Tidal motion, and the seston supply to the Benthic macrofauna in the Oosterschelde

Report on investigations

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APPENDIX A

TABLES 1 - 3

FIGURES 12 - 18 and 22 - 25
1. Introduction

In the Oosterschelde the production of suspension feeding bottom animals like mussels and cockles seems to be higher near the mouth than at a more inner location of the estuary (SMAAL et al, 1985; see also Table 1 and Table 2).

The question is: which processes are the most important in determining the growth of mussels and cockles in the Oosterschelde? If these factors were known, it would perhaps be possible to predict the effect of the storm surge barrier on the production of the various mussel culture plots in the Oosterschelde.

This study tried to answer this question.

In the first part of this report a theoretical approach has been followed. This theoretical approach starts from the idea put forward by WILDISH AND KRISTMANSON, 1979, that benthic filter feeders may be food limited and that an important limiting factor is tidal current velocity immediately above the sediment-water interface.

In the second part of this report more attention has been paid to the results of the variation in seston parameters during the tidal cycle above several mussel plots.

The theoretical results from the before mentioned approach has been compared with those data. It appeared, however, that depletion of the seston concentrations in the benthic boundary layer could not be observed in the measurements. Therefore also other factors have to be considered to understand the interaction between seston and suspension feeders.

In the third part of this report, several alternative hypotheses are postulated. The processes behind these hypotheses have been formulated and quantified as good as possible. The results can explain the data. Further research is recommended to test these hypotheses.

The research described in this report is started within the framework of the WABASIM-salt project.
The research and reporting is carried out by Ir. J.H.G. Verhagen. The research activities are executed in cooperation with the WABASIM-suspension feeders working group consisting of the following members:

Drs. A.C. Smaal, (DDMI), chairman
Ir. J.H.G. Verhagen, (DHL), secretary
Drs. J. Coosen (DIHO)
Drs. L. van Geldermalsen (DIHO)
Ing. H. Haas (DDMI)
Drs. O. Klepper (DIHO)
Drs. F.H.I.M. Steyaert (RIVO).
2. The seston supply by tidal motion to the benthic suspension feeders

When current speeds above a musselbed are low and the horizontal dimensions of the bed are very large compared to the water depth, the mussels remove food particles (= seston) more rapidly than the process of advective horizontal transport and vertical diffusive transport can supply seston to the mussels. In this situation, the seston concentration is reduced near the sediment-water interface and suspension feeders can become food limited. WILDISH and KRISTMANSON (1979) developed a mathematical model to quantify the relationship between growth of suspension feeders and tidal current velocity. This approach has been extended mainly to include the effect of water depth.

2.1 Development of a simple seston balance model

The model of limited mixing proposed by WILDISH and KRISTMANSON (1979) is extended to include the effects of water depth, primary production, tidal motion and mixing by the activity of the filter feeders. WILDISH and KRISTMANSON considered the case of a parallel flow over a horizontal flat bottom as an idealization of the tidal motion in a small part of the estuary containing one musselbed.

2.1.1 The horizontal flow velocity

The time averaged turbulent flow velocities are assumed to vary in the vertical direction but not in the flow direction. The flow near the sediment-water interface will depend on the roughness of the bottom. If the average height of the roughnesses is much greater than the thickness of the viscous sublayer, we have the fully-rough-wall condition with no effective viscous sublayer. From NIKURADSE's experiments on flow through pipes with walls of uniform sand-grain roughness it is found in literature that the fully rough wall condition is reached for

\[
\frac{u^* k}{v} > 55
\]

where:
\( u^* \) the wall-friction velocity  
\( k \) the average height of the bottom roughnesses  
\( \nu \) the kinematic viscosity of water

with \( u^* \approx 0.05 \, U \) (\( U \) is the free stream velocity)

\[ \approx 1 \pm 3 \, \text{cm/s} \]

\[ k \approx 1 \pm 2 \, \text{cm} \]

\[ \nu = 1.4 \cdot 10^{-2} \, \text{cm}^2/\text{s} \]

the fully rough-wall criterium is usually fulfilled.

The velocity distribution in this case is affected only by the roughness and not by the viscosity of the fluid.

The turbulent velocity distribution in pipes and channels (depth \( H \)) is sometimes represented by a simple power law:

\[
\frac{U}{U_{\text{max}}} = \left( \frac{z}{H} \right)^{1/n}
\]

The exponent \( 1/n \) in this fully rough-wall situation does not depend on fluid viscosity and is therefore independent of the Reynolds number. The exponent depends only on the bottom roughness and is equal to

\[
\frac{1}{n} = \frac{1.13}{\ln \left( \frac{12 \, H}{k} \right)}
\]

(a)

With \( H = 1 \pm 5 \, \text{m} \) we obtain \( 1/n = 1/5.7 \pm 1/7.7 \) so \( n \approx 6.7 \).

\[
\frac{U}{U_{\text{max}}} = \left( \frac{z}{H} \right)^{0.15}
\]

where

\( z \) the coordinate perpendicular to the wall
Consider now the case of a bed of suspension feeders of uniform density extending from $x_0 < x < x_0 + L$. So $L$ is the length of the bed in flow direction.

It is assumed that the flow field is unchanged by the presence of the animals. Since the value of the exponent $1/n$ varies only slightly with a change in bottom roughness $k$ according to equation (a) the above assumption is not unrealistic.

We take $1/n = 0.17$ to account for the increased roughness of a bumpy musselbed.

2.1.2 The vertical mixing coefficient

Since seston is being removed by the suspension feeders, its concentration is reduced near the bottom. The supply of seston to the suspension feeders occurs by vertical mixing and is according to Fick's law proportional to the eddy viscosity $\varepsilon_m$ and the vertical gradient in the seston concentration $c$.

$$\varepsilon_m \frac{3c}{3z} \text{ at } z = 0$$

In the region near the wall $0 < z/H < 0.25$ the size of the large eddies which are responsible for the eddy viscosity are usually taken proportional to the distance from the wall, so

$$\varepsilon_m = \kappa u^* z$$

where

$\kappa = 0.4$ Von Kármán's constant.

There are also turbulent eddies produced by the filtering suspension feeders. Those eddies will have a dimension $l$ of a few times the size of the suspension feeders, say $l$ is about 10 up to 20 cm.

This means that the eddy viscosity in a thin layer above the musselbed is more or less constant and equal to:

$$\varepsilon_m = \kappa u^* l$$
Far away from the wall $z/H > 0.25$ the eddy viscosity is more or less constant and equal to $\varepsilon_m \approx 0.06 \pm 0.07 \, u^*H$.

The distribution of the eddy viscosity above the musselbed is shown in the next figure.

region in which the turbulence is influenced by the activity of the suspension feeders

2.1.3 Production and consumption of seston

The density of the musselbed is denoted by $N$ individuals per square centimetre. Assume that an average mussel filters water at the rate of $\phi \, cm^3/s$.

The rate at which seston is removed by the mussels per square centimetre is

$$\phi \, N \, c_{z=0}$$

If it is assumed that all the seston filtered is removed from the water, then a balance must exist between the vertical seston supply by vertical mixing and the seston consumption both per unit bottom area.

So, the boundary condition for $z = 0$ is:

$$\varepsilon_m \frac{\partial c}{\partial z} = \phi \, N \, c$$

We apply the seston balance to a control volume above the musselbed as depicted below.
Control volume \( x_0 \leq x \leq L \),
\( 0 \leq z \leq H \).

The mass balance reads:

\[
\frac{\partial c}{\partial t} + u \frac{\partial c}{\partial x} - \frac{\partial}{\partial z} \epsilon m \frac{\partial c}{\partial z} - \frac{PR}{H} = 0
\] (1)

The effect of the horizontal mixing on the \( c \)-distribution is assumed to be negligible small. So the term \( D_x (\partial^2 c / \partial x^2) \) is not included in the balance. The production of seston per unit water surface is denoted by \( PR \) and is supposed to be constant. Because we assumed in this section that 'u' did not change in \( x \)-direction, there are according to the continuity equation, no vertical velocities and therefore the water depth does not change with time. In fact, we are considering only the steady flow situation.

If it considered worthwhile to solve the unstationary two-dimensional mass conservation problem, this can be done in the future. In that case, however, the vertical water velocities are also important and to obtain them we have to start with a flow calculation of a tidal motion (not necessarily over a horizontal bottom). The costs of such a calculation has to be weighed against the benefits. (Costs order of magnitude FL. \( 10^4 \) per case).

We assumed

\[
\frac{U}{U_{\text{max}}} = \left( \frac{z}{H} \right)^{0.17}
\]

and
\[ e_m = 0.0025 \ U_{\text{max}} \ H \]

over the main part of the water column

\[ e_m = 0.4 \ u^* \ z \]

near the bottom outside the region directly influenced by the filtering mussels

\[ e_m = 0.4 \ u^* \ l \]

near the bottom inside the region \( 0 < z < l \) directly influenced by the filtering mussels.

The boundary conditions are

\[ e_m \ \frac{\partial c}{\partial z} = \emptyset \ N \ c \]

for \( z = 0 \)

\[ \frac{\partial c}{\partial z} = 0 \]

for \( z = H \)

\[ c = c_0 \text{ is constant} \]

for \( x = x_o \ (U_{\text{max}} > 0) \).

The initial condition is

\[ c = c_0 \]

for \( t = 0 \)

This problem can be solved numerically.

(Costs order of magnitude F1. \( 10^2 \) per case).

2.2 Approximate solutions of the seston balance equation

To get an impression of the model results approximate solutions are obtained for some specific situations.

2.2.1 The deep water situation and steady motion

The 2-D steady state solution appropriate for the deep water situation.

The assumptions are:

Steady state, or \( \partial c/\partial t = 0 \).

Seston production negligible \( PR/H = 0 \).

The vertical dispersion coefficient \( e_m \) is a function of \( z \) and is from now on denoted by \( D \). Over the main part of the water column \( D \) is equal to \( D_o \), where
\[ D_0 = 0.0025 U_0 H \text{ (FISCHER et al, 1979).} \]

Near the bottom \( D \) is equal to \( D_1 \), where

\[ D_1 = 0.4 u^* \cdot 1 = 0.02 U_0 \]

The length scale \( l \) of the turbulent eddies produced by the filtering mussels is taken as 20 cm.

The horizontal velocity \( u \) is assumed to be time independent. Over the main part of the water column \( u \) is taken constant and equal to \( u_0 \). Nearer to the bottom \( u \) diminishes according to

\[ u = u_0 - (u_0 - u_1) e^{-kz} \]

where \( u_1 \) is the flow velocity over the bottom \( z = 0 \).

The assumed distribution of \( u \) and \( D \) over \( z \) are graphically displayed in Figure 1.

The seston balance equation in this case becomes:

\[ u \frac{\partial c}{\partial x} - \frac{\partial}{\partial z} D \frac{\partial c}{\partial z} = 0 \]

Figure 1. The distribution of velocity \( u \) and vertical diffusion \( D \) over \( z \).
As long as the seston boundary layer thickness $\delta(x)$ does not reach the water surface, which will usually be the case in a deep water situation, the boundary conditions are:

\[
\text{at the bottom } z = 0 \quad D_1 \frac{\partial c}{\partial z} = \emptyset N c
\]

and at \( z = \delta(x) \quad c(x, \delta(x)) = c_0 \)

At the front of the mussel bed \( x = 0 \) and \( c(0, z) = c_0 \), where \( c_0 \) is a given constant.

The first boundary condition states that all the seston filtered by the mussels \( \emptyset N c_{z=0} \) is removed from the water column. So it is assumed that no resuspension of faeces or pseudo-faeces takes place.

In Appendix A the solution method of the case I situation is given.

The solution is graphically displayed in Figure 2.

![Figure 2. Development of seston boundary layer and seston depletion.](image)

The seston boundary layer thickness appears to increase proportional to the square root of the horizontal distance. At the front of the mussel bed the proportionality depends on the values of the vertical dispersion coefficient and the velocity just above the mussel bed as follows:

\[
\delta = \sqrt{\frac{6 D_1 x}{u_1}}
\]
The bottom values $D_1$ and $u_1$ are substantial lower than those in the main part of the water column, see Figure 1.

At larger distances from the front of the bed, the seston boundary layer thickness appears to behave like

$$\delta = \sqrt{\frac{\phi N}{2 D_1}} (x - x_0)$$

in which $x_0$ is a (negative) integration constant.

The solution of the seston concentration above the mussel bed is (see Appendix A):

$$c(x, 0) = \left(1 - \frac{\phi N \delta(x)}{2 D_1}\right) c_0$$

The seston depletion above the bed is denoted by \textit{DEPL}, defined as

$$\text{DEPL} = \frac{c_0 - c(x, 0)}{c_0} \quad \text{which is equal to} \quad \frac{\phi N \delta(x)}{2 D_1}$$

So the seston depletion over the largest part of the bed is equal to

$$\text{DEPL} = \frac{\phi N}{u_0} \sqrt{\frac{3 u_0 (x - x_0)}{2 D_1}} \quad \text{see Figure 3}$$

The conclusion is that the seston depletion in the benthic boundary layer above a mussel bed is:

1) proportional to the filtration rate of the mussels per unit bed surface $\phi N$;
2) inverse proportional to the square root of the horizontal flow velocity $u_0$ in the main part of the water column
3) inverse proportional to the square root of the vertical dispersion coefficient in the benthic boundary layer itself
4) proportional to the square root of the horizontal distance measured in flow direction.

The solution is valid in the case of sufficient deep water $H > \delta(x)$ and for $\frac{\phi N \delta}{D_1} << 1$ i.e. for rather small values of the seston depletion.
In the beginning of section 2.2.1 the assumption was made that 
\( D_1 = 0.02 \frac{u}{\varpi} 1 \) where 1 is the length of the eddies produced by the filtering mussels (1 = 20 cm).

In that case we may write:

\[
\text{DEPL} = \frac{\varphi N}{u_0} \sqrt{\frac{3(x - x_0)}{0.04 1}}
\]

Figure 3:
Seston depletion as function of \( \frac{\varphi N}{u_0} \) for different length of a mussel bed in deep water.

This Figure could be compared to Figure 9 for small values of \( \frac{\varphi N}{u_0} \) in the paper of SMAAL et al (1985).

2.2.2 The shallow water situation and tidal motion

The difference in seston concentration between bottom and water surface decreases with decreasing water depth.

For shallow water the assumption of homogeneous mixed water column can be made. In that case the seston balance equation applied to a control volume above the mussel bed becomes:

\[
\frac{\partial c}{\partial t} + u \frac{\partial c}{\partial x} = \frac{PR}{H} - \frac{V}{H} c \tag{a}
\]

where \( V \) is the filtration rate per unit bottom surface.

In this situation the seston production per unit surface \( PR \) is not neglected. The term \( PR \) contains two contributions:

1) the production of the phytoplankton component in the seston
2) the resuspension of seston including faeces and pseudofaeces from the bottom.
The first contribution will be proportional to the phytoplankton biomass which is usually a small and time dependent fraction of \( c \).
The second contribution depends on the current velocity \( u \) and on the availability of seston on the bottom.
To simplify calculations the production \( PR \) per unit surface is assumed constant so, the production per unit volume increases sharply for \( H \to 0 \). An alternative formulation of \( PR \) is presented at the end of this chapter.
The flow velocity \( u \) is assumed constant over the water depth.

In a coordinate system moving with the water particles we have

\[
\frac{dc}{dt} = \frac{PR - Vc}{H} \tag{b}
\]

Say \( H \) is only a function of \( t \) \( H = H(t) \)

\[
H = H_o + \eta \sin \omega t
\]

Say \( u \) at \( x = L/2 \) is \( u_o \cos \omega t \).
The velocity at \( x \not= 0 \) follows from the continuity equation:

\[
\frac{\partial u}{\partial x} + \frac{1}{H} \frac{dH}{dt} = 0 \tag{c}
\]

or \( u = u_o \cos \omega t - \frac{x - \frac{L}{2}}{H(t)} \frac{dH}{dt} \)

The path of the particle as a function of time follows from

\[
\frac{dx}{dt} = u_o \cos \omega t - \left(\frac{x - \frac{L}{2}}{H} \frac{dH}{dt}\right) \tag{d}
\]

Together with the boundary conditions

\[
c = c_o \quad \text{for} \quad x = 0 \quad \text{and} \quad -\frac{\pi}{2} < \omega t + 2k\pi < \frac{\pi}{2}
\]

\[
c = c_o \quad \text{for} \quad x = L \quad \text{and} \quad \frac{\pi}{2} < \omega t + 2k\pi < \frac{3\pi}{2}
\]

\( k = 0, 1, 2, \ldots \)

Equation (b) and (d) can be solved numerically for each particle starting at the boundaries at time \( t_o \).
Example parameter values:

\( H = 150 \text{ cm} \)
\( \eta = 100 \text{ cm} \)
\( \omega = 2\pi/6 \times 3600 \text{ s}^{-1} \)
\( u_0 = 40 \text{ cm/s} \)
\( V = 0.055 \text{ cm/s} \)
\( \text{PR/Vc}_o = 0.1 \)

Figures 6 and 7 show some results.

Figure 6 The seston concentration above a musselbed in shallow water for various moments in the tidal cycle
Figure 7. The tidal variation in the seston concentration $c/c_0$ at the front $x = 0$ and at the end $x = L$ of the mussel bed in shallow water.

Figure 6 shows the dimensionless seston concentration $c/c_0$ as a function of $x$ for several moments in the tidal cycle.

Figure 7 shows the seston concentration $c/c_0$ at the front $x = 0$ and at the end $x = L$ of the mussel bed as a function of time.

We observe a remarkable difference in the severeness of the food limitation during the tidal slack periods.

The bottom pictures in Figure 7 show that food limitation is much more severe during the tidal slack period at low water than during the tidal slack period at maximum water-level.

The reason is that the food content in a shallow water-layer is less and therefore faster depleted than at maximum flood height.
The considerations in this section are based on the assumption that the production of seston per unit surface PR is constant. As mentioned already this assumption is not realistic. Erosion of seston from the bottom will occur if the flow velocity is higher than a given critical value \( u_c \). See also chapter 4.1 and 4.2. The effect of the variation in erosion intensity during the tidal period can be formulated as follows

\[
\begin{align*}
PR &= PR^0 \quad \text{is constant for } u > u_c \\
PR &= 0 \quad \text{for } u < u_c
\end{align*}
\]

Equation (b), valid in a coordinate system moving with the water particles, has been solved again. Taking \( PR^0 = 0.25 V c_b \) the solution is shown in Figure 7a. Here \( c_b \) is a measure for the seston (or POC) concentration on the bottom.

![Figure 7a](image)

Compare this figure also with Figure 19.

The tidal variation in the seston concentration is such that it is maximal in the second half of the ebb and flood tide. The tidal averaged level is according to equation (b) equal to

\[
\bar{c} = \frac{PR}{V} = \tau \frac{PR^0}{V} = 0.25 \tau c_b
\]
where $T$ is the fraction of the tidal period in which the tidal velocity is higher than $u_c$. So it is concluded that the average seston concentration in the water $c$ is proportional to the seston concentration on the bottom. The proportionality constant is an increasing function of the tidal velocity amplitude.

2.3 Comparison with results of Wildish and Kristmanson

WILDISH and KRISTMANSON (1984) conducted an experiment in a 5 m long by 50 cm wide flume in which a turbulent boundary layer flow was created over a bed of actively pumping mussels. They measured the depletion of the seston concentration at a point 1 cm above the flume bottom at a distance $x = 360$ cm behind the inlet of the flume for various boundary conditions.

Their results are shown in Figure 9 from [WILDISH et al., 1984]. In this figure the seston depletion is expressed as

$$C = \frac{c_o - c_{bot}}{c_o}$$

where

$c_o$ is the concentration of seston in the inlet water
$c_{bot}$ is the concentration 1 cm above the bottom at $x = 360$ cm.
The front of the mussel bed is beginning at $x = x_o = 25$ cm.

The filtration rate of an average mussel is estimated as $\theta = 0.56$ cm$^3$/s. The dimensionless number $P$ is equal to the ratio between the filtration rate per unit bottom surface $\theta N$ and the average horizontal velocity in the seston boundary layer $a u$.

$$P = \frac{\theta N}{a u}$$

where

$N$ is the number of individuals per cm$^2$
$u$ is the free stream velocity in cm/s
$\alpha$ is the ratio between average velocity in the seston boundary layer and free stream velocity (taken by the authors as 0.8).
Fig. 8. Typical velocity profiles as measured by the hydrogen bubble probe at (A) 100 cm and (B) 360 cm from the inlet screen.

Fig. 9. ATP-seston depletion (C) observed at the outlet (X = 360 cm) as a function of parameter P.

Fig. 10. Seston boundary layer thickness at x = 360 cm according to present theory.
Figure 9 shows also the result of a mathematical model developed by the same authors for parameter values consistent with the experimental conditions. Their model is also based on a seston balance applied to the benthic boundary layer.

A few comments on the model of WILDISH and KRISTMANSON seems at this place to be appropriate.

A. The first comment is of minor importance and concerns only the solution method.

They stated "There does not appear to be a straight forward analytical solution and it was therefore solved numerically". However, the analytical solution, for the parameter value \( b = 0.5 \) as used by the authors can easily be obtained.

The parameter value \( b \) expresses the thickness increase in the downstream direction of the seston boundary layer

\[
\delta = a(x - x_o)^b
\]

The analytical solution from their seston balance equation (2) turns out to be

\[
C = 1 - \frac{a}{2b} \exp \left\{ \frac{2b}{a} (\sqrt{x} - \sqrt{x_o}) \right\} - \frac{a}{2b} \sqrt{x} \left[ 1 - \exp \left\{ \frac{2b}{a} (\sqrt{x} - \sqrt{x_o}) \right\} \right]
\]

The numerical solution given by WILDISH and KRISTMANSON and shown in their Figure 9 appears to be in perfect agreement with the above analytical solution.

B. A second comment seems to be more important.

The seston balance is expressed in terms of the average concentration of seston over the thickness of the boundary layer denoted by \( \delta \).

The concentration profile at a given \( x \) will have a more or less parabolic shape, as depicted in the Figure below.

![Figure 11](image-url)
The rate at which seston is removed is not proportional to the average concentration as assumed by the authors, but proportional to the concentration near the bottom.

The difference between the free stream concentration and the bottom concentration is in the case of a parabolic concentration profile equal to \( c_1 = 3(c_o - c) \).

Therefore, the seston balance equation of WILDISH and KRISTMANSON should have read (in their notation):

\[
(2') \quad \frac{d(C_0)}{dx} = P(1 - 3c)
\]

instead of \( = P(1 - C) \) as written in their equation (2).

An analytical solution of the revised equation \((2')\) can also be found. The results of that solution are in good agreement with the results of my own model presented in the next page.

A comparison of the experimental results of WILDISH and KRISTMANSON with the seston balance model as developed and presented in this report is interesting, because that model calculates not only the seston depletion but also the thickness of the seston boundary layer.

The seston depletion according to my own model is:

\[
C = \frac{c_1}{c_o} = \frac{1}{1 + \frac{2D}{\varphi N \delta}}
\]

(see equation 2a in Appendix A)

In Appendix A, the relation between \( C \) and the two parameters \( \varphi N / u_o \) and \( u_o / D l \) is derived and given in equation (11).

If the assumption is made that the mixing length of the actively pumping mussels on this experiment will be no more than 15 cm, we get a dispersion coefficient in \( \text{cm}^2/\text{s} \) equal to \( D = 0.3 \) \( u \) (where \( u \) is in \( \text{cm/s} \)).

The results of the here developed model at \( x = 360 - 25 = 335 \) cm are also depicted in Figure 9 and Figure 10.

Figure 9 shows the calculated seston depletion. The results of my model appear to be in better agreement with the experimental results than WILDISH's and KRISTMANSON's model. The scatter in the experimental data, however, is too large to draw firm conclusions.
Figure 10 shows the calculated thickness of the seston boundary layer as a function of the filtration rate/current speed ratio $P$. This theoretical result can be compared with the velocity boundary layer thickness measured at 360 cm from the inlet by WILDISH and KRISTMANSON as shown in their Figure 8 (B).

2.4 Discussion of model results

The results of the mathematical model show that the seston concentration in the flow over a mussel bed of sufficient length and mussel density can be nearly depleted.

The seston depletion depends on:

. the mussel bed length and density
. the filtration rate of an average mussel in the bed
. the current velocities
. the water depth
. the seston concentration at the front of the mussel bed
. the production rate of seston.

Taking realistic values of mussel bed length (1000 m), mussel density (1000 individuals.m$^{-2}$) and filtration rate of an average mussel (0.55 cm$^3$/s) the following results are obtained.

The seston depletion at the downstream end of the mussel bed in deep water appeared to be insensitive to the depth and approximately equal to

$$C = \frac{\sqrt{\frac{3L}{2u_o D_1}}}{1 + \sqrt{\frac{3L}{2u_o D_1}}}$$

Deep water in this context means $H > \delta(L)$

or

$$H > \sqrt{\frac{6D_1 L}{u_o}}$$

With $D_1 = 0.02 u_o l$, $l = 20$ cm$^2$ and the values for $L$, $\delta$, and $N$ as mentioned before, we get deep water for

$H > 5$ m
and \( C = \frac{33.7}{33.7 + u_o} \) \( u_o \) in cm/s.

From the last expression the effect of a reduction in the tidal current velocity on the severeness of the food limitation at the downstream end of this specific mussel bed can be easily obtained.

For shallow water where the benthic boundary layer in the seston concentration reaches the water surface already in the front part of the mussel bed, the seston depletion above the bed is nearly equal to the seston depletion at the water surface. In that case the depletion at the downstream end of the bed is approximately equal to

\[
C = \frac{C_1}{C_o} \approx (1 - \frac{PR}{\frac{\phi N L}{uH}}) \left[ 1 - \exp\left(\frac{-\frac{\phi N L}{uH}}{uH}\right) \right]
\]

Again for realistic values of the seston production rate per unit water surface and for the other parameters we get:

\[
C = \frac{C_1}{C_o} \approx 0.9 \left[ 1 - \exp\left(-\frac{5500}{uH}\right) \right] \quad uH \text{ in cm}^2/s
\]

So the conclusion is that for shallow waters \((H < 3 \text{ m})\) current velocity and water depth have quantitatively the same influence on the seston depletion at the downstream end of the mussel bed.

So according to this model a 20% reduction in tidal currents has the same influence as a 20% reduction in water depth.

However, it must be remembered that most of the model results are based on the simplifying assumption that resuspension of faeces and pseudofaeces at the musselbed could be neglected.

Therefore, before drawing too much conclusions from the model, pertaining to the real Oosterschelde situations, and indication of the value of this assumption has to be obtained. In the next section a comparison with Oosterschelde data will be made.
3. Data on seston supply and growth of suspension feeders

A review of the data on biomass and growth of mussels and cockles in the Oosterschelde is given by SMAAL et al (1985).
Part of the information given in that paper is reproduced in the next section.

3.1 Biomass and growth of cockles and mussels

The southern branch of the Oosterschelde estuary is divided into three areas, viz.: 1 (west), 2 (middle) and 3 (east). See Fig. 12.
The biomass, density and standing stock of mussels (Mytilus edulis) in these three areas is given in Table I and of cockles (Cerastoderma edule) is presented in Table 2.
Area 3 is not a mussel culture area, it contains only rewatering places and stock-yards.
Growth of adult mussels from May to September 1983 on culture plots in area 1 is 4.6 mg/day and in area 2 3.04 mg/day.
Growth of adult mussels in net bags hanging freely in the water near the surface showed in the growing season 1985 the values 4 mg/day in area 1, 2.36 mg/day in area 2 and 3.71 mg/day in area 3.
Growth of cockles for year class 1 and 2 in 1984 was about 2 mg/day in area 1 and 0.75 mg/day in area 3.
Those numbers contained, however, a considerable variance.

From the data it seems that there is a decrease in biomass per m², standing stock and production of bottom cultured mussels and of cockles, going from the west to the east.
The growth of mussels hanging in net bags near the water surface, however, showed no significant difference between area 1 and 3.

3.2 The seston concentration and composition in the Oosterschelde

Fig. 13 shows the mean concentration over 10 years (1972-1982) of seston, POC and chlorophyll-a as a function of the time of the year on two locations near mussel plots. Location I corresponds to ZM 12 (west) and location II to Z 5 (middle), see also Figure 14.
Table 3 shows the differences between the 3 areas in these seston components, averaged over the year and over the season. From these data a gradient in chlorophyll can be observed. In area 1 the chl.-a values are about 25% higher than in area 3. The POC and seston concentrations show not the same tendency, but only lower values in area 2 compared to 1 and 3.

Figure 15 shows the variation of POC and chlorophyll during the tide above mussel beds. The concentration values at the bottom averaged over the tidal period are about 30% higher for POC and 20% for chlorophyll compared to the values at half water depth. The tidal variation in POC seems to follow the tidal variation in current velocities with a phase lag of about one hour, but that relation is not very clear. The tidal variation in chlorophyll clearly differs from the variation in current velocities. Only one instead of two peaks are in general observed during one tidal cycle. That peak occurs in general around highwater slack. Note that the data are averaged over several locations at different times of the year. Figures 16 and 17 show the tidal variation in chlorophyll-a and currents on several locations and dates (HAAS, 1984, 1985). It seems that the maximum chlorophyll values during the tide are reached just before highwater slack. The ratio between maximum and minimum value could well be a factor two. (Note: The hydraulic situation on day 2-10-'85 as presented in Figure 16 is not normal. A large part of the storm surge barrier in the northern gully was closed in this period.)

3.3 Comparison of model results with data of seston components

The model is based on the idea that the mussels remove food particles more rapidly than it is supplied by the tidal motion. As a result the food concentration is reduced near the sediment-water interface. The data on POC and chlorophyll-a above the mussel plots show the contrary, namely 25 to 30% higher values at the bottom than at half depth. The reason is that the model neglects sedimentation and erosion of particulate matter. During the development of the model the implicit assumption has been made that the sedimentation rate of particulate organic matter and chlorophyll is at most order 1 m/day. This value is commonly used in phytoplankton models.
Apparently this is not justified in the Oosterschelde situation. The net sedimentation rate can be calculated from the data as follows:

If it is assumed that there is no vertical transport of particulate matter, then

\[ v \frac{dc}{dz} - D \frac{\partial^2 c}{\partial z^2} = 0 \]

where
\( c \) is the concentration of particulate matter and
\( v \) is the settling velocity.

So

\[ v = \frac{D}{c} \frac{\Delta c}{\Delta z} = \frac{D}{c} \frac{\Delta c}{\text{UH}} \]

where

- \( \frac{\Delta c}{c} = 0.25 \) for chlorophyll-a and
- \( 0.3 \) for POC
- \( D = 0.0025 \text{ UH} \)

The mean tidal velocity above several mussel plots is \( U = 50 \text{ cm/s} \), resulting into a settling velocity \( v \) of 0.625 mm/s for chlorophyll-a or 54 m/day and 0.75 mm/s for POC or 64.8 m/day.

These values are extremely high. Nevertheless as SMAYDA (1970) shows, sinking rates of marine phytoplankton in this order of magnitude has been measured. The higher sinking rates are usually found for unproductive senescent cells. This information might be important for the Oosterschelde situation.

Could it be that the allochtone phytoplankton which is adapted to the North Sea situation does not feel very healthy in the estuarine environment and therefore gets a higher settling rate?

In the eastern part of the estuary the renewal time of the water is much longer and therefore the phytoplankton population in area 3 must be mainly autochtone with much lower sedimentation rates. Also it is known that the phytoplankton turnover rate is higher in the eastern part. The primary production per unit surface does not differ that much between east and west (see nota Balans 1985-11) despite a lower biomass (Table 3) and a 50% shallower depth in area 3 compared to area 1. As a consequence of the higher vitality the vertical gradients in chlorophyll in area 3 could be much less than 0.25. It would be interesting to test this idea with the data of area 3. It has not been done here.
The measured tidal variation in chlorophyll above a mussel bed could be compared with results of the model for the shallow water situation. Figure 18 (83 06 28) shows the tidal variation in chlorophyll-a on a mussel plot in area 2 in water of 5 m depth. The specific plot forms part of a mussel culture area and it is situated more in the western part of those plots.

The model results as presented in Figure 7 are valid under the assumption that c is constant at the edges of the front of the bed (x = 0) during flood tide.

In fact this is not realistic. During flood the concentration at x = 0 will increase because of the production PR and the absence of filtration during the tidal excursion of a fluid particle during flood at x < 0. Correcting for this aspect gives a model result valid for x = 0 as shown in the lower half of Figure 18.

The figure shows that at the front part of the bed the production of chlorophyll dominates the grazing loss of chlorophyll during flood tide and vice versa during ebb.

There is some resemblance between theory and measurements. However, it concerns only one example. For instance, the strong and sudden increase in the chlorophyll concentration as is shown in Fig. 22 measured at a mussel plot in area 1 cannot be explained with the presented model.

The conclusion is that apart from the depletion of chlorophyll in the flow above a mussel bed in downstream direction also other factors have to be considered to understand the interaction between seston and suspension feeders.
4. Alternative hypotheses about determining factors

4.1 Sedimentation and erosion of chlorophyll

In the preceding section the large settling rate of chlorophyll has been discussed.
The chlorophyll balance of a vertical segment moving with the depth averaged tidal velocity \( u \) which includes the processes of erosion and sedimentation reads:

\[
\frac{dc}{dt} + \frac{v_{\text{eff}}}{H} c - E - \mu c = 0 \quad (a)
\]

in which
- \( c \) the vertical averaged chlor concentration
- \( E \) represents the erosion of \( c \) from the bottom
- \( v_{\text{eff}} \) represents the effective settling rate of \( c \), defined as \( v_{\text{eff}} = v - \frac{D}{c} \frac{dc}{dz} \)
- \( \mu \) the relative production rate of \( c \).
The dispersion term is not taken into account, see also DRONKERS, 1985.

4.1.1 Quantification of this mechanism

Estimating the consequences of these processes, assume:

\[
v_{\text{eff}} = v_0 \quad \text{for} \quad u < u_s \quad \text{and} \quad \text{and}\]

\[
v_{\text{eff}} = v_1 \quad \text{for} \quad u > u_s
\]

where \( v_0 >> v_1 \)

\[
E = 0 \quad \text{for} \quad u < u_e \]

\[
E \neq 0 \quad \text{for} \quad u > u_e \quad u_e > u_s
\]

If \( E = 0 \), the solution of equation \( (a) \) is shown as in Fig. 19.
If the effect of erosion is taken into account, the curve for \( c \) will be somewhat higher for \(|u| > u_e\). It is felt, however, that erosion of chlorophyll (apart from perhaps microphytobenthos erosion) is not very common. It has to be remembered that the effect of resuspension is already incorporated in \( v_{\text{eff}} \).

The result of this model says nothing about the variation of \( c \) in a fixed coordinate system. It states only that the loss of \( c \) by settling is compensated by production alone. The effect of horizontal dispersion has been neglected. Introducing this aspect again but now in a fixed coordinate system, we get for tidal averaged chlorophyll concentration \( \overline{c} \):

\[
\frac{3}{\partial x} \frac{\partial}{\partial x} \frac{\partial c}{\partial x} = \left( \frac{v_{\text{eff}}}{H} - \overline{u} \right) \overline{c}
\]

In the eastern part of the Oosterschelde \( \overline{v_{\text{eff}}} \) could be small (is not proved), and, as mentioned already in section 3.3, there are indications that net growth \( \overline{u} \) is high. On the other hand, in the western part \( \overline{v_{\text{eff}}} \) could be high and \( \overline{\mu} \) somewhat lower than in the eastern part.

If the import of \( c \) in the estuary, if any, is limited then \( \overline{v_{\text{eff}}} - \overline{\mu} \) averaged from west to east must be small. Consequently \( \frac{\overline{v_{\text{eff}}}}{H} - \overline{\mu} \) is probably smaller than 0 in the east and larger than zero in the west.

With \( \frac{3\overline{c}}{\partial x} = 0 \) for \( x = L \), the solution of \( \overline{c} \) can be as depicted in Figure 20.
The result corresponds more or less to the measured distribution of the yearly averaged values of chlorophyll and POC in the 3 areas of the Oosterschelde as is shown in Table 3. According to Table 3 the gradient in chlorophyll along the tidal excursion in area 1 and 2 could at most be about 25%. So the amplitude of the tidal variation in $c$ at a fixed point could be at most 25% of the mean value.

Summing up the two processes, we get a tidal variation in $c$ as shown below.

The variation in $c$ behaves in a comparable way as the measured tidal variation in chlorophyll. Only one peak is observed occurring just before high-water slack.

The resemblance would be better if the tide averaged chlorophyll concentration $\bar{c}$ had a higher gradient in longitudinal direction. This could well be possible,
because the gradient of 25% is based on an average of 10 years monthly data, while the tidal variations in chlorophyll are taken from measurements on fixed dates which are not chosen at random (only time series are used which show a pronounced behaviour).

The hypothesis as explained and quantified in this section is especially relevant in those parts of the Oosterschelde where the process of sedimentation is highest and the subsequent erosion during the tidal cycle is limited. These parts will be found especially in the inner part of the northern gully of the Oosterschelde in the region called the Hammen. The sediment composition in this particular area shows a grainsize distribution with a substantial amount of fine grained sand, 60 - 150 μm, which is a feature of a sedimentation region with still a limited erosion (because no mud is present).

A consequence of the hypothesis of net sedimentation of chlorophyll in the Hammen is that there must be a net import of POC or in each case of chlorophyll from the North Sea through the northern gully. This seems in contradiction with results obtained by DRONKERS pointing to an export of organic material to the North Sea. However, the latter result is based on a consideration of the transport over the transect Roompot - Schaar van Roggenplaat, the two southern gullies.

Applying the method developed by DRONKERS to the POC and seston data in the northern gully, leads to the conclusion of an import of these components in that gully, of the same order of magnitude as the export calculated by DRONKERS (1985)!!

This calculation has been carried out by W. VAN PAMPUS, student report 1986 LH-Wageningen, Department of Hydraulics and Catchment Hydrology (in preparation).

4.2 Floating of microphytobenthos

Changes in concentration of particular matter due to processes like sedimentation and erosion will be rather smooth and gradual over the tidal cycle.

The strong and sudden increase in chlorophyll as shown in Fig. 22 measured at a mussel plot at the east side of the Roggenplaat cannot be explained by such gradual processes.
Another hypothesis is presented to explain such situations. It is postulated that the sudden increase in chlorophyll-a in Fig. 22 is due to benthic diatoms brought into suspension. The mechanism behind this process is not the velocity regulated erosion, but it is the buoyancy of the microphytobenthos layer which is saturated with gasbubbles after a period of high production. The period with high production coincides with the emergence period of the flats.

Pieces of the originally connected benthic layer therefore only dislodge during the subsequent flood period. L. DE JONG (personal communication) observed occasionally a large scale disruption of the microphytobenthos mat at the Roggenplaat just after the location got flooded.

The detached pieces of about 2 cm diameter bumped against each other and against the bottom and finally they disintegrated. The water became very turbid by this resuspension of microphytobenthos pieces together with the adhesive silt.

The suspended material is transported by the flood currents to the east end of the flats. It is interesting to observe that mussel culture areas are usually found at the east side of tidal flats. This points to a possibility of a causal relation between the both phenomena. Figure 23.

4.2.1 Quantification of this mechanism

The microphytobenthos production is $2 \text{ g C m}^{-2} \text{ day}^{-1}$ (LINDEBOOM, 1985)

Production is mainly limited to the ebb period, so in one ebb period the production is $1 \text{ g C m}^{-2} = 25 \text{ mg chlor m}^{-2}$. The biomass of benthic microalgae remains remarkably constant at a level of $130 \text{ mg chlor m}^{-2}$, so the production must be equal to the loss rate.

We assume that this loss rate is totally due to the described updrifting process, so $25 \text{ mg chlor m}^{-2}$ per tidal cycle is disrupted. The flow velocity during flood is $0.25 \text{ m/day}$ at the specific date and location of Fig. 22 (HAAS, 1985). The increase in chlorophyll in Fig. 22 took four hours. In four hours the water is displaced $4 \cdot 0.25 \cdot 3600 = 3600 \text{ m}$. This displacement should match the length of the flat over which the benthic microflora layer is disrupted. It corresponds to about half the total length of the Roggenplaat. Therefore the amount of bottom diatoms passing a transect at the end of the flat will be $3600 \cdot 1 \cdot 25 = 80 \text{ gr chlorophyll/m}$.
This estimated amount has to be checked with the measured flux through the transect per m times the duration of the flux. The measured amount is depth times the increase in chlorophyll in the 4 hours period times this period times the transport velocity. Hence:

with a mean depth of 5 m a chlor increase of 7.5 mg chlor/m² and a transport velocity of 0.25 \( \times \) 3600 = m/hr, the measured amount becomes

\[
5 \times 7.5 \times 4 \times 900 = 135 \text{ g chlorophyll/m.}
\]

In view of the uncertainty in the given estimates, we conclude that the given hypothesis could also explain the order of magnitude of the measured tidal variation in chlorophyll.
5. Discussion and conclusions

The question, which factors are the most important in controlling the growth of suspension feeding bottom animals in the Oosterschelde has not yet been solved. However, some insight has been gained during this study about the plausibility or probability of a number of possible determining factors. The method which has been followed in this study is to bring forward certain hypotheses and estimate its implications as far as possible using various conceptual models.

By comparing model results with field data, an impression can be obtained of the value of a given hypothesis. If field data are not available or not appropriate to judge the value of a certain hypothesis, the hypothesis cannot be rejected. By showing the implications of those hypotheses, a background is obtained from which ideas how to measure it could perhaps evolve.

The discussion will be centered around the four hypotheses which have been studied:

Hypothesis I:
Food depletion at the sediment-water interface above the musselbed due to insufficient currents and vertical mixing.

The hypothesis is originally put forward by WILDISH and KRISTMANSON in 1979. In the original version of the hypothesis resuspension of seston is neglected. Also settling of seston is neglected. All seston filtered by suspension feeders is removed from the water column.

The result of a model based on this hypothesis shows that food depletion is an increasing function of the ratio between the filtration rate per unit surface of the musselbed and of the horizontal current velocity above the bed (see Figure 9).

The results are more or less in agreement with experimental data of WILDISH and KRISTMANSON obtained in a flume on laboratory scale. However, the results are not in agreement with Oosterschelde data of seston components in the water above musselplots.
Instead of a food depletion at the sediment-water interface, the Oosterschelde data show the contrary, namely a 25% to 30% higher values at the bottom than at half depth for POC and chlorophyll-a.

There are two main reasons for this discrepancy.

Firstly, the model neglects sedimentation of particulate matter. This appeared to be not justified. Data on vertical gradients of POC and chlorophyll show that settling velocities must be about 65 respectively 55 m/day. This is extremely high. A value of the settling velocity commonly used in phytoplankton models is 0 - 1 m/day.

It is suggested here that the phytoplankton in the western and central part of the Oosterschelde is mainly of North Sea origin, and might feel not very healthy in the estuarine environment.

It is known (SMAYDA, 1970) that unproductive senescent cells usually have higher settling velocities.

Secondly, the model neglects resuspension of particulate matter. This appears also not realistic. Apart from sedimentation and resuspension also the process of filtration and biodeposition of seston exists. SMAAL et al (1985) show that 20% of the seston per day is filtered and biodeposited. Because no seston depletion in the water column can be observed over one tidal cycle, most of this material must be resuspended again in the same tidal cycle.

Hypothesis II:

Food depletion in a given area of the Oosterschelde due to insufficient supply by currents and resuspension.

Resuspension and erosion are difficult processes to handle. The processes become even more complicated because we are interested primarily in a specific component of the resuspended material, namely in the degradable fraction of the organic matter.

In order to avoid too much uncertainties, it is wise to consider the mentioned processes first on an estuarine wide scale.

Let us concentrate on POC which is believed to be an important food source for suspension feeders.

It is expected that the growth of suspension feeders increases with an increase in the POC concentration in the water column.

The POC concentration in the water on its turn depends on the total amount of POC in the estuary and on the ratio between the amount in the water and in the bottom. The total amount follows from the balance between production and mineralisation and from the import or export from the estuary to the
North Sea. The distribution of POC between bottom and water pool depends on the balance between sedimentation and resuspension of POC. We consider in the following only the tidal averaged situation. Resuspension is higher in areas where the bottom currents are higher. However, if bottom currents are too high, not only the freshly settled POC is resuspended, but also sand which inhibits suspension feeders growth. So the optimal bottom tidal currents has to be between an upper and lower limit. The optimal velocity is such that faeces and pseudofaeces are brought into resuspension, but not the fine grained sand.

Figure 24 shows the grain size distribution of the sediment in the Hammen. Observe that there are locations consisting of sand with a substantial amount of fine grained particles.

The lower the tidal velocities the less POC is brought into suspension. Apart from velocities the resuspension of POC depends also on the availability of this organic material in the bottom.

Figure 25 from the BALANS report 1985-11 shows that the POC distribution in the bottom of the Oosterschelde is not homogeneously distributed. This aspect together with the aspect of the currents yields a POC distribution in the main gully of the Oosterschelde as shown in Figure 25, copied from the mentioned BALANS report 1985-11.

Also Table 2 shows more or less the same distribution of POC in the three areas of the Oosterschelde.

Hypothesis II cannot be rejected on the basis of available data. At present a measuring program at DDMI is going on in which the relation between growth of suspension feeders and seston quantity and quality is studied (SMAAL, PRINS).

Hypothesis III:
Phytoplankton depletion in a certain area containing musselbeds due to insufficient supply by currents and local production in comparison with the effective settling rate (see section 4.1.1).

This hypothesis is in some sense a modification of the foregoing one. The only difference is that in this case only chlorophyll is considered as food for the suspension feeders and that more attention is paid to the production of phytoplankton which can be different in various parts of the Oosterschelde.

The question of the food supply (POC, chlorophyll) by currents for the estuary as a whole is extensively studied in the BALANS project.
One of the results is that an export of organic material exists over a transect containing the two southern gullies of the Oosterschelde. The question is whether the result is also valid for the northern gully. This question has recently been studied by a LH-student (PAMPUS, W. van, 1986). He concluded that an import of organic matter in the northern gully of the Oosterschelde of a comparable order of magnitude as the measured export in the other two gullies could be possible.

The results of a model based on this hypothesis gives a chlorophyll gradient in the Oosterschelde which is higher in area 1 than in area 2 which corresponds with measurements (see Table 2). Also one peak is observed in the calculated tidal variation in chlorophyll occurring just before high-water slack, which also corresponds with data.

Hypothesis IV:
Suspension feeders situated at the edges of tidal flats can profit from a food supply caused by updrifting of parts of the microphytobenthos layer during flood tide. The hypothesis needs further study to judge its validity. It is mentioned by one of the members of the suspension-feeders working group that the extensive microphytobenthos areas in the eastern part of the Oosterschelde apparently are not accompanied by a corresponding stock of suspension feeders.

On the other hand other arguments can be found which support the hypothesis. As said, further research is needed.
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APPENDIX A: Solution method of case I

Seston balance

\[ u \frac{\partial c}{\partial x} - u \frac{\partial c}{\partial z} (D \frac{\partial c}{\partial z}) = 0 \]  

(1)

where

\[ u = u_o - (u_o - u_i) e^{-kz} \]

\[ D = D(z) \text{ at } z = 0 \quad D = \ \text{const.} \]

Boundary conditions

For \( z = 0 \)

\[ D \frac{\partial c}{\partial z} = \phi N C \]

For \( z = \delta \)

\[ c = c_o \quad \text{and} \quad \frac{\partial c}{\partial z} = 0 \]

For \( x = 0 \)

\[ c = c_o \]

A reasonable description of the concentration profile seems:

\[ c = c_o - c_1(x) \left(1 - \frac{z}{\delta(x)}\right)^2 \]

(2)

For \( z = 0 \) we get

\[ \frac{2 D_1}{\delta} c_1 = \phi N (c_o - c_1) \Rightarrow c_1 = \frac{\phi N \delta c_o}{2 D_1 + \phi N \delta} \]  

(2a)

To simplify the calculations we assume that \( \frac{\phi N \delta}{2 D_1} \ll 1 \), which is quite reasonable for practical values of the various parameters.

So:

\[ c_1 = \frac{\phi N \delta}{2 D_1} c_o \]

(3)

Integrating equation (1) over \( z \) between 0 and \( \delta \) and using the boundary conditions at \( z = \delta \) and \( z = 0 \) gives:

\[ \phi^o \delta u \frac{\partial c}{\partial x} \, dz + \phi N c_{z=0} = 0 \]

(4)
Substitution of (2) and (3) in (4) gives:

\[
\frac{\varphi N c_o}{2 D_1} \int_0^\delta u^\prime \left( -1 - \frac{z}{\delta} \right)^2 \frac{d\delta}{dx} - 2 \left( 1 - \frac{z}{\delta} \right) \frac{z}{\delta} \frac{d\delta}{dx} \right) \, dz + \varphi N c_o = 0
\]  

(5)

With \( u = u_o - (u_o - u_1) e^{-kz} \), the integral can easily be solved. The solution is:

\[
\left[ \frac{2}{3} u_o \delta + \frac{(u_o - u_1) \delta}{k_0} \left( -1 - 2 \frac{e^{-k_0 \delta}}{k_0} - \frac{2}{k_0^2 \delta^2} (e^{-k_0 \delta} - 1) \right) \right] \frac{d\delta}{dx} = 2 D_1
\]  

(6)

The asymptotic behaviour of the above solution for \( k_0 \ll O(1) \) is

\[
\left[ \frac{2}{3} u_o \delta + \frac{(u_o - u_1) \delta}{k_0} \left( - \frac{2}{3} k_0 \delta + O(k_0^2 \delta^2) \right) \right] \frac{d\delta}{dx} = 2 D_1
\]

or

\[
\frac{d \delta^2}{dx} = \frac{6 D_1}{u_1}
\]

With \( \delta = 0 \) for \( x = 0 \) we get:

\[
\delta = \sqrt{\frac{D_1 x}{u_1}}
\]  

(7)

The asymptotic behaviour of the solution (6) for large values of \( k_0 \) i.e. \( k_0 \gg O(1) \) is

\[
\left[ \frac{2}{3} u_o \delta + (u_o - u_1) \delta \cdot O(k_0^{-1}) \right] \frac{d\delta}{dx} = 2 D_1
\]

or

\[
\frac{d \delta^2}{dx} = \frac{6 D_1}{u_o}
\]

or

\[
\delta = \sqrt{\frac{6 D_1 (x - x_o)}{u_o}} \quad \text{where} \; x_o \; \text{is an integration constant.}
\]
The seston balance equation (1) can also be solved analytically without any assumption on the order of magnitude of the filtration rate in the case \( u(z) = u_0 \) is constant.

In that case the seston balance equation integrated over \( z \) between 0 and becomes:

\[
\begin{align*}
\int_{0}^{\delta} \left\{ \frac{d c_1}{dx} (1 - \frac{z}{\delta})^2 - 2 c_1 (1 - \frac{z}{\delta}) \frac{d \delta}{dx} \right\} dz + 2 \frac{D_1 c_1 \delta}{\delta^2} &= 0 \\
\int_{0}^{\delta} \left\{ \frac{d c_1}{dx} (1 - \frac{z}{\delta})^2 - 2 c_1 (1 - \frac{z}{\delta}) \frac{d \delta}{dx} \right\} dz &= -2 \frac{D_1 c_1 \delta}{\delta^2}
\end{align*}
\]

or

\[
- \frac{1}{3} u_0 \frac{d}{dx} (c_1 \delta) + \frac{2 D_1 c_1}{\delta} = 0
\]

With \( c_1 = \frac{\Theta N \delta c_0}{2 D_1 + \Theta N \delta} \) we get a first order differential equation in \( \delta(x) \) which can be integrated to yield

\[
\frac{1}{2} \delta^2 + \frac{2 D_1}{\Theta N} \delta - \left( \frac{2 D_1}{\Theta N} \right)^2 \ln \left( 1 + \frac{\Theta N \delta}{2 D_1} \right) = \frac{6 D_1 x}{u_0}
\]

The integration constant is equal to zero, because \( \delta = 0 \) for \( x = 0 \). Observe that if the dimensionless parameter \( \frac{\Theta N \delta}{2 D_1} \) is small compared to one, the above equation reduces in a good approximation to

\[
\delta^2 = \frac{6 D_1 x}{u_0}
\]

or

\[
\delta = \frac{6 D_1 x}{u_0} \quad \text{and} \quad \text{DEPL} = \frac{\Theta N \sqrt{\frac{3L}{2 u_0 D_1}}}{1 + \Theta N \sqrt{\frac{3L}{2 u_0 D_1}}}
\]

The above equation can also be expressed in terms of DEPL as follows:

\[
\frac{1}{2} \gamma^2 + \gamma - \ln(1 + \gamma) = \left( \frac{\Theta N}{2 D_1} \right)^2 \cdot \frac{6 D_1 x}{u_0}
\]

in which \( \gamma = \frac{\text{DEPL}}{1 - \text{DEPL}} \)

The solution of this equation for \( x = 335 \) cm and \( D_1 = 0.02 u_0 \), \( l = 15 \) cm is presented in Fig. 9.
### Table 1. Biomass, Density and Standing Stock of *Mytilus Edulis* in 3 Areas of the Oosterschelde: Mean Values ± S.D. from 1979 to 1983.

<table>
<thead>
<tr>
<th>AREA</th>
<th>1 (west)</th>
<th>2 (middle)</th>
<th>3 (east)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Surface (m²)</strong></td>
<td>135.43</td>
<td>94.58</td>
<td>88.40</td>
</tr>
<tr>
<td><strong>Biomass (g ADW/m²)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juveniles</td>
<td>0.4</td>
<td>5.59</td>
<td>0</td>
</tr>
<tr>
<td>Adults</td>
<td>4.22</td>
<td>3.61</td>
<td>4.2</td>
</tr>
<tr>
<td><strong>Density (N/m²)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juveniles</td>
<td>115.7±17.2</td>
<td>111.8±16.7</td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>340.0±21.3</td>
<td>230.0±51.0</td>
<td>211.0±147.0</td>
</tr>
<tr>
<td><strong>Standing Stock (tons ADW)</strong></td>
<td>1482±89</td>
<td>1458±239</td>
<td>886±617</td>
</tr>
</tbody>
</table>

### Table 2. Biomass, Density and Standing Stock of *Cerastoderma Edule* in 1984.

<table>
<thead>
<tr>
<th>AREA</th>
<th>1 (west)</th>
<th>2 (middle)</th>
<th>3 (east)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Surface (m²)</strong></td>
<td>24.10</td>
<td>31.05</td>
<td>38.05</td>
</tr>
<tr>
<td><strong>Biomass (g ADW/m²)</strong></td>
<td>63.4</td>
<td>35.0</td>
<td>19.7</td>
</tr>
<tr>
<td><strong>Density (N/m²)</strong></td>
<td>244</td>
<td>135</td>
<td>78</td>
</tr>
<tr>
<td><strong>Standing Stock (tons ADW)</strong></td>
<td>11.48</td>
<td>10.63</td>
<td>11.93</td>
</tr>
<tr>
<td><strong>Biomass</strong></td>
<td>26.9</td>
<td>17.3</td>
<td>5.0</td>
</tr>
<tr>
<td><strong>Density</strong></td>
<td>103</td>
<td>66.5</td>
<td>19.7</td>
</tr>
<tr>
<td><strong>Standing Stock (tons ADW)</strong></td>
<td>1844</td>
<td>1273</td>
<td>812</td>
</tr>
</tbody>
</table>

### Table 3. Mean Seston Concentrations per Year and Growth Season (April-September) from 1977-1983 in 3 Areas.

<table>
<thead>
<tr>
<th>AREA</th>
<th>1 (west)</th>
<th>2 (middle)</th>
<th>3 (east)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CHL-a (µg/l)</strong></td>
<td>6.60</td>
<td>9.68</td>
<td>5.70</td>
</tr>
<tr>
<td><strong>POC (mg/l)</strong></td>
<td>1.49</td>
<td>1.41</td>
<td>1.03</td>
</tr>
<tr>
<td><strong>SPM (mg/l)</strong></td>
<td>27.5</td>
<td>21.5</td>
<td>19.3</td>
</tr>
</tbody>
</table>

**Table 3. Mean seston concentrations per year and growth season (April-September) from 1977-1983 in 3 areas.**
Sections:
1. west
2. middle
3. east

CIRCULATION CELLS

Figure 12
Figure 13 Mean seston concentration over the year on locations I and II from surface sampling in monthly routine programs over 1972-1982.
Sampling locations
"MOKWE"

1. Hanneken Noord
2. Hanneken Zuid
3. Hanneken Roggeplant 20
4. Hanneken Roggeplant Z
5. Brab. Varen, Kilde Tannen Vijver
6. Brab. Varen, Midden

Vessels
7. Molenvliet
8. Bokkagat
9. Lodijke

Figure 14
Fig 15. Mean seston concentrations from 13-hour sampling programs on several mussel plots during ebb and flood (n = 10). — 0.5 m above the bottom — — — half depth.
<table>
<thead>
<tr>
<th>Datum</th>
<th>Schip</th>
<th>Plaats</th>
<th>MOKWE</th>
<th>LH</th>
<th>HH</th>
<th>Rijkswaterstaat</th>
<th>Milieu en Inrichting</th>
<th>Deltadienst M'burg</th>
</tr>
</thead>
<tbody>
<tr>
<td>851002</td>
<td>Molenvliet</td>
<td>LAMMEN 16</td>
<td>18.03</td>
<td>16.06</td>
<td></td>
<td>Rijkswaterstaat</td>
<td>Milieu en Inrichting</td>
<td>Deltadienst M'burg</td>
</tr>
<tr>
<td>851002</td>
<td>Bokkegat</td>
<td>BRAB.V.W.17</td>
<td>11.15</td>
<td>17.40</td>
<td></td>
<td>Rijkswaterstaat</td>
<td>Milieu en Inrichting</td>
<td>Deltadienst M'burg</td>
</tr>
<tr>
<td>851002</td>
<td>Lodycke</td>
<td>LG PK (KOM)</td>
<td>11.28</td>
<td>17.25</td>
<td></td>
<td>Rijkswaterstaat</td>
<td>Dienst Getijd Wateren</td>
<td>Middelburg</td>
</tr>
</tbody>
</table>

Figure 16
Datum: 850508
Schip: Orisant
Plaats: HAMMEN (H16)

Datum: 850508
Schip: Aggar
Plaats: KOM (LG/PK)

Figure 17
Figure 18. (a) Tidal variation in chlorophyll at the "Slikken Dortsman"; normal tide

(b) Result of food depletion theory at the front of a musselbed in shallow water
Figure 22 Tidal variation in chlorophyll on a musselplot at the east side of the Roggenplaat
Figure 23 Locations of mussel culture plots in Oosterschelde
Figure 24 Grainsize distribution of sediments of musselplots in the Hammen (from STEYAERT, 1985)
Figure 25 Organic carbon distribution in the bottom and the distribution of POC and suspended matter in the water near the surface in the Oosterschelde (yearly averaged values). Reprinted from Nota BALANS 1985-II.