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Delayed Nutrient Conversion for a Single Species Periodic Chemostat

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Authors' contributions

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 with periodic nutrient input modelled using Fourier series and incorporate delays in nutrient conversion. We show that both periodicity and delays have complementing influence in the long term behaviour of the species. Numerical results show that periodicity has bigger influence on species density variations for delays below the Hopf Bifurcation point, while for delays above the Bifurcation point,the delay effect is more influential.

Keywords: DDE; Periodic Chemostat; Fourier series; Hopf Bifurcation.

2010 Mathematics Subject Classification: 34H20, 34K18, 37C75.

1 INTRODUCTION

The chemostat is an important piece of laboratory apparatus that occupies a central place in ecological studies. It 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 such as PH, cell density, nutrient concentration etc. When studying the interrelationships of organisms and

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their environments it's difficult to trace the mathematics, but the chemostat makes the mathematics easily traceable (see for instance Watman [1] and Zhao [2]).

The nature of many processes in modelling, dictates use of time delays. Time delays occur so often in real life that to try and snub them in modelling is ignoring reality [3]. Nutrient consumption for example, does not imply instant growth, there must be time taken before further reactions take place. In economics, money supply is not direct consequence to change in economy, their is time involved in price change. Moreover, all humans without exclusions take some time between conception and birth. There's also time involved in nutrient conversion and maturation. In almost all applications in sciences, there is a great need for incorporating time delays due to the presence of process time. Recent theoretical and computational advancements in delay differential equations reveal that delay differential equations are capable of generating rich and plausible dynamics with realistic parameter values [2].

Organisms live and interact in a fluctuating environment. In pursuing the description of natural processes, we search for periodic patterns since they are useful in helping us predict what they will do in future [4]. Even though autonomous systems have been extensively studied, non-autonomous systems are more realistic because real-world models often require incorporating temporal inhomogeneity in the models. 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 with the same period of the time variable [5]. 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.

Past studies have shown that when creating a periodic environment in a Chemosat model, introducing the Fourier series is better than the commonly used sine function [6] since Fourier series enables one to demonstrate periodic functions as infinite trigonometrical series including functions that contain discontinuity. In our study we use an appropriate Fourier series to vary the nutrient input periodically.

2 THE MODEL

The chemostat model with periodic nutrient input and nutrient conversion delay is given by

$$\begin{aligned}\dot{S}(t) &= \left(S^0(t) + \frac{b}{\omega}\sum_{j=1}^{n}\frac{(-1)^{j-1}}{2j-1}\cos(2j-1)t - S(t)\right)D - \frac{\mu c x(t)S(t)}{k+S(t)} \\ \dot{x}(t) &= x(t)\left(\frac{\mu S(t-\tau)}{k+S(t-\tau)} - D\right) \qquad (2.1)\end{aligned}$$

where:

$S^0(t)$ is the input concentration at time.
S(t) is the concentration of the substrate at time t.
$x(t)$ is the concentration of the species at time t.
D is the dilution rate
μ is the maximum specific growth rate for the species
k is the Michaelis-Menten constant for the species
c is the constant of proportionality and the content of the nutrient in the species
τ is the delay term.

The nutrient input is given by a Fourier series function as

$S^0(t) = \left(S^0 + \frac{b}{\omega} \sum_{j=1}^{n} \frac{(-1)^{j-1}}{2j-1} \cos(2j-1)t \right)$ models prolonged seasonal nutrient variations better than the commonly used sine function [5],[7]).

System 2.1 has two rest points. The boundary rest point is given by $(\overline{S}^*, 0)$ and an interior one given by $(\overline{S}^*, \overline{x}^*)$ where $0 < \min(S(t)) \leq \overline{S}^* \leq \max(S(t))$ and $0 \leq \min(x(t) \leq \overline{x}^* \leq \max(x(t))$. For the boundary rest point we have $0 < S^0 - |\frac{b}{\omega} \sum_{j=1}^{n} \frac{(-1)^{j-1}}{2j-1} \cos(2j-1)t| \leq \overline{S}^* \leq S^0 + |\frac{b}{\omega} \sum_{j=1}^{n} \frac{(-1)^{j-1}}{2j-1} \cos(2j-1)t \mid$. We denote $(\overline{S}^*, \overline{x}^*)$ as $\xi^*(S^*, x^*)$.

The interior equilibrium point $\xi^*(S^*, x^*)$, can be translated to the origin by letting $S_1(t) = S(t) - S^*$ and $x_1(t) = x(t) - x^*$ and still denote them as $S(t)$ and $x(t)$ respectively. With the new transformations of $S_1(t)$ and $x_1(t)$, system 2.1 now becomes:

$$\begin{aligned} \dot{S}(t) &= \left(S^0(t) - S(t) - S^*\right) D - \frac{\mu c(S(t) + S^*)(x(t) + x^*)}{(k + S(t) + S^*)} \\ \dot{x}(t) &= -D(x(t) + x^*) + \frac{\mu(S(t-\tau) + S^*)(x(t) + x^*)}{k + S(t-\tau) + S^*} \end{aligned} \tag{2.2}$$

For brevity, we let

$$\begin{aligned} f &= \left(S^0(t) - S(t) - S^*\right) D - \frac{\mu c(S(t) + S^*)(x(t) + x^*)}{(k + S(t) + S^*)} \\ g &= D(x(t) + x^*) + \frac{\mu(S(t-\tau) + S^*)(x(t) + x^*)}{k + S(t-\tau) + S^*} \end{aligned} \tag{2.3}$$

We note that $S(t) = x(t) = 0$ and

$$\begin{aligned} \frac{\partial f}{\partial x(t)} &= \frac{-\mu c S^*}{k + S^*} \\ \frac{\partial f}{\partial S(t)} &= -D - \frac{k x^* \mu c}{(k + S^*)^2} \\ \frac{\partial g}{\partial x(t)} &= -D + \frac{\mu S^*}{k + S^*} and \\ \frac{\partial g}{\partial S(t-\tau)} &= \frac{k \mu x^*}{(k + S^*)^2} \end{aligned}$$

The linearized system becomes

$$\begin{aligned} \dot{S}(t) &= -\frac{\mu c S^*}{k + S^*} x(t) - \left(D + \frac{k x^* \mu c}{(k + S^*)^2}\right) S(t) \\ \dot{x}(t) &= \left(-D + \frac{\mu S^*}{k + S^*}\right) x(t) + \left(\frac{k \mu x^*}{(k + S)^2}\right) S(t-\tau) \end{aligned} \tag{2.4}$$

Let $m = \frac{k \mu x^*}{(k + S^*)^2}$ and $n = \frac{\mu S^*}{(k + S^*)}$

The characteristic equation of 2.4 is given by

$$\lambda^2 + (2D - n + cm)\lambda + (D^2 + cmD - Dn - cmn) + cmce^{-\lambda\tau} = 0 \tag{2.5}$$

Letting $n - D = k$, $\beta = cm + D$, and $l = cmn$,the characteristic equation 2.5 simplifies to:

$$\lambda^2 + (\beta - k)\lambda - \beta k + le^{-\lambda\tau} = 0 \tag{2.6}$$

We now show that under suitable conditions system 2.1 undergoes Hopf Bifurcation. Hopf Bifurcation requires that the equilibrium point $\xi(S^*, x^*)$ be asymptotically stable, 2.6 has imaginary roots, and Re $\left(\frac{d\lambda}{d\tau}\right)^{-1} |_{\tau=\tau_j} > 0$, $j = 1, 2, 3...$, simultaneously where τ_j is as defined in 2.10(see for instance [8], [9] and [10].

Theorem 2.1. *If*

1. $\tau = 0$ *and* $(\beta - k) > 0$,
2. $l > \beta k$, *and*
3. $\lambda(\tau) = \alpha + i\omega(\tau)$ *be a root of 2.1 near* $\tau = \tau_j$ *satisfying* $\alpha(\tau_j) = 0$ *for* $\omega(\tau_j) = \omega_0$,

then, as τ *increases from zero, there exist a critical value say* $\tau = \tau_\eta$ *such that the equilibrium point* $\xi^*(S^*, x^*)$ *is locally asymptotically stable and unstable as the delay term* τ *rises greater than the critical value. Furthermore, the system 2.1 undergoes a Hopf bifurcation at the positive equilibrium point* $\xi^*(S^*, x^*)$ *for* $\tau = \tau_j, (j = 0, 1, 2, ...)$ *as delay increases past the critical value*

When $\tau = 0$ and $(\beta - k) > 0$ we show that the equilibrium point $\xi^*(S^*, x^*)$ of the system 2.2 is asymptotically stable.

When $\tau = 0$, the characteristic equation 2.6 becomes:

$$\lambda^2 + (\beta - k)\lambda - \beta k + l = 0 \tag{2.7}$$

Solving 2.7 by the quadratic equation yields:

$$\lambda_1 = \frac{-(\beta - k) \pm \sqrt{(\beta - k)^2 - 4(-\beta k + l)}}{2}$$

But since $\beta - k > 0$ then, the real parts of λ_1 will be negative, implying that the system is asymptotically

If $l > \beta k$ the characteristic equation 2.6 has a pair of purely imaginary roots $\pm i\omega_0$, where

$$\omega_0 = \left(\frac{-(\beta^2 + k^2) + \sqrt{(\beta^2 + k^2) - 4(\beta^2 k^2 - l^2)}}{2}\right)^{\frac{1}{2}}$$

and when $\tau = \tau_j$ then

$$\tau_j = \frac{1}{\omega_0}\left(\cos^{-1}\frac{\omega_0^2 + \beta k}{l} + 2j\pi\right) j = 0, 1, 2...$$

To show this, we let $i\omega_0$ (where ω is non negative) be a root of 2.6 then $(i\omega_0)^2 + (\beta - k)\omega i - \beta k + l(\cos\omega\tau - i\sin\omega\tau) = 0$ or:

$$-\omega^2 + i(\beta - k)\omega - \beta k + l(\cos\omega\tau - i\sin\omega\tau) = 0 \tag{2.8}$$

We separate the real part and the imaginary part to get:

$$\begin{aligned} -\omega^2 - \beta k + l\cos\omega\tau &= 0 \\ (\beta - k)\omega_0 - l\sin\omega\tau &= 0 \end{aligned}$$

Which means:

$$\begin{aligned} l\cos\omega\tau &= \omega^2+\beta k \\ l\sin\omega\tau &= (\beta-k)\omega \end{aligned} \tag{2.9}$$

squaring and adding both sides yields:

$l^2(\cos^2\omega\tau+\sin^2\omega\tau)=\omega^4+\omega^2(2\beta k+(\beta-k)^2)+\beta^2k^2$

Which means $\omega^4+(\beta^2+k^2)\omega^2+\beta^2k^2-l^2=0$. Therefore:

$$\omega^2=\frac{-(\beta^2+k^2)\pm\sqrt{(\beta^2+k^2)^2-4(\beta^2k^2-l^2)}}{2}$$

or:

$$\omega=\left(\frac{-(\beta^2+k^2)\pm\sqrt{(\beta^2+k^2)^2-4(\beta^2k^2-l^2)}}{2}\right)^{\frac{1}{2}}$$

Assuming that $l>\beta k$ it then implies

$$\omega_0=\left(\frac{-(\beta^2+k^2)+\sqrt{(\beta^2+k^2)-4(\beta^2k^2-l^2)}}{2}\right)^{\frac{1}{2}}$$

Furthermore, from the first part of 2.9 we have

$\cos\omega\tau=\dfrac{\omega^2+\beta k}{l}$

or

$$\omega\tau=\left(\cos^{-1}\frac{\omega^2+\beta k}{l}+2j\pi\right)j=0,1,2...$$

When $\tau=\tau_j$ and $\omega=\omega_0$

$$\tau_j=\frac{1}{\omega_0}\left(\cos^{-1}\frac{\omega_0^2+\beta k}{l}+2j\pi\right)j=0,1,2... \tag{2.10}$$

If we let $\lambda(\tau)=\alpha+i\omega(\tau)$ be a root of 2.1 near $\tau=\tau_j$ satisfying $\alpha(\tau_j)=0$ for $\omega(\tau_j)=\omega_0$. Then the following transversal condition will hold:

$(\alpha\prime(\tau)^{-1})\mid_{\tau}=\tau_j=Re\left(\dfrac{d\lambda}{d\tau}\right)^{-1}\mid_{\tau=\tau_j}>0,\ j=1,2,3...$

We differentiate λ implicitly on the characteristic equation 2.6 on both sides with respect to τ to obtain:

$2\lambda\dfrac{d\lambda}{d\tau}+(\beta-k)\dfrac{d\lambda}{d\tau}+le^{-\lambda\tau}(-\lambda(1)-\tau\dfrac{d\lambda}{d\tau)}=0$

Make $\dfrac{d\lambda}{d\tau}$ the subject of the formula to obtain: $\dfrac{d\lambda}{d\tau}(2\lambda+(\beta-k)-le^{-\lambda\tau}\tau)=l\lambda e^{-\tau\lambda}$ or:

$$\frac{d\lambda}{d\tau}=\frac{l\lambda e^{-\lambda\tau}}{2\lambda+(\beta-k)-l\tau e^{-\lambda\tau}} \tag{2.11}$$

and as defined above; $\tau=\tau_j$ where $j=1,2,3...$ and $\lambda=i\omega_0$ is a root where $(\omega>0)$ Substituting these values equation 2.11 becomes:

$$\frac{d\lambda}{d\tau}=\frac{l(i\omega_0)e^{-i\omega_0\tau_j}}{2(i\omega_0)+(\beta-k)-l\tau_je^{-\omega_0i\tau j}} \tag{2.12}$$

But from equation 2.8 $le^{-i\omega_0\tau_j} = \omega_0^2 - i(\beta-k)\omega_0 + \beta k$ Therefore 2.12 becomes:

$$\frac{d\lambda}{d\tau} = \frac{(i\omega_0(\omega_0^2 - i(\beta-k)\omega_0 + \beta k)}{2(i\omega_0) + (\beta-k) - \tau_j(\omega_0^2 - i(\beta-k)\omega_0 + \beta k} \tag{2.13}$$

0r:

$$\frac{d\lambda}{d\tau} = \frac{\omega_0^3 i + (\beta-k)\omega_0^2 + \beta k\omega_0}{((\beta-k) - \omega_0^2\tau_j - \beta k\tau_j) + (2\omega_0 + (\beta-k)\omega_0\tau_j)i} \tag{2.14}$$

We multiply both the numerator and the denominator by the conjugate of the denominator and we only take the real parts to get:

$$Re\left(\frac{d\lambda}{d\tau}\right) = \frac{2\omega_0^4 + (\beta-k)^2\omega_0^2 + 2\beta k\omega_0^2}{((\beta-k) - \omega_0^2\tau_j - \beta k\tau_j)^2 + (2\omega_0 + (\beta-k)\omega_0\tau_j)^2} \tag{2.15}$$

Hence:

$$Re\left(\frac{d\lambda}{d\tau}\right) = \alpha\prime(\tau_j) = \frac{\omega_0^2(2\omega_0 + \beta^2 + k^2)}{((\beta-k) - \omega_0^2\tau_j - \beta k\tau_j)^2 + (2\omega_0 + (\beta-k)\omega_0\tau_j)^2} > 0 \tag{2.16}$$

This completes the proof.

2.1 Numerical Results for Single Species with Delay

In this section we present the numerical findings based on the above given theorem. The figures below clearly agree with the theorem. For our numerical analysis we will use the following parameters except for Fig. 1. where $b = 0$

Table 1. Parameter values used to graph 1, 2, 3 and 4

History	Time	S0	c	D	μ	k	b	ω
[6,5]	[0,900]	11	1	0.4675	0.571	0.5	8	π

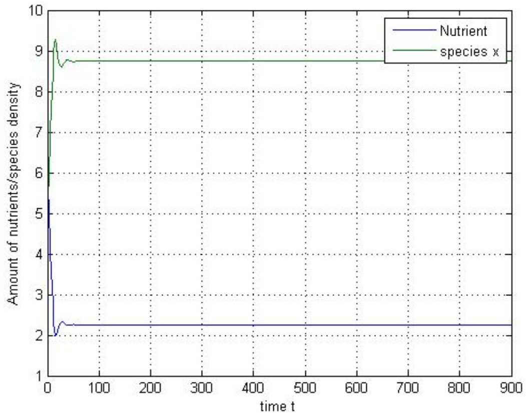

Fig. 1. A graph of single species at equilibrium point, $\tau = 2.8$

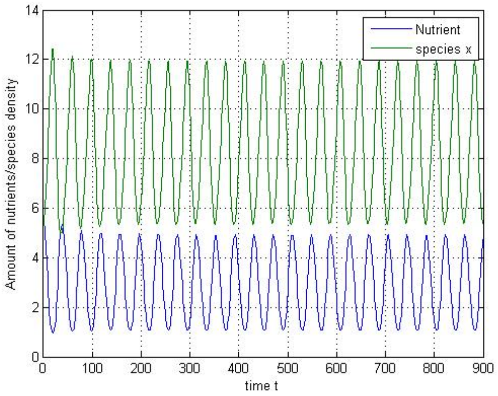

Fig. 2. A graph of single species at the bifurcation point $\tau = 8.3$

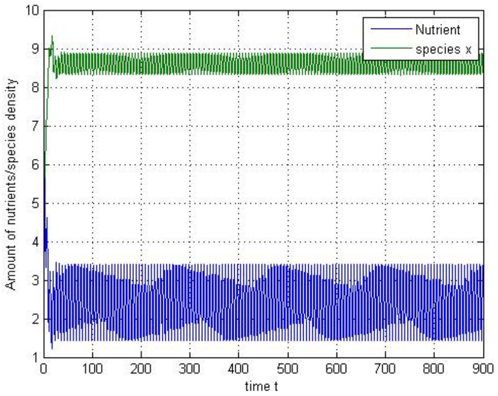

Fig. 3. A graph of single species with periodic nutrient input and a delay term $\tau = 2.3$

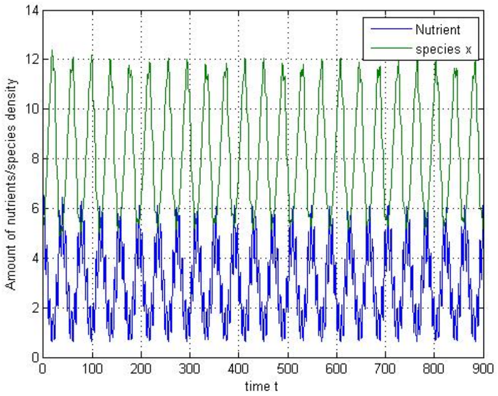

Fig. 4. A graph of single species with periodic nutrient input and $\tau = 8.5$

Delay values are given in each graph.

When $\tau = 2.8$ the system 2.1 is asymptotically stable and the equilibrium points are as follows:

$(S^*, x^*) = (2.2601, 8.7415)$

Graphical representation is:

Fig. 1. is generated with $S^0(t) = S^0$(constant).

It indicates that with small delays, the density of the species remains constant for $0 \leq t < \infty$. We know that this is not true in nature. Therefore besides delay, another factor must be at play that causes the variations of species density even for species with quick nutrient conversion time.

When we increase the delay from $\tau = 2.8$ to $\tau = 8.3$ which is our bifurcation point, the periodic solutions occurs. The graphical representation is:

In this Fig. 2. when τ is equal to the bifurcation point, variations of species density is observed from the beginning. This is what is observed in nature. Clearly we need to modify these parameters so that variations (in species density) are observed both with small or large delays. This is achieved by adding a periodicity term previously defined as:

$$S^0(t) = S^0 + \frac{b}{\omega} \sum_{j=1}^{n} \frac{(-1)^{j-1}}{2j-1} \cos((2j-1)t \quad (2.17)$$

The graph with this modification are present below.

In Fig. 3, both the periodicity and delays are at play. We see that even for small delays, variations of species density is well accounted for, just as they are for large delays.

We note that when delay is increased above the bifurcation point, the periodicity appears to be more influenced by the delay other than the periodic term in the nutrient input concentration.

3 CONCLUSION

An interesting observation is made when we compare figs 1-4, it is demonstrated that for small delays ($\tau <$ bifurcation point) the periodic nutrient input has a more pronounced effect on the density variation of species compared to the effect of the delay. (Fig 1 vs 3). The effect of periodic nutrient input on the species is masked (atleast partially) by large delays ($\tau >$ bifurcation value). In other words, periodicity has bigger influence of species density variations for small delays while for large delays,the delay effect is more influential compared to the periodicity. Further, if we let the nutrient input concentration vary periodically using the Fourier series function and amalgamate it with the delay term. The seasonal variations of nutrients are clearly seen from the graph. It is essential to note that incorporating the delay at the same time varying the input has significant results and evidently they compliment each other and they are both critical modification of the chemostat to ensure a better chemostat equation for studying biological systems.

COMPETING INTERESTS

The authors declare that no competing interests exist.

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