Working Paper

On the Dominance of Filamentous Blue-Green Algae in Shallow Lakes

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WP-94-67
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ABSTRACT

The algal community of eutrophic shallow lakes is often dominated by filamentous cyanobacteria. In this paper we follow two independent approaches to show that this state should be an alternative equilibrium over a range of conditions to the state dominated by green algae and diatoms. First, we analyze the patterns of blue-green dominance observed in the field, and show that in view of the dynamical systems theory, those patterns imply that the algal community must be a hysteretic system. Then, we construct a minimal competition model to show that hysteresis should, in fact, be expected from differences in physiology between cyanobacteria and algae measured in the laboratory. The basic mechanism behind this is that cyanobacteria are the superior competitors under conditions of low light, but also promote such conditions as they cause a higher turbidity per unit of phosphorus than other algae. This theory of hysteresis explains why blue-green dominance is so resistant to restoration efforts by means of nutrient reduction. It also suggests that a shock therapy, such as temporary flushing, can suffice to get rid of blue-greens.

ON THE DOMINANCE OF FILAMENTOUS BLUE-GREEN ALGAE IN SHALLOW LAKES

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INTRODUCTION: OBSERVATIONS ON BLUE-GREEN DYNAMICS IN LAKES

It is a well established fact that the concentrations of phytoplankton and chlorophyll-a in a lake increase with the nutrient loading. In shallow lakes, filamentous cyanobacteria tend to become abundant in the course of the eutrophication process (Berger, 1975; Schindler, 1975; Sas, 1989). When these "blue-green algae" are present, they often dominate the algal community completely. Although in some cases they appear only in the summer, they often stay dominant during all seasons (Sas, 1989).

An especially bothersome phenomenon from the water-quality managers' point of view is the fact that the turbidity of a lake becomes higher if it is dominated by cyanobacteria. This is most obvious if a lake switches from one state to another. Figure 1 shows three examples of such lakes. In lake Usselmeer the summer algal community has been dominated by filamentous blue-greens twice over the last 15 years and in both summers the chlorophyll-a were exceptionally high. Lake Eemmeer is usually dominated by blue-greens. In 1991 blue-greens density was low most of the summer, which coincided with a drop in Chl-a. Even more conspicuous is the drop in Chl-a that occurred in the Schlachtensee, when this lake switched from blue-green dominance to an alternative algal assemblage.

To check the observation that blue-greens enhance turbidity against more data, information was analyzed on 103 shallow Dutch lakes. An interpolated response surface of chlorophyll-a against total-P and the percentage of algal biovolume consisting of filamentous blue-greens (Fig. 2) supports the idea that lakes with a higher percentage of blue-greens have higher Chl-a concentrations at the same total-P level. In a multiple linear regression through the same data, both the percentage blue-greens and total-P were highly significant in explaining Chl-a ($p<<0.0001$).

Although blue-green dominance in shallow lakes is typically associated with hypertrophic conditions, it can be seen from Figures 1 a and b that there is no critical total-P concentration that determines whether a lake is dominated by blue-greens. For a range of nutrient levels cyanobacteria may or may not be dominant. The data points in any specific lake do seem to be separated, however, with respect to their chlorophyll-a levels. The blue-green dominated states always have a higher Chlorophyl-a concentration than the other states.

If the nutrient loading of blue-green dominated lakes is reduced, the response of the system to the decreasing nutrient concentration is typically discontinuous (Sas, 1989). At first, the chlorophyll-a level responds only slightly. This period of little response to the change in total-P ends with a relatively fast transition to a non-blue-green dominated situation with a lower chlorophyll level. The turbidity at which this switch occurs is higher if the (mixed) depth of the lake is smaller, and it has been stated that the switch tends to occur at a fixed ratio of euphotic depth to mixed depth (Z_{eu}/Z_{mix}) for all shallow lakes. The behavior of the algal community of the Schlachtensee (Figs. 1 c and 3) is a good example of this discontinuous response.

Although most of the literature is about temperate lakes, abrupt changes between persistent blue-green dominance and other algal assemblages have been described for tropical lakes as well (Fig. 4). Here, the blue-green species involved is *Spirula platensis*. Although accurate data is scarce, some of these lakes are actually known to switch back and forth repeatedly without obvious external forcing (Melack, 1989).

Because of the notorious resistance of blue-green dominance to restoration efforts by means of nutrient reduction, additional ways to get rid of them have been tried. In lakes where the hydrology can be manipulated, an increase of the through-flow ("flushing") has proved effective in breaking the blue-green dominance.

To facilitate further discussion the above observations are condensed into eight premises:

1. *Shallow lakes are often dominated by filamentous blue-green algae at high total-P concentrations.*
2. *In some lakes, but not all, blue-green dominance is interrupted in winter.*

3. *In a given lake blue-greens can be either dominant or rare at the same total-P level.*
4. *In a given lake the chlorophyll-a concentrations associated with blue-green dominance are higher than those corresponding to other states.*
5. *Abrupt changes between blue-green dominance and other persistent states have been observed with no evidence of large changes in environmental factors.*
6. *The response of the algal community to decreasing total-P concentration can be discontinuous.*
7. *The ratio of euphotic depth to lake depth at which blue-green dominance ends is approximately the same for all shallow lakes.*
8. *Flushing can end blue-green dominance.*

A THEORY OF HYSTERESIS BASED ON FIELD OBSERVATION

Combining the above information, the patterns depicted in Figure 1 can be generalized to a diagram of the equilibrium states of the algal community of a lake as a function of the control variable total-P (Fig. 5). Since the algal community is a dynamical system, the geometry of this picture implies that it must be a "hysteretic" system: at low total-P levels, only the non-blue-green state is possible, whereas at very high total-P levels, only the blue-green dominated state exists. Over a range of intermediate nutrient levels, however, both states are possible.

The consequences of this situation become clear if we imagine the response to changing nutrient levels. When, starting from a low total-P level, we slowly increase the nutrient load, the chlorophyll-a level will gradually increase (see Fig. 5) until the critical total-P value (P_2) is reached, above which only the blue-green dominated state exists. When this "breakpoint" is passed, the system will show a "catastrophic transition" to a higher chlorophyll level at the blue-green dominated upper branch of the hysteresis. If, from this point, we start lowering the total-P gradually, the algal community will stay on the blue-green dominated branch until the lower critical nutrient concentration (P_1) is reached, and the jump back to the lower branch occurs.

Normally, catastrophic dynamical systems of this kind show a hysteretic response to changes in all relevant parameters. In this case, it is known that flushing can tip the competitive balance. Obviously, it should be expected that the response to flushing should be hysteretic as well. Departing from conditions for which the two equilibria exist, a consequence is that an increase of the through-flow needs in principle to be only temporal to get rid of blue-green dominance permanently.

In addition, the system should show hysteresis in its response to the seasonal change of conditions. Apparently, winter can, but does not always, bring the system past the breakpoint below which blue-green dominance ends (premise 2). Many conditions vary simultaneously over the season, but to clarify the argument it could be assumed that the drop in temperature is the main factor causing the disappearance of blue-greens in winter. Then, hysteresis would imply that the disappearance in winter occurs at a lower temperature than the reappearance in summer. Generally speaking, conditions at which blue-greens appear and disappear should be different.

Obviously, the view of the algal community as a hysteretic system is well in line with the observed discontinuities in behavior summarized in premises 5 and 6.

A MODEL OF COMPETITION FOR LIGHT AND NUTRIENTS

The above reasoning is based solely on the patterns observed in the field. In this and the next paragraph, a competition model is constructed and used to analyze a completely independent set of information, namely the physiological characteristics of algae that can be measured in the laboratory. Instead of analyzing competition between many species as occurs in the field, a simplification is introduced by considering only one typical blue-green (*b*) and one typical non-blue-green (*g*) species. For finding parameter values *Oscillatoria agardhii* and *Scenedesmus protuberans* has been taken as examples of the two respective groups.

To build up the growth equations the productivity of the algae is assumed to depend on the availability of nutrients and light and from that the losses due to mortality, respiration and flushing are subtracted.

For the dependence upon the nutrient concentration (*n*) the classical Monod form is used with a half-saturation concentration (*h*):

$$\frac{n}{n + h} \qquad (1)$$

For simplicity the total nutrient concentration in the system (*P*) is considered to be constant, and it is defined as the sum of free nutrients (*n*) and nutrients present in blue-green (*b*) and green (*g*) algae:

$$n = P - g - b \qquad (2)$$

The dependence of productivity upon the underwater light climate is more difficult to write in a simple form. Obviously, light intensity varies in the course of the day and decreases also with depth. Integration of the photosynthesis over time and depth, however, yields awkward formulations that are still far from perfect in describing any real situation because, for instance, the depth of the water column varies from site to site as well. Since it is obvious, nonetheless, that available light, and therefore productivity declines with turbidity, the overall light limitation function is simply defined as:

$$\frac{1}{1 + qE} \qquad (3)$$

where q is the sensitivity to turbidity and E is the Lambert-Beer light extinction coefficient, depending on the density of algae and their specific extinction coefficients (k_g and k_b):

$$E = k_g g + k_b b \qquad (4)$$

Clearly the sensitivity coefficient (q) should decrease with incoming irradiation (I) and increase with the (mixed) depth (Z) of the lake and the half-saturation light intensity (i_g and i_b) needed by the two algal species for photosynthesis:

$$q_g \equiv \frac{i_g Z}{I} \qquad q_b \equiv \frac{i_b Z}{I} \qquad (5)$$

Assuming the effect of nutrient limitation and light limitation to be multiplicative the complete model becomes:

$$\frac{dg}{dt} = g\left[\, r_g \frac{1}{1 + q_g\,(k_g g + k_b b)} \frac{P - b - g}{h + P - b - g} - d_g - f \,\right] \qquad (6a)$$

$$\frac{db}{dt} = b\left[\, r_b \frac{1}{1 + q_b\,(k_g g + k_b b)} \frac{P - b - g}{h + P - b - g} - d_b - f \,\right] \qquad (6b)$$

where d_g and d_b are the rates of respiration and mortality losses of both groups, and f is the loss rate due to flushing. The incoming water is assumed to be free of algae and have a nutrient concentration equal to P in order not to affect mass balance.

The dimensions of the parameter and the default values used to produce the figures that follow are listed in Table 1. The points made in the formal model analysis, however, depend only on inequalities of pairs of parameters, not on the specific values that are assigned to produce the figures. All qualitative results follow from the assumption that blue-green algae have a lower maximum productivity (r), loss rate (d), and sensitivity to turbidity (q), but cause a higher turbidity per unit of nutrients (k) than other algae.. Thus the four basic inequalities are:

$$r_b < r_g \qquad d_b < d_g \qquad q_b < q_g \qquad k_b > k_g \qquad (7)$$

MODEL ANALYSIS AND RESULTS

To analyze the behavior of the model the formula is first written in a lumped form:

$$\frac{dg}{dt} = g\,G\,(g, b, f, N) \qquad (8a)$$

$$\frac{db}{dt} = b\,B\,(g, b, f, N) \qquad (8b)$$

where the functions G and B are the ones presented in eqs. (6a) and (6b), respectively. As all competition models, this model (6) has three trivial equilibria:

. absence of both species ($g=0;\ b=0$)

. absence of blue-green algae ($g=g^{*}>0;\ b=0$)

. absence of green algae ($g=0;\ b=b^{*}>0$)

The values of g^{*} and b^{*} can be computed by solving the equations:

$$G\,(g, 0, f, P)=0 \qquad B(0, b, f, P)=0$$

with respect to g and b. Since G and B are decreasing with g, b, and f and increasing with P, it follows from the implicit function theorem that g^{*} and b^{*} are increasing with P and decreasing with f, as should be expected (see premise 1).

For suitable values of the control parameters (f, P) the model can also have one non-trivial (i.e. strictly positive) equilibrium (g^{+}, b^{+}) which can be obtained by solving the equations

$$G\,(g, b, f, N) = 0 \qquad (9a)$$

$$B\,(g, b, f, N) = 0 \qquad (9b)$$

with respect to g and b. This equilibrium corresponds to coexistence of both groups. In the appendix it is proven that such a coexistence is always unstable (i. e. the equilibrium (g^{+}, b^{+}) is a saddle for all parameter values satisfying inequalities (7)).

These results can be summarized in three state portraits (Fig. 6) showing the trajectories of simulations starting from different initial states. Portraits [*g*] and [*b*] correspond to situations where the same species wins the competition irrespective of the initial conditions. At the same time, portrait [*g/b*], shows the situation in which both trivial equilibria ($(g^*,0)$ and $(b^*, 0)$) are stable. In this case, the boundary of their basins of attraction is the stable manifold of the saddle, namely the trajectory connecting the origin with (g^+, b^+). Simulations end in either of the trivial "monoculture" equilibria, depending on which side of this boundary they start.

Now, the dependence of the state portrait on total-P level and flush rate is explored, assuming that for a given pair (f, P) the portrait is [*g/b*]. If departing from this situation the parameters will be perturbed, the equilibria of the system will vary. However, the two trivial equilibria will remain on the axis and, by continuity, the saddle (g^+, b^+) will remain in the positive quadrant if the perturbation is sufficiently small. Consequently, the trajectories of the system are perturbed, but qualitatively the state portrait remains the same. This situation ends when the saddle (g^+, b^+) disappears from the positive quadrant by colliding with one of the trivial equilibria. This happens when $(g^+,b^+)=(g^*, 0)$, i.e., when the two equations:

$$G(g, 0, f, P) = 0 \qquad B(g, 0, f, P) = 0 \qquad (10)$$

have a solution with $g>0$, or when $(g^+,b^+) = (0,b^*)$ i.e., when the two equations

$$G(0, b, f, P) = 0 \qquad B(0, b, f, P) = 0 \qquad (11)$$

have a solution with $b>0$. Eqs. (10) with $g>0$ implicitly define a curve, called bifurcation curve, in the parameter space (f, P). On one side of this curve are systems with the state portrait [*g*], while on the other side of the curve and close to it the state portrait is [*g/b*] with the saddle (g^+, b^+) very close to the trivial equilibrium $(g^*, 0)$. Similarly, eqs.(11) with $b>0$) define another bifurcation curve: points (f,P) on this curve correspond to systems which have the state portrait [*b*], but close to this curve there are points which correspond to systems with the state portrait [*g/b*]. The two bifurcation curves can be obtained by means of any package suitable for drawing implicitly defined curves. The result is shown in Fig.7, where the labels [*g*], [*g/b*], [*b*] identify the corresponding state portrait. The figure shows that one can always get rid of the blue-green algae (i.e., enter region [*g*]) by lowering the total-P concentration and/or by increasing the flush rate (see premises 6 and 8).

An alternative and more classical way of looking at the problem is to show the dependency of the systems' equilibria upon the control parameters. Since turbidity is one of the main concerns of lake water quality managers, it is shown how the extinction E in equilibrium (in fact, a linear combination of both state variables) varies with P and f (Fig. 8). The system shows hysteresis with respect to both P and f. In an intermediate range of the control parameter, where the state portrait is [*g/b*], there are two possible values of extinction; the lower one (E_g) associated with dominance of green algae, and the higher one (E_b) associated with the dominance of blue-green algae. The values P_1 and P_2 in the first hysteresis correspond to the values of P that can be read in Fig. 7 for $f=0.03$. Similarly, the two values f_1 and f_2 in the second hysteresis picture can be read from Fig. 7 for $P=0.4$. It can be seen from those diagrams that a transition from blue-green to green dominance is always associated with a conspicuous drop in turbidity, and that in the vicinity of the breakpoints, a small variation of a control parameter can be sufficient to induce the transition (see premise 6). Note that the hysteresis with respect to P corresponds to the pattern extracted from the field data (Fig. 5) in the second paragraph.

The figures also show that the upper branch of the hysteresis, is entirely above the lower branch. However, this does not imply that in a given lake extinction associated to blue-green algae dominance is always greater than that associated to green algae dominance, as stated in premise 4. For example, Fig. 8a shows that for $f=0.03$ and $P=P_1$ the extinction E_b associated with blue-green dominance is equal to 1, while Fig. 8b shows that for $f > f_1$ and $P = 0.4$ the extinction E_g associated to green algae dominance is approximately equal to 2. More precisely, premise 4 says that

$$E_b\,(f_b,\, P_b) \;\geq\; E_g\,(f_g,\, P_g) \quad \forall\,(f_b,\, P_b,\, f_g,\, P_g)$$

while from Fig. 7 it can only be conjectured that:

$$E_b\,(f,\,P_b) \geq E_g\,(f,\,P_g) \quad \forall\,(f,\,P_b,\,P_g)$$

$$E_b\,(f_b,\,P) \geq E_g\,(f_g,\,P) \quad \forall\,(f_b,\,P,\,f_g)$$

Indeed, this conjecture holds for all lakes and for all values of parameters satisfying inequalities (7). To prove this, notice first that the two branches of the first hysteresis are increasing with respect to P (recall that it has already been proven that g^* and b^* are increasing with P), while the two branches of the second hysteresis are decreasing with f (because g^* and b^* decrease with f). Then, it suffices to show that the extinction E^+ associated to the saddle $(g^+,\,b^+)$ (shown as dotted line in Fig. 8) is not dependent on P and increases with f. For this, write eqs. (9) (defining g^+ and b^+, and hence E^+) in the form (see eqs. (6)):

$$r_g \,\frac{P - g - b}{P - g - b + h}\,\frac{1}{1 + q_g\,E} = m_g + f$$

$$r_b \,\frac{P - g - b}{P - g - b + h}\,\frac{1}{1 + q_b\,E} = m_b + f$$

and then take the ratio of these two equations, thus obtaining

$$\frac{r_g}{r_b}\,\frac{1 + q_b\,E}{1 + q_g\,E} = \frac{m_g + f}{m_b + f} \qquad (12)$$

This equation shows that E^+ does not depend upon the total-P concentration. Moreover, the inequalities $q_g > q_b$ and $m_g > m_b$ (see (7)) imply that the functions on the left and right-hand sides of (12) are decreasing with E and f, respectively. Hence E^+ (which is the solution of (12)) increases with f.

With respect to the independence of the breakpoint turbidity upon P, it is possible to be actually more specific. Recalling that $q \equiv i\, Z/I$ (see (5)) and assuming that I/EZ is positively related to the ratio Z_{eu}/Z_{mix}, eq. (12) can be rewritten in the form

$$\frac{r_g}{r_b}\;\frac{1 + \alpha\, i_b \dfrac{Z_{eu}}{Z_{mix}}}{1 + \alpha\, i_g \dfrac{Z_{eu}}{Z_{mix}}} = \frac{m_g + f}{m_b + f}$$

where a is a suitable parameter, independent upon the lake characteristics. Thus, the critical value of (Z_{eu}/Z_{mix}), at which blue-green dominance starts and the one at which it ends should be roughly the same for all lakes with comparable flush rates. These results imply an extension of premise 7, which makes reference only to the switch from blue-green dominance, but also shows that the critical value of (Z_{eu}/Z_{mix}) is not really "universal" as it decreases with flush rate.

DISCUSSION

In the first part of this paper it is shown that the presence of hysteresis in the algal community can be deduced from the patterns observed in the field. In the second part, a model is used to show that competition between blue-greens and other algae is a plausible explanation for this hysteresis, in view of their physiological characteristics measured in the laboratory. However, obviously, many mechanisms other than the ones included in this clean competition model will operate in real lakes. Some will enhance the hysteresis, while others will tend to promote coexistence instead. Indeed, in some lakes a rather stable coexistence with other algae is observed. In the following paragraphs some nuances to the view presented in this paper are added by reviewing four mechanisms that are likely to be involved in real lakes.

An explanation that has been suggested to explain the absence of filamentous blue-greens in relatively clear water is the fact that their photosynthesis is reduced at high light intensities. Obviously, this photo-inhibition, which is not included in the model, will tend to enhance hysteresis, as it emphasizes the competitive inferiority of blue-greens in situations of low turbidity.

Another physiological peculiarity of filamentous blue-greens that enhances hysteresis is their ability to maintain a high biovolume at very low P-levels. This explains why, in some lakes, the turbidity hardly decreases in response to decreasing total-P levels as long as blue-greens are dominant (Hosper, 1984). In terms of our competition model it means that the specific extinction of blue-greens should, in fact, increase with decreasing total-P concentrations, postponing the arrival at the critical turbidity that leads to the collapse of blue-green dominance.

An important aspect that has yet to be considered is spatial heterogeneity. Both the field data and the model indicate that depth is one of the main factors in determining whether blue-greens will dominate or not. As many lakes have more-or-less distinct shallow and deep parts, the competitive balance may be in favor of blue-greens only in part of the lake. The consequences of this can be shown by extending the model to include, for instance, different compartments with diffusion between them. These consequences are, however, straightforward enough to grasp intuitively. Obviously, in case of complete isolation of the parts, blue-greens can dominate in the deeper part and be absent in the shallow part. By continuity, it can be seen that slight mixing will cause just a small input of the competitive inferior group in each part without destroying the dominance of the other group. At the same time, very strong mixing between the parts will cause the system to be homogeneous again, and blue-greens will be either dominant or absent from the whole lake. Without going into quantitative details, it can be inferred from this thought experiment that coexistence is favored if areas with different depths exist and horizontal mixing is not too strong.

A topic of much discussion with respect to blue-green algae is their inedibility. Even large herbivorous zooplankters are unable to effectively consume filamentous blue-greens under most conditions. Selective grazing is generally considered the explanation for the fact that blue-greens often dominate in summer after the rise in zooplankton density that induces the clear water phase. In the case of filamentous blue-greens, however, this view is too simple. Not only are they hardly consumed themselves, they also hinder large Daphnids in eating edible algae by clogging their filtering systems. It has been shown experimentally that Daphnia populations will collapse if they are fed at constant concentrations of edible algae with increasing addition of filamentous blue-greens. Thus, selective grazing may allow blue-greens to invade the system, but depending on the situation the threshold to complete dominance may not be reached because the necessary grazing collapses due to the above mechanism. Specific experiments and modelling would be required to understand the impact of grazing on the dynamics of those blue-greens in more detail, but the potential for causing coexistence with other algae can be easily seen from the above discussion.

Although spatial heterogeneity, grazing and other mechanisms that are not included in the model may counteract the potential for hysteresis, the field patterns suggest that the overall system is still hysteretic in many cases. The case for the modelled mechanisms as an explanation for the observed patterns seems strong. Nonetheless it would be worthwhile to experimentally check some of the more specific model predictions, such as the result that the extinction at which the system switches between blue-green dominance and the alternative state should depend on the flushing rate.

ACKNOWLEDGEMENTS

The authors thank Paul Boers, Diederik van der Molen, Egbert van Nes and Jef Huisman for useful discussions, Alessandra Gragnani for carrying out the numerical analysis needed to produce Figures 6 to 8 and STORA for allowing the use of the data represented in Figure 2.

APPENDIX

Assume that the dynamical system

$$\frac{dg}{dt} = g\ G$$

$$\frac{db}{dt} = b\ B$$

has a non trivial equilibrium. Then,

$$G = B = 0$$

for a positive pair (g, b). The Jacobian matrix evaluated at the equilibruim is therefore

$$J = \begin{vmatrix} g\frac{\partial G}{\partial g} & g\frac{\partial G}{\partial b} \\ b\frac{\partial B}{\partial g} & b\frac{\partial B}{\partial b} \end{vmatrix}$$

Following equation (6), the functions G and B can be written in the form:

$$G = r_g\ R(g+b)\ S_g(k_g g + k_b b) - m_g - f$$

$$B = r_b\ R(g+b)\ S_b(k_g g + k_b b) - m_b - f$$

where:

$$R(x) = \frac{P-x}{P-x+b}$$

$$S_g(x) = \frac{1}{1+q_g x}$$

$$S_b(x) = \frac{1}{1+q_b x}$$

Hence:

$$\frac{\partial G}{\partial g} = r_g\left(R'S_g + R\,S'_g\,k_g\right)$$

$$\frac{\partial G}{\partial b} = r_g\left(R'S_g + R\,S'_g\,k_b\right)$$

$$\frac{\partial B}{\partial g} = r_b\left(R'S_b + R\,S'_b\,k_g\right)$$

$$\frac{\partial B}{\partial b} = r_b\left(R'S_b + R\,S'_b\,k_b\right)$$

so that the determinant of the Jacobian matrix

$$\det\ J = g\,b\left(\frac{\partial G}{\partial g}\frac{\partial B}{\partial b} - \frac{\partial G}{\partial b}\frac{\partial B}{\partial g}\right)$$

can be computed explicitly in terms of the functions R, S_g, S_b and their derivatives. After some algebra

$$\det J = r_g\ r_b\ g\ b\ R R'(k_b - k_g)(S_g S'_b - S_b S'_g)$$

is obtained. But

$$S_g S'_b = -\ S_g S_b{}^2 q_b$$
$$S_b S'_g = -\ S_b S_g{}^2 q_g$$

so that

$$(S_g S'_b - S_b S'_g) = S_g S_b (S_g q_g - S_b q_b)$$

Moreover,

$$S_g q_g = \frac{q_g}{1 + q_g x}$$

$$S_b q_b = \frac{q_b}{1 + q_b x}$$

and the inequality $q_b < q_g$ implies $S_g q_g > S_b q_b$.

Thus the determinant of the Jacobian is negative, since it is given by:

$$\det J = r_g r_b g b R R'(k_b - k_g) S_g S_b (S_g q_g - S_b q_b)$$

and all its terms but one, namely R', are positive (recall that $k_b > k_g$). This implies that the nontrivial equilibrium is a saddle.

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TABLE 1

Parameter dimensions and the values used to produce the figures. All values are taken from published or unpublished results of lab experiments by Mur on *Scenedesmus protuberans (g)* and *Oscillatoria agardhii (b)*. The q values are estimated using equation (5) for a temperate lake with a depth of 3 m from a lab experiment in mixed water columns with varying turbidity.

	g	b	dimensions
r	1.2	0.4	day^{-1}
d	0.15	0.06	day^{-1}
h	0.003	0.003	$mgP\ l^{-1}$
k	5	15	$l\ m^{-1}(mgP)^{-1}$
q	2	1	m

FIGURES

Fig. 1Average summer chlorophyll-a concentrations as a function of total-P concentration in different years for three eutrophic shallow lakes. Blue-green dominated years are marked as heavy dots. (Schlachtensee after Sas, 1989)

Fig. 2Interpolated surface showing the response of the chlorophyll-a concentration in the period July-August to the total-P concentration and percentage of algal biovolume accounted for by blue-green algae for 103 shallow Dutch lakes.

Fig. 3Percentage of the algal biomass accounted for by blue-green algae as a function of the ratio of euphotic depth to mixed depth in the Schlachtensee (after Schreurs, 1992).

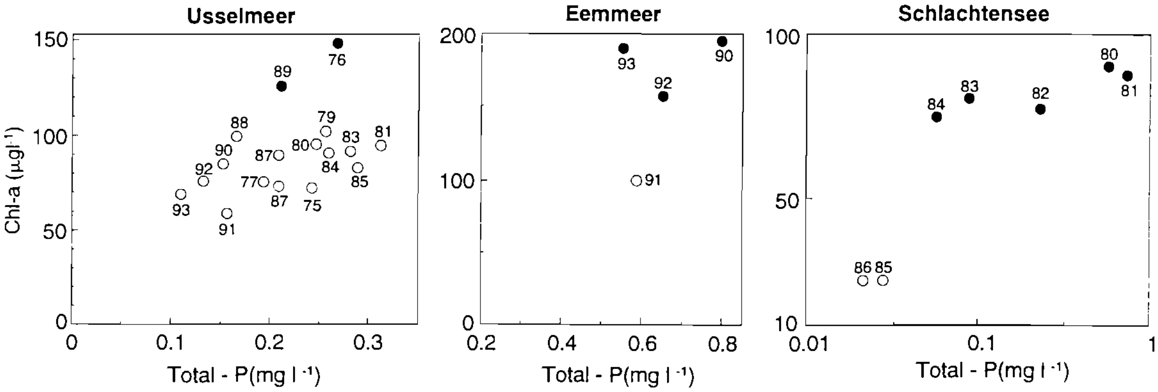
Fig. 4Abrupt change from high to low chlorophyll-a levels with the disappearance of the blue-green alga *Spirula platensis* in lake Nakuru (after Melack, 1979).

Fig. 5Generalized diagram of the equilibrium states of the algal community of shallow lakes inferred from the patterns observed in the field.

Fig. 6Sets of simulated trajectories illustrating the three possible state portraits of the model: [*g*] a monoculture of green algae is the only stable equilibrium; [*g/b*] initial conditions determine the final state; [*b*] a monoculture of blue-green algae is the only stable equilibrium.

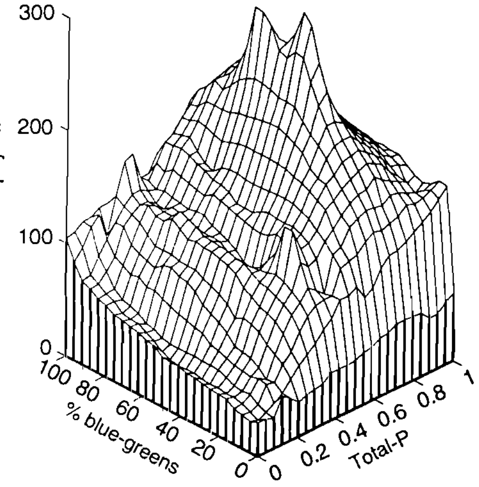
Fig. 7Bifurcation diagram of the model showing for which combinations of flush rate (f) and total-P concentration (P) blue-green algae [*b*] or other algae [*g*] will dominate, and for which combinations those states are alternative equilibria [*g/b*].

Fig. 8Hysteresis shown as the response of the turbidity (E) with respect to the control parameters total-P (P) and flush rate (f).


Usselmeer
Eemmeer
Schlachtensee
Chl-a (μgl⁻¹)
150
100
50
0
0
0.1
0.2
0.3
Total - P(mg l⁻¹)
89
76
88
79
90
87
80
83
81
92
84
77
85
93
87
75
91
200
100
0
0.2
0.4
0.6
0.8
93
90
92
91
10
50
100
0.01
0.1
1
80
83
82
81
84
86
85

(a) *(b)* *(c)*

Fig.1



Chlorophyll-a
300
200
100
0
100
80
60
40
20
0
% blue-greens
0
0.2
0.4
0.6
0.8
1
Total-P

Fig.2

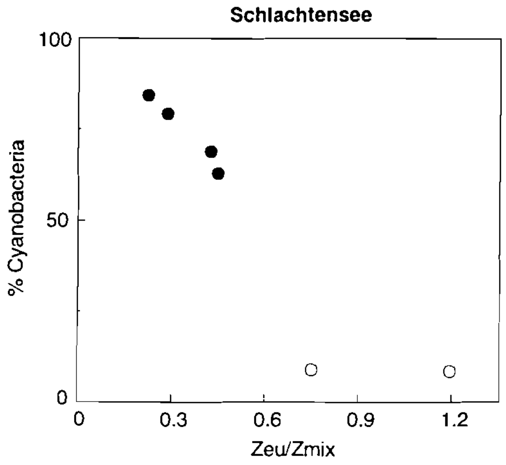


Fig.3

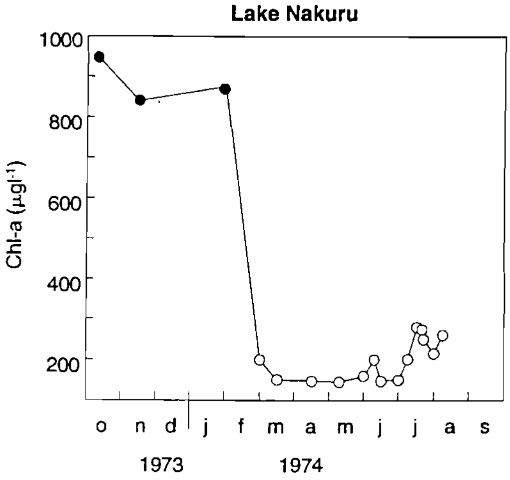

Lake Nakuru
Chl-a (µgl-1)
1000
800
600
400
200
o
n
d
j
f
m
a
m
j
j
a
s
1973
1974

Fig.4

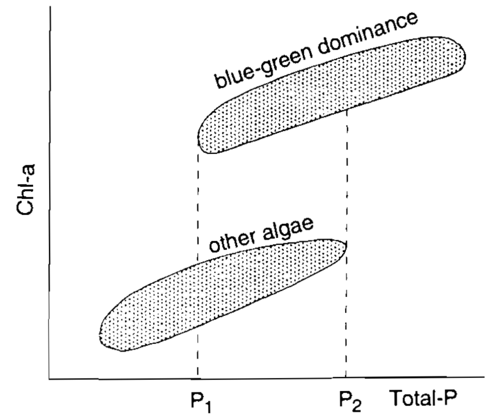


Fig.5

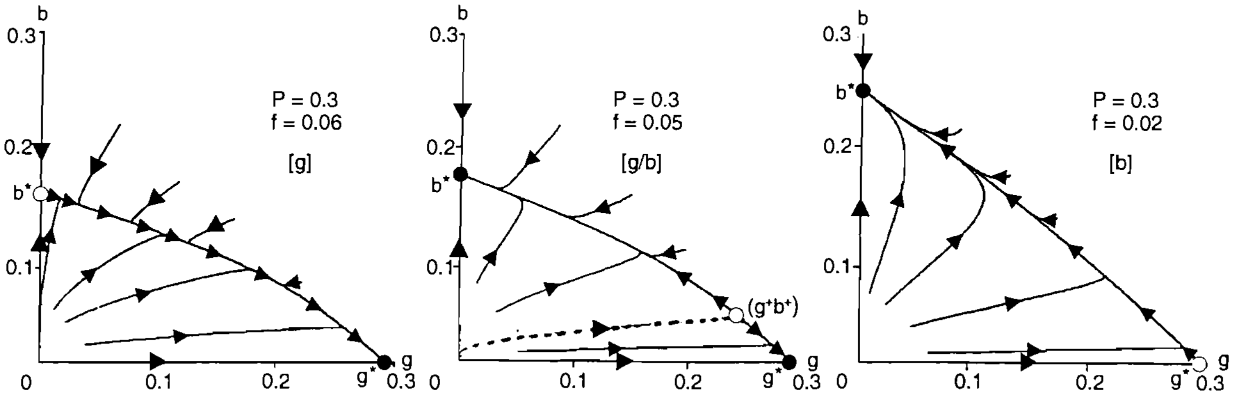
b
0.3
0.2
b*
0.1
0
0.1
0.2
g*
0.3
g
P = 0.3
f = 0.06
[g]
b
0.3
0.2
b*
0.1
0
0.1
0.2
g*
0.3
g
(g⁺b⁺)
P = 0.3
f = 0.05
[g/b]
b
0.3
b*
0.2
0.1
0
0.1
0.2
g*
0.3
g
P = 0.3
f = 0.02
[b]

Fig.6

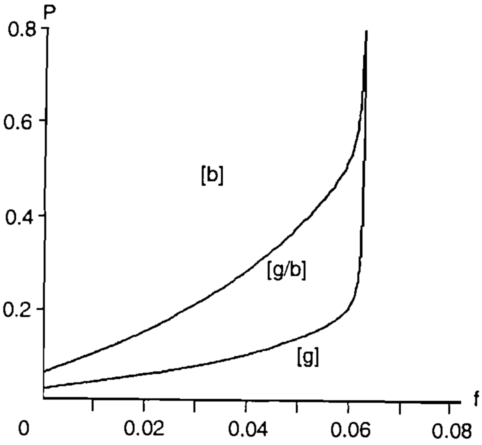
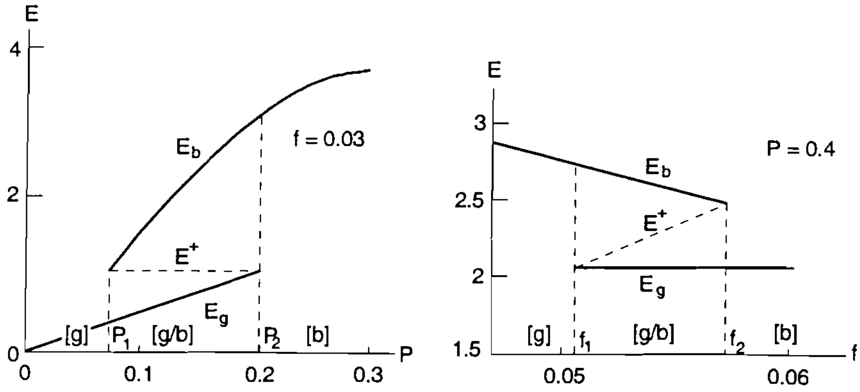


Fig.7


E
4
2
0
0
0.1
0.2
0.3
P
E_b
E^+
E_g
f = 0.03
[g]
P_1
[g/b]
P_2
[b]
E
3
2.5
2
1.5
0.05
0.06
f
E_b
E^+
E_g
P = 0.4
[g]
f_1
[g/b]
f_2
[b]

(a)

(b)

Fig.8