Stability Analysis of a Plankton System with Delay

A. K. Sharma \textsuperscript{a} and A. Sharma \textsuperscript{b}\textsuperscript{*}

\textsuperscript{a}Department of Applied Sciences, L.R.D.A. V. College, Jagran, Punjab, India.
\textsuperscript{b} Department of Applied Sciences, D.A.V. Institute of Engineering and Technology, Jalandhar-144008, Punjab, India.

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Abstract. This paper is evolved to have insight of Plankton-Nutrients interactions in the presence of delay in the growth term of phytoplankton species. The conditions for asymptotic stability about endemic equilibrium are derived in the absence of delay. The Nyquist criteria is used to estimate the length of delay to preserve stability. Analytic criterion for the existence of hopf-bifurcation is also discussed.

Keywords: Planktons, Nyquist criterion, Length of delay, Stability and Hopf- Bifurcation.

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1. Introduction

Differential equations with delay in various interaction terms have already been extensively used by many researchers to model population dynamics which also includes plankton-nutrient interactions. Delayed models were initially proposed by volterra [17, 18] to study the fish models. Many delayed biological models are the monographs of cushing[3], gopalsamy [6] and kuang [7]. They observed that the delayed differential equation models exhibited more complicated dynamics than ODE’s as time delay may transfer a stable equilibrium to unstable and induce bifurcations. Moreover, the mathematical analysis of Plankton-Nutrient systems has been studied by many authors [8–14]. Lot of work has also been done which deals with physical and chemical aspects of phytoplankton growth [6]. Beretta et al.[1] and Ruan [15] studied chemostat models to stimulate the growth of plankton with limited nutrient supply at a constant rate and also studied the effect of delay on the stability of the system by taking delay as bifurcation parameter. Das and Ray[4] has studied a detritus based plankton system with delay on nutrient cycling and showed that delay in nutrient cycling does not effect the stability of the system

\textsuperscript{*} Corresponding author. Email: annjumati@yahoo.com
under certain conditions. In this paper we will investigate a Plankton-Nutrient system with limited nutrient supply at a constant rate $D_0$ with delay in the growth term of phytoplankton species due to nutrient uptaking. The deriving equations of the system considered are as follows:

$$\frac{dP}{dt} = rDP(t - \tau) - \delta_1 P - \beta_1 \frac{P}{a+P} Z$$ (1)

$$\frac{dD}{dt} = \gamma(D_0 - D) - \alpha_1 DP$$ (2)

$$\frac{dZ}{dt} = \beta_2 \frac{P}{a+P} Z - \delta_2 Z$$ (3)

$$P(0) > 0, D(0) > 0, Z(0) > 0.$$ 

The following assumptions of the above model are made:
1. The variable $P(t), Z(t)$ and $N(t)$ are the population densities of the phytoplankton, zooplankton and concentration of nutrient respectively at any time $t$.
2. $r$ is the growth rate of phytoplankton and $\gamma$ the rate of replenishment of nutrient. Here $\beta_1$ and $\beta_2$ are the grazing and conversion rate of the biomass by zooplankton respectively (satisfying the condition $\beta_1 > \beta_2$).
3. $D_0$ is the constant rate of nutrient supply, $a$ is the half saturation constant and $\alpha_1$ is the uptake rate of nutrients by the phytoplankton. Further $\delta_1, \delta_2$ are the death rate of phytoplankton and zooplankton species respectively.

The initial conditions of the system (1-3) has the form $P(\theta) = \phi_1(\theta), D(\theta) = \phi_2(\theta), Z(\theta) = \phi_3(\theta)$, $\phi_1(\theta) \geq 0, \phi_2(\theta) \geq 0, \phi_3(\theta) \geq 0, \theta \in [-\tau, 0], \phi_1(0) \geq 0, \phi_2(0) \geq 0, \phi_3(0) \geq 0$, where $\phi_1(\theta), \phi_2(\theta), \phi_3(\theta) \in C([-\tau, 0], R^3_+)$, the space of continuous functions mapping the interval $[-\tau, 0]$ into $R^3_+$ where $R^3_+ = \{(x_1, x_2, x_3) : x_i \geq 0, i = 1, 2, 3\}$.

Now from the fundamental theorem of differential equations the existence, uniqueness and continuous dependence on initial conditions of the system (1-3) are evidently satisfied. The solutions curves must be positive as the populations has to survive [5, 6]. So in order to check the positivity we put the system of equations in the matrix form $X = F(X)$, where $X = (P, D, Z)^t \in R^3$ and

$$F(X) = \begin{bmatrix} F_1(X) \\ F_2(X) \\ F_3(X) \end{bmatrix} = \begin{bmatrix} P(t - \tau)D - \delta_1 P - \beta_1 \frac{P}{a+P} Z \\ \gamma(D_0 - D) - \alpha_1 DP \\ \beta_2 \frac{P}{a+P} Z - \delta_2 Z \end{bmatrix}.$$ 

Let $F : R^3_+ \to R^3$ be locally lipschitz and satisfy the condition $F_i(X)|_{X_i = 0} \geq 0, X \in R^3_+$, where $R^3_+ = [0, \infty)^3$ a nonnegative octant in $R^3$. Therefore by some lemma in [19] and theorem A4 in [16], any solution of (1-3) with positive initial conditions exist uniquely and each component of $X$ remain in $[0, k)$ for some $k > 0$ and if $k < \infty$ then $\lim \sup [P + D + Z] = +\infty$.

2. Stability of Model without Delay

We will first recall a definition from [2, 7]

**Definition**: The Equilibrium $E^*$ is called asymptotically stable if there exist a $K > 0$ such that $\sup_{-\tau \leq \theta \leq 0} ||\phi_1(\theta) - P^*|| + ||\phi_2(\theta) - D^*|| + ||\phi_3(\theta) - Z^*|| < \delta$ which implies that $\lim_{t \to \infty} (P(t), D(t), Z(t)) = (P^*, D^*, Z^*)$, where $(P(t), D(t), Z(t))$ is the solution of the system (1 - 3) with given initial conditions.
The boundary and planar equilibria of the system are $E_0 = (0, D_0, 0)$ which is always trivial, $E_1 = \left( \frac{\gamma (\delta_1 - r D_0)}{\alpha_1 a_1}, \delta_1, 0 \right)$ exists if $r D_0 < \delta_1$ and an interior equilibrium $E^* = \left( \frac{a_2 \beta_2 - \delta_2}{\beta_2}, \frac{\gamma D_0 (\delta_2 - \delta_1)}{\gamma (\delta_2 - \delta_1) + \alpha_1 \delta_2}, \frac{a_2 \beta_2 - \delta_2}{\beta_2} \right)$ where $\frac{\gamma D_0 (\delta_2 - \delta_1)}{\gamma (\delta_2 - \delta_1) + \alpha_1 \delta_2} - \delta_1 > 0$ and $r D_0 > \delta_1 (1 + \frac{\alpha_1 \delta_2}{\gamma (\delta_2 - \delta_1)})$ holds. Here we discuss the flow of the system only around the interior equilibrium $E^*$. The characteristic equation of the system about $E^*$ is given by

$$
\begin{vmatrix}
rd^*e^{-\lambda \tau} - \delta_1 - \frac{a_2 \beta_2 Z^*}{(a + P^*)^2} - \lambda & rP^* - \frac{\beta_1 P^*}{a + P^*} - \delta_2 - \lambda \\
-\alpha_1 D^* & -\gamma - \alpha_1 P^* - \lambda & 0 \\
\end{vmatrix} = 0
$$

$$
\triangle(\lambda, \tau) = \lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 + (B_1 \lambda^2 + B_2 \lambda + B_3) e^{-\lambda \tau} = 0,
$$

(4)

where $A_1 = \gamma + \alpha_1 P^* \delta_1 + \frac{a_2 \beta_2 Z^*}{(a + P^*)^2} + \delta_2 - \frac{\beta_1 P^*}{a + P^*}$.

$$
A_2 = (\delta_1 + \frac{a_2 \beta_2 Z^*}{(a + P^*)^2}) (\gamma + \alpha_1 P^* - \frac{\beta_1 P^*}{a + P^*} + \delta_2) + (\gamma + \alpha_1 P^*)(\delta_2 - \frac{\beta_1 P^*}{a + P^*}) + r \alpha_1 P^* D^* + \frac{a_2 \beta_2 P^* \gamma}{(a + P^*)^2} - \frac{\alpha_1 \beta_2 P^* (\gamma + \alpha_1 P^*)}{a + P^*} - \frac{\alpha_1 \beta_2 P^* \gamma}{a + P^*}.
$$

$$
B_1 = -r D^*, \quad B_2 = r D^* (\frac{\beta_1 P^*}{a + P^*} - \delta_2) - r D^*(\gamma + \alpha_1 P^*)
$$

For $\tau = 0$, the transcendental equation (4) reduces to following form

$$
\triangle(\lambda, 0) = \lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 + (B_1 \lambda^2 + B_2 \lambda + B_3) = 0.
$$

(5)

where,

$$
A_1 + B_1 = \gamma + \frac{\beta_2 - \delta_2}{\beta_2} + \frac{\alpha_1 \delta_2}{\beta_2} + \left[ \frac{\gamma D_0 (\beta_2 - \delta_2)}{\gamma (\beta_2 - \delta_2) + \alpha_1 \delta_2} - \delta_1 \right] > 0
$$

$$
A_2 + B_2 = (a - 1) \left[ \frac{\gamma D_0 (\beta_2 - \delta_2)}{\gamma (\beta_2 - \delta_2) + \alpha_1 \delta_2} - \delta_1 \right] [\gamma + \frac{\alpha_1 \delta_2}{\beta_2} ] > 0.
$$

$$
A_3 + B_3 = \frac{\alpha_1 \beta_2 \delta_2}{\beta_2 - \delta_2} \left[ \frac{\gamma D_0 (\beta_2 - \delta_2)}{\gamma (\beta_2 - \delta_2) + \alpha_1 \delta_2} - \delta_1 \right] [\gamma + \frac{\alpha_1 \delta_2}{\beta_2} ] > 0
$$

Now by using Routh-Hurwitz Criteria we know that all the roots of equation (5) have negative real parts i.e. the interior equilibrium $E^*$ is locally asymptotically stable provided that the condition $(A_1 + B_1)(A_2 + B_2) - (A_3 + B_3) > 0$ holds.

**Theorem 1:** The sufficient conditions such that the endemic equilibrium $E^*$ exist and the system $(1 - 3)$ will remain asymptotically stable around $E^*$ are

$$
\frac{\gamma D_0 (\beta_2 - \delta_2)}{\gamma (\beta_2 - \delta_2) + \alpha_1 \delta_2} \geq \delta_1 , \quad a > 1 \text{ and } (\delta_1 + a \delta) (\beta_2 - \delta_2)^2 \geq a^2 \delta_2 \beta_2^2 \text{ and the populations will also persistent.}
$$

3. Estimation of the Length of Delay to Preserve Stability

We consider the system $(1 - 3)$ and the space of all real valued continuous functions defined on $[-\tau, \infty)$, satisfying the given initial conditions on $[-\tau, 0]$. We linearize the given system about $E(P^*, D^*, Z^*)$ by using perturbations $x = P - P^*$, $y = D - D^*$, $z = Z - Z^*$.
\[
\frac{dx}{dt} = a' x + b' y + c' z + d' x(t - \tau) \\
\frac{dy}{dt} = a'' x + b'' y \\
\frac{dz}{dt} = a''' x
\]

where
\[
a' = -(\delta_1 + \frac{(\beta_2 - \delta_2)\delta}{\beta_2}) , \quad b' = \frac{ar_2}{2}, \quad c' = -\frac{\beta_2 \delta_2}{\beta_2}, \quad d' = \frac{r_D \delta_2}{2}, \delta = \frac{r_D \delta_2}{2}
\]
\[
a'' = -\frac{\gamma D_0 (\beta_2 - \delta_2)}{\gamma (\beta_2 - \delta_2) + \alpha_1 \delta_2}, \quad b'' = (-\gamma - \frac{a_1 \delta_2}{\beta_2 - \delta_2}), \quad a''' = \frac{(\beta_2 - \delta_2)\delta}{\beta_2},
\]

Taking laplace transform of the system \((6-8)\), we get
\[
(s - a' - d' e^{-s\tau})\bar{x} = b'\bar{y} + c'\bar{z} + d'e^{-s\tau}k_1(s) + x(0) \\
(s - b'')\bar{y} = a''\bar{x} + y(0) \\
s\bar{z} = a'''\bar{x} + z(0)
\]

where
\[
k_1(s) = \int_{-\tau}^{0} e^{-st} x(t) dt
\]

and \(\bar{x}, \bar{y}, \bar{z}\) are the laplace transform of \(x(t), y(t)\) and \(z(t)\) respectively.

Now following along the lines of [5]and using Nyquist criteria, it can be shown that the condition for local asymptotic stability of \(E^*\) is given by
\[
ImH(i\eta_0) > 0, \quad (9)
\]
\[
ReH(i\eta_0) = 0, \quad (10)
\]

where \(H(\phi) = \phi^3 + A_1 \phi^2 + A_2 \phi + A_3 + (B_1 \phi^2 + B_2 \phi + B_3)e^{-\phi \tau}\) and \(\eta_0\) is the smallest positive root of \((10)\).

In our case \((9)\) and \((10)\) gives
\[
A_3 - A_1 \eta_0^2 = B_1 \eta_0^2 \cos \eta_0 \tau - B_3 \cos \eta_0 \tau - B_2 \eta_0 \sin \eta_0 \tau, \quad (11)
\]
\[
A_2 \eta_0 - \eta_0^3 > -B_1 \eta_0^2 \sin \eta_0 \tau + B_3 \sin \eta_0 \tau - B_2 \eta_0 \cos \eta_0 \tau \quad (12)
\]
Sufficient conditions are given by if (11) and (12) are satisfied simultaneously. We shall now from the above sufficient conditions give an estimate on the length of delay. Our aim is to find an upper bound \( \eta_+ \) on \( \eta_0 \) independent of \( \tau \) and then to estimate \( \tau \) so that (12) hold for all values of \( \eta \), \( 0 \leq \eta \leq \eta_+ \) and in particular at \( \eta = \eta_0 \). Now from (11), we have

\[
A_1 \eta_0^2 = A_3 + B_3 \cos \eta_0 \tau + B_2 \eta_0 \sin \eta_0 \tau - B_1 \eta_0^2 \cos \eta_0 \tau \tag{13}
\]

Maximizing \( A_3 + B_3 \cos \eta_0 \tau + B_2 \eta_0 \sin \eta_0 \tau - B_1 \eta_0^2 \cos \eta_0 \tau \) subject to \( |\sin(\eta_0 \tau)| \leq 1 \), \( |\cos(\eta_0 \tau)| \leq 1 \), we get

\[
A_1 \eta_0^2 \leq A_3 + |B_3| + |B_2| \eta_0 + |B_1| \eta_0^2 \tag{14}
\]

and if

\[
\eta_+ = \frac{|B_2| + \sqrt{B_2^2 + 4(A_1 - |B_1|)(A_3 + |B_3|)}}{2(A_1 - |B_1|)} \tag{15}
\]

we then have \( \eta_0 \leq \eta_+ \).

Now from (12), we can write

\[
\eta_0^2 \leq A_2 + B_4 \eta_0 \sin \eta_0 \tau + B_2 \cos \eta_0 \tau - B_3 \frac{\sin \eta_0 \tau}{\eta_0} \tag{16}
\]

As \( E^* \) is locally asymptotically stable for \( \tau = 0 \), thus for sufficiently small \( \tau > 0 \), inequality (14) will continue to hold.

Substituting (13) in (16) and rearranging we get,

\[
(B_3 - A_1 B_2 - B_1 \eta_0^2)[\cos \eta_0 \tau - 1] + (B_2 - A_1 B_1) \eta_0 + \frac{A_1 B_3}{\eta_0} \sin \eta_0 \tau < (A_1 A_2 - A_3 - B_3 + A_1 B_2 + B_1^2 \eta_0) \tag{17}
\]

To find the upper bound of (17), we have

\[
(B_3 - A_1 B_2 - B_1 \eta_0^2)[\cos \eta_0 \tau - 1] = 2(B_3 - A_1 B_2 - B_1 \eta_0^2) \sin^2 \frac{\eta_0 \tau}{2} \leq \frac{|B_3 - A_1 B_2 - B_1 \eta_0^2| \eta_0^2 \tau^2}{2}
\]

and \( [(B_2 - A_1 B_1) \eta_0 + \frac{A_1 B_3}{\eta_0}] \sin \eta_0 \tau \leq [(B_2 - A_1 B_1) \eta_0^2 + A_1 |B_3|] \tau \),

Thus (12) must be satisfied if we have \( K_1 \tau^2 + K_2 \tau < K_3 \), where \( K_1 = \frac{1}{2} |B_3 - A_1 B_2 - B_1 \eta_0^2| \), \( K_2 = |B_2 - A_1 B_1 \eta_0^2 + A_1 |B_3| \) and \( K_3 = |A_1 A_2 - A_3 - B_3 + A_1 B_2 + B_1^2 \eta_0| \).

Hence, if \( \tau_+ = \frac{1}{2K_1}(-K_2 + \sqrt{K_2^2 + 4K_1 K_3}) \), then stability is preserved for \( 0 \leq \tau \leq \tau_+ \).
Thus we are now in a position to state the following lemma.

**Lemma 1:** If there exists a $\tau$ in $0 \leq \tau \leq \tau_+$ such that $K_1 \tau^2 + K_2 \tau < K_3$, then $\tau_+$ is the maximum value of $\tau$ i.e. length of delay for which $E^*$ is asymptotically stable.

### 4. Stability Analysis and Bifurcation Results

Let us take $\tau \neq 0$, $\lambda = u + iv$ in (4) and separating the real and imaginary parts, we get

\[ u^3 - 3uv^2 + A_1 u^2 - A_1 v^2 + A_2 u + A_3 + (B_1 u^2 - B_1 v^2 + B_2 u + B_3) e^{-\nu} \cos v \tau + (2B_1 uv + B_2 v) e^{-\nu} \sin v \tau = 0 \]

(18)

and

\[ -v^3 + 3u^2v + 2A_1 uv + A_2 v - (B_1 u^2 - B_1 v^2 + B_2 u + B_3) e^{-\nu} \sin v \tau + (2B_1 uv + B_2 v) e^{-\nu} \cos v \tau = 0 \]

(19)

Let us take $\lambda$ and hence $u$ and $v$ as a function of $\tau$ and we are interested to know the change of stability around $E^*$ at some particular value of $\tau = \hat{\tau}$ for which $u = 0$ and $v \neq 0$.

Therefore from equation (18) and (19), we have

\[ A_1 \hat{v}^2 - A_3 = (B_3 - B_1 \hat{v}^2) \cos \hat{v} \hat{\tau} + B_2 \hat{v} \sin \hat{v} \hat{\tau} \]

\[ \hat{v}^3 - A_2 \hat{v} = B_2 \hat{v} \cos \hat{v} \hat{\tau} - (B_3 - B_1 \hat{v}^2) \sin \hat{v} \hat{\tau} \]

(20)

Eliminating $\hat{\tau}$ from (20), we get an equation in $\hat{v}$ as

\[ \hat{v}^3 + (A_1^2 - 2A_2 - B_1^2) \hat{v}^4 + (A_2^2 - B_2^2 - 2A_1A_3 + 2B_1B_3) \hat{v}^2 + A_3^2 - B_3^2 = 0 \]

(21)

and the value $\hat{\tau}$ of the form

\[ \hat{\tau}_n = \frac{1}{n} \arccos \left( \frac{A_1 \hat{v}^2 - A_3 (B_3 - B_1 \hat{v}^2) + (\hat{v}^2 - A_2 \hat{v}) B_2 \hat{v}}{B_3 - B_1 \hat{v}^2} \right) + \frac{2n\pi}{\hat{v}}, n = 0, 1, 2, 3, \ldots \]

(22)

This implies that as $\tau$ bifurcates from $\tau = 0$, infinitely many branches of $u(\tau)$ appears, of which one crosses $u(\tau) = 0$ at each $\tau_n$. To establish Hopf bifurcation at $\tau = \tau_n$, we need to show that $\frac{du(\hat{\tau})}{d\tau} \neq 0$. From (18) and (19), differentiating with respect to $\tau$ and setting $u = 0$, $v = \hat{v}$ and $\tau = \hat{\tau}$, we have
\[ P \frac{du(\tau)}{d\tau} + Q \frac{dv(\tau)}{d\tau} = R \]
\[ -Q \frac{du(\tau)}{d\tau} + P \frac{dv(\tau)}{d\tau} = S. \]  \hspace{1cm} (23)

where 
\[ P = A_2 - 3v^2 + 2B_1 v \sin \nu \tau + (B_1 v^2 - B_3) \cos \nu \tau + B_2 \cos \nu \tau - B_2 \nu \tau \sin \nu \tau \]
\[ Q = -2A_1 \nu + B_2 \sin \nu \tau + (B_1 v^2 - B_3) \tau \sin \nu \tau - 2B_1 \nu \cos \nu \tau + B_2 \nu \tau \cos \nu \tau \]
\[ R = -(B_1 \nu^2 - B_3) \nu \sin \nu \tau - B_2 \nu^2 \cos \nu \tau \]
\[ S = B_2 \nu^3 \sin \nu \tau - (B_1 \nu^2 - B_3) \nu \cos \nu \tau \]

Now solving (23), we have
\[ \left( \frac{du(\tau)}{d\tau} \right)_{\tau = \rho} = \frac{RP - QS}{P^2 + Q^2} \]  \hspace{1cm} (24)

where \( \frac{du(\tau)}{d\tau} \) has the same sign as that of \( RP - QS \).

Now
\[ RP - QS = \nu^2(3v^4 + 2(A_1^2 - 2A_2 - B_1^2)v^2 + (A_2^2 - B_2^2 - 2A_1A_3 + 2B_1B_3)) > 0 \]  \hspace{1cm} (25)

Suppose we let
\[ \phi(z) = z^3 + (A_1^2 - 2A_2 - B_1^2)z^2 + (A_2^2 - B_2^2 - 2A_1A_3 + 2B_1B_3)z + A_3^2 - B_0^2 \].

which is the left side of (21) with \( z = \nu^2 \) and \( \phi(\nu^2) = 0 \).

Then from (24) and (25), we have
\[ \frac{du(\tau)}{d\tau} = \frac{\nu^2}{P^2 + Q^2} \frac{d\phi}{dz}(\nu^2) \]

Hence if \( \nu = \nu_0 \) is the first positive root of (21) then \( \frac{du}{d\tau} > 0 \) at \( \tau = \rho \) and the smallest \( \tau \) at which stability occur about \( E^* \) is given by (22).

i.e. \( \rho_0 = \frac{1}{\nu_0} \arccos \left( \frac{A_3 \nu_0^2 - A_3 (B_3 - B_1 \nu_0^2) + (A_1 \nu_0^2 - A_3 \nu_0 B_2 \nu_0)}{(B_3 - B_1 \nu_0^2)^2 + (B_2 \nu_0)^2} \right) \).

**Theorem 2:** Let \( \nu = \nu_0 \) be the first positive root of Equation (21), then a Hopf bifurcation occur and the interior equilibrium \( E^* \) become unstable as \( \tau \) passes through.

![Figure 1](image-url)
Figure 2. Figure 3(a) and 3(b) gives numerical solutions calculated at $\tau = 64$, which again showing the convergent nature of the trajectories around $E^*$ with same set of values of parameters.

Figure 3. 3D graph shows small amplitude oscillations of Phytoplankton, Nutrient and Zooplankton in figure 4(a), 4(b) and 4(c), which disappear after certain time.

5. Conclusion

In this paper, we first obtained the conditions for local stability of the system about the interior equilibrium i.e. $E^*$ in the absence of delay and it had been shown
through numerical simulation in figure 1 for suitable set of parameters. Further it was established that the delay in the system did not disturb its stability so long it had been satisfying the stability conditions given in lemma-3 for how so ever long the value of delay may be taken and can be verified through numerical simulation in figure 2, 3 and 4 where the population exhibit small amplitude oscillations around their steady-state value and disappeared after certain time. The length of delay for preserving the stability of the system is also estimated. The critical value of the delay i.e. $\tau = \tau_0$ has also been calculated for the existence of small amplitude oscillations by considering delay as a bifurcation parameter.

References