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MODELLING PRIMARY PRODUCTION IN THE NORTH SEA USING THE EUROPEAN REGIONAL SEAS ECOSYSTEM MODEL

RAMIRO A. VARELA, ANTONIO CRUZADO and JESÚS E. GABALDÓN

Centre d'Estudis Avançats de Blanes, Camí de Santa Bàrbara s/n, E-17300 Blanes (Girona), Spain

ABSTRACT

The primary production module incorporated in the European Regional Seas Ecosystem Model (ERSEM) is described in detail. It considers two phytoplankton groups, diatoms and autotrophic flagellates, and four different nutrients: nitrate, ammonia, phosphate and silicate (only for diatoms). All the related state variables and fluxes are represented in terms of carbon, nitrogen, phosphorus and silicon.

The potential carbon growth rate process is estimated by considering that nutrient availability acts as a limitation factor on the maximum growth rate which is itself a function of light and water temperature. Respiration, excretion of organic matter, lysis and sinking are the main carbon and nutrient loss processes. Results indicate that the model simulates well the annual phytoplankton dynamics in the central regions of the North Sea, underestimating primary production and chlorophyll in the southern North Sea. The model gave good correlations with the main dissolved nutrients, such as silicate, phosphate or nitrate. The primary production module proved to be especially sensitive to the flagellate/diatom interaction and competitive behaviour for inorganic nutrients as well as with regard to grazing losses. It is suggested that a major improvement could be made by including a third phytoplankton group (*e.g., Phaeocystis*) in the model structure, and that comparison with other phytoplankton growth schemes based on the Droop formulation is advisable.

1. INTRODUCTION

The aim of this paper is to describe a detailed primary production model hindcasting the seasonal phytoplankton cycle in the entire North Sea as well as a thorough sensitivity analysis in which many of the related parameters have been subject to a scaled modification. The model is, in fact, a module of the European Regional Seas Ecosystem Model (ERSEM) and simulates phytoplankton growth in terms of carbon and several nutrients (N, P and Si) for two algal groups: diatoms and autotrophic flagellates. The whole ERSEM model includes several modules (*e.g.,* zooplankton, pelagic bacteria and heterotrophic flagellates as well as benthic organisms) for 15 boxes in the entire North Sea.

Many models have been developed and applied to the North Sea area. Fransz *et al.* (1991) did an excellent review of the most important ones and they also focused on the mechanisms applied by North Sea modellers to simulate, among other processes, the nutrient uptake, phytoplankton growth or zooplankton grazing. Therefore, we would like to confine the usual literature review to this extensive reference and directly begin with the model description and features.

2. DESCRIPTION OF THE PRIMARY PRODUCTION MODULE

2.1. GENERAL ASSUMPTIONS

Horizontally, the North Sea is divided into ten boxes (Fig. 1). Among them, 5 boxes spanning the deeper regions and where stratification occurs are vertically resolved into a surface and a deep water box. Advection and diffusion were computed using the time and space averaged circulation provided by the hydrodynamic submodel (Radach & Lenhart, 1995). In general, the evolution of the non-conservative primary production terms can be viewed as a balance between the several production and destruction terms:

$$SPx = \text{production terms - destruction terms} \quad (1)$$

where SPx are the source terms for both phytoplankton groups which are our main concern here. Chlorophyll *a* values were calculated by adding the chlorophyll contents of diatoms and autotrophic flagellates, using a carbon to chlorophyll conversion factor (Eq. 2). This conversion factor was different for each phytoplankton group. A complete list of the sym-

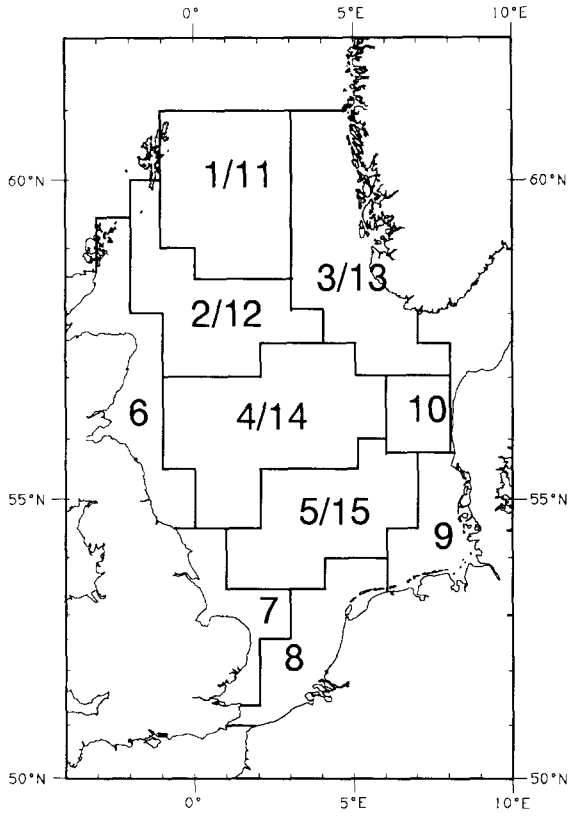


Fig. 1. ERSEM North Sea box structure.

bols used can be found in Appendix I.

$$chl = \left(\frac{P1c}{uhP1c\$} + \frac{P2c}{uhP2c\$}\right) \quad (2)$$

The primary productivity module considers various processes schematically shown in Fig. 2. Phytoplankton is assumed to be composed of two functional groups, diatoms and autotrophic flagellates. Each phytoplankton group is represented by independent state variables including carbon, nitrogen, phosphorus and silicon (the latter only for diatoms). Besides the requirement for silicate by the diatoms, another difference between the two groups is the grazing pressure that acts upon each one: diatoms, assumed to be of cell sizes greater than 20 μm, are grazed by mesozooplankton, while autotrophic flagellates are assumed to have a cell size below 20 μm and are eaten by both microzooplankton and mesozooplankton. Their respective response to temperature and light conditions and to nutrient limitation, in conjunction with grazing and sinking, control the differential behaviour of these components of phytoplankton. The grazing terms, though included in the figure, are detailed in Broekhuizen *et al.* (1995) and Baretta-Bekker *et al.* (1995).

Nutrients are supplied by lateral and vertical hydrodynamical processes from other spatial boxes, by river discharges as well as by biological activity. In particular, dissolved inorganic nitrogen was assumed to be composed by nitrate and ammonia supporting two different fractions of production, new and regenerated (Dugdale, 1967). New production, based on the oxidized forms, is provided from advection and diffusion mechanisms while regenerated production is based mainly on ammonia and is produced by heterotroph excretion and by bacteria remineralization from detritus. Phosphate and silicate have similar source and sink terms.

2.2. GENERAL PHYTOPLANKTON EQUATIONS

The formulation for both phytoplankton functional groups is similar. The major rates involved are: photosynthetic carbon fixation and nutrient uptake among the positive ones and carbon respiration, lysis, excretion of organic carbon and grazing among the negative ones. The source terms for phytoplankton can be introduced by (fluxes due to grazing are left out):

change in phytoplankton =
production term - (respiration + lysis + excretion)

In standard ERSEM notation:

$$SP1c = sumP1 \cdot eNIP1 \cdot P1c - (fP1O3c + fP1R6c + fP1R1c) \quad (3)$$

$$SP1n = fN4P1n + fN3P1n - (fP1R6n + fP1R1n) \quad (4)$$

$$SP1p = fN1P1p - (fP1R6p + fP1R1p) \quad (5)$$

$$SP1s = fN5P1s - (fP1R6s + fP1R1s) \quad (6)$$

while the equivalent source terms for flagellates are:

$$SP2c = sumP2 \cdot eNIP2 \cdot P2c - (fP2O3c + fP2R6c + fP2R1c) \quad (7)$$

$$SP2n = fN4P2n + fN3P2n - (fP2R6n + fP2R1n) \quad (8)$$

$$SP2p = fN1P2p - (fP2R6p + fP2R1p) \quad (9)$$

See Appendix I for explanation of the terms used.

2.3 CARBON GROWTH RATE PROCESSES

The module assumes that carbon-based population growth rate can be limited by water temperature and light availability, following a fully synergistic multiplicative approach represented by:

potential carbon growth rate =
maximum photosynthetic rate · temperature dependence · light dependence):

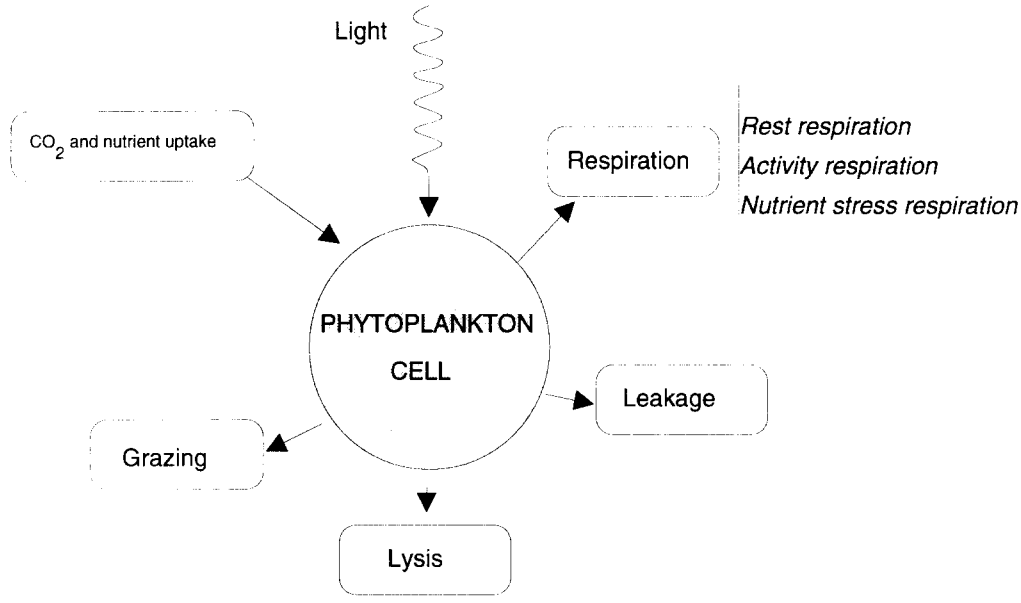


Fig. 2. Scheme of the main processes involved in the primary production module.

$$sumPX = sumPx\$ \cdot etPx \cdot eiPI \tag{10}$$

where x is 1 or 2, one of the phytoplankton groups. A similar approach was used by Baretta *et al.* (1988) in the simulation of the Estuary. This formulation is based on maximum photosynthetic rate estimations done by Colijn (1983) at rather constant temperature, and flagellates generally showed to have higher photosynthetic rate values than diatoms.

Temperature affects the potential growth rate parameter $sumPx$ through an exponential factor ($etPx$) which, for the temperature range found in the North Sea, varies between 0.5 and 2.5 and is estimated according to Pichot (1980):

$$etPx = q10Px\$^{0.1 \cdot (ETW - \overline{ETW})} \tag{11}$$

where the parameter $q10Px\$$ corresponds to the well known physiological parameter Q10 which is different for each phytoplankton group, ETW is the water temperature and $\overline{ETW}$ is the annual mean water temperature (in the model set to 10°C). Temperature is then considered as a regulation factor influencing the potential photosynthetic activity.

The dimensionless light factor $eiPi$ takes into account the daily average total radiation in a given box (EIR, W·m^{-2}), the length of daylight time ($sunq$, h) and the extinction coefficient ($xEPS$, m^{-1}). The average light in the box, parameterized with an optimal irradiance (I_{OPT}, W·m^{-2}), gives rise to $eiPI$ which ranges between 0 and 0.66. First, irradiance is converted into *P*hotosynthetically *A*vailable *R*adiation (PAR) using a conversion factor:

$$IPAR+EIR \cdot pEIR\_EOW\$ \tag{12}$$

The ratio of the PAR to an optimal irradiance (I_{OPT}) at the top of the box (I_0) and at the bottom (I_z) is then evaluated:

$$I_0 = \frac{I_{PAR}}{I_{OPT}} \tag{13a}$$

$$I_z = I_0 \cdot e^{-xEPS \cdot depth\$} \tag{13b}$$

following Brock (1981) and the traditional Beer-Lambert attenuation law. Light extinction $xEPS$ is computed through a linear relationship with the phytoplankton, detritus and suspended matter concentrations as independent variables (Baretta *et al.*, 1988). Optimal irradiance (Steele, 1962) is estimated as:

$$I_{OPT} = \left(I_{PAR} \cdot \frac{1}{xEPS} \cdot \left(1 - e^{-xEPS \cdot f} \right) + clPIi\$ \cdot (depth\$ - f) \right) \cdot \frac{1}{depth\$} \tag{14}$$

where f is a factor obtained comparing the I_{PAR} with a predetermined minimum value (*clPIi$*, near 40 W·m^{-2}). If I_{PAR} is less than this minimum, f is set to zero; otherwise, f is computed following Eq. 15):

$$f = \min\left(depth\$, -\log\left(\frac{clPIi\$}{I_{PAR}}\right)\cdot\frac{1}{xEPS}\right) \quad (15)$$

The average light limitation factor for each box is finally estimated by adding a correction for the thickness of the box (*depth$*) and day length (*sunq*):

$$eiPI = \frac{\left[\left(e^{1-I_z}\right)-\left(e^{1-I_0}\right)\right]}{xEPS\cdot depth\$}\cdot sunq\cdot\frac{1}{24} \quad (16)$$

The final actual growth rates are estimated including a composite nutrient limiting factor based on Michaelis-Menten relationships (*eNIPx*, see Eqs 3 and 7). This nutrient limitation is estimated for the three main nutrients (nitrogen, phosphorus and silica) with a geometrical mean approach. Nitrogen is assumed to be further divided into nitrate and ammonia, while silica limitation is taken into account only when diatoms are concerned. These formulations are expressed using the Michaelis-Menten equation in the classical way (Dugdale, 1967):

$$eN1Px = \frac{N1p}{N1p + chPxp\$} \quad (17)$$

$$eNIPxn = \frac{NIn}{NIn + chPxn\$} \quad (18)$$

$$eN5P1 = \frac{N5s}{N5s + chP1s\$} \quad (19)$$

where NIn is obtained adding the nitrate and ammonia concentration terms: $NIn = N3n+N4n$.

The combined nutrient limitation factor for diatoms is given by:

$$eNIP1 = \sqrt[3]{eN5P1\cdot eN1P1\cdot eNIP1n} \quad (20)$$

and for autotrophic flagellates by

$$eNIP2 = \sqrt{eN1P2\cdot eNIP2n} \quad (21)$$

Since the Michaelis-Menten equation gives results ranging from 0 to 1, the formulation used (Eqs 20-21) for nutrient limitation also gives values between 0 and 1.

The complete effect of the various growth rate controlling factors is shown in Fig. 3. Before the nutrient limitation acts, the potential photosynthetic rate follows a curve which, for box 5, ranges between 0.20 and 1.20. During the winter and early spring, the potential growth rate stays at its lowest values (0.20 d^{-1}), increasing steadily from May to August and declining again until it reaches the low December values. As shown by the growth/nutrient factors to the left of Fig. 3, the nutrient determined growth rate is not greatly depressed until the nutrients are very depleted.

2.4. NUTRIENT UPTAKE PROCESSES

Uptake of each nutrient is computed by multiplying the net primary production of each phytoplankton component by the nutrient quota (ratio of phytoplankton nutrient to phytoplankton carbon), and by a correction which ensures that nutrient in excess of that required to maintain the fixed internal quota is released back to the water. For phosphorus this is:

phosphorus uptake =
phosphorus quota·(gross carbon production - total respiration) - correction term

or in ERSEM notation:

$$fN1Pxp = qpPxc\$\cdot(fO3Pxc - fPxO3c) - \max(0., qpPxc - qpPxc\$)\cdot Pxc \quad (22)$$

where the max( ) term takes into account the phosphorus taken up in excess of a maximum quota set equal to parameter *qpPxc$*. The *fO3Pxc* term is equivalent in the model to the gross production, (*fO3Pxc=sumPx·eNIPx·Pxc*, see Eqs 3 and 7). A similar formulation is used for the nitrogen or silicate terms.

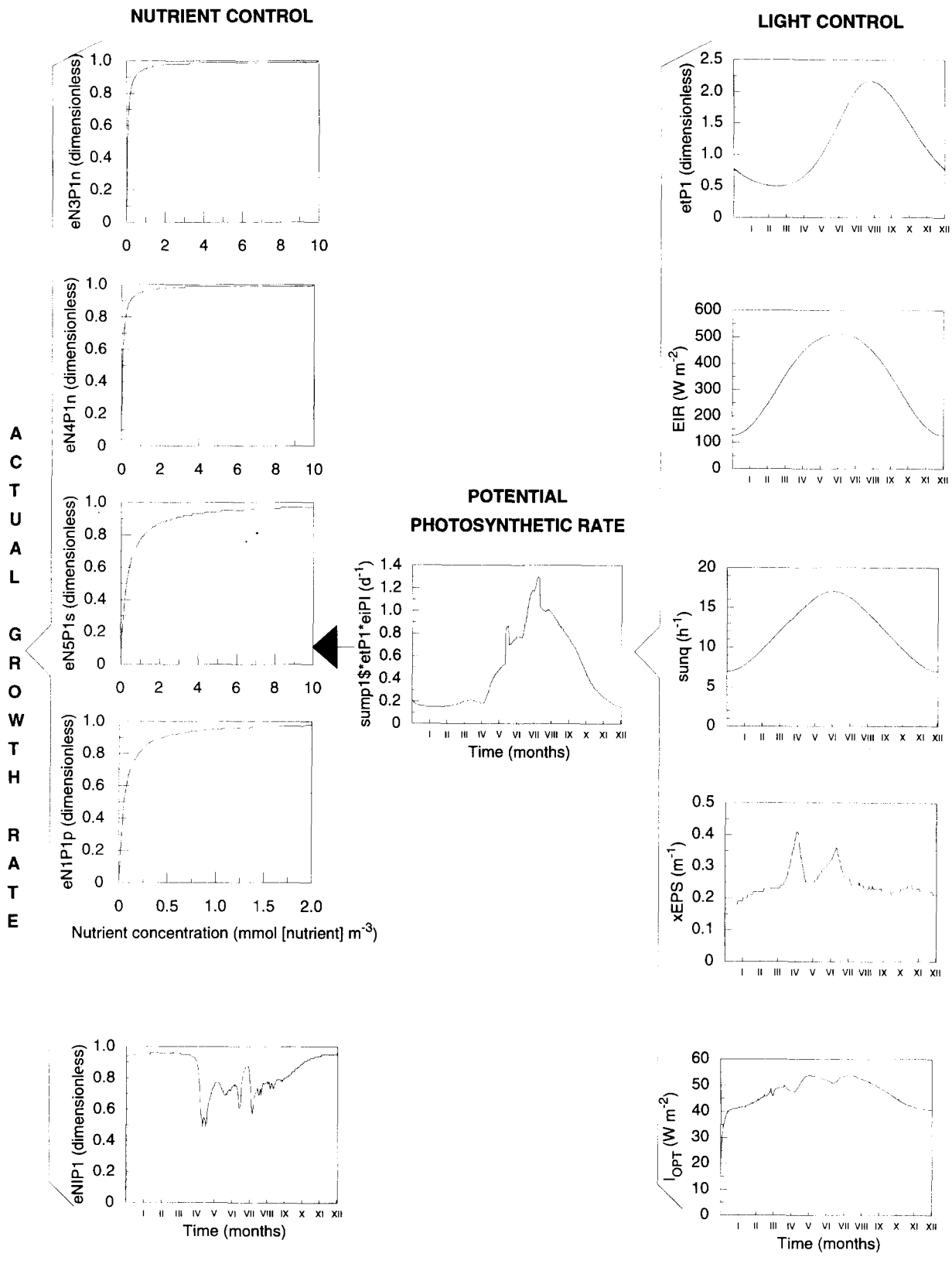
Nitrogen partitioning between ammonia and nitrate is based on a preferential ammonia uptake over nitrate. This was established with a simple formula, using the term *xpref_N4$*. When *xpref_N4$* is set to 1, no preference is allowed. At larger *xpref_N4$* values (>1) the preference for ammonia increases

$$pu\_N4Pxn = \frac{\frac{N3n}{N3n + chPxn\$}}{xpref\_N4\$\cdot\left[\frac{N4n}{N4n + chPxn\$}\right] + \left[\frac{N3n}{N3n + chPxn\$}\right]} \quad (23)$$

$$fN3Pxn = fNIPxn\cdot pu\_N4Pxn \quad (24)$$

$$fN4Pxn = fNIPxn - fN3Pxn \quad (25)$$

Fig. 3. Schematic description of the production processes involving phytoplankton growth in the standard ERSEM model. Growth rate stands for carbon-based phytoplankton population growth rate. Symbols used can be found in Appendix I. Curves shown are for diatoms (P1) in ERSEM box 5. →


NUTRIENT CONTROL
LIGHT CONTROL
POTENTIAL PHOTOSYNTHETIC RATE
ACTUAL GROWTH RATE
eN3P1n (dimensionless)
eN4P1n (dimensionless)
eN5P1s (dimensionless)
eN1P1p (dimensionless)
Nutrient concentration (mmol [nutrient] m-3)
etP1 (dimensionless)
EIR (W m-2)
sump1$*etP1*eiPI (d-1)
sunq (h-1)
xEPS (m-1)
eNIP1 (dimensionless)
IOPT (W m-2)
Time (months)
I II III IV V VI VII VIII IX X XI XII

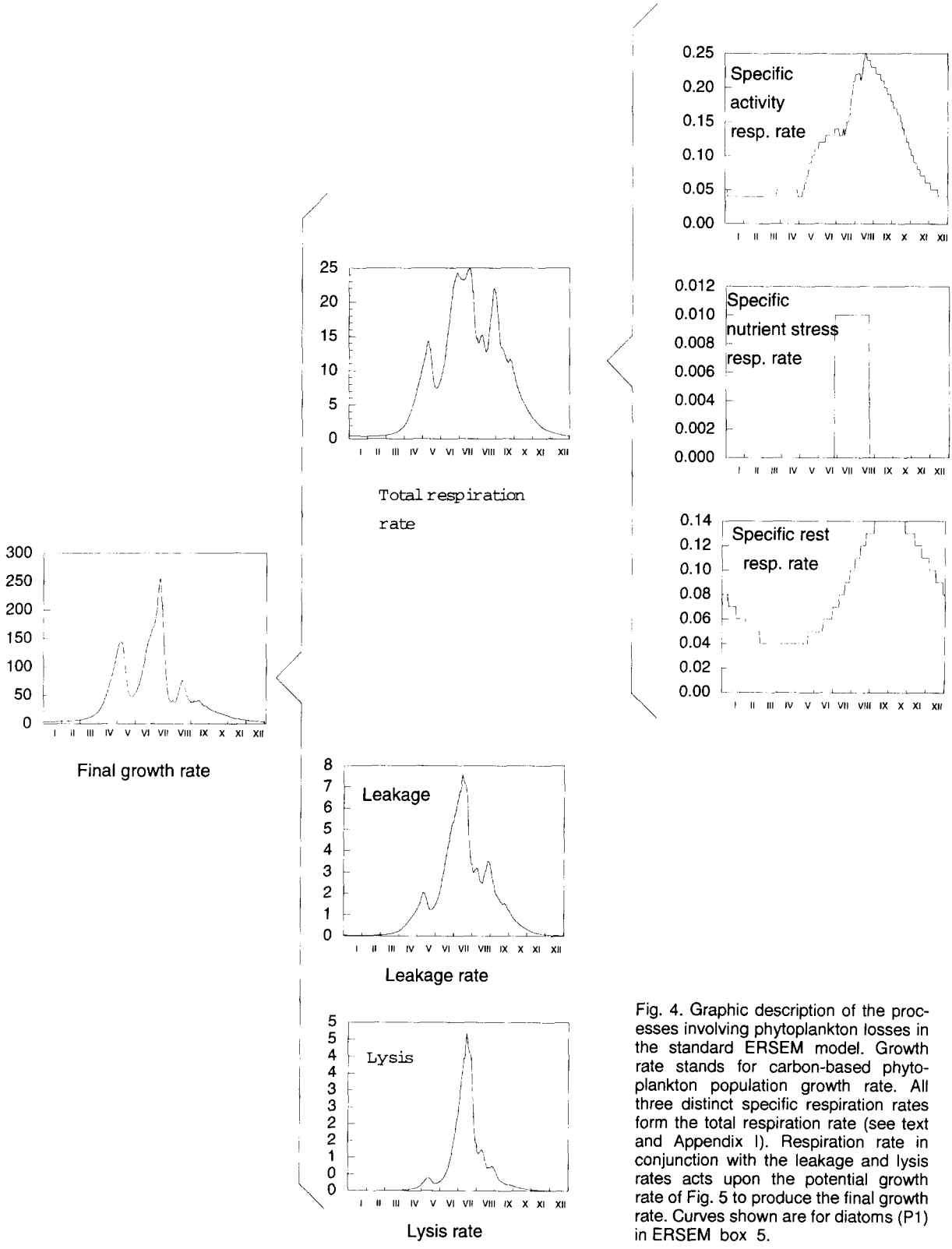


Fig. 4. Graphic description of the processes involving phytoplankton losses in the standard ERSEM model. Growth rate stands for carbon-based phytoplankton population growth rate. All three distinct specific respiration rates form the total respiration rate (see text and Appendix I). Respiration rate in conjunction with the leakage and lysis rates acts upon the potential growth rate of Fig. 5 to produce the final growth rate. Curves shown are for diatoms (P1) in ERSEM box 5.

2.5. CARBON LOSS RATE PROCESSES

2.5.1. RESPIRATION

In the model, carbon losses due to respiration are assumed to be composed of three distinct processes: activity respiration, nutrient stress respiration and resting respiration. The specific activity respiration rate *sraPx* is assumed to be proportional to the specific gross growth rate (*sumPx·eNIPx*, Baretta *et al.*, 1988):

$$sraPx = pu\_raPx\$ \cdot sumPx \cdot eNIPx \quad (26)$$

The nutrient specific stress respiration rate *sroPx* is proportional to the difference between the specific maximal (nutrient-rich) potential growth rate (*sumPx*) and the specific actual gross growth rate (*sumPx·eNIPx*, Baretta *et al.*, 1988).

$$sroPx = pum\_roPx\$ \cdot (1 - eNIPx) \cdot sumPx \quad (27)$$

As a consequence, when nutrients are scarce *sroPx* is maximal. This directly influences the magnitude of the phytoplankton peak, since at this time nutrients are almost at their lowest level and the growth rate is still high.

The specific rest respiration rate is a function of seawater temperature and day length. Higher *srsPx* rates are typically found immediately after the summer, when seawater temperature is still high and day length begins to decrease.

$$srsPx = srsPx\$ \cdot etPx \cdot \left(1 - \frac{sunq}{24}\right) \quad (28)$$

The final (total) respiration rate is obtained adding together the activity respiration, the nutrient stress respiration and the rest respiration rates (Baretta *et al.*, 1988):

$$fPxO3c = (sraPx + sroPx + srsPx) \cdot Pxc \quad (29)$$

2.5.2. LYSIS AND DISSOLVED ORGANIC MATTER EXCRETION

Like the nutrient stress respiration, lysis is assumed to be proportional to the difference between the maximal and the actual growth rate (Baretta *et al.*, 1988):

$$seoPx = pum\_eoPx\$ \cdot sumPx \cdot (1 - eNIPx) \quad (30)$$

The lysis rate in diatoms (Eq. 30) is enhanced by a factor dependent on the activity of bacterial proteases:

$$seoP1 = seoP1 + seoP1 \cdot \left[\frac{B1c}{chB1eP2c\$ + B1c}\right] \quad (31)$$

An amount of carbon corresponding to the lysis rate is transferred into particulate detritus:

$$fPxR6c = \max(0, pe\_R1Pxc\$ \cdot seoPx \cdot Pxc) \quad (32)$$

while the rest of the biomass lost through lysis goes to the dissolved organic matter pool (DOM, Eq. 33). Lancelot (1983) suggested that the formation of excretion products occurs at an enhanced rate under nutrient limitation conditions. A second loss term was therefore added (*pu_eaPx$·sumPx·eNIPx*), proportional to the activity respiration rate (activity dependent excretion) which also contributes to the leakage process.

$$fPxR1c = ((1 - pe\_R1Pxc\$) \cdot seoPx + pu\_eaPx\$ \cdot sumPx \cdot eNIPx) \cdot Pxc \quad (33)$$

A graphic representation of all the loss rate processes involved in the standard ERSEM module is shown in Fig. 4.

2.5.3. SINKING

Only sedimentation of diatoms and flagellates will be considered here. After Steele & Yentsch's (1960) work and until the experiments by Bienfang *et al.* (1982) it has been widely accepted that nutrient limitation *per se* results in elevated sinking velocities. However, this is not the case for all the nutrients and for all the species. In fact, only silicate seems to be significant for diatoms (Bienfang *et al.*, 1982) and nitrate for dinoflagellates (Culver & Smith, 1989). In the standard module, sedimentation is based on two parameters, a maximum sinking rate and a nutrient limitation value under which this phenomenon occurs. The formulation used allows for increased sedimentation when nutrient availability decreases. In the standard run only diatoms were allowed to sink, since parameter *resP2m$* was set to zero.

$$SEDIP1 = esP1m\$ \cdot \max(0, (esNIP1\$ - eNIP1)) \quad (34)$$

2.6. NUTRIENT LOSS RATE PROCESSES

Nutrients are lost in the primary production module in connection with the loss of phytoplankton carbon. Excretion of dissolved organic nitrogen with lysis and the production of particulate organic nitrogen with lysis and activity-dependent excretion are represented by:

$$fPxRIn = (fPxR1c + fPxR6c) \cdot qnPxc \quad (35)$$

$$fPxR1n = \min(fPxRIn, fPxR1c \cdot qnPxc \cdot xR1n\$) \quad (36)$$

$$fPxR6n = fPxRIn - fPxR1n \quad (37)$$

TABLE 1
Biomass values and timing of the spring peak of the diatoms and of the flagellates.

box number	*diatoms spring peak (P1c)*		*flagellates spring peak (P2c)*	
surface (bottom)	*biomass (mg C·m^{-3})*	*day*	*biomass (mg C·m^{-3})*	*day*
1 (11)	234 (78)	122 (126)	413 (18)	132 (153)
2 (12)	224 (141)	125 (134)	450 (131)	143 (148)
3 (13)	243 (49)	120 (125)	445 (16)	135 (153)
4 (14)	282 (228)	123 (127)	232 (114)	140 (138)
5 (15)	323 (350)	123 (127)	145 (133)	126 (126)
6	167	144	88	146
7	320	120	142	124
8	300	120	129	121
9	359	114	269	128
10	278	117	317	136

Phosphate and, for diatoms, also silicate have similar formulations.

2.7. NUMERICAL INTEGRATION AND SIMULATION ENVIRONMENT

The numerical integration of the routines and the general simulation environment are described in Ruardij *et al.* (1995).

3. RESULTS

The ERSEM model was run for a number of years using 1988 forcing conditions to obtain a 'long-term steady state' which would provide the 'equilibrium' initial conditions for a given set of parameter values. These values, together with the forcing functions, boundary and initial conditions, constitute the so-called 'standard' model. Standard parameters values were mostly derived from the literature (in some minor cases when this was impossible a reasonable guess was assumed) but small adjustments were also done during the model calibration process. The results reported here are the solutions of such a 'standard' model as well as those resulting from a systematic modification of all the parameter values (see Appendix II) by 33% above and below the standard value.

3.1. STANDARD RUN

3.1.1. CARBON BIOMASS

Diatoms generally exhibited two main peaks, one in spring and the other during autumn. Spring simulated biomass ranged from 100 to more than 350 mg C·m^{-3} depending on the area considered. With the exception of box 5 in the central North Sea and box 6 along the UK coast, the diatom spring bloom is larger in coastal boxes (numbers 6 to 10) than in the surface boxes of the two-layer stratified boxes (1/11-5/15). Also, the deeper boxes consistently showed lower biomass concentration with the exception of box 5 (Table 1).

The diatom spring peak generally appears around day 120 and lasts for about 20 days; a tendency to peak about one week earlier in coastal and deeper regions can also be detected. On the other hand, the diatom autumn bloom is noticeably lower than the spring one and could not always be clearly distinguished in the coastal boxes where carbon levels are maintained with some fluctuations between 10 and 30 mg C·m^{-3} from late spring to early winter. The autumn bloom is also present below 30 m depth in the deeper boxes, with the exception of boxes 14 and 15 in the central North Sea where the autumn increase is practically undetectable. A representative example of the diatom annual evolution for both a coastal and a offshore region is shown in Fig. 5.

Autotrophic flagellates exhibited a more variable behaviour, with large biomass variations among regions. Simulated biomass values varied from less than 20 mg C·m^{-3} in deeper areas to more than 400

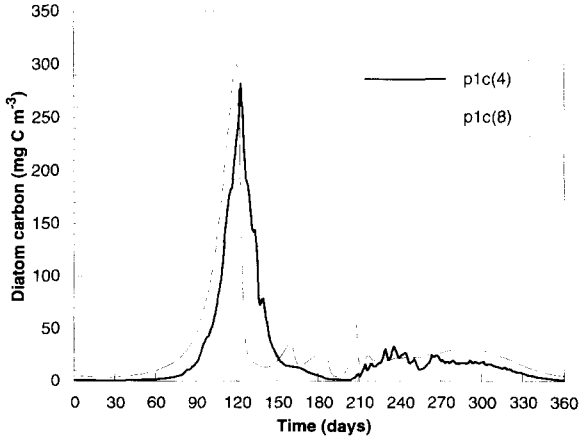


Fig. 5. Diatom carbon annual evolution in a coastal (ERSEM box 8) and offshore (ERSEM box 4) box according to the standard model results.

TABLE 2
Seasonally averaged chlorophyll *a* (mg chl $a \cdot m^{-3}$).

*season**	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*
winter	0.01	0.03	0.03	0.20	0.39	0.03	0.42	0.65	0.59	0.35	0.01	0.02	0.02	0.17	0.38
spring	3.03	5.19	3.88	5.58	5.13	2.40	4.86	4.73	5.87	5.25	1.23	2.74	0.92	4.03	5.04
summer	1.11	2.09	1.69	2.50	2.28	1.59	2.14	2.27	2.06	1.97	0.17	0.39	0.22	0.96	1.84
autumn	0.55	0.48	0.46	0.67	0.70	0.23	0.65	1.03	0.69	0.79	0.34	0.35	0.20	0.57	0.65
mean	1.17	1.94	1.51	2.23	2.12	1.06	2.01	2.16	2.30	2.09	0.43	0.87	0.34	1.43	1.97

*winter=January-March, spring=April-June, summer=July-September, autumn=October-December.

mg $C \cdot m^{-3}$ in some open areas. Unlike diatoms, flagellate biomass is much higher in the stratified regions than near shore (Table 1). Again box 5 in the central North Sea is the exception, with relatively low flagellate biomasses. Box 11 in the northern North Sea and box 13 along the Norwegian coast has the lowest simulated flagellate biomass values of the whole North Sea region.

During spring, flagellates consistently peak 10 to 20 days after the diatoms bloom and the peaks also last for about 20 days. No significant difference in the duration of the spring bloom among the different areas could be detected. Unlike diatoms, the flagellate autumn bloom is relatively more important when compared to the spring peak and occurs earlier than the equivalent diatom autumn peak. As a consequence, the flagellate autumn bloom sometimes equals or even exceeds spring values.

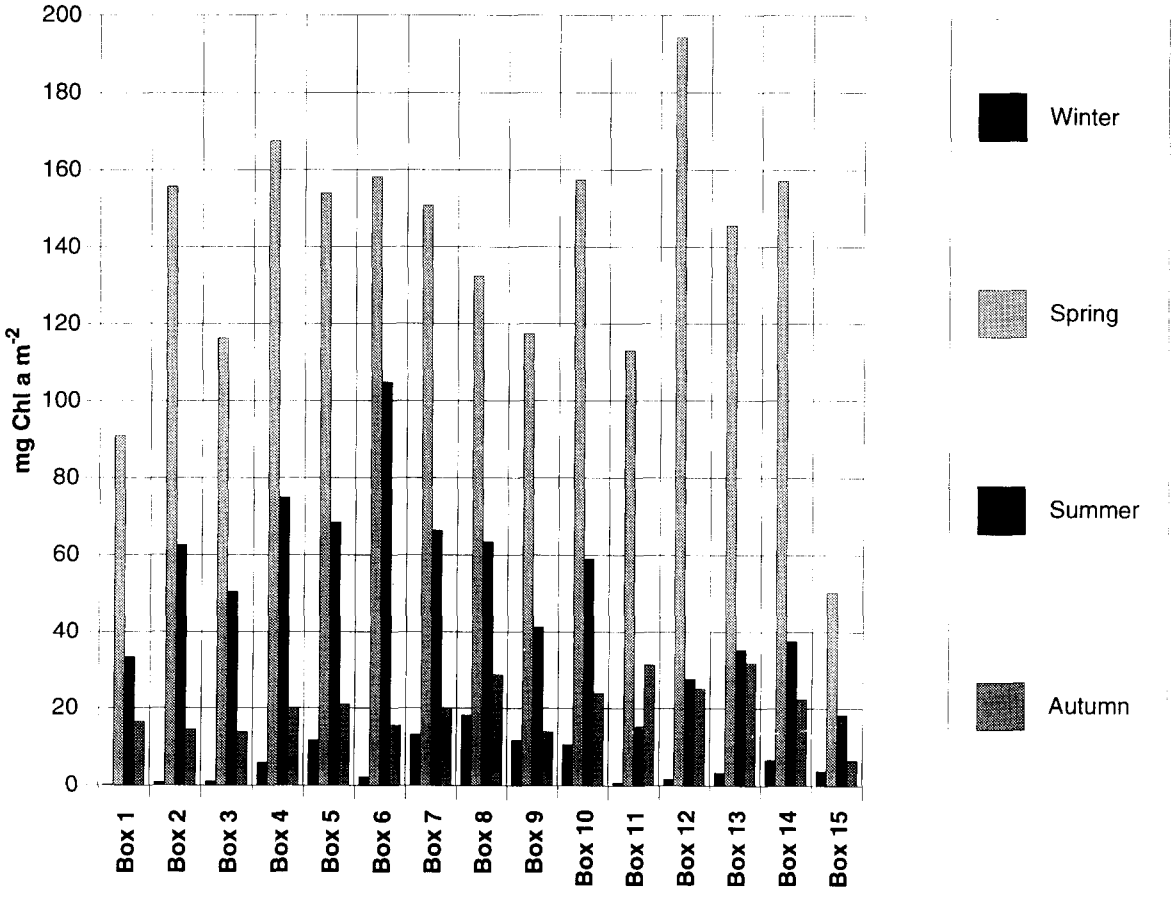


Fig. 6. Integrated seasonal chlorophyll mean concentrations calculated from daily values.

TABLE 3
The annual gross and net primary production (g $C \cdot m^{-2} \cdot a^{-1}$) for diatoms and flagellates for the 15 ERSEM boxes with the mean depth.

		gross primary production		*net primary production**	
box number	*mean depth (m)*	*diatoms*	*flagellates*	*diatoms*	*flagellates*
1 (11)	30 (92)	31.1 (1.4)	193.0 (1.4)	16.6 (-4.9)	50.3 (-2.7)
2 (12)	30 (71)	88.4 (1.1)	317.8 (1.2)	45.8 (-10.0)	143.3 (-6.8)
3 (13)	30 (158)	47.5 (0.3)	186.9 (0.3)	23.3 (-3.8)	69.2 (-2.2)
4 (14)	30 (39)	113.9 (1.3)	311.5 (1.9)	56.2 (-17.9)	148.1 (-12.5)
5 (15)	30 (10)	98.3 (0.2)	208.9 (0.4)	42.3 (-30.1)	101.8 (-26.5)
6	66	80.7	114.4	12.9	22.2
7	31	95.6	196.1	35.8	87.5
8	28	112.3	201.2	47.3	101.5
9	20	85.8	181.3	57.5	133.3
10	30	101.6	226.2	42.7	105.1

*net primary production values are calculated taking into account the effects of respiration (activity respiration rate, stress respiration rate and nutrient respiration rate) and activity excretion.

3.1.2. CHLOROPHYLL *A*

Chlorophyll *a* simulated values range from winter near-zero values to more than 15 mg chl $a \cdot m^{-3}$ during the spring peak. Seasonal mean chlorophyll concentrations estimated from daily values are shown in Table 2. The spring values are consistently higher for all the simulated regions, and summer values also

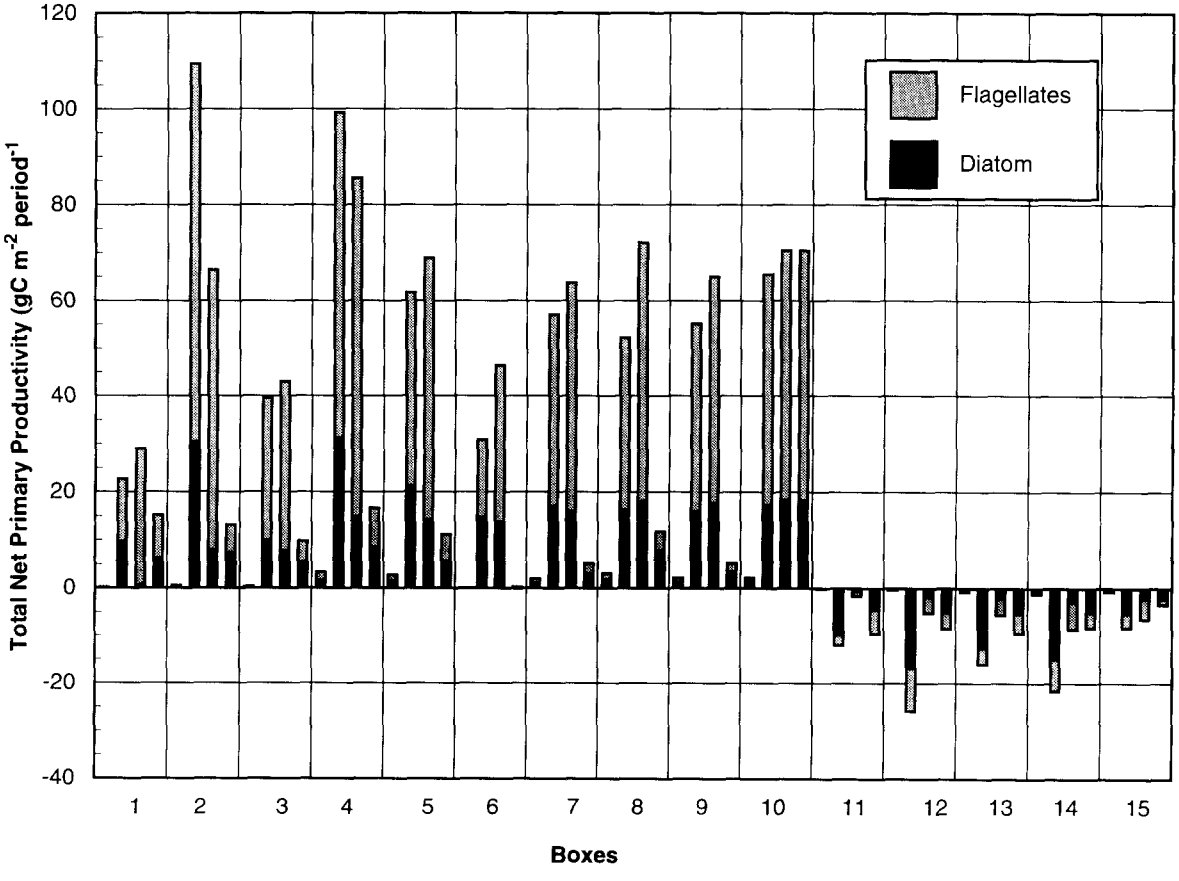


Fig. 7. Simulated total net primary production per season (winter, spring, summer and autumn) in the different boxes of the North Sea region.

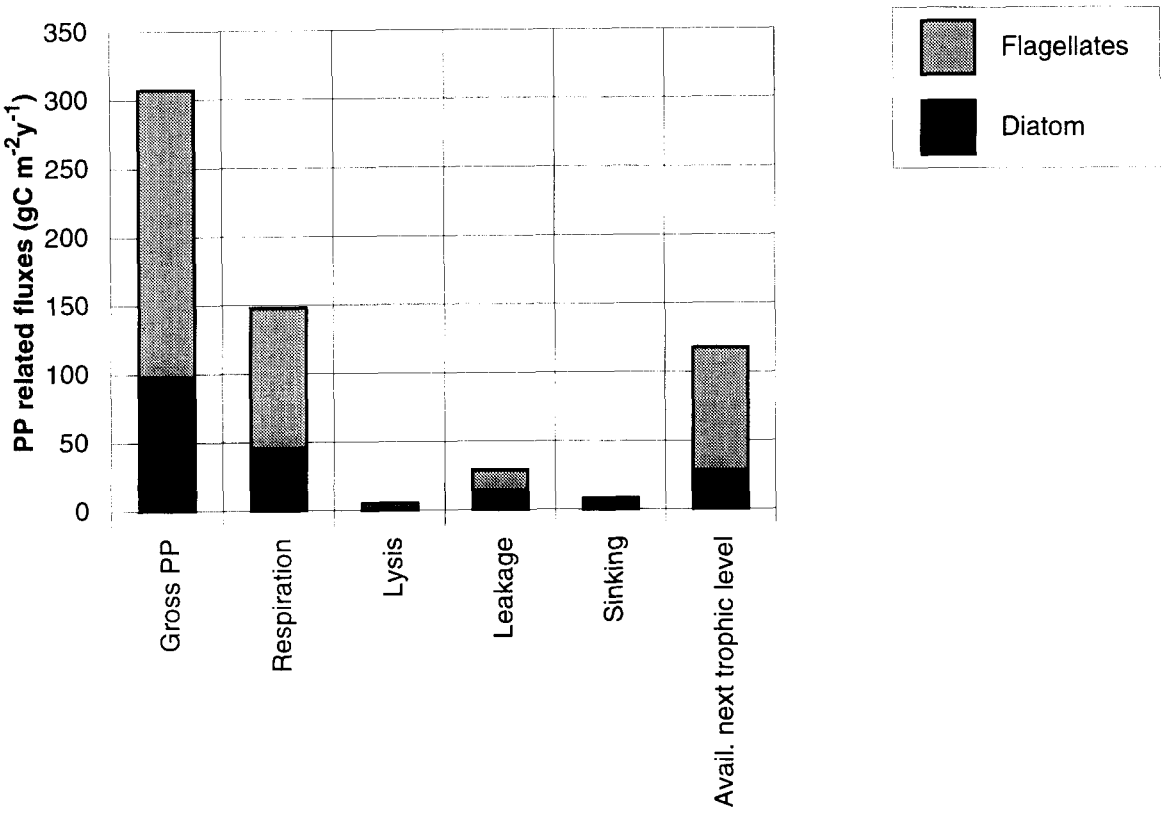


Fig. 8. Annual primary production related fluxes in the offshore box 5 (central North Sea) for both diatoms and autotrophic flagellates. Grazing fluxes were not included.

generally exceed autumn concentrations, the only exception being the deep box 11 in the northern North Sea. Coastal boxes generally had the highest concentrations together with boxes 4 and 5 in the central North Sea.

Seasonally and vertically integrated chlorophyll values show a similar trend, with spring concentrations which are generally double the summer or autumn values (Fig. 6). The highest time-integrated chlorophyll values were found in the central North Sea (2/12 and 4/14). The northern and deeper regions (specially box 13) show the lowest chlorophyll concentrations. Contrary to the chlorophyll averaged values of Table 2, depth-integrated chlorophyll concentrations in the coastal areas could not be clearly distinguished from the deeper and stratified offshore regions.

3.1.3. INTEGRATED PRIMARY PRODUCTION

The total annual gross primary production, *i.e.* the gross production of diatoms and autotrophic flagellates, calculated per region of the North Sea ranges from about 200 g $C{\cdot}m^{-2}{\cdot}a^{-1}$ to more than 400 g $C{\cdot}m^{-2}{\cdot}a^{-1}$ (Table 3). Values are particularly high in box 4 in the central North Sea and in box 2. The model gives the lower primary production values along the eastern coast of the UK (box 6).

Diatom gross primary production is, on average, higher in coastal boxes than in the stratified regions of the North Sea. On the other hand, flagellate gross primary production values are two or three times higher than the corresponding diatom values and, generally, more important in deeper boxes than in coastal regions.

Total net primary production is generally less than half the gross primary production, with the lower layer of the deeper boxes always giving negative values. Values range from less than 15 g $C{\cdot}m^{-2}{\cdot}a^{-1}$ to near 150 g $C{\cdot}m^{-2}{\cdot}a^{-1}$. Coastal regions have, on the average, about a 50% higher primary production than offshore areas, while higher total net primary production values are found in the German Bight (box 9) and again in box 2 in the northern North Sea. The lowest net production is found in box 6 along the coast of the UK. As in the case of gross primary production, flagellate net production always exceeds the corresponding diatom values.

When diatom and flagellate net primary production seasonal distribution is analysed (Fig. 7), some more features are revealed. Simulated results show that

spring is not always the season of maximum total net primary production, since summer and even autumn values are often higher. Net primary production is negative even during the spring or summer seasons in the deeper boxes.

If diatoms and autotrophic flagellates are analysed independently, results are somewhat different, since diatoms almost always have the maximum net primary production during the spring, with the exceptions of the coastal boxes 8, 9 and 10 in, respectively, the southern Bight, the German Bight and the eastern Danish coast. Flagellates, on the other hand, have large primary production values during summer and/or autumn.

3.2. PRIMARY PRODUCTION RELATED FLUXES

3.2.1. CARBON FLUXES

The primary production module produces some very crucial fluxes of matter for the rest of the ERSEM model. It is thus important to analyse these fluxes and to try to make an overall balanced picture of the module. This 'module picture' can also be used later to compare model results to experimental or measured data and discuss the appropriateness of the module.

Diatoms and autotrophic flagellates grow by fixing carbon dioxide from the water. In the primary production module, respiration, lysis, leakage and excretion of organic matter together with grazing and sinking are the loss term processes.

In box 5, the total respiration accounts for more than 40% of a total gross primary production of 307 g $C \cdot m^{-2} \cdot a^{-1}$ (Fig. 8). Lysis is less than 2% of the total gross primary production, while sinking (which is only allowed for diatoms) accounts for 2-3% of the total production. Leakage, also an important loss factor, accounts for 10% of the total production. As a result, the next trophic level can only graze on roughly 1/3 of the initial gross growth rate. The annual evolution of the simulated phytoplankton carbon leakage rate shows that rates are higher immediately after the spring bloom in offshore zones, while coastal areas have the maximum leakage rates in summer. The lowest simulated values are found during winter, and leakage rates are also generally higher in the offshore regions than in coastal ones.

Although not shown here, values along the eastern coast of the UK (box 6) are similar to those of box 5. The relative diatom proportion in the total gross production is much higher, while integrated gross production itself is only slightly lower (Table 3). In this coastal box respiration is again the dominant loss factor while lysis and leakage are almost negligible. However, the contribution of diatoms to the sediment by sinking is higher than in the pelagic box 5.

3.2.2. NUTRIENT FLUXES

The main nutrient fluxes related to nutrient assimilation are shown in Table 4. Values vary widely among the different areas simulated but a more consistent pattern can be distinguished if values within the same box are analysed. Flagellates generally have larger values of nutrient uptake (with the obvious exception of silicate) and nutrient leakage is consistently more important (by up to one order of magnitude) than the nutrient losses by lysis. However, the latter is not true for silicate, whose losses by leakage are almost negligible. When the uptake of the various nutrients is compared, phosphorus has the lowest values in both regions, while total nitrogen uptake is always the largest.

According to Table 4, silicate constitutes an important nutrient source term for diatoms, and its uptake values are highly linked with the maximum growth periods in the pelagic regions. In coastal waters uptake of silicate is more evenly distributed through the year, and maxima are always related to the phytoplankton peaks.

3.3. SENSITIVITY ANALYSIS

The ERSEM model with the primary production mod-

TABLE 4
Nutrient fluxes (mmol nutr.$\cdot m^{-2} \cdot a^{-1}$) for diatoms, flagellates and total phytoplankton in the boxes 5 and 6.

	offshore box 5			*coastal box 6*		
process	*diatoms*	*flagellates*	*total*	*diatoms*	*flagellates*	*total*
Nitrate uptake	259.20	513.6	772.80	187.700	249.100	436.800
Ammonia uptake	691.20	1929.7	2620.90	370.100	662.900	1033.000
Phosphorus uptake	73.30	95.0	168.30	43.000	35.400	78.400
Silicate uptake	1080.00	-	1080.00	689.000	-	689.000
Nitrogen leaked	216.00	266.8	482.80	133.056	124.978	258.000
Nitrogen loss by lysis	0.16	8.6	8.76	0.015	0.070	0.085
Phosphorus leaked	16.94	10.4	27.34	10.217	4.873	15.100
Phosphorus loss by lysis	0.01	0.3	0.31	0.001	0.003	0.004
Silicate leaked	24.52	-	24.52	14.814	-	14.814
Silicate loss by lysis	248.40	-	248.40	151.888	-	151.888

ule was run several times with different parameter values to test the sensitivity of the model. A total of 29 parameters were chosen and, to make the simulations, the pre-determined 'standard values' were changed up and down by 1/3 of the standard value. This made 58 different simulations. A summary of the results with regard to the annual gross primary production (GPP) are shown in Appendix II. Values are presented as a percentage of variation in relation to the standard, and are in bold typeface when results were at least 50% different from those given by the standard run.

3.3.1. GROSS PRODUCTION

The parameters having a direct control on the growth rate of diatoms and flagellates strongly affect the model solutions when modified. Low values of *sumP1$* cause the virtual disappearance of the diatom component in all boxes (diatom GPP ranges from 0.7 to 32% of the standard solution). As expected, flagellates show greater biomasses all year round and particularly in spring, blooming earlier and with higher biomass values. Their annual GPP increases everywhere from 23 to 60%. On the contrary, high parameter values cause the diatom component to bloom earlier (faster) in spring while the flagellate bloom is somewhat reduced and delayed in some of the boxes.

The flagellates do not disappear with low values of *sumP2$*. However, the spring bloom of this phytoplankton component is very much delayed and reduced (flagellate GPP ranges from 20 to 63% of the standard value) without affecting the diatom biomass. The high values of the flagellate growth parameter do not significantly alter their biomass but heavily suppress the diatom component in all boxes. The diatom GPP is reduced to values of 12 to 80% of the standard ones.

3.3.2. NUTRIENT HALF-SATURATION CONSTANTS

The Michaelis-Menten limitation terms for phytoplankton growth set the differential ability of each phytoplankton component to grow under nutrient stress. The half-saturation constants for the various nutrients, have hardly noticeable effects in the phytoplankton and nutrient distributions.

3.3.3. NUTRIENT/CARBON QUOTA

The ratio of nutrient-elements to carbon is fixed in the nutrient uptake terms by their respective quota. Nutrient uptake is computed from the carbon-based growth times these quota and any nutrient elements in excess of these quota are released immediately back to the dissolved phase. Changing the maximum allowable nutrient quotas in diatoms drastically reduces their biomasses in terms of carbon, though the annual GPP is not changed by more than about 15% up and down. Changing the maximum allowable nutrient quota in flagellates reduces this component carbon-based biomass without altering the diatom biomass. The annual flagellate GPP changes by as much as 20% but in no systematic way, the sign of the change differing from box to box.

3.3.4. AMMONIA PREFERENCE

Ammonia is known to be taken up preferentially over nitrate. The ammonia preference coefficient sets the weight that ammonia concentrations exert over the overall value of nitrogen uptake. The effect of changing this parameter on the phytoplankton biomass is negligible.

3.3.5. SPECIFIC RESPIRATION RATES

Activity respiration rate The activity respiration coefficients control the proportion of the GPP lost (recycled) through respiration presumably during the light hours. Their effect on the phytoplankton biomass is rather noticeable, more so for flagellates. The largest value of the diatom respiration rate parameter causes smaller diatom peaks to appear during the spring with greater flagellate peaks. The annual diatom GPP varies by less than about 15% below and above the standard run values for box 1 and much less for other upper boxes. The annual flagellate GPP variations are somewhat smaller. The effects of increasing the flagellate respiration rate parameter are opposite to those described above, with increased diatoms and decreased flagellate biomass. The change caused by this parameter on the annual diatoms GPP is of about 30% above and below, while the flagellate GPP is only affected by 18% at most.

Nutrient stress respiration The parameters used in the nutrient stress respiration terms determine what fraction goes to respiration of the difference between the GPP in optimal nutrient conditions and that in the real conditions. When these parameters are changed, no effect is observed on the diatom biomass and only a relatively small effect is shown by the flagellate biomass, particularly during summer in some of the boxes. The most noticeable effect is a decrease of the summer flagellate peak for the higher value of the parameter. The annual GPP of diatoms and flagellates shows practically no change.

Rest respiration The rest (dark) respiration rate, a function of the temperature factor and the length of the night period, is extremely important by controlling both the time and the intensity of the diatom and flagellate spring bloom. The GPP for diatoms decreases by more than 50% with the high respiration rate and increases by more than 100% with the low respiration rate. The GPP for flagellates is also affected by the diatom respiration increasing by more than 30% in some boxes for the high diatom respiration rate and

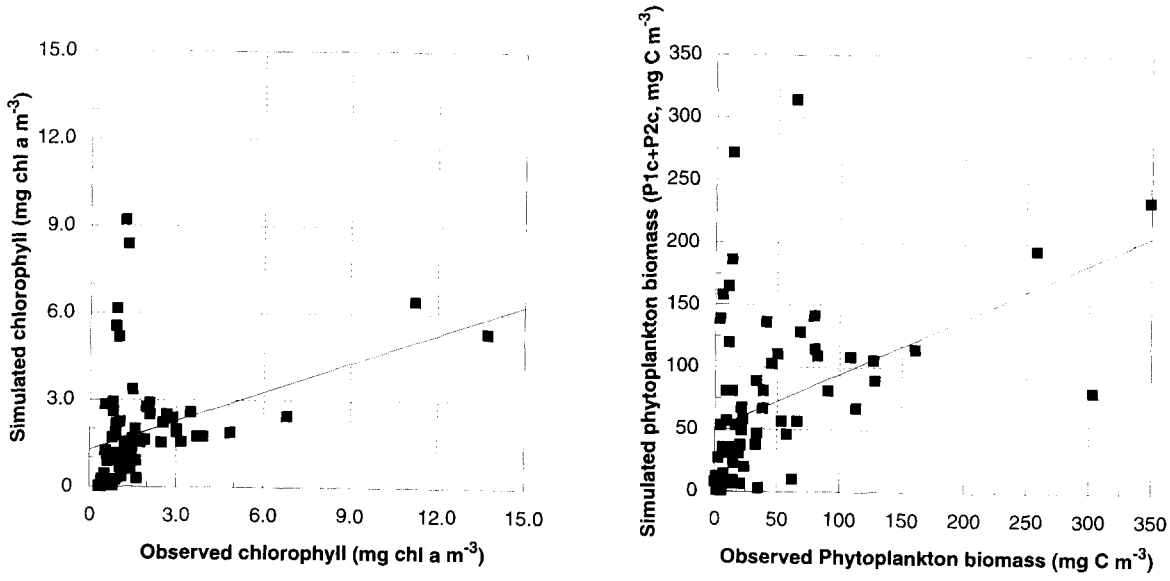


Fig. 9. Predicted model results against observed (BODC) data for total phytoplankton carbon (P1c+P2c, right) and chlorophyll (left). This comparison includes ERSEM boxes 4 to 9.

decreasing by about 12% for the low rate. The changes are in the opposite direction with regard to the two phytoplankton components with enhanced flagellate respiration rate, the diatoms increasing and the flagellates decreasing.

3.3.6. NUTRIENT STRESS LYSIS

The nutrient-stress lysis parameters determine what fraction goes to detritus (both DOC and POC) of the difference between the GPP in optimal nutrient conditions and the GPP in the real conditions. The effect of changing the diatom lysis rate on the biomasses of both components of phytoplankton is very small, with substantial increases in the summer flagellate peak in some boxes. Only small changes in both diatom and flagellate annual GPP are observed with negative covariation in the case of the diatoms and positive in the case of the flagellates. The effect of changing the flagellate lysis rate on the diatom biomass is insignificant but the flagellates show somewhat smaller biomasses in most boxes, particularly during the summer peak period. The effects on the annual GPP for diatoms are small (less than 6%) and covary with the parameter value while the annual GPP for flagellates, also small, shows the opposite sign.

3.3.7. ACTIVITY-DEPENDENT EXCRETION

The activity-dependent excretion parameters determine what fraction of the GPP goes to detritus (both DOC and POC). During the spring bloom the diatom and flagellate biomasses slightly change with changes in the diatom fraction that goes to detritus while the flagellate biomass decreases with increasing the flagellate fraction that goes to detritus. The opposite is true during the summer peak. The annual GPPs for diatoms show small variations positively covarying with the parameter values while those for flagellates covary mostly in a negative way.

The half-saturation constant of the bacterial protease contribution to activity-dependent excretion in diatoms has a rather negligible effect on the diatom biomasses while that on the flagellate biomasses is considerable in several boxes during the summer peak, decreasing in both cases with respect to the standard run.

3.3.8. APPORTIONING OF DOC AND POC EXCRETION

The fraction of the material that is lost in the lysis in the form of POC (the remaining being DOC) affects neither the nutrients nor the phytoplankton biomasses.

TABLE 5
Annual mean chlorophyll values in different North Sea areas (mg Chl $a \cdot m^{-3}$) from several sources.

ICES region	*ERSEM box*	*NERC-BODC*	*model results*
3	6-7	1.24	1.59
4	8	1.13	2.16
5	9-10	3.07#	2.19
7	4-5	1.04	1.64

*These values are taken from contour lines and must be considered only approximations.
Value calculated using only ERSEM box 10 area.

4. DISCUSSION

Even though the North Sea is one of the most intensively studied regions in the world, it is difficult to obtain a dataset big enough to allow a full comparison with a complex model like ERSEM. In the validation of the primary production module, model simulations have been mainly compared against the existing BODC (British Oceanographic Data Centre) data, but results are also going to be related with a series of more specific references. The central and southern regions of the North Sea are relatively well sampled, but the lack of primary production/chlorophyll data is particularly notorious for the northern regions, where we were unable to establish comparisons between model simulations and field data.

4.1. CARBON BIOMASS AND CHLOROPHYLL *A*

According to BODC data (monthly means extracted from a two-year data base and geographically averaged according to the ERSEM boxes situation) and considering all the central and southern ERSEM boxes, the main differences arise from the magnitude and timing of the spring bloom. Observed carbon peaks in the southern areas are found mostly during April-June, while in the simulated data the spring blooms are somewhat earlier (March-April) and with lower biomasses. While there is no distinct spring bloom in the observations in the central boxes (4 and 5), there is in the simulations, where the phytoplankton carbon can sometimes be double the observed values. The overall (boxes 4 to 9) total simulated carbon biomass compared to NERC-BODC observations is shown in Fig. 9 (r=0.44, n=80).

Simulated total chlorophyll, on the other hand, varied from near 0.1 to as much as 8.4 mg chl $a \cdot m^{-3}$ in boxes 4 and 5 and from 0.17 to 9.2 mg chl $a \cdot m^{-3}$ in the southern regions (boxes 7 to 9). Monthly chlorophyll means estimated from the 1988-1989 BODC data base fluctuate from 0.4 to 3.5 mg chl $a \cdot m^{-3}$ in the central regions. In the southern North Sea (boxes 7 to 9), chlorophyll ranges from near 0.5 mg chl $a \cdot m^{-3}$ to values as high as 13.74 mg chl $a \cdot m^{-3}$. The overall (boxes 4 to 9) relation between observed and simulated chlorophyll data is depicted in Fig. 9 (r=0.40, n=82; see also Table 5). Again here, the major discrepancy between the observed and modelled chlorophyll data is similar to the one mentioned for carbon biomass. The magnitude of the chlorophyll spring bloom does not correspond to the observations in the central regions, while the simulated peak is earlier and lower in the southern boxes. Overall, the model seems not to reproduce very well the difference between central and coastal areas of the North Sea (an explanation of this behaviour will be suggested below).

4.2. PRIMARY PRODUCTION

Reid *et al.* (1990) described the phytoplankton dynamics of the North Sea and reviewed some empirical measurements and calculations of primary production in different North Sea areas. According to their compilation, the mean net primary production in the central North Sea is 250 g $C \cdot m^{-2} \cdot a^{-1}$, in the northern North Sea values ranged from 150 to 200 g $C \cdot m^{-2} \cdot a^{-1}$, and in the southern North Sea production is about 200 g $C \cdot m^{-2} \cdot a^{-1}$. Simulated results in the northern North Sea (boxes 1/11, 2/12 and 3/13) averaged 106 g $C \cdot m^{-2} \cdot a^{-1}$, in the same order of magnitude but below the lower end of these data. In the central North Sea (boxes 4/14, 5/15 and 10) and in southern regions (boxes 7 to 9) simulated net primary productivity values averaged respectively 136 g $C \cdot m^{-2} \cdot a^{-1}$ and 154 g $C \cdot m^{-2} \cdot a^{-1}$, also lower than what could be expected from Reid *et al.* (1990).

Recently, Joint & Pomroy (1993) intensively sampled the southern and central North Sea (ICES boxes 3, 4, 5 and 7) for 15 months, to measure chlorophyll *a* and primary production. Most primary production values were obtained using a regression procedure linked with the chlorophyll measurements, in order to expand the primary production data to fit the much larger chlorophyll dataset. They reported values of primary production of 79 g $C \cdot m^{-2} \cdot a^{-1}$ for ICES region 3, 199 g $C \cdot m^{-2} \cdot a^{-1}$ for region 4, 261 for region 5 and

TABLE 6
Primary production values in different North Sea areas (g $C \cdot m^{-2} \cdot a^{-1}$) from several sources.

ICES region	*ERSEM box*	*Gieskes & Kraay (1984)*	*Joint & Pomroy (1993)*	*model results*
3	6-7	150	79	79.2
4	8	150	199	149.0
5	9-10	250	261	169.3
7	4-5	250	119	130.0

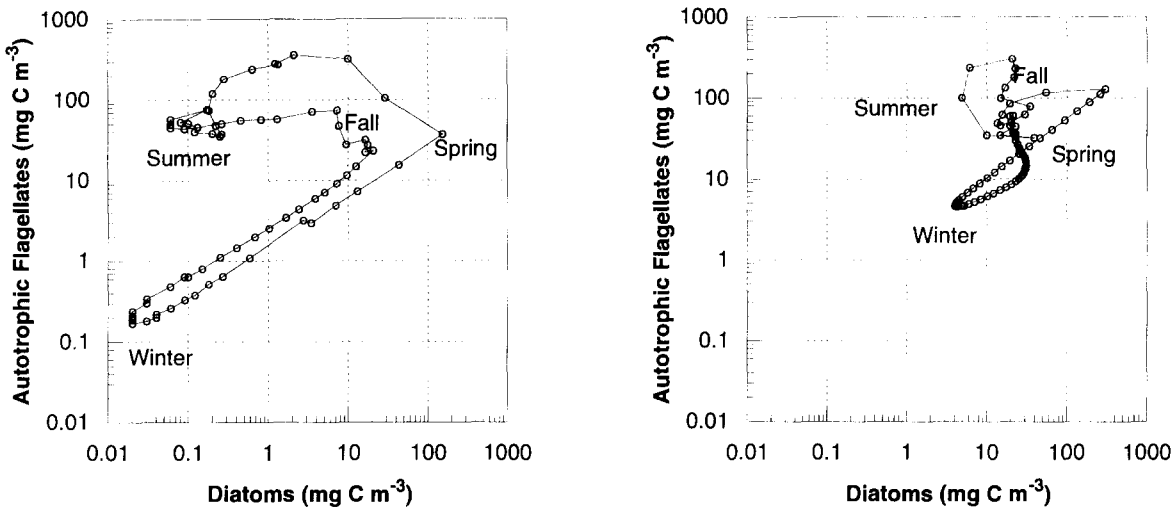


Fig. 10. Log-log plot of diatoms *vs* autotrophic flagellates. Left graph shows results for offshore box 1 in the northern North Sea while the right-hand graph depicts results for coastal box 8 in the Southern Bight. For clarity, symbols shown are at a 5-day interval.

119 g $C \cdot m^{-2} \cdot a^{-1}$ for region 7 (Table 5). These values are much lower than those indicated by Reid *et al.* (1990) for the central North Sea, which in turn come from Gieskes & Kraay (1984). The possible explanation suggested by Joint & Pomroy, is that Gieskes & Kraay measured primary production only over three months (May, July and September) and then extrapolated the data to obtain the annual production. This is likely to overestimate primary production for the whole year. Joint & Pomroy's primary production data compare well with modelled results in the UK coastal and central regions, but the model results in the southern North Sea boxes (8, 9 and 10) are again somewhat low.

It is clear that many factors influence the spatial pattern of primary production and biomass in the North Sea. However, only few of them seem to be crucial, *e.g.,* bottom topography, water circulation and nutrient discharge by rivers. According to several different research studies on nutrients, chlorophyll and primary production during the whole year (*i.e.*, Owens *et al.*, 1990; Reid *et al.*, 1990; Joint & Pomroy, 1993), coastal regions generally keep a higher level of nutrients during the whole year, allowing a more sustained (and differentiated) phytoplankton growth. This feature was also present in the simulations, since relatively high levels of nutrients (and phytoplankton) were maintained in these regions during the winter and summer seasons. According to the formulation, the phytoplankton evolution is assumed to be exponential (dependent on the existent biomass at a given moment), and higher initial levels of phytoplankton will allow a faster development. In coastal regions, this could result in earlier peaks than in offshore areas. This can be confirmed both in the model simulations (Table 1) and in nature (*e.g.* Reid *et al.*, 1990, who found the diatom bloom to develop as early as February near the Belgian coast). Model results, however, failed to explain the high primary production and biomass that direct measurements (Joint & Pomroy, 1993) have revealed in the southern regions of the North Sea. It is possible that the model structure, based on only two phytoplankton groups, is not suitable to reproduce the known *Phaeocystis* algal blooms that develop in these areas and that another specific variable concerning this group should be included. Another possible explanation is that the model's coarse spatial resolution is not suitable to adequately reproduce the strong environmental gradients (nutrient supply from rivers, sediment concentration, *etc.*) found near the coast, and so the *a posteriori* 'box averaged' data would be invalid. Finally, a better tuning of the whole model with respect to the ammonia concentration could possibly enhance the results.

Diatom growth in the North Sea is classically assumed to be limited by the availability of silicate (*e.g.,* Reid *et al.,* 1990), while flagellate behaviour is thought to be dependent on nitrogen or phosphorus. Model results indicate that the value of the diatom peak of the offshore regions is limited by silicate especially during the spring blooms, while incident light is the determinant factor the rest of the year. Near the shore, nutrient is a less determinant factor; light and possibly the site-dependent hydrodynamical conditions are the key components. This is in agreement with results from the strategic fjord ecosystem model of Ross *et al.* (1993), who recently suggested that primary production is controlled by physical fac-

tors (mainly temperature and irradiance) and the activities of higher trophic levels in a sea-loch ecosystem.

In fact, modelled phytoplankton appears to be especially sensitive to grazing when stressed by nutrients. After the spring bloom, the progressive nutrient limitation promotes a competitive exclusion between diatoms and flagellates. Grazing appears to be important during this nutrient-limited period, and generates random fluctuations. Bottom-up and top-down forces may coexist in the same community history (Hunter & Price, 1992) but this top-down force keeps a highly non-linear relationship that, if forced, could decouple and de-stabilize the 'upper' control (Hastings & Powell, 1991).

It is also interesting to analyse the relative contribution of each phytoplankton group to the total production. Earlier data from Louis *et al.* (1974) showed that diatoms predominated in the south while dinoflagellates were more abundant in the north. However, they found marked seasonal differences in this distribution. According to the same authors, diatoms generally dominate (cell numbers) in all months. More recently, Brockmann *et al.* (1990) found that phyto-

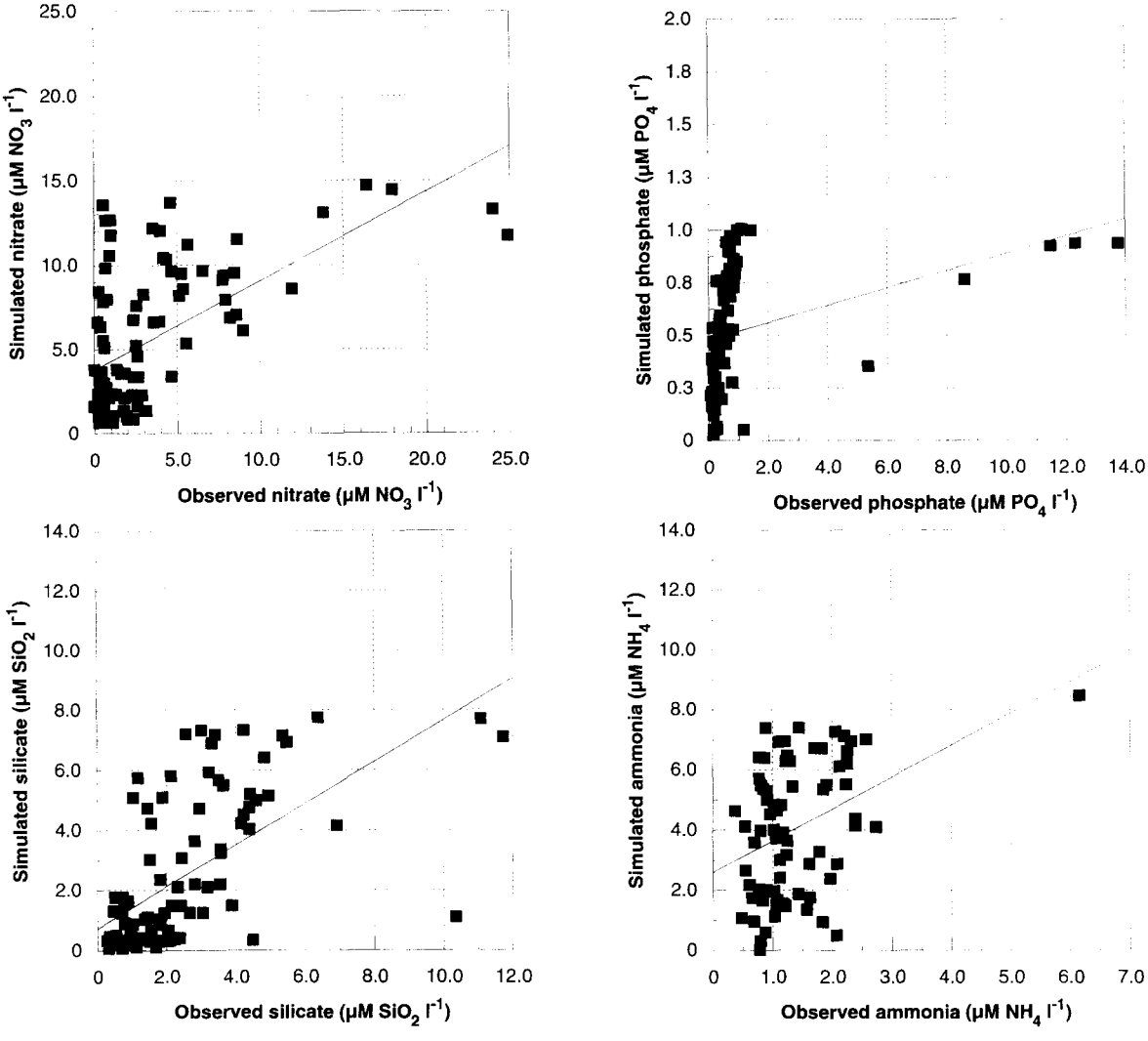


Fig. 11. Predicted model results against BODC data. Depth and regionally averaged BODC data for a. phosphate; b. silicate; c. nitrate and d. ammonia against predicted model results for ERSEM boxes 4, 5, 6, 8 and 9.

plankton carbon values during the spring peak ranged from 100 to 500 mg $C \cdot m^{-3}$ for the whole North Sea. Owens *et al.* (1990) carried out an extensive survey of 1987 data and showed that more than 75% of primary production was attributable to cells <5 μm small in diameter in the stratified regions. This proportion varies greatly in coastal regions, where organisms >5 μm accounted for most of the primary production.

There are many indications that the relative proportions of diatoms to autotrophic flagellates are very variable. Among these are the results of the sensitivity tests done, which indicate that the parameters directly, or even indirectly, related with the maximum growth rate of either group are the most sensitive ones. Simulation results showed that flagellate biomass and associated primary production predominate almost all the time. In fact, this is the opposite of what the general results of Louis *et al.* (1974) showed. However, flagellates in the primary production module were assumed to be organisms of cell sizes below 20 μm and model parameterization was according to that. If smaller organisms dominate primary production, simulation results agree with the more recent observations of Owens *et al.* (1990), being also within the range mentioned by Brockmann *et al.* (1990).

In offshore areas, the simulated diatom to flagellate proportion varies with the seasons of the year (Fig. 10, left). The relatively high temperatures and low nutrients of the summer especially favour the predominance of the flagellates over the diatoms, the latter growing strongly during spring but competing for nutrients with the flagellates the rest of the time. During the winter, both phytoplankton are strongly limited by light and water temperature. Physiological constants such as maximum uptake rate or half-saturation constants should play a major role in determining the relative preponderance of one group over the other. Nearshore values show both components concentrated over a narrow area (Fig. 10, right). Optimal temperatures and large nutrient availability, along with higher incident light levels, allowed both groups to maintain relatively high levels of biomass all through the year. The influence of one phytoplankton group over the other is less significant.

The particular behaviour of the module relative to the autotrophic flagellate/diatom proportions may also be based on the relative proportions of the different nutrient species involved. According to BODC data, model results are well related with observed phosphate (r=0.86, n=78) and also fairly good correlations are obtained for nitrate (r=0.73, n=78) and silicate (r=0.58, n=78, Fig. 11). A season-dependent $SiO_4/(NO_3+NH_4)$ proportion was found to exist in model results, since values for box 5 in the central North Sea during winter (0.4) and summer (0.8) are higher than in spring (0.15) and autumn (0.20). Data from Brockmann *et al.* (1990) and Owens *et al.* (1990) indicate a similar $SiO_4/(NO_3+NH_4)$ for the same region. However, the same comparison with coastal boxes (6, 7, 8 and 9) indicates that the silicate to nitrogen proportion is as much as an order of magnitude lower than it should be (an average of 0.3 (model results) against 2.0 (field measurements), same authors). This suggests that modelled dissolved nitrogen in coastal environments is higher than in observations, perhaps excessively enhancing the flagellate growth. Here the same comments concerning primary production differences between the model and field measurements near the shore apply.

4.3. SENSITIVITY TEST

The results of the sensitivity test show a great influence of the growth and respiration/excretion parameters on the model solutions. Low growth rates destabilize each component of phytoplankton, promoting the development of the other one. On the contrary, high growth rates for each phytoplankton component stabilize that component while destabilizing the other one through a fiercer competition for nutrients without, in the case of diatoms, increasing significantly their own biomass. The effect on the nutrients is, in both cases, in the direction of a faster uptake of those nutrients which are more specific of the phytoplankton components: silicate and ammonia for diatoms and phosphate and nitrate for flagellates.

The half-saturation constants as well as the ammonia preference parameter have very little effect on the model solutions indicating that the nutrient concentrations do not limit the growth rates except in some short periods when either diatoms or flagellates are blooming. However, it should be stressed that this behaviour is strongly dependent on the nitrogen tuning of the model.

The large ammonia concentrations found in many boxes most of the time cannot upset the competition between diatoms and flagellates in favour of the latter and are not controlled by the ammonia preference parameter or by the ammonia uptake formulation.

The respiration terms modify the net growth rate and therefore the division rate of the phytoplankton population. As a matter of fact, the portion of GPP that goes to respiration causes the net phytoplankton growth rate to be smaller the larger the respiration rate is. On the other hand, the annual net primary production is controlled mainly by the nutrient availability, nutrients being (unlike carbon or light) the only limiting resource. As a result, the larger the respiration rate is for any of the two phytoplankton components, the larger the joint GPP should be (even though the phytoplankton populations grow more slowly). As an example, the combined annual GPP of diatoms and flagellates for the standard run in box 5 is 854 mg $C \cdot m^{-2} \cdot d^{-1}$. When the *srsP1$* takes the larger value, the combined GPP is 995 and when the *srsP1$* takes the smaller value, the combined GPP is 839 mg

$C \cdot m^{-2} \cdot d^{-1}$. The NPP instead should remain stable.

Overall, it seems that the phytoplankton growth rates are unrealistically low either through the growth parameters tested or through the temperature/light effects. The phytoplankton and nutrient evolution would be crisper with larger growth rates without great changes in the peak biomasses or annual NPPs (export to the other trophic levels). The overall growth rates in the standard run are extremely low ($<0.2\ d^{-1}$) during the spring bloom when organisms, particularly diatoms, should be in their best condition. One doubling per day is not unrealistic during the blooming season, while the model parameters only allow for one doubling every five or more days. A comparison with other phytoplankton growth schemes, like the Droop formulation (Droop, 1973, 1975; Tett *et al.*, 1986) which is based on the internal nutrient content, can probably clarify this point, but again it should be noted that other model runs trying to adjust the ammonia concentrations and/or increasing the growth rate with a lower fixed nutrient content seem advisable.

Another issue addressed in the sensitivity test is the long-term stability of the model when the parameter values change, causing important deviations of the distribution of nutrient concentrations and biomasses, particularly the year-end values. It is rather difficult to assess the long-term effect of slight changes in the phytoplankton biomasses at the year end without running the model for a sufficiently large number of years with the new set of parameter values. The difference between year-end values and those at the beginning of the year may lead to multi-year variations and eventually to instabilities. Phosphate and ammonia values at the end of the year are strongly affected by changes in most parameters, particularly those in the maximum growth rates, the nutrient quota, the respiration and excretion, the bacterial protease and the sedimentation velocity. The silicate year-end values are also affected by the growth rates, the rest respiration of diatoms and the sedimentation parameters.

5. CONCLUSIONS

1. According to Joint & Pomroy's (1993) extensive survey, the ERSEM primary production module simulates reasonably well primary production in the central regions of the North Sea. However, model results are lower than what could be expected in coastal boxes, specially in the southern North Sea.
2. The model generally gives an unexpectedly high autotrophic flagellate to diatom ratio. Suggested explanations are parameterization of maximum growth rate but most likely the relatively large nitrogen to silicate dissolved nutrient proportions in near-shore areas.
3. The primary productivity module is especially sensitive to the flagellate and diatom interaction and competitive behaviour for inorganic nutrients. This could be extended to those parameters or functions directly affecting the maximum growth rate values such as the temperature regulation factor, water temperature, *etc.*
4. Among the loss rate processes, respiration was by far the most important factor, even more than excretion of dissolved organic matter or lysis. Sinking, even though simulated only for diatoms, is slightly more significant than lysis but considerably less important than leakage.
5. Simulated phytoplankton growth in the North Sea seems to be limited by different processes according to the area. Coastal areas tend to be more dependent on local hydrodynamics and light extinction mechanisms, while offshore regions are mostly controlled by nutrients and incident light. Zooplankton seems to play its major role on phytoplankton stressed by nutrients after the blooms.
6. The module does not seem to adequately reproduce the differences between coastal and central regions of the North Sea. There is a need of further investigation by better tuning of the model with respect to the ammonia concentration, the growth rates or including at least a third phytoplankton group (*e.g., Phaeocystis*) in the model structure. If the other possibilities do not enhance the model performance, this latter inclusion will probably help obtain more accurate estimates of primary production and biomass in coastal areas, as well as a more realistic dissolved silicate:total dissolved nitrogen ratio.
7. Due to the method used in the sensitivity analysis, a number of non-sensitive processes can be lumped, specially those referring to the phytoplankton respiration and excretion. The sensitivity results depend on the values of the other parameters, and may vary if these values are changed. As a consequence, conclusions derived from this sensitivity test must always be drawn with great caution.

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The model used for the present work was a collective effort of the ERSEM participants while the primary productivity module was developed, before the project started, by the NIOZ team. The authors had no direct involvement in either the module development or in the selection of the parameter values used in the standard run.

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Appendix I

Primary production module .

symbol	*name*	*value*	*units*
State variables			
P1c	Diatoms carbon		mg C·m^{-3}
P1n	Diatoms nitrogen		mmol N·m^{-3}
P1p	Diatoms phosphorus		mmol P·m^{-3}
P1s	Diatoms silicate		mmol Si·m^{-3}
P2c	Flagellates carbon		mg C·m^{-3}
P2n	Flagellates nitrogen		mmol N·m^{-3}
P2p	Flagellates phosphorus		mmol P·m^{-3}
N3n	Dissolved inorganic nitrate		mmol N·m^{-3}
N4n	Dissolved inorganic ammonia		mmol N·m^{-3}
N1p	Dissolved inorganic phosphate		mmol P·m^{-3}
N5s	Dissolved inorganic silicate		mmol Si·m^{-3}
B1c	Bacterial biomass, carbon		mg C·m^{-3}
Derived quantities			
Chl	Total chlorophyll *a*		mg chl *a*·m^{-3}
Terms for the overall biological fluctuations			
SP1c	Overall diatoms biological fluctuation, carbon		mg C·m^{-3}·d^{-1}
SP1n	Overall diatom biological fluctuation, nitrogen		mmol N·m^{-3}·d^{-1}
SP1p	Overall diatom biological fluctuation, phosphorus		mmol P·m^{-3}·d^{-1}
SP1s	Overall diatom biological fluctuation, silicate		mmol Si·m^{-3}·d^{-1}
SP2c	Overall flagellate biological fluctuation, carbon		mg C·m^{-3}·d^{-1}
SP2n	Overall flagellate biological fluctuation, nitrogen		mmol N·m^{-3}·d^{-1}
SP2p	Overall flagellate biological fluctuation, phosphorus		mmol P·m^{-3}·d^{-1}
Limitation and regulation factors			
etP1	Temperature regulation factor, *P1c*		-
etP2	Temperature regulation factor, *P2c*		-
eiPI	Light limitation factor		-
eN3P1n	Nitrate limitation factor, *P1c*		-
eN4P1n	Ammonia limitation factor, *P1c*		-
eNIP1n	Total nitrogen limitation factor, *P1c*		-
eN3P2n	Nitrate limitation factor, *P2c*		-
eN4P2n	Ammonia limitation factor, *P2c*		-
eNIP2n	Total nitrogen limitation factor, *P2c*		-
eN1P1	Phosphorus limitation factor, *P1c*		-
eN1P2	Phosphorus limitation factor, *P2c*		-
eN5P1s	Silicate limitation factor, *P1c*		-
eNIP1	Global limitation factor, *P1c*		-
eNIP2	Global limitation factor, *P2c*		-
Main Carbon factors and fuxes			
sumP1	Actual carbon growth rate, *P1c*		d^{-1}
sumP2	Actual carbon growth rate, *P2c*		d^{-1}
qnP1c	Nitrogen overall cell quota, *P1c*		mmol N·(mg C)$^{-1}$
qpP1c	Phosphorus overall cell quota, *P1c*		mmol P·(mg C)$^{-1}$
qsP1c	Silicate overall cell quota, *P1c*		mmol Si·(mg C)$^{-1}$
qnP2c	Nitrogen overall cell quota, *P2c*		mmol N·(mg C)$^{-1}$
qpP2c	Phosphorus overall cell quota, *P2c*		mmol P·(mg C)$^{-1}$
fP1O3c	Total respiration rate, *P1c*		mg C·m^{-3}·d^{-1}
fO3P1c	Gross production, *P1c*		mg C·m^{-3}·d^{-1}
fP2O3c	Total respiration rate, *P2c*		mg C·m^{-3}·d^{-1}
fO3P2c	Gross production, *P2c*		mg C·m^{-3}·d^{-1}
sraP1	Specific activity respiration rate, *P1c*		d^{-1}
sraP2	Specific activity respiration rate, *P2c*		d^{-1}

Primary production module (continued).

symbol	*name*	*value*	*units*
sroP1	Specific nutrient stress respiration rate, *P1c*		d^{-1}
sroP2	Specific nutrient stress respiration rate, *P2c*		d^{-1}
srsP1	Specific rest respiration rate, *P1c*		d^{-1}
srsP2	Specific rest respiration rate, *P1c*		d^{-1}
fP1R1c	DOM excretion rate, *P1c*		mg $C \cdot m^{-3} \cdot d^{-1}$
fP2R1c	DOM excretion rate, *P2c*		mg $C \cdot m^{-3} \cdot d^{-1}$
fP1R6c	Lysis rate, *P1c*		mg $C \cdot m^{-3} \cdot d^{-1}$
fP2R6c	Lysis rate, *P2c*		mg $C \cdot m^{-3} \cdot d^{-1}$
SEDIP1	Actual sedimentation, *P1c*		$m \cdot d^{-1}$
SEDIP2	Actual sedimentation, *P2c*		$m \cdot d^{-1}$
Main Nitrogen fluxes			
fNIP1n	Total nitrogen uptake rate, *P1c*		mmol $N \cdot m^{-3} \cdot d^{-1}$
fNIP2n	Total nitrogen uptake rate, *P2c*		mmol $N \cdot m^{-3} \cdot d^{-1}$
fN3P1n	Nitrate uptake rate, *P1c*		mmol $N \cdot m^{-3} \cdot d^{-1}$
fN4P1n	Ammonia uptake rate, *P1c*		mmol $N \cdot m^{-3} \cdot d^{-1}$
fN3P2n	Nitrate uptake rate, *P2c*		mmol $N \cdot m^{-3} \cdot d^{-1}$
fN4P2n	Ammonia uptake rate, *P2c*		mmol $N \cdot m^{-3} \cdot d^{-1}$
fP1R1n	DOM excretion rate, *P1n*		mmol $N \cdot m^{-3} \cdot d^{-1}$
fP1R6n	Lysis excretion rate, *P1n*		mmol $N \cdot m^{-3} \cdot d^{-1}$
fP2R1n	DOM excretion rate, *P2n*		mmol $N \cdot m^{-3} \cdot d^{-1}$
fP2R6n	Lysis excretion rate, *P2n*		mmol $N \cdot m^{-3} \cdot d^{-1}$
Main Phosphorus fluxes			
fN1P1p	Phosphate uptake rate, *P1c*		mmol $P \cdot m^{-3} \cdot d^{-1}$
fN1P2p	Phosphate uptake rate, *P2c*		mmol $P \cdot m^{-3} \cdot d^{-1}$
fP1R1p	DOM excretion rate, *P1p*		mmol $P \cdot m^{-3} \cdot d^{-1}$
fP1R6p	Lysis excretion rate, *P1p*		mmol $P \cdot m^{-3} \cdot d^{-1}$
fP2R1p	DOM excretion rate, *P2p*		mmol $P \cdot m^{-3} \cdot d^{-1}$
fP2R6p	Lysis excretion rate, *P2p*		mmol $P \cdot m^{-3} \cdot d^{-1}$
Main Silicate fluxes			
fN5P1s	Silicate uptake rate, *P1c*		mmol $Si \cdot m^{-3} \cdot d^{-1}$
fP1R1s	DOM excretion rate, *P1s*		mmol $Si \cdot m^{-3} \cdot d^{-1}$
fP1R6s	Lysis excretion rate, *P1s*		mmol $Si \cdot m^{-3} \cdot d^{-1}$
Diatom parameters, carbon			
sumP1$	Maximum specific growth rate, *P1c*	2.50	d^{-1}
q10P1$	Doubling temperature, *P1c*	4.00	-
pu_raP1$	Activity respiration rate, *P1c*	0.10	-
pum_roP1$	Nutrient stress respiration rate, *P1c*	0.05	-
srsP1$	Rest respiration rate, *P1c*	0.25	d^{-1}
pe_R1P1c$	Labile organic carbon excretion, *P1c*	0.20	-
pum_eoP1$	Nutrient dependent lysis rate, *P1c*	0.30	-
pu_eaP1$	Activity dependent excretion, *P1c*	0.05	-
chB1eP2c$	Bact. biom. where lysis doubles due to prot. activity	600.0	mg $C \cdot m^{-3}$
Diatom parameters, nitrogen			
qnP1c$	Maximum nitrogen quota	0.0143	mmol $N \cdot (mg\ C)^{-1}$
chP1n$	Nitrogen half saturation constant, *P1c*	0.10	mmol $N \cdot m^{-3}$
chPIn$	Nitrogen half sat. constant, whole phytoplankton	0.05	mmol $N \cdot m^{-3}$
Diatom parameters, phosphorus			
qpP1c$	Maximum phosphorus quota	1.096E-3	mmol $P \cdot (mg\ C)^{-1}$
chP1p$	Phosphate half saturation constant	0.10	mmol $P \cdot m^{-3}$
Diatom parameters, silicate			
qsP1c$	Maximum silicate quota	0.0175	mmol $Si \cdot (mg\ C)^{-1}$
chP1s$	Silicate half saturation constant	0.30	mmol $Si \cdot m^{-3}$

Primary production module (continued).

symbol	*name*	*value*	*units*
Flagellate parameters, carbon			
sumP2c$	Maximum specific growth rate, *P2c*	2.00	d^{-1}
q10P2$	Doubling temperature, *P2c*	4.00	-
pu_raP2$	Activity respiration rate, *P2c*	0.25	-
pum_roP2$	Nutrient stress respiration rate, *P2c*	0.05	-
srsP2$	Rest respiration rate, *P2c*	0.15	d^{-1}
pe_R1P2c$	Labile organic carbon excretion, *P2c*	0.50	-
pum_eoP2$	Nutrient dependent lysis rate, *P2c*	0.30	-
pu_eaP2$	Activity dependent excretion, *P2c*	0.05	-
Flagellate parameters, nitrogen			
qnP2c$	Maximum nitrogen quota	0.0157	mmol N·(mg C)$^{-1}$
chP2n$	Nitrogen half saturation constant, *P2c*	0.05	mmol N·m^{-3}
Flagellate parameters, phosphorus			
qpP2c$	Maximum phosphorus quota	0.612E-3	mmol P·(mg C)$^{-1}$
chP2p$	Phosphate half saturation constant, *P2c*	0.05	mmol P·m^{-3}
Light Parameters			
EIR	Daily average total light in a given box		W·m^{-2}
I_z*	Available light at bottom of box		W·m^{-2}
I_0*	Incident light at top of box		W·m^{-2}
I_{PAR}	Photosynthetically available irradiance (surface)		W·m^{-2}
I_{OPT}	Optimum irradiance		W·m^{-2}
clPIi$	Minimum parameter in Steele´s equation	40.0	W·m^{-2}
pEIR_eow$	Conversion factor to PAR	0.50	-
ruPIi$	Maximum daily shift in optimal irradiance	0.25	W·m^{-2}
*xEPS**	Extinction coefficcient		m^{-1}
*sunq**	Daylength		h
Sinking parameters			
esNIP1$	Threshold value below which sinking starts, P1	0.75	
esNIP2$	Threshold value below which sinking starts, P2	0.75	-
resP1m$	Maximum sinking rate, P1	45.0	m·d^{-1}
resP2m$	Maximum sinking rate, P2	0.0	m·d^{-1}
Other symbols used in this manuscript			
*depth$**	Average depth for each box		m
Limnut$	Switch to select multiplicative or Liebig nutrient limitation	0 or 1	-
uhP1c$	Carbon to chlorophyll conversion parameter, P1	50	mg C·(mg chl *a*)$^{-1}$
uhP2c$	Carbon to chlorophyll conversion parameter, P2	25	mg C·(mg chl *a*)$^{-1}$
xpref-N4n$	Preference of ammonia over nitrate	3.0	-
xR1n$	Nitrogen content in cytoplasma *vs* structural comp.	1.2	-
xR1p$	Phosphorus content in cytoplasma *vs* structural comp.	1.2	-
xR1s$	Silicate content in cytoplasma *vs* structural comp.	0.1	-
x	One of the phytoplankton classes	1 or 2	-
w	Vertical advection coefficient		m·d^{-1}
λ	Turbulent vertical diffusivity		m^2·d^{-1}

* *estimated in the physical model*

Appendix II

Sensitivity analysis Table

Standard values are shown in mg $C \cdot m^{-2} \cdot d^{-1}$, all other values are presented as a percentage of variation in relation to the standard, and are in bold typeface when results are at least 50% different from those given by the standard run.

parameter	*diatoms gross primary production*														
	boxes														
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*
standard	*86.4*	*245.5*	*132.0*	*316.4*	*273.1*	*224.3*	*265.6*	*312.1*	*238.4*	*282.3*	*3.8*	*3.0*	*0.8*	*3.5*	*0.6*
sumP1$	**350.1**	**156.5**	**195.9**	126.7	115.2	148.2	117.8	129.7	123.3	129.6	**318.4**	**363.3**	**391.3**	**258.5**	**159.2**
(-)	**0.8**	**0.9**	**3.0**	**2.1**	**8.5**	**0.7**	**9.0**	**14.5**	**31.7**	**10.6**	**0.0**	**0.0**	**0.0**	**2.9**	**16.7**
sumP2$	**12.5**	**16.5**	**25.6**	**36.6**	79.6	**25.2**	71.5	71.3	72.2	71.3	**10.5**	**16.7**	**25.0**	**31.4**	66.7
(-)	**170.5**	130.9	126.4	115.8	108.3	126.2	113.3	115.0	116.2	115.7	**331.6**	**386.7**	**387.5**	**302.9**	**166.7**
chP1p$	78.2	82.4	87.0	96.7	98.7	88.4	97.7	96.4	94.6	92.6	84.2	83.3	87.5	88.6	100.0
(-)	134.0	114.7	113.0	105.0	101.6	107.0	102.9	103.6	105.7	105.6	123.7	123.3	125.0	114.3	100.0
chP1n$	94.8	96.7	98.7	100.0	100.1	99.4	100.0	99.9	98.7	99.9	97.4	100.0	100.0	100.0	100.0
(-)	107.6	103.6	100.8	100.1	100.0	100.6	100.1	100.2	100.2	100.1	105.3	103.3	100.0	100.0	100.0
chP1s$	88.3	92.5	94.3	96.8	98.3	91.6	97.7	97.0	97.4	96.1	92.1	93.3	87.5	94.3	100.0
(-)	111.0	108.0	105.8	103.8	101.8	108.3	102.8	103.5	103.0	104.6	113.2	110.0	112.5	108.6	116.7
chP2p$	117.6	109.5	106.2	102.8	100.3	104.0	101.8	102.1	104.2	102.6	115.8	116.7	112.5	114.3	116.7
(-)	83.0	85.0	91.5	98.0	101.1	93.0	98.7	97.5	94.5	95.1	86.8	86.7	87.5	88.6	100.0
chP2n$	104.7	102.4	100.5	100.0	100.1	100.3	100.0	100.1	100.1	100.0	105.3	103.3	100.0	100.0	100.0
(-)	95.7	97.1	99.3	100.1	100.0	99.8	100.0	100.0	100.0	100.1	97.4	100.0	100.0	100.0	100.0
chPIn$	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
(-)	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
xpref_N4n$	100.9	100.4	102.4	102.1	111.5	100.1	102.9	101.8	100.6	103.2	102.6	100.0	100.0	97.1	100.0
(-)	101.2	100.5	102.3	102.6	115.1	100.5	103.9	102.5	101.3	103.2	102.6	100.0	100.0	97.1	**33.3**
pu_eaP1$	126.2	113.3	111.4	106.6	103.7	111.8	104.4	105.6	103.9	105.6	134.2	126.7	125.0	120.0	116.7
(-)	132.3	113.6	113.8	107.8	104.3	113.3	105.1	106.4	104.4	106.6	139.5	130.0	137.5	125.7	116.7
pu_raP1$	84.7	91.6	94.9	98.3	101.0	89.3	100.1	98.0	99.7	98.8	84.2	80.0	87.5	85.7	100.0
(-)	119.0	105.3	105.5	101.1	98.7	106.5	99.4	100.9	99.7	101.0	126.3	123.3	125.0	117.1	100.0
pum_eoP1$	87.4	92.3	95.0	96.6	98.2	92.3	97.9	97.6	97.8	97.0	89.5	90.0	87.5	91.4	100.0
(-)	112.3	107.4	105.2	104.1	102.1	106.8	102.4	102.4	102.4	103.0	115.8	113.3	112.5	111.4	116.7
chB1eP2c$	100.7	100.5	100.2	100.2	100.0	100.3	100.2	100.2	100.2	100.1	102.6	103.3	100.0	100.0	100.0
(-)	99.3	101.3	99.9	99.8	99.8	99.6	100.0	99.9	99.9	99.8	100.0	100.0	100.0	100.0	100.0
pum_roP1$	98.8	99.9	100.2	100.3	100.5	99.3	100.4	100.3	100.3	100.2	100.0	100.0	100.0	100.0	100.0
(-)	101.6	100.6	100.0	99.8	99.6	100.6	99.8	99.9	99.9	99.9	102.6	103.3	100.0	102.9	100.0
srsP1$	**47.8**	64.3	74.2	74.3	85.5	61.3	80.7	78.9	89.1	83.1	**34.2**	**40.0**	**50.0**	**51.4**	83.3
(-)	**214.1**	118.7	138.6	106.7	101.2	122.6	100.8	106.7	100.8	106.0	**239.5**	**253.3**	**275.0**	**200.0**	133.3
qsP1c$	80.6	78.5	78.3	79.8	79.9	81.5	78.7	80.7	79.3	80.7	86.8	96.7	87.5	88.6	83.3
(-)	135.3	137.0	136.7	137.5	136.2	132.7	133.6	130.4	132.2	128.4	139.5	116.7	137.5	128.6	133.3
resP1m$	94.9	96.1	97.5	99.6	100.0	100.5	99.7	99.6	98.6	99.1	102.6	100.0	100.0	100.0	100.0
(-)	108.7	105.5	103.9	100.8	99.9	99.1	100.4	100.5	101.8	100.9	100.0	100.0	100.0	100.0	100.0
esNIP1$	**3.6**	**4.0**	**9.1**	**24.7**	**46.6**	**2.9**	**34.8**	**37.2**	**38.2**	**35.3**	**2.6**	**6.7**	**12.5**	**31.4**	66.7
(-)	134.4	118.9	114.8	102.7	100.0	94.8	100.8	101.5	105.7	101.2	92.1	90.0	87.5	91.4	100.0
srsP2$	124.4	109.9	108.1	107.7	105.5	116.5	105.9	107.5	104.8	105.1	**181.6**	**183.3**	**187.5**	**162.9**	133.3
(-)	68.4	75.5	87.3	78.7	85.4	69.8	84.8	85.1	92.7	124.8	60.5	56.7	75.0	65.7	83.3
qnP2c$	96.2	92.1	100.3	101.2	107.0	102.0	101.2	100.6	100.3	103.2	134.2	106.7	112.5	100.0	100.0
(-)	102.8	102.2	98.6	100.2	98.6	99.7	101.5	101.9	100.5	96.1	78.9	100.0	100.0	105.7	116.7
qpP2c$	83.7	89.7	83.0	94.7	95.8	96.4	95.6	97.4	85.5	83.4	97.4	103.3	125.0	114.3	116.7
(-)	114.6	105.9	106.9	105.8	108.5	105.4	103.4	102.5	102.3	103.2	118.4	103.3	100.0	94.3	100.0
esNIP2$	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
(-)	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
pum_eoP2$	106.5	104.7	102.8	101.3	100.1	101.7	100.7	100.8	102.0	101.2	118.4	110.0	112.5	105.7	100.0
(-)	95.5	95.7	97.6	99.2	99.9	97.8	99.5	99.4	98.1	98.3	84.2	96.7	87.5	97.1	100.0
pu_eaP2$	106.4	103.7	102.0	101.6	100.7	104.2	101.3	101.9	101.8	101.3	113.2	113.3	112.5	108.6	100.0
(-)	93.8	95.8	98.0	98.5	99.5	95.1	98.6	98.1	98.2	98.8	92.1	90.0	87.5	91.4	100.0
pu_raP2$	133.4	115.0	110.7	107.5	103.8	115.0	106.0	107.7	107.9	106.6	**165.8**	**170.0**	**175.0**	**151.4**	133.3
(-)	72.8	73.8	84.3	87.4	97.0	80.0	91.8	89.8	92.5	94.5	73.7	60.0	75.0	65.7	83.3

Standard values are shown in mg $C \cdot m^{-2} \cdot d^{-1}$, all other values are presented as a percentage of variation in relation to the standard, and are in bold typeface when results are at least 50% different from those given by the standard run.

parameter	*flagellates gross primary production*														
	boxes														
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*
standard	*535.9*	*882.7*	*519.3*	*865.3*	*580.2*	*317.8*	*514.8*	*558.9*	*503.5*	*628.4*	*3.8*	*3.5*	*0.9*	*5.3*	*1.2*
sumP1$	91.0	91.2	94.1	95.1	99.0	92.3	102.7	98.1	85.0	93.0	**43.4**	79.8	63.2	85.7	101.0
(-)	123.0	125.6	130.0	144.9	**164.5**	**160.1**	**159.2**	148.6	143.1	137.6	147.0	**165.7**	**166.7**	141.5	125.0
sumP2$	**150.0**	149.8	148.4	**166.2**	**182.0**	**208.9**	**175.8**	**166.3**	**167.0**	**158.9**	**244.9**	**232.3**	**241.9**	**175.2**	112.2
(-)	76.9	66.6	74.6	65.5	58.2	**31.7**	63.7	57.8	60.4	59.9	**26.3**	**42.9**	**33.3**	50.9	58.4
chP1p$	101.9	105.2	103.6	102.7	102.7	105.9	107.8	101.8	104.2	104.4	110.7	106.1	98.9	99.9	103.6
(-)	96.7	95.0	96.6	96.9	97.5	96.0	103.4	98.2	95.2	96.3	89.5	97.3	88.9	98.1	100.1
chP1n$	100.2	101.3	100.4	100.1	100.0	100.3	105.2	100.0	100.0	99.9	102.8	100.4	88.0	99.9	103.6
(-)	99.0	98.5	99.5	99.9	99.9	99.6	105.2	99.8	99.7	99.8	97.3	100.1	100.0	100.0	100.1
chP1s$	100.7	102.2	101.4	101.5	101.6	104.7	106.9	101.0	101.5	101.7	105.5	103.3	98.9	99.9	103.6
(-)	98.7	97.4	98.4	98.3	98.3	94.9	104.4	98.8	98.1	97.8	94.7	97.2	88.9	98.1	100.1
chP2p$	97.1	93.8	95.0	94.0	93.8	92.6	100.3	95.1	92.1	92.7	92.3	97.5	88.0	98.0	103.6
(-)	103.1	107.6	106.6	107.0	107.1	107.8	110.8	105.4	109.1	109.9	110.5	105.8	100.0	99.9	100.1
chP2n$	99.3	98.7	99.5	99.8	99.8	99.7	105.6	99.8	99.7	99.8	100.2	100.4	99.0	99.8	103.6
(-)	100.4	101.6	100.4	100.1	100.1	100.0	107.6	100.1	100.0	99.9	102.7	97.2	100.0	99.9	100.1
chPIn$	100.5	100.0	100.0	100.0	99.9	100.1	105.8	100.1	99.9	100.0	100.2	100.4	99.0	99.8	103.6
(-)	100.6	99.9	100.0	100.0	100.1	99.7	105.7	100.1	100.1	99.9	100.0	100.0	100.0	99.9	100.1
xpref_N4n$	99.9	100.4	102.4	105.9	110.4	99.7	111.9	104.1	109.9	106.8	100.2	97.5	88.0	92.4	95.0
(-)	100.0	100.5	102.8	106.4	112.9	99.2	112.5	104.5	111.9	107.4	100.0	97.1	88.9	92.4	83.3
pu_eaP1$	97.6	96.3	97.4	95.9	96.1	91.2	103.1	98.2	95.7	96.3	87.0	94.6	88.0	96.1	103.6
(-)	97.3	95.5	96.9	95.2	95.9	89.9	102.6	98.2	95.4	95.6	84.2	91.4	88.9	94.3	100.0
pu_raP1$	101.2	102.7	101.4	102.5	103.3	107.2	107.3	102.1	83.2	102.3	113.4	106.1	99.0	103.6	103.6
(-)	98.6	97.9	98.8	98.0	97.9	94.1	103.9	98.6	97.4	97.7	89.5	94.2	88.9	96.2	100.0
pum_eoP1$	101.4	103.0	102.2	102.8	101.9	104.7	107.0	100.8	102.2	102.1	105.4	100.3	99.0	99.9	103.6
(-)	97.9	96.8	97.7	96.7	97.9	95.2	104.4	99.3	97.6	97.6	94.8	97.0	88.9	98.1	100.0
chB1eP2c$	99.8	99.8	99.8	99.8	99.6	99.8	105.6	99.7	99.6	99.9	100.2	97.4	99.0	99.9	103.6
(-)	100.2	100.2	100.2	100.2	100.3	99.9	105.5	100.0	100.2	99.8	100.1	99.9	100.1	100.0	100.0
pum_roP1$	100.1	100.2	100.2	100.1	99.9	100.5	105.7	99.9	99.9	100.2	100.2	100.3	99.0	99.9	103.6
(-)	99.8	99.6	99.7	99.8	100.0	99.2	105.4	99.8	99.9	99.5	100.1	97.0	100.1	100.0	100.0
srsP1$	110.3	85.1	109.2	116.9	130.4	129.5	129.4	119.9	118.1	114.1	144.9	126.0	142.9	120.7	95.0
(-)	93.6	92.8	95.4	94.6	96.9	87.7	101.2	97.3	94.8	93.2	**50.0**	82.7	66.7	86.8	100.0
resP1m$	104.0	105.8	106.7	110.5	110.6	114.3	115.8	107.8	112.5	110.1	110.7	106.0	98.9	101.9	112.3
(-)	93.2	87.3	87.4	80.8	82.3	76.9	90.5	88.9	78.4	82.4	86.9	94.1	89.0	94.3	83.3
resP1m$	100.1	101.4	100.7	100.3	99.9	100.4	106.5	100.5	100.9	100.8	102.9	100.3	98.9	99.9	103.7
(-)	100.0	98.1	99.0	99.4	100.0	99.5	104.0	99.1	98.5	98.6	97.5	99.9	100.1	100.0	100.0
esNIP1$	122.1	125.0	128.8	139.2	155.6	159.7	115.3	144.0	144.2	133.2	147.7	163.3	153.9	126.3	103.7
(-)	97.9	94.0	96.9	98.4	100.2	99.5	100.8	96.8	93.5	94.8	94.8	99.9	89.0	100.0	100.0
srsP2$	97.2	97.1	99.6	95.1	90.4	188.7	100.7	94.2	94.7	95.2	55.4	66.0	54.9	75.4	95.1
(-)	110.2	105.0	102.5	110.6	118.2	129.9	117.2	111.2	106.6	105.5	195.0	174.1	189.1	141.5	108.3
qnP2$	88.8	92.9	86.4	106.1	109.0	99.7	110.1	102.8	106.9	104.6	124.0	114.8	98.9	96.1	95.1
(-)	116.4	98.3	95.3	92.5	90.6	100.7	99.0	95.5	92.2	92.2	81.7	97.0	100.0	100.0	99.9
qpP2c$	100.6	87.9	88.5	82.7	99.5	100.9	93.2	93.5	82.3	85.9	102.9	129.1	109.9	126.3	112.4
(-)	101.1	104.6	109.5	120.2	111.9	98.6	110.1	99.9	111.4	107.1	105.4	88.4	88.9	79.2	91.6
esNIP2$	99.9	100.0	100.1	99.9	99.8	100.2	105.8	99.9	99.7	99.9	100.2	100.4	98.9	99.9	103.7
(-)	100.0	100.0	99.9	99.9	100.2	99.9	105.6	100.0	100.2	99.8	100.1	99.8	100.0	100.0	100.0
pum_eoP2$	97.9	97.6	98.1	97.8	98.0	97.8	104.2	98.6	97.2	97.6	105.5	100.4	98.9	99.9	103.7
(-)	102.6	102.5	101.6	101.8	101.8	102.3	106.7	101.0	102.2	102.1	94.8	96.9	88.9	98.1	100.0
pu_eaP2$	99.9	98.7	98.9	97.7	96.4	94.3	103.0	97.1	96.4	97.4	92.4	94.7	87.9	96.1	103.7
(-)	100.2	101.5	101.1	102.3	104.0	106.1	108.4	102.7	103.4	102.3	108.0	102.7	100.0	101.8	100.0
pu_raP2$	102.1	98.4	101.9	96.1	90.9	77.8	99.5	92.5	91.3	93.7	71.2	80.3	76.9	88.6	103.7
(-)	100.0	103.8	100.9	107.8	115.3	122.0	115.2	110.2	111.1	106.9	144.8	134.1	122.3	115.0	100.0