ON STABILITY AND PERIODICITY IN PHOSPHORUS NUTRIENT DYNAMICS*

By E. M. ARNOLD (*Battelle, Pacific Northwest Laboratory, Richland, Washington*)

Abstract. The stability of an equilibrium and the existence of limit cycles in a three-dimensional dynamical system arising in predator-prey-nutrient dynamics are demonstrated, using center manifold theory. Some implications of this result for limnological applications are discussed.

1. Introduction. This brief note deals with the stability and long run behavior of a three-dimensional system which arises in phosphorus nutrient cycling in freshwater plankton communities. This system forms part of several widely used lake ecosystem models (see, for example, Di Toro, et al. [1]). The existence of limit cycles in the ω-limit sets of trajectories and the stability of an isolated equilibrium point will be established. The method used is general enough to be useful in studying dynamical systems in contexts different than that considered here. The system under consideration is:

$$\begin{aligned} \dot{x}_1 &= x_1(G_p(x_3) - ex_2 - d) \\ \dot{x}_2 &= x_2(G_z(x_1) - c) \\ \dot{x}_3 &= mx_1(f - G_p(x_3)) \end{aligned} \tag{A}$$

where $G_p(x_3)$ and $G_z(x_1)$ are C^1 monotone increasing functions which are often of the rational form $G_p(x_3) = ax_3/x_3 + K$, $G_z(x_1) = bx_1/x_1 + L$ in limnological applications.

This system models zooplankton, phytoplankton and phosphorus nutrient dynamics with x_1, x_2, and x_3, denoting phytoplankton, zooplankton and phosphorus concentrations, and $G_z(x_1)$, $G_p(x_3)$, denoting (respectively) zooplankton and phytoplankton growth rate functions. The remaining parameters are positive constants which may be interpreted as follows: m = phosphorus-to-carbon ratio in phytoplankton, c = zooplankton death rate, e = zookplankton grazing rate, d = endogenous respiration rate, and f = phosphorus replenishment rate due to living phytoplankton. The constant f is assumed to be greater than d, the excess being due to phosphorus containing excretions from phytoplankton. This model is conservative with respect to phosphorus, which is renewable via biomass from dying phytoplankton and excretions from living phytoplankton. It is assumed that both types of plankton die in proportion to the number presently alive, and that there are no time lags in the system.

2. Results. Some preliminary facts about the dynamics of the system A are collected in the following proposition:

Proposition 1. The plane $x_3 = G_p^{-1}(f)$ (henceforth called M) is invariant under the flow of A. M is monotonically attracting and its phase portrait consists of concentric

* Received February 5, 1979.

cycles about a rest point $E = (G_z^{-1}(c), (f-d)/e, G_p^{-1}(f))$, which is stable with respect to the two-dimensional flow on M.

Remark. By saying that M is monotonically attracting, it is meant that if $x(x_0, t)$ is the solution starting at $x_0 \notin M$, that $d(x(t)), M) \to 0$ monotonically, where d is the Euclidean distance in R^3.

Proof (sketch). An examination of the derivative of $D^2 = [G_p(x_3(t)) - f]^2$ in light of the monotonicity of G_p shows that D^2 decreases and hence that M is attracting. The phase portrait within M can be obtained by an argument like that in Hirsch and Smale [2, pp. 261–262], with the Liapounov function $V(x_1, x_2) - V(G_z^{-1}(c), (f-d)/e)$, where:

$$V(x_1, x_2) = \int^{x_1} \frac{G_z(\xi) - c}{\xi}\, d\xi - \int^{x_2} \frac{(f-d) - e\eta}{\eta}\, d\eta.$$

This sketch appears with slightly more detail in Arnold [3]. A similar version with less general growth rate functions is given in Freedman and Waltman [4].

The facts that M is attracting and E is stable under small perturbations, within M, of initial conditions are convincing evidence that E is stable under small perturbations in any direction in the phase space R^3 of A. A proof of this assertion can be based on the center-stable manifold Theorem. As a consequence, trajectories through points outside M, but sufficiently close to E, do not spiral out to "infinity" as they approach M.

Proposition 2. The equilibrium point E is stable.

Proof. Since M is attracting, there can be no unstable manifold through E and the (x_1, x_2, x_3) phase space is a center-stable manifold. Next, to show that M is a center manifold, the eigenvalues of the linear part of A written as $\dot{x} = f(x)$, with $f\colon R^3 \to R^3$, will be calculated.

$$\{Df\}_{E=(x_E, y_E, w_E)} = \left[\frac{\partial f^i}{\partial x_j}\right] E = \begin{bmatrix} 0 & -G_z^{-1}(c)e & G_z^{-1}(c)G_p'(f) \\ \dfrac{(f-d)}{e} G_z'(c) & 0 & 0 \\ 0 & 0 & -mG_z^{-1}(c)G_p'(f) \end{bmatrix}$$

where the primes denote differentiation. The eigenvalues of this matrix are $\lambda_1 = -mG_z^{-1}(c)G_p'(f) < 0$, $\lambda_2 = i(G_z^{-1}(c)(f-d)G_z'(c))^{1/2}$ and $\lambda_3 = -i(G_z^{-1}(c)(f-d)G_z'(c))^{1/2}$. The monotonicity of G_z and G_p imply that λ_1 is negative and λ_2 and λ_3 are imaginary. Thus, there is a one-dimensional stable manifold and a two-dimensional center manifold through E. That M is a center manifold can be verified by a straight forward computation showing that $M = V_c \cap R^3$, where V_c is the complex vector space spanned by the eigenvectors v_2 and v_3 corresponding to λ_2 and λ_3. The proof now follows from Proposition 1 and an application of the center-stable manifold theorem (Kelley [5]). The method used to prove Proposition 2 can be generalized to higher-dimensional systems when stability can be decided in an extracted center manifold.

Since M is attracting and has a phase portrait consisting of concentric cycles, it is natural to ask if bounded solutions starting outside M approach these cycles as limit cycles. This assertion also follows from center manifold theory.**

** The author is grateful for the referee's suggestions on this point.

Proposition 3. The ω-limit set of a bounded solution $x(x_0, t)$ of A with $x(x_0, 0) = x_0$, $x_0 \notin M$, contains a cycle. (Proposition 2 insures the existence of bounded solutions through x_0 near E.)

Proof. The cycles in M are stable in M, so the center stable manifold theorem insures their stability in R^3. Since M attracts and consists of stable oscillations, the approach to M is to a cycle with asymptotic phase.

3. Discussion. The method used in this note allows the use of properties of a known planar system to determine the stability of an equilibrium point for the overall system. In this example the subsystem turns out to be a good indicator of system behavior evolving from points outside but nearby the center manifold M. Indeed, numerical experiments have shown that the approach to M is quite rapid. Thus each orbit C in M serves as an approximate model of the system behavior for initial states (such as those whose distance from M is measured by a physically reasonable phosphorus concentration) on the trajectory approaching C which are not far removed from M. The periods of the orbits in M can be estimated by averaging techniques. For the Michaelis–Menten growth rate functions mentioned above, Lin and Kahn [6] give some results which can be used for this purpose.

To indicate some implications of the phase portrait of this system for applications, consider the problem of an undesirably high and persistent level of phosphorus concentration in a eutrophic lake. The fact that the solution trajectories of our system tend to M (in a short time) means that the problem can't be solved or even relieved for long by removing a quantity from the lake at some time. The model says that long-term control can be achieved only by modification of the phosphorus pool by external means. This suggests that the kinetics between the lake sediments and phosphorus pool is an important consideration in the design of phosphorus control strategies.

References

[1] D. M. DiToro, D. J. O'Connor and R. V. Thomann, *A dynamic model of phytoplankton population in the Sacramento-San Joaquin Delta*, Adv. Chem. Series **106**, Am. Chem. Soc., pp. 131–180 (1971)

[2] M. Hirsch and S. Smale, *Differential equations, dynamical systems and linear algebra*, Academic Press, New York, pp. 261–262, 1974

[3] E. M. Arnold, *Aspects of a zooplankton, phytoplankton, phosphorus system*, Ecological Modeling **5**, 293–300 (1978)

[4] H. I. Freedman and P. Waltman, *Perturbation of two-dimensional predator-prey equations*, SIAM J. Appl. Math. **28**, 1–11 (1975)

[5] A. Kelley, *Stability of the center-stable manifold*, J. Math. Anal. Appl. **18**, 336–344 (1967)

[6] J. Lin and P. B. Kahn, *Averaging methods in predator-prey systems and related biological models*, J. Theor. Biol. **57**, 73–102 (1976)