

NUTRIENT DYNAMICS IN THE NORTH SEA: FLUXES AND BUDGETS IN THE WATER COLUMN DERIVED FROM ERSEM

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ABSTRACT

Nutrient dynamics for phosphate, nitrate, ammonium and silicate have been simulated with ERSEM, the European Regional Seas Ecosystem Model. From the model results budgets for the dissolved inorganic nutrients and the corresponding particulate fractions have been calculated. The annual cycles of the nutrients phosphate and silicate compare quite well with the observed ranges of variability. This does not hold for ammonium and nitrate. Biologically mediated transformations such as nutrient uptake and pelagic and benthic mineralization are the dominant processes in changing the nutrient concentrations with the horizontal advective contributions playing a minor role during the productive season.

Vertical advection and vertical diffusion have a clear seasonal signal, with a maximum in February. The decay of the advective nutrient transport in summer is caused by the depletion of the upper layer of dissolved inorganic nutrients by algal uptake. The inflow of nutrients in the northwest is almost balanced by the outflow in the northeast, without causing large nutrient transports into the shallower areas from the north. However, from the coastal areas there is a nutrient flow towards the central North Sea, enhancing primary production in the central area.

1. INTRODUCTION

The North Sea ecosystem has been modelled by applying the European Regional Seas Ecosystem Model (ERSEM), version 5.2, for the simulation of the dynamics during 1988 and 1989. The general ideas and the concept of ERSEM are described in Baretta *et al.* (1995). In ERSEM the North Sea was divided into ten boxes of volumes between 404 and 12815 km³, and five of the boxes in the deep North Sea were split into an upper box (0 to 30 m) and a lower box, to grossly represent the horizontal and vertical structure of the North Sea (Fig. 1).

The spatial distributions and the temporal developments of the state variables are modulated by the currents in the North Sea. The transports of nutrients and biota obtained from ERSEM result from the water transports, introduced into ERSEM by using the results of a general circulation model for the North Sea (Backhaus, 1983, 1985; Pohlmann, 1991; Lenhart *et al.*, 1995). The physical transport mechanisms were introduced into the box model ERSEM as described in Radach (1994) and Lenhart *et al.* (1995).

For the standard simulation with ERSEM the transports for 1988 were used as hydrodynamical forcing. The ERSEM simulation was run for 30 years with repeated forcing to obtain repeating annual cycles for all state variables; the results discussed here are derived from the 31st year of simulation.

The focus of this paper will be on the dissolved nutrient cycling in the water as simulated by ERSEM by calculating all the fluxes which contribute to the actual concentrations of these nutrients. Based on the conservation equations for the nutrients phosphate, nitrate, ammonium and silicate, budgets for each of these nutrients have been calculated from model results. These budgets are complemented by budgets of phosphorus, nitrogen and silicon in the particulate matter.

There are earlier attempts at nutrient budget calculations, partly by using data sets, partly by using simulations. Ursin & Andersen (1978) investigated the response of the North Sea to eutrophication with an ecosystem model and estimated changes in *e.g.* primary production. Nixon *et al.* (1986) discussed aspects of the N and P budgets in relation to other estuarine and coastal marine ecosystems. Based on measurements Nelissen & Stefels (1988) estimated inputs and outputs of phosphorus and nitrogen for the whole North Sea and for the coastal continental strip. Radach *et al.* (1990a) revised these budgets. Radach (1992) reviewed and updated the budgets for the North Sea and the coastal continental strip.

By using the results of an ecological model, budgets can be derived in a more complete way than from observations, because the simulated systems are closed systems with values for all fluxes included. The nutrient budgets present a good testing object of

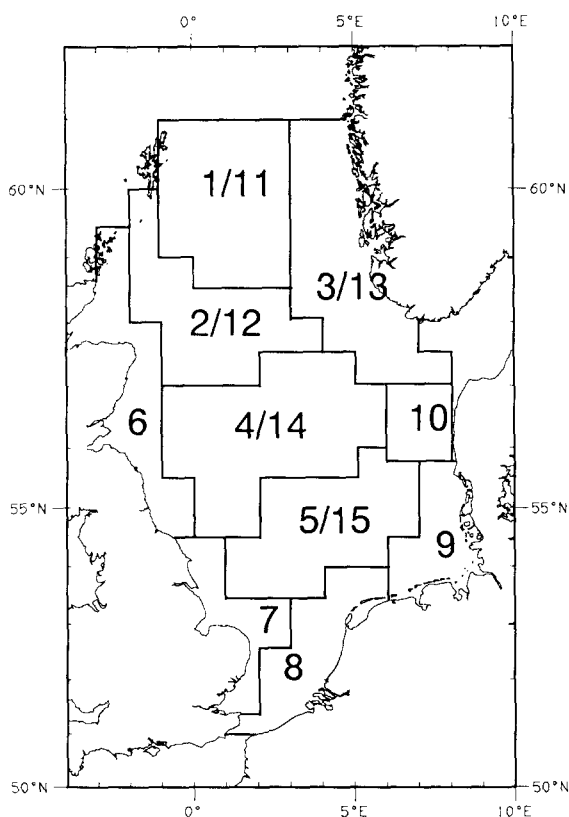


Fig. 1. The box structure of ERSEM.

TABLE 1

Initial values of nutrient concentrations on 1 January 1988 for the ERSEM boxes, for phosphate, nitrate, ammonium and silicate.

box	phosphate $\text{mmol P}\cdot\text{m}^{-3}$	nitrate $\text{mmol N}\cdot\text{m}^{-3}$	ammonium $\text{mmol N}\cdot\text{m}^{-3}$	silicate $\text{mmol Si}\cdot\text{m}^{-3}$
1	0.745	8.598	3.063	4.483
2	0.702	7.538	3.486	3.967
3	0.664	7.302	3.287	4.032
4	0.716	7.440	4.359	4.215
5	0.821	8.556	5.759	5.072
6	0.706	7.403	3.947	4.277
7	0.888	9.620	6.086	5.863
8	0.970	10.813	6.922	6.610
9	0.978	10.720	7.392	6.525
10	0.793	8.096	5.336	4.915
11	0.751	8.640	3.069	4.520
12	0.702	7.533	3.493	3.968
13	0.662	7.287	3.258	4.023
14	0.717	7.440	4.370	4.228
15	0.822	8.559	5.773	5.093

the full ERSEM, because far more nutrient data exist for the North Sea than other chemical and biological data, and because nutrient availability determines potential primary production, the basis of ecosystem dynamics.

2. NUTRIENT DATA USED IN ERSEM

Nutrient data are used in the standard simulation to prescribe the boundary and initial conditions as well as the river input. No atmospheric input is prescribed in ERSEM. Furthermore, nutrient data are used for comparing the simulation results with observations, as validation data.

2.1. INITIAL AND BOUNDARY CONDITIONS FOR NUTRIENTS

The initial values (Table 1) used for the standard simulation have been obtained by running the full model for 30 years with boundary conditions as described below in order to let the slow benthic processes adjust fully to the perpetual-year forcing. The values of the state variables on the last day of year 30 were taken as initial values. Due to the boundary conditions used for this run the initial values reflect the major nutrient distribution within the North Sea. For instance coastal and northern boxes obtain larger concentration values than the central boxes of the North Sea. This mirrors the fact that the coastal areas receive large amounts of nutrients from the rivers and that a tongue of nutrient-rich water enters the North Sea from the North Atlantic (Radach, 1992).

The concentration values at the open boundaries (Fig. 2) have been taken from compilations of the North Sea Task Force (RWS, 1992). There are ten box interfaces adjacent to the Atlantic Ocean, the English Channel and the Baltic Sea, where nutrient concentrations have to be prescribed as boundary conditions over the year. For the boundary conditions there were time series of data available, averaged over a longer period (month). The estimation of daily values from these monthly means can be done in several ways. The most obvious method is a linear interpolation between the monthly means. From a biological point of view there was a preference for using a smoothed step function. The reasoning is that in periods with lower mean values of the time series, the effect on the phytoplankton production of using too high values for the nutrient boundary concentrations can be significant, while this effect will not be 'averaged' by too low values during the higher mean values in the time series, due to non-linearity in the phytoplankton response to different nutrient concentration.

Generally the nutrient concentrations of the surface boundary boxes show much lower values in summer than in winter because of algal uptake in spring and summer. The boundaries of the lower boxes exhibit

weaker or no annual variation, because these depths are less influenced by primary production. For ammonium no boundary data are available. Therefore a so-called reflecting boundary condition was applied which identifies the value on the boundary as equal to the interior value of the adjacent box. This leads to advective ammonium fluxes, because there is a net water flow into or out of the boundary boxes.

The river loads (Table 2) have also been taken from compilations of the North Sea Task Force (RWS, 1992), provided as monthly mean values. In total about 43 kt·a⁻¹ of phosphate-P, 668 kt·a⁻¹ of inorganic dissolved nitrogen and 234 kt·a⁻¹ of silicate-Si are transported into the coastal strip by rivers during one year. The nutrient contributions by the rivers are introduced into the coastal areas, reaching from the Scottish Coast to the German Bight (boxes 6 to 9).

2.2. NUTRIENT DATA FOR VALIDATION

For validating the pelagic nutrient variables in ERSEM we use the data provided by the ECOMOD data base at the Institut für Meereskunde in Hamburg compiling data sets from various sources, including the data from the NERC (Natural Environmental Research Council) North Sea Community Research Programme, covering the southern North Sea and the ICES nutrient data holdings up to 1984. In total for phosphate, nitrate, ammonium and silicate 72553, 41925, 32452 and 17832 data have been used for the whole of the North Sea, respectively. The medians and the 16.6%- and 83.3%-quantils derived from the data set provide the observational validation measures for as many months as possible. In the presentations of the annual cycles (Figs 3 to 6) these statistical measures were only given when at least 15 data were available to estimate variability. Large ranges may result from many data as well as from few.

3. NUTRIENT CONCENTRATIONS AND FLUXES IN THE STANDARD SIMULATION OF ERSEM

In general the conservation equations for dissolved inorganic nutrients are very similar to each other, differing only in a few process terms. For phosphate of concentration C it reads, for example

$$\frac{dC}{dt} =$$

$$\begin{aligned} & \{ \text{horiz. advective inflow} \} - \{ \text{horiz. advective outflow} \} \\ & + \{ \text{vertic. advective inflow} \} - \{ \text{vertic. advect. outflow} \} \\ & + \{ \text{vertic. diffusive inflow} \} - \{ \text{vertic. diffusive outflow} \} \\ & + \{ \text{river inflow} \} \\ & - \{ \text{algal uptake} \} + \{ \text{algal respiratory release} \} \\ & + \{ \text{phytoplankton excretion} \} \\ & + \{ \text{bacterial excretion} \} \\ & + \{ \text{excretion of heterotrophic flagellates} \} \end{aligned}$$

$$\begin{aligned} & + \{ \text{excretion of microzooplankton} \} \\ & + \{ \text{excretion of mesozooplankton} \} \\ & + \{ \text{fish excretion} \} \\ & + \{ \text{benthic regeneration} \} \end{aligned} \quad (1)$$

For ammonium and nitrate this equation is supplemented by a term describing nitrification. In the nitrate equation, however, the terms for excretion by bacteria, heterotrophic flagellates, microzooplankton and fish do not occur since nitrogen excretion is in the form of ammonium. In the silicate equation these excretion terms have to be replaced by a term representing regeneration of silicate from labile organic dissolved matter.

The standard simulation provides the evolution of the nutrient concentrations (on the left-hand side of Eq. 1) as the combined effect of all processes on the right-hand side of Eq. 1. The importance of the single terms to the temporal change of the concentrations will be discussed later.

3.1. SIMULATED ANNUAL CYCLES OF NUTRIENT CONCENTRATIONS

The annual cycles of phosphate, nitrate, ammonium and silicate in the surface layer (Figs 3 to 6) differ considerably from box to box. The concentrations of PO₄, NO₃ and SiO₄ show an increase from the start of the year up to the beginning of the spring bloom, mainly caused by benthic mineralization. After the spring bloom the dissolved inorganic nutrients are depleted. In the upper layers of the northern North Sea (boxes 1, 2 and 3) the nutrient concentrations exhibit steep decays in April and May. For phosphate, nitrate and ammonium this is different in the rest of the surface layer of the North Sea (boxes 4 to 10), where the spring decay is slow, because nutrient regeneration from the benthos replenishes the water column.

While the summer depletion of phosphate (Fig. 3) and nitrate (Fig. 4) lasts from May to September in boxes 1, 2 and 3, depletion occurs in the other surface boxes for phosphate only in June and/or July and for nitrate in August/September, if at all. Ammonium (Fig. 5) exhibits depletion in boxes 4 to 10 at the end of April and in May only. The development of the silicate concentration (Fig. 6) is different, showing generally a depletion phase from May to September, interrupted by strong events of concentration increases caused by vertical diffusion (see section 3.3.2).

The deep North Sea (boxes 11, 12, 13) shows a modulation of the concentration of dissolved inorganic nutrients according to the development in the upper layer. In the central North Sea the lower boxes 14 and 15 have evolutions of their concentrations which resemble those of the upper layer, since the boxes are shallow and well-mixed throughout summer (Lenhart *et al.*, 1995).

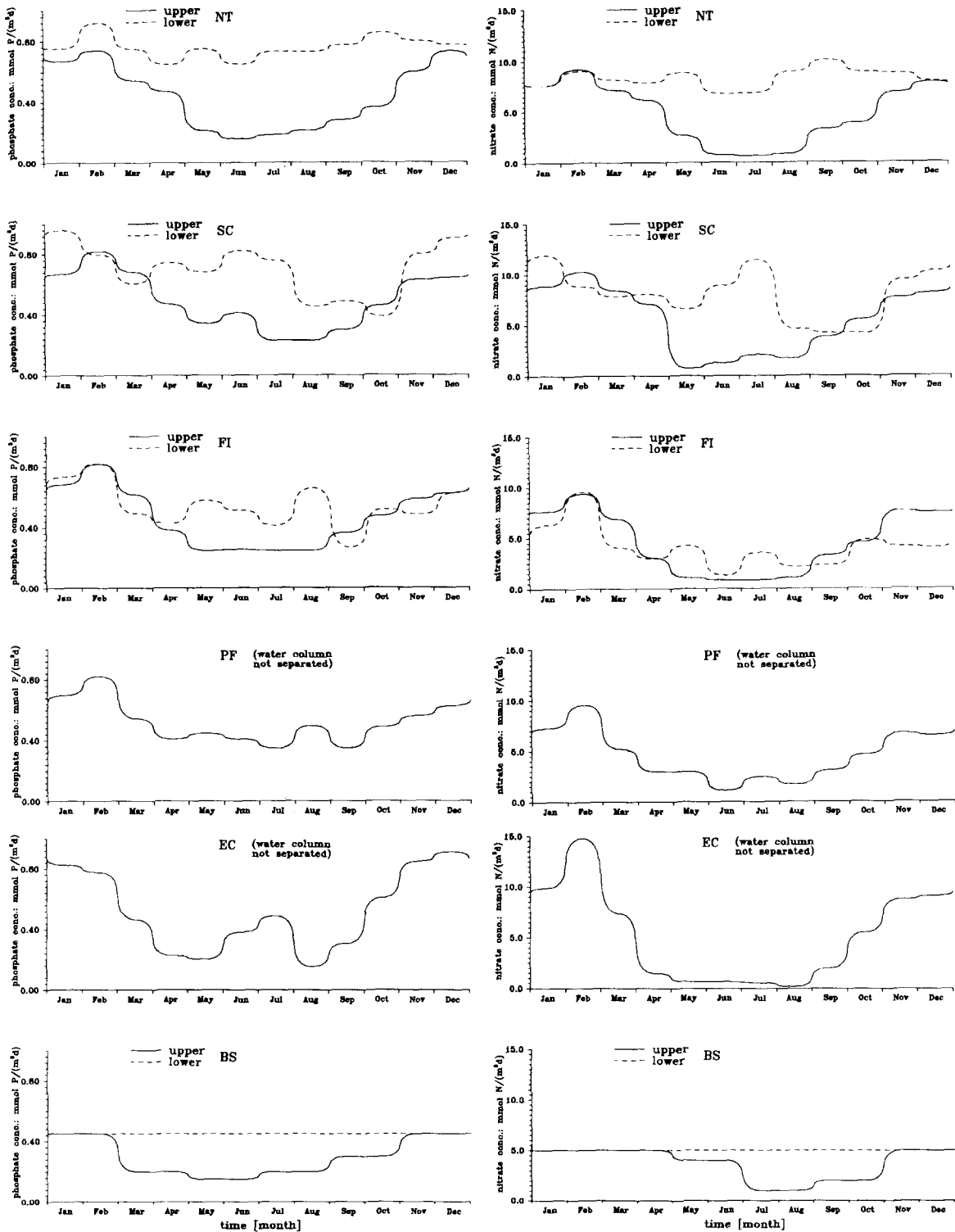
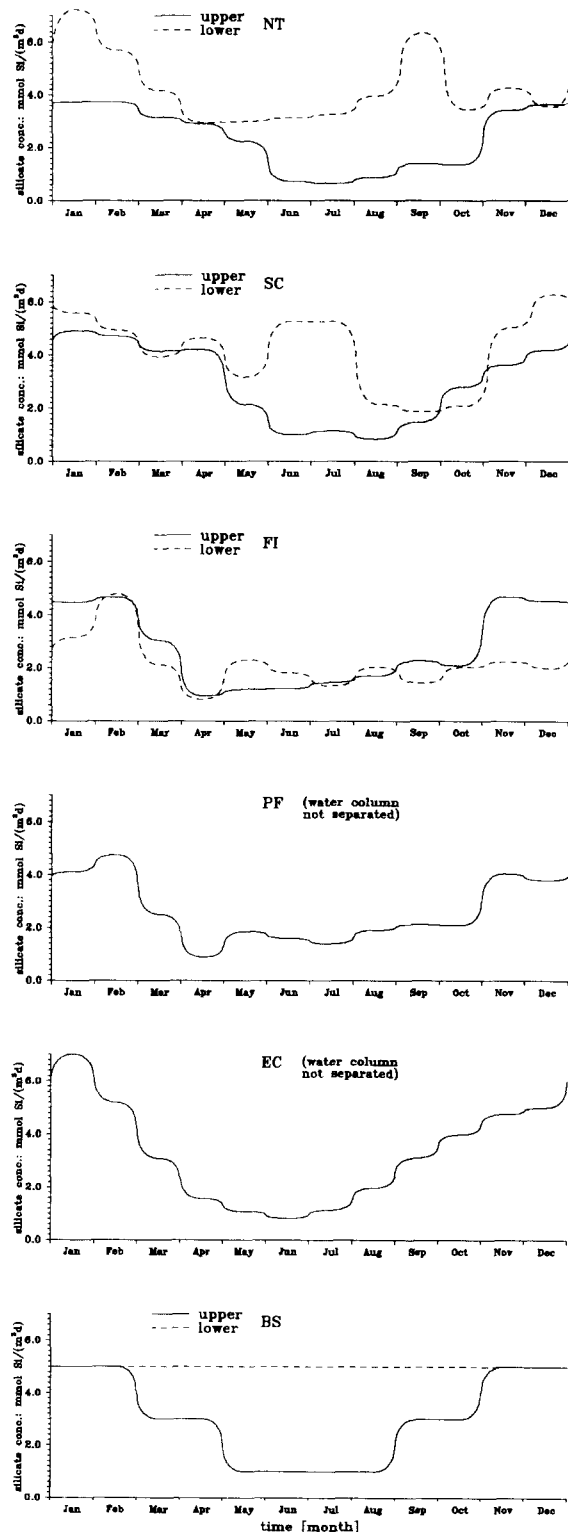


Fig. 2. Boundary values of main macronutrients for all boxes as monthly mean values (in $\text{mmol} \cdot \text{m}^{-3}$) a. for phosphate, b. for nitrate and c. for silicate; the abbreviations for the connections to the Atlantic and the Baltic Sea are as follows: NT = Norwegian Trench, SC = Shetland Channel, FI = Fair Isle Channel, PF = Pentland Firth, EC = English Channel, BS = Baltic Sea; the dashed lines denote the concentrations on the lateral interface of the lower boxes.



From the simulated annual cycles of dissolved inorganic nutrient concentrations we have calculated the annual cycles of the ratio of inorganic nitrogen nutrients to inorganic phosphate concentration (N:P ratio) (Fig. 7). Three areas with different dynamics can be distinguished. In the northern North Sea the surface areas (boxes 1 and 2) exhibit a decrease of the initial N:P=16 down to very small values due to the stronger depletion of inorganic dissolved nitrogen compared to phosphate depletion from May to August. The Norwegian Trench (box 3) shows an intermediate behaviour, with nitrogen depletion in May changing to phosphate depletion (N:P around 40) in June and July, returning to weak nitrogen deficiency in August. The central North Sea (box 4) and the coastal areas (box 9) are characterized by enhanced phosphate depletion, starting to build up in May, being strongest in June, July, and changing to a weak phosphate dominance with a value of N:P=14 in August.

Maximum N:P ratios of 80 to 90 occur in English and Dutch coastal waters (boxes 7 and 8); the dynamics are similar to those in the northern central North Sea (box 4). The southern central North Sea exhibits by far the largest maxima of about 140 (box

TABLE 2

River inputs used in the ERSEM simulations: annual river inputs of dissolved nutrients for all relevant rivers around the North Sea.

river	enters box	tons P	tons N	tons Si
Firth of Forth	6	186	420	11
Tyne/Tees	6	593	14735	9309
Humber	7	5891	60636	17928
Thames	7	3786	26214	14931
Ems	8	614	25736	6805
Noordzeekanaal	8	1767	10877	3912
Lauwer	8	143	333	25
Lake IJssel/ Kornwerderzand	8	461	12320	3588
Lake IJssel/ Den Oever	8	820	21232	5170
Meuse	8	4400	91159	34402
Rhine	8	14194	191543	69623
Scheldt	8	2116	31670	15077
Yzer	8	109	267	37
Elbe	9	3822	126314	34520
Jade	9	3	8	2
Schleswig- Holstein rivers	9	3	8	2
Weser	9	3420	52862	18470
Danish rivers	9	513	1227	136
sum box 6		778	15155	9319
sum box 7		9677	86850	32858
sum box 8		24624	385137	138638
sum box 9		7762	180419	53129
total		42842	667561	233946

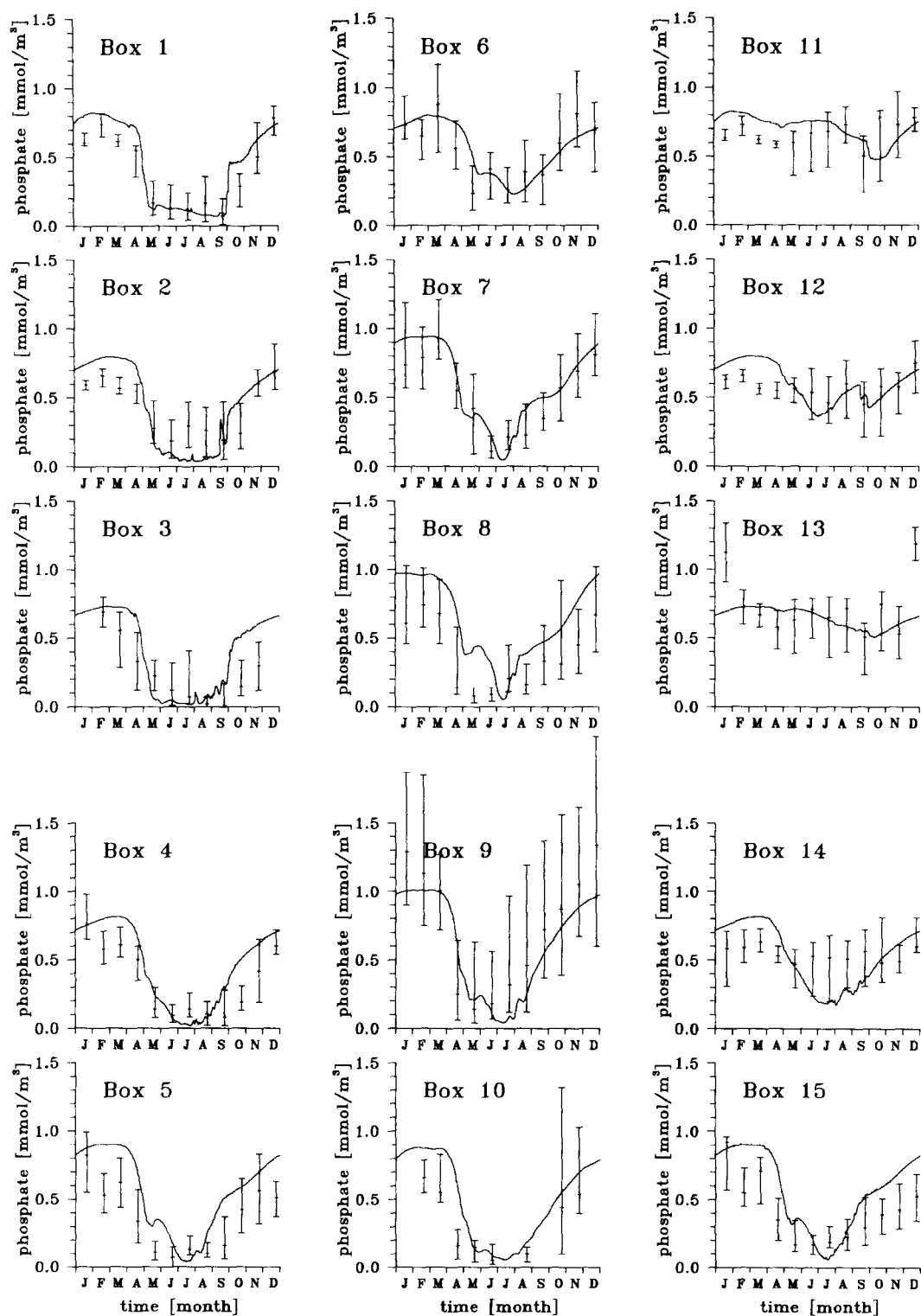


Fig. 3. Annual cycles for phosphate for all boxes for 1988, together with observational ranges of variability.

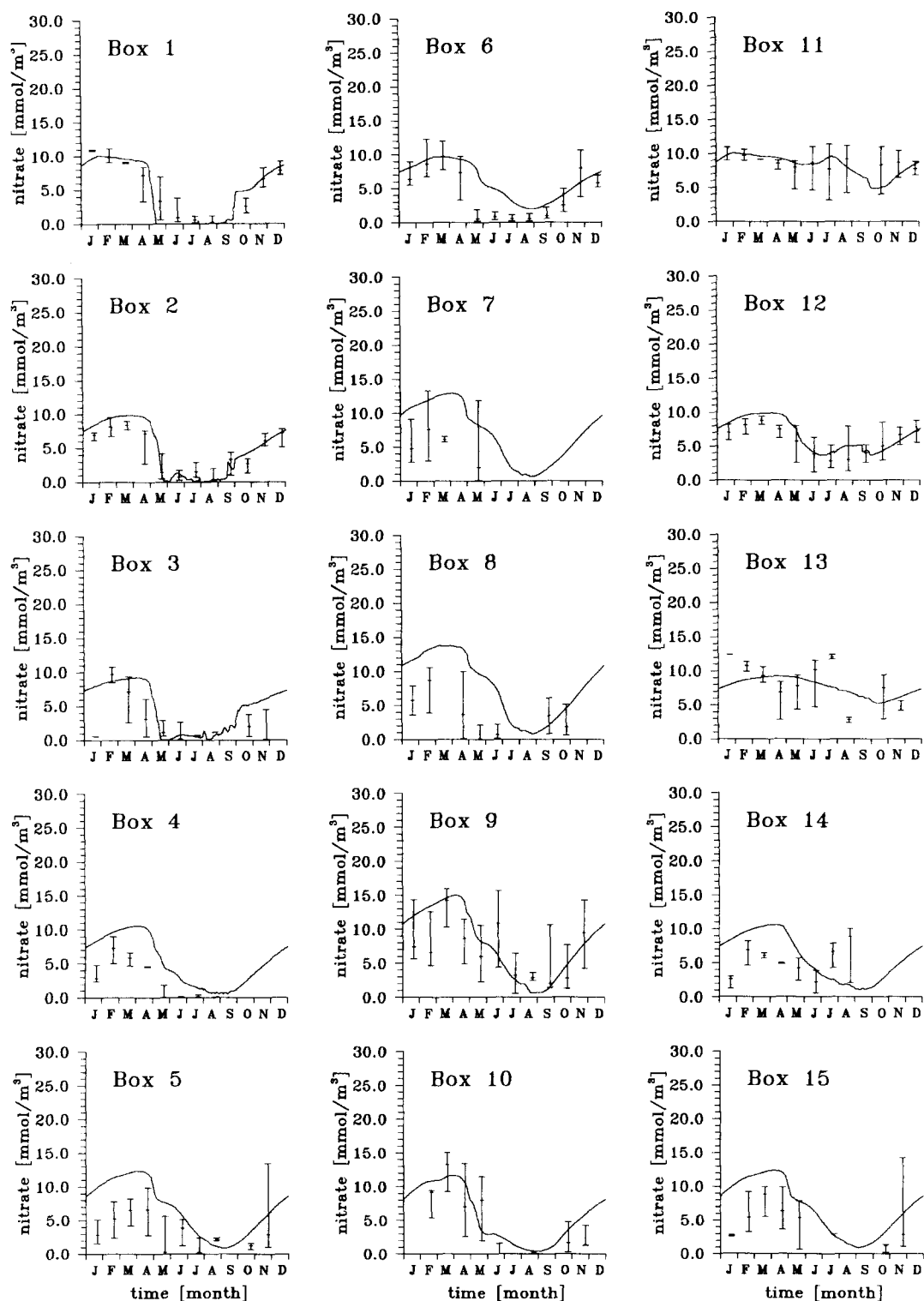


Fig. 4. Annual cycles for nitrate for all boxes for 1988, together with observational ranges of variability.

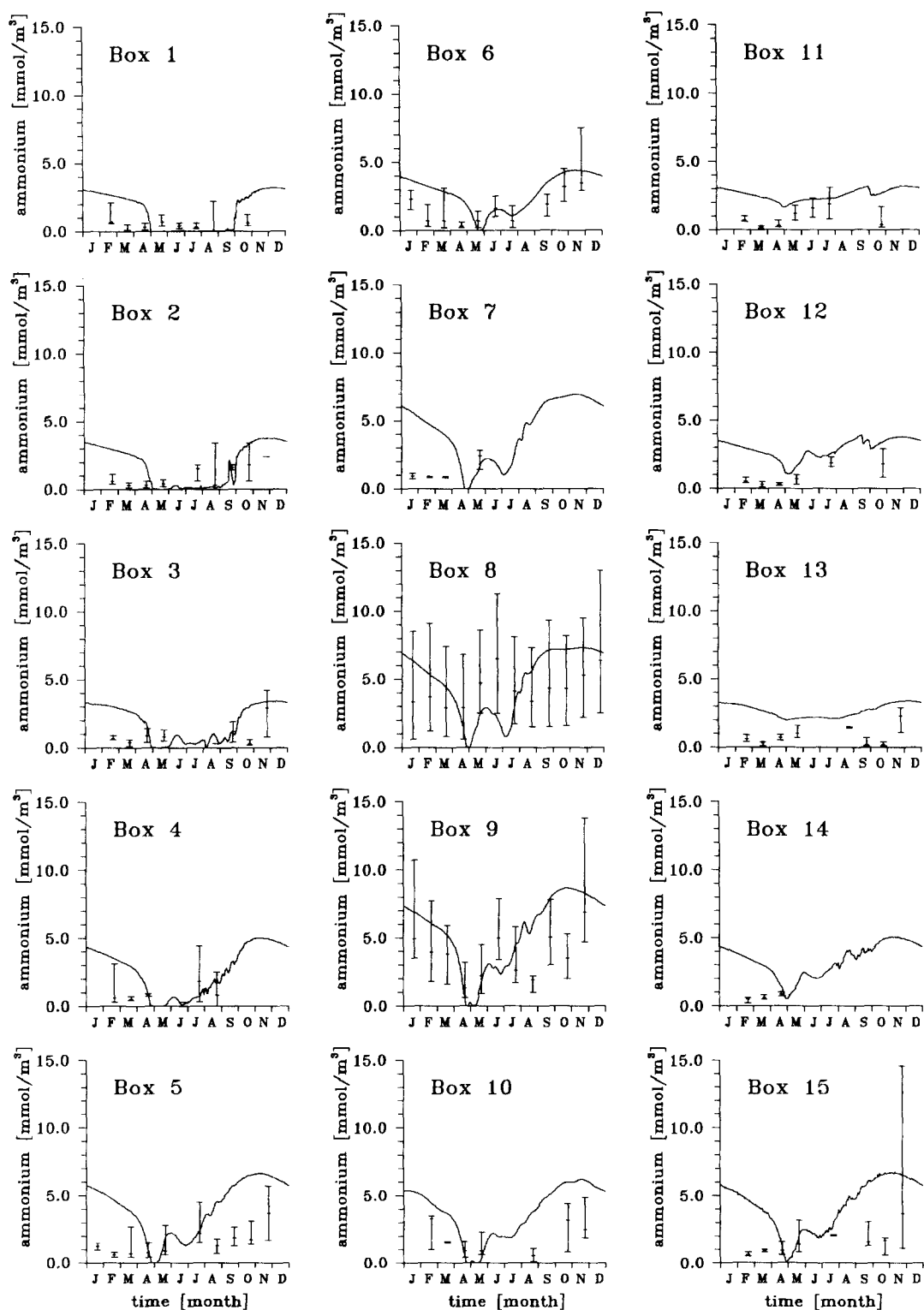


Fig. 5. Annual cycles for ammonium for all boxes for 1988, together with observational ranges of variability.

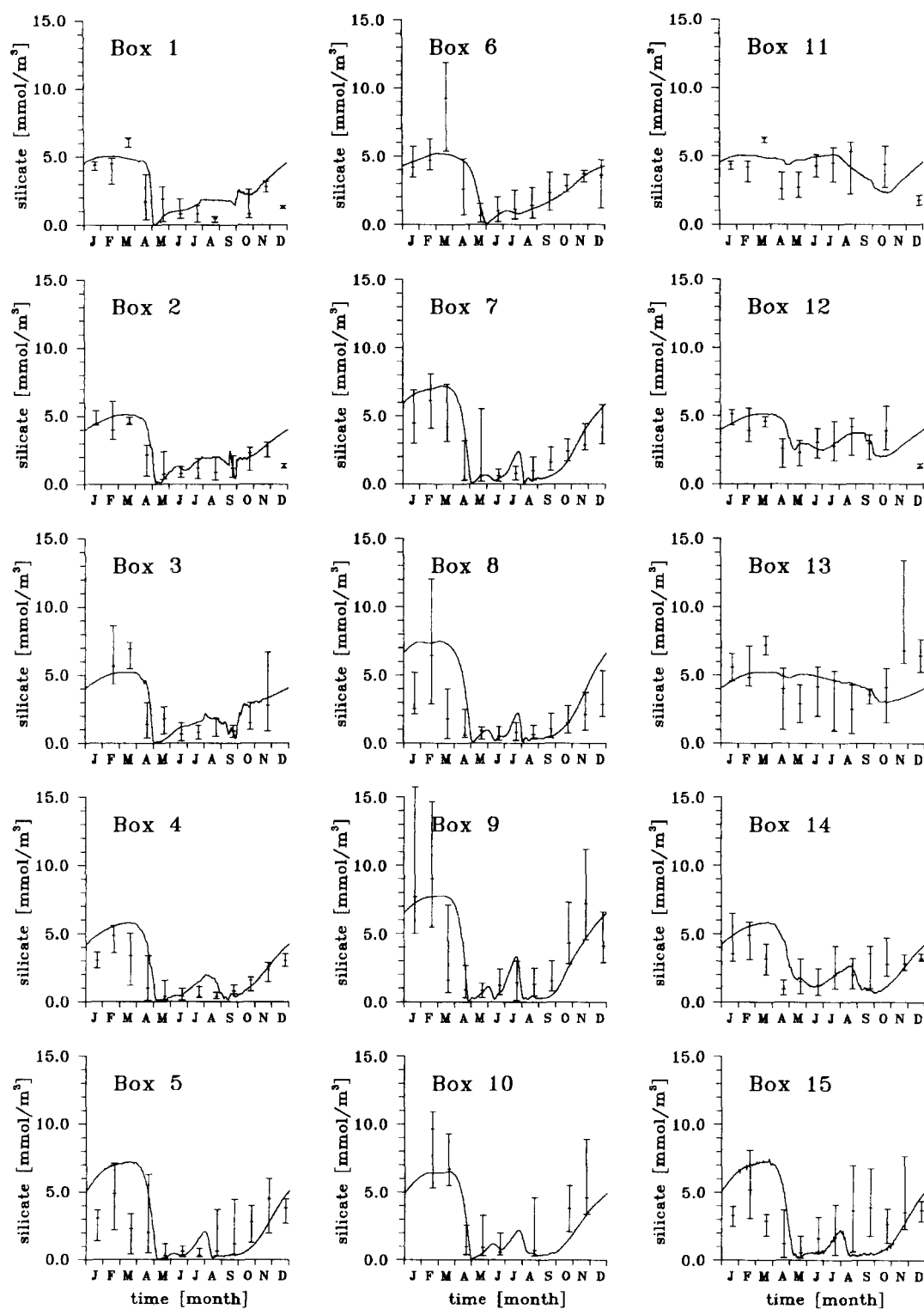


Fig. 6. Annual cycles for silicate for all boxes for 1988, together with observational ranges of variability.

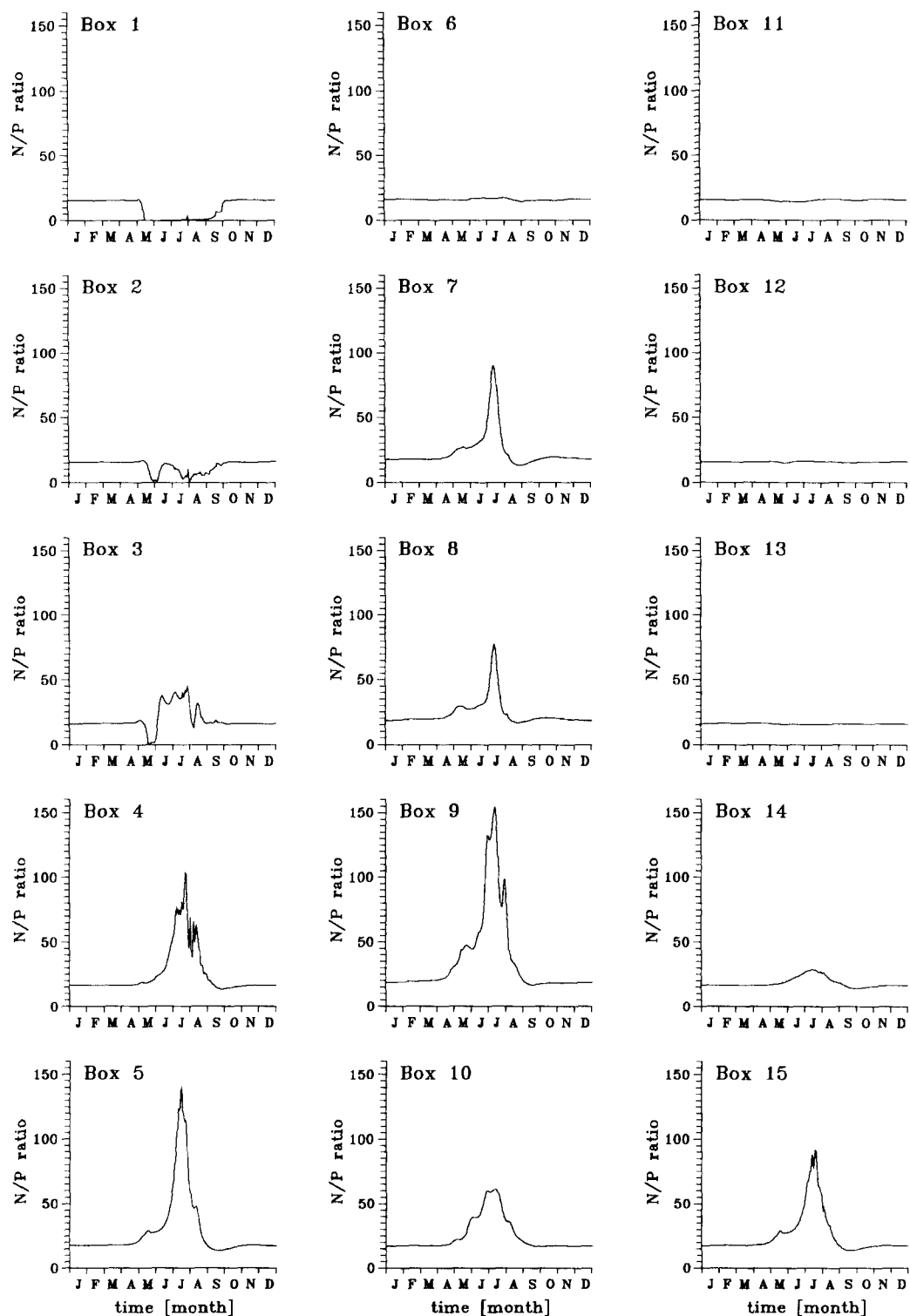


Fig. 7. Annual cycles for the N:P ratio for all boxes.

5) and 160 (box 9), which express a relative nitrogen excess over phosphate during summer conditions. In the deeper parts of the central North Sea (box 15) the structure of the N:P ratio, with a maximum value of about 80, resembles that of the surface water (box 5), because the water column is mixed. In the deep water in the north (boxes 11 to 14), but also in the Scottish coastal waters, only minor changes of the N:P ratio occur.

3.2. SIMULATED ANNUAL CYCLES OF BIOLOGICALLY INDUCED NUTRIENT FLUXES

The biologically mediated nutrient fluxes of gross nutrient uptake, algal respiration, pelagic and benthic regeneration contribute the largest changes to the nutrient concentrations. For all nutrients gross uptake and algal release run parallel in the upper boxes; in the lower boxes respiration acts as a source of nutrients. The microbial regeneration and benthic regeneration prove to be of different importance for the different nutrients.

Nutrient uptake. Phosphate uptake by diatoms (Fig. 8a) occurs mainly in spring and autumn in the central North Sea, when the thermocline establishes and when it decays. In addition, uptake by diatoms also occurs in summer in the southern central (box 5) and coastal areas (boxes 6 to 10). Ammonia uptake by diatoms (Fig. 9a) occurs first; nitrate uptake (not shown) follows two weeks later, when ammonium concentrations decrease in late April and early May. In spring the uptake of phosphate extends into May in most of the boxes, covering both peaks of uptake of ammonium and nitrate.

Also for flagellates net uptake of phosphate (Fig. 8b) and ammonium (Fig. 9b) runs parallel over the annual cycle. The spring peak dominates the uptake curves in the north (boxes 1 to 3), but the peak uptake values are shifted towards summer in the south; there the main uptake activity extends throughout summer, because regenerated nutrients from the benthos are immediately available and need not penetrate the thermocline. In boxes 7 to 10 distinct effects of the spring, summer, and autumn blooming of algae can be seen, with summer and autumn peaks being the largest in boxes 8 and 9.

Nutrient regeneration in the pelagic. Excretion of phosphate by the small heterotrophs, comprising bacteria, heterotrophic nanoflagellates and microzooplankton (Fig. 8c) in the surface layer is strongest before and after their spring peak, and the absolute maximum activity occurs in summer, as it is closely related to the flux of dissolved organic matter which is mostly produced by phytoplankton under nutrient stress. The annual cycle of ammonium excretion by all small heterotrophs together looks totally different, with a broad summer maximum in the surface layer (Fig. 9c). The annual cycles of excretion of phosphate and ammonium by heterotrophic flagellates, however,

are both very similar in shape, showing mostly a sharp spring maximum and levelling off towards summer, with a dip of very small values at the end of July.

Annual cycles of excretion of phosphate and ammonium by mesozooplankton (Figs 8d and 9d) show similarities, but while ammonium excretion has about the same magnitude for zooplankton and for the small heterotrophs (Figs 9c and d), phosphate regeneration by the small heterotrophs is much larger than mesozooplankton excretion (Figs 8c and d).

Nutrient regeneration from the benthic domain.

As examples we present benthic regenerated phosphate and ammonium (Figs 8e and 9e) for boxes 11, 14 and 9, which exhibit slightly different annual cycles. Both start with regeneration peaks right after the spring bloom. A broad cycle follows, from May to December, with maxima in July/August for both dissolved inorganic nutrients. Concentrations are mostly affected in the coastal boxes, by up to 0.04 mmol P·m⁻³·d⁻¹ and 0.4 mmol N·m⁻³·d⁻¹ in several boxes.

The lower layer is most active in box 15, the shallowest deep box. Only small values of benthic regeneration last throughout the winter, until activity increases again in May. Phosphate regeneration rates are of the same order of magnitude as phosphate uptake rates, but the bulk of regeneration occurs after the blooms, with a maximum in August. The same holds for ammonium. The high regeneration activity is in accordance with findings from the NERC North Sea Community Research Programme (Howarth *et al.*, 1994).

3.3. SIMULATED ANNUAL CYCLES AND HORIZONTAL DISTRIBUTIONS OF PHYSICAL TRANSPORTS OF NUTRIENTS

Physical transport of nutrients is realized in ERSEM by horizontal and vertical advection and by vertical diffusion as detailed in Lenhart *et al.* (1995).

3.3.1. HORIZONTAL TRANSPORTS

Gross horizontal advective transports of dissolved inorganic nutrients into as well as out of all of the boxes have a clear seasonal signal. Also net horizontal nutrient transports show a seasonal signal (Fig. 10). The transports are at their maximum in February, decay until June/July, and they increase again towards the end of the year. The effect on the concentration is largest in the coastal boxes 7 to 10 because of their relatively small volumes. The decay of the advective transport in summer is caused by the fact that depletion of nutrients in spring and summer leaves little dissolved inorganic nutrients in the upper layer all over the North Sea to be advected.

The spatial pattern of the annual horizontal advective flow for the total water column (as the sum for surface and deep boxes) shows that the inflow in the northwest is almost balanced by the outflow in the

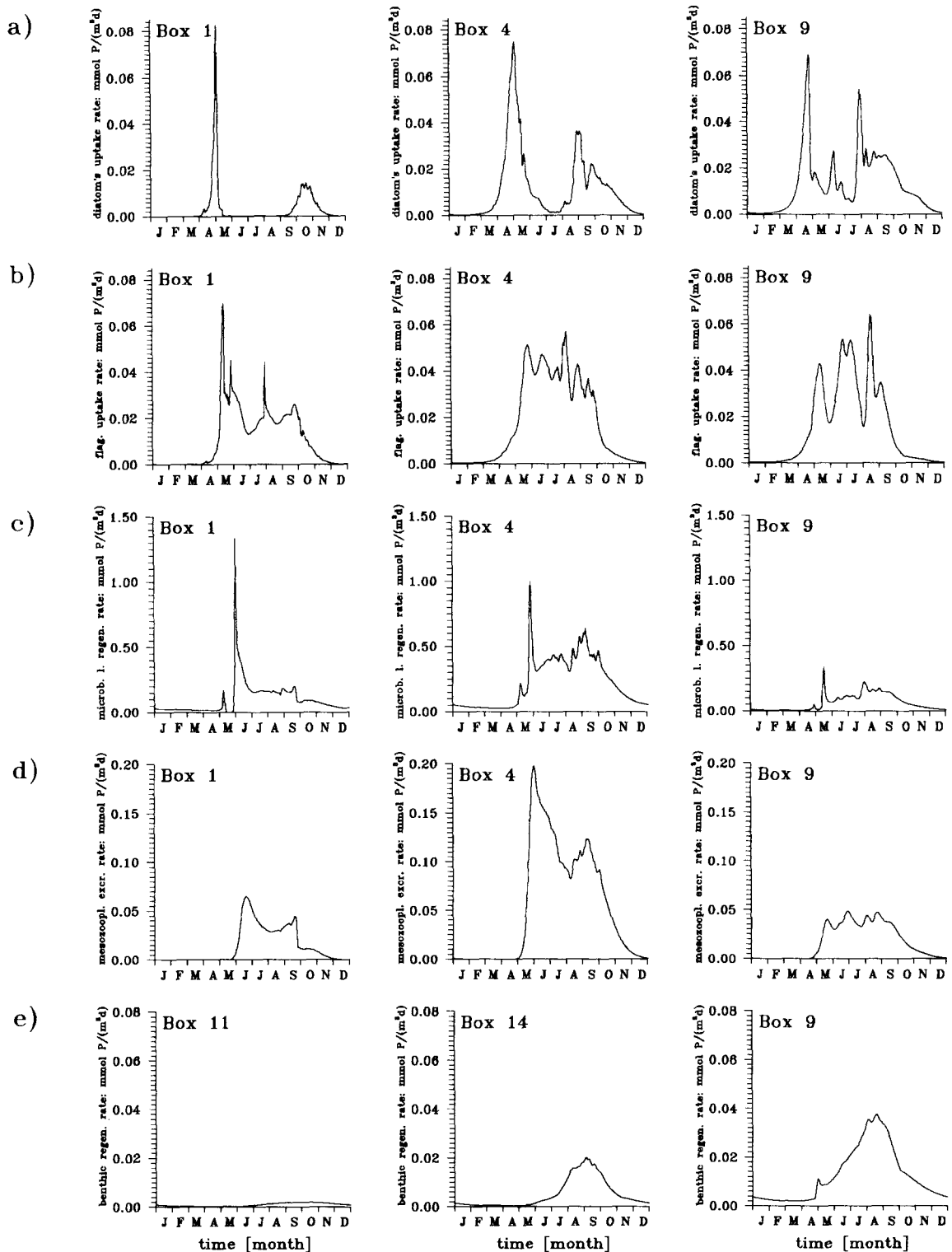


Fig. 8. Annual cycles of net uptake by a. diatoms and b. flagellates, c. pelagic regeneration by small heterotrophs, d. mesozooplankton excretion and e. benthic regeneration of phosphate for the boxes 1, 4 and 9.

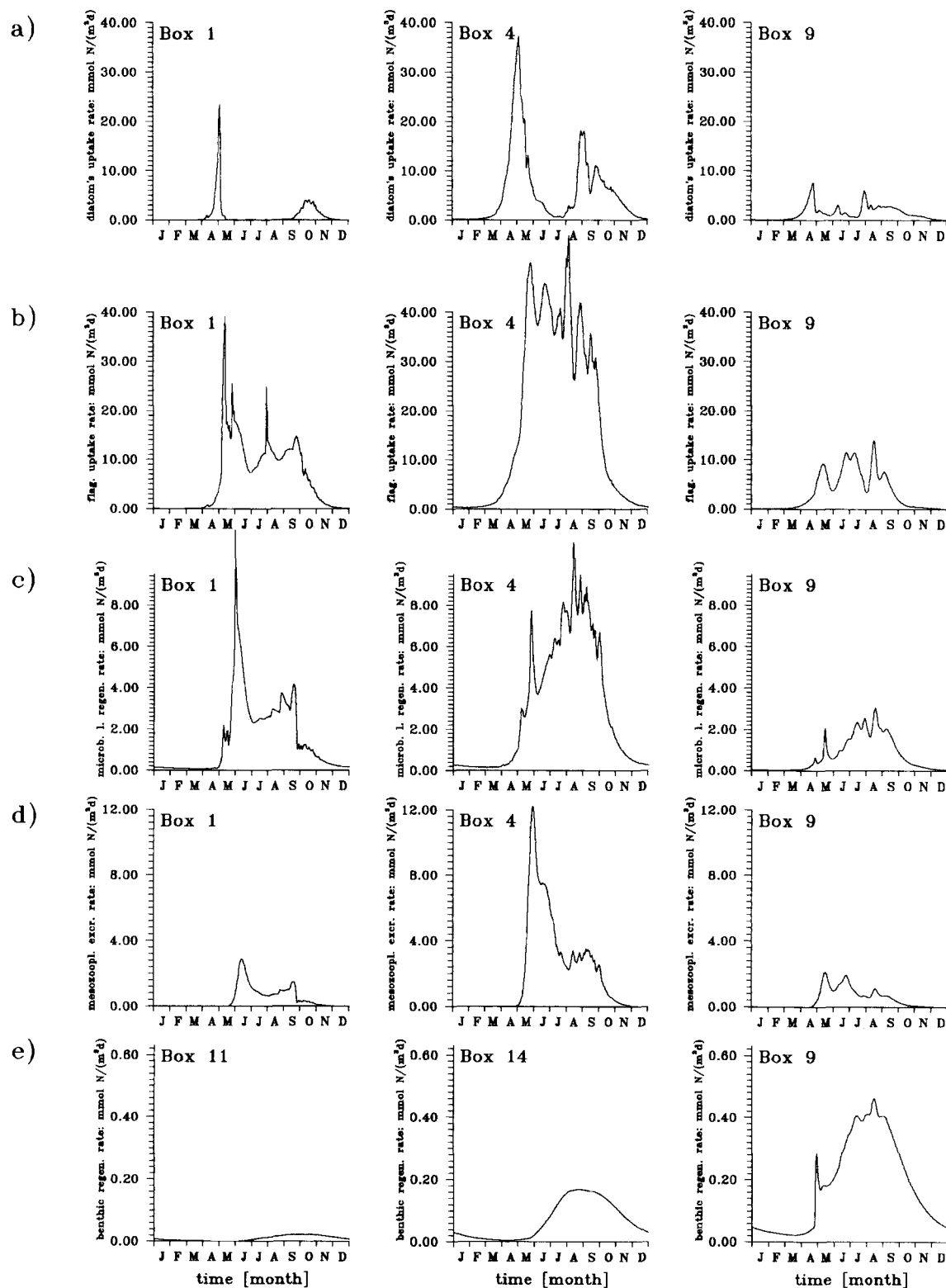


Fig. 9. Annual cycles of net uptake by a. diatoms and b. flagellates, c. pelagic regeneration by small heterotrophs, d. mesozooplankton excretion and e. benthic regeneration of ammonium for boxes 1, 4 and 9.

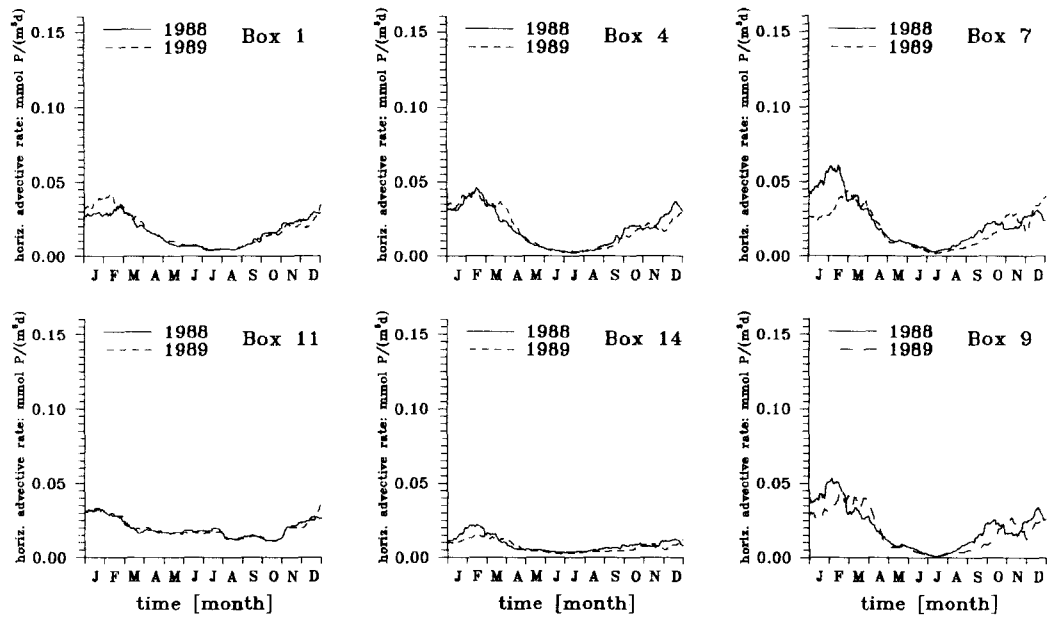


Fig. 10. Annual cycles for horizontal advective inflow of phosphate for boxes 1, 11, 4, 14, 7 and 9, for 1988 and 1989.

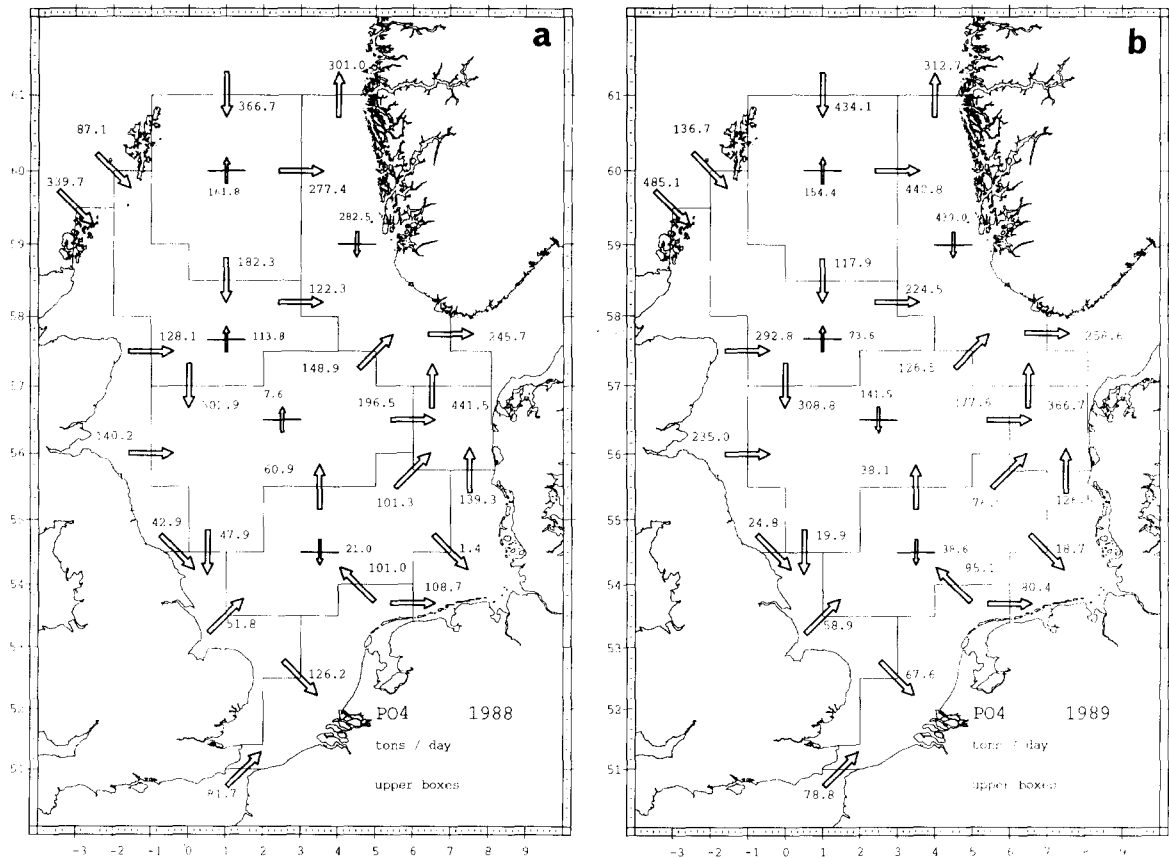


Fig. 11. Regional distribution of net advected phosphate within the system of the upper layers a. in 1988 and b. in 1989. Vertically advected flow is indicated by an arrow (in $\text{t} \cdot \text{d}^{-1}$) in the centre of the boxes. For comparison with numbers in Table 4 multiply by 360.

northeast. The general structure of the phosphate transport follows the general cyclonic circulation pattern (Radach, 1992; Lenhart *et al.*, 1995). The pattern for all net nutrient transports within the upper box system (Fig. 11) is imposed by the circulation and can be characterized as follows: Large amounts of nutrients are introduced from the North Atlantic Ocean in the northwest, then circulate mostly in the northern half of the North Sea, and leave the North Sea through the Norwegian Trench to the Atlantic and through the Skagerrak to the Baltic. Part of the nutrient import from the northwest flows along the British coast and to the central North Sea, but only a small fraction enters the southern North Sea, following the coastline in an anti-clockwise path to finally enter the Norwegian Trench. However, nutrients flow from the coastal areas (enriched by river loads) towards the central North Sea and further north, following the cyclonic circulation.

The deep boxes (not shown) are dominated by the flow through the northern boundary, entering in the northwest and leaving in the northeast. Most of the imported nutrients are not transported further south than box 4 and leave the North Sea via box 3, from which $2589 \text{ t PO}_4\text{-P}\cdot\text{d}^{-1}$ and $13902 \text{ t NO}_3\text{-N}\cdot\text{d}^{-1}$ leave the deep parts of the Norwegian Trench. Thus, it turns out that the net advective flows across the box boundaries form important contributions to the budgets of each single box.

The separation into horizontal flow within the surface and the deep boxes, respectively, reveals a more complicated pattern, where the surface boxes border the deep boxes (e.g. where boxes 8 and 9 border box 5). A net flow of $136 \text{ t}\cdot\text{d}^{-1}$ of phosphate crosses the line of $54^\circ 30' \text{ N}$ into the southern North

Sea. All other transports cross this line or the borders of box 5 northwards and are much higher than the southbound transports. There is phosphate flow of $126 \text{ t}\cdot\text{d}^{-1}$ from box 7 into box 8 and considerably more outflow from box 8 to the northeast, viz. $287 \text{ t}\cdot\text{d}^{-1}$. Box 8 also has an inflow of phosphate of about $80 \text{ t}\cdot\text{d}^{-1}$ from the English Channel.

The situation is structurally similar for nitrate, although much larger amounts are transported. There is an outflow of $15501 \text{ t}\cdot\text{d}^{-1}$ out of the Norwegian Trench, which is a little larger than the input on the western side of the northern boundary. The flux towards south across $54^\circ 30' \text{ N}$ is only $630 \text{ t}\cdot\text{d}^{-1}$. The advective export from the continental coastal boxes 8 and 9 is much larger than the advective input to them; most of the export is transported into the central North Sea area in this spatial setup of the model.

3.3.2. VERTICAL TRANSPORT

Vertical transports of water carry dissolved inorganic nutrients between the upper and the lower box. Vertical advection of these nutrients has a strong seasonal signal (not shown). In most of the boxes the largest vertical advective transports occur from January to March; smaller transports occur in autumn, from October to December. However, in boxes 1 and 3 stronger events may also happen in summer. The influence of vertical advection on the concentration is only of the order of $5\cdot 10^{-3} \text{ mmol P}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ and 2 to 3 $\text{mmol N}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ for nitrate. Thus usually the effect is marginal, though sometimes noticeable.

Vertical diffusion of dissolved inorganic nutrients results from wind activity, combined with strong vertical gradients of the nutrients between upper and

TABLE 3
Budgets of inorganic and particulate phosphorus, nitrogen and silicon for the whole North Sea.

	phosphorus budget			nitrogen budget			silicon budget		
	PO_4	POM-P	$\text{PO}_4+\text{POM-P}$	NO_3+NH_4	POM-N	$\text{NO}_3+\text{NH}_4+\text{POM-N}$	SiO_4	POM-Si	$\text{SiO}_4+\text{POM-Si}$
in kt :									
content at first day	911	131	1042	6708	7356	14064	4986	603	5589
content at last day	911	131	1042	6715	7361	14076	5007	600	5607
in $\text{kt}\cdot\text{a}^{-1}$:									
advective inflow	1864	550	2414	13108	3189	16297	11519	2285	13804
advective outflow	-1933	-540	-2473	-13893	-3111	-17004	-11726	-2312	-14038
river input	43	23	66	668	154	822	233	24	257
net algal uptake	-1843	1843	0	-17621	17621	0	-9568	9568	0
micro. pel. min.	665	-665	0	7190	-7190	0	-	-	-
mesoz. excretion	151	-151	0	3900	-3900	0	-	-	-
fish excretion	69	45	114	345	227	572	-	-	-
fish grazing	-	-76	-76	-	-309	-309	-	-	-
sinking + filter. f.	-	-1031	-1031	-	-6690	-6690	-	-9579	-9579
benthic mineraliz.	988	-	988	6332	-	6332	9597	-	9597

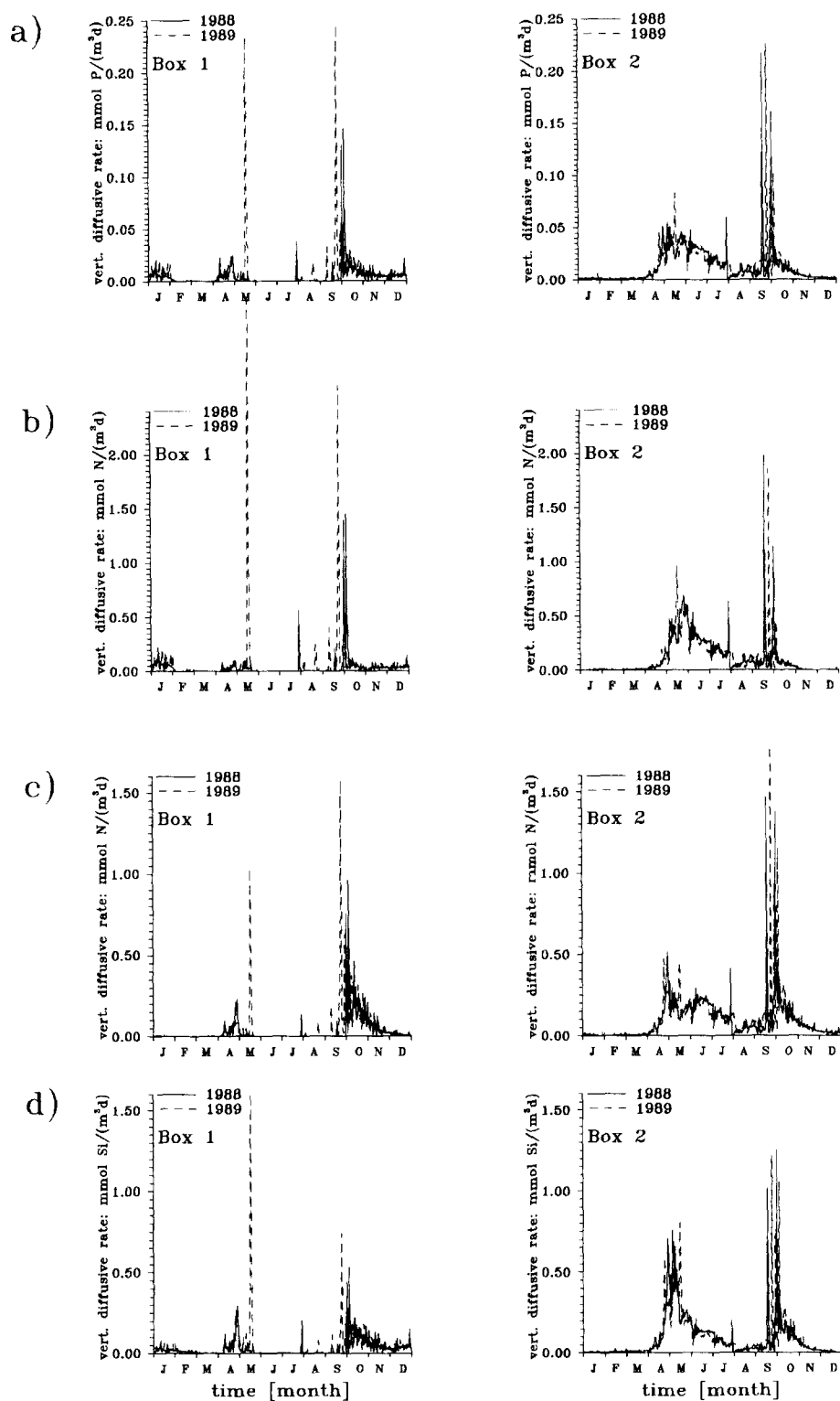


Fig. 12. Annual cycles for vertical diffusion of a. phosphate, b. nitrate, c. ammonium, and d. silicate, for boxes 1 and 2.

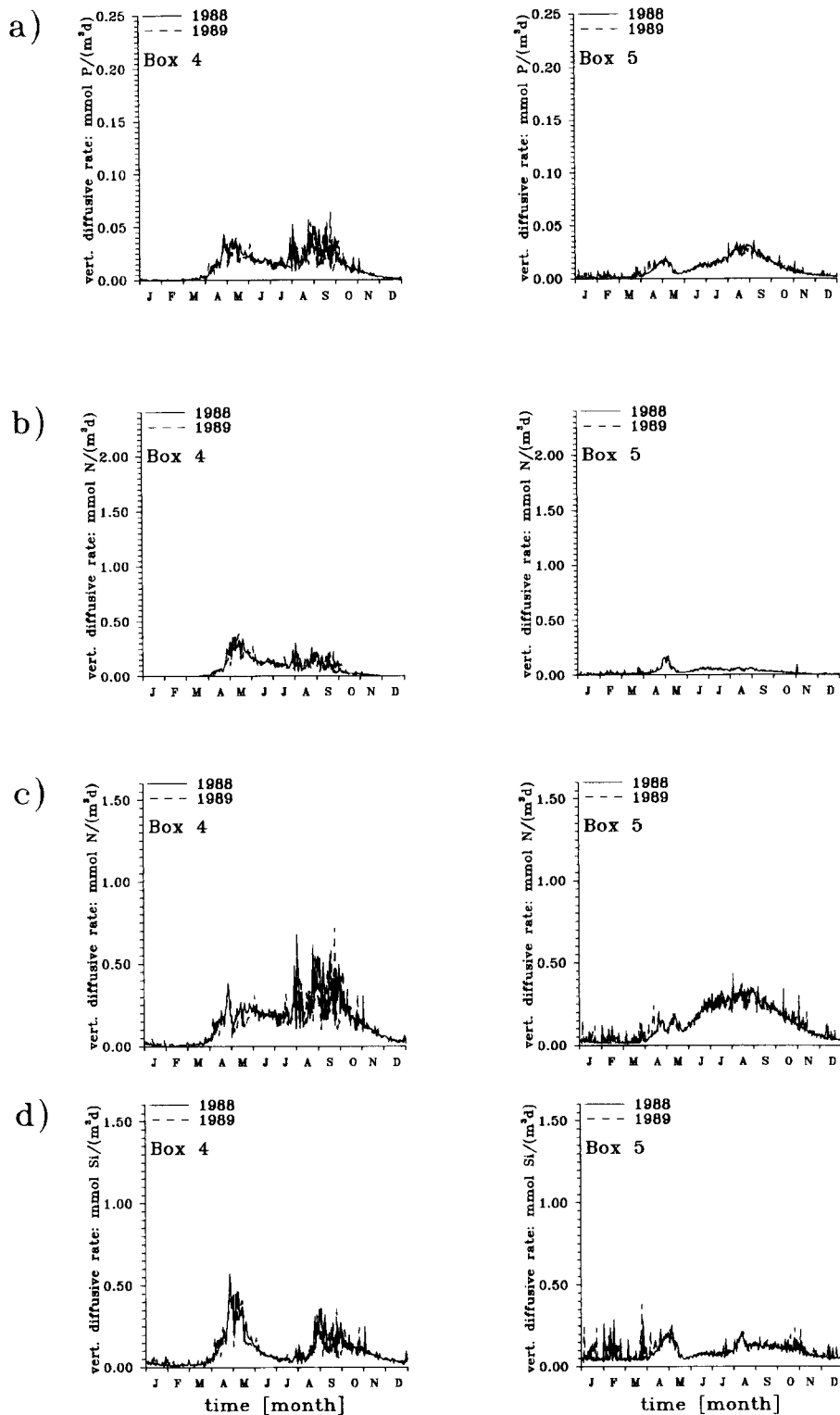


Fig. 12. (Cont.) Annual cycles for vertical diffusion of a. phosphate, b. nitrate, c. ammonium, and d. silicate, for boxes 4 and 5.

lower boxes. Occasional summer storms and the regular storm activity during September and October stir up the sea to layers deeper than 30 m, thus causing turbulent entrainment of nutrients into the upper layer (boxes 1 to 3), where these effects change the concentrations up to $0.25 \text{ mmol P} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ and up to $3 \text{ mmol N} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ for nitrate (Fig. 12). In such cases in summer the concentration of nitrate may be doubled or even tripled within one day, as occurred in box 3 in summer 1988 (Fig. 4).

4. NUTRIENT BUDGETS FROM THE STANDARD SIMULATION OF ERSEM

Annual budgets for the nutrients calculated from the results of the standard simulation for each of the boxes provide integral quantities to compare our previous knowledge with and thus to test the realism of the ERSEM model. They provide insight into the dominant processes acting in nutrient dynamics and thus help to understand the system. For each box the budget equations for nutrients are derived from the box-integrated conservation Eq. 1 by integration over one year, from $t=0$ (1 January) to $t=T$ (last day of year), yielding

$$C(T) - C(0) = \int_0^T [\text{right-hand side of eq. 1}] dt \quad (2)$$

This means that the difference between the final and the initial content of nutrients in the box for the year under consideration is equal to the sum of the contributions of all processes. This leads to changes in the concentration of the nutrients cumulated over one year.

The detailed budgets for the inorganic dissolved fractions of phosphorus, nitrogen and silicon are supplemented by budgets of particulate phosphorus, nitrogen and silicon, which are restricted to the input and output of the respective elements, without going into the details of the many trophic interactions. In Table 3 the budgets for the dissolved and the particulate fractions are compiled for the whole of the North Sea.

The box-specific budgets are presented in Tables 4 to 8. In parts a. of these tables we give phytoplankton uptake and pelagic and benthic remineralization. Pelagic remineralization consists of respiratory algal release and the excretion of algae, bacteria, heterotrophic flagellates, micro- and meso-zooplankton and fish. For ammonium and nitrate the contribution of nitrification is also considered. The budget for silicate contains, in addition, the remineralization of labile dissolved organic matter. Concerning the physical processes, the contributions by horizontal and vertical advection are given as net transports; further horizontal advection across the exterior lateral boundaries is given (Tables 4 to 8, parts b.). In parts c. the budgets

for the particulate fractions are given.

Benthic mineralization fluxes occur in boxes with an interface to the sediment (boxes 6 to 15). The vertical diffusion as well as the vertical advection only acts at the 30-m thermocline interface, separating the upper layer (boxes 1 to 5) from the deep water (boxes 11 to 15). Therefore there is no contribution by these vertically acting processes within the coastal areas (boxes 6 to 9). The processes acting at the 30-m thermocline transport a definite amount of nutrients from the deep box into the surface box (or downwards), which appears as outflow for the first and inflow for the second box. Therefore, within the budget, the contributions from vertical advection and vertical diffusion cancel when summed over all boxes.

4.1. PHOSPHORUS BUDGET

The phosphorus budgets for the whole of the North Sea and each of the 15 boxes are given in Tables 3 and 4. In winter about 911 kt of phosphorus are dissolved in the water of the North Sea while only 131 kt are bound in particulate matter. The largest biotic fluxes are gross algal uptake of $3655 \text{ kt} \cdot \text{a}^{-1}$, algal respiratory release of $1812 \text{ kt} \cdot \text{a}^{-1}$, microbial pelagic regeneration of $665 \text{ kt} \cdot \text{a}^{-1}$, and benthic regeneration of $988 \text{ kt} \cdot \text{a}^{-1}$, which is 4, 2, 0.7 and 1.1 times the winter content, respectively. Bacterial, heterotrophic flagellates and microzooplankton excretion is 4.4 times of the mesozooplankton excretion of $151 \text{ kt} \cdot \text{a}^{-1}$.

The annual total gross advective transports of phosphate into (or out of) the boxes amount to about $8200 \text{ kt} \cdot \text{a}^{-1}$, which is 9 times the winter content, but only a net loss of $69 \text{ kt} \cdot \text{a}^{-1}$ results from the transport, and for the single boxes the range of net transport is between -130 and $+59 \text{ kt} \cdot \text{a}^{-1}$. An amount of $550 \text{ kt} \cdot \text{a}^{-1}$ of particulate phosphorus is advected into the North Sea, and an almost identical quantity is advected out.

The river input is $43 \text{ kt} \cdot \text{a}^{-1}$ of phosphate and $23 \text{ kt} \cdot \text{a}^{-1}$ of particulate phosphorus. This amount seems small compared to the other contributions to the total budget, but it is a significant input into the coastal boxes (Table 4).

Fish take out $76 \text{ kt} \cdot \text{a}^{-1}$ of POM-P by feeding in the water column and provide $114 \text{ kt} \cdot \text{a}^{-1}$ of dissolved and particulate phosphorus by excretion. The excretion by fish is higher than consumption by fish because fish also feed on benthos not included in the budget for the water. Particulate excretion enters the detritus pool. The particulate material sinking to the bottom and ingested by filter feeders is about $1031 \text{ kt} \cdot \text{a}^{-1}$ and reappears (96%) as benthic mineralization. All biological transfers of phosphate amount to about $7300 \text{ kt} \cdot \text{a}^{-1}$.

Horizontal advection transports about $1864 \text{ kt} \cdot \text{a}^{-1}$ of phosphate in and $1933 \text{ kt} \cdot \text{a}^{-1}$ out of the North Sea across the borders, yielding a flushing time for the North Sea of half a year (175 days). About $7650 \text{ kt} \cdot \text{a}^{-1}$, i.e. 8.4 times the winter content are exchanged

TABLE 4
Budgets for phosphorus for all boxes in 1988.
a. all biological process contributions to the dissolved inorganic phosphate budget.

box	algae gross uptake $kt P \cdot a^{-1}$	algae respir. release $kt P \cdot a^{-1}$	microbial pelagic regener. $kt P \cdot a^{-1}$	meso-zoopl. excretion $kt P \cdot a^{-1}$	fish excretion $kt P \cdot a^{-1}$	benthic regener. $kt P \cdot a^{-1}$
1	-246.	103.	38.	5.	2.	0.
2	-505.	187.	44.	11.	2.	0.
3	-353.	144.	47.	10.	3.	0.
4	-883.	331.	77.	19.	8.	0.
5	-505.	210.	58.	17.	4.	0.
6	-236.	122.	46.	14.	4.	75.
7	-255.	117.	34.	11.	5.	93.
8	-360.	165.	45.	14.	5.	135.
9	-191.	78.	23.	6.	5.	84.
10	-104.	45.	13.	3.	3.	39.
11	-4.	38.	33.	2.	4.	50.
12	-3.	65.	46.	10.	8.	86.
13	-1.	63.	76.	7.	5.	71.
14	-7.	105.	66.	16.	10.	196.
15	-1.	39.	21.	6.	2.	160.
total NS	-3655.	1812.	665.	151.	69.	988.

b. all transport process contributions to the dissolved inorganic phosphate budget.

box	initial content $10^3 t$	final content $10^3 t$	net horizontal advective flow $kt P \cdot a^{-1}$	net vertical advective flow $kt P \cdot a^{-1}$	vertical diffusive inflow $kt P \cdot a^{-1}$	vertical diffusive outflow $kt P \cdot a^{-1}$	river inflow $kt P \cdot a^{-1}$
1	36.	36.	-34.	58.	77.	-3.	0.
2	37.	37.	-10.	41.	232.	-1.	0.
3	42.	42.	162.	-103.	107.	-16.	0.
4	60.	60.	40.	3.	409.	-4.	0.
5	53.	53.	-4.	-8.	238.	-10.	0.
6	70.	69.	-25.	0.	0.	0.	1.
7	31.	31.	-14.	0.	0.	0.	10.
8	40.	40.	-29.	0.	0.	0.	25.
9	18.	18.	-12.	0.	0.	0.	8.
10	10.	10.	1.	0.	0.	0.	0.
11	111.	111.	10.	-58.	3.	-77.	0.
12	86.	86.	61.	-41.	1.	-232.	0.
13	221.	221.	-233.	103.	16.	-107.	0.
14	78.	77.	22.	-3.	4.	-409.	0.
15	19.	19.	-5.	8.	10.	-238.	0.
total NS	912.	912.	-69.	0.	1096.	-1096.	43.

c. budget contributions for particulate organic phosphorus.

box	net advective transport $kt P \cdot a^{-1}$	net vertical diffusion $kt P \cdot a^{-1}$	net sinking of algae and detritus $kt P \cdot a^{-1}$	net primary production $kt P \cdot a^{-1}$	plankton excretion $kt P \cdot a^{-1}$	excretion by fish $kt P \cdot a^{-1}$	uptake by fish $kt P \cdot a^{-1}$	river inflow $kt P \cdot a^{-1}$
1	3.	-19.	-83.	144.	-43.	2.	-4.	0.
2	-25.	-111.	-126.	318.	-54.	1.	-4.	0.
3	8.	-31.	-126.	209.	-57.	2.	-5.	0.
4	-34.	-172.	-241.	552.	-96.	5.	-13.	0.
5	9.	-56.	-169.	295.	-75.	3.	-7.	0.
6	24.	0.	-79.	114.	-60.	2.	-2.	0.
7	1.	0.	-98.	138.	-45.	3.	-3.	4.
8	-8.	0.	-140.	195.	-60.	3.	-2.	12.
9	0.	0.	-90.	113.	-29.	3.	-4.	7.
10	-1.	0.	-41.	59.	-16.	2.	-2.	0.
11	20.	19.	32.	-34.	-35.	3.	-3.	0.
12	-26.	111.	32.	-62.	-55.	5.	-5.	0.
13	62.	31.	54.	-62.	-83.	3.	-6.	0.
14	-23.	172.	39.	-98.	-82.	7.	-14.	0.
15	1.	56.	8.	-38.	-27.	1.	-2.	0.
total NS	10.	0.	-1031.	1843.	-816.	45.	-76.	23.

horizontally between the boxes. Vertical advection redistributes $518 \text{ kt}\cdot\text{a}^{-1}$ and vertical diffusion exchanges $1096 \text{ kt}\cdot\text{a}^{-1}$ between surface and deep layers (about 57% and 120% of the layer contents, respectively).

Regeneration is strongest in the southern central North Sea (Table 4). In box 15 an amount of phosphate corresponding to 8.4 times the winter content in the water is regenerated by the benthos yearly. In the southern coastal areas the range is 3- to 4.6-fold. Gross uptake of phosphate amounts to 14.7 times the

winter content in box 4 as the maximum value; this is considerably higher than the turnover rate of 2.6 to 3.2 derived from the simulations by Radach & Moll (1993) for the central North Sea. From ERSEM we get a range between 3.4 (box 6) and 10.5 (box 9) times in the coastal boxes. The second highest turnover rate for uptake is in box 2, which is far from coastal areas. Excretion by the microbial loop constituents may also reach 120% of the winter content (boxes 2, 4, 9 and 10).

4.2. BUDGETS OF NITROGEN-NUTRIENTS

4.2.1. NITRATE BUDGET

Nitrate provides the bulk of the nitrogen-nutrients in winter. About 4473 kt of nitrate are dissolved in the water of the North Sea in winter. At the end of the integration the amount is 4487 kt .

The largest biotic fluxes are gross algal uptake of $10802 \text{ kt}\cdot\text{a}^{-1}$, algal respiratory release of $5044 \text{ kt}\cdot\text{a}^{-1}$, and nitrification of $5618 \text{ kt}\cdot\text{a}^{-1}$, both of which together nearly sum up to gross uptake (Table 5). Direct benthic regeneration of $489 \text{ kt}\cdot\text{a}^{-1}$ constitutes a less important source of nitrate.

Again, horizontal advection transports large amounts: About $9303 \text{ kt}\cdot\text{a}^{-1}$ flow in and $10176 \text{ kt}\cdot\text{a}^{-1}$ flow out of the North Sea across the borders, and from $41239 \text{ kt}\cdot\text{a}^{-1}$ to $42113 \text{ kt}\cdot\text{a}^{-1}$ are exchanged between the boxes. However, the net advective transport summed over all boxes amounts to $874 \text{ kt}\cdot\text{a}^{-1}$ and thus the North Sea as a whole seems to lose about 15% of its nitrate contents. The single net advective contributions of nitrate to the nitrate budgets of the boxes are of second-order importance. The

TABLE 5

Budget for nitrate for all boxes in 1988.
a. all biological process contributions to the budget.

box	algae gross uptake $\text{kt N}\cdot\text{a}^{-1}$	algae respir. release $\text{kt N}\cdot\text{a}^{-1}$	benthic nitrification regener. $\text{kt N}\cdot\text{a}^{-1}$	kt $\text{N}\cdot\text{a}^{-1}$
1	-885.	363.	0.	105.
2	-1911.	723.	0.	141.
3	-1223.	507.	0.	168.
4	-2591.	990.	0.	377.
5	-1318.	554.	0.	479.
6	-602.	310.	40.	435.
7	-649.	302.	25.	289.
8	-845.	388.	34.	397.
9	-467.	193.	35.	197.
10	-277.	121.	12.	88.
11	-8.	71.	80.	510.
12	-7.	125.	70.	519.
13	-2.	116.	117.	1163.
14	-15.	202.	52.	569.
15	-3.	79.	24.	184.
total NS	-10802.	5044.	489.	5618.

b. all transport process contributions to the budget

box	initial content kt N	final content kt N	net horizontal advective flow $\text{kt N}\cdot\text{a}^{-1}$	net vertical advective flow $\text{kt N}\cdot\text{a}^{-1}$	vertical diffusive inflow $\text{kt N}\cdot\text{a}^{-1}$	vertical diffusive outflow $\text{kt N}\cdot\text{a}^{-1}$	river inflow $\text{kt N}\cdot\text{a}^{-1}$
1	189.	189.	-137.	317.	258.	-20.	0.
2	177.	178.	-62.	200.	922.	-13.	0.
3	211.	211.	691.	-532.	498.	-107.	0.
4	283.	283.	250.	0.	999.	-21.	0.
5	249.	250.	21.	-39.	324.	-16.	0.
6	329.	330.	-195.	0.	0.	0.	14.
7	153.	154.	-44.	0.	0.	0.	79.
8	200.	201.	-302.	0.	0.	0.	330.
9	90.	91.	-99.	0.	0.	0.	141.
10	46.	46.	57.	0.	0.	0.	0.
11	578.	580.	-90.	-317.	20.	-258.	0.
12	418.	420.	407.	-200.	13.	-922.	0.
13	1098.	1101.	-1528.	532.	107.	-498.	0.
14	363.	365.	173.	0.	21.	-999.	0.
15	89.	89.	-15.	39.	16.	-324.	0.
total NS	4473.	4487.	-874.	0.	3179.	-3179.	564.

TABLE 6
Budget for ammonium for all boxes in 1988.
a. all biological process contributions to the budget.

box	algae gross uptake $kt\ N\ a^{-1}$	algae respir. release $kt\ N\ a^{-1}$	microbial pelagic regeneration $kt\ N\ a^{-1}$	meso-zoopl. excretion $kt\ N\ a^{-1}$	fish excretion $kt\ N\ a^{-1}$	benthic regeneration $kt\ N\ a^{-1}$	nitrification $kt\ N\ a^{-1}$
1	-1661.	722.	580.	145.	9.	0.	-105.
2	-2988.	1128.	650.	450.	9.	0.	-141.
3	-2247.	936.	664.	321.	11.	0.	-168.
4	-5659.	2148.	1038.	699.	30.	0.	-377.
5	-3221.	1323.	659.	417.	16.	0.	-479.
6	-1386.	705.	379.	294.	22.	412.	-435.
7	-1633.	733.	383.	258.	27.	571.	-289.
8	-2304.	1035.	519.	329.	28.	854.	-397.
9	-1248.	505.	271.	164.	25.	555.	-197.
10	-666.	284.	152.	97.	16.	259.	-88.
11	-22.	208.	239.	23.	21.	226.	-510.
12	-21.	365.	340.	172.	45.	480.	-519.
13	-6.	341.	516.	60.	26.	295.	-1163.
14	-45.	592.	587.	336.	47.	1207.	-569.
15	-8.	223.	210.	134.	11.	982.	-184.
total NS	-23114.	11250.	7190.	3900.	345.	5842.	-5618.

b. all transport process contributions to the budget.

box	initial content $kt\ N$	final content $kt\ N$	net horizontal advective flow $kt\ N\ a^{-1}$	net vertical advective flow $kt\ N\ a^{-1}$	vertical diffusive inflow $kt\ N\ a^{-1}$	vertical diffusive outflow $kt\ N\ a^{-1}$	river inflow $kt\ N\ a^{-1}$
1	67.	67.	-27.	100.	237.	-2.	0.
2	82.	82.	17.	95.	782.	-3.	0.
3	95.	95.	606.	-230.	218.	-112.	0.
4	166.	165.	80.	8.	2056.	-25.	0.
5	168.	167.	-64.	-28.	1442.	-66.	0.
6	176.	175.	5.	0.	0.	0.	2.
7	97.	97.	-60.	0.	0.	0.	8.
8	128.	128.	-122.	0.	0.	0.	54.
9	62.	62.	-117.	0.	0.	0.	40.
10	30.	30.	-55.	0.	0.	0.	0.
11	205.	205.	149.	-100.	2.	-237.	0.
12	194.	194.	10.	-95.	3.	-782.	0.
13	491.	490.	-194.	230.	112.	-218.	0.
14	213.	213.	-118.	-8.	25.	-2056.	0.
15	60.	60.	-22.	28.	66.	-1442.	0.
total NS	2234.	2228.	89.	0.	4942.	-4942.	104.

coastal boxes 8 and 9 together lose about $400\ kt\ a^{-1}$. Vertical advection redistributes $2638\ kt\ a^{-1}$ and vertical diffusion exchanges $3179\ kt\ a^{-1}$ between upper and lower layers. Both processes transport nitrate efficiently into the upper layer. The river input is about $564\ kt\ a^{-1}$.

4.2.2. AMMONIUM BUDGET

There are $2234\ kt$ of ammonium dissolved in the water of the North Sea in winter, at the beginning of the year. The largest biotic fluxes are gross algal

uptake of $23114\ kt\ a^{-1}$ (10.3-fold), which is also the largest contribution to the budget (Table 6). The next largest contribution is the respiratory release of $11250\ kt\ a^{-1}$. Then pelagic regeneration of $7190\ kt\ a^{-1}$ and benthic regeneration of $5842\ kt\ a^{-1}$ (about 2.6-fold) follow. Mesozooplankton excretion amounts to $3900\ kt\ a^{-1}$. The relations between the process contributions for ammonium are different from those for phosphate; ammonium is much more often recycled by uptake, release and excretion.

Horizontal advection transports about $3805\ kt\ a^{-1}$ into and $3716\ kt\ a^{-1}$ out of the North Sea across the

TABLE 7
Budget for nitrogen for all boxes in 1988.
a. all biological process contributions to the dissolved inorganic nitrogen budget.

box	algae gross uptake $kt\ N\ a^{-1}$	algae respir. release $kt\ N\ a^{-1}$	microbial pelagic regeneration $kt\ N\ a^{-1}$	meso-zoopl. excretion $kt\ N\ a^{-1}$	fish excretion $kt\ N\ a^{-1}$	benthic regeneration $kt\ N\ a^{-1}$
1	-2546.	1085.	580.	145.	9.	0.
2	-4899.	1851.	650.	450.	9.	0.
3	-3470.	1443.	664.	321.	11.	0.
4	-8250.	3138.	1038.	699.	30.	0.
5	-4539.	1877.	659.	417.	16.	0.
6	-1988.	1014.	379.	294.	22.	452.
7	-2282.	1035.	383.	258.	27.	596.
8	-3148.	1423.	519.	329.	28.	888.
9	-1714.	698.	271.	164.	25.	590.
10	-943.	405.	152.	97.	16.	271.
11	-30.	280.	239.	23.	21.	306.
12	-28.	491.	340.	172.	45.	550.
13	-9.	457.	516.	60.	26.	413.
14	-60.	794.	587.	336.	47.	1259.
15	-10.	302.	210.	134.	11.	1007.
total NS	-33915.	16294.	7190.	3900.	345.	6332.

b. all transport process contributions to the dissolved inorganic nitrogen budget.

box	initial content $kt\ N$	final content $kt\ N$	net horizontal advective flow $kt\ N\ a^{-1}$	net vertical advective flow $kt\ N\ a^{-1}$	vertical diffusive inflow $kt\ N\ a^{-1}$	vertical diffusive outflow $kt\ N\ a^{-1}$	river inflow $kt\ N\ a^{-1}$
1	256.	256.	-164.	418.	495.	-22.	0.
2	259.	260.	-45.	295.	1705.	-16.	0.
3	305.	306.	1297.	-762.	715.	-218.	0.
4	448.	449.	329.	8.	3056.	-46.	0.
5	417.	417.	-43.	-68.	1766.	-83.	0.
6	505.	505.	-190.	0.	0.	0.	15.
7	250.	250.	-104.	0.	0.	0.	87.
8	329.	329.	-424.	0.	0.	0.	384.
9	153.	153.	-216.	0.	0.	0.	182.
10	76.	76.	2.	0.	0.	0.	0.
11	783.	785.	59.	-418.	22.	-495.	0.
12	612.	613.	416.	-295.	16.	-1705.	0.
13	1589.	1591.	-1722.	762.	218.	-715.	0.
14	577.	577.	55.	-8.	46.	-3056.	0.
15	149.	149.	-37.	68.	83.	-1766.	0.
total NS	6708.	6715.	-785.	0.	8120.	-8120.	668.

c. budget contributions for particulate organic nitrogen.

box	net advective transport $kt\ N\ a^{-1}$	net vertical diffusion $kt\ N\ a^{-1}$	net sinking of algae and detritus $kt\ N\ a^{-1}$	net primary production $kt\ N\ a^{-1}$	plankton excretion $kt\ N\ a^{-1}$	excretion by fish $kt\ N\ a^{-1}$	uptake by fish $kt\ N\ a^{-1}$	river inflow $kt\ N\ a^{-1}$
1	10.	-165.	-571.	1460.	-725.	6.	-16.	0.
2	-201.	-921.	-816.	3047.	-1100.	6.	-16.	0.
3	34.	-240.	-824.	2027.	-985.	7.	-19.	0.
4	-246.	-1594.	-1503.	5112.	-1737.	20.	-53.	0.
5	77.	-627.	-1018.	2662.	-1076.	11.	-28.	0.
6	176.	0.	-486.	973.	-674.	15.	-8.	2.
7	15.	0.	-634.	1247.	-641.	18.	-12.	7.
8	-53.	0.	-934.	1725.	-849.	19.	-9.	100.
9	-5.	0.	-624.	1016.	-435.	17.	-14.	45.
10	-1.	0.	-287.	537.	-249.	10.	-10.	0.
11	122.	165.	223.	-249.	-262.	14.	-13.	0.
12	-161.	921.	205.	-463.	-512.	30.	-21.	0.
13	428.	240.	361.	-449.	-576.	17.	-24.	0.
14	-128.	1594.	218.	-734.	-924.	31.	-58.	0.
15	12.	627.	0.	-292.	-344.	7.	-10.	0.
total NS	79.	0.	-6690.	17621.	-11090.	227.	-309.	154.

boundaries; this means a flushing time of about six months (206 days). About $19000 \text{ kt}\cdot\text{a}^{-1}$ are exchanged between the boxes. Thus, the currents transport 8.5 times the winter nutrient content of the North Sea during one year. Again, the net advective transport, summed over the whole of the North Sea, is small. The North Sea gained only $89 \text{ kt}\cdot\text{a}^{-1}$ from the adjacent seas. This is the difference between the in- and outflow across the borders. Vertical advection redistributes $1153 \text{ kt}\cdot\text{a}^{-1}$ and vertical diffusion exchanges $4942 \text{ kt}\cdot\text{a}^{-1}$ between upper and lower layers. These transports correspond to half and 2.2 times the winter contents. The river input of ammonium of $104 \text{ kt}\cdot\text{a}^{-1}$ is small in comparison with the contents of the whole of the North Sea, viz. less than 5% of the contents.

In total, the winter content of ammonium is transported as often (10.8 times) as transformed (10.3 times) by gross primary production during one year. At the end of the year the total content is 2228 kt.

4.2.3. BUDGET FOR TOTAL NITROGEN

To judge the phosphorus transfers in relation to the transfers of nitrogen it is useful to make up the budget also for nitrate plus ammonium and for particulate nitrogen. Tables 3 and 7 give the budgets for dissolved inorganic and particulate nitrogen in the whole of the North Sea and in each of the boxes.

Nitrate plus ammonium sum up to about 6708 kt of total nitrogen nutrients dissolved in the water of the North Sea in winter. Particulate nitrogen in the North Sea is even larger, namely 7356 kt. The largest biotic flux is still gross algal uptake of $33915 \text{ kt}\cdot\text{a}^{-1}$. Respiratory release regenerates $16294 \text{ kt}\cdot\text{a}^{-1}$. Pelagic regeneration amounts to $7190 \text{ kt}\cdot\text{a}^{-1}$, and benthic regeneration to $6332 \text{ kt}\cdot\text{a}^{-1}$. Mesozooplankton excretion is only half of these amounts, namely $3900 \text{ kt}\cdot\text{a}^{-1}$. At the end of the year the content of nitrogen nutrients is 6715 kt.

Horizontal advection across the borders transports about $13108 \text{ kt}\cdot\text{a}^{-1}$ of dissolved inorganic nitrogen into and $13893 \text{ kt}\cdot\text{a}^{-1}$ out of the North Sea. The corresponding numbers for the particulate fraction are $3189 \text{ kt}\cdot\text{a}^{-1}$ and $3111 \text{ kt}\cdot\text{a}^{-1}$, respectively. Advection results in a loss of total nitrogen of $707 \text{ kt}\cdot\text{a}^{-1}$ from the North Sea. The river input consists of $658 \text{ kt}\cdot\text{a}^{-1}$ of dissolved inorganic and of $154 \text{ kt}\cdot\text{a}^{-1}$ of particulate nitrogen. It is thus of the same order of magnitude as the advective loss.

4.3. SILICON BUDGET

The budgets for silicon are given for the whole of the North Sea and each of the boxes in Tables 3 and 8.

The winter content of silicate in the North Sea is about 4986 kt, that of particulate silicon 603 kt. Dominant processes for the silicate budget are gross algal uptake of $21880 \text{ kt}\cdot\text{a}^{-1}$, benthic silicate regeneration

of $9597 \text{ kt}\cdot\text{a}^{-1}$, and algal respiratory release of $9028 \text{ kt}\cdot\text{a}^{-1}$. Gross uptake utilizes 4.4 times the winter content of the water of the North Sea. Net uptake is almost balanced by benthic regeneration. Algal excretion is $3015 \text{ kt}\cdot\text{a}^{-1}$. From regeneration of labile organic matter $270 \text{ kt}\cdot\text{a}^{-1}$ enter the silicate pool.

Advection of silicate across the borders into the North Sea sums up to about $11519 \text{ kt}\cdot\text{a}^{-1}$ and out of the North Sea to $11726 \text{ kt}\cdot\text{a}^{-1}$, yielding a flushing time of about 160 days and causing a net loss of $207 \text{ kt}\cdot\text{a}^{-1}$ from the whole of the North Sea, which is about 4% of the initial amount.

The amount of $45095 \text{ kt}\cdot\text{a}^{-1}$ of silicate is advected into the boxes. The advective inflow of particulate silicate into the North Sea is $2285 \text{ kt}\cdot\text{a}^{-1}$; the outflow is $2312 \text{ kt}\cdot\text{a}^{-1}$. Vertical advection redistributes $2886 \text{ kt}\cdot\text{a}^{-1}$ of silicate, and vertical diffusion mixes $8045 \text{ kt}\cdot\text{a}^{-1}$ between upper and lower boxes.

The river input sums up to $233 \text{ kt}\cdot\text{a}^{-1}$ of inorganic silicon and to $24 \text{ kt}\cdot\text{a}^{-1}$ of particulate silicon. The river input enters only boxes 7 to 9, i.e. the southern North Sea, where the big Atlantic inflows from the north do not go.

The difference in the contents at the end and at the beginning of the year is 21 kt for silicate and -3 kt for particulate silicon.

4.4. N:P RATIOS OF THE CONTRIBUTIONS TO THE BUDGETS

From the budget terms for inorganic nitrogen and for phosphate N:P ratios can be calculated for every single contribution to the budgets (Table 9). The annual bulk N:P ratios show regional differences for all processes.

Uptake has N:P ratios from 23 (box 1) to 18 (box 12). The coastal boxes have smaller N:P ratios (around 19.8) than the open sea surface boxes (about 21). The regional differences in the N:P ratio mirror the different proportions of diatoms and flagellates, sharing the nutrient pools. Bacterial excretion shows N:P ratios from 25 to 34, except for box 6 and the deep boxes (N:P from 16 to 23). Fish excretion shows N:P ratios of between 10 and 13.5 in boxes 6 to 15, but a fixed ratio of 9 in boxes 1 to 5. For zooplankton excretion N:P ratios from 18 to 95 are calculated. The N:P ratios for benthic mineralization range from 13 (box 13) to 15.5 (box 9).

The net transports have also varying N:P ratios, from 4 to 40, differing also between inflow and outflow for a certain box. Vertical diffusion, however, depending on the gradients across the thermocline, provides nutrients to the upper layer with an N:P ratio prevalent in the deep water, viz. about 16.

4.5. DIFFERENCES IN THE BUDGETS FOR N, P AND SI AND REGIONAL COMPARISON OF BUDGETS

The budgets for total phosphorus, total nitrogen and

TABLE 8
Budget for silicon for all boxes in 1988.
a. all biological process contributions to the dissolved silicate budget.

box	algae gross uptake $kt Si \cdot a^{-1}$	algae respiration release $kt Si \cdot a^{-1}$	algae excretion $kt Si \cdot a^{-1}$	benthic regeneration $kt Si \cdot a^{-1}$	labile organics $kt Si \cdot a^{-1}$
1	-803.	268.	17.	0.	10.
2	-2465.	804.	47.	0.	33.
3	-1622.	594.	15.	0.	20.
4	-5135.	1820.	162.	0.	68.
5	-3397.	1435.	159.	0.	44.
6	-1942.	1021.	13.	913.	20.
7	-1752.	843.	2.	933.	20.
8	-2652.	1273.	1.	1323.	29.
9	-1289.	528.	1.	793.	16.
10	-683.	299.	1.	363.	8.
11	-36.	36.	367.	387.	0.
12	-31.	31.	585.	788.	0.
13	-10.	10.	675.	672.	0.
14	-57.	57.	806.	1859.	0.
15	-8.	8.	164.	1567.	0.
total NS	-21880.	9028.	3015.	9597.	270.

b. all transport process contributions to the dissolved silicate budget.

box	initial content $kt Si$	final content $kt Si$	net horizontal advective flow $kt Si \cdot a^{-1}$	net vertical advective flow $kt Si \cdot a^{-1}$	vertical diffusive inflow $kt Si \cdot a^{-1}$	vertical diffusive outflow $kt Si \cdot a^{-1}$	river inflow $kt Si \cdot a^{-1}$
1	197.	197.	-254.	320.	457.	-13.	0.
2	187.	187.	-118.	222.	1483.	-4.	0.
3	233.	234.	817.	-630.	886.	-78.	0.
4	320.	322.	215.	57.	2860.	-42.	0.
5	295.	297.	46.	-37.	1989.	-234.	0.
6	380.	381.	-32.	0.	0.	0.	9.
7	187.	187.	-77.	0.	0.	0.	33.
8	245.	245.	-110.	0.	0.	0.	138.
9	110.	110.	-101.	0.	0.	0.	53.
10	56.	56.	13.	0.	0.	0.	0.
11	605.	608.	14.	-320.	13.	-457.	0.
12	441.	443.	332.	-222.	4.	-1483.	0.
13	1213.	1218.	-1155.	630.	78.	-886.	0.
14	413.	415.	215.	-57.	42.	-2860.	0.
15	106.	106.	-12.	37.	234.	-1989.	0.
total NS	4986.	5007.	-207.	0.	8045.	-8045.	233.

c. budget contributions for particulate silicon.

box	net advective transport $kt Si \cdot a^{-1}$	net vertical diffusion $kt Si \cdot a^{-1}$	net sinking of algae and detritus $kt Si \cdot a^{-1}$	net primary production $kt Si \cdot a^{-1}$	plankton excretion $kt Si \cdot a^{-1}$	river inflow $kt Si \cdot a^{-1}$
1	107.	-78.	-536.	517.	-10.	0.
2	-61.	-353.	-1167.	1614.	-33.	0.
3	151.	-86.	-1055.	1013.	-20.	0.
4	-232.	-328.	-2526.	3153.	-68.	0.
5	-25.	161.	-1895.	1802.	-44.	0.
6	20.	0.	-910.	907.	-20.	1.
7	39.	0.	-928.	907.	-20.	2.
8	-47.	0.	-1317.	1378.	-29.	15.
9	41.	0.	-790.	760.	-16.	6.
10	-14.	0.	-361.	383.	-8.	0.
11	139.	78.	148.	-367.	0.	0.
12	-147.	353.	378.	-585.	0.	0.
13	199.	86.	382.	-675.	0.	0.
14	-196.	328.	673.	-806.	0.	0.
15	-1.	-161.	326.	-164.	0.	0.
total NS	-27.	0.	-9579.	9838.	-270.	24.

total silicon differ in their structure. While particulate phosphorus and silicon account for 12 to 14% of the dissolved fraction in winter, particulate nitrogen is twice as much, namely 24% of the dissolved fraction in winter. When the fluxes integrated over the year are related to the initial winter content, it appears that advective transport amounts to 1.1 to 1.2 times the winter content for nitrogen, 2.3 to 2.4 times for phosphorus and 2.4 to 2.5 times for silicon. The river input is the same for all three elements, namely 5 to 6% of the total winter content. Uptake converts 1.25 times the winter content of nitrogen within one year, but 1.7 to 1.8 times the winter content of phosphorus and silicon. Sinking affects amounts of half the total winter nitrogen content, all winter phosphorus content and 1.7 times the winter silicon content. Benthic minerali-

zation returns the same amounts to the water within one year. On the spatial scale of the entire North Sea and the temporal scale of one year the fastest conversions occur for silicon, the slowest for nitrogen, when measured in relation to the winter contents of the elements.

The comparison of the budgets for the different regions shows remarkable differences, mainly determined by their morphology. As an example, consider Table 4 for the phosphate budgets for each of the boxes. The three types of hydrodynamically characterized boxes can be recognized again, the shallow coastal boxes, and, in the deeper North Sea, the surface and the deep boxes. The surface boxes in the deep North Sea have the gross algal uptake strongly fed by vertical diffusion of nutrients from the lower

TABLE 9
N:P ratios all boxes in 1988.
a. N:P ratios for biological budget contributions.

box	algae gross uptake	algae respiration release	microbial pelagic regeneration	meso-zooplankton excretion	fish excretion	benthic regeneration
1	22.8	7.8	34.1	62.7	8.9	-
2	21.4	8.5	32.8	94.6	8.9	-
3	21.7	7.7	31.0	72.5	8.9	-
4	20.6	6.6	29.6	82.1	8.9	-
5	19.8	5.8	25.1	55.1	8.9	-
6	18.6	5.6	18.3	46.9	13.2	13.3
7	19.7	5.6	24.8	54.1	12.9	14.1
8	19.3	5.1	25.3	51.0	13.4	14.6
9	19.8	5.4	26.5	58.2	12.3	15.5
10	20.0	5.9	26.3	63.0	12.0	15.4
11	17.5	4.1	16.0	23.2	12.1	13.5
12	17.9	4.2	16.5	39.7	12.7	14.1
13	17.7	4.0	15.0	18.1	10.9	12.8
14	18.7	4.2	19.7	46.1	10.1	14.2
15	19.6	4.5	22.5	49.6	10.9	13.9

b. N:P ratios for transport budget contributions.

box	initial content	final content	net horizontal advective flow	net vertical advective flow	vertical diffusive inflow	vertical diffusive outflow	river inflow
1	15.6	15.6	10.6	15.8	14.1	17.5	-
2	15.7	15.7	9.6	15.8	16.2	43.5	-
3	15.9	15.9	17.7	16.3	14.7	30.2	-
4	16.4	16.5	18.2	6.6	16.5	37.9	-
5	17.4	17.4	25.4	19.6	16.4	19.7	-
6	16.0	16.0	17.0	-	-	-	44.0
7	17.6	17.6	16.5	-	-	-	20.2
8	18.2	18.2	32.7	-	-	-	34.5
9	18.5	18.5	39.3	-	-	-	51.8
10	16.9	16.9	3.8	-	-	-	-
11	15.5	15.6	12.6	15.8	17.5	14.1	-
12	15.6	15.7	14.9	15.8	43.5	16.2	-
13	15.9	15.9	16.3	16.3	30.2	14.7	-
14	16.4	16.5	5.5	6.6	37.9	16.5	-
15	17.4	17.4	15.8	19.6	19.7	16.4	-

boxes. About 40% of gross uptake is released by algal respiration again. The regenerative activities of the small heterotrophs provide up to 7 to 15% of gross algal uptake. The lower boxes (11, 12, 14 and 15) in the deep provide nutrients to the upper ones; their loss is partly replenished by benthic regeneration, partly by algal respiratory release and by the microbial web activity. In the shallow boxes 6 to 10 large parts of the net nutrient uptake by algae is replenished by benthic regeneration. The microbial loop is the third important source of phosphate, compared to the annual amounts.

The percentages of any flux in relation to the winter content show strong regional variations. Not even within each of the three groups of boxes do the same dynamics prevail. For instance, nutrient uptake in the ten upper boxes transforms between 3.4 times (box 6) and 14.7 times (box 4) the winter amount of phosphate; in the continental coastal boxes this ratio varies from 8.2 to 10.5. Vertical diffusion transports between 12 times (box 15) and 0.4 times (box 13) the winter amount of phosphate in the box. Gross advection transports even 5 times (box 14, 15) to 24 times (box 10) the initial content through the respective box, and even the net flows transport between 13% and 137% of the initial contents into or out of a box. The inflows across the boundaries are also rather variable and provide several times the initial content, e.g. 4.7 times for box 1 and 6.7 times for box 11.

While the northern boxes 2 and 12 gain PO_4 from the Atlantic, boxes 4, 14 and 10 gain PO_4 from interior boxes by advective transport. Boxes 5 to 9 lose PO_4 thus levelling off the gradients fed by river input, and the deep boxes 11 and 13 serve as sinks for the whole of the North Sea: The North Sea is fertilized from the Atlantic and from the coastal zones, and primary production incorporates the nutrients at maximum rates in the central North Sea (boxes 2, 4 and 5) and in the continental coastal areas (boxes 8 to 10). The central North Sea (boxes 2 and 4), with the highest net phosphate gain (303 and 450 $\text{kt}\cdot\text{a}^{-1}$, resp.) exhibits the highest PO_4 uptake (13.3 and 14.7 times the initial value, resp.). In the upper boxes 1 to 5 microbial regeneration of PO_4 is always the main regeneration mechanism, but it is of less importance than diffusive transport into the upper layer. Where benthic regeneration occurs (boxes 6 to 15), pelagic microbial regeneration is usually less important. In all boxes the mesozooplankton excretion is of minor importance as a regenerative mechanism.

The budget for dissolved inorganic nitrogen shows similar features. In addition to vertical diffusion, pelagic and benthic regeneration and uptake, provides zooplankton an important contribution, viz. 5% to 10% of the amount for gross uptake. Here the small heterotrophs provide between 15% and 23% of algal uptake on an annual basis. While gross nitrogen uptake varies from 9.4 times (box 10) to 82 times (box 4) the winter content in the upper boxes, the excretion

by smaller heterotrophs results in 1.5 to 10.4 times the winter content and that by zooplankton 1 to 7 times.

From all budgets we learn that they are dominated by regional, i.e. box-specific processes, and that horizontal advective transports of nutrients are of second-order importance, modulating the regional budgets and imposing additional regional characteristics.

Several models for the North Sea exist, which could in principle be used to evaluate fluxes of nutrients (Fransz & Verhagen, 1985; Radach & Moll, 1993; Van den Berg *et al.*, 1995). Radach & Moll (1993), simulating the primary production and its variability in the central North Sea by using 25 annual cycles of meteorological driving functions, were able to give ranges for the flow of phosphate within the water column for a number of processes, ending the trophic hierarchy at herbivorous zooplankton. One of the main results was that the nutrients taken up by algae amount to 2.6 to 3.2 times the winter concentration of that layer which in summer is situated above the seasonal thermocline. This is far less than estimated for single boxes by ERSEM.

5. DISCUSSION

Eutrophication is an ongoing process in the coastal waters, especially along the continental coast (Nelissen & Stefels, 1988; Radach, 1992). As the nutrients form one of the basic essentials for primary production, it is important to assess the effects of continuous, if not increased, anthropogenic nutrient loads. Do they lead to a persistently increased primary production, which —when the algae are decaying in massive amounts— may cause severe oxygen depletion in the deeper layers of the coastal seas and may thus damage the ecosystem, as was observed occasionally by Von Westernhagen *et al.* (1986)? Only from model simulations can we estimate how much of the large amounts of nutrients flowing through the North Sea ecosystem will remain in the North Sea or be exported across its open boundaries to the Atlantic Ocean and possibly to the Baltic Sea. In this section we discuss to which degree ERSEM can serve to improve the understanding of the nutrient dynamics. The model simulation has not been manipulated to yield a best fit to the observations, but to produce the ecosystem dynamics on the basis of state-of-art knowledge about the North Sea ecosystem. The results concerning the nutrients are compared with available observations to determine the strengths and weaknesses of the results.

5.1. COMPARISON OF ANNUAL CYCLES WITH OBSERVATIONS

The coincidence of simulated and observed dissolved inorganic nutrient cycles is of different quality for the different state variables and different regions.

Phosphate concentrations in the central North Sea boxes (4, 5 and 15) and in the coastal boxes (7, 8 and 9) start close to the observed mean winter value, but decrease too slowly in spring and reach only 30 to 50% of the observed value, e.g. in May. Concentrations are partly lower than observed in summer, and they recover faster in autumn than observations show (e.g. in boxes 2, 3 and 15). Generally speaking, the simulated annual signal is more pronounced than the observed one at any time of the year (Fig. 3). The concentrations in the coastal areas (boxes 6 to 9), but also in the deep boxes (1 to 3, 11 to 13) fit well into the observed ranges for most of the months. There is also a tendency for a slow spring decay (e.g. in box 8). In general phosphate concentrations are well simulated.

For nitrate (Fig. 4) the annual cycles in the deep boxes 1 to 3, 11 and 12 are well simulated, but the starting values for the central North Sea boxes (4, 5, 14 and 15) and for the coastal boxes (7 and 8) were about a factor of two higher than observed. Therefore, until spring the concentrations are much higher than observed; moreover they increase slightly by advection and, in April, by regenerative processes. Decay in spring is insufficient to reduce concentrations to those observed in May, June and July. Depletion is accomplished in August. The concentrations are driven to higher values already in October, while observations remain at a lower level. The coastal areas (boxes 7 to 9) exhibit a large observational variability in nitrate values, which is well simulated for box 9; the decay in May and June in box 8 is not reproduced. The concentrations in the northern British coastal areas (box 6), showing small observational variability per month, suffer also from insufficient spring decay. Thus the nitrate concentration pattern in the North Sea is not so well simulated as phosphate by ERSEM.

Observed ammonium concentrations (Fig. 5) are low all year round in all areas, except for boxes 8 and 9. The Scottish coastal waters (box 6) and the Dutch coast (box 8) are the only areas where the simulations nearly fit the data ranges, not least because of the large observational ranges. Everywhere else the simulated concentrations are higher by a factor of 2 to 4 from January to April and from July to December. It is only in May and June that the simulation in nearly every area drops to the observed low concentration level. The reason may lie in the high initial values, but on the other hand ammonium dynamics build up the high concentrations again in summer and autumn, after a full depletion phase. This state variable seems not to be properly simulated. Regeneration and excretion processes of ammonium, causing these dynamics, are further discussed in Ruudij & Van Raaphorst (1995) and Varela *et al.* (1995). Probably the process of nitrification in the water is not modelled properly.

The simulation starts with too high silicate values in

the central North Sea (boxes 4, 5 and 15) and some coastal areas (boxes 7 and 8), compared to the data ranges (Fig. 6). This high level extends until April; after that the spring bloom depletes the silicate pool very efficiently, and the simulation and the observations coincide quite well for all boxes, for which data are available.

The extremely high maximum values of the N:P ratio follow from the fact that nitrate concentrations do not decrease fast enough or at least exhibit a phase shift compared to observations in spring, and therefore the concentration remains too high in June and July. Observed mean N:P ratios in the German Bight are 37, 6, 3 for June, July and August, as obtained from BODC data.

Summarizing, the annual cycles for the dissolved inorganic nutrient concentrations of phosphate and silicate compare well with the observed ranges of variability. For nitrate the simulation fails to reproduce the observations in the central and the coastal North Sea. For ammonium a coincidence with data ranges is very rare. The spring decrease is generally too slow.

5.2. COMPARISON OF NUTRIENT INVENTORY FROM ERSEM WITH ESTIMATES FROM DATA ANALYSIS

The nutrient contents in the surface and deep boxes are given in Fig. 13 during the winter half year (1 November - 31 March) and the summer half year (1 April - 31 October). Also the difference in the contents of the upper boxes is given between 'winter' and 'summer' contents, to enable a comparison between earlier estimates of nutrient depletion and primary production estimates given by Radach *et al.* (1990a) and Radach (1992).

For phosphate ERSEM yields a winter content of 911 kt P in 1988, compared to an estimate from data of 843 kt P, which is about 8% more phosphate in the model. In the upper 30 m of the whole of the North Sea the estimates from data (355 kt P) and from the model (356 kt P) are practically the same. However, the summer content in the model is 148 kt P, which is about 24% more than the 119 kt P estimated from data. Thus in general the North Sea loses too little phosphate from winter to summer (206 kt in the model simulation compared to 236 kt estimated from data).

For nitrate the estimate from data yields a 'winter' content of 5146 kt $\text{NO}_3\text{-N}$, which is 11% higher than the model contents of 4636 kt N. However, the difference between 'winter' values for the upper 30 m (2134 kt N estimated from data, 1800 kt N from the model) and summer values (344 kt N from data, 827 from ERSEM) is much smaller in the model, viz. less than 54% of the difference from data analysis. Thus, the summer depletion is estimated to be much stronger from data analysis than from the ERSEM model.

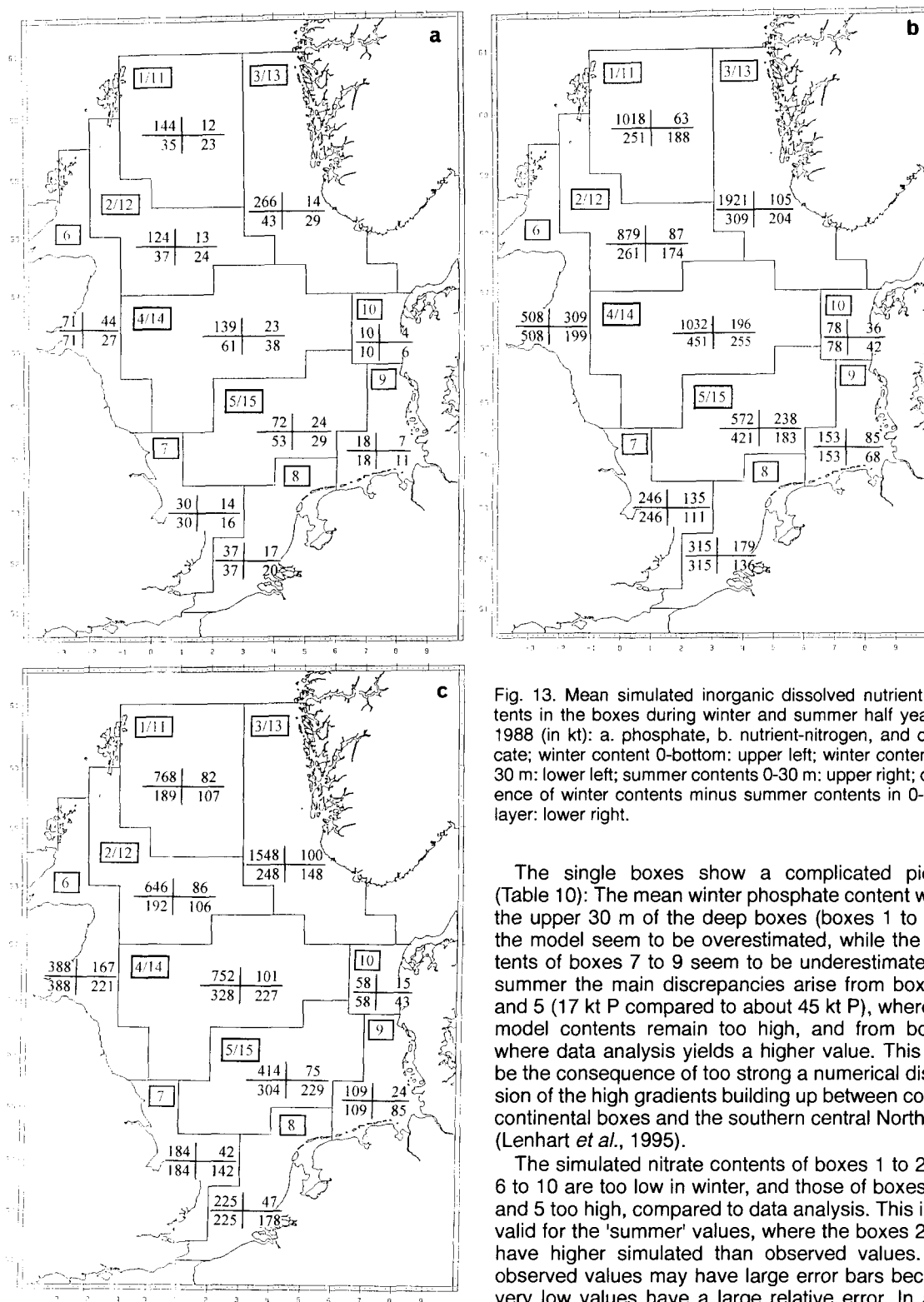


Fig. 13. Mean simulated inorganic dissolved nutrient contents in the boxes during winter and summer half years of 1988 (in kt): a. phosphate, b. nutrient-nitrogen, and c. silicate; winter content 0-bottom: upper left; winter contents 0-30 m: lower left; summer contents 0-30 m: upper right; difference of winter contents minus summer contents in 0-30 m layer: lower right.

The single boxes show a complicated picture (Table 10): The mean winter phosphate content within the upper 30 m of the deep boxes (boxes 1 to 5) in the model seem to be overestimated, while the contents of boxes 7 to 9 seem to be underestimated. In summer the main discrepancies arise from boxes 4 and 5 (17 kt P compared to about 45 kt P), where the model contents remain too high, and from box 8, where data analysis yields a higher value. This may be the consequence of too strong a numerical dispersion of the high gradients building up between coastal continental boxes and the southern central North Sea (Lenhart *et al.*, 1995).

The simulated nitrate contents of boxes 1 to 2 and 6 to 10 are too low in winter, and those of boxes 3, 4 and 5 too high, compared to data analysis. This is not valid for the 'summer' values, where the boxes 2 to 9 have higher simulated than observed values. The observed values may have large error bars because very low values have a large relative error. In addition, the estimates from data analysis may be biased

TABLE 10

Mean contents of phosphate and nitrate (in kt) in the surface layer (0-30 m) and in the whole water column (0-bottom) during winter and summer. Values calculated from observations (in table: data) and from ERSEM simulations (1988 and 1989)

<i>phosphate</i>										
<i>surface layer</i>							<i>water column</i>			
<i>box</i>	<i>winter</i>			<i>summer</i>			<i>box</i>	<i>winter</i>		
	<i>data</i>	<i>sim. '88</i>	<i>sim. '89</i>	<i>data</i>	<i>sim. '88</i>	<i>sim. '89</i>		<i>data</i>	<i>sim. '88</i>	<i>sim. '89</i>
1	30	35	35	12	12	14	1 + 11	122	144	143
2	31	37	36	16	13	13	2 + 12	105	124	123
3	35	43	42	11	14	14	3 + 13	246	266	264
4	49	61	60	12	23	22	4 + 14	112	139	137
5	35	53	52	5	24	22	5 + 15	47	72	71
6	35	32	32	18	20	19	6	72	71	70
7	42	30	31	11	14	13	7	42	30	31
8	66	37	38	26	17	16	8	66	57	38
9	24	18	18	7	7	6	9	24	18	18
10	7	10	10	2	4	3	10	7	10	10
sum	355	356	354	119	148	142	sum	843	911	905

<i>nitrate</i>										
<i>surface layer</i>							<i>water column</i>			
<i>box</i>	<i>winter</i>			<i>summer</i>			<i>box</i>	<i>winter</i>		
	<i>data</i>	<i>sim. '88</i>	<i>sim. '89</i>	<i>data</i>	<i>sim. '88</i>	<i>sim. '89</i>		<i>data</i>	<i>sim. '88</i>	<i>sim. '89</i>
1	200	189	187	78	50	58	1 + 11	817	765	759
2	190	185	182	26	67	65	2 + 12	648	622	610
3	212	220	219	20	79	78	3 + 13	1615	1365	1359
4	251	297	289	5	134	126	4 + 14	572	678	661
5	215	265	262	42	145	150	5 + 15	237	359	355
6	187	142	154	14	99	94	6	378	345	338
7	239	158	162	32	81	87	7	239	158	162
8	463	201	210	65	106	121	8	463	201	210
9	125	94	96	29	47	50	9	125	94	96
10	52	49	49	33	19	17	10	52	49	49
sum	2134	1800	1810	344	827	846	sum	5146	4636	4599

by spatial heterogeneity in the data which may favour summer data off the coasts.

Comparing the simulated N:P ratios (Table 11) for the summer and winter half years, it can be seen that the 'winter' N:P ratios of slightly below 16 (boxes 1 to 3, 11 to 13) or above 16 (boxes 5, 7 to 9 and 15) or equal to 16 (boxes 4, 10 and 14) differ from those in summer. Only the deep water (boxes 11 to 13) does not change its composition. In the model simulation the northern North Sea (boxes 1 and 2) exhibits N-limitation (N:P=6 or 11), while all other areas except box 6 deviate strongly in the direction of P-limitation. The overall N:P ratios increase from the north down the British coast, anticlockwise around the North Sea, with a maximum in the German Bight (N:P=46). Also the central North Sea is affected: In box 4 we find N:P=31, in box 5 N:P=36, more than in the continental coastal strip off Belgium and The Netherlands. This pattern was already observed in the discussion

of the annual cycles of the N:P ratios, and it can also be detected in the bulk differences between the winter and summer half years. The pattern can be interpreted as the combined effect of northern inflow with N:P ratios of a little less than 16 and the river input from the continent, which has N:P ratios of 35 (rivers entering box 8) to 52 (rivers entering box 9).

To summarize, there are three possibilities (which do not exclude each other) to explain the considerable discrepancies between model and data derived estimates of box contents: First, the estimates from data may not be correct, for instance because the low nutrient concentrations in the data set are not fully representative of the area; this is not very likely. Secondly, the discrepancy between model results and validation data is a consequence of the initial and boundary conditions prescribed. In addition, nitrate starting levels are certainly too high in boxes 4, 5, 14 and 15. As these values are simulation results they

TABLE 11

N:P ratio for summer and winter mean contents of the boxes.

box	summer content	winter content
1	5.9	15.6
2	10.9	15.6
3	21.1	16.0
4	30.7	16.3
5	36.0	17.6
6	15.7	15.8
7	26.8	18.0
8	26.6	18.9
9	46.3	18.9
10	29.7	17.2
11	15.1	15.6
12	15.6	15.6
13	15.6	15.9
14	19.6	16.3
15	30.3	17.6
mean	19.2	16.8

may be partly an effect of too strong a levelling off of the gradients between coastal areas and the central North Sea (Lenhart *et al.*, 1995). Thirdly, the mechanism of nutrient removal in the model is too weak. The effect can be seen from both the phosphate and the nitrate content. The last possibility is the most likely (Ruurdij & Van Raaphorst, 1995).

5.3. DEPENDENCE OF NUTRIENT DYNAMICS ON THE FORCING

5.3.1. FORCING BY LONG-TERM MEAN CURRENTS

The simulations depend to a certain degree on the realization of the transport terms. To get an impression of this dependence the simulation was repeated with modified physical forcing. First, instead of daily advective rates, temporal mean rates were introduced, averaging the flow fields for the 11 years 1982 to 1992, resulting in an identical current velocity field for each day. The resulting budget terms resemble those obtained from the standard run within 23% at the maximum. Again, local biological and chemical transformations together with vertical diffusion determine, to a large degree, the dynamics in each of the regions.

The in- and outflow driven by annually averaged water transports is reduced by about 5% for the deep northern boxes compared to about 15% for the shallow coastal boxes 7 to 9, where strong gradients build up against their neighbouring boxes. This effect is due to the stronger dispersive action of daily currents. This is in accordance with the results of the model FYFY (Van den Berg *et al.*, 1995) on a finer spatial scale (about 20 km), which gave higher nutrient concentrations in annually averaged current fields than in daily currents.

As an example we present the contributions of all the processes of the phosphate budget in Table 12. These values have to be compared to those given in Table 4. Net transports change between 8% and 23%. The processes most affected are gross horizontal and vertical advective transports, both of which are about 11 to 13% less in this run than in the runs with the specific current field for 1988. Note that the biological transformations are only marginally affected by about 1 to 3%.

5.3.2. LOCAL DYNAMICS

The standard run was then repeated without any horizontal and vertical advection, thus treating the box water columns as isolated from each other, but maintaining vertical diffusive exchange across the interfaces at 30 m. This run allows us to estimate the role of horizontal water transports for the budgets.

When comparing the phosphate budgets for this run (Table 13) with those of the standard run (Table 4), the biological transformations turn out to be modified. For instance phosphate uptake is lower in boxes 1 to 3 by 11% to 23% in case of local dynamics, showing that production in these boxes is dependent on the Atlantic inflow of nutrients. Production in the central North Sea and in the continental coastal boxes 4 to 10 is enhanced only by about 2% to 5%, except for box 6 (22%) and box 8 (15%). In box 8 the benthic regeneration is increased. The structure of the annual cycles is also altered. Without advection the phosphate concentration dropped more rapidly in spring, but later than in the standard run.

5.3.3. TEMPORAL VARIABILITY

When implementing daily varying water transports, we hoped to introduce a major source for observed biological variability, because in certain areas and at certain times of the year transports depend strongly on the meteorological conditions, and effective vertical diffusion of nutrients depends on wind activity combined with strong vertical gradients of nutrients. Thus the weather should be an important agent causing algal blooms at different times in the two years simulated (1988 and 1989). The differences between the two years are noticeable, but in general relatively small, which was to be expected when using the same boundary condition for both years. The general features are the same, but events occur which are differently distributed within each year, and time shifts occur of the temporal developments.

Nutrient transports depend on the meteorological conditions. For relatively small amounts of horizontal advective nutrient transports the interannual variability solely due to physical transport may reach a factor of two. The simulations for the years 1988 and 1989 show that the outflow from the lower box 13 into the Baltic of $100.6 \text{ t} \cdot \text{d}^{-1}$ in 1988 may change to an inflow

TABLE 12
Budgets for phosphorus for all boxes in 1988 with mean annual advective forcing.
a. all biological process contributions to the budget.

box	algae gross uptake $kt P \cdot a^{-1}$	algae respiration release $kt P \cdot a^{-1}$	microbial pelagic regeneration $kt P \cdot a^{-1}$	meso-zooplankton excretion $kt P \cdot a^{-1}$	fish excretion $kt P \cdot a^{-1}$	benthic regeneration $kt P \cdot a^{-1}$
1	-253.	104.	38.	6.	2.	0.
2	-504.	184.	43.	11.	2.	0.
3	-366.	146.	48.	11.	3.	0.
4	-884.	329.	78.	19.	8.	0.
5	-509.	210.	58.	17.	4.	0.
6	-233.	120.	47.	14.	4.	75.
7	-255.	117.	34.	11.	5.	93.
8	-360.	166.	46.	15.	5.	134.
9	-194.	79.	23.	6.	5.	87.
10	-106.	45.	13.	4.	3.	40.
11	-3.	38.	35.	3.	4.	54.
12	-3.	62.	46.	10.	8.	85.
13	-1.	64.	82.	9.	6.	78.
14	-7.	100.	66.	17.	10.	204.
15	-1.	38.	21.	6.	2.	169.
total NS	-3680.	1801.	677.	158.	70.	1018.

b. all transport process contributions to the budget.

box	initial content $10^3 t$	final content $10^3 t$	net horizontal advective flow $kt P \cdot a^{-1}$	net vertical advective flow $kt P \cdot a^{-1}$	vertical diffusive inflow $kt P \cdot a^{-1}$	vertical diffusive outflow $kt P \cdot a^{-1}$	river inflow $kt P \cdot a^{-1}$
1	36.	37.	-21.	52.	76.	-3.	0.
2	37.	37.	4.	33.	228.	-1.	0.
3	42.	43.	153.	-88.	101.	-9.	0.
4	60.	62.	69.	-23.	407.	-1.	0.
5	53.	55.	-2.	-11.	242.	-8.	0.
6	70.	70.	-28.	0.	0.	0.	1.
7	31.	32.	-13.	0.	0.	0.	10.
8	40.	41.	-27.	0.	0.	0.	25.
9	18.	19.	-13.	0.	0.	0.	8.
10	10.	10.	2.	0.	0.	0.	0.
11	111.	113.	-2.	-52.	3.	-76.	0.
12	86.	87.	55.	-33.	1.	-228.	0.
13	221.	225.	-229.	88.	9.	-101.	0.
14	78.	79.	-5.	23.	1.	-407.	0.
15	19.	19.	-11.	11.	8.	-242.	0.
total NS	912.	929.	-68.	0.	1076.	-1076.	43.

of $3.6 t \cdot d^{-1}$ in 1989. From the central North Sea (lower box 14) about $43 t \cdot d^{-1}$ of phosphate enter the Scottish coastal waters (box 6) in 1988, whereas in 1989 about $122 t PO_4-P \cdot d^{-1}$ leave box 14 to box 6. Even the largest transports of nutrients change from 1988 to 1989 by about 7%: about $2589 t \cdot d^{-1}$ of phosphate leave the Norwegian Trench to the north in 1988 in the deep water, whereas in 1989 the amount is $192 t \cdot d^{-1}$ larger.

Especially vertical diffusive transport is dependent on weather events. For instance in the phosphate

cycle, a sharp increase in concentration in box 2 occurred in September 1988, whereas in 1989 there was no such increase. However, in 1989 a similar event occurred in box 1 in May, which did not happen in 1988. Such peaks are caused by injections of nutrients from the lower layer created by wind events which enforce vertical turbulent transport of nutrients into the upper layer (Fig. 12). They may double the nutrient concentration in the upper layer within one day.

In the deep northern areas the difference in nutrient

TABLE 13
Budgets for phosphorus for all boxes without horizontal and vertical advection (local dynamics).
a. all biological process contributions to the budget.

box	algae gross uptake $kt P \cdot a^{-1}$	algae respir. release $kt P \cdot a^{-1}$	microbial pelagic regeneration $kt P \cdot a^{-1}$	meso-zooplankton excretion $kt P \cdot a^{-1}$	fish excretion $kt P \cdot a^{-1}$	benthic regeneration $kt P \cdot a^{-1}$
1	-189.	87.	33.	0.	0.	0.
2	-447.	184.	46.	7.	2.	0.
3	-296.	129.	43.	4.	2.	0.
4	-899.	351.	77.	19.	8.	0.
5	-516.	218.	56.	16.	4.	0.
6	-280.	160.	36.	9.	3.	80.
7	-268.	124.	36.	11.	5.	93.
8	-415.	188.	51.	18.	5.	157.
9	-199.	81.	24.	7.	5.	77.
10	-108.	47.	13.	4.	3.	43.
11	-5.	34.	22.	0.	2.	28.
12	-2.	63.	50.	6.	7.	81.
13	-1.	35.	48.	3.	3.	44.
14	-6.	114.	69.	16.	11.	282.
15	-1.	40.	20.	6.	2.	151.
total NS	-3630.	1857.	624.	125.	61.	1037.

b. all transport process contributions to the budget.

box	initial content $10^3 t$	final content $10^3 t$	net horizontal advective flow $kt P \cdot a^{-1}$	net vertical advective flow $kt P \cdot a^{-1}$	vertical diffusive inflow $kt P \cdot a^{-1}$	vertical diffusive outflow $kt P \cdot a^{-1}$	river inflow $kt P \cdot a^{-1}$
1	36.	39.	0.	0.	73.	-1.	0.
2	37.	35.	0.	0.	208.	0.	0.
3	42.	45.	0.	0.	121.	0.	0.
4	60.	79.	0.	0.	466.	-3.	0.
5	53.	49.	0.	0.	227.	-8.	0.
6	70.	79.	0.	0.	0.	0.	1.
7	31.	41.	0.	0.	0.	0.	10.
8	40.	69.	0.	0.	0.	0.	25.
9	18.	21.	0.	0.	0.	0.	8.
10	10.	12.	0.	0.	0.	0.	0.
11	111.	120.	0.	0.	1.	-73.	0.
12	86.	83.	0.	0.	0.	-208.	0.
13	221.	234.	0.	0.	0.	-121.	0.
14	78.	101.	0.	0.	3.	-466.	0.
15	19.	18.	0.	0.	8.	-227.	0.
total NS	912.	1025.	0.	0.	1106.	-1106.	43.

uptake between 1988 and 1989 is considerable: while weather conditions lead to one algal bloom in spring 1988, two distinct spring blooms occur in 1989 in boxes 1 and 2. The interannual variation of nutrient regeneration from the benthic, induced solely by the hydrodynamical differences between the two years, is largest in summer at the maximum of the regeneration activity (up to about 20% of the maximum value).

Although physical variability creates some biological variability, the overall quantities of annual budgets are affected only marginally. To compare the simulated annual cycles to observations there is no need

to discriminate between the simulations for 1988 and 1989, because they are fairly similar in relation to the ranges of observed variability. Thus the ecosystem model seems to buffer the physical variability.

The impact of the physical variability on the biological system has been studied using one-dimensional ecological simulation models. The effects of short term meteorological forcing on the pelagic plankton system of the central North Sea was recently investigated by Radach & Moll (1990, 1993), who have driven a one-dimensional plankton model by forcing functions derived from three-hourly standard meteor-

ological measurements over 25 years. The resulting 25 annual cycles of mixed layer depths compare well with observations. It was shown that the plankton dynamics in the one-dimensional model were largely dependent on the physical situation in the water column, especially on the turbulent mixing intensity. The simulations with the differential one-dimensional physical upper layer model yield time-dependent profiles of turbulent diffusion intensity in the form of local mixing coefficients, which serve as forcing fields in the plankton model, determining the vertical distribution of the plankton and thus deciding about the relation of production to respiration, within the whole water column, *i.e.* gain or loss of phytoplankton biomass. Radach & Moll (1993) found that although the phytoplankton blooming events occurred at different times within these 25 years, the cumulative primary production was similar for all 25 years, in spite of the relatively large physical variability, especially during spring (see fig. 16 in Radach & Moll, 1993). The biological model system seemed to buffer the physically imposed variability on the annual time scale. This supports the findings from ERSEM.

A comparison of the one-dimensional model simulation results and observed time series revealed that natural variability appeared to be larger than the simulated, especially on time scales of less than one year. It seemed that circulation contributed to the biological variability observed at a fixed station such as Helgoland (Radach *et al.*, 1990b) by moving horizontal inhomogeneities through the point of observation. Thus, the observations showed a much larger variability than has been modelled. So far the large natural variability has not yet been reproduced by any model we know of.

The ERSEM model is far more complex than the model by Radach & Moll (1993), and we can argue that there must be internal mechanisms in nature that create variability, which are not existent in this ecosystem model or have not yet been activated by the variability of the physical forcing alone.

There are, however, several sources of variability that have not yet been included in ERSEM. River discharge is an important source of variability in coastal areas. The Elbe discharge has a weakly varying mean annual cycle; the variability, however, is large (see fig. 3 in Radach *et al.*, 1986; Radach *et al.*, 1990b). Single discharge events dominate the annual cycles. This variability acts together with direct meteorological variability on the North Sea circulation. In the ERSEM simulations presented river input was only included as monthly means.

One further possible agent could be the highly variable solar radiation, which should replace the smooth formulation of radiation used so far in ERSEM. Actual solar radiation at the sea surface depends on cloudiness and thus on the weather. Moll & Radach (1990) have shown the considerable variability of heat and radiative fluxes at LV ELBE 1 in the German Bight for

the years 1962 to 1986. To activate the mechanisms in ERSEM which could transform temporal physical variability into biological variability it seems to be necessary to use smaller regional units that include the spatial variability of radiation to a certain degree.

6. CONCLUSIONS

The comparison of model results with data shows that some features of the model results are realistic, but not all. The annual cycles of the nutrients phosphate and silicate compare quite well with the observed ranges of variability. This does not hold for ammonium and nitrate. The spring decrease is, however, generally a little too slow for all nutrients. Local biological and chemical transformations together with vertical diffusion largely determine the nutrient dynamics of the ecosystem in each of the regions. The biologically mediated transformations of nutrient uptake and pelagic and benthic regeneration of nutrients are the most important processes in changing the nutrient concentrations. The nutrient uptake by algae may recycle phosphate up to 4 times per year and nitrogen up to 10 times per year, compared to the winter content of nutrients in the water, according to the simulation. The percentages vary strongly regionally. The higher trophic levels play a minor role in nutrient dynamics, as sources for nutrients through excretion, comparable to vertical advection in magnitude. The budgets for the four nutrients support the findings from the simulated annual cycles.

The horizontal advective contributions turn out to modify these local dynamics. Vertical advection and vertical diffusion have a clear seasonal signal, with a maximum in February. The decay of the advective nutrient transport in summer is caused by the depletion of the upper layer from nutrients due to algal uptake. The inflow of nutrients in the northwest is nearly balanced by the outflow in the northeast, without causing strong nutrient transports into the shallower areas from the north. However, from the coastal areas there is nutrient flow towards the central North Sea. The nutrient flow from the north and from the coastal zones into the central North Sea leads to an enhanced algal production there. Possibly the nutrient flow from the continental coastal zone into the central North Sea is overestimated because of the relatively high intrinsic numerical diffusion of the box setup. A refinement of the boxes would allow us to obtain more reliable estimates of this nutrient flux perpendicular to the continental coast. The simulation without horizontal advection (section 5.3.2.) shows that the advective and diffusive flows cannot be neglected when aiming at a model simulation for the whole of the North Sea that will bring out the regional differences.

We also present the nitrogen budgets (although the state variables nitrate and ammonium are not well simulated) in addition to those for phosphorus and

silicon to give the orders of magnitude of the fluxes involved. We believe that these fluxes will not be totally altered by improving the coincidence of simulated nitrogen nutrients with observations.

The budgets for phosphorus, nitrogen and silicon show that the particulate fraction of total P, N and Si in winter, at the beginning of the simulation, is 13%, 52% and 11% of total P, N and Si, respectively. In the river input the particulate fraction is 34%, 18% and 10%, respectively. Compared to the internal cycling activity, the net effect of horizontal transport is small during the growing season. River input seems small, but as a permanent source over the last 50 years it has created the conditions under which the high nutrient transformations as given in the budgets take place.

A basic feature of all budgets is that the advective import and export across the boundaries of the North Sea nearly cancel each other for all compounds. The net effect of transport is marginal for the whole of the North Sea under the given model setup and boundary conditions. Note that no atmospheric input of phosphorus and nitrogen has been included in the simulation. The atmospheric N input of about $577 \text{ kt} \cdot \text{a}^{-1}$ (Radach, 1992) might have a noticeable effect on the dynamics.

The N:P ratios for the observed winter and summer contents of nutrients in the boxes support the findings that the northern North Sea is nitrogen limited. Under the given boundary constraints, which hold for the late 1980s, the simulation shows that the North Sea is widely governed by phosphate limitation in summer, except for the very north, where nitrogen limitation occurs. However, in the light of the available data this statement has to be considered with great caution. The question which nutrient limits primary production when in which area cannot be answered by the present model setup.

An improvement of the model results compared to observations can be obtained by 1. refining the box structure, to reduce the artificial diffusivity and to better resolve spatial gradients along the continental coast, 2. improving the estimates of input by rivers and at the northern and southern boundaries of the North Sea and by introducing atmospheric N input, 3. a more realistic light forcing of primary production by including cloudiness in the formulation of radiation, and 4. improving the description of nitrification in the water.

Such modifications will result in a much more reliable simulation which should also contain more of the observed temporal and spatial variability now damped out.

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