

University of Northern Iowa  
UNI ScholarWorks

---

Presidential Scholars Theses (1990 – 2006)

University Honors Program

---

1994

# The modeling of phosphorus dynamics in a lake system

Todd N. Swift  
*University of Northern Iowa*

Follow this and additional works at: <https://scholarworks.uni.edu/pst>

 Part of the [Biological and Chemical Physics Commons](#), and the [Water Resource Management Commons](#)

*Let us know how access to this document benefits you*

---

## Recommended Citation

Swift, Todd N., "The modeling of phosphorus dynamics in a lake system" (1994). *Presidential Scholars Theses (1990 – 2006)*. 161.  
<https://scholarworks.uni.edu/pst/161>

This Open Access Presidential Scholars Thesis is brought to you for free and open access by the University Honors Program at UNI ScholarWorks. It has been accepted for inclusion in Presidential Scholars Theses (1990 – 2006) by an authorized administrator of UNI ScholarWorks. For more information, please contact [scholarworks@uni.edu](mailto:scholarworks@uni.edu).

# The Modeling of Phosphorus Dynamics in A Lake System

Todd N. Swift and H. K. Macomber, Advisor

We have constructed a basic closed stock and flow model of lake phosphorus cycling that includes three stock concentrations: inorganic phosphorus, phosphorus in living organic material, and phosphorus in dead organic material. Stocks are connected by flows that are made stock dependent in a plausible manner. The model exhibits two equilibrium points, one stable and the other unstable, with an interesting crossover between them. Below a certain total phosphorus threshold, stable equilibrium is characterized by all of the phosphorus stock residing in the inorganic form, suggesting the collapse of the biological system. Above the threshold, this is not true. We then used STELLA® II, a computer program for dynamic modeling, to study the dynamics of the basic model and some extensions and modifications to it, including the addition of another stock and external loading of the system. When the system is perturbed from equilibrium, the model shows eutrophication blooms and other interesting behavior.

## Introduction

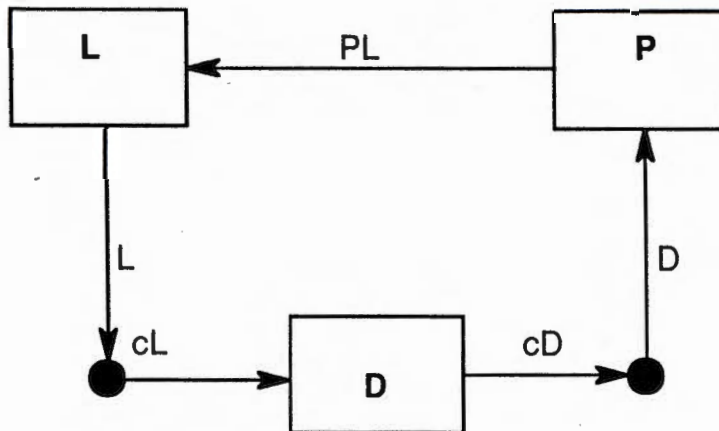
The element phosphorus is essential to the growth of all plants, including algae. Phosphorus is often not freely available in natural waters and is one of the elements whose availability is a major constraint on the production of large crops of plankton algae (Reynolds, p. 202). When large amounts of phosphorus are added to a lake, algae grow rapidly in a process called eutrophication. When these algae exceed the carrying capacity of the lake and die out, the bacteria that thrive on their decay consume large amounts of oxygen. This can kill fish in the lake.

The implications of human disruption of phosphorus cycles in populated lake areas are not always clear. Small amounts of additional phosphorus may be beneficial, but large amounts may be disastrous. The biological cycling of phosphorus and the attendant disruptions can be extremely rapid (Reynolds, p. 202).

The purpose of this project is to develop a basic model for the phosphorus cycle in a lake and to study its behavior under various conditions. The dynamic modeling of biological systems is an important activity in many areas, ranging from terrestrial environmental science to closed life-support systems in space vehicles. The modeling of space biological systems may become more important as the length of time that astronauts spend in space continually increases, while the weight of resources that may be used for life support remains constrained.

## The Basic Model

The basic model (from Harte, pp. 45-49) is a very simple closed box model of the interrelationships of living, inorganic, and dead organic phosphorus concentrations in a lake. Figure 1 shows the model in its dimensionless form. (See the Appendix for the development of this and other mathematical details not given in the main body of the paper.)



**Figure 1.** Diagram of the basic model, where the boxes labeled L, P, and D represent dimensionless concentrations of phosphorus in living organic material, inorganic material, and dead organic material, respectively, and  $c$  is a dimensionless rate constant. The dark circular areas represent single unit converters.

The three corresponding governing equations are:

$$\frac{dL}{dt} = PL - L, \quad (1)$$

$$\frac{dP}{dt} = D - PL, \quad (2)$$

$$\frac{dD}{dt} = cL - cD, \quad (3)$$

where  $L$ ,  $P$ , and  $D$  represent dimensionless concentrations of phosphorus in living organic material, inorganic material, and dead organic material, respectively, and  $t$  is the dimensionless time.

Note from the figure and equations above that the conversion to a dimensionless form requires that the flows into and out of the  $D$  box be unit converted. This form is preferable to the dimensional one because the number of rate constants appearing in the equations is reduced from three to one, making analysis of the system more straightforward.

In a closed lake system, phosphorus must be conserved. This is seen in the dimensional equations by summing the right-hand sides of all three

equations and noting that the result is zero. In the dimensionless variables adopted here, conservation implies that

$$L + P + \frac{D}{c} = K \quad (4)$$

where  $K$  is the dimensionless total phosphorus concentration in all forms.

### Analytic Study of the Basic Model

The three governing equations given above can be reduced to two to facilitate analysis. By using (4) to eliminate  $D$  in (2), we arrive at the two governing nonlinear equations:

$$\frac{dL}{dt} = PL - L, \quad (1)$$

$$\frac{dP}{dt} = c(K - P - L) - PL \quad (5)$$

for  $L$  and  $P$ .  $D$  can then be obtained from (4).

At equilibrium,  $L$  and  $P$  will be constant, so that by setting the right-hand sides of (1) and (5) to zero, the equilibrium conditions may be obtained. When this is done, two equilibrium points are found:  $L=0$ ,  $P=K$  and  $L=c(K-1)/(c+1)$ ,  $P=1$ . A linear stability analysis of each of these equilibrium points can be performed by examining the exponential time dependence of small perturbations from equilibrium. The exponents are calculated as eigenvalues, and the signs of the real parts of these determine stability. A negative sign indicates decay to the equilibrium point for long times and hence stability, while a positive sign indicates instability.

For the first equilibrium point,  $L=0$ ,  $P=K$ , we find that the eigenvalues are  $-c$  and  $K-1$ . Perturbations  $L^*$  and  $P^*$  in the neighborhood of the point are then given by

$$\begin{bmatrix} L^* \\ P^* \end{bmatrix} = W_1 \begin{bmatrix} 0 \\ 1 \end{bmatrix} e^{-ct} + W_2 \begin{bmatrix} 1 \\ \frac{c+K}{1-c-K} \end{bmatrix} e^{(K-1)t} \quad (6)$$

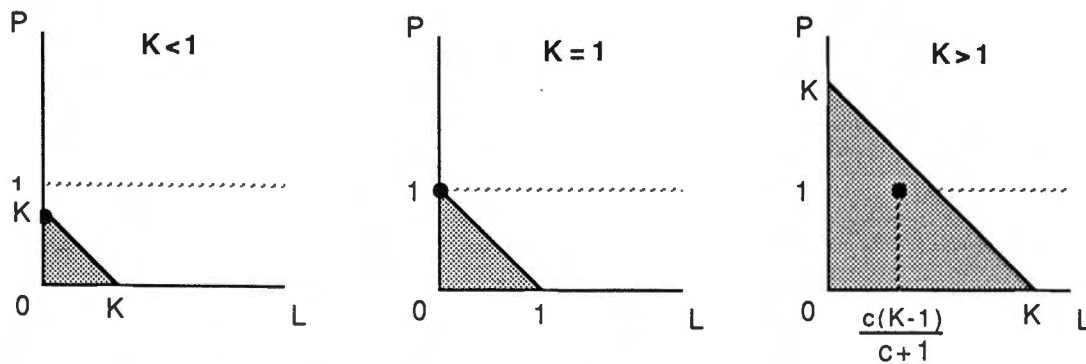
where  $W_1$  and  $W_2$  are constants determined by the initial conditions. Thus, if  $K < 1$ , this equilibrium point is stable. If  $K > 1$ , it is clearly unstable.

Linear stability analysis fails in the case  $K=1$  for the two equilibrium points coalesce. We then find, by graphical means, that this single equilibrium point has both stable and unstable attributes but is stable in the domain of interest.

For the second equilibrium point,  $L=c(K-1)/(c+1)$ ,  $P=1$ , the eigenvalues are not so easily calculated. However, we can show that if  $K<1$ , the equilibrium point is unstable, and if  $K>1$ , it is stable. In the latter case, solutions approach equilibrium in an oscillatory or monotonic manner depending on the value of  $K$ . Larger  $K$  values produce eigenvalues that are real and negative, resulting in a monotonic approach to equilibrium. Smaller  $K$  values result in eigenvalues that are complex conjugates of each other, resulting in an oscillatory approach to equilibrium. Note that the condition for stability of the second equilibrium point is opposite to that for the first point.

We see that the long-term behavior of the system depends on the single constant  $K$ , measuring the concentration of phosphorus in the system. If it is too low,  $K<1$ , the system will eventually settle down to equilibrium at  $L=0$ ,  $P=K$ . The condition  $L=0$  means that there is no phosphorus and suggests that the biological system has collapsed due to insufficient phosphorus. This may also mean that if we perturb a dead system ( $L=0$ ) by adding sufficient phosphorus to make  $K>1$ , we can bring the system back to life (provided there is a "seed" of algae or living material to begin the growth).

Figure 2 below shows the stable equilibrium point and physically admissible regions ( $L, P, D \geq 0$ ) of the LP-plane for  $K<1$ ,  $K=1$ , and  $K>1$ .



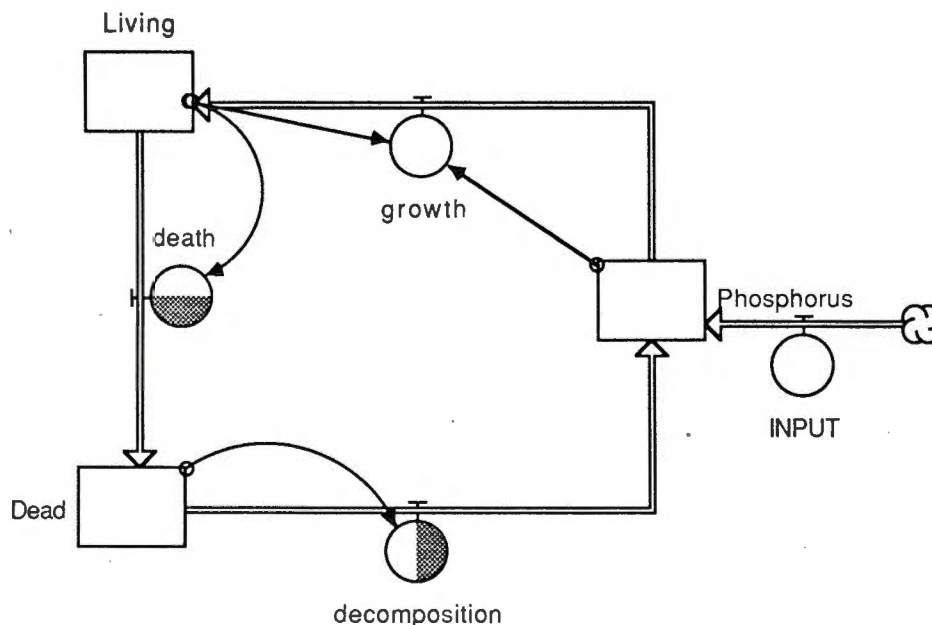
**Figure 2.** Stable equilibrium point, black dot, and physically admissible region, shaded, in the LP-plane for  $K<1$ ,  $K=1$ , and  $K>1$ .

As  $K$  increases, the physically admissible boundary line moves outward from the origin while maintaining a slope of magnitude unity. As can be seen from the two graphs on the left, when  $K \leq 1$  the system will settle down to  $L=0$ .

## STELLA® II and the Dynamics of the Basic Model

The long-term behavior of the basic model is completely determined by the analysis above, but the analysis tells us very little about what the system does on its way to final equilibrium. Also, when the model is extended to improve its realism, analytic studies become very difficult and we must turn increasingly to computational numeric studies. STELLA® II (hereafter referred to as STELLA) is a simulation program designed to model dynamic systems in a relatively simple manner. It is powerful and has the potential to significantly lessen the programming demands for any dynamical modeling project.

Figure 3 below shows the basic model as constructed in STELLA, and can be used to explain the workings of STELLA.



**Figure 3.** The basic model, as constructed in STELLA. The cloud attached to the INPUT flow represents an infinite source of phosphorus and the shaded circles represent single unit conversions.

There are four basic building blocks used to represent dynamical systems in STELLA. They are stocks, flows, converters, and connectors. The rectangular boxes are *stocks* and, in this case, represent the three kinds of phosphorus. Every stock accumulates one type of phosphorus.

The stocks are connected by *flows* that have "spigots" on them to control the flows. The half-shaded flow circles represent flows in which unit conversions are performed. This is necessary in the dimensionless model used here. The cloud represents an infinite stock. In this case, there is an infinite amount of phosphorus (from the lake's point of view) that

can be added to the lake to perturb it.

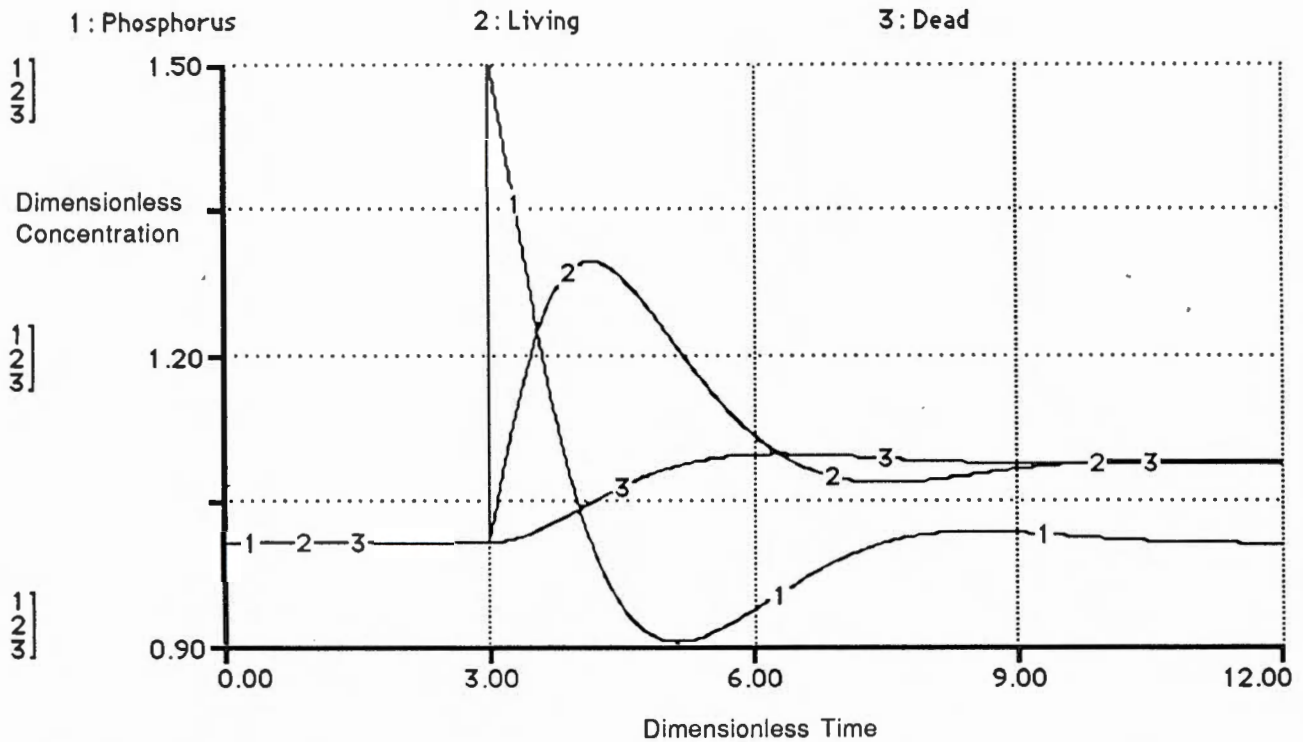
Circles that are used to modify flows and stocks are called *converters*. There are none used in this model, but these can be used when more complexity is required.

Finally, *connectors* are used to connect parts of the model that depend on each other. These are the curved arrows seen on the diagram above. The nonlinear term in the basic model appears because the growth rate depends on both the living phosphorus concentration and the inorganic phosphorus concentration. This can be seen by the connectors coming from both of these stocks to the growth flow.

After designing the system graphically, the user of STELLA must then define all of the quantities and relationships between the various components of the model. When this is done, the model can be run and adjusted so that it is in equilibrium. The dynamics of the model when perturbed from equilibrium can then be studied.

The basic model requires only initial values for the three stocks and a value for  $c$  (see (3)). The constant  $c$  acts in the unit converted flows in Figure 3 above and thus controls the flow rate between the appropriate stocks. The value used for  $c$  was 0.2, which is realistic for a lake system. In the dimensionless model, the  $L, P, D$  point of 1,1,1 (which corresponds to  $K=7$ ) is a stable equilibrium point, so we start with all three of the stock concentrations at unity and then perturb the system by using a STELLA function called *pulse* to rapidly increase the concentration in the inorganic phosphorus stock to a new value. The added phosphorus comes from the infinite cloud of phosphorus.

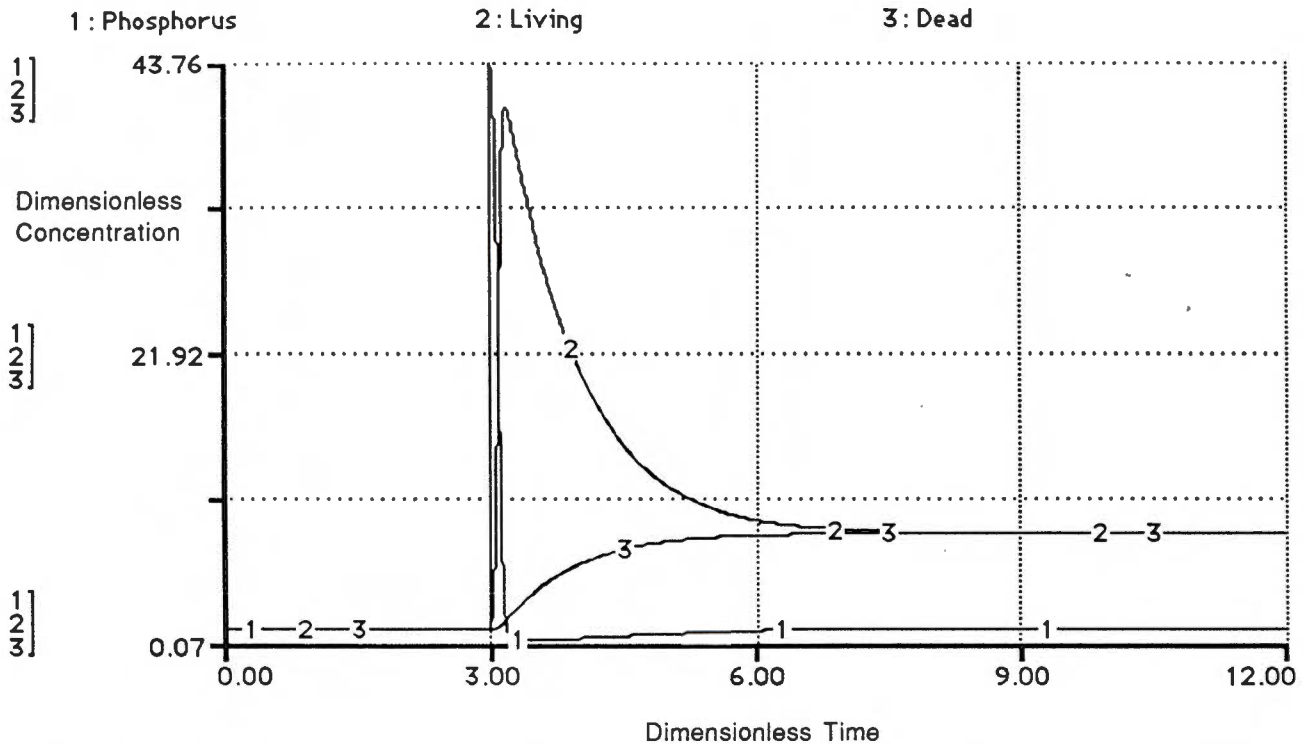
One way that lakes are perturbed is by the phosphorus from fertilizers and detergents that are commonly used today, so we begin by simulating a perturbation of this sort. When we perturb the system by adding a pulse of height 0.5 (a 50% increase) and width of one time step to the inorganic phosphorus ( $P$ ) stock at time  $t=3.00$ , we obtain the result shown in Figure 4 below.



**Figure 4.** Results of increasing the inorganic phosphorus concentration by 0.5 units at time  $t=3.00$ . Note the initial rapid increase in the living concentration followed by a rapid decrease to the new equilibrium values:  $P=1$  and  $L=D=1.083$ .

It can be seen in Figure 4 that the solutions are oscillatory and the concentrations overshoot their equilibrium values several times. This means that the eigenvalues are complex conjugates of each other with negative real parts. If our perturbation results in a much larger  $K$  value, analysis shows that we should obtain solutions that monotonically approach their new equilibrium values. This is seen in Figure 5 below which shows the solutions when we pick an extremely large initial perturbation that results in a  $K$  value of 50.





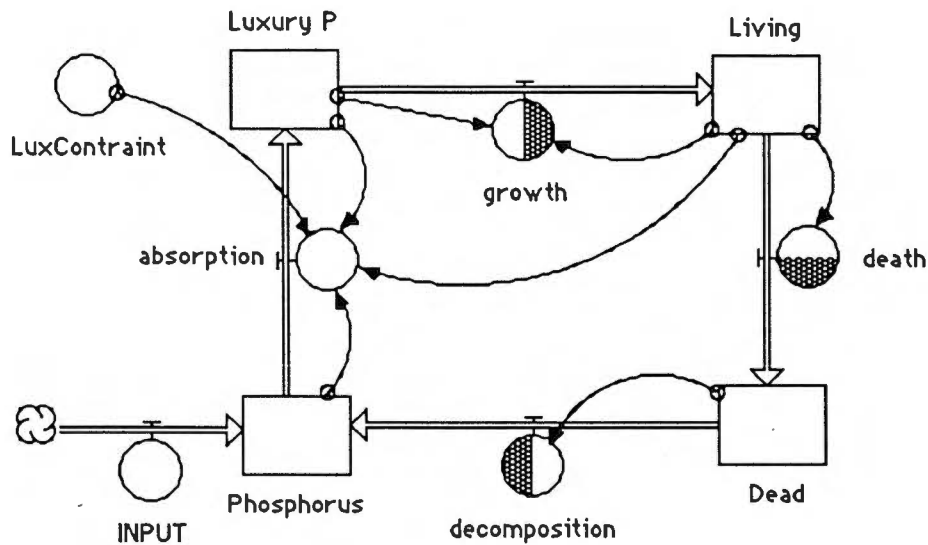
**Figure 5.** Results of increasing the dimensionless concentration of phosphorus by 43 units at  $t=3.00$ . Note the monotonic approach to the new equilibrium values:  $P=1$ ,  $L=D=8.167$ .

There are many ways to run and perturb even this basic model. The initial perturbation could be of a different stock (representing for example, the dumping of organic waste into the lake) or it could be a sudden removal of phosphorus from one stock (representing, for example, heavy fish harvesting in the lake). We do know, however, from the analysis how to predict the equilibrium values that will result from a given perturbation.

The basic model is very simple but does provide plausible results. The next step is to make the model more realistic by adding a new stock and then to experiment by perturbing the new system.

### Extending the Model

Any realistic phosphorus lake model must distinguish between absorption and growth, so this is where we make our extension. Absorption is the process by which algae rapidly absorb nutrients at a rate several times faster than they can use them to grow. The nutrients, called luxury nutrients, are "stored" until the algae can grow. To accommodate this, we modified the model to include one additional stock, called luxury phosphorus. This extended model is shown in Figure 6 below.



**Figure 6.** The model extended to include luxury phosphorus as an additional stock. The converter, LuxConstraint, is used to restrict the luxury phosphorus concentration (see text).

The dimensionless equations for this extended model are:

$$\frac{dP}{dt} = D - P, \quad (7)$$

$$\frac{dLux}{dt} = P - \frac{c_2 LuxL}{c_1 c_3 (1+Lux)}, \quad (8)$$

$$\frac{dL}{dt} = c_2 \frac{LuxL}{(1+Lux)} - c_3 L, \quad (9)$$

$$\frac{dD}{dt} = L - c_1 D, \quad (10)$$

where  $P$ ,  $Lux$ ,  $L$ , and  $D$  represent dimensionless concentrations in the respective compartments,  $t$  is the dimensionless time, and  $c_1$ ,  $c_2$ , and  $c_3$  are dimensionless rate constants.

There is one additional part of this system that is seen in Figure 6 as the converter called LuxConstraint. The concentration of phosphorus in luxury form cannot exceed six percent of the total concentration of phosphorus in living material. In dimensionless terms,

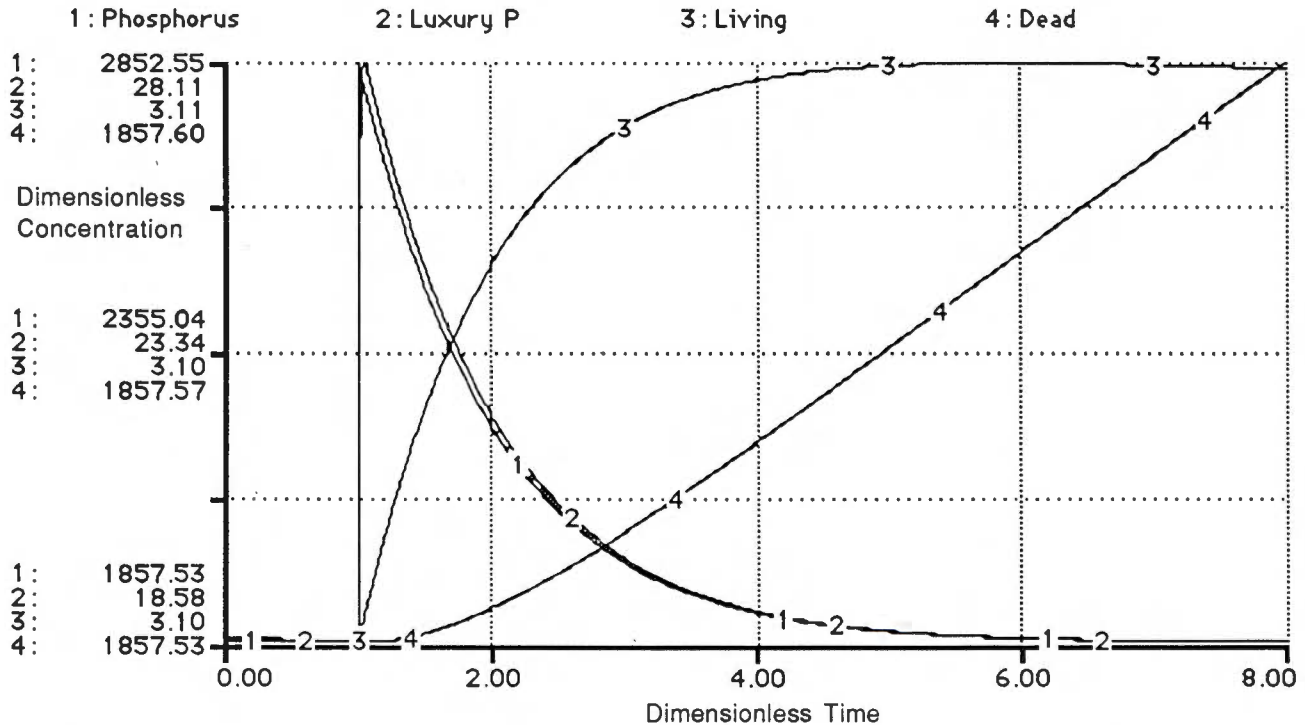
$$Lux \leq \frac{0.06}{c_1 c_3} L. \quad (11)$$

This constraint means the second term in the right-hand side of (8) and the first term in the right-hand side of (9) should be set to zero when the luxury concentration exceeds its allowable amount. This was implemented in STELLA by multiplying these terms by a function of the form

$$\frac{1}{1+e^{(-x/a)}} \quad (12)$$

where  $x$  is the difference between  $Lux$  and its maximum value determined by (11). When  $Lux$  is significantly below its maximum value, (12) is nearly unity. But when  $Lux$  is significantly above its maximum value, (12) is nearly zero, and the absorption flow in Figure 6 is effectively disabled. The constant  $a$  determines how quickly the transition takes place.

The model was first run until an equilibrium point was established. The resulting equilibrium concentrations were then converted to their dimensional counterparts to see if the numbers were realistic. The concentrations seemed realistic, so we began perturbations of the model to see what would happen. Figure 7 below shows the results of an increase of 50% (1000 units) in the concentration of inorganic phosphorus at  $t=1.00$ .



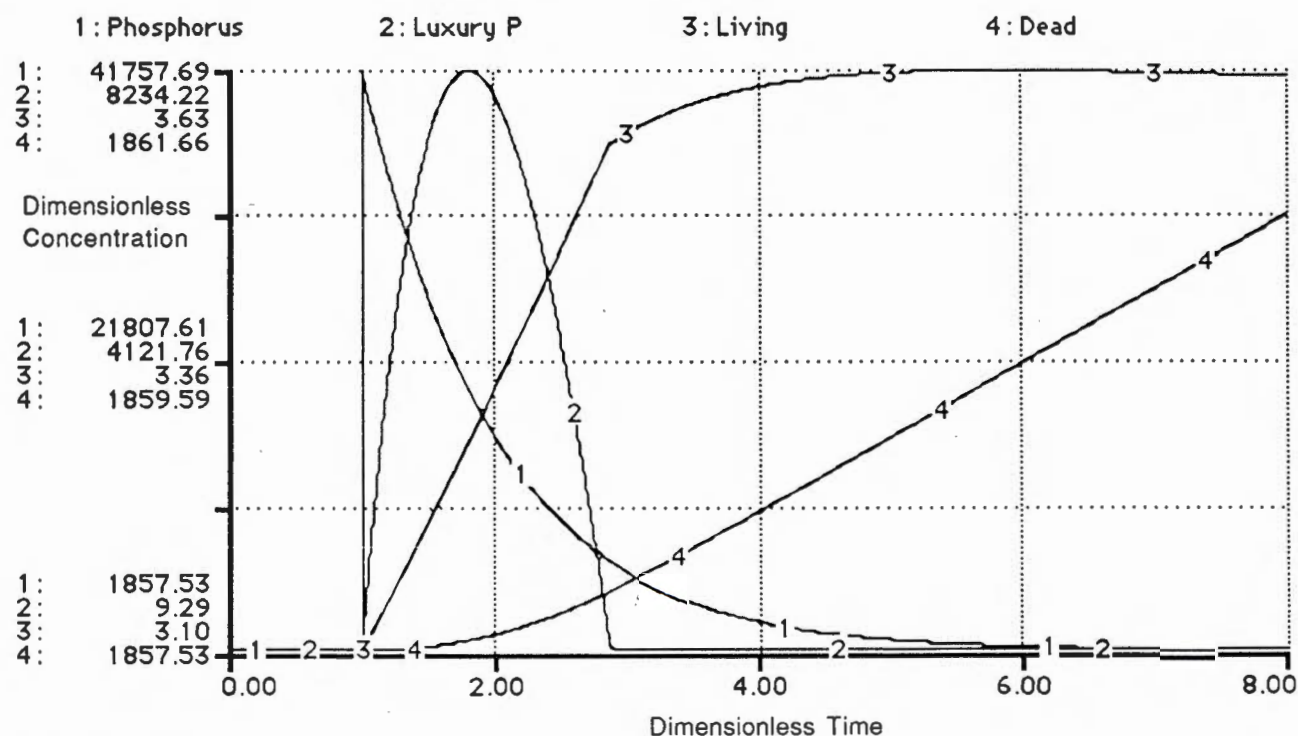
**Figure 7.** Early time response to an increase of 1000 units (50% increase) in the dimensionless concentration of inorganic phosphorus at  $t=1.00$ . Note the dynamics of the luxury stock closely follow those of the phosphorus stock.

We can see that the dynamics of the luxury stock closely follow the phosphorus stock. This is because the absorption rate constant is very large, thus allowing the luxury concentration to rise very rapidly. As the luxury concentration rises, the growth rate increases and we see a rapid increase in the living concentration. This is followed by a decrease in the

growth rate and a leveling off of the living concentration as the luxury and phosphorus concentrations are reduced close to their new equilibrium values. The living and dead concentrations are not yet in equilibrium after eight dimensionless units of time (about 6 hours of real time). The living concentration has begun to decline and the dead concentration continues to rise.

The long-term behavior of the solutions is not shown in Figure 7 or the following figures due to memory limitations in the computer being used and insufficient time to implement a convenient method to accurately capture the early dynamics of the system and retain the long-term dynamics without running out of memory. An adaptive step size Runge-Kutta algorithm would be convenient, but unfortunately is not available in STELLA. Another method that could be used will be discussed later.

Figure 8 below shows the results when the inorganic phosphorus concentration is increased by 40,000 units.



**Figure 8.** Early time response to an increase in dimensionless phosphorus concentration of 40,000 units at  $t=1.00$ .

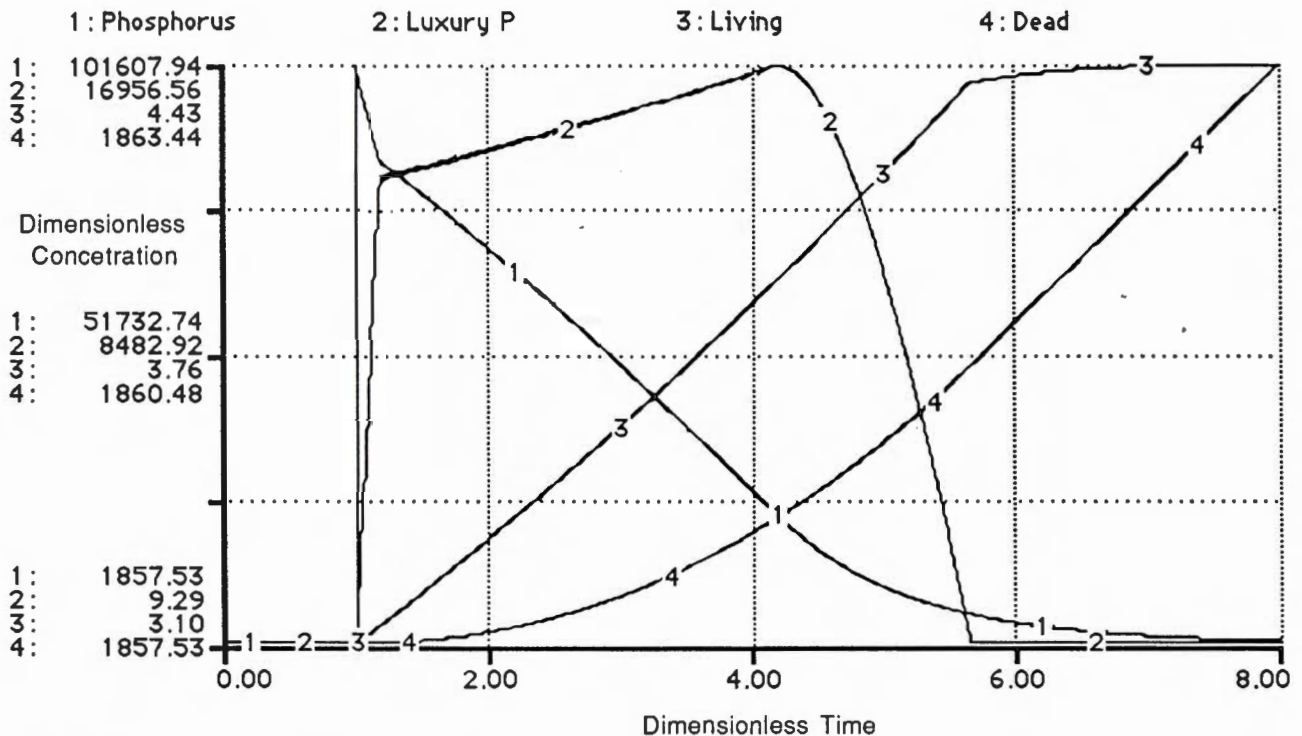
There are several interesting things happening after this perturbation. The increase in luxury concentration is not as abrupt as in the previous case. This is because there is so much more inorganic phosphorus available that, even with a very large rate constant, the absorption flow takes some time to fill the luxury stock concentration to

its maximum.

We can also see that the high rate of decrease of the luxury concentration after  $t=2.00$  causes the concentration to become nearly zero. This is very interesting behavior and may be a defect in the model. STELLA will not allow the stock to go below zero, so the luxury concentration becomes a very small number and there is a discontinuity in the growth rate. However, we see that the growth rate is still positive meaning that there is some flow into the living stock. This result seems to make sense in the real world: the algae deplete their luxury stock to zero and begin growing directly from the inorganic phosphorus stock. But we are not sure how STELLA is producing this result as there is no direct connection between the phosphorus and living stocks. We do not see any discontinuities in the slope of the phosphorus curve, suggesting that the flow from it has not been disrupted. If the non-negativity requirement is relaxed, the curves do not have any kinks and the luxury concentration will become negative. More work needs to be done to better understand this situation.

The dynamics of the phosphorus, living, and dead curves are similar to those in Figure 7 except for the discontinuities mentioned above. Also, the living curve does not appear to be bending over as it was in Figure 7. This may be because there is more total phosphorus available, thus extending the period of rapid growth. The maximum luxury concentration constraint has not been reached in either of these situations.

Figure 9 below shows the results of a perturbation that is large enough to make the luxury concentration reach its maximum allowable amount.



**Figure 9.** Early time response to an extremely large increase of 100,000 units in the phosphorus concentration at  $t=1.00$ . Note the discontinuity in the luxury stock when the luxury concentration reaches its maximum at  $t=1.20$ .

This result is similar to that in Figure 8 except that at  $t=1.20$ , the luxury concentration has reached its maximum value relative to the living concentration. We see the constraint come into effect as the absorption rate is rapidly decreased and the luxury concentration switches to a new path that rises as the concentration in the living stock raises the maximum allowable luxury concentration. Later, the luxury concentration nearly reaches zero, as in Figure 8, and causes a discontinuity in the growth rate.

These numerical experiments are interesting in themselves but also indicate problems that need to be solved. The model needs to be constructed in such a way that the long-term and the short-term behaviors can be observed. Choosing a time step that is small enough to accurately capture the short-term dynamics currently requires too much memory to see the long-term equilibrium. One method we are attempting to use to avoid this problem is to change the time scale of the model at a point in time that we can choose. This should make it possible to include the long-term equilibrium and the early dynamics on the same graph.

Perhaps the biggest problem is discovering what STELLA is doing when the luxury concentration drops to nearly zero. We must also decide if the result we obtain, algae using up all of their luxury phosphorus, is

realistic and if it is not, we must modify the model further before making any other extensions.

Additionally, the initial rate constants and relations chosen when building the dimensional model should be further studied. Different sets of realistic values should be used and the resulting effects examined.

## Conclusions

The modeling of phosphorus dynamics in a lake environment is indeed a complicated matter. Both of the models constructed in this report demonstrate plausible behavior but generate as many or more questions than they answer.

The governing equations for the basic model are simple enough to be studied analytically, which helps immensely in subsequent numeric study. However, adding just one more equation, or stock, to the model makes analytical study very difficult. The complicated numeric results are hard to interpret when there is little fundamental understanding of the model. It is hard to be convinced by them when so little is known about what is happening within the equations that produce them.

There is much left to be done in this study. The "kinks" in solutions of the extended model must be better understood, the long-term behavior of the system needs to be incorporated into the study, the inner workings of STELLA when confronted with discontinuities must be discovered, and the assumptions made during construction of the extended model need to be carefully studied and evaluated.

All this must be done before extending the model further to include such things as sedimentation, inflowing streams, seasonal variations, and different forms of life competing for the same phosphorus. Seemingly simple additions to the model greatly increase its complexity.

## References

- Brown, Edward J., Robin F. Harris, and Joseph Koonce. 1978. "Kinetics of Phosphate Uptake by Aquatic Microorganisms: Deviations From a Simple Michaelis-Menton Equation." *Limnology and Oceanography* 54: 26-34.
- Emsley, John and Dennis Hall. 1976. *The Chemistry of Phosphorus: Environmental, Organic, Inorganic, Biochemical, and Aspects*. Harper and Row, New York, NY.

Harte, John. 1988. *Consider a Spherical Cow: A Course in Environmental Problem Solving*. University Science Books, Mill Valley, CA.

High Performance Systems, Inc. 1992. STELLA® II software. Hanover, NH.

Molot, Lewis and Edward Brown. 1986. "Method for Determining the Temporal Response of Microbial Phosphate Transport Affinity." *Applied and Environmental Microbiology*, **51**: 524-531.

Reynolds, C. S. 1978. "Phosphorus and the Eutrophication of Lakes - a Personal View." *Phosphorus in the Environment: its Chemistry and Biochemistry*, from the Ciba Foundation Symposium 57. Elsevier, New York, NY.

## Appendix

### Recasting the Basic Model Equations Into a Dimensionless Form:

The dimensional equations and rate constants for the basic model are (Harte, pp. 45-49):

$$\frac{dL}{dt} = \beta PL - \gamma L, \quad (1A)$$

$$\frac{dP}{dt} = \alpha D - \beta PL, \quad (2A)$$

$$\frac{dD}{dt} = \gamma L - \alpha D, \quad (3A)$$

where  $L$ ,  $P$ , and  $D$  are the phosphorus concentrations in the respective forms,  $t$  is the time, and representative values of the rate constants  $\alpha$ ,  $\beta$ , and  $\gamma$  are 0.05/day, 2.5/(day  $\mu\text{M}$ ), and 0.25/day, respectively.

To put these equations into dimensionless form, we write

$$L=L_C L^*, \quad P=P_C P^*, \quad D=D_C D^*, \quad \text{and} \quad t=t_C t^*, \quad (4A)$$

where  $L_C$ ,  $P_C$ ,  $D_C$ , and  $t_C$  are characteristic dimensional values of the respective quantities and  $L^*$ ,  $P^*$ ,  $D^*$ , and  $t^*$  are dimensionless variable values. Substitution of the expressions (4A) into (1A), (2A), and (3A) yields the equations:

$$\frac{dL^*}{dt^*} = (\beta t_C P_C) P^* L^* - (\gamma t_C) L^*, \quad (5A)$$



$$\frac{dP^*}{dt^*} = \left(\frac{\alpha t_c D_c}{P_c}\right) D^* - (\beta t_c L_c) P^* L^*, \quad (6A)$$

$$\frac{dD^*}{dt^*} = \left(\frac{\gamma t_c L_c}{D_c}\right) L^* - (\alpha t_c) D^*, \quad (7A)$$

which contain six constant coefficients. We now chose the four characteristic values in an effort to reduce the number of constant coefficients. A convenient choice is:

$$t_c = \frac{1}{\gamma}, L_c = \frac{\gamma}{\beta}, P_c = \frac{\gamma}{\beta}, D_c = \frac{\gamma^2}{\alpha\beta}. \quad (8A)$$

This gives us the dimensionless equations (1,2, and 3) in the main part of the paper:

$$\frac{dL}{dt} = PL - L, \quad (9A)$$

$$\frac{dP}{dt} = D - PL, \quad (10A)$$

$$\frac{dD}{dt} = cL - cD, \quad (11A)$$

where  $c = \alpha/\gamma$  and the asterisk (\*) has been suppressed. The equations now only contain one rate constant,  $c$ , which makes the system easier to study analytically. Since  $c$  does not depend on  $\beta$ ,  $\beta$  enters into the dynamics of the system only through its effect on the initial values of the dimensionless variables.

### Conservation of Phosphorus:

If the original dimensional equations are added together, the right-hand side becomes zero, implying that the total phosphorus concentration  $L+P+D$  is conserved, as it must be. Using (4A) above this may be expressed in the form

$$L_c L^* + P_c P^* + D_c D^* = \text{constant total phosphorus concentration} \quad (12A)$$

This is easily rewritten in the form

$$L + P + \frac{D}{c} = K, \quad (13A)$$

where the asterisk (\*) has again been suppressed and  $K$  is the dimensionless total phosphorus concentration. This is (4) in the main part

of the paper.

### Equilibrium Points:

At equilibrium, the concentrations are not changing. Then (1) and (5) in the main body of the paper imply that

$$PL - L = 0, \quad (14A)$$

$$c(K - P - L) - PL = 0. \quad (15A)$$

The first equation tells us that  $P=1$  or  $L=0$ . We can then use the second equation to solve for the  $L$  or  $P$  values that go with  $P=1$  and  $L=0$ , respectively. We arrive at the two equilibrium points  $L=0, P=K$  and  $L=c(K-1)/(c+1), P=1$ .

### Linear Stability Analysis of Equilibrium:

In the neighborhood of the equilibrium point  $L=0, P=K$ , let us write  $L=0+L^*$  and  $P=K+P^*$  where  $L^*$  and  $P^*$  now represent small perturbations of the equilibrium solution. Substituting into (1) and (5) and neglecting all nonlinear terms, assumed small, yields

$$\frac{d}{dt} \begin{bmatrix} L^* \\ P^* \end{bmatrix} = \begin{bmatrix} K-1 & 0 \\ -c-K & -c \end{bmatrix} \begin{bmatrix} L^* \\ P^* \end{bmatrix}. \quad (16A)$$

This equation has exponential solutions of the form

$$\begin{bmatrix} L^* \\ P^* \end{bmatrix} = \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} e^{\lambda t}, \quad (17A)$$

where

$$\begin{bmatrix} K-1 & 0 \\ -c-K & -c \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} = \lambda \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} \quad (18A)$$

which tells us that

$$(K-1-\lambda)c_1 = 0, \quad (19A)$$

$$(-c-K)c_1 + (-c-\lambda)c_2 = 0.$$

We can easily solve (19A) for the two possible values of  $\lambda$  and associated values of  $c_1$  and  $c_2$  and express our perturbed solution in the form:

$$\begin{bmatrix} L^* \\ P^* \end{bmatrix} = W_1 \begin{bmatrix} 0 \\ 1 \end{bmatrix} e^{-ct} + W_2 \begin{bmatrix} 1 \\ \frac{c+K}{1-c-K} \end{bmatrix} e^{(K-1)t} \quad (20A)$$

where  $W_1$  and  $W_2$  are constants determined by the initial conditions. This is (6) in the paper.

We now move to the second equilibrium point,  $L=c(K-1)/(c+1)$ ,  $P=1$ . Finding the eigenvalues in this case is not as easy as for the first equilibrium point, but by proceeding as before we arrive at a quadratic equation for the eigenvalues:

$$\lambda^2 + c \left( \frac{c+K}{c+1} \right) \lambda + c(K-1) = 0, \quad (21A)$$

where the two roots of this equation are the eigenvalues. This tells us that

$$\lambda_1 \lambda_2 = c(K-1), \quad (22A)$$

$$-(\lambda_1 + \lambda_2) = \frac{c(K+c)}{c+1}, \quad (23A)$$

where  $\lambda_1$  and  $\lambda_2$  are the eigenvalues.

The discriminant of the quadratic equation (21A) for the eigenvalues is positive if  $K < 1$ ; thus both eigenvalues will then be real numbers. In addition, if  $K < 1$  (22A) tells us that the signs of the two eigenvalues must be opposite, and thus we have one positive and one negative eigenvalue and an unstable saddle around the equilibrium point. Note that when  $K < 1$ , the first equilibrium point is stable.

If  $K > 1$ , the analysis becomes more complicated because, depending on the sign of the discriminant (which depends on the value of  $K$ ), the eigenvalues may be complex. The discriminant has two roots for  $K$ :

$$K_{\pm} = \frac{(c^2 + 4c + 2) \pm 2(c+1)^{3/2}}{c} \quad (24A)$$

If  $1 < K < K_-$ , the discriminant is positive and both roots are both real. Then (22A) tells us that the eigenvalues must have the same sign, while (23A) tells us that their sum must be negative. Thus, both of them must be negative, making this equilibrium point stable. Similarly, when  $K > K_+$ , both of the eigenvalues are again real and negative.

When  $K_- < K < K_+$ , the discriminant is negative, and the eigenvalues are complex. However, their real parts are still negative and so the solution is still stable. In this case, near-equilibrium solutions will spiral in towards the equilibrium point, oscillating around their new equilibrium

values. This was the case in Figure 4 if the main body of the paper.

Linear stability analysis fails in the case  $K=1$ , in which case the two equilibrium points coalesce. We then find, by graphical means, that this single equilibrium point has both stable and unstable attributes but is stable in the domain of interest.

### Recasting the Extended Model Equations Into a Dimensionless Form:

The model was extended by adding an additional stock, called luxury phosphorus. We first assumed that the absorption (uptake) rate, or the flow from phosphorus to luxury phosphorus was very fast. One source reported that within twenty minutes of adding  $H_3PO_4$  to a system, more than ninety percent of the added phosphorus was incorporated into algae (Emsley and Hall, p. 22). A somewhat less rapid rate of about ninety percent in forty-five minutes was assumed to arrive at a rate constant of 30/day (called  $\phi$ ).

The second assumption was that algal growth follows the Michaelis-Menten equation (Molot and Brown, p. 524). The form of this equation is seen in the right hand sides of (26A) and (27A) below. The remaining rate constants were chosen to be similar to those in the basic model.

The dimensional equations are then:

$$\frac{dP}{dt} = \alpha D - \phi P, \quad (25A)$$

$$\frac{dLux}{dt} = \phi P - \left( \frac{\theta Lux}{Z + Lux} \right) L, \quad (26A)$$

$$\frac{dL}{dT} = \left( \frac{\theta Lux}{Z + Lux} \right) L - \gamma L, \quad (27A)$$

$$\frac{dD}{dt} = \gamma L - \alpha D, \quad (28A)$$

where  $P$ ,  $Lux$ ,  $L$ , and  $D$  are the phosphorus concentrations in the respective forms,  $t$  is the time,  $\alpha$ ,  $\gamma$ ,  $\phi$ , and  $\theta$  are rate constants with representative values of 0.05/day, 0.25/day, 30/day, and 2.5/day, respectively, and  $Z$  is the luxury concentration where the growth rate is one-half its maximum value in the Michaelis-Menten relation.

We follow a procedure similar to that described in the first section of the Appendix and choose the following characteristic quantities to reduce the number of constant terms:

$$t_c = \frac{1}{\phi}, P_c = Z, Lux_c = Z, L_c = \frac{\phi^2}{\alpha\gamma} Z, D_c = \frac{\phi}{\alpha} Z. \quad (29A)$$

This gives us (7)-(10) in the main part of the paper:

$$\frac{dP}{dt} = D - P, \quad (30A)$$

$$\frac{dLux}{dt} = P - \frac{c_2}{c_1 c_3} \frac{LuxL}{(1+Lux)}, \quad (31A)$$

$$\frac{dL}{dt} = c_2 \frac{LuxL}{(1+Lux)} - c_3 L, \quad (32A)$$

$$\frac{dD}{dt} = L - c_1 D, \quad (33A)$$

where  $c_1$ ,  $c_2$ , and  $c_3$  are  $\alpha/\phi$ ,  $\theta/\phi$ , and  $\gamma/\phi$  respectively.

The constraint on the luxury phosphorous concentration (11) is described in the main body of the paper.

### Stability Testing of STELLA Differential Equation Solvers:

STELLA was initially tested using two sets of three differential equations with known analytic solutions. The first set had an exponential solution. Using Euler's method in STELLA required a time step smaller than 0.001 to achieve less than one percent error after 3000 iterations, while the fourth order Runge-Kutta algorithm had an error of less than 0.001 % after 3000 iterations with a time step of 0.05. The Runge-Kutta method is clearly more accurate with this system of equations.

The second system of equations had an oscillatory solution. The fourth order Runge-Kutta method had an error of less than 0.05 % with a time step of 0.02 after 2500 iterations.

The fourth order Runge-Kutta method and a time step equal to or less than 0.02 was used for all of the results contained in this paper.