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A modelling study of ecosystem dynamics and nutrient cycling in the Humber plume, UK

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Abstract

The European Regional Seas Ecosystem Model (ERSEM) has been coupled with a two-dimensional depth-averaged transport model of the Humber plume region and run to simulate 1988–1989. Simulations of the spatial and temporal variations in chlorophyll-*a*, nitrate, phosphate and suspended particulate matter distributions in winter, spring and summer show how the development of the spring bloom and subsequent maintenance of primary production is controlled by the physicochemical environment of the plume zone. Results are also shown for two stations, one characterised by the high nutrient and suspended matter concentrations of the plume and the other by the relatively low nutrient and sediment concentrations of the offshore waters. The modelled net primary production at the plume site was $105 \text{ g C m}^{-2} \text{ a}^{-1}$ and $127 \text{ g C m}^{-2} \text{ a}^{-1}$ offshore. Primary production was controlled by light limitation between October and March and by the availability of nutrients during the rest of the year. The phytoplankton nutrient demand is met by in-situ recycling processes during the summer. The likely effect of increasing and decreasing anthropogenic riverine inputs of nitrate and phosphate upon ecosystem function was also investigated. Modelling experiments indicate that increasing the nitrogen to silicate ratio in freshwater inputs increased the production of non-siliceous phytoplankton in the plume. The results of this model have been used to calculate the annual and quarterly mass balances describing the usage of inorganic nitrogen, phosphate and silicate within the plume zone for the period of the NERC North Sea survey (September 1988 to October 1989). The modelled Humber plume retains 3.9% of the freshwater dissolved inorganic nitrogen, 2.2% of the freshwater phosphate and 1.3% of the freshwater silicate input over the simulated seasonal cycle. The remainder is transported into the southern North Sea in either dissolved or particulate form. The reliability of these results is discussed. © 1997 Elsevier Science B.V. All rights reserved.

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1. Introduction

A key factor in controlling coastal primary production and global geochemical cycling may be chemical transports and biogeochemical interactions within estuarine plume zones. It remains possible

that they are major factors in regulating the fluxes of land-derived natural and pollutant chemicals into shelf seas (Jouanneau and Latouche, 1982; Fichez et al., 1992; Morris et al., 1995).

An estuarine plume can be characterised by a relatively weak salinity gradient extending offshore from the mouth of an estuary. The offshore boundary of the plume is difficult to define as it tends to merge with a near-shore band of low salinity water. A spe-

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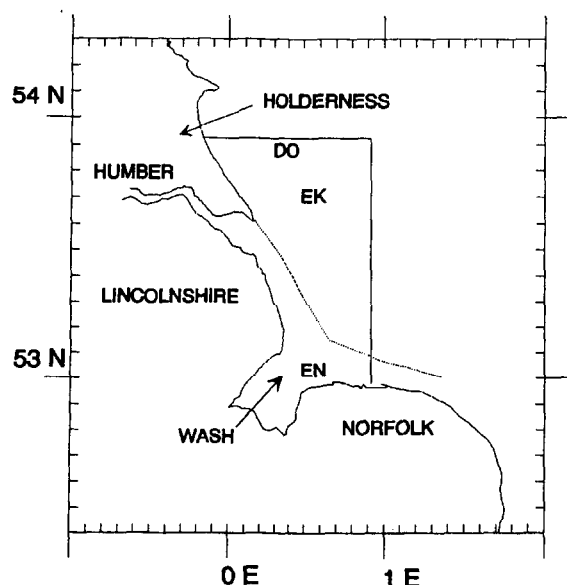


Fig. 1. Map of the Humber estuary and the coastal plume zone. The approximate extent of the low salinity plume is indicated by the dashed line. The boundaries of the mass balancing box (Morris et al., 1995) are shown by solid lines. The position of survey sites EN, EK and DO are indicated.

cific isohaline is often selected from the observed salinity field for practical purposes (Jouanneau and Latouche, 1982). Plumes are also characterised by enhanced nutrient concentrations compared with off-shore waters, due to land-derived inputs from the contiguous estuary. High nutrient levels can lead to enhanced phytoplankton growth and potentially to eutrophication.

The Humber plume extends south from the Humber mouth along the Lincolnshire coast and then eastward along the Norfolk coast (Morris et al., 1995). Fig. 1 shows the approximate extent of the plume as defined by an isohaline of salinity 34.0‰. Essentially the plume is highly energetic and its morphology depends strongly on the river discharge, tidal conditions and wind stress. This means that the boundary of the plume is difficult to define, hence the dynamics of the system are also difficult to define. It is characterised by high nutrient and suspended sediment concentrations, both of which play a major part in controlling the ecosystem. A secondary source of freshwater into the region are the rivers that empty into the Wash. They carry nutrient loads that are similar to or exceed on occasions those carried by the

Humber (Fichez et al., 1992). The Holderness coast, to the north of the river Humber, undergoes constant erosion, providing a major source of suspended inorganic particulates. Suspended sediment and nutrient concentrations decrease away from the coast.

The Humber plume region has been the focus for a number of field studies, including the Natural Environment Research Council (NERC) North Sea survey (Lowry et al., 1992; Simpson, 1994; Morris et al., 1995), and the ongoing, at the time of writing, Land Ocean Interaction Study (LOIS). One of the major aims of both of these studies has been to quantify the fate of land-derived nutrients, both dissolved and particulate as they pass from the estuary to the sea.

The effects of anthropogenic modifications to land-derived nutrient inputs upon the function of the ecosystem in coastal seas can include eutrophication in extreme cases. Diatoms are a basic food source for mesozooplankton and filter-feeding fish in inshore waters, they have short life cycles, are grazed heavily and rarely create a nuisance. Conversely flagellates persist for longer periods of time and represent poor food sources for grazers. Furthermore, flagellate blooms are often related to undesirable eutrophication effects such as anoxia and toxic algal blooms. Officer and Ryther (1980) have hypothesised that silicate is the controlling nutrient in determining whether the ecosystem is flagellate or diatom dominated. The alternation between these systems is governed by the relative magnitudes of land-derived fluxes of nitrogen, phosphorus and silicon into the coastal zone and the recycled fluxes of these elements from zooplankton grazing, phytoplankton respiration and decomposition in the sediments.

In this paper a model has been described that reproduces the observations of the North Sea Survey, using the best available forcing functions in order to establish a validatable baseline. The purpose of this was to test the applicability of the generic ERSEM model in a shallow coastal environment. Results are shown for two stations, one inside the plume (EN) and one offshore (EK) to contrast the two distinct biological regimes in the model domain (Fig. 1). The model has been rerun with 0.5 and 1.5 times the observed riverine nitrate and phosphate inputs, to determine the likely impact of changes in an-

thropogenic inputs upon the plankton composition and to assess the potential for eutrophication in the plume.

An application of the model has been a calculation of detailed budgets of the cycling of dissolved and particulate nutrients through the coastal ecosystem. The results are then compared with previous estimates of nutrient fluxes in the region to assess the performance of the model and to identify which processes require further study.

To calculate a mass balance of an element we need to identify and quantify all of the processes affecting that element. A combination of the limitations in current sampling techniques and logistical problems means that it is difficult to fully quantify the spatial and temporal variation of all the processes taking place in the plume zone over a seasonal cycle. One way to circumvent this problem is to use a fine scale ecological model. The results of ecological models allow budgets to be derived in a far more complete way than can be made from observations because the simulated systems are closed with values for all the fluxes. Comparison of nutrient budgets compiled from quantitative analysis of available data and model output provided a good objective test for the models (Radach and Lenhart, 1995). The discrepancies between the budgets can be used as an indicator for future investigations into the nutrient cycling of estuarine plumes.

2. Model structure

The model developed for this task is a combination of two well established modelling initiatives, ERSEM v11 (European Regional Seas Ecosystem Model, version 11) and a 2D depth-averaged hydrodynamic and transport model of the Humber plume (Wood, 1993), developed from the North Sea model of Prandle (1984).

The open boundaries of the model domain are defined by latitude 54°00'N in the north and longitude 1°48'E to the east. The southern and western boundaries of the model are defined by land. The grid size is approximately 4.5 × 4.5 km, giving 359 biologically active cells within the model domain.

In order to make a mass balance for a dynamic system such as the Humber plume the boundaries of the region need to be defined. As has been pre-

viously stated the boundaries of an estuarine plume are mobile and difficult to define. In order to make a budget calculation we therefore have to assume fixed geographical boundaries for the region. These are defined by a box between 53°51.5'N 0°57.5'E, the coast and the freshwater limits of the estuaries. The seaward boundaries mark the approximate limits of the wind driven excursions of the plume and they are consistent with those used for previous flux estimates of both nutrients and trace metals in the region (Wood, 1993; Huthnance et al., 1994; Morris et al., 1995; Millward et al., 1996). The nutrient budgets presented are an aggregation of the 250 linked grid points within the defined mass balancing box (Fig. 1).

2.1. Transport model

The advection diffusion model was driven by residual velocities. The rate of change of a contaminant C with time is given by:

$$\frac{dC}{dt} + U \frac{dC}{dt} + V \frac{dC}{dt} = K_x \frac{dC}{dx} + K_y \frac{dC}{dy} + \sum S \quad (1)$$

where U and V are residual velocities in a northerly and easterly direction, K_x and K_y are coefficients of horizontal diffusion and $\sum S$ represents the sum of any source and sink terms including biogeochemical processes. The nonlinear advection term is split into two components to take account of the directional properties of the residual velocity field. The range of magnitude of residual velocities (0.01 to 0.1 m s⁻¹) means that artificial diffusion is found to be equivalent to a diffusion coefficient in the range of 23 to 225 m² s⁻¹ using the formulae given by Roach (1972). The transport equations were solved using an upwind difference, flux-corrected scheme (Book et al., 1973). This method was chosen to maintain the concentration gradients within the model domain by minimising the effects of artificial diffusion. The diffusion coefficients are assumed to be variable over the whole grid and are parameterised to represent the dispersion caused by tidal mixing. A tidal velocity amplitude dependent form of K_x , K_y has been used (Wood, 1993):

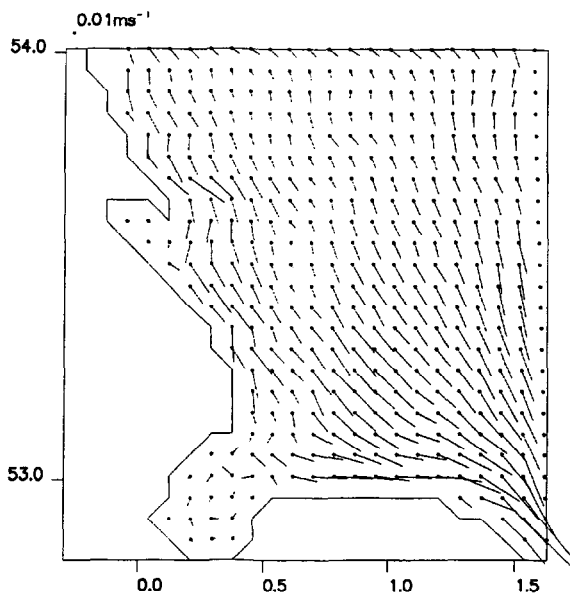


Fig. 2. Simulated residual velocity flow field for January 1988.

$$K_x = \alpha U_m (V_m^2 + U_m^2)^{1/2}, \quad K_y = \alpha V_m (V_m^2 + U_m^2)^{1/2} \quad (2)$$

where V_m and U_m are tidal velocity amplitudes and α is a constant with a value of 50 s. This value was chosen because it generates plausible winter salinity fields.

A two-dimensional depth-averaged hydrodynamic model (Prandle, 1984), which solves the shallow water wave equations on the same grid as the transport model was used to determine the residual velocities. It was forced by M2 tidal elevations at the open boundaries, monthly average river flows and wind stresses. Monthly residual velocities were calculated from the hydrodynamic model to force the transport model. A sample simulated residual velocity field is illustrated in Fig. 2. The residual flow is from north to south along the Holderness/Lincolnshire coast and then turns east along the Norfolk coast. This basic pattern is repeated throughout the simulation. However, the magnitude of the residual velocities fluctuate with changes in the wind forcing.

2.2. Ecosystem model

The ecosystem described in ERSEM is considered to be a series of interacting physical, chemical and biological processes which together exhibit a coher-

ent system behaviour and is reviewed by Baretta et al. (1995). State variables have been chosen in order to keep the model relatively simple without omitting any component that exerts a significant influence upon the energy balance of the system. ERSEM uses a 'functional' group approach to describe the ecosystem whereby biota are grouped together according to their trophic level (subdivided according to size classes or feeding method). The dynamics of biological functional groups are described by both physiological (ingestion, respiration, excretion and egestion) and population processes (growth, migration and mortality). The biological variables in the model are, phytoplankton (Varela et al., 1995; Ebenhöh et al., 1997), functional groups related to the microbial food web (Baretta-Bekker et al., 1995, 1998), mesozooplankton (Broekhuizen et al., 1995), fish (Bryant et al., 1995) and benthic fauna (Ebenhöh et al., 1995; Blackford, 1997). The chemical dynamics of nitrogen, phosphate, silicate and oxygen are coupled to the biologically driven carbon dynamics. The phytoplankton pool is described by four functional groups based on size and ecological properties (diatoms, flagellates, picoplankton and inedible phytoplankton). All phytoplankton groups contain internal nutrient pools and thus have dynamically varying C:N:P ratios. The nutrient uptake is controlled by the external nutrient concentration and the internal nutrient pool. The microbial food web contains bacteria, heterotrophic flagellates and microzooplankton, each with dynamically varying C:N:P ratios. Bacteria act to decompose detritus and can compete for inorganic nutrients with phytoplankton. Heterotrophic flagellates feed on bacteria and picoplankton, are grazed by microzooplankton and are cannibalistic. Microzooplankton consume diatoms, autotrophic and heterotrophic flagellates, are grazed by mesozooplankton and are cannibalistic. Mesozooplankton consume diatoms, autotrophic flagellates and microzooplankton and are cannibalistic. The top predators in the ecosystem are fish and are represented by static predation and excretion rates (Bryant et al., 1995).

The benthic submodel contains a food web which describes nutrient and carbon cycling via both aerobic and anaerobic bacterial pathways, bioturbation/bioirrigation and the vertical transport in the sediment of particulate matter due to the activity of

benthic biota. The benthic nutrient dynamics submodel describes the mineralisation of organic matter coupled to diagenetic nutrient processes in the sediments (Ruurdij and Van Raaphorst, 1995). The vertical positions of the oxygen, sulphide horizons and nutrient profiles in the sediments are determined and are used to calculate the flux of these variables to or from the pelagic system. These processes are strongly dependent on the benthic community structure and activity. The benthic pelagic coupling is described by the inputs of settling organic detritus into the sediments and diffusional nutrient fluxes into or out of the sediment. ERSEM v11 has been used in this application and a technical description is given in Radford (1996).

The physical submodel in addition to transport describes irradiance, temperature, river inputs and seaward boundary conditions. In this application inorganic suspended particulate matter (SPM) and salinity have been included as conservatively transported tracers, because of their influence upon light attenuation and dissolved oxygen saturation respectively.

2.3. Model coupling

The simulations have been made using SESAME (Software Environment for Simulation and Analysis of Marine Ecosystems) which is described in Ruurdij et al. (1995). SESAME uses variable time step integration. The time step varies between a maximum and minimum value and is dynamically adjusted to prevent the rate of change from exceeding pre-set limits in order to avoid negative concentrations. Every time step the transport model is integrated for each pelagic variable over the maximum biological time step, to calculate the net transport flux of that variable for each grid box. The net transport flux of each variable is then passed into SESAME where it is integrated along with the fluxes due to biogeochemical processes.

2.4. Initial conditions and external forcing

The initial conditions for the model were taken from the standard ERSEM 15-box North Sea model, the set-up of which is described in Baretta et al. (1995). A uniform field of all state variables was applied to the model domain. The model was then spun

up to a quasi steady state by applying the river forcing, seaward boundary conditions and the ecology. The northern boundary was forced and the eastern boundary was open, using a non-reflecting Orlanski boundary condition (Chapman, 1985). Northern boundary conditions for phosphate, nitrate, ammonium, silicate and SPM were taken from North Sea survey site DO (53°54'N 0°24'E; Fig. 1) (Lowry et al., 1992). Otherwise, results from the ERSEM 15-box North Sea model were used to prescribe boundary conditions for all other transported ecological variables. The northern boundary is assumed to have no east–west offshore gradient. For nutrients and SPM this is a reasonable assumption, except near to the coast (within 10–15 km, that is 2 or 3 grid points) where a concentration gradient clearly exists due to land runoff and coastal erosion (LOIS unpublished data). However, no data exist to define these gradients over a seasonal cycle.

Daily freshwater inputs from the Humber and Wash rivers were taken from Lowry et al. (1992). The monthly mean freshwater nitrate and silicate inputs were estimated by calculating the theoretical zero salinity concentration from mixing curves (Boyle et al., 1974). The assumption of conservative mixing is valid for nitrate and silicate in the outer Humber estuary (Morris et al., 1995) and the Great Ouse/Wash (Fichez et al., 1992). Phosphate inputs were estimated from measurements of the freshwater concentrations (Lowry et al., 1992). Inputs of ammonium were taken from Fichez et al. (1992). The river inputs of particulate organic matter (POM) were taken from compilations made by the North Sea Task Force (Anonymous, 1992).

Bed sediments were assumed to be uniform over the region, consisting of coarse sandy gravel with a mean porosity of 0.4 (Watson and Frickers, 1994). Phosphate adsorption parameters for the benthic nutrient submodel were parameterised as described in Ruurdij and Van Raaphorst (1995).

SPM is assumed to be conservatively transported through the Humber plume. Mixing curves show that fine SPM (<63 μm) is primarily estuarine in origin and conservatively mixed (Morris and Allen, 1995). The land-derived inputs of SPM have been estimated for the Humber (Lowry et al., 1992), the Wash (Fichez et al., 1992) and the Holderness cliffs (McCave, 1987).

The model has been forced with daily sea surface irradiance (Pätsch, 1995) and daily water temperatures extracted from a North Sea circulation model (Pohlmann, 1995).

2.5. Period of simulation

The simulations referred to in this paper are for 1988–1989, the period of the NERC North Sea survey, from September 1988 to October 1989. The southern North Sea including the Humber plume region was systematically surveyed at monthly intervals for a wide range of biogeochemical parameters (Simpson, 1994). This time period has been chosen

because it corresponds with the best available forcing and validation data for the model and is coincident with previous budget calculations.

3. Results

Two survey sites have been chosen to compare and contrast the behaviour of the model ecosystem inside and outside of the plume, EN a typical plume site strongly influenced by the river runoff, and EK an offshore site which is uninfluenced by the fresh-water inputs but strongly influenced by the northern boundary especially in winter. The positions are indicated in Fig. 1.

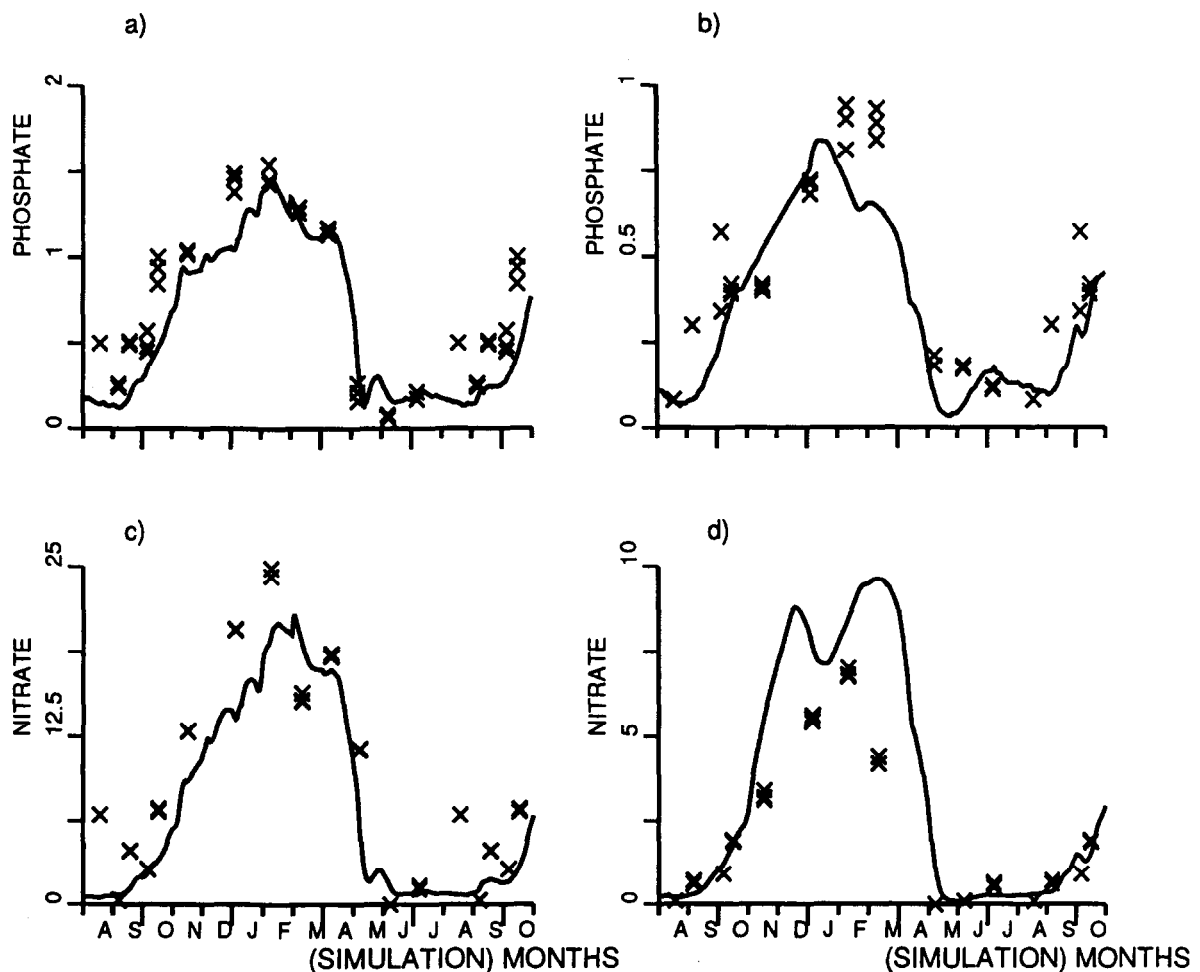


Fig. 3. Modelled seasonal cycles of phosphate (mmol m^{-3}) at (a) EN and (b) EK, and nitrate (mmol m^{-3}) at (c) EN and (d) EK, plotted with validation data for the period August 1988 to October 1989.

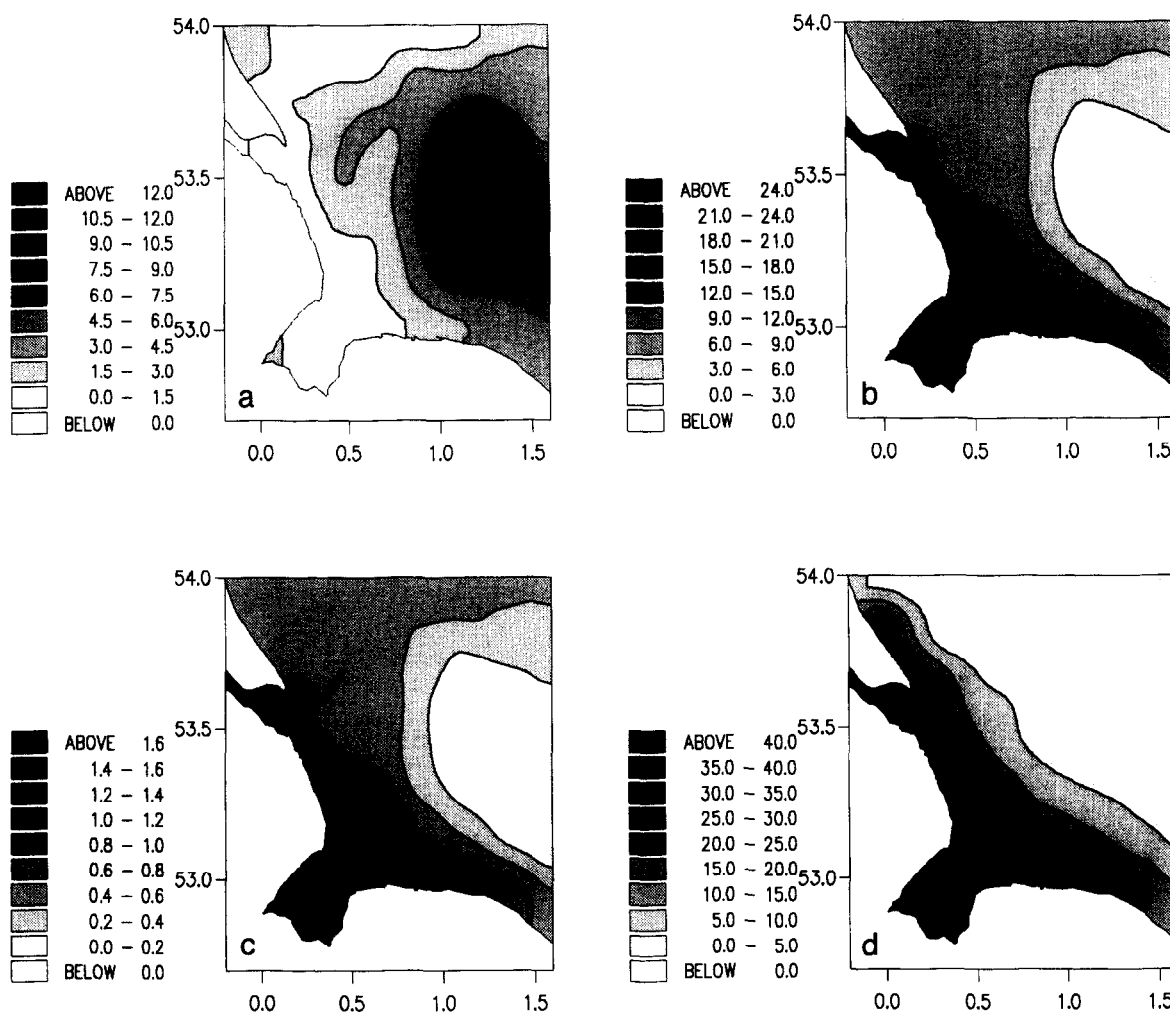


Fig. 6. Modelled spatial distributions of (a) chlorophyll (mg Chl m^{-3}), (b) nitrate (mmol m^{-3}), (c) phosphate (mmol m^{-3}), and (d) suspended particulate matter (mg m^{-3}), in April 1989 (Julian day 460).

nutrient and SPM concentrations extend from the Humber mouth, in a southerly direction. The plume is augmented by the inputs from the Wash rivers and turns east along the Norfolk coast. Modelled distributions are similar to the observed spatial patterns of the nitrate and phosphate plumes in December 1988 reported by Morris et al. (1995). However, the modelled concentrations of nitrate in the plume mouth are about 50% less than the observations suggesting that either the riverine nitrate inputs may be underestimated, or the modelled plume spreads too far from the coast. The hydrodynamic model contains no process description of density effects. The

strong horizontal salinity gradients at the edge of the Humber plume produce horizontal pressure gradients (since the freshwater plume is less dense than the offshore seawater) which act to confine the plume along the Lincolnshire coast. This effect will help to maintain high nutrient concentrations in the vicinity of the plume mouth. The plume boundary isolines for nitrate (10.0 mmol m^{-3}) give an indication of the extent of the influence of the northern boundary conditions on the model domain at this time.

By early April 1989 (Julian day 460), the spring phytoplankton bloom is already taking place outside the plume (Fig. 6a). There is a distinct patch of

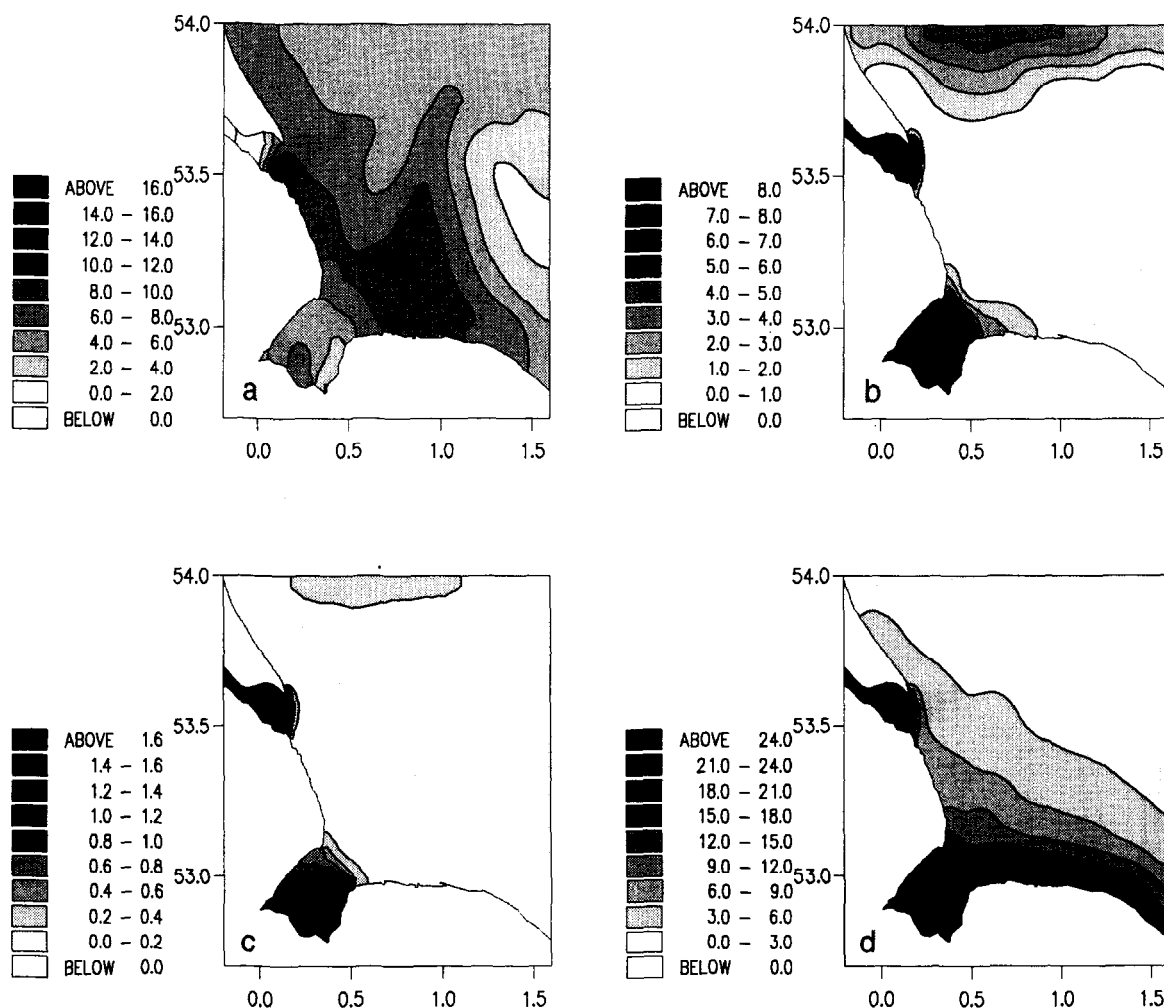


Fig. 7. Modelled spatial distributions of (a) chlorophyll (mg Chl m^{-3}), (b) nitrate (mmol m^{-3}), (c) phosphate (mmol m^{-3}), and (d) suspended particulate matter (mg m^{-3}), in May 1989 (Julian day 490).

high chlorophyll-*a* concentrations ($>8 \text{ mg Chl m}^{-3}$) offshore near the eastern boundary of the model domain, while within the plume zone the bloom has yet to start (chlorophyll-*a* $<2.0 \text{ mg Chl m}^{-3}$). Nitrate (Fig. 6b) and phosphate (Fig. 6c) are depleted in the areas where the phytoplankton bloom has already taken place. The SPM plume is shown in Fig. 6d, and corresponds with areas of high nutrient loads and low chlorophyll. This indicates that primary production is light limited in the plume zone at this time. The intensity and length of the bloom may be extended by the influence of the northern boundary conditions. The prevailing residual flow field of the

model transports nutrients from the northern boundary into the region of phytoplankton growth. The bloom moves towards the coast (Fig. 6a) as nutrients become limiting until it reaches the sediment plume when it becomes light limited. In May 1990 the spring bloom as evidenced by nutrient depletion was found to have taken place outside the plume before it took place inside the plume (Morris et al., 1995).

By mid May (Julian day 490) strong phytoplankton growth is taking place in the plume, having chlorophyll-*a* concentrations $>7.5 \text{ mg Chl m}^{-3}$ (Fig. 7a). Nitrate (Fig. 7b) and phosphate (Fig. 7c)

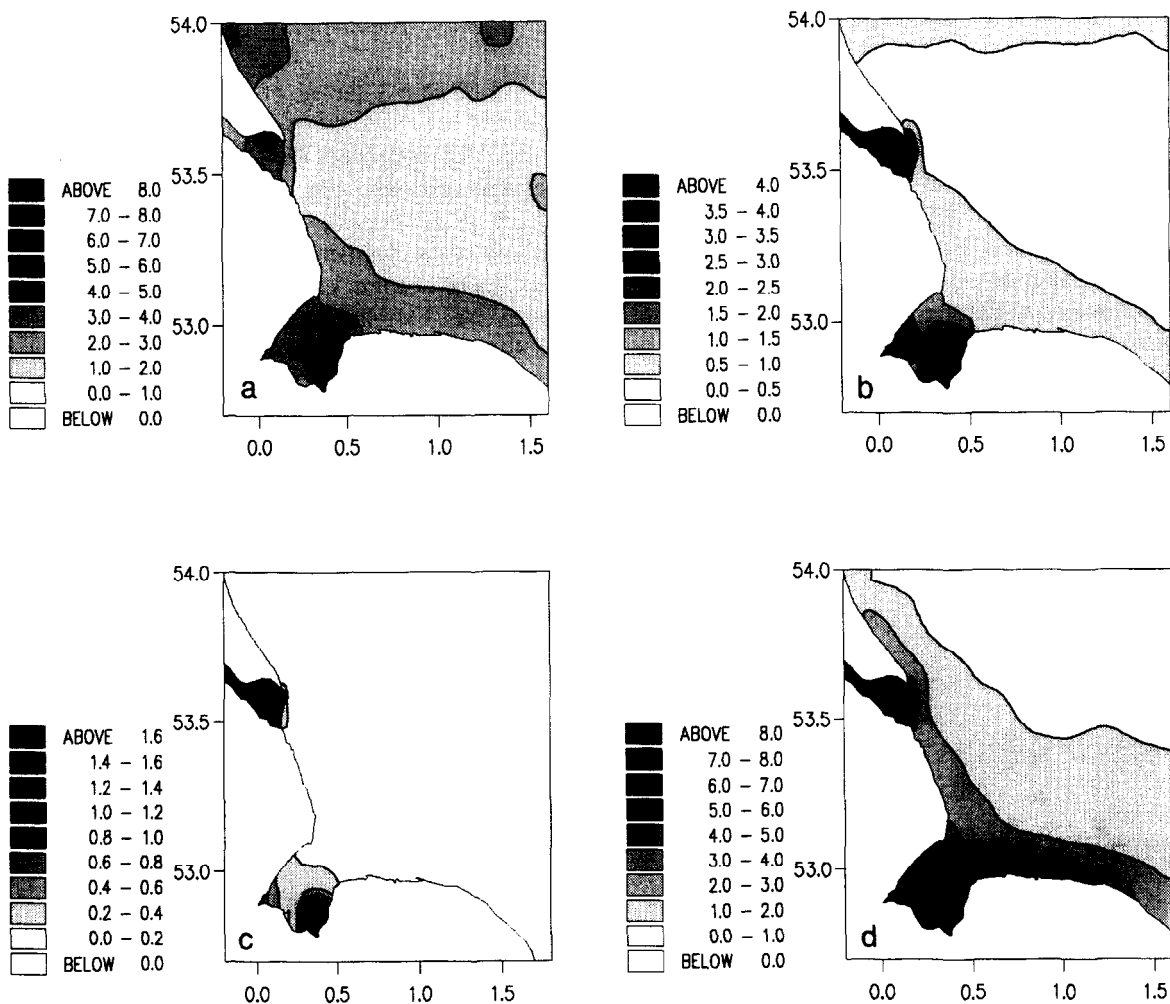


Fig. 8. Modelled spatial distributions of (a) chlorophyll (mg Chl m^{-3}), (b) nitrate (mmol m^{-3}), (c) phosphate (mmol m^{-3}), and (d) suspended particulate matter (mg m^{-3}), in July 1989 (Julian day 540).

are depleted except in the vicinity of the Humber mouth, the Wash and along the Norfolk coast. These patches of high nutrient concentrations correspond with areas of high SPM (Fig. 7d). During the spring, both freshwater loads and coastal erosion rates tend to decrease, with a corresponding decrease in the concentrations of SPM within the plume.

By midsummer (Julian day 570) the distribution of chlorophyll-*a* throughout the region is fairly even with concentrations of $>2 \text{ mg Chl m}^{-3}$ (Fig. 8a). Nitrate (Fig. 8b) and phosphate (Fig. 8c) are uniformly depleted except in the vicinity of freshwater sources. A weak SPM plume exists extending in a southeasterly direction from the Humber mouth

(Fig. 8d). This suggests that primary production is nutrient rather than light limited throughout the region. The modelled distributions of nitrate, phosphate and chlorophyll-*a* exhibit similar patterns to those observed in July 1990 (Morris et al., 1995).

Figs. 7 and 8 also illustrate the adaptation of the northern boundary conditions to the model domain. In both sets of figures there are strong isolines parallel to the northern boundary for nitrate and phosphate which give an indication of the extent of the influence of the boundary conditions in spring and summer. The uneven distribution of chlorophyll-*a* along the northern boundary (Fig. 8a), where a uniform set of boundary conditions for phy-

toplankton biomass was applied, is a reflection of the rapid adaptation of the phytoplankton to the topographic and hydrodynamic variations within the model domain. There is an inevitable inconsistency between the observed dissolved nutrient boundary conditions and the particulate nutrient boundary conditions taken from ERSEM. The internal nutrient ratios of modelled biota and detritus are a function of the parameterisation and the ambient nutrient concentrations within the 15-box North Sea model. Therefore the modelled boundary conditions are independent of the observed nutrient concentrations. The biological model reconciles this inconsistency in the grid cells adjacent to the northern boundary.

3.3. Primary production

Fig. 9 shows the fit of modelled, (a) SPM with data and (b) net primary production at site EN. Modelled SPM reproduces the seasonal trends in the data, but underestimates the concentrations. The difficulties in prescribing land-derived SPM loads and the lack of a mechanism for sediment resuspension in the model account for the major discrepancies between the observations and the simulations. The role of SPM in the model is to determine the marked differences in the spatial and temporal variation in the light limitation of phytoplankton growth. The light limitation factor (0 means total limitation, 1 means

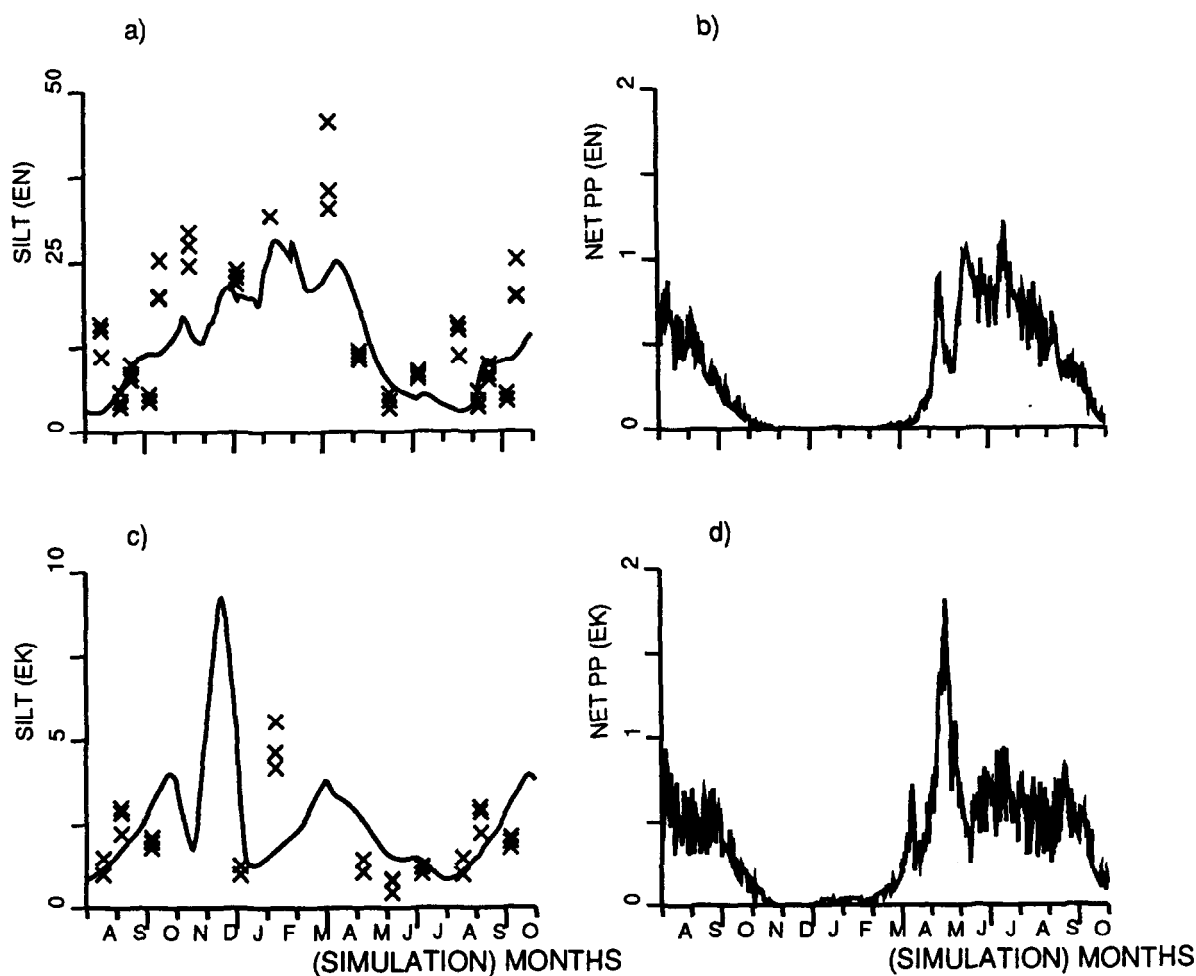


Fig. 9. Modelled seasonal cycles of suspended particulate matter (g m^{-3}) at (a) EN and (c) EK, and net primary production ($\text{g C m}^{-2} \text{d}^{-1}$) at (b) EN and (d) EK, plotted with validation data for the period August 1988 to October 1989.

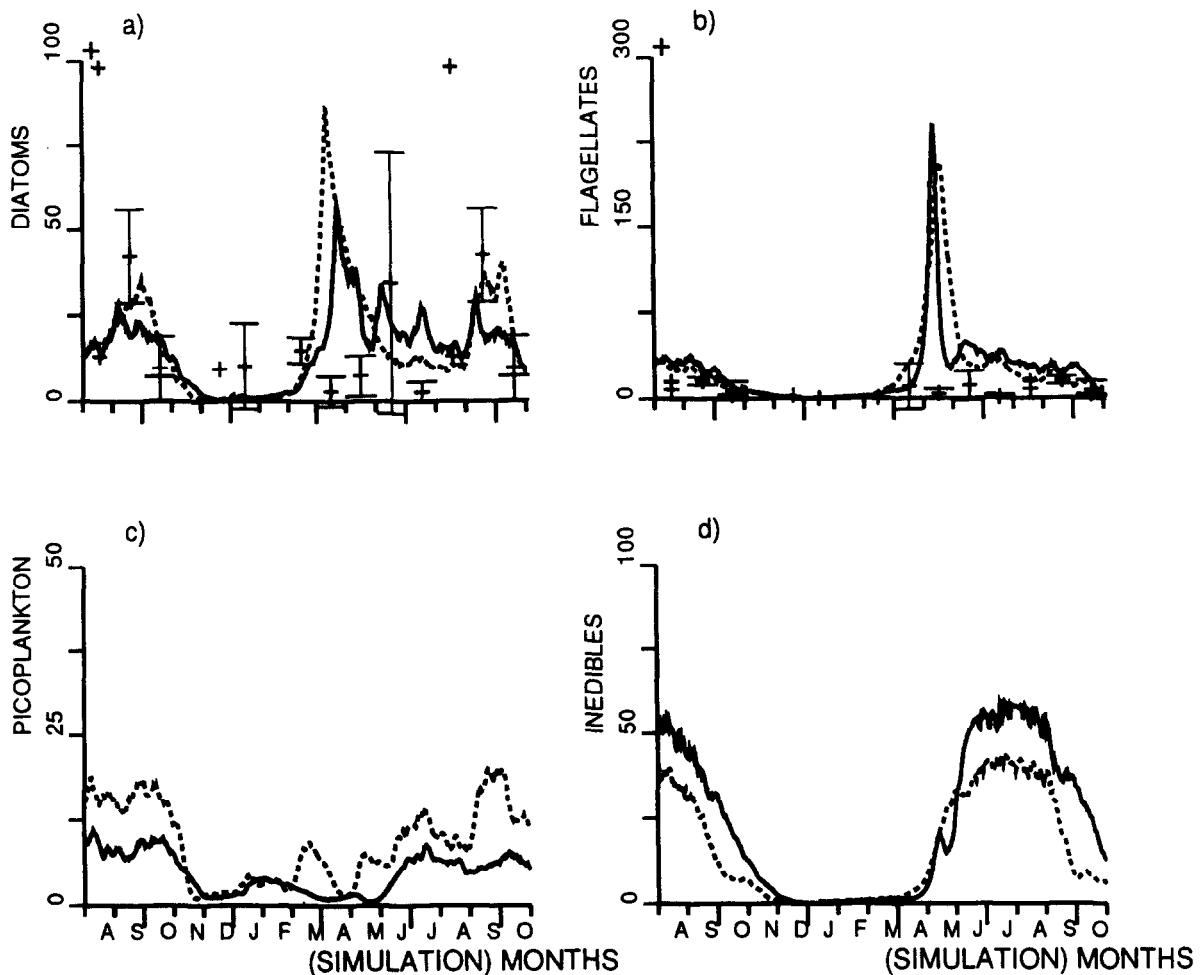


Fig. 10. Modelled seasonal cycles of the carbon biomass of (a) diatoms, (b) flagellates, (c) picoplankton, (d) inedible phytoplankton plotted with validation data where available for the period August 1988 to October 1989 for sites EN (solid line) and EK (dashed line). The units are mg C m^{-3} .

no limitation) for primary production (not shown) doubled in magnitude between mid April and mid May corresponding to a sharp decrease in the SPM concentration at this time. This change allows the abrupt increase in primary production.

At the offshore site (EK), SPM concentrations are much smaller and have a less well defined seasonal trend (Fig. 9c). In spring, the seasonal cycle of light limitation (not shown) increases earlier and more slowly than in the plume zone. As a consequence of this, primary production starts a month earlier and is more pronounced in the summer (Fig. 9d).

The seasonal cycles of modelled (a) diatoms (silicate consumers), (b) flagellates ($2\text{--}20\ \mu\text{m}$), (c) pi-

coplankton ($<2\ \mu\text{m}$) and (d) inedible phytoplankton ($>20\ \mu\text{m}$) are shown in Fig. 10. The validation data are monthly regionally averaged biomass (Lowry et al., 1992) for the English coastal ICES box, 3'' (ICES, 1983). At site EK the diatom bloom occurs in April and is followed by a flagellate bloom in May, while inside the plume, the diatom and flagellate blooms take place simultaneously. The differences in timing of the spring bloom and phytoplankton succession are probably attributable to the marked difference in light regimes between the sites. A secondary diatom bloom occurs inside the plume in the autumn. Modelled diatom and flagellate biomass are consistent with the observed data. Diatoms were ob-

served to be abundant at many sites in the southern North Sea in spring and autumn of 1988/89 (Tett and Walne, 1995). Simulated picoplankton is consistently more abundant offshore than it is within the plume and dominates the total phytoplankton biomass in the winter. Inedible phytoplankton are more abundant at the nutrient-rich plume site than they are offshore. There are currently no validation data available for picoplankton and inedible phytoplankton.

The net annual modelled primary production was $106 \text{ g C m}^{-2} \text{ a}^{-1}$ for the plume site and $127 \text{ g C m}^{-2} \text{ a}^{-1}$ for the offshore site. These values are larger than the ^{14}C determinations reported in Joint and Pomroy (1993) which gave $79 \text{ g C m}^{-2} \text{ a}^{-1}$ as the annual production for the English Coast (Box 3', ICES, 1983) for the period August 1988 to August 1989. However, the primary production in the adjacent central North Sea area (Box 7'', ICES, 1983) which has similar conditions to those at site EK was $119 \text{ g C m}^{-2} \text{ a}^{-1}$ (Joint and Pomroy, 1993), suggesting that the modelled production at this site may not be overestimated. The modelled estimate at site EN may partly be a reflection of the high nutrient concentrations in the vicinity of the Humber plume compared with the rest of the English coast.

The seasonal variations in modelled and observed primary production are given in Table 1. During the spring and summer the model overestimates the pri-

mary production 1.5 to 2 times. In winter the model underestimates it. The data indicates that 11.5% of the annual primary production took place in the winter, compared with <3% in the model. Diatoms have approximately the same amount of production at both sites, whereas flagellates and picoplankton are more productive at the offshore site. Inedible phytoplankton production is highest inside the plume. Overall the offshore site has the highest primary production except during the summer when the plume is more productive. Measurements made in July 1987 in this region (Owens et al., 1990) show that 75% of the primary production was by phytoplankton $>5 \mu\text{m}$ and less than 5% by phytoplankton $<0.8 \mu\text{m}$. The general trend in the data is for large phytoplankton to dominate in nutrient-rich coastal water and smaller phytoplankton to dominate offshore. This trend is reproduced by the model.

3.4. Bacteria and zooplankton

Fig. 11 shows the modelled seasonal cycles of (a) bacteria and (b) heterotrophic flagellates. The seasonal cycles of bacteria are similar at both sites. The minimum biomass occurs in December and reaches a maxima in mid summer. Bacterial biomass is higher at the offshore site during the spring reflecting the rapid response of bacteria to the earlier

Table 1

Modelled net primary production for the four phytoplankton classes in ERSEM plus observations of the net seasonal primary production from Howarth et al. (1994) and the net annual primary production from Joint and Pomroy (1993) for ICES Box 3' (ICES, 1983)

	Modelled net primary production ($\text{g C m}^{-2} \text{ quarter}^{-1}$)					Data
	Diatom	Flagellate	Picoplankton	Inedibles	Total	Net ^{14}C production
<i>Autumn</i>						10.0
EN	174	1.23	1.04	0.708	4.56	
EK	4.05	2.00	2.40	0.50	8.70	
<i>Winter</i>						9.00
EN	0.19	0.11	0.10	-0.01	0.41	
EK	1.46	0.85	1.85	0.12	4.64	
<i>Spring</i>						37.00
EN	11.96	20.14	0.62	9.92	43.39	
EK	11.42	37.38	2.45	9.07	61.10	
<i>Summer</i>						23.00
EN	12.37	18.55	2.40	24.58	57.46	
EK	11.53	15.71	6.96	18.86	52.62	
<i>Annual</i>						79.00
EN	26.26	40.03	4.15	35.21	105.79	
EK	28.63	55.95	13.66	28.55	127.06	

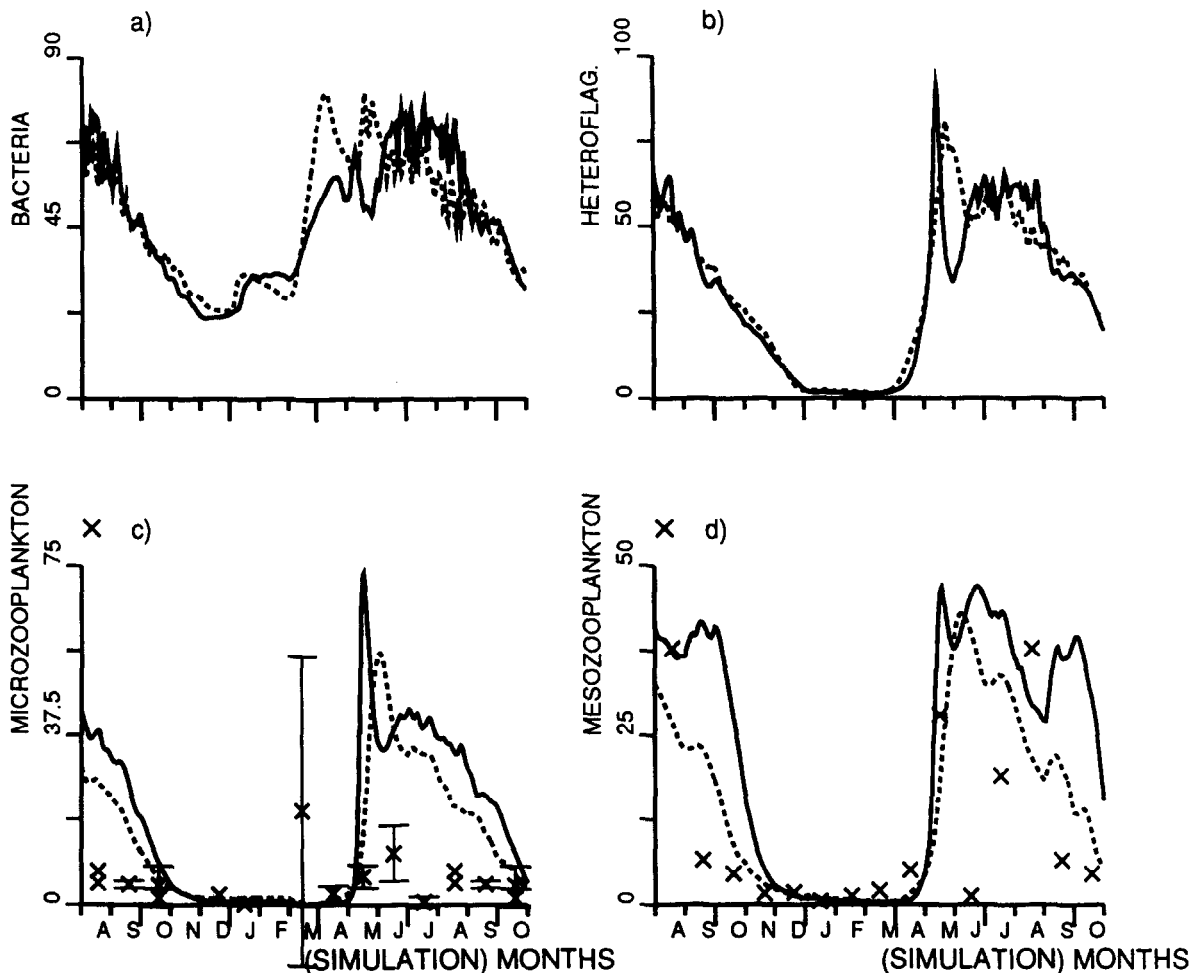


Fig. 11. Modelled seasonal cycles of the carbon biomass of (a) bacteria, (b) heterotrophic flagellates, (c) microzooplankton, (d) mesozooplankton plotted with validation data where available for the period August 1988 to October 1989 for sites EN (solid line) and EK (dashed line). The units are mg C m^{-3} .

spring bloom. Modelled heterotrophic flagellates exhibit similar trends. There are no data available with which to validate these results.

The fit of modelled microzooplankton with regional averaged data is shown in Fig. 11c. The model correctly reproduces the seasonality of the data but underestimates the biomass. The biomass data were determined from lugol or formaldehyde preserved samples (Lowry et al., 1992), and are probably underestimates due to the disintegration of many species upon preservation (Baretta-Bekker et al., 1995).

The modelled seasonal cycle of omnivorous mesozooplankton along with the fit to region-

ally averaged data for the English coast is shown in Fig. 11d. The mesozooplankton data were derived from continuous plankton recorder surveys by Broekhuizen et al. (1995). Seasonal trends and the biomass of mesozooplankton are simulated well at both sites.

In all cases the modelled zooplankton respond rapidly to the spring bloom. The response is faster at the plume site than offshore, despite the lower primary production and later spring bloom. This implies that the modelled spring bloom is to some extent grazer controlled in the plume, and may explain why the modelled chlorophyll peak is lower than observations suggest. This is a consequence of

the earlier spring bloom outside of the plume and the prevailing residual flow field transporting zooplankton biomass into the plume (Fig. 2).

3.5. Simulated quarterly and annual nutrient budgets for the humber plume mass balancing box

The nutrient budgets referred to in this section are made from a simulation of the Humber plume ecosystem between October 1988 and September 1989, the period of the NERC North Sea Survey. For the purpose of budget making the seasons are defined as tri-monthly units starting from 1 October 1988.

The net change in concentration of dissolved inorganic nitrogen and phosphate can be given by the following equation:

$$\begin{aligned} dC/dt = & \text{net transport (advection/diffusion and river} \\ & \text{inputs} - \text{net algal uptake} - \text{net bacterial uptake} \\ & + \text{microzooplankton excretion (microzooplankton} \\ & + \text{heterotrophic flagellates)} + \text{fish excretion} \\ & + \text{benthic regeneration.} \end{aligned} \quad (4)$$

Similarly the rate of change of POM-N and POM-P can be written as:

$$\begin{aligned} dC/dt = & \text{net transport (advection/diffusion and river} \\ & \text{inputs)} + \text{net algal uptake} + \text{net bacterial uptake} \\ & - \text{microzooplankton excretion (microzooplankton} \\ & \text{and heterotrophic flagellates)} + \text{fish (detrital} \\ & \text{excretion and mesozooplankton consumption)} \\ & - \text{input to benthos (sedimentation} + \text{suspension} \\ & \text{feeders)} \end{aligned} \quad (5)$$

The equations for silicate do not have terms for bacterial uptake, microzooplankton and fish excretion.

3.5.1. Nitrogen and POM-N

The quarterly and annual budgets of dissolved inorganic nitrogen are given in Fig. 12a. The annual budget is approximately in balance, there is a net increase of 2.61×10^7 moles of DIN over the simulated period. On an annual basis, phytoplankton uptake is the largest sink for DIN, removing 80% of total uptake, the remainder being consumed by bacteria.

These removal processes are balanced by the benthic efflux (63%), heterotrophic cycling (25%) and net input (import–export) (12%).

Over the period of the budget calculation the river Humber and the Wash rivers input 365.2×10^7 moles of DIN into the plume box, of which 71% is exported into the southern North Sea, the remainder being retained to meet biological demand.

In the autumn the net DIN content of the plume increases by 80.2×10^7 moles. The total influx of DIN from all sources is approximately twice the phytoplankton uptake. The single largest input is from the benthic efflux (60%), the remainder being made up by river inputs and microzooplankton. About 50% of the freshwater input is retained in the plume box at this time. During the winter there is a small increase of the total mass of the plume box. Biological activity is low, the requirements of phytoplankton are matched by the inputs from the river and the benthos. River inputs are largest at this time (making up 60% of the annual freshwater DIN input), with about 90% being exported from the plume. In the spring there is a large removal of DIN from the plume box, which is largely driven by primary production. Phytoplankton and bacteria consume approximately 3.5 times the decrease in DIN in the plume box over the season. Benthic regeneration and microbial cycling make up the excess requirement which implies that in-situ recycling processes are very fast. Biological DIN requirements are matched by internal recycling (98%) during the summer. In the spring about 15% of the freshwater input is exported from the plume while in summer this increases to 50%.

Land-derived inputs of POM-N to the Humber plume box (Fig. 12b) are much smaller than their dissolved inorganic counterparts, (POM-N = 14% of DIN input). The largest inputs occur in the autumn and winter. POM-N is advected out of the plume all year round, the largest removal occurring in the autumn, (41% of the annual removal). This is coincident with an increase in the magnitude of physical transport processes (Howarth et al., 1994). A substantial efflux of POM-N also occurs in winter (24%) and spring (24%). The annual removal of POM-N from the plume is approximately three times the freshwater input, indicating the role of the plume as a producer of organic particulate material.

Algal uptake is the largest source of POM-N, with

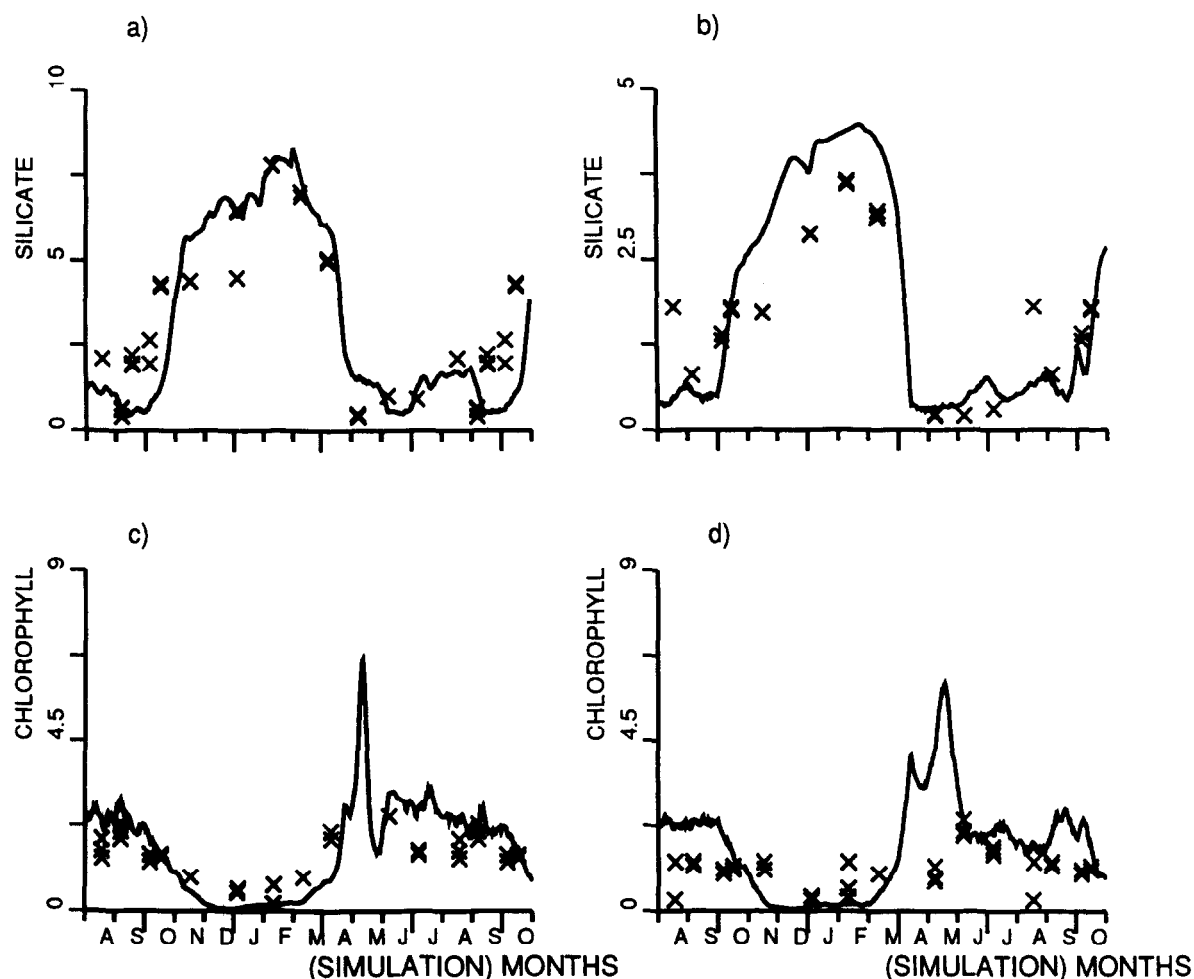


Fig. 4. Modelled seasonal cycles of silicate (mmol m^{-3}) at (a) EN and (b) EK, chlorophyll-*a* (mg Chl m^{-3}) at (c) EN and (d) EK, plotted with validation data for the period August 1988 to October 1989.

3.1. Seasonal cycles of nutrients and chlorophyll-*a*

The modelled seasonal cycles of nitrate, phosphate, silicate and chlorophyll-*a*, at North Sea survey sites EN and EK are shown in Figs. 3 and 4 together with the monthly observations (Lowry et al., 1992).

The model reproduces the seasonal trends and concentrations of the nitrate, silicate and phosphate data very well. Nutrient concentrations are at a minimum in summer, and are slowly replenished to their maximum value between September and January. This is due to the seasonal decrease in phytoplankton activity and for the site influenced by the plume, to the increase in river runoff. In winter nutrient

concentrations are underestimated. In May the rapid depletion of nutrients is caused by the spring phytoplankton bloom. There is a slight tendency to underestimate the nutrient concentrations in the autumn.

The fit of modelled chlorophyll-*a* with data is generally good. Growth starts in March and reaches its peak in May. The monthly sampling interval used during the NERC North Sea survey (Lowry et al., 1992) means that the peak of the spring bloom was not observed. However, a continuous monitoring fluorometer deployed in the southern North Sea at this time (Tett et al., 1994) did record a peak of similar magnitude to that predicted by the model at site EK. Similarly, a continuous monitoring fluorometer de-

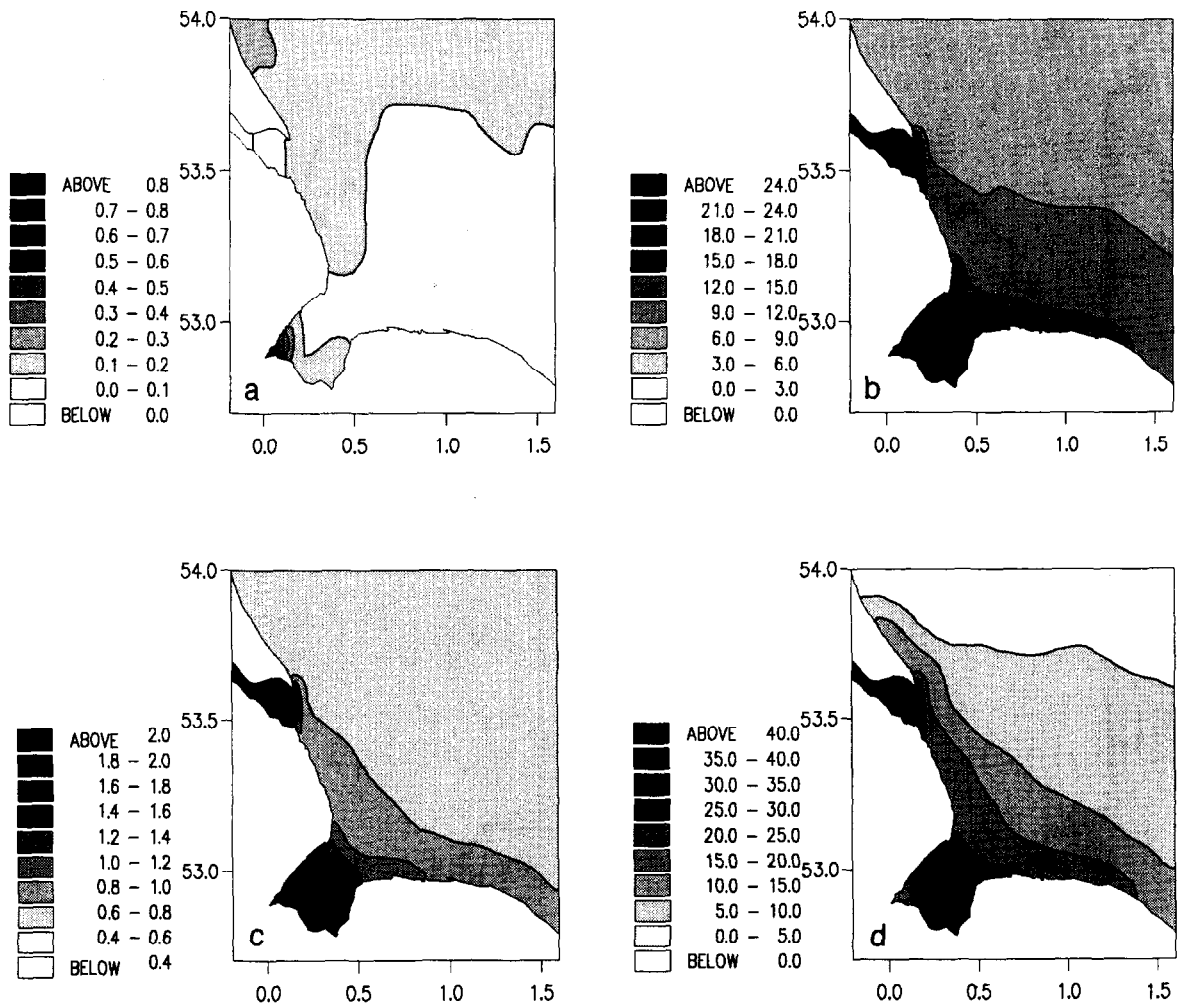


Fig. 5. Modelled spatial distributions of (a) chlorophyll (mg Chl m^{-3}), (b) nitrate (mmol m^{-3}), (c) phosphate (mmol m^{-3}), and (d) suspended particulate matter (mg m^{-3}), in January 1989 (Julian day 360).

ployed 10 km northeast of the Wash in the Humber plume during May and June 1995 also recorded a chlorophyll peak lasting about two weeks of $> 12 \text{ mg Chl-}a \text{ m}^{-3}$ (LOIS, unpubl. data) which suggests that the modelled spring bloom may be too small at EN. During the summer and autumn the fit with data is good, but there is a tendency to underestimate the chlorophyll-*a* concentration in the winter.

3.2. The development of the spring phytoplankton bloom

The spatial and temporal development of the modelled spring bloom and its effects on the distribution

of nutrients in the plume zone are shown in Figs. 5–8.

The simulated distributions of (a) chlorophyll-*a*, (b) nitrate, (c) phosphate and (d) SPM at the beginning of January 1989 are illustrated in Fig. 5. Modelled chlorophyll concentrations are very low ($< 0.2 \text{ mg Chl-}a \text{ m}^{-3}$) with the highest concentrations in the north of the model domain. This compares well with surface observations of chlorophyll made in December 1989 where values of 0.1 to $0.15 \text{ mg Chl-}a \text{ m}^{-3}$ were measured (Lowry et al., 1992). The modelled distributions of nitrate, phosphate and SPM show a distinct river plume which is coincident with the modelled salinity distribution (not shown). High

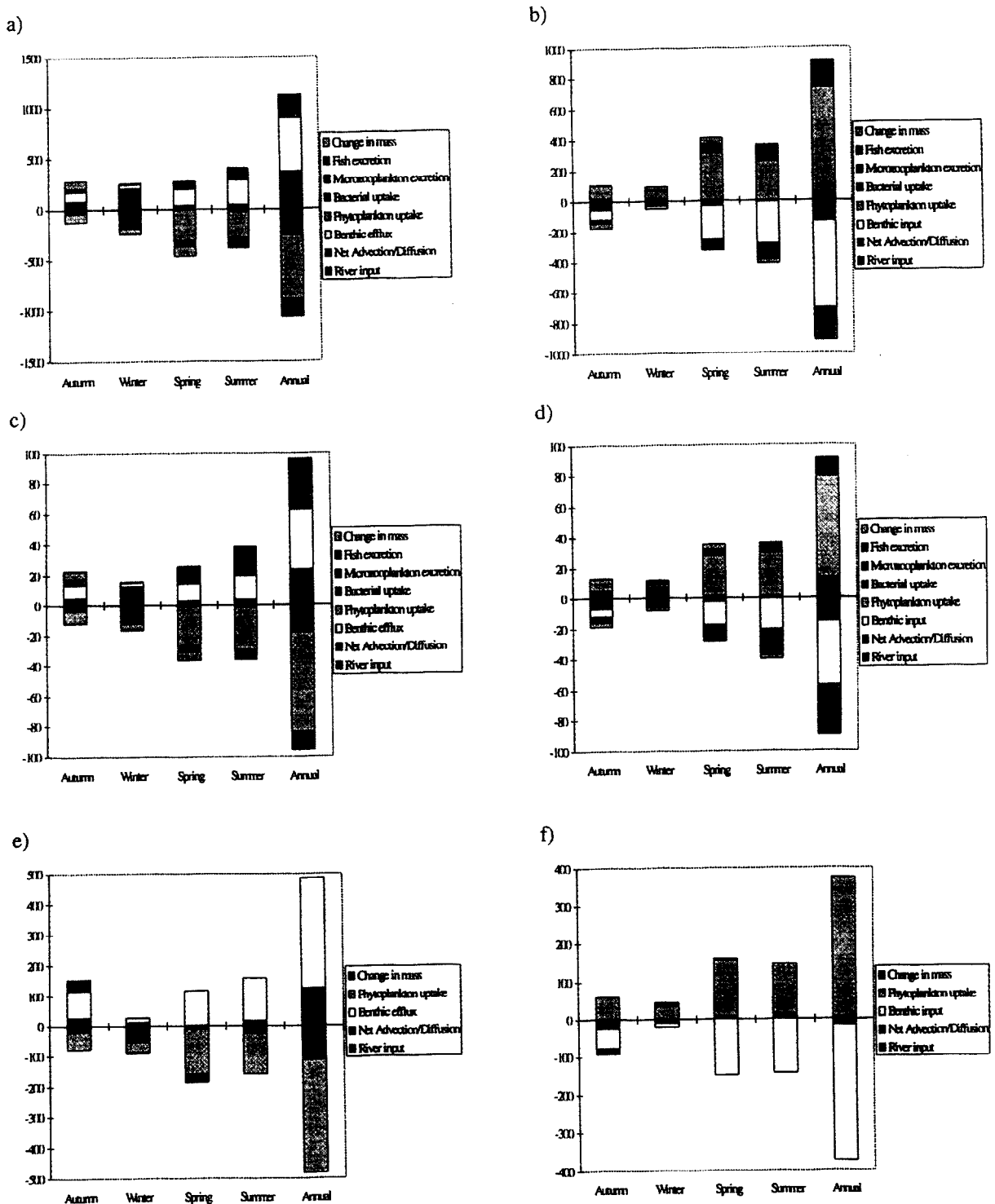


Fig. 12. Modelled annual and quarterly fluxes of nutrient cycling in the plume box. (a) DIN fluxes, (b) POM-N fluxes, (c) phosphate fluxes, (d) POM-P fluxes, (e) silicate fluxes, and (f) POM-Si fluxes for the period October 1988 to September 1989. Units of 10^7 moles quarter⁻¹ and 10^7 moles a⁻¹. A negative number implies removal from the pelagic system.

the maximum input occurring in the spring. Bacteria provide a secondary source, with the maxima occurring in the summer. The benthos is the largest sink for POM-N, consuming about 67% of the net POM-N production over a year, with the largest fluxes occurring in spring and summer (39% and 47% respectively). Excretion by microzooplankton accounts for the remainder of the POM-N loss, with the biggest fluxes in the spring and summer.

Modelled fish act to remove POM-N by grazing mesozooplankton and also to create it by excretion of detritus. The fish are generally net suppliers of POM-N because they also feed upon benthic suspension feeders.

3.5.2. Phosphate and POM-P

Annual and quarterly phosphate budgets are given in Fig. 12c. Over the simulated period there is a small increase in the phosphate content of the plume. The annual phosphate cycling is similar to that described for DIN. Biological demand for phosphate is matched by the benthic efflux (51%) and microbial cycling (44%). Net input (input–export) provide the remaining 6% of the annual biological requirement.

Over the seasonal cycle, 78% of the freshwater phosphate input is exported from the plume box. In the winter the entire freshwater input is exported which makes up 66% of the annual efflux from the plume box. During spring and summer biological activity in the plume consumes 75% and 58% of the freshwater input respectively.

In the autumn the net increase in mass in the plume box is exceeded by the benthic efflux and the release from microzooplankton. There is a small net input of phosphate into the box. In winter the total mass of the plume box increases slightly. The biological demand is balanced primarily by the benthic efflux. In the spring phytoplankton and bacteria remove 30.4×10^7 moles from the plume box. In-situ recycling processes match the majority of this demand (benthic efflux 38%, pelagic recycling 35%). Biological phosphate demand is about 5.5 times larger than the net loss from the system over the spring season, thus indicating the importance of in-situ biogeochemical recycling in regulating primary production in the coastal zone. Similar behaviour is exhibited during the summer, biological phosphate demand is met by in-situ cycling, with microzoo-

plankton providing the largest source of phosphate to the system.

The behaviour of particulate organic phosphate (POM-P) is similar to that of POM-N, and is shown in Fig. 12d. The modelled plume box exports POM-P all year round. The largest removals occurring in the autumn and spring, exporting 87% of the annual efflux. Annually, freshwater POM-P inputs are about 50% of the freshwater phosphate input, indicating that it is a major source of phosphorus to the plume zone. Advective export of POM-P from the plume box exceeds the freshwater inputs at all times except in the summer. Algal uptake is the primary source of POM-P with the largest inputs occurring in spring and summer. Bacteria and fish provide secondary sources. The removal processes are dominated by the flux to the benthos (53%) and microzooplankton excretion (42%) of the annual POM-P production. These sinks are most significant in the spring and summer.

3.5.3. Silicate and POM-Si

Diatom production and benthic regeneration regulate the biogeochemical cycling of silicate in the plume. On an annual time scale the silicate demand of diatoms is matched by the benthic regeneration of silicon (Fig. 12e). There is a small net influx of about 2% of the biological demand. The plume stores silicate in the autumn and winter, benthic effluxes and net transport fluxes (rivers–advection) exceed the biological demand. In spring, diatom uptake is about 4 times the net loss of silicate over the season, the balance is made up by the benthic efflux, along with a small net transport contribution. During the summer the plume is a net exporter of silicate to the North sea, benthic regeneration exceeds the phytoplankton demand for silicate.

The freshwater silicate input is almost entirely exported into the southern North Sea, with only 7% being retained in the plume box over the annual cycle. In autumn, winter and spring the plume exports 76%, 89% and 70% respectively, the remainder being consumed by diatoms. During the summer the plume exports 1.75 times more silicate than the freshwater sources provide, because the benthic effluxes exceed the silicate requirements of diatoms at this time.

On an annual time scale POM-Si is exported from the Humber plume box. It is exported in the autumn

and winter and imported in the summer (Fig. 12f). This means there is a net influx of diatoms and diatom detritus into the plume during the summer. Silicate is exported from the plume during the summer suggesting the plume is recycling POM-Si and releasing it into the North Sea. The source of the POM-Si is 93% algal growth and 7% land-derived. The sediments are the major sink for POM-Si consuming 97.5% of the algal uptake.

3.5.4. Benthic inputs and recycling

Fig. 13 shows the inputs of POM-N to the benthic model and the return fluxes of DIN. Annually, the influx of POM-N exceeds the efflux of DIN by about 7.2%. This corresponds to the quantity of nitrogen trapped in the seabed or lost due to denitrification. The seasonal variation in both influx and efflux are driven by the seasonal changes in primary production. Less than 50% of the model input to the benthos is via sedimentation, the remainder is mediated via suspension feeding organisms. In spring and summer the influx of POM-N exceeds the efflux of DIN, in the autumn and winter the system is reversed. POM-P and POM-Si (data not shown) show similar trends. There is a net input into the benthos of 5% of the total influx of POM-P on an annual basis. On an annual time scale there is a small net efflux of silicate into the water column.

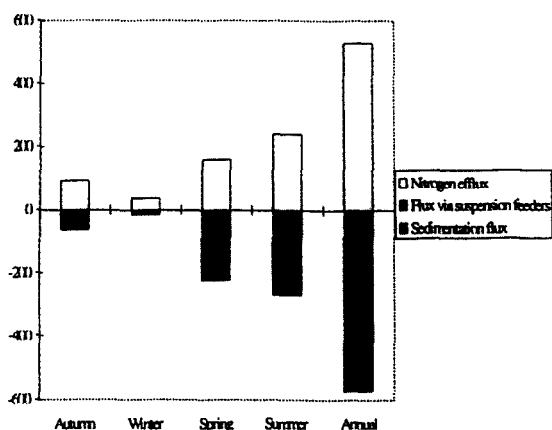


Fig. 13. Modelled annual and quarterly fluxes of benthic inputs of nitrogen and recycling in the plume box for the period October 1988 to September 1989. Units of 10^7 moles quarter⁻¹ and 10^7 moles a⁻¹. A negative number implies removal from the pelagic system.

4. Sensitivity analysis

4.1. Influence of external forcing on ecosystem dynamics

The external forcing of the model may exert a considerable influence upon the simulations. In order to assess this influence the model has been run with the ecology switched off so that all of the variables are treated as conservative tracers. The model has been run for two years with the same initial conditions and external forcing as the previous simulation. A comparison of this run with the standard simulation for nitrate and diatom biomass at sites EK and EN is shown in Fig. 14. At site EK, which is uninfluenced by the Humber estuary, the simulations are very similar between late summer and March, the period of low biological activity. As the spring bloom begins the two traces diverge as the ecologically active simulation switches from hydrodynamic control to biological control. The diatom biomass in the non-ecological simulation shows the biological signal from the northern boundary conditions. In late summer and in autumn the two traces converge as biological activity slows. Similar results are shown at site EN where the river inputs are the dominant input. This indicates the external forcing is very important in determining the simulation in the autumn and winter, but during the spring and summer the biology controls the system. It also indicates the quality of the simulations during the summer is a consequence of the process descriptions in the biological model and not the external forcing. Furthermore, it may be crucial to have accurate boundary conditions in the period prior to and during the spring bloom, as this will determine the amount of new primary production in the spring and hence the quantity of nutrients available for recycling during the summer.

4.2. Effects of varying riverine nutrient loads on primary production

In order to ascertain the short term effects of changes in land-derived inputs upon the primary production in Humber plume the model has been rerun with freshwater nitrate and phosphate inputs of 0.5 and 1.5 times the observed inputs. The same initial conditions were used as in the standard run and the

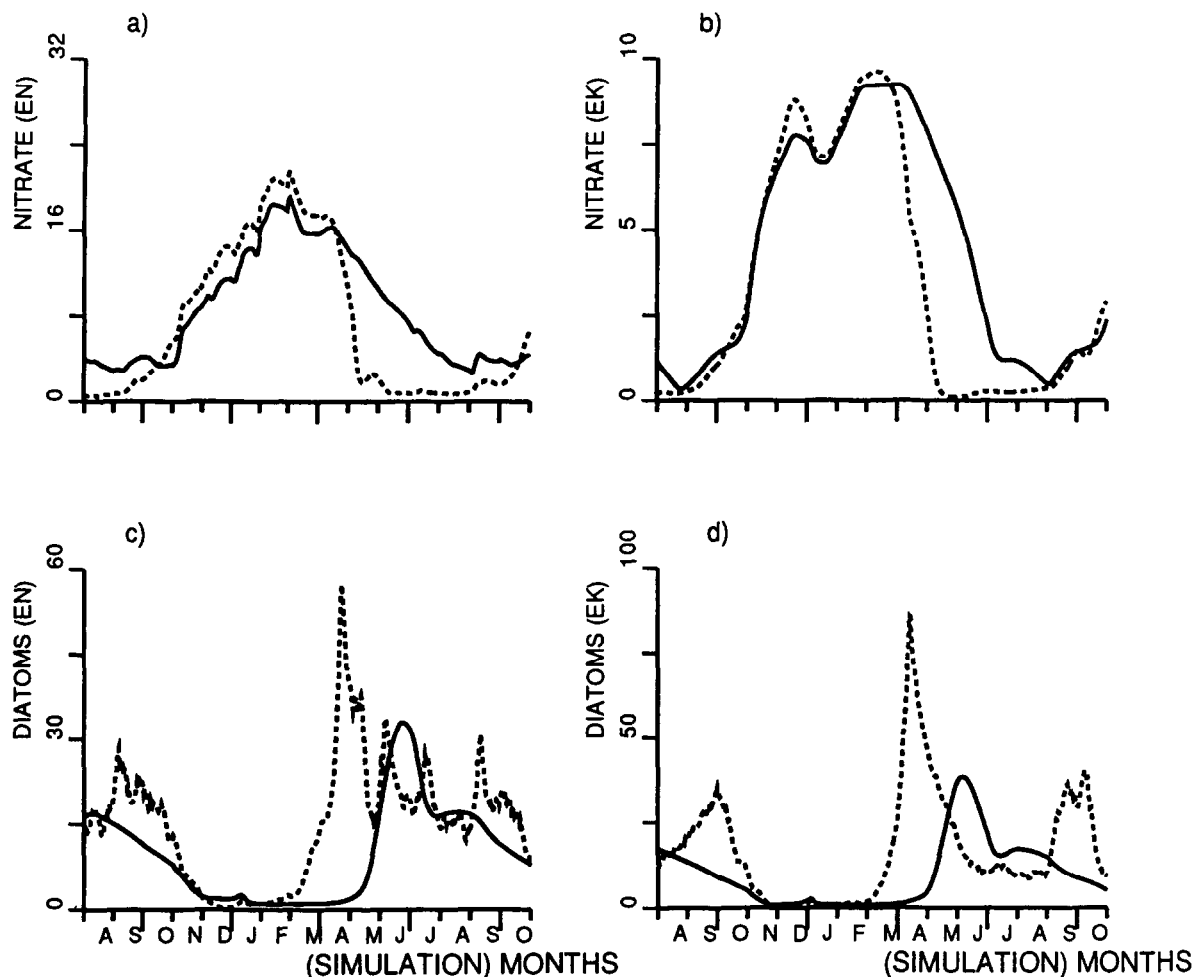


Fig. 14. Modelled seasonal cycles of nitrate (mmol m^{-3}) at (a) EN and (b) EK, and diatoms (mg C m^{-3}) at (c) EN and (d) EK. Simulation with ecology switched on (dashed line) and without ecology (solid line).

model was run for a two-year period using external forcing for 1988–1989. Annual net primary production estimates are quoted for the four phytoplankton groups and the net production for the simulation period 1 October 1988 to 30 September 1989.

The resulting variations in annual primary production are shown in Table 2. Site EN showed significant increases in total net production as the nutrient loads increase. Net production does not alter in proportion with the changes in river fluxes. This is because during the period of biological activity the supply of nutrients for phytoplankton growth is primarily controlled by in-situ recycling processes (Fig. 12) and not by net transport fluxes. The net

production was limited by the quantity of nutrients available prior to the spring bloom and the rate of in-situ recycling during the summer. The bulk of the freshwater nutrient inputs occur in winter. Biological activity is low, so a large part of the input is exported over the eastern boundary of the model without any biological modification. The transport time through the modelled plume is 10 to 15 days for a conservative tracer (Wood, 1993).

Diatom production increased slightly with increasing nutrient load, while non siliceous phytoplankton production increased markedly. The biggest changes are in flagellate production. Diatoms are limited by the rate of benthic recycling of silicate

Table 2

Modelled net annual primary production ($\text{g C m}^{-2} \text{ a}^{-1}$) for the four phytoplankton classes in ERSEM, for model runs with 0.5, 1.0 and 1.5 times the freshwater nitrate and phosphate loads

	Diatoms			Flagellates			Picoflagellates			Inedibles			Total		
	0.5	1.0	1.5	0.5	1.0	1.5	0.5	1.0	1.5	0.5	1.0	1.5	0.5	1.0	1.5
EN	21.52	26.26	28.33	31.39	40.03	49.18	4.25	4.15	5.76	26.25	35.21	38.11	83.4	105.7	121.4
EK	28.63	28.63	28.63	55.95	55.95	55.95	13.66	13.66	13.66	28.55	28.55	28.55	126.8	126.8	126.8

and therefore cannot compete as effectively for nutrients. This supports the hypothesis of Officer and Ryther (1980) that increasing the N:Si and P:Si ratios will force the ecosystem to become flagellate dominated, thus increasing the risk of eutrophic events occurring in the region. The offshore site EK remained unaffected by all of the changes which indicates that it is not influenced by the river inputs. Comparison of Figs. 1 and 2 shows that EK is effectively 'upstream' of the mouth of the Humber estuary and is instead strongly influenced by the Northern boundary conditions. The long term effects of changes in anthropogenic nutrient inputs and their retention in or flushing from the bed sediments remains unquantified.

5. Discussion

5.1. Blackbox fluxes

To compare the results of the model with previous blackbox calculations of plume processes (i.e. comparison of the freshwater input with the net fluxes across the seaward boundaries) we need to consider the net transport fluxes. Table 3 shows literature

estimates of the net input/output of nutrients from the plume box for different seasons. Monthly mean net transport fluxes from the model are included for comparison. Blackbox calculations made by Morris et al. (1995) found that the plume exported nitrate, phosphate and silicate in December 1988. Wood (1993) found the plume consumed phosphate and silicate in May 1989, and, consumed nitrate and phosphate, but exported silicate in July 1989. The observed direction and magnitude of the fluxes are reproduced by the model. The errors in the blackbox calculations are about 45% (Wood, 1993), estimated by using the method of Kjerfve et al. (1981), by taking subsets of data and comparing the different estimates of the outflow for each subset.

A time-evolving box model for nitrate in the Humber plume box for the same period as the simulation was reported in Huthnance et al. (1994). North Sea survey data were used to calculate inflow and outflow functions. Chlorophyll-*a* survey data were used to estimate nutrient uptake using fixed stoichiometric ratios. The river inputs in both models are similar as they were calculated from the same daily gauged riverflow data (Lowry et al., 1992). The net advective and diffusive fluxes of DIN from the

Table 3

Blackbox fluxes (river input + flux across northern boundary-flux across eastern boundary)

	Nitrate		Phosphate		Silicate	
	from data	model	from data	model	from data	model
December 1988	-1.80 ^a -1.10 ^b	-0.46	-0.04 ^a -0.02 ^b	-0.01	-0.30 ^a -0.20 ^b	-0.43
May 1989	0.70 ^b	0.58	0.05 ^b	0.03	0.50 ^b	0.03
July 1989	0.80 ^b	0.02	0.04 ^b	0.00	-0.20	-0.30

Units are $10^7 \text{ moles d}^{-1}$.

^a Flux calculated from surface nutrient data (Morris et al., 1995).

^b Flux estimated from North Sea survey stations (Wood, 1993).

A negative sign indicates a net outflow from the box.

ERSEM model are of the same order of magnitude (approximately 1.0×10^7 moles d^{-1}) as those reported by Huthnance et al. (1994). The box model shows the plume exporting nitrate throughout the year except in the spring when there is a net influx to help sustain the spring bloom. The ERSEM model shows a small net influx in the spring and a larger influx of DIN in the autumn which helps to replenish the nitrogen content of the plume box.

5.2. Phytoplankton uptake

Estimates of nutrient consumption by phytoplankton have been made using the monthly net primary production estimates for the English coastal region given in Howarth et al. (1994) for the period of the simulation. The calculation assumes that nutrients are taken up according to the following ratios, C:P:N:Si = 106:16:1:23 (Chester, 1990). The area of the plume box has been estimated as $0.532 \times 10^{10} \text{ m}^2$ from the domain of the model. To estimate the silicate uptake, diatoms are assumed to make up 40% of the primary production. The results are shown in Table 4. The error in the primary production data is 22% (Joint and Pomroy, 1993), which means that the estimates of the uptake of nitrogen and silicate from data compare very well with the model, as does the mean annual modelled primary production for the plume box. However, the modelled uptake of phosphate is about twice the estimate based on observation. In the ERSEM primary production model phytoplankton have variable C:N:P ratios (Baretta-Bekker et al., 1997) and internal nu-

trient pools. The average modelled N:P ratio for phytoplankton uptake over the simulation period is 10.5 which is much lower than the ratio of 16 used in the estimates from data. The modelled N:P ratio of dissolved nutrients is 12.5 over the same period. This implies that modelled phytoplankton nutrient uptake is largely determined by the N:P ratio of dissolved nutrients. Thus, the modelled uptake is 1.5 times larger than expected, which suggests a potential uncertainty of about 50% due to an artefact of the primary production model. The excess phosphate uptake by phytoplankton may be due to the lack of a mechanism for the sorption/desorption of phosphate to SPM in the model, which will act to buffer the plume phosphate concentrations (Froelich, 1988) and restrict its availability to phytoplankton. The potential significance of this effect can be illustrated by sensitivity analysis. Increasing the porosity of the sediments (poro) and the phosphate adsorption coefficient (pm1\$) will enhance the retention of phosphate by the sediments. With poro = 0.4 and pm1\$ = 100 the N:P ratio of phytoplankton uptake is 10.5, with poro = 0.5 and pm1\$ = 250 the N:P ratio is 16 and with poro = 0.7 and pm1\$ = 400 the N:P ratio = 20.5. This indicates that the sorption/desorption of phosphate, in the sediments or onto SPM, could exert a significant control upon the availability of phosphate for phytoplankton growth in the modelled plume.

On a seasonal time scale the model tends to overestimate the uptake of DIN and silicate in the summer and under estimate it in the winter. This is consistent with the trends in modelled primary

Table 4

Estimates of phytoplankton uptake in the Humber plume box during the period of the NERC North Sea survey using the monthly primary production estimates of Howarth et al. (1994) and assuming uptake according to Chester (1990), C:N:P:Si = 106:16:1:23

	Net primary production		Nitrogen uptake/ 10^7		Phosphate uptake/ 10^7		Silicate uptake/ 10^7	
	data	model	data	model	data	model	data	model
autumn	10.0	8.12	66.88	83.81	4.18	7.63	39.29	57.55
winter	9.0	3.97	60.23	45.89	3.76	3.59	34.62	30.99
spring	37.0	44.11	257.60	302.07	15.47	26.10	142.32	-147.02
summer	23.0	42.07	154.50	251.64	9.58	28.07	89.90	-131.12
Annual	79.0	98.17	528.66	683.61	33.04	65.39	303.97	-366.68

Silicate calculation assumes 40% of production is diatoms. The area of the box is $0.532 \times 10^{10} \text{ m}^2$. Flux units are 10^7 moles quarter $^{-1}$ and 10^7 moles a^{-1} , respectively. Primary production is in units of $\text{g C m}^{-2} \text{ quarter}^{-1}$ and $\text{g C m}^{-2} \text{ a}^{-1}$, respectively. The modelled mean primary production for the mass balancing box is also given.

Table 5
Estimates of the quarterly benthic efflux of nutrients in the Humber plume box

	Winter (1988/89)	Spring (1990)	Summer (1990)
Nitrate	−69.24 ± 88.25	−40.50 ± 93.21	103.5 ± 15.24
Ammonia	0.0 ± 47.88	38.3 ± 38.3	129.0 ± 130.0
Phosphate	1.69 ± 5.0813	4.10 ± 3.65	5.53 ± 3.20
Silicate	11.73 ± 19.37	19.36 ± 18.19	83.34 ± 69.84

Based on mean and standard deviation daily flux estimates reported in Watson and Frickers (1994) extrapolated over the whole plume box and each season. The area of the box is $0.532 \times 10^{10} \text{ m}^2$. Flux units are $10^7 \text{ moles quarter}^{-1}$. A negative sign implies removal from the pelagic system.

production (Table 1). Phosphate follows a similar trend, but the modelled uptake is consistently 40 to 60% above the estimates from primary production.

5.3. Benthic nutrient fluxes

Quarterly benthic effluxes of nutrients based on the data of Watson and Frickers (1994) are given in Table 5. To obtain an order of magnitude estimate of seabed fluxes the median and range of the observations have been calculated and scaled over the area of the plume box. No attempt has been made to spatially correlate the fluxes with sediment type. Suitable sediment cores for flux measurements can only be obtained from sites where the sediment is reasonably cohesive and the majority of the bed sediments in the plume region lacks enough cohesive sediment for sampling to occur.

The modelled effluxes of DIN are within the range of observations at all three sampling times. However, the model fails to reproduce the influxes of DIN in the observations in the winter and spring. Modelled phosphate fluxes are larger than those observed, which is consistent with the modelled phytoplankton uptake. The benthic effluxes of silicate are within the observed range in the winter and summer and twice the maximum observed value in the spring.

The modelled efflux of DIN from the seabed is 7.2% less than the influx of POM-N over a season, which is within the 7 to 12% loss of nitrogen due to denitrification estimated by Law and Owens (1990) for North Sea sediments.

5.4. Particulate organic matter

The budgets of POM are more difficult to quantify due to the lack of spatial and temporal data. The

validation of the model shows that it reproduces the observed mass and seasonal trends of chlorophyll-*a* at specific sites within the plume box. The model also reproduces biomass estimates for diatoms, flagellates and mesozooplankton that are consistent with regionally averaged observations, although microzooplankton biomass may be overestimated. This suggests that the net transport fluxes of POM determined by the model are of the correct order of magnitude and have realistic seasonal trends.

Phytoplankton and bacteria compete for dissolved inorganic nutrients in the modelled plume. This is influenced by both the ambient growth conditions for algae and the availability of dissolved organic material for bacterial growth. (In ERSEM all dissolved organic material is assumed to be immediately consumed by bacteria and is not explicitly represented.) The regeneration of mineral nutrients resulting from predation (heterotrophic flagellates on bacteria, microzooplankton on heterotrophic flagellates) provides a feedback for some of the material flows within the microbial loop (Azam et al., 1983). The role of the microbial loop in sustaining primary production during the summer remains unquantified in the Humber plume zone.

With the exception of phosphate, the modelled phytoplankton uptake, benthic effluxes and transport fluxes are consistent with other estimates of these processes. This implies that the recycling of DIN by microzooplankton may be of the correct order of magnitude, while phosphate is overestimated. Howarth et al. (1994) estimated that 70% of the increase in nitrate in the southern North Sea between November 1988 and January 1989 was due to regeneration from suspended particulate matter, which is considerably more than the 30% determined by the model. This may be in part due to the lack

of sediment resuspension processes in the model. Resuspension would make more particulate organic bound nutrients available for recycling in the pelagic rather than benthic. Resuspension may also reduce the uptake of nutrients by phytoplankton due to the increased effects of light limitation upon growth. Another possible cause of this discrepancy could be the difference in mean depth (and consequent water volume/bottom area ratio) between the shallow Humber plume and the deeper southern North Sea.

6. Conclusions

Primary production within the plume zone is controlled by the balance between available nutrients (land-derived and through benthic/pelagic recycling processes), and the light limitation in the water column due to the seasonal variation in incident solar radiation and suspended sediment loads. The behaviour of the plume ecosystem over a seasonal cycle can be split into two periods.

Between October and March, phytoplankton development is inhibited by high SPM loads which are responsible for a decrease in light penetration and hence the ecosystem is relatively inactive. This is especially true at the plume site. This corresponds to previous observations of phytoplankton inhibition in the well-mixed turbid waters of the Humber/Wash region (Fichez et al., 1992; Morris et al., 1995). Nutrients were conservatively transported in the plume (Morris et al., 1995) and benthic fluxes were minimal (Watson and Frickers, 1994), as was indicated by the model. Modelled nutrient concentrations are primarily determined by the external forcing. River inputs dominate inside the plume and the northern boundary outside the plume. In the second period (April to September) the ecosystem is active. After the initial spring bloom, phytoplankton nutrient demand is primarily met by in-situ recycling processes which also determine the phytoplankton composition.

There are distinct differences between the two sites EK and EN. The offshore site has higher primary production, which is partly a reflection of the lower SPM at this site compared with inshore, where light limitation means the phytoplankton growth season is shorter. The model consistently underestimates SPM concentrations at the plume site. This can be attributed to both a lack of knowledge of the land-

derived inputs of SPM and the lack of a sediment resuspension mechanism in the model. Intermittent resuspension events (tidal and storm) may exert a significant effect on the ecosystem dynamics. Resuspended SPM acts to inhibit phytoplankton growth due to absorption of light. Resuspension will also increase the quantities of POM in the water column, which may cause a shift in nutrient recycling processes from the benthic to the pelagic.

Increasing the N:Si ratio in the freshwater inputs causes an increase in both primary production and flagellate growth in the summer in the area of the model dominated by the river plume. This suggests that inflated anthropogenic inputs of nitrogen and phosphate could push the system towards eutrophication. However, the strong vertical mixing in the region and light limitation would suggest that the plume is very unlikely to become anoxic in the late summer. This highlights an important distinction between the potential of excess nutrients to enhance primary production and the environmental conditions being suitable for this potential to be exploited.

Over the simulated seasonal cycle the modelled Humber plume acts to remove 30% of the freshwater DIN, 22% of the freshwater phosphate and 7% of the freshwater silicate inputs, the rest being transported into the southern North Sea. Of the dissolved inorganic freshwater inputs retained in the plume 87%, 90% and 81% of the nitrogen, phosphate and silicate is then exported in a particulate organic form into the southern North Sea. These values can be rescaled to show that 3.9%, 2.2% and 1.3% of the freshwater DIN, phosphate and silicate are retained within the plume over the simulated year. The percentage of land-derived nutrients retained are probably underestimated. The loss of nitrogen by denitrification has been measured at up to 50% (Smith et al., 1984) in estuaries and up to 12% in the sediments of the southern North Sea (Law and Owens, 1990). This suggests that the loss of land-derived nitrogen in the modelled plume may be underestimated. Similarly, the retention of land-derived phosphate may also be underestimated. Modelled benthic phosphate effluxes are much larger than those measured, suggesting that the model may be underestimating the capacity of the sediments to absorb phosphate. The errors in fluxes calculated from data are in the range 45 to 100% and the errors in the modelled fluxes

are at least 50% (potential error in the phytoplankton uptake of phosphate), due to parameter uncertainties.

If, as the model suggests, the plume is exporting POM into the southern North Sea, it may exert a significant control on the fates of land-derived particle reactive pollutants from the Humber into the North Sea. For example, Turner et al. (1992) showed that the partition coefficients for the adsorption of dissolved trace metals onto particles are enhanced by 1 to 2 orders of magnitude in the presence of the organic material in the Humber plume. There is a continuous movement of fine suspended sediment from west to east across the North Sea, with deposition occurring to the north of the Dutch and German coasts, in the German Bight and the Norwegian trench (Howarth et al., 1994). Therefore it seems likely that POM generated in the Humber plume will be transported across the southern North Sea and deposited in the aforementioned regions.

Oreskes et al. (1994) proposed that the primary value of models is heuristic, providing guidance for further studies. Models can test hypotheses, strengthening what has been established by other means and illuminating which parts of the system are most in need of further study and where empirical data are needed most. Comparison of modelled fluxes with previous estimates of these fluxes suggest that the model produces benthic and cross boundary fluxes of the correct order of magnitude for nitrogen and silicate. There are problems with the phytoplankton uptake fluxes, the primary production appears too high in summer and too low in winter and the phosphate assimilation is probably too high. Further work is therefore required to look at the photoadaptation of phytoplankton in highly turbid water and the phosphate uptake mechanism. A number of potentially important pathways have yet to be quantified via process studies. These are the role of heterotrophic nutrient cycling, the fluxes of POM to the seabed and into the North Sea, the significance of the resuspension of SPM/POM and phosphate sorption/desorption reactions.

ERSEM has been coupled to a 2D depth-average transport model of the Humber plume region and can successfully simulate the observed behaviour of the plume ecosystem. It is an extremely powerful tool for exploring the dynamics of potentially eutrophic marine systems. The biological complexity of the

model is fully justified, because it allows us to explore the complexities of the causal linkages between land-derived nutrient inputs, marine ecosystem function and ultimately man.

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