TWO COMPONENT POPULATION DYNAMICS OF DISSOLVED NUTRIENT AND PHYTOPLANKTON: EXISTENCE OF STABILITY SWITCHES

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Abstract. The paper presents a detailed study of two component population dynamics of dissolved nutrient $N(t)$ and phytoplankton $P(t)$ based on laboratory observations obtained at the University of Brunei Darussalam. Certain experiments were set up with constant input of nutrient introduced into the system. It was assumed that the conversion of dead phytoplankton into nutrient was not immediate. Biologically, some finite time is required for the chemical process of decay to occur. In other words, dead phytoplankton becomes available as nutrient only after some finite time $\tau$. Mathematically, this delay is introduced by a term of the type $P(t - \tau)U(t - \tau)$ as a source term in the governing dynamic equations for the two components obtained from the generalised equations for modelling three interacting components (phytoplankton, herbivores zooplankton and dissolved nutrient) analysed in a recent article by Busenberg et al. [2]. It is shown through a linear analysis that the stability of the steady state is dependent on certain conditions holding between the parameters of the model. Deduction of stability switches upon variation of the parameter $\tau$ constitutes an important aspect of our study.

1. Introduction

The dynamics of marine plankton has been the subject of extensive study through various mathematical models. Since the pioneering work of Riley et al. [11], a number of models with increasing complexity were developed by several authors. Steele [12] and Steele and Frost [13] looked at phytoplankton-herbivore interactions. Explicit incorporation of nutrients in phytoplankton-herbivore interactions can be seen in the models of Evans and Parslow [3], Frost [4], Taylor [14] and Wroblewski et al. [16].

This paper looks at the population dynamics of phytoplankton $P(t)$ in the presence of dissolved nutrient $N(t)$ as a two component model. In order to study the effects of feeding nutrient at a constant rate during the process, several laboratory experiments were set up at the University of Brunei Darussalam. It was assumed that the dead phytoplankton was not immediately available as nutrient. Biologically, the conversion took some finite time $\tau$ in which some chemical process of decay occurred. In order to construct a suitable model to describe the dynamics as observed, we introduce a delay term of the type $P(t - \tau)U(t - \tau)$, where $\tau$ is a finite time delay and $U(t - \tau)$ a unit step function, into the generalised equations developed for three components (phytoplankton, herbivores zooplankton and dissolved nutrient) by Busenberg et al. [2].

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In accordance with the above constraints, the dynamics of dissolved nutrient and phytoplankton interaction is assumed to be described by the following equations:

\[
\begin{align*}
\frac{dN}{dt} &= c_1 P(t - \tau)U(t - \tau) - \frac{aNP}{N + k} + i, \\
\frac{dP}{dt} &= \left(\frac{aN}{N + k} - c_2\right)P, \\
(N(0), P(0)) &= (N_0, P_0)
\end{align*}
\]

The components, \(N = N(t)\) and \(P = P(t)\), are measured in terms of their nitrate concentrations, \(\mu g\ atom\ NO_3 dm^{-3}\). The term \(i\) that denotes the constant input of dissolved nutrient during the dynamical process can be rescaled as \(i = bk\). Thus, various parameters introduced in this model with their respective units, are defined as follows:

- \(a\): maximal nutrient uptake rate for the phytoplankton; \(day^{-1}\)
- \(k\): Michealis–Menton half saturation constant; \(\mu g\ atom\ NO_3 dm^{-3}\)
- \(c_1\): conversion rate of dead phytoplankton into nutrient; \(day^{-1}\)
- \(c_2\): phytoplankton mortality rate; \(day^{-1}\)
- \(b\): constant input rate of nutrient into the system; \(day^{-1}\)
- \(\tau\): finite time delay at which dead phytoplankton is available as nutrient; \(days\).

It is assumed that \(c_1 < c_2\) due to the consideration of the decaying process and also there is a constant input rate of nutrient. The values of the parameters and initial conditions are chosen such that

\[
\begin{align*}
N_0, P_0 &> 0, \\
a, k, c_1, c_2, b, \tau &> 0
\end{align*}
\]

2. Linear Stability Analysis

The main objective of the analysis is to look at the local stability of the steady state of the system (1.1). In other words, we examine the qualitative behaviour of solutions \((N, P)\) of the system (1.1) near the steady state.

2.1. Steady State.

The system (1.1) has a unique steady state represented as

\[
(N_s, P_s) = \left(\frac{c_2k}{a - c_2}, \frac{bk}{c_2 - c_1}\right).
\]

This steady state is independent of the delay parameter \(\tau\), and the dynamics of the system (1.1) when \(\tau = 0\) also possess a similar steady state as (2.1). For (2.1) to represent a feasible steady state we have

\[
0 < c_1 < c_2 < a.
\]
2.2. Linear System.

The standard approach for obtaining the corresponding linear system of (1.1) is by making the substitutions,

\[ N = N_s + n(t), \quad P = P_s + p(t) \]  

(2.3)

into the system (1.1), where \( n(t) \) and \( p(t) \) represent small perturbations of \( (N, P) \) near \( (N_s, P_s) \). Thus, the dynamical behaviour of \( (N, P) \) near \( (N_s, P_s) \) for \( t \geq \tau \) is described by the following linear system

\[
\begin{align*}
\frac{dn}{dt} &= -\Omega n - c_2 p + c_1 p(t - \tau) \\
\frac{dp}{dt} &= \Omega n
\end{align*}
\]

(2.4)

where

\[ \Omega = \frac{b(a - c_2)}{a(c_2 - c_1)}. \]  

(2.5)

Observe that \( \Omega > 0 \) due to the conditions (1.2) and (2.2). The equilibrium point of the linear system (2.4) is simply the origin of the \( n, p \) plane, i.e.

\[ (n, p) = (0, 0). \]  

(2.6)

2.3. Characteristic Equation.

It is known from the theory of delay differential equations (see Bellman and Cooke [1]) that if the equilibrium point (2.6) is asymptotically stable, then the steady state (2.1) is locally asymptotically stable. The stability of the equilibrium point (2.6) is governed by the real parts of the roots \( \lambda \) of the associated characteristic equation given by

\[ F(\lambda, \tau) = \lambda^2 + \Omega \lambda + \Omega(c_2 - c_1 e^{-\lambda \tau}) \]  

(2.7)

where

\[ \lambda = \mu + i\nu, \quad \text{where} \quad \mu, \nu \in \mathbb{R} \]  

(2.8)

Since the roots \( \lambda \) occur in conjugate pairs, we shall consider only \( \nu > 0 \).

2.4. Instantaneous Dynamics.

Let us consider, prior to analysing the equation (2.7), the system (1.1) when \( \tau = 0 \). Basically, the conversion of dead phytoplankton into nutrient becomes instantaneous. Moreover, the instantaneous dynamics has the same steady state (2.1) and one can easily see that its linear system is (2.4) by putting \( \tau = 0 \). Thus the corresponding characteristic equation becomes

\[ \lambda^2 + \Omega \lambda + \Omega(c_2 - c_1) = 0 \]  

(2.9)

whose roots are expressed as

\[ \lambda = \frac{1}{2} \left(-\Omega \pm \sqrt{\Omega^2 - 4\Omega(c_2 - c_1)}\right). \]

Since \( \Omega > 0 \) and \( c_2 > c_1 \), the real parts of these roots are always negative which implies that the equilibrium point (2.6) is asymptotically stable when \( \tau = 0 \). Figure 1 below illustrates a phase plot of (1.1) when \( \tau = 0 \).
2.5. Stability Switches.

In analysing the characteristic equation (2.7), the delay parameter $\tau$ is considered as a continuous variable. Thus we may think $F(\lambda, \tau)$ as a continuous function of $\tau$. Correspondingly, the roots (2.8) are functions of $\tau$. We then may write (2.7) equivalently as

$$\lambda(\tau)^2 + \Omega \lambda(\tau) + \Omega(c_2 - c_1 e^{-\lambda(\tau)\tau}) = 0.$$ 

As $\tau$ is increased from $\tau = 0$, the real parts of (2.8) may change sign and accordingly the stability of the equilibrium point may change. This phenomenon is referred to as stability switches (see for instance MacDonald [9], Gopalsamy [5] and Kuang [8]).

We have shown that the equilibrium point (2.6) is asymptotically stable when $\tau = 0$. If this point switches its stability at some $\tau = \tilde{\tau} > 0$, then (2.8) become pure imaginary roots i.e. $\mathcal{R}(\lambda) = \mu = 0$. Let $\lambda = i\nu$ where $\nu > 0$. Upon substitution into (2.7), we have

$$-\nu^2 + \Omega c_2 - \Omega c_1 \cos \nu \tau = 0$$

$$\Omega \nu + \Omega c_1 \sin \nu \tau = 0$$

Eliminating $\tau$, we obtain

$$(\Omega c_1)^2 = (-\nu^2 + \Omega c_2)^2 + (\Omega \nu)^2$$

and by rearranging we have a quadratic equation in $\nu^2$ i.e.

$$\nu^4 + \nu^2(\Omega^2 - 2\Omega c_2) + \Omega^2(c_2^2 - c_1^2) = 0.$$  

(2.11)

The roots of (2.11) are

$$\nu^2 = \frac{\Omega}{2} \left((2c_2 - \Omega) \pm \sqrt{(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2)}\right).$$  

(2.12)

We know that $\Omega > 0$ and $(c_2^2 - c_1^2) > 0$ due to the conditions (1.2) and (2.2).
Since $\nu$ is real, the existence or nonexistence of pure imaginary roots will depend entirely on the values of $\Omega$, $c_1$ and $c_2$. Thus we consider the following cases

Case i : $(2c_2 - \Omega) \leq 0$,

Case ii : $(2c_2 - \Omega) > 0$ and $(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2) < 0$,

Case iii : $(2c_2 - \Omega) > 0$ and $(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2) > 0$, and

Case iv : $(2c_2 - \Omega) > 0$ and $(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2) = 0$.

In Cases i and ii, pure imaginary roots cease to exist and this implies that $\bar{\tau}$ will not occur. Consequently, stability switches will not occur. All roots (2.8) of the characteristic equation (2.7) are located on the left-half of the complex $\lambda$ plane and stay boundedly away from the imaginary axis as $\tau$ is increased. The equilibrium point (2.6) remains asymptotically stable for all $\tau \geq 0$. We conclude therefore that the coexisting steady state (2.1) is locally asymptotically stable.

Pure imaginary roots exist if the conditions of either Case iii or Case iv are satisfied. In Case iii, there are two positive values of $\nu$ denoted as $\nu_+$ and $\nu_-$ where

$$\nu_+^2 = \frac{\Omega}{2} \left( (2c_2 - \Omega) + \sqrt{(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2)} \right)$$

$$\nu_-^2 = \frac{\Omega}{2} \left( (2c_2 - \Omega) - \sqrt{(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2)} \right)$$

and obviously,

$$0 < \nu_- < \nu_+. \quad (2.14)$$

Both $\nu_+$ and $\nu_-$ are simple positive roots of (2.11). In Case iv, there exists only one positive value of $\nu$ denoted as $\nu_0$ which is of multiplicity 2. Its value is given as

$$\nu_0 = \sqrt{\frac{\Omega}{2} (2c_2 - \Omega)}. \quad (2.15)$$

The existence of these pure imaginary roots at $\bar{\tau}$, in both Cases iii and Case iv, may give rise to stability switches of the equilibrium point. Switches may occur whenever the roots (2.8) cross the imaginary axis as $\tau$ passes $\bar{\tau}$. Crossing to the right may result in the loss of stability, whereas crossing to the left may result in the gain of stability.

2.6. Direction of Crossing.

To determine the direction of crossing at $\bar{\tau}$, we work out the sign of $\Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu}$. Differentiating (2.7) with respect to $\tau$, we obtain

$$2\lambda \frac{d\lambda}{d\tau} + \Omega \frac{d\lambda}{d\tau} + \Omega c_1 \left( \frac{d\lambda}{d\tau} + \lambda \right) e^{-\lambda\tau} = 0$$

that gives

$$\frac{d\lambda}{d\tau} = \frac{-\Omega c_1 \lambda e^{-\lambda\tau}}{2\lambda + \Omega + \Omega c_1 \tau e^{-\lambda\tau}}. \quad (2.16)$$

For convenience, we choose to work with the reciprocal of (2.16) written as

$$\left( \frac{d\lambda}{d\tau} \right)^{-1} = \frac{-2\lambda + \Omega - \tau}{\Omega c_1 \lambda e^{-\lambda\tau}}. \quad (2.17)$$
Substituting $e^{\lambda \tau}$ from (2.7) into (2.17), we obtain

$$
\left( \frac{d\lambda}{d\tau} \right)^{-1} = -\frac{2\lambda + \Omega}{\lambda(\lambda^2 + \Omega \lambda + \Omega c_2)} - \frac{\tau}{\lambda}.
$$

At $\tau = \tilde{\tau}$ where $\lambda = i\nu$ occur as the only roots of (2.7), the sign of $\Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu}$ is

$$
\text{sgn} \left\{ \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu} \right\} = \text{sgn} \left\{ \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu}^{-1} \right\} = \text{sgn} \left\{ \frac{\Omega(\Omega - 2c_2) + 2\nu^2}{(\Omega c_2 - \nu^2)^2 + \Omega^2 \nu^2} \right\}.
$$

Since $(\Omega c_2 - \nu^2)^2 + \Omega^2 \nu^2 > 0$,

$$
\text{sgn} \left\{ \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu} \right\} = \text{sgn} \{ \Omega(\Omega - 2c_2) + 2\nu^2 \}.
$$

Inserting the expression of $\nu^2$ from (2.12),

$$
\text{sgn} \left\{ \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu} \right\} = \text{sgn} \left\{ \pm \Omega \sqrt{(2c_2 - \Omega)^2 - 4(c_2^2 - \overline{c_2}^2)} \right\}. \quad (2.18)
$$

For Case iii,

$$
\text{sgn} \left\{ \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu_+} \right\} = 1 \Rightarrow \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu_+} > 0.
$$

This means that at the eigenvalue $\lambda = i\nu_+$ there exists a sequence of values of $\tau$ which correspond to the roots of (2.7) crossing the imaginary axis from left to right. Consequently, the equilibrium point (2.6) changes its stability from asymptotically stable to unstable. Moreover,

$$
\text{sgn} \left\{ \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu_-} \right\} = -1 \Rightarrow \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu_-} < 0.
$$

In this case, the roots of (2.7) will cross the imaginary axis from right to left as $\tau$ passes through $\tilde{\tau}$ that corresponds to the eigenvalue $\lambda = i\nu_-$. Consequently, the unstable equilibrium point becomes asymptotically stable.

For Case iv,

$$
\text{sgn} \left\{ \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu_0} \right\} = 0 \Rightarrow \Re \left( \frac{d\lambda}{d\tau} \right)_{\lambda=i\nu_0} = 0.
$$

The roots of (2.7) will never cross the imaginary axis. This is obvious since the root $\nu_0$ of (2.11) given in (2.15) is not simple.

2.7. Switching Values of $\tau$ (Case iii).

Let us denote the switching values $\tau = \tilde{\tau}$ that correspond to the imaginary roots $\lambda = i\nu_+$ and $\lambda = i\nu_-$ as $\tilde{\tau} = \tau_+$ and $\tilde{\tau} = \tau_-$ respectively. We have shown that there will occur crossing of roots from left to right of the imaginary axis when $\tau$ increases through $\tau_+$, and crossing of roots from right to left when $\tau$ increases through $\tau_-$. 
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These values of \( \tau \) can be easily determined from (2.10), and are given in (2.19) and (2.21) as follows:

\[
\tau_{+,n} = \frac{\theta_+}{\nu_+} + \frac{2n\pi}{\nu_+} \quad (2.19)
\]

where \( 0 \leq \theta_+ < 2\pi \), \( n = 0, 1, 2, 3, \ldots \) and

\[
\begin{align*}
\cos \theta_+ &= \frac{\Omega c_2 - \nu_+^2}{\Omega c_1} = \frac{\Omega - \sqrt{(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2)}}{2c_1} \\
\sin \theta_+ &= -\frac{\nu_+}{c_1}
\end{align*}
\]

and,

\[
\tau_{-,n} = \frac{\theta_-}{\nu_-} + \frac{2n\pi}{\nu_-} \quad (2.21)
\]

where \( 0 \leq \theta_- < 2\pi \), \( n = 0, 1, 2, 3, \ldots \) and

\[
\begin{align*}
\cos \theta_- &= \frac{\Omega c_2 - \nu_-^2}{\Omega c_1} = \frac{\Omega + \sqrt{(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2)}}{2c_1} \\
\sin \theta_- &= -\frac{\nu_-}{c_1}
\end{align*}
\]

Since \( \theta_+ \), \( \theta_- \), \( \nu_+ \) and \( \nu_- \) are all fixed while \( n \) varies, both \( \tau_{+,n} \) and \( \tau_{-,n} \) represent arithmetic sequences. From (2.20),

\[
\begin{align*}
\pi < \theta_+ < \frac{3\pi}{2} & \text{ if } (\Omega - \sqrt{(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2)}) < 0 \\
\frac{3\pi}{2} < \theta_+ < 2\pi & \text{ if } (\Omega - \sqrt{(2c_2 - \Omega)^2 - 4(c_2^2 - c_1^2)}) > 0
\end{align*}
\]

whereas from (2.22), we see that

\[
\frac{3\pi}{2} < \theta_- < 2\pi.
\]

Thus, from (2.14), (2.23) and (2.24), we can verify easily that

\[
\tau_{+,0} < \tau_{-,0} \quad (2.25)
\]

Thus the equilibrium point (2.6) remains asymptotically stable for all \( 0 \leq \tau < \tau_{+,0} \) since all roots (2.8) have negative real parts. As \( \tau \) passes \( \tau_{+,0} \), two roots of (2.7) cross the imaginary axis towards the right-half of the complex \( \lambda \) plane, and consequently the equilibrium point becomes unstable for all \( \tau_{+,0} < \tau < \tau_{-,0} \). As \( \tau \) passes \( \tau_{-,0} \), the two eigenvalues with positive real parts return back to the left-half plane joining others with negative real parts. Thus the equilibrium point regains its stability for all \( \tau_{-,0} < \tau < \tau_{+,1} \). These exchanges of stability continue as long as the sequences (2.19) and (2.21) obey the following pattern

\[
0 < \tau_{+,0} < \tau_{-,0} < \tau_{+,1} < \tau_{-,1} < \cdots < \tau_{+,n} < \tau_{-,n} < \cdots \quad (2.26)
\]

However the above pattern (2.26) ceases to hold after a certain value of \( n \), due to the following

\[
\tau_{+,n+1} - \tau_{+,n} = \frac{2\pi}{\nu_+} < \frac{2\pi}{\nu_-} = \tau_{-,n+1} - \tau_{-,n} \quad (2.27)
\]
i.e. the common difference of sequence \( \tau_{+,n} \) is less than the common difference of sequence \( \tau_{-,n} \). Thus, there exists a finite number \( n = k \) (say) where \( \tau_{+,k} \) and \( \tau_{+,k+1} \) occur successively before \( \tau_{-,k} \). As a result, the equilibrium point remains unstable for all \( \tau > \tau_{+,k} \). In fact the 'finiteness' of \( n = k \) depends on the values of the fixed parameters.

2.8. Case iv.

Let us denote the values of \( \tau = \tilde{\tau} \) that correspond to the occurrence of pure imaginary eigenvalue \( \lambda = i\nu_0 \) as \( \tilde{\tau} = \tau_0 \). Their values are given in (2.28) as follows:

\[
\tau_{0,n} = \frac{\theta_0}{\nu_0} + \frac{2n\pi}{\nu_0}
\]

(2.28)

where \( 0 \leq \theta_0 < 2\pi \), \( n = 0, 1, 2, 3, \ldots \) and

\[
\begin{align*}
\cos \theta_0 &= \frac{\Omega c_2 - \nu_0^2}{\Omega c_1} = \frac{\Omega}{2c_1} \\
\sin \theta_0 &= -\frac{\nu_0}{c_1}
\end{align*}
\]

(2.29)

We have shown that there is no crossing of roots as \( \tau \) passes \( \tau_0 \). Thus, stability switches will not occur. We can conclude therefore that the equilibrium point (and hence the coexisting steady state) remains asymptotically stable (locally asymptotically stable) for all \( \tau \geq 0 \) except at various \( \tau_0 \) as given in (2.28).

3. Numerical Analysis

The dynamics of the system (1.1) is further illustrated through numerical calculations and simulations which are shown by the following Tables and Figures. The parametric values as given in Table 1 and Table 2, are such that \( c_1, c_2, a, k, N_0 \) and \( P_0 \) are fixed while the parameter \( b \) is adjusted to provide examples in the different cases.

<table>
<thead>
<tr>
<th>parameters</th>
<th>values</th>
</tr>
</thead>
<tbody>
<tr>
<td>( c_1 )</td>
<td>0.4 day(^{-1} )</td>
</tr>
<tr>
<td>( c_2 )</td>
<td>0.5 day(^{-1} )</td>
</tr>
<tr>
<td>( a )</td>
<td>0.1 day(^{-1} )</td>
</tr>
<tr>
<td>( k )</td>
<td>0.2 ( \mu g ) atom ( NO_3 ) dm(^{-3} )</td>
</tr>
<tr>
<td>( (N_0, P_0) )</td>
<td>(0.5, 0.5) ( \mu g ) atom ( NO_3 ) dm(^{-3} )</td>
</tr>
</tbody>
</table>

Table 1. Parametric values used in all calculations and simulations in this paper. The values of \( c_2, a, \) and \( k \) are adopted from Wroblewski et al. [16].
EXISTENCE OF STABILITY SWITCHES

<table>
<thead>
<tr>
<th>cases</th>
<th>range of values of $b \text{day}^{-1}$</th>
<th>chosen values of $b \text{day}^{-1}$</th>
<th>$(N_s, P_s)$ $\mu g \text{atom NO}_3 \text{dm}^{-3}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>i</td>
<td>$b \geq 0.4$</td>
<td>0.5</td>
<td>(0.2,1.0)</td>
</tr>
<tr>
<td>ii</td>
<td>$0.16 &lt; b &lt; 0.4$</td>
<td>0.2</td>
<td>(0.2,0.4)</td>
</tr>
<tr>
<td>iii</td>
<td>$b &lt; 0.16$</td>
<td>0.1</td>
<td>(0.2,0.2)</td>
</tr>
<tr>
<td>iv</td>
<td>$b = 0.16$</td>
<td>0.16</td>
<td>(0.2,0.32)</td>
</tr>
</tbody>
</table>

**Table 2.** Range of values of the parameter $b$ that satisfies the parametric conditions of each case. Third and fourth columns represent the chosen values of $b$ and calculated values of $(N_s, P_s)$ of each case respectively.

3.1. Cases i and ii.

The dynamics of the system (1.1) of Case i (as shown by Figures 2a and 2b) and Case ii (as shown by Figures 2c and 2d) are illustrated.

**Figure 2A.**

**Figure 2B.**

**Figure 2C.**

**Figure 2D.**
3.2. Case iii.

Various simulations of the system (1.1) are shown in Figures 3a–g. Table 3 below contains the calculated values of $\tau_{+, n}$ and $\tau_{-, n}$ for $n = 0, 1, 2, \ldots, 10$. The occurrence of stability switches of the system (1.1) can be readily observed as $\tau$ passes $\tau_{+, n}$ and $\tau_{-, n}$. In this example the steady state loses its linear asymptotic stability permanently for $\tau \geq \tau_{+, 0}$.

\begin{table}[h]
\centering
\begin{tabular}{|c|c|c|c|c|c|}
\hline
$n$ & $\tau_{+, n}$ & $\tau_{-, n}$ & $n$ & $\tau_{+, n}$ & $\tau_{-, n}$ \\
\hline
0 & 11.5149 & 29.8364 & 6 & 108.8536 & 224.5138 \\
1 & 27.7380 & 62.2827 & 7 & 125.0767 & 256.9600 \\
2 & 43.9611 & 94.7289 & 8 & 141.2998 & 289.4063 \\
3 & 60.1843 & 127.1751 & 9 & 157.5229 & 321.8525 \\
4 & 76.4074 & 159.6213 & 10 & 173.7460 & 354.2987 \\
5 & 92.6305 & 192.0676 & & & \\
\hline
\end{tabular}
\caption{Various values of $\tau_{+, n}$ and $\tau_{-, n}$ that correspond to the occurrence of respective pure imaginary eigenvalues. Observe that $\tau_{+, 0}$ and $\tau_{+, 1}$ occur successively before $\tau_{-, 0}$. Consequently, the steady state (0.2, 0.2) becomes unstable as $\tau$ passes $\tau_{+, 0}$.}
\end{table}

\textbf{Figure 3A.} \hspace{1cm} \textbf{Figure 3B.}
3.3. Case iv.

The dynamics of the system (1.1) are illustrated by Figures 4a–d. Table 4 below shows the calculated values of $\tau_{0,n}$ at which the system (1.1) possesses periodic solutions. It is shown that the steady state is asymptotically stable for all $\tau \neq \tau_{0,n}$. 
Table 4. The values of $\tau_{0,n}$ at which eigenvalues $\lambda = i\mu_0$ occur.

<table>
<thead>
<tr>
<th>$n$</th>
<th>$\tau_{0,n}$</th>
<th>$n$</th>
<th>$\tau_{0,n}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>15.1150</td>
<td>6</td>
<td>123.9430</td>
</tr>
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<td>8</td>
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<td>69.5290</td>
<td>9</td>
<td>178.3570</td>
</tr>
<tr>
<td>4</td>
<td>87.6670</td>
<td>10</td>
<td>196.4950</td>
</tr>
<tr>
<td>5</td>
<td>105.8050</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

4. Results and Discussions

Results of the linear stability analysis of the steady state $(N_s, P_s)$ of the system (1.1) and the numerical analysis are brought out for four different cases.

In Cases i and ii, $(N_s, P_s)$ always remains locally asymptotically stable for all $\tau \geq 0$. 
In Case iii, \((N_S, P_s)\) remains locally asymptotically stable for \(0 \leq \tau < \tau_{+,0}\) or \(\tau_{-,n} < \tau < \tau_{+,n+1}\) where \(n = 0, 1, 2, \ldots, k\). Otherwise, it gives up its asymptotic stability when \(\tau_{+,n} < \tau < \tau_{-,n}\) where \(n = 0, 1, 2, \ldots, k\). The finiteness of \(n = k\) that depends on the values of the fixed parameters has resulted in the loss of the stability of \((N_s, P_s)\) permanently for \(\tau > \tau_{+,k}\). It is shown that when \(\tau = \tau_{+,n}\), the corresponding linear system of (1.1) exhibits a periodic solution of period \(T = \frac{2\pi}{\nu_+}\) where \(\nu_+\) is given by (2.13). In fact, as it is hoped to report in a later paper, the system (1.1) experiences a periodic solution of period \(T = \frac{2\pi}{\nu_+}\) approximately. One can refer to recent works of Verhulst [15], Hale and Koçak [7], Gopalsamy [5] and Gopalsamy and Leung [6] for such a bifurcation. Our objective will be to calculate (or at least approximate) such a periodic solution and prove its stability for \(\tau \in (\tau_{+,0}, \tau_{+,0} + \delta)\) where \(\delta\) is positive and small.

In Case iv, \((N_s, P_s)\) is locally asymptotically stable for all \(\tau \geq 0\) except at various \(\tau = \tau_{0,n}\) where \(n = 0, 1, 2, \ldots\).

The incorporation of the delay term of such type \(P(t - \tau)U(t - \tau)\) into the system (1.1) leads to the following generalisation. The instantaneous dynamics of (1.1), i.e. when there is no delay, always exhibits solutions that approach \((N_s, P_s)\) asymptotically and monotonically (see Figure 1). Varying the input rate (i.e. \(b\)) of nutrient into the system only affects the level, \(P_s\), of the steady state. Such asymptotic and monotonic nature of phytoplankton and nutrient interaction is also typical of the phytoplankton-nutrient system analysed in Mohamad [10]. Thus the need for the delay term in our model to observe oscillatory phytoplankton-nutrient interaction is apparent. Such oscillatory behaviour was observed in the laboratory experiments as illustrated by Figure 5 below. The graph consists of two sets of experimental data collected after 80 days and, as we can see, the phytoplankton population appears to oscillate around 40 million cell/ml. In these experiments nitrate concentration was initially maintained at 0.02 g/l and then nitrate was added every 5 days.

![Figure 5](image_url)
References


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