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MODELLING NITRATE AND AMMONIUM UPTAKE BY PHYTOPLANKTON. INFLUENCE OF THE FORMULATION IN AN ECOSYSTEM MODEL

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Abstract

We examine the response and behavior of an ecosystem model subjected to five different formulations proposed in the literature for expressing nitrate and ammonium uptake by phytoplankton. The formulations all take into account the inhibition of nitrate uptake in the presence of ammonium. Eight state variables are considered in the model, developed for an enclosed water column with selective nutrient additions. The results of 70-day simulations of food web dynamics show that the results of the five formulations differ not only in the amplitude of the peaks but also in the number of peaks, their relative importance and their timing. Apparent effects increase with the trophic level. To obtain the same simulated evolution of the ecosystem with the five formulations, the parameter values have to be largely modified from those given by the original authors, and to vary greatly from one formulation to another. These results underline the differences of results between the formulations. They also show that care must be taken in the choice of functions, and corresponding parameter values, used in models of systems with periodic external nutrient inputs.

Keywords : nitrate, ammonium, model, ecosystem.

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Introduction

Most of the simulation models of the pelagic ecosystem are derived from a common ancestor (e.g. Steele, 1974) and include the same basic representation of biological processes. But depending on the subject and the space and time scales of interest, different mathematical formulations are used to represent the same biological process. It is not clear that all are of equal validity and that their use in different contexts is correct.

There are some studies which compare the adequacy of different mathematical functions in representing a given biological process by testing the goodness of fit to experimental data. For example, this has been done for the photosynthesis-light relationship (Lederman and Tett, 1981; McBride, 1992), nutrient limitation of phytoplankton growth by total phosphorus and total nitrogen (Morrison *et al.*, 1987), and ingestion by copepods as a function of food concentration (Mullin *et al.*, 1975). Franks *et al.* (1986) studied the behavior of a phytoplankton-herbivore-nutrient model, with two different grazing functions. But such comparative studies are rare and usually modelers dare only to change the values of coefficients and perform sensitivity analysis (e.g. O'Brien and Wroblewski, 1973; Horwood, 1982; Cochrane *et al.*, 1991). It appears therefore that there is a need to investigate the responses of ecosystem models to different empirical formulations.

An important topic is the mathematical representation of nitrate and ammonium uptake. Nitrate uptake is considered to represent new production, in contrast to ammonium uptake, which is regenerated production; under steady-state conditions, new production should be balanced by the export of organic matter from the euphotic zone (Dugdale and Goering, 1967). In the context of global carbon cycle studies, accurate parameterization of nitrate (NO3) and ammonium (NH4) uptake is therefore essential. Numerous studies have shown that phytoplankton cells take up ammonium preferentially, with nitrate uptake being inhibited by the presence of ammonium; however mechanisms are unclear and inhibition of NO3 uptake by NH4 appears to be a highly variable process (see the reviews by McCarthy, 1981; Syrett, 1981; Collos, 1989; Dortch, 1990). Detailed ecosystem models generally distinguish between NO3 and NH4 (e.g. Walsh, 1975; Wroblewski, 1977; Taylor and Joint, 1990) and several functions have been used to represent their differential uptake by phytoplankton.

In this paper we investigate the effect of five different formulations of NO3 and NH4 uptake by phytoplankton on the output of an ecosystem model, developed in an environment not perturbed by hydrodynamics processes. The choice of these formulations has been driven by the fact that they have been used in previous literature ecosystem models. Our purpose is to show the influence of the choice of a given formulation and of its parameter values on the dynamics of the food web and to point out the care which must be taken in this choice, not to determine which formulation is the best.

Model description

Model general formulation

In order to avoid the effect of forcing of biological processes by physical ones, this model has been developed for an enclosed water column, but with selective nutrient additions performed by the experimenters. This model is based on the models developed by Andersen *et al.* (1987) for the large-volume enclosures of the Controlled Ecosystem Population Experiment

(CEPEX). The study of Andersen *et al.* concerned the ecosystem of enclosure CEE3 (Controlled Experimental Ecosystem) of the Foodweb I experiment carried out in Saanich Inlet during the summer of 1978; detailed results of this experiment have been taken from Grice (1980) and Grice and Reeve (1982).

We consider the 0-8 m layer of the 23 m deep enclosure. Eight state variables are taken into account (Fig. 1): diatoms, flagellates, herbivores, carnivores, silicate, nitrate, ammonium and non-living particulate organic matter (POM). Compared to the model of Andersen *et al.* (1987), we do not differentiate between copepods and appendicularians as copepods are dominant, but we introduce ammonium. The POM compartment is considered as a sink which receives dead or settling organisms and fecal pellets, as POM accumulated at the bottom in enclosure CEE3 and was not resuspended.

Three forcing variables drive the food-web: irradiance, temperature and nutrient supply. In fact, subsequent nitrate additions were made during the experiment: the first one during day 4 in order to stimulate a diatom bloom which collapsed in a few days following the removal of silicate from the water column; the next additions (on days 21 and 40) were made to maintain the flagellate populations.

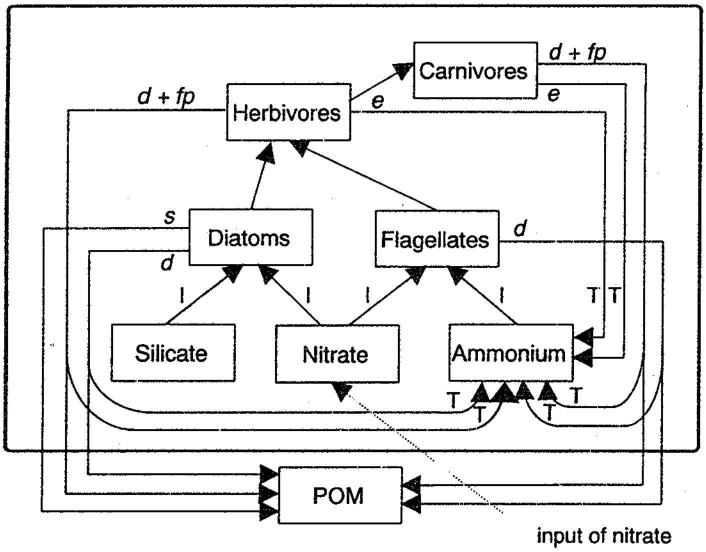

Fig. 1. Diagram of the model. POM: particulate organic matter; I: irradiance; T: temperature; d: death; e: excretion; fp: fecal pellet production; s: sedimentation

In order to simplify and easily compare the different formulations used for uptake of NO3 and NH4 by phytoplankton, we assume that flagellate growth depends on nitrate and ammonium concentrations while diatom growth depends on silicate and on nitrate only. As, in the enclosure, the bloom of diatoms is very restricted in time, depending almost exclusively on the availability of silicate, this simplification will not have a large influence. As NH4 is taken into account in this model, we consider that part of dead organisms and fecal pellets is directly remineralized as NH4 and that this regeneration is a function of temperature. We ignore bacterial oxidation of ammonia into nitrite and subsequently into nitrate, as well as pathways of dissolved organic nitrogen.

Table 1. Variables and parameters used in the model
*μM-N is equivalent to μmol of nitrogen per liter ; *, see text and Table 4 for details ; (1)(2), mortality rate of the diatoms when silicate (1) or nitrate (2) is limiting.*

Symbol	Definition	Unit	Value				
State variables			*Initial conditions*				
D	Diatoms	μM-N	1.5				
F	Flagellates	μM-N	0.4				
H	Herbivores	μM-N	0.06				
C	Carnivores	μM-N	0.05				
NH4	Ammonium	μM-N	1.22				
NO3	Nitrate	μM-N	5.0				
Si	Silicate	μM-Si	17.9				
POM	Particulate organic matter	μM-N	0.04				
Forcing variables							
I	Irradiance	$\mu E\ m^{-2}\ s^{-1}$					
T	Temperature	°C					
Phytoplankton parameters			*D*	*F*			
μ_{mD}	maximum growth rate	day^{-1}	3.0	-			
υ_m	maximum uptake rate of nitrate and ammonium	day^{-1}	-	1.2			
k_I	half-saturation constant for NO3	μM-N	2.0	*			
k_{Si}	half-saturation constant for Si	μM-Si	1.0	-			
I_s	optimal irradiance	$\mu E\ m^{-2}\ s^{-1}$	250	360			
β	photoinhibition parameter	-	-0.4	-0.8			
$r_{Si/N}$	ratio of silicate over nitrogen	mol-Si mol-N^{-1}	0.8	-			
s	sedimentation rate of diatoms	day^{-1}	0.33	-			
Zooplankton parameters			*H*	*C*			
a_H, a_C	assimilation coefficients	-	0.7	0.8			
r_m	maximum ingestion rate	day^{-1}	0.96	1.3			
k	Ivlev's coefficient	μM-N^{-1}	0.35	0.35			
B_o	threshold concentration for feeding	μM-N	0.05	0.01			
e_D, e_F	capture efficiency of phytoplankton	-	1, 0.8	-			
a_e	excretion rate at 0°C	day^{-1}	0.0855	0.0760			
b_e	slope of the excretion curve	-	1.0305	1.0450			
Mortality parameters			*D(1)*	*D(2)*	*F*	*H*	*C*
d_{max}	maximum mortality rate	day^{-1}	0.10	0.045	0.18	0.06	0.0427
d_o	minimum mortality rate	day^{-1}	0.03	0.03	0.018	0.0375	0.03
a_d	slope of the mortality curve	μM-N day^{-1}	0.035	0.105	1.134	0.36	0.006
B_{min}	threshold of the mortality curve	μM-N	0.5	7.0	7.0	1.6	0.47
Regeneration parameters							
a_m	regeneration coefficient at 0°C	-	0.05				
b_m	slope of the regeneration curve	-	0.039				

Most of the mathematical formulations representing the different biological processes, except the uptake of NO3 and NH4 by phytoplankton, are those used in Andersen *et al.* (1987) where their appropriateness and their underlying assumptions are discussed in detail. The corresponding parameters and their values, the mathematical formulations and the differential equation system are listed in Tables 1, 2 and 3. µM-N refers to µmol of nitrogen per liter.

Table 2. Processes represented in the model
(see text and Table 4 for uptake rate of nitrate and ammonium by flagellates)

Process	Construct
Phytoplankton growth	
μ_D growth rate of diatoms	$\mu_D = \mu_{mD}\, l_{SN}\, l_I$
l_{SN} limitation of growth by nutrients	$l_{SN} = MIN(l_N, l_{Si})$
l_N limitation by nitrate	$l_N = NO3 / (k_I + NO3)$
l_{Si} limitation by silicate	$l_{Si} = Si / (k_{Si} + Si)$
l_I limitation by irradiance	$l_I = 2\,(1 + \beta)\, r / (r^2 + 2\,\beta r + 1)$ with $r = I / I_s$
μ_F growth rate of flagellates	$\mu_F = \upsilon\, l_I$
υ uptake rate of nitrate and ammonium	$\upsilon = \upsilon_m\, [f(NO3)+f(NH4)]$
Zooplankton predation	
r_x ingestion rate of variable x	if $B \le B_o$ then $r_x = 0$
for herbivores $B = e_D\, D + e_F\, F$	if $B > B_o$ then $r_x = r_m\, [1 - exp(-k\,(B-B_o))]$
for carnivores $B = H$	
i_D predation rate of herbivores on diatoms	$i_D = v\, e_D\, D$ with $v = r_x / B$
i_F predation rate of herbivores on flagellates	$i_F = v\, e_F\, F$
Phyto- and zooplankton mortality	
d_x mortality rate of variable x	if $B \le B_o$ then $d_x = d_{max}$
for diatoms $B = NO3$ if $l_{SN} = l_N$	if $B > B_o$ then $d_x = a_d / B + d_o$
$B = Si$ if $l_{SN} = l_{Si}$	
for flagellates $B = NO3 + NH4$	
for herbivores $B = e_D\, D + e_F\, F$	
for carnivores $B = H$	
Zooplankton excretion	
e_x excretion rate of variable x	$e_x = a_e\, b_e^T$
Regeneration	
m regeneration rate	$m = a_m\, exp(b_m\, T)$

Table 3. System of differential equations. For NO3 and NH4 uptake, switching functions (s_1 and s_2 ; see Table 4) are used with the Jamart formulation

$$\frac{dD}{dt} = (\mu_D - d_D - s)\, D - i_D\, H$$

$$\frac{dF}{dt} = (\mu_F - d_F)\, F - i_F\, H$$

$$\frac{dH}{dt} = (a_H\, r_H - d_H - e_H)\, H - r_C\, C$$

$$\frac{dC}{dt} = (a_C\, r_C - d_C - e_C)\, C$$

$$\frac{dNH4}{dt} = m\,[d_D\, D + d_F\, F + (d_H+(1-a_H)r_H)\, H + (d_C+(1-a_C)r_C)\, C] + e_H\, H + e_C\, C - \upsilon_2\, F$$

$\text{with } \upsilon_2 = s_2\, \upsilon_m\, [f(NO3)+f(NH4)]\, l_I$ *for the Jamart formulation*

$\upsilon_2 = \upsilon_m\, f(NH4)\, l_I$ *for the four other formulations*

$$\frac{dNO3}{dt} = -\,\mu_D\, D - \upsilon_1\, F$$

$\text{with } \upsilon_1 = s_1\, \upsilon_m\, [f(NO3)+f(NH4)]\, l_I$ *for the Jamart formulation*

$\upsilon_1 = \upsilon_m\, f(NO3)\, l_I$ *for the four other formulations*

$$\frac{dSi}{dt} = -\,\mu_D\, r_{Si/N}\, D$$

$$\frac{dPOM}{dt} = (1-m)\,[d_D\, D + d_F\, F + (d_H+(1-a_H)r_H)\, H + (d_C+(1-a_C)r_C)\, C] + s\, D$$

Differential uptake of NH4 and NO3 by flagellates

Flagellate growth is assumed to depend on the uptake of NO3 and NH4 and to be limited by irradiance (*cf.* Tab. 2). We consider five different mathematical formulations representing the differential uptake of NO3 and NH4 by flagellates, υ (day^{-1}). Parker (1993) used his formulation in a simple model (particulate nitrogen-NO3-NH4) and compared the results with phytoplankton culture data. The other parameterizations (Walsh, 1975; Jamart *et al.*, 1977; Wroblewski, 1977; Taylor and Joint, 1990) have been proposed and used in various ecosystem models.

Formulations of nutrient uptake rate as a function of nutrient concentration N use generally a hyperbolic relationship of the form N/(k+N) where k is the half-saturation constant. In the Jamart formulation N is equal to NO3+NH4 (Table 4). The other four formulations can be written, for an easier comparison, on the same basic scheme:

$$\upsilon = \upsilon_1 \frac{NO3}{k_1 + NO3} F_i + \upsilon_2 \frac{NH4}{k_2 + NH4}$$

with υ_1, υ_2 : maximum specific uptake rates (day^{-1}); k_1, k_2 : half-saturation constant (µM-N) for NO3 and NH4 respectively; F_i : inhibitory function of NO3 uptake by NH4 concentration.

Table 4. Uptake rate of nitrate and ammonium by flagellate (υ, day^{-1})
υ_m maximum uptake rate; υ_1, υ_2, specific uptake rate of NO3 and NH4 respectively ; k_1, k_2, half-saturation constant for NO3 and NH4 respectively

Construct		Value		Unit
	case 1	case 2	case 3	
1- Jamart *et al.* (1977)				
$\upsilon = \upsilon_m \frac{NO3 + NH4}{NO3 + NH4 + k_1}$	k_1=f(N)	1.0	f(N)	μM-N
	k=1.0	-	0.8	-
if $0 \leq N \leq 5$ μM *then* $k_1 = k\,(0.2 + 0.16\,N)$	N_{cr}=0.5	0.5	0.5	μM-N
if $N \geq 5$ μM *then* $k_1 = k\,(1.0)$ $\quad N = NO3 + NH4$				
and switching functions s_1 *and* s_2				
if $NH4 \geq N_{cr}$, $s_1 = 0$ *and* $s_2 = 1$				
if $NH4 < N_{cr}$ *and* $NO3 \geq N_{cr}$, $s_1 = 1$ *and* $s_2 = 0$				
if $NH4 < N_{cr}$ *and* $NO3 < N_{cr}$, $s_1 = NO3/N$ *and* $s_2 = NH4/N$				
2- Wroblewski (1977)				
$\upsilon = \upsilon_m \left[\frac{NO3}{k_1 + NO3} F_i + \frac{NH4}{k_2 + NH4}\right]$	k_1=1.0	1.0	1.0	μM-N
	k_2=1.0	1.0	0.351	μM-N
with $F_i = e^{-\Psi NH4}$	Ψ=1.462	1.462	1.462	μM-N^{-1}
3- Parker (1993)				
$\upsilon = \upsilon_m \left[\chi \frac{NO3}{k_1 + NO3} F_i + \frac{NH4}{k_2 + NH4}\right]$	k_1=3.69	1.0	1.2	μM-N
	k_2=0.25	1.0	1.2	μM-N
with $F_i = \frac{1}{1 + NH4 / k_2}$ *and* $\chi = \frac{\upsilon_1}{\upsilon_2}$	χ=0.575	0.575	1.0	-
4- Walsh (1975)				
$\upsilon = \upsilon_m \left[\frac{NO3}{k_1 + NO3} F_i + \frac{NH4}{k_2 + NH4}\right]$	k_1=1.5	1.0	1.5	μM-N
	k_2=1.5	1.0	0.6	μM-N
with $F_i = 1 - \alpha\, NH4$	α=0.25	0.25	0.45	μM-N^{-1}
if $NH4 \geq 1/\alpha$ *then* $F_i = 0$				
5- Taylor and Joint (1990)				
$\upsilon = \upsilon_m \frac{k_2\, NO3 + k_1\, NH4}{k_2\, NO3 + k_1\, NH4 + k_1\, k_2}$	k_1=0.2	1.0	0.9	μM-N
	k_2=0.1	1.0	0.45	μM-N
OR $\upsilon = \upsilon_m \left[\frac{NO3}{k_1 + NO3} F_i + \frac{NH4}{k_2 + NH4} F_i^{\prime}\right]$				
with $F_i = (k_2\, NO3 + k_1\, k_2) / (k_2\, NO3 + k_1\, NH4 + k_1\, k_2)$				
and $F_i^{\prime} = (k_1\, NH4 + k_1\, k_2) / (k_2\, NO3 + k_1\, NH4 + k_1\, k_2)$				

Parker (1993) used two different values for υ_1 and υ_2 while the others considered that υ_1 and υ_2 were equal. We therefore adopt a unique value of maximum uptake rate of nitrogen, υ_m equal to 1.2 day^{-1} (*cf.* Tab. 1), for the five formulations and parameterize the different υ_1 and υ_2 of the Parker formulation by the ratio χ (υ_1 over υ_2). Concerning the other coefficients and the inhibitory function F_i, the Taylor-Joint formulation uses two different values for k_1 and k_2 and the function F_i is related to them. In this equation, each nutrient concentration influences the uptake of the other and there is not only an inhibition of NO3 uptake by NH4 but also an inhibition of NH4 uptake by NO3. Parker (1993) also used two different values of k_1 and k_2 and the function F_i is related to k_2. In contrast, Walsh (1975) and Wroblewski (1977) adopted the same value for k_1 and k_2 and used a third parameter to formulate the inhibition of NO3 uptake by NH4. In the Jamart formulation, the half-saturation constant for nitrogen is assumed to vary with the inorganic nitrogen concentration. This formulation, with switching functions, is rather idealized as selective uptake by phytoplankton is probably not as mutually exclusive as represented by this formulation. In contrast to the other four formulations, NO3 and NH4 differential equations are therefore slightly different (see Tab. 3). We do not consider formulations such as this used by Carothers and Grant (1983) which differs from the others in that process rates are functions of the most limiting nutrient (i.e. Liebig's law of the minimum). We neglect diel periodicity of nutrient uptake and phytoplankton growth that some authors, such as Walsh (1975), took into account.
Three sets of parameter values are tested for the formulations: 1- the original values used by the authors, 2- same values of k_1 and k_2 for the five formulations, 3- a set of values providing a great similarity of simulations. The choice of these values and the criteria of choice will be discussed with the results.

Numerical integration, boundary conditions

The initial concentrations of the state variables (cf. Tab. 1) correspond to the measurements made on the first day of the experiment. The rate of change with time was calculated by the Runge-Kutta fourth-order method with a constant time step of 1 hour. Model results were also tested with time steps of 30 min and 2 h. Maximum differences between simulated concentrations with 30-min and 2-h time steps were of 0.1 µM-N, while the results for simulation showed no appreciable difference with either 30 min or 1 h as time step. A 1-h time step was therefore sufficient and it adequately corresponds to the biological rates of this modeled ecosystem. Models were run for seventy days to see clearly the influence of the different functions and permit simulations, in most cases, of two peaks of flagellates and zooplankton. This period also corresponded to the period for which values of the forcing variables (irradiance, temperature) are available. Irradiance and temperature are considered to be constant on a day scale. Nitrate additions are of 28, 6 and 2.5 µM-N on days 4, 21 and 40 respectively. During the first 70 days of the experiment, nutrient concentrations measured in the first 8 meters were of <0.1-30.7 µM-N for NO3, with values generally lower than 15 µM-N, and of 0.1-4.3 µM-N for NH4.

Results

Case 1: original parameter values

The first case deals with the original parameter values used by the authors, values which cover large ranges, 0.20-3.69 μM-N for k_1, 0.10-1.50 μM-N for k_2. Variation of the inhibitory function F_i with increasing NH4 concentration is presented on Figure 2. Two groups of curves can be distinguished : 1- the curves of Parker and Wroblewski which show a rapid decrease of f_i when NH4 increases between 0 and 1 μM-N and an important inhibitory effect ($F_i<0.1$ when NH4=2.5 μM-N), 2- the curves of Taylor-Joint and Walsh, with a more or less linear decrease and a small inhibitory effect ($F>0.37$ when NH4=2.5 μM-N). Moreover, the curve of Taylor-Joint is presented for a NO3 concentration of 5 μM-N; higher NO3 concentrations gives higher F_i values.

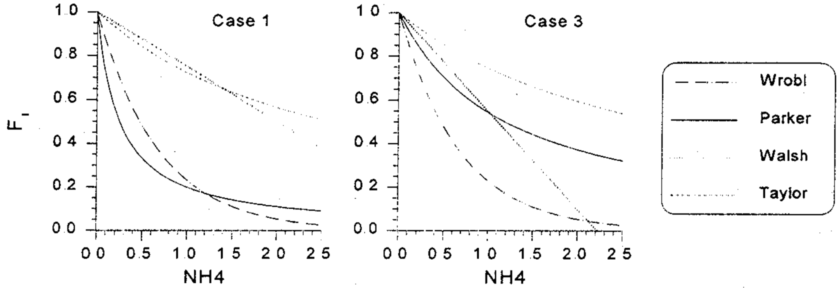

Fig. 2 Variation of the inhibitory function F_i on NO3 uptake with increase of NH4 concentration for two sets of parameter values (see Tab. 4). F_i is calculated with a NO3 concentration of 5 μM-N for the Taylor-Joint curve.

Figure 3 shows the isocontours of nutrient uptake by flagellates (υ) for the five formulations in the variable space NO3 (0-15 μM-N) - NH4 (0-2.5 μM-N). The Jamart formulation produces a simple pattern with parallel isocontours. Same values of υ correspond to the same concentration of NO3 and NH4; for example, the 0.95-isocontour intercepts the NO3-axis and the NH4-axis at a same value of 1.94 μM-N. In this case, differences in the NO3 and NH4 uptake are parameterized by switching functions in the NO3 and NH4 differential equations. The Taylor-Joint formulation produces a similar pattern with parallel isocontours. Values of uptake are very high ($\upsilon>1.1$ day^{-1}) in nearly all the NO3-NH4 space, due to the low values of k_1 and k_2 and the resulting high value of f_i. With the Parker equation, the inhibition of NO3 uptake appears more clearly for the lowest NH4 concentrations. With these two formulations, all highest values of υ occur for the highest NH4 and NO3 concentrations. In contrast, with the Walsh and Wroblewski equations, high υ values occur with median or relatively low NH4 concentration (particularly in the case of Wroblewski) and appear therefore near the lower right corner of the NO3-NH4 space; inhibition of NO3 uptake by NH4 appears very clearly. Figure 4 displays the simulated time courses of six of the state variables of the model obtained with the five formulations of nutrient uptake by flagellates. POM and silicate are not represented as POM is a sink and silicate nearly exhausted after day 7. In the reference data (see Andersen *et al.*, 1987) as well as in the simulated results, the first input of nitrate on day 4 promoted a large diatom peak which collapsed in a few days as silicate was exhausted; it was replaced by a flagellate peak. Peaks succeeded in the order phytoplankton, then herbivores, and lastly carnivores. Inputs of nitrate, on days 4, 21 and 40, appear clearly. As it could be expected, the variation of diatoms is not influenced by the type of formulation used for flagellates.

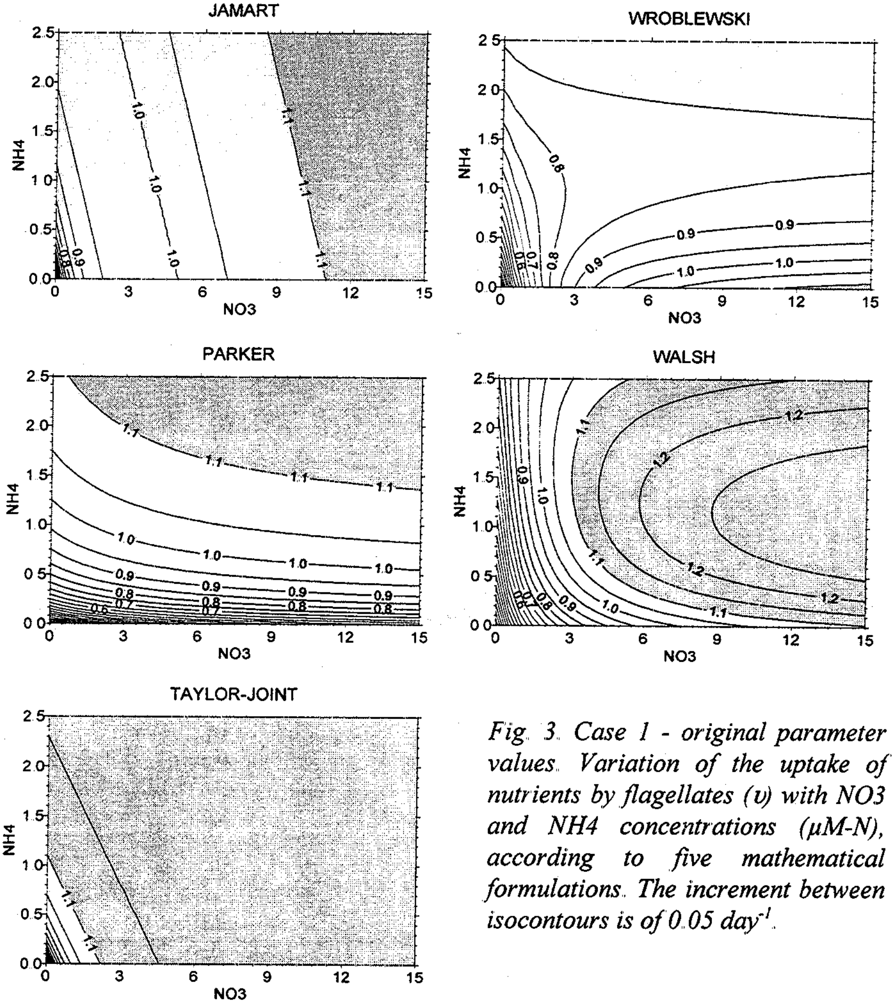

Fig. 3. Case 1 - original parameter values. Variation of the uptake of nutrients by flagellates (υ) with NO3 and NH4 concentrations (µM-N), according to five mathematical formulations. The increment between isocontours is of 0.05 day^{-1}.

The formulation used influences greatly the simulated dynamics of the ecosystem as well as in the number of peaks for each variable, the amplitude of these peaks, their relative importance and their timing. To simplify the comparison we can consider three groups: 1- Parker, 2- Wroblewski, 3- Jamart, Walsh and Taylor-Joint. The behavior of the second group appears somewhat intermediate between those of the first and third groups. The Parker simulation is characterized by a nearly complete inhibition of NO3 uptake after day 7, a reduced NH4 peak and small first peaks of flagellates, herbivores and carnivores. The second peak of flagellates is, compared to the other four simulations, moderate in maximum concentration but extended in time; this leads to large second peaks of zooplankton. Note also the occurrence of a third flagellate peak (~day 54) with this formulation.

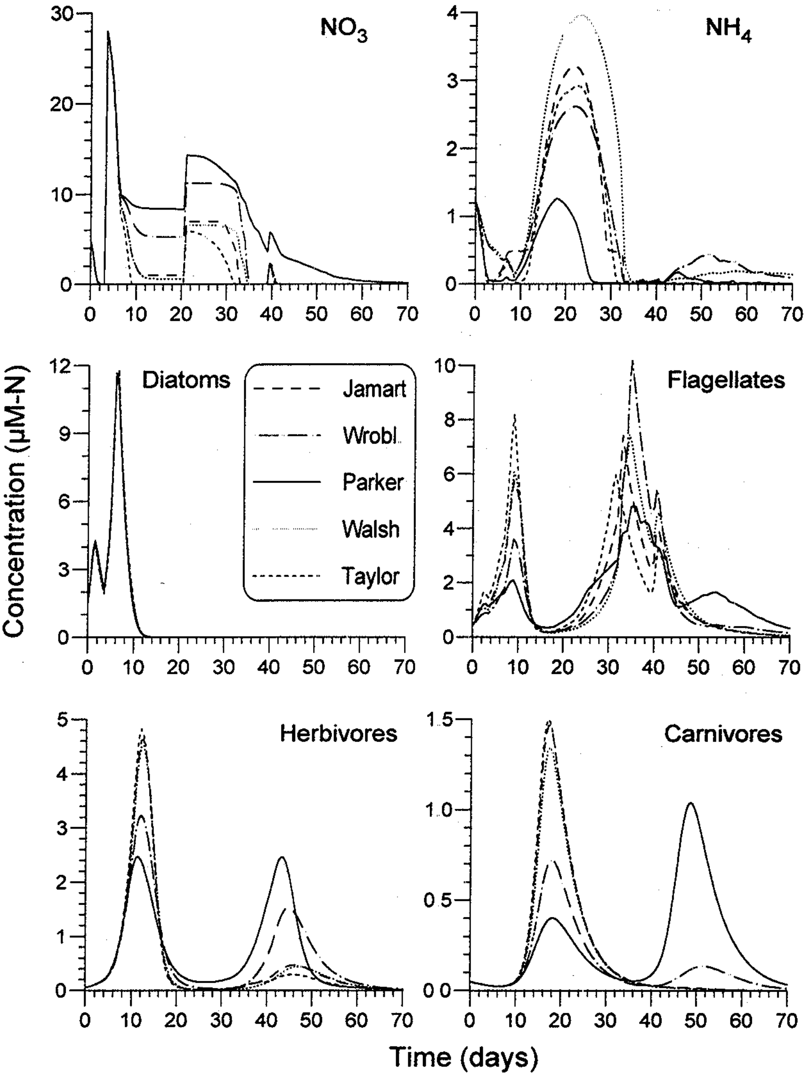

Fig. 4. Case 1 - original parameter values. Simulated temporal variations during 70 days of 6 state variables of the model, with the five formulations for nutrient uptake by flagellates.

Opposite features are observed for the third group of formulations (and intermediate for the second group): 1- the quasi-exhaustion of NO3 in group 3 after the first NO3 input (NO3 concentration remains relatively important in group 2), 2- important first and second peaks of flagellates of somewhat similar amplitude (in group 2 the second peak is much higher than the first one), 3- important first peaks of herbivores and carnivores (intermediate feature for Wroblewski, group 2), 4- a well developed NH4 peak (due to excretion of zooplankton and remineralization of fecal pellets and dead organisms), 5- a reduced second peak of herbivores and the absence of a second peak of carnivores (intermediate feature in group 2). We also note the following qualitative differences: the first peaks of herbivores and carnivores are equal or much lower than the second ones in the Parker simulation, while they are much higher in groups 2 and 3.

Apparent effects, such as differences in maximum concentration of the variables, propagate up the food-chain and increase with the trophic level. If we consider the second peaks of phyto- and zooplankton, which do not depend on diatoms, maximum amplitude of flagellates varies from 4.8 to 10.2 μM-N, i.e. a two-fold increase, those of herbivores from 0.3 to 2.5 μM-N, i.e. a eight-fold increase, and the maximum concentration of carnivores at that time (around day 50) is even more different, from 0.01 to 1.04 μM-N. If we consider absolute values, these differences in maximum amplitude are of course higher for flagellates than for herbivores and carnivores (differences of 5.4, 2.2 and 1.03 μM-N respectively).

Case 2: same values of k_1 and k_2 for the five formulations

We adopted the same value of 1 μM-N for k_1 and k_2 for the five formulations. k_1 and k_2 were set to the same value by Wroblewski (1 μM-N) and Walsh (1.5 μM-N) and Jamart *et al.* considered a unique half-saturation constant (cf. Tab. 4). This value of 1 μM-N is a reasonable value for k_1 in eutrophic waters (MacIsaac and Dugdale, 1969).

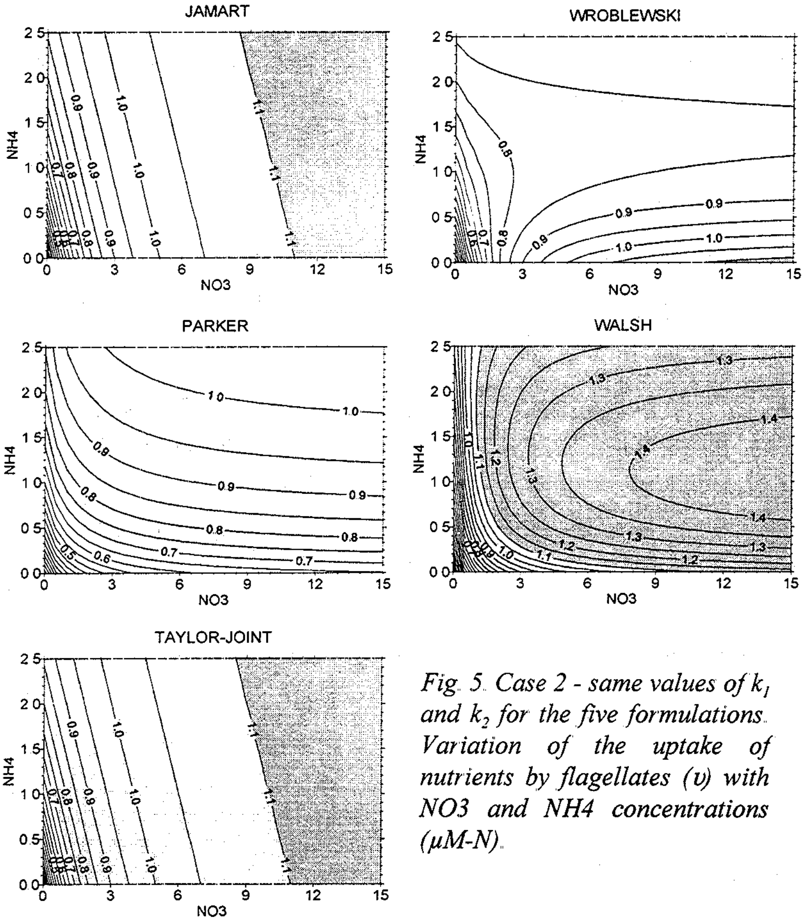

Fig. 5. Case 2 - same values of k_1 and k_2 for the five formulations. Variation of the uptake of nutrients by flagellates (υ) with NO3 and NH4 concentrations (μM-N).

The isocontours of nutrient uptake by flagellates are presented on Figure 5 for the five formulations, the Wroblewski formulation being unchanged. Adopting a unique value of k_1 and a unique value of k_2 for the five formulations forces the isocontours to have the same values on the axes. This appears clearly with the 1.0-isocontour which intercepts the NO3-axis at a value of 5 µM-N and with the 0.6-isocontour which crosses the NH4-axis at a value of 1 µM-N. When adopting a constant value of k_1 for the Jamart formulation and $k_1=k_2$, the formulations of υ by Jamart and Taylor-Joint become equivalent (*cf.* Tab. 4), as it appears clearly on the graphs. Following a decrease or increase of k_1 and k_2, uptake is, respectively, globally higher (Walsh) or lower (Taylor-Joint). In the case of Parker, higher uptake of NO3 is induced by the decrease of k_1 and the increase of k_2, but, uptake of NH4 is reduced by the increase of k_2, resulting in a globally lower uptake.

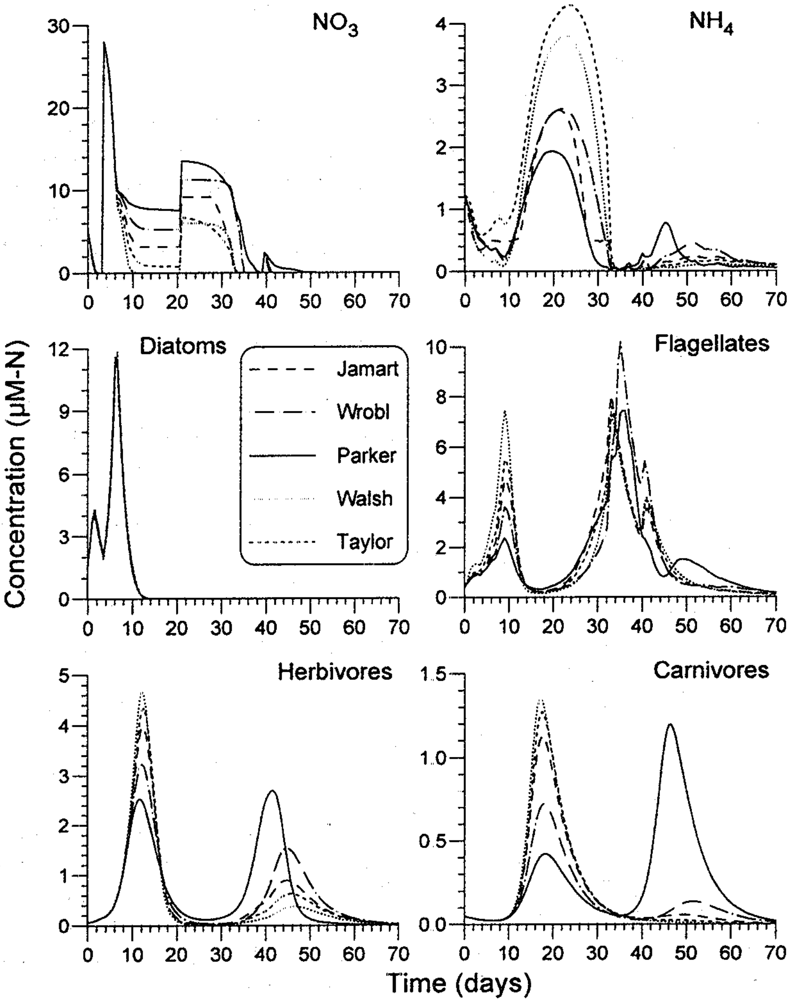

Fig. 6. Case 2 - same values of k_1 and k_2 for the five formulations. Simulated temporal variations during 70 days of 6 state variables of the model.

With this set of parameters the simulated dynamics of the model appears more similar with the Walsh and Taylor-Joint formulations (Fig. 6), some similarity having previously noted in case 1 between Jamart, Walsh and Taylor-Joint simulations. Although values of υ are identical for the Jamart and Taylor-Joint formulations, simulated curves are different. This results from the switching functions used by Jamart. Except for the second peak of flagellates, where the three simulated curves of Jamart, Taylor-Joint and Walsh are nearly confounded, the Jamart simulation with a constant value of k_1 appears more different from these two other simulations than in case 1. It is particularly obvious for NO3 and NH4 evolutions. The simulated dynamics with the Parker formulation is more similar to the four others in the cases of NO3, NH4 and flagellates. NO3 is more assimilated, particularly after day 32; the NH4 and the flagellate peaks are higher (with value of 7.3 μM-N instead of 4.8 μM-N for the second flagellate peak). But large differences remain, for herbivores and carnivores particularly.

Case 3: similarity of the simulated ecosystem evolution

A set of parameter values which induces similar simulated evolution of the ecosystem variables with the five formulations has been obtained (cf. Tab. 4) with the following criteria and constraints in mind. As much as possible we tried to keep the original coefficient values of the authors and the shape of the inhibitory curve f_i. Authors'values of k_1 were conserved in the Wroblewski and Walsh formulations; the variation of k_1 with inorganic nitrogen concentration was kept in the Jamart formulation. The inhibitory coefficient Ψ of Wroblewski was unchanged as its value was determined from a fitting to some experimental data. Keeping a ratio of 2 between k_1 and k_2 for Taylor-Joint formulation minimized the change of the curve F_i (cf. Fig. 2).

Uptake rates of nitrate and ammonium have been much more studied than inhibition of nitrate uptake by ammonium, and values of the coefficients k_1 and k_2 have been determined for various species or populations and in different environmental conditions (e.g. Eppley *et al.*, 1969; MacIsaac and Dugdale, 1969). Therefore, we remain in a reasonable range for k_1 (0.16-1.5 μM-N) and k_2 (0.35-1.2 μM-N). Both in the field and in the laboratory, k_1 values generally exceed or equal k_2 values (see the review by Dortch, 1990). Choosing $k_2<k_1$ in the formulations of Wroblewski and Walsh, where inhibition of NO3 uptake is not related to k_2, allowed us to control the simulated NH4 evolution more independently of the NO3 one. This appeared necessary to obtain the same simulation curves for the five formulations.

Figure 7 shows the corresponding isocontours of υ. Some global similarity of these graphs is observed between Wroblewski and Walsh, and between Jamart, Parker and Taylor-Joint. One solution to obtain similarity of these five graphs would be to increase k_1 to very high values of 3.5-4 μM-N for Wroblewski and Walsh formulations, values which are rarely observed. We preferred to keep biologically reasonable values.

Figure 8 shows that, with this set of values, the same dynamics of the ecosystem are simulated for the five formulations. Only the Parker simulation differs slightly from the four others. Not enough NO3 is assimilated. Modifying the evolution of NO3 without changing that of NH4 would require a large decrease of k_1, but in that case k_2 would be greater than k_1, in contrast to that generally observed. Note also that is was not possible to keep the different specific uptake rates (ratio χ) considered by Parker. To obtain these similar simulations, k_1 and k_2 have to be arbitrarily set to different values according to the formulation used; for example, k_1 is set to 0.9 μM-N in the Taylor-Joint formulation and to 1.5 μM-N in the Walsh one, and k_1 varies from 0.16 to 0.8 μM-N in the Jamart formulation. The values of k_1 and k_2 used are also very different from the original given by the authors: the value of k_1 is increased from 0.2 up to 0.9 μM-N (Taylor-Joint), the value of k_2 from 0.25 up to 1.2 μM-N (Parker).

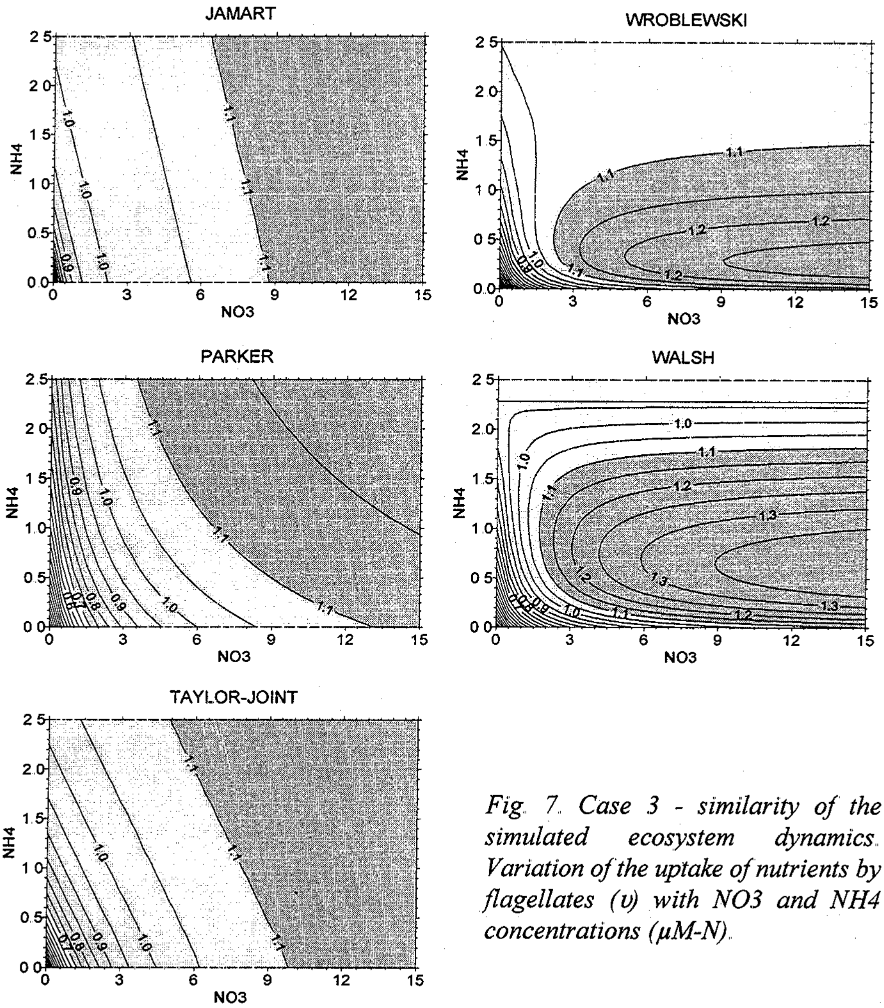

Fig. 7. Case 3 - similarity of the simulated ecosystem dynamics. Variation of the uptake of nutrients by flagellates (υ) with NO3 and NH4 concentrations (μM-N).

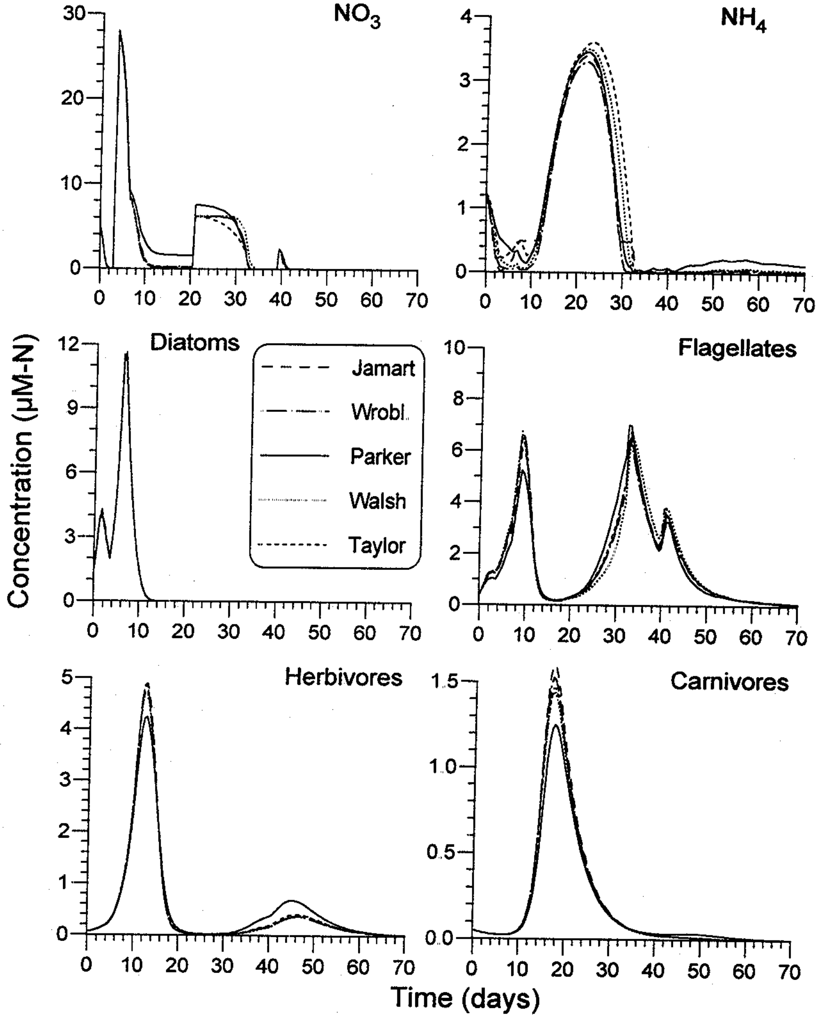

Fig. 8. Case 3. Similarity of the simulated temporal variations of the state variables of the model obtained with the five formulations.

Discussion

The results show how the output of an ecosystem model vary with the formulation used to represent the uptake of NO3 and NH4 by phytoplankton. This holds either when the original parameters are used or when the same biologically significant parameters (k_1 and k_2) are used. The simulated results differed not only in the amplitude of the peaks but also in the number of the peaks, the relative importance of first and second peaks and their timing. These differences were even observed with the formulations used in models of somewhat similar ecosystems, such as upwelling ecosystem (Walsh, 1975; Jamart *et al.*, 1977; Wroblewski, 1977). Nevertheless, it is possible to obtain the same simulated evolution of the ecosystem dynamics with the five formulations tested: the original parameter values had to be largely modified. We found such a set of values in which, for example, the extreme values of half-saturation constants used by Taylor and Joint (1990) or by Parker (1993) had to be modified. The parameter values also had to be set to different values for each formulation.

External inputs of nitrate were added in the experimental enclosure and consequently in the model. It can be argued that important effects will probably only occur when modelling systems with periodic external nutrient inputs. However, such systems may be more common and more important than generally thought. In open systems, inputs of nitrate from deep layers to euphotic layer following a wind event have been reported (Marra *et al.*, 1990; Nielsen and Kiørboe, 1991), and they induce an enrichment in chlorophyll of the upper layers. Nutrient pulses play a large role in oligotrophic areas in generating new production. Effects of physical processes on the availability of nutrients have also been studied in different physical models. For example, Klein and Coste (1984) showed in their one-dimensional model that nutrient input into the upper layer was mainly controlled by turbulent vertical transport through the thermocline. Simulated results of Flierl and Davis (1993) suggested that vertical motions resulting from mesoscale oceanographic features could be an important source of new nutrients. Although such *in situ* inputs are not as high as those made in the CEPEX enclosure, these phenomena stress the need for appropriate formulation of nutrient uptake.

Our purpose was not to determine the best formulation. Parker (1993) tested his parameterization of differential NO3 and NH4 uptake in a simple model (particulate nitrogen-NO3-NH4). He found a good agreement of the simulated concentrations of NO3, NH4 and phytoplankton with a data set of about thirteen measurements from the literature. In contrast, Wroblewski (1977) based his formulation on a good fit of uptake rates (i.e. on physiological processes and not on resulting concentrations as did Parker). From a literature data set of 4 values, he determined a value of 1.462 μM-N^{-1} for Ψ, the NO3 uptake inhibition parameter. Hofmann and Ambler (1988) used the Wroblewski function in their ecosystem model, but with a rather different Ψ value of 5.59 μM-N^{-1} determined from a fit to five experimental values. The Wroblewski equation has been used in several ecosystem models (e.g. Fasham *et al.*, 1990; Kumar *et al.*, 1991) but with different values for the parameters often not experimentally justified. Inhibition of NO3 uptake by NH4 has been shown as a highly variable process (see the reviews by McCarthy, 1981; Syrett, 1981; Collos, 1989; Dortch, 1990). On one hand more studies coupling experimental data and adjustment of mathematical functions have to be performed; on the other hand, modelers need to be careful in the choice of the formulation of nutrient uptake and of the corresponding parameter values, and to test how this choice affect the model results.

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