REPRESENTATION OF *EMILIANIA HUXLEYI* IN PHYTOPLANKTON SIMULATION MODELS. A FIRST APPROACH

DAG L. AKSNES, JORUN K. EGGE, RUNE ROSLAND & BERIT R. HEIMDAL

SARSIA

AKSNES, DAG L., JORUN K. EGGE, RUNE ROSLAND & BERIT R. HEIMDAL 1994 12 30. Representation of *Emilania huxleyi* in phytoplankton simulation models. A first approach. – *Sarsia* 79:291–300. Bergen. ISSN 0036-4827.

Emiliania huxleyi (LOHMANN) HAY et MOHLER is represented as a state variable in a general phytoplankton model that also includes one diatom group and one phytoplankton group encompassing the 'other flagellates' than *E. huxleyi*. Furthermore, three nutrient variables (nitrogen-, phosphorus-, and silicon-nutrients) are included. The main features of the model are that *E. huxleyi* has been given a higher growth affinity for orthophosphate than the two other groups, and that diatoms, besides being dependent on silicon, have been given a higher maximal growth rate than the two flagellate groups. The output from the simulation model is compared with observations made in mesocosm experiments loaded with different amounts of nitrate and orthophosphate. The simulated *E. huxleyi* is not able to grow as well as the real *E. huxleyi*, and this applies especially to the experiments low in orthophosphate. It is difficult to account for the high observed numbers of *E. huxleyi* in terms of the available inorganic othophosphate in these experiments. The literature, however, gives some evidence that *E. huxleyi* is able to utilise organic phosphorous sources. By assuming an organic phosphorus source that adds phosphorus to the orthophosphate pool, however, the fit between the model and the observations is improved. Furthermore, simulations indicate that the phosphorus originating from organic substances should be more available for the *E. huxleyi* than for the other groups. In simulation models this is achieved by defining a higher *E. huxleyi* uptake affinity for orthophosphate, but it may also be assumed that the orthophosphate originating by enzymatic activity on organic substances are spatially (at the scale of the uptake process) more close to the *E. huxleyi* cell than to the other phytoplankters present in the water body.

Dag L. Aksnes, Jorun K. Egge, Rune Rosland & Berit R. Heimdal, Department of Fisheries and Marine Biology, University of Bergen, Bergen High Technology Center, N-5020 Bergen, Norway.

INTRODUCTION

The carbonate pump is believed to be an important component of the global carbon cycle, and the amount of carbonate mineral produced depends on the evolutionary and ecological succes of calcifying pelagic organisms (WESTBROEK & al. 1993). The formulation of adequate predictive carbonate pump models raises the problem that the dynamics of the highly diverse set of calcifying pelagic organisms needs to be taken into account. As a first step, *Emiliania huxleyi* has been selected as a 'model organism' in order to achieve insight about the role of calcifying pelagic organisms for biological climate forcing. Within a modelling context, it is important to represent two kinds of phenomena: 1) The processes of carbonate formation and sinking and their influence on the CO_2 levels in the bloom areas, and 2) the bloom phenomena themselves. The last subject, or more precisely; under what kind of environmental conditions are *E. huxleyi* likely to have success, is the focus of the present study. *E. huxleyi* competes for nutrients with non-calcifying species, and consequently it is crucial to have quantitative knowledge about the competitive abilities of *E. huxleyi*. These abilities have to be explained on the basis of detailed knowledge of the general biology and the physiology of this species. Several hypothesis for success have been suggested, and the possible functions of the coccoliths have received much attention (BRAARUD & al. 1952; PAASCHE 1964; PAASCHE & KLAVENESS 1970; BAUMANN & al. 1978; SIKES & al. 1980; SIKES & WILBUR 1982; LINSCHOOTEN & al. 1991) and have been reviewed by PAASCHE (1992) and WESTBROEK & al. (1993). Furthermore, *E. huxleyi* is reported to compete successfully for phosphorus at low orthophosphate concentrations (RIEGMAN & al. 1992). This property may depend on the ability to produce alkaline phosphatase in phosphorus deficient media so that organic phosphorus compounds may be utilised (KUENZLER 1965; KUENZLER & PERRAS 1965). On this background, we have assumed that *E. huxleyi* has a higher growth affinity for phosphorus than other phytoplankton species. In addition to the experimental evidence, this assertion is also based on the

fact that *E. huxleyi* has become a dominating species in several mesocosm experiments with low orthophosphate concentrations (EGGE 1993; EGGE & HEIMDAL 1994). Another important observation made in such experiments is that *E. huxleyi*, and other flagellates as well, are not able to compete successfully (i.e. become dominant) with diatoms when silicate is non-limiting (above approximately 2 μM, EGGE & AKSNES 1992) and orthophosphate and nitrate are present (> 0.1 μM, EGGE 1993). An earlier version of the simulation model (AKSNES & al. in press), including one diatom group and one flagellate group has been independently validated against measurements obtained in mesocosm experiments. Here, independent validation means that no adjustments were applied to the model coefficients in order to obtain improved fit between model predictions and observations. This model gave fairly good correspondence for the diatom/flagellate ratio in mesocosm experiments having different nutrient loadings (AKSNES & al. in press). The main model structure and the values of the model coefficients are based on the model developed by ANDERSEN & al. (1987) and ANDERSEN & NIVAL (1989) for the CEPEX enclosures. In the present paper we introduce an '*E. huxleyi*' state variable that is separated from the other flagellate group by having a higher affinity for phosphorus. The results from the model is discussed on the basis of the time development in several mesocosm experiments having different degree of orthophosphate loadings.

The present study is part of a long term project aiming for increased predictability of general phytoplankton models. Alterations of the model (including the values of the coefficients) will be based on theoretical and empirical evidence rather than on case-specific tuning (see LOEHLE 1983). Enclosure experiments are conducted to validate the biological source and sink terms. Water movements as a source for bloom dynamics may be ignored (or controlled) in such enclosures. A main goal of these efforts are to develop a simple and robust biological compartment that may be driven by 3D-hydrodynamical models in order to simulate ocean phytoplankton dynamics (AKSNES & LIE 1991; AKSNES & al. in press; SKOGEN & al. in press).

METHODS

The simulation model

The biological processes are summarized in Table 1. Maximal phytoplankton growth is a function of temperature (EPPLEY 1972), light limitation, nitrogen, phosphorus and silicon (diatoms) limitations (Eqs 1-3 in Table 1). Following AKSNES & EGGE (1991) and D. L. Aksnes and coworkers own obs, the saturation curves of growth rate versus the different nutrients and light are based on constant affinity coefficients rather than on constant half-saturation coefficients. This means that the half-saturation parameter increases with temperature in the same way as maximal growth rate (AKSNES & EGGE 1991). Eqs 2 and 3 (Table 1) show that all limitations are expressed as non-dimensional terms at the range 0 to 1. The 'law of the minimum' is used for simultanenous limitations due to several nutrients, i.e. only the most limiting nutrient is limiting the phytoplankton growth at a particular time (Eq. 2 in Table 1). Simultaneous light and nutrient limitation, however, is represented by multiplicative limitation, i.e. the product of the limitations from both light and the most limiting nutrient is used to compute the realized growth rate (Eq. 3 in Table 1). The three loss terms; mortality, metabolic loss and diatom sinking are included in the model. The mortality rate is assumed constant, the metabolic loss rate is temperature dependent (Eq. 4 in Table 1) while diatom sinking rate depends on silicate concentration (Eq. 5 in Table 1) according to ANDERSEN & NIVAL (1989). All the present experiments, however, were continuously stirred and we assumed that this stirring overrided the sinking, and the diatom sinking rate was therefore not applied. Each state variable (nitrogen-, phosphorus- and silicon-nutrients together with one diatom, one flagellate and one *E. huxleyi* variable) of the model is represented by a differential equation as shown in Table 3. Except for the phosphorus affinity, the values of the other *E. huxleyi* coefficients are the same as for the other flagellate group, while the diatom and flagellate coefficients (Table 2) are identical to those used by AKSNES & al. (in press). As an alternative to the use of fixed coefficient values, the values may be adjusted (by least square minimisation or other similar techniques) in order to improve the fit between model predictions and the observations. This process, termed 'calibration' or 'tuning', is a common practise in ecological modelling and represents an efficient way of reducing the variance between models and observations. Tuning, however, is not likely to improve the gener-

Table 1. Process equations (explanations to the symbols are given in Tables 2 and 3). T and I represents ambient temperature and irradiance. The equations below is expressed for the diatom group, but the same equations (although different coefficients) are used for the flagellate and the *E. huxleyi* group. In these two groups, however, there are no silicate limitation (Eq. 2) and no sinking (Eq. 5).

Temperature specific growth rate: $\mu_{d.max}(T) = \mu_{d.max0}\, e^{a_1 T}$	(1)
The non-dimensional environmental limitation term: $S_{d.lim} = MIN(N/(\mu_{d.max}/\alpha_{d.N}+N), P/(\mu_{d.max}/\alpha a_{d.P}+P), Si/(\mu_{d.max}/\alpha_{d.Si}+Si))$	(2)
Diatom realized growth rate: $\mu_d = \mu_{d.max}\, I/(\mu_{d.max}/\alpha_{d.I}+I)\, S_{d.lim}$	(3)
Diatom metabolic loss rate: $e_d = e_0\, e^{a_2 T}$	(4)
Diatom sinking rate: If $Si \leq Si_t$ then $w_d = w_{max}$ If $Si > Si_t$ then $w_d = (a_3 / Si + w_{min})$	(5)

Table 2. Values of the coefficients (see text). The term affinity refers to the growth affinity.

Symbol	Value/unit	Explanation
Maximal growth versus temperature		
$\mu_{d.max0}$	1.5 10-5 s^{-1}	Maximum growth rate for diatoms at 0° C
$\mu_{f.max0}$	1.0 10-5 s^{-1}	Maximum growth rate for flagellates at 0° C
μ_{emax0}	1.0 10-5 s^{-1}	Maximum growth rate for *E. huxleyi* at 0° C
a_1	0.063° C^{-1}	Temperature dependency of growth; diatoms, flagellates and *E. huxleyi*
Growth limitations		
$\alpha_{d.N}$	1.7 10^{-5} $s^{-1}\mu M^{-1}$	Diatom affinity for nitrogen-nutrients
$\alpha_{d.P}$	2.7 10^{-4} $s^{-1}\mu M^{-1}$	Diatom affinity for phosphorus-nutrients
$\alpha_{d.Si}$	2.5 10^{-5} $s^{-1}\mu M^{-1}$	Diatom affinity for silicon-nutrients
$\alpha_{d.I}$	3.6 10^{-7} $m^2\mu mol^{-1}$	Diatom affinity for light
$\alpha_{f.N}$	1.5 10-5 $s^{-1}\mu M^{-1}$	Flagellate affinity for nitrogen-nutrients
$\alpha_{f.P}$	2.3 10^{-4} $s^{-1}\mu M^{-1}$	Flagellate affinity for phosphorus-nutrients
$\alpha_{f.I}$	1.1 10^{-7} $m^2\mu$ mol^{-1}	Flagellate affinity for light
α_{eN}	1.5 10^{-5} $s^{-1}\mu M^{-1}$	*E. huxleyi* affinity for nitrogen-nutrients
α_{eP}	4.1 10^{-4} $s^{-1}\mu M^{-1}$	*E. huxleyi* affinity for phosphorus-nutrients
α_{eI}	1.1 10^{-7} $m^2\mu mol^{-1}$	*E. huxleyi* affinity for light
Mortality		
m_d	1.6 10^{-6} s^{-1}	Diatom mortality rate
m_f	1.6 10^{-6} s^{-1}	Flagellate mortality rate
m_e	1.6 10^{-6} s^{-1}	*E. huxleyi* mortality rate
Metabolic losses		
e_0	8.1 10-7 s^{-1}	Metabolic loss rate for diatoms, flagellates and *E. huxleyi* at 0° C
a_2	0.07° C^{-1}	Temperature dependency of metabolic losses for diatoms, flagellates and *E. huxleyi*
Diatom sinking rate		
Si_t	1.0 μM Si	Threshold silicate concentration
w_{max}	3 m day^{-1}	Maximum sinking rate
w_{min}	0.3 m day^{-1}	Minimum sinking rate
a_3	2.7 μM m day^{-1}	Shape factor for the sinking function
Cellular elemental composition (mol-ratio)		
r_1	0.063	P : N ratio in diatoms
r_2	0.063	P : N ratio in flagellates
r_3	0.031	P : N ratio in *E. huxleyi*
r_4	0.875	Si : N ratio in diatoms

ality of models, but is more likely to mask errors in both the model and in the observations. For example, good fit may be obtained because a wrong process representation is balancing wrong coefficient values, or wrong/irrelevant measurements are used to alter correct model coefficients.

Solar elevation and self-shading from phytoplankton biomass was taken into account in the calculation of subsurface irradiance. The diffuse light (I_{dif}) and direct (I_{dir}) light at depth z was calculated as:

$$I_{dif}(z,t) = b_1 R_{dif}(t) e^{-k_{dif} z}$$
$$I_{dir}(z,t) = b_1 R_{dir}(t) e^{-k_{dir} z} \quad (1)$$

where $R_{dif}(t)$ and $R_{dir}(t)$ are the diffuse and direct components of the surface irradiation which are converted into PAR by the constant b_1. The coefficients k_{dif} and k_{dir} are the diffuse and direct attenuations of the water column given by:

$$k_{dif} = (b_2 + b_3 (D+F+E))/z_m$$
$$k_{dir} = (b_2 + b_3 (D+F+E))/(\cos\theta) \quad (2)$$

where the coefficients represent attenuation due to sea water and dead particulate matter and dissolved compounds (b_2), and attenuation (b_3) due to diatoms (D) flagellates (F) and *E. huxleyi* (E). z_m represents the mean path length per unit vertical distance in the water column for the diffuse light rays and is equal to 0.83 (Sathyendranath & Platt 1990), and finally θ is the zenith angle of the direct light in the water column computed from Snell's formula. The values of the coefficients b_1, b_2 and b_3 were chosen according to Aksnes & Lie (1990) and were 0.25, 0.14 m^{-1} and 1.25 10^{-3} mgN^{-1} m^{-1}, respectively. Fig. 1 shows the modelled average light in two of the enclosures.

Enclosure experiments

In Raunefjorden at the western coast of Norway, six enclosures (4 m deep and a volume of 11 m^3) were attached to a floating laboratory in the periods 23 May–18 June 1991, and 22 April–29 May 1992. In 1991, two bags (parallels) had nitrate and inorganic orthophosphate added to them in the ratio of 13 : 1.5 (termed the 1991-low experiment), two bags were fertilized with a nitrate:phos-

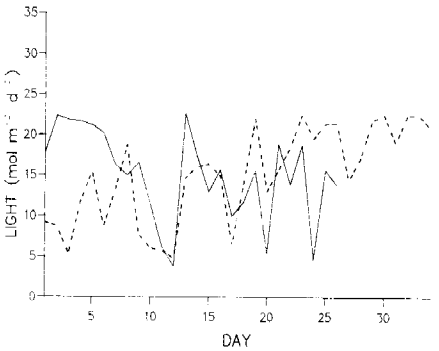

Fig. 1. Light conditions (mol m^{-2} day^{-1}) during 1991- (solid line) and 1992-experiments (broken line). The values represent the average sum of direct and diffuse irradiance inside the enclosure 1991-low and 1992-low (i.e. the light used for the computation of the light limitation term, I in Eq. 3 in Table 1).

phate ratio of 13 : 0.4 (1991-medium), and the last two bags were fertilized with a 13 : 0.1 ratio (1991-high). In 1992, two bags (parallels) had nitrate and inorganic orthophosphate added to them in the ratio of 16 : 5 (1992-low experiment), two bags were fertilized with a nitrate : phosphate ratio of 16 : 1 (1992-medium), and the last two bags were fertilized with a 16 : 0.2 ratio (1992-high). Water was pumped continuously (about 40 l min^{-1}) from the bottom to the top of the enclosure in order to ensure a homogenous distribution of nutrients and phytoplankton. Each bag was renewed with natural water from the outside of the bags at a rate of 10 % per day.

Table 3. The simulation model. The coefficient k_1(= 1.16 10^{-6} s^{-1}) represents the 10 % per day water renewal of the enclosures while N_b and N_{add} represent the nitrogen nutrient concentration in the incoming water and the added nitrogen fertiliser respectively. μ_d, μ_f and μ_e are the realized diatom flagellate and *E. huxleyi* growth rates given by Eq. (3), while e_d, e_f and e_e are the realized metabolic loss rates given by Eq. 4 in Table 1.

Nitrogen nutrients (N):
$dN/dt = -k_1 (N-N_b) + N_{add} - D(\mu_d - e_d) - F(\mu_f - e_f) - E(\mu_e - e_e)$

Phosphorus nutrients (P):
$dP/dt = -k_1 (P-P_b) + P_{add} - r_1 D(\mu_d - e_d) - r_2 F(\mu_f - e_f) - r_3 E(\mu_e - e_e)$

Silicon nutrients (Si):
$dSi/dt = -k_1 (Si-Si_b) + Si_{add} - r_4 D\mu_d$

Diatoms (D):
$dD/dt = -k_1 (D-D_b) + D(\mu_d - e_d - m_d)$

Flagellates (F):
$dF/dt = -k_1 (F-F_b) + F(\mu_f - e_f - m_f)$

E. huxleyi (E):
$E/dt = -k_1 (E-E_b) + E(\mu_e - e_e - m_e)$

Samples for nutrients (nitrate, orthophosphate and silicate) and phytoplankton enumeration and identification were obtained with intervals from 1 to 3 days. Determination of nitrate, phosphate and silicate were performed on fresh samples. Enumeration and identification of phytoplankton were carried out on samples preserved by neutralized formaldehyde and acid Lugol using the sedimentation method of UTERMÖHL (1931). In order to compare phytoplankton counts with simulation results (given in nitrogen units) time-invariant nitrogen content was assumed for the different groups: 1.5 pg N per *E. huxleyi* cell, 4 pg N per diatom cell and 2 pg N per flagellate cell. The flagellate community in 1992, however, was characterised by large dinoflagellates and a nitrogen content of 15 pg N per cell was assumed. As emphasised in the Discussion, however, measurements and simulation results should not be too rigorously compared (in absolute terms). The conversion from cell number to biomass can only be viewed as an approximate scaling of cell counts into the units represented in the simulation model.

Forcing of the simulations

Initial values of the state variables were measured in each of the sea enclosures, and the forcing of the model included measurements of surface irradiance, water temperature, nutrient addition, and measurements of the state variables in the incoming water (boundary conditions). As the water of the bags was mixed continuously, we assumed that all phytoplankton experienced the same light regime which was assumed to be the average light of the water column. Surface measurements of hourly incident radiation (accounting for both the diffuse and the direct component, see Eqs 1 and 2) were provided by the Radiation Observatory at the University of Bergen (ANON 1992, 1993).

In the basic run we assumed that a rather high amount (0.1 μmol orthophosphate per day) was added continuously to the phosphorus state variable and hence became available to all the three phytoplankton groups. The presence of an, at times, extensive pool of organic phosphorus compounds in natural fjord environments as well as in enclosure experiments is substantiated by measurements made by THINGSTAD & al. (1993).

A second run was made without an organic phosphorus compounds. (dotted lines in Figs 2–7), and finally a run (Fig. 8) with increased (10 times) growth affinities for light for all phytoplankton groups were made to demonstrate the light limitation of the model during the initial phase of the experiments (when the nutrients were at non-limiting levels).

RESULTS

First, we make some comments on the interpretation of the measured versus the simulated state variables. The simulation model does not differentiate between different nitrogen nutrients, while the measurements does. The metabolic nitrogen loss is normally dominated by ammonium and other non-nitrate compounds, but in the present model metabolic loss from the phytoplankton is added to a common nitrogen (and phosphorus as well) nutrient variable. The measurements shown in Fig. 2 represent nitrate and hence, the measured and simulated

state variables are not identical (same argument applies to phosphorus). Comparisons of measured and simulated phytoplankton state variables are even more non-trivial than the nutrient comparisons. The 'measurements' of the biomass (N-content) of each phytoplankton state variable in Figs 5–7 are based on cell counts and time-invariant assumptions about the cellular N-content of the three groups, while the model predictions represent the simulated N-content of each group. Thus, a strict comparison between model predictions and simulation is hardly feasible. Although seldom pointed out, such incompatibilities between measurements and models are quite common in ecological modelling.

Nutrients

As explained in the Methods we assumed a pool of organic phosphorus adding at a constant rate to the phosphorus-nutrient state variable during the entire run (solid lines in Figs 2–7). Such additional supply of phosphorus did not alter the simulated dynamics of the 1991-low, 1992-low and the 1992-medium experiments, but the simulated dynamics of the 1991-medium, 1991-high and 1992-high experiments were seriously altered as demonstrated by comparison with the run where no organic phosphorus pool was assumed (dotted lines in Figs 2-7). Hence, the simulation experiments clearly indicate orthophosphate limited growth for the 1991-medium, 1991-high and 1992-high experiments, but not for the other three. For these last three light rather than nutrient limitation was indicated as the nutrients were at non-limiting levels (discussed later).

The measured nitrate concentrations show that the initial nutrient consumption (interpreted as the decrease in nitrate) was higher in 1991 than in 1992 (Fig. 2). This is also reflected by the model. For the model, and probably also for the enclosures, the much better light conditions prevailing the first week in 1991 compared to 1992 (see Fig. 1) was responsible for the higher initial nitrate consumption in 1991 (Fig. 2). A rapid decline in nitrate, however, was also observed in 1992 along with the increased radiation around day 15. This feature was also simulated, although the response of the model (both in 1991 and 1992) was slower than indicated by the measurements (as demonstrated later improved fit is obtained by setting higher growth affinities for light). Due to light limitation, the simulated nitrogen-nutrient concentrations were consistently higher than the measured nitrate observations in the experiments high in both phosphorus and nitrogen nutrients (1991-low, 1992-low and 1992-medium,

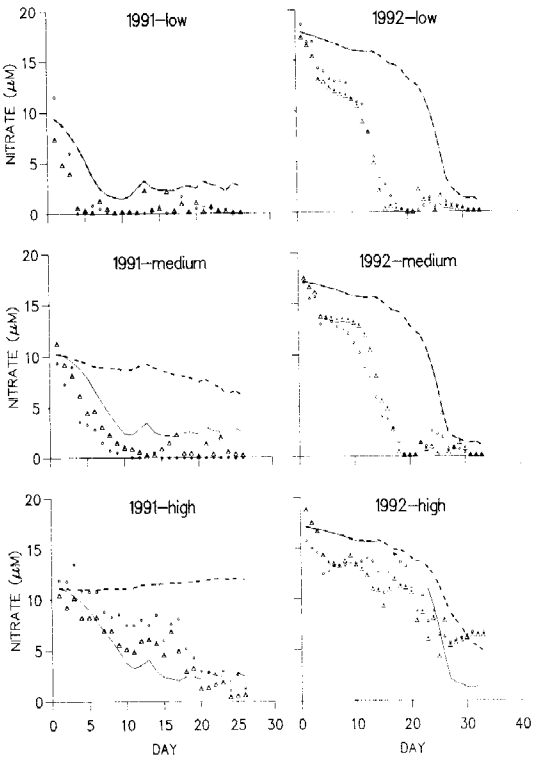

Fig. 2. Nitrate measurements (different symbols indicate parallel enclosures) and model predictions (lines). Solid line represents the simulation where an organic phosphorus source is assumed, while results of the simulation where no such source is assumed is indicated by the broken line. One solid line means exact overlap. This should be interepreted as there is no phosphorous limited growth in the simulation.

Fig. 3). In the three experiments low in orthophosphate (1991-medium, 1991-high and 1992-high), the nitrate consumption was highly underestimated by the model in the case where no organic phosphorus source was assumed (dotted line in Fig. 2). The 1991-high experiment having the most pronounced orthophosphate shortage, clearly indicates that the simulation model cannot account for the nitrate consumption (nor the *E. huxleyi* increase, see below) without assuming an extra phosphorus source.

Phytoplankton

As can be seen from the nutrient concentrations (Figs 2, 3) the phytoplankton growth in the 1991-low simulation is not severly limited by nutrients (nitrogen-nutrients and phosphorus-nutrients are above 2 and 1 μM respectively), but the simulated *E. huxleyi* (Fig. 5) is not able to grow as obser-

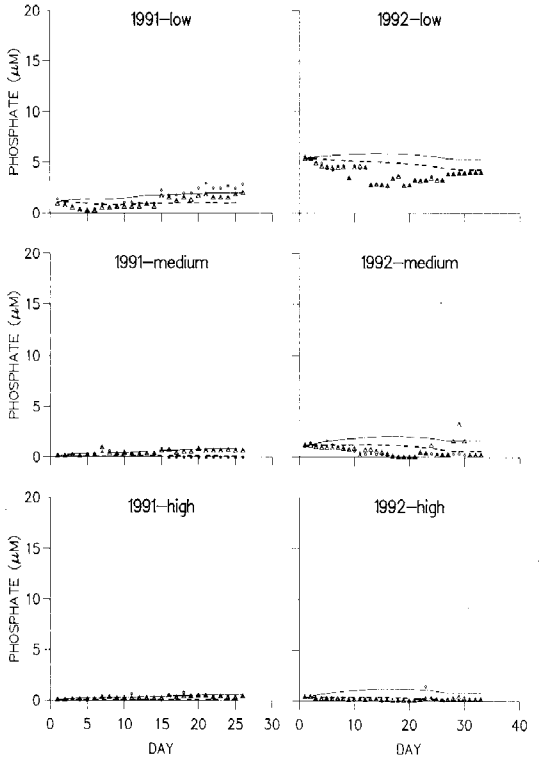

Fig. 3. Orthophosphate measurements (different symbols indicate parallel enclosures) and model predictions (lines). Solid line represents the simulation where an organic phosphorus source was assumed, while results of the simulation where no such source is assumed is indicated by the broken line.

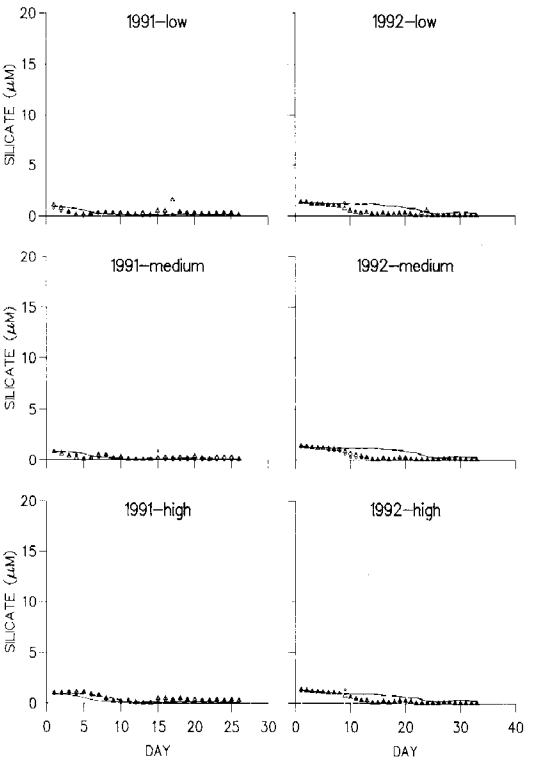

Fig. 4. Silicate measurements (different symbols indicate parallel enclosures) and model predictions (lines). Solid line represents the simulation where an organic phosphorus source is assumed, while results of the simulation where no such source was assumed is indicated by the broken line.

ved, especially after the reduction in incoming light after day 10 (Fig. 1). Hence, as also indicated by the nutrient dynamics, a too strong light limitation may act upon *E. huxleyi* in the present model. The diatoms, having a higher growth affinity for light ($3.6\ 10^{-7}\ m^{-2}\ \mu mol^{-1}$ versus $1.1\ 10^{-7}\ m^{-2}\ \mu mol^{-1}$), respond more in accordance with the observations. Although all the experiments were run at low initial silicate concentration (Fig. 4) and with no silicate additions, the diatoms responded with an increase in numbers the first days (Fig. 6), a response that was well reflected by the model. As in previous mesocosm experiments (Aksnes & al. in press), the flagellate group is responding with a decrease rather than an increase during the initial period of the experiments (Fig. 7), and this feature cannot be explained by the present model. *E. huxleyi*, however, responded with an immediate increase in numbers, both in nature as well as in the simulations. The correspondence between measurements and model predictions was best in the experiments low in phosphate (Fig. 5), and the *E. huxleyi* measurements seemed rather unaffected by the low phosphate concentrations. On the other hand, the simulated *E. huxleyi* development was very sensitive to whether an organic phosphorus source was present or not (dotted versus solid line in Fig. 5), and in the 1991-high experiment positive growth was not possible to achieve unless extra phosphorus was made available during the simulation.

DISCUSSION

Fig. 5 shows that the simulated *E. huxleyi* was not able to grow as well as the real *E. huxleyi*. This applies especially to the experiments low in orthophosphate (dotted line in Fig. 5). More *E. huxleyi*were produced in the enclosures than can be accounted for in terms of inorganic orthophosphate. By assuming an organic phosphorus source, however, the fit between the model and the observations was improved. Hence, utilisation of organic

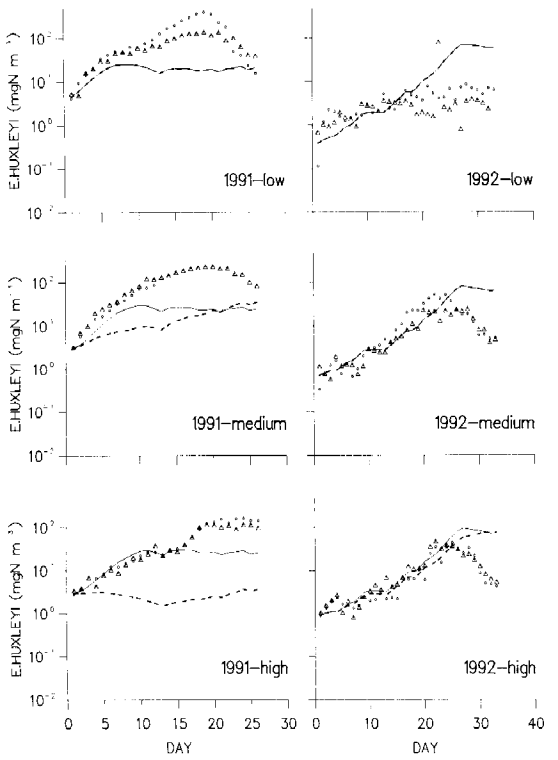

Fig. 5. Observations of *Emiliania huxleyi* (different symbols indicate parallel enclosures) and model predictions (lines). Solid line represents the simulation where an organic phosphorus source is assumed, while results of the simulation result where no such source is assumed is indicated by the broken line. One solid line means exact overlap. This should be interepreted as there is no phosphorous limitation in the simulated run. The *E. huxleyi* observations are based on cell counts and converted to biomass by assuming a constant cellular N-content (see text). Logarithmic scale on y-axis.

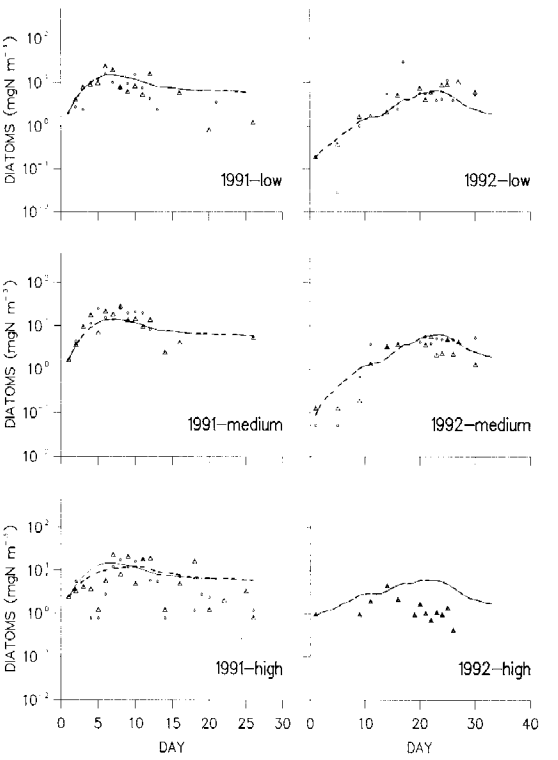

Fig. 6. Observations of diatoms (different symbols indicate parallel enclosures) and model predictions (lines). Solid line represents the simulation where an organic phosphorus source is assumed, while results of the simulation where no such source is assumed is indicated by the broken line. The difference between the two runs is small according to the strong silicate limitation overriding any phosphorus effects. The diatom observations are based on cell counts and converted to biomass by assuming a constant cellular N-content (see text). Logarithmic scale on y-axis.

phosphorus compounds seems important for the realized growth of *E. huxleyi* in the present experiments. The ability of *E. huxleyi* to produce alkaline phosphotase (KUENZLER 1965; KUENZLER & PERRAS 1965) gives support to this interpretation. There is one problem, however, with the representation of the organic phosphorus pool in the simulation model; we asume that orthophosphate is released from the organic compounds into a common pool available for all three phytoplankton groups. Fig. 7 shows the 'other flagellates' as well as *E. huxleyi* are stimulated by this supply (the diatoms are silicon-limited and not able to utilise the orthophosphate). The relatively high growth affinity for orthophosphate that is assumed for *E. huxleyi* is directing a higher proportion of phosphorus to this group than to the flagellate group. More phosphorus may have been channeled to *E. huxleyi* if the growth affinity was set even higher. Another way to channel the organic phosphorus to the *E. huxleyi,* rather than to the other flagellates, is to assume that the orthophosphate originating from organic substances is spatially (at the scale of the uptake process) more close to the *E. huxleyi* cell than to the other phytoplankters present in the water body (which may be the case if *E. huxleyi* releases substances that decompose organic phosphorus compounds close to the cell membrane). In this case the othophosphate released from the organic substances should not be put into the common phosphorus state variable, but rather be kept exclusively for *E. huxleyi.* In the simulation model this may have been represented as a direct *E. huxleyi* utilisation of organic phosphorus compounds rather than set-

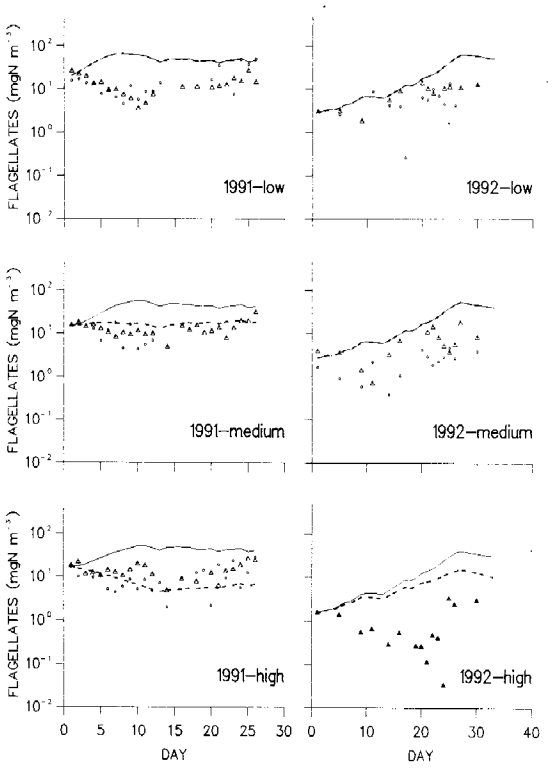

Fig. 7. Observations of flagellates (different symbols indicate parallel enclosures) and model predictions (lines). Solid line represents the simulation where an organic phosphorus source is assumed, while results of the simulation result where no such source is assumed is indicated by the broken line. One solid line means exact overlap. This should be interepreted as there is no phosphorous limitation in the simulated run. The flagellate observations are based on cell counts and converted to biomass by assuming a constant cellular N-content (see text). Logarithmic scale on y-axis.

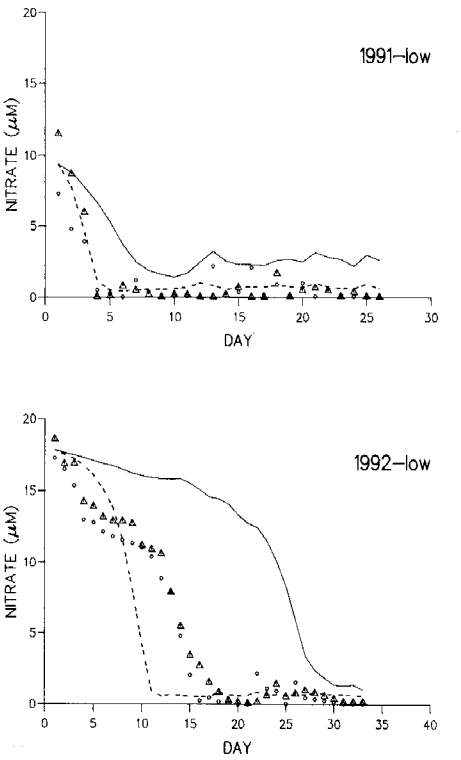

Fig. 8. Indication of light limitation in the model. A too slow nitrate utilisation is indicated for the basic run (solid lines). An increase in the light affinities with one order of magnitude (for all phytoplankton groups) cause a much more rapid nitrate utilisation (broken lines). This clearly indicates that the basic model is light limited during the initial period, and that the light limitation is stronger in 1992 than in 1991. This is in accordance with the irradiance shown in Fig. 1.

ting a higher *E. huxleyi* growth affinity for orthophosphate. This would require a separate parameterisation of the consumption of the organic phosphorus compounds. Measurements indicate that the rate limiting step (and hence the cruical process from a modelling viewpoint) in the utilisation of dissolved organic phosphorus (DOP) compounds are the conversion from polymer DOP into monomer DOP (T. F. Thingstad pers. commn, but see also THINGSTAD & al. 1993) and little is known about how this process works in the water column. Obviously, a realistic quantitative representation of the apparently enhanced phosphorus utilisation in *E. huxleyi* requires more knowledge of the mechanisms involved. An interesting observation made by ANDERSEN (1981) is that extensive coccolith production can be induced by phosporous shortage, and that the process of calcification and coccolith crystal growth is linked to the phosphorus metabolism of *E. huxleyi*. This of course does not mean that the coccolith formation enables enhanced phosphorus uptake, but in one or another way the success of the *E. huxleyi* may be linked to the adaptive significance of the coccoliths.

The hypothesis, put forward in the Introduction, that *E. huxleyi* is efficient in utilising phosphorus seems appropriate, but is apparently not sufficient in order to simulate the success of *E. huxleyi* in the present enclosure experiments. Another feature indicated by the model, however, is that too strong light limitation acts upon *E. huxleyi* in the present model. This is especially evident from the low growth computed by the model in the 1991-low experiment (Fig. 5). Here, light was the major

limiting factor during the entire period as both phosphate and nitrate concentrations were high. This is substaniated by the simulation shown in Fig. 8. An increase of the light affinities with one order of magnitude causes a much more rapid nitrate utilisation (and higher phytoplankton growth – not shown). This clearly indicates that the basic model is light limited during the initial period, and that the light limitation is stronger in 1992 than in 1991. This agrees with the irradiance-plot in Fig. 1.

In the forthcoming validation experiments, we should put more emphasis on the measurements of organic compounds and formulate some alternatives to the present phosphorus representation. The light limitation should probably be reconsidered as improved fit could be obtained by tuning of the growth affinties for light. Such tuning, however, may equally well balance other errors of the model such as the applied mortality and the use of multiplicative limitation between nutrients and light. Here, new experiments are required to provide insight. The main conclusion that should be drawn from the present experiments and simulations is that organic phosphorus may be an important source for phytoplankton growth, and that this may be especially important to consider in simulation models of *E. huxleyi*.

ACKNOWLEDGEMENTS

This is EHUX contribution No. 24, supported by the Norwegian Research Council. Thanks to Toby Tyrell, Arnold Taylor and two anonymous referees for valuable suggestions.

REFERENCES

Aksnes, D.L. & J.K. Egge 1991. A theoretical model for nutrient uptake in phytoplankton. – *Marine Ecology Progress Series* 70:65–72.

Aksnes, D.L. & U. Lie 1991. A coupled physical-biological pelagic model of a shallow sill fjord. – *Estuarine, Coastal and Shelf Science* 31:459–486.

Aksnes, D.L. & K.B. Ulvestad, B.M. Balino, J. Berntsen, J.K. Egge & E. Svendsen in press. Ecological modelling in coastal waters: towards predictive physical-chemical-biological simulation models. – *Ophelia.*

Andersen. O.K. 1981. *Coccolithdannelse og kalsifieringsgrad i en N-celle kultur av* Emiliania huxleyi *ved fosfatbegrenset vekst i kolbekultur og kjemostat.* – Dr. scient. thesis, University of Oslo. 66 pp.

Andersen, V. & P. Nival 1989. Modelling of phytoplankton dynamics in an enclosed water column. – *Journal of the Marine Biological Association of the United Kingdom* 69:625–646.

Andersen, V., P. Nival & R.P. Harris 1987. Modelling of a planktonic ecosystem in an enclosed water column. – *Journal of the Marine Biological Association of the United Kingdom* 67:407–430.

Anon. 1992. *Radiation observations in Bergen, Norway 1991. The radiation observatory. Radiation yearbook.* – Meteorological Geophysical Institute. University of Bergen.

— 1993. *Radiation observations in Bergen, Norway 1992. The radiation observatory. Radiation yearbook.* – Meteorological Geophysical Institute. University of Bergen.

Baumann, F.G., H.D. Isenberg & J. Gennaro, jr. 1978. The inverse relationship between nutrient nitrogen concentration and coccolith calcification in cultures of the coccolithophorid *Hymenomonas* sp. – *Journal of Protozoology* 25:253–256.

Braarud, T., K.R. Gaarder, J. Markali & E. Nordlie 1952. Coccolithophorids studied in the electron microscope. – *Nytt Magasin for botanikk* 1:129–134.

Egge, J.K. 1993. *Nutrient control of phytoplankton growth: Effects of macronutrient composition (N, P, Si) on species succession.* – Dr. scient. thesis, University of Bergen. 104 pp.

Egge, J.K. & D.L. Aksnes 1992. Silicate as regulating nutrient in phytoplankton competition. – *Marine Ecology Progress Series* 83: 281–289

Egge, J.K. & B.R. Heimdal 1994. Blooms of phytoplankton including *Emiliania huxleyi* (Haptophyta). Effects of nutrient supply in different N : P ratios. – *Sarsia* 79:333–348.

Eppley, R.W. 1972. Temperature and phytoplankton growth in the sea. – *Fishery Bulletin* 70:1063–1085.

Kuenzeler, E.J. 1965. Glucose -6-phosphate utilisation by marine algae. – *Journal of Phycology* 1:156–164.

Kuenzeler, E.J. & J.P. Peras 1965. Phosphatases of marine algae. – *Biological Bulletin* 128:271–284.

Linschooten, C., J.D.L. van Bleijswijk, P.R. van Emburg, J.P.M. de Vrind, E.S. Kempers, P. Westbroek & E.W. de Vrind-de Jong 1991. Role of the light-dark cycle and medium composition on the production of coccoliths by *Emiliania huxleyi* (Haptophyceae). – *Journal of Phycology* 27:82–86.

Loehle, C, 1983. Evaluation of theories and calculation tools in ecology. – *Ecological Modelling* 19:239–247.

Paasche, E. 1964. A tracer study of the inorganic carbon uptake during coccolith formation in photosynthesis in the coccolithophorid *Coccolithus huxleyi.* – *Physiologia Plantarium* 18:138–145.

— 1992. The physiology of *Emiliania huxleyi* 1992. – In: Westbroek, P., J.E. van Hinte, M. Knappertbusch & Janneke Ottens (eds). *The Global Modelling Initiative.* Report on the third international GEM Workshop Chateau de Blagnac, September 13–18, 1992.

Paasche, E. & D. Klaveness 1970. A physiological comparison of cocclith forming and naked cells of *Coccolithus huxleyi.* – *Archiv für Mikrobiologie* 73: 143–152.

Riegman, R., A.A.M. Noordeloos & C. Cadée 1992. *Phaeocystis* blooms and euthrophication of the continental coastal zones of the North Sea. – *Marine Biology* 112:479–484.

Sathyendranath, S. & T. Platt 1990. The light field in the ocean: Its modification and exploitation by the pelagic biota. – Pp. 333–344 in: Herring, P.J. (ed.). *Light and Life in the Sea.* Cambridge University Press.

Sikes, C.S., R.D. Roer & K.M. Wilbur 1980. Photosynthesis and coccolith formation: inorganic carbon and net inorganic reaction of deposition. – *Limnology and Oceanography* 25:248–260.

Sikes, C.S. & K.M. Wilbur 1982. Calcification by coccolithophorids: effect of pH and Strontium. – *Journal of Phycology* 16:433–436.

Skogen, M.D., E. Svendsen, J. Berntsen, D.L. Aksnes & K. Ulvestad in press. Modelling the primary production in the North Sea using a coupled 3 dimensional physical chemical biological ocean model. – *Estuarine, Coastal and Shelf Sciences.*

Thingstad, T.F., E.F. Skjoldal & R.A. Bohne 1993. Phosphorus cycling and algal-bacterial competition in Sandsfjord, Western Norway. – *Marine Ecology Progress Series* 99:239–259.

Utermöhl, H. 1931. Neue wege in der quantitativen Erfassung des Planktons. (Mit besonderer Berücksichtigung des Ultraplanktons). – *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 5:567–596.

Westbroek, P., C.W. Brown, J. van Bleijswijk, C. Brown Lee, G. J. Brummer, M. Conte, J. Egge, E. Fernandez, R. Jordan, M. Knappertsbusch, J. Stefels, M. Veldhuis, Paul van der Wal, J. Young 1993. A model system approach to biological climate forcing. The example of *Emiliania huxleyi.* – *Global and Planetary Changes* 8:27–46.

Accepted 21 September 1994.