACT

Carbon/Chlorophyll-a ratios were determined for benthic diatom populations at 6 stations in the Ems estuary. For mixed field populations previous data are not available. Measurements were carried out over a period of nearly 3 years. The data were statistically analysed. Statistically significant differences in ratio values were indicated within and between years. No indications were found for a statistically significant station effect upon the ratio values. The ratio values over the 3 year period investigated ranged from 10.2 up to 153.9 with yearly averages and standard deviations of 40.3 ± 13.8; 41.2 ± 20.4 and 61.4 ± 22.0, respectively. It was concluded that chlorophyll-*a* measurements in itself are insufficient to describe fluctuations in benthic diatom standing stock. Mechanisms possibly regulating the Carbon/Chlorophyll-*a* ratios are discussed.

INTRODUCTION

The sediments on the bottom of shallow lakes and shallow seas, including their intertidal mud and sand flats, contain variable quantities of micro-algae. It is customary to determine their amount by means of measurements of chlorophyll-a. In primary production studies, however, biomass increase is normally given in terms of organic carbon. Thus the expression of algal standing stock in terms of organic carbon reflects an appreciable relationship with the primary production process. However, a simple conversion from chlorophyll-*a* to organic carbon is only possible under the assumption that the ratio between both components is more or less constant or that the fluctuations are at least well known. Organic carbon to chlorophyll-*a* ratios for natural benthic diatom populations were not available until now. The published data on organic carbon to chlorophyll-*a* ratios derived from natural phytoplankton populations are variable, scarce and mostly obtained during short bloom periods. Data for well-growing populations are given in Table 1.

Steemann-Nielsen & Hansen (1959), Rodhe *et al.* (1966), Anderson (1969), Sayo *et al.* (1969), Takahashi *et al.* (1972), Eppley *et al.* (1973) and Fee (1976) suggest the existence of light adaptation by a cell chlorophyll-*a* increase under low light intensities. Harvey (1953), Brown & Richardson (1968), Beale & Appleman (1971) and Sheridan (1972) found an inverse proportion between light intensity and chlorophyll-*a* concentrations for algal cells. Steele & Baird (1962), Antia *et al.* (1963), Coombs *et al.* (1967), Eppley (1968), Strickland *et al.* (1969), Hobson & Pariser (1971), Thomas & Dodson (1972) and Perry (1976) showed that deficiency of P, N and Si could lead to a considerable increase in the organic carbon to chlorophyll-*a* ratios. Caperon & Meyer (1972), Eppley & Renger (1974) and Perry (1976) described a negative correlation between specific growth rate and the organic carbon to chlorophyll-*a* ratio.

Table 1. C/Chl-*a* ratios determined for well-growing natural algae populations.

Authors	C/Chl-a ratios
Parsons & Strickland (1959)	39.6
Antia et al. (1963)	25
Eppley (1968)	22.2-47.5
Eppley et al. (1971)	60
Eppley et al. (1977)	10-90

A list of the data available is given in Table 2.

All investigations referred to show that chlorophyll-*a* is not necessarily a good and conservative unit to describe the quantity of algal biomass. Further, it is uncertain whether the phytoplankton carbon to chlorophyll-*a* ratios also hold for benthic diatom populations.

Table 2. Organic carbon to chlorophyll-*a* ratios determined during exponential growth and nutrient limitation of cultures and natural algae populations.

Authors	C/Chl-a ratios	Nature of investigated populations
Steel & Baird (1962)	29.2 - 714.3	Culture of Skeletetonema sp.
Antia et al. (1963)	23.5 - 114	Induced bloom; mixture of 6 diatoms and 1 dinoflagellate
Coombs et al. (1967)	23.5 - 29.6	Si-deficiency; Navicula pelliculosa phytoplankton
Eppley (1968)	(22.2 - 47.5)	No detectable N; natural population, open sea, composition unknown
Strickland et al. (1969)	(71.4 - 125.0)	N limitation; deep tank population of Caclonia niei
Hobson & Pariser (1971)	34.5 - 83.3	NO_3 deficiency; Thalassiosira fluviatilis
Caperon & Meyer (1972)	14.7- 100.0	N limitation; chemostat culture of Thalassiosira pseudonana
Thomas & Dodson (1972)	55.0- 500.0	N limitation; chemostat culture of Chaetoceras gracilis
Eppley & Renger (1974)	19.0- 61.8	N and P limitation; chemostat culture of Thalassiosira pseudonana
Perry (1976)	28.6- 91.4	

Therefore, organic carbon to chlorophyll-*a* ratios were determined for intertidal mobile benthic diatom populations, it will be demonstrated that there are clear fluctuations in the organic carbon to chlorophyll-*a* ratios (C/Chl-*a*) for benthic diatoms and some other micro-algae over the year and between years. Data were collected over about three years at 6 sampling stations in the estuary of the River Ems.

MATERIALS AND METHODS

Collection and trapping of benthic diatom populations. Surface sediment of about 2 mm thickness, coloured brown by diatoms, was collected from 6 arbitrarily chosen stations in the estuary of the River Ems (Fig. 1). The sediments were scraped off and a volume of about 1½ l was mixed with some seawater until a very thick and tough slurry was obtained.

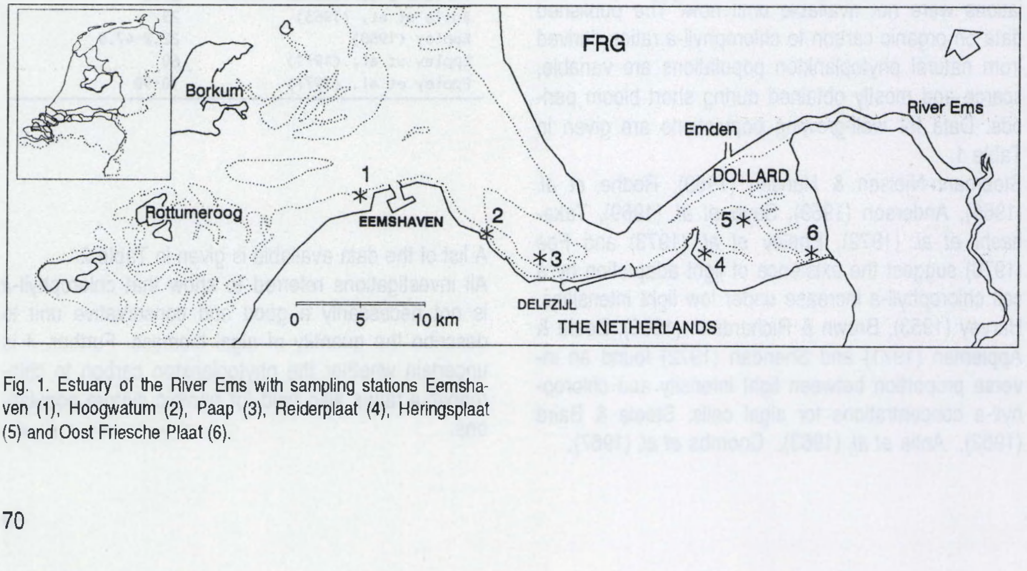

Fig. 1. Estuary of the River Ems with sampling stations Eemshaven (1), Hoogwatum (2), Paap (3), Reiderplaat (4), Heringsplaat (5) and Oost Friesche Plaat (6).

The slurry was put into a rectangular container (60 x 40 x 12 cm) and spread out to a flat layer. Water present on the sediment surface was removed. The sediment surface was covered with an 0.5 to 1 mm thick layer of flamed and acid washed sand (Merck, No. 7536 or Brocacef ZA 152). Then a monolayer of Whatman's Grade 105 lens tissue (46 x 57 cm) was brought lengthwise upon the sediment and was pasted with some water against the container's wall. After this, two other lens tissues were placed together across the former one. The containers were covered with transparent plastic to prevent desiccation and placed for about 16 to 24 h under conditions of 12 °C, 65 - 80 μE m^{-2} s^{-1} and a light period of 6 - 8 h.

Harvesting procedures

After at least 16 h the two upper lens tissues only were carefully removed, torn up in a number of pieces, and put into a beaker partly filled with organic carbon free salt water (30.77 g NaCl, 0.88 KCl, 1.10 g Na_2SO_4 and 0.20 g $NaHCO_3$ per litre distilled water, being isotonic with sea water with a salinity of 35). The salt water used was diluted to within 10% of the salinity of the water of the sampling station. After that the beaker was closed and vigorously shaken by hand for about 10 seconds. The suspension was poured out over three layers of about 2.5 mm thick foam plastic followed by a 55 µm nylon sieve. The lens tissue fibres were separated from the diatoms by the foam plastic barrier. The bulk of the harpacticoid copepods were caught by the 55 µm sieve. Microscopic inspections affirmed that the clear, light brown-coloured suspension contained only diatoms and nearly no microscopically visible bacteria.

Additional procedures for other algal groups

When mixtures of different algal groups and of protozoa were obtained (e.g. Station Oost Friesche Plaat, Fig. 1), further processing was necessary. These mixtures were separated with a slightly modified version of the technique described by de Jonge (1979). The procedure followed is based on density gradient centrifugation of the samples in Ludox-TM. *Euglena* species (Euglenophyceae) could normally be harvested from the 30% Ludox-TM layer, benthic diatoms (Bacillariophyceae) from the 70% layer and *Merismopedia* species (Cyanophyceae) from the 15% layer.

Determinations

The suspension obtained was used to determine the C/Chl-*a* ratio per station (Fig. 1) per date. Samples with a volume between 10 and 25 ml were used for chlorophyll-*a* determination. The sample was put into a centrifuge tube and centrifuged for 5 min at 760 x *g* on top of the tubes. The greater part of the supernatant was removed by a pipette connected with a vacuumpump, the remaining sample in the tube frozen (-20 °C), lyophilized and the chlorophyll-*a* content determined according to Lorenzen (1967). Four replicas from the suspension were used for the analysis.

For determination of organic carbon a sample of 100 ml was used, filtered over Whatman GF/C glass fibre filters under low vacuum and quickly washed with carbon-free salt water to remove possible dissolved organic as well as inorganic carbon. Filters were dried for at least 2 h at 50 °C, stored in a desiccator and the carbon content determined using a Coleman C and H analyzer, Model 33 (Coleman Instruments Inc., Maywood, Illinois, USA). Also for this analysis four replicas were used.

Statistical methods

The k sample test of Kruskal & Wallis (1952) supplemented by the multiple comparison test of Dunn (1964), the two sample test of Wilcoxon (1945) and the test of Friedman (1937) for testing the agreement between rankings were applied to establish station, season and year effects on C/Chl-*a* ratios.

RESULTS

Field observations

Figure 2 shows the C/Chl-*a* ratios obtained over the total period investigated regardless of the sampling station. There are remarkable differences in the values over the period investigated.

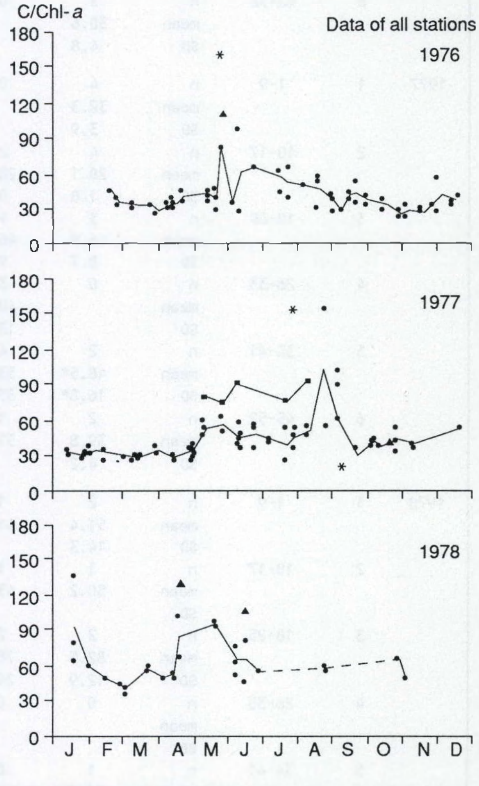

Fig. 2. Organic carbon to chlorophyll-*a* ratios for the 6 stations investigated. Solid and dotted lines: curve based on averages per week (cf. Table 3) The sharp maximum observed in May/June 1976 is possibly an artefact caused by only a single observation. ●: Bacillariophyceae (benthic mobile species); ■: *Merismopedia* species; ▲: Euglenophyceae; *: Cyanophyceae other than *Merismopedia* speciea (mainly *Oscillatoria* species).

Table 3. C/Chl-*a* ratios obtained for the stations investigated. n: number of observations; mean and standard deviations (SD) of C/Chl-*a* ratios per period per station and per period irrespective of station (total). For explanation of station numbers see Figure 1.

				Station no.						
Period	No.	Week no.		1	2	3	4	5	6	Total
1976	1	1-9	n	1	0	0	0	1	1	3
			mean	45.6				33.3	39.3	39.5
			SD							6.2
	2	10-17	n	4	2	3	1	1	1	12
			mean	33.9	39.4	33.1	33.1	35.0	30.2	34.3
			SD	2.3	10.5	5.1				4.8
	3	18-25	n	2	3	4	1	1	0	11
			mean	37.9	57.9	45.3	35.3	83.1		49.9
			SD	11.2	33.0	15.4				22.1
	4	26-33	n	2	2	2	1	1	1	9
			mean	47.6	39.6	59.7	65.0	63.4	44.3	51.8
			SD	13.2	12.2	8.3				12.4
	5	34-41	n	4	1	4	1	1	2	13
			mean	38.9	29.2	38.8	28.9	38.4	41.2	37.7
			SD	3.1		9.9			4.4	6.6
	6	42-52	n	3	0	5	1	2	2	13
			mean	30.6		31.5	30.3	25.8	44.7	32.4
			SD	4.8		6.3		2.3	16.0	8.5
1977	1	1-9	n	4	0	4	1	1	1	11
			mean	32.3		28.4	31.0	26.7	28.7	29.9
			SD	3.9		2.4				3.3
	2	10-17	n	4	2	4	2	1	2	15
			mean	28.1	28.6	32.2	29.8	38.8	27.3	30.1
			SD	1.8	0.4	5.0	0.5		2.3	4.0
	3	18-25	n	3	4	4	1	1	0	13
			mean	46.9	46.5	49.7	47.3	56.1		48.3
			SD	8.7	9.4	9.3				8.0
	4	26-33	n	0	3	3	1	1	1	9
			mean		40.2	47.0	52.0	46.8	35.2	43.9
			SD		13.4	4.8				8.8
	5	34-41	n	2	4	3	2	1	0	12 *
			mean	48.5*	53.5	54.7	27.0	15.4		45.4*
			SD	16.8*	35.3	30.4	23.8			27.9*
	6	45-52	n	2	1	3	0	0	0	6
			mean	39.8	51.3	41.7				42.7
			SD	4.2		9.7				7.7
1978	1	1-9	n	2	1	3	1	1**	0	8**
			mean	51.4	41.0	56.2	39.1	45.6**		50.4**
			SD	14.3		21.0				13.9
	2	10-17	n	1	1	1	1	2	1	7
			mean	50.2	45.8	99.8	45.6	58.4	55.6	59.1
			SD					7.6		19.0
	3	18-25	n	2	2	1	1	1	0	7
			mean	82.5	78.0	51.5	43.3	79.8		70.8
			SD	12.9	24.7					19.9
	4	26-33	n	0	0	1	0	0	0	1
			mean			52.8				52.8
			SD							
	5	34-41	n	1	0	1	0	0	0	2
			mean	56.8		53.7				55.3
			SD							2.2
	6	42-52	n	1	0	1	0	0	0	2
			mean	62.9		47.1				55.0
			SD							11.2

* Without outlier: 153.9.

** Without outlier: 133.1.

Also between the stations at about the same sampling date differences are observed. Data obtained from algal groups other than benthic diatoms were scarce. Therefore, it was not possible to analyse them statistically. However, Figure 2 shows that the C/Chl-*a* ratios obtained for Cyanophyceae such as *Merismopedia* sp. (mainly *Merismopedia glauca* f. *mediterranea*) are rather high as compared with the values obtained for the benthic diatoms. The available data obtained for other groups of Cyanophyceae, mainly consisting of *Oscillatoria* and *Phormidium* species, even exceed the values of *Merismopedia* sp. However, their values are less constant than the values determined for the *Merismopedia* species, possibly due to changing species composition.

STATISTICAL ANALYSES

Analyses between stations

Because the numbers of data obtained from the 6 stations (Fig. 1) were very different and only few for each month, each of the investigated years was divided into 6 periods of approximately equal length. Some variation in the lengths of the periods was introduced in order to reduce the variation in number of data available for each period. Using this procedure further evaluation of the data was possible with distribution free statistical tests.

The test of Kruskal & Wallis was applied to the data of Table 3 (including the two outliers, mentioned at the end of the table) in order to test the hypothesis that the ratios of the 6 stations could be considered as random samples from the same population. Because the numbers of data per station per period were too low to obtain a reliable test result, this test was carried out for combinations of always two successive periods (Table 4).

Table 4. Significance levels (P) of Kruskal-Wallis test for comparing C/Chl-*a* ratios of different stations for pairs of successive periods as distinguished in Table 3.

Years	1976			1977			1978		
Periods	1,2	3,4	5,6	1,2	3,4	5,6	1,2	3,4	5,6
Significance level (P)	0.98	0.61	0.33	0.82	0.61	0.57	0.51	-	-

The test could not be applied to weeks number 18-52 of 1978 because of shortage of data. According to the Kruskal-Wallis k sample test no significant relation could be established between the ratios and the stations. This means that within these pairs of periods no significant differences between the observations from different stations could be established.

An objection against this test is that the stations are compared on the basis of data which are obtained during relatively long time intervals. The most reliable method to establish a pure station effect on C/Chl-*a* ratios would be a comparison of simultaneous samples from all 6 stations. Such data were not available but 6 relatively short periods could be selected (Table 5) in which for all 6 stations at least one C/Chl-*a* ratio value was available. If for a station two or more data were available for one such period, the mean value was used. For each of these periods the 6 values obtained were ranked and the concordance between the 6 rankings was tested with Friedman's test. The test result ($P = 0.07$) was nearly significant. This means that the possibility of systematic differences in simultaneous C/Chl-*a* values between the 6 stations cannot be fully excluded.

Analyses between periods

The possible station effect as indicated above was neglected in the analyses which were carried out to investigate a period or year effect upon the C/Chl-*a* ratios. The data of the 6 distinguished periods for 1976 and 1977 (Table 3, including the outliers) were investigated with the test of Kruskal & Wallis (Table 6). For 1978 the test could not be carried out because for the second half of that year too few data were available. Subsequently the periods were compared two by two by means of the simultaneous test of Dunn (1964). Applied at the level α, the probability that any difference between two samples will be significant is at most α under the hypothesis that all samples are drawn from the same population. The results of both tests (Table 6) give evidence of a strong period effect in the C/Chl-*a* ratio. These effects, however, are quite different for the two years. In 1976 there is one peak at about the middle of the year (Table 3, Week No. 18-33). In 1977 the values are relatively low at the beginning of the year (Table 3, Week No. 1-17). Thereafter they increase and maintain a relatively high level during 1977 and 1978 (Table 3, 1977 Week No. 18-52 and 1978).

By the forementioned shortage of data the high level could not be statistically established for the second half of 1978.

Table 5. C/Chl-a ratios obtained within relatively short time intervals for the stations investigated. For station numbers see Figure 1. Agreement between the ranks of stations was calculated with the test of Friedmann.

		Station no.											
	Week	1		2		3		4		5		6	
Year	no.	Ratio	R	Ratio	R	Ratio	R	Ratio	R	Ratio	R	Ratio	R
1976	14-15	35.1*	5	32.0	2	37.6	6	33.1	3	35.0	4	30.2	1
	28-31	38.2	1	48.2	3	65.6	6	65.0	5	63.4	4	44.3	2
	35-37	41.4	5	29.2	2	38.5	4	28.9	1	38.4	3	44.3	6
1977	15-17	27.0*	1	28.3	2	31.7*	5	30.1	4	38.8	6	28.9	3
	25-30	51.6	5	34.8*	1	48.8*	4	52.0	6	46.8	3	35.2	2
1978	12-16	50.2	3	45.8	2	99.8	6	45.6	1	58.4*	5	55.6	4
	Total		20		12		31		20		25		18

*Mean value of the ratio over the period considered.
R: Rank of ratio (according to increasing value).

Because of the established period effects the 3 years under consideration were compared separately for each period (including the outliers) by means of the test of Kruskal & Wallis. For the last 3 periods only the years 1976 and 1977 could be compared by means of Wilcoxon's two sample test.

The results, summarized in Table 7, are significant for all three periods analysed with the Kruskal-Wallis test and significant only for the last period (Table 3, Week No. 42-52) analysed with the Wilcoxon test. The results of Dunn's test (Table 7) clearly show that the significances obtained in the Kruskal & Wallis test are due to the high C/Chl-*a* ratios as measured in 1978 in particular for the first two periods (Table 3, Week No. 1-17). It is remarkable that for the last period (Table 3, Week No. 42-52) the level of the ratio in 1977 is significantly higher than in 1976. At the end of 1977 the level did not decrease as was the case in 1976 (compare results in Table 6).

DISCUSSION

Tables 1 and 2 give C/Chl-a ratios as published by a number of authors. The values presented in the present paper are mainly within the range of the literature values (Fig. 2) in spite of the fact that all published values were obtained from phytoplankton species. The clear differences in ratio level for the benthic diatoms and other phytobenthos groups (Fig. 2) strongly indicate that biomass fluctuations cannot simply be described in terms of chlorophyll-*a*. It is necessary to discriminate between different phytobenthos groups. This also means that the species composition should always be studied.

The statistical tests which were carried out indicate differences in C/Chl-*a* ratios within and between years. Further, no station effect could be indicated. Based on these statistical results some remarks can be made and some possible explanations for the fluctuations observed will be given.

Nutrient deficiency

Table 2 shows the influence of nutrient deficiency on the C/Chl-*a* ratio. In nearly all cases there is a reasonable increase in the C/Chl-*a* ratio caused by a decrease of cell chlorophyll-*a* and increase of cell carbon. Only Eppley & Renger (1974) reported a cell carbon decrease while Thomas & Dodson (1972) found changing cell carbon levels.

It is remarkable that the phenomenon of C/Chl-a increase appears regardless of the kind of limiting nutrient. Perry (1976) emphasizes the relation between the influence of nutrient deficiency on the one hand and decreasing growth rate and increasing C/Chl-*a* ratio on the other hand. Thus an increasing ratio level could indicate a decreasing growth rate due to any kind of nutrient limitation. Because the observations presented in Figure 2 show statistically significant differences in ratio levels for different parts of the year (Table 6). It seems not unlikely to explain this in terms of possible nutrient deficiency.

Table 6. C/Chl-a ratios obtained in the six periods distinguished (cf. Table 3) compared by means of the tests of Kruskal & Wallis and of Dunn. The periods are arranged in order of increasing mean rank.

Year 1976						
Period no.	6	2	5	1	3	4
Week no.	42-52	10-17	34-41	1-9	18-25	26-33
n	13	12	13	3	11	9
Mean rank	17.5	23.3	31.4	35.8	40.1	47.4

Test of Kruskal and Wallis: P<0.001
Test of Dunn: 6 and 4 (P = 0.0015);
6 and 3 (P = 0.028);
2 and 4 (P = 0.030)

Year 1977						
Period no.	1	2	5	4	6	3
Week no.	1-9	10-17	35-41	26-33	42-52	18-25
n	11	15	13	9	6	13
Mean rank	17.6	18.4	39.8	42.4	42.6	50.2

Test of Kruskal and Wallis: P<0.00001
Test of Dunn: 1 and 3 (P = 0.0001);
1 and 4 (P = 0.069);
1 and 5 (P = 0.082);
2 and 3 (P = 0.0002);
2 and 4 (P = 0.051);
2 and 5 (P = 0.056)

Table 7. C/Chl-a ratios of the years 1976, 1977, 1978 compared by means of the test of Kruskal and Wallis or Wilcoxon and Dunn's multiple comparison test.

			Year			P (test of Kruskal & Wallis or Wilcoxon)	P (test of Dunn)		
			1976	1977	1978		'76/'77	'76/'78	'77/'78
Period. no.	1	n	3	11	9				
Week no.	1-9	R	14.2	6.3	18.3	0.004	n.s.	n.s.	0.0003
Period. no.	2	n	12	15	7				
Week no.	10-17	R	8.4	10.6	30.7	<0.0001	n.s.	0.028	0.00003
Period no.	3	n	11	13	7				
Week no.	18-25	R	12.8	14.8	23.3	0.047	n.s.	0.05	n.s.
Period no.	4	n	9	9	1				
Week no.	26-33	R	11.4	7.6	-*	0.136**			
Period no.	5	n	13	13	2				
Week no.	36-41	R	12.1	14.9	-*	0.36**			
Period no.	6	n	13	6	2				
Week no.	42-52	R	7.8	14.8	-*	0.012**			

R: Mean rank of ratio (according to increasing value).
* Year 1978 not involved in test because of shortage of observations.
** Wilcoxon's two-sample test.
n: Number of observations.
n.s.: Not significant (P> 0.10).

However, chemical data suggest that nutrient levels in the water of the greater part of the estuary of the River Ems are possibly not a limiting factor. The sediment composition on the stations investigated ranges from coarse sandy to fine silty. The organic carbon content as well as the bacterial population density increases with changing sediment composition from sandy to fine silty (Schröder & van Es, 1980). Parallel to this there is also an increase in mineralisation activity in the sediment, possibly leading to differences in nutrient supply in the top layer. The results given in Tables 4 and 5 lead to the conclusion that no statistically significant station effect upon the C/Chl-*a* ratios could be indicated. This means that changes in nutrient supply caused by differences in sediment composition and mineralisation activity cannot be a main factor in controlling the C/Chl-*a* ratios. If we are still dealing with nutrient deficiency we must think of an influence which is not site-coupled but algae-layer-coupled. It is not unlikely that in diatom populations nutrient deficiency may appear by a decreased diffusion as a function of diatom density and excreted mucilaginous products such as extra cellular and autolytic products of all kinds of microorganisms (Frankel & Mead, 1973).

The variation in C/Chl-*a* ratios determined during summer and autumn (Fig. 2) suggests that if deficiency plays an important role, this factor does not influence the ratio levels constantly. This would be not unrealistic because the investigated diatom populations live on relatively unstable sediments which are reworked with changing intensity by waves induced by wind, tide and benthic fauna.

Species composition

The results of Tables 4 and 5 indicate that, in spite of existing gradual differences in species composition along the main axis of the estuary (van den Hoek *et al.*, 1979), this alone cannot be an important factor in explaining the changes in C/Chl-*a* ratios. This might be due to the fact that not only the species composition changes but also the number of individuals per species, smoothing out the species specific ratios.

Another point of importance is that diurnal changes in the C/Chl-*a* ratio for populations containing one or more benthic diatom species were not studied. This aspect cannot be excluded since for phytoplankton Eppley *et al.* (1971) observed C/Chl-*a* ratios with a coefficient of variation of about 200%. Such phenomenon in relation to the very different vertical positions of the stations and thus also different photoperiods might partly explain the variation in C/Chl-*a* ratios per sampling date.

Abiotic factors

A statistically significant effect was indicated for similar periods in successive years (Table 7). This was mainly due to a 50% increase in the average ratio level for 1978 as compared with the same periods in the previous years. The minimum value was also higher in 1978 as compared with 1976 and 1977 (Table 8). Such a multi-year-coupled factor or combination of factors must be due to still unknown macro-influences.

Table 8. Mean, standard deviation (SD), maximum and minimum values for C/Chl-*a* ratios obtained over the periods investigated. For individual data see Figure 2.

	Years investigated		
	1976	1977	1978
Mean	40.3	41.2	61.4
SD	13.8	20.4	22.0
Minimum	23.6	10.2	34.7
Maximum	96.0	153.9	133.1

The absence of a station effect is remarkable because the vertical position of the stations ranged from about 1.1 m above to about 0.7 m below mean sea level. Since the mean tidal amplitude in the middle of the estuary is about 2.75 m, this means a difference in immersion time of at least hours per tide. Apparently this is only of little importance to the ratio level. The absence of a station effect means that on the same date different sites in the estuary are directly comparable on the basis of only chlorophyll-*a* measurements. The statistically significant changes in C/Chl-*a* ratios for different periods of the year mean that comparison of biomass distributions over periods longer than about a week are not possible on the basis of chlorophyll-*a* determinations alone.

Methodological remarks

Some remarks on the method of C/Chl-*a* ratio determination should be made. Samples were only collected from places which were light or dark brown coloured by diatoms. This means that there is no information on differences in the C/Chl-*a* ratio between diatom populations collected from localities with high and very low biomass densities.

Another possibly still more important restriction was the fact that from the natural populations only specimens could be harvested which were able to creep into the tissues within the given harvesting period. This certainly resulted in a selection between immobile or less mobile and highly mobile species. Also for the mobile species fraction a possible selection has been made as cells could be in different physiological conditions. It was not possible, however, to develop a rather simple method to isolate all benthic diatom cells quantitatively and alive from sediment. With the density separation method developed earlier (de Jonge, 1979) diatom cells could be quantitatively isolated from inorganic sediments together with part of the organic matter; however, the detritus (organic matter) content of the fractions containing diatoms (0-70% Ludox-TM) was too high to make any estimation of the diatom carbon possible. The separation method applied to raw field samples is only suitable for a chlorophyll-*a* determination, diatom identification and counting.

CONCLUSION

Biomass fluctuations can be described most accurately if C/Chl-*a* ratios are actually determined. Information on relative biomass distributions by means of chlorophyll-*a* determinations are only possible if samples are taken within a short period. The values given in Table 8 show that the use of a constant ratio (e.g. an annual average) to convert chlorophyll-*a* to organic carbon may involve errors varying from 34-50% (overestimation and underestimation, respectively). The actual differences (Table 8 and Fig. 2 maxima and minima) are even greater. The values determined over the 3 years (Table 8) also show that an additional error may be introduced if the annual average used dates from a previous year.

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DYNAMICS OF MICROPHYTOBENTHOS BIOMASS IN THE EMS ESTUARY MEASURED AS CHLOROPHYLL-*A* AND CARBON

V.N. de Jonge and F. Colijn

ABSTRACT

The dynamics of microphytobenthos biomass in the Ems estuary (The Netherlands, NW Europe) were studied over 3 years on 6 transects with 41 stations in total. Six of these stations (one per transect) were sampled frequently.

The vertical and horizontal distributions of chlorophyll-*a* were measured. The organic carbon content of the microphytobenthos was calculated, using carbon to chlorophyll-*a* ratios. These organic carbon values were compared with estimates of chlorophyll-*a*, which are usual measure of biomass.

The mean annual concentrations of chlorophyll-*a* varied per station. For the 6 main stations they ranged from 28.6 to 247.0 mg m^{-2} in the top 0.5 cm of sediment. For the other 35 transect stations they ranged from 15.3 to 309.7 mg m^{-2}. Per transect the difference between the averaged annual means of the transect stations and the mean annual value of solely the main station was usually small and less than 15%.

The vertical distribution of chlorophyll-*a* in the sediment of the main stations reveals a profile which is similar for 5 of the 6 stations investigated. The relative distribution of chlorophyll-*a* from vital cells was reconstructed from the typical vertical distributions of chlorophyll-*a*. These graphs were used to calculate the total chlorophyll-*a* from vital cells in the sediment. Multiplying the chlorophyll-*a* by the C/Chl-*a* ratio results in a value for microphytobenthos biomass expressed in organic carbon.

The smallest mean annual value for microphytobenthos biomass at the six main stations is 3.1 g C m^{-2} and the largest value is 16.7 g C m^{-2}. The average values over the three years range from 3.2 to 11.0 g C m^{-2}.

For the main stations the ratio between the biomass from the 0.5 to 2.0 cm sediment layer and the biomass from the 0 to 2 cm sediment layer gradually changes from 0.6 in the lower reaches of the estuary to 0.4 in the upper reaches of the estuary. These ratios show that sampling only the top 0.5 cm of the sediment to determine the microphytobenthos chlorophyll-*a* and multiplying this figure by a C/Chl-*a* ratio results in the real biomass being grossly (100 to 150%) underestimated. The use of an incorrect C/Chl-*a* ratio (which varies from 40 to 70 per annum) in this multiplication can increase this deviation by a further 50%.

INTRODUCTION

In estuaries such as the Ems (Fig. 1) phytoplankton and microphytobenthos are the main primary producers. This microphytobenthos mainly consists of benthic diatoms. Measurements of primary production in the water column of the Ems estuary (Colijn, 1983) and on the intertidal flats (Colijn & de Jonge, 1984) have shown the contribution made by both to the total primary production. The relative importance of phytoplankton and microphytobenthos varies with area. In the lower reaches, between the barrier islands and the mainland, the primary production in the water column is more important than the benthic primary production. This is due to the low turbidity of the water. In the upper reaches (Dollard and lower Ems) the converse is true. In total the benthic primary production should account for c. 20% of the total production, (including the production of excretion products) (Colijn, 1983). In order to determine the relationships between grazers and benthic algae it is not sufficient to know the production values (Ludden *et al.*, 1985). The grazing efficiency of zooplankton, nematodes, harpacticoid copepods, filter feeding bivalves, etc. depends on the concentration of food relative to the density of the grazers (Admiraal *et al.*, 1988). To find this, a relevant set of parameters must be determined, from which the algal biomass can be calculated.

There are several different ways of determining algal biomass. These techniques usually involve cell counting, followed by conversion to biovolume or organic carbon (Mullin *et al.*, 1966; Strathmann, 1967), or calculations using concentrations of chlorophyll-*a* and organic carbon (Banse, 1977), or the C^{14} labelling of chlorophyll-*a* (Redalje & Laws, 1981; Redalje, 1983). All these techniques have their limitations. The method developed by Banse (1977) cannot be applied to sediment-inhabiting algae in the Ems estu-

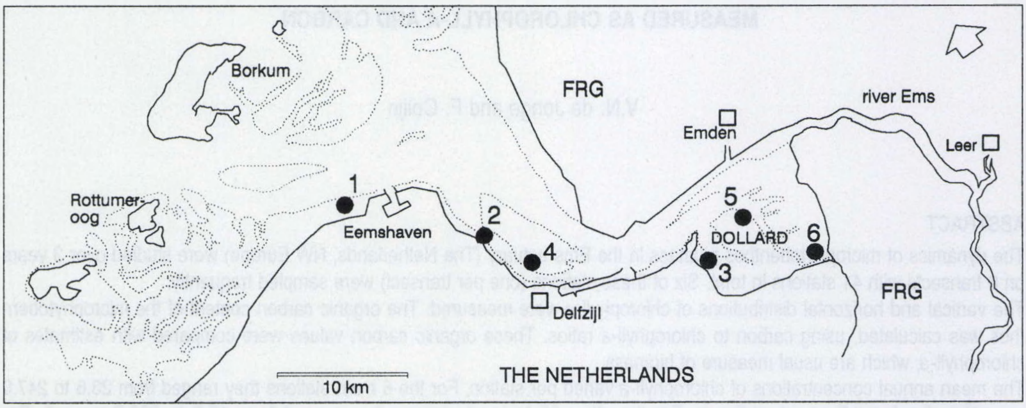

Fig. 1. Map of the Ems estuary, showing transects 1 to 6.

ary because the living algae represent only a small fraction of the total organic carbon (de Jonge, 1979). Until very recently (Gould & Gallagher, 1990) labelling of chlorophyll-*a* with C^{14} to determine the microphytobenthos biomass was little used. Because the chlorophyll-*a* has to be determined for primary production measurements, in most studies therefore chlorophyll-*a* is used for routine estimates of biomass.

However, without additional information from the field and measured on the same populations, neither cell counts nor chlorophyll-*a* measurements represent a parameter that can adequately be used as an estimate for algal biomass. This is simply because the organic carbon content varies per cell, per cell volume and per unit of chlorophyll-*a*.

A technique to determine the seasonal variations in the C/Chl-*a* ratio for mixed field populations of motile, benthic diatoms in the Ems estuary has been described previously (de Jonge, 1980). This very simple technique is based on a modification of the lens-tissue technique published by Eaton & Moss (1966). The results revealed that C/Chl-*a* ratios vary from c. 10 to 90. Statistical analyses showed the ratios did not differ significantly between stations when the samples were taken on the same date. Seasonal differences were very significant. This paper presents biomass distributions and fluctuations based on chlorophyll-*a* measurements and on chlorophyll-*a* data converted to organic carbon using the C/Chl-*a* ratios published previously for the same study period and the same stations (de Jonge, 1980). Data series are presented to show that the biomass of microphytobenthos differs between areas, between locations within the same area but situated at different elevations within the tidal range, and at different depths in the sediments of permanent plots on the tidal flats.

The implications of the results for ecological studies is discussed.

MATERIALS AND METHODS

Study area

The Ems estuary (Fig. 1) is a coastal plain estuary which crosses the Wadden Sea at the border between the Netherlands and Germany. The estuary is separated from the North Sea by barrier islands, from the mainland by dikes and from adjacent tidal basins by high-lying tidal flats (tidal watersheds). It is c. 75 km long between the tidal inlet and the town of Leer and is c. 500 km^2 in area, the outer delta excluded. Approximately 40% of the lower reaches and as much as 80% of the Dollard (upper reaches, Fig. 1) comprise intertidal flats. The tidal prism of the estuary is c. 1×10^9 m^3 and the tidal range varies from 2.25 m in the tidal inlet to over 3.0 m near Emden and in the southeastern part of the Dollard. For more hydrographical information, see de Jonge (1988).

Investigations were carried out in 6 areas distributed over the entire estuary (Fig. 1). In each of these areas one transect, indicated by a single number (1 to 6) was chosen. The transects were situated perpendicular to the main tidal channel.

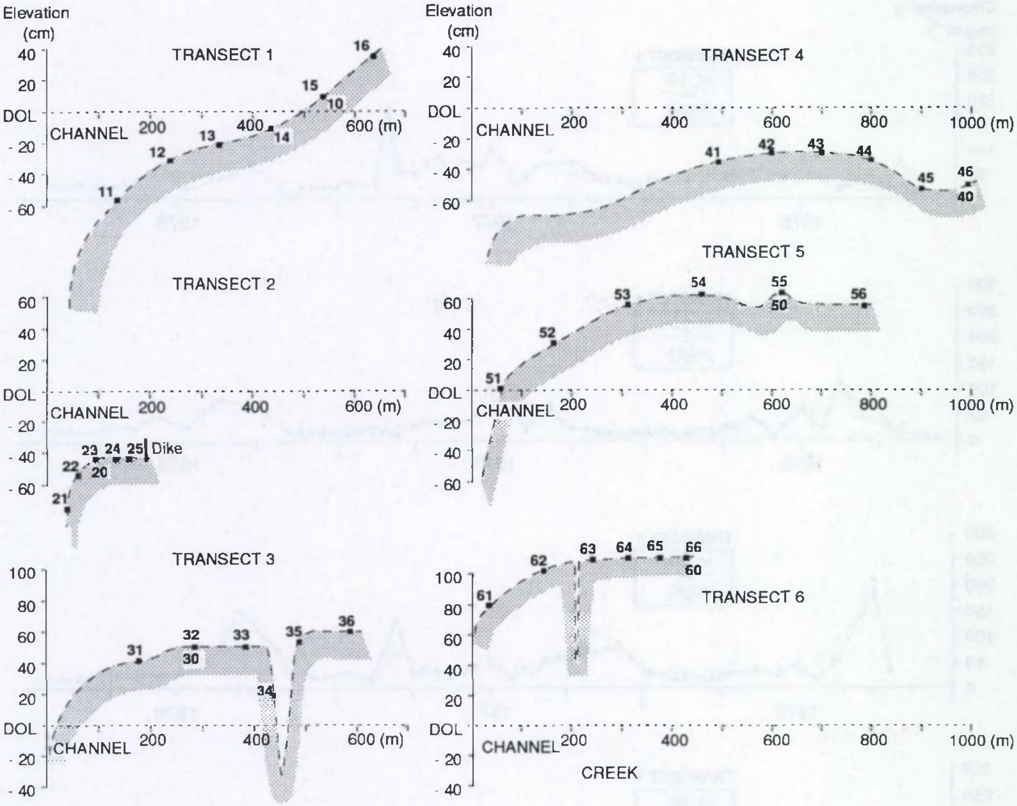

Fig. 2. Cross-sectional view of the elevation of all sampling stations. DOL (Dutch Ordnance Level) represents mean sea level. The first digit in the combination of numbers indicates the transect. The second digit indicates the transect station. Code 0 (second digit) indicates the main stations and codes 1 to 6 the other transect stations.

In each of these transects one main station, indicated by a two-digit number, with the first digit being the transect number (1 to 6) and the second a zero, was chosen. Moreover an additional number of stations were chosen along the transect, usually 100 m from each other. The main station was usually situated in the middle. The transect stations are indicated by two-digit numbers, with the first number indicating the transect itself and the second the transect station (Fig. 2). In each transect, one of these stations was situated at one of the corners of the 50 x 50 m plot that formed the main station. The stations were positioned so that they covered most of the range in elevation (Fig. 2).

The sediments of the main stations can be characterized as follows. Sandy sediments with a clay content of only 1.5-2% $(^{w}/_{w})$ were found at station 10. In these lower reaches the clay content varies strongly, between 0.3 and 3.5%, depending on the degree of exposure to waves and currents. Muddy sand is found at station 20. Here the clay content is 10-15%. The sediments of station 30 can be characterized as sandy mud with a clay content of 10-20%. In the middle reaches of the estuary where station 40 was situated the clay content was only 2-5% indicating a sandy sediment. Stations 50 and 60 were situated in the Dollard. The former had a clay content of 5-10% and could therefore be characterized as muddy sand, whereas the sediments of station 60 were muddy, with a clay content of 30-35%.

Sampling

Two series of twenty cores (inner diameter of 2.4 cm each) were taken from the main stations, to determine the chlorophyll-*a*. The sediment column was cut into slices of different thickness. The uppermost sediment layer had a thickness of 0.5 cm because the chlorophyll-*a* concentrations determined in that layer

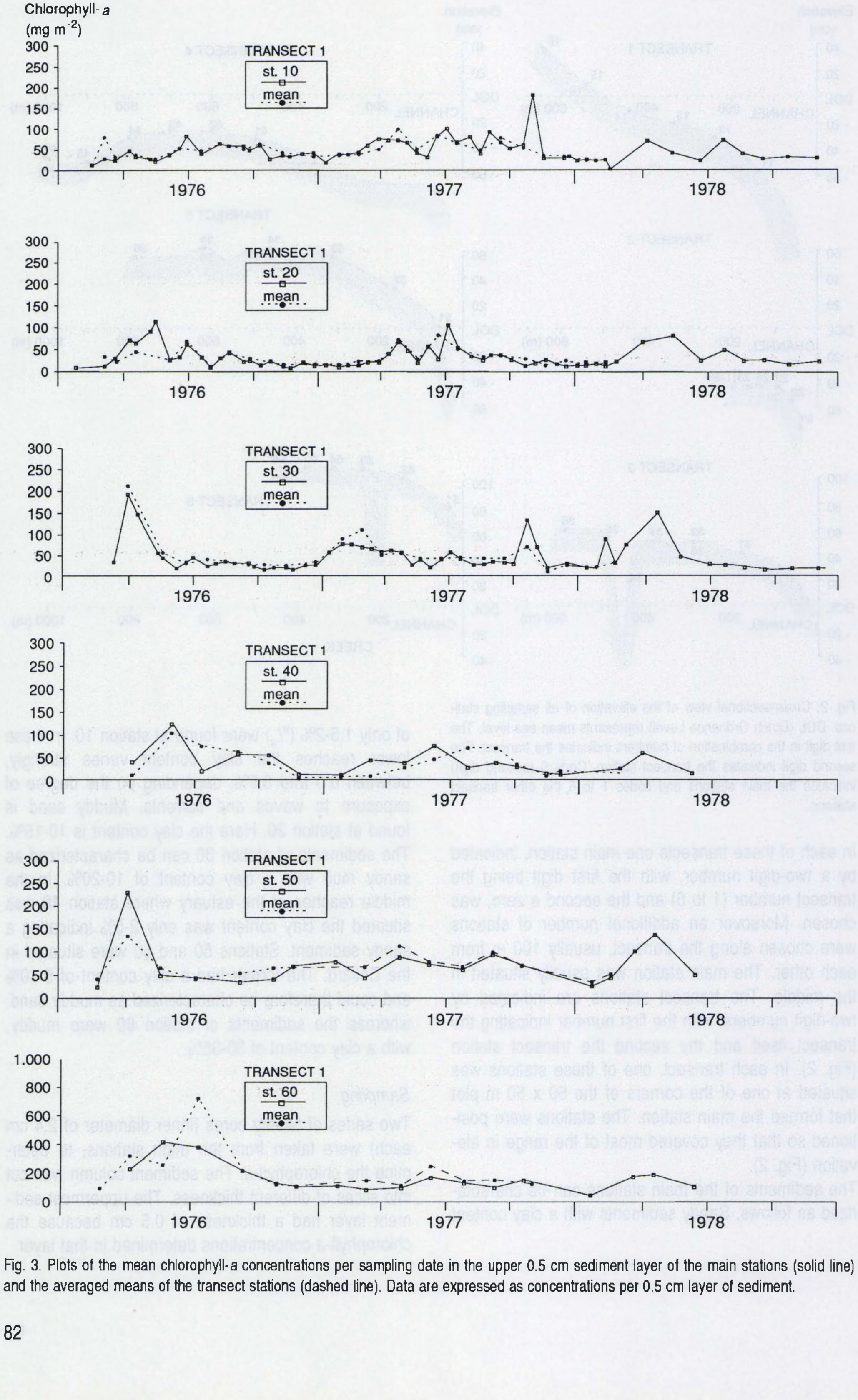

Fig. 3. Plots of the mean chlorophyll-*a* concentrations per sampling date in the upper 0.5 cm sediment layer of the main stations (solid line) and the averaged means of the transect stations (dashed line). Data are expressed as concentrations per 0.5 cm layer of sediment.

were also used in the primary production measurements (Colijn & de Jonge, 1984). The upper 0.5 cm layer of the first series of twenty cores was stored separately at -20 °C until the determination of chlorophyll-*a*. This procedure was followed to determine both the means and the standard deviations. The twenty cores of the second series were also sliced. Samples taken from the sediment layers at 0-0.5 cm, 0.5 to 2.0 cm, 2.0 to 5.0 cm, 5.0 to 10.0 cm and 10.0 to 15.0 cm depth were pooled per depth category, mixed thoroughly and subsampled. Three subsamples were taken from each depth category and stored at -20 °C until determination of chlorophyll-*a*. Only the mean values for chlorophyll-*a* were obtained, because it was physically impossible to determine values for all samples from all depths. Moreover, mean values in chlorophyll-*a* per location were considered sufficient. For the procedures of mixing and subsampling, see de Jonge (1979).

The transect stations were sampled following the same technique as described for the main stations. This time, five sediment samples were taken. Only the upper 0.5 cm was removed for analysis. Samples were stored separately at -20 °C until chlorophyll-*a* determination.

Stations 1 to 3 were sampled monthly in 1976 and 1978 and fortnightly in 1977. Stations 4 to 6 were sampled approximately every two months, because they could not be reached without a vessel.

The replica samples from the main stations and the transect stations were taken at regular distances from each other.

Laboratory analyses and calculations

Chlorophyll-*a* was determined spectrophotometrically after the samples had been lyophilized. Pigment concentration was measured using a modification (Moed & Hallegraeff, 1978) of Lorenzen's method (1967).

The chlorophyll-*a* concentrations were converted to organic carbon using C/Chl-*a* ratios of vital, mobile, benthic diatom populations and, when present, other benthic algae like the Cyanophyceae *Merismopedia glauca* at transect 1 (de Jonge, 1980).

When algae other than diatoms were abundantly present, their contribution to the total biomass was distinguished by applying the Ludox-TM separation technique (de Jonge, 1979).

RESULTS

The mean chlorophyll-*a* values (series of non-pooled samples) for the upper 0.5 cm sediment layer of the main stations (solid line) and the transect stations (dashed line) are presented in Fig. 3. A subjective assessment of the graphs shows dissimilarity in chlorophyll-*a* between the six main stations. There are year-to-year variations which differ with station. In 1976 the main stations 20 to 50 showed chlorophyll-*a* maxima in spring followed by a sudden or gradual decrease. In 1976 station 10 did not show a clear peak but station 60 showed a summer maximum which was also observed in 1977 for all stations (except main station 30). In 1978 the main stations 10 to 30 again peaked in spring. Generally, most of the stations are characterized by relatively high chlorophyll-*a* concentrations in summer. Only at main station 30 did the chlorophyll-*a* values peak mainly during spring.

The plots in Fig. 3 show a good correspondence between the variations of the mean chlorophyll-*a* of the main stations (solid line) and the mean values of all the transect stations (dashed line). It is not possible to give here the graphs of all 35 transect stations, so the mean chlorophyll-*a* concentrations per sampling date for the transect stations have been averaged in order to calculate the annual means (Table 1).

Usually, the chlorophyll-a values of the main stations lie between the maximum and minimum values of the transect stations per sampling date.

To facilitate the general comparison of all these data we calculated the annual means of the main stations and of the transect stations, as well as the average of the annual means of the transect stations (Table 1).

A comparison of the means of the main stations and those of the transects clearly indicates that these values do not differ strongly over the year (less than 25-30% in two cases and less than 15% in all others). This indicates that the main stations chosen were fairly representative of their transect even though the transects and the stations initially were chosen arbitrarily. A second point of interest is the higher chlorophyll-*a* concentrations in the Dollard (Table 1: transect 6) as compared with the rest of the estuary. Finally, the lowest chlorophyll-*a* concentrations were measured at stations on transect 2 and the highest at stations on transect 6 (Table 1, Fig.1).

In Fig. 3 only the mean values of the top 0.5 cm sediment layer were considered for the different

Table 1. Annual mean chlorophyll-*a* values for main stations, transect stations and the transect average from the means of the transect stations. Values given as mg chlorophyll-*a* m^{-2} for a 0.5 cm slice of sediment.

Main stations		Transects							
Station	10	Transect mean	Transect station	11	12	13	14	15	16
1976	41.4	46.2		34.5	39.6	43.5	47.4	47.9	64.6
1977	60.2	54.8		32.0	43.0	51.2	52.3	60.7	89.7
1978	32.5			-	-	-	-	-	-
Station	20	Transect mean	Transect station	21	22	23	24	25	
1976	35.1	31.5		26.0	33.9	32.2	30.8	34.8	
1977	33.1	36.4		15.3	32.6	41.2	46.3	46.8	
1978	28.6	-		-	-	-	-	-	
Station	30	Transect mean	Transect station	31	32	33	34	35	36
1976	44.1	55.3		46.9	45.6	54.6	62.8	55.1	66.9
1977	50.2	52.9		40.6	51.6	45.6	62.1	46.6	71.2
1978	41.9	-		-	-	-	-	-	-
Station	40	Transect mean	Transect station	41	42	43	44	45	46
1976	52.8	50.9		60.2	34.0	67.4	60.5	37.2	46.4
1977	33.2	34.0		18.2	26.8	35.5	50.2	41.0	32.2
1978	34.4	-		-	-	-	-	-	-
Station	50	Transect mean	Transect station	51	52	53	54	55	56
1976	70.7	67.5		62.7	67.6	72.8	90.3	59.6	52.1
1977	73.5	84.1		78.8	84.0	79.0	90.6	84.2	87.8
1978	71.9	-		-	-	-	-	-	-
Station	60	Transect mean	Transect station	61	62	63	64	65	66
1976	247.0	263.9		271.9	309.7	236.2	272.8	272.3	220.4
1977	123.8	159.2		170.2	180.0	165.0	149.3	150.3	140.3
1978	127.8	-			-	-	-	-	-

sampling dates and years. However, standard deviations were also calculated for all these values. As an example, the mean chlorophyll-*a* concentrations in 1977 as well as the standard deviations are given in Fig. 4 for the main stations only. The graphs show that the standard deviations increase with increasing chlorophyll-*a* concentrations. The relatively large coefficients of variation are caused by the irregular or patchy distribution of the benthic chlorophyll-*a* (cf. van den Hoek et al, 1979).

The chlorophyll-*a* concentrations for the different depths (obtained from the pooled series of twenty cores) are given in Fig. 5. To ensure a valid comparison all concentrations are expressed per 0.5 cm of sediment slice. The graphs show that in general the chlorophyll-*a* values are greatest in the upper 0.5 cm of the sediment. However, there are some exceptions. On some occasions during early spring and in autumn and at all stations except 60 (where limited data are available) the chlorophyll-*a* concentrations in the 0.5-2.0 cm sediment layer were larger than those of the top 0.5 cm. Furthermore, the chlorophyll-*a* fluctuations in the top 0.5 cm of the sediment also occurred in the 0.5-2.0 cm layer and sometimes even in the 2.0 to 5.0 cm layer. However, the deeper in the sediment, the weaker the fluctuations in the chlorophyll-*a* concentrations (Fig. 5) although there were also differences between stations. For the main stations 10 and 50 (and to a lesser extent for station 40), which have rather sandy sediments, the chlorophyll-*a* concentration of the 5.0 to 10.0 cm layer differed from that of the 10.0 to 15.0 cm layer. This is certainly not the case for the main stations 20 and 30, which had muddy sand to sandy mud sediments. Main station 60 had very stiff, clay-rich sediments under anoxic conditions that were difficult to sample at

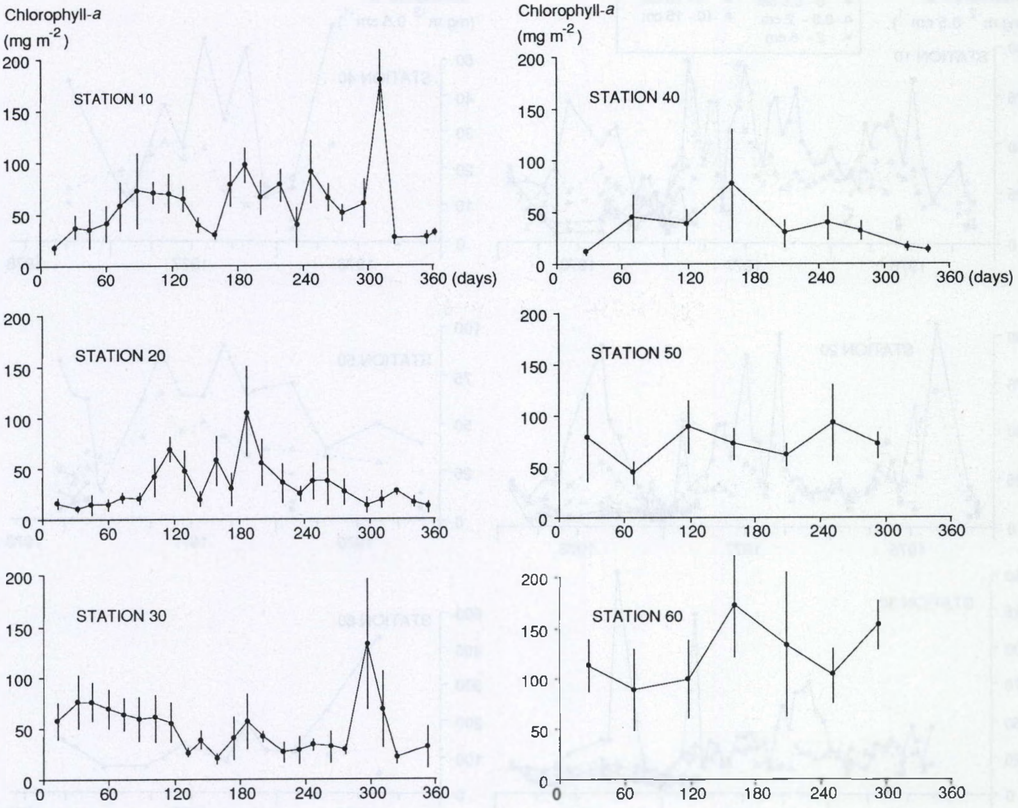

Fig. 4. Plots of the mean chlorophyll-*a* concentrations in the upper 0.5 cm sediment layer of the six main stations in 1977. Bars represent standard deviations.

depths below 2 cm, presumably also falls into the latter group. These figures indicate the depths to which benthic diatoms may be found (see also Fig. 6).

The chlorophyll-*a* values per station, per depth were averaged for those sampling dates when also sediment layers deeper than 2 cm were sampled.

These mean values were plotted as a percentage of the value for the uppermost 0.5 cm, which was considered to be unity (100%). The resulting relative depth distributions of the total chlorophyll-*a* concentrations are given in Fig. 6a. Before the relative chlorophyll-*a* distributions were used for further calculations, Spearman's rank correlation coefficients were calculated to test the hypothesis that the chlorophyll-*a* at the different levels fluctuated independently. The test results in Table 2 show that this hypothesis usually holds for depths greater than 2 cm. But it also held for the two upper layers of the sandy stations 40 and 50. Nevertheless, there is evidence for considering that the chlorophyll-*a* fluctuations in the two upper sediment layers of 4 out of 6 stations are related.

The available data indicate that the vertical distribution of chlorophyll-*a* of all the stations cannot simply be described as a function of the surface value. For depths below 2 cm the chlorophyll-*a* concentrations steadily decrease, as is demonstrated by the relative vertical distribution profile (Fig. 6a). Except for station 60, the relative decrease (slope of graph) in vertical concentration of chlorophyll-*a* seems to be independent of the surface value. This is an important indication for that the deeper sediment contains chlorophyll-*a* that has little to do with the transient surface concentrations derived from vital surface populations. Despite this, the relative vertical distribution of chlorophyll-*a* can be used to reconstruct roughly the mean original vertical distribution of chlorophyll-*a* for vital microphytobenthos cells. To do this the value for the 2.0 to 5.0 cm layer (the depth from which the steady decrease in chlorophyll-*a* was ascertained; Fig.6a)

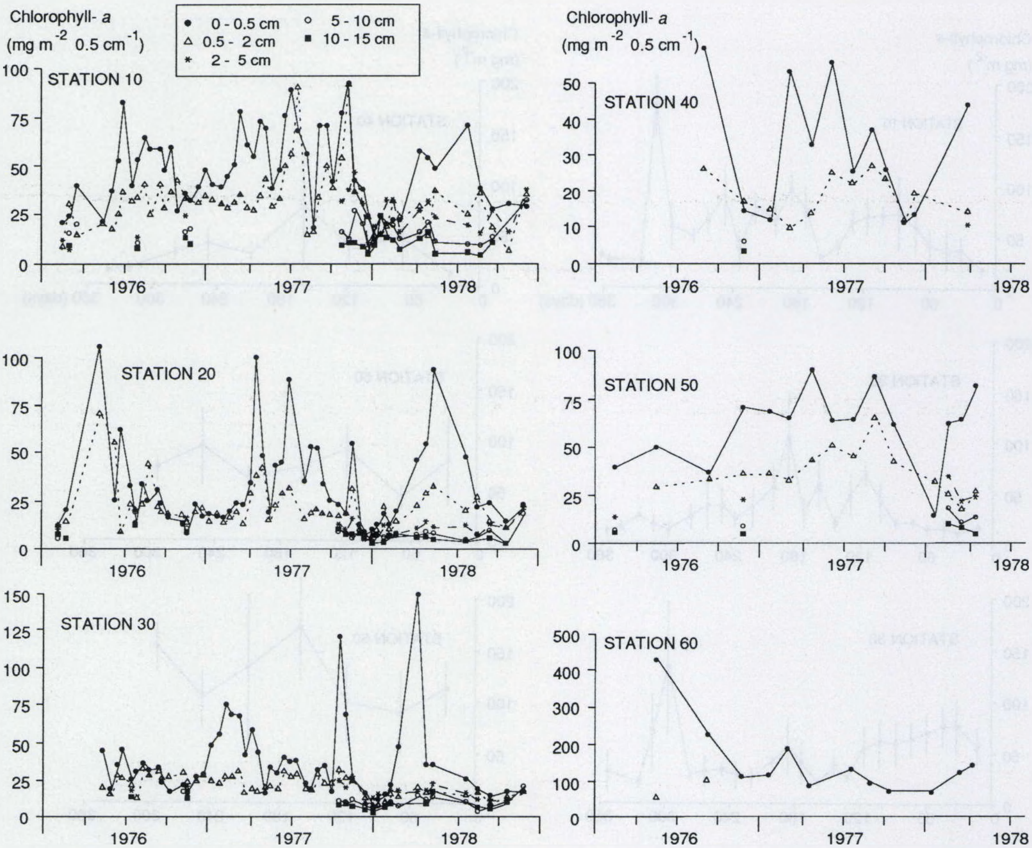

Fig. 5. Plots of the mean chlorophyll-*a* concentrations per depth (0-0.5 cm; 0.5-2.0 cm; 2.0-5.0 cm; 5.0-10.0 cm and 10.0-15.0 cm) for the six main stations. Data expressed as concentrations per 0.5 cm sediment layer.

was connected with the 0% value at the surface (Fig. 6b). This results in the graphs presented in Fig. 6c. These represent the vertical gradient in chlorophyll-*a* from sources other than vital algal cells. The graphs in Fig. 6d then represent the mean relative vertical distribution of chlorophyll-*a* from vital algal cells. This graph is assumed to reach a level of 0% chlorophyll-*a* from vital algae at a depth of 2.0 to 5.0 cm, which of course is an approximation and which is not necessarily completely true (cf. Admiraal *et al.*, 1988). The distribution in Fig. 6c is thought to be mainly derived from dead and partly degraded microphytobenthos.

The present estimation of the depth distribution of chlorophyll-*a* from vital algal cells also implies that in the 2.0-5.0 cm layer (cf. Fig. 6d) a small percentage of algal chlorophyll-*a* is still present (this is confirmed by Fig. 5, where it is shown that rather strong fluctuations can occur in chlorophyll-*a* at this depth too). Because of the calculation procedure, this amount must be assumed to be zero (cf. Fig. 6d). The same holds for the value of chlorophyll-*a* from non vital microphytobenthos in the top layer, which consequently is also assumed to be zero. Of course, also this assumption is not completely true, either. However, the distinction between chlorophyll-*a* from vital microphytobenthos or other sources ('detrital material') is necessary because without it the bulk of the algal chlorophyll-*a* (65 to 93%, cf. Table 3) is present far below the euphotic layer in the sediment which has a maximum thickness of 3 mm (Colijn, 1982). This means that only a very small percentage of the algal chlorophyll-*a* from vital cells is available to sustain this total mass or even to let it grow. From the graphs in Fig 6a and 6d a factor was calculated to convert the chlorophyll-*a* values from the pooled 0.5 to 2.0 cm layers, where a mixture of chlorophyll-*a* from vital algal cells as well as other sources is assumed to be present, into chlorophyll-*a* from vital microphytobenthos (cf. Table 3).

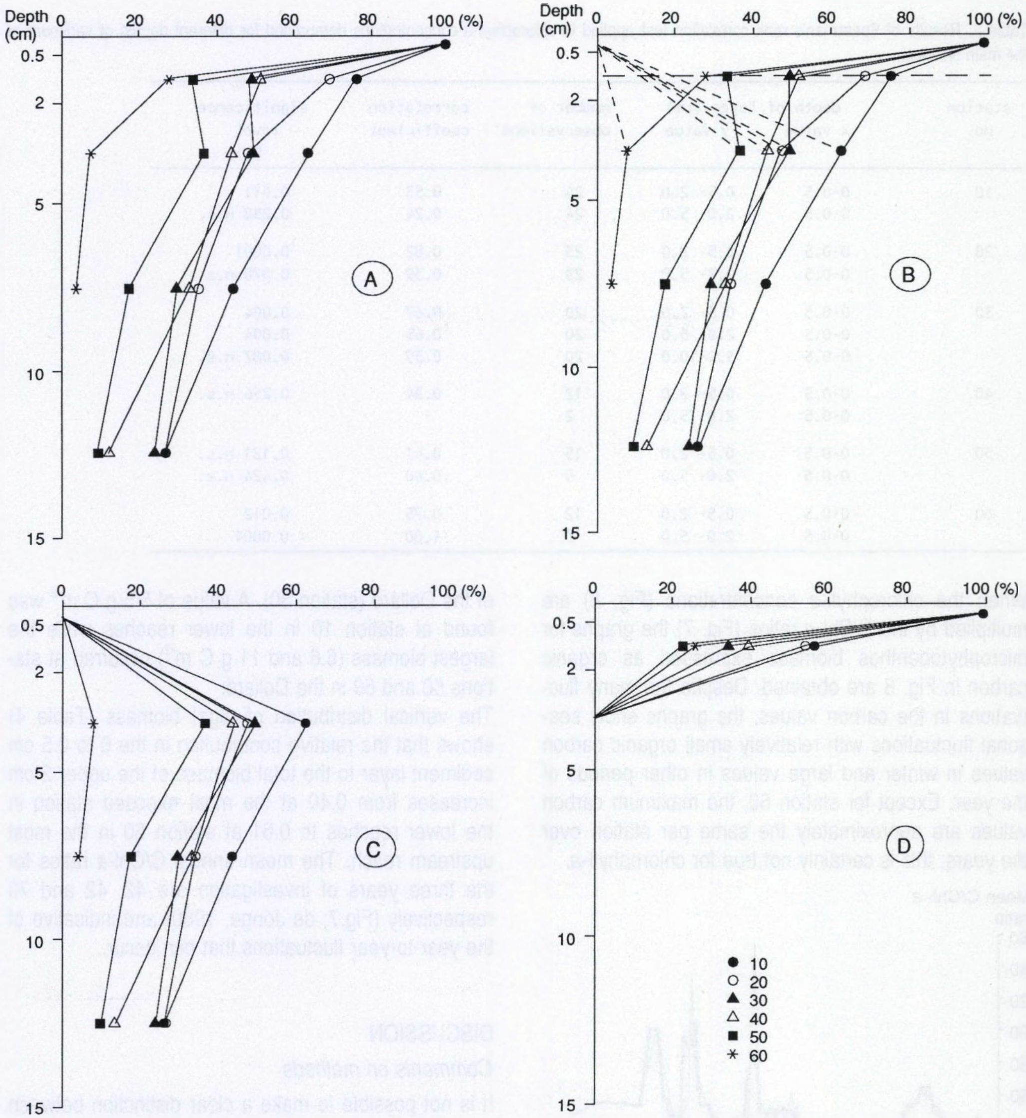

Fig. 6. Relative depth distributions of chlorophyll-*a* for the six main stations. A: distribution of mean total chlorophyll-*a*; B: proposed distinction between chlorophyll-*a* from vital microphytobenthos and other sources ('detrital') C: distribution of 'detrital' chlorophyll-*a*; D: distribution of chlorophyll-a from vital microphytobenthos.

Data published by de Jonge (1980) were used to calculate *running* C/Chl-*a* ratios over a period of five weeks (Fig. 7). This was done to prevent carbon biomass changing suddenly after the chlorophyll-*a* values had been multiplied by sometimes strongly fluctuating C/Chl-*a* ratios (cf. both graphs in Fig. 7). These values fluctuate seasonally. In general relatively small values were found in late winter or early spring and relatively large values occurred in summer (Fig. 7).

The seasonal pattern in the ratio is, however, not a simple sinusoidal one. As expected, the chlorophyll-a values in the 0-2.0 cm layer (Fig. 8, open triangles) show larger values during summer and smaller values during winter, but with the exception of station 20 a pronounced seasonal pattern is absent. This is true not only for the upper 2 cm but also for the upper 0.5 cm layer (Fig. 3).

Table 2. Results of Spearman's rank correlation test applied to chlorophyll-*a* concentrations determined for different depths of sediment at the main stations.

station no.	depth of layer (cm) x value	depth of layer (cm) y value	number of observations	correlation coefficient	significance level p
10	0-0.5	0.5- 2.0	24	0.53	0.011
	0-0.5	2.0- 5.0	24	0.24	0.258 n.s.
20	0-0.5	0.5- 2.0	23	0.82	0.0001
	0-0.5	2.0- 5.0	23	0.39	0.070 n.s.
30	0-0.5	0.5- 2.0	20	0.67	0.004
	0-0.5	2.0- 5.0	20	0.65	0.004
	0-0.5	5.0-10.0	20	0.39	0.087 n.s.
40	0-0.5	0.5- 2.0	12	0.34	0.256 n.s.
	0-0.5	2.0- 5.0	2	-	-
50	0-0.5	0.5- 2.0	15	0.41	0.121 n.s.
	0-0.5	2.0- 5.0	5	0.40	0.424 n.s.
60	0-0.5	0.5- 2.0	12	0.75	0.012
	0-0.5	2.0- 5.0	3	-1.00	< 0.0001

When the chlorophyll-*a* concentrations (Fig. 8) are multiplied by the C/Chl-a ratios (Fig. 7) the graphs for microphytobenthos biomass expressed as organic carbon in Fig. 8 are obtained. Despite the many fluctuations in the carbon values, the graphs show seasonal fluctuations with relatively small organic carbon values in winter and large values in other periods of the year. Except for station 60, the maximum carbon values are approximately the same per station over the years; this is certainly not true for chlorophyll-*a*.

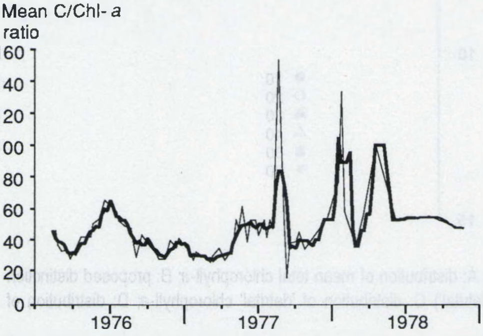

Fig. 7. Plot of the running mean C/Chl-*a* ratios of benthic diatom populations in the Ems estuary as calculated over a period of 5 weeks given as the fat solid line; the thin solid line represents weekly averages. After de Jonge (1980).

For comparison, Table 4 presents the mean annual values of chlorophyll-*a* and organic carbon for the different stations and sediment layers. The smallest total biomass (Table 4) with an overall mean value of approximately 3.5 g C m^{-2} was found in the middle reaches of the estuary (stations 20 and 40) and part of the Dollard (station 30). A value of 5.5 g C m^{-2} was found at station 10 in the lower reaches while the largest biomass (6.6 and 11 g C m^{-2}) occurred at stations 50 and 60 in the Dollard.

The vertical distribution of algal biomass (Table 4) shows that the relative contribution in the 0 to 0.5 cm sediment layer to the total biomass of the upper 2 cm increases from 0.40 at the most exposed station in the lower reaches to 0.61 at station 60 in the most upstream reach. The mean annual C/Chl-*a* ratios for the three years of investigation are 42, 42 and 70 respectively (Fig.7; de Jonge, 1980) and indicative of the year-to-year fluctuations that can occur.

DISCUSSION

Comments on methods

It is not possible to make a clear distinction between the biomass of vital microphytobenthos cells living on and in the sediment surface and detritus, using the available techniques. Every value produced is an estimate because none of the available parameters that can be measured (cell counts, organic carbon, chlorophyll-*a*, intact diatom frustules, etc.) unambiguously leads to the biomass expressed in organic carbon. Therefore, a calculation procedure was applied in this paper to obtain the best possible estimate of the chlorophyll-*a* in vital microphytobenthos.

We could have used a different procedure to correct for 'detrital' chlorophyll-*a*, starting from the assumption that the smallest chlorophyll-*a* concentration below the top layer is the 'detrital' chlorophyll-*a*.

Table 3. Relative and absolute chlorophyll-a values for layers sampled between the surface and 15 cm depth for all main stations. Further the corrected relative vertical distribution of chlorophyll-a, from which a correction factor for converting total chlorophyll-a in the 0.5-2.0 cm layer to chlorophyll-a from vital microphytobenthos (cf. the graphs in Fig. 6) is given. Concentrations are given per square metre and per 0.5 cm sediment layer. See table 2 for number of observations.

sediment layer	main stations 10		20		30		40		50		60	
	(mg Chl-a m^{-2})	(%)		(%)		(%)		(%)		(%)		(%)
0- 0.5	38.3	100	25.5	100	35.4	100	28.7	100	62.8	100	122.4	100
0.5- 2.0	29.0	76	17.6	69	17.3	49	15.1	52	21.7	34	34.2	28
2.0- 5.0	24.1	63	12.3	48	17.4	49	12.5	44	23.2	37	9.8	8
5.0-10.0	16.7	44	9.0	35	10.8	30	9.7	34	11.6	18	5.2	4
10.0-15.0	10.3	27	6.8	27	8.6	24	3.6	13	6.3	10	-	-
	Relative distribution of chlorophyll-a from vital microphytobenthos											
0- 0.5		100		100		100		100		100		100
0.5- 2.0		56.5		54.5		34		39		23		25.5
2.0- 5.0		0		0		0		0		0		0
5.0-10.0		0		0		0		0		0		0
10.0-15.0		0		0		0		0		0		0
Chl-a correction factor for 0.5-2.0 cm depth layer		0.74		0.79		0.69		0.75		0.68		0.91

Table 4. Mean annual values of chlorophyll-*a* and organic carbon for the main stations and the sediment layers.

		chlorophyll-a (mg m^{-2})			n	biomass (gC m^{-2})			n	biomass ratio
station	year	0-0.5 cm	0.5-2.0 cm	0-2.0 cm		0-0.5 cm	0.5-2.0 cm	0-2.0 cm		0-0.5 cm/ 0-2.0 cm
10	1976	44.2	66.2	110.4	19	1.93	2.76	4.69	19	
	1977	56.4	87.1	143.5	24	2.30	3.68	5.98	24	
	1978	34.1	51.0	85.1	13	2.49	3.50	5.99	12	
	mean	47.1	71.6	118.7	56	2.21	3.32	5.54	15	0.40
20	1976	29.3	59.6	88.8	16	1.28	2.42	3.70	16	
	1977	32.5	47.8	80.4	28	1.42	1.99	3.41	28	
	1978	26.4	40.6	67.0	17	1.99	3.00	4.99	16	
	mean	30.0	48.9	78.9	61	1.51	2.34	3.84	60	0.40
30	1976	28.7	51.2	79.9	15	1.31	2.20	3.51	15	
	1977	43.6	48.0	91.6	23	1.66	1.98	3.64	23	
	1978	32.0	28.4	60.4	13	2.67	2.07	4.74	12	
	mean	36.3	43.9	80.2	51	1.80	2.07	3.87	50	0.46
40	1976	73.0	47.8	120.8	2	1.34	1.72	3.06	2	
	1977	29.1	40.8	69.9	9	1.29	1.90	3.19	9	
	1978	43.1	30.8	73.9	1	2.40	1.71	4.11	1	
	mean	37.6	41.1	78.7	12	1.39	1.85	3.24	12	0.43
50	1976	48.2	50.6	98.8	4	1.83	1.92	3.75	4	
	1977	70.1	89.5	159.6	7	2.98	3.98	6.96	7	
	1978	55.1	50.8	105.9	4	4.52	4.35	8.87	4	
	mean	60.2	68.8	129.0	15	3.08	3.53	6.61	15	0.47
60	1976	247.4	172.1	419.5	3	10.16	6.51	16.67	3	
	1977	108.8	84.5	193.3	6	4.21	2.97	7.18	6	
	1978	107.3	66.7	174.0	3	8.32	4.73	13.05	3	
	mean	143.1	102.0	245.0	12	6.72	4.20	11.02	12	0.61

This implies that the chlorophyll-*a* concentration in the uppermost 2 cm should be reduced by this background value, because it can be hypothesized that the 'detrital' chlorophyll-*a* at depth equals the surface value, because of sediment turbation.

However, many negative biomass values are obtained for the top 0.5 cm layer of sediment when this assumption is applied to the available data. This suggests that the assumption that the 'detrital' chlorophyll-*a* is zero at the surface and increases with depth is more feasible. We calculated the difference in mean annual biomass for 1977 for stations 10 and 30, using both assumptions.

We found that the values for total biomass over the uppermost 2 cm at stations 10 and 30 was respectively 24% and 29% lower when the initial assumption was used. Despite this difference, the result is surprisingly good; but, as already mentioned, the disadvantage of the second procedure is that many negative biomass values occur and this restricts the usefulness of this correction method. Negative values may also have been caused partly by methodological inaccuracies because during these investigations the HPLC technique was not available to separate chlorophyll-*a* from other pigments (Riaux-Gobin *et al.*, 1987).

Another reason for reservation in the use of chlorophyll-*a* values from greater depths is caused by Lorenzen's, (1967) method in which two large values (acidified and non-acidified) are subtracted to obtain the required value. Also this is due to the lack of the HPLC method during our measurements. Thus, the deeper in the sediment the more unreliable values.

Meaning of the results obtained here.

It is important to determine the biomass of microphytobenthos accurately because this material provides food for grazers. As shown here part of this food is distributed through the sediment column whereas another part reaches the water column during high tide from where it is redistributed. To be able to convert chlorophyll-*a* into organic carbon accurately, reliable C/Chl-*a* ratios must be available for the different parts of the ecosystem (water, sediment surface and deeper sediment layers). But, these values are not available. We did, however, know the concentrations of chlorophyll-*a* at different depths in the sediment and the C/Chl-*a* ratios for living motile benthic diatoms collected from the top layer of the sediment. Still, it can be assumed that beneath the euphotic zone the general pool of organic carbon is utilised more rapidly than the chlorophyll-*a* (Admiraal and Peletier, 1979; Admiraal, 1984) and that the carbon extraction of the cells below the upper 2 cm layer, in which the chlorophyll-*a* levels follow each other closely, is more rapid than that of the upper 2 cm. This will result in the C/Chl-*a* ratios in the sediment declining. The deeper in the sediment, the smaller the ratio. This assumption formed the basis for the correction used here (cf. Fig. 6) to estimate the total biomass of the microphytobenthos.

The observations that chlorophyll-*a* can be found in significant concentrations at depths of 15 cm far below the 3 mm (at maximum) thick euphotic zone are consistent with data published by Moul & Mason (1957), Hopkins (1963), Taylor & Gebelein (1966), Pamatmat (1968), Steele & Baird (1968), Fenchel & Staarup (1971), Cadée & Hegeman (1974) and Colijn (1982). Only a few examples that are indicative for the relative depth distribution of vital algae cells in intertidal sediments are available. Joint (1981) published data on the depth distribution of both chlorophyll-*a* and fluorescing cells for an English estuary and showed that chlorophyll-*a* declined over the top cm. Below this depth the concentrations stabilized up to a depth of 9 cm. This is comparable with the figures presented here. The decline in cell numbers is also noteworthy. Most of the cells are present in the top 2 cm and the relative contribution of cells beneath 4 cm depth is insignificant. Baillie (1987) working on soft sediments showed that the bulk of the microphytobenthos cells are present within the upper 2 to 3 cm. Larger cells were most numerous at a depth of approximately 2 cm. Admiraal *et al.* (1988) gave some examples of a depth distribution at 3 different localities in the Ems estuary. The distributions clearly show the restricted depth to which diatoms are found at station 60 (cf. also Fig. 6; station). Benthic diatoms from station 50 had a distribution that reached depths of approximately 10 cm, whereas small (most probably sand-adhered) diatom cells at station 10 reached depths of 15 cm. Cell numbers declined over the top 2 to 5 cm here too. Note, however, that the cell numbers in sandy sediments like those occurring at transect 1 can reach reasonable numbers even at depths of 15 cm. These cells, however, are very small and despite their numbers do hardly contribute to the biomass. Although, the figures published elsewhere do not show how microphytobenthos biomass varies with depth they partly illustrated that microphytobenthos biomass is not important at depths below 5 cm, the boundary condition used in the calculations.

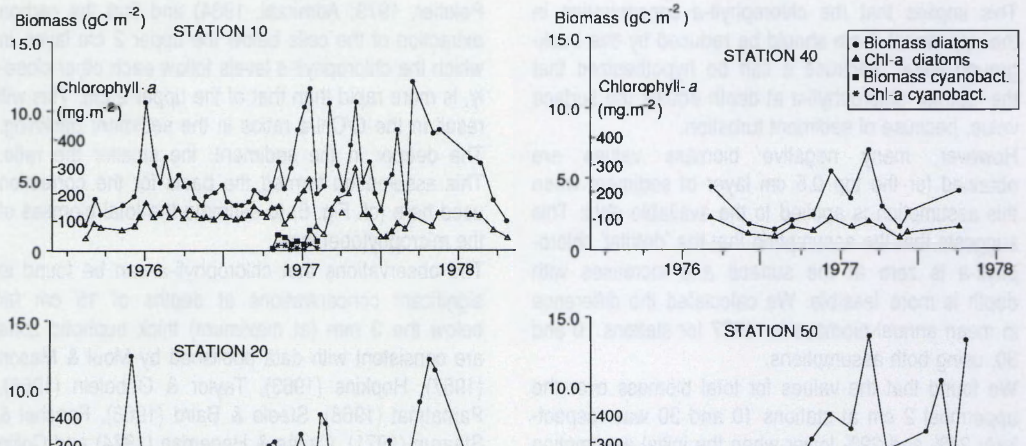

Fig. 8. Plots of the microphytobenthic biomass in the uppermost 2 cm expressed in chlorophyll-*a* and organic carbon per sampling date for the main stations. Carbon values obtained by multiplying the C/Chl-*a* ratios (Fig. 7) by the sum of the chlorophyll-*a* values of the 0.5 cm sediment layer (Fig. 3) and the corrected values for the 0.5-2.0 cm layer (cf. Fig. 6).

Buried diatoms can play an important role in the survival of certain populations, by employing adaptation mechanisms as the uptake of dissolved organic compounds (Admiraal, 1984).

The distribution of biomass with depth (Fig. 6d) of the benthic diatoms should be assessed under field conditions. Although the present analysis of the depth distribution of the microphytobenthos was not available at the time of the final BOEDE report on modelling the ecosystem of the Ems estuary (Baretta & Ruardy, 1988), the graphs presented in Fig. 6d correspond very well with the graphs of relative biomass in Baretta & Ruardy (op cit., Fig. 7.3). Interestingly, the previously published graphs were not solely based on preliminary analyses of field data but also on practical considerations as food availability for grazers and theoretical considerations as P/B ratios. When the biomass values calculated in this study for the upper 0.5 cm and the upper 2.0 cm layers are compared with model calculations (Baretta & Ruardij, 1988; p. 206), the values are found to be of the same order of magnitude. In that study the total biomass in a sediment column of 30 cm was calculated to range from 2 - 25 g C m^{-2} whereas the amount in the top 0.5 cm ranged from 1 - 10 g C m^{-2}. Thus, the total biomass in the total column was, on average, only twice that of the 0.5 cm top layer, except for station

60 where 75% of the total biomass was present in that layer. Within the top 5 cm the mean total biomass ranged from 97% (in the area of station 60) to 87% (in the area of station 10). These values correspond very well with our results.

In our study we disregarded the differences in the relative distribution of microphytobenthos with depth between stations (Admiraal *et al.*, 1988) because only a limited data set was available on this vertical distribution (cf. Fig. 5 and Table 3).

Chlorophyll-*a* measurements from the top 0.5 cm are often used to calculate the microphytobenthos biomass in the sediment, but this leads to two significant underestimations of the available biomass for grazers. The first underestimation is caused by the seasonal change in C/Chl-*a*, resulting in a clear seasonal fluctuation in algal carbon but not in chlorophyll-*a* (Fig. 8). This seasonal figure for chlorophyll-*a* seems very common at our latitude. Steele & Baird (1968), Pamatmat (1968), Leach (1970), Cadée & Hegeman (1974) and Colijn & de Jonge (1984) also reported only moderate differences if at all in microphytobenthos chlorophyll-*a* between winter and summer, suggesting that biomass differences between summer and winter are small. The second important underestimation is caused by using only the top 0.5 cm of the sediment. In that case only 50-75% of the total biomass is taken into account; this results in a "biomass" value which is 100-150% too small (cf. Table 4). The use of an 'incorrect' C/Chl-*a* ratio can increase this deviation by a further 50% (see above). This underlines the importance of using the proper depth distribution of the diatom chlorophyll-*a* as well as the proper C/Chl-*a*.

Processes controlling the dynamics of microphytobenthos

The biomass (organic carbon) graphs presented in Fig. 8 show an irregular seasonal pattern. The causes for temporary reductions in the microphytobenthos biomass could be grazing, bad light conditions because of overcast skies, bioturbation, mortality, lunar-induced changes in tidal currents and changes in wave action caused by changing wind speed. There is a seasonal fluctuation in the activity of the biotic components (grazers and burrowers) that can cause a biomass reduction in microphytobenthos (cf. Admiraal, *et al.* 1983). Despite, calculations presented by Montagna (1984) and Gould & Gallagher (1990), it is improbable that mainly grazers and burrowers are responsible for the sometimes strong changes in the biomass concentrations observed within a period of only 14 days (cf. Fig. 8: 1977 carbon graphs). This leaves us with light (clear or dull summers), tidal currents (spring - neap cycle) and wind-induced waves as the most likely factors to have caused the irregularities. Considering the changes in wind speed, and given the results of a study of the resuspension process in this estuary (de Jonge & van Beusekom, this thesis.) it seems probable that the strong reductions in microphytobenthos biomass in the upper sediment layers coincide with periods of relatively high wind speed (cf. also Colijn & Dijkema, 1981). As explained by de Jonge & van Beusekom (op cit.) not only wind-induced waves but also the tidal currents contribute to the resuspension of microphytobenthos. However, their results indicate that the wind-induced waves are far more important than the tidal currents. This means that the wind-induced waves remain as the main cause for resuspension (transport between tidal flats and channels is brought about by the tidal currents) whereas the light conditions [indicated by station elevation (Admiraal & Peletier, 1980), solar radiation and water turbidity (Colijn, 1983: p 104)] are responsible for microphytobenthos growth as reported by Colijn & de Jonge (1984). The combined effect of these factors leads to a pattern as presented in Fig. 9 when the mean biomass over the whole research period per station is plotted as a function of the station elevation. Of course this picture is very similar to the relation between annual primary production of the

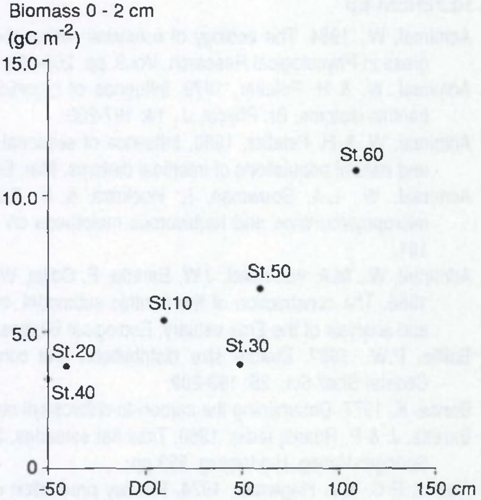

Fig. 9. Plot of the 3-year mean values of the microphytobenthos organic carbon against the elevation of the sampling station. Main stations only.

microphytobenthos reported for the same stations by Colijn & de Jonge (1984) who found a fair correlation between the mean annual chlorophyll-*a* concentrations in the uppermost 0.5 cm sediment layer and the annual primary production.

CONCLUSIONS

1. The seasonal variation of microphytobenthos biomass expressed in terms of carbon significantly differs from that expressed in chlorophyll-*a*.
2. The bulk of the organic carbon of the microphytobenthos is present in the uppermost 2 cm sediment layer. Within this layer 40 to 60% of this biomass is present in the uppermost 0.5 cm sediment layer.
3. The mean annual value for total microphytobenthos biomass in the uppermost 2 cm sediment layer and measured over a period of three years on six permanent plots ranges from 3.1 g C m^{-2} (28.6 mg Chl-*a* m^{-2}) to 16.7 g C m^{-2} (247 mg Chl-*a* m^{-2}).
4. The strong dynamics in the biomass of microphytobenthos are ascribed to resuspension by wind-induced waves rather than to grazing by herbivores.

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PRIMARY PRODUCTION OF MICROPHYTOBENTHOS IN THE EMS ESTUARY

F. Colijn and V.N. de Jonge

ABSTRACT

From 1976 through 1978 primary production of microphytobenthos was measured at 6 stations on intertidal flats in the Ems estuary using the ^{14}C method. The purpose of the measurements was to estimate the annual primary production at different sites in the estuary and to investigate the factors that influence the rates of primary production. Therefore benthic chlorophyll-*a* and a set of environmental factors were measured. Only primary production correlated significantly with chlorophyll-*a* concentration in the superficial (0.5 cm) sediment layer; other factors (temperature, *in situ* irradiance) did not correlate with primary production, primary production rate or assimilation number. Annual primary production ranged from c. 50 g C m^{-2} to 250 g C m^{-2} and was closely related to elevation of the tidal flat station. However, highest values were also recorded at the station closest to a waste water discharge point in the inner part of the estuary. Annual primary production can be roughly estimated from the mean annual content of chlorophyll-*a* in the sediment. Use of different calculation methods results in annual primary production values that do not differ greatly from each other. Also productivity rates did not differ much over most of the estuary, except at the innermost station which showed a high production rate in combination with high microalgal biomass; this could not be explained by the high elevation of the station alone. A hypothesis is offered to explain the limited primary production of microphytobenthic vegetations.

INTRODUCTION

The radio carbon (^{14}C) method (Steemann Nielsen, 1952), although subject to several errors (cf. Colijn *et al.*, 1983) (for review see Peterson, 1980), has been widely adopted to measure phytoplankton primary production in different habitats. With modifications, this method has also been used several times for the measurement of phytobenthos primary production in intertidal areas and shallow coastal seas (Grøntved, 1960; Steele & Baird, 1968; Gargas, 1970; Leach 1970; Cadée & Hegeman, 1974, 1977; Plante-Cuny, 1978). In other, similar habitats, primary production has further been measured by means of the oxygen bell-jar technique (Pomeroy, 1959; Pamatmat, 1968; van Es, 1982a; Lindeboom & de Bree, 1982). All these studies aimed essentially at estimating annual primary production and community respiration (in case of oxygen method) and at explaining how these processes are affected by abiotic and biotic factors.

The soft, sandy and muddy, sediments of the Ems estuary do not harbour a conspicuous vegetation of macroalgae; however, a thin film of diatoms and cyanobacteria covers the sediment surface. These are the main primary producers on intertidal flats (Cadée & Hegeman, 1974; Admiraal, 1980; Colijn & Dijkema, 1981). The purpose of our study was to measure *in situ* photoautotrophic carbon fixation of sediments at different sites. The programme included measuring chlorophyll-*a* content of the superficial layers of sediment; solar radiation; temperature; salinity; tidal emersion during daylight; and characterization of the type of sediment. Considerable effort was devoted to estimating the annual primary production, which can be calculated using a combination of data on tidal emersion and daylight periods. Physiological experiments and field investigations on benthic diatoms from the same estuary were made by Admiraal (l977a, b, c) and Admiraal & Peletier (1980). Results of recent measurements of primary production in the same estuary obtained with the oxygen method, were also available (van Es, 1982a).

In addition to the factors that directly regulate primary production - such as light and nutrients - we were also interested in the effects of indirect factors - such as grazing, burial, transport, sedimentation, resuspension and mortality of microphytobenthos and phytoplankton. Measurements of both phytoplanktic and microphytobenthic production (Colijn, 1978) should elucidate the quantitative importance of organic matter input derived from primary producers in the Ems-Dollard ecosystem as opposed to the allochthonic organic matter input from the North Sea (cf. de Jonge & Postma, 1974), the River Ems and the River Westerwoldsche Aa (van Es, 1982b).

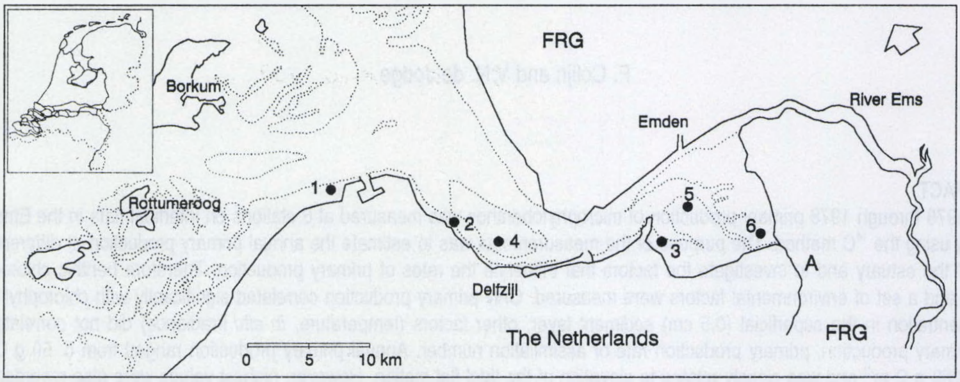

Fig. 1. Ems-Dollard estuary with location of sampling stations:(1-6). A = Westerwoldsche Aa.

MATERIAL AND METHODS

Area and sampling stations

The Ems estuary (Fig. 1) is one of the larger estuaries in the Wadden Sea. A particular feature of this estuary is the Dollard, a shallow sheltered embayment into which the Westerwoldsche Aa discharges only small amounts of freshwater, loaded with high concentrations of organic matter. For our research, measurements were regularly taken at 6 stations on intertidal flats (Fig. 1); all stations, except Station 2, were situated ca. 600 m from a larger tidal channel (Station 2: 50 to 100 m) to avoid the direct scouring influence of channel water. Stations 3, 5 and 6 were located in the Dollard, and station 6 is in the direct vicinity of the wastewater outlet. The sediment type at each station has been described by van Es (1982a: Table 1) and is fairly representative of the range of sediments found in the estuary. No macroalgal growth was found at the stations; however, diatoms with gelatinous tubes occasionally formed macroscopic tufts; their patchy distribution made adequate sampling difficult. All the sampling and measuring were done at low tide.

Incubation techniques and sample preparation

Benthic primary production was measured in 3 perspex cylinders (2 light and 1 dark), each 6.0 cm in diameter and 15 cm long, as described by Leach (1970). Immediately after being mixed with 2 to 20 µC ^{14}C, 50 ml water was carefully added to each cylinder through a rubber cap. Remaining air was expelled by pressing the cylinders more deeply into the sediment. The incubators were kept in the sediment for 2 to 3 h. The incubation water was obtained from shallow pools on the tidal flats or from nearby gullies. Following the incubation period, the cylinders were brought to the laboratory or the research vessel in a dark box and processed within h. Inorganic carbon was measured in the incubation water according to the method of Strickland and Parsons (1972). The added amount of ^{14}C was determined threefold. Light and dark serum bottles containing 50 ml of unfiltered incubation water were used as controls: fixation rates in these bottles were negligible and therefore no corrections were applied to fixation rates of the sediments itself. The temperature of the superficial sediments was measured at the beginning and end of the incubation period. For chlorophyll-*a* analysis, 20 sediment samples were taken regularly distributed over a 50 x 50 m permanent plot with a corer (internal diameter 2.4 cm). Chlorophyll-*a* was measured according to Lorenzen's (1967) method with slight modifications: the upper 0.5 cm thick sediment layer was cut off and put into a centrifuge tube; all samples were deep-frozen and lyophilized to prevent inaccuracies resulting from differences in water content and to facilitate extraction; the dried sediments were extracted in 10 or 15 ml of aqueous aceton (90%) with the addition of magnesium carbonate, centrifuged off and the supernatants measured in a colorimeter at 664 nm. No corrections for turbidity at 750 nm were made. A correction for pheopigments was made by acidification (Lorenzen, 1967). Irradiance in J cm^{-2} was measured continuously at 10 min intervals at Delfzijl (Fig. 1) with a Kipp solarimeter (Fig. 2).

Measuring ^{14}C activity

Uptake of label was measured as follows: incubation water with a little suspended sediment was filtered through a glass fibre filter (Whatman GF/C)(Fraction 1). Then a layer of sediment, 0.5 to 1.0 cm thick, was sliced off the sediment column. Approximately a quarter of this layer was used to make a slurry which was filtered (Fraction 2) and washed with filtered seawater to remove the added inorganic ^{14}C. Both fractions (1 and 2) and the remainder of the sediment were wrapped in weighted alufoils and immediately dried in a stove at 70°C to prevent further biological activity.

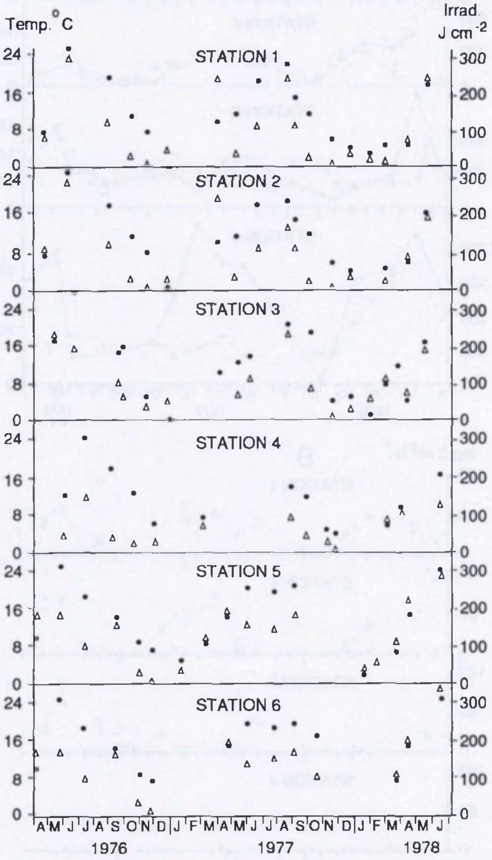

Fig. 2. Temperature (•) and irradiance (J cm^{-2} h^{-1})(△) during field incubations

Excretion rate was not measured, because other researchers (Cadée & Hegeman, 1974; Darley *et al.*, 1976) have shown that excretion in microphytobenthos is very low (a few % of the totally fixed carbon; see also Chapman & Rae, 1969; Hall & Fischer, 1982). To avoid problems in scintillation counting, a combustion method (Packard 306 Sample Oxidizer) was tested and used for dried sediments as well as for phytoplankton samples on filters loaded with sediment. The method was tested with labelled algae mixed with increasing amounts of sediment. In all cases the recovery of ^{14}C exceeded 95% (cf. Revsbech *et al.*, 1981). Drying at 70°C did not result in loss of activity as compared with samples combusted immediately after filtration. Quench curves were made with hexadecane ^{14}C (by weight) as an internal standard, and later with the direct combustion of labelled methyl-methacrylate-^{14}C (New England Nuclear, 35000 dpm) and paper strips with a ^{14}C standard which contained 5000 dpm (Radiochemical Centre). The scintillation mixture for counting the concentration of added ^{14}C in aqueous samples was composed of BBS-3 (Beckman) 20% in toluene, and later in an Aquasol Phenethylamine mixture (5:1 v/v) (Iverson *et al.*, 1976). The counting efficiencies were almost the same (ca. 80%) in these 2 mixtures.

After drying and mixing well in a mortar, 3 sediment subsamples were weighed (ca. 100 mg) and each combusted separately in a piece of filter paper. For all calculations of the total ^{14}C uptake, the weight of the sediment fraction was used, together with the radioactivity of the two filters and in both fractions (1 and 2). All data were expressed in mg C m^{-2} h^{-1}.

Calculations

Hourly fixation rates (Fig. 3B) (not corrected for dark uptake of ^{14}C) were assumed to reflect the net assimilation rates (Williams *et al.*, 1979). These rates were multiplied by the actual emersion period of the day on which these samples were taken, to calculate the daily production (Fig. 3A). The emersion period was determined from the actual recorded tidal curves (Rijkswaterstaat, Meet- en Adviesdienst, Delfzijl) and the elevation of each station. Five different methods were used to estimate annual production (Table 1) and to evaluate possible differences in annual production caused by different calculation methods.

For these calculations average emersion periods during daylight for each station were calculated from a linear regression of the measured annual effective photoperiods against the elevation of the stations (Table 3). Annual production per station was taken as the means of the values over two successive years. Effective photoperiods in Method V were derived from the interaction of daylength and tidal emersion (Colijn, 1982).

For all calculations given, we assumed that no irradiance reached the surface of the sediment during submersion (see 'Discussion').

Table 1. Methods for calculation of annual primary production. Effective photoperiod = emersion during daylight

Method I:	Interpolation of hourly rates between measurements x effective photoperiods for all days = production value per day; summation of all daily values gives annual production
Method II:	Hourly rate x effective photoperiod = production value per measuring day; planimetry of resulting annual graph (Fig. 3A)
Method III:	Hourly rate x mean annual emersion period (%) x daylength of measuring day = production value per day; planimetry of resulting annual graph
Method IV:	Monthly average of hourly rates (Stations 1 to 5 and 6) x actual monthly effective photoperiods = monthly production value; summation of monthly values
Method V:	Monthly average of hourly rates (Stations 1 to 5 and 6) x calculated monthly effective photoperiod from model = monthly production value; summation of monthly values

RESULTS

Production and chlorophyll-a measurements

Daily production values (mg C m^{-2}) and mean chlorophyll-*a* data (mg m^{-2}) are given in Fig. 3A, and the actual hourly rates are given in Fig. 3B. Production values per day were calculated by multiplying the hourly rate by the actual effective photoperiod on the day of measurement. Low daily values were found at all stations in winter, especially in November and December. High daily values were recorded both in spring and summer. The measurements at Station 6 were atypical: both chlorophyll-*a* and production showed comparatively high values during a large part of the year. The mean hourly rates per month showed a large month to month variation in these fixation rates; hourly rates were lowest in November and December, and during the rest of the year higher fixation rates were found almost irrespective of the season. However, if the data from Station 6 were omitted, the mean hourly rate was highest in April.

The fixation rates at Station 6 reached values of up to 100 mg C m^{-2} h^{-1}, or 1300 mg C m^{-2} d^{-1}. The mean hourly rate for all stations over 2 year was c. 37 mg C m^{-2} h^{-1}. However, this mean hourly rate was twice as high at Station 6. The mean assimilation number (production rate per unit of chlorophyll-*a*, mg C mg Chl-a^{-1} h^{-1}) for all measurements was 0.67. The maximum mean value (0.49) per station was found at Station 2, the minimum mean value (0.43) at Station 6. However, owing to the wide range in assimilation numbers per station, these mean assimilation numbers per station did not differ significantly from each other (ANOVA, F_0 (5,89) = 2,57; 0.05> P > 0.025).

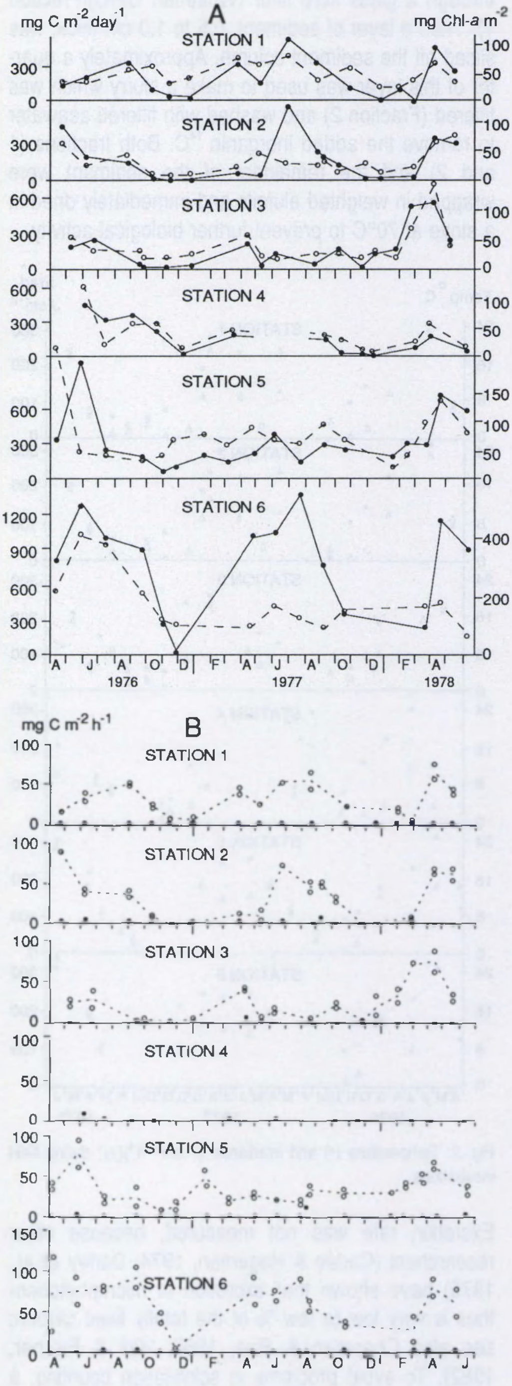

Fig. 3(A). Daily primary production and chlorophyll-a at the 6 stations ((•) mg C m^{-2} d^{-1}; (o) mg Chl *a* m^{-2})

Fig. 3(B) Primary production rates and dark uptake rates (mg C m^{-2} h^{-1}). Means of light values (o) are connected; dark values (•)

Chlorophyll-*a* concentration ranged from low winter values of 10 mg m^{-2} at Station 2 to high summer values of up to 400 mg m^{-2} at Station 6. At the other stations, values above 100 mg m^{-2} were occasionally measured during short blooms. Mean values ranged from c. 30 mg m^{-2} at Station 2 to c. 190 mg m^{-2} at Station 6. Stations 1 to 4 showed approximately the same average value, whereas Station 5 showed a higher value, intermediate between those of Stations 1 to 4 and Station 6. A linear regression of all production rates against all chlorophyll-*a* concentrations revealed a positive correlation between these 2 variables ($r = 0.5515$, $n = 95$, $P < 0.001$, Fig. 4).

A positive correlation was also found between these variables for each of the Stations 1 to 4, but not for Stations 5 and 6 (Table 2). This special feature of Stations 5 and 6 is caused by the comparatively low fixation rates at high chlorophyll-*a* concentrations (Fig. 4) which suggests that carbon fixation reached saturation values at higher chlorophyll-*a* values.

Station	n	Slope	Y intercept	r^2	P
1	16	0.6652	-1.98	0.3351	0.05
2	17	0.9938	1.26	0.4465	0.01
3	17	0.6431	-0.38	0.6416	0.01
4	13	0.6871	7.99	0.5826	0.01
5	18	0.1043	25.95	0.0811	n.s.
6	14	0.0854	50.54	0.0846	n.s.
1-6	95	0.2220	21.74	0.3042	0.01
1-4	63	0.6705	4.01	0.4422	0.001

Table 2. Regression of primary production rate against chloro-phyll-*a* concentration in the top 0.5 cm of sediment, for each of the 6 stations.

Temperatures and irradiances measured simultaneously with the field incubations are presented in Fig. 2. Both temperature and irradiance reflected seasonal changes and showed a weak positive correlation ($r = 0.4487$), which was statistically significant ($P < 0.001$). Both factors correlated positively, but weakly with the hourly production rate ($r = 0.3843$ and 0.3643, $n = 95$, $P < 0.01$, respectively). This correlation was not significant for the data of each individual station, because of the marked variation in production rates and the paucity of observations.

Also, the assimilation number did not show a significant correlation, either with irradiance, or with temperature.

Annual production

The estimates of annual production as calculated by the 5 methods described above are presented in Table 3. Methods, I II and III gave almost identical results. Surprisingly, annual production values based on the accurately determined photoperiods (I) were almost the same as those based on the rougher Methods II and III. The results obtained by Methods IV and V were in close agreement with each other but differed from the results obtained by Methods I to III: at all stations except at Station 3, annual production on the basis of mean monthly production values mg C m^{-2} h^{-1}) was lower than on the basis of actually measured production values. The differences in annual production values calculated by Methods IV and V are completely determined by the elevation of the stations and the tidal range, in other words, by the effective photoperiod. The percentual agreement between the results obtained by Methods IV and V proves that the calculation of the effective photoperiods with the model is in accord with actually measured photoperiods (Table 3, Methods IV and V).

The linear extrapolation of the tidal emersion effect (Table 3, Methods IV to V) would result in an expected production of c. 110 g C m^{-2} a^{-1} at Station 6. The actual value was roughly twice as high, because of the much higher production rate at this station, notwithstanding the relatively low mean assimilation number. The atypicality of this station in the estuary is also reflected by the very high chlorophyll-*a* values (Fig. 3A).

Dark ^{14}C fixation values (Fig. 3B) showed no correlation with production rate, temperature, or station number. The mean value was 2.09 mg C m^{-2} h^{-1}, which is 5.6% of the mean hourly production rate. As pointed out under Material and Methods we assumed that primary production only occurred during emersion. Obviously, this holds for the turbid inner part of the estuary, but not for the outer part with much clearer waters. Therefore, we calculated, using the characteristic values of Station 1, the effective light period which is defined now as the emersion period plus the submersion time, when photosynthetic active radiation (PAR) at the sediment surface exceeded 25 W m^{-2}. This value is assumed to equal the saturation irradiance (Colijn & Van Buurt, 1975). With these assumptions the total effective light period increases by 25%.

Table 3. Annual primary production in g C m^{-2} at 5 stations in the Ems estuary as based on 1 set of data and 5 different methods of calculation ('Material and Methods'), together with the mean chlorophyll-*a* concentration and the mean emersion period (as % of tidal cycle) of each station. All annual production values are exclusively based on the emersion periods of the stations. DOL = Dutch Ordnance Level = approximately mean sea level

Method	Station					
	1	2	3	4	5	6
I	81	62	62	62	99	245
II	77	56	59	61	106	256
III	76	57	67	58	101	245
IV	73	57	82	53	99	200
V	70	54	84	51	98	214
Mean chlorophyll-a (mg m^{-2})	49	33	42	40	77	184
Station elevation (m DOL)	0	-.4	+.3	-.5	+.7	+1.1
Average annual emersion (%) during daylight	49	37	57	35	69	80

For Station 1 this would increase the annual primary production from 70 to 89 g C m^{-2} (Method V). Although we had no measurements during submersion to check this estimate, it seems to be realistic (cf. Cadée & Hegeman, 1974).

DISCUSSION

Methodology

The problem of self-absorption normally encountered when one determines radiocarbon in sediment samples can be solved in several ways. In liquid scintillation counting, high counting efficiencies are easily obtained by suspending the sediment in a gelling scintillation cocktail (Skauen *et al.*, 1971; Cadée & Hegeman, 1974, 1977). However, only small amounts of sediment can be subjected to this procedure, especially as the sediment contains silt with high quenching properties. The acid digestion method (van Raalte *et al.*, 1974) has proved to be unsuccessful, because of an unexplained low recovery. The combustion method which we adopted lacks the above disadvantages. Thus we could process samples of up to a few 100 mg of dry sediment with almost 100% recovery and reach counting efficiencies of c. 75 %. However, the non-uniform distribution of the labelled incubation solution in the upper sediment layer is a problem (cf. Colijn & van Buurt, 1975). Also, the concentrations of inorganic carbon in the upper sediment layers may differ from the concentration in the incubation water (Klein, 1981; Revsbech *et al.*, 1981; Lindeboom & de Bree, 1982). A few measurements of the concentration of total inorganic carbon showed (unpublished results of F. Colijn) that the surface water film and the 0 to 2 mm deep layer had minor differences in inorganic carbon content (cf. Revsbech *et al.*, 1981). Because we did not measure the specific activity of $H^{14}CO_3^-$ in the upper sediment layers, there is some uncertainty about the actual fixation rates in these layers. According to Revsbech *et al.*, (1981) this may cause an underestimation of the fixation rate in deeper layers up to a factor of 2 to 5. The very small light penetration in our sediments (Colijn, 1982) may well reduce this error, because the maximal photosynthetic rates take place within a layer of only 0.5 mm (Revsbech and Jørgensen, 1983). An advantage of the in situ method is that the sediment with the microalgal layer stays intact and that the flux of nutrients including bicarbonate from the deeper sediment layers is not disrupted. Measurements of nutrient concentrations in channel waters in the Dollard have shown that these nutrient concentrations usually are high (de Jonge & Postma, 1974; Rutgers van der Loeff *et al.*, 1981).

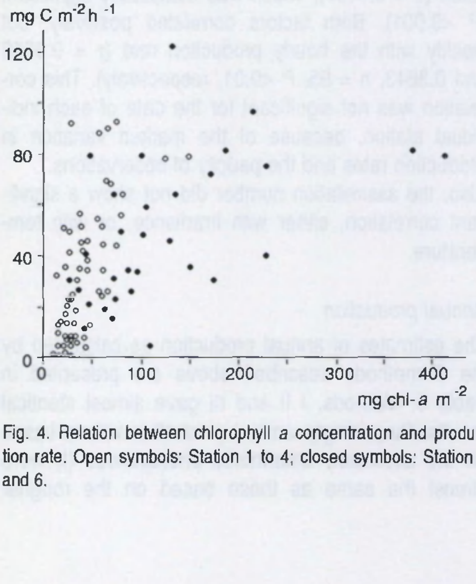

Fig. 4. Relation between chlorophyll *a* concentration and production rate. Open symbols: Station 1 to 4; closed symbols: Station 5 and 6.

Nutrient limitation is not necessarily occurring in the thin film of water overlying the mud flat since nutrient uptake and photosynthesis are not always coupled (Eppley, 1981). We think that, generally, nutrients will not act as a limiting factor for the growth of the microphytobenthic vegetation in the Ems estuary (cf. Admiraal *et al.*, 1982).

In our investigation, the sample surface (c. 28 cm^2) was large enough to prevent 'edge effects' from playing an important role, as can easily occur with very small samples (Marshall *et al.*, 1973; cf. Cadée & Hegeman, 1974). The water flow, which is an inevitable consequence of the bell-jar technique (van Es, 1982a), creates a major problem. Generally, stirring stimulates both macroalgae and sediment-inhabiting microalgae to give higher production values (UNESCO manual, 1973; Boynton *et al.*, 1981; Revsbech *et al.*, 1981), possibly by improving CO_2 exchange (Admiraal *et al.*, 1982), or by removing inhibiting O_2, or by suspending algae and thereby increasing their average illumination. An increase in production, however, is not always found (Hargrave *et al.*, 1983). In our view, microphytobenthos on intertidal flats is not subjected to any appreciable water flow during emersion, and therefore the best imitation of the natural emerged environment should be a non-stirred incubator. Not even such a non-stirred incubator fully reproduces conditions on a natural emerged sand- or mudflat (Darley *et al.*, 1976). However, Darley *et al.* found that during 1 h experiments air-incubated samples showed a linear uptake of label at a rate comparable with that shown by submerged samples. A recent study (Holmes & Mahall, 1982) revealed that flooding with a 1 to 2 mm layer of agitated water reduced net photosynthetic rates by c. 50%. Although the cause of this reduction was not given, it is reasonable to infer that the reduction was the result of the microalgae migrating into deeper layers. During our measurements we never observed a visual downwards migration of diatoms.

Production rate, algal biomass and environmental factors

Possible relationships between primary production and environmental factors can be established by applying stepwise multiple regression analysis (van Es, 1982a). This analysis showed that only chlorophyll-*a* values explained the variation in production values for all station, but other factors (temperature and irradiance) made a very inconsistent contribution to the variance. Although the main goal of our study was to establish the annual primary production in the Ems estuary (with an area of c. 500 km^2), knowledge on the factors regulating this production is also important. The significant positive correlation between algal biomass (expressed as mg Chl-*a* m^{-2}) and the production rate (Colijn & Venekamp, 1977; Plante-Cuny, 1978) should enable us to make rough estimates of the primary production over greater areas without time consuming production measurements. A statistically significant correlation was found between mean annual production (Method I) and mean chlorophyll-*a* concentration over the same period ($r = 0.9973$, $n = 6$, $P < 0.001$; without Station 6: $r = 0.9689$, $n = 5$, $P < 0.01$) (Table 2, Fig. 5).

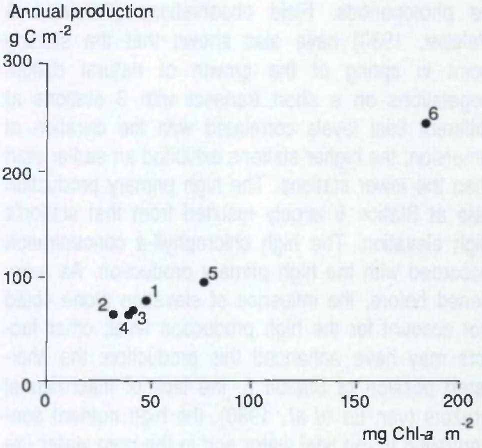

Fig. 5. Relation between annual mean chlorophyll-*a* concentration and annual primary production for 6 stations studied.

A similar, close correlation between mean annual chlorophyll-*a* content and annual production was found by Cadée & Hegeman (1977) in the Western Wadden Sea. However, the slope of their regression line is less steep than ours; the reason for this difference is that their chlorophyll-*a* measurements included sediment to a depth of 1 cm, while ours included sediment only to a depth of 0.5 cm. Thus, we agree with Cadée and Hegeman, that the annual microphytobenthic production can be estimated on the basis of relatively few chlorophyll-*a* samples distributed over the year. On the other hand, this method yields only a limited insight into the year-round variability of the primary-produced organic carbon available for estuarine processes of grazing, burial, transport and mortality. Daily production rates and chlorophyll-*a* concentrations were expected to increase with increasing elevation of the stations.

However, biomass only increased in this way at Stations 5 and 6, and production rates were only relatively high at Station 6. A significant positive correlation between primary production and tidal level was also found by Cadée & Hegeman (1977), and we agree that this is caused by the longer effective photoperiods on the more elevated tidal flats. This is supported by Admiraal (1977a) who investigated the minimum irradiance requirement of benthic diatoms in culture. Extrapolation of these and other literature data (Colijn, 1982) shows that a minimum irradiance for saturating diatom growth occurs during most of the year; only during winter may irradiance be limiting (Colijn & Dijkema, 1981; Colijn, 1982) through the combination of low solar irradiance and short effective photoperiods. Field observations (Admiraal & Peletier, 1980) have also shown that the starting point in spring of the growth of natural diatom vegetations on a short transect with 3 stations at different tidal levels correlated with the duration of emersion; the higher stations exhibited an earlier start than the lower stations. The high primary production rate at Station 6 largely resulted from that station's high elevation. The high chlorophyll-*a* concentration accorded with the high primary production. As mentioned before, the influence of elevation alone could not account for the high production level; other factors may have enhanced this production: the sheltered position of Station 6, the lack of macrofaunal grazers (van Es *et al.*, 1980), the high nutrient concentration in the tidal water and in the pore water (de Jonge, unpublished), combined with the high mineralization rate of allochthonic organic material (van Es, 1982b) that supplies inorganic carbon. The population of benthic algae mostly consisted of diatoms, but it also contained blue-green algae and Euglenophyceae, particularly in summer. This vegetation had a lower specific production rate than the diatom vegetations of the other stations. However, interpreting the assimilation numbers raises problems, the depth of the photic layer in the sediment strongly depends on the composition of the sediment (Colijn, 1982). When the specific production rates were calculated from the chlorophyll-*a* contents of the top 0.5 cm of sediment, it was assumed that all chlorophyll in this layer contributes to the primary production, because it was impossible to measure chlorophyll-*a* in the photic layer properly. Consequently, the assimilation number was always underestimated. The absence of a significant correlation between primary production rate and temperature or irradiance was surprising at first sight. Laboratory experiments with small cores (Colijn & van Buurt, 1975) have shown that both temperature and irradiance enhance the primary production rate unless irradiance reaches saturation levels. That no correlation between irradiance and photosynthetic rate, and assimilation number was found can be explained by the incubation irradiances, which nearly always exceeded a saturation level of 11-25 W m^{-2} (PAR) (recalculated from Colijn & van Buurt, 1975). Our field incubations in November, December, January and February were performed with lower irradiance values only.

The lack of correlation between production rate and assimilation number with temperature contrasts with results obtained by Admiraal & Peletier (1980). They observed that doubling rates of cultures in enclosed incubators increased from c. 0.2 d^{-1} in winter to more than 2 d^{-1} in late spring. However, simultaneously observed doubling rates of natural populations were always much lower (max. 0.1 d^{-1}) even under high (>20°C) temperatures. Apparently, in our field incubations the effect of temperature on production rate is obscured by other factors. The observed low doubling rates (Admiraal & Peletier, 1980) and the relatively low chlorophyll-*a* concentrations at Stations 1 to 4 are probably caused by grazing, burying and transport. In other studies, the removal of epibenthic grazers resulted in a significant increase in algal biomass and productivity (Pace *et al.*, 1979; Darley *et al.*, 1981). These results, however, are not in accordance with those obtained by Connor *et al.* (1982), who observed a positive feedback between grazing by mud snails and the chlorophyll standing stock, at least at low densities of animals. If the microcosms were raked daily and densities of snails were high, the algal biomass and rates of photosynthesis fell. Also the removal of a proportion of the actively growing diatoms from the photic zone into the aphotic sediment layers and suspension and transport by tidal currents (Cadée & Hegeman, 1974; Ballie and Welsh, 1980; de Jonge, 1983) can keep the benthic diatom population at a low level.

High primary production and chlorophyll-*a* concentrations at Station 6 probably form the limit for microphytobenthic vegetations. This limit can be set by high concentrations of 0_2, low diffusion flux of $C0_2$ into the microalgal layer (Admiraal *et al.*, 1982) and absorption of PAR by chlorophyll-*a* and fine sediment particles (Fenchel & Staarup, 1971; Colijn, 1982). This hypothesis is supported by the saturation of production rate (Fig. 4) and by the low assimilation numbers at very high chlorophyll-*a* concentrations at Station 6 during favourable conditions of temperature

Table 4. Comparison of annual production rates in intertidal and shallow coastal sediments. Upper part: ^{14}C-values; lower part: O_2-values

Locality (Lat.)	Sediment type, depth (m)	Method	Annual production (g C m^{-2})	Production rate (mg C m^{-2} h^{-1}) range; mean	Chlorophyll (mg m^{-2})	Dominating microphytes	References
Danish fjords (55° N)	Littoral sand & mud, 0.2-1.8 m	^{14}C	116	25-90;60	n.d.	Pennate diatoms	Grøntved (1960)
Danish Wadden Sea (55° N)	Intertidal sands	^{14}C	571 (sheltered) 892 (exposed)*	25-300 25-500	n.d.	Pennate diatoms	Grøntved (1962)
Loch Ewe, Schotland (57° 50' N)	Sandy beach	^{14}C	4-9	0.14-1.78 mg C mg Chl^{-1} h^{-1}	3-20 µg g^{-1} dry sediment	Sand-attached diatoms	Steele and Baird (1968)
Ythan estuary, Scotland (57° N)	Intertidal muds	^{14}C	31	4-26;10	25-34 µg g^{-1} dry sediment	Motile pennate diatoms	Leach (1970)
South New England, USA (41° N)	Intertidal mixed sediment	^{14}C	81	8.2-30.8;20.1	100	Pennate diatoms dinoflag., filamentous algae	Marshall et al. (1971)
Niva Bay, Øresund, Denmark (56° N)	Shallow sands, 0.5 m	^{14}C	n.d.	125-300*	n.d.	Free-living and attached diatoms	Gargas (1970)
Madagascar (13° S)	Marine sands, 5-60 m	^{14}C	150 (5 m) 66 (mean)	9.22	38-78	Cyanophyceae, diatoms, symbiotic dinoflag	Plante-Cuny (1978)
Madagascar (13° S)	Marine sands, 5-38 m	^{14}C	n.d.	(5 m) 410 mg C m^{-2} d^{-1} (15) 232 mg C m^{-2} d^{-1} (25) 40 mg C m^{-2} d^{-1} (38) 9 mg C m^{-2} d^{-1}	3-34	Ditto	Plante-Cuny (1973)
Mediterranean coast, France (43° N)	Marine sands, up to 12 m	^{14}C	n.d.	120-194 mg C m^{-2} d^{-1}	24-64	n.d.	Colocoloff (1972)
Falmouth Bay, USA (41° N)	Salt marsh muds	^{14}C	105.5±12.5	5-80	n.d.	n.d.	van Raalte et al. (1976)

Locality (Lat.)	Sediment type, depth (m)	Method	Annual production (g C m^{-2})	Production rate (mg C m^{-2} h^{-1}) range; mean	Chlorophyll (mg m^{-2})	Dominating microphytes	References
Chuchi Sea, USA (71° N)	Fine muds and sands, 5 m	^{14}C	5	0.5-57	40-320	Diatoms and Euglenophyceae	Matheke and Horner (1974)
Wadden Sea, Netherlands (53° N)	Intertidal flats (sandy-mud)	^{14}C	100±40	50-100 (winter) 100-1100 (summer)	7.1 µg g^{-1} dry sediment 100; 40-400	Attached and suspendable diatoms	Cadée and Hegeman (1974)
River Lynher estuary, SW England (50° N)	Intertidal mudflats	^{14}C	143	5-115	30-80 µg g^{-1} dry sediment	n.d.	Joint (1978)
Balgzand Wadden Sea (53°N)	Intertidal flats, 4 transects	^{14}C	85 (29-188) (15 stations)	0-900 (d^{-1})	3-13 µg g^{-1} dry sediment	Diatoms	Cadée and Hegeman (1977)
Bolsa Bay, USA (34° N)	Barren estuarine mudflats	^{14}C	115-246	26-59 (4 stations)	185-385 (annual mean)	Motile & non-motile diatoms, bluegreens, dinoflagellates	Riznyk et al. (1978)
Ems-Dollard estuary (53° N)	Intertidal mudflats	^{14}C	62-276 (6 stations)	1-120; 37.0	33-184 (annual mean)	Diatoms, occ. Euglenophyceae bluegreens	This study
Ems-Dollard estuary (53° N)	Intertidal mudflats	O_2	69-314 (6 stations)	0-1900 mg C m^{-2} d^{-1}	n.d.	Diatoms, occ. Euglenophyceae bluegreens	van Es (1982a)
False Bay, USA (48° N)	Intertidal sandflats	O_2	143-226 (3 stations)	0-100	30-70 µg g^{-1} dry sediment	Diatoms (<u>Navicula</u> spp.)	Pamatmat (1968)
Georgia salt marshes, USA (31° N)	Intertidal mudflats	O_2	200	5-140	n.d.	Pennate diatoms flagellates, bluegreens, dinoflagel.	Pomeroy (1959)
Bay of Fundy Canada (45° N)	Intertidal flats	O_2	47-83	10-800	10-500	Microalgae	Hargrave et al. (1983)

n.d. = not determined; * = potential rates and irradiance: 0.19 and 0.20 mg C mg Chl-a^{-1} h^{-1} were measured at Station 6 on 25.V. and 14.VII. 1976, respectively, as opposed to a mean value of 1.37 for 8 other measurements at temperatures above 19 °C, irradiance> 150 W m^{-2}, and chlorophyll-*a* concentrations below 50 mg m^{-2}.

Recently, Admiraal *et al.* (1983) have discussed 2 different interpretations of the term primary production; the first was based on the photosynthetic rate on an hourly basis, as in this study, the second on the biomass increase over 24 h periods. They showed that in the latter case at a biomass density of 4 g C m^{-2} (roughly equivalent to 100 mg Chl-*a* m^{-2}) biomass net production might be as low as zero. That we were still able to measure positive fixation rates reflects the inherent property of the ^{14}C method that neither excretion nor respiration rates are subtracted from the fixation rates on a 24 h basis. Thus it is still not clear how much fixed carbon is available for primary consumers per year.

Comparison with other areas

Data on primary production form intertidal flats and shallow coastal areas around the world have been compiled in Table 4. Two important results are obvious from this table: Firstly, the annual production data measured with a bell-jar technique in the Ems estuary and partly during the same period (van Es, 1982a) fit in with ^{14}C fixation rates: $r = 0.9699$, $n = 6$, $P < 0.01$, (slope = 1.27). Thus both techniques give roughly identical estimates of annual primary production (Hunding & Hargrave, 1973). However, the individual, actually measured hourly rates per station showed large variations, probably because the measurements could not be performed at exactly the same spot; patchy distribution of microalgae (van den Hoek *et al.*, 1979) can lead to a 2- to 10-fold difference in chlorophyll-*a* concentration and cell numbers over a distance of a few centimetres. Secondly, the values for annual primary production at stations in the Western Wadden Sea (Cadée & Hegeman, 1974, 1977) are in the same range as the data from our Stations 1 to 5, again with the exception of our Station 6, with higher values than those of their Station 1 (188 g C m^{-2} a^{-1}). Leach (1970) showed that with relatively high chlorophyll-*a* values (400 to 600 mg m^{-2}) the annual production was rather low (31 g C m^{-2} a^{-1}). This might be caused by the muddy sediments (Station 3) with a thin photic layer and a high chlorophyll-*a* content in the deeper sediment layers. Surprisingly, as Table 4 shows, on a more global scale most of the annual production values are within a narrow range from 50 to 200 g C m^{-2}, even though they were determined at very different geographical latitudes. An exception are the data obtained by Steele & Baird (1968) who found a very low annual production, probably a result of the washout of free-living diatoms from their wave-exposed sands and the dispersal of viable cells to at least 20 cm depth. Other very low values have been found in polar regions and can be ascribed to the short growing season (Matheke & Horner, 1974). The high values given by Grøntved (1962) are based on potential measurements and do not reflect *in situ* production conditions.

As pointed out also by Cadée & Hegeman (1974), the spreading of small sediment cores results in much higher primary production. There is a possible explanation for the small range of annual production values. The abiotic environment in tidal areas largely precludes the existence of stable, permanent microalgal vegetations, because the cells are continually being suspended and removed. Moreover, the photic layer in sediments is too thin to enable all availabe cells to contribute optimally to the process of primary production. Thirdly, if an algal layer is formed, its growth is reduced through its own photosynthesis products or because the diffusion of carbon dioxide and nutrients is hampered in the algal film. All these processes limit the formation of a considerable microalgal biomass and restrict the concomitant net primary production.

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4. PHYSICS AND BIOLOGY

THE OCCURRENCE OF 'EPIPSAMMIC' DIATOM POPULATIONS: A RESULT OF INTERACTION BETWEEN PHYSICAL SORTING OF SEDIMENT AND CERTAIN PROPERTIES OF DIATOM SPECIES

V.N. de Jonge

ABSTRACT

The role of 'sand' (particles >55 µm) as a substratum for benthic diatoms was investigated, using sediments collected from tidal flats and main channels in the Ems estuary. On average, 13% of the sand grains were occupied by one or more diatom cells. It appeared that 80% of the diatom cells in this fraction were present in or on mud coating the sand grains. Of the sand grains in the water, 7% were occupied by diatom cells. The presence of benthic diatoms on the mud coatings rather than the bare parts of the sand grains stresses the importance of 'mud' (particles <55 µm) as a substratum for diatoms on the tidal flats. This was confirmed by separate cell counts for the mud and sand fractions.

Of the sand grains with attached diatoms, the mean number of diatom cells per grain in the water was similar to that on the tidal flats. This indicates a large exchange of sand between tidal flats and channels. A similar exchange between tidal flats and channels for benthic diatoms living on mud aggregates was suggested by the striking similarities in cell number distribution and species composition in samples from these two habitats. However, on exposed tidal flats certain species were present in lower numbers than in the channels, indicating that loosely attached diatoms can be scoured off their substratum. Consequently, two factors are assumed to contribute to the dynamics of the species composition of benthic diatoms. The first is the adhesion capacity of diatoms and the second is sediment sorting by currents and waves. These factors cause a differential but significant flux of benthic diatoms to and from the channels, followed by changes over time in the diatom populations on the tidal flats and possibly a shift in the species composition. These processes show that the terms 'epipelic' and 'epipsammic' are not helpful to classify the main components of the diatom flora in this estuary.

INTRODUCTION

The estuarine areas around the North Sea are very dynamic environments. This is caused by a combination of factors which include a small mean water depth, strong tidal currents, and variable wave action. The tide-generated water movement in the estuary influences the transport of suspended matter through the estuary: furthermore, the associated processes of deposition and resuspension of sediment affect the formation and erosion of the tidal flats (Postma, 1967).

The microphytobenthos populations, mainly consisting of benthic pennate diatoms that live in and on the tidal flats, can be suspended and deposited, as Grøntved (1949), Cadée & Hegeman (1974) and Oertel & Dunstan (1981) have already indicated. These authors reported the presence of large numbers of benthic diatom cells in the channel waters of tidal basins. On the basis of this information and the work of Round (1965), Harper & Harper (1967) and Harper (1969) it has been postulated (Van den Hoek *et al.*, 1979) that motile diatoms with low adhesion capacity tend to congregate near the thin surface layer of the sediment. Such diatoms are termed 'epipelic' by Round (1965). It follows that these diatoms should easily be suspended from substrata that are exposed to currents and waves, resulting in them being transported to the channels. Consequently, diatoms with low motility that are firmly attached to sand particles [Round's (1965) so-called 'epipsammic' diatoms] tend to dominate such habitats. This hypothesis has been supported by Harper & Harper (1967), who found that some diatom species adhered strongly to their substratum, whereas others could easily be removed.

Given the processes that regulate the sediment composition of tidal flats (Postma, 1967), it seems improbable that currents and waves remove epipelic diatoms from their substratum without also moving some of the epipsammic diatoms and the sediment. It seems likely that during sediment sorting loose diatom cells and diatoms attached to sediment particles are suspended, together with sediment. This material is then redistributed over tidal flats and also transported to the main channels. Because of their relatively high density (de Jonge, 1979), the solitary suspended diatoms are probably subject to the same accumulation processes as those for fine-grained sediment (Postma, 1967). Both the suspended diatoms and those adhered to bottom sediments will

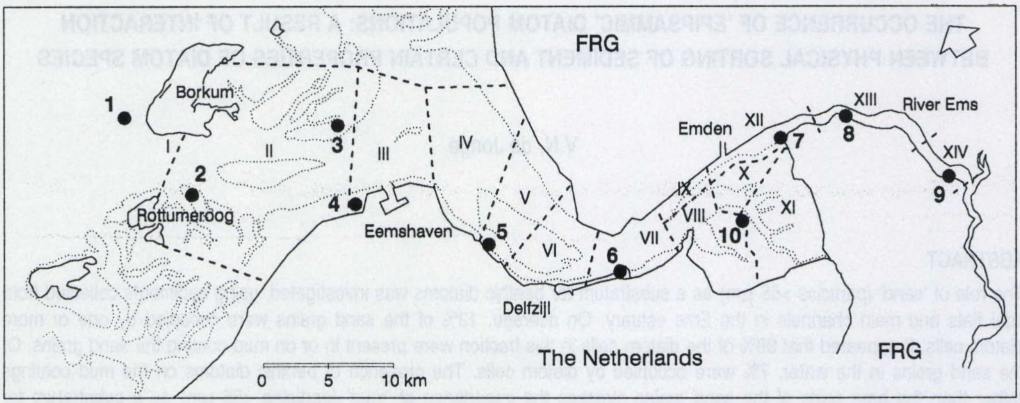

Fig. 1. Map of the area investigated. Roman numerals refer to channels in sectors and arabic numerals to stations on tidal flats.

contribute to the dynamics of the species composition, the former by multiplying after they have been deposited and the latter by responding to the improved growth conditions resulting after part of the sediment and the diatom population has been removed.

At present the significance of water movement and the erosion-sedimentation cycle for the constitution of sediment-inhabiting diatom assemblages is not well understood. The present study intends to contribute to a better understanding of the relationship between this erosion-sedimentation cycle and the composition of diatom assemblages.

MATERIALS AND METHODS

Sampling procedure

The study area was the estuary of the River Ems (Fig. 1). This estuary is part of the Wadden Sea and lies on the border between the Netherlands and The Federal Republic of Germany. The estuary extends from Leer (F.R.G.) to the islands of Borkum and Rottumeroog, over a length of approximately 80 km.

The total area of the estuary is approximately 500 km^2; 45% of the area consists of intertidal flats (in the Dollard, intertidal flats account for 80% of the area whereas in the River Ems they account for less than 25%). Samples were collected from different tidal flats and from the main channels in the Ems estuary. Samples were separated into 'mud' and 'sand' fractions and cell number and species composition were determined in each fraction.

The stations on the tidal flats (Fig. 1) were fairly regularly spaced along the axis of the Ems estuary.

Table 1. Sampling dates for the channel water and the tidal flats. The stations, sectors and sediment fractions that were analysed on the different sampling dates are listed.

Samples	Unfractionated samples	Fractionated samples	
		Particle fraction <55 µm (mud)	Particle fraction >55 µm (sand)
Samples from:			
Tidal flat station nos	4-9	-	1-10
Date	18/3	-	14/4
Results presented in	Table 3 Figures 2,3	-	Table 5
Channel sector nos	-	II-XIV	I-XIV
Date	-	18/3	14/4
Results presented in	-	Table 3 Figures 2,3	Table 6

Stations 1 - 4 were situated in the outer region which has predominantly sandy sediments. The composition of the sediment at stations 5 and 10 can be characterized as silty fine sand, station 6 as sandy silt and stations 7-9 as sandy clay (cf. van Es, 1982).

The estuary was divided into 14 sectors (Fig. 1). Within these sectors water was sampled in the main channels so that a comparison could be made between suspended and sediment-inhabiting benthic diatoms. The surface area of the exposed tidal flats and the water volume of the channel sectors are given for half-tide (Table 2).

Table 2. Surface area of exposed tidal flats and water volume of the channels for a number of sectors of the Ems estuary at half-tide.

	Main estuary axis between North Sea and the town of Leer										Dollard		
Sector no.	II	III	IV	V	VI	VII	IX	XII	XIII	XIV	VIII	X	XI
Tidal flat area (x 10^6 m^2)	80	20	21	22	16	4.1	3.2	4.8	2	1.5	21	13.6	40
Water volume (x 10^6 m^3)	460	345	225	165	85	95	18	31	24	15	44	16	13

Tidal flats

Sediment samples from the tidal flats (Fig. 1) were collected on 18 March 1980 and on 14 April 1980. Because of bad weather in March, the three most seaward stations could not be sampled (Table 1). At each station 20 samples of the uppermost 0.5 cm of the sediment were taken at random from an area of 0.25 km^2 using cores with a diameter of 2.4 cm. The samples were amalgamated, mixed and subsampled according to the method described by de Jonge (1979). The subsamples collected in April were processed further (Table 1). These subsamples were mixed with some water, vigorously shaken by hand and sieved through a 55-µm mesh plankton gauze to separate out the sand particles including the sand-associated diatoms (Round, 1965). These sand fractions were used for microscopic observations.

Channels

The channels (Fig. 1) were sampled at half-tide when only the main channels contained water. The advantage of this timing was that the total estuarine water mass could be sampled. The samples were taken approximately 1 m below the water surface. A pump was used to take a 25-l mixed sample over the total length of each of the sectors. This was done because the suspended material is not homogeneously distributed in the water but is present as clouds. A 55-µm mesh plankton gauze was used to separate sand from finer-grained sediment components. The 'mud' fraction (particles <55 µm) was examined in March, and the 'sand' fractions (particles >55 µm) in April (Table 1).

The sand fraction consisted of pure bare grains or grains partly coated with mud particles. These mud particles were composed of aggregates of quartz, clay minerals and organic material, and coarse detritus particles.

The mud fraction itself was composed of the same constituents, plus remnants of animal skeletons. All samples were fixed according to van der Veer (1982) and immediately stored at -20 °C.

COUNTING PROCEDURE

Tidal flats

In the unfractionated samples of March (Table 1) the mean number of benthic diatoms was determined per square metre of the tidal flat per sector and for the total tidal area per sector. The sand fraction of all stations in April was used to ascertain how many cells were present per sandgrain. Cells on bare surfaces of the sand grains were counted separately from cells present in or on mud particles coating the sand grains.

Channels

In the mud fraction of the water samples taken in March (Table 1), the total numbers of pennate diatom cells were determined. They were expressed in numbers per cubic metre of water and in numbers per total water mass per sector. The pennate diatoms in the sand fraction were not counted for three reasons: first, the sand concentrations only accounted for 10% of the total dry weight of the suspended matter; secondly, the bottom sediments consist mainly of sand (>90%) which means that a low percentage of

Table 3. Percentages and total numbers of 12 dominant benthic diatom species in the suspended matter (particle fraction <55 μm) of the channel water and on seven tidal flat stations (total sediment from 0 to 0.5 cm depth). For explanation of the station and sector numbers, see Fig. 1. Samples were collected on 18 March 1980

Species	Main estuary axis										Dollard		
Channels													
Sector no.	II	III	IV	V	VI	VII	IX	XII	XIII	XIV	VIII	X	XI
Plagiogramma brockmannii	7	4	5	4	1	1	1	2	-	-	1	1	-
Navicula crytocephala	2	6	<0.5	1	-	1	2	-	-	-	0.5	1	1
Navicula aequorea	1	-	1	1	1	1	-	-	-	-	<0.5	-	-
Navicula salinicola	-	2	1	3	2	-	-	-	-	-	2	1	-
Opephora pacifica	-	1	-	1	1	<0.5	-	<0.5	2	-	1	1	-
Achnanthes hauckiana	1	3	2	2	2	2	-	1	-	-	1	1	-
Catenula adhaerens	-	-	-	<0.5	-	<0.5	0.5	-	-	-	<0.5	1	<0.5
Opephora martyi	-	1	1	-	-	1	-	-	-	-	<0.5	<0.5	1
Raphoneis minutissima	16	25	29	23	24	15	18	13	19	5	12	6	-
Cymatosira belgica	19	17	19	17	12	8	9	12	12	16	10	5	4
Navicula diserta	13	12	14	10	7	8	11	20	16	16	3	1	-
Navicula flanatica	8	5	2	12	18	30	25	20	14	12	49	66	75
Total no. of cells (x 10^6 m^{-3})	3184	2729	2764	2325	1790	1720	4144	2990	1062	247	2688	7531	18021
Tidal flat													
Station no.		4	5			6		7	8	9	10		
Plagiogramma brockmannii		-	<0.5			2		<0.5	1	-	1		
Navicula cryptocephala		-	1			1		<0.5	<0.5	-	2		
Navicula aequorea		36	12			2		<0.5	1	1	1		
Navicula salinicola		17	3			<0.5		-	-	-	<0.5		
Opephora pacifica		5	1			2		1	2	1	1		
Achnanthes hauckiana		14	5			2		1	3	1	2		
Catenula adhaerens		2	1			<0.5		<0.5	<0.5	<0.5	1		
Opephora martyi		2	1			-		<0.5	1	3	<0.5		
Raphoneis minutissima		-	12			6		3	8	18	8		
Cymatosira belgica		1	13			14		2	10	12	6		
Navicula diserta		<0.5	11			15		3	26	17	9		
Navicula flanatica		3	19			27		76	8	2	46		
Total no. of cells (x 10^7 m^{-1})		2180	855			2535		3570	1102	1200	732		

Rough sediment characterization: Station 4: fine sand; station 5: silty fine sand; station 6: sandy silt; station 7: clayey fine sand; station 8: sandy clay; station 9: sandy clay; station 10: silty fine sand.

the total sand is resuspended by tidal currents; thirdly, in contrast with the mud fraction of the suspended matter, the sand concentrations fluctuate strongly because of the tidal currents. Consequently, representative sampling of this material was impossible, given the equipment available. In the sand fraction taken in April (Table 1) the number of individual diatom cells per sand grain was determined. As described for the tidal flat samples, the diatom cells that were present on bare surfaces were counted separately from those present on the mud-coated surfaces of the grains. The species compositions of the unfractionated tidal flat samples and of the mud fraction of the water samples (both taken in March) were determined. To count the total numbers of diatom cells the benthic diatoms were removed from their substratum by shaking a suspension of sediment in water using a Braun cell homogenizer MSK (for details see de Jonge, 1979). Then the diatom cells were counted with a microscope counting chamber (Neubauer, improved; 0.1 mm deep) using fluorescence microscopy.

The presence of benthic diatoms on individual sand grains was studied microscopically. Cells associated with bare parts of sand grains were scored separately from those associated with mud coatings on the grains.

To do this these samples were stained with alcian blue, which preferentially stains mucopolysaccharide (Parker & Diboll, 1966). It was observed that these compounds were usually present in the particles of the mud fraction or the mud particles coating sand grains. Switching between fluorescence and normal light enabled the cells associated with bare parts of sand grains to be differentiated from those associated with mud coatings on sand grains.

To assess the species composition of the samples, the benthic diatoms of all types of samples were removed from their substratum using the homogenizer procedure described above. For the mud fraction of the water samples (Table 1), this procedure was followed by density separation of intact diatom cells from the suspended matter (de Jonge, 1979). This method was not used for the tidal flat sediment samples because few empty pennate diatom frustules were found. Using the method of Hasle & Fryxell (1970) all samples were prepared for microscopic identification.

Species were identified using Peragallo & Peragallo (1897-1908), Hustedt (1930, 1939, 1959, 1961-1966) and Brockmann (1950).

RESULTS

Distribution of diatoms

The basic results of the March observations are given in Table 3. The total number of benthic diatoms at the tidal flat stations along the estuarine axis varied (Table 3). At stations 4, 6 and 7 the populations were much denser (2200-3500 x $10^7 m^{-2}$) than at the other stations (700-1200 x $10^7 m^{-2}$).

The abundance of a species at the tidal flat stations sampled is only given in the tables when the relative abundance of that species represented at least 2% of the species assemblage at one of the tidal flat stations. This was done to limit the table length. Twelve species fulfilled this requirement.

The relative abundance of these species in the water samples was also calculated (see Table 3). The dominant species were present at nearly all sampling stations. However, the numbers per species differed strongly.

The total numbers of the benthic diatoms in the water (Table 3) also varied, decreasing from 3000 x 10^6 m^{-3} in sector II to 200 x 10^6 m^{-3} in the water of the River Ems near Leer. In sectors IX and XII numbers of benthic diatoms were relatively high, as in other sectors of the Dollard (VIII, X and XI). Values increased from 2700 x 10^6 m^{-3} near the mouth of the Dollard in the northwestern part to 18000 x 10^6 m^{-3} in the southeastern part of the Dollard.

Fig. 2 gives graphs of the cell numbers in the estuarine sectors. Some 60% of all the benthic diatoms were present in the water column (Table 4). The high correspondence between total numbers of diatoms cells on the tidal flats and in the channel water, when the total surface area and water content per sector are taken into account, is striking. Figure 2 strongly indicates that there is a relationship per sector between the cell numbers in the water and those in the sediment. In Fig. 3 the numbers of benthic diatoms of the seven most abundant species in the channels and on the tidal flats are plotted per sector. The cell abundance of the species shown in Fig. 3 was either higher or lower in the water column than on the tidal flats (Table 4).

The gradient of cell numbers in the channel water was always steep. Highest densities occurred in the region near the tidal inlet and decreased gradually upstream, with the lowest values being found in the River Ems. The steepness of this gradient is, of course, partly caused by the water volumes per sector decreasing upstream (Table 2). The species *Navicula aequorea*, *N. salinicola* and *Achnanthes hauckiana*, which were less abundant in the water than on the flats (Table 4) showed, however, a steep gradient in cell numbers on the tidal flats [Fig. 3(a-c)]. But a second group of species, consisting of *Raphoneis minutissima*, *Cymatosira belgica* and *Navicula diserta*, which were more abundant in the water column (Table 4), had a weak gradient in cell numbers on the flats [Fig. 3(e-g)] and occurred in fewer numbers on the sediments in the lower reaches (see sector III, station 4) than did the former group of species [Fig. 3(a-c)].

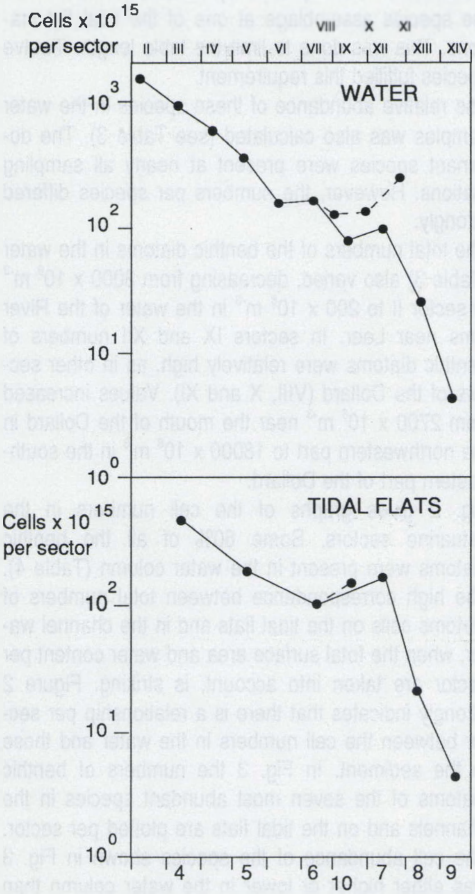

Fig. 2. Distribution of total numbers of diatom cells along the estuarine axis on 18 March 1980 in the water and on tidal flats.

The distribution of the species *Navicula flanatica* [Fig. 3(d)] was intermediate between the two groups of species. Figs. 2 and 3 indicate that suspension of benthic diatoms does occur, but the process seems different for different species [Fig. 3(a-c)], and (e-g)], and may be also dependent on the location of the tidal flats.

Table 4. Cell numbers per species present in the channel water expressed as a percentage of the sum of the cell numbers of that species present in the water and on the tidal flats.

Species		%
Plagiogramma brockmannii	Hust.	90.9
Navicula cryptocephala	Kütz	92.1
Navicula aequorea	Hust.	6.9
Navicula salinicola	Hust.	28.1
Opephora pacifica	(Grun) Petit	41.2
Achnanthes hauckiana	Grun.	36.7
Catenula adhaerens	Mereschk.	25.5
Opephora martyi	Héribaud	49.4
Raphoneis minutissima	Hust.	91.5
Cymatosira belgica	Grun.	85.1
Navicula diserta	Hust.	80.3
Navicula flanatica	Grun.	54.5

Attachment of pennate diatoms to sand grains

The attachment of pennate diatom cells to sand grains was studied in April at all ten tidal flat stations (Table 5). On average, 88.2% of all sand grains were free from diatoms (Table 5, 6th column). Of the diatoms found on sand grains, 79.2% (4th column) were present on mud coatings. The remaining 20.8% of the diatom cells (3rd column) were present on the bare parts of sand grains. Table 5 also shows that the mean number of diatom cells per sand grain varied between the different estuarine sectors: it was low (0.02-0.44) at stations 1-3 but for stations 4-6 it was less variable and was higher (1.02-1.29), whereas at stations 7-10 the value decreased again. A different pattern was shown in the mean number of cells per attached sand grain (5th column): the figure increased gradually from 3.48 (station 1) to 5.88 (station 5), but further upstream this mean cell number decreased gradually again.

Table 6 presents data on diatom cells attached to suspended sand grains in the channel water.

Generally, the average number of cells per sand grain (Table 6, 2nd column) was lower than on the tidal flat sediments (Table 5). However, the average difference was not greater than a factor of two. The mean numbers of cells attached to bare parts of occupied sand grains (Table 6, 3rd column) were clearly lower than the values found for the sediments (Table 5). This did not hold for the mean cell numbers present in or on the mud coatings of sand grains (Tables 5 and 6, 4th column), which reached an overall value of 3.3 both in the water and in the sediments. It is evident that the percentage of sand grains without diatom cells in the water column (Table 6, 6th column) was only slightly higher than that in the corresponding fraction from the tidal flats.

Table 5. Mean cell numbers and percentages of benthic diatom species found attached to sand grains from tidal flats on 14 April 1980. Location of the stations (nos 2-10) is given in Fig. 1. Data for station no. 10 are given separately because this station lies in the Dollard and does not fit in the estuarine gradient proper (see Fig. 1).

	Tidal flat station no.	Mean number of attached cells per sand grain	Mean cell number per sand grain (for the sand fraction with attached cells)			Percentage of sand grains	
			on bare parts	in/on mud-coated parts	total	without attached cells	with attached cells
Main estuary axis	1	0.43	0.96	2.52	3.48	87.7	12.3
	2	0.02	0.00	4.00	4.00	99.5	0.5
	3	0.44	0.44	4.05	4.49	90.3	8.7
	4	1.29	2.29	3.09	5.38	76.0	24.0
	5	1.02	2.03	3.85	5.88	82.7	17.3
	6	1.20	0.49	3.70	4.19	71.4	28.6
	7	0.34	1.01	3.27	4.28	92.0	8.0
	8	0.25	0.93	2.47	3.40	92.7	7.3
	9	0.06	0.00	2.73	2.73	97.8	2.2
Dollard	10	0.26	0.31	2.76	3.07	91.4	8.6
Mean value		0.53±0.47	0.85±0.78	3.24±0.64	4.09±0.99	88.15±9.01	11.75±9.04
percentage			20.8	79.2	100%		

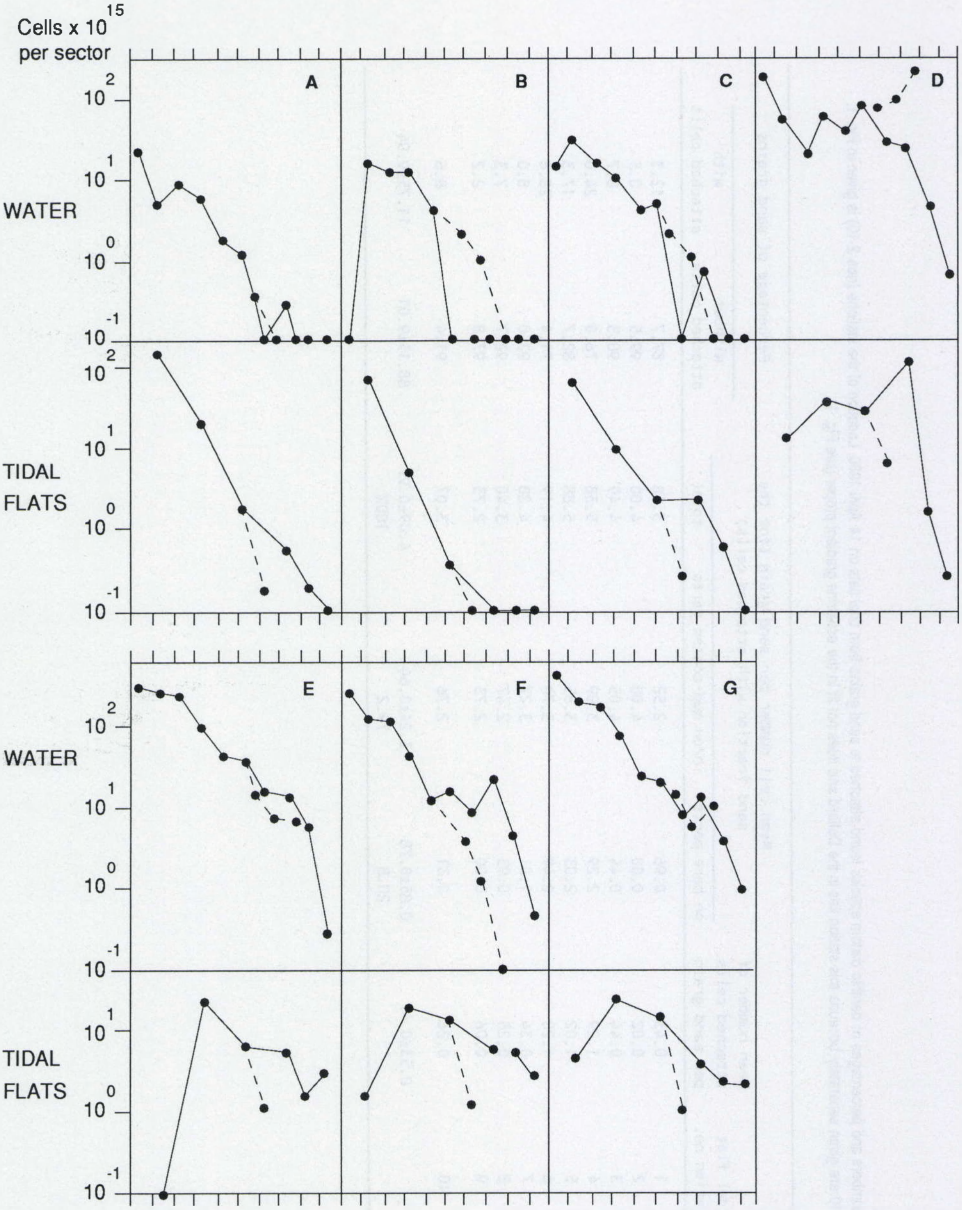

Fig. 3. Cell number distribution of selected diatom species in the water (fraction <55 μm) and on the tidal flats (total sample) along the estuarine axis on 18 March 1980. Sampling sectors and tidal flat stations as in Fig. 2. A, *Navicula aequorea*; B, *Navicula salinicola*; C, *Achnanthes hauckiana*; D, *Navicula flanatica*; E, *Raphoneis minutissima*; F, *Navicula diserta*; G, *Cymatosira belgica*.

In Table 5 (5th column) the mean number of diatom cells per sand grain increased up the estuary until station 5 and then tailed off. No such clear curve was found for the sand fraction in the channel water (Table 6, 5th column). A comparison of Tables 5 and 6 shows that with the exception of the gradient in cell numbers mentioned above, generally no clear differences were observed between the values presented for the sand grains from the tidal flat sediments and those from the channel water.

Table 6. Mean cell numbers and percentages of benthic diatoms found attached to sand grains collected from the water column of the main channels on 14 April 1980. Location of sectors is given in Fig. 1. Sectors where sand was absent in the samples have been omitted.

		Mean number of cells per sand grain (for the sand fraction with attached cells)			Percentage of sand grains	
Sector no.	Mean number of cells attached per sand grain	on bare parts	in/on mud-coated parts	total	without attached cells	with attached
I	0.29	0.51	3.49	4.00	92.8	7.2
II	0.29	0.14	3.29	3.43	91.6	8.4
IV	0.21	0.24	3.29	3.53	94.1	5.9
V	0.13	0.30	2.42	2.72	95.3	4.7
VII	0.31	0.36	2.95	3.31	90.7	9.3
IX	0.13	0.00	1.97	1.97	93.3	6.7
XIII	0.16	0.20	4.01	4.21	96.1	3.9
VIII	0.15	0.54	2.69	3.23	95.3	4.7
X	0.27	0.38	3.34	3.72	92.8	7.2
XI	0.91	0.64	6.45	7.09	87.2	12.8
Mean	0.29±0.23	0.33±0.20	3.39±1.22	3.72±1.34	96.92±2.63	7.08±1.34

Table 7. Relative abundance and total numbers of cells of the dominant benthic diatom species in the sand fraction and in the mud fraction for two tidal flat stations on 14 April 1980. Data obtained from 0.5 cm sediment top layer. For location of the stations, see Fig. 1.

	Station 1			Station 4		
Sediment characterization	coarse sand			fine sand		
Sediment fraction Species	sand (%)	mud (%)	total (%)	sand (%)	mud (%)	total (%)
Plagiogramma brockmannii	-	-	-	-	-	-
Navicula cryptocephala	3	5	8	0.5	-	0.5
Navicula aequorea	-	-	-	8	4	12
Navicula salinicola	2	2	4	6	3	9
Opephora pacifica	<0.5	-	<0.5	5	2	7
Achnanthes hauckiana	<0.5	-	<0.5	9	8	17
Catenula adhaerens	-	-	-	1	-	-
Opephora martyi	-	-	-	-	-	-
Raphoneis minutissima	<0.5	9	9	0.5	0.5	1
Cymatosira belgica	<0.2	10	10	-	1	1
Navicula diserta	0.5	5	5.5	5	1	6
Navicula flanatica	-	-	-	2	8	10
Cell numbers ($x10^7 m^{-2}$)			371			6675

This indicates that there is a significant exchange of sand particles with attached benthic diatoms between the channels and the tidal flats.

Having demonstrated the unimportance of bare sand as a substratum for diatoms, an attempt was made to separate the sand from the mud. This was done to show that there were proportionately more cells in the mud than in the sand. The sediment separation of samples from stations 1 and 4 was successful.

For all other samples, detritus hampered the separation of sediment components and therefore reliable cell counts up to the species level could not be carried out. The results given in Table 7 indicate that in spite of the low percentage of mud (less than 5% $^{w}/_{w}$ for both stations) this fraction was disproportionately rich in diatoms. These results reinforce the conclusion inferred from Tables 5 and 6, namely that mud is the significant fraction of a substratum for diatoms.

DISCUSSION

Suitability of sand and mud as substrata for benthic diatoms

Sand grains act as a physical substratum for colonization by benthic diatoms. The role of mud particles, however, is quite different. Mud is often present in the form of aggregates roughly consisting of clay minerals, detritus particles including bacteria, and organic substances that act as an adhesive. Within these flocculi small quartz particles and inorganic remainders of organisms are often present. The flocculi vary in biogenetic nature and composition (Meadows & Anderson, 1968; Frankel & Mead, 1973; Eglington & Barnes, 1978). It is known that organic compounds are associated with mineral particles (Brümmer, 1968) and that humic acids and polysaccharides are adsorbed by mineral particles (Neihof & Loeb, 1972, 1974; Cauwet, 1981). This is important, because organic compounds can stimulate diatom growth (Admiraal & Peletier, 1979). Moreover, nutrients are also adsorbed by sediments (see review by Aston, 1980). This means that compounds are present in a releasable or exchangeable form and this can be advantageous for algal growth. Consequently, the varying and complex spatial structures of mud flocculi can offer a favourable substratum for diatoms. The foregoing explanation of the suitability of mud as a substratum for benthic diatoms conforms with the results presented in Table 5 and 7. The information in Table 7 suggests that an important part of the diatom populations is present in the mud fraction, whereas Table 5 illustrates that even in the sand fraction most diatoms are in fact present on or in mud particles that are coating the sand grains. These data show that diatoms mainly use mud as a substratum.

Apart from being a source of organic compounds and nutrients, mud can also protect diatom cells against mechanical damage. Further, diatoms might contribute to the formation of flocculi by producing mucopolysaccharides (Darley, 1977), but it seems improbable that they create their own microniche entirely by this process, because the mud coatings on sand grains were usually ten times the size of the diatom cells. It is more likely that the diatom cells usually take advantage of existing flocculi.

Influence of currents and waves on composition and transport of sediments

Tidal flats are influenced by currents and waves. During submersion the currents rework and sort the sediments (Postma, 1967). These processes are amplified by the wind-induced waves. Resuspended material can be transported from tidal flats into neighbouring channels when currents are strong enough. Once arrived in the tidal channels the suspended material is partly dispersed by the complex mixing process of the water (Zimmerman, 1976), but at the same time is subject to estuarine accumulation processes (Postma, 1967). This results in the suspended matter being transported in the direction of the tidal flats and upstream. This net inland transport can be estimated from the rate of accretion (0.8 cm a^{-1}; Reenders & van der Meulen, 1972; van der Goes *et al.*, 1979). On a short time-scale there is near equilibrium between the sediment transport from outside via the tidal channels to the tidal flats and the resuspension of freshly deposited sediment fractions from the tidal flats to the channels (Fig. 4; cf. de Jonge, 1983).

Relation between suspended and settled populations of benthic diatoms

That benthic diatoms become suspended and transported in estuarine systems has previously been inferred from a decrease in biomass (Baillie & Welsh, 1980; Colijn & Dijkema, 1981) or from the presence of benthic diatoms in the water column (e.g. Grøntved, 1949; Cadée & Hegeman, 1974; Baillie & Welsh, 1980; Oertel & Dunstan, 1981). However, no satisfactory explanation of the process that causes the presence of these diatoms in the water column could be advanced, because the aforementioned authors studied the water column or the tidal flat sediments rather than the exchange processes. The results presented in Fig. 2 and 3 show great similarities in cell numbers per species between the channels and neighbouring tidal flats. The results presented in Tables 5 and 6 show that on average, the cell numbers associated with sand grains from the tidal flats do not differ strongly from those associated with grains suspended in the water in the channels (Tables 5 and 6, 5th column). The overall mean (2nd column in both tables) in the water column was lower than that of the tidal flats by less than a factor of two. The values in Tables 5 and 6 indicate two interesting phenomena.

The first is that the diatom cells attached to sand grains on the tidal flats most likely reached the channels coupled to these grains: as most of these cells are present in the mud particles coating the sand grains the same probably holds for diatoms found in the mud fraction. The second phenomenon is the implied high cycling rate of sand grains (and

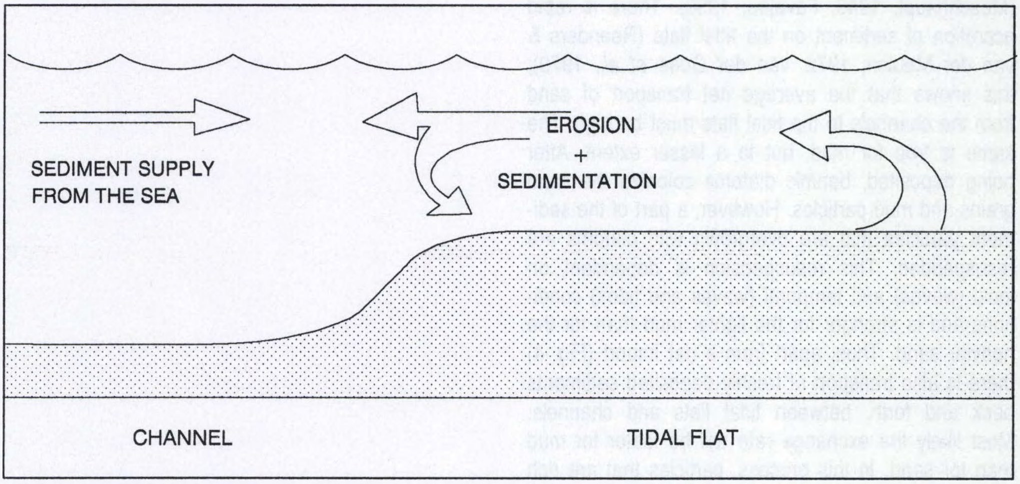

Fig. 4. Diagram representing the relative importance of the net sediment transport between channel and tidal flat and the relative quantities of freshly deposited sediment cycling between tidal flats and channels.

consequently of attached diatom cells) between tidal flats and channels. This is inferred from the fact that in spite of the large amounts of sediment that are deposited in the Ems estuary (Fig. 4) the numbers of cells per sand grain in the channels tally well with those on the tidal flats. However, not all benthic diatoms reach the water column coupled to sediment. This was demonstrated by direct microscopical observations on board ship and can also be derived from Fig. 3. In this figure it is shown that in the water downstream, the numbers of cells of *Navicula flanatica*, *Raphoneis minutissima*, *Cymatosira belgica* and *N. diserta* were disproportionately high compared with those of the other species. This suggests that the adhesion capacity of these four species is lower than that of other species. These examples show that differences in adhesion capacity (Harper & Harper, 1967; Harper, 1969) may be significant under natural conditions. It is of course extremely difficult to ascertain whether the loosely attached diatoms do reach the water column coupled to mud particles. Even sampling and processing can cause these specimens to become detached from their substrata.

Possible relation between dynamics of sediment composition and species composition of benthic diatoms

If the information discussed so far is synthesized, the following possible relation between the dynamics of sediment and benthic diatoms is obtained: the sediments of tidal flats mainly consist of sand (Maschhaupt, 1948; Favejee, 1960). There is rapid accretion of sediment on the tidal flats (Reenders & van der Meulen, 1972; van der Goes *et al.*, 1979); this shows that the average net transport of sand from the channels to the tidal flats must be high. The same is true for mud, but to a lesser extent. After being deposited, benthic diatoms colonize the sand grains and mud particles. However, a part of the sediment particles that are overgrown with diatoms are resuspended. This resuspension is dependent on local (waves) and temporal (waves and tides) conditions and is stronger for the lighter mud than for the heavier sand. Thus, apart from a net import (Fig. 4) there is also transport of freshly deposited sediments back and forth, between tidal flats and channels. Most likely the exchange rate will be faster for mud than for sand. In this process, particles that are rich or poor in diatoms (this depends on the season) from the tidal flats are exchanged for particles poorer or richer in diatoms from the channels. Moreover, with the resuspension of sediment, loosely attached species become suspended as individuals. This resuspension results in losses being greatest for loosely attached and unattached diatoms and even greater for diatoms attached to mud particles than those attached to sand grains. Only those diatoms that are strongly attached to sand particles can usually remain on the tidal flats. Thus the previously discussed processes result in a selection of species assemblages based on both adhesion capacity and presence in or on mud or sand. Therefore, the term 'epipelic' and 'epipsammic' do not seem to be very appropriate to characterize the different components of the diatom flora in the Ems estuary.

To sum up, physical conditions contribute to the formation of characteristic diatom species assemblages. However, it must be kept in mind that factors other than those connected with water movement can regulate the presence of species at different estuarine localities (Admiraal, 1980).

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EXPERIMENTS ON THE RESUSPENSION OF ESTUARINE SEDIMENTS CONTAINING BENTHIC DIATOMS

V.N. de Jonge and J. van den Bergs

ABSTRACT

A laboratory system was used to test the effect of water flow on the resuspension of mud and sand sediments and, specifically, benthic diatoms from the Ems estuary, The Netherlands. Current velocities generated by two rotating cylinders in a cylindrical tank were determined by a small float and a laser Doppler velocimeter. At low angular velocities, the amount of suspended matter increased linearly with angular velocity and the float current velocity. However, at higher angular velocities, the increase in current velocity was less because of the strong turbulence: concomitantly, the current velocity boundary layer (δ) became thinner and the suspended matter concentration increased rapidly. The dominant diatom species from the sandy sediment were suspended in two distinct groups, one of which consisted of the species *Navicula aequorea*, *Navicula salinicola*, *Ophephora martyi* and *Opephora pacifica*, and was more exclusively bound to sand grains than the other. The benthic diatom species inhabiting the silty sediment did not show this difference. The most important shortcoming in the experiments was the inability to determine the radial and vertical velocity components. This precluded reliable calculations of the shear stress. The data presented emphasize the importance of finding a method to determine the shear stress under experiments and field conditions so that direct comparisons can be made. Despite this it is assumed that, just as under the experimental conditions discussed, under natural conditions in shallow waters resuspension starts at current velocities as low as c. 10 cm s^{-1}.

INTRODUCTION

The intertidal flats of the estuary of the River Ems are rich in microphytobenthos populations, mainly consisting of benthic diatoms (van den Hoek *et al.*, 1979; Admiraal, 1980; Colijn & de Jonge, 1984; de Jonge, 1985). During the last decade much effort has been spent in measuring the distribution of biomass and the primary production of these populations (Colijn & de Jonge, 1984). Environmental effects on cell growth (Admiraal, 1980) and grazing by nematodes (Romeyn & Bouwman, 1973, Admiraal *et al.*, 1983; Romeyn *et al.*, 1983) and by harpacticoid copepods have been investigated in an integrated study of the Ems estuary (BOEDE, 1985).

Large numbers of benthic diatoms can be present in the water column of estuarine systems (Grøntved, 1949; Cadée & Hegeman, 1974; de Jonge, 1985). This suspended microphytobenthos in shallow estuarine systems may have significance as an additional food source for benthic and pelagic filter-feeding communities (Roman & Tenore, 1978; Baillie & Welsh, 1980). The suspension of all benthic diatoms does not occur simultaneously but different groups of species become suspended in sequence (de Jonge, 1985). The available data suggest that this is caused by the interaction of the physical sorting of sediment and certain properties of the benthic diatoms, e.g. cell size and adhesion capacity, and the nature of the particles on which they live. Thus, it seemed worthwhile to study the suspension mechanism of benthic diatoms in more detail. No direct observations of this process during changing current velocities have previously been made.

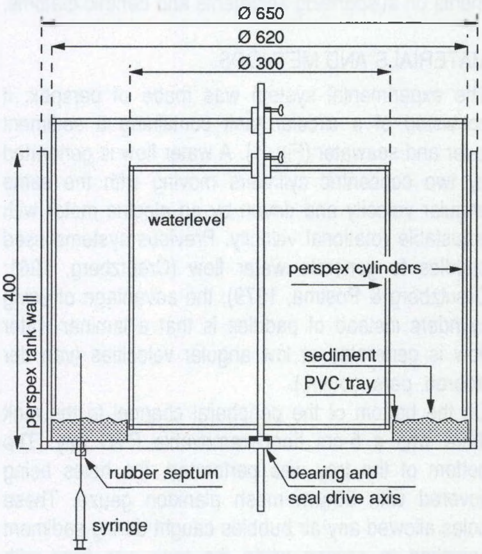

Fig. 1. Schematic diagram of the cylindrical tank used. Sizes are given in mm.

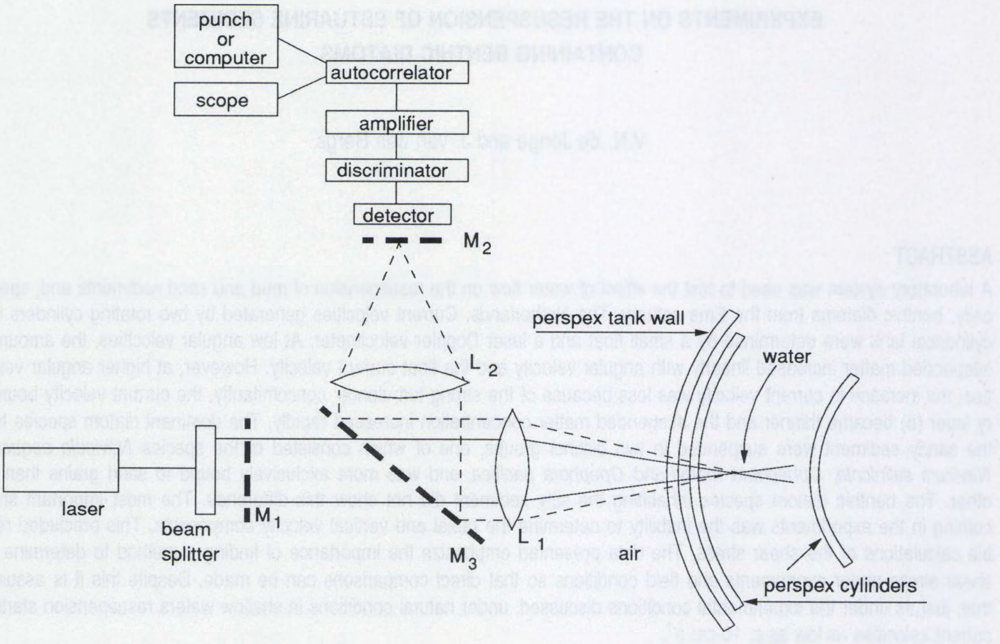

Fig. 2. Diagram of the laser Doppler velocimeter in the backscattering mode. L_1 and L_2 are lenses, M_1 and M_2 are black marks with small holes and M_3 is a mirror. Solid lines represent the first order diffracted light beams. Dotted lines represent the backscatter light signals. The dectector is a photomultiplier.

Because it is difficult to make observations under complex natural conditions, we designed a system in which variable current velocities could be generated. This paper presents the results of laboratory experiments on suspending sediments and benthic diatoms.

MATERIALS AND METHODS

The experimental system was made of perspex; it consisted of a circular tank containing a sediment layer and seawater (Fig. 1). A water flow is generated by two concentric cylinders moving with the same angular velocity and driven by an electric motor with adjustable rotational velocity. Previous systems used paddles to generate water flow (Creutzberg, 1961; Creutzberg & Postma, 1979); the advantage of using cylinders instead of paddles is that a laminar water flow is generated at low angular velocities (van der Vooren, pers. comm.).

On the bottom of the peripheral channel to the tank there was a 5-cm deep removable PVC tray. The bottom of the tray was perforated, the holes being covered with 55-µm mesh plankton gauze. These holes allowed any air bubbles caught during sediment sampling to escape when the tank was filled with seawater. A rubber septum was mounted in the bottom of the middle of the channel to enable the water column to be sampled at half depth. Sampling was carried out using a 50-ml syringe the needle of which had been replaced by a 25 cm long tube of stainless steel (inner diameter 1 mm).

The relation between the angular velocity (rad s^{-1}) of the cylinders and the bulk rotation of the water mass in the central part of the channel was determined using a small float, constructed of a table-tennis ball weighted with a thin needle. At half water depth a cross made of two thin 3 x 3 cm^2 PVC sheets was mounted on the shaft of the needle. A frame of thin copper wire on top of the float ensured that the float stayed positioned in the middle of the channel.

In addition to the above described measurements with a float, other series of measurements were carried out using a laser Doppler velocity meter (LDV) operating in the backscattering mode (Fig. 2). The instrument consisted of an He-Ne laser (Spectra-physics stabilite TM, model 124A), an optical device (type 400, Technical Physical Serve TNO-TPD, Delft, The Netherlands), an amplifier and a discriminator (Spring Lane Trading Estate, Malvern, Worcestershire, England). The instrument measured the vertical tangential current velocity profile in the middle of the channel without disturbing the current velocity field.

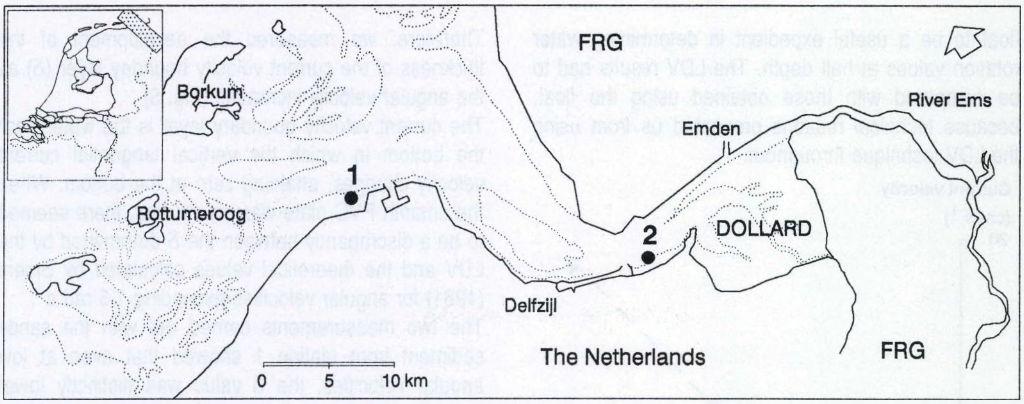

Fig. 3. Map of the Ems estuary showing the location of the sampled stations.

Current velocities could be determined down to approximately 1 mm above the bottom or the sediment. To study the influence of bottom roughness on the current velocity of the water, experiments were carried out either with a PVC plate on the tray or with different types of sediment in the tray. Current velocities were determined with both the LDV and the float. The data obtained were compared with the results of the numerical analysis of the current velocity field at low Reynold numbers for the circular tank (Bloem, 1981). A disadvantage of the laser Doppler velocity meter was that at angular velocities above 1 rad s^{-1} strong resuspension of sediment occurred, resulting in a high turbidity that hampered the detection of back scattering.

Two stations in the estuary of the Ems were sampled (Fig. 3). Sandy sediment was collected at station 1 (3.2% composed of sediment <55 m) and sandy-silty sediment at station 2 (46.5 % composed of sediment <55 m). In addition water was sampled from pools at both stations.

Samples (5 cm thick) were taken with a shovel whose shape had been adapted to the shape of the tray. At the station, the sediment was carefully transferred to the PVC tray as nearly undisturbed as possible. In the laboratory the tray was placed in the tank and the water was filtered and siphoned into the tank. Experiments were carried out at a constant temperature of 4 °C; light/dark cycle 9:15 h and a light intensity of 15-20 $\mu E\ m^{-2}\ s^{-1}$ at the water surface. During the adjustment period of two days, a constant air supply was maintained, to ensure oxygenous conditions.

Experiments were carried out for angular velocities ranging from 0.6 to 3.4 rad s^{-1}. Samples were taken 30 min after the system had been adjusted to a new angular velocity. The concentrations of suspended matter and chlorophyll-*a* in two sediment fractions were determined. Using 55-µm mesh plankton gauze, samples were separated into a sediment fraction <55 µm (mainly consisting of aggregates of organic matter, silt and clay) referred to as mud in this publication, and a sediment fraction >55 µm (mainly sand). The sand fraction was resuspended in water and both sediment fractions were filtered using dried (110 °C) and preweighed 5.5-cm diameter Whatman GF/C glass-fibre filters. After filtering, the filters were rinsed with 5 ml distilled water, deep frozen, freeze-dried and weighed to determine the suspended matter concentration of both sediment fractions. Afterwards, the chlorophyll-*a* content was determined by using a modified version (Moed & Hallegraeff, 1978) of Lorenzen's (1967) method.

Three samples from the experiment carried out with the sandy sediment of station 1 and two samples from the experiment carried out with the silty sediment of station 2 were used to ascertain the species composition and cell numbers. The samples were processed according to the method of Hasle and Fryxell (1970). The diatoms were identified from the descriptions in Peragallo & Peragallo (1897-1908), Hustedt (1930, 1939, 1959, 1961-1966) and Brockmann (1950). The cell numbers were counted under the microscope, using a counting chamber (Neubauer, improved; 0.1 mm deep).

RESULTS

Current velocity

Both the angular velocity (rad s^{-1}) and the tangential current velocity (determined by the LDV and by the float at half depth) with a smooth PVC plate on the tray gave similar estimates (Fig. 4), indicating the float to be a useful expedient in determining water rotation values at half depth. The LDV results had to be compared with those obtained using the float, because technical reasons prevented us from using the LDV technique throughout.

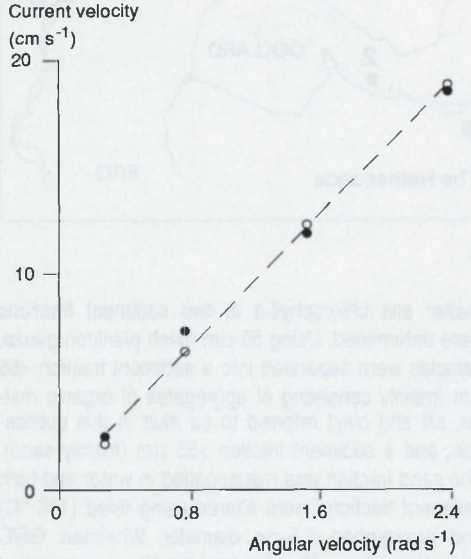

Fig. 4. Relation between angular velocity and tangential current velocity determined by float (O) for the upper half of the water column and by the laser Doppler velocimeter (●) at half depth, in the middle of the peripheral channel and for a smooth PVC bottom.

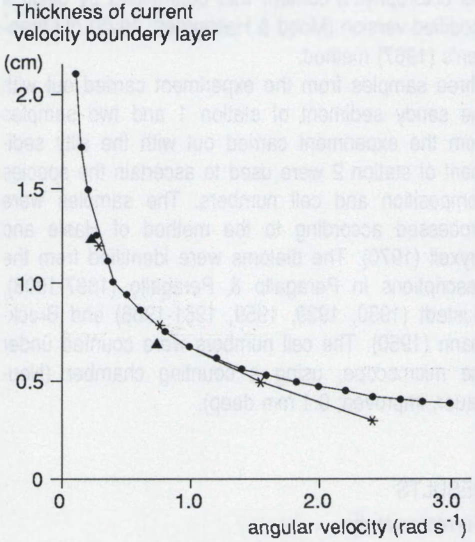

Fig. 5. Relation between angular velocity and the thickness of the current velocity boundary layer calculated by numerical analysis (●) and some LDV measurements done for a smooth PVC bottom plate (✱), and sediment from station 1 (▲).

Therefore, we measured the development of the thickness of the current velocity bounday layer (δ) as the angular velocity increased (Fig. 5).

The current velocity boundary layer is the water near the bottom in which the vertical tangential current velocity changes, attaining zero at the bottom. When the smooth PVC plate was on the tray, there seemed to be a discrepancy between the δ determined by the LDV and the theoretical values calculated by Bloem (1981) for angular velocities exceeding 1.5 rad s^{-1}.

The two measurements carried out with the sandy sediment from station 1 showed that even at low angular velocities, the δ value was distinctly lower than the calculated values.

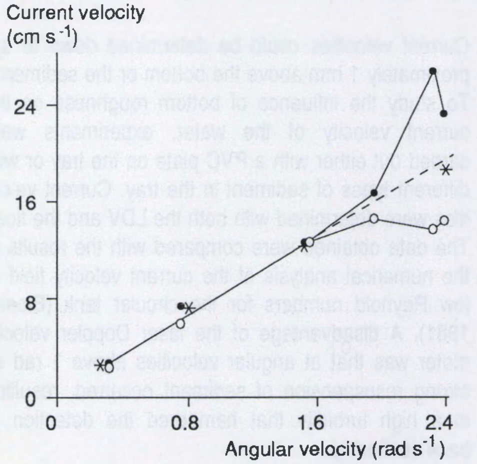

Fig. 6. Plot of angular velocity and tangential current velocity determined by LDV for a smooth PVC bottom plate (✱) as well as for sediment from station 1 (●), and the current velocity determined by float (O) for sediment from station 1.

The development of current ripples and turbidity made it impossible to use the LDV at higher angular velocities.

Fig. 6 gives the relation between angular velocity and current velocity for two different set-ups: a smooth PVC plate on the tray, and the tray filled with washed sand collected from station 1. The relation was determined in two different ways: using the LDV and the float. The sand had to be washed because after resuspension the fine sediment fractions in the original sediment hampered the detection of the backscattering signal. The curves for the float and the LDV were identical when a smooth, stable bottom was present (cf. Fig. 4). However, they differed for angular velocities >1.56 rad s^{-1} when the bottom was composed of washed, sandy sediment.

The dramatic changes in current velocity for angular velocities >2.0 rad s^{-1} were particularly striking. This phenomenon coincided with the formation of current ripples on the bottom. The difference between the curve of the LDV measurements and that of the float measurements for the experiment with a sandy bed indicates that the unmeasured changes in radial and vertical velocity components were larger than the tangential changes at angular velocities above 2.0 rad s^{-1} (the float velocity clearly decreased whereas the LDV increased). When the PVC bottom plate was used no such turbulent conditions occurred (Fig. 4).

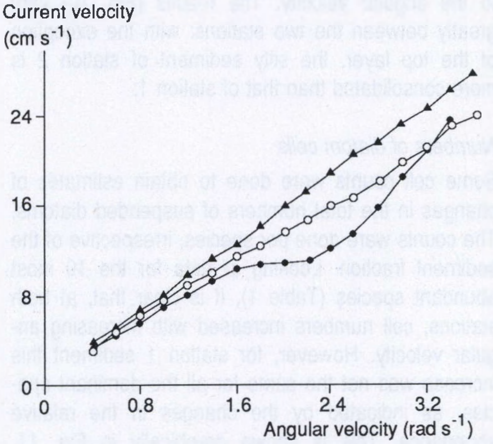

Fig. 7. Relation between angular velocity and the current velocity determined by float for a smooth PVC bottom plate (▲), sediment from station 1 (●) and sediment from station 2 (O).

Fig. 7 presents current velocities measured with the float, for three different bottom types (PVC plate, sandy sediment from station 1 and the sandy-silty sediment from station 2). Values for the sandy-silty sediment were intermediate between those for the PVC plate and for the sandy sediment of station 1 (cf. Fig. 6). The current velocities measured when sediment was used instead of the smooth PVC plate were lower because of an increase in bottom roughness and the consequently increased energy dissipation to the bottom sediment; similarly, the current velocity boundary layer of the station 1 sediment was thinner than when the PVC plate was used (Fig. 5).

Suspended matter and chlorophyll-a

The current velocity field in the peripheral channel can be divided into three velocity components: tangential, radial and vertical. Only the tangential component could be measured with the equipment available and, therefore, a causal relationship between the flowing water and the resuspension of bottom sediment could not be calculated. Instead, suspended matter and chlorophyll-*a* concentrations were plotted against the angular velocity of the cylinders (see Fig. 8 for the sandy sediment of station 1 and the sandy-silty sediment of station 2). The relation between angular velocity and the suspended matter concentrations is not linear but seems to consist of two approximately linear parts with a bend at 2.0-2.4 rad s^{-1}. Compared with the sediment composition, the curves of both fractions show that the water flow resulted in discriminatory suspension of the sediment, with the finer sediment being suspended more easily. The experiment with the sediment of station 1 clearly shows that, despite the low percentage of mud (3.2%) in the natural bottom sediment, much more mud than sand was suspended.

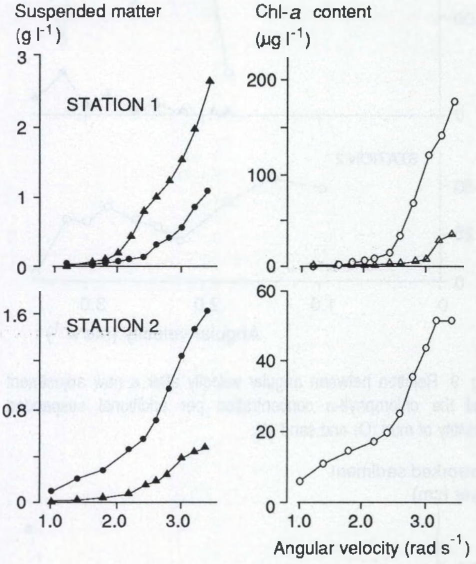

Fig. 8. Relations between angular velocity, suspended matter and chlorophyll-*a* of the sand fraction and the mud fraction from both stations. Open and closed triangles refer to the sand fraction, open and closed circles to the silt fraction.

The chlorophyll-*a* curves (Fig. 8) resemble those for the suspended matter. The chlorophyll-*a* of the sand fraction is derived from algae associated with sand grains, because most of the free-living pennate diatoms can easily pass through a sieve of 55-µm mesh. The chlorophyll-*a* for the mud fraction could belong to algae attached to mud aggregates as well as to free-living diatoms. The chlorophyll-*a* content of the sand fraction of station 2 was too low to be measured.

After each increase in angular velocity the chlorophyll-*a* concentration of the additionally-suspended sediment was calculated. These values indicate the vertical distribution of chlorophyll-*a* in the sediment layer. For both stations chlorophyll-*a* is unevenly distributed along the depth of the bottom sediment (Fig. 9).

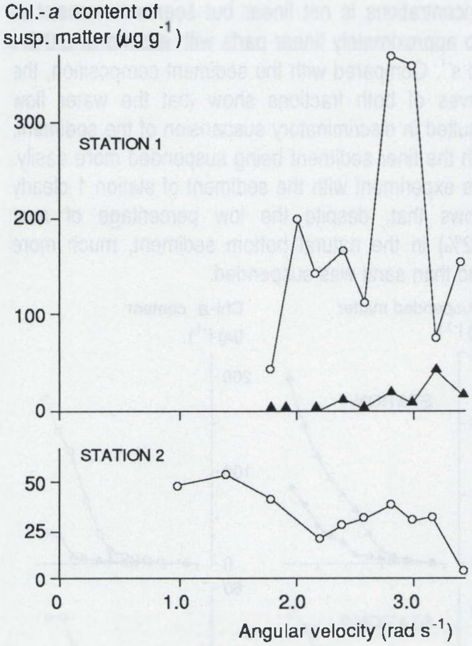

Fig. 9. Relation between angular velocity after a new adjustment and the chlorophyll-a concentration per additional suspended quantity of mud (O) and sand (▲).

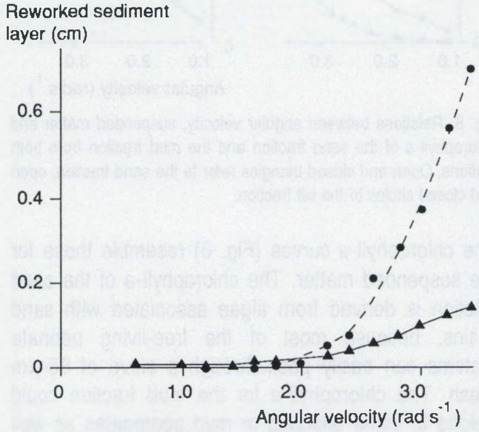

Fig. 10. Plot of angular velocity against the calculated volume of reworked sediment expressed as cm reworked sediment layer. ●, Station 1; ▲, Station 2.

Furthermore, the chlorophyll-*a* content of the sediment that was suspended first, (i.e. the top layer of the sandy sediment of station 1) is lower than that of the layers subsequently exposed. Conversely, in the sandy-silty sediment of station 2 the chlorophyll-*a* of the subsequently suspended sediments was the lower.

Calculations done on the layers of reworked sediment

To obtain information about the effects of a water flow on different types of sediment, we calculated the thickness of the reworked sediment layer in relation to the angular velocity. The results (Fig. 10) vary greatly between the two stations: with the exception of the top layer, the silty sediment of station 2 is more consolidated than that of station 1.

Numbers of diatom cells

Some cell counts were done to obtain estimates of changes in the total numbers of suspended diatoms. The counts were done per species, irrespective of the sediment fraction. Looking at data for the 10 most abundant species (Table 1), it is clear that, at both stations, cell numbers increased with increasing angular velocity. However, for station 1 sediment this increase was not the same for all the dominant species, as indicated by the changes in the relative abundance. This is shown graphically in Fig. 11, where the curves show that the 10 diatom species can be divided into two groups. At an angular velocity of 1.8 rad s^{-1}, the species *Achnanthes hauckiana*, *Amphora coffaeiformis*, *Catenula adhaerens*, *Navicula flanatica*, *Navicula forcipata*, and *Raphoneis minutissima* reached relatively high densities in suspension. In contrast, at the same angular velocity, the cell numbers of the species *Navicula aequorea*, *Navicula salinicola*, *Opephora martyi* and *Opephora pacifica* were low. Between 1.8 and 2.4 rad s^{-1}, the increase in the cell numbers of the second group of species was much larger than that of the first group.

DISCUSSION

Recently, Jumars & Nowell (1984) discussed the influence of benthic organisms living at the sediment/water interface on the resuspension of bed sediments. They related the effects (i.e. changes in bed material discharge (cf. O'Brien & Rindlaub, 1934) to the bed shear stress (τ). However, under both natural (Bohlen, 1979) and experimental conditions, the problem is how to determine the bed shear stress (τ) correctly.

Table 1. Number of suspended cells from the main pennate diatom species on stations 1 and 2 at three angular velocities: n, cell numbers x $10^4 1^{-1}$; %, relative cell abundance.

	Angular velocity (rad s^{-1})					
	18		24		34	
Species	n	%	n	%	n	%
Station 1						
1. Navicula flanatica Grun.	53.4	38	262.6	22	702.2	15
2. Opephora martyi Hérebaud	3.0	2	223.4	19	1062.4	23
3. Achnanthes hauckiana Grun.	20.2	14	133.0	11	465.2	10
4. Raphoneis minutissima Hust.	15.4	11	96.2	8	223.6	5
5. Navicula forcipata Grev.	16.2	12	80.8	7	187.0	4
6. Navicula salinicola Hust.	1.6	1	98.6	8	529.0	12
7. Catenula adhaerens Mereschk.	9.2	7	85.6	7	278.2	6
8. Amphora coffaeiformis (Agardh) Kütz.	8.6	6	77.2	7	214.4	5
9. Navicula aequorea Hust.	2.4	2	39.2	3	355.6	8
10. Opephora pacifica (Grun.) Petit	2.4	2	34.4	3	187.0	4
Remaining species	7.6	5	57.0	5	355.6	8
Total	140		1188		4560	
Station 2						
1. Navicula flanatica Grun.	322.2	44			590.0	30
2. Cymatosira belgica Grun.	128.0	27			410.0	20
3. Raphoneis minutissima Hust.	104.4	14			292.0	15
4. Gyrosigma fasciola (Ehr.) Cleve	23.0	3			122.0	6
5. Achnanthes hauckiana Grun.	28.8	4			84.0	4
6. Navicula salinarum Grun.	26.2	3			78.0	4
7. Fragilaria brevistriata Grun.	0.4	3			72.0	3
8. Rhaphoneis amphiceros Ehr.	14.4	2			78.0	4
9. Pleurosigma aestuarii (Bréb.) W. Smith	14.4	2			54.0	3
10. Catenula adhaerens Mereschk.	17.8	2			36.0	2
Remaining species	46.6	6			184.0	9
Total	756				2000	

The numerical analysis of the water flow in our circular tank (Bloem, 1981) indicates that, at increasing angular velocities, the radial (v) and vertical (w) velocity components develop in a complex and disproportionally strong way concomitantly with the tangential velocity component (u). Unfortunately, we could not determine all three velocity components with the equipment available. Consequently, the bed shear stress could not be estimated because $\tau = \sqrt{\tau^2_{xz} + \tau^2_{yz}}$ in which τ_{xz} is based on u and τ_{yz} is based on the unknown v. We were wary of estimating the bed shear stress simply by taking the tangential current velocity component (Gordon, 1975) and inserting it in the quadratic friction law. Therefore, we merely plotted the relation between the angular velocity (rad s^{-1}) of the cylinders in the flow generator, and suspended sediment, chlorophyll-*a*, and suspended benthic diatoms. These plots enabled a causal relationship to be identified between angular velocity (bed shear stress or dissipated energy) and resuspension. However, the comparison between the concentrations of the total suspended matter for both stations and the current velocities determined by the float (cf. Fig. 7) revealed the need to ascertain all three velocity components (Fig. 12). Total concentrations of suspended matter were used because the sand and mud were not resuspended independently from each other. At low angular velocities, the increase in total suspended matter developed linearly with angular velocity as well as with the current velocity (Fig. 12). The steep increase in suspended matter at higher angular velocities (c. 2 rad s^{-1} corresponding with c.10 cm s^{-1}) corresponds very well with the smaller increase in the current velocity shown by the float. Increased suspended matter can only be the result of increased bed shear stress and consequently of more energy being dissipated to the bottom. Thus, current-velocity components other than the tangential velocity component must be responsible for the steep-increase in suspended matter. This agrees with Bloem's numerical analysis (Bloem, 1981). These other current-velocity components caused strong vortices; at station 1 at angular velocities above 1.6 rad s^{-1} the current velocity determined by the float developed

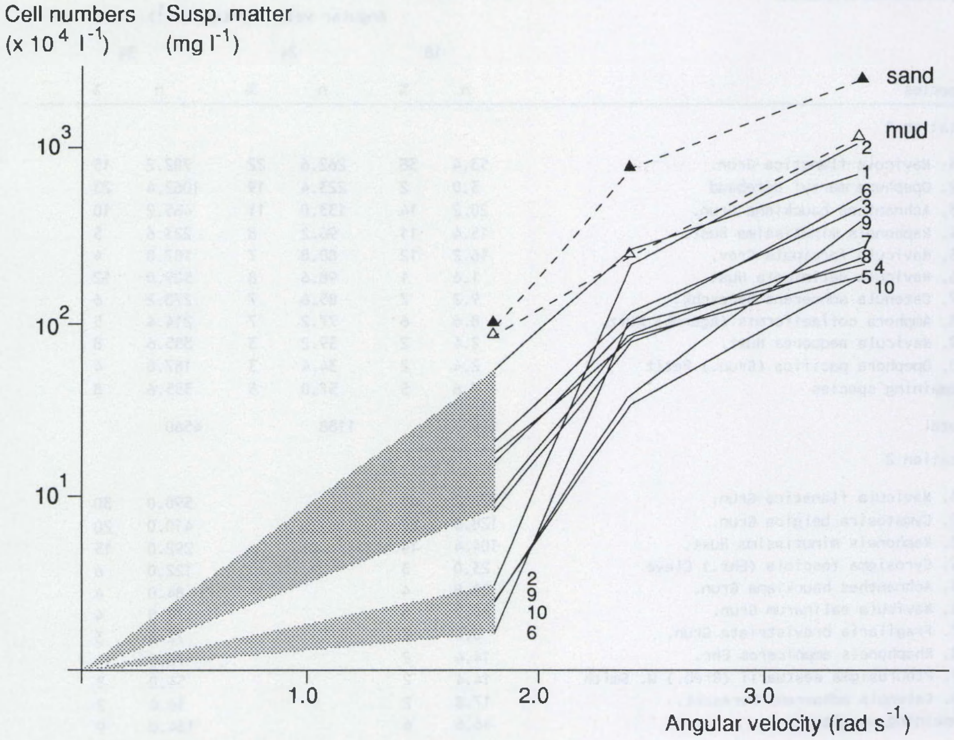

Fig. 11. Plot of angular velocity against the numbers of suspended cells of the 10 most abundant species, and the concentrations of suspended mud and sand for station 1. (1) *Navicula flanatica*; (2) *Opephora pacifica*; (3) *Achnanthes hauckiana*; (4) *Raphoneis minutissima*; (5) *Navicula forcipata*; (6) *Navicula salinicola*; (7) *Catenula adhaerens*; (8) *Amphora coffaeiformis*; (9) *Navicula aequorea*; (10) *Opephora pacifica*.

very differently and partly contrary to that determined by the LDV (Fig. 6). Obviously, the presence of current ripples at an angular velocity of 1.8 rad s^{-1} may have contributed to these vortices and to the intensified resuspension (cf. Fig. 10). The sediments of station 2 were more consolidated because they were clayey and fine-grained (Postma, 1967) and therefore rich in organic substances and micro-organisms (Schröder & van Es, 1980) which increased the binding (Meadows & Anderson, 1968). Consequently, no current ripples were formed.

Mud and even sand are driven into the water column at relatively low angular velocities (Fig. 8). During the motion of the bed sediment, the mud fraction was washed out, which means that the amount of mud suspended was disproportionate to the initial sediment composition. This has significance for the field situation, because some of this material is transported to the channels, where it is dispersed and mixed with other suspended matter. During the next tide the mixture of this freshly-suspended and older-suspended material is redistributed over the tidal flats in the estuary and finally accumulates according to processes explained by Postma (1954, 1961) and van Straaten & Kuenen (1957, 1958). Long-term changes in the composition of the estuarine sediments have not been observed (BOEDE, data file), thus under field conditions a dynamic equilibrium might be maintained between resuspension and redeposition of sediments (de Jonge, 1983).

More than 80% of the benthic diatoms on sand grains live associated with mud particles coating these grains (de Jonge, 1985): this stresses the importance of mud aggregates as a substrate and confirms observations made by Meadows & Anderson (1968). Because the mud fraction of the sediment washed out faster than the sand fraction, diatom species or specimens that are free-living or are associated with mud particles will be suspended at lower current

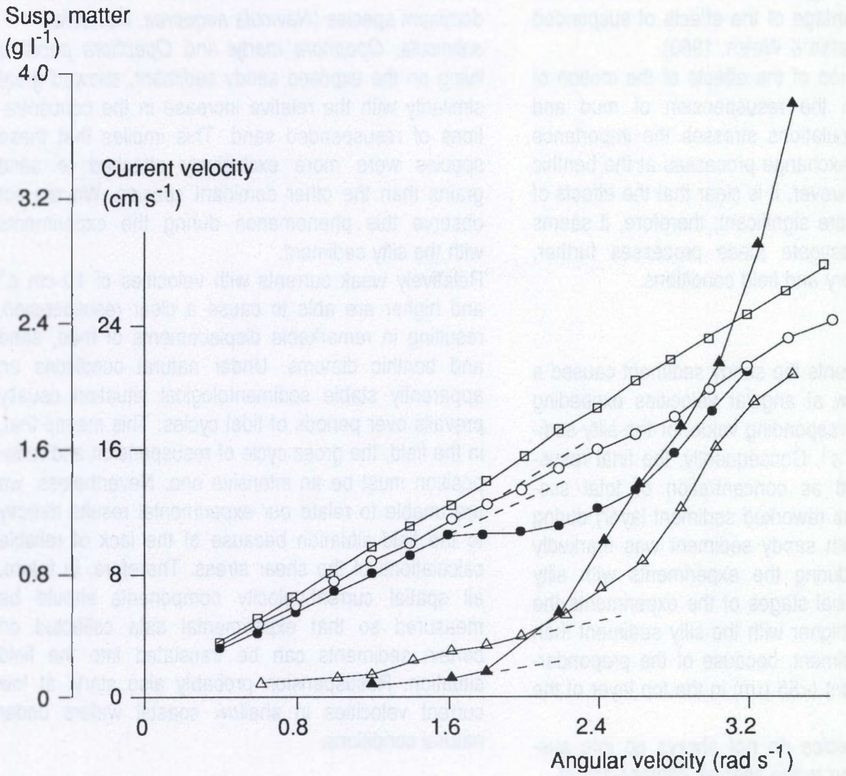

Fig. 12. Relation between angular velocity and current velocity determined by float for a smooth PVC bottom plate (☐), sediment from station 1 (●), sediment from station 2 (O), and angular velocity and total suspended matter for station 1 (▲), and total suspended matter for Station 2 (△).

velocities than the cells associated with the heavy sand grains. This should then result in a differential suspension of diatom cells, as indicated in Fig. 11 (cf. Table 1, station 1): the relative abundance of the species *Navicula aequorea*, *Navicula salinicola*, *Opephora martyi*, and *Opephora pacifica* increased considerably at higher angular velocities. A significant number of these diatom cells were presumably associated with sand grains and in the transport processes were dependent on the behaviour of the sand. This also agrees with the explanation given in an earlier paper (de Jonge, 1985) for some direct field observations. In that study the species *Navicula aequorea* and *Navicula salinicola* were also recognized as species associated with sand grains. The only discrepancy between both data sets is caused by *Achnanthes hauckiana*, which was formerly also recognized as a sand-associated species. Interestingly, the four species mentioned above are not among the 10 most abundant species present in the silty sediment of station 2 (Table 1, station 2). The species composition and cell numbers in the channel water are very similar to those of the sediments of the tidal flat (de Jonge, 1985). This and the results published here show that diatoms seem to be swept away from tidal flats at relatively low current velocities. Therefore, the processes of resuspension, mixing and redeposition can be assumed to happen very fast. Besides sediment resuspension, sediment reworking occurs (Fig. 9 and 10). The diatom cells associated with sand grains are particularly subject to this process. The values calculated for the reworked sediment layer (Fig. 10) clearly show that benthic diatoms can be transported to depths beneath the photic layer, which is less than 2 mm for sand and less than 0.2 mm for silty sediments (Colijn, 1982).

Under natural conditions, the transport of benthic diatoms to the channels can be important because in winter, when phytoplankton populations are virtually absent, these suspended pennate diatoms can form an additional, high-quality food source for small herbivorous plankton organisms. Further, filter-feeders can also take advantage of the effects of suspended benthic diatoms (Baillie & Welsh, 1980).

The above discussion of the effects of the motion of bed sediments on the resuspension of mud and benthic diatom populations stresses the importance of currents on the exchange processes at the benthic boundary layer. However, it is clear that the effects of waves are even more significant; therefore, it seems worthwhile to investigate these processes further, under both laboratory and field conditions.

CONCLUSIONS

During the experiments the sandy sediment caused a turbulent water flow at angular velocities exceeding 1.6 rad s^{-1}. The corresponding value for the silty sediment was c. 2 rad s^{-1}. Consequently, the final resuspension (expressed as concentration of total suspended matter or as reworked sediment layer) during the experiments with sandy sediment was markedly higher than that during the experiments with silty sediment. In the initial stages of the experiments the resuspension was higher with the silty sediment than with the sandy sediment, because of the preponderance of fine sediment (<55 µm) in the top layer of the silty sediment.

Benthic diatom species do not always go into suspension in proportion to the species composition of the sediment. The relative increase in cell numbers of dominant species (*Navicula aequorea*, *Navicula salinicola*, *Opephora martyi* and *Opephora pacifica*) living on the exposed sandy sediment, showed great similarity with the relative increase in the concentrations of resuspended sand. This implies that these species were more exclusively attached to sand grains than the other dominant species. We did not observe this phenomenon during the experiments with the silty sediment.

Relatively weak currents with velocities of 10 cm s^{-1} and higher are able to cause a clear resuspension, resulting in remarkable displacements of mud, sand and benthic diatoms. Under natural conditions an apparently stable sedimentological situation usually prevails over periods of tidal cycles. This means that, in the field, the gross cycle of resuspension and redeposition must be an intensive one. Nevertheless, we are unable to relate our experimental results directly to the field situation because of the lack of reliable calculations of the shear stress. Therefore, in future, all spatial current-velocity components should be measured so that experimental data collected on certain sediments can be translated into the field situation. Resuspension probably also starts at low current velocities in shallow coastal waters under natural conditions.

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WIND AND TIDE INDUCED RESUSPENSION OF SEDIMENT AND MICROPHYTOBENTHOS IN THE EMS ESTUARY

V.N. de Jonge and J.E.E. van Beusekom

ABSTRACT

The resuspension of microphytobenthos (mainly benthic diatoms) and of the sediment fraction $< 55\ \mu m$ from tidal flats was studied in the Ems estuary (Netherlands/Germany). Resuspension is already achieved at low wind speeds of 2 m s^{-1}. Waves generated by winds between 5 and 10 m s^{-1} contribute 2 to 5 times more to resuspension than tidal currents. Measured in the main channels the resuspended microphytobenthos already reach significant values (10% of the total microphytobenthos biomass) at wind speeds of 3 m s^{-1}. Over most of the estuary suspended matter and chlorophyll-*a* increased linearly with antecedent winds ranging from 2 to 14 m s^{-1} and averaged over three high water periods preceding sample collection. Resuspended material measured during high tide in the water covering the tidal flats correlated with the wind speed during the sampling period.

Wind-induced waves cause resuspension of sediments and microphytobenthos, whereas tidal currents are mainly responsible for the redistribution of the resuspended material.

The lateral mixing scale for the lower and upper reaches of the estuary is estimated to be in the order of 3 ± 1 tidal cycles.

INTRODUCTION

The terms 'phytoplankton' and 'phytobenthos' suggest that these groups are sharply defined. However, in estuaries phytoplankton can contain significant numbers of benthic species (Grøntved, 1949; Cadée & Hegeman, 1974; de Jonge, 1985).

Resuspension of benthic diatoms appears related to the resuspension of the substrate. Most benthic diatoms live adhering to aggregates of clay minerals and organic matter, some of which form coatings on sand grains (Meadows & Anderson, 1968; de Jonge, 1985). Expressed per estuary reach there can be as many benthic diatoms in the water of the channels as there are diatom cells in the top 0.5 cm of the tidal flats (de Jonge, 1985). Because, species composition in the water and on the tidal flats is also nearly the same (de Jonge, 1985) a high turnover of sediment as well as of benthic algae occurs between the tidal flats and channels in the estuary.

The resuspension of algae has rarely been studied in the field. Gabrielson & Lukatelich (1985) showed that chlorophyll-*a* increase in the water is caused by resuspension. This process may increase the efficiency of food chain relationships, especially in shallow systems where phytoplankton biomass is very small or in systems where phytoplankton is nearly absent during winter (Roman & Tenore, 1978, Baillie & Welsh, 1980; Fréchette & Bourget, 1985; de Jonge, 1985; Demers *et al.*, 1987). The present study was carried out to assess the importance of the resuspension and to quantify the relationship between on the one hand suspended amounts of sediment and microphytobenthos and on the other hand the key factors tidal currents and wind-induced waves.

MATERIALS AND METHODS

Study area

The study was done in the Ems estuary on the border between the Netherlands and the Federal Republic of Germany (NW Europe) (Fig. 1). Including the outer delta this estuary is approximately 100 km long. The average discharge of the River Ems is 115 m^3s^{-1}. The tidal prism in the inlet between the barrier islands of Rottumeroog and Borkum is approximately 10^9 m^3. The mean tidal range increases from 2.3 m near the island of Borkum to 3.2 m at Emden (de Jonge, 1983). Strong tidal currents, result in much dispersion (Helder & Ruardij, 1982) and a steep salinity gradient (de Jonge, 1988, 1991). There is a suspended matter gradient, from approximately 20 g m^{-3} near the tidal inlet to 400 g m^{-3} in the most turbid part of the estuary close to the River Ems (de Jonge, 1988). This steep gradient in suspended matter is maintained by local accumulation processes (Postma, 1967).

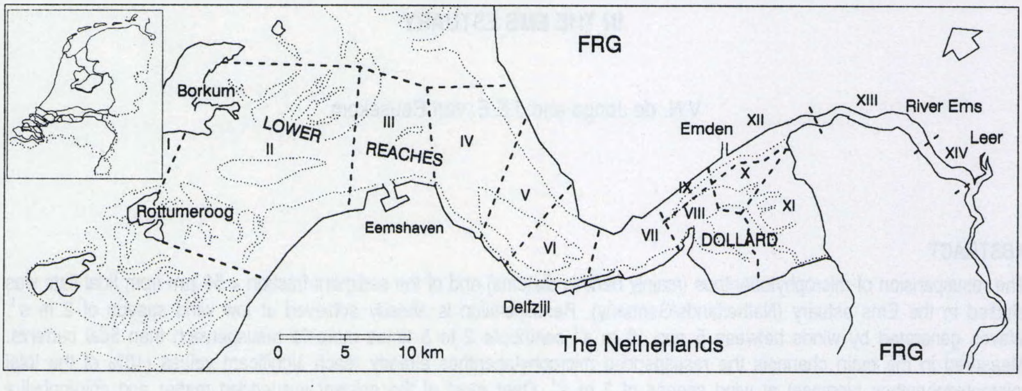

Fig. 1. Map of the Ems estuary, with the boundaries of the 14 sectors (I - XIV). Dotted lines indicate mean low water level.

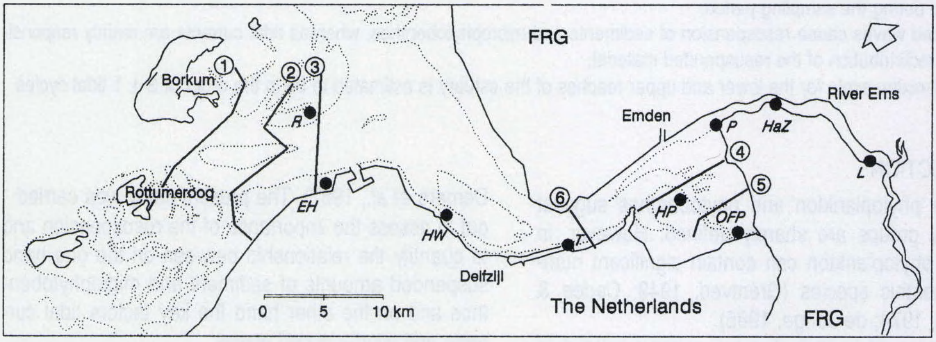

Fig. 2. Map of the Ems estuary with the cross sections (1 - 6) and stations on tidal flats: R= Randzel; EH= Eemshaven; HW= Hoogwatum; T= Termunten; HP= Heringsplaat; OFP= Oost Friesche Plaat; P= Pogum; HaZ= Hatzumer Zand and L= Leer.

The mean annual primary production in the Ems estuary during the mid 1970s was approximately 200 gC m^{-2} a^{-1} (Colijn, 1983; Colijn & de Jonge, 1984), of which about 75% is attributable to permanently suspended algae (phytoplankton) and the rest to microalgae (mostly diatoms) living on and in the tidal flats and forming the microphytobenthos.

Field measurements

Longitudinal surveys - The estuary was sampled 11 times in 1980-81 (Table 1) during high tide, to determine the longitudinal distribution of chlorophyll-*a* and of suspended matter in the main channels. In two surveys (March 1980 and December 1980) the species distribution of microphytobenthos and phytoplankton (mainly centric diatoms) in the water was determined, as well as the suspended matter and chlorophyll-*a* concentrations.

Because microphytobenthos chlorophyll-*a* can reach significant concentrations in winter and spring, these periods were chosen as the main sampling periods to minimize the contribution of phytoplankton to the total chlorophyll-a content in the water column. However, two surveys were done in April 1980 and June 1981 when an abundant phytoplankton standing stock was present.

The Ems estuary was divided into 14 sectors for sampling (Fig. 2). Water was continuously pumped (at 300 m^3 min^{-1}) from 2 m depth using a manifold during passage of each sector. The inflowing volume was split into four flows. Water from the smallest tube (50 ml s^{-1}) was sieved through 55 μm plankton gauze, and collected, yielding an integrated subsample of c. 25 l per sector. After mixing, a single subsample of 250 to 1000 ml was filtered over a weighed and dried glass fibre filter (Whatman GF/C), washed

Table 1 Listing of all cruises in this study. For cross sections see Fig. 2; for drogue tracks see Fig. 5

LONGITUDINAL SURVEYS		CROSS-SECTIONAL SURVEYS			DROGUE EXPERIMENTS	
Cruise	Date	Cruise	Date	Cross section	Cruise	Date
1	4 - 6 Feb 1980	12	2 - 4 Dec 1980**	3	23	21 May 1980
2	17 - 19 Mar 1980***	13	2 - 4 Dec 1980**	6	24	21 May 1980
3	15 - 16 Apr 1980*	14	17 Mar 1981	1	25	21 May 1980
4	2 - 4 Dec 1980***	15	17 Mar 1981	3	26	16 Jun 1980
5	16 - 17 Mar 1981	16	25 Mar 1981	4	27	17 Jun 1980
6	18 Mar 1981	17	25 Mar 1981	5	28	18 Jun 1980
7	19 Mar 1981	18	26 Mar 1981	1	29	18 Jun 1980
8	23 Mar 1981	19	26 Mar 1981	3	30	19 Jun 1980
9	25 Mar 1981	20	24 Jun 1981	2	31	9 Sep 1980
10	26 Mar 1981	21	26 Jun 1981	4		
11	24 - 26 Jun 1981*	22	26 Jun 1981	5		

* rich in phytoplankton. ** main channel only. *** determination of numbers of phytoplankon cells and of benthic diatom cells.

with 10 ml of distilled water, wrapped in aluminium foil and immediately stored at -20 °C. This subsample was used for determination of suspended matter and chlorophyll-*a*.

A second 20 l subsample was used to enumerate diatoms passing a 55 µm mesh plankton gauze, after first concentrating it in a modified version of the flow-through centrifuge (1400 rpm) described by Donze and de Groot (1982). The inner side of the rotating drum of this centrifuge was covered with soft synthetic material impressed with a honeycomb pattern. Each honeycomb "cell" functioned as a very small sedimentation chamber in which a layer not more than about 1 mm thick accumulated. The sample was led into the centre but towards the bottoms of the rotating drum at a rate of approximately 250 ml min^{-1}. Under these conditions, the recovery of this centrifuge was nearly 100%; this was checked by sampling the water after centrifugation. After removing the "honeycomb" from the centrifuge drum, the sedimented material was flushed out of the cells with a syringe dispensing filtered sea water. The resulting concentrated sample was first subsampled, then filtered (Whatman GF/C) and stored as described above. For cell counting by fluorescence microscopy and species analysis, three extra subsamples were taken and preserved with a mixture of acrolein, glutaraldehyde and tannin (van der Veer, 1982) before being stored at -20 °C.

Cross-sectional surveys - Cross sectional surveys were carried out during high tide and under varying weather conditions (see Fig. 2 and Table 1) to determine the differences in chlorophyll-*a* and suspended matter over the tidal flats, as compared to discrete channels. Above the flats 1 l water samples (one per sampling station) were taken manually. Sampling depths were 0.3 m over the flats vs. 2 m in the channels. Samples were collected from distinct stations within the cross section. Two subsamples were sieved and filtered and the filter discs of suspended matter were processed and stored as described under longitudinal surveys.

Drogue experiments - These observations, carried out in May, June and September, 1980 were done to investigate the fluctuations in chlorophyll-*a* content and the suspended matter content in the same water mass during one tidal cycle. The drogues were long and thin and had a length that covered c. 75% of the local water depth. Only 5 to 7 cm of the drogues was above the water surface and the visibility was increased by use of phosphorescent red paint. Consequently, the tracks represent the mean pattern of a certain water mass and drifting of the drogue by wind was excluded. The observations started at high tide. The drogues were followed by a boat. Every 30 or 60 minutes, depending on the displacement of the drogue, water samples were taken manually from a depth of c. 0.3 m. On board, the water samples were immediately sieved, filtered and stored as described above. The mean current velocities of the water column were calculated from the distance the drogue travelled between two samplings.

Effective wind speed - Hourly measurements from the coastal station Lauwersoog were obtained from the Royal Dutch Meteorological Institute (KNMI). Mean wind speed was calculated for each 6 hr interval bracketing high tide (when most tidal flats are submerged). Using regression we then tested which combination of "high water wind speeds" correlated best with suspended matter or the resuspended fraction of the microphytobenthos.

Sampling the tidal flats - At some stations on the intertidal flats the sediment was sampled to determine the biomass distribution of the microphytobenthos during the longitudinal surveys (Fig. 2). At each station 20 to 25 samples of 2.4 cm diameter each were taken using perspex tubes and rubber stoppers or a modified ball-stoppered corer. On board the ship, the upper 0.5 cm of each core was sliced off. The samples were pooled and mixed thoroughly, after which 5 subsamples of 1 ml each were taken and stored separately at -20 °C (for details see de Jonge, 1979).

Laboratory analysis - Before analysis of suspended matter content and chlorophyll-*a* the water samples and the sediment samples were lyophilized. Chlorophyll-*a* (mg m^{-3}) was measured spectrophotometrically at 664 nm using the method published by Lorenzen (1967), modified according to Moed & Hallegraeff (1978). Suspended matter content was determined gravimetrically (g m^{-3}) after drying for 1 hour at 105 °C.

In samples of the surveys of March 1980 and December 1980 inorganic particles and empty diatom frustules were separated from intact pennate and centric diatom cells by a modification of the Ludox separation method (de Jonge, 1979) considerably shortened by not treating a second sample to establish the recovery. Recovery was now determined in the same sample that was used to separate the intact diatom cells from empty frustules and inorganic compounds. The method was streamlined further by pooling the different Ludox fractions after the first washing of the various density fractions in which the separated diatom cells were present. After pooling, the washing procedure was continued as described by de Jonge (1979).

The separated samples were oxidized and processed to microscopic slides according to Hasle & Fryxell (1970). The total cell numbers and the ratio between pennate and centric diatoms was determined by fluorescence microscopy on the concentrated integrated field sample. The diatom cells were counted using 0.1 ml blood-counting chambers (Neubauer improved 0.1 mm deep).

RESULTS

Surveys and field experiments

Longitudinal surveys - The graphs in Fig. 3A show the importance of the numbers of benthic diatoms in the water as compared with planktonic diatoms in winter and early spring. For both cruises, the longitudinal distribution of chlorophyll-*a* in the estuary (Fig. 3B) corresponds well with the distribution of the numbers of benthic diatom cells (Fig. 3A). There is one deviation: the chlorophyll-*a* concentration in the water of the River Ems in March 1980. This may have been caused by the development of phytoplankton in the River Ems. The graphs for the cell numbers of pennate diatoms (Fig. 3A) and those for suspended matter (Fig. 3C) also agree, but the longitudinal gradient in chlorophyll-*a* of the tidal flats (not given) and the water column did not.

Although sectors XIII and XIV of the river Ems did not fit into the general pattern, the graphs in Fig. 3 indicate relations between suspended matter and benthic diatoms (chlorophyll-*a*) in the Ems estuary. For most sectors the presented data suggest that part of the chlorophyll-*a* in the water column is derived from pennate diatoms. Regression analyses (Table 2, cruises 1 to 10) indicated that in the estuary during winter and early spring the concentrations of suspended matter and chlorophyll-*a* were correlated with each other. Another result is that based on these calculations two subareas (lower reaches and Dollard) and possibly a third (lower Ems) can be distinguished. This subdivision of the estuary in three areas was retained in further calculations.

Cross-sectional surveys - At low wind speeds (less than c. 6 m s^{-1}) most of the values for suspended matter in the channels and above the flats were roughly the same (Fig. 4). However, the concentrations of suspended matter above the flats at locations not far from the edge of the channel were usually lowest. Maximum concentrations were found close to the shoreline or near the hydraulic boundary (tidal watershed) between two tidal basins.

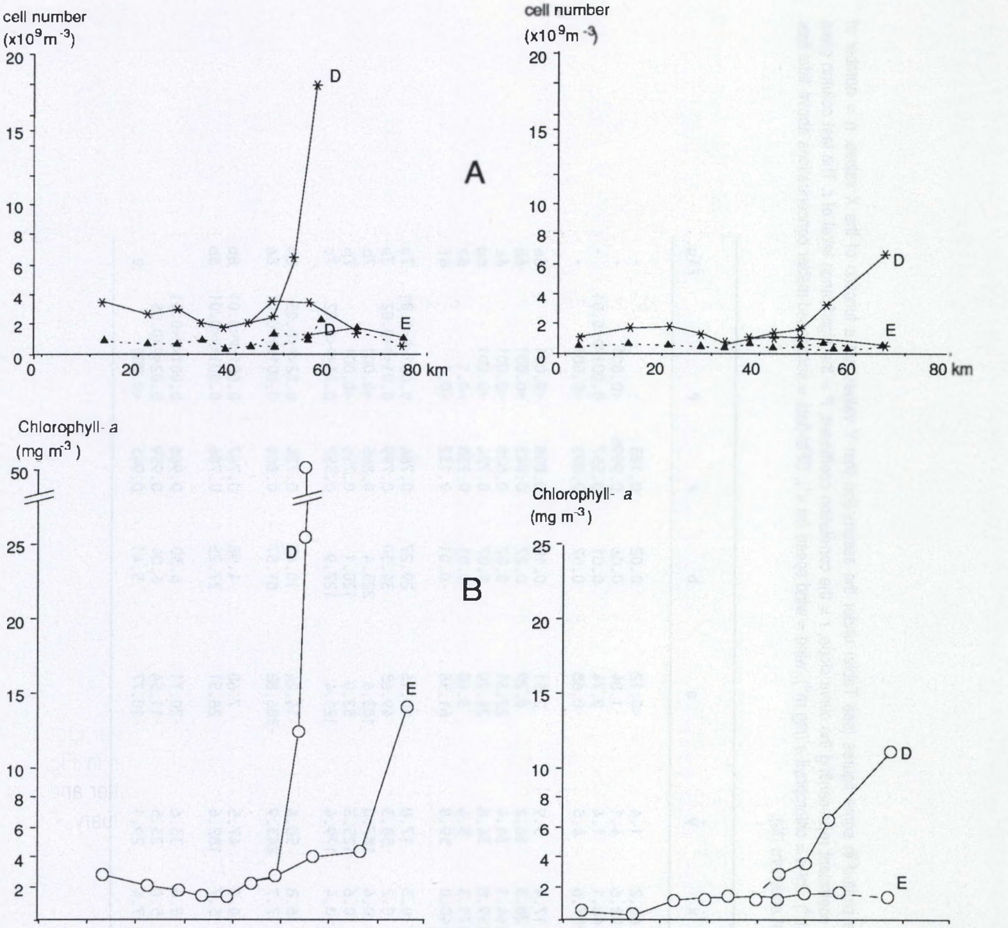

Fig. 3. Longitudinal gradients of concentrations of phytoplankton diatom cells (A:▲) and numbers of benthic diatom cells (A:✱), chlorophyll-*a* (B) and suspended matter (C) in March 1980 and December 1980. For statistics see Table 2. Roman numerals refer to the sectors.

Table 2. Results of regression analysis applied to different data whose values are plotted in some figures (see Table) under the assumption that Y values are a function of the X values. n = number of observations, x = mean X value, y = mean Y value, a = y intercept, b = regression coefficient representing the curve slope, r = the correlation coefficient, P = the significance level of r. The last column gives the figures in which the basic data have been plotted. SPM = suspended matter (g m^{-3}), chl-*a* = chlorophyll-*a* (mg m^{-3}), wind = wind speed (m s^{-1}), SPM-flats = suspended matter concentrations above tidal flats (g m^{-3}) and % resusp. chl-*a* = resuspended microphytobenthos from the top 0.5 cm of sediment (%).

X	Y	Area	Cruise	n	$\bar{x}$	$\bar{y}$	a	b	r	P	Fig.
SPM	chl-*a*	Lower reaches	1	4	66.2	1.4	-0.12	0.02	0.183	-	-
		Dollard	1	5	102.6	4.1	-1.84	0.06	0.9996	<0.001	-
		Lower reaches	5 to 10	22	46.1	1.4	0.74	0.01	0.557	0.001<P<0.01	-
		Dollard	5 to 10	24	197.6	4.5	-0.68	0.02	0.893	<0.001	-
SPM	chl-*a*	Lower reaches	28	14	17.4	5.9	2.51	0.19	0.808	<0.001	6a
		Lower reaches	29,30	27	28.3	16.2	8.29	0.27	0.943	<0.001	6b
		Dollard	24	11	164.1	34.4	22.31	0.07	0.826	<0.001	6c
		Dollard	23	17	159.8	34.8	24.20	0.07	0.724	<0.001	6d
		Dollard	26,27	24	171.3	5.4	3.40	0.01	0.238	>0.1	6e
		Dollard	25	15	140.0	59.8	61.58	-0.01	0.132	>0.1	6f
Current velocity	SPM	Lower reaches	28	12	0.3	17.8	10.16	29.27	0.784	0.001<P<0.01	7a
		Lower reaches	30	8	0.2	58.3	49.63	34.50	0.799	0.01<P<0.02	7a
		Dollard flats	23,24,25	16	0.4	187.0	103.6	225.4	0.865	<0.001	7b
		Dollard chan.	23,24,25	22	0.6	125.3	52.0	120.1	0.755	<0.001	7b
		Dollard	26,27	20	0.4	179.4	121.4	127.9	0.557	0.01<P<0.02	7c
SPM flats	wind	Lower reaches	-	8	6.8	56.6	-14.24	10.43	0.724	0.02<P<0.05	8a
		Dollard	-	9	7.7	243.9	-386.88	81.57	0.804	0.001<P<0.01	8a
SPM channels	wind	Lower reaches		11	8.0	47.5	7.68	4.98	0.767	0.001<P<0.01	8b
		Dollard		11	5.7	182.6	28.51	27.25	0.786	0.001<P<0.01	8b
% resusp. chl-*a*	wind	Lower reaches		5	8.6	33.6	-20.71	6.30	0.966	0.001<P<0.01	
		Dollard		4	5.8	23.5	-11.54	6.04	0.959	0.02<P<0.05	
		total estuary		9	7.4	29.1	-10.77	5.41	0.945	<0.001	9

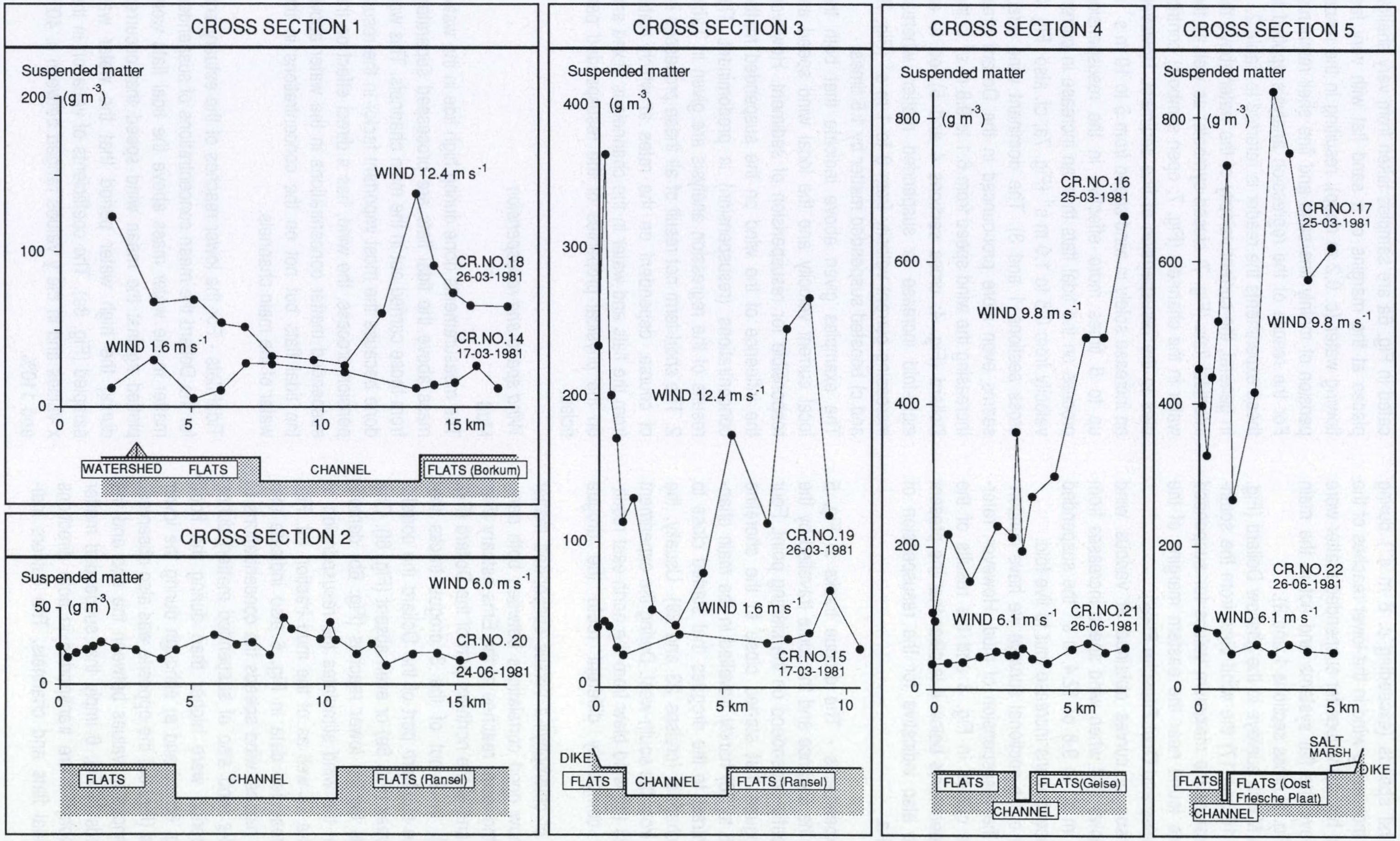

Fig. 4. Plot of the suspended matter concentrations as measured during the cross-sectional surveys and excluding cross section 6 (which represents a channel). For location of the different cross sections see Fig. 2. The mean wind speed of the high water period during sampling is given.

At high wind speeds (exceeding c. 6 m s^{-1}) during periods of increasing wind in the lower reaches of the estuary the highest values for suspended matter were always above the flat systems and not in the main channel (Fig. 4, cross sections 1 and 3).

During the March surveys in the shallow Dollard (Fig. 4, cruises 16 and 17) the wind blew from the south-west. Therefore the maximum values for suspended matter were found near the eastern margins of the Dollard (Geise and Oost Friesche Plaat).

A comparison of curves obtained at various wind speeds shows that when wind speed increases from 1.6 or 6.1 m s^{-1} to 9.8 or 12.4 m s^{-1} the suspended matter concentrations increase four to five-fold.

During the cross sectional surveys we have concentrated on the resuspension of mud. However, referring to the curves in Fig. 3 and the results of the drogue experiments below it is clear that the present results are also indicative for the resuspension of chlorophyll-*a*.

Drogue experiments - The drogue tracks in Fig. 5 show that the distance and the route travelled by the drogue greatly dependend on the starting point. Four of the drogues that started close to the shoreline (cruises 25 to 28) hardly travelled in the main channel, in contrast to the drogues that started close to the main channel (cruises 23 and 29). Usually, the wind blew from the south-west. During the experiment of cruise 25 the wind blew from the north-east resulting in a completely different route the drogue travelled.

The plots of chlorophyll-*a* versus suspended matter (Fig. 6) show good correlations between both parameters in the lower reaches of the Ems estuary (Fig. 6a and b) and in the northern part of the Dollard (Fig. 6c and d). In 2 out of the 3 drogue tracks that crossed the southern part of the Dollard the correlations are weak (Fig. 6e) or even absent (Fig. 6f). One of the plots for the lower reaches (Fig. 6b) demonstrates that the wind stimulates the resuspension of chlorophyll-*a* as well as of the mud fraction (cf. Fig. 4). The presented data in Fig. 6 also indicate that during the highest wind speeds the concentrations of chlorophyll-*a* (and also of suspended matter) during the ebb period were higher than during the flood period (Fig. 6b,c,d and e) although during the lower wind speed (Fig. 6a) the opposite was also observed. The differences in values between the ebb and the flood periods in Fig. 6 imply that suspended matter and chlorophyll-*a* are transported in both directions between tidal flats and channels. The outliers indicated in Fig. 6a are samples taken from very shallow places at the margins of a sand flat with very fast flowing water (c. 0.2 m deep), resulting in the resuspension of mainly fine sand and fine shell remnants. For the results of the regression analysis applied to these experiments the reader is referred to Table 2.

In general, the current velocity of the water above the intertidal flats (Fig. 7; closed symbols) as well as the water in the channels (Fig. 7; open symbols) contributes to the resuspension of fine sediment. However, an increase solely in wind speed from 5 to 10 m s^{-1} is up to 5 times more effective in the resuspension process on the tidal flats than an increase in current velocity from 0.5 to 1.0 m s^{-1} (Fig. 7a; cf. also Fig. 4: cross sections 1 and 3). The dominant wind effect seems even more pronounced in the Dollard area. Increasing the wind speed from 6.1 to 9.8 m s^{-1} in the Dollard (Fig. 4; cross sections 4 and 5) led to an eight-fold increase in suspended matter, whereas increasing current velocity from 0 to 1 m s^{-1} (Fig. 7b and c) boosted suspended matter by 1.5 times.

The examples given above indicate that both the local current velocity and the local wind speed are responsible for resuspension of sediment. However, the influence of the wind on the suspended matter concentrations (resuspension) is predominant. The results of the regression analysis are given in Table 2. The short-term net result of all these processes is, of course, dependent on the rates at which water from the flats and water in the channels is mixed and on the physical properties of the resuspended particles.

Wind speed and resuspension

Mud

The measurements done during high tide in the water mass above the tidal flats are processed separately from those carried out in the main channels. This was done because the most important factor in the resuspension process, the wind, has a direct effect on the suspended matter concentrations in the water above the tidal flats but not on the concentrations in the water of the main channels.

Tidal flats - For the lower reaches of the estuary and for the Dollard the mean concentrations of suspended matter in the water mass above the tidal flats were plotted against the mean wind speed that occurred during the high water period that the water was sampled (Fig. 8a). The coefficients of variation in the x values and in the y values ranged between c. 40% and 110%.

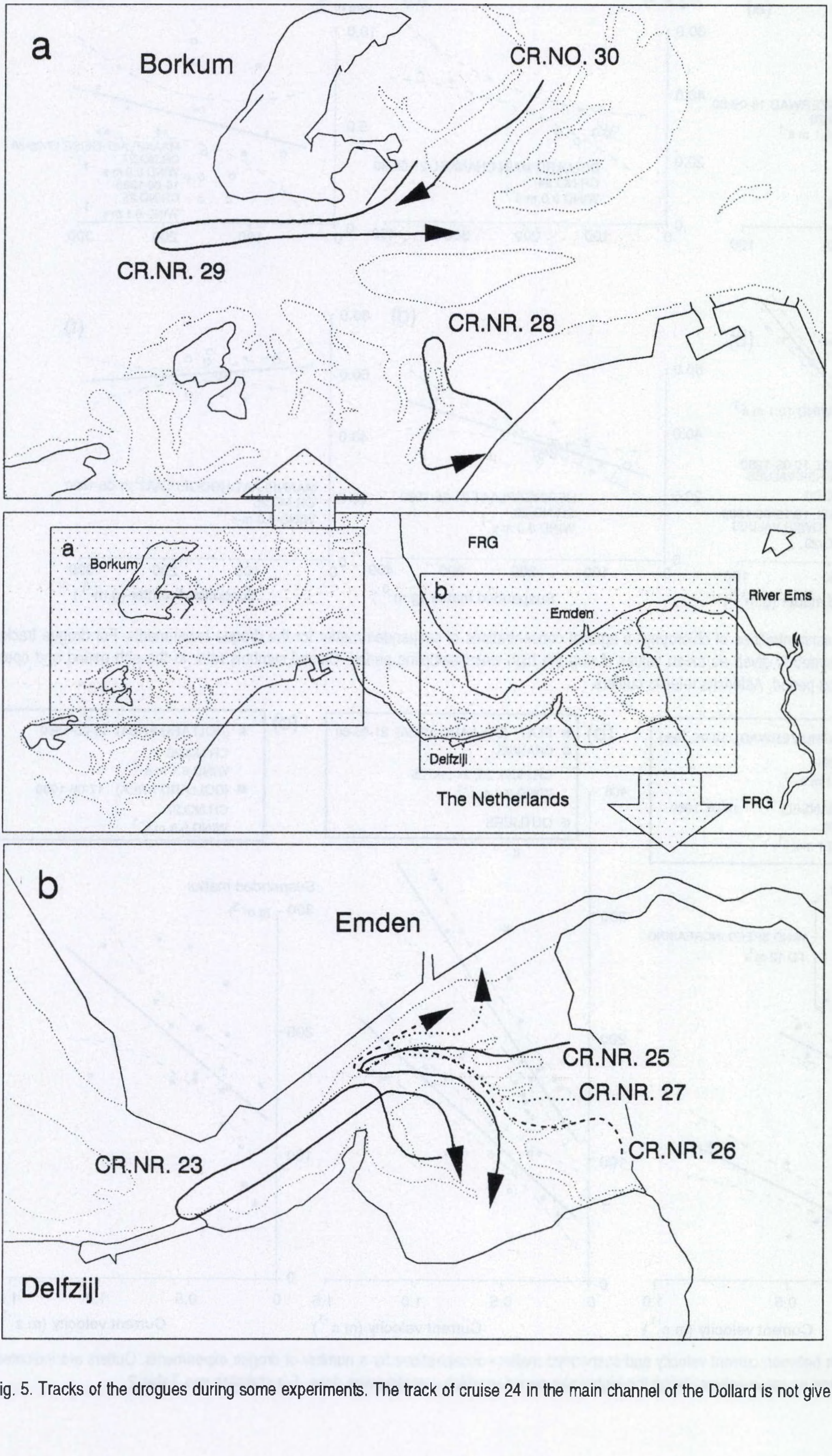

Fig. 5. Tracks of the drogues during some experiments. The track of cruise 24 in the main channel of the Dollard is not given.

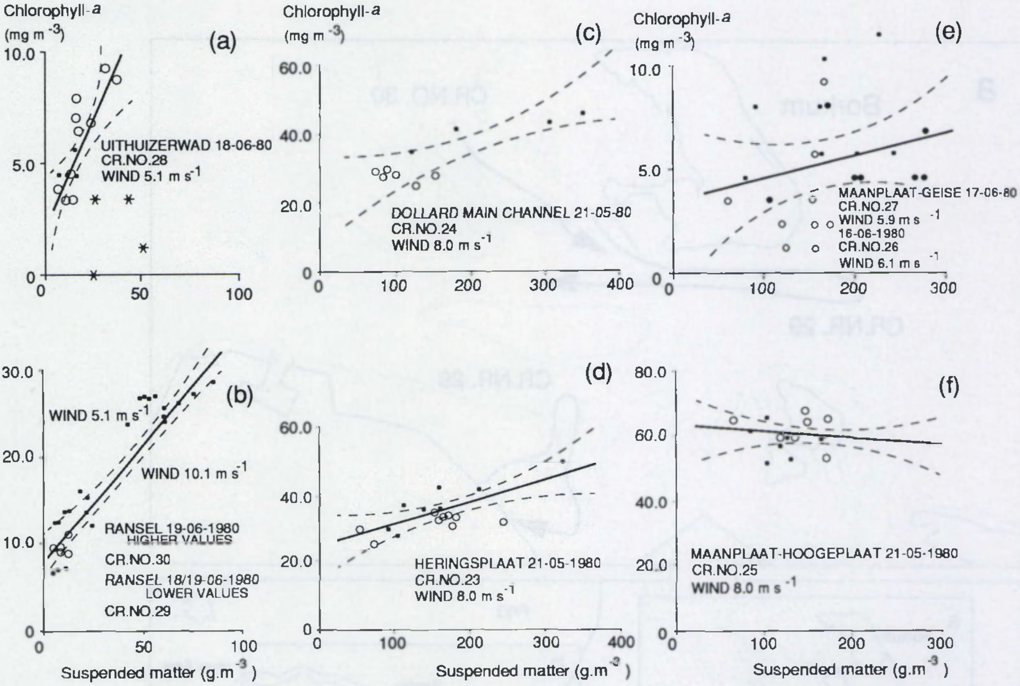

Fig. 6a-f. Plots of concentrations of chlorophyll-*a* against concentrations of suspended matter for the drogue experiments. For drogue tracks see Fig. 5. Wind speed is given as mean values during the high water sampling period. Closed symbols refer to the ebb period and open symbols to the flood period. Asterisks refer to outliers.

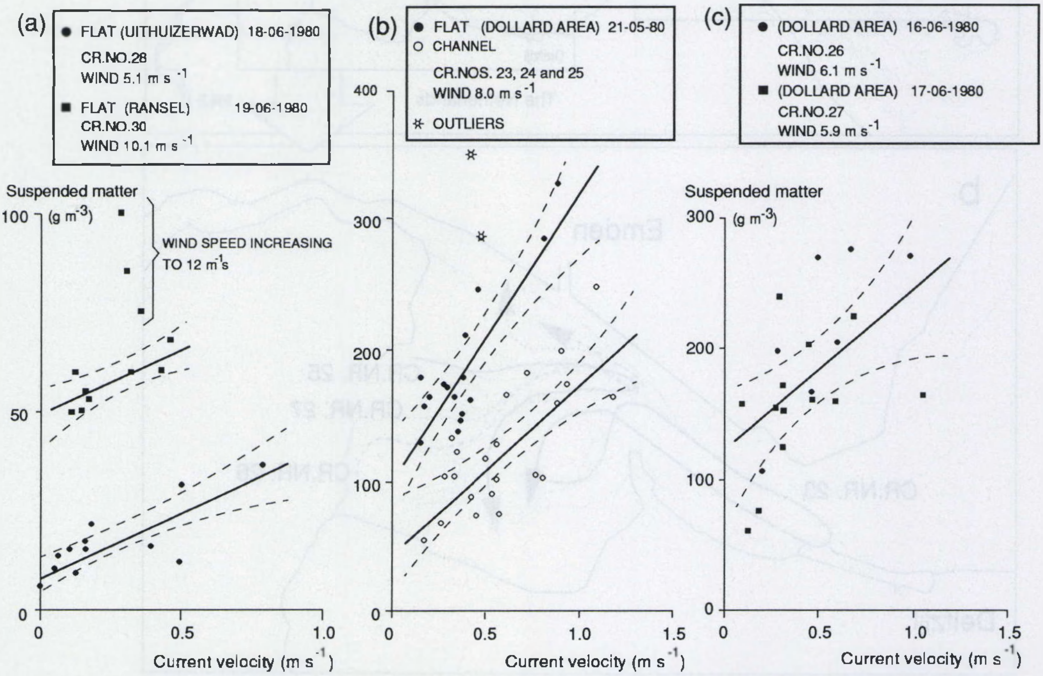

Fig. 7a-c. Relation between current velocity and suspended matter concentrations for a number of drogue experiments. Outiers are indicated. Wind speed is given as mean values during the high water period in which sampling was done. For statistics see Table 2.

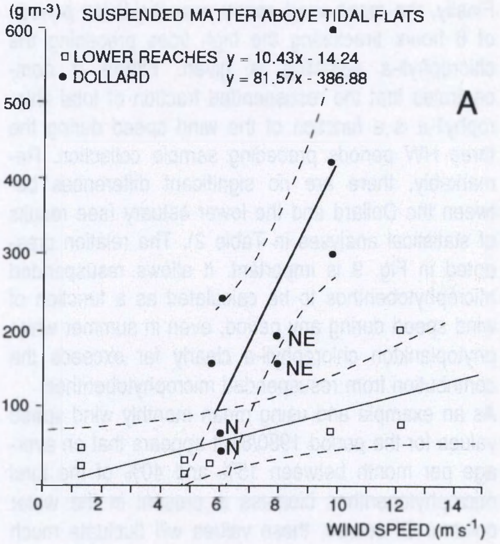

Fig. 8a. Relation between mean suspended matter concentrations in the water above the tidal flats during high tide and the mean wind speed during the same high water period in two parts of the Ems estuary.Wind was south-west unless indicated otherwise. The 95% confidence limits are indicated. For further statistics see Table 2. Values are derived from surveys 14 to 30.

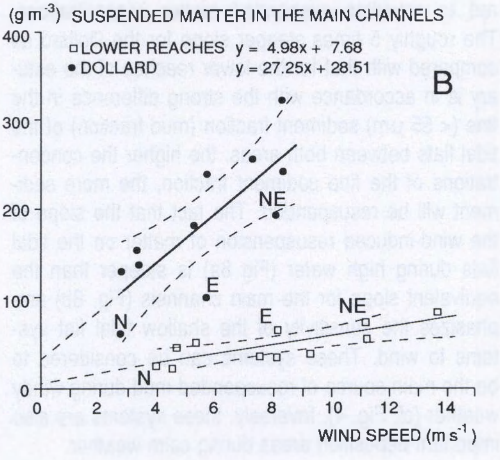

Fig. 8b. Relation between mean concentrations of suspended matter in the water of the channels and the 'effective wind speed' (mean wind speed during three high water periods preceding sample collection) in two parts of the Ems estuary. The 95% confidence limits are given. For further statistics see Table 2. Values derived from surveys 1 to 11 and 20.

The correlation coefficients are 0.724 for the lower reaches and 0.804 for the Dollard and are statistically significant (Table 2).

According to the plots in Fig. 8a resuspension already occurs at very low wind speeds in the lower reaches and at wind speeds above 5 m s^{-1} in the Dollard area. The curve slope for the Dollard is much steeper than that for the lower reaches. However, it appears that winds from the north and north-east (see indications in Fig. 8a) stimulate resuspension less than the wind coming from the opposite directions (south to south-west). The regression functions in Fig. 8a also indicates that resuspension in the lower reaches of the estuary occurs at lower wind speeds than in the Dollard. The remarkable difference in the onset of resuspension between the Dollard and the lower reaches does not agree with the graphs of Fig. 8b (see below) and may be the result of wind direction and fetch.

The drogue experiments (Fig. 5) also indicate that the water running above the tidal flats during high tide is not thoroughly mixed with the channel water during a single tide. Thus, resuspension from tidal flats will not directly result in increased suspended matter concentrations in the central part of the channels (cf. Fig. 4).

Main channels - To investigate the time lag between the resuspension from tidal flats and the response of the suspended matter concentration along the axis of the main channels, regression analysis was performed on data from the longitudinal surveys.

In Fig. 8b the concentration of mean suspended matter in the channels per survey per area (lower reaches and Dollard) is plotted against the mean wind speed that occurred during the 3 high tide periods preceding sample collection of suspended matter.

This was done because this relation resulted in the highest correlation coefficient between suspended matter along the axis of the main channels and wind speed. The standard deviations in the mean suspended matter concentrations and the wind speeds were low with coefficients of variation ranging from 38 to 42 %. This relationship indicates that about 3 tidal cycles are needed to transport fine suspended matter (mud) from the tidal flats to the axis of the main channels, and vice versa. Surprisingly, the available data indicate wind direction is less important than wind speed.

Microphytobenthos

The relation between wind speed and the fraction of resuspended chlorophyll-*a* derived from microphytobenthos was investigated for the same subareas used when studying the suspended matter. The resuspended amount was defined as the fraction of the chlorophyll-*a* mass present in the water of the sectors under consideration and the sum of the total mass present in the water and the top 0.5 cm of the sediments of the tidal flats situated above mean low water level. Because of the few data, the biomass values of station HW in sector 5 were also used when calculating the resuspension of microphytobenthos in sectors I to IV. Table 3 gives the mean concentrations as well as the total masses per area. Moreover, the fraction of the chlorophyll-*a* in the water (% resuspended microphytobenthos) is given.

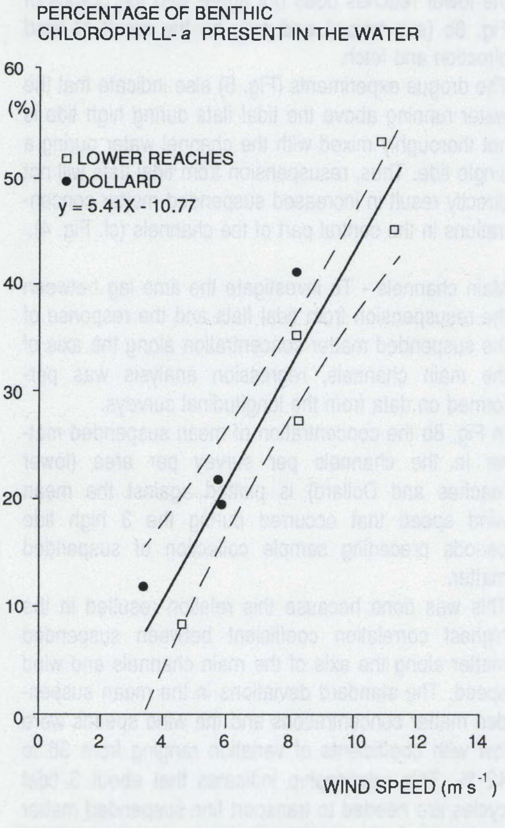

Fig. 9. Relation between the fraction of resuspended chlorophyll-*a* (mainly benthic diatoms) and the 'effective wind speed' for the lower reaches and the Dollard area. The resuspended chlorophyll-*a* fraction is $\frac{B_w}{(B_w + B_b)} \times 100$,

where B_w = chlorophyll-*a* mass in the water of a certain sector divided by B_b = chlorophyll-*a* mass present in the top 0.5 cm of the tidal flats in the same sector. See for basic data Table 3 and for statistics Table 2.

Finally, the mean wind speed over the three periods of 6 hours bracketing the high tides preceding the chlorophyll-*a* sampling is given. Figure 9 demonstrates that the resuspended fraction of total chlorophyll-*a* is a function of the wind speed during the three HW periods preceding sample collection. Remarkably, there are no significant differences between the Dollard and the lower estuary (see results of statistical analyses in Table 2). The relation presented in Fig. 9 is important. It allows resuspended microphytobenthos to be calculated as a function of wind speed during any period, even in summer when phytoplankton chlorophyll-*a* clearly far exceeds the contribution from resuspended microphytobenthos.

As an example and using mean monthly wind speed values for the period 1980/81 it appears that on average per month between 15% and 40% of the total microphytobenthos biomass is present in the water column. Of course, these values will fluctuate much more if tidally or daily wind speeds are used to calculate the resuspended fractions.

DISCUSSION

Relations between wind speed and resuspension

The relations in figures 8 and 9 represent the most simple models to calculate resuspension in the Ems estuary. Only data on the local wind speed are required to calculate suspended matter concentrations. The roughly 5 times steeper slope for the Dollard as compared with that for the lower reaches of the estuary is in accordance with the strong difference in the fine (< 55 μm) sediment fraction (mud fraction) of the tidal flats between both areas: the higher the concentrations of the fine sediment fraction, the more sediment will be resuspended. The fact that the slope of the wind-induced resuspension of matter on the tidal flats during high water (Fig 8a) is steeper than the equivalent slope for the main channels (Fig. 8b) emphasizes the sensitivity of the shallow tidal flat systems to wind. These systems can be considered to be the main source of resuspended mud during windy weather (cf. Fig. 4). Inversely, these systems are also important deposition areas during calm weather.

The nature of the relation between wind speed and suspended matter is unclear for wind speeds below 3 m s^{-1} and above 13 m s^{-1} (see Fig. 8a and b). As Kullenberg (1971, 1972, 1976), Therriault *et al.* (1978), Demers *et al.* (1987), and Levasseur *et al.* (1983) suggest, there may be a threshold value of wind speed somewhere between 0 and 3 m s^{-1}., below which sediment is not resuspended. However, the

Table 3. Mean chlorophyll-*a* concentrations measured in the top 0.5 cm of tidal flats (mg m^{-2}) and in water (mg m^{-3}). The area of the tidal flats in the lower reaches (sectors II, III, IV and tidal flat stations R, EH and HW) is 121 x 10^6 m^2 and in the Dollard (sectors VII, VIII, X, XI and tidal flat stations T, HP and P) it is 78 x 10^6 m^2. The volume of the lower reaches at mean sea level (midtide) is 1030 x 10^6 m^3 and in the Dollard it is 168 x 10^6 m^3. From these surface and volume values the total chlorophyll-*a* mass (x 10^9 mg) was calculated for the tidal flats and the water. Moreover, the percentage of chlorophyll-a in the water as compared with the sum of the chlorophyll-a present on the tidal flats and in the water, and the effective wind speeds (m s^{-1}) are given.

Date of sampling	Mean chlorophyll-*a* (mg m^{-2})	(mg m^{-3})	Chlorophyll-*a* mass (x 10^9 mg)	Chlorophyll-*a* in water (%)	Effective wind speed (m s^{-1})
LOWER REACHES					
8 Feb 1980 flats	31.8		3.8		
4 Feb 1980 water		1.4	1.4	27	8.2
18 Mar 1980 flats	18.2		2.2		
19 Mar 1980 water		2.4	2.5	53	10.9
3 Dec 1980 flats	12.7		1.5		
2 Dec 1980 water		0.8	0.8	35	8.2
16 Mar 1981 flats	57.8		7.0		
16 Mar 1981 water		0.6	0.6	8	4.6
24 Mar 1981 flats	23.9		2.9		
23 Mar 1981 water		2.3	2.4	45	11.2
DOLLARD					
8 Feb 1980 flats	35.4		2.8		
4 Feb 1980 water		4.1	0.7	20	5.8
18 Mar 1980 flats	44.4		3.5		
19 Mar 1980 water		14.0	2.4	41	8.2
3 Dec 1980 flats	42.0		3.3		
2 Dec 1980 water		5.2	0.9	21	5.8
16 Mar 1981 flats	66.5		5.2		
16 Mar 1981 water		4.0	0.7	12	3.4
24 Mar 1981 flats	-				
23 Mar 1981 water		5.0	0.8	?	8.4

values referred to in those studies were obtained from shallow subtidal systems and not from tidal flat systems. For tidal areas it is not easy to relate resuspension to wind-induced waves because of the changing water depth during the tidal cycle (Carper & Bachmann, 1984).

Kamps (1962) measured the relation between mean wind speed and the clay content in the water column near high tidal flats just in front of land reclamation works. From his data it could be inferred that the lowest clay content occurs at a mean wind speed of 1 m s^{-1} or less. Our data indicate that the wind threshold value in the Ems estuary is below 3 m s^{-1} (Fig. 8a). From the relation between wind speed and resuspension of microphytobenthos, given in Fig. 9, this threshold value can be estimated to be a wind speed of 1 to 2 m s^{-1}. These observations correspond very well with the findings of the authors cited above.

Linear extrapolation of the regressions in Figs. 8b and 9 for wind speeds above 13 m s^{-1} is statistically inadmissable. Above this value the regression line might be expected to deflect towards a "saturation" level at high wind velocities because all "mobile" sediment is suspended. But in the Elbe estuary, under westerly winds blowing from the sea, Dücker (1982) found a sharp increase in suspended matter for a wind speed between 12.3 and 20 m s^{-1} instead of a deflection. This might be because he made no distinction between different sediment size fractions. It is therefore possible that only the fine sediment fractions (mud) achieve a saturation level at high wind speeds whereas the sand concentrations (which in the Ems estuary were not included in the measurements) continue to rise steeply.

The relationship between suspended matter concentrations in the main channels and the average wind speed over the three high water periods preceding sample collection (Fig. 8b) indicates that wind is the major cause of the resuspension process. Tidal currents are of minor importance in this respect (see Fig. 7; cf. also Demers *et al.*, 1987). In terms of resuspension the Ems estuary seems to be behave like a simple system consisting of a sediment compartment and a water body making contact twice a day. During high wind speed, strong wave action and thus high orbital (wave-induced) current velocity and consequently much turbulence, a relatively large part of the mud fraction in the superficial sediment layer is resuspended. The resuspended material from the tidal flats is transported to the main channels by the ebb tidal currents. In the channels, the longitudinal transport of material is caused by residual currents and river discharge (de Jonge, 1991). There, residual currents are generated by topographical structures in the channels and on the tidal flats, and by drift currents and lateral differences in density (Dronkers & Zimmerman, 1982). This implies that the initial redistribution of resuspended sediments may depend on the location of the tidal flats within the current field while further transport is achieved by estuarine mechanisms of accumulation (Postma 1954; Groen, 1967; Postma, 1967; Dronkers; 1986). The magnitude of this upstream transport largely depends on tidal characteristics (such as differences in current velocities between flood and ebb), water depth, and the size and specific mass of the particles under consideration. As indicated under the Results, the best fit between suspended matter concentrations in the main channels and wind speed (Fig. 8b and 9) implicitly also gives a rough estimate of the local time scale for lateral mixing. From the drogue tracks (Fig. 5) it can be inferred that this mixing must last longer than one tidal period. These tracks show that a water mass close to the mainland or tidal watershed rarely reaches the main channel at low tide, whereas water close to the main channel even reaches the middle part of some channels. Thus, it seems that the time scale of the lateral mixing of the water masses, which is difficult to determine in the field, is somewhere in the order of 3 ± 1 tidal cycles for both the Dollard area and the lower reaches of the Ems estuary. It is remarkable that this lateral mixing time seems to be approximately the same for Dollard and the lower estuary, although these areas differ hydrographically.

Resuspendable amount

Although suspended matter was not sampled within 1 or 2 cm from the sediment bed of the tidal flat, our observations presented in Figs 8a and b are consistent with the Yalin bedload equation (cf. Drake & Cacchione, 1989) in which the "near bed" reference concentration is a function of certain parameters that include the volume concentration of resuspendible material in the bed. This consistency implies that the Yalin bedload equation can be applied to calculate how resuspension in the Ems estuary depends on wind speed, using shear stress related to wind and waves. The same may hold for the resuspension of microphytobenthos.

Because the wind speed in the lower reaches is, on average, higher than in the Dollard, and the resuspension for both areas follows the same function, the resuspension of microphytobenthos is relatively more important in the lower reaches than in the Dollard area.

Microphytobenthos and sediment stability

The observed positive effect of microphytobenthos biomass on sediment stability has been observed under laboratory conditions and also in the field (Rhoads *et al.*, 1978; Delgado *et al.*, 1991; Vos *et al.* 1988). Seasonal changes in sediment stabilization can be attributed to this phenomenon (Yingst & Rhoads, 1978; Grant *et al.*, 1982 and Frostick & McCave, 1979). Other studies suggest that mucus exuded by benthic algae can inhibit sediment transport because it stabilizes the sediment bed (Neumann *et al.*, 1970; Holland *et al.*, 1974; Coles, 1979; de Boer, 1981; Grant *et al.*, 1986; Paterson, 1989). However, our present study shows that under

field conditions and for large areas there is no clear indication that a greater microphytobenthos biomass on the tidal flats results in the sediment bed being significantly more stable (Table 3 and Fig. 9).
We also showed that the response of suspended matter to wind speed changes was very rapid, meaning that sediment, microphytobenthos included, is very rapidly exchanged between the tidal flats and the overlying water.

CONCLUSIONS

1. We conclude that the concentrations of suspended matter in the Ems estuary are heavily and predominantly influenced by wind-induced waves. The current velocity also contributes to the processes of deposition and resuspension, but to a lesser extent.
2. In the Ems estuary resuspension of fine sediment size fractions (mud) can be described as a function of the "effective wind speed" which is defined as the wind speed averaged over 3 high water periods preceding sampling. The same relation holds for the resuspended microphytobenthos fraction from the top 0.5 cm layer of sediment.
3. The time scale of lateral mixing of fine suspended material in the upper reaches and lower reaches of the estuary was estimated to be 3 ± 1 tidal cycles.

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5. APPLICATION OF KNOWLEDGE AND DISCUSSION

WIND DRIVEN TIDAL AND ANNUAL GROSS TRANSPORT OF MUD AND MICROPHYTOBENTHOS IN THE EMS ESTUARY, AND ITS IMPORTANCE FOR THE ECOSYSTEM

V.N. de Jonge

ABSTRACT

Wind driven fluxes of different particulate materials were quantified for two main regions in the Ems estuary on the border between the Netherlands and the Federal Republic of Germany (north-western Europe). The annual flux of mud (fraction < 50 µm) between the tidal flats and the water is c. 12 x 10^6 tonnes in the lower reaches (274 x 10^6 m^2) and c. 7.5 x 10^6 tonnes in the Dollard (102 x 10^6 m^2). The longitudinal annual gross flux of mud was calculated to be c. 32 x 10^6 tonnes in the tidal inlet of the estuary but the net flux is calculated to be no more than 1.4 x 10^6 tonnes.

The annual flux of microphytobenthos carbon between the top layer of the sediment and the water is c. 20 x 10^3 tonnes in the lower reaches and c. 10 x 10^3 tonnes in the Dollard. The fluxes between the top 0.5 cm of the sediment and the 0.5 to 2.0 cm layer are c. 12.5 x 10^3 tonnes organic carbon in the lower reaches and c. 5 x 10^3 tonnes organic carbon in the Dollard.

Calculations indicate that 30% of the primary production in the water column of the lower reaches is caused by suspended microphytobenthos; in the Dollard this proportion is much greater (c. 90%). In the total estuary 53% of the primary production is caused by real phytoplankton, 22% by microphytobenthos living on the tidal flats and c. 25% by suspended microphytobenthos.

INTRODUCTION

To date studies on microphytobenthos in shallow coastal areas have been mainly restricted to the role (presence, production and behaviour) of these organisms in the benthic system (for references see de Jonge & Colijn, in prep.; Colijn & de Jonge, 1984). Benthic diatoms are the main constituents of this microphytobenthos. They live in the boundary layer between the sediment and the water and are therefore susceptible to resuspension. The possible role of these resuspended populations for the pelagic system was discussed earlier by Baillie & Welsh (1980), Admiraal (1984), de Jonge (1985) and de Jonge & van den Bergs (1987). Recently, de Jonge & van Beusekom (this thesis) succeeded in relating diatom resuspension to wind speed. That study was a step forward in clarifying the role of benthic diatom populations in the functioning of estuarine systems. When used with data on the biomass distribution of benthic diatoms on the tidal flats, the relationship discovered enables the diatom carbon fluxes resulting from wind driven resuspension to be quantified. In addition, the biomass fluxes of the diatoms between different layers of sediment can be estimated on the basis of the depth distribution of the benthic diatoms (de Jonge & Colijn, this thesis).

A second factor of ecological importance is the wind induced resuspension of mud (fraction < ca. 55 µm) from the tidal flats. This process occurs simultaneously with the diatom resuspension (de Jonge & van Beusekom, in prep.) and can also be described as a function of wind speed. It can be argued that this is the process mainly responsible for the short-term fluctuations in light conditions in the Ems estuary. Consequently, this phenomenon will play an important role in the primary production of the phytoplankton.

This paper presents data for the Ems estuary (Fig. 1) on tidal fluxes of microphytobenthos. The fluxes are presented as chlorophyll-*a* and organic carbon. Two fluxes were measured: between the uppermost 0.5 cm sediment on the tidal flats and the water column, and between that layer and the underlying 0.5 - 2.0 cm layer of sediment. The contribution of suspended microphytobenthos to the phytoplankton primary production and the phytoplankton biomass will be estimated. Moreover, tidal fluxes of mud and associated detritus between the tidal flats and the water column (lateral fluxes) will be given and compared with the estimated longitudinal gross fluxes and net fluxes upstream from the coastal area.

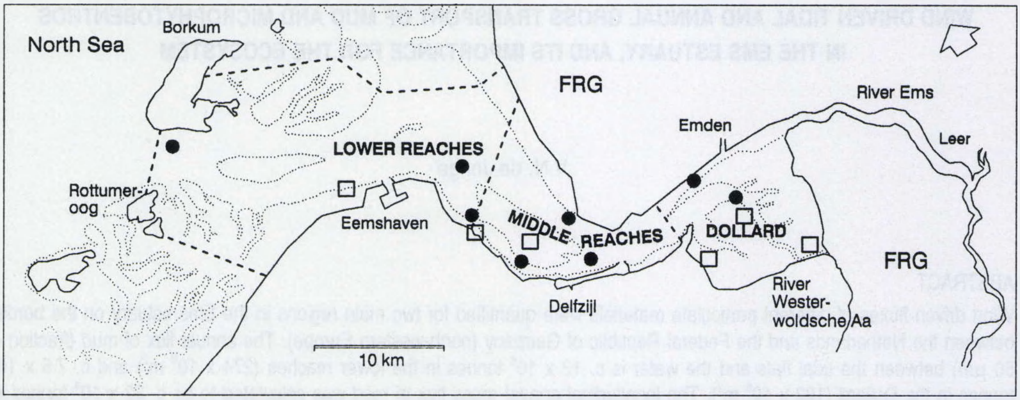

Fig. 1. Map of the Ems estuary, with 3 subareas: lower reaches, middle reaches and Dollard. Dots are sampling stations for chlorophyll-*a* in the main channels. Squares represent stations on the tidal flats used for measurements of biomass and primary production of microphytobenthos.

MATERIALS AND METHODS

Study area

The study was carried out in the estuary of the River Ems, situated on the border between the Netherlands and the Federal Republic of Germany (N.W. Europe) (Fig. 1).

The estuary is c. 100 km long. The average discharge of the River Ems is c. 115 $m^3 s^{-1}$. The tidal prism in the inlet between the barrier islands of Rottumeroog and Borkum is approx. 10^9 m^3. The mean tidal range increases from 2.3 m near the barrier islands to 3.2 m at Emden (de Jonge, 1983).

A complicated geomorphology and strong tidal currents result in a complex pattern of water currents and a steep salinity gradient (de Jonge, 1991). There is a suspended matter gradient from approx. 20 g m^{-3} near the tidal inlet to approx. 400 g m^{-3} in the most turbid part of the estuary (de Jonge, 1988). In the Dollard (Fig. 1) the mean suspended matter concentration is roughly 200 g m^{-3}.

Some morphological parameters of the three areas distinguished are given in Table 1.

Phytoplankton

It was originally intended to present calculations for one specific year: 1977. However, samples for measuring primary production were taken during part of 1977 only. Therefore the values for phytoplankton primary production and phytoplankton chlorophyll-*a* over the period 1975 - 1980 were used for the calculations.

During 1975 and 1976 chlorophyll-*a* was measured routinely every month at approximately 30 stations (Figs. 1, 2 and 3). From 1976 to 1980 chlorophyll-*a* was measured at a number of stations selected for primary production (Colijn, 1983). Water samples of 1 litre were taken with a sampler developed by Postma (1954). Aliquots were filtered over Whatman GF/C glass fibre filters, quickly washed with 10 ml of distilled water, wrapped in aluminium foil and immediately stored at -20 °C. In the laboratory the samples were lyophilized. Chlorophyll-*a* was measured spectrophotometrically at 664 nm using the method of Lorenzen (1967), modified according to Moed and Hallegraeff (1978).

Microphytobenthos

The data on the spatial and temporal distribution of microphytobenthos on the tidal flats in the Ems estuary in terms of chlorophyll-*a* and organic carbon come from de Jonge & Colijn (this thesis). In 1977 these authors sampled once every two weeks at 3 locations in the estuary, two of which were in the lower reaches and one in the Dollard (Fig. 1). Every two months two additional stations in the Dollard were sampled.

Chlorophyll-a was determined by collecting 20 sediment cores (inner diameter of 2.4 cm each). The cores were sliced. The samples from the top 0.5 cm were pooled, mixed thoroughly and subsampled. The samples from the 0.5-2.0 cm layer were treated similarly. For more details, see de Jonge (1979) and de Jonge & Colijn (this thesis).

Effective wind speed

Data from the Royal Dutch Meteorological Institute (KNMI) met. station at Eelde (c. 40 km southwest of Delfzijl) were used to calculate the "effective wind

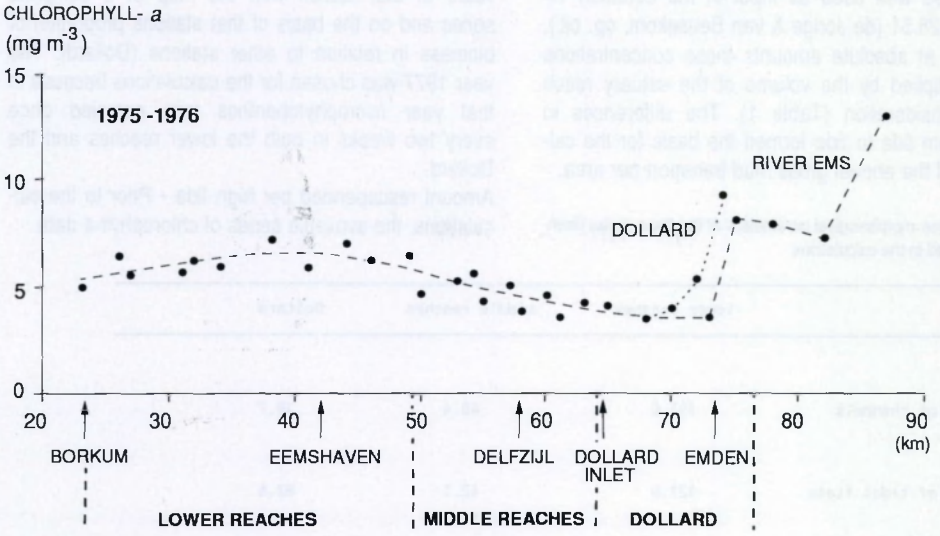

Fig. 2. Longitudinal gradient of chlorophyll-*a* concentrations in the water of the Ems estuary for the years 1975-1976.

speed" for each high water (HW) period in 1977. The "effective wind speed" (de Jonge & van Beusekom, this thesis) is defined as the wind speed at which resuspension is induced; it is the average wind speed over three high water periods preceding the sampling of suspended matter or microphytobenthos [in this case the high water period for which resuspended mud (fraction < 55 µm) or resuspended microphytobenthos is calculated]. A high water period is defined here as the period running from 3 hours before to 3 hours after the astronomical time of high water. The values from the met. station at Eelde were converted to obtain the wind speed in the lower reaches and the Dollard. These values are 1.18 for the lower reaches and 0.82 for the Dollard. The conversion factors used are means and based on long-term measurements (30-year) of the wind speed (Anonymous, 1974).

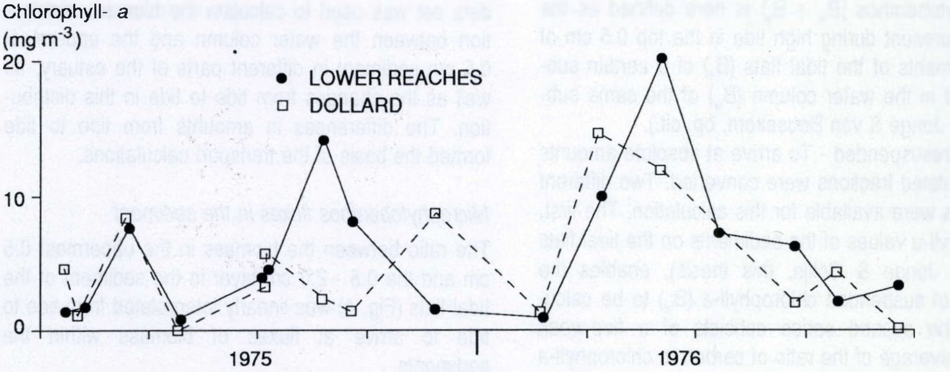

Fig. 3. Seasonal variation in phytoplankton chlorophyll-a in the lower reaches of the Ems estuary and the Dollard. Values are means per subarea for the period 1975-1976.

Resuspended mud

The effective wind speed (m s^{-1}) was used as input in the equation Y= 4.98X + 7.68 (de Jonge & van Beusekom, in prep.) to calculate the mud (g m^{-3}) resuspended in the lower reaches at high tide.

To obtain these values in the Dollard the effective wind speed was used as input in the equation Y= 27.25X + 28.51 (de Jonge & van Beusekom, op. cit.). To arrive at absolute amounts these concentrations were multiplied by the volume of the estuary reach under consideration (Table 1). The differences in values from tide to tide formed the basis for the calculation of the annual gross mud transport per area.

Table 1. Three morphological parameters of the three areas distinguished, used in the calculations.

Area	lower reaches	middle reaches	Dollard
Surface of channels x $10^6 m^2$	153.0	48.4	19.7
Surface of tidal flats x $10^6 m^2$	121.0	42.1	82.6
Water volume at mean high water level x $10^6 m^3$	1300	460	220

Resuspended microphytobenthos

Resuspended fraction - The effective wind speed ($m\ s^{-1}$) was used as input in the equation Y= 5.41X - 10.77 (de Jonge & van Beusekom, this thesis) to calculate the resuspended fraction of total microphytobenthos [$B_w/(B_w + B_s)$] during high tide. The total microphytobenthos ($B_w + B_s$) is here defined as the amount present during high tide in the top 0.5 cm of the sediments of the tidal flats (B_s) of a certain subarea and in the water column (B_w) of the same subarea (de Jonge & van Beusekom, op. cit.).

Amount resuspended - To arrive at absolute amounts the calculated fractions were converted. Two different data sets were available for this calculation. The first, chlorophyll-*a* values of the sediments on the tidal flats (see de Jonge & Colijn, this thesis), enables the amount of suspended chlorophyll-*a* (B_w) to be calculated. The second series consists of a five-week running average of the ratio of carbon to chlorophyll-*a* (de Jonge, 1980) and enables the chlorophyll-*a* values to be converted to organic carbon.

For this paper the biomass values (organic carbon and chlorophyll-*a*) given in de Jonge and Colijn (in prep.) were averaged per sampling date per subarea (e.g. lower reaches) or (when data series for different stations were of different lengths) by converting the value of that station with the help of a complete series and on the basis of that stations proportion of biomass in relation to other stations (Dollard). The year 1977 was chosen for the calculations because in that year microphytobenthos was sampled once every two weeks in both the lower reaches and the Dollard.

Amount resuspended per high tide - Prior to the calculations, the available series of chlorophyll-*a* data was converted to a series based on a tidal time step. This was done simply, by linear interpolation of the total chlorophyll-*a* amount per area ($B_s + B_w$). This data set is crucial. It forms the forcing curve for the calculations from tide to tide, based on data interpolation over periods of approximately fourteen days. This data set was used to calculate the biomass distribution between the water column and the uppermost 0.5 cm sediment in different parts of the estuary, as well as the changes from tide to tide in this distribution. The differences in amounts from tide to tide formed the basis of the transport calculations.

Microphytobenthos fluxes in the sediment

The ratio between the biomass in the uppermost 0.5 cm and the 0.5 - 2.0 cm layer in the sediment of the tidal flats (Fig. 4) was linearly interpolated from tide to tide to arrive at fluxes of biomass within the sediments.

The depth distribution of chlorophyll-a in the sediments of the tidal flats was found to be relatively stable (cf. de Jonge & Colijn, this thesis). Therefore, it was assumed that changes in the 0.5-2.0 cm layer were a function of the concentrations in the 0-0.5 cm layer. Thus, after calculating the distribution of the

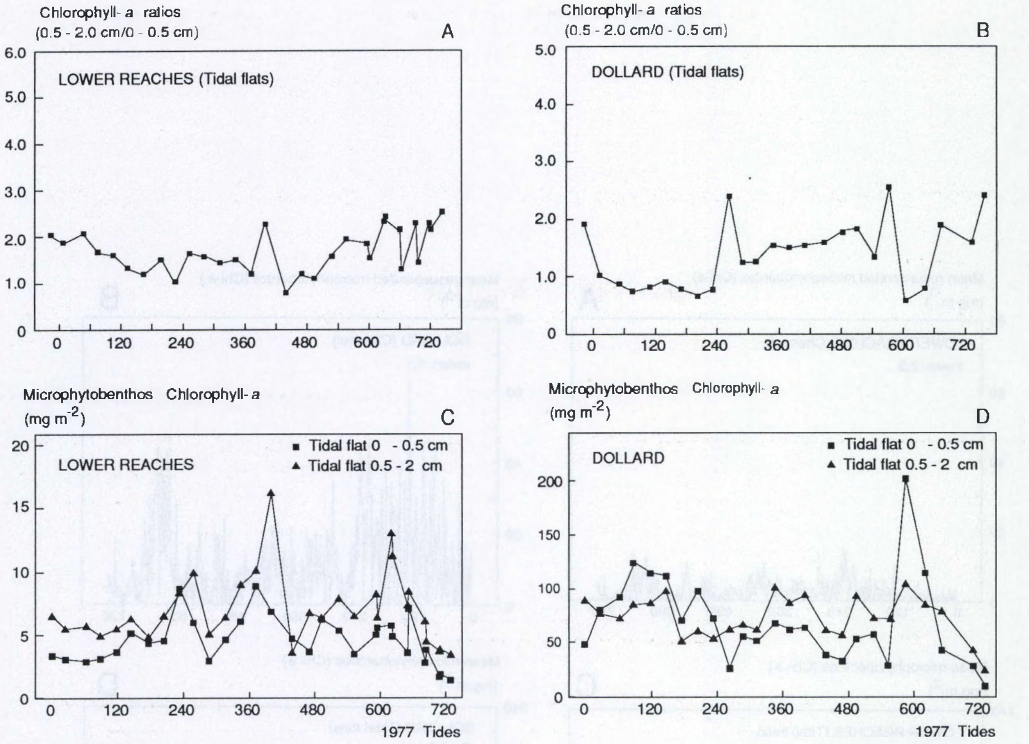

Fig. 4. A and B Ratio of chlorophyll-*a* content of the 0.5 - 2.0 cm layer to that of the uppermost 0.5 cm sediment in the lower reaches and the Dollard in 1977.

C and D Seasonal variation in chlorophyll-*a* masses in the two sediment layers in the lower reaches and the Dollard in 1977.

microphytobenthos chlorophyll-*a* between the water and the 0-0.5 cm layer, the amount in the 0.5-2.0 cm layer was simply to estimate from the ratio of chlorophyll-*a* between both layers. These data formed the basis for calculating the transport between both layers.

RESULTS

Basic data on chlorophyll-a in water and sediment

Phytoplankton - An example of the mean annual longitudinal distribution of chlorophyll-*a* concentrations in the Ems estuary is given in Fig. 2. The chlorophyll-*a* concentrations in the lower reaches are slightly higher than those in the tidal inlet and those in the middle reaches and the Dollard. The mean annual chlorophyll-*a* concentrations in the Dollard inlet are relatively low. Within the Dollard the values increase steeply upstream from the inlet. The concentrations in the River Ems also increase upstream. An example of the seasonal variation in chlorophyll-*a* concentrations in the lower reaches and the Dollard is also presented (Fig. 3). The curve for the lower reaches roughly represents the common seasonal variation in phytoplankton chlorophyll-*a*, with relatively low values in autumn and winter and relatively high values during the growing season. The curve for the Dollard (Fig. 3) is less clear, with peaks in between the seasons too.

Microphytobenthos - In Fig. 4 the two-weekly values of measured chlorophyll-*a* in the uppermost 0.5 cm of the tidal flats (B_s), in the 0.5 - 2.0 cm layer and the chlorophyll-*a* ratios between the 0.5-2.0 cm and the uppermost 0.5 cm sediment layers.

Calculated data on amounts of biomass and mud

The annual data on the effective wind speed, responsible for the suspension of microphytobenthos and mud, will be presented under 'suspended matter'. The calculated variation in the chlorophyll-*a* concentrations in the water column, the uppermost 0.5 cm of sediment and the 0.5-2.0 cm layer from one high water to the next (Fig. 5) illustrate strong variations in the distribution of the microphytobenthos chlorophyll-*a*.

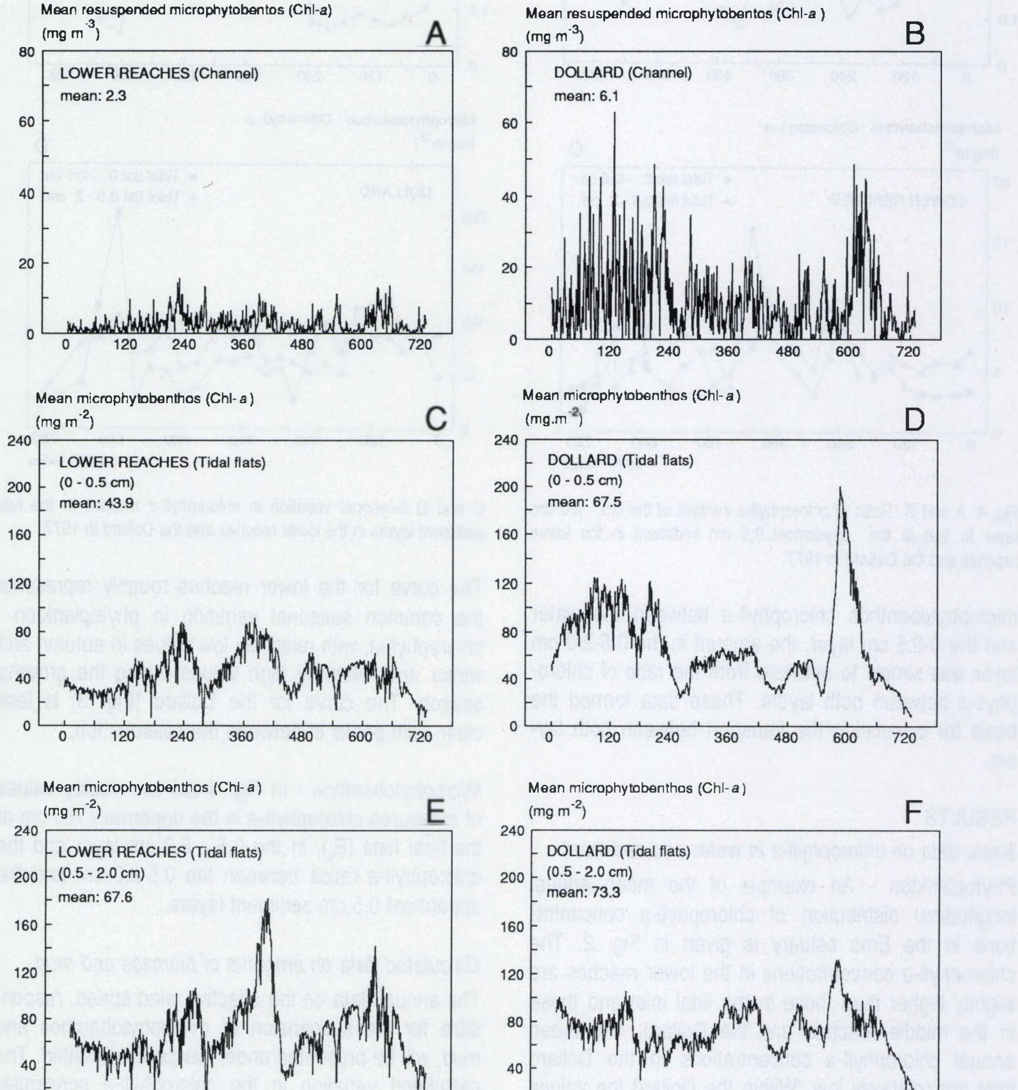

Fig. 5. Calculated changes of chlorophyll-*a* from tide to tide in the water column (A, B), the uppermost 0.5 cm layer of sediment (C, D), and the 0.5-2.0 cm layer of sediment (E, F) for lower reaches and Dollard in 1977. The mean annual values are also shown. For calculation procedure see text.

The main part of the total micro-phytobenthos chlorophyll-*a* is present in the 0.5-2.0 cm sediment layer.

In the lower reaches 8.18 tonnes or c. 50% of the chlorophyll-*a* mass is present in this layer; the figure for the Dollard is 6.05 tonnes chlorophyll-*a* or c. 47% (Table 2). The relative amount of microphytobenthos chlorophyll-*a* present in the water column in the lower reaches is almost twice that in the Dollard (2.95 tonnes or c. 18% compared with 1.35 tonnes or c. 10%). These values do not correspond to the differences in biomass in the top 0.5 cm of sediment in the two areas (Table 2). The calculated chlorophyll-*a* mass in the top 0.5 cm of the tidal flats is on average, 5.31 tonnes (c. 32 %) in the lower reaches and 5.57 tonnes (c. 43%) in the Dollard.

Table 2. Some data for 1977 resulting from the measurements[1] and calculations presented in this study.

	mean concentrations		mean masses (tonnes per area)	
	lower reaches	Dollard	lower reaches	Dollard
water column				
total Chl-a[1,2]	7.6 (mg m^{-3})	6.6		
phytoplankton Chl-a	5.3 (mg m^{-3})	0.5	6.89	0.11
microphytobenthos Chl-a	2.3 (mg m^{-3})	6.1	2.95	1.35
phytoplankton Carbon	-	-	-	-
microphytobenthos Carbon	87.6 (mg m^{-3})	233	113.8	51.3
suspended matter	46.9 (g m^{-3})	178.2	60970	39200
tidal flats (0-0.5 cm depth)				
microphytobenthos Chl-a[1]	43.9 (mg m^{-2})	67.5	5.31	5.57
microphytobenthos Carbon	1736 (mg m^{-2})	2577	210	212.9
tidal flats (0.5-2.0 cm depth)				
microphytobenthos Chl-a[1]	67.6 (mg m^{-2})	73.3	8.18	6.05
microphytobenthos Carbon	2578 (mg m^{-2})	2915	312	240.8
total				
microphytobenthos Chl-a			16.45	12.97
microphytobenthos Carbon			635	505

[1] **own measurements**

[2] calculated for the period 1975-1980 from data from Colijn (1983) for 1977-and own data for 1975 and 1976

The chlorophyll-*a* concentrations and consequently the algal carbon in the water can be distinguished into two categories. One is formed by real phytoplankton and the other by resuspended microphytobenthos. The distinction can be made by subtracting measured chlorophyll-a in the water column and the calculated chlorophyll-*a* from suspended microphytobenthos.

The data (Table 2) indicate that each year a substantial amount of the chlorophyll-*a* in the water is derived from suspended microphytobenthos. Assuming that the values of suspended microphytobenthos for 1977 hold for other years too, this contribution amounts to 30% for the lower reaches and 92% for the Dollard, when compared with the mean total chlorophyll-*a* in the water concentrations for the period 1975 - 1980 (Fig. 2 and Table 2). The amounts of suspended microphytobenthos carbon are not given here separately because these values are converted from chlorophyll-*a* data (see Materials and Methods).

Relevant data are given in Table 2.

Suspended matter - The values of the calculated effective wind speed used for estimating the mean suspended matter concentrations (Fig. 6) show considerable differences between the two areas.

The lower reaches are more exposed to the wind and therefore the values for this area (Fig. 6A) are higher than those in the Dollard (Fig. 6B). Surprisingly, the effective wind speeds do not show a pronounced seasonal pattern even though calm conditions prevail in the period June to August.

Not surprisingly the calculated concentrations of wind-induced suspended matter mirror the pattern of the plotted effective wind speed (Fig. 7). The mean suspended matter concentration in the lower reaches is almost a quarter that in the Dollard (46.9 g m^{-3} compared with 178.2 g m^{-3}; Table 2) because of the differences in slope of the equations applied. Elsewhere, these differences are attributed to the differences in sediment composition of these two areas (de Jonge & van Beusekom, this thesis).

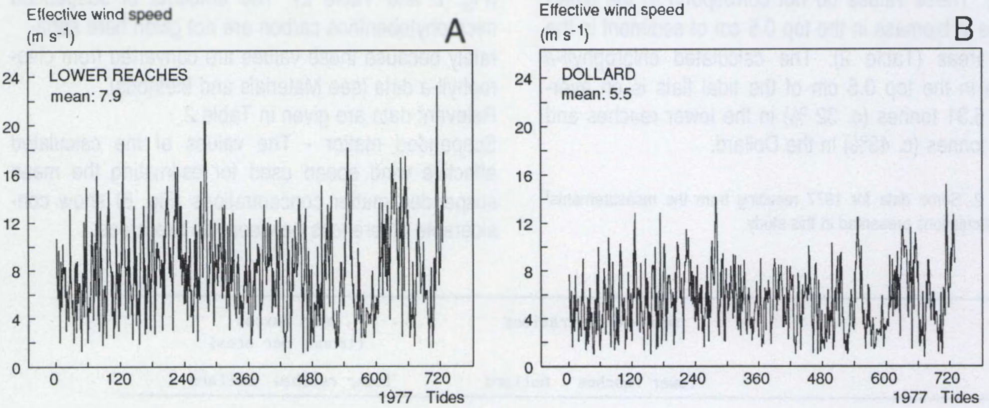

Fig. 6. Plot of the effective wind speeds in lower reaches (A) and Dollard (B) used for calculating the mean suspended matter concentrations per tidal period and the resuspended amount of microphytobenthos

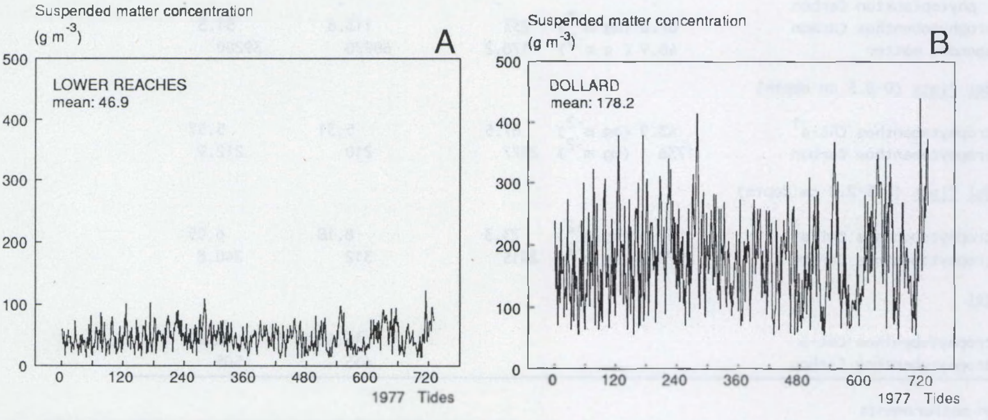

Fig. 7. Plot of the calculated concentrations of suspended matter in the lower reaches (A) and the Dollard (B). Values are averages per tide per area.

Fluxes of microphytobenthos biomass and mud

The fluxes of microphytobenthos and mud are calculated as the sum of the absolute differences in the material available in the water during the consecutive high water periods.

Microphytobenthos - The transport of microphytobenthos is expressed in terms of carbon because this enables easy comparison with carbon budgets.
In Fig. 8 the tidal fluxes between the uppermost 0.5 cm layer of the sediment and the water column (Fig. 8A and B) as well as between this uppermost layer and the 0.5-2.0 cm layer in the sediment (Fig. 8C and D) are shown for the lower reaches and the Dollard. According to the equations applied, during increasing wind speed there is a flux from the uppermost 0.5 cm layer of the sediment to the water column and into the 0.5-2.0 cm layer of the sediment (positive value). During decreasing wind speed there is a flux to the surface of the tidal flats (negative value). The total annual fluxes in microphytobenthos carbon are given in Fig. 8 as tonnes per area and represent gross values. The amounts are considerable.

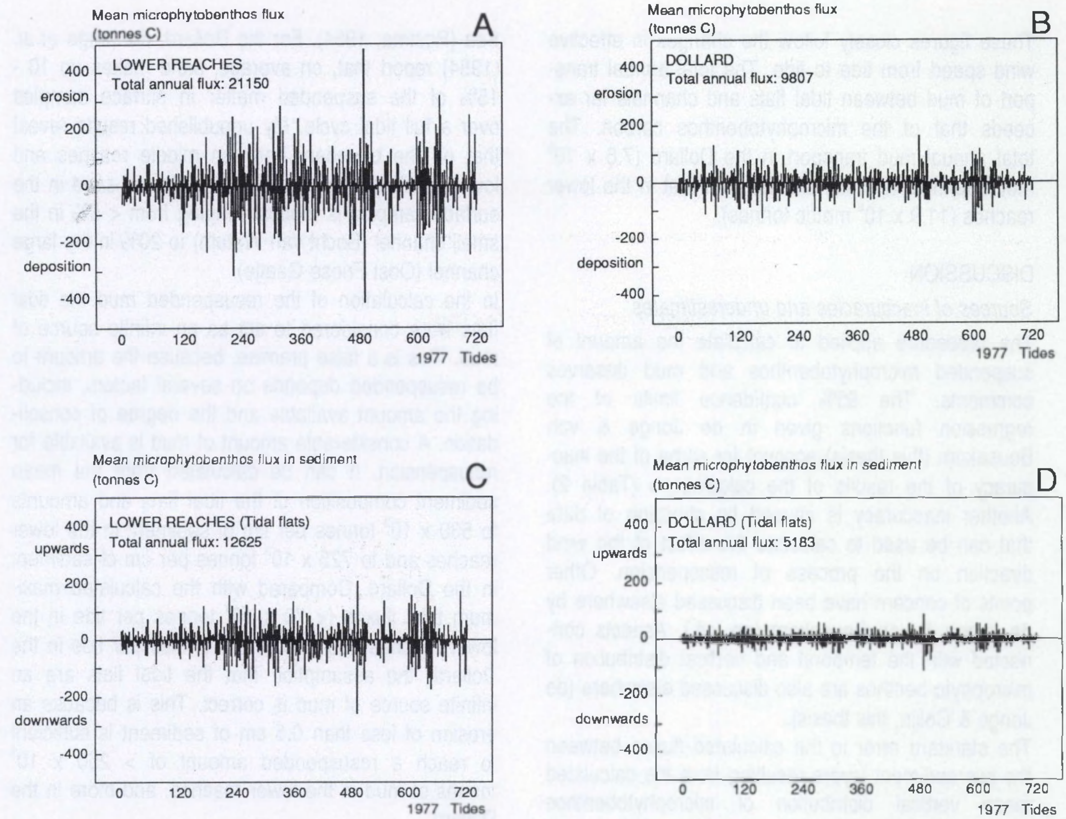

Fig. 8.Calculated wind-induced tidal transports of microphytobenthos carbon between the 0-0.5 cm sediment layer and the water for the lower reaches (A) and the Dollard (B) and the calculated wind induced tidal flux between the 0-0.5 cm and the 0.5-2.0 cm sediment layer for the lower reaches (C) and the Dollard (D).

Over 21 000 metric tonnes of carbon are transported from sediment to water in the lower reaches and almost 10 000 metric tonnes are transported in the Dollard. The annual transports (upwards + downwards) between the two sediment layers are much smaller: over 12 500 metric tonnes of carbon in the lower reaches and nearly 5000 tonnes in the Dollard.

Mud - Fig. 9 shows the lateral tidal transports for the lower reaches and the Dollard.

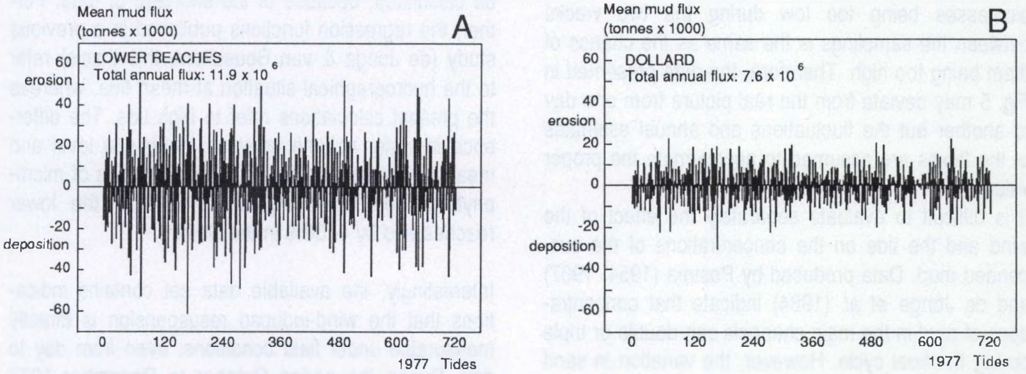

Fig. 9. Calculated wind induced tidal fluxes of mud between the tidal flats and the water column for the lower reaches (A) and the Dollard (B). Values are given as tonnes per area per tide.

These figures closely follow the changes in effective wind speed from tide to tide. The total annual transport of mud between tidal flats and channels far exceeds that of the microphytobenthos carbon. The total annual mud transport in the Dollard (7.6 x 10^6 metric tonnes) is much smaller than that in the lower reaches (11.9 x 10^6 metric tonnes).

DISCUSSION

Sources of inaccuracies and underestimates

The procedure applied to calculate the amount of suspended microphytobenthos and mud deserves comments. The 95% confidence limits of the regression functions given in de Jonge & van Beusekom (this thesis) account for some of the inaccuracy of the results of the calculations (Table 2). Another inaccuracy is caused by shortage of data that can be used to calculate the effect of the wind direction on the process of resuspension. Other points of concern have been discussed elsewhere by de Jonge & van Beusekom (op. cit.). Aspects connected with the temporal and vertical distribution of microphyto-benthos are also discussed elsewhere (de Jonge & Colijn, this thesis).

The standard error in the calculated fluxes between the two sediment layers resulting from the calculated mean vertical distribution of microphytobenthos biomass is 4% for the lower reaches and 5% for the Dollard; these values do not significantly influence the accuracy of the results.

The linear interpolation of the data on the biomass of the microphytobenthos on the tidal flats in the various reaches may have resulted in inaccuracies. However, systematic errors are unlikely because the chance of biomasses being too low during the two weeks between the samplings is the same as the chance of them being too high. Therefore, the data presented in Fig. 5 may deviate from the real picture from one day to another but the fluctuations and annual estimates of the fluxes are assumed to approximate the proper value.

It is difficult to evaluate separately the effect of the wind and the tide on the concentrations of the suspended mud. Data produced by Postma (1954, 1967) and de Jonge *et al.* (1984) indicate that concentrations of mud in the main channels can double or triple during the tidal cycle. However, the variation in sand concentrations is usually much greater. The presence of this sand in the water column may be a source of inaccuracies in the calculations. However, sand generally makes up only a small part of the total suspended matter near the water surface in the Wadden Sea (Postma, 1954). For the Dollard, de Jonge *et al.* (1984) report that, on average, sand makes up 10 - 15% of the suspended matter in surface samples over a full tidal cycle. My unpublished results reveal that on the boundary between middle reaches and lower reaches (Fig. 1) the contribution of sand in the surface samples is modest ranging from < 5% in the small channel (Bocht van Watum) to 20% in the large channel (Oost Friese Gaatje).

In the calculation of the resuspended mud the tidal flats were considered to act as an infinite source of mud. This is a false premise, because the amount to be resuspended depends on several factors, including the amount available and the degree of consolidation. A considerable amount of mud is available for resuspension. It can be calculated from the mean sediment composition of the tidal flats and amounts to 530 x 10^3 tonnes per cm of sediment in the lower reaches and to 725 x 10^3 tonnes per cm of sediment in the Dollard. Compared with the calculated maximum tidal fluxes (< 70 x 10^3 tonnes per tide in the lower reaches and < 40 x 10^3 tonnes per tide in the Dollard) the assumption that the tidal flats are an infinite source of mud is correct. This is because an erosion of less than 0.5 cm of sediment is sufficient to reach a resuspended amount of > 250 x 10^3 tonnes of mud in the lower reaches, and more in the Dollard.

The calculated fluxes of mud and microphytobenthos are assumed to represent minimum amounts because the suspended matter values increase from the surface to the bottom (Postma, 1954; de Jonge *et al.*, 1984). But the available surface values could, not be calculated, because of the shortage of data. Further, the regression functions published in a previous study (de Jonge & van Beusekom, this thesis) refer to the hydrographical situation at mean tide, whereas the present calculations refer to high tide. The difference in water volume between mean sea level and mean high water results in the actual fluxes of microphytobenthos increasing by c. 25% in the lower reaches and by c. 30% in the Dollard.

Interestingly, the available data set contains indications that the wind-induced resuspension is directly measurable under field conditions, even from day to day. During the period October to December 1977 the two stations on the tidal flats in the lower reaches (nos. 10 and 20; cf. de Jonge & Colijn, this thesis) were sampled once every two weeks but twice on two

Table 3a. Mean annual primary production in the Ems estuary over the period 1976-1980 (data borrowed from Colijn, 1983, Colijn & de Jonge, 1984 and own calculations). For location of areas see Fig.1. Values between brackets include excretion.

Parameters		lower reaches	middle reaches	Dollard
PRIMARY PRODUCTION				
total phytoplankton in channels (1)	(gC m^{-2} a^{-1})	411 (514)	146 (161)	62 (62)
above tidal flats (1)	(gC m^{-2} a^{-1})	50 (62)	115 (127)	19 (19)
mean values for total area (calculated from date above)	(gC m^{-2} a^{-1})	252 (314)	132 (145)	27 (27)
real phytoplankton	(gC m^{-2} a^{-1})	176 (219) 57% (63%)	95 (104) 59% (61%)	2 2%
microphytobenthos (water column)	(gC m^{-2} a^{-1})	76(4) 25% (22%)	37(4) 23% (22%)	25 26%
microphytobenthos (tidal flats)	(gC m^{-2} a^{-1})	55 18% (16%)	29 18% (17%)	68 72%
total microphytobenthos	(gC m^{-2} a^{-1})	131 43% (37%)	66 41% (39%)	93 98%
total algae	(gC m^{-2} a^{-1})	307 (350) 100% (100%)	161 (170) 100% (100%)	95 (0) 100% (0%)
CHLOROPHYLL-A				
Chl-a concentration (2) mean 1975-1980	(mg m^{-3})	7.6	6.1	6.6
resuspended Chl-a (Table 2)	(mg m^{-3})	2.3	ca. 1.7(3)	6.1
fraction Chl-a from resuspended microphytobenthos		0.30	0.28	0.92

1): Data borrowed from Colijn, 1983

2): Data 1977-1980 borrowed from Colijn (1983: p.50) and 1975-1976 own data

3): Value estimated from the relative distribution of pennate diatom cells in water and on tidal flats (de Jonge, 1985) cf. also Fig. 11

4): Values calculated under the assumption that excretion of microphytobenthos is insignificant.

Table 3b. Total annual primary production in tonnes per annum in different parts of the Ems estuary. For location of areas see Fig. 1. Values in brackets include excretion.

	lower reaches	middle reaches	Dollard	total estuary
total primary production				
real phytoplankton	48224 (60000)	8598 (9412)	205	57027 (69722)
resusp. microphytobenthos	20825	3348	2560	26733
microphytobenthos on tidal flats	15070	2624	6956	24650
Total	84119 (95895)	14570 (15384)	9721	108410 (121000)

successive days (for more details see de Jonge & Colijn, this thesis). In agreement with the results of de Jonge & van Beusekom (this thesis) the differences in microphytobenthos biomass between these days corresponded very well with the changes in effective wind speed.

Distribution of primary production and biomass over benthic and pelagial.

The values on the relative contribution of chlorophyll-a derived from suspended microphytobenthos can be used to estimate the proportion of the primary production caused by 'real phytoplankton' and the part caused by suspended microphytobenthos. The calculations were done assuming that under the same conditions the growth efficiency of phytoplankton (consisting of diatoms and flagellates) equals that of the suspended microphytobenthos (mainly diatoms). The calculations were based on values for primary production published by Colijn (1983) for this estuary (Table 3) and on the chlorophyll-*a* data presented in Table 2.

From the values in Table 3A it is concluded that the mean annual primary production caused by real phytoplankton in the lower reaches and the middle reaches (57% and 59% respectively) exceeds the contribution of total microphytobenthos. In the Dollard the contribution of real phytoplankton to the total primary production is extremely small (2%); consequently, 98% of the primary production is caused by microphytobenthos. The annual primary production for the two categories is given per reach in Table 3B. From these data it is concluded that the microphytobenthos primary production in the water column is c. 25% for the entire estuary, a feature which was not explicitly included in the model of the Ems estuary ecosystem (Baretta & Ruardij, 1988). The annual primary production in the entire estuary (121 x 10^3 metric tonnes, Colijn, 1983) agrees very well with the results of the ecosystem model (ca. 102 x 10^3 metric tonnes). Roughly the same holds when total phytoplankton and microphytobenthos on tidal flats are considered separately.

Colijn (1983) reported that no excretion products were produced by the phytoplankton in the Dollard. This finding corresponds with the present results (Table 3A) from which it appears that in the Dollard the primary production by real phytoplankton is unimportant. The absence of excretion products from microphytobenthos (cf. Baretta & Ruardij, 1988; p 216: 36% of the primary production in the Dollard is excreted) is not correct but results from the inability of the ^{14}C method to measure the exuded compounds.

The information presented in Figures 5 and 8 and in Tables 2 and 3 is summarized in Fig. 10 and illustrates the relative importance of biomass, primary production, and fluxes of phytoplankton and microphytobenthos in the lower reaches and Dollard. Values are given both per reach and per square metre.

Role of microphytobenthos for grazers

In the previous section it is indicated that, in terms of quantities, the most important feeding environment for populations of estuarine grazers is certainly not the water column but the tidal flats. Another ecologically important fact is that in the uppermost layers of the tidal flats the concentrations of microphytobenthos are much greater than in the water column. Based on this it can be hypothesized that the tidal flats are a very important food source. Schwinghammer *et al.* (1983) analysed $\delta^{13}C$ ratios of benthic fauna and concluded that the bulk of their food was derived from benthic diatoms. The same conclusion was reached by Incze *et al.* (1982) for the clam *Macoma balthica* and by Fenchel & Kofoed (1976) and Levinton & Bianchi (1981) for *Hydrobia* snails. This phenomenon might be related to the resuspension. During the process of resuspension different fractions of the sediment become hydraulically separated. The resuspension starts with small particles and material of low density such as mud aggregates. This separation could be advantageous for the grazers' energy budget. Also, the specialized deposit feeders take advantage from the life style of microphytobenthos and therefore their biomass concentration is greatest near the sediment surface (de Jonge & Colijn, this thesis).

From the foregoing it is clear that the ecology of microphytobenthos living at the interface between sediment and water is highly complex. The algae are easily suspended (de Jonge & van Beusekom, this thesis) and it seems reasonable to assume that their primary production in the water column is as effective as it is on the tidal flats.

Only a few studies have dealt with the effect of resuspension on the concentration of microphytobenthos biomass in the water. Most of these studies qualitatively describe the process of algal resuspension (Neumann *et al.*, 1970; Roman & Tenore, 1978; Baillie & Welsh, 1980; Frechette & Bourget, 1985; Gabrielson & Lukatelich, 1985; de Jonge, 1985;

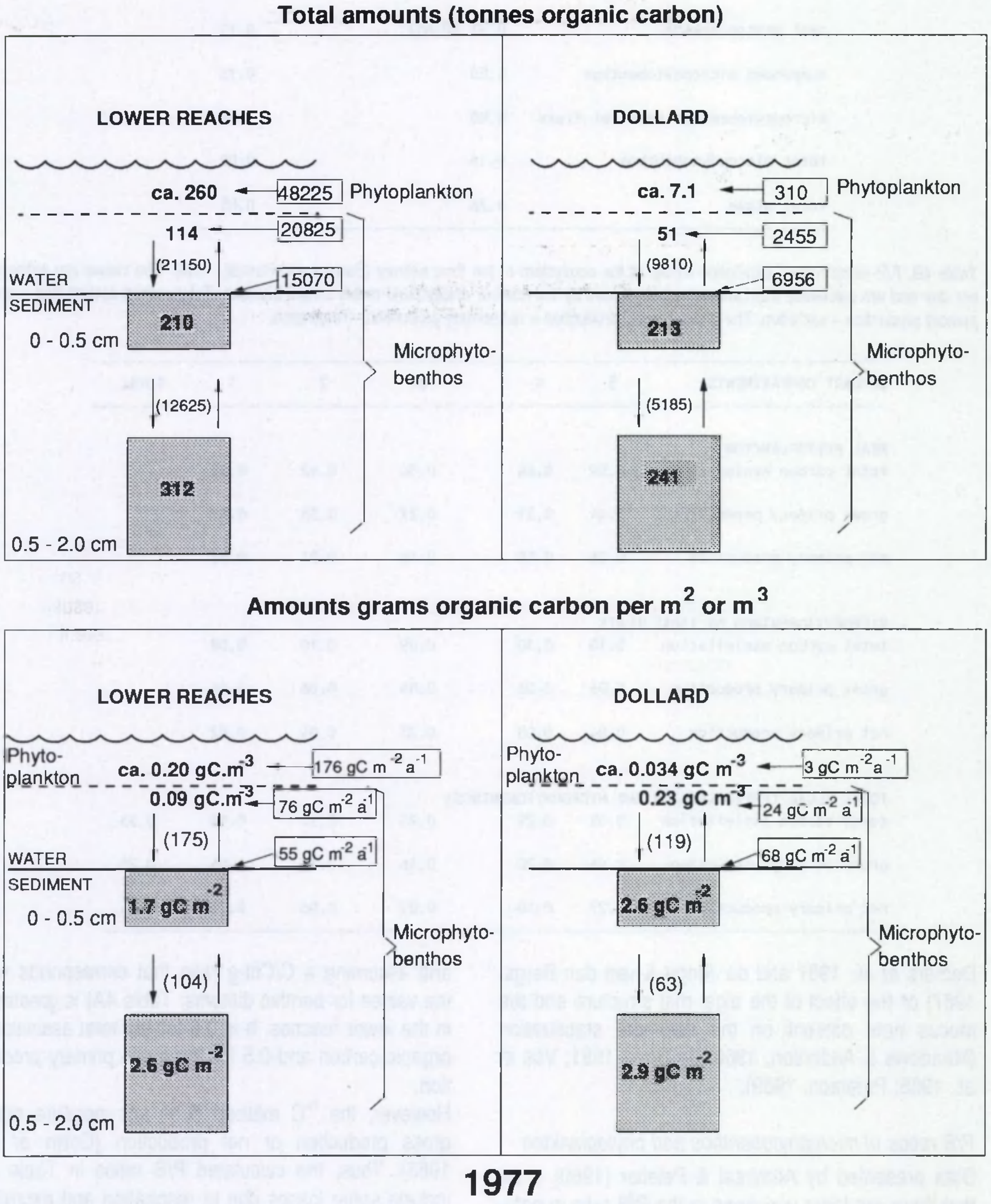

Fig. 10. Diagrams representing the mean annual biomass, the annual primary production and the annual gross fluxes of biomass between the water column and the two sediment layers for two parts of the Ems estuary (the lower reaches and the Dollard).
Values in brackets are fluxes. Values in rectangles represent annual primary production and other values represent mean annual biomass. Biomass values for phytoplankton are estimated from chlorophyll-*a* values (cf. Fig. 2) using C/Chl-*a* ratio of 38 (de Jonge, 1980).

Table 4A. P/B ratios expressed as mean primary production per day, divided by mean annual biomass. Values include respiration and therefore roughly correspond to the gross primary production given in Table 4B. Values in brackets include excretion and roughly correspond to total C assimilation.

	LOWER REACHES	DOLLARD
real phytoplankton	0.51 (0.63)	0.11
suspended microphytobenthos	0.50	0.13
microphytobenthos on tidal flats	0.08	0.04
total microphytobenthos	0.16	0.05
total algae	0.26	0.05

Table 4B. P/B ratios from a simulation model of the ecosystem of the Ems estuary (Baretta and Ruardij, 1988). The values are expressed per day and are calculated from annual values divided by the number of days and mean annual biomass. Total carbon assimilation = gross primary production + excretion. The gross primary production = net primary production + respiration.

ESTUARY COMPARTMENTS:	5	4	3	2	1	TOTAL
REAL PHYTOPLANKTON						
total carbon assimilation	0.59	0.44	0.34	0.42	0.55	
gross primary production	0.44	0.31	0.27	0.33	0.48	
net primary production	0.26	0.15	0.16	0.21	0.37	
MICROPHYTOBENTHOS ON TIDAL FLATS						
total carbon assimilation	0.10	0.10	0.09	0.10	0.08	
gross primary production	0.06	0.06	0.05	0.06	0.04	
net primary production	0.04	0.03	0.03	0.04	0.02	
TOTAL ALGAE (PHYTOPLANKTON AND MICROPHYTOBENTHOS)						
total carbon assimilation	0.63	0.29	0.21	0.15	0.10	0.35
gross primary production	0.46	0.20	0.16	0.11	0.06	0.25
net primary production	0.27	0.10	0.09	0.06	0.04	0.14

Demers *et al.*, 1987 and de Jonge & van den Bergs, 1987) or the effect of the algal mat structure and the mucus nets present on the sediment stabilization (Meadows & Anderson, 1968; de Boer, 1981; Vos *et al.*, 1988; Paterson, 1989).

P/B ratios of microphytobenthos and phytoplankton

Data presented by Admiraal & Peletier (1980) show that there are large variations in the P/B ratio in natural microphytobenthos populations. The P/B ratio of the different groups of primary producers calculated from the present study shows that the productivity of the phytoplankton (based on the field measurements and assuming a C/Chl-a ratio that corresponds with the values for benthic diatoms; Table 4A) is greatest in the lower reaches. It is 0.6 for the total assimilated organic carbon and 0.5 for the gross primary production.

However, the ^{14}C method does not measure either gross production or net production (Colijn *et al.*, 1983). Thus, the calculated P/B ratios in Table 4A include some losses due to respiration and excretion products and therefore underestimate the real value.

When the ratios for phytoplankton and resuspended microphytobenthos calculated for the lower reaches under natural conditions are compared with those obtained from the ecosystem model (compartments 4 and 5 representing the lower reaches) (Table 4A and B) there is reasonable agreement. In the case of the Dollard (Dollard in Table 4A and compartments 1 and 2 in Table 4B), the values for the natural situation and the results from the model differ diametrically from each other and from those of the lower reaches. The values based on field measurements reveal daily P/B ratios of ca. 0.1 but the P/B ratios based on the model results are much larger: c. 0.2 to 0.5. This difference might be caused by the relatively large biomass (mainly resuspended microphytobenthos) in the water under field conditions (Table 2 and 4A).

The overall daily P/B ratio in Table 4A based on the sum of microphytobenthos and phytoplankton agrees very well with the values (Table 4B: total algae) calculated from the model results. This indicates that observed differences between the field and the model may be mainly based on differences in the distribution of the total biomass pool over sediment and water, rather than on differences in mean annual biomass and/or annual primary production.

The P/B ratio for microphytobenthos is substantially smaller than that of phytoplankton and resuspended microphytobenthos: it is 0.08 in the lower reaches and 0.04 in the Dollard. In the Dollard this value is so small that the P/B ratio for the net primary production may result in a value of approx. 0.02 (cf. Table 4B). Although so small, this value is enough to sustain the local population of the microphytobenthos which is grazed by several organisms, among them harpacticoid copepods, oligochaetes and nematodes. The mean annual primary production of microphytobenthos on the tidal flats in the Dollard is (Table 3) 68 gC m^{-2} a^{-1}, which corresponds to 0.19 gC m^{-2} d^{-1}. From the model results (Baretta & Ruardij, 1988) the net primary production can be estimated to be c. 25% of the total carbon assimilation, resulting in a net production of c. 0.05 gC m^{-2} d^{-1} for the field situation. The total grazing pressure by copepods and nematodes in the Dollard is less than 0.03 gC m^{-2} d^{-1} (Admiraal *et al.*, 1983; Baretta & Ruardij, 1988). Thus the total net primary production is enough to supply food to all the meiofauna and to sustain the local microphytobenthos population. However, losses caused by other grazers such as polychaete larvae and by permanent burial and mortality were not included in this calculation. For the Boston coast (USA) Gould & Gallagher (1990) found large losses of 1.7 gC m^{-2} d^{-1} which were ascribed to grazing pressure. These values possibly included wind driven resuspension. A very interesting aspect is that when the suspended populations of microphytobenthos and those on the tidal flats are taken into account the P/B ratio increases from 0.08 to 0.16 in the lower reaches and from 0.04 to 0.05 in the Dollard. This suggests that growth of microphytobenthos in the water column is a very helpful mechanism for sustaining the local population.

Comparison of annual gross fluxes and net fluxes

The resuspension of fine sediment material "mud" has long been a topic of study (Kamps, 1962; Kullenberg, 1971, 1972, 1976; Gordon, 1974; Heathershaw, 1974; Therriault *et al.*, 1978; Dyer, 1979; Levasseur *et al.*, 1983; Carper & Bachmann, 1984, Demers *et al.*, 1987 and de Jonge & van Beusekom (this thesis). However, so far the impact of mud resuspension on the total annual flux of material between tidal flats and channels has not been quantified.

The magnitude of the net annual upstream transport of mud and organic carbon from the North Sea coastal zone can be estimated from data on the accretion rate of the area (Reenders & van der Meulen, 1972) and from the carbon content of the suspended matter in the tidal inlet of the estuary.

The calculations are based on an accretion of 0.008 m a^{-1}, a mean silt content of 30% in the tidal flats in the Dollard of 30% (Maschhaupt, 1948) and ca. 22% in the rest of the estuary (van Heuvel, 1991) and an organic carbon content of 4.9% in the suspended matter in the tidal inlet (own data). Fig. 11 provides an overview of mean annual amounts of mud and organic carbon present, the calculated annual flux of mud and organic carbon between tidal flats and channels, the local annual longitudinal transport, the local annual primary production and an estimate for the net annual influx of mud and organic carbon for the entire estuary and the Dollard. The data indicate that in the tidal inlet of the Ems estuary the net annual influx of both organic carbon (69 x 10^3 tonnes) and mud (1410 x 10^3 tonnes) is very small and amounts only to a few percent in comparison with the gross longitudinal fluxes (1600 x 10^3 tonnes of organic carbon and 32 000 x 10^3 tonnes of mud) and the lateral fluxes (587 x 10^3 tonnes of organic carbon and 12 000 x 10^3 tonnes of mud). This implies that the net annual flux in the tidal inlet of the estuary is unmeasurable under field conditions if convential measuring techniques are used, largely because inaccuracies of water transport alone are already in the order of 5% (cf. de Jonge, in press). An interesting alternative procedure for measuring such transports was recently published by Pejrup (1988).

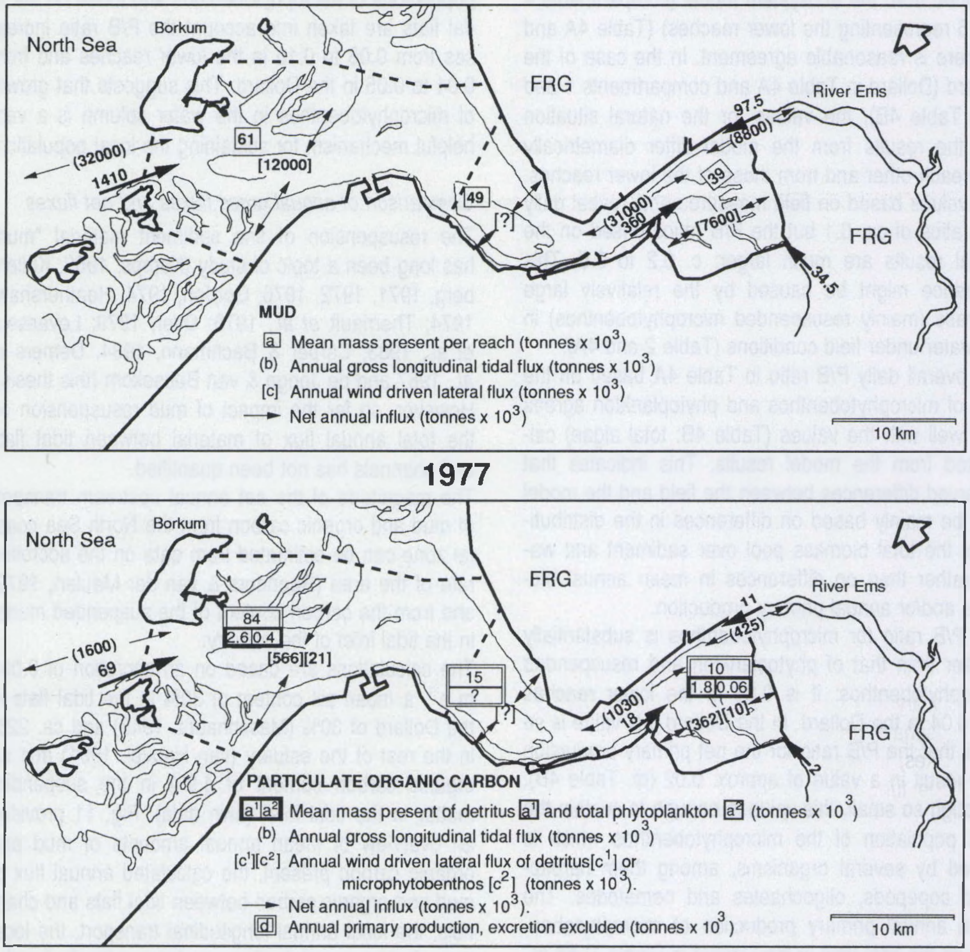

Fig. 11. Fluxes of mud and organic carbon from different sources.

The wind-driven lateral transports are considerably larger than the values for water transport given above.

When the fluxes presented above are compared with the results of the computer simulation model for the Ems estuary we find that in that model a considerable amount of mud transport from the North Sea coastal zone into the Ems estuary is assumed to be attributable to flows of "fluid mud" that are needed to reach a balance between total import and export of silt. There is no theoretical basis for this assumed fluid mud transport in the tidal inlet of the estuary and it was not confirmed by field measurements.

In the simulation model (Baretta & Ruardij, 1988) only mean monthly values of the wind speed were used to simulate the annual cycle in turbidity. Consequently, the effects of short-term wind events were not simulated. The results of the present study clearly illustrate the magnitude of these wind-induced changes in suspended matter and thus of turbidity (Fig. 7). In combination with daily insolation these dynamics directly influence the primary production in the water column.

Comparison of the net annual influx of organic carbon to the Dollard with data given by van Es (1977) reveals some differences. The earlier published particulate carbon supply was estimated as 37 x 10^3 tonnes annually whereas according to the present study it is to 28 x 10^3 tonnes.

In the present study the total annual supply of particulate organic carbon from the coastal area to the estuary is estimated to be 69 x 10^3 tonnes C annually (corresponding to 148 gC m^{-2} a^{-1}) whereas the supply in the simulation model (Baretta & Ruardij, 1988) is 37.9 x 10^3 tonnes of organic carbon annually (81 gC m^{-2} a^{-1}). The estimate from the simulation model is c. 45% less than the supply calculated in this paper. Moreover, the present value is, in turn, c. 45% less than the estimated supply of c. 225 gC m^{-2} a^{-1} for the early 1970s for the western Dutch Wadden Sea (de Jonge & Postma, 1974).

Short term fluctuations in light extinction

At present it seems that the procedure followed here is one of the rare ways of calculating fluxes without using a complex simulation model and its inherent uncertainties.

The present calculations have ecological significance, for several reasons. Changes in light extinction need to be quantified realistically, to serve as input for ecosystem models. For the Ems estuary the wind induced suspended matter concentrations can be converted to light extinction coefficients (k) by applying the equation $k = 0.4 + 0.04\ SM$ (Colijn, 1982). Changes in the turbidity of the water caused by wind or human activities lead to a proportional change in primary production of the phytoplankton (DeGroodt & de Jonge, 1990). However, the mud fraction in the Ems estuary is also an important carrier of nutrients e.g. phosphate (de Jonge & Villerius, 1989; de Jonge & Engelkes, in prep.). The quantitative effect of the very large turn-over of mud between tidal flats and channels on the nutrient supply of the water column is as yet unclear and needs to be evaluated further. Therefore, it would be worth applying the present findings in models simulating mud transport between tidal flats and tidal channels.

As mentioned above, in the paper by de Jonge & van Beusekom (this thesis) the relation between effective wind speed and resuspended mud in the central part of the main channels implicitly also provides some indication of the time scale of the lateral mixing rate. When the generalized pattern of residual currents (de Jonge, 1991: Fig. 9; Robaczewska, 1990: Fig. 35) is considered it seems that the lateral mixing of mud is influenced by the presence of the complex residual cells in lower reaches and Dollard. This pattern suggest that these cells effectively contribute to the dispersion of fine particles during the tidal cycle. Analysing the lateral transport routes of resuspended mud further with the models available may clarify the phenomenon (Ridderinkhof & Zimmerman, 1990).

Anthropogenic effects

As well as natural events, such as tide and wind, anthropogenic factors such as dredging can also change the estuarine gradient of suspended matter concentrations (de Jonge, 1983). It is assumed that on average the changes induced by dredging activities will not influence the wind driven lateral fluxes of the mud (and organic carbon) but that they influence the background light extinction of the water in the estuary.

Unstudied aspects

The tide induced dynamics of mud and sand in the system were not considered in the present paper but are of importance in the estuary. The same holds for the role of the tide in the longitudinal transport of mud.

CONCLUSIONS

1. The resuspension and redistribution may be described in three different phases. These are:
   a. a wind induced phase in which wave induced oscillatory bottom currents are responsible for sediment resuspension;
   b. a tide induced phase in which above a certain threshold value tidal current velocity is mainly responsible for the local transport of resuspended material on tidal flats (in the main channels the tidal currents determine both the longitudinal and lateral transport of the resuspended material.);
   c. an anthropogenically induced phase in which changes in estuarine geometry, e.g. as a result of dredging, lead to changes in suspended matter concentrations.
2. Resuspended microphytobenthos contributes, on average, 30% to the total amount of chlorophyll-*a* biomass present in the water of the lower reaches of the Ems estuary. In the Dollard this value is much higher (c. 85%). Consequently, the microphytobenthos is also assumed to contribute the same percentages to the annual primary production of the water column.
3. In the lower reaches ca. 40% of the total microalgal chlorophyll-*a* biomass is present in the water. In the Dollard this amount is much smaller (c. 10%), the remainder being present on the large intertidal flats.
4. Approximately 25% of the total primary production in the Ems estuary is caused by resuspended microphytobenthos, 53% by real phytoplankton and c. 22% by microphytobenthos living on the tidal flats.

5. The total algal biomass and its concentration in the uppermost 0.5 cm layer of the tidal flats is much greater than the total biomass and concentration in the water. In terms of providing food for grazers the tidal flats seem to be more important than the water column.
6. The short-term dynamics in turbidity in the Ems estuary are mainly caused by the wind driven lateral fluxes of mud. This results in concentrations being higher in the Dollard than in the lower reaches.

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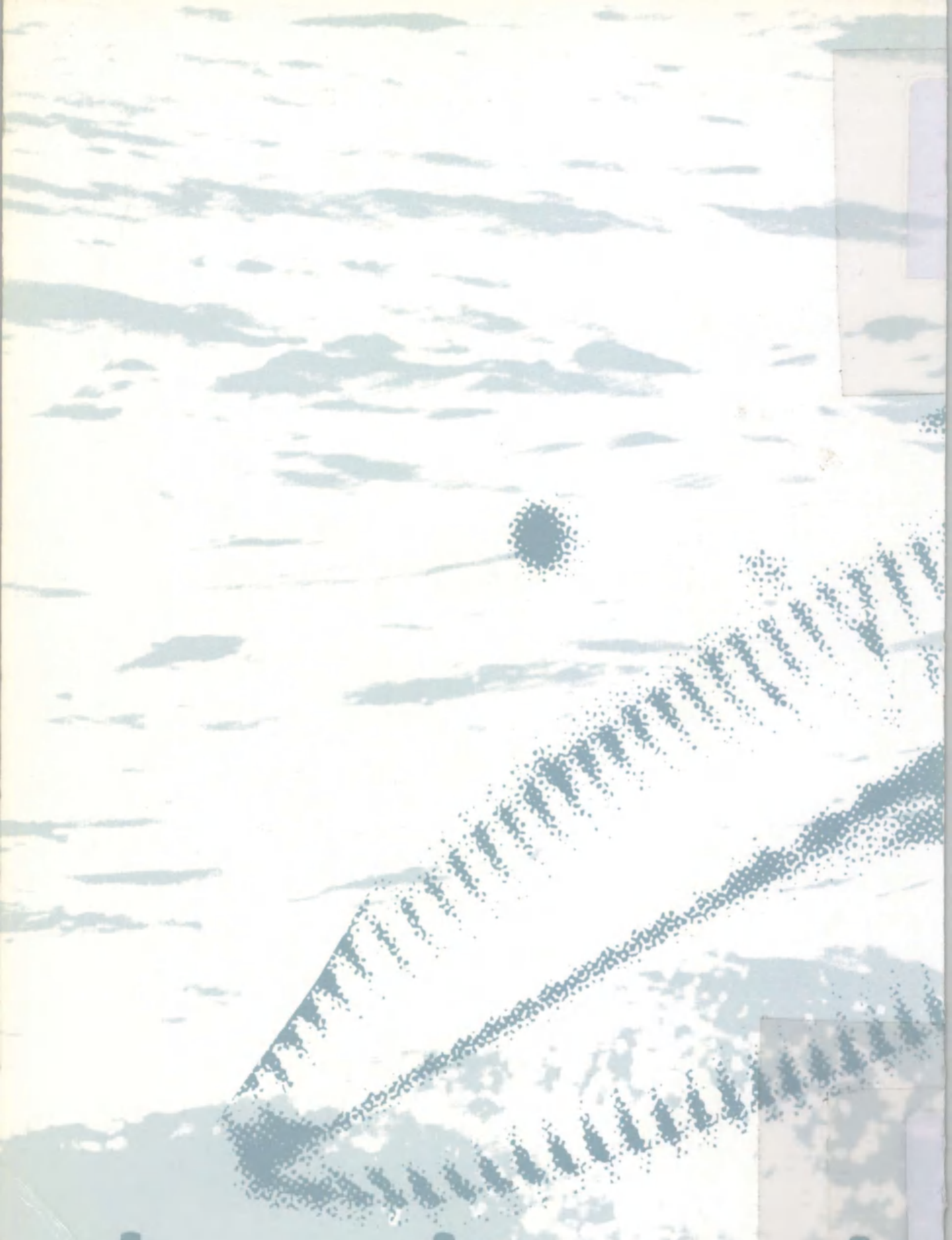

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