

# Chaos and Control Action in a Kolmogorov Type Model for Food Webs with Harvesting or Replenishment

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**ABSTRACT** In this paper, we apply the feedback decoupling technique to a Kolmogorov type model for three species food webs with harvesting or replenishment. A feedback control law is derived to decouple the effect of predators from prey dynamics. It is found that the necessary and sufficient conditions for the existence of the decoupling control law rely on the persistence of the prey population and the fact that the specific growth rate of prey depends explicitly on the superpredator population density at any moment in time. It is shown that, without any control action of regulated replenishment or harvesting, irregular or chaotic behavior is possible in such a process for certain ranges of the system parameters. This is illustrated by the construction of a bifurcation diagram for a model of a three-species food web with response functions of the Holling type II. To make the system output or variables less sensitive to irregular disturbances, the feedback control technique is applied which produces the desirable effect of stabilizing the system. When such a model is applied to an activated sludge process, the objective of the control action can also be to regulate the inputs in order to obtain satisfactory water quality.

**KEYWORDS:** Kolmogorov model - control - chaos - stabilization.

## INTRODUCTION

Ecological models may be classified as either strategic or tactical, as identified by Holling (1966). Tactical models are relatively more complex. They usually rely on a great amount of supporting data, and are used for making specific predictions. Strategic models, on the other hand, can provide broader insights into possible behaviors of the system based on simple assumptions (McLean and Kirkwood, 1990), such as the model considered by Hader and Freedman (1989) for predator-prey populations with parasitic infection, or the model of continuous bioreactor analyzed by Lenbury and Orankitjaroen (1995).

As Mosetti (1992) has observed, the control of ecological systems for management purposes is a difficult task due to the amount of supporting data needed as well as the conflicting management goals. In this respect, a simple reduced strategic model which requires fewer data for calibration can be quite a useful tool as a building block for the study of real problems in order to give a decision-maker some preliminary results.

The Kolmogorov model of population growth is, mathematically, probably the most general model of the types considered to date. It incorporates the

principle that the growth rate of species is proportional to the number of interacting species present. The classical ecological models of interacting populations have typically focussed on two species. The first Kolmogorov model, developed in 1936, was expanded on by several researchers, including May (1972) and Albrecht et al (1974). Such models have been applied to plant and animal dynamics both in aquatic and terrestrial environments (Hastings and Powell, 1991). However, mathematical developments reveal that community models involving only two species as the building blocks may miss a great deal of important ecological behavior. In fact, it is now recognized that in community studies the essence of the behavior of a complex system may only be understood when attempts are made to incorporate the interactions among a larger number of species.

Researchers in the last decade or so have turned their attention to the theoretical study of food webs as the "building blocks" of ecological communities and have been faced with the problem of how to couple the large number of interacting species. Behavior of the entire community is then assumed to arise from the coupling of strongly interacting pairs. The approach is attractive by its virtue of being tractable to theoretical analysis (Hastings and Powell, 1991). Yet, many researchers have demonstrated that

very complex dynamics can arise in model systems with three species (Gilpin, 1979; Rai and Sreenivasan, 1993). For example, an investigation by Hastings and Powell (1991) showed that a continuous time model of a food chain incorporating nonlinear functional responses can exhibit chaotic dynamics in long-term behavior when reasonable parametric values are chosen. The key feature observed in this chaotic dynamics is the sensitive dependence on initial conditions.

In this paper, we first study the possibility of making the ecosystem output or variables less sensitive to irregular disturbances by applying the feedback control technique in order to stabilize the system. A feedback control law is derived to decouple the effect of the predators from the prey dynamics in a three-species food web of the Kolmogorov type. It is found that the necessary and sufficient conditions for the existence of the decoupling control law rely on the persistence of the prey population and the fact that the specific growth rate of prey depends explicitly on the superpredator population density at any moment in time.

We demonstrate by the construction of a bifurcation diagram for a model with response functions of the Holling type II that, without any control action, chaotic behavior may result through period doubling bifurcations. Once, the feedback decoupling control action is in place, the system can be stabilized and, in this context, we obtain a process which is more easily controllable.

Moreover, when the Kolmogorov type model with input / removal terms is applied to an activated sludge process, the main objective is perhaps to regulate the inputs in order to obtain satisfactory water quality. By simply fine-tuning the point in time when the control action is set in motion, the control technique considered here can be adjusted to give the desirable outcome.

### THE KOLMOGOROV TYPE MODEL AND THE STATIC DECOUPLING PROBLEM

We consider a general Kolmogorov type model of n-species food webs, which may be written as follows

$$\dot{X}_i = X_i F_i + u_i, \quad i = 1, 2, \dots, n \quad (1)$$

where  $X_i$  is the  $i$ -th species population density,  $u_i$  is the input/removal (replenishment/harvesting) rate

of the species which depends on the population densities of all n-species in the food web, and

$$F_i = F_i(X_1, X_2, \dots, X_n), \quad i = 1, 2, \dots, n$$

Such a system (1) can be used to model population dynamics of plant or animal interactions in an aquatic or terrestrial environment such as in the work of Lenbury and Siengsanon (1993), where an activated sludge process was analyzed using a three-species Kolmogorov type model. Also, in the study by Lenbury and Likasiri (1994), the dynamic behavior of a model for a food web was investigated through the application of the singular perturbation technique.

To formulate the static feedback decoupling problem, we let

$$\begin{aligned} X &= (X_1, X_2, \dots, X_n)^t \\ F &= (F_1, F_2, \dots, F_n)^t \\ U &= (u_1, u_2, \dots, u_{n-1})^t \end{aligned}$$

and

$$G(X) = \begin{pmatrix} 1 & 0 & 0 & \dots & 0 \\ 0 & 1 & 0 & \dots & 0 \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \cdot & \cdot & \cdot & \dots & 0 \\ 0 & 0 & 0 & \dots & 1 \\ 0 & 0 & 0 & \dots & 0 \end{pmatrix}$$

an  $n \times (n - 1)$  matrix.

Then, the system of equations (1) with  $u_n = 0$  can be rewritten as

$$\dot{X}_i = X_i F_i + [GU]_i, \quad i = 1, 2, \dots, n \quad (2)$$

If we now take  $X_1$  to be the state variable which is more easily regulated externally, the "outcome" or output of equation (2) is then assumed to be

$$H(X) \equiv (X_n, X_2, \dots, X_{n-1})^t \quad (3)$$

The static feedback decoupling problem, as stated in the work by Mosetti (1992) and explained in greater detail by Isidori (1985), can be defined as follows. "Given equations (2) and (3), we need to find a feedback law  $\alpha(X)$  and a state-dependent change of coordinates  $\beta(X)$  in the input space  $\mathcal{R}^m$  such that the closed-loop system formed by the combination of (2) and (3) with the control law

$$U = \alpha(X) + \beta(X)V \quad U \in \mathfrak{R}^{n-1}, V \in \mathfrak{R}^{n-1},$$

$$\alpha(X) = -A^{-1}(X)J$$

and

$$\beta(X) = A^{-1}(X)$$

has the *i*-th output dependent only on the *i*-th component of the new input *V*".

In order to accomplish this, we introduce the following notation. Letting

where

$$\nabla^* = \left( X_1 \frac{\partial}{\partial X_1} \quad X_2 \frac{\partial}{\partial X_2} \quad \dots \quad X_n \frac{\partial}{\partial X_n} \right)'$$

$$J = (\nabla_F^{\rho_1+1} H_1, \nabla_F^{\rho_2+1} H_2, \dots, \nabla_F^{\rho_n+1} H_n)'$$

provided that the decoupling matrix *A*(*X*) is nonsingular.

then the operator  $\nabla_F$  is defined as

$$\nabla_F H_i = F \nabla^* H_i$$

*Proof* We refer readers to Isidori's work (1985) for the proof of this theorem in the general case.

where *H<sub>i</sub>* is the *i*-th component of the vector *H*(*x*) defined in (3).

In order to establish the control law for the Kolmogorov type model, we need to first prove the following Lemma.

We then understand that

**Lemma 1** The characteristic number  $\rho_1 = 1$  and  $\rho_i = 0, i = 2, 3, \dots, n - 1$ .

$$\nabla_F^k H_i = \nabla_F (\nabla_F^{k-1} H_i)$$

*Proof* In the case of  $\rho_1 (i = 1)$ , we first consider  $\text{grad} (\nabla_F^k H_1) G_j, j = 1, 2, \dots, n - 1$ , when  $k = 0$ . We find that

while  $\nabla_F^0 H_i = H_i$ ,

$$\text{grad} (\nabla_F^0 H_1) G_j = \text{grad} (X_n) G_j$$

Further, the characteristic number  $\rho_i$  associated with the output *H<sub>i</sub>* can be defined as the largest integer such that for all  $k < \rho_i$

$$\text{grad}(\nabla_F^k H_i) G_j = 0 \quad , j = 1, 2, \dots, n - 1$$

where *G<sub>j</sub>* is the *j*-th column of the matrix *G*.

Accordingly, the decoupling matrix *A*(*X*) associated with equations (2) and (3) is the  $(n - 1) \times (n - 1)$  matrix

$$A(X) = (a_{ij})$$

$$= \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \\ \frac{\partial X_n}{\partial X_1} \quad \frac{\partial X_n}{\partial X_2} \quad \dots \quad \frac{\partial X_n}{\partial X_n} \\ 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} \leftarrow j\text{-th row}$$

where

$$a_{ij} = \text{grad}(\nabla_F^{\rho_i} H_i) G_j$$

$$= \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \\ 0 \\ 0 \\ \dots \\ 0 \\ 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} \leftarrow j\text{-th row}$$

The static state-feedback decoupling theory (Mosetti, 1992) can be stated as follows.

**Theorem 1** A necessary and sufficient condition for the existence of  $(\alpha, \beta)$  which solves the decoupling problem is that the decoupling matrix *A*(*x*) is nonsingular. If this is the case then a possible decoupling control is given by

= 0  
since  $j < n$ .

However, when  $k = 1$ , we find

$$\begin{aligned} \text{grad} \left( \nabla_{F_n}^1 H_1 \right) G_j &= \text{grad} \left( \nabla_{F_n}^1 X_n \right) G_j \\ &= \text{grad} \left\{ \left( F_1 \quad F_2 \quad \dots \quad F_n \right) \begin{pmatrix} X_1 \frac{\partial X_n}{\partial X_1} \\ X_2 \frac{\partial X_n}{\partial X_2} \\ \vdots \\ X_n \frac{\partial X_n}{\partial X_n} \end{pmatrix} \right\} G_j \\ &= \text{grad} \left( F_n X_n \right) G_j \end{aligned}$$

$$= \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \\ 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} \leftarrow j\text{-th row}$$

$$\begin{aligned} &= \frac{\partial}{\partial X_j} \left( X_n F_n \right) = X_n \frac{\partial F_n}{\partial X_j} \\ &\neq 0 \end{aligned}$$

if we assume that  $F_n$  is an explicit function of  $X_j$  for all  $j = 1, 2, \dots, n - 1$ . Therefore,  $\rho_1 = 1$ .

Now, for  $\rho_i, i = 2, 3, \dots, n - 1$ , we consider

$\text{grad} \left( \nabla_{F_i}^k H_1 \right) G_j$  for  $i \geq 2$  when  $k = 0$ , and obtain

$$\text{grad} \left( \nabla_{F_i}^0 H_i \right) G_j = \text{grad} \left( X_i \right) G_j$$

$$= \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \\ \frac{\partial X_i}{\partial X_1} \quad \frac{\partial X_i}{\partial X_2} \quad \dots \quad \frac{\partial X_i}{\partial X_j} \quad \dots \quad \frac{\partial X_i}{\partial X_n} \\ 0 \\ \vdots \\ 0 \end{pmatrix} \leftarrow j\text{-th row}$$

$$= \begin{cases} 1 & \text{if } i = j \\ 0 & \text{if } i \neq j \end{cases}$$

Thus,  $\text{grad} \left( \nabla_{F_i}^0 H_i \right) G_j \neq 0$  for some  $j$ , which means that  $\rho_i = 0$  for  $i = 2, 3, \dots, n - 1$ .

We can now derive the entries  $a_{ij}$  of the decoupling matrix  $A(x)$  as follows.

$$\begin{aligned} a_{ij} &= \text{grad} \left( \nabla_{F_i}^1 H_1 \right) G_j \\ &= \text{grad} \left\{ \left( F_1 \quad F_2 \quad \dots \quad F_n \right) \begin{pmatrix} X_1 \frac{\partial X_n}{\partial X_1} \\ X_2 \frac{\partial X_n}{\partial X_2} \\ \vdots \\ X_n \frac{\partial X_n}{\partial X_n} \end{pmatrix} \right\} G_j \\ &= \text{grad} \left( F_n X_n \right) G_j \\ &= X_n \frac{\partial F_n}{\partial X_j} \end{aligned}$$

for  $j = 1, 2, \dots, n - 1$ .

On the other hand, for  $i \geq 2, \rho_i = 0$ , we therefore obtain

$$\begin{aligned} a_{ij} &= \text{grad} \left( \nabla_{F_i}^0 H_i \right) G_j \\ &= \begin{cases} 1 & \text{if } i = j \\ 0 & \text{if } i \neq j \end{cases} \end{aligned}$$

for  $j = 1, 2, \dots, n - 1$  and  $i = 2, 3, \dots, n - 1$ . Thus, the decoupling matrix is

$$A(x) = \begin{bmatrix} X_n \frac{\partial F_n}{\partial X_1} & X_n \frac{\partial F_n}{\partial X_2} & \dots & \dots & \dots & X_n \frac{\partial F_n}{\partial X_{n-1}} \\ 0 & 1 & 0 & 0 & \dots & 0 \\ 0 & 0 & 1 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \dots & \vdots \\ 0 & 0 & 0 & 0 & \dots & 1 \end{bmatrix}$$

### APPLICATION TO THREE SPECIES FOOD WEBS

**The control law**

We now derive the control law for the Kolmogorov type model for a three species food web which can be written as

$$\dot{x} = x f(x, y, z) + u_1 \tag{4}$$

$$\dot{y} = y g(x, y, z) + u_2 \tag{5}$$

$$\dot{z} = z h(x, y, z) \tag{6}$$

where  $z$  is the prey population density,  $y$  and  $x$  are the predator and superpredator, respectively, while  $u_1$  and  $u_2$  are the corresponding input rates. Then,

$$X = (x \quad y \quad z)'$$

$$F = (f \quad g \quad h)$$

$$U = (u_1 \quad u_2)'$$

$$G(X) = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 0 \end{pmatrix}$$

and the output is

$$H(X) = (z \quad y) \tag{7}$$

The main result of the static state-feedback decoupling theory can be stated as follows.

**Theorem 2A** necessary and sufficient condition for the existence of  $(\alpha, \beta)$  which solves the decoupling problem for equations (4)-(6) is that the prey population persists and the specific growth rate of prey  $h$  depends explicitly on the superpredator population density. If this is the case, then a possible decoupling control is given by:

$$\alpha(X) = \left( -xf - \frac{h}{h_x}(zh_z + h) - yg \right)'$$

$$\beta(X) = \begin{pmatrix} \frac{1}{zh_x} & \frac{h_y}{h_x} \\ 0 & 1 \end{pmatrix}$$

and

$$u_1 = -xf - \frac{h}{h_x}(zh_z + h) + \frac{1}{zh_x}v_1 - \frac{h_y}{h_x}v_2 \tag{8}$$

$$u_2 = -yg + v_2 \tag{9}$$

*Proof* From Lemma 1, we found that  $\rho_1 = 1$  and  $\rho_2 = 0$ . We then obtain

$$\nabla^* H_1 = (0 \quad 0 \quad z)'$$

so that  $\nabla_F^1 H_1 = zh$ , and  $\nabla_F^0 H_2 = y$ . Therefore, we are led to the decoupling matrix

$$A(X) = \begin{pmatrix} zh_x & zh_y \\ 0 & 1 \end{pmatrix} \tag{10}$$

Thus,  $A(X)$  is nonsingular if and only if  $\det A \neq 0$ , namely

$$zh_x \neq 0 \tag{11}$$

This leads to the requirement that prey persists, in which case  $z > 0$ , and that  $h_x \neq 0$  or, equivalently,  $h$  depends explicitly on  $x$ .

Moreover, we have

$$\nabla_F^{\rho_1+1} H_1 = \nabla_F^2(z) = \nabla_F \{ \nabla F(z) \}$$

$$= \nabla_F \left\{ \begin{pmatrix} f & g & h \end{pmatrix} \begin{pmatrix} x \frac{\partial z}{\partial x} \\ y \frac{\partial z}{\partial y} \\ z \frac{\partial z}{\partial z} \end{pmatrix} \right\}$$

$$= \nabla_F(hz)$$

$$= \begin{pmatrix} f & g & h \end{pmatrix} \begin{pmatrix} x \frac{\partial}{\partial x}(hz) \\ y \frac{\partial}{\partial y}(hz) \\ z \frac{\partial}{\partial z}(hz) \end{pmatrix}$$

$$= xzfh_x + yzgh_y + z^2hh_z + zh^2$$

Also,

$$\nabla_{F'}^{\rho_2+1} H_2 = \nabla_{F'}^1 (J)$$

$$= \begin{pmatrix} f & g & h \end{pmatrix} \begin{pmatrix} x \frac{\partial y}{\partial x} \\ y \frac{\partial y}{\partial y} \\ z \frac{\partial y}{\partial z} \end{pmatrix}$$

$$= gy$$

Therefore,

$$J = (\nabla_{F'}^{\rho_1+1} H_1 \quad \nabla_{F'}^{\rho_2+1} H_2)$$

$$= \begin{pmatrix} xzf h_x + yzgh_y + z^2 h h_z + zh^2 \\ gz \end{pmatrix}$$

which leads us to

$$\alpha(X) = -A^{-1}(X)J$$

$$= - \begin{pmatrix} 1 & h_y \\ zh_x & h_x \end{pmatrix} \begin{pmatrix} xzf h_x + yzgh_y + z^2 h h_z + zh^2 \\ gz \end{pmatrix}$$

$$= \begin{pmatrix} -xf - zh \frac{h_z}{h_x} - \frac{h^2}{h_x} \\ -gy \end{pmatrix}$$

while

$$\beta(X) = A^{-1}(X)$$

$$= \begin{pmatrix} 1 & h_y \\ zh_x & h_x \end{pmatrix}$$

as claimed.

If we now let

$$\xi = \frac{dz}{dt} \tag{12}$$

then, since  $\dot{z} = zh$ , we have

$$\frac{d\xi}{dt} = \frac{\partial(zh)}{\partial x} \dot{x} + \frac{\partial(zh)}{\partial y} \dot{y} + \frac{\partial(zh)}{\partial z} \dot{z}$$

$$= zh_x(xf+u_1) + zh_y(yg+u_2) + (zh_z+h)zh = v_1$$

by applying the law in equations (8) and (9). Also, using (9), we find

$$\frac{dy}{dt} = yg + u_2 = v_2$$

Therefore, in the new coordinate system  $(\xi, y, z)$  we have

$$\frac{d\xi}{dt} = v_1 \tag{13}$$

$$\frac{dy}{dt} = v_2 \tag{14}$$

$$\frac{dz}{dt} = \xi \tag{15}$$

which clearly shows the decoupled structure, namely, each of the control variables acts only on one state variable. In fact, to keep the system decoupled, one approach is to set  $v_1 = 0$ . Then,  $\xi$  now remains constant, say at  $\xi(t_0)$ .

Integrating (15), we obtain

$$z(t) = \xi(t_0)t = z(t_0)$$

Thus, if  $\xi(t_0) = 0$  at a given initial time  $t = t_0$  when the control is activated, then

$$z(t) = z(t_0)$$

for any subsequent time  $t$ , whatever the fluctuation of  $v_2$ . This means that the prey population will not depend upon variations in the predator or superpredator. This is the essential feature of this technique, whereby the variations in the predator and superpredators are decoupled from the prey dynamics.

**Persistence conditions**

The question of persistence has been dealt with in various literature in all its versions : weak persistence; strong persistence; and uniform persistence

(Huaping and Zhien, 1991). We shall give, in the following Lemma, the persistence conditions for the standard food web consisting of equations (4)-(6) with

$$f(x, y, z) \equiv \frac{c_2 y}{b_2 + y} + \frac{c_3 z}{b_3 + z} - d \quad (16)$$

$$g(x, y, z) \equiv \frac{c_1 z}{b_1 + z} + \frac{a_2 x}{b_2 + y} - d \quad (17)$$

$$h(x, y, z) \equiv r\left(1 - \frac{z}{k}\right) - \frac{a_1 y}{b_1 + z} - \frac{a_3 x}{b_3 + z} \quad (18)$$

where  $d$  is the specific removal rate, and the terms

$$\frac{c_i z}{b_i + z}, \quad i = 1, 3$$

and

$$\frac{c_2 y}{b_2 + y}$$

are the population response functions of the Holling type II in which  $c_i$  is the maximum growth rate and  $b_i$  is the so-called half-saturation constant. The construction and analysis of the model in the case that  $u_1 = u_2 = 0$  may be found in the work of Lenbury and Likasiri (1994).

A standard food web given by equations (4)-(6) with (16)-(18) generally possesses only one positive equilibrium  $\hat{E} = (0, \hat{y}, \hat{z})$  and possibly only one

positive limit cycle  $\hat{\Gamma} = (0, \hat{y}(t), \hat{z}(t))$  for its subsystem (5)-(6) with  $x$  set equal to zero. Under this assumption, we are led to the following Lemma.

**Lemma 2**The food web given by equations (4)-(6) with (16)-(18) is persistent if

$$\frac{c_2 \hat{y}}{\hat{b}_2 + \hat{y}} + \frac{c_3 \hat{z}}{\hat{b}_3 + \hat{z}} > d \quad (19)$$

and (in the case that  $\hat{\Gamma}$  exists)

$$\frac{1}{T} \int_0^T \left( \frac{c_2 \hat{y}(t)}{\hat{b}_2 + \hat{y}(t)} + \frac{c_3 \hat{z}(t)}{\hat{b}_3 + \hat{z}(t)} \right) dt > d \quad (20)$$

where  $T$  is the period of the limit cycle  $\hat{\Gamma}$ , provided that  $u_1$  and  $u_2$  are identically zero. Otherwise, the population persists if

$$u_1(0, \hat{y}, \hat{z}) > 0 \quad (21)$$

and (in the case that  $\hat{\Gamma}$  exists)

$$\frac{1}{T} \int_0^T u_1(0, \hat{y}(t), \hat{z}(t)) dt > 0 \quad (22)$$

*Proof* This is a straight forward extension of the result given in one of our earlier papers (Lenbury and Likasiri, 1994) with the addition of the input/removal terms  $u_1$  and  $u_2$ .

Consequently, on substituting (16)-(18) into (8) and (9), one obtains the following decoupling feedback law.

$$u_1 = -x \left( \frac{c_2 y}{b_2 + y} + \frac{c_3 z}{b_3 + z} - d \right) + \frac{z(b_3 + z)}{a_3} \left( r \left( 1 - \frac{z}{k} \right) - \frac{a_1 y}{b_1 + z} + \frac{a_3 x}{b_3 + z} \right) \left( r \left( 1 - \frac{2z}{k} \right) - \frac{a_1 b_1 y}{(b_1 + z)^2} + \frac{a_3 b_3 x}{(b_3 + z)^2} \right) - \frac{b_3 + z}{a_3 z} v_1 - \frac{a_1 (b_3 + z)}{a_2 (b_1 + z)} v_2 \quad (25)$$

$$u_2 = -y \left( \frac{c_1 z}{b_1 + z} - \frac{a_2 x}{b_2 + y} - d \right) + v_2 \quad (26)$$

Figure 1 shows the time courses of the three state variables and the discharge rates  $u_1$  and  $u_2$  under normal conditions. We then chose to start our control action at the time  $t = t_0$  shown in the Figure

where  $\dot{z} = \xi(t_0) = 0$ . Thus, the effect of the control action is seen in Figure 2 when the new input  $v_1$  is set equal to zero and  $v_2$  is taken to be of the form

$$v_2 = A e^{-\gamma t} \sin \omega t$$

which corresponds to a damped sinusoidal input. The prey population density  $z$  becomes constant after the time  $t_0$ , while the predator and superpredator vary in a sinusoidal fashion with damping amplitude. As time passes, the new input rate  $v_2$  becomes negligibly small and the corresponding population densities of all three species are maintained at constant levels as a result.

**CONTROL ACTION ON A CHAOTIC SYSTEM**

In the work by Lenbury and Likasiri (1994), the model of a food web given by equations (4)-(6) with (16)-(18) and  $u_1 = u_2 = 0$  have been analyzed using the singular perturbation method. Explicit conditions were derived which separate the various dynamic structures and identify the limit cycles composed of alternately slow and fast transitions. In particular, it was found that the system will have a unique global attractor in the first octant which is a low-frequency limit cycle with a period of high-frequency oscillation if the following conditions hold on the system parameters.

$$\frac{4a_1b_1b_2c_1k}{(b_1+k)^2} < \frac{r(b_3-b_1)[c_1(k-b_1)-d(b_1+k)]}{2b_3+k-b_1} \tag{27}$$

$$k(c_1-d) > b_1(c_1+d) \tag{28}$$

$$\frac{b_2(c_1k-b_1d-dk)}{a_2(b_1+k)} < \frac{b_1b_3(a_1+r)[c_1(k-b_3)-d(2b_1+k-b_3)]}{(a_1b_3-a_3b_1d)(2b_1+k-b_3)+a_3b_1c_1(k-b_3)} \tag{29}$$

and  $\frac{c_i}{d}$  ( $i=1,2,3$ ) are sufficiently high.

We now carry out a numerical investigation to determine the ranges of parametric values where chaotic dynamics were likely. Our choice of parameters was guided by two factors. First, we follow the example of the work by Lenbury and Likasiri (1994) and assume that the ecological system under study may be characterized by highly diversified dynamics. Accordingly, we chose parametric values so that the time response of the

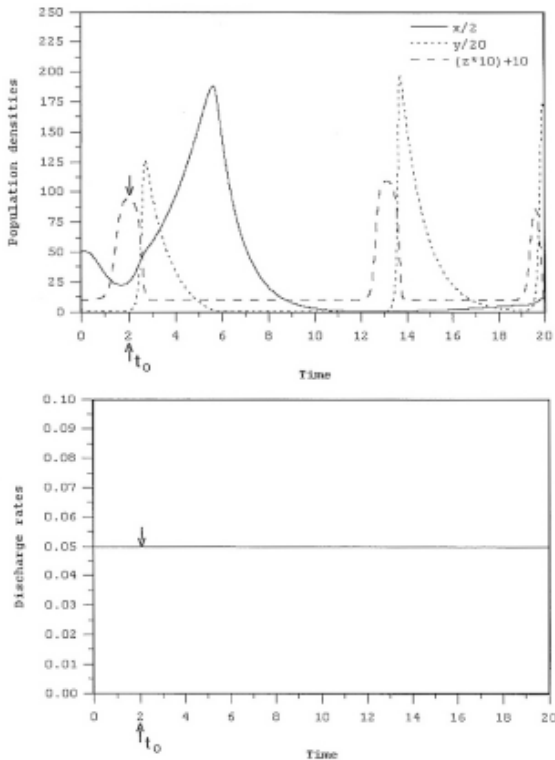


Fig 1. Time evolution of superpredator  $x$  (—), predator  $y$  (.....), and prey  $z$  (-----), and constant discharge rates  $u_1$  and  $u_2$  with no control action. Here,  $a_1 = 0.05$ ,  $a_2 = 0.5$ ,  $a_3 = 0.5$ ,  $b_1 = 4.0$ ,  $b_2 = 8.0$ ,  $b_3 = 8.0$ ,  $c_1 = 15.0$ ,  $c_2 = 1.5$ ,  $c_3 = 1.5$ ,  $d = 1.0$ ,  $k = 10.0$ ,  $r = 10.0$ ,  $u_1 = 0.05$ , and  $u_2 = 0.05$ .

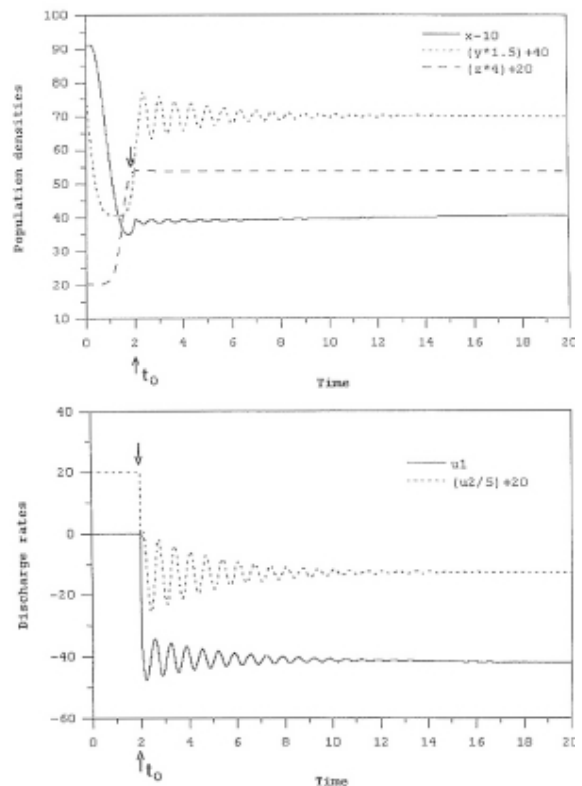


Fig 2. Time evolution of superpredator  $x$ , predator  $y$ , and prey  $z$ , and discharge rates  $u_1$  and  $u_2$  under control operations starting at  $t = t_0$  with  $v_1 = 0$  and  $v_2 = 100e^{t/3} \sin 3\pi t$ , and other system parameters as in Figure 1.



system equations (4)-(6) increases from top to bottom. The prey is assumed to have very fast dynamics, while the predator and superpredator have intermediate and slow dynamics, respectively. Phytoplankton - zooplankton - fish is a typical example of an ecosystem where the time response increases with the trophic levels. In fact, most food chains observed in nature have time responses increasing along the chain from top to bottom.

Second, as has been noted by many previous workers (Hastings and Powell, 1991; Rai and Sreenivasan, 1993), one may be able to generate chaos in a nonlinear system which already exhibits limit cycle behavior. We therefore chose parametric values to satisfy the conditions (27)-(29) found by Lenbury and Likasiri (1994) to lead to a solution trajectory on a low frequency limit cycle with bursts of high frequency oscillations.

Our investigation involves letting the system run for 100,000 time steps and examining only the last 80,000 time steps to eliminate transient behavior. We use values of  $b_1$  between 4.0 and 4.5, changing  $b_1$  in steps of 0.01. The relative maximum values  $x_{max}$  of  $x$ , collected during the last 80,000 time steps, are plotted as a function of  $b_1$  as shown in Figure 3.

We discover in this bifurcation diagram the appearance of a period doubling route to chaos, similar to those exhibited by one-dimensional difference equations such as the logistic population model. Apparently, the system of equations (4)-(6) with (16)-(18) exhibits chaotic dynamics for the values of  $b_1$  between 4.22 and 4.32. Windows in the bifurcation diagram are observed for  $b_1$  in the ranges of  $4.26 < b_1 < 4.32$  and  $4.34 < b_1 < 4.40$ , for example, where periodicity is re-established.

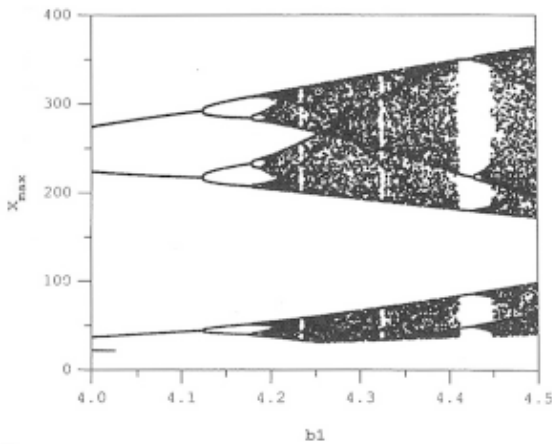


Fig 3. Bifurcation diagram for the model system (4)-(6) with (16)-(18), using the value of  $b_1$  from 4.0 to 4.5, and other parametric values as in Figure 1. Plots are of the relative maximum values of  $x$  vs  $b_1$ .

Figure 4 shows the solution trajectory of the model system (4)-(6) with (16)-(18) using  $b_1 = 4.3$  in the chaotic range identified in the bifurcation diagram. The strange attractor is projected onto the  $(y, z)$ -plane in Figure 4, and the corresponding chaotic time courses of  $x$ ,  $y$  and  $z$  in uncontrolled conditions are shown in Figure 5 with the discharge rates  $u_1$  and  $u_2$ .

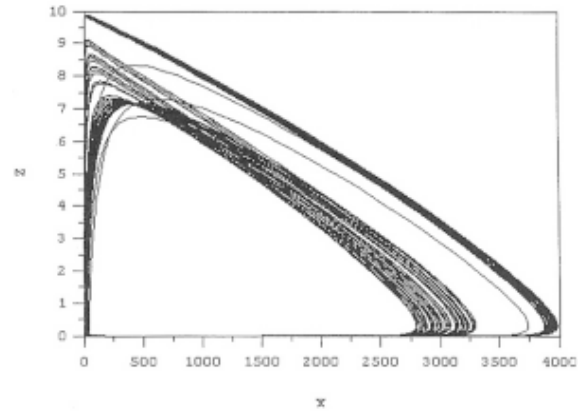


Fig 4. Projection onto the  $(y,z)$ -plane of the strange attractor obtained on simulating the model system (4)-(6) with (16)-(18) using  $b_1 = 4.3$  in the chaotic range identified in the bifurcation diagram, and other parametric values as in Figure 1.

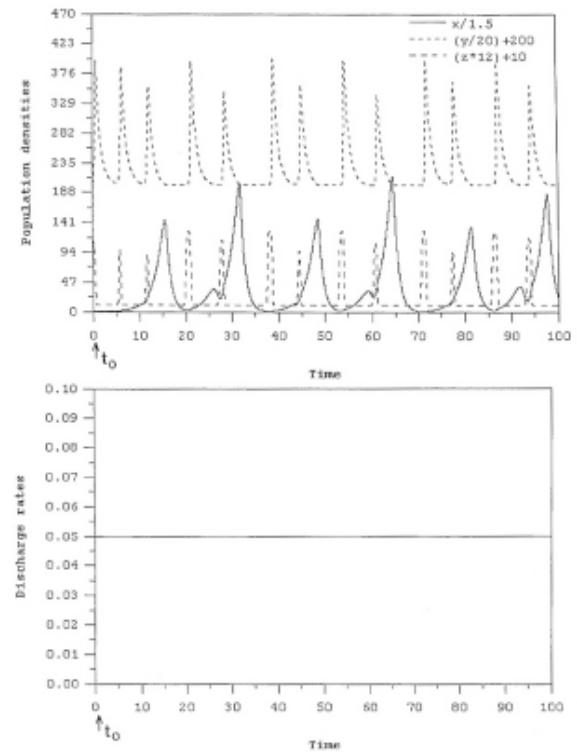


Fig 5. Time courses of the three state variables exhibiting chaotic behavior when there is no control action, and parametric values are as in Figure 4.

Figure 6 shows the time courses of  $z$  starting from two different initial conditions. The difference in the two starting values of  $z$  is merely 0.01. We observe that, while the two plots follow indistinguishable paths during the initial short period, they begin to diverge and follow noticeably different paths eventually. This clearly demonstrates the sensitivity to initial conditions which is the essential characteristics of chaotic behavior.

Figure 7 then shows the effect of the control action on the chaotic system of Figure 4 with  $v_1$  set equal to zero and  $v_2$  irregular. Here, the control is initiated at the point where  $\dot{z}(t_0) = 0$  and  $\ddot{z}(t_0) < 0$ . Once the control action is in place, prey is maintained at a constant high level, while the variations in predator, superpredator, and the discharge rates  $u_1$  and  $u_2$  are irregular.

On applying the model to an activated sludge process, the state variables can be nutrient-bacteria- protozoa, for example, and the objective of the control action is perhaps to regulate the inputs in order to obtain satisfactory water quality. In such a case, it is desirable to start the control action when the variable  $z$  falls to its first lowest point ( $\dot{z}(t_0) = 0$  and  $\ddot{z}(t_0) > 0$ ). We will then be able to maintain  $z$  at a constant low level.

## CONCLUSION

It has been demonstrated that while some inherent properties of a nonlinear model permit the emergence of chaotic dynamics, they also allow the existence of a feedback decoupling control mechanism. Since the behavior of the entire community is believed to arise from the coupling of these strongly interacting species, the detection and possibility of control of a chaotic system is of critical importance. If a generalization from a food web model depends crucially upon behavior after a long time, then the role of chaos may be extremely relevant.

On a cautious note, the question of whether or not deterministic chaos actually occurs in a real ecosystem is still open to discussion. As has been observed by Sabin and Summers (1993), "... there is still no generally accepted example of a chaotic ecosystem in nature. Moreover, some traditional ecologists believe that irregular oscillations in natural populations are attributed to random perturbations or noise in the environment rather than being the result of the intrinsic nonlinear dynamics of the system".

Perhaps the first concrete example of occurrence of chaos in nature is due to Sugihara and May (1990) who showed that there underlies a three-dimensional chaotic attractor in the dynamics of marine planktonic diatoms. Despite the fact that the corresponding time series is very noisy, they have been able to extract the information which allows them to describe some of the dynamics as deterministic chaos.

Such irregular behavior is not desirable when one is interested in managing a system, since chaos allows

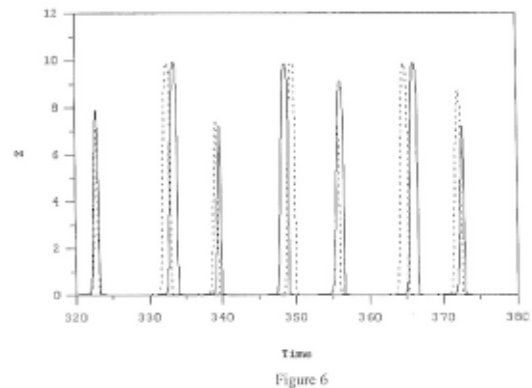


Figure 6. Divergence of solutions when the system exhibits chaotic dynamics. Prey densities are plotted for two different initial conditions (— and - - -), differing only by 0.01 in  $z$ .

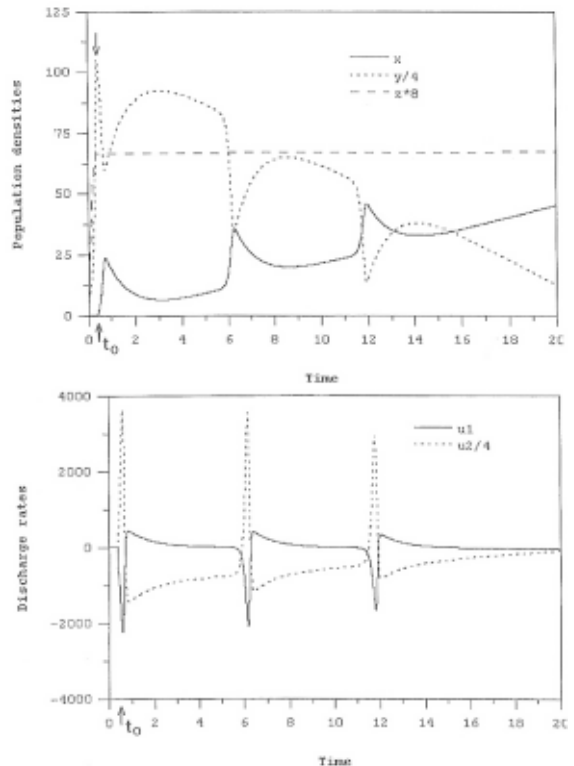


Figure 7. Time evolution of the three state variables, using parametric values of Figure 5. The chaotic system becomes stabilized when the control action is initiated at  $t = t_0$  with  $v_1 = 0$  and  $v_2$  irregular.

only short-term predictions. Thus, a feedback control mechanism such as the one we have been discussing provides an attractive and useful tool to regulate the process since it can stabilize the system and make it less sensitive to the exogenous disturbances or noise input. The present study has potential to act as a spring board for a generalization to more complex models in the hope of obtaining a more manageable system.

## ACKNOWLEDGMENT

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