Applications of Mathematics

Banibrata Mukhopadhyay; Rakhi Bhattacharyya

Modeling the role of constant and time varying recycling delay on an ecological food chain

Applications of Mathematics, Vol. 55 (2010), No. 3, 221–240

Persistent URL: http://dml.cz/dmlcz/140396

55 (2010) APPLICATIONS OF MATHEMATICS No. 3, 221–240

MODELING THE ROLE OF CONSTANT AND TIME VARYING RECYCLING DELAY ON AN ECOLOGICAL FOOD CHAIN*

Banibrata Mukhopadhyay, Rakhi Bhattacharyya, Kolkata

(Received October 1, 2007)

Abstract. We consider a mathematical model of nutrient-autotroph-herbivore interaction with nutrient recycling from both autotroph and herbivore. Local and global stability criteria of the model are studied in terms of system parameters. Next we incorporate the time required for recycling of nutrient from herbivore as a constant discrete time delay. The resulting DDE model is analyzed regarding stability and bifurcation aspects. Finally, we assume the recycling delay in the oscillatory form to model the daily variation in nutrient recycling and deduce the stability criteria of the variable delay model. A comparison of the variable delay model with the constant delay one is performed to unearth the biological relevance of oscillating delay in some real world ecological situations. Numerical simulations are done in support of analytical results.

Keywords: autotroph, herbivore, nutrient recycling, global stability, Hopf-bifurcation, variable delay, two-timing expansion

MSC 2010: 34C25, 34D23, 92D25, 92D40

1. Introduction

Understanding the relationship between producers and consumers is a long standing topic of interest in ecological food webs. Contemporary modeling studies involving these interactions in the presence or absence of decomposers have occupied a significant volume in mathematical ecology ([41], [35], [36], [13], [15], [23]). The basic trophic levels of an ecological food chain consist of (i) primary producers and (ii) primary consumers. The primary producers, commonly known as autotroph, can manufacture their own organic requirement from inorganic materials independent of other sources of organic substrates. These autotroph are either phototrophic

* The present research is performed under a project supported by the Department of Science and Technology, Ministry of Human Resource Development, Govt. of India (Grant No. SR/S4/MS:296/05).

or chemoautotrophic—energy being derived either by photosynthesis, where chlorophyll is present, or from inorganic oxidation, where it is absent. Herbivores, that feed on these autotroph, play the role of primary consumers. There are mainly two types of autotroph-herbivore ecosystems: (i) terrestrial plant-herbivore systems ([21], [9], [12], [36], [37], [27], [13], [15], [6]), (ii) marine phytoplankton-zooplankton systems ([16], [30], [2], [31]–[34], [19], [29], [24]–[26]). In the terrestrial environment, photosynthetic organisms are the main producers. They provide the initial source of food in the food chain as well as habitats for other organisms. They are the primary agents in soil formation and in modifying the nonliving environment [8]. The herbivores are normally the insects or mammals. In the marine environment on the other hand, the autotrophic phytoplankton are unicellular microscopic organisms which play the key role at the base of the aquatic food chain. The animal species zooplankton live on these phytoplankton. These aquatic organisms have a relatively short life span. As soon as they get exposed to air, water diffuses and evaporates quickly from their bodies and as a result the cellular metabolism is disrupted and finally destroyed.

A salient feature of a natural ecosystem is the *regeneration of nutrient* due to decomposition of dead biotic elements ([42], [30]). The effect of nutrient recycling on food chain dynamics has been extensively studied. Nisbet et al. [28] studied the effect of nutrient recycling for closed ecosystems. Usually, nutrient recycling is considered as an instantaneous process and the time required to regenerate nutrient from dead organic matter is neglected ([31], [11], [14]). However, in a natural ecosystem, such a delay is always present. Beretta et. al. [5] considered an open ecosystem with limiting nutrient which is partially recycled after death. They have used a distributed delay in the recycling term and studied stability aspects around the positive equilibrium. Bischi [7] considered the effect of recycling delay on resilience, namely, the rate at which a system returns to a stable steady state following a perturbation [10]. Ruan [33] compared plankton models with nutrient recycling in the presence and absence of time delay. Bandyopadhyay et. al. [1] studied a nutrient-autotroph-herbivore system, where nutrient recycling is modeled by a discrete time delay. They have performed a stability and bifurcation analysis of the system and estimated an interval of recycling delay that preserves the stability of the system. Finally they have shown the existence of a stability switch for the particular model.

From the above review, it is clear that the effect of nutrient recycling (both instantaneous and delayed) on nutrient-autotroph-herbivore dynamics has been studied in great detail. In the context of delayed recycling, either discrete or distributed delays has been used so far. However, nutrient recycling in a real world ecosystem does not take place in a uniform fashion. As is pointed out by Whittaker [43], this recycling delay increases as temperature decreases and hence the regeneration time is very

likely to be shorter during daytime than at night as well as during summer than in winter [38]. This has motivated us to study the impact of time varying recycling delay on an ecological food chain. Consequently, we, in the present analysis, consider a three species nutrient-autotroph-herbivore model with nutrient recycling. A discrete time delay, both in constant and in variable form, is incorporated into the term representing recycling of nutrient from dead herbivore.

The organization of the paper is as follows. Section 2 deals with the stability aspect of the ODE model around different equilibrium points. In Section 3 we introduce constant recycling delay and examine the role of delay on the stability aspects of the system. Finally, in Section 4, we make the recycling delay time dependent and analyze the impact of variable delay on the dynamical behavior of the system.

2. The basic model

We consider the following nonlinear nutrient-autotroph-herbivore model with nutrient recycling

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= N(N_0 - pN) - aNA + c_1A + b_1H, \\ \frac{\mathrm{d}A}{\mathrm{d}t} &= a_1NA - cA - \frac{\beta AH}{k+A}, \\ \frac{\mathrm{d}H}{\mathrm{d}t} &= \frac{\beta_1 AH}{k+A} - bH, \end{aligned} \tag{2.1}$$

where $N(t)$, $A(t)$, and $H(t)$ denote the density of nutrient, autotroph and herbivore population respectively at time t. The initial conditions are $N(0) \geqslant 0$, $A(0) \geqslant 0$, $H(0) \geqslant 0$, N_0 is the external nutrient input into the system and p is the loss rate of nutrient biomass due to leaching. It is assumed that the input of external nutrient to the system is dependent on the amount of nutrient present in the system. Consumption of nutrient by autotroph is assumed to follow the simple mass action kinetics with a and a_1 representing respectively the interaction and conversion rates. Autotroph biomass is lost from the system at a rate c due to litter fall, grazing etc. Herbivore grazing is modeled by using the Michaelis-Menten Holling type-II functional response [18] which is an ecologically realistic interaction for an autotroph-herbivore system. It is assumed that nutrient is regenerated from the dead biomass of both autotroph and herbivore species and c_1 and b_1 represent the corresponding recycling rates.

We first prove the biological validity of the model. For this, we consider $W = N + A + H$. Then $W(0) = N(0) + A(0) + H(0) \geqslant 0$ and

$$\dot{W} = N(N_0 - pN) + (a_1 - a)NA + (c_1 - c)A + (b_1 - b)H + \frac{(\beta_1 - \beta)AH}{k+A}.$$

As $a_1 < a$, $\beta_1 < \beta$ we have $\dot{W} \leqslant N_0 N + c_1 A + b_1 H \leqslant k_{\min} W$, where $k_{\min} = \min\{N_0, c_1, b_1\}$. So, $W(t) \leqslant W(0)\mathrm{e}^{k_{\min} t}$. Therefore, every solution of (2.1) starting from $\mathbb{R}^+_3$ will lie within this region; that is, every solution is defined on $[0, \infty)$ and it is bounded on arbitrary compact sub-intervals of $[0, \infty)$.

The stationary points of the system (2.1) are

(i) the trivial equilibrium point $E_T \equiv (0, 0, 0)$;

(ii) the axial equilibrium point $E_A \equiv (N_0/p, 0, 0)$;

(iii) the boundary equilibrium point

$$E_B \equiv \Big(\frac{c}{a_1}, \frac{c(pc/a_1 - N_0)}{a_1 c_1 - ac}, 0\Big) \equiv (N_1, A_1, 0);$$

(iv) the interior equilibrium point $E^* \equiv (N^*, A^*, H^*)$, where $A^* = kb/(\beta_1 - b)$, N^* is the positive root of

$$px^2 + \Big[aA^* - N_0 - \frac{a_1 b_1 \beta_1 A^*}{\beta b}\Big]x + (cb_1\beta_1 - \beta c_1 b)\frac{A^*}{b} = 0, \tag{2.2}$$

and $H^* = [(a_1 N^* - c)(k + A^*)]/\beta$.

The boundary equilibrium point exists if $N_0/p > c/a_1 > c_1/a$ or $N_0/p < c/a_1 < c_1/a$. The interior equilibrium point exists if the following conditions hold

$$b < \beta_1 < \frac{c_1 b\beta}{cb_1}, \quad N_0 < \frac{(ab\beta - a_1 b_1 \beta_1)k}{\beta(\beta_1 - b)}, \quad N^* > N_1. \tag{2.3}$$

So, we see that the input concentration of nutrient plays an important role in controlling the dynamics of the system.

Next we perform the stability analysis around various stationary points. Clearly, the trivial equilibrium point E_T is unstable. Stability analysis of the axial equilibrium point reveals that it is unstable if the boundary equilibrium point exists. The characteristic equation of the Jacobian matrix at the boundary equilibrium point E_B is

$$\Big(\frac{\beta_1 A_1}{k + A_1} - b - \lambda\Big)[\lambda^2 - \lambda(N_0 - 2pN_1 - aA_1) + A_1(a_1 c_1 - ac)] = 0. \tag{2.4}$$

Now, all the roots of the equation (2.4) will have negative real parts if $a_1 c_1 > ac$ and $b > (\beta_1 A_1)/(k + A_1)$ as $(N_0 - 2pN_1 - aA_1)$ is always negative. Therefore, the system will be locally asymptotically stable around E_B if

$$N_0 < \frac{pc}{a_1} < \frac{pc_1}{a} \tag{2.5}$$

and

$$b > \frac{\beta_1(pc^2 - N_0 c a_1)}{pc^2 + ka_1^2 c_1 - aa_1 kc - ca_1 N_0}. \tag{2.6}$$

So for large b, the system will be stable around the boundary equilibrium point E_B.

Let us now study the most interesting interior equilibrium point E^*. The characteristic equation in this case takes the form

$$\lambda^3 + P_1\lambda^2 + P_2\lambda + P_3 = 0, \tag{2.7}$$

where

$$\begin{aligned} P_1 &= aA^* + 2pN^* - N_0 - M, \\ P_2 &= M(N_0 - 2pN^* - aA^*) + \frac{kbM}{A^*} - a_1A^*(c_1 - aN^*), \\ P_3 &= -(N_0 - 2pN^* - aA^*)\frac{kbM}{A^*} - \frac{a_1b_1kb^2H^*}{\beta_1A^*}, \\ M &= \frac{b^2\beta H^*}{\beta_1^2A^*}. \end{aligned} \tag{2.8}$$

Next we state the stability criteria around this equilibrium point in the form of the following theorem.

Theorem 2.1. *The system* (2.1) *will be locally asymptotically stable around the interior equilibrium point if*

(i) $P_1 > 0$,

(ii) $P_1P_2 > P_3 > 0$,

where P_1, P_2 *and* P_3 *are given by* (2.8).

After studying the local stability behavior we perform a global analysis around the equilibrium point of coexistence. For this, we first consider the transformations $N = N^* + N_1$, $A = A^* + A_1$, and $H = H^* + H_1$. With these transformations, the model system (2.1) reduces to

$$\begin{aligned} \frac{\mathrm{d}N_1}{\mathrm{d}t} &= N_1(N_0 - 2pN^* - pN_1) - \alpha(N^*A_1 + N_1A^* + N_1A_1) \\ &\quad + c_1A_1 + b_1H_1, \\ \frac{\mathrm{d}A_1}{\mathrm{d}t} &= \alpha_1(N^*A_1 + N_1A^* + N_1A_1) - cA_1 \\ &\quad - \frac{\beta}{k + A^*}\Big[b(H_1 + H^*)A_1 + A^*H_1 \\ &\quad - \frac{1}{k + A^*}\{A_1^2(H_1 + H^*) + A^*A_1H_1 + A_1A^*H^*\}\Big], \\ \frac{\mathrm{d}H_1}{\mathrm{d}t} &= \frac{\beta_1}{k + A^*}\Big[A_1(H + H^*) + A^*H_1 \\ &\quad - \frac{1}{k + A^*}\{A_1^2(H_1 + H^*) + A^*A_1H_1 + A_1H^*A^*\}\Big] - bH_1. \end{aligned} \tag{2.9}$$

Then, $(0,0,0)$ is an equilibrium point of (2.9). Next we define

$$U = \frac{1}{2}N_1^2 + \frac{\sigma_1}{2}A_1^2 + \frac{\sigma_2}{2}H_1^2 \geqslant 0, \tag{2.10}$$

where $\sigma_1, \sigma_2 > 0$ are to be chosen. U will be a Lyapunov function if $\dot{U} \leqslant 0$ when $(N_1, A_1, H_1) \neq (0,0,0)$. Now,

$$\begin{aligned}
\dot{U} = {} & N_1^2(N_0 - 2pN^* - pN_1 - \alpha A^* - \alpha A_1) \\
& + A_1^2\Big[\sigma_1\Big\{\alpha_1(N_1 + N^*) - c \\
& - \frac{\beta}{k + A^*}\Big(H_1 + H^* - \frac{A_1(H + H^*) + A^*(H_1 + H^*)}{k + A^*}\Big)\Big\} \\
& \qquad\qquad - \frac{\beta_1}{(k + A^*)^2}H_1 H^* \sigma_2\Big] \\
& + H_1^2\sigma_2\Big[\frac{\beta_1(A_1 + A^*)}{k + A^*} - \frac{\beta_1}{(k + A^*)^2}A_1(A_1 + A^*) - b\Big] \\
& + N_1 A_1(-\alpha N^* + c_1 + \alpha_1 A^* \sigma_1) \\
& + A_1 H_1\Big[-\frac{\beta A^* \sigma_1}{k + A^*} + \frac{\beta_1 H^* A^*}{(k + A^*)^2}\sigma_2\Big] + N_1 H_1 b_1.
\end{aligned} \tag{2.11}$$

Using the inequality

$$xy \leqslant \frac{1}{2}\varepsilon_i x^2 + \frac{1}{2\varepsilon_i}y^2, \tag{2.12}$$

we have

$$\begin{aligned}
\dot{U} \leqslant {} & N_1^2\Big[N_0 - p(2N^* + N_1) - \alpha A^* - \alpha A_1 \\
& + \frac{\varepsilon_1}{2}(\sigma_1\alpha_1 A^* + c_1 - \alpha N^*) + \frac{\varepsilon_3 b_1}{2}\Big] \\
& + A_1^2\Big[\sigma_1\alpha_1(N_1 + N^*) - c \\
& - \frac{\beta\sigma_1}{k + A^*}\Big\{H + H^* - \frac{A_1(H_1 + H^*) + A^*(H_1 + H^*)}{k + A^*}\Big\} \\
& - \frac{\beta_1 H_1 H^*}{(k + A^*)^2}\sigma_2 + \frac{1}{2\varepsilon_1}(-\alpha N^* + c_1 + \alpha_1\sigma_1 A^*)\Big] \\
& + \frac{\varepsilon_2}{2}\Big[\frac{\beta_1 H^* A^* \sigma_2}{(k + A^*)^2} - \frac{\beta A^* \sigma_1}{k + A^*}\Big] \\
& + H_1^2\Big[\frac{\sigma_2\beta_1}{(k + A^*)^2}(A_1 + A^*)(k + A^* - A_1) - b\sigma_2 + \frac{b_1}{2\varepsilon_3} \\
& + \frac{\sigma_1\varepsilon_2}{2}\Big\{\frac{\beta_1 H^* A^*}{(k + A^*)^2} - \frac{\beta A^*}{k + A^*}\Big\}\Big].
\end{aligned} \tag{2.13}$$

Next we set

$$
\begin{aligned}
(2.14)\quad \sigma_1 &= \frac{\alpha N^* - c_1}{\alpha_1 A^*} - \xi_1,\\
\varepsilon_1 &= \frac{\alpha N^* - c_1 - \alpha_1 A^* \sigma_1}{2\alpha_1 \sigma_1 (N_1 + N^*)},\\
\varepsilon_2 &= 1,\\
\varepsilon_3 &= \frac{2(2pN^* - N_0)}{b_1},\\
\sigma_2 &= \frac{\beta\sigma_1}{k + A^*} \frac{A^* + H^* + H_1 - (A_1 + A^*)(H_1 + H^*)(k + A^*)^{-1}}{\beta_1 H^* (H_1 + A^*)(k + A^*)^{-2}} - \xi_2,
\end{aligned}
$$

with $\xi_1, \xi_2 > 0$. By choosing ξ_1, ξ_2 properly it is possible to set σ_1 and σ_2 such that $\dot{U}_1 < 0$, that is, we can choose ξ_1 and ξ_2 such that

$$
\begin{aligned}
(2.15)\qquad \sigma_2 \Big[\frac{\beta_1}{(k + A^*)^2} (A_1 + A^*)(k + A^* - A_1) - b \Big]\\
+ \frac{\sigma_1}{2} \Big[\frac{\beta_1 H^* A^*}{(k + A^*)^2} - \frac{\beta A^*}{k + A^*} \Big] + \frac{b_1}{2\varepsilon_3} \leqslant 0.
\end{aligned}
$$

We summarize the above analysis into the following:

Theorem 2.2. *The model system* (2.1) *will be globally asymptotically stable if* (2.15) *holds, where* σ_1, σ_2, ε_1, ε_2, ε_3 *are given by* (2.14).

From (2.15), it can be said that for small b, we can choose ξ_1 and ξ_2 sufficiently large so that $\dot{U} \leqslant 0$. Hence, for small values of b, the system will be globally asymptotically stable around the interior equilibrium point E^*. Interestingly, our analysis of the boundary equilibrium point (E_B) showed that stability around this point is possible for large values of b (2.6). Thus, global stability around the equilibrium point of coexistence implies instability around the boundary equilibrium of herbivore extinction.

A numerical study of the model is performed using Matlab and the resulting stable population time graph is shown in Fig. 1.

3. Constant recycling delay

In this section, we consider the basic model (2.1) with constant recycling delay. It is well established that reconversion of dead biomass into nutrient is not an instantaneous process but is mediated by some time lag required for bacterial decomposition. This delay will be present in reconversion of both autotroph and herbivore into nutrient. However, the decomposition of herbivore will take much longer time than that

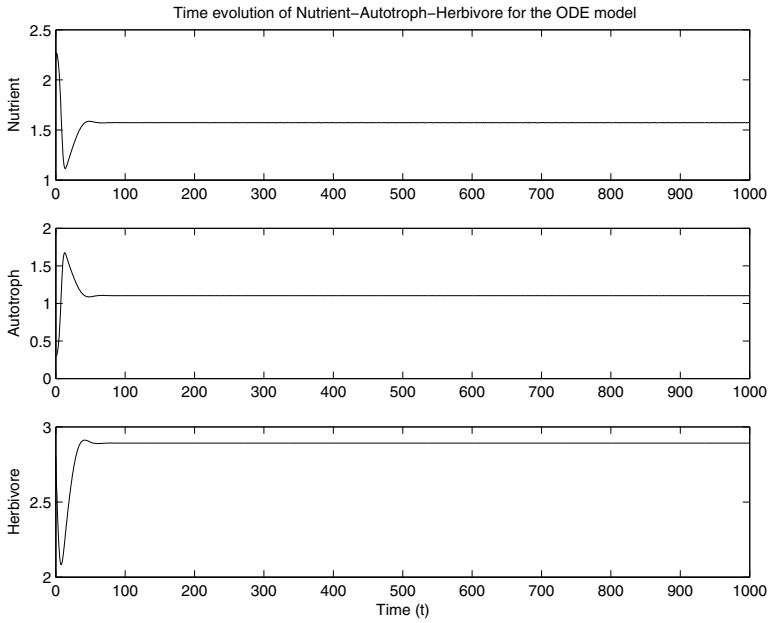

Figure 1. Time evolution of nutrient, autotroph, and herbivore population for the ODE model. Parameter values are $N_0 = 2.5$, $p = 1$, $a = 1$, $c_1 = 0.12$, $b_1 = 0.05$, $a_1 = 0.5$, $k = 0.95$, $c = 0.215$, $\beta = 0.4$, $\beta_1 = 0.2$, and $b = 0.109$. Initial conditions are $N^* = 2.2$, $A^* = 0.3$, and $H^* = 2.8$. The figure exhibits stable behavior for all the populations.

of autotroph. So we consider the recycling delay in the term representing nutrient regeneration from herbivore and assume autotroph recycling as instantaneous. The effect of autotroph-nutrient recycling delay on a similar type model has already been studied in a previous work [1]. With these assumptions, we write down the delay model as

$$\begin{aligned} \dot{N} &= N(N_0 - pN) - aNA + c_1 A + b_1 H(t-\tau), \\ \dot{A} &= a_1 NA - cA - \frac{\beta AH}{k+A}, \\ \dot{H} &= \frac{\beta_1 AH}{k+A} - bH, \end{aligned} \tag{3.1}$$

where τ represents the constant recycling delay. The initial conditions are $N(0) = \overline{N} \geqslant 0$, $A(0) = \overline{A} \geqslant 0$ and $H(t) = \overline{H}(t) \geqslant 0$, where $\overline{H}(t)$ is a continuous nonnegative function for $-\tau \leqslant t \leqslant 0$.

The characteristic equation corresponding to the interior equilibrium point of the system (3.1) is given by

$$\lambda^3 + P_1\lambda^2 + P_2\lambda + P_{31} + P_{32}\mathrm{e}^{-\lambda\tau} = 0, \tag{3.2}$$

where

$$P_{31} = -\frac{(N_0 - 2pN^* - aA^*)\beta\beta_1 A^* H^* k}{(k + A^*)^3}, \tag{3.3}$$
$$P_{32} = \frac{a_1\beta_1 A^* H^* k b_1}{(k + A^*)^2}.$$

The characteristic equation (3.2) is a transcendental equation and has infinitely many eigenvalues. Consequently, the classical Routh-Hurwitz criteria can not be used to analyze this equation. We shall study the distribution of the roots of (3.2) analytically. For this, we consider a root of (3.2) in the form $\lambda = u + \mathrm{i}v$. The system will undergo a stability change if the real part of the root is zero (namely if the root is purely imaginary), that is, $u = 0$. We denote the corresponding v by v_0. Routine calculations show that the system will undergo a stability change for an infinite number of values of τ given by

$$\tau_n = \frac{1}{v_0}\Big[n\pi + \arctan\frac{v_0(P_2 - v_0^2)}{P_1 v_0^2 - P_{31}}\Big], \tag{3.4}$$

where $n = 0, \pm 1, \pm 2, \ldots$ and v_0 is the largest positive root of

$$\Phi(v_0^2) = v_0^6 + v_0^4(P_1^2 - 2P_2) + v_0^2(P_2^2 - 2P_1P_{31}) + P_{31}^2 - P_{32}^2 = 0. \tag{3.5}$$

The derivative of the real part of the root of (3.2) with respect to τ is given by

$$\Big[\frac{\mathrm{d}u}{\mathrm{d}\tau}\Big]_{\tau=\tau_0,\, v=v_0} = \frac{v_0^2}{E^2 + F^2}\Big[\frac{\mathrm{d}}{\mathrm{d}v_0^2}\Phi(v_0^2)\Big], \tag{3.6}$$

where

$$E = P_2 - 3v_0^2 - P_{32}\tau\cos(v_0\tau), \tag{3.7}$$
$$F = 2P_1 v_0 + P_{32}\tau\sin(v_0\tau).$$

Now for large v_0^2, $\Phi(v_0^2) > 0$ and hence $\mathrm{d}\Phi/\mathrm{d}v_0^2 \neq 0$. Thus, the transversility condition holds and consequently the system will undergo a Hopf-bifurcation [17].

From the above analysis it is seen that for $\tau = 0$, the system remains stable if the conditions of Theorem (2.1) are satisfied. For $\tau \neq 0$, if $0 < \tau < \tau_0$, the delayed system will remain stable. But for $\tau > \tau_0$, the system will become unstable and exhibit Hopf-bifurcation for an infinite number of values of the delay parameter τ. A numerical study of the delay model is performed and the results are shown in Figs. 2–5. Fig. 2 shows the graph when the delay lies in $0 < \tau < \tau_0$ exhibiting stable

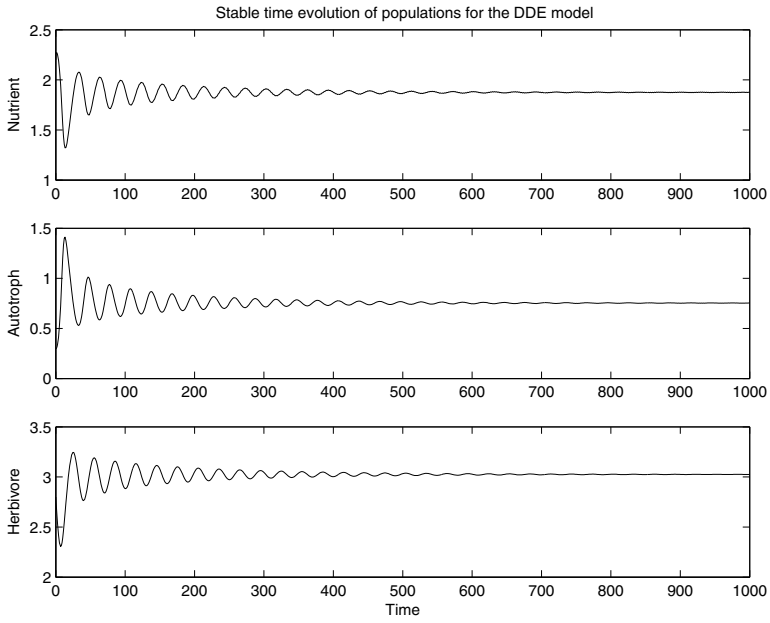

Figure 2. Time evolution of the populations for the DDE model. Parameter values are $N_0 = 2.5$, $p = 1$, $a = 1$, $c_1 = 0.12$, $b_1 = 0.05$, $a_1 = 0.5$, $k = 1$, $c = 0.215$, $\beta = 0.4$, $\beta_1 = 0.2$, $b = 0.09$, and $\tau = 10$. Initial conditions are $N^* = 2.2$, $A^* = 0.3$, and $H^* = 2.8$. The figure exhibits stable behavior for all the populations.

behavior. In Fig. 3 we demonstrate the onset of delay-induced instability for $\tau = 13$ which numerically exemplifies the existence of τ_0. Fig. 4 shows periodic oscillation in population density for $\tau > \tau_0$. In Fig. 5 we draw the phase portrait of the DDE model showing the stable limit cycle arising from Hopf-bifurcation.

4. Time varying recycling delay

In this section, we consider time dependent recycling delay to model the day/night variation in recycling. The model with time varying nutrient recycling takes the form

$$\begin{aligned} \dot{N} &= N(N_0 - pN) - aNA + c_1 A + b_1 H(t - \tau(t)), \\ \dot{A} &= a_1 NA - cA - \frac{\beta AH}{k + A}, \\ \dot{H} &= \frac{\beta_1 AH}{k + A} - bH. \end{aligned} \tag{4.1}$$

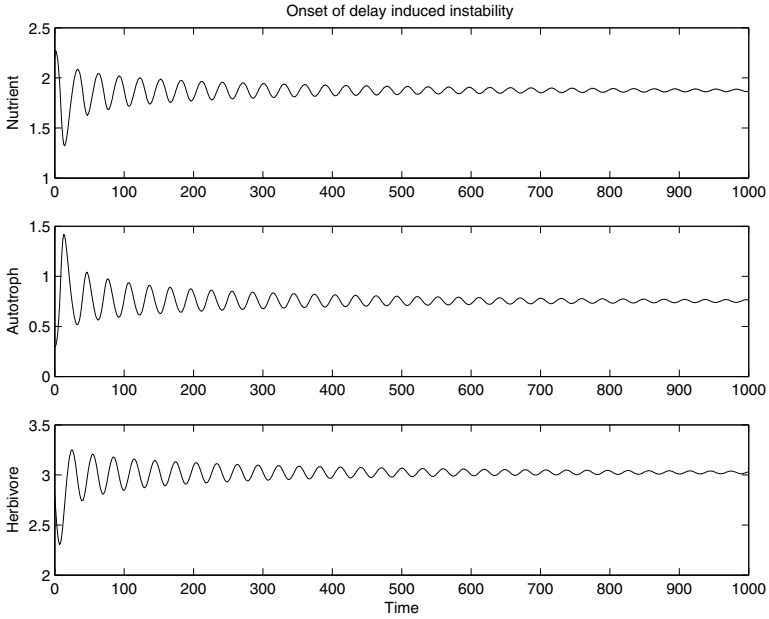

Figure 3. Time evolution of the populations for the DDE model showing onset of delay induced instability with $\tau = 13$.

To start the analysis, we first introduce the linear operator

$$L\begin{pmatrix} u(t) \\ q(t) \\ w(t) \end{pmatrix} \equiv \begin{bmatrix} \dfrac{\mathrm{d}u}{\mathrm{d}t} - a_{11}u - a_{12}q - b_1 w(t-\tau_0) \\ \dfrac{\mathrm{d}q}{\mathrm{d}t} - a_{21}u - a_{22}q - a_{23}w \\ \dfrac{\mathrm{d}w}{\mathrm{d}t} - a_{32}q \end{bmatrix}, \tag{4.2}$$

where

$$\begin{gathered} a_{11} = N_0 - 2pN^* - aA^*, \quad a_{12} = c_1 - aN^* < 0, \\ a_{21} = a_1 A^*, \quad a_{22} = \frac{\beta A^* H^*}{(k+A^*)^2}, \quad a_{23} = -\frac{\beta A^*}{k+A^*}, \\ a_{32} = \frac{\beta_1 H^* k}{(k+A^*)^2}, \quad u = N - N^*, \quad q = A - A^*, \quad w = H - H^*, \end{gathered} \tag{4.3}$$

and τ_0 is defined by (3.4) with $n = 0$. The linearized version of (4.1) can then be written in the form

$$L\begin{pmatrix} u(t) \\ q(t) \\ w(t) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}. \tag{4.4}$$

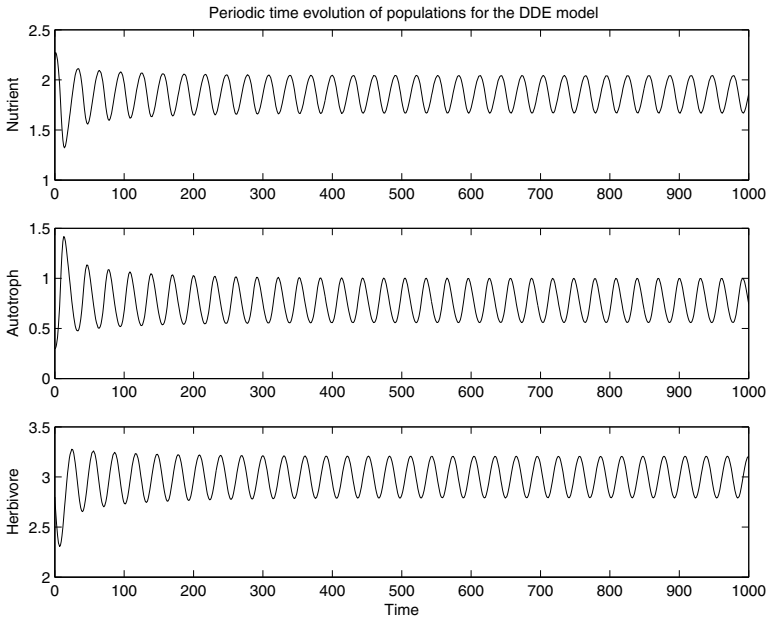

Figure 4. Time evolution of the populations for the DDE model. Parameter values are $N_0 = 2.5$, $p = 1$, $a = 1$, $c_1 = 0.12$, $b_1 = 0.05$, $a_1 = 0.5$, $k = 1$, $c = 0.215$, $\beta = 0.4$, $\beta_1 = 0.2$, $b = 0.09$, and $\tau = 20$. The figure exhibits unstable behavior for all the populations.

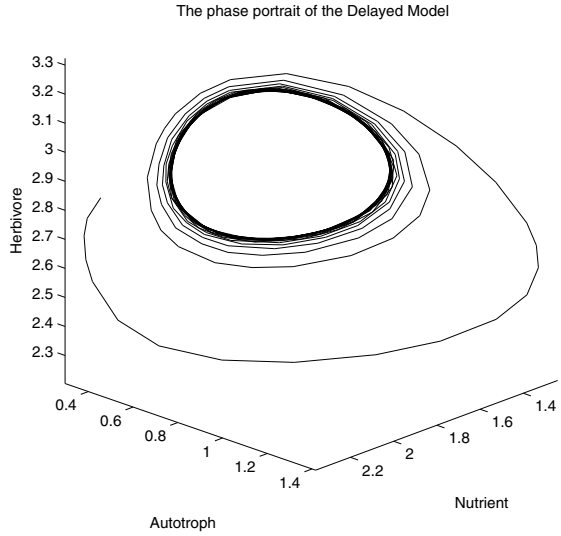

Figure 5. Phase portrait of the delay model with same parameter values as above.

The solution of (4.4) is

$$\begin{aligned}\begin{bmatrix} u(t) \\ q(t) \\ w(t) \end{bmatrix} &= M \begin{bmatrix} -(a_{32} + a_{22}\mathrm{i}v_0 + v_0^2)/a_{21} \\ \mathrm{i}v_0 \\ a_{32} \end{bmatrix} \mathrm{e}^{\mathrm{i}v_0 t} + \text{c.c.t.} \\ &\equiv M \begin{bmatrix} \nu_1 \\ \nu_2 \\ \nu_3 \end{bmatrix} \mathrm{e}^{\mathrm{i}v_0 t} + \text{c.c.t.},\end{aligned} \tag{4.5}$$

where c.c.t. denote the complex conjugate terms.

Next we study the stability criteria of the system around the interior equilibrium point E^* with oscillating delay

$$\tau(t) = \tau_0 + \varepsilon f(t), \tag{4.6}$$

where ε is a small positive quantity and $f(t)$ is a periodic function of t. The corresponding linearized system is

$$\begin{aligned}\frac{\mathrm{d}u}{\mathrm{d}t} &= a_{11}u + a_{12}q + b_1 w(t - \tau(t)), \\ \frac{\mathrm{d}q}{\mathrm{d}t} &= a_{21}u + a_{22}q + a_{23}w, \\ \frac{\mathrm{d}w}{\mathrm{d}t} &= a_{32}q.\end{aligned} \tag{4.7}$$

We look for a solution of the type

$$\begin{pmatrix} u \\ q \\ w \end{pmatrix} = \sum_{i=0}^{\infty} \varepsilon^i \begin{bmatrix} u_i(t, \sigma) \\ q_i(t, \sigma) \\ w_i(t, \sigma) \end{bmatrix}, \tag{4.8}$$

where $\sigma = \varepsilon t$. Now from (4.7), collecting the coefficients of like powers of ε we find that

$$L \begin{pmatrix} u_0 \\ q_0 \\ w_0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}. \tag{4.9}$$

So from (4.5) we can say that

$$\begin{pmatrix} u_0 \\ q_0 \\ w_0 \end{pmatrix} = M(\sigma) \begin{pmatrix} \nu_1 \\ \nu_2 \\ \nu_3 \end{pmatrix} \mathrm{e}^{\mathrm{i}v_0 t} + \text{c.c.t.} \tag{4.10}$$

Using (4.10), we have

$$L\begin{pmatrix} u_1 \\ q_1 \\ w_1 \end{pmatrix} = \begin{bmatrix} b_1 f(t)\mathrm{i}v_0 M(\sigma)\nu_3 + b_1\tau_0 M'(\sigma)\nu_3 - M'(\sigma)\nu_1 \\ -\nu_2 M'(\sigma) \\ -\nu_3 M'(\sigma) \end{bmatrix} \mathrm{e}^{\mathrm{i}v_0 t} + \text{c.c.t.}, \tag{4.11}$$

where $M' = \mathrm{d}M/\mathrm{d}\sigma$.

Next we consider the Fourier series expansion of $f(t)$ in the form

$$f(t) = \sum_{n=-\infty}^{\infty} \alpha_n \exp(\mathrm{i}wnt). \tag{4.12}$$

Using (4.11) and (4.12), we obtain

$$\begin{aligned} L\begin{pmatrix} u_1 \\ q_1 \\ w_1 \end{pmatrix} = {} & \begin{bmatrix} b_1 \mathrm{i}\alpha_0 v_0 \nu_3 M(\sigma) + M'(\sigma)(b_1\tau_0\nu_3 - \nu_1) \\ -\nu_2 M'(\sigma) \\ -\nu_3 M'(\sigma) \end{bmatrix} \mathrm{e}^{\mathrm{i}v_0 t} \\ & + \sum_{n\neq 0} \begin{bmatrix} \mathrm{i}b_1\alpha_n v_0 \nu_3 M(\sigma) \\ 0 \\ 0 \end{bmatrix} \mathrm{e}^{\mathrm{i}(v_0+wn)t} + \text{c.c.t.} \end{aligned} \tag{4.13}$$

To solve (4.13) we find a particular solution corresponding to each term on the right-hand side. For $n \neq 0$, it is easy to find a particular integral. To find the solutions when $n = 0$, we apply Fredholm theory.

We define the inner product in the space of periodic functions with period $2\pi/v_0$ by

$$\langle \underline{u}, \underline{v} \rangle = \int_0^{2\pi/v_0} \tilde{u}(t)\overline{\tilde{v}(t)}\,\mathrm{d}t. \tag{4.14}$$

The adjoint operator L^* of L is [20]

$$L^*\begin{pmatrix} u \\ q \\ w \end{pmatrix} = \begin{bmatrix} a_{11}u + a_{21}q - \dfrac{\mathrm{d}u}{\mathrm{d}t} \\ a_{12}u + a_{22}q + a_{32}w - \dfrac{\mathrm{d}p}{\mathrm{d}t} \\ b_1 u(t+\tau_0) + a_{23}q - \dfrac{\mathrm{d}w}{\mathrm{d}t} \end{bmatrix}, \tag{4.15}$$

and the kernel of this adjoint operator is given by

$$\begin{bmatrix} u^*(t) \\ q^*(t) \\ w^*(t) \end{bmatrix} = B \begin{bmatrix} d_1 \\ d_2 \\ d_3 \end{bmatrix} \mathrm{e}^{\mathrm{i}v_0 t} + \text{c.c.t.}, \tag{4.16}$$

where

$$d_1 = a_{12}a_{32}, \quad d_2 = \frac{a_{12}^2 a_{32}}{\mathrm{i}v_0 - a_{11}},$$
$$d_3 = \frac{a_{12}a_{32}}{(a_{11} - \mathrm{i}v_0)(a_{22} - \mathrm{i}v_0) - a_{12}a_{21}}.$$

The particular integral of (4.13) exists if the right-hand side of (4.13) is orthogonal, which implies

$$\frac{M'(\sigma)}{M(\sigma)} = \frac{d_1 b_1 \alpha_0 v_0 \nu_3}{\nu_1 d_1 + \nu_2 \overline{d_2} + \nu_3 \overline{d_3} - b_1 d_1 \tau_0 \nu_3} \frac{2\pi}{\tau_0}. \tag{4.17}$$

If $v_0^2 < v_0^{2^+}$ with $\alpha_0 > 0$ then $M(\sigma) \to 0$ as $t \to \infty$, and if $v_0^2 > v_0^{2^+}$ with $\alpha_0 < 0$ then $M(\sigma) \to 0$ as $t \to \infty$. But for $v_0^2 < v_0^{2^+}$, $M(\sigma) \to \infty$ as $t \to \infty$ if $\alpha_0 < 0$. Here

$$v_0^{2^+} = \frac{a_{32} - a_{11}^2 - a_{12}a_{21} + \sqrt{(a_{32} - a_{11}^2 - a_{12}a_{21})^2 - 4a_{11}^2 a_{32}}}{2}. \tag{4.18}$$

So it is seen that when the mean delay is less (greater) than τ_0, the system may become unstable (stable) depending on the system parameters and is controlled by $v_0^{2^+}$.

Now, for large b, $(a_{32} - a_{12}a_{21})$ is large and N^* is small. Consequently, $v_0^{2^+}$ is large. Thus, for *large death rate of herbivore*, the system with time varying delay exhibits characteristics opposite to those of the system with constant delay.

Let us now study the case when $\alpha_0 = 0$. To this end, we use the two timing method with $\sigma = \varepsilon^2 t$. This ensures that the analysis is sensitive to smaller rates of growth or decay. Equating the like powers of ε, we get

$$L \begin{pmatrix} u_0 \\ q_0 \\ w_0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \tag{4.19}$$

$$L \begin{pmatrix} u_1 \\ q_1 \\ w_1 \end{pmatrix} = \begin{pmatrix} b_1 f(t) w_{0,t}(t - \tau_0, \sigma) \\ 0 \\ 0 \end{pmatrix}, \tag{4.20}$$

$$L \begin{pmatrix} u_2 \\ q_2 \\ w_2 \end{pmatrix} = \begin{pmatrix} b_1 f(t) w_{1,t}(t - \tau_0, \sigma) + b_1 \tau_0 w_{0,\sigma}(t - \tau_0, \sigma) + \{f(t)\}^2 \\ -q_{0,\sigma} \\ -w_{0,\sigma} \end{pmatrix}. \tag{4.21}$$

As $\alpha_0 = 0$, the Fourier series expansion of $f(t)$ becomes

$$f(t) = \sum_{n=-\infty,\, n\neq 0}^{\infty} \alpha_n \exp(\mathrm{i}wnt),$$

and the solution of (4.20) is

$$\begin{bmatrix} u_1(t) \\ q_1(t) \\ w_1(t) \end{bmatrix} = b_1 \mathrm{i} v_0 M(\sigma) \times \sum_{n=-\infty,\, n\neq 0}^{\infty} B_n \begin{bmatrix} -\dfrac{(wn+v_0)^2 - a_{32}a_{23} - a_{22}\mathrm{i}(wn+v_0)}{a_{21}} \\ \mathrm{i}(wn+v_0) \\ a_{32} \end{bmatrix}, \tag{4.22}$$

where

$$B_n = \frac{\alpha_n}{\xi^3 - (a_{11}+a_{22})\xi^2 + (a_{11}a_{22} - a_{21}a_{23} - a_{12}a_{21})\xi - a_{11}a_{23} + b_1 a_{21}\mathrm{e}^{-\mathrm{i}\xi\tau_0}}$$

with $\xi = (wn + v_0)$. Substituting (4.22) into (4.21), we get

$$L \begin{bmatrix} u_2 \\ q_2 \\ w_2 \end{bmatrix} = \begin{bmatrix} \Delta M'(\sigma) + \displaystyle\sum_{m,n=-\infty,\, m,n\neq 0}^{\infty} \alpha_m \alpha_n \mathrm{e}^{\mathrm{i}w(m+n)t} M_n M(\sigma) \\ -M'(\sigma)\nu_2 \\ -M'(\sigma)\nu_3 \end{bmatrix} \mathrm{e}^{\mathrm{i}v_0 t} + \text{c.c.t.},$$

where $\Delta = (b_1\tau_0\nu_3 - \nu_1)$ and $M_n = b_1^2 \mathrm{i} v_0 a_{32} B_n \exp(-\mathrm{i}wn\sigma_0) - \nu_3 v_0^2$. To find the non-secular solution, applying the Fredholm orthogonality condition, we get

$$\{(b_1\tau_0\nu_3 - \nu_1)d_1 - \nu_2\overline{d_2} - \nu_3\overline{d_3}\}M'(\sigma) + \sum_{n\neq 0} \alpha_{-n}\alpha_n M_n M(\sigma) = 0. \tag{4.23}$$

Therefore,

$$\frac{M'(\sigma)}{M(\sigma)} = \frac{\displaystyle\sum_{n\neq 0} |\alpha_n|^2 M_n}{d_1\nu_1 + \overline{d_2}\nu_2 + \overline{d_3}\nu_3 - d_1 b_1 \tau_0 \nu_3}. \tag{4.24}$$

Let us denote the right-hand side of (4.24) by $K(w, b_1)$. Then

$$M(\sigma) = C \exp\left[K(w, b_1)\varepsilon^2 t\right]. \tag{4.25}$$

So the system will be linearly asymptotically stable if $\mathrm{Re}\{K(w, b_1)\} < 0$. We are now in a position to summarize the analysis in the following:

Theorem 4.1. *Consider the system* (4.1)*, where the recycling delay* $\tau(t)$ *has the form* $\tau(t) = \tau_0 + \varepsilon f(t)$*, where* τ_0 *is given by* (3.4)*,* ε *is a small constant and* $f(t)$ *is a periodic function with the Fourier expansion* $f(t) = \sum \alpha_n \exp(\mathrm{i}wnt)$*. Then*

(i) *If $\varepsilon = 0$, the interior equilibrium point is marginally stable according to the linearized criteria.*

(ii) *If $\varepsilon > 0$, $\alpha_0 > 0$ (< 0) the system will be locally asymptotically stable around E^* if $v_0^2 < v_0^{2+}$ ($> v_0^{2+}$). If $v_0^2 < v_0^{2+}$ ($> v_0^{2+}$) together with $\alpha_0 < 0$ (> 0), then the system will become unstable.*

(iii) *If $\varepsilon > 0$ and $\alpha_0 = 0$, then the steady state will be locally asymptotically stable if $\mathrm{Re}\{K(w, b_1)\} < 0$, where $K(w, b_1)$ is the right-hand side of* (4.24).

5. Discussion

A real ecological food web is distinguished from the corresponding mathematical model in a number of aspects. The factors that contribute to these deviations are manifold, e.g., seasonal and/or daily variations, environmental fluctuations and so on. The study of seasonal and daily variations in different ecological contexts has drawn the attention of mathematical ecologists for a long time. For example, variation in species dispersal using reaction-diffusion equations with variable diffusion coefficients have been well studied ([22], [3], [4], [39], [40], [26]). Advanced mathematical tools have been utilized for analyzing models that incorporate these ecologically realistic characteristics of natural system.

In the present analysis, we have concentrated on such a practical aspect of an ecological food chain, namely, the time variability in nutrient recycling. Unlike most of the existing literature on ecological food chains, the external nutrient input to the system is assumed to depend upon the existing nutrient concentration. In Section 2, we studied the basic non-delayed model around the various steady states. Our analysis around the boundary state of herbivore extinction demonstrated that a high mortality rate of the herbivore population (together with a low external nutrient input) has a stabilizing effect around this boundary state. On the contrary, our investigation of the coexistent steady state revealed that a low value of this mortality rate ensures global stability around this interior equilibrium. Thus, the *herbivore mortality rate* plays a major role in controlling the local and global dynamics of the basic model around the various stationary states; and *there is a connection between the boundary equilibrium stability and the global asymptotic stability of the interior equilibrium in terms of this mortality rate.*

Next we have studied the model with constant, discrete recycling delay in the term modeling herbivore recycling. An initial interval of the delay parameter (namely, $(0, \tau_0)$) is obtained that imparts stability to the system. However, when the delay crosses this interval, the system becomes unstable through the occurrence of Hopf-bifurcation. Thus a regeneration delay of sufficient magnitude ($> \tau_0$) is able to

destabilize the system resulting in periodic fluctuation of various species. Finally, we have made the recycling delay time dependent by allowing the delay to oscillate around the constant value with small amplitude of oscillation. This ecologically accommodates the daily variation in nutrient regeneration into the model equations. We have derived the stability criteria in terms of the Fourier coefficients of $f(t)$ together with different system parameters. It has been found that for *large mortality rate of the herbivore* population, the system with oscillating delay exhibits stability characteristics opposite to those of the model with constant delay. Thus with the introduction of variable delay, the system becomes stable under the parameter restrictions for which the constant delay model exhibits oscillatory behavior. These observations suggest that *in a real world ecosystem, where the delay term undergoes daily and/or seasonal fluctuation, use of models with constant delay as an approximation could give rise to conclusions that are inappropriate as well as unrealistic.*

To end, we want to add a few lines. We have modeled only daily variation in nutrient recycling by using small amplitude oscillating delay. It is worthwhile to study the impact of seasonal fluctuation on nutrient regeneration through temporal fluctuations of large amplitude. We leave these for future consideration.

Acknowledgement. The authors are grateful to the learned referee for his/her valuable comments.

References

[1] *M. Bandyopadhyay, R. Bhattacharyya, B. Mukhopadhyay*: Dynamics of an autotroph-herbivore ecosystem with nutrient recycling. Ecol. Model. *176* (2004), 201–209.
[2] *E. Beltrami, T. O. Carroll*: Modeling the role of viral disease in recurrent phytoplankton blooms. J. Math. Biol. *32* (1994), 857–863.
[3] *D. L. Benson, J. A. Sherratt, P. K. Maini*: Diffusion driven instability in an inhomogeneous domain. Bull. Math. Biol. *55* (1993), 365–384.
[4] *D. L. Benson, P. K. Maini, J. A. Sherratt*: Pattern formation in reaction-diffusion models with spatially inhomogeneous diffusion coefficients. Math. Comp. Model. *17* (1993), 29–34.
[5] *E. Beretta, G. I. Bischi, F. Solimano*: Stability in chemostat equations with delayed recycling. J. Math. Biol. *28* (1990), 99–111.
[6] *R. Bhattacharyya, B. Mukhopadhyay*: Oscillation and persistence in a mangrove ecosystem in presence of delays. J. Biol. Syst. *11* (2003), 351–364.
[7] *G. I. Bischi*: Effects of time lags on transient characteristics of a nutrient recycling model. Math. Biosci. *109* (1992), 151–175.
[8] *P. Colinvaux*: Ecology II. John Wiley & Sons, Chichester, 1993.
[9] *M. J. Crawley*: Herbivory. The dynamics of animal plant interaction. Studies in Ecology Vol. 10. University of California Press, Berkley, 1983.
[10] *D. I. De Angelis, S. M. Bartell, A. L. Brenkert*: Effect of nutrient recycling and food chain length on the resilience. Amer. Naturalist *134* (1989), 778–805.
[11] *D. L. De Angelis*: Dynamics of Nutrient Recycling and Food Webs. Chapman & Hall, London, 1992.

[12] *M. Farkas, H. I. Freedman*: The stable coexistence of competing species on a renewable resource. J. Math. Anal. Appl. *138* (1989), 461–472.
[13] *D. Ghosh, A. K. Sarkar*: Oscillatory behaviour of an autotroph-herbivore system with a type-III uptake function. Int. J. Syst. Sci. *28* (1997), 259–264.
[14] *D. Ghosh, A. K. Sarkar*: Stability and oscillations in a resource-based model of two interacting species with nutrient cycling. Ecol. Model. *107* (1998), 25–33.
[15] *D. Ghosh, A. K. Sarkar*: Qualitative analysis of autotroph-herbivore system with nutrient diffusion. Korean J. Comput. Appl. Math. *6* (1999), 589–599.
[16] *T. G. Hallam*: Structural sensitivity of grazing formulations in nutrient controlled plankton models. J. Math. Biol. *5* (1978), 261–280.
[17] *B. D. Hassard, N. D. Kazarinoff, Y.-H. Wan*: Theory and Applications of Hopf Bifurcation. Cambridge University Press, Cambridge, 1981.
[18] *C. S. Holling*: The functional response population regulation. Mem. Entomol. Soc. Can. *45* (1965), 1–60.
[19] *S. R.-J. Jang*: Dynamics of variable-yield nutrient-phytoplankton-zooplankton models with nutrient recycling and self-shading. J. Math. Biol. *40* (2000), 229–250.
[20] *E. Kreysig*: Introductory Functional Analysis with Applications. John Wiley & Sons, New York, 1978.
[21] *D. Ludwig, D. D. Jones, C. S. Holling*: Qualitative analysis of insect outbreak systems: the spruce budworm and forest. J. Anim. Econ. *47* (1978), 315–332.
[22] *P. K. Maini, D. L. Benson, J. A. Sherratt*: Pattern formation in reaction-diffusion models with spatially inhomogeneous diffusion coefficients. IMA J. Math. Appl. Med. Biol. *9* (1992), 197–213.
[23] *D. Mukherjee, S. Ray, D. K. Sinha*: Bifurcation analysis of a detritus-based ecosystem with time delay. J. Biol. Syst. *8* (2000), 255–261.
[24] *B. Mukopadhyay, R. Bhattacharyya*: A delay-diffusion model of marine plankton ecosystem exhibiting cyclic nature of blooms. J. Biol. Phys. *31* (2005), 3–22.
[25] *B. Mukopadhyay, R. Bhattacharyya*: Modelling phytoplankton allelopathy in a nutrient-plankton model with spatial heterogeneity. Ecol. Model. *198* (2006), 163–173.
[26] *B. Mukhopadhyay, R. Bhattacharyya*: Modeling the role of diffusion coefficients on Turing instability in a reaction-diffusion prey-predator system. Bull. Math. Biol. *68* (2006), 293–313.
[27] *S. Muratori, S. Rinaldi*: Low- and high-frequency oscillations in three-dimensional food chain systems. SIAM J. Appl. Math. *52* (1992), 1688–1706.
[28] *R. M. Nisbet, J. Mckinstry, W. S. C. Gurney*: A "strategic" model of material cycling in a closed ecosystem. Math. Biosci. *64* (1983), 99–113.
[29] *O. Pardo*: Global stability for a phytoplankton-nutrient system. J. Biol. Syst. *8* (2000), 195–209.
[30] *T. Powell, P. J. Richardson*: Temporal variation, spatial heterogeneity and competition for resources in plankton systems: theoretical models. Am. Nat. *125* (1985), 431–463.
[31] *S. Ruan*: Persistence and coexistence in zooplankton-phytoplankton-nutrient models with instantaneous nutrient recycling. J. Math. Biol. *31* (1993), 633–654.
[32] *S. Ruan*: The effect of delays on stability and persistence in plankton models. Nonlinear Anal., Theory Methods Appl. *24* (1995), 575–585.
[33] *S. Ruan*: Oscillations in plankton models with nutrient recycling. J. Theor. Biol. *208* (2001), 15–26.
[34] *S. Ruan, G. Wolkowicz*: Uniform persistence in plankton models with delayed nutrient recycling. Can. Appl. Math. Q. *3* (1995), 219–235.
[35] *A. K. Sarkar, D. Mitra, S. Roy, A. B. Roy*: Permanence and oscillatory co-existence of a detritus-based prey-predator model. Ecol. Model. *53* (1991), 147–156.

[36] *A. K. Sarkar, A. B. Roy*: Oscillatory behavior in a resource-based plant-herbivore model with random herbivore attack. Ecol. Model. *68* (1993), 213–226.
[37] *A. Sikder, A. B. Roy*: Limit cycles in a prey-predator systems. Appl. Math. Lett. *6* (1993), 91–95.
[38] *D. Schley, S. A. Gourley*: Linear stability criteria for population models with periodically perturbed delays. J. Math. Biol. *40* (2000), 500–524.
[39] *J. A. Sherratt*: Turing bifurcations with a temporally varying diffusion coefficient. J. Math. Biol. *33* (1995), 295–308.
[40] *J. A. Sherratt*: Diffusion-driven instability in oscillating environments. Eur. J. Appl. Math. *6* (1995), 355–372.
[41] *O. L. Smith*: Food Webs. Chapman & Hall, London, 1982.
[42] *Y. M. Svirezhev, D. O. Logofet*: Stability of Biological Communities. Mir, Moscow, 1983.
[43] *R. H. Whittaker*: Communities and Ecosystems. Macmillan, New York, 1975.

Authors' addresses: *B. Mukhopadhyay*, Department of Science, Central Calcutta Polytechnic, 21, Convent Road, Kolkata-700 014, India, e-mail: banibrat001@yahoo.co.in; *R. Bhattacharyya*, Department of Science, The Calcutta Technical School, 110, S. N. Banerjee Road, Kolkata-700 013, India.