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

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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

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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

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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, con-
sider 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 nu-
trient recycling

\[
\begin{align*}
\frac{dN}{dt} &= N(N_0 - pN) - aNA + c_1A + b_1H, \\
\frac{dA}{dt} &= a_1NA - cA - \frac{\beta AH}{k + A}, \\
\frac{dH}{dt} &= \frac{\beta_1AH}{k + A} - bH,
\end{align*}
\]

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 \( N(0) \geq 0, A(0) \geq 0, \)
\( H(0) \geq 0, N_0 \) 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. Consump-
tion 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. Herbi-
vore 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 \( W(0) = N(0) + A(0) + H(0) \geq 0 \) 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 \( \dot{W} \leq N_0 N + c_1 A + b_1 H \leq k_{\text{min}} W \), where \( k_{\text{min}} = \min \{ N_0, c_1, b_1 \} \). So, \( W(t) \leq W(0) e^{k_{\text{min}} t} \). 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 \( E_B \equiv (c_1 a_1, c_1 (pc_1/a_1 - N_0), 0) \equiv (N_1, A_1, 0) \);
(iv) the interior equilibrium point \( E^* \equiv (N^*, A^*, H^*) \), where \( A^* = kb/((\beta_1 - b) \), \( N^* \) is the positive root of
\[
px^2 + \left[ AA^* - N_0 - \frac{a_1 b_1 \beta_1 A^*}{\beta b} \right] x + \left( cb_1 - \beta c_1 b \right) A^* \frac{A^*}{b} = 0,
\]
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
\[
b < \beta_1 < \frac{\beta_1 b_1}{cb_1}, \quad N_0 < \frac{(ab - a_1 b_1 \beta_1)k}{\beta (\beta_1 - b)}, \quad N^* > N_1.
\]
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
\[
\left( \frac{\beta_1 A_1}{k + A_1} - b - \lambda \right) \left[ \lambda^2 - \lambda (N_0 - 2pN_1 - aA_1) + A_1 (a_1 c_1 - ac) \right] = 0.
\]
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
\[
N_0 < \frac{pc}{a_1} < \frac{pc_1}{a}
\]
and
\[
b > \frac{\beta_1 (pc^2 - N_0 ca_1)}{pc^2 + ka_1^2 c_1 - ca_1 kc - ca_1 N_0}.
\]
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

\[(2.7) \quad \lambda^3 + P_1 \lambda^2 + P_2 \lambda + P_3 = 0,\]

where

\[(2.8) \quad P_1 = aA^* + 2pN^* - N_0 - M,\]
\[P_2 = M(N_0 - 2pN^* - aA^*) + \frac{kbM}{A^*} - a_1 A^*(c_1 - aN^*),\]
\[P_3 = -(N_0 - 2pN^* - aA^*)\frac{kbM}{A^*} - \frac{a_1 b_1 k^2 H^*}{\beta_1 A^*},\]
\[M = \frac{b^2 \beta H^*}{\beta_1^2 A^*}.\]

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) $P_1 P_2 > P_3 > 0$,

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

\[(2.9) \quad \frac{dN_1}{dt} = N_1(N_0 - 2pN^* - pN_1) - \alpha(N^* A_1 + N_1 A^* + N_1 A_1)
+ c_1 A_1 + b_1 H_1,
\]
\[\frac{dA_1}{dt} = \alpha_1 (N^* A_1 + N_1 A^* + N_1 A_1) - cA_1
- \frac{\beta}{k + A^*} [b(H_1 + H^*) A_1 + A^* H_1
- \frac{1}{k + A^*} \{A_1^2 (H_1 + H^*) + A^* A_1 H_1 + A_1 A^* H^* \}],\]
\[\frac{dH_1}{dt} = \frac{\beta_1}{k + A^*} [A_1 (H + H^*) + A^* H_1
- \frac{1}{k + A^*} \{A_1^2 (H_1 + H^*) + A^* A_1 H_1 + A_1 H^* A^* \}] - bH_1.\]
Then, \((0,0,0)\) is an equilibrium point of (2.9). Next we define

\[
U = \frac{1}{2}N_1^2 + \frac{\sigma_1}{2}A_1^2 + \frac{\sigma_2}{2}H_1^2 \geq 0,
\]

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

\[
\dot{U} = N_1^2(N_0 - 2pN^* - pN_1 - \alpha A^* - \alpha A_1)
+ A_1^2\left[\sigma_1 \left\{\alpha_1(N_1 + N^*) - c \frac{\beta_1}{(H_1 + H^*)} \left(H_1 + H^* - \frac{A_1(H_1 + H^*) + A^*(H_1 + H^*)}{k + A^*} \right) \right. \right.
\left. \left. - \frac{\beta_1}{(k + A^*)^2}H_1H^*\sigma_2 \right\} \right]
+ H_1^2\sigma_2 \left[\frac{\beta_1(A_1 + A^*)}{k + A^*} - \frac{\beta_1}{(k + A^*)^2}A_1(A_1 + A^*) - b \right]
+ N_1A_1(-\alpha N^* + c_1 + \alpha A^*\sigma_1)
+ A_1H_1\left[\frac{\beta A^*\sigma_1}{k + A^*} + \frac{\beta_1H^*A^*}{(k + A^*)^2}\sigma_2 \right] + N_1H_1b_1.
\]

Using the inequality

\[
xy \leq \frac{1}{2} \varepsilon_i x^2 + \frac{1}{2\varepsilon_i} y^2,
\]

we have

\[
\dot{U} \leq N_1^2\left[N_0 - p(2N^* + N_1) - \alpha A^* - \alpha A_1 \right.
+ \frac{\varepsilon_1}{2}(\sigma_1\alpha_1A^* + c_1 - \alpha N^*) + \frac{\varepsilon_3b_1}{2}] 
+ A_1^2\left[\sigma_1\alpha_1(N_1 + N^*) - c \frac{\beta_1}{(H_1 + H^*)} \left(H_1 + H^* - \frac{A_1(H_1 + H^*) + A^*(H_1 + H^*)}{k + A^*} \right) \right.
\left. \left. - \frac{\beta_1}{(k + A^*)^2}H_1H^*\sigma_2 \right\} \right]
+ H_1^2\left[\frac{\varepsilon_2}{2}\frac{\beta_1H^*A^*\sigma_2}{(k + A^*)^2} - \frac{\beta A^*\sigma_1}{k + A^*} \right]
\left. \left. + \frac{\sigma_1\varepsilon_2}{2}\left[\frac{\beta_1H^*A^*}{(k + A^*)^2} - \frac{\beta A^*}{k + A^*} \right] \right\} \right].
\]
Next we set

\[
\sigma_1 = \frac{\alpha N^* - c_1}{\alpha_1 A^*} - \xi_1, \\
\varepsilon_1 = \frac{\alpha N^* - c_1 - \alpha_1 A^* \sigma_1}{2\alpha_1 \sigma_1 (N_1 + N^*)}, \\
\varepsilon_2 = 1, \\
\varepsilon_3 = \frac{2(2pN^* - N_0)}{b_1}, \\
\sigma_2 = \frac{\beta \sigma_1}{k + A^*} \left[ \frac{H^* + H_1 - (A_1 + A^*)(H_1 + H^*)(k + A^*)^{-1}}{\beta H^*(H_1 + A^*)(k + A^*)^{-2}} - \xi_2 \right],
\]

with $\xi_1, \xi_2 > 0$. By choosing $\xi_1, \xi_2$ properly it is possible to set $\sigma_1$ and $\sigma_2$ such that $\dot{U}_1 < 0$, that is, we can choose $\xi_1$ and $\xi_2$ such that

\[
\sigma_2 \left[ \frac{\beta_1}{(k + A^*)^2} (A_1 + A^*)(k + A^* - A_1) - b \right] + \sigma_1 \left[ \frac{\beta_1 H^* A^*}{(k + A^*)^2} - \frac{\beta A^*}{k + A^*} \right] + \frac{b_1}{2\varepsilon_3} \leq 0.
\]

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 $\sigma_1, \sigma_2, \varepsilon_1, \varepsilon_2, \varepsilon_3$ are given by (2.14).

From (2.15), it can be said that for small $b$, we can choose $\xi_1$ and $\xi_2$ sufficiently large so that $\dot{U} \leq 0$. 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

\[
\begin{align*}
\dot{N} &= N(N_0 - pN) - aNA + c_1A + b_1H(t - \tau), \\
\dot{A} &= a_1NA - cA - \frac{\beta AH}{k + A}, \\
\dot{H} &= \frac{\beta_1AH}{k + A} - bH,
\end{align*}
\]

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

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

\[
\lambda^3 + P_1\lambda^2 + P_2\lambda + P_3 + P_3e^{-\lambda\tau} = 0,
\]
where

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

The characteristic equation (3.2) is a transcendental equation and has infinitely many eigenvalues. Consequently, the classical Routh-Hurwitz criteria cannot 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 \(\lambda = u + iv\). 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 \(\tau\) given by

\[
\tau_n = \frac{1}{v_0} \left[ n\pi + \arctan \frac{v_0(P_2 - v_0^2)}{P_1v_0^2 - P_{31}} \right],
\]

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

\[
\Phi(v_0^2) = v_0^6 + v_0^4(P_2 - 2P_2) + v_0^2(P_2^2 - 2P_1P_{31}) + P_{31}^2 - P_{32}^2 = 0.
\]

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

\[
\left[ \frac{du}{d\tau} \right]_{\tau=\tau_0, v=v_0} = \frac{v_0^2}{E^2 + F^2} \left[ \frac{d}{dv_0^2} \Phi(v_0^2) \right],
\]

where

\[
E = P_2 - 3v_0^2 - P_{32}\tau \cos(v_0\tau),
\]
\[
F = 2P_1v_0 + P_{32}\tau \sin(v_0\tau).
\]

Now for large \(v_0^2, \Phi(v_0^2) > 0\) and hence \(d\Phi/dv_0^2 \neq 0\). Thus, the transversality 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 \(\tau\). 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
behavior. In Fig. 3 we demonstrate the onset of delay-induced instability for $\tau = 13$ which numerically exemplifies the existence of $\tau_0$. 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{align*}
\dot{N} &= N(N_0 - pN) - aNA + c_1A + b_1H(t - \tau(t)), \\
\dot{A} &= a_1NA - cA - \frac{\beta AH}{k + A}, \\
\dot{H} &= \frac{\beta_1AH}{k + A} - bH.
\end{align*}

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.
To start the analysis, we first introduce the linear operator

\[ L \begin{pmatrix} u(t) \\ q(t) \\ w(t) \end{pmatrix} = \begin{pmatrix} \frac{du}{dt} - a_{11}u - a_{12}q - b_1w(t - \tau_0) \\ \frac{dq}{dt} - a_{21}u - a_{22}q - a_{23}w \\ \frac{dw}{dt} - a_{32}q \end{pmatrix}, \]

where

\[ a_{11} = N_0 - 2pN^* - aA^*, \quad a_{12} = c_1 - aN^* < 0, \]
\[ a_{21} = a_1A^*, \quad a_{22} = \frac{\beta A^* H^*}{(k + A^*)^2}, \quad a_{23} = -\frac{\beta A^*}{k + A^*}, \]
\[ a_{32} = \frac{\beta_1 H^* k}{(k + A^*)^2}, \quad u = N - N^*, \quad q = A - A^*, \quad w = H - H^*, \]

and \( \tau_0 \) is defined by (3.4) with \( n = 0 \). The linearized version of (4.1) can then be written in the form

\[ L \begin{pmatrix} u(t) \\ q(t) \\ w(t) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}. \]
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

\[
\begin{bmatrix}
  u(t) \\
  q(t) \\
  w(t)
\end{bmatrix} = M
\begin{bmatrix}
  -(a_{32} + a_{22}i v_0 + v_0^2)/a_{21} \\
  iv_0 \\
  a_{32}
\end{bmatrix} e^{i\nu_0 t} + \text{c.c.t.}
\]

(4.5) \equiv M \begin{bmatrix}
  \nu_1 \\
  \nu_2 \\
  \nu_3
\end{bmatrix} e^{i\nu_0 t} + \text{c.c.t.},

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

Next we study the stability criteria of the system around the interior equilibrium point \( E^\ast \) with oscillating delay

\[
\tau(t) = \tau_0 + \varepsilon f(t),
\]

(4.6) where \( \varepsilon \) is a small positive quantity and \( f(t) \) is a periodic function of \( t \). The corresponding linearized system is

\[
\begin{align*}
\frac{du}{dt} &= a_{11} u + a_{12} q + b_1 w(t - \tau(t)), \\
\frac{dq}{dt} &= a_{21} u + a_{22} q + a_{23} w, \\
\frac{dw}{dt} &= a_{32} q.
\end{align*}
\]

(4.7)

We look for a solution of the type

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

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

\[
L \begin{bmatrix}
  u_0 \\
  q_0 \\
  w_0
\end{bmatrix} = \begin{bmatrix}
  0 \\
  0 \\
  0
\end{bmatrix}.
\]

(4.9) So from (4.5) we can say that

\[
\begin{bmatrix}
  u_0 \\
  q_0 \\
  w_0
\end{bmatrix} = M(\sigma) \begin{bmatrix}
  \nu_1 \\
  \nu_2 \\
  \nu_3
\end{bmatrix} e^{i\nu_0 t} + \text{c.c.t.}
\]

(4.10)
Using (4.10), we have

\[
L \begin{pmatrix} u_1 \\ q_1 \\ w_1 \end{pmatrix} = \begin{bmatrix} b_1 f(t)i\nu_0 M(\sigma)\nu_3 + b_1 \tau_0 M'(\sigma)\nu_3 - M'(\sigma)\nu_1 \\ -\nu_2 M'(\sigma) \\ -\nu_3 M'(\sigma) \end{bmatrix} e^{i\nu_0 t} + \text{c.c.t.,}
\]

where \( M' = \frac{dM}{d\sigma} \).

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

\[
f(t) = \sum_{n=-\infty}^{\infty} \alpha_n \exp(\text{i}wn t).
\]

Using (4.11) and (4.12), we obtain

\[
L \begin{pmatrix} u_1 \\ q_1 \\ w_1 \end{pmatrix} = \begin{bmatrix} b_1 \alpha_0 v_0 \nu_3 M(\sigma) + M'(\sigma)(b_1 \tau_0 \nu_3 - \nu_1) \\ -\nu_2 M'(\sigma) \\ -\nu_3 M'(\sigma) \end{bmatrix} e^{i\nu_0 t} \\
+ \sum_{n \neq 0} \begin{bmatrix} i b_1 \alpha_n v_0 \nu_3 M(\sigma) \\ 0 \\ 0 \end{bmatrix} e^{i(v_0 + wn) t} + \text{c.c.t.}
\]

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

\[
\langle \mathbf{u}, \mathbf{v} \rangle = \int_0^{2\pi/v_0} \tilde{u}(t) \tilde{v}(t) \, dt.
\]

The adjoint operator \( L^* \) of \( L \) is [20]

\[
L^* \begin{pmatrix} u \\ q \\ w \end{pmatrix} = \begin{bmatrix} a_{11} u + a_{21} q - \frac{du}{dt} \\ a_{12} u + a_{22} q + a_{32} w - \frac{dp}{dt} \\ b_1 u(t + \tau_0) + a_{23} q - \frac{dw}{dt} \end{bmatrix},
\]

and the kernel of this adjoint operator is given by

\[
\begin{bmatrix} u^*(t) \\ q^*(t) \\ w^*(t) \end{bmatrix} = B \begin{bmatrix} d_1 \\ d_2 \\ d_3 \end{bmatrix} e^{i\nu_0 t} + \text{c.c.t.,}
\]

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where
\[
d_1 = a_{12}a_{32}, \quad d_2 = \frac{a_{12}^2a_{32}}{iv_0 - a_{11}}, \quad d_3 = \frac{a_{12}a_{32}}{(a_{11} - iv_0)(a_{22} - iv_0) - a_{12}a_{21}}.
\]
The particular integral of (4.13) exists if the right-hand side of (4.13) is orthogonal, which implies
\[
\frac{M'(\sigma)}{M(\sigma)} = \frac{d_1 b_1 \alpha_0 v_0 \nu_3}{\nu_1 d_1 + \nu_2 d_2 + \nu_3 d_3 - b_1 d_1 \tau_0 \nu_3} - \frac{2\pi}{\tau_0}.
\]
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
\[
v_0^{2+} = \frac{a_{32} - a_{11}^2 - a_{12}a_{21} + \sqrt{(a_{32} - a_{11}^2 - a_{12}a_{21})^2 - 4a_{11}^2a_{32}}}{2}.
\]
So it is seen that when the mean delay is less (greater) than \(\tau_0\), 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 \(\varepsilon\), we get
\[
L \begin{pmatrix} u_0 \\ q_0 \\ w_0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix},
\]
\[
L \begin{pmatrix} u_1 \\ q_1 \\ w_1 \end{pmatrix} = \begin{pmatrix} b_1 f(t)w_0, t(t - \tau_0, \sigma) \\ 0 \\ 0 \end{pmatrix},
\]
\[
L \begin{pmatrix} u_2 \\ q_2 \\ w_2 \end{pmatrix} = \begin{pmatrix} b_1 f(t)w_1, t(t - \tau_0, \sigma) + b_1 \tau_0 w_0, t(t - \tau_0, \sigma) + \{f(t)\}^2 \\ -q_0, \sigma \\ -w_0, \sigma \end{pmatrix}.
\]
As \(\alpha_0 = 0\), the Fourier series expansion of \(f(t)\) becomes
\[
f(t) = \sum_{n=-\infty, n \neq 0}^{\infty} \alpha_n \exp(iwnt),
\]
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and the solution of (4.20) is

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

where

\[
B_n = \alpha_n \xi^3 - (a_{11} + a_{22})\xi^2 + (a_{11}a_{22} - a_{21}a_{23} - a_{11}a_{23} + b_1a_{21}e^{-i\xi\tau_0})
\]

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

\[
L \begin{bmatrix}
u_2 \\ q_2 \\ w_2
\end{bmatrix} = \begin{bmatrix}
\Delta M'(\sigma) + \sum_{m,n=-\infty, m,n \neq 0}^{\infty} \alpha_m \alpha_n e^{iw(m+n)t} M_n M(\sigma) \\
-M'(\sigma)\nu_2 \\
-M'(\sigma)\nu_3
\end{bmatrix} e^{iv_0 t} + \text{c.c.t.},
\]

where \( \Delta = (b_1\tau_0\nu_3 - \nu_1) \) and \( M_n = b_1^2 i v_0 a_{32} B_n \exp(-iwn\sigma) - \nu_3v_0^2 \). To find the non-secular solution, applying the Fredholm orthogonality condition, we get

\[
(4.23) \quad \{(b_1\tau_0\nu_3 - \nu_1)d_1 - \nu_2d_2 - \nu_3d_3\} M'(\sigma) + \sum_{n \neq 0} \alpha_{-n}\alpha_n M_n M(\sigma) = 0.
\]

Therefore,

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

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

\[
(4.25) \quad M(\sigma) = C \exp[K(w, b_1)\varepsilon^2 t].
\]

So the system will be linearly asymptotically stable if \( \text{Re}\{K(w, b_1)\} < 0 \). 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 \( \tau_0 \) is given by (3.4), \( \varepsilon \) is a small constant and \( f(t) \) is a periodic function with the Fourier expansion \( f(t) = \sum \alpha_n \exp(iwn t) \). 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 $\text{Re}\{K(w, b_1)\} < 0$, 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.

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