ELSEVIER

In Collaboration with
the Netherlands Institute for Sea Research

Journal of Sea Research 38 (1997) 311-331

JOURNAL OF
SEA RESEARCH

The impact of thermal stratification on phytoplankton and nutrient dynamics in shelf seas: a model study

Piet Ruardij *, Hans Van Haren, Herman Ridderinkhof

Netherlands Institute for Sea Research, P.O. 59, NL-1790 AB Den Burg, Texel, The Netherlands

Received 29 October 1996; accepted 30 June 1997

Abstract

Local heating rate within the water column depends on energy input by solar radiation and on heat exchange across the surface as controlled by wind and convection. The heating results in thermal stratification of the water column, which in turn affects the vertical transport of, for example, nutrients. In this paper the implications of the stratification on the biota by focusing on the time of its onset and its variability in time and (vertical) space are evaluated. Especially the consequences of the stratification on the phytoplankton dynamics and the trophic interactions are shown. For this purpose, an integrated ecosystem model is developed which includes a physical submodel and an ecological model. The model is calibrated with data from a mooring project, during which a large number of physical and biological parameters have been measured at a site on the Oyster Grounds in the North Sea over a 15-month period. The physical model is a one-dimensional entrainment/detrainment model. The ecological model consists of submodels which are part of the ERSEM ecological model and which describe the biological and chemical processes in the water column and in the benthos. Results show that stratification has a major impact on the biota. Especially the timing of the onset of the stratification has major consequences for the production and succession of phytoplankton and the structure of the food web during the entire growing season.

Keywords: stratification; phytoplankton nutrients; primary production; ecosystem model; ERSEM

---

1. Introduction

During summer the deeper parts of shelf seas are thermally stratified. Since the availability of nutrients and light to the phytoplankton is controlled by the vertical density structure of the water column, such stratification has a major impact on the primary production in the water column (Tett et al., 1993; Tett and Walne, 1995). This holds not only for the distribution of primary production in the water column, but also for the nutrient dynamics (Tett and Walne, 1995). Several two-layer coupled models exist describing primary production in a stratified shelf sea (e.g. Radach and Lenhart (1995); Tett and Walne (1995)). Only a few vertically fully resolved coupled physical–biological models exist in the literature (Radach, 1983; Stramska and Dickey, 1993; Sharples and Tett, 1994; Eigenheer et al., 1996). None of them discusses the consequences of the timing of the onset and the extent of the stratification for the phytoplankton production, the succession and trophic interactions during a full growth season. Only one model (Eigenheer et al., 1996) shows the

---

* Corresponding author. Tel: +31 (0)222 369 300; Fax: +31 (0)222 319 674; E-mail: rua@nioz.nl

1385-1101/97/$17.00 © 1997 Elsevier Science B.V. All rights reserved.
PII S1385-1101(97)00042-7

response of phytoplankton and nutrients for different types of stratification, but for the spring period only. Nevertheless, one may speculate that the timing of the onset of stratification in spring, when the succession of dominating phytoplankton species proceeds rapidly (≈ weeks) (Riegman et al., 1993), may determine the species composition for at least several months. In addition, irregular short-term declines or even breakdowns of stratification, both resulting in enhanced mixing may have a longer-term effect on the physical and biological properties of the water column. Hence the entire growth season should be considered and not just the spring period. Ridderinkhof (1992), for instance, showed that wind mixing events do not only influence the short-term variability of the surface mixed layer depth, but also the total heat content of a water column on a longer, seasonal, time scale.

It is our hypothesis that short-term mixing events are responsible for the supply of nutrients to the surface mixed layer during summer, and as such may have a major impact on the summer phytoplankton production. The primary objective of the present study is thus to examine the consequences of the timing of the onset of the stratification in spring and the impact of the variability of the stratification during summer, when forced by wind, air temperature, humidity, irradiation and tidal friction, on primary production, nutrient–phytoplankton interactions and interactions of phytoplankton with higher trophic levels on the continental shelf. To achieve this aim the physical model of Ridderinkhof (1992) has been combined with the ERSEM-II ecosystem model (Baretta et al., 1995) and the extensive data set available from a mooring site in the Oyster Grounds, North Sea (Fig. 1) into a new physical–biological model (STRAECOS). The observations are applied as forcing for the model (mainly the physical part) and for calibration, e.g. for chlorophyll-a, vertical extinction and nutrients.

The ERSEM model has been jointly developed by eight institutes in Europe and it is claimed that the model is generic for shelf seas. The original 2D version of the model describes in an appropriate way pelagic and benthic processes as well as sediment–water exchanges in the North Sea (Broekhuizen et al., 1995; Ebenhöh et al., 1995; Radach and Lenhart, 1995; Ruardij and Van Raaphorst, 1995; Varela et al., 1995). As a secondary objective this study provides an independent test of the genericity of, in particular, the pelagic submodel of ERSEM for its applicability in a 1D setup, but with a different physical model component and at a different space scale than the 2D version as developed and tested for the entire North Sea. Also, the underlying physical model could be tested extensively for the first time in combination with biological submodels.

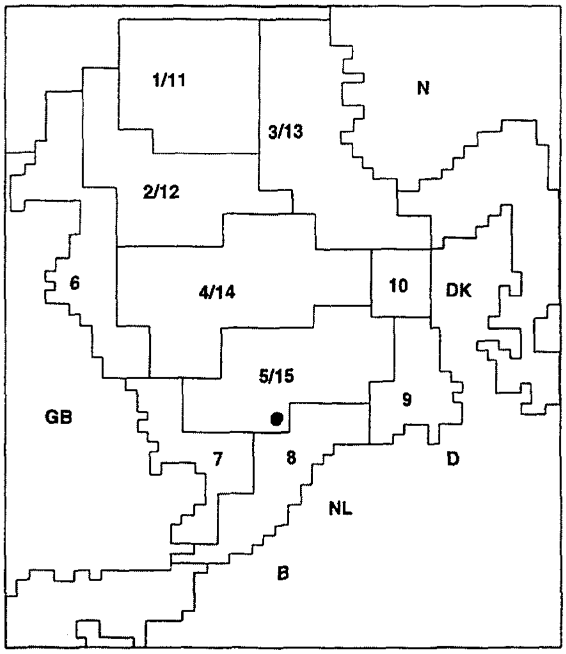

Fig. 1. Schematic map of box division as applied in the original ERSEM model. The filled circle indicates the INP-mooring site in the Oyster Grounds.

2. The model

The STRAECOS model described here is a direct coupling of a physical and an ecological model. The model runs within the simulation environment SESAME (Ruardij et al., 1995). The physical model is a mixed-layer model in which vertical transport is induced by shifting of layers ('boxes'). For the coupling of the physical model to the ecological model the possibility of a two-step integration is introduced in the SESAME environment at each time step. In the STRAECOS model in the first step the rates of change of the biochemical processes are calculated and integrated by SESAME for all layers. Subsequently the new (temporary) values of the state variables are used in the second step in which the rates of change induced by physical processes resulting in shifting of the layers are calculated for all state variables. These rates are integrated again by SESAME to the new (definitive) values of the state variables at the next time step.

2.1. The physical model

The mixed-layer model used is based on a model of Van Aken (1984) which has been modified by Ridderinkhof (1992). This model approach has advantages from a numerical point of view. First, the model results are not affected by numerical dispersion between layers. Second, complete mixing between layers is modelled by averaging concentrations instead of using unrealistically large turbulent diffusive transport between fixed layers. Third, a mixed surface or bottom layer is represented by one layer in the model with instantaneous mixing. The main drawbacks of this approach are the problems such as mass conservation which are related to the variable volume of the layers.

The main characteristics of this model are summarised in Fig. 2. It is assumed that the physical structure of the water column can be represented by three main layers:

- the turbulent surface mixed layer (SML) with a temperature T_s and a thickness H_s. The entrainment velocity w_s parameterises the turbulent fluxes to the layer below. Turbulence in this layer is mainly generated by atmospheric forcing;
- the thermocline layer (WTIL: weak turbulence intermediate layer), which consists of a variable number of sublayers of 1 m thickness;
- the turbulent bottom mixed layer (BML) with a temperature T_b and thickness $D - H_b$. The entrainment velocity (w_b) parameterises the turbulent fluxes at the top of this layer to the WTIL. Vertical turbulence in the bottom layer is assumed to be generated by the tidal currents only.

Temperature changes are caused by heating through irradiation, counteracted by the heat efflux across the air–sea interface. This efflux is controlled by the turbulence in the SML, the air–water temperature difference and the humidity (Van Aken, 1984).

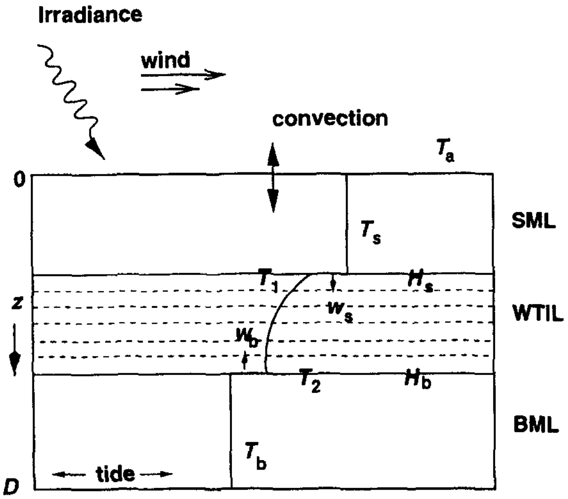

Fig. 2. Schematic picture of a water column with depth D comprising a surface mixed layer (*SML*) and a bottom mixed layer (*BML*), separated by a thermocline with weak turbulence (*WTIL*) and interfaces at H_s and H_b. T_a, T_s and T_b are the temperatures of the air above the water column, of the surface layer and of the bottom layer, respectively. T_1 and T_2 are the temperatures at the top and bottom of the thermocline. w_s and w_b are the entrainment velocities.

Vertical transport in the water column is induced by shifting of the layer boundaries. Direct exchange between the SML and the BML is only possible if the boundaries of the WTIL overlap, i.e. when the WTIL has disappeared.

This approach differs from models which solve the advection–diffusion equation on a vertical grid and in which the diffusion coefficients are derived from a turbulence–closure scheme (Mellor and Yamada, 1974, 1982; Radach, 1983; Stramska and Dickey, 1993).

During the calibration of the model it turned out, however, that the lack of any exchange between the upper and bottom mixed layers once stratification occurs, leads to unrealistic temperature distributions. Consequently a (weak) background turbulent diffusivity in the WTIL was necessary to match the model results with the observed data on the vertical temperature distribution. Others (Sharples and Tett, 1994) came to the same conclusion about this background diffusion.

A second modification of the original physical model is the extension with resuspension and deposition processes for suspended particles. Basically, suspended particle dynamics are modelled similarly as by Tett and Walne (1995). Resuspension is assumed to be proportional to the friction at the sea-bed (induced by the tidal current and the wave orbital velocity) in excess of a threshold level. The parameters involved were all calibrated by comparing the model results with the available field data.

2.2. The ecological model

The ecological part of the model consists of a number of submodels of the ERSEM-II model (Baretta et al., 1995), which are interlinked and which describe the biological and chemical processes in the water column and in the benthic system (Blackford and Radford, 1995). The dynamics of the biological functional groups are described by physiological processes (ingestion, respiration, excretion, egestion, etc.) and population processes (growth, migration and mortality). Biological variables in the model are phytoplankton, variables related to the microbial loop, zooplankton and benthic fauna (Baretta-Bekker et al., 1995, 1998; Broekhuizen et al., 1995; Ebenhöh et al., 1995, 1997; Varela et al., 1995; Blackford, 1997). The nutrients dynamics are fully coupled to the biologically driven carbon dynamics. Early diagenetic transformations and fluxes of organic matter and nutrients in the sediment are included in the model (Ruardij and Van Raaphorst, 1995).

Based on size and ecological properties, the total phytoplankton pool is subdivided into four functional groups, which are diatoms, flagellates, picophytoplankton and inedible phytoplankton (Fig. 3). Picophytoplankton rapidly grows and is grazed by heterotrophic flagellates. Despite their larger size diatoms grow faster than flagellates (Varela et al., 1995). Inedible phytoplankton is a slow grower due to the fact that the maintenance of its inedibility is an energy consuming process. All phytoplankton groups contain internal nutrient pools and thus have dynamically varying C : N : P: (Si) ratios. The nutrient uptake by phytoplankton is controlled by the difference between the external nutrient concentration and the internal nutrient pools. The growth rate is dependent on the internal quota (Droop, 1973). The consumers consist of five groups, also based on their ecological function and size (see Fig. 3).

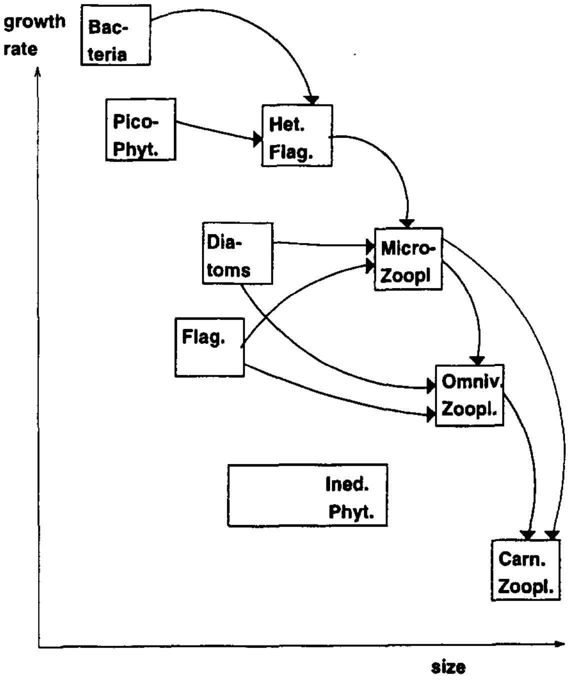

Fig. 3. Schematic outline of the functional groups and their grazing interactions in the pelagic submodel in ERSEM. The position of each functional group indicates its size and its growth rate (*Het. Flag.*: heterotrophic flagellates, *Ined. Phyt.*: inedible phytoplankton).

An important interaction between physics and biology is the light availability in the water column, where stratification may (indirectly) cause a higher average light availability for the phytoplankton in the SML (Tett et al., 1993). On the other hand, a high phytoplankton biomass in the SML will cause a lower light availability in the whole water column and especially in the BML.

The relation between light and production is described in the ERSEM model with the equation of Steele (1962) to allow for the effect of light inhibition at high irradiance close to the water surface. Here, Steele's equation is replaced by that of Smith (1936) which seems more appropriate for several reasons. Smith's equation (see Table 1) assumes light saturation instead of photo-inhibition above a certain irradiance I_0.

According to Kirk (1983) photo-inhibition is not as frequent a phenomenon as was originally supposed, and is likely to be of negligible importance during periods of even small wind speeds, which

Table 1

Equations of irradiance according to Smith (1936) and Steele (1962) as used in the model. The values of the parameters are found in the text or in Table 2.

P/I relations:

Steele: $$P(I) = \mu\alpha\frac{I}{I_0}\exp\left(1-\alpha\frac{I}{I_0}\right)$$

Smith: $$P(I) = \frac{\mu\alpha\frac{I}{I_0}}{\sqrt{\mu^2+\left(\alpha\frac{I}{I_0}\right)^2}}$$

Productions integrated over depth z (m):

Steele: $$P(I,z) = \frac{\mu}{kz}\left[\exp\left(1-\alpha\frac{I}{I_0}\mathrm{e}^{-kz}\right)-\exp\left(1-\alpha\frac{I}{I_0}\right)\right]$$

Smith: $$P(I,z) = \frac{\mu}{kz}\left[{}^{\mathrm{e}}\log\left(1+\sqrt{\left(\frac{\mu I_0}{\alpha I}\right)+1}\right)-{}^{\mathrm{e}}\log\left(\mathrm{e}^{-kz}+\sqrt{\left(\frac{\mu I_0}{\alpha I}\right)^2+\mathrm{e}^{-2kz}}\right)\right]$$

where:

$P(I)$	actual specific primary production (d^{-1})
μ	specific growth rate of phytoplankton (d^{-1})
I	actual irradiation ($\mathrm{W\ m}^{-2}$)
I_0	irradiation to which phytoplankton is adapted ($\mathrm{W\ m}^{-2}$)
α	factor representing the initial slope (x at $I = 0$) of the P/I curve (–)
z	depth of box column (m)
k	vertical extinction (m^{-1})
$P(I,z)$	specific column primary production ($\mathrm{m\ d}^{-1}$)

creates sufficient turbulence to move algal cells away from the sea surface. Jassby and Platt (1976) showed that Smith's equation fits the observed production–irradiation curves better than that of Steele. Other equations such as the one of Jassby and Platt (1976) are not taken into consideration because they need more than one parameter and cannot simply replace the Steele's equation with only I_0 as parameter.

Following the argument by Kirk (1983) it is assumed in the model that phytoplankton in that part of the water column can profit optimally from high irradiance close to the water surface when their residence time is much smaller than the length of a day. By relating the term α (Table 1), representing the initial slope of the P–I curve, to the level of turbulence in the water column, the primary production remains optimally to larger depths, despite the low light energy at depth (Fig. 4). In the model α is set to 1 for layers which are part of the WTIL which is a low turbulence area by definition. For the mixed layers α depends on the total net kinetic energy due to wind and the tidal friction near the bottom. The actual value of α is determined during the calibration. The I_0 values of the phytoplankton depend on the average light circumstances in a layer and so decrease with depth. This is in accordance with observations by Ryther and Menzel (1959).

The benthic system is important with respect to the regeneration of nutrients originating from material deposited on the sea floor. The essential process in this submodel is the mineralisation of organic material, coupled to diagenetic processes of nutrients (Ruardij and Van Raaphorst, 1995).

3. Data

All data used in this study are from a consistent data set which have been collected in the framework of the Integrated North Sea program (INP) at the mooring site in the Oyster Grounds (54°25′N 04°02′E, 45 m depth, Fig. 1). The array of moored instruments, consisting of fluorometers, transmission

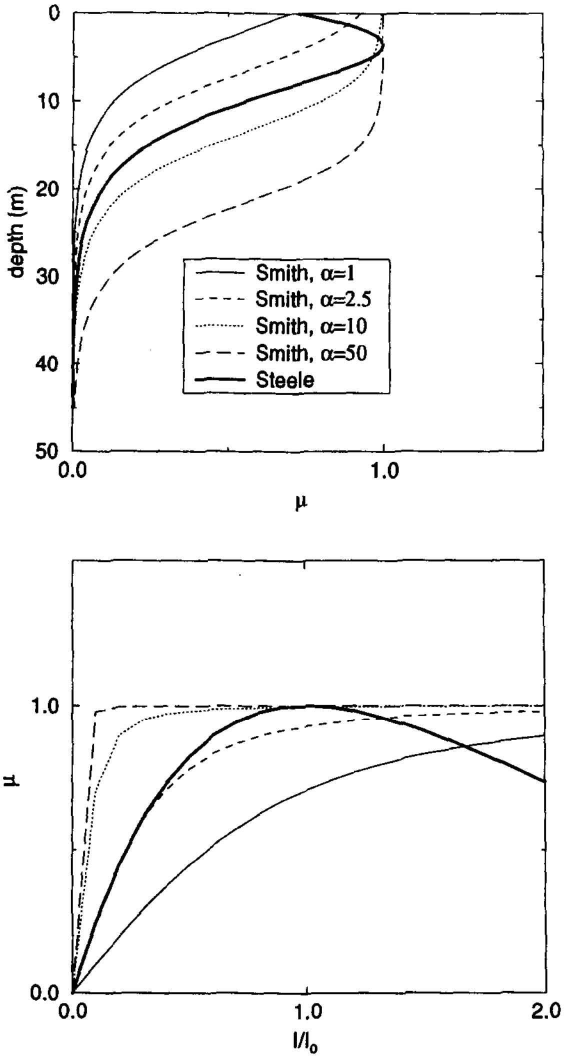

Fig. 4. Primary production (μ) as function of depth (upper panel) and the relation between primary production (μ) and irradiation (I/I_0) (lower panel) as calculated with the equation of Steele (thick line) and the equation of Smith for different α values.

meters, light, current and temperature meters sample at least at a rate of once per hour (Van Haren et al., 1997) during the full year 1994. The mooring site was visited at least once per month for instrument revising and additional sampling. Most of the physical data are used to force the model with the exception of the temperature data, which have been used to calibrate the model. All other types of data (of chemical and biological variables) are also used to calibrate the model.

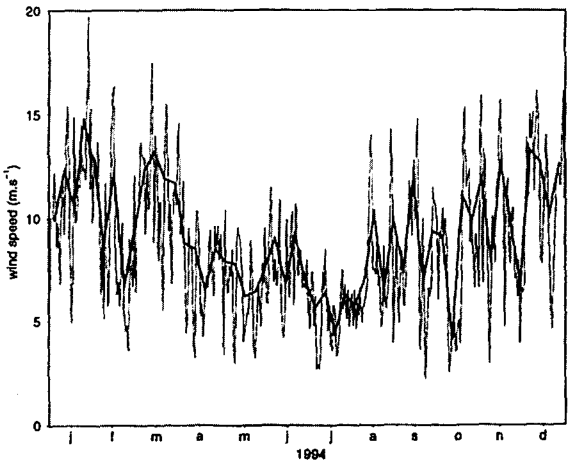

Fig. 5. Wind speed as measured near the mooring site in 1994. The grey area indicates the surface below the daily averaged wind speed. The thick line indicates the weekly averaged wind speed.

3.1. Forcing data

The forcing data exist of time series of either daily or weekly averages. Normally daily averages are used for forcing. The model is not forced with hourly data, because the processes defined in the biological model are formulated on a daily averaged basis. During 1994 meteorological data were collected on sites near the mooring site. The solar radiation was obtained from measurements at the mooring site. Wind velocity (Fig. 5) was measured on an oil platform in the central North Sea, 150 km northeast of the mooring site. Other variables necessary to calculate the turbulent heat flux at the sea surface (air temperature, humidity) were measured at the site. To calculate the (vertical) behaviour of the bottom mixed layer daily averaged values of the vertically averaged current velocity were used.

3.2. Calibration data

The calibration data can be divided in two groups.

3.2.1. Daily averaged data

Temperatures were measured every 2 m depth. Chlorophyll-*a* concentrations and the vertical extinction coefficient are derived from fluorescence and transmission measurements and both are measured at 13 m and 38 m depth.

3.2.2. Biweekly averaged data

All nutrients were measured every two weeks. Part of the data were measured directly on board (Malschaert, Van Ooyen, Van Raaphorst, unpublished data) and another part was measured during the routine monitoring program of the Dutch ministry of public works (RWS/DNZ, The Hague). The different sources of the nutrient data are identified by different symbols in all figures. The measurements are done with standard nutrient auto-analysis techniques.

4. Calibration

The main criterion for the calibration is the minimising of the deviations between simulated and observed data for the different sets available. The most appropriate setting is found by trial and error, i.e. rerunning the model for different sets of parameters.

With the temperature data the physical part of the model is calibrated. With the other observations (chlorophyll-*a*, nutrients) at least the most important part of the pelagic model of ERSEM can be tested.

4.1. Initial values

The setting of the initial values is as follows. In winter, the entire water column is well-mixed and concentrations are uniform throughout the water column. When available, initial values were taken from the field data. For the initial values of the other state variables it is assumed that they are in dynamical equilibrium, i.e. the values after a one-year run should be near the initial values. By trial these values are estimated.

4.2. The physical model

In Fig. 6 the evolution with time of the temperature is given for 1 and 43 m depth. The model works pretty well for the surface but poorly for the bottom layer when transport only takes place through entrainment and detrainment (= no turbulent diffusion). By incorporating weak background turbulent diffusion into the model, (with a coefficient $k = 4.5 \times 10^{-5}$ m^2 s^{-1}), we are able to reproduce the seasonal temperature at 43 m reasonably. The model can reproduce the seasonal dynamics quite well but does not show the short-term disturbances ($\leq$ week) apparent in the data, especially in the middle layers (not shown) but also at 43 m. For the calibration of the resuspension process only values of periods with relatively high wind speed and low phytoplankton concentrations are used. In principle, all data of winter and autumn are suitable for this aim. However, only data obtained in the winter are used, because

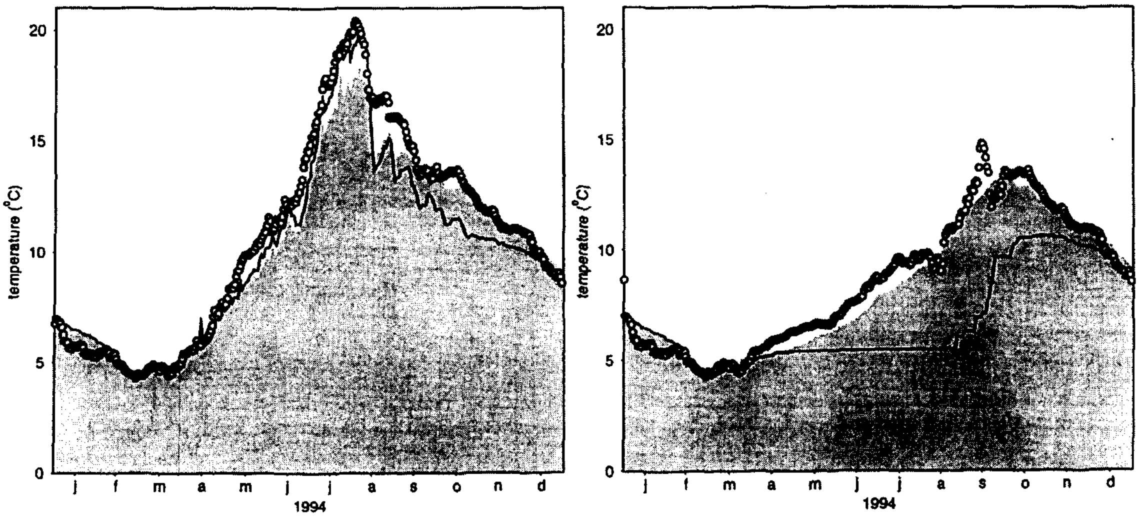

Fig. 6. Seasonal evolution of temperature at (left) 1 m and (right) 43 m depth for a simulation without a constant eddy background diffusion (solid line), a simulation with a background turbulent diffusion coefficient ($k = 4.5 \times 10^{-5}$ m^{-2} s^{-1}) (grey area) and observations (dots).

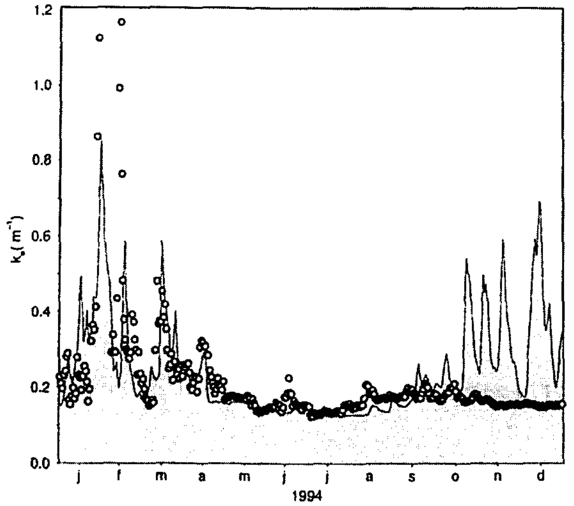

Fig. 7. Seasonal variation of the vertical light extinction coefficient (k_e) in a surface layer with a depth of 13 m: model (solid lines) and from observations (dots). The observations are from transmission meters and underwater light meters.

the field observations show contradictory dynamics during storms during winter (first three months of 1994) and during autumn (last three months of 1994) (Fig. 7). Apparently, the particulate matter near the sediment surface cannot be resuspended after a summer of consolidation of the sediment or it is already exported after resuspension during the last storms in early spring. The data of the first three months are selected because in this period the concentration suspended matter in the water column may have a large impact on the start and timing of the spring bloom, which on its turn may have consequences in the rest of the growing season for phytoplankton and nutrient dynamics.

4.3. The ecological model

To facilitate calibration of the ecological model against the field data two criteria were selected which are ranked in order of importance.

(1) The model has to reproduce the observed chlorophyll-*a* dynamics in the surface layer (at 13 m) and in the bottom mixed layer (at 38 m) as closely as possible (cf. Fig. 8). Prediction of the constant biomass level during the winter months is important for the proper condition at the start of the spring bloom.

(2) The model has to reproduce the observed low nutrient concentrations in the surface layer in the summer and possibly also the low values found in the bottom layer (cf. Fig. 9).

However, from the data we do have virtually no knowledge about the composition of the phytoplankton. The only certain facts are:

- just before the start of the thermal stratification an important sedimentation event of diatoms occurs (Van Haren et al., 1997). In the same period of the

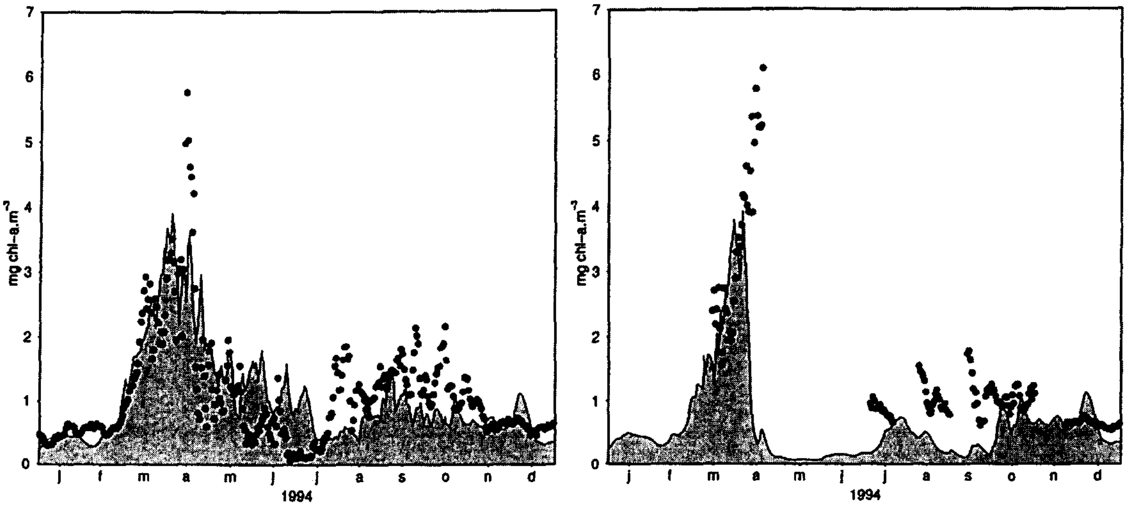

Fig. 8. Seasonal dynamics of chlorophyll-*a* at 13 m (left) and at 38 m (right) for the standard simulation (solid line), and observations (dots).

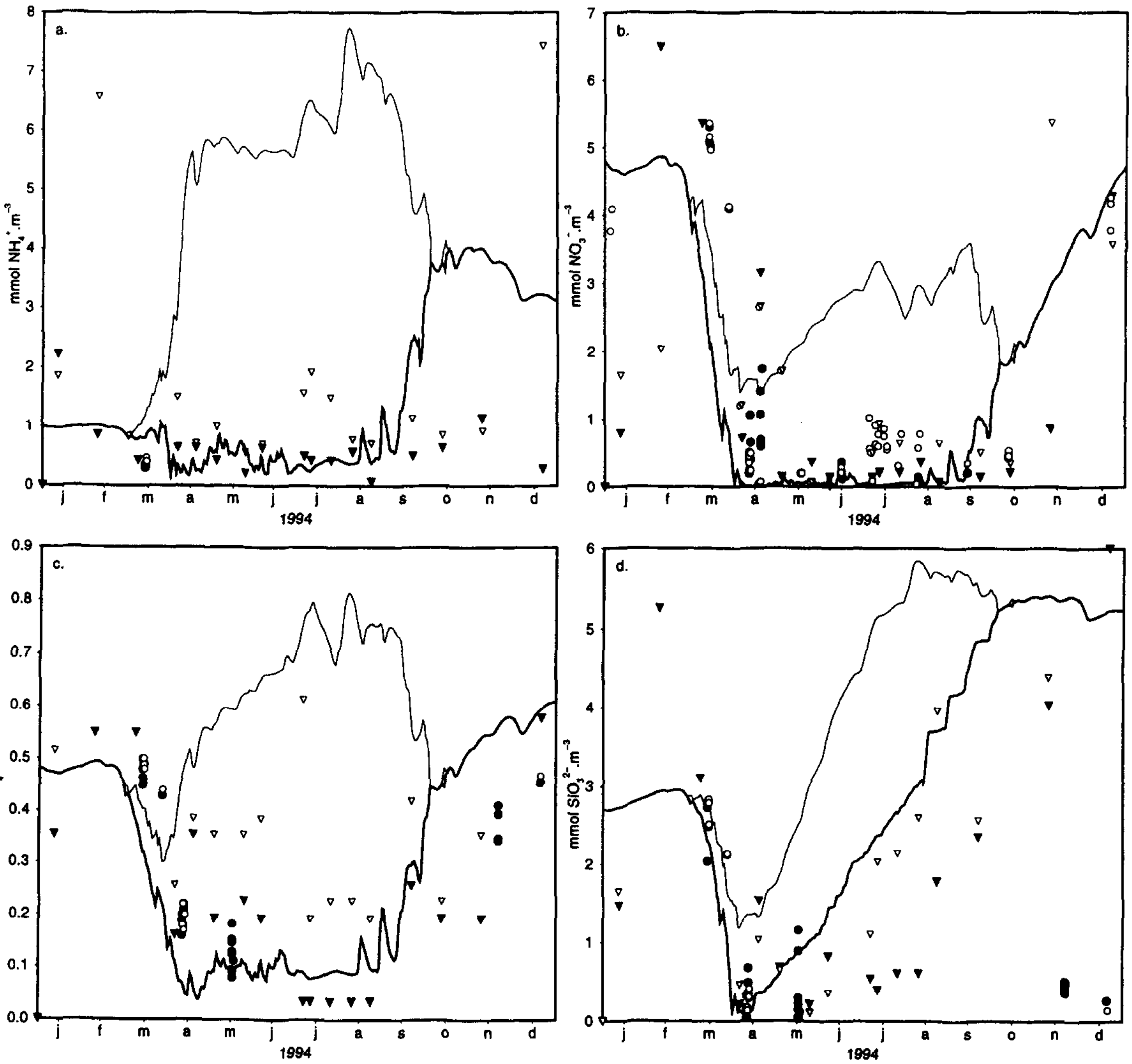

Fig. 9. Seasonal variations of ammonium concentration as simulated with the standard model (lines) and observations (symbols). The thick line and the filled symbol are for 10 m depth, the thin line and the open symbols for 40 m depth. (Values represented by triangles are measured by RWS, those represented by dots by NIOZ).

year the same phenomenon has been observed at other locations in the North Sea (Jago et al., 1993);

– the group of inedible phytoplankton appears only in periods in which the grazers control the net growth of phytoplankton (Ebenhöh et al., 1997). A major part in this functional group consists of (toxic) dinoflagellates.

These facts resulted in an extended sinking behaviour for diatoms. In the model, diatoms not only sink under severe nutrient conditions, but also as soon as they appear in a (sub)layer with low turbulence (a box of the WTIL). A number of parameters were adjusted after recalibration (Table 2). The main changes with respect to the original ERSEM model appeared for the C/chl-*a*-ratio and the increased light sensitivity. Both changes have been made in order to maximise the uptake of silicate per unit of chlorophyll-*a* in order to reach a better calibration for chlorophyll-*a*. This is necessary because the uptake only takes place in a fully mixed water column before the onset of the stratification. After that moment the diatoms sink to the BML where light conditions

Table 2
Overview of the values of model parameters in the original ERSEM (E) model and this STRAECOS (S) model. The proportional rate is defined as the proportional growth rate relative to the one of flagellates.

	Picophytopl.		Flagellates		Diatoms		Inedible phytopl.	
	E	S	E	S	E	S	E	S
Proportional growth rate (–)	2.00	1.18	1.00	1.00	1.25	0.73	0.50	0.63
C:Chl-a (mg C (mg Chl)$^{-1}$)	50	25	25	25	25	25	25	25
Stress sinking rate (m d^{-1})	–	–	–	–	45	22.50	5	45
WTIL sinking rate (m d^{-1})	–	–	–	–	–	15	–	–

are worse and growth stops. The growth rates of the other groups differ less from those in the ERSEM model (Table 2).

Changes in micro- and mesozooplankton values are limited to the two most important parameters. One describes the maximal uptake. The other describes the concentration below which the food uptake is food dependent according to a Monod relation (Baretta-Bekker et al., 1998). Nothing has been changed in the food web itself. The only aim for this part of the model was to obtain a seasonal cycle in which initial and end values are of the same order of magnitude.

5. Results

5.1. The physical model

The modelled stratification starts in March, after a short period in February, when the irradiation and the air temperature increase (Fig. 10). The results of the model as well as the observations show a stable WTIL development from mid-April onwards (Fig. 11). In the model between the beginning of March and mid-April the stratification is regularly disturbed with well mixed periods. In this period the model deviates clearly from the observations, which show most of the time a total mixing with only very short-time intervals with stratification. At times, the thickness of the WTIL varies within a few days from 30 to 20 m and vice versa (observed and modelled) (Fig. 10). In July and August the wind speed is considerable lower than in the other months of 1994. In these two months the WTIL is thickest. After the end of the summer wind events cause the WTIL to disappear intermittently. In the autumn, after two periods with strong winds, the stratification is finally terminated in the model. The field observations, however, show that until the end of the year the water column is stratified during short periods. Despite the exclusion from the model of other processes such as horizontal advection it may be concluded that the model roughly shows the same seasonal variation as the field observations. The most clear deviation occurs at the end of June when the observed thickness of the WTIL is much larger than modelled.

5.2. The ecological model

The timing of the spring bloom depends on the physical conditions in the entire water column and on the phytoplankton concentration in the winter period. The field observations of chlorophyll-*a* show

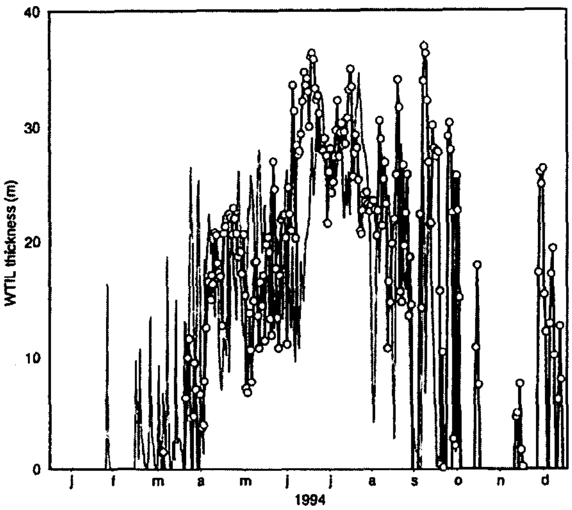

Fig. 10. The thickness of the non-turbulent intermediate layer (WTIL) as modelled (the grey area) and calculated from the data (dots).

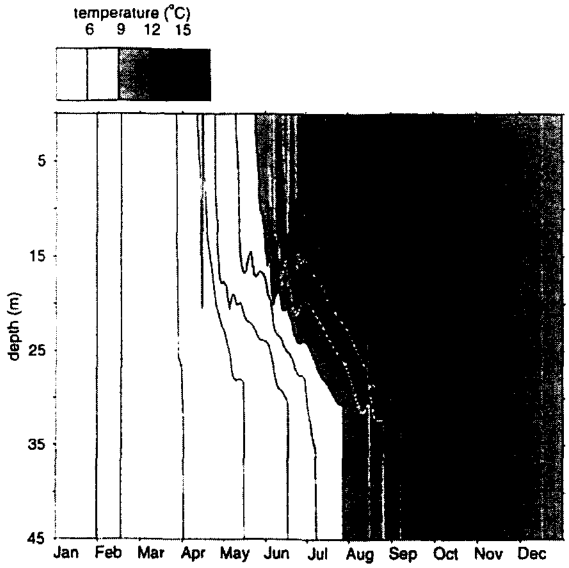

Fig. 11. Seasonal dynamics of the vertical distribution of temperature (°C) in the water column according the standard run. The lines are the 1-°C-isotherms.

a very stable concentration in winter despite the high vertical extinction values (Van Haren et al., 1997). These high vertical extinction values (Fig. 7) are caused by the resuspension of silt and should result in a poor light climate. As the effects of high winds on the turbulent diffusion and indirectly on the average amount of light available for the phytoplankton growth have been included in the P/I calculation, the model does reproduce a stable biomass as observed in the field during such a period (Fig. 8).

The spring bloom of phytoplankton is initiated after a considerable decrease of the vertical light extinction at the end of February directly after the last storm (Figs. 7 and 12). All phytoplankton groups react to this change according to their functional behaviour which results in a succession of phytoplankton types during the bloom period according to their ecological behaviour in interaction with the physical environment. The bloom and this succession are halted in mid-April after the onset of stable stratification (Fig. 10) and the depletion of the nutrients in the euphotic zone. This month-long spring bloom consists of successive blooms of two phytoplankton groups, diatoms and flagellates, preceded by a small picophytoplankton bloom (Fig. 13). This small bloom of picophytoplankton is controlled by the heterotrophic flagellates which can react very quickly to the variations in the availability of food. The first large diatom bloom is stopped by the deple-

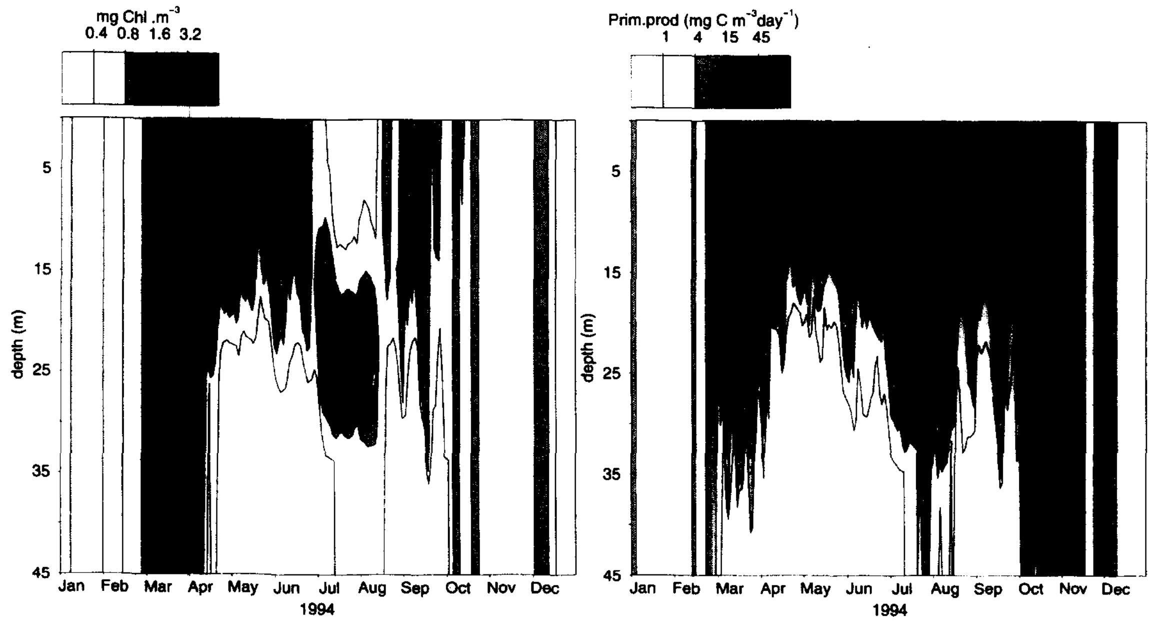

Fig. 12. Seasonal dynamics of the vertical distribution of chlorophyll-*a* (left figure) and of primary production (right figure) in the water column from the standard run.

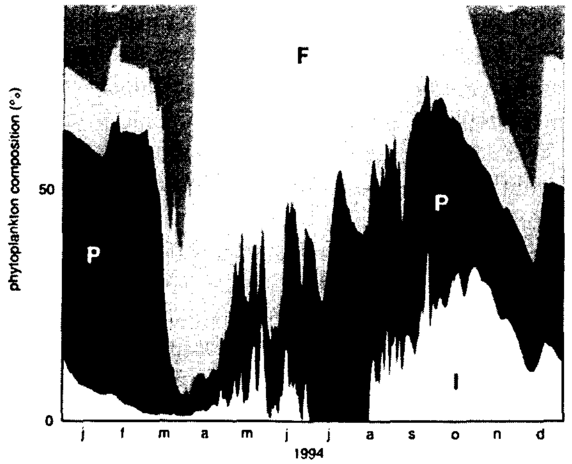

Fig. 13. Seasonal dynamics of the composition of phytoplankton succession at 13 m for the standard simulation. (*D*: diatoms, *F*: flagellates, *P*: picophytoplankton and *I*: inedible phytoplankton).

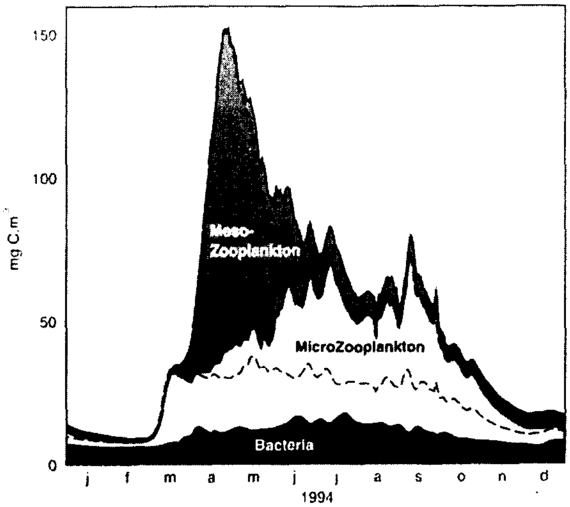

Fig. 14. Cumulative representation of seasonal dynamics of consumers for the standard simulation. The dotted lines refer for microzooplankton to the subdivisions in heterotrophic flagellates and other microzooplankton and refer for mesozooplankton to the subdivisions in omnivorous and carnivorous zooplankton.

tion of silicate and the start of the stratification. The uptake of nutrients by phytoplankton in the surface mixed layer in spring and the associated decrease of nutrients seem fairly well modelled, although the response in the model is about one month too early for nitrate and silicate when compared with observations. This difference in timing is due to the earlier start of the stratification in the model: the input of nutrients from the bottom mixed layer into the SML is decreased too soon.

The successive blooms of diatoms and flagellates respectively are succeeded in the model by a summer biomass minimum when mainly flagellates and picophytoplankton are active. The bloom of inedible phytoplankton appears after mid-August when stratification is disturbed shortly and grazers succeed in controlling the edible phytoplankton.

The modelled chlorophyll-*a* content in the bottom mixed layer (Fig. 8) shows the same peak in mid-April as in the field observations. This peak is caused by the sinking of diatoms from the upper layer due to low turbulence levels in the water column at the onset of the stratification. The model value of the peak is lower than the observations, probably because the model produces a too early stratification of the water column. The separation of a part of the column leads, due to the better light climate in the upper layer to a subsequent higher primary production and subsequently to a higher phytoplankton concentration and a coupled higher vertical light extinction in this layer (Fig. 7). This leads to an unfavourable light climate in the bottom layer and to a reduction of the primary production in this layer (Fig. 12).

During the summer period there is a stable stratification and hence a low input of nutrients from the bottom mixed layer. This leads to a typical summer depression in the phytoplankton biomass (Fig. 12) and nutrient concentrations in the upper mixed layer. At the end of the summer the stratification is disturbed by high wind speeds which result in an autumn bloom of the phytoplankton. The modelled chlorophyll-*a* concentration in the period between June and August (Fig. 8) is markedly different from the observed values, which show a period with very low chlorophyll-*a* concentrations which is succeeded, after a sudden increase, by a period with higher values. The model shows nearly the reverse tendency. This difference can be partly explained by the differences in thickness of the WTIL between model and observations (Fig. 10). A larger WTIL thickness leads to a lower diffusive transport of nutrient upwards and this leads to a strong limitation of the primary production and hence to a lower phytoplankton biomass.

The seasonal dynamics of the consumers (Fig. 14) shows a behaviour which can be expected from the modelled succession of phytoplankton. The heterotrophic flagellates, part of the microzooplankton, respond directly to the growth of the picophytoplankton. The bloom of the diatoms and flagellates leads to a fast increase of the omnivorous mesozooplankton. After the spring bloom, microzooplankton is the dominant consumer which grazes on bacteria, picophytoplankton, flagellates and on the heterotrophic flagellates. The omnivorous zooplankton is succeeded by carnivorous zooplankton, mainly because the autotrophic part of the food is too small to maintain the omnivorous zooplankton biomass.

The decrease of the nutrient concentration in the bottom mixed layer stops as soon as stratification starts; the adverse light availability in this layer and the vertical barrier of the WTIL reduces the loss of nutrients due to upward vertical transport and primary production nearly zero in the model. The relatively high values of modelled phosphate and silicate in the bottom mixed layer during the summer, as compared with the field observations, can be considered as a failure of the model. This failure may have several reasons such as a too low light sensitivity, a too high nutrient regeneration in the sediment and, last but not least, due to horizontal advective transport which is not represented in this model. The most probable reason may be a too early reduction of the modelled phytoplankton growth in the BML due to an accelerated start of the stratification, which effectively results in a cutting off from the light source. In Section 6 this discrepancy between model and observations will be further analysed.

6. Sensitivity analysis

To evaluate the effects of the physical stratification a sensitivity analysis has been performed in which the control of the physical environment on the biota, the productivity of the ecosystem, the succession of the phytoplankton and the competition between the consumers is monitored. The control on the biota mainly takes place by limiting the vertical transport of nutrients and changes in the light availability (self shading). The stratification itself is determined by physical processes which have a high variability in space and time since these processes are forced by meteorological factors like irradiation and wind. The synergetic effect of these processes can be summarised as follows:

- the magnitude of the turbulent background diffusion in the WTIL
- the time of onset and the duration of the stratification
- short time disturbances (2–5 days) in the stratification leading to alternation in time of periods of stratification and mixing.

In the following sections the net results of these effects on the functioning of the ecosystem will be shown. This will be done by comparing the standard runs with a model run in which one or two parameter values or process descriptions are changed which directly or indirectly describe one of the mechanisms or processes.

6.1. The impact of the turbulent background diffusion

In Section 4 it has been shown that the turbulent background diffusion is very important in reproducing the observed temperature variations over time. Due to the stratification the transport from the lower layers is limited and hence the nutrient depletion leads to very low chlorophyll-*a* concentrations in the surface layers. The background diffusion is responsible for an increase of about 25% of the total primary production in the water column (Fig. 15). It has a large impact on the phytoplankton biomass in and above the WTIL.

In the summer months there are obvious differences between the standard run and the run without diffusion. It also makes clear that the observed low chlorophyll-*a* concentrations may be caused by intermittently lower vertical diffusion than the background value (Fig. 16). A low concentration in the upper layers can have a dramatic effect on the bottom mixed layer, especially in a water column of 45 m, where the compensation depth of the primary production (the depth at which gain and loss processes of phytoplankton are in equilibrium) may exceed the total depth, thereby inducing primary production in the BML (Fig. 16). This has consequences for the consumers in the run without diffusion. Mesozooplankton (Fig. 17) then has a second peak during summer and this results in about twice as large a mesozooplankton production in the entire water column.

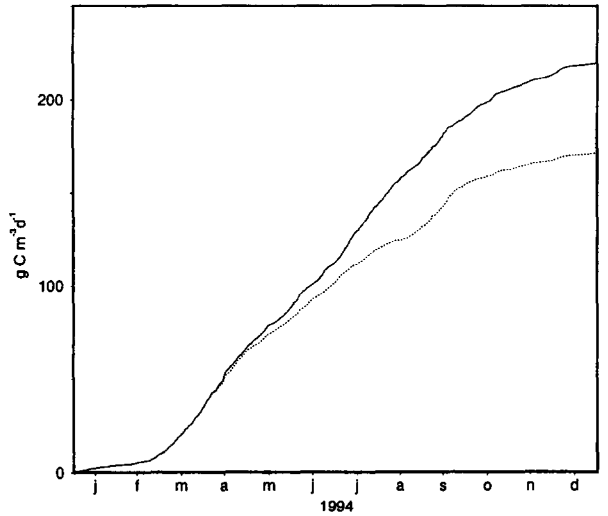

Fig. 15. Primary production integrated over time of the standard simulation (solid line) and a run without turbulent background diffusion (dotted line).

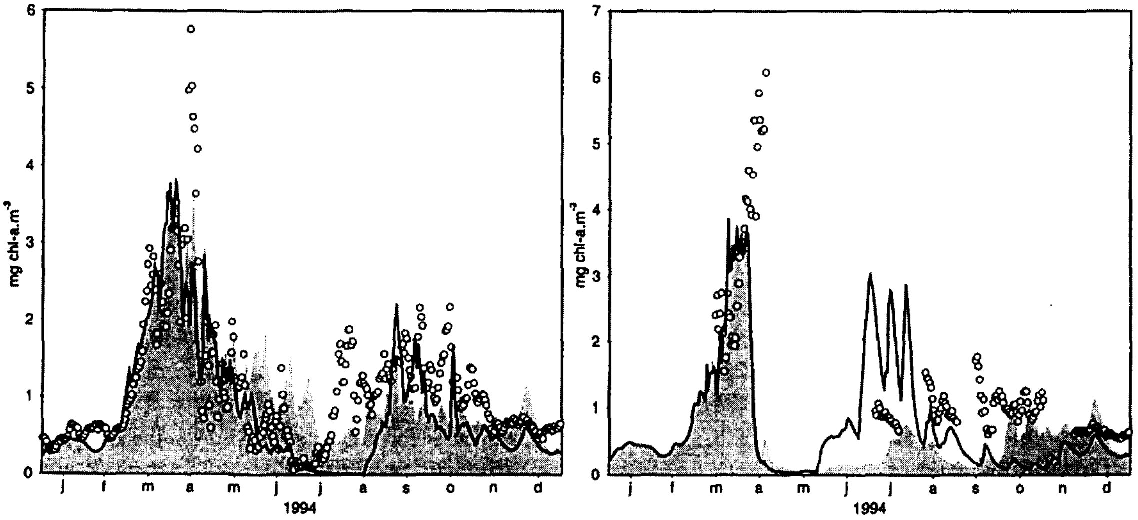

Fig. 16. Seasonal dynamics of chlorophyll-a at 13 m (left) and 43 m (right) for the standard run (grey area), a run without turbulent background diffusion (solid line), and observations (dots).

6.2. The impact of the start of the stratification on the phytoplankton bloom and the consequences for the rest of the growing season

In Section 5.1 it has been noted that in the model the start of the stable stratification is about three weeks earlier than observed in the field. In these three weeks the stratification is not very stable with time, but during this period there is some stratification present (Fig. 10). Thus, the exchange between bottom and surface mixed layer will be decreased by this stratification. In this sensitivity analysis the consequences of a too early stratification in the model will be tested by conditioning the model so that the stratification does not start before a certain day (day 115 = 25 April). This large intervention in the model made a recalibration of the diatom growth necessary. By reducing the C/chl-a-ratio of diatoms to its origi-

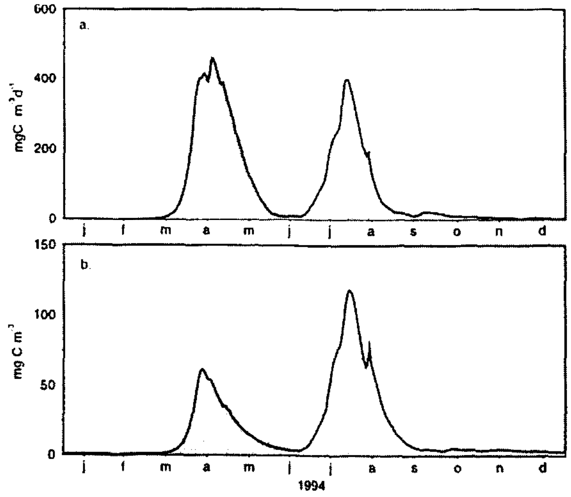

Fig. 17. Seasonal dynamics of (top) net column production of zooplankton and (bottom) mesozooplankton biomass at 38 m for the 'standard' simulation (grey area), and for a run without background turbulent diffusion (solid line).

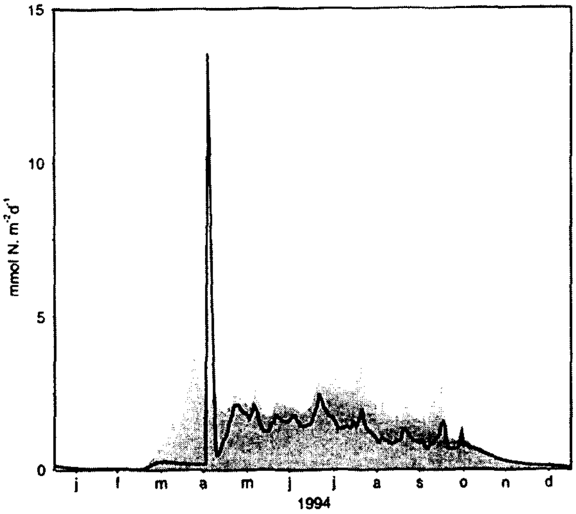

Fig. 18. Seasonal dynamics of the sedimentation of particulate N (detritus + diatoms) in the standard simulation (grey area) and in a simulation run with a delayed start of the stratification (solid line).

nal higher value in the ERSEM model (see Table 2) we could avoid that the chlorophyll-*a* concentration shows a decrease instead of an increase in early spring.

After this adaptation, the model shows a remarkable improvement compared to the standard run in both the biotics (chlorophyll-*a*) and the abiotics (nutrients). These improvements are mainly caused by the better average light availability in a totally well-mixed water column, the subsequent higher primary production during the spring bloom and the associated large sedimentation of nutrient stressed diatoms sinking to the sediment (Figs. 18 and 19).

Such a sedimentation event is not present in the standard runs, because there the diatom bloom is terminated much earlier by the stratification and succeeded by a flagellate bloom. This bloom does not settle out but is locally consumed or is ended by nutrient depletion. This leads to a production of detritus which in its turn sediments slowly.

The sinking of diatoms in this sensitivity run also results in a coupled sedimentation of particulate nutrients which subsequently lead to a removal of the nutrients from the pelagic system for a longer time.

The higher primary production in spring leads also to a better agreement between modelled and observed chlorophyll-*a* concentrations at 38 m (Fig. 19). The large removal of nutrients results in a decrease of the nutrient concentrations in the bottom mixed layer which is much more in agreement with the observed values (Fig. 20). Also, the chlorophyll-*a* concentrations in the surface mixed layer (Fig. 19) now reach the observed low summer values, although still at a wrong moment in time. These low chlorophyll-*a* values in the surface layer do not lead to a summer bloom in the bottom mixed layer like in the first sensitivity analysis. The removal of nutrients from the pelagic system also results in limiting nutrient concentrations in the bottom mixed layer. It may be concluded that the unrealistic modelling of the stratification structure in the water column during three weeks in spring has consequences for the model results of the biota for the rest of the year.

6.3. The effect of daily disturbances of the stratification on the ecosystem

The effects of different averaging periods for the meteorological forcing are studied by averaging the hourly observations over weekly intervals. A linear averaging procedure was applied. For the wind forcing the energy is considered and therefore the

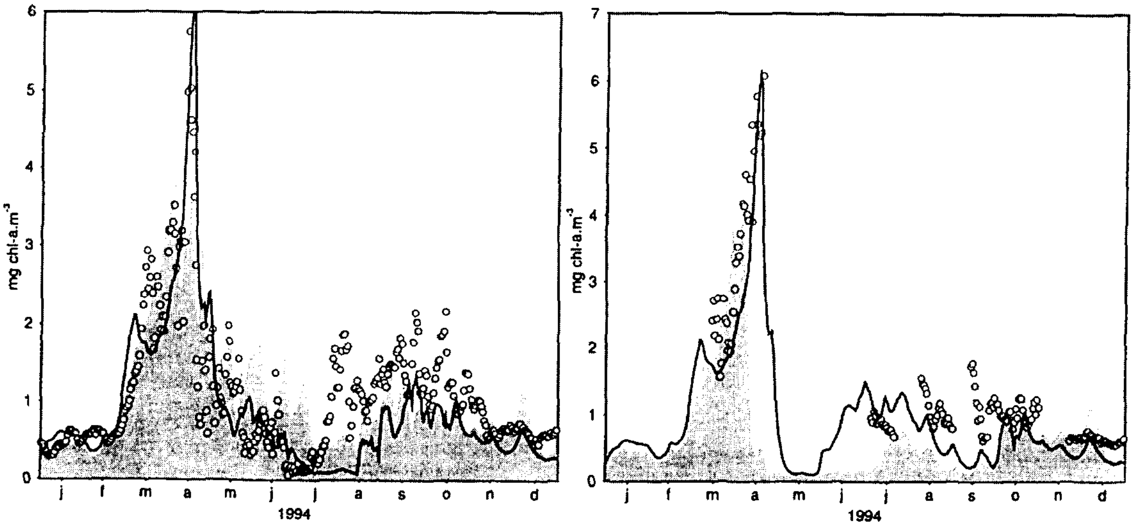

Fig. 19. Seasonal dynamics of chlorophyll-*a* at 13 m (left) and chlorophyll-*a* and 38 m (right) in the standard simulation (grey area) and in a simulation run with a delayed start of the stratification (solid line) together with observations (dots).

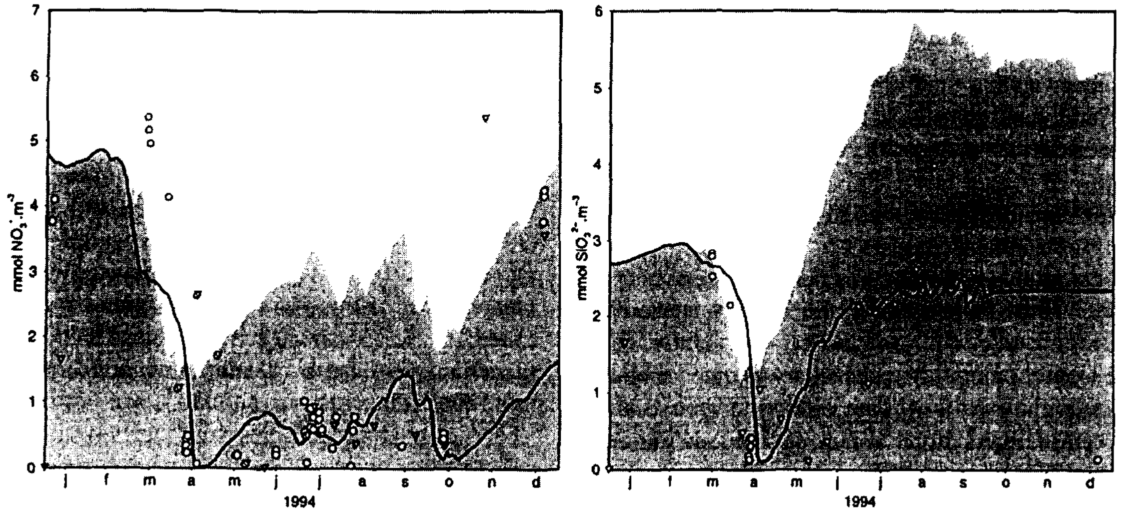

Fig. 20. Seasonal dynamics of nitrate at 40 m (left) and silicate at 40 m (right) in the standard run (grey area) and in a run with a forced delayed start of the stratification (solid line) together with observations (triangles represent values measured by RWS, dots by NIOZ).

quadratic values of the observations are used to calculate the mean. In this way extreme daily values are suppressed and short disturbances are smoothed out. Ridderinkhof (1992) has shown that the depth of the surface mixed layer is much less when the forcing of the model is based on weekly averages. Entrainment of the WTIL into the surface mixed layer occurs less frequently and moreover less intensely when the strong wind events are filtered out. This reduction of the cross-thermocline exchange results in a larger temperature difference between the surface and bottom mixed layers for weekly averaged forcing. However Ridderinkhof (1992) showed this, with the original model without turbulent background diffusion. Fig. 21 shows the cumulative primary productions for daily (standard run) and weekly averaged forcing in the different main layers. It can be concluded that the forcing with weekly averages has no significant influence on the total primary production in the water column.

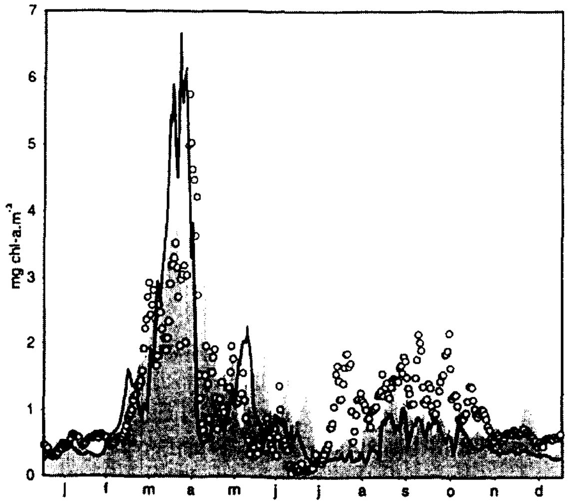

Fig. 24. Seasonal dynamics of chlorophyll-*a* at 13 m for the standard simulation (grey area) (all forcing from 1994) and a run with wind forcing of 1986 (solid line), and observations (dots).

7. Discussion

The seasonal stratification dynamics are fairly well modelled with a mixed layer model with exceptions for periods in early spring and a period in August. Eigenheer et al. (1996) also concluded that a mixed layer model predicts a too early start of the stratification in spring when compared to observations of the FLEX-experiment (Weber, 1980) but also earlier than when using a turbulence closure model (Mellor and Yamada, 1982). A possible reason for this too early start could be that in this application and the one of Eigenheer et al. (1996) daily averaged forcing are used in which diurnal effects are neglected. The deviation between model and observations in august is caused by inertial shear which cannot be included in a 1D-model Van Haren et al. (1997).

The seasonal cycle as modelled with the combined stratification–ERSEM model shows the existence of a 'classical' seasonal cycle of phytoplankton, with a short-lived spring diatom bloom that occurs about the same time as the beginning of thermal layering, a summer period of low phytoplankton biomass in the surface mixed layer together with a maximum in the WTIL, and an autumn increase due to the remixing of the entire water column. The chlorophyll-*a* observations at the mooring site (Van Haren et al., 1997) and observations made during the NERC UK North Sea project in 1988–1989 (Mills et al., 1983; Howarth et al., 1993; Joint and Pomroy, 1993; Tett et al., 1993) generally support the results of the model.

Tett and Walne (1995) indicate that, according to their model, the spring bloom is initiated by the net irradiance in the upper mixed layer of the water column. This net irradiance depends on the light extinction of the water column and on the thickness of the surface layer. This model confirms their conclusions: as soon as the light availability is sufficient the spring bloom starts. With this model we have shown that continuation of this bloom and the total production during the bloom depends heavily on the physical structure of the water column. A thinner surface mixed layer will lead to higher concentrations, however but will not enhance the total primary production as is shown in the sensitivity analysis. An earlier start of the stratification will also limit the production in the surface layer sooner and will result in a lower production during the spring bloom.

The modelled succession fits well with other observations of the contributions of different size fractions of the phytoplankton in a water column at mid-latitudes. Durbin et al. (1975) showed that in Narragansett Bay (USA) phytoplankton in the size class smaller than 2 μm (picophytoplankton in our model) is abundant in winter and had an early peak before the spring bloom. The spring bloom mainly consists of large algae (diatoms in our model) and is succeeded in summer by phytoplankton in the smaller size classes (flagellates and picophytoplankton in our model).

The seasonal variations of the microzooplankton fit very well with data of the BODC (Baretta-Bekker et al., 1995). The omnivorous zooplankton showed too early a larger peak in comparison with climatological data compiled by Broekhuizen et al. (1995). It seems that the parameter change, after the calibration, has not lead to reasonable results for zooplankton. However, when taking into account the seasonal dynamics of the main food sources for zooplankton, viz. flagellates and diatoms (Figs. 8 and 13), it cannot be expected that with our model their maximal biomass could be simulated at such a late moment in time. The only way to model such peak is by assuming a lower growth rate, active migration of

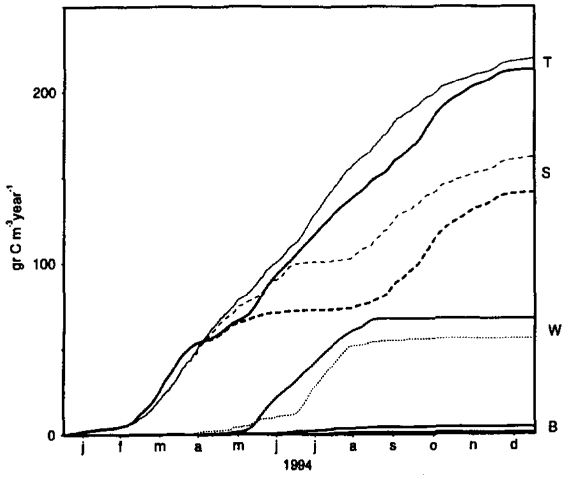

Fig. 21. Cumulative primary production for the total water column (*T*; solid lines), the surface mixed layer (*S*: broken lines), the weak turbulent intermediate layer (*W*: dotted lines), and the bottom-mixed layer (*B*: solid lines) in the standard simulation (daily forcing: thin lines) and in a run with weekly forcing (thick line).

The effects shown are the same as in the first sensitivity analysis but to a lesser extent. Again there is a shift of the primary production to the lower layers. Also, the same effect on the chlorophyll-*a* concentrations (Fig. 22) as shown in the first sensitivity analysis can be seen. The shift in time of the primary production is explained by the better light availability in the lower layers. It can be concluded that when weekly averages, instead of daily averaged values, are used vertical exchange is artificially suppressed which may lead to unexpected events in the lower layers.

6.4. The effect of the variability and dynamics of the wind forcing on the system

Wind is an important forcing for the disturbance of the stratification. Also the onset of the stratification requires a period of relatively low winds. Therefore, the standard run (1994) has been compared with a run in which the wind forcing is from 1986. Especially the spring period of that year included a period with quiet weather (Fig. 23). The results show that the response of chlorophyll-*a* to the different wind forcing is large (Fig. 24). Due to the quiet weather in early spring, according to the model the diatoms are not able to reach high values during the spring bloom. They are replaced by the flagellates which accordingly reach much higher values than in 1994. The timing of the succeeding smaller blooms in the summer period is also different. It can be concluded that the timing of the onset and the maximal concentration of the spring bloom is dependent on incidental events such as storms and may strongly differ from year to year.

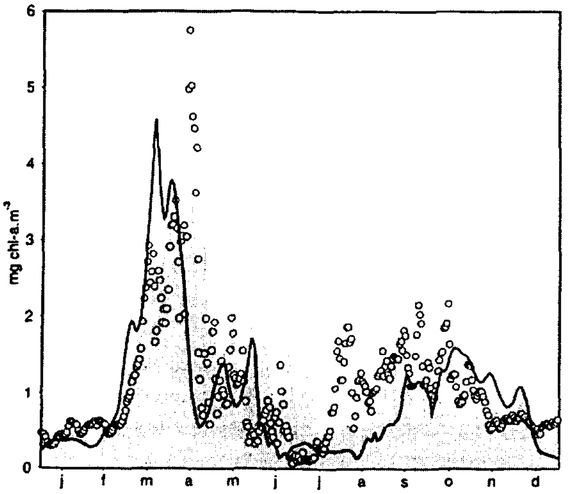

Fig. 22. Seasonal dynamics of chlorophyll-*a* at 13 m in the standard simulation (grey area) with daily forcing, in a simulation run with weekly forcing (solid line), and observations (dots).

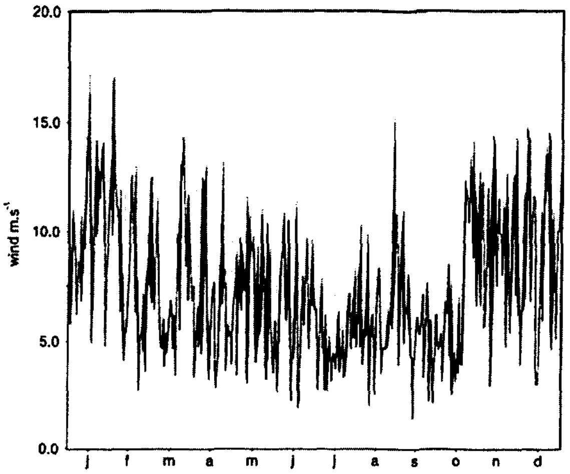

Fig. 23. The wind forcings as used in the standard simulation (1994) and in the sensitivity run with wind forcing of 1986. A positive difference between the wind speeds (1994 higher than 1986) is given in grey and a negative in black.

zooplankton to the layers with highest food concentration and a more efficient use of the (scarce) food, especially by microzooplankton during the summer season.

The largest differences between observed and modelled chlorophyll-*a* values are found during the summer. These could only partially be explained by the differences in the thickness of the WTIL between the model and observations. From other observations it is clear why; it has been shown that sometimes there is considerable advective transport (Van Raaphorst et al., 1998) but also apparently internal mixing induced by inertial shear (Van Haren et al., 1997). To account for these processes in our model we have to replace our physical model by a 3D transport model including turbulence closure. We have shown that it is possible to study a water column in a shelf sea with a closed one-dimensional model although at times tidal transport may not be negligible. The remaining problems are the wrong timing of the spring bloom and the intermittent exchange during the summer period. The first problem is probably caused by the use of daily forcing during the period of unstable stratification, where hourly forcing would be better. The second problem is related to the exclusion of a few specific physical processes which cannot be integrated in a 1D-model. They sometimes could induce disturbances in the vertical stratification and indirectly on the biota.

Finally our model showed that the winter 'pools' of nutrients are the main substrate source for the phytoplankton, and that during the rest of the year local regeneration of nutrients is much more important than the advective input from other areas. This is in agreement with results of Radach and Lenhart (1995) who showed that in the ERSEM application for the entire North Sea the advective input of nitrogen in the (large) boxes is only 3% of the annual uptake by primary production.

8. Conclusions

From our model study we made the following conclusions.

Diatoms play a crucial role in the ecological system (model). They are probably responsible for the fast decrease of nutrients in spring, which has consequences for the rest of the growing season.

The role of the microbial loop is predominant during nutrient-limited periods: it recycles a major part of the nutrients in the water column.

With the physical mixed-layer model the stratification processes and the forcing of these processes can be modelled quite well with daily forcing. However, small discrepancies between modelled and observed timing of the onset of the stratification may lead to large discrepancies between observed and modelled biota. In such a period hourly forcing is apparently necessary to include the diurnal effects on the heating and cooling of the water column.

The introduction of a turbulent background diffusion coefficient is very relevant for the biological system. In this way nutrients are transported to the upper layers which results in enhanced total primary production.

Short wind disturbances do not have the major impact as suggested by Ridderinkhof (1992). The field observations show that the effects of tides and waves are not implemented well in the original set-up of the mixed layer model and can be included by introducing a turbulent background diffusion.

Lateral transport of nutrients seems unimportant for the functioning of the ecosystem. Some effects which are induced by physical processes such as inertial shear, horizontal advective water transport. can only be resolved by a turbulence closure model incorporated in a fully 3D model.

The overall conclusion is that the physical environment is the determining factor for the seasonal variations of the dynamics of the biota. The wind regime during spring may advance or delay the stratification. In turn this leads to a decrease or increase, respectively, of the primary production during the spring bloom. The presence of silt on the sediment during a windy spring can lead to resuspension of silt, depress the primary production by light limitation and may counteract the positive effects of the wind-delayed onset of the stratification. The magnitude of the primary production during spring has implications for the entire growth season, especially when the spring bloom has resulted in a large sedimentation of phytoplankton. The nutrients in the surface mixed layer as well as in the bottom mixed layer are affected. The consequence may be that from year to year large inter-annual differences can appear in the magnitude, seasonal variation and succession of phytoplankton. This effect will be certainly reflected in the secondary production of micro- and mesozooplankton.

Acknowledgements

This research was partly funded by the European Community under MAST II contract number MAS2-CT92-0032. Additional funds were supplied by BEON. H. Van Haren has been supported by a grant from NWO, the Dutch organisation for the advancement of scientific research. Most field data were obtained from cruises financially supported by the Netherlands Marine Research Foundation (grant 39104). We thank Wim Van Raaphorst, Job Baretta and Bouwe Kuipers for their critical reading of the manuscript.

References

Baretta, J.W., Ebenhöh, W., Ruardij, P., 1995. The European Regional Seas Ecosystem Model, a complex marine ecosystem model. Neth. J. Sea Res. 33, 233–246.

Baretta-Bekker, J.G., Baretta, J.W., Rasmussen, E.K., 1995. The microbial food web in the European Regional Seas Ecosystem Model. Neth. J. Sea Res. 33, 363–379.

Baretta-Bekker, J.G., Baretta, J.W., Hansen, A.S., Riemann, B., 1998. An improved model of carbon and nutrient dynamics in the microbial food web in marine enclosures. Aquat. Microb. Ecol., 14, 91–108.

Blackford, J., 1997. A quantitative analysis of benthic biological dynamics in a North Sea ecosystem model. J. Sea Res. 38, this issue.

Blackford, J., Radford, P., 1995. A structure and methodology for marine ecosystem modelling. Neth. J. Sea Res. 33, 247–260.

Broekhuizen, N., Heath, M.R., Hay, S.J., Gurney, W.S.C., 1995. Predicting the dynamics of the North Sea's mesozooplankton. Neth. J. Sea Res. 33, 381–406.

Droop, M., 1973. Some thoughts on nutrient limitation in algae. J. Phycol. 9, 264–272.

Durbin, E., Krawiec, G., Smayda, T., 1975. Seasonal studies on the relative importance of different size fractions in Narragansett Bay, USA. Mar. Biol. 32, 271–287.

Ebenhöh, W., Kohlmeier, C., Radford, P., 1995. The benthic biological submodel in the European Regional Seas Ecosystem. Neth. J. Sea Res. 33, 423–452.

Ebenhöh, W., Baretta, J.W., Baretta-Bekker, J.G., 1997. The primary production module in the marine ecosystem model ERSEM II with emphasis on the light forcing. J. Sea Res. 38, this issue.

Eigenheer, A., Kühn, W., Radach, G., 1996. On the sensitivity of ecosystem box model simulations on mixed-layer depth estimates. Deep Sea Res. 43, 1011–1027.

Howarth, M.J., Dyer, K.R., Joint, I.R., Hydes, D.J., Purdie, D.A., Edmonds, H., Jones, J.E., Lowry, R.K., Moffat, T.J., Pomroy, A.J., Proctor, R., 1993. Seasonal cycles and their spatial variability. Phil. Trans. R. Soc. 343, 383–402.

Jago, C.F., Bale, A.J., Green, M.O., Howarth, M.J., Jones, S.E., Mc-Cave, I.N., Millward, G.E., Morris, A.W., Rowden, A.A., Williams, J.J., 1993. Resuspension processes and seston dynamics, southern North Sea. Phil. Trans. R. Soc. 343, 475–488.

Jassby, A.T., Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21, 540–547.

Joint, I., Pomroy, A., 1993. Phytoplankton biomass and production in the southern North Sea. Mar. Ecol. Prog. Ser. 99, 169–182.

Kirk, J.T.O., 1983. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Cambridge, 400 pp.

Mellor, G., Yamada, T., 1974. A hierarchy of turbulence closure models for planetary boundary layers. J. Atmos. Sci. 31, 1791–1806.

Mellor, G., Yamada, T., 1982. Development of a turbulence closure models for geophysical fluid problems. Rev. Geophys. Space Phys. 20, 851–875.

Mills, D.K., Tett, P., Novarino, G., 1983. The spring bloom in the south-western North Sea in 1989. Neth. J. Sea Res. 33, 65–80.

Radach, G., 1983. Simulations of phytoplankton dynamics and their interactions with other system components. In: Sundermann, J., Lenz, W. (Eds.), Proceedings of the Symposium on North Sea Dynamics, Hamburg, September 1981. Springer-Verlag, Berlin, pp. 584–610.

Radach, G., Lenhart, H., 1995. Nutrient dynamics in the North Sea: fluxes and budgets in the water column derived from ERSEM. Neth. J. Sea Res. 33, 301–335.

Ridderinkhof, H., 1992. On the effects of variability in meteorological forcing on the vertical structure of a stratified water column. Cont. Shelf Res. 12, 25–36.

Riegman, R., Kuipers, B.R., Noordeloos, A.A.M., Witte, H.J., 1993. Size-differential control of phytoplankton and the structure of phytoplankton communities. Neth. J. Sea Res. 31, 255–265.

Ruardij, P., Van Raaphorst, W., 1995. Benthic nutrient regeneration in the ERSEM ecosystem model of the North Sea. Neth. J. Sea Res. 33, 453–483.

Ruardij, P., Baretta, J.W., Baretta-Bekker, J.G., 1995. SESAME, Software Environment for Simulation and Analysis of Marine Ecosystems. Neth. J. Sea Res. 33, 261–270.

Ryther, J., Menzel, D., 1959. Light adaptation by marine phytoplankton. Limnol. Oceanogr. 4, 492–497.

Sharples, J., Tett, P., 1994. Modelling the effect of physical variability on the midwater chlorophyll maximum. J. Mar. Res. 52, 219–238.

Smith, E.L., 1936. Photosynthesis in relation to light and carbon dioxide. Proc. Natl. Acad. Sci. Wash. 22, 504–511.

Steele, J., 1962. Environmental control of photosynthesis in the sea. Limnol. Oceanogr. 7, 137–150.

Stramska, M., Dickey, T., 1993. Phytoplankton bloom and the vertical thermal structure of the upper ocean. J. Mar. Res. 51, 819–842.

Tett, P., Walne, A., 1995. Observations and simulations of hydrography, nutrients and plankton in the southern North Sea. Ophelia 42, 371–416.

Tett, P., Joint, I., Purdie, D., Baars, M., Oosterhuis, S., Danreri, G., Hannah, F., Mills, D., Plummer, D., Pomroy, A., Walne, A., Witte, H.J., 1993. Biological consequences of tidal stirring gradients in the North Sea. Phil. Trans. R. Soc. A 343, 493–508.

Van Aken, H., 1984. A one-dimensional mixed-layer model for stratified shelf seas with tide- and wind-induced mixing. Dt. Hydrogr. Z. 37, 3–27.

Van Haren, H., Ruardij, P., Ridderinkhof, H., Mills, D., 1997. High frequency long time series measurements of phytoplankton biomass in the central North Sea. In: Stel, J.H. et al. (Eds.), Operational Oceanography, ther Challenge for European Cooperation. Proc. 1st Int. Nat. Conf. Eurogoos, Elsevier, Amsterdam, pp. 529–538.

Van Raaphorst, W., Malschaert, J.F.P., Van Haren, J.J.M., 1998. Tidal resuspension and deposition of particulate matter in the Oyster Grounds, North Sea, J. Mar. Res. 56, in press.

Varela, R.A., Cruzado, A., Gabaldón, J.E., 1995. Modelling primary production in the North Sea using ERSEM. Neth. J. Sea Res. 33, 337–361.

Weber, G.R.J.T.A., 1980. The chlorophyll development at the central station during FLEX'76. Two data sets. Proc. Final ICES/JONSIS Workshop on JONSDAP'76, Liège, Belgium, 29 April–2 May 1980. ICES Council Meeting 1980 C 13-24, 3.