Linearizing Ecological Models with Time-Varying Parameters

GEOFFREY T. EVANS
Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

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ABSTRACT

An ecological model with time-varying parameters can be linearized about a point which is either a local equilibrium or fixed in time, but not in general both. Each choice has its advantages, but neither choice is anywhere near as useful as the linearization of a model with constant parameters. Linearizations of a model of annual plankton cycles can capture some qualative behavior of the original nonlinear model.

Given a system of coupled, nonlinear, autonomous differential equations which describe the dynamics of an ecosystem (or anything else), one of the first methods of analysis is to find a fixed point of the system and look at a linear expansion of the equations about that point. Since the system is autonomous, we end up with a system of homogeneous linear equations with constant coefficients whose behavior is fully understood. However, many problems in ecology involve the effects of large periodic changes in the environment: for example, daily or annual cycles of light or temperature. Discussion of such problems involves equations in which some of the parameters are functions of time. Now when we try to linearize about some point, it is in general not possible to find a point which is both fixed in time and always an equilibrium. We can meet one requirement or the other, but there is no longer a single natural point to linearize about, and different choices have different properties. Moreover, the linear approximation will no longer be a homogeneous equation, and will generally not have constant coefficients. This has good and bad consequences. On the one hand, it leads to linear approximations which have richer behavior; on the other hand, there is less analytical machinery to apply to them.

Present address: Northwest Atlantic Fisheries Centre, PO Box 5667,
St. John's, Newfoundland, Canada A1C 5X1

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52 Vanderbilt Ave., New York, NY 10017 0025-5564/82/08155+07$02.75

Suppose we start with a differential equation

$$\frac{dX}{dt} = F(X,t), \tag{1}$$

where X can be a vector. We make a linear approximation about a general reference point $X_0(t)$ as follows:

$$\begin{aligned}\frac{d}{dt}[X(t)-X_0(t)] &= \frac{dX}{dt}-\frac{dX_0}{dt}\\ &= F(X,t)-\frac{dX_0}{dt}\\ &\simeq F(X_0,t)+J_0(t)(X-X_0)-\frac{dX_0}{dt},\end{aligned} \tag{2}$$

where $J_0(t)$ is the Jacobian or community matrix $\frac{\partial F}{\partial X}(X_0,t)$. This approximation is a linear differential equation in $X-X_0$, nonhomogeneous, with variable coefficients.

There are some natural choices for the reference point $X_0(t)$. One choice is the quasiequilibrium trajectory $X^*(t)$ [1] which satisfies $F(X^*(t),t)=0$: each point on the trajectory is a point which would be in equilibrium if the parameters were held constant at their current values. We then have

$$\frac{d}{dt}(X-X^*) \simeq J^*(t)(X-X^*)-\frac{dX^*}{dt}. \tag{3}$$

Another choice is to fix X_0 at a value at which the system is in equilibrium for some average value of the parameters. (We're on somewhat shaky ground here, not knowing what sort of averaging is appropriate for the original nonlinear equation.) Then

$$\frac{d}{dt}(X-X_A) = F(X_A,t)+J_A(t)(X-X_A). \tag{4}$$

Intuitively, the quasiequilibrium and average linearizations are appropriate, respectively, for perturbations which vary slowly and quickly relative to some internal time scale of the equations: one expects a system to track slow perturbations and average over fast ones.

A linear differential equation can incorporate nonlinear functions of the independent variable, and our approximations so far haven't tried to linearize them. Indeed, approximating with nonconstant, linear functions of t would be a silly way to represent periodic perturbations. Silvert and Smith [4] consider (1) in the form

$$\frac{dX}{dt} = G(X,\phi(t))$$

where ϕ is a periodic function of t (or possibly a vector of such functions).

They then make a bilinear expansion of G in X and ϕ: if $G(X_A,0)=0$, then

$$\frac{d}{dt}(X-X_A)\simeq\frac{\partial G}{\partial X}(X_A,0)\cdot(X-X_A)+\frac{\partial G}{\partial\phi}(X_A,0)\cdot\phi(t). \qquad (5)$$

This carries linearization as far as one reasonably can: let us call it the ultralinear approximation. It is a nonhomogeneous linear equation, with time-dependent forcing and constant coefficients, and its behavior is fully understood. [The ultralinear approximation is not uniquely defined. For example, in a model driven by square wave forcing, it would be natural to think of $\phi(t)$ as a square wave, but legitimate to think of it as a sine wave, with a different form of G and a different ultralinearization.]

An approximation is useful if it preserves some properties of the original equation, while simplifying calculations. For equations with constant parameters, local stability is preserved under linearization, and is easy to decide for the linear model. The ultralinear approximation to equations with time-varying parameters does not always possess this property. Consider, for example, the Mathieu equation

$$\ddot{x}+\delta\dot{x}+(\rho+a\sin\omega t)x=0,$$

or, in the notation used above,

$$\begin{pmatrix}\dot{x}\\ u\end{pmatrix}=\begin{pmatrix}0 & 1\\ -(\rho+a\sin\omega t) & -\delta\end{pmatrix}\begin{pmatrix}x\\ u\end{pmatrix}.$$

The ultralinear approximation using $\phi(t)=\sin\omega t$ is

$$\ddot{x}+\delta\dot{x}+\rho x=0.$$

$x=0$ is a stable equilibrium for the ultralinear, damped linear oscillator equation, but may be an unstable equilibrium for the original Mathieu equation [2, 3]. (The Mathieu equation is its own quasiequilibrium and average approximation.)

For the example considered in [4]

$$\begin{aligned}\dot{x}&=rx(1-x/k)-xy+a\phi(t),\\ \dot{y}&=-ky+xy,\end{aligned}$$

the ultralinear approximation is the same as the average equilibrium approximation. However, in this model the term $a\phi(t)$ looks a bit strange: a fluctuating source or sink of prey organisms unrelated to any existing population. A possibly more realistic perturbation of the Lotka-Verhulst equation was considered in [5]:

$$\begin{aligned}\dot{X} &= r(t)X - qX^2 - CXY,\\ \dot{Y} &= XY - Y\end{aligned} \tag{6}$$

(at least with these equations the populations cannot become negative). The quasiequilibrium approximation is

$$\ddot{x} + q\dot{x} + [r(t) - q]x = r'(t);$$

the average equilibrium approximation is

$$\ddot{x} + [q + \bar{r} - r(t)]\dot{x} + (\bar{r} - q)x = r'(t);$$

and the ultralinear approximation is

$$\ddot{x} + q\dot{x} + (\bar{r} - q)x = r'(t).$$

Strogatz and Evans [5] compared the quasiequilibrium and average equilibrium approximations with the original model for a range of frequencies of $r(t)$. They found that the intuitive ideas of quasiequilibrium as slow change and average equilibrium as fast change held up quite well. For example, the quasiequilibrium approximation came close to the nonlinear model when r varied slowly, but diverged further and sometimes exhibited subharmonic resonance when r varied quickly. The resonant frequency of the ultralinear model provides a reasonable estimate of the boundary between fast and slow time.

Linear models can account for many of the features of the nonlinear model of annual plankton cycles of Evans and Parslow [1]. The model is

$$\begin{aligned}\frac{dP}{dt} &= \alpha(t)P - \frac{P-0.1}{P+0.9}H,\\ \frac{dH}{dt} &= \frac{0.5(P-0.1)}{P+0.9}H - 0.07\,H,\end{aligned} \tag{7}$$

where $\alpha(t) = 0.118 - 0.114\cos\omega t$, $\omega = 2\pi/T$ (the numbers are chosen to represent conditions in the North Atlantic), and the steady annual cycle, after starting transients have died out, is shown in Figure 1 for various values of T. Straightforward calculation yields the various linearizations:

$$\begin{aligned}\text{quasi:}\ &\ddot{p} + 0.388\alpha(t)\dot{p} + [0.097\alpha(t) + 0.388\alpha'(t)]p = 0.263\alpha'(t),\\ \text{average:}\ &\ddot{p} + [0.163 - \alpha(t)]\dot{p} + [0.011 - \alpha'(t)]p = 0.263\alpha'(t),\\ \text{ultra:}\ &\ddot{p} + 0.163\,\dot{p} + 0.011\,p = 0.263\alpha'(t),\end{aligned}$$

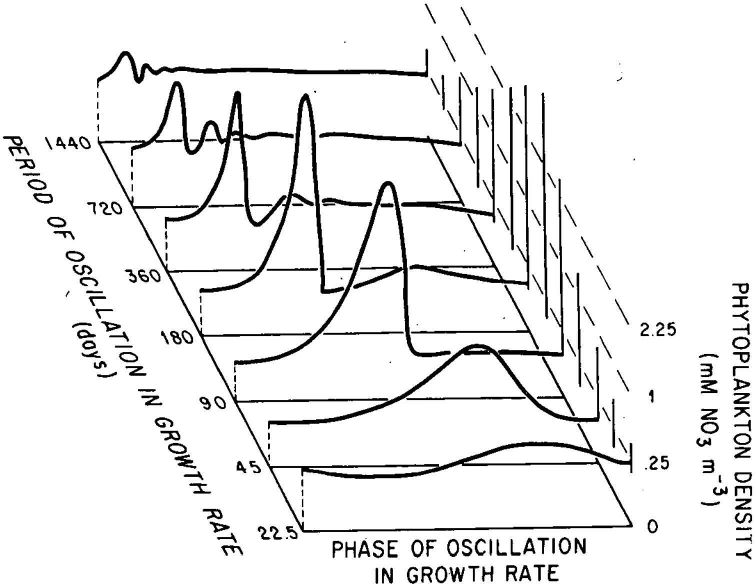

FIG. 1. The steady cycle of phytoplankton in the nonlinear model (7), for various values of T.

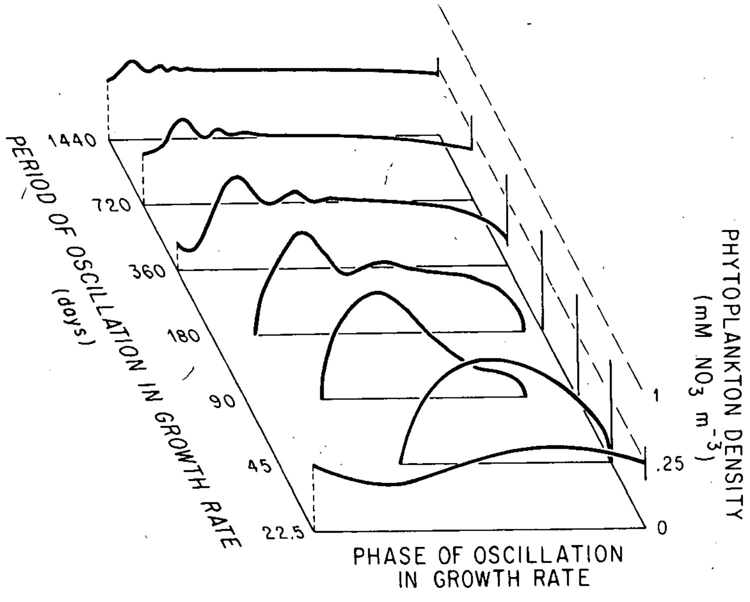

FIG. 2. The steady cycle of phytoplankton in the quasiequilibrium approximation.

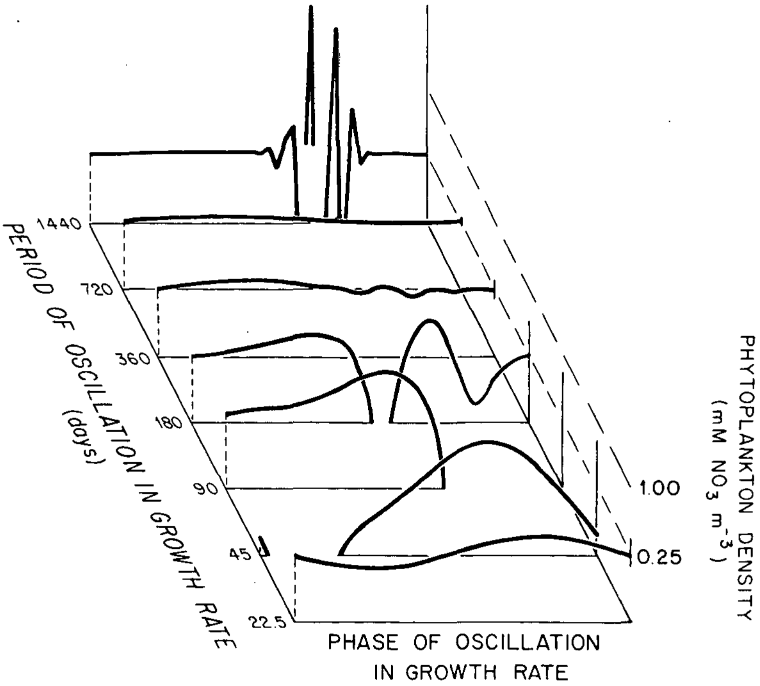

FIG. 3. The steady cycle of phytoplankton in the average equilibrium approximation.

whose steady cyclic solutions are graphed in Figures 2–4. When $T = 360$ (much longer than the resonant period) we would expect the quasiequilibrium approximation to work best, and it does. For very large T, the average equilibrium (short period) approximation breaks down completely, a victim of negative damping. Both long and short period linearizations display nonsinusoidal response to sinusoidal input (the ultralinear model of course does not). Many of the features of the annual cycle, including the spring outburst, various aftershocks in the summer, and the necessity of being reasonably near to resonance in order to have blooms, are captured in the quasiequilibrium model. The main difference between it and the nonlinear model is the size of the peak, which appears to be due to the influence of the other equilibrium at $P = 0$, $H = 0$ which the linear model doesn't know about. By contrast, the ultralinear model captures almost none of the interesting features.

One message of this work may be that linear approximations to equations with varying parameters have little to offer. The quasiequilibrium approximation does look qualitatively like the original, and it is interesting to see that

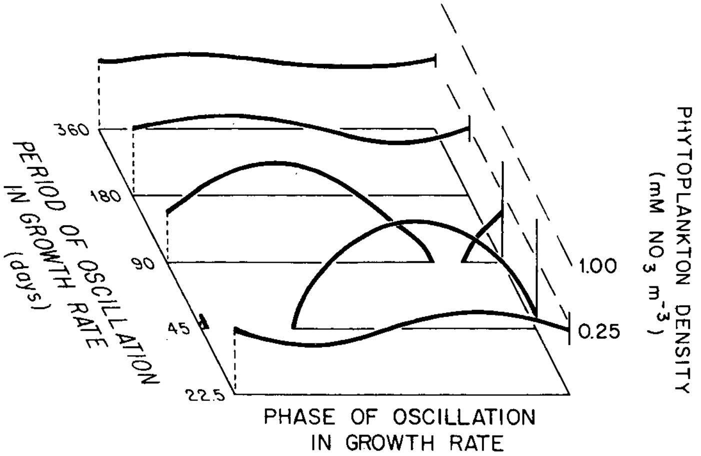

FIG. 4. The steady cycle of phytoplankton in the ultralinear approximation.

features like the aftershocks following the main bloom are in fact features of a system of linear equations. However, the quantitative agreement is often poor, computations are no easier than for the nonlinear original, and there is no theory linking the original and its approximation. The ultralinear approximation is poor even qualitatively, and although its stability properties are easy to compute, we have seen that they need not be those of the equation it approximates.

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