

# A Model of Phytoplankton Blooms

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*Submitted August 28, 2000; Accepted July 16, 2001*

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**ABSTRACT:** A simple model that describes the dynamics of nutrient-driven phytoplankton blooms is presented. Apart from complicated simulation studies, very few models reported in the literature have taken this “bottom-up” approach. Yet, as discussed and justified from a theoretical standpoint, many blooms are strongly controlled by nutrients rather than by higher trophic levels. The analysis identifies an important threshold effect: a bloom will only be triggered when nutrients exceed a certain defined level. This threshold effect should be generic to both natural blooms and most simulation models. Furthermore, predictions are given as to how the peak of the bloom  $P_{\max}$  is determined by initial conditions. A number of counterintuitive results are found. In particular, it is shown that increasing initial nutrient or phytoplankton levels can act to decrease  $P_{\max}$ . Correct predictions require an understanding of such factors as the timing of the bloom and the period of nutrient buildup before the bloom.

**Keywords:** phytoplankton blooms, nutrient-phytoplankton models, bottom-up control, threshold model.

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Phytoplankton are the source of almost all energy passing through aquatic food webs and comprise some 40% of the total fixed global primary productivity (Falkowski 1994). A large component of this productivity can be attributed to the occurrence of both seasonal and sporadic algae blooms that form as patches over the ocean's surface in areas of localized nutrient enrichment (Lohrenz et al. 1992; Berman et al. 1995; Flynn et al. 1997; Lucas et al. 1999). Once triggered, bloom events lead to rapid rates of increase in phytoplankton growth. Biomass can sometimes increase by several orders of magnitude, only to decrease or crash as suddenly as the bloom mysteriously appeared. As phy-

toplankton sink out of the water column, they transport large quantities of carbon in a manner that intimately connects these primary producers with the earth's global carbon cycle. Hence phytoplankton have the capability of directly affecting large-scale global processes such as ocean-atmosphere dynamics and climate change. In freshwater lakes, rivers, and reservoirs, phytoplankton communities can have a major impact on ecosystem dynamics. Here, the appearance of algae blooms are often a signal of dangerous eutrophication and may result in major water-quality problems.

Until recently, there has been little research describing the generic mathematical mechanisms that underlie the dynamics of phytoplankton succession and blooms, except for direct simulation approaches (Evans and Parslow 1985; Evans 1988; Fasham et al. 1990). In this respect, Truscott and Brindley (1994b) made notable progress in modeling a bloom as a nonlinear “excitable system.” Their formulation depends on “top-down” control, with zooplankton strongly controlling the initiation of blooms both in freshwater lakes and upwelling ocean systems. However, top-down control is an unlikely mechanism for the many blooms that are toxic or largely inedible and that can thus hardly be affected by zooplankton grazing. Here, we attempt to overcome this shortcoming by designing a model that is based on bottom-up nutrient control. In this model, a threshold level of nutrients is required to trigger the bloom. Although there have been a number of bottom-up models reported in the literature (Patten 1968; O'Brien 1974; Evans 1988; DeAngelis 1992; Stone and Berman 1993; Franke et al. 1999; Litchman and Klausmeier 2001), to our knowledge the threshold effect described here has not been identified previously either in simulation approaches or in theoretical studies of bloom dynamics. (Note, however, that threshold effects have been reported for chemostat [Smith and Waltman 1994] and resource competition models [Grover 1997] but in the context of equilibrium behavior rather than the transient dynamics discussed here.) Yet the concept has been anecdotal among limnologists for a long time now and has on occasion even been identified. For example, some 70 yr ago, Pearsall, in his landmark studies of phytoplankton blooms (1932, p. 245) in the English Lake District, provided one of the first

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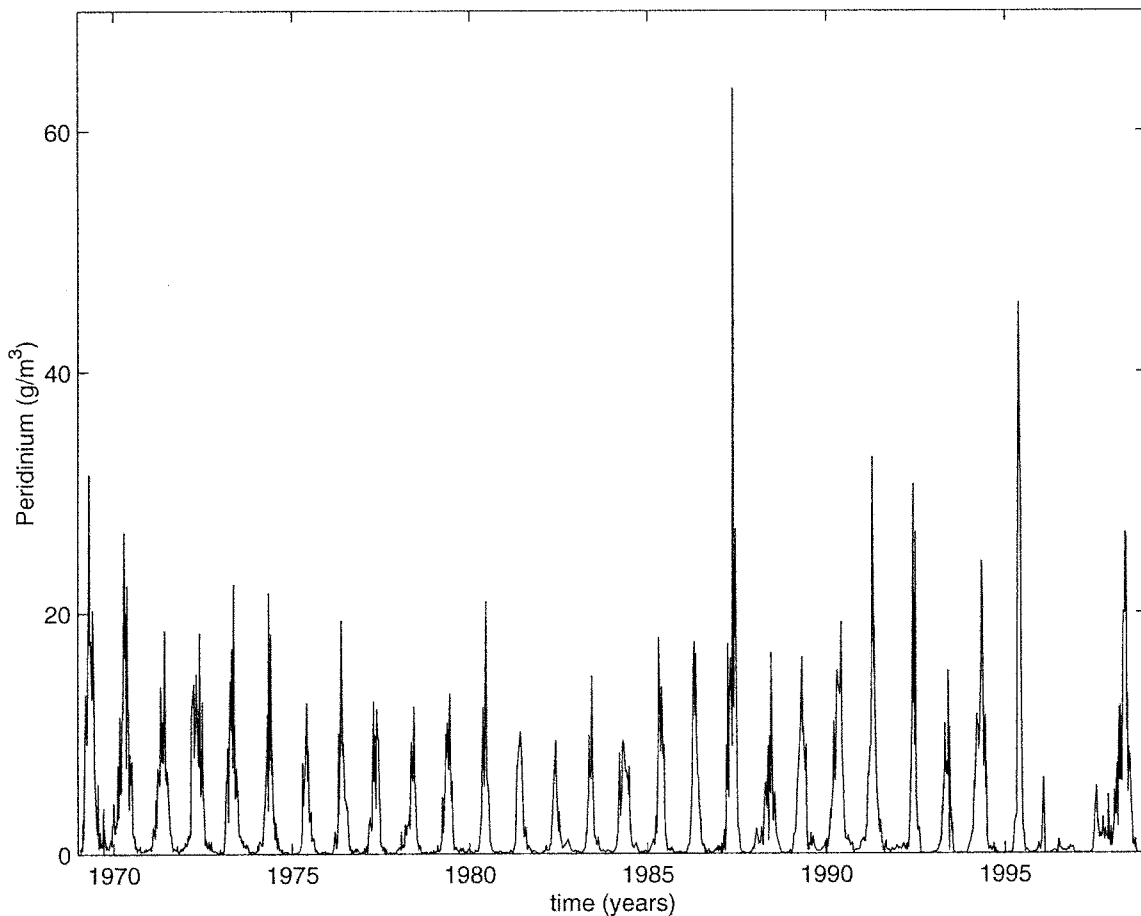
records of the threshold: “it seems probable that ... substantial increases in the proportions of diatoms will not take place in these lakes if silica [nutrients] is below 0.5 mg per litre.”

The model is also able to shed light on what are currently difficult questions in the study of phytoplankton dynamics still today, namely, What are the mechanisms that lead to the triggering of blooms, and what then causes their subsequent demise or collapse? What determines the time at which a bloom is triggered, and what then limits the peak of the bloom event?

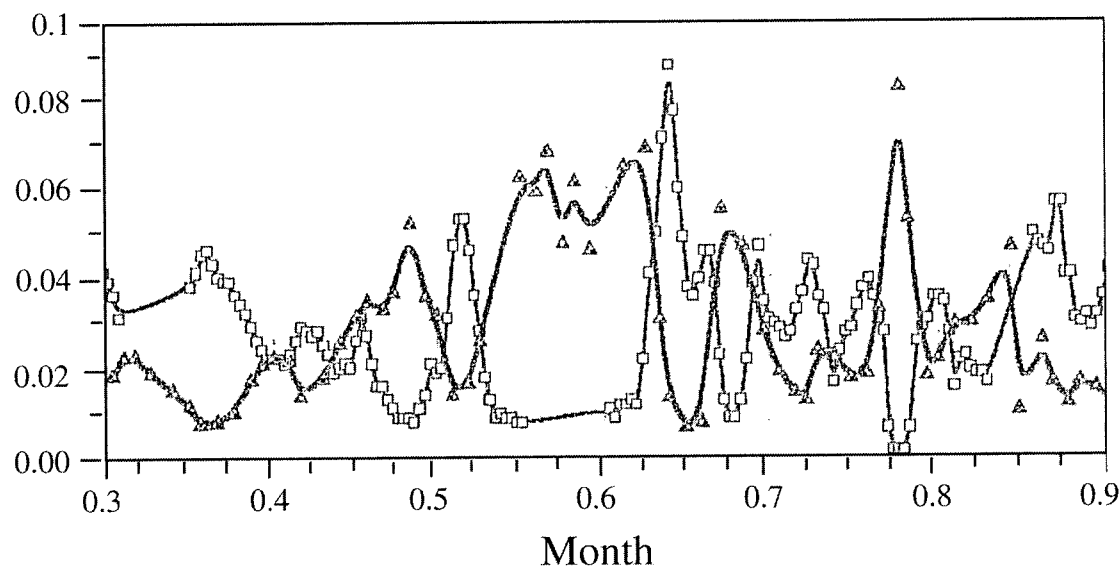
The annual phytoplankton bloom dynamics at Lake Kinneret (Sea of Galilee), Israel, are illustrated in figure 1, which displays the biomass time series of the dinoflagellate *Peridinium gatunense*. The Kinneret is one of the best monitored lakes in the world, with a long-term data set that extends over 25 yr (Berman et al. 1995). Despite intensive study, the dynamics of these bloom events are still poorly understood. The bloom generally occurs in

spring every year, not long after the “turnover” of the water column and the injection of nutrients and phytoplankton cysts from the sediment into the lake’s surface waters. Yet, strangely, in 1997 there was an irregular “non-*Peridinium*” year when the bloom mysteriously failed to appear. Furthermore, when examined on an annual basis, there is great variability from one bloom to the next. Although there is no evidence that the collapse of the bloom is solely due to strong nutrient limitation, this is one of the only plausible theories available to explain these crashes in *Peridinium* biomass. Since *Peridinium* is rarely grazed by zooplankton and fish, top-down control of the bloom dynamics is out of the question (Hart et al. 2000).

Figure 2 illustrates what appears to be a cause-effect relationship between nutrient and phytoplankton dynamics occurring in the Danube River, Germany (data collected by G. Volkmar). Large nutrient increases are generally followed by bloom events, which in turn tend to draw heavily on nutrient supplies, thus depleting them considerably. A



**Figure 1:** Time series from Lake Kinneret, Israel, of *Peridinium gatunense* phytoplankton blooms from 1970–1999. Data courtesy of Utza Pollinger and Tamar Zohary. The bloom peak varies considerably from year to year, and in unusual cases, there might be no bloom at all.



**Figure 2:** Time series from the Danube River, Germany, showing the relationship between chlorophyll measured in milligrams per liter (a proxy for phytoplankton) and nutrients  $\text{PO}_4 - \text{P}$  measured in milligrams per liter, from March to October 1998. Phytoplankton data (*thick line, triangles*) courtesy of Gerhardt Volkmar (University of Regensburg); nutrient data (*thin line, squares*) courtesy of Kopf and Pöhlmann (Bavarian State Office for Water Management, Munich). In general, high nutrient levels lead to rapid phytoplankton growth and therefore depletion of nutrients. This in turn causes a collapse in the phytoplankton numbers.

long phase of high chlorophyll levels is thus associated with low nutrient concentrations, but, because of the difficulty in supporting large phytoplankton levels, this extended period of productivity breaks down soon enough. The successive triggering of further blooms is most likely due to the discharge of nutrient sources into the river.

These features, both for the Kinneret and the Danube, make a strong case for bottom-up nutrient control of blooms. However, apart from isolated simulation studies (O'Brien 1974), the basic underlying dynamics have yet to be addressed from a theoretical perspective. We examine this behavior in depth below and formulate a generic model to gain new insights into the interplay between factors such as the timing of the bloom, its peak height, and the role of initial conditions for both nutrients and phytoplankton.

#### A Simple Nutrient-Phytoplankton Model

Here, we present a model that illustrates the important dynamic properties of phytoplankton blooms. Although the model is of a very simple structure, it is an extremely useful one, and its dynamics are inherently generic to more complex  $N$ - $P$  models. Later, we return to discuss the con-

sequences of adding further realistic features and explain why our initial model captures the essential dynamics.

The model consists of only two variables: nutrients levels,  $N$ , and phytoplankton biomass,  $P$ . It is assumed that small levels of nutrients enter the system at a slow but constant rate, and we first seek to determine how these nutrient "inputs" might influence phytoplankton dynamics. Phytoplankton,  $P$ , rely on nutrient "uptake" for growth and are removed from the water column through mortality and sinking. This gives the following system:

$$\begin{aligned}\dot{N} &= \text{input} - \text{uptake} - \text{loss}, \\ \dot{P} &= \text{uptake} - (\text{death} + \text{sinking}).\end{aligned}\quad (1)$$

It is possible to learn a great deal about the general dynamics of models of the above form by examining the particularly simple system

$$\begin{aligned}\dot{N} &= a - bNP - eN, \\ \dot{P} &= cNP - dP,\end{aligned}\quad (2)$$

with initial conditions  $N(0) = N_0 > 0$  and  $P(0) = P_0 > 0$ .

There are five parameters in this first model. Nutrient inputs flow into the system at a constant rate,  $a$ , and

nutrient uptake rates of phytoplankton are determined by the parameters  $b$  and  $c$ . In equations (2), nutrients and phytoplankton are treated as though they are part of an “interacting-particle system” (Durrett and Levin 1994), where the bilinear Lotka-Volterra interaction,  $NP$ , implies that the probability of a phytoplankton utilizing a nutrient is determined by the product of their relative abundances (or proportional probabilities). Michaelis-Menten uptake dynamics (Dugdale 1967) might provide a more realistic reflection of nutrient uptake dynamics (as discussed later), but in the interest of simplicity, we have chosen to retain the Lotka-Volterra term, which is a good first approximation to the former. The parameters  $d$  and  $e$  are the per-capita-mortality/loss rates of phytoplankton and nutrients, respectively, which we have taken to be constant here.

Units of  $N$  are given in milligrams solute per meter cubed water,  $P$  is in units of kilograms solute per meter cubed water, and the time  $t$  is measured in days. The parameter  $a$  is the flux entering the system and can be given in units of milligrams per day per meter cubed, while  $b$  and  $c$  are the coefficient rates with units of meters cubed per kilogram per day and meters cubed per milligram per day, respectively. The death and loss rates  $d$  and  $e$  are given in units per day.

The analysis of the model can be greatly simplified by rescaling to nondimensional variables:

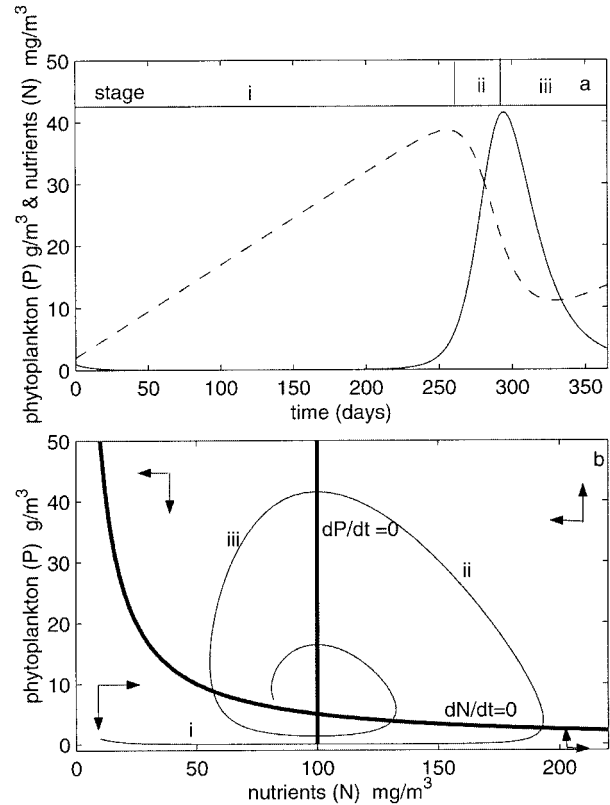
$$\begin{aligned} N' &= \frac{c}{d} N, \quad P' = \frac{b}{d} P, \quad t' = dt, \\ I &= \frac{ac}{d^2}, \quad q = \frac{e}{d}. \end{aligned} \quad (3)$$

When the dashes are dropped, the model becomes

$$\begin{aligned} \dot{N} &= I - NP - qN, \\ \dot{P} &= NP - P. \end{aligned} \quad (4)$$

Here, three of the five original parameters have effectively scaled out, leaving only the two dimensionless parameters  $I$  and  $q$ , which can be interpreted as effective influx and nutrient loss rate, respectively.

A typical simulation of the nutrient-phytoplankton dynamics in the time domain is presented in figure 3. In the first phase, the nutrient level slowly builds up due to the constant external nutrient input  $I$  in a manner that is similar to that observed in many temperate lakes and oceans during winter and early spring. After a time delay, when the nutrients finally reach a threshold level, the phytoplankton dynamics trigger, initiating the bloom. However, when the phytoplankton growth rates attain high levels, the nutrient supply is quickly depleted, causing the



**Figure 3:** *a*, Time-series plot of equations (4) with phytoplankton ( $P$ ) in grams per meter cubed (solid line) and limiting nutrient ( $N$ ) in milligrams per meter cubed (dashed line). Nutrients slowly build up linearly until initiation of the bloom. This occurs just before nutrients reach their maximum level. Parameters are as follows:  $I = 0.075$ ,  $q = 0$  ( $a = 0.00075$ ,  $b = c = 1$ ,  $d = 0.1$ ,  $e = 0$  in eqq. [2]), with initial conditions  $P_0 = 0.05$ ,  $N_0 = 0.0005$ . For the purposes of illustration, nutrient levels were rescaled and reduced by a factor of five. *b*, Phase-plane diagram of the phytoplankton bloom. The arrows indicate the direction that the trajectory “flows” in the phase plane. The motion in the phase plane is always counterclockwise (see below). The different stages *i*, *ii*, and *iii* are indicated at the top of the graph. Nutrients are in units of the model. The  $NP$ -phase plane provides a simple graphical means to understand the dynamics of the model. The  $N$  nullcline of the equations is defined by the line in the phase plane, where  $\dot{N} = 0$ . For equations (4), this is given by  $P = (I/N) - q$ , which is a line that divides the  $NP$ -phase plane into two. In the region of the phase plane that lies below the  $N$  nullcline,  $\dot{N} > 0$ , and nutrients accumulate in the system accordingly. In the region above the  $N$  nullcline,  $\dot{N} < 0$ , and nutrient levels decline. The  $P$  nullcline  $\dot{P} = 0$  is given by the equation  $N = 1$ . There is no phytoplankton growth ( $\dot{P} < 0$ ) when the trajectory is on the left side of the  $P$  nullcline, whereas phytoplankton increase ( $\dot{P} > 0$ ) when the trajectory is to the right. The point  $\dot{N} = \dot{P} = 0$  at which the  $N$  nullcline intersects the  $P$  nullcline defines an equilibrium point. The two nullclines divide the plane into four quadrants, and the model’s dynamic behavior is determined by the region into which its initial conditions ( $N_0$ ,  $P_0$ ) fall. The phase plane may be used as a guide to trace out how the trajectory of the model changes in time as it is attracted toward equilibrium. A careful examination of  $\dot{N}$  and  $\dot{P}$  in the four regions shows that the trajectory must move counterclockwise through the phase plane in its approach to equilibrium.

bloom to crash in turn. Thus, the time evolution of the simulation may crudely be divided into three stages: stage i, linear nutrient buildup; stage ii, phytoplankton bloom (rapid rise in  $P$ ) and subsequent depletion in nutrients ( $N$ ); stage iii, bloom crash (rapid decline in  $P$ ).

This motivates the following simple working definition of a bloom as a rapid increase in phytoplankton biomass by over at least one order of magnitude, contemporaneous to a depletion of nutrients. These events are followed immediately by a rapid decline in phytoplankton levels. Note, however, that a phytoplankton bloom is not necessarily a singular event. Sometimes the major bloom is succeeded by a number of smaller secondary blooms (see fig. 3).

The phase plane of figure 3b provides a convenient means for understanding the three stages in bloom dynamics (see legend for an explanation of phase-plane analysis). Here, the initial conditions are such that  $(N_0, P_0)$  lies in the lower left region ( $\dot{P} < 0$  and  $\dot{N} > 0$ ). Hence, initially, the phytoplankton levels decline, and there is a slow constant nutrient buildup due to the inflow  $I$  (stage i). The nutrient levels  $N$  continue to build up until they reach the threshold level  $N_c = 1$ , and the algae bloom is then triggered (stage ii). At this point, the trajectory crosses into the lower-right region ( $\dot{P} > 0$  and  $\dot{N} > 0$ ) of the phase plane, and both nutrient and phytoplankton levels are on the rise. Next, the trajectory crosses the  $N$  nullcline and moves into the upper-right region ( $\dot{P} > 0$  and  $\dot{N} < 0$ ) of the phase plane. In this region, phytoplankton dramatically increases while nutrients plummet in their attempt to fuel the bloom.

However, at some point nutrients can no longer support further increase in  $P$ . This occurs when the trajectory passes from the upper-right into the upper-left region and crosses the  $P$  nullcline ( $\dot{P} = 0$ ) where the bloom attains its maximum level  $P_{\max}$ . Now  $\dot{P} < 0$  and  $\dot{N} < 0$  so that both the phytoplankton and the nutrient levels crash in the final phase (stage iii) of the bloom. The phytoplankton population crashes mainly because the large nutrient pool has been depleted and the daily replacement of nutrients is now not enough to support a swelling standing stock of phytoplankton. This feature, namely that the nutrient depletion is directly responsible for initiating the crash in phytoplankton levels, was astutely noted by O'Brien (1974).

To illustrate how well these equations approximate the dynamics of real data, a time series of the *Peridinium* biomass in Lake Kinneret over 1982 (an arbitrarily chosen year) has been superimposed over a model simulation in figure 4. It is somewhat surprising that a model of such simple structure fits the data so well. One sees that even the asymmetry of the plankton data (compare the fast rise to the slow fall) is reproduced by the model.

### Underlying Threshold Dynamics of Minimal Model: $I = q = 0$

We start the analysis of model (4) with the simple case when  $I = q = 0$ , and there are no external nutrient input and output fluxes whatsoever. The equations simplify to

$$\begin{aligned}\dot{N} &= -NP \\ \dot{P} &= (N - 1)P\end{aligned}\quad (5)$$

and the model is parameter free. Equations of the above form are also used in the epidemiological literature (Murray 1989; Banks 1994) and have been referred to as the Kermack and McKendrick SIR (susceptible-infected-removed) model, hinting that epidemic and bloom dynamics might not be unrelated.

Model (5) has the single equilibrium

$$P^* = 0, \quad N^* = k,$$

where the constant  $k$  is determined by the model's initial conditions (see below). A stability analysis reveals that the two eigenvalues of the system's Jacobian, when evaluated at equilibrium, are

$$\lambda_1 = 0 \quad \text{and} \quad \lambda_2 = k - 1.$$

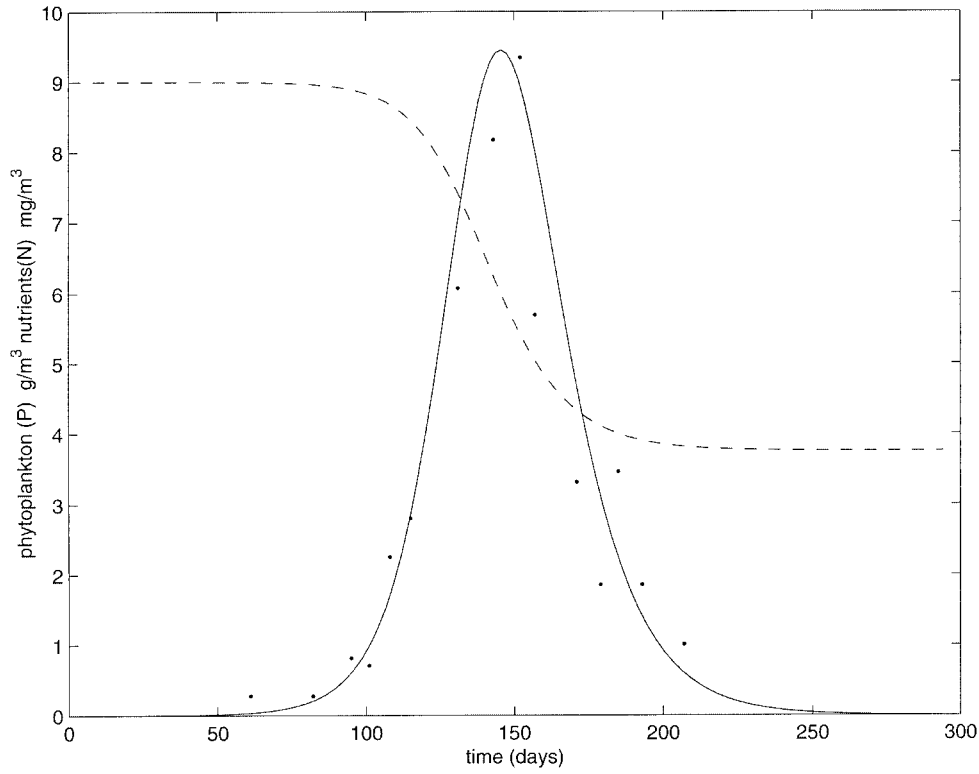
That one eigenvalue is 0 reflects the fact that the equilibrium is neutrally stable; for the same model parameters, the equilibrium solution is essentially determined by the initial conditions and is sensitive to perturbations.

Of particular interest are the model's transient dynamics to equilibrium since, as seen in figure 4, they describe the characteristic features of a bloom's growth and demise well. Looking at model equations (5) in more detail, we see that for positive initial conditions, the nutrient level  $N$  must monotonically decrease in time,  $\dot{N} < 0$ .

Consider now equations (5) governing phytoplankton dynamics when  $t = 0$ :

$$\dot{P}_{t=0} = P_0(N_0 - 1).$$

In this equation, the critical nutrient level  $N_c = 1$  takes on the simple interpretation of a "threshold." If  $N_0 < 1$  (i.e., the initial nutrient levels are below the threshold  $N_c$ ), then  $\dot{P}_{t=0} < 0$ . This is true for all  $t$  thereafter, since, as has already been established,  $N$  decreases with time to equilibrium. The plankton levels are thus condemned to decrease monotonically to 0, and there can be no bloom. If, however,  $N_0 > 1$  (i.e., initial nutrient levels exceed the threshold  $N_c$ ), phytoplankton growth is positive,  $\dot{P}_{t=0} > 0$ , and a bloom develops, as seen in figure 4 passing



**Figure 4:** Simulation of equations (4) with parameters  $I = 0$  and  $q = 0$  ( $a = q = 0$ ,  $b = c = 1$ ,  $d = 0.1$  as in eqq. [2]) and initial conditions  $N_0 = 15$  and  $P_0 = 0.0002$ . Units as in figure 3. The bloom is triggered even though there are no nutrient inputs ( $I = 0$ ) because the initial nutrient levels are above the threshold ( $N_0 > 1$ ). The nutrients (*dashed line*) monotonically decay to a positive nonzero equilibrium level, while the phytoplankton (*continuous line*) display a typical bloom that eventually crashes. Superimposed on the simulation is observed data from the 1982 Lake Kinneret *Peridinium gatunense* bloom (*dots*) in real units. For the purposes of illustration, nutrient levels have been rescaled appropriately (by a factor of 9/15).

through stages ii and iii. We have just identified one of the most important features of the model, namely the underlying threshold behavior of the bloom.

The peak height of the bloom  $P_{\max}$  can then be readily obtained in the same manner as for the SIR epidemic model (e.g., Murray 1989; Banks 1994). Dividing the equations in (5),

$$\frac{dP}{dN} = \frac{N-1}{-N}. \quad (6)$$

This can be integrated and has the solution

$$P = P_0 + N_0 - N + \ln \frac{N}{N_0}. \quad (7)$$

Recall that a bloom can occur only if  $N_0 > 1$ . Given that the phytoplankton bloom reaches its peak height  $P_{\max}$  when  $N = 1$  (where  $\dot{P} = 0$ ), then

$$P_{\max} = P_0 + N_0 - 1 + \ln \frac{1}{N_0}. \quad (8)$$

From this equation, it is easy to see that  $P_{\max}$  increases with either an increase in  $P_0$  or  $N_0$ , as one might intuitively expect.

Since  $P^* = 0$ , equation (7) also makes it possible to calculate the nutrient equilibrium  $N^*$  in terms of the initial conditions:

$$N^* = N_0 + P_0 + \ln \frac{N^*}{N_0}. \quad (9)$$

The above transcendental equation can be shown to have a single positive root (see Murray 1989, p. 614) for  $N^*$ , which may be solved by numerical techniques. That  $N^*$  is nonzero has the interesting implication that when the bloom finally crashes and all phytoplankton is removed from the water column, nutrients nearly always remain—a

feature that occurs in lakes but is considered somewhat puzzling. Hence, although the crash of algae blooms is often attributed to strong nutrient limitation, nutrients are in fact never fully utilized. This leaves the paradoxical impression that the bloom must in some ways have a life and death of its own.

#### Bloom Dynamics When Nutrient Fluxes $I > 0$

Examine now the effects of incorporating a small constant inflow of nutrients ( $I > 0$ ) into system (4) and possibly a small nutrient loss  $q \geq 0$ . The system is characterized by two equilibria that we examine in turn. The equilibrium we will be most concerned with is

$$P^* = I - q, \quad N^* = 1. \quad (10)$$

Its stability may be determined from the eigenvalues  $\lambda_{1,2}$  of the system's Jacobian, and a calculation shows that

$$\lambda_{1,2} = \frac{-I}{2} \pm \frac{1}{2} \sqrt{I^2 + 4(q - I)}.$$

The equilibrium is locally stable only if both eigenvalues have negative real parts (i.e.,  $\text{Re}(\lambda_{1,2}) < 0$ ; Murray 1989). Hence, for  $I > 0$ , this equilibrium is locally stable only if  $q < I$ . Note for future reference that if  $q < I(1 - I/4)$ , the eigenvalues have imaginary components causing trajectories to spiral in phase space as they approach equilibrium through damped oscillations (see fig. 5). However, as a consequence of Dulac's criterion, it is impossible for the model to attain limit-cycle behavior.

The model also has a second equilibrium at which the phytoplankton population is extinct:

$$\tilde{P} = 0, \quad \tilde{N} = \frac{I}{q}. \quad (11)$$

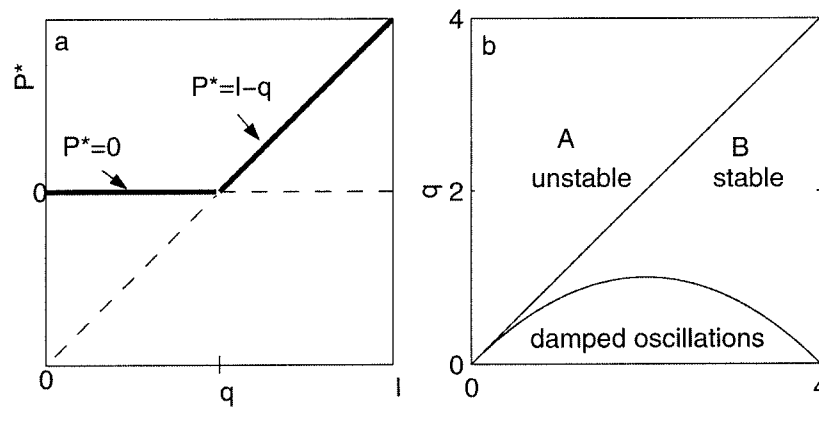
At this equilibrium, the eigenvalues of the Jacobian are

$$\lambda_{1,2} = -q \frac{I - q}{q}.$$

Hence, the second equilibrium is stable only for  $q > I$  and is an unstable saddle point otherwise. This condition tells us that if nutrient inflows  $I$  are small and below a distinct threshold level, a phytoplankton population cannot be sustained. Thus, in addition to the threshold level  $N_c$  discussed already in the context of the bloom formation, there is yet another threshold effect.

A full picture of the system's dynamics can be understood better by examining the stability of the equilibria as a function of the control parameter  $I$ , as is shown in figure 5a. As  $I$  increases above  $I = q$ , we see an exchange of stability whereby  $(\tilde{N}, \tilde{P})$  becomes unstable while  $(N^*, P^*)$  stabilizes. This exchange of stability caused by a change in  $q$  is referred to as a transcritical bifurcation. In figure 5b, we summarize the stability of the system in the  $(I, q)$  parameter space. Above the line  $I = q$ , the equilibrium  $(\tilde{N}, \tilde{P})$  is stable, while below it, the second equilibrium  $(N^*, P^*)$  is stable.

From here on, we deal only with equilibrium equations (10), which have a feasible phytoplankton population, and we are thus concerned with the case  $q < I$ . In particular,



**Figure 5:** a, Stability of the two equilibria  $P^* = 0$  and  $P^* = I - q$  plotted as a function of the bifurcation parameter  $I$ . The solid line represents the stable equilibrium for a given value of  $I$ , while the dashed line indicates the unstable equilibrium. Note the exchange of stability at  $I = q$ . b, Equilibrium  $(P^*, N^*) = (I - q, 1)$  is locally unstable in region A of parameter space and locally stable in region B. The parabolic line  $q = I(1 - I/4)$  demarks the boundary of the region for which there are damped oscillations (see text).

we attempt to identify the model's threshold under conditions of nutrient inflow  $I > 0$ . At the beginning of the simulation shown in figure 3, the initial conditions of the system  $P_0$  and  $N_0$  are both well below equilibrium so that  $N_0 P_0 \ll N^* P^* = I$ . Hence, equations (4), describing nutrient dynamics, may be approximated as

$$\dot{N} = I - qN. \quad (12)$$

Integration leads to the increasing nutrient buildup

$$N(t) = \begin{cases} N_0 + It, & q = 0, \\ \frac{I}{q} + \left(N_0 - \frac{I}{q}\right)e^{-qt}, & q \neq 0, \end{cases} \quad (13)$$

and the nutrients increase monotonically with time. Numerical simulations have shown that for  $q < I/2$ , it is reasonable to develop the exponential up to first order  $e^{-qt} \approx 1 - qt$ . (In practice, the bloom triggers rapidly enough to make the linearization a good approximation because higher-order terms remain negligible.) For this approximation, the nutrient dynamics are again characterized by a slow linear buildup:

$$N(t) = N_0 + (I - N_0 q)t. \quad (14)$$

We note that if  $I/2 < q < I$ , the buildup is nonlinear at the final stage only (i.e., just before the bloom triggers), and the linear approximation equation (14) is still reasonable for our purposes. Equation (14) shows that  $q$  may effectively be scaled out by reparameterizing  $I$ ,

$$I' = I - N_0 q, \quad (15)$$

or, alternatively, if initial nutrient levels  $N_0$  are small, then  $q$  has a negligible effect. Thus, since  $q$  has little qualitative impact on the dynamics as long as  $q < I$ , from here on we need concentrate only on the case  $q = 0$ .

In terms of the phytoplankton dynamics,

$$\dot{P} = (N - 1)P = (N_0 + It - 1)P \quad (16)$$

which can be integrated and solved for  $P(t)$ , yielding

$$\ln \frac{P(t)}{P_0} = N_0 t + \frac{I t^2}{2} - t. \quad (17)$$

Combining (13) and (17), we find the form of the trajectory in the  $NP$ -phase plane:

$$I \ln \frac{P}{P_0} = (N_0 - 1)(N - N_0) + \frac{1}{2}(N - N_0)^2. \quad (18)$$

### Evolution and Intensity of the Bloom Event

We now attempt to fully characterize the evolution of the bloom dynamics. Two cases have to be distinguished in terms of whether the state variables  $N$  and  $P$  are below or above the  $N$  nullcline  $N^* P^* = I$ .

*Case A.* If  $N$  and  $P$  are such that  $NP \ll N^* P^* = I$  (i.e., the initial conditions are below the  $N$  nullcline), then stage i, the first phase of the bloom, may be approximated according to our results for  $I > 0$ . This is the regime of slow nutrient buildup.

*Case B.* If the conditions are such that  $NP \gg N^* P^* = I$  (i.e., the initial conditions are above the  $N$  nullcline), then  $I$  has little effect on the dynamics of interest, and the previous analysis for the parameter-free model in which  $I = 0$  is relevant. The simple parameter-free model thus describes the main bloom itself, that is, stages ii and iii.

A typical bloom event begins with low initial conditions ( $N_0, P_0$ ) where the predictions of case A apply and there is a nutrient buildup. This is followed by the initiation of the bloom event as specified by the predictions of case B. Next, we locate the switching point where dynamics change from case A to B. However, this must occur just as the trajectory (which is initially below the  $N$  nullcline  $NP \ll N^* P^* = I$ ) cuts the  $N$  nullcline ( $\dot{N} = 0$ ). Hence, the switching occurs at the point of maximal nutrient levels when  $\dot{N} = 0$  or, that is, when  $N = N_{\max}$ .

Let  $t = \hat{t}$  be the time when the nutrients attain their maximum levels  $N_{\max}$  (i.e., when  $dN/dt = 0$ ); phytoplankton levels will thus be  $P(\hat{t}) = \hat{P}$ . The maximum nutrient level achieved is  $N_{\max} = N_0 + \hat{I}t$  (see eq. [13]). After some mathematical maneuvering, the details of which are described in appendix A, it is possible to approximate  $\hat{t}$  to find the maximum nutrient levels  $N_{\max}$ :

$$N_{\max} = 1 + \sqrt{(N_0 - 1)^2 + 2I \ln \left( \frac{I}{P_0} \right)}. \quad (19)$$

To recap, beginning with relatively small initial conditions ( $N_0, P_0$ ), we use case A to model the nutrient buildup until  $t = \hat{t}$  and  $N = N_{\max}$ . At this point, we change over to case B, where we take as initial conditions  $N_0 = N(\hat{t}) = N_{\max}$  and  $P_0 = P(\hat{t}) \approx I$  (see app. A). Remember that case B is just the simple parameter-free threshold model we first examined. When these initial conditions are plugged into equation (8), the bloom height is given as

$$P_{\max} = I + N_{\max} - 1 + \ln \left( \frac{1}{N_{\max}} \right). \quad (20)$$



We can use the above analysis to gain a deeper understanding of the factors that control the intensity of the bloom. Whereas intuition might lead us to expect that bloom height  $P_{\max}$  increases as the initial number of phytoplankton cells ( $P_0$ ) or nutrient levels ( $N_0$ ) increases, this is not always the case. Figure 6a displays the results of simulations of equations (4), with  $P_{\max}$  plotted as a function of  $P_0$  while  $N_0$  is held fixed. The bloom height can both decrease and increase as the initial level of phytoplankton cells increases, which gives the graph an unusual and counterintuitive “V shape.”

The pattern can be explained using the algebraic expression (20) for the peak of the phytoplankton bloom,  $P_{\max}$ . A plot of the prediction for  $P_{\max}$  as a function of  $P_0$  (with  $N_0$  fixed) is given in figure 6a. This should be compared with the simulation results given in the same figure. As can be seen, up to a small constant offset, equation (20) provides an excellent fit to the basic trend produced by the simulations. The graph indicates that  $P_{\max}$  first decreases and then increases (i.e., in a V shape) as a function of the initial condition  $P_0$ . A similar relationship is seen in figure 6b, which plots  $P_{\max}$  as a function of  $N_0$  when  $P_0$  is fixed.

The reasons for the V shape are explained in more detail in appendix B, where equation (20) is investigated for specific initial conditions to simplify the analysis. In these specific cases, the origin of the V shape is immediately evident. Another approach, also outlined in appendix B, is to approximate the nutrient dynamics in the neighborhood of the nutrient threshold  $N_c = 1$ . This gives a very simple formula for the phytoplankton maximum:

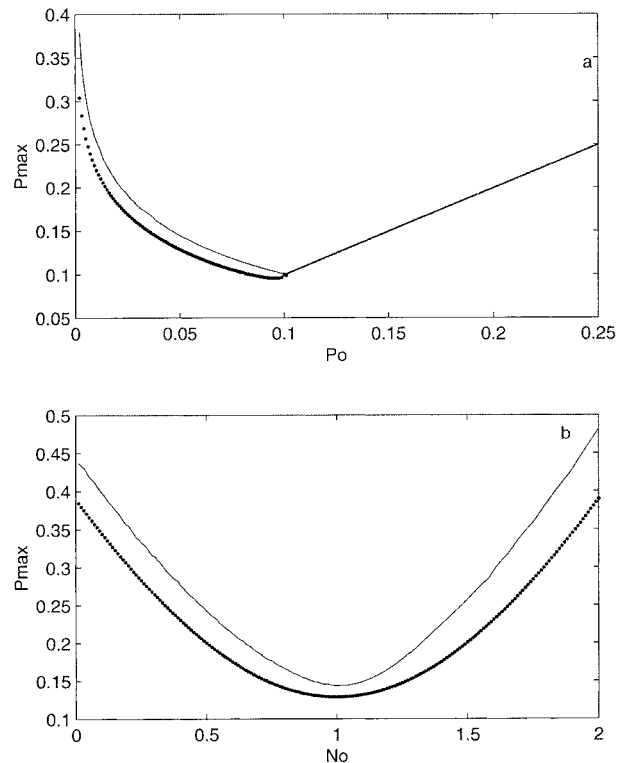
$$P_{\max} = \frac{1}{2}(N_0 - 1)^2 + I \left( 1 + \ln \frac{I}{P_0} \right), \quad (21)$$

where  $P_{\max}$  is a simple quadratic function of  $N_0$  and thus has a trivial V shape. This explains the parabolic form in figure 6b.

### Phase-Plane Analysis

Phase-plane analysis provides a simple qualitative graphical interpretation of the changes in bloom height  $P_{\max}$  as a function of the initial conditions. Figure 7b plots several model runs in the phase plane for different initial phytoplankton levels but for the same initial level of nutrients  $N_0$ . For the different simulations shown in figure 7b, it is useful to locate the points on the  $N$  nullcline where nutrients reach their maximum,  $N_{\max}$ , and points on the  $P$  nullcline where phytoplankton reaches maximal levels,  $P_{\max}$ .

The phase plane shows that the smaller the initial phy-

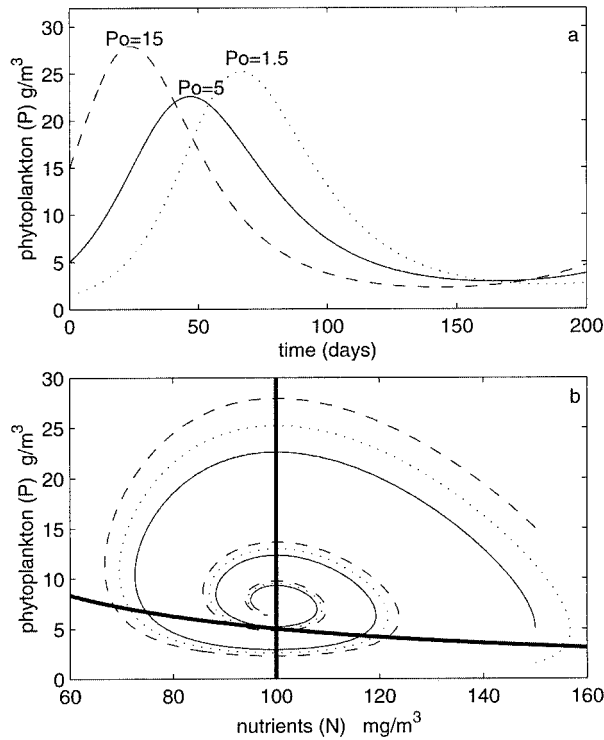


**Figure 6:** a, Simulations of model equations (4) with parameters  $I = 0.1$  and  $q = 0$  and initial condition  $N_0 = 1$ . The  $P_{\max}$  value was monitored and plotted as a function of initial phytoplankton levels  $P_0$ . The graph results in a V shape. The solid line represents solutions of model equations (4), while the dotted line is the approximation calculated from equation (20). b, Parameters as in a but now fixing  $P_0 = 0.0001$  and varying  $N_0$ .

toplankton level,  $P_0$ , the more the trajectory is pulled toward the horizontal  $N$  axis, which ultimately leads to a larger  $N_{\max}$ . Squeezing the trajectory toward the lower horizontal axis for a long period of time results in a slow buildup of nutrients; it is this nutrient buildup that delays the triggering of the bloom. Hence, smaller levels of  $P_0$  increase  $N_{\max}$  simply due to the way trajectories are forced to flow geometrically in the phase plane under the restriction (intrinsic to dynamical systems) that trajectories cannot intersect (Boyce and Diprima 1969; Lin and Segel 1974).

The phase plane shows that  $N_{\max}$ , the final amount of nutrients accumulated, is the key element in determining the bloom height  $P_{\max}$ . The more the nutrient levels build up (as reflected in the excursion of the trajectory to the farthest right side of the phase plane), the larger is the bloom that can be fueled.

If, however, the initial phytoplankton levels,  $P_0$ , are relatively high (more specifically, above the  $N$  nullcline), one sees from the phase plane that the opposite effect must



**Figure 7:** *a*, Three time series generated from model equations (4) with parameters  $I = 0.075$  and  $q = 0$  ( $a = 0.00075, b = c = 1, d = 0.1, e = 0$  for eqq. [2]) and initial condition  $N_0 = 0.15$  for three different initial conditions:  $P_0 = 1.5$  (dotted line);  $P_0 = 5$  (solid line);  $P_0 = 15$  (dashed line). The bloom peaks of the time series ( $P_{\max}$ ) make evident the basic V-shaped pattern that arises as  $P_0$  increases. *b*, Time series of figure 7a are plotted in the phase plane.

hold. Namely, for the same initial nutrient level, the larger the  $P_0$ , the bigger the bloom. This is because when  $P_0$  is relatively high, the nutrients are unable to build up in the manner just described (fig. 7b).

A similar argument can help to explain the changes in bloom height  $P_{\max}$  found when the initial condition  $N_0$  is varied while  $P_0$  is held fixed. For trajectories starting with  $N_0 < 1$ , increasing  $N_0$  serves to decrease  $P_{\max}$ . However, if  $N_0 > 1$ , increasing  $N_0$  leads to larger blooms. Now the  $P$  nullcline proves to be the dividing line where the qualitative behavior of the graph changes to form a characteristic V shape.

#### Parameters and Model Variants

Given a fixed-model structure, the results obtained so far allow interesting predictions to be made for variations in the model parameters such as nutrient inflow and mortality/loss rate of the phytoplankton. From an ecological perspective, these parameters are important and clearly

vary over different systems. We have therefore summarized the effects of parameter changes on the model in table 1.

Despite the simplicity of the above model, the main results appear to be robust to structural changes. We extended our study of the model and replaced the Lotka-Volterra interaction terms that describe nutrient-phytoplankton dynamics with several other more complicated forms in an attempt to add realism. For example, Dugdale (1967) proposed Michaelis-Menten enzyme kinetics specifically to describe nutrient-phytoplankton interactions. The Michaelis-Menten equations are of the same form as the well-known Monod equations (see DeAngelis 1992) used, say, in the Droop equations, and they have formed the basis of a number of modeling studies intended to simulate phytoplankton blooms (e.g., O'Brien 1974). In addition, we examined the effects of including several other realistic features, both biological factors such as nutrient recycling and higher predation and physical factors such as sinking out of nutrients and phytoplankton into the water column. The more generalized model configuration has the following structure:

$$\begin{aligned} \dot{N} = & \text{input} - \text{uptake} - \text{loss} \\ & + \text{mixing} + \text{recycling}, \end{aligned} \quad (22)$$

$$\begin{aligned} \dot{P} = & \text{uptake} - \text{death} - \text{sinking} - \text{mixing} \\ & - \text{predation} - \text{recycling}. \end{aligned} \quad (23)$$

$$\begin{aligned} \dot{N} = & I - F(N, P) - qN + k(N_0 - N) + rP \\ \dot{P} = & F(N, P) - DP - (s + k)P - G(P) - rP \end{aligned} \quad (24)$$

$$F = \begin{cases} \frac{N}{a + N}P & \text{(Monod),} \\ \frac{N}{e + N} \frac{a}{b + cP}P & \text{(Edwards and Brindley 1996, 1999),} \end{cases} \quad (25)$$

$$G = \begin{cases} \frac{P}{b + P}Z, & \text{(Holling Type II),} \\ \frac{P^2}{\mu^2 + P^2}Z, & \text{(Holling Type III).} \end{cases} \quad (26)$$

In equations (26), the variable  $Z$  represents the zooplankton, which is held constant as a first approximation.

**Table 1:** Effect of parameter changes

Parameter change	Effect
An increase in effective nutrient inflow $I$	Increases the phytoplankton equilibrium $P^* = I - q$ . Has no effect on the nutrient equilibrium $N^* = 1$ . Has no effect on the threshold level $N_c = 1$ controlling the initiation of the bloom. Reduces the time $\hat{t}$ (eq. [A1]) at which the nutrients reach their maximum height $N_{\max}$ . In principal, this shortens the time it takes for nutrients to reach the threshold level $N = 1$ , at which the bloom is triggered, and also the time at which the peak of the bloom $P_{\max}$ occurs. Increases the peak of the nutrient buildup $N_{\max}$ (when $N_0 P_0 < N^* P^*$ ). Increases the peak of the phytoplankton bloom $P_{\max}$ .
Increasing the nutrient loss $q$	Gives rise to a second equilibrium $\tilde{P} = 0$ , $\tilde{N} = I/q$ that is unstable for $q < I$ . This equilibrium does not exist if $q = 0$ . Decreases the phytoplankton equilibrium $P^* = I - q$ . Slows down the triggering of the bloom due to delayed nutrient buildup, that is, $\hat{t}$ (eq. [A1]) is reduced. (Recall that the effective $I$ rescales according to eq. [15].) Decreases the peak of the nutrient buildup $N_{\max}$ (when $N_0 P_0 < N^* P^*$ ). Decreases the peak of the phytoplankton bloom $P_{\max}$ .
Spiral behavior	When $q < I(1 - I/4)$ (see fig. 5b), secondary blooms can arise as the trajectory spirals in the phase plane.

The model structure now closely resembles those given in several other recent food-web studies (Edwards and Brindley 1996, 1999). A full study of this system is beyond the scope of this article. However, it should be emphasized that the powerful techniques of nullcline analysis often makes it possible to understand the effects of each of these factors rapidly. For example, we examined a more “realistic” model in which the equations (4) are modified by incorporating Michaelis-Menten kinetics:

$$\begin{aligned}\dot{N} &= I - P \frac{N}{a + N} - qN, \\ \dot{P} &= P \frac{N}{a + N} - DP.\end{aligned}\quad (27)$$

We reanalyzed the above equations in detail with realistic parameter values taken from DeAngelis (1992, p. 49). The nullclines of the above model ( $\dot{N} = 0$ ,  $\dot{P} = 0$ ) when plotted in phase space are plotted in DeAngelis (1992, his fig. 3.4, p. 50) and are extremely similar to those of the original equations (4) (see fig. 3b), that is, with Lotka-Volterra terms. For this reason, the two models share many of the same dynamic features. Simulations reveal that there are no qualitative differences between the responses of the

above model to changes in  $P_0$  and  $N_0$  (e.g., in terms of  $P_{\max}$ ,  $N_{\max}$ , threshold behavior, nutrient buildup, etc.).

We also investigated several other interaction terms (e.g., the Holling-type interaction terms used in the Edwards and Brindley [1996, 1999]  $N$ - $P$ - $Z$  model) and confirmed that their behaviors are not substantially different from the simpler model of equations (4).

## Discussion

O'Brien (1974) developed one of the first successful models describing the dynamic properties of nutrient-phytoplankton interactions. Despite its simplicity, the model provides fascinating insights into many of the events occurring in the epilimnion of lakes and oceans. O'Brien (1974) suggests that the “most interesting property of the model is the consistent occurrence of population crashes during simulations. The shape of the curve describing these crashes markedly resembles spring phytoplankton pulses and the subsequent crashes which occur in many lakes and portions of the ocean” (O'Brien 1974, p. 136). Our study attempts to provide a general theoretical analysis of this phenomenon observed repeatedly in the many simulation models reported in the literature over the last dec-

ades (Patten 1968; Fasham et al. 1990; Truscott and Brindley 1994a, 1994b; Edwards and Brindley 1996, 1999).

The model described here demonstrates that nutrient-phytoplankton dynamics may be governed by a generic threshold effect, a possibility not yet discussed in the literature pertaining to simple aquatic models. That is, a critical buildup of nutrients is required before a phytoplankton bloom can be triggered. Such an effect has been referred to by limnologists (Lund 1950) as the Pearsall hypothesis (see also Pearsall 1932), but it is only poorly understood and is usually anecdotal. In Lake Kinneret, for example, there have been several years (in the late 1990s; data not shown in the time series) on record when, against all expectations, the annual *Peridinium* bloom strangely did not appear. In the Kinneret system and many other lakes, algal blooms are often regular events. However, blooms can also be sporadic and formed by transient events (Dickey et al. 1988; Lohrenz et al. 1992; Cloern and Jassby 1995). One interesting and not atypical study (Glover et al. 1988) demonstrated that only transient nanomolar changes in nitrate concentration in surface Sargasso Sea water were required for the formation of a nitrate-dependent bloom. This type of behavior, where a slight suprathreshold change in nutrients initiates bloom formation, is consistent with the threshold predictions described here.

Another interesting facet of the model lies in the propensity of the bloom to oscillate so that after the first major bloom there will be signs of a secondary smaller bloom. These secondary blooms can arise when  $q < I(1 - I/4)$ . Hence, the nutrient-phytoplankton trajectory spirals in phase space, as seen, for example, in the model time series of figure 3a. Secondary blooms are also to be found in time series of many other modeling studies (Evans 1988; Fasham et al. 1990; Franke et al. 1999) and have been observed in a number of natural systems (Lund 1950; Fasham et al. 1990; Jassby et al. 1992; Ross et al. 1993).

In real systems, the intensity of blooms are often difficult to predict in advance. Some of the results found here give us an indication as to why this might be so. In particular, we have demonstrated that bloom intensity does not necessarily increase with an increase in initial nutrients or

phytoplankton cells—something that a linear systems paradigm might lead us to expect. With higher initial conditions, it becomes possible to trigger the bloom more rapidly; however, this means that nutrients have less chance to build up, and the bloom itself is thus less productive. This effect is another outcome of the model's intrinsic threshold, which controls the timing of the bloom.

The model also gives insights concerning the unpredictable timing of the sudden crash observed in many phytoplankton blooms. As O'Brien (1974) mentions, although zooplankton have often been implicated as the agents responsible for crashes in many spring and summer phytoplankton blooms, the model shows that the key factor is more likely to be the large-scale reduction of nutrients used up in supporting the phytoplankton bloom. As soon as  $N$  drops below  $N_c = 1$ , the model predicts that the phytoplankton crash will be initiated. Zooplankton may in fact increase the death rate of phytoplankton, thus serving to speed up the occurrence of the phytoplankton crash, but the crash in itself could well be inevitable with or without the presence of zooplankton. In the English lakes, Lund (1950) and Macan (1970) argue similarly: "Grazing by animals has no appreciable effects on the fluctuations in [phytoplankton] numbers" (Lund 1950, p. 31).

We are currently investigating a suite of oscillatory, excitable, and chaotic bottom-up phytoplankton-nutrient models in order to understand the more complicated temporal dynamics seen in empirical data such as that of the river Danube and Lake Kinneret.

### Acknowledgments

We thank T. Berman, N. Cohen, and W. Eckert for their contributions and many suggestions. V. Gerhardt, U. Pollinger, and T. Zohary kindly allowed us to make use of their field data collected at Lake Kinneret and the river Danube. We gratefully acknowledge support from the James S. McDonnell Foundation and the European Union Fifth Framework grant "Phytoplankton On-Line." B.B. was supported by the German Volkswagen Stiftung.

## APPENDIX A

Here, we estimate the bloom height  $P_{\max}$  for the case when initial conditions are such that  $N_0 P_0 \ll N^* P^* = I$ . The  $P_{\max}$  value is estimated in a two-step procedure. In the first step, an approximation is made for the maximum nutrient level,  $N_{\max}$ , attained in the initial phase of nutrient buildup. In the second step, we use this peak nutrient level as an initial condition for model equations (5) where we can assume  $I = 0$ . The peak height of the bloom can then be estimated from the previous analytic prediction, equation (8).

*Step 1.* Let  $t = \hat{t}$  be the time at which the nutrients attain their maximum levels  $N_{\max}$ , and thus  $\dot{N} = 0$ . Define the phytoplankton levels at this time as  $\hat{P} = P(\hat{t})$ . Since  $\dot{N} = 0$ , clearly  $\hat{P} = I/N_{\max}$ . Solving equation (17) for  $t = \hat{t}$  and taking the maximal root (which is the only consistent solution) gives

$$\hat{t} = \frac{1 - N_0 + \sqrt{(N_0 - 1)^2 + 2I \ln\left(\frac{I}{N_{\max} P_0}\right)}}{I}. \quad (\text{A1})$$

Thus, a good approximation for  $N_{\max} \simeq N_0 + I\hat{t}$  can be obtained by solving

$$N_{\max} = f(N_{\max}) = 1 + \sqrt{(N_0 - 1)^2 + 2I \ln\left(\frac{I}{N_{\max} P_0}\right)} \geq 1. \quad (\text{A2})$$

This transcendental equation may be solved using the iterated Newton-Raphson scheme:

$$N_{\max}^{i+1} = f(N_{\max}^i), \quad i = 0, 1, 2, \dots \quad (\text{A3})$$

At equilibrium,  $N^* = N_{\max}^{i+1} = N_{\max}^i$ . Clearly, the fixed point of the difference equation must also be the solution to equation (A2).

In iterating (A3), a reasonable first approximation for  $N_{\max}$  is its lower bound (see eq. [A2])  $N_{\max}^0 = 1$ . A better approximation for  $N_{\max}$  is thus  $N_{\max}^1$ , the first iterate of the map (A3), namely,

$$N_{\max} \approx N_{\max}^1 = 1 + \sqrt{(N_0 - 1)^2 + 2I \ln\left(\frac{I}{P_0}\right)}. \quad (\text{A4})$$

Numerical simulations show that this estimate for  $N_{\max}$  gives excellent predictions and certainly captures the main trend we seek. (We have found that the Newton-Raphson scheme converges over the relevant parameter ranges of interest. Convergence is ensured if  $|f'(y)| < 1$ , which can be shown to hold when  $I$  is relatively small, that is,  $I < 2$  as a first approximation.)

*Step 2.* The bloom height  $P_{\max}$  may now be estimated as follows. We take  $\bar{N}_0 = N_{\max}$  and  $\bar{P}_0 = \hat{P} = I/N_{\max}$  as initial conditions for equations (5), where the ensuing bloom dynamics may be reasonably approximated by assuming  $I = 0$ . The  $P_{\max}$  value may then be approximated directly by applying equation (8). We have found that an even better approximation may be obtained by taking  $\bar{N}_0 = N_{\max}$  and  $\bar{P}_0 = \hat{P} = P^* = I$  as initial conditions since now  $\bar{N}_0 \bar{P}_0 > N^* P^* = I$ , and this brings us even further into the range for which the approximation  $I = 0$  is valid. By equation (8), the bloom height may be approximated as

$$P_{\max} = I + N_{\max} - 1 + \ln\left(\frac{1}{N_{\max}}\right).$$

## APPENDIX B

Here, we provide further details as to why  $P_{\max}$ , when plotted as a function of the initial conditions  $P_0$  or  $N_0$ , has a characteristic V shape, as seen in figure 6. Our aim is to explore equations (A2) and (20) for specific initial values. Consider the predictions for  $N_{\max}$  and  $P_{\max}$  in dependence of  $N_0$  for the special choice of  $P_0 = 1$ . (A similar analysis holds for the case when  $N_0 = 1$  is fixed and  $P_0$  is free to vary.) Now the equations simplify to

$$N_{\max} = 1 + |N_0 - 1|, \quad (\text{B1})$$

$$P_{\max} = \begin{cases} I + 1 - N_0 + \ln\left(\frac{1}{2 - N_0}\right), & N_0 < 1, \\ I + N_0 - 1 + \ln\left(\frac{1}{N_0}\right), & N_0 > 1. \end{cases} \quad (\text{B2})$$

The derivative of  $P_{\max}$  in equation (20) with respect to  $N_0$  is

$$\frac{dP_{\max}}{dN_0} = \begin{cases} -1 + \frac{1}{2 - N_0} < 0, & N_0 < 1, \\ 1 - \frac{1}{N_0} > 0, & N_0 > 1. \end{cases} \quad (\text{B3})$$

In this way, we see that the bloom height  $P_{\max}$  is a decreasing function of  $N_0$  for  $N_0 < 1$ ; yet once  $N_0 > 1$ ,  $P_{\max}$  increases with  $N_0$ . Thus,  $N_0 = 1$  proves to be the dividing line between decreasing and increasing bloom height when the initial condition  $N_0$  is varied.

We now show that the V shape is a generic phenomenon in this plankton model by solving equations (5) when nutrient levels are slightly perturbed from equilibrium  $N^* = 1$ . We take advantage of the fact that nutrient levels typically stay close to  $N^* = 1$ , whereas plankton levels change dramatically. This allows us to approximate the first equation of (5) as

$$\dot{N} = -NP \approx -P. \quad (\text{B4})$$

Using equations (5), we obtain  $dP/dN = 1 - N$ , which can be integrated exactly to obtain

$$(P - P_0) = (N - N_0) - \frac{1}{2}(N^2 - N_0^2). \quad (\text{B5})$$

Therefore, in this approximation, the trajectory follows a parabola with a phytoplankton maximum at the threshold level  $N_c = 1$ .

We can calculate  $P_{\max}$  similar to the derivation of (20) by evaluating equation (B5) at the threshold value  $N_c = 1$  and taking the special initial values  $\bar{P}_0 = I$  and  $\bar{N}_0 = N_{\max}$ . Thus, we obtain the new formula for  $P_{\max}$ :

$$P_{\max} = \bar{P}_0 + 1 - \bar{N}_0 - \frac{1}{2}(1 - \bar{N}_0^2) = I + \frac{1}{2}(N_{\max} - 1)^2. \quad (\text{B6})$$

Using equation (A2) for  $N_{\max}$ , we finally obtain the simple formula for the maximal phytoplankton levels:

$$P_{\max} = I + \frac{1}{2}\left[(N_0 - 1)^2 + 2I \ln \frac{I}{P_0}\right]. \quad (\text{B7})$$

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Associate Editor: Donald L. DeAngelis