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"A mathematical model for a *Phaeocystis sp.* dominated plankton community dynamics. I: The basic model"

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A mathematical model for a *Phaeocystis sp.* dominated plankton community dynamics. I: The basic model

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Abstract. Many factors interact to control vernal blooms of *Phaeocystis sp.* in polar and temperate waters, which makes it difficult to predict when or how these blooms will develop or terminate. Here, we construct a mathematical model that includes nutrients (nitrogen and phosphorus), grazers (ciliates and copepods), and *Phaeocystis* (single cell and colonial forms) compartments to analyze the role and the magnitude of the effect of several controlling factors in bloom dynamics. The model focuses on two aspects of plankton ecology: community dynamics and the role of life history attributes at the population level. Employing combinations of physiological and ecological processes, our models generate abrupt changes in plankton densities as often observed in the oceans.

We illustrate dynamic sensitivity by varying a parameter over a reasonable range of values and noting that there exist thresholds where a small variation can produce a significant change in the dynamic outcome, transforming the system from one type of dynamic behavior to another. The results indicate that colonies are important community structuring agents in certain environments; for example, in some settings, colonies do not develop to large sizes and contribute to high removal rates by sinking unless grazers keep *Phaeocystis* single cell densities below threshold levels. In particular, initial microzooplankton densities, the character of the microzooplankton functional response to algal abundance (as described by the half-saturation constant K_1), and the timing of copepod grazing indirectly determine nutrient utilization between single and colonial forms in the *Phaeocystis* population. The results of our simulations indicate that the system has a strong dependence on the balance between growth rates and removal rates in both *Phaeocystis* and protozoan populations during the first days of the bloom, the nutrients and the copepods playing alternate roles as indirect controls as the bloom progresses. Because of the importance of the timing of events, the structure of the colonial population, and the complexity of underlying feedback mechanisms, the system does not exhibit the classical pattern of trophic chain oscillations.

Introduction

Phaeocystis spp. are unicellular algae with a complex life cycle. Although discovered over a century ago, much of the research to understand its developmental life history and its role as a dominant primary producer in different environments has been accomplished only in the last decade. *Phaeocystis spp.* can be large contributors to primary production in both polar (Smith et al. 1991) and temperate regions (Lancelot et al. 1987). This article focuses upon understanding the dynamics of planktonic communities containing *Phaeocystis* populations and their role in oceanic transport. Our objective is to analyze the relative importance of different physiological and ecological factors that cause the sudden density changes often observed in planktonic systems and determine the relative dominance of single cell or colonial forms under various environmental conditions.

The complexity of the life history of *Phaeocystis spp.*, the ecological intricacies of the timing and the magnitude of the densities of zooplankton (such as ciliates and copepods), and the roles of the processes of sinking and sedimentation, suggest that prediction of the development of characteristic community dynamics as well as the fate of the *Phaeocystis* bloom is a nontrivial task. Here we consider issues relating to bloom dynamics including the role of nutrients (nitrogen, *N*, and phosphorous, *P*), the importance of grazing as a control of community structure, including the timing of the appearance of size-specific grazers, and the importance of sinking and sedimentation as factors contributing to vertical fluxes.

Review of *Phaeocystis* life history and ecology

Phaeocystis sp. (Prymnesiophyceae, earlier called Haptophyceae), was first identified by M. G. Pouchet in 1892. Found in temperate oceans (Lancelot et al. 1991), polar seas (Palmisano et al. 1986), where it produces massive blooms, as well as in tropical waters (Guillard and Hellebust 1971), it occurs in at least two different forms, solitary and colonial (Parke et al. 1971), and is characterized by a complex life cycle (Lancelot et al. 1991, Davidson and Marchant 1992, Rousseau et al. 1994).

In the solitary cell form *Phaeocystis* is free-living, 3 to 10 μm in diameter (Kornmann 1955, Gieskes and Kraay 1975, Moestrup 1979, Chang 1983, Weisse and Scheffel-Moser 1990b), and can be either flagellated or non-motile (Parke et al. 1971, Hallegraeff 1983, Chang 1984). Colonies are formed from non-motile cells and consist of cells embedded in a mucilaginous matrix (Chang 1983). While in the colony, cells can grow and divide (Kornmann 1955). The signal for initiation of colony formation is unknown, and although many environmental factors have been considered as triggers (temperature, decreased concentrations of nutrients, trace metals, etc.), no conclusive evidence has been yet found

(Verity et al. 1991). Colonies can break into smaller colonies (Kornmann 1955, Verity et al. 1988, Rousseau et al. 1990), but two colonies do not aggregate to form a larger one. Colonial sizes generally vary from 10 μm to 3 mm in diameter, normally contain from 2 to 10,000 cells, but under particular environmental conditions, larger sizes and numbers can be attained. Both single and colonial forms can coexist in the same population (Davidson and Marchant 1992).

The number of species in this genus remains a matter for debate (Parke et al. 1971, Sournia 1988, Baumann et al. 1994). At present *P. pouchetii*, *P. globosa* and *P. scrobiculata* are considered to be separate species, although there is evidence for the existence of an Antarctic strain with particular characteristics (Baumann et al. 1994). *P. scrobiculata* has been found in New Zealand (Moestrup 1979) and in the North Atlantic (Estep et al. 1984) and exhibits small morphological differences relative to the other two. *P. pouchetii* and *P. globosa* do not have any detectable morphological difference in the single stage, and only seem to differ in the form of the colony and the fragility of the matrix (Kornmann 1955, Chang 1983, Jahnke and Baumann 1987). *P. pouchetii* is found in colder waters (−2 to 14°C) while *P. globosa* seems to survive in warmer waters (−0.6 to 22°C)(Jahnke and Baumann 1987, Baumann et al. 1994).

Phaeocystis blooms can occur in a wide range of environments, in regions of high nutrient concentrations (North Sea) or low nutrient concentrations (tropical Atlantic), of strong stratification (marginal ice zones) or weak stratification (Norwegian fjords), in various coastal environments, and under low or high grazing pressure (Wassmann 1994). After the bloom reaches a peak, usually a sudden disappearance of *Phaeocystis* occurs. Possible causes for the rapid biomass change include grazing, cell lysis, microbial degradation and sedimentation.

Phaeocystis sp. can serve as food resource for numerous types of grazers (Davidson and Marchant 1992, Weisse et al. 1994, Hansen et al. 1994) because of the spectrum of *Phaeocystis sp.* size availability (over three orders of magnitude). Tintinnids, ciliates, dinoflagellates, and other microzooplankton feed on single cells (Admiraal and Venekamp 1986, Weisse and Scheffel-Moser 1990a, Weisse et al. 1994). Colonies up to 300 μm in diameter are eaten by metazooplankton, mainly copepods (Jones and Haq 1963, Weisse 1983, Huntley et al. 1987, Tande and Bamsted 1987, Hansen and van Boekel 1991). Copepods may prefer senescent colonies (Estep et al. 1990) possibly because in the growth phase, cells produce dimethylsulphonio-propionate (DMSP) (Liss et al. 1994), which generates acrylic acid and dimethyl sulphide (DMS), both of which could result in colonies being less palatable to some grazers. Grazing by protozoans (North Sea, Weddell Sea), copepods, or krill (Weddell Sea, Bransfield Strait) can be a significant factor in the termination of blooms (Tande and Bamstedt 1987, Weisse and Scheffel-Moser 1990a).

Methods

A mathematical model, constructed in modular form based on the relationships indicated in the *Phaeocystis* community diagram (Fig. 1), is formulated and parameterized utilizing information and data on the processes found in the literature. In addition to *Phaeocystis* in single cell and colonial forms, model compartments include two nutrients, nitrogen and phosphorus; two grazers populations, microzooplankton (e.g. ciliates) and metazooplankton (e.g. copepods). Simulations were performed to evaluate the effects of various scenarios represented by different sets of parameter values and initial conditions.

The physical environment of our model assumes a mixed layer of given depth z with constant temperature and salinity, hence water density and viscosity do

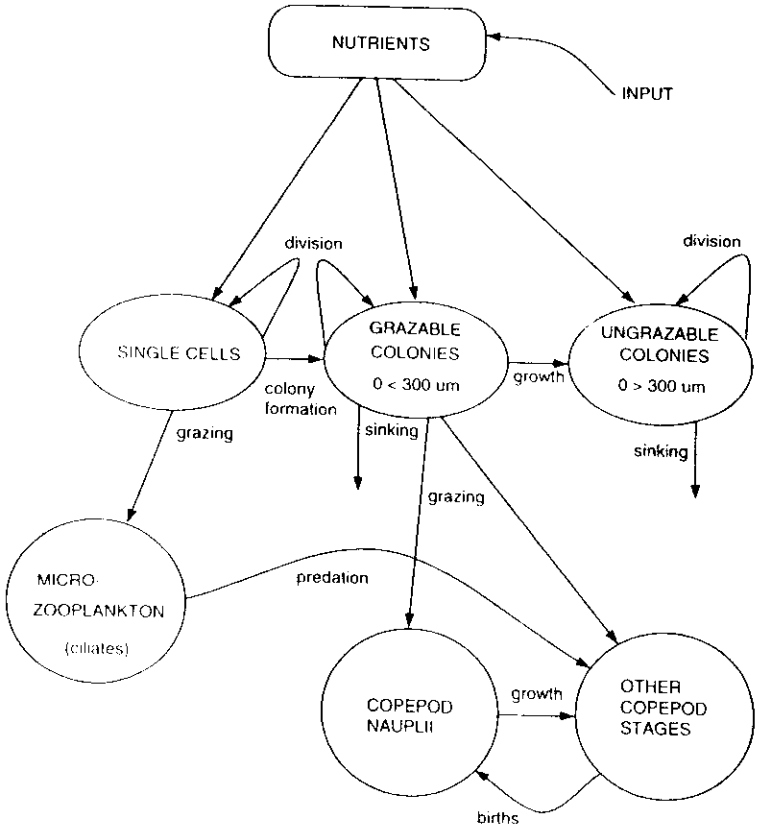

Figure 1. Diagram of compartments and connections in the basic model. Horizontal arrows represent movement to other classes by growth, while vertical arrows represent removal by consumption or by sinking out of mixed layer.

not vary. Even though the mixed layer is a very patchy environment, all variables are assumed to be homogeneously distributed. Nutrient concentrations and population densities can vary within a distance of a few centimeters or less. Measurements taken from a fixed station at sea do not always refer to the same population or environment because currents move water masses and all plankton they contain. Hence we take a Lagrangian perspective as the individual members of the populations are followed as they move together with their environment. If we keep in mind that the purpose of our model is not prediction but analysis of the behavior of a system and its response to different environmental conditions, then the assumption of a homogeneous distribution seems reasonable. Removal of colonies by sinking refers to removal from the mixed layer.

The basic model

Individual *Phaeocystis* cell models. To analyze the relative importance of factors involved in the life cycle of *Phaeocystis sp.*, we develop an individual-based model that tracks cells, both in single and colonial forms, as they grow and divide in the mixed layer.

A newly formed cell has a minimum volume V_0; it grows until it reaches a maximum volume $2V_0$ and then divides. We assume that the cell uptakes the nutrients in the surrounding water following a Monod-type model. The nutrients are absorbed through the outer membrane so that uptake is proportional to surface area and depends on the concentration of the nutrients in the water. The losses (respiration, maintenance) are proportional to the volume of the cell. The growth rate is proportional to the balance of uptake and losses. The basic model of the single cell is

$$\frac{dV}{dt} = F_s(N, P)(a_s V^{2/3} - b_s V) = f_s(V, t) \tag{1}$$

where $N(t)$ and $P(t)$ are the concentrations of nitrogen and of phosphorus in the water at time t, $V(t)$ is the volume of the cell at time t, and a_s and b_s represent growth and loss rates, respectively. The function

$$F_s(N, P) = \frac{NP}{k_P^s N + k_N^s P + NP} \tag{2}$$

represents an additive model, a variation of the Monod function for the simultaneous limitation of growth by two nutrients, where k_N^s, k_P^s are half saturation constants for nutrient uptake (O'Neill et al., 1989).

An initial cell size distribution is assumed to be a truncated normal distribution covering the range between a minimum, $V_{\min}$, and a maximum, $V_{\max}$, cell size

for the species, with mean $\frac{V_{\min} + V_{\max}}{2}$. This originates a set of initial volumes $V_0^{(\ell)}$ corresponding to a discrete set of cell sizes (ℓ).

Colonial cells follow the same growth process but are governed by the equation

$$\frac{dV}{dt} = F_c(N, P)(a_c V^{2/3} - b_c V) = f_c(V, t) \tag{3}$$

where a_c and b_c represent growth and maintenance rates respectively, and $F_c(N, P)$ is an additive functional response similar to Equation (2), with half saturation constants k_N^c, k_P^c. When a colonial cell divides, the two daughter cells remain in the mucilaginous envelope.

Because each colony originates from one cell and all cells in a colony are subject essentially to the same environmental conditions, we assume synchronous divisions that result in the doubling of colonial cell number (Kornmann 1955, Rousseau et al. 1994). In order to track colonies individually, a system of colony size classes containing 2^n cells is constructed.

Nutrient model. As the dynamic algal population evolves, nitrogen and phosphorus concentrations vary according to the equations

$$\frac{dN}{dt} = I_N - u_{N_s} S_s F_s(N, P) - u_{N_c} S_c F_c(N, P) \tag{4}$$

and

$$\frac{dP}{dt} = I_P - u_{P_s} S_s F_s(N, P) - u_{P_c} S_c F_c(N, P) \tag{5}$$

where $N(t)$, $P(t)$ represent concentrations of nitrogen and phosphorus in the water, $S_s(t)$ is the total surface of single cells and $S_c(t)$ is the total surface of colonial cells (per unit volume of water) at time t. We are assuming that the colonial matrix is permeable so that colonial cells perceive the same nutrient concentration as is in the surrounding water. Here u_{N_s}, u_{N_c}, u_{P_s}, u_{P_c} are maximum uptake rates and $F_s(N, P)$, $F_c(N, P)$ are the respective additive functions for the simultaneous limitation of growth by two nutrients. I_N and I_P are time dependent functions representing nutrient input to the system.

Maximal growth rates (a_s, a_c) and uptake rates (u_N, u_P) are computed from known population doubling times and carbon content at volume V_0 of single and colonial cells by using the exact solution to our equations when nutrients are abundant ($F_s(N, P) = 1$, $F_c(N, P) = 1$) and assuming the ratios $C : N : P$ within cells to be constant 106 : 16 : 1. Although ratios change as the bloom progresses, this is a reasonable approximation that helps maintain numerical simplicity.

Ciliate population model. Structured feeding is not imposed for ciliates because they generally consume only single celled *Phaeocystis* forms. The model ciliate grazer population is represented in an aggregated form (Steele 1974, Scheffer 1991) rather than modeled with an individual-based approach. The ciliate population growth is assumed given by

$$\frac{dG_1}{dt} = g_1 s_1 \frac{AG_1}{A + K_1} - \frac{\mu_1 G_1^2}{\kappa} \tag{6}$$

where

$$A(t) = \int_{V_{\min}}^{V_{\max}} \alpha(V) \rho_0(V, t) dV \tag{7}$$

is the algal biomass density in terms of carbon, $\alpha(V)$ is the carbon mass of a cell of volume V, $\rho_0(V, t)$ is the density of single cells of volume V, and $G_1(t)$ is the density of ciliates at time t. Here K_1 represents the half saturation constant in a Type II functional response, g_1 is the maximum grazing rate, s_1 is the assimilation rate, and μ_1 is the mortality rate. Note that the form of this equation is similar to the logistic equation. In the latter, the density dependent mortality term includes a parameter related to resource abundance (carrying capacity). In our case resource is abundant and not a limitation to growth, but an increasing population can be limited by space or predators. Thus we uncouple effects by introducing an independent parameter κ to represent crowding. This simple way of modeling the ciliate population appears sufficient to obtain a descriptive, qualitative behavior of the system.

Copepod population model. In contrast to the ciliate population, the copepod population is structured because individuals in different stages of development graze on colonies of different sizes. We represent the population in five different groups: nauplii, early copepodites (CI–CIII), late copepodites (CIV–CVI), female adults and male adults. Each cohort is followed through its development into consecutive stages by using the individual growth equation:

$$\frac{dm}{dt} = (\phi_2(j(m)) s_2 - b_2) m = f_2(m) \tag{8}$$

where $m(t)$ denotes the carbon mass of the individual at time t; $\phi_2(j(m))$ denotes the ingestion rate of an individual at stage j with mass m; and s_2 and b_2 denote assimilation and maintenance rates respectively. We assume that the ingestion rate depends only on the developmental stage, that individual growth does not depend solely on *Phaeocystis* abundance, and that the copepod population is not resource limited.

Let $G_2(m, t)$ be the density of copepods of mass m at time t, then the copepod population follows the size structured McKendrick–von Foerster equation

$$\frac{\partial G_2}{\partial t} + \frac{\partial}{\partial m}(f_2 G_2) = -\mu_2(j(m))G_2 \tag{9}$$

where $f_2(m)$ is the individual growth function, and $\mu_2(j(m))$ is the size dependent mortality function. The boundary condition is

$$G_2(m_0, t) = \int_{m_4}^{m_M} \beta(m, t)G_2(m, t)dm \tag{10}$$

where m_0 is the mass at hatching, m_4 and m_M the minimal and maximal masses, respectively, for adult females, and $\beta(m, t)$, the birth function, is a pulse function equal to the average number of nauplii produced after each reproductive interval by a female of mass m when t is a multiple of the reproductive interval τ_2, and zero for all other t.

***Phaeocystis* population model.** For each cell type (ℓ) we denote by $\rho_0(V^{(\ell)}, t)$ the density of single cells of this type that have a volume $V^{(\ell)}$ at time t, and $\rho_i(V^{(\ell)}, t)$ the density of colonies having $2^{(i-1)}$ cells of volume $V^{(\ell)}$ at time t, for $i = 1, \ldots, n_{\max}$.

The *Phaeocystis* population is described by the $(n_{\max} + 1)$ equations

$$\frac{\partial \rho_i}{\partial t} + \frac{\partial}{\partial V}(f_* \rho_i) = -losses \tag{11}$$

for $i = 0, 1, \ldots, n_{\max}$, where f_* denotes the individual growth function f_s or f_c, depending on the case. The boundary conditions are

$$\rho_0(V_0^{(\ell)}, t) = (2 - \chi)\rho_0(2V_0^{(\ell)}, t) \tag{12}$$

$$\rho_1(V_0^{(\ell)}, t) = \chi\rho_0(2V_0^{(\ell)}, t) \tag{13}$$

where χ is a number such that $0 < \chi < 1$, and represents the probability of a single cell generating a colony; and for $i > 1$,

$$\rho_i(V_0^{(\ell)}, t) = 2\rho_{i-1}(2V_0^{(\ell)}, t). \tag{14}$$

Losses modules

The term labelled *losses* on the right hand side of (11) is composed of one or more of the following terms:

Sinking. We assume that flagellated cells do not sink, but that all colonies obey Stokes' Law for small spherical particles. There are physiological factors that need to be taken into account when considering the sinking of microzooplankton in the water column. These factors are mostly related to shape, density, and surface characteristics (such as smoothness, stickiness, spikes, surface to volume ratio, etc.) and to the ability of organisms to change them. Healthy colonies are either spherical or ellipsoidal so that spherical seems reasonable approximation. Moreover, healthy colonies seem to be able to vary their density but not their shape or surface characteristics. Under this assumption, Stokes' Law appears to be an adequate representation for sinking. A colony of size i will sink with velocity

$$v_i = \frac{2}{9} g r_i^2 \frac{\delta_i - \delta_w}{\eta \delta_w} \tag{15}$$

for all sizes $i = 1, \ldots, n_{\max}$, where g is the gravitational force constant, η is the viscosity of sea water and δ_w is the density at a given temperature and salinity, r_i is the radius of the colony, computed using the relationship between number of cells in a colony and colonial volume developed by Rousseau et al. (1990)

$$\log(2^{(i-1)}) = a \log V + b, \tag{16}$$

and δ_i is the size dependent density of the colony. We compute the density of a colony by expressing its volume in terms of the number of cells and the mass as the sum of cell mass and matrix mass, assuming that the matrix has the density of sea water. δ_i can be expressed as

$$\delta_i = \delta_w + \alpha(2^{(i-1)})^\beta \tag{17}$$

where α and β are constants. The values obtained are $\alpha = 0.4$ and $\beta = -1$ by fitting our equation to data communicated from C. Lancelot (Université Libre de Bruxelles).

The loss term due to sinking is then

$$sinking = \frac{v_i}{z}\rho_i \tag{18}$$

where z is the depth of the mixed layer, and $i = 1, \ldots, n_{\max}$.

Ciliate grazing. We assume that ciliates graze only on single cells, yielding grazing loss represented by the equation:

$$grazing_1 = \frac{A(t)}{A(t) + K_1} g_1 G_1(t) \tag{19}$$

where $A(t)$ is as defined in (7).

Copepod grazing. The grazing impact on the *Phaeocystis* population is realized through two different controls: a "preferred size" function $p(i, j(m))$ that depicts the size distribution of particles ingested at each stage j of development (Bergreen et al. 1988), and a stage dependent "diet" function $D(j(m))$ that determines the portion of the individual's daily total demand, in terms of carbon, met by consuming *Phaeocystis* cells.

We assume that nauplii feed both on single cells and colonies, and that other copepod stages feed only on colonies, all following the preferred particle size distribution function $p(i, j(m))$. The proportion of cells and colonies removed from size class i by copepods is

$$grazing_2 = \int_{m_0}^{m_M} D(j(m)) p(i, j(m)) G_2(m, t) dm \tag{20}$$

for $i = 0, 1, \ldots, n_{\max}$.

Additional modules

Predation. If $D_c(j(m))$ is the stage dependent "diet" function that determines the portion of the individual copepod's daily carbon demand met by consumption of ciliates, then predation on ciliates by copepods is

$$\frac{1}{\alpha_c} \int_{m_0}^{m_M} D_c(j(m)) G_2(m, t) dm \tag{21}$$

where α_c is the carbon mass of an individual ciliate. When predation is included, Eq. 9 is replaced by

$$\frac{dG_1}{dt} = g_1 s_1 \frac{AG_1}{A + K_1} - \frac{\mu_1 G_1^2}{\kappa} - \frac{1}{\alpha_c} \int_{m_0}^{m_M} D_c(j(m)) G_2(m, t) dm. \tag{22}$$

The equations describing the *Phaeocystis* population remain unchanged.

Nutrient input. Eqns. 4 and 5 describe temporal variations in the concentration of nitrogen, $N(t)$, and phosphorus, $P(t)$. They include time dependent functions $I_N(t)$ and $I_P(t)$ which represent daily nutrient input to the system. In the early steps of our simulations, nitrogen and phosphorus input will be assumed to be equal to zero. Later we will assume these functions to be of the form

$$I_*(t) = \begin{cases} 0 & \text{if } t < t_s \\ \text{constant} & \text{if } t_s \le t \le t_e \\ 0 & \text{if } t > t_e \end{cases} \tag{23}$$

where $I_*(t)$ designates either $I_N(t)$ or $I_P(t)$, and t_s and t_e represent the times at which nutrient inflow begins and ends respectively.

Table 1 presents a summary of variables, functions and parameters, as well as their units, as used in the model. Tables 2 and 3 show the values of parameters and initial conditions employed in the simulations.

Table 1. Glossary of symbols in the model

Name	Description	Units
	a. *Phaeocystis* models	
a_s	maximum growth rate for single cell	$\mu m\ d^{-1}$
a_c	maximum growth rate for colonial cell	$\mu m\ d^{-1}$
b_s	maintenance rate for single cell	d^{-1}
b_c	maintenance rate for colonial cell	d^{-1}
$f_s(V)$	individual growth function for single cell	$\mu m^3\ d^{-1}$
$f_c(V)$	individual growth function for colonial cell	$\mu m^3\ d^{-1}$
k_N^s	half-saturation constant for N in single cell	μM
k_P^s	half-saturation constant for P in single cell	μM
k_N^c	half-saturation constant for N in colonial cell	μM
k_P^c	half-saturation constant for P in colonial cell	μM
$N(t)$	concentration of nitrogen in water	μM
$P(t)$	concentration of phosphorus in water	μM
u_{Ns}	maximum uptake rate for N in single cells	$\mu M\ d^{-1}\ mm^{-2}$
u_{Ps}	maximum uptake rate for P in single cells	$\mu M\ d^{-1}\ mm^{-2}$
u_{Nc}	maximum uptake rate for N in colonial cells	$\mu M\ d^{-1}\ mm^{-2}$
u_{Pc}	maximum uptake rate for P in colonial cells	$\mu M\ d^{-1}\ mm^{-2}$
$V^{(\ell)}$	volume of cell of type ℓ	μm^3
$V_0^{(\ell)}$	initial cell volume for cell of type ℓ	μm^3
χ	probability of a single cell turning into a colony	–
$\rho_0(V^{(\ell)}, t)$	density of cells of volume V (type ℓ) at t	ind. l^{-1}
$\rho_i(V^{(\ell)}, t)$	density of colonies of size i having cells of volume V (type ℓ) at time t	col. l^{-1}

Table 1. (cont.) Glossary of symbols in the model

Name	Description	Units
	b. Ciliate model	
$A(t)$	algal biomass (single cells)	μgC
$\alpha(V)$	carbon mass in cell of volume V	μgC
$G_1(t)$	ciliate density	ind. l^{-1}
g_1	grazing rate of ciliates	d^{-1}
K_1	half-saturation constant for ciliates	$\mu gC\ l^{-1}$
κ	crowding effect constant	ind. l^{-1}
s_1	assimilation rate of ciliates	..
μ_1	mortality rate of ciliates	d^{-1}
	c. Copepod model	
b_2	maintenance rate for copepods	d^{-1}
$f_2(m)$	individual growth function for copepods	$\mu gC\ d^{-1}$
$G_2(m, t)$	density of copepods of mass m	ind. l^{-1}
$j(m)$	stage copepod is in when mass is m	..
m_0	initial C mass of naupli	μgC
m_1	C mass when entering stage CI	μgC
m_2	C mass when entering stage CIV	μgC
m_3	C mass when entering adult stage	μgC
m_4	minimal C mass for spawning females	μgC
$D(j(m))$	percentage of daily C demand met by ingesting *Phaeocystis* cells when of mass m	..
$p(i, m)$	portion of colonies of size i out of total ingested by copepod of mass m	..
R_2	sex ratio in adult copepods	..
s_2	assimilation rate	..
$\beta(m, t)$	birth function in copepods	..
$\mu_2(j(m))$	stage dependent mortality rate of copepods	d^{-1}
$\phi_2(j(m))$	ingestion rate of copepods in stage $j(m)$	$\mu gC\ d^{-1}$
τ_2	reproductive interval in copepods	d
	d. Sedimentation model	
δ_w	density of seawater	$\mu g\ l^{-1}$
δ_i	density of colony of size i	$\mu g\ l^{-1}$
η	viscosity of seawater	$\mu g\ mm^{-1}\ d^{-1}$
g	gravitational acceleration	$m\ d^{-2}$
r_i	radius of colony of size i	mm
v_i	sinking velocity of colony of size i	$m\ d^{-1}$
z	depth of mixed layer	m
α_M	carbon content in matrix	$ngC\ mm^{-3}$

Table 2. Fixed parameter values

Name	Value	Units	Reference
minrad	3	μm	Weisse and Scheffel-Moser (1990)
maxrad	3.8	μm	≪»
ρ_0	5×10^5	ind. l^{-1}	created
b_s	0.0336	d^{-1}	Lancelot et al. (1991)
b_c	0.0336	d^{-1}	≪»
α_s	10.8 ± 3.5	pgC	Rousseau et al. (1990)
α_c	4.28 ± 5.3	pgC	≪»
α_M	335 ± 42	$ngC\ mm^3$	≪»
δ_w	1.0246	$\mu g\ l^{-1}$	Parsons et al. (1984)
η	0.119664×10^9	$\mu g\ mm^{-1}\ d^{-1}$	≪»
z	100	m	
μ_1	0.17	d^{-1}	Scheffer (1991)
κ	3000	ind. l^{-1}	created
m_0	0.019	μgC	computed from Bergreen et al. (1988)
m_1	0.32	μgC	≪»
m_2	1.15	μgC	≪»
m_3	2.7	μgC	≪»
m_4	3.0	μgC	≪»
$\phi_2(1)$	0.593	d^{-1}	computed from Harris and Paffenhofer (1976) and Bergreen et al. (1988)
$\phi_2(2)$	0.934	d^{-1}	≪»
$\phi_2(3)$	0.752	d^{-1}	≪»
$\phi_2(4)$	0.411	d^{-1}	≪»
$\phi_2(5)$	0.205	d^{-1}	≪»
$D(1)$	0.8	..	inspired in Estep et al. (1991)
$D(2)$	0.7	..	≪»
$D(3)$	0.5	..	≪»
$D(4)$	0.1	..	≪»
$D(5)$	0.1	..	≪»
b_2	0.81	d^{-1}	Bergreen et al. (1988)
s_2	0.44	..	≪»
τ_2	1.0	d	Harris and Paffenhofer (1976)
R_2	0.47	..	≪»
$\mu_2(1)$	0.12	d^{-1}	estimated from Harris and Paffenhofer (1976)
$\mu_2(j)$	0.10	d^{-1}	Lancelot et al. (1991), Hansen & van Boekel (1991)

Table 3. Variable parameter values and initial conditions

Name	Range	Units	Value	Reference
k_N^1	0.3-4.5	μM	0.5	Lancelot et al. (1991)
k_N^2	0.3-4.5	μM	0.4	≪»
k_P^1	0.01-0.2	μM	0.1	Veldhuis et al. (1987)
k_P^2	0.05-1.4	μM	0.7	≪»
s_1	0.5-0.7	..	0.5	Verity (1985)
		..	0.6	Raymont (1983)
K_1	20-300	$\mu gC\ l^{-1}$	107	Verity (1985)
		$\mu gC\ l^{-1}$	25	computed from Lancelot et al. (1991)
G_1	0.25-80	ind. l^{-1}		
copepods	0.5-5.0	ind. l^{-1}	5	Harris and Paffenhofer (1976)
		ind. l^{-1}	8	Lancelot et al. (1991)
T_1	0.8-1.0	d	0.84	Grimm and Weisse (1985)
		d	1.0	Kornmann (1955)
		d	1.61	Rousseau et al. (1990)
T_2	0.9-1.4	d	1.2	Grimm and Weisse (1985)
		d	1-1.25	Verity et al. (1988)
		d	1.72	Rousseau et al. (1990)
T_3	0.65-2.8	d	0.65	Verity (1985)
γ	0.001-0.1	..	0.001-0.02	Veldhuis and Admiraal (1987)
N	1.0-50.0	μM	7-96	Lancelot el al. (1991) (North Sea)
		μM	1-12	Wassmann et al. (1990) (Barents Sea)
		μM	0.3-9.0	Muggli and Smith (1993) (Greenland Sea)
P	0.5-1.8	μM	0.4-2.0	Lancelot el al. (1991) (North Sea)
		μM	0.1-0.8	Wassmann et al. (1990) (Barents Sea)
		μM	0.15-0.74	Muggli and Smith (1993) (Greenland Sea)
		μM	0.5-74.2	Veldhuis and Admiraal (1987) (laboratory)
$D_c(1)$	0.0	..		created
$D_c(2)$	0.0-0.25	..		≪»
$D_c(3)$	0.0-0.5	..		≪»
$D_c(4)$	0.1-0.7	..		≪»
$D_c(5)$	0.1-0.7	..		≪»

Results

To take advantage of the modular form of the model, simulation experiments are performed including a new factor at each step and analyzing its effects in the increasingly complex system. Evaluations of the modeling efforts are based upon benchmarks (Table 4) obtained from laboratory experiments and field studies on *Phaeocystis* communities. These include aspects of nutrient availability and limitations, bloom peak and period, grazer effects on single cells and colonies, and sedimentation fluxes. To determine attainment of these benchmarks, simulations are performed in a modular manner, investigating first the interactions of nutrients and *Phaeocystis* populations, then ciliate grazing is added, followed by addition of copepod grazing. Finally, copepods are allowed to prey on ciliates. We also investigate the effects of a continuous inflow of nutrients over a fixed period of time, in the dynamics of the system.

All model simulations reported are initialized at day zero with *Phaeocystis* single cell density at 10^5cells l^{-1}.

Nutrient-*Phaeocystis* population dynamics

Given the wide range of concentrations of nutrients N and P in the water column in areas where *Phaeocystis* blooms occur (Riegman et al. 1990, Wassman et al. 1990, Lancelot et al. 1991, Muggli and Smith 1993), the effect of various nutrient concentrations in the simulations is evaluated at all levels in the module hierarchy. We first consider a system initialized with a prescribed nutrient

Table 4. Benchmarks

a. Bloom peak densities

Reference	Single cells (cells l^{-1})	Colonies (col. l^{-1})
Lancelot (1982, 1984), Belgian coastal waters	3×10^7	
Eilertsen et al. (1981), Balsfjorden (Norway)	10^6	
Jones and Haq (1963), Eastern Irish Sea	10^6	5×10^3-1.6×10^4
Cadée and Hegeman (1986), Wadden Sea	10^7-10^8	
Weisse et al. (1986), Wadden Sea	2.8×10^7-4.7×10^7	
Weisse et al. (1986), List Harbour		3.1×10^4
Bajte and Michaelis (1986), German Bight		10^3-10^4
Weisse and Scheffel-Moser (1990a), Southern Bight	2.7×10^7	3×10^4
Wassmann et al. (1990), Barents Sea		1.35×10^4

Table 4. (cont.) Benchmarks

b. Ciliate peak densities

Reference	Density ($ind.\ l^{-1}$)	Species
Lancelot and Mathot (1985)	3×10^3	ciliates
Admiraal and Venekamp (1986)	2.4×10^3-1.18×10^5	tintinnids
Verity et al. (1991)	1.1×10^3-1.7×10^4	oligotrich ciliates
	2.1×10^4-4.9×10^4	dinoflagellates

c. Removal by sinking

Reference	Value	Description
Wassmann (1994)	4-33%	daily loss rates via colonies
	6.6%	daily average loss rate
	$3.5\%.d^{-1}$	mass sedimentation average

d. Sinking velocity

Reference	Value	Description
Taguchi and Hargrave (1978)	$4.9\text{m}\ d^{-1}$	average
van Boeckel et al. (1992)	$7\text{m}\ d^{-1}$	average
Wassmann (1994)	$1.5\text{-}13.3\text{m}\ d^{-1}$	

concentration and assume that no nutrients are added to the system so that only nutrient depletion occurs during the simulation. In the system composed of the nutrient and the *Phaeocystis* compartments, cells grow and colonies are assumed to be formed with constant probability per day.

Within the range of concentrations between 1.0 to 50 μM for nitrogen and 0.5 to 1.4 μM for phosphorus, the peak of the bloom – the day when algal densities are at their highest value – (and subsequent depletion) occurs in general between days 11 and 12 with a maximum density within the same orders of magnitude in almost all cases, $10^7 - 10^8$cells l^{-1} for single cells and $10^4 - 10^5$col l^{-1} for colonies (Fig. 2A). These values are within range for single cells, but higher than observed in nature for colonies (see Table 4a). The average number of cells per colony remains close to 2 (Figs. 2C & 3C), so that sedimentation flux is small (less than 0.002% of total cell numbers per day). With the initial concentration of nutrients in the range usually found in the sea, the peak *Phaeocystis* cell density depletes nutrients in a very short time interval (Fig. 2B). Because population doubling occurs almost daily, variation in the initial concentration of nutrients does not significantly change the timing of the peak *Phaeocystis* density, except for extremely low initial concentrations. If the concentrations are initially very low (e.g. 1 μM for N, 0.5 μM for P) the whole process slows considerably (Fig. 3), resulting in a significant delay in the peak of the bloom and in lower peak densities.

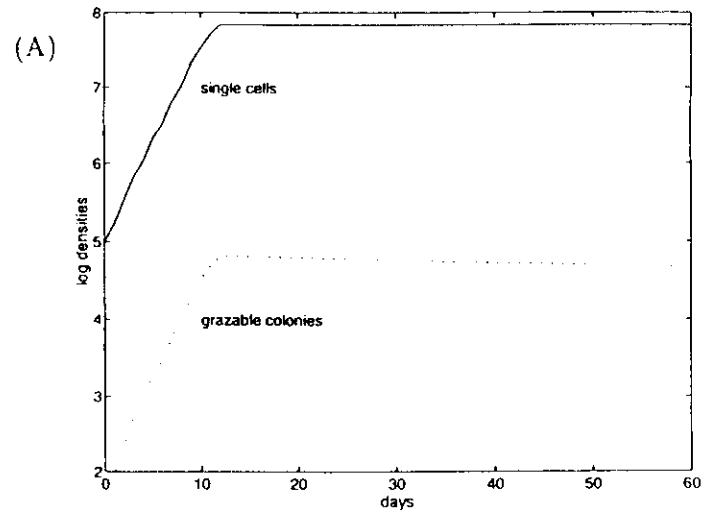

Figure 2A.

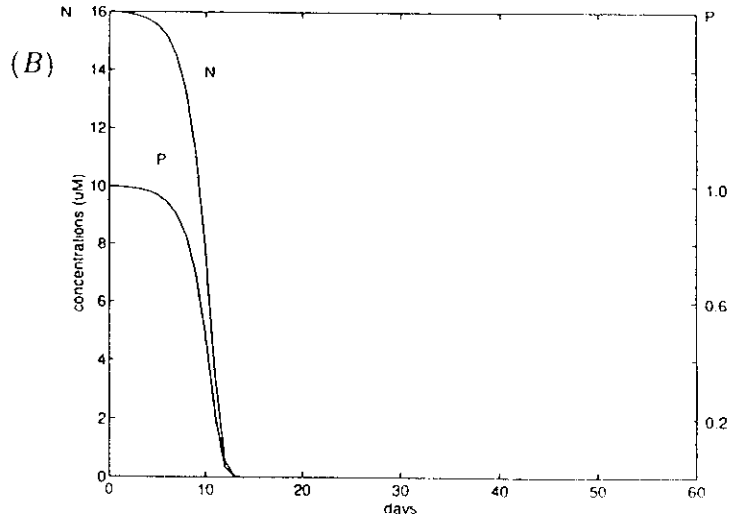

Figure 2B.

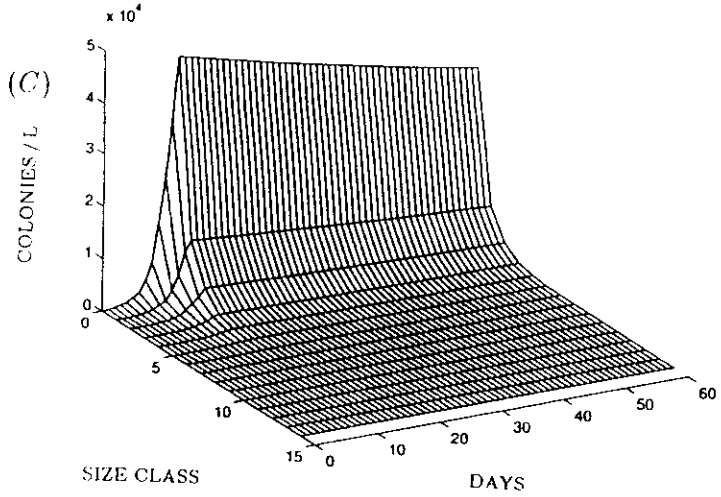

Figure 2C.

Figure 2A–C. Output of the Nutrient-*Phaeocystis* model when initial concentrations are 16 μM for nitrogen and 1 μM for phosphorus: (A) single cell and colonial densities, (B) nitrogen and phosphorus concentrations, (C) colonial size distribution.

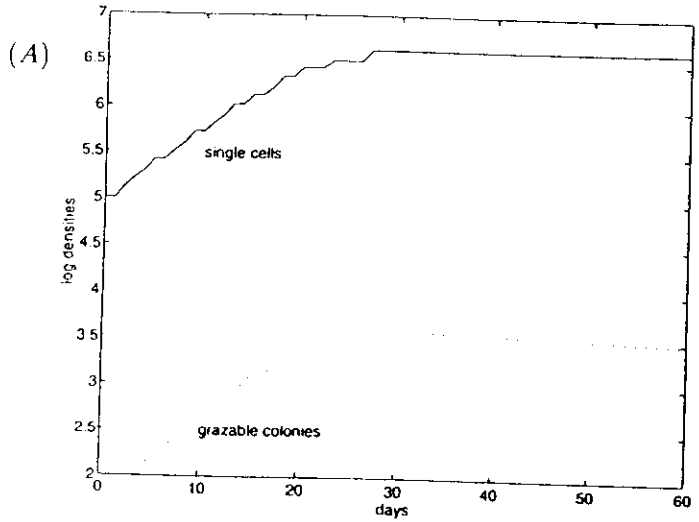

Figure 3A.

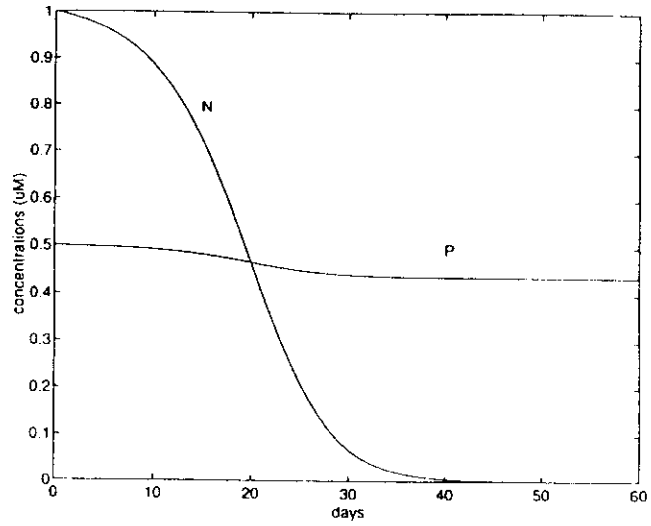

Figure 3B.

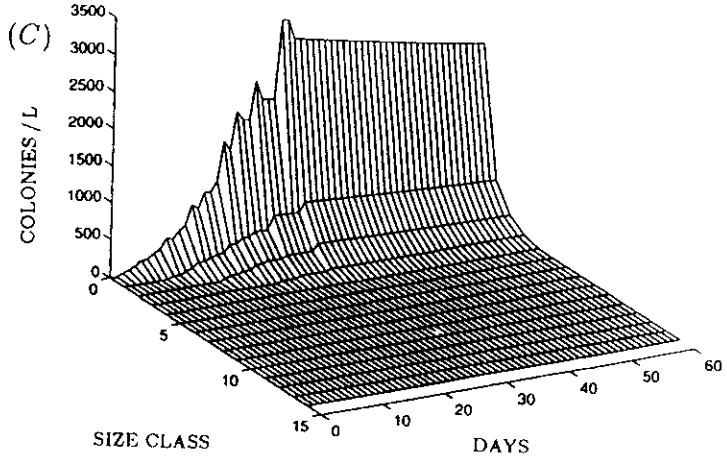

Figure 3C.

Figure 3A–C. Output of the Nutrient-*Phaeocystis* model as in Fig. 2, when initial concentrations are 1 μM for nitrogen and 0.5 μM for phosphorus: (A) single cell and colonial densities, (B) nitrogen and phosphorus concentrations, (C) colonial size distribution. Note same scale for N and P.

Sensitivity analysis

***C.N.P* ratios.** The $N : P$ ratio is assumed fixed within the cell, equal to 16 : 1, but can be quite variable in the water column over the bloom period. As growth proceeds, for cases with low initial $N : P$ ratios, the *Phaeocystis* population is N limited, while for initial high $N : P$ ratios, P is the limiting nutrient. The switch from nitrogen to phosphorous limitation occurs at an initial $N : P$ value close to the Redfield ratio. The computation of the maximal uptake rates for N and P from the doubling time for both single and colonial cells and the C content of the cells considers the $C : N : P$ ratios to be constantly 106 : 16 : 1. In our simulations at an initial ratio of 16, the $N : P$ value in the water column remains at equilibrium throughout the removal process until both nutrients are depleted.

We decided to keep the $C : N : P$ ratios in the cell constant for numerical simplicity. The effects of an increase in $N : P$ and $C : N$ ratios are a delay in the timing of the peaks because of depressed nitrogen and phosphorus consumption relative to carbon, and also larger cell densities at the peak. These changes do not affect peak colony sizes.

Uptake half-saturation constants. The sensitivity of the model to the half-saturation constants in the functions $F_s(N, P)$ and $F_c(N, P)$ was investigated by utilizing variations of up to 100% in these parameters. This variation produced only a minor effect on the total number of colonies obtained at the peak of the bloom (time when nutrients are depleted) as reflected in small perturbations (up to 4%) in the ratio of total colonial cells to total single cells, as well as in the average number of cells per colony. When initial nutrient concentrations are high, independent of $N : P$ ratios, no changes in the time of the peak are observed. However, at low initial nutrient concentrations, growth slows as the half-saturation constants increase or accelerates as they decrease, resulting in a delay in the time of the peak of up to 4 days or an advance of up to 5 days. Here variations in colonial to single cell ratios and average numbers of cells per colony are reduced to a maximum of 2.5%, essentially because of the scarcity of nutrients.

Doubling time. The time required for a *Phaeocystis* population in the sea to double during the exponential growth phase is about one day (Kornmann 1955, Grimm and Weisse 1985, Weisse et al. 1986, Verity et al. 1991). We assume a cell in a colony takes a longer time to double (Guillard and Hellebust 1971, Rousseau et al. 1990). Simulations with doubling times within the range 0.8 to 1 day for single cells and 1 to 1.4 days for colonial cells indicate that peak densities did not vary and that peak occurrence was delayed as doubling times increased. The number of cells per colony increased slightly as the ratio of single cell doubling time to colonial cell doubling time increased.

Probability of starting a colony. Single cells are assumed to turn into colonies with constant probability. In laboratory experiments, Veldhuis and Admiraal (1987) observed that the number of colony-forming cells was very small, varying

between 0.1 and 2% of the total single cell number. For different $N : P$ ratios and the colonial creation probability varying from 0.001 to 0.025, simulations yield single cell densities that do not vary significantly at the peak (at most 1%) and colonial densities that are more sensitive to variations in these parameters (25 fold increase). For example, for concentrations of 28 μM for nitrogen and 1.0 μM for phosphorus, peak single cell densities vary from 6.82×10^7 to 6.76×10^7cells l^{-1}, while colonial densities vary from 6.7×10^3 to 1.3×10^5col l^{-1}. Another perspective is to consider the ratio of total numbers of cells in colonies to total numbers of single cells per liter, which varied one order of magnitude, from 0.17×10^{-3} to 3.5×10^{-3}, independent of $N : P$ ratios. An increase in the probability of colony formation to an unrealistic 0.1 yields peak densities of 4.9×10^7cells l^{-1} for single cells and 4.8×10^5col. l^{-1} for colonies, implying a ratio of 0.18×10^{-1}. Within the range of probabilities utilized, the colonial to single cell ratio at the peak appears to depend linearly on the probability of a single cell generating a colony. We conclude that if the probability remains within the range proposed by Veldhuis and Admiraal (1987), it does not have a significant effect in the structure of the bloom.

Main results. An increase in $C : N$ or $N : P$ ratios produces a delay in the timing of peak densities as well as an increase in peak values, but does not change relative colonial sizes. Variations in the values of the uptake half-saturation constants have some minor effects on the system, but only when initial nutrient concentrations are low. Variations within observed values of doubling times do not have significant effects on the dynamics of the system. Variations within observed values of the probability of a single cell starting a colony have a very slight effect on single cell and a small effect on colonial densities. Population structure is not drastically altered, and densities remain within benchmark ranges.

In the cases discussed, the average number of cells per colony at the peak is at most 2.01 with the largest colonies having no more than 64 cells. So with no grazers present, the bloom quickly reaches a peak, after which one or both nutrients are quickly exhausted. Because colonies are small, their removal from the mixed layer by sinking is extremely slow, in general well below 0.1% of the population per day.

Nutrient-*Phaeocystis*-ciliate community dynamics

In the next iteration to attain community benchmarks, a ciliate grazer population, such as tintinnids, that consume single *Phaeocystis* cells but not colonial cells, is introduced into the nutrient-*Phaeocystis* model. The ciliate population module was studied in this environment by varying the ciliate doubling time within the range of 0.55 to 2.8 days, the assimilation rate from 0.5 to 0.7, and the initial ciliate densities. A general trend is that both single cell and colonial densities, as well as the times of peak densities, decrease with decreasing doubling times and with decreasing assimilation efficiencies, and increase with decreasing initial ciliate densities. The peak average cell numbers per colony increases as doubling

time, assimilation efficiency and initial ciliate density decreases. Given an initial ciliate density and an assimilation rate, there seems to be an optimal doubling time which maximizes peak colony density and peak ciliate density.

Sensitivity analysis. Increases in $C : N : P$ ratios at the *Phaeocystis* cellular level do not affect the observed pattern of behavior, although lower ciliate densities can have a greater impact on the *Phaeocystis* population.

The half-saturation constant K_1. The effect of variations in the half-saturation constant K_1 in the ciliate model is reported here for the two extreme situations of a ciliate population with small assimilation efficiency (0.5) and short doubling time (0.65 day) and one with large assimilation efficiency (0.7) and long doubling time (2.8 days) with K_1 in the range between 10 and 200 $\mu gC/l$ (Fig. 5). In both cases, peak single cell density increases steadily with K_1, while colonial density seems to reach a plateau at some K_1. Peak ciliate density increases with K_1 and then decreases; the "optimal" value of K_1 is the same threshold for the colonial density plateau. The day of maximal *Phaeocystis* density occurs earlier with small values of K_1, is delayed slightly and then returns to a nominal level as K_1 increases, the threshold value is again the same as above. Small

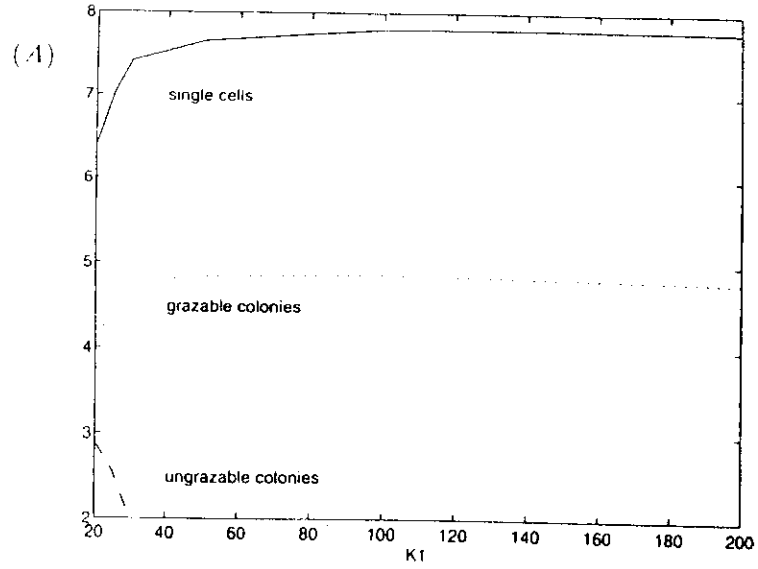

Figure 4A.

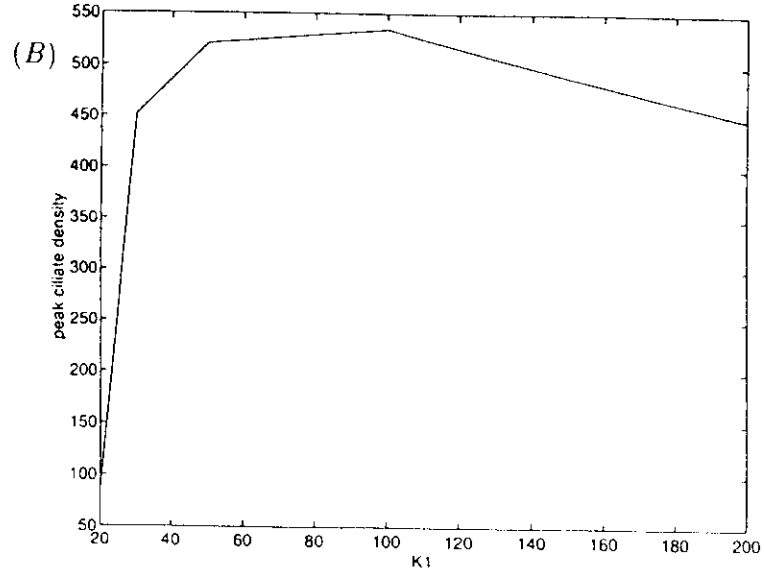

Figure 4B.

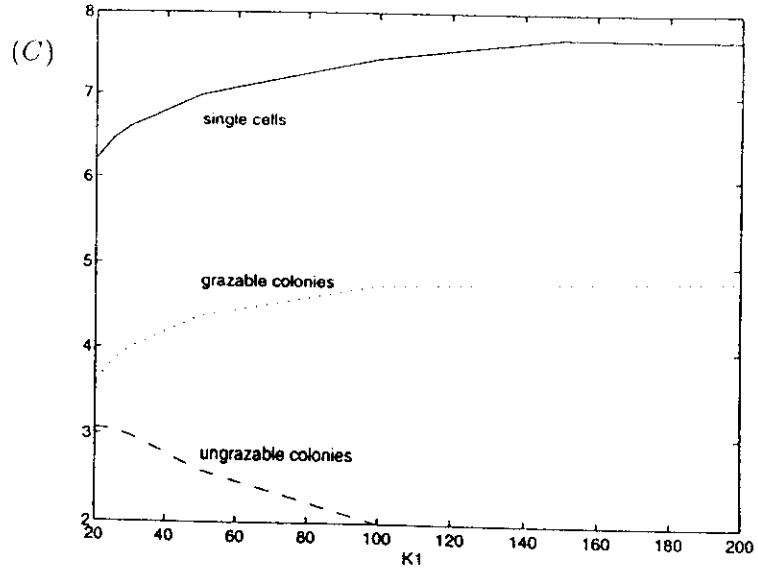

Figure 4C.

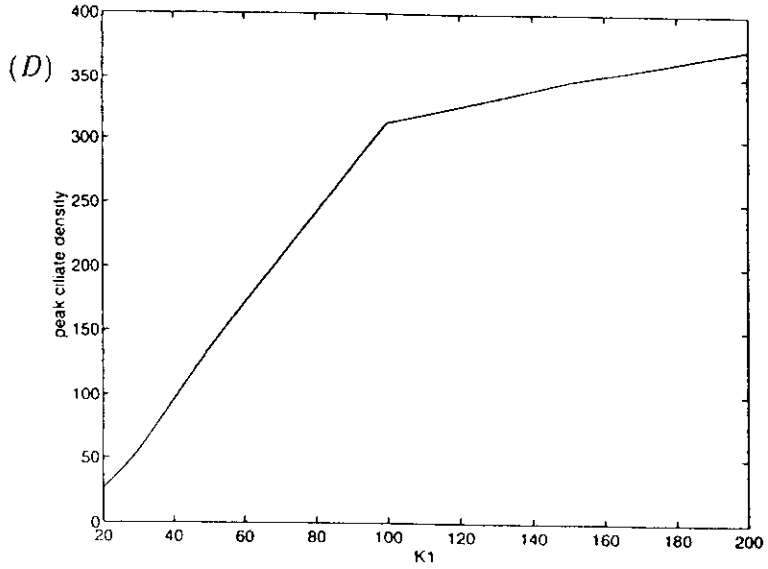

Figure 4D.

Figure 4A–D Effects of variations in the half-saturation constant K_1 for the functional response in the ciliate population. Case 1: (A) peak densities of single cells, grazable colonies and ungrazable colonies and (B) peak ciliate density, for a population having a doubling time of 2.8 days and an assimilation efficiency of 0.7. Case 2: (C) peak densities of single cells, grazable colonies and ungrazable colonies, and (D) peak ciliate density, for a population having a doubling time of 0.65 day and an assimilation efficiency of 0.5.

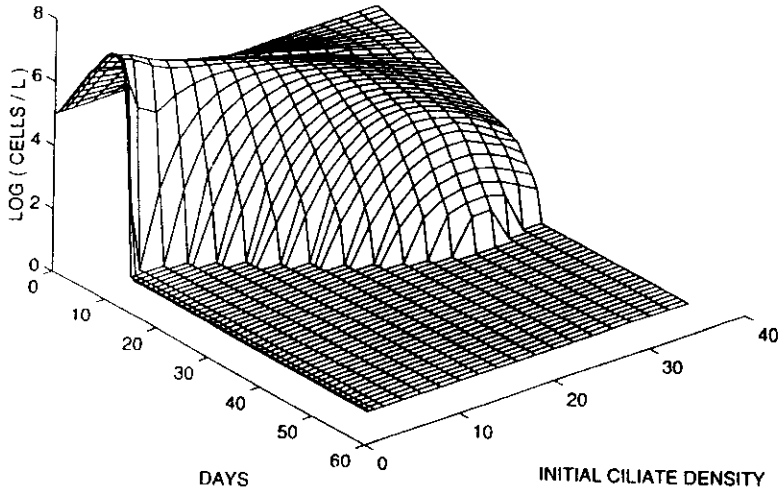

Figure 5A.

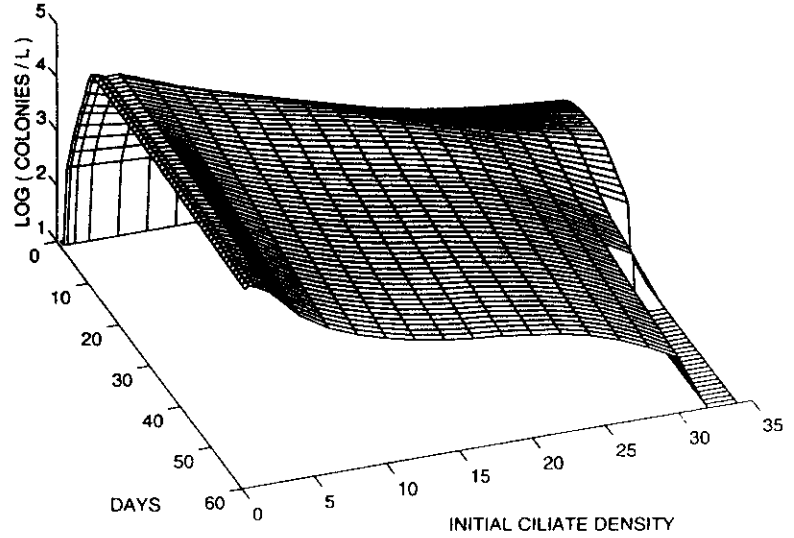

Figure 5B.

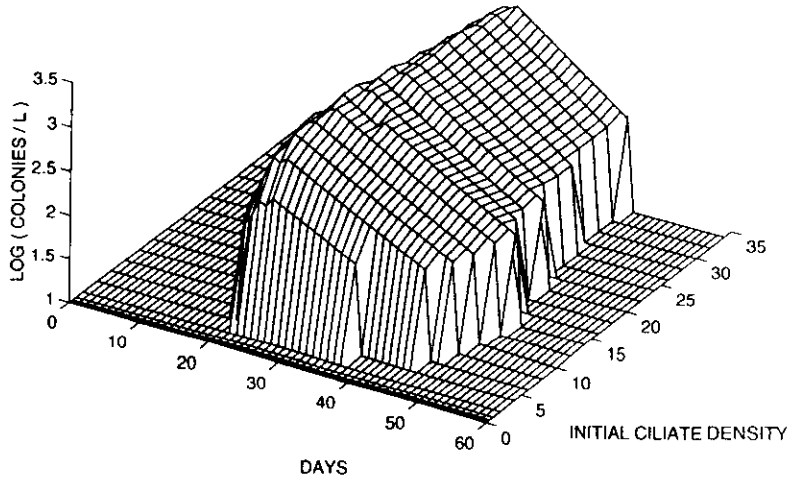

Figure 5C.

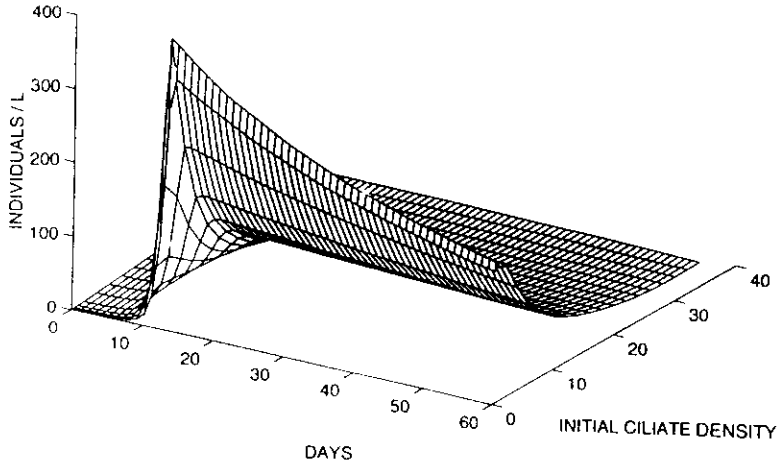

Figure 5D.

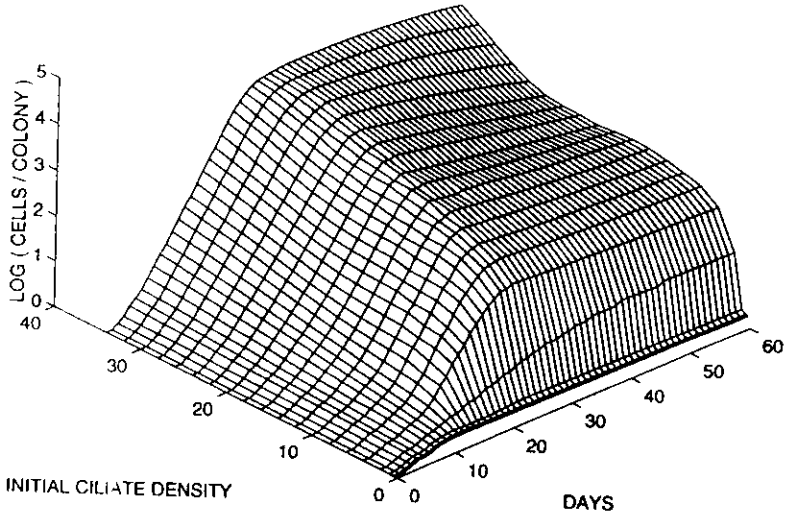

Figure 5E.

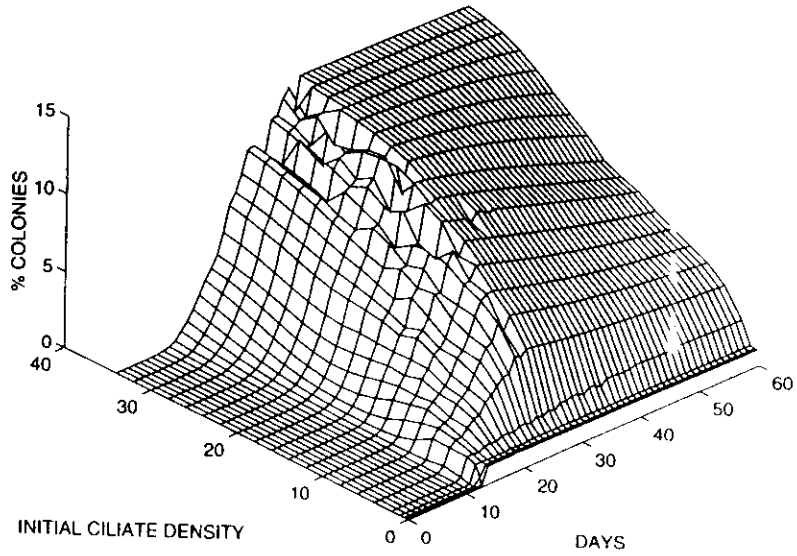

Figure 5F.

Figure 5A–F. Dynamic output of the Nutrient-*Phaeocystis*-Ciliate community model when the ciliate population has a doubling time of 0.65 day, an assimilation efficiency of 0.5, as initial ciliate density varies: (A) single cell population, (B) grazable colonial population, (C) ungrazable colonial population, (D) ciliate population, (E) colonial sizes, and (F) removal rate.

half-saturation values produce small *Phaeocystis* and ciliate densities and allow colonies to grow large (average well above 1,000 cells per colony) while large K_1 values result in large densities and small average cell numbers per colony (2 to 3).

At the beginning of the bloom, when cell densities are low, the slope of the Monod function is steep for small values of K_1, resulting in a rapid increase of cell removal rates as cell densities increase. For large values of K_1 this slope is shallow, resulting in a slow increase of removal rates as *Phaeocystis* single cell densities grow. Because cell removal increases more slowly, cell densities can increase faster and reach higher peak values, producing at the same time a rapid depletion of nutrients and smaller colonies.

Initial ciliate density. To better describe the qualitative features of the behavior of this community (Figs. 5, 6 & 7), we take as an example a ciliate population assumed to have a doubling time of 0.65 days, an assimilation efficiency of 0.5, and a half-saturation constant for the functional response K_1 equal to $107\,\mu gC\ l^{-1}$ (Verity 1985); other model populations with different values of these parameters yield analogous results.

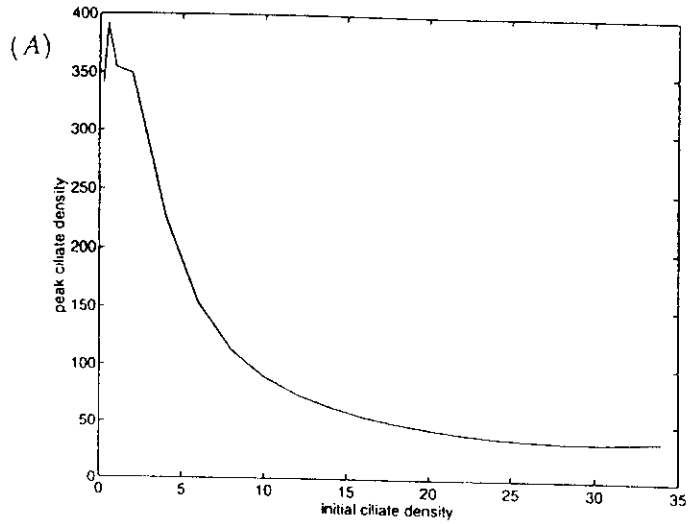

Figure 6A.

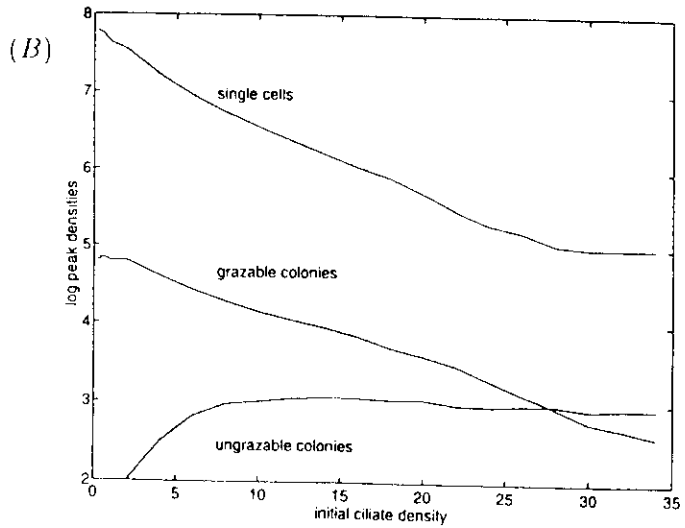

Figure 6B.

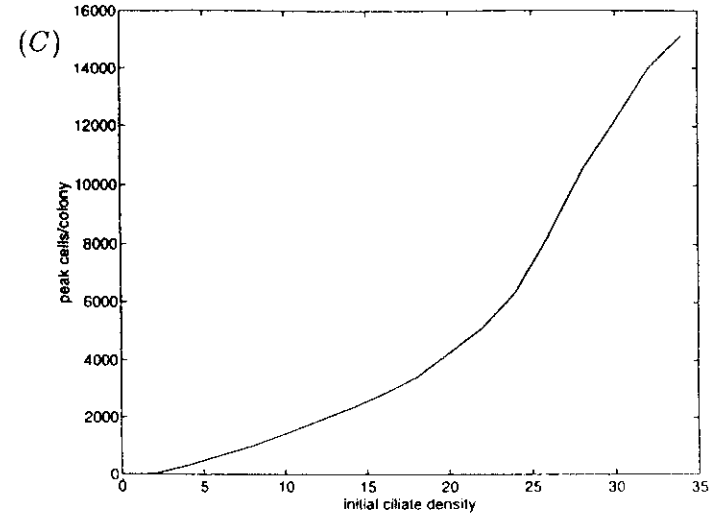

Figure 6C.

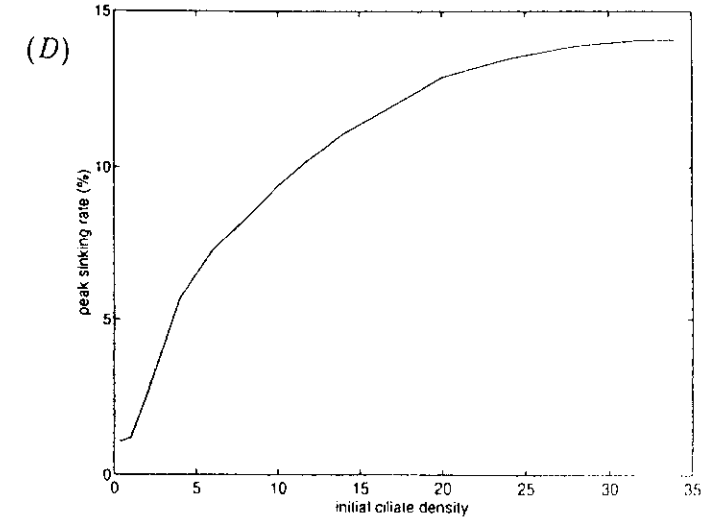

Figure 6D.

Figure 6A–D. Effect of variations in the initial ciliate density on the peak values of the model output: (A) peak ciliate density, (B) peak single cell, grazable colonies and ungrazable colonies densities respectively, (C) peak average number of cells per colony, and (D) peak removal rate by sinking.

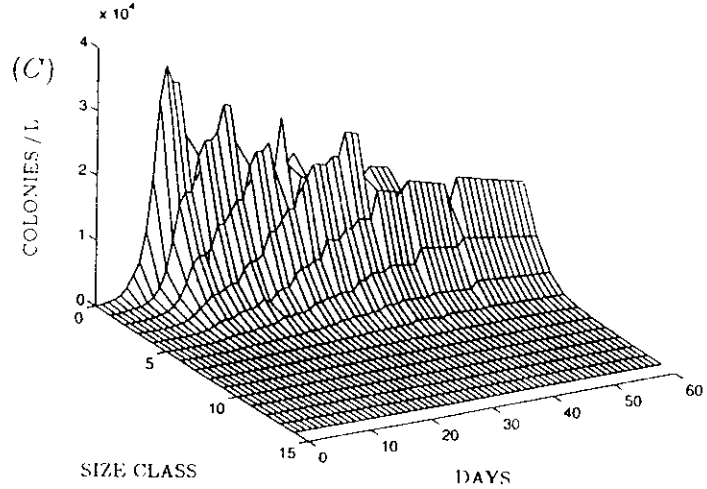

Figure 7A.

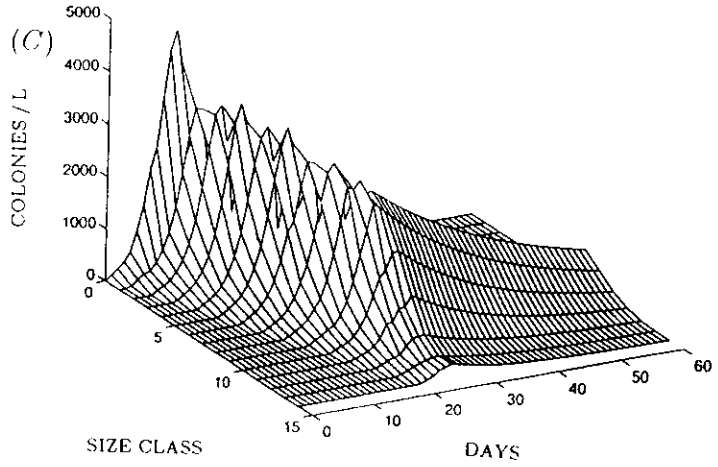

Figure 7B.

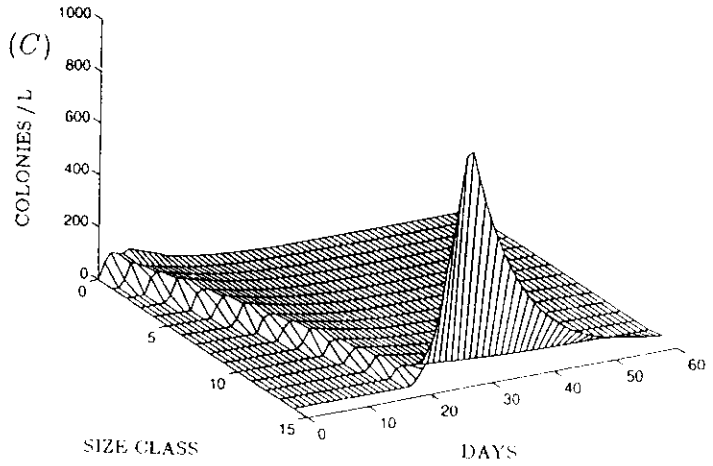

Figure 7C.

Figure 7A–C. Dynamics of the colonial size distribution corresponding to the nutrient-*Phaeocystis*-ciliate model when inicial ciliate density is: (A) low, (B) moderate, and (C) high.

If ciliates are present at small initial densities, their density follows the density of the algal bloom until they become numerous and graze the single cell population to extinction. The remaining nutrients are utilized by the colonial form that can then grow larger. Sinking controls the abundance of large colonies. The peak is reached between days 10 to 11, and the peak single cell densities before the crash are between 6×10^7 and 3.5×10^7cells l^{-1}, while colonial densities remain almost constant at about 6.5×10^4col. l^{-1}. Although some colonies may contain over 256 cells, the average cell number per colony is at most 2.2 (Fig. 7A). The maximal removal rate by sinking is 2.6% of the population per day (Fig. 6D).

A similar behavior is observed when ciliates are initially present in moderate numbers; but, in this case, peak single cell densities are lower (9×10^6 to 1.1×10^6cells l^{-1}) because of more intense grazing. Colonial densities reach 2.7×10^4 to 7×10^3col. l^{-1}. Under these conditions ciliate populations reach peaks that are two to six times lower than in the previous case (Figs. 5D & 6A). Because less nutrient has been consumed, a striking change occurs in the average cell number per colony which becomes much higher (663 to 2,830) than in the previous case (Fig. 7B). In fact, colonies can grow significantly above 300 μm in diameter contributing to the "ungrazable" class with peak densities of 6.8×10^2 to 1.1×10^3col. l^{-1}. (Fig. 6B). The maximal removal rates are between 7 and 11% of the population per day (Fig. 6D).

When ciliates are initially present in high numbers, the bloom does not occur and the ciliate population does not grow much, remaining at the same level because of food limitation. Single cells that escape predation grow into colonies

that have sufficient available nutrient to allow them to accumulate to a very large size and sink. The maximal removal rate by sinking reaches 14% of the population per day (Fig. 6D). In these cases, the average cell number per colony reaches 6,340 to 15,118 cells per colony (Fig. 7C), while peak densities of ungrazable colonies reach values of 9.3×10^2 to 8.8×10^2col. l^{-1} (Figs. 5C & 6B).

Main results. The basic model is sensitive to the half-saturation constant K_1 that describes the character of the microzooplankton functional response to algal abundance. This parameter is species dependent. The initial ciliate density is another parameter that causes significant changes in the dynamic outcome, transforming the system from one type of behavior to another. We can observe this sensitivity in Fig. 6, which illustrates how peak values change as the initial ciliate density increases from 0.25 ind. l^{-1} to 34 ind. l^{-1}. Densities of the *Phaeocystis* are within ranges observed in nature (see Table 4a).

It is worth noting the impact that initial ciliate densities have on the colonial sizes (reflected on average number of cells per colonies, Fig. 5E) and their distribution (Fig. 7), as well as on sinking rates (Fig. 5F). Also note the variety of non-linear responses to ciliate density (Fig. 6).

Nutrient-*Phaeocystis*-ciliate-copepod community dynamics

The copepod module is now included in the system. We are modelling small sized copepods such as *Temora longicornis* and *Acartia tonsa*. Estimates of the size spectrum consumed by each stage (Fig. 8) were obtained from data of Bergreen et al. (1988), while other vital rates were taken from Harris and Paffenhofer (1976) and Lancelot et al. (1991). Based on observations reported in Estep et al. (1990), we (somewhat arbitrarily) selected the consumption of *Phaeocystis* at different stages to be 80% of their demand for nauplii, 70% for CI – CIII stages, 50% for CIV – CVI stages, and 10% for adults. As mentioned previously, nauplii graze both on single cells and small colonies (Verity and Smayda 1989, Estep et al. 1990), while other life stages graze on colonies.

Because copepods do not seem to graze on colonies until they enter the senescent stage (Estep et al. 1990), or at least until acrylic acid production is reduced, and because there is a paucity of data about the timing of these processes, we varied the time at which copepods start grazing on the *Phaeocystis* population from day 0 of the run to day 20, i.e., 10 days after the peak of the bloom occurs when copepods are not present.

We let copepod initial density vary from 0.5 ind. l^{-1} to 5 ind. l^{-1} in stages CIV to adult. With an initial density of 5 ind. l^{-1} the copepod model yields a peak density of 33 ind. l^{-1}, rather excessive for this type of organism. An initial density of 2 ind. l^{-1} gives a more realistic peak of 13 ind. l^{-1}, and an average close to 8 ind. l^{-1}; thus this value is taken as the initial copepod density for the examples that follow, and the initial ciliate density is varied within the moderate range.

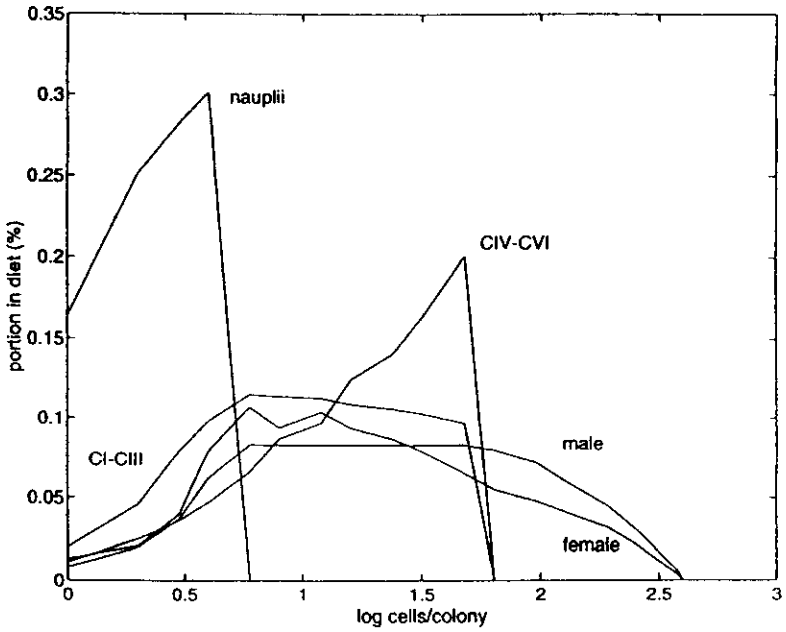

Figure 8. Representation of the "preferred size" function $p(i, j(m))$ that depicts the size distribution of particles ingested by copepods at each stage of development. (Data from Bergreen et al., 1988).

Sensitivity analysis

Timing of copepod grazing. If copepods are allowed to start grazing at any time between day 0 and day 8, the *Phaeocystis* population is driven to extinction by grazing, independently of initial grazers densities (Figs. 9A, 9B & 9C). The average number of cells per colony is at most 4.1 which occurs when both grazers densities are the lowest; however, in most cases the number remains below 2 cells per colony. As expected, the earlier the copepods are introduced, the sooner *Phaeocystis* is driven to extinction, the smaller the colonial size and the more negligible is the sinking (Figs. 9D & 10). In all these cases, nutrient consumption is very low.

When the copepods start grazing on day 9 (one day before the peak of the bloom occurs), a few colonies have the opportunity to grow sufficiently large to escape predation. Nutrient concentrations remain high; hence those colonies can grow rapidly into the largest colonial size in the model (16384 cells per colony or equivalently 2.8 mm in diameter) by day 21 or 22. (Fig. 10C). Because colonies are so large, a maximal sinking rate of 14.1% is reached by day 33 or 34 (Fig. 9E). A similar behavior is obtained if copepods start grazing when the peak of the bloom occurs.

As the introduction of copepods is delayed relative to the peak of the bloom, their impact decreases. The later the introduction, the smaller the impact on single cells and grazable colonies, the larger the nutrient consumption, which ultimately leads to lower nutrient concentrations and reduced growth rates. For example, if they enter the community at day 15, ungrazable colonial densities are maximized (7.4×10^2 to 12.2×10^2col. l^{-1}) (Fig. 9C), but the average colonial size is reduced (to a range of 950 to 4,735 cells per colony compared to a range of 6,340 to 15,118 cells per colony when they are not present) as is the maximal removal rate by sinking (range of 7.8 to 11.5 % compared to 14 %). (Figs. 9D & 9E). If grazing starts at day 20, ungrazable colonial densities, colonial sizes, and removal rates by sinking decrease (6.8×10^2 to 11.1×10^2cells l^{-1}; 685 to 2,095 cells per colony; 7.3 to 10.3% respectively).

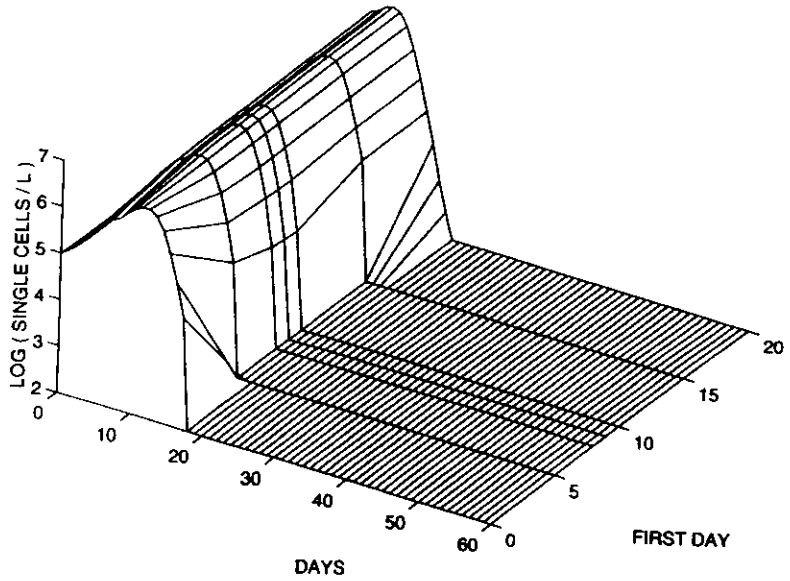

Figure 9A.

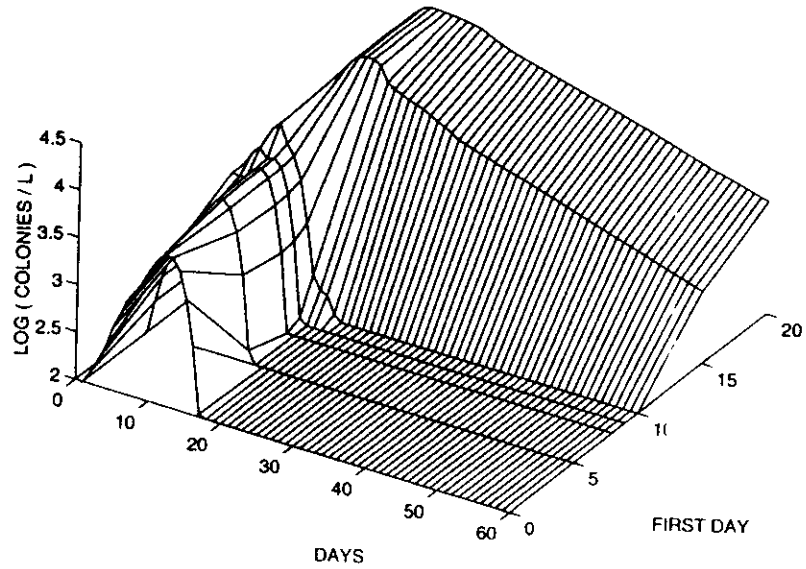

Figure 9B.

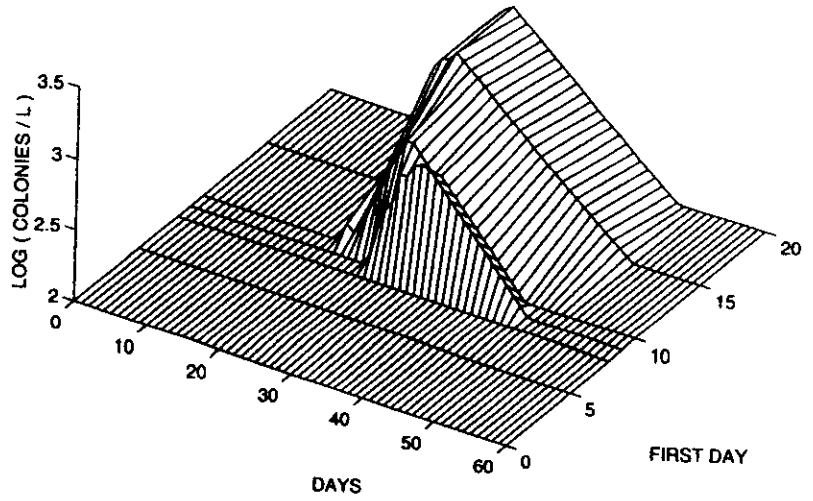

Figure 9C.

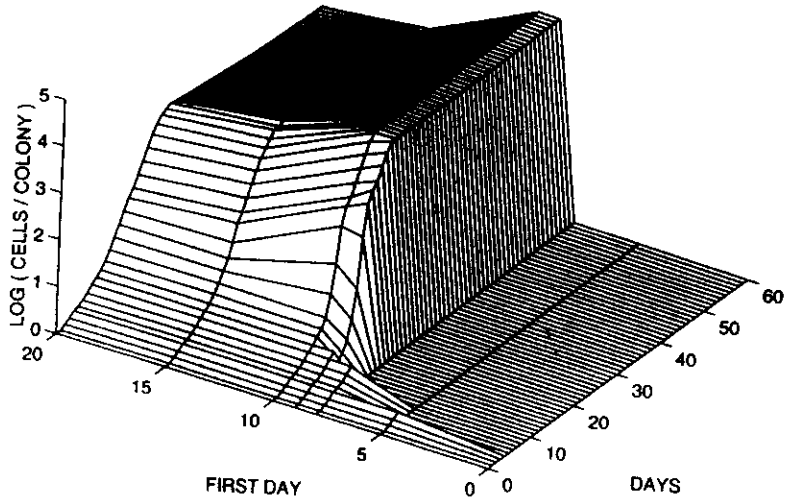

Figure 9D.

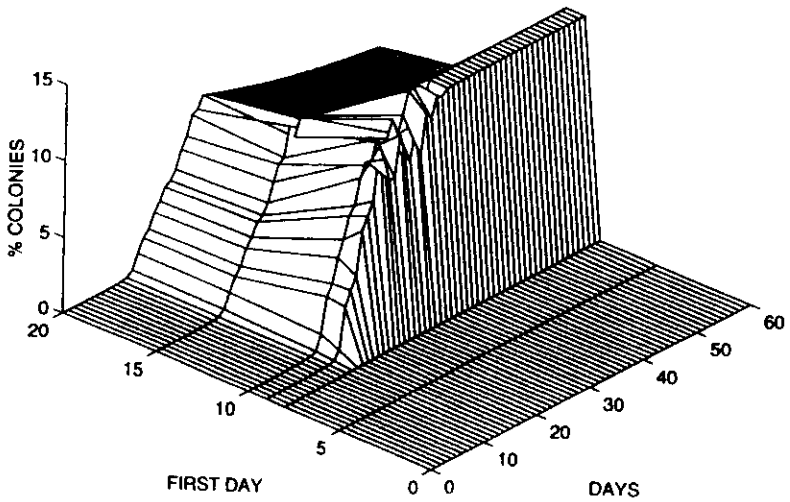

Figure 9E.

Figure 9A–E. Dynamic output of the Nutrient-*Phaeocystis*-Ciliate-Copepod community model for a moderate initial ciliate density and an initial adult copepod density of 2 ind. l^{-1}, as the first day of copepod grazing varies: (A) single cell population, (B) grazable colonies, (C) ungrazable colonies, (D) colonial sizes, and (E) removal rates by sinking.

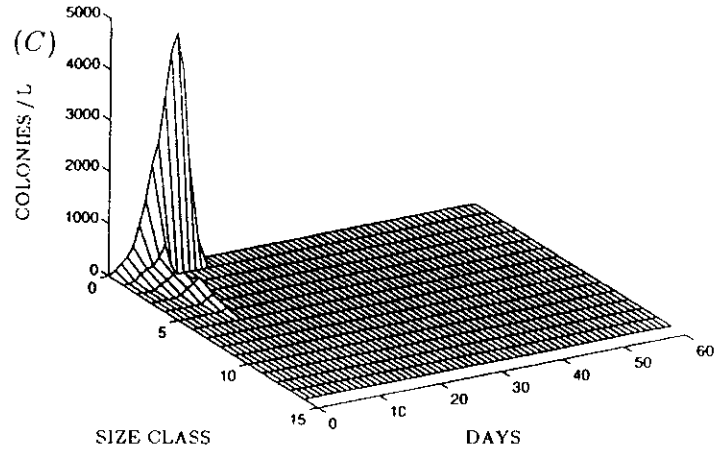

Figure 10A.

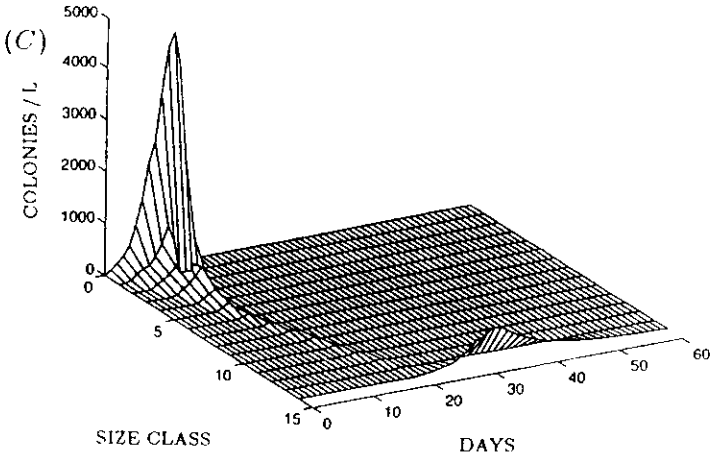

Figure 10B.

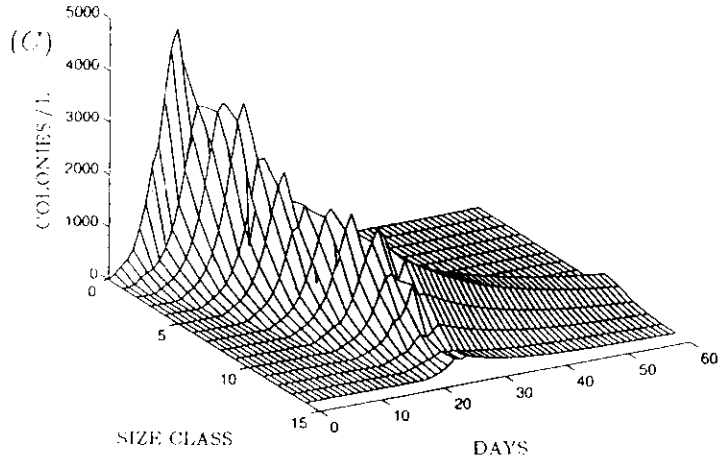

Figure 10C.

Figure 10A–C. Dynamics of the colonial size distribution in the Nutrient-*Phaeocystis*-Ciliate-Copepod community model for a moderate initial ciliate density and an initial adult copepod density of 2 ind. l^{-1}, as the first day of copepod grazing varies: (A) day 8, (B) day 9, and (C) day 15. Compare the latter with Fig. 7B (copepods not present).

Initial copepod density. Variations in initial copepod densities do not seem to have as large of an effect on the peak *Phaeocystis* densities as variations in initial ciliate densities do. For example, at low initial ciliate density, a variation of initial copepod densities from 0.5 to 5 ind. l^{-1} produces a variation of less than 7 % in peak single cell densities and 23 % on colonial densities, and at high initial ciliate density the variation is less than 17 % and less than 30 %, respectively.

Main results. The response of the system to the timing of copepod grazing varies drastically depending on whether copepods come into the system early or close to the day where the *Phaeocystis* population reaches its peak density. While varying initial ciliate densities have a strong effect on single cell densities, variations in the timing of copepod grazing strongly influence colonial densities (Fig. 11). The initial copepod density does not have a detectable effect if within densities observed in the field, and even tripled above normal.

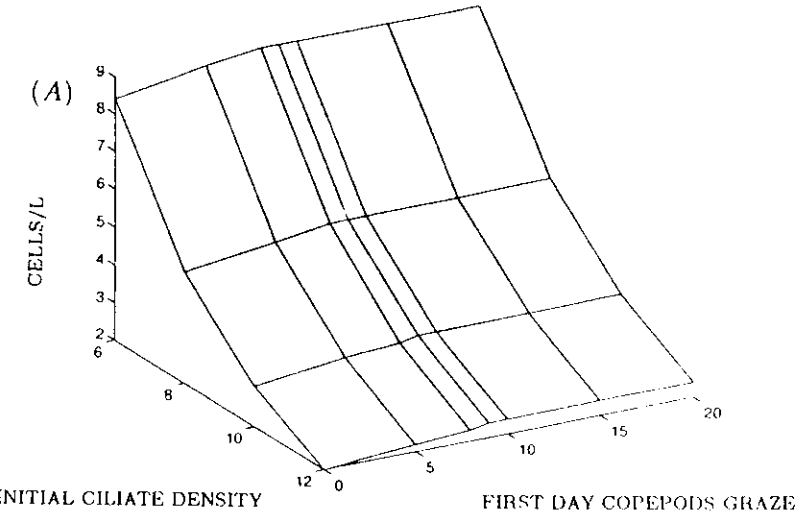

Figure 11A.

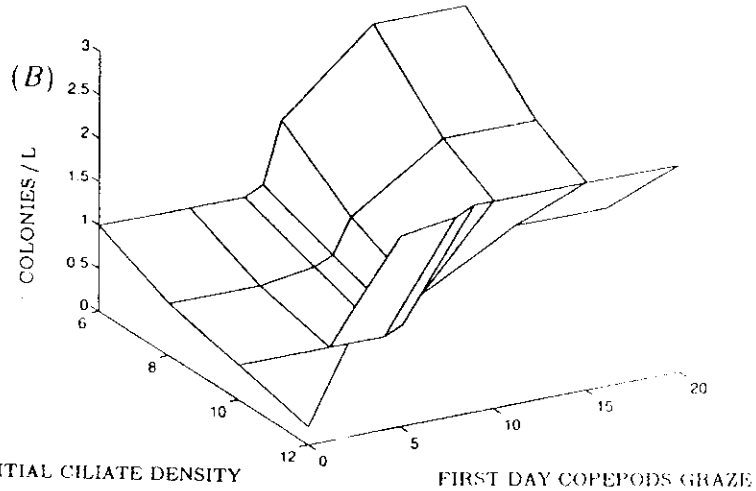

Figure 11B.

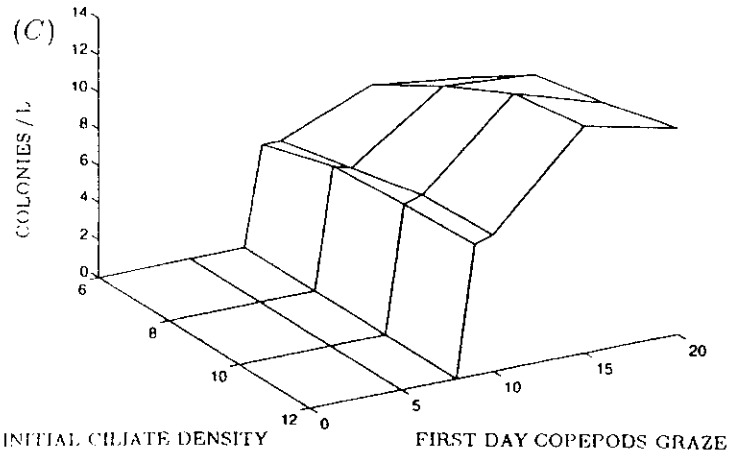

Figure 11C.

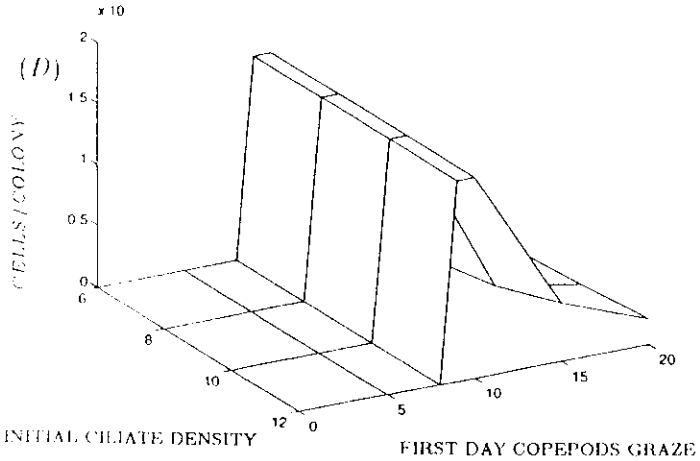

Figure 11D.

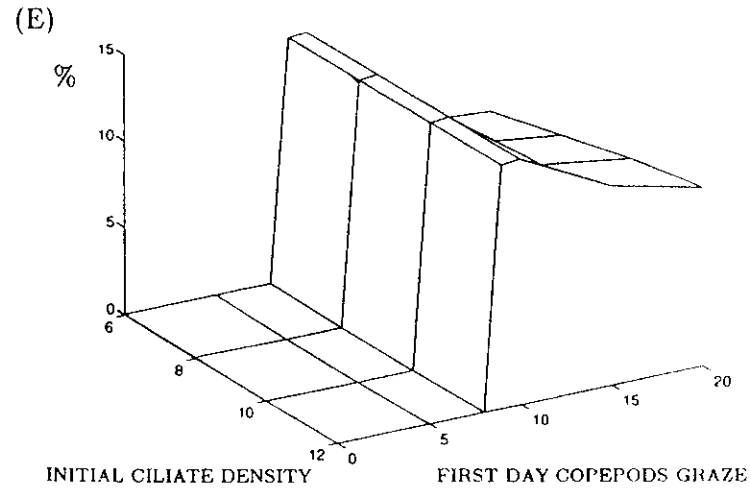

Figure 11E.

Figure 11A–E. Combined effects of initial ciliate density and the timing of the copepods grazing on *Phaeocystis* cells and colonies on: (A) peak single cell density, (B) peak grazable colony density, (C) ungrazable colony density, (D) peak average cell number per colony, (E) peak removal rate by sinking.

Effects of predation

In the examples discussed here, we represent the ciliate population by a species having a body mass of $0.868 \times 10^{-2}\ \mu gC$, a doubling time of 0.65 days, an assimilation rate of 0.5, and a half-saturation constant for the functional response equal to $107\ \mu gC.l^{-1}$ (Verity 1985). As mentioned earlier, the copepod population represents relatively small copepods such as *Temora longicornis* or *Acartia tonsa* and its initial density is $2ind\ l^{-1}$. Copepods are assumed to start consuming *Phaeocystis* colonies on day 9 of the bloom but prey on ciliates from the initial time of the simulation.

Because of the omnivorous feeding of the copepods, development of the copepod population is assumed to be independent of either *Phaeocystis* or ciliate abundance. At each time step, energetic needs are estimated in terms of carbon. We assume that at each developmental stage, copepods satisfy these needs by consuming a different proportion of ciliates and *Phaeocystis*. Although these stage dependent proportions, defined by the functions $D_c(j(m))$ and $D(j(M))$ respectively, are not time dependent, the composition of the copepod population does change, resulting in a carbon demand that varies with time. We allow adult copepods to take from 10 to 70% of their demand from the ciliate population, while late copepodites take 0 to 50% and early copepodites 0 to 25%. Most of

the simulations were performed on the range 10 to 30%, 0 to 10%, and 0 to 5% respectively because of the interesting characteristics of the results. We also let adult copepods cover as before 10% of their carbon demand with *Phaeocystis* colonies, while late copepodites cover 50% and early copepodites 70%, and nauplii 80% of their demand with small *Phaeocystis* colonies and single cells. We assume that nauplii can not consume ciliates. We will refer to this coupling of the energetic demand of the structured population and a chosen set of proportions as a predation pressure or strategy of the copepods on the ciliate population.

Effects on the *Phaeocystis* and ciliate populations. In a first set of simulation experiments we investigate the model composed of the nutrient, *Phaeocystis*, ciliate, and copepod compartments as in the previous step and, in addition, link the ciliate and copepod populations, letting the predatory strategy of copepods on ciliates vary within the ranges described above. We also vary the initial ciliate density.

When the initial ciliate density is low to moderate, the ciliate population grows to a peak that occurs approximately at day 15, the time when the *Phaeocystis* single cell population reaches its peak before being driven to extinction by grazers. Then the ciliate density decreases because of copepod predation and resource limitation. Around day 50, the ciliate population becomes extinct independently of the predators' pressure, although predation does have an effect on how rapidly their density decreases.

For a given initial ciliate density, increasing predation pressure causes an unexpected result: both the peak ciliate density and the peak *Phaeocystis* single cell density increase (Figs. 12 & 14). By depressing the ciliate population during the first few days, copepods allow *Phaeocystis* densities to increase faster. Then *Phaeocystis* reach a level that, since the growth rate of ciliates depends on the algal biomass, allows ciliates to overcome the effects of predation by reproducing faster until they become so numerous that the single cell population crashes. As a consequence of the rapid increase of single cell density, nutrients are consumed faster, resulting in larger colonial densities but smaller colonial sizes as copepod pressure increases.

If we fix now the predation strategy and let the initial ciliate density increase from very low to moderate, we observe that both the peak ciliate density and the peak single cell and grazable colony densities decrease while ungrazable colony densities show a slight increase (Fig. 13). This occurs because when more ciliates consume more *Phaeocystis* cells, the reduced availability of single cells decreases both the ciliate growth rate and the generation of colonies, at the same time reducing the consumption of nutrients which then are available to support larger colonies growth.

Now we consider high initial ciliate densities. In these cases, ciliates overgraze *Phaeocystis* cells, depressing the phytoplankton population and inhibiting ciliate growth. Copepod predation on the non-increasing ciliate population drives it to extinction in 25 to 5 days depending on the predatory pressure. The remaining

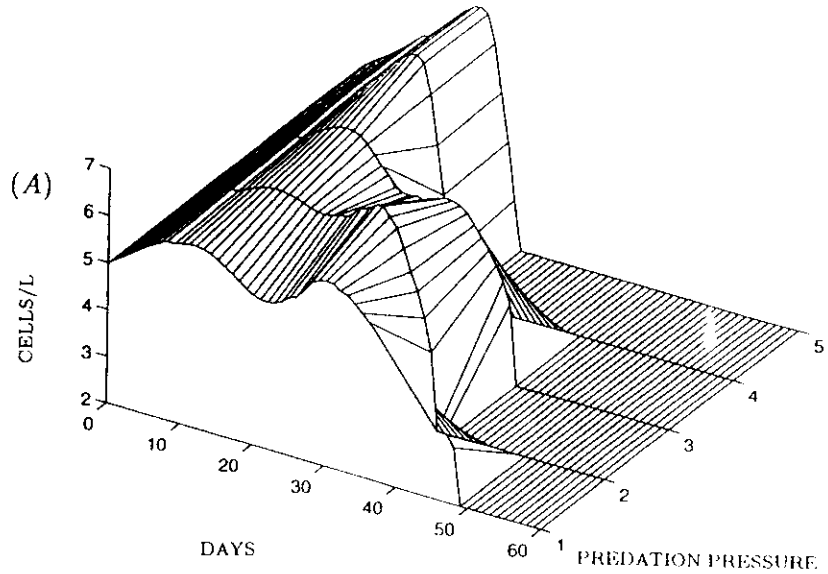

Figure 12A.

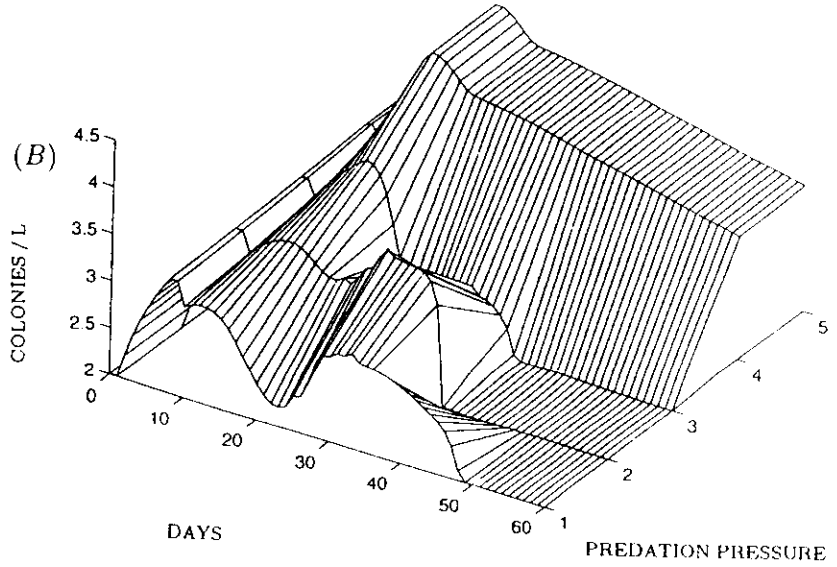

Figure 12B.

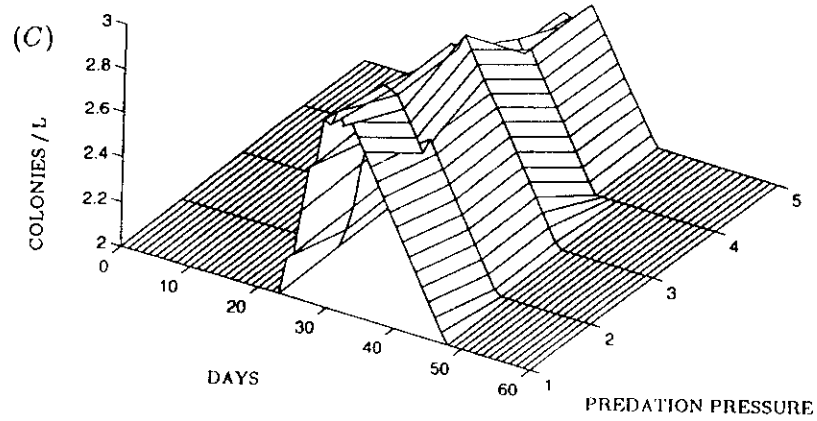

Figure 12C.

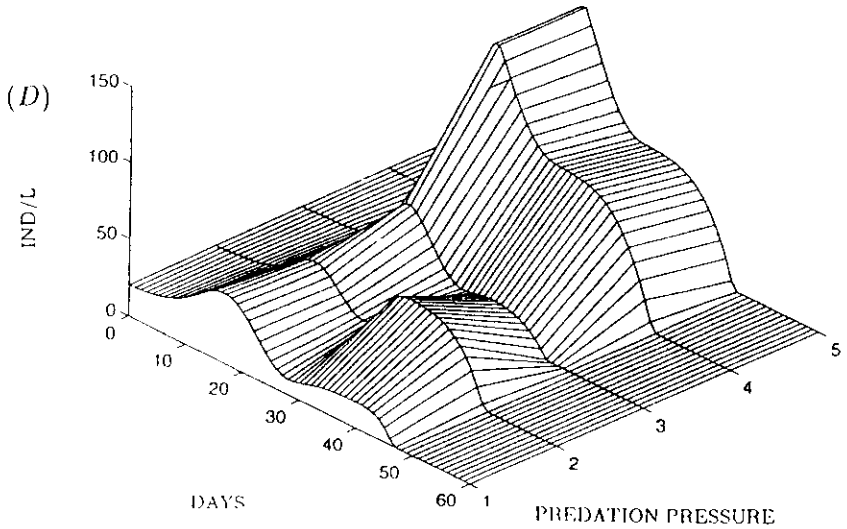

Figure 12D.

Figure 12A–D. Effects of increasing predation pressure given a fixed initial ciliate density (20ind./ l^{-1}) on (A) single cell and (B) grazable colony dynamics, (C) ungrazable colony and (D) ciliate population dynamics.

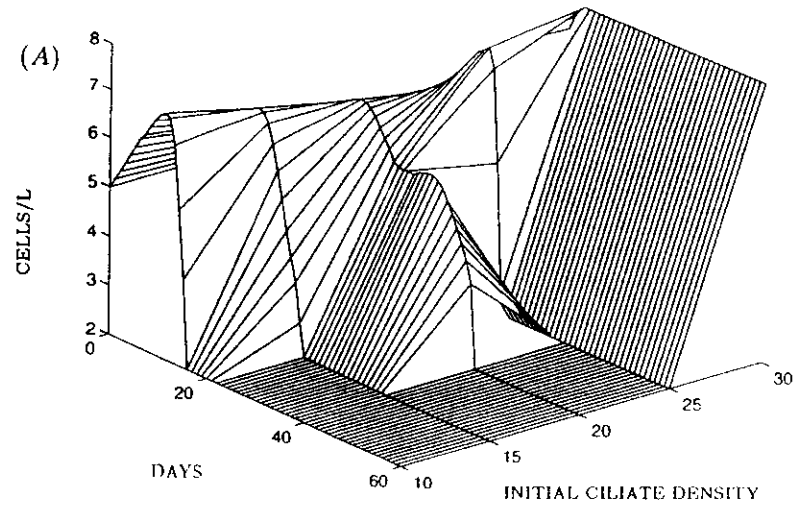

Figure 13A.

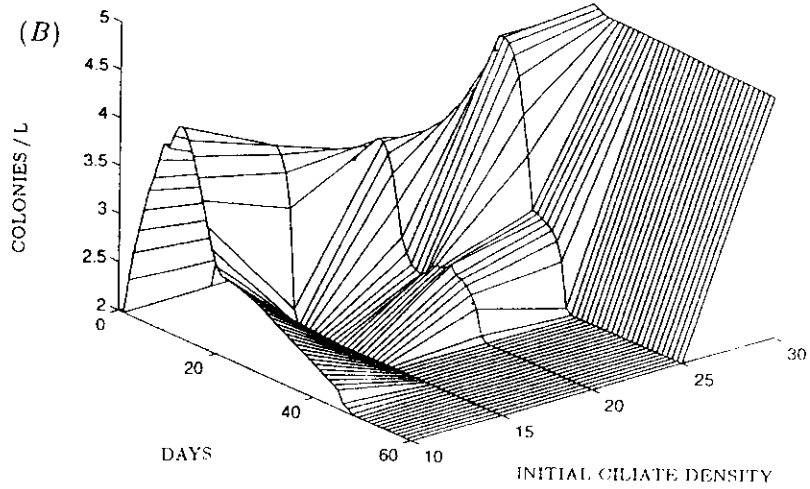

Figure 13B.

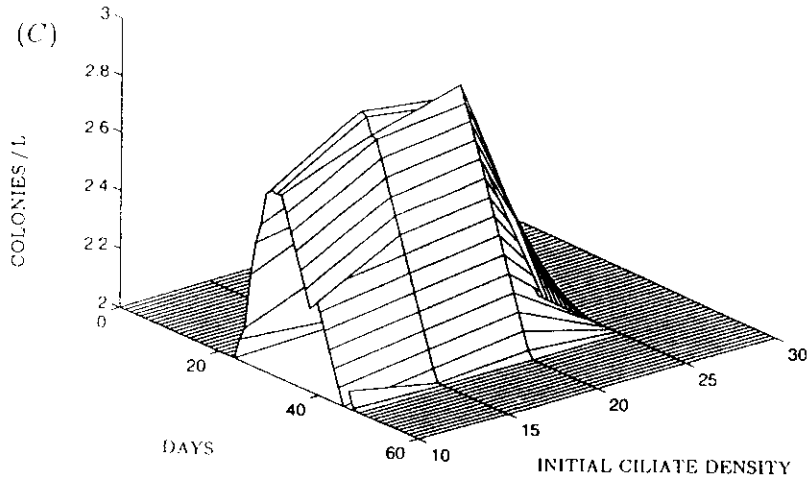

Figure 13C.

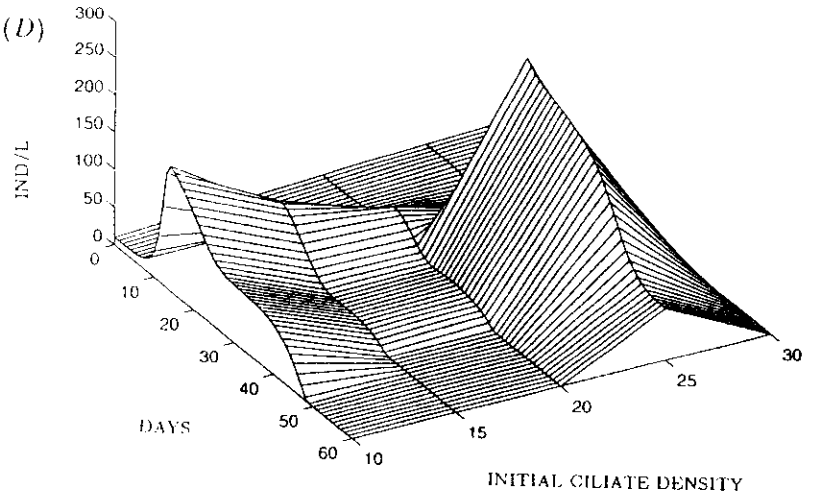

Figure 13D.

Figure 13A–D. Effects of increasing initial ciliate density given a fixed predation pressure on (A) single cell and (B) grazable colony dynamics, (C) ungrazable colony, and (D) ciliate population dynamics.

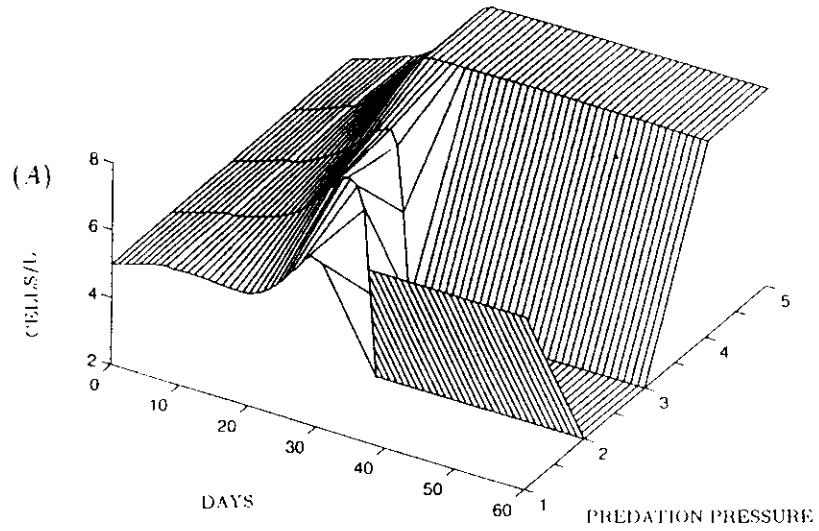

Figure 14A.

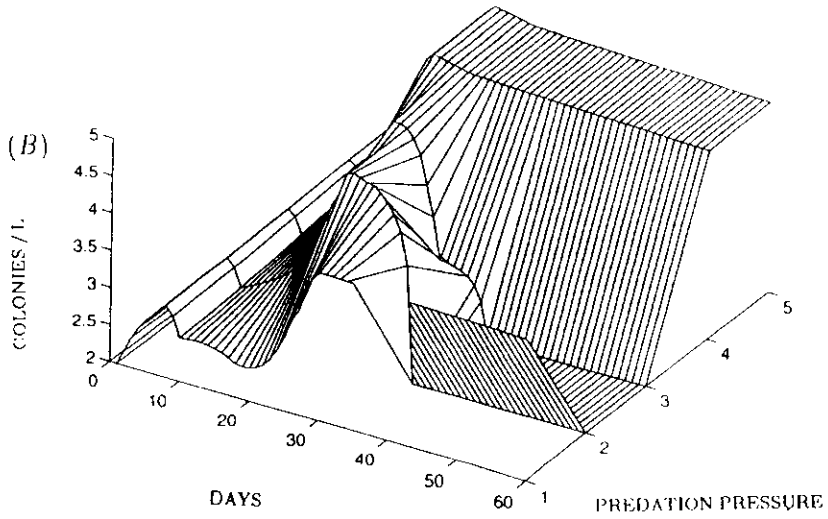

Figure 14B.

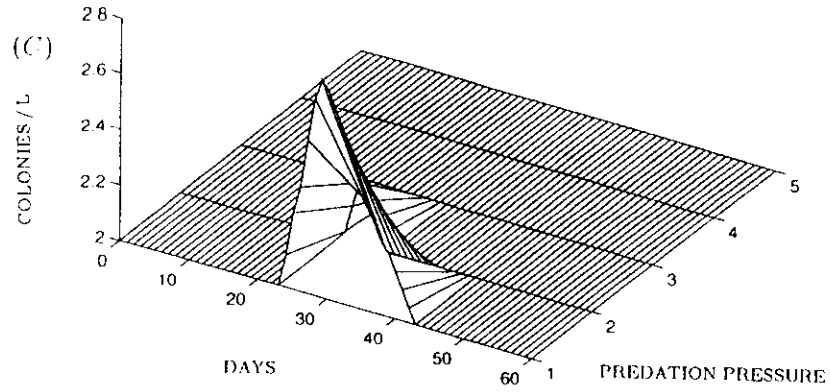

Figure 14C.

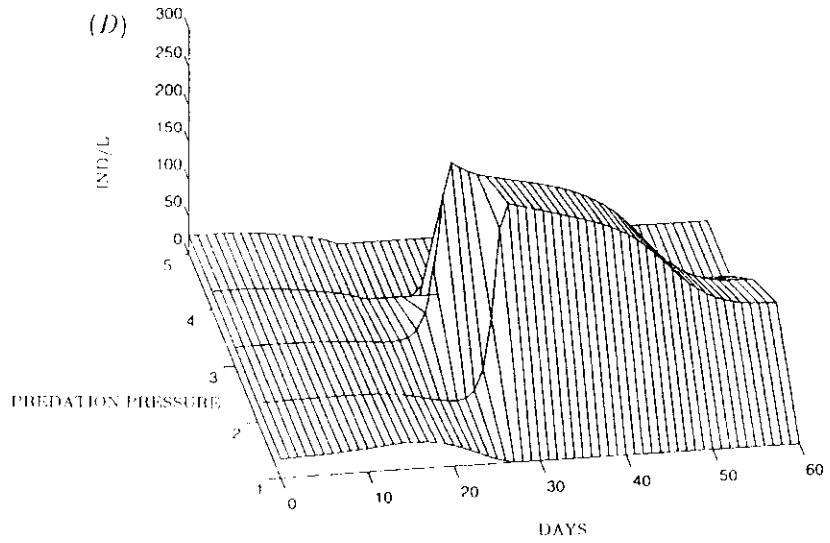

Figure 14D.

Figure 14A–D Effects of increasing predation pressure given a fixed initial ciliate density ($25 ind.l^{-1}$) on (A) single cell and (B) grazable colony dynamics, (C) ungrazable colony and (D) ciliate population dynamics.

Phaeocystis cells and colonies are not controlled by copepod grazing and continue to grow until nutrients are depleted. As the predation pressure increases, the less control ciliates have on single cells dynamics and the earlier nutrients are depleted, so that ungrazable colony sizes are only attained when predation

on ciliates is very low (Fig. 14C). Otherwise, colonial sizes remain in the very small range.

It is in the boundary between moderate to high initial ciliate densities that interesting dynamics occur, because of a delicate balance between algal growth and removal rates and ciliate growth and removal rates. These processes are controlled from the bottom, by nutrient abundance, and from the top by a variable demand of the copepod population. Only in these cases do we observe an oscillatory behavior in both *Phaeocystis* and ciliate populations. In some cases, a very small change in either initial ciliate density or predatory pressure can cause the *Phaeocystis* population to crash, while in others the ciliate population crashes and the *Phaeocystis* population grows rapidly with nutrient abundance as the only control. These phenomena apparently occur in no predictable pattern (Fig. 14).

If the copepod density is increased, say by multiplying it by a factor, the effects are not exactly the same as obtained by multiplying the "diet" function by the same factor. Although similar, they are "skewed" as if also a slight increase in the ciliate initial density had occurred; this is another demonstration of the nonlinearity of the interactions.

Main results. The behavior of the system strongly depends on the balance between growth rates and removal rates in both *Phaeocystis* and microzooplankton populations during the first days of the bloom.

When copepods prey on microzooplankton, the variety of responses of the system to changing predation pressure and initial microzooplankton densities increases. The responses are not necessarily the expected ones because of the existence of the colonial stage and the underlying feedback mechanisms. The *Phaeocystis* population is not necessarily driven to extinction.

Mortality

One parameter that affects the ciliate population is the mortality rate μ_1, a parameter not related to copepod predation. We let the value of μ_1 vary between 0.02 and 0.14 d^{-1}. The patterns in the dynamics of the ciliate population do not change, and even when predation is very low, the changes in peak values are very small, suggesting that predation has a stronger effect on the behavior of the ciliate population than the other type of mortality. In the cases with oscillatory behavior there is a small increase in the amplitude of the oscillations as μ_1 increases, both in the ciliate and the *Phaeocystis* populations.

Effects of nutrient input

We next examined the effect of the introduction of an input into the nutrient pool during a fixed interval at different times along the span of the bloom. First, a constant daily input of both nutrients, N and P, flow continuously into the pool

for a fixed period of ten days, starting at days 10, 20, 30 and 40 respectively. Subsequently, the period is extended to fifteen days. The effects of inputs of different concentrations were also tested. These tests may represent the effect of remineralization of organic compounds within the mixed layer as well as external inflow due to the presence of a river or other similar source.

With a daily input of $10^{-3}\,\mu M$ of nitrogen and $10^{-4}\,\mu M$ of phosphorus, changes in the nutrient levels were almost imperceptible. If daily inputs are increased to $10^{-2}\,\mu M$ for nitrogen and $10^{-3}\,\mu M$ for phosphorus, changes in nutrient levels become more pronounced the earlier the inflow starts because total nutrient uptake increases as the *Phaeocystis* population grows. At this concentration, any input after day 30 is consumed almost instantly. The changes in the *Phaeocystis* population are small and are reflected only in the size distribution and the density of ungrazable colonies. If the input occurs earlier, the single cell population is almost at the point of being overgrazed by the ciliates, so it can not fully utilize the nutrient inflow. Colonies do use the nutrient to grow to larger sizes and escape copepod grazing. If the inflow starts later, then the larger colonies exploit those nutrients and the effects, though small, can be observed in the size distribution of colonies.

If the daily input is increased to $10^{-1}\,\mu M$ for nitrogen and $10^{-2}\,\mu M$ for phosphorus, the changes at nutrient concentration level are enormous. For example, if the initial nutrient concentration is $16\,\mu M$ for nitrogen and $1\,\mu M$ for phosphorus, and the inflow starts at day 10, then by day 20 nutrients have accumulated to reach concentrations peaks of 30 to $19\,\mu M$ for nitrogen and 2.7 to $1.8\,\mu M$ for phosphorus depending on predation pressure. That is, the more copepods prey on ciliates, the more abundant are *Phaeocystis* cells and colonies and the faster nutrients are consumed. If the inflow starts at day 20, when *Phaeocystis* densities are higher, the concentrations, after reaching low levels, increase back to 16 to $11\,\mu M$ for nitrogen and 1.3 to $1.1\,\mu M$ for phosphorus, depending on predation levels. In all cases, nitrogen is totally depleted at about day 30. As before, the changes in the *Phaeocystis* population are reflected only in the size distribution and density of ungrazable colonies, and, though small, the changes are easier to observe than in the previous cases.

Extending the interval of nutrient inflow to 15 days yields no differences relative to the cases where the interval is only 10 days can, except in the cases of higher predation pressure. But even then, changes are minimal and relate to slight increases in densities in the ungrazable colonies.

Main results. No significant effects on the *Phaeocystis* population can be observed when a continuous nutrient inflow over a fixed number of days occurs during the bloom.

Dicussion

A model, necessarily a simplification of the real world, can serve many purposes, including delineation of the main traits and mechanisms of a given system and indication of its dynamics. The success of a model often depends on the inclusion of all essential compartments and connections and the exclusion of those factors whose variations may not have a significant impact on the questions asked about the system. In a system as complex and as intricate as a *Phaeocystis* community, it is absolutely necessary to make simplifications. Here we consider only the most basic compartments and relationships. Other factors, such as the effect of shear on colonial division and the colonial size distribution, and an alternate resource for microzooplankton are important but are omitted at present.

Although both temperature and irradiance have been observed to be important in colony formation and cell growth (Kayser 1970, Gieskes and Kraay, 1975, Jahnke 1989, Verity et al. 1988, Verity et al. 1991), the sharp differences in these environmental parameters observed at the onset of *Phaeocystis* blooms from year to year (Cadée and Hegeman 1986, Weisse et al. 1986) suggest that other conditions more variable or local in character, such as nutrient concentrations, *Phaeocystis* "seed" population, or the grazer community composition, could be more fundamental. We assume a constant temperature of 10 °C, in order to determine parameters involved in the model such as the water density δ_w, the seawater viscosity η, and the half-saturation constant K_1 for the functional response of ciliates.

If we consider only the nutrient-*Phaeocystis* module, a bloom occurs independently of initial concentrations. The cells multiply until depletion of one or both nutrients, in such a way that the higher the initial concentration, the more rapid the depletion. Under these conditions, colonies do not have sufficient time to grow beyond 64 cells, giving an average of 2 cells per colony at the peak. Sinking is the only removal process considered in this scenario. Because colonies are so small, they remain for a long period in the mixed layer so that the peak daily removal rate is at most 0.002% of the total cell numbers, a negligible loss by sinking (Figs. 2A & 3A). To obtain daily loss rates and average colonial sizes closer to those reported in the literature (Wassmann et al. 1990, Wassmann 1994, Weisse and Scheffel-Moser 1990b, Verity et al. 1991) nutrients could be added continuously, or at least frequently, to the pool; however, in this case of a restricted nutrient-*Phaeocystis* system, this would lead to excessively high *Phaeocystis* single cell densities.

The inclusion of grazer compartments in the model drastically changes the outcome. The presence of microzooplankton that feed on single cells reduces *Phaeocystis* abundance and slows the overall consumption of nutrients, allowing the remaining cells to continue growth and division. Under these conditions, colonies grow to much larger sizes (up to a peak average of 2,800 cells per colony) and the daily loss rate due to sinking increases to peak values of 5 to 11% of total cell numbers, values which are realistic. Initial ciliate density is

one of the parameters that causes significant changes in the dynamic outcome, transforming the system from one type of behavior to another. We can observe this sensitivity in Fig. 6, which illustrates how peak values change as the initial ciliate density increases from 0.25 ind. l^{-1} to 34 ind. l^{-1}. Depending on the initial densities of ciliates and initial nitrogen and phosphorus concentrations, nutrients may not be totally depleted even after 30 days.

Note that in the sample chosen to illustrate our results, ciliate peak densities are much lower than levels reported in the literature (see Table 4b.). It is worth noting that the ciliate model is sensitive to variations in the assimilation and ingestion rates, and particularly in the functional response to algal abundance. As we varied these species-dependent parameters over a reasonable range, we were able to obtain ciliate densities on the order of 1,000 cells l^{-1}, close to the 3,000 cells l^{-1} reported by Lancelot et al. (1991) and to the range of 1,500 to 24,000 reported by Weisse and Scheffel-Moser (1990a), but still quite low compared to peaks of 24,000 to 118,000 cells l^{-1} reported by Admiraal and Venekamp (1986), who noted that their densities are much higher than the highest values usually found in well developed tintinnid populations. In our case, the lower densities may be due to our assumption that the ciliate population depends exclusively on single *Phaeocystis* cells for its survival.

The fact that the ciliate population model is formulated in a very generic manner allows the representation of any other microzooplankton species, such as dinoflagellates, whose life cycle is similar to that of ciliates and that would feed on single *Phaeocystis* cells, provided we know the corresponding doubling time, assimilation efficiency and functional response to algal abundance.

The copepod compartment functions in the community model differently from the ciliate compartment because evidence does not seem to exist to indicate that a *Phaeocystis* bloom can sustain a copepod population of the type we are modeling here (*Temora longicornis* or *Acartia tonsa*); hence, it would not be reasonable to impose a sole resource assumption similar to the one utilized for the ciliate population. Moreover, there is evidence that large copepodites and adult copepods do not graze on *Phaeocystis* in the early stages of the bloom (Estep et al. 1990). By assuming that the copepod population is not food limited and that at different developmental stages they are able to cover a different percentage of their nutritional needs by consuming *Phaeocystis*, we tested the effect copepods may have on the bloom dynamics.

There is considerable controversy regarding the role of grazing in the decline of blooms. Our results indicate that the observation by Estep et al. (1990), that copepods do not graze on *Phaeocystis* in the early stages of the bloom is valid, and show that copepods have a dramatic impact if they start consuming colonies approximately when the bloom is peaking. The timing of their intervention is crucial, essentially because they indirectly "control" how the nutrients are utilized by the *Phaeocystis* population. The model suggests that in most cases grazing does not terminate a bloom situation, but by depressing phytoplankton

densities, it controls nutrient consumption and contributes to the formation of larger colonies which sink faster.

Note the combined effects of variations in initial ciliate densities and copepod timing on various peak values. Fig. 11 shows that small variations in initial ciliate density have a remarkable effect on peak single cell and grazable colonial densities, while the copepod timing is crucial in determining how large colonies can grow and, consequently, the impact of removal by sinking.

When predation by copepods on the ciliates is permitted, we observe that the behavior of the system strongly depends on the balance between growth rates and removal rates in both *Phaeocystis* and ciliate populations during the first days of the bloom. *Phaeocystis* growth rates depend on nutrient abundance, while removal rates depend not only on the abundance of grazers and on sinking rates, but also on physiological and ecological characteristics of the grazers. In particular, grazing and assimilation rates and functional response to phytoplankton abundance of the protozoans are fundamental because they control the single cell population from which colonies are generated. By varying the parameters of these processes over realistic ranges, different peak values and timings are found. The results we presented here refer to simulation experiments performed using parameters corresponding to one particular species of ciliates, which is in a certain way a 'worst case' because its low assimilation rate and short doubling time make it a voracious consumer. When we mention low, moderate, or high ciliate densities we are assuming them relative to the species in consideration, so we can concentrate on the pattern in the behavior of the system rather than in particular cases.

The simulation experiments performed with predation of copepods on ciliates yield some results that are interesting because of the variety of responses to changing predation pressure and initial ciliate density and because responses, although very logical, are not necessarily the expected ones. For example, there are cases in which increasing predation pressure on ciliates results in higher peak densities in **both** *Phaeocystis* **and** ciliate populations. The explanation for such unexpected indirect effects behavior is the complexity of the system and, particularly, the underlying feedback mechanisms. The rate at which ciliates remove solitary cells controls their abundance, which in turn affects other compartments resulting in less single cells, less colonies, more nutrient available, higher *Phaeocystis* growth rates, and ultimately larger colonies. Copepods control ciliate abundance affecting ciliate grazing capability. Copepods graze over a range of sizes, so that if colonies grow to ungrazable sizes too fast, copepods ability to control *Phaeocystis* is diminished. By depressing ciliates, copepods allow *Phaeocystis* to consume nutrients faster, with the consequence that colonies remain in the grazable size classes where they can be consumed. These chains of indirect effects make the system not a top-controlled or bottom-controlled one, but rather one under a ping-pong control, because growth, consumption, grazing and removal rates, as well as system feedbacks, are **variable** because they are determined by abundances that change with time.

Contrary to what we expected, the inflow of nutrients, even at high concentrations does not have an observable effect on the *Phaeocystis* population. The accumulation is visible in the nutrient pool if the inflow starts relatively early in the bloom, but it does not translate to any remarkable change in the population. If the inflow starts later in the bloom, nutrients are consumed instantly and no discernible effects result.

As mentioned previously, for those cases when the *Phaeocystis* population is formed primarily by very large colonies, the removal rate by sinking reaches a maximum of 14.2 % of the population per day, which is, in general, above daily loss rates reported in Wassmann et al. (1990) and Wassmann (1994) (Table 4c). The choice of the maximal colonial size in our model has been determined by the maximal radius for which Stokes' Law is valid. The maximal sinking velocity is that of the largest colonial size: 6.6 $m.d^{-1}$. Wassmann (1994) reports average sinking velocities of 4.9 $m.d^{-1}$ (from Taguchi and Hargrave 1978) and 6 $m.d^{-1}$ (from van Boekel et al. 1992), so that sinking velocities in our model are well within range (Table 4d). An increase in the range of colonial sizes may, of course, allow for higher removal rates. Also, we consider a constant water temperature throughout the bloom. Even a slight increase in temperature would mean a decrease in δ_w, the water density, which translates into an increase in sinking velocities. Furthermore, we could assume that colonies can increase their density after the peak of the bloom (Davidson and Marchant 1987, Lubbers et al. 1990), which also would imply an increase in sinking velocities. It remains to be seen if by including these modifications in our model, we could reach peak daily removal rates of 33% (Wassmann 1994). Under our current assumptions, sinking is important at the end of the bloom, only when colonies are large.

In summary, the primary implications of the analysis relate to the roles of grazers in controlling the colonial size distribution in *Phaeocystis* communities. If grazers are not present, *Phaeocystis* cells exhaust nutrients before colonies grow sufficiently large to sediment at observed rates. If grazers are present, their initial densities are important in controlling the abundances and size distribution of the *Phaeocystis* population. The earlier grazers are present, the slower the depletion of nutrients, and the higher the removal of smaller colonies, permitting enhanced growth of the remaining colonies. The relative abundance of large colonies accelerates the sinking flux of *Phaeocystis* colonies and contributes to bloom termination. The arrangement is fragile because if grazers densities are too high or if the grazing starts too early, the *Phaeocystis* population is grazed to extinction and a bloom does not result.

The control exerted by copepods in preying on ciliates reveals a complex feedback in the *Phaeocystis*-dominated community. Increased predation on ciliates may enhance both *Phaeocystis* and ciliate population densities. Because the community appears to be driven by delicately balanced relationships between density dependent (nutrient-*Phaeocystis*; cells-ciliates; colonies- copepods; and ciliates-copepods) removal rates, the multitude of apparently distinct field observations in the literature seem feasible and non-contradictory. Community dynamics, coupled with environmental factors, can explain variability of observed dynamic behavior.

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