



## Bottom–Up Excitable Models of Phytoplankton Blooms

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A simple nutrient–phytoplankton model is used to explore the dynamics of phytoplankton blooms. The model exhibits excitable behaviour in the sense that a large scale outbreak can only be triggered when a critical nutrient threshold is exceeded. The model takes into account several features often neglected but whose combined effect proves very important: (i) rapid nutrient recycling associated with the microbial loop and patch formation; (ii) self-shading; and (iii) a bottom–up approach, whereby nutrient levels are responsible for both the triggering and the demise of the bloom. Although the literature is replete with studies of ‘top–down’ models in which zooplankton grazing control the triggering and demise of the bloom, bottom–up models are nevertheless appropriate in many circumstances. We provide a full mathematical investigation of the effects of these three different features in an excitable system framework.

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### 1. INTRODUCTION

One of the striking features associated with many phytoplankton populations is the occurrence of rapid and massive bloom formations. Such events are characterized by a dramatic sharp rise in algae population numbers of up to several orders of magnitude (Beltrami and Carroll, 1994) followed shortly afterwards by a sudden collapse, whereby the phytoplankton population returns to its original low level as if nothing had ever occurred. Early records of the sudden appearance of blue–green algae date back to at least 1183 where they were described as thick films or scums on the surface of an English lake (Griffiths, 1939; Goldman and Horne, 1983). But phytoplankton blooms are a widespread phenomenon present in rivers, lakes and oceans spanning the globe. There is no single generic type of phytoplankton bloom. Some blooms appear regularly every year (e.g., the classic Spring blooms), while others occur in an erratic fashion and may be sporadic both in time and space.

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The appearance of a bloom can have devastating implications. Many phytoplankton species are toxic, and their appearance in large numbers have the potential to damage or kill higher organisms such as zooplankton, shellfish, and fish as their toxins mobilize up through the foodchain, sometimes leading to human poisoning via ingestion of contaminated food sources. Given the impact of the many different types of phytoplankton blooms, it is of interest to develop modelling approaches for understanding the mechanism which governs their dynamics.

Truscott and Brindley (1994a,b) made significant progress in this direction by using a nonlinear ‘excitable systems’ appropriate for red-tide blooms. Their model rests on the assumption that phytoplankton are controlled by zooplankton grazers and could, with a perturbation, reach an ‘excited’ state thereby initiating a bloom. This is often referred to as a ‘top–down’ approach since the bloom is very much controlled by zooplankton grazers. Ecologically, however, ‘top–down’ models are in many cases inadequate as a general description of phytoplankton blooms. For example, zooplankton are hardly expected to graze many toxic red-tide algae. Similarly other types of algae have spines, cellulose cell walls and/or are large in size which protects the phytoplankton from being grazed. Much work by the ‘Leeds group’ (Truscott and Brindley, 1994a,b; Edwards and Brindley, 1996, 1999; Pitchford, 1997; Clothier and Brindley, 1999; Pitchford and Brindley, 1999) has been devoted to examining the robustness of the excitable paradigm as the ‘top–down’ mechanism underlying algae outbreaks. Here we try and extend their work by showing how the concept can be applied to ‘bottom–up’ schemes where nutrients control the initiation and demise of the bloom.

## 2. THE EXCITABLE BOTTOM–UP MODEL

A general model for describing nutrient–phytoplankton growth is given by the equations:

$$\begin{aligned}\dot{N} &= I - g(N)P - e(N) \\ \dot{P} &= g(N)P - Pf(P),\end{aligned}\tag{1}$$

where the variable  $N$  describes the concentration of the limiting nutrient in units of (mg) solute ( $\text{m}^{-3}$ ) water and  $P$  the phytoplankton biomass in units of (kg) solute ( $\text{m}^{-3}$ ). It is assumed that external nutrient inputs flow into the system at a constant rate  $I$  in units of ( $\text{mg day}^{-1} \text{m}^{-3}$ ), and that the time  $t$  is measured in days. The *per capita* phytoplankton uptake rate of nutrients is governed by the function  $g(N)$ , for which several choices are possible. For example: (a)  $g(N) = N$ . In this case the gross uptake rate  $g(N)P$  is given by the usual Lotka–Volterra bilinear term ( $NP$ ). Nutrients and phytoplankton are treated as though part of an ‘interacting-particle system’ (Durrett and Levin, 1994) where the probability of phytoplankton utilizing a nutrient is determined by the product of their relative abundances

(or proportional probabilities). (b)  $g(N) = N/(k + N)$ . This is the classical Michaelis–Menten uptake term (Dugdale, 1967; DeAngelis, 1992). Note that for  $N \ll k$  the gross uptake  $g(N)P \approx NP$  and thus approximates the Lotka–Volterra interaction. However, for large  $N \gg k$ , the *per capita* uptake function  $g(N)$  saturates reflecting the fact that there is some upper ceiling constraining the uptake of a single phytoplankton cell when surrounded by an abundance of nutrients.

The model (1) assumes that nutrients are lost from the water column at the rate  $e(N)$ . The function  $f(P)$  represents the *per capita* mortality rate of the phytoplankton and also subsumes the rate at which these cells sink out of the water column.

In perhaps its simplest incarnation, the nutrient–phytoplankton model would have the following form:

$$\begin{aligned}\dot{N} &= I - \alpha NP \\ \dot{P} &= \beta NP - Pf(P),\end{aligned}\tag{2}$$

where  $\alpha$  and  $\beta$  are constants and interactions are of the Lotka–Volterra type. We have assumed that the nutrient loss rate is negligible [ $e(N) = 0$  in equation (2)] which might typically represent a tightly recycling and stratified system where nutrients are sealed in the epilimnion. Although minimal in structure, the model makes it possible to investigate the main ideas behind excitable dynamics found in more complex systems. Typically the *per capita* mortality rate  $f(P)$  should be constant [i.e.,  $f(P) = \gamma$ ] representing the usual density independent mortality and/or sinking out of the water column.

When zooplankton grazes upon phytoplankton it is usual to model  $f(P)$  with a Holling type II or III functional form [i.e.,  $f(P) = Z/(k + P)$ ,  $f(P) = (PZ)/(k + P^2)$  with  $Z$  representing a constant zooplankton presence]. Pitchford (1997) showed that a nutrient–phytoplankton model with Holling type III term (representing zooplankton grazing) and a term describing self-shading effects can lead to excitable behaviour. However, we refrain from using such functional forms because our main concern is to model blooms of inedible algae, making predator interactions irrelevant in our models.

In formulating the model, we also intend to incorporate two further realistic features:

- (a) *Patch formation and recycling*: We suppose that there is some critical level of phytoplankton biomass at which patch formation becomes prominent (Mitchell *et al.*, 1985). As is well known, such aggregation leads to a more efficient microbial loop and nutrient cycling in general (Goldman, 1984).
- (b) *Self-shading*: Large phytoplankton levels significantly reduce the amount of light penetrating the water column. Without light, phytoplankton at deeper levels have difficulties surviving (Huisman and Weissing, 1994; Kirk, 1994).

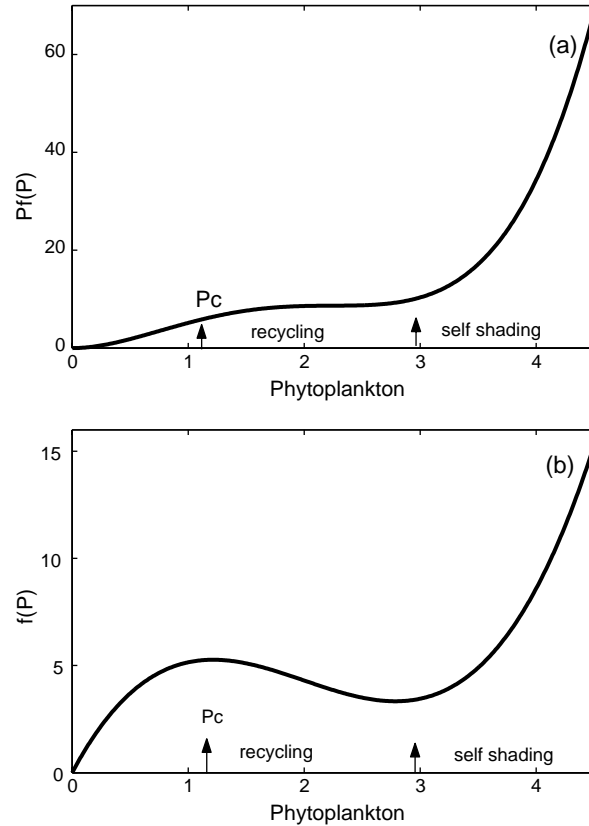


Figure 1. (a) The gross loss function  $Pf(P)$  plotted as a function of  $P$  where  $f(P) = (P - a)^3 - bP + c$  ( $a = 2$ ,  $b = 1.85$  and  $c = 8$ ). 'Arrows' indicate critical values of  $P$  where recycling and then self-shading take effect. (b) The *per capita* loss function  $f(P)$  plotted as a function of  $P$ .

As a first approximation these features might be implemented, at least in a qualitative manner, by appropriate modification of the *gross* loss function  $Pf(P)$ . Consider, for example, the function  $Pf(P)$  plotted as a function of  $P$  in Fig. 1(a). One sees that the curve is monotonic increasing over the full range and reasonably linear for low  $P$ , thereby capturing the usual density independent mortality effects. At intermediate levels of  $P$ , the gradient of the curve is less steep, reflecting that patch formation and its attendant recycling keeps the phytoplankton growing in the water column for a longer time. Although this is a first approximation, we later explicitly show that it is indeed reasonable. Finally, for larger values of  $P$  the effects of self-shading become more prominent and the mortality rate increases accordingly. When these effects are combined together, the *net per capita* growth rate  $f(P)$  resembles a cubic curve as shown in Fig. 1(b). The cubic character is an important factor that endows the system with excitability, as we shall see below.

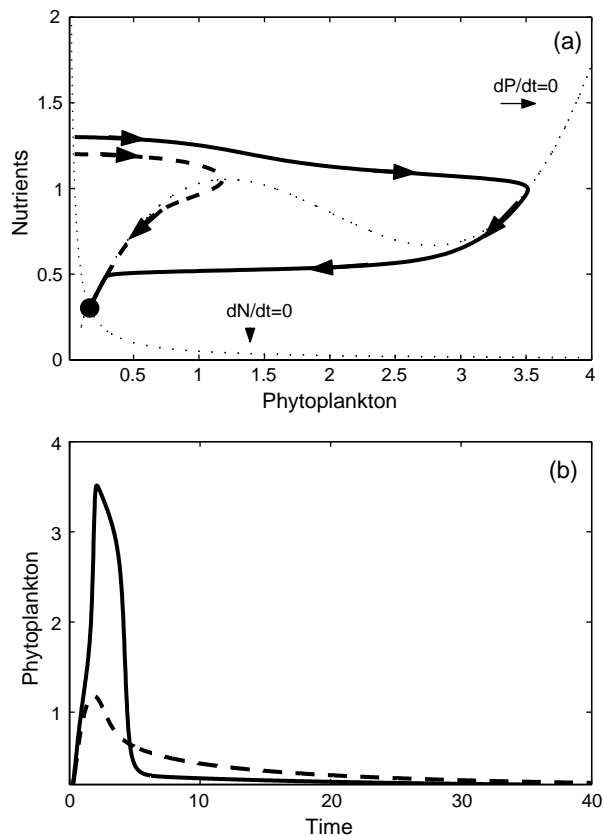


Figure 2. (a) Phase-plane diagram of the phytoplankton bloom. The arrows indicate the direction that the model trajectory of equation (2) ‘flows’ in the phase-plane. The  $N$ - and  $P$ -nullclines are indicated as dotted lines. The  $P$ -nullcline divides the  $N$ - $P$  phase-plane into two. In the region of the phase-plane that lies to the top/bottom of the  $P$ -nullcline,  $\dot{P} > 0$ ,  $\dot{P} < 0$ , and phytoplankton grows/declines respectively. The threshold of the excitable system can be seen by comparing the dashed and solid lines. If initial nutrient levels are below threshold the trajectory is attracted to the equilibrium (marked by the circle) without triggering a bloom. If initial nutrient levels are above threshold the trajectory snaps to the right side and encircles the phase-plane giving rise to the bloom. Parameters are:  $\alpha = 0.1$ ,  $\beta = 5$ ,  $l = 0.005$ ,  $a = 2$ ,  $b = 1.85$ ,  $c = 8$ . The initial conditions for the case of no bloom are:  $N_0 = 1.2$ ,  $P_0 = 0.05$  and for the bloom  $N_0 = 1.3$ ,  $P_0 = 0.05$ . (b) Plots of the phytoplankton dynamics in the time domain for above threshold initial conditions (solid line) and below threshold initial conditions (dashed line).

We make use of the phase-plane (i.e., plotting curves of  $N$  against  $P$ ) to help understand the dynamics of equation (2). The  $N$ - and  $P$ -nullclines (the manifolds on which the derivatives  $dN/dt = 0$  and  $dP/dt = 0$ ) provide a guide to the model’s flow in the phase-plane (see Fig. 2 legend for details). The  $P$ -nullcline is given by the equation  $N = f(P)$  which as discussed above, we suppose is qualitatively cubic in shape, as in Fig. 2(a). The  $N$ -nullcline is hyperbolic having

the form  $N = I/\alpha P$ . Using phase-plane simulations (Fig. 2) we illustrate how the excitable mechanism works for model equation (2). When the initial level of nutrients is low (below threshold) the trajectory is attracted directly to the equilibrium (the point where the two nullclines cross) without triggering a phytoplankton bloom. If however the initial level of nutrients is above threshold, the trajectory follows a solution in phase space that is of a quite different nature and is governed by the model's different slow and fast time-scales. Once above threshold, the trajectory makes a large excursion in phase space by rapidly snapping to the right side of the  $P$ -nullcline, dropping slowly down the nullcline, quickly snapping back to the left-hand side of the  $P$ -nullcline and then eventually reaching equilibrium. The cubic shape of the  $P$ -nullcline facilitates the excitability. Thus when the trajectory first snaps to the  $P$ -nullcline, this gives rise to a full-scale bloom. The height of the bloom is set by the separation of the turning points associated with the cubic nullcline. In Fig. 2(b) the dynamics of the model with  $f(P)$  as in Fig. 1 are plotted as a function of time. In the time domain it is possible to see once again the clear differences between a full developed bloom [solid line, Fig. 2(a) and 2(b)] and the nonbloom [dashed line, Fig. 2(a) and 2(b)].

Until now we have used the term 'excitable system' in a rather loose way. In fact there is no single formal definition. By convention, the main mathematical features characterizing 'excitability' within the context of the phytoplankton bloom example are:

- (i) The existence of a threshold; when the nutrients (i.e., the triggering variable) are below a fixed threshold level the bloom will not appear, while if above threshold an outbreak will take place.
- (ii) The bloom is very rapid compared to changes in the nutrient levels.
- (iii) Phytoplankton abundance may be associated with two states: one that is very low with almost no growth, and the other that is associated with the bloom maximum itself. The latter level is fixed by the cubic nullcline [see Fig. 2(a)] ensuring that the variability in the peak height of bloom events is minimal.

### 3. A BLOOM MODEL WITH EXPLICIT RECYCLING

The above model, and in particular the function  $f(P)$ , might appear to be somewhat contrived, or even pathological, from a biological perspective. Here, we study a more natural model that explicitly includes nutrient recycling and patch formation, making clear the relevance and generality of the previous example. We focus on nutrient recycling because in recent times there has been a much greater appreciation of the role of the microbial loop whereby bacteria rapidly remineralize and recycle large fluxes of material and energy through the aquatic foodweb (Azam *et al.*, 1983). Previously it was assumed that nearly all primary production passes through a vertical food chain from phytoplankton to grazing metazoans and ultimately to fish. However, this picture of a linear food chain is vastly

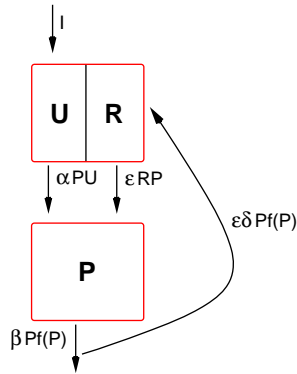


Figure 3. A schematic flow diagram of model equation (3) which describes the influxes and outfluxes between the different compartments ( $U$  = unrecycled nutrients;  $R$  = recycled nutrients;  $P$  = phytoplankton).

simplified and often misleading. Instead, it is now understood that some 50% of phytoplankton cell constituents may simply bypass the traditional food chain and pass through a complex ‘microbial loop’ in which nutrients are rapidly recycled. Thus a large portion of phytoplankton may be diverted, either directly or indirectly, into microbial pathways rather than passing up to higher trophic levels (Stone and Weisburd, 1992; Stone and Berman, 1993). Seen in this way, microbial communities can greatly enhance nutrient recycling at the very base of the food web. Goldman (1984) likened the intense microbially mediated recycling to a rapidly turning ‘spinning wheel’ with short time-scales ( $<1$  day) for nutrient turnover with minimal losses. As Goldman (1984) writes with regard to the spinning wheel hypothesis: ‘One simple way to reconcile the seemingly incompatible concept that phytoplankton may be growing fast in oligotrophic waters is to suggest that small amorphous aggregates of organic matter in the water column represent self-contained microhabitats . . . . Each aggregate then is a floating ‘oasis’ in the desert, serving as a life-support system for its resident population of autotrophs and heterotrophs’. As is currently understood, rapid recycling is only plausible with the development of microbial consortia consisting of phytoplankton, bacteria and protozoa (Azam *et al.*, 1990). The assembly of such a consortia is density dependent controlled by chemotaxis (Mitchell *et al.*, 1985).

In order to explicitly model the effects of microbially enhanced recycling we divide the nutrient pool into two different forms: those that have at some point been recycled ( $R$ ) and those that are unrecycled ( $U$ ). Using Fig. 3 as a guide, the new model becomes:

$$\begin{aligned}\dot{U} &= I - \alpha U P \\ \dot{R} &= \epsilon P(\delta f(P) - R) \\ \dot{P} &= \beta P(\alpha U + \epsilon R - f(P)).\end{aligned}\tag{3}$$

Now the equation for  $R$  represents the recycling of nutrients enhanced via the microbial loop. The actual speed of the recycling is controlled by the term  $\epsilon$ . In the model we suppose recycling can only occur when the phytoplankton ( $P$ ) has attained a critical biomass density ( $P_c$ ). Thus we take the term  $\delta(P)$  controlling fluxes from phytoplankton to recycled nutrients as:

$$\delta = \begin{cases} c, & P \geq P_c \\ 0, & P < P_c \end{cases} \quad (4)$$

where  $c$  is a constant. Our rationale for this ‘switch’ is due to the fact that patch formation is classically understood to be a threshold process. The classical KiSS model [see Martin (2003), Slobodkin (1999) for reviews] predicts that for a circular patch to survive its radius,  $l$ , must exceed the critical value  $L_{\text{KiSS}}$ .

Although the function used here might be seen as a sudden switch, the main results remain unchanged should the switching effect be made gentler. This can be achieved, for example, by using a Holling type III function with  $\delta = \frac{P^2}{k+P^2}$  where  $k$  is a constant. Detailed numerical simulations show that the Holling type III functional form does not alter the model’s qualitative behaviour. More specifically all three criteria for excitability described above hold. However to simplify the mathematical analysis from here on we use equation (4) rather than the Holling type III function.

Phytoplankton growth ( $\dot{P}$ ) itself depends on the uptake of both recycled and unrecycled nutrients (controlled by  $\beta$ ), and is lost through death or falling out of the water column at a rate ( $f(P)$ ) given by:

$$f(P) = \gamma_1 P + \gamma_2 \quad (5)$$

where  $\gamma_1$  and  $\gamma_2$  are constants. The term  $\gamma_1 P$  should be interpreted as the growth restriction or self limitation imposed by shelf-shading, while  $\gamma_2$  is the usual density independent *per capita* mortality rate.

The number of parameters in the above equations can be reduced further by taking the scaling  $P' = \alpha P$ ,  $U' = \alpha U$ ,  $R' = \epsilon R$ ,  $I' = \alpha I$ ,  $\gamma_1' = \gamma_1/\alpha$ ,  $\theta = \epsilon/\alpha$ ,  $c' = \epsilon c$ ,  $P_c' = \alpha P_c$ ,  $f'(P') = \gamma_1' P' + \gamma_2$ . After dropping dashes the equations reduce to:

$$\begin{aligned} \dot{U} &= I - UP \\ \dot{R} &= \theta P(\delta f(P) - R) \\ \dot{P} &= \beta P(U + R - f(P)). \end{aligned} \quad (6)$$

Simulations of the above model show that there are two qualitative different scenarios which need to be distinguished. As Fig. 4(a) and 4(b) reveals, for the same initial phytoplankton level  $P_0$ , these scenarios depend only on the initial nutrient level  $N_0$ , namely

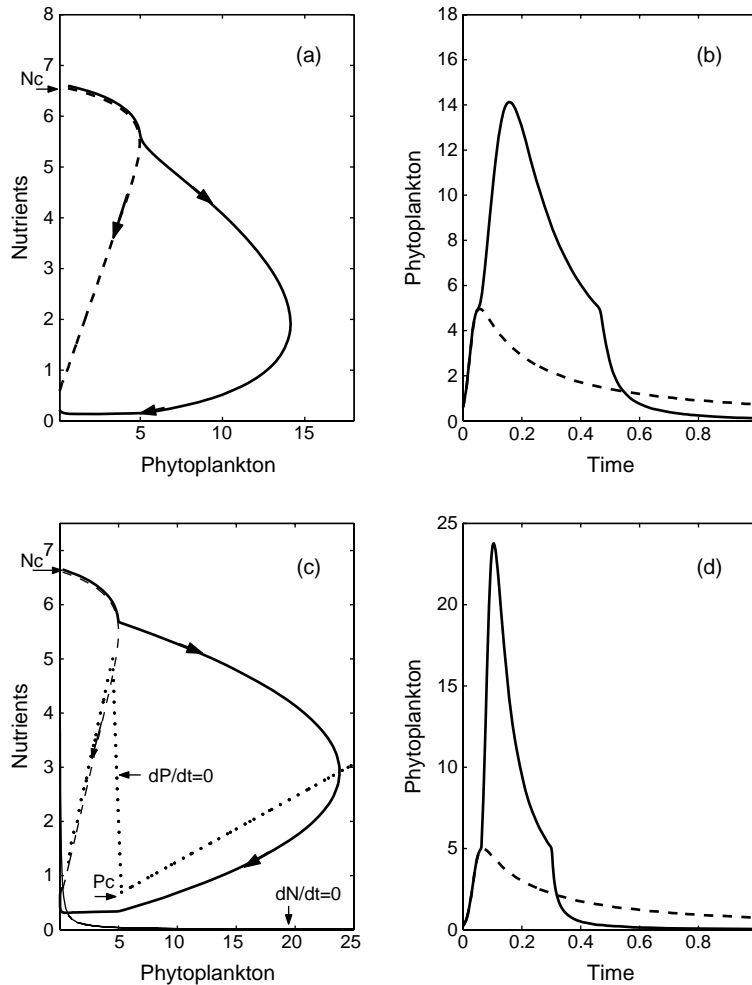


Figure 4.  $NP$ -phase-plane and phytoplankton time series for two different cases (a, b) the full **URP** system given by equation (3) with parameters ( $\alpha = 1, \beta = 15, \gamma_1 = 1, \gamma_2 = 0.5, P_c = 5.0, I = 0.2, c = 0.11, \epsilon = 8$ ). Below threshold initial conditions (dotted line) are:  $N_0 = 6.55, P_0 = 0.6, R_0 = 0$ . Above threshold initial conditions (solid line)  $N_0 = 6.6, P_0 = 0.6, R_0 = 0$ . (c, d) The two level reduced system **UP** of equation (7). Note that parameters and initial conditions are identical to that in Fig. 4(a) and 4(b).

- (i) if  $N_0 > N_c$  a full-scale phytoplankton bloom develops (solid line); while
- (ii) if  $N_0 < N_c$  there is no bloom (dashed line)

where  $N_c$  is the critical nutrient threshold.

This threshold effect can be understood as follows. If initial nutrient levels are large enough phytoplankton are able to attain the critical phytoplankton density  $P_c$ . At this point the microbial loop ‘kicks’ into action and rapid nutrient recycling begins. As a consequence recycled nutrients are injected into the phytoplankton compartment enhancing phytoplankton growth and resulting in a full-scale

bloom. On the other hand if initial nutrient levels are below  $N_c$ , phytoplankton levels fail to ever reach  $P_c$ . In such a case, the phytoplankton grow until they attain levels which the nutrient pool  $U$  can no longer sustain. Phytoplankton levels then start to decline to equilibrium without a bloom ever being triggered.

It is possible to show more formally why equation (6) exhibits seemingly excitable behaviour. The first order differential equation (6) can be approximated by a system of two first order ODE's, by taking advantage of the fact that the recycling process works at a fast time-scale (i.e.,  $\epsilon \gg 1$ ) relative to the nutrient uptake. As such, we take the steady-state solution of  $\dot{R} = 0$  which is given by  $R = \delta f(P)$ , and plug this into the equation for  $\dot{P}$ . This leaves two equations:

$$\begin{aligned}\dot{U} &= I - UP \\ \dot{P} &= \beta P(U + \delta f(P) - f(P))\end{aligned}\quad (7)$$

where again

$$\delta = \begin{cases} c, & P \geq P_c \\ 0, & P < P_c. \end{cases}\quad (8)$$

The  $U$ - and  $P$ -nullclines of equation (7) are given by:

$$P = \frac{I}{\alpha U}\quad (9)$$

$$U = \begin{cases} f(P)(1 - c), & P \geq P_c \\ f(P), & P < P_c \end{cases}\quad (10)$$

and plotted in Fig. 4(c). The  $P$ -nullcline (dotted line) bears some resemblance to a piece-wise linear approximation to a cubic, and phase-plane serves as the origin of the model's excitable behaviour. Once phytoplankton densities exceed  $P_c$  the effective nullcline changes from the left-hand branch to the right-hand branch as seen in Fig. 4(c). Biologically at this switching point the 'spinning wheel' is turned on and rapid recycling begins. The recycled nutrients fuel the phytoplankton which respond by rapid growth and a full-scale bloom develops. The  $P$ -nullcline controls both the triggering of the bloom ( $P > P_c$ ) and the maximum plankton levels (i.e., the trajectories are confined in phase space by cubic nullclines which set bounds to the amplitude of the bloom).

Fig. 4 allows a direct comparison of the original system of equation (3) with the reduced two equation system [equation (7)]. From the phase-plane [Fig. 4(a) and 4(c)] and the time series [Fig. 4(b) and 4(d)], it is clear that the behaviour of the two systems is not qualitatively different.

#### 4. DISCUSSION

The excitable  $N$ - $P$  bloom models described above belong to a class of simplified ecological models (Beltrami, 1989; Truscott and Brindley, 1994a,b;

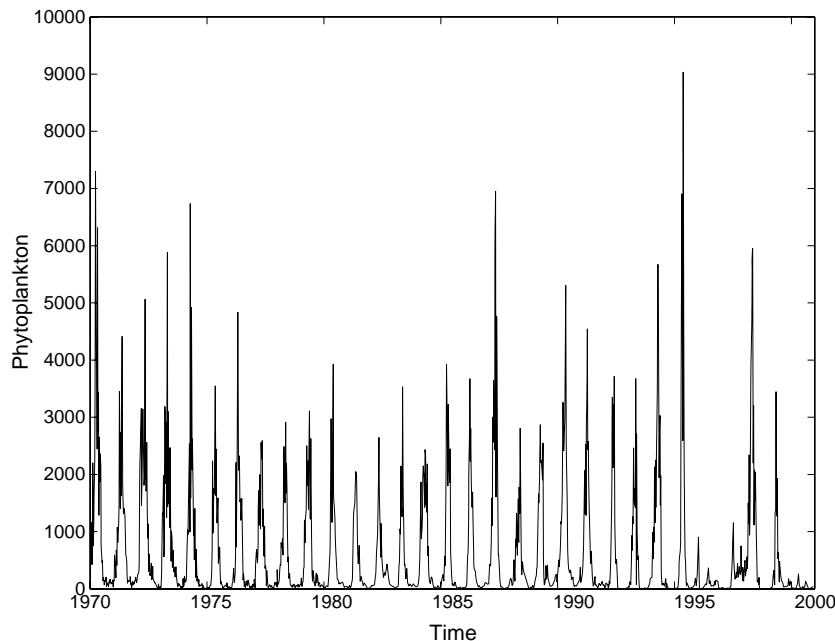


Figure 5. Time series of annual *Peridinium gatunense* blooms in Lake Kinneret, Israel. Previous to 1996 the bloom occurred annually. However, from 1996 until 2001 the bloom often failed to trigger. Data courtesy of Utza Pollinger and Tamar Zohary.

Huppert *et al.*, 2002) which aim at understanding the processes and mechanisms leading to phytoplankton outbreaks. The excitable mechanism is particularly attractive for modelling phytoplankton outbreaks because of the distinctive **threshold mechanism**. The threshold explains in simple terms how very small differences in initial nutrient levels can determine if a bloom will trigger or not. This characteristic perhaps gives insights into the limnological enigma of why blooms are sometimes so difficult to predict. For example, at Lake Kinneret, Israel, the regular long-term annual Spring bloom suddenly failed to appear in 1996, 1997 and 2000 (see Fig. 5). This motivated intense scientific research activity (Sukenik *et al.*, 2002), but as yet it is still difficult to explain why the bloom mysteriously failed to appear in some years. However, if the bloom were controlled by a threshold mechanism, small changes in nutrient levels can have enormous influence on the triggering of bloom events. Such small shifts in nutrient levels might be extremely difficult to detect in practice, and therefore explain why limnologists may have overlooked them. Yet the concept has been anecdotal amongst limnologists for decades now, and has on occasion even been identified. For example, some seventy years ago Pearsall (1932, p. 245), in his landmark studies of phytoplankton blooms in the English Lake district, provides one of the first 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  $0.5 \text{ mg l}^{-1}$ ’.

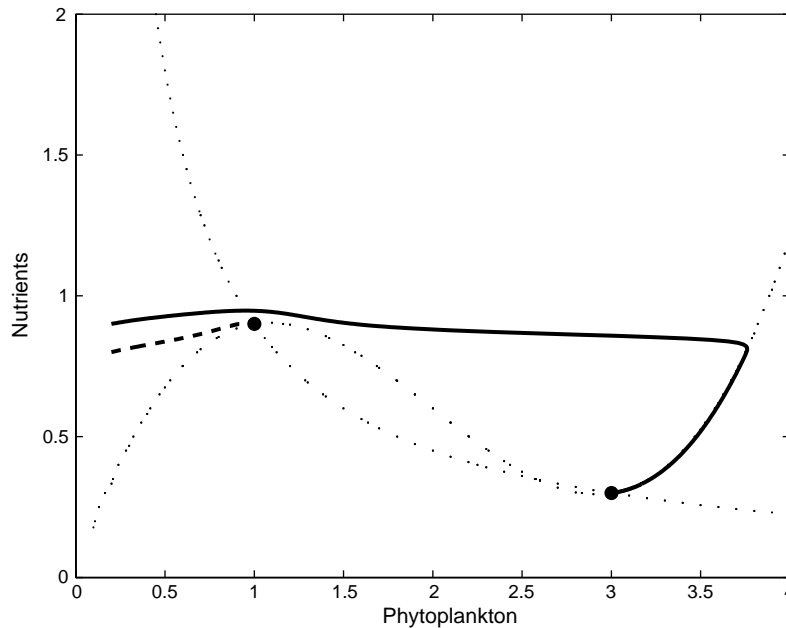


Figure 6. The  $N$ - and  $P$ -nullclines are indicated as dotted lines while the trajectory is a solid line. The two stable equilibria are notated by solid circles at the intersection of the nullclines. Different initial conditions lead to different equilibria solutions. Parameters:  $\alpha = 0.1$ ,  $\beta = 5$ ,  $I = 0.005$ ,  $a = 2.0$ ,  $b = 2.5$ ,  $c = 8$  using equation (2) and  $f(P)$  as in Fig. 1 (legend).

The nonlinearity of the model has many other important implications. According to a linear systems approach, a gradual and continuous increase in nutrient loadings of a water body is expected to result in a continuous increase in productivity. However, the model presented here can have drastic switches due to the presence of intrinsic nonlinearities. This can be seen as follows. Fig. 2(a) makes clear that the model nullclines cross at a single point and there is thus only one equilibrium state. Under higher nutrient loadings however, the nullclines for equation (2) with increased  $I$  appear as in Fig. 6. Now the  $N$ -nullcline cuts the  $P$ -nullclines at three different points and there are three equilibria: two which are stable separated by an equilibrium that is unstable (see Fig. 6, legend). There are two alternative stable states where phytoplankton densities are either at high or low population levels. In such a case the equilibrium to which the system is attracted depends on the initial conditions. This is consistent with the recent findings of Scheffer *et al.* (2001) who investigated human-induced eutrophication in shallow lakes. They found that ‘water clarity often seems to be hardly affected by increased nutrient concentrations until a critical threshold is passed, at which the lake shifts abruptly from clear to turbid’. In their review, Scheffer *et al.* (2001) argue that many ecosystems are bistable and changes in environmental conditions can shift the system from one equilibrium to another. As we

have shown, this could well be expected if the system nullclines are cubic-like in form.

Entering the 21st century water quality has become one of the most crucial environmental issues on the scientific agenda. Lakes and rivers are exposed to increasing anthropogenic inputs and higher nutrient loadings. While we might expect such loadings to increase productivity, simple ecological models show that the outcome could quite easily be worse than intuition predicts. In the presence of threshold phenomena (May, 1977), minimal changes in external nutrient loading could lead to sudden phytoplankton bloom events or abrupt eutrophication shifts, or both. This qualitative behaviour is predicted by simple nutrient–phytoplankton models and also observed in numerous ecosystems. Water resource managers are facing enormous difficulties in conserving the quality of existing water bodies quality in order to keep it usable for drinking and tourism. As Anderson (1995) writes ‘few people seem to like swimming in blue–green algal blooms, and that is without consideration of the health risks associated with algal toxins: even if the owner survives, the dog might not (fifteen dogs died swimming in a *Microcystis* bloom in Rutland Water, UK)’.

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