THE EUROPEAN REGIONAL SEAS ECOSYSTEM MODEL,
A COMPLEX MARINE ECOSYSTEM MODEL

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Mathematics may be compared to a mill of exquisite workmanship which grinds you stuff of any degree of fineness; but, nevertheless what you get out depends upon what you put in; and as the grandest mill in the world will not extract wheat flour from peascod, so pages of formulae will not get a definite result out of loose data.

T.H. Huxley, 1897, quoted in J.E. Schindler, 1988.

ABSTRACT

This paper presents an overview of the concept, structure and implementation of the European Regional Seas Ecosystem Model (ERSEM). The model dynamically simulates the biogeochemical seasonal cycling of carbon, nitrogen, phosphorus and silicon in the pelagic and benthic food webs of the North Sea, and is forced by irradiance, temperature and transport processes.

The model has a coarse spatial resolution into ten boxes, the ICES boxes, of which the five deepest have been resolved into surface (0 to 30 m) and deep (30 m to bottom) boxes.

At the open boundaries, time series are prescribed for dissolved and particulate nutrients. River loads of nutrients for the rivers discharging into the North Sea are prescribed at monthly intervals. A general circulation model has been used to aggregate the exchange volumes across the box boundaries into daily in- and outflows. From these, the horizontal transports of dissolved and suspended constituents are calculated. Vertical transport is in the form of sinking and sedimentation for particulates and in the form of turbulent diffusion for dissolved constituents.

The physical model contains all information specific to the area to be modelled, whereas the biological/chemical submodels have been constructed not to be site-specific.

The biological variables are represented as functional groups expressed in units of organic carbon and the chemical variables as the internal pools in the biological variables and as the dissolved inorganic pools in water and sediment, expressed in units of N, P and Si.

The model runs in a software environment (SESAME) developed for enabling the development of large and complex models in a modular way by a consortium of institutes, each focusing on different aspects of the ecosystem, translating these into modules within the model. With the exception of fish populations, where size- and age-structure are explicitly represented, all the other biological components have been modelled as unstructured populations aggregated into functional groups. This approach is shown to be appropriate for taxa having short generation times in relation to the annual cycle and for taxa which do not span more than one trophic level during their lifetime.

1. INTRODUCTION

The last two decades have seen an increasing number of attempts to integrate the knowledge derived from process studies into simulation models of marine ecosystem components. The usual approach has been to select a few functional groups ('phytoplankton', 'zooplankton', 'nutrients') and try to construct a mathematical model. Many modellers took a steady-state approach, assuming the system to be in dynamical equilibrium (Steele, 1974; Billen, 1978; Mommaerts *et al.*, 1984). Others, arguing that

the dominant forcing of the system was meteorological and hence very variable, preferred a dynamical time-evolving approach (Fransz & Verhagen, 1985; Billen & Lancelot, 1988). A recent review by Fransz et al. (1991) gives an overview of all models that have been constructed to represent aspects of North Sea ecosystem functions. At the same time a few attempts have been made to model estuarine/marine ecosystems as a whole, taking into account benthic and pelagic processes as well as advection and dispersion (Kremer & Nixon, 1978; Radford & Joint, 1980; Baretta & Ruardij, 1988; 1991).

The one thing all these models have in common is that the biological components have been aggregated and abstracted into functional groups. The trophic interactions between the functional groups are defined using fixed parameters, with very uncertain values, depending strongly on the definition of the interacting functional groups. This approach precludes the adaptation and self-organisation of the functional groups when the trophic interactions are organized in a food chain. However, if the trophic interactions occur in a model food web, i.e. if functional groups have multiple food sources and multiple predators, the system can dynamically adapt to spatial or temporal variability in the environment by channelling mass fluxes through different components of the food web, even though the food web structure is fixed. The transfers of particulate organic carbon in these food webs are not restricted to predator-prey interactions but, by including decomposition/mineralization processes also encompass detrital processes. This is made explicit by including detritus as a state variable. Changes in the food web dynamics thus result in changes in the balance between detrital and living matter, and the coupling between the benthic and pelagic systems. The microbial food web may play an important role in these processes, being able to respond very fast to changes in its biotic and abiotic environment (Baretta-Bekker et al., 1994), although scientific opinion is still divided as to whether the main role of the microbial system is to transform dissolved organic matter produced by excretion and lysis into particulate matter or to recycle nutrients (Pomeroy, 1974; Azam et al., 1983).

Usually ecosystem models use either carbon or one of the macronutrients (nitrogen, phosphorus or silicon) as their unit of currency. Other nutrients, if present, are carried as an external variable. By carrying all the macronutrients as well as carbon as state variables the ERSEM model is able to adjust dynamically to spatial and temporal differences in carbon and nutrient availability. In combination with the inclusion of detritus as a state variable (containing dynamically varying ratios of C, N and P) this approach allows an evaluation of the role of sedimentation in benthic-pelagic coupling (Ebenhöh et al., 1995) and of benthic nutrient regeneration (Ruardij & Van Raaphorst, 1995). Keeping track of the macronutrients

after they have been transformed from their dissolved inorganic form into organic particulates provides a first approximation of the tight coupling between the cycling of carbon and nutrients in aquatic systems that has been observed experimentally by tracer studies (Owens et al., 1990; D'Elia, 1988).

The time frame of most marine ecosystem models is one to a few years, due to the predominance of the seasonal signal in most temperate and high-latitude systems. However, when benthic processes are included in a model, even with climatological forcing runs of about 25 to 40 years may be required before the system settles into a climatological seasonal cycle (cf. Ebenhöh et al., 1995; Ruardij & Van Raaphorst, 1995). With interannual variability in physical forcing and boundary conditions (Lenhart et al., 1995), it is unlikely that a marine ecosystem, or even a model containing sufficiently slow processes, will ever achieve a dynamical steady state.

The purpose of this paper is to sketch the main mechanisms and processes implemented in the European Regional Seas Ecosystem Model, with the details of the numerous submodels being given elsewhere (Varela et al., 1995; Baretta-Bekker et al., 1995; Broekhuizen et al., 1995; Bryant et al., 1995; Ebenhöh et al., 1995; Ruardij & Van Raaphorst, 1995; Lenhart et al., 1995). The scientific objective has been to develop a generalized model of the cycling of carbon and the associated (re)cycling of the macronutrients nitrogen, phosphorus and silicon. Oxygen dynamics are also included because of the potential impact of oxygen depletion on benthic carbon and nutrient dynamics.

2. A SHORT DESCRIPTION OF THE EUROPEAN REGIONAL SEAS ECOSYSTEM MODEL

2.1. GENERAL FEATURES

The model consists of an interlinked set of modules, describing the biological and chemical processes in a water column, which may be stratified or mixed and in the benthic system. Horizontal transport is included by driving the model with the output of physical circulation and dispersion models, whilst irradiance and temperature are supplied as external forcing.

Each module consists of a coupled set of ordinary differential equations which may be solved by a straightforward explicit method (Euler integration) or by an implicit higher-order Runge-Kutta method. The whole model is run on Unix workstations using the simulation modelling package SESAME (Software Environment for Simulation and Analysis of Marine Ecosystems) developed at the Netherlands Institute for Sea Research (Ruardij et al., 1995). An overview of the ERSEM model as applied to the North Sea may be found in ERSEM (1993). The structure of ERSEM-North Sea has been described in Blackford & Radford (1995), a technical description of the modules can be
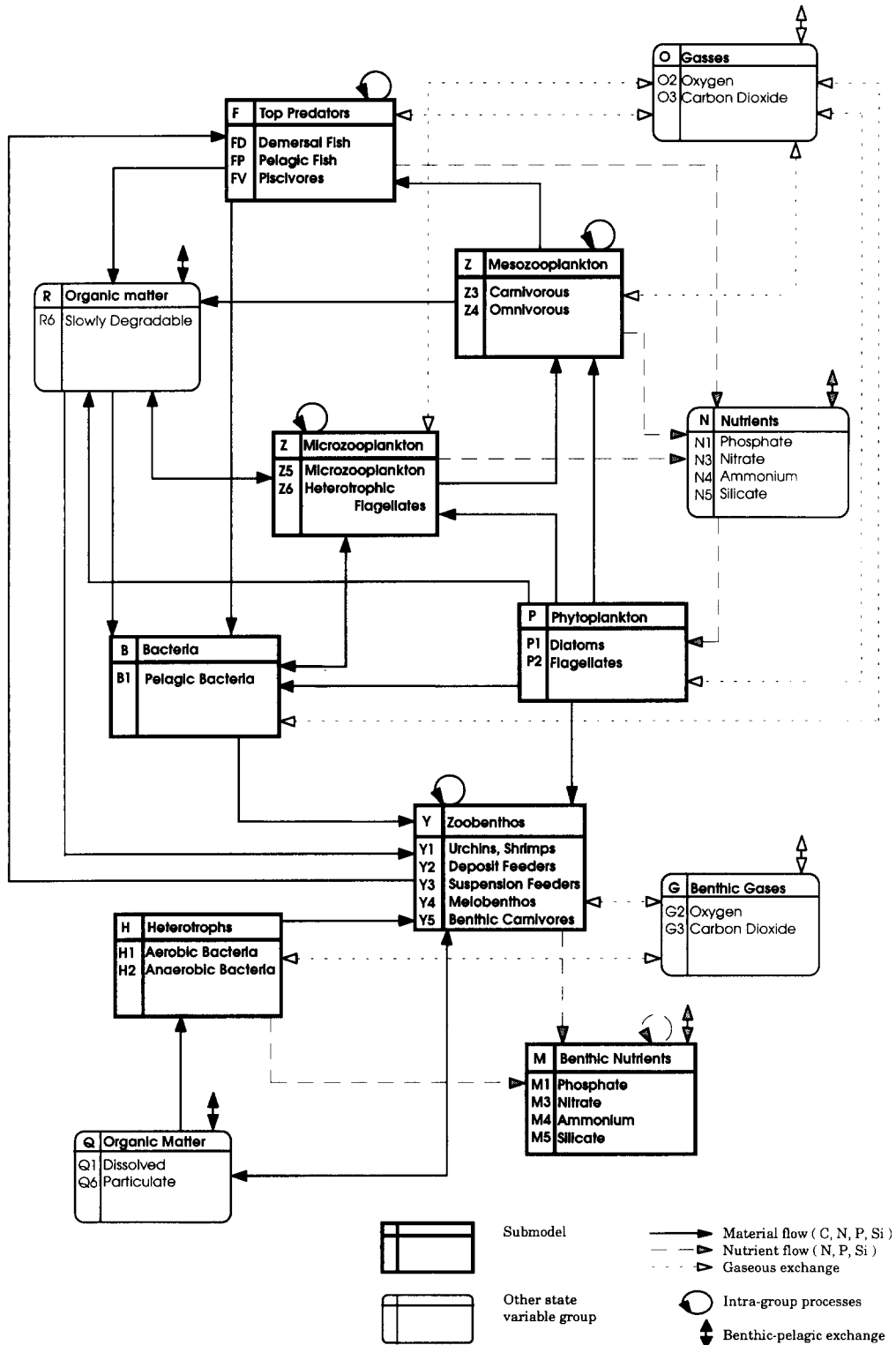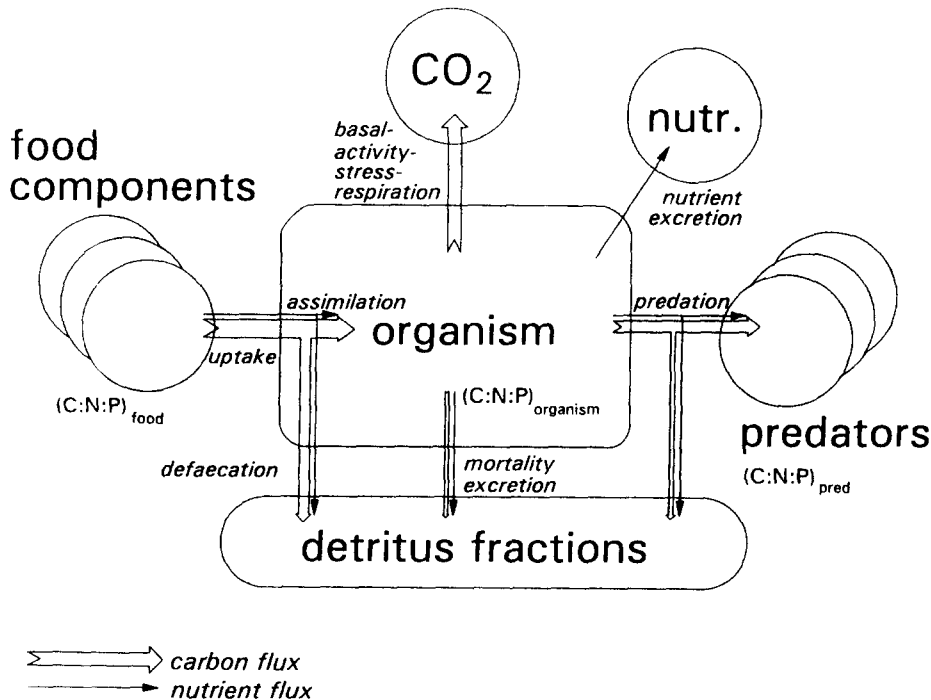
Fig. 1. ERSEM process flow diagram.

Fig. 2. Standard organism, as used as base for the modelling of the functional groups in ERSEM.

found in Radford (1993), and the model code itself is available on request from the Plymouth Marine Laboratory.

An essential feature of aquatic ecosystem models is the combination of biology and physics, which cannot completely be separated (migration with currents, sedimentation due to biological actions, sinking of senescent phytoplankton); however, a rough separation is possible. The biological dynamics of the functional groups are described in terms of physiological processes (ingestion, respiration, excretion, egestion, etc.) and population processes (growth, migration, and mortality) with trophic interactions defined in the food web structure. The physical processes affecting the biological constituents are advection and dispersion in the horizontal, and sedimentation and dispersion in the vertical, with the horizontal processes operating on scales of tens of kilometres and the vertical processes on tens of metres.

2.1.1. THE BIOLOGY

The biological constituents of the model are organized into functional groups, both in the pelagic submodel and in the benthic submodel (Fig. 1). These do not have an internal size structure (except for the fish module which has annual cohorts) but each forms an implicit size-class in its own right. Feeding/grazing relationships in the pelagic subsystem are generally restricted to the next-smaller functional group(s) and

the same functional group ('cannibalism'), but in the benthic system the size difference between food and feeder may be much larger, as for example in deposit-feeding macrobenthos.

All biological functional groups except fish are modelled according to the concept of the 'standard organism' (Fig. 2). The universal biological processes of food uptake, assimilation, respiration, excretion, egestion, etc. are defined in this concept. The differences between the functional groups mainly lie in the rate constants, which are derived experimentally from the literature or from allometric considerations, and in the food components on the uptake side. There are three classes of standard organisms: primary producers, consumers and decomposers. This concept works well for those groups where data usually are derived from population or even community studies, especially the single-celled components of the system.

There are two main problems in modelling functional groups that represent larger, longer-lived organisms, where experimental data usually are derived from individuals. First data have to be scaled from the individual to the species level and then from the species level to the population (functional group) level. In this process it is difficult to accomodate the fact that biomass increase in these populations is mostly by growth of individuals and not by increasing numbers of identically sized individuals (cf. Broekhuizen et al., 1995). As most, if not all, biological rates

decrease with increasing size and age, using fixed specific rates for those groups is a coarse approximation. A partial solution would be to keep track of the time-varying size-frequency structure within the population.

The phytoplankton groups (diatoms and flagellate phytoplankton) contain internal nutrient pools, and thus have dynamically varying C:N:P:(Si) ratios. The consequence is that detritus also has variable C:N:P:Si ratios. This allows the recycling of detrital material, both in the water column and in the sediments, to be dependent on the actual C:N:P ratio, thus effectively taking the 'history' of detritus into account when defining the prevailing rate of mineralization.

The microbial food web, converting dissolved excretion products and labile organic carbon, into particulate forms, has been resolved in ERSEM in order to quantify its role in nutrient (re)cycling.

All the biological functional groups contribute to the detrital pools by lysis, egestion, sloppy feeding and mortality. The representation of sinking by particulate detritus in the model allows the emergence of a realistic seasonal cycle in the vertical distribution of inorganic nutrients. The underlying mechanism is simply that sinking removes organic-bound nutrients from the euphotic zone, thus depleting the recycling nutrient pool in the upper layers and passing control of the nutrient resupply rate from biotic to hydrodynamic processes. Horizontal near-bed transport of detritus via resuspension/deposition processes is neglected at present, but is recognized as a major process generating spatial variability in benthic processes.

Clearly, modelling the carbon and nutrient cycles in shelf sea systems necessitates the inclusion of benthic/pelagic interactions and hence a benthic system submodel. In ERSEM, the benthic submodel contains a food web model describing carbon and associated nutrient cycling, and a bioturbation/bioirrigation module to calculate the diffusion of dissolved substances and the vertical transport in the sediment of particulate matter according to the presence and activity of the benthic biota. Additionally, benthic nutrient dynamics are described in a separate benthic nutrient dynamics module. In this module the changes in the vertical positions of the oxygen and sulphide horizons, the nutrient profiles and the resultant nutrient flux from or to the sediment by diffusion across the sediment surface are dependent on redox-conditions in the sediment, which in turn depend on benthic community structure and activity.

2.1.2. THE PHYSICAL FORCING FOR THE NORTH SEA IMPLEMENTATION

Computational constraints dictated a rather coarse horizontal spatial resolution for the model. The ICES boxes were adopted as the spatial compartments (Fig. 3), subdividing the deeper parts of the North

Sea, where thermal stratification occurs in summer, into surface and deep boxes at 30 m depth.

Water movement is represented indirectly in the model in the form of daily advection volumes and (vertical) diffusion coefficients, prescribing daily exchanges of water across box boundaries, both horizontally and vertically (Lenhart et al., 1995). These are used to derive the transport of dissolved and particulate material. Daily horizontal exchange volumes and the daily varying vertical diffusion coefficients were compiled from flow fields produced by a baroclinic general circulation model (GCM), having a grid size of approximately 20 km, and a vertical resolution of 19 layers. This model has been described by Backhaus (1985) and Pohlmann (1991). The procedure for adapting the GCM flow field to the box structure used in ERSEM is described in Lenhart et al. (1995).

The whole model is forced by incident radiation, with the integrated energy over one day at the sea surface in the absence of cloud cover being calculated from the solar constant according to Evans & Parslow (1985) with day length dependent on latitude and Julian day number. The underwater light climate
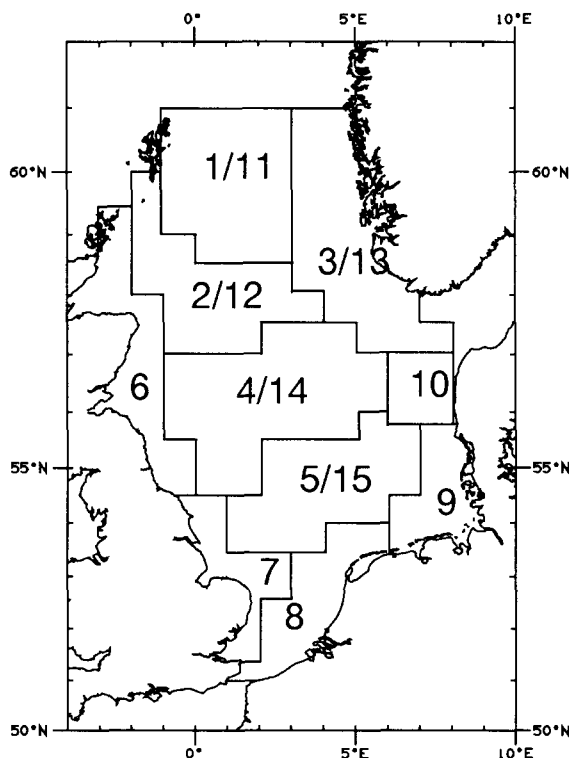

Fig. 3. ERSEM box structure. The deep boxes are divided into two layers, the top 30 m labelled as boxes 1 to 5 whilst the deep boxes are labelled 11 to 15.
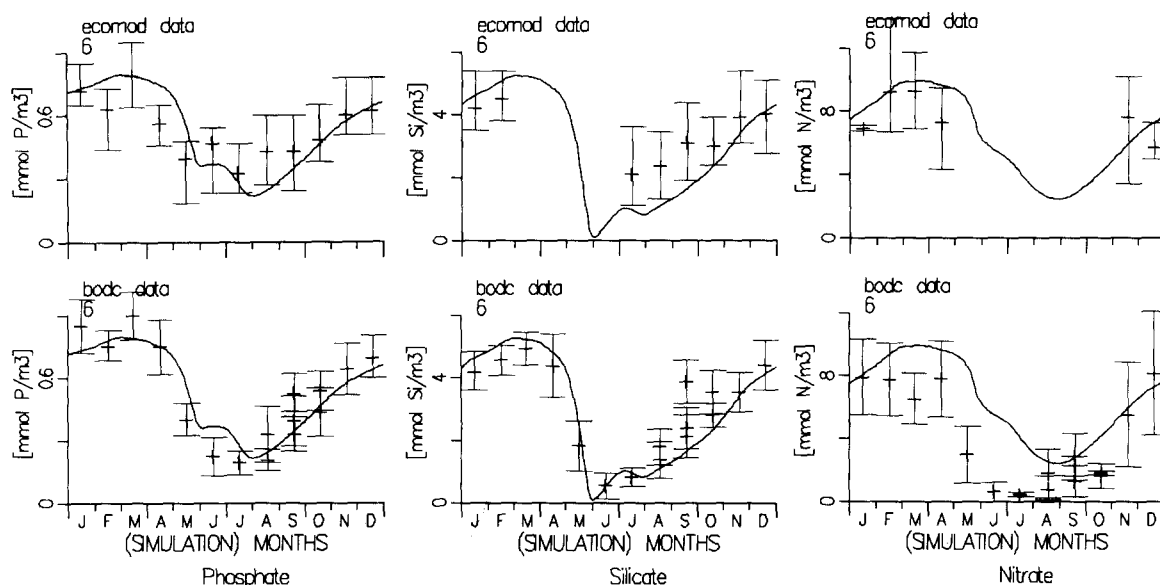
Fig. 4. Field data for box 6 from the ECOMOD dataset (upper panel) and the BODC data set (lower panel).

is calculated from the surface irradiance and integrated over the thickness of each spatial box, according to Steele (1962), with the extinction coefficient calculated from suspended matter concentration according to an empirical equation derived by Colijn (1982). Calculating the extinction coefficient from the background extinction and the actual suspended matter concentration (i.e. the sum of suspended sediment, detritus and phytoplankton) automatically introduces self-shading.

Mean water temperature in each box is prescribed as a sinusoidal function. These functions were derived from temperatures produced by the GCM of Pohlmann (1991) and box-averaged. All physiological rates have a temperature dependence, defined for the system's annually-averaged temperature (10°C) and multiplied by a factor containing the prevailing temperature dependence value (Q10) and the actual water temperature.

Freshwater inflows from the 14 major freshwater sources are given as fortnightly time series for the year 1985. The data have been made available by the Department of Public Works acting on behalf of the North Sea Task Force (NSTF).

2.1.3. THE NUMERICS

The model contains both fast processes, with rates in the order of 1 d^{-1}, and much slower processes. This generally creates problems for most numerical methods of solving ordinary differential equations. The high daily rates of change caused by the fast processes are handled by a dynamical time-step adjustment in the Euler integration routine, which automatically adjusts the step size such that the largest change in any state variable does not exceed 50% of the mass present, thus striking a balance between numerical accuracy and computational overhead. Another numerical problem is caused by the discontinuity of some of the forcing functions (irradiance, advection, diffusion) which throughout are provided as daily averages. These appear as step functions, causing the numerically more accurate Runge-Kutta integration methods to be computationally very inefficient.

As the conceptual time step in the model is a day, diurnal cycles are not explicitly resolved. Therefore, the time step adjustment to smaller steps does not produce a higher resolution of biological phenomena.

2.2. MODEL VERIFICATION

Two data sets were used for model verification. For the area south of 55°30' N the data set assembled in the North Sea Project of the Natural Environment Research Council was available, distributed by the British Oceanographic Data Centre (BODC) on CD-ROM. These were collected during monthly surveys of the southern and central North Sea, roughly covering the ERSEM boxes 4/14, 5/15 and 6 to 10, during a 15-month period in 1988-1989. Data for the northern areas, the ERSEM boxes 1/11, 2/12 and 3/13 were kindly made available by the Marine Laboratory Aberdeen and ICES and collated by the Institut für Meereskunde in Hamburg in a data base (ECOMOD).

All samples within an ERSEM box during one survey period were treated as replicates and averaged. Range bars were used to indicate the spatial variabil-
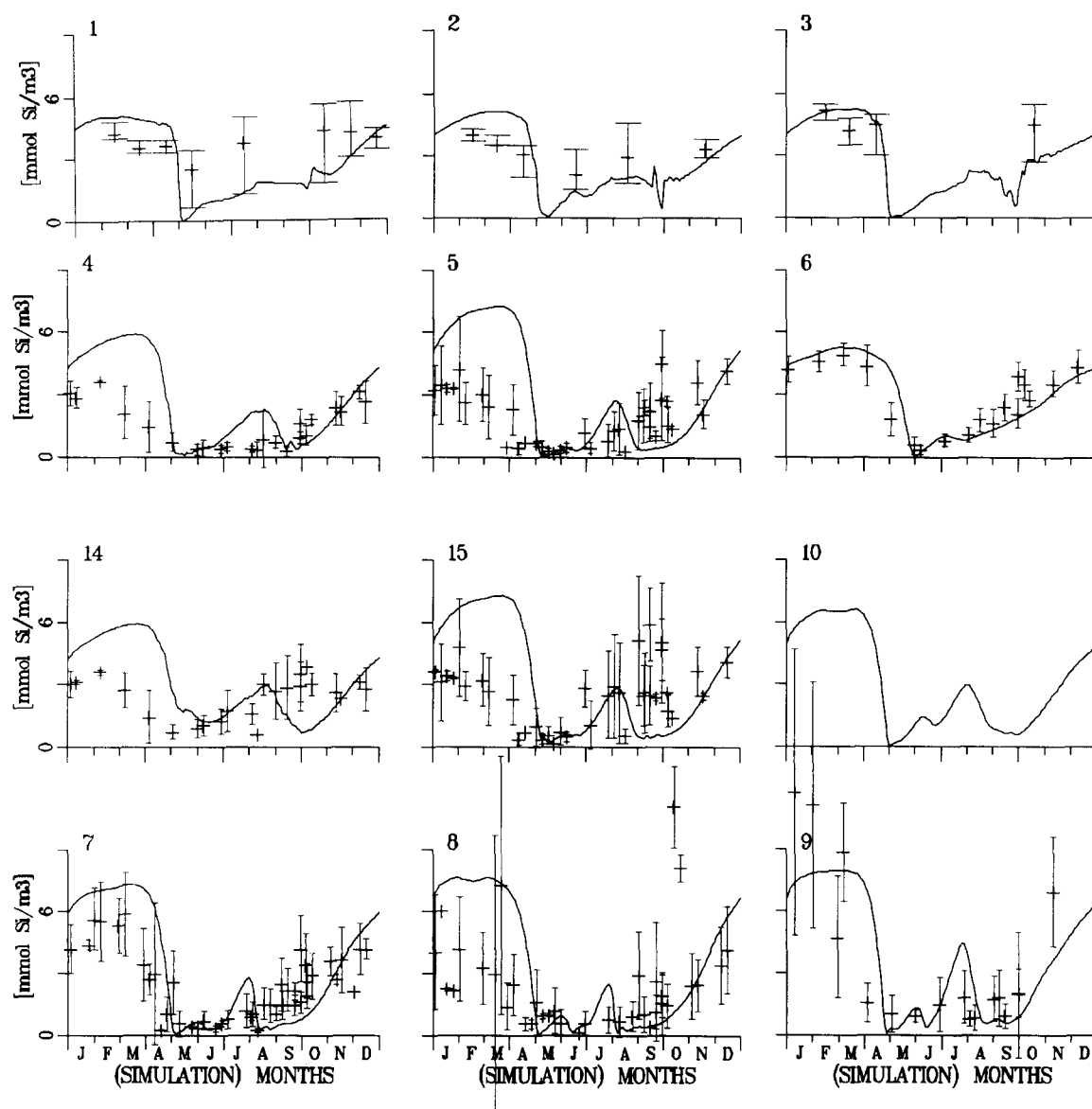
Fig. 5. Simulated seasonal dynamics of silicate, with validation values of the BODC data set for all boxes except for the boxes 1 to 3, where the ECOMOD data set has been used.

ity within the boxes (Fig. 4).

The data show the coastal boxes to have a very high spatial variability for all nutrients with the exception of box 6 along the north-east coast of the UK. The explanation for this is the presence of large and variable nutrient sources in the coastal boxes, such as the Thames, Scheldt, Rhine and Elbe, and the existence of steep but variable gradients in nutrients and suspended matter concentrations normal to the coast. These gradients cannot be resolved on the scale of the ICES boxes with the consequence that they appear as variability in the data. Box 6 does not

have these gradients, because, though deep, it is generally well-mixed and receives relatively little nutrients from land.

Despite the high variability in the aggregated data, the seasonal dynamics are very clear: all nutrients, except NH_4, reach maximum concentrations in winter, decrease rapidly during March and April, have variable but low concentrations during summer and increase rapidly in autumn to winter values. This seasonality was observed both in the well-mixed coastal areas and in the seasonally stratified surface (0 to 30 m) and deep boxes (30 m to bottom) of the central
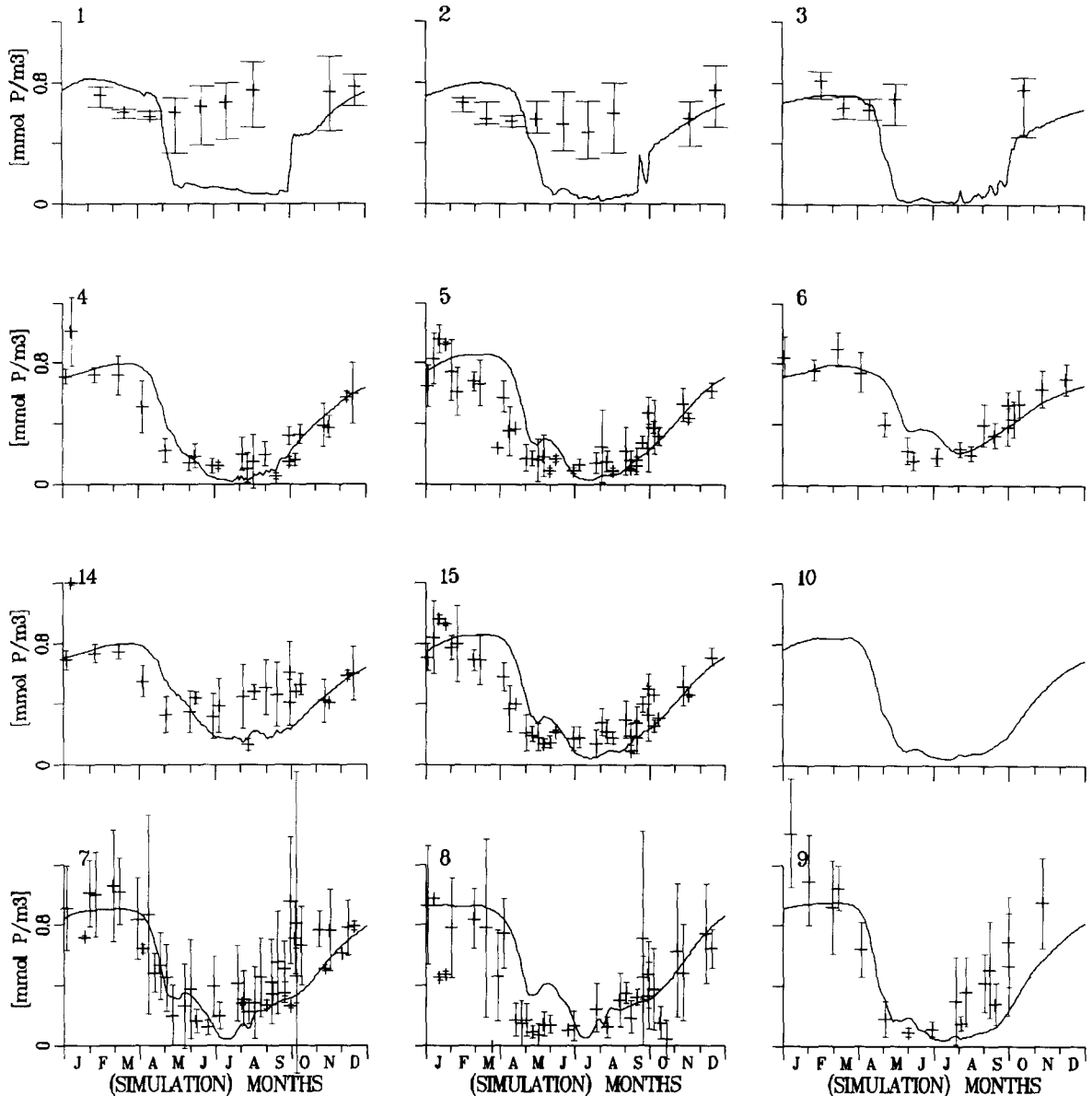
Fig. 6. Simulated seasonal dynamics of phosphate, with validation values of the BODC data set for all boxes except for the boxes 1 to 3, where the ECOMOD data set has been used.

North Sea, with the deep boxes (e.g. 14 and 15) maintaining higher nutrient concentrations during summer than the surface boxes, due to both benthic-pelagic nutrient fluxes and to reduced nutrient uptake by phytoplankton because of light limitation. However, the seasonality of nutrient concentrations in the surface boxes in the northern North Sea (boxes 1 and 3) seems to be rather different at least for PO_4. In those regions, PO_4 concentrations are relatively constant throughout the year, with a tendency towards a late summer maximum. As the ECOMOD data for the northern area are from a different source than the

BODC data, inconsistency between the data sets might be responsible for the apparent difference in seasonality. However, as both data sets overlap in box 6 (Fig. 4) and are completely coherent there, this is unlikely to be the case.

3. RESULTS

Nutrients The observed seasonal dynamics of the nutrients (Figs 5-8) are qualitatively reproduced by the model, with the regional differences being more pronounced in the data than in the model results. The
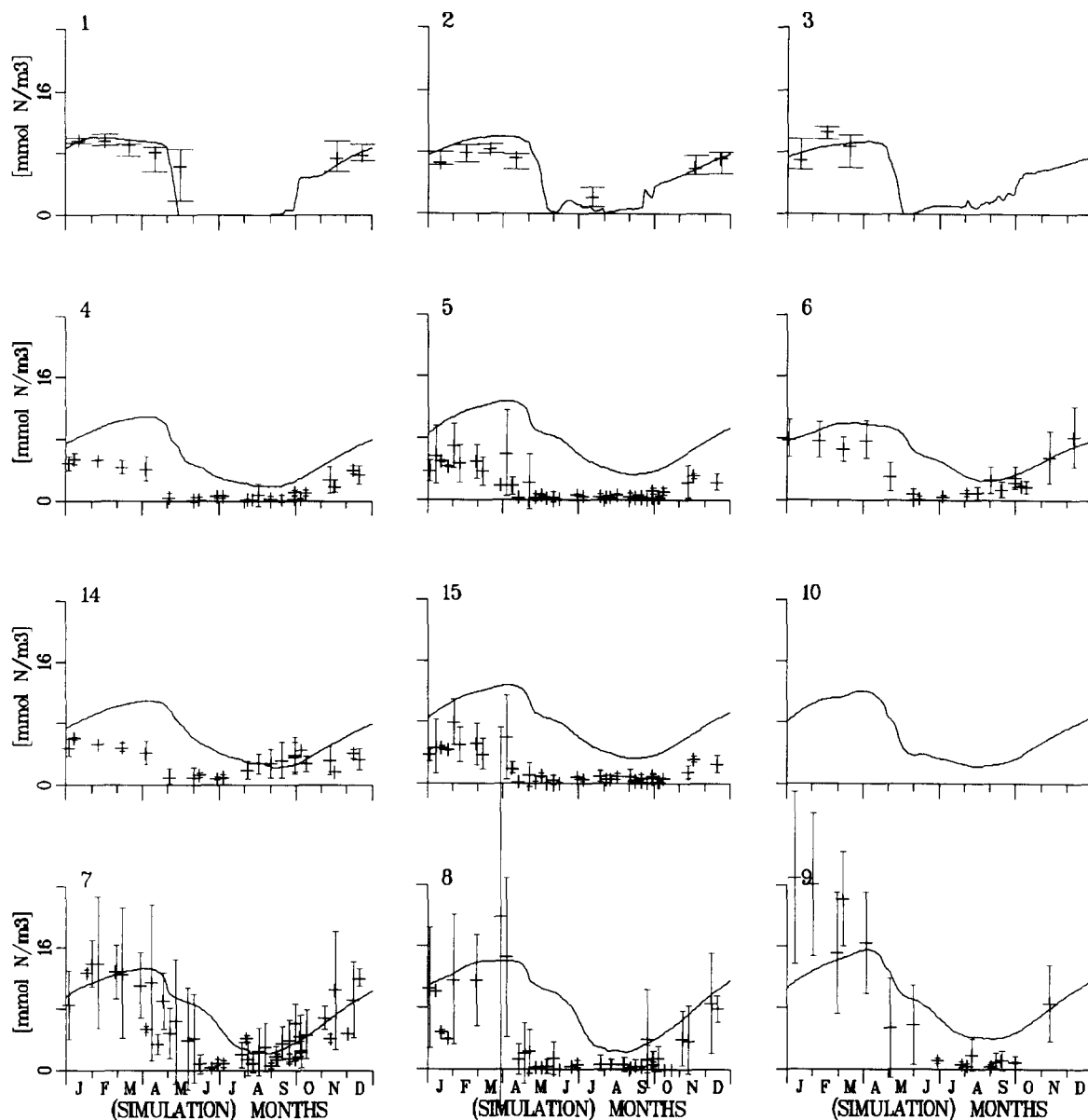
Fig. 7. Simulated seasonal dynamics of nitrate, with validation values of the BODC data set for all boxes except for the boxes 1 to 3, where the ECOMOD data set has been used.

differences in nutrient cycling between surface and deep boxes are well reproduced. This indicates that the vertical scale of the model matches the physical forcing rather well and captures the controlling physical processes, whereas the horizontal scale is (much) too large, averaging out existing gradients.

The strikingly different seasonal dynamics in box 6 (the UK north-east coast box) vs the continental coastal boxes are reproduced very well by the model, with the exception of NH_4, which has no clear seasonality in the data and is extremely variable in the model especially in box 6.

An overall budget of the major terms in the annual nutrient fluxes through the system, compiled from the model results (Radach & Lenhart, 1995), is given in Table 1.

For nitrogen and phosphorus, the river input is nearly balanced by outflow over the boundaries, mainly through compartments 3/13. This close balance is not surprising, as the system is in dynamic equilibrium. There are striking differences between N, P and Si with 64% of the total nitrogen mineralization taking place in the water column, 45% of the total phosphorus mineralization and only 3% of the total
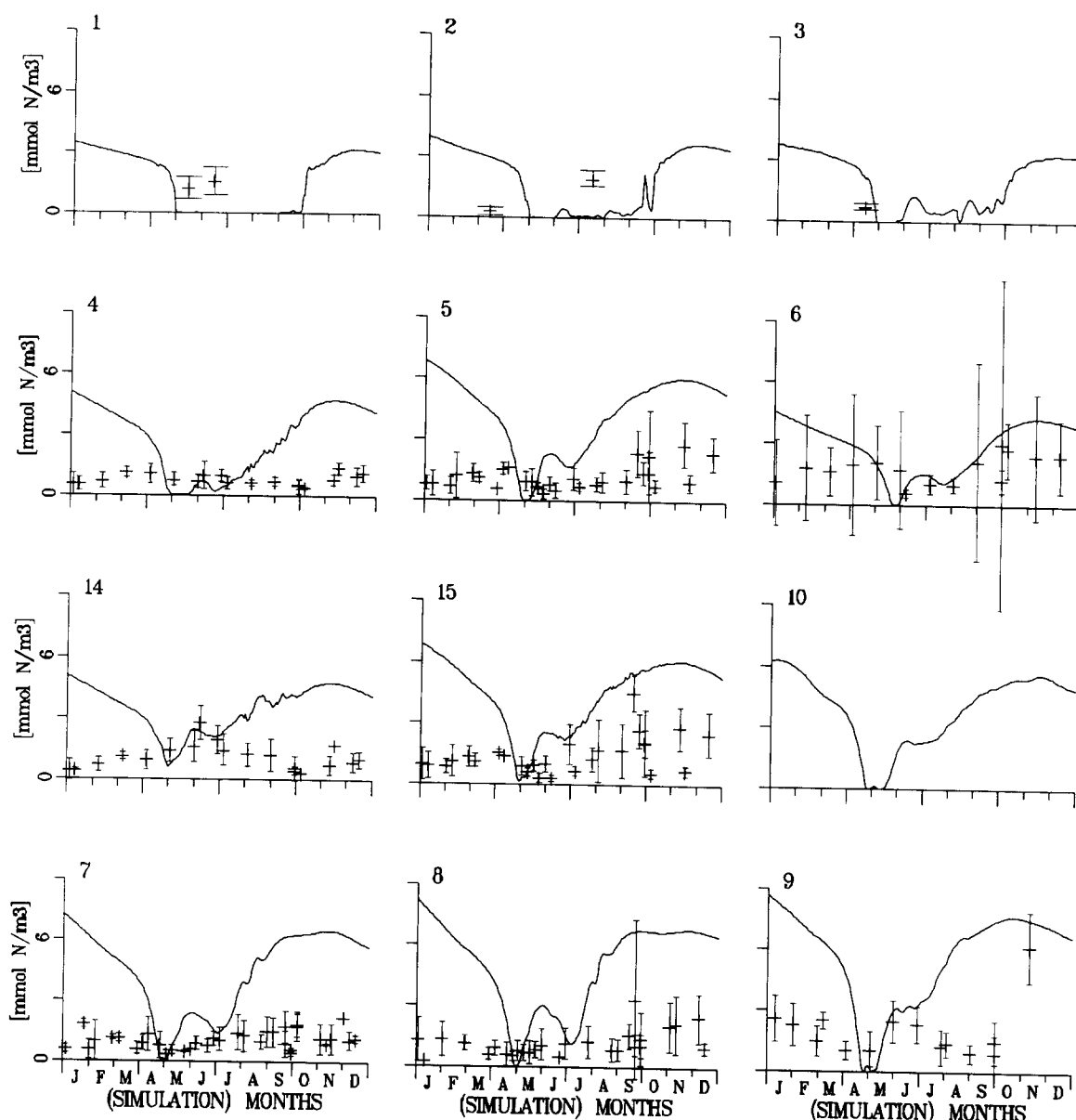
Fig. 8. Simulated seasonal dynamics of ammonium with validation values of the BODC data set for all boxes except for the boxes 1 to 3, where the ECOMOD data set has been used.

silicate mineralization. The implication is that nitrogen mineralization is faster than P mineralization in the model. This explains why the model predicts that large parts of the North Sea are P-limited, which is rather unlikely. This may also (partly) explain why the predicted ammonium concentrations in summer are higher than observed.

Other interesting aspects are the large in- and out-flows of dissolved silicate which exceed the uptake flux by diatoms, reflecting the poor utilization in autumn and winter.

Finally the small contribution of the rivers to total nutrient flows in the North Sea can be pointed out, which explains why we only see local effects of the river contribution and no detectable effects on the system as a whole.

Phytoplankton The spring bloom of diatoms predicted by the model is not evident in the data. The standing stock in winter is underestimated but the biomass during summer is in general agreement with the data. The data are based on phytoplankton counts converted to carbon biomass (cf. Baretta-Bekker et al., 1995). Primary production in the model is lower than observed for the coastal boxes, but higher than

observed for the offshore boxes (Joint & Pomroy, 1993), probably as a consequence of the spatial setup of the model, which exaggerates the dispersion of nutrients.

Flagellate phytoplankton biomass distribution is in qualitative agreement with the available data, with a maximum occurrence in the German Bight (box 9).

Microzooplankton The model reproduces the seasonality seen in the data reasonably well. However, the data were derived from counts of Lugol- or formaldehyde-preserved samples, and the biomass estimates based on these counts are probably underestimates, since many microzooplankton species desintegrate on preservation (cf. Sorokin, 1981). Instead of overpredicting concentrations of microzooplankton the model may thus underpredict abundance.

Mesozooplankton dynamics are in good correspondence with the data for the second half of the year, but show unrealistic behaviour in the first half, partially due to the absence of zooplankton immigration across the northern boundaries in spring.

Fish In view of the coarse spatial resolution of ERSEM, fish migration, or rather fish distribution,

over the modelled area is prescribed using catch data (cf. Bryant et al., 1995). The predation mortality imposed by fish as a static load on the rest of the system is very low but, not being density-dependent, is still sufficient to drive some benthic components to extinction. Dynamic fish growth is implemented as a global object in the model.

Benthic biology The seasonal and spatial distribution and activity of benthic organisms as predicted by the model cannot directly be verified with existing data. Such data do not exist. However, the observed regional differences in annually-averaged standing stocks of the different benthic functional groups are broadly reflected in the model results. Progress in modelling of benthic biological dynamics is, and will be, strongly dependent on marine benthic ecology becoming more process-oriented and less descriptive.

Benthic nutrient dynamics as predicted by the model as well as the oxic/anoxic transition depths are in good correspondence with benthic nutrient flux experiments but cannot reflect the spatial variability observed in the field due to the coarse spatial resolution and the absence of bed-load transport of particu-

TABLE 1
Annual budgets in kt of the dissolved compounds of nitrogen, phosphorus and silicon in the water column in the North Sea.

	N		P		Si	
	in	out	in	out	in	out
dissolved						
transport over the boundaries	13108	13893	1864	1933	11519	11726
import from rivers	668		43		233	
uptake		17621		1843		9838
pelagic mineralization	11090		816		270	
fish excretion dissolved	345		69			
benthic mineralization	6332		988		9597	
subtotal	31543	31514	3780	3776	21619	21564
particulate						
transport over the boundaries	3189	3111	550	540	2285	2312
import from rivers	154		23		24	
uptake	17621		1843		9838	
pelagic mineralization		11090		816		270
fish grazing		309		76		
fish excretion	227		45			
sedimentation		6690		1031		9579
subtotal	21191	21200	2461	2463	12147	12161
total						
transport over the boundaries	16297	17004	2414	2473	13804	14038
import from rivers	822		66		257	
fish excretion	572		114			
fish grazing from pelagic		309		76		
benthic mineralization	6332		988		9597	
sedimentation		6690		1031		9579
overall total	24023	24003	3582	3580	23658	23617

lates. The model results indicate that the recycling of organic matter and the associated nutrients in the benthic system in this relatively shallow system occurs within a year of deposition and that there is generally no long-term accumulation of organic matter in the North Sea.

4. DISCUSSION

The importance of treating production and mineralization processes symmetrically in modelling the cycling of organic matter and nutrients was pointed out by Mommaerts (*cf.* Fransz *et al.*, 1991). He gave both a flow diagram (fig. 21 in Fransz *et al.*, 1991) and the conservation equations (table 5 in Fransz *et al.*, 1991) for an idealized marine ecosystem model. A comparison with the flow diagram for ERSEM (Fig. 1) shows ERSEM to be an implementation of this idealized marine ecosystem model with some significant refinements: The Z (zooplankton) compartment of the idealized model is resolved into heterotrophic flagellates, microzooplankton and two groups of mesozooplankton as state variables, and not prescribed as forcing functions. However, the most extensive differences are in the representation of benthic processes. Whereas in the idealized model all benthic-pelagic interactions perforce are aggregated into particulate detritus arriving in the sediment and the associated nutrients being remineralized by benthic bacteria, in ERSEM the benthic nutrient concentrations themselves are dependent on biological activity (*cf.* Ebenhöh *et al.*, 1995) and early diagenetic processes (*cf.* Ruardij & Van Raaphorst, 1995), and directly interact with water-column concentrations to define the direction and magnitude of benthic-pelagic nutrient fluxes. The model thus dynamically simulates the cycling of N, P, and Si from the uptake of dissolved inorganic forms by phytoplankton, and the various transitions into dissolved and particulate organic forms in the detrital and biological state variables in the water column. It does not short-circuit this cycling at the sediment-water interface but resolves benthic nutrient dynamics fully.

The uncertainty as to the correct parameterization of benthic processes has led most modellers to avoid explicit representation of any benthic constituent except benthic bacteria and/or detritus. In ERSEM we take advantage of the fact that the consequences of incorrect parametrizations of benthic processes will show up in unexplainable discrepancies elsewhere in the system between model results and observations. Sensitivity analyses of uncertain parameters can thus be used to identify those benthic processes where we most urgently need experimental data in order to improve our system description (Ebenhöh *et al.*, 1995).

Marine ecosystem models usually describe a spatially delimited subsystem of the global ocean. This implies open boundaries with mass and energy flows across these boundaries. This exchange over the boundaries reduces the autonomy of the dynamic behaviour of the system, since the boundary conditions act in the same way as forcing functions, modifying system function without feedback from the system itself. It is therefore important that the spatial extent of the system be defined such that the internal dynamics of the system are not dominated by the boundary conditions. Ideally, on the time-scale of dominant biological processes (weeks), an approximation of the system as being mass-closed, should be valid. At the very least, the spatial resolution should be chosen such that the mass flows generated in a spatial box by the internal dynamics dominate the mass flows generated by advection and dispersion across the boundaries. The sea outside the systems boundaries is also a dynamic system and behaves according to similar dynamical rules. Hence, too large deviations between boundary concentrations and dynamically calculated system-internal concentrations may point to serious model faults or to errors in the boundary conditions.

The seasonal signal imposed by solar radiation drives the annual cycle of heating and cooling that defines the long-term and large-scale vertical structure in the water column. At the other end of the scale, diel cycles of heating and cooling determine the daily depth of mixing, while intermediate events, with periodicities of days to months are generated by major weather patterns and the passage of storms. The effects of these periodic events on the vertical structure of the water column are expressed in the model in the daily varying vertical diffusive exchange between surface and deep boxes. As the vertical scale in the model is a few tens of metres, vertical processes can be comfortably represented at physiological levels and time scales (Schindler, 1988). In the horizontal plane the spatial scale in the model is of the order of 200 km, due to the size of the boxes, which implies a time scale of a few months for environmental fluctuations to be observable on this scale (Harris, 1980). This discrepancy between horizontal and vertical space scales and thus —implicitly— time scales may very well have consequences in that the tacit assumption of homogeneity over length scales of hundreds of kilometres is rather less realistic than assuming homogeneity over tens of metres, as is the case for the vertical.

The model contains many feedback mechanisms, many of them implicit, because of the tight coupling between the carbon and nutrient cycles and between benthic and pelagic processes. These make the model system self-organizing to some extent and dynamically very persistent. This self organization can clearly be seen in the regional differences in the relative fluxes through the system components (fig. 8 in Baretta-Bekker *et al.*, 1995). Even if some functional groups go extinct in some of the spatial compartments, due to predation pressure or to starvation,

this leads to a different routing of energy flows through the benthic system, but not to a collapse of the system. A corollary of this property is that the model system exhibits great persistence in terms of total metabolic functions, such as photosynthesis, respiration and nutrient cycling, which is also a feature in most real ecosystems (Pomeroy & Alberts, 1988). This feature should not be interpreted as being in any way relevant for system shifts whereby species occupying a certain niche are replaced with others since individual species are hidden in the model by the functional group approach.

An aspect which reduces the self-organizational capability of our model system is the fact that we prescribe the trophic interactions between functional groups by way of availability coefficients. These coefficients reflect the size-relationship between functional groups which are presumed to be constant.

5. CONCLUSIONS

The dynamics of the lower trophic levels are very much determined by the abiotic environment (hydrodynamics, the structure of the water column, horizontal and vertical transport of nutrients and particulates), which control the resource supply. The dynamics of higher trophic levels may both be resource-controlled (bottom-up control) and predation-controlled (top-down control).

As pointed out by Ebenhöh et al. (1995), the present model, as a consequence of the functional group approach, should be seen as a complicated model of simple trophic interactions instead of as a complex model, since competition for the same resource mainly occurs within the functional groups, thus excluding explicit resource competition between species or groups of species. This prevents the model from expressing chaotic behaviour. However, Ebenhöh et al. (1995) show that by introducing a modest degree of explicit resource competition, chaotic behaviour can be elicited immediately in the benthic system, without this having negative effects on long-term system stability. They even argue that it increases system stability.

The results of the model, making a hindcast for 1988 and 1989, indicate that the major controls on the seasonal cycling of nutrients and organic carbon are represented in the model, since the model results closely reproduce the observed values for this period of silicate and phosphate (Figs 5 and 6).

The model results for NO_3 and NH_4^+ (Figs 7 and 8) do not reproduce the observations well, with NO_3 remaining too high in summer and NH_4^+ concentrations being too high overall. This discrepancy has been traced in part to the absence of a specified boundary condition for NH_4 at the English Channel boundary. This again illustrates the importance to system function of correct boundary conditions. At the same time, since obtaining correct boundary condi-

tions for periods longer than one year is very difficult, the sensitivity of this type of model to the boundary conditions bodes ill for long-term trend analysis runs, unless it can be shown that the boundary conditions can be treated as climatological. As we have seen indications (Lenhart et al., 1995) that the numerical dispersion inherent to the use of large spatial boxes 'smears out' the regional differences between the system components and that these large boxes damp the variability in the system, the next step in our modelling work should be to refine the spatial grid. The advantage of the box-model approach with regard to the representation of transport processes has been that it allowed us to neglect small-scale interactions between hydrodynamics and biology and the associated steep gradients in favour of getting the overall description of processes interacting appropriately in a consistent way. Another approach could be to directly force the ecological processes with a general circulation model. This would also allow us to address the unresolved problem of dynamically modelling resuspension/deposition processes, bed-load transport of detritus and the adsorption/desorption of nutrients during deposition and resuspension. These closely related processes may be expected to be key processes in the interaction between the coastal zone and the open ocean and our capability to model them at present is woefully lacking.

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