



# Review of three-dimensional ecological modelling related to the North Sea shelf system

## Part 1: models and their results

Andreas Moll \*, Günther Radach

*Institut für Meereskunde, Troplowitzstr. 7, 22529 Hamburg, Germany*

Received 28 February 2002; accepted 28 April 2003

### Abstract

The state-of-the-art in modelling the marine ecosystem of the greater North Sea is reviewed, providing an overview especially about three-dimensional models that describe and predict how the marine ecosystem of the greater North Sea area functions and how concentrations and fluxes of biologically important elements vary in space and time, throughout the shelf and over years, in response to physical forcing. Articles with a strong concentration on modelling were selected from the available literature, and all articles around the existing “ecological modelling groups” dealing with the area of the North Sea were sorted in chronological order of their appearance in the literature. We found eleven of such groups and described their different modelling efforts. Selecting the seven three-dimensional models (NORWECOM, GHER, ECOHAM, ERSEM, ELISE, COHERENS and POL3dERSEM), we characterized the complexity of the models, by comparing the resolution in time and space, and the resolution of the trophic structure by discussing the number and kind of state variables and of the processes relating these state variables to each other.

The review of biogeochemical/ecological modelling for the greater North Sea shows that important findings by model simulations have either confirmed existing knowledge derived from field work or have given new insight into the mechanisms of the functioning of the North Sea system: the temporal and spatial development and magnitude of primary production, its spreading from the coasts to the north-west over the open North Sea, its mechanisms of limitation, the functioning of the pelagic small food web and of the benthic web, the mechanisms of nutrient regeneration, the effects of riverine and atmospheric nutrient inputs causing eutrophication of coastal waters, the extent of eutrophication in the North Sea, and the budgets for nitrogen, phosphorus, and silicon. The three-dimensional ecological models of the greater North Sea have provided consistent distributions and dynamics of the lower trophic levels on their regional, annual and decadal scales which cannot be derived to this degree of coverage by observations.

The state-of-the-art in validation for these models is presented in part 2

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**Keywords:** Atlantic; European Continental Shelf; North Sea; Phytoplankton dynamics; Ecosystem dynamics; Nutrient dynamics; Eutrophication; Pelagic-benthic coupling; External forcing; Biogeochemical modelling; Ecological modelling; Three-dimensional modelling; Model evaluation

\* Corresponding author. Tel.: +49 40 42838 2526; fax: +49 40 5605724.

E-mail address: [moll@ifm.uni-hamburg.de](mailto:moll@ifm.uni-hamburg.de) (A. Moll).

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## 1. Introduction: from societal needs to Grand Challenges in research

As many shelf ecosystems, the North Sea is under growing stress caused by the various and partly conflicting human demands. The large populations in the coastal areas have strong impacts on the natural environment. The most important challenges, the so-called “Grand Challenges” to North Sea research (Sündermann, 2001; Sündermann et al., 2001) concern the questions (1) “What changes of the North Sea system are to be expected in the next decades?”, (2) “To what degree are these changes anthropogenic (e.g. due to over fishing, contaminants or human-induced climate change) and thus principally controllable?”, and (3) “What operational strategies (e.g. monitoring, coastal management, reduction measures) are necessary for sustainable development in the North Sea?” The challenges demand knowledge of the dynamics and driving forces of North Sea subsystems (Fig. 1), i.e. of the pelagic and the benthic division in stratified areas offshore and in non-stratified coastal waters. When focussing on the subsystems one notices that they are inevitably coupled with each other (Murray, Barthel, Barth & Fragakis, 2001).

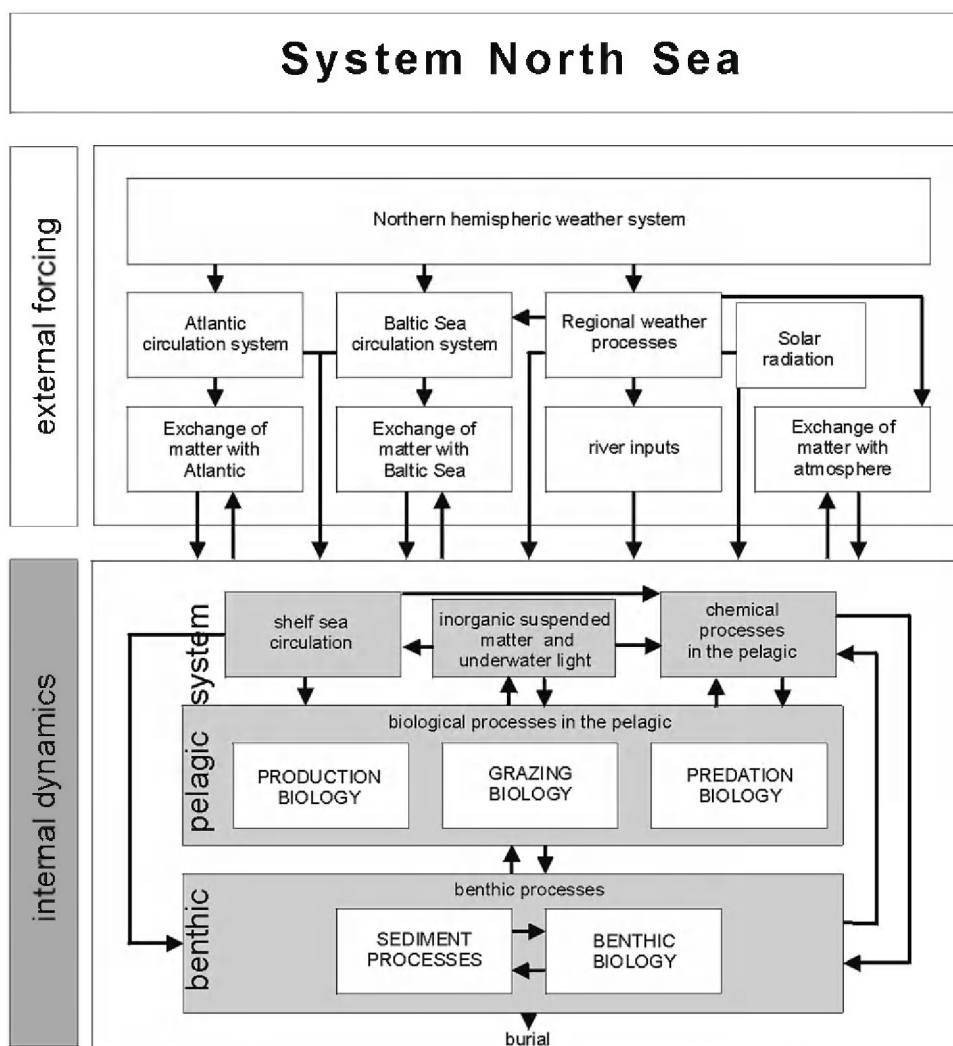


Fig. 1. The North Sea ecosystem is embedded in its geological, physical and chemical environment, which modelling of its ecosystem must take this into account. The “System North Sea” is divided into internal dynamics and external forcing to illustrate the coupling of the driving forces with its pelagic and the benthic subsystems. These subsystems are coupled as illustrated by arrows. Ecosystem function cannot be understood without its relations to the environment that are characterised by the general shelf sea circulation and chemical processes. The external forcing acts on the dynamics of the ecosystem as exchange of matter with adjacent sea areas (Atlantic, Baltic Sea) and the atmosphere, and as river inputs. Additionally, solar radiation acts as forcing. Altogether the external forcing causes variability in ecosystem processes.

The general problem when trying to tackle the Grand Challenges to North Sea research is the complexity of the environmental compartments and their interconnections. On one hand, our growing understanding of environmental problems leads to the necessity to deal with more of this complexity. On the other hand, our relative ability to investigate environmental problems by field experiments at the necessary level of complexity decreases as the questions become more complex! One way out of this dilemma is to use adequate simulation models, in combination with field experiments.

The overall aim of this paper is to review the state-of-the-art in modelling related to the marine ecosystem

of the greater North Sea. We concentrate on models using ordinary and partial differential equations, which are usually conservation equations. We would like to provide an overview about three-dimensional (3D) models that describe and predict how the marine ecosystem of the North Sea functions and how concentrations and fluxes of biologically important elements (carbon (C), nitrogen (N), phosphorus (P), silicon (Si), oxygen (O)) vary in space and time, throughout the shelf and over periods of years, in response to physical forcing. Our objective is to describe the modelling approaches and modelling groups dealing with the North Sea, their history, evolution and important results.

The review includes nutrient cycle models (N, P, Si) with rudimentary biology, models with detailed biologically mediated fluxes of elements (C, N, P, Si, O) through the ecosystem, and ecosystem models representing the full nutrient and/or carbon cycle including trophodynamics. We include models of specific aspects of the ecosystem like primary productivity, nutrient regeneration, (harmful) algal blooms, oxic conditions, eutrophication, species successions, trophic interactions, recruitment of stocks, sedimentary processes and benthic-pelagic coupling. Such models often form the basis for three-dimensional model versions.

It is well-known that the physical environment is of great importance for the development of the biological components of the ecosystem (Mann & Lazier, 1991), and therefore our review has a focus on models which incorporate a strong physical component. The North Sea is embedded in larger ecosystems, and modelling must take that into account in respect to the forcing factors as shown in Fig. 1, where the ecosystem is represented as composed of pelagic and benthic subsystems. We neglect the littoral zones, estuaries and the wadden seas. External forcing factors include exchange of matter with adjacent sea areas (Atlantic, Baltic Sea), exchange of matter and energy with the atmosphere and river inputs. Additionally, solar radiation acts as forcing. Altogether the external forcing causes variability in model ecosystem responses, as is certainly the case in the actual North Sea. With respect to future problems in the region, a decadal time frame has to be considered to give models predictive utility.

The number of models published per year has increased exponentially, and consequently a number of reviews have been published since the 1960s. Models about ecological aspects of the North Sea appearing in the literature up to 1989 were reviewed by Fransz, Mommerts and Radach (1991), so we make only limited reference to them. They were mostly vertically integrated box models, vertical section models or one-dimensional water column process models. We concentrate on the last decade in considering papers on models with three-dimensional ecological representations. Ecological modelling of fjords was reviewed by McClimans, Loed and Thendrup (1992). The overview by Wroblewski and Hofmann (1989) focused on models investigating transport of biogenic material among estuarine, nearshore, shelf, slope and oceanic regimes. General plankton- and ecosystem models are usually formulated as advection-diffusion-reaction equations (ADREs). Overviews about the status of such models were given by Hofmann (1991) and Hofmann and Lascara (1998). Evans and Fasham (1993) and contributors to their book dealt with a general model of biogeochemical processes, especially for the oceanic system. Carlotti, Giske and Werner (2000) give a good overview about the methodology for building zooplankton models and about the existing literature on zooplankton models. Approaches for modelling processes transporting contaminants (including nutrients) in water, biota and suspended matter for the pelagic and benthic systems were summarised by GESAMP (GESAMP Joint Group of Experts on the Scientific Aspects of Marine Pollution, 1991).

Twenty five years after the introduction of the first coupled physical-biological models (Jamart, Winter, Banse, Anderson & Lam, 1977; Radach & Maier-Reimer, 1975), and ten years after the review on ecological models for the North Sea by Fransz et al. (1991), it is appropriate to assess the current status of modelling marine ecosystems and to look to the future, especially for three-dimensional modelling in the greater North Sea area.

## 2. Survey of three-dimensional ecological models

Three-dimensional ecological modelling became feasible when computer power reached a stage where the necessary trophic resolution could be combined with the desired spatial and temporal resolution. The development of these models has followed the availability of circulation models for the oceans and the shelf seas that could be used as forcing in ecological modelling.

About 1986 the development of three-dimensional ecological models started in Japan and in the USA. The first differential three-dimensional models were developed for the East Seto Inland Seas in the Pacific (Kishi & Ikeda, 1986), for the mid-Atlantic Bight (Walsh, Dieterle & Meyers, 1988), and for the limnic system Lake Okeechobee in Florida (Dickinson, Huber & Pollman, 1992). It was only a few years later, namely in the year 1993, that the development of three-dimensional ecological models for the North Sea started in several institutions around its perimeter.

Global three-dimensional biogeochemical modelling started in the late 1980s on the basis of dynamical ocean general circulation modelling, e.g. by Maier-Reimer and Bacastow (1990). Development of global or basin-scale models and that of shelf sea models has run in parallel, with little exchange or model coupling so far, although many of the problems in modelling the biogeochemical cycles are the same. Large-scale ecological models have mostly been used to investigate problems connected to climate change, in particular effects of naturally varying carbon dioxide partial pressure ( $p\text{CO}_2$ ) and anthropogenic carbon dioxide ( $\text{CO}_2$ ) uptake in the oceans. Ecological models for the shelf seas were mostly concerned with the investigation of the functioning of the ecosystem with regard to eutrophication problems, e. g. for the north-west European shelf seas (Zevenboom, 1994).

The first three-dimensional ‘ecosystem’ model for the North Sea was the NORWECOM (1993), followed by the GHER model (1994), ECOHAM and ERSEM in 1995. Two of these models were updated into NORWECOM2 and ERSEM-II. The model ELISE was restricted to the English Channel only. The bulk of model articles appeared relatively recently. The advantage of three-dimensional modelling compared to one-dimensional modelling is that all transport processes, both advection and turbulent diffusion, are included.

Several research groups around the North Sea are working on (three-dimensional) ecosystem models. All were based on ecological, zero-dimensional models, one-dimensional water column process models or two-dimensional vertically-integrated or section models. These are considered here in addition to the papers on the three-dimensional models. We aggregated the key articles of the “ecological modelling groups” according to the names of the models.

Table 1 lists the names of North Sea “ecological models”, gives references to articles in the literature applying those names and shows the institutional affiliations of the modelling groups. All articles on models reviewed here are referenced in Moll and Radach (2001).

Several one-dimensional models have been extended to three-dimensional models for the North Sea. These spatially simpler models were in one case a zero-dimensional, preliminary model of biological processes (Aksnes & Egge, 1991) and in another a model for a mesocosm study (Aksnes et al., 1995). Often a one-dimensional water column process model was extended to three spatial dimensions (Aksnes & Lie, 1990; Allen, Blackford & Radford, 1998a; Menesguen, 1991; Radach & Moll, 1993; Ruurdij, van Haren & Ridderinkhof, 1997; Tett & Walne, 1995; Varela, Cruzado, Tintore & Ladona, 1992).

The three-dimensional models of the greater North Sea initially addressed pelagic habitats only (Skogen, 1993), but later versions included a simple bottom detritus compartment (Moll, 1995) introducing benthic remineralisation. Another line of modelling treated all chemical and biological compartments at once, leading to extended box modelling in three dimensions during the 1990’s MAST project called “European Regional Seas Ecosystem Model (ERSEM)”. This complex ERSEM ecosystem model has been developed for the North Sea and was used for investigating many aspects of this ecosystem (Baretta, Ebenhöh & Ruurdij, 1995; Baretta-Bekker & Baretta, 1997). Blackford and Radford (1995) gave the rationale for the



Table 1  
Models of North Sea "ecological modelling groups" and their evolution

No	Model name	0d Biogeochemical model	1d Water Column model	2d Applications	3d Circulation model	3d Ecosystem model
1	NORWECOM 1/2 Norwegian Ecological Model System, IMR, Bergen	(Asknes & Egge, 1991; Asknes et al., 1995)	(Asknes & Lie, 1990)	(Balino, 1996)	(Svendsen, Saetre & Mork, 1991; Svendsen, Bernitsen, Skogen, Ulvestad, 1995; Adlandsvik & Martinsen, 1996)	(Skogen, 1993; Skogen, Svendsen, Bernitsen, Aksnes & Skogen, 1995; Asknes et al., 1995; Skogen et al., 1998; Skogen & Soiland, 1998; Soiland & Skogen, 2000)
2	GHER Geo-Hydrodynamics and Environment Research Model, ULG, Liege	none	(Varela, Cruzado, Tintore & Ladona, 1992; Delhez et al., 1993)	none	(Nihoul, Deleersnijder & Djenidi, 1989; Delhez & Martin, 1992; Delhez, 1996)	(Delhez & Martin, 1994; Delhez, 1998)
3	ECOHAM1 Ecological North Sea Model, Hamburg, IfM, Hamburg	none	(Radach & Maier-Reimer, 1975; Moll, 1989; Radach & Moll, 1993; Moll, 1997c)	(Lenhart, 1990)	(Hainbucher et al., 1987; Pohlmann, 1991; Pohlmann, 1996)	(Moll, 1995; Moll, 1997b; Moll, 1997a; Moll, 2000; Moll, 1999)
4	ERSEM I/II European Regional Seas Ecosystem Model, EU-Mast Project	(Baretta-Bekker, Baretta, Hansen & Riemann, 1998)	(Ruurdij, van Haren & Ridderinkhof, 1997)	(Baretta & Ruurdij, 1987; Baretta & Ruurdij, 1989)	(Pohlmann, 1991; Lenhart, Radach, Backhaus & Pohlmann, 1995)	22 articles in: (Baretta, Ebenhöh & Ruurdij, 1995; Baretta-Bekker & Baretta, 1997)
5	ELISE Ecological Modelling Software for interactive modelling, Ifremer, Brest	(Menesguen, 1991)	(Menesguen, 1991)	(Chapelle, Lazure & Menesguen, 1994; Hoch & Menesguen, 1997; Menesguen & Hoch, 1997; Guillaud, Andrieux & Menesguen, 2000)	2d: (Salomon & Breton, 1993; Cugier, 1999)	(Hoch and Garreau, 1998; Cugier and Le Hir, 2000)

(continued on next page)

Table 1 (continued)

No	Model name	0d Biogeochemical model	1d Water Column model	2d Applications	3d Circulation model	3d Ecosystem model
6	COHERENS Coupled Hydrodynamical Ecological model for Regional Northwest-European Shelf seas, EU-Mast Project	none	(Tett, 1990; Tett & Walne, 1995)	CD-ROM Test cases	(Luyten, Deleersnijder, Ozer & Rudnick, 1996; Luyten, 1996)	CD-ROM (Luyten et al., 1999)
7	POL3dERSEM Proudman Oceanographic Laboratory 3d ERSEM Model, POL, Liverpool; PML, Plymouth	none	(Ruurdij, van Haren & Ridderinkhof, 1997; Allen et al., 1998a; Allen, Howland, Bloomer & Uncles, 1998b)	(Allen, 1997)	(Proctor & James, 1996; Holt & James, 1999)	(Allen et al., 2001)
8	MIRO after the Spanish painter, (EU-Project) FU, Belgium	(Lancelot, Mathot & Owens, 1986)	none	(Lancelot, 1990; Lancelot, Billen & Barth, 1991; Lancelot, Rousseau, Billen & van Eeckhout, 1997)	none	none
9	CSM-NZB/DYNAMO Continental Shelf Model — Noordzee-Bloom/Dynamic eutrophication Model, (MANS) Delft Hydraulics, NL	ECOLUMN-BLOOM II (Ecological water column model), (de Vries et al., 1998)	none	(MANS, 1991, Peeters et al., 1995; Los & Bokhorst, 1997)	GENO/ZUNOWAK (de Kok, 1996)	none
10	FYFY Fysisch Fytoplankton model, NIOZ, Texel	(Michielsen et al., 1994)	none	(van den Berg et al., 1996a, van den Berg et al., 1996b)	(Hainbucher, Pohlmann & Backhaus, 1987)	none
11	DYMONNS Dynamic Model of Nutrients in the North Sea, SOC, Southampton	none	(Tett, 1990; Tett and Walne, 1995)	(Hydes, Kelly-Gerrey, Thomson, Proctor & Prandle, 1997; Kelly-Gerrey, Gellers-Barkmann & Hydes, 1997)	2d: (Prandle, 1984; Jones & Howarth, 1995)	none

ERSEM modelling. In the first phase the North Sea was divided into a 15 box system (10 surface and 5 deep boxes), and during ERSEM II the resolution was increased to 130 boxes (85 surface and 45 deep boxes). Nutrient budgets were calculated on the basis of the coarse configuration (Radach & Lenhart, 1995). Scenarios for both reduction of nutrient inputs (Lenhart, Radach & Ruurdij, 1997) and long-term eutrophication of the North Sea (Pätsch & Radach, 1997) were simulated on the basis of the finer box configuration.

Regional-scale models (some of lower dimensionality) exist for specific areas of the North Sea. An application of box modelling (Hoch & Menesguen, 1997; Menesguen & Hoch, 1997) treated the English Channel as a quasi-three-dimensional ecological system. Two-dimensional models exist for different bays along the French Atlantic coast (Chapelle et al., 1994; Guillaud et al., 2000; Le Pape & Menesguen, 1997). The Southern Bight of the North Sea was modelled by Luyten et al. (1999) in the EU project “Coupled Hydrodynamical Ecological model for Regional northwest-European Shelf seas (COHERENS)”. Skogen (1998) and Skogen et al. (1998) investigated eutrophication problems in the Skagerrak. Joint modelling efforts within the EU-project “Phaeocystis blooms in nutrient enriched coastal zones of the Channel and the North Sea” focussed on the *Phaeocystis* blooms at the continental coast, developing the MIRO model (1990). Lancelot (1990) and Lancelot, Billen & Barth (1991) provided an ecological model for *Phaeocystis*-dominated coastal areas with three groups of phytoplankton, dissolved organic matter, bacteria and their predators, detritus in the pelagic, and a coupling to benthic detritus and nutrient pools. A final description of applications was given in Lancelot, Rousseau, Billen and van Eeckhout (1997). MIRO had no three-dimensional model version.

Another regional-scale effort for the coastal strip off The Netherlands evolved from the Dutch MANS project (1986–1992) (MANS, 1991), which produced DELWAQ (Postma, 1989) for transport of conservatively mixed matter, DYNAMO to simulate nutrient pools (van der Giessen, 1989) and ECOLUMN-BLOOM II (Peeters et al., 1995) to simulate phytoplankton blooms. The last was originally developed for freshwater systems (de Vries and Michielsen, 1992; Los, 1991; van der Molen et al., 1994). All these modules form the two-dimensional application DCM-NZB for the coastal strip off The Netherlands (Los & Bokhorst, 1997). There exists also a version CSM-NZB for the greater North Sea shelf. Although DCM-NZB and CSM-NZB were documented in a number of reports the results were only sparsely published in journals (de Vries et al., 1998; Peeters et al., 1995). None of the modules has a three-dimensional set-up. Van den Berg et al., 1996a) developed the vertically-integrated, two-dimensional FYFY model, with no further three-dimensional applications. The DYMONNS model (Hydes et al., 1997) is also a vertically integrated two-dimensional model with no three-dimensional application. These models in fewer than three dimensions are not discussed further.

The two most recent models, COHERENS (1999) and POL3dERSEM (2000), are not as well documented by publications as the other models. COHERENS was distributed on a CD-ROM with an excellent documentation of the model program and an easy-to-use file structure. The first application describes the implementation of the model code to study eutrophication in the southern North Sea, including light attenuation by inorganic suspended particulate matter (Luyten et al., 1999). The POL3dERSEM model covers the whole north-west European Shelf system, and the first application illustrates how spatial and temporal variations in physical processes determine the onset of the spring bloom in the north-west European Shelf (Allen et al., 2001).

### 2.1. Achievements of selected three-dimensional ecological models

The three-dimensional models listed in Table 1 were designed to describe the horizontal and vertical ecosystem dynamics of the North Sea, in more or less detail. Physical, chemical and biological processes are closely coupled on the scales relevant for ecosystem dynamics. The fluxes of matter determine the dynamics of the shelf system, which means that their correct representation is a key for the understanding



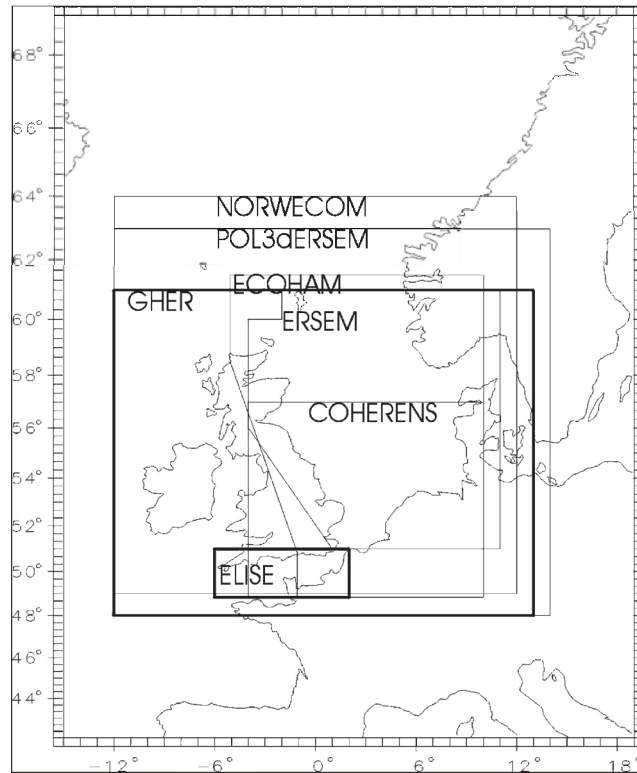


Fig. 2. Spatial extensions for the selected North Sea models, for details see Table 2.

of the entire system. Therefore, we present first the space and time scales resolved in the selected North Sea models and then we describe the applications.

All models except for COHERENS and ELISE include at least the whole North Sea area (Fig. 2). Models for the greater North Sea area have a longitudinal extension from 48° N to 64° N and a latitudinal extension from 12° W to 14° E. The COHERENS model resolves the southern North Sea only, while the ELISE model simulates only the English Channel.

Table 2

Space and time scales in the selected three-dimensional North Sea models and their geographical area of model domain (see Fig. 2). (\*) approximated for NORWECOM which has polar stereographic coordinates

No	Model name	Spatial resolution $\Delta h$ (km)	Longitude (°)	Latitude (°)	Spatial extent (km)	Temporal resolution $\Delta t$ (sec)	Temporal range (years)
1	NORWECOM(*)	20	−12.0, 12.0	49.0, 64.0	1.600	900	1985–1994
2	GHER	18	−12.0, 13.0	48.0, 61.0	1.400	69	1989
3	ECOHAM	20	−04.5, 10.0	49.0, 61.5	1.400	900	1985–1994
4	ERSEM	110	−04.0, 11.0	51.0, 61.0	1.100	86,400	1955–1993
5	ELISE	4	−06.0, 02.0	48.5, 51.0	300	1000	1978–1992
6	COHERENS	7	−04.0, 10.0	48.5, 57.0	900	600	1989
7	POL3dERSEM	12	−12.0, 14.0	48.0, 63.0	1.700	1080	1995

To illustrate the resolution of the physical and biological scales for the selected models the numerical values of the horizontal space scales ( $\Delta h$ ,  $H$ ) and the time scales ( $\Delta t$ ,  $T$ ) are given in Table 2. For the North Sea models the finest horizontal resolutions are 7 km (COHERENS) and 12 km (POL3dERSEM); most models work with a resolution of 18 km to 20 km (GHER, ECOHAM and NORWECOM). ERSEM adopted a  $1^\circ$  box structure, which corresponds to a spatial resolution of about 110 km in north–south direction and 50 km in east–west direction. Except for ERSEM, all models resolve the diurnal cycle. The duration of the simulation is the annual cycle for all models. Long-term simulations of 10 years duration are available from NORWECOM and ECOHAM (Skogen & Moll, 2000). For ERSEM a simulation of 39 years was performed to simulate the eutrophication of the North Sea during 1955–1993 (Pätsch & Radach, 1997).

Using a horizontal resolution of about 7 km and a time step of 15–20 minutes, the characteristics of fluid motions except for temporally short waves and small-scale turbulence would be resolved. Both small-scale processes are usually parameterised in the circulation models. The biological time scales of the population dynamics of phytoplankton and of the small bacterioplankton are also resolved. However, the spatial scales of bacterioplankton, phytoplankton and partly also zooplankton are only partially resolved. Especially horizontal patchiness on scales of 1000s of metres and less cannot be resolved in current shelf seas circulation models, and thus cannot be simulated yet in three-dimensional ecological models. Patchiness has to be parameterised.

#### 2.1.1. NORWECOM (Norwegian Ecological Model System)

NORWECOM was developed in 1993, and the first user guide was published by Skogen (1993). The current version was documented by Skogen and Soiland (Skogen & Soiland, 1998). Aksnes et al. (1995) applied the model first to simulate mesocosm experiments and then to simulate the plankton dynamics in February–June 1988 in the North Sea, including the bloom of *Chrysochromulina polylepis* in the Kattegat-Skagerrak in May, which was stimulated by anthropogenic nutrients. Aksnes et al. (1995) tested the predictive power of NORWECOM, finding that several features of the bloom could be reproduced, as well as the progression of nutrient concentrations and abundances of diatoms and flagellates. The model area was next extended to the greater North Sea, and in the papers by Skogen, Eriksrod and Svendsen (1997) and Skogen, Svendsen, Berntsen, Aksnes and Ulvestad (1995) regional distribution of primary production was estimated for 1985. The simulated amounts of annual primary production were in fairly good agreement with the sparse observations. Further attempts to obtain credibility for NORWECOM followed. Skogen and Moll (2000) compared the modelled variability of primary production from simulations for 1985–1994 of NORWECOM and ECOHAM and showed rather similar ranges of variability from both models. Skogen, Aure, Danielssen and Svendsen (1998) simulated the natural fertilisation of the Skagerrak by a flooding event of the Glomma River in May–June 1995, one of the largest floods during the last century. The effects of this model scenario on the marine plankton system were studied in contrast to the model scenario without river input. The model failed to reproduce the observed very fresh surface layer, probably due to the high vertical mixing in the model as a result of insufficient vertical resolution. Although the flooding event was unusual, the simulated effect on total primary production of diatoms in the Skagerrak was small. While the data showed a total lack of flagellates, the simulated flagellates were responsible for 50% of primary production. Over the years the model was extended into NORWECOM2 (Skogen, 1998) to include oxygen, silicate shells and suspended particulate matter. Soiland and Skogen (2000) continued validation of the extended NORWECOM2 using nutrient observations in the North Sea for the period 1980–1989, measuring the deviation between simulated and observed nutrient concentrations. While inorganic nitrogen was simulated rather badly, the nutrients phosphate and especially silicate were simulated much better.

### 2.1.2. *GHER (Geo-Hydrodynamics and Environment Research Model)*

North Sea modelling by this group started very early (Nihoul, 1976), but was not continued during the 1980s. In the 1990s Delhez and Martin (1994) were among the first who presented a three-dimensional model study for the north-west European continental shelf, coupling a meso-scale circulation model (with resolution of  $1/6^\circ$  in both horizontal directions) with a simple ecosystem model, containing the state variables nitrogen-nutrients, phyto- and zooplankton and detritus. The phytoplankton showed a maximum on the Dogger Bank; but the results of the ecological test simulation were not really evaluated. A biologically and chemically more complex version of a macro-scale ecohydrodynamic model for the north-west European continental shelf was presented by Delhez (1998), describing the nitrogen and carbon cycles by 17 state variables representing the 9 compartments nitrate, ammonium, small and large phytoplankton, heterotrophic flagellates, zooplankton, bacteria, detritus, and DOM; in all compartments of the food web the C/N ratios can vary. Climatological mean data for January were taken as initial conditions for the simulated year 1989. The dynamics of the primary production responded to the physical forcing and were characterized by differences between stratified and non-stratified regimes.

### 2.1.3. *ECOHAM (Ecological North Sea Model, Hamburg)*

ECOHAM is a three-dimensional model for estimating the annual primary production in the North Sea (Moll, 1995; Moll, 1997b; Moll, 1998). It is a spatial extension of the one-dimensional water column model by Radach and Moll (1993). The plankton system was represented by one phytoplankton bulk variable, triggered by one nutrient, namely phosphate or dissolved inorganic nitrogen (DIN). The mechanism for nutrient regeneration was represented by immediate regeneration of part of the dead organic matter in the water and by a linear process for regenerating the detritus at the bottom. Coupling of the benthic nutrient reservoir to the water column was achieved by regeneration of inorganic nutrients from detritus and transfer into the water column by bottom boundary conditions. The model was documented in a user guide by Moll (1997a). The simulation of the annual cycle for 1986 shows the development of the spring phytoplankton bloom starting in the continental coastal zone, extending first into the area of the Baltic outflow along the Norwegian Trench and covering the whole of the North Sea by April. Due to shortage of nutrients caused by stratification, the phytoplankton concentration decreased at first in the southern central and then in the northern central North Sea. Heavy depletion was reached in July in the total North Sea, except for the coastal margins (Moll, 1998). The annual primary production was largest in the continental coastal zone ( $>300 \text{ gC m}^{-2} \text{ y}^{-1}$ ), decreasing to the northwest. Primary production showed its minimum ( $<100 \text{ gC m}^{-2} \text{ y}^{-1}$ ) in the northern central area. A phosphate budget derived from annual simulations for 1985–1992 was given in Moll (1997d); the model was validated by using two larger data sets, one from ICES and one from the ERSEM project (Moll, 2000). The effects of advection and diffusion on the amounts of annual primary production were investigated by Moll and Pohlmann (1997). It could be shown that horizontal advection achieved a nutrient distribution with higher annual primary production as if vertical diffusion were only acting. Thus, the structure of the currents is very important for the annual sum of primary production in the North Sea. Using realistic atmospheric forcing for driving the circulation, the variability of annual primary production was estimated for a simulation range of ten years (1985–1994) (Moll, 1999; Skogen & Moll, 2000). Comparisons of the primary production estimates from ECOHAM and from NORWECOM showed regional differences in primary production larger than the differences between the two models in each area inspected. ECOHAM suggested that the interannual variability of primary production in the North Sea was around 15% of the mean, similar to one-dimensional, 25-year simulations at Ocean Weather Station Farnes (57°30' N, 3°0' E) (Radach & Moll, 1993).

### 2.1.4. *ERSEM (European Regional Seas Ecosystem Model)*

Although it is a box model, ERSEM (Baretta et al., 1995) was included in the review of the three-dimensional models because its spatial structure is quasi three-dimensional. In the horizontal the North

Sea was represented by 85 boxes in the surface layer and by 45 boxes in the bottom layer. The model was developed within a MAST project over 7 years (1990–1996) and resulted in two volumes of reports: Netherlands Journal for Sea Research 33, 1995, and Journal for Sea Research 38, 1997. Blackford and Radford (1995) discussed the structure and methodology for ERSEM. Radach and Lenhart (1995) described the nutrient dynamics in the North Sea from fluxes and budgets derived with ERSEM. Boundary conditions for nutrients in the water entering the North Sea were prescribed, leading to the important result that the advective nutrient import and export across the open North Sea boundaries nearly cancelled for all compounds. A number of valuable contributions in respect to the North Sea ecology have been made with ERSEM: A calculation of total primary production was done by Varela, Cruzado and Gabaldon (1995) and Ebenhöh, Baretta-Bekker and Baretta (1997), microbial dynamics with decoupled carbon assimilation and nutrient uptake (in ERSEM II) were simulated by Baretta-Bekker, Baretta and Ebenhöh (1997); Broekhuizen, Heath, Hay and Gurney (1995) modelled the dynamics of the North Sea meso-zooplankton and Bryant, Heath, Gurney, Beare and Robertson (1997) followed the development of *Calanus finmarchicus* in a three-dimensional structured population model that they applied to the northern North Sea, where Bryant et al. (1995) modelled the predation, growth and population dynamics of fish, and an analysis of benthic biological dynamics was performed by Blackford (1997).

A long-term simulation covering 1955–1993 to reproduce the effects of eutrophication of the North Sea was performed by Pätsch and Radach (1997). Main features of the process were reproduced. Studies showed that ERSEM is capable of simulating a continuum of food webs (Baretta-Bekker et al., 1997; Lenhart, Radach & Ruudij, 1997; Radach & Lenhart, 1995), that is to represent the change from a system dominated by a multivorous web (Baretta-Bekker et al., 1997) in the eutrophic coastal zone to a system dominated by the microbial loop in the relatively oligotrophic offshore areas.

Lenhart, Radach and Ruudij (1997) and Lenhart (1999) used a refined box set up of ERSEM to study reduced nutrient loads from the major rivers around the North Sea under different scenarios. They started from a steady state solution adapted to the new river forcing. A 50% reduction of the inorganic and organic loads of nitrogen and phosphorus resulted in remarkably little change in primary production, about 12–17% in the continental coastal zone, 11% in the southern central North Sea and only 4–7% in the central North Sea; the northern North Sea remained nearly unaffected and showed a decrease of less than 5%. The nitrogen budget for the region where the river Rhine entered showed that the majority of nitrogen fluxes were reduced by 15–20% by the reduction of the river loads by 50%. However, zooplankton grazing on bacteria and mortality of phytoplankton remained nearly unaffected by the reduction.

#### 2.1.5. *ELISE (Ecological Modelling Software for interactive modelling)*

The ELISE system (Menesguen et al., 1995) concentrated on two-dimensional applications for different areas. Menesguen and Hoch (1997) simulated the temporal development of phytoplankton over the English Channel, splitting the area into 71 boxes for two vertical layers. A realistic, fine-mesh flow field of two-dimensional tidal residual currents drove the ecological model consisting of 8 state variables, carrying dissolved inorganic nitrogen and silicate as nutrients. Zooplankton and higher trophic levels were not included as either prognostic or diagnostic state variables. Areas in the western English Channel which were stratified during summer exhibited the lowest production to biomass ratios in comparison to the other areas; coastal boxes were the most productive. However, productivity per unit surface area was highest for deeper, transparent and well-mixed waters and lowest for coastal waters, which were too turbid and shallow to support high production per surface unit. A sensitivity analysis for this model was performed by Hoch and Menesguen (1997). The biological model (Menesguen & Hoch, 1997) was set into a quasi-three-dimensional frame by Hoch and Garreau (1998), based on a fine-grid with a mesh size of two nautical miles. Essentially, this version is a vertical one-dimensional model embedded in a two-dimensional depth-integrated, advection-dispersion model. For the year 1980 instantaneous solar radiation was prescribed. In comparison to the box-model results, the three-dimensional model results differed mostly in two areas, in



the north of Brittany and in the Bay of Seine. Both discrepancies were explained by physical features: in the estuary of the Seine the haline structure was captured in the two-layer box model, but was not resolved in the three-dimensional model, and in contrast the stratification in the box model was too coarse, and the 3-d model was advantageous because a frontal zone was resolved. It was suggested to step to a fully three-dimensional model set-up.

#### *2.1.6. COHERENS (Coupled Hydrodynamical Ecological model for Regional Northwest-European Shelf seas)*

This three-dimensional, multi-purpose model (Luyten et al., 1999) is really a modelling tool developed by a series of MAST projects (PROFILE, NOMADS and COHERENS). It enables a potential modeller of the north-west European shelf to set up a model system from basic building blocks like a physical model for simulating the general circulation of the shelf sea, a biological model, a sediment model, and a contaminant transport model. The biological module is based on Tett (1990) and Tett and Walne (1995) and contains eight state variables: microplankton carbon and nitrogen, detrital carbon and nitrogen, nitrate, ammonium, oxygen, and zooplankton nitrogen. The biological model has no benthic state variables. The simulation for the southern North Sea covered a full yearly cycle for 1989. Comparisons have been made at the NERC North Sea Project site CS for 1989. The rapidly-sinking spring bloom and the mid-summer, midwater chlorophyll maximum seem well simulated. Nitrate is realistically simulated during the spring bloom, but not during the autumn, which may be explained by the missing benthic mineralisation. The excellent user manual describes the structure of the program step by step, including preparation of the input and output. It is supplemented by a reference manual describing the modules. So far beside a water column application to the northern North Sea (Lee et al., 2002) with extensive comparison to previous ERSEM and ECOHAM1 model results, no other publication is available beside these manuals that come with the CD-ROM. User friendly support of all necessary modelling tools and data sets is available on the CD-ROM.

#### *2.1.7. POL3dERSEM (Proudman Oceanographic Laboratory 3d ERSEM Model)*

The latest model development is POL3dERSEM. Allen et al. (2001) implemented the biology of the ecosystem model ERSEM into a three-dimensional circulation scheme for the North Sea at a spatial resolution of 12 km. We separated this fully three-dimensional version from the box model version of ERSEM, because it is based on a real three-dimensional grid, and the programme uses advanced numerical handling (Proctor, Lockey & James, 1999) with massively parallel programming. The model was applied to the north-west European continental shelf to illustrate how spatial and temporal variations in physical and chemical driving forces determine the onset of the spring bloom in the North Sea. It was shown how the surface chlorophyll grows first along the continental coastal zone in April, then covers the Atlantic area south of Ireland and England, fills the southern North Sea, the Skagerrak and Kattegat and reaches out into the North Sea along the Norwegian Trench in May, and finally, in July, covers nearly all of the North Sea and the surrounding waters, except for the northern central North Sea. Comparison with climatological monthly mean data shows good coincidence for phosphate, summer nitrate, summer silicate, and chlorophyll; other variables have not yet been so accurately matched. POL3dERSEM sets new standards in the three-dimensional ecosystem modelling of the North Sea, because the complex trophic relations of ERSEM have been integrated into a fully three-dimensional circulation model, with the finest spatial resolution of all model systems mentioned.

### *2.2. Comparison of state variables and process representations*

Fransz et al. (1991) depicted in an idealised diagram (their Fig. 21) a trophic resolution for the North Sea ecosystem including the standard functional units of producers, consumers and decomposers in the



pelagic and benthic subsystems. The diagram represents state variables for nutrients, phytoplankton, zooplankton, dead organic (dissolved and particulate) matter, and bacteria in the pelagic system, and bacteria and dead organic matter for the benthic system and the transfers of matter among the state variables.

The three-dimensional models for the north-west European shelf or the North Sea system have a trophic resolution which distinguishes the main functional units (nutrients, phytoplankton, zooplankton, and detritus, dissolved organic matter and bacteria in the pelagic and diagenesis and zoobenthos for the benthic compartment). Higher trophic levels like fish, birds or mammals are not included in ecosystem models as prognostic state variables up to now. With respect to the real complexity of ecological processes, models remain relatively simple. We describe the trophic resolution of the model systems in Table 3 considering the resolved matter cycles and chosen state variables for the different functional units, for the pelagos and benthos. Except for COHERENS, all models simulate the pelagic and benthic system. ECOHAM simulates the phosphorus cycle only, while COHERENS and GHER simulate the nitrogen cycle only. Cycles of phosphorus, nitrogen and silicon are included in NORWECOM, ELISE, POL3dERSEM and ERSEM, with separate state variables for the pelagic and benthic systems. Representation of phytoplankton ranges from one bulk state variable to four: picophytoplankton (0.2–2  $\mu\text{m}$  equivalent spherical diameter, ESD), flagellates (2–20  $\mu\text{m}$  ESD), diatoms (20–200  $\mu\text{m}$  ESD), and dinoflagellate-like “inedible” phytoplankton (20–200  $\mu\text{m}$  ESD) that is not grazed by zooplankton. The state variable chlorophyll was defined as the sum of the chlorophyll content of the sub-groups. Zooplankton state variables are not included in two models; ECOHAM and COHERENS prescribed the observed biomass of mesozooplankton. GHER used a bulk formulation, and only the two ERSEM models included different size-dependent zooplankton units. Dissolved organic matter and bacteria were not represented as state variables in four models; there is a bulk

Table 3

State variables in the selected North Sea models, sorted by the number of pelagic state variables

No	Name	Pelagic				Benthic	
		Matter cycle State variables	Nutrients DOM	Phytoplankton Bacteria	Zooplankton Detritus/POM	Matter cycle State variables	Nutrients Zoobenthos
3	ECOHAM	P 2	one bulk no	one bulk no	not explicit no	P 1	not explicit no
6	COHERENS	no 8	two explicit no	one bulk no	not explicit two functional	N,O 0	no no
1	NORWECOM	N,P,Si 8	three bulk no	two functional no	no two functional	N,P,Si,O 5	not explicit no
4	ELISE	N,P,Si 10	three bulk no	two functional no	no three functional	N,P,Si 3	three bulk no
2	GHER	N 16	two explicit one bulk	two functional one bulk	one bulk one bulk	N 1	not explicit no
7	POL3dERSEM	N,P,Si,O 35	four explicit one bulk	three functional one bulk	three functional one bulk	N,P,Si,O 18	four explicit three functional
4	ERSEM II	N,P,Si,O 43	four explicit four bulk	four functional three functional	three functional four functional	N,P,Si,O 22	four explicit three functional

representation included in GHER and POL3dERSEM, and a full representation is incorporated in ERSEM only. Except for ECOHAM all the models have resolved the detritus in the water column using one or more state variables.

The benthic system was introduced to provide for nutrient remineralisation on medium and long-time scales. Thus, except for COHERENS, all models have formulated the nutrient regeneration by indirect mechanisms or used up to four explicit state variables for nutrients in the benthic bottom layer. A zoobenthos compartment is resolved only by the two ERSEM models after Blackford (1997), with state variables for meiobenthos, suspension and deposit feeders.

Because of the huge manifold of processes grouped in each functional unit, state variable or species, it is common to define “standard processes” for the biological and chemical reactions linking the state variables. The numbers of the state variables and processes yield a characterisation of the resolution of the complexity of the trophic web. The models have been developed to investigate the specific questions mentioned in section 2.1 and, therefore, do not include all the possible processes.

ECOHAM simulates phytoplankton biomass, phosphate concentration and sedimented detritus, the last at the bottom of the sea only, aiming at the estimation of primary production during the annual cycle. Pelagic detritus and dissolved organic phosphorus are not prognostic variables, but enter the model by a simple parameterisation of the “small food web”. Also the benthic regeneration of phosphate is a much simplified parameterisation of the complicated processes at and in the bottom. The simple structure is, however, sufficiently complex to estimate the annual cycle of primary production in the North Sea as well as more complicated representations like NORWECOM, ERSEM or POL3dERSEM.

NORWECOM separates the phytoplankton into two functional groups, the diatoms and the flagellates, which necessitates the introduction of silicate as a nutrient, as well as phosphate and inorganic nitrogen. A zooplankton state variable is missing, although it is known that zooplankton grazing is important in cases of abundant nutrients for the decline of phytoplankton blooms. Thus, this model intrinsically estimates too much primary production. The benthic regeneration is modelled in a more complicated manner than in ECOHAM, though it is still simple. All nutrients, inorganic nitrogen, silicate and phosphate are regenerated from detritus, which has a pool in the water in addition to benthic detritus.

GHER separates the phytoplankton into small and large compartments (Delhez, 1998) (his fig. 2). Heterotrophic flagellates and mesozooplankton graze on small and large phytoplankton, separately. GHER introduced bacteria as a state variable, and as in ERSEM the bacteria compete with phytoplankton for nutrients. COHERENS based the pelagic sub-module on work by Tett and Walne (1995) (their Fig. 4). The nitrogen cycle included one phytoplankton and detritus state variable. Oxygen was additional. ELISE combined the nitrogen, phosphorus and silicon cycles (Hoch & Garreau, 1998) (their Fig. 3) to investigate general features of competition between diatoms and dinoflagellates, which do not require silicon. Zooplankton was not taken into account, but the grazing pressure was introduced through a higher mortality rate. Dead organic matter was defined in the water column and in the benthos. Microbial biomass was not explicitly simulated, and decomposition processes were expressed through temperature-dependent rates.

The most complex model structure was that of ERSEM in which the trophic web was represented by four groups each of phytoplankton, zooplankton and benthic organisms (Fig. 3). Particulate and dissolved organic matter contains the elements C, N, P, and Si. The sediment is layered, and anoxic or oxic layers may develop. The sediment plays a role as deposit for the elements. The cycles of these elements are represented by the prognostic nutrients nitrate, ammonium, phosphate, silicate, and carbon dioxide as state variables. POL3dERSEM used a slightly reduced trophic resolution. The trophic and chemical representation in ERSEM is by far the most complex used up to now in ecological modelling for shelf seas, as well as for oceans.

To build management tools for societal concerns like “eutrophication”, it is convenient to aggregate different state variables and their standard processes into “key processes” and to describe their implementation into the models (Table 4). Such “key processes” are, e.g., spring algal blooms, annual phytoplankton

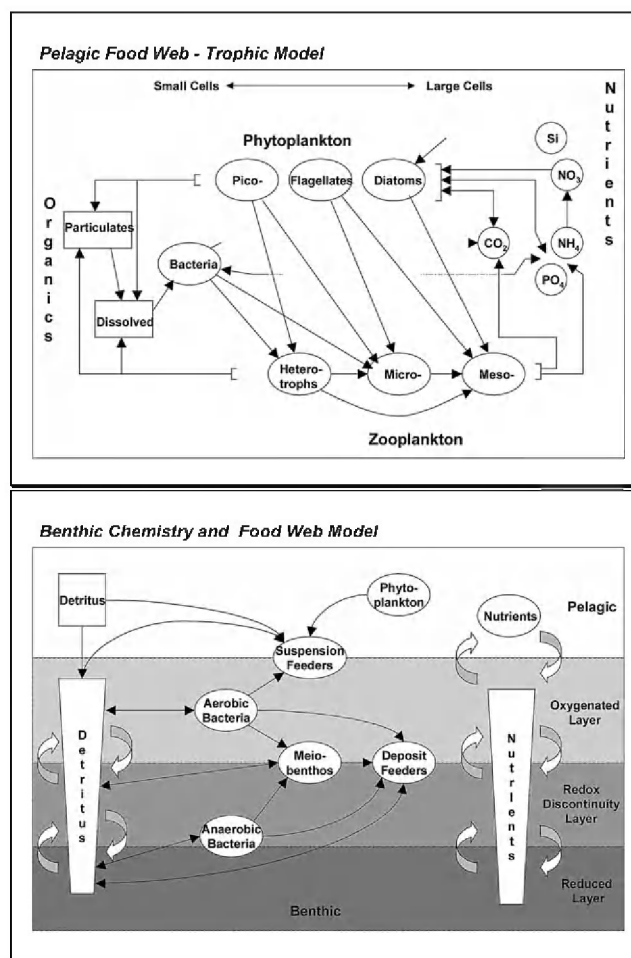


Fig. 3. Interaction diagram for the complex ecosystem model ERSEM (Allen et al., 2001).

cycles, nutrient regeneration, eutrophication, trophic relations in the food web, recruitment of fishes, pelagic-benthic coupling, and contaminant dynamics.

To understand and analyse “algal blooms”, the phytoplankton has to be separated into several distinct state variables with different parameterisations for nutrient limitation to cover the annual cycle and successions of different groups. For the simulation of “nutrient regeneration” it is necessary to differentiate several particulate and dissolved organic compartments for the regeneration of the C, N, P, and Si cycles. “Eutrophication” has by far the widest demands. It is necessary to simulate N:P nutrient ratios and to separate the microbial food web from the classical food chain for larger plankton particles. Oxygen demands have to be included. To study “trophic relations” state variables must be connected as a food web. Study of fish “recruitment” makes it necessary to simulate populations as structured size or stage classes and take individual based species information into account. Characterizing “pelagic-benthic coupling” requires both pelagic and benthic subsystems with appropriate physical forcing at the benthic boundary layer. And finally, evaluating contaminant effects requires at least a module for heavy metals (hydrophilic particles) or organic contaminants (hydrophobic particles) including the relevant dissolved and particulate substance cycles.

Table 4

Implementation of 'key process complexes' in the selected models. For each 'key process complex' a short list of necessary criteria was defined, with SV = state variables, FU = functional units, SPmodel = structured population model, IBmodel = individual based model, HM = heavy metal, PCB = polychlorinated biphenyl. The evaluation of the seven models is judged due to these criteria as: first line "Yes" = necessary state variables included; second line: explanation if necessary

No	Model name	Algae blooms	Nutrient regeneration	Eutrophication	Tropic relations	Recruitment	Pelagic-benthic coupling	Contaminants
Criteria		phytoplankton succession; nut. limitation	particulate and dissolved organic matter	nut: N/P ratio; phyto/zoo-bacteria/oxygen	number of FU and SV; relations	Zooplankton: SPmodel/IBmodel	Processes between pelagos and benthos	HM module; PCB module
1	NORWECOM	Partly: only two groups	Partly:only POM	Partly:no microbial loop	No:only phy	No	Yes/restricted:no zoobenthos	Yes:HM/PCB modules
2	GHER	Partly: only two groups	Yes:one DOM	No:only N cycle	Partly:phy/zoo/bac sum param.	No	Partly:Very crude parameterisation	No
3	ECOHAM	No: bulk formulation	Partly:only POM	No:only P cycle	No:only phy	No	Partly:Very crude parameterisation	No
4	ERSEM	Yes: four groups	Yes	Yes/restricted: coarse resolution	Yes	No	Yes/restricted: large boxes	No
5	ELISE	Partly: only two groups	Partly:only POM	Partly:no microbial loop	No:only phy	No	Yes/restricted: no zoobenthos	Partly: PCB/Cd under progress
6	COHERENS	No: bulk formulation	Partly:only POM	No:only N cycle	No:only phy	No	No:only SPM	No
7	POL3d-ERSEM	Yes: three groups	Yes:one DOM	Yes	Yes	No	Yes:nutrients, POM zoobenthos	No

The potential of the seven three-dimensional models to contribute to the understanding of the dynamics characterised by the "key processes" has been assessed; the results are given in Table 4. At the present time the models are suited only for investigating a very restricted scope of key process complexes. No model is suited for the recruitment problem; only one model (NORWECOM) has a module incorporated that could be used for the simulation of special contaminant dynamics. ERSEM and its three-dimensional derivative POL3d-ERSEM are suitable for all the key process complexes, except for recruitment and contaminant dynamics. The spatial resolution of ERSEM is, however, too coarse in its present box-model versions.

### 3. State-of-the-art in ecosystem understanding through modelling

This section is devoted to examples of achievements by three-dimensional modelling of the ecological functioning of the north-west European shelf seas system, organised according to the key processes as mentioned in the last section. The main ecological processes and phenomena of the shelves were discussed in several reviews (Alongi, 1998; Baird & Ulanowicz, 1989; Charnock et al., 1994; Evans & Fasham,

1993; Jorgensen & Richardson, 1996; Malone, Malej, Harding, Smolaka & Turner, 1999; Postma & Zijlstra, 1988; Reynolds, 1997; Sündermann, 1994; Walsh, 1988).

Overall, the three-dimensional ecosystem models have given improved understanding of the interaction of the processes regulating biological production in marine systems; they have provided conceptual frameworks for testing hypotheses, and they were useful in ensuring data consistency and in synthesising large and disparate data sets.

Here important modelling results are identified and presented

- (i) for the pelagic system to show characteristics of its functioning as the main primary production system,
- (ii) for the benthic system that receives organic material from the pelagic system which is then consumed by the zoobenthos, providing regenerated nutrients,
- (iii) for the cycling of matter in the whole system due to different concepts of interaction for the different nutrients, and finally,
- (iv) for the whole ecosystem with its connections to the external world and its reaction potential and variability.

### 3.1. *Plankton system*

The main controls of phytoplankton growth due to light, nutrients and physics on the shelves are summarised in reviews, e.g. Reid, Lancelot, Gieskes, Hagmeier and Weichart (1990). All of these processes are included in the three-dimensional models in simplified forms. In the turbid waters of coastal oceans sessile algae, the phytobenthos, are of importance only along the very shallow coasts due to the strong light attenuation. These algae were usually neglected in the models we review here; however, they play a role in models for the Wadden Sea (Dittmann, 1999; Lindeboom, 1988).

#### 3.1.1. *Algae blooms and primary production*

The key process “algal blooms” comprises several aspects, e.g. the annual dynamics of phytoplankton, its regional variations, its successions and its regulations. Ecological models have given insight for all of these aspects.

**3.1.1.1. Primary production** Of special interest are the regional differences in the horizontal distributions of the annual primary production (Fig. 4). All models reproduced the main regional features of the annual total for the North Sea similarly: they yield high production in coastal regions (above  $200 \text{ gC m}^{-2} \text{ y}^{-1}$ ) and a minimum in the central area (below  $100\text{--}150 \text{ gC m}^{-2} \text{ y}^{-1}$ ). Lower production values off the British south coast (below  $100 \text{ gC m}^{-2} \text{ y}^{-1}$ ) were not produced by the models.

The ability to reproduce regional differences by three-dimensional modelling will be shown by model comparisons for ten specific regions (so-called ERSEM boxes) of the North Sea (Fig. 5). The annual variability for selected boxes in the North Sea was less than the regional differences for these boxes, which is evident e.g. when comparing box 9 in the German Bight and box 4 in the central North Sea.

Annual variability of primary production was so far observed only rudimentary, but could be estimated by several three-dimensional model simulations already for one to four decades. The variability of primary production derived with the three-dimensional ERSEM box model for the years 1955–1994 was in the range of  $100\text{--}175 \text{ gC m}^{-2} \text{ y}^{-1}$ .

Because of the importance of the total amount of annual primary production, we present estimates of the mean annual net primary production for the North Sea for different years (Table 5). The range of annual production from the two long-term simulations of NORWECOM and ECOHAM (Skogen & Moll, 2000) varied between  $120$  and  $140 \text{ gC m}^{-2} \text{ y}^{-1}$  for ten different simulated years. The GHER model calcu-



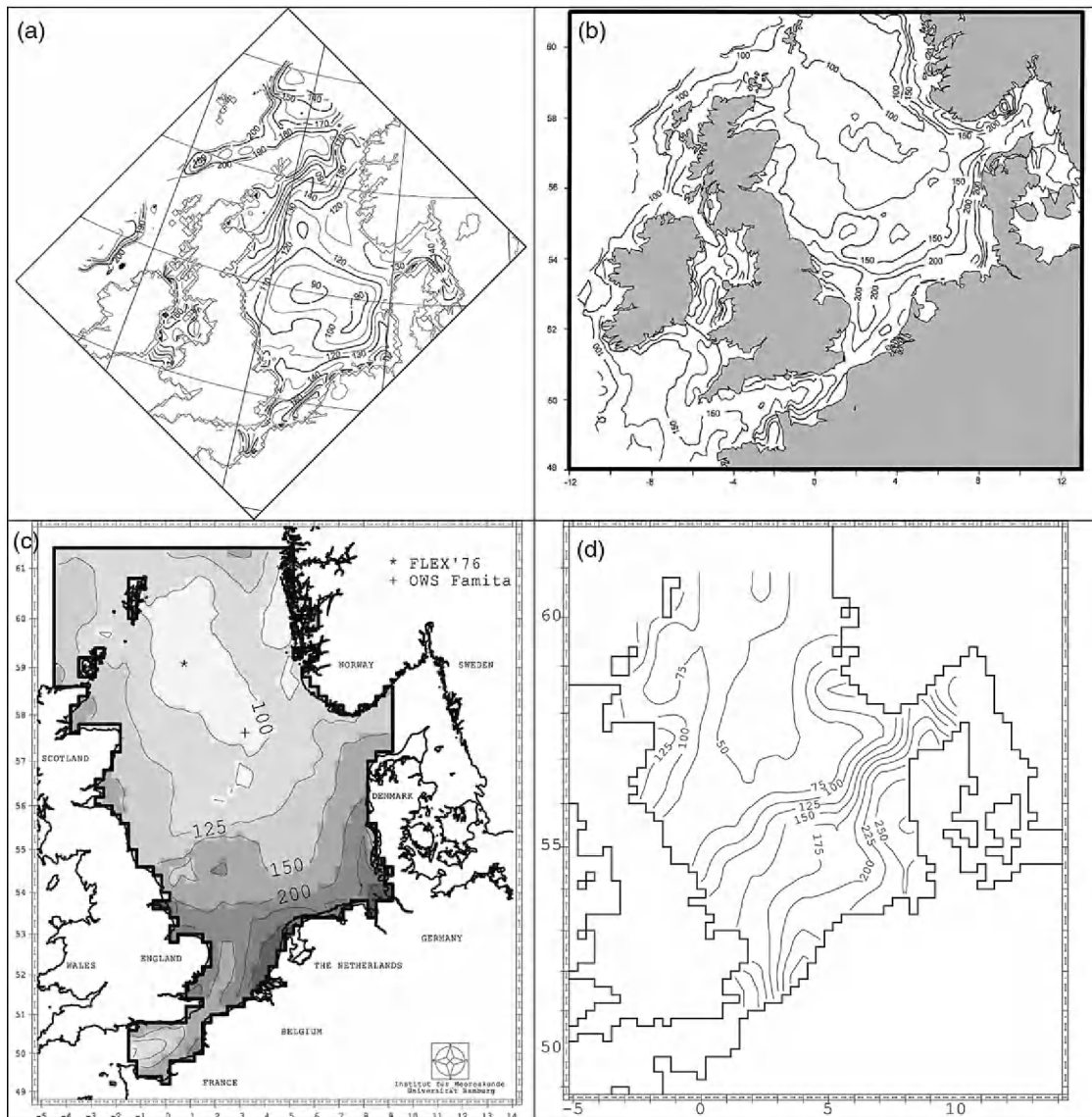


Fig. 4. Regional distribution of annual primary production for different ecosystem models. (a) NORWECOM (Skogen et al., 1995), (b) GHER (Delhez, 1998), (c) ECOHAM (Moll, 1998), (d) ERSEM (Pätsch & Radach, 1997).

lated only one year, and the two most recent models COHERENS and POL3dERSEM have not yet been used to quantify annual production.

**3.1.1.2. Succession** Primary production estimates for specific phytoplankton groups were produced by the GHER model by separating large and small phytoplankton, by the NORWECOM model by introducing diatoms and flagellates, in the POL3dERSEM model by adding picophytoplankton to diatoms and flagellates and in the ERSEM model by using these three algal groups plus inedible phytoplankton (e.g. large *Phaeocystis* colonies). ERSEM reproduced the annual succession of the algal groups (Fig. 6). Diatoms started

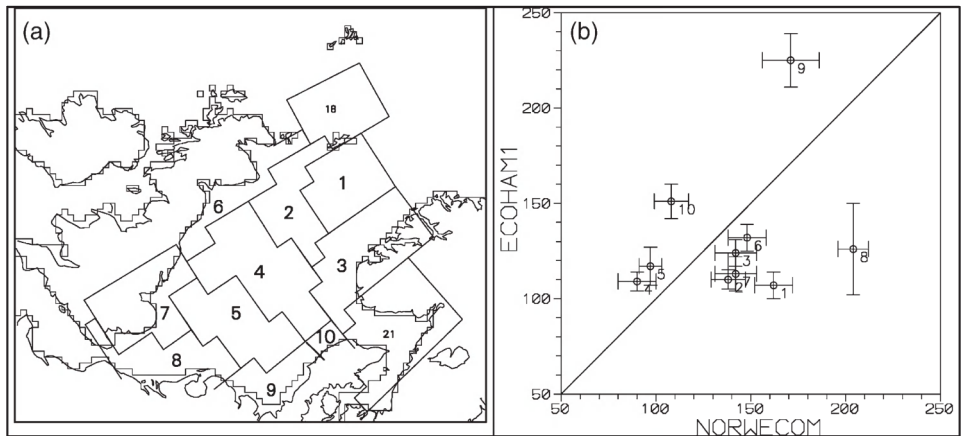


Fig. 5. Annual mean primary production in gC m<sup>-2</sup> y<sup>-1</sup> and standard deviation for ten years in different ERSEM boxes in the North Sea. (a) ERSEM boxes (1–10), (b) NORWECOM versus ECOHAM annual production (Skogen & Moll, 2000).

Table 5  
Mean annual water column net primary production estimates (gC m<sup>2</sup> y<sup>-1</sup>) for the North Sea for the models NORWECOM (Skogen & Moll, 2000), GHER (Delhez, 1998), ECOHAM (Skogen & Moll, 2000), ERSEM (Pätsch & Radach, 1997), COHERENS and POL3d-ERSEM (n.q.y.= year simulated, but not quantified yet)

Year	NORWECOM	GHER	ECOHAM	ERSEM	COHERENS	POL3d-ERSEM
1984				100–175		
1985	127		133	100–175		
1986	139		135	100–175		
1987	130		129	100–175		
1988	135		119	100–175		
1989	137	150	118	100–175	n.q.y.	
1990	143		112	100–175		
1991	131		123	100–175		
1992	132		120	100–175		
1993	134		127	100–175		
1994	134		121	100–175		
1995						n.q.y.
Mean	134		124	100–175		
std	45		29			

in early spring and declined when silicate was depleted; flagellates took over when phosphate was nearly depleted, and picophytoplankton and inedible *Phaeocystis* filled the gaps between in the central and southern North Sea.

Up to now, a detailed simulation of algal species is not possible because the necessary dynamical constants for the different species have not yet been determined experimentally.

**3.1.1.3. Annual cycles** Simulation results of the three-dimensional models gave the first consistent pictures of the spatial and temporal development of the phytoplankton bloom over the whole of the North Sea. The plankton bloom in spring starts in the south east and progresses as a wave to the north-west, following the depth gradient from shallow to deep waters (Moll, 1998). The observed annual cycles (Colebrook, 1982) were reproduced by the models (OSPAR et al., 1998). The ERSEM box model rep-

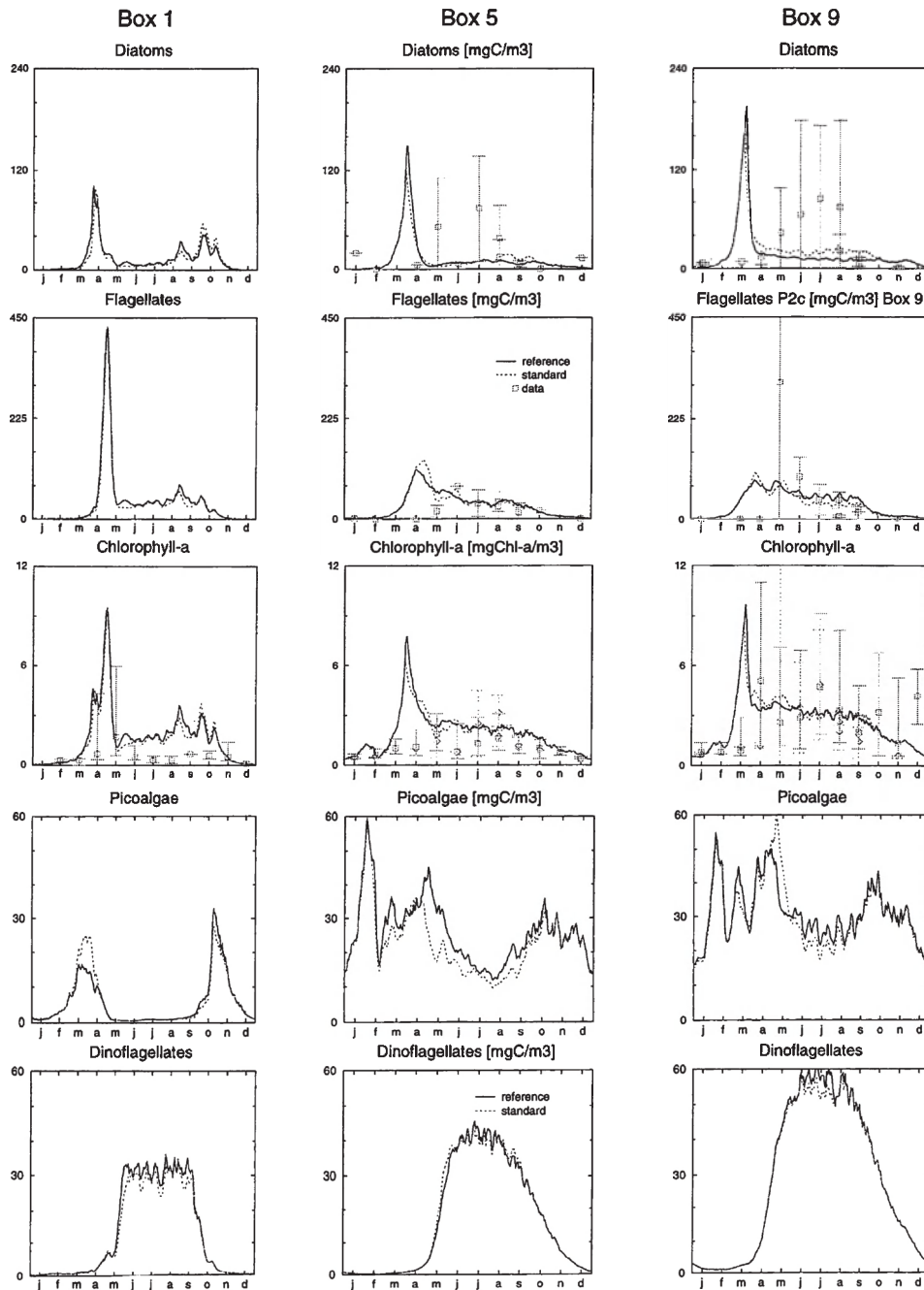


Fig. 6. ERSEM-II-simulated versus observed concentrations of diatoms, flagellates, chlorophyll, picophytoplankton and dinoflagellates for three different boxes in the North Sea (Ebenhöh, Baretta-Bekker & Baretta, 1997). Box numbers are given in Fig. 5. The observations are indicated by monthly median values plus 17%, and 83% quantil data (Radach & Pätsch, 1997). "Reference" and "standard run" indicate the use of different benthic nutrient modules.

resented the phytoplankton and primary production system best. To judge the ability of the models in representing algal blooms, we compare only the results of ERSEM to field data (Fig. 6). We show simulation results for the northern North Sea (Box 1), the central North Sea (Box 5) and the German Bight (Box 9). The amount and the onset of the spring, summer, and fall blooms differ for the three regions. There was no good agreement with the observations for diatoms, flagellates and picoalgae. And even chlorophyll (as the sum of the four phytoplankton groups), with a distinct annual cycle, differed from the monthly mean observations for the regions selected.

*3.1.1.4. Limitation by nutrients and by light* The mechanisms regulating algal growth in the models were nutrient and light limitation. When only one nutrient was used in the model, it served as rough trigger for the phytoplankton blooming, rather than representing the regulatory mechanisms in detail. This was usually the case in the beginning of three-dimensional modelling. The latest models used several nutrients and consequently implemented limitation mechanisms for each and for light (Ebenhöh et al., 1997; Pätsch & Radach, 1997). The authors have shown how variably the limitation mechanisms come into play for the four algal groups of the model ecosystem, depending on the temporal and regional state of the environment (Pätsch & Radach, 1997) (their Fig. 8). When comparing the regional differences with increasing distance from the coast, the most striking feature is that diatoms as well as flagellates are not limited by nitrogen close to the coast, but by phosphate at least in the inner German Bight. Both taxa are limited by nitrogen and not by phosphate in the more distant areas of the central North Sea.

So far, the presentation of the model simulations has been mainly restricted to overall descriptions of the dynamics, but many more regional and temporal details of the dynamics could and should be investigated by looking closely at the simulations. Effects of stratification on the phytoplankton dynamics, effects of currents and nutrients, the influence of irradiance variation in time and in the horizontal/vertical dimensions, and also of interactions among nutrient and light limitations have only been analysed and illustrated in rudimentary fashion, if at all.

### *3.1.2. Eutrophication*

To study eutrophication effects the model ecosystem must include several different state variables of nutrients and phytoplankton and also a representation of the microbial loop. This degree of complexity was more or less implemented in NORWECOM2, ERSEM, and POL3dERSEM.

Simulations reproducing eutrophication in the continental coastal areas are still few. Only one long-term simulation exists. Pätsch and Radach (1997) attempted, using ERSEM, to hindcast the long-term trends in nutrients, algae and primary production over four decades (Fig. 7). No corresponding observations exist for this period, except for a few time series of nearly that duration close to the coast. The simulation data provided a consistent overall picture of the process of eutrophication in the North Sea. Maximum primary production occurred in the mid-1980s, then primary production decreased. Comparison to available data shows agreement in the long-term component, but deficiencies, e.g., in the phasing of the nutrient concentrations. Improvements should be made to reach a better coincidence with observations in the coastal regions.

The measures to be taken against eutrophication can only be investigated by simulations of so-called “reduction scenarios”. The possible effects 50% reduction of riverine nutrient inputs were the subject of a modelling workshop (OSPAR et al., 1998). Model results from three-dimensional and two-dimensional (vertically integrated) ecological models were analysed for different amounts of P or N reduction, as well as simultaneous P and N reduction. The goal was to illustrate effects of 80, 50 or 10% reduction in all the rivers. Output variables of the simulations were created for ten different areas, namely the mean winter concentration of DIP and DIN, the mean summer, the mean winter and the maximum of weekly averaged chlorophyll concentration values, the annual primary production and the maximum weekly averaged production, the area having more than 10% decrease in primary production, the diatom/non-diatom ratio, and

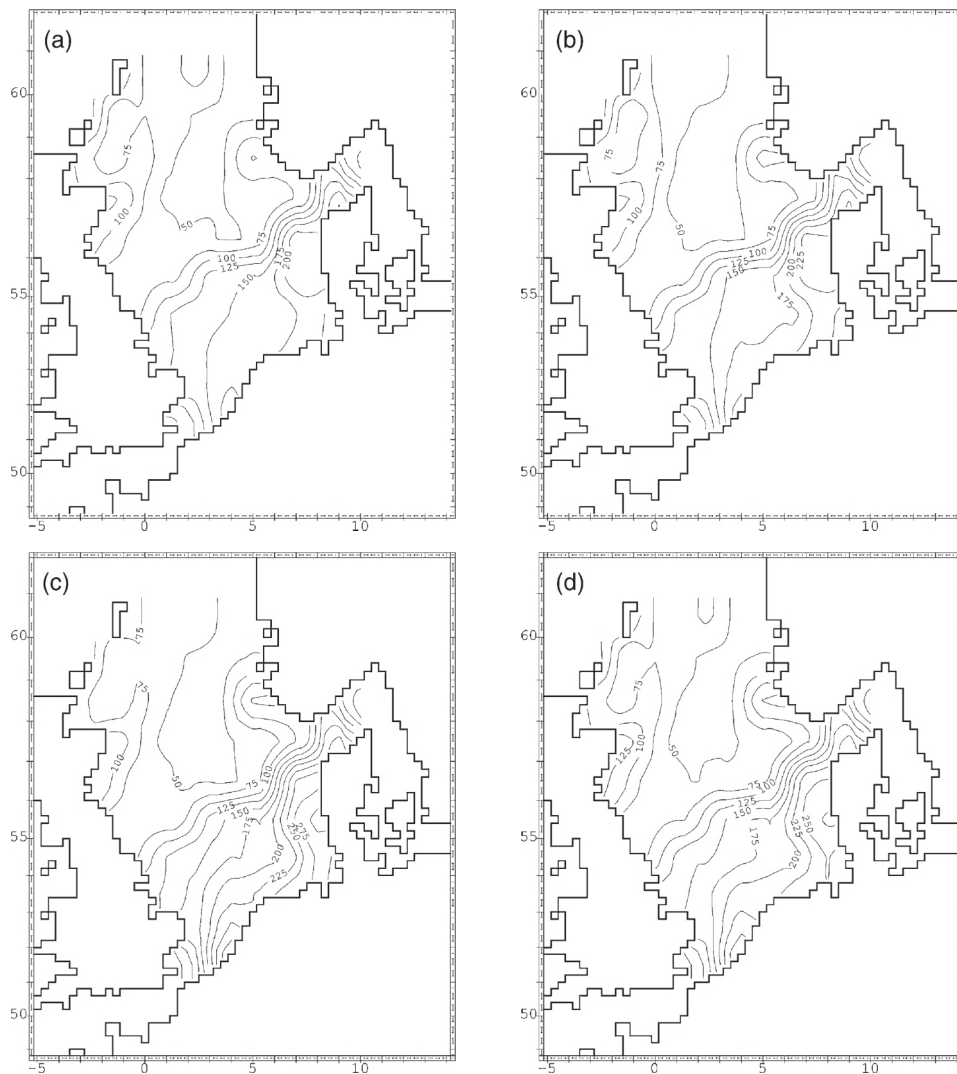


Fig. 7. Horizontal distribution for simulated annual primary production ( $\text{gC m}^{-2} \text{y}^{-1}$ ) in the North Sea for four ten-year periods (Pätsch & Radach, 1997).

finally the area and days with oxygen depletion. Not all of the models were able to calculate all of the selected variables. Models which did not include both N and P as nutrients could not calculate the effect of P reductions or N and P reductions. Most models were unable to calculate oxygen depletion in the bottom waters.

The overall effect of riverine nutrient load reductions can be seen best from annual primary production (Pätsch & Radach, 1997). A reduction of N and P inputs in almost all cases lead to a predicted decrease in primary production (Table 6). The extent of the predicted reduction ranges from 0–24% for P reductions only and from 0–43% for P and N reduction, depending on the model and the model area. As to be expected, the predicted reductions in primary production were of greater importance in the continental coastal region than in the central or northern North Sea, where the effects tended to zero. Further studies of the nutrient reduction scenarios with the ERSEM box model by using a finer spatial resolution were



Table 6

Effect of nutrient load reductions on primary production ( $\text{gC m}^2 \text{y}^{-1}$ ) by (OSPAR et al., 1998) for different coastal zones (CZ) of the North Sea (NS). The column "Base Case" quantified the absolute annual primary production of the standard run. The following two columns indicate the scenario of only P reduction and N plus P reduction

Area	Model	Base case	50% P (abs)	reduction (%)	50% NP (abs)	reduction (%)
Channel	ELISE	193	176	−9	176	−9
	CSM-NZB	238	237	0	233	−2
Belgium CZ	ECOHAM1	234	200	−14		
	ERSEM	216	181	−16	177	−18
	NORWECOM	198	178	−10	175	−11
	MIRO	475	399	−16	269	−43
	CSM-NZB	294	287	−2	270	−8
Dutch CZ	ECOHAM1	307	269	−13		
	ERSEM	267	215	−19	205	−23
	NORWECOM	207	171	−17	172	−17
	MIRO	1103	841	−24	688	−39
	DCM-NZB	314	299	−5	289	−8
German Bight	CSM-NZB	359	330	−8	304	−15
	ECOHAM1	325	277	−15		
	ERSEM	290	221	−24	213	−27
	NORWECOM	197	164	−17	165	−16
	CSM-NZB	340	297	−13	264	−22
Danish CZ	ECOHAM1	225	219	−2		
	ERSEM	303	260	−14	244	−19
	NORWECOM	122	114	−2	114	−6
	CSM-NZB	292	277	−5	239	−18
UK E Coast S.	ECOHAM1	222	202	−9		
	ERSEM	113	110	−3	106	−7
	NORWECOM	137	135	−2	131	−5
	CSM-NZB	282	275	−2	252	−11
UK E Coast N.	ECOHAM1	149	149	0		
	ERSEM	129	126	−2	128	−1
	NORWECOM	182	182	0	182	0
	CSM-NZB	255	253	−1	251	−2
Skagerrak	NORWECOM	168	168	0	164	−3
	DYMONNS	117			108	−8
Southern NS	ECOHAM1	227	211	−7		
	ERSEM	193	171	−11	165	−15
	NORWECOM	139	129	−7	127	−8
	CSM-NZB	269	260	−3	247	−8
	ECOHAM1	119	119	0		
Northern NS	ERSEM	140	137	−2	137	−2
	NORWECOM	157	157	0	156	0
	CSM-NZB	207	206	−1	203	−2
	MIRO	470	363	−23	308	−34

performed by Lenhart (2001). The simulation study demonstrated how the nitrogen and phosphorus fluxes in the trophic web change from the quasi-oligotrophic open regime towards the eutrophicated coastal regime. In the reduction run all processes decrease, but the microbial loop is quantitatively more important in the reduction run, with higher mass flows relative to the net uptake by phytoplankton.

### 3.2. Benthic system

The current state-of-the-art in three-dimensional ecosystem modelling of sediment biology and chemistry is characterised by ERSEM-I and ERSEM-II (Blackford, 1997; Ebenhöh et al., 1995; Ruardij and van Raaphorst, 1995). These models resolved a complex trophic structure, reproducing the general functioning of the North Sea benthos quite well. The benthic system was represented by a detritus pool and seven functional groups of aerobic and anaerobic bacteria, meiofauna, deposit and filter feeders, epibenthic and infaunal predators. The benthic subsystem was cast in a one-dimensional representation of vertical structure of organic carbon, oxygen and the nutrient fluxes for the nitrogen, phosphorus and biogenic silicate cycle in a three-layered sediment. It was linked to the pelagic system mainly by the sedimentation and filtering of organic matter, the export of dead organic material by all trophic levels and nutrient release from the sediments.

ERSEM-II gave reasonable pictures for the seasonal benthic dynamics (Blackford, 1997) and reproduced the regional differences in macrofaunal patterns fairly well on a large North Sea scale. Fig. 8 shows the correlation of modelled annual mean macrofaunal biomass together with data from the North Sea Benthic Survey (NSBS) (Künitzer et al., 1992). The spatial coverage of NSBS was excellent, but the seasonality was not recorded as each station was sampled only once a year (in April/May for the southern and central regions and in January for the northern North Sea). Macrofauna was calculated from ERSEM simulation as the sum of deposit feeders, suspension feeders and infaunal predators. For the  $1^\circ$  by  $1^\circ$  boxes 0–5 sampling stations fell into each box (Fig. 8(a)). The comparison of model and data at this scale showed an underestimation of the biomasses by the model in areas with a biomass over about  $13 \text{ gC m}^{-2}$ . Biomass of this magnitude was observed on the continental coast in shallow areas in the vicinity of major river plumes.

The model overestimated the faunal biomass of the German Bight. If the model results were transformed to the large ERSEM-I boxes, the number of samples within each model box increased by an order of magnitude and the correlation was greatly improved. Thus, the ERSEM model made a good prediction of the north-south trend in biomass, but did not reproduce the small-scale features in the vicinity of major estuaries. Anaerobic bacteria dominated in the southern North Sea, with aerobic bacteria gaining importance towards the better oxygenated north.

The relation between depth and modelled net primary production, detrital input, suspended food and macro-benthic biomass derived from the simulation (Fig. 9) has no counterpart from observations. The relationship between simulated available food (net primary production in the overlying water column) and water depth shows a break in slope at about 70 m depth. This is in accordance with observations by Künitzer et al. (1992) of a division of the infauna into northern and southern assemblages along the 70 m depth contour. The factors structuring species distribution are attributed by Künitzer et al. (1992) to be temperature, water masses, the type of sediment and the food supply to the benthos, all of which are included in ERSEM.

Besides the ecosystem approach, recently a prognostic diagenetic model was developed to close deficits in the simulation of marine biogeochemical processes at the sediment-water interface (Middelburg, Soetaert, Herman & Heip, 1996; Soetaert, Middelburg, Herman & Kerst, 2000). It provided a one-dimensional simulation of deposition and mineralisation rates and the fluxes of organic carbon, oxygen, nitrate and ammonium along vertical sediment and water profiles. The nitrogen budget by Soetaert et al. (2001) at the shelf-break area demonstrated the impact of the euphotic zone, the water column below, as well as the sediments on the nitrogen cycling. The amount of organic nitrogen sinking out of the water column is  $187 \text{ mmol N m}^{-2} \text{ yr}^{-1}$  which are incorporated in the sediment. Due to nitrification the derived ammonium is nearly completely oxidised (95%) into nitrate and 44% of the nitrate thus formed is denitrified in the sediment, the other part of  $107 \text{ mmol N m}^{-2} \text{ yr}^{-1}$  is returned to the water column. In contrast ERSEM simulated the regional differences of nutrient fluxes across the sediment-water interface for the North Sea

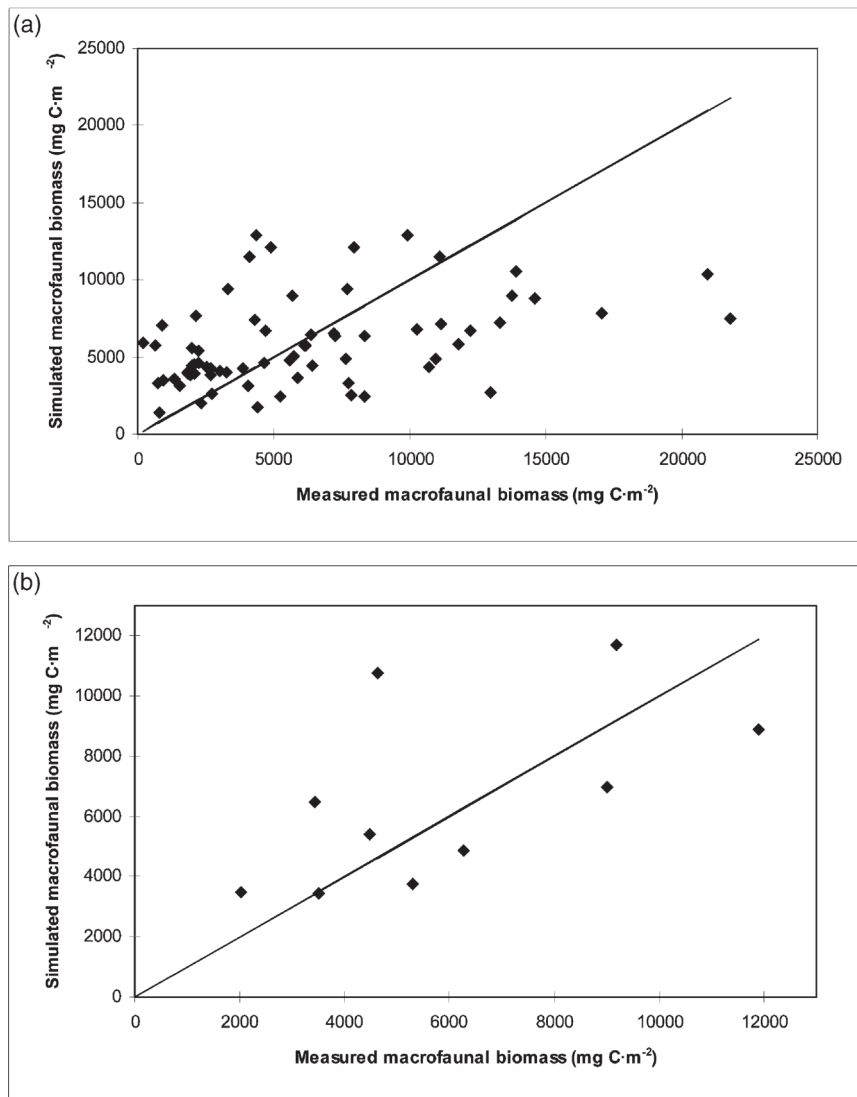


Fig. 8. Correlations for macrofauna from North Sea Benthic Survey data and ERSEM simulation for (a) ERSEM-II with 130 boxes and (b) ERSEM-I with 15 boxes structure (Blackford, 1997).

area for nitrogen (with a mean of  $1 \text{ mol N m}^{-2} \text{ yr}^{-1}$ ), phosphorus ( $62 \text{ mmol P m}^{-2} \text{ yr}^{-1}$ ) and silicon ( $653 \text{ mmol Si m}^{-2} \text{ yr}^{-1}$ ) (Radach & Lenhart, 1995), and the benthic biology of ERSEM had a very significant effect on the nutrient fluxes across the sediment-water interface (except for nitrate) (Blackford, 1997). Another application to North Sea sediments illustrated the bioturbation effects on nutrient remineralisation under different POM loads (Dauwe, Herman & Heip, 1998). Strong mixing by bioturbation was observed at the Frisian Front and minimal bioturbation at the German Bight station depending on the quality of the arriving organic matter. In the high amount and high quality POC sediment at the German Bight station, most organisms were found at shallow sediment depths ( $<2 \text{ cm}$ ), mainly feeding on freshly deposited or (re-)suspended material as interface or suspension feeders. Sediments, containing a large amount of refrac-

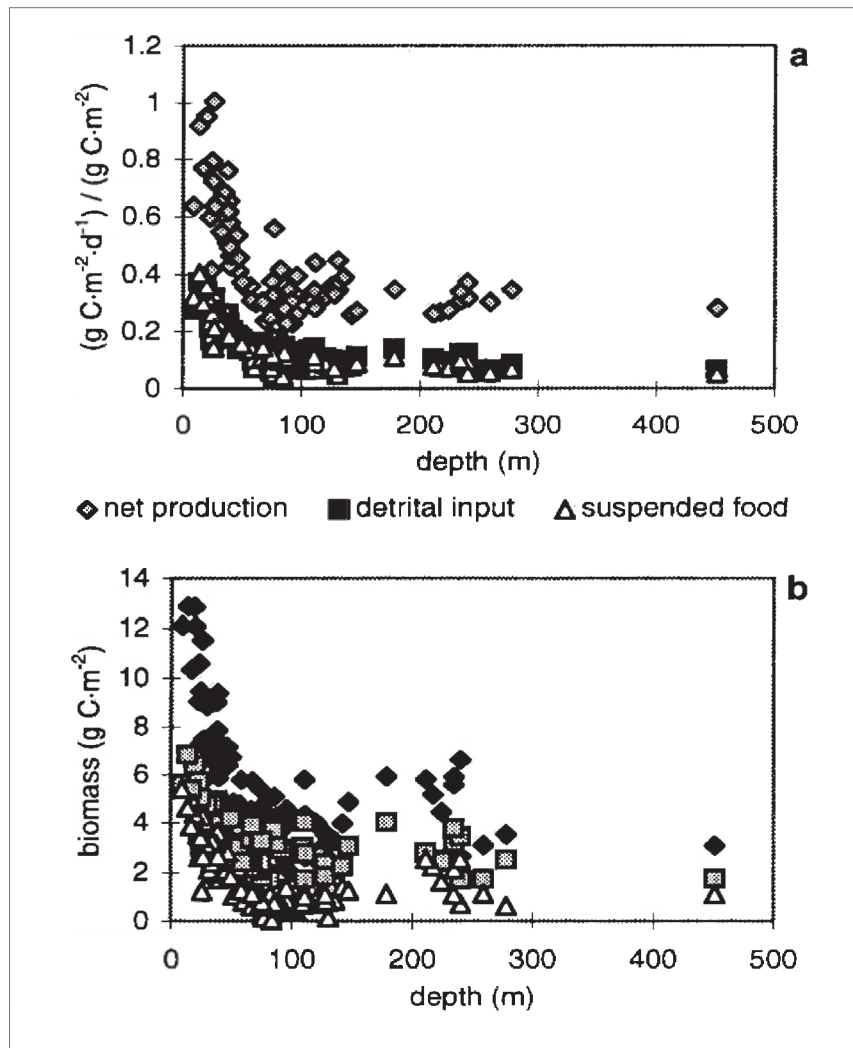


Fig. 9. Relations from ERSEM-II simulations for the macrofauna of the North Sea (Blackford, 1997). (a) the relation between depth and net primary production, detrital input and suspended food, (b) the relation between benthic biomass and depth.

tory organic matter, supported a small-sized deeply penetrating fauna (up to 20 cm) consisting mainly of deep-living deposit feeders.

For improving the regeneration mechanism in the ecosystem models a benthic diagenetic module of medium complexity should be developed and implemented in the three-dimensional ecosystem models according to the classification for describing sediment-water exchange processes by Soetaert, Middelburg, Herman and Kerst (2000).

### 3.3. Cycling of matter

The different model systems are best characterised in terms of their N, P, Si, and C budgets for the whole or for parts of the North Sea.

The construction of conceptual models for the flow of matter started around 1980 for the elements phosphorus (Ursin & Andersen, 1978), carbon (Joiris et al., 1982) and nitrogen (Mommaerts, Pichot, Ozer, Adam & Baeyens, 1984) for the North Sea. Fasham (1985) constructed a generic ecosystem model of the deep-sea euphotic zone using only nitrogen. A highlight for modelling the coastal ocean with a really complete web was provided for the Chesapeake Bay by Baird and Ulanowicz (1989). A flow analysis for all dissolved inorganic nutrients through the ecosystem of the North Sea was provided by Radach and Lenhart (1995) using ERSEM. Except for ERSEM and ECOHAM (using phosphorus, (Moll, 1997d), none of the three-dimensional models (Table 1) have been used so far for calculating budgets. But budgets for smaller regions of the North Sea were given by Allen (1997) and Hydes, Kelly-Gerreyn, Thomson, Proctor and Prandle (1997). A flow analysis of both simulated inorganic and organic carbon pools does not exist as yet.

Radach and Lenhart (1995) used ERSEM results to characterize changes in nutrients. Biological processes, gross nutrient uptake, algal respiration, and pelagic and benthic regeneration, contributed the largest changes to concentrations. For all nutrients gross uptake and algal release are the largest fluxes in the surface layer. In the lower layer respiration acted as a net source for nutrients. Microbial regeneration and benthic regeneration proved to be of different importance for the different nutrients. Local biological and chemical transformations together with vertical diffusion largely determined the nutrient dynamics of the ecosystem in each of the regions of the ERSEM simulation. Nutrient uptake by algae might recycle phosphate up to 4 times per year (Radach & Lenhart, 1995) (their Tab. 4), nitrogen up to 5 times per year (Radach & Lenhart, 1995) (their Tab. 7), and silicon up to 4 times per year (Radach & Lenhart, 1995) (their Tab. 8), compared to the winter content of nutrients in the water simulated for 1988. The percentages varied strongly regionally. The higher trophic levels played a minor role in nutrient dynamics as sources for nutrients through excretion.

Vertical diffusion was maximal in winter. The horizontal advective contributions turned out to modify the local dynamics. Decreases of the advective nutrient transport in summer was caused by the depletion of nutrients from the upper layer due to algal uptake. From the coastal areas there was a nutrient flow toward the central North Sea. Refinement of the boxes would allow a better representation of the gradients of nutrient concentrations perpendicular to the continental coast and thus to obtain more reliable estimates of the nutrient fluxes.

For the continental coastal area, Lenhart et al. (1997) used ERSEM with smaller boxes of  $1^\circ$  (east–west) and  $0.5^\circ$  (north–south) to obtain budgets for silicon, nitrogen and phosphorus. The N/P ratio was not fixed and allowed for differences in the flows of the elements through the food web. The nitrogen budgets near the Rhine (box 91) and for a region 100 km north (box 82) showed remarkable differences: Most of the inorganic nutrients from rivers were advected out of the region; in the onshore region the heterotrophic loop (zooplankton—detritus—bacteria) was weaker than in the off-shore region, and more organic material was lost to the sediment. The off-shore region received no river inputs and thus had a lower nutrient level (Fig. 10). The phosphorus budget showed relatively much lower river inputs than the nitrogen budget (relative to primary production). In the offshore region the heterotrophic loop exhibited increased phosphorus fluxes relatively larger than those in the nitrogen budget (Lenhart et al., 1997).

Lenhart et al. (1997) showed detailed analyses of budgets for the nutrient elements Si, N, and P under the assumption of non-Redfield ratios. These results proved to be very useful for understanding the eutrophicated system; on the other hand, there was and will be only little observational evidence to compare with most of the simulated fluxes. The study also pointed to the practical problem of defining a limited number of criteria for judging eutrophication, because the whole system reacts to eutrophication.

### 3.4. *Ecosystem dynamics under external forcing*

In the previous sections we illustrated aspects of the internal dynamics of the North Sea system (Fig. 1). Now we present the state of understanding of the system in its connections to external forcing.



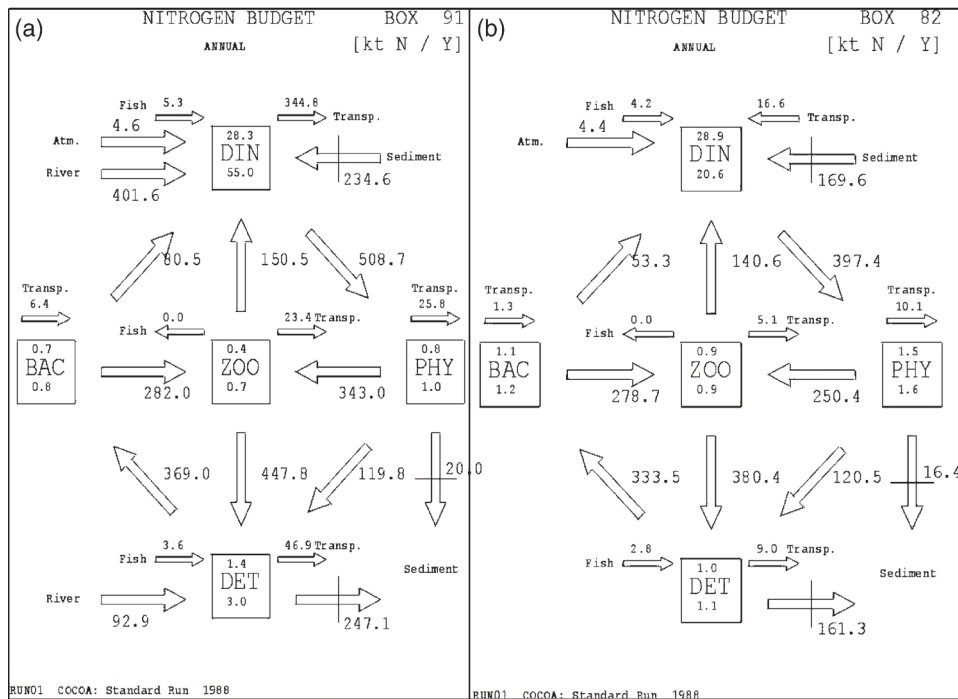


Fig. 10. Annual nitrogen budget for 1988 for (a) box 91 off the Rhine delta, (b) box 82 about 100 km north. DIN represents the sum of nitrate plus ammonium with river inputs and atmospheric nitrogen loads indicated (Lenhart, Radach & Ruurdij, 1997). Numbers in the boxes indicate the amount at the beginning and end of the year. Fluxes are given in  $10^6 \text{ Kg yr}^{-1}$ .

Of special interest are the variability and potential of reactions of the ecosystem to trends and shifts in the forcing and anthropogenic changes. External forcing functions of interest (Fig. 1) are hydrodynamics, solar radiation, riverine and atmospheric inputs and exchanges with the Atlantic and Baltic.

A prerequisite for 3D ecological simulation is the availability of (preferably non-climatological) meteorological and oceanographic forcing data, especially long-term hydrodynamic simulations.

### 3.4.1. Role of hydrodynamic forcing

The influence of stratification and water column processes was extensively discussed in previous reviews, e.g. by Fransz et al. (1991). Coupled water column process models had shown already the importance of the stability of the water column for the start of the spring plankton bloom. The GHER 3D ecosystem model of the North Sea first illustrated this importance in a synoptic manner by presenting the annual evolution of the temperature and chlorophyll concentrations in a vertical section from the shallow Southern Bight to the deeper northern part (Delhez, 1998) (his Fig. 5).

It is the influence of horizontal and vertical advection that is of special interest in 3D modelling. Moll and Pohlmann (1997) used ECOHAM simulations to test the coupling of advection and biological processes; four simplified scenarios showed the influence of horizontal transports on the regional distribution of primary production. Omitting horizontal advection and diffusion while keeping vertical turbulent diffusion and the biological dynamics unchanged, yielded a representation of the local dynamics (Fig. 11). The full 3D dynamics of 1986 yielded a mean integrated annual water column net production of  $143 \text{ gC m}^{-2} \text{ y}^{-1}$ , differing regionally between  $92\text{--}345 \text{ gC m}^{-2} \text{ y}^{-1}$ . Horizontal advection smoothed all regional distributions, and the transports were necessary to reproduce the annual periodicity of the nutrient cycles

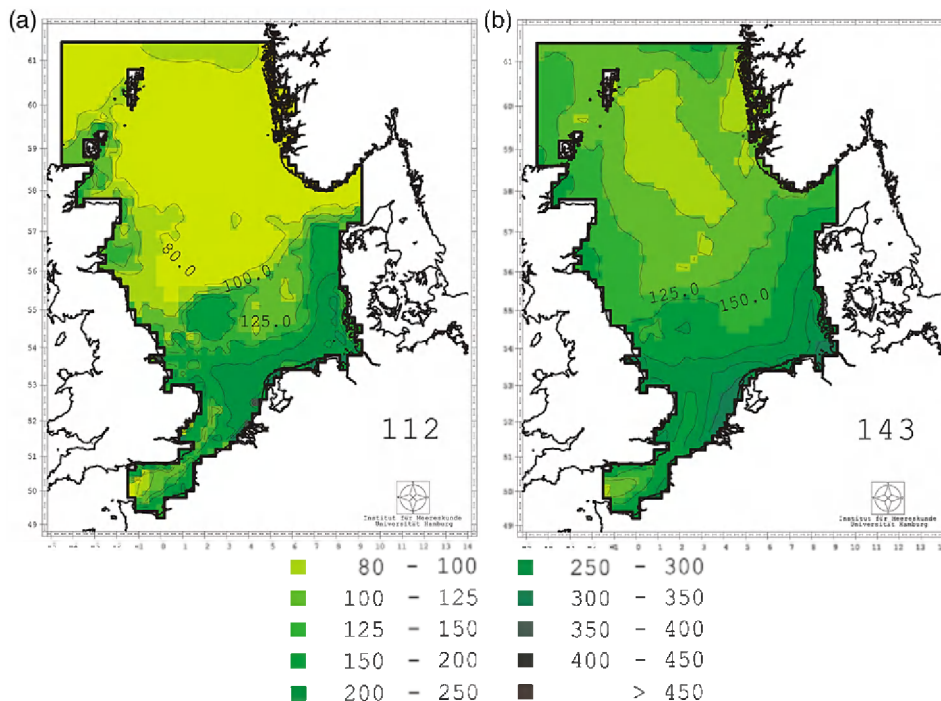


Fig. 11. Influence of advection and diffusion on simulated annual primary production in the North Sea for the year 1986: (a) local dynamics of the water column with an annual mean production of only 112  $\text{gC m}^{-2} \text{y}^{-1}$ , (b) full three-dimensional simulation with an annual mean production of 143  $\text{gC m}^{-2} \text{y}^{-1}$  (Moll & Pohlmann, 1997).

in the northern North Sea with its regional production minimum. The scenarios showed that local dynamics mainly determined the primary production. Primary production increased by 12, 25 and 28% in adding horizontal diffusion, horizontal advection and the full 3D dynamics, respectively.

Several models have been used to quantify primary production and its spatial variability. Skogen and Moll (2000) studied variations in primary production (Fig. 5) with NORWECOM and ECOHAM. When they found differences in the primary production and its variability, the simulated physics also differed. While the interannual variability in the primary production of the northern North Sea was driven in the NORWECOM simulation largely by the Atlantic inflow, and thus by an increase in nutrients, production in the ECOHAM simulation was determined mainly by the stratification regime and was modulated by the transports. The difference in results was mainly due to the use of two different physical models. The horizontal transports from four North Sea circulation models compared by Smith, Damm, Skogen, Flather and Pätsch (1996) showed large differences. A realistic, well-tested and validated 3D circulation model is therefore essential for primary production and further ecosystem studies in this area, including realistic horizontal advection and exchange with the Atlantic and correct simulation of the vertical density structure.

### 3.4.2. Role of solar radiative forcing

Solar radiation as a trigger initiating algal blooms was also extensively discussed in previous reviews, e.g. Frantz et al. (1991). No publication about 3D ecosystem models illustrated the water column dynamics in relation to the processes of solar radiation, attenuation and self shading. It is the influence of the horizontal differences in the annual cycle of the radiation which is of special interest in 3D modelling, but studies of this are sparse. Pätsch and Radach (1997) simulated a 39 years hindcast for the North Sea with ERSEM-II and studied the influence of solar radiation versus that of anthropogenic river inputs. The interannual

variability of the net primary production was not correlated to light variability in the north, but 62.5% of the variance of production in the south could be explained by radiation variance (Fig. 12). Pätsch and Radach (1997) concluded that the influence of radiation dominated in the southern North Sea because phytoplankton are light-limited in the well-mixed zones, in contrast to the stratified, and therefore nutrient-limited, northern North Sea.

#### 3.4.3. Role of riverine and atmospheric inputs

River inputs are commonly implemented as external forcing in ecological models, and reductions of those are common in modelling (OSPAR et al., 1998). However, atmospheric inputs are not yet commonly implemented.

Skogen et al. (1995) presented simulation results from NORWECOM with river nutrient input reduced by 50%. Their investigation responded to the 2nd International Conference on the Protection of the North Sea in London 1987, at which all countries around the North Sea agreed to achieve a 50% reduction between 1985 and 1995 in areas where nutrients caused pollution. Later it was agreed to evaluate the effects of nutrient reduction by the percentage decrease of primary production (Fig. 13). The main effect of reduced nutrients was decreased production of flagellates, because there was no reduction in the input of silicate, which is rate-limiting for the diatoms. The strongest local effects occurred close to the continental coast, with reductions between 5–10% of annual primary production compared to the business-as-usual scenario. The latest application of NORWECOM aimed at the quantification of the effect of the flooding of the Norwegian river Glomma in May–June 1995 (Skogen et al., 1998).

While the NORWECOM results depended only on dissolved inorganic nitrogen and phosphorus reductions, simulations with ERSEM-II included the riverine input of all four dissolved and particulate nutrients as well as particulate organic carbon on an annual basis (Lenhart et al., 1997). The most recent ERSEM-II simulations (Lenhart, 2001) compared reduction scenarios, different nutrient limitation functions, and annual P versus N budgets for a series of boxes off the coast of The Netherlands. While the reduction scenario of 50% results in decreased winter concentrations of nitrogen and phosphorus of up to 40%, the decrease in net primary production reached only up to 20% in small areas in the coastal zone. There were significant changes in the strength and timing of the nutrient limitation in all phytoplankton groups in the model, but the diatom concentration did not change much. All fluxes of the microbial loop show higher relative process contributions in the reduction run. The results of the ecosystem model ERSEM

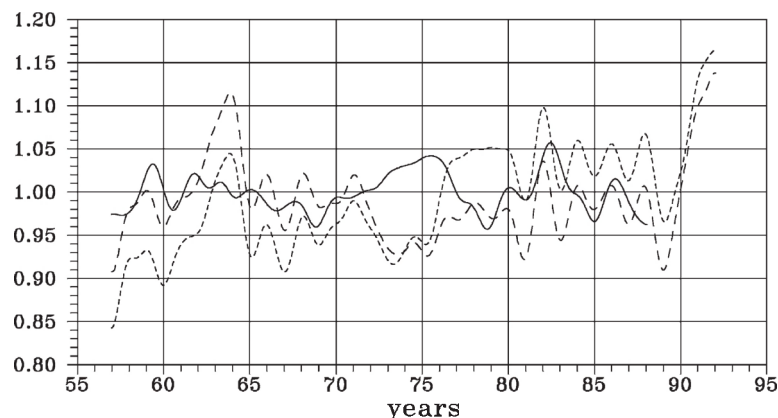


Fig. 12. Anomalies of the solar radiation (solid line), net primary production in the 1955–1993 hindcast simulation (long-broken line), and the net primary production of the standard run without anthropogenic nutrient inputs (dotted line) in the southern North Sea (Pätsch, 1997).

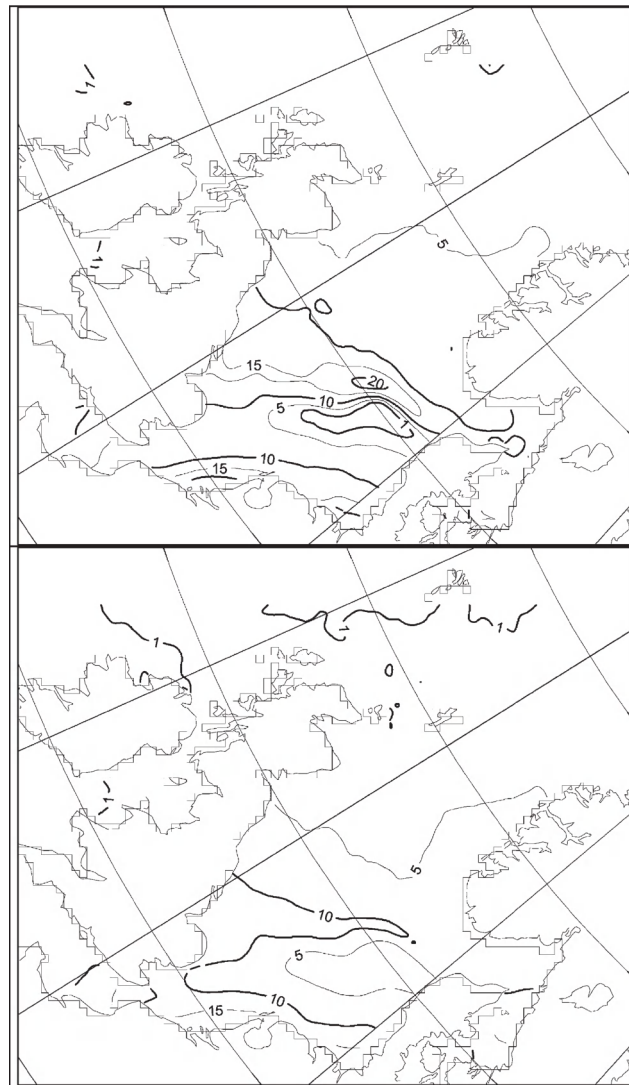


Fig. 13. Reduction in percentage of flagellate production simulated with NORWECOM for the year 1985 (Skogen, Svendsen, Berntsen, Aksnes & Ulvestad, 1995) during June (top), and per annum (bottom) with a 50% reduction in river loads.

showed, that a reduction in the nutrient load by 50% for N and P cannot be linearly transferred to a similar reduction in primary production. To show how far the river-induced eutrophication penetrated into the central North Sea, Pätsch and Radach (1997) plotted the annual differences of primary production in an ERSEM-II simulation against the corresponding increments of annual river inputs of phosphate and dissolved inorganic nitrogen for areas ranging from the continental coast seaward (Fig. 14). The relation showed steep initial increases of additional primary production for small increments of river inputs in the German Bight (box 71). Further increases of production with increasing river inputs were not possible because the carrying capacity was reached, which seems to be limited by the available solar energy within the upper layer of decreasing transparency, not by the plentiful nutrients. A clear influence of eutrophication was shown to be expected even for the south-eastern central North Sea (box 58), but not for the central

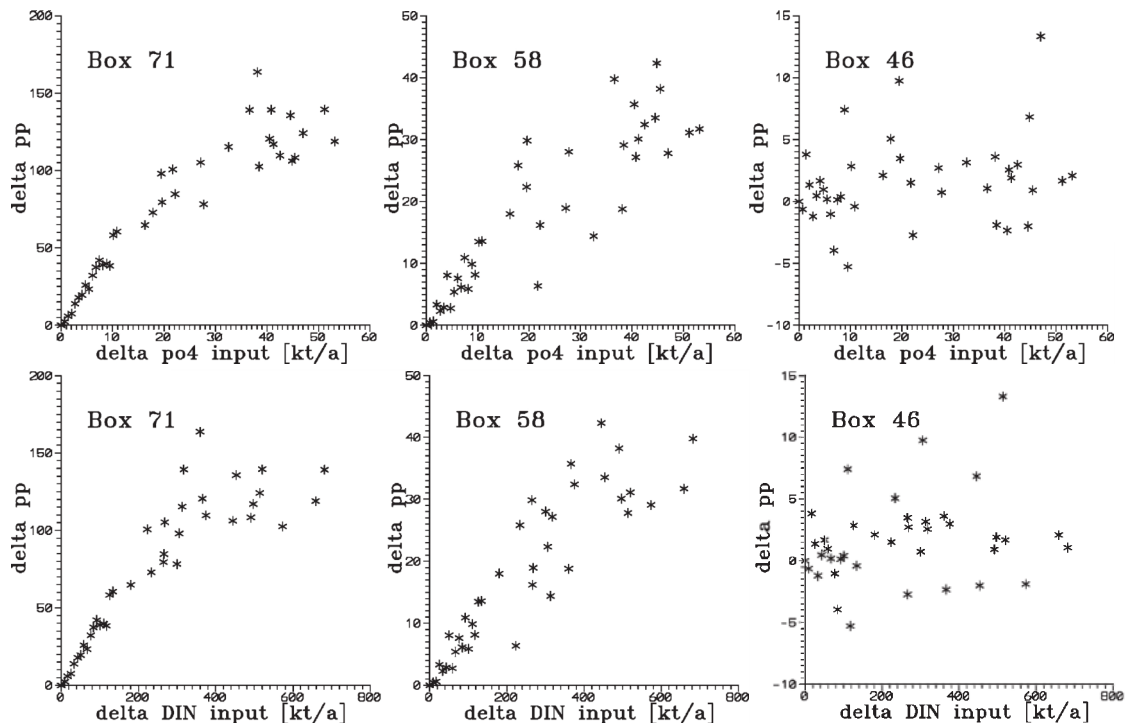


Fig. 14. Relation of simulated annual increase of primary production (delta pp) versus the annual increase of river inputs for the years 1955–1993 (Pätsch & Radach, 1997), for phosphate (upper panel) and dissolved inorganic nitrogen (lower panel) in the boxes 71 (inner German Bight), 58 and 46 (central North Sea).

North Sea (box 46). Studies of river nutrient input should be repeated with fully 3D ecological models of the ERSEM type.

Only a few ecological models have included atmospheric nitrogen inputs. Among the 3D models only ERSEM (Pätsch & Radach, 1997) and NORWECOM (Soiland & Skogen, 2000) used annual mean input values for the whole North Sea. Intensive air-sea coupling has to be included in the next generation of models. The necessary atmospheric loads have to be provided by aggregation of observations and atmospheric model data.

#### 3.4.4. Role of the exchanges with the Atlantic and the Baltic Sea

Water and nutrient flows across the northern boundaries of the North Sea, derived from observed nutrient concentrations and simulated circulation data, gave no indications of any trend over the four decades investigated by Pätsch (1997) using ERSEM-II. The hypothesis of Lindeboom et al. (1996) that water entering from the Atlantic had changed its composition and caused major changes in the North Sea ecosystem could not be substantiated (Pätsch & Radach, 1997). Unfortunately, there is a lack of continuous, long-term, nutrient observations in the non-coastal areas of the North Sea. It is known that the Atlantic circulation influences the circulation in the North Sea, e.g. in connection with the NAO (Dickson, Lazier, Meincke, Rhines & Swift, 1996). Circulation models for the North Atlantic, which are forced by realistic atmospheric conditions, could provide the necessary boundary conditions for modelling the circulation of shelf seas under this same forcing.

The influence of the Baltic outflow on the North Sea system has to be investigated by coupling ecological models for both systems. Development of circulation models for that area is underway (Janssen, Schrum,



Hübner & Backhaus, 2001; Schrum & Backhaus, 1999). The best way to study the influences of the adjacent sea areas on the dynamics of the north-west European shelf seas would base the ecological models on a circulation model including the Atlantic Ocean and all shelf seas of northwest Europe.

### 3.4.5. Variability of the ecosystem dynamics

Data for studying variability in the open North Sea are sparse (Radach & Gekeler, 1996; Radach & Pätsch, 1997), and include no long-time series. In the MAST NOWESP project (Laane et al., 1996) time series were compiled for temperature, salinity, nutrients, chlorophyll, suspended matter and plankton at several sites in the North Sea. Data sets suitable for a comparison with ecosystem models in the North Sea were the Dutch monitoring data (NOWESP site 5–2) and the Helgoland Roads data (NOWESP site 6). These two sites are situated in the continental coastal zone with strong influence from the Rhine and Elbe rivers and thus are located in strong gradients perpendicular to the coast. Pätsch and Radach (1997) used ERSEM-II to provide long-term simulations for these NOWESP sites. We present their statistical analysis in a condensed form in Tables 7–9 to illustrate comparisons between observed long-time series and consecutive simulations. First the authors defined the correspondence of NOWESP sites and ERSEM-II boxes. The middle and lower panel provided statistical measures of the coincidence of simulation and observations for the Dutch monitoring data (1976–1988) and Helgoland Roads data (1962–1993), separately for “all months” together, for “winter” (December–February) and for “summer” (April–September). The long-term means and standard deviations were given for both, the simulation results and the observations. Root mean square (rms) differences between simulated and observed monthly means, normalised by the standard deviation of observations, were used to quantify the fit.

Dutch monitoring data for phosphate showed good agreement with model winter concentrations (Table 8), but during the most eutrophicated years several relative maxima in summer were not reproduced, yielding an rms distance of 1.23 standard deviations and no correlation. The overall fit for nitrate was better than for phosphate; mean observed levels were close to the simulated ones. However, the observed standard deviations were all larger than simulated ones by a factor of two. The winter concentrations were strongly underestimated in nearly every year, as expressed by the relatively high rms distance of 1.03 standard deviations. Silicate observations were simulated well; both the start of depletion and the autumn increase were simulated. The overall correlation was good, but standard deviation was high due to sporadic, very high silicate concentrations in winter. Moreover, while simulated concentrations for summer are very low, relative maxima occurred frequently in the observations, raising the mean, standard deviation and rms error. The agreement of simulated and observed chlorophyll was satisfactory for all months, although the simulation did not reach the maximal observed values of chlorophyll.

The observations at Helgoland Roads in the German Bight (Table 9) included the separation of diatoms and flagellates. Similarity between simulated and observed diatom abundance was satisfactory. Timing of

Table 7

Correspondence of NOWESP sites and ERSEM boxes, and interpolation weights for comparison of simulation results and NOWESP time series of the given state variables (Pätsch & Radach, 1997)

NOWESP site	Position	ERSEM ND130 box	weights>0.02 (rounded)	data source	state variable
Site 5–2	3°48′ E–4°08′ E, 52°12′ N–52°32′ N	81, 82, 85	0.71, 0.23, 0.06	RWS, Den Haag	PO4, NO3, SiO4,
Site 5–3	3°18′ E–3°48′ E, 52°22′ N–52°42′ N	74, 75, 80, 81, 82	0.14, 0.05, 0.14, 0.65, 0.13	RWS, Den Haag	PO4, NO3, SiO4, Chl
Site 6	6°40′ E–8° E, 54° N–54°45′ N	70, 71	0.64, 0.36	BAH, Hamburg	PO4, NO3, NH4, SiO4, Chl, diatoms, flagellates

Table 8

Statistical analysis of coincidence of simulated and observed time series for state variables (SV): nutrients at site 5–2 and chlorophyll at site 5–3 (Dutch coastal waters) (Pätsch & Radach, 1997)

SV	phosphate			nitrate			silicate			chlorophyll		
	all mo.	winter	summer	all mo.	winter	summer	all mo.	winter	summer	all mo.	winter	summer
mean												
sim	0.69	1.15	0.37	12.91	20.20	8.09	4.50	10.44	0.60	2.09	0.65	3.13
obs	0.70	1.10	0.41	16.29	26.16	10.47	4.11	8.97	1.30	2.19	1.21	2.55
standard deviation												
sim	0.41	0.16	0.18	7.73	4.64	4.88	4.73	1.99	0.14	1.24	0.12	0.81
obs	0.42	0.33	0.29	13.07	10.70	10.49	4.73	4.77	1.08	1.67	0.65	1.80
further statistical properties												
N	144	36	72	204	51	102	144	36	72	192	48	96
rms	0.81	0.89	1.23	0.70	1.03	0.77	0.72	0.86	1.21	0.95	1.28	0.92
corr	0.66	0.45	−0.08	0.78	0.49	0.73	0.74	0.62	−0.12	0.43	0.22	0.50
5%	yes	yes	no	yes	yes	yes	yes	yes	no	yes	no	yes
1%	yes	yes	no	yes	yes	yes	yes	yes	no	yes	no	yes

The means and standard deviations are given for the simulation results (sim) and the observations (obs) for phosphate, nitrate, silicate and chlorophyll for the whole year (all months) and winter and summer. In the lowest panel further statistical measures are given: N is the number of available data, the rms error (rms) and correlation (corr) between simulation and observations is given together with the 5% and 1% confidence limit of the correlation.

Table 9

Statistical analysis of coincidence of simulated and observed time series for state variables (SV) at NOWESP site 6 (German Bight) (Pätsch & Radach, 1997)

SV	phosphate			nitrate			diatoms			flagellates			silicate		
	all mo.	winter	summer	all mo.	winter	summer	all mo.	winter	summer	all mo.	winter	summer	all mo.	winter	summer
mean															
sim	0.54	1.00	0.22	13.42	21.76	7.69	28.67	4.09	44.73	39.07	3.41	69.94	6.40	15.30	0.70
obs	0.74	0.96	0.51	14.27	17.15	12.80	24.48	1.83	45.47	23.97	8.63	38.43	7.19	9.77	5.01
standard deviation															
sim	0.43	0.27	0.17	8.91	6.76	4.94	33.19	3.64	39.25	53.48	1.77	61.46	6.91	2.79	0.46
obs	0.35	0.21	0.28	11.49	11.21	10.85	38.75	1.80	45.69	40.71	6.39	53.43	5.81	5.21	5.46
further statistical properties															
N	382	96	190	381	95	190	384	96	192	384	96	192	316	78	159
rms	1.10	1.00	1.42	0.91	0.92	0.96	1.08	2.70	1.26	1.63	1.28	1.75	1.23	1.51	1.28
corr	0.66	0.65	0.36	0.50	0.56	0.55	0.33	−0.17	0.09	0.07	0.17	−0.18	0.39	0.11	−0.11
5%	yes	yes	yes	yes	yes	yes	yes	no	no	no	no	no	yes	no	no
1%	yes	yes	yes	yes	yes	yes	yes	no	no	no	no	no	yes	no	no

For further explanation see footnote to Table 8 above.

the spring diatom bloom in the model was close to that observed, although the simulated bloom occurred about one month earlier than the observed bloom during many years. Observed and simulated mean concentrations in summer were nearly equal, and the observed standard deviations were well simulated. The comparison between observations and the simulation of flagellates was not satisfactory. Both the means

and standard deviations of flagellate abundance were larger in the simulation than in the observations during all months. The maximum of the flagellates occurred in spring, as for diatoms, which was different from observations, where flagellates peaked later, in summer.

The interannual variability was generally underestimated by ERSEM-II. The cause may lie in the use of climatological annual cycles of temperature and salinity, on which the hydrodynamic simulation was based (Pätsch & Radach, 1997). Also a mean annual cycle for particulate suspended matter was prescribed. Future models should certainly simulate the parameters temperature, salinity and suspended particulate matter prognostically. Then we can expect better results in the future.

### 3.5. Available simulation data from three-dimensional ecosystem models

The model results described above show the potential of 3D ecosystem models. Such models produce huge amounts of simulated data, which should be available for further use and analysis. Moll and Radach (2001) summarised the availability of the simulation runs up to date. The simulated data were not stored regularly from all models, and when they were, the simulated data were usually not stored in public or institutional data bases; they are usually available only on request from the scientist performing the simulation, and the approach is mostly by direct or email contact. Most of the simulated ERSEM state variables and process contributions, which became output parameters were stored for the configuration of the 1° boxes, on which the long-term simulation was based. For the fully 3D models fewer parameters are available, but for these models the hydrodynamic data are also available on a 12–20 km grid.

## 4. Conclusions

Model results reviewed here have either confirmed existing knowledge derived from field work or have given new insight into the mechanisms of the North Sea system: the temporal and spatial development and magnitude of primary production, its limitation, the function of the small food web and of the benthic web, the mechanisms of nutrient regeneration, the effects of coastal eutrophication, the extent of eutrophication in the North Sea, and the budgets for phosphorus, nitrogen and silicon.

The three-dimensional ecological models of the greater North Sea have provided consistent regional and annual distributions and dynamics of state variables representing the lower trophic levels, results which cannot be derived to this degree of coverage by observations. They have given an understanding of the quantitative dynamics of primary production, especially about its spreading from the coasts to the northwest over the open North Sea.

This review has also shown apparent deficiencies of the ecosystem models. At present most models are suited only to investigate a very restricted scope of processes. For example, modelling of algal succession depends on detailed knowledge not yet available regarding the physiological demands of algal species or groups of species, concerning nutrients, light, and turbulence intensity. No model developed so far is suited for the recruitment problem, and only one has incorporated state variables for the simulation of specific contaminant dynamics. The complexity of all models, except perhaps of ERSEM-type models, needs to be enhanced. Sediment chemistry is not represented in a way that would enable realistic long-term simulations, since burial of organic matter and subsequent remobilisation of nutrients are not included in any model formulation. Algal growth could be much better simulated in respect to the regional effects of stratification, of currents and nutrient availability and of the influence of light intensity as they vary with latitude, season, and depth.

All models are well suited for establishing budgets for estimating the fluxes in their simulated area and time period. However, calculation and publication of fluxes and budgets are not common. Budgets have an importance per se, as well as for comparisons among models and between models and data.

The functioning of the ecosystem, as represented in ecological models, should be investigated taking into account the atmospheric and hydrodynamic shifts induced by global change. These changes in the meteorological forcing and in the circulation system on the shelf may considerably alter the annual primary production in coming decades.

The advantage of box models is their relatively small demand for computer time, which gives the possibility to perform many simulation runs, e.g. to investigate the sensitivity of the model to parameter changes. However, the resolution of the box models restricts the study of meso-scale and smaller features. From the comparisons between the models for the greater North Sea and observations, it has become clear that ecosystem models should be 3D and should be coupled with or forced by state-of-the-art circulation models. For example, scenarios of eutrophication and of reduced atmospheric and riverine inputs of nutrients have not yet been studied using finely resolved, 3D ecosystem models to confirm results from simulations with coarser resolution.

Because the Atlantic circulation influences the circulation in the North Sea, e.g. in connection with the NAO, circulation models for the North Atlantic forced by realistic atmospheric conditions, could provide the necessary boundary conditions for modelling shelf seas' circulation under this same forcing. This is not yet achieved.

The trophic resolution implemented in North Sea ecological models seems arbitrary and was not determined systematically. Research is needed seeking a more rational determination of the complexity required for the problem under consideration. Processes on scales below the meso-scale have to be parameterised, and much testing is needed of the commonly used parameterisations and to derive appropriate parameterisations where they are lacking. Evaluations of spatially extensive models requires mapping of distributions for the main phytoplankton groups (diatoms, nanoflagellates, and dinoflagellates) and zooplankton groups (at least micro- and mesozooplankton) over the annual cycle.

The validation procedure will be presented in Part 2 of this series of papers.

## Acknowledgements

The results presented here emerged to a large extent from the research project "Synthesis and Conception of North Sea Research (SYCON)", 1998–2000/2001, which was funded by the Bundesministerium für Bildung und Forschung (BMBF) under contract 03F0215A. We are very much obliged to our colleagues in this project SYCON, who helped us with advice and deep interdisciplinary knowledge during the project and afterwards when this paper was written. We also want to thank all our colleagues in the modelling teams around the North Sea very much for providing us with valuable information about their models. Without this help the review could not have been written. Furthermore we wish to thank two anonymous reviewers for constructive comments which improved and condensed the manuscript. Finally, we deeply thank the editor Dr. Charlie Miller for his great effort in revising the paper into a proper English version.

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