



Hopf Bifurcation Analysis for a Two Species Periodic Chemostat Model with Discrete Delays

Jane Ileri^{1*}, Ganesh Pokhariyal² and Stephene Moindi²

¹Catholic University of Eastern Africa, P.O. Box 62157-00200, Nairobi, Kenya.

²University of Nairobi, P.O. Box 30197-00200, Nairobi, Kenya.

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This work was carried out in collaboration among all authors. JI designed the study, performed the mathematical analysis, wrote the protocol, and wrote the first draft of the manuscript. GP and SM managed the numerical analyses of the study. All authors read and approved the final manuscript.

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Abstract

In this paper we analyze a Chemostat model of two species competing for a single limiting nutrient input varied periodically using a Fourier series with discrete delays. To understand global aspects of the dynamics we use an extension of the Hopf bifurcation theorem, a method that rigorously establishes existence of a periodic solution. We show that the interior equilibrium point changes its stability and due to the delay parameter it undergoes a Hopf bifurcation. Numerical results shows that coexistence is possible when delays are introduced and Fourier series produces the required seasonal variations. We also show that for small delays periodic variations of nutrients has more influence on species density variations than the delay.

Keywords: Coexistence; competition; competitive exclusion; DDE; Periodic Chemostat; Fourier series; Hopf Bifurcation; stability.

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*Corresponding author: E-mail: jireri@daystar.ac.ke;

1 Introduction

The study of Chemostat is important in ecology and has seen many researchers devote themselves to studying and analyzing its models. Its an important piece of laboratory apparatus that is designed for production and functional study of micro-organisms. One of the reasons why a chemostat is very useful is that it can grow micro-organisms in a physiologically steady state and it has the capacity to keep constant all environmental conditions hence making mathematics easily traceable ([1], [2], [3]). Mathematical modelling with time delays has proven to be very valuable in understanding various dynamics both natural and man-made. Delays are common in many natural processes [4]) and ([5]). When environments being modelled are not instantaneous, then they should include delays. Such environments include those of the Chemostat [6], [7], [8] and [9]. The environments of natural populations undergo temporal variation, causing changes in the growth characteristics of populations. One of the methods of incorporating temporal non-uniformity of the environments in models is to assume that the parameters are periodic. A good example of physical environmental conditions that fluctuates with time is temperature, humidity, PH, and availability of important resources such as water and food. All this vary with time and seasons. Researchers (see for instance [10], [11], [12], [13] and [14]), have succeeded in showing that after adding a periodic function to the Chemostat model, coexistent can occur. For some it is the reservoir nutrient concentration that they varied periodically and for others it is the washout rate function. Either way, both results proved coexistence was possible.

In this study we incorporate discrete delay to model the lag in the process of nutrient conversion as well as vary the nutrient supply periodically by a Fourier series as opposed to the commonly used sine function.

2 The model

The chemostat model of two species competing for a single, essential and growth limiting nutrient with a periodic nutrient input and a delay term of $\tau > 0$ is described by:

$$\begin{aligned} \dot{S}(t) &= \left(S^0 + \frac{b}{\omega} \sum_{j=1}^n \frac{(-1)^{j-1}}{2j-1} \cos(2j-1)t - S(t) \right) D_0 - \frac{\mu_1 c_1 x_1(t) S(t)}{k_1 + S(t)} - \frac{\mu_2 c_2 x_2(t) S(t)}{k_2 + S(t)} \\ \dot{x}_1 &= x_1(t) \left(\frac{\mu_1 S(t - \tau_1)}{k_1 + S(t - \tau_1)} - D_1 \right) \\ \dot{x}_2 &= x_2(t) \left(\frac{\mu_2 S(t - \tau_2)}{k_2 + S(t - \tau_2)} - D_2 \right) \end{aligned} \tag{2.1}$$

where:

$S^0(t)$ is the input concentration at time.

$S(t)$ is the concentration of the substrate at time t.

$x_i(t)$ is the concentration of the i^{th} species at time t.

D_0 is the dilution rate

D_i is the death rate for species i.

μ_i is the maximum specific growth rate for the i^{th} species

k_i is the Michaelis-Menten constant for the i^{th} species

c_i is the constant of proportionality and the content of the nutrient in the i^{th} species

$S(0) \geq 0, x_1 \geq 0, x_2 \geq 0$, and the delay term τ is given as τ_1 for the first species and τ_2 for the second species. The nutrient input is given by a Fourier series function as

$S^0(t) = \left(S^0 + \frac{b}{\omega} \sum_{j=1}^n \frac{(-1)^{j-1}}{2j-1} \cos(2j-1)t \right)$. This models prolonged seasonal nutrient variations better than the commonly used sine function ([10], [14]).

The interior equilibrium point defined by model 2.1 is $\xi = (S^*, x_1^*, x_2^*)$.

We translate $\xi = (S^*, x_1^*, x_2^*)$ to the origin by letting $S(t) = S(t) - S^*$, $x_1(t) = x_1(t) - x_1^*$, $x_2(t) = x_2(t) - x_2^*$

With this new transformation, model 2.1 now becomes:

$$\begin{aligned} \dot{S}(t) &= (S^0(t) - S(t) - S^*)D_0 - \frac{\mu_1 c_1 (x_1(t) + x_1^*) (S(t) + S^*)}{(k_1 + S(t) + S^*)} \\ &\quad - \frac{\mu_2 c_2 (x_2(t) + x_2^*) (S(t) + S^*)}{(k_2 + S(t) + S^*)} \\ \dot{x}_1(t) &= -D_1 (x_1(t) + x_1^*) + \frac{\mu_1 S(t - \tau_1) + S^*}{k_1 + S(t - \tau_1) + S^*} (x_1(t) + x_1^*) \\ \dot{x}_2(t) &= -D_2 (x_2(t) + x_2^*) + \frac{\mu_2 S(t - \tau_2) + S^*}{k_2 + S(t - \tau_2) + S^*} (x_2(t) + x_2^*) \end{aligned} \tag{2.2}$$

For simplicity we let:

$$\begin{aligned} f &= (S^0 - S(t) - S^*)D_0 - \frac{\mu_1 c_1 (x_1(t) + x_1^*) (S(t) + S^*)}{(k_1 + S(t) + S^*)} - \frac{\mu_2 c_2 (x_2(t) + x_2^*) (S(t) + S^*)}{(k_2 + S(t) + S^*)} \\ g &= -D_1 (x_1(t) + x_1^*) + \frac{\mu_1 (S(t - \tau_1) + S^*) (x_1(t) + x_1^*)}{k_1 + S(t - \tau_1) + S^*} \\ h &= -D_2 (x_2(t) + x_2^*) + \frac{\mu_2 (S(t - \tau_2) + S^*) (x_2(t) + x_2^*)}{k_2 + S(t - \tau_2) + S^*} \end{aligned}$$

We now linearize 2.2 around $\xi = (S^*, x_1^*, x_2^*)$ by taking the partial derivatives as follows:

$$\begin{aligned} \frac{\partial f}{\partial x_1} &= \frac{-\mu_1 c_1 S^*}{k_1 + S^*} \\ \frac{\partial f}{\partial x_2} &= \frac{-\mu_2 c_2 S^*}{k_2 + S^*} \\ \frac{\partial f}{\partial S(t)} &= -D_0 - \frac{k_1 x_1^* \mu_1 C_1}{(K_1 + s^*)^2} - \frac{k_2 x_2^* \mu_2 C_2}{(K_2 + s^*)^2} \\ \frac{\partial g}{\partial x_1(t)} &= -D_1 + \frac{\mu_1 S^*}{k_1 + S^*} \\ \frac{\partial g}{\partial S(t - \tau_1)} &= \frac{k_1 \mu_1 x_1^*}{(k_1 + S^*)^2} \\ \frac{\partial h}{\partial x_2(t)} &= -D_2 + \frac{\mu_2 S^*}{k_2 + S^*} \\ \frac{\partial h}{\partial S(t - \tau_2)} &= \frac{k_2 \mu_2 x_2^*}{(k_2 + S^*)^2} \end{aligned}$$

Combining all the three equations, our linearized system now becomes:

$$\begin{aligned}
 \dot{S}(t) &= \left(\frac{-\mu_1 c_1 S^*}{k_1 + S^*} \right) x_1(t) + \left(-\frac{\mu_2 c_2 S^*}{k_2 + S^*} \right) x_2(t) + \left(-D_0 - \frac{k_1 x_1^* \mu_1 c_1}{(K_1 + s^*)^2} - \frac{k_2 x_2^* \mu_2 c_2}{(K_2 + s^*)^2} \right) S(t) \\
 \dot{x}_1(t) &= \left(-D_1 + \frac{\mu_1 S^*}{k_1 + S^*} \right) x_1(t) + \left(\frac{k_1 \mu_1 x_1^*}{(k_1 + S^*)^2} \right) S(t - \tau_1) \\
 \dot{x}_2(t) &= \left(-D_2 + \frac{\mu_2 S^*}{k_2 + S^*} \right) x_2(t) + \left(\frac{k_2 \mu_2 x_2^*}{(k_2 + S^*)^2} \right) S(t - \tau_2)
 \end{aligned} \tag{2.3}$$

For brevity we can let:

$$\begin{aligned}
 a_{11} &= -\frac{\mu_1 c_1 S^*}{k_1 + S^*} \\
 a_{12} &= -\frac{\mu_2 c_2 S^*}{k_2 + S^*} \\
 a_{13} &= -\left(D_0 + \frac{k_1 x_1^* \mu_1 c_1}{(k_1 + S^*)^2} + \frac{k_2 x_2^* \mu_2 c_2}{(k_2 + S^*)^2} \right) \\
 a_{21} &= \left(-D_1 + \frac{\mu_1 S^*}{k_1 + S^*} \right) \\
 a_{23} &= \left(\frac{k_1 \mu_1 x_1^*}{(k_1 + S^*)^2} \right) \\
 a_{32} &= \left(-D_2 + \frac{\mu_2 S^*}{k_2 + S^*} \right) \\
 a_{33} &= \left(\frac{k_2 \mu_2 x_2^*}{(k_2 + S^*)^2} \right)
 \end{aligned}$$

The linearized equation now becomes:

$$\begin{aligned}
 \dot{S}(t) &= a_{11}x_1(t) + a_{12}x_2(t) + a_{13}S(t) \\
 \dot{x}_1(t) &= a_{21}x_1(t) + 0x_2(t) + a_{23}S(t - \tau_1) \\
 \dot{x}_2(t) &= 0x_1(t) + a_{32}x_2(t) + a_{33}S(t - \tau_2)
 \end{aligned} \tag{2.4}$$

The characteristics equation corresponding to 2.4 is given by the polynomial

$$\lambda^3 - a_{11}\lambda^2 - a_{21}a_{12}\lambda - a_{13}a_{21}a_{32} + (-a_{33}\lambda^2 + a_{11}a_{33} - a_{21}a_{12}a_{33})e^{-\lambda\tau_2} + (-a_{32}a_{23}\lambda + a_{32}a_{23}a_{11})e^{-\lambda\tau_1} = 0 \tag{2.5}$$

For brevity we can let:

$$\begin{aligned}
 A &= -a_{11} \\
 B &= -a_{21}a_{12} \\
 C &= -a_{13}a_{21}a_{32} \\
 D &= -a_{33} \\
 E &= a_{11}a_{33} \\
 F &= -a_{21}a_{12}a_{33} \\
 G &= -a_{32}a_{23} \\
 H &= a_{32}a_{23}a_{11}
 \end{aligned}$$

The characteristics equation 2.5 is now simplified to:

$$\lambda^3 + A\lambda^2 + B\lambda + C + (D\lambda^2 + E\lambda + F)e^{-\lambda\tau_2} + (G\lambda + H)e^{-\lambda\tau_1} = 0 \tag{2.6}$$

3 Stability and Local Hopf Bifurcation

We will now analyze the stability of this characteristic equation and analyze when the Hopf Bifurcation occurs.

In circumstances when either $\tau_1 \neq 0$ or $\tau_2 \neq 0$ we show that the interior equilibrium point $\xi = (S^*, x_1^*, x_2^*)$ undergoes a Hopf bifurcation as either τ_1 or τ_2 increases from zero.

Theorem 3.1. *From the characteristic equation 2.6 when $\tau_1 = 0$ and $\tau_2 \neq 0$ and we let $\lambda = \omega i$ be a root of 2.6, where ($\omega > 0$) then:*

$$\tau_2 = \frac{1}{\omega} \left[\cos^{-1} \left(\frac{(E - AD)\omega^4 + (EB_1 + AF - DB_2)\omega^2 + FB_2}{D^2\omega^4 - 2DF\omega^2 + F^2} \right) + 2j\pi, \right] j = 0, 1, 2, \dots$$

Where the new terms;

$$\begin{aligned} B + G &= B_1 \\ C + H &= B_2 \end{aligned}$$

And all the other terms are as defined above.

Proof. when $\tau_1 = 0$ and $\tau_2 \neq 0$ the characteristic equation 2.6 will now become:

$$\lambda^3 + A\lambda^2 + (B + G)\lambda + (C + H) + (D\lambda^2 + E\lambda + F)e^{-\lambda\tau_2} = 0$$

For simplicity we can let:

$$\begin{aligned} B + G &= B_1 \\ C + H &= B_2 \end{aligned}$$

The equation now becomes:

$$\lambda^3 + A\lambda^2 + B_1\lambda + B_2 + (D\lambda^2 + E\lambda + F)e^{-\lambda\tau_2} = 0 \tag{3.1}$$

We then let $\lambda = \omega i$, ($\omega > 0$) be a root of 3.1, therefore we shall have:

$$-\omega^3 i - A\omega^2 + B_1\omega i + B_2 + (-D\omega^2 + E\omega i + F)e^{-\omega i\tau_2} = 0$$

Which we can write as

$$-\omega^3 i - A\omega^2 + B_1\omega i + B_2 + (-D\omega^2 + E\omega i + F)(\cos \omega\tau_2 - i \sin \omega\tau_2) = 0$$

Which implies

$$-\omega^3 i - A\omega^2 + B_1\omega i + B_2 - D\omega^2 \cos \omega\tau_2 + E\omega i \cos \omega\tau_2 + F \cos \omega\tau_2 + D\omega^2 i \sin \omega\tau_2 + E\omega \sin \omega\tau_2 - iF \sin \omega\tau_2 = 0$$

Separating the real and the imaginary parts yields:

$$\begin{aligned} -\omega^3 + B_1\omega + E\omega \cos \tau_2 + D\omega^2 \sin \omega\tau_2 - F \sin \omega\tau_2 &= 0 \\ -A\omega^2 + B_2 - D\omega^2 \cos \omega\tau_2 + F \cos \omega\tau_2 + E\omega \sin \omega\tau_2 &= 0 \end{aligned}$$

and we re-write it as

$$\begin{aligned} E\omega \cos \tau_2 + (D\omega^2 - F) \sin \omega\tau_2 &= \omega^3 + B_1\omega \\ E\omega \sin \omega\tau_2 + (F - D\omega^2) \cos \omega\tau_2 &= A\omega^2 + B_2 \end{aligned} \tag{3.2}$$

This leads to:

$$(E^2\omega^2 - (F - D\omega^2)^2) \cos \omega\tau_2 = (E\omega(\omega^3 + B_1\omega)) - (D\omega^2 - F)A\omega^2 + B_2$$

Which yields

$$\tau_2 = \frac{1}{\omega} \left(\cos^{-1} \left(\frac{E\omega(\omega^3 + B_1\omega) - (D\omega^2 - F)A\omega^2 + B_2}{E^2\omega^2 - (F - D\omega^2)^2} \right) + 2j\pi \right), j = 0, 1, 2, \dots$$

Collecting the like terms together the equation further simplifies to:

$$\tau_2 = \frac{1}{\omega} \left[\cos^{-1} \left(\frac{(E - AD)\omega^4 + (EB_1 + AF - DB_2)\omega^2 + FB_2}{D^2\omega^4 - 2DF\omega^2 + F^2} \right) + 2j\pi, \right] j = 0, 1, 2, \dots \quad (3.3)$$

Which completes the proof

Theorem 3.2. *If there exist a polynomial of the form:*

$$\omega^6 + p\omega^4 + q\omega^2 + r = 0 \quad (3.4)$$

and let $S = \omega^2$ then, the polynomial 3.4 has atleast 3 positive roots $\omega_n = \sqrt{S_n}$ where $n = 1, 2, 3$ and therefore $\pm i\omega_n$ are purely imaginary roots of equation 3.1

Proof. If solve simultaneously system 3.2 and Square both sides we shall have:

$$\begin{aligned} E\omega^2 \cos^2 \omega\tau_2 + 2(D\omega^2 - F)E\omega \cos \omega\tau_2 \sin \omega\tau_2 + (D\omega^2 - F)^2 \sin^2 \omega\tau_2 &= \omega^6 + 2B_1\omega^4 + B_1\omega^2 \\ E^2\omega^2 \sin^2 \omega\tau_2 - 2(D\omega^2 - F)E\omega \cos \omega\tau_2 \sin \omega\tau_2 + (F - D\omega^2)^2 \cos^2 \omega\tau_2 &= A\omega^4 + 2AB_2\omega^2 + B_2^2 \end{aligned}$$

Adding up the two equations yields:

$$\omega^6 + (2B_1 + A - D^2)\omega^4 + (B_1^2 + 2AB_2 - E^2 + 2DF)\omega^2 - F^2 + B_2^2 = 0 \quad (3.5)$$

For simplicity we can let:

$$\begin{aligned} (2B_1 + A - D^2) &= p \\ (B_1^2 + 2AB_2 - E^2 + 2DF) &= q \\ -F^2 + B_2^2 &= r \end{aligned}$$

Therefore equation 3.5 now becomes:

$$\omega^6 + p\omega^4 + q\omega^2 + r = 0 \quad (3.6)$$

If we denote $S = \omega^2$ then, we obtain:

$$S^3 + pS^2 + qS + r = 0 \quad (3.7)$$

According to Routh-Hurwitz criterion, [15] the polynomial 3.7 holds the following results:

- If $S < 0$ then, the equation 3.7 has atleast one positive root.
- If $S \geq 0$ then, the equation 3.7 has no positive root.
- If $S \geq 0$ and $\eta = p^2 - 3q > 0$ then, equation 3.7 has positive roots iff $S = \frac{-P + \sqrt{\eta}}{3} > 0$

If 3.7 has positive roots then without loss of generality we can assume that the 3 roots are all positive defined by S_1, S_2, S_3 . Its then true to conclude that equation 3.6 has three positive roots defined by $\omega_n = \sqrt{S_n}$ where $n = 1, 2, 3$.

Consequently, when $n = 1, 2, 3$ then, equation 3.3 is denoted by

$$\tau_n^j = \frac{1}{\omega_n} \left[\cos^{-1} \left(\frac{(E - AD)\omega_n^4 + (EB_1 + AF - DB_2)\omega_n^2 + FB_2}{D^2\omega_n^4 - 2DF\omega_n^2 + F^2} \right) + 2j\pi, \right]$$

where:

$$(j = 0, 1, 2, \dots) \text{ and } (n = 1, 2, 3)$$

With $\pm i\omega_n$ being the purely imaginary roots that has negative real parts for τ_n , which completes the proof.

Theorem 3.3. Let $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ be the root of 3.1 near $\tau = \tau_j$ satisfying $\alpha\tau_j = 0, \omega(\tau_j) = \omega_0$ then the following transversal condition holds:

$$\alpha'(\tau_2)^{-1} \Big|_{\tau=\tau_n^j} = \operatorname{Re} \left[\frac{d\lambda}{d\tau_2} \right]_{\tau_2=\tau_n^j}^{-1} \neq 0$$

Where: $n = 1, 2, 3$ and $j = 0, 1, 2, \dots$

Proof. We consider the characteristic polynomial labelled 3.1 and evaluate the derivative of λ implicitly with respect to τ_2 to get:

$$3\lambda^2 \frac{d\lambda}{d\tau_2} + 2A\lambda \frac{d\lambda}{d\tau_2} + B_1 \frac{d\lambda}{d\tau_2} + (D\lambda^2 + E\lambda + F) \left(-e^{-\lambda\tau_2} \lambda - e^{-\lambda\tau_2} \tau_2 \frac{d\lambda}{d\tau} \right) + e^{-\lambda\tau_2} \left(\frac{d\lambda}{d\tau} + E \frac{d\lambda}{d\tau} \right) = 0$$

leading to

$$\frac{d\lambda}{d\tau} = \frac{\lambda e^{-\lambda\tau_2} (D\lambda^2 + E\lambda + F)}{3\lambda^2 + 2A\lambda + B_1 - \tau_2 e^{-\lambda\tau_2} (D\lambda^2 + E\lambda + F) + e^{-\lambda\tau_2} (2D\lambda + E)} \quad (3.8)$$

or:

$$\left(\frac{d\lambda}{d\tau} \right)^{-1} = \frac{3\lambda^2 + 2A\lambda + B_1 e^{\lambda\tau_2}}{\lambda (D\lambda^2 + E\lambda + F)} + \frac{(2D\lambda + E)}{\lambda (D\lambda^2 + E\lambda + F)} - \frac{\tau_2}{\lambda} \quad (3.9)$$

with $\lambda = \omega_n i$ and $\tau_2 = \tau_n^j$, simply denoted here as τ_j , equation 3.9 becomes:

$$\left(\frac{d\lambda}{d\tau} \right)^{-1} = \frac{(-3\omega_n^2 + 3A\omega_n i + B_1) e^{\omega_n i \tau_j}}{-Di\omega_n^3 - E\omega_n^2 + F\omega_n i} + \frac{(2D\omega_n i + E)}{-Di\omega_n^3 - E\omega_n^2 + F\omega_n i} - \frac{\tau_j}{\omega_n i} \quad (3.10)$$

which leads to

$$= \frac{1}{\Omega} (-3\omega_n^2 \cos \omega_n \tau_j - 3\omega_n^2 i \sin \omega_n \tau_j + 2A\omega_n i \cos \omega_n \tau_j - 2A\omega_n \sin \omega_n \tau_j + B_1 \cos \omega_n \tau_j + B_1 i \sin \omega_n \tau_j + 2D\omega_n i + E) - \frac{\tau_j}{\omega_n i} \quad (3.11)$$

where $\Omega = (-E\omega_n^2 + (F\omega_n - D\omega^3)i)$

or

$$\begin{aligned} \left(\frac{d\lambda}{d\tau} \right)^{-1} &= \frac{1}{\Theta} \left(3E\omega_n^4 \cos \omega_n \tau_j + 3F\omega_n^3 i \cos \omega_n \tau_j - 3iD\omega_n^5 \cos \omega_n \tau_j + \right. \\ & 3E\omega_n^4 \sin \omega_n \tau_j - 3F\omega_n^3 i \sin \omega_n \tau_j - 3iD\omega_n^5 \sin \omega_n \tau_j - \\ & 2AE\omega_n^3 i \cos \omega_n \tau_j + 2AF\omega_n^2 \cos \omega_n \tau_j - 2AD\omega_n^4 \cos \omega_n \tau_j + \\ & + 2AE\omega_n^3 \sin \omega_n \tau_j + 2AF\omega_n^2 i \sin \omega_n \tau_j - 2ADi\omega_n^4 \sin \omega_n \tau_j - \\ & B_1 E\omega_n^2 \cos \omega_n \tau_j - B_1 F\omega_n i \cos \omega_n \tau_j + B_1 Di\omega_n^3 \cos \omega_n \tau_j - \\ & B_1 E\omega_n^2 i \sin \omega_n \tau_j + B_1 F\omega_n \sin \omega_n \tau_j - B_1 D\omega_n^3 \sin \omega_n \tau_j - 2DE\omega_n^3 i + \\ & \left. 2DF\omega_n^2 - 2D^2\omega_n^4 - E^2\omega_n^2 - FE\omega_n i + EID\omega_n^3 \right) + \frac{\tau_j i}{\omega_n} \end{aligned} \quad (3.12)$$

Where:

$$\Theta = E^2\omega_n^4 + (F\omega_n - D\omega_n^3)^2$$

The real part of this complex function is:

$$\begin{aligned} \operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1} = & \frac{1}{\Theta} \left(3E\omega_n^4 \cos \omega_n \tau_j - 3F\omega_n^3 \sin \omega_n \tau_j + 3D\omega_n^5 \cos \omega_n \tau_j + \right. \\ & 2AF\omega_n^2 \cos \omega_n \tau_j - 2AD\omega_n^4 \cos \omega_n \tau_j + 2AE\omega_n^3 \sin \omega_n \tau_j - \\ & B_1E\omega_n^2 \cos \omega_n \tau_j + B_1F\omega_n \sin \omega_n \tau_j - B_1D\omega_n^3 \sin \omega_n \tau_j + \\ & \left. 2DF\omega_n^2 - 2D^2\omega_n^4 - E^2\omega_n^2 \right) \neq 0 \end{aligned} \tag{3.13}$$

This completes the proof.

Lemma 3.4. *When theorem 3.1, 3.2 and 3.3 hold, then as τ_2 increases from zero, there exist a critical value say α such that the equilibrium point $\xi = (S^*, x_1^*, x_2^*)$ is locally asymptotically stable and unstable as τ_2 rises greater than the critical value such that $\tau_2 > \tau_\alpha$. In addition, the system 2.1 demonstrates Hopf bifurcation at the positive equilibrium point $\xi = (S^*, x_1^*, x_2^*)$ for $\tau_2 = \tau_n^j, (j = 0, 1, 2, \dots)$ as delay increases past the critical value.*

4 Numerical Results

Numerical results when $\tau_1 = 0$ and $\tau_2 \neq 0$ given in the figures below are agreement with the analytical results presented in the Theorems above including lemma 3.4.

Table 1. Parameter values used to graph figures when $\tau_1 = 0$ and $\tau_2 \neq 0$

History	Time	S0	c_1	c_2	$D_0 = D_1 = D_2$	$\mu_1 = \mu_2$	$k_1 = k_2$	b	ω
[6,5,4]	[0,900]	11	1	1	0.4675	0.571	0.5	8	π

The graphical representation with $\tau_1 = 0$ and $\tau_2 = 1$ with $b = 0$ is

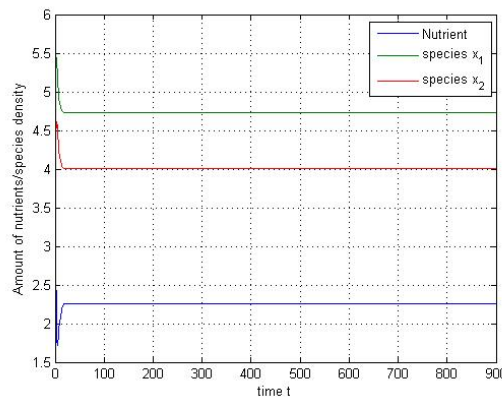


Fig. 1. A graph showing coexistence of two species at the equilibrium point, $\tau_2 = 1$

The positive equilibrium of the system 2.1 is locally asymptotically stable for $\tau_1 = 0$ and $\tau_2 = 1$, with the equilibrium points being $(S^*, x_1^*, x_2^*) = (2.2579, 4.7342, 4.007)$

Fig. 1. demonstrates that even with small delays and no periodicity, coexistence of the two competing species is possible. This contrasts sharply with the results from a Chemostat model without delays, which usually predicts competitive exclusion. Hence incorporating delays results in a chemostat model that more closely predicts natural like environments.

A major weakness in this figure is that the density of both species is constant. This is not what is observed in natural environment. clearly, there is need to modify the model so that even with small delays, the naturally observed variations are reproduced.

As we increase the delay τ_2 , the density of species x_2 keeps increasing while that of x_1 keeps decreasing. At $\tau_2 = 7$, the species x_2 is the dominant species with the changeover taking place at $\tau_2 = 3.8$

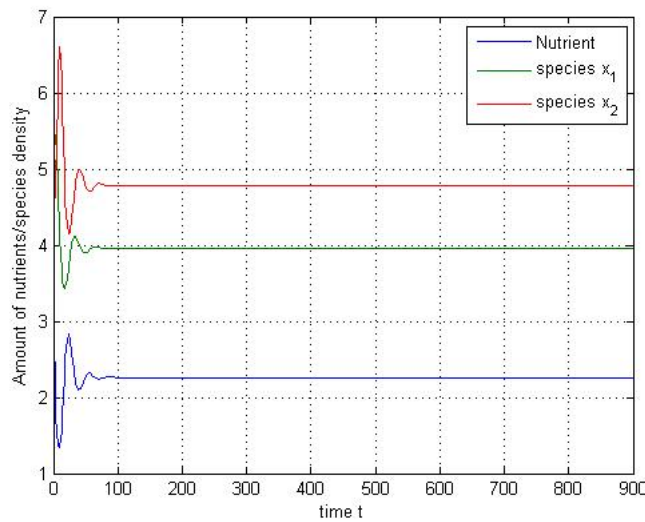


Fig. 2. A graph showing Coexistence at , $\tau_2 = 7$

However when we get near the bifurcation point which occurs at $\tau_2 = 24$, periodic variations keeps being persistence for longer. The diagram is as shown in the Fig. 3.

The Figure illustrates the effects of large delays. The results are similar to those in Fig. 2. in terms of coexistence. In the event we have competing species, coexistence is guaranteed and variations on species density is clearly demonstrated. However in order to model variations for both small and large variations we incorporate periodicity in form of Fourier series function.

Incorporation of periodic nutrient input through a Fourier series function results in an even better model on natural environments as demonstrated by figure 4 with $\tau_1 = 0$ and $\tau_2 = 1$. The simulations gives interesting insights into the model. We see that even in times of below-average nutrient supply, there are occasional spices as expected in natural environments. In nature, assuming nutrients is washed into a lake by rain water, we do expect occasional rains that add nutrients. This is especially true in the tropics. The results agree with those obtained in Fig. 1. and as τ_2 increases, so does its average density.

It is important to note that in chemostat equations, when we use a Fourier series to vary the nutrients periodically as well as evaluate the discrete delay at the bifurcation point $\tau_2 = 24$, then

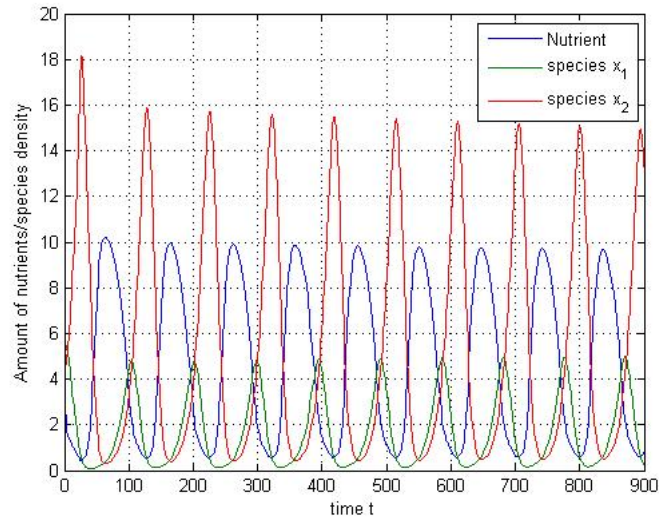


Fig. 3. A graph showing Bifurcation at , $\tau_2 = 24$

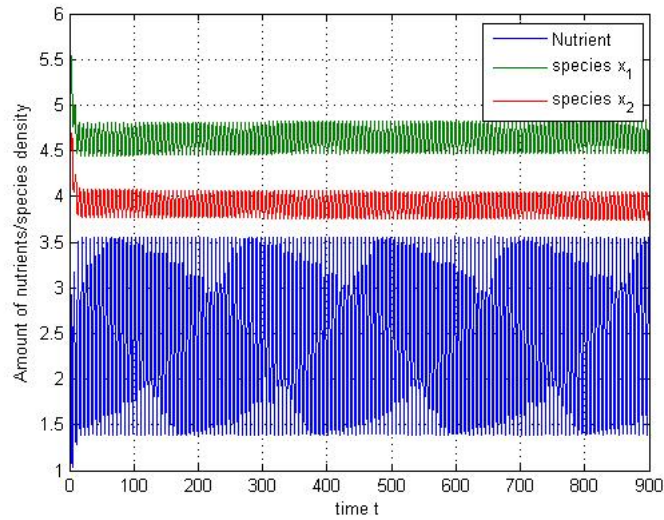


Fig. 4. A graph of two species at, $\tau_2 = 1$ with periodic nutrient

periodicity seems to be caused more by the delay other than the periodic term.

Fig. 3. shows a diagram for a model without periodic nutrient input while Fig. 5. shows the same diagram with periodic nutrient input. While the equilibrium points remain similar in both diagrams, Fig. 5. shows regions where the influence of either the periodic nutrient input or delays play a major role. Fig. 4. clearly confirms that when the delay is small, then periodicity is more significant and both play a big role in modelling natural environments.

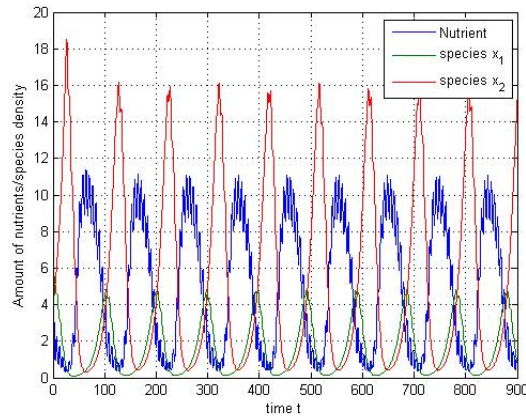


Fig. 5. A graph of two species at the bifurcation point, $\tau_2 = 24$ with periodic nutrient

These results are replicated if we let $\tau_1 \neq 0$ and $\tau_2 = 0$

When we have $\tau_1 > 0$, and $\tau_2 > 0$, and nutrient input varied periodically, numerical computation show that species coexist.

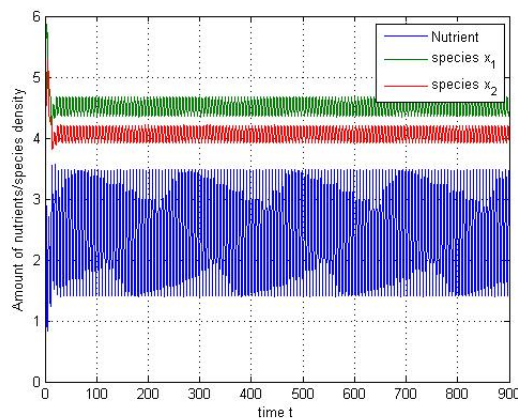


Fig. 6. A graph of two species with two distinct delays $\tau_1 = 1$ and $\tau_2 = 3$ and periodic nutrient input

This is the situation that mimics nature more accurately. Species naturally lives in the same ecosystem even in cases where we have some limited nutrients. In addition, species usually contain delays even though some species may have smaller or larger delays compared to others and depending on the problem being modelled. It's unlikely that any of the delays will be zero at any time. In addition when both delays are greater than zero, we note that the species with the larger delay seems to persist in higher density than those with smaller delay. When delay terms are incorporated with periodic nutrient, they also mimic the natural environment closely. Naturally, even though competing species coexist, they comprise of distinct delay terms.

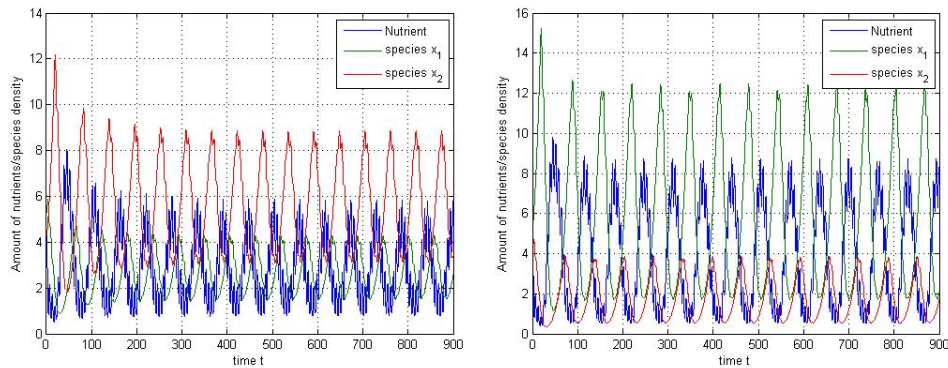


Fig. 7. Graph of $\tau_1 = 1$ and $\tau_2 = 17$ and Fig. 8. Graph of $\tau_1 = 17$ and $\tau_2 = 1$ and periodic nutrient input

5 Conclusion

The inclusion of discrete delays in a periodic chemostat model to cater for the time taken in nutrient conversion is not just an approach to ensure coexistence holds but also a natural fact to explain that consumption cannot at any time imply instant growth. Both numerical and analytical computations show that incorporating delay terms provokes periodic solutions. It is also clear that incorporating both delays and periodicity results in a much better prediction of natural environments and both play an important role in determining how species coexist with each other. The model where the two delays are distinct are more realistic because species do not contain the same delays in size, growth and development, as well as age, which are the main factors that define maturity. The species with larger delay exists in a greater density compared to the one with small delays as shown in Fig. 7 and 8.

Competing Interests

Authors have declared that no competing interests exist.

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