

**A model of carbon flows in relation to  
macrobenthic food supply  
in the Oosterschelde estuary  
(S.W. Netherlands)**

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A model of carbon flows in relation to  
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#### **ABSTRACT**

The first part of this thesis describes a simulation model of the carbon flows in the Oosterschelde estuary, S.W. Netherlands. Aim of the model is to describe the availability of food for macrobenthic filterfeeders, and possible changes in this as a result of the construction of a half-open storm-surge barrier. Major aspects of the model are transport, primary production, zooplankton grazing, mineralization, microphytobenthos production and zoobenthos grazing.

In the second part of the thesis the question how to assess uncertainty in model results of such a relatively complicated model is addressed. In a sensitivity analysis the parameters are classified into a limited number of groups with separate effects on model results. This classification is used to facilitate the calibration procedure. Calibration is treated as a method to reduce uncertainty in model output, and not as a procedure to test hypotheses concerning model formulations.

The reduced uncertainty is used in the calculation of the effects of several scenarios. Despite the considerable physical changes as a result of the barrier the carbon flows in the Oosterschelde appear to remain near their old values. There is a limited possibility to extend the mussel culture in the seaward part of the Oosterschelde, but with a risk of causing overgrazing, with negative effects on mussel yields and the natural system. The risk of eutrophication of the Oosterschelde as a result of direct nutrient discharges is slight, but the impact on the Oosterschelde of further eutrophication of the adjacent North Sea would be larger.



## STELLINGEN

- 1) Ecosysteemmodellen zijn in het algemeen te complex om individuele modelformuleringen te testen. Parameterschattingstechnieken gericht op hypothese tests zijn dan niet toepasbaar.
- 2) De methode die Finn (1978) gebruikt om een 'cycling index' te berekenen komt niet overeen met zijn oorspronkelijke definitie (1976).

Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. *J. Theor. Biol.* 56: 363-380.

Finn, J.T., 1978. Cycling index: a general definition for cycling in compartment models. In: Adriano, O., Brisbin, I.L. (eds.), *Environmental chemistry and cycling processes*. U.S. Dept. energy symp. 45. National Technical Information Centre, Springfield, Va. pp 148-164.

- 3) In een budgetstudie dienen alle termen onafhankelijk te worden gemeten of althans geschat.
- 4) De in aquatisch-ecologische modellen vaak gemaakte veronderstelling dat de koolstof-chlorofyl ratio constant is, is een grove simplificatie die meestal niet wordt beargumenteerd.
- 5) Een verklarend karakter is voor een ecosysteemmodel geen doel op zich.

Kremer, J.N. and S.W. Nixon, 1978. *A coastal marine ecosystem: simulation and analysis*. Springer Verlag, Berlin.

- 6) Een deel van de door Fransz beschreven dynamiek van het zoöplankton in de Noordzee berust vermoedelijk op numerieke instabiliteiten in de door hem gebruikte oplossingsmethode.

Fransz, H.G. (1979) Carbon dynamics in the food web of the south-eastern North Sea: a simulation study. In: *Progress in ecological engineering and management by mathematical modelling*. Proceedings 2<sup>nd</sup> conference on state-of-the-art in ecological modelling.

- 7) Als de claim van Gordon *et al.* dat "The code has been verified to ensure that all programming errors have been removed" inderdaad een methode om programmerfouten op te sporen beschrijft en niet slechts wishful thinking zou dit een veel grotere betekenis hebben voor de ontwikkeling van ecologische modellen dan het door hun beschreven model zelf.

Gordon Jr., D.C., Keizer, P.D., Daborn, G.R., Schwinghamer, P. and W.L. Silvert, 1986. Adventures in holistic ecosystem modelling: the cumberland basin ecosystem model. *Neth. J. Sea Res.* 20(2/3): 325-335.

- 8) Het gebruik van de term "gezond functionerend ecosysteem" suggereert een onjuiste analogie met een levend organisme. Een dergelijke beoordeling van een ecosysteem is een subjectieve zaak en geen objectieve realiteit.

Saeijs, H.E.F (1982) Changing estuaries. Rijkswaterstaat communications 32, Government Publications Office, The Hague.

- 9) Door de overheid geforceerde grote wetenschappelijke samenwerkingsverbanden leiden evenmin tot efficiënt onderzoek als gedwongen collectivisatie tot efficiënte landbouw.

- 10) Het belangrijkste positieve milieu effect van de Oosterschelde dam is vermoedelijk uitstel of afstel van andere grote en dure infrastructuurle werken geweest.

Stellingen behorende bij het proefschrift van O. Klepper:

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## 1. GENERAL INTRODUCTION

### 1.1 Introduction

In 1987 a storm-surge barrier was completed in the mouth of the Oosterschelde (S.W. Netherlands, see figure 1.1); it serves the purpose of protecting the area behind it from floods, and at the same time to keep the rich ecosystem of the Oosterschelde intact: a simple closure of the Oosterschelde would have destroyed the present ecosystem, in which the movements of the tide and the large intertidal areas play a key role (Knoester et al., 1983; Saeijs and Baptist, 1980).

The construction of the barrier and several dams in the Eastern and Northern branches of the Oosterschelde (see figure 1.1) form a large investment in the conservation of the ecosystem; as a result of these and earlier engineering works the ecosystem is now to a considerable degree under human control (e.g., freshwater and nutrient input, tidal range). This makes it necessary to investigate the effect on the ecosystem of engineering works and their management. Since 1980, the Oosterschelde has been studied intensively in order to know the original situation and changes as a result of the engineering works. These studies concerned hydraulics (current velocities, tidal range -Dronkers, 1980), geomorphology (Kohsiek et al., 1987), biomass of birds and their food-uptake (Meininger et al., 1984) and the conditions for mussel culture (Steijaert, 1983, 1985).

The present report forms part of this research effort and describes a simulation model of the carbon and nutrient flows in the Oosterschelde ecosystem. The model is based on the results of an interdisciplinary program, the BALANS project (Stortelder, 1979) executed jointly by the Rijkswaterstaat (former Delta Department, present Tidal Waters Division) and the Delta Institute for Hydrobiological Research. The aim of the project was to gain insight into the processes regulating the main carbon flows in the ecosystem.

The management interest in a model of the Oosterschelde is to know the possibilities of the natural system for human use and the effect of storm-surge barrier and possible management strategies on this. The mussel culture is the most important use of the Oosterschelde, both in terms of economic value and effect on the entire ecosystem. The model aims at the calculation of food concentrations (phytoplankton, suspended detritus) for mussels and other suspension feeders. In order to calculate phytoplankton production, the concentrations of inorganic nutrients necessary for growth have to be calculated also. It is generally assumed that the effect of mussel culture on the system is mainly via food and nutrients: food concentration for other organisms may be lowered, and nutrient regeneration is possibly increased. The most important human influences on this are the presence of the storm-surge barrier (reducing exchange with the North Sea), manipulations with the numbers of mussels (possibly reducing their own food levels) and the freshwater input (containing nutrients for phytoplankton growth). The time-scale on which these manipulations may show effects (on phytoplankton, mussel growth) is weeks to years. The spatial scale that is relevant is 10 to 20 km.

Of course, there are a number of other aspects of human influence on the ecosystem. These concern smaller time-scales (e.g. the effect of closing the storm-surge barrier for 1 or 2 days), larger time-scales (e.g. the possible geomorphological changes after several decades), smaller spatial scales (e.g. the effect of the construction of an artificial beach on bottom fauna), or flows of matter other than carbon and nutrients (e.g. heavy metals). These problems are not considered by the present model.

A second aim of the present model is to integrate the main results of the research in the BALANS-project. In this way the results are quantitatively

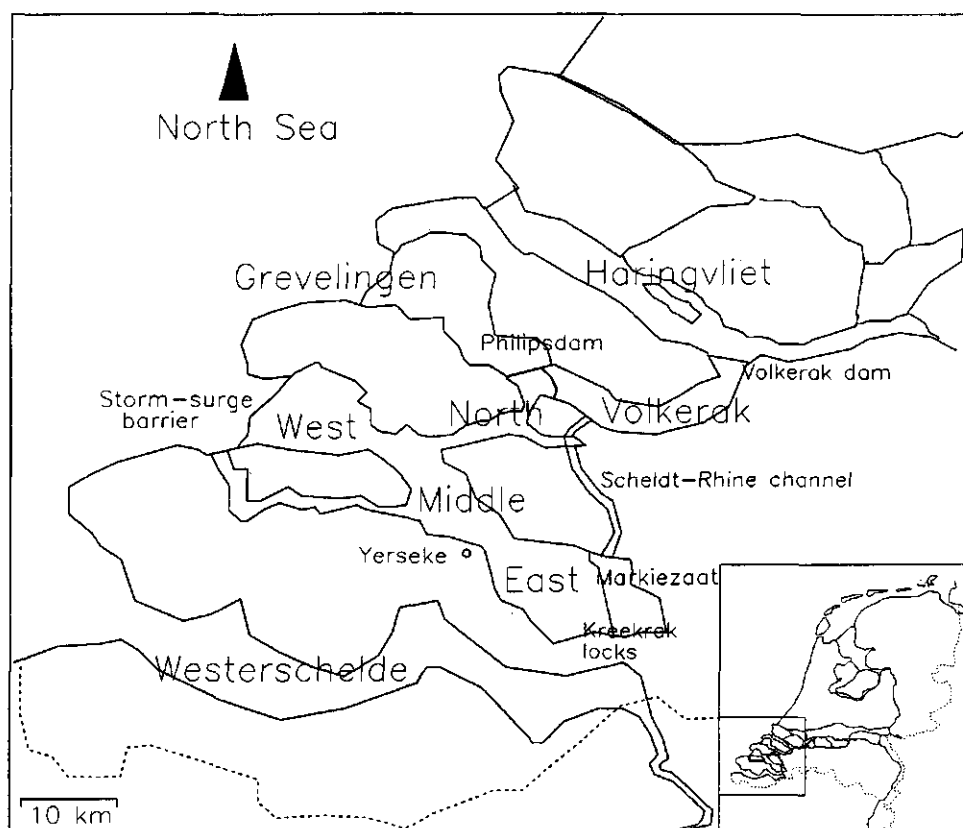
vely summarized and may be compared with each other: which processes are important, and which are less important, what is accurately known, and what not.

In a previous study (Klepper and Van de Kamer, 1987, 1988), the BALANS results were also combined, but only in accounting terms (i.e. no process information) and on a yearly-averaged basis. The questions underlying this steady-state model were whether a closed carbon budget for the Oosterschelde can be found on the basis of experimental results, and what the most important carbon-flows in this budget are. The conclusion was that the data are not inconsistent with a closed carbon budget. However, they show a considerable uncertainty. From the yearly averaged budget it can be concluded that the major carbon flows are all on the first and second trophic levels: the higher food chain (fish, birds) is quantitatively negligible, and can therefore be safely omitted in more detailed carbon flow models.

The incorporation of the processes underlying the major carbon flows required a finer spatial and temporal scale than in the above-mentioned model. The major practical difference between the steady-state model and the present model is that now it is possible to calculate the effect of changed environmental conditions on the carbon flows in the Oosterschelde.

In this chapter a brief general description of the Oosterschelde ecosystem is followed by an outline of the model, paying particular attention to the limitations and possibilities of the model.

## 1.2 The Oosterschelde ecosystem



**Figure 1.1:** Map of the Oosterschelde in the SW part of the Netherlands, showing the subdivision into four subregions (west, middle, east and north) and some locations mentioned in the text.

### Situation 1983

The landscape of the Oosterschelde has been changed by engineering works for centuries, and in particular in the last decades. The construction of the storm-surge barrier started in 1984/85, and the situation of the estuary around 1983 is here described as the reference situation.

In former times the Oosterschelde was part of the multiple branched estuary of the rivers Rhine, Meuse and Scheldt. As a result of the Delta Project, the flow of the rivers Rhine and Meuse through the southern part of the region was restricted: the Volkerak dam, completed in 1969, cut off southward flow almost completely. The link with the Westerschelde estuary had already been cut in the nineteenth century. The Oosterschelde (see fig. 1.1) can therefore be regarded as an estuary subject to only very limited freshwater influence.

The mean tidal range varies from 2.8 m at the entrance to 3.7 m at the most inland site. The maximum flow velocity during flood and ebb is about  $1 \text{ m.s}^{-1}$ , with deviations for location of no more than  $\pm 20\%$  (Knoester et al., 1983). With the movement of the tides a parcel of water travels a distance of about 10-15 km backwards and forwards (horizontal component) (Dronkers, 1980; see figure 7.7). In each tidal cycle about 1,250 million cubic meters of water flow into and out of the Oosterschelde, with the average rate of flow being approximately  $56,000 \text{ m}^3.\text{s}^{-1}$ . Average discharges into the Oosterschelde are approximately  $55 \text{ m}^3.\text{s}^{-1}$ : from the Volkerak locks, 28%; from inflowing small rivers, 30%; and excess water from the Veerse Meer and Lake Grevelingen, 15% (Havermans, 1983).

As a result of the relatively small freshwater inflow, water quality in the Oosterschelde is primarily influenced by the sea, but locally, the larger sources will have a noticeable impact on water quality, in particular in the most eastern part ("Kom" area), and the northern branch ("Volkerak" area). The water quality is good in the entire Oosterschelde (Stortelder et al., 1984); nutrient levels are low to moderate (both inorganic nitrogen and silicon  $< 2 \text{ mg.l}^{-1}$ ; phosphorus  $< 0.2 \text{ mg.l}^{-1}$ ), chlorophyll concentrations are low (average  $5-10 \text{ } \mu\text{g.l}^{-1}$ ), and toxic materials such as heavy metals have low concentrations (both in water and sediment).

The morphology of the Oosterschelde is mainly characterized by tidal channels, intertidal sand- and mudflats and salt marshes. The latter form relatively small scattered areas between the intertidal flats and the dikes: almost the entire Oosterschelde area is directly bordered by dikes. The maximum depth of the tidal channels in the Oosterschelde is about 50 meters. Such depths are found mainly in the central and western part of the estuary; in the eastern and northern part of the estuary the depth of the channels does not exceed 25 m.

The large intertidal areas consist in the west mainly of sand shoals and in the east and north of great stretches of mud flats. Both types occur in the central area. Both shoals and mud flats are covered by the tide twice a day. Apart from ripple marks and shell banks the intertidal areas are flat, cut across by a few shallow water courses. For the most part the areas are not higher than 0.50 m above mean sea level, the highest points reaching to 1.50 above mean sea level (Knoester et al., 1983).

The bed of the Oosterschelde consists almost entirely of mobile loose sediment (mainly sand of  $100-200 \text{ } \mu\text{m}$ ). Although large quantities of sediment are set in motion by the tides (Dronkers, 1986), changes in the position of channels, shoals and mud flats and in the total area of the intertidal zone have become noticeable only over periods of several decades in the past (Van den Berg, 1986), and geomorphological changes as a result of the storm-surge barrier are expected to take a similar period (Kohsiek et al., 1987).

Mainly in the central and eastern parts of the Oosterschelde, salt marshes are found on the highest parts of the tidal flats, close to the dikes. The frequency with which they are covered by water varies from twice a day to just a few times a year. The salt marshes differ from the rest of the area in their morphology and the high clay content (20% or more) of the soil. Their morphology is characterized by a complex branching system of creeks which are around two meters deep and can be many meters wide. The ecosystem of the salt marshes is characterized by a large number of higher plants, birds and mammals. The carbon and nutrient cycles of these marshes are, in spite of occasional inundations, only loosely connected with those of the water and the tidal flats. There is an exchange of nutrients and detritus between the marshes and the pelagic system (Groenewegen, pers.



comm.), but this exchange is negligible compared to exchange with the North Sea and input from the Volkerak (Klepper et al., 1985).

The ecosystem in the water is closely connected with that on the (intertidal) bottom. The combined system is dominated by phytoplankton, filterfeeding bivalves (cockles and mussels) and tunicates, and zooplankton. With respect to species diversity it is estimated that about 1000 species can be found in the water and on intertidal and subtidal bottoms. Phytoplankton, among which diatoms and flagellates are the most common, amount to about 240 species; zooplankton, mainly ciliates, and copepods, to about 75. In the period 1961-1981 88 species of fish were observed, 12 of which abundantly (Knoester et al., 1983). The Oosterschelde serves as a nursery for fish like plaice, dab, flounder, sole, herring and sprat. Some of the species are bound to the tide, as they feed at high tide on the intertidal flats (Knoester et al., 1983).

An essential factor, besides salinity and water quality, with regard to the species diversity is the type of substratum available; a distinction can be made between soft and hard substrata. The soft substrata are the (natural) sandy and muddy intertidal regions and the adjacent shallow water areas. This habitat is the most common, and is important as a link to higher trophic levels (e.g. from phytoplankton via cockles to birds) because of its intertidal character. In addition to this, a large variety of organisms are also to be found on and near the hard substratum (Van den Hurk, 1987). This last comprises both hard peat layers and the materials and structures introduced by man: stone dike facings, harbors, bridge supports and wrecked vessels. This hard substratum is important because it is a relatively rare habitat along the Dutch coast. The species on the hard substratum contribute little to the carbon-flows in the Oosterschelde, but comprise a large fraction of the total number of species. Species are found whose normal habitats are the rocky coasts of Scandinavia, southern England and northern France; these include sponges, hydras, many species of sea anemones, barnacles and lobsters (Knoester et al., 1983).

The Oosterschelde is rich in bird species, especially waders and ducks. There are probably two factors of importance in this connection: the food-supply from benthic organisms and the fact that the Oosterschelde and its surroundings are a relatively quiet area where birds can find refuge at high water (Saeijs and Baptist, 1980). The delta region lies on one of the migration routes of the northern European bird population.



Figure 1.2: The storm surge barrier.

#### Present situation

The recently finished Oosterschelde works consist of a storm-surge barrier in the mouth of the Oosterschelde, and two dams in the eastern and northern branches (see fig. 1.1). The storm surge barrier is intended to protect the area from floods, the two other dams create a stagnant fresh-water lake, which serves agriculture (irrigation water) and ship traffic (tide-free passage from Antwerp to the Rhine). In addition, the two dams prevent the tidal range in the Oosterschelde from dropping too low.

A description of the present situation in the Oosterschelde is given by Holland et al. (1986). The average tidal range has been reduced from 3.5 m to 3.26 m at Yerseke. The area under tidal influence is reduced mainly as a result of the exclusion of the areas behind the dams in the northern and eastern branches: of the present 16.2 km<sup>2</sup> of salt marshes, 10.2 km<sup>2</sup> is no longer subject to tidal influence, while 46 km<sup>2</sup> of the former 160 km<sup>2</sup> of mud and sand flats have also lost their tidal characteristics.

The maximum flow velocities in the tidal channels have been reduced roughly from 1 m.s<sup>-1</sup> to 0.5-0.75 m.s<sup>-1</sup>. This reduction has lead to lower levels of turbulence in the channels, with impacts on the distribution of sand and mud, and water transparency. This influences filterfeeders both directly (they need to filter less inorganic material) and indirectly: the greater transparency leads to more light for phytoplankton growth. Finally,

the reduced currents have also diminished mixing of the water, and thus caused a reduced exchange with the North Sea. This could lead to a lower salinity and higher nutrient concentrations, but its influence is countered by a lower freshwater input as a result of the two dams.

As a result of the reduced exchange volume, the present tidal channels are too wide and deep. It is therefore expected that they will partly silt up: partly with sediment imported from the North Sea, but mainly with sediment from the Oosterschelde itself, in particular from the intertidal flats. As a result, average depth will decrease, and intertidal area will decrease eventually (Kohsiek et al., 1987). As has been mentioned, the expected duration of these changes is several decades.

### 1.3 Outline of the simulation model

The Oosterschelde model describes the flows of carbon, nitrogen and silicon in the water column and bottom. The species diversity described in the previous paragraph is reduced to a small number of state variables, by leaving out a large number of groups, and lumping others. The spatial differences within the Oosterschelde is described by considering four compartments (see figure 2.2): east, middle west and north. Within each compartment, a distinction is made between water column, intertidal bottom and subtidal bottom. The processes are modelled identically in the four compartments, although the compartments may differ in e.g. depth, suspended sediment concentration, and so on. A simplified schematic representation of the model in a single compartment is given in figure 1.3.



species) belong to the second group: in this way the fraction of diatoms may be used as an indicator of phytoplankton "quality".

The zooplankton is divided into two groups in the zooplankton sub-model: the first consists of the true zooplankton (having their entire life-cycle in the water), the second of the larvae of benthic animals. The first group is a state-variable in the model, the second group is modelled as a time series. Biomass and grazing activity of both groups have been measured in the Oosterschelde; concerning the other processes (respiration, assimilation), the zooplankton sub-model is based on literature data.

Mineralization of organic detritus in the water column has been modelled using a simple first-order formulation by lumping the microbiota and meiofauna together with the dead organic material in a single state-variable "labile detritus". The main problem in the estimation of the decay coefficient from oxygen-consumption and POC-decay measurements is the estimation of the amount of substrate, i.e. the labile fraction of the detritus.

Mineralization in the bottom is treated separately, as a part of the microphytobenthos sub-model. The production and decay processes in the benthos are closely coupled because the benthic diatoms are either nutrient- or  $\text{CO}_2$ -limited for most of the year: their supply of these substances is mainly from the mineralization in the sediments on which they are attached.

The biomass of mussels, cockles and other bottom-fauna is described by a time-series in the model, estimated (for the mussels) from market-data, and (for the other zoobenthos) from field-surveys. There is an abundant literature on the activity of filterfeeders, in particular the mussel. On a number of significant points this literature contains contradictions, in particular on the influence of temperature, the influence of suspended sediment concentration, and the possibility to select food from the filtered material. In the macrobenthos sub-model it is attempted to formulate the model in a way which makes it possible to express the various results from the literature as parameter ranges, e.g.: the effect of temperature between no effect and a fairly strong effect may be expressed in a temperature coefficient ( $Q_{10}$ ) between 1 and 3.

In order to couple the nitrogen-, silicon-, carbon- and oxygen cycles in the model, conversion factors are needed. In the model these factors are assumed to be fixed; they are estimated on the basis of literature data.

#### 1.4 sensitivity analysis and calibration

The model as formulated on the basis of process-information from the literature and the Oosterschelde itself cannot be considered finished: in the first place, there is often a considerable uncertainty in these formulations, which is expressed here as a range for a parameter (example: the range for the  $Q_{10}$  of mussels described above); secondly, it is clearly necessary to check whether the model correctly describes the old situation before using it to calculate the impact of some scenario.

The effect of uncertainty in the parameter values has been quantified using a Monte Carlo analysis: by running the model a large number of times using randomly selected values of the parameters from their ranges, a range of output-values for every model-output emerges. From these, it is possible to decide which parameters have the most influence on model-output (are the most sensitive).

The results of the sensitivity analysis are used in the model calibration: from the entire range of all parameters, a very broad range in output of e.g. chlorophyll (say, yearly average 1-50  $\mu\text{g/l}$ ) may be obtained, whereas the actual range is much more narrow (e.g. 3-8  $\mu\text{g/l}$ ). This narrow range

coincides with a similar more narrow range of parameter-values. Therefore, the calibration of the model to field data reduces initial uncertainty.

This reduced uncertainty is then used in the calculation of the effect of several possible scenarios on the Oosterschelde. It is felt that the (usual) presentation of a single model-output representing an optimal set of parameters may be misleading: perhaps a different set of parameter values (within the uncertainty range) would have given quite different results.

The first "scenario" to be calculated is a comparison of the situation before and after the construction of the storm-surge barrier and compartmentalization dams for a "standard year", i.e.: with averaged inputs for temperature, irradiation, and so on. Other scenarios are: doubling or halving of nutrient inputs; dumping of manure into the Oosterschelde and the extension of the mussel culture.

In summary, the following procedure is followed to handle uncertainty in the model: all parameters values are formulated as an initial range; this initial range is reduced by a comparison to field data to a calibrated range, and this reduced uncertainty is then used in the application of the model.

### 1.5 Limitations and use of the model

Some limitations to the use of the model have already been mentioned. They are related firstly to the substances being modelled: the major carbon- and nutrient flows in the Oosterschelde. Excluded are therefore e.g. toxic substances, species composition (with the exception of the distinction diatoms/ other algae, which is related to the nutrient flows), geomorphological changes and so on.

Within the group of questions related to the carbon- and nutrient flows, the use of the model is restricted to a certain temporal and spatial scale. Although it would seem desirable to have a model with a very small spatial and temporal scale (it is possible to integrate to a coarser scale, not the reverse), the present model uses only a fairly broad spatial description of the Oosterschelde (regions west, middle, east and north), and a time-scale of days or longer. This has been done for a number of practical reasons. Many important data are available on a similar scale only, e.g.: there are a dozen water-sampling stations in the Oosterschelde with a sampling interval of 2-4 weeks, but other important variables are known only on a much coarser temporal scale (e.g. zoobenthos biomass, only a few complete surveys) or spatial scale (e.g. zooplankton biomass, only two sampling stations). Clearly, it is not useful to build a detailed model for which many of the input-data have to be estimated from less detailed information, and which can not be checked with equally detailed field data. In addition, an ecological model with e.g. a time-scale of hours and a spatial scale of kilometers would require an enormous amount of computer time, making it virtually impossible to simulate a few years.

The choice for the present scale should not be considered as a negative one, merely on the basis of lack of information and computer time: a more detailed model takes more time to formulate (e.g. all kinds of processes within the daily cycle and within the tidal cycle play a role), to inspect the results (more spatial compartments), and therefore to calibrate and so on. If a coarser model is able to answer most of the questions, it is clearly preferable.

Typical questions that cannot be answered by the present model concern (transport) processes within a compartment: for example the supply of food from the water column to a mussel "bed". The model calculates a compartment-average surface value, but in a particular situation of low current speed and high mussel density the supply to the bottom may be the limiting factor

(Frechette and Bourget, 1985; Verhagen, 1986; Smaal et al., 1987). Another example would be a closure of the storm-surge barrier. In this case, the assumption that dissolved substances are completely mixed over the water column is probably no longer valid (depending on wind conditions and possible salinity stratification), and the vertical transport of oxygen towards the bottom may cause problems.

Questions which can be answered are related to direct manipulations with these flows (e.g. nutrient discharges), or indirect impacts (e.g. via the cultivation of mussels). It should be noted that, although higher trophic levels are not included in the model because their contribution to carbon flows is negligible, the major carbon flows are, of course, very relevant in the other direction as the primary source of food for fish and birds. Therefore, the results of the model may be also relevant for questions related to these groups of organisms.

A final restriction on the use of the model is its reliability. It is attempted to incorporate this aspect directly into the model-output, by presenting the results including an uncertainty-interval, based on the calibration of the model, discussed above. In this way, it may be seen immediately whether predicted changes are large relative to the uncertainty in these predictions.

## 2. THE TRANSPORT MODEL

### 2.1 Introduction

In an estuarine environment transport processes play a major role in determining the concentrations of both biotic and abiotic substances. Therefore, an ecological model of the Oosterschelde has to include a model to describe input of substances from the land, surrounding lakes and the atmosphere, transport within the estuary, and exchange with the North Sea. This chapter is divided into two parts, describing the transport models for dissolved substances and for particulate matter respectively.

The transport of dissolved substances is a well-known process and existing models yield satisfactory results. In estuarine environments the horizontal distribution of salinity gives valuable information on transport because firstly, salt is a conservative substance, and secondly, a gradient in concentration is present. The conservativity ensures that the concentration is determined by transport processes only, while the existence of a gradient makes it possible to calculate the balance between mixing with sea water (which increases salinity) and the flushing with fresh water (which decreases salinity).

In the Oosterschelde the horizontal distribution of salinity has been modelled by Dronkers (1980), Ockhuysen (1983) and Van der Wekken (1986) with one-dimensional, steady state models which are solved analytically. These are of limited use for the present model, because the time-scale of the ecological model is days, which is in general too short to assume steady-state transport conditions. Also, the incorporation of source- and sink terms would make an analytical solution of the equations impossible.

Therefore, the present model is based on numerical models without steady-state assumptions, which allow for arbitrary complex source- and sink terms. Examples of these are the models by Bella and Dobbins (1968), O'Kane (1980), Helder and Ruardij (1982), Van Es and Ruardij (1982) and Bos (1985). For the Oosterschelde, information from steady-state models (compartment borders, initial estimates of mixing terms) has been included.

In contrast to the models for dissolved substances, the situation for particulate matter is less satisfactory. Modelling the transport of particulate matter is complicated by the fact that no conservative substance like salt exists in this field: the suspended sediment has sources and sinks in the form of erosion and sedimentation. Furthermore, the time-scale of the process is much smaller: within a tidal cycle the salinity of the estuary changes only slightly, but suspended sediment concentrations vary rapidly with current velocity. Finally, suspended matter concentrations are more difficult to measure than salinity.

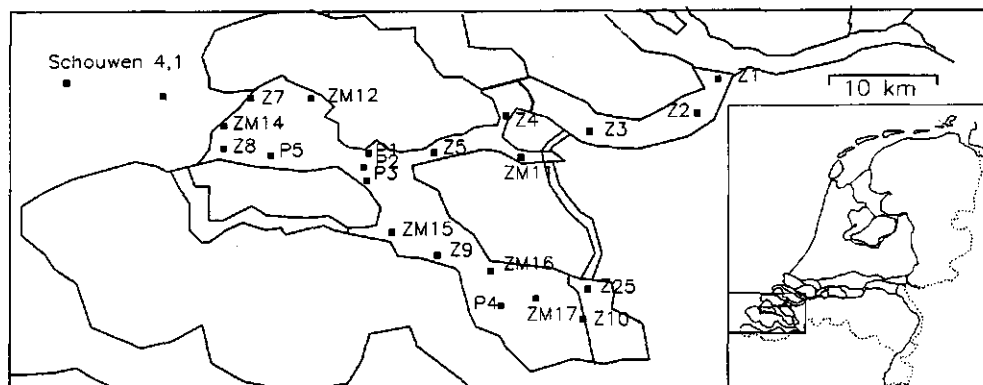
In existing models of particulate transport operating on the same temporal and spatial scale as the present model, these problems are solved in different ways (Ebenhöh; 1984, Dronkers, 1984, 1986a; Laane and Ruardij, 1986). The present model follows the simple parametrization of the transport process that is proposed by Dronkers.

In the first section of the chapter the transport model for dissolved substances is treated. The numerical scheme for the solution of the transport-equations and the elimination of the tidal movements from the total transport are discussed. The next section discusses the horizontal transport of suspended sediment and in particular the estimation of the coefficients in the Dronkers-model. Finally the application of the sediment-transport model to particulate organic carbon and algae is discussed in relation to the vertical distribution of these substances.

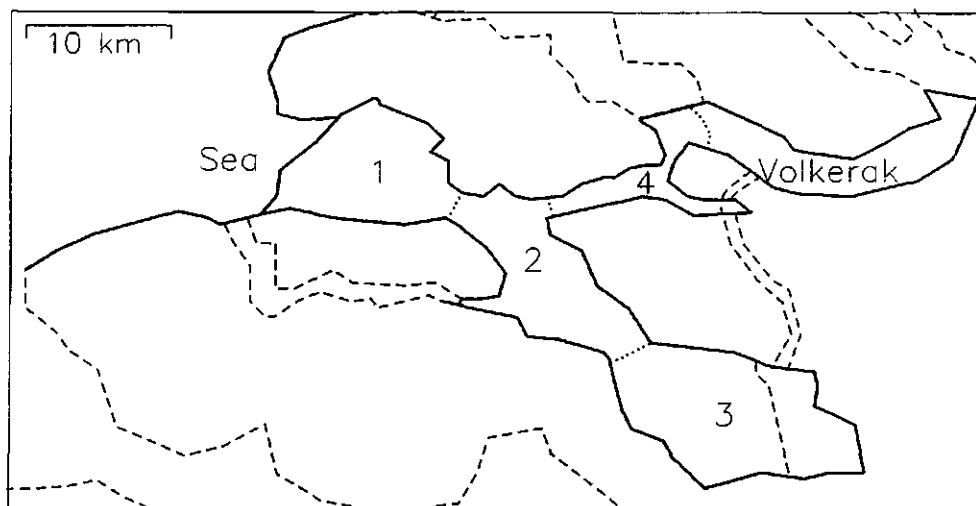


## 2.2 COMPARTMENTS

The Oosterschelde is divided into five compartments (see figure 2.2), four of which are modelled. The fifth (most northern) compartment is treated as a border of the system. The schematization is a slight adaptation of the one used by Dronkers (1980). Detailed morphological data on the compartments are given by Duin (1986).



**Figure 2.1:** The location of sampling stations in the Oosterschelde and those serving as boundary conditions.



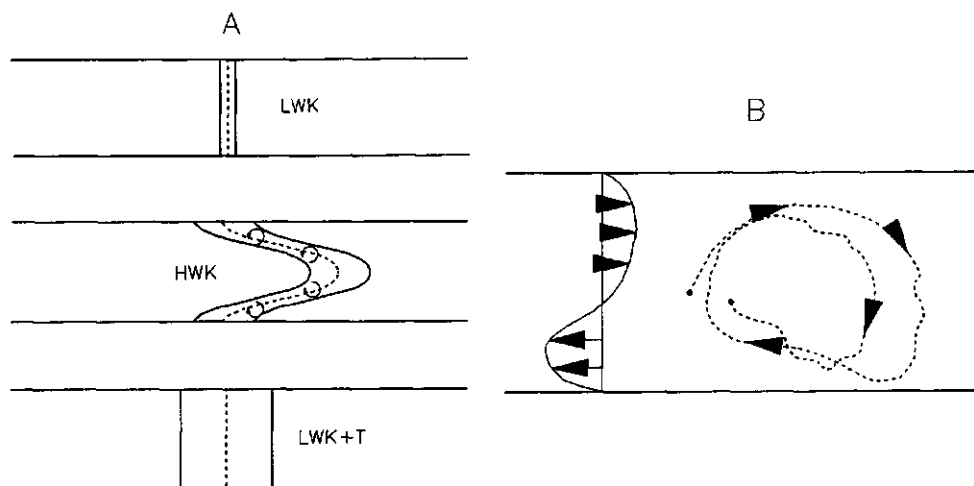
**Figure 2.2:** The division of the Oosterschelde into four compartments with boundaries indicated.

## 2.3 THE TRANSPORT OF DISSOLVED SUBSTANCES

### Introduction

In this section several problems concerning the transport of dissolved matter in the Oosterschelde will be discussed. The first point is the elimination of tidal movements from the transport equations. The oscillating water movement induced by the tide plays an important role in the transport by increasing mixing (see figure 2.3). However, this mixing can be adequately described by a single parameter, and the oscillating movements can be subtracted to obtain the (much smaller) net displacement.

The strong lateral and vertical mixing in the Oosterschelde make it possible to describe the distribution of dissolved substances in one dimension only: the (branched) axis of the estuary (Dronkers, 1980). The next point is the conversion of the resulting one dimensional partial differential equation describing mixing and flushing into a stable finite-difference scheme. Finally, a summary is given of the calculations of discharges into, and subtractions from the Oosterschelde.



**Figure 2.3:** (from Dronkers and Zimmerman, 1982) Two of the mechanisms that cause mixing in an estuary.

A: plan view of an hypothetical estuary; LWK- low water slack, HWK- high water slack, T- tidal period. The tidal flow is generally not homogeneously distributed over the cross-section of the estuary, but stronger in the centre of a channel. As a result, a hypothetical tracer substance forming a narrow band at LWK would be stretched out at HWK. A stretched patch of tracer is both longer and has a stronger concentration gradient in the direction perpendicular to the direction of stretching. As a result, the turbulence causes a much stronger mixing than in a homogeneous flow, and the band of tracer has spread considerably after one tidal cycle.

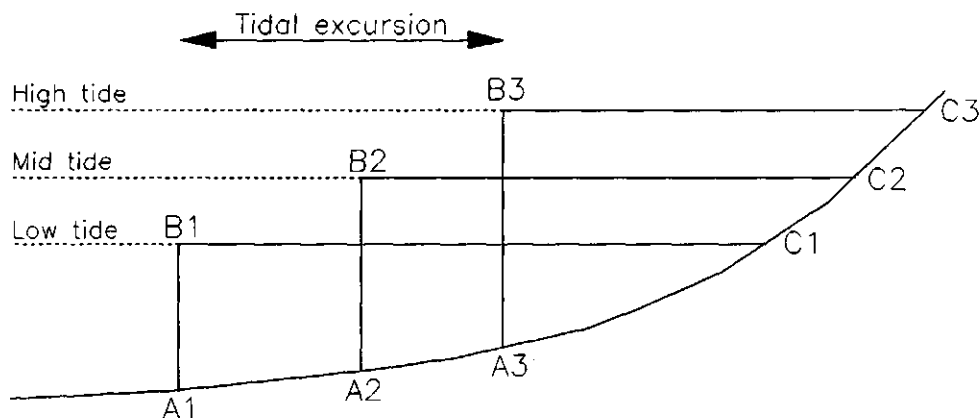
B: The net flow after one tidal cycle (residual flow) often shows a reversion from one side of the estuary to the other (residual flow pattern shown in the left of the figure). Relatively small displacements of a particle during several tidal cycles may be the result of turbulence. In combination with the residual flow the particle moves over considerable distances along the axis of the estuary and mixing is increased.

#### Fixed volume reference frame

In some situations, e.g. during the construction of the storm-surge barrier in the Oosterschelde, information on water levels and -movements during the tidal cycle is needed. Even a one-dimensional model giving this information (IMPLIC) takes a large amount of computer time to compute a few tidal cycles. For the present model, with a time-scale of days, detailed information on the movements of substances during a tidal cycle is not necessary, and it would be desirable if the detailed computations could be avoided.

A considerable simplification results if observations of the system are not taken from a fixed point on the bank of the estuary ( $x$ ), but from a reference frame moving with the water ( $x'$ ) (O'Kane, 1978, 1980). At the moment of mid-tide the positions of  $x'$  and  $x$  are the same; at other times  $x'$  is defined by a constant upstream volume: the volume of the estuary upstream (landward) of a cross-section through  $x'$  perpendicular to the axis of the

estuary (see figure 2.4). During high water  $x'$  will be landward (upstream) of  $x$ , during low tide downstream. The movement of an imaginary buoy moving with the water can now be described in the fixed-volume reference frame by a slow net displacement seaward, which corresponds to the freshwater input into the estuary.



**Figure 2.4** Sketch of the transformation from fixed-bank to fixed-volume reference frame: cross section of an estuary along its axis; the areas ABC represent the same volume. The value of  $x'$  at low, mid and high tide equals the  $x$ -coordinate at A1, A2, A3 respectively.

Considering the Oosterschelde in a fixed-bank reference frame, the buoy would be moving upstream at a speed of  $1-2 \text{ m.s}^{-1}$  during flood, and downstream during ebb at approximately the same speed. The movement in the fixed-volume reference frame is:

$$U = \frac{Q}{A} \quad (\text{m.s}^{-1}) \quad (2.1)$$

with:  $Q$  = net freshwater input ( $\text{m}^3.\text{s}^{-1}$ )  
 $A$  = average cross-sectional area ( $\text{m}^2$ )  
 $U$  = current velocity ( $\text{m.s}^{-1}$ )

In the Oosterschelde approximate values are (Dronkers, 1980):

$$Q = 50 \text{ m}^3.\text{s}^{-1}$$

$$A = 2.10^4 \text{ m}^2$$

which results in:

$$U = 2.5 \cdot 10^{-3} \text{ m.s}^{-1}$$

This net velocity fits into the required time-scale of days for the ecological model.

The actual movement of a buoy in a fixed-volume Oosterschelde would be very different from this average figure: local differences in current velocity and morphology, large and small-scale eddies and so on, would make the movement of the buoy highly random. These random movements of individual particles result in a strong mixing of the Oosterschelde. Two of the tide-induced mixing mechanisms are illustrated in figure 2.3. The mixing can be described by a dispersion coefficient; a derivation of the dispersion coefficient from a random-movement model can be found in Fischer et al. (1979).

According to Dronkers (1980, 1982), the strong mixing results in a homogeneous distribution of dissolved substances over the cross-section of the Oosterschelde. Only in the northern branch some vertical stratification (higher salinity near the bottom) may occur near the Volkerak sluices. Even here, this effect is not very pronounced, and a one-dimensional description of the Oosterschelde can be considered adequate. The present schematisation is not strictly one-dimensional, but consists of two one-dimensional branches: it is assumed that each branch is homogeneously mixed across its cross-section; a cross-section cutting through two branches (near the middle compartment) would not be necessarily homogeneously mixed.

One dimensional net flow and dispersion are included in the advection-dispersion equation (Owen, 1984; Dronkers and Zimmerman, 1982):

$$\frac{\delta C}{\delta t} = \frac{1}{A} \frac{\delta}{\delta x} \left( D A \frac{\delta C}{\delta x} - Q C \right) + P \quad (2.2)$$

with: A - cross-section ( $m^2$ )

C - concentration ( $g \cdot m^{-3}$ )

D - dispersion coefficient ( $m^2 \cdot s^{-1}$ )

Q - net flow ( $m^3 \cdot s^{-1}$ )

P - process term; input ( $P > 0$ ), output ( $P < 0$ ) ( $g \cdot m^{-3} \cdot s^{-1}$ )

the P-term includes discharges to and extractions from outside the Oosterschelde -which will be discussed at the end of this chapter- and all biological processes, which are the subject of the other chapters.

O'Kane (1980) discusses the effects of the assumptions that the cross-section A (which depends on the water level) and the dispersion coefficient D (which varies with current velocity) are constant. It appears that the resulting approximation is a very good one, certainly in comparison to the uncertainty in most ecological data.

It may be mentioned that equation (2.2) can also be used to describe the average concentration distribution in the original x-reference frame. This requires averaging the data over a sufficient number of tidal cycles (depending on residence time, see Dronkers, 1982). This approach has not been followed, because the P-term (sources, sinks, processes) must be formulated also in terms of, e.g., a two-week average. It is more convenient for the rest of the model to be able to treat the concentration distribution as an instantaneous distribution, and the processes as instantaneous rates.

Some remarks must be made on the effect of the fixed-volume reference frame on the comparison with field data. The fixed-volume transformation implies that the model describes the concentration in a volume-element that is constantly moving in the fixed-bank reference frame. The locations of concentration measurements are recorded in the fixed-bank reference frame, and therefore must be transformed to be able to compare them with the model results. From water-level recordings and water-level/volume data (Duin,

1986) it is possible to transform fixed-bank coordinates  $x(t)$  to fixed-volume coordinates  $x'(t)$  (see figure 2.4).

The model concerns the average concentration of a variable in a compartment. To enable comparison with field data, the average concentration in a compartment has to be calculated. This is approximated by fitting a line through the  $(x'(t), C(t))$  data, and calculating the expected value at the middle of the compartment. This procedure was chosen in stead of simple averaging because the  $x'$ -values are often not distributed homogeneously over a compartment. For the Oosterschelde data set this work was done by Van Loon (1987b).

Note that the  $x$ - $x'$  transformation of measurements does not imply any judgement on the nature of the transport process involved. For example, encountering at some point of the tidal excursion of a volume-element a high concentration of sand, it is likely that this sand originates from the bottom below it. Yet it is necessary to transform the  $x$ -coordinate of this sand-measurement, because the moving volume element is being modelled, and not because it is assumed that the sand is actually moving through the estuary.

The description in the fixed-volume frame implies that all components in the model that are attached to the bottom (e.g. mussels) or to the bank (e.g. discharges) are oscillating (O'Kane, 1978, 1980). The implications of this for the discharge of freshwater and nutrients are moderate, as lateral inflows are relatively small compared to the inflow at the Volkerak en Kreekrak sluices (endpoints of Northern and Southern branches). There may be some consequences for the interaction between phytoplankton and benthic filterfeeders however. This will be discussed in the zoobenthos chapter.

#### Finite difference scheme

To solve equation (2.2) in practice, the partial differential equation has to be converted into an approximately equivalent ordinary differential equation. A one-dimensional finite-difference approximation to (2.2) usually follows a "forward time centered space" (FTCS) scheme (Owen, 1984; O'Kane, 1980; Helder and Ruurdij, 1982). As has been mentioned, the  $P$ -term is not considered here; the remainder is split into a dispersive part (the first part, involving the  $D.A.\delta C/\delta t$ -term) and an advective part (the second part, involving the  $Q.C$ -term). Further, because of the different volumes of the compartments, it is more convenient to consider changes in total mass of a substance than in concentration: therefore we multiply concentration ( $C$ ) with volume ( $A.\delta x$ ). This gives for the advective transport:

$$T_A = -\delta(Q.C)$$

or, approximated:

$$T_{A\ i} = \frac{1}{2} Q_{i-1} (C_{i-1} + C_i) - \frac{1}{2} Q_i (C_i + C_{i+1}) \quad (2.3)$$

with:  $T_A$  - advective transport ( $g.s^{-1}$ )  
 $i$  - compartment-index  
 $Q$  - net flow ( $m^3.s^{-1}$ )  
 $C$  - concentration ( $g.m^{-3}$ )

For dispersive transport we have to approximate:

$$T_D = \delta \left( D A \frac{\delta C}{\delta x} \right)$$

with:  $T_D$  - dispersive transport ( $\text{g.s}^{-1}$ )

To simplify the finite-difference expression for dispersive transport, first an exchange coefficient is defined:

$$E = \frac{D A}{l} \quad (2.4)$$

with:  $E$  - exchange coefficient ( $\text{m}^3.\text{s}^{-1}$ )  
 $D$  - dispersion coefficient ( $\text{m}^2.\text{s}^{-1}$ )  
 $A$  - average cross-sectional area between two adjacent compartments ( $\text{m}^2$ )  
 $l$  - average distance between midpoints of two adjacent compartments ( $\text{m}$ )

Dispersive transport now can be approximated as:

$$T_{D,i} = E_{i-1} (C_{i-1} - C_i) - E_i (C_i - C_{i+1}) \quad (2.5)$$

The use of relatively large presumably homogeneous compartments causes artificial dispersion as a result of the advective transport: even if dispersion coefficient equals zero, the concentration of some substance is spread out over the neighboring compartments during transport. The FTCS scheme has the advantage over other schemes (e.g., using the concentration in the upstream compartment instead of the average concentration of two adjacent compartments) that artificial dispersion is small (Owen, 1984). In the schematization and time-step used in the present model, artificial dispersion is negligible compared to true dispersion (Bos, 1985).

Some caution should be applied in using (2.3): Owen (1984) points out that if  $C_{i+1} \neq 0$ , and all other  $C_i$ 's are zero, equation 2.3 results in a negative advection term at compartment  $i$ , although the concentration is zero. This problem is dependent on the compartment size  $\Delta x$  and current velocity  $U$ . Thomann (1972) defines the condition:

$$U \Delta x < 2 D \quad (2.6)$$

in words: true dispersion should be large enough to counteract negative advective transport at zero concentration in (2.3). Data from Dronkers, the map in figure 2.2 and equation 2.1, yield approximately  $U = 2.5 \cdot 10^{-3} \text{ m.s}^{-1}$ ,  $\Delta x = 15 \text{ km}$  and  $D = 100 \text{ m}^2.\text{s}^{-1}$ , which fulfills condition 2.6.

Finally, stability of the scheme requires that no more than the total volume of the compartment may be exchanged in one time-step (Thomann, 1972):

$$2 D \Delta t < \Delta x^2 \quad (2.7)$$

This condition has also been fulfilled in the present model.

#### The calculation of flows between the compartments

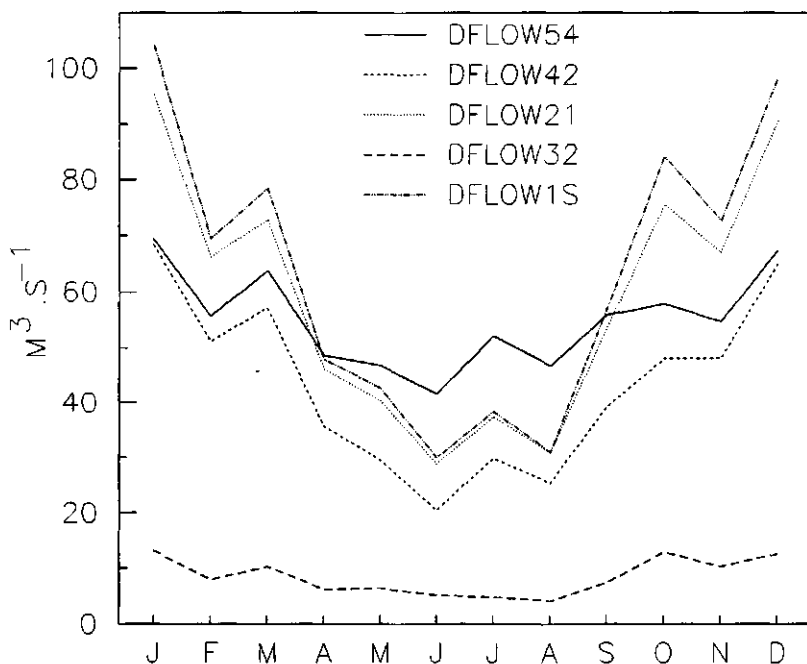
The calculation of the net water flow between adjacent compartments (advective transport;  $Q$ ) is based on calculation of the water balance: the sum of discharges, precipitation, evaporation and extraction.

These data were compiled by Havermans (1983) for the period 1980-1981, and by Van Loon (1987a) for the period 1982-1985. Sources of freshwater are

mainly discharges from the Haringvliet and some small rivers in the northern compartment ( $\pm 66\%$  of total input), precipitation ( $\pm 15\%$ ) and polder water discharges ( $\pm 7\%$ ). Most of this flows to the North Sea, although some water is lost on its way through the Oosterschelde: by evaporation as a main factor ( $\pm 11\%$  of total input), as a result of the operation of locks (6%) and of seeping of the water to the surrounding polders. To reduce the amount of input into the model as much as possible, the following simplifications were made (treating the larger flows more accurately):

- only monthly averaged precipitation and evaporation data were used (KNMI data, station Vlissingen)
- the three-monthly average polder water discharges per unit area of polder appear to be closely correlated ( $r^2 = 0.94$ ) to net precipitation (precipitation minus evaporation). Therefore discharges were calculated from precipitation and evaporation data.
- the seeping of water into the surrounding polders is dependent on the season. This seasonal pattern is similar for all compartments, and can be approximated ( $r^2 = 0.84$ ) by a cosine-function with a period of one year.
- extraction to Haringvliet and discharge from Kreekrak locks is approximately constant.
- salinities of discharges are assumed to be constant.

Remaining input is obtained from linear interpolation of monthly values. The calculated flows between the compartments are presented in figure 2.5.



**Figure 2.5:** Average net flows between compartments in the the Oosterschelde during 1980-1985. DFLOW $ij$  indicates flow from compartment  $i$  to compartment  $j$  (see figure 2.2). DFLOW1S: flow from compartment 1 to sea.



### Boundary conditions

The boundary conditions in the model can be considered as additional compartments "North Sea" and "Volkerak". The difference with inner compartments is that here concentrations are not calculated from model equations but interpolated from measurements. This choice of boundary conditions (prescribed concentration) is known as a Dirichlet-boundary; it is the usual choice for estuarine models (O'Kane, 1978). It may be noted that the use of a fixed-volume reference frame makes it unnecessary to distinguish between ebb and flood boundary-situations, as is the case in a fixed frame (O'Kane, 1978, 1980).

As seaward boundary concentrations the average of the recordings at the stations Schouwen 1 and Schouwen 4 (RIZA sampling grid) was chosen. These stations are situated at the North Sea, approximately 8 kilometers from the storm-surge barrier, see figure 2.1. Due to the sharp seaward increase in depth and width of the tidal channel, the horizontal tide and thus the transformation from fixed-bank to fixed-volume is negligible at this point (Van Loon, pers. com.). Daily values are obtained from monthly measurements by linear interpolation.

A second boundary is situated at the site of the Philipsdam. The compartment to the north of it forms part of the Oosterschelde, but has not been incorporated into the model for the following reasons: due to the low salinity, the biology of this region differs markedly from that in the rest of the Oosterschelde; little biological research has been done here, and the region is no longer part of the Oosterschelde after 1987 anyway.

The concentrations at this second boundary are calculated from fixed-volume transformed data; in the same way as for the other compartments the expected concentration at the middle of the compartment is calculated. This time-series is again interpolated for daily values.

### Estimation of dispersion coefficients

The calculation of the net flows between the compartments and the boundary conditions leaves only the mixing term in the transport equation 2.2. The value of the dispersion coefficient is dependent on basin morphology and tidal characteristics, and can be estimated only approximately on a theoretical basis. In practice, it is estimated from salinity data (Fischer et al., 1979; Dronkers and Zimmerman, 1982; O'Kane 1980)

Previous estimates of dispersion coefficients in the Oosterschelde are available from Dronkers (1980; steady-state model) and Bos (1985; dynamical model). Methods and results of estimating the dispersion coefficients for the present schematization of the Oosterschelde will be discussed in the calibration chapter.

## 2.4 THE TRANSPORT OF SUSPENDED MATTER

### Introduction

In this section an attempt is made to arrive at a transport equation for suspended matter. This transport equation is of importance for the phytoplankton and detritus state variables in the model.

The reason the transport of particulate matter is different from that of dissolved matter stems from the settling and resuspension of particles to- and from the bottom. Suspended, the particle moves with the ebb- or flood current, but lying on the bottom the particle can be considered not to move. This results in a residual transport that may be very different from that of the water. A model developed by Dronkers (1984, 1986a,b) describing this residual transport in terms of residual flows will be briefly discussed.

The first problem with this residual-flow description of particulate transport is to estimate the residual flows of suspended sediment. For this purpose the data by ten Brinke (1987) on suspended sediment concentration measurements and on sedimentation/erosion in the Oosterschelde will be used.

The second problem that will be discussed is the applicability of the transport model for suspended fine sediment to other particulate matter. A comparison between vertical profiles of salinity, chlorophyll, particulate organic carbon (POC; consisting mainly of detritus) and total suspended matter (mainly inorganic) reveals that chlorophyll (phytoplankton) and POC show vertical profiles intermediate between salinity and total suspended matter. The assumption is made that horizontal transport rates for POC and chlorophyll are in a similar way intermediate between salinity and suspended sediment.

Finally, the vertical transport of suspended matter is discussed. During the tidal cycle, large amounts of sediment are settling and being resuspended again. Because of this large exchange between water and bottom, it is assumed in the model that the pools of suspended matter in water and bottom can be considered as a single pool.

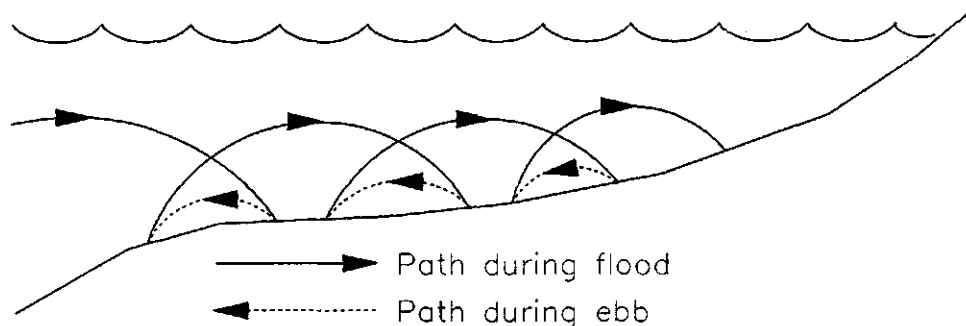
Apart from the fast, short-term exchange of particulate matter between water and bottom, there is a slower, long-term change in the average amount of sediment suspended in the water: in winter the concentration of suspended sediment is approximately two times higher than in summer. This is apparently the result of storms. Because of different process-rates (e.g. detritus decomposition, grazing) in water and bottom, it is necessary to describe the shift in the relative amounts of particulate matter that are suspended and residing in the bottom. This is achieved by using observed suspended matter concentrations in the Oosterschelde.

### Horizontal transport of suspended matter

Dissolved substances are, by definition, moving with the water. Their average net displacement during one tidal cycle is -in the absence of sources and sinks- equal to net water displacement, which is roughly equal to fresh-water inflow. In contrast, particulate matter is not always moving with the water mass: if current velocity drops below a certain level (deposition velocity - Postma, 1967) the particles settle to the bottom. If the current velocity increases again, the sediment is eroded as the critical erosion velocity (Postma, 1967) is reached. This process of settling and resuspension is in general not symmetric (Postma, 1967; Dronkers, 1984, 1986a):

- deposition velocity is lower than critical erosion velocity;
- the particle is transported immediately after erosion, but if the current velocity drops below deposition velocity, it needs some time to reach the bottom;
- current velocity is not a symmetric function of time.

Depending on morphology and tidal characteristics, this asymmetry may result in an import or export of sediment (see figure 2.6). The process is termed tide-induced residual transport. Models describing this process were developed by Postma (1967) and Dronkers (1984, 1986a,b).



**Figure 2.6:** An example of residual transport of a particle as a result of repeated settling and resuspension (From Dronkers, 1986b). In the figure the particle moves landward because its path during flood is longer than its path during ebb tide.

The time-scale of a model describing the fate of a particle during a tidal cycle is not appropriate for its incorporation into the present model: only the resulting net transport over a tidal cycle is of interest in this context. In the models of Postma and Dronkers and also in that of Ebnerh h (1984), the amount of sediment transported is proportional to the sediment concentration in the water column. For this reason the residual net transport can be formulated similar to 2.2:

$$T_{\Delta}' = Q' C \quad (2.8)$$

with:  $T_{\Delta}'$  - residual transport of suspended sediment  
( $\text{g} \cdot \text{s}^{-1}$ )

$Q'$  - apparent flow ( $\text{m}^3 \cdot \text{s}^{-1}$ )

$C$  - susp. sediment concentration ( $\text{g} \cdot \text{m}^{-3}$ )

In this formulation,  $Q'$  is simply a proportionality factor with the dimension of flow ( $\text{m}^3 \cdot \text{s}^{-1}$ ). Instead of a net-flow  $Q$  equal to net water transport however, now an apparent flow  $Q'$  is used, determined by the tide-induced residual transport (Dronkers, 1984). Usually, the terminology will not cause confusion; if necessary the  $Q'$ -term will be indicated as "apparent" or "particulate flow rate" in order to distinguish it from the residual transport of water,  $Q$ .

Apart from the residual transport particulate matter is subject to mixing. This process also can be described in a way similar to that of

dissolved substances by a dispersion coefficient. Strictly, a coefficient  $D'$  for particulate matter differing from  $D$  for dissolved matter should be defined (Dronkers, 1984). However, as has been discussed above, most of the mixing in the Oosterschelde is caused by the tidal movements, or the "gross" displacements. Although the net displacements of dissolved matter and particles may be quite different, their (much larger) gross displacements are very similar, and it seems reasonable to assume that dispersion coefficients are equal too.

#### Estimation of residual flow $Q'$ for suspended sediment

Fixed-point measurements of sediment transport in the Oosterschelde have been made by Elgershuizen (1983) and ten Brinke (1987). This method is based on measurements of suspended sediment concentration and current velocity from several ships on a transect at several depths during a tidal cycle. Multiplying current velocity and concentration, an instantaneous transport flux is obtained, which is summed to obtain net transport during a tidal cycle.

A major problem concerning this method is the fact that gross inflow almost equals gross outflow, which makes estimating the relatively small difference difficult (Cadee, 1982): subtracting two almost identical figures causes a strong magnification of relative error. In fact, the results of Elgershuizen reported by Dronkers (1986) show errors larger than 100 per cent.

An alternative is the use of moving-frame measurements. In this approach, sediment concentration measurements are taken from a vessel moving with the tide during one tidal cycle (Dronkers, 1986; Ten Brinke, 1987). The amount of sediment eroded or sedimented (estimated from concentration measurements) combined with the path that the suspended sediment travels landward or seaward (from current measurements) the net transport can be calculated. This method has the advantage that estimated parameters have a physical interpretation (e.g. erosion velocity, settling rate) which should be more or less constant. This makes it possible to use the estimated parameters in other situations (e.g. using current velocities estimated from models). However, it requires again the subtraction of two nearly identical figures with resulting low accuracy.

A third method to estimate long-term suspended sediment fluxes is to calculate them from bottom soundings. Erosion and sedimentation of the Oosterschelde compartments is recorded by Van den Berg (1986). A large part of the observed sediment transport can be attributed to sand, which makes up on the average 96% of the bottom sediment (Daemen, 1985). Sand transport is mainly the result of movement of sand-"waves" along the bottom of the tidal channels; this transport mechanism is not relevant for the transport of particulate carbon in the water column and will not be discussed here. The sedimentation and erosion of fine sediment can be calculated with the aid of Van den Berg's data by taking bottom composition in the eroding and accumulating areas into account (Ten Brinke, 1987). For this purpose Ten Brinke has used the clay fraction ( $< 16\mu\text{m}$ ) in a large number of sediment cores. From the sedimentation/erosion rates in the different compartments an average sediment flux between the compartments can now be calculated. Uncertainty in these data are mainly caused by uncertainty regarding bottom composition (clay content is recorded in rather wide intervals (e.g. 0-8%, 8-25%, 25-35% and so on), and water content of the sediment has to be estimated also), and to a lesser extent by uncertainty concerning sedimented or eroded volume.

In table 2.1 the calculated fluxes for the three methods are listed.

To estimate total sediment flux through a compartment border from the moving-frame measurements Ten Brinke suggests multiplying the data from the southern channel in the mouth with 1.4, and those from the southern channel in the middle compartment with 1.2.

**Table 2.1:** Estimates of transport of fine suspended sediment in the Oosterschelde. Positive sign: landward flux, negative sign: seaward flux. All data in  $10^6$  kg/tide. The range reported by Dronkers is probably one standard deviation. Ten Brinke gives minimum and maximum values.

**1. fixed-point measurements**

compartments:	flux $10^6$ kg/tide	source of data:
sea-1 (south.channel)	$-1.3 \pm 2.0$	average reported by
2-3	$-0.9 \pm 1.0$	Dronkers (1986a)
sea-1 (south.channel)	-0.96	on 870211;
sea-1 (north.channel)	0.48	on 870428; from
		Ten Brinke (1987)

**2. moving-frame measurements**

sea-1 (south.channel)	-0.2	Dronkers (1986a)
2-3 (main channel)	-0.4	„
sea-1 (north.channel)	0.05	Van Pampus (1987)
1 (south.channel)	$0.38 \pm 0.86$	850418 Ten Brinke (1987)
„	$0.48 \pm 0.42$	860206 „
„	$-0.08 \pm 0.73$	using average parameters
		obtained in 1985
„	$-0.10 \pm 0.26$	860626
„	$-0.34 \pm 0.31$	870226
2 (south.channel)	$-0.06 \pm 0.14$	850509 Ten Brinke (1987)
„	$-0.38 \pm 0.41$	860213 „
„	$0.05 \pm 0.28$	using average parameters
		obtained in 1985
„	$-0.16 \pm 0.17$	860618
3 (main channel)	$-0.22 \pm 0.25$	850606 Ten Brinke (1987)
„	$0.02 \pm 0.05$	860220 „
„	$-0.04 \pm 0.11$	using average parameters
		obtained in 1985
„	$-0.12 \pm 0.19$	860611
„	$-0.44 \pm 0.34$	870219
4 (main channel)	$-0.84 \pm 0.46$	870106 Ten Brinke (1987)
„	$-0.04 \pm 0.10$	870428

**3. from sedimentation/erosion data:**

sea-1	$-0.99 \pm 0.72$	average 1960-1980, Ten
1-2	$-0.75 \pm 0.57$	Brinke (1987)
2-3	$0.03 \pm 0.01$	„
2-4	$0.41 \pm 0.30$	„
4-5	$0.11 \pm 0.06$	Ten Brinke (pers.comm.)

Although the sedimentation/erosion data form the most reliable set, it should be noted that these long-term trends are possibly not representative for the normal situation in the Oosterschelde. A large fraction of the transport of sediment occurs during a few severe storms (Dronkers, 1986b; Kohsiek et al., 1987); it is therefore possible that some region is continuously importing fine sediment during the year, which is eroded in one or two storms: such a continuous import could feed the ecosystem during the growing season. Obviously, the situation with a continuous export is quite different from an ecosystem viewpoint: therefore the applicability of the sedimentation/erosion data for the present purpose is uncertain in itself, although the data are the most reliable.

Therefore, the ranges for the transport flux to be used in the model are based on the results of the direct transport measurements; these ranges are wider than the ranges obtained from sedimentation/erosion data. A summary of the ranges in table 2.1 is approximately:

from	to	flux ( $10^6$ kg/tide)
sea	1	$-0.5 \pm 1.2$
1	2	$-0.3 \pm 0.7$
2	3	$-0.3 \pm 0.4$
2	4	$-0.6 \pm 0.7$
4	5	$0.1 \pm 0.1$

With the aid of these flux-estimates the apparent flow  $Q'$  in equation 2.8 may be estimated. It should be noted that the data in table 2.1 concern total transport; i.e. both the dispersive and the advective ( $Q'$ ) components (equation 2.2). The dispersive transport causes an import of sediment, as the suspended sediment concentration at sea is on the average higher than in the Oosterschelde. Dispersion coefficients for the present model have been estimated on the basis of salinity data by Van Loon (1987a); these estimates are discussed in detail in chapter 10. Substitution of the average concentration gradient in equation 2.5 yields the dispersive flux, which can be subtracted from the total fluxes above; division by average concentration yields the apparent flow rates  $Q'$  (table 2.2).

**Table 2.2:** estimation of apparent flow rates  $Q'$  calculated from advective flux minus dispersive flux divided by average concentration at compartment border; range indicates maximum and minimum values used in the sensitivity analysis of the model.

from	to	disp.flux (kg/s)	adv.flux (kg/s)	avg. conc. (g/m <sup>3</sup> )	$Q'$ (10 <sup>3</sup> m <sup>3</sup> /s)
sea	1	3.42	-11.2	27.5	-0.53 ± 0.98
1	2	1.35	-6.7	21.0	-0.38 ± 0.75
2	3	0.07	-6.7	19.6	-0.35 ± 0.46
2	4	0.07	-13.4	19.6	-0.68 ± 0.80
4	5	0.28	2.2	15.9	0.12 ± 0.14

#### Horizontal transport of particulate carbon and chlorophyll

The discussion in the preceding paragraph was concerned with the transport of all suspended materials. Particulate organic carbon (POC), including algae (identified with Chlorophyll) form small ( $\pm 5\%$  and  $\pm 1\%$ , respectively) but important fractions of the seston, and may show a different behavior. The problems in estimating total suspended matter fluxes from field measurements make clear that it is impossible to answer from direct flux measurements the more detailed question how different fractions of this flux behave. The non-conservativity of both fractions makes the calculation of fluxes from erosion/sedimentation budgets impossible. Therefore, indirect evidence based on vertical distributions of the two fractions will be used.

It appears that salinity is almost perfectly mixed over the water column in the Oosterschelde, but seston concentration increases twofold from surface to bottom. This increase apparently is the result of the sinking and resuspension of the particulate matter. The profiles of POC and Chlorophyll are intermediate between those of salinity and seston. As the settling and resuspension of particulate matter are the underlying cause of both vertical profiles and horizontal transport mechanism, the assumption will be made that the transport rate  $Q'$  of detritus and Chlorophyll is in a similar way intermediate between those of salinity and seston.

A data set on the vertical distribution of the three seston components is available from the routine sampling stations P1 to P5 (see figure 2.1). During the period 1980-1982 samples were collected weekly at three depths simultaneously: at the surface, at 60% of total depth, and at 1 meter above the bottom. Absolute depth values range from 10m (P2) to 30 m (P5). Additional data are provided by Ten Brinke (1987), who compares surface to bottom concentrations of total suspended sediment and POC obtained during the moving-frame transport measurements.

Table 2.3: Relative increase in concentration from surface to 60% of total depth and from surface to bottom with 95% confidence interval.

variable	to 60%:	to bottom:
salinity	1.010 ± 0.006	1.009 ± 0.002
seston*	1.613 ± 0.088	1.968 ± 0.143
**		1.92 ± 0.23
POC *	1.301 ± 0.050	1.486 ± 0.070
**		1.37 ± 0.11
Chlorophyll	1.146 ± 0.040	1.190 ± 0.056
* routine sampling stations ** average values from ten Brinke (1987)		

There were no significant relations found between relative concentration increase and either location (depth) or season; this may be due to the large variance of the data. The vertical increase in POC and Chlorophyll appears to be substantially less than that of total seston. A simple model to deal with these differences and their influence on horizontal transport is to define a fraction (x) of every seston component which behaves as dissolved substances, and a fraction (1-x) which has the same vertical distribution as total seston. An identical vertical distribution means an identical settling velocity, which is in its turn is closely related to the tide-induced residual transport of the particles.

For a seston component y now the flow term  $Q_y$  can be calculated by taking the weighted average of seston-like behavior (the  $Q'$ -term from the preceding section) and dissolved-like behavior (the  $Q$ -term from the dissolved transport model):

$$Q_y = (1-x) Q' + x Q \quad (2.9)$$

The fraction x may be calculated by assuming an increase towards the bottom of 0% in x and 97% in (1-x). Using the confidence intervals in table 2.3 yields the following estimates of x:

"dissolved fraction" x, calculated from vertical profiles with 95% confidence intervals derived from table 2.3

Chlorophyll	0.79 ± 0.09
POC	0.48 ± 0.15

Apart from transport-calculations the inhomogeneous distribution of detritus and chlorophyll has relevance for the biological submodels. For example, the column-average concentration of detritus available for zooplankton grazing is approximately 25 per cent higher than surface values. However, because most measurements concern surface concentrations, these



will be presented as model-output. If necessary, bottom- or water-column average concentrations can be calculated from these using the relations in table 2.3.

#### Vertical transport of particulate matter

In the Oosterschelde there is a large exchange of mass between particulate matter in suspension and on the bottom. In this paragraph, an equilibrium formulation for this exchange, and the shift of the equilibrium due to the seasonal (wind) influences will be discussed. This shift is of ecological interest because different process-rates (grazing, mineralization) operate on the suspended and bottom fractions of the organic seston components. The main difficulty in this paragraph is estimation of the total amount of bottom sediment involved in the exchange process.

Time series of measurements of suspended particulate matter concentrations, both *in situ* (Dronkers, 1986a, Ten Brinke, 1987) and in settling-tubes (Elgershuizen, 1983) show that a large portion (40-80 per cent) of the suspended particulate matter settles from the water column and is resuspended again during each tidal cycle. This is confirmed by *in situ* measurements of the effective settling velocity (Elgershuizen, 1983) and recent measurements of settling velocities in settling-tubes by Van Geldermalsen (pers. comm.), which show velocities of 1 to 4 mm.s<sup>-1</sup>, or 80-350 m.day<sup>-1</sup>.

As has been mentioned, this relatively rapid settling and resuspension of particulate matter makes it inconvenient to incorporate these processes explicitly into the present simulation model which has a time scale of days. In fact, this fast exchange at a time-scale of hours causes the bottom- and suspended pools of two substances to be in mutual equilibrium on the time scale of interest. Therefore, in the present model the state variables that make up the suspended matter (inorganic silt, detritus and phytoplankton) are modelled as single pools, containing both bottom- and suspended fractions.

The incorporation of a bottom compartment into the model raises the question which part of the bottom can be considered part of the ecosystem. A maximum for the pool of particulate matter would be almost infinite, if the entire sediment thickness under unit area of Oosterschelde would be taken into account. A minimum value would be the maximum amount of particulate matter that can be found suspended in the water column: obviously, the total amount should be at least as large as the suspended fraction.

By means of this minimum value for particulate matter per square meter, a rough estimation of the total particulate pool will be made. From this estimated total amount and the observed concentrations in the Oosterschelde the fraction in suspension at some time can be derived. This distribution of suspended and settled fractions will also be applied to the "particulate part" of the partly dissolved/partly particulate substances POC and Chlorophyll.

For inorganic seston (silt) two fractions are defined:

$$\text{Silt}_{\text{water}} + \text{Silt}_{\text{bottom}} = \text{Silt}_{\text{total}} \quad (\text{g.m}^{-2}) \quad (2.10)$$

The total amount of silt is assumed to have a constant value in the model. This implies that a decrease in the total amount of silt in some compartment by export is compensated by a downward shift in the position of the bottom compartment; in the case of sedimentation the bottom layer shifts upwards. This is equivalent to the assumption that the thickness of the ecologically relevant bottom-layer is not influenced by a possible import or export into/from a compartment.

The pool in the water can be calculated from the surface concentration, taking into account water depth, and the approximately 2-fold increase in concentration toward the bottom (see previous paragraph). Because  $Silt_{bottom}$  in (2.10) can not be negative, this maximum amount of suspended sediment in the water represents a lower bound for the total amount of silt. Maximum concentrations of seston (consisting mainly of silt) during the period 1972-1985, and the resulting minima for  $Silt_{total}$  are given in table 2.4.

**Table 2.4:** Average and maximum suspended matter concentrations during 1972-1985, average depth, calculated maximum amount of suspended matter, assumed total amount in model ( $Silt_{total}$ ) and the average thickness of the bottom-layer resulting from this assumed total amount.

comp.	concentration ( $g \cdot m^{-3}$ )		depth (m)	max. ( $g \cdot m^{-2}$ )	model total ( $g \cdot m^{-2}$ )	bottom layer (cm)
	avg.	max.				
1	23.1	55.6	12.2	970	1000	1.15
2	19.0	42.7	10.4	635	660	0.73
3	20.2	56.1	3.9	301	330	0.38
4	19.0	52.8	8.2	604	625	0.78

To give a more tangible idea of the effect of the model assumptions, the average thickness of the bottom layer that is assumed to constitute part of the ecosystem may be calculated. For this purpose the values of  $Silt_{total}$  may be compared with the average amount suspended in the water. The remaining fraction of the fine sediment in this average situation may be converted to a bottom thickness by assuming 4 per cent fine particles in bottom sediments (Daemen and De Leeuw-Vereecken, 1985) and a bulk density of (wet) sediment of  $1.3 \text{ kg} \cdot l^{-1}$  (Dronkers, 1986a). The resulting average sediment-layers in the four compartments are listed in table 2.4. The average thickness of the sediment layer that is treated in the model as being in equilibrium with the suspended sediment ranges from 3 mm in the sheltered compartment 3 (east) to 1.2 cm in the mouth of the Oosterschelde (compartment 1). It seems that the definition of a single bottom-compartment is very uncertain. A more realistic model would probably include a multi-layered bottom, in which exchange with the water column decreases with depth, from very fast (equilibrium) at the surface to slow (days) at several centimeters depth to very slow (years, centuries) at a depth of half a meter or more. However, no information on these vertical exchange rates of sediment in the Oosterschelde (or, in fact, in any other tidal system) is available. The present model can be regarded as the simplest possible approximation to a bottom-exchange model: the upper part of the bottom is lumped with the ecologically most important- "fast" top layer and is assigned an "infinite" exchange rate, the lower, slower-exchanged parts of the bottom are lumped with the deep bottom and assigned an exchange rate of zero, or stated otherwise: simply excluded from the model.

In table 2.4 it was illustrated that the average amount of suspended sediment is approximately half the maximum. The minimum concentration in its turn is approximately half the average concentration. The maxima and minima

show a seasonal pattern: low in summer and high in winter. This implies that seasonally a different fraction of the total particulate matter is suspended in the water column.

For the calculation of the suspended fractions of the organic seston components in relation to the inorganic seston (silt) behavior, the same approach will be used as for the calculation of the different horizontal transport rates. The ratio between surface concentration and total amount of silt is called E:

$$E = \frac{\text{Silt}_{\text{surface}}}{\text{Silt}_{\text{total}}} \quad (2.11)$$

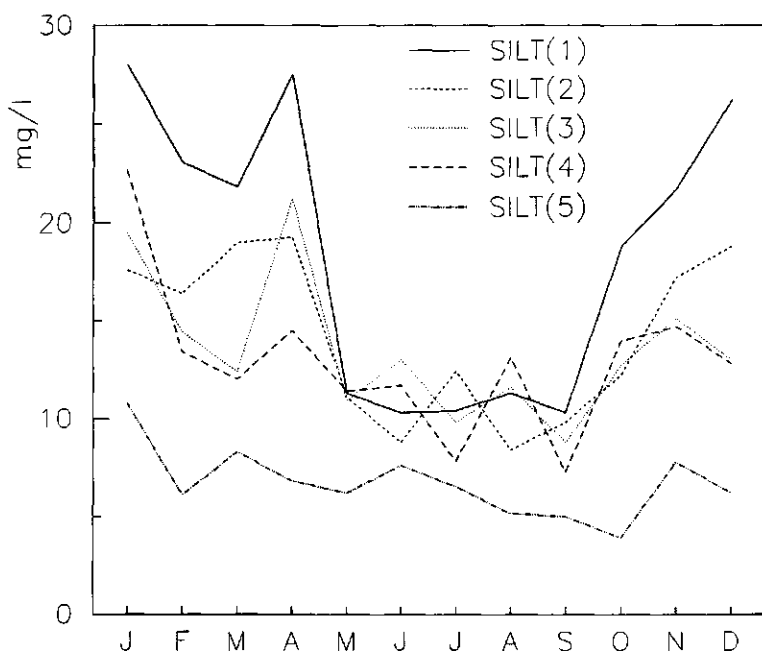
with E - expressed in  $\text{m}^{-1}$   
 $\text{Silt}_{\text{total}}$  in  $\text{g} \cdot \text{m}^{-2}$   
 $\text{Silt}_{\text{surface}}$  in  $\text{g} \cdot \text{m}^{-3}$

It was assumed previously that the organic seston components show partly "dissolved behavior" (fraction x) and partly "silt-like" behavior (fraction 1-x). In this context the same fractions will be used also. It is assumed that, for example, detritus has a fraction ( $\pm 50\%$ , see previous section) which is homogeneously distributed over the water column, and a fraction ( $\pm 50\%$ ) which has a relative distribution over water-column and bottom comparable to silt. Then the relation between total amount of some organic seston component  $Y_{\text{total}}$  and surface concentration  $Y_{\text{surface}}$  may be written as:

$$Y_{\text{total}} = (x Z + (1 - x) / E) Y_{\text{surface}} \quad (2.12)$$

with: x - "dissolved-like" fraction of Y  
 Z - average depth (m)  
 $Y_{\text{surface}}$  - surface concentration of Y ( $\text{g} \cdot \text{m}^{-3}$ )  
 $Y_{\text{total}}$  - total amount of Y in  $\text{g} \cdot \text{m}^{-2}$   
 E - defined in equation 2.11; in  $\text{m}^{-1}$

The coefficient E in equation 2.11 has not been modelled explicitly: this would have required a detailed physical sub-model, dealing with wind speed and -direction in relation to wave height, influence of morphology, North-Sea waves, and so on. Instead, the observed concentrations of silt have been used in combination with the estimated  $\text{Silt}_{\text{total}}$  to calculate E. The measured concentrations are presented in figure 2.7.



**Figure 2.7:** Measured surface concentrations of inorganic suspended sediment in the Oosterschelde compartments 1-5 (see fig. 2.2) averaged over 1980-1985.

The export of sediment from some compartments implies erosion of the bottom: the bottom layer will shift down to some extent. As a result of this shift, POC from deeper layers will enter the bottom/water system. The question arises whether this supply of detritus to the system plays a role in the food chain. At the moment, this has to be discussed as a theoretical question, because data on the nutritive value of this old POC are lacking. However, it seems reasonable to assume that it has none: the eroding POC was deposited centuries ago; if it would be biodegradable it seems strange that it still exists at all.

The assumption of refractory POC in the old bottom-deposits is modelled as follows. In the case of erosion, a fixed amount of refractory POC is added to the system per unit of silt eroded (parameter QPOCSEQ); this ratio is approximately 5% (range 0.1-10%), reflecting the approximate POC:silt ratio in the Oosterschelde. For reasons of symmetry, only refractory POC is deposited in case of sedimentation. In the latter case the amount is determined by the refractory POC:silt ratio as calculated by the model. Other state variables are neither permanently buried nor eroded. In order to be able to investigate the effect of the assumption that the eroded POC is refractory, a parameter SEDLABQ is introduced, which gives the labile fraction of eroded POC; the value of this parameter is normally set to zero.

## 2.5 Summary of model assumptions

The transport model describes transport of dissolved and particulate substances in a one-dimensional four-compartment model of the Oosterschelde. The concentrations to be modelled are the average surface concentrations in a compartment. A 'fixed upstream volume' coordinate system is used.

The transports of dissolved substances are calculated using a FTCS finite difference scheme. As a result of the use of the constant upstream volume coordinate system only net flows between the compartments are needed. These flows are calculated from the water balances of the compartments.

Dispersion coefficients describing longitudinal mixing are estimated using salinity data. Transversal mixing is assumed to be sufficient for a one-dimensional approach.

Horizontal advective transport of inorganic particulate matter ("silt") is described by an apparent flow rate  $Q'$ , similar to the description of the advective flow of dissolved substances. The value of  $Q'$  is estimated from sediment transport measurements. The dispersive transport of suspended matter is assumed to be equal to that of dissolved substances.

The advective transport of particulate organic carbon (POC) and chlorophyll are intermediate between those of suspended sediment ( $Q'$ ) and net water flow ( $Q$ ). This formulation is based on vertical concentration gradients of POC and chlorophyll, which are in a similar way intermediate between the vertical profiles of salinity and of suspended sediment.

A bottom compartment representing the top layer of the sediment is defined. It is assumed that the suspended- and bottom state variables in the model form a single pool of particulate matter: suspended and bottom fractions are in equilibrium on the time scale of days. The silt concentration measurements at the surface are used to estimate the equilibrium coefficient by assuming a fixed total amount of silt in bottom plus water column. The equilibrium coefficient is used to calculate the fraction of an organic seston component residing in the bottom.

The concentration of refractory POC is determined by the erosion or sedimentation as calculated from silt transport. In case of erosion, refractory POC is introduced into the system; in case of sedimentation it is buried. Other state variables are neither eroded nor deposited below the approximately 1 cm thick bottom compartment.

### 3 THE PHYTOPLANKTON MODEL

#### 3.1 Introduction

A model of phytoplankton dynamics in the Oosterschelde forms an important part of the present Oosterschelde model: phytoplankton is the main food source of the macrobenthic filterfeeders (Smaal et al., 1987) and phytoplankton production is the primary source of the detritus (Klepper & V/d Kamer 1988), which forms an additional food-supply for the filterfeeders. In this chapter the supply of phytoplankton to the ecosystem is described; the transport of phytoplankton has been described in the previous chapter, and the demand will be described in the chapters on grazing by zooplankton and filterfeeders.

The photosynthetic rate of phytoplankton is determined by light, nutrient concentrations and temperature. The first factor differs from the latter two in that the changes in light-intensity are much more rapid, mainly as a result of the mixing of the phytoplankton through the vertical light-gradient in the water column. The influence of light on photosynthesis is modelled following the approach of Eilers and Peeters (1981a,b; 1988). Their model has been used to estimate the effects of the light-fluctuations (too rapid to be incorporated directly into the model) on the daily integrated photosynthesis. In the Oosterschelde, the factors temperature and nutrient concentrations change slower than the time-step of the model; they have been modelled by changing the characteristics of the photosynthesis/light response. This chapter first discusses their effects on photosynthesis separately, followed by a discussion of their interactions.

The photosynthetic rate of the phytoplankton is also called the gross production rate; the growth rate or net production rate of the phytoplankton is equal to the photosynthetic rate minus respiration and excretion rates. Excretion rate appears to increase with the nutrient-limitation of the phytoplankton. Respiration rate is a function of growth rate, showing a minimum at zero growth rate (called maintenance respiration), and a respiration associated with biosynthesis. Maintenance respiration is dependent on environmental conditions, the fraction of photosynthesis respired in biosynthesis is a function of the biochemical composition of the algae.

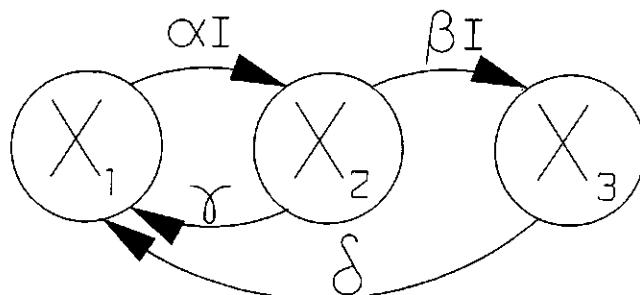
An important aspect of the present model is the treatment of chlorophyll content. The chlorophyll content has a direct influence on phytoplankton dynamics because it determines the capacity to capture light; furthermore, most field measurements of algal biomass are obtained indirectly by measuring chlorophyll concentration. In the present model a dynamic description of chlorophyll content is included.

#### 3.2 The Eilers/Peeters model of photosynthesis

In this section a brief description of a model relating photosynthesis to light intensity is given; a more detailed description of the model, and especially of the underlying physiological processes is given by Eilers and Peeters (1981a,b; 1988). The model may be characterized by three parameters describing the steady-state production vs. light curve: the initial slope of the curve, i.e. the response under light-limited conditions; the optimal light-intensity and the maximal production rate, i.e. at optimal light intensity. Changes in light intensity occur much more rapidly than those in temperature or nutrient concentrations; the first step in the modelling of photosynthesis in the Oosterschelde is therefore to integrate the photosynthetic response to a daily rate. For the present, it is assumed that the steady-state characteristics of the phytoplankton light-response are fixed;

in subsequent sections the effect of environmental conditions on the parameters in the expression for daily photosynthesis will be discussed.

In the Eilers/Peeters model it is assumed that the photosynthetic units may exist in three states: the variables  $X_{1-3}$  represent the fractions in each state ( $X_1 + X_2 + X_3 = 1$ ).  $X_1$  is the fraction in resting condition,  $X_2$  is the fraction in activated condition, and  $X_3$  is the fraction in inactivated condition. The possible transactions between the states are illustrated in figure 3.1: activation rate ( $1 \rightarrow 2$ ) is proportional to light intensity; return rate to  $X_1$  is independent of light intensity; from  $X_2$ , inactivation may occur, with a rate that is proportional to light intensity; the return from  $X_3$  to  $X_1$  is again independent of light intensity. It is assumed that carbon fixation is proportional to the rate of transition from  $X_2$  to  $X_1$ .



**Figure 3.1:** The state transitions of the photosynthetic units under the influence of light.  $X_1$ : resting state,  $X_2$ : activated state,  $X_3$ : inactivated state.

From this description the following differential equations relating the states  $X_{1-3}$  to light intensity evolve:

$$\begin{aligned} dX_1/dt &= -\alpha I X_1 + \gamma X_2 + \delta X_3 \\ dX_2/dt &= \alpha I X_1 - (\gamma + \beta I) X_2 \\ dX_3/dt &= \beta I X_2 - \delta X_3 \end{aligned} \quad (3.1)$$

After a long exposure to a constant light intensity, a steady state is reached. It was assumed that photosynthesis is proportional to  $X_2$ , which yields:

$$P = \frac{k \alpha \delta I}{\alpha \beta I^2 + (\alpha + \beta) \delta I + \gamma \delta} \quad (3.2')$$

reparameterization yields:

$$P = \frac{I}{a I^2 + b I + c} \quad (3.2)$$

From the model equations (3.1) it is clear that both the original parameters and those in expression (3.2) should be positive.

The shape of the family of curves described by (3.2) is illustrated in figure 3.2; the curves may be characterized by the initial slope of the curve ( $s$ ), the maximal photosynthesis ( $P_{max}$ ), which is obtained at the

optimal light intensity ( $I_{opt}$ ). These characteristics of the steady state response are also used to characterize the photosynthetic response in general, but it should be noted that the transient response may show e.g. a different value for maximal production rate than  $P_{max}$ . The optimal light intensity can be expressed as:

$$I_{opt} = \sqrt{c/a} = \sqrt{\frac{\delta \gamma}{\alpha \beta}} \quad (3.3)$$

A dimensionless expression for the steady state curve may be obtained by defining:

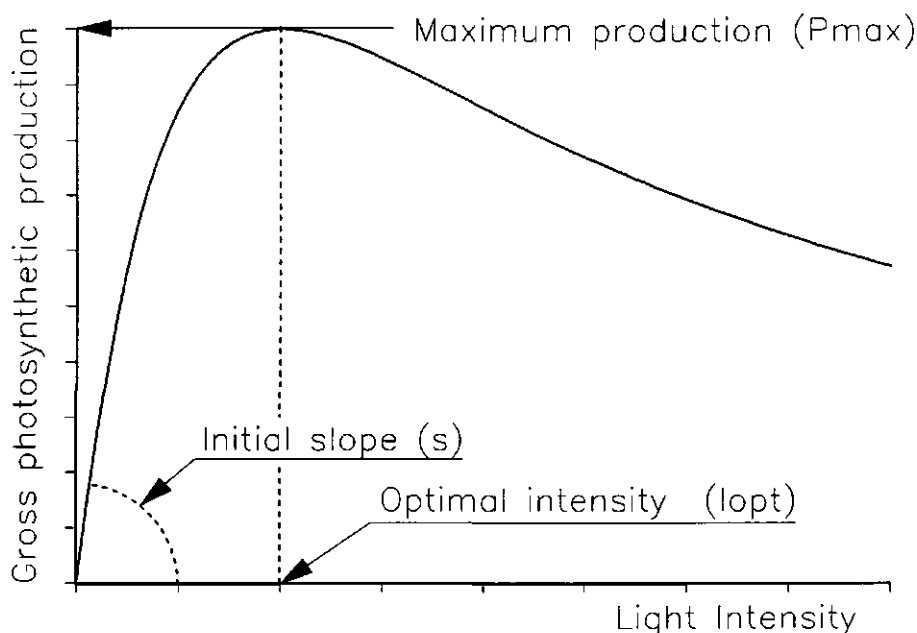
$$U = I / I_{opt}$$

$$e = P / P_{max}$$

$$W = b / \sqrt{ac}$$

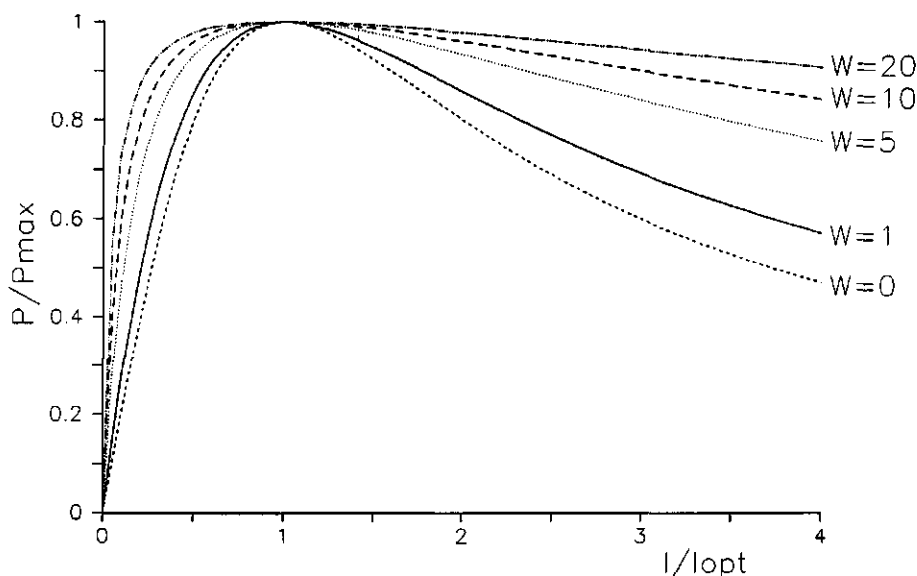
$$e = \frac{U (W + 2)}{U^2 + W U + 1} \quad (3.4)$$

The parameter  $W$  characterizes the shape of the production-curve; several values for  $W$  are illustrated in figure 3.3.



**Figure 3.2:** Steady-state photosynthesis/light curve illustrating the three photosynthetic parameters: initial slope ( $s$ ), maximal production rate ( $P_{max}$ ) and optimal light intensity ( $I_{opt}$ ).

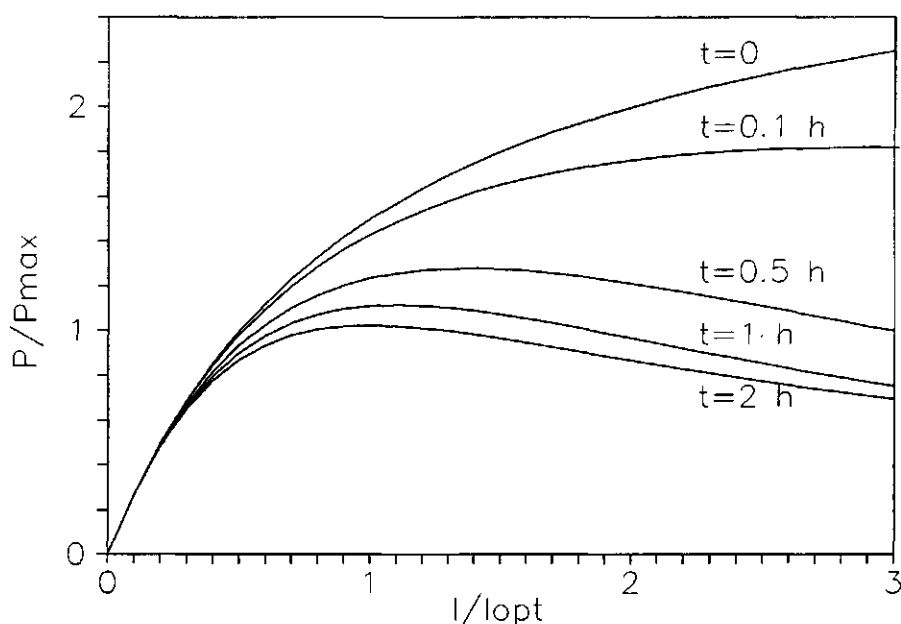




**Figure 3.3:** Dimensionless form of the steady-state photosynthesis/light curve illustrating the shape-parameter  $W$ .

### 3.3: Calculation of daily and vertically integrated photosynthesis

In the application of the Eilers/Peeters model to the Oosterschelde, it should be taken into account that the photosynthetic response of phytoplankton is a function of time: at light intensities above  $I_{opt}$  the initial production decreases rapidly and reaches a steady-state after some hours (MacCaull and Platt, 1977; Belay and Fogg, 1978; Parsons et al., 1977; Belay, 1981; Powles and Björkman, 1982; Vincent et al., 1984; Vermij et al., 1985; Neale and Richerson, 1987); this process is known as photo-inhibition (see figure 3.4). After several hours in the dark the cells recover from the effect of exposure.



**Figure 3.4:** The time-course of photosynthetic response curves after transition from the dark. The parameters used for this curve represent typical values for shape of the curve (Oosterschelde data) and time-dependence (literature data). From Klepper et al., 1987.

Vertical mixing of the water column causes light-to-dark transitions of the phytoplankton with a times-scale of minutes (Klepper et al., 1987). As a result of this mixing the production at the surface is higher due to a decrease of the effect of photoinhibition. Although the production in deeper layers is lower as a result of the arrival of inhibited cells, the net effect of mixing for the whole column is positive: most of the production takes place in the surface layers. The effect of mixing on productivity depends on several variables, of which the surface light intensity and the shape of the steady-state production curve are the most important (Gallegos and Platt, 1985; Klepper et al., 1987). In the Oosterschelde, the calculated increase due to mixing is usually negligible, but may sometimes be as high as 40 to 60% (Klepper et al., 1987). The largest increase coincides with a combination of high surface light intensities and a sharply peaked production-curve (low value of  $W$ ). Although these results have not been confirmed by actual measurements in the Oosterschelde, literature reports on experiments with fluctuating light show the same range of values from negligible (Jewson and Wood, 1975; Marra and Heinemann, 1982) to 50-90% (Marra, 1978b; Gallegos and Platt, 1982). Although both this range of values and the most important parameters (shape of production curve, surface light intensity) coincide with model predictions, this comparison cannot be regarded as an actual model-validation, because the published data all lack one or more of the

required input-parameters for the model, which makes a rigorous comparison between calculated and observed data impossible.

The integration of photosynthesis over the water column of the Oosterschelde has to take into account the decrease in light intensity with depth and basin morphology. The decrease in light intensity may be approximately described by an exponential curve:

$$I(Z) = I(0) \exp (-K*Z) \quad (3.5)$$

with  $Z$  - depth (m)

$I(Z)$  - light intensity at depth  $Z$  ( $W/m^2$ )

$I(0)$  - light intensity at the surface ( $W/m^2$ )

$K$  - extinction coefficient ( $m^{-1}$ )

Basin morphology in the Oosterschelde is characterized by extensive shallow areas and some deep channels (Duin, 1986). For the purpose of the present calculations, the situation may be described by an exponential curve (Klepper et al., 1987):

$$A(Z) = A(0) \exp (-C*Z) \quad (3.6a)$$

with  $A(Z)$  - horizontal area of water surface at depth  $Z$

$C$  - coefficient ( $m^{-1}$ )

Integrating this function over depth gives the volume of a compartment; because the maximal depth in a compartment is considerably (5-10 times) greater than average depth, it makes little difference whether we integrate to the actual maximal depth or to infinite depth. Therefore, we have as a good approximation:

$$C = 1/Z_{avg} \quad (3.6b)$$

with  $Z_{avg}$  - average depth (m)

Extinction and basin morphology interact with mixing and surface light intensity in the determination of column averaged production. For example, in shallow areas where a substantial part of the surface light reaches the bottom, the effect of mixing will be different from that in deep channels where the light intensity at the bottom is effectively zero.

The general case of the dynamic Eilers-Peeters model (equations 3.1) applied to the Oosterschelde does not lead to an analytic solution but has been solved numerically (Klepper et al., 1987). Incorporation of the results of these calculations into the present model has been achieved by varying the parameters of the model independently and fitting an empirical relation through the calculated photosynthetic rates. The following range of parameter-values was used, coinciding with observed ranges in the Oosterschelde:

nominal:	range	dimension	meaning in model
W = 4	0 - 15	( )	shape of production curve
K = 1	0.5 - 2	(m <sup>-1</sup> )	extinction coefficient
U <sub>avg</sub> = 0.75	0.25 - 3	( )	average surface intensity in units of I <sub>opt</sub>
Z <sub>avg</sub> = 8	3 - 12	(m)	average depth

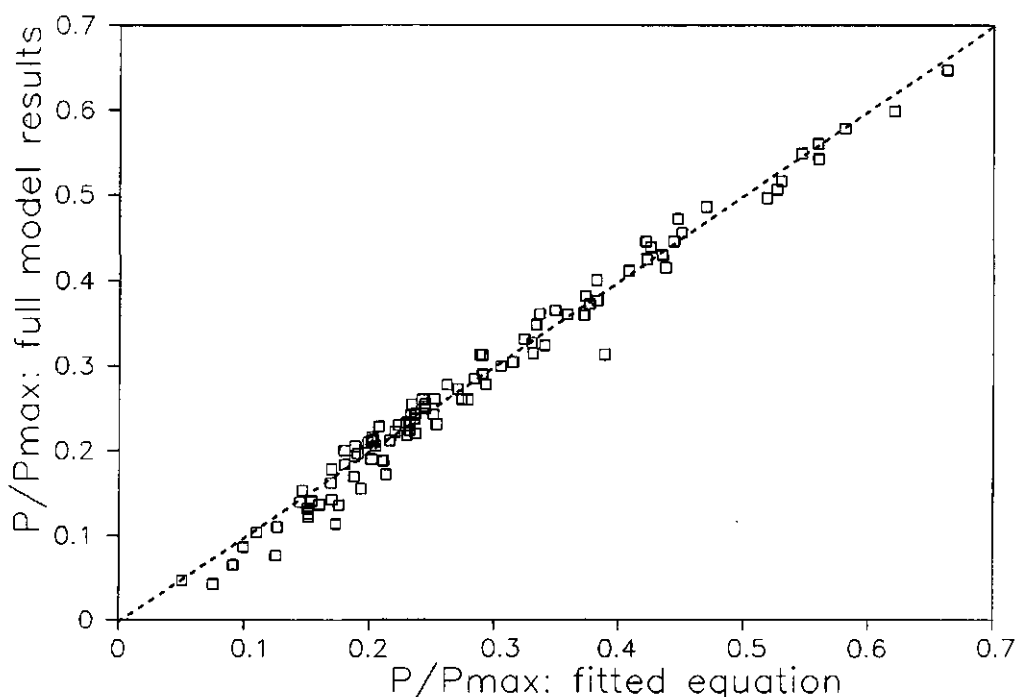
the following equation was fitted with an r<sup>2</sup> of 0.95:

$$Pg = D1 * Pmax * F1 \quad (3.7a)$$

$$F1 = \frac{4.66 * (1 - \exp(-2.15 * U_{avg})) * (W + 2)}{(K + 2.55/Z_{avg}) * (W + 4.95) * Z_{avg}} \quad (3.7b)$$

with: Pg - daily integrated gross primary production per  
unit volume per unit biomass (day<sup>-1</sup>)  
D1 - daylength in hours per day  
Pmax - maximal production rate in h<sup>-1</sup>  
F1 - dimensionless reduction function  
U<sub>avg</sub> - average surface irradiance in units of I<sub>opt</sub>  
W - shape-parameter of production-curve (see fig. 3.4)  
K - light extinction coefficient (eq. 3.5)  
Z<sub>avg</sub> - average depth (m)

The fit between numerical results and expression 3.7 is illustrated in figure 3.5.



**Figure 3.5:** Results of Eilers/Peeters model (expressed per unit of  $P_{max}$ ) for 100 randomly chosen parameter-sets within ranges representing Oosterschelde conditions compared with the dimensionless reduction function in expression 3.7.  $r^2 = 0.95$

### 3.4 The influence of environmental factors on photosynthetic parameters

In the previous section, attention was focused on processes with a time-scale shorter than one day. In that case it can be assumed that both temperature and nutrients as well as the parameters characterizing the steady-state photosynthetic curve are constant. In this paragraph the photosynthetic parameters will be considered as functions of (slowly changing) environmental conditions. The response to these conditions will first be focused on a single factor before discussing their interactions.

#### Maximum production rate: temperature

In many modelling studies (e.g. Platt et al., 1977; Kremer and Nixon, 1978; Smith, 1980; De Vries, 1987) the influence of temperature on maximum production rate is derived from the relation between growth rate and temperature as reviewed by Eppley (1972). Phytoplankton growth rate can be conveniently measured both in continuous- and batch-cultures. For individual species the relation between growth rate and temperature can be described by an initial increase, an optimum and a sharp drop at high temperatures (figure 3.6). For a mixed assemblages of species and a slow change in temperature, a much simpler formulation results from the displacement of low-temperature species by high-temperature species with increasing temperatures (see figure 3.6). As the present model is not concerned with individual species and

temperature changes only slowly in a marine environment, the simple curve of the mixed population may be used. Eppley collected a large number of growth rate measurements and fitted an upper bound to them, thus correcting for the response of individual species and situations where light or nutrients are not optimal.

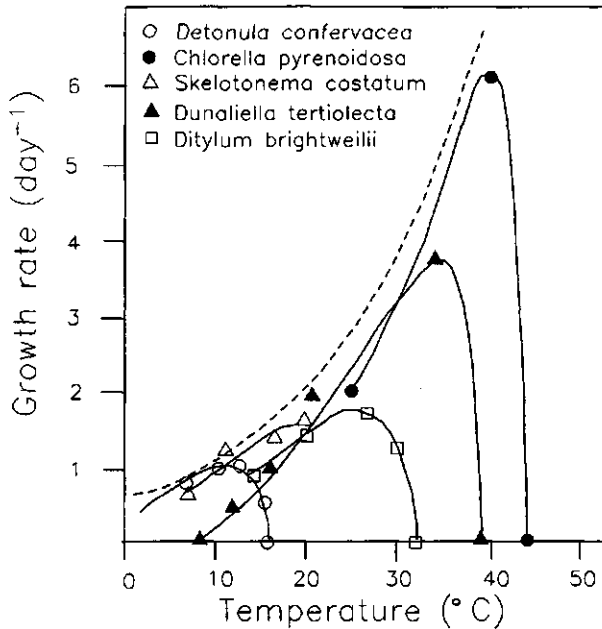


Figure 3.6: (from Eppley, 1972) The relation between temperature and growth rate for five species of algae: for slowly changing temperatures, a mixed population reacts according to the upper drawn line.

The resulting curve can be described as:

$$\text{Pnt}(T) = \text{Pnt}(10) * \exp((T-10)*T\text{coef}) \quad (3.8)$$

with  $T$  - temperature in °C

$\text{Pnt}(T)$  - net production in  $\text{d}^{-1}$  at temperature  $T$

$T\text{coef}$  - temperature coefficient ( $^{\circ}\text{C}^{-1}$ )

$T\text{coef}$  can be converted to a  $Q_{10}$  (relative increase in  $\text{Pnt}$  with a 10 °C increase in temperature) with the expression:

$$Q_{10} = \exp(10 * T\text{coef}) \quad (3.9)$$

Eppley reports a  $\text{Pnt}(10)$  of 1.11 ( $\text{d}^{-1}$ ), and a  $T\text{coef}$  of 0.063 ( $^{\circ}\text{C}^{-1}$ ). With the use of (3.9) this leads to a  $Q_{10}$  of 1.88: slightly less than a doubling of the growth rate with a 10 degrees increase in temperature. The coefficients in equation (3.8) can be estimated fairly accurately: Eppley (1972) reviews older literature showing  $Q_{10}$ -values from 2.1 to 2.3; Slagstad (1982),

using more recent data additionally, reports a Q10 of 1.79 and a Pnt(10) of 1.32 (d<sup>-1</sup>).

Assuming that respiration and excretion are either a negligible fraction of production or show a similar reaction to temperature changes, the Q10 value may be used for Pmax also; the actual level of Pmax can only be calculated if respiration and excretion are known. As the estimation of respiration shows considerable uncertainty (as will be discussed below), this unknown difference between gross and net production is a serious problem in the application of Eppley's formula to gross Pmax.

An alternative to the use of Eppley's equation for net production is to obtain nutrient- and light saturated production rate from gross production measurements; in the Oosterschelde, <sup>14</sup>C incorporation has been measured regularly at several stations (Wetsteijn et al., 1985; Vegter and De Vischer, 1987). In the interpretation of these measurements the problem arises that they have been expressed in units of carbon per unit of chlorophyll-a per hour, which requires a knowledge of the chlorophyll content of the algae. Furthermore it is possible that some nutrients may be limiting during summer. Therefore, these Oosterschelde measurements will not be used directly as model-input but rather to check the combination of several model assumptions (Pmax-formulation, nutrient-limitation formulation, chlorophyll content) with field data.

In conclusion, the following formulation will be used for the maximum production rate:

$$P_{max_d} = P_{max10_d} \exp ((T-10) \cdot T_{coef}) \quad (3.10)$$

with Pmax<sub>d</sub> - maximal production rate in day<sup>-1</sup>  
 T - temperature in °C  
 Tcoef - temperature coefficient (°C<sup>-1</sup>)  
 Pmax10<sub>d</sub> - maximum production at 10 °C in day<sup>-1</sup>

from the observation that maximal net growth rates at 10 °C are in the range 1.1-1.3 (d<sup>-1</sup>) it follows that the coefficient Pmax10<sub>d</sub> (representing maximal gross production) should be at least 1.3; Tcoef should be in the range 0.06-0.083.

#### Maximum production rate and nutrient concentration

The relation between the concentration of a single nutrient and maximum production rate can be expressed by a dimensionless saturation curve giving the fraction of nutrient-saturated production achieved as a function of concentration. Several formulations for such a curve have been proposed in the literature (see discussion by Chen and Christensen, 1985), which are almost equivalent: initially, the response is proportional to nutrient concentration; at higher concentrations there is a more or less smooth transition to a saturation level of unity (= no limitation). The most widely used (e.g. Dugdale, 1967, Platt et al., 1977, Kremer and Nixon, 1978, DiToro, 1980) is a hyperbolic function:

$$F_n(C) = \frac{C}{K_s + C} \quad (3.11)$$

with F<sub>n</sub> - dimensionless reduction function  
 C - concentration of nutrient (mg.l<sup>-1</sup>)  
 K<sub>s</sub> - half saturation concentration (mg.l<sup>-1</sup>)

The same type of formulation is used to describe nutrient uptake of phytoplankton cells. The coefficients obtained from uptake experiments should not be used for the present purpose to describe algal growth however. Uptake experiments typically take only a few hours, during which time algae may be able to store nutrients temporarily (luxury uptake). Only under steady-state conditions, both formulations are equivalent (DiToro, 1980). This implies that the hyperbolic expression for growth can not be used in environments where nutrient concentrations vary rapidly as compared with the time-scale of phytoplankton growth (e.g. in tropical waters with significant diurnal variations). In the Oosterschelde, nutrient concentrations typically vary on a time-scale of weeks, which justifies the use of the expression 3.11.

If more than one nutrient may be limiting, a number of limitation functions have to be combined. De Groot (1983) discusses several formulations that are used for this purpose. Some of these do not meet the following two consistency criteria:

- when one of the nutrients is absent, growth should be zero
- when all nutrients are in abundance save one, the original single-nutrient curve should be reproduced.

These criteria leave in essence only two methods of combination: a multiplication of the  $F_n$ -values or taking the minimum of the  $F_n$ 's. If the nutrient-function is a step-function rising to unity for even a small concentration of the nutrient, both expressions are equivalent, as we have only two possible function values:

$$\begin{aligned}\min \{0,1\} &= 0 * 1 = 0 \\ \min \{1,1\} &= 1 * 1 = 1\end{aligned}$$

In practice, in many experiments the response of the algae approaches a step-function closely (perhaps reflecting a poor choice of experimental nutrient-concentrations), and the minimum- and multiplicative model are hard to distinguish (Chen and Christensen, 1985). As the minimum-formulation appears to fit experimental data slightly better (Jørgensen and Johnson, 1981; De Groot, 1983), this will be used for the present model:

$$F_n(Si,N) = \min \{ F_n(Si), F_n(N) \} \quad (3.12)$$

The  $K_s$ -values for the two nutrients in the model are reviewed by Dugdale (1967), Kremer and Nixon (1978), Jørgensen (1979) and DiToro (1980): see table 3.1.

**Table 3.1:** Literature values of half-saturation concentrations ( $K_s$ ) for nutrient-limited growth.

source:	mg N.l <sup>-1</sup>	mg Si.l <sup>-1</sup>
Dugdale (1967)	0.0035 - 0.035	
Parsons et al. (1984)	0.0001 - 0.14	
Kremer and Nixon (1978)	0.014 - 0.42	0.002 - 0.1
Jørgensen (1979)	0.025 - 0.20	
DiToro (1980)		0.02 - 0.13



### Initial slope and carbon to chlorophyll ratio

The initial slope of the P/I-curve represents the ability of the algae to capture photons under light-limiting conditions. Dubinsky (1980) expresses this efficiency as moles C assimilated per Einstein (=1 mole of photons) absorbed by the chlorophyll-a molecules and reports a constant value of 8 einsteins per mole C. The amount of light absorbed by the chlorophyll at a certain light intensity will depend on cell morphology and the presence of other pigments. In spite of this, in models of photosynthesis a constant value of the initial slope of the P/I curve per unit of chlorophyll-a is found to be an adequate description (Steele, 1962; Jassby and Platt, 1976; Smith, 1980). An inspection of measurements of the initial slope in the Oosterschelde (Wetsteijn, unpubl. results) shows no seasonal pattern, nor correlation with temperature or light conditions. Although the range of values is quite broad (mean  $\pm$  std. dev.:  $0.23 \pm 0.17$  mg C/mg Chl/f/h/(W/m<sup>2</sup>)), the deviations from the mean value appear as random errors.

The chlorophyll content of phytoplankton cells is not a fixed amount but shows substantial fluctuations. In laboratory cultures, chlorophyll-to-carbon ratios vary between 1:1600 and 1:8 (w/w; Steele, 1962); in natural populations values range from 1:500 (Lingeman-Kosmerchok, 1979a to 1:10 (Strickland et al., 1969; Tolstoy, 1979).

The time-scale of these fluctuations is apparently related to cell division rate, and is much shorter in tropical waters and laboratory cultures, where significant changes occur during the day (e.g. Yentsch and Ryther, 1957; Prezelin and Matlick, 1980; Post et al., 1984; Mortain-Bertrand et al., 1987); on the other hand, phytoplankton chlorophyll content in temperate waters shows a typical time-scale of adaptation of days (Steeman-Nielsen and Jørgensen, 1968a,b; Saijo et al., 1969; Marra, 1978a, 1980a; Rivkin et al., 1982).

The adaptation of the chlorophyll-content of algae can be broadly described by the observation that they have as much chlorophyll as they need to capture light for growth, but not more than this. The resulting chlorophyll content is a function of both nutrient- and light conditions: if there is a surplus of light relative to the availability of nutrients, the amount of chlorophyll per cell decreases; if on the other hand light is limiting, the chlorophyll content increases. Natural populations of phytoplankton adapted to low light intensities by high chlorophyll content are described by Fee (1976), Saijo et al. (1969), Gieskes et al. (1978), Morris and Foster (1971) and Lingeman-Kosmerchok (1979a). Natural population of phytoplankton with low chlorophyll content are described by Bienfang and Gundersen (1977), Tolstoy (1979) and Lingeman-Kosmerchok (1979a).

A model of this adaptation was first developed by Steele (1962):

$$\text{Chlfq} = \frac{\text{Dl Fn}}{1.34 \text{ I}_0} \quad (3.13)$$

with Chlfq - chlorophyll-a content (w/w)

Dl - daylength (hours)

Fn - nutrient limitation function (-)

I<sub>0</sub> - surface irradiance (cal/cm<sup>2</sup>)

The formula was compared to data from the central North Sea (Steele and Baird, 1962, 1965) and appeared to reproduce the observations satisfactorily.

A theoretical problem with the formula is that it depends on surface light intensity only: it seems improbable that algae would react in the same way to some surface light intensity in a shallow and clear water as in a deep and turbid water, where the average light intensity would be much lower.

A model with a more detailed treatment of light intensity has been developed by Bannister (1979) and Bannister and Laws (1980). Their work is based on results obtained with continuous cultures of algae. In a continuous culture, a well-stirred vessel of algae is diluted with fresh culture medium while the suspension of algae is flowing out at the same rate. Under steady-state conditions the algal growth rate equals the dilution rate. By manipulation of culture conditions (nutrient concentrations in the inflow, dilution rate and light intensity) it is possible to obtain a light-limited or nutrient-limited culture with a predetermined growth rate.

The results of experiments with these cultures support the model of Steele under nutrient-limiting conditions. In this case the chlorophyll to carbon ratio is approximately proportional to the growth rate. This relation is independent of the nutrient that is limiting.

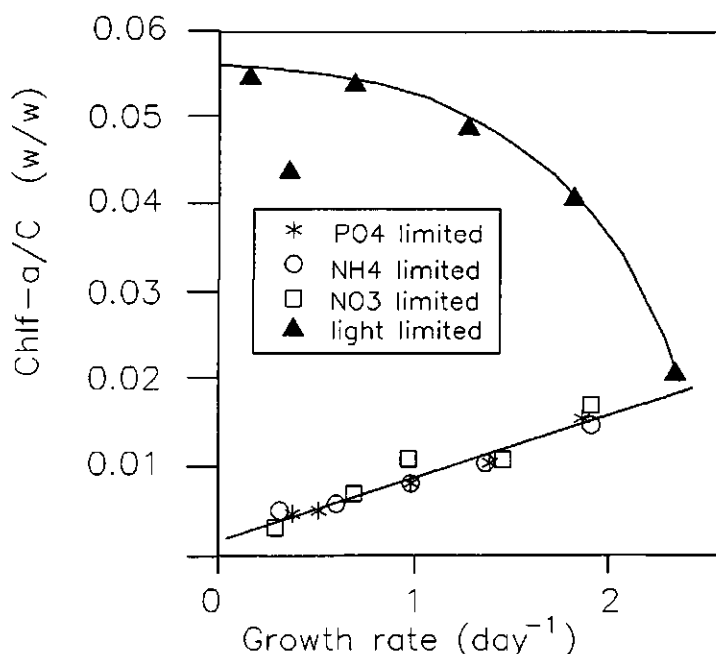


Figure 3.7: (from Bannister and Laws, 1980). Chlorophyll-a to carbon ratio as a function of growth conditions

Under light-limited conditions, the chlorophyll-a content increases with growth rate, which is under these conditions approximately proportional to the light-limitation function. Bannister and Laws (1980) use a rather complicated model to explain their data. A simplified expression appears to give an adequate fit also:

$$\text{Chlfq} = \text{Chlfq}_{\text{max}} * F_n * (1 - F_l)^{0.5} \quad (3.14)$$

with Chlfq - chlorophyll-a content (w/w)  
 Chlfq<sub>max</sub> - max. chlorophyll-a content (w/w)  
 Fn, F1 - nutrient, light limitation functions

the maximum chlorophyll content in the data by Bannister and Laws is approximately 1:18; using other literature references this value may be in the range of 1:8 to 1:20.

Equation 3.14 relates chlorophyll-a content to light limitation function F1. However, chlorophyll plays a role in the determination of the initial slope, and therefore of possible light-limitation itself: therefore, it is necessary to find the chlorophyll content that leads to a value of F1 which satisfies both sides of equation 3.14. In practice, this may be done by assuming some Chlfq-value, calculating a F1-value and thus obtaining a new Chlfq-value, etc.; after one or two iterations the value of Chlfq remains virtually unchanged. In the Oosterschelde simulation model light conditions vary only relatively slowly, and the calculated Chlfq of the integration-step (day) before is simply used for the calculation of F1.

#### Temperature and optimal light intensity

According to the model of Eilers and Peeters (1981a, 1988) the optimal light intensity (equation 3.4) is a function of the ratio of the enzymatic reaction rates ( $\alpha$ ,  $\delta$ ) involved in photosynthesis to the photochemical reaction rates ( $\alpha$ ,  $\beta$ ). Only the first rates are a function of temperature; therefore the model predicts that Iopt is a function of temperature also (Eilers and Peeters, 1981a). This is confirmed by Oosterschelde measurements (Wetsteijn, unpubl. results), in which Iopt as a function of temperature can be fitted to the equation:

$$I_{opt} = I_{opt10} \exp ((T-10) \cdot T_{coef}) \quad (3.15)$$

with T - temperature in °C  
 Tcoef - temperature coefficient (°C<sup>-1</sup>)  
 Iopt10 - optimal light-intensity at 10 °C in W.m<sup>-2</sup>

The parameters have values ( $\pm$  95% conf.interv.) of:

$$I_{opt10} = 117 \pm 7 \text{ W.m}^{-2}$$

$$T_{coef} = 0.055 \pm 0.011$$

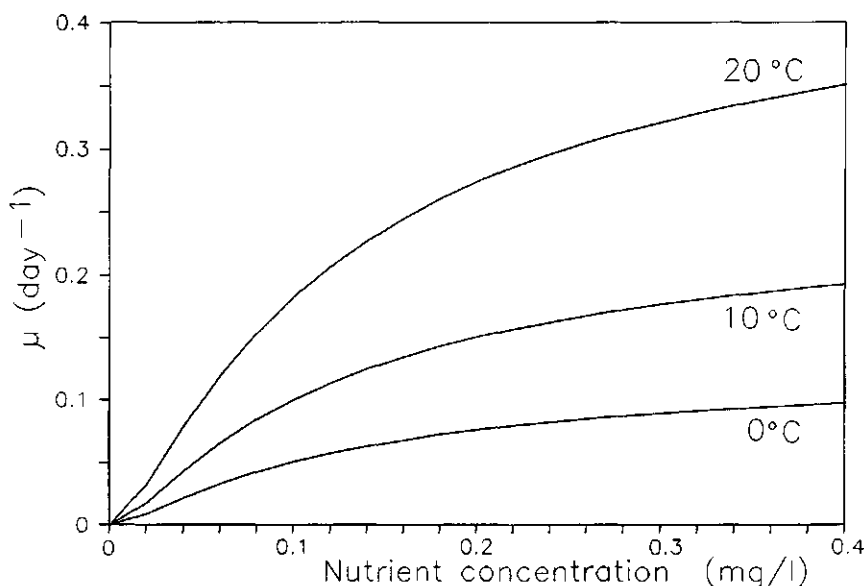
with an  $r^2$  of 0.28 (n=334). Although the remaining scatter is considerable, it does not show any apparent seasonal pattern or relation with light intensity.

#### Interactions between environmental parameters

The interaction between several environmental influences can in general be described by two types of response: a multiplicative response, in which case an increase in one factor raises the response-curve for another factor over its entire range, and a Blackman-type ("law of the minimum") response, in which case only a single factor is limiting, and the levels of other factors have no influence on the response. An example of a Blackman-

type response was already given for the interaction between two nutrients (3.12).

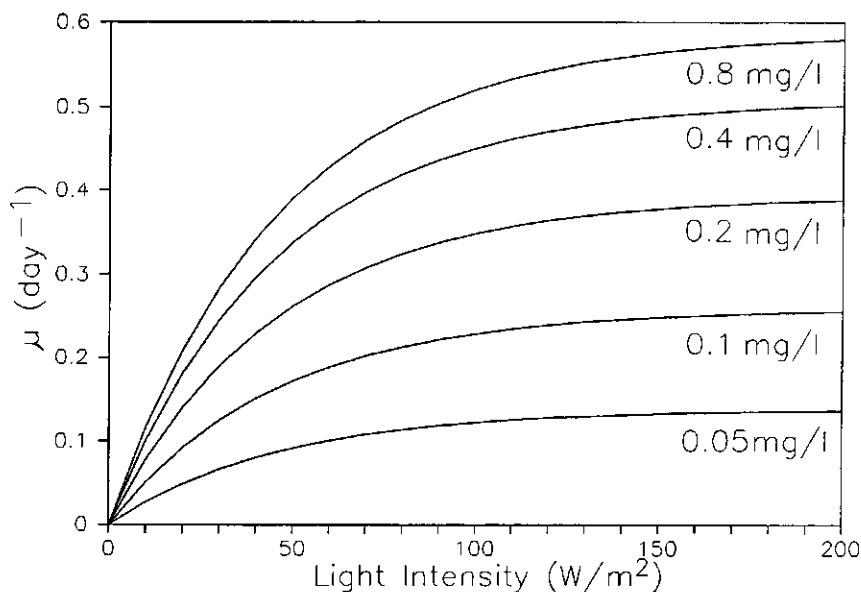
The interaction between temperature and nutrients is discussed by Parsons et al. (1984). Most of the available data fit to a multiplicative model: apparently a higher temperature facilitates both nutrient-uptake and saturated growth rate. The nutrient-limitation function (3.12) is multiplied by the maximum production rate (3.10), which is an exponential function of temperature. Parsons et al. report that in some cases it was found that the half-saturation coefficient  $K_s$  (equation 3.11) increased with temperature, thus changing the multiplicative response into a Blackman-type response. These instances were mainly limited to temperature above the optimum; in general  $K_s$  seems to be independent of temperature. The multiplicative response has been therefore been used in the present model, it is illustrated in figure 3.8.



**Figure 3.8:** Steady-state response of the present phytoplankton sub-model as a function of nutrient concentration ( $K_s = 0.1$  mg/l) for different temperatures. Average surface light intensity is 75% of  $I_{opt}$ ; extinction coefficient  $1. m^{-1}$ ; average depth = 8 m.

The interaction between nutrients and light appears to be multiplicative also (Parsons et al., 1984). The combined response can be inferred from the observation that (1) the production per unit of chlorophyll is approximately constant under light limiting conditions (as discussed above) and (2) the amount of chlorophyll per cell increases proportional to nutrient-limited growth rate (see figure 3.7). Thus, increased amounts of nutrients increase growth-rate not only directly, but also cause an increased ability to capture light. This interaction is illustrated in figure 3.8, where the response of the present phytoplankton sub-model under steady-state conditions are shown. The response to increased nutrient concentrations is initially (in the range 0-0.05 mg/l) somewhat more than proportional to nutrient concentration (note

inflexion point near 0.05 mg/l), because of a concomitant decrease in light-limitation.



**Figure 3.9:** Steady-state response of the present phytoplankton sub-model as a function of light intensity ( $I_{opt} = 100 \text{ W/m}^2$ ) for different nutrient concentration ( $K_s = 0.1 \text{ mg/l}$ ). Temperature is  $10^\circ\text{C}$ ; extinction coefficient  $1.\text{m}^{-1}$ ; average depth = 8 m.

The interaction between temperature and light-intensity is a Blackman-type response, as there seems to be no relation between temperature and chlorophyll content (Bannister and Laws, 1979, 1980). The capture of light by the photosynthetic pigments (which is the rate-limiting step under light-limitation) is independent of temperature (Dubinsky, 1980), and only when the enzymatic reactions become rate-limiting a clear effect of temperature is observed. The steady-state response of the present model follows these observations, as illustrated in figure 3.10.

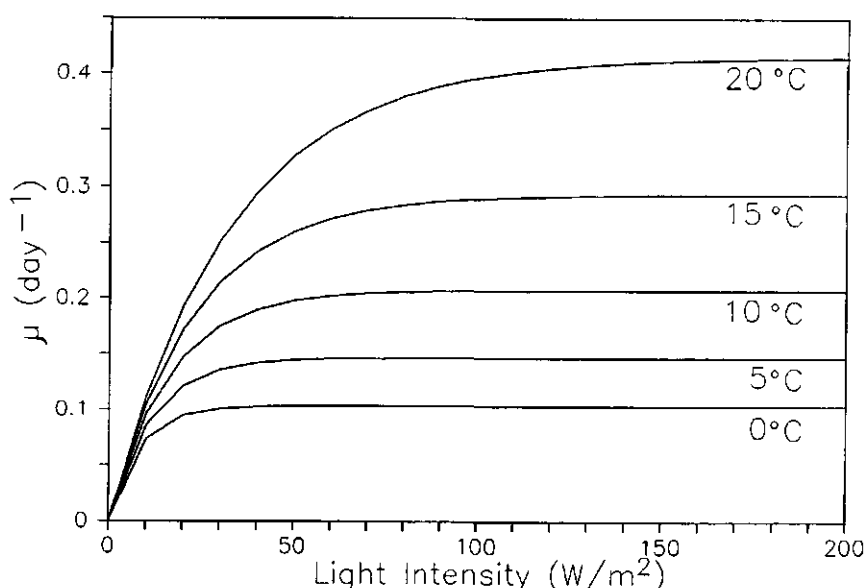


Figure 3.10: Steady-state response of the present phytoplankton sub-model as a function of light intensity for different temperatures.  $I_{opt} = 100 \text{ W/m}^2$ ; nutrients are not limiting; extinction coefficient  $1. \text{m}^{-1}$ ; average depth = 8 m.

### 3.5 Respiration

The respiration rate of phytoplankton has been related in the literature either to biomass (e.g. Steele, 1962; DiToro et al., 1971; Laws, 1975; Gieskes and Kraay, 1977; Lingeman-Kosmerchok, 1979c; Slagstad, 1982) or to light-saturated production rate (e.g. Steemann-Nielsen and Jørgensen, 1968a,b; Steel, 1972; Parsons et al., 1984). A more general approach is to be followed by Platt et al. (1977) and Bannister (1979) who express respiration as a linear function of growth rate. Their expression can be recalculated as:

$$R = R_o + (1-pv) * (Pg - R_o) \quad (3.16)$$

with  $R$  - respiration ( $\text{d}^{-1}$ )

$R_o$  - maintenance respiration ( $\text{d}^{-1}$ )

$pv$  - production value, the amount of biomass produced per unit of primary production (w/w)

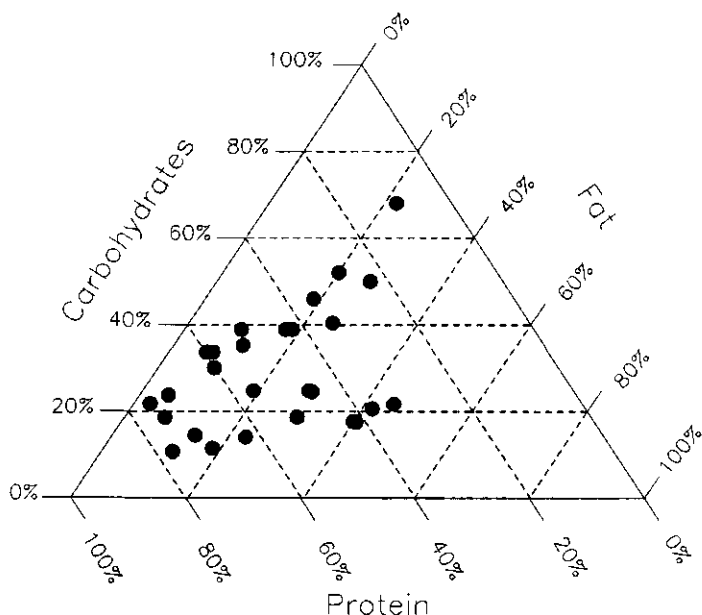
$Pg$  - gross production ( $\text{d}^{-1}$ )

A considerable range of values is found for both coefficients  $R_o$  and  $pv$  in (3.16); A review by Wetsteijn (1984) gives:

$$\begin{aligned} 0 < R_o < 0.10 \\ 0.55 < pv < 0.90 \end{aligned}$$

A model that is able to explain most of the wide scatter in observations in pv was developed by Penning de Vries (1973). It appeared that the fraction of substrate (glucose) respired during the biosynthesis of a certain end-product could be accurately predicted by simply adding the requirements for the intermediate reactions in the biochemical pathway for this particular end-product. Moreover, by making some assumptions on the average composition of carbohydrates, proteins and fats, Penning de Vries was able to simplify the necessary calculations into a consideration of the fractions of these three groups of molecules only. Apart from the overall biochemical composition, the use of either  $\text{NO}_3$  or  $\text{NH}_4$  as a nitrogen source appeared important: the use of nitrate (which has to be reduced before incorporation in protein) costs more energy.

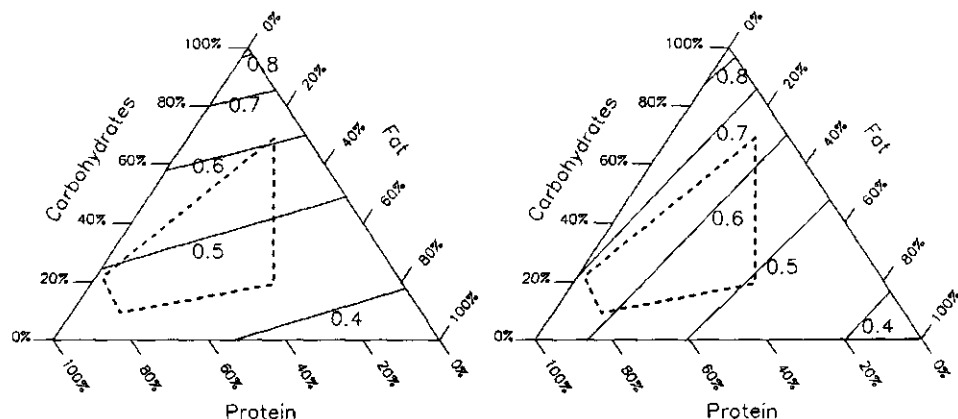
In figure 3.11 the composition of a number of algal cultures and natural phytoplankton is shown. The composition depends on growth conditions and (to a lesser extent) on species: in general N-limited cultures showed a lower protein/fat ratio. The composition is also time dependent, for example there is a clear daily pattern in carbohydrate content as a result of accumulation during the daylight period and depletion in the dark.



**Figure 3.11:** The composition of some algae from laboratory cultures and from the field. The sum of carbohydrates, proteins and fat is normalized to 100%. References: Parsons et al., 1984; Raymont, 1980; Payer et al., 1980; Darley, 1977.

Combining the data on algal composition with the results of Penning de Vries (figure 3.12) it is possible to obtain a narrower estimate on biosynthesis-related respiration than the above-cited results by Wetsteijn. From the diagrams it appears that the weight of organic matter produced per unit weight of substrate (glucose) for  $\text{NH}_4$ -utilizing algae is in the range 0.50-0.70; for  $\text{NO}_3$ -using algae it is 0.45-0.55. A submodel of the biochemical

composition of algae would considerably complicate the present model, and it would not be possible to compare such a model with field data, which are lacking from the Oosterschelde. Despite the uncertainty on algal composition in the Oosterschelde, the data on algal composition in general allow an estimate of  $p_v$  in the range of 0.45 to 0.7, which is narrower than the initial experimental range.



**Figure 3.12:** (redrawn from Penning de Vries 1973) The production value ( $p_v$ ) as a function of biomass composition.  $p_v$  equals the weight of biomass of the given composition per unit weight of glucose used. The diagram to the left gives the  $p_v$  for growth on  $\text{NO}_3^-$ , the diagram to the right for  $\text{NH}_4^+$ . The sum of carbohydrate, protein and fat has been normalized to 100%; the dotted region contains the observations on phytoplankton composition.

Maintenance respiration appears to be determined by several environmental factors (Penning de Vries, 1973), mainly related to protein turnover and the cost of osmoregulation and ion exchange with the environment. These processes are influenced by temperature, with a  $Q_{10}$  of approximately 2. The actual level of maintenance respiration is hard to predict however; protein turnover rates differ strongly for different proteins (Penning de Vries, 1973) and protein content per cell is quite variable (figure 3.11). Osmoregulation is also variable among species. For instance, naked flagellate cells are known for their high respiration (Parsons et al., 1984), which is probably associated with the leakage of ions at the site of the flagella rather than with the direct energy requirements for motility (Peeters, pers. comm.). It seems that there are insufficient data to obtain a better estimate for  $R_0$  than the range of values from direct measurements cited above.

### 3.6 Excretion

Data on the excretion of dissolved organic carbon by phytoplankton have been reviewed by Sharp (1977), Fogg (1983) and Wetsteijn (1984). Excretion rates are negligible in exponentially growing populations and under light-limiting conditions. Under conditions of nutrient-limitation however,



an excretion of 10 to 40 per cent of the carbon fixation is reported. This mechanism has been incorporated into the model by making the excretion rate a function of nutrient limitation:

$$E = E_{max} * (1 - F_n) * P_g \quad (3.17)$$

with:  $E$  - excretion rate ( $d^{-1}$ )  
 $E_{max}$  - maximal excretion expressed as a fraction of gross production (-)  
 $F_n$  - nutrient-limitation function - equation 3.12 (-)  
 $P_g$  - gross production rate ( $d^{-1}$ )

The value of  $E_{max}$  is treated as a constant in the model, with a value in the range of 0.1 to 0.4. It should be noted that the above expression is based on its extreme values ( $F_n \approx 0$  and  $F_n \approx 1$ ) only, reflecting the general statements in the literature on nutrient- or light-limited cultures. There appears to be no systematic investigation of excretion rate as a function of nutrient concentrations to check intermediate values predicted by (3.17) however.

### 3.7 Two phytoplankton groups

In phytoplankton ecology a distinction is often made between diatoms and other algae. Diatoms contain relatively large amounts of silicon in their cell (in some cases even more than carbon; see ch. 8), other algae contain no silicon. The spring bloom of phytoplankton usually consists exclusively of diatoms, which causes a depletion of silicate in the water (Parsons et al. 1984; Wetzel, 1975). During summer, the diatoms are in many cases replaced by other species, often smaller and having flagellae.

As a result of eutrophication during the past decades, the concentrations of phosphate and nitrate have been increasing in both fresh and coastal waters. The supply of silicate on the other hand is not affected by pollution: this has caused a relative shortage of silicate, which in its turn causes a relative decline in diatoms compared to other algae (Officer and Ryther, 1980). This process is considered as one of the negative effects of eutrophication, because some of the non-diatoms are not attractive as food for grazing organisms (e.g. *Phaeocystis* spp.), or they may be even toxic (e.g. some *Dinoflagellates*).

In the Oosterschelde, data on species composition have been collected since 1983. They show an almost complete dominance of diatoms throughout the year (Bakker, unpubl. results; Peperzak, 1986). In order to gain some insight into the possible development of the two species groups under changing circumstances, they are treated as separate state-variables in the model. Unfortunately, most of the information on the physiological differences between the groups is only qualitative or hypothetical, which makes it difficult to model these differences.

The explanation given in the literature for the often observed absence of diatoms in summer is silicate depletion; the explanation given for the initial predominance of diatoms is either a higher energy-efficiency (Steele and Frost, 1977; Parsons et al., 1984) or a flatter temperature-response (De Vries, 1987). In the present model the energy-disadvantage of the non-diatoms has been modelled by assuming higher losses by respiration and excretion. Instead of doubling the number of loss-parameters ( $R_0$  and  $p_v$  in 3.16;  $E_{max}$  in 3.17) by choosing separate values for the two groups, the difference between diatoms and other algae has been expressed in the single parameter "ARAT", by which diatom respiration and excretion rates are multip-

lied for the non-diatoms. The flatter temperature-response may be modelled by choosing a lower Q10-value for diatoms.

It should be stressed that the differences between the two algal groups are based on the observation that diatoms must have some advantage over other groups, at least in winter. Otherwise, their silicon requirement would lead to their rapid extinction in nature. In the model, this advantage has to be expressed using the physiological parameters in the carbon budget. However, actual physiological measurements show widely overlapping ranges in the properties of the two groups, both in production parameters (Eppley, 1972; Parsons et al., 1984) and in loss rates (Lingeman-Kosmerchok, 1979a,c). There seems to be no lower grazing on diatoms as compared to other algae either; on the contrary, the species of algae that are unattractive as food for grazers (because of toxicity, large colonies, slime etc.) are all non-diatoms. Nevertheless, there are many aspects of phytoplankton ecology that are not incorporated in the present model, which could form an explanation of the success of diatoms despite their silicon-"handicap": e.g. vulnerability to diseases, sensitivity for toxic substances, requirements for micro-nutrients and vitamins etc. As these processes are not modelled, the assumption has to be made that the difference lies in the energy budget of the two groups which does form part of the model.

The values to be used for ARAT (presumably some value higher than unity) and the Q10's in the model will have to be found by calibrating model results to chlorophyll, silicate and inorganic nitrogen data.

### 3.8 Summary of model assumptions

The model for gross photosynthesis is based on the dynamical description of production and inhibition by Eilers and Peeters (1981a,b; 1987). This model makes it possible to incorporate the effect on photosynthesis of rapid fluctuations in light intensity as a result of vertical mixing. Their model is reduced to an empirical expression relating vertically and daily integrated gross photosynthesis to light-limited production rate, optimal light intensity, maximal production rate, average surface light intensity, average depth and vertical light extinction coefficient.

The initial slope of the photosynthesis/light curve (light-limited production rate) is modelled as proportional to the chlorophyll content of the algae. Maximal production is the product of an exponential function of temperature ( $Q_{10} \approx 2$ ) and the hyperbolic equation for nutrient limitation; for diatoms only the most limiting of either nitrogen or silica is considered ("minimum law"). Optimal light intensity is a function of temperature only.

The carbon to chlorophyll ratio plays a role (for the phytoplankton) in adaptation to light and nutrient conditions and (for the interpretation of field results) because phytoplankton biomass is usually determined indirectly via chlorophyll concentration. The chlorophyll content of algae is modelled as proportional to the hyperbolic expression for nutrient limitation and a decreasing function of light limitation.

The phytoplankton is divided into two species-groups: diatoms and non-diatoms. The latter do not need silicate for growth, show a higher respiration and excretion rate, and a higher Q10.

#### 4. THE ZOOPLANKTON MODEL

##### 4.1 Introduction

The zooplankton is defined as the group of animals that are passively transported by the water. A major subdivision within the group is formed by the holoplankton ("true plankton"), species that live in the water during their entire life-cycle and the meroplankton, consisting of species that live in the water only during the juvenile stage. In the Oosterschelde, both groups are present in approximately equal densities. The holoplankton consists mainly of copepoda of the genera Temora, Acartia and Centropagus. The meroplankton is formed mainly by the larvae of the barnacle Balanus.

Another major subdivision is into micro-, meso and macrozooplankton. The border between micro- and mesozooplankton is drawn at 100  $\mu\text{m}$ , between meso- and macrozooplankton at 1000  $\mu\text{m}$ . Of these groups, only the mesozooplankton has been studied in the Oosterschelde and is included in the present model as it is the largest in biomass (Bakker et al., 1985, Tackx, 1987); it is further indicated as the zooplankton.

The microzooplankton grazes on small particles (bacteria, microflagellates) and plays a role in the decomposers food web (Fenchel and Barker Jørgensen, 1977). The decomposition of organic matter in the Oosterschelde is not well understood, and is modelled here as a simple first-order decay (see chapter 5). The microzooplankton is not included in this decomposition model. The macrozooplankton consists of small jelly-fish (predominantly the genus Pleurobrachia) and grazes on the first two groups. In the Wadden Sea, its biomass shows one or two sharp peaks during the year; during these periods the biomass of its prey is grazed down to very low levels. The absence of the macrozooplankton group from the model implies that mesozooplankton mortality has to be estimated empirically.

Grazing by zooplankton is often the major loss-process for phytoplankton in deep water, where bottom fauna plays an insignificant role. In shallow water, the bottom fauna plays a more important role, but still a considerable fraction of total grazing on phytoplankton is due to zooplankton (DiToro et al., 1971; Verhagen, 1985; Baretta, 1980; Tackx et al., 1986, Tackx, 1987). Interest in zooplankton dynamics originates not only from its role in controlling phytoplankton biomass, but also from its role in the further food chain: it is the food source for a number of fishes (Andersen and Ursin, 1977). For the present model, the grazing by zooplankton is the primary interest; as has been mentioned the higher food chain is omitted from the model and grazing on zooplankton is treated in a simple empirical fashion.

In the Oosterschelde biomass and grazing rates of zooplankton have been measured by Tackx and coworkers (Tackx et al., 1986, Tackx, 1987). Additional information was necessary on zooplankton loss-processes: loss by faeces, respiration and mortality. For these processes, the model follows the approach by DiToro (1971) and Kremer and Nixon (1978).

In the models by Kremer and Nixon (1978) and Fransz (1979) zooplankton population dynamics is modelled by a large ( $\pm 10$ ) number of state-variables for the various life-stages. The life stages show differences in grazing and loss-rates. Of course, the information provided by these models on population structure cannot be provided by a single state variable model (for example, those of DiToro (1971) and Anderson and Ursin (1977)). However, for the present calculation of phytoplankton grazing this would not seem very important (Tackx, 1987). A more serious problem with the single state variable approach is that it lacks the time-lag typical of actual population dynamics. For example, if there is abundant food after a period of shortage, the adults will invest more energy in egg-production, which will cause a

population increase only after some weeks. In a single state-variable model, individual and population growth rate are identical, and the population would have reacted immediately.

In spite of this problem, the present model follows the single state-variable approach of DiToro (1971) for reason of its simplicity. It will be attempted to calibrate the parameters in his simple model to the observed population dynamics in the Oosterschelde as reported by Bakker and Van Rijswijk (1987, and unpublished results).

For the meroplankton (the benthic larvae) the single state variable approach of the true (holo) zooplankton is even too complicated: here a further simplification is made. In this case the biomass is determined only to a very limited extent by growth, respiration and so on: the meroplankton is only a temporary stage between spawning of macrobenthos and the settlement of the larvae. Furthermore, the amount of benthic larvae depends strongly on chance. For example, it is estimated that less than 10% of the eggs of mussels are fertilized (Verhagen, 1982); the number of mussel larvae depends more on favorable temperature, current and salinity conditions during spawning than on mussel biomass. For this reason no attempt is made to model the number of benthic larvae as a state variable. Instead, their number is approximated by an empirical curve. Their activity is assumed to be equal to that of true zooplankton. The two groups are lumped by Tackx et al. (1986) also (see for example figure 4.3): their work does not show significant differences in e.g. ingestion rates between the groups.

The transport of zooplankton resembles that of dissolved substances, i.e.: zooplankton biomass is not determined by feeding and loss-processes only, but also by mixing with adjacent water masses and residual currents. In the present model, these processes can not be fully included, as data on zooplankton abundance at both the North Sea and the Volkerak border of the model are lacking. Further, the possibility of vertical movements which may be correlated with the tidal cycle makes the residual transport of zooplankton difficult to estimate.

#### 4.2 Grazing

In this section three questions are discussed: what constitutes the food of the zooplankton, what is the relation between food concentration and food uptake and what is the influence of temperature on grazing rate.

##### Food

Grazing by zooplankton is not a passive sieving of the particles in the water: the animals are able to select particles both on the basis of size (Cowles, 1979; Lingeman-Kosmerchock, 1979b; Tackx, 1987) and on the basis of taste (Poulet and Marsot, 1980). Phytoplankton appears to be preferred above detritus as a food source (Tackx et al., 1986; Tackx, 1987). Both Kremer and Nixon (1978) and Verhagen (1985) assume that a fraction of the detritus may serve as food in periods when phytoplankton biomass is low. The maximum fraction of detritus that may serve as food is the fraction of particulate organic carbon larger than 3  $\mu\text{m}$  (in the Oosterschelde 72%; Tackx, 1987) which is the lower size limit for particle retention by zooplankton (Tackx, 1987). In the present model it is assumed that phytoplankton is the primary food source for zooplankton; if food concentration drops below a certain threshold (discussed in the next section), phytoplankton is supplemented by the fraction of the detritus larger than 3  $\mu\text{m}$ .

Part of the phytoplankton is smaller than the lower size limit of 3  $\mu\text{m}$  also. The occurrence of small algal cells is in general related to the nutrient supply: at low nutrient concentrations, cells are usually smaller

(Gieskes, 1972; Eppley, 1972; Parsons and Takahashi, 1973; Wetzel, 1975; Laws, 1975 and Steele and Frost, 1977). This is apparently the result of the large surface-to-volume ratio of small cells, which facilitates nutrient uptake. A simple but crude way to model the size of phytoplankton is to use the nutrient-limitation function: it is assumed that the fraction of cells that is available to zooplankton grazing is the same as the fraction of maximum growth rate achieved by the phytoplankton as a result of nutrient limitation.

#### Grazing and food concentration

The dependence of grazing on food concentration has been described by several relations, which are essentially identical. All show a saturation of ingestion at increasing food concentrations. DiToro (1971) uses a Monod-type function:

$$R_t = R_{max_t} \frac{F}{F + F_{half}} \quad (4.1)$$

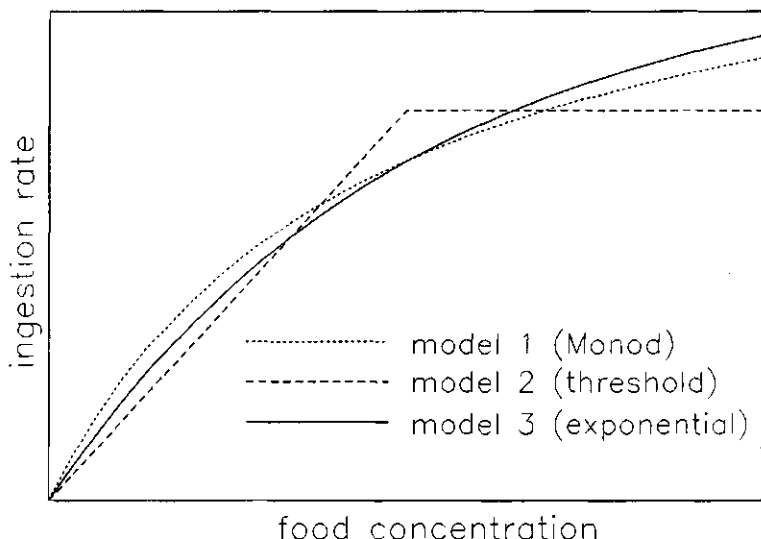
Kremer and Nixon (1978) discuss two equations:

$$R_t = R_{max_t} * \min \left( 1, \frac{F}{F_{lim}} \right) \quad (4.2)$$

$$R_t = R_{max_t} * (1 - e^{-F*k}) \quad (4.3)$$

with:  $R_t$  - (temperature-dependent) ingestion per unit of biomass ("daily ration") in  $\text{mgC.mgC}^{-1}.\text{d}^{-1}$   
 $R_{max_t}$  - (temperature dependent) maximal daily ration ( $\text{mgC.mgC}^{-1}.\text{d}^{-1}$ )  
 $F$  - food concentration ( $\text{mgC.l}^{-1}$ )  
 $F_{half}$  - half-saturating food concentration ( $\text{mgC.l}^{-1}$ )  
 $F_{lim}$  - threshold food concentration ( $\text{mgC.l}^{-1}$ )  
 $k$  - saturation coefficient ( $\text{l.mgC}^{-1}$ )

The three equations are illustrated in figure 4.1.



**Figure 4.1:** Three equations relating zooplankton ingestion to food concentration (eqs. 4.1-3). X-axis: food concentration; y-axis: ingestion. Units and coefficients arbitrary.

Kremer and Nixon (1978) remark that a choice between the three formulations on the basis of experimental data is difficult: by adjusting the parameters of the models, the difference between the models can in general be made smaller than the uncertainty in measured ingestion. For the present, the second model is used, as it expresses limitation directly in terms of a threshold food concentration which is convenient for the calculation of the fraction of detritus in the diet.

An estimation of the concentration  $F_{lim}$  ranges from  $0.08 \text{ mg C.l}^{-1}$  to  $5 \text{ mg C.l}^{-1}$ ; most values are in the range  $0.2$  to  $0.3 \text{ mg C.l}^{-1}$  (Kremer and Nixon, 1978). DiToro et al. (1971) report values for their half-saturation concentration of  $0.25$  to  $0.55 \text{ mg dry wt.l}^{-1}$ , i.e. approximately  $0.12$  to  $0.20 \text{ mg C.l}^{-1}$ , which appears to agree with the data of Kremer and Nixon. In the present model, a value of  $0.25$  (range  $0.2$ - $0.3$ )  $\text{mgC.l}^{-1}$  is used. This implies that food concentrations are in general not limiting zooplankton food uptake in the Oosterschelde; the ingestion rates reported by Tackx are therefore interpreted as maximum rations.

This relative food abundance implies that the model assumptions regarding the "undersized fraction" of the food (28% of detritus; nutrient-limitation function for phytoplankton) are not very critical: if the model is able to reproduce normal phytoplankton and detritus levels, the phytoplankton is sufficient to feed the zooplankton, at least in summer. The exclusion of a limited fraction of the phytoplankton below the  $3\mu\text{m}$  size limit does not affect the ingestion rate of the zooplankton under these conditions.

#### Temperature

The maximal daily ration increases with increasing temperature. This increase can be described by an exponential function:

$$R_{max_t} = R_{max_{15}} \exp ((t-15) \ln(Q_{10})/10.)$$

(4.4)

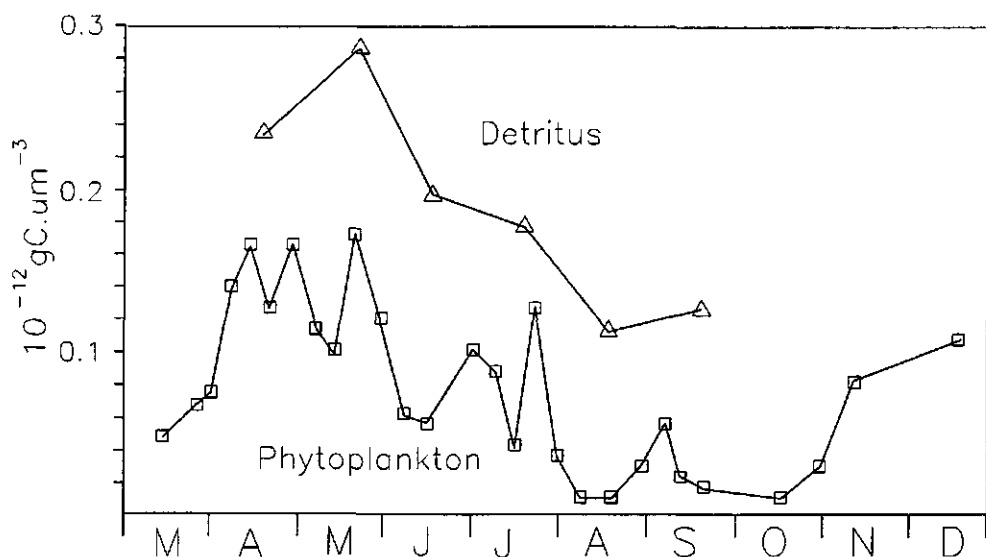
with:  $R_{max_{15,t}}$  - maximal daily ration ( $d^{-1}$ ) at 15 and  $t$  °C  
 $t$  - temperature in °C  
 $Q_{10}$  - coefficient giving relative increase in activity at a 10°C increase in temperature

The effect of temperature on zooplankton grazing has been reviewed by DiToro et al., (1971), Kremer and Nixon (1978) and Lingeman-Kosmerchok (1979b). These authors report a range of  $Q_{10}$  values from 1.6 to 3.3. The Data used by DiToro et al. (1971) show a difference between freshwater Daphnia species and estuarine species of the genera Acartia and Centropagus: the latter display a steeper temperature response. Bakker and Van Rijswijk (1987) report literature values on development time from Nauplius larval stage to adults of the copepod Temora longicornis (the dominant species in the Oosterschelde), which decreases from 127 days at 5 °C to 37 days at 20 °C, resulting in an overall  $Q_{10}$  of 2.3. For model calculations a range of  $Q_{10}$ -values of 2-3 is used.

#### Maximum daily ration

The values of  $R_{max}$  from literature values show a wide range of 0.02 to 4.8  $d^{-1}$  (literature review in Tackx et al., 1986).

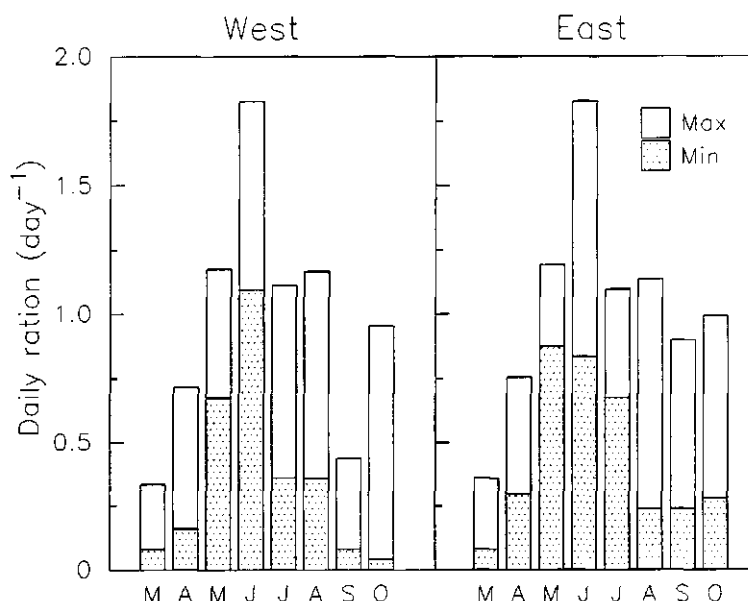
In the Oosterschelde, grazing has been measured by determining the volume of the ingested particles. To convert this to units of carbon, the carbon content of the particles has to be known. This strongly depends on the size and the type of particles: small particles contain relatively more carbon than larger ones; detritus contains more carbon than phytoplankton. The average carbon content of the phytoplankton in the Oosterschelde is illustrated in figure 4.2: it is on the average much lower ( $0.05 \cdot 10^{-12}$  gC. $\mu m^{-3}$ ) than the average carbon content of all suspended organic matter ( $0.2 \cdot 10^{-12}$  gC. $\mu m^{-3}$ ). This makes an estimation of maximal daily ration strongly dependent on assumptions regarding the diet of zooplankton. There are two hypotheses regarding zooplankton feeding, discussed extensively by Tackx (1987): the first is that zooplankton eats mainly phytoplankton, the second that feeding is indiscriminate. Because of the higher carbon content of the detritus, the second hypothesis would result in a higher carbon-ingestion for the same (measured) ingested volume than the first hypothesis.



**Figure 4.2:** Carbon content of phytoplankton and total organic matter (mainly detritus) in the Oosterschelde during 1983 (from Tackx, 1987).

The daily rations calculated on the basis of the two assumptions are illustrated in figure 4.3. Tackx et al. (1986) and Tackx (1987) conclude that the daily rations ranging from 20% per day in spring and autumn to 80% per day in summer calculated on the basis of the selective feeding hypothesis are the most reliable.





**Figure 4.3:** Seasonal distribution of monthly averaged daily ration of zooplankton in the Oosterschelde, expressed in percentage of body weight ingested per day. (From Tackx et al., 1986). Upper histograms calculated on the basis of a-select feeding; lower (shaded) histograms: phytoplankton as sole food source.

#### 4.3 Loss processes

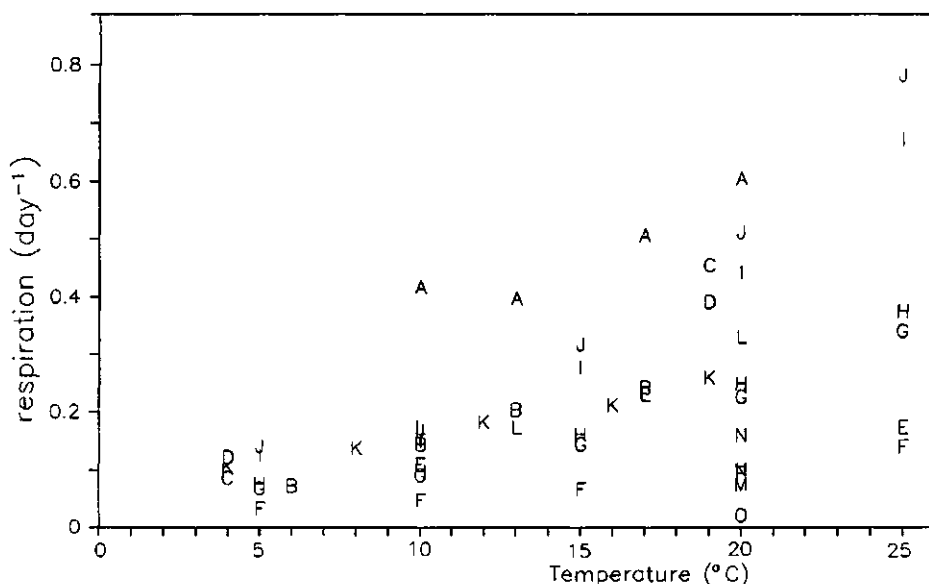
The processes discussed in this section are: loss of ingested food as faeces, respiration and mortality by predation. These processes have not been investigated in the Oosterschelde. This implies that we have to rely on -often rather wide ranges of- literature values. In the section on mortality, an empirical formulation replaces the absence of fish and macrozooplankton from the model.

#### Assimilation efficiency and respiration

The assimilation efficiency is the fraction of the ingested food that is actually taken up in the animal. This fraction ranges from 7 to nearly 100% (Jørgensen, 1979). Most values are in the range of 40 to 80% (Lingeman-Kosmerchok, 1979b; Kremer and Nixon, 1978; DiToro et al., 1971). It is found to be independent of ingested amount, body size and temperature. Kremer and Nixon (1978) mention only ash content of the phytoplankton as having a negative effect on assimilation efficiency: a high ash content means a relatively low organic fraction of the dry weight. However, they do not mention whether this effect of organic matter content on assimilation is very strong; in their own model a fixed assimilation efficiency is used. The same assumption is made by DiToro (1971) and is used in the present model also; its value is in the range of 0.4-0.8.

Respiration is expressed in units of carbon respired per unit of animal carbon per day (unit  $d^{-1}$ ). It can again be described by an exponential function of temperature (equation 4.4). Kremer and Nixon (1978) use a Q10-

value of 2, but uncertainty is considerable: the data show a range of 1.5 to 2.5. The response at some fixed temperature is very variable (Kremer and Nixon, 1978, Jørgensen, 1979; see figure 4.4): the respiration rate at, for example, 10 °C ranges from 0.04 to 0.4 d<sup>-1</sup>.



**Figure 4.4:** Zooplankton respiration data from Jørgensen (1979). Recalculated from oxygen and dryweight data assuming 1 ml O<sub>2</sub> = 1.43 mg O<sub>2</sub> = 0.54 mg C = 1.34 mg drywt (see chapter 8). Every symbol represents a different experiment or species.

#### Mortality

The death rate in the present model represents grazing by higher trophic levels. In the Kremer and Nixon model, these higher levels are explicitly present. As has been mentioned, this is not possible in the Oosterschelde model, as data on macrozooplankton are lacking. DiToro et al. (1971) formulate zooplankton mortality as a fixed fraction of biomass per day, to be obtained from calibration. The use of a constant rate is in disagreement with the fact that both predator biomass and activity is highest in spring and early summer. One of the reasons for this is, of course, that predator biomass depends on zooplankton biomass: the macroplankton reproduces rapidly, and will increase in biomass soon after a zooplankton bloom. Furthermore, some of the zooplankton itself grazes on (juvenile stages of) other species of zooplankton (Kremer and Nixon, 1978).

A simple way to incorporate a non-constant mortality rate into the model is to assume that predator biomass (and thus zooplankton mortality rate) is proportional to zooplankton biomass:

$$Z_{\text{mort}} = \text{mortq} * B$$

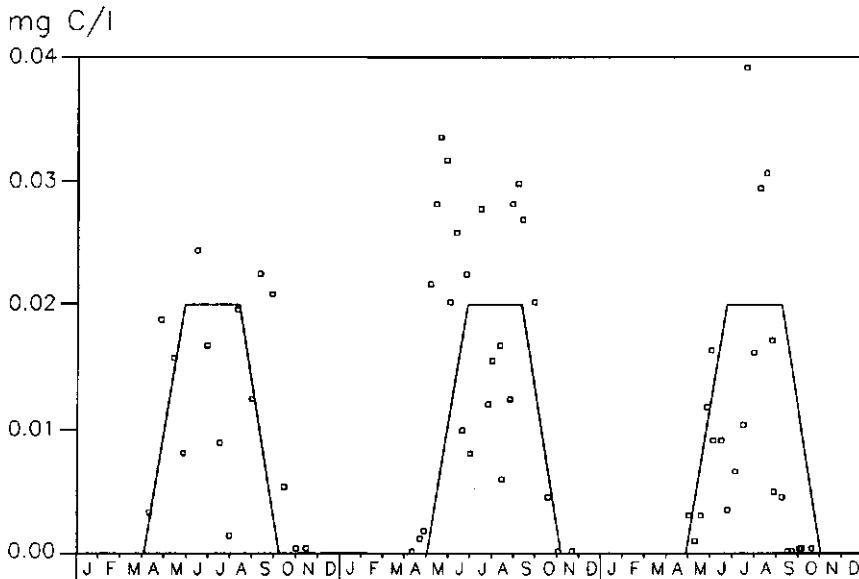
(4.5)

with:  $Z_{\text{mort}}$  - zooplankton mortality rate ( $\text{day}^{-1}$ )  
 $\text{mortq}$  - proportionality constant ( $\text{day}^{-1} \cdot (\text{gC} \cdot \text{m}^{-3})^{-1}$ )  
 $B$  - zooplankton biomass ( $\text{gC} \cdot \text{m}^{-3}$ )

The proportionality constant is to be determined from calibration.

#### 4.4 Biomass of benthic larvae

The biomass of benthic larvae as measured in compartments 1 (mouth) and 3 (east) of the Oosterschelde is shown in figures 4.5 and 4.6. No attempt was made to model these data by means of a state-variable. Instead, they were approximated by a periodic function as shown in the figures: the same function is used for years of which no measurements are available. For the average summer biomass a value of  $0.02 \text{ mg C.l}^{-1}$  was used in the mouth (comp. 1; figure 4.5), and a value of  $0.05 \text{ mg C.l}^{-1}$  in the eastern compartment (no. 3; figure 4.6). For the middle and north compartments, intermediate values of these two compartments were used, as there are no observations available here.



**Figure 4.5:** Empirical function and observed biomass of benthic larvae in compartment 1 (West). Unpublished data from Bakker.

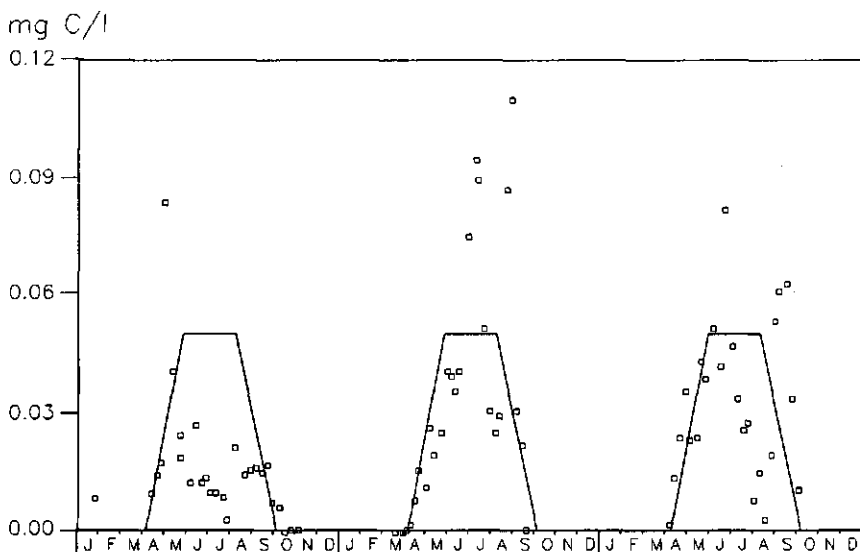


Figure 4.6: Empirical function and observed biomass of benthic grazers in compartment 3 (East). Unpublished data from Bakker.

#### 4.5 Transport

This section discusses the estimation of border conditions and residual flows in the transport equations for zooplankton.

Although a number of papers describe zooplankton biomass at the North sea (e.g.: Fransz and Gieskes, 1984; Fransz, 1979; Joiris et al., 1982), there is no detailed data set for the region near the mouth of the Oosterschelde comparable to the data by Tackx (1987). For the northern border of the model, the Volkerak, there are no data at all. This makes it impossible to calculate exchange of zooplankton biomass across these borders.

A necessarily crude assumption to solve this problem is to assume that the biomass at the North Sea is equal to that at the first compartment, and in the Volkerak to that of the adjacent fourth compartment, i.e.: that there is no exchange across these borders. An exception to this is the situation where calculated Oosterschelde biomass reaches a very low level; in this case the North Sea biomass is assumed to be at least equal to some threshold (COPMIN), which may prevent a possible extinction of copepoda in the model. For exchange between the inner compartments of the model, the same dispersion coefficient as used for dissolved matter is used.

A second problem in the evaluation of the transport equations for zooplankton is the estimation of the residual flow  $Q$ . In chapter 2, this residual flow was calculated for the particulate state variables depending on their vertical distribution in the water column. A non-uniform vertical distribution of some substance during the tidal cycle may cause a large difference in residual flow from that of the water itself. In the case of particles this is primarily the result of passive settling and resuspension. Zooplankton may be assumed to remain free of the bottom, and is not subject to the same mechanism. However, there is also a vertical gradient in current velocity (Verhagen, 1986): if vertical movements of an animal are not random

but correlated with the tidal cycle, its net displacement could be even much larger than that of a sediment particle. For example, it is assumed (B. Kuipers, pers. comm.) that the migration of fish-larvae from the North Sea into the Wadden Sea is accomplished by remaining close to the bottom during the ebb tide.

Bakker et al. (1985) have shown that there are variations in zooplankton biomass at the surface in the Oosterschelde of approximately 50% around the mean value during the tidal cycle. The variations are possibly caused by vertical migration of the zooplankton. These vertical movements could have a potentially large effect on zooplankton residual transport. However, at the present not enough data are available to make even an estimate of the direction of this residual flow: into or out of the Oosterschelde. It is thought (Bakker, pers. comm.) that there may be a net migration of zooplankton from the North Sea into the Oosterschelde in spring, and possibly an outward migration in autumn.

Despite the considerable uncertainty, it is not likely that migration plays a major role in zooplankton population dynamics: the Oosterschelde population is probably self-sustaining (i.e.: not dependent on a permanent import from the North Sea) and it is not likely that there is an important export of zooplankton from the Oosterschelde either. Even if there would be a net export or import, it is probably a relatively minor term in the population budget compared to e.g. assimilation or respiration. In view of the uncertainty in the latter terms, it seems unnecessary to include residual flow term: the (uncertainty in) model results is probably hardly influenced by assuming that net zooplankton migration is zero.

#### 4.6 Summary of model assumptions

The zooplankton model aims at the calculation of phytoplankton mortality as a result of zooplankton grazing. It describes the permanently planktonic zooplankton in the size range of 100 to 1000  $\mu\text{m}$  by a single state variable. The biomass of benthic larvae is described by an empirical periodic function of time. Their behavior is assumed to be identical to that of the true zooplankton.

Zooplankton feeds primarily on phytoplankton; the diet is supplemented by detritus if food concentration drops below a (low) threshold concentration. Particles smaller than 3  $\mu\text{m}$  diameter cannot be captured by zooplankton. In the model, it is assumed that a fixed fraction (28%) of the detritus falls below this size limit; of the phytoplankton, this fraction is set equal to the nutrient-limitation function of the phytoplankton.

The ingestion of zooplankton is independent of food concentration for the normal food levels found in the Oosterschelde. In the model, a linear dependence of ingestion on food concentration is assumed only below the above-mentioned threshold concentration. The ingestion rate further depends on temperature; this is modelled by an exponential function.

Assimilation is a fixed fraction of ingestion; literature values range from 40 to 80% of ingestion. Respiration is modelled as a temperature-dependent fraction of bodyweight per day. The temperature dependence is modelled again as an exponential function.

Mortality rate is modelled as proportional to zooplankton biomass itself, in order to simulate cannibalism and increased predation by macrozooplankton in periods of high zooplankton biomass.

Transport of zooplankton is modelled by exchange between the compartments within the Oosterschelde only. Exchange across the external model boundaries is unknown and set to zero. Residual flow is unknown for both internal and external boundaries in the model; it is set to zero throughout.

## 5 MINERALIZATION OF SUSPENDED AND DISSOLVED DETRITUS

### 5.1 Introduction: the choice of a mineralization model

This chapter discusses the modelling of mineralization, which can in general be defined as the conversion of dead organic carbon and organic nutrients to inorganic form. Excluded from this discussion are the processes taking place in the sediments on the intertidal flats: the processes of mineralization and primary production on these flats are closely coupled and are treated together in the chapter on microphytobenthos.

Two types of detritus are distinguished in the model: the first consists of organic carbon and nitrogen, the second of organic silicon. The reason for this distinction is that the cycles of carbon and nitrogen are closely coupled (all organisms contain carbon and nitrogen in similar ratios), but the silicon cycle is quite distinct, as only diatoms contain a significant amount of this element. The silicon in the remains of dead diatoms is further indicated as "detrital silicon", the other dead organic material simply as "detritus".

The main source of both types of detritus is the phytoplankton, which enters the detritus pool mainly via the faeces produced by benthic filter-feeders and zooplankton. This conclusion is based on the high filtration rates in the Oosterschelde (Smaal et al., 1987): it is estimated that the entire volume is filtered in a few days. Other sources of detritus are transport across the boundaries of the system and excretion by phytoplankton. The high grazing rate implies that the average age of the phytoplankton is low; it is therefore probably not necessary to take causes of mortality of the phytoplankton like senescence and fungal infections (Lund, 1965; Vermij, 1987) into account: these factors are thought to play a role in "old" populations (i.e., with a low turnover rate) of phytoplankton only (Lund, 1965). Apart from mineralization, detritus is consumed by filter-feeders and (to some extent) by zooplankton.

The various organic fractions in the detritus have very different decay rates (Laane, 1982; Van Es and Meyer-Reill, 1982). The entire range of decay rates is conveniently lumped into two fractions, a readily decomposable fraction and a fraction that resists decomposition for a long time, termed "labile" and "refractory", respectively (Smits, 1980). At the source (e.g. a dead organism), nearly all material is labile and only a small fraction refractory (Jewell and McCarthy, 1971). In the field, the composition of the detritus is usually shifted towards a high refractory fraction as a result of slow accumulation of the refractory material, and rapid disappearance of the labile part.

Another distinction is between dissolved and particulate detritus. The detrital silicon is particulate, but the organic carbon is partly particulate and partly dissolved. The distinction in two fractions may be important for their mode of transport, as was discussed in chapter 2.

In the mineralization process, three factors play a role: the concentration and nature of the substrate, environmental conditions (temperature, oxygen concentration) and the number and species composition of the heterotrophic bacteria which mediate most of the mineralization. The role of the last of these factors is at present not well understood. Although it is possible to count bacteria by special staining techniques (Van Es and Meyer-Reill, 1982), these counts are very time-consuming. In the Oosterschelde, only a limited number of bacterial counts is available (Laanbroek en Verplanke, 1984; Bijkerk, 1985). A major problem in the interpretation of these data is that only a fraction of the counted bacteria is actually active. Van Es and Meyer-Reill estimate this fraction at 6 to 60%. This uncertainty concer-

ning active biomass is increased by uncertainty concerning specific activity. There does not seem to exist a single, widely accepted technique to measure activity (Van Es and Meyer Reill, 1982; Laanbroek and Verplanke, 1984).

One point seems to be undisputed however: bacterial activity may not be exactly known, but it is certainly high. Bacterial growth rates may reach a doubling of biomass per hour if food and oxygen are not limiting. Paradoxically, their high activity makes it possible to exclude bacterial biomass from the present model: it will implicitly assumed that substrate availability is always the limiting factor in mineralization; this assumption results in a simple first-order model for mineralization.

For the detrital silicon a first-order model seems also appropriate. In this case, mineralization is not a biological process but is caused by the dissolution of the (particulate) detrital silicon (Smits, 1980; Yamada and D'Elia, 1984).

The following elements of the mineralization model are discussed in this chapter: the distinction of labile and refractory detritus in relation to decay rate, the temperature dependence of the process rates and the distinction of dissolved and particulate detritus.

## 5.2 The estimation of the parameters in the mineralization model

A first order model of mineralization can be formulated as:

$$M = k(T) * DET \quad (5.1)$$

with:  $M$  - mineralization ( $\text{mg.l}^{-1}.\text{day}^{-1}$ )

$k(T)$  - mineralization rate as a function of temperature ( $\text{day}^{-1}$ )

$DET$  - concentration of detritus ( $\text{mg.l}^{-1}$ )

$T$  - temperature

It should be noted that the distinction between labile and refractory detritus is more or less arbitrary: in fact there exist a large number of decay-rates ranging from very fast (time-scale of hours) for e.g. amino acids to very slow (years) for e.g. humic acids. In a detailed model, a subdivision of several classes of substrates could be made, but data are scarce for the Oosterschelde and such a distinction cannot be supported.

Data on mineralization of organic carbon in the Oosterschelde have been collected by Laanbroek and Verplanke (1984), Haas (1984) and Lemstra (1986). In these papers severe methodological problems are encountered. In the work of Laanbroek and Verplanke two methods are compared: oxygen-uptake and  $^3\text{H}$ -thymidine incorporation. Estimates of mineralization based on the first method are on the average 50 times higher than those of the second method; the authors are not able to indicate one of the two methods as wrong however. Further, they do not relate their results to the available substrate or environmental conditions, which makes these data not very useful for the estimation of parameters in the present model. Haas and Lemstra have monitored total, dissolved and particulate organic carbon in incubated samples for 10-14 days. Due to the low accuracy of their organic carbon determinations (10-20%), they are only rarely able to detect a decrease in total organic carbon at all.

In view of this uncertainty, it will be simply assumed that all detritus has a single decay rate. It will be assumed also that dead algae are entirely degradable: i.e. the refractory fraction of the algae is set to zero. Conversely, the decay-rate of refractory detritus is also set to zero, and it is further assumed that this detritus is neither a food-source for some animal. The refractory detritus is part of the model only to make a



comparison with observed particulate organic carbon (POC) measurements possible: it is, by definition, not part of the food-chain.

The labile and refractory fractions may also be distinguished by different nitrogen-to-carbon ratios: the N/C ratio of detritus is on the average lower than of living biomass (Parsons et al., 1984) and decreases with age (Stuart, 1982); a decrease in N/C ratio makes the substrate more refractory (Goldman et al., 1987). These observations can be incorporated into the model by assuming that the N/C-ratio of labile detritus is the same as of living biomass, but that of refractory detritus much lower. This assumption implies that the amount of nitrogen released during mineralization is simply the (fixed) N/C ratio times the amount of C-mineralization. A further discussion of the choice of a fixed N/C-ratio and its value in the model can be found in chapter 8.

In a review by Smits (1980) nearly all values of the decay rate of the labile fraction decomposing at 20 °C are in the range of 0.01 to 0.20 day<sup>-1</sup>. In models for oxygen concentration in relation to wastewater discharges (Streeter-Phelps models, e.g. Bella and Dobbins, 1968; Lee and Choi, 1985) all waste water is considered to have a single decomposition rate of 0.2 to 0.3 day<sup>-1</sup>. O'Kane (1980) presents a model that uses two decomposition rates at 20 °C: 0.05 day<sup>-1</sup> for the slow fraction and 0.25 day<sup>-1</sup> for the fast fraction. According to O'Kane the higher values are typical for situations with untreated fresh sewage; in natural waters the decay rate is lower. Therefore, the range mentioned by Smits will be used for the mineralization of carbon and nitrogen Oosterschelde model.

Dissolution rates for suspended detrital silicon vary from approximately 0.005-0.01 day<sup>-1</sup> (review by Lingeman-Kosmerchok, 1978; temperatures not mentioned), 0.02 day<sup>-1</sup> (Van Bennekom et al., 1974; temperature 12 °C) to values of 0.03 (10 °C) to 0.06 (20 °C) day<sup>-1</sup> (Kamatani, 1969). In the bottom sediments dissolution is slower as a result of the slow diffusion of silicate to the overlying water: silicate concentrations in the interstitial water may increase to an equilibrium concentration of approximately 10 mg.l<sup>-1</sup>, at which point net dissolution stops. Although maximal sediment-dissolution rates (i.e., at zero concentration of silicate) are in the same range as for suspended detrital silicon (0.004-0.025 day<sup>-1</sup>; Smits, 1980), actual sediment fluxes are considerably lower and range from negligible to 0.0025 day<sup>-1</sup>.

The decay rate of organic carbon and nitrogen is an increasing function of temperature. According to Smits (1980) and O'Kane (1980) this increase can be described by the usual Q<sub>10</sub>-formulation: the relative increase at 10 °C temperature increase is a constant (the Q<sub>10</sub>). Q<sub>10</sub>-values obtained in different experiments range from 1.5 to 2.5 (Smits, 1980; O'Kane, 1980).

The influence of temperature on the dissolution of particulate silicon appears to be fairly strong. The experiments of Kamatani (1969) give a  $Q_{10}$  of 2; Kremer and Nixon (1978) use a  $Q_{10}$  of 3 in their model on the basis of bell-jar experiments in Narragansett Bay, and the results of Yamada and D'Elia (1984) show a  $Q_{10}$  of 4.

In the treatment of the transport of detritus, it is assumed that all detritus is particulate. There are two observations supporting this assumption: in the first place more than 90% of the dissolved organic carbon (DOC) in the Oosterschelde is refractory (Wortelboer, 1984), as was found in the Ems-Dollard estuary also (Laane, 1982). The refractory DOC consists of large organic molecules; the small molecules (amino acids, small fatty acids) are present in very low concentrations, as they are an attractive substrate for the bacteria. The second observation is the fact that most of the bacteria can be found attached to particles (Laanbroek and Verplanke, 1984). Mineralization proceeds for the larger part by extracellular release of hydrolyzing enzymes by the particle-bound bacteria, followed by rapid uptake of the hydrolysis products (Van Es and Meyer-Reill, 1982).

The assumption that all labile detritus is particulate has a practical purpose only: in this way it is possible to treat detritus transport in the same way as POC transport, and to compare calculated detritus plus phytoplankton with measured POC. In theory, the state-variable LDET comprises all degradable detritus, and it is therefore possible to add the (soluble) extracellular release of phytoplankton to the LDET in the model.

Although the detrital silicon is entirely particulate, there is also some uncertainty concerning its transport: in the transport model, the behavior of the various particulate substances is not identical: for example, inorganic sediment shows a strong increase towards the bottom, phytoplankton hardly so, and POC shows an intermediate behavior. There are no data to estimate the behavior of detrital silicon in this respect; it is possible that it is homogeneously suspended over the water column, or that it behaves as suspended sediment with an inhomogeneous distribution over the water column and a large fraction resting on the bottom. This uncertainty may be translated into a range for the "dissolved-like fraction"  $x$  defined in chapter 2 between 0 and 1.

### 5.3 Summary of model assumptions

This chapter describes the decomposition of dead organic material. The microorganisms involved in the decomposition process are not modelled: their growth rate is sufficiently high to make substrate availability the limiting factor. It is assumed in the model that all biologically produced material can be decomposed. This decomposable material (labile detritus) represents only a part of all detritus in the Oosterschelde, because of the slow accumulation of refractory material. This accumulation is not modelled: refractory detritus is only passively transported in the present model.

Decomposition is modelled as a first-order decay. The decay rate at 20°C has been determined from literature values and ranges from 0.01 to 0.20 day<sup>-1</sup>. The decay rate is temperature dependent, with a  $Q_{10}$  of 1.5 to 2.5. The mineralization of nitrogen is modelled in the same way as that of carbon, assuming a fixed N/C ratio for the detritus, identical to that of living biomass.

The regeneration of silicate is not biologically mediated, but results from the slow dissolution of particulate silicon of biogenic origin; it is modelled as a first-order process. The decay rate is characterized by a  $Q_{10}$  of 2 to 4. Its value at 10 °C is 0.01-0.03 day<sup>-1</sup> in the water column and 0-0.0025 day<sup>-1</sup> in the sediment.

## 6. MICROBENTHOS: PRODUCTION AND MINERALIZATION ON INTERTIDAL FLATS

### 6.1 Introduction

The submodel describing primary production and mineralization on the intertidal flats is not described in detail in this thesis. Experimental results are given by Hofman et al. (1987, 1988) and De Jong et al. (1987a,b; 1988a,b); a model based on this work has been developed by Scholten, and is described elsewhere (Scholten et al., 1988). The present chapter is a summary of this last paper.

There are several links between the processes on the intertidal flats and those in the water column. In the first place, there is the rapid exchange of detritus between the sediment and the overlying water due to settling and resuspension. In the model there is only a single detritus state-variable, which is distributed over the suspended- and sediment-phases (with a seasonally varying distribution-coefficient, see chapter 2). This detritus forms a direct link between sediment and water. A second link is formed by the nutrients, of which the main pool is in the water column. They are consumed by benthic primary production and (for nitrogen only) denitrification; they are produced by benthic mineralization. Thirdly, oxygen from the water column is consumed by benthic mineralization during immersion of the flats; this is not balanced by oxygen production during photosynthesis: the produced oxygen is lost to the atmosphere, as benthic diatoms photosynthesize only when the flats are dry.

### 6.2 Microbenthos model summary

The physiology of benthic diatoms is quite similar to that of pelagic diatoms; the relations between light-intensity and primary production is modelled using the Eilers-Peeters model (see figure 3.2); the relation between nutrient concentration and growth rate is modelled using an hyperbolic saturation function (3.11), using the "minimum-law" for the combination of the nitrogen- and silicon limitations (3.12). In contrast to the phytoplankton-submodel, the microphytobenthos-submodel uses a fixed carbon-to-chlorophyll ratio.

Despite the similarities however, the benthic and pelagic diatoms require different models because of their different habitats. In the water column there is on the average 6  $\mu\text{g}$  chlorophyll per liter, or, with an average depth of 8 m, approximately 50  $\text{mg}\cdot\text{m}^{-2}$ . On the intertidal flats total biomass is higher (on the average 50-100  $\text{mg}\cdot\text{m}^{-2}$  chlorophyll; Daemen and De Leeuw-Vereecken, 1985), but the most important difference is that it is concentrated in a thin layer at the top of the sediment: half of the total biomass can be found in the upper millimeter (De Jong et al., 1987a).

This high concentration of biomass means that the pools of available nutrients are relatively very small; in particular, the inorganic carbon (benthic diatoms are probably able to use both  $\text{CO}_2$  and  $\text{HCO}_3^-$  -Ludden et al., 1985) is depleted within a few hours or less, if light conditions are favorable. If this happens, primary production can proceed only at a rate equal to the supply rate of inorganic carbon from the atmosphere and from mineralization.

Estimates of the  $\text{CO}_2$  flux from the atmosphere from literature data are very variable. The flux is determined by processes at the air/water boundary. A gradient develops both in a thin (micrometers) layer of air and in the water near the surface. Across this boundary,  $\text{CO}_2$  concentration decreases from its normal atmospheric value to its concentration in the water. The gradient in the air surface layer is strongly influenced by windspeed, in the water surface layer by  $\text{CO}_2$  consumption. Low estimates of the flux would make

its contribution to total CO<sub>2</sub>-availability for the diatoms negligible, high estimates of this flux would make it the major CO<sub>2</sub>-source for the diatoms.

The mineralization in the sediment is concentrated on the intertidal flats. In the sediment of the deep channels, the mineralization rate is less because of the lower oxygen concentrations (there is no primary production) and because of the lower substrate concentration (this is partly because detritus from dead benthic diatoms is largely absent and further because the instability of the sediment does not permit the settlement of the detritus from the water column (the channel bottoms are mostly sandy)).

In the deeper sediment layers oxygen is absent, and several anaerobic processes take place, where nitrate, organic compounds or sulphate are used as an electron-acceptor in mineralization. Of these processes, denitrification is the most important, in the first place because of its higher rate and also because the reduced organic and sulphur compounds generally do not accumulate in the sediment: at some later stage they are oxidized with oxygen in the upper sediment layers or the water column, and this pathway can in fact be regarded as a two-stage aerobic mineralization; the oxygen consumption by the oxidation of reduced organic and sulphur compounds is included in the estimates of aerobic mineralization. In contrast, denitrification is an irreversible process, and the N<sub>2</sub> escapes to the atmosphere.

The model of denitrification is a temperature-dependent first order decay of the detritus of which the rate is a hyperbolic saturation function of the dissolved inorganic nitrogen concentration in the water:

$$Dc = C \cdot r_{10} \cdot f(T) \frac{N}{K_m + N}$$

with:

- Dc        - denitrification rate (gC.m<sup>-2</sup>.day<sup>-1</sup>)
- C         - benthic labile detritus (gC.m<sup>-2</sup>)
- r<sub>10</sub>      - relative rate at 10°C and saturating DIN (day<sup>-1</sup>)
- f(T)      - exponential (Q<sub>10</sub>) temperature-function (-)
- N         - inorganic nitrogen concentration in water column (mg.l<sup>-1</sup>)
- K<sub>m</sub>       - half-saturation coefficient (mg.l<sup>-1</sup>)

The coefficient r<sub>10</sub> represents the maximal relative mineralization rate by denitrification at 10 °C attained at an abundant supply of nitrate in the water column. This rate is determined by transport-processes, i.e. the flux of nitrate from the water column. This flux is determined by a number of physical and biological processes (sediment porosity, diffusion coefficient, bioturbation). It has been estimated from literature data, but shows a wide range of values.

The sediment of the Oosterschelde is inhabited by a large number of grazers. For the model they have been classified into three groups: the depositfeeders, the meiobenthos and the snail *Hydrobia ulvae*. The depositfeeders and most of the meiobenthos are indiscriminate feeders that simply "filter" the sediment free from detritus and diatoms; the difference between the depositfeeders (e.g. *Arenicola marina*) and the meiobenthos (mainly Nematodes) is that the meiobenthos crawls through the pores of the sediment leaving it largely undisturbed, while the depositfeeders are responsible for a considerable reworking of the sediment (*bioturbation*): apart from direct consumption of benthic diatoms, diatoms die because they are buried too deep to reach the surface again. The third group of grazers lives on the surface of the sediment and grazes specifically on the diatoms at the surface.

The biomass of benthic grazers is a forcing function in the model. As in the case for the filterfeeders (see chapter 7), the accumulation and loss of biomass during the season is not incorporated in the carbon and nitrogen budget of the system; it is simply assumed that the grazed detritus and diatoms are immediately lost, partly as faeces and partly as respiration. The biomasses of the depositfeeders and snails have been estimated by Coosen and Van den Dool (1983); of the meiobenthos by Smol (1986). Grazing and bioturbation rates have been estimated by De Vooy (1986, 1987) and Smol (1986).

Apart from grazing losses, benthic diatoms may suffer from erosion, in particular during storms. As a result of the wave action, benthic diatoms may become buried deep under the sediment (Vos, 1986), or they are brought into suspension and deposited on the bottoms of the tidal channels. The resuspension of sediment as a result of storms is not modelled explicitly; instead the higher concentration in winter as a result of this resuspension is directly incorporated as a forcing function (equation 2.11). In the microphytobenthos model it is assumed that losses of biomass due to erosion are proportional to the ratio of sediment in suspension to total sediment.

## 7. MACROBENTHIC FILTERFEEDERS

### 7.1 Introduction

Macrobenthic filterfeeders in the Oosterschelde belong for the larger part to two taxonomically related species: the mussel (*Mytilus edulis*) and the cockle (*Cerastoderma edule*). A third group of filterfeeders is formed by species living on hard substrate: tunicates, brittle stars, oysters and sponges.

As the latin name implies, both mussel and cockle are edible and they are fished in the Oosterschelde. There are some important differences between the two species. The presence of mussels in the Oosterschelde is largely artificial: first year-class mussels ("seed") are collected in the Wadden Sea, and deposited in the Oosterschelde on special plots; during their life-cycle they are moved within the Oosterschelde several times by the mussel-growers (Coosen and Schoenmaker, 1985). Cultivation plots on the bottom are indicated on maps, and distributed among the mussel-growers by the Ministry of Agriculture and Fisheries. The population dynamics of cockles on the other hand are, apart from the fishery on adult cockles, completely natural. Another major difference between the two species is that cockles live for the larger part on intertidal flats, and mussels for the larger part subtidal.

The filterfeeders in the Oosterschelde have large biomasses (Coosen and Schoenmaker, 1985; Coosen and Smaal, 1985; Van den Hurk, 1987; Leewis, 1987), and exert a considerable influence on the ecosystem (Smaal et al., 1987). Suspended matter (seston) is filtered in large quantities and for the larger part deposited as pseudofaeces and faeces. This process influences phytoplankton mortality (Wetsteyn et al., 1985), sediment composition (Steyaert, 1983, 1985) and mineralization (Oenema, 1988).

The impact of the filterfeeders on the system can be considered as proportional to the product of their weight-specific activity coefficients and biomass; biomass can be separated into numbers and individual weights. Biomass of the three groups has not been treated as a state-variable, of which the value is calculated from growth and decline as the result of environmental conditions. It appears to be impossible to model the numbers of filterfeeders because they are determined almost entirely by processes outside the ecosystem. The number of mussels brought into the Oosterschelde from the Wadden Sea is determined by market prices and conditions in the Wadden Sea; the number of cockles is determined by reproductive success, which is not yet well understood (Beukema, 1982) and by fishery. Finally, the biomass of hard-substrate filterfeeders is limited by the subsurface area of bridges, dikes, and so on. For these reasons the number of filterfeeders is described as a forcing function in the model.

The individual weight of the filterfeeders is determined by factors that do form part of the model, like food and suspended sediment concentration, temperature and so on. However, food and filterfeeder weights were not treated as state-variables in a single model simultaneously, but treated separately. A coupled model (Radford, 1978; BOEDE, 1986) is difficult to manage and to calibrate as errors in the filterfeeder rate-coefficients tend to be compensated by (erroneous) food concentrations: for example, if filtration rate is overestimated, filterfeeder growth is initially too high also; however, as a result of the overestimated phytoplankton mortality, food concentrations drop, and filterfeeder growth returns to normal. In general, models treat either food concentration as a state variable (Kremer and Nixon, 1978; De Vries, 1987) or filterfeeder biomass (Verhagen, 1982), but not both. In the present case, where numbers could not be a state variable anyway, the individual weights were treated also as a forcing function. However, in order

to estimate the rate coefficients a separate model was developed in which the weights were a state variable and the food concentrations a forcing function; this model is described in appendix I.

The present model focuses on the grazing impact, and will try to establish a relation between filterfeeders biomass and large-scale food concentrations. The major process involved is the filtration of a large fraction of the volume of the Oosterschelde per day, which is the main cause of phytoplankton mortality. Part of the filtered material is converted to filterfeeders biomass, part to detritus. Eventually, all filtered organic matter is converted to inorganic carbon and nutrients. As will be discussed below, the filtration can be regarded as the major factor in this cycle; whether the organic matter is recycled via the detritus pathway or via assimilation followed by respiration by the filterfeeders is of secondary importance, as both pathways have similar rates. For this reason, attention is focused in the present discussion on filtering activity only.

From the viewpoint of filterfeeder growth, it does make a significant difference whether the filtered material is assimilated and respired later or lost as faeces. Therefore, assimilation efficiency and respiration are discussed in detail in appendix I. Although the formulations for these processes are not used directly in the present model (individual weights are forcing functions), they are included in the model in order to be able to calculate potential growth rate: this potential growth rate is used as an indicator of the overall effect of phytoplankton-, detritus-, suspended sediment concentrations and so on. For example, if phytoplankton biomass drops as a result of some change in the system (e.g.: lower nutrient supply, increased mussel cultivation), then the effect of this lower food supply on the filterfeeder growth rate would be of more interest for the mussel cultivation and cockle fishery than the phytoplankton concentration in itself.

The activity of the filterfeeders causes a strong coupling between the benthic and the pelagic system. In the chapter on transport it was discussed how a fixed-volume reference frame (that is moving with respect to the bottom) results in a considerable simplification of the transport-equations. In the model it is assumed that the benthos found at the bottom of a compartment in the mid-tide situation is fixed in that compartment, although in reality the watermasses are moving and filterfeeders from one compartment are filtering water from neighboring compartments for part of the time. The implications of this assumption are discussed in this chapter.

In the present model small-scale processes are not included. They may be of considerable interest because mussels (and, to a lesser extent, cockles also) occur in concentrated "beds": in the neighborhood of these beds, the deposition of faeces and pseudofaeces may cause problems (Kohsiek and Misdorp, 1983; Steyaert, 1983, 1985), or seston supply may be insufficient (Fretchette and Bourget, 1985; Verhagen, 1986; Dijkema et al., 1987). A model of these small-scale processes requires a detailed description of flows and mixing in the neighborhood of the mussel bed, on a time-scale of hours. This is beyond the scope of the present model. Therefore, the model should be considered useful only for the calculation of food availability for a more or less hypothetical potential mussel bed: it is possible that in an actual situation of low current speed, seston supply or the removal of (pseudo)-faeces would be insufficient for the cultivation of mussels, or that a too high current speed would erode the mussel bed.

The chapter starts with a discussion of the biomass data. Filtration activity is estimated and the effect of the fixed-volume reference frame on concentration distribution is discussed. In the final section, model assumptions are summarized.

## 7.2 Biomass of filterfeeders

In this section the elements of the forcing functions that describe macrobenthic filterfeeders biomass in the Oosterschelde are discussed.

### Cockles

The density of all soft-bottom macrozoobenthos in the Oosterschelde has been surveyed in 1983/1984; for the cockle additional surveys have been done in 1984 and 1985. A detailed study of numbers and individual weights of cockles has been done on a limited number of locations.

Biomass is calculated from density (weight per unit area) and the area of the compartments. For this purpose, the area of a compartment is split into three parts: a subtidal area proper, mainly consisting of the bottom of deep gullies which is morphologically very active (Van den Berg, 1986) and biologically poor; the intertidal flats, where most of the biomass is concentrated and the subtidal borders of these flats (from mean low water level (MLW) to MLW-1). Surface areas of these subdivisions of the compartments (for compartment borders, see figure 2.2) are given in table 7.1. The area of compartment 3 has been considerably reduced after 1983 because of the construction of a dam that closed off the Markiezaat area in the eastern part of the compartment (see figure 2.2).

Table 7.1: Surface area of the four Oosterschelde compartments in  $10^6 \text{ m}^2$ . Compartment no. 1 = west ("mouth"), 2 = middle, 3 = east ("kom"), 4 = north. In compartment 3 a dam has closed off the Markiezaat area in 1984: this is indicated by the "incl" (Markiezaat inclusive) and "excl" (exclusive) columns. "Hard substrate" indicates the subtidal area of stones etc. Data from Duin (1985) and Van den Hurk (pers. comm.)

compartment.:	1	2	3 excl.	3 incl.	4
intertidal	24.69	35.90	46.55	70.63	21.82
border	6.22	4.93	12.33	14.39	2.54
subtidal					
ex. border	74.98	65.76	32.69	38.16	20.27
inc. border	81.20	70.69	45.02	52.55	22.81
hard substrate	6.32	1.20	1.09	1.09	2.40

The density of cockles obtained from the 1983 zoobenthos survey and the 1984/1985 cockle-surveys are given in table 7.2. For the model-input the average value of both is used; furthermore, it is assumed that the difference between the two surveys (7-30% of average, mean 17%) is indicative of year-to-year variability.



**Table 7.2:** Yearly averaged density of cockles in the Oosterschelde compartments in gram ash-free dry weight (ADW) per square meter. Data from Coosen and Smaal (1985), table XVII. Densities in compartments 2 and 4 are lumped in their work.

compartment:	1	2+4	3	note
intertidal	53	26	9	(a)
	63		20	(b)
border	15	7	1	(c)
subtidal	0.6	0.3	0.07	(a)

(a) Oosterschelde zoobenthos inventory 1983

(b) Cockle survey 1984/1985

(c) J. Coosen, unpublished results of 1987

The activity of cockles is usually described by means of allometric relations ( $aW^b$ ), making it necessary to split the cockle population in year-classes; in the Oosterschelde, a distinction of three classes (0, 1 and  $\geq 2$  year) appears sufficient: cockles of 3 years and older are very rare (Pouwer, 1985). A description of the seasonal pattern of activity requires a description of both numbers and individual weights of the three classes. For this purpose, it is assumed that all cockle-populations in the Oosterschelde show a similar seasonal development with respect to mortality and growth.

Cockle mortality is caused by a number of factors which show a their most pronounced effects in different age-classes and seasons. Mortality due to physical factors (e.g. being buried too deep under the sand) acts most strongly in winter and on juvenile individuals; mortality due to fisheries acts more strongly on the adults; predation is mainly due to birds and to some extent to crabs and sea-stars; it is more pronounced in summer and spread out more or less evenly over the age-classes (big cockles are more attractive as prey but more difficult to handle).

A detailed description of the decrease in numbers with age is not available because of the high variability in the available records (see figure 7.1). This variability is due to sampling errors (the spatial distribution of the cockles can be very patchy) and to the fact that mortality is often strongly local: e.g. when a certain part of an intertidal flat is fished clear of cockles. For a description of the average decrease in numbers per square meter, it is assumed that relative mortality is a constant: this simple model is in agreement with the similar mortalities for different seasons and age-classes, and requires the estimation of a single coefficient only. It results in the following forcing function:

$$N(T) = N(0) * \exp(-cT) \quad (7.1)$$

with  $N(T)$  - no. of cockles at time  $T$

$T$  - time in days

$c$  - mortality rate ( $d^{-1}$ )

The differences in mortality rate, and therefore, age-structure of the populations within a compartment (Pouwer, 1985; Schoenmaker, 1985; Dijkema

et al., 1987) are of the same order of magnitude as those between the Oosterschelde compartments (Coosen and Smaal, 1985), which justifies the use of a single age-structure for all compartments in the present model.

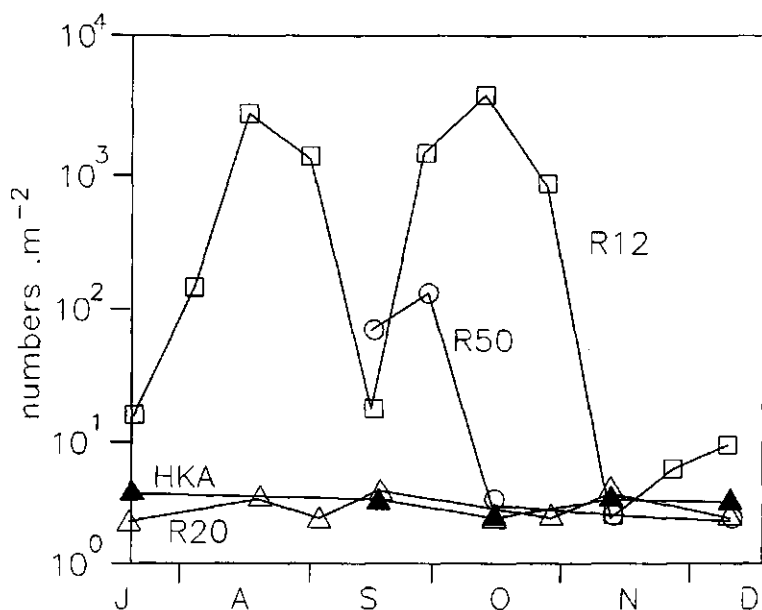
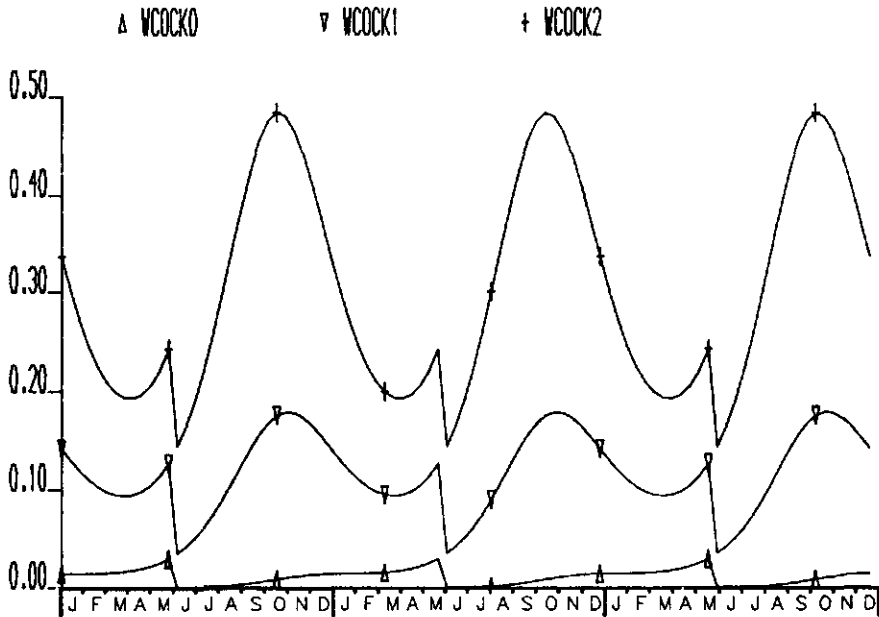


Figure 7.1: An illustration of the seasonal fluctuations in cockle density (in numbers per m<sup>2</sup>; logarithmic scale). Data from Pouwer, 1985. R12, R20 and R50 are three stations on the "Roggenplaat" in the mouth of the Oosterschelde, HKA is a station on the "Hooge Kraayer" flat in the eastern part of the Oosterschelde.

For a description of the development of individual weights the curve in figure 7.2 has been used. Again, this development appears to be highly variable, and local situation (e.g. exposition, density) causes differences in growth-rates within the compartments that are in the same order of magnitude as those between the compartments (Pouwer, 1985; Schoenmaker, 1985; Dijkema et al., 1987). Different growth-curves usually show a similar shape (peak in October, decline until April), but the maximum weight of a 2-year old cockle may vary between 300 and 600 mg adw. It may be expected that average figures show a considerably smaller variability however, and are close to the curve in figure 7.2. Furthermore, uncertainty in calculated activity resulting from differences in individual weights and population-structure of the biomasses from tables 7.1 and 7.2 are relatively small compared to uncertainty in biomass itself and in activity-coefficients (see below).



**Figure 7.2:** Seasonal development of individual weight of cockles (g adw) as used in the model; after J. Coosen, pers. comm. WCOCK<sub>i</sub> - weight of cockles in yearclass *i*. The sharp drop near dayno. 150 (modulo 360) marks the "birthday" of the cockles: 0-year old cockles reach the 1-yearclass, and new 0-year cockles are introduced. Note that the 0-, 1- and 2-year curves form a single smooth curve across the "birthdays".

#### Biomass of mussels

For the determination of mussel biomass, Coosen and Schoenmaker (1985) have interviewed a representative selection of the Oosterschelde mussel growers about the amount of juvenile mussels necessary to produce a given amount of adult mussels in different years and different areas in the Oosterschelde. From these data and the average amount of adult mussels that is brought to the market at Yerseke they have calculated total input of mussels into the Oosterschelde.

The distribution of the mussels over the three compartments that are used for cultivation is given in table 7.3. In compartment 3 (east) no mussels are cultivated.

Table 7.3: Fractions of the biomass of mussels of the three age classes in the three Oosterschelde compartments. Fractions do not add up to unity, because mussels are also grown in the Volkerak compartment (5), which was not included in the present model, but did form part of the analysis of Coosen and Schoenmaker.

comp.	seed	half.	cons.
1	.04	.04	.54
2	.52	.52	.30
4	.04	.04	.04

The input-output calculations of Coosen and Schoenmaker (1985) exclude natural populations of mussels. These are estimated to form less than 5 per cent of cultured stock. They are included in the "hardsub"-group.

The data from Coosen and Schoenmaker provide description of total biomass at the beginning and end of the season; because individual weights of mussels at the start and end of the season are known also, the data can be simply converted into numbers of mussels. Information on the development of numbers during the season is of a more indirect nature. In the middle and western compartments, numbers are slowly decreasing as a result of mortality. Mortality is distributed fairly evenly over the year: in spring, mussels suffer from the after-effects of being redistributed by the growers; in summer mortality is mainly caused by predation (sea-stars and birds), and in autumn and winter, storms cause mortality by erosion of the mussel beds. Therefore, the same equation (7.1) has been used to describe mussel mortality as for cockles.

The development of individual weights can be described by a sigmoidal growth curve, with a superimposed seasonal influence. The increase in shell-length stops in winter, and the body weight even decreases (Craeymeersch et al., 1986). The model uses as a forcing function an average seasonal curve for the Oosterschelde constructed on the basis of data from Coosen (pers. com.): see figure 7.3.

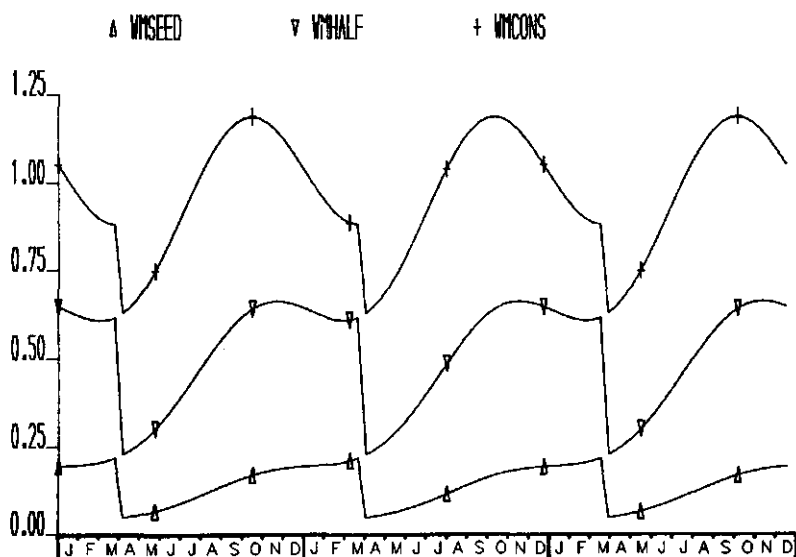
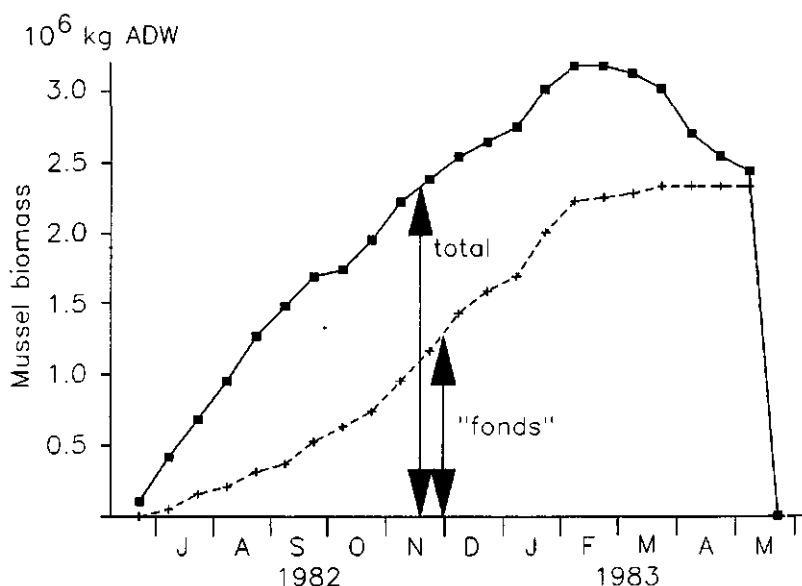


Figure 7.3: Seasonal development of individual weight of mussels (g adw) as used in the model; after J. Coosen, pers. comm. WMSEED: seed-mussels; WMHALF: juvenile mussels; WMCONS: adult mussels.

The eastern compartment of the Oosterschelde plays a special role in the mussel culture. It is not used for the usual mussel cultivation. Large quantities of mussels are brought in, both from the Oosterschelde and the Wadden Sea to be cleaned of sand and mud before they are sold. For this purpose, the mussels are stored for some days on areas with peat-bottoms. In addition, the compartment is used to store mussels in case the market prices drop too low. These mussels are distributed over the mussel growers and brought to other parts of the Oosterschelde at the end of the winter (April; see figure 7.4). In this way, the biomass in the eastern compartment depends strongly on market conditions and shows a high year-to-year variability (see table 7.4).



**Figure 7.4:** Typical development of biomass of mussels in eastern compartment. Lower curve gives "fonds" mussels, i.e. mussels dumped as a result of price-regulations. Upper curve gives cumulative amount of fonds-mussels plus mussels temporary stored for cleaning. (From Coosen and Schoenmaker, 1985).

The average amount of mussels in the eastern compartment shows large yearly fluctuations. Average biomasses for the 10-month mussel season are given in table 7.4. In the model seasonal biomass is modelled using a triangular function, with a steady increase during the season and a sharp drop at the end. The average height of this triangle is taken from table 7.4.

**Table 7.4:** Average biomass of mussels in eastern compartment during the mussel-season (july-april). In this compartment only adults occur. Data from Coosen and Schoenmaker (1985).

season	79/80	biomass	4.0	$10^6$ kg ADW
	80/81		3.9	„
	81/82		10.7	„
	82/83		16.8	„

#### Biomass of suspension feeders living on hard substrate

The hard substrate to which tunicates, sponges, limpets, oysters and other organisms are attached is mostly man-made: only small areas of hard-substrate occur naturally in the Oosterschelde: the fossil peat-banks in the eastern part. The remainder is made up of the subtidal stone reinforcements of the dikes, concrete constructions like the Zeeland-bridge and the storm-surge barrier. The total subtidal surface of these works is estimated by Van

den Hurk (1987) as 10.9 km<sup>2</sup>. This is mainly concentrated in the western compartment: see table 7.1.

Density has been estimated from five surveys during 1984-1986 (Van den Hurk, 1987; Leewis, 1987). The results are summarized in table 7.5. In this table the data from several stations and from autumn and spring-surveys are lumped. The variability of individual density determinations was too high (30-50% variability coefficient) to detect significant differences between them. The group "remainder" consists partly of detritus and micro-organisms, which are, of course, no filterfeeders. Also included in this group are the sea-anemones. These may be regarded as filterfeeders in some sense, but they are not included here as they are carnivores.

Table 7.5: Average density (in g ADW m<sup>-2</sup>) of organisms attached to hard substrate in the Oosterschelde. Data from Van den Hurk (1987).

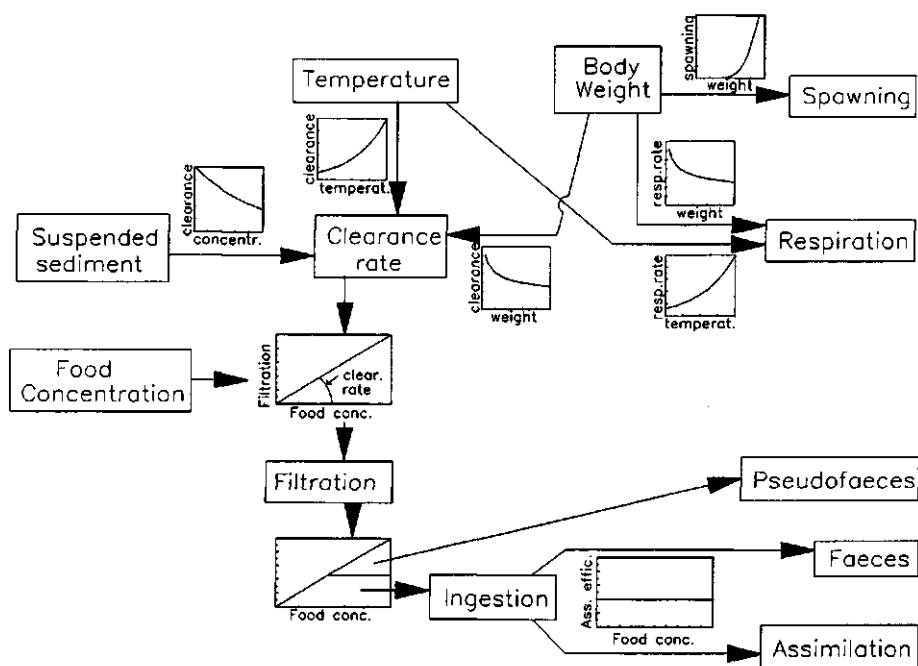
Group I	Tunicates	33	73
	Limpets and Mussels	19	
	Oysters	21	
Group II	Sponges	54	85
	Hydroids	27	
	Brittle stars	4	
Remainder			85
(of which Sea-anemones		46)	

### 7.3 Activity of filterfeeders

#### Introduction

In this section attention is focused on the activity of the filterfeeders in relation to large-scale carbon and nutrient flows: filterfeeders play a key role in phytoplankton mortality and nutrient regeneration. A different viewpoint is taken in Appendix I, where the activity of cockles and mussels is related to their observed growth in order to estimate the parameters in the activity model.

A generalized description of the activities of filterfeeders is given in figure 7.5: the animal pumps water through the gills and part of the particles is retained (filtration); this process is influenced by body weight, temperature and particle concentration. Part of the filtered material is rejected before ingestion (pseudofaeces), the rest is ingested. Of the ingestion, a fraction is assimilated, the rest is faeces. The respiration is again a function of bodyweight and temperature, and finally the adult animals lose weight in spring by spawning.



**Figure 7.5:** Processes in filterfeeder carbon budget; the graphs give the approximate form of the functional relationships. Both respiration and clearance rate (expressed per unit of bodyweight) are decreasing functions of weight and are positively influenced by temperature; suspended sediment concentration has a negative effect on clearance rate. Filtration is the product of clearance rate and seston concentration; above a certain threshold part of the filtration is rejected as pseudofaeces, the rest is ingested. Of the ingested material, part is assimilated and part becomes faeces.

The energy budget of macrobenthic filterfeeders is summed up by Bayne and Newell (1983):

$$C = P + G + R + F + U \quad (7.2)$$

- with: C - gross consumption (the amount of food filtered from the water)  
 P - somatic production (growth)  
 G - reproductive output (spawning)  
 R - respiration  
 F - egestion (faeces + pseudofaeces)  
 U - excretion

The P and G-terms are lumped as total production. The excretion of organic matter (e.g. slime) forms part of the digestion process and is usually small; in practice it is included in measurements of faeces and pseudofaeces. If



production is not measured directly but inferred from the budget, it is called scope-for-growth (SFG; Bayne and Newell, 1983):

$$\text{SFG} = C - R - F (-U)$$

(7.3)

A rough estimate of the terms in the budget learns that the production term is much lower than the consumption. For mussels, yearly production per unit of biomass (P/B) is in the order of  $0.5-4 \text{ y}^{-1}$  (Craeymeersch et al., 1986); filtration rate for an average mussel ( $\pm 0.4 \text{ g C}$ ) is approximately  $1 \text{ l.h}^{-1}$  (discussed below), with POC concentrations in Oosterschelde of  $1-2 \text{ mg.l}^{-1}$ , this would give a consumption of approximately  $30 \text{ gC.gC}^{-1}.\text{year}^{-1}$ . For the cockle a similar low efficiency can be calculated (Coosen and Smaal, 1985). Clearly, most of the gross consumption is not converted to biomass, but lost either as respiration or egestion.

In the carbon cycle of the Oosterschelde, the filterfeeder activity may be broadly summarized as (1) they cause a flow from phytoplankton to the detritus pool and (2) they enhance nutrient regeneration both directly (by their own respiration) and indirectly (by the formation of detritus). The distinction between direct and indirect regeneration is meaningful only if the respiration rate of the filterfeeders would be significantly different from the mineralization rate of detritus. For the mussels we have an estimated rate (discussed in appendix I) of  $0.005-0.02 \text{ day}^{-1}$ , for the cockles of  $0.01-0.03 \text{ day}^{-1}$  and for aerobic decomposition of suspended detritus (see chapter 5) of  $0.01-0.20 \text{ day}^{-1}$ ; the decomposition rate of detritus in the subtidal sediment is not known, but probably considerably lower (see chapter 6). These figures suggest that both pathways result in comparable regeneration rates of the nutrients. Stated otherwise: for the nutrient- and carbon cycles in the Oosterschelde, the consumption is the most important process, the subsequent division between assimilation, and (pseudo)faeces is of secondary importance. Therefore, attention in this section focuses on consumption; assimilation efficiency is treated in less detail.

The treatment of filterfeeder biomass as a forcing function poses a technical problem in the nutrient bookkeeping. If biomass is a state-variable, the addition of organic nutrients to this pool by assimilation and the release of inorganic nutrients by respiration are implicitly balanced by increase or decrease in biomass, which is zero in the long run. This is both the case for the cockle population (which is neither continually increasing nor decreasing in size) and for the mussels, where the input in total biomass of juvenile mussels from the Wadden sea approximately equals the harvest of adult mussels (Coosen and Schoenmaker, 1985).

If biomass is not a state variable, the same equations (assimilation, respiration) for nutrient uptake and -release can still be used, but now there is no longer an implicit check whether the budget is balanced, and a permanent "sink" of nutrients (in case we underestimate respiration relative to assimilation) or alternatively a source could be created. This danger is not imaginary, as the gain- and loss-terms in the budget are nearly equal (discussed above) and only approximately known (see appendix I). Instead, a simple alternative has been used by neglecting the pool-addition and depletion terms: respiration is simply equated to assimilation in the model.

This approach is attractive because of its simplicity, its closed budget, and because the resulting seasonal pattern of assumed respiration is approximately correct: temperature and bodyweight have similar influences on both assimilation and respiration. However, it is clear that there is a

systematic error because, in reality, organic nutrients are stored in the filterfeeder biomass during summer, with a net release during winter.

The magnitude of this error in relation to the size of the total nutrient pool can be estimated as follows. An estimate of nutrients in inorganic form ( $\pm 0.7$  mg/l) and organic form (N:C-ratio times POC content:  $0.14 \times 1.5$  mg/l) in the watercolumn (average depth  $\pm 8$  m) gives a N-pool of  $7.3$  g/m<sup>2</sup>. An average (over the entire Oosterschelde surface) biomass of cockles (the main filterfeeders) of  $11$  g ADW/m<sup>2</sup> is approximately  $5.8$  gC/m<sup>2</sup> or  $0.82$  gN/m<sup>2</sup>. A typical seasonal pattern in biomass (combining the effect of numbers and individual biomass) is a twofold increase from spring to autumn, i.e. seasonal fluctuations constitute  $1/3$  of the average biomass, or  $0.27$  gN/m<sup>2</sup>. This comparison is not complete (nutrients are present also in e.g. bottom detritus, microphytobenthos and so on, and filterfeeders should include mussels also). However, it can be concluded that nutrients stored in filterfeeders constitute only a few per cent of total nutrient pool so that the assumption of a respiration equal to assimilation has a negligible effect on nutrient budgets only.

Because of this assumption, the only terms of the filterfeeder budget are gross consumption and assimilation. However, a description of respiration is not omitted even though respiration is not included as an independent term in the carbon budget. Without actually using the scope-for-growth (equation 7.3) in growth calculations, it is calculated, both as a check as on calculated terms in the budget and to be used as a "filterfeeder-oriented" summary of the model results. As the reproductive effort is not included in the definition of scope for growth, it can be omitted entirely in the present context.

In order to estimate the rate coefficients in the present model, a separate model has been developed in which individual biomass is not a forcing function but a state-variable. This makes it possible to compare calculated biomass with observed values in order to decrease the uncertainty in the rate coefficients resulting from literature and experimental data. As has been mentioned before: from the viewpoint of filterfeeder growth, small differences in assimilation efficiency or the question of reproductive effort do make a big difference. Therefore, appendix I contains a more thorough discussion of the processes of assimilation, respiration and reproductive output.

#### Clearance rate

Filterfeeders feed by pumping water containing food-particles over the gill, which sieves part of them out of the water. Instead of measuring pumping rate and retention efficiency separately their combined effect is directly obtained by measuring the decrease in particle concentration in an experimental vessel. The total decrease in suspended matter is called the filtration (mg/h), division by particle concentration (mg/l) gives the clearance rate (l/h). The measurements could be biased because the filterfeeders produce particles also, both in the form of material rejected before ingestion (pseudofaeces) and as faeces. However, these particles are generally much larger than the food particles and they settle on the bottom near the filterfeeder; their (negative) contribution to clearance rate is usually considered negligible.

The clearance rate of macrobenthos is generally related to body weight, temperature and suspended matter (seston) concentration. The clearance for a fixed temperature ( $t$ ) and seston concentration ( $s$ ) is written as  $CR_{t,s}$ . The relation to body weight is expressed as:

$$CR_{c,s} = a W^b$$

(7.4)

with:  $CR_{c,s}$  - clearance rate in  $l.h^{-1}$  for temperature  
 $t$  and seston concentration  $s$   
 $W$  - body weight (gram dry flesh weight)  
 $a, b$  - coefficients

As the influence of both temperature and seston concentration are not clear (discussed below), literature values for the coefficients  $a$  and  $b$  (listed in table 7.6) are discussed first without reference to these environmental conditions.

**Table 7.6:** Literature values for the coefficients relating clearance ( $l.h^{-1}$ ) to body weight (g dry flesh):  $CR = a W^b$  for the mussel *Mytilus edulis*. To make a comparison easier, the clearance for a 0.8 g mussel has been calculated.

$a$	$b$	$CR_{(W=0.8g)}$	$t^{\circ}C$	reference:
1.27	0.38	1.17	14	Review by Bayne (1976)
1.66	0.49	1.49	15	,,
2.21	0.27	2.08	-	,,
3.85	0.25	3.64	10	,,
4.79	0.26	4.52	10	,,
4.21	0.11	4.11	21	,,
3.05	0.34	2.83	21	,,
2.41	0.74	2.04	12	,,
3.90	0.60	3.41	10	,,
1.94	0.39	1.78	15	,,
1.31	0.73	1.11	12	Winter (1978)
7.45	0.66	6.43	12	Mohlenberg & Riisgard ('79)
1.63	0.39	1.49	0	Thompson (1984)
1.87	0.50	1.87	0	,,
1.49	0.23	1.41	2	,,
1.64	0.47	1.47	5	,,
1.94	0.40	1.77	5	,,
1.70	0.51	1.52	7	,,
1.99	0.38	1.83	8	,,
1.75	0.48	1.57	9	,,
1.84	0.41	1.68	10	,,
1.35	0.34	1.25	15	,,
1.08	0.10	1.06	-	Smaal (1985)
1.28	0.44	1.16	-	,,
0.98	0.85	0.81	-	,,
2.03	0.71	1.73	-	,,
2.87	0.36	2.65	-	,,

The extremely high values obtained by Mohlenberg and Riisgard (1979) have not been considered further. Excluding these values, a range in  $a$ -values of approximately 1.0 - 4.8 and in  $b$ -values of 0.1-0.8 results. This yields clearance rates for an averaged-sized mussel (0.8-gram) from 1.2 to 4.5  $l.h^{-1}$ .

Data on the relation between body weight and clearance for the cockle are more scarce. Literature values are listed in table 7.7

Table 7.7: Literature values for the coefficients relating clearance ( $l.h^{-1}$ ) to body weight (g dry flesh):  $CR = a W^b$  for the cockle Cerastoderma edule. To make a comparison easier, the clearance for a 0.4 g cockle has been calculated.

a	b	CR <sub>(w=0.4)</sub>	t°C	reference:
2.00	0.58	1.18	10	Vahl (1973)
11.6	0.70	6.11	11	Mohlenberg & Riisgard ('79)
1.93	0.30	1.47	16	Newell & Bayne (1980)
1.53	0.55	0.92	16	„
4.90	0.73	2.51	8	„
12.2	2.45	1.29	11	„
2.34	1.31	0.70	13	„
3.89	1.66	0.85	14	„
0.74	0.24	0.59	13	„
2.66	0.45	1.76	15	Vonck & Smaal (1986)
2.82	0.42	1.92	14	„
2.50	0.44	1.67	14	„
3.20	0.56	1.92	13	„
3.02	0.55	1.82	12	„
2.24	0.50	1.42	12	„
2.69	0.57	1.60	11	„
2.02	0.53	1.24	10	„
2.54	0.63	1.43	10	„

The value reported by Mohlenberg and Riisgard is again much higher than other clearance rates, and is further disregarded. Two of the combinations of (a,b)-values of Newell and Bayne (1980) appear to be out of the normal range also: in the combination (12.2,2.45) both a and b are higher, and in the combination (0.74,0.24) both are lower than the normal range. Excluding these values, a range of a-values of 1.5-5, and in b-values of 0.3-1.0 results. Clearance for an averaged-sized cockle (0.4 gram) ranges from 0.7 to 2.5  $l.h^{-1}$ .

For hard-substrate organisms Van den Hurk (1987) has reviewed existing literature, and performed additional measurements in the Oosterschelde. Data on the relation between clearance and body weight are listed in table 7.8. For some of the data, clearance is expressed in  $l.h^{-1}.gram$  body-weight $^{-1}$ , implicitly assuming a b-value of 1.

**Table 7.8:** Relation between clearance and body-weight from literature review and measurements by Van den Hurk (1987) for several species of hard-substrate filter-feeders. Clearance in  $l.h^{-1}$ , weight in g dry flesh; a and b values in equation  $CR = a W^b$ .

	a	b	
Tunicates:			
<u>Ascidella aspersa</u>	54.4	1.05	(1)
„	46.4	0.84	(1)
<u>Pyura stolonifera</u>	8.15	0.70	(1)
„	15.6	1.08	(1)
<u>Molgula manhattensis</u>	10.0	1	(2,3)
<u>Ascidella scabra</u>	4.0	1	(2,3)
<u>Styela clava</u>	0.83	0.44	(3)
„	1.90	0.84	(3)
<u>Ciona intestinalis</u>	4.7	1	(2,3)
Brittle star:			
<u>Ophiotrix fragilis</u>	1.6	1	(2,3)
Sponge:			
<u>Halichondria panicea</u>	0	-	(3)
(1)	literature review by Van den Hurk (1987)		
(2)	b value of 1 assumed		
(3)	measurements by Van den Hurk (1987)		

Table 7.8 clearly shows the heterogeneity of the hard-substrate organisms, even if only the taxonomically related tunicates are considered. For the Oosterschelde, an accurate species composition is not known, and furthermore, for a number of species no filtration data exist: the zero-value for the sponge in table 7.8 reflects, of course, experimental problems in measuring low filtration rates rather than the absence of any feeding in sponges. The total filterfeeding hard substrate biomass consists for approximately 45% of bivalves and tunicates (group I in table 7.5) and for 55% of sponges and brittle stars (group II in table 7.5). For this mixed group a rough estimate of average clearance of 1.5 (range 1-2)  $l.g^{-1}.h^{-1}$  at 15 °C is used in the model.

#### Temperature and clearance

In the discussion of the effect of temperature two restrictions are made. Firstly, only temperatures below the optimal temperature are considered. Water temperature, at least in the subtidal areas, seldom exceeds 20 °C. It is not to be expected that filterfeeders suffer from a decline in activity as a result of too high temperatures (i.e. temperatures above  $\pm 25$  °C). Therefore, only the intermediate range of temperatures that have a positive (or at least non-negative) effect on activity can be considered.

A second restriction is that only slow temperature-changes are considered. It is known that sudden changes in temperature have a very different

effect on activity during the first days than after one or more weeks (Widdows and Bayne, 1971; Schulte, 1975): for marine animals, the reactions typical of sudden temperature-changes can be regarded as laboratory-artifacts and have little relevance in nature.

Data on acclimated temperature response of the mussel Mytilus edulis range from no response at all (Widdows and Bayne, 1971; Widdows, Fieth and Worral, 1979; Thompson, 1984) to a fairly high  $Q_{10}$  of 3. (Schulte, 1975 for the range 5-20 °C). In view of the uncertainty about any temperature effect at all, it seems unnecessary to describe the temperature-response of the mussel by different  $Q_{10}$ 's for various ranges in temperature (as in Schulte, 1975).

For the cockle Cerastoderma edule there is only one paper on the relation between filtration and temperature: Newell and Bayne (1980) found no significant relation between them. Apart from direct measurements there is some indirect evidence for an increase in activity of the cockle with temperature. De Vooys (1985) mentions the remarkably fast growth of cockles in southern Portugal. Also, the growth-rings of cockles and mussels that are caused by a slower growth in winter point to a lowered activity. Perhaps a  $Q_{10}$  -range of 1 to 3 would be applicable for the cockle also.

For tunicates, a clear temperature-dependent increase in activity was found by Van den Hurk (1987). He reports a five-fold activity increase as a result of a temperature-increase from 4.3 to 11 °C. These results are based on a limited number of data, and an extrapolation to a 100-fold increase in activity in the entire range of 0 to 20 °C in the Oosterschelde would probably be an exaggeration. For this group, the model uses a  $Q_{10}$  of 3, range 2-4.

The uncertainty in the effect of temperature on cockles and mussels implies that it is not possible to correct the a- and b-values in tables 7.6 and 7.7 for temperature dependency. The uncertainty in a- and b-values for hard-substrate organisms is mainly a result of the heterogeneity of this group: it is hardly reduced by a temperature correction.

#### Particle concentration and clearance rate

It is generally found that high particle concentrations cause a depression in clearance rate of both Mytilus and Cerastoderma. However, the concentration at which this occurs differs markedly for various experiments.

In experiments with algal cultures, the concentrations are recorded in cells.ml<sup>-1</sup>. It appears however (Foster-Smith, 1975a) that the species of algae used has a considerable effect on the results: smaller cells cause less inhibition than larger cells. It seems therefore more appropriate to express seston concentration in mg ash-free dry weight (ADW).l<sup>-1</sup>. For the most commonly used species of algae (Phaeodactylum tricornutum), the approximate conversion of 10<sup>6</sup> cells = 0.07 mg ADW (Widdows, 1978) has been used.

Widdows (1978) found no effect on the clearance of Mytilus edulis (concentrations up till 1.4 mg.l<sup>-1</sup> pure algae). Foster-Smith (1975b) found no depression until 50 mg ADW.l<sup>-1</sup> (both pure algae and mixture of algae and inorganic particles). Vonck and Smaal (1985) and Prins and Smaal (1987) found no depression in clearance with natural seston concentrations in the range of 0-22 mg ADW.l<sup>-1</sup>. In contrast to these results, Schulte (1975) found a steady decline in filtration from 10<sup>6</sup> - 10<sup>8</sup> cells.l<sup>-1</sup> (pure culture of Platymonas suecica; equivalent to approximately 0.7-7 mg.l<sup>-1</sup>). Widdows et al. (1979) found a decline in clearance for the entire range of (natural) seston between 3 to 100 mg.l<sup>-1</sup>.

It appears that a functional relation of the form

$$CR_{T,W}(S) = CR_{T,W}(0) e^{-q S} \quad (7.5)$$

with:  $CR_{T,W}(S)$  - clearance rate as a function of  
seston concentration for some fixed  
body weight and temperature ( $l.h^{-1}$ )

$S$  - seston concentration ( $mg.l^{-1}$ )

$q$  - coefficient ( $l.mg^{-1}$ )

would fit the data of both Widdows et al. (1979) and Schulte (1975). Values of  $q$  range from 0 (no depression) to  $5.10^{-3} l.mg^{-1}$ .

For the cockle Cerastoderma edule there are less data on the relation between particle concentration and clearance. Foster-Smith (1975a) found a decrease in clearance at relatively (compared to the mussel) low concentrations of  $1-2 \cdot 10^6$  cells. $l^{-1}$  (pure Phaeodactylum culture; approx.  $7-14 mg.l^{-1}$ ). On the other hand, Newell and Bayne (1980) and Prins and Smaal (1987) found no significant relation between natural seston concentration (range  $5-25 mg.l^{-1}$ ) and clearance rate. Using the same formulation as for the mussel, the value of  $q$  would be in the range 0 (no effect) to  $0.02 l.mg^{-1}$  (clearance approximately halves from 0 to  $30 mg.l^{-1}$ ).

It is not known whether for the hard-substrate filterfeeders a relation between seston concentration and clearance rate exists. In the model, clearance is assumed to be independent of seston concentration.

The uncertainty regarding the relation between seston concentration and clearance makes it impossible to correct the a- and b-values in tables 7.6-7.8 for seston concentration.

#### Effects of aerial exposure

The influence of aerial exposure on filterfeeders in the Oosterschelde is limited to cockles, juvenile and "wild" (uncultivated) mussels. These groups are immersed approximately 18 hours per day (Coosen and Smaal, 1985; Craeymeersch et al., 1986). Cultured adult mussels and hard-substrate filterfeeders grow sub-tidally.

The effects of exposure on clearance rate, assimilation and respiration are discussed by Widdows and Shick (1985). It appears that there is no effect on assimilation efficiency. Of course, clearance stops during exposure, but the mussel recovers again soon after immersion. For the cockle, recovery is slower, but after 30 minutes 75% of normal clearance is already reached (Widdows and Shick, 1985). In the model, daily clearance is therefore proportional to immersion time.

#### Pseudofaeces

Although there is probably some reduction in clearance rate of cockles and mussels with higher seston concentrations, this effect is not very strong, and filtration increases (almost) linearly with suspended matter (seston) concentration. Instead of reducing their clearance, mussels and cockles limit their ingestion by rejecting an increasing part of the filtered material as pseudofaeces (see figure 7.6). Part of the ingestion is rejected later as faeces. The hard-substrate filterfeeders show a different mechanism: in this group, there is an increasing ingestion with seston concentration, but a negative relation between ingestion and assimilation efficiency (discussed below).

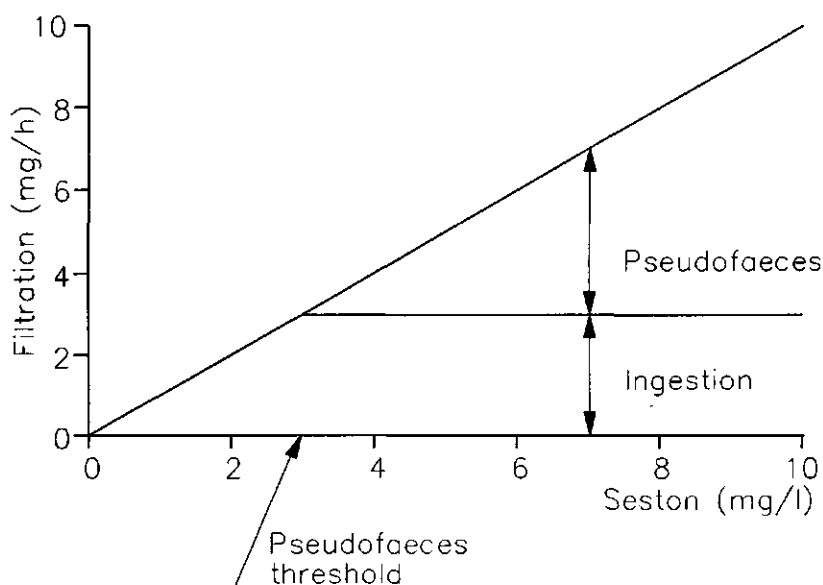


Figure 7.6: Filtration, pseudofaeces and ingestion according to the model of Verhagen (1982). The slope of the line through the origin represents clearance rate (here  $1 \text{ l.h}^{-1}$ ). Pseudofaeces threshold concentration is variable in the model; here  $3 \text{ mg.l}^{-1}$ .

In appendix I two possible models of pseudofaeces-production are discussed. In the first model, pseudofaeces is rejected in the same composition as the filtered material; according to the second model, the cockles and mussels are able to select (at least part of) the food from the pseudofaeces. The two models are incorporated into the present model by means of the concept "aselect-pseudofaeces" (APSF), which is defined as the pseudofaeces rejected without selection; the organic material is ingested from the remainder of the faeces. In the first model, all pseudofaeces is rejected without selection and APSF is simply equal to the standard concept of pseudofaeces. The other extreme is that the filterfeeders are able to select all food from the filtered material, i.e. the pseudofaeces consists entirely of inorganic material; there is no organic pseudofaeces, and ingestion is equal to the filtered amount. This situation may be modelled by setting the APSF-threshold to a concentration higher than that observed in the field. Of course, the selection efficiency may be lower than 100%, and probably decreases with filtered amount. This may be expressed by setting the APSF threshold to some intermediate value: above the level of pseudofaeces formation, but below the concentration in the field. A numerical example of the model is given in table 7.9



**Table 7.9:** Three examples which show the effect of the "aselect pseudofaeces model". In all examples the concentrations of organic and inorganic matter are 1 mg/l and 9 mg/l, respectively. clearance rate is 1 l/h; pseudofaeces threshold is 3 mg/l, and assimilation efficiency is 40%. All data in the table are in mg/h.

1. no selection: APSF-threshold = 3 mg/l  
(equivalent to model of Verhagen, 1983)

	organic	inorganic
aselect pseudofaeces	0.7	6.3
selected pseudofaeces	-	-
ingestion	0.3	2.7
assimilation	0.12	
faeces	0.18	2.7

2. complete selection: APSF threshold > 10 mg/l

aselect pseudofaeces	-	-
selected pseudofaeces	0.0	6.3
ingestion	0.3+0.7	2.7
assimilation	0.4	
faeces	0.6	2.7

3. partial selection: APSF threshold = 6 mg/l

aselect pseudofaeces	0.4	3.6
selected pseudofaeces	0.0	2.7
(selection efficiency = $0.4/0.7 = 57\%$ )		
ingestion	0.3+0.3	2.7
assimilation	0.24	
faeces	0.36	2.7

The calibration of the mussel and cockles models to observed weights in appendix I supported the selection-model: the APSF-levels were 20-60 for cockles and 30-70 for mussels, which is generally above the actual pseudofaeces thresholds for both groups, and in the upper range of seston concentrations observed in the Oosterschelde.

#### Assimilation efficiency

Assimilation efficiency of cockles and mussels is treated as a constant in the present model. Several relations with physiological and environmental variables that have been proposed in the literature (e.g. with weight, temperature, ingestion) are discussed in appendix I. It appears that these relations are either not consistent (e.g.: a positive effect was found in some experiments, but no or even a negative effect in others) or that they are based on apparent experimental artifacts (e.g., feeding mussels pure algal cultures or very low food concentrations). A calibration of the model to mussel and cockle data gave a range of values of 10-50% and 5-35%, respectively.

For the hard-substrate filterfeeders, there are data only for the Tunicates, measured by Van den Hurk (1987), who has also done a literature-

survey. Both in the Oosterschelde and in the literature, a relation between the fraction of organic matter in the food and the assimilation efficiency is found: in his own work the AE increases from 30-40% at 10% organic material, to 75-85% AE at 50% organic material. In the model the following functional relation is used:

$$AE = AE_{max} \cdot POMq / (POMq + 0.15) \quad (7.6)$$

with: AE - assimilation efficiency

$AE_{max}$  - maximum assimilation efficiency

POMq - fraction of organic material in the food

The value of  $AE_{max}$  has a range of 0.85 to 0.95.

### Respiration

As has been mentioned, respiration is calculated in the present model only to estimate scope-for-growth of cockles and mussels; it is not used in further calculations. The relation between body weight and respiration is expressed in the same manner as in equation 7.4:

$$R_e = x W^y \quad (7.7)$$

with  $R_e$  - respiration in ml  $O_2 \cdot h^{-1}$  at some fixed temperature

W - dry body weight in gram

x,y - coefficients

x is described as a function of temperature using the standard Q10 formulation. The calibration to cockle and mussel weights in appendix I yielded the following ranges:

	mussels	cockles
x	0.16 - 0.23	0.2 - 0.33
y	0.45 - 0.9	0.7 - 1.0
Q10	1.0 - 2.0	1.2 - 2.2

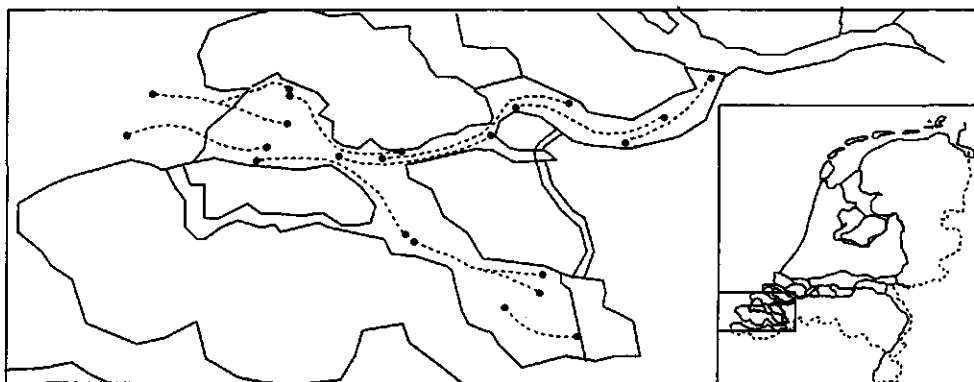
## 7.4 Benthic filterfeeders in a moving reference frame

### Introduction

In chapter 2 the fixed-volume reference frame of the model was introduced: the model describes water masses which are moving with respect to the shore (and bottom) as a result of the horizontal tide. From a pelagic viewpoint this choice is obviously convenient, but it causes problems in the coupling with the benthic system: in a fixed-volume reference frame the bottom is moving with a period of the tidal cycle. In the Oosterschelde, the tidal excursion is approximately 15 km (see figure 7.7), which means that the water which resides at mid-tide in compartment 2 is partly moved to compartment 1 at low tide, and to compartment 3 at high tide. This implies that filterfeeders fixed at the bottom of a compartment, may feed from the water from different compartments.

It should be stressed that these problems are not easily solved by choosing a fixed-bank reference frame: this choice would increase the complexity of nearly all model formulations and would reduce the time-step from days to hours. For example, the description of a stationary salinity or nutrient distribution in a moving frame would change from a constant into a periodic function; the calculation of primary production would be complicated by similar rapidly changing concentrations of phytoplankton (see, for example, results of fixed-point 13-hour measurements of Bijkerk, 1986) and by the changing volumes of the compartments (e.g. Gmelig, 1981).

Therefore, the present model uses a moving reference-frame; further it is assumed that the benthic filterfeeders feed from their mid-tide compartment only. Both approximations are examined in this section. It will be shown that the transition to the moving reference frame is actually a minor point; the second assumption has a potentially larger effect, but errors in the spatial distribution of the calculated phytoplankton concentrations appear to be acceptable relative to the scale of the model.



**Figure 7.7:** tidal excursions at various points in the Oosterschelde. The dotted lines describe the average paths of a volume-element during an entire tidal cycle. Redrawn after Dronkers, 1980.

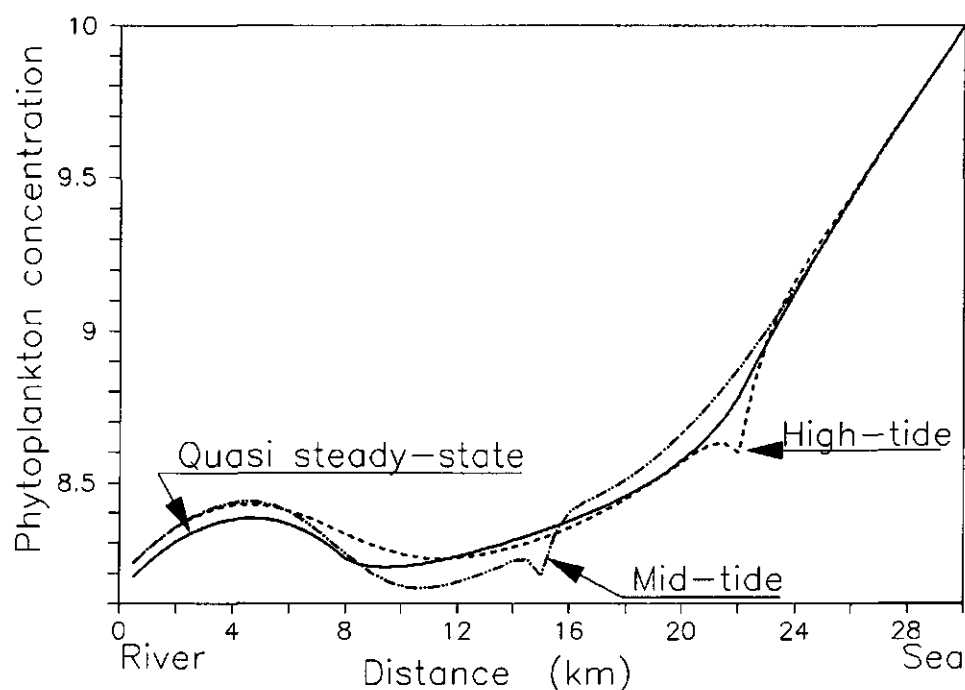
#### Quasi steady state approximation

For the purpose of illustrating these issues, a separate simplified model (allowing small time-steps) with a fine grid has been developed. The Oosterschelde is modelled as a 30 km long one-dimensional channel with a compartment-length of 500 m. For dispersion coefficient a value of  $200 \text{ m}^2 \cdot \text{s}^{-1}$  is used, with a residual transport of  $2.5 \text{ mm} \cdot \text{s}^{-1}$ . Primary production has a value of 0.1 unit of biomass per unit of volume per hour; "background" mortality is 1% per hour. This results in a steady-state concentration (slightly diminished by flushing) of 10 units, and a turnover of 24% per day. An amount of filterfeeders is added to this system capable of removing 10% of the phytoplankton per hour from a single compartment. Apart from putting these filterfeeders into a single compartment, they are also spread out in various ways in order to illustrate the effects of different model assumptions.

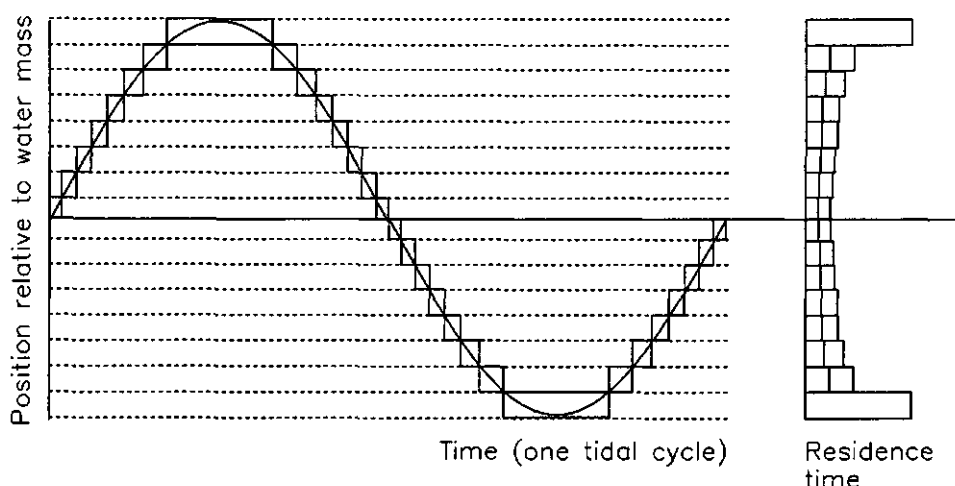
In the first run the filterfeeders are all located in a single compartment in the middle of the Oosterschelde. The moving reference frame was modelled by giving the filterfeeders a sinusoidal displacement with an amplitude of 7 km in the model. The resulting concentration distribution is given for mid-tide and high tide in figure 7.8. It can be seen that the two distributions are slightly different: in the high-tide solution a "dip" in the concentration can be observed at km 22 (this corresponds to the compartment where the filterfeeders are active at that moment); in the mid-tide solution a "dip" can be observed at km 15; more upstream the concentration is relatively low (these compartments have just passed the filterfeeders), more downstream the concentration is relatively high (these compartments have not been filtered for the longest time).

In a second run this distribution is approximated by spreading the filtering activity over the tidal excursion, taking into account the residence time, and applying this average filtration rate continuously. The filterfeeders are now no longer assigned a fixed position on the bottom, but distributed over the various compartments from which they feed: for example, if the filterfeeders feed for 1 hour during the tidal cycle (12.4 hours) from one of the compartments, then  $1/12.4$  part of the filterfeeders is assigned permanently to this particular compartment.

The procedure is analogous to that followed for discharges by O'Kane (1980): in the modelling of waste water discharges into an estuary, there is the problem of a moving water mass and a fixed discharge site. O'Kane spreads the discharges in a similar manner over the tidal excursion of the water to obtain a "quasi-steady-state" waste-water distribution. The term "quasi" points to the fact that this approach resolves the small time-scales of the tidal movement, but it is still possible to model longer-term changes dynamically. The quasi-steady state approach results in a filtration-distribution with two sharp peaks at the end-points of the tidal excursion: these represent slack water, and the longest residence times (figure 7.9).



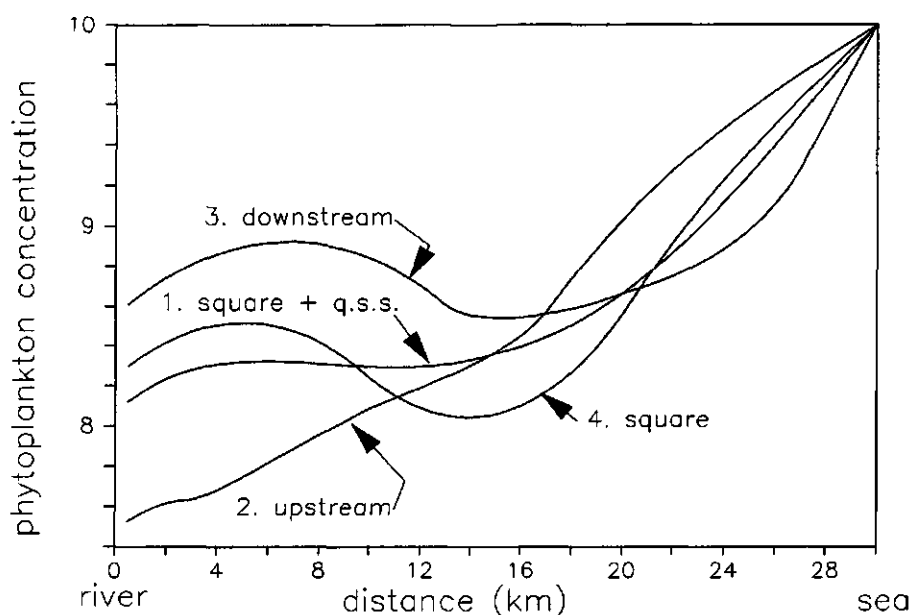
**Figure 7.8:** concentration of phytoplankton (arbitrary units) calculated using filterfeeders moving with respect to the water, shown for mid-tide and high-tide, and using the quasi steady-state approximation (see text).



**Figure 7.9:** The calculation of a "quasi-steady state" approximation of filterfeeder grazing. In the diagram to the left the position of the filterfeeders relative to the watermasses moving with the tide is shown. The rectangles give the time during which the filterfeeders are in a particular compartment. To the right these residence times are shown for all compartments; the quasi steady state approximation is obtained by permanently assigning to each compartment a fraction of the total filterfeeder grazing proportional to its respective residence time.

Figure 7.8 shows that the differences between the dynamical calculations (shown at two points in the tidal cycle) and the quasi-steady state approach are small. The difference between e.g. 11.4 hours of un-grazed phytoplankton growth and 1 hour of strong grazing on the one hand, or a permanent grazing with  $1/12.4$  of the peak-intensity on the other hand are apparently small.

It should be noted that this result can not be generalized: in a situation with a much lower dispersion coefficient or a much higher filtration (or analogously: the discharge of very reactive waste water) the quasi-steady state approximation would be less satisfactory. Obviously in these situations the present model with its time and space-scale would not be adequate. Field-measurements in the Oosterschelde (H. Haas, unpublished results) have never shown phytoplankton depletion near mussel beds, which appears to confirm the choice of parameters for the present model.



**Figure 7.10:** concentration of phytoplankton (arbitrary units) calculated by: 1) using the quasi-steady state approach, assuming that all filterfeeders are spread out evenly over the compartment ("square+qss"); 2) idem, assuming that they are concentrated at the upstream part of the compartment ("upstream"); 3) idem, assuming all filterfeeders at the downstream end ("downstream"); 4) filterfeeders spread out evenly over the compartment without taking into account water movements (as in the main model, termed "square").

#### Spatial distribution of filterfeeders

In the previous paragraph a single patch of filterfeeders, moving with respect to the fixed-volume reference frame was compared with the same amount of filterfeeders with a spatial distribution based on the residence time of the first peak. It appeared that such a two-peaked spatial distribution gave a good approximation of the effect of the moving filterfeeders. This indicates a method to calculate the filtration of bottom-fauna in a fixed-volume reference frame: calculate the filterfeeder density for every point along the axis of the estuary, approximate it with a quasi-steady-state distribution of filtration, and sum all the resulting distributions.

However, in the Oosterschelde a detailed spatial description of the distribution of the filterfeeders is not available. Even for the present coarse grid, which requires only the estimation of 4 average figures, data are relatively scarce and have a large uncertainty range. It is not possible to describe the distribution within the compartments further on the basis of the present data.

The effects of this coarse grid were investigated by introducing a coarse compartment of 10 km length (from km 10 to km 20) into the present detailed model. Four model-runs were compared in which the same amount of filterfeeders is spread out in different ways. In the first three, filter-

feeders are spread out according to the quasi-steady-state curve: 1) the filterfeeders are spread out evenly over the coarse compartment; 2) they are concentrated at the upstream or 3) at the downstream side of the compartment; in the fourth run, the filterfeeders are again spread out evenly over the coarse compartment, but now with the assumption that the filterfeeders feed only from their "own" (mid-tide) compartment without taking into account the tidal movement.

Within the coarse grid it would not be possible to distinguish runs 1, 2 and 3: they may be regarded as bounds to the error introduced by the coarse grid; run 4 is a convenient simplification: the error involved in this simplification can be compared with the error-bounds resulting from the coarse grid.

In figure 7.10 it can be observed that the simple rectangular block-filtration (run 4) remains for the larger part within the bounds set by runs 1, 2 and 3; only in the middle of the compartment the calculated concentration is too low. It should be noted that the actual situation the differences would be less, because in the present simulations it was assumed that there are no filterfeeders outside the middle compartment; in reality the filtration of filterfeeders that takes place outside their "own" compartment is largely compensated by filtration by animals from neighboring compartments.

It may be concluded that the error introduced by assuming that filterfeeders reside permanently in their respective mid-tide compartments is acceptable for the spatial resolution of the model.

### 7.3 Summary of model assumptions

In the Oosterschelde model the biomass of mussels, cockles and hard-substrate filterfeeders is described by empirical functions.

Mussel biomass is calculated from yearly numbers, obtained from market-supply and mortality data. These are multiplied by a seasonal description of individual weight. For cockles, numbers and individual weights are derived from field surveys. Both groups are distinguished into three size-classes. For the hard-substrate filterfeeders biomass is treated as a constant value.

Feeding by cockles and mussels is described as a slowly increasing function of body weight. Feeding decreases with suspended matter concentration and increases with temperature, both according to exponential functions. Part of the filtered amount is rejected without selection. This is termed a-select pseudofaeces to distinguish it from true pseudofaeces which may be subject to selection. The assimilation of ingested material is a fixed fraction, independent of food concentration and -composition, body weight and temperature. In order to have a closed budget for nutrient cycling, it is assumed that filterfeeder respiration is equal to assimilation.

Feeding by hard-substrate organisms differs from that of mollusks by the absence of a relation with particle concentration, the absence of pseudofaeces, and an assimilation efficiency that decreases with the fraction of inorganic material in the ingestion.

In the calculation of filterfeeder clearance, the movement of the water is not taken into account. A further simplification is made by assuming that the filterfeeders feed permanently from their respective mid-tide compartments.



## 8. STOICHIOMETRY

### 8.1 Introduction

The present model is primarily a carbon model, but includes also inorganic nitrogen and silica. This coupling of the cycles of several nutrients in a model requires information about the composition of all state variables. Another reason to know the stoichiometry of the state variables is the fact that many of the biomasses and processes are measured indirectly. For example, phytoplankton biomass is measured as chlorophyll (for a discussion of carbon to chlorophyll ratio: see chapter 3); benthic primary production is measured as oxygen production.

The composition of the state variables in terms of carbon and nutrients is in general different, and even a single group (e.g. phytoplankton) may show a composition that is dependent on environmental conditions. This may make a model which attempts to conserve mass during changing environmental conditions, and during for example, the conversion of phytoplankton biomass into zooplankton biomass and detritus, quite complicated. In theory, keeping track of carbon and two nutrients makes it necessary to include three state variables for every ecological group in the model.

A solution to this cumbersome bookkeeping is to use the pool of dissolved nutrients in order to conserve mass in the system. If organic matter is transferred to a state variable with a lower nutrient content, then the nutrient is released in the dissolved inorganic pool and vice versa. Examples of this approach for the conversion of algae to zooplankton are the models by DiToro et al. (1971) and Kremer and Nixon (1978). De Vries, 1987) make use of the dissolved nutrient pool for seasonal fluctuations in composition of algae: if during summer the nutrients levels decrease, the nutrient content of the phytoplankton decreases also, and nutrients are released into the dissolved pool.

The use of the dissolved pool to solve stoichiometric bookkeeping is not completely satisfactory. Although zooplankton does release some inorganic nutrients (ammonium) during feeding, a considerable fraction of the excess nutrients is released in organic form in the faeces (DiToro et al., 1971). The uptake and excretion of nutrients into/from the dissolved pool to model time-variable stoichiometries appears to be a model artefact also (Baveco et al., 1986).

In the Oosterschelde there are no data on the stoichiometry of algae, zooplankton and detritus. Literature data show an overlapping range in composition of these groups.

In the present model a single, fixed stoichiometry of all state variables will be assumed. A complete multiple bookkeeping would make the model unmanageable; existing approximations to variable stoichiometry appear to be not quite realistic, and the simplest assumption is within the range of data anyway.

In this chapter literature data on dry weight-, nitrogen-, oxygen-, and silica-to-carbon ratios are summarized, and ranges that will be used in the model are selected.

### 8.2 Dry weight

Dry weight of phytoplankton is only of interest in the present context because some of the literature expresses nutrient content as a fraction of dry weight. The data in Jørgensen (1979) show systematic differences in carbon fraction of dry weight between diatoms and non diatoms. In diatoms the carbon content is lower, presumably because of the high fraction of silica (see below), which is lacking in other algal groups. In diatoms the

average C/W ratio from the literature review by Jørgensen (1979) (in weight per weight) is 33%, range 15-50%. In other algae, the average value is 42% (range 25 to 70%). In the recalculation of N/C and Si/C ratios, only the average values will be used.

In literature on filterfeeders, biomass is usually expressed in ash-free dry weight. In the present model, filterfeeders are no state-variable, and it is not necessary to use a conversion factor. Conversion is only necessary for the separate model of individual weight that is used in the calibration of the present model. The ash-free dry weight of invertebrates is some 3 to 20 % lower than total dry weight (Jørgensen, 1979). The average carbon to ash-free dry weight ratio in the invertebrates listed by Jørgensen (1979) is 51% (range 45 to 56%).

### 8.3 Nitrogen: a summary of the nitrogen cycle

The nitrogen concentrations in the Oosterschelde are for a considerable part determined by transport processes. This is in some contrast to the situation for phytoplankton and labile detritus, where -at least in the inner compartments- concentrations are not strongly influenced by boundary conditions, and inputs of organic matter are negligible compared to primary production (Holland et al., 1986). For nitrogen, the seasonal pattern in concentration (see figures 10.18-21) can be partly explained by higher inputs in winter in combination with lower concentrations at the North Sea in summer. A detailed account of nitrogen-input to the Oosterschelde is given by Stortelder et al (1984) and Holland et al. (1986): the main source is the discharge from the Haringvliet through the Volkerak dam (see figure 1.1) and from small rivers from the province of Brabant in the North (77%); remaining inputs are mainly from the Kreekrak locks and another small river in the Eastern compartment (10%), polderwater discharges (6%) and precipitation (3%).

In general, the biological cycle of nitrogen runs parallel to that of carbon. Possible exceptions to this are: fixation of nitrogen by blue-green algae, evaporation and denitrification. As has been mentioned (chapter 3), the phytoplankton is at present dominated by Diatom species; nitrogen fixing species are absent both from the Oosterschelde and from adjacent North Sea and lake Grevelingen. Evaporation of nitrogen may take place according to the following reaction:



under near-neutral pH conditions however, this equilibrium lies strongly to the left and in the Oosterschelde (pH 7.5-8.5; Stortelder et al., 1984), this process is probably nearly absent. The role of denitrification is potentially larger. In chapter 6 the modelling of denitrification in the intertidal flat sediments is discussed. Denitrification in the water column is unlikely because it is always close to oxygen-saturation; denitrification in the sediment of the tidal channels is probably small because of the low organic matter content of these sandy sediments.

### N/C ratios

Nitrogen content of phytoplankton is reviewed by Lingeman-Kosmerchock (1978) and Jørgensen (1979). There seems to be no difference in this ratio between diatoms and other algal groups. The nitrogen content expressed in N/C ratio (weight basis) is illustrated in figure 8.1. Most values are in the range of 6 to 20 %. Extreme value range from 2.5 to 45 per cent. The 6 to 20% range will be used in the calibration.

The nitrogen content of zooplankton is reviewed by Jørgensen (1979). Data are more scarce, but show in general the same range as the phytoplankton: see figure 8.1.

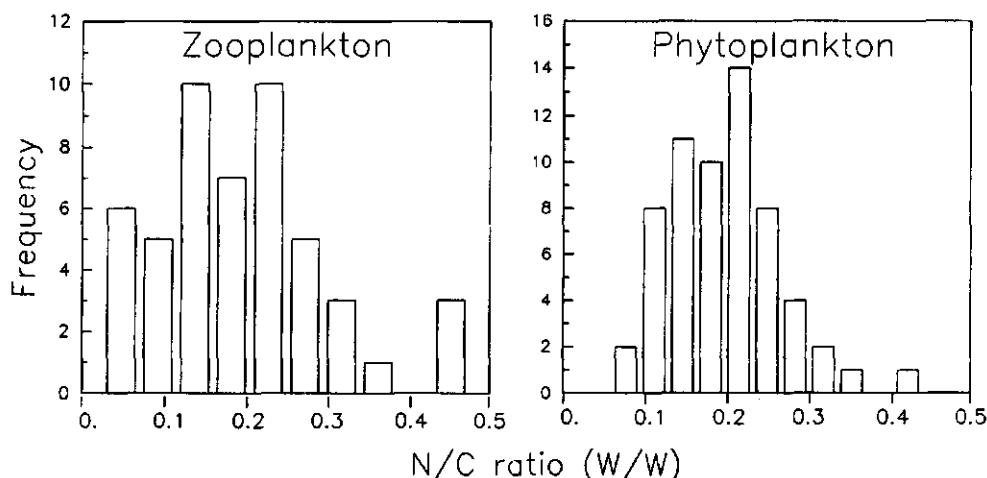


Figure 8.1: N/C ratio (w/w) in phytoplankton (data from Lingeman-Kosmerchok -1978, and Jørgensen -1979) and in zooplankton (data from Jørgensen -1979).

The N-content of detritus depends on its average age. Young detritus has the same composition as its parent material; old detritus (refractory detritus), consisting of humic substances, lignin and so on, has a very low N-content. The problem of dividing the detritus into a refractory and a degradable part has been discussed in the mineralization chapter. It was assumed that all organic material that is produced is degradable also: the amount of refractory detritus produced each year is negligible compared to total production, although the accumulated amount on a time scale of many years may be large. Further, it was assumed that mineralization of N and C occurs at the same rate. Therefore, the fraction of nitrogen of the degradable detritus is (in the model) the same as that of phytoplankton.

#### 8.4 Silica

The silica content plays a role in diatoms only; as has been discussed in the mineralization chapter the silicon skeletons of dead diatoms are treated in the model as a separate state variable which consists for 100% of silicon.

The Si/C ratio in diatoms may be very high (Lingeman-Kosmerchok, 1978; Jørgensen, 1979). A diatom may contain considerably more silica than carbon: see figure 8.2. In the model calibration a Si/C ratio of 30 to 150% will be used.

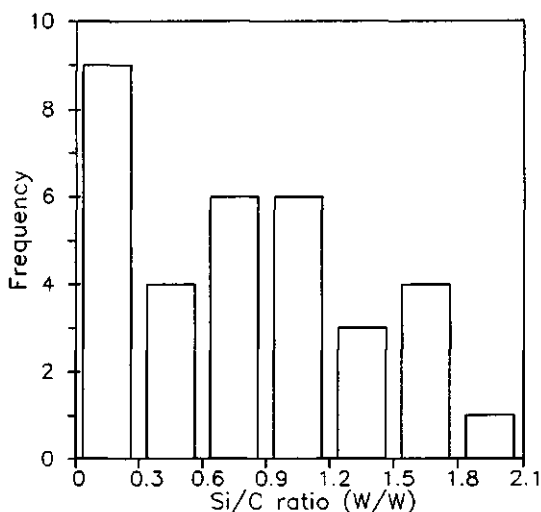


Figure 8.2: Si/C ratio (w/w) in phytoplankton. Data from Lingeman-Kosmerchok (1978) and Jørgensen (1979).

### 8.5 Oxygen

The oxygen to carbon ratio of organic matter is of interest for the conversion of respiration to carbon loss for zooplankton and filterfeeders, for the conversion of oxygen produced by benthic diatoms to carbon production and for the possible future coupling of an oxygen budget for the Oosterschelde to the present carbon budget.

The oxygen requirement for the oxidation of organic matter is expressed as a respiratory quotient O/C, in moles. If this quotient is 1.25 in, for example, some diatom, then this diatom produces on the average  $1/1.25=0.8$  mole of oxygen per mole of carbon fixed during photosynthesis. Data on O/C ratios from literature concern respiratory quotients; O/C ratios for primary production will not be discussed separately, but are assumed to be the inverse of the respiratory quotient.

The oxygen to carbon ratio in the formation and degradation of carbohydrates is unity if expressed in moles:



Lipids and proteins contain less oxygen, which implies that the oxygen requirement for the oxidation of organic matter is always higher than 1 mole  $O_2$  per mole C, depending on the composition. The data by Lingeman-Kosmerchok (1979c) show an average of 1.03. Parsons et al. (1984) give a range of 1.1 to 1.3. Wetzel (1975) uses a value of 1.2 in calculations. Gieskes and Kraay (1977) and Ryther and Yentsch (1957) use a value of 1.25. In the present model a respiratory quotient of 1.2 will be used, with a range from 1.1 to 1.3.

## 9 PRELIMINARY RESULTS AND SENSITIVITY ANALYSIS

### 9.1 Introduction

In this chapter, some preliminary model results will be discussed in relation to a sensitivity analysis. The treatment of sensitivity analysis anticipates to some extent the chapter on calibration; therefore, some of the concepts that will be developed in more detail in the following chapter are briefly discussed at this point.

In the foregoing chapters a model was developed on the basis of laboratory and field experiments; with the exception of the individual weights of cockles and mussels and the boundary conditions, no reference was made to observations of the state-variables in the Oosterschelde. Although a model could be based on this a priori information alone, the use of additional information on the state-variables is clearly desirable:

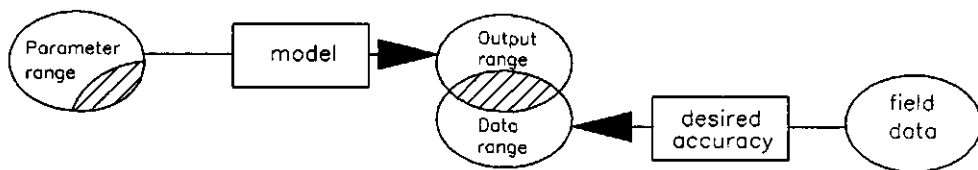
- 1) to test the assumptions made in the model;
- 2) to reduce uncertainty in model parameters.

It has been attempted to treat both points simultaneously in the present case, by formulating two alternative hypotheses by means of two parameter values in a single equation. If equation f1 represents the outcome of a first possible model, and f2 the outcome of an alternative model, we may formulate the choice between the two by defining the outcome of a hybrid model f' as:

$$f'(p) = p f1 + (1-p) f2$$

Usually, an intermediate value between f1 and f2 is a possible hypothesis also, and the uncertainty about either f1 or f2 may be expressed as a continuous range for the parameter p in the hybrid model between 0 and 1. For example, phytoplankton transport is interpolated between suspended sediment transport and water transport; the uncertainty about the behavior of phytoplankton between these two extremes may be expressed by a range in the parameter x in equation 2.12. In this way both the uncertainty in model assumptions and in process rates may be formulated in terms of parameter ranges. The use of these ranges in model calculations leads to an model-output range.

The reduction of the parameter range is done by comparing the model-output range with the field data. In this comparison two points should be noted: field measurements are also uncertain, and the purpose of the model should be taken into account. For example, if measurements have an accuracy of 10%, model results and data will differ on the average at least this amount; however, it may be that the model will be used only to indicate a general trend resulting from some long-term scenarios, and that an order-of-magnitude agreement between model and data on a yearly-averaged basis is already sufficient. In this way, the scatter in field data and the desired accuracy lead to a data-range, which can then be compared (and hopefully overlaps with a part of) the model-output range.



**Figure 9.1:** An outline of model identification. The hatched area in the parameter range corresponds to the intersection of model- and data range.

If there is no overlap between the two ranges, either parameter ranges should be made broader or model formulations should be revised. This situation may be problematic, as it is often not clear which of the assumptions in the model is unjustified (Beck, 1987).

If model and data range do overlap, the restricted parameter range corresponding to the intersection of the two ranges represents the reduced uncertainty resulting from the use of both a priori information and field data. The process of matching model-output and data ranges is known as model identification or calibration. The (restricted) parameter uncertainty should be taken into account if the model is used for predictions. It can be misleading to present model results for a single set of parameters that represents a best choice in a range of values: the range of model-results resulting from parameter uncertainty should be presented as well.

In this chapter, the calculation of a model-output range is discussed; a detailed discussion of the calibration procedure can be found in chapter 10. The calculation of model-behavior as a result of parameter uncertainty is known as sensitivity analysis.

In a model with a large number of parameters, sensitivity analysis poses a technical problem, as it is difficult to investigate the ranges of all parameters simultaneously for reason of limitation on computer memory; in the present implementation of the sensitivity analysis procedure, it is only possible to do so for 50 parameters at a time. This implies that the parameters have to be investigated in several batches, keeping the remaining parameters fixed. This procedure may lead to a biased estimate of the influence of some parameters (Van Straten, 1985), because:

- the effect of parameter uncertainty depends on model behavior itself;
- the effect of a parameter directly depends on the values of the other parameters.

As an example of the first point we may consider for the nutrient-limitation expression:

$$f(N) = \frac{N}{K_m + N} \quad (9.1)$$

$f(N)$  is very sensitive for  $K_m$  for low values of  $N$ , but hardly so for large  $N$ . Usually, only the sensitivity of the model in the range of the actual system-behavior is of interest. For example, for it is possible to generate very low nutrient-concentrations with the model using unrealistically high

growth-rates of algae or strongly reduced nutrient-inputs; in this situation the model is very sensitive for  $K_m$ , but this is probably not the case for the simulation of the present Oosterschelde. Therefore, it is important to ascertain that model behavior is not outside the range of system-behavior when performing a sensitivity analysis.

An example of a direct interaction is:

$$G(N) = P1 * P2 * N \quad (9.2)$$

Multiplication of parameters occurs for example in the calculation of grazing (biomass times filtering activity), in the transport model (residual flow  $Q$  times dissolved fraction  $x$ ) and in the zooplankton model (daily ration times assimilation efficiency). In addition, parameters are sometimes added together (e.g.: grazing on microphytobenthos is the sum of several biomass-times-activity terms; light extinction is the sum of several specific light-absorbing components), or more complicated interactions may occur (for example, respiration is expressed by a rate at 10 °C times an exponential expression with a  $Q_{10}$ , specific activity of macrobenthos is expressed as  $a.W^{0.75}$ ).

Obviously, if one is interested only in improving model-output during the calibration of the model, it would be sufficient to adjust one of the interacting parameters, keeping the other(s) fixed. If one is interested in the "true value" of the parameters however, the choice of the other value is important. For the present model, it is believed that most parameters are largely abstract entities, whose value depends on the scale (in time and space) and the abstraction level of the state-variables in the present model of the Oosterschelde. As a result, the values of the parameters have only a limited intrinsic meaning: if the same model-structure would be used in an other estuary, or if parts of the model would be incorporated in a model of e.g. a lake, the parameter values would probably have to be quite different: sensitivity analysis and calibration would have to start afresh from the a priori parameter ranges, and it would not be possible to use the reduced parameter range obtained from the present model. Keeping this restriction in mind, we may, in the case of two directly dependent parameters, keep one of them fixed at a more or less arbitrary value.

With direct interactions only the above-mentioned relations where parameters occur together in a single calculation are meant; an example of indirect interactions would be: a low mineralization rate leads to low nutrient concentrations, and thus to a high sensitivity for  $K_m$ -values. This kind of interaction via the state variables would be an example of the effect of parameter uncertainty depending on model behavior itself.

The influence of the state-variables on the sensitivity analysis and the necessity of keeping some parameters fixed while varying others makes it necessary to have a first guess for the parameters which yields values of the state-variables "sufficiently close" to the actual system behavior, i.e.: close enough to allow an acceptable estimate of the actual parameter-sensitivities.

This first stage proceeds necessarily more or less intuitively: some promising parameters are selected and calibrated by hand. During the development of the model and the many trial runs involved in this process, it becomes -without a formal sensitivity analysis- clear which parameters have a large influence on the results; these are adjusted to bring model results and data into agreement, without a formal goodness-of-fit measure however. In this chapter the model output of this preliminary calibration and the field measurements are presented; the parameter values of this run are then the starting point of the sensitivity analysis. The major aim of the sensitivity analysis is a selection of parameters to be used in the calibration procedu-

re. This selection should present a minimal number of parameters which span most of the original model-output range, i.e.: parameters which have a very small influence may be omitted, and from clusters of parameters with interchangeable effects (e.g. equation 9.2), only a single parameter may be chosen.

This procedure may lead to erroneous results if the hand-calibration leads to a model-output which is so far removed from the actual system behavior that a set of parameters is chosen which does not cover the actual system behavior. It should be noted that it is quite possible that the first calibration is not very good, but does lead to a limited set of calibration parameters which cover the entire model-output range: wrong values for the parameters do not necessarily mean that their sensitivity coefficients are estimated wrong also. Therefore, a set of good starting-values for the parameters is not as essential as it would possibly seem to be. If, however, the above-mentioned situation would occur, it appears very hard to detect it; a first intuitive stage in the calibration procedure seems unavoidable.

In the calculations, model inputs such as temperature, irradiance and so on, will be kept fixed for the moment to focus on uncertainty concerning model content. In a later stage (for example, in the calculation of the impact of some management scenario) these inputs could be varied also.

## 9.2 Preliminary model results compared with measurements

The parameter values that were used in the preliminary model run are listed in table 9.1; part of the corresponding model output is shown in figure 9.2. Only compartments 1 and 3 (West and East) are shown for brevity; in general the results in compartments 2 and 4 (middle and North) are intermediate between these two.

The calculated phytoplankton-chlorophyll concentration is on the average somewhat lower than the measured values, notably in compartment 3 in the third quarter of the year. In compartment 1 the general trend of the data (highest values in 1982) is reproduced, this is not the case in compartment 3. The simulated values of particulate organic carbon (consisting for the larger part of refractory detritus) are close to the observed values. The calculated values of light-saturated primary production (PMAX) are in agreement with average observed values; the seasonal pattern is less pronounced than in the measured values. The calculated carbon-to-chlorophyll ratio shows a relatively flat curve; a comparison with observed values (for 1983 and 1984 only) is difficult due to the large scatter in the data.

Calculated benthic chlorophyll concentration can only be compared with measurements in 1982 and 1983. Although the average value is reproduced satisfactorily, the seasonal pattern of the model results seems too pronounced and out of phase.

For copepoda also, there are measurements only during 1982 and 1983. The measurements show generally higher values in 1983, model output calculates higher values for 1982. The average level of the simulated values appears to be too low in the Western compartment.

The data on dissolved inorganic nitrogen (DIN) show a decreasing trend during 1980 and 1981, with a considerable scatter in the data these first years; the model reproduces this trend to some extent. In the eastern compartment, simulated values are generally too high; in the Western compartment, the average levels are modeled in agreement with the data, but the seasonal fluctuations reproduced by the model are too small. Silicate concentrations in winter are reproduced accurately; in summer the concentrations are usually too high, notably in the Western compartment.



The calculated oxygen concentrations are close to the saturation level. In the Eastern compartment, calculated values are nearly always higher than observed.

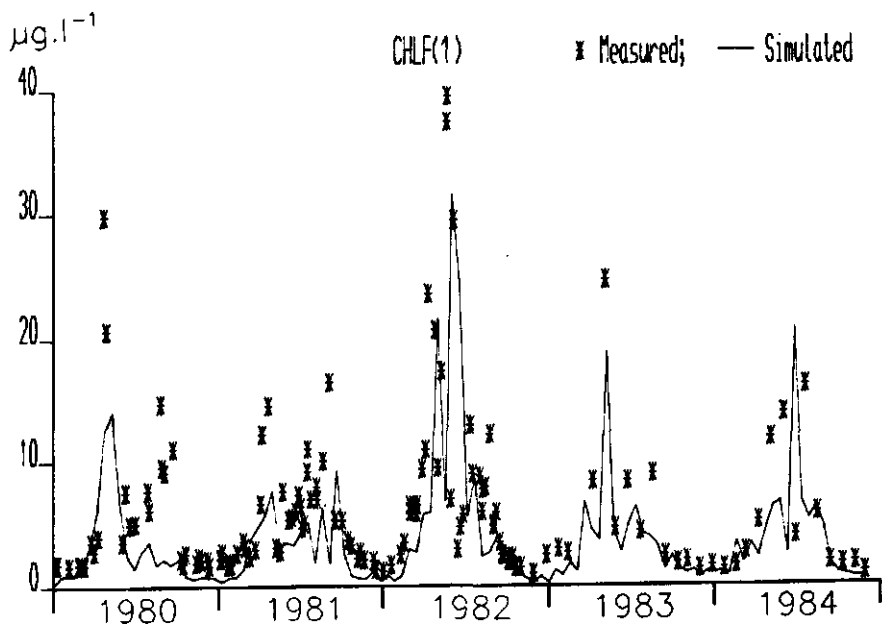


Figure 9.2a: Phytoplankton chlorophyll-a content: preliminary model results and observed values in compartment 1 (West).

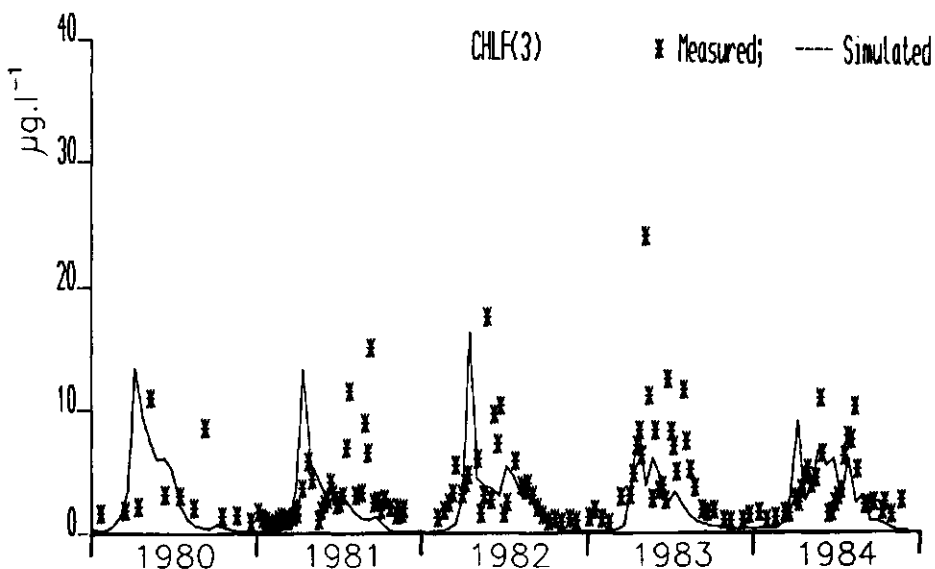


Figure 9.2b: Phytoplankton chlorophyll-a content: preliminary model results and observed values in compartment 3 (East).

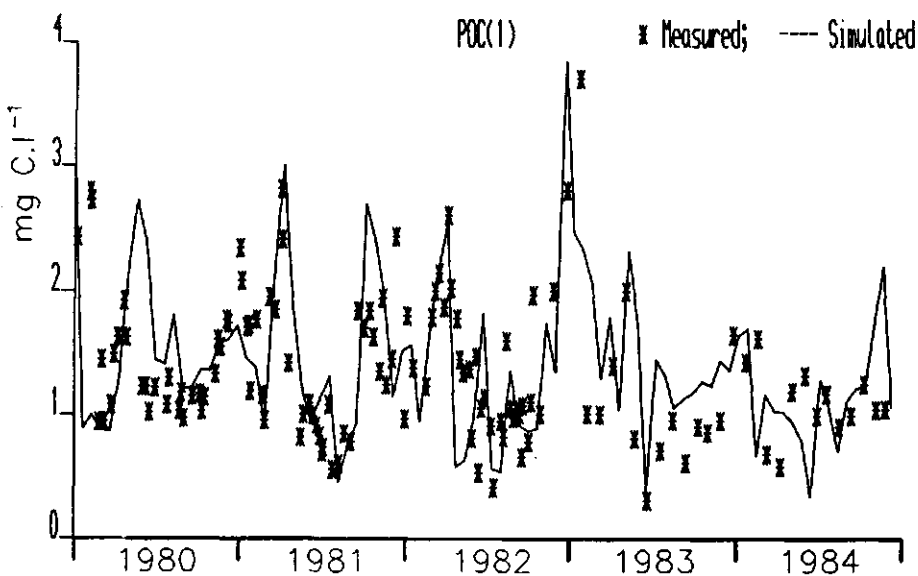


Figure 9.2c: Particulate organic carbon content: preliminary model results and observed values in compartment 1 (West).

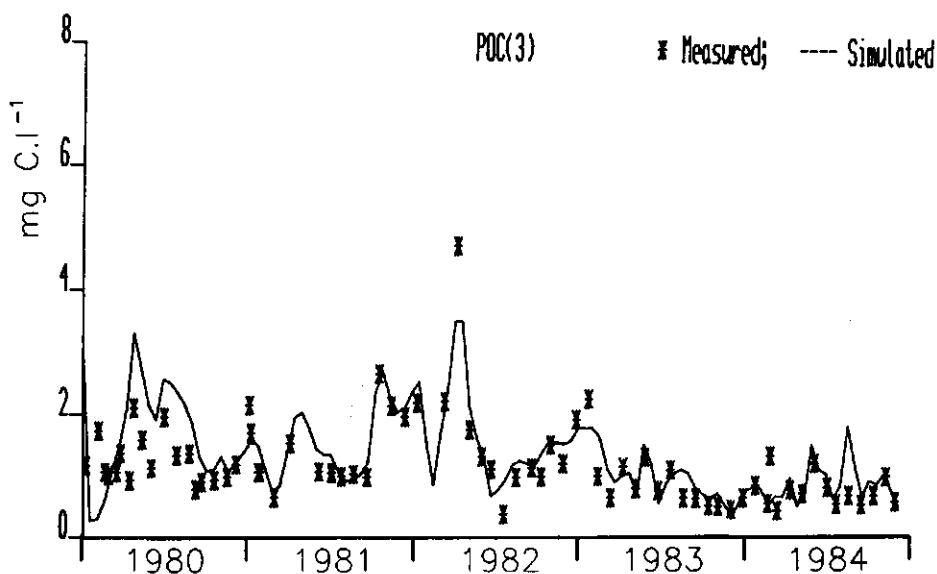


Figure 9.2d: Particulate organic carbon content: preliminary model results and observed values in compartment 3 (East).

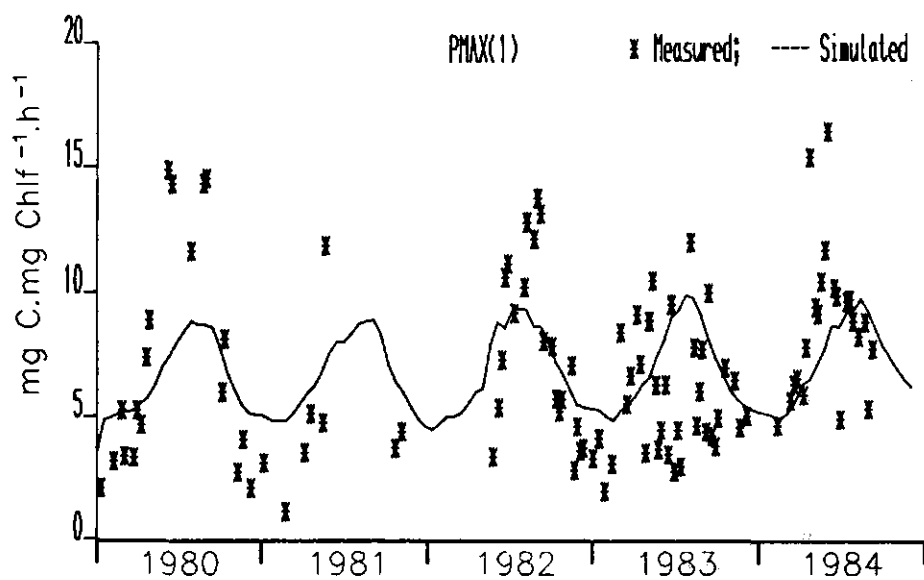


Figure 9.2e: Light-saturated production rate: preliminary model results and observed values in compartment 1 (West).

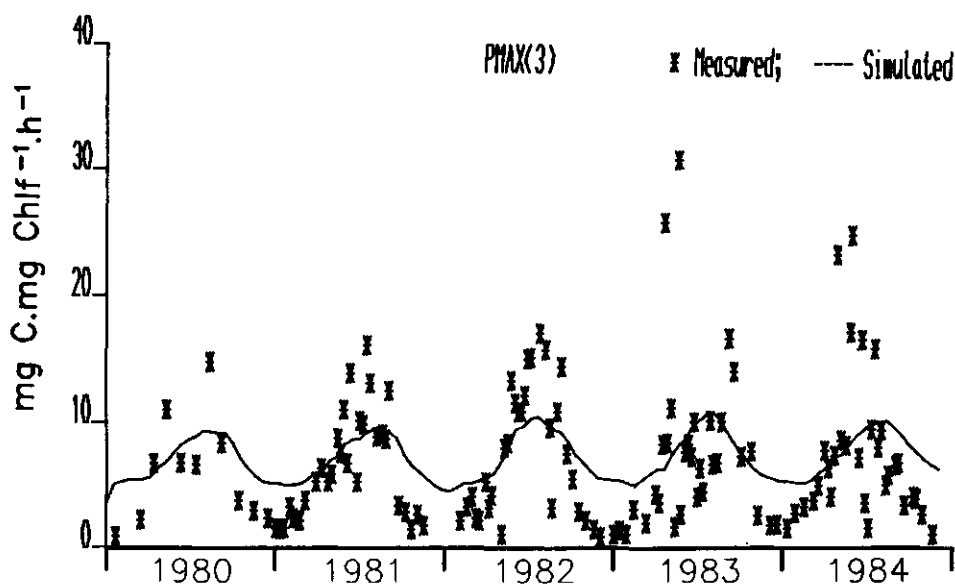


Figure 9.2f: Light-saturated production rate: preliminary model results and observed values in compartment 3 (East).

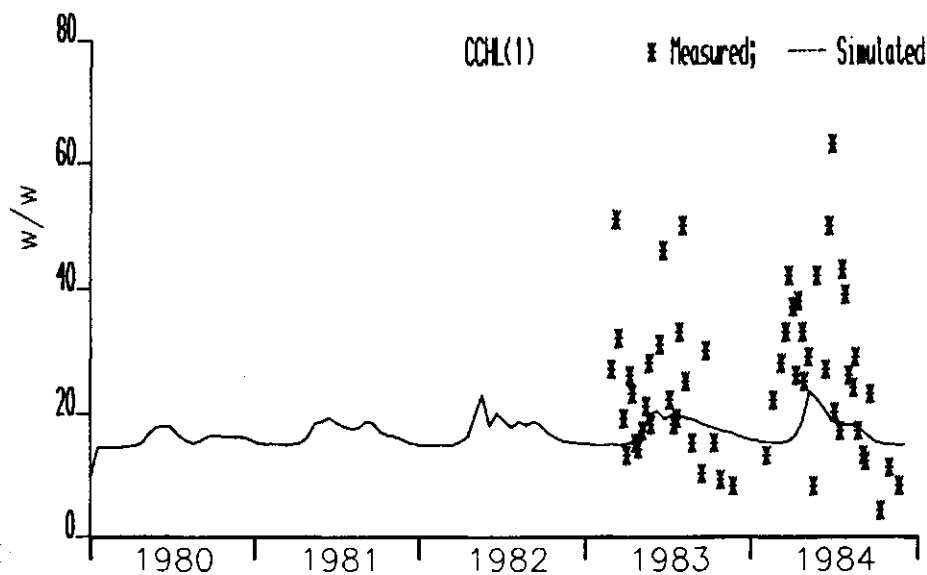
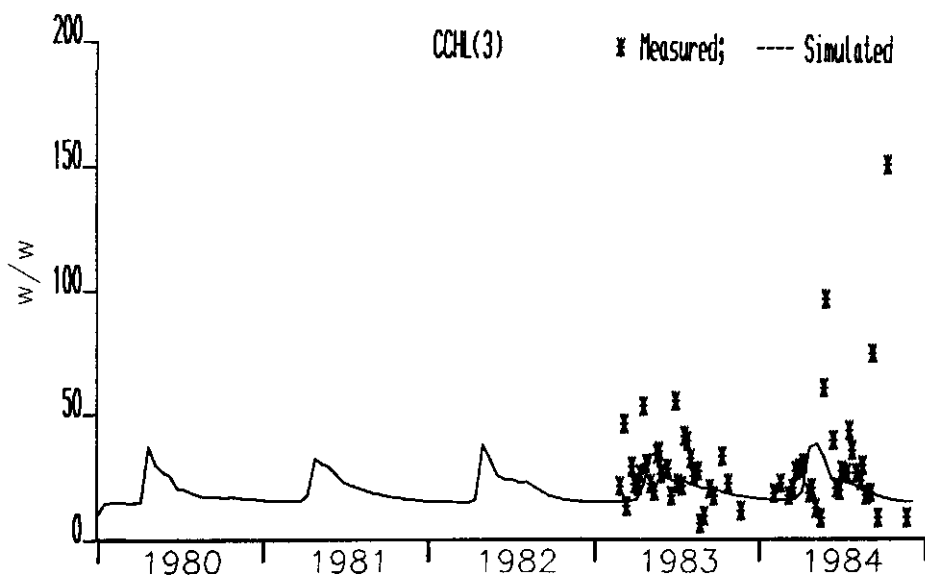
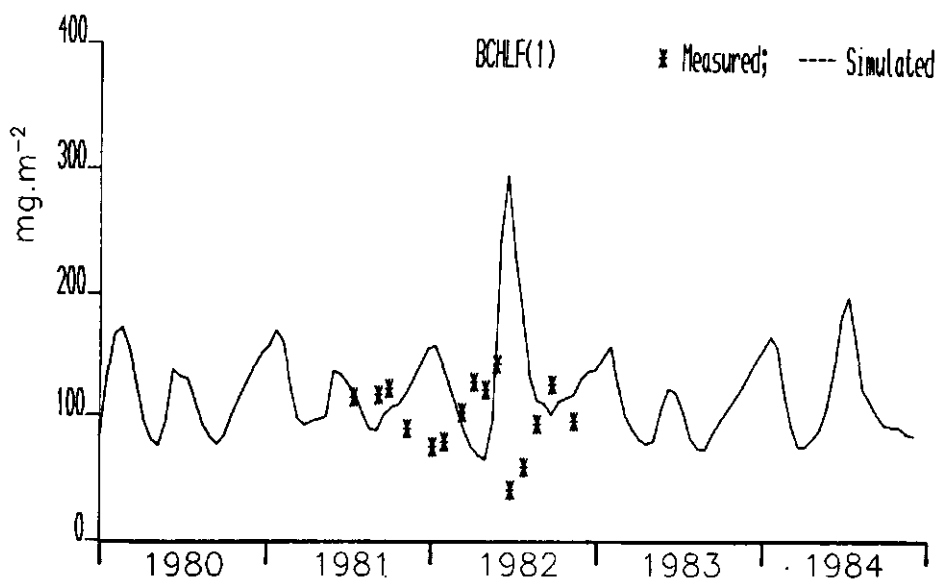


Figure 9.2g: Phytoplankton carbon to chlorophyll ratio: preliminary model results and observed values in compartment 1 (West).



**Figure 9.2h:** Phytoplankton carbon to chlorophyll ratio: preliminary model results and observed values in compartment 3 (East).



**Figure 9.2i:** Phytobenthos chlorophyll-a content: preliminary model results and observed values in compartment 1 (West).

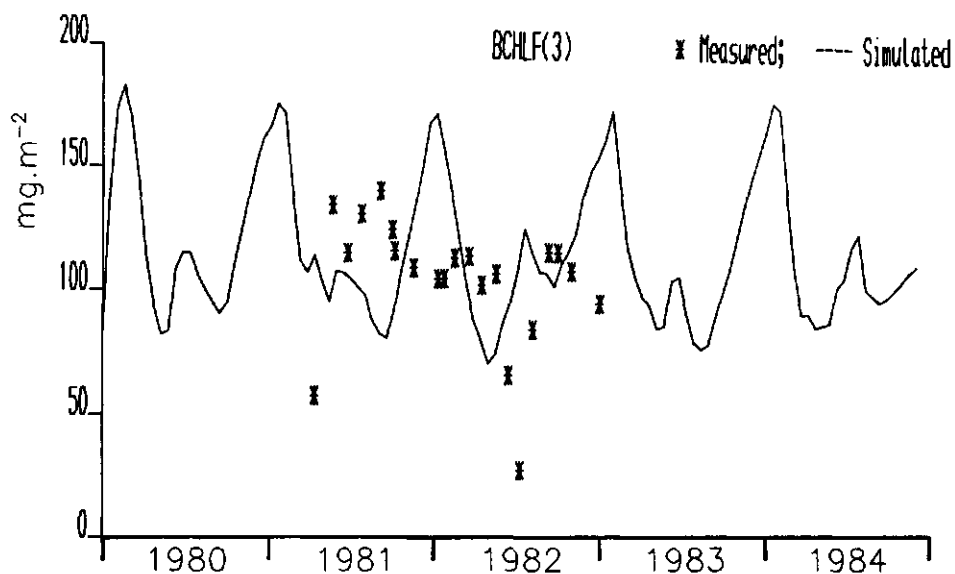


Figure 9.2j: Phytobenthos chlorophyll-a content: preliminary model results and observed values in compartment 3 (East).

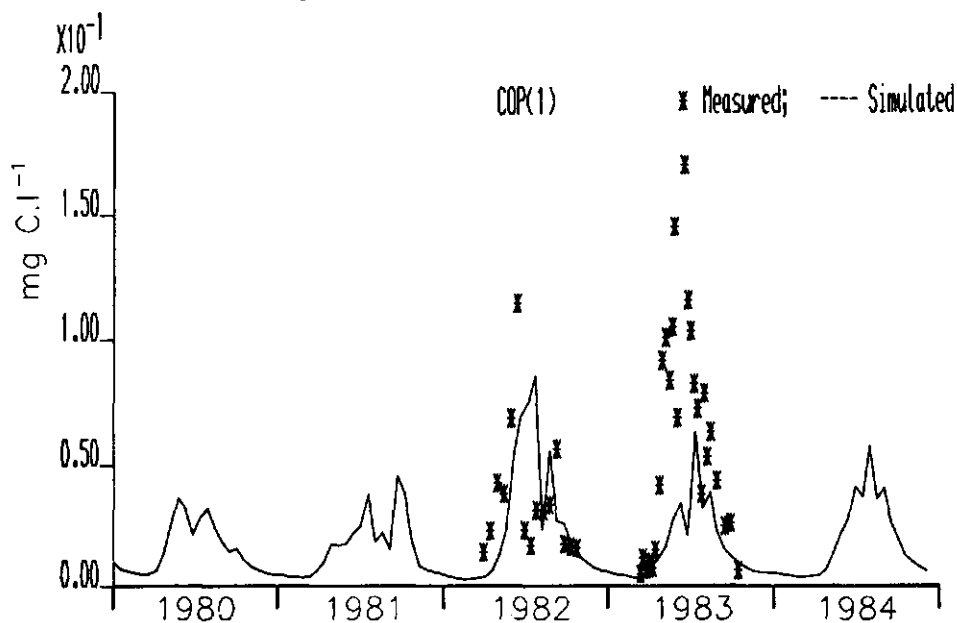
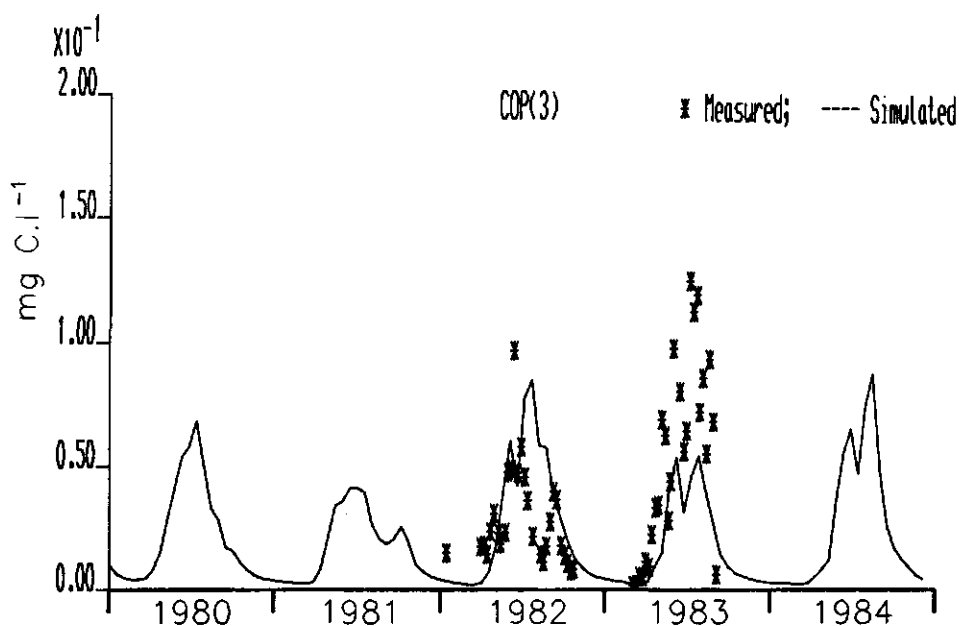
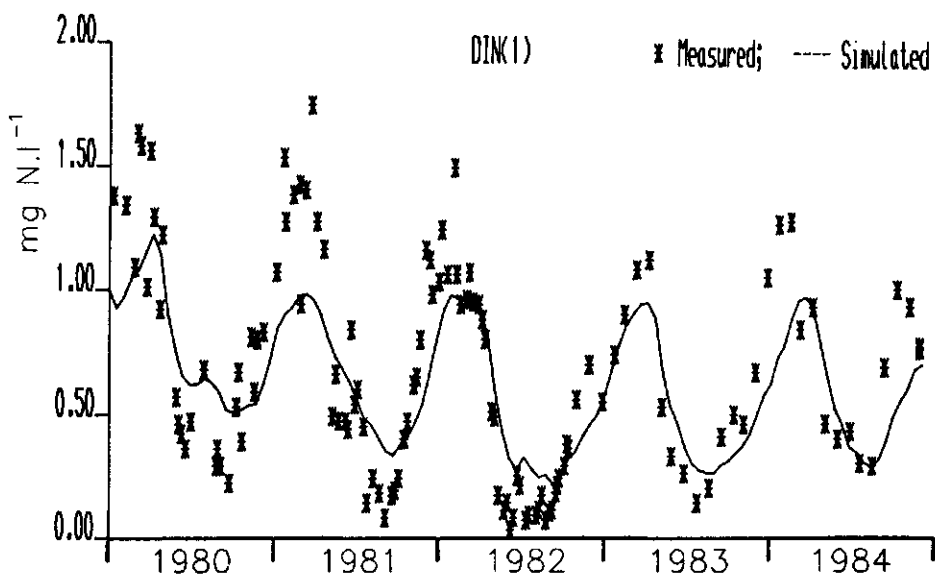


Figure 9.2k: Copepod biomass: preliminary model results and observed values in compartment 1 (West).



**Figure 9.21:** Copepod biomass: preliminary model results and observed values in compartment 3 (East).



**Figure 9.2m:** Dissolved inorganic nitrogen concentration: preliminary model results and observed values in compartment 1 (West).

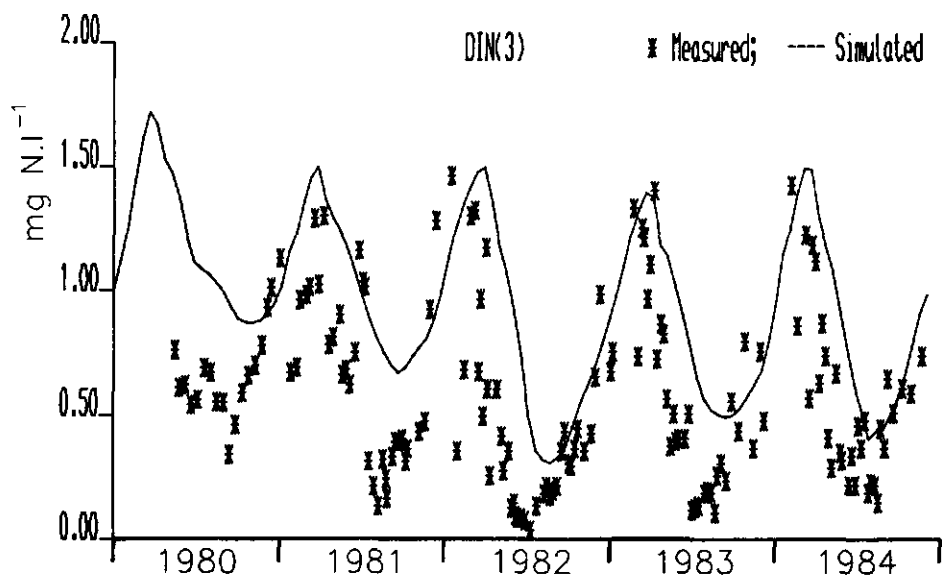


Figure 9.2n: Dissolved inorganic nitrogen concentration: preliminary model results and observed values in compartment 3 (East).

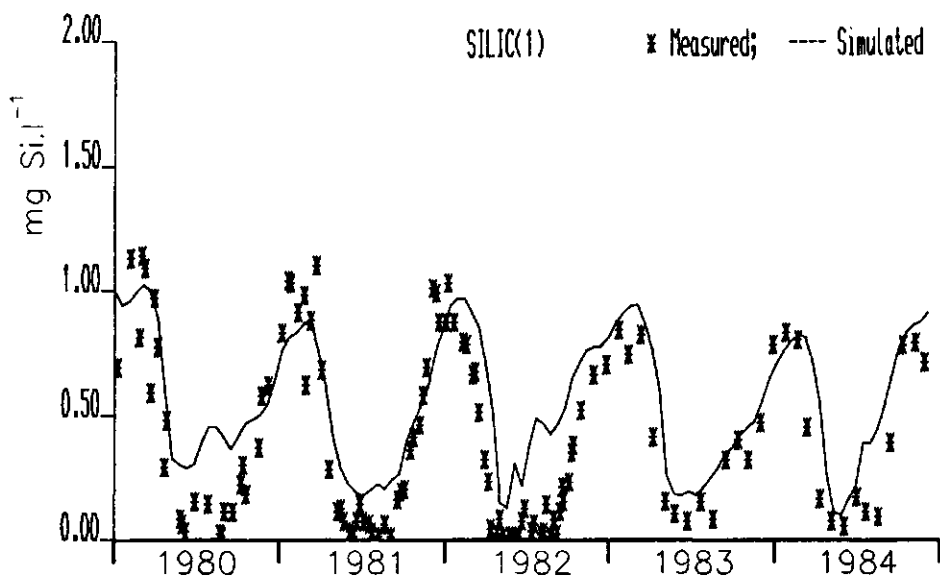


Figure 9.2o: Silicate concentration: preliminary model results and observed values in compartment 1 (West).



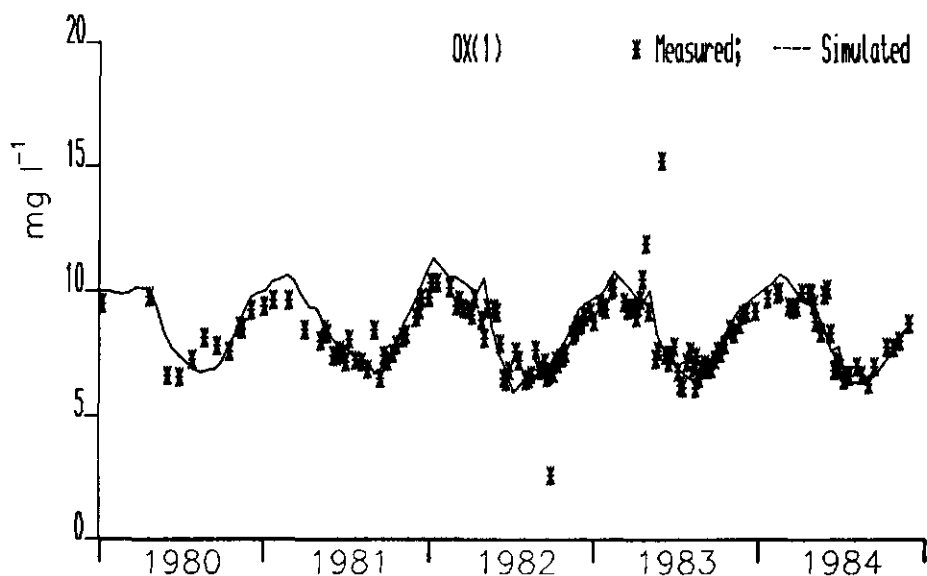


Figure 9.2p: Silicate concentration: preliminary model results and observed values in compartment 3 (East).

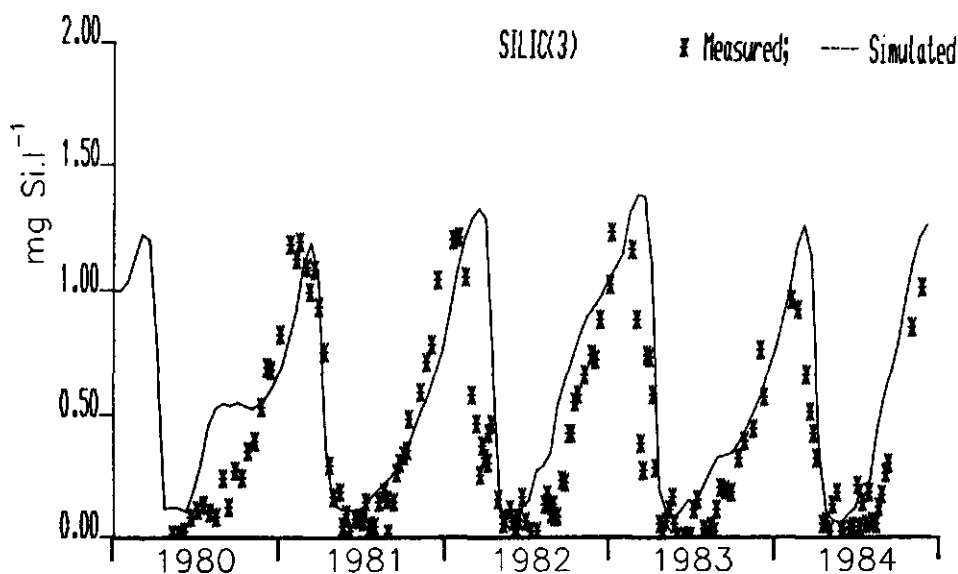


Figure 9.2q: Oxygen concentration: preliminary model results and observed values in compartment 1 (West).

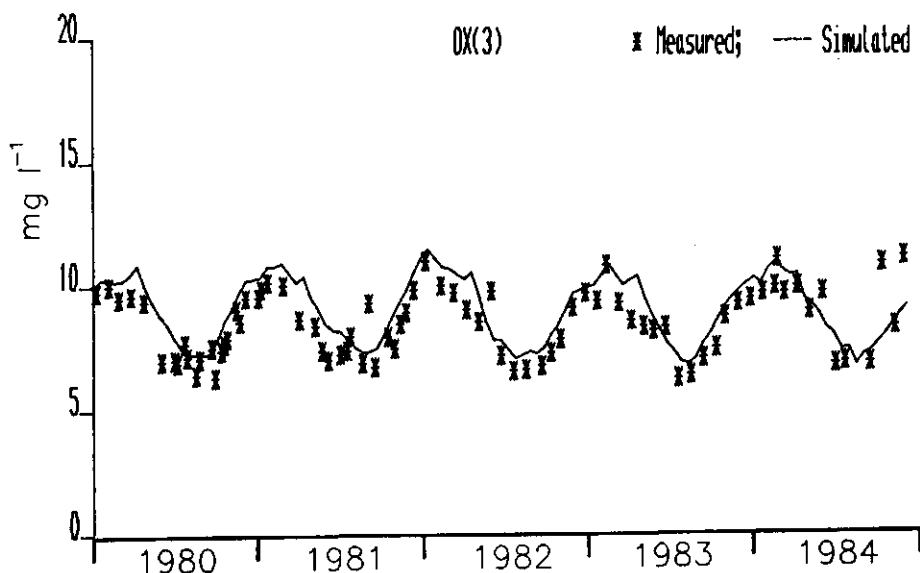


Figure 9.2r: Oxygen concentration: preliminary model results and observed values in compartment 3 (East).

### 9.3 Method of sensitivity analysis

Model equations that can be solved analytically provide an ideal case for sensitivity analysis. In this case, model results can be directly computed for different parameter values, and a graph of model outcome versus parameter value can be drawn. For the present model, this is not possible, and sensitivity analysis can only be performed by running the model several times with different parameter values.

A straightforward way to investigate the influence of, say, 10 parameters on model outcome  $j$  at time  $t$  ( $M_{j,t}$ ) would be to choose a number, say, 5 of values in every parameter range, and to calculate model results for all combinations of parameter values. In this example, this would imply almost 10 million model runs, which may illustrate why this technique is seldom applied for even moderately complicated models. (See, however Draper and Smith (1981) for examples of this technique in the context of the calibration of small nonlinear models).

A solution that can be successfully applied when parameter uncertainty is relatively small is linearization, also called first-order uncertainty analysis (Van de Kamer, 1983). If the model yields a value of  $M'_{j,t}$  near the parameter vector  $P'$  ( $=[p'_1, p'_2, \dots, p'_n]$ ), then the model results for parameter values in the neighborhood of  $P$  can be approximated as:

$$M_{j,t} = M'_{j,t} + \sum_{i=1}^n a_{i,j,t} (p_i - p'_i) \quad (9.3)$$

with:  $a_{i,j,t} = \delta M_{j,t} / \delta p_i$ , the first derivative of  $M_{j,t}$  to  $p_i$

In this way only the coefficients  $a_{1,j,t}$  need to be known, which can be determined by a single model run each. The problem with this approach is that parameter uncertainty is often large, which makes the restriction "in the neighborhood" of  $P'$  no longer valid (Cukier et al., 1978). If the model-response to parameter variations is linear, equation 9.3 is, of course, valid for the entire parameter range. In the nonlinear case, the approximation may still be accurate, but often it is not.

A more robust approach to the problem is Monte Carlo analysis (Spear and Hornberger, 1978; Van de Kamer, 1983; Fedra et al, 1981; O'Neill et al., 1982; Warwick and Cale, 1986). In this method the parameters are not varied systematically but chosen from some probability distribution. In its simplest form, all parameters are chosen independently from uniform distributions, i.e. every parameter value in the range has an equal probability of being selected. This resembles the first approach in which every parameter was varied while keeping the other parameters fixed. Here, the other parameters are not fixed, but because they are varied independently, their average effect is usually cancelled out. This averaging effect requires that Monte Carlo analysis must be based on considerably more runs than there are parameters. The actual number of runs required is dependent on the interaction between parameters and to the non-linearity in model response: if both are absent, then a number of runs equal to the number of parameters would already be sufficient. In Monte Carlo analysis, results can be interpreted only statistically. Compared to a complete scan of all possible parameter values, Monte Carlo analysis is still very efficient; compared to first order uncertainty analysis it is more generally applicable.

The reason to choose parameter values in Monte Carlo analysis independently at this point is purely technical: it allows a straightforward estimate of the  $a_{1,j,t}$ -coefficients in (9.3). If the combined effect of all parameter uncertainties on model outcome is to be investigated to calculate the model-output range (see figure 9.1), it is probably no longer correct to assume that the parameters are independent: for example the values of several physiological parameters in the phytoplankton model (maximal production rate, respiration rate) are probably positively correlated. Nevertheless, at this stage the assumption of independence still has to be made because the parameters of the model have been measured in nearly all cases in separate experiments, which does not allow the estimation of their correlations. After applying the calibration procedure however, there is usually a clear correlation between the calibrated parameter values; in the final assessment of calibrated model-output range these correlations can and should be used.

The simplest statistical treatment of the Monte Carlo results is to draw a straight line through the  $(p_1, M_{j,t})$ -results. This resembles the approach in equation 9.3, but now the linearity assumption is made posteriori, and not, as in first-order uncertainty analysis a priori. It may be checked if the model-response can be represented as linear satisfactorily, and whether it may be necessary to introduce, for instance, quadratic terms. Even if the effect of a parameter on model-output is nonlinear, the regression line may be useful as it gives the average effect of the parameter over its uncertainty range. Considering model-output  $j$  at time  $t$ , the regression line is:

$$M_{j,t} = M'_{j,t} + a_{1,j,t} * (p_1 - p'_1)$$

A sensitivity coefficient can now be defined as:

$$S_{i,j,t} = \frac{a_{i,j,t} * [\text{range in } p_i]}{M_{j,t}} \quad (9.4)$$

it gives the relative change in  $M_{j,t}$  as a result of changing  $p_i$  over its uncertainty range.

It should be stressed that the calculated sensitivity coefficients should be treated with considerable caution. In the first place, sensitivity of a parameter depends on other parameter-values and on model-input as has been discussed previously. Therefore, the calculation of sensitivity-coefficients in "batches" of 50 parameters may bias the results, depending on the non-linearity of the model, and on whether interacting parameters are included in the same batch or not. Secondly, the Monte Carlo procedure yields  $s$ -values with a limited accuracy only: in practice, computation-time limits the number of runs to 200 per batch of parameters.

In order not to miss important interactions between parameters in different batches, the most sensitive parameters from the first batch were included in the second batch also, and so on. Because of this there are a number of "replicates" in the parameters: some parameters have been included several times.

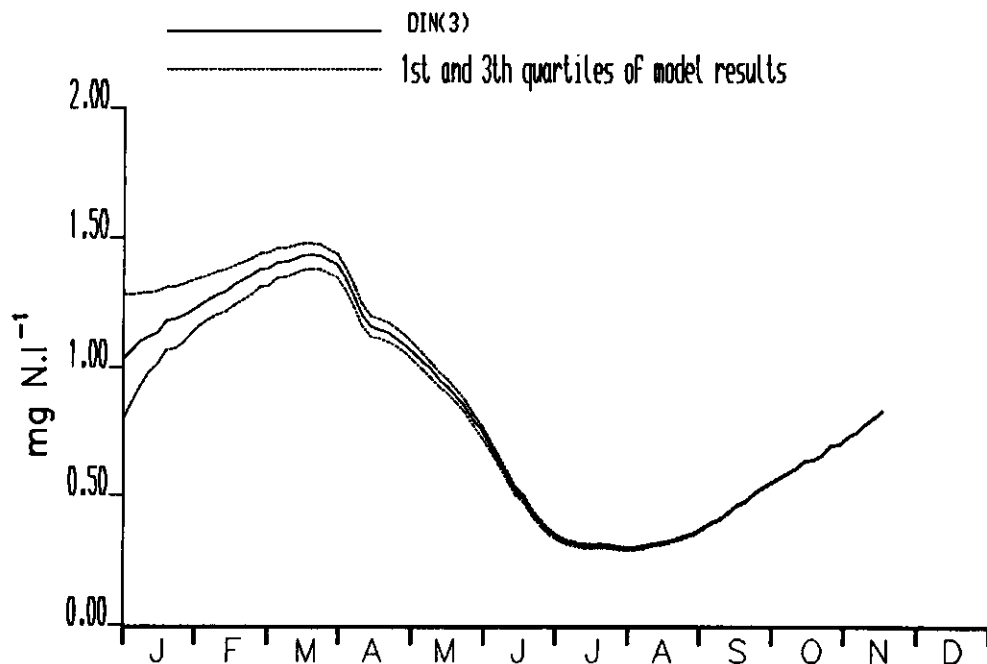
Some of the results of the sensitivity analysis have been presented graphically (see for example figure 9.3). For this purpose, the results have to be summarized in a compact way. The standard deviation of the model results is not sufficiently informative, as the results may be highly skewed; the minimum and maximum values attained in the simulations can not be used, as this range tends to increase with the number of simulation runs. An adequate measure is provided by the quartiles of the distribution of the results, i.e. the points which divide the model-outputs into four equal parts (Chambers et al., 1983). It should be noted in the interpretation of the graphs that the band produced by the 1-3th quartiles (which represents 50% of the model-output range only) is considerably more narrow than the 95%-confidence band.

#### 9.4 Results of preliminary sensitivity analysis

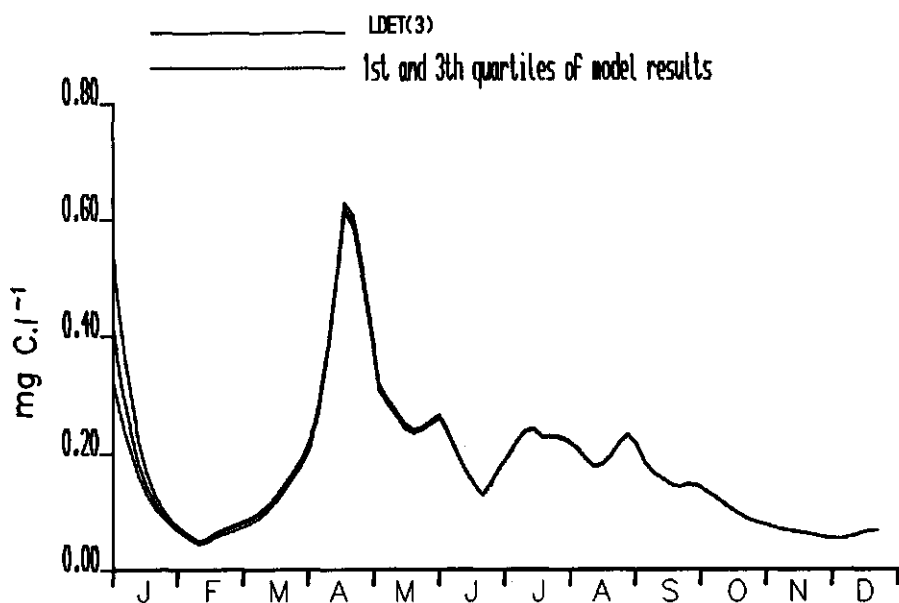
The sensitivity coefficients defined by equation 9.4 have been calculated only for a limited number of cases. In the first place, only a single year has been simulated (1982) and only three points in time have been investigated (day number 90, 180 and 270, representing early spring, summer and autumn); further, only a limited number of output-variables has been considered. Included in the analysis were all parameters concerning process formulations, excluded were (for the present) parameters related to inputs (e.g. the biomass of filterfeeders, nutrient discharges, boundary conditions and so on).

Apart from parameter values, boundary conditions and inputs, model results are influenced by initial conditions of the state-variables. It appears however, that this influence is largely limited to the first three simulated months. This is illustrated by figures 9.3a-c for three typical state-variables (dissolved: nitrogen, suspended particulate: labile detritus, and benthic: benthic chlorophyll) in the Eastern compartment (were initial conditions may be expected to show the most persistent effect). This conclusion is in contrast with pessimistic statements by Platt et al (1977); these were, however, based on atmospheric circulation models where (errors in) initial conditions tend to dominate the solution relatively rapidly.

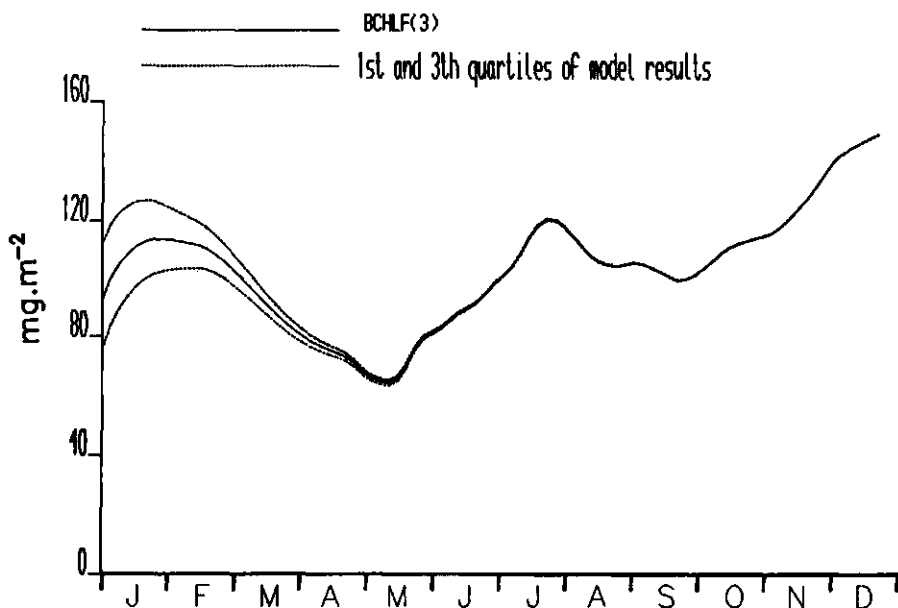
Apparently, negative feed-back effects in the present model dominate the effect of initial conditions in the present case. To eliminate the effect of the initial conditions the model calculations have been started with a period of two months previous to producing output.



**Figure 9.3a:** The effect of changing the initial concentration of dissolved inorganic nitrogen on model results in compartment 3 (East).

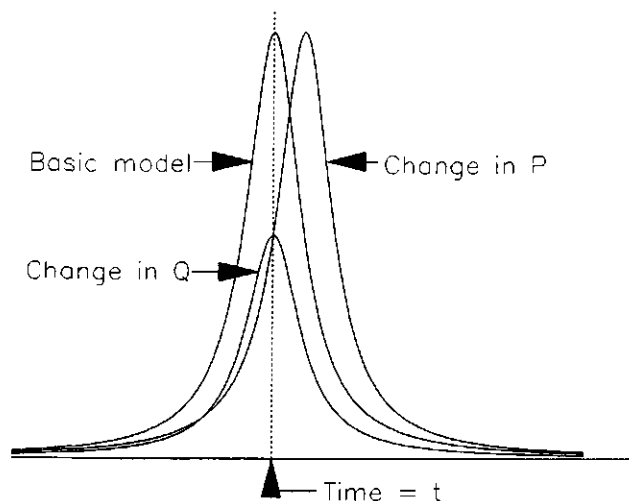


**Figure 9.3b:** The effect of changing the initial concentration of labile detritus on model results in compartment 3 (East).



**Figure 9.3c:** The effect of changing the initial concentration of benthic chlorophyll on model results in compartment 3 (East).

A parameter may show a high sensitivity coefficient if variations in its value cause shifts in time in the output of a sharply-peaked variable: this problem is illustrated in figure 9.4. These sensitivities would be of interest if the model was intended to calculate the output at a narrowly defined point in time. However, the present model is concerned with broader categories (like "spring bloom", "summer average") rather than with the exact value at, say, 16 March 1983. In order to avoid very large sensitivities associated with temporal shifts, a moving average of 15 days was applied to the model output before calculating sensitivity coefficients.



**Figure 9.4:** a change in parameter P causes a small shift in the timing of the output; a change in Q reduces the entire level of the output. Without the application of moving averaging they would have the same sensitivity coefficient at time t; moving averaging strongly reduces the sensitivity to P, but hardly to Q.

**Table 9.1: Sensitivity coefficients (equation 9.4) in preliminary model run.**  
Parameter values for this run are indicated in the first column.

Variable:		CHLF(1)			CHLF(3)			DIN(1)			DIN(3)			SILIC(1)			SILIC(3)		
Time:		90	180	270	90	180	270	90	180	270	90	180	270	90	180	270	90	180	270
Parameter	value																		
ACCOC	0.07	0.0	0.0	-0.1	0.2	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.2	0.1	0.1
ACMUS	0.06	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	-0.1
AIRFAC	1	0.0	0.0	0.0	0.0	-0.2	-0.2	0	0	0	0	0	0	0	0.1	0.0	0.1	0.1	0.1
AIRFAC	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ARAT	2	-0.4	-0.3	-0.1	-0.8	-0.3	-0.4	0.1	0.2	0.1	0.2	0.3	0.1	0.0	-0.1	0	0.0	-0.1	-0.1
ARAT	2	-0.1	-0.3	-0.2	-0.2	-0.3	-0.4	0	0.2	0.1	0.0	0.3	0.1	0.0	0.1	0.1	0.0	0.2	0.1
ARAT	2	0.0	-0.1	-0.1	0.0	-0.3	-0.3	0.0	0.1	0	0.0	0.1	0	0.0	-0.1	0.0	0.0	-0.1	0.0
ARCOC	0.006	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
ARCOC	0.006	0	0.0	0.0	0.1	0.0	0.1	0	0.0	0.0	0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.1
ARMUS	0.005	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0
BCCOC	0.4	0.0	0.1	0.1	0.0	0.0	0.0	0	0	0	0.0	-0.1	-0.1	0.0	0.1	0.0	0.0	0.0	0.0
BCMUS	0.64	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BIOTURQ	0.017	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.1	0.1
BLVIC	0.02	0.0	0.0	-0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.1
BLV3C	0.05	-0.1	-0.1	0.0	-0.3	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BN10COEF	0.01	0.0	0.0	0.0	0.0	0.0	0.0	0	-0.1	-0.1	0	-0.3	-0.1	0.0	0.1	0.0	0.0	0.1	0.0
BN10COEF	0.01	0.0	-0.1	0.0	0.0	-0.2	-0.1	0	-0.1	-0.1	0	-0.1	-0.2	0.0	0.0	0.0	0.0	0.0	0.0
BOTRAT	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.0	0.2	0.2
BOTRAT	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0	0.0	0.1	0.1
BRCOC	0.75	-0.2	0.0	-0.1	0.0	0.0	-0.2	0	0	0	0.1	0.0	0	0.1	0.0	0.0	0.0	0.0	0.0
BRESFRAC	0.0375	0.0	0.1	0.0	0.0	0.0	0.0	0	-0.1	0	0.0	-0.1	0.0	-0.1	0.0	0.0	-0.2	0.0	0.0
BRESMIN	0.058	-0.1	0.0	-0.1	0.0	0.0	0.0	0	0.1	0	0.0	0.1	0	0.1	0.0	0.0	0.2	0.1	0.1
BRESMIN	0.058	0	0.1	0	0.2	0.1	0.2	0.0	-0.1	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
BRMUS	0.56	-0.1	-0.1	0.0	0.0	0.0	0.0	0	0.1	0	0	0.1	0	0.0	-0.1	0.0	0.0	0.0	0.0
BRMUS	0.56	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	-0.1	0	0.0	0.0	0.0
BSILT	1.97	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0	0.0	0.0	0.0	0.0	0.0	0.0
CCHLB	0.03	0.0	0.0	0.0	-0.2	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CCHLB	0.03	0.0	-0.1	0.0	0.0	-0.2	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
CCHLMIN	0.012	-0.2	0.0	-0.1	-0.3	0.0	-0.2	0.0	0.0	0	0.0	-0.1	0.0	-0.1	0.2	0.0	0.0	0.3	0.0
CCHLMIN	0.012	0.0	0.1	0.0	0.0	0.1	0.0	0	0.1	0	0.0	0.1	0	-0.1	0.2	0.0	-0.1	0.2	0.1
CCHLMIN	0.012	0	0.0	0.0	-0.2	0.0	0.0	0.0	0.1	0	0.0	0.1	0.0	0	0.2	0.0	0.0	0.2	0.1
CFLUX	1.35	0.0	0.0	0.0	-0.1	0.0	-0.2	0	0.0	0	0	0	0	-0.1	-0.1	-0.1	-0.3	-0.3	-0.3
CFLUX	1.35	-0.1	0.0	-0.1	0.0	0.0	-0.3	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	-0.1	-0.2	-0.2	-0.3
CFLUX	1.35	0.0	0.1	0	0.0	0.0	0.0	0	-0.1	-0.1	0.0	-0.1	-0.1	0.0	0.0	-0.1	0.0	-0.1	-0.2
CRTRATE	0.038	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CHMIN10Q	0.07	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.1	0	0.0	0.1	0	0.0	-0.1	0	0.0	-0.1	-0.1
DAYRZOO	0.6	-0.3	-0.4	-0.2	-0.3	-0.6	-0.3	0.1	0.1	0	0.1	0.2	0.1	0.4	0.3	0.1	0.6	0.3	0.1
DAYRZOO	0.6	-0.1	-0.3	-0.1	-0.2	-0.6	-0.4	0	0.0	0.0	0	0.0	0.0	0	0.1	0.0	0.1	0.1	0.0
DCOEF	0.0007	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.2	0.0	0.0
DISLITF	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
DISP12	226	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DISP15	373	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0	0.0	0.0	-0.1
DISP23	144	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0	-0.1	0.0	0.0	-0.1	-0.1
DISP24	360	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DQALG	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0	0.0	0.0	-0.1	0.0	0	0.0	-0.1	-0.1
DQDET	0.35	0.2	0.1	0.1	0.3	0.2	0.2	0.0	0.0	0	-0.1	-0.1	0	0.0	0.1	0.0	0.0	0.0	0.0
DQDET	0.35	0.0	0.0	0.0	0.0	0.0	0.0	0	0.1	0	0.0	0.1	0	0	0.1	0	0	0.1	0.1
DQPSIL	0.47	-0.1	-0.1	-0.1	0.0	0.0	-0.2	0	0.1	0.1	0.1	0.1	0.1	0.1	-0.4	-0.1	0.2	-0.2	-0.1
DQPSIL	0.47	0.0	-0.1	0.0	0.0	-0.2	-0.2	0.0	0.0	0	0.0	0	0	0	-0.3	-0.2	-0.1	-0.3	-0.3
DQPSIL	0.47	0	0.1	0.1	0.0	0.1	0.1	0.0	-0.1	0	0.0	-0.1	0.0	0	-0.3	-0.1	0.0	-0.3	-0.2
EFFCOC	0.2	-0.2	-0.1	0.0	0.0	0.0	0.0	0	0.1	0	0	0.1	0	0.0	-0.1	0.0	0.0	0.0	0.0
EFFMUS	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EFFZOO	0.42	-0.2	-0.1	-0.1	0.0	0.0	-0.2	0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	-0.1
EPTMAX	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EXMAXQ	0.25	0.0	0.0	-0.1	0.0	0.0	-0.3	0	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.1
EXMAXQ	0.25	-0.1	-0.2	-0.1	0.0	-0.4	-0.4	0	0.1	0	0	0.1	0.1	0.1	0.0	0.0	0.0	0.1	0.0
FAECDFRAC	0.32	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FAECHFRAC	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FAECHFRAC	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FAECHFRAC	0.5	0.0	0.0	0.0	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0



Table 9.1 (continued): Sensitivity coefficients (equation 9.4) in preliminary model run. Parameter values for this run are indicated in the first column.

Variable: Time:	CHLF(1)				CHLF(3)				DIN(1)				DIN(3)				SILIC(1)				SILIC(3)			
Parameter value	90	180	270		90	180	270		90	180	270		90	180	270		90	180	270		90	180	270	
FOODLIM	0.25	0.3	0.3	0.4	0.5	0.5	0.6	-0.1	-0.2	-0.1	-0.2	-0.4	-0.2	-0.3	0.0	-0.1	-0.6	-0.2	-0.1					
FOODLIM	0.25	0.1	0.2	0.2	0.4	0.4	0.6	0	0.0	0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0
HCOEF	0.02	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
IOPT10	120	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
IOPTB10	69	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
IOPTB10	69	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0	0.0	0.0	-0.1	0.0	0.0	0.0	0.0	0.0
IOPTB10	69	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
KMDIN	0.1	-0.1	0.0	-0.1	0.0	0.0	-0.2	0	0.1	0.1	0	0.1	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
KMSIL	0.19	-0.1	0.0	0	-0.1	0.0	0.0	0	0.0	0	0	0.0	0	0	0.1	0.1	0.1	0.1	0.1	0.2				
KMSIL	0.19	0	0.0	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.1	0.0	0.1	0.2				
KMSIL	0.19	-0.2	-0.1	-0.1	0.0	0.0	0.0	0	0.1	0	0	0.1	0.1	0.2	0.1	0.1	0.2	0.2	0.3					
HCOEF	0.011	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0				
MRTQ	3.8	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0	0.0	-0.2	0.0				
MRTQ	3.8	0.2	0.3	0.1	0.3	0.3	0.2	0	-0.1	0	-0.1	-0.2	-0.1	-0.2	0.0	0	-0.4	-0.1	0.0					
MRTQ	3.8	0.0	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0	-0.1	0.0				
MUFAC	0.28	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MUFAC	0.28	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NCRAT	0.14	0.0	0.0	0.0	-0.4	0.0	0.0	0	0.1	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FACTOF	4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	-0.1	0	0.0	-0.1				
PFLQ	1	0.0	-0.1	0	-0.2	-0.2	-0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1			
PFLQ	1	0.0	0.0	0.0	-0.2	-0.2	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	-0.1	0	0.0	-0.1	-0.1				
PMAX10	0.5	0.1	0.1	0.1	0.4	0.1	0.2	0	-0.1	-0.1	-0.1	-0.2	-0.1	-0.1	-0.1	-0.1	-0.3	-0.3	-0.1					
PMAX10	0.5	0.1	0.1	0.1	0.5	0.2	0.3	0	0.0	0.0	0	0	0.0	0	0	-0.1	0.0	0	-0.1	-0.1	0.0			
PMAXB10	0.365	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PSIL10	0.06	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.2	0.2				
Q10ALG	1.5	0	0.0	0.1	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10BP	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10CMIN	2	0	0.0	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10COCC	1.9	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10DIA	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10GRAZ	2.8	0.0	0.0	0.0	0.1	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10MUSC	2	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10PBRES	2	0.0	0.0	0.0	0.0	0.2	0.2	0	0	0.0	0	0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10SMIN	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1			
Q10ZIN	3	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10ZRS	2	0	-0.1	-0.1	-0.2	-0.3	-0.3	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
QPOCSED	0.05	0	-0.1	-0.1	0.0	-0.2	-0.2	0	0.0	0.0	0	0.0	0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0	0.0
QPOCSED	0.05	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.1			
QPSILSED	0	0	0.1	0.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0			
RESFRAC	0.287	-0.1	-0.1	-0.1	-0.3	-0.3	-0.3	0	0.1	0	0	0.1	0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1			
RESFRAC	0.287	0	0.0	0.0	-0.1	0.1	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.1	0.0	0.0					
RESQMIN	0.005	-0.2	-0.4	-0.3	-0.3	-0.5	-0.5	0	0.5	0.2	0	0.6	0.2	0.2	0.5	0.2	0.3	0.5	0.2					
RESQMIN	0.005	-0.1	-0.4	-0.2	-0.3	-0.6	-0.6	0	0.2	0.1	0	0.2	0.1	0.1	0.3	0.1	0.1	0.3	0.1					
RESQZ	0.03	0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SEDLABQ	0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SESQC	0.002	0	-0.1	-0.1	0.0	-0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.1	0.1	0	0.2	0.1					
SESQM	0.002	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SFLOW1S	530	-0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0	0	-0.1	0.0	0.0	-0.1	-0.1					
SFLOW21	380	0.0	0.0	0.0	0.0	-0.1	-0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0	-0.1	0.0					
SFLOW32	350	0.0	0.0	0.0	-0.2	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1				
SFLOW42	680	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SFLOW54	120	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	-0.1	0.0	0.0					
SICRAT	0.58	0	-0.1	-0.1	-0.3	-0.2	-0.2	0	0.0	0.0	0	0.0	0.0	0	0.3	0.1	-0.1	0.2	0.1					
SLOPEB	0.0035	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	-0.1	0.0	0.0					
SLOPEB	0.0035	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0					
SLOPECHL	0.22	0.0	0.0	0.0	0.2	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0					
SLOPECHL	0.22	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TSILI(1)	1170	0	0.1	0.1	0.2	0.0	0.2	0.0	0.1	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TSILI(2)	1160	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0	0.0	0.0					
TSILI(3)	370	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TSILI(4)	1050	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
WINDRATE	0	0.0	0.0</																					

Table 9.1 (continued): Sensitivity coefficients (equation 9.4) in preliminary model run. Parameter values for this run are indicated in the first column.

Variable: Time: Parameter	value	COP(2)			CX(2)			PMAX(2)			POC(2)			CCHL(2)			BCHLF(2)		
		90	180	270	90	180	270	90	180	270	90	180	270	90	180	270	90	180	270
ACCOG	0.07	0.0	0.1	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0	-0.1	0.0	0	0.0	0.0	0.0	0.0
ACHUS	0.06	-0.1	0.0	-0.1	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	-0.0	0.0	0.0	0.1	0.0	0.0	0.0
AIRFAC	1	0.0	0.0	0.0	0	0.1	0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	-0.1	0.0	0.0
AIRFAC	1	0.0	0.0	0.0	0.0	0.1	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0
ARAT	2	0.0	0.0	0.0	-0.1	0	0	0.0	0.0	0.0	-0.1	-0.1	0	0.2	-0.1	0.1	0.0	0.0	0.0
ARAT	2	0.0	0.0	-0.2	0	-0.1	0	0.0	0.0	0.0	0.0	-0.1	0.0	0	-0.1	0.0	0.0	0.0	-0.1
ARAT	2	0.0	-0.1	-0.1	0.0	0	0	-0.1	-0.1	-0.1	0.0	0	0.0	-0.1	-0.1	0	0.0	0.0	0.0
ARCOG	0.006	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ARCOG	0.006	0.1	0.3	0.3	0	0.0	0	0.1	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
ARMUS	0.005	0.0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
BCCOG	0.4	0.0	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0	0.1	0	0.1	0.1	0.1	0.0	0.0	0.0
BCMUS	0.64	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.1
BIOTURQ	0.017	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.2	0.0	-0.1
BLVIC	0.02	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	-0.1	-0.1
BLV3C	0.05	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0
BN10COEF	0.01	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0
BN10COEF	0.01	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.1	0.0	0	0.0	0.1	0	-0.2	0.0	0.0
BOTRAT	0.7	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	-0.1	0	0.0	-0.1	0	-0.1	0.2	0.1
BOTRAT	0.7	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.2	0.1
BRCCG	0.75	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0
BRESFRAC	0.0375	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0
BRESMIN	0.058	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	-0.4	-0.1	0.0
BRESMIN	0.058	-0.1	-0.1	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.6	-0.2	-0.1
BRMUS	0.56	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0
BRMUS	0.56	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	-0.1	-0.1
BSIL7	1.97	0.0	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CCHLB	0.03	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.3	-0.3	-0.3
CCHLB	0.03	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	-0.2	-0.3	-0.2
CCHLMIN	0.012	0.0	0.1	0.1	0.0	0	0.0	0.2	0.2	0.2	0.0	0.1	0.0	0.2	0.2	0.2	0.0	0.1	0.0
CCHLMIN	0.012	0.0	0.0	0.0	0	0.0	0.0	0.3	0.3	0.3	0.0	0.1	0.0	0.3	0.2	0.2	0.0	0.1	0.0
CCHLMIN	0.012	0.1	0.2	0.4	0	0	0	0.2	0.2	0.2	0.0	0.1	0	0.2	0.3	0.2	0.1	0.2	0.1
CFLUX	1.35	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.1	0.3	0.4	0.5
CFLUX	1.35	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.3	0.5
CFLUX	1.35	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.1	0.1	0.2	0.3	0.4
CRTRATE	0.038	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
CWMIN10Q	0.07	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0	0.2	0.1
DAYRZOO	0.6	0.4	0.1	0.2	0	0.0	0	0.0	0.0	0.0	-0.1	-0.2	0	-0.2	-0.2	0.0	0.0	-0.1	-0.1
DAYRZOO	0.6	0.5	0.1	0.2	0	0	0	0	0	0	0	0.0	0	0.0	-0.1	0.0	0.0	-0.1	0.0
DCOEF	0.0007	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
DISLITF	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	-0.1
DISP12	226	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DISP15	373	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DISP23	144	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DISP24	360	0.0	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
DQALG	0.2	0.0	-0.1	-0.1	0	0	0.0	0.0	0.0	0.0	0.1	0.0	0	0.1	0.0	0.0	0.0	0.0	0.0
DQDET	0.35	-0.1	-0.1	-0.1	0	0.0	0	0	0	0	0.1	0.1	0.1	0.0	0.0	0	0.0	0.0	0.0
DQDET	0.35	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
DQPSIL	0.47	0.0	0.0	0.1	0	0.0	0	0.0	0	0.0	0	0.0	0	-0.1	0.0	0.0	0.0	-0.1	-0.1
DQPSIL	0.47	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.1	0.0	-0.1	-0.1
DQPSIL	0.47	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	-0.1	-0.1	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0
EFFCOG	0.2	0.1	0.1	0.1	0	0.0	0	0.0	0.0	0.0	-0.1	0	0	0.0	-0.1	0.0	0.0	0.0	0.0
EFFMUS	0.6	-0.1	0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
EFFZOO	0.42	0.2	0.1	0.1	0	0	0.0	0.0	0.0	0.0	-0.1	0	0	0.0	0.0	0.0	0.0	0.0	0.0
EFTMAX	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EXMAXQ	0.25	0.0	-0.1	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0
EXMAXQ	0.25	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	0	-0.1	0	-0.2	-0.1	0	0.0	-0.1	0.0
FAECDFRAC	0.52	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FAECDFRAC	0.6	0.1	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	-0.1	-0.1
FAECDFRAC	0.5	0.1	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0
FAECDFRAC	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0

Table 9.1 (continued): Sensitivity coefficients (equation 9.4) in preliminary model run. Parameter values for this run are indicated in the first column.

Parameter	value	COP(2)			OX(2)			PMAX(2)			POC(2)			CCEL(2)			BCHLF(2)		
		90	180	270	90	180	270	90	180	270	90	180	270	90	180	270	90	180	270
FOODLIM	0.25	0.0	0.0	-0.2	0.1	0	0	0.0	0.0	0.0	0.1	0.1	0	0.1	0.3	0.1	0.0	0.0	0.0
FOODLIM	0.25	-0.5	-0.2	-0.5	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BCOEF	0.02	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0	0.0	0.0
IOPT10	120	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
IOPTB10	69	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
IOPTB10	69	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	0	0.0	0.0	0.5	0.0	-0.1
IOPTB10	69	-0.2	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0
KMDIN	0.1	0.0	0	0.0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
KMSIL	0.19	-0.1	-0.2	-0.2	0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0.0	-0.1	0.0	-0.2	0.0	-0.1
KMSIL	0.19	0.0	0.0	-0.1	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	-0.1
KMSIL	0.19	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	-0.1	0	0	0.0	0.0	0.1	0.0	0.0	-0.1
MCOEF	0.011	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MRTQO	3.8	-0.4	-0.5	-0.4	0.0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.1
MRTQO	3.8	-0.5	-0.3	-0.4	0	0.0	0	0.0	0.0	0.0	0.1	0.1	0	0.1	0.1	0.0	0.0	0.0	0.0
MRTQO	3.8	-0.2	-0.8	-0.7	0.0	0	0	0	0	0.1	0.1	0.1	0	0.0	0.0	0.0	-0.1	0.0	0.0
MUFAC	0.28	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	0.0	-0.1	0	0.0	0.0	0.0
MUFAC	0.28	-0.1	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	-0.1	-0.1	-0.1
MCRAT	0.14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
FACTQF	4	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0
FFLOWQ	1	-0.1	-0.2	-0.3	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0
FFLOWQ	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.1	0.0	0.0	0.0	-0.1	-0.1	-0.1
PMAX10	0.5	0.1	0.0	0.0	0	0	0	0.3	0.3	0.3	0.0	0.0	0.0	0.1	0.1	0	0.0	0.0	0.0
PMAX10	0.5	0.0	0.0	0.0	0	0	0	0.3	0.3	0.3	0.0	0.0	0.0	0	0.1	0	0.0	0.0	0.0
PMAXB10	0.365	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PSIL10	0.06	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	-0.1	-0.1	0.0	0.0	0.0
Q10ALG	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10BP	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0
Q10CHIN	2	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10COCC	1.9	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0
Q10DIA	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0
Q10GRAZ	2.8	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.1
Q10MUSC	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1
Q10PERES	2	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q10SHIN	2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0
Q10ZIN	3	-0.3	0.1	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-0.1	-0.1	-0.1
Q10ZRS	2	0.2	0.1	0.2	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
QPOCSED	0.05	0.2	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.3	0.2	0.2	0	-0.1	0	0.0	0.0	0.0
QPOCSED	0.05	-0.1	-0.2	-0.2	0	0.0	0.0	0.0	0.0	0.0	0.3	0.2	0.2	0	0.0	0.0	-0.1	0.0	0.0
QPSILSED	0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0
RESFRAC	0.287	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	0.0	0	0	0	0	0.0	0.0	-0.1	0.0
RESFRAC	0.287	-0.1	-0.2	-0.2	0	0.0	0.0	0.0	0.0	0.0	-0.1	0.0	0	-0.1	0.0	0.0	0.0	0.0	0.0
RESQMIN	0.005	-0.2	-0.2	-0.6	0	-0.1	0	0.0	0.0	0.0	-0.1	-0.2	0	-0.1	-0.3	-0.1	0.0	-0.1	0.0
RESQMIN	0.005	0.0	-0.1	-0.1	0	-0.1	0	0.0	0.0	0.0	0.0	-0.1	0.0	0.0	-0.1	0.0	0.0	-0.1	0.0
RESQZ	0.03	-0.2	-0.1	-0.1	0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0
SEDLABQ	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	-0.1	0	0.0	0.0	0.0	0.0	0.0	0.0
SESOQ	0.002	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0
SESOQ	0.002	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0
SFLOW1S	530	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
SFLOW21	380	0.0	0.0	0.0	0.0	0.0	0	-0.1	0	0	0.0	0.0	0	0.0	0.0	0.0	0.0	-0.1	0.0
SFLOW32	350	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SFLOW42	580	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SFLOW54	120	-0.1	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	0	0.0	0	0.1	0.0	0.0
SICRAT	0.58	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0
SLOPEB	0.0035	0.1	0.0	0.2	0	0.0	0.0	0.1	0.1	0.1	0.1	0.1	0	0.1	0.1	0	0.0	0.0	0.0
SLOPEB	0.0035	-0.2	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0
SLOPECHL	0.22	-0.1	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SLOPECHL	0.22	0	-0.2	-0.2	0	0.0	0.0	-0.1	-0.1	-0.1	0	0.0	0	0.0	0.0	0.0	0.2	0.0	0.0
TSILT(1)	1170	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TSILT(2)	1160	-0.1	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
TSILT(3)	370	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TSILT(4)	1050	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0
WINDLRATE	0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0	0.0	0	0	0	-0.2	-0.1
WINDLRATE	0	0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.1	0	-0.1	0	0.0

### 9.5 The reduction of the initial parameter set

The data in table 9.1 may be used to reduce the initial set of parameters to a manageable set number. For this purpose, we will group the parameters together in clusters having similar effects, and choose from each cluster the one with the largest effect on output. Consider the following matrix of S:

**Table 9.2:** A theoretical example of sensitivity coefficients  $s_{i,j,t}$

	$M_{1,1}$	$M_{1,2}$	$M_{1,3}$	$M_{2,1}$	$M_{2,2}$	$M_{2,3}$
$p_1$	0.1	0.3	0.1	0.0	0.0	0.0
$p_2$	0.0	0.0	0.0	-0.2	-0.4	-0.3
$p_3$	0.3	0.9	0.3	0.0	0.0	0.0
$p_4$	-0.2	-0.6	-0.2	0.0	0.0	0.0
$p_5$	0.1	0.3	0.1	0.2	0.4	0.3

It is clear that parameters  $p_1$  and  $p_3$  have the same effect on the model results;  $p_4$  appears to have the very opposite effect, but this is merely a matter of sign: a decrease of  $p_4$  has the same effect as an increase in e.g.,  $p_1$ . Further,  $p_2$  has an effect on the M's that is quite different from that of the  $\{p_1, p_3, p_4\}$ -group. Finally, the effect of  $p_5$  appears to be intermediate between those of the other two groups: the same effect on the M's can be obtained by a combined increase in  $p_1$  and a decrease in  $p_2$ . In fact, the matrix S in the table has a rank of only two: two rows are sufficient to describe the entire model-output behavior.

This example suggests the following procedure to cluster the parameters into separate groups:

- 1) determine the number of independent rows of the matrix S; this number (N) is called the rank of the matrix.
- 2) for a first qualitative grouping, scale all rows of S to unit length:

$$L_i = \sqrt{(\sum_{j,t} (S_{i,j,t})^2)} \quad (9.5)$$

$$S'_{i,j,t} = \frac{S_{i,j,t}}{L_i}$$

this scaling would make  $p_1'$  equal to  $p_3'$  in the example above.

- 3) perform a cluster analysis on the rows, forming N clusters. As a distance measure the absolute value of the sine of the angle between the two columns is used:

$$D_{i,k} = \sqrt{(1 - \sum_{j,t} (S'_{i,j,t} * S'_{k,j,t}))} \quad (9.6)$$

in this way the distance between two parameters having (apart from scaling) the same effect is zero, two independent parameters have a (maximal) distance of 1.

4) select from each of the N clusters the row which had the largest length before scaling

5) check whether linear combinations of the selected rows (parameters) are in fact able to reproduce the original S-matrix.

In this procedure it should be kept in mind that there is considerable noise in the actual matrix S in table 9.1. In our example, this would mean that the zero values would actually have some small random value, which makes the rows 1, 3 and 4 no longer strict linear combinations of each other. Therefore, the objective should not be to reproduce S exactly, but only approximately. A technique to determine the approximate rank of a matrix is principal component analysis (Pielou, 1984). By means of an analysis of the correlations between the columns of S, orthogonal linear combinations of the columns of S are determined which represent decreasing fractions of the original variance in the matrix. In our case, 95% of the variance could be represented by the first 15 principal components, 99% of the variance by the first 22 components.

This analysis implies that it would in theory be sufficient to represent 95% of the effect of the entire set of parameters by only 15 new ones. However, it would be quite awkward to work with linear combinations of the old parameters representing such an optimal parameter choice: "0.3 times zooplankton respiration - 0.1 times phytoplankton mortality + ...". The use of the original parameters is less efficient (we have to use a few more), but much more convenient.

A weighted group-average clustering algorithm (Davis, 1973; Pielou, 1984) was implemented using (9.6) as a distance-measure. The results are represented in figure 9.5. It can be observed that at the higher cluster-levels the links are almost at a distance of unity, i.e.: the groups represent completely independent (orthogonal) parameters. At the lowest levels, it can be observed that none of the parameters has exactly the same effect as others; this is remarkable as the table contains a number of "replicates": as each batch of parameters in the sensitivity analysis included the parameters with the largest effect in the other batches. These replicates are usually grouped together (e.g. PMAX10, CCHLMIN), but are also found far apart (e.g. ARAT).

A special case is formed by a few parameters (PMAXB10, TSILT(3), EFTMAX, FAECDFRAC) whose influence on model was (rounded to) zero throughout. These parameters could not (and obviously need not) be clustered; a bordering case is formed by the parameter DISPl2, which has a slight effect on a single output-variable (CCHL(2)); as a result of the large number of zero's this row is almost orthogonal to all other rows, and it appears to be very unique (see figure 9.5; because of its negligible value however (L = 0.04) it was not considered further.

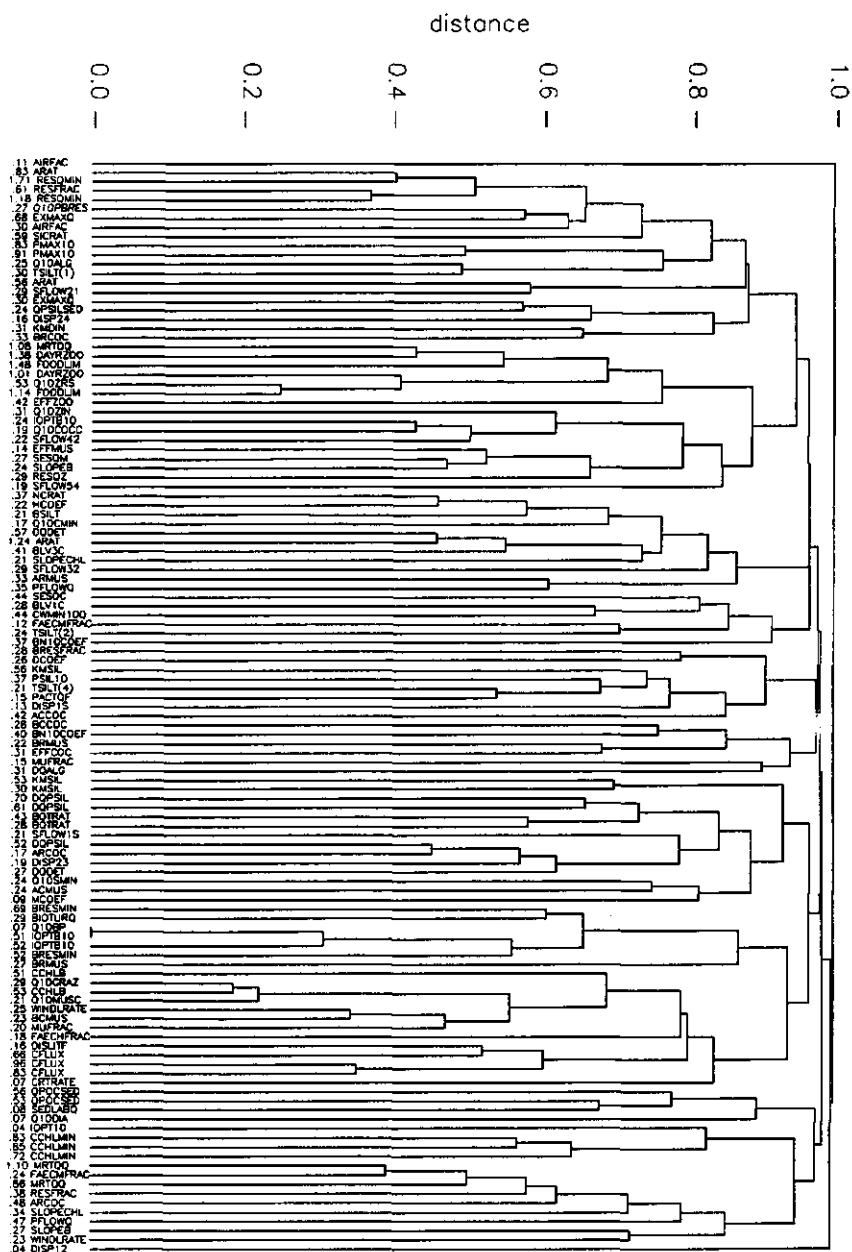


Figure 9.5: Dendrogram obtained by clustering the rows of table 9.1 using the distance-measure (9.6). The number in front of the parameter-name represents the original length (equation 9.5) before scaling of the row.

Taking into account that the number of parameters should probably be somewhat higher than the number of principal components to represent the same output-space, the dendrogram in fig. 9.5 was separated at a distance-level of 0.88 into 21 clusters. The parameters having the greatest average effect (greatest length according equation 9.5 in each cluster are listed in table 9.3.

**Table 9.3:** 21 parameters selected as the ones with the greatest length (=average impact on the model) from the 21 clusters that result from figure 9.5 by splitting at an inter cluster distance of 0.88

AIRFAC	FOODLIM
ARAT	KMSIL
BN10COEF	MRTQQ
BRESFRAC	MUFRAC
BRESMIN	PSIL10
CCHLMIN	RESQMIN
CFLUX	RESQZ
CWMIN10Q	Q10SMIN
DQALG	QPOCSED
DQPSIL	Q10DIA
EFFCOC	

A check on the choice of parameters was performed by finding for each row in S the linear combination of the parameters in table 9.3 that gave the best fit (in a least-squares sense) to this row. For each of these approximations the fraction of variance "explained" by the 21 parameters was never less than 0.78; the average explained variance was even 0.97.

There remain some issues not entirely resolved by the procedure presented above. In the first place, only a limited number (36) of output-variables and time-steps was considered. With a total number of 12 state-variables (in 4 compartments) and a simulation period of 5 years, it would have been (theoretically) possible to calculate an S-matrix with  $4 \times 12 \times 365 \times 5$  columns. Apart from the practical impossibility to calculate such a matrix, it would obviously contain an enormous amount of redundant information. The assumption that the present 36-column matrix (considering only three points in time and 12 output-variables) contains sufficient information to characterize the entire model-response to the variations in some parameter cannot be rigorously checked; it appears to be supported however by the fact that 15-20 columns appear to contain this information already.

A second problem is that although the reduced set of parameters contains all the qualitative behavior of the original full parameter set, the absolute amount of model-output variation as a result of the parameter-variations has become smaller. For example, parameter p1 was omitted from table 9.2, because it had an effect similar to the larger p3; however, although the effects of p1 and p3 may be interchangeable, the combined effect may be expected to be larger than that of p3 alone. The fact that a parameter from the reduced table 9.3 represents on the average 5 "old" parameters does not necessarily mean that a large amount of variance is lost: in the first place the assumption that two related parameters may vary independently

(which would allow us to sum their variance) is probably not true, and in the second place, the assumption that their effect are linear (which would allow us to add their sensitivity coefficients) is true neither.

As an example of the first point: zooplankton-researchers have measured food-uptake, assimilation and respiration rates of copepoda, usually in separate experiments. Therefore, it is not possible to determine the interdependence of these rates, and in the sensitivity analysis their uncertainties are treated as independent. However, this is probably not true: combining lowest food-uptake and assimilation rates with highest respiration leads to a permanently negative food-budget for the copepoda, while the combination of favorable rates would lead to a "super-copepod" showing unrealistically high growth-rates. In reality, respiration is probably positively correlated with food-uptake and assimilation negatively. Putting assimilation and respiration at some intermediate value and varying only food-uptake rate gives us probably a much more realistic picture of variations in growth rate than independent variations.

The non-linearity in model response makes it impossible to add the effects of two independent parameters: in theory, their combined effect could be larger or smaller, but in practice it will usually be smaller. In ecological systems (or at least, in ecological models) there are numerous negative feed-backs, which cause the response of the system to be less than proportional to the perturbation applied; i.e.: the response to variations in parameter values resembles a saturation curve (Von Bertalanffy, 1968). If the largest of two independent parameters covers most of the saturation-like response of the model, the additional effect of the second parameter is only small, and it would not be correct to add the second response to that of the first.

In conclusion, the assumption that the selected parameters cover (nearly) the entire model-output range not only qualitatively (in terms of independent types of model-response) but also quantitatively (in terms of absolute ranges of output-variables) appears to be reasonable.

#### 9.6 Summary

In this chapter the effect of parameter uncertainties on model output is investigated. For this purpose a Monte-Carlo analysis is used because this method has a relatively high computational efficiency without the need to assume that model-response is linear.

In this analysis, it is not possible to vary all parameters simultaneously. As the model-response to parameter variations depends both on other parameters and on the values of the state variables, it is necessary to have a first estimate of the parameters. It is argued that the actual value of the parameters in this first guess is of secondary importance, but that the values of the state-variables should "sufficiently" resemble the actual system behavior in order to obtain a realistic picture of parameter-sensitivities. Whether the resemblance is sufficient is tested by visual inspection of the output; there appears to be no rigorous mathematical proof available.

In the sensitivity analysis, the response of 90 parameters on 12 variables at three times in 1983 was investigated. By means of a principal component and a cluster analysis, 21 groups of parameters are selected that represent the different independent types of response of the model to parameter variations. It is argued that the selection of the parameter with the largest influence from each group is sufficient to reproduce most of the model-output variability not only qualitatively, but also quantitatively.



## 10 MODEL CALIBRATION

### 10.1 Introduction

In the previous discussion of sensitivity analysis, the subject of calibration has already been briefly introduced, as both are closely related. In the present discussion, calibration is seen as an instrument to reduce the a priori uncertainty on parameter values using field data. Calibration is comparable to model validation; in both procedures the model results are compared with field data. In calibration, the initial uncertainty in parameter values is reduced by rejecting those sets of parameter values which give model results not in accordance with the field data; in validation, the model structure is tested by comparing the calibrated model with a fresh data set (Wigan, 1972).

Calibration is sometimes referred to as "curve-fitting", but in fact the two activities differ considerably because in curve-fitting any convenient curve (polynomials, splines, etc.) can be used, while calibration concerns a model with a pre-defined structure. This implies, firstly, that it is in general not possible to fit a model with  $n$  parameters through any  $n+1$  data-points. Further, parameter values are not determined by the observed data alone, but there is usually some additional information available.

The most important advantage of a physically and biologically realistic model structure occurs if the model is used to predict a new situation, i.e. in extrapolation. Extrapolation of a fitted curve leads in general to meaningless results; in the case of a structured model one may have more confidence in the predictions. The additional information on parameter values that may be used in a structured model is an obvious advantage, and (in theory at least) could make it possible to have a model that is better than the field data.

Needless to say, extrapolation remains a highly uncertain undertaking; De Wit and Arnold (1976) use the term "speculative models" for models of unique systems like the Oosterschelde, because they cannot be validated experimentally, but only more or less verified by observations of the real system over time. An example of true experimental validation would be the application of e.g. a model of maize growth, calibrated on data from the Netherlands and Botswana, to a third data-set from North America. Two data-sets from the Oosterschelde obtained during different periods cannot be used for validation as they are hardly independent: they merely represent two observations of the system in approximately the same state, and hardly increase the confidence we have in the model results if we make predictions on future scenarios. Although the available data have been split into two periods on which the model was calibrated separately, this should therefore not be viewed as a true validation of the model, but rather as a test for the calibration procedure.

In most treatments of calibration, a statistical viewpoint is taken: some probability distribution of the deviations between model and data is assumed (nearly always: normally distributed, constant variance, independent in time), which leads to a probability distribution for the parameters (Draper and Smith, 1981; DiToro, 1984; Legett and Williams, 1981; Halfon, 1985). The a priori information on the parameters is used in on-line estimation techniques (Kalman-filtering), in which the parameters are updated as new field-data become available (DiToro, 1984; Walters, 1986; Beck, 1987). A very general approach is followed by Tarantola (1987), who discusses both the use of a priori information and the influence of the choice of probabi-

lity distributions instead of the usual Normal distribution (robust estimation, see also Chambers et al., 1983).

The statistical approach makes it possible to test whether some parameters are significantly different from those in a more simple model, in which case the simple model is to be preferred (e.g. reduce model  $y = a + b.x$  to  $y = a$  or perhaps  $y = b.x$  or even  $y = 0$  etc.). It is also possible to calculate the probability that the observed residuals are actually a realization of the assumed probability distribution. If this probability is very low, then either the assumptions on the statistical behaviour of the residuals are wrong and must be adjusted, or the model structure itself should be rejected (e.g. Draper and Smith, 1981). It must be noted however that these calculations should be applied with caution: often, the underlying assumptions (e.g. Normal distribution) are difficult to check and influence the results to a considerable degree (Tarantola, 1987, Press et al., 1987). However, an important problem in this approach is that it does not take into account that the acceptance or rejection of a model by the user is not a purely technical question, but depends on whether the model adequately addresses the objectives for which it was developed.

Even in a purely scientific context (testing and improving hypotheses on real-world behavior) there are some conflicts with an "objective" approach to judge model performance. If the model is developed to assist management decisions, the criteria by which it is judged may be completely different from statistical considerations: for example, a model may be chosen that systematically over-predicts the data to be on the safe side in making decisions.

To illustrate these issues we may consider a regional model of fish populations which includes primary production, zooplankton and fish; in such a model it may be assumed that the primary production in a given region is a constant. Confronted with actual primary production data, this description would be invalid (seasonal, local variations) but this simplification appears to be acceptable because, obviously, the model is meant to be compared with the observed fish stocks and the relation with primary production is only indirect. Less obvious would be a comparison with zooplankton data: to what extent is the model invalidated if zooplankton dynamics are described poorly, but fish-stocks are more or less correct? A close fit of the model to both fish and zooplankton dynamics would be optimal, but if this is not possible, the zooplankton-deviations are probably judged less severely than the fish-deviations: this weighing decision is subjective, depending on the purpose of modelling, and not on a statistical measure such as the variance of the zooplankton or fish field-data.

This illustrates a general problem with an "objective" approach to calibration: as more data are introduced, it is possible to invalidate almost any ecological model. The solution may be sought in ever expanding and refining the model, but this is clearly not very practical; the practical alternative is to orient the model to some well-defined objective, and to judge it accordingly. In contrast to the situation in some of the basic physical sciences, an ecological model usually has a very limited scope: in the example above, the scope was a single trophic level; another restriction is usually the geographic range (for instance, some model of algal growth may be applicable only during the stratified period in the Northern North Sea; another only in shallow phosphorus-limited lakes), a further restriction may be the time-scale, and so on. Clearly, the validation/calibration procedure should take this limited scope into account.

The present model is predominantly a management-oriented model: it aims at the calculation of the impact of human activities on the first

trophic levels in the Oosterschelde, in particular the effects of construction of the storm-surge barrier and the cultivation of mussels on the food supply for the filterfeeders. This aim has several consequences for model content. It has often been stated that a model should be kept "as simple as possible"; in the present context, this implies that processes that are (presumably) least related to the aim of the model have been the most simplified. In other words, modeling errors are deliberately introduced in order to keep the model within its limited scope.

The emphasis on an objective-oriented judgement of model results does not mean that calibration should be an entirely subjective and ill-defined procedure. Calibration of a complex model probably most often proceeds via the "manual method": a few parameters are selected to be adjusted, and the model-results are judged qualitatively. Obviously, this method can be very time-consuming and generally yields irreproducible results (Tarantola, 1987). Furthermore, its results are not conclusive: if manual tuning does not yield satisfactory results, should model structure be adapted or should tuning be applied with more intuition or perseverance? The possible danger of this point is that model structure is adjusted too soon, and is made too complicated. In addition, the manual calibration yields only a single best parameter set, but no information on its uncertainty. Therefore, some well-defined calibration procedure (algorithm), in which the objective-oriented weighing of the model output and the uncertainty concerning the calibrated parameters are incorporated explicitly is in general to be preferred.

As will be discussed below however, there is no "perfect" calibration-algorithm; there remains a chance that calibration fails, giving incorrect information on parameter uncertainty or stimulating the over-development of the model. Nevertheless, the calibration procedure presented below aims at reducing the chance of such failure, and to be more efficient than manual tuning.

In this chapter, a weight will be attached to each output-variable. This weight will be used in judging model performance, and will be defined according to the above-mentioned criteria. A method to obtain parameters yielding model results within acceptable ranges will be discussed. The calibrated parameter- and model-output ranges are then presented.

## 10.2 Methods

The three major points in the calibration procedure are (see figure 9.1):

- 1) parameter- and model-output range. In the calculations a parameter is characterized by a minimum and maximum value, which represent literature data or other a priori information (e.g. non-negativity constraints etc.) on parameter values. This minimum and maximum define the parameter range. Running the model for a particular set of parameters and other input values (initial conditions, forcing functions, boundary conditions; these are here considered as fixed) gives one particular model output. Model output is very generally defined as some multivariate function of the variables and parameters in the model. In this way, the combination of model-equations and a certain fixed input maps the parameters (a single point in parameter space) onto a point in the model-output space. Similarly, the set in parameter-space formed by the parameter-ranges is mapped onto a set in model-output space. Assuming that the model produces a continuous mapping, the image of the parameter range will be a connected set. This set in model-output range represents all possible model-outcomes which can be obtained by using all possible parameter-values for this particular set of input-values. It is called the model-output range.

2) data range. Presumably some of the model-output variables have also been measured: this set of measurements can be represented as a point in output-space. Similar to the model-output, this point is characterized by a certain set of input-values; for example the measurements for one particular year. The set of measurements generally forms a lower-dimensional subset of the output-space. For the present discussion of calibration, only the part of the output which corresponds to measured values is of interest, and it will be assumed that measurements and model-output have the same dimension. The data range is a set of points here defined by maximum deviation from measured data: all points in output-space with smaller deviation from the data fall in the data range.

3) An algorithm to obtain the overlap between these two ranges, i.e.: the parameter values leading to model-output within the data range.

#### Theoretical definition of data range

To obtain a practical working definition of a data range, two aspects have to be considered: the measurement of a deviation around the measured data for an individual output-variable ( $C'$ ), and the combination of these measurements for the entire ensemble of output-variables into a single number  $C$ . The concept of a data range can then be simply translated into a range for  $C$ .

A possible criterion is to judge relative error, using (Carver, 1980; Legett and Williams, 1981):

$$C_1' = \frac{1}{n} \sum_{k=1}^n (\log y_k - \log x_k)^2 \quad (10.1)$$

or (Carver, 1980):

$$C_2' = \frac{1}{n} \sum_{k=1}^n (y_k/x_k - 1)^2 \quad (10.2)$$

with:  $n$  - number of measurements through time

$y_k$  - time-series of measurements ( $k=1..n$ )

$x_k$  - time-series of corresponding calculated values ( $k=1..n$ ).

Related measures are discussed by Legett and Williams (1981) and Stroo (1986). These measures are usefull if errors increase proportional to the magnitude of the variables (due to measurement errors, increased natural variability or both) or if the variables span a very wide range of values (e.g. in a models for bioaccumulation of toxic substances, concentrations in various species may differ several orders of magnitude; judging absolute values in this case would focus attention on the calculated and measured concentrations in a single species only). These measures are not suitable for the present case: the scatter in the measured variables (figures in chapter 9) appears to be fairly constant in most cases. Small data values are generally not more accurately measured. On the other hand, for some variables, notably chlorophyll, there does appear to be an increased variability at higher values: therefore, relative errors between model and data may be expected to decrease with chlorophyll concentration initially (the constant measurement accuracy decreases relative to measured values), and to increase again with higher concentrations (increased patchiness in time and

space not covered by the model). Judging model results by absolute errors can therefore be regarded as a compromise in this case. Another argument in favour of considering absolute errors is that most model-outputs like mussel growth are linear rather than logarithmic functions of the state variables: if chlorophyll concentration increases from 1 to 1.5  $\mu\text{g/l}$ , mussel growth will hardly change and remain zero or negative; if it changes from 10 to 15  $\mu\text{g/l}$ , mussel growth will show a much stronger increase.

The most widely used measure for  $C'$  is the sum of squared residuals. (Or, equivalently the square-root of this: a bound on  $C'$  in the form of a sum of squares can be directly translated to a bound on the square root of  $C'$ , as the square root is a monotonic function).

The quadratic (or square-roots of quadratic) measures treated so far have the undesirable property that they are relatively sensitive to outliers (Chambers et al., 1983; Tarantola, 1987): the value of  $C'$  may be dominated by some large residuals, which may be, of course, very exceptional and revealing cases, but which can in practice not be distinguished from large measurement errors. Chambers et al. (1983) give an iterative scheme to detect outliers: the model is fitted using equal weights and a quadratic distance; residuals are examined and if some exceptionally large residual is detected, it receives a lower weight, after which the model is fitted again and so on, until no new outliers occur. A simpler solution which also gives a more robust (unsensitive for outliers) measure is to use the absolute values of the residuals ( $L_1$ -norm -Tarantola, 1987). For a single output-variable:

$$C_3' = \frac{1}{n} \sum_{k=1}^n |e_k| \quad (10.3)$$

with  $e_k$  the  $k$ 'th residual ( $e_k = y_k - x_k$ ;  $k=1..n$ )

Another alternative to the quadratic treatment is the use of the maximum residual, known as the  $L_\infty$  norm (Tarantola, 1987). For a single output-variable:

$$C_4' = \max \{e_1, e_2, \dots\} \quad (10.4)$$

Examples of the use of the  $L_\infty$ -norm can be found in Fedra et al. (1981), Belforte and Bona (1985) and Klepper and Van de Kamer (1987, 1988). An obvious drawback of (10.4) is the above-mentioned danger of outliers, for which this measure is maximally sensitive; a major advantage is the fact that the concept of a data-range is intuitively very clear: model and data are never more than  $C_4'$  units apart. This may make it an attractive measure, if used in combination with some data-smoothing.

For the present model, the  $L_1$ -norm ( $C_3'$ ) was chosen as a criterion for an individual output-variable in view of its robustness and simplicity.

So far, only measures for individual output-variables have been considered. For a multivariate model these have to be combined. The simplest method is to sum the squares of all residuals, both over time and over all output variables (e.g., Roberts and DiCesare, 1982). This method is in general not satisfactory, as the output will be usually differently judged for different output variables (different dimensions, different measurement accuracy; different importance).

The most generally used measure for multivariate models is to take a weighted sum of the individual sums of squares, where the weights are

different for every output variable but constant through time (Jorgensen et al., 1981; Beck, 1984; Beck and Young, 1976; Carver, 1980):

$$C_s = \frac{\sum e_{1k}^2}{w_1} + \frac{\sum e_{2k}^2}{w_2} + \dots + \frac{\sum e_{nk}^2}{w_n} \quad (10.5)$$

with  $1/w_1$  - i-th weight  
 $e_{1k}$  - k-th residual of i-th output variable

If the variance of the residuals is known a priori, its inverse can be used for the weights in (10.5). This yields the least-variance (Markov) estimate of the parameters (Halfon, 1985). Therefore,  $C_s$  is related to the statistical approach discussed above. However, in practice the weights are often estimated using "engineering judgement" (Beck, 1984).

The summation of the individual sums of squares resembles the  $L_1$ -approach above in that it is not very sensitive to some individual values of the  $C$ 's (individual "residuals"). In this context however, this may imply that a model that is close to the data for most output-variables but very far from one or two others is still considered close to the data. An individual data-point that is very far from the model may be safely considered an outlier without much loss of information, but this is probably not the case for an entire output-variable. If a model is required to describe a system consisting of several variables (for which the individual desired (and obtainable) accuracies are specified using weights), it would be intuitively reasonable to demand a similar performance for every output. It would not make sense to compensate, say, a very bad chlorophyll-output with very good nutrient- and oxygen performance; the model would still be unacceptable. (Unless, of course, chlorophyll is not needed, in which case it should not be considered as output at all).

Therefore the present model combines the individual weighted  $L_1$ -norms by means of a  $L_\infty$  norm:

$$C_s = \max \left\{ \frac{C_{s,1}}{w_1}, \frac{C_{s,2}}{w_2}, \dots \right\} \quad (10.6)$$

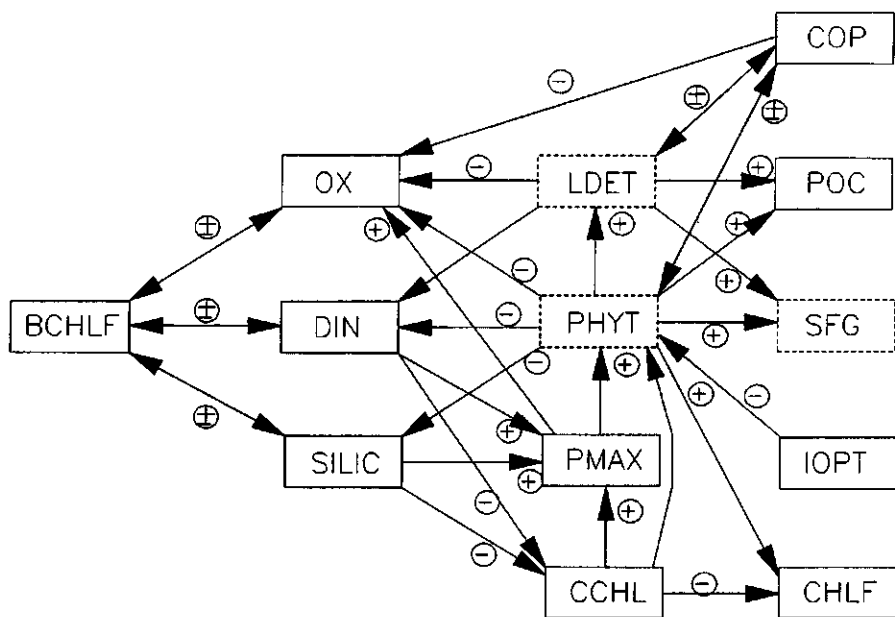
with  $1/w_1$  - i-th weight  
 $C_{s,1}$  - individual  $L_1$ -norms; see equation 10.3

#### Calculation of weights for individual output-variables

In view of the purpose of the present model, it is natural to judge the model performance on the calculated food-availability for filterfeeders. This approach presents two problems: in the first place, there are no direct observations on the most relevant state-variables: phytoplankton biomass and labile detritus (see fig. 10.1). There are, of course, observations on chlorophyll and particulate carbon (POC), but chlorophyll has to be converted to carbon using the carbon-to-chlorophyll ratio, and labile detritus forms only a fraction of total organic carbon; most of it is made up of refractory detritus. Therefore, we cannot compare the relevant model-output with observations directly, but have to rely on indirect observations. Of course, some variables are good indirect indicators (e.g. chlorophyll), others of secondary importance (e.g. it can be argued that high phytoplankton production leads to both a high phytoplankton biomass and high oxygen

concentrations; therefore, oxygen can serve as an indirect indicator for mussel food availability). In the second place, the model intends to be more than a black-box prediction of mussel-food availability, but claims to include a number of relevant processes (primary production, nutrient cycles etc.) and secondary variables (nutrients, copepods) related to this food supply; the advantage of a biologically realistic structure in a model when making predictions has been discussed previously: it would be desirable if this aspect of model performance (i.e.: are secondary variables in agreement with measured values?) could be judged as well. Again, some of the processes and variables are of less importance than others; for example benthic chlorophyll is linked to phytoplankton biomass only indirectly via the nutrients, which would make this variable seem less relevant for mussel growth than the nutrients themselves.

Both points can be considered from the same viewpoint: any observed variable is more important (either as an indirect indicator of food supply or as an indicator of food-supply related processes) as it is more closely correlated to the (unobserved) mussel food supply. The question is therefore how to measure the strength of the relation between mussel growth and observed variables. In figure 10.1, the relations between the different variables have been indicated with arrows, with the sign of the effect indicated. The calculation of the overall effect from the separate relations between the variables appears to be a complicated task, as all the possible direct and indirect paths have to be taken into account. However, the added effect of all direct and indirect paths, including correlations between variables resulting from common causes, is simply the correlation coefficient (Sokal and Rohlf, 1972).



**Figure 10.1:** relations between observed (drawn boxes) and unobserved (dotted boxes) variables in the model and mussel food supply. For abbreviations of the variables: see appendix II.

In order to have a single measure of the mussel-food supply the yearly averaged potential growth (or scope for growth, SFG; see equation 7.3) has been used as a weighting factor. Although the absolute value of this variable shows a considerable uncertainty (see discussion on the calibration of cockle and mussel growth models in appendix 1), this is of secondary importance for the present discussion, where SFG is only used as a weighing function to summarize model-output.

The scope for growth was calculated in the model for the three weight-classes of mussels: seed, half-grown and adult. It appeared that these three variables were very closely correlated: the absolute levels differ (due to the allometric coefficients) but changes in, e.g. phytoplankton biomass have the same relative effect. Therefore, only the SFG for half-grown mussels was used for the present analysis.

The output-variables for which measurements in the Oosterschelde are available were varied by means of a sensitivity analysis using the parameters in table 9.3. The yearly averaged output was then correlated with SFG, giving a correlation coefficient  $r$  and a regression coefficient  $b$ . The absolute value of  $b/0.01$  can now be used as a weight for the output-variables: if an output-variable changes with an amount  $0.01/b$  this corresponds to a change in SFG of 1% per day.

The results are listed in table 10.1. In some cases (e.g. benthic chlorophyll, IOPT) the correlations are negligible. This may imply either that there is hardly any relation between these variables and mussel growth, or that different chains of relations (paths) cancel each other: for example, it may be expected that there is a clear positive relation between SFG and copepod biomass as both groups use the same food-supply; on the other hand, a high copepod biomass will reduce the amount of food available for mussels, so that on the whole a high or low copepod biomass does not give much information on conditions for mussel growth.

**Table 10.1:** Correlation coefficients between yearly-averaged values of different output-variables and scope for growth of half-grown mussels calculated for compartment 2 in 1983. The variable-ranges ( $W$  in equations 10.6) are calculated from regression coefficients  $b$  as  $|0.01/b|$ : a wide range relative to the magnitude of measured values indicates a weak relation between the variable and SFG.

name:	definition:	corr. coef.	$W$
CHLF	Chlorophyll concentr.	0.91	1.29 $\mu\text{g/l}$
OX	oxygen concentration	0.67	0.47 $\text{mg/l}$
DIN	dissolved inorganic nitrogen	-0.60	0.10 $\text{mg/l}$
CCHL	carbon to chlorophyll ratio	0.53	6.33 (w/w)
PMAX	light-saturated prod.rate	0.42	4.31 $\text{gC/gChlf/h}$
SILIC	silicate concentration	-0.31	0.38 $\text{mg/l}$
POC	particulate organic carbon	0.19	1.25 $\text{mg/l}$
COF	copepod biomass	-0.14	0.22 $\text{mgC/l}$
BCHLF	benthic chlorophyll	0.13	314 $\text{mg/m}^2$
IOPT	optimal light int. phytop.	0.11	30.5 $\text{W/m}^2$



### An algorithm for model calibration

Only in the case of a linear model and the use of the quadratic distance is it possible to obtain a calibrated parameter-range analytically. In the general case this is not possible and the following procedure is usually followed (e.g. Beck and Young, 1976; Carver, 1980; Draper and Smith, 1981; DiToro, 1984; Birta, 1984; Tarantola, 1987):

- 1) choose an initial parameter set (P), calculate distance C(P) from data;
- 2) follow a path through the parameter-space from this set leading to lower C-values until C(P) can not be further decreased (e.g. steepest descent, quasi-Newton methods, etc.). This defines  $P_{min}$ ;
- 3) estimate a range of P-values around  $P_{min}$  from the local behavior of C(P).

This approach has some weak points, of which the importance depends on the model being calibrated and the C-function. Firstly, the initial choice in (1) not only determines the speed at which the algorithm under (2) converges, it may also determine the point  $P_{min}$ , because C(P) may show local minima. Secondly, the algorithms under (2) may show poor convergence. In the case of a quadratic C-function and without constraints on the parameters P, convergence is usually good; problems arise in the case of minima lying on constraints, or non-quadratic C-functions (Tarantola, 1987; Press et al., 1986). Finally, the estimation of the P-range around  $P_{min}$  is in general problematic; it is usually assumed that the model may be linearized locally: this assumption is crucial for the resulting estimates and may not be realistic (Draper and Smith, 1981).

An algorithm which overcomes these difficulties is due to Price (1979). It is related to the method of "simulated annealing" (Tarantola, 1987; Press et al., 1986) and was proposed as a method of (constrained) function-minimization only, but it also solves the problem of calculating an arbitrary complex (e.g. skewed; even disjoint) P-range.

For the minimization of n parameters the algorithm requires storage of N parameter sets, with  $N \gg n$ . It starts by choosing the N parameter-sets at random from the initial parameter ranges, and calculating the corresponding C-values; these (P,C)-sets are stored. A new parameter-set is generated by randomly selecting n+1 parameter sets from the N stored ones. The first n points of this set are used to calculate a centroid G:

$$G(i) = \frac{1}{n} \sum_{j=1}^n P_j(i) \quad \text{for } i=1..n \quad (10.7)$$

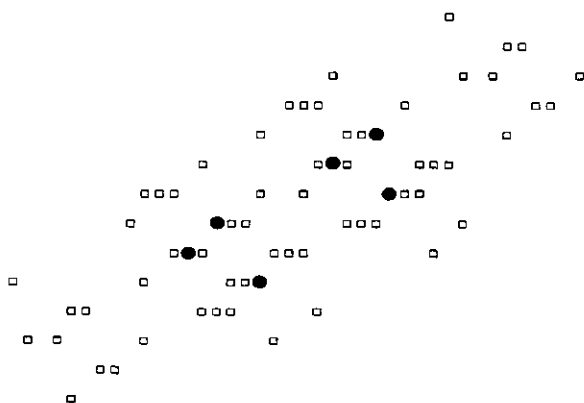
with:  $i=1..n$  index for parameter-values  
 $j=1..n$  index for parameter-sets

the new point is now the (n+1)st point reflected in this centroid G:

$$P'(i) = 2 * G(i) - P_{n+1}(i) \quad \text{for } i=1..n$$

The new C-value is then calculated, and if it is lower than one of the stored (P,C)-sets, the new set replaces this, and so on. In this way, the initial homogeneous distribution of P-values is steadily replaced by values around the minima (!) of C; the set of stored points represents the corresponding parameter-range.

The generation of new trial points from the stored points is illustrated in figure 10.2. It can be observed that the algorithm shows a "reasonably intelligent pattern recognition capability" (Price, 1979): in the example, the stored points appear to be in two clusters, and seem to lie on two parallel lines; new trial points are generated mainly around the two old clusters and on the two lines, without too much rigidity in adhering to this pattern (if any, of course). The rigidity with which an established pattern is followed can be adjusted by varying the ration  $N:n$ . If this ratio is low, the algorithm is relatively successful in finding improved parameter sets, but is in danger of adhering too rigidly to an erroneous initial pattern. An example in two dimensions would be: if we store three points only, and these happen to form an equilateral triangle, we can only generate new equilateral triangles, but could never reach a minimum inside the triangle. A high  $N:n$  ratio effectively prevents these kinds of degeneration but slows down the progress of the algorithm considerably.



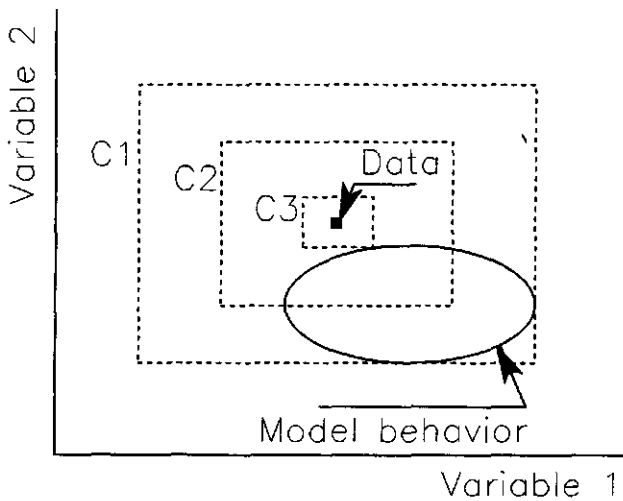
- configuration of 6 stored points in 2 dimensions
- set of 60 possible trial points

**Figure 10.2:** The generation of new trial points in the Price algorithm. Closed circles are the 6 stored points; the new trial point is one of the small squares.

Because only the worst parameter set is removed, the parameters retain an approximately uniform distribution over their increasingly narrow range; however, the marginal distributions for a single parameter may show a non-uniform distribution (see, for example figures 10.9-11 and A1.16-17).

A final note on the application of the algorithm concerns a stopping criterion: at what level of  $C$  are we satisfied? The ranges ( $W$ ) in the calibration procedure (table 10.1) were chosen on the basis of the relations between the output-variables and the scope-for-growth (SFG) of mussels. Although this provides a model-objective oriented way to obtain relative weights for the different output-variables, the choice of the "effect-level" of a variable of  $0.01 \text{ .day}^{-1}$  in SFG was rather arbitrary. Therefore, there is no clear choice of a level of  $C_*$  (equation 10.6) which represents the acceptable data-range, and indirectly the calibrated parameter-ranges. A too high value of  $C$  may not reduce output-uncertainty at all: all model-results

are acceptable; a too low value of C may make all model-results unacceptable: see figure 10.3.



**Figure 10.3:** In the choice of a threshold for the distance between model and data a low value (C3) leads to a single or very limited number of acceptable model-runs only, and thus to a too narrow range of parameters. A high value (C1) makes all model-outcomes acceptable, and thus does not reduce parameter uncertainty. The boundaries of the different C values are rectangular (instead of square) because the second variable has a closer relation to mussel scope-for-growth than the first.

A comparable problem occurs in statistical parameter-estimation techniques like least-squares (Draper and Smith, 1981) or maximum-likelihood estimation (Walters, 1986). After the optimal set of parameters has been calculated, the deviations between model and data are examined to see whether these optimal parameters do in fact yield an acceptable model; furthermore, the uncertainty in estimated parameters is calculated, with the general result that high average residuals give a high parameter uncertainty.

In practice, the problem of giving an *a priori* bound on  $C_e$  has been avoided analogously to the statistical approach: the model was calibrated using the weights in table 10.1, seeking a minimum value of  $C_e$ . All parameter-values giving model-results within 10% of these minima have been defined as acceptable. A visual inspection of the results afterwards has been used to judge whether the "acceptable" model runs are in fact acceptable or not.

The first point in this strategy (seeking an optimal parameter set and judging its acceptability afterwards) appears to be straightforward: it would be hard to imagine setting a too low bound on  $C_e$  and after failure of the algorithm not even inspecting the optimal (but unacceptable) results. This would not be the case (unlike the present) where there is some alternative model. If this alternative model would give an optimal  $C_e$ -level, the same level could be used to put a bound on the model under consideration.

The second point is the rule of accepting all parameter-sets giving

$C_0$ -values within 10% of the optimum. The attractive side of this rule is that it coincides with the intuitively reasonable requirement that a bad fit should lead to a high uncertainty: if the average residual is high, a 10% increase in this average will coincide with a wider range in model-behavior (and parameter values) than when the average residual is small. The problem is of course: why accept a 10% increase in  $C_0$ , and not 5% or 25% or any other value? Again, the only answer appears to be an a posteriori inspection of the results: does this rule give an acceptable uncertainty range or does it seem too small (i.e.: there are more acceptable parameter-values) or too large (some of the parameter values lead to unacceptable model-results).

### 10.3 Results: dispersion coefficients

The calibration of dispersion coefficients may be treated separately from that of other parameters because there is an output-variable (salinity) that is influenced by these parameters only and not by the biological processes.

It is difficult to give a priori estimates of the value of the dispersion coefficients as they are only to a limited extent physical quantities: included in the dispersion-term are also all advective processes not described in the schematization of the model, e.g.: residual circulation patterns in a one-dimensional model (Fischer et al., 1979). In similar one-dimensional residual-flow models (Oosterschelde: Bos, 1985; Ems-Dollard: Helder and Ruudij, 1982), values for the dispersion coefficient range from 10 to 400  $m^2.s^{-1}$ .

A practical difficulty in the estimation of the dispersion coefficients in the present model is that there are two boundaries, one at the sea and one at the Volkerak side (see figure 2.1 and 2.2 for position of boundary compartments; figure 10.4 shows measured concentrations at the boundaries). The dispersion coefficients at these two boundaries cannot be estimated simultaneously. For example, a high dispersion across the sea boundary causes a high influx of salt; this may be compensated by a high dispersion at the Volkerak boundary, thus transporting the salt upstream and keeping the salinity in the Oosterschelde near measured values. However, the result would be a constant import of salt into the Volkerak, which would not be realistic. Therefore, the additional constraint was made that the dispersion coefficient DISP45 should cause net transport of salt into the Volkerak (calculated using measurements in compartments 4 and 5) over a long period to be zero.

For the calibration, the available data were split into two periods: 1980-1982 and 1983-1984. The constraint on the Volkerak salt-budget yielded two remarkably similar values for DISP45: for 1980-82 a value of 214  $m^2/s$ , for 83-84 of 218  $m^2/s$ . A uniform value of 215  $m^2/s$  was further used.

The accuracy of salinity-data used for calibration depends only to a very limited extent on the accuracy of measurement. Most of the error is caused by patchiness as a result of incomplete horizontal and vertical mixing of the watermasses; in addition there are model-errors caused by the one-dimensional description of the estuary (e.g. an uneven transversal or vertical distribution), and errors in the fixed-volume transformation. Most of these errors will be more pronounced in a situation with a strong salinity gradient, i.e. in compartment 4. Therefore, the weight for compartment 4 was chosen 2 times higher than for the other compartments.

The calibrations of both periods ended with an average absolute residual of 0.8 ‰ for the first three compartments, and 1.6 ‰ for the fourth compartment. However, the estimation of the dispersion coefficients resulting from the first three years was much better than that of the second period. The resulting calibrated parameter ranges are summarized by an

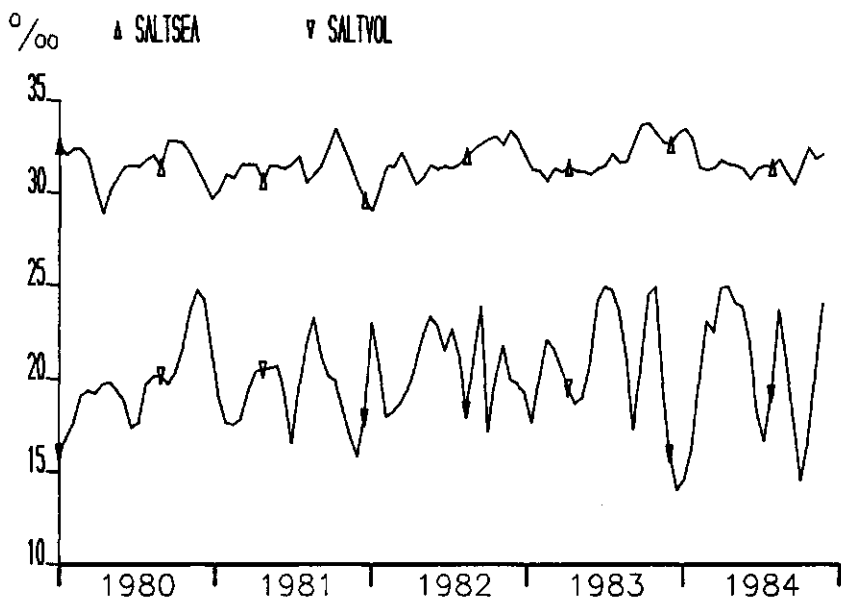
average and standard deviation in table 10.3. It may be observed that the calibrated ranges from the second period overlap those of the first period in all cases: there is no conflict between the data from the first and second periods, but this is hardly surprising as the data from the second period contained apparently less information. This is also apparent from the parameter-values obtained for the entire period: they are nearly equal to those obtained from the first period. The better estimation that is possible in the first period may be explained by the greater number of observations and the larger fluctuations in freshwater flow through the Oosterschelde, resulting in larger fluctuations in salinity.

Table 10.3: results of the calibration of the dispersion coefficients. DISPi<sub>j</sub>: dispersion coefficient between compartments i and j; DISP1S: between 1 and sea. Units: m<sup>2</sup>/s. The initial range for all parameters was 10-400 m<sup>2</sup>/s

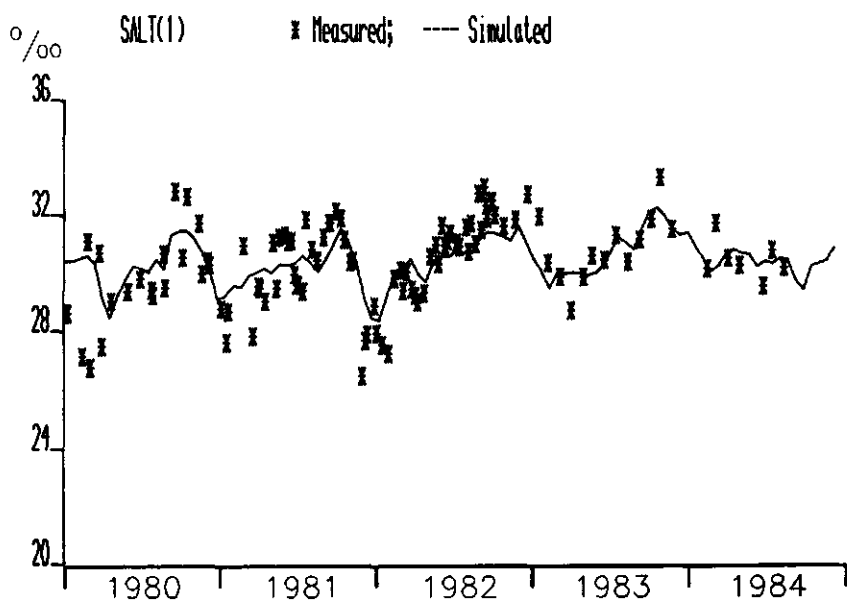
parameter:	1980-1982		1983-1984		1980-1984	
	avg.	st.dv.	avg.	st.dv.	avg.	st.dv..
DISP1S	378 ± 11		316 ± 38		373 ± 11	
DISP12	226 ± 6		223 ± 39		226 ± 6	
DISP23	141 ± 24		182 ± 84		144 ± 23	
DISP24	361 ± 5		330 ± 32		360 ± 5	

correlations (1980-84):

	DISP1S	DISP12	DISP23	DISP24
DISP1S	1			
DISP12	-0.60	1		
DISP23	-0.28	0.02	1	
DISP24	0.40	-0.65	-0.40	1



**Figure 10.4:** measured salinities at North Sea (upper curve) and Volkerak (lower curve) boundaries



**Figure 10.5:** measured and calculated salinities in compartment 1.

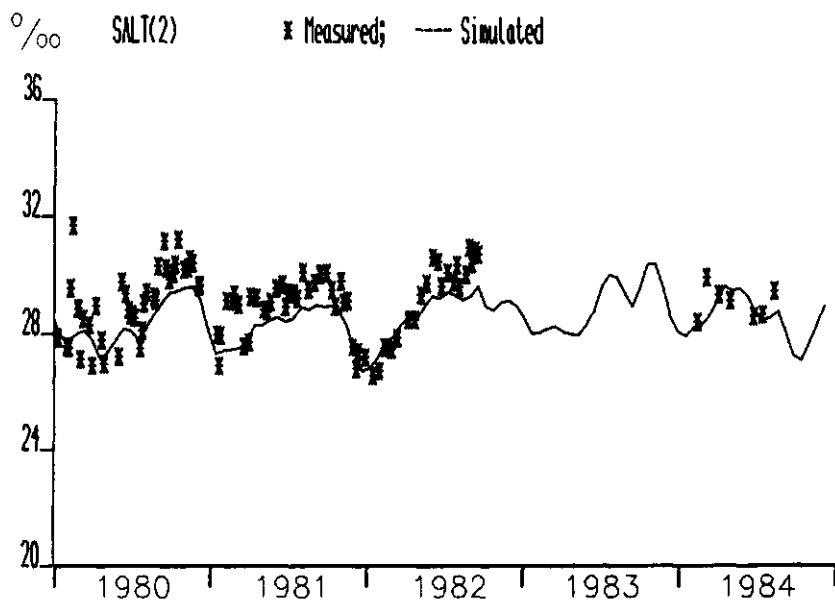


Figure 10.6: measured and calculated salinities in compartment 2.

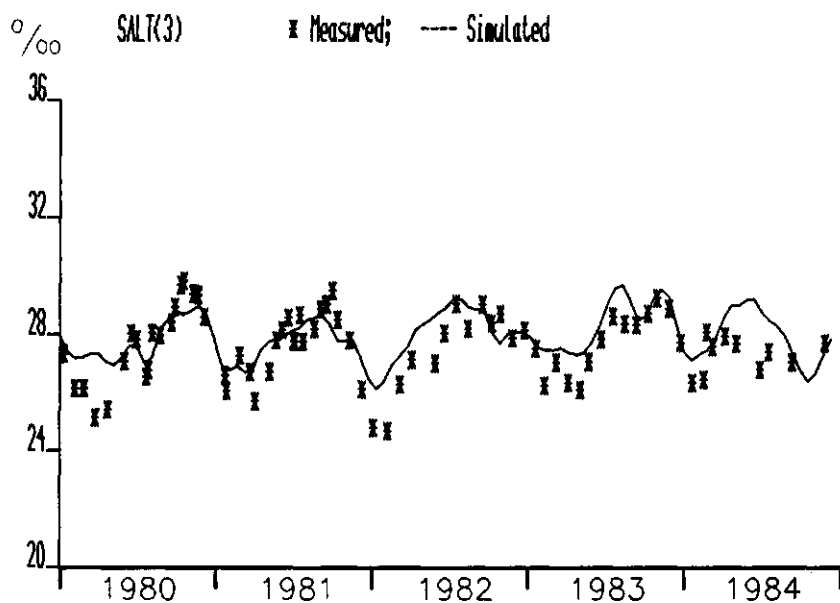


Figure 10.7: measured and calculated salinities in compartment 3.

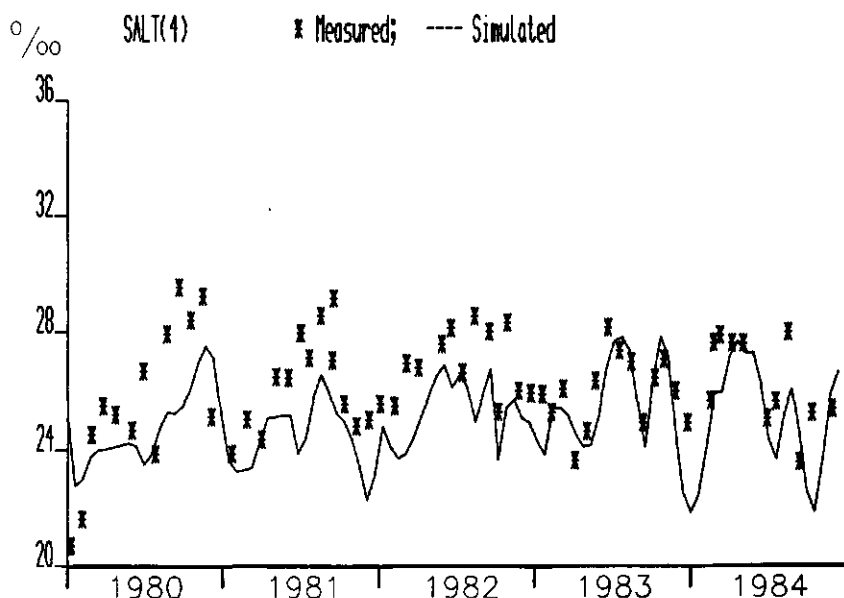


Figure 10.8: measured and calculated salinities in compartment 4.

The results are in general satisfactory, although there are some periods with a systematic under or over-estimation of the salinities by the model, notably in 1980/81 where calculated salinities are too low in compartments 2 and 4. The situation could probably be improved by choosing a higher dispersion coefficient between compartments 1 and 2, and at the same time between 1 and sea. This last point is necessary to prevent too low calculated salinities in compartment 1 as a result of the increased mixing with the relative fresh compartment 2. It may be noted that this increased dispersion between 1 and sea is not possible in the assumed initial range of the dispersion coefficients: DISP1S is already close to its upper limit of  $400 \text{ m}^2.\text{s}^{-1}$ .

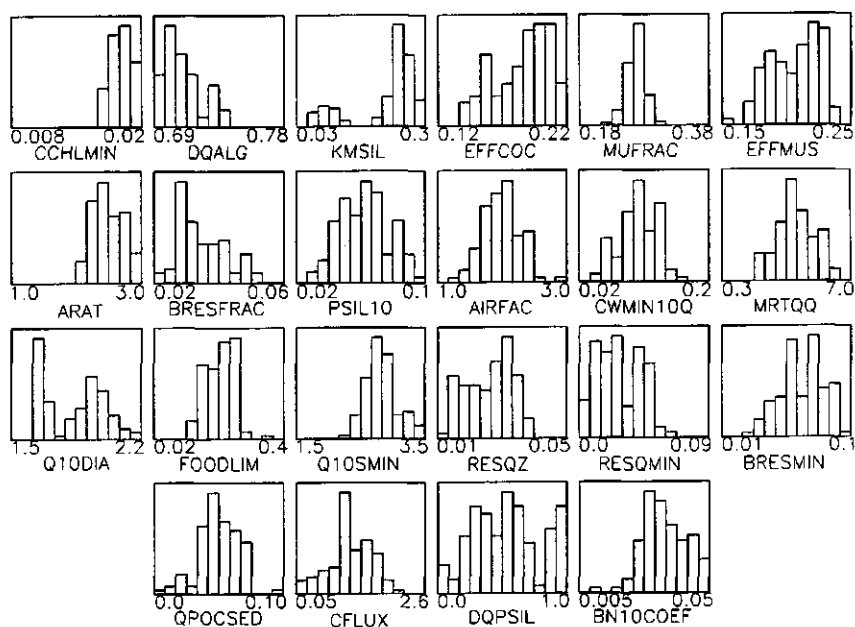
Values for the dispersion coefficients higher than  $400 \text{ m}^2.\text{s}^{-1}$  (the upper limited for reported values in similar estuaries) would probably lead to some improvement in calculated salinities. It should be noted however that freshwater discharges and boundary conditions are known with a limited accuracy only: although as a first approximation it seems reasonable to assume that all uncertainty lies in the dispersion coefficients (which are therefore used as parameters in the calibration), this assumption should not lead to unrealistic values of the dispersion coefficients. Instead of calibrating the dispersion coefficients outside their a priori bounds, it will be assumed that the (moderate) systematic errors in the calculated salinities can be attributed to errors in discharges or boundary conditions.

#### 10.4 Results: other parameters

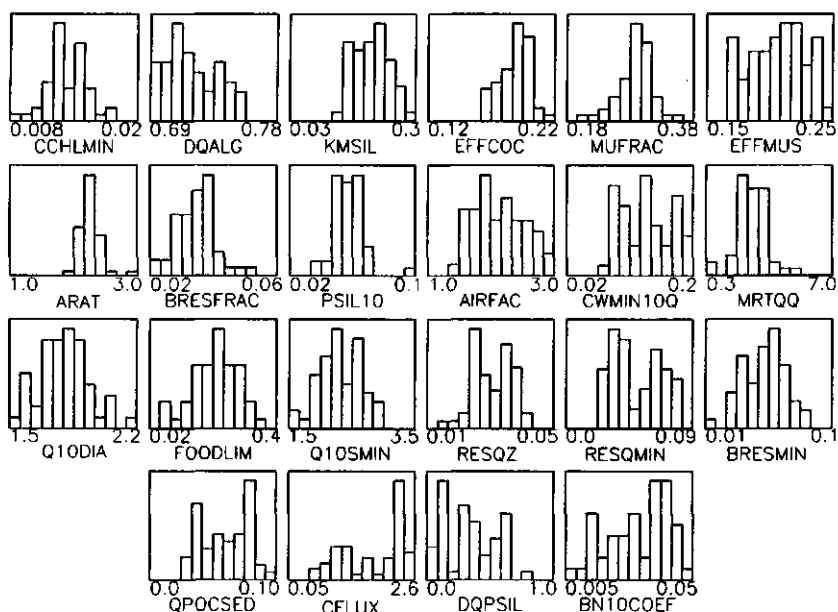
The parameters from table 9.3 were calibrated three times, again using the data from 1980-82, 1983-84 and the entire period 1980-84. It appeared that the three calibrations gave in general similar results for the calculated output (figures 10.14-10.17), but there were some differences in



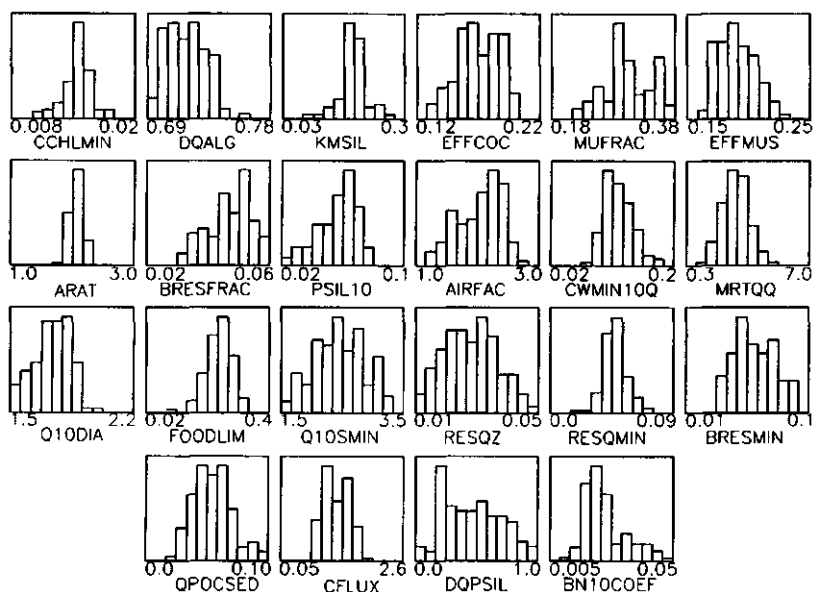
calculated parameter ranges. For the majority of the parameters, the results from the 80/84 runs most resembled those of the 83/84 runs; in contrast to the situation for the calibration of the dispersion coefficients in the previous section, it appears that for the biological processes the measurements from the second period are the most informative. In figures 10.9-10.11 the calibrated parameter-ranges are shown. It can be noted that a number of parameter-ranges are substantially reduced; in most cases the reduction in the 80/84 run resemble those in the 83/84 run, e.g. parameters CCHLMIN (min. chlorophyll content of phytoplankton), ARAT ("disadvantage coefficient" of non-diatoms), and MRTQQ (coefficient in mortality equation for zooplankton); in some cases the three runs give almost identical results, e.g. QPOCSED (fraction refractory POC in sediment) and DQALG ("dissolved-like" fraction of phytoplankton). By taking linear combinations of the original parameters it is possible to distinguish the three parameter-sets from each other (a multiple-discriminant analysis Pielou, 1984; see figure 10.12), but this distinction is not as clear for any combination of single parameters. The best separation between the three parameter-sets based on two parameters is given in figure 10.13.



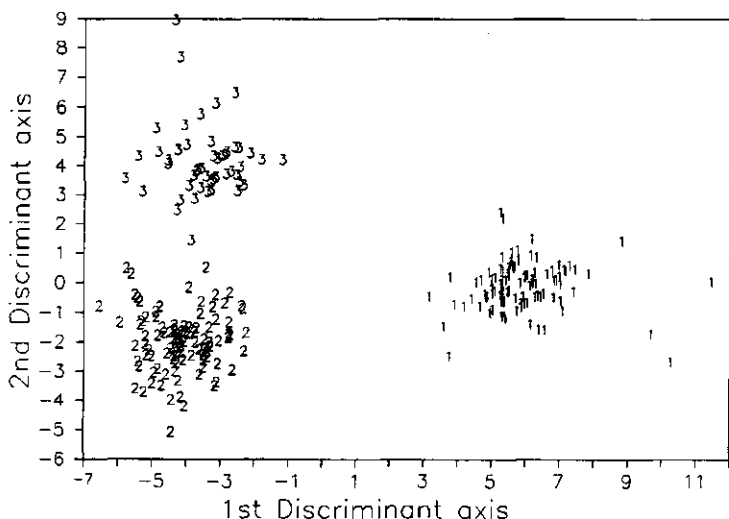
**Figure 10.9:** The parameter distributions resulting from the calibration of the model on data from 1980-1982. The x-axis shows the initial range of each parameter.



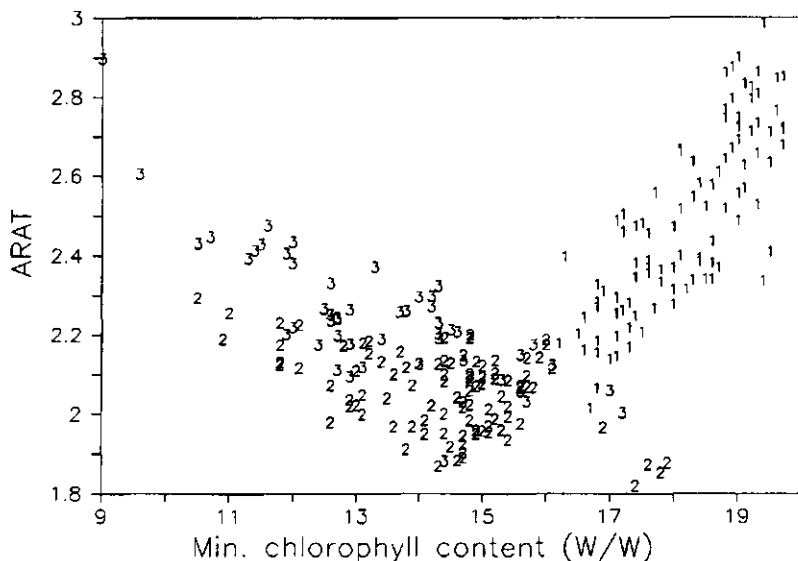
**Figure 10.10:** The parameter distributions resulting from the calibration of the model on data from 1983-1984. The x-axis shows the initial range of each parameter.



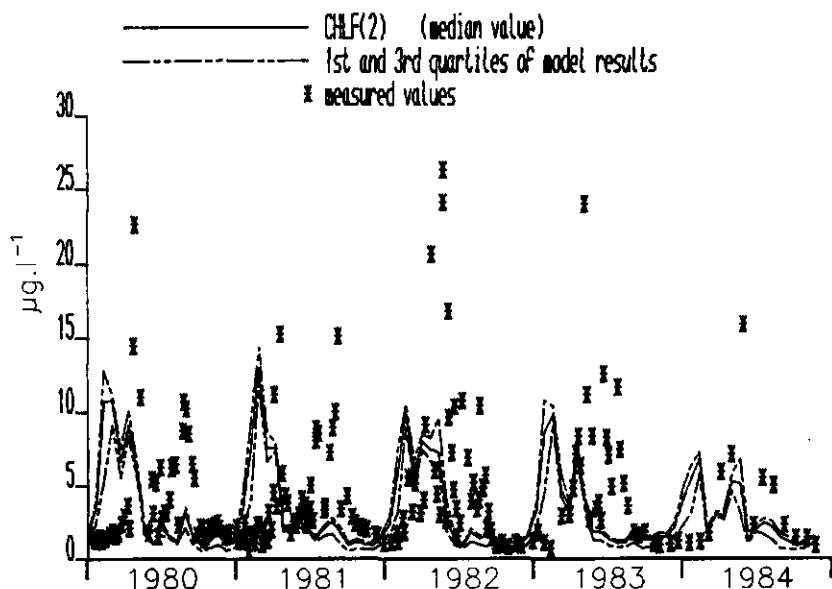
**Figure 10.11:** The parameter distributions resulting from the calibration of the model on data from 1980-1984. The x-axis shows the initial range of each parameter.



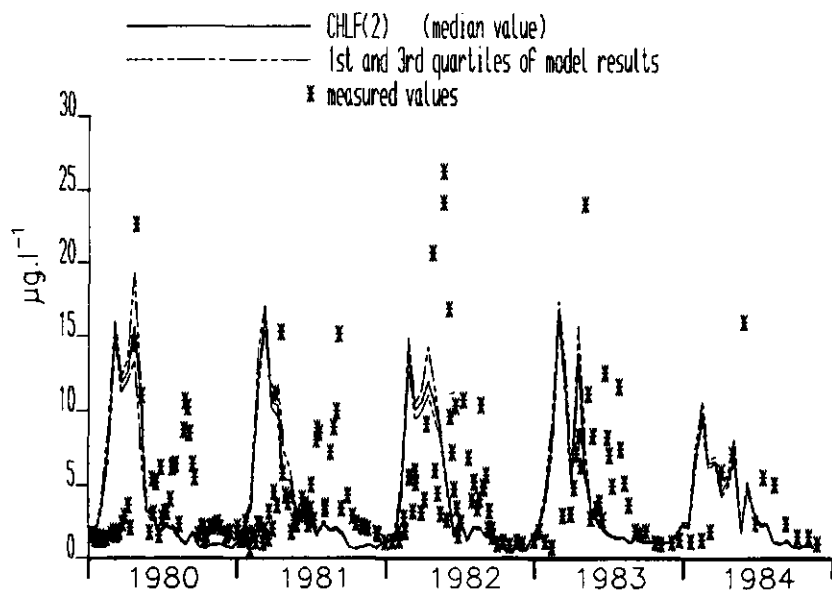
**Figure 10.12:** The three parameter-sets obtained from the three separate calibrations (coded as: (1) using 1980/82 data; (2) using 1983/84 data; (3) using 1980/84 data) are shown to form distinct clusters by means of a discriminant analysis (Pielou, 1984). The axes in the figure are linear combinations of the original parameters which give an optimal separation.



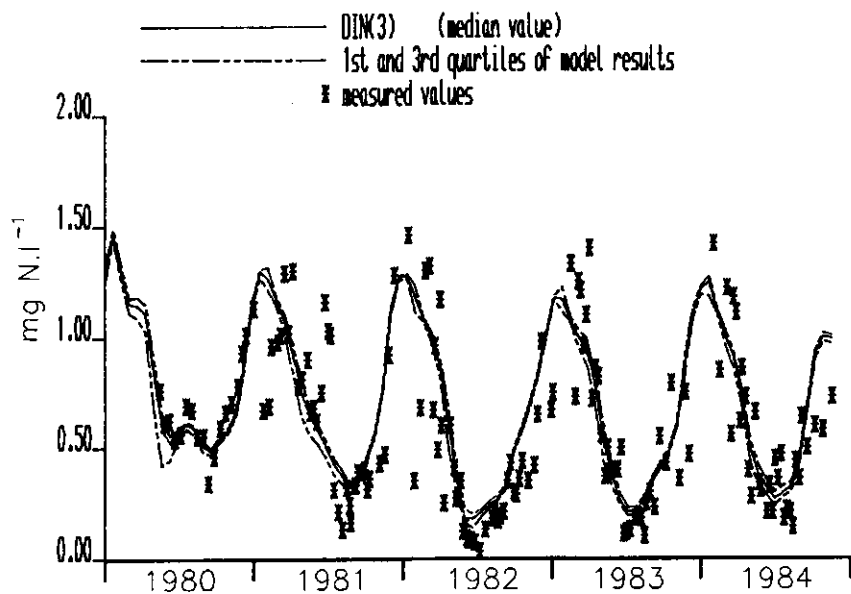
**Figure 10.13:** The three parameter-sets obtained from the three separate calibrations (coded as: (1) using 1980/82 data; (2) using 1983/84 data; (3) using 1980/84 data) can not be separated as clearly as in the previous figure by any two parameters (here: ARAT and CCHLMIN). The 83/84 and the 80/84 show a considerable overlap.



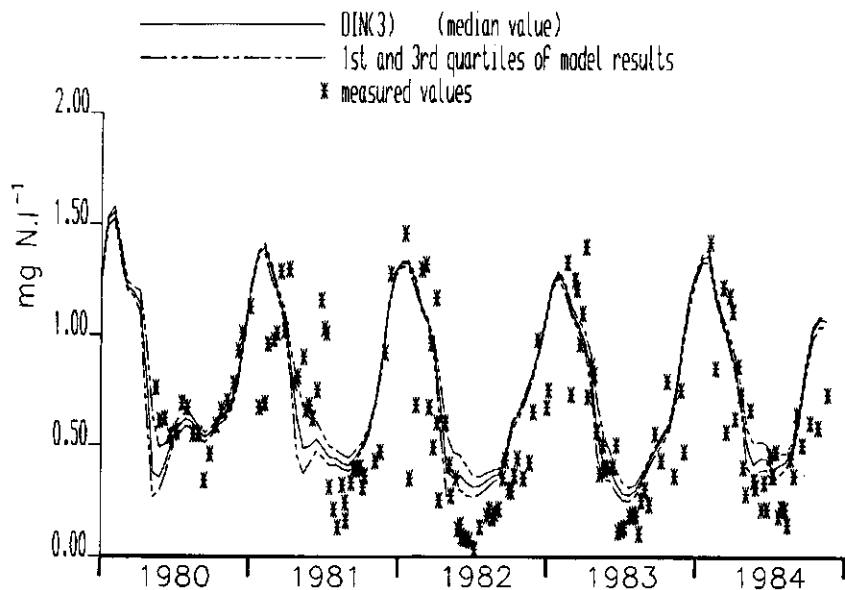
**Figure 10.14:** Model results (using parameter ranges from 1980/82 calibration) and measured values of chlorophyll-a in water column in compartment 2.



**Figure 10.15:** Model results (using parameter ranges from 1983/84 calibration) and measured values of chlorophyll-a in water column in compartment 2.



**Figure 10.16:** Model results (using parameter ranges from 1980/82 calibration) and measured values of dissolved inorganic nitrogen in water column in compartment 3.



**Figure 10.17:** Model results (using parameter ranges from 1983/84 calibration) and measured values of dissolved inorganic nitrogen in water column in compartment 3.

The effect of the calibration is a considerable reduction in model-output uncertainty. This may be observed by comparing the results of the model using the initial ranges of the parameters with the calibrated ranges. In particular, some of the parameter-combinations from the initial ranges lead on the average to much too high chlorophyll-concentrations in the eastern compartment, and correspondingly to too low values for dissolved nitrogen (figures 10.18-21). In contrast, the initial parameter ranges lead to a model-output range that more or less overlaps with the data in the western compartment.

In the interpretation of these graphs, it should be noted that the uncertainty-limits represent the 1-3th quartiles of the model-output distribution: the 95% limits would be (depending on the shape of the distribution) probably 3-4 times wider.

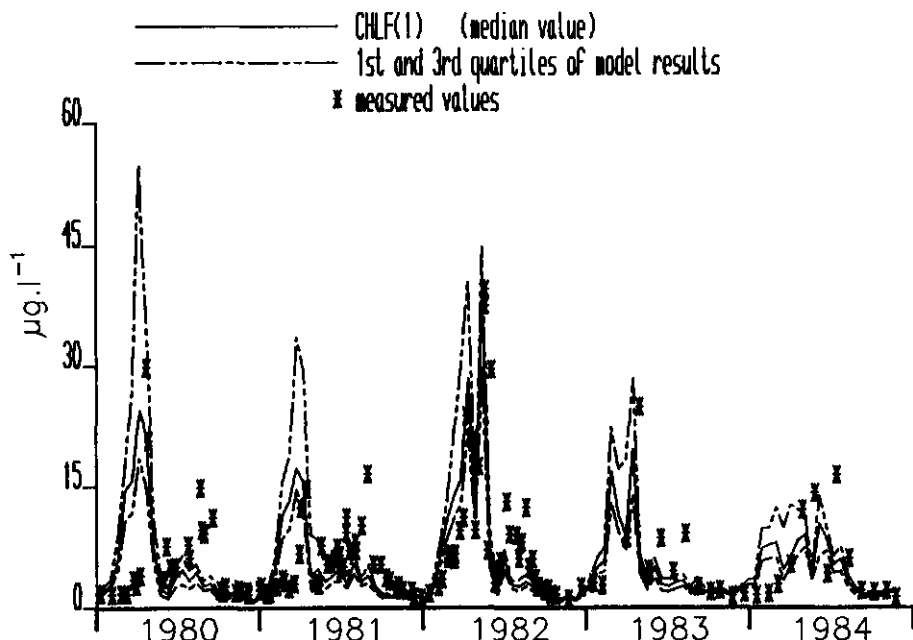


Figure 10.18: The initial uncertainty (using initial parameter ranges) in chlorophyll concentration in the water column in compartment 1.

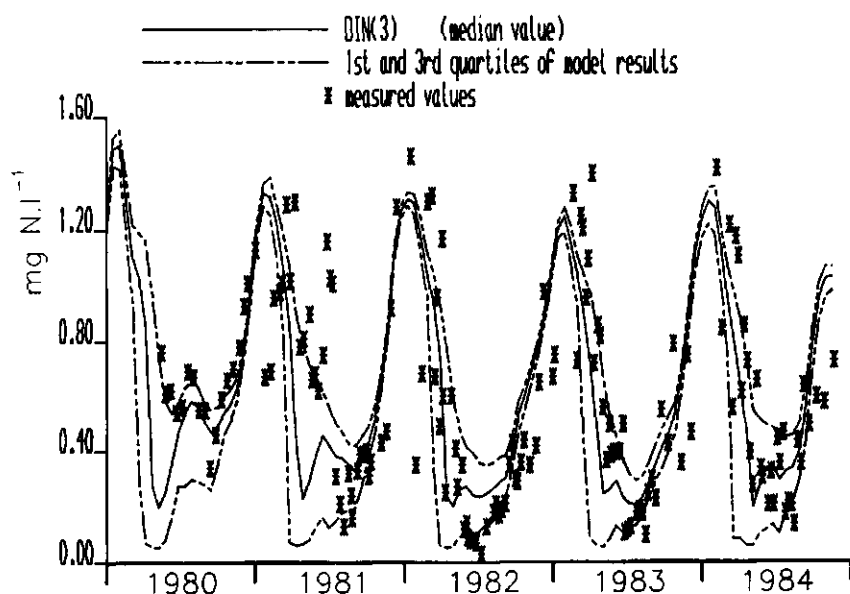


Figure 10.19: The initial uncertainty (using initial parameter ranges) in chlorophyll concentration in the water column in compartment 3.

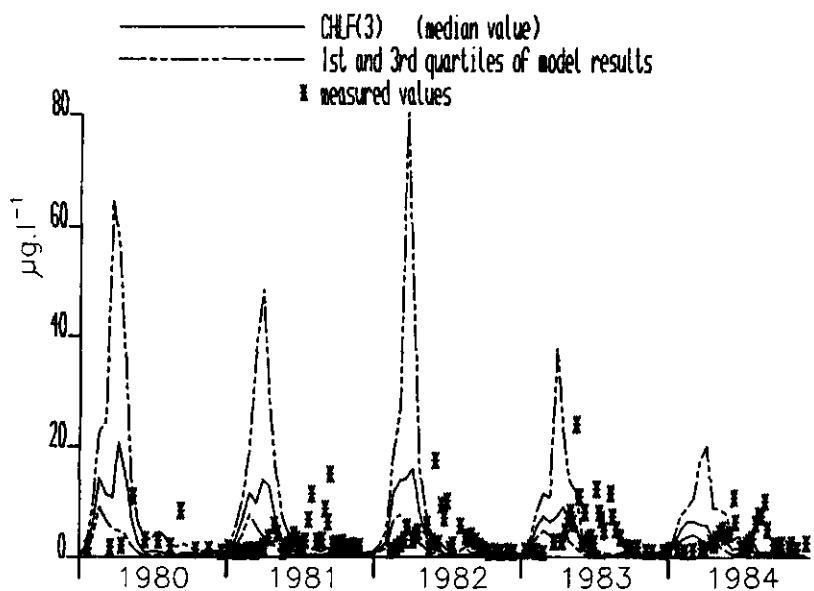


Figure 10.20: The initial uncertainty (using initial parameter ranges) in dissolved inorganic nitrogen concentration in compartment 3.

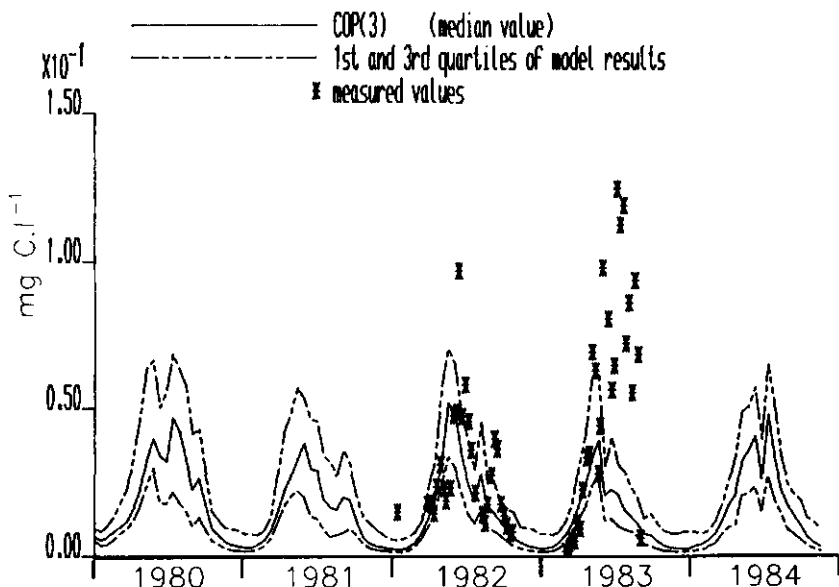


Figure 10.21: The initial uncertainty (using initial parameter ranges) in copepod biomass in compartment 3.

The average and maximum levels in the calibrated results for chlorophyll-a in the water column are accurately reproduced, but the timing is often out of phase: maximum values are modelled too early, and late-summer and autumn values are too low.

The simulated primary production may be compared with measurements only indirectly, because primary production in the field can only be calculated from the measured photosynthetic parameters. The most important parameter is the light-saturated production rate ( $P_{max}$ ) which is reproduced satisfactorily compared with the apparently considerable scatter in the measurements; only the winter values appear to systematically overestimated by the model. The measured values of the optimal light intensity are well reproduced in compartments 1 and 2; in the eastern compartments the model is not able to reproduce the low values obtained during the first years of measurements. The measured carbon-to-chlorophyll ratio shows a very large scatter; model results can therefore not be said to fit the data well, but are obviously neither in contrast with them. The vertical extinction coefficient is reproduced satisfactorily. The primary production calculated from the above-mentioned variables ( $P_{max}$ ,  $I_{opt}$ , extinction and so on) is shown in figures 10.45 and 10.46)

The results for dissolved inorganic nitrogen in the western compartment largely coincide with measured values in summer, but simulated values are too low in winter. In the other compartments, both summer and winter values are reproduced.

The model output of silicate agrees with measured results in summer; in winter the levels are modelled in general too low, notably in compartment 1.



Copepod biomass is reproduced satisfactorily for 1982 but is too low for 1983. The timing of the model-output is too early in the eastern compartment, but this may probably be attributed to the phytoplankton biomass, which shows a similar early timing of its bloom in this compartment.

Benthic chlorophyll measurements are scarce; although the model reproduces average levels in all compartments except the middle (no. 2), the seasonal dynamics seem to be shifted exactly a half period. The uncertainty in this output-variable is considerable.

Simulated oxygen concentrations agree with measured values satisfactorily, except for a shift in timing; this can again be attributed to the too early timing of the phytoplankton bloom. Further, there are some apparent outliers in measured values (in 1983 in compartment 1, in 1980 in compartment 2, and in 1984 in compartments 3 and 4).

The simulated particulate organic carbon (POC) consists mainly of refractory detritus. Measured values show a considerable scatter. Simulated values generally agree with these data, except in compartment 4, where the model overestimates the POC concentration, in particular in 1980 and 1981.

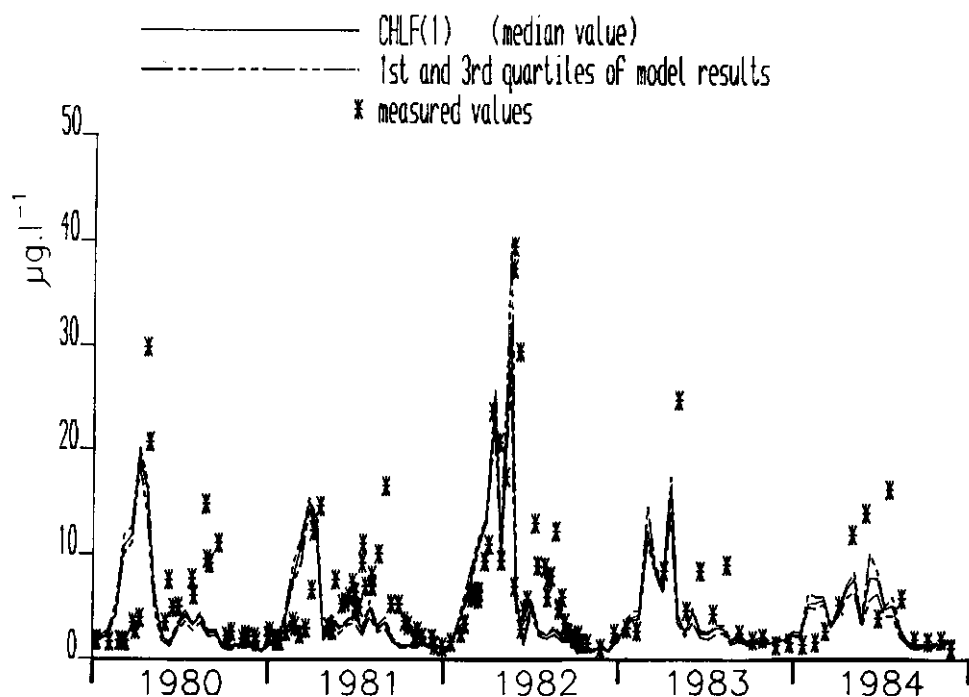
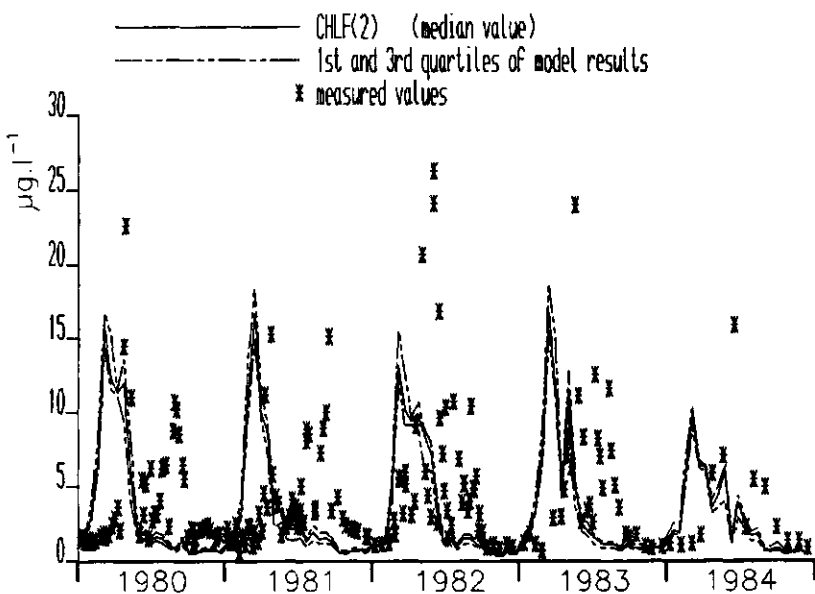
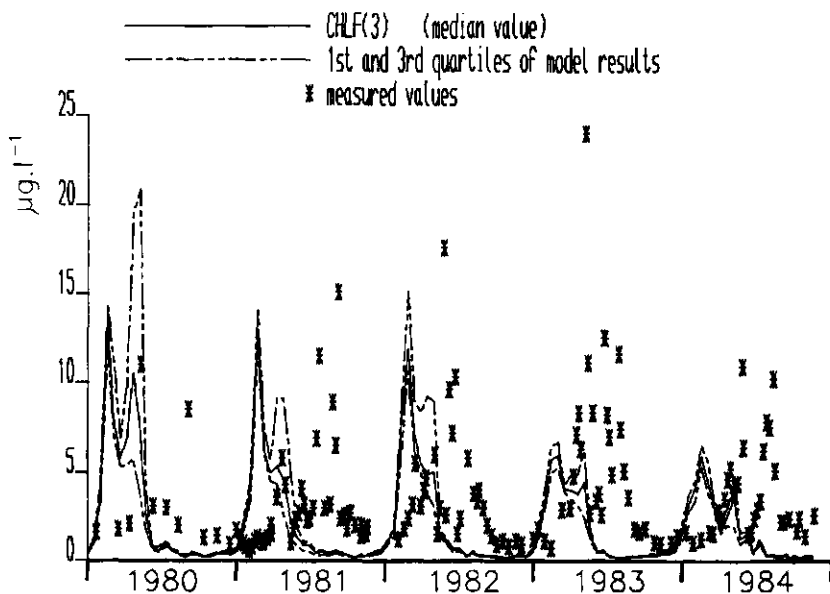


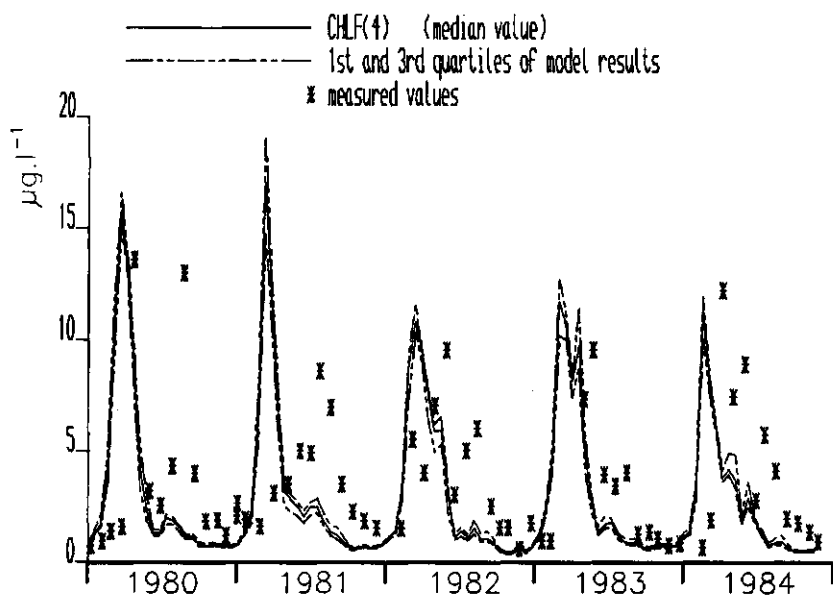
Figure 10.22: Model results (showing effect of calibrated parameter ranges) and measured values of chlorophyll-a in water column in compartment 1.



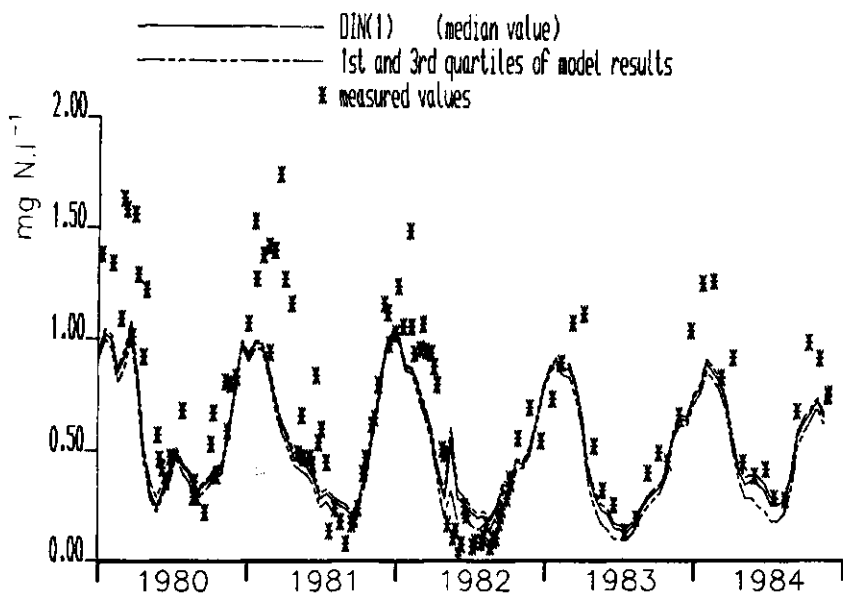
**Figure 10.23:** Model results (showing effect of calibrated parameter ranges) and measured values of chlorophyll-a in water column in compartment 2.



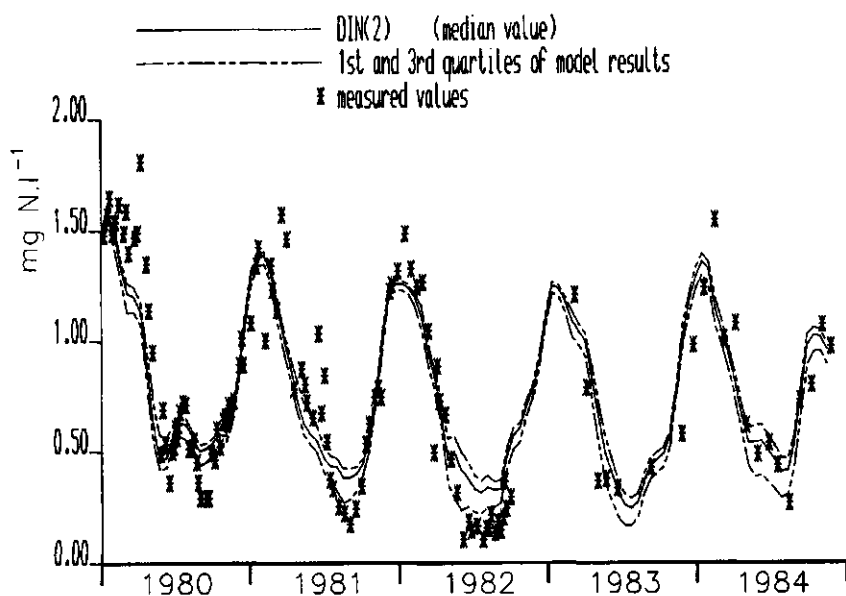
**Figure 10.24:** Model results (showing effect of calibrated parameter ranges) and measured values of chlorophyll-a in water column in compartment 3.



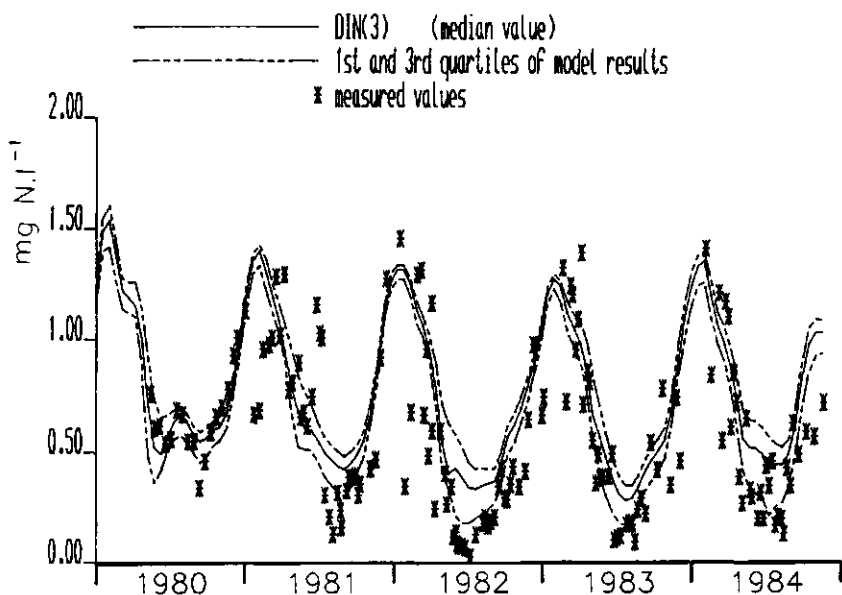
**Figure 10.25:** Model results (showing effect of calibrated parameter ranges) and measured values of chlorophyll-a in water column in compartment 4.



**Figure 10.26:** Model results (showing effect of calibrated parameter ranges) and measured values of dissolved inorganic nitrogen in compartment 1.



**Figure 10.27:** Model results (showing effect of calibrated parameter ranges) and measured values of dissolved inorganic nitrogen in compartment 2.



**Figure 10.28:** Model results (showing effect of calibrated parameter ranges) and measured values of dissolved inorganic nitrogen in compartment 3.

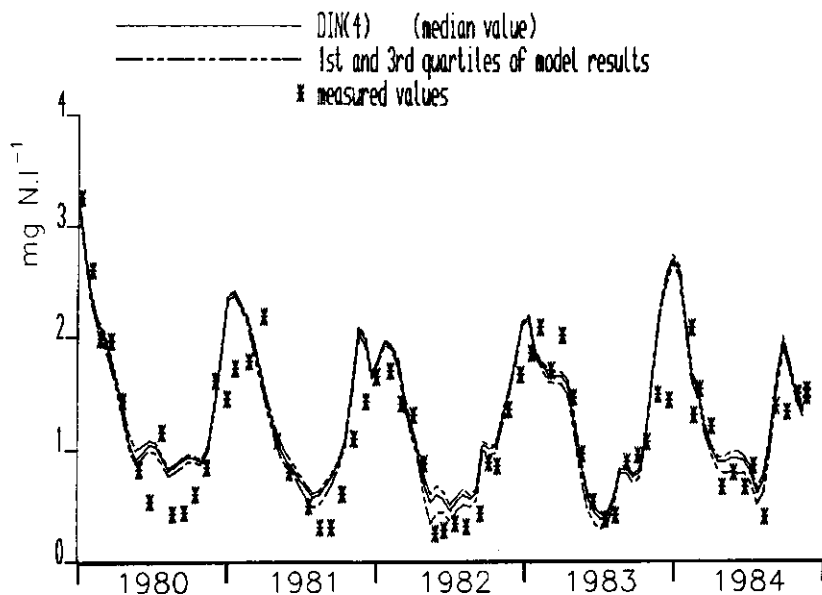


Figure 10.29: Model results (showing effect of calibrated parameter ranges) and measured values of dissolved inorganic nitrogen in compartment 4.

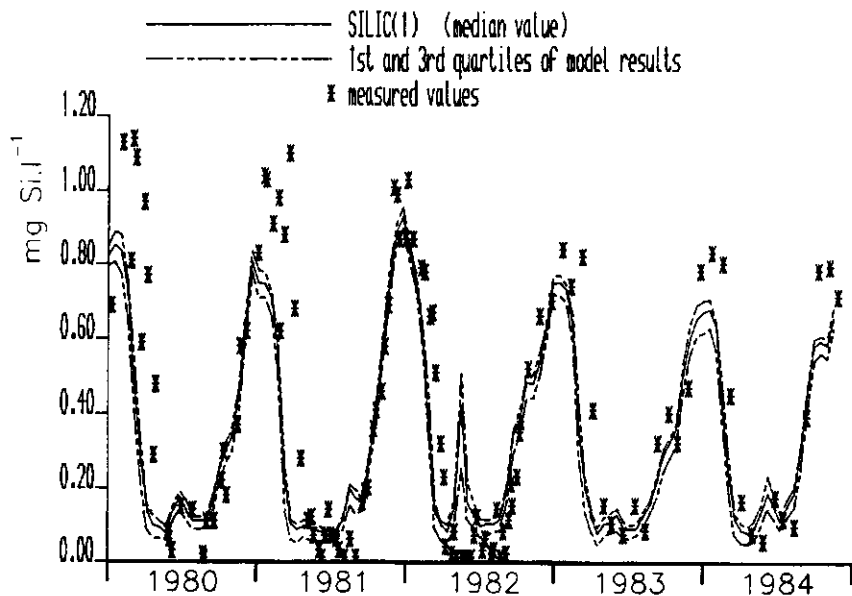
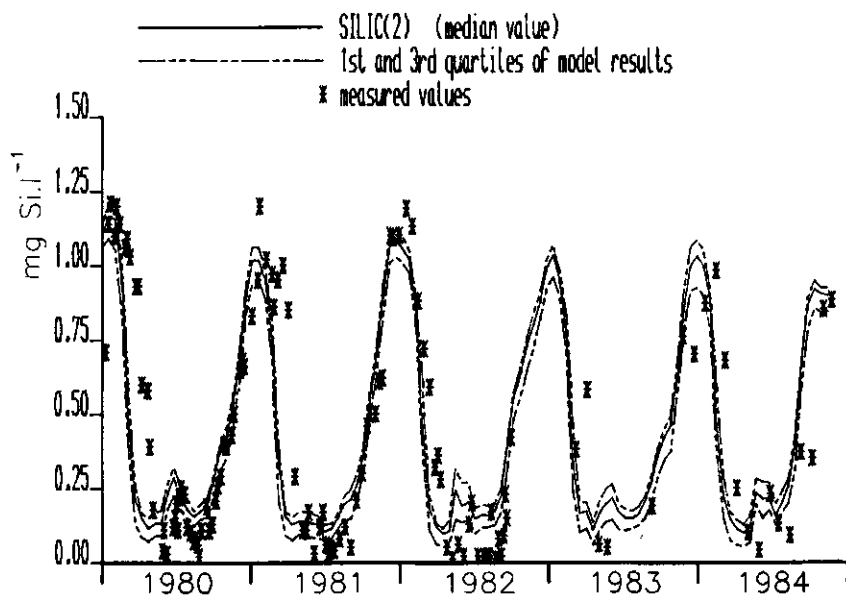
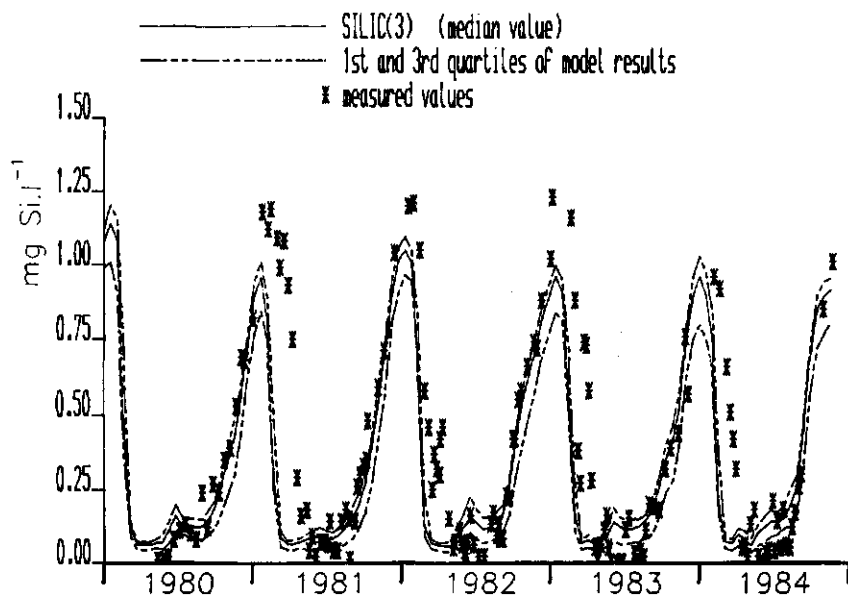


Figure 10.30: Model results (showing effect of calibrated parameter ranges) and measured values of silicate in compartment 1.



**Figure 10.31:** Model results (showing effect of calibrated parameter ranges) and measured values of silicate in compartment 2.



**Figure 10.32:** Model results (showing effect of calibrated parameter ranges) and measured values of silicate in compartment 3.

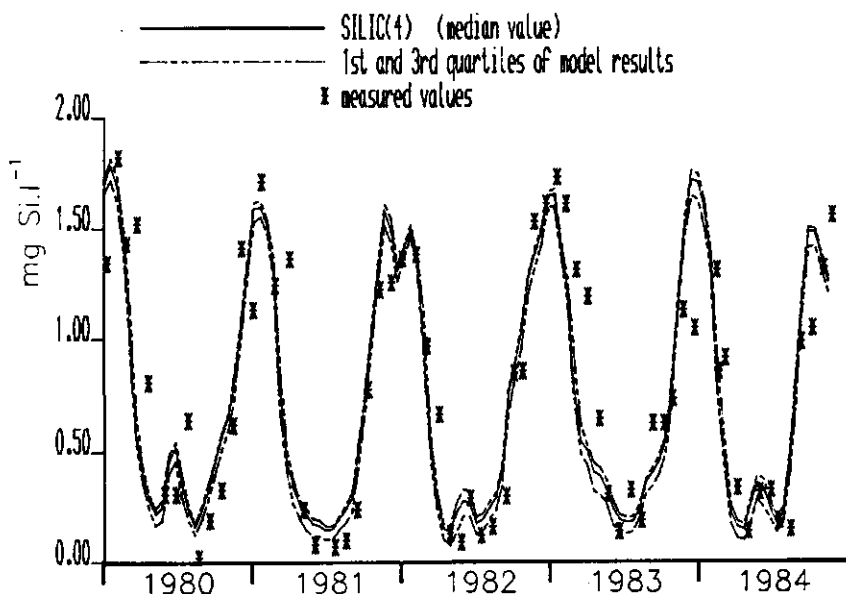


Figure 10.33: Model results (showing effect of calibrated parameter ranges) and measured values of silicate in compartment 4.

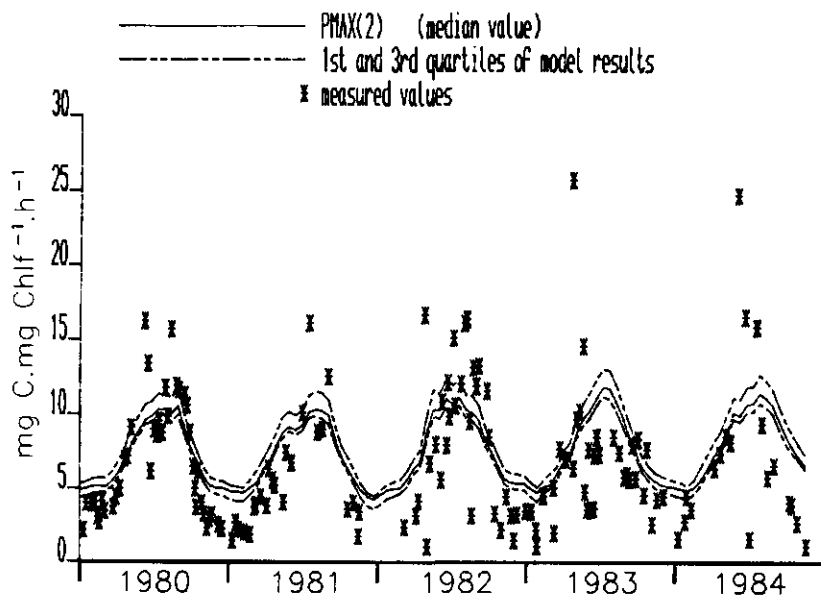
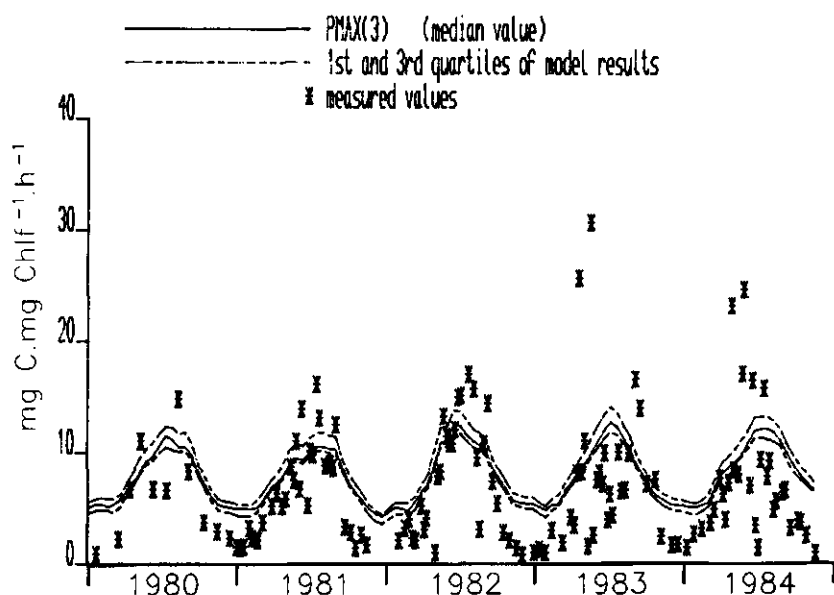
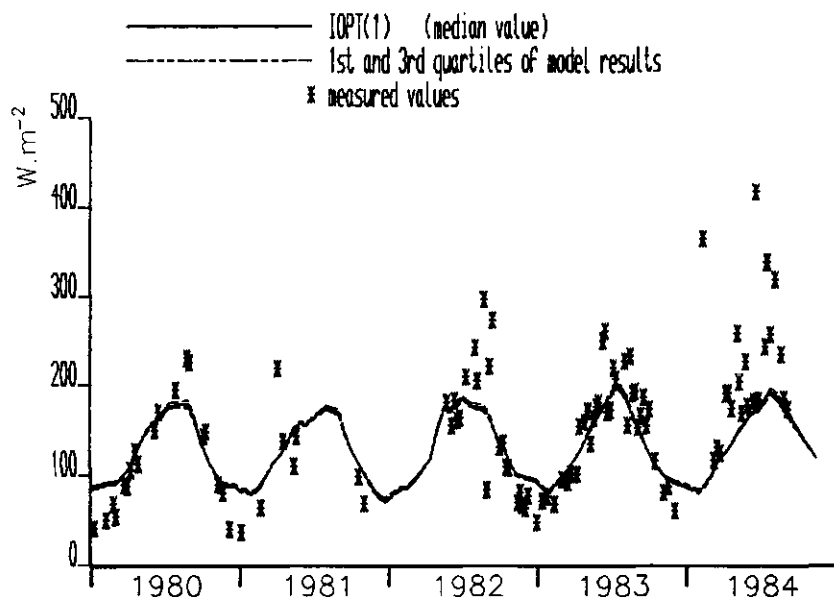


Figure 10.34: Model results (showing effect of calibrated parameter ranges) and measured values of light-saturated production rate of phytoplankton (in mg C/mg Chlf/h) in compartment 2.



**Figure 10.35:** Model results (showing effect of calibrated parameter ranges) and measured values of light-saturated production rate of phytoplankton (in mg C/mg Chl/h) in compartment 3.



**Figure 10.36:** Model results (showing effect of calibrated parameter ranges) and measured values of optimal light intensity in compartment 1.



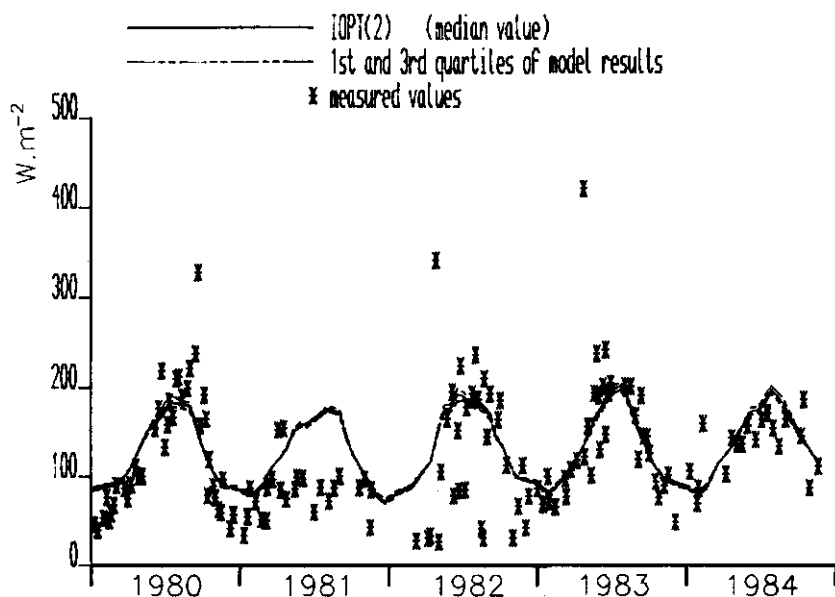


Figure 10.37: Model results (showing effect of calibrated parameter ranges) and measured values of optimal light intensity in compartment 2.

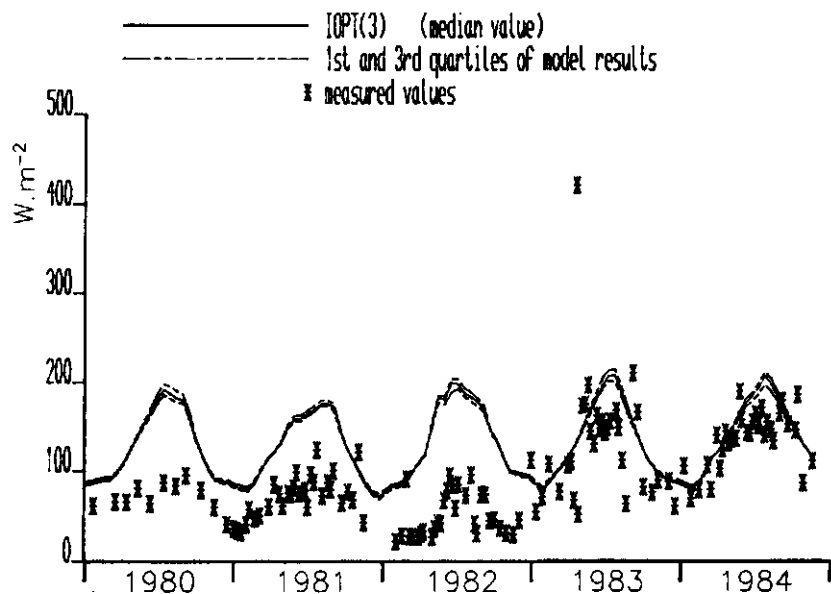


Figure 10.38: Model results (showing effect of calibrated parameter ranges) and measured values of optimal light intensity in compartment 3.

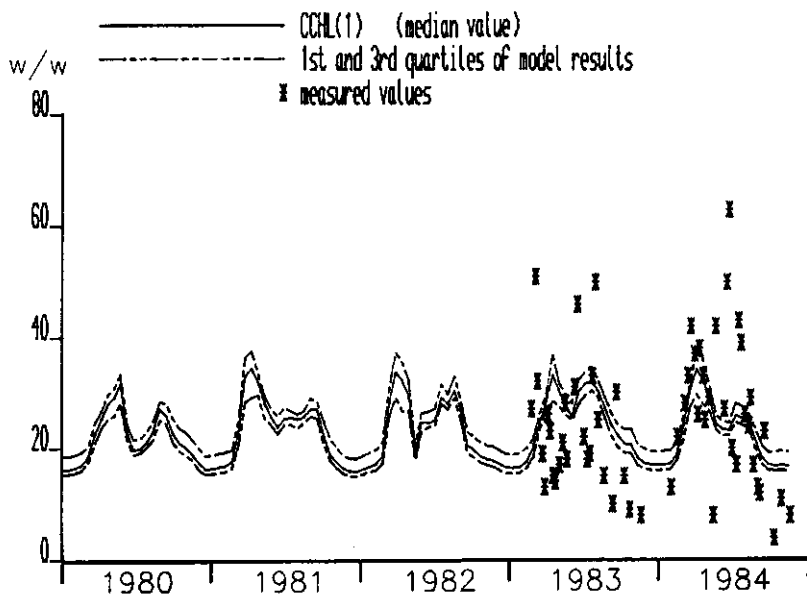


Figure 10.39: Model results (showing effect of calibrated parameter ranges) and measured values of carbon to chlorophyll ratio of phytoplankton in compartment 1.

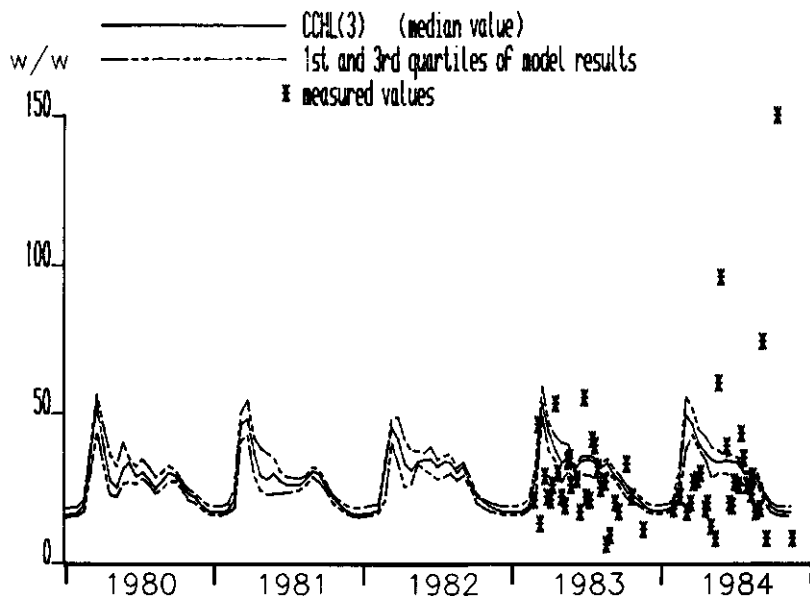


Figure 10.40: Model results (showing effect of calibrated parameter ranges) and measured values of carbon to chlorophyll ratio of phytoplankton in compartment 3.

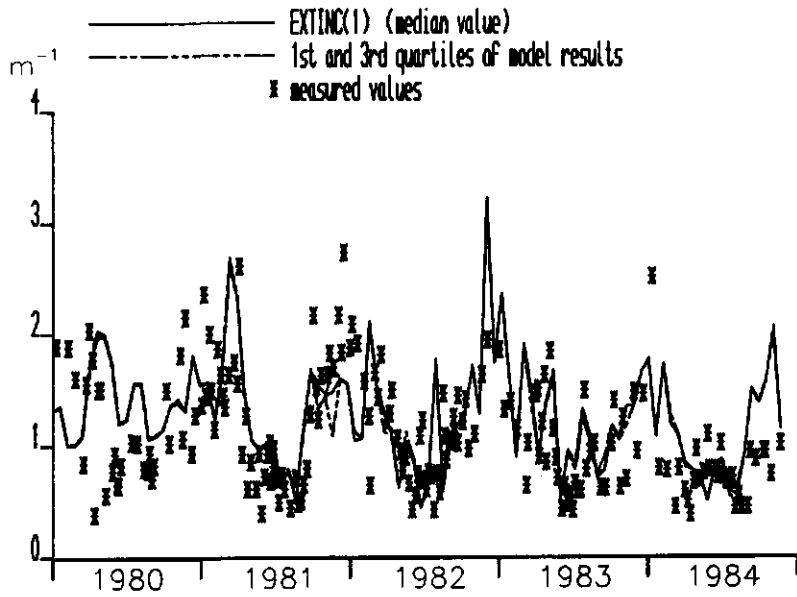


Figure 10.41: Model results (showing effect of calibrated parameter ranges) and measured values of vertical light extinction coefficient in compartment 1.

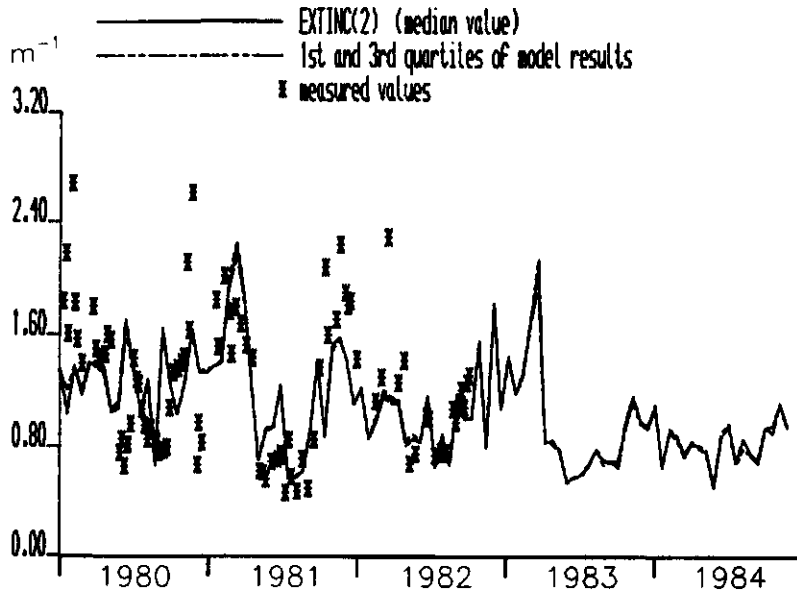


Figure 10.42: Model results (showing effect of calibrated parameter ranges) and measured values of vertical light extinction coefficient in compartment 2.

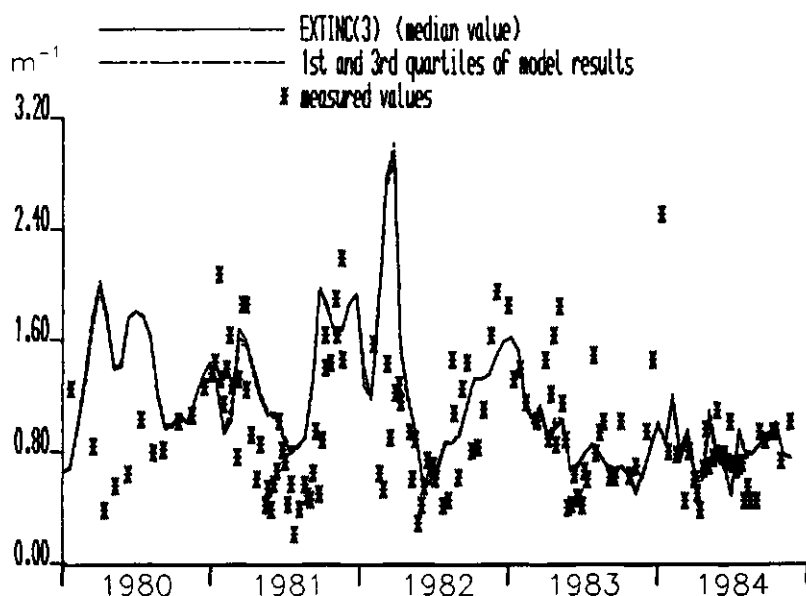


Figure 10.43: Model results (showing effect of calibrated parameter ranges) and measured values of vertical light extinction coefficient in compartment 3.

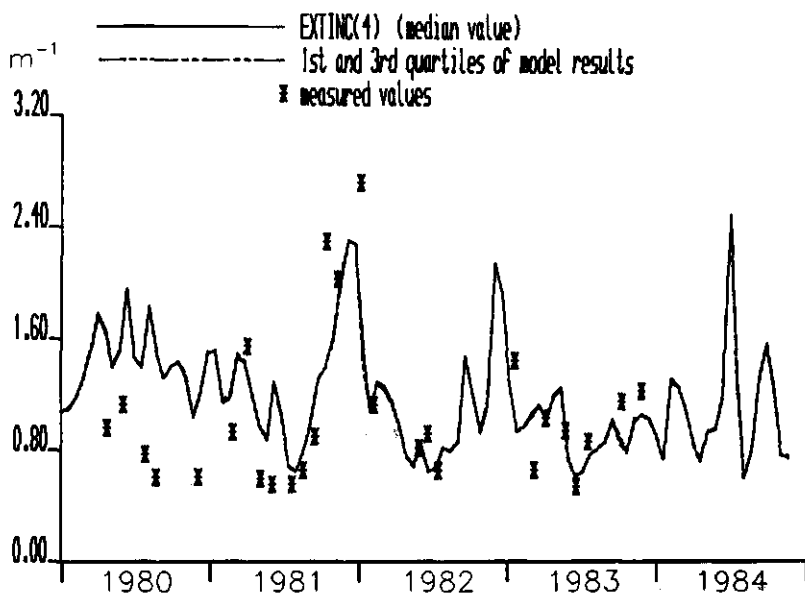


Figure 10.44: Model results (showing effect of calibrated parameter ranges) and measured values of vertical light extinction coefficient in compartment 4.

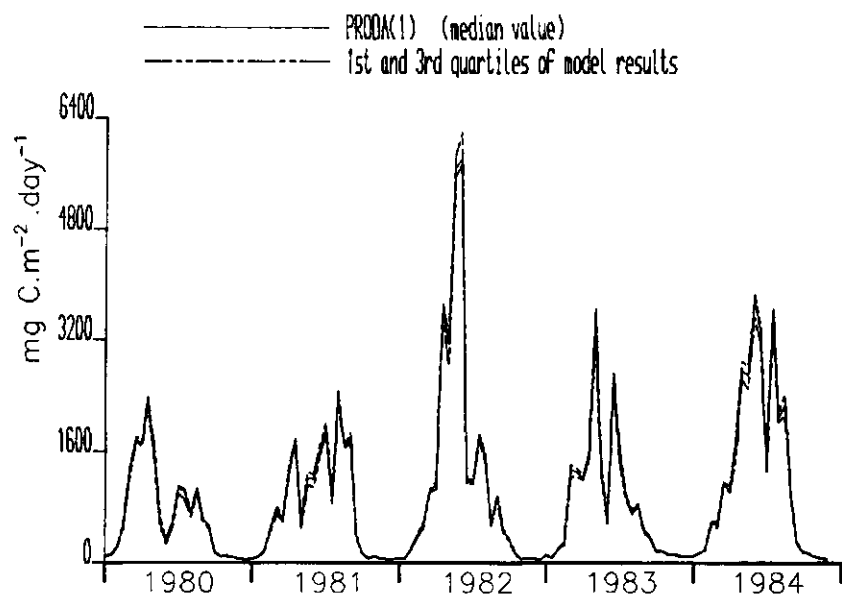


Figure 10.45: Primary production calculated by the model (in  $\text{mg C/m}^2/\text{day}$ ) in compartment 1 (showing effect of calibrated parameter ranges).

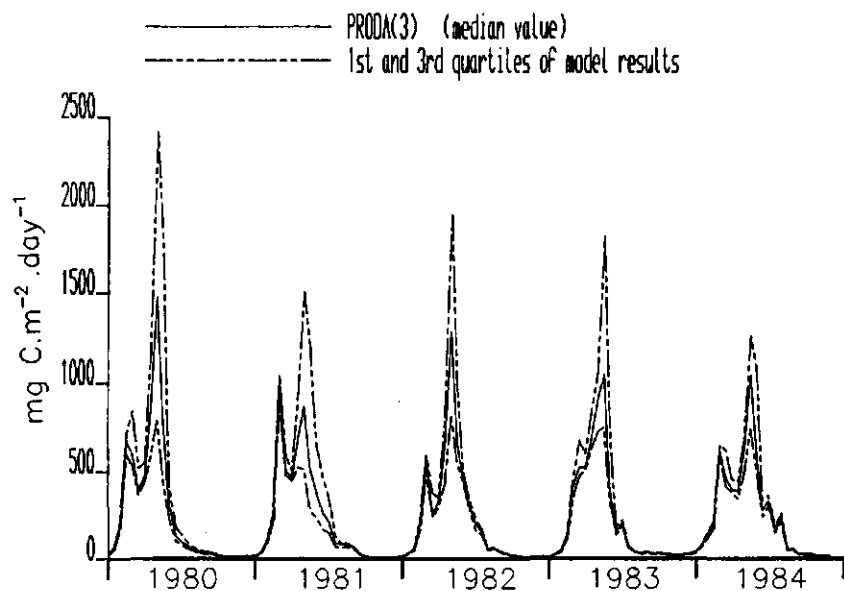
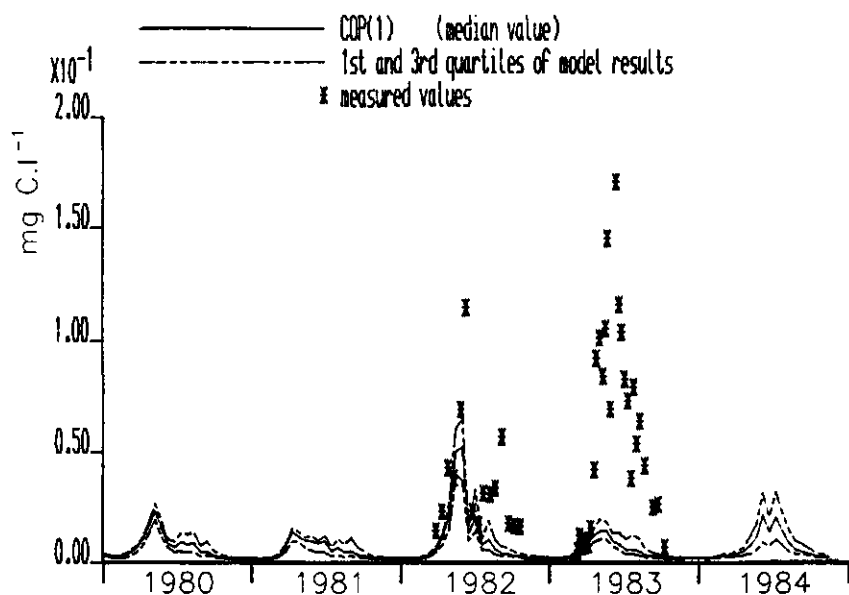
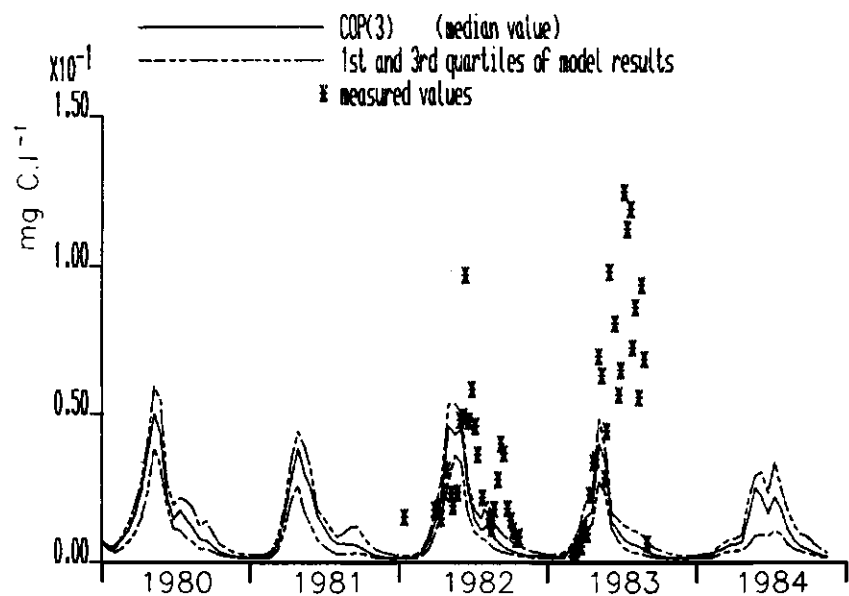


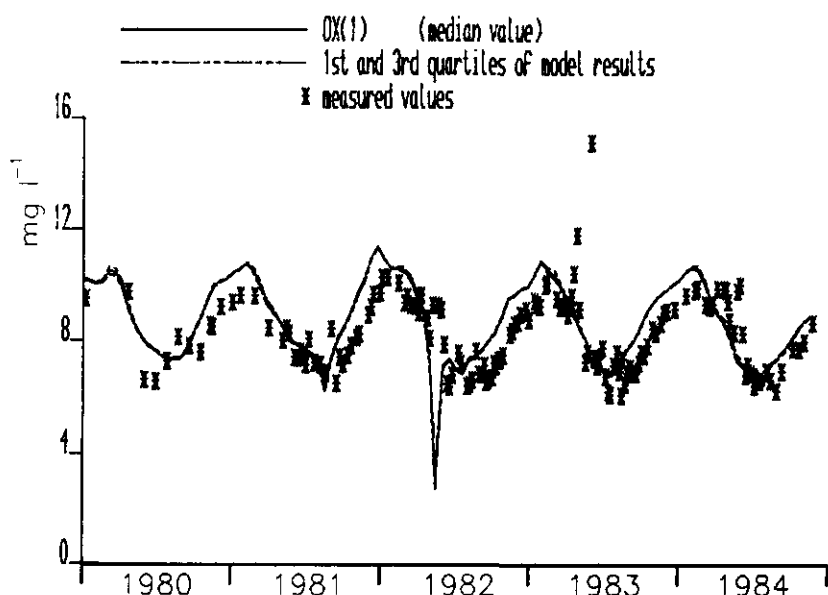
Figure 10.46: Primary production calculated by the model (in  $\text{mg C/m}^2/\text{day}$ ) in compartment 3 (showing effect of calibrated parameter ranges).



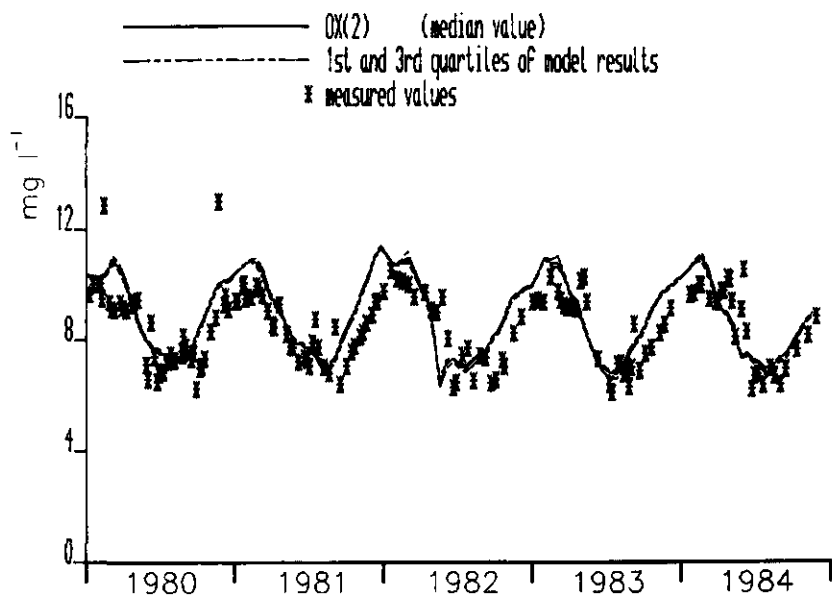
**Figure 10.47:** Model results (showing effect of calibrated parameter ranges) and measured values of copepod biomass in compartment 1.



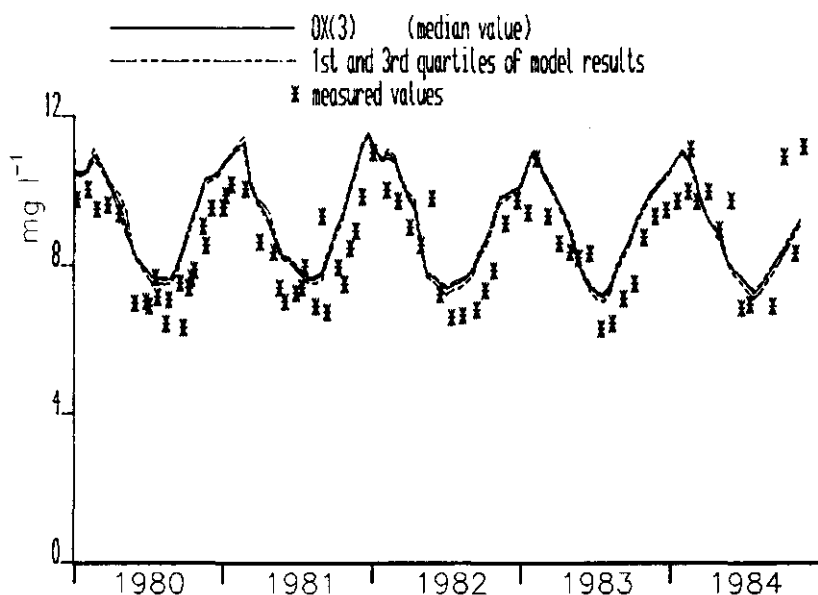
**Figure 10.48:** Model results (showing effect of calibrated parameter ranges) and measured values of copepod biomass in compartment 3.



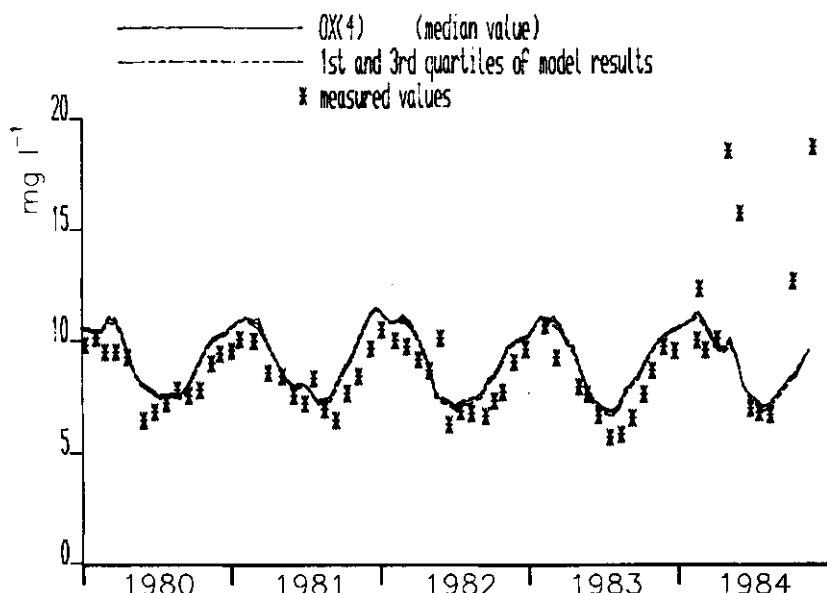
**Figure 10.49:** Model results (showing effect of calibrated parameter ranges) and measured values of oxygen concentration in compartment 1.



**Figure 10.50:** Model results (showing effect of calibrated parameter ranges) and measured values of oxygen concentration in compartment 2.

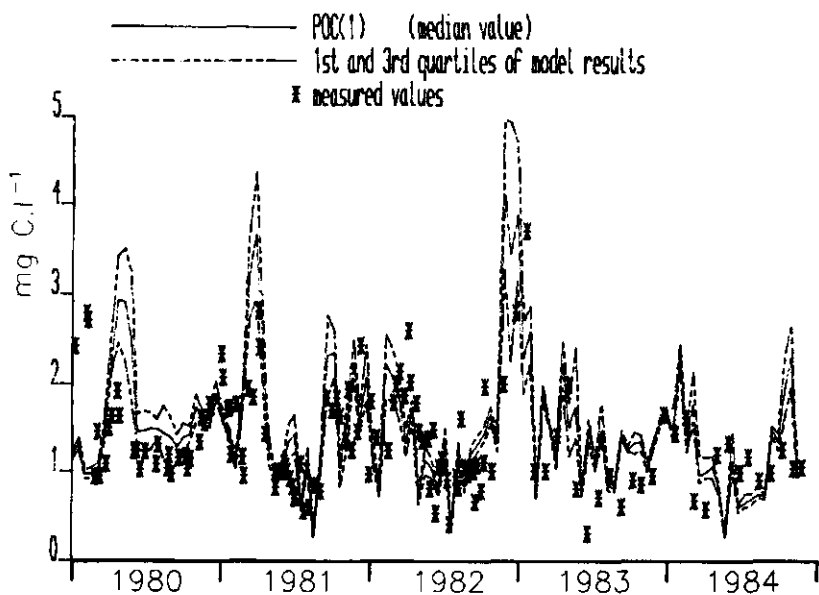


**Figure 10.51:** Model results (showing effect of calibrated parameter ranges) and measured values of oxygen concentration in compartment 3.

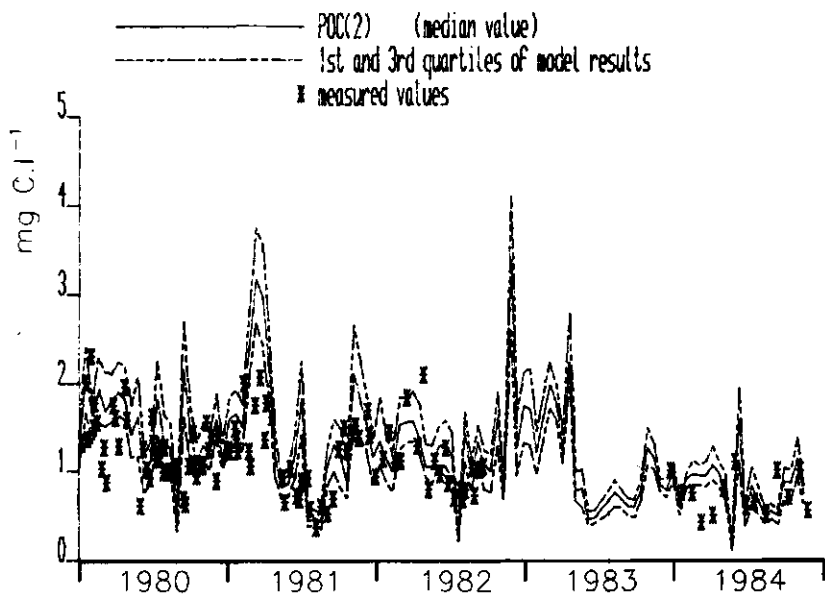


**Figure 10.52:** Model results (showing effect of calibrated parameter ranges) and measured values of oxygen concentration in compartment 4.

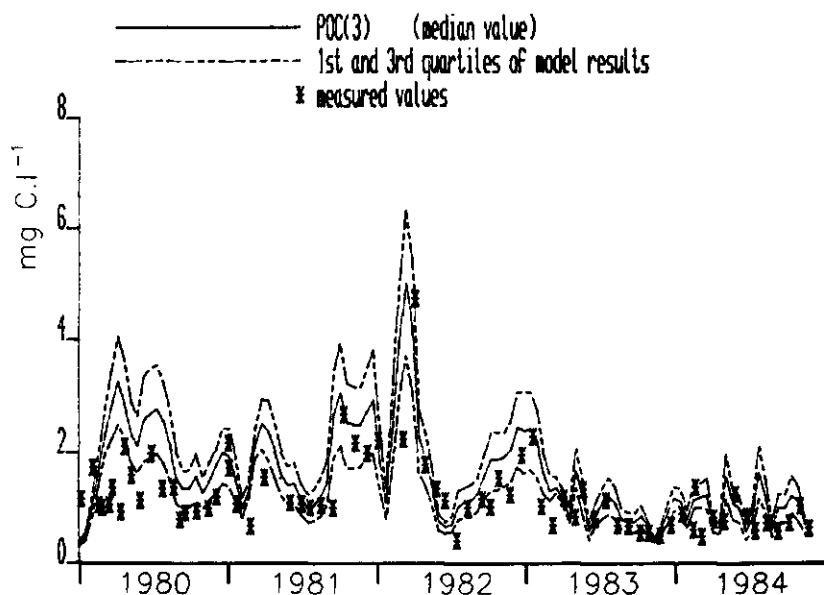




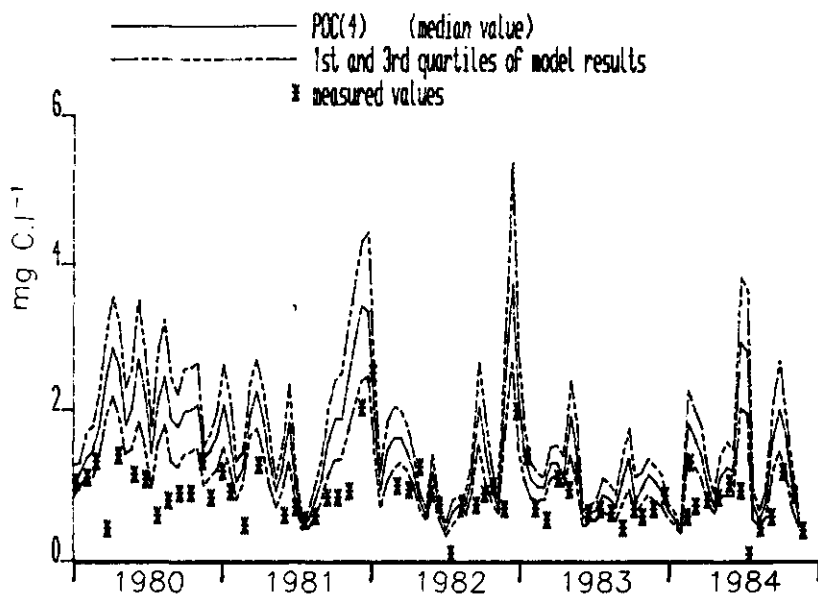
**Figure 10.53:** Model results (showing effect of calibrated parameter ranges) and measured values of particulate organic carbon in compartment 1.



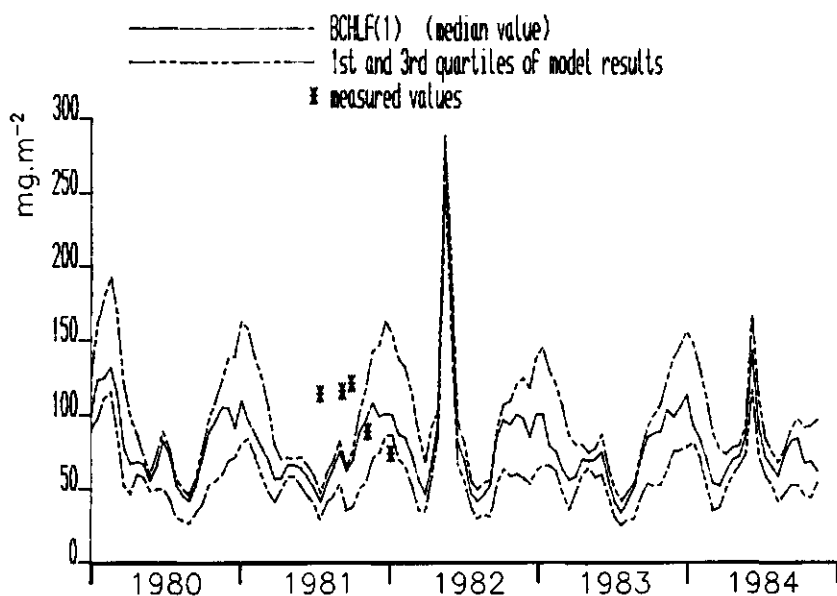
**Figure 10.54:** Model results (showing effect of calibrated parameter ranges) and measured values of particulate organic carbon in compartment 2.



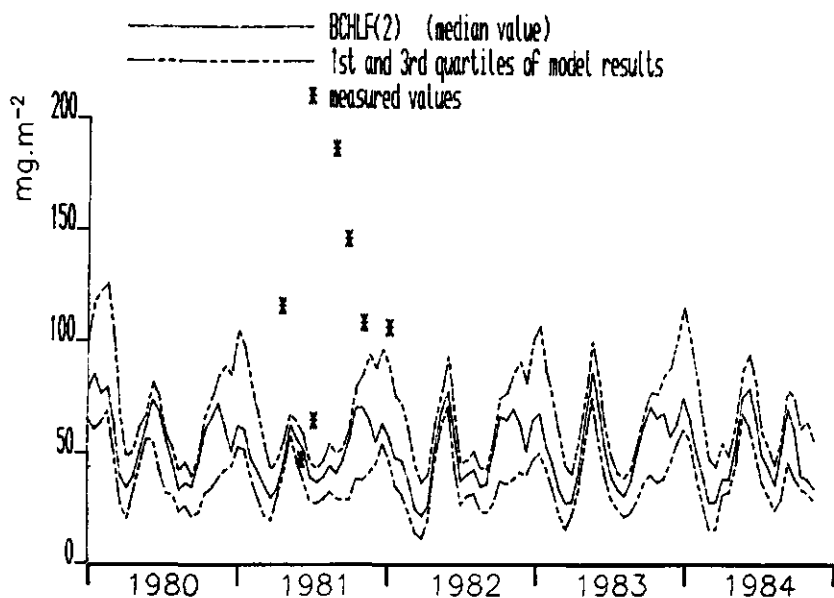
**Figure 10.55:** Model results (showing effect of calibrated parameter ranges) and measured values of particulate organic carbon in compartment 3.



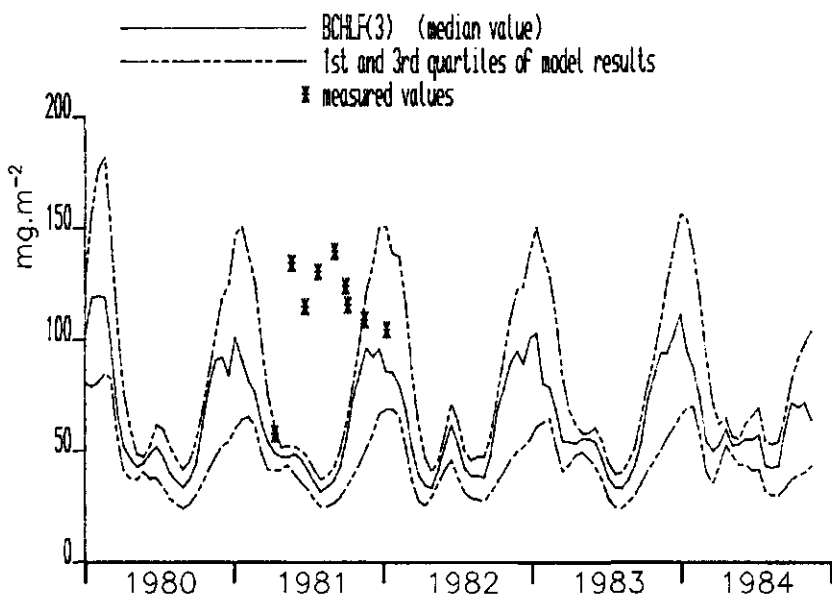
**Figure 10.56:** Model results (showing effect of calibrated parameter ranges) and measured values of particulate organic carbon in compartment 4.



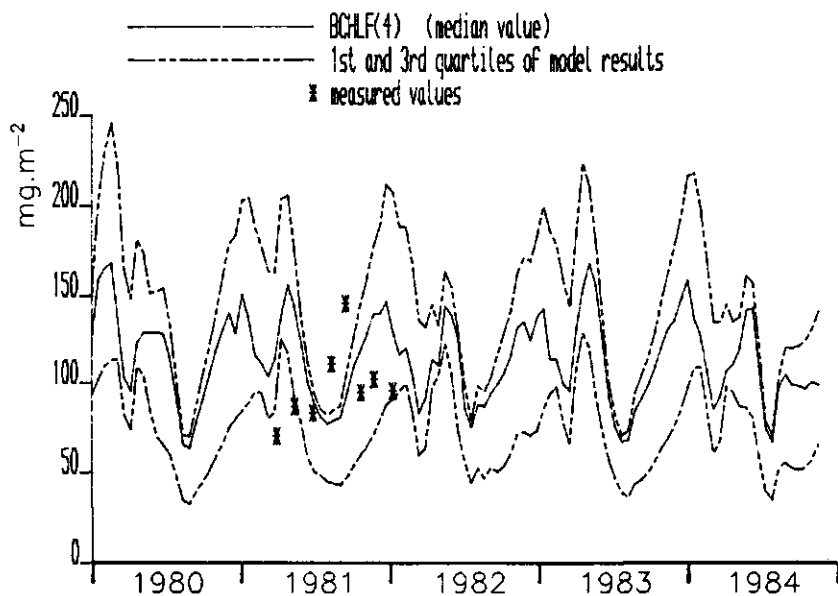
**Figure 10.57:** Model results (showing effect of calibrated parameter ranges) and measured values of benthic chlorophyll content in compartment 1.



**Figure 10.58:** Model results (showing effect of calibrated parameter ranges) and measured values of benthic chlorophyll content in compartment 2.



**Figure 10.59:** Model results (showing effect of calibrated parameter ranges) and measured values of benthic chlorophyll content in compartment 3.



**Figure 10.60:** Model results (showing effect of calibrated parameter ranges) and measured values of benthic chlorophyll content in compartment 4.

### 10.5 Discussion

The smaller uncertainty in the model output for compartment 1 (e.g., figure 10.18, 10.22) is partly the result of the nearby boundary with the North Sea. The effect of this depends on the parameter values in the model: if primary production would be set to zero (i.e. phytoplankton is transported and grazed only), there would still be some chlorophyll in compartment 1 with even a more or less realistic seasonal pattern; this pattern could then be explained entirely by the boundary conditions (input from the North Sea). For the actual choice of parameter values, the relative effect of the boundary conditions is obviously smaller. The influence of boundary conditions has been quantified by changing the boundary concentrations of chlorophyll at random around their mean value; the parameters in the model were kept fixed. The resulting variations in summer chlorophyll concentrations for the 4 compartments were fitted by multiple regression:

$$\text{CHLF}(i) = a + b * \text{CHLFSEA} + c * \text{CHLFVOL}$$

The dimensionless regression coefficients  $b$  and to what extent concentrations in a compartment are determined by boundary concentrations. The results were a decrease in  $b$ -value from 0.34 in compartment 1, 0.11 in compartment 2 to 0.02 and 0.04 in compartments 3 and 4, respectively. The  $c$ -value was negligible in the compartments 1-3 (0.01, 0.02 and 0.01 respectively) and had a value of 0.18 in compartment 4. It may be concluded that the influence of the boundary conditions is pronounced only in compartment 1, but even in this compartment the boundary conditions do not dominate the model results.

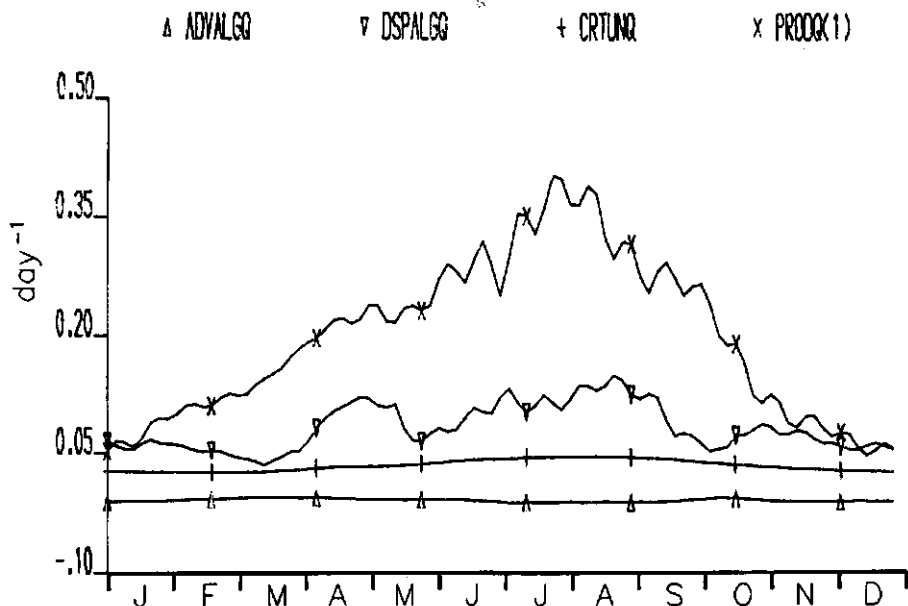
In addition to the effect of the boundary conditions another reason for the more moderate behaviour of the model output in response to parameter uncertainty in compartment 1 is its greater depth (12.4 m compared to 3.5 m in the eastern compartment). Many processes, like primary production and filterfeeder filtration can be best expressed per unit surface: primary production because of its close relation to incoming radiation, and filtration because the filterfeeders live on the bottom. Expressed per unit surface, the pools of the major state-variables (chlorophyll, nutrients) are much larger (because of the greater depth) in the western compartment; consequently, we may expect changes in concentrations to occur slower in this compartment.

Although the comparison between model results and observed concentrations is in general satisfactory, there appear to be three major problems: the timing of the algal blooms is in general too early; the simulated copepod biomass is too low in 1984, and there are some systematic discrepancies between measured and simulated values for the nutrients and light-saturated production rate in the winter period.

The first point may be related to the description of seasonal activity of macrobenthic filterfeeders, in particular cockles. In figures 10.61 and 10.62 the relative activity (fraction of volume filtered per day) of the major grazers is shown. The model calculates a very strong increase in activity from spring to autumn; during the latter period phytoplankton productivity (also express in units of  $d^{-1}$ ) is less than the grazing rate, resulting in the low algal biomass. The macrobenthic filterfeeder activity is the result of an increased biomass in autumn and specific activity. The peak values of biomass in autumn of both cockles and mussels seems to be a well-established fact, but the seasonal pattern of activity is uncertain. In the present model, activity is related to temperature only. The available data on the relation between temperature, clearance and respiration were reviewed in chapter 7; they showed a range of temperature effects (expressed as a  $Q_{10}$ ) between zero (no effect) and 3 (three-fold increase with 10 °C).

Some of the conflicts in the data could probably be resolved, and the model improved, by taking into account an hysteresis effect: temperature not only influences activity directly, but also indirectly via the spawning cycle. In spring, activity is higher as a result of gametogenesis than in autumn at the same temperature (Bayne et al., 1977; Newell and Bayne, 1980).

Another source of an early timing of the spring bloom in compartment 3 (east) may be the function used to describe the seasonal pattern of "fonds" mussels and mussels to be cleaned (see figure 7.4): this stock of mussels is removed suddenly from the compartment in april. Although this stock is in fact auctioned in a single day, the removal of the mussels probably takes one or a few weeks. Inclusion of this in the model would probably cause a slower increase in algal biomass in spring in the eastern compartment.



**Figure 10.61:** some of the major components in the phytoplankton budget in the western compartment, all expressed per unit of biomass per day: ADVALGQ -advective transport; DSPALGQ -dispersive transport; CRTUNQ -clearance by hard-substrate organisms; PRODQ(1) -gross photosynthetic productivity.

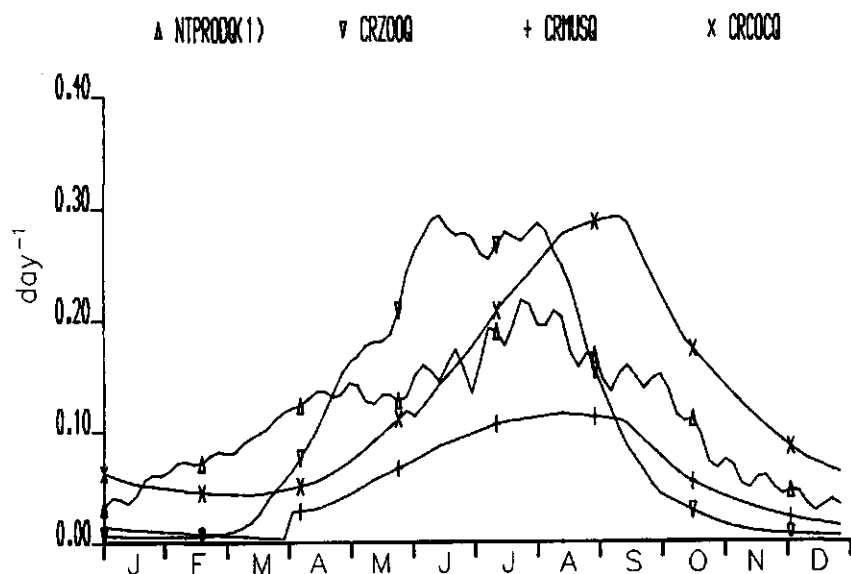


Figure 10.62: Some of the major components in the phytoplankton budget in the western compartment, all expressed in units of biomass per day: NTPRODQ -net photosynthetic production; CRZOOQ -zooplankton clearance rate; CRMUSQ-mussel clearance rate; -CRCOCQ -cockle clearance rate.

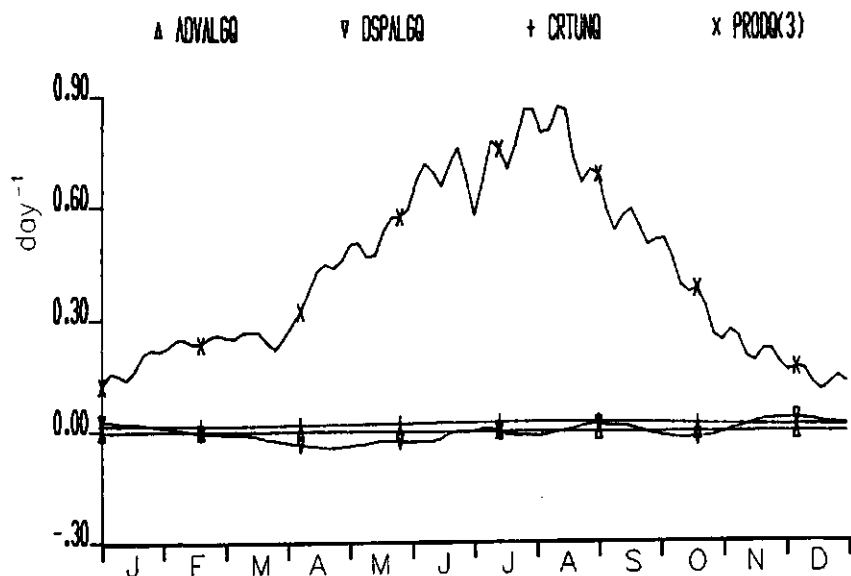


Figure 10.63: some of the major components in the phytoplankton budget in the eastern compartment, all expressed per unit of biomass per day: ADVALGQ -advective transport; DSPALGQ -dispersive transport; CRTUNQ -clearance by hard-substrate organisms; PRODQ -gross photosynthetic productivity.

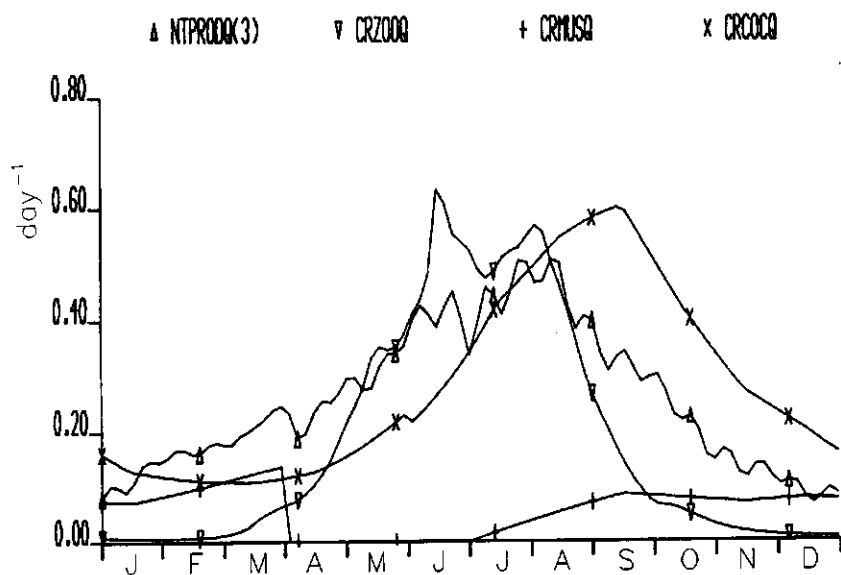


Figure 10.64: Some of the major components in the phytoplankton budget in the eastern compartment, all expressed in units of biomass per day: NTPRODQ -net photosynthetic production; CRZOOQ -zooplankton clearance rate; CRMUSQ -mussel clearance rate; -CRCOCQ -cockle clearance rate.

The lower simulated value for the copepod biomass in 1984 as compared to 1983 is the reverse of the measured situation, which shows a higher biomass in 1984. The model results appear to be a structural deficiency of the model, and independent of parameter values: it can be observed in the preliminary run (fig. 9.21) and using the initial parameter ranges also (fig. 10.21). It is apparently not possible to reproduce the measured values better with the present simple model structure. It should be noted however that simulated values are in reasonable agreement with the data, and that the relation between copepod biomass and mussel food supply is only very limited (see section 10.2, table 10.1).

In a number of cases, the model performs better in summer than in winter: dissolved inorganic nitrogen and silicate concentrations in the West and to some extent in the middle compartment are underestimated in winter, light-saturated production rate is underestimated in winter. Although the discrepancy in light-saturated production rate appears unimportant (light intensity is far below the saturation level in winter), the underestimation of nutrient concentrations appears to be more serious. In a closed system the sum of inorganic and organic nutrients is constant, and an underestimation of the inorganic nutrient-pool in winter (when most nutrients are in inorganic form) would lead to an underestimate of summer-phytoplankton concentration (which incorporates most of the nutrients at its peak) also. As has been discussed in chapter 9 however, the influence of initial conditions in the Oosterschelde lasts only for 1-2 months; it seems that the winter nutrient levels probably determine spring bloom peaks but not the summer concentrations. As the spring bloom peaks are (apart from their timing) reproduced satisfactorily, and the winter-nutrient concentrations are in themselves not



very important (nutrients are not limiting in this period anyway), it appears to be not very important to improve the model in this respect.

Apart from the separate calibration of the dispersion coefficients, the parameters related to horizontal transport have played a relatively minor role in the calibration procedure. The parameter DQALG ("dissolved-like" fraction of phytoplankton) is related to both horizontal transport and vertical distribution of phytoplankton; its influence on model-output may be related to phytoplankton productivity (it determines the ratio of algae at the surface vs. total amount of algae in the column) and grazing (giving the concentration increase towards the bottom, i.e. the filterfeeders), more than to horizontal transport.

The relatively low importance of horizontal transport in the total phytoplankton budget is illustrated in figures 10.61-10.64, where advective and dispersive transport are compared with gross and net productivity and grazing rates, all in the same units ( $\text{day}^{-1}$ ). It appears that transport flux plays a relatively small role both in compartment 1 and 3, although the dispersive flow (positive, i.e.: import from North Sea) in compartment 1 is not negligible.

#### 10.6 Conclusion

The most important deficiency of the model appears to be a too early timing of the phytoplankton bloom. Strong points are the average and maximal level of phytoplankton biomass, and nutrient, oxygen and POC concentrations.

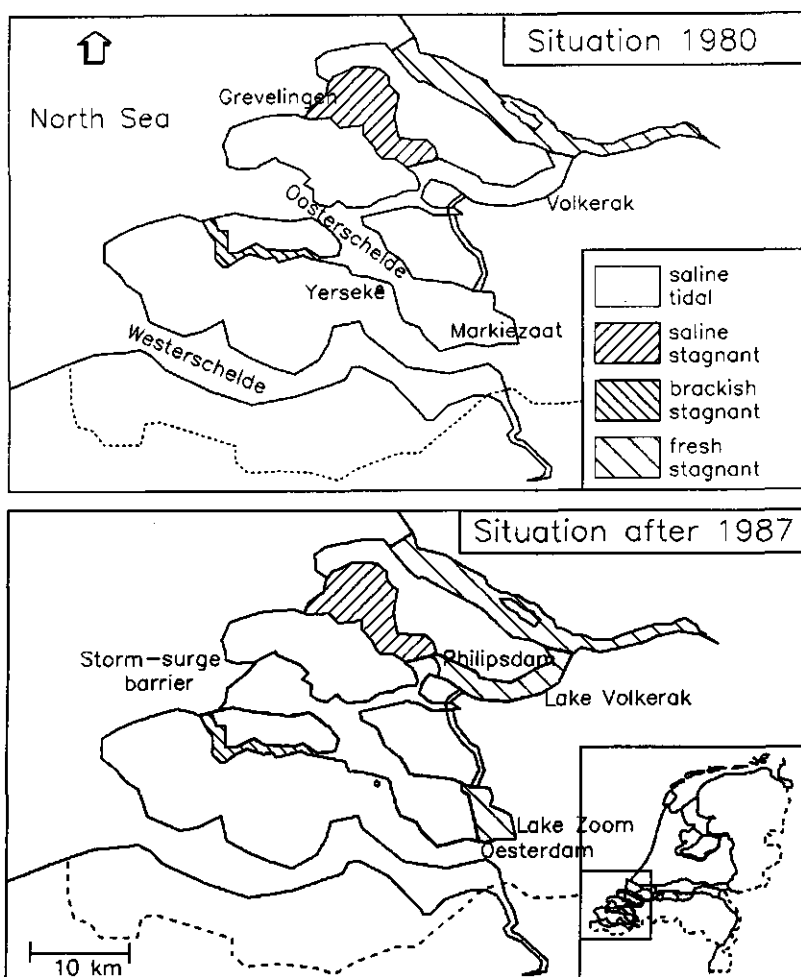
## 11. APPLICATION OF THE MODEL TO SOME MANAGEMENT SCENARIOS

### 11.1 Introduction

In this chapter the model will be applied to calculate the impact of several management options on the Oosterschelde, in particular on food-supply for the macrobenthic filterfeeders. The first (and probably most important) scenario is no longer an "option" but a reality: the storm-surge barrier. Although the model has been developed far too late to be of any value in the decision-making process whether to build a storm-surge barrier or not, the calculation of the impact of the barrier on the system is not altogether useless: in the first place, the changes that are occurring in the Oosterschelde have a stochastic character. For example, the year 1987/88 after the completion of the barrier was very wet and had a very mild winter: it is difficult to compare this year with the previous years, which showed a sequence of very severe winters. Feeding the model with long-term average inputs can give an impression of the average impact of the barrier, which otherwise would require several years of measurements. Further, it is not possible to continue the very broad research program which accompanied the construction works on the same scale; therefore, a model which predicts where the largest changes may be expected can be very useful to guide a reduced measurement programme.

The other scenarios can be viewed as actual management options, but also as an extended sensitivity analysis: what would be the impact of reduced or increased nutrient loads, of an increased mussel cultivation, of a dumping of manure into the Oosterschelde? In the first scenario the post storm-surge barrier situation was compared with the situation before the construction, in the other scenarios the comparison is between barrier alone and barrier plus increased nutrient loads, etc.

All scenarios have been calculated for a "standard year", using the averaged inputs for the period 1980-1985. Uncertainty in the results has been calculated using the parameter ranges obtained from calibration (see previous chapter).



**Figure 11.1:** The Oosterschelde before (1980) and after (1987) the construction of the storm-surge barrier and compartmentalization dams.

## 11.2 The impact of the storm surge barrier

### Description of abiotic changes

The effects of the storm-surge barrier and related works has been described by Holland et al. (1986). The principal effect of the storm-surge barrier is a reduction of the wet cross-section of the Oosterschelde mouth from approximately 80,000 m<sup>2</sup> to 16,650 m<sup>2</sup>, causing a strongly increased hydraulic resistance. The effect of this on the tidal amplitude is largely compensated as a result of the construction of the two dams closing of the Markiezoat area and the Volkerak (see figure 11.1); these reduce the total volume of the Oosterschelde, and as a result the tidal range at Yerseke (at the border of compartments 2 and 3) decreases only slightly, from 3.5 m to

3.26 m. Although the current velocity increases close to the barrier, the overall effect of the reduced cross-section and volume is a reduction in current velocities: maximum velocities are reduced from  $\pm 1 \text{ m.s}^{-1}$  to  $0.5\text{--}0.75 \text{ m.s}^{-1}$ . This has a marked effect on the suspended sediment concentrations (table 11.1).

Table 11.1: reduction in suspended sediment concentrations in the four Oosterschelde compartments, based on observations during 1986 and 1987 (Ten Brinke and Wetsteyn, pers. comm.). In the model calculations it is assumed that seasonal pattern remains the same, but all concentrations are lowered with a fixed percentage.

compartment:	new concentration as fraction of old:
West	30-65%
Middle	35-55%
East	20-50%
North	5-70%

Because the decrease in tidal range is only slight, there is initially hardly a reduction in intertidal surface area (with the exception, of course, of the Markiezaat and Volkerak areas). However, the channels in the Oosterschelde are at present relatively large in comparison to present tidal volume, and it is expected that they will be partly filled with sediment in the long term (Kohsiek et al., 1987). It is thought that this sediment will originate mainly from the tidal flats, and not (or hardly) from the North Sea: as a result, the tidal flats will be eroded: it is expected that from the initial 10,900 hectares of tidal flats, 300 ha (3%) will be eroded in 1992, and 1500 ha (14%) in 2020. Kohsiek et al. (1987) calculate an eventual loss of approximately 30% of the tidal flats over several centuries, but by that time the conditions determining the geomorphology of the Oosterschelde have probably changed to such an extent (e.g. sea-level rise), that the this final equilibrium state will not be actually reached.

The closure of the Volkerak and Markiezaat areas reduces the freshwater and nutrient input to the Oosterschelde: the polder water sluices and the small rivers of the province of Brabant will now be discharging on the freshwater lake Zoom. The total inflow of freshwater into the Oosterschelde is reduced from approximately  $25 \cdot 10^6 \text{ m}^3/\text{yr}$  to  $14 \cdot 10^6 \text{ m}^3/\text{yr}$ ; taking into account the reduced area of the Oosterschelde itself, the relative decrease in discharge is smaller: from approximately  $5.3 \text{ m}^3/\text{m}^2/\text{year}$  to  $3.7 \text{ m}^3/\text{m}^2/\text{year}$  (Holland et al., 1986).

As dispersion is approximately proportional to the square of the current speed, a marked reduction in dispersion coefficients, in particular in the northern branch may be expected (table 11.2). As a result of the combination of reduced freshwater input (potentially causing a increase in salinity) and a reduced dispersion (decreasing mixing with saline North Sea water), salinity remains approximately the same. If nutrients could be described conservatively, their concentration would not change markedly either.

Table 11.2: reduction in dispersion coefficients in the Oosterschelde, based on calculations of current velocities in the new situation and a quadratic relation between current velocity and dispersion (Pieters, pers. comm.)

between compts:                      new dispersion as fraction of old:

Sea -West	0.56
West -Middle	0.56
Middle -East	0.64
Middle -North	0.09

In the present calculations of the effect of the barrier, the long-term morphological changes (erosion of tidal flats, siltation of channels) have not been taken into account, but only the more or less short-term changes. This choice has been made because management options are concerned with these short-term changes. For example, it is very difficult to predict the long-term development of mussel culture in the Netherlands. Moreover, it appeared that the tidal-flat part and the pelagic part of the model are not very strongly coupled. Therefore, it may be expected that the pelagic system is not much influenced by a decrease in surface area of the tidal flats; further, assuming that the processes on the flats are not influenced by the total area of the flats, the model predictions concerning production and mineralization on the tidal flats themselves (expressed per unit surface) are still correct.

The changes in the Oosterschelde as a result of the construction of the storm-surge barrier and related works may be summarized as follows:

- tidal range is reduced only slightly
- intertidal area is reduced by the exclusion of the Markiezaat and Volkerak areas, but remains otherwise (initially) almost the same
- freshwater input is reduced by approximately 30%
- current velocities are reduced by 30-50%, and as a result suspended sediment concentrations and horizontal mixing are strongly reduced.

#### Calculated ecological changes

In the calculation of the expected changes in the Oosterschelde, the input-data from 1980-84 have been averaged to obtain a "standard year". The calculations have been performed taking into account the sensitivity for uncertainty in model parameters. This concerns, firstly, the uncertainty that remained after the calibration procedure, and secondly, the uncertainty of the effects of the barrier, mainly in suspended sediment concentrations and dispersion coefficients. As a result the model-output consists of two intervals: the first band ("nominal parameter values") gives the results for the old standard year, including parameter uncertainty; the second ("projected parameter values") gives the results after the closure of the barrier, including parameter uncertainty and uncertainty concerning the actual mixing, suspended sediment concentration and so on.

As a general result, it can be stated that the expected effects of the Oosterschelde works are mostly smaller in the western compartment than in the east and north. This is a result of the fact that some of the abiotic changes are relatively large in the eastern and in particular in the nor-

thern compartment, and of the reduced influence of the (unchanged) boundary condition at the North Sea.

The expected changes in phytoplankton concentrations are similar in all parts of the Oosterschelde. The yearly-averaged concentrations increase, but only slightly. On a seasonal basis they are characterized by an earlier spring bloom with lower peak values and by higher values in summer. There is a decrease in chlorophyll concentration (figs. 11.2-3), but this can be attributed to a lower chlorophyll content (fig. 11.4): biomass in carbon is higher (fig. 11.5). In its turn, the increase in carbon-to-chlorophyll ratio is a result of the improvement in light-conditions (fig. 11.6), and the decrease in nutrient-conditions (fig. 11.7 and 11.8).

The primary production rate is on the average higher in the new situation (figure 11.9). However, this is the result of a higher biomass rather than of a higher relative production rate: this rate is approximately the same for the old and new situations because the higher values in winter are compensated by lower values in summer (figure 11.10).

The silicon concentrations are expected to decrease slightly (figs. 11.11 and 11.12), but dissolved nitrogen much stronger (figs. 11.13-14). As a consequence, the non-diatoms, which were previously hardly nutrient-limited (fig. 11.7) suffer a relatively large decrease in growth-conditions, and it is expected that the ratio of diatoms to non-diatoms will increase (fig. 11.15).

The effect of the storm-surge barrier on the scope for growth of mussels is positive (figs. 11.16-17). This is partly the result of the increased phytoplankton biomass, which is moreover spread more equally over the growing season. Furthermore, labile detritus concentrations are expected to be higher (fig. 11.18) as a result of the higher excretion by phytoplankton as a consequence of the lower nutrient concentrations (equation 3.16). Another reason for improved scope for growth is that clearance rates are slightly higher because clearance is a decreasing function of suspended sediment concentrations (equation 7.5).

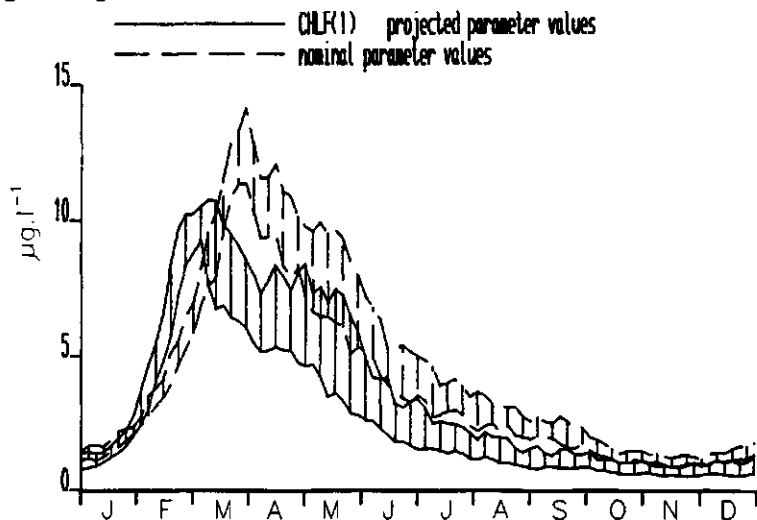
The "wild" grazers in the model (cockles and zooplankton) experience the same conditions as the mussels: their food supply increases, resulting in a higher scope-for growth for cockles and a higher biomass for the zooplankton (fig. 11.19).

In the new situation there is a shift of sediment in suspension towards the bottom. The same holds for suspended detritus, both organic carbon and particulate silicon (diatom remains). As a consequence, it is expected that an increased fraction of mineralization takes place in the sediment; an effect of this is an increase in denitrification (fig. 11.20), which is one of the causes of the decrease in dissolved inorganic nitrogen in the water (figs. 11.13-14). Other causes are the changed inputs and transport, and the increased amount of nitrogen stored in organic form (phytoplankton, detritus, zooplankton).

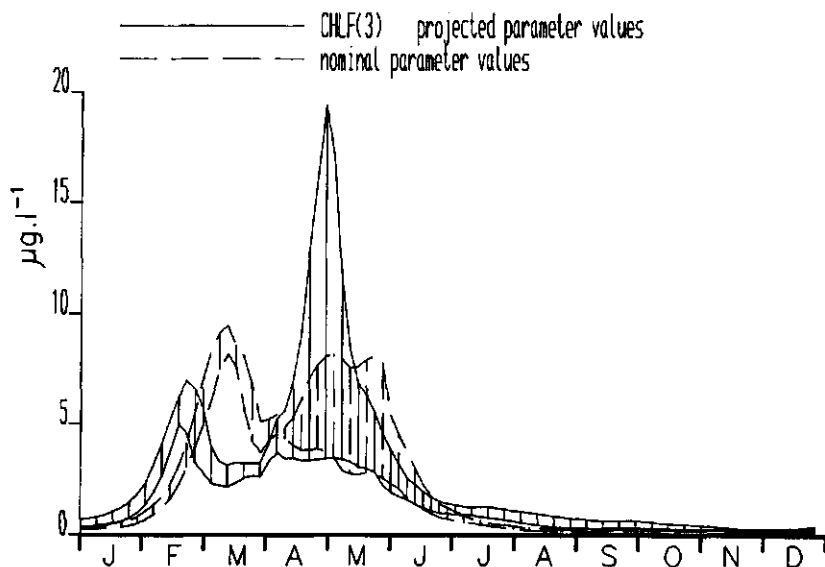
The effect of the shift in silicon-regeneration towards the bottom is a slight increase in phytobenthos biomass in summer (figure 11.21): the benthic diatoms are silicon-limited in summer, and the fact that the silicate regeneration occurs for the larger part via the sediment means an increased production and biomass for the benthic diatoms.

The yearly-averaged oxygen concentrations in the Oosterschelde hardly change as a result of the barrier. The average is slightly below saturation because oxygen production on the tidal flats (which takes place at low tide) is lost to the air, while consumption during immersion is derived from the water column. In spring there is supersaturation (phytoplankton bloom) in

summer and winter undersaturation; this seasonal pattern remains virtually unchanged (fig. 11.22).



**Figure 11.2:** predicted changes (for a standard-year) in suspended chlorophyll concentrations in compartment 1 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



**Figure 11.3:** predicted changes (for a standard-year) in suspended chlorophyll concentrations in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.

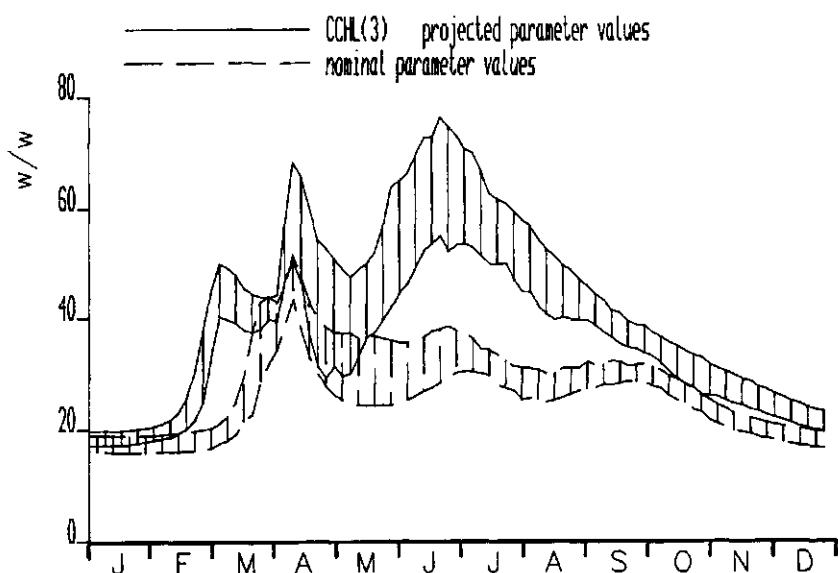


Figure 11.4: predicted changes (for a standard-year) in carbon to chlorophyll ratio in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.

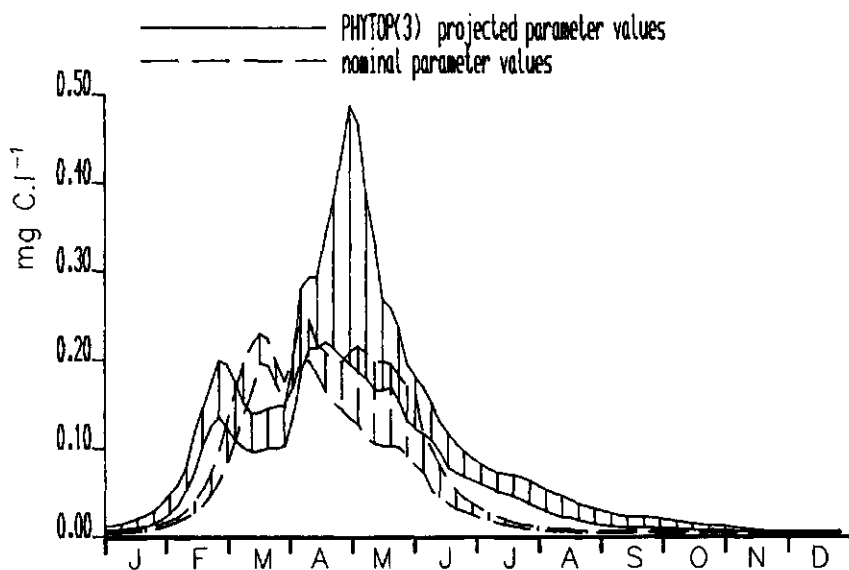
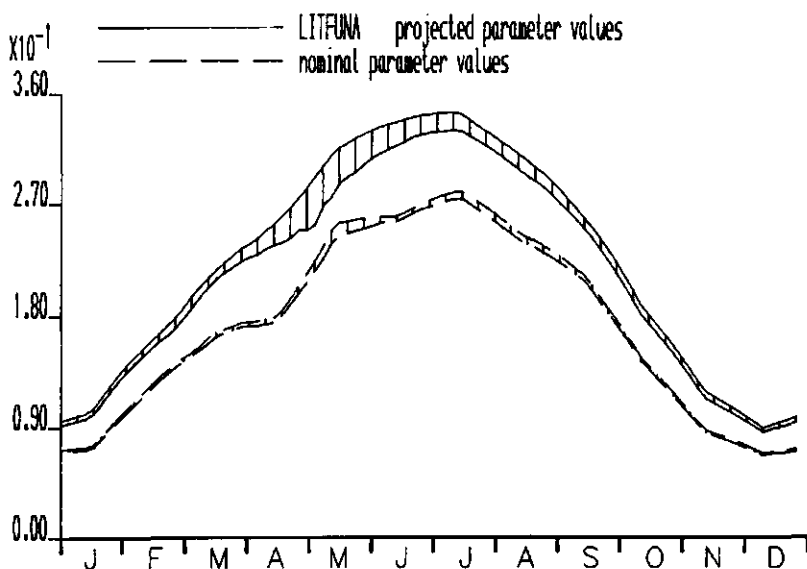
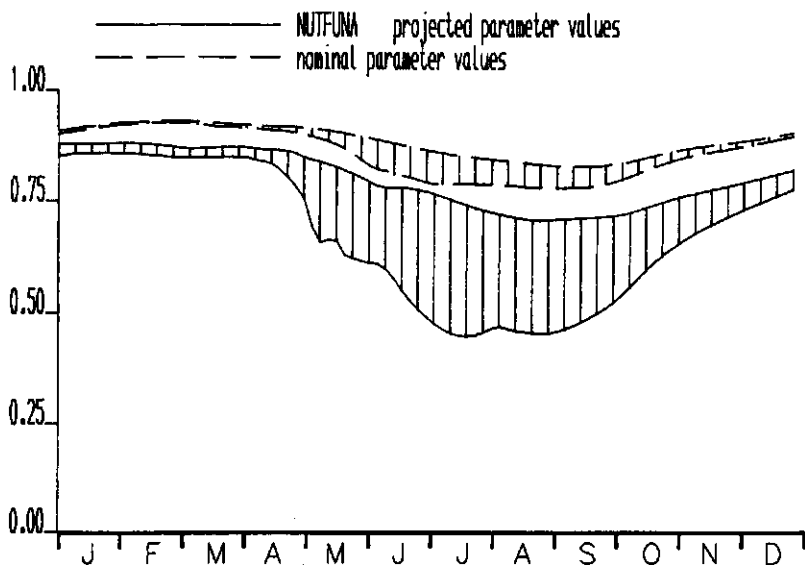


Figure 11.5: predicted changes (for a standard-year) in phytoplankton biomass (in carbon) in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.





**Figure 11.6:** predicted changes (for a standard-year) in light-limitation function for phytoplankton in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



**Figure 11.7:** predicted changes (for a standard-year) in nutrient-limitation function for non-diatoms in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.

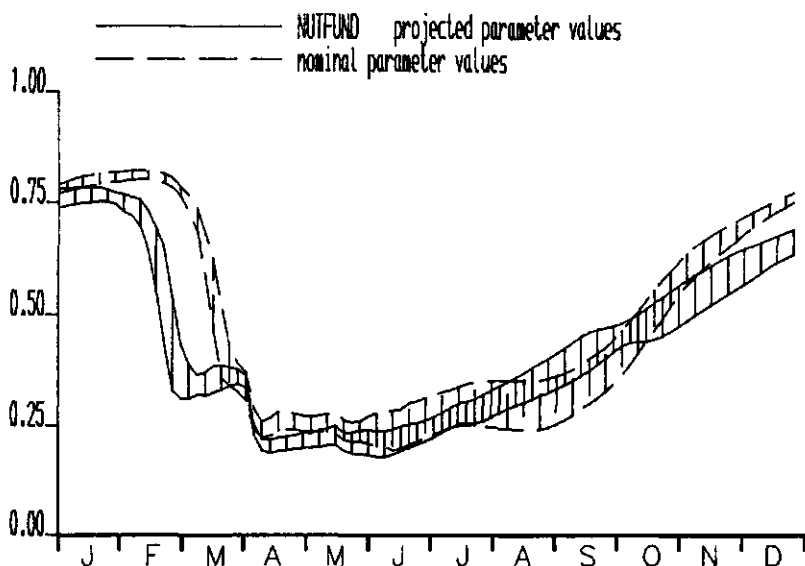


Figure 11.8: predicted changes (for a standard-year) in nutrient-limitation function for diatoms in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.

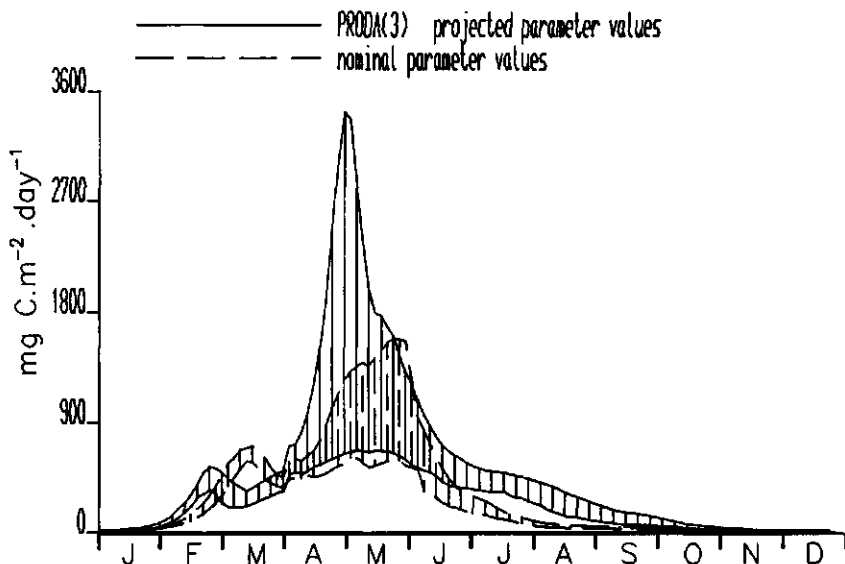


Figure 11.9: predicted changes (for a standard-year) in gross primary production of phytoplankton in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.

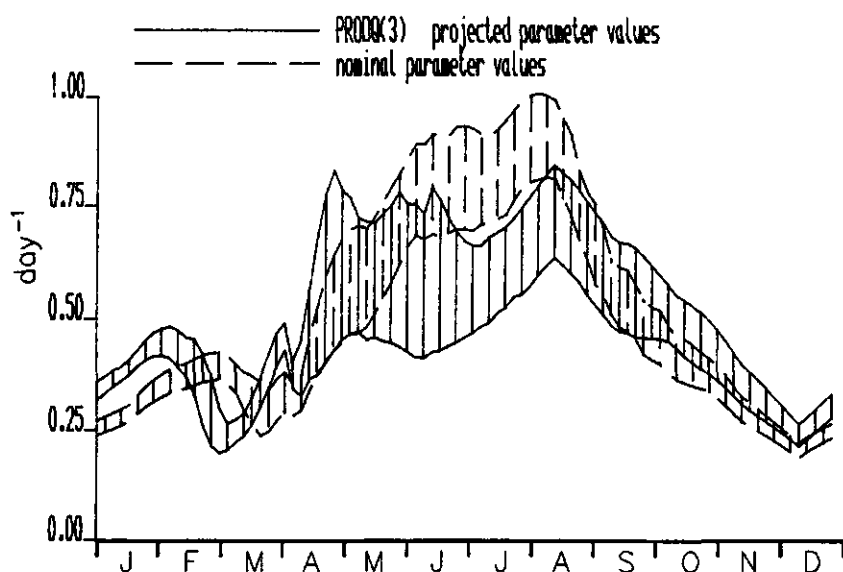


Figure 11.10: predicted changes (for a standard-year) in relative gross primary production rate of phytoplankton in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.

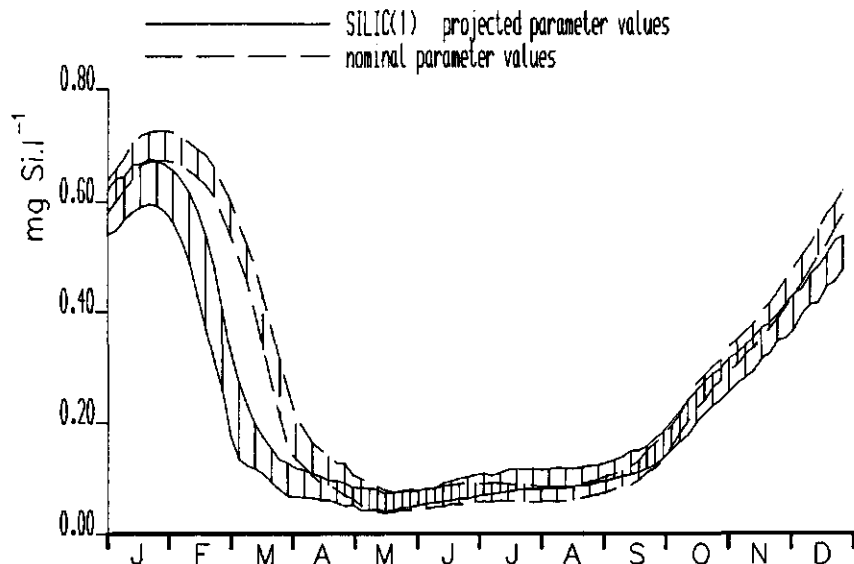
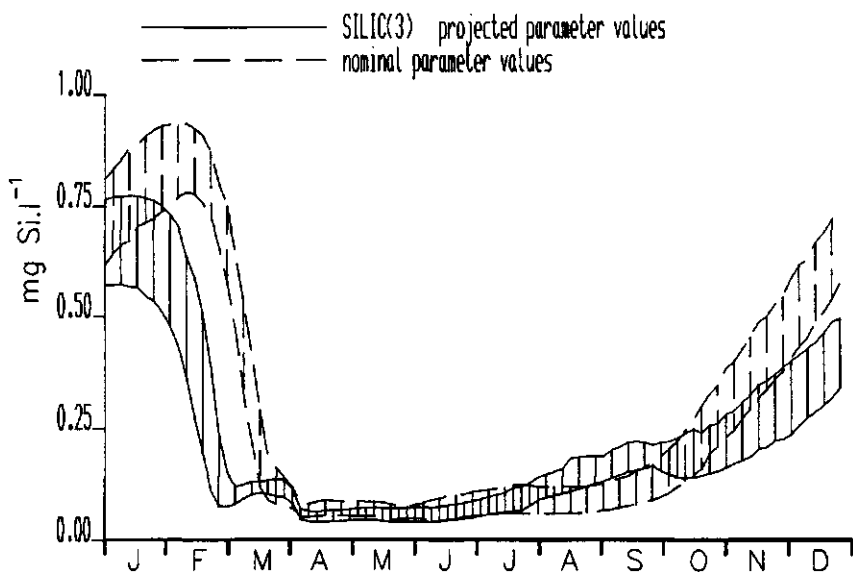
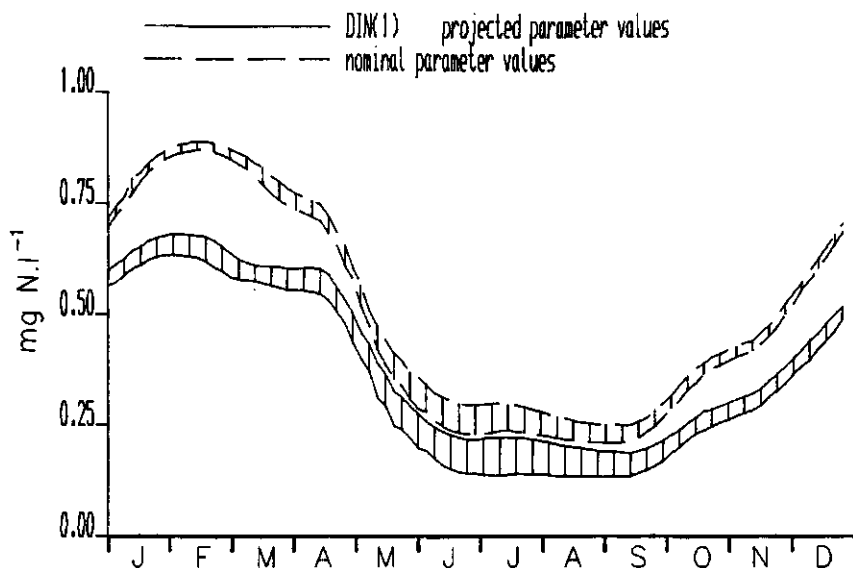


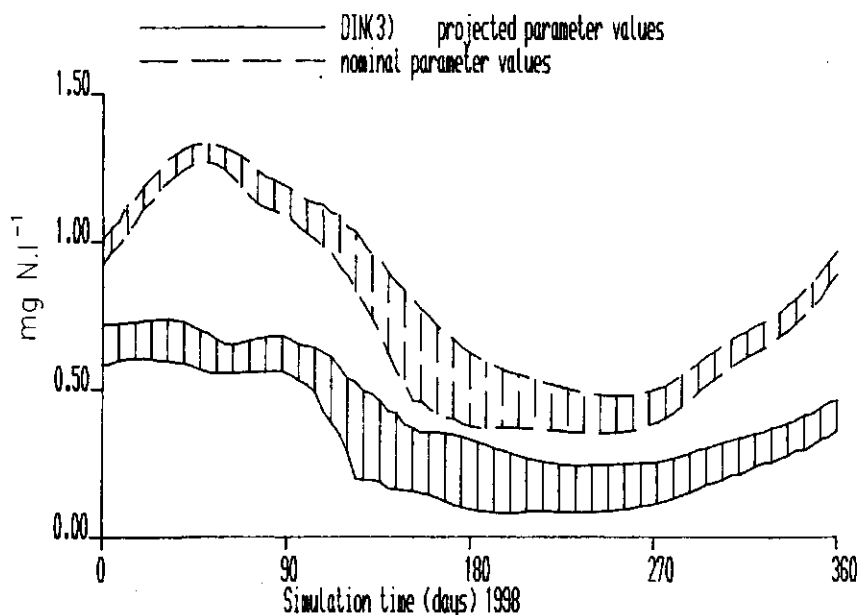
Figure 11.11: predicted changes (for a standard-year) in silicate concentrations in compartment 1 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



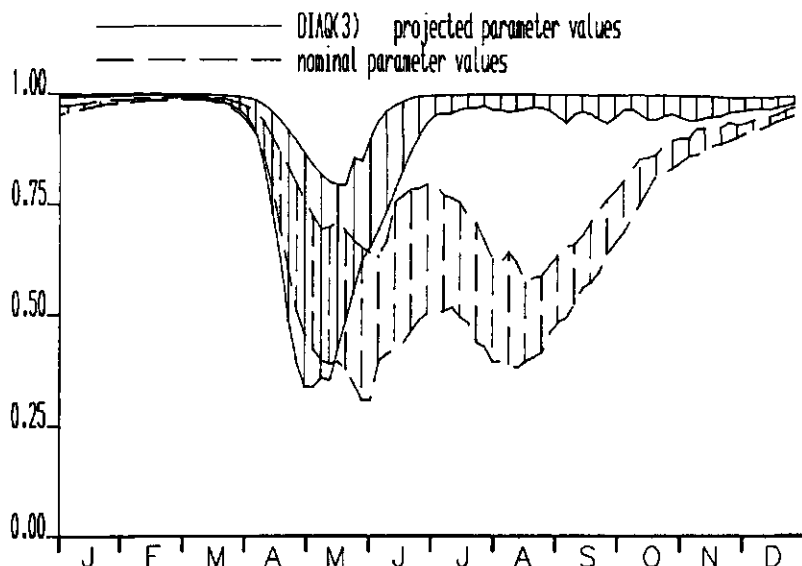
**Figure 11.12:** predicted changes (for a standard-year) in silicate concentrations in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



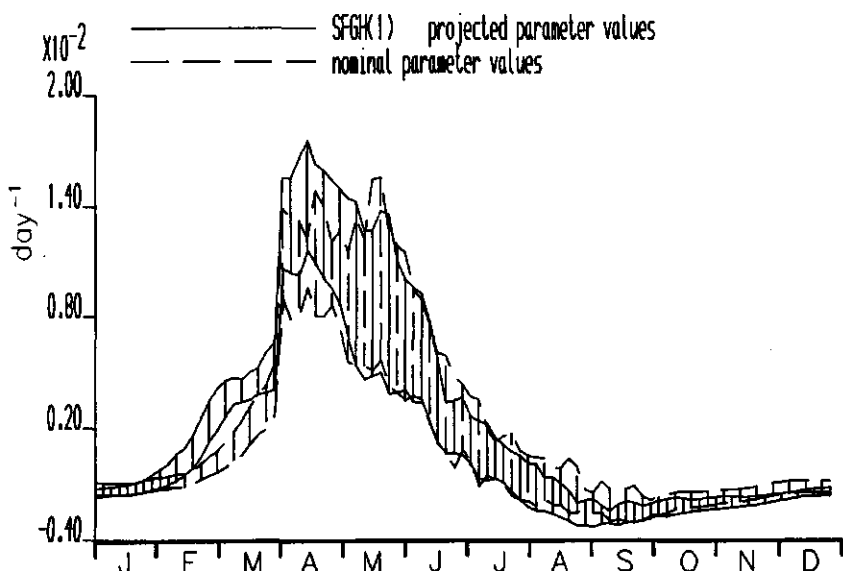
**Figure 11.13:** predicted changes (for a standard-year) in inorganic nitrogen concentrations in compartment 1 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



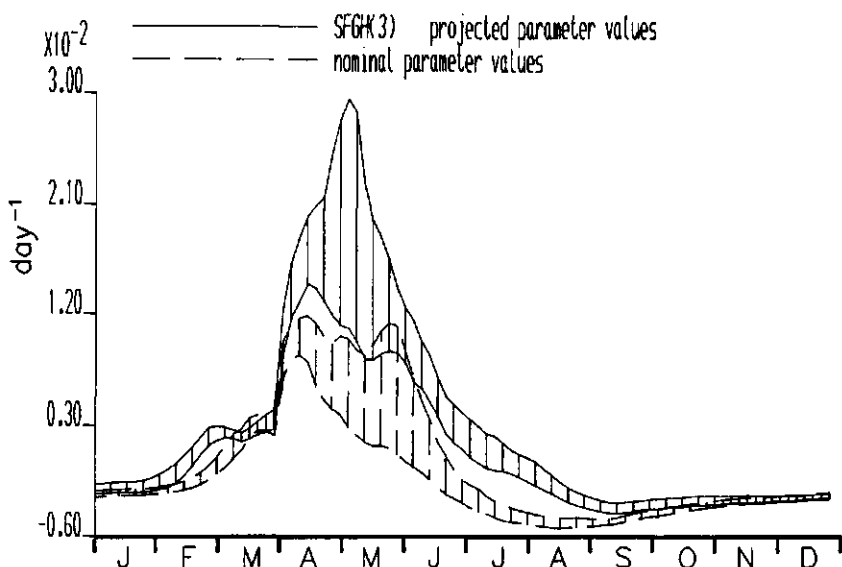
**Figure 11.14:** predicted changes (for a standard-year) in inorganic nitrogen concentrations in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



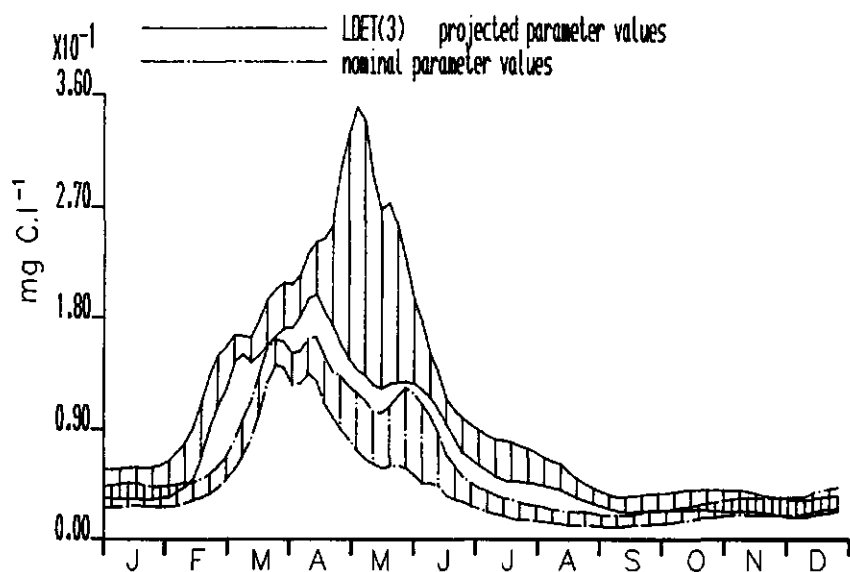
**Figure 11.15:** predicted changes (for a standard-year) in the fraction of diatoms in the phytoplankton in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



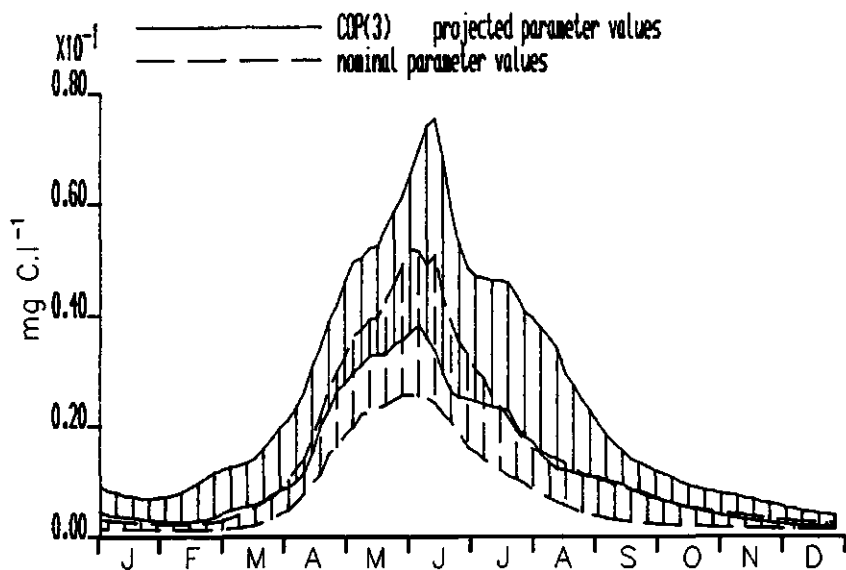
**Figure 11.16:** predicted changes (for a standard-year) in scope-for-growth of half-grown mussels in compartment 1 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



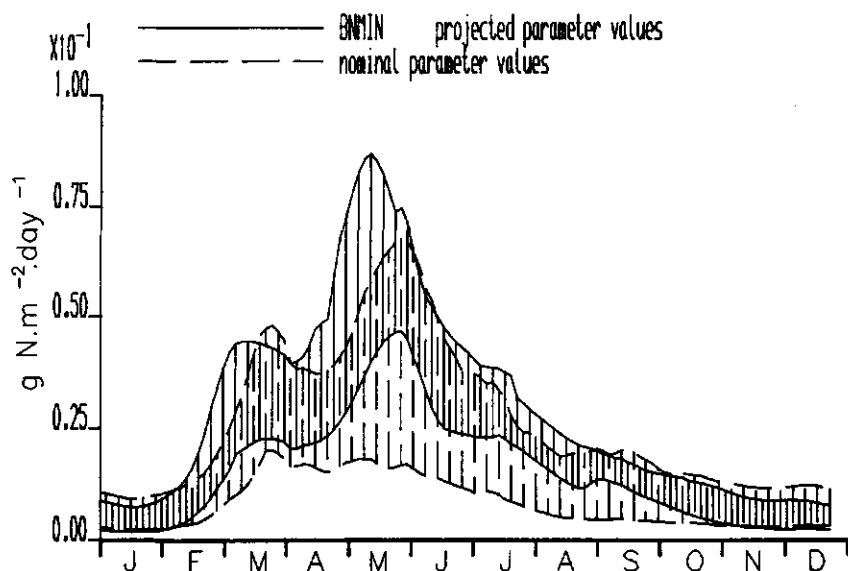
**Figure 11.17:** predicted changes (for a standard-year) in scope-for-growth of half-grown mussels in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



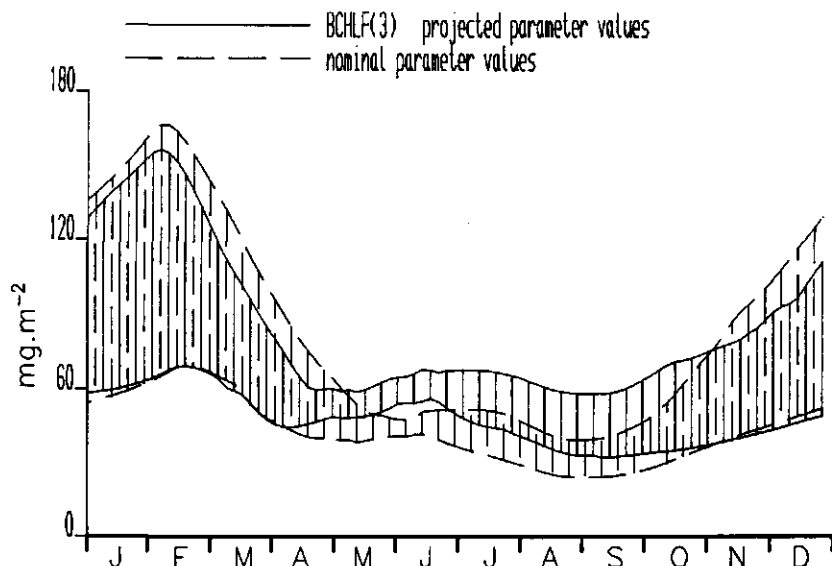
**Figure 11.18:** predicted changes (for a standard-year) labile detritus concentration in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



**Figure 11.19:** predicted changes (for a standard-year) in copepod biomass in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



**Figure 11.20:** predicted changes (for a standard-year) in denitrification rate in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



**Figure 11.21:** predicted changes (for a standard-year) in benthic chlorophyll concentrations in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.



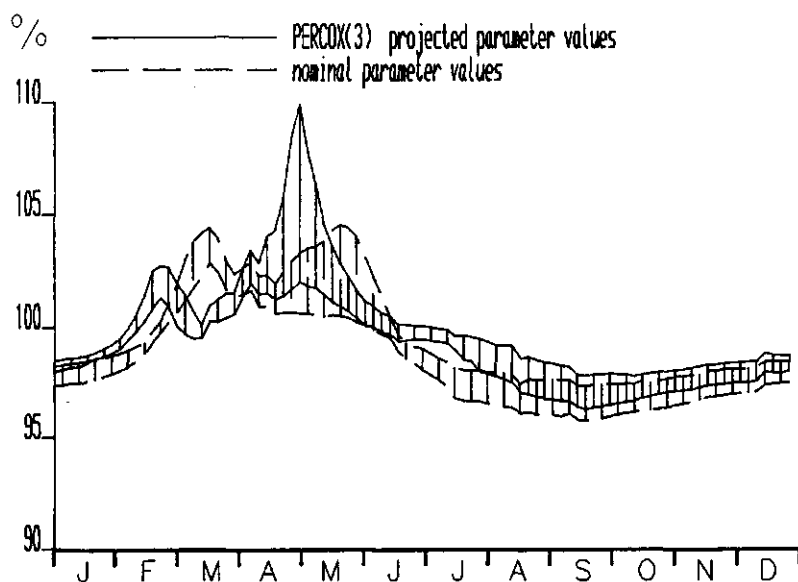


Figure 11.22: predicted changes (for a standard-year) in oxygen concentration (expressed as percentage saturation) in compartment 3 as a result of the Oosterschelde works. The bands represent 1st and 3th quartiles of model results. Nominal values: pre-barrier situation; projected: after barrier.

#### Discussion of effects

It should be noted that the present model may be used to predict changes in large-scale carbon- and nutrient- and oxygen-flows only. Therefore, some of the changes predicted by the model may not be relevant in practice because other effects are more important. An example of this is the prediction that the fraction of diatoms will increase. As the "undesirable" phytoplankton species (toxic species, foam-causing species) belong to non-diatom groups, the predicted relative increase in diatoms would point to an increased "quality" of the phytoplankton. However, in the summer of 1987 there was, for the first time in the Oosterschelde, a bloom of the toxic genus *Dinophysis* in the northern compartment. This first occurrence of the genus has been attributed (Peeters, pers. comm.) to the fact that this mobile genus is adapted to more or less stagnant water. This direct physical effect of the reduced mixing has not been incorporated into the model.

Another direct physical effect of mixing is related to mussel culture. Although the model predicts an improvement of growth conditions for mussels, in practice there proved to be problems on the existing mussel cultivation plots in 1987, because current velocities are at present insufficient to remove biodeposition. However, formerly there were large areas where current velocities were too high for mussel cultivation: these areas can now be exploited, and part of the old plots abandoned. The present model predicts that such a shift in cultivation plots is indeed worthwhile, because the large-scale food supply has not diminished as a result of the barrier.

Although there is a considerable uncertainty in the denitrification rate calculated with the model (figure 11.20), a shift in mineralization from water column to bottom, and at the same time an increase in the relative

ve importance of anaerobic processes seems likely to occur. More important however, is that the decreased inputs and exchange with the North Sea means that the relative importance of denitrification will increase. In the old situation the denitrification rate was  $10 \text{ gN.m}^{-2}.\text{year}^{-1}$  on the tidal flats, or an average  $6 \text{ gN.m}^{-2}.\text{year}^{-1}$  for the entire area (model results) and total N-input was  $28 \text{ gN.m}^{-2}.\text{year}^{-1}$  (Holland et al., 1986); in the new situation the N-input decreases to  $13 \text{ gN.m}^{-2}.\text{year}^{-1}$  and denitrification will increase to approximately  $8 \text{ gN.m}^{-2}.\text{year}^{-1}$ . In this respect the "new" Oosterschelde appears to resemble the neighboring stagnant saline lake Grevelingen, where denitrification plays a major role in the removal of nitrogen from the system.

The predicted oxygen concentrations hardly differ from old values; the predicted oxygen concentrations are still well above the threshold of 50% saturation, below which some sub-lethal effects (e.g.: reduction in growth rate in fish) may be observed (Peeters, pers. comm.). However, it must be noted that the model predicts an horizontally and vertically averaged value only: it is possible that the oxygen concentrations near the bottom may drop lower than 50%, because the vertical mixing of the water column has decreased. This may cause risks for the mussel culture, but it may be expected that these risks are limited to the northern branch (where current speed has decreased most) and situations with a closed barrier.

### 11.3 Some management scenarios

In the calculation of the following scenarios the storm-surge barrier is always assumed present. Therefore, "nominal parameter values" now represent the standard year with reduced exchange, suspended sediment concentrations, etc., including uncertainty model-parameters and these barrier-related changes, and the "projected parameter values represent an extension of these parameters with changed nutrient loads, mussel biomass, etc.

#### Changing nutrient discharges and boundary conditions

In these scenarios it is assumed that nutrient (both N and Si) conditions change. This is simulated by changing the concentrations in the freshwater discharges (they are either halved or doubled) and by changing boundary conditions.

Inputs include discharges from polders, surrounding lakes (lake Zoom, lake Veere) and the atmosphere. Increases in nutrient concentrations in the future could be the result of further eutrophication of the surrounding lakes and of excessive use of fertilizers in agriculture; reduction of nutrient discharges could be the result of eutrophication-control measures and fertilizer regulations.

It appears that a doubling of discharges has its most pronounced effect in the northern compartment: the nutrient concentrations increase almost proportional with the discharges (see figure 11.23-24). The yearly-averaged concentration of chlorophyll is increased approximately twofold also (see figure 11.25), but this is partly caused by a higher chlorophyll content of the cells: the yearly-averaged phytoplankton biomass expressed in carbon units increases with approximately 60% only. For the other compartments the changes are smaller: in compartments 1, 2 and 3 the increase in phytoplankton-carbon is 2%, 17% and 22%, respectively.

The halving of the discharges has a smaller effect than the doubling scenario: in compartment 4, chlorophyll concentrations drop with approximately 30%, and phytoplankton-carbon with approximately 20%. Again, the changes in the other compartments are less pronounced (<10%).

The effect of changes in nutrient-inputs seems to be largely restricted to the northern compartment. The main explanation for this is that freshwater influence in the southern branch of the Oosterschelde is small: the average fraction of fresh water that may be calculated from average salinity is approximately 10% only, which clearly strongly reduces the effects of changes in concentration of this fraction. Apparently, the boundary conditions at the North Sea are more important in determining the nutrient concentrations than the freshwater inputs. Another explanation for the moderate effect is a partial compensation for the increased N-input by an increased denitrification (see figure 11.26). As has been discussed above, the denitrification accounts for a substantial N-removal in the new Oosterschelde.

To investigate the apparently substantial influence of the boundary conditions on the nutrient concentrations in the southern branch the model was run with doubled boundary concentrations for nitrogen at sea. In this scenario the silicate concentrations were kept constant. The effect of this scenario is a marked increase in chlorophyll concentrations, notably in the eastern compartment (figures 11.27). Due to the fact that only nitrogen concentrations have been increased at the boundary in this scenario and that silicon is limiting the diatoms, the increased biomass during the summer bloom is nearly entirely due to non-diatoms.

In view of the preceding remarks on the relative importance of boundary conditions and inputs, a strong increase chlorophyll is not unexpected, but it seems surprising that this effect is more than proportional to the increase in concentration and that the increase is strongest in the eastern compartment, which is the most distant from the boundary.

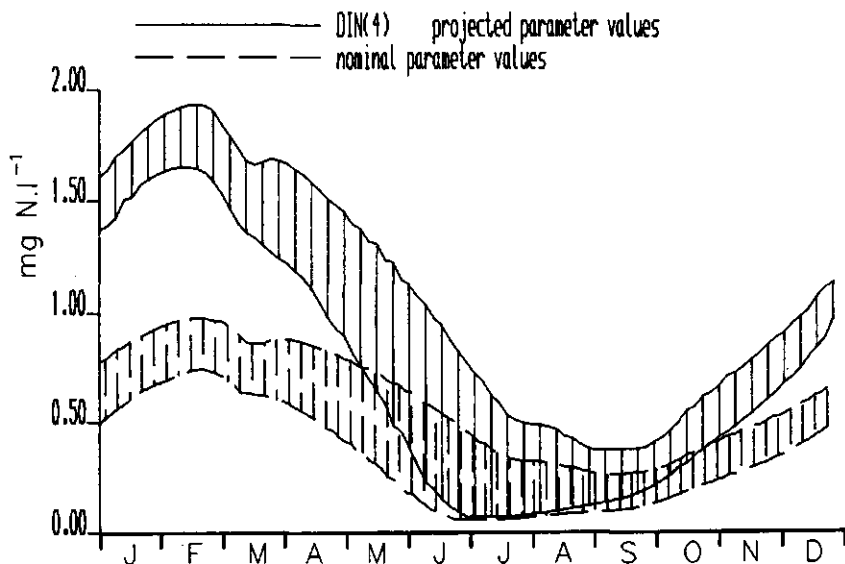
The more than proportional increase may be explained by the effect of grazing: most of the grazing on phytoplankton is due to filterfeeders, of which the biomass was not changed in this scenario. If grazing remains constant, an increase in phytoplankton production could have a strongly magnified effect on net population increase, which is the difference between net production and grazing rates. For example, if during some period the production was  $0.5 \text{ day}^{-1}$  and grazing rate was  $0.4 \text{ day}^{-1}$ , and the first term is changed to  $0.9 \text{ day}^{-1}$ , then the net population growth is increased with a factor 4, although the effect of the nutrients was less than a doubling in rate coefficient.

The second point can be explained by the fact that the long-term effect of the seaward boundary on nutrient concentrations hardly differs between compartments west and east: at sea, salinity is approximately 32 ‰, in the west approximately 30 ‰, and in the east approximately 28 ‰. The average fraction of seawater therefore hardly differs between the compartments: 94 and 88%, respectively. This long-term view is approximately valid for the total amount of nitrogen (i.e. the sum of organic and inorganic forms), which behaves -apart from denitrification- as a conservative substance. For chlorophyll, which has a high turnover, this high fraction of seawater in the eastern compartment has little significance: the amount of phytoplankton reaching the eastern compartment from the North Sea is probably negligible due to grazing losses under way. In fact, the relative independence of chlorophyll concentrations from boundary conditions is one of the reasons for the stronger reaction to the increased nitrogen concentrations. Another reason for the more pronounced reaction in the eastern compartment is its smaller depth as was discussed previously.

However, a scenario with strongly changed boundary conditions is not very realistic. Although nutrient discharges into the North Sea have rapidly increased in the past decades and eutrophication problems are developing,

these problems are at present confined to relatively small areas, e.g. in the German bight and near the Danish coast. Due to the prevailing south-westerly current, the North Sea water in front of the Oosterschelde consists for at least (depending on wind direction) 90% of so-called Channel water originating from the Atlantic Ocean (De Ruijter et al., 1987), which is not noticeably influenced by river discharges. A doubling of the nutrient concentrations at the Oosterschelde mouth would therefore require much more than a doubling in nutrient discharges into the North Sea.

In general therefore, it may be concluded that there is little danger of strong changes in phytoplankton biomass as a result of changing nutrient conditions in the Oosterschelde: changes in the concentration at the North Sea are probably moderate: even in pessimistic scenarios a doubling of nutrient concentrations at the North Sea are not foreseen. The effects of increased discharges into the Oosterschelde are largely limited to the northern compartment.



**Figure 11.23:** predicted changes (for a standard-year) in dissolved inorganic nitrogen concentration in compartment 4 as a result of doubling nutrient content in freshwater inputs. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with doubled nutrient inputs.

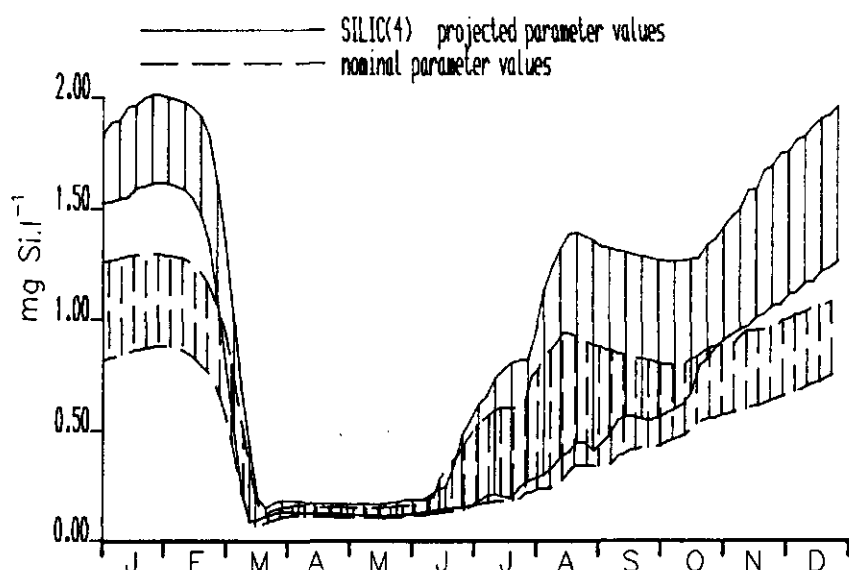


Figure 11.24: predicted changes (for a standard-year) in silicate concentration in compartment 4 as a result of doubling nutrient content in freshwater inputs. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with doubled nutrient inputs.

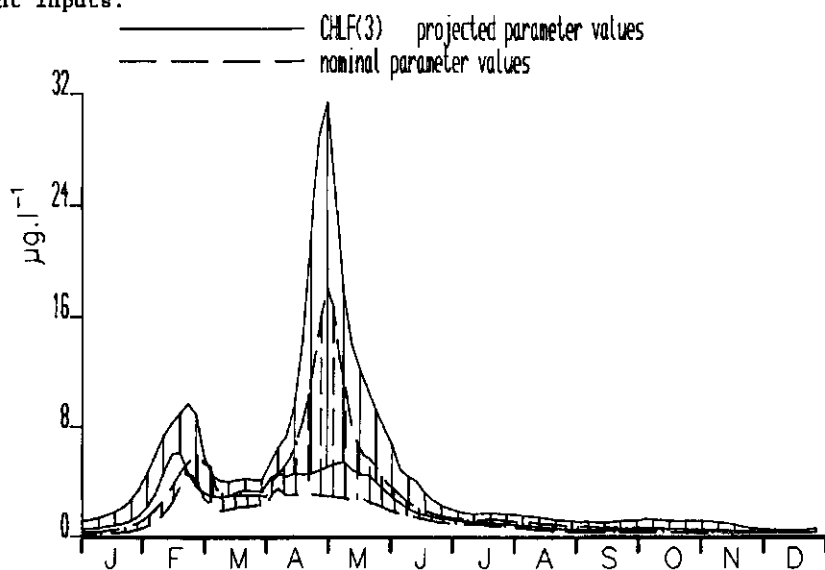


Figure 11.25: predicted changes (for a standard-year) in chlorophyll concentration in compartment 3 as a result of doubling nutrient content in freshwater inputs. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with doubled nutrient inputs.

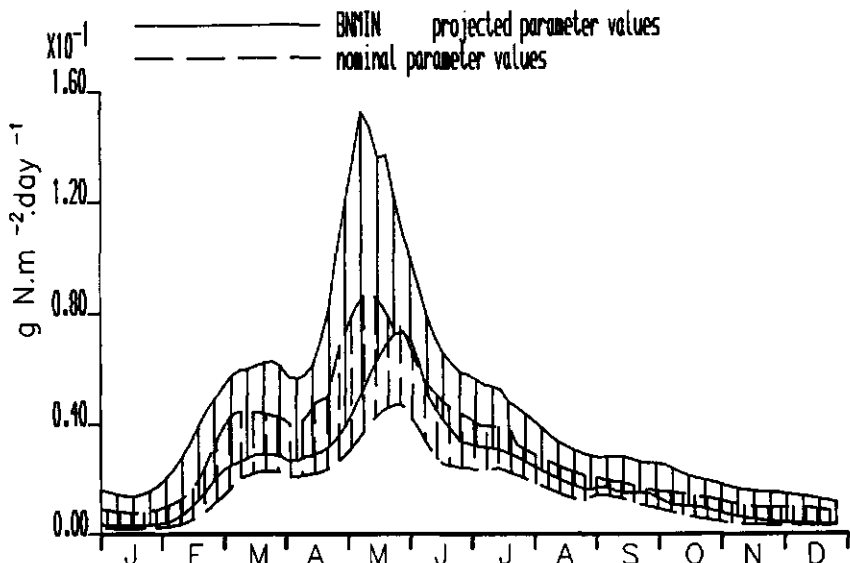


Figure 11.26: predicted changes (for a standard-year) in denitrification rate in compartment 3 as a result of doubling nutrient content in freshwater inputs. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with doubled nutrient inputs.

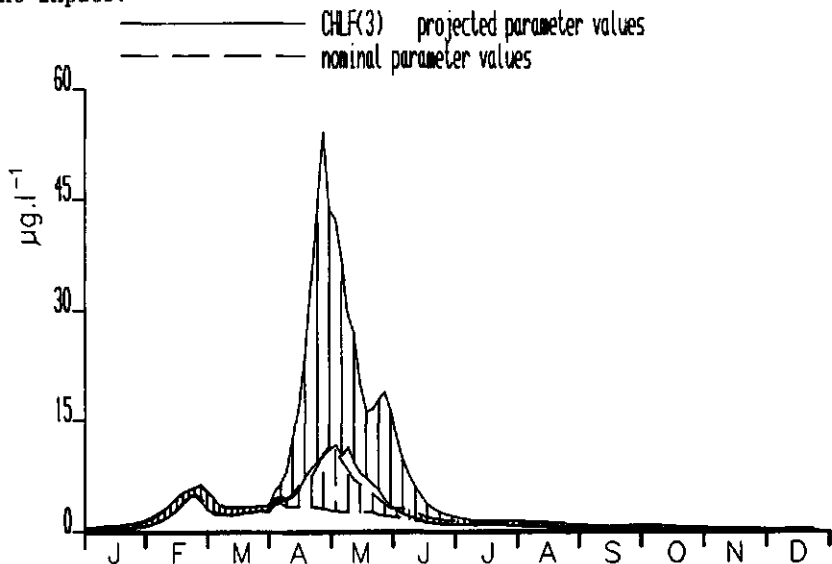


Figure 11.27: predicted changes (for a standard-year) in chlorophyll concentration in compartment 3 as a result of doubling nitrogen concentration at the North Sea boundary. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with doubled nutrient inputs.

#### Dumping of manure

The rapid development of intensive animal husbandry in the Netherlands, largely based on imported fodder, has created a large surplus of manure. It is estimated that the present surplus amounts to  $37.5 \cdot 10^6$  tons (wet weight) per year. In view of the fact that until recently organic fertilizer was considered as a useful substance to increase plant productivity, it seems obvious to ask whether the surplus of manure can be used for this purpose, instead of treating it in costly installations. For instance, it has been suggested to dump the manure in the North Sea in order to enhance fish production.

Following the line of such thought-experiments, the model was used to calculate the effect of dumping 10% of the Dutch manure surplus into the middle compartment of the Oosterschelde. For this purpose wet manure was converted to organic carbon (state-variable labile detritus) by using its  $BOD_5$ -value of 15 g  $O_2/l$ , a conversion of  $BOD_5$  (i.e. oxygen demand during the first 5 days) to total oxygen demand of 2.8, and a conversion of oxygen to carbon of 1/3.

The results show that phytoplankton biomass increases as a result of the added nutrients (fig. 11.28). The effect on phytoplankton is tempered because of increased grazing: the zooplankton, feeding on the detritus, is now able to survive winter food-shortage, and is already present before the spring-bloom of phytoplankton. The high detritus concentration further causes an increase in denitrification rate (figure 11.29). The favorable effect on mussel production can be attributed to the increased detritus concentrations also (fig. 11.30).

However, these positive effects are countered by the decrease in oxygen concentration (figure 11.31). As has been mentioned, problems start to develop only below 50% saturation, but the compartment-average values for a standard year may be much more favorable than, e.g. near-bottom values during a hot and quiet period in summer. Furthermore, the assumption that the compartment is completely mixed over its cross-section is only valid because there are no important lateral inflows. In the present scenario, the assumption of complete mixing would no longer be tenable: near the sewage-outfall there would probably develop an area with strongly reduced oxygen concentrations, anaerobic bottoms and so on. Clearly, even judging strictly from the viewpoint of mussel-yield, an increase in productivity would be of little benefit if there is a fair chance on mass mortality as a result of anoxic conditions.

Thus it appears that from the viewpoint of productivity, dumping of manure would yield dubious results. Besides this, there is the problem of the copper in the manure, which is highly toxic for nearly all marine organisms, and the problem of the transportation costs. It may be concluded that there is nothing to recommend the dumping scenario.

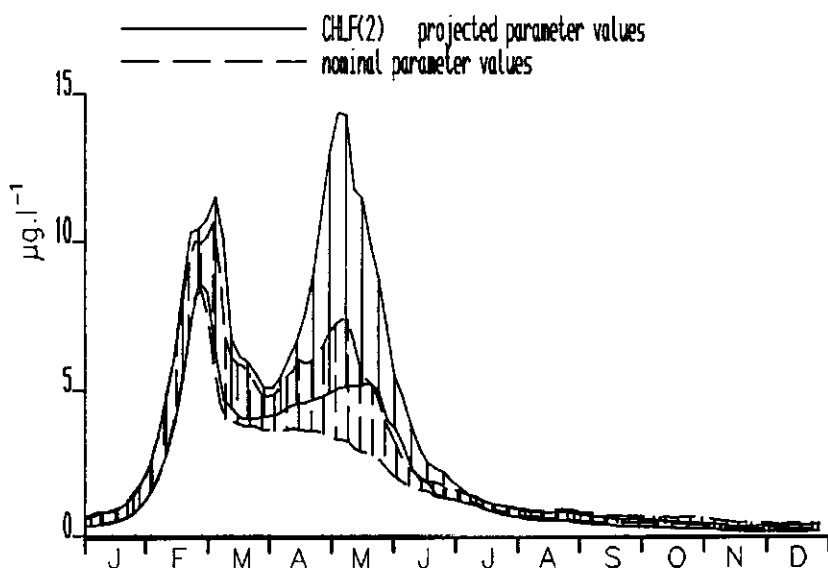


Figure 11.28: predicted changes (for a standard-year) in chlorophyll concentration in compartment 2 as a result of dumping manure in the Oosterschelde. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with manure.

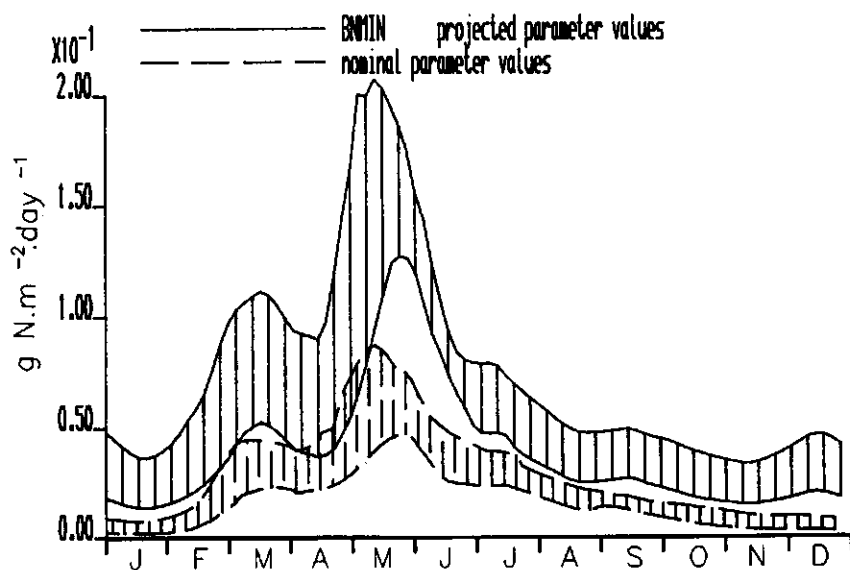
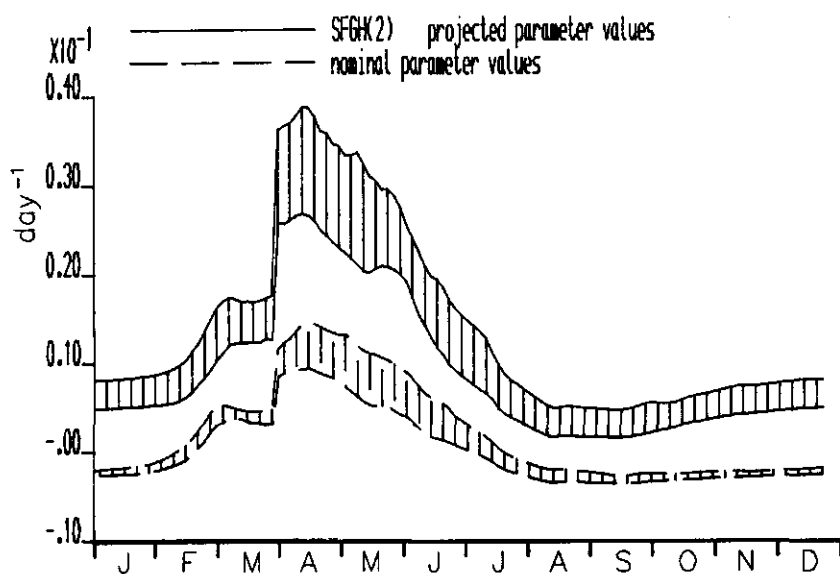
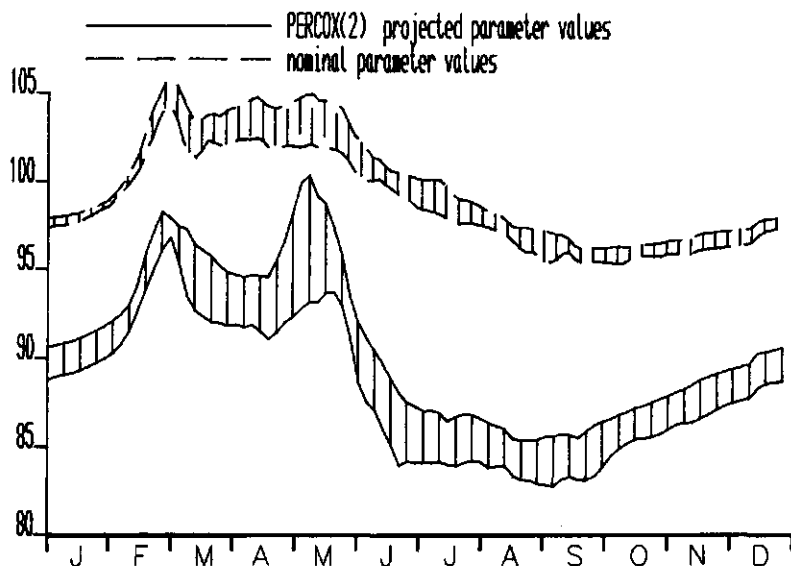


Figure 11.29: predicted changes (for a standard-year) in denitrification rate in compartment 3 as a result of dumping manure in the Oosterschelde. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with manure.





**Figure 11.30:** predicted changes (for a standard-year) in half-grown mussel scope-for-growth in compartment 2 as a result of dumping manure in the Oosterschelde. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with manure.



**Figure 11.31:** predicted changes (for a standard-year) in oxygen concentration (expressed as percentage saturation) in compartment 2 as a result of dumping manure in the Oosterschelde. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with manure.

### Increasing mussel biomass

The expected improved growth conditions could make an extension of the mussel culture in the Oosterschelde attractive. Such an extension has been investigated by adding an amount of mussels per unit of subtidal area in the various compartments corresponding to the present subtidal density of mussels in the western compartment.

The simulation results show that the eastern compartment is more sensitive for an increase in mussel biomass than the western compartment. Adding the same amount of biomass per unit surface, yearly-averaged chlorophyll-a concentrations decreases with 22% in the eastern compartment and 7.5% in the western compartment (see figs. 11.32-3). The increased grazing is partly compensated by a higher productivity of the phytoplankton as a result of the increased nutrient concentrations (figure 11.34). The yearly average scope-for-growth of a half-grown mussel decreases with 22% and 33% in the western and eastern compartments respectively. As a result of the decrease in food concentration copepod biomass decreases markedly in compartment 3 (fig. 11.36), but hardly in the western compartment. Other components of the system (oxygen) are less or not at all (microphytobenthos) influenced by the increase in biomass. The stronger effect of mussel cultivation in the eastern compartment may again be mainly attributed to the difference in depth and the exchange with the North Sea; the fact that scope-for-growth reacts stronger than food concentrations is a result of the fact that it is the difference between feeding and loss terms of the mussels.

The effect of increasing mussel biomass has been studied in more detail by adding several amounts of mussels to the compartments. It appears that the scope for growth is a linear function of mussel biomass for a wide range of biomass values. For the two compartments we have:

West:  $SFGH = 0.0024 - 0.00054 * B$

East:  $SFGH = 0.0018 - 0.00060 * B$

with: -SFGH: yearly average scope for growth, expressed in  $\text{day}^{-1}$

-B: additional mussel density in units of present density in western compartment (range of values in the runs: 0-8).

by assuming that the profit for the mussel grower per mussel is proportional to the yearly-averaged scope-for-growth (yield), we may calculate the optimal density of mussels. The total yield is a function which initially increases with mussel density (scope for growth is high and total yield is approximately proportional to numbers of mussels), but decreases at higher densities (the mussels exhaust their food supply and scope for growth is small or even negative).

The assumption that profit per mussel is proportional to SFGH gives for the total profit ( $SFGH * B$ ) a simple quadratic expression in B, which may be differentiated to obtain the optimal B.

West:  $B_{opt} = 2.1$

East:  $B_{opt} = 1.5$

This would mean that the mussel culture in the western compartment could be extended by 2 times the present intensity; in the east (where there is at present no cultivation), it would be optimal to have a density 1.5 times higher than that in the western compartment at present.

However, the assumption that profit is proportional to mussel scope-for growth seems rather optimistic: the mussel grower has some expenses also. Again, we can assume that expenses are proportional to the amount of cultivated mussels. This gives the model:

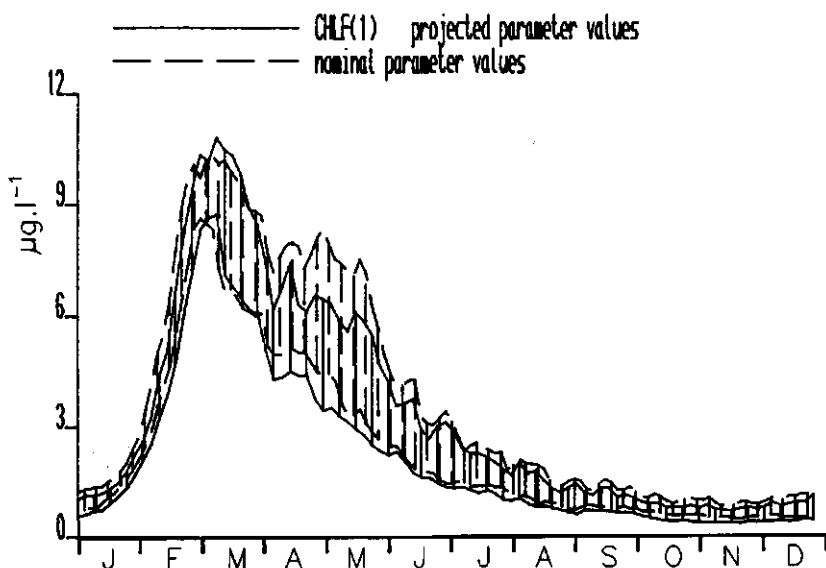
$$Y = (x - y B) B - z B$$

Clearly, we should have  $z < x$ , or the cultivation of mussels would never be profitable. If we assume that at present, a mussel-grower in the western compartment spends half his profits in fishing the seed-mussels, sowing them, harvesting and so on, we have  $z = \frac{1}{2} x = 0.0012$ . For this value, the optimal solutions would be 1.05 and 0.5, for the western and eastern compartments respectively.

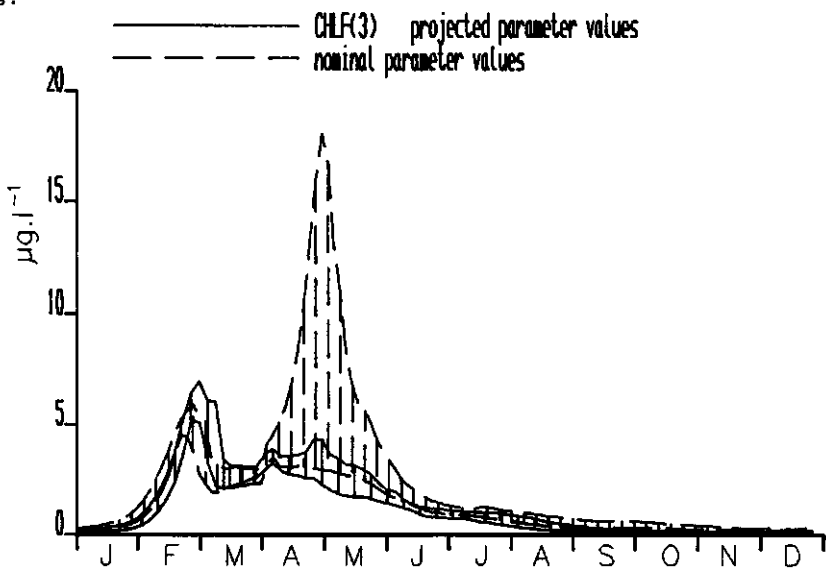
The foregoing calculations are valid for a "standard year" (i.e., with averaged inputs and forcing functions), and without taking into account parameter uncertainty. In making predictions, it is useful to take into account not only some average or most likely value, but uncertainty as well. This is illustrated in figure 11.36 which illustrates the yearly-averaged scope-for-growth (SFGH) values, calculated with the model using the calibrated parameter ranges. These histograms can be compared with figures 11.16-17, which also show the (slight) increase in SFGH in the western compartment, and the substantial increase in the East. It can also be observed that the higher average value in the West is caused by a number of runs with substantially higher SFGH-values; the lower range is approximately the same.

Interpreting the histograms as probabilities, it may be concluded that the expected SFGH in the western compartment is higher, but that the chance of getting a low SFGH has not diminished. If mussel culture would be extended, the histogram would be shifted towards lower values of SFGH. Despite the fact that there might still be a higher expected SFGH, it would actually increase the risk of obtaining a low mussel growth. As the growth rates of other grazers (cockles, zooplankton) are closely correlated to the scope for growth of mussels, the same would hold for these organisms. In the management of ecosystems, a sub-optimal management with a low risk is often preferred over a management that has a higher expected value (here: in terms of growth rates) but a higher risk (Walters, 1986).

Summarizing: the model predicts a higher expected growth rate for mussels and other grazers; this would leave room for a considerable extension of the mussel culture in the western compartment, but only a moderate increase in the eastern compartment. However, such an extension would increase the risk of low growth rates above the present level; if the management of the Oosterschelde prefers the minimization of risk over an higher expected value, there is no room for an extension of mussel culture.



**Figure 11.32:** predicted changes (for a standard-year) in chlorophyll concentration in compartment 1 as a result of doubling mussel biomass in the compartment. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with extra mussels.



**Figure 11.33:** predicted changes (for a standard-year) in chlorophyll concentration in compartment 3 as a result of adding the same density of mussels as presently in compartment 1. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with extra mussels.

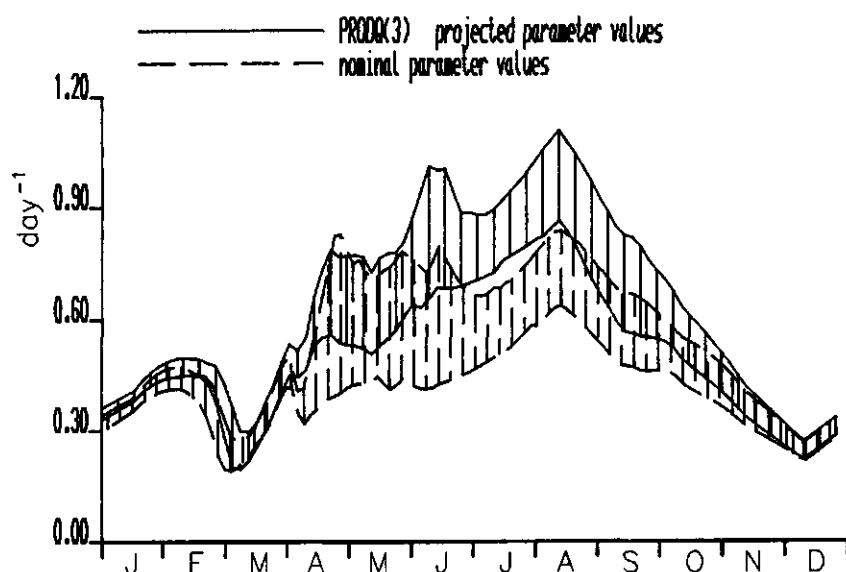


Figure 11.34: predicted changes (for a standard-year) relative gross primary production rate in compartment 3 as a result of adding the same density of mussels as presently in compartment 1. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with extra mussels.

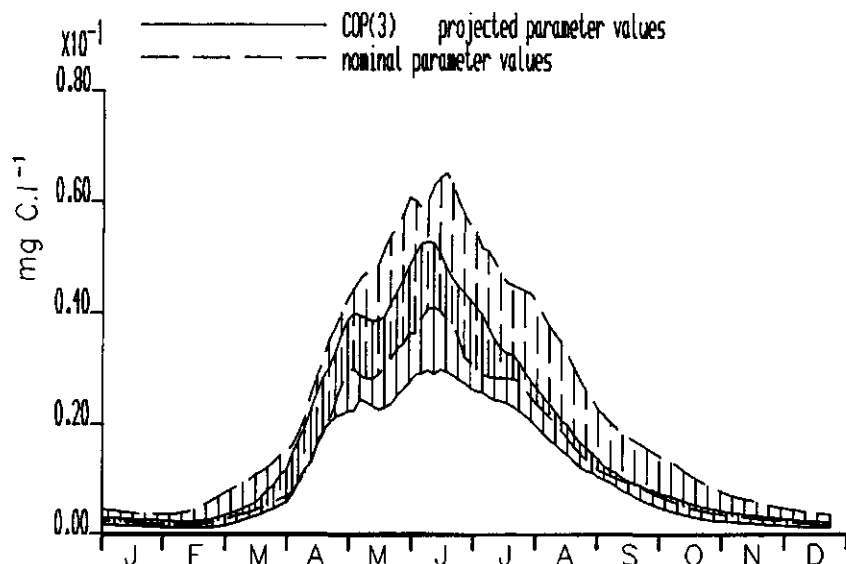
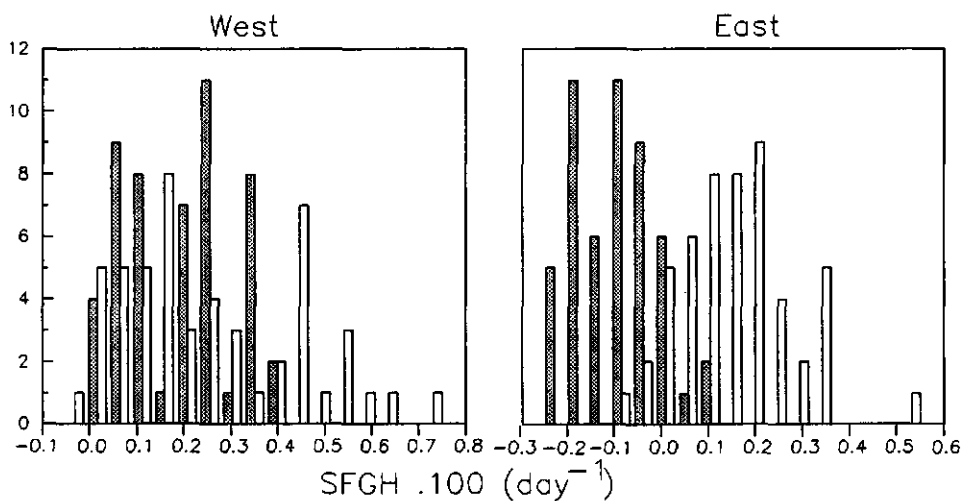


Figure 11.35: predicted changes (for a standard-year) in copepod biomass in compartment 3 as a result of adding the same density of mussels as presently in compartment 1. The bands represent 1st and 3th quartiles of model results. Nominal values: present situation (including barrier); projected: with extra mussels.



**Figure 11.36:** Yearly-averaged scope-for-growth values calculated using calibrated parameter values. Dark bars: old situation; open bars: after storm-surge barrier.

#### 11.4 Summary and conclusions

In this chapter the model is applied to calculate the effect of some human manipulations on the Oosterschelde ecosystem. The first and major manipulation of the system has been the construction of the storm-surge barrier and compartmentalization dams. It appears that the expected ecological changes are moderate in most respects, because changes tend to compensate each other. Two examples are: the improved light-condition for phytoplankton, which is compensated by a decrease in nutrient concentrations, and the decrease in freshwater load, which is compensated by reduced mixing. As a result, phytoplankton biomass will increase slightly only. The lowered nutrient concentrations will increase phytoplankton excretion, which is the main reason for an increased detritus concentration. The combination of higher phytoplankton biomass and higher detritus concentrations lead to improved growth conditions for the grazers in the system.

The reduced mixing causes a shift in sediment concentration in suspension toward the bottom. Combined with the higher detritus concentrations this leads to an increase in bottom mineralization.

The increased mineralization means an increase in nutrients and  $\text{CO}_2$  available for the phytobenthos, leading to a small increase in production and biomass. Another consequence of this increased benthic mineralization is an increase in denitrification; combined with the decreased nitrogen-input, this leads to a marked decrease in dissolved inorganic nitrogen, and thus to the increased nitrogen limitation of the phytoplankton, already noted above.

The decrease in mixing may cause oxygen problems in the northern compartment. Although the expected compartment-average values for a standard year are well above 50%, problems may occur near the bottom or in quiet periods, especially at the end of the summer.

Changes in nutrient concentrations in the freshwater discharges appear to have a marked influence on the nutrient concentrations in the northern compartment only; in the other compartments, nutrient concentrations and phytoplankton biomass are less influenced. The moderate effects in the southern branch of the Oosterschelde can be explained by the predominance of marine influence on nutrient concentrations. If boundary conditions at the North Sea are changed, the effects on phytoplankton biomass (and thus on the rest of the ecosystem) are large; however, it is unlikely that the boundary conditions at the North Sea will change very strongly in the future.

A dumping of excess manure in the Oosterschelde would influence grazing organisms mainly directly as food; phytoplankton productivity and biomass would increase slightly. Oxygen concentrations would be severely reduced, and could reach problematic levels.

An increase in mussel cultivation could be attractive as a result of the improved growth conditions for mussels. Such an extension is feasible in the western compartment only, in the eastern compartment food supply is rapidly diminished by increased grazing. Although the extension would be profitable in terms of expected growth rates, an extension of mussel culture would increase the risk of low growth rates for all grazers above the present levels.

If the expected changes are brought in relation to future field work, it appears that the following subjects are of particular interest: the predicted increase in mussel growth rates, the increased benthic mineralization, in particular the denitrification, and the possible oxygen problems in the northern branch.

## 12. GENERAL DISCUSSION

In this chapter the development of the present model is placed in the context of the development of ecological models for similar situations: what types of models can be distinguished, what is the role of the intended use of the model in its development, and how can uncertainty be incorporated in modelling studies. This discussion is not meant to be exhaustive, and will be generally limited to modelling studies of the water quality and ecology of estuaries.

### A functional classification of models

Mathematical models can be classified according to many criteria, e.g. linear vs. nonlinear, steady-state vs. dynamic, spatially distributed vs. point models etc. (Jørgensen, 1983). For the present discussion, models are classified on the basis of their intended use, as scientific and qualitative; scientific and quantitative, and applied.

The use of models is closely linked with their complexity. The simplest models fall into the scientific and qualitative class. The purpose of these models is to study some type of system-behavior in its purest form, stripped of all its unessential aspects. An example of this type of model are the Lotka-Volterra equations for the interaction between a predator and its prey (Walters, 1986). The model shows that a biological system may show periodic behavior purely as the result of the interactions between two species, and allows the investigation of the stability, frequency etc. of these cycles. Other examples of this type of model are behavioral models (e.g. "optimal foraging" theory, Taghon, 1981), models to investigate the effect of cycling on ecosystem stability (DeAngelis, 1980), the effect of disturbances on species diversity (Verhagen and Csetenui, 1987).

The advantage of the qualitative models is their simplicity and the resulting possibility to analyze them: e.g., solve the equations analytically, analyze the model behavior for all combinations of parameter values and inputs. Many concepts in ecosystem analysis like stable cycles, stability and resilience, catastrophic behavior, chaotic behavior are due to this type of modelling research.

The disadvantage of the qualitative type of models is that a direct comparison between these "bare" models and a real system is hardly possible due to the complexity of actual systems. Although there have been attempts to compare the results of e.g. the Lotka-Volterra model to actual field data (e.g., there is a famous time-series of the catch of hares and snow-foxes in the records of the Canadian Hudson Bay Company which shows cyclic behavior), this comparison is necessarily only qualitative, as the model lacks aspects like the climate, hunting pressure and food supply for the hares, which probably determine to a large extent the behavior of the actual observed system.

An extension of the model with measured inputs, and replacement of the abstract parameters representing "a predator" and "a prey" with e.g. the actual rate coefficients measured for fish and zooplankton, brings the model into the second class: the scientific/quantitative models. The purpose of this kind of modelling effort is an extension to that of the previous class: the qualitative models have primarily a hypothesis-generating purpose; with quantitative models it is also possible to test hypotheses. Although the model has now a more restricted applicability as a result of replacing the abstract entities with actual variables, its intention is still to be as general as possible. Their use should not be limited to a single system, but are intended to analyze characteristics of a (certain type of) ecosystem in general. Examples of questions that have been successfully answered by this



type of model are: "Can the typical two-peaked chlorophyll curve in the North Sea be reproduced by a model with only phytoplankton and detritus but without zooplankton?" (Fedra, 1981, 1983) or "Is it necessary to include a bacteria-microzooplankton food-chain in a model of the pelagic zone of the Atlantic Ocean?" (Vezina and Platt, 1988).

The third type of models distinguished in this discussion are the applied models. These are necessarily quantitative, as they are not concerned with some abstract question but always with some particular system: e.g., "What happens with the primary productivity of the North Sea if the present load of herbicides is reduced as planned?" Obviously, it is in theory equally possible that this has no effect or a positive effect; the interesting point is what we may actually expect in view of the present concentrations, phytoplankton sensitivity, expected load reduction etc.

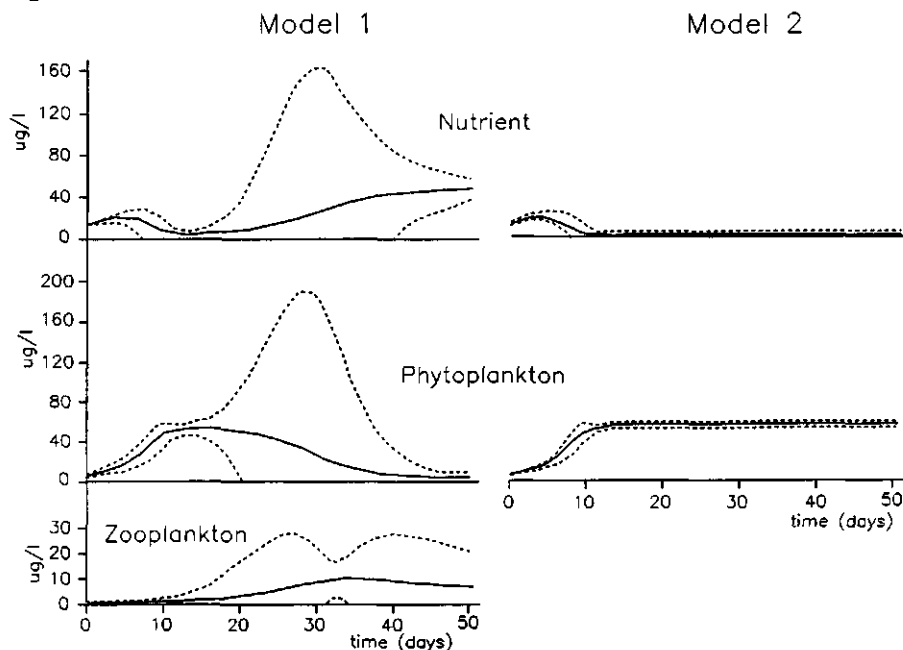
The applied models differ from the previous class in that they are concerned with predictions and not with hypothesis testing. This distinction is not clear-cut as hypotheses can be tested by comparing model predictions with actual observed behavior. However, the emphasis is quite different. In hypothesis-testing, it is a bad sign if a particular piece of model content can not be tested; this is not necessarily a problem in applied models. Beck (1987) considers the development of water quality models from the hypothesis-testing viewpoint:

"First, Popper has drawn a distinction between science and nonscience as a matter of whether the hypotheses associated with any attempt at a description of nature can be formulated in a manner whereby they can be unambiguously falsified. Given the currently available field observations of the behavior of environmental systems, 'comprehensive' models, which have become enormously complex assemblies of very many hypotheses, cannot be effectively falsified. This is partly a function of uncertainty in the field data, certainly a function of current limitations in the methods of system identification, and essentially a function, in the event of a significant mismatch between the model and observations, of being unable to distinguish which among the multitude of hypotheses have been falsified. In fact the detailed spatial patterns of water circulation and equally detailed differentiation of ecological behavior described by the more complex models would demand experimental observations that are simply not technically feasible."

The argument seems quite sound: if we want to be able to reject some hypothesis (proving a hypothesis or model to be correct remains, of course, an impossibility) or choose between two alternative hypotheses then a complex model is generally not suitable. More in general, this appears to be true of the complex natural system itself: for example, in an estuary, the gradient of salinity runs parallel to that of nutrients, suspended sediment concentration, chlorophyll content and many others; furthermore, the seasonal patterns in some of these variables run parallel too. In such a system, it is difficult or impossible to distinguish the effect of one of these factors from the others on e.g., the growth rate of some organism. If we want to separate the effects of salinity, chlorophyll and suspended sediment concentrations on mussel growth rate, the best solution is obviously to conduct some controlled laboratory experiments. This allows the development and testing of model formulations for these effects, which would have been impossible in the framework of a complex model of the real system.

As one wants to avoid "nonscience", it seems better to construct very simple models only, of which all parameters may be determined from the available field measurements. This solution to the problem seems unattractive: models are always simplifications but should not become caricatu-

res. For example, in the estuarine example we can not distinguish the salinity, suspended sediment and chlorophyll effects on mussel growth; suppose we solve this by incorporating salinity effects only, which can then be neatly calibrated. Clearly, this model yields nonsense if one of the factors (sediment, chlorophyll) is changed and salinity remains constant. A similar example is given by Beck (1983): two eutrophication models of different complexity were calibrated to some (artificial) data set. Only the parameters of the simple version (containing nutrients and phytoplankton only) could be estimated with some accuracy; this was not possible with a more complicated version (which contained zooplankton also). Using the simple model it was possible to make predictions with quite narrow uncertainty bands; the more complicated gave different predictions with much wider uncertainty bands. The predictions by the two models are illustrated in figure 12.1.



**Figure 12.1:** (from Beck, 1983) Two models of different complexity are calibrated to the same (artificial) data set and subsequently used for predictions; Model 2 contains the state-variables nutrient and phytoplankton, model 1 contains in addition zooplankton. The dotted bands represent  $\pm$  the standard deviations of predicted values.

Beck (1983) considers the situation a dilemma: "With a large model (M1) it may well be possible to predict the 'correct' future, but one would have little or no confidence in the prediction. In contrast, with a small model (M2) it may be that a quite 'incorrect' future is predicted, and, worse still, one might place considerable confidence in that prediction".

It seems that there is hardly a dilemma in this case as the more complicated model appears clearly preferable: not only are its predictions better (after all, zooplankton does form part of the ecosystem), it also gives a more realistic picture of the uncertainty. Obviously, if we have

insufficient data we can not make up for this by using an insufficient model! Model simplification can be justified only if some particular process has little or no influence on the model-output, which is clearly not the case in this example. If we want to make better predictions for this system we need more data on zooplankton; this is a very important model result in itself, and should certainly not be "covered up" by leaving the zooplankton out of the model.

The fact remains however that many ecological models have a far greater complexity than the available field data seem to support. It is perhaps better to admit that complex ecological models like the present are not scientific in the sense of "scientific discovery", but fall into the third category, the applied one. This kind of models is not suitable to develop and test new hypotheses, and in this sense they could be called "unscientific", although the usual derogatory connotation of this word may be hopefully avoided.

De Wit and Arnold (1976) place the development of ecological simulations models in the engineering tradition, where complex models have been applied for several decades. For example, during the building of the Oosterschelde storm-surge barrier, models were used to predict currents near the construction site using typically 10,000 grid cells in which water level and current speed were calculated. Clearly, the verification of the calculations would also require "experimental observations that are simply not technically feasible" (Beck) even by the Rijkswaterstaat; the purpose of these models is obviously not to test and improve the equations of fluid dynamics but to provide predictions for the construction works. Although the model outputs are compared with some current speed and water level recordings, there is a large amount of "surplus content", defined as model content that cannot be identified from the field data (Beck, 1987). Similarly, an ecological model may contain a large amount of surplus content which can not be justified from a hypothesis-testing viewpoint but is thought to be necessary for the predictive purpose of the model.

The emphasis on the application of models in the third category has two consequences: the purpose of the model should be clear, and the role of statistics in model development is different. As the development of complex models (and because natural ecosystems are usually complex, most ecosystem models will be complex) can, in view of Beck's argument, only be justified as applied science, this application should be clear and be kept in mind in the modelling effort.

The special role of statistics in relation to model purpose has already been discussed in chapter 10. The usual statistical techniques are developed for the models of the scientific category: they aim at the testing of hypotheses and the estimation of parameters; although some of the same issues recur in applied models, the emphasis is different, as model results are viewed in relation to model use. For example, Beck (1987) considers parameters which hardly influence the results as undesirable, as they can not be identified. On the other hand Swartzman and Kaluzny (1987), who implicitly take the applied view, state: "...the sensitivity of model output to parameter changes is used as a test of the robustness of model performance to changes in parameter estimates. Under this criterion a model is interpreted as good if it is insensitive to small ( $\pm 10\%$ ) changes in model parameters".

### The development of applied models

In a report on Oosterschelde before the construction of the storm-surge barrier and on expected changes in the system as a result of the barrier, Holland et al. (1986) also discussed some of the expected changes in the ecosystem, without however using a model. For example:

"The consequences of the decrease in nutrient discharges on primary production are probably small. In the Oosterschelde the primary production is at present limited by light extinction as a result of the turbidity, in other words: nutrient are present in relative abundance. It is not unthinkable that the primary production will be higher after 1986 as a result of the on the average improved light climate under water because this production is at present limited by the available amount of light".

This statement may be used to show the limits of qualitative reasoning to arrive at predictions: as long as a chain of causes and effects runs in one direction (e.g.: lower current speed -> less suspended sediment -> more light -> more primary production), one does not need a quantitative model to reach a (qualitative) conclusion. When two factors that change as a result of the barrier have opposite effects then the outcome is no longer clear, and predictions become little more than a guess ("not unthinkable"). In this situation it is obviously necessary to weigh the light- and nutrient effects against each other quantitatively, in other words: to use some quantitative model.

In the initial phase of the development of a model the spatial and time-scale, variables and structure of the model should be chosen on the basis of the required output, and the management options that are considered for the system. There is no intrinsic "best" representation of the system: the same system may be considered at different time- and spatial scales, and emphasizing different aspects by different choices of input-, output- and state variables scales. The Oosterschelde is an example of a system where at least ten different models were used to answer hydraulic, geomorphologic and biologic questions at different time and spatial scales.

At this point it has proved very useful to involve the model-users, experimental scientists and model-builders in a workshop in which the first version of an ecological model is formulated (Ruadij and Baretta, 1982; Walters, 1986). A preliminary model is most useful as a learning tool rather than to make accurate predictions: in the first place, the development of a model stimulates discussions on system boundaries, important processes and variables and so on; furthermore, the preliminary model may be used to develop promising management scenarios. At this early stage, the model can also be important to guide the measurement program in the laboratory and the field (Hornberger and Spear, 1981).

The procedure to develop a new model for each specific question and system under consideration may seem wasteful: why not formulate, e.g.: "a more generalized model which could then be fine tuned to fit all salt marsh ecosystems" (Hopkinson et al., 1988)? If there is a number of similar ecosystems with similar problems it is in fact possible to deal with all of them with a single model. Examples are the shallow Dutch lakes, which are very similar and have similar eutrophication problems. A single model was used successfully for a large number of them (Los, 1982). Usually however, this is not the case. For example, the estuaries along the Dutch coast are superficially similar (similar tidal range, all have large soft-bottomed intertidal flats with similar species composition), but all show some specific characteristics and problems: the Westerschelde and Ems-Dollard are true estuaries, with a considerable fresh-water input; the Oosterschelde and

Wadden Sea have only a relatively limited freshwater input. The Westerschelde resembles the Ems-Dollard in that they are polluted with organic matter and have no mussel culture; the Westerschelde differs from the Ems-Dollard because it suffers in addition from considerable pollution by heavy metals and pesticides. The Wadden Sea and Oosterschelde are both used for mussel culture, and neither receives organic pollution; the Wadden Sea differs from the Oosterschelde however because it is strongly eutrophied. A model that would incorporate all these characteristics would obviously be much more complicated than any of the models for a separate system; such a model would be very cumbersome to handle, both in the development (sensitivity analysis, calibration) and in use (calculation of scenarios), so that the seemingly wasteful method to develop separate models (Boede, 1986; Ouboter, 1988; EON, 1988; this report) is quite likely more efficient than the development of a single large model. Nevertheless, in this case a single model is in theory still feasible, because we still have a limited number of systems and associated management problems in mind; this is no longer the case for a model that would be suitable for any estuary: such a "generally applicable" model would require that we take into account all characteristics and all possible problems and uses of estuaries, which seems an impossibility.

Obviously, the development of different models for different systems or even for different problems in a single system does not mean that "the wheel has to be re-invented" each time. There is a large literature on specific processes like transport or primary production, which can be applied for a specific problem at hand. Furthermore, the development of suitable model-formulations is usually only a minor part of the modelling work; the collection of input-data, calibration data and the sensitivity analysis and calibration usually take up most of the time.

#### The role of uncertainty

The use of a model may be restricted to its role as a tool in the preliminary analysis of the system, but often it will be used for quantitative predictions. In this case the modeler may replace the cautious predictions by Holland et al. cited above by statements like: "primary production in the Oosterschelde will increase from 308 gC.m<sup>-2</sup>.year<sup>-1</sup> to 322 gC.m<sup>-2</sup>.year<sup>-1</sup>". The main result of such seemingly very accurate predictions is probably to decrease the credibility of ecological modelling. Any prediction should be accompanied by an estimate of its uncertainty.

The sources of uncertainty in predictions are classified by O'Neill and Gardner (1979) and Walters (1986) as:

- 1) uncertainty resulting from model construction
- 2) uncertainty resulting from parameter estimation errors
- 3) uncertainty resulting from system inputs

The first type of uncertainty is the hardest to quantify. In some cases, if it concerns some relatively simple and isolated part of the model, a quantification is straightforward. For example, Walters (1986) discusses the effect of using several growth-curves in fishery models; in the present model alternative formulations in e.g. phytoplankton transport or filter-feeder activity were incorporated using a parameter which interpolates between the several possible model-outcomes (see chapter 9). The assessment of this kind of uncertainty is much more complicated if it concerns some more fundamental choices in model formulation, like the number of state variables or spatial compartments, the time scale etc. An example of this kind of structural uncertainty was already given above in the phytoplankton/nutrient model with and without zooplankton; this category of uncertainty also includes "unforeseen circumstances" like the occurrence of new species in a system, unexpected geomorphological changes, etc.

To a large extent, structural uncertainty will be unavoidable as the number of choices to be made in the initial model formulation is very large, and there is no formal way of examining the effect of each of them, as is done in a sensitivity analysis for different parameter values. The only solution is to consider the assumptions carefully, especially in relation to the intended use of the model, and to state them clearly to the prospective user of the model.

The second kind of uncertainty is discussed in detail in chapters 9 and 10. In the present model, the following procedure has been followed to quantify and decrease the parameter uncertainty:

- formulate all parameter values as a range;
- calculate model-output uncertainty as a result of this;
- reduce parameter and model-output uncertainty by comparing calculated and observed values.

The procedure followed in the present report resembles to some extent the Bayesian approach in which both a priori knowledge on the parameter values and information based on observed output is used for an a posteriori parameter and model-output uncertainty estimation (Fedra et al., 1981; DiToro, 1984; Tarantola, 1987; Walters, 1986; Beck, 1987); it differs however in the emphasis placed on the model-objective oriented weighing of the output variables.

In practice a formal uncertainty analysis for more complicated models is seldom followed however. Beck states in his review (1987): "In the following review of the literature there is only one example of an approximate implementation of [the Bayes' equation] and no example of an maximum likelihood estimator applied without the assumption of Gaussian probability density functions." and: "Should such statistics be of interest, we may observe that DiToro and Van Straten (1979) and Van Straten (1983) can claim to have addressed one of the largest scale problems of estimation. They have used a 12-state variable model with in all, 20 parameters to be estimated."

It is probably a coincidence that in the present model a similar number of parameters (22) have been estimated. Although the problem seemed initially far more formidable with a number of 90 parameters (which would have been beyond the capability of available computer memory and time), the present model proved to conform to the observation of Hornberger and Spear (1981): "sensitivity analyses of large ecological models inevitably show that a surprising large fraction of the total number of parameters is simply unimportant to the critical model behavior".

The third kind of uncertainty, that concerning inputs, is here also understood to include boundary conditions, forcing functions and initial conditions. This kind of uncertainty is typically small for model runs using historical data (where inputs have been measured), but may increase dramatically for future scenarios when inputs have to be predicted also. Uncertainty of this type limits the predictive power of a model: if phytoplankton dynamics in some system are determined completely by the weather (solar radiation, suspended sediment as a function of wind speed, nutrient inputs from precipitation and runoff) then the best predictions of phytoplankton dynamics would be worse than the predictions of future weather, because there would be also parameter and model-structure uncertainty in addition to the weather-uncertainty. The question may be raised whether it is worth the trouble to make a model of the biology if we cannot predict the weather anyway.

In practice however, the uncertainty in future inputs is not considered in ecological models as the model is not used to make absolute predictions, but rather conditional predictions: what will happen if a certain

management is applied to the system compared to the effect of another management under the same conditions? The situation may be compared to buying a raincoat of dubious quality: one is not interested in the chance to get wet on a particular day when wearing this coat (which is the product of the chance that it rains times the chance that the coat leaks) but rather in the chance to get wet if it rains, i.e. the quality of the raincoat only. If we want to differentiate between the effects of a high-nutrient scenario and a low-nutrient scenario, we will ordinarily keep the weather and other inputs fixed and change nutrients inputs into the model only. The interesting kind of uncertainty is then in the model predictions given these scenarios, i.e. the uncertainties of the first and second kind.

Although it is evident that predictions without an indication of their uncertainty are misleading, it is not so clear how to deal with the uncertainty in the decision process (Van der Meer, 1986; Walters, 1986). The typical approach is to base the decision on the most likely model outcome, and to be more conservative as the estimates are more uncertain. A more formal way of treating uncertainty is based on statistical decision theory (discussed by Walters, 1986), in which odds are placed on each possible model-outcome, and these odds are used in the decision making, for example by maximizing expected value (the average of the possible returns predicted by the model weighted by their odds) or by a "min-max" criterion (the management option is chosen whose worst possible outcome gives the highest return).

It seems that the formal approach to decision making is very difficult to realize for ecological models: in the first place, these models usually do not have a single value from which to calculate a return (like income per capita or yield per hectare). The output is multivariate (nutrients, phytoplankton, oxygen etc.), and we could furthermore consider minimum, maximum, average levels of each output-variable. In order to use a formal decision procedure the output would have to be weighted somehow into a single number (Anonymus, 1986). The second step is the calculation of an uncertainty level for the possible model-outcomes. This question has been addressed in some detail in the present report, but it should be realized that the uncertainty-estimates are very uncertain in themselves. This does not cause problems if we use uncertainty in a more or less relative sense (e.g., which variables can be predicted with more or less accuracy; how large is the uncertainty in the predictions compared to the expected difference between two scenarios), but it seems dangerous to base further calculations on these estimated uncertainties. Thirdly, it will be difficult to decide which criterion should be used for the decision (maximize expected value, minimize risk, etc.). It may be concluded that formal methods can not be applied yet to most ecological decision problems.

## SUMMARY AND CONCLUSIONS

In this chapter models for ecological systems have been classified on the basis of their purpose as scientific/qualitative, scientific/quantitative and applied. Models of natural ecosystems are usually unsuitable for hypothesis testing, and as such could be called unscientific; they can be justified however by their applied use.

The emphasis on application makes it usually necessary to develop a new model for a specific system and a specific problem; a generally applicable model of e.g. all temperate estuaries is not possible. A preliminary version of the model may be used as a learning tool; it may also be used to indicate research priorities.

Uncertainty in model predictions is usually restricted to uncertainty in parameter estimates: uncertainty in model structure can not be quantified, and uncertainty in future inputs is usually irrelevant as the model is used for predictions given a certain input. The role of uncertainty in the decision making process is at present qualitative and informal; ecological models are not suitable (yet) for the techniques of statistical decision theory.



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## Appendix 1 COMPARISON OF FILTERFEEDER ACTIVITY WITH OBSERVED GROWTH

### A1.1 Introduction

In this appendix a simple model of the activity of the cockle (*Cerastoderma edule*) and the mussel (*Mytilus edulis*) is compared with data on individual weights in the Oosterschelde in order to test whether the model describes the observed growth satisfactorily, and to obtain a parameter estimation for the filterfeeder sub-model in the Oosterschelde simulation model. An improved estimate of the parameters describing the activity of cockles and mussels is of considerable importance: this activity has a large influence on the carbon cycle, and the ranges of parameters obtained from literature data are often very wide. For example: if filtration is proportional to  $W^{0.3}$ , the activity of the cockle population per unit of biomass is approximately (depending on size-distribution) 2 times as high as in the case that filtration behaves as  $W^{0.7}$ .

The activity of mussels has received a great deal of attention, both in the literature and in the Oosterschelde biological research. Some attempts have been made to incorporate the available data into a model (Bayne, 1976; Bayne and Newell, 1983; Verhagen, 1982). The reason to develop a new model for the present case is that there are several papers containing data that do not agree with these models. Probably not because the existing models are "wrong", but because a great deal of local, temporal and individual variation in mussel activity exists. Therefore, it is attempted to incorporate this variability in the model in the form of an uncertainty range for the parameters. To keep the number of parameters manageable, and also in view of the considerable uncertainty, the model has been kept as simple as possible, containing only the most important relations in previous models. Of the parameters that evolve, ranges based on literature data will be given.

For the cockle, the same model structure appears to be applicable as for the mussel, although with different parameter values. In this case literature data are more scarce, resulting in wider ranges.

### A1.2 The activity model

#### Introduction

The energy budget of macrobenthic filterfeeders is summed up by Bayne and Newell (1983):

$$C = P + G + R + F + U \quad (A1.1)$$

with: C - gross consumption (the amount of food filtered from the water)

P - somatic production (growth)

G - reproductive output (spawning)

R - respiration

F - egestion (faeces + pseudofaeces)

U - excretion

The excretion of organic matter (e.g. slime) forms part of the digestion process and is usually small; in practice it is included in measurements of faeces and pseudofaeces.

The production-term is to be calculated from the remaining terms in the budget. For these, a formulation relating them to body-size and environmental variables is sought.



### Clearance rate

The gross consumption term in the budget (clearance rate times food concentration) is the most relevant for the carbon- and nutrient cycles in the ecosystem. A description of clearance rate as a function of body-size, temperature and seston concentration is discussed in the chapter 7. The relevant equations are:

$$CR_{T..} (W) = a W^b \quad (A1.2)$$

with:  $CR_{T..} (W)$  - clearance rate in  $l.h^{-1}$  for temperature  $T$   
and seston concentration  $S$  as a function of  
weight

$W$  - body weight (gram dry flesh weight)  
 $a, b$  - coefficients

$$CR_{w..} (T) = CR_{w..} (15) e^{(T-15)/10 \ln(Q_{10})} \quad (A1.3)$$

with:  $CR_{w..} (T)$  - clearance rate for some specific weight  
and seston concentration as a function of  
temperature ( $l.h^{-1}$ )

$T$  - temperature in  $^{\circ}C$   
 $Q_{10}$  - specific increase for 10  $^{\circ}C$  temperature  
increase, e.g.:  $Q_{10} = 2$  means a two-times  
higher activity at 15  $^{\circ}C$  than at 5  $^{\circ}C$ .

$$CR_{T.w} (S) = CR_{T.w} (0) e^{-q S} \quad (A1.4)$$

with:  $CR_{T.w} (S)$  - clearance rate for some fixed  
body weight and temperature ( $l.h^{-1}$ ) as a  
function of seston concentration

$S$  - seston concentration ( $mg.l^{-1}$ )  
 $q$  - coefficient ( $l.mg^{-1}$ )

### Pseudofaeces

Mussels and cockles reject part of the filtered material as pseudofaeces. This fraction is zero below a certain threshold and increases asymptotically with seston concentration to 100% (Foster-Smith, 1975a). A simple model of pseudofaeces production is given by Verhagen (1982) and Bayne and Newell (1983): above the pseudofaeces threshold, ingestion remains constant; the rest of the filtration becomes pseudofaeces (see fig. 7.6).

There are several differences between pseudofaeces and faeces: the first is rejected before ingestion, the latter after, they look different and are ejected from different parts of the animal. This makes it possible to collect and analyze them separately. The main difference from an ecosystem-viewpoint would seem to be that the pseudofaeces is rejected in the same composition as the seston, whereas faeces consists only of material that cannot be used by the mussel. This view of a non-selective rejection of the pseudofaeces by mussels is supported by Foster-Smith (1975a,b), Bayne (1976) and Winter (1978). However, it was found by Bayne et al. (1977) that mussels may show selection; Kiorboe and Mohlenberg (1981) and Prins and

Smaal (1987) found that both cockles and mussels are able to select phytoplankton relative to natural inorganic material: the fraction of chlorophyll in ingested particles was 3-9 (mussels) and 4 (cockles) times higher than in the water.

The wide range in selectivity that these authors found could be explained by morphological adaptation of the animals: selection occurs at the labial palps, and animals living in very turbid waters showed relatively larger labial palps and a greater ability to select particles than animals in clearer water. Investigations by Essink and coworkers (1986) showed that animals are able to adapt themselves to the turbidity of the water by increasing or decreasing their relative palp-size. This adaptation requires a period of several weeks.

The possible ability to select particles may have a large effect on our understanding of the ecology of the filterfeeders. This can be illustrated using the "classical" view of a-select formation of pseudofaeces: a fixed ingestion above a relatively low concentration of seston implies that the amount of food available for the mussel is generally proportional to the fraction of food particles in the seston. The model therefore predicts that a turbid environment is detrimental to mussels. This would imply for instance that the decreasing turbidity in the Oosterschelde as a result of the storm-surge barrier would be beneficial to mussel growth (assuming the same food concentrations).

In the present model the possible ability to select material from the pseudofaeces is described using the concept of aselect pseudofaeces. For this aselect pseudofaeces (PSFCON) the model of Verhagen will be used (see figure 7.6), i.e.: initially, ingestion increases with seston concentration, but above the pseudofaeces-threshold, ingestion remains constant, and the remainder of the filtered material is rejected. Using the same pseudofaeces-threshold as Verhagen (1982) or Bayne and Newell (1983), this results in the standard pseudofaeces model. If the animal is capable of selecting part of its food from the pseudofaeces, this can be described by splitting the pseudofaeces in a part which is not selected (PSFCON) and a part from which all organic material is removed. An increasing selection efficiency can now be modelled by increasing the PSFCON-threshold: the animal is capable of removing an increasing fraction of the organic material from the pseudofaeces. A threshold above the range of observed seston levels results in the absence of PSFCON: in this case the animal selects all food from the pseudofaeces and the entire filtration is used in the calculation of assimilation (see below).

Pseudofaeces threshold concentrations are reported by Foster-Smith (1975a): 2 mg.l<sup>-1</sup> for the mussel and 3-3.5 mg.l<sup>-1</sup> for the cockle. In a review by Winter (1978) pseudofaeces-free cell densities of 30-40 .10<sup>6</sup> cell.l<sup>-1</sup> (Phaeodactylum: 2-3 mg.l<sup>-1</sup>) and 35-40 .10<sup>6</sup> cell.l<sup>-1</sup> (Platymonas suecica, approximately 2.5-3 mg.l<sup>-1</sup>) are given. There seem to be insufficient data to derive a body-weight dependency, as used by Bayne (1976). The present model will use a aselect pseudofaeces threshold in the range of 2 to 75 mg.l<sup>-1</sup> for both cockle and mussel. The upper limit (75) is above observed seston concentrations in the Oosterschelde, and thus represents the absence of aselect pseudofaeces formation.

#### Assimilation efficiency and particle concentration

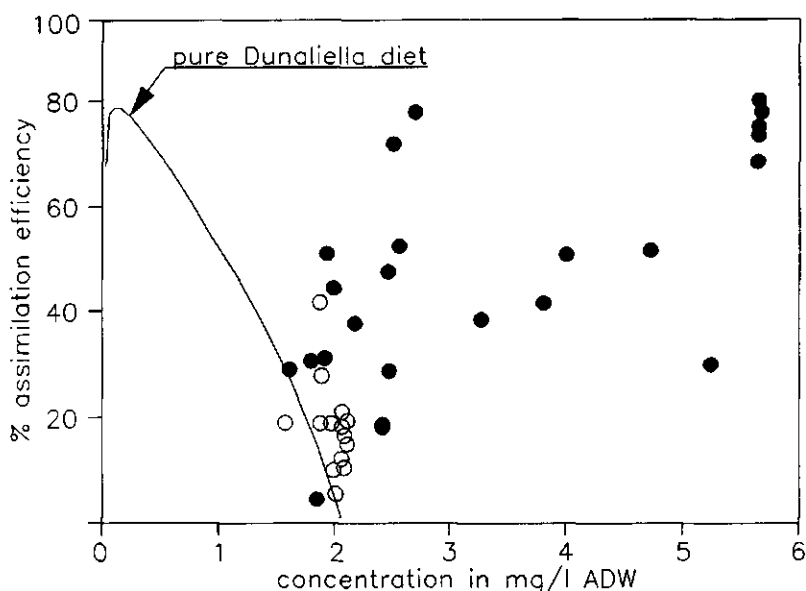
A fraction of the ingested food is assimilated. Of this process, there are in general two models (Taghon, 1981): assimilation efficiency is a fixed fraction, or it decreases with increasing ingestion.

A problem with the interpretation of the results in the literature is that two definitions of assimilation efficiency are used for the same term. In the first (the standard) definition, assimilation efficiency (AE) is calculated relative to the ingestion only. Using the second definition, assimilation efficiency (AE') is calculated relative to the entire filtration, i.e.: both faeces and pseudofaeces are lumped. Although usually the first definition is purported to be used, in practice the faeces and pseudofaeces are often collected together, which implies the use of the second definition (Smaal, pers. comm.).

The use of the two definitions has serious consequences for some of the reported relations between particle concentration and assimilation efficiency. Taking the view of an absence of, or at least a limited selectivity at the pseudofaeces level, it follows AE' decreases with increasing pseudofaeces formation, i.e.: with increasing particle concentrations. The papers of Widdows and Bayne (1971), Widdows (1978) and Bayne et al. (1984) describe a decreasing assimilation efficiency with increasing particle concentration, but probably use the second definition (AE'). In the following discussion it will be assumed that all papers that do not explicitly mention the exclusion of pseudofaeces are probably using the second definition.

In some papers an increase of assimilation efficiency with food concentration is reported. Stuart (1982) uses the second definition of assimilation efficiency (AE') and reports an increase in AE' with particle concentration for the mussel Aulacomia ater. A similar increase (using the first definition however) is reported for the mussel Perna perna by Berry and Schleyer (1983). Bayne et al. (1987) report a remarkably sharp increase of AE with organic ingestion, from approximately -50% at 0.07 mg organic ADW/l to +70% at 0.5 mg/l. A similar increase in assimilation of both cockles and mussels in the Oosterschelde was found by Prins and Smaal (1987). The results of Bayne et al., Prins and Smaal may possibly be explained by the very low food concentrations that they use (<1% to 25% of natural concentrations), causing a relatively large contribution of the excretion term to the food-budget, which leads to the negative values of AE. However, the fact that AE-values found at 10-25% of the normal food concentration are already normal (50-70%), confirms the observation by Berry and Schleyer (1983) that excretion is usually negligible.

In other experiments, a decrease in assimilation efficiency with food concentration is reported. Foster-Smith (1975b) describes a decrease in AE from over 90% to 50% with increasing ingestion of Phaeodactylum tricornutum culture. His results were not influenced by the addition of aluminum particles. However, it is possible that his results can be attributed to the fact that a pure algal culture was the only food source. It is shown by Griffiths (1980) for the mussel Choromytilus meridionalis that the relation between AE and ingestion is different for natural food (mainly detritus) and pure cultures: see figure A1.1.



**Figure A1.1:** (from Griffiths, 1980): Assimilation efficiency for the mussel *Choromytilus meridionalis* when feeding on natural detritus in field (closed symbols) and laboratory (open symbols). The curve of assimilation efficiency when feeding on pure *Dunaliella primoluta* is given for comparison.

Other papers report no relation between assimilation and food concentration. Thompson (1984) found no relation between AE' and (natural) food concentration for *Mytilus*, and Hawkins and Bayne (1985) and Smaal (1985) obtained the same result for AE.

Finally, it should be mentioned that some of the experiments under laboratory conditions may show transient effects which are actually artifacts: Bayne et al. (1987) found different AE-values for populations from sites of different turbidity; these differences disappeared after two weeks acclimation. This may imply that some of the decreases or increases in AE with food concentration found in short-term experiments are the result of using mussels adapted to different food-concentrations, e.g.: there is a decrease in AE with ingestion, but a number of short-term experiments are performed at relatively low seston concentrations with animals adapted to high concentrations, which thus show an increase in AE with concentration).

In conclusion, it seems that there is little evidence to support a relation between ingestion and assimilation efficiency for *Mytilus edulis*. Most of the results can be attributed either to a calculation of assimilation efficiency on the basis of both pseudofaeces and faeces, or to different laboratory artifacts (pure algal cultures, very low food concentrations or unacclimated animals). In the present model, a value independent of ingestion is used.

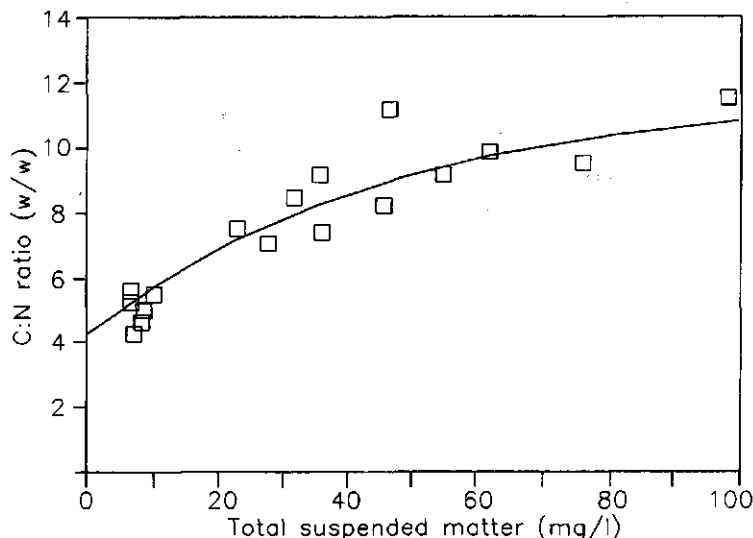
Data on the assimilation efficiency of the cockle (*Cerastoderma edule*) are scarce: there are only the papers by Foster-Smith (1975b), Newell and Bayne (1980) and Vonck and Smaal (1985). Again, Foster-Smith reports a decrease in efficiency from 90 to 50% with increasing ingestion of *Phaeodac-*

tylum/alumina mixtures. The other authors, using natural seston, find no such relation. In the model an assimilation efficiency independent of ingestion is assumed.

#### Assimilation and diet

In the previous discussion assimilation efficiency was related to the ingested amount of organic matter in general. It is also possible to distinguish between assimilation of different fractions of the diet: e.g. N-compounds and C-compounds, or algae and detritus.

In the chapter on mineralization detritus was distinguished in a labile and a refractory part, defined by its role as a possible food-source for bacteria; it is generally found that the refractory detritus has a lower N-content. In the Oosterschelde there is a close correlation between POC-concentration in the water and total seston content (Elgershuizen, 1983): apparently a large part of the POC is associated with the sediment. Data on N/C-ratios in the Oosterschelde are scarce, but the work by Gols (1987) shows a clear negative correlation between N/C-ratio and seston concentration. This supports the hypothesis that the sediment-associated detritus is refractory. It seems plausible that this refractory detritus cannot be digested by the zoobenthos; this is confirmed by the results of Prins and Smaal (1987) who found a marked decrease in carbon-AE as a result of the addition of suspended sediment but a much smaller decrease in nitrogen-AE. It appears that in general the N-assimilation efficiency is higher than that of carbon (Hawkins and Bayne, 1985). Stated otherwise, carbon may be for a substantial part refractory; nitrogen not or at least less so. In conclusion, it seems probable that assimilation efficiency is positively related to the N/C-ratio; this relation is incorporated in the model by means of the distinction between labile and refractory detritus.



**Figure A1.2:** (from Gols, 1987) relation between suspended matter content and C/N-ratio in the Oosterschelde.

A possible further distinction between the assimilation of algae and labile detritus appears to be unnecessary; there is no evidence to assume a

higher assimilation efficiency for algae. A comparison between feeding on algae and detritus showed that a diet of pure algae is inhibitory for the assimilation of mussels. It is possible that this inhibition is caused by the fact that the culture is pure, and would disappear in a mixed culture. The assimilation efficiency of mussels and cockles feeding on (almost) pure detritus is normal to high (Griffiths, 1980; Stuart, 1982; Smaal, 1985; Vonck and Smaal, 1985), with the exception of (sediment-associated) refractory detritus discussed above. This seems to leave little room for a possibly even higher assimilation efficiency of mixed algal cultures.

#### Assimilation efficiency: other factors

Data on a relation between body size and assimilation efficiency for filterfeeders are conflicting. Widdows (1978) reports an increase in AE' with body size for *Mytilus*. However, Winter (1978), Bayne and Newell (1983) and Smaal (1985) did not find any relation for *Mytilus*. For the cockle we have only the work by Vonck and Smaal (1985), who found no relation between body size and assimilation efficiency. For Tunicates, Van den Hurk mentions literature results showing a relation between body size and AE, but did not find any relation in the Oosterschelde.

In general no relation is found between temperature and assimilation efficiency. Widdows (1978) and Thompson (1984) found no relation for *Mytilus*; this relation was absent also for the cockle *Cerastoderma edule* (Newell and Bayne, 1980). Widdows and Bayne (1971) and Bayne and Newell (1983) found a slight decrease with temperature in *Mytilus*. Winter (1978) report that there is no relation between AE and temperature for the mussels *Modiolus modiolus* and *Arctica islandica* in the natural range of temperature, but a slight increase at a (high) temperature of 20 °C. In the Oosterschelde, Smaal (1985) and Vonck and Smaal (1985) found no relation for either the mussel or the cockle. In the model, AE is described as independent of temperature.

From the previous discussion no consistent description of assimilation efficiency for cockles and mussels as a function of ingestion, food composition, body size and temperature emerges. In the model the AE is treated as a constant. Literature values of AE (not AE'!) are listed in table A1.1 they show a very wide range of approximately 5 to 90 per cent; the single paper treating cockles and mussels simultaneously (Foster-Smith, 1975b) shows no difference in assimilation efficiency between the two species. It is possible that the assimilation efficiency is, in fact, a constant, and that the wide range of reported values reflects experimental problems (note the scatter in figure A1.1); it is also possible that the possible determining factors discussed above do explain most of the variation, but that the functional relation is obscured by experimental artifacts or, finally, that there are still other factors determining AE which have not been considered. Clearly, these questions can be resolved only by additional experiments: at present, there is no basis for a more complicated model of assimilation efficiency than a simple constant.

**Table A1.1:** Assimilation efficiency of cockles and mussels.

Only literature data in which pseudofaeces is explicitly mentioned or where labeled food is used are included to avoid confusion with AE'.

Species	AE (range in %)	reference
<i>Choromytilus meridionalis</i>	2 - 90	Griffiths (1980)
<i>Perna Perna</i>	30 - 90	Berry & Schleyer (1983)
<i>Mytilus edulis</i>	38 - 50	Hawkins & Bayne (1985)
..	5 - 55	Foster-Smith (1975b)
..	-73 - 78	Bayne et al. (1987)
<i>Cerastoderma edule</i>	5 - 55	Foster-Smith (1975b)
..	79 - 83	Vonck & Smaal (1985)

### Respiration

In this section the respiration of cockles and mussels is discussed in relation to filtering activity, particle concentration, body size and temperature.

The respiration of filterfeeders is closely connected with filtering activity. During short-term variations in filtering activity, respiration increases or decreases also. However, as the present model is concerned with the daily average of clearance rate and respiration (the "routine rate"-Bayne, 1976), the short-term relation between these two processes is not relevant: on a seasonal basis, a correlation between the two processes is not always found (Widdows, 1978; Thompson, 1984). The significant correlation between the two processes that was found by Newell and Bayne (1980) can perhaps be better explained by a simultaneous dependence on other factors (e.g., body size, temperature).

An increase in respiration with increasing concentrations of algal suspensions was reported by Widdows and Bayne (1971) and Widdows (1978). However, for natural food sources, no such relation was found (Widdows et al., 1979; Newell and Bayne, 1980; Stuart, 1982; Berry and Schleyer, 1983; Thompson, 1984). In the model, the respiration is treated as independent of seston concentration.

The relation between body weight and respiration is expressed in the same manner as in equation A1.3:

$$R_c = x W^y \quad (A1.5)$$

with  $R_c$  - respiration in ml  $O_2 \cdot h^{-1}$  at some fixed temperature

$W$  - dry body weight in gram

$x, y$  - coefficients

The values that were obtained for the coefficients  $x$  and  $y$  for mussel and the cockle are listed in tables A1.2 and A1.3.

**Table A1.2:** Literature values for the coefficients relating respiration ( $\text{ml O}_2 \cdot \text{h}^{-1}$ ) to body weight (dry flesh weight):  $R_e = x W^y$  for the mussel Mytilus edulis. To make a comparison easier, the respiration for a 0.8 g mussel has been calculated.

x	y	$R_{(w=0.8g)}$	$t^\circ\text{C}$	reference:
0.70	0.66	0.60	16	Bayne (1976)
0.52	0.93	0.42	15	,,
0.32	0.70	0.27	15	,,
0.56	0.60	0.49	12	,,
0.26	0.72	0.22	15	,,
0.55	0.77	0.46	15	,,
0.16	0.67	0.14	15	,,
0.34	0.70	0.29	15	,,
0.37	0.75	0.31	10	,,
0.57	0.51	0.51	12	Bayne et al. (1977)
0.56	0.36	0.52	18	,,
0.52	0.38	0.48	20	,,
0.44	0.35	0.41	8	,,
0.30	0.72	0.26	8	,,
0.33	0.49	0.30	9	,,
0.69	0.44	0.63	12	,,
0.63	0.84	0.52	16	,,
0.42	0.28	0.39	15	,,
0.47	0.66	0.41	17	,,
0.34	0.50	0.30	16	,,
0.25	0.81	0.21	10	,,
0.35	0.77	0.29	9	,,
0.55	0.59	0.48	8	,,
0.24	0.67	0.21	5	Widdows (1978)
0.28	0.62	0.24	10	,,
0.21	0.67	0.18	10	,,
0.30	0.70	0.26	15	,,
0.41	0.60	0.36	20	,,
0.55	0.58	0.48	25	,,
0.37	0.75	0.31	10	Review by Winter (1978)
0.32	0.70	0.27	15	,,
0.55	0.77	0.46	15	,,
0.26	0.72	0.22	(winter)	Review by Bayne & Newell
0.16	0.67	0.14	(summer)	,, (1983)
0.42	0.87	0.35	?	,,
0.40	0.78	0.34	?	,,
0.23	0.71	0.20	7	Thompson (1984)
0.10	1.04	0.08	2	,,
0.17	1.04	0.13	0	,,
0.21	0.82	0.17	5	,,
0.23	0.28	0.22	8	,,
0.42	0.86	0.35	15	,,
0.27	0.60	0.24	11	,,
0.28	1.11	0.22	9	,,
0.13	0.40	0.12	4	,,
0.16	0.96	0.13	0	,,



**Table A1.3:** Literature values for the coefficients relating respiration ( $\text{ml O}_2 \cdot \text{h}^{-1}$ ) to body weight (dry flesh weight):  $R = x W^y$  for the cockle *Cerastoderma edule*.

To make a comparison easier, the respiration for a 0.4 g cockle has been calculated.

x	y	$R_{(W=0.4)}$	t°C	reference:
0.37	0.77	0.18	10	review by Winter (1978)
0.58	0.43	0.39	16	Newell & Bayne (1980)
0.67	0.66	0.36	16	„
0.40	0.30	0.30	14	„
0.20	0.09	0.18	9	„
0.67	0.85	0.31	8	„
0.49	1.00	0.20	8	„
0.66	0.38	0.47	7	„
0.60	0.34	0.44	12	„
0.55	0.81	0.26	13	„
0.65	0.23	0.53	14	„
0.68	0.75	0.34	13	„
0.41	0.53	0.25	?	review by Bayne & Newell
0.20	0.44	0.13	?	„ (1983)

Tables A1.2 and A1.3 show an increase in respiration with temperature for both mussel and cockle. Linear regression yields a  $Q_{10}$  for mussel respiration of 1.84 (95% confidence interval: 1.48-2.27) and for cockles of 1.62 (conf. interval: 0.77-3.41). The values of parameters x and y were not correlated.

In addition to the general data in table A1.2 there are a number of papers specifically investigating the relation between temperature and respiration for the mussel. Again a distinction should be made between "acute" and acclimated temperature response: for the present, only the latter is of interest. Widdows and Bayne (1971) found no significant temperature effect in the range 10-20 °C; Bayne (1976) mentions unpublished data by Bayne and Widdows which would show a "relative independence" of temperature. Widdows (1973) found  $Q_{10}$ -values for acclimated respiration in a temperature range of 10-25°C of 1.3-1.7. A range in  $Q_{10}$ -values from 1 (no effect) to 2.5 summarizes the available information. For cockles we have to rely on the scarce data from table A1.3 only.

A final remark concerns the calculation of the respiration in units of carbon: this is required for a comparison with the other terms in the food-budget (eq. A1.1). Hawkins and Bayne (1985) give a range of 0.38 to 0.53 mg C·ml  $\text{O}_2^{-1}$ , thus increasing the uncertainty of respiration rate. The resulting ranges are indicated in table A1.4.

Table A1.4: uncertainty range and average value for parameters x and y (at 15 °C) in equation A1.5 and Q10-value.

Parameter x' equals x, but is expressed in mg C.h<sup>-1</sup>.

	min:	avg:	max:
mussel: x	0.39	0.45	0.51
x'	0.12	0.20	0.27
y	0.20	0.67	1.10
Q <sub>10</sub>	1.0	1.84	2.5
cockle: x	0.53	0.63	0.75
x'	0.20	0.29	0.40
y	0.23	0.54	1.00
Q <sub>10</sub>	0.77	1.62	3.41

#### Reproductive effort

In the process of spawning a considerable fraction of the body weight is released. Furthermore, respiration is high during the spawning period. Bayne (1976) relates the fraction of the weight that is spawned each season to approximately the square of body weight:

$$S = 0.073 W^{1.79} * 100\% \quad (A1.6)$$

with: S - yearly fraction of bodyweight spawned (%)  
W - dry body weight in g

The reproductive effort is highly variable between different populations of mussels (Bayne, 1976). In the model a range from 0.01 to 0.80 is used for the proportionality constant in A1.6 (the factor 0.73 of Bayne) for mussels, and 0.02-0.5 for cockles.

#### Effects of aerial exposure

The influence of aerial exposure on filterfeeders in the Oosterschelde is limited to cockles and juvenile mussels. These groups are immersed approximately 18 hours per day (Coosen and Smaal, 1985).

The effects of exposure on clearance rate, assimilation and respiration are discussed by Widdows and Shick (1985). It appears that there is no effect on assimilation efficiency. Of course, clearance stops during exposure, but the mussel recovers again soon after immersion. For the cockle, recovery is slower, but after 30 minutes 75% of normal clearance is already reached (Widdows and Shick, 1985). In the model, daily clearance is therefore proportional to immersion time.

The effect of exposure on respiration is different for cockles and mussels. Cockles are able to respire in air. They show a reduced respiration of 50 to 75 % of aquatic rate (Widdows and Shick, 1985). Mussels keep their shell closed in air. They possess a facultative anaerobic metabolism and show a strongly reduced metabolism during aerial exposure (14 to 20% of aquatic

rate -Widdows and Shick, 1985). Taking this reduced respiration into account the model calculates daily respiration rate for e.g. a cockle that is immersed during 75% of the day as  $88 (0.75 \times 100 + 0.25 \times 50)$  to  $92 (0.75 \times 100 + 0.25 \times 75)$  per cent of aquatic respiration.

### A1.3 Calibration to field data

#### Methods and data

The present application of the filterfeeder-activity model differs from that in main model because here, weight is a state variable (in the main model it is a forcing function) and all other variables (the state variables in the main model) are forcing functions. For this purpose, measurements of POC, temperature, chlorophyll and suspended matter (obtained from the Rijkswaterstaat routine sampling stations; measuring interval 2-4 weeks) were interpolated. The conversion of chlorophyll to carbon was assumed constant ( $C:Chl = 40$ ; in the main model this is a function of light and nutrient conditions, see chapter 3), and the fraction of labile detritus is a parameter to be calibrated (in the main model labile and refractory detritus are two state variables, see chapter 5).

The cockle weights were collected every two weeks at three sites: two in the mouth (on the Roggenplaat R6 and R20) and one in the eastern compartment (on the Hooze Kraayer HKA). The sampling procedures are described by Schoenmaker (1985) and Pouwer (1985).

An analysis of the growth of a population of "wild" mussels on an intertidal station in compartment 4 is given by Craeymeersch et al. (1986). They obtained weight-data indirectly from an analysis of growth-rings (giving a relation between shell-length and shell-growth) and an analysis of the seasonal pattern in the relation between shell-length and ash-free dry weight. Combining these relations, the development of individual biomass shown in figure A1.14 is obtained: it appears that this curve has the same shape as the curve in figure 7.4, which gives growth of cultivated mussels in the Oosterschelde, but apparently growth on commercial beds is much better: "wild" mussels take longer to reach their adult weight, which is moreover considerably lower than that of cultivated ones. Although the curve in figure 7.4 is "synthetic" (not obtained from a data set like that of Craeymeersch et al.), the data on initial and adult weights, development time and so which were obtained from mussel-growers (Coosen and Schoenmaker, 1985) are probably quite reliable. Because the large difference between the data by Craeymeersch et al. and the "synthetic" curve, both curves have been used to calibrate the model, which allows a comparison between the different parameter values thus obtained.

For the cockles data from 1984-1985 were used. The growth-ring data of Craeymeersch et al. go back for approximately 7 years from 1984; The cockles weights form a single series per site; the three sites were treated separately.

The procedure followed for calibration is explained in detail in chapter 10. Briefly, an initial range is indicated for every parameter and an acceptable range around the observed data for the model-behavior. Initially, parameter values are chosen at random and independently from all parameter ranges, i.e. all combinations of different parameters values within their ranges are equally likely. For every set of parameters the model-output is compared with observed values, and from this the deviation between model and data is calculated. By rejecting parameter-sets with a high deviation the initial random-search is gradually changed into a search in the neighborhood of the optimal parameter sets, and the initial indepen-

dence of the values for different parameters in a set is replaced by the observed interdependency of the parameters (e.g.: it is possible that both a high and a low clearance give acceptable model-output, but only in combination with a high and low respiration, respectively). The calibration procedure ends with a number of parameter-sets that show model-behavior within the initially specified range. From this calibrated parameter range it is possible to see which part of the initial uncertainty range leads to acceptable model-behavior, whether there are correlations between the parameters, and so on.

In the calibration, 11 physiological parameters were varied:

**Table A1.5:** parameters in activity models for cockles and mussels

no:	name	dim.	meaning:
1	ACLR	$l.h^{-1}$	a-value in $CR=aW^b$ at 15 °C, no seston
2	ARES	$mg\ C.h^{-1}$	a-value in $R=aW^b$ at 15 °C
3	ASPW	(-)	b-value in $CR=aW^b$
4	BCLR	(-)	b-value in $CR=aW^b$
5	BRES	(-)	b-value in $R=aW^b$
6	DETRED	(-)	fraction labile detritus
7	EFFPOMQ	(-)	assimilation efficiency
8	PSFCON	$(mg\ l^{-1})$	aselect pseudofaeces concentration
9	Q10CLR	(-)	Q10 for clearance rate
10	Q10RES	(-)	Q10 for respiration rate
11	SESQM	$(l.mg^{-1})$	reduction in clearance from seston

The initial ranges for the parameters were (see chapter 7 and previous section):

no:	name:	initial range:	
		mussels	cockles
1	ACLR	1.0 - 4.8	1.5 - 5.0
2	ARES	0.12 - 0.27	0.2 - 0.4
3	ASPW	0.02 - 0.8	0.02 - 0.7
4	BCLR	0.1 - 0.8	0.4 - 0.7
5	BRES	0.2 - 1.1	0.23 - 1.0
6	DETRED	0.0 - 1.0	0.0 - 1.0
7	EFFPOMQ	0.05 - 0.95	0.05 - 0.95
8	PSFCON	2.0 - 75.	2.0 - 75.0
9	Q10CLR	1.0 - 3.0	1.0 - 3.0
10	Q10RES	1.0 - 2.5	0.8 - 3.4
11	SESQM	0.0 - 0.005	0.0 - 0.02

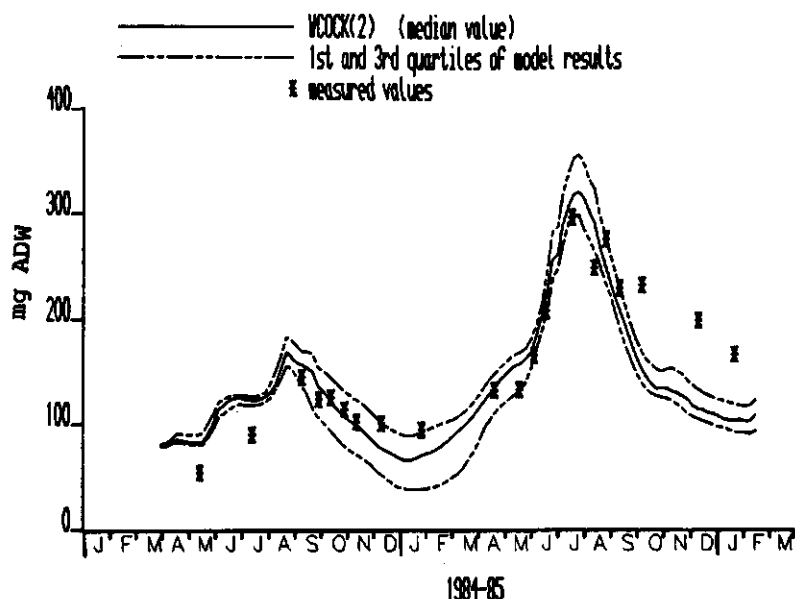


Figure A1.3: Results of simulated (using calibrated parameter values) and measured weights of cockles at station HKA (eastern compartment), yearclass 1983.

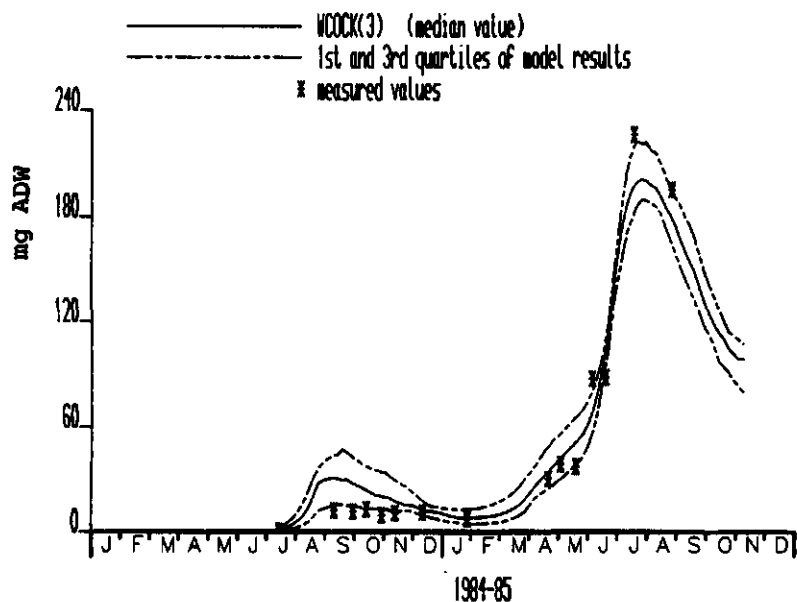


Figure A1.4: Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of cockles at station HKA (eastern compartment), yearclass 1984.

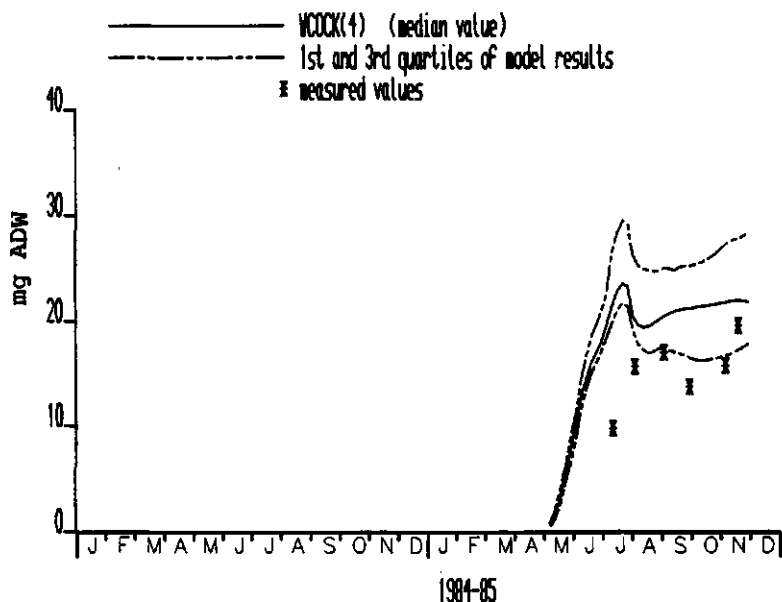


Figure A1.5: Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of cockles at station HKA (eastern compartment), yearclass 1985.

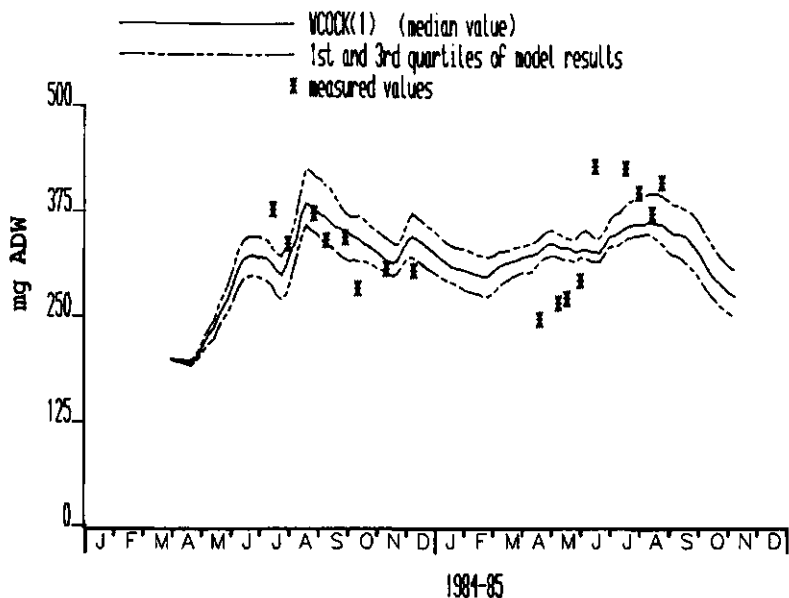


Figure A1.6: Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of cockles at station Roggenplaat-6 (western compartment), yearclass 1982.

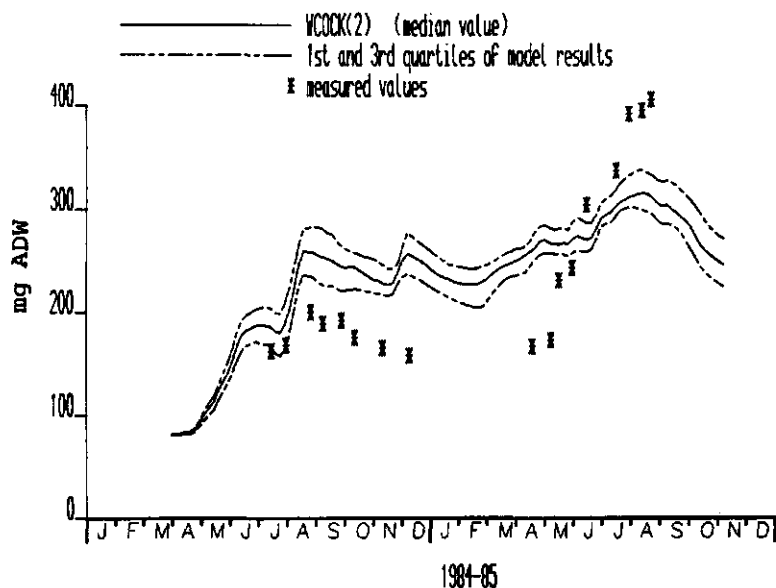


Figure A1.7: Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of cockles at station R6 (western compartment), yearclass 1983.

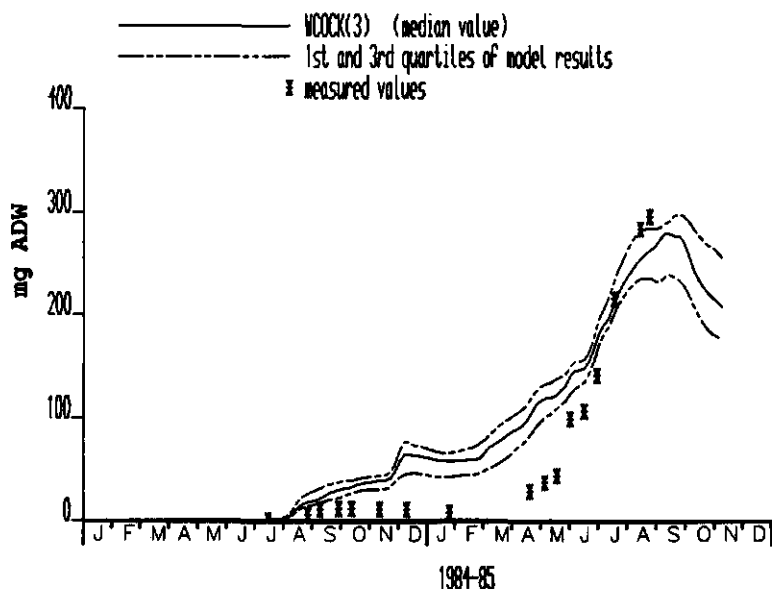
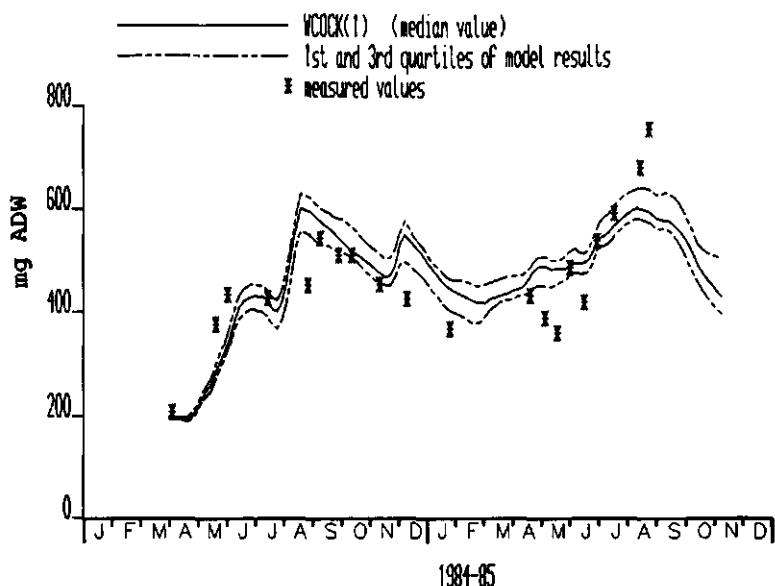
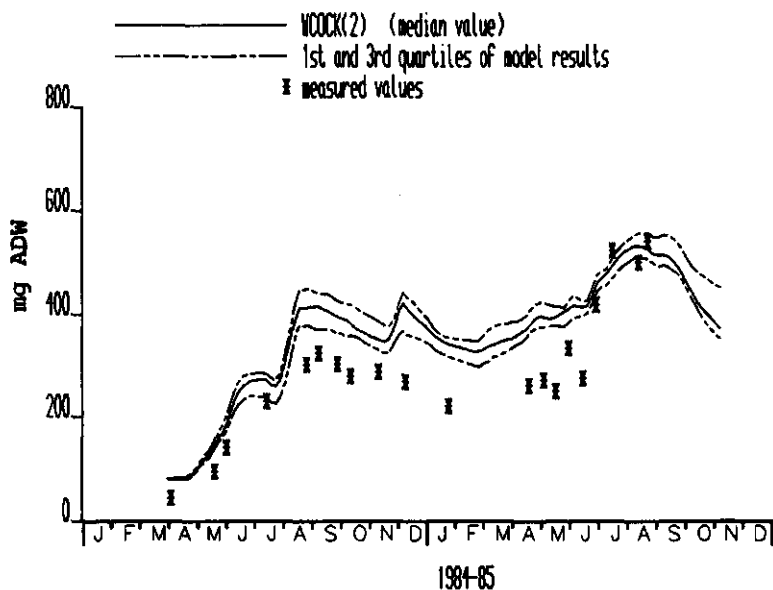


Figure A1.8: Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of cockles at station R6 (western compartment), yearclass 1984.



1984-85  
**Figure A1.9:** Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of cockles at station R20 (western compartment), yearclass 1982.



1984-85  
**Figure A1.10:** Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of cockles at station R20 (western compartment), yearclass 1983.



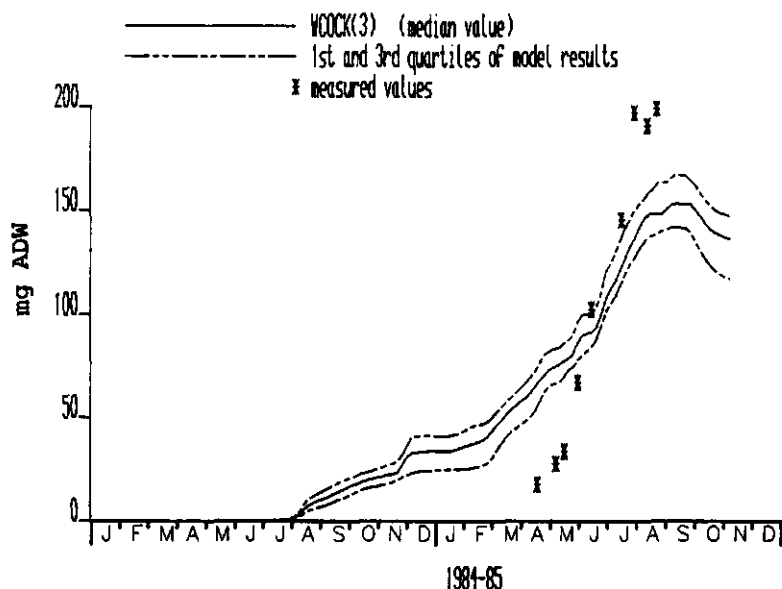


Figure A1.11: Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of cockles at station R20 (eastern compartment), yearclass 1984.

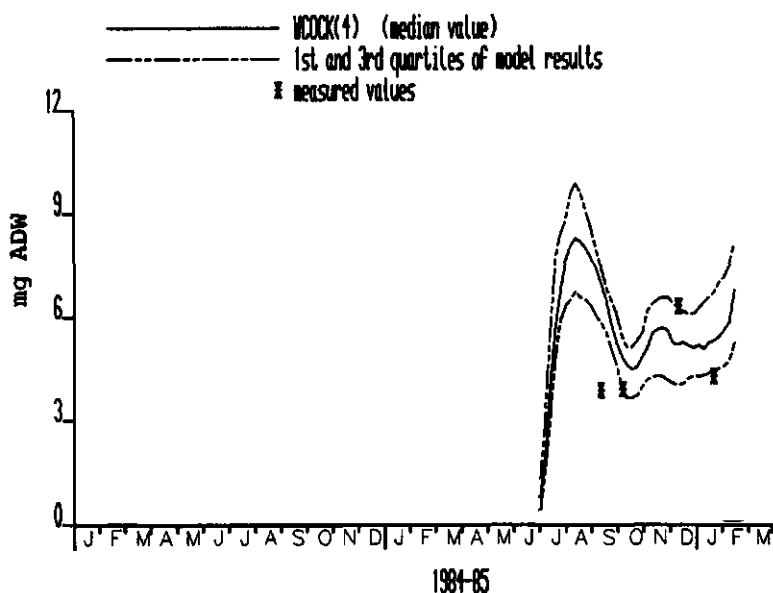


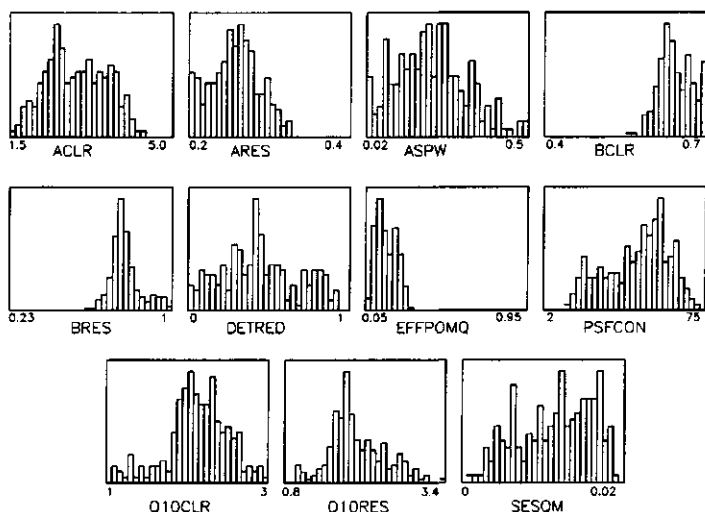
Figure A1.12: Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of cockles at station R20 (western compartment), yearclass 1985.

### Results: cockles

For the cockle data-set the calibrated model shows in general a satisfactory agreement with the observations (see figures A1.3-A1.12). The results for the comparison with the HKA population (figs. A1.3-5) is particularly good, although there seems to be a slight over-emphasis on seasonal dynamics in model-results as compared to field data. For the Roggenplaat stations, the reverse appears to be true, and the simulated seasonal pattern has too small fluctuations (in particular figure A1.7, but hardly in A1.9 however). Another systematic deviation for these stations are the too high simulated values for small cockles. The growth pattern of a cockle is mainly determined by the difference in allometric parameters for food-uptake and loss (Von Bertalanffy, 1968): the loss-processes (here respiration) tend to grow faster with body weight than the food-uptake. This results in a decrease in relative growth rate with weight, and a maximal weight, where loss equals gain. In the present model with fixed allometric coefficients, this implies that the maximal weight (which is more or less correct) together with the proportionality coefficients (a value in  $aW^b$ -relation) which determine average growth rate determine also the juvenile growth rate. The present results give a reasonable compromise between average growth rate (3-year old cockles do have the proper weight), maximal weight and juvenile growth. For an improvement of the results, a more flexible model would be required.

The parameter-sets that resulted from the cockle-calibration were significantly different for the three sites. These differences concerned mainly difference in the fraction of detritus assumed edible (parameter DETRED) and in assimilation efficiency (EFPOMQ). The model parameters obtained from comparison with the data-set in the mouth (Roggenplaat stations 6 and 20) showed in general a higher DETRED and a lower assimilation efficiency. In addition there were some small (but significant) differences in the allometric coefficients for respiration and clearance. In this respect, results from the site in the Eastern compartment did not differ from the results from Roggenplaat-6, but the two Roggenplaat stations showed significant differences.

An analysis of the differences in calibrated parameter ranges between the sites is outside the scope of this discussion; for the present purpose of reducing the uncertainty in input-parameters for the main model, only the combined range of parameter values is considered: if, for example, the ranges in assimilation efficiencies obtained from different calibrations would be 5-15%, 10-15% and 7-20%, then the range to be used in the main model would be 5-20%. The differences between the sites therefore diminish the overall reduction in parameter ranges. Despite this, there is a strong reduction in the ranges of most of the parameters, notably in the allometric coefficients for clearance and respiration, respiration rate and  $Q_{10}$ -values. The aselect pseudofaeces threshold is consistently higher than the actual pseudofaeces concentration of approximately  $2 \text{ mg.l}^{-1}$ : this means that the amount of not-selected pseudofaeces (PSFCON) is lower than the amount of pseudofaeces, pointing to a selection of organic matter from the pseudofaeces.



**Figure A1.13:** Frequency histograms of the calibrated parameter sets in the cockle calibrations. The x-axis shows the initial range for the parameters: an (approximately) homogeneous distribution over the initial range means that the parameter range is not reduced by calibration; a narrowly peaked distribution means that only the a limited range of values leads to an acceptable model-output. The abbreviations for the parameters are explained in table A1.5.

The reduction in uncertainty concerning the allometric coefficients is important, as most of the population consists of cockles much smaller than 1 g adw: for these low W's, the value of the expression  $a \cdot W^b$  (for clearance, respiration) depends strongly on the b-value, even more than on the a-value. Both the range of the Q10 for respiration and for clearance are reduced considerably.

Not reduced is the uncertainty concerning the effect of suspended matter concentration on clearance (parameter SESQM); however, if average seston concentration is 15 mg/l, then the effect of increasing SESQM from 0 to 0.02 is only a relatively minor reduction in clearance rate of 25% (equation A1.4). The ranges of the parameters DETRED (edible fraction of detritus) and ASPW (spawned fraction) are hardly reduced compared to initial range, but these do not play a role in the main model: the fraction of labile detritus is calculated in the model itself, and not an input-parameter, and the loss of weight as a result of spawning is incorporated in the empirical weight-curves (figures 7.2, 7.3).

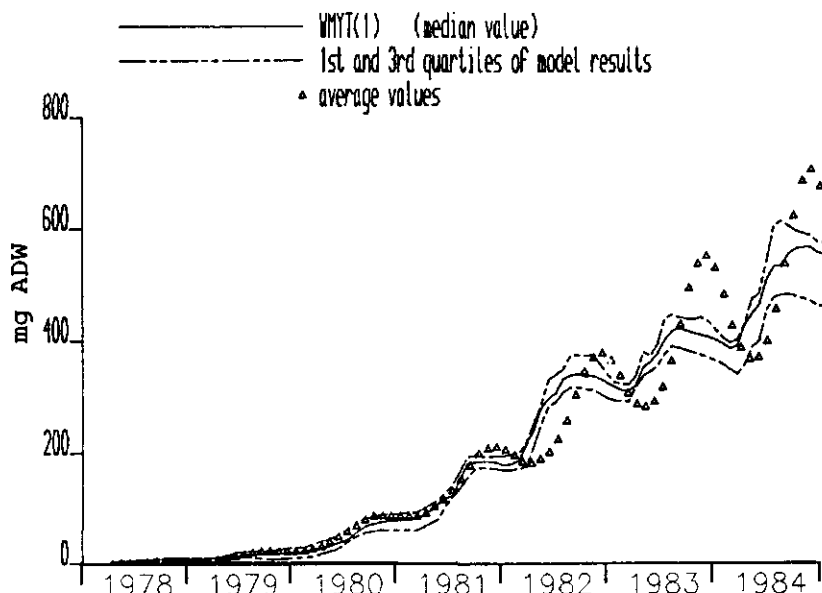


Figure A1.14: Results of simulated (using calibrated parameter values) and measured individual weights (in mg ash-free dry weight) of mussels. The data were obtained from the growth curve for an intertidal population of mussels published by Craeymeersch et al. (1986)

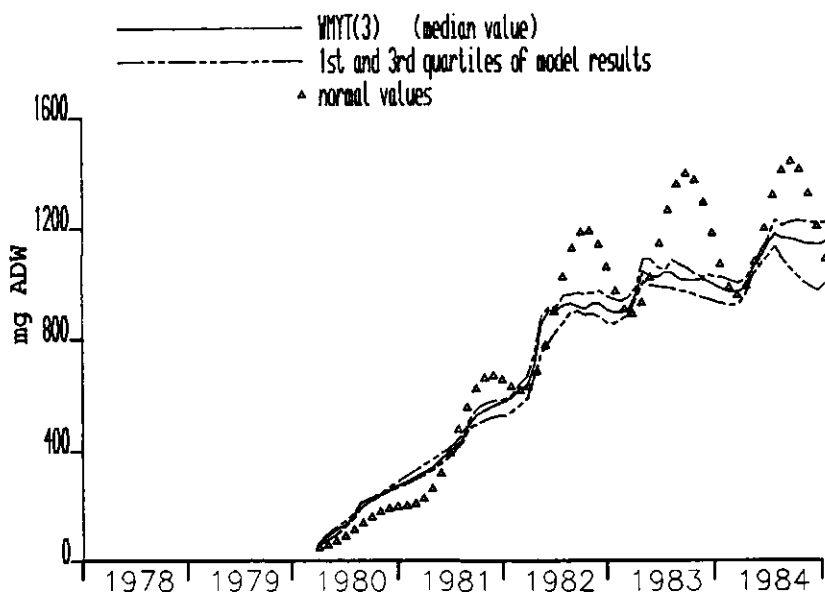


Figure A1.15: Results of simulated (using calibrated parameter values) and "normal" individual weights (in mg ash-free dry weight) of mussels. The "data" were obtained as a smooth curve on the basis of information from mussel growers (Coosen, pers. comm.).

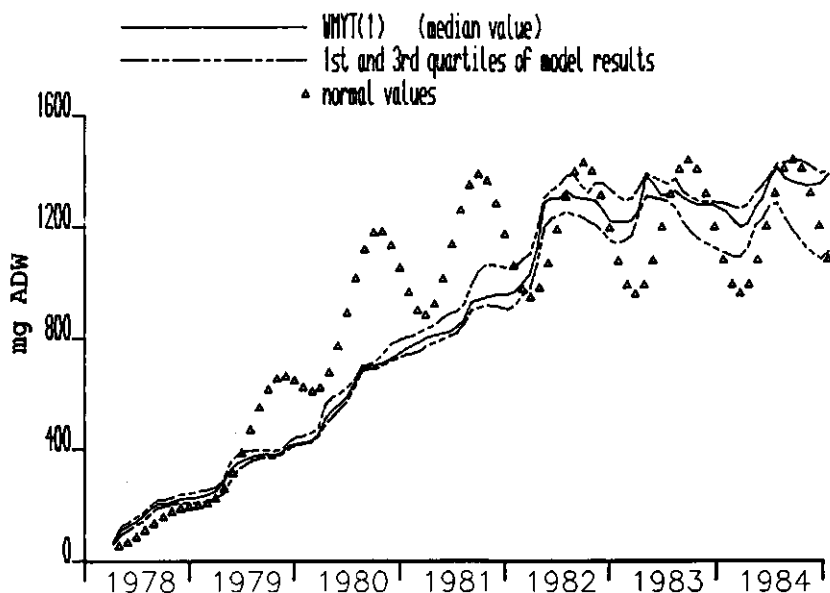


Figure A1.16: Results of simulated (using calibrated parameter values) and "normal" individual weights (in mg ash-free dry weight) of mussels. The "data" were obtained as a smooth curve on the basis of information from mussel growers (Coosen, pers. comm.).

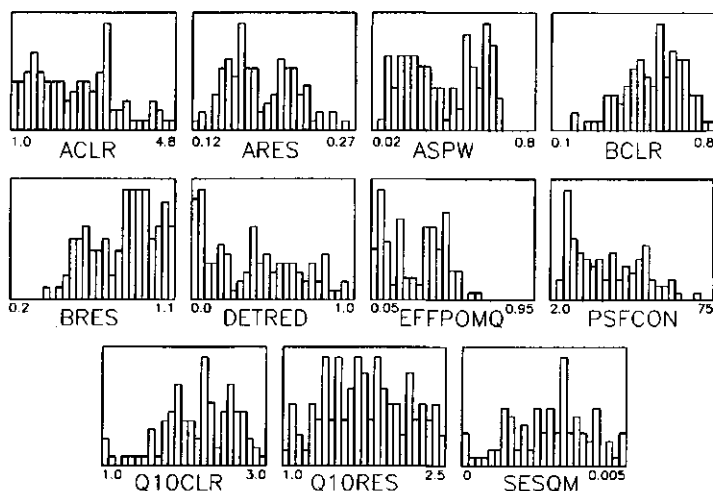
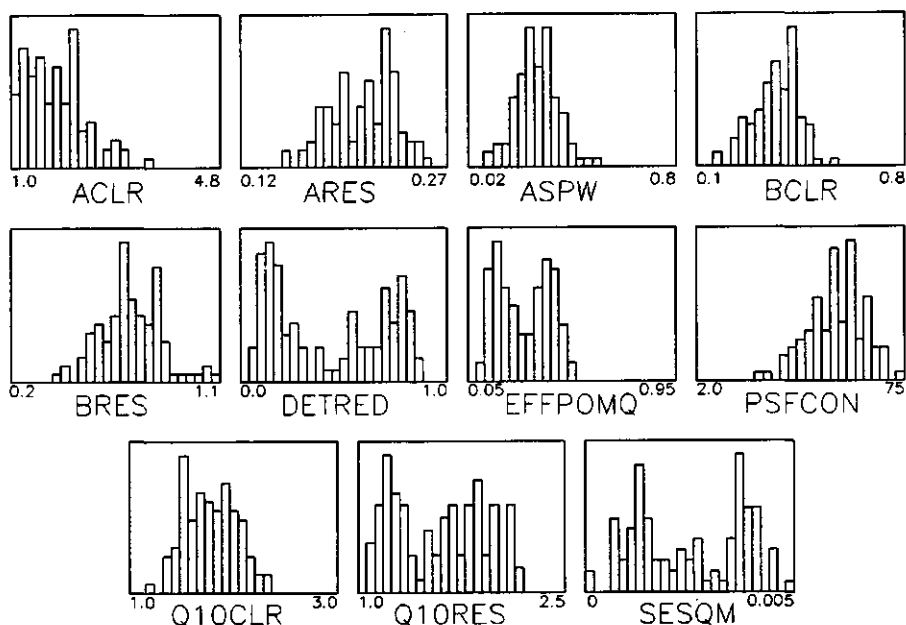


Figure A1.17: Frequency histograms of the calibrated parameter sets in the calibration of the mussel model to the data set by Craeymeersch et al. (1986). The x-axis shows the initial range for the parameters: an (approximately) homogeneous distribution over the initial range means that the parameter range is not reduced by calibration; a narrowly peaked distribution means that only a limited range of values leads to an acceptable model-output. The abbreviations for the parameters are explained in table A1.5.



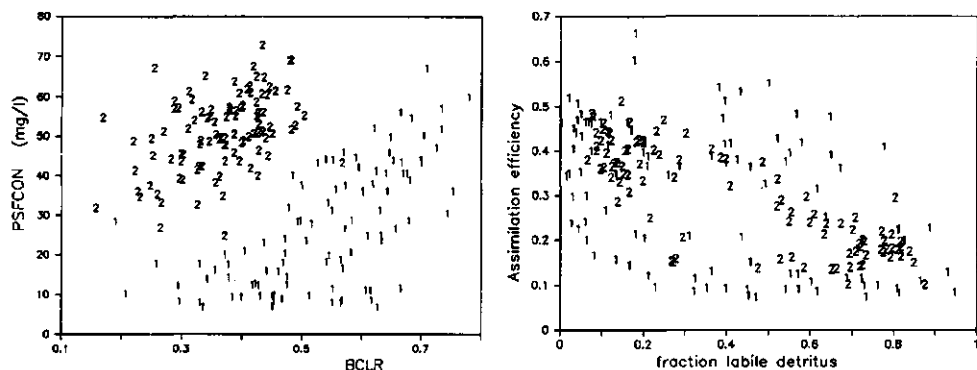
**Figure A1.18:** Frequency histograms of the calibrated parameter sets in the calibration to growth on cultivation plots. The x-axis shows the initial range for the parameters: an (approximately) homogeneous distribution over the initial range means that the parameter range is not reduced by calibration; a narrowly peaked distribution means that only the a limited range of values leads to an acceptable model-output. The abbreviations for the parameters are explained in table A1.5.

#### Results: mussels

The range of model-output from the calibrated set of parameters is shown in figures A1.14-A1.16. Both for the data set from Craeymeersch et al (1986) and for the growth-curves of cultivated mussels the agreement is satisfactory. It can be observed that average growth rate and maximal weights are reproduced fairly accurately, but that seasonal dynamics are less well reproduced. In particular the adult mussels tend to show a too early spring growth and insufficient decrease in winter. A probable explanation for this is the assumption that the carbon to chlorophyll ratio is a constant. According to calculations with the main model, the phytoplankton contains 1.5 to 2 times more carbon per unit of chlorophyll in summer than in winter. This result is not in disagreement with measured values (which show a wide scatter however), but has not been used in the present model because the mussel-model was meant to provide input for the main model.

The calibrated ranges of the parameters are illustrated in figures A1.17 and A1.18. It appears that the most important differences between the calibrated parameter ranges are found in the allometric coefficients for clearance and respiration (BCLR, BRES) and in the aselect-pseudofaeces threshold (PSFCON). It appears that the proportionality coefficient ( $a$  in  $a \cdot W^b$ ) in the equation for clearance (ACLR) is generally higher for the Craeymeersch' data (which is unexpected, because they grow slower), but this is apparently compensated by the higher allometric coefficient ( $b$  in  $a \cdot W^b$ )

BCLR, which decreases the activity of the smaller mussels ( $W < 1$ ). Another difference between the two calibrations is the lower selectivity (lower a-select pseudofaeces threshold) obtained for calibration on the Craeymeersch' data, which also results in lower calculated growth rates. It can be observed that the model is over-parameterized, at least relative to the data; this results in correlations between the calibrated parameter ranges. For example, there is a positive correlation between the allometric coefficient in the clearance relation (BCLR) and the pseudofaeces-selection parameter (PSFCON): the first has a negative influence on calculated growth, the second a positive. It can be noted that a similar correlation exists between the two parameters for both calibrations, but on a different level (see figure A1.19). Another correlation is between the fraction of edible detritus (DETRED) and the assimilation efficiency: here both calibration give similar correlations and the averages are approximately equal also.



**Figure A1.19:** Illustration of some of the correlations between calibrated parameters in the mussel model. The points give parameter values with a similar fit; code 1 refers to the calibration to the Craeymeersch' data, code 2 to the average cultivated "data".

It appears that the difference in inundation time alone (the cultivated mussels grow sub-tidally, the Craeymeersch' mussels are inundated approximately 20 hours per day) is insufficient to explain the differences in growth rate, and that there are additional differences in physiological parameters between the mussel populations. Again, an analysis of the differences between parameter values obtained from the two data sets is outside the scope of the present discussion.

In the calculation of reduced uncertainties, only the calibration to the growth of cultivated mussels has been used, as cultivated mussels are by far the most abundant in the Oosterschelde (Coosen and Smaal, 1985). The ranges resulting from the calibrations are listed below.

no:	name:	calibrated range:			
		mussels		cockles	
1	ACLR	1.0	- 2.4	1.5	- 4.5
2	ARES	0.16	- 0.23	0.2	- 0.33
4	BCLR	0.2	- 0.5	0.6	- 0.7
5	BRES	0.45	- 0.9	0.7	- 1.0
7	EFFPOMQ	0.10	- 0.50	0.05	- 0.35
8	PSFCON	30.	- 70.	10.	- 70.
9	Q10CLR	1.4	- 2.2	1.8	- 2.7
10	Q10RES	1.0	- 2.0	1.2	- 2.2
11	SESQM	0.0	- 0.005	0.0	- 0.02



# APPENDIX II: parameter listing of model

Abbreviations for sub-models: b - microphytobenthos  
p - pelagial (phytoplankton, zooplankton)  
t - transport  
f - forcing functions  
z - zoobenthos

name	b	p	t	f	z	dimension	description	min	max	actual
ACOC						1 m3/d	A-value in A*W**B cockle clearance at 10 oC	0.024	0.091	0.046
ACMUS						1 m3/d	A-value in A*W**B mussel clearance at 10 oC	.03	.094	.033
AIRFAC						1 m/d	resorption coefficient	0.5	3.0	2.0
ARAT						1	coeff.descr.higher energy requir.algae comp.to diat.	1	?	2.7
AROC						1 gC/d	A-value in A*W**B cockle respiration at 10 C	0.0048	0.0096	0.007
AREALj						1 m2	cross section area between comp.i and comp.j			see comm
ARMUS						1 g C/g ADW/d	A-value in A*W**B mussel respiration	0.0029	0.0048	
AVC3(1)						1 g adv	av.biom.of cons. muss.comp. 3 in season '79/'80			4.0E8
AVC3(2)						1 g adv	av.biom.of cons. muss.comp. 3 in season '80/'81			3.9E8
AVC3(3)						1 g adv	av.biom.of cons. muss.comp. 3 in season '81/'82			10.7E8
AVC3(4)						1 g adv	av.biom.of cons. muss.comp. 3 in season '82/'83			16.8E8
AVC3(5)						1 g adv	av.biom.of cons. muss.comp. 3 in season '83/'84			8.8E8
AVC3(6)						1 g adv	Av. biom. of muss.in comp. 3 in year 1978+1Y			8.8E8
BCOC						1	b-value in A*W**B equation for Cockle clearance	0.6	0.7	0.64
BCE10COEF						1 d-1	mineralisation rate on bottom of tidal channels			0.01
BCHUS						1	B-par. in A*W**B for mussel & cockle-clearance	0.4	0.7	0.56
BIOTURQ						1 d-1/(gDPFD/m2)	bioturbation coeff.of depositfeeders in bottom			0.017
BLV1C						1 gC/m3	avg. summer conc.of benthic larvae in comp. 1 (west)	0.015	0.025	0.02
BLV3C						1 gC/m3	av. summer conc. of benthic larvae in comp 3 (east)	0.03	0.07	0.05
BN10COEF						1 d-1	denitr. rate in carbon /carbon /day units	0.		0.025
BOTFAC						1	switch to incr.total amount of silt-->bottom thickness	1		1
BOTRAT						1 1 1	ratio of microbial act.in bottom comp. with water	0	1	
BPRODQ						1 1/u/(W/m2)	production/biomass/intensity coefficient microph.benth.	0.001	0.1	0.085
BCROC						1	b-value in A*W**B cockle-respiration	0.23	1.00	0.54
BRESFRAC						1	fraction of phytobenthos production that is respired			0.05
BRESMIN						1 d-1	phytobenthos maintenance respiration (at PROD=0)			0.02
BRMUS						1	b-value in A*W**B mussel respiration	0.20	1.10	0.80
BSILT						1 1 1 1	ratio of near-bottom conc. of silt to surface conc.	1.90	2.04	1.97
CCHLB						1 ng C/ug Chlf	carbon/chlorophyl ratio of phytobenthos	0.016	0.029	0.040
CCHLMIN						1 ng C/ug CHL	min. carbon/chlorophyl ratio (nutfun=1; lincfun=0)	0.008	0.020	
CCOEFK1						1	coeff.for calc. extinction coefficient			0.054
CCOEFK2						1 m2/mg chlF	coeff. for relation extinction coeff. /chlorophyll			0.0088
CFLUX						1 g C/m2/d	CO2-flux at air/water interface	0.046	2.76	1.35
COCKMORT						1 1/d	mortality rate cockles	0.0029	0.0035	0.0036
CONSO(1)						1	fraction of consumption mussels in comp.1			see comm
CRTRATE						1 m3/d/g adv	clearance rate tunicate at 10 oC	0.024	0.05	0.038
CWIN10Q						1 d-1	mineralisation rate in water at 10 oC	0.004	0.13	0.045
CWRAT						1 gC/g adv	carbon/dry weight ratio	0.45	0.56	0.53
DATR200						1 d-1	max daily ration at 15 oC of Copepods	0.5	2.0	1.5
DAYSEC						1	total seconds in a day			86400
DCOEF						1 (gC/m2)-1 d-1	fr.of phytob. eaten /g dep.feeder /day at 20 oC			0.015
DEMITNC						1 gN/gC	N(O3)-cons.per unit of C-cons. in denitr.			1
DEPTH(1)						1 1 1 1 m	mean depth of comp. 1:12.15, 10.35, 3.86, 8.24			
DGRAZ						1 gC/m2/d	grazing by depositfeeders			
DIAMAX						1	maximum fraction of diatoms at border	DIAMIN	1	0.9
DIAMIN						1	minimum fraction of diatoms at border	0	DIAMAX	0.1
DINPMAX						1 gN/m3	maximum DIN in polderwater			7
DINPMIN						1 gN/m3	minimum DIN in polderwater			2
DINPR						1 gN/m3	mean conc. of DIN in precipitation			3
DINVMAX						1 gN/m3	maximum DIN in Veersemeer			2.0
DINVMIN						1 gN/m3	minimum DIN in Veersemeer			0.
DINZKMAX						1 gN/m3	maximum DIN in Zoom and at Kreekraksluices			6.16
DINZKMIN						1 gN/m3	minimum DIN in Zoom and at Kreekraksluices			2.88
DIS1j						1 m	distance between comp.i and comp.j			
DISINTCP						1 mm/month	polderwater discharge at net precipitation of zero			31.3
DISLITF						1	parameter in calculation cichlf ratio from LITFUN		1	0.6
DISP12						1 m2/sec	dispersion between comp.1 and comp. 2	220	232	226
DISP15						1 m2/sec	dispersion between comp.1 and North-sea boundary	362	384	373
DISP23						1 m2/sec	dispersion between comp. 2 and comp. 3	121	167	144
DISP24						1 m2/sec	dispersion between comp. 2 and comp. 4	355	365	360
DISP45						1 m2/sec	dispersion between comp. 4 and Volkerak boundary	214	218	215
DISSLOPE						1	fr. of net precipit.that is discharged from polders			0.34
DQALG						1 1 1 1	fr.of algae showing dissolved-like transp. behaviour	0.75	0.80	0.78
DQDET						1 1 1 1	fr.of detritus showing dissolved-like transp. behaviour	0.49	0.51	0.50
DQPSIL						1 1 1	"dissolved-like fraction" of particulate silicate	0	1	
DRYQ(1)						1	mean fr.of the day tidal flats are dry			see comm
DUMP						1 gC/d	used in scenario to add manure to comp. 2	0		0
EFFCOC						1	assimilation efficiency cockles	0.12	0.22	0.17

name	b	p	t	f	z	dimension	description	min	max	actual
EFFMUS						1 -	assimilation efficiency mussels	0.09	0.43	0.25
EFFZOO	1					-	assimilation efficiency zooplankton	0.40	0.90	0.80
EXTMAX						1 -	max.assimilation eff. Tunicates	0.85	0.95	
EXT3MAX	1					m3/sec	maximum extraction from comp.4 to Kreekraksluices			1.3
EXT3MIN	1					m3/sec	minimum extraction from comp.3 to Kreekraksluices			0.3
EXT4MAX	1					m3/sec	maximum extraction from comp.4 to Grevelingen			22.9
EXT4MIN	1					m3/sec	minimum extraction from comp.4 to Grevelingen			4.9
EXTMAXQ	1					-	max.exor. as fr. of gross prod. when nutrients are nil	0.01	0.70	0.55
EXTBACK						1 m-1	background extinction			0.44
FAECDFRAC	1					-	fr. of ingestion to faeces prod. by dep.feeders			0.60
FAECHFRAC	1					-	fr. of ingestion to faeces production by Hydrobia			0.40
FAECMFRAC	1					-	fr.of ingestion to faeces prod. by meiobenthos			0.72
FLATQ(I)	1					1 -	fr.of surface covered by tidal flats:49,.37,.71,.68			
HCOEF	1					(gC/m2)-1 d-1	fr. of phytob. eaten /g. hydrobia /day at 20 oC			0.017
HGRAZ	1					g C/m2/d	grazing by Hydrobia			
IOP10	1					W/m2	opt.light int. at 10 oC phytopl. photosynthesis	110	130	120
IOP10	1					W/m2	optimal light int.in phytob. prod. curva at 10 oC			80
JUVQ(I)	1					1 -	fr. of juvenila (seed+halfgrown) mussels in comp.I			see comm
KHDIN	1	1				g N/m3	Michaelis-Menten half-saturation conc. for DIN	0.005	0.2	
KMSIL	1	1				gSi/m3	Michaelis-Menten half-saturation conc.for silicium	0.002	0.1	
LONGDAY						hr	max. daylength			16.4
MAXSEEP	1					m3/sec	maximum of OS total of seepage to polders			2.0
MCOPF	1					(gC/m2)-1 d-1	fr. of phytob. eaten /g. meiobenthos /day at 20 oC			0.0067
MDPFED(I)	1					gC/m2	mean yearly dep.feeders biom.on tidal flats in comp (I)			see comm
MEYDROB(I)	1					gC/m2	mean yearly benthic graser biomass in comp (I)			see comm
MINSEEP	1					m3/sec	minimum seepage to polders			0.7
MHEIO	1					gC/m2	mean yearly meiobenthos biomass in Oosterschelde			see comm
MHRTQ	1					1/d	mortality rate mussels			2.93E-4
MRTQ	1					1/((gC/m3).d)	mortality rate rate copepoda			5
MUFAC	1					-	fr. of LDET too small to eat (< 3 u) for zooplankton	0.12		0.28
NCOMS(1)						1 -	init.no. of cons.mussels (adult) E.S.in 79/80			
NCOMS(2)						1 -	init.no. of cons.mussels (adult) E.S.in 80/81			2.92E9
NCOMS(3)						1 -	init.no. of cons.mussels (adult) E.S.in 81/82			3.17E9
NCOMS(4)						1 -	init.no. of cons.mussels (adult) E.S.in 82/83			2.00E9
NCOMS(5)						1 -	init.no. of cons.mussels (adult) E.S.in 83/84			3.05E9
NCOMS(6)						1 -	init.no. of cons.mussels (adult) E.S.in 84/85			3.43E9
NCRAT	1	1				1 g N/g C	nitrogen/carbon ratio	0.06	0.20	
NHALF(1)						1 -	init.no. of halfgrown muss. E.S.in '79/'80			2.55E9
NHALF(2)						1 -	init.no. of halfgrown muss. E.S.in '80/'81			4.06E9
NHALF(3)						1 -	init.no. of halfgrown muss. E.S.in '81/'82			4.36E9
NHALF(4)						1 -	init.no. of halfgrown muss. E.S.in '82/'83			4.40E9
NHALF(5)						1 -	init.no. of halfgrown muss. E.S.in '83/'84			4.12E9
NHALF(6)						1 -	init.no. of halfgrown muss. E.S.in '84/'85			"
NSEED(1)						1 -	initial no. of seed mussels in E.S.in '79			2.03E10
NSEED(2)						1 -	initial no. of seed mussels in E.S.in '80/'81			2.51E10
NSEED(3)						1 -	initial no. of seed mussels in E.S.in '81/'82			2.58E10
NSEED(4)						1 -	initial no. of seed mussels in E.S.in '82/'83			1.25E10
NSEED(5,6)						1 -	initial no. of seed mussels in E.S.in '83/'84;84/85			2.09E10
NUTFAC						1 -	may be used for reduction in nutrient input scenario	0		1
OCRAT	1	1				1 g O2/g C	oxygen to carbon ratio	3.3	3.9	3.2
FACTQF	1					g C/m2	coef. in calc. of active fraction of phytobenthos			4.
PFLQWQ	1					-	interp.part.flows between Q'model and dissolved model	0	1	1
PLUS(I)						1 -	switch for scenarios with extra mussels in comp. I	0		0
PMAX10	1					ugC/ugC/h	PMAX at 10 C and no nutrient limitation	0.16	0.38	0.3
PMAXB10	1					1/h	max. production rate at 10oC			0.3
POLDAR(I)	1					m2	area of polder discharging on comp.I			see comm
PRECONV	1					-	precipit. conversion coeff. from mm/month to m/day			3.81E-10
PSFCMUS						1 g adw/m3	pseudo faeces threshold conc.	27	75	40
PSFCOC						1 g adw/m3	virtual pseudo faeces threshold conc. cockles	5	21	25
PSIL10	1	1				1/d	mineralisation rate of part. silicon at 10 oC	0.01	0.03	
PSINTC						1	intercept of corr.function seston and POC at sea			
PSSLOPE	1					g C/g adw	slope of corr.function seston and POC at sea			0.036
Q10ALG	1					-	Q10 non-diatoms	1.6	2.3	
Q10BP	1					-	Q10 microphytobenthos production			2.5
Q10COCC						1 -	Q10 cockle clearance	1.6	3.0	
Q10COCR						1 -	Q10 cockle respiration	1.1	1.9	
Q10DLA	1					-	Q10 for diatoms	1.6	2.3	
Q10GRAZ	1					-	Q10 of gras.by Hydrobia, dep.feeders, meiobenthos			2.
Q10MIN	1	1				-	Q10 for mineralisation	1.5	2.5	1.8
Q10MUSC						1 -	Q10-mussel clearance	1.1	3.0	2.0
Q10MUSR						1 -	Q10-mussel respiration	1.0	1.8	1.5
Q10PBRES	1					-	Q10 microphytobenthos respiration			2.
Q10ZIN	1					-	Q10 for zooplankton ingestion	1.5	4	4
Q10ZRS	1					-	Q10 of zoopl.respiration	1.5	3	2
QEXHAR	1					m3/sec	fixed extraction to Haringvliet from comp.5			
QINZOKR	1					m3/sec	fixed input from Zoom + Kreekraksluices into Oostersch.			5.21
QPCOSED	1					-	ratio RDET incr. at surface to SILT export-erosion			0.05
RESFRAC	1					-	fraction of gross production that is respired	0.09	0.43	
RESQMIN	1					d-1	min.diatom resp.at 10 oC	0	0.09	
RESQZ	1					1/d	respiration rate zooplankton	0.05	0.25	0.05

name	b	p	t	f	z	dimension	description	min	max	actual
RFRACP	1	-	-	-	-	-	refractory fraction of POC in sea and Volkerak	0.8	0.95	0.90
SALPOL	1	-	-	-	-	o/oo	salinity of polderwater			6.3
SALPR	1	-	-	-	-	o/oo	mean salinity in precipitation			0.04
SALVEER	1	-	-	-	-	o/oo	salinity in Veersemeer			21.7
SALZOKR	1	-	-	-	-	o/oo	salinity in Zoom and at Kraekraksluices			10.7
SOEFK	1	-	-	-	-	m2/g adw	seston-coeff.in calc.of extinction coefficient			
SEDLABQ	1	-	-	-	-	-	fraction labile POC in deep-bottom sediments	0	0.05	0
SEEPQ(1)	1	-	-	-	-	-	fraction of seepage in comp.1 compared with TOTSEEP			see comm
SESQC	1	-	-	-	-	m3/g adw	param.in reduction function cockle clearance SESFUNG	0	.004	.002
SESQM	1	-	-	-	-	m3/g adw	red.fact. seston clear.mussels	0	.005	.002
SETTLE(1)	1	-	-	-	-	-	avg. no. of cockles settling in comp. 1	1.7E11	5.7E11	3.8E11
SETTLE(2)	1	-	-	-	-	-	avg. no. of cockles settling in comp. 2	8.5E10	2.6E11	1.7E11
SETTLE(3)	1	-	-	-	-	-	avg. no. of cockles settling in comp. 3	1.6E10	4.8E10	3.2E10
SETTLE(4)	1	-	-	-	-	-	avg. no. of cockles settling in comp. 4	7.0E10	2.1E11	1.4E11
SFLOW1S	1	-	-	-	-	m3/s	particulate flow from comp.1 to comp.1	-450	1510	530
SFLOW21	1	-	-	-	-	m3/s	advective transport rate of particulate matter	-370	1130	380
SFLOW32	1	-	-	-	-	m3/s	advective transp.rate of particulate matter comp 3->2	-110	810	350
SFLOW42	1	-	-	-	-	m3/s	advective transp.rate of particulate matter comp 4->2	-120	1480	680
SFLOW54	1	-	-	-	-	m3/s	advective transp.rate of particulate matter comp 5->4	-20	260	120
SHORTDAY	1	-	-	-	-	hr	daylength of the shortest day			7.6
SICRAT	1	1	1	-	-	-	silicium carbon ratio	0.3	1.5	
SILICKMAX	1	-	-	-	-	gSi/m3	max.silicium content of Zoom and Kraekraksluices			3.77
SILICKMIN	1	-	-	-	-	gSi/m3	min.silicium content of Zoom and Kraekraksluices			0.65
SILICPR	1	-	-	-	-	gSi/m3	mean conc. of silicium in precipitation			0.12
SILICVMAX	1	-	-	-	-	gSi/m3	maximum silicium content of Veersemeer			3.77
SILICVMIN	1	-	-	-	-	gSi/m3	minimum silicium content of Veersemeer			0.65
SIPMAX(1)	1	-	-	-	-	gSi/m3	maximum silicium conc.of polderwater			see comm
SIPMIN(1)	1	-	-	-	-	gSi/m3	min.silicium conc.of polderwater disch. in comp. 1			see comm
SLOPE	1	-	-	-	-	(1/h)/(w/m2)	initial slope of production curve			0.004
SLOPECHL	1	-	-	-	-	((mgC/mgCHL)/h)/(W/m2)	slope phytoplankton	0.21	0.28	
SHORTO	1	-	-	-	-	-	initial seed mortality			0.78
SSB	1	1	-	-	-	-	switch to indicate presence (=1) of storm-surge barrier	0	1	0
SSBRAN	1	1	-	-	-	-	may be used to simulate uncertainty in some effects SSB	0	2	1
STARTYEAR	1	1	1	-	-	-	first year of simulation	'80	'86	
SURMAX(1)	1	-	-	-	-	m2	water surface at max.flood level (for calc.of prec)			see comm
SURNAP(1)	1	1	-	-	-	m2	wat.surf.at u.sea-level:94.7,96.2,99.8,31.9*10**6			
TDIAMAX	1	-	-	-	-	d	daynumber at which DIAFRAC is DIAMAX			20
TEXJMAX	1	-	-	-	-	d	daynumber max.extr. from comp.3 to Kraekraksluices			206
TEXJMAX	1	-	-	-	-	m3/sac	daynumber max.extraction from comp.4 to Gravelingen			195
TLONGDAY	1	-	-	-	-	d	dayno. longest day (June 21)			191
TMAXDINP	1	-	-	-	-	d	daynumber of maximum DIN in polderwater			
TMAXDINV	1	-	-	-	-	d	daynumber of maximum DIN in Veersemeer			30
TMAXDINZK	1	-	-	-	-	d	daynumb.of max. DIN in Zoom, Kraekraksluices			46
TMAXSEEP	1	-	-	-	-	d	daynumber of max.total seepage to polders (here 352)			352
TMAXSILICK	1	-	-	-	-	d	daynumber of max.Si cont.of Zoom and Kraekraksluices			44
TMAXSILICV	1	-	-	-	-	d	daynumber of max.Si1 content of Veersemeer			15
TMAXSIP(1)	1	-	-	-	-	d	daynumber of max.Si conc.polderwater			see comm
TSILT(1)	1	-	-	-	-	g/m2	fixed amount total silt (bottom + suspended) in comp. 1	970		1000
TSILT(2)	1	-	-	-	-	g/m2	fixed amount total silt (bottom + suspended) in comp. 2	635		660
TSILT(3)	1	-	-	-	-	g/m2	fixed amount total silt (bottom + suspended) in comp. 3	245		265
TSILT(4)	1	-	-	-	-	g/m2	fixed amount total silt (bottom + suspended) in comp. 4	604		625
TUNIC(1)	1	-	-	-	-	g ADW	biomass of hard-substrate filterfeeders comp. 1			1.0E9
TUNIC(2)	1	-	-	-	-	g ADW	biomass of hard-substrate filterfeeders comp. 2			1.9E8
TUNIC(3)	1	-	-	-	-	g ADW	biomass of hard-substrate filterfeeders comp. 3			1.7E8
TUNIC(4)	1	-	-	-	-	g ADW	biomass of hard-substrate filterfeeders comp. 4			3.8E8
VOL(1)	1	1	-	-	-	m3	volume compartment 1: 1.15;0.996;0.386;0.262 km**3			
WETMCONS	1	-	-	-	-	-	fraction of day adult mussel under water		1	1
WETMHAF	1	-	-	-	-	-	fraction of day half-grown mussel under water	0.7	0.8	0.75
WETMSEED	1	-	-	-	-	-	fraction of day musselseed under water	0.7	0.8	0.75
WINDLRATE	1	-	-	-	-	1/d	coefficient to calculate WINDL from WINDFAC	0.		0.
WMAXQ	1	-	-	-	-	-	used in calculation of mussel weights			1.2
WMINQ	1	-	-	-	-	-	used in calc. of av.seasonal develop.of musselwt.			0.8
Y,TA-YD	1	-	-	-	-	(various)	parameters in empirical description of cockle -weight			

## SAMENVATTING

In 1976 werd besloten de aanvankelijk geplande gesloten dam in de Oosterschelde mond te vervangen door een afsluitbare stormvloedkering, aangevuld met twee kleinere gesloten dammen achterin het estuarium (compartimenteringsdammen). Deze constructies geven een compromis tussen verschillende tegenstrijdige belangen met betrekking tot het Oosterschelde gebied: het land achter de dijken moest beschermd worden tegen een herhaling van de overstromingsramp van 1953, en wel zo snel mogelijk; de unieke natuur en de schelpdier kwekerij in het gebied moesten behouden blijven en de scheepvaart tussen Rotterdam en Antwerpen moest een getijde-vrije doorvaart hebben. In 1987 werd de stormvloedkering in gebruik genomen, en enkele maanden later werden met het klaarkomen van de compartimenteringsdammen de Oosterscheldewerken afgesloten.

Op het moment dat de beslissing werd genomen de Oosterschelde half-open te houden waren alle betrokkenen weliswaar overtuigd van het unieke karakter van het gebied (het enige relatief schone getijdegebied in Nederland) en het belang van de mosselkwekerij voor de lokale economie, maar over kwantitatieve aspecten van het ecosysteem en de bedrijfsvoering in de mosselkwekerij en van relaties tussen ecosysteem en de mosselkwekerij was nog erg weinig bekend. Tegelijk met de voorbereiding voor de bouw van de kering werd dan ook een onderzoekprogramma gestart om de voedselkringloop in de Oosterschelde te kwantificeren. Het onderzoek was een samenwerkingsverband tussen de Deltadienst van Rijkswaterstaat en het Delta Instituut voor Hydrobiologisch Onderzoek. De ontwikkeling van een mathematisch model was onderdeel van dit onderzoek.

Doelstelling van het model-onderzoek was tweeledig: enerzijds een ondersteuning van het veld- en laboratoriumonderzoek door de resultaten van verschillende deelonderzoeken onder één noemer te brengen (de koolstofkringloop), en ze zo beter vergelijkbaar te maken. Dit maakt het mogelijk het relatieve belang van verschillende processen te vergelijken en eventuele lacunes op te sporen. Anderzijds ondersteunt het model het beheer van de Oosterscheldewerken: door met het model verschillende scenario's door te rekenen kan het effect van voorgenomen ingrepen of een bepaald beheer vooraf worden beoordeeld.

Het model beschrijft de stromen van koolstof, stikstof, silicium en zuurstof in waterkolom en bodem van de Oosterschelde. De grote diversiteit aan soorten wordt gereduceerd tot een beperkt aantal toestandsvariabelen, door een groot aantal groepen (vooral van de hogere trofische nivo's) weg te laten, en anderen te combineren tot een. De ruimtelijke diversiteit binnen de Oosterschelde wordt beschreven door vier compartimenten: oost, midden, west en noord. Binnen elk compartiment wordt verder een onderscheid gemaakt tussen waterkolom, intergetijdebodem en onderwaterbodem. De procesbeschrijvingen in elk compartiment zijn dezelfde, hoewel ze onderling verschillen in diepte, troebelheid, oppervlakte, etcetera.

In het transport-submodel wordt het transport van opgelost en zwevend materiaal tussen de compartimenten onderling en tussen de Oosterschelde en de grenzen van het systeem (de Noordzee in het westen, en het Volkerak in het noorden) beschreven. De belangrijkste problemen die hiervoor moeten worden opgelost zijn: de schatting van de uitwisseling van opgeloste stof tussen de compartimenten, de beschrijving van het transport van zwevende stof, en de schatting van de parameters in de hiervoor gekozen beschrijving.

Het fytoplankton vormt de belangrijkste groep van primaire producenten in de Oosterschelde. In het fytoplankton-submodel worden de brutoproductie en

de verliesprocessen van deze groep beschreven. Hierbij zijn vooral de invloed van de lichtintensiteit onder water en nutriëntenconcentraties op het chlorofylgehalte van de algen, en de invloed van verticale menging en morfologie van het bekken op de kolom-gemiddelde productie van belang. Het fytoplankton wordt beschreven door twee toestandsvariabelen: diatomeeën en andere algen. Het fysiologische verschil tussen de twee groepen is dat alleen diatomeeën silicium voor hun groei nodig hebben; het ecologische verschil tussen de twee groepen is dat alle ongewenste soorten (bijvoorbeeld slijm-producerende of toxische soorten) tot de tweede groep behoren. Op deze manier kan de fractie van diatomeeën worden gebruikt als een indicator voor de fytoplankton "kwaliteit".

In het zoöplankton-submodel wordt het zoöplankton verdeeld in twee groepen: het echte zoöplankton (d.w.z.: dieren die hun hele levenscyclus in het water doorbrengen) en de larven van benthische dieren. De eerste groep is een toestandsvariabele in het model, de tweede groep wordt gemodelleerd als een tijdserie. De biomassa en graasactiviteit van beide groepen zijn in de Oosterschelde gemeten; de beschrijving van andere processen (respiratie, assimilatie) is gebaseerd op literatuurgegevens.

De mineralisatie van organisch detritus in de waterkolom is gemodelleerd door een eenvoudige eerste-orde formulering. Hierin worden de microbiota en de meiofauna met het dode organische materiaal samengevoegd tot één toestandsvariabele, het "labiele detritus". Daarnaast is er een toestandsvariabele die het niet-afbreekbare (refractaire) detritus beschrijft. Bij de schatting van de afbraak-coëfficiënt uit zuurstof-consumptie en POC-afbraak-experimenten is het moeilijkste probleem de schatting van de hoeveelheid substraat, d.w.z. de labiele fractie van het detritus.

De mineralisatie in de bodem wordt afzonderlijk beschreven, als onderdeel van het microfytobenthos-submodel. De productie en afbraak van organisch materiaal zijn direct gekoppeld, omdat gedurende het grootste deel van het jaar de benthische diatomeeën ofwel nutriënt- ofwel CO<sub>2</sub>-gelimiteerd zijn: de aanvoer van deze stoffen is grotendeels afkomstig van mineralisatie in het sediment waarop de diatomeeën groeien.

De biomassa van mosselen, kokkeis en andere bodemfauna worden beschreven door een tijdserie in het model. Deze wordt (voor de mosselen) geschat uit marktgegevens en (voor het overige zoöbenthos) uit veldopnames. Er bestaat een uitgebreide literatuur over de activiteit van filterfeeders, met name over de mossel. Op een aantal belangrijke punten bevat deze literatuur echter tegenstrijdigheden, bijvoorbeeld op het gebied van de invloed van temperatuur, van zwevend sedimentgehalte, en over de mogelijkheid voedsel uit het gefiltreerde materiaal te selecteren. In het macrobenthos-submodel wordt geprobeerd het model zó te formuleren dat de verschillende literatuurgegevens vertaald kunnen worden in een parameter-range: bijvoorbeeld de invloed van temperatuur variërend van 'geen effect' tot 'een tamelijk sterk effect' kan worden uitgedrukt als een temperatuur coëfficiënt (Q<sub>10</sub>) tussen 1 en 3.

Om de stromen van stikstof, silicium, koolstof en zuurstof in het model met elkaar te verbinden zijn conversiefactoren nodig. In het model worden deze conversiefactoren constant verondersteld. Ze worden geschat op basis van literatuurgegevens.

Het model zoals geformuleerd op basis van de proceskennis uit Oosterschelde en literatuurgegevens is slechts een halfproduct: in de eerste plaats is er vaak een grote onzekerheid in de formulering, die hier uitgedrukt wordt als een parameter-range (voorbeeld: bovenbeschreven range voor de Q<sub>10</sub> van mosselen). In de tweede plaats is het vanzelfsprekend nodig te

controleren of het model de werkelijke Oosterschelde correct beschrijft vóór het te gebruiken om de gevolgen van een scenario te berekenen.

Het effect van onzekerheid in de parameterwaarden is gekwantificeerd door een Monte Carlo analyse: door het model een groot aantal malen te laten lopen met "at random" geselecteerde waarden voor de parameters binnen hun range wordt een range van modeluitkomsten verkregen. Hieruit is het mogelijk te bepalen welke parameters het meeste invloed hebben op de modeluitkomsten (de meest gevoelige parameters).

De resultaten van de gevoeligheidsanalyse worden gebruikt in de modelcalibratie. Uit de volledige range van de parameters resulteert een wijde range modeluitkomsten. Bijvoorbeeld jaargemiddelde waarden van het chlorofylgehalte van 1-50  $\mu\text{g/l}$ . De werkelijke range van waarden in het veld is veel beperkter (bijvoorbeeld 3-8  $\mu\text{g/l}$ ). Deze nauwere range komt overeen met een gedeelte van de oorspronkelijke range van de parameters. Op die manier wordt door een vergelijking met veldgegevens de oorspronkelijke onzekerheid verkleind.

Het bepalen van dat gedeelte van de parameter ranges dat modeluitkomsten binnen de range van gemeten waarden oplevert is technisch een lastig probleem. In de eerste plaats is het aantal parameters waarover onzekerheid bestaat erg groot (90), in de tweede plaats zou het bepalen van alle op grond van de parameter-ranges mogelijke modeluitkomsten en daarna pas elimineren van onwerkelijke uitkomsten erg veel rekentijd vragen.

Daarom is allereerst op grond van de Monte Carlo analyse een selectie gemaakt van een beperkt aantal (20) parameters, die samen het overgrote deel van de onzekerheid in modeluitkomsten bepalen. Hierbij is met behulp van multivariate statistische technieken allereerst bepaald hoeveel verschillende typen modelgedrag kunnen worden onderscheiden, en vervolgens is een even grote groep parameters gekozen die elk een verschillend effect hebben op de modeluitkomsten. Alleen met deze groep is verder gerekend.

Bij het vinden van parameterwaarden die modeluitkomsten opleveren die overeenkomen met velddata is gebruik gemaakt van een techniek waarbij aanvankelijk at random wordt gezocht in het gebied van alle mogelijke parameterwaarden. Na verloop van tijd wordt het zoeken in gebieden die slechte modeluitkomsten leveren echter gestaakt, en in de goede gebieden geïntensiveerd. Zo blijkt het mogelijk om relatief snel de parameter ranges te verkleinen.

Deze gereduceerde onzekerheid wordt vervolgens gebruikt in de berekeningen van de gevolgen van scenario's. Hierbij wordt dus een range van modeluitkomsten verkregen die corresponderen met de (gereduceerde) range van parameterwaarden.

Het eerste "scenario" is een vergelijking tussen de Oosterschelde vóór en na de stormvloedkering en compartimenteringsdammen. Het blijkt dat de biologische effecten van de kering over het algemeen gering zijn, doordat abiotische invloeden elkaar grotendeels compenseren. Twee voorbeelden zijn: de hogere gemiddelde lichtintensiteit (gunstig voor primaire productie) gecompenseerd door de verminderde nutriëntenbelasting (ongunstig), en de verminderde zoetwaterbelasting die gecompenseerd wordt door de verminderde menging. De gebieden waar naar verwachting de grootste veranderingen zullen optreden zijn: de verslechterende zuurstofsituatie in de noordelijke tak, en de grotere mineralisatie en denitrificatie in het sediment.

Een eventuele verandering in de nutriëntenbelasting heeft alleen effect op de noordelijke tak van de Oosterschelde. In de rest van het gebied is de invloed van de Noordzee dominant. Eventuele veranderingen in de

nutriëntenconcentraties op de Noordzee zouden daarom wél veel invloed op de Oosterschelde hebben.

Een uitbreiding van de mosselkweek in het westelijk deel van de Oosterschelde zou -in economische termen- lonend zijn. Het gevolg van een dergelijke uitbreiding is echter een verminderde opbrengst van wilde schelpdieren, en is aldus negatief voor de natuurlijke voedselketen. In het oostelijk deel van de Oosterschelde, waar op dit moment geen mosselen worden gekweekt, is de invoering van mosselkwekerij ook na het gereedkomen van de kering nauwelijks mogelijk omdat zij hier hun eigen voedselaanbod spoedig zouden uitputten.

In een slotbeschouwing wordt ingegaan op de plaats van het huidige model in de ontwikkeling van ecologische modellen in het algemeen. In volgorde van toenemende complexiteit kunnen kwalitatieve modellen, kwantitatieve modellen met een wetenschappelijk doel en toegepaste modellen worden onderscheiden. Het huidige model valt in de laatste categorie. Het model is niet geschikt om hypothesen te toetsen, zowel vanwege zijn complexiteit en ook omdat het een uniek ecosysteem beschrijft, waarmee experimenteren niet mogelijk is. Veel van de bestaande methoden van onzekerheidsanalyse zijn op hypothese-toetsen gericht en daarom hier niet van toepassing. De hier gepresenteerde calibratieprocedure is dan ook niet gericht op het al of niet verwerpen van bepaalde hypothesen, maar op verkleinen van de onzekerheid bij het doen van voorspellingen met het model.

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### Curriculum vitae

Olivier Klepper werd op 5 december 1958 geboren in Rotterdam. In 1977 deed hij eindexamen Atheneum-b aan het Herman Jordan Lyceum te Zeist en begon hij biologie te studeren aan de Universiteit van Amsterdam. In 1980 behaalde hij zijn kandidaatsexamen wiskundige biologie (B2). Tijdens de doctoraalstudie liep hij onder meer stage bij de vakgroep Aquatische Ecologie, het Laboratorium voor Microbiologie en het NIOZ/BOEDE. In 1984 slaagde hij met lof voor het doctoraalexamen.

In 1984 werkte hij een half jaar bij het NIOZ/BOEDE, en trad hetzelfde jaar in dienst bij het Delta Instituut voor Hydrobiologisch Onderzoek te Yerseke. Vanaf 1986 werkte hij voor de Deltadienst van Rijkswaterstaat. Bij deze twee instellingen werd het huidige onderzoek verricht. Daarnaast werkte hij bij Rijkswaterstaat mee aan modellering van vervuiling in Noordzee en Westerschelde. In 1988 trad hij in dienst van het Asian Wetland Bureau in Bogor, Indonesië. Hier nam hij deel aan een ecologische inventarisatie van een moerasgebied in Zuid Kalimantan.

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