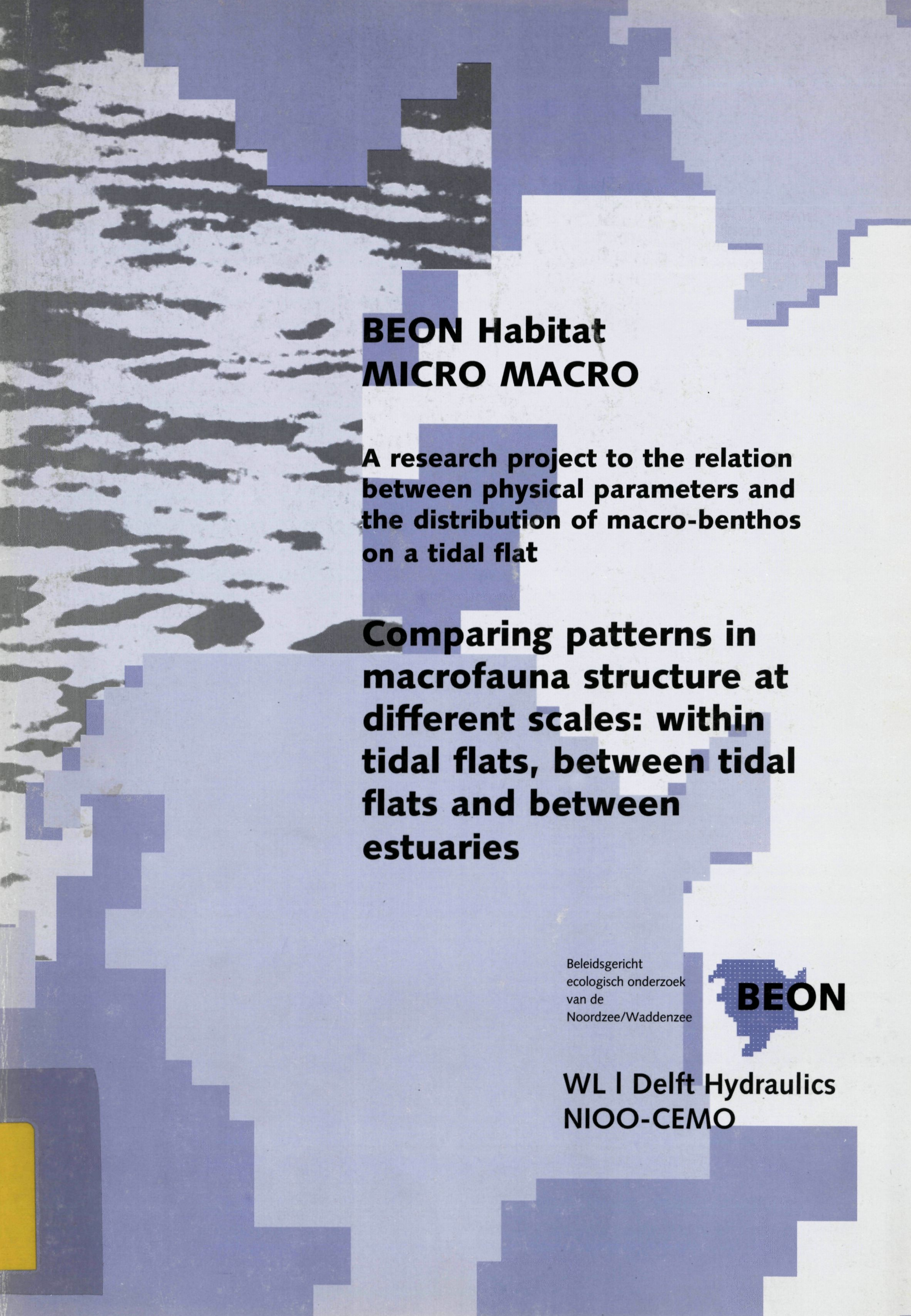

BEON Habitat
MICRO MACRO

A research project to the relation between physical parameters and the distribution of macro-benthos on a tidal flat

Comparing patterns in macrofauna structure at different scales: within tidal flats, between tidal flats and between estuaries

Beleidsgericht
ecologisch onderzoek
van de
Noordzee/Waddenzee

BEON

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Overzicht BEON habitatrapporten, verschenen in het kader van het project 'Kartering van habitats/ecotopen in de Nederlandse zoute wateren'

In het kader van BEON (Beleidsgericht Ecologisch Onderzoek in Noordzee/Waddenzee) worden een aantal speerpunten onderscheiden. Bij het speerpunt 'verstoring habitats' staat als prioriteit onder systeemkennis vermeld dat onderzocht moet worden welke ecotopen onderscheiden kunnen worden, waar ze zich bevinden en wat hun karakteristieken zijn. Het tweede prioritaire onderwerp stelt de vraag naar het belang van bepaalde ecotopen voor bepaalde soorten. Het uitgevoerde project sluit aan bij deze vragen.

Beleidsrelevantie

Het beleid in de kustwateren en de Waddenzee is gericht op het duurzaam functioneren en gebruiken van het systeem. Door het multifunctionele karakter van het gebruik wordt verweving van functies als uitgangspunt genomen. Indien dat niet mogelijk is, wordt zonering toegepast. Bij verweving van functies wordt uitgegaan van optimalisatie van de verschillende functies; bij scheiding wordt in de onderscheiden gebieden veelal gestreefd naar maximalisatie. Door indeling in ruimte en tijd wordt ernaar gestreefd de negatieve effecten op de overige functies zo klein mogelijk te houden, zowel bij verweving als scheiding. Voor beleid en beheer is het essentieel de habitatkarakteristieken te kennen waarop elke functie gebaseerd is. Bovendien is het noodzakelijk te weten waar de betreffende karakteristieken voorkomen. In een voorgaand BEON-project wordt voor een aantal organismengroepen aangegeven wat de belangrijkste habitatkarakteristieken zijn. Vooral fysische parameters blijken belangrijk. Deze zijn nog maar zeer ten dele op bestaande kaarten weergegeven.

Het project heeft eveneens als doel om door middel van een case-study een basis te leggen voor een generieke methodiek en ondersteunend instrumentarium om de geschiktheid van ruimtelijk inhomogene gebieden voor verschillende soorten en gebruiksfuncties te kunnen evalueren en presenteren.

Het in kaart brengen van ecotopen en habitats is essentieel voor de toepassing van de EU-Habitatrichtlijn en de regelingen die getroffen moeten gaan worden in het kader van het Biodiversiteitsverdrag van Rio.

Als afsluiting van het project zijn een viertal rapporten uitgebracht:
Omdat het voorkomen van organismen niet uitsluitend wordt bepaald door de duidelijk waarneembare fysische en biologische eigenschappen van de locatie is onderzocht of de microverspreiding van voedsel een belangrijke factor was. Hierover wordt gerapporteerd in de rapportage van NIOO-CEMO en WL (BEON rapport nr. 98-14: BEON Habitat. MICRO MACRO. A research project to the relation between physical parameters and the distribution of macro-benthos on a tidal flat (WL). Comparing patterns in macrofauna structure at different scales: within tidal flats, between tidal flats and between estuaries (NIOO-CEMO)). Het onderzoek werd uitgevoerd in de Westerschelde

De tweede rapportage bevat twee onderdelen uitgevoerd door RIVO-DLO en NIOZ. In deze rapportage wordt de verspreiding van vissen in kustwateren en Waddenzee beschreven in relatie tot abiotische en biotische (voedsel) gegevens (BEON rapport nr. 98-16: Wetenschappelijke eindverantwoording en korte samenvatting van de RIVO-DLO bijdrage aan het BEON-project 'Kartering van habitats/ecotopen in de Nederlandse zoute wateren (RIVO-DLO). Benthos-Epibenthos interactions in the Dutch Wadden Sea (NIOZ).

In een rapportage van RIVM, IBN-DLO, en RIKZ wordt het gebruik van het habitat en ecotoopbegrip nader uitgewerkt (BEON rapport nr. 98-11: Naar een ecotopensysteem zoute wateren Nederland). Hiertoe is een hiërarchisch systeem ontwikkeld dat algemeen toepasbaar is in Kustwateren.

Voorgesteld wordt de term habitat te reserveren voor een benadering waarbij vanuit een organisme gedacht wordt. Een habitat kan dan gedefinieerd worden als **'het type omgeving waarin een organisme leeft'**; het wordt bepaald door de eisen die dat organisme aan zijn omgeving stelt. Deze benadering is belangrijk bij het beschermen van bedreigde organismen.

Bij een integraal beleid waarbij van een aantal functies wordt uitgegaan, heeft het meestal voordelen het ecotoopbegrip te hanteren. Binnen een bepaald ecotoop is ruimte voor een aantal organismen of een levensgemeenschap. Als definitie voor ecotoop wordt aangehouden **'een geografische eenheid die binnen bepaalde grenzen homogeen is wat betreft de belangrijkste hydraulische, morfologische en fysisch-chemische omgevingsfactoren die relevant zijn voor de biota'**.

In de vierde rapportage (RIKZ, IBN-DLO, RIVM) wordt op basis van de ontwikkelde theorie een voorbeeld gegeven van een ecotopenkaart van de Waddenzee (BEON rapport nr. 98-13: Naar ecologische kaarten van de Waddenzee). Door middel van overlays en door de gebruiker samen te stellen legenda's en klassegrenzen kunnen ecotoop en habitatkaarten gemaakt worden. Het inbrengen van informatie betreffende het voorkomen van organismen en het ontwikkelen van rekenmodules om optimale ontwikkelingsomstandigheden in kaart te brengen is onderdeel van projecten buiten BEON, en is voor de Waddenzee reeds uitgevoerd voor Zeegras en voor de Westerschelde voor de Kokkel. Een kaart die de optimale ontwikkelingsmogelijkheden voor mosselbanken wordt ontwikkeld door IBN-DLO, RIVO-DLO en RIKZ.

In opdracht van de HID-Noordzee werd gelijktijdig gewerkt aan de ontwikkeling van ecotopenkaarten voor de Noordzee waarbij gestreefd moest worden naar afstemming. De toegepaste methoden en ontwikkelde applicaties zijn in gezamenlijk overleg ontwikkeld. Het **'Ecotopen GIS Noordzee'** (Auteur J.G. Hartholt) is onlangs uitgebracht.

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Contents

1 Introduction

1.1 History

The BEON 'MICRO-MACRO' project is part of the Dutch project 'Preparation of an Integral mapping of Habitats in the Dutch part of the Continental Shelf and the Dutch Coastal Waters'. The project is charged by BEON to several Dutch co-operating institutes in contract no. RKZ-163 (1995).

This Report contains a description of the activities of Delft Hydraulics carried out in 1996 and 1997. The present subject of research is a follow up of the study which started in 1995 (see Delft Hydraulics, 1995). The first part of the study carried out in 1995 focussed on the development of a two dimensional hydrodynamic and transport model covering a tidal flat in the Western Scheldt in detail. In the transport model a formula for the growth of macro-benthos was implemented as well.
First simulations were carried out simulating the distribution of suspended and deposited nutrients and sediments on the tidal flat. The results were compared to the observed distribution and biomass of suspension and deposit feeders. It was concluded that a correlation exists between the flow velocity and the distribution of filter feeders and deposit feeders on the scale of a tidal flat. It appeared not to be possible to predict the growth of the macro-benthos with the implemented formula. This can be due to the formula applied, but also to the ability of the model to properly predict the food distribution during a tide.

In the study described in this Report, above study results are investigated in more detail, together with results of new transport simulation runs and the biological data available from the 1995 survey.

1.2 Goal and Objectives

The general goal of the entire MICRO-MACRO study (covering the period of 1995-1997) is to obtain insight in the processes that determine the geographical distribution of macro-benthos on a tidal flat. Keywords are *food availability* and *hydrodynamic parameters*. The question to such a research project was raised since the geographical distribution of macro-benthos in estuarine systems shows a large patchiness and variability in biomass. This makes it very difficult to give a clear description of the role of macro-benthos in the food chain of estuarine systems. Sampling gives too little insight in seasonal dynamics and mean food assimilation. Long year trends in species distribution and biomass are difficult to observe.

In this project it is assumed that insight in these processes can be obtained by analyses of factors that determine/influence the variability and biomass of macro-benthos. Then it is important to distinguish two different scales: the large (MACRO) scale concerns the entire estuarine system; the smaller (MICRO) scale concerns the scale of a tidal flat. This distinction is made since it appears that the processes that determine/influence the distribution and density of biomass on a MACRO scale do not necessarily determine those on a MICRO scale, and vice versa. The biomass, distribution and species composition in the

Western Scheldt on the estuary scale is driven by salinity and system productivity. On a smaller spatial scale however, substrate composition and inundation time or depth are probably the key factors, besides hydrodynamics and substrate dynamics. High dynamic sandy parts (with megaripples) usually have a fairly low biomass. Low dynamic muddy parts usually have a rather high biomass. Hydrodynamical conditions therefore define the habitats of benthos, both by affecting the substrate (composition, stability) as well as the overlying water (food availability, inundation time, scouring). These small scale processes are subject of this study.

Delft Hydraulics' activities focusses in the present part of the study only on the MICRO scale, since it appeared very difficult to cover both the MICRO and MACRO scale in a thorough way without becoming superficial. For the understanding of the several biological and hydrodynamic processes occurring on a MICRO scale a number of time consuming discussions were necessary, as well as to find the boundaries of the simulation possibilities of the transport model.

2 Description and analysis of data

2.1 Hydrodynamics, available data

In the present study two hydrodynamic models are available from the study carried out in 1995:

1. The Scaldis Model
2. The Molenplaat Model

The Scaldis Model is a two dimensional hydrodynamic Model covering the entire Western Scheldt with a resolution of 100-400 m2, developed by RIKZ (Rijks Instituut voor Kust en Zee: National Institute for Coastal and Marine Management). In this study it is used to compute the hydrodynamic boundary conditions for the Molenplaat model, which is a detailed model covering a smaller part of the Western Scheldt with a resolution of 30-100 m2. The Molenplaat model is used to compute the water movement in the Molenplaat area and to predict the transport of suspended matter during a tide.

The available hydrodynamic data consisted of water levels and current velocities sampled at several locations on the Molenplaat in the Western Scheldt in 1995. These data are already analysed in 1995 see (Delft Hydraulics,1995).

For the set-up of the hydrodynamic models carried out in the first part of the study, bathymetric data was used from 1988 (in the larger part of the Western Scheldt) and from 1994 (in the area of the Molenplaat). Using this bathymetric data and the water level and velocity data the Molenplaat model was calibrated.
During the present study for the entire Western Scheldt, bathymetric data of 1995 came available. This data was used to create a new more recent bottom schematisation for both the Scaldis model and the Molenplaat model. Hereafter both models were verified on there hydrodynamic performance at the Molenplaat.

2.2 Macrozoobenthos on a tidal flat, theories

2.2.1 Introduction

As mentioned in Chapter 1, this study focusses on the relation between the abundance, distribution and species composition of macrozoobenthos with hydrodynamics, substrate dynamics and substrate composition.

The faunal composition of an estuary may be interpreted in terms of the trophic group mutual exclusion hypothesis (Wildish & Peer, 1983). This hypothesis states that species composition and productivity are limited directly or indirectly by tidal current velocity. Mutual exclusivity arises because each of the trophic groups can tolerate a different range of tidal velocities. Thus, deposit feeders are favoured at low current velocities in net depositional areas, and suspension feeders in higher current velocities where deposition and erosion are low or absent. Where tidal dynamics cause the sediment to undergo significant erosion-deposition cycles, suspension feeders are absent and only a few hardy deposit feeders may be found (Wildish & Peer, 1983).

So hydrodynamical factors control food supply for suspension feeders as well as deposit feeders. Suspension feeders feed by filtering particles (phytoplankton) from the water column. Thereby it is important how many particles flow by. Deposit feeders feed by collecting deposited material from the bottom. Thereby it is important how many particles drop down. As a result of different feeding behaviour of these groups, different optimal hydrodynamic conditions exist. Hydrodynamics also influences the resuspension of microphytobenthos which can be an important food source for suspension feeders. In addition, hydrodynamical factors can cause stress when current velocities, or bottom shear stress is high. At places with high bottom shear stress the constant reworking of the sediment can result in collapsed holes and washed away animals.

Experimental evidence that feeding rates of suspension feeders are inhibited by high concentrations of inorganic sediment particles in suspension is available for some species (Wildish & Peer, 1983; Essink, 1993). Other possibilities are that high current speeds directly inhibit feeding above a threshold speed, or that high concentrations of food particles themselves inhibit feeding (Wildish & Peer, 1983).

2.2.2 Controlling processes

Several factors and processes influence the abundance, distribution and species composition of the macrozoobenthos on a tidal flat. This list provides a very short overview of significant processes and the relevance of these processes for this project.

- *Weather and climate*. Temperature and light define primary production and the activity of the benthos is temperature dependent. When winter temperatures are severely cold mortality of sensitive benthos species can occur. In this study a very short time period is considered during summer, so the influence of wheather and climate is neglected.
- *Salinity*. Salinity is known to influence the distribution of benthos species. In this study the salinity is considered constant in the study area.
- *Biotic interactions*. There is predation, competition, and facilitation on a tidal flat. These processes affect the composition and distribution of benthos. In this study we focus on abiotic interactions rather than biotic interactions.
- *Primary production*. The primary production of benthic diatoms is affected by light, temperature, nutrient availability, wave action, current velocity, grazing by zooplankton, and salinity. The process of photosyntheses requires light, when the water is turbid the photosyntheses of benthic diatoms is dependent on emersion time. The gross benthic primary production is about 17% of the total gross primary production in the Western Scheldt. Benthic diatoms are a food source for deposit feeders and suspended benthic diatoms are a food source for suspension feeders.
- *Substrate*. The substrate composition as well as the substrate dynamics are important. Substrate composition is measured as siltcontent, median grain size, and organic matter content. Substrate dynamics is defined as the mobility of the elements (grains, aggregates) and the mobility of the surface. Composition and dynamics are influenced by hydrodynamics and the presence of benthos on the flat (bioturbation, stickiness). A lot of the unsolved correlation between the abundance of benthos and the abiotic processes is subscribed to substrate dynamics.
- *Hydrodynamics*. This can affect the establishment of larvae, rinsing out of animals, and supply of food. Bottom shear stress can be limiting as a stress factor or as a minimum

boundary rule for food supply. Sedimentation and resuspension of food particles is driven by the hydrodynamic conditions.

- *Inundation*. The abundance of benthos is influenced by the inundation time, which is dependent on water depth relative to NAP and the tidal range. Inundation time relates to food availability, predation pressure and a gradient in physical stress (temperature, salinity, oxygen).

2.2.3 Food in the vertical layer

It is assumed that bivalves, particularly dense populations, reduce the concentration of suspended food in the overlaying water column (Dame, 1996). The depletion of food from the boundary layer is dependent on the ratio between current speed (in vertical direction) and vertical mixing. Field observations of mussel beds of different sizes show higher mussel growth along the leading edges and reduced growth along the direction of flow and in the central portions of beds (Dame, 1996).

Smaal (1997) found that seston concentrations (inorganic matter, detritus, algae) in the Eastern Scheldt were higher at the bottom than at the surface. The ratio between bottom and surface concentrations was higher for suspended matter than for POC and chlorophyll. The *organic fraction* of the seston however was higher at the surface. These phenomena can be ascribed to (Smaal, 1997):

1. Resuspension of low quality inorganic sediment in combination with hydrodynamic sorting in the benthic boundary layer near the bottom (Muschenheim, 1987),
2. Food depletion near the bottom by the selective filtration activity of the suspension feeders (Muschenheim & Newell, 1992),
3. Filtration and selective ingestion of POC and chlorophyll by suspension feeders and subsequent resuspension of their biodeposits with a lower organic matter content (Prins et al., 1996),

or a combination of these phenomena.

Ad 1. Particles with different settling velocities, when exposed to the same flow, will be subject to hydrodynamic sorting. This means that particles with the highest density have a higher concentration near the bottom than particles with a lower density.

This results in the effect that particles with a higher organic matter content (which have lower densities) can be found with a maximum concentration several centimeters above the bottom (Muschenheim, 1987).

Resuspension and hydrodynamic sorting can explain the higher SPM concentrations near the bottom in the Eastern Scheldt, but not the existing difference between POC and chlorophyll, assuming that the hydrodynamic behaviour is similar (Smaal, 1997).

Ad 2. Food depletion is unlikely to occur in the Eastern Scheldt, because the chlorophyll concentrations near the bottom were higher than at the surface (Smaal, 1997).

Ad 3. Selective uptake of algae by suspension feeders leads to pseudofaeces with a relative low fraction of chlorophyll compared to the seston. Pseudofaeces have a very loose structure and a low settling velocity and are resuspended easily (Prins et al., 1996). The formation of biodeposits and their resuspension probably contributes to the observed effect (Smaal, 1997).

There are no dense suspension feeder beds on the Molenplaat, therefore depletion of food near the bottom is unlikely to occur. A vertical profile of suspended sediments in the Western Scheldt can be found, but this is caused by the hydrodynamical conditions (tidal velocities). At slack tide, current velocities are near zero, so the suspended solids will settle and concentrate near the bottom. In between this events the water of the Western Scheldt is well mixed. In this study food availability in horizontal direction (depth averaged) is considered.

2.2.4 Model parameters

Assuming that suspended solids form their main source of food, the flux of suspendend solids in the water column can be an explaining factor for the distribution of suspension feeders. From the combined hydrodynamic and water quality models one can derive the *cumulative advective flux*, this is a measure for the total flow of suspended particles over a tidal period. The cumulative advective flux is calculated as:
(flow * concentration * time) / area,
and thus expressed as g/m^2. We like to find out whether the spatial variance of the cumulative advective flux explains the spatial variance of the suspension feeders.

The *net sedimentation flux* declares the net transport of suspended solids to the bottom. It is to be expected that deposit feeders will live at places with a high deposition rate. The *gross sedimentation* and *gross resuspension* fluxes can act as limiting factors.

Substrate dynamics is hard to express. In the field high dynamic parts are recognised by the megaripples, steep slopes and sand banks and low dynamic parts by the flat surface. Wave energy, maximum current velocities, shear stresses and tidal range can be used as parameters to describe the substrate dynamics. It can be expected that at places with high substrate dynamics the gross resuspension and sedimentation rates are high. In the water quality model the *product of the gross resuspension flux and the gross sedimentation flux* is calculated to express substrate dynamics. In addition, the *maximum bottom shear stress* over a tidal period gives an indication for substrate dynamics, as well as substrate composition and stressfull hydrodynamic conditions, like scouring.

Inundation time is a well known parameter to explain the distribution of macrozoobenthos. Inundation time follows directly from the bathymetry and tidal ranges in the study area.

2.3 Biological survey, available data

From the 1995 survey the following data was available for comparison with the modelparameters (section 2.2.5):

- distribution of grain sizes (mean, median, sorting, skewness, kurtosis in μm and phi-units)
- percentage sediment composition: %medium sand (250-500μm), %fine sand (125-250μm), %very fine sand (63-125μm) and %silt (<63μm).
- surface deposit feeders (N/m^2 and g $AFDW/m^2$)
- deposit feeders (N/m^2 and g $AFDW/m^2$)
- filter feeders (N/m^2 and g $AFDW/m^2$)
- omnivores (N/m^2 and g $AFDW/m^2$)
- predators (N/m^2 and g $AFDW/m^2$)
- bottom chlorophyll concentrations (μg/g ds)

These data were gathered in March, June, September and December. The density and biomass distribution over the tidal flat shows a seasonality caused mainly by biological factors. In this study the data for June were used, since the water movement is computed using boundary conditions (water levels/velocity) representing an average tide in june 1995.

3 Transport modelling: small scale

3.1 Model verification hydrodynamics

As described in section 2.1, the hydrodynamic models were verified for their modelperformance at several locations on the Molenplaat, applying an updated bottom schematisation (run P02).
Figures 3.1.A and 3.1.B show the computed depth averaged tidal velocity and computed water levels versus measured velocity and water levels. For comparison reasons the former (1995) model performance applying the old bottom schematisation (1988/1994) are given in Figures 3.1.C and 3.1.D.
It is concluded that no significant differences exist between the 'old' and 'new' models in the Molenplaat area, so a recalibration of the Molenplaat Model is not necessary. For the Transport simulations described in section 3.2 the new bathymetry has been applied.

3.2 Model calibration siltcontent

3.2.1 Introduction

Assuming that the food availability of suspension feeders and deposit feeders is mainly determined by the concentration of suspended solids and deposited solids, it is important that the transport model is capable of properly predicting the suspended solid (silt) transport, and its deposition and resuspension pattern.
The Molenplaat model is a depth averaged two dimensional model, which means that in the model the suspended solids are well mixed over the vertical. For the transport computations the model requires

1. Suspended sediment conditions at the open boundaries of the model
2. Settling velocity of suspended sediment concentrations
3. Critical shear stress for erosion
4. Critical shear stress for deposition
5. Dispersion coëfficiënt
6. Numerical parameters (time step, simulation period, ..)

In the computations resuspension of deposited sediment can only occur if indeed sediment is present on the bed. This means that, if we start the computations with a 'clean' bottom, resuspension will occur not earlier than when sediment is deposited. So the model needs a 'spin-up' time in which it can create a proper initial condition. This is done by defining a cyclic tide which is repeated several times to obtain an 'equilibrium' between resuspension and deposition. In our computations, at the end of the 4th tide the obtained sediment distribution defines the initial condition for the eventual computation.
It is noted that the obtained 'equilibrium' after 4 tides is not really an equilibrium. At some locations in the area there exists net deposition during a tide. Repeating the same tide again and again will cause an increase of the sediment concentrations at the bed. In nature this will eventually lead to a change in the bathymetry which effects the bed shear stress. So in

nature finally a (dynamic) equilibrum developes. This cannot be included in our transport model, since we do not adjust the bathymetry after the computation of several tides.
So the initial condition we compute with the procedure described above does not represent the real observed concentrations at the bottom, but merely gives an indication of the relative distribution of deposited sediments.

In the model no emissions of suspended sediments occur. The sedimentation and erosion processes are modelled according to Partheniades-Krone (Partheniades, 1962; Krone, 1962; Delft Hydraulics' Delwaq Manual; 1995). Both advection and diffusion/dispersion of suspended solids are included. It is furthermore possible to incorporate the effect of wind and waves on the bed shear stress.

3.2.2 Model Input

The required values for the model input parameters described in the preceding section were chosen from literature as follows:

Suspended sediment boundary conditions. These were chosen varying between 23 mg-ds/l eastern boundary and 37 mg-ds/l western boundary, representing suspended silt concentrations of silt with a median grain size smaller than 63 μm. The concentrations were obtained from the WAKWAL-database. The long-term mean for June between 1982 and 1993 was used, for the locations WS100, Hansweert and WS130, Terneuzen.

The settling velocity of suspended sediment is related to the median grain size. From literature it is known that a settling velocity of 8,64 m/day (=0.1 mm/s) corresponds to grain sizes smaller than 63 μm. So this value was kept constant in all simulation runs.

The value for the critical shear stress for deposition depends not only on the median grain size but also on the suspended sediment concentration, the organic grade of the silt, and the shape of the grain. From literature a value 0.1 Pa was chosen, assuming a 'round shape', and no flocculation.

The value for the critical shear stress for erosion was varied in two runs. In the first run a critical shear stress of 1 Pa was chosen, in accordance with the value used in 1995. The results however showed that possibly a smaller value was allowed. This is also substantiated by experiments carried out in 1996 with bed material from several locations of the Molenplaat (database Ecoflat). The 'measured' critical shear velocity amounts 0.2-0.3 m/s which corresponds more or less with a critical shear stress for erosion of 0.5 Pa.

The dispersion coëfficiënt was taken 10 m^2/s and was kept unchanged, since there was no data available to calibrate on this parameter.

3.2.3 Model simulations

Introduction

The simulation results of the silttransport can actually only be influenced by variation of the settling velocity, the critical shear stresses for deposition and erosion and the dispersion coefficient. Remaining parameters which will however also effect the silttransport are the modelled bed roughness and the local depth schematisation. Changing these parameters will also change the water movement, whereas in this study the hydrodynamic model is considered calibrated. So these parameters were as much as possible kept unchanged during the transport simulations.

The calibration runs used an aggregated grid (4 cells united to 1), which decreased the computational time and the size of the output files considerably. The accuracy of the computations with an aggregated grid is less, but for calibration purposes it gives sufficient information while varying several parameters in several runs. The 'final' calibration run was repeated with the original fine grid to obtain more detailed results. An overview of all runs is given below:

Run Id	**description**
P03b	Run to verify the transport results of 1995
P03c	Critical shear stress for erosion has decreased with respect to run P03b
P06b	Roughness coefficient has changed locally with respect to P03c
P06d	Critical shear stress for erosion has further decreased with respect to run P06b
P07d	A wind of 5 m/s was included in this run which is further identical to P06b

Run P03b

This run was performed to verifiy the first silt transport results obtained in the study of 1995. It appeared that there were differences in the computed maximum shear stresses computed in 1995 and those computed with run P03b. This is due to an incorrect transformation of the computed water volumes from the flow model to the silt transport model applied in 1995. However, although the computed bed shear stresses showed differences with the same run in 1995, the computed net sedimentation pattern appeared to be the same: large amounts of net sedimentation (cumulative, after 1 tide) along the northern, eastern, southern and western boundary of the Molenplaat model. This pattern contradicts our expectations and observations, since at the central part of the Molenplaat the velocities are lowest and most silt is observed.

The (computed) net sedimentation is determined by the difference between the cumulative gross sedimentation and the cumulative gross resuspension. Given the computational results, it was concluded that the cumulative gross resuspension in these areas is too small. Therefore it was decided to decrease the critical shear stress for resuspension in the next transport run (P03c) to 0.5 Pa.

Run P03c

The results of run P03c show an improvement with respect to the net silt deposition pattern, when compared to the results of run P03b, although especially the eastern part is still characterised by a large amount of deposited silt. This can be seen in Figure 3.2A which shows the net cumulative sedimentation for runs P03b and P03c.

As explained in the report of 1995, the roughness parameter in the central part and eastern part of the Molenplaat was taken equal to $n = 0.013$, assuming that dunes and ribs are not present in this area, and assuming a median grain size of 290 µm. However, sediment data show that the eastern part of the Molenplaat is characterised by larger grain sizes, so a larger roughness parameter in this area is allowed. Therefore a new run, P06b, was defined where a larger roughness coefficient of n = 0.033 was applied in the eastern part of the Molenplaat. Since in this area no water level or velocity measurements were available, the effect on the calibration results of the hydrodynamics in this area could not be assessed. A sensitivy run showed that the effects on the hydrodynamics in the available observation stations were negligible.

Run P06b

At the eastern part of the Molenplaat the results of run P06b show an improvement with respect to the net silt deposition pattern, when compared to the results of run P03c and the observations, indicating that the schematised bottom roughness largely influences the simulation results.

Figures 3.3 and 3.7 show that there exists a correlation between the maximum shear stress < 0.5 Pa and the inner area with a siltpercentage between 30% and 60%. However, this correlation is not valid at the north-western boundary. Here the computed maximum shear stress amounts between 0.3 and 0.5 as well, but no significant amount of silt is found here. The small computed maximum shear stresses are probably due to the small schematised bottom roughness (n = 0.013) in this area. As is shown in Figure 3.2.B in this area exactly an artificial boundary of schematised bottom roughness from n = 0.045 to n = 0.013 is present.

Figures 3.4 and 3.7 show that there exists more or less a correlation between the maximum shear stress < 0.5 Pa and the central area where 10-20% of very fine sand is observed.

Figures 3.5, 3.6 and 3.7 show that there exists a correlation between the maximum shear stress > 1 Pa and the eastern area where 30-50% of fine/medium sand is observed. This correlation does not exist in the western area where large dunes are observed and which is more characterised by the presence of fine sand only.

The computed gross cumulative sedimentation flux (see fig 3.8B) appears to correlate with the schematised depth but also with the maximum shear stress. This is to be expected, since at the areas which have the shortest inundation times, sedimentation can only occur during a short period, and most silt will be deposited at lower shear stresses.

The small computed gross cumulative resuspension flux (see fig 3.8A) corresponds only in the central area with the computed maximum shear stress < 0.5 Pa. This is due to the fact that in the areas with a large maximum shear stress, where we expect the resuspension to be large as well, the amount of deposited silt is small, and as such also is the gross resuspension.

The net result of the resuspension and sedimentation is named the ‘net sedimentation flux’. Figure 3.8C shows the net cumulative sedimentation flux after 1 tide. It appears that most sediment is deposited in the northern and southern part of the central Molenplaat. This is also observed when we do not look to the net sedimentation flux, but to the absolute concentration of deposited silt (after 1 tide). At the same time silt is deposited at the western side of the Molenplaat. As explained with the description of the maximum shear stress, the latter is probably explained by the simulated bottom roughness.
The fact that most silt is deposited at the northern and southern part is explained by the pattern of computed max. shear stress. The area of deposited silt is almost included in the area with max. shear stress < 0.5 Pa, except for several grid cells in the northern part and in the southern part. It appears that in these areas the gross sedimentation flux is so large, that

it cannot all be resuspended during 1 tide. This is probably due to, again, the schematised bottom roughness in combination with the depth schematisation. The depth values are not measured on the scale of the gridsizes, so local inconsistencies with real depths may be present. This is not observed in the hydrodynamic calibration results since only a limited number of flow velocity data was available.

Run P06d

This run was performed as a sensitivity run, to investigate the effect of further decreasing the critical shear stress for erosion from 0.5 Pa to 0.3 Pa. From the results (see Figure 3.9) it is observed that in general the net amount of deposited silt is decreased with a factor 4 - 5, and even in the western part with a factor 20 (in this area in fact the net amount of silt disappears). However, the sedimentation pattern on the Molenplaat in general remains the same as in the other simulation runs: in the northern and southern part more net silt is deposited than on the central part where the largest silt fraction is observed.

Conclusions/Discussion

Regarding the results of the calibration runs the following conclusions can be drawn:

The computed maximum shear stress corresponds very well with the observed silt percentage in the area of the Molenplaat.

The computed net sedimentation flux is difficult to compare with the silt percentage, since it represents a silt concentration instead of a percentage. For example: the observed silt percentage is largests in the central area of the Molenplaat, whereas the computed sedimentation flux (and the absolute deposited silt concentration) is largest for all runs in the northern and western part of the central part. It is to be expected that in the central part of the Molenplaat, which has the shortest inundation time and the smallest maximum shear stresses hardly any other sediment fractions will be deposited except silt fractions. In the northern and western part it is to be expected that also larger sediment fractions will be deposited. Simulations of several sediment fractions prescribing reliable concentrations and corresponding settling velocities and critical shear stresses would be necessary to be able to translate the net silt simulation results to the observed silt percentages. Another way of comparing results and observations would be the gathering of silt sedimentation fluxes at several locations on the Molenplaat .

The model results are very sensitive to the schematised bottom roughness. The bottom roughness is mainly responsible for the resuspension capability of the flow. As such, a detailed analyses of the grain sizes, gullies and dunes on the Molenplaat is necessary to refine the schematised bottom roughness.

In the model the applied critical shear stress for resuspension and erosion was chosen, based on the median grain sizes of the modelled silt content. However, also the biology may play an important role in the resuspension process. Some areas on the Molenplaat are characterised by net siltation. During a period of time, algae may grow / develop on the silt layer, resulting in a silt layer where the individual parts stick together. This will especially occur in summer times, whereas the biological growth differs geographically depending on physical parameters as inundation time, temperature etc.
This means that the model should allow for a critical shear stress for erosion which is not only coupled to the simulated sediment fraction, but also to the geographical position, and

the fact whether the sediment fraction is in suspension or deposited during a specific period. This requires a sophisticated model. In the present transport model this can only be simulated by allowing two sediment fractions with the same settling velocities, the same critical shear stress for deposition but a different critical shear stress for erosion: analyses of the results of the two fractions must then be restricted to the areas where their respective critical shear stresses for erosion 'holds'.

In the calibration runs only the shear stress generated by the tide is responsible for deposition and erosion of silt. However, in reality shear stresses generated by wind waves play an important role in the process as well, especially in shallow areas. In the next section an analyses is made of the magnitude of the shear stress generated by wind waves and the tide.

It is possible to define many simulation runs, varying the critical shear stresses for deposition and erosion, the settling velocity, the dispersion coefficient, the schematised bed roughness and the bathymetry. However, from the data available, it is not possible to obtain better values for these parameters as used at this moment, except possibly the schematisation of the bottom roughness. This means that carrying out more calibration runs would be 'wild guesses' not providing any more information than we have now.
Given the above four calibration runs it was concluded that the results of run P06b were closest to the observations. From the results (especially regarding the correlation between the maximum shear stresses and the measured/observed silt pattern on the Molenplaat) we can conclude that the model is capable of predicting the locations where silt is deposited. However, from these results we cannot immediately conclude that the transport model is capable of properly predicting the suspended and deposited silt concentrations.

3.3 2D Application runs Molenplaat

3.3.1 Average Tide: No Wind: parameter analysis versus observations

Introduction to the figures

The figures present both field measurements and model results. The field measurements can be recognised by the line "June '95", which is the date of sampling and this is written down in the corner of the figure. The modelled results are the results from run P06b, which is also written down in the corner where appropriate.

Sediment composition

The measurements of sediment composition in June 1995 are presented in figures 3.3 through 3.6. All figures are created from the measurements at the sample locations using linear triangular interpolation to obtain a two-dimensional surface plot.
Figure 3.3 shows that the silt content can reach high levels, over 70%, in the mid section of the Molenplaat. At the western side of the Molenplaat the sediment almost completely consists of fine sand (Figure 3.5). Medium sand can be found in the eastern part, the southern border and a strip along the western side (Figure 3.6). Very fine sand can be found in relatively low percentages mainly in the mid section (Figure 3.4).

The maximum bed shear stress over a tidal period is presented in Figure 3.7. This parameter correlates very well with the sediment composition. The spatial distribution of medium sand corresponds with the spatial distribution of maximum bed shear stress, except for the most south-western part of the flat. The relation between the maximum bed shear stress and the percentage silt is presented in Figure 3.10. In this figure the silt percentages in each sampling grid cell are compared to the maximum shear stress in the same grid cell. It follows that high silt percentages occur at low bed shear stress and low silt percentages coincide with high bed shear stress (see also section 3.2.3).

Suspension feeders

The biomass and density of the functional group 'suspension feeders' is presented in Figures 3.11 and 3.12. The biomass is expressed as g AFDW/m^2, the density is expressed as numbers/m^2. The density distribution correlates well with the distribution of muddy parts. This is not in accordance with the hypothesis that suspension feeders favour those parts with higher current velocities and where deposition and erosion are low or absent (Wildish and Peer, 1983). The distribution of biomass shows a slightly different pattern, this distribution is mainly affected by the density of the cockle, which has a high bodyweight.

The spatial variance of suspension feeders is affected by the flow of food particles. According to Dame (1996) dense beds of suspension feeders are able to reduce the concentration of suspended food in the overlying water column. The highest densities of suspension feeders therefore are to be expected at places where the advective flow of food particles is highest (Dame, 1996). Figure 3.13 presents the cumulative advective flux, over one tidal period, of suspended solids, shown in the same grid cells as the presentation of density. The highest fluxes are found at the boundaries of the tidal flat near the channels, where the current velocities reach the highest values. These high fluxes do not correlate with high densities of suspension feeders, in contrary, it almost seems that there is an inverse correlation with density. It may well be that there exists an optimal advective flux, where the overlying water column is refreshed, and the scour of high current velocities is not limiting. Figures 3.14 and 3.15 present the relation between cumulative advective flux and suspension feeder density and biomass for each sampling location (see Figure 3.16). This relation supports the hypothesis of an optimum.
Lowest advective fluxes occur at places with a low inundation time, these parts are devoid of food for a relative long period. Inundation time itself therefore is a parameter that describes the spatial distribution of suspension feeders over a tidal flat. A common assumption is that suspension feeders do not live at places with an inundation time lower than 50%. Figure 3.17 gives the inundation time over the Molenplaat, the density of suspension feeders in the highest parts (compare with Figure 3.12) is indeed low. The inundation percentage against the density of suspension feeders for each sampling location is presented in Figure 3.18. Apparently the sampling points are located either in the subtidal area, or in the intertidal area with an inundation percentage between 36% and 56%. There's no evidence for limitation by inundation.

The maximum bed shear stress (Figure 3.7) can be an indicator for food supply and stress. Figure 3.19 presents the relation between this parameter and the density of suspension feeders at the sampling locations. This relation indicates that suspension feeders choose to live at places with quiet conditions. The highest densities occur at places with a maximum bed shear stress of about 0.5 Pa. These are also the places with a high silt content.

In this study, substrate dynamics is expressed as the product of gross sedimentation flux and gross resuspension flux. At places with high values for this parameter we assume that there are significant erosion-deposition cycles which can cause stressful conditions. Figure 3.20 presents this parameter for the Molenplaat and its surroundings. Highest erosion-deposition cycles can be found at the edges of the tidal flats. Figure 3.21 gives the substrate dynamics for the Molenplaat. The pattern of substrate dynamics is not similar to that of the maximum bed shear stress, this has to do with the amount of sediment available to deposit and resuspense. Figure 3.22 presents the relation between substrate dynamics and suspension feeder density for each sampling point. There is no clear relation, but there is evidence to believe that suspension feeders avoid high deposition-erosion places.

Surface deposit feeders

The biomass and density of the functional group 'surface deposit feeders' is presented in figures 3.23 and 3.24. This group feeds by eating deposited material from the surface of the tidal flat. Its main species is *Macoma balthica*. The distribution is limited to net deposition areas, i.e. the muddier parts. The locations of the sample points visualised within the 'active' grid points for surface deposit feeders are shown in Figure 3.25.

The measurements of siltcontent and density of surface deposit feeders in all samples are drawn against each other in Figure 3.26. There is a clear trend of higher densities at higher siltpercentages.

The maximum bed shear stress (Figure 3.7) can be indicative for stressful conditions. It's expected that the densities of surface deposit feeders will reach highest values at low shear stress. Figure 3.27 presents the relation between maximum shear stress and density of surface deposit feeders at the sampling locations. There is a similar relation between shear stress and the abundance of surface deposit feeders as for suspension feeders, but the highest densities of surface deposit feeders seem to occur at a slightly less shear stress of about 0.4 Pa.

Deposit feeders

The functional group 'deposit feeders' is a very heterogeneous one. The biomass and density of deposit feeders is presented in figures 3.28 and 3.29. This group contains a diversity of species, like *Heteromastus* and *Arenicola*. 'Deposit feeders' are not limited to net deposition areas, but the density distribution correlates well with silt content.

The locations of the sample points visualised within the 'active' grid points for deposit feeders are shown in Figure 3.30. Maximum bed shear stress against density shows that this group too doesn't like high shear stresses (Figure 3.31). Highest densities are found at a maximum shear stress of about 0.4 Pa, where the silt content is high.

Microphytobenthos

In the Western Scheldt the average chlorophyll concentration *in the water column* in June, apart from algal blooms, from 1982 to 1993 is 19 µg/l (WAKWAL-database, location WS100, Hansweert). The chlorophyll content of the top 1.0 centimeter *of the bed* in June, averaged over all sampling locations of the Molenplaat, is 7.8 µg/g dry sediment. This converts to about 0.20 g/m^2. When it is assumed that all off the microphytobenthos is resuspended in a water column of 5.0 meter depth, this leads to a chlorophyll concentration of about 40 µg/l. This can be compared to the present concentration of 19 µg/l. When taken into account that not all phytobenthos will resuspend at once, but there is primary production of

phytobenthos, the chlorophyll present might well be phytoplankton as well as resuspended phytobenthos. Microphytobenthos production therefore can act as an important food-source for both suspension feeders as deposit feeders.
The spatial distribution of microphytobenthos (in µg/g dry sediment) is shown in Figure 3.32.
The maximum bed shear stress against the chlorophyll-a content doesn't show a very clear relation (Figure 3.33). However, most datapoints are found at a shear stress of 0.5 Pa and a maximum shear stress of 2.2 Pa seems to be limiting for densities over 10 µg/g.
A reason for this can be that a relative thick mat of microphytobenthos is harder to erode than a sparse distribution of phytobenthos. Furthermore the type of microphytobenthos can play a role. The resuspension of benthic diatoms in the *Eastern* Scheldt for example was of minor importance because epipsammic diatoms dominate over epipelic diatoms. Epipsammic diatoms resuspend less easily (Smaal, 1997). It is not known precisely what benthic diatom species live on the Molenplaat at the moment.

Conclusions and Discussions

All benthos functional groups seem to prefer silty areas with low shear stresses (figures 3.19, 3.27 and 3.31). This is to be expected for (surface) deposit feeders. Silt content and maximum bed shear stress are correlated with each other (Figure 3.10).
The cumulative advective flux against the biomass of suspension feeders shows an optimum (Figure 3.15). The left side of this optimum shows the food-limitation by advective flow, and the right side of this optimum shows the stress caused by high current velocities.
In the graphs for maximum bed shear stress against density of the benthos functional groups there's one outlier at about 1.8 Pa. This relatively high value for shear stress indicates a low silt content in the field, but this is not in accordance with the field measurements. According to the bathymetry the depth at this location is 1.93 meters. It is questionable whether this depth is correct.

This study focussed on a limited set of parameters that are however considered the most important hydrodynamic and sedimentary aspects relevant to macrobenthos. These include:

- Depth of water (inundation, exposure)
- Composition of the sediment/bed roughness
- Stability of the habitat (shifting or stable for burrow maintenance, maximum current speeds)
- Food supply and availability (deposition/advection)

The biomass and distribution of macrobenthos on a tidal flat is affected by several other factors, such as:

- Space (density of colonisation, competition)
- Vulnerability to predation
- Larval dispersal and settling (may depend on tidal current patterns)
- Life history stages (e.g. migration/recruitment, seasonally)
- Antecedent conditions (previous winters)
- Extremes that create zonal limits (light limitation, floods, temp, salinity)
- External actions e.g. dredging, water quality effects (DO, toxic substances)

These biological and temporal processes are not explicitly taken into account in this study and may therefore blur the results.

3.3.2 Average Tide: effect of wind and waves

Introduction

The magnitude of the bottom shear stress causes the suspended silt to deposit or the deposited silt to resuspend. The bottom shear stress can in general be divided into two parts: a part originating from the tidal flow, and a part originating from the orbital flow caused by wind waves.
In our transport model the shear stress caused by the tidal flow is copied from the hydrodynamic simulations. The shear stress caused by the wind waves is computed following the formulations for the wave parameters of (Groen & Dorresteijn, 1976; Holthuijsen, 1980) and for the friction factor according to Bijker.
Very strong winds blowing over large areas will genate an upset or downset of the water level causing the tidal flow to decrease or increase in the direction of respectively increasing or decreasing water level. For smaller wind speeds this effect is negligible. In the present analyses the magnitude of the shear stresses caused by the wind is compared analytically to the shear stresses caused by the tide only. So the latter mentioned effect of the wind on the tidal velocities has not been taken into account.

The bathymetry of the Molenplaat varies from NAP+1.3 m at the shallowest part to ca.NAP-1.0 m at most boundaries and to ca NAP-5.0 m at the southern boundary near the gully (see Figure 3.2.C).
The maximum shear stresses caused by the tide occurs when the velocities are highest, i.e. when the water depth is about equal to NAP (equals ca. MSL), or, when the bed is located above NAP, as soon as that specific location is flooded. The maximum shear stress caused by the tidal flow (as computed by run P06b) varies from about 0.2 Pa to 3.0 Pa.

The shear stress caused by the wind waves is independent of the tidal flow and is a function of depth, bottom roughness, wind speed, gravity, air density and fetch. The latter is defined as the distance along which the wind can develop wind waves.
In the Molenplaat model we distinguish 4 different areas of bed roughness: n = 0.013 (Ks = 0.00087 m), n = 0.022 (Ks = 0.034 m), n = 0.033 (Ks = 0.24 m) and n = 0.045 (Ks = 0.706 m).

Comparing Shear stresses in the Molenplaat area: wind 5 m/s

Figure 3.34A shows the shear stress caused by wind waves as a function of waterdepth, when a wind of 5 m/s is blowing. To create this graph the formulas referred to in the introduction were used, varying the bottom roughness as schematised in our transport model, and applying a wind fetch of 10 km. The latter was chosen assuming a south western wind, which is the most common in this area.
It is concluded that at the lowest bed roughness (the central part of the Molenplaat), the shear stress induced by the wind waves does not exceed 0.2 Pa. The waterdepth where this maximum is reached amounts ca. 0.5 m. The maximum shear stress induced by the tide varies in this area from ca. 0.3 Pa to ca. 0.6 Pa. If this maximum is reached at a water depth equal to 0.5 m, the total maximum shear stress becomes 0.2 Pa higher in this area. This means that resuspension of silt will occur more frequently since the critical shear stress for erosion is taken 0.5 Pa in the model.
At the turn of the tide the tidal velocities are lowest, and also are the shear stresses induced by the tide. These are the periods that silt is deposited. However, the shear stress induced by

wind waves can hinder this process: If the water depth is in between 0.5 m and 1.5 m (and this occurs almost everywhere on the Molenplaat during an 'average tide') the wind waves temporarily prevent silt to be deposited, since the critical shear stress for deposition is 0.1 Pa.

In areas with a higher bed roughness the wind waves have stronger effects on the resuspension/siltation pattern. Figure 3.34A shows that at depths from 0 - 2 m the wind waves cause a shear stress from 0.2 Pa - 1.8 Pa, which will effect the resuspension process during a large period of the tide. The deposition process is even longer effected during water depths between 0 and 2.5 m.

Run P07d

Run P06b has been repeated (run p07b) applying a south western wind of 5 m/s to investigate the effect of the wind not only on the maximum shear stress but also on the sedimentation pattern.
It appears that the maximum shear stress in the eastern part is twice as large as when no wind is included, and also in the (south) western part of the Molenplaat the maximum shear stress is larger. These are just the areas with an increased bed roughness.
The gross sedimentation pattern is also different from the pattern observed when no wind is applied. In the southern part the gross sedimentation is less than computed with run P06b. In the northern and western part the gross sedimentation is much less, and in the remaining area it is almost zero. As a result the gross resuspension is also much less: it is still encountered in the northern and southern part. The net sedimentation is almost zero on the entire Molenplaat.

Comparing Shear stresses in the Molenplaat area: wind 10 m/s

Figure 3.34B shows the shear stress caused by wind waves as a function of waterdepth, when a south-western wind of 10 m/s is blowing.

It is concluded that at the lowest bed roughness (the central part of the Molenplaat), the shear stress induced by the wind waves does not exceed 0.4 Pa. The waterdepth where this maximum is reached amounts ca. 1.0 m. Regarding the critical shear stress for resuspension and the maximum shear stresses caused by the tide, the resuspension process is effected at wind shear stresses larger than 0.2 Pa, which occurs at depth between 0 and 2.5 m.

Regarding the critical shear stress for deposition, if the water depth is in between 0 m and 3.5 m the wind waves temporarily prevent silt to be deposited.

In areas with a higher bed roughness, Figure 3.34B shows that during the entire tidal range occurring on the Molenplaat the wind waves cause shear stresses larger than 0.2 Pa, to a maximum of more than 5 Pa at a depth of ca 1 m. These values are of the same order of magnitude as the shear stresses induced by the tide.

Comparing Shear stresses in the Molenplaat area: wind 15 m/s

Figure 3.34C shows the shear stress caused by wind waves as a function of waterdepth, when a south-western wind of 15 m/s is blowing.

It is concluded that during the entire tidal period these strong winds have a large effect on the erosion/sedimentation process. At low bed roughness the shear stress induced by the wind is still of the same order of magnitude as the shear stress induced by the tide. However, at larger bed roughness, the shear stress induced by the wind largely exceeds the shear stress induced by the tide. So here the silt deposition/erosion process in dominated by the wind waves.

Conclusions

Wind waves can have a large effect on the sedimentation/erosion process on a shallow tidal flat with mean water depths between 0 and 5 m. In our analyses we have only looked at a constant wind speed, blowing during a constant time. In reality this process will be much more complicated due to wind coming from varying directions at different speed.
The present study shows that severe winds can temporarily remove all silt from the tidal flat or drive the sedimenattion/resuspension process and hence determine the net siltation pattern. For weak winds the tide remains the dominating factor.
In areas with a bed consisting of larger grain sizes and/or sand dunes and ribs, the effect of the wind is more pronounced than on a flat and smooth bed.

3.3.3 Average Tide: No Wind: particle tracks

Introduction

The water movement used for transport runs P06b and P06d was simulated again with run E01. In this run some particles (here we think of chlorophyll) were released in the gullies and on several (silty) locations on the Molenplaat. The suspended particles are transported by the water and we are able to follow their tracks during rising and falling tide. The simulations give insight in the transport process and we might conclude whether chlorophyll particles present on the Molenplaat originate from the gullies or originate from the Molenplaat itself by primary production and redistribution during the tide.
It is noted that in this simulation sedimentation and/or deposition of the particles does not occur. It is assumed that the settling velocity of these particles is very low and that the critical shear stress for erosion is much smaller than 0.5 Pa. For chlorophyll particles this is a rather valid assumption.The particles are transported as soon as the flow velocity is larger than 0 m/s. For the particles released on the Molenplaat, the most interesting tidal period to look at is from low water to high water. At low water it is assumed that the particles are present on the Molenplaat and that they resuspend as soon as the water floods the tidal flat. Then, when high water is reached, the velocities are lowest and the particles:

1. might settle down again, or
2. remain in suspension and are transported by the falling tide to another location.

For particles released in the south-western part of the Molenplaat model, the rising tide is the most interesting period if we want to see whether the particles are able to reach and settle on the Molenplaat.
For the particles released in the eastern part of the model the falling tide is the most interesting period.

Simulations

Figure 3.35A shows particles released at the central silty part of the Molenplaat during low water. The first 3 hours this area remains dry. Then the particles are resuspended and transported in northern direction. Here they settle down, or, if they remain in suspension, are transported with the falling tide into the gully as shown in figure 3.35B.

Figure 3.36A shows particles released at the eastern part of the Molenplaat. Some locations remain dry during the first three hours. Particles resuspended at these locations do not leave the Molenplaat during rising tide. Particles released at the location which is already wet during low water are transported into the gully. Figure 3.36B shows that during falling tide all particles are transported into south western direction off the Molenplaat. The first hour with an average speed of ca 30 cm/s, the second hour with an average speed of ca 75 cm/s and the third hour with an average speed of 90 cm/s.

In figure 3.37A tracks of particles released at the south western part of the Molenplaat are plotted. Some locations remain dry during a few hours, but as soon as the particles are resuspended they are transported in north eastern direction. Here they might settle down or they are transported into the gully as shown in figures 3.35Band 3.36B.

Figure 3.38A shows that particles released in the gully are only transported in the gully and do not arrive on the Molenplaat. Also particles released at the south western side near the Molenplaat are transported in the gullies and do not cross the tidal flat (figure 3.39A). The same holds for particles released during high water at the eastern side of the Molenplaat (fig 3.40A).

Conclusions

From the simulation results described above we can conclude that (chlorophyll) particles transported in the gullies in general do not arrive on the Molenplaat and will not settle down here during turning of the tide. A redistribution of particles resuspended on the Molenplaat itself is possible, especially when resuspension occurs in the south western part during rising tide. This means that chlorophyll present on the bed of the Molenplaat most likely originates from local primary production.

4 Dicussion and suggestions for further research

The hypothesis that states that resuspension feeders are abundant at relatively high current velocities or bottom shear stress is not correct, according to the results of this study. It was found that suspension feeders are abundant at low shear stresses and a subsequently high silt content. A reason for this can be the species of suspension feeders that is found at the Molenplaat. The group of suspension feeders mainly exists of cockles, which have a different way of feeding than for example mussels. Cockles have their siphon closer to the bottom and are therefore maybe more dependent on locally resuspended food-particles, while mussels reach several centimeters above the bottom. Further research remains to be done into the relationship between high silt content and high densities of suspension feeders, and the type of suspension feeders.

The measurements on the Molenplaat have been carried out in different seasons. This study only considered June, because the water quality model is calibrated on that month. Of course there are strong seasonal differences between densities and biomasses, not only as an effect of biological processes such as growth, spawning, competition and mortality, but also as an effect of physical processes and events, such as autumn-storms and settlement of larvae. Further research remains to be done into the magnitude and relative importance of the biological and physical processes.

The relationship between bottom shear stress and silt content on the Molenplaat holds well, but it appeared that this is not the case on other tidal flats in the Western Scheldt. Several reasons for this can be that:
1. The modelled bathymetry of the tidal flats is not correct
2. Wind-stress is not included in the computation of shear stress
3. The grid size of the applied SCALDIS model (60x60 meters) is too large

A more detailed model with an updated bathymetry and incorporation of wind generated waves will probably give a better correlation. To validate the results of this study and to scale up the applicability to an estuary scale it is crucial to apply this improved model.

5 Literature

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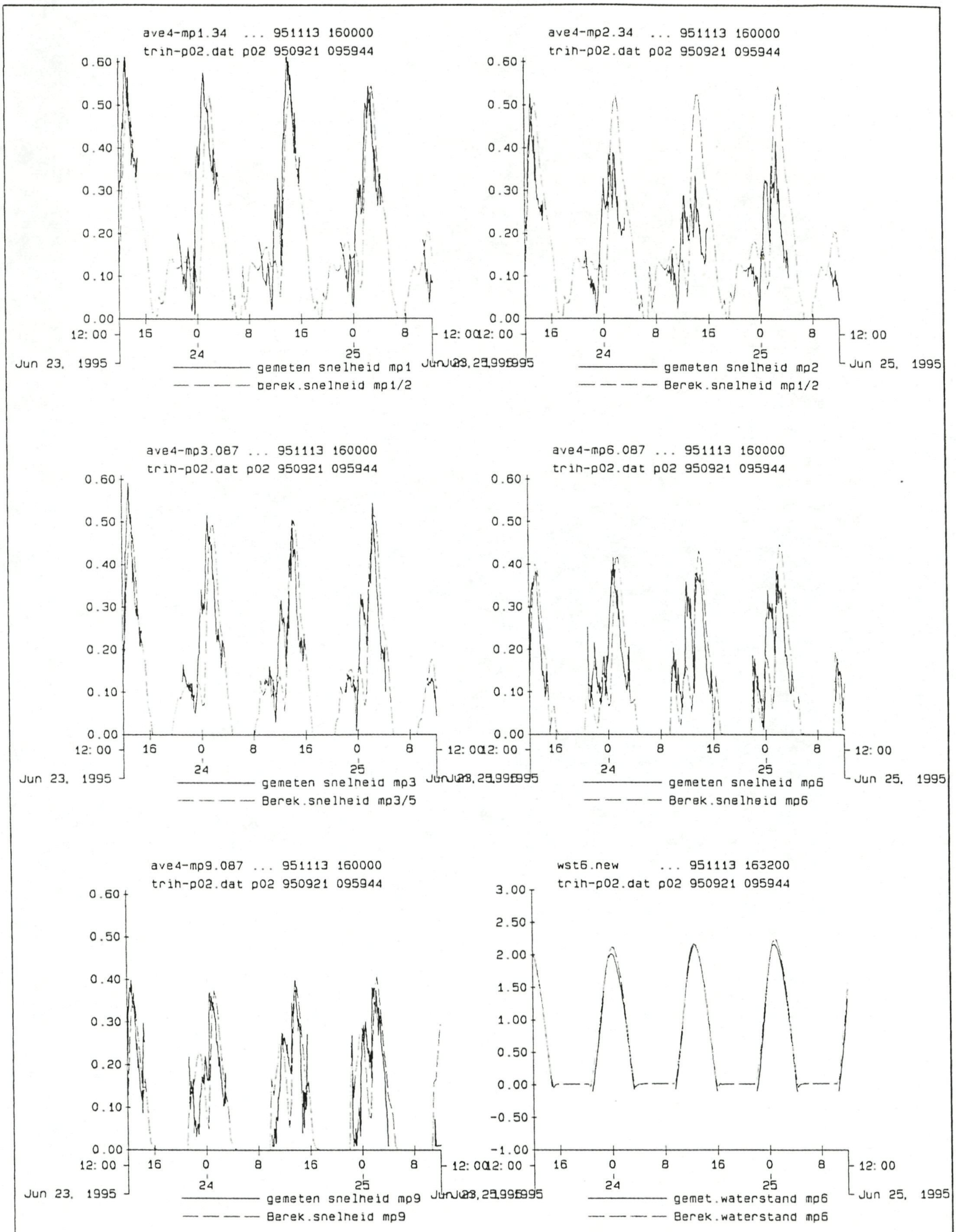
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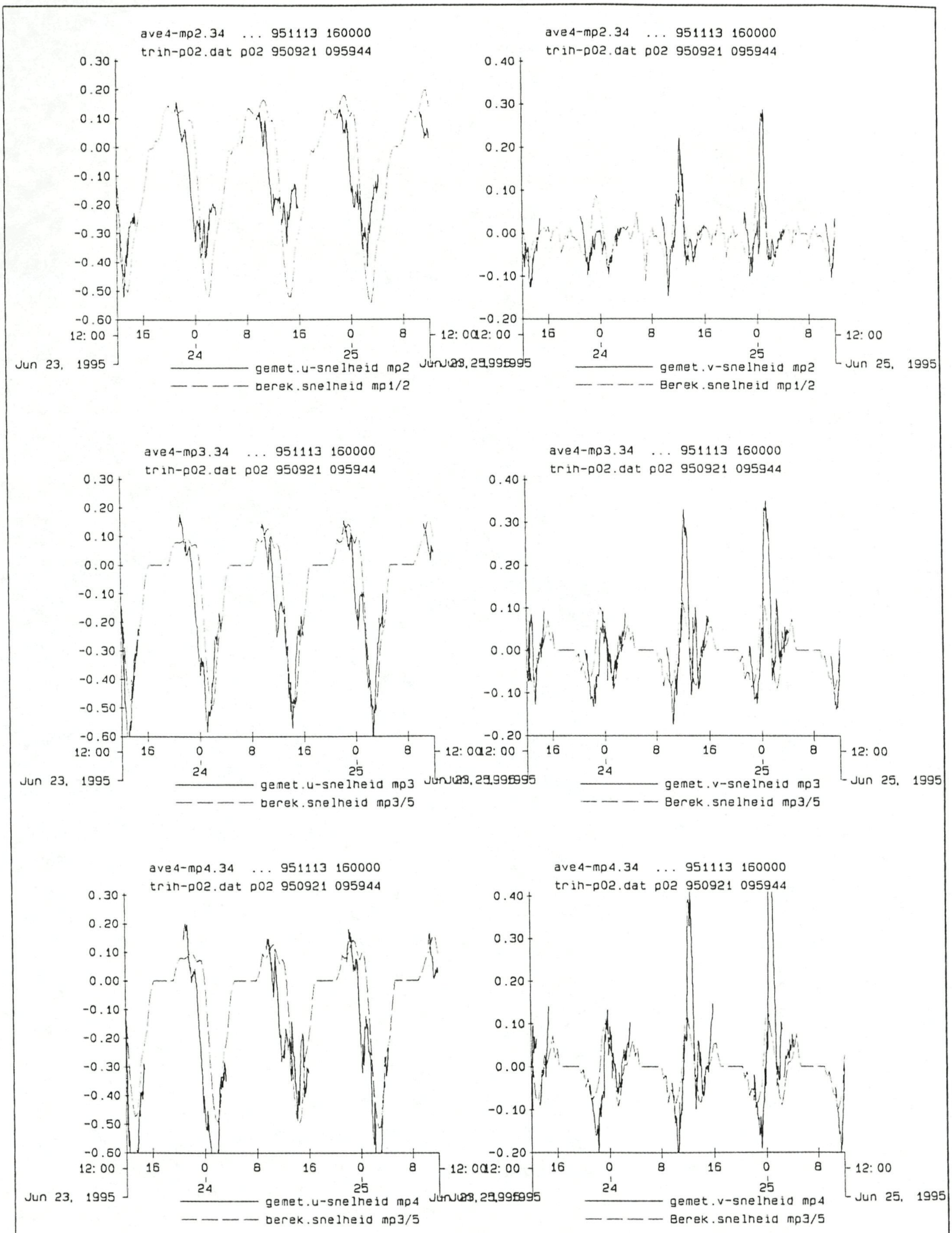
Run p02
Berekende tegen gemeten snelheden, mp1/2, mp3/5,
mp6 en mp9. Berekende tegen gemeten waterstand, mp6

1995-11-13
16:36:15

WATERLOOPKUNDIG LABORATORIUM

Fig 3.1.a

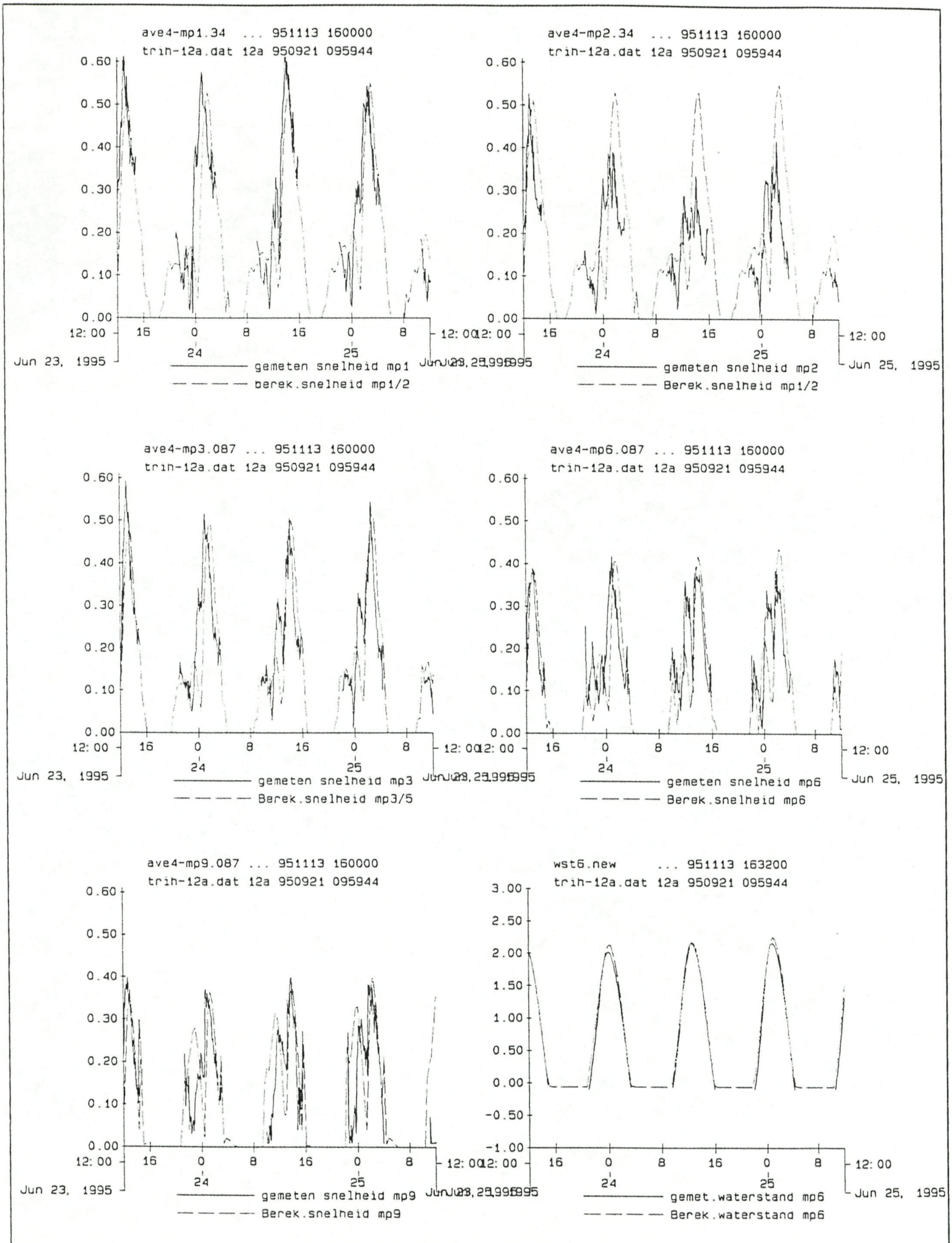


Run p02
Berekende tegen gemeten snelheidscomponenten
Meetpunt 1/2 en Meetpunt 3/5

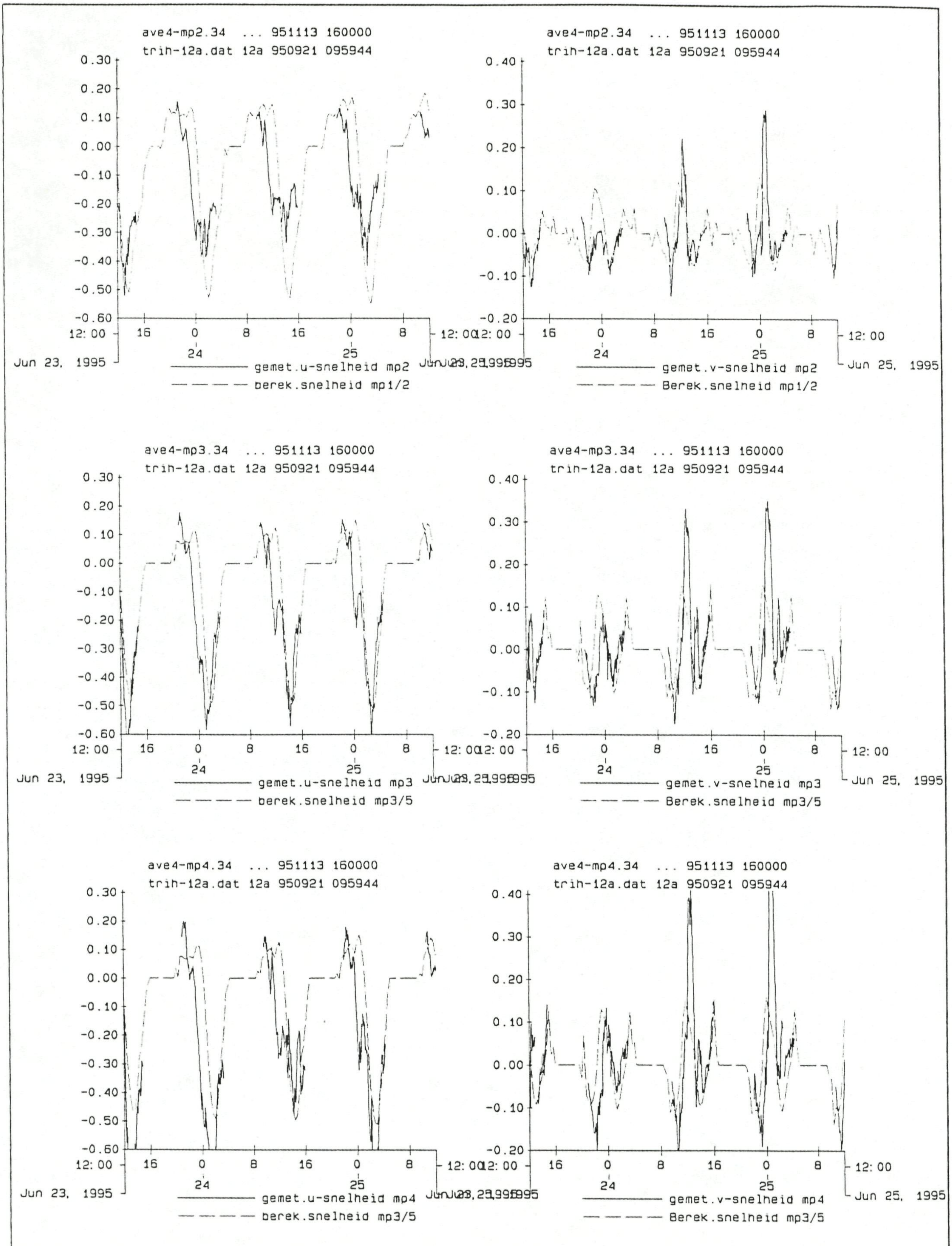
1995-11-13
17:05:25

WATERLOOPKUNDIG LABORATORIUM

Fig 3.1.b



Run 12a Berekende tegen gemeten snelheden, mp1/2, mp3/5, mp6 en mp9. Berekende tegen gemeten waterstand, mp6		1995-11-13 16:36:15
WATERLOOPKUNDIG LABORATORIUM		Fig 3.1.c

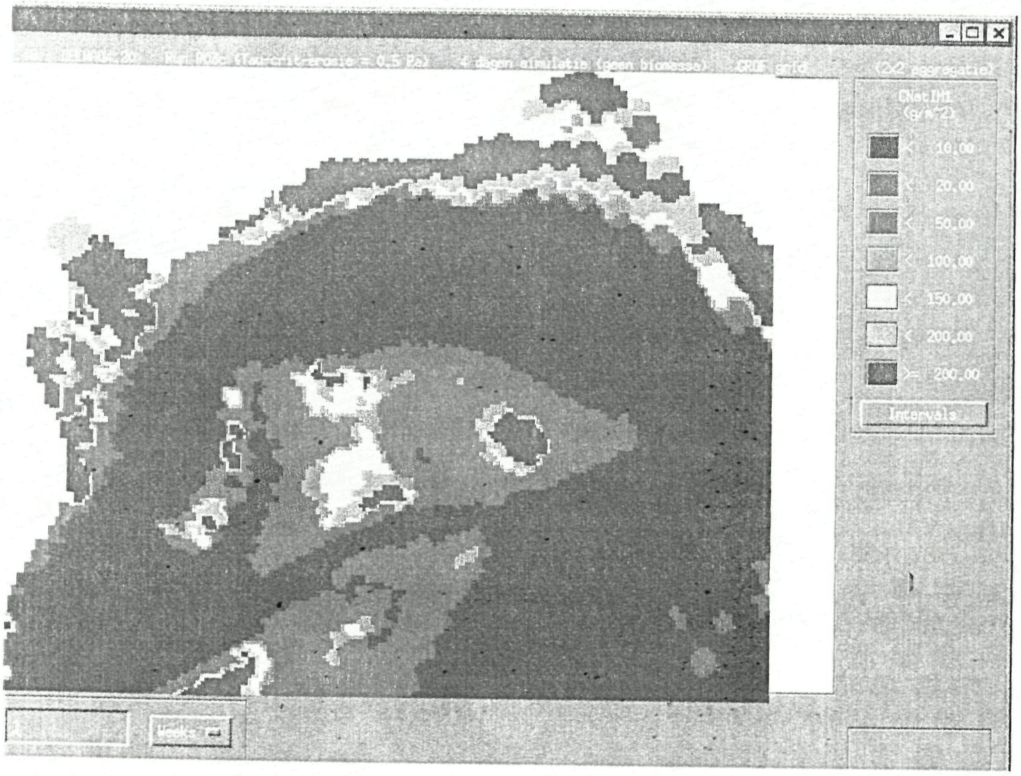


Run 12a
Berekende tegen gemeten snelheidscomponenten
Meetpunt 1/2 en Meetpunt 3/5

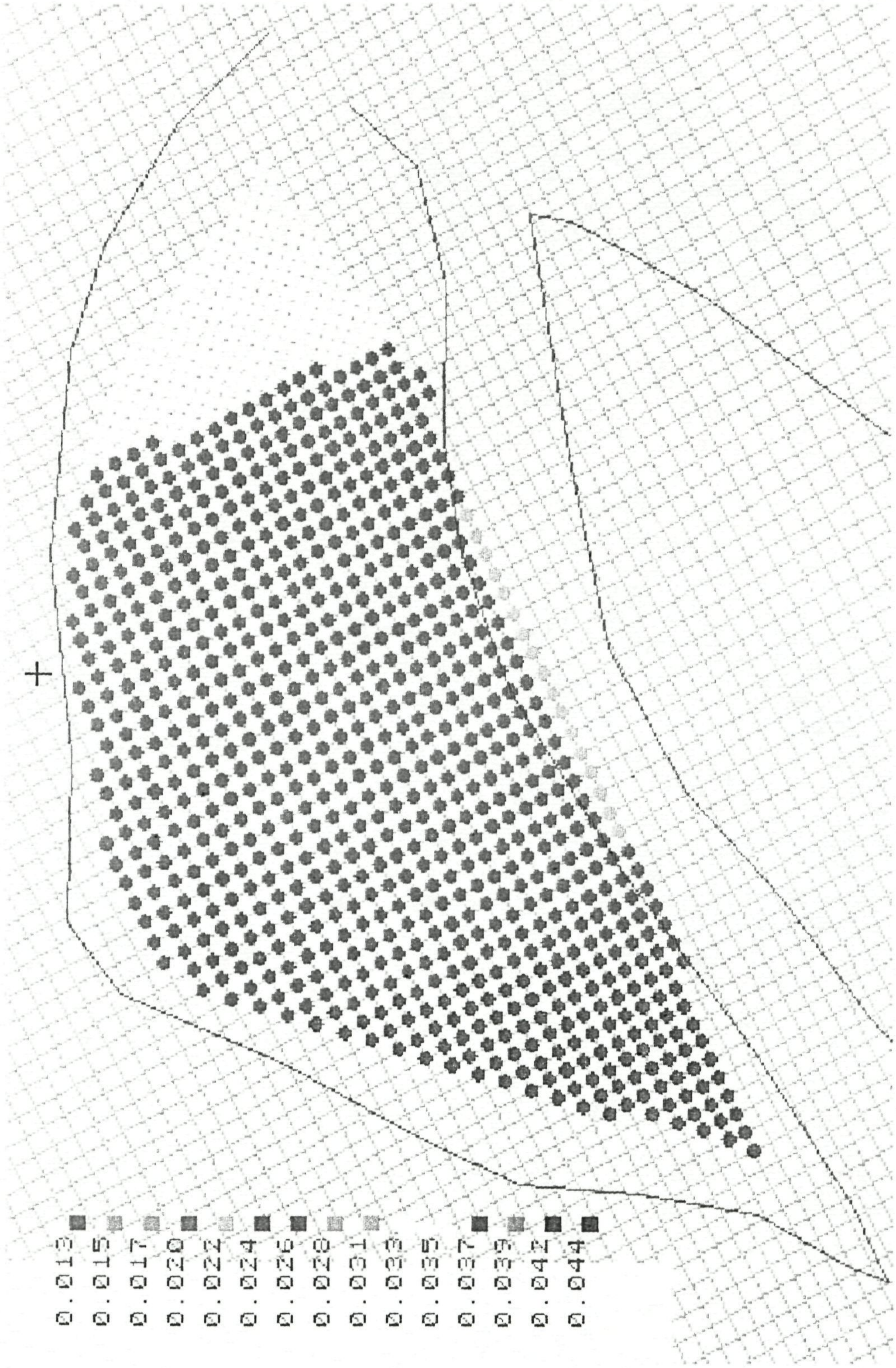
1995-11-13
17:05:25

WATERLOOPKUNDIG LABORATORIUM

Fig 3.1.d



Net cumulative sedimentation for runs P03b (top) and P03c (bottom)	BEON micro/macro	
DELFT HYDRAULICS	Fig. 3.2.A	



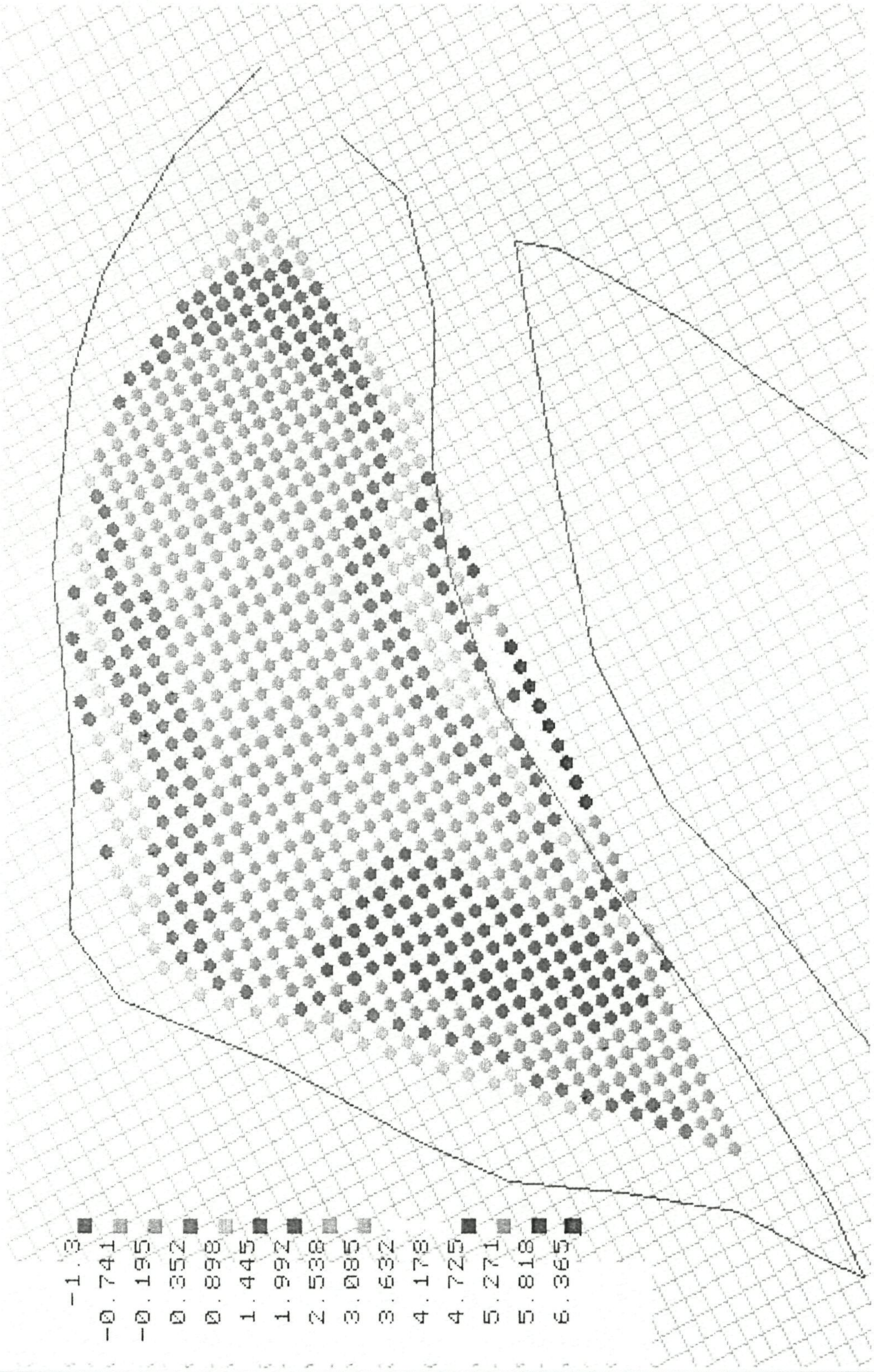
Bottom roughness coefficient

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.2.B

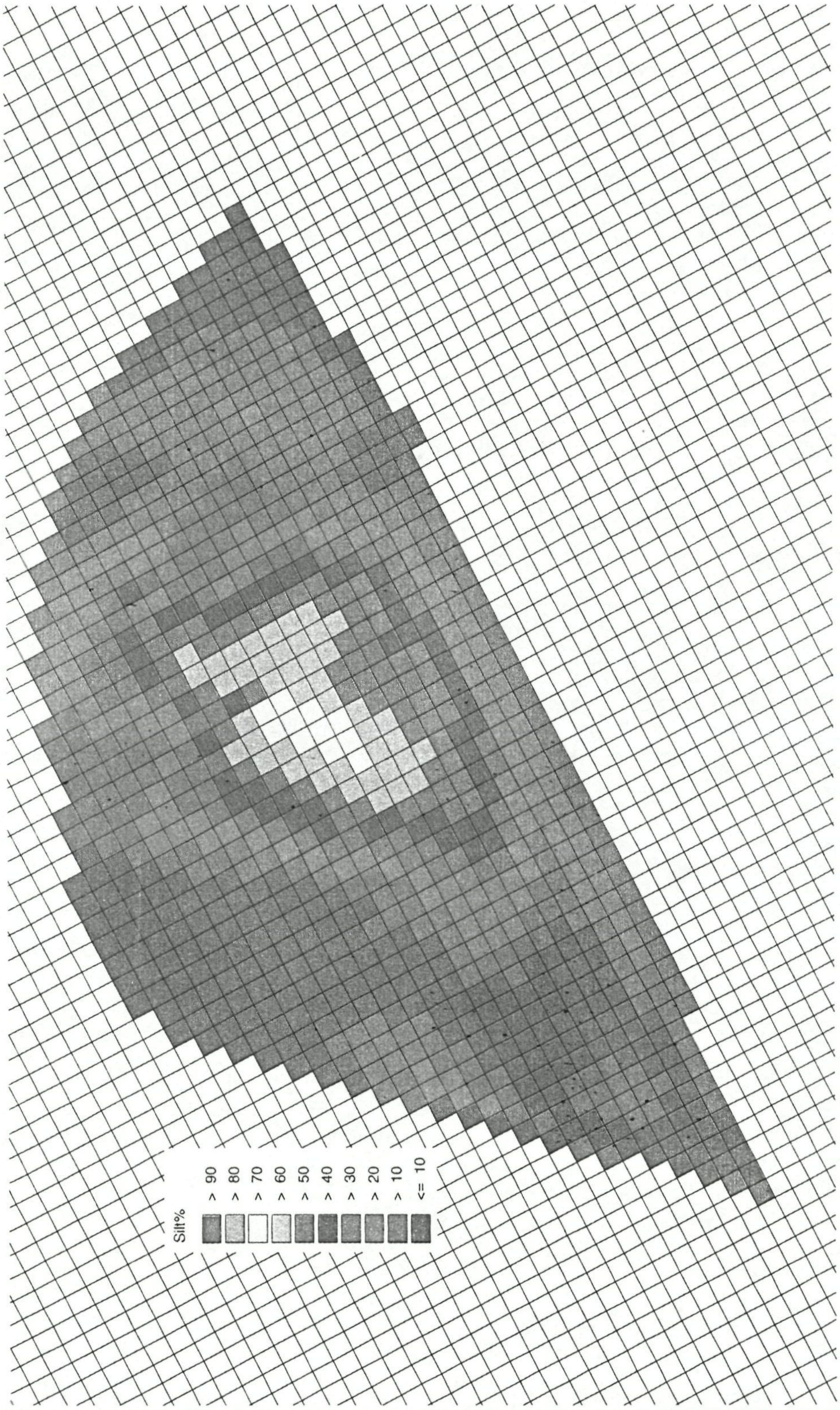


Bathymetry

BEON micro/macro

DELFT HYDRAULICS

Fig. 3.2.C



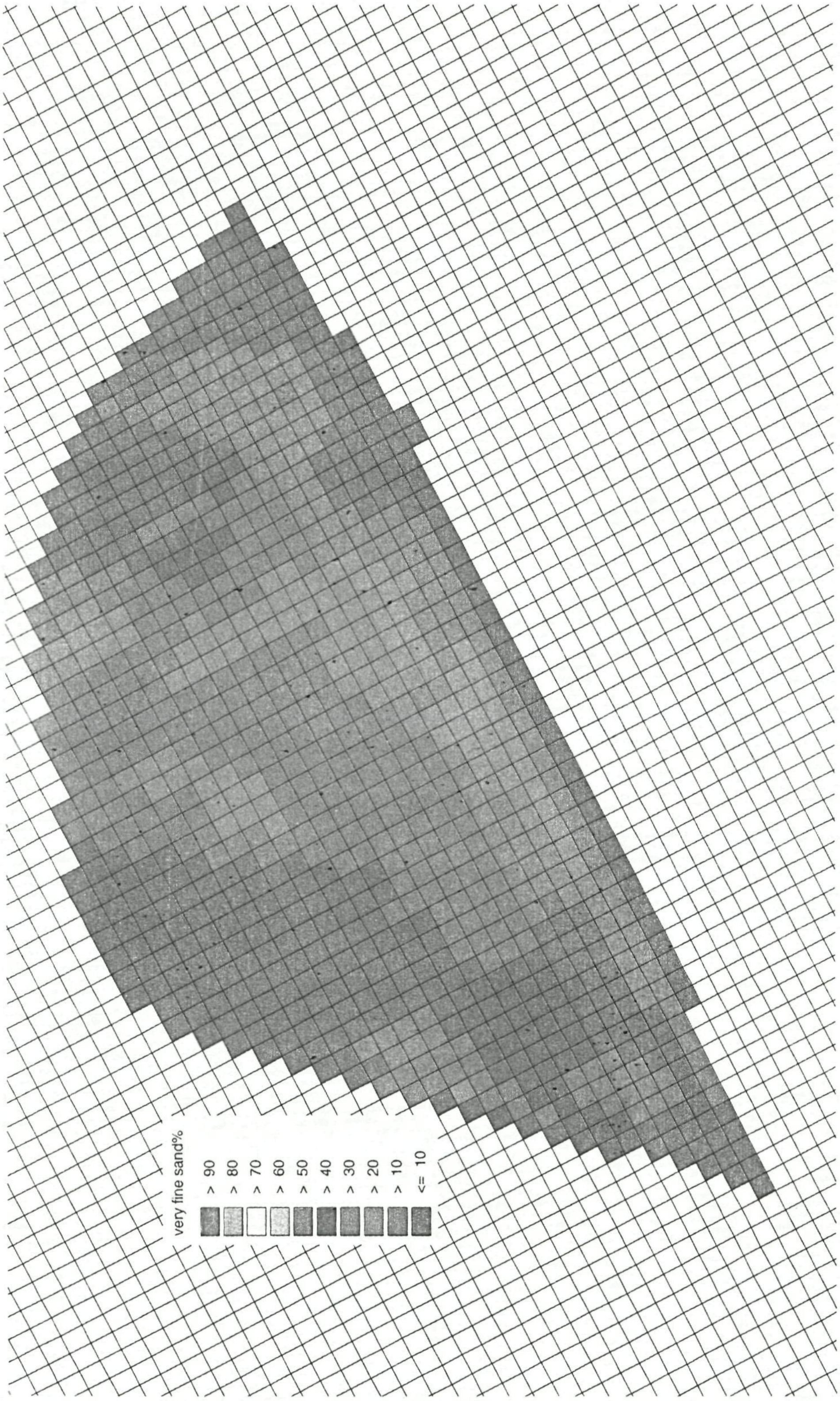
Silt percentage

BEON micro/macro

June '95

DELFT HYDRAULICS

Fig. 3.3



Very fine sand percentage

BEON micro/macro

June '95

DELFT HYDRAULICS

Fig. 3.4

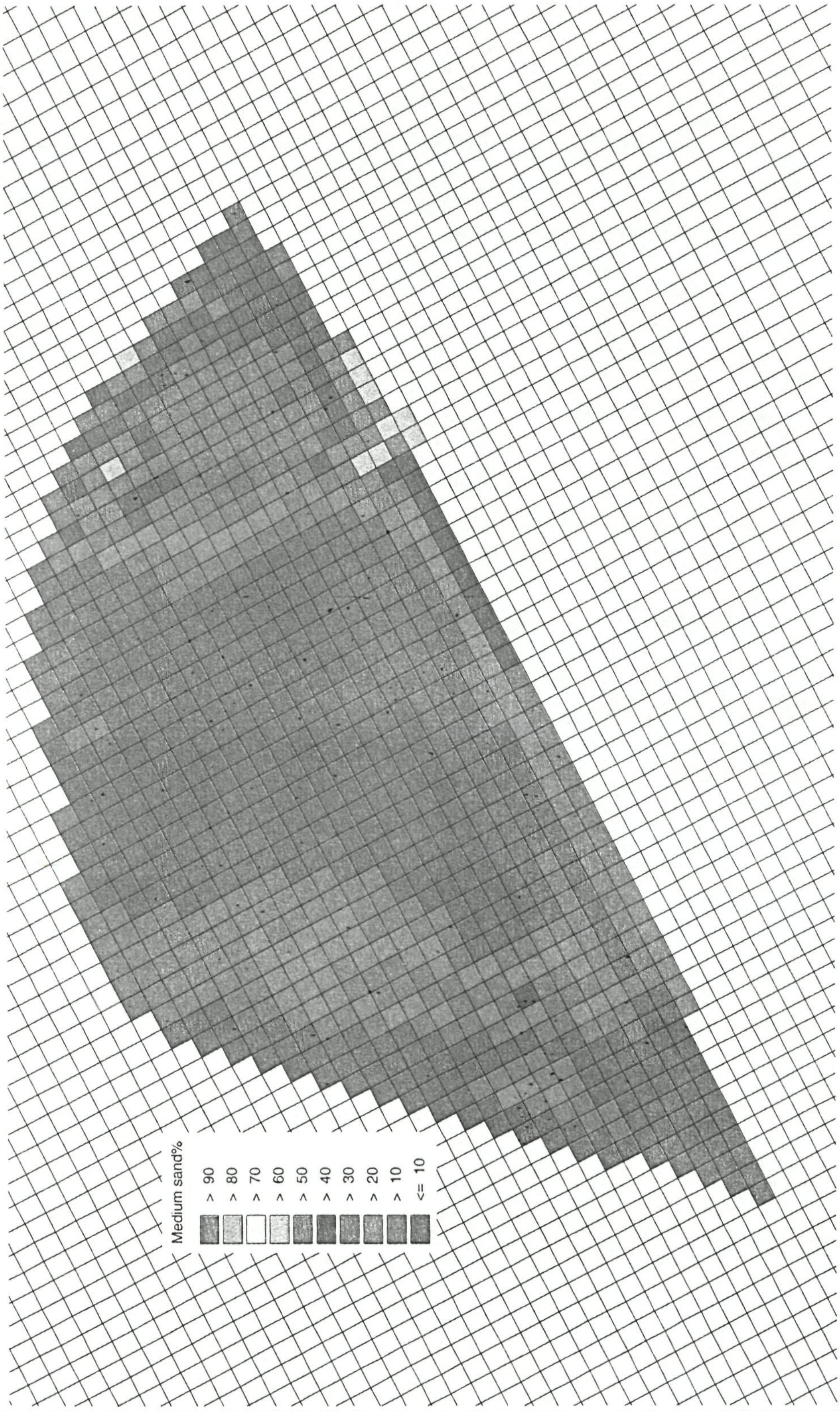
Fine sand percentage

BEON micro/macro

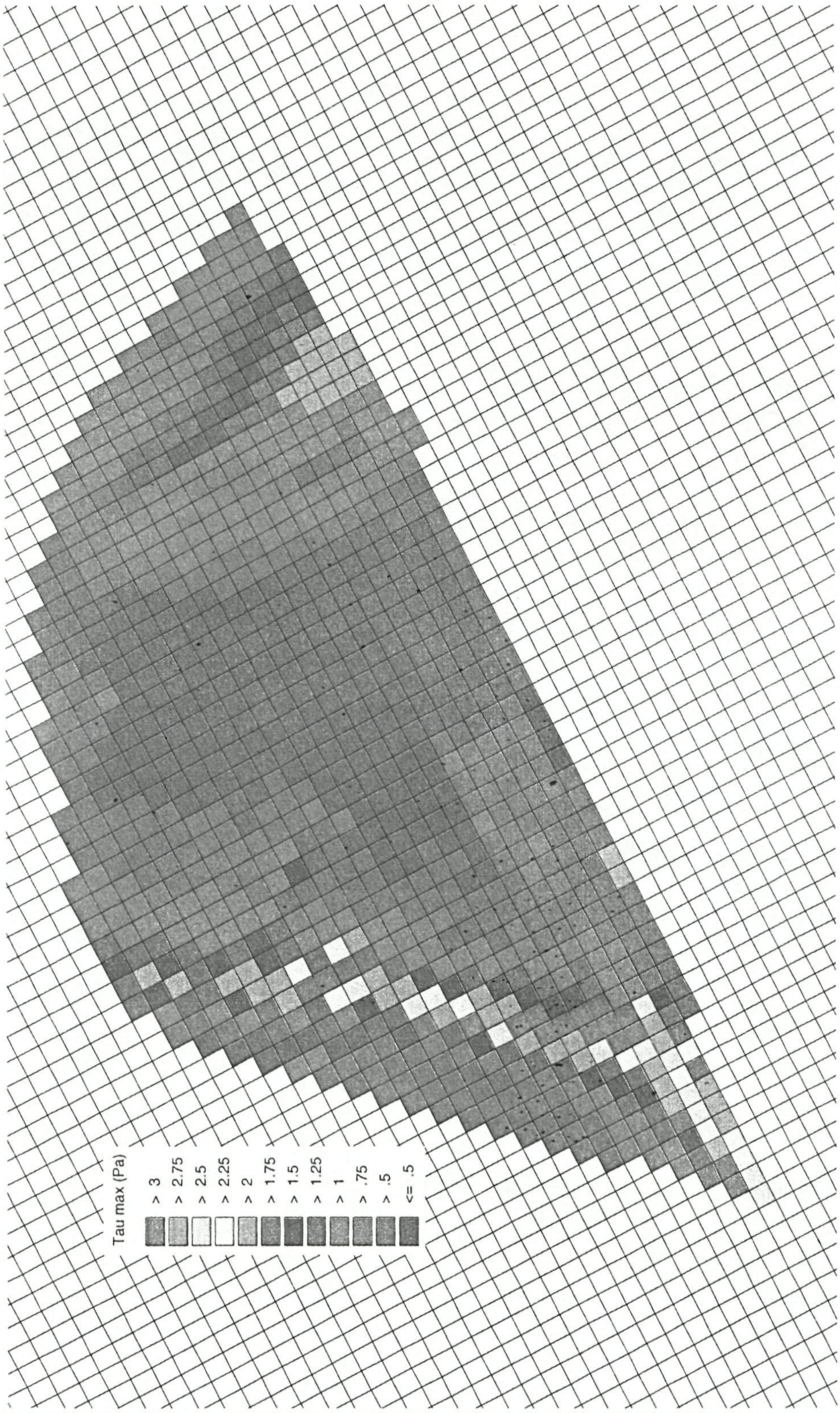
June '95

DELFT HYDRAULICS

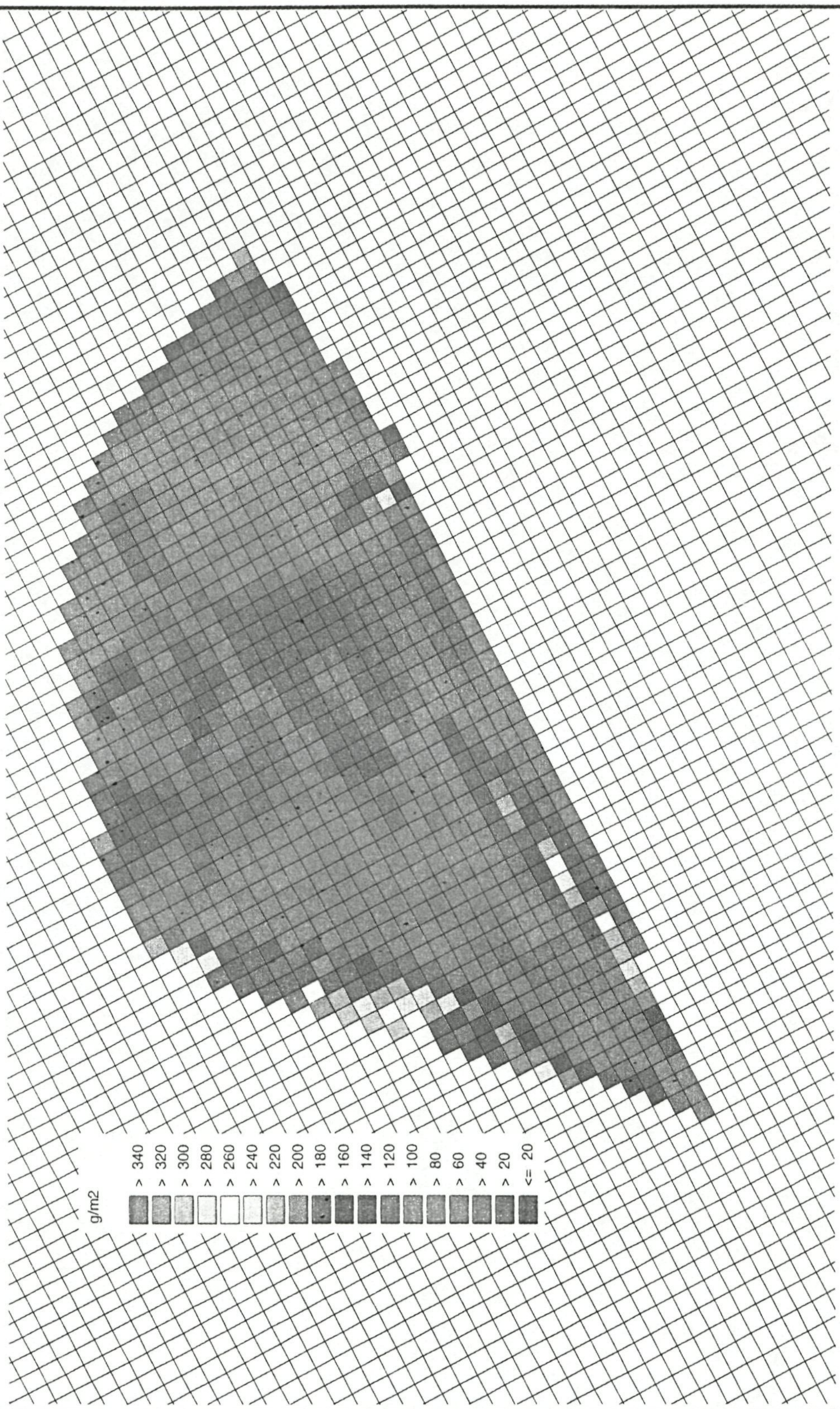
Fig. 3.5



Medium sand percentage	BEON micro/macro June '95
DELFT HYDRAULICS	Fig. 3.6



Maximum bed shear stress (Pa)	BEON micro/macro	
	P06b	
DELFT HYDRAULICS	Fig. 3.7	



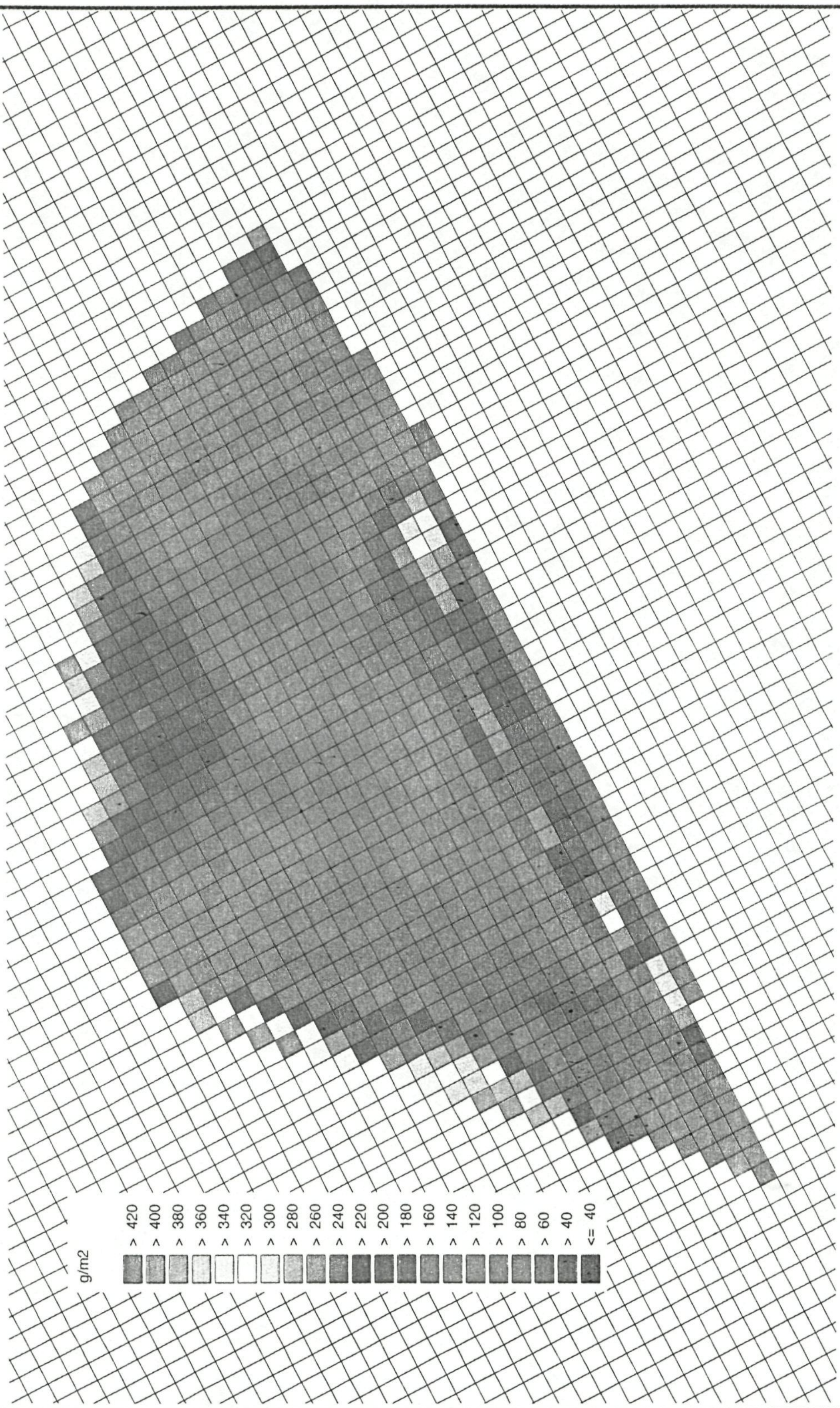
Gross Cumulative Resuspension Flux

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.8.A



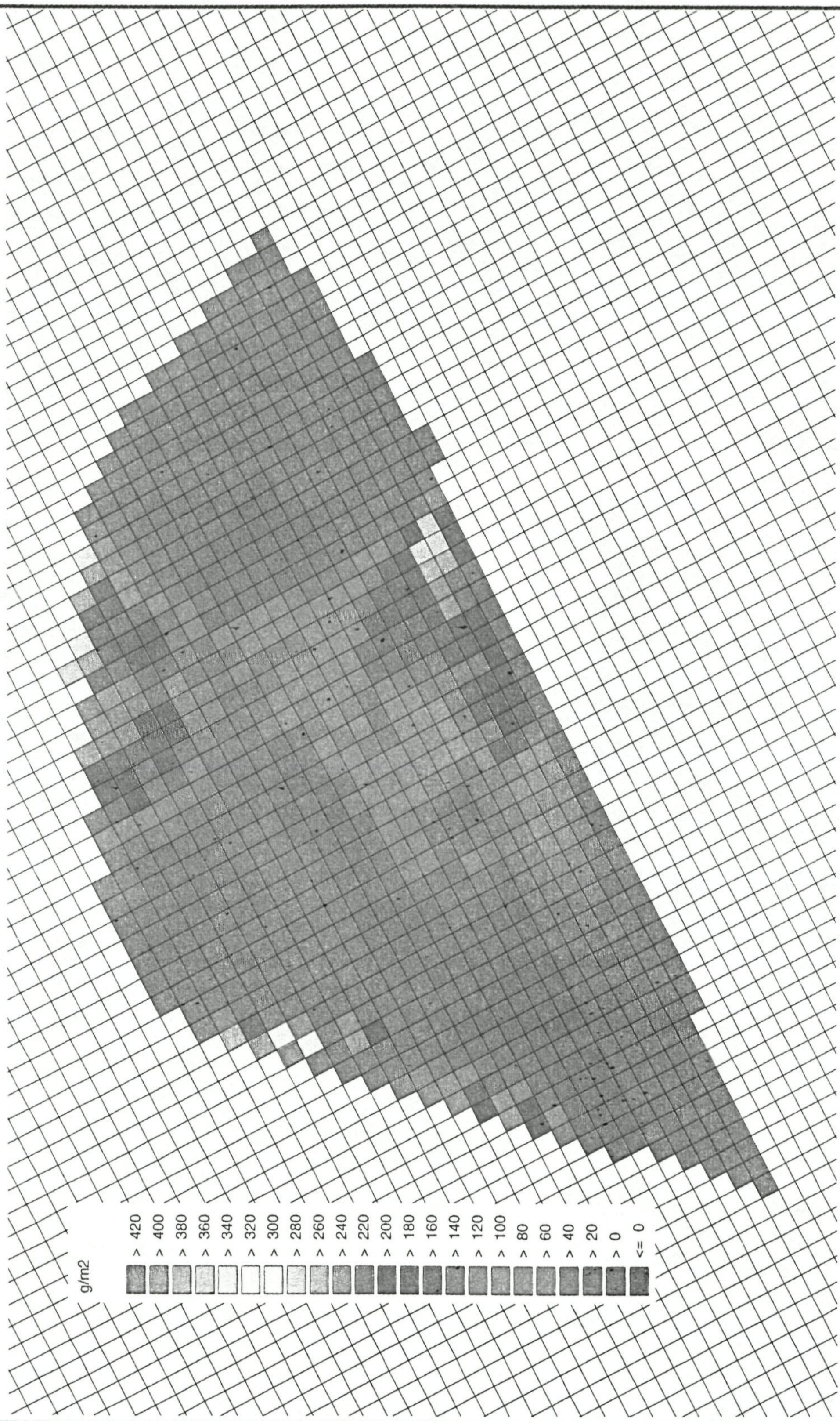
Gross Cumulative Sedimentation Flux

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.8.B



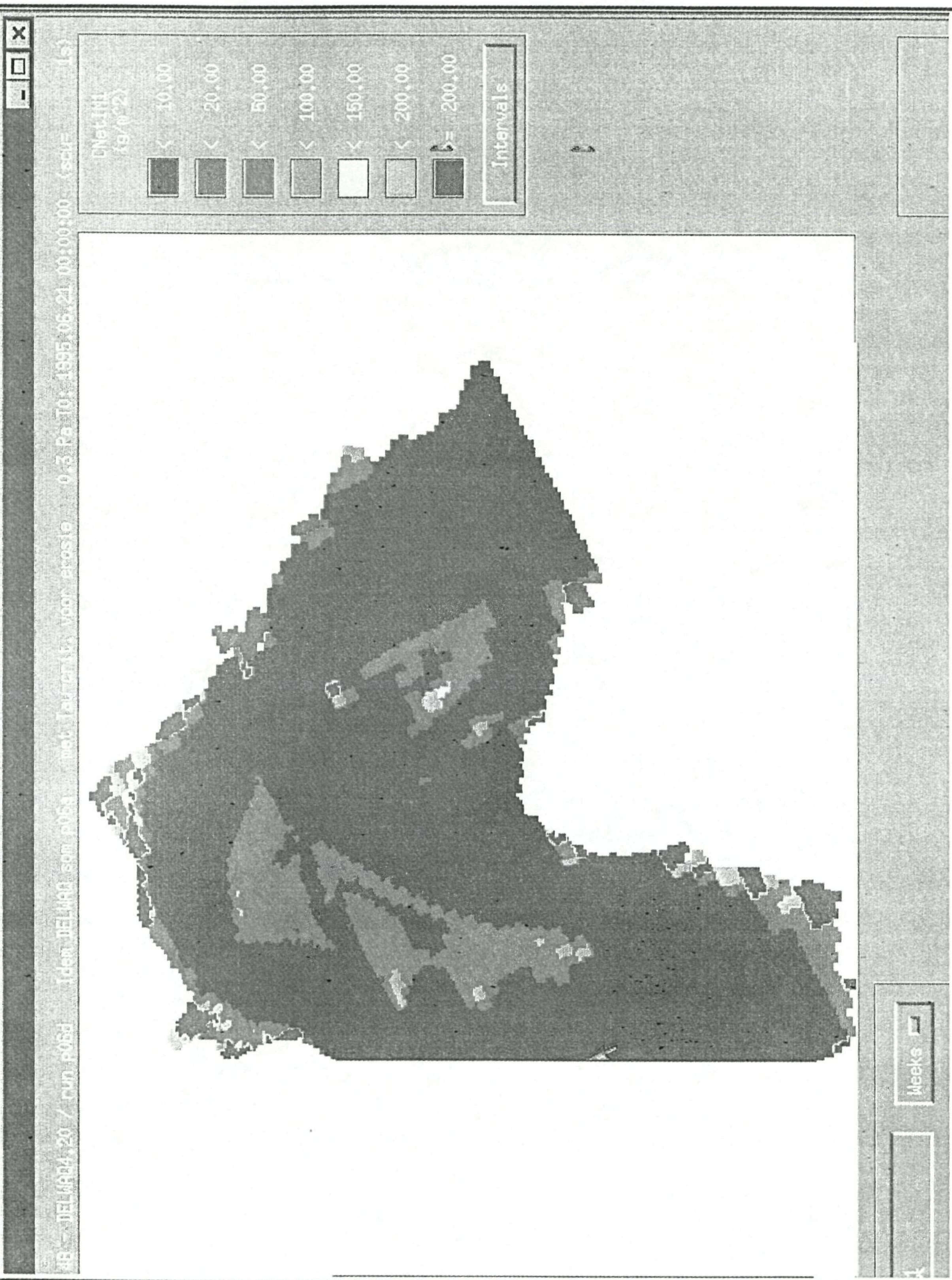
BEON micro/macro

Net Cumulative Sedimentation Flux

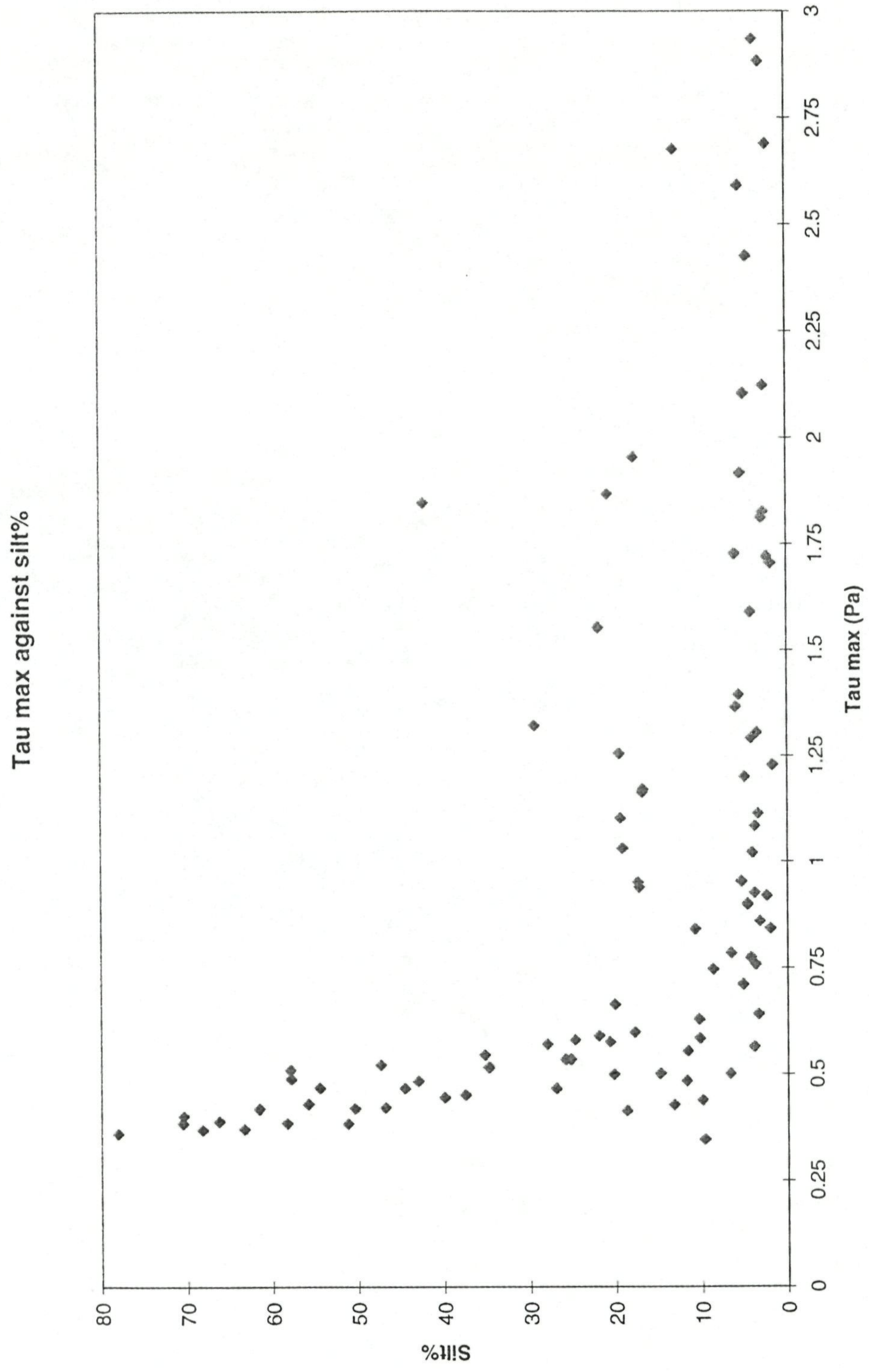
P06b

DELFT HYDRAULICS

Fig. 3.8.C



Net Cumulative Sedimentation Flux	BEON micro/macro	
	P06d	
DELFT HYDRAULICS	Fig. 3.9	



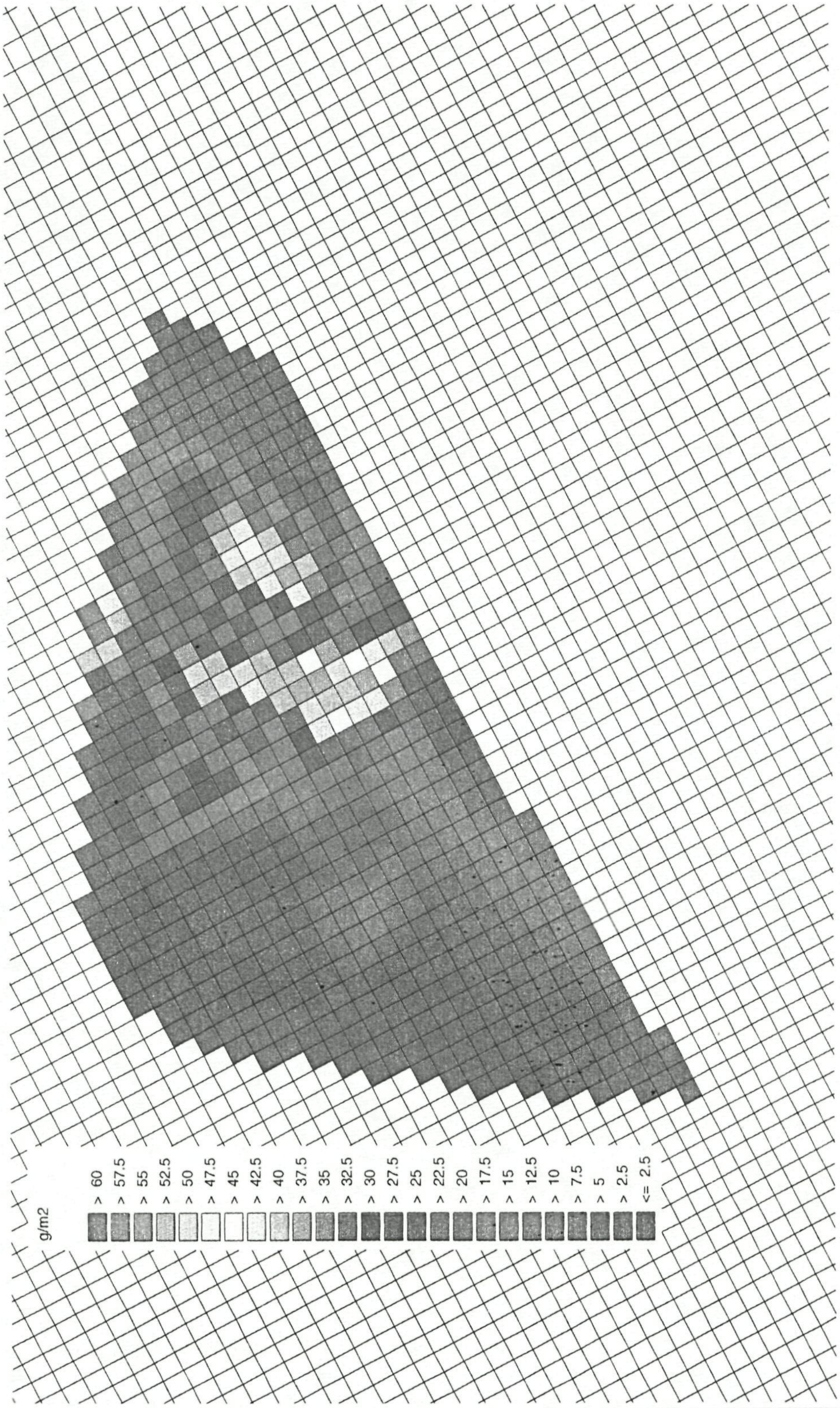
Tau max (Pa) against % silt

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.10



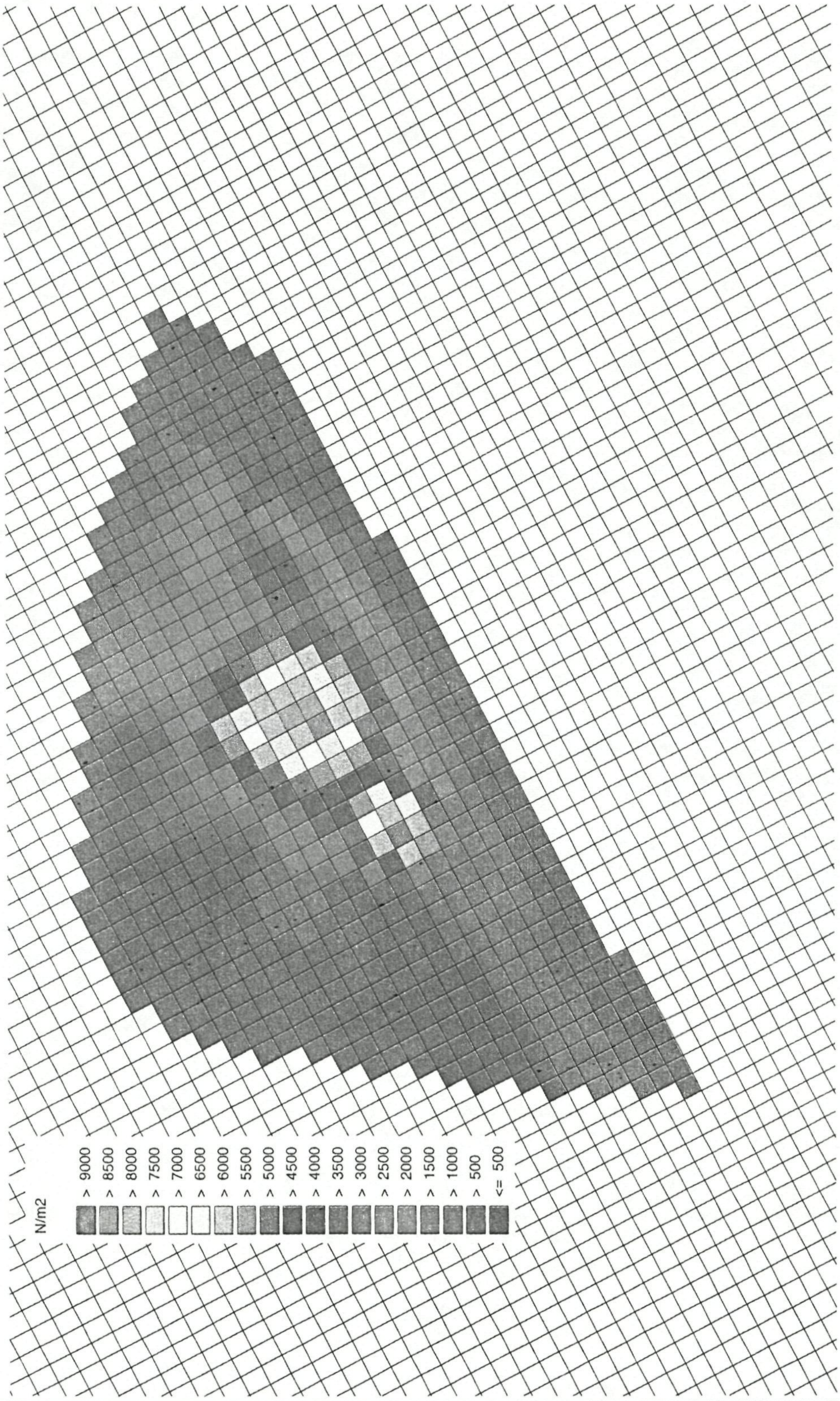
Biomass suspension feeders (g AFDW/m^2)

BEON micro/macro

June '95

DELFT HYDRAULICS

Fig. 3.11



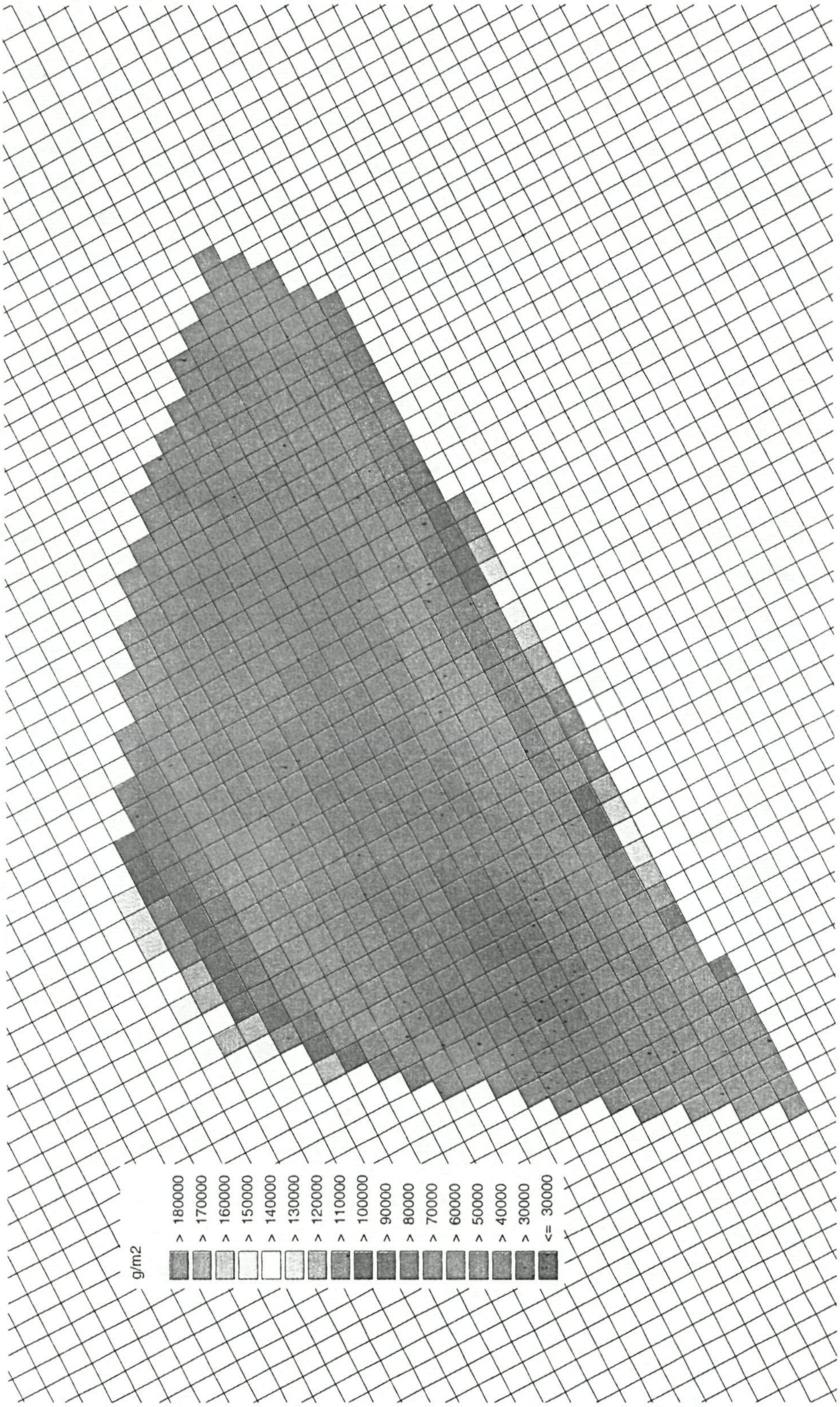
Density suspension feeders (N/m^2)

BEON micro/macro

June ‘95

DELFT HYDRAULICS

Fig. 3.12



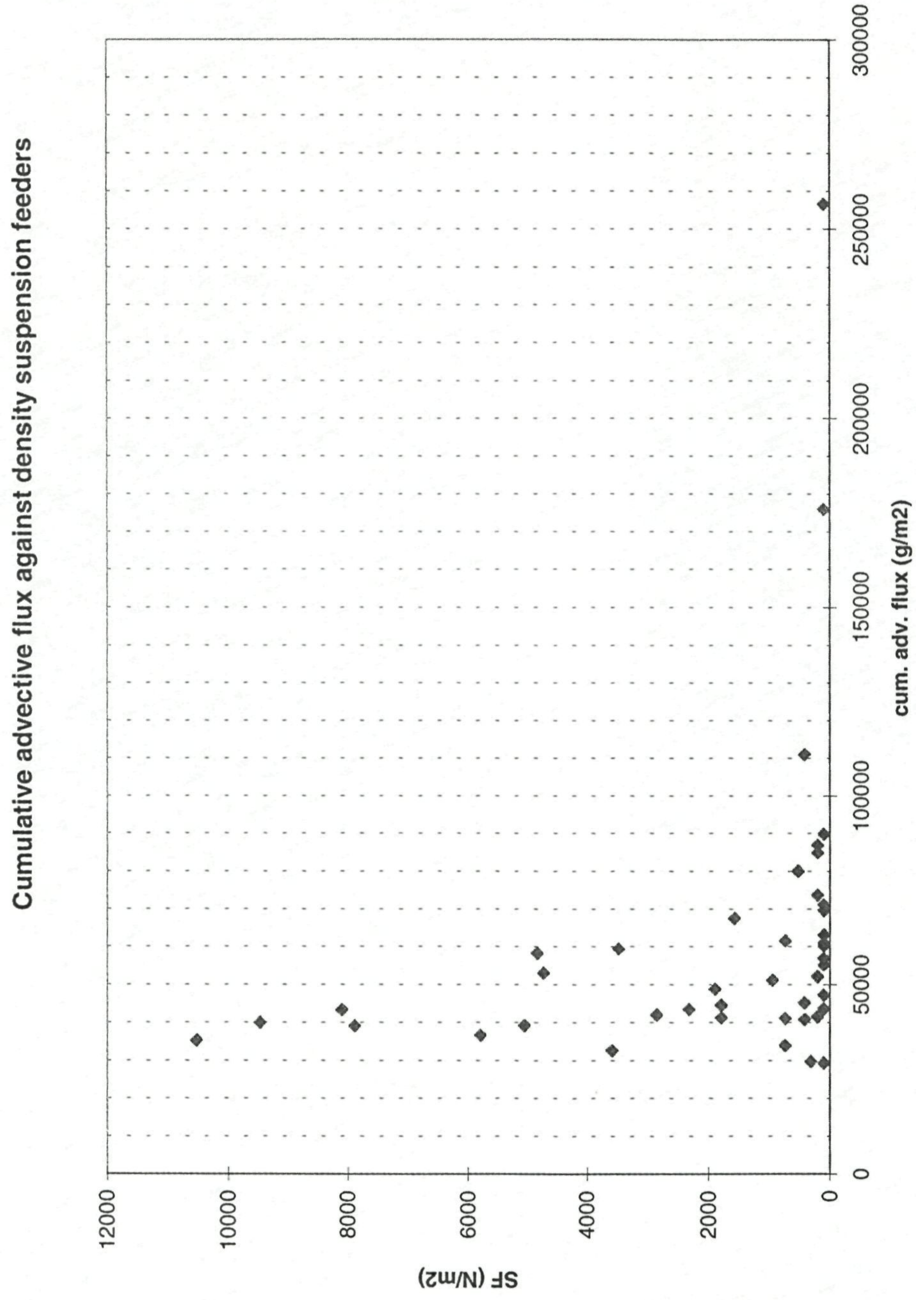
Cumulative advective flux (g/m^2)

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.13



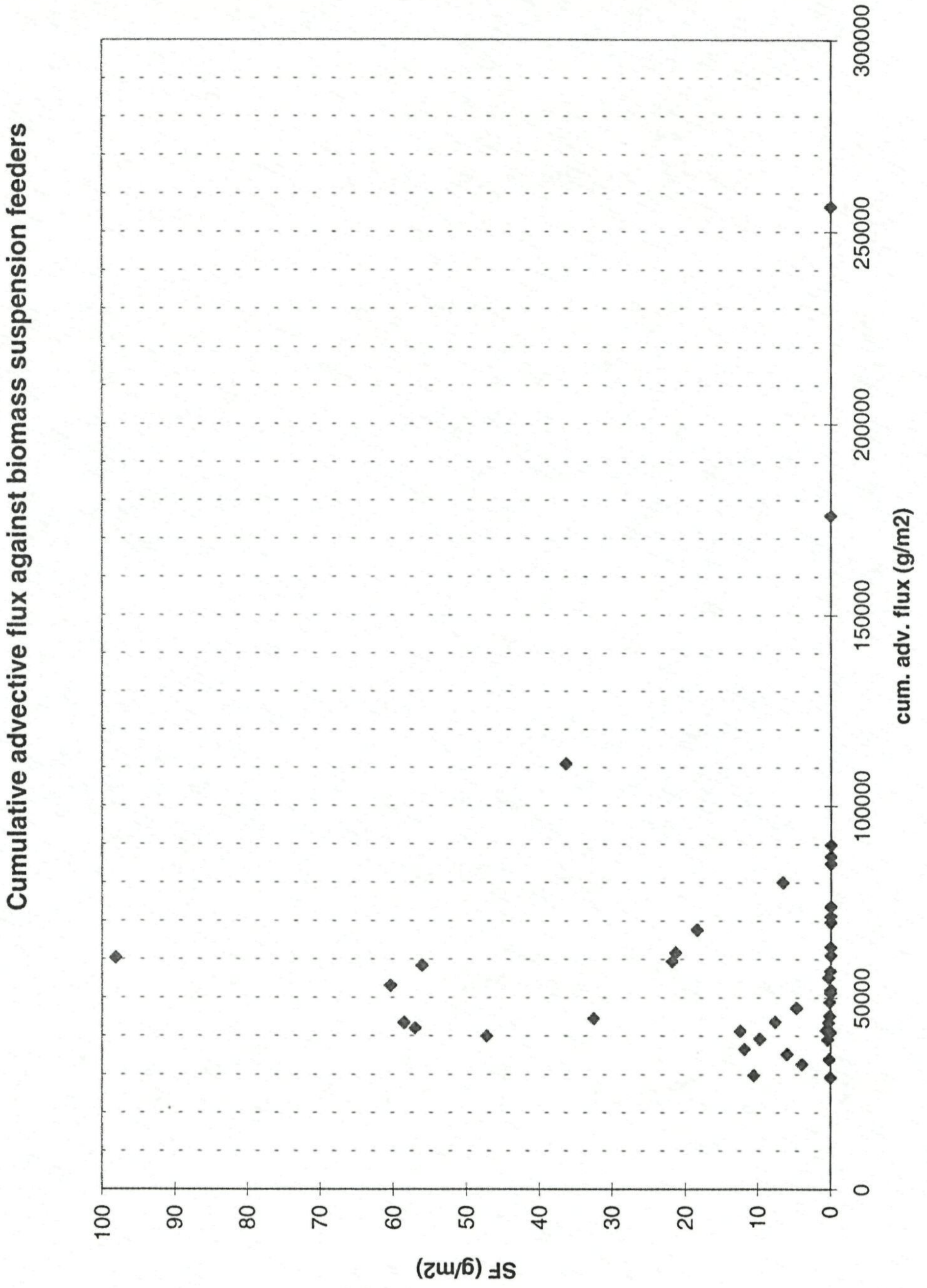
Cumulative advective flux against density SF

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.14



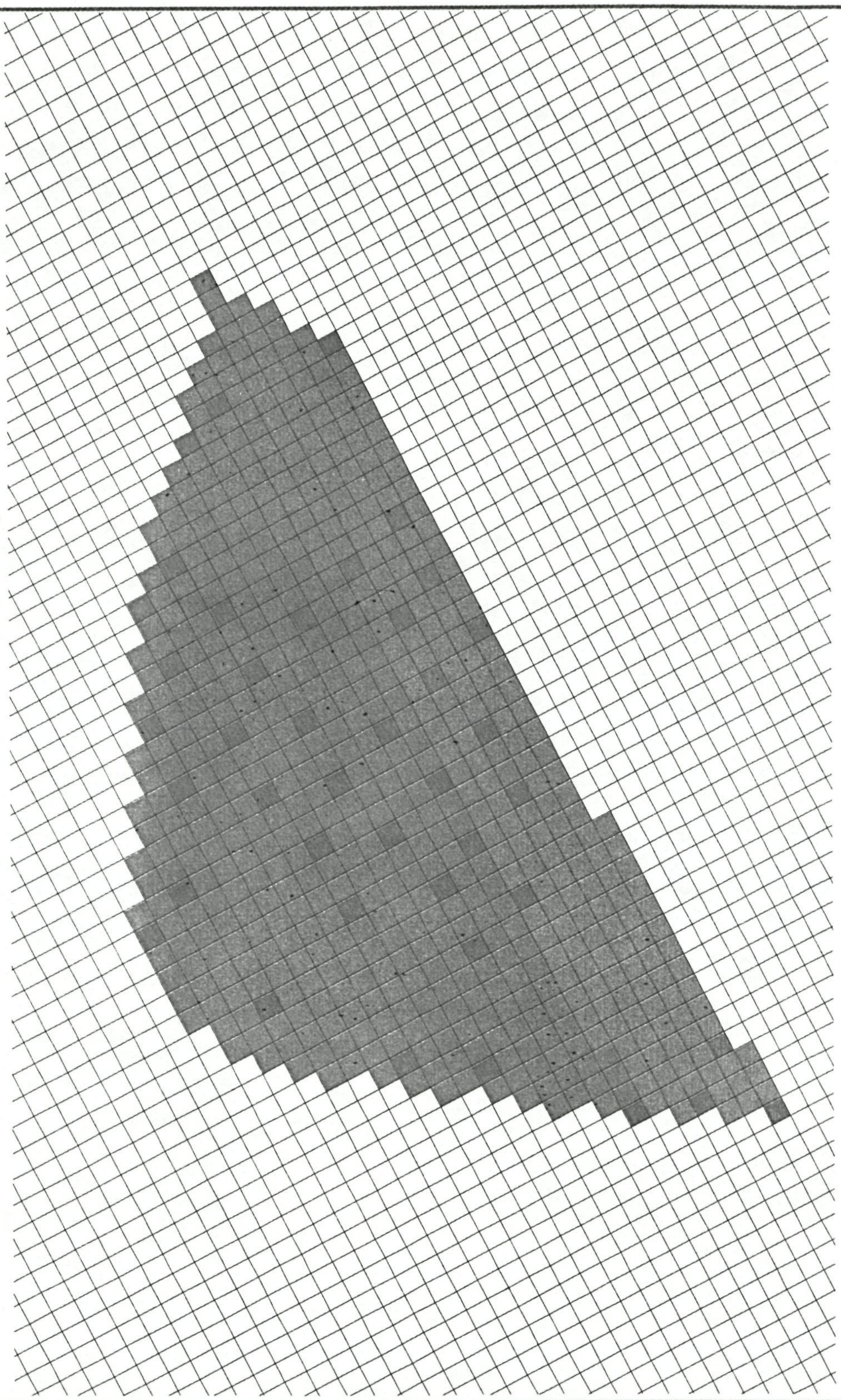
Cumulative advective flux against biomass SF

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.15



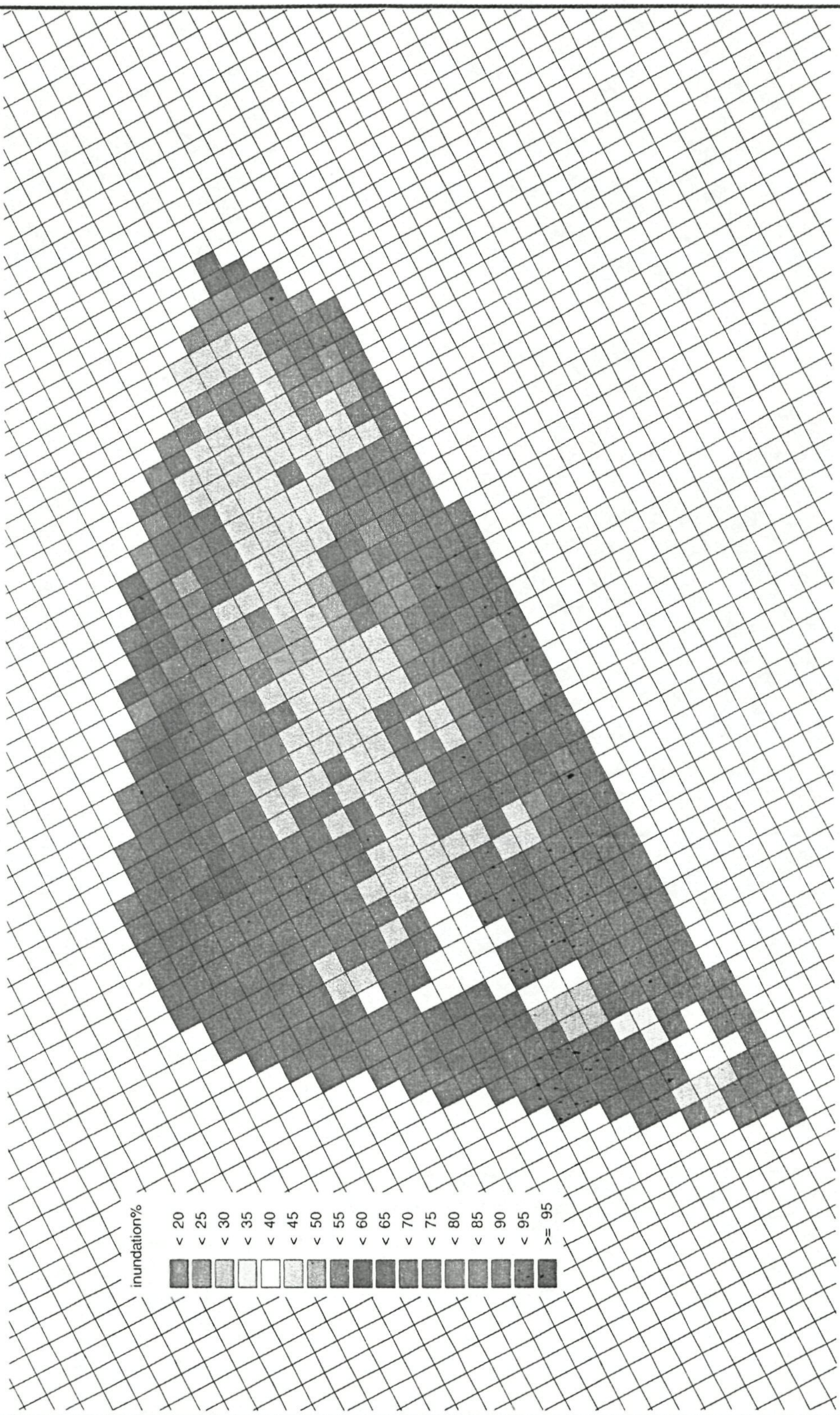
Sampling points of suspension feeders

BEON micro/macro

June '95

DELFT HYDRAULICS

Fig. 3.16



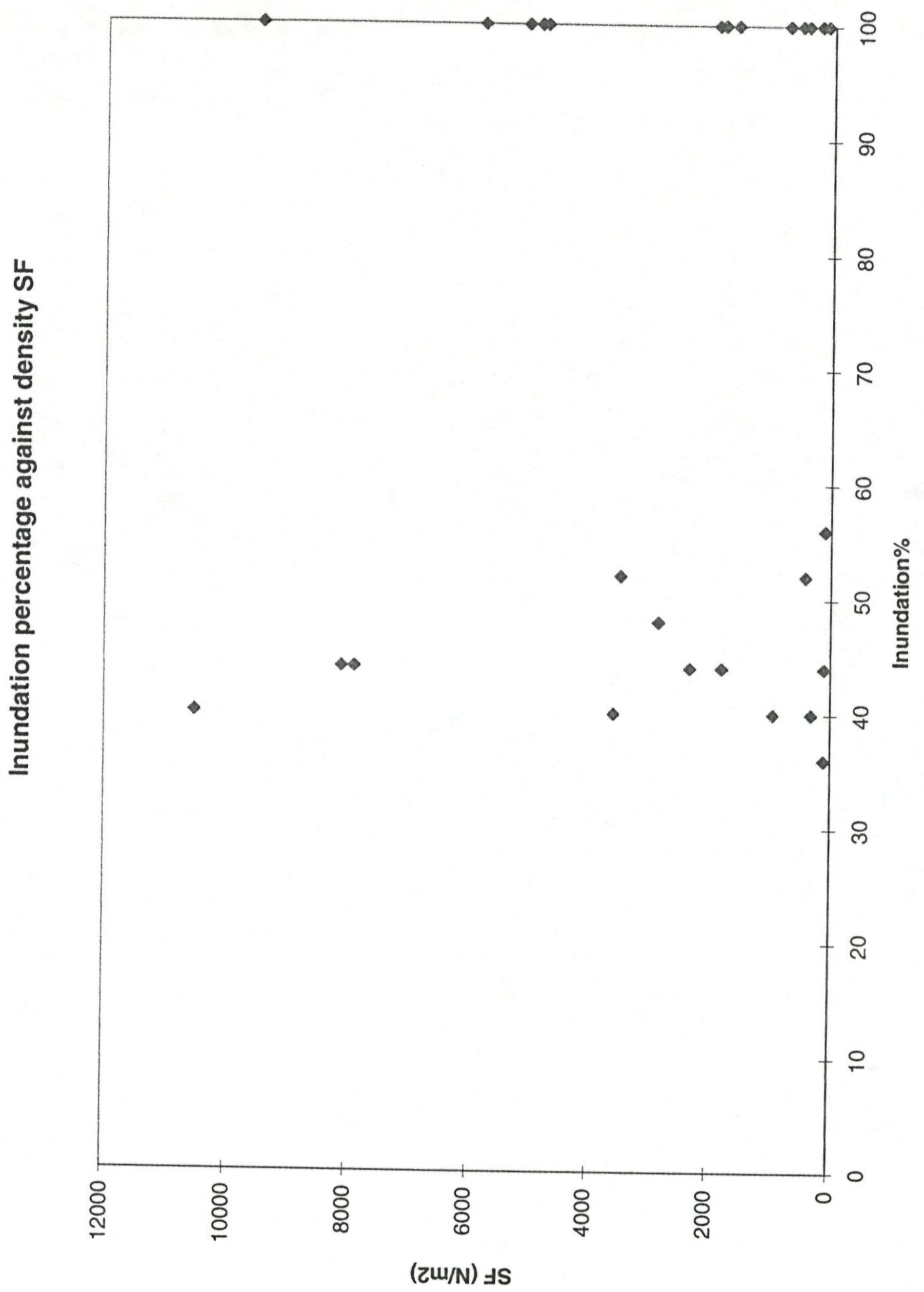
Inundation percentage

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.17



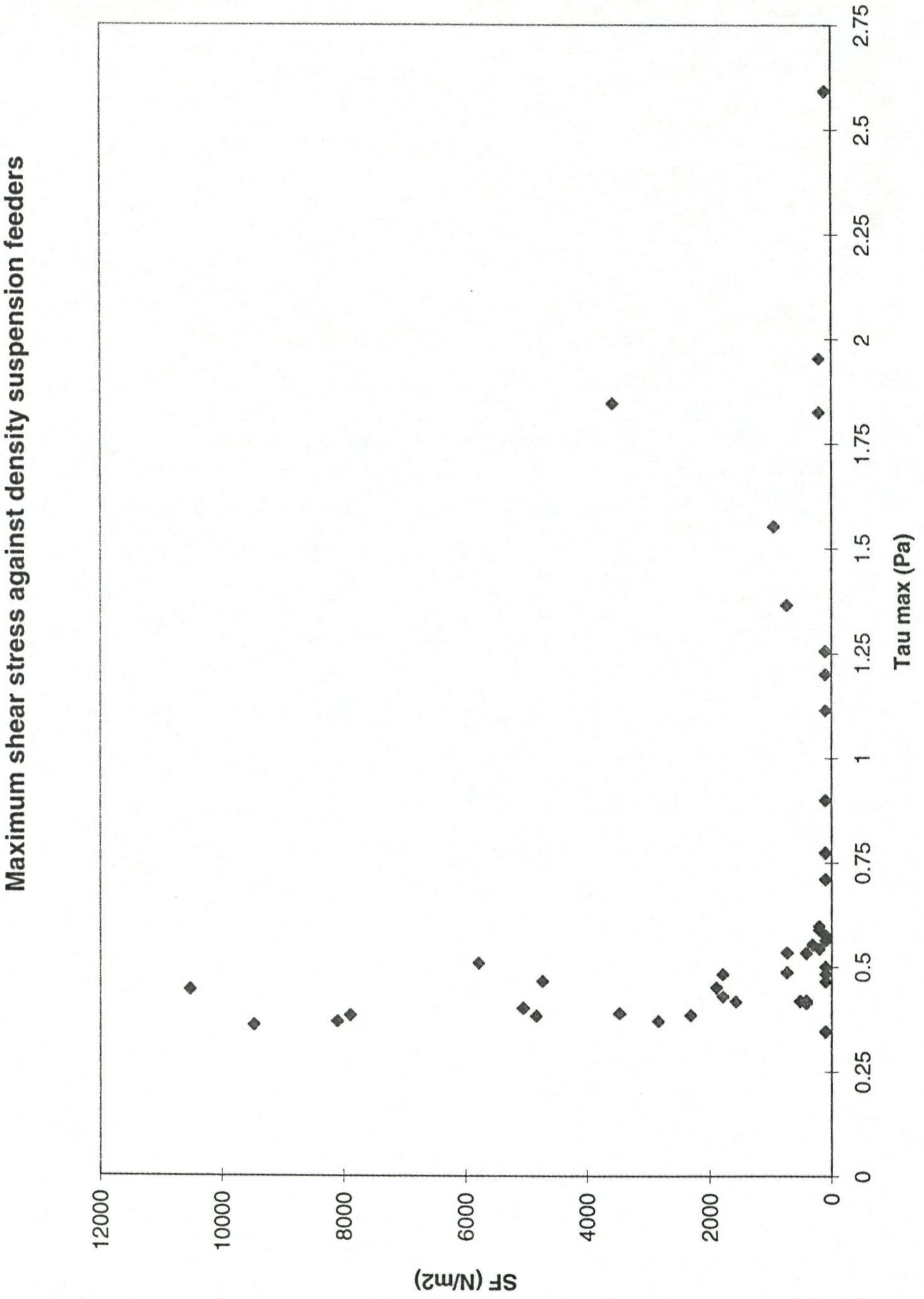
Inundation percentage against density SF

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.18



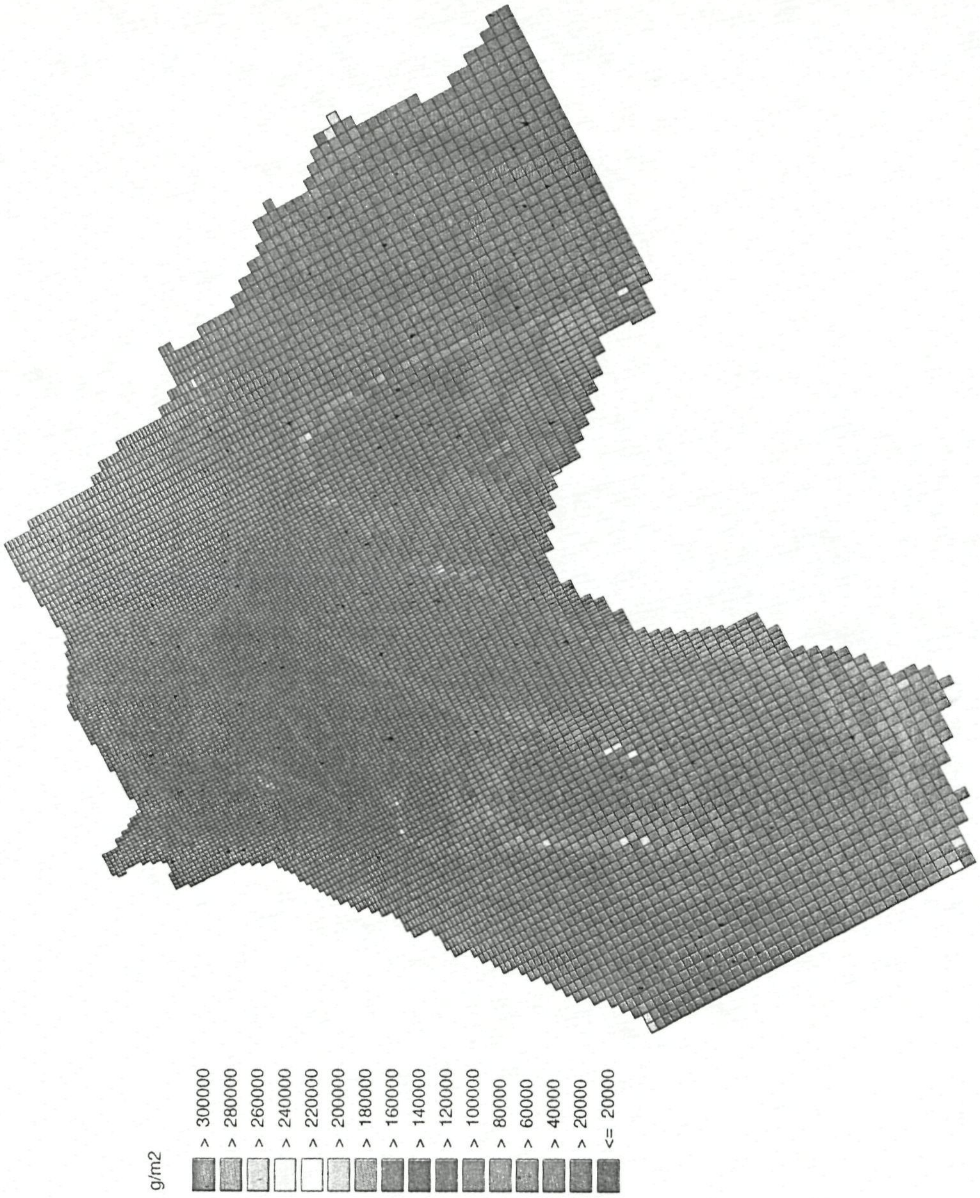
Maximum bed shear stress against density SF

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.19



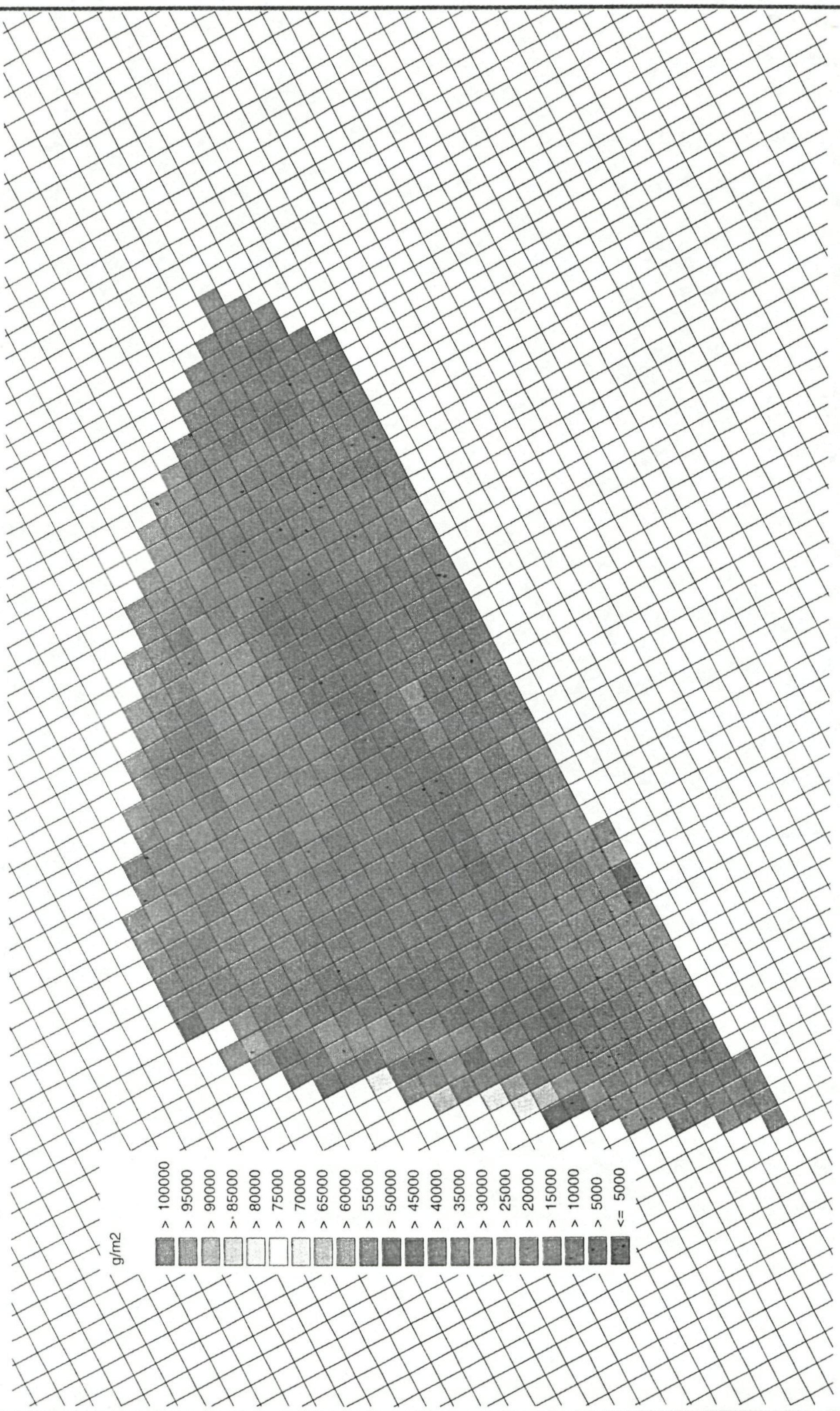
Substrate dynamics for entire area (g/m^2)

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.20



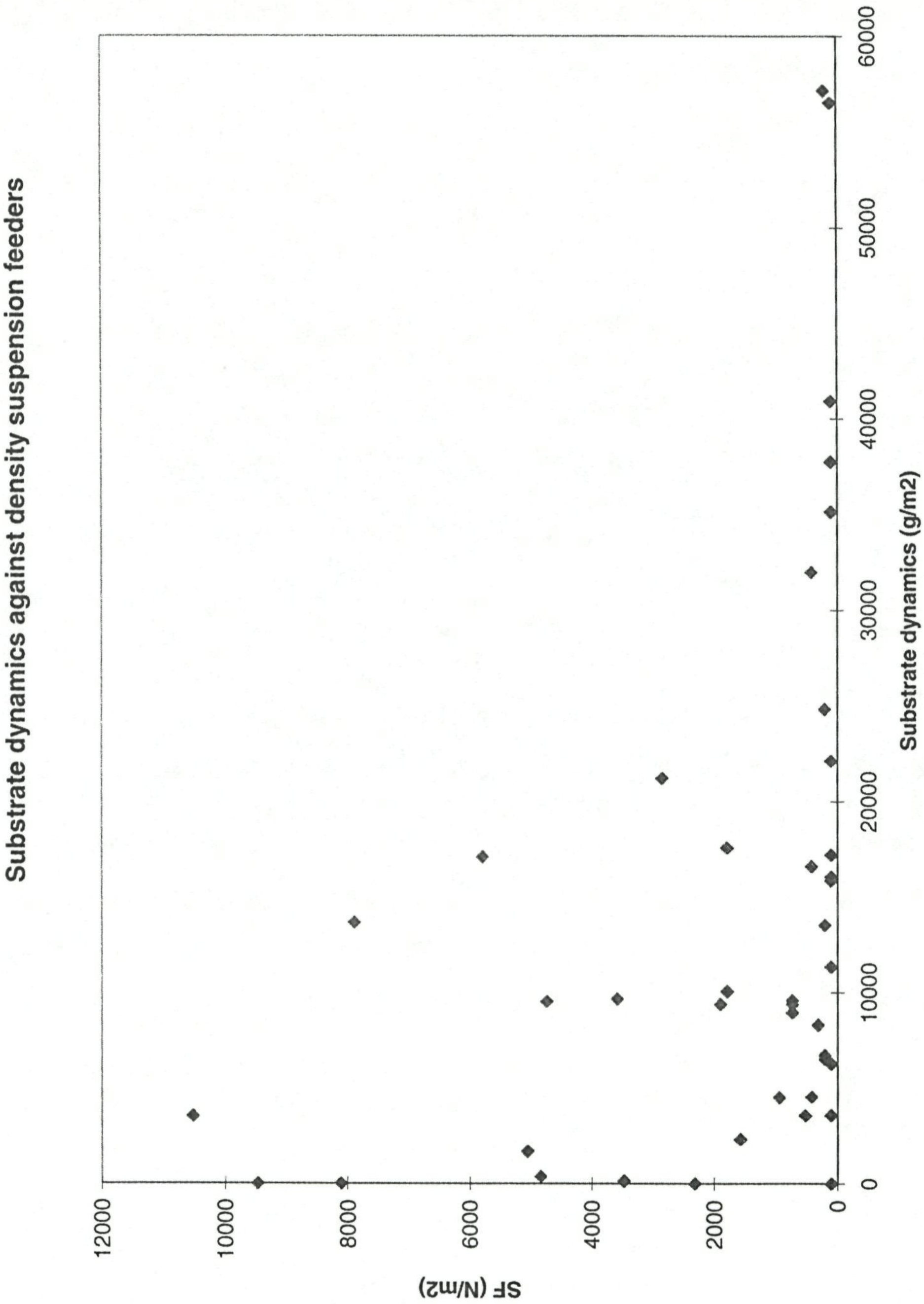
BEON micro/macro

Substrate dynamics for Molenplaat area (g/m^2)

P06b

DELFT HYDRAULICS

Fig. 3.21



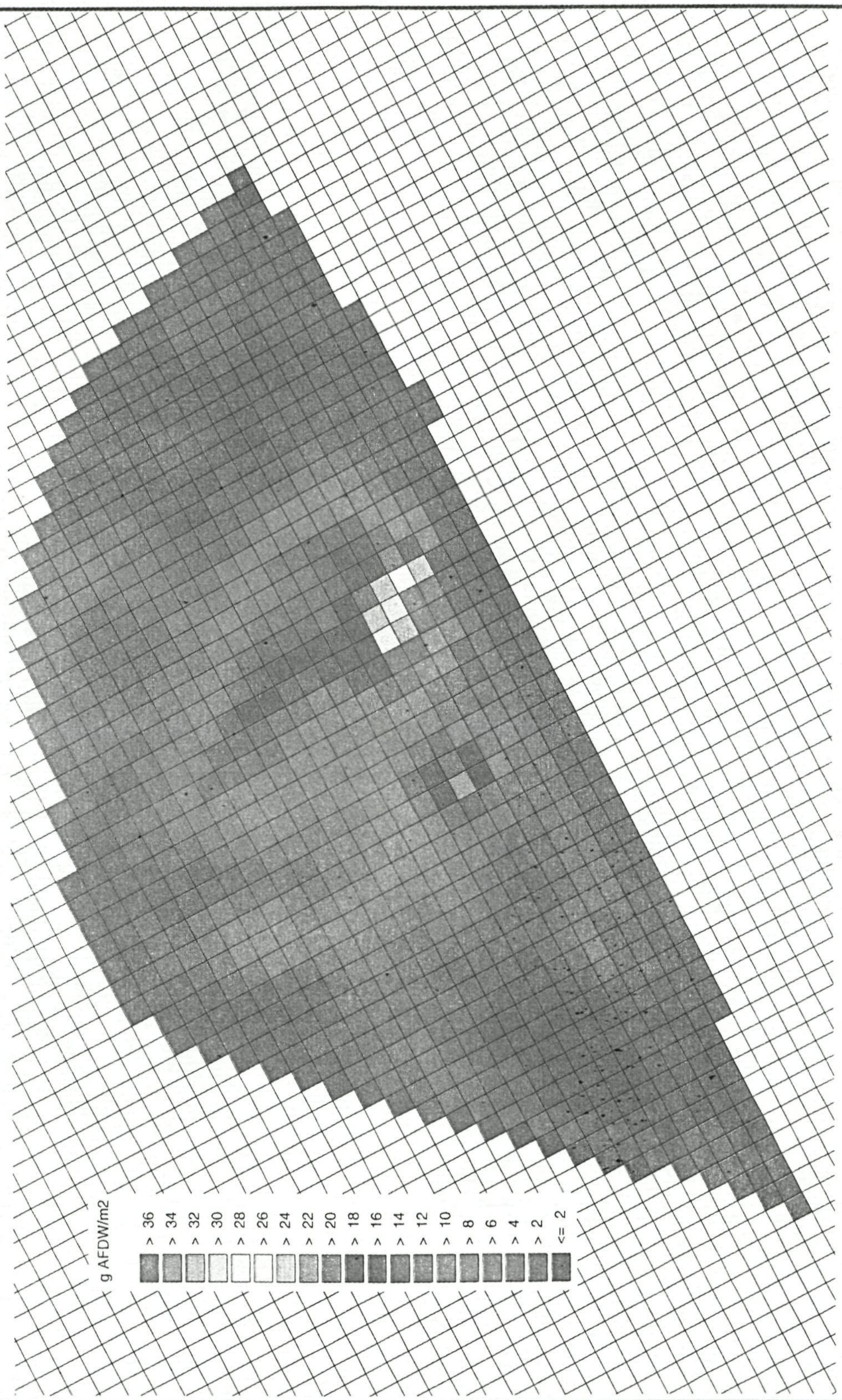
Substrate dynamics against density SF

DELFT HYDRAULICS

BEON micro/macro

P06b

Fig. 3.22



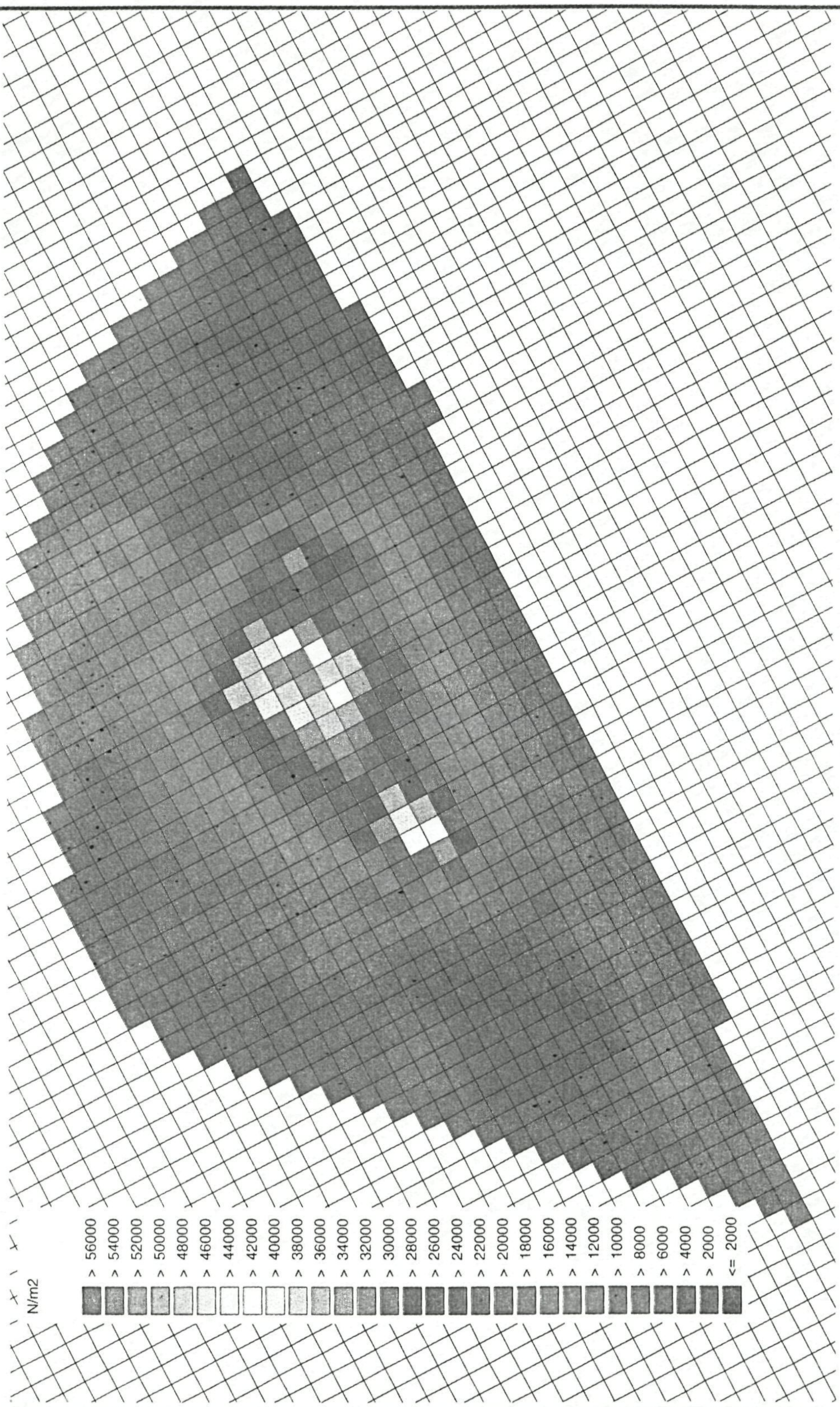
BEON micro/macro

Biomass surface deposit feeders (g AFDW/m^2)

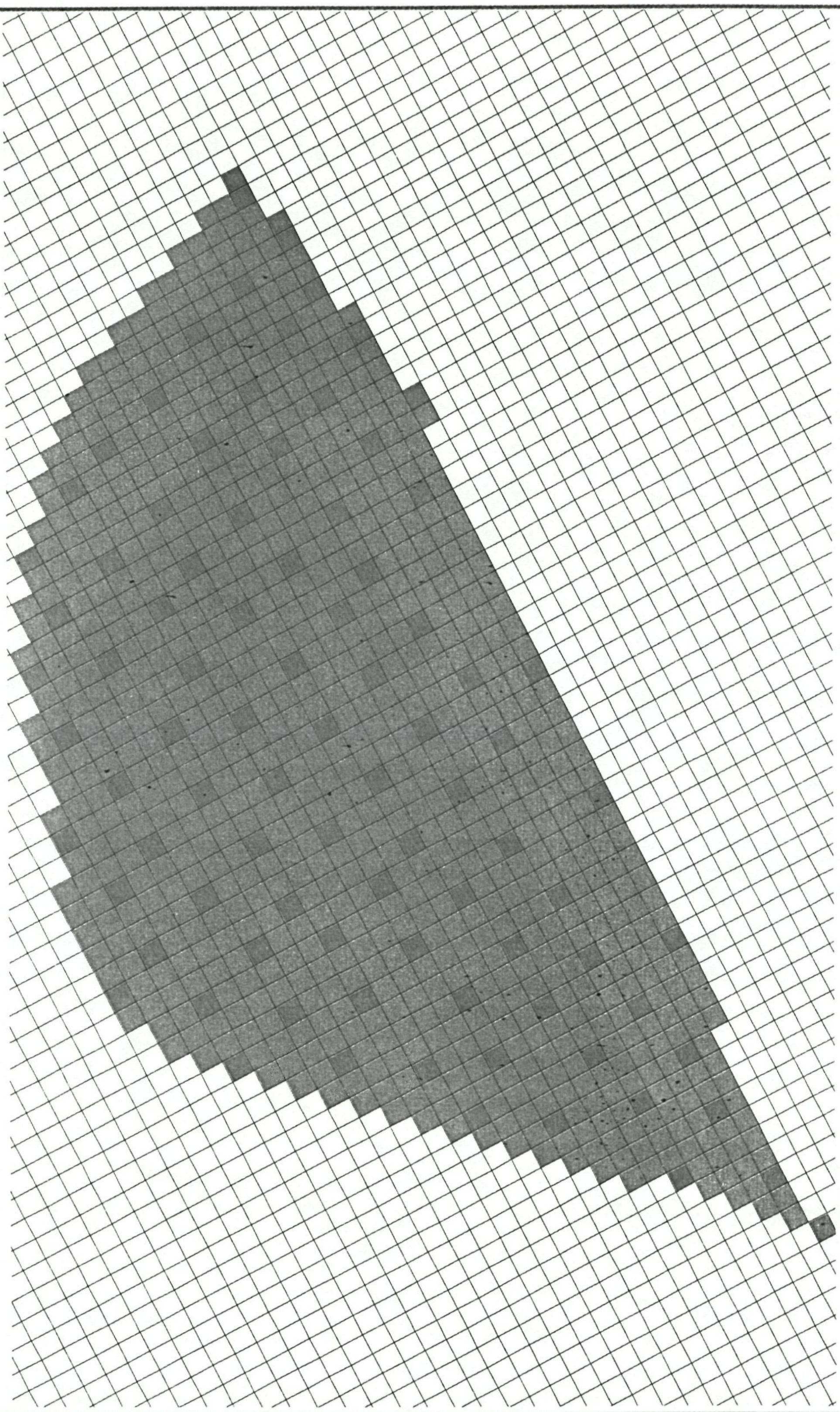
June '95

DELFT HYDRAULICS

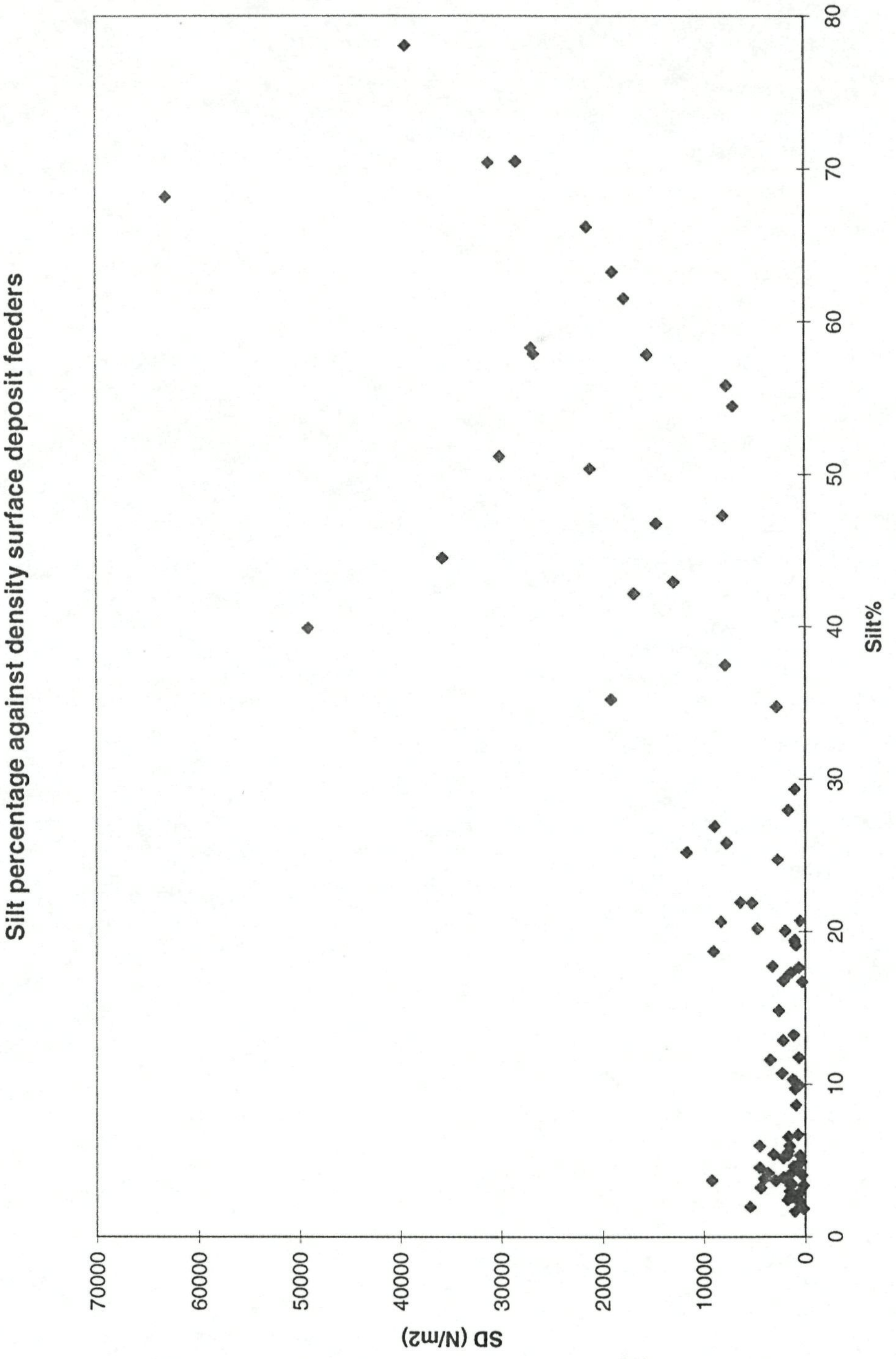
Fig. 3.23



Density surface deposit feeders (N/m^2)	BEON micro/macro June '95
DELFT HYDRAULICS	Fig. 3.24



Sample points for surface deposit feeders	BEON micro/macro
	June '95
DELFT HYDRAULICS	Fig. 3.25



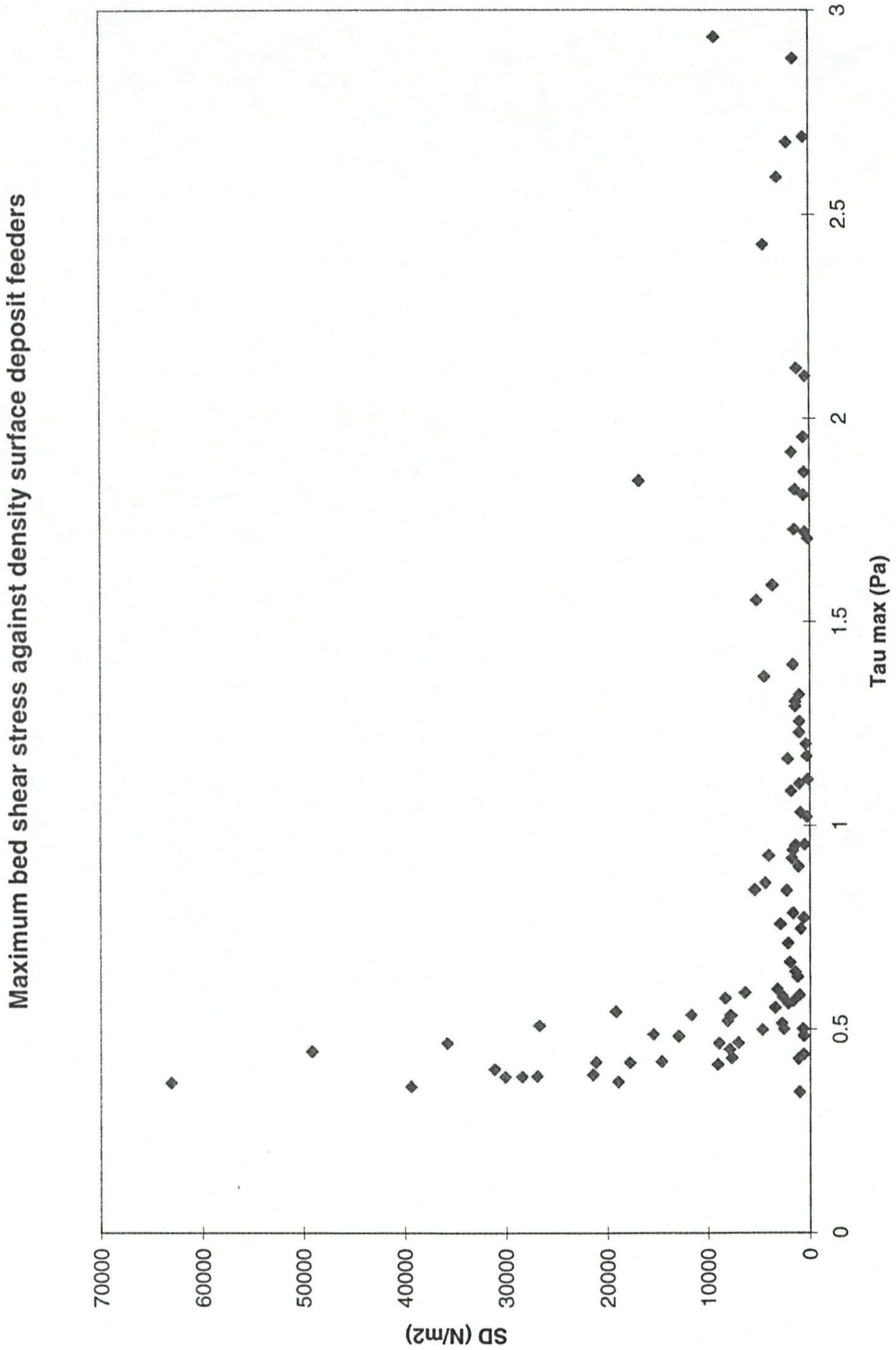
Silt percentage against density SD

BEON micro/macro

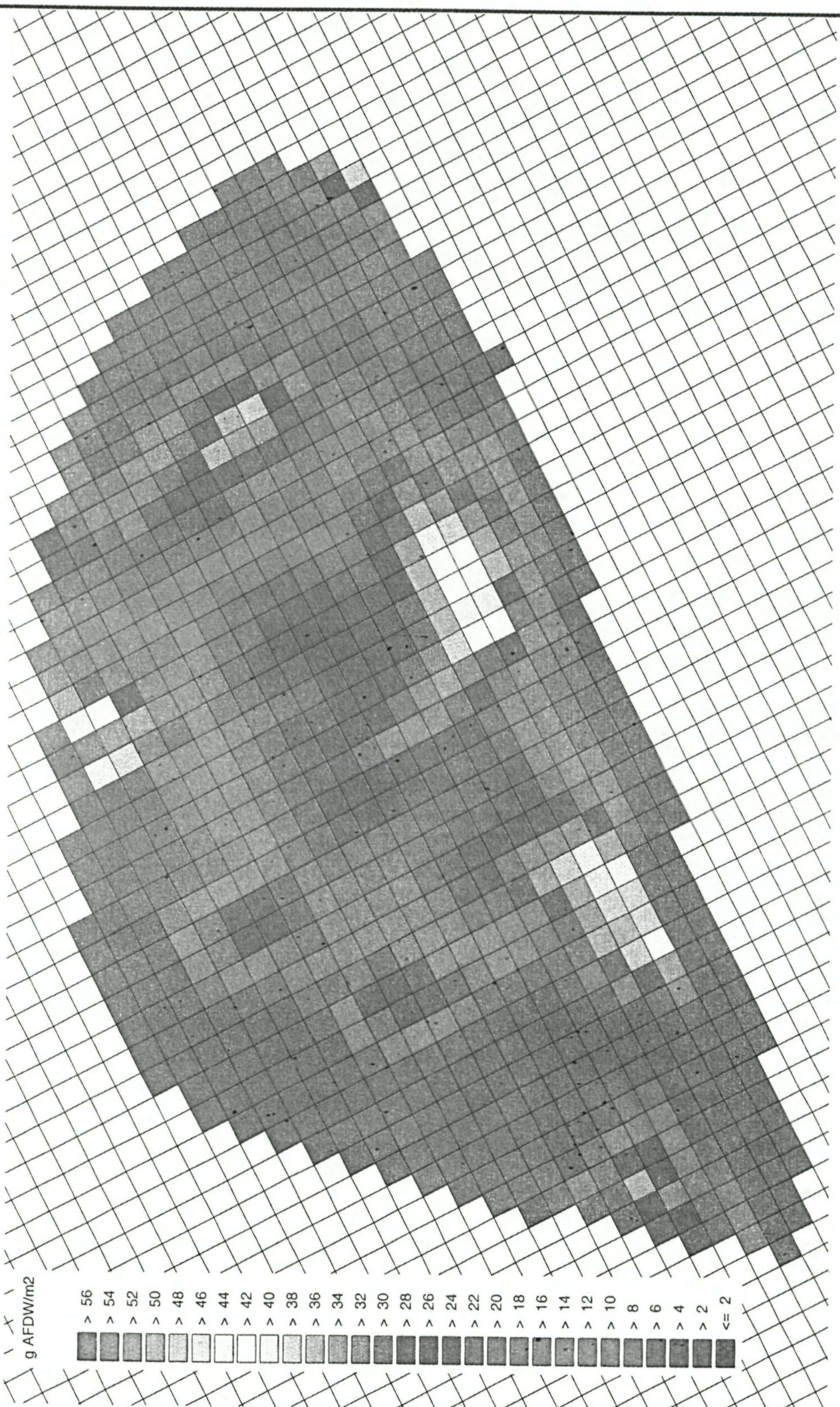
P06b

DELFT HYDRAULICS

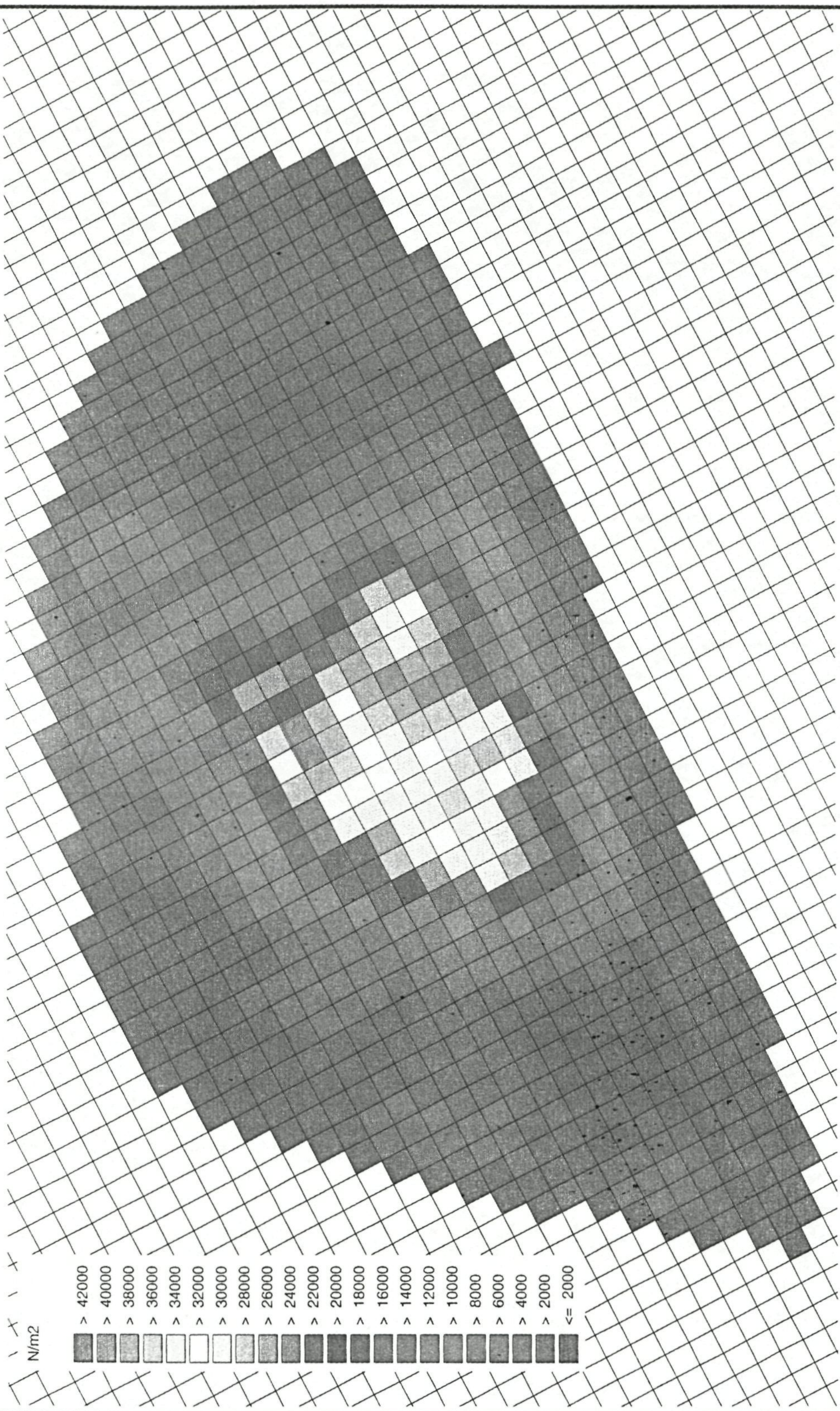
Fig. 3.26



Maximum bed shear stress against density SD	BEON micro/macro	
	P06b	
DELFT HYDRAULICS	Fig. 3.27	



Biomass deposit feeders (g AFDW/m²)	BEON micro/macr
	June '95
DELFT HYDRAULICS	Fig. 3.28



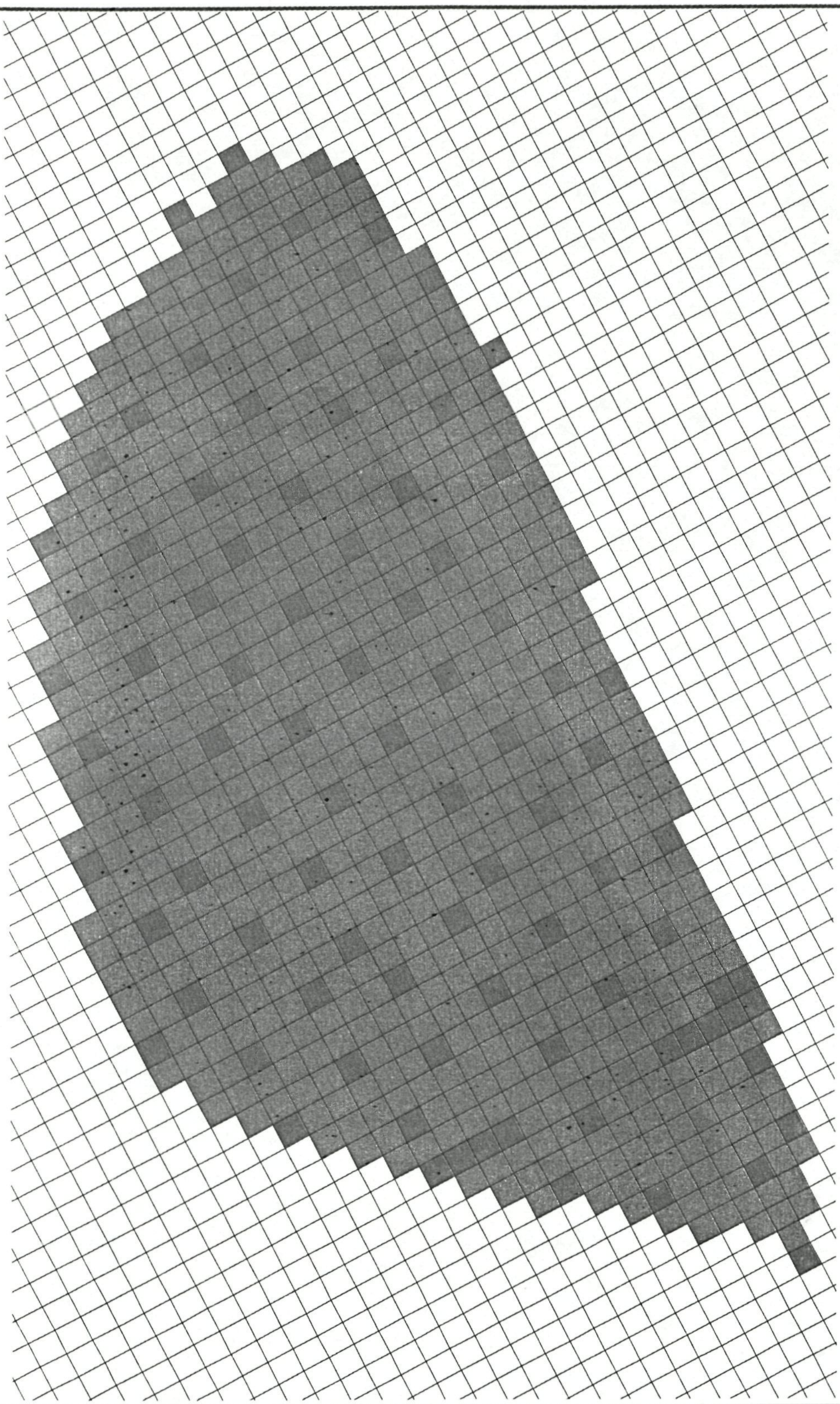
Density deposit feeders (N/m^2)

BEON micro/macro

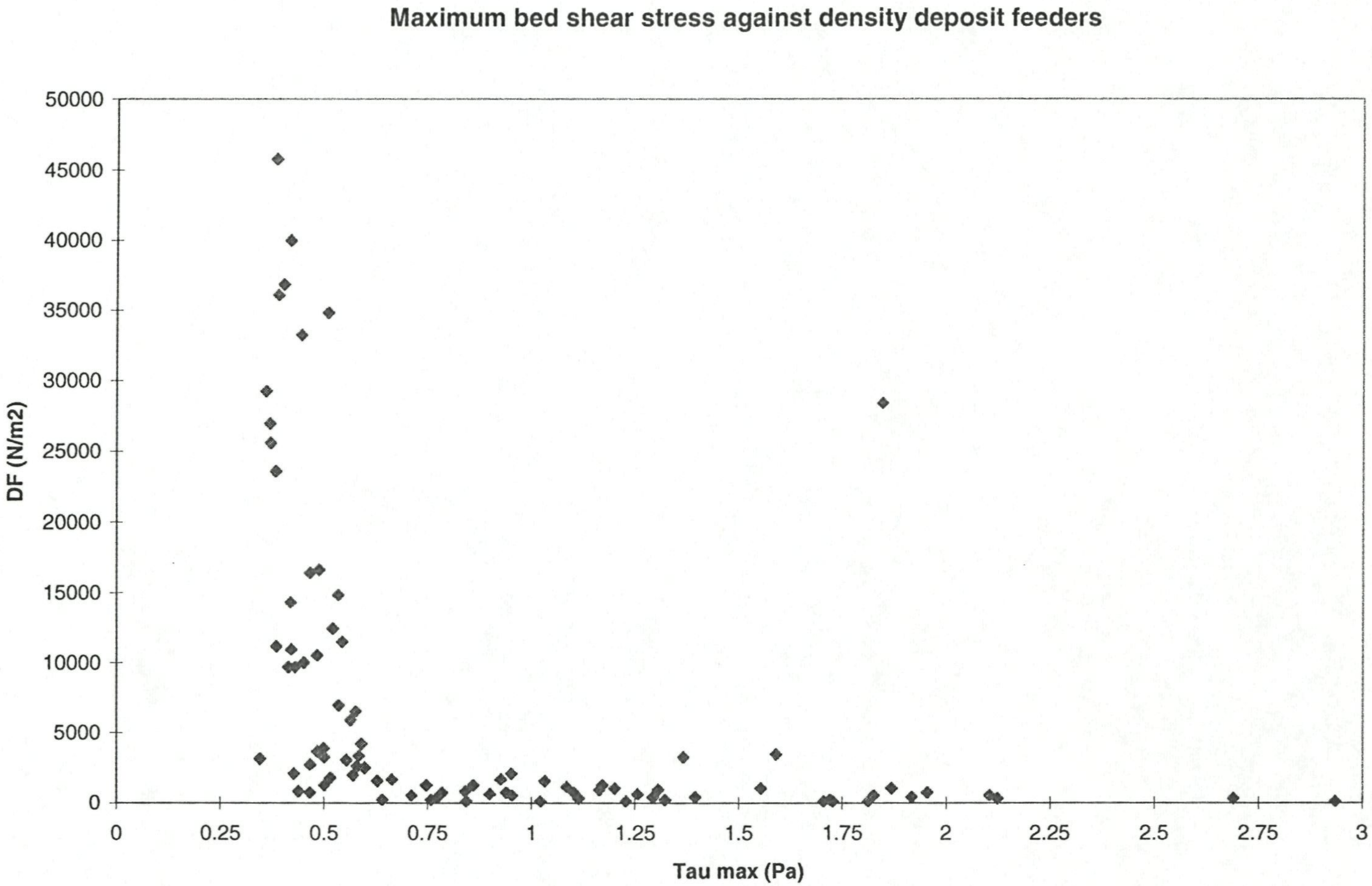
June '95

DELFT HYDRAULICS

Fig. 3.29



Sample locations of deposit feeders	BEON micro/macro
	June '95
DELFT HYDRAULICS	Fig. 3.30



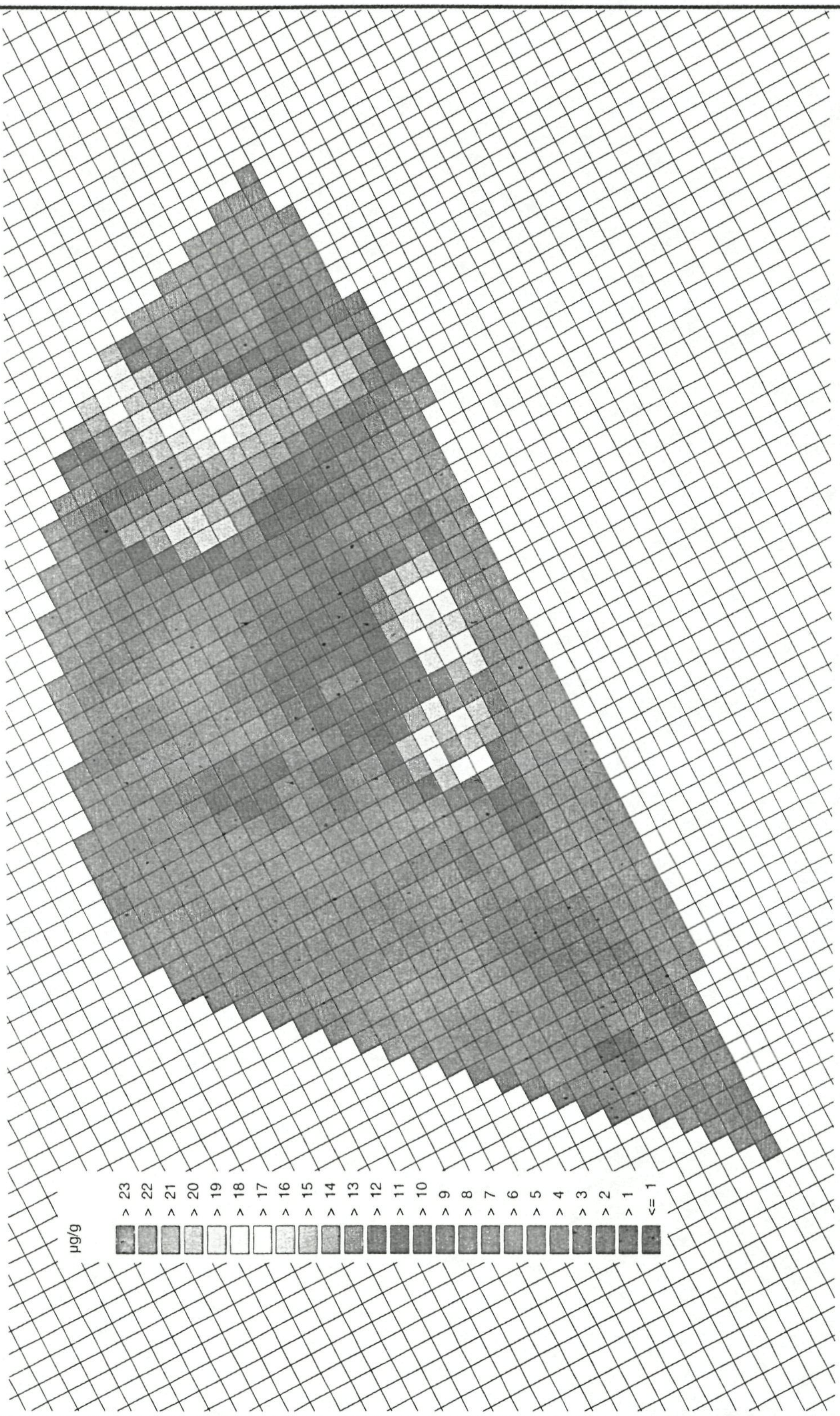
DELFT HYDRAULICS

Maximum bed shear stress against density DF

BEON micro/macro

P06b

Fig. 3.31



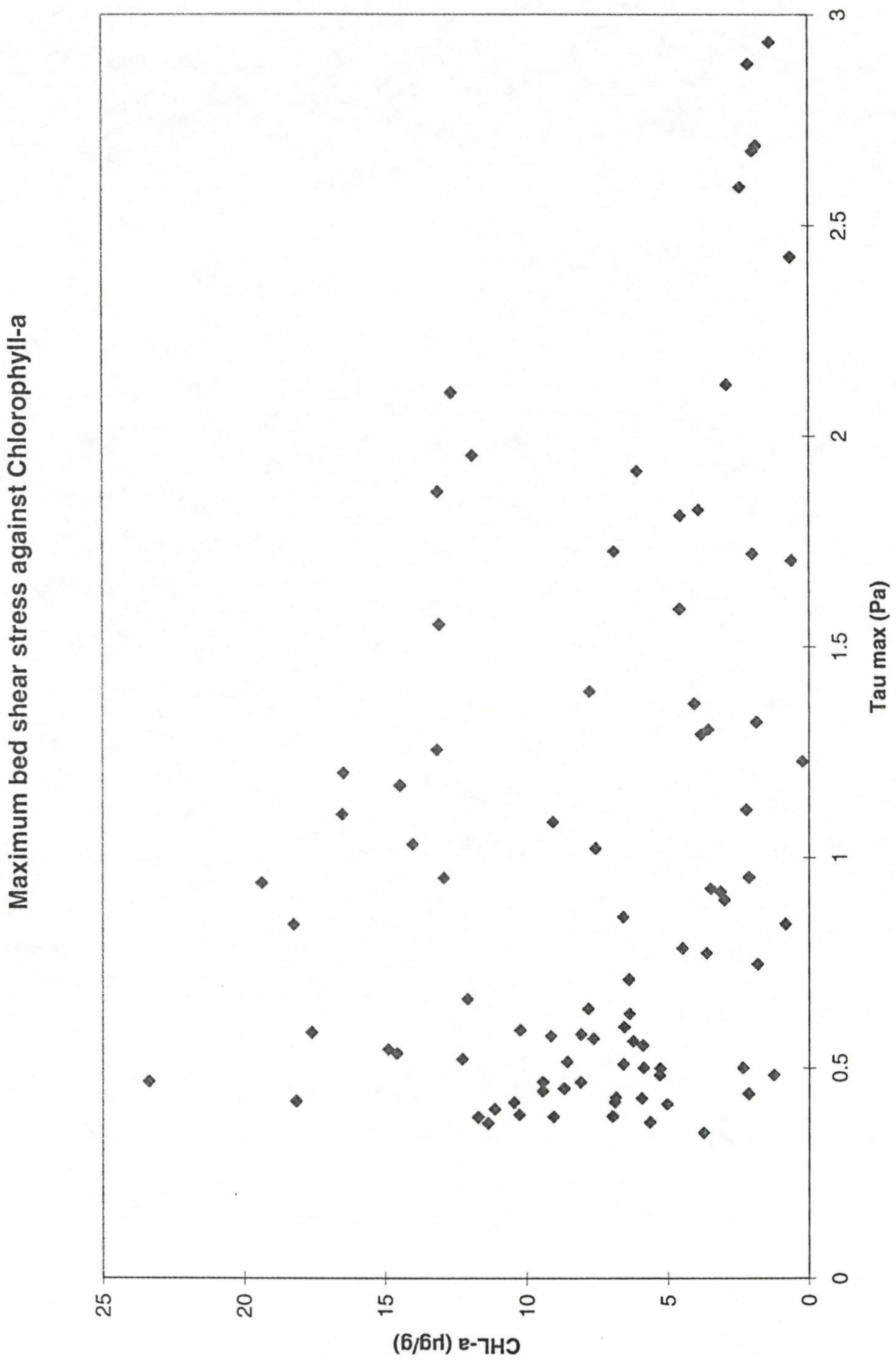
Chlorophyll-a content (µg/g dry sediment)

BEON micro/macr

June '95

DELFT HYDRAULICS

Fig. 3.32



Maximum shear stress against Chlorophyll-a

BEON micro/macro

P06b

DELFT HYDRAULICS

Fig. 3.33

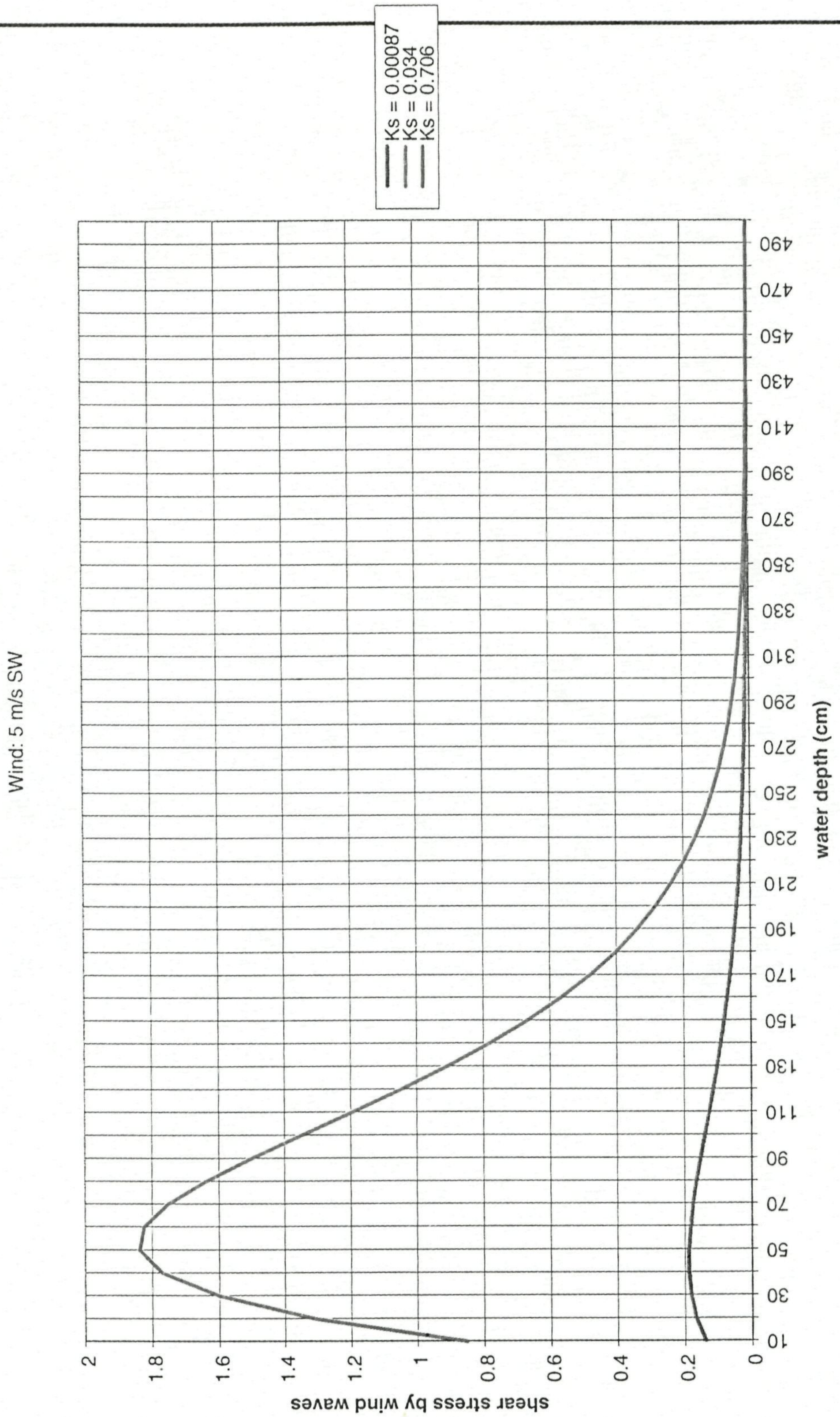
Maximum shear stress BEON model

BEON micro/macr

P06b

DELFT HYDRAULICS

Fig. 3.34

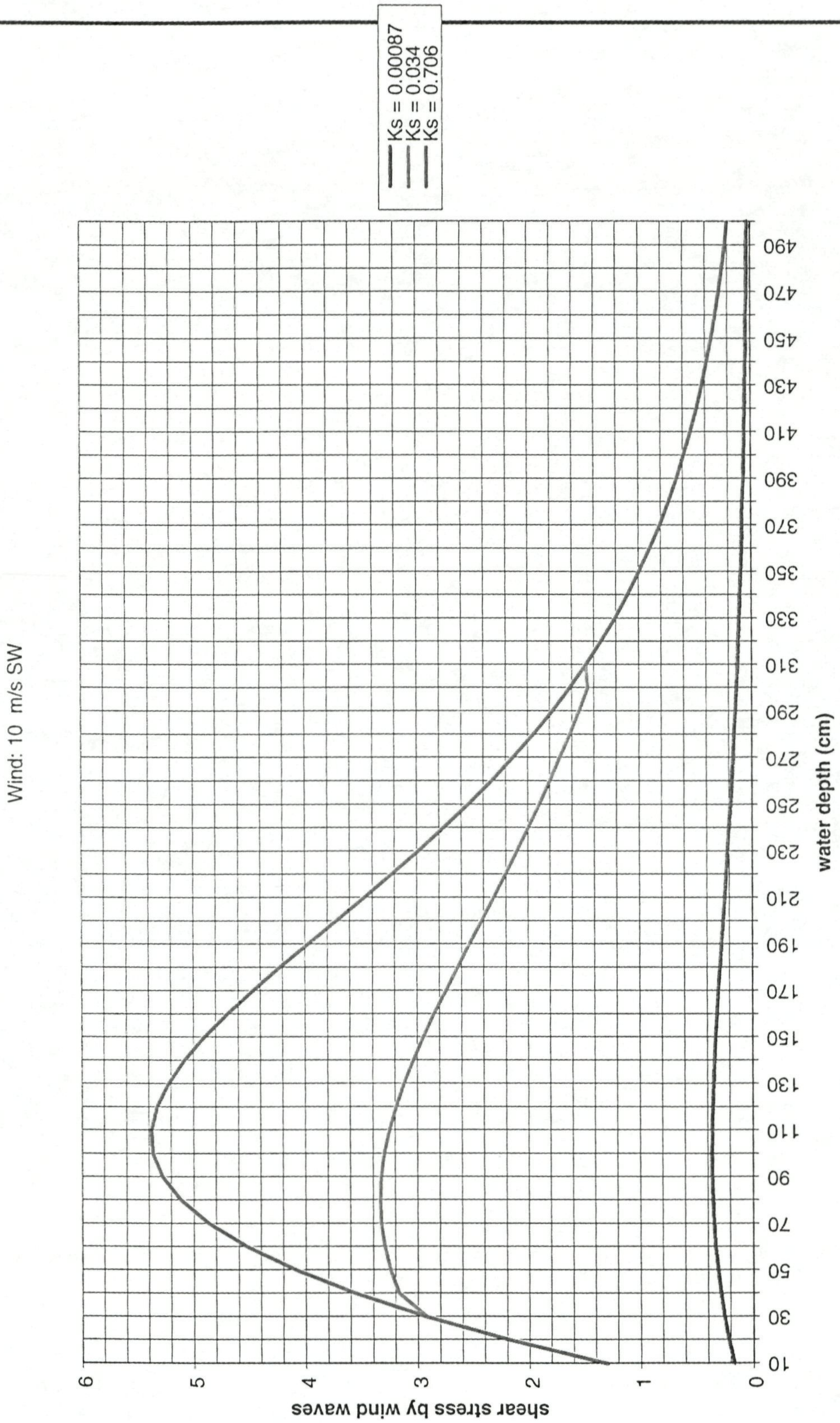


Shear stress by wind waves 5 m/s

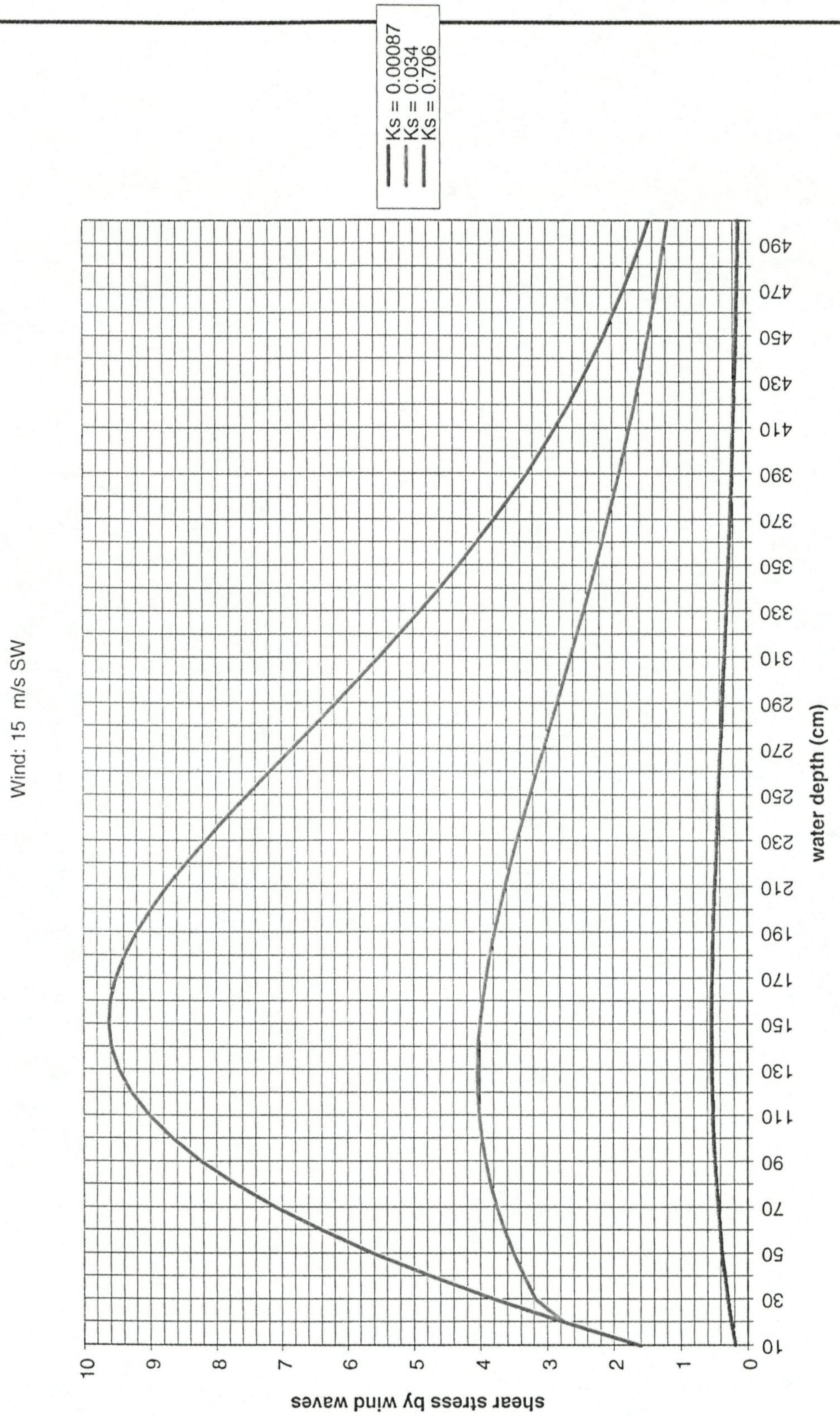
BEON micro/macro

DELFT HYDRAULICS

Fig. 3.34.A



Shear stress by wind waves 10 m/s	BEON micro/macro
DELFT HYDRAULICS	Fig. 3.34.B



Shear stress by wind waves 15 m/s

BEON micro/macro

DELFT HYDRAULICS

Fig. 3.34.C

Comparing patterns in macrofauna structure at different scales: within tidal flats, between tidal flats and between estuaries

Peter Herman (NIOO-CEMO)

Contents

Introduction

In the present report we describe the results of a sampling campaign focused on larger scale variation in the intertidal benthos of the Westerschelde. Previously, we reported on the results of a detailed survey performed on the Molenplaat, a small intertidal flat near Hansweert. The results obtained during these surveys indicate that, contrary to the original hypothesis underlying this work, suspension feeders and, in fact, macrobenthos in general, attain the highest biomass and density values at the stations with a relatively high silt content and a low bottom shear stress as calculated from a detailed hydrodynamic model. The aim of the larger scale work reported here was to investigate whether larger-scale gradients in system productivity modify the relationship as determined at small scales on the Molenplaat. Field and model studies on primary productivity (Soetaert et al., 1994) show that there is a strong gradient in net primary productivity in the Westerschelde, from negative values around the Belgian-Dutch border, to values in the order 100 gC $m^{-2}y^{-1}$ near the mouth. It was anticipated that this variation in primary productivity of the pelagic system would be reflected in the biomass of the benthos found on four intertidal flats, spanning more than half of the distance between the border and the mouth.

In order to make the four flats sampled as comparable as possible, we chose 4 flats that shared with the Molenplaat their general size, and the feature that they are situated upstream of a larger flat. The Molenplaat was one of the four, in order to confirm general consistency with the previous more detailed survey. The number of samples per flat was approximately equal to give them comparable weight in the analysis, and all sampling was performed on systematic grids.

Apart from a general descriptive aspect, questions asked in this study are the existence of a general monotonous trend in biomass, the existence of differences in the relationship between hydrodynamics (or its proxies sediment grain size) and benthic composition and biomass, and the possibilities to extrapolate relationships obtained within the Molenplaat to the whole estuary.

The data obtained in the Westerschelde during this campaign, are compared to an existing database on the benthos of the Oosterschelde. These data have been published by Meire et al., 1994. Three tidal flats in the Oosterschelde have been extensively sampled, once in autumn 1985, once in autumn 1989. The flats are the Roggenplaat in the mouth of the estuary, the Galgeplaat in the centre of the estuary, and the Krabbenkreek in the northern branch. This data base provides a useful comparison, because it allows investigation of another within-estuary trend and the comparison between the Westerschelde, where pelagic primary production is very limited, and the Oosterschelde with a much more elevated level of pelagic primary production.

Material and methods.

Field sampling.

A grid was designed on the four tidal flats, that would result in app. 100 samples. The grid had a spacing of app. 200 m between the sampling points, except on the Valkenisse flat, where the spacing was app. 300 m. The co-ordinates and maps with the sampling locations are given in Fig. 1. Sampling points were located in the field using a portable dual GPS system, with a precision of app. 5 m.

At each sampling location, one sediment core of inner diameter 11 cm, was taken to a depth of 30 cm. The material was sieved in the field over a 1 mm sieve, and the residue fixed in buffered formaldehyde (4 % final concentration). A sample for sediment grain size analysis was taken with a small core, of which the top 1 cm was sampled.

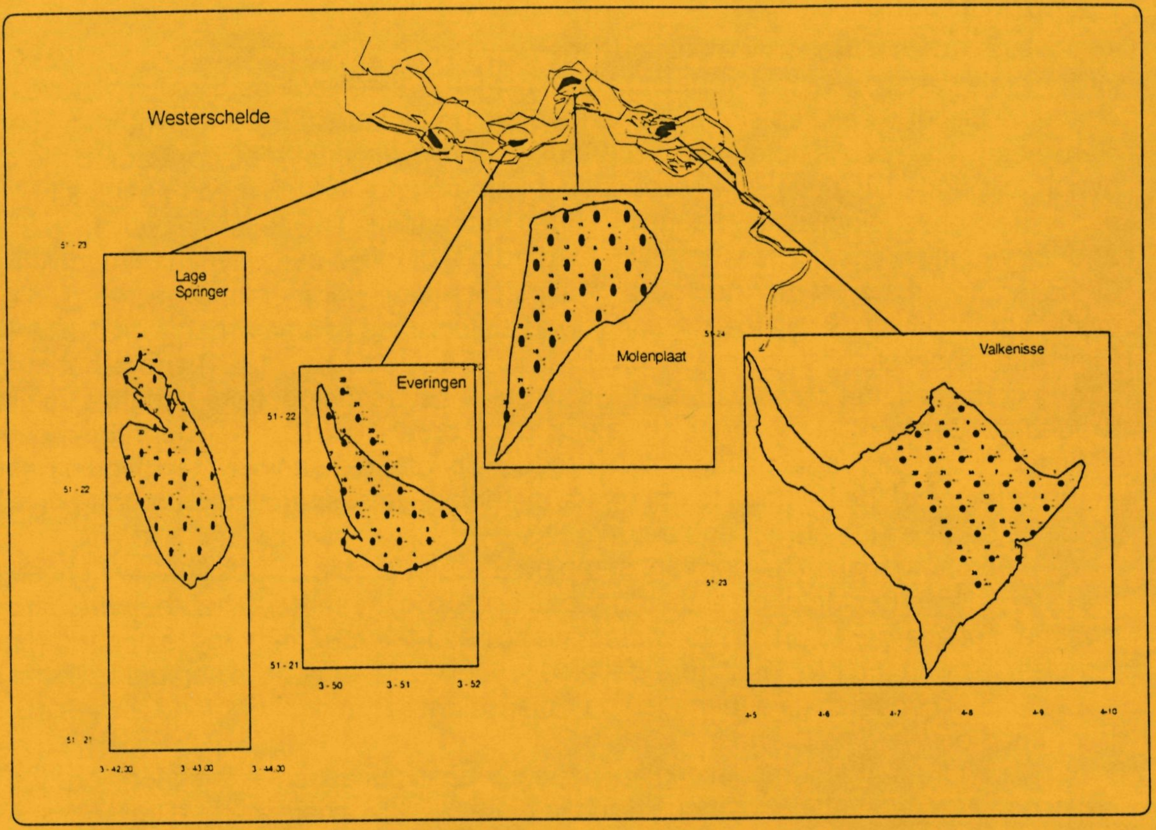


Fig. 1 Map of the Westerschelde, indicating the four intertidal flats sampled. Contours of the flats are based on 1994 bathymetry, dots indicate sampling points. Where dots fall outside the contours, the position of the flats has changed.

Laboratory Analysis

In the laboratory, all animals were picked out under a dissecting microscope, and identified to species when possible. Higher taxonomic levels had to be used in exceptional cases. Animals were counted, and their biomass determined with one of the two following methods. For bivalves, shell length was measured and converted into ash-free dry weight (AFDW), including the organic portion of the shell, using length-weight regressions obtained for the same species, season and estuary. For other species the blotted wet weight was determined and converted using established conversion factors for the species in the Delta area. It was checked that these conversion factors were valid for the Westerschelde.

Sediment grain size composition was determined with a Malvern laser sizer, using a focal length of 300 mm. Median, sorting and kurtosis have been calculated in μ and phi units. % of the total samples has been calculated in the classes (< 16 μm, 16-50 μm, 50-63 μm, 63-118 μm, 118-234 μm, > 234 μm).

Data analysis

The abundance data have been classified using TWINSPAN. Cut levels were set at . In the resulting diagram, the indicator species and their cut level have been indicated. For each TWINSPAN group thus determined, the mean density and biomass have been calculated. The groups have been characterised by the feeding types of the constituent species. On the basis of literature data, each species was accorded to one of the following feeding types: Deposit feeders, Omnivores, Predators, Surface deposit feeders and

Suspension feeders. The relative contribution of each of the feeding groups was calculated by summing the biomass of all the species belonging to the feeding group over all the sampling points in the TWINSPAN group, and dividing by the total biomass in the TWINSPAN group.

The TWINSPAN groups were characterised by the average % silt (< 16 µm) in the stations of the group. Of all available grain size parameters, this measure correlated best with the average biomass in the groups. The relation between biomass and % silt (< 16 µm) was further analysed by regression.

For the analysis of the relation between grain size distribution and feeding types of the benthos, five classes of stations have been produced, each representing 20 percentile classes of the distribution of silt (<16 µm) content. For each of the five classes the average composition in terms of feeding groups has been calculated. As a check on the calculations, they have also been repeated using the content of very fine sand as an independent variable.

Maximum bottom shear stress values (TauMax, Pa) have been obtained from a run of the Scaldis model, provided by M. Baptist and P. Thoolen (Delft Hydraulics). These values have been related to sediment grain size composition and composition of the fauna.

Maps of several variables have been produced. In these maps, a column proportional in height to the variable, is plotted with its base at the position of the sampling point. The location of the four tidal flats relative to one another reflects their position in the estuary, but the size of the flats is largely exaggerated to make the graphs readable.

Results

TWINSPAN analysis

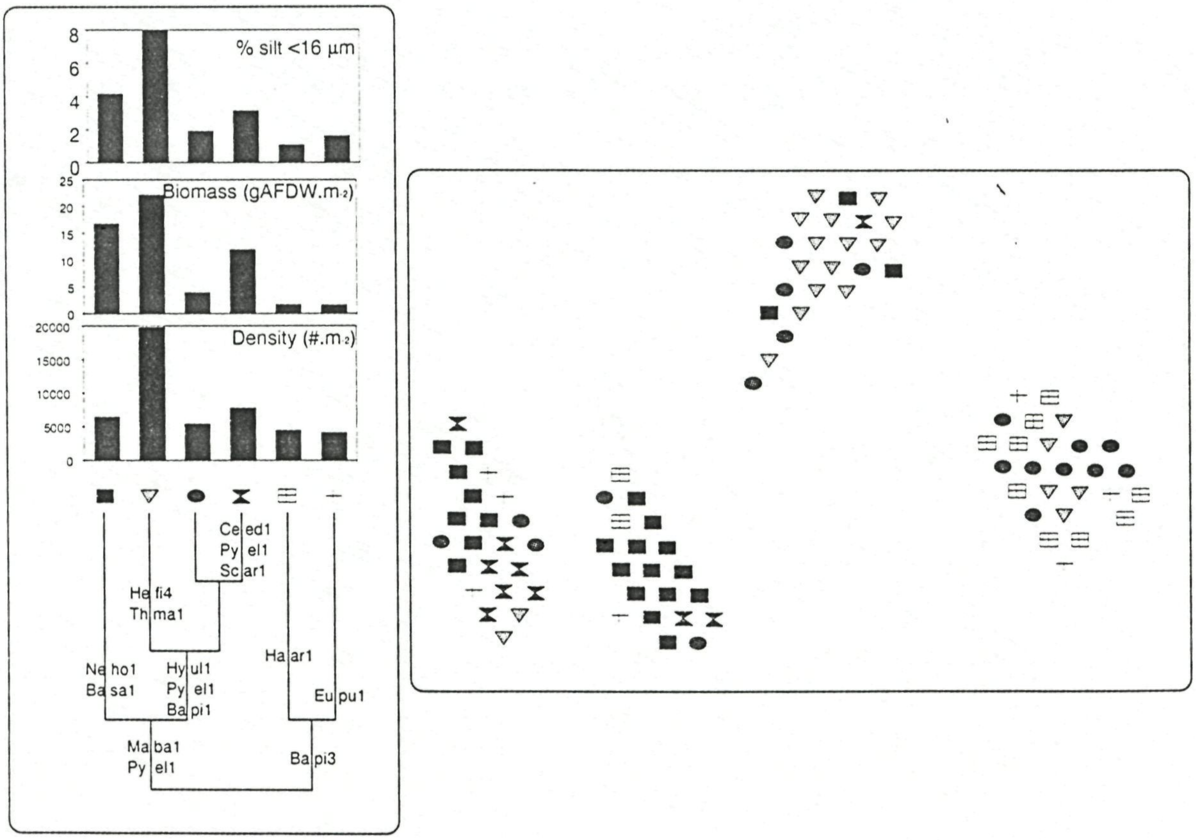


Fig. 2. Results of the TWINSPAN analysis. The diagram shows the division. For each group the average density, biomass and sediment silt content is shown. The map shows the spatial distribution of the groups.

The results of the TWINSPAN analysis are shown in Fig. 2. Six groups have been retained.

The division diagram shows that the first distinction was made on the basis of high abundance (cut level three) of *Bathyporeia pilosa*. This is a mobile surface deposit feeding crustacean typically occurring in mobile sand stations. Within the group of stations showing this species in high abundance, a further distinction was made on the basis of the occurrence of either *Haustorius arenarius* or *Euridyce pulchra*. It is unclear what factor is responsible for this distinction. In their spatial distribution both groups of stations are restricted to the outer margins of the flats, typically the places where the sand bars occur. This region was most extended on the Valkenisse flat. Both TWINSPAN groups (5 and 6) had low silt content and low biomass. They were largely dominated by surface deposit feeders (Fig. 3).

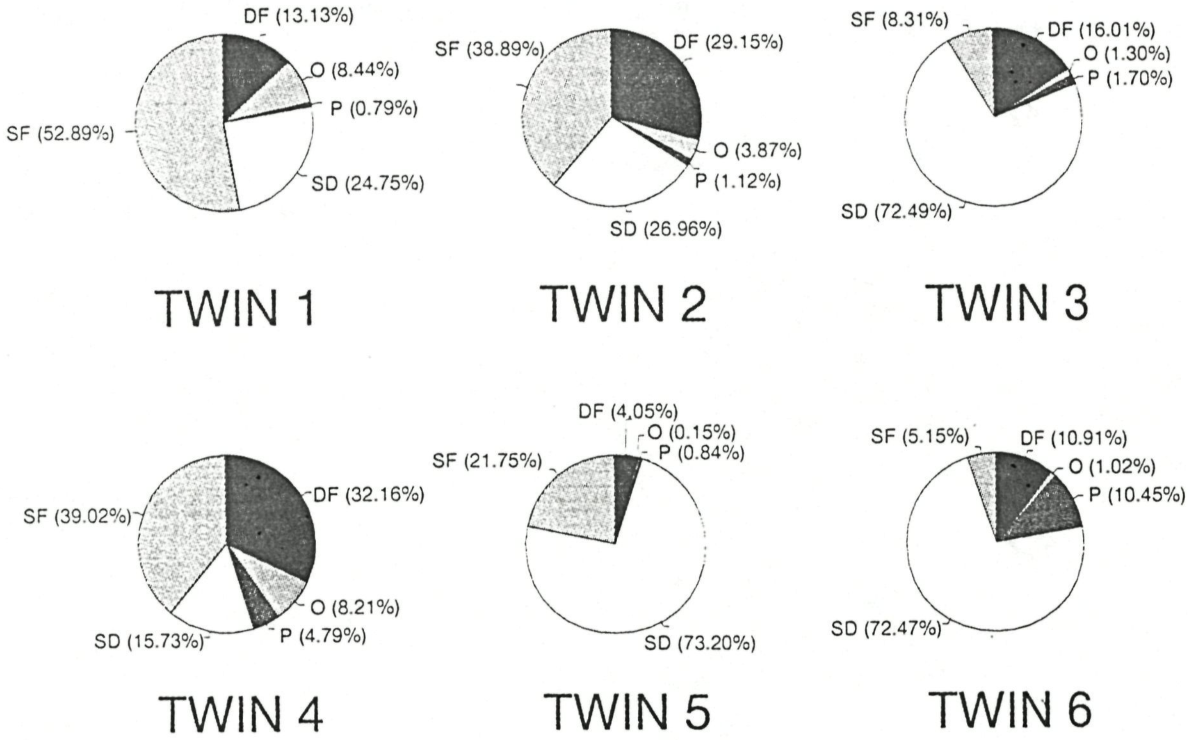


Fig. 3. Feeding group composition of the different twinspan groups. SF: suspension feeders, DF: deposit feeders, O: omnivores, P: predators, SD: surface deposit feeders

The other group, less subject to extreme physical stress, was first subdivided in a group identified by *Nephtys hombergii* and *Bathyporeia sarsi*. Both species tend to occur mainly in the more marine part of the estuaries in the south-west of the Netherlands. They typify an assemblage with a high dominance of suspension feeders (mainly cockles) (Fig. 3) and a relatively fine sediment. The high biomass in these sediments was mainly due to large individual size, since it was not reflected in high density values (Fig. 2).

The alternative group in this distinction was characterised by *Hydrobia ulvae, Pygospio elegans* and *Bathyporeia pilosa*. It subdivided into TWIN 2 (high abundance of *Heteromastus filiformis*; presence of *Tharyx marioni*) and the cluster of TWIN 3 and TWIN 4. TWIN 2 was the richest assemblage, with highest abundance and biomass. This group occurred in the finest sediments. It was most prominent on the central part of the Molenplaat, with a few occurrences elsewhere. It had an approximately equal composition of surface deposit feeders, deep deposit feeders and suspension feeders.

TWIN 3 was a relatively poor (in density and biomass) assemblage of mainly surface deposit feeders living in sandy, silt-poor sediments. It had no indicator species associated to it. Its occurrence was mostly on the Valkenisse flat, where it occupied the relatively stable, sandy stations. TWIN 4 (indicators *Cerastoderma edule*, *Pygospio elegans*, *Scoloplos armiger*) was more diverse in feeding types, contained a considerable portion of suspension feeders, and had higher biomass and density in a slightly more silty sediment. It occurred mostly on the two seaward flats.

Spatial distribution of density and biomass

Fig. 4 shows the relative distribution of biomass over the tidal flats, together with the average (± standard error) for each tidal flat. Average biomass was highest on the Molenplaat, followed by the Everingen flat, Lage Springer and Valkenisse. The distribution was markedly more even in the two most landward flats. On the Everingen and Lage Springer flat the differences between highest and lowest biomass values were much more expressed.

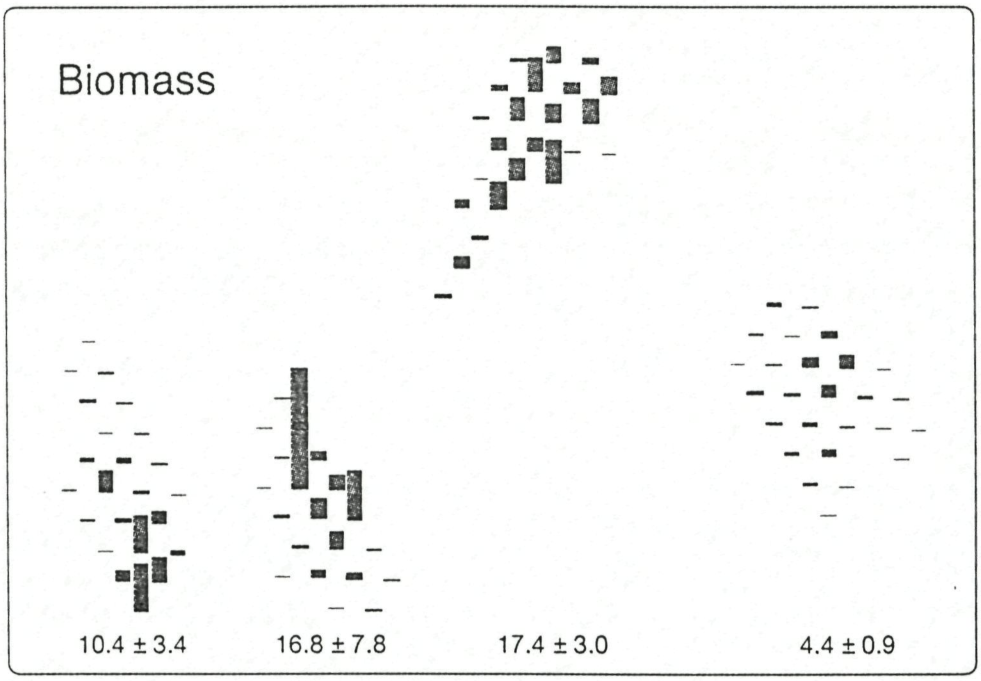


Fig. 4. Spatial distribution of total sample biomass (g AFDW m^{-2}). The bars placed at the location of the samples have a height proportional to the sample biomass. Below each flat the average ± standard error for the flat is shown.

The distribution of density (Fig. 5) shows that the average size of individuals was not equal between flats. The smallest individuals occurred on the Valkenisse flat, followed by the Lage Springer, the Molenplaat and the Everingen flat. In general, the distribution of density values over the samples was more even than the distribution of biomass. This indicates that high biomass values were usually obtained due to large individual size of the animals, rather than to very high density.

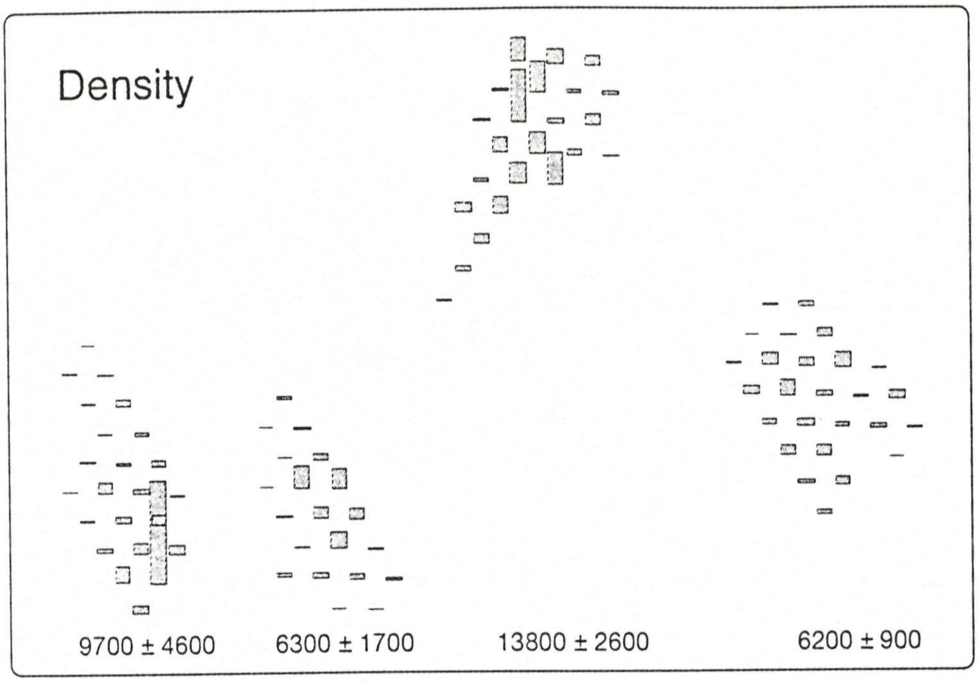


Fig. 5. Spatial distribution of total sample density (number m^{-2}). The bars placed at the location of the samples have a height proportional to the sample density. Below each flat the average ± standard error for the flat is shown.

Sediment grain size

Of the different grain size variables obtained, we show in Fig. 6 the relative spatial distribution of the silt fraction smaller than 16 µm. The finest sediments occurred on the

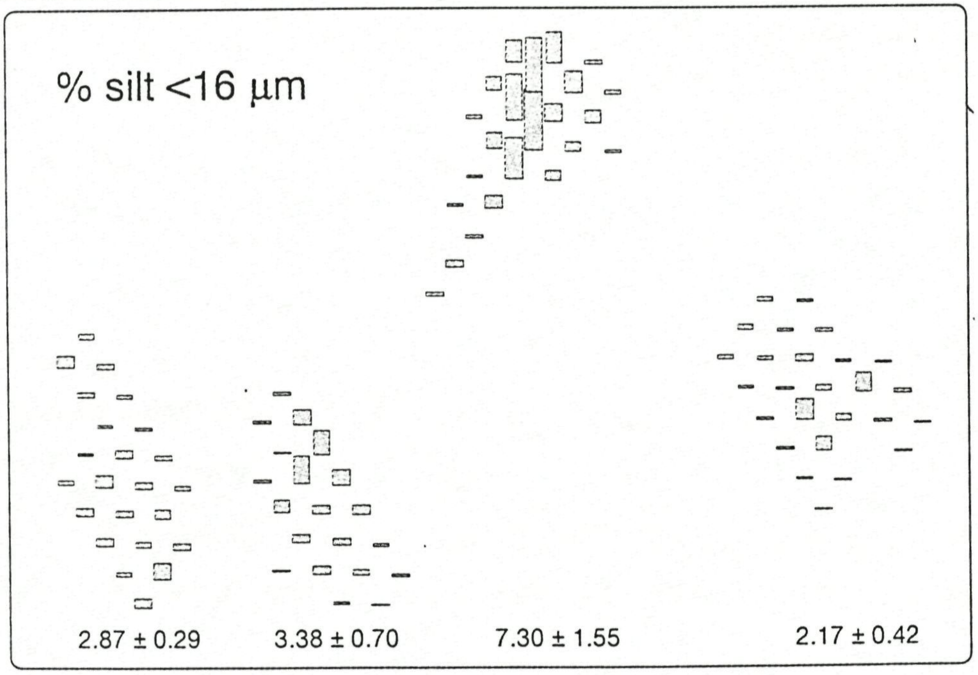


Fig. 6. Spatial distribution of sediment fine silt content (%). The bars placed at the location of the samples have a height proportional to the sample silt content. Below each flat the average ± standard error for the flat is shown.

Molenplaat, where they also occupied the largest surface. On the Valkenisse and Lage Springer flats, stations with high silt content were scarce. The relative spatial distribution of the fine sand fraction was well correlated with the silt distribution.

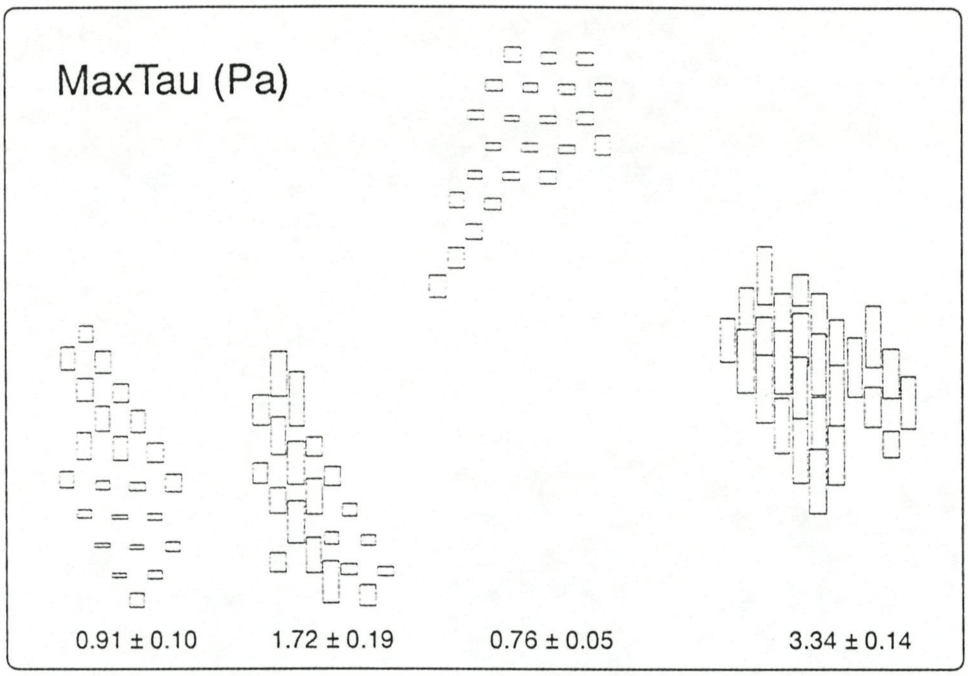


Fig. 7. Spatial distribution of maximal bottom shear stress during a tidal cycle (Pa). The bars placed at the location of the samples have a height proportional to the bottom shear stress. Below each flat the average ± standard error for the flat is shown.

Correlation between variables

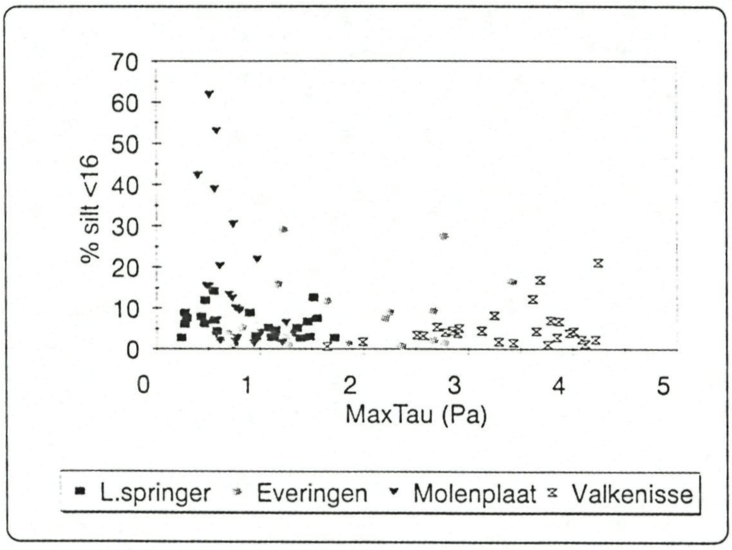


Fig. 8. % fine silt in the sediment, plotted as a function of maximum bottom shear stress during a tidal cycle

Surprisingly, we found no correlation between maximal bottom shear stress (Fig. 7) during the tidal cycle and the sediment grain size composition. Such a correlation is expected on theoretical grounds; the reason for the lack of correlation (Fig. 8) is unclear and will be the subject of further investigations. Only within the Molenplaat, a correlation was found.

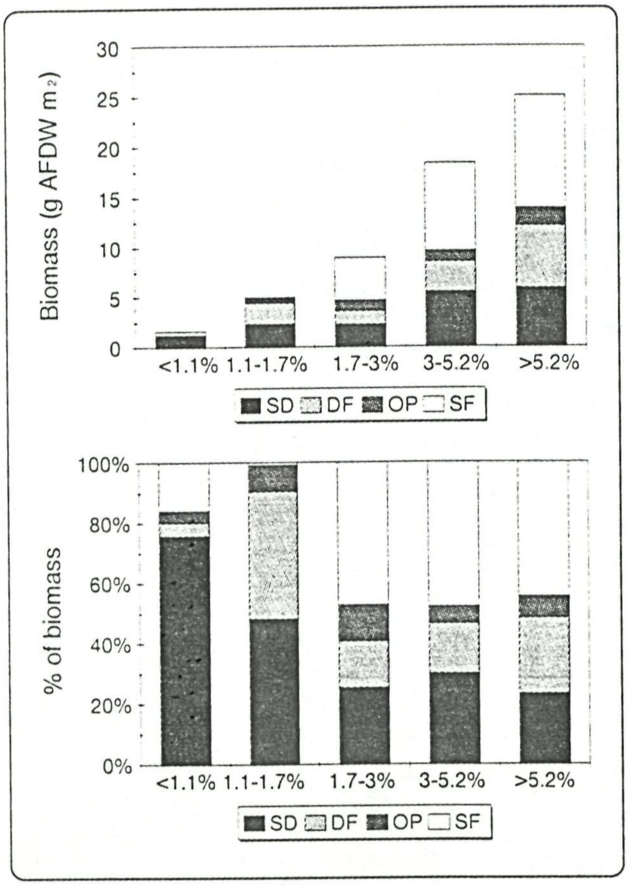


Fig. 9. Composition of the fauna in terms of feeding groups for five silt content classes (each representing 20 percentiles of the silt distribution). SD: surface deposit feeders, DF: deposit feeders, OP: omnivores/predators, SF: suspension feeders

Silt content of the sediment appeared to be a good predictor of macrobenthic biomass in general. Considering the average values for each of the flats, a 1:1 correspondence in ranking of the flats is found. The grouping of stations in 20-percentile classes of silt content showed a strong correlation with total biomass, and with composition of the macrobenthos in terms of feeding groups (Fig. 9). The exponential increase of average biomass with increasing silt content is apparent in Fig. 9a, while Fig. 9b shows that the relative composition of the feeding groups shifted abruptly twice: below 1.1 % silt content deep deposit feeders were nearly absent, and the fauna was largely dominated by surface deposit feeders. Around 1.7 % silt content a second shift showed the appearance of suspension feeders, which however remained a remarkably constant proportion of total biomass in the higher silt content classes.

Also for individual sampling points, a significant (log-log) correlation between silt content and total biomass was found. This relation, however, was not constant across the different tidal flats. Analysis of covariance showed a significant difference in slope between the regression lines for the different flats. These regression lines appeared to fall in two groups (Fig. 10). Lage Springer and Everingen flat had a much steeper regression line than did Molenplaat and Valkenisse. Within the latter group, the slopes were not significantly different, but the intercept was significantly higher in the Molenplaat.

Analyses for the correlation between

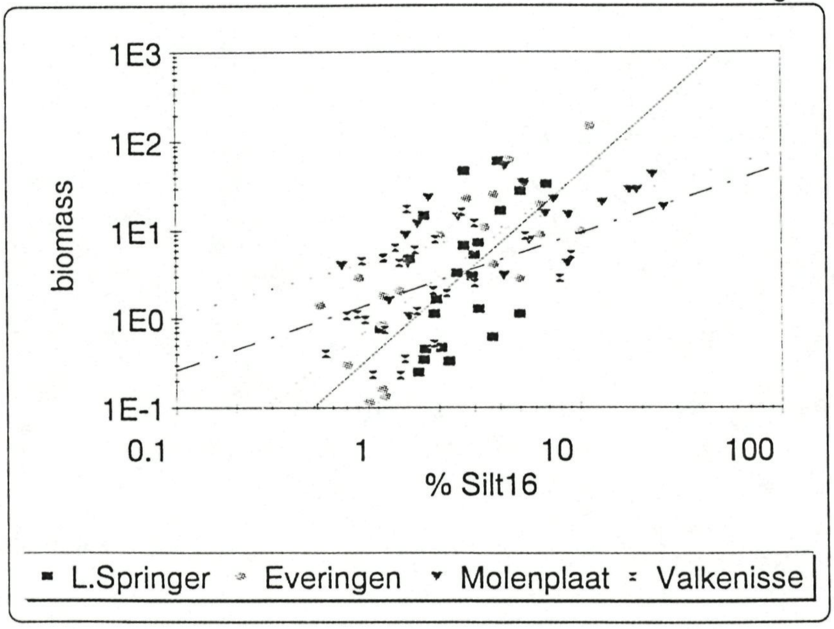


Fig. 10. Correlation between total biomass and sediment silt content, with regression lines for the four flats.

TauMax and biomass showed no significant relation at all.

Oosterschelde data set

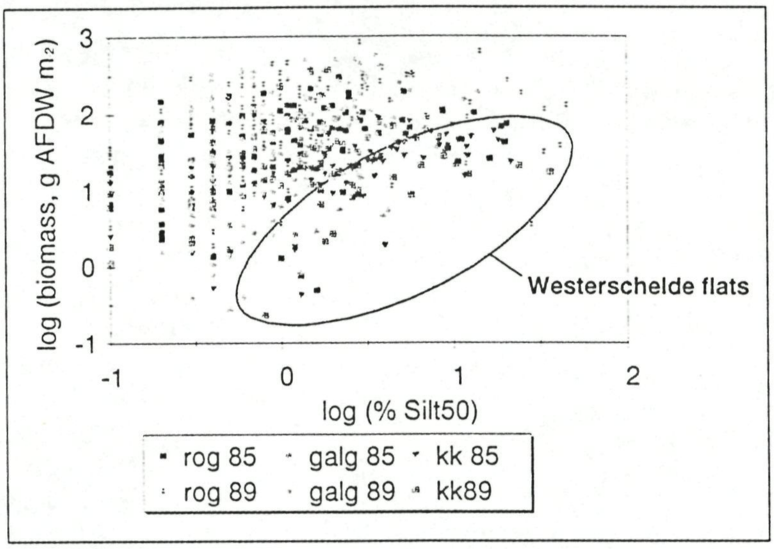


Fig. 11. Relation between total biomass and sediment silt content for the Oosterschelde data set. The ellipse encompasses the Westerschelde data on the same scales.

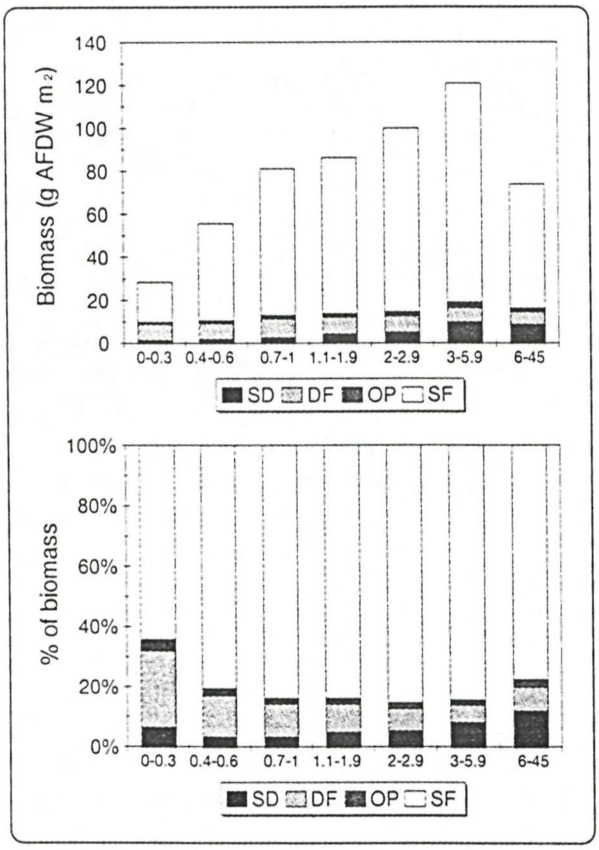


Fig. 12. Feeding types in silt classes in the Oosterschelde. Abbreviations as in Fig. 9.

Fig. 11 illustrates the relation between silt content of the sediment and benthic biomass for the Oosterschelde data set. Silt content lower than 50 μm was used, since these were the only data available. For the Westerschelde data, silt < 50 μm was well correlated with silt < 16 μm, so that no qualitative differences in the relations described is noted when 50 μm instead of 16 μm is used. The ellipse in fig. 11 encompasses the Westerschelde data set. It can be noted that biomass in general is much higher for the Oosterschelde samples, especially at the lower silt content. A very weak correlation (r=0.32, n=595) between log (silt content) and log (biomass) was found for the Oosterschelde data. The absolute values of the silt content should be considered with some caution, as different measurement methodologies have been used in the two different data sets, but this does not explain the order-of-magnitude differences between the two systems, nor the difference in strength of the relationship.

Broken up by feeding types (fig. 12) the difference between the two systems appears to be entirely due to a difference in biomass of the suspension feeders. The absolute values of the biomass of the other feeding groups was quite comparable for both systems (compare figs. 12 and 9). Surface deposit feeders, deposit feeders and omnivores/predators summed up to maximum 10 -20 g AFDW m^{-2}, but in the Oosterschelde suspension feeders occurred in all sediment classes and attained much higher biomass values. This was also reflected in the percentage composition according to feeding groups, which was largely dominated by suspension feeders in all classes in the Oosterschelde.

Discussion

After the analysis of the spatial pattern of the macrobenthos on the Molenplaat (previous BEON report), the original hypothesis underlying this project had largely been falsified. The demonstration that benthic suspension feeders were mostly restricted to quiet areas on the flat, with high silt content of the sediment, falsified the hypothesis that they would be restricted to areas of high turbulence facilitating their access to pelagic resources. The results of the present survey in the Westerschelde seem to confirm this conclusion. Within each of the four tidal flat systems, benthic suspension feeders were restricted to the stations with a (relatively) high silt content of the sediment. The more exposed stations, usually at the margins of the flats, mainly had a surface deposit feeding fauna. A monotonous increase of biomass with increasing silt content has been demonstrated, and a restriction of suspension feeders to sediments with app. > 2% silt.

The second part of the hypothesis stated that the average biomass of suspension feeders would increase with increasing productivity of the water column, and that in these higher productivity areas, the suspension feeders would tend to occupy a broader niche (in terms of turbulence conditions) than in the lower productivity areas. This part of the hypothesis relied heavily on the assumption of a direct dependence between suspension feeder biomass and pelagic productivity. Between the four flats sampled in the Westerschelde, little evidence has been found to corroborate this hypothesis. There was no gradient in biomass from the mouth to the inner estuary, even when corrected for the differences in average silt content of the sediment on the flats. In fact, the correlation between average (log) silt and average (log) biomass over the four flats was very high, whereas the order of the flats in terms of silt content differed from their order in terms of (pelagic) system productivity.

Direct observations of the vertical gradients in suspended matter and chlorophyll during a tidal cycle (Herman, unpublished) suggested that the benthic fauna on the Molenplaat (and most probably also on the other Westerschelde flats) depends on erosion/deposition, rather than on turbulence mechanisms. Typically, the profiles of chlorophyll a content of the water column above the Molenplaat showed two features. First, the vertically integrated concentration was maximal at the peak of the ebb and flood currents. Second, if any vertical gradients occurred, they were systematically towards a higher concentration below, near the sediment-water interface. These two features lead to the conclusion that the bulk of the chlorophyll available to benthic suspension feeders in these systems must come from resuspension of benthic algae. The strong correlation between chlorophyll content and total suspended matter, and the fact that uptake efficiency of suspension feeders generally decreases with the concentration of inorganic suspended solids, may imply that the peak chlorophyll concentrations are relatively inaccessible to suspension feeders, but it is doubtful whether other food sources than those derived from sediment resuspension are ever of great importance as food.

It should be concluded, therefore, that in the Westerschelde flats there was no essential distinction between suspension feeders and other benthic groups in terms of their dependence on deposition, rather than on turbulence mechanisms. Nevertheless, as it was observed earlier on the Molenplaat, the number of stations where suspension feeders occurred (46 % of all stations) was much more restricted than for the occurrence of deposit feeders (77 %) and surface deposit feeders (98%). The average silt content of stations with suspension feeders (5.26 %) was higher than for stations with deposit feeders (4.55 %) or for stations with surface deposit feeders (3.95 %, which is very near to the overall mean of 3.89 % for all stations). There was a clear restriction of suspension feeders to the more silty stations, but this restriction was not responsible for the whole increase of biomass with silt content, as can be seen from Fig. 9a: the other groups also increased in biomass with increasing silt content.

The interpretation of the Westerschelde results is hampered by the lack of correlation between tidal bottom shear stress and silt content of the sediments. This result is surprising and contradictory to what was (and is again in this study) observed in the Molenplaat. The possibility that the problem is methodological cannot be excluded. Several of these flats are highly mobile. We observed in the field that the intertidal zone did not correspond with the available bathymetry maps which we used to set out the sampling grid. These maps were two years old at the time of sampling, and the net movement of the flats was at places several hundreds of meters, up to 1 km. Discrepancy in the bathymetry could be a possible explanation for the lack of fit between the model-generated shear stress and observed grain size distribution. This problem is least pronounced for the Molenplaat, which is relatively sheltered and has not been observed to move a lot over the last years. Closer examination of Fig. 6 and Fig. 7 also suggests that some patterns in both graphs are similar, but located at slightly different absolute places. A second methodological problem is the non-inclusion of wind stress in the model. This could omit an important factor in the resuspension of silt from some more exposed sediments. Finally, the availability of silt in the water could be of importance. It can be expected that in the eastern part of the estuary, where suspended silt concentrations are higher in the water, more possibilities for the deposition of silt exist than in the western part. A closer examination of these results is surely called for. Without a proper explanation of the relation between shear stress and silt content, we will use sediment silt content as a relative measure of hydrodynamic stability of the sediments.

A controversy which has arisen within the group working on this BEON project is on the relative importance of food, as opposed to hydrodynamical stress, in the determination of the spatial pattern of occurrence of macrobenthic intertidal animals. Our original hypothesis stressed the importance of food availability, and assumed that hydrodynamic stress was only important in limiting the areas where animals would have access to food particles produced in the pelagic zone. This hypothesis was refuted in the Westerschelde results presented. The cross-comparison with the Oosterschelde, however, was most instructive in the interpretation. There are a number of points deserving attention in this comparison.

The biomass values in the Oosterschelde were generally much higher than in the Westerschelde data. There were some differences in the data sets between 1985 and 1989, but these differences were more pronounced in the density data than in the biomass data (Meire et al., 1994). In 1989 density was much lower (a factor 4-5) but biomass was higher (by a factor 2-3). This was related to the strong recruitment of young animals after the severe winter 1984-1985 (Meire et al., 1994). Almost all this difference was caused by the benthic suspension feeders (Fig. 13), which were by far the most variable group in time. It is possible that in 1985 the environment was undersaturated, because it takes some time for

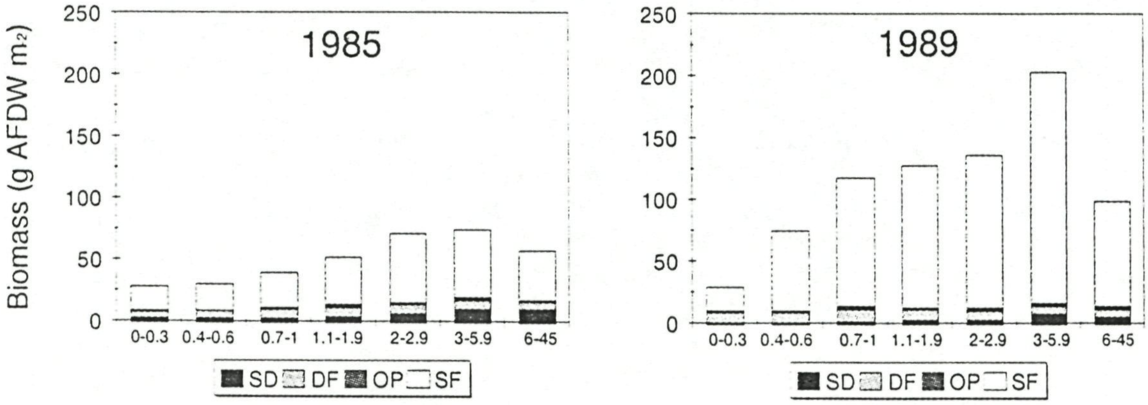


Fig. 13. Oosterschelde data set. Feeding group composition of biomass in 1985 and 1989.

these relatively large, long-lived animals to build up biomass after a severe decimation of the population. It is striking too to observe that the average biomass in the low-silt station groups was not different between the two years. In the stations containing more silt, the absolute difference tended to grow with the silt content, but the relative difference was a factor 2-3 throughout. In the low-silt stations density too was comparable between the years; it is well possible that the autumn population in these stations consists of recruits of the year that do not survive winter. When comparing Westerschelde with Oosterschelde stations, one again remarks that the suspension feeders are the only group responsible for the differences in total biomass. The other feeding groups together tend towards a maximum biomass of 20 g AFDW m^{-2}, although for the lower silt content classes it may have been slightly higher in the Oosterschelde than in the Westerschelde. However, compared with the difference in suspension feeders, this small difference is almost negligible. One concludes from these comparisons that the suspension feeders are by large the most variable feeding group in the benthic assemblages.

On a system comparison level, the difference between Oosterschelde and Westerschelde is in accordance with the hypothesis originally put forward. Primary production in the water column is much higher in the Oosterschelde than in the Westerschelde. This difference seems to enlarge the scope for deposit feeding in the low-silt stations slightly, probably because of a higher organic content of the deposited material. However, it most importantly influences the biomass of the suspension feeders, that may be directly dependent on the concentration of food in the water column. One further observes that in the Oosterschelde, where the average biomass of suspension feeders is much larger than in the Westerschelde, these animals occupy a much broader niche (in terms of sediment silt content). In the Westerschelde they are confined to the most silty stations, whereas in the Oosterschelde an increasing trend with silt content is visible but much less pronounced; suspension feeders were observed in virtually all stations, even in the lowest silt content. This is probably a reflection of the season, as the indications are strong that most of these animals are recruits of the year. Winter storms may restrict the suspension feeders to the more protected areas, and it is likely that benthic suspension feeder biomass is physically determined at the high energy sites.

Summarising the data obtained in this project, we can reformulate the hypothesis as follows:

- Suspension feeders are much more dependent on food concentration in the water column than other groups in the macrobenthos. Lack of food will limit their biomass to lower levels, and this is a reflection of either the local productivity or of the import of food from external sources (the sea)
- In food-poor conditions, one can then expect that food limits the biomass of suspension feeders. Suspension feeders will be restricted to optimal habitats providing the best conditions for their feeding. These will likely be places of net sedimentation and concentration of material resuspended elsewhere.
- In richer systems (either with more production or more food import), density-dependent mechanisms will limit the benthic suspension feeder biomass in the optimal habitats. Likely candidates for these mechanisms are bird and fish predation, if predators tend to concentrate on the richest food patches. Other mechanisms may have to do with competition between suspension feeders, which may suffer a certain degree of food depletion near the bottom at high clearance rates, even in turbulent tidal systems. As a consequence of these density-dependent limitations, it is expected that animals spread out over less optimal habitats, and will occupy a broader niche than in food-poor systems.
- In all systems, mechanical limitations seem to exist for suspension feeder biomass at high energy sites. Long-term average biomass seems to be low there, and even in food-rich systems, the population may be limited to recruits of the year, that cannot survive winter conditions.

At this moment, our results permit to make the following predictions:

- in the Oosterschelde, suspension feeders will feed more on pelagic food components than in the Westerschelde, where resuspended benthic algae may be their primary food source
- In the Oosterschelde, when going from the mouth to the inner estuary, one expects a decreasing importance of imported food from the North Sea in the diet of the suspension feeders
- Predation should be more important as a factor determining population structure and biomass of suspension feeders in food-rich than in food-poor systems. Predation in food-rich systems should be disproportionally concentrated in high biomass areas.
- Shellfish fisheries will have little impact on the system when practised in the high energy sediments, where winter storms would remove the suspension feeders anyway. It will have a high and years-lasting impact on the benthic biomass in the areas where suspension feeders are regulated by density-dependent factors. Fisheries will therefore be in direct competition with bird predation.
- Primary recruitment of larvae to the sediment does not seem to limit suspension feeder biomass. However, recruitment into the 1+ year class could very will limit biomass in the high energy areas.

Several aspects of this hypothesis are testable. These tests will be the subject of further investigations. In particular, we will investigate the composition of cockle diet in Westerschelde, Oosterschelde and Waddenzee.

Reeds verschenen BEON rapporten:

BEON rapport nr.	1.	BEON Meerjarenplan 1988-1993.	1987
BEON rapport nr.	2.	BEON Jaarwerkplan 1988.	1988
BEON rapport nr.	3.	BEON Modellering.	1988
BEON rapport nr.	4.	BEON meerjaren Uitvoeringsprogramma 1988-1993.	1989
BEON rapport nr.	5.	BEON Jaarwerkplan 1989.	1989
BEON rapport nr.	6.	Findings of the BEON Workshop in preparation for the Third North Sea Conference.	1989
BEON rapport nr.	7.	Beleidspresentatie BEON 23 juni 1989 Den Haag.	1989
BEON rapport nr.	8.	Effects of Beamtrawl Fishery on the Bottom Fauna in the North Sea.	1990
BEON rapport nr.	9.	BEON Jaarwerkplan 1990.	1990
BEON rapport nr.	10.	BEON Voortgangsrapport 1988-1989.	1990
BEON rapport nr.	11.	Beleidspresentatie BEON 31 mei 1990 Den Haag.	1990
BEON rapport nr.	12.	Beleidspresentatie BEON 20 juni 1991 Den Haag.	1991
BEON rapport nr.	13.	Effects of Beamtrawl Fishery on the Bottom Fauna in the North Sea. II. The 1990 - studies.	1990
BEON rapport nr.	13 A.	BEON Jaarwerkplan 1991.	1991
BEON rapport nr.	14.	BEON Jaarwerkplan 1992.	1992
BEON rapport nr.	15.	Beleidspresentatie BEON 19 juni 1992 Den Haag.	1992
BEON rapport nr.	16.	Effect of Beamtrawl Fishery on the Bottom Fauna in the North Sea. III. The 1991 - studies.	1992
BEON rapport nr.	17.	Beleidspresentatie BEON 12 december 1991.	1992
BEON rapport nr.	18.	Trace Element Geochemistry at the Sediment Water Interface in the North Sea and the Western Wadden Sea.	1993
BEON rapport nr.	19.	Effecten van met benzo(a)pyreen verontreinigd sediment op de Helmkrab (Corystes cassivelaunus). Rapportage Project BEONADD I/II.I	1993
BEON rapport nr.	20.	Scavenging seabirds behind fishing vessels in the Northeast Atlantic. (With emphasis on the Southern North Sea).	1993
BEON rapport nr.	21	Brug tussen Beleid en Onderzoek (Rapportage over het eerste BEON Meerjarenprogramma 1988-1992).	1993
BEON rapport nr.	93-1	Naar een duurzame ontwikkeling van de Noordzee. (Tweede Meerjarenprogramma BEON1993-1997).	1993
BEON rapport nr.	93-2	The appearance of scars on the shell of Arctica Islandica L. (Mollusca, Bivalvia) and their relation to bottom trawl fishery.	1993
BEON rapport nr.	93-3	BEON Jaarwerkplan 1993.	1993
BEON rapport nr.	93-4	BEON Beleidspresentatie "Zee en Wadvogels. "Voorkomen en invloeden daarop" d.d. 10 december 1993.	1993

1994

BEON rapport nr. 94-1	Effecten van verschuivingen van nutriëntenconcentraties op biota in de Nederlandse kustwateren. Philippart, C.J.M. & E.G. de Groodt, A.G. Brinkman, R.G. Jak, M.C.Th. Scholten (IBN 93 E 02).
BEON rapport nr. 94-2	Vervalt; zie 96-3
BEON rapport nr. 94-3	Jaarwerkplan 1994.
BEON rapport nr. 94-4	Jaarverslag 1993: Algenonderzoek in mesocosms en modelleringlering. Riegman, R. (NIOZ 93 E 01).
BEON rapport nr. 94-5	Impact of anthropogenic activities on the productivity of the western Wadden Sea ecosystem. Veer, H.W. van der. (NIOZ 93 E 02).
BEON rapport nr. 94-6.1	Bentic nutriënt generation in the ERSEM ecosystem model of the North Sea. Ruardij, P. and W. van Raaphorst. (NIOZ 93 E 03)
BEON rapport nr. 94-6.2	The EcoWasp model and it's environment. Smit, J.P.C., A.G. Brinkman, E.G.M. Embsen, P. Ruardij, and W. van Raaphorst. (NIOZ 93 E 03)
BEON rapport nr. 94-7	Risico-analyse Mariene Systemen (RAM*2 project) Eindrapport van de RAM-Auditgroep.
BEON rapport nr. 94-8	Comparison of models describing species composition of marine phytoplankton Michielsen, H & Berg, A. van den & Joordens, J., et al.(project MANS-FYFY, WL 93 E 01).
BEON rapport nr. 94-9	Verslag BEON Workshop Risico-analyse, d.d. 27 april 1994, Den Haag.
BEON rapport nr. 94-10	BEON Beleidspresentatie "Microverontreinigingen: effecten en trends", d.d. 21 juni 1994.
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