THE BENTHIC BIOLOGICAL SUBMODEL IN THE EUROPEAN REGIONAL SEAS ECOSYSTEM MODEL

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ABSTRACT

The submodel describing benthic biology including a bioturbation module as incorporated in the European Regional Seas Ecosystem Model (ERSEM) is discussed. It is linked to a nutrient dynamic model. The structure of the benthic model food web is presented. There are four macrobenthic functional groups, meiofauna and aerobic and anaerobic bacteria. The modelling uses 'standard organisms' as basic building blocks. The choice of parameter values is discussed. The results demonstrate the dependence of the benthic system on the pelagic system. The importance of features such as predation within functional groups for stability of the system is investigated. Detritus input from the pelagic system and detritus recycling is most important in the benthic food web. The web of carbon and nutrient fluxes through the system is analysed. On the basis of the food web analysis, the trophic positions of the functional groups are calculated. Besides the benthic biology, the mathematical formulation of the bioturbation and diffusion enhancement is discussed. Macrobenthic presence and activity enhance diffusion in the sediment and contribute essentially to vertical transport of particulate matter. This is of great importance for the vertical distribution of detritus, and as a consequence, for microbial activity in the sediment layers.

1. INTRODUCTION

ERSEM (ERSEM, 1993; Baretta et al., 1995) is an attempt to construct an extensive model of the North Sea. The model consists of pelagic, benthic and transport submodels. The benthic submodel in ERSEM consists of three separate parts: 1. benthic biology; 2. bioturbation and bioirrigation; 3. nutrient profiles (Ruardij & Van Raaphorst, 1995) which exchange information according to pathways illustrated in Fig. 1.

The modelled benthic system is driven by input from the pelagic system; pelagic detritus and diatoms sink to form benthic detritus, and benthic suspension feeders actively feed on pelagic biomass. The seasonality of these inputs produces the benthic seasonality. The direct temperature or light dependence is much less important. Also, the differences in input are the chief source of spatial gradients, because in the present version of the benthic biology module differences in sediment-type are not taken into account, although they are taken into account in the nutrient profiles (Ruardij & Van Raaphorst, 1995), where diffusion constants and adsorption processes depend on the nature of the ERSEM geographical boxes.

Much less is known about benthic processes than about pelagic ones. This is because there are far fewer benthic ecologists and because sampling of benthos is much more time consuming and problematic than sampling of plankton. As a direct result there are far fewer benthic models or modules and those that exist admit to many unknown processes. Warwick et al. (1979) used a benthic model 'to investigate the effect on the system as a whole of a variety of hypothetical trophic relationships which are (were) poorly understood, particularly the interactions between meiofauna and macrofauna'. Radford (1994) used the model GEMBASE to demonstrate the importance of benthic interactions, particularly those of deposit feeders and suspension feeders on the total productivity of an estuary. He demonstrated that increased pelagic productivity resulted in a commensurate increase in benthic productivity. The benthic subsystem of the Ems model (Admiraal et al., 1988) was very detailed and included aerobic and anaerobic bacteria which alone needed 30 parameters to be modelled. Representations of bioturbation and vertical diffusion were also included although few measurements were available to justify the parameter values. This situation has hardly changed up to the
Present but the overriding need to account for the ultimate fate of all system carbon and nutrients has led to their inclusion in ERSEM (this paper). An attempt has been made to simplify the benthic submodel by defining the standard (benthic) animal with common processes such as intake, assimilation, respiration, mortality and nutrient release but with different parameters for each functional group, allowing for different food preference factors, sources and vertical distributions. A similar approach is adopted in modelling aerobic and anaerobic bacteria.

The enhancement of diffusion leads to an important input to the benthic nutrient profiles submodel. The transport of dissolved substances in the pore water is modelled similar to a diffusion process, with the diffusion constant depending on the density of the macrobenthic population (section 3.4.).

Mixing in the sediment as transport of particulate matter is denoted as 'turbation' (section 3.5.). Macrobenthic organisms contribute essentially to the turbarion ('bioturbation'). They 'mix' the sediment and effectively transport freshly sedimented material from the surface of the sediment to deeper layers, where it fuels the biological processes. Equations are derived which allow the calculation of the depth distribution of detritus and the changing composition of detritus with depth. Consumption and excretion of detritus at various depths, and addition of detritus to the surface by sedimentation act as input to the bioturbation model.

The vertical transport of particulate matter in the sediment is not an easy mathematical problem. The concepts of 'diffusion' and advection work well in the water column, but are only crude approximations for shifting particles in the sediment. Some theoretical models have been developed, but they seem to be too complicated for an implementation in ERSEM (Matisof, 1982; Boudreau & Imboden, 1987; Goldberg & Koide, 1962). Some observations and experiments are done in mesocosms (De Wilde & Kuipers, 1977), others in natural sediments (Gerino, 1990; Bianchi, 1988).

Turbation is a slow process; no equilibrium distribution of the particle fractions can be assumed. The vertical distributions of detritus components (C, N, P, Si) change dynamically under the influence of turbarion, decomposition and production processes. These distributions are important both for microbial activities and activities of deposit feeders. The bioturbation model presented in this paper does not claim to be a new theory. It works pragmatically within the ERSEM framework.

The feedback from a biotic system to the abiotic environment is generally of extreme interest. This became especially obvious by Watson & Lovelock's (1983) parable of the daisy world, where the biotic system keeps the 'world' inhabitable. On a smaller scale, the principle is well known in the Wadden Sea, where the physical properties of the sediment surface are modified by algae and cyanobacteria, where the biotic system provides for instance sediment traps. Another example is the soil community. These feedback mechanisms from the biotic system act generally positively to its abiotic environment, improving the conditions. This is a typical property of a complex system in the sense of the theory of complexity (e.g. Waldrop, 1993). Such positive effects are important prerequisites for self-organized structure forming, self-organized criticality leading to surprising behaviour and robustness due to adaptability. Unfortunately, the ERSEM model is only a complicated simple model. It does not aim to reproduce these properties of the ecosystem; it only aims to reproduce average mass flows. Nevertheless, we think that at least a simple and rudimentary description of the feedback between macrobenthos and sediment properties has to be included in the ERSEM model for this purpose.

2. TROPHIC INTERACTIONS

As in other ERSEM modules, the food web in the benthic submodel is not constructed from species, but the state variables represent functional groups. They can be considered collections of species with a similar function in the ecosystem. The method of defining these functional groups is by subdividing the infinitely complex real food web into a few artificial parts, not by combining single species into mathematical aggregates. Even if these two procedures may, at first glance, lead to the same result, there is a difference in the interpretation which may be essential for the complicated task of parametrization. By subdividing the ecosystem into functional groups according to some selected rules, everything will be included somewhere, but the mathematical formulation of the processes (uptake, excretion, etc.) belonging to these functional groups may be difficult, because different mechanisms and different rates
and thresholds have to be combined. This is a problem; hence, modellers tend to identify a functional group with one or two common species and then assign their properties (functions and parameters) to the whole functional group. This corresponds to an incomplete aggregation of species.

Benthic primary producers are not taken into account in the present implementation of the ERSEM model because the depth of the shallowest compartment is below the euphotic zone.

2.1. CONSUMER-FOODWEB (MACRO- AND MEIOBENTHOS)

A straightforward method of aggregation is the subdivision of all species into size classes. The only remaining 'functions', which then have to be separated, are primary production, secondary production and decomposition of detritus. This method is successful in the pelagic lower food web. In the benthic system there are, however, distinct 'functions' of organisms with similar size. The four macrobenthic organisms comprise all species above 1 mm, excluding 'demersal fish' (Bryant et al., 1995). They are subdivided into four functional groups in the benthic model:

- suspension feeders feed directly from the pelagic system, all other organisms use food which is part of the benthic system (possibly with pelagic origin).
- deposit feeders feed on benthic detritus and benthic organisms which may be several orders of magnitude smaller than the animals themselves.
- infaunal predators collect the food in a completely different manner to suspension and deposit feeders and have prey of a size comparable to themselves.
- epifaunal predators are often mobile and large (megabenthos). They act on the sediment surface. However, immobile epifauna and small epifaunal predators exist and have to be included here.

The feeding behaviours of macrobenthic functional groups have important consequences for their contribution to bioturbation and bioirrigation. Infaunal predators are quite active in reworking the sediment, deposit feeders act at greater depth, while epibenthic predators disturb the surface and suspension feeders do not contribute very much. The other type of influence on the vertical transport in the sediment is the enhancement of the 'effective' diffusion constant for interstitial water by burrows and pumping.

Another functional group is meiobenthos, including all heterotrophs between protozoa and animals of a size of about 1 mm. Compared to the number of species in the macrobenthic functional groups there are far more meiobenthic species, with widely different specializations, aggregated into a single functional group. Meiobranchia are of minor importance for bioturbation and bioirrigation. Hence, the subdivision of functions into macrobenthos and the aggregation of meiofauna can be justified on the basis of these physical effects. The meiofaunal functional group, as defined here, represents in itself a complex food web. In the aggregated form, meiobenthos has to be omnivorous, feeding to a considerable extent on itself. This predation within the meiofauna increases the trophic position of meiobenthos to the value it would have on average if the food web were resolved (see section 5.4).

2.2. DECOMPOSER-FOODWEB (BACTERIA AND DETRITUS)

The main input of biomass to the benthic system is pelagic detritus. In the present model two different groups of microbial decomposers are considered: aerobic bacteria and anaerobic bacteria. The food web for the benthic submodel is shown in Fig. 2.

Detritus consists of a wide spectrum of dead organic matter with different composition (nutrient poor - nutrient rich) and degradability. Benthic detritus in the sense of the ERSEM is particulate organic matter (POM) and it is described by its composition in terms of carbon, nitrogen and phosphorus. The silicate component is important only in the benthic nutrient model (Ruardij & Van Raaphorst, 1995). Only the labile fraction of dissolved organic matter (DOM) is considered; refractory DOM is neglected altogether.

Detritus arrives at the sediment surface by sedimentation of pelagic detritus and diaatoms. It is transported vertically in the sediment by bioturbation and physical actions. It is decomposed and reprocessed by bacteria, meiofauna and deposit feeders. Because the easily degradable parts have a shorter residence time in the sediment than the more refract-

![Fig. 2. Benthic food web in ERSEM. The horizontal axis represents a compromise between size and trophic position. H1 aerobic benthic bacteria, H2 anaerobic benthic bacteria, Y1 epibenthic predators, Y2 deposit feeders, Y3 suspension feeders, Y4 meiofauna, Y5 infaunal predators, R6 & Q6 particulate detritus, P1 diatoms, P2 autotrophic flagellates.](image-url)
Horizons and layers in the benthic submodel. The horizons $d_o$ and $d_n$ depend on time; they move according to the strength of different redox processes and diffusion.

<table>
<thead>
<tr>
<th>horizons</th>
<th>surface</th>
<th>$d_o$(time)</th>
<th>$d_n$(time)</th>
<th>30 cm</th>
</tr>
</thead>
</table>

Layers:
- aerobic layer: $0 - d_o$
- oxidized (nitrate dominated) layer: $d_o - d_n$
- anoxic (reduced) layer: $d_n - 30$ cm

In the ERSEM, the degradability is coupled to the nutrient content of the detritus (see section 3.2.), and hence the nitrogen and phosphorus components of detritus have a smaller penetration depth in the sediment than the carbon component.

The vertical distribution of the detritus is dynamically calculated in a separate bioturbation submodel. Consumption and production at different depths, addition at the surface and macrobenthic activity act as input, the parameters of the depth functions describing the distribution of the detritus components over depth are the output of this submodel. Presently the distribution function is an exponential decrease, cut off at a depth of 30 cm. The parameter of this exponential function is the average penetration depth, which dynamically changes with time and location (box).

In the present ERSEM formulation, the sediment consists of three layers, separated by moving horizons as shown in Table 1. The horizons move dynamically as described in Ruardij & Van Raaphorst (1995). These layers correspond to the main decomposers for particulate detritus which are aerobic and anaerobic bacteria. The aerobic bacteria live and act in the uppermost (aerobic) layer. The anaerobic bacteria live below the oxygen horizon in the oxidized and in the anoxic (reduced) layer. The benthic functional groups, decomposers and secondary producers, have access to detritus at different depths (Table 2). Detritus derived from benthic faecal production is assumed to occur in the middle of the given depth intervals, predators excrete close to the surface. This is of relevance for the dynamical calculation of the detritus distribution parameters.

### 3. THE STRUCTURE OF THE BENTHIC BIOLOGICAL SUBMODEL

Using standard organisms, the construction of the model is relatively simple. One must specify:
- the food web with preference factors;
- dynamic parameters;
- depth intervals relating to the functional groups;
- deviations from the standard organisms (e.g. suspension feeders and anaerobic bacteria);
- environmental conditions (temperature, light, oxygen, etc.).

The most important features of the standard organisms are described. A standard organism is represented by a set of fluxes and processes which are essentially controlled by the biomass of the standard organism.

#### 3.1. STANDARD SECONDARY PRODUCER

A standard secondary producer is described by a vector $Y$ containing a carbon component $Y.c$ in mg C m$^{-2}$ and N- and P-components $Y.n$, $Y.p$ in mmol m$^{-2}$. The atomic ratio is fixed. The vector $Y$ follows a differential equation

$$\dot{Y} = \text{uptake} - \text{faeces} - \text{respiration} - \text{mortality} - \text{nutrient excretion} - \text{predation losses}$$

The terms on the right side of Eq. 1 are fluxes with C-, N- and P-components in mg C m$^{-2}$d$^{-1}$ and mmol m$^{-2}$d$^{-1}$. All fluxes are temperature dependent with a Q10-value, dependent on the functional group. This temperature factor is included in the model but omitted in the following discussion of the processes to keep the formulas simple.

**Predation losses** Predation losses are modelled in the predators as uptake term. They simply appear here as consequent loss terms. In this sense 'predation losses' are processes associated not with the considered standard organism but with its predators.

**Uptake** Most of the secondary producers eat from more than one food source. In addition, they are omnivores due to species aggregation. Hence, uptake is a sum over different food sources:

$$\text{uptake} = \sum_i \text{uptake}_i(F_i, F)$$

Here $F_i$ is the concentration vector (C, N, P) of food source $F_i$, which can be another secondary producer,
a primary producer or a detritus fraction. In the case of predation within the functional group \( F_i \) is identical with \( Y \). \( F \) is a food sum. In the present version of the standard model \( F \) is defined as

\[
F = \sum_i \bar{F}_i \text{ with } \bar{F}_i = \frac{p_i F_i}{p_i F_i c + L_{up}}
\]  

The uptake fluxes are

\[
up(F_i, F) = r^{up} \frac{\bar{F}_i}{F_i c + K^{up}} Y c
\]  

The parameter \( L^{up} \) is similar to a lower food threshold. However, there is no sharp cut off of uptake for food densities below \( L^{up} \) but a gradual reduction. With \( L^{up} = 0 \) the effective food concentrations \( \bar{F}_i \) are proportional to the real food concentrations \( F_i = p_i F_i \). A non-zero \( L^{up} \) stabilizes the system numerically, because in this case sparse food sources are saved if parallel rich food sources boost the presence of \( Y \) as predator. The parameters \( p_i \) denote preference factors, which may be different for the food sources. For instance, detritus may be less preferred. The parameter \( K^{up} \) is the half saturation constant for food uptake, and the constant \( r^{up} \) (in \( d^{-1} \)) describes the maximum specific uptake. In the soft threshold term defining \( \bar{F}_i \) and in the saturation term (Monod forms) only the carbon components \( F_i c \) and \( F c \) of food sources and food sum are used. The C:N:P composition of the uptake flux \( up(F_i, F) \) is the same as that of the food source \( F_i \).

Faeces A part of the food uptake is released faeces

\[
faeces.c = \sum_i q_i^{fec} up(F_i, F).c
\]

\[
faeces.np = \sum_i q_i^{fec} up(F_i, F).np e^{ex}
\]  

These fluxes produce particulate detritus (POM) in the model. In reality these wastes are not necessarily particulate. A corresponding extension of the model is simple, but requires another unknown parameter (compare mortality). The composition of the faecal products is not the same as that of the food; they contain less nutrients. In the model this is necessary because reprocessed detritus must have a lower quality. This is taken into account by a dilution factor \( e^{ex} \) for the nitrogen and phosphorus components of the faeces. The silicate component of the food is completely defaecated. The difference between uptake and faeces is considered as assimilated:

\[
ass(F_i, F).c = \left(1 - q_i^{fec}\right) up(F_i, F).c
\]  

Respiration Respiration is a carbon flux, producing CO\(_2\) and consuming oxygen:

\[
respiration = \text{basal respiration} + \sum_i q_i^{res} ass(F_i, F).c + \text{stress respiration}
\]  

Basal respiration is proportional to the biomass of the secondary producer \( Y \):

\[
\text{basal respiration} = r^{res} Y c
\]  

Activity respiration is interpreted as energy costs of uptake and assimilation and is assumed to be proportional to the assimilation fluxes. Stress respiration (dependent on oxygen stress or salinity stress) is implemented but not used in the present version of ERSEM.

Nutrient release Due to uptake of food with varying C:N:P-ratios and due to carbon losses by respiration, the secondary producer must readjust its own fixed C:N:P ratio. Generally there will be a surplus of nutrients which will be released. No additional parameter is necessary for this adjustment. In the case of nutrient-poor food there may be a nutrient demand, and then the surplus carbon is respired. Nutrient release is a process with N and P fluxes leading to dissolved ammonium and phosphate.

Mortality Mortality in this sense is non-predation mortality due to old age (unimportant), physical trauma or other causes not specified in the model. This mortality is taken to be proportional to the biomass of \( Y \). Stress mortality due to oxygen shortage or salinity stress is implemented but not used in ERSEM:

\[
\text{non-predation mortality} = \text{natural mortality} + \text{stress mortality}
\]

\[
\text{natural mortality} = r^{m} Y
\]  

The flux has the same composition as \( Y \). It splits into two parts leading to particulate and dissolved (LOC) dead organic matter (fraction \( q^{dis} \), presently 0).

3.2. STANDARD DECOMPOSER

A standard decomposer is described by a vector \( H \), similar to the standard secondary producer, with fixed atomic ratios. It follows the differential equation

\[
\dot{H} = \text{decomposition} \cdot \text{DOM-excretion} \cdot \text{respiration} \cdot \text{mortality} \cdot \text{nutrient uptake/excretion} \cdot \text{predation losses}
\]  

\[
H = \text{decomposition} \cdot \text{DOM-excretion} \cdot \text{respiration} \cdot \text{mortality} \cdot \text{nutrient uptake/excretion} \cdot \text{predation losses}
\]
A temperature factor is included in the model but omitted from the following formulas.

**Predation losses** see secondary producers.

**Decomposition** The standard decomposer is assumed to possess three decomposition pathways for detritus:

\[
\text{decomposition} = \text{POM-fast} + \text{POM-slow} + \text{DOM-uptake}
\]  
(11)

The flux \( \text{POM-fast} \) is dependent on the \( \text{POM} \) composition and slows down if the nutrient contents (N or P) become low:

\[
\begin{align*}
\text{POM-fast}_c &= r_{ Pf } \varepsilon \text{POM}_c \\
\text{POM-fast}_{np} &= r_{ Pf } \varepsilon \text{POM}_{np} e_{Pf} 
\end{align*}
\]  
(12)

In this flux \( r_{ Pf } \) is a rate constant \((1^t)\), \( \text{POM} \) is the density of the particulate detritus and \( \varepsilon \) is a factor depending on the detritus composition in relation to the bacterial atomic ratios:

\[
\varepsilon = \min \left( 1, \frac{\text{POM}_n \cdot \text{H}_n \cdot \text{POM}_p \cdot \text{H}_p}{\text{POM}_c \cdot \text{H}_c \cdot \text{POM}_c \cdot \text{H}_c} \right)
\]  
(13)

The composition of the flux differs from the composition of detritus itself, because the nutrient-rich fraction is assumed to be decomposed first. This deviation is described by a concentration factor \( e_{ Pf } \) for the nitrate and phosphate component. The flux \( \text{POM-slow} \) is not dependent on the nutrient content of detritus \((c = 1)\), but is constructed similar to \( \text{POM-fast} \) with a much smaller rate constant \( r_{ Ps } \) and \( e_{ Ps } = e_{ Pf } \). The flux \( \text{DOM-uptake} \) is simply proportional to the labile DOM concentration (LOC):

\[
\text{DOM-uptake} = r_{ D } \text{DOM}
\]  
(14)

The decomposition fluxes are not modelled as being proportional to the bacterial biomass. This reflects the view that the decomposition process is limited by amount and quality of the substrate. The flux represents the production of bacterial biomass. Decomposition of detritus is also assumed to be oxygen dependent. The particulate rates in Eq. 11 get an additional factor \( p (\text{oxygen}) \), described in the section about mortality.

**DOM-excretion** A part of POM is decomposed by extracellular enzymes. This is formally described as

\[
\text{DOM-excretion} = q_{ ex } (\text{POM-fast} + \text{POM-slow})
\]  
(15)

The difference is considered as assimilated:

\[
\text{assimilation} = \text{decomposition} \cdot \text{DOM-excretion}
\]  
(16)

**Respiration** Similar to standard secondary producer.

\[
\text{respiration} = r^{ res } \text{H.c} + q^{ res } \text{assimilation}
\]  
(17)

**Nutrient uptake and excretion** Contrary to the secondary producers in the model, microorganisms (decomposers) can take up inorganic nutrients. Under nutrient-limited conditions in the pelagic system, they may compete with primary producers (Rothhaupt, 1992). There is evidence that this may also occur in the benthic system (Schwinghamer et al., 1991; Schwinghamer & Kepkay, 1987). The standard decomposer takes in nutrients proportional to the decomposition flux and dependent on the external nutrient concentration. It adjusts its C:N:P ratio as described for secondary producers.

\[
\text{nutrient uptake/excretion}.n = \frac{H.n \cdot \text{decomposition} \cdot \text{NH}_4}{\text{NH}_4 + K^n} - \text{excretion}.n
\]  
(18)

The constant \( K^n \) describes the dependence of the nutrient uptake on the ammonium concentration. A similar formula is assumed for the P-component with \( \text{PO}_4 \) as source/sink.

**Mortality** Similar to the standard secondary producer.

\[
\text{non-predation mortality} = \text{stress mortality}
\]  
(19)

For benthic bacteria there is a stress mortality modelled. If the aerobic layer or the oxidized layer vanishes, so does the living space for the corresponding types of microorganisms. Then stress mortality occurs:

\[
\text{stress mortality} = r^{ m r } \text{H} (1 - \rho)
\]  
(20)

\[
\text{reduction factor} = \rho = \min \left( 1, \frac{d}{d^{ cr } r} \right)
\]  
(21)

Here \( d \) is the thickness of the layer, \( d^{ cr } \) the critical thickness and \( r^{ m r } \) in \((1^t)\) the maximum mortality rate. \( \rho \) is also used as factor for decomposition rates.

**Anaerobic bacteria** With minor modifications the standard decomposer module can be used. Anaerobic bacteria do not live in the standard environment. Oxygen availability is substituted by availability of other electron acceptors, mainly nitrate. Sulphate reducers are treated implicitly which is a questionable feature of the present biological model. Here, as in many other places in the model it is very easy to make changes as soon as more information is available and the need for extensions becomes obvious. The model is presently frozen in a developmental
stage which is preliminarily satisfying, but it is not the final state.

3.3. SUSPENSION FEEDERS

Some modifications of the standard secondary producer are necessary to fit it to this functional group. Suspension feeders are not only filterers, but in the following it is assumed that the grazing rate must be derived from a filtration volume and other parameters (K_{up}, d_{up}, d_{Q}, see below). Because resuspension is not explicitly modelled, benthic detritus as food source needs a special treatment. The specific filtered volume (m^3·mg C·d^{-1}) depends on the food concentration \( F \). It is assumed that this dependence has the form

\[
\text{filt}(F) = \text{filt}_{\text{max}} \frac{K_{up}}{F+c+K_{up}} \tag{22}
\]

With a Michaelis constant \( K_{up} \) (mg C·m^{-3}) the product filt_{\text{max}} \cdot K_{up} \) can be considered as uptake rate constant \( r_{up} \) (in d^{-1}) according to Eq. 4. The model food concentrations \( F \) for suspension feeders are \( P1 \) (diatoms), \( P2 \) (flagellates), \( R6 \) (particulate pelagic detritus) and \( Q6 \) (benthic detritus). The first three are given in mg C·m^{-3} as averages over the water column. The last is given in mg C·m^{-2}. The effective food concentrations \( F_i \) in Eq. 3 are calculated in the model by using factors \( p_i \) as described in Table 3.

The factor \( d_{up} \) describes the unequal distribution of particulate organic matter in the water column, with higher concentration close to the sediment surface. For a convenient comparison with the other benthic functional groups this factor can have the dimension m. For example a value \( d_{up} = 3 \) m can mean a concentration factor 10 and a 30 cm layer available for suspension feeders (see Table 2).

The uptake flux is temperature dependent and can also be reduced by oxygen deficiency and by high silt concentrations. The latter can be important, if the model is applied to coastal areas. At present, however, this factor is ignored, but it may be essential to the correct representation of the ratio of deposit to suspension feeders, which is different for silty and sandy areas.

3.4. 'BIO-IRRIGATION' - DIFFUSION ENHANCEMENT

Dissolved and particulate substances are treated differently in the model. The considered dissolved substances are nutrients (NH_4, NO_3, PO_4, SiO_4), gases (O_2, CO_2, N_2) and dissolved organic matter (DOM). They are all transported with the interstitial water, and may be adsorbed to sediment particles. Their concentrations are modified by biological and chemical reactions. Transport and adsorption/desorption are described in the nutrient profile model (Ruardij & Van Raaphorst, 1995). The transport of solutes is generally simplified to an 'effective diffusion', which means that the equations are like diffusion equations. The 'diffusion' constant reflects molecular diffusion and convection of the interstitial water through the space between sediment particles and the burrows of organisms. The convection is induced by pressure gradients and pumping activities of the organisms. Hence, organisms enhance the 'diffusion' by both, providing holes and pumping water. These two processes are sometimes called 'bio-drainage' and 'bio-ventilation'. They are combined to the term 'bio-irrigation'.

In the ERSEM model the influence of the biotic system on diffusion is described as the dependence of the diffusion constant on the macrobenthic biomass. It is assumed that a diffusion constant \( \alpha_0 \) can be defined if macrobenthos is absent. The effective diffusion constant \( \sigma \) is written in the form of a product

\[
\sigma = \alpha_0 \varepsilon (Y_{irr}) \tag{23}
\]

Here \( Y_{irr} \) is a weighted sum (Eq. 25) of the macrobenthic and meiobenthic densities \( Y_i \) (biomass per m^-2) (see Appendix A.3). \( \varepsilon \) — the diffusion enhancement function — has the form

\[
\varepsilon (Y_{irr}) = 1 + \mu_{irr} \frac{Y_{irr}}{Y_{irr} + K_{irr}} e_{temp} \tag{24}
\]

with

\[
Y_{irr} = \sum_{i=1}^{s} \alpha_i Y_i \tag{25}
\]

\( \mu_{irr} \) is the maximum enhancement of diffusion depending on the chosen value of \( \alpha_0 \). The biomass weighting coefficients \( \alpha_i \) represents the different degrees to which the functional groups contribute. In the ERSEM model \( \mu_{irr} \) is assumed to be 10, and \( K_{irr} \) corresponds roughly to the average density present. The temperature dependence of the macrobenthic activity is taken into account by the factor \( e_{temp} \).

Because the burrows last even after the death of the occupant and because the ventilation depends on the activity and not on biomass itself, a more elabo-

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| Food fractions for suspension feeders and weight factors for the food sum \( F = \sum p_i F_i \). For \( d_{up}, p^0, d_{Q} (Y3) \) see text. |
|---|---|
| \( F_i \) | \( p_i \) |
| \( P1 \) | \( d_{up} \) |
| \( P2 \) | \( d_{up} \) |
| \( R6 \) | \( p^0 d_{up} \) |
| \( Q6 \) | \( p^2 \) times fraction in \([0,d_{Q}(Y3)]\) |
rate description would take these factors into account. However, this elaboration awaits experimental underpinning.

The diffusion constant is certainly depth dependent, the enhancement is depth dependent, and the different functional groups act at different depths. However, this dependence is neglected in the present version of the ERSEM model. It may turn out that this depth dependence of diffusion is extremely important for the reproduction of observed profiles, especially if the model is applied to coastal areas or the Wadden Sea. Then it also has to be taken into account that microorganisms will influence diffusion by excretion of organic matter which could form diffusion barriers. Chemical gradients in the sediment could be enhanced to steplike shapes.

3.5. BIOTURBATION – DEPTH PROFILE OF DETRITUS DENSITIES

The well-elaborated models which describe the mixing in the sediment (Boudreau & Imboden, 1987; Matlissof, 1982) are too cumbersome to act as submodels for a single process alongside the hundreds of other processes in an ecosystem model. A simple and robust description of vertical transport of particulates is needed which nevertheless captures the essential feature of the process. Such a model is presented in this section.

The main purpose of the bioturbation model is the dynamic calculation of the depth profile of the detritus density, differentiating between carbon, nitrogen, phosphorus and silicate components of detritus. By treating these components individually, the detritus composition may change with depth. Microbiological activity and nutrient production by decomposition depend on detritus density and composition at different depths.

Particulate transport is much more difficult to model than diffusion, because there is nothing like a ‘diffusion equation’ for particulates which can be simply reparameterized. Rather, the process is non-local, which means it cannot be described by partial differential equations (like diffusion). The local changes depend not only on local concentrations and their local spatial derivatives, but also on distant concentrations (integro-differential equations). The nonlocality reflects the fact that worms often transport sediment, not to an adjacent layer, but to the surface, or feed in funnels from the surface. Very crude approximations have to be accepted to simplify this process.

In this simple model, the density profiles are parameterized and differential equations for the parameters are derived. Hence, the parameters are new dynamic state variables. All detritus components (C, N, P, Si) are modelled in the same way, but differently parameterized. For simplicity, a single parameter \( D \) is used for each component. It has the meaning of a mean intrusion depth of this detritus component into the sediment. The depth is denoted as \( x \). The detritus density \( q(x) \) is expressed by a surface concentration \( q_0 \) and a normalized shape function \( \rho(x, D) \) with \( \rho(0, D) = 1 \):

\[
q(x) = q_0 \rho(x, D)
\]

Let \( Q \) be the total amount of detritus under 1 m\(^2\) between the surface and a maximum depth \( d_{\text{max}} \) then

\[
\int_0^{d_{\text{max}}} q(x) \, dx = Q
\]

defines \( D \) as average intrusion depth

Now a differential equation for the parameter \( D \) has to be derived, because it changes dynamically. Two types of changes of \( D \) must be described:
- changes due to production or consumption of detritus at given depths \( D_i \). The index \( i \) indicates the different production and consumption processes (sources and sinks). They are associated with the benthic functional groups. A special case is the addition of new detritus at the surface by sedimentation,
- a change of \( D \) due to particulate transport, denoted by \( \gamma \) in Eq. 29.

Using mass balance and conservation of the centre of mass, production and consumption change \( D \) in a simple way, if \( D \) is the average detritus depth:

\[
D = \sum_i (D_i - D) f_i Q + \gamma
\]

This is valid for any distribution function \( \rho(x, D) \) in Eq. 26. The sum runs over different production and consumption processes \( i \) including sedimentation. The \( f_i \) are the production rates of detritus (negative for sinks) in mg C m\(^{-2}\) d\(^{-1}\) or mmol m\(^{-2}\) d\(^{-1}\), the \( D_i \) are the production depths with 0 for sedimentation.

Because there is not enough quantitative information, the modeller has considerable freedom in the formulation of a bioturbation model. It can be assumed that the bioturbing organisms move a layer \( \Delta \) (m\(^{-1}\)) from depth \( \delta \) (m) to the surface, shifting down all sediment above. Alternatively, the bioturbation mechanism could assume that a surface layer \( \Delta \) (m\(^{-1}\)) would be moved down to depth \( \delta \), shifting upward all above. The two mechanisms are not equivalent. Or, thirdly, a layer \( \Delta \) (m\(^{-1}\)) could be exchanged between the surface and a depth \( \delta \). In any case, exchange and shift of sediment layers change \( D \) and a further ‘smoothing’ of the new distribution is
assumed to lead to a shape (Eq. 26) with a new $D$.

To have an analogue to the diffusion constant $\sigma$ ($\text{m}^2 \text{d}^{-1}$), a parameter $\tau = \Delta \cdot \delta$ ($\text{m}^2 \text{d}^{-1}$) is introduced instead of $\Delta$. With the first of the above mechanisms, the bioturbation contribution $\gamma$ in Eq. 27 becomes

$$\gamma = \frac{\tau}{D^2} \int_0^\delta (q(x) - q(0)) \, dx \quad (30)$$

The term $\gamma$ also contains the physical mixing, but generally the biological effect will be quite large. The separation of the two processes is done by writing $\tau$ as product of a physical $\tau_0$ and a biological modification (Eq. 36). The term $\gamma$ obviously depends on the assumed functional form of $\rho(x,D)$ for the density $q(x)$. In the present version of $\rho(x,D)$, a simple exponential decline is assumed:

$$\rho(x,D) = e^{-\frac{x}{D}} \quad (31)$$

Then the integral in Eq. 30 can be calculated and leads to

$$\gamma = \frac{\tau}{D^2} \left[ 1 - \left(1 + \frac{\delta}{D}\right)e^{\frac{-\delta}{D}} \right] \quad (32)$$

The second mechanism leads to

$$\gamma = \frac{\tau}{D^2} \int_0^\delta (q(0) - q(x)) \, dx \quad (33)$$

and with Eq. 31 to

$$\gamma = \frac{\tau}{D^2} \left[ e^{\frac{-\delta}{D}} - \left(1 + \frac{\delta}{D}\right) \right] \quad (34)$$

In the present ERSEM model a similar somewhat simpler formula is incorporated, corresponding to the third mechanism (exchange)

$$\gamma = \frac{\tau}{D^2} \left(1 - e^{\frac{-\delta}{D}} \right) \quad (35)$$

For $\delta < D$ all three formulas are nearly equivalent, if $\tau$ in Eq. 35 is taken half as large as in Eq. 32 and 34. It is not easy to say which formula (Eq. 32, 34 or 35) is closer to reality. This depends on the specific nature of bioturbation. In all cases, if only bioturbation acts, the intrusion depth $D$ increases continuously and asymptotically ($D \gg \delta$) according to $D \approx \text{const} D^2$.

This leads to $D \approx \frac{1}{2} l$, which is a very slow increase. With constant sedimentation and decomposition processes, the intrusion depth $D$ will approach an equilibrium value.

The turbation constant $\tau$ in the model depends on the macrobenthic biomasses in a way similar to the diffusion constant $\sigma$ (Eqs 23 to 25)

$$\tau = \tau_0 e^{y_{tut} \tau} \quad (36)$$

$$\varepsilon (y_{tut}) = 1 + \mu_{tut} \frac{y_{tut}}{y_{tut} + K_{tut} e^{\text{temp}}} \quad (37)$$

with

$$y_{tut} = \sum_{i=1}^5 \beta_i Y_i \quad (38)$$

Here $\mu_{tut}$ is the maximum enhancement of turbation, and $\tau_0$ is the turbation if no macrobenthic organisms are present (physical mixing). The Michaelis constant $K_{tut}$ (for half maximum enhancement) is again chosen to correspond roughly to the average macrobenthic densities; $e_{\text{temp}}$ is a temperature factor. The weights $\beta_i$ may differ from the $\alpha_i$ in Eq. 25. Because the functional groups contribute to bioturbation at different depths in the sediment, the weights should be dependent on the intrusion depths $D$. Again, this requires data for typical depth distributions of the benthic functional groups.

4. PARAMETRIZATION

Parametrization is usually a complicated task for the following reasons:

- often there are many parameters;
- parameters are often defined only in the context of the model and cannot be measured before the model is constructed;
- measurements are expensive and complicated, especially for benthic parameters;
- the measured values are very uncertain, because there is a high degree of natural variability;
- parameters may be ascribed to functional groups, not to species, while most measurements are carried out at the species level;
- parameters derived from laboratory measurements cannot easily be extrapolated to community parameters;
- model input consists of rarely measured dynamic parameters for regulation of processes.

It is clear that direct parametrization is the exception. Rather, educated guesses and calibration by comparison of simulation results with measured biomasses and fluxes is the norm for parametrization.

An interesting example of the use of laboratory data in the ecosystem model is the formulation of uptake for suspension feeders (section 3.3.). There are more parameters than needed. The uptake rate is the product of the maximum filtration volume, a Michaelis constant, and an empirical factor describing concentration increase toward the sediment surface.

In principle it is enough to define an uptake rate $r^m$ (Eq. 4) which should be about 0.1 $\text{d}^{-1}$ for physiological reasons. However, filtered volumes are easy to measure, so they appear in the formulas. There are
TABLE 4
Macrobenthic standing stocks (spring values) in the ERSEM boxes (in mg C m⁻²), derived by Bryant et al. (1995), from observations. Values are rounded.

<table>
<thead>
<tr>
<th>box</th>
<th>standing stocks of</th>
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<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Y1</td>
<td>Y2</td>
<td>Y3</td>
<td>Y4</td>
<td>Y5</td>
</tr>
<tr>
<td>6</td>
<td>30</td>
<td>2100</td>
<td>1400</td>
<td>70</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>30</td>
<td>1400</td>
<td>900</td>
<td>50</td>
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</tr>
<tr>
<td>8</td>
<td>30</td>
<td>4700</td>
<td>3100</td>
<td>160</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>30</td>
<td>3600</td>
<td>2400</td>
<td>120</td>
<td></td>
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<tr>
<td>10</td>
<td>120</td>
<td>1800</td>
<td>1200</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>60</td>
<td>1900</td>
<td>350</td>
<td>120</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>60</td>
<td>1100</td>
<td>200</td>
<td>70</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>60</td>
<td>2500</td>
<td>300</td>
<td>150</td>
<td></td>
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<tr>
<td>14</td>
<td>60</td>
<td>2500</td>
<td>1600</td>
<td>80</td>
<td></td>
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<tr>
<td>15</td>
<td>60</td>
<td>2900</td>
<td>2900</td>
<td>120</td>
<td></td>
</tr>
</tbody>
</table>

often good reasons to separate a model parameter in a product of two factors:

model parameter = laboratory value • modification

The modification includes all the problems, going from the lab to the natural system and from the natural system to the model. It is often an immeasurable new parameter, giving the modeller on the one hand the opportunity to introduce a measured value as it is, and on the other hand enough freedom to take into account the difference of field, laboratory and model situations. It is the art of the modeller to develop a feeling for the necessary modifications. Ideally, the modification is 1, but in most cases the value has finally to be fixed by calibration. Another thing is that the laboratory value itself generally has a broad range in the literature, and that the modeller may like to go to one or the other just acceptable extreme.

There are some features of the model which make parametrization easier than it seems:
- sophisticated process descriptions define the parameter in such a way that preliminary values can easily be derived from existing general knowledge on physiology and by intuition;
- allometric relations can be used;
- the model itself develops an internal coherence which reduces the sensitivity to many parameters.

The latter is only true if the model reaches a high level of complexity where several regulation mechanisms act on the same process, and where one regulation mechanism can partly take over if another fails. This coherence also leads to mutualism in the model system: different parts support each other indirectly in a positive way, even if the direct effects are negative (Patten et al., 1990). This, in turn, complicates parametrization, because despite the large number of parameters in a complex model it is not at all easy to tune a model in a desired direction. Generally, simultaneous changes of several parameters are necessary.
are derived by Bryant et al. (1995), from many observations. They suffer, as the authors state, from various errors, especially the error due to the assignment of the functional groups. They are given in Table 4.

The parameters of the bioturbation/bio-irrigation model are collected in Appendix A.3 and preliminary values are assigned to them.

5. RESULTS

5.1. INPUT FROM THE PELAGIC SYSTEM

The benthic system depends most strongly on input from the pelagic system. The production of the pelagic system is determined by physical conditions (light, temperature, mixing, advection) which are mainly functions of depth. For the model it is very important how the vertical structure of the water column and vertical transport are described.

ERSEM divides the North Sea into ten geographical compartments, closely related to the ICES boxes (Lenhart et al., 1995). The five geographical compartments with summer stratification (Lenhart et al., 1995) are divided at the 30-m depth line, forming 15 spatial compartments, 5 of them without benthos (numbered 1-5) and 10 with benthos (numbered 6-15). In Fig. 3 the depths of all spatial ERSEM compartments ('boxes') are presented.
It is assumed that there is no vertical density gradient within these 15 boxes but a density difference between upper and lower boxes exists, if there is a subdivision. This somewhat arbitrary setting influences the concentrations of phytoplankton and pelagic detritus acting as food for the suspension feeders.

The concentrations in the deeper boxes 11, 12, 13 are low because there is not enough light for a self-sustaining phytoplankton population. Input from the upper boxes by sedimentation and mixing is necessary. Suspension feeders do not survive well in these three boxes. Similarly, box 6 is deep and assumed to be well mixed, with the consequence of low phytoplankton concentrations because of low average light conditions. In contrast, boxes 7 to 10 are well illuminated and support a rich population of suspension feeders. This simple relation is visible in all results and can be modified only to a minor extent by benthic dynamic parameters. Phytoplankton concentrations and suspension feeder biomass (yearly averages) are compared in Fig. 4.

Deposit feeders and microbial activity depend on the abundance of benthic detritus, which in turn is determined by the sedimentation of organic matter. The spatial distribution of deposit feeders over the North Sea can only be reproduced by the model if the sedimentation process is correctly modelled. Presently, in ERSEM, sedimentation is described by a sedimentation rate, given in m·d⁻¹. Therefore, the input to the sediment depends not on the depth of the water column, but only on the concentration within the

---

**Fig. 6.** Comparison of the results (annual means in a stable cycle) of the standard model and measured data/estimates given in Table 4. The full rectangles represent the results with the standard parameter set, the open rectangles represent the observations (deposit feeders, suspension feeders and infaunal predators) and estimations (epibenthic predators).
Fig. 7. Effect of predation by demersal fish on deposit feeders Y2, infaunal predators Y5, suspension feeders Y3 and epibenthic predators Y1. The full rectangles represent the simulated densities (mg C·m$^{-2}$) in the standard situation (with fish predation), the open rectangles give the densities without fish predation.

Water column which roughly reflects the phytoplankton production. Hence, there is not much variability in the detritus input to the sediment of different columns (see Fig. 5). The upper compartments 1 to 5 lose organic matter only to the lower compartments 11 to 15 and not to the sediment. Diatoms form about 1/4 of the total detritus input. But because in the model diatoms sink only under nutrient depletion conditions, which never occur in the lower boxes, no diatoms reach the benthic systems in boxes 11 to 14. Decaying diatoms release some DOM into the sediment.

Another factor determining the benthic system is sediment type. The grain sizes of the upper sediment layers are, in principle, externally determined by currents and dispersion factors. The physical models are not yet prepared to predict sediment types well enough, and the biological model does not take the sediment type into account. Only the benthic nutrient model makes adsorption/desorption processes dependent on the sediment type. Internal factors which may influence the spatial distribution of macrobenthic functional groups are discussed in later subsections.

5.2. SPATIAL DISTRIBUTION AND SEASONAL DEPENDENCE

In most cases the simulation was continued until a stable seasonal cycle was reached (after 10-40 simulated years). Here and in all following figures and discussions (except section 6.3) the model results represent such a stable cycle. In this situation there is
no dependence on the initial conditions with the exception of zero start values. Therefore, functional groups which are 'extinct' in some boxes in the standard run have to get an initial seed.

In most cases annual means are discussed, because the seasonal variations of macrobenthic groups are not very strong. The autumn values exceed the spring values by a factor of about 2. Fig. 6 shows the results of the standard run compared to measured data (compare Table 4). While the spatial distribution of the suspension feeders is roughly reproduced, the spatial distribution of the deposit feeders deviates strongly from observations. The problem in box 15 is caused by high fish predation (next section). The biomass of the predators is badly reproduced. Some basic modelling work is needed.

5.3. INFLUENCE OF HIGHER TROPHIC LEVELS (DEMERAL FISH)

Aside from input of plankton detritus, the distribution of macrobenthos over the different regions of the North Sea is determined by another process external to the benthic system: predation by demersal fish. This process is described by Bryant et al. (1995). But here some implications for the benthic system are presented. The macrobenthic system in the model consists of two parallel, only weakly connected predator-prey systems. Epibenthic predators feed mainly on suspension feeders (Y1 on Y3), and infaunal predators feed mainly on deposit feeders (Y5 on Y2) (see Fig. 2). Predation by demersal fish — as it is now formulated in ERSEM (Bryant et al., 1995) — acts on all four functional groups, especially on infaunal predators. Hence, demersal fish are seen as superpredators.

There are two representations of the predation by demersal fish in ERSEM: static loadings, and a dynamic fish model (Bryant et al., 1995). Only the first and simple method has been used here, because at the time the dynamic fish model was still under construction. In the static fish model, mortalities are imposed on the benthic functional groups which depend on season and box, but fish do not react dynamically to the available food. In the dynamic fish model the fish population reacts as a whole, but the spatial distribution of mortalities is fixed. In a still more elaborate model the spatial distribution of fish should also vary, because a single population with fixed distribution could result in unreasonably strong or weak local predation pressure.

In connection with the predation by fish a principal difficulty of the present preliminary ERSEM version becomes obvious: composition, parameters and properties of the functional groups are not as well defined as they should be. The benthos modellers cut the benthic biological system into somewhat arbitrary pieces and name one of the pieces 'infaunal predators', Y5. Some biologists answer the requests for physiological parameters with data for some species, which the modellers average and modify according to the needs of the model. Other biologists add up some observed species biomasses to a standing stock value for the functional group, and a third group of biologists collect and process data on predation by fish on the species belonging to the functional group. Do all the different scientists really have the same 'object' in mind? Remember, the object is an artificial creation of the modeller!

The biomass of infaunal predators is less than 10% of the macrobenthic biomass in the data of Bryant et al., 1995 (Table 4) and in the simulation results which are adjusted to these data. The predation by fish, in contrast, is focused on the infaunal predators. In that way, the role of Y5 changed during the modelling process. Originally it was intended to be the key predator in the benthic system, controlling the macrobenthic deposit feeders Y2 and meio-benthos Y4, if fish predation on these groups does not suffice. Now Y5 is a link connecting benthic secondary production to pelagic predators. This change in 'function' of the group created some problems in the parameter adjustment and interpretation of preliminary simulation results. In Fig. 7, the simulation results (standard parameter set) with and without predation by demersal fish are compared.

In Fig. 7 a positive population effect of predation by fish can be detected in some boxes. This well-known chain effect is shown in Fig. 8.

It can be considered the most simple example of how, in a complex network with mainly negative direct interactions, indirect positive interactions can develop. More generally, such indirect positive interactions (Patten et al., 1990) become dominant in complex food webs, leading to collective and coherent behaviour of complex models. They are the base of 'complexity' in still more evolved model systems, which show the properties of self-organization, surprising behaviour as a consequence of self-organized criticality, balancing at the edge of chaos, and other interesting types of behaviour. The ERSEM cannot
TABLE 5
Feeding matrix (P phytoplankton, R pelagic and benthic detritus, H aerobic and anaerobic benthic bacteria, Y4 meiobenthos, Y2, Y3 deposit and suspension feeders, Y5, Y1 infaunal and epibenthic predators). The numbers give \( a \text{ priori} \) estimates of relative importance of a food source (row) for a feeder (column). Formally detritus is treated similarly with defaecation and mortality as additional source terms. P as a primary producer has no input from within the system.

<table>
<thead>
<tr>
<th></th>
<th>P</th>
<th>R</th>
<th>H</th>
<th>Y4</th>
<th>Y2</th>
<th>Y3</th>
<th>Y5</th>
<th>Y1</th>
</tr>
</thead>
<tbody>
<tr>
<td>P</td>
<td>.7</td>
<td>.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>1</td>
<td>.3</td>
<td>.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>.05</td>
<td>.3</td>
<td>.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y4</td>
<td>.05</td>
<td>.4</td>
<td>.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y2</td>
<td>.05</td>
<td>.5</td>
<td>.3</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Y3</td>
<td>.05</td>
<td>.5</td>
<td>.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y5</td>
<td>.05</td>
<td>.2</td>
<td>.1</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y1</td>
<td>.05</td>
<td>.3</td>
<td>.5</td>
<td>.2</td>
<td>.1</td>
<td>.1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

reproduce such properties, which the real system may have.

Because the standard simulation run represents a long-term equilibrium situation, which is seasonally periodic, continuously declining populations disappear. The input to the benthic boxes is spatially variable (section 5.1.), hence there are richer and poorer boxes. The maximum mortality which a functional group can withstand depends on the box. As can be seen in Fig. 7 the cumulated mortalities in some boxes exceed the capacities for some functional groups in the model. In boxes 14 and 15 deposit feeders can be wiped out by fish predation. In boxes 11 and 13, suspension feeders do not survive in the model because the plankton concentration in these boxes is low. Here it is obvious that the present ERSEM version needs improvements. Substituting fish by a fixed mortality which is the same in all boxes makes the situation worse.

The biology in all boxes is modelled with the same rules and the same set of parameters. The outcome of the simulations differs in the boxes only due to different physical conditions and topography. Hence, only an adaptive predation could help to allow the survival of all groups everywhere, when fixed mortalities lead to extinction. However, we may ask: should all groups survive everywhere?

5.4. TROPHIC POSITIONS

In this subsection, an extension of the term 'trophic level' is discussed. A trophic level of a species describes how often biomass is passed on by uptake and predation until it becomes part of the species biomass. This number is not an integer if recycling of matter via detritus, predation on different levels and predation within functional groups are taken into account. Then it is better called 'trophic position'. The food web shown in Fig. 2 can also be expressed in matrix form as in Table 5, where the web is slightly compressed. Let \( A \) be a matrix as given in Table 5. The columns of \( A \) represent the acceptors (predators), the rows of \( A \) represent the donors (prey), the numbers in \( A \) (not negative) give the relative contribution of the sources to the input of an acceptor. They are \( a \text{ priori} \) estimates which can later be substituted by normalized fluxes to the functional groups. In a closed system the numbers in each column have to add up to 1. Then biomass would be reprocessed \textit{ad infinitum} and trophic levels in the above mentioned sense would be meaningless. If external sources exist, the corresponding column sums are less than 1. In the classical form the matrix has one column primary producers containing only zeros, and a detritus loop and other loops are not considered. The adaptation to the benthic situation requires the introduction of detritus as a very important food source and, as well, recycling terms to detritus. Further, diagonal elements in \( A \) representing predation within a functional group as an expression of food web aggregation have to be taken into account.

Such a matrix allows the calculation of the trophic positions (Ulanowicz, 1986). In this paper Ulanowicz's method is extended by allowing recycling loops and cannibalism. Taking into account artificial cannibalism—as discussed with meiobenthos— the calculated trophic positions become independent of the degree of aggregation. This is extremely remarkable and a good support for the use of quite large functional groups with inhomogeneous aggregation, as usual in the ERSEM formulation.

For the following definition of trophic positions the matrix \( A \) must not have closed (input free) loops. Then, the sum of powers of \( A \) converges (\( I \) is the unit matrix):

\[
B = (I - A)^{-1} = \sum_{n=0}^{\infty} A^n
\]

The column sums of \( B \) represent the trophic positions. Assume for instance a simple food chain. Then \( A, A^2, A^3... \) have the forms

\[
A = \begin{bmatrix}
0 & 1 & 0 & 0 \\
0 & 0 & 1 & 0 \\
0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0
\end{bmatrix}, \quad A^2 = \begin{bmatrix}
0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}, \quad A^3 = \begin{bmatrix}
0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}
\]

and \( B \) is

\[
B = \begin{bmatrix}
1 & 1 & 1 & 1 \\
0 & 1 & 1 & 1 \\
0 & 0 & 1 & 1 \\
0 & 0 & 0 & 1
\end{bmatrix}
\]

The sums of the columns of \( B \) are 1, 2, 3, 4,... and
correspond to the position in the food chain. In the case of Table 5 matrix \( A \) becomes

\[
\begin{bmatrix}
0 & 1 - 6\varepsilon & 0 & 0 & 0.6 & 0 & 0 \\
0 & 0 & 1 & 0 \cdot 3 & 0.3 & 0.4 & 0 \\
0 & \varepsilon & 0 & 0.3 & 0.6 & 0 & 0 \\
0 & \varepsilon & 0 & 0.4 & 0.1 & 0.3 & 0 \\
0 & \varepsilon & 0 & 0 & 0 & 0 & 0.5 \\
0 & \varepsilon & 0 & 0 & 0 & 0 & 0.5 \\
0 & \varepsilon & 0 & 0 & 0 & 0 & 0.2 \\
0 & \varepsilon & 0 & 0 & 0 & 0 & 0.1
\end{bmatrix}
\]

Columns and rows correspond to \( P, R, H, Y_4, Y_2, Y_3, Y_5, Y_1 \) (Table 5). The parameter \( \varepsilon \) symbolizes recycling by excretion. For specific \( \varepsilon \)-values the matrix \( B = (I - A)^{-1} \) can be calculated. In the most simple case \( (\varepsilon = 0) \) \( B \) becomes

\[
\begin{bmatrix}
1 & 1 & 1 & 1 & 1 & 1 & 1 \\
0 & 1 & 0.5 & 0.65 & 0.59 & 0.28 & 0.67 \\
0 & 0 & 1.67 & 0.17 & 0.73 & 0.14 & 0.40 \\
0 & 0 & 0 & 1 & 0.63 & 0.40 & 0.56 \\
0 & 0 & 0 & 0 & 1 & 0 & 0.14 \\
0 & 0 & 0 & 0 & 0 & 1.25 & 0.14 \\
0 & 0 & 0 & 0 & 0 & 0 & 1.11
\end{bmatrix}
\]

The trophic positions of the benthic functional groups are the column sums of \( B \) (Table 6). Here the trophic position of phytoplankton is 1, which is the lowest possible value for biomass (\( CO_2 \) has level 0). In the case of \( \varepsilon = 0 \) detritus is a pure product of phytoplankton and has the value 2 as base of the benthic food web. With \( \varepsilon > 0 \) the detritus level increases and the other levels rise correspondingly. Clearly, it is a matter of definition if the passing of organic matter through the state 'detritus' is considered to be of the same quality as the passing through the organisms\(^1\). The trophic positions of \( H, Y_4, Y_2, Y_5 \) do not change relative to detritus. Further it is remarkable that deposit feeders have a lower trophic position than meio-benthos which feeds on itself. Suspension feeders \( Y_3 \) are one level above the weighted average of \( P \) and \( R \), and epibenthic predators \( Y_1 \) have a lower value than infaunal predators \( Y_5 \), because they feed strongly on \( Y_3 \).

Such a food web analysis is of special interest in the case of the benthic system with its dense web of links due to predominant artificial or true omnivory and the importance of detritus recycling. The numbers in matrix \( A \) and the corresponding trophic positions are based on \textit{a priori} estimates, which are given here as a kind of aim for the simulation. There are several reasons to present these estimates: It is interesting to compare the expectations of the modellers and the result of the model.

In the present stage of calibration the model results are not 'better' than the estimates.

The model results will depend on space and season. One has to select a box and consider time averages.

Taking the modelling results instead of the \textit{a priori} estimates will change the numbers. Table 7 gives an extended overview over the carbon fluxes in the ben-

\begin{table}[h]
\centering
\caption{Calculated trophic positions based on \textit{a priori} estimates.}
\begin{tabular}{lcc}
\hline
\textbf{functional group} & \textbf{trophic position} \\
\hline
phytoplankton, \( P \) & 1 & - \\
detritus, \( R \) & 2\(^1\) & 3.12\(^1\) \\
bacteria, \( H \) & 3 & 4.12 \\
meiobenthos, \( Y_4 \) & 4.17 & 5.29 \\
deposit feeders, \( Y_2 \) & 3.82 & 4.94 \\
suspension feeders, \( Y_3 \) & 2.40 & 3.17 \\
inhaunal predators, \( Y_5 \) & 5.20 & 6.3 \\
epifaunal predators, \( Y_1 \) & 4.30 & 5.06 \\
\hline
\end{tabular}
\end{table}

\begin{table}[h]
\centering
\caption{The gross carbon fluxes through the benthic system in box 8 (aggregated yearly averages in mg C m\(^{-2}\) d\(^{-1}\)).}
\begin{tabular}{llllllllllllll}
\hline
\textbf{P} & \textbf{R6} & \textbf{Q6} & \textbf{Q1} & \textbf{H} & \textbf{Y4} & \textbf{Y2} & \textbf{Y3} & \textbf{Y5} & \textbf{Y1} \\
\hline
\hline
\end{tabular}
\end{table}

\(^1\) After finishing the manuscript it became clear, that the passing through the state 'detritus' should not be counted. This leads to minor changes in theory and results.
TABLE 8
Trophic positions of the functional groups (simulation result).

<table>
<thead>
<tr>
<th>functional group</th>
<th>trophic position</th>
</tr>
</thead>
<tbody>
<tr>
<td>phytoplankton, P</td>
<td>1</td>
</tr>
<tr>
<td>pel. detritus, R5</td>
<td>2</td>
</tr>
<tr>
<td>ben. detritus, Q6</td>
<td>4.43</td>
</tr>
<tr>
<td>bacteria, H</td>
<td>5.43</td>
</tr>
<tr>
<td>meiobenthos, Y4</td>
<td>6.42</td>
</tr>
<tr>
<td>deposit feeders, Y2</td>
<td>6.41</td>
</tr>
<tr>
<td>suspension feeders, Y3</td>
<td>3.42</td>
</tr>
<tr>
<td>infaunal predators, Y5</td>
<td>7.56</td>
</tr>
<tr>
<td>epifaunal predators, Y1</td>
<td>5.58</td>
</tr>
</tbody>
</table>

The trophic system of box 8. For this table a new matrix $A$ can be derived by normalizing the columns to 1. On the basis of this matrix, the trophic positions of the functional groups in the model can be calculated as described above. Phytoplankton P is trophic position 1 and pelagic detritus R5 is level 2. The latter is an approximation, because there is some detritus production from pelagic sources other than algae, and hence the level of R5 should be slightly higher than 2. Neglecting this, the trophic positions of the groups are as given in Table 8. There are some deviations from expectations in Table 6, but the general picture remains. In the a priori estimate, the detritus recycling was underestimated and the importance of the within-group fluxes was overestimated.

5.5. CARBON AND NUTRIENT FLUXES THROUGH THE BENTHIC BIOLOGICAL SYSTEM

In this section the discussion is again limited to yearly averages in box 8, which was selected because of the existence of a flourishing macrobenthic community.

FIG. 9. Carbon fluxes through the benthic biological system of box 8 (aggregated yearly averages). The standing stocks are given in mg C m$^{-2}$. The fluxes are given in mg C m$^{-2}$ d$^{-1}$.

<table>
<thead>
<tr>
<th>stocks and fluxes</th>
<th>C : N : P</th>
</tr>
</thead>
<tbody>
<tr>
<td>a. stocks:</td>
<td></td>
</tr>
<tr>
<td>particulate detritus, Q6</td>
<td>1000 : 70 : 5.0</td>
</tr>
<tr>
<td>dissolved org. matter, Q1</td>
<td>1000 : 195 : 14.4</td>
</tr>
<tr>
<td>bacteria, H</td>
<td>1000 : 200 : 15.0 (fixed)</td>
</tr>
<tr>
<td>meio/macrobenthos, Y</td>
<td>1000 : 143 : 9.5 (fixed)</td>
</tr>
<tr>
<td>pelagic detritus, R5</td>
<td>1000 : 136 : 9.6</td>
</tr>
<tr>
<td>diatoms, P1</td>
<td>1000 : 136 : 10.0</td>
</tr>
<tr>
<td>flagellates, P2</td>
<td>1000 : 172 : 13.2</td>
</tr>
<tr>
<td>b. fluxes:</td>
<td></td>
</tr>
<tr>
<td>sedimentation → Q6</td>
<td>1000 : 133 : 9.8</td>
</tr>
<tr>
<td>sedimentation → Q1</td>
<td>1000 : 194 : 14.4</td>
</tr>
</tbody>
</table>

In its most aggregated form, the benthic biological system contains carbon in the state variables:
- particulate detritus, Q6
- dissolved organic matter, Q1
- bacterial biomass, $H=\{H_1, H_2\}$
- meio- and macrobenthic biomass, $Y=\{Y_4, Y_2, Y_5, Y_3, Y_1\}$

The input to the benthic system originates from pelagic algae P1, P2 and detritus R6, mainly by sedimentation but partly also by suspension feeding. The carbon fluxes and standing stocks (yearly averages) on this aggregated level are given in Fig. 9. The figure demonstrates that detritus recycling is important in the benthic system. Most of the decomposition is done by bacteria which respire a large fraction of carbon. Suspension feeding is an important input to the benthic system, even if it is much smaller than sedimentation input. A more detailed overview of carbon

FIG. 10. Distribution of carbon fluxes (in mg C m$^{-2}$ d$^{-1}$) between the aerobic and microaerobic/anaerobic layers in the sediment of box 8. Compare Fig. 9. The C:N:P atomic ratios of the fluxes are given in brackets, with carbon normalized to 1000.
fluxes in the benthic system is given in Table 7.

The nutrient fluxes through the biological system are only qualitatively parallel to the carbon fluxes if respiration is substituted by nutrient excretion, because the C:N:P atomic ratios change. In Table 9 these ratios are given for the stocks and some fluxes of Fig. 9. The recycling flux of $H \rightarrow Q6$ consists mainly of dying bacteria and has high nutrient ratios, the recycling flux $Y \rightarrow Q6$ consists mainly of faeces which are nutrient depleted compared to the food source. The atomic ratio C:N:P of the various fluxes show differences, but these are not striking. The average detritus composition in the equilibrium is a result of balancing all processes. In the model it is mainly determined by one stabilizing negative feedback mechanism: the decomposition rate of detritus diminishes with decreasing nutrient content. There is, however, a general difficulty in the present standard version of ERSEM: pelagic detritus $R6$ arriving in the benthic system is too rich in nutrients.

![Diagram](image1)

Fig. 11. Carbon fluxes between functional groups in box 8. The fluxes to detritus are net fluxes. Respiration fluxes, sedimentation fluxes and fluxes to fish are omitted. All fluxes are yearly averages in mg C·m⁻²·d⁻¹.

![Diagram](image2)

Fig. 12. Diffusion and bioturbation enhancement factors for ERSEM boxes 7 and 12.

![Diagram](image3)

Fig. 13. Penetration depths of carbon(POC)-and nitrogen(PON)-components of detritus for ERSEM boxes 7 and 12.
Box 7
Oxygen penetration depth(7)
Nitrate penetration depth(7)

Box 12
Oxygen penetration depth(12)
Nitrate penetration depth(12)

Fig. 14. Oxygen and nitrate/sulphide horizon of ERSEM boxes 7 and 12.

Deposit Feeders

Suspension Feeders

Infaunal Predators

Epibenthic Predators

Fig. 15. Comparison of the two parameter sets given in Table A.1.1 and Table A.1.4. The full rectangles represent the results with the standard parameter set, the open rectangles the results with the alternative set.
The distribution of decomposition processes over aerobic and anaerobic bacteria is of special interest. Fig. 10 represents the carbon fluxes, stocks and atomic ratios as yearly averages. Detritus below the oxygen horizon is older and nutrient poorer than detritus in the aerobic sediment. In the analysed box 8 the average depth of the oxygen horizon is 0.73 cm, and the average depth of the sulphide horizon 9.7 cm. Because of the continuous reprocessing of detritus, its nutrient content in the lower layers of the sediment is reduced.

The model further allows a closer look at the carbon and nutrient fluxes connected with each functional group. These fluxes are simulation results, and may change considerably if better estimates of physiological parameters become available. They are not given here. The web of the carbon fluxes is represented in Fig. 11, but sedimentation input is omitted.

Fig. 16. Qualitative dependence of prey (X*) and predator (Y*) equilibrium densities as functions of resource concentration R and saturation constant K (see text).

Deposit Feeders

Suspension Feeders

Infaunal Predators

Epibenthic Predators

Fig. 17. Sensitivity to uptake saturation: The full rectangles represent the standard simulation run, the open rectangles represent the results with about 30% reduced saturation values.
5.6. BIOTURBATION AND 'BIO-IRRIGATION'

Due to the temperature dependence and the seasonal variation of the biomass of deposit feeders, a seasonal periodicity of the enhancement factors can be observed. In Fig. 12, the enhancement factors for the boxes 7 and 12 are given. In box 7 the deposit feeder biomass in the model is low (−1800 mg C·m⁻²), in box 12 it is the highest (−8000 mg C·m⁻²). (Fig. 6).

The intrusion depths of detritus are the result of many processes: physical mixing and bioturbation, detritus production, decomposition, and sedimentation. In Fig. 13, the depths for the carbon and nitrogen components of detritus are given for the two boxes used in Fig. 12. During summer, the average depth decreases, because material is deposited on the surface by sedimentation. The average depth of the nutrient components is less than of carbon in both boxes, because of the repeated reprocessing of detritus leading to aging in deeper layers (section 2.2).

Bioturbation is the effect of biological activity on the vertical transport of particulates. Bioturbation, diffusion enhancement, the sedimentation rate, the position of the oxygen horizon and the position of the nitrate/sulphide horizon are interdependent in a complex way. Ultimately, all biological activity in the benthic system is determined by the rate of detritus which is added to the system by sedimentation (see section 5.1). More sedimentation causes higher oxygen consumption and a less deep penetration of oxygen. It also causes higher macrobenthic biomass and, hence, diffusion enhancement which increases the oxygenation of the sediment. Too high oxygen consumption can lead to a collapse of the oxygenated layer, and of macrobenthos. A reduced bioturbation transports less detritus into the deeper sediment layers, where then the microbial activity is diminished. Less nitrate is reduced and the nitrate/sulphide horizon shifts downwards (Fig. 14). High bioturbation rates remove detritus from the layers close to the sediment and, hence, decrease the availability of benthic detritus for suspension feeders. The thickness of the oxygenated layer influences the nitrification process. These different positive and negative feedback mechanisms interact, and the final model results depend strongly on the input from the pelagic system and the parametrization.

6. SENSITIVITY ANALYSIS

6.1. PARAMETRIZATION OF PHYSIOLOGICAL PROCESSES

The standard set of macro- and meio-benthos parameters and an alternative set are given in Appendix A.1 (Table A.1.1 and A.1.4). In Fig. 15 the results of the two parameter sets are compared. All parameters in both sets are a priori estimates. Only the mortalities of the macrobenthic groups are chosen to achieve reasonable average values. The results demonstrate that there is still freedom to choose optimal parameter sets. However, the conclusion that any desired result can be reached by changing the parameters would be wrong. On the contrary, the similarity of the results should be seen as an expression of a robust collective behaviour of the system: sensitivity to many parameters is low. An exception is the dependence on 'natural mortality', which is not a well-justified parameter, and is used only to roughly reproduce the observed abundances.

The parameters for uptake saturation are of special importance for the spatial distribution of the macrobenthic functional groups in the model. Roughly speaking, low saturation values equalize the distribution because differences in food availability have a minor effect. Theoretically, this can be derived from
Lotka-Volterra approximations:

\[
\begin{align*}
\dot{X} &= \left( \frac{BR}{R + K} - \frac{\gamma Y}{1 + \sigma X} - \epsilon X \right) X \\
\dot{Y} &= \left( \frac{\gamma Y}{R + \sigma K} - \delta \right) Y 
\end{align*}
\]

Here \( R, X, Y \) are resource, prey and predator densities. The saturation constant for the growth of the prey is \( K \). The other constants \( B, \gamma, \gamma', \sigma, \epsilon, \delta \) are kept fixed. The equilibrium values \( X^*, Y^* \) can be investigated as functions of \( R \) and \( K \):

\[
Y^* = \begin{cases} 
\frac{\beta R}{R + K} - \frac{\epsilon \delta}{\gamma' - \delta \gamma} & \text{if } Y^* > 0 \\
0 & \text{otherwise}
\end{cases}
\]

\[
X^* = \begin{cases} 
\frac{\delta}{\gamma' - \delta \gamma} & \text{if } Y^* > 0 \\
\frac{BR}{\epsilon} & \text{if } Y^* = 0
\end{cases}
\]

The dependence is presented qualitatively in Fig. 16. If the saturation constant \( K \) is too high, a lower resource concentration (mainly detritus \( Q6 \) in the model) leads to reduction of prey (\( Y2, Y3 \)) and extinction of predators (\( Y5, Y1 \)). Such spatial variations in the distribution of detritus input into the benthic system enhance the abundances of macrobenthos in the model if \( K \) is large, or diminish the abundances if \( K \) is small.

In the model an increase of the saturation constants by 30\% leads to an extinction of some functional groups in several boxes, while a reduction by 30\% leads to a more homogenous distribution (Fig. 17).

6.2. STABILITY AND PREDATION WITHIN FUNCTIONAL GROUPS

ERSEM contains several, sometimes artificial, features which stabilize the simulation results. These features are:

- predation within functional groups;
- feeding thresholds;
- maximum uptake rates;
- multiple food sources (artificial omnivores);
- multiple predators (higher aggregation in the lower parts of the food web);
- other non-linearities.

Some of these features may also have a destabilizing effect. A maximum uptake rate stabilizes the food web 'upwards' but destabilizes 'downwards'. Omnivorous behaviour has the same effects.

In the benthic system feeding within functional groups is of great importance. It is not only a stabilizer, it also represents the part of the food web which is hidden within the functional groups. It cannot be removed without misrepresentation of the biological system. Another formulation may have to be found. In its present form feeding within functional groups adds quadratic mortality terms to the meiobenthos and infaunal and epibenthic predators (\( Y4, Y5, Y1 \)). (In fact, the quadratic mortality exists only with moderate densities. Due to the saturation formulation it becomes linear again at high densities).

In the benthic ERSEM model such a second predator can be artificially introduced as a density-dependent 'parasite' or 'pathogen' of deposit feeders \( Y2 \) as a second predator.

6.3. STABILITY AND CHAOTIC BEHAVIOUR

An interesting way to destabilize the model is by introduction of chaos generators. If a prey is subject to predation by two different predators, then usually one predator is eliminated as a result of the competition-exclusion principle. However, if both boundary systems (1 predator, 1 prey) show limit cycles, the other predator may invade the system and both predators may coexist (Keener, 1983; Yodzis, 1989). In the benthic ERSEM model such a second predator can be artificially introduced as a density-dependent 'parasite' or 'pathogen' of deposit feeders \( Y2 \) (Fig. 19).

The results will demonstrate that, in principle, ERSEM is able to show chaotic behaviour, if not suppressed. For this purpose another state variable \( X \) (= parasite) was introduced, acting as a further mortality term on the deposit feeder \( Y2 \):
\[ x = \beta x \left( \frac{Y_2}{Y_0} - \frac{x}{X + X_0} \right) \]

additional mortality on \( Y_2 = \delta Y_2 \)

\( X \) is assumed to be dimensionless. It grows rapidly, if the density \( Y_2 \) exceeds a critical level, which is about \( Y_0 \). At very low infestation levels, below \( X_0 \), the decline of \( X \) is hyperbolic, not exponential.

Simulations were carried out without feeding within \( Y_5 \), with static fish predation, and without the predation link from \( Y_4 \) to \( Y_5 \). Also some physiological parameters of \( Y_2 \) and \( Y_5 \) were changed compared to the standard run. The parameters are given in Table 10. With these parameters, the chaotic results illustrated in Fig. 20 were obtained. The long-term averages of deposit feeders and infaunal predators in this simulation run agree roughly with observations (Table 4). The results should be interpreted with care, because the model treats the large ERSEM boxes as internally homogeneous. In reality, outbreaks of such parasite epidemics, predator overpopulations, and high prey densities are always limited to smaller areas with internal chaotic dynamics. Hence, the simulation results in Fig. 20 should be partly interpreted as a reproduction of spatial patchiness. The spatial average over the large ERSEM box should correspond to the long-term average in a small area (ergodic behaviour). Only one box is shown in Fig. 20. The chaotic behaviour occurs in all boxes and looks different everywhere.

This chaotic behaviour is not only of limited academic interest. Rather, it reproduces an important feature of reality: high variability. Further, the chaotic

**Table 10** Parameters for ‘parasite’ dynamics and modified macrobenthic parameters for achieving chaotic behaviour (compare with Table A.1.1 in Appendix A.1).

<table>
<thead>
<tr>
<th>symbol</th>
<th>meaning</th>
<th>value</th>
<th>unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \beta )</td>
<td>rate of increase, decrease</td>
<td>0.05</td>
<td>( d^{-1} )</td>
</tr>
<tr>
<td>( Y_0 )</td>
<td>threshold density</td>
<td>3000</td>
<td>mg C m(^{-2})</td>
</tr>
<tr>
<td>( X_0 )</td>
<td>low ‘parasite’ level</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>( \delta )</td>
<td>additional mortality at ( X=1 )</td>
<td>0.002</td>
<td>( d^{-1} )</td>
</tr>
<tr>
<td>( r^{MP} )</td>
<td>maximum specific growth rate</td>
<td>0.15</td>
<td>( d^{-1} )</td>
</tr>
<tr>
<td>( \rho^{MP} )</td>
<td>natural mortality</td>
<td>0</td>
<td>( d^{-1} )</td>
</tr>
<tr>
<td>( K^{MP} )</td>
<td>food saturation level</td>
<td>1000</td>
<td>mg C m(^{-2})</td>
</tr>
<tr>
<td>( L^{MP} )</td>
<td>lower food threshold</td>
<td>200</td>
<td>mg C m(^{-2})</td>
</tr>
<tr>
<td>( p(Y_5) )</td>
<td>predation within ( Y_5 )</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>( p(Y_4) )</td>
<td>predation on meio-benthos</td>
<td>0</td>
<td>-</td>
</tr>
</tbody>
</table>

system seems to be quite robust and more persistent. The regulation of population densities is of a different type, than the simple standard differential equations with few interactions and stable steady states. This numerical observation is an important subject for further investigations.

**7. Conclusions**

The benthic submodel contains many new features compared with older benthic models. It allows the calculation of nutrient profiles (Ruardij & Van Raaphorst, 1995) and the dynamic determination of oxygen and nitrate horizons. It treats the feedback of the biological system on the physical system by a bioturbation/‘bioirrigation’ module (sections 3.4., 3.5.). It contains a complex food web with many links (Fig. 2). The trophic positions of the functional groups can be calculated using a method of Ulanowicz (1986). The method was extended by explicit treatment of trophic links within functional groups. So trophic positions are independent of species aggregation in functional groups as defined by the modeller (section 5.4.).

The benthic submodel contains parameters of which many could only be guessed and roughly estimated. However, a sensitivity analysis led to results which were surprising at the first glance: the dependence of model behaviour on most parameter values is weak. If the model system is sensitive to a single parameter, this may indicate poor representation of ecological reality by the model. This robust behaviour
is an expression of the complexity of the model. It contains many feeding links and a large number of feedback mechanisms and non-linearities, which together enable the model system to behave coherently and to show collective dynamical modes. A modification of a single process by changing some parameters is compensated for by a collective reaction of all other processes. Therefore, it is not easy at all to achieve desired results simply by playing with uncertain parameter values. It is important to identify the critical points in the model.

An example of a sensitive feature in the model is feeding links within the macrobenthic predator group. They stabilize the system in that removing these links leads to a breakdown of both predator and prey populations.

Another important feature of the model is its stability. Is the stability of the model in agreement with the stability of the real system? Is it too stable? Without answering these questions any predictions of the model remain questionable. The modellers willingly use several mechanisms to artificially stabilize the model system because it is easier to work with a stable model. It could be demonstrated that a small change in the food web — splitting a predator into two different but parallel predators — can force the system into chaotic oscillations. Then the often-discussed sensitivity of complex systems to initial conditions can be observed. The standard ERSEM formulation is not chaotic; it is — unfortunately — too stable: it forgets initial values in months or years of simulation time. In fact, the ERSEM is a complicated simple model, which does not represent essential features of complex systems such as 'self-organized criticality' and 'edge of chaos'. This was not the aim of the ERSEM modelling project.

The bioturbation 'bio-irrigation' module fulfills a need in the ERSEM model despite its relative simplicity. The feedback between the biotic system and its physical base, and the intrusion of degradable material into deeper layers of the sediment are fundamental features of the system, because they may be positive feedback mechanisms. This should be investigated by further sensitivity analysis. Lack of information makes reasonable parametrization a difficult task; presently there seems no other way than using the model to refine initial guesses. Because of the importance of this part of the model, future developments in the ERSEM model should focus on the improvement of the bioturbation and 'bio-irrigation' submodule.

As all the other parts of ERSEM, the benthic model does not work in isolation, but needs to be coupled to the other subsystems. The results strongly depend on the input of the other model parts, especially on the pelagic system. The input by sedimentation (passive) and suspension feeding (active) on the one hand, and predation by demersal fish on the other, determine the spatial distribution (box-to-box differences) of macrobenthos in the model. Some of the assumptions in the description of sedimentation processes are certainly questionable and will be improved in the next ERSEM version, because detritus input is the most important determinant of the spatial distribution of deposit feeders and microbenthic activity in the North Sea.

The model allows a close inspection of regulation mechanisms. All single fluxes from and to functional groups can be graphically represented as functions of time of year and by their dependence on state variables and parameters. As the predictive power of the model is still low, at present its greatest value consists in its communication power. It forms a consistent picture of the complex natural system.

8. REFERENCES


Keener, G.E., 1983. Oscillatory coexistence in the chemo-


APPENDIX

A.1. MACRO- AND MEIOBENTHOS PARAMETERS

Temperature dependence:
All Q10-values are taken to be 2.0.

Oxygen dependence:
not included due to lack of information

Maximum specific uptake rate: $r^{P}$ (Eq. 4)
This rate should roughly follow an allometric relation. Starting with the standard description (Fenchel, 1974; Borgmann, 1987)

$$rate\ (per\ animal)\sim\ (weight)^b$$

a length relation can be derived:

$$specific\ rate\ (per\ g\ C)\sim\ (length)^\alpha$$

with $\alpha = 3(b-1)$. With an estimated power $b = 0.75$ (Fenchel, 1974) it follows that $\alpha = -0.75$, Borgmann (1987) uses $\alpha = -0.72$ and Schwinghamer et al. (1986), find $\alpha/3 = -0.208$ in intertidal communities. For the functional groups Y1 to Y5 in the benthic system, assumed length relations (spherical equivalent diameters in mm, see Schwinghamer et al., 1986) are:

$$Y4 : (Y2,Y3) : Y5 : Y1 = 0.2 : 1.5 : 4 : 8$$

Approximate relations for the specific uptake rates (in d$^{-1}$) can be derived with $\alpha = 2/3$:

$$Y4^\alpha : (Y2,Y3)^\alpha : Y5^\alpha : Y1^\alpha = 0.38 : 0.10 : 0.05 : 0.03$$
### TABLE A.1.1

Macrobenthos and meiobenthos parameters (Y1 epibenthic predators, Y2 deposit feeders, Y3 suspension feeders, Y4 meiobenthos, Y5 infaunal predators). Food sources H1, H2 benthic bacteria, P1, P2 pelagic algae, R6 pelagic detritus, Q6 benthic detritus. The parameters are described in sections 3.1, 3.3 and Appendix A.1.

<table>
<thead>
<tr>
<th>symbol</th>
<th>meaning</th>
<th>Y1</th>
<th>Y2</th>
<th>Y3</th>
<th>Y4</th>
<th>Y5</th>
<th>unit</th>
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<tbody>
<tr>
<td>Q10</td>
<td>Q10-value</td>
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<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>( r^{up} )</td>
<td>specific uptake rate</td>
<td>0.06</td>
<td>0.04</td>
<td>0.13</td>
<td>0.30</td>
<td>0.10</td>
<td>d(^{-1})</td>
</tr>
<tr>
<td>( K^{up} )</td>
<td>food saturation</td>
<td>3000</td>
<td>2000</td>
<td>1000</td>
<td>1000</td>
<td>3000</td>
<td>mg C.m(^{-2})</td>
</tr>
<tr>
<td>( L^{up} )</td>
<td>lower food threshold</td>
<td>500</td>
<td>200</td>
<td>60</td>
<td>200</td>
<td>500</td>
<td>mg C.m(^{-2})</td>
</tr>
<tr>
<td>( F_i )</td>
<td>food sources</td>
<td>Y3,Y5,Y2,Y1</td>
<td>H1,H2,Y4,Q6</td>
<td>P1,P2,R6,Q6</td>
<td>H1,H2,Y4,Q6</td>
<td>Y2,Y4,Y5</td>
<td></td>
</tr>
<tr>
<td>( p_i )</td>
<td>preference factors</td>
<td>1,1,1,3</td>
<td>1,1,1,0.2</td>
<td>see Table 3</td>
<td>1,1,1,0.2</td>
<td>1,1,1,0.2</td>
<td></td>
</tr>
<tr>
<td>( d_Q )</td>
<td>available detritus layer</td>
<td>-</td>
<td>0.2</td>
<td>0.003</td>
<td>0.03</td>
<td>-</td>
<td>m</td>
</tr>
<tr>
<td>( q_i^{sec} )</td>
<td>defaecated fractions</td>
<td>0.2</td>
<td>0.35</td>
<td>0.25</td>
<td>0.25</td>
<td>0.3</td>
<td>-</td>
</tr>
<tr>
<td>( e^{ex} )</td>
<td>dilution factor (excretion)</td>
<td>0.8</td>
<td>0.7 (Q6)</td>
<td>0.7(Q6,R6)</td>
<td>0.4 (Q6)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>( q_i^{res} )</td>
<td>respired fractions</td>
<td>0.25</td>
<td>0.25</td>
<td>0.15</td>
<td>0.45</td>
<td>0.25</td>
<td>d(^{-1})</td>
</tr>
<tr>
<td>( \rho^{es} )</td>
<td>basal respiration</td>
<td>0.0027</td>
<td>0.0027</td>
<td>0.0027</td>
<td>0.01</td>
<td>0.0027</td>
<td>d(^{-1})</td>
</tr>
<tr>
<td>( r^n )</td>
<td>natural mortality</td>
<td>0.0055</td>
<td>0</td>
<td>0.0025</td>
<td>0</td>
<td>0.0125</td>
<td>d(^{-1})</td>
</tr>
</tbody>
</table>

These rates are about ten times the turnover rates estimated by Schwinghamer et al. (1986). A net growth efficiency of 10% is low but not unreasonable. The rates in the standard parameter set deviate from these theoretical values. As newest 'best' estimates the given rates are assumed (Table A.1.1).

**Preference factors: \( p_i \) (Eq. 3)**

The macrobenthic groups and meiobenthos being omnivores, different food sources are added with weights (=preference factors) to a food sum. The preference factors are generally taken to be 1.0, due to lack of information, with two exceptions: detritus and within-group predation. Detritus is given the low preference factor of 0.2. Further it must be observed that generally only a part of detritus is spatially available for Y3 and Y4 (see below). In the case of Y1 and Y5, within-group predation can be an important food source only if the corresponding preference factor balances the much lower densities of Y1 and Y5 compared to Y3 and Y2. Hence, the preference factors for predation of Y1 on Y1, Y4 on Y4 and Y5 on Y5 are chosen to have values in the range from 1.0 to 3.0.

**Availability of detritus: \( d_Q \) (section 2.2, Table 2)**

The benthic detritus feeders have limited access to detritus, distributed over the upper 30 cm of the sediment. It is assumed that deposit feeders can utilize the detritus in the upper 20 cm, suspension feeders have access to the upper 3 mm and meiobenthos will reach the detritus in the upper 3 cm.

**Food uptake, half saturation constant: \( K^{up} \) (Eq. 4)**

These constants were chosen to correspond roughly to the average food concentration (Table A.1.2). The treatment of the pelagic food sources of Y3 (suspension feeders) with the parameter \( d_w \) is discussed separately below. The values for Y1, Y2, Y3, Y5 are based on sampling estimates (Table A.1.1); the other values are educated guesses, partly based on preliminary simulation runs. The food sums for Y1 to Y5 can be derived from these values as weighted sums (with preference factors). They are first approximations to the half saturation constants (Table A.1.3). In the case of Y3 and Y4, the weights reflect that not all Q6 is accessible (see section 2.2).

**Food uptake, lower threshold: \( L^{up} \) (Eq. 3)**

These constants were chosen quite arbitrarily at about 10% of the expected average concentrations of single food sources. They do not have a great influence on the result as long as they are not completely neglected. They save the sparse food sources from becoming completely consumed, as described in section 3.1. The threshold is soft; there is no sharp cut-off, only a
TABLE A.1.2
Expected average food concentration for derivation of the uptake half saturation constant. The pelagic values correspond to a 1 m layer with a concentration factor 3 (or a 30 cm layer with concentration factor 10).

<table>
<thead>
<tr>
<th>food source</th>
<th>expected concentration (mg C·m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>benthic:</td>
<td></td>
</tr>
<tr>
<td>Q6</td>
<td>5000</td>
</tr>
<tr>
<td>H1 + H2</td>
<td>1500</td>
</tr>
<tr>
<td>Y1</td>
<td>100</td>
</tr>
<tr>
<td>Y2</td>
<td>2500</td>
</tr>
<tr>
<td>Y3</td>
<td>1300</td>
</tr>
<tr>
<td>Y4</td>
<td>1000</td>
</tr>
<tr>
<td>Y5</td>
<td>100</td>
</tr>
<tr>
<td>pelagic:</td>
<td></td>
</tr>
<tr>
<td>R6</td>
<td>300 (year)</td>
</tr>
<tr>
<td>P1 + P2</td>
<td>150 (year)</td>
</tr>
</tbody>
</table>

TABLE A.1.3
Expected food sums. They give first estimates for the uptake half saturation constants.

<table>
<thead>
<tr>
<th>feeder</th>
<th>weighted sum</th>
<th>food sum (mg C·m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y1</td>
<td>3·Y1+Y3+Y4+Y5</td>
<td>2700</td>
</tr>
<tr>
<td>Y2</td>
<td>0.2·Q6+H1+H2+Y4</td>
<td>3500</td>
</tr>
<tr>
<td>Y3</td>
<td>0.05·Q6+(0.2·R6+P1+P2)·3m</td>
<td>460-850</td>
</tr>
<tr>
<td>Y4</td>
<td>0.1·Q6+H1+H2+Y4</td>
<td>3000</td>
</tr>
<tr>
<td>Y5</td>
<td>Y2+Y4+3·Y5</td>
<td>3800</td>
</tr>
</tbody>
</table>

TABLE A.1.4
An alternative set of physiological parameters. Compare with Table 3. Only those parameters are listed which have changed values compared to Table 3.

<table>
<thead>
<tr>
<th>symbol</th>
<th>meaning</th>
<th>Y1</th>
<th>Y2</th>
<th>Y3</th>
<th>Y4</th>
<th>Y5</th>
<th>units</th>
</tr>
</thead>
<tbody>
<tr>
<td>ρ⁰</td>
<td>specific uptake rate</td>
<td>0.03</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
<td>0.10</td>
<td>d⁻¹</td>
</tr>
<tr>
<td>Kₚ₀</td>
<td>food saturation</td>
<td>2000</td>
<td>1500</td>
<td>500</td>
<td>2000</td>
<td>food</td>
<td></td>
</tr>
<tr>
<td>Lₚ₀</td>
<td>lower food threshold</td>
<td>200</td>
<td>50</td>
<td>200</td>
<td>food</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pᵢ</td>
<td>preference factors</td>
<td>1,1,1,1</td>
<td>1,1,1,0.2</td>
<td>ρₚ=0.2 (R6,Q6)</td>
<td>1,1,1</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>qᵢᶠₑᶜᵉ</td>
<td>defaecated fractions</td>
<td>0.25</td>
<td>0.25</td>
<td>0.2</td>
<td>0.25</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>qᵢᵣᵉˢ</td>
<td>respired fractions</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
<td>d⁻¹</td>
<td></td>
</tr>
<tr>
<td>ρₙ</td>
<td>natural mortality</td>
<td>0.008</td>
<td>0.018</td>
<td>0.010</td>
<td>0.006</td>
<td>d⁻¹</td>
<td></td>
</tr>
</tbody>
</table>
mortality was used as *deus ex machina*. The mortality rates were calibrated such that the medians over the ten spatial compartments of the concentrations of $Y_1, Y_2, Y_3, Y_5$ agree with the medians of the values, given in Table 4. Unfortunately, some functional groups die out in some ERSEM boxes (see section 5).

**Stress mortality:**
Not estimated.

**Soluble fraction in dying biomass:**
Not estimated.

**Nutrient excretion:**
No parameters necessary. This process re-establishes the fixed C:N:P ratio after uptake and respiration. The ratio is assumed to be 1000:143:9.5.

**Suspension feeders and pelagic food sources:** $d_w, d_q(Y_3)$ (section 3.3, and Table A.1.1)
Presently, the pelagic food concentrations in mg C m$^{-3}$ are multiplied by $d_w = 3$ m (available water layer multiplied by a concentration factor) to arrive formally at food concentrations in mg C m$^{-2}$, consistent with the benthic densities. The resuspension layer $d_q(Y_3) = 3$ mm gives the suspension feeders access to the upper 3 mm of the sediment. With these values, benthic resuspended detritus and the pelagic food sources contribute roughly the same amount to the food.

**A.2. MICROBENTHIC PARAMETERS**

**Temperature dependence:**
A Q10-value of 2.0 is assumed throughout.

**Oxygen dependence:** $d^{ot}$ (Eq. 18)
In the case of benthic bacteria oxygen availability is described by the thickness of the aerobic layer (aerobic bacteria) and the oxic, nitrate dominated layer (anaerobic bacteria). It is assumed that the layer thicknesses are about 1 cm for the aerobic and several cm for the oxic layer. If these thicknesses fall to about 10% of these values, decomposition of detritus slows down in the model and mortality rises.

**Maximum decomposition rates of particulate detritus:** $r^{df}, r^{mu}$ (Eq. 12)
Detritus decomposition in the model is purely substrate limited. It only depends on the concentration and composition of detritus and not on the actual bacterial biomass. If the C:N:P ratio of detritus corresponds to the C:N:P ratio of the bacteria, the decomposition rate is about 20% per day. If the detritus becomes lower in nutrients, the rate slows down to a minimum value of 2% per day.

**Composition of assimilated detritus:** $c^{df}$ (Eq. 12)
Because the more nutrient-rich fractions of detritus are decomposed more rapidly than nutrient-poor fractions, at any moment the decomposed and assimilated part of the detritus is richer in nutrients than the average detritus. It is assumed that

$$(N/C)_{decomposed} = c^{df} (N/C)_{average}$$

In this way the remaining detritus becomes progressively nutrient depleted. $c^{df}$ is arbitrarily assumed to be 2.

**Uptake of dissolved organic matter:** $r^{oi}$ (Eq. 14)
Dissolved organic matter in the benthos originates as lysis products of sinking diatoms and as by-products of decomposition of particulate detritus. It is taken up at a rate of 50% of its mass per day. Because the diffusion of DOM (Q1) has not yet been modelled, the anaerobic bacteria H2 do not use or produce DOM in the model.
Excretion of DOM: $q^{ex}$ (Eq. 15)

The fraction $q^{ex} = 0.1$ of the decomposed particulate detritus is not assimilated but released in soluble form. This reflects the fact that exoenzymes are important in the decomposition process (only H1).

Respired fraction: $q^{res}$ (Eq. 17)

It is assumed that 30% of the decomposed and assimilated detritus POM and DOM is respired.

Basal respiration: $\rho^{res}$ (Eq. 17)

2% of biomass per day is taken as an arbitrary estimate of basal respiration.

Natural mortality:

Bacteria are assumed to be immortal barring predation or stress.

Stress mortality: $\rho^{str}$ (Eq. 21)

A maximum mortality of 5% per day is assumed if the thickness of the layer in which the bacteria live approaches zero (see oxygen dependence, $d^{str}$ above).

Composition: $q^{dis}$

The fraction $q^{dis} = 0.1$ of dying bacteria is released as DOM (only H1).

Nutrient uptake and excretion: $K'^n, K'^p$ (Eq. 17)

In general the excess nutrients are excreted. In this way the fixed C:N:P ratio is re-established after uptake and respiration. In the case of nutrient-poor detritus it may be necessary to take up nutrients to compensate for the low quality of food. This process is modelled, but because it does not normally occur, the corresponding Michaelis constants are set to zero. The C:N:P ratio is assumed to be 1000:200:15.

<p>| TABLE A.2.1 Parameters for aerobic and anaerobic benthic bacteria H1 and H2. The parameters are explained in section 3.2 and Appendix A.2. |</p>
<table>
<thead>
<tr>
<th>symbol</th>
<th>meaning</th>
<th>H1</th>
<th>H2</th>
<th>unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Q_{10}$</td>
<td>Q10-value</td>
<td>2</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>$\rho^{tr}$</td>
<td>fast degradation of POM</td>
<td>0.2</td>
<td>0.2</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$\rho^{rs}$</td>
<td>slow degradation of POM</td>
<td>0.02</td>
<td>0.02</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$\rho$</td>
<td>DOM-uptake</td>
<td>0.5</td>
<td>0</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$\alpha^{df}$</td>
<td>concentration factor (uptake)</td>
<td>2</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>$q^{res}$</td>
<td>DOM-release (fraction)</td>
<td>0.1</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>$\rho^{res}$</td>
<td>respired fraction</td>
<td>0.3</td>
<td>0.3</td>
<td>-</td>
</tr>
<tr>
<td>$\rho^{str}$</td>
<td>basal respiration</td>
<td>0.02</td>
<td>0.02</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$\rho^{str}$</td>
<td>stress mortality</td>
<td>0.05</td>
<td>0.05</td>
<td>d$^{-1}$</td>
</tr>
<tr>
<td>$d^{str}$</td>
<td>threshold thickness</td>
<td>0.001</td>
<td>0.1</td>
<td>m</td>
</tr>
<tr>
<td>$\delta^{dis}$</td>
<td>soluble fraction of dead bac.</td>
<td>0.1</td>
<td>0</td>
<td>-</td>
</tr>
</tbody>
</table>

A.3. BIOTURBATION AND 'BIO-IRRIGATION' PARAMETERS

The parameter values are given in Table A.3.1.

Weights: $\alpha_i$, $\beta_i$ (Eqs 25 and 38)

The weights reflect the assumptions that deposit feeders Y2 are the most important 'bio-irrigators' and 'bioturbators' and that suspension feeders Y3 do not contribute very much. Because the predators Y1 and Y5 have low biomass but are relatively active they are assigned greater
weights (presently 1) so their contribution should be comparable to that of the deposit feeders. Meiobenthos Y4 contributes slightly to 'bio-irrigation' but not to bioturbation in the model.

Bioturbation depth: δ (Eq. 35)
The shallow bioturbation depth δ (2 cm) is the result of calibration attempts with preliminary simulation runs. This value cannot be chosen independently of the mixing constant τ₀, or of the functional form ρ (Eq. 31), which is an exponential. Further calibration work is necessary. All ERSEM results are calculated with the present preliminary parametrization given in Appendix A (Table A.1.1, A.2.1 and A.3.1).

Mixing value τ₀: (Eq. 36)
The mixing value τ₀ may be compared with Gerino's (1990) value of 10⁻⁶ m²·d⁻¹.

<table>
<thead>
<tr>
<th>symbol</th>
<th>meaning</th>
<th>unit</th>
<th>value</th>
</tr>
</thead>
<tbody>
<tr>
<td>σ₀</td>
<td>molecular diffusion</td>
<td>m²·d⁻¹</td>
<td>~10⁻⁴</td>
</tr>
<tr>
<td>μₘᵢᵣ</td>
<td>maximum diffusion enhancement</td>
<td>-</td>
<td>10</td>
</tr>
<tr>
<td>Kᵣᵢᵣ</td>
<td>Michaelis constant for enhancement</td>
<td>mg C·m⁻²</td>
<td>5000</td>
</tr>
<tr>
<td>αᵢ</td>
<td>weights (Y₁, Y₂, Y₃, Y₄, Y₅)</td>
<td>-</td>
<td>0,1,0,0,2,1</td>
</tr>
<tr>
<td>Q10-value</td>
<td>-</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>symbol</th>
<th>meaning</th>
<th>unit</th>
<th>value</th>
</tr>
</thead>
<tbody>
<tr>
<td>τ₀</td>
<td>physical mixing</td>
<td>m²·d⁻¹</td>
<td>2·10⁻⁶</td>
</tr>
<tr>
<td>δ</td>
<td>bioturbation depth</td>
<td>m</td>
<td>0.02</td>
</tr>
<tr>
<td>μᵣᵢᵣ</td>
<td>maximum diffusion enhancement</td>
<td>-</td>
<td>10</td>
</tr>
<tr>
<td>Kᵣᵢᵣ</td>
<td>Michaelis constant for enhancement</td>
<td>mg C·m⁻²</td>
<td>5000</td>
</tr>
<tr>
<td>βᵢ</td>
<td>weights (Y₁, Y₂, Y₃, Y₄, Y₅)</td>
<td>-</td>
<td>1,1,0,0,1</td>
</tr>
<tr>
<td>Q10-value</td>
<td>-</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>

TABLE A.3.1
Parameters in the bioturbation and 'bio-irrigation' model. (Y₁=epibenthic predators; Y₂=deposit feeders; Y₃=suspension feeders; Y₄=meiobenthos; Y₅=infaunal predators.)