

# Chemostat Model with Periodic Nutrient Input Described by Fourier Series

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## Abstract

In this paper we present a periodic Chemostat model of two species competing for a single nutrient available in limiting supply. The nutrient input is varied periodically using a Fourier series function to take into account the changing patterns as seasons vary. We show both analytically and numerically that varying the nutrient input using a Fourier Series function results in a better model to describe coexistence of species in natural environments.

*Keywords: Coexistence; Competition; Competitive Exclusion; Periodic Chemostat; Fourier Series; Stability*

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## 1 Introduction

The system being discussed here models a Chemostat, which 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. Species no matter how close they are to each other, naturally do not compete with each other as long as all the desired resources such as water, light, heat, temperature, and food are in excess. Once the supply of any one necessary resource falls below a certain level, then competition begins. Competition can be between individuals of the same species or different species. In reality species cannot survive without a certain degree of interaction either within themselves or with other species and the environment. The type of these interactions usually vary depending on the evolutionary context and environmental circumstances in which they occur. When studying the interrelationships of organisms and their environments it's difficult to trace the mathematics, but the chemostat makes the mathematics easily traceable ([1], [2]). It is a model of a simple lake

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and is also used to model waste water treatment. Commercially, the chemostat plays a fundamental role in certain fermentation processes, particularly in commercial production of genetically altered organisms [5].

When considering the chemostat model in its simplest form, there are two constants that are kept under the control of the experimenter, the concentration of the input nutrient and the overflow rate. Naturally one expects that these will vary with time. The variations are brought about by periodic environments. One can chose to vary the washout rate [4], the nutrient input concentration [6] or better still one can actually vary both parameters [7]. Experimentally, these variations have proved to be of great effect in an experiment done by Herbert et al in [3]. In some cases the periodic functions have been varied at a commensurate period and in others cases the parameters have been made to vary at different periods. The later case has proven to mimic nature more since ecologically a population may be of inherent period variations and this causes seasonal effects. Unlike the commonly used sine function, the Fourier series ensures fluctuations within the season are well captured and captures extended periods of time when the nutrient is higher than average, same as when lower than average. This is what happens in nature. For example, in a simple lake, during the dry season nutrients are low for some of the competing species. However, there are days during this dry season when it rains and serves to replenish these nutrients. Similarly, during the wet season, there are periods (sometimes several days) when it does not rain. This causes intraseason variations that are best modelled using a Fourier Series function instead of the commonly used Sine Function [6], [7].

## 2 The Model

The chemostat model being analyzed here consists of two species that are competing for a single, essential and growth limiting nutrient varied periodically in time. It is described as follows:

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

$$S(0) > 0, x_1(0) \geq 0, x_2(0) \geq 0 \text{ for } 0 \leq t < \infty$$

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  $i$ .

$\mu_i$  is the maximum specific growth rate for the  $i^{th}$  species

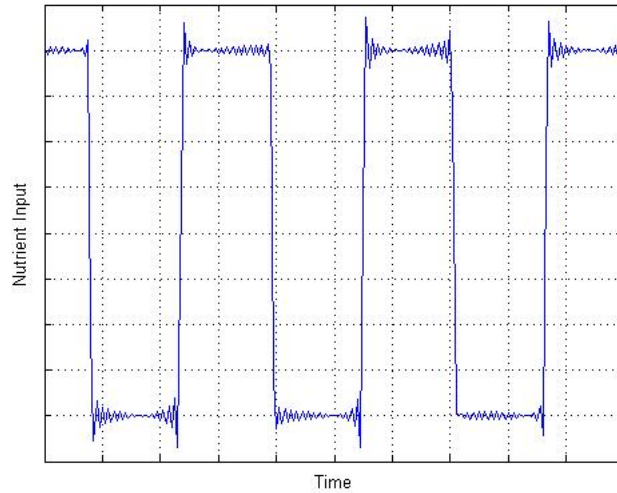
$k_i$  is the Michaelis-Menten constant for the  $i^{th}$  species

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

The nutrient input given by a Fourier series function

$S^0(t) = \left( S^0 + \frac{b}{\omega} \sum_{j=1}^n \frac{(-1)^{j-1}}{2j-1} \cos(2j-1)t - S(t) \right)$  models intraseason variations effectively as show in the figure below.

Figure 1: Nutrient Input Described by Fourier Series Function



The last two equations of 2.1 can be rewritten in integral form as

$$x_i(t) = x_i(0) \exp \int \left( \frac{\mu_i S(t)}{k_i + S(t)} - D_i \right) dt \tag{2.2}$$

## 2.1 Boundedness and Positivity of the Solution

It should be noted that for  $x_i(0) \geq 0$ ,  $x_i(t) \geq 0$  for  $0 \leq t \leq \infty$  which is a major requirement of Chemostat models. This statement ensures non-negativity of the species. Non-negativity and boundedness of both nutrients and competing species is generally a prerequisite of any chemostat model since no species can take negative values and no species can grow infinitely.

**Theorem 2.1.** *The system has a positive solution of the form  $v(t) = S(t) + x_1(t) + x_2(t)$  where  $(S(t), x_1(t), x_2(t)) \in R_+^3$  is positive set of vector space. Further,  $v(t) = S(t) + x_1(t) + x_2(t) < \infty$  for  $0 \leq t < \infty$*

**Proof** We shall start by showing that  $S(t) > 0$ . We prove by contradiction and so we assume that  $S(t) < 0$  for all  $t \geq 0$ . The first part of equation 2.1 can be written as:

$$\dot{S}(t) = S^0(t)D_0 - S(t)D_0 - \sum_{i=1}^2 \frac{\mu_i c_i x_i(t) S(t)}{k_i + S(t)}, 1 \leq i \leq 2$$

Therefore it follows that since  $S^0(t) = \left( S^0 + \frac{b}{\omega} \sum_{j=1}^n \frac{(-1)^{j-1}}{2j-1} \cos(2j-1)t - S(t) \right) \geq 0$  and  $D_0 \geq 0$ ,

$$\dot{S}(t) \geq - \left( S(t)D_0 + \sum_1^2 \frac{\mu_i c_i x_i(t) S(t)}{k_i + S(t)} \right), 1 \leq i \leq 2$$

or

$$\dot{S}(t) \leq S(t) \left( D_0 + \sum_1^2 \frac{\mu_i c_i x_i(t)}{k_i + S(t)} \right)$$

since  $S(t)$  is assumed to be negative then  $\frac{\dot{S}(t)}{S(t)} \geq \left( D_0(t) + \frac{1}{s(t)} \sum_1^2 \frac{\mu_i c_i x_i(t)}{k_i + S(t)} \right)$

Integrating this equation from 0 to  $T_0$  yields

$$S(t) \geq S(0) \exp \int_0^{T_0} \left( D_0 + \frac{1}{S(\xi)} \sum_1^2 \frac{\mu_i c_i x_i(t)}{k_i + S(t)} \right) S(t) d\xi \tag{2.3}$$

The quantity on the right hand of equation 2.3 is positive which this contradicts the assumption that  $S(t) < 0$ . This implies that  $S(t) > 0$  for all  $t \geq 0$ .

The integral representation of the second part of 2.1 is given by

$$x_1(t) = x_1(0) \exp \int_0^{T_0} \left( \frac{\mu_1 S(\xi)}{k_1 + S(\xi)} - D_1 \right) d(\xi)$$

The right hand side of the equation implies that  $x_1(t) \geq 0$  for all  $t$  provided that  $S(\xi) \neq -k_1$  for  $x_1(0) \geq 0$ . In any case, both  $S(t)$  and  $k_1$  are positive quantities thus  $k_1 + s(t) \neq 0$ . The proof for  $x_2(t)$  will follow analogously. This means that the solution  $S(t)$ ,  $x_1(t)$  and  $x_2(t)$  are positive for all  $t \geq 0$

To prove boundedness, we let  $v(t) = S(t) + x_1(t) + x_2(t)$  where  $s(t), x_1(t),$  and  $x_2(t) \in R_+^3$  is positive set of vector space, and assume that  $v(t)$  is also a continuous and  $\omega$ -periodic function. Using 2.1 we find that:

$$\dot{V}(t) = S^0(t)D_0 - (S(t)D_0 + x_1(t)D_1 + x_2(t)D_2)$$

Therefore it follows that :

$$\dot{V}(t) = S^0(t)D_0 - (S(t)D_0 + x_1(t)D_1 + x_2(t)D_2) \leq S^0(t)D_0$$

From the fundamental theorem of calculus, it means that:

$$V(t) \leq \int_0^t S^0(\xi)D_0 d(\xi) < \infty, \forall t \geq 0$$

Since  $V(t) < \infty, 0 \leq t < \infty$ , it follows that, individually,  $S(t) < \infty, x_i(t) < \infty, 1 \leq i \leq 2, 0 \leq t < \infty$ , meaning that the solution is bounded. This completes the proof.

## 2.2 Explicit Solutions

**Theorem 2.2.** Let  $S(t), x_i(t)$  for  $i = 1, 2$  be solutions of 2.1. Then:

$$S(t) = S^0 + Ae^{-Dt} + \sum_{j=1}^n B \cos((2j - 1)t - \theta) + c_1 g_1(t) + c_2 g_2(t) \tag{2.4}$$

$$x_i(t) = x_i(0) \exp \int_0^t \left( (\mu_i - D_i) - \frac{k_i \mu_i}{k_i + S(t)} \right) d\xi \quad (2.5)$$

where:

$$\begin{aligned} A &= S(0) - S^0 + \sum_{j=1}^n \frac{\beta D^2}{D^2 + ((2j-1)t)^2} + c_1 x_1(0) + c_2 x_2(0) \\ g_i(t) &= \sum_{j=1}^n (D - D_i) \int_0^t x_i(\xi) e^{-D(t-\xi)} d\xi - x_i(t) d\xi \\ B &= \frac{\beta D}{\sqrt{D^2 + ((2j-1)t)^2}} \\ \theta &= \tan^{-1} \left( \frac{(2j-1)}{D} \right) \end{aligned}$$

**Proof**

The first part of 2.1 is given as:

$$\dot{S}(t) = \left( S^0 + \sum_{j=1}^n \beta \cos((2j-1)t) - S(t) \right) D - \frac{\mu_1 c_1 x_1(t) S(t)}{k_1 + S(t)} - \frac{\mu_2 c_2 x_2(t) S(t)}{k_2 + S(t)}, \text{ where for simplicity,}$$

we have written  $\beta$  in place of  $\frac{b}{\omega} \frac{(-1)^{j-1}}{2j-1}$  in the first equation in 2.1.

This translates to

$$\dot{S}(t) + DS(t) = \left( S^0 + \sum_{j=1}^n \beta \cos((2j-1)t) \right) D - \sum_{i=1}^2 \frac{\mu_i c_i x_i(t) S(t)}{k_i + S(t)} \quad (2.6)$$

but from the second equation of model 2.1 we have:

$$\dot{x}_i(t) = x_i(t) \left( \frac{\mu_i S(t)}{k_i + S(t)} - D_i \right)$$

multiplying this equation by  $c_i$  on both sides yields:

$$\frac{\mu_i c_i x_i(t) S(t)}{k_i + S(t)} = \dot{x}_i(t) c_i + D_i c_i x_i(t)$$

Replacing this term in 2.6 yields:

$$\dot{S}(t) + DS(t) = \left( S^0 + \beta \sum_{j=1}^n \cos((2j-1)t) \right) D - \sum_{i=1}^2 (\dot{x}_i(t) c_i + D_i c_i x_i(t)) \quad (2.7)$$

By Product Rule of differentiation, equation 2.7 is equivalent to:

$$\frac{d}{dt} [S(t) e^{Dt}] = \left( S^0 + \beta \sum_{j=1}^n \cos((2j-1)t) \right) D e^{Dt} - \sum_{i=1}^2 (\dot{x}_i(t) c_i + D_i c_i x_i(t)) e^{Dt}$$

meaning

$$S(t)e^{Dt} = \int \left( S^0 + \beta \sum_{j=1}^n \cos((2j-1)t) \right) De^{Dt} - \sum_{i=1}^2 \int c_i e^{Dt} (\dot{x}_i(t) + D_i x_i(t)) dt$$

or

$$S(t)e^{Dt} = \int_0^t \left( S^0 + \beta \sum_{j=1}^n \cos((2j-1)\xi) \right) De^{D\xi} d\xi - \sum_{i=1}^2 \int_0^t c_i e^{Dt} (\dot{x}_i(\xi) + D_i x_i(\xi)) d\xi$$

Integrating and dividing both sides by  $e^{Dt}$  yields:

$$S(t) = S(0)e^{-Dt} + \int_0^t \left( S^0 + \beta \sum_{j=1}^n \cos((2j-1)\xi) \right) \frac{De^{D\xi}}{e^{Dt}} d\xi - \sum_{i=1}^2 \int_0^t c_i (\dot{x}_i(\xi) + D_i x_i(\xi)) \frac{e^{D\xi}}{e^{Dt}} d\xi$$

which is equivalent to:

$$S(t) = S(0)e^{-Dt} + \int_0^t \left( S^0 + \beta \sum_{j=1}^n \cos((2j-1)\xi) \right) De^{-D(t-\xi)} d\xi - \sum_{i=1}^2 \int_0^t c_i (\dot{x}_i(\xi) + D_i x_i(\xi)) e^{-D(t-\xi)} d\xi \tag{2.8}$$

We integrate 2.8 term by term by the use of the integration techniques such as integration by parts and the integral formula cited in [8] to obtain

$$S(t) = S(0)e^{-Dt} + S^0 - S^0 e^{-Dt} + \sum_{j=1}^n \beta D \left( \frac{1}{D^2 + ((2j-1))^2} (D \cos((2j-1)t) + ((2j-1)) \sin((2j-1)t)) \right) + \frac{De^{-Dt}}{D^2 + ((2j-1))^2} \left( \sum_{i=1}^2 c_i (x_i(t) - e^{-D(t-\xi)}) - D \int_0^t x_i(\xi) e^{-D(t-\xi)} d\xi \right) - \sum_{i=1}^2 c_i D_i \int_0^t x_i(\xi) e^{-D(t-\xi)} d\xi \tag{2.9}$$

The term

$\sum_{j=1}^n \beta D \frac{1}{D^2 + ((2j-1))^2} (D \cos((2j-1)t) + ((2j-1)) \sin((2j-1)t))$  in 2.9 can be rewritten as

$$\sum_{j=1}^n \frac{\beta D^2}{D^2 + ((2j-1))^2} \left( \cos((2j-1)t) + \frac{((2j-1))}{D} \sin((2j-1)t) \right)$$

which is equivalent to:

$$\sum_{j=1}^n \frac{\beta D}{\sqrt{D^2 + ((2j-1))^2}} \left( \frac{D}{\sqrt{D^2 + ((2j-1))^2}} \cos((2j-1)t) + \frac{((2j-1))}{\sqrt{D^2 + ((2j-1))^2}} \sin((2j-1)t) \right) \tag{2.10}$$

From elementary algebra, we have

$$\sin \theta = \frac{(2j-1)}{\sqrt{D^2 + ((2j-1))^2}}$$

$$\cos \theta = \frac{D}{\sqrt{D^2 + ((2j-1))^2}}$$

$$\tan \theta = \frac{(2j-1)}{D}$$

$$\theta = \tan^{-1} \frac{(2j-1)}{D}$$

Using the trigonometry identity  $\cos(u-v) = \cos u \cos v + \sin u \sin v$ , equation 2.10 can further be rewritten as

$$\sum_{j=1}^n \frac{\beta D}{\sqrt{D^2 + ((2j-1))^2}} (\cos((2j-1)t) - \theta) \tag{2.11}$$

Inserting 2.11 in 2.9 gives

$$S(t) = S^0 + Ae^{-Dt} + \sum_{j=1}^n B(\cos((2j-1)t) - \theta) + c_1 g_1(t) + c_2 g_2(t)$$

To show that

$$x_i(t) = x_i(0) \exp \int_0^t (\mu_i - D_i) - \frac{k_i \mu_i}{k_i + S(t)} d\xi \tag{2.12}$$

we note that the last two equations of 2.1 can be represented in integral form as:

$$x_i(t) = x_i \exp \int \left( \frac{\mu_i S(t)}{k_i + S(t)} - D_i \right) dt, 1 \leq i \leq 2$$

Inserting limits from 0 to t yields:

$$x_i(t) = x_i(0) \exp \int_0^t \left( \frac{\mu_i S(\xi)}{k_i + S(\xi)} - D_i \right) d\xi$$

which is equivalent to:

$$x_i(t) = x_i(0) \exp \int_0^t \frac{\mu_i S(\xi) - D_i k_i - D_i S(\xi)}{k_i + S(\xi)} d\xi$$

If we add and subtract the term  $k_i \mu_i$  to the integral part we obtain

$$x_i(t) = x_i(0) \exp \int_0^t \frac{\mu_i S(\xi) - D_i k_i - D_i S(\xi) + k_i \mu_i - k_i \mu_i}{k_i + S(\xi)} d\xi$$

or

$$x_i(t) = x_i(0) \exp \int_0^t \frac{(S(\xi) + k_i) (\mu_i - D_i) - k_i \mu_i}{k_i + S(\xi)} d\xi$$

which is equivalent to

$$x_i(t) = x_i(0) \exp \int_0^t (\mu_i - D_i) - \frac{k_i \mu_i}{k_i + S(t)} d\xi$$

which completes the proof.

The break even concentration for a given number  $D > 0$  is given by

$$\lambda_i = \frac{k_i D}{\mu_i - D}.$$

Species have distinct break-even concentrations and without loss of generality can be enumerated by indices such that  $\lambda_1 < \lambda_2 < \dots < \lambda_n$ . This parameter is important because it determines the survival of  $i^{th}$  species. If this parameter is small, the corresponding the  $i^{th}$  species will continue to survive till competition decides its fate. If it were not for the seasonal effects, then it is factual to say that the species with the lowest  $\lambda$  will always win.

**Theorem 2.3.** If we let  $\eta_i = \frac{\mu_i - D_i}{k_i \mu_i} - \frac{1}{\sqrt{(k_i + S^0)^2 - B^2}} < 0, 1 \leq i \leq 2$  then  $\lim_{t \rightarrow \infty} x_i(t) = 0$  as  $t \rightarrow \infty$ .

Where:

$$B = \frac{\beta D}{\sqrt{D^2 + ((2j - 1))^2}}$$

**Proof**

For  $\lim_{t \rightarrow \infty} x_i(t) = 0$ ,

It follows from 2.5 that

$$\lim_{t \rightarrow \infty} \int_0^t (\mu_i - D_i) - \frac{k_i \mu_i}{k_i + S(t)} d\xi = -\infty \tag{2.13}$$

We substitute the term  $S(t)$  with the new value of  $S(t)$  given in 2.4 as:

$$S(t) = S^0 + Ae^{-Dt} + \sum_{j=1}^n B \cos((2j - 1)t - \theta) + c_1 g_1(t) + c_2 g_2(t)$$

Also note that if  $\lim_{t \rightarrow \infty} x_i(t) = 0$ ,

the term  $Ae^{-Dt}$  and  $c_1 g_1(t) + c_2 g_2(t)$  will tend to zero, and this abridges the new term of  $S(t)$  as

$$S(t) = S^0 + \sum_{j=1}^n B \cos((2j - 1)t - \theta).$$

Equation 2.13 can thus be written as



$$\lim_{t \rightarrow \infty} \int_0^t \left( (\mu_i - D_i) - \frac{k_i \mu_i}{k_i + S^0 + \sum_{j=1}^n B \cos((2j-1)t - \theta)} \right) d\xi = -\infty$$

The integrand of this equation is a periodic function of period  $\frac{2\pi}{\omega}$ , which means for  $t \geq t_0$ , we can change the limit to run from  $t_0$  to  $t_0 + \frac{2\pi}{\omega}$  and further rewrite 2.13 as:

$$\int_{t_0}^{t_0 + \frac{2\pi}{\omega}} \left( (\mu_i - D_i) - \frac{k_i \mu_i}{(k_i + S^0) + \sum_{j=1}^n B \cos((2j-1)t - \theta)} \right) d\xi \tag{2.14}$$

This integration can be simplified by letting  $n = 1$  to attain:

$$\eta_i = \int_{t_0}^{t_0 + \frac{2\pi}{\omega}} \left( (\mu_i - D_i) - \frac{k_i \mu_i}{(k_i + S^0) + B \cos(\omega\xi - \theta)} \right) d\xi$$

which is equivalent to:

$$\eta_i = (\mu_i - D_i) \frac{2\pi}{\omega} - \frac{k_i \mu_i}{\omega} \int_{t_0 - \theta}^{t_0 + \frac{2\pi}{\omega} - \theta} \frac{1}{(k_i + S^0) + B \cos \xi} d\xi \tag{2.15}$$

Using an integral formula provided in the integral table in [8] as:

$$\int \frac{1}{a + b \cos x} dx = \frac{2}{\sqrt{a^2 - b^2}} \tan^{-1} \frac{(a - b) \tan(\frac{x}{2})}{\sqrt{a^2 - b^2}},$$

and letting  $a = (k_i + S^0)$  and  $b = B$ , equation 2.15 can be written as

$$\eta_i = (\mu_i - D_i) \frac{2\pi}{\omega} - \frac{k_i \mu_i}{\omega} \left( \frac{2}{\sqrt{(k_i + S^0)^2 - B^2}} \tan^{-1} \frac{((k_i + S^0) - B) \tan(\frac{\xi}{2})}{\sqrt{(k_i + S^0)^2 - B^2}} \right) \Big|_{t_0}$$

Which simplifies to

$$\eta_i = (\mu_i - D_i) \frac{2\pi}{\omega} - \frac{k_i \mu_i}{\omega} \frac{2}{\sqrt{(k_i + S^0)^2 - B^2}} \times \pi$$

Which is equivalent to:

$$\eta_i = \frac{2\pi}{\omega} k_i \mu_i \left( \frac{\mu_i - D_i}{k_i \mu_i} - \frac{1}{\sqrt{(k_i + S^0)^2 - B^2}} \right)$$

but since  $\eta_i < 0$ ,

then, it follows that:

$$\eta_i = \frac{\mu_i - D_i}{k_i \mu_i} - \frac{1}{\sqrt{(k_i + S^o)^2 - B^2}} < 0$$

This completes the proof.

**Lemma 2.4.**  $\eta_i < 0$  iff  $\mu_i \leq D_i$ . In addition, if  $0 < \eta_1 < c_2$ , then,  $\lim_{t \rightarrow \infty} x_i(t) = 0$  and  $\limsup_{t \rightarrow x_2(t) > 0} > 0$  and due to the periodicity term in the nutrient input the species  $x_1$  and  $x_2$  may coexist.

### 3 Numerical Results

We now turn to numerical simulations to verify the theorems we have presented so far.

Figure 3 is a graphical representation of system 2.1 with the Fourier Series describing periodic nutrient input. As a demonstration of the appropriateness of the Fourier Series function in modeling the Chemostat over the commonly used Sine function, we plot them side by side using the same parameters. The Figure on the right is a representation of model 2.1 while that on the left is a representation of 3.1.

$$\begin{aligned} \dot{S}(t) &= (S^0 - b \sin(\omega t) - S(t))D_0 - \frac{\mu_1 c_1 x_1(t) S(t)}{K_1 + S(t)} - \frac{\mu_2 c_2 x_2(t) S(t)}{K_2 + S(t)} \\ \dot{x}_1(t) &= x_1(t) \left( \frac{\mu_1 S(t)}{K_1 + S(t)} - D_1 \right) \\ \dot{x}_2(t) &= x_2(t) \left( \frac{\mu_2 S(t)}{K_2 + S(t)} - D_2 \right) \end{aligned} \tag{3.1}$$

Table 1: Parameter values used to graph figure 3

$S^0$	$x_1^0$	$x_2^0$	$c_1$	$c_2$	$D_0$	$D_1$	$D_2$
6	5	5	0.236842117	0.904813608	1	1.26689	1

$\mu_1$	$\mu_2$	$k_1$	$k_2$	$b$	$\omega$
2.1	1.6578	2	2.0001	1.9108280	0.1

Clearly, the figure demonstrates that in addition to fluctuations of the nutrient, the species also undergo frequent fluctuations as is evident in nature. While the fluctuations are frequent, the amplitude of the fluctuations is small, meaning the nutrients do not deviate too far from their equilibrium point.

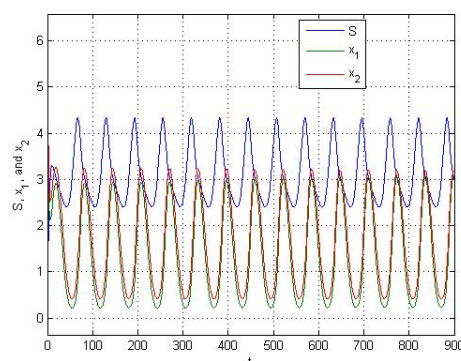


Figure 2: Graph of periodic nutrient input varied using sine function

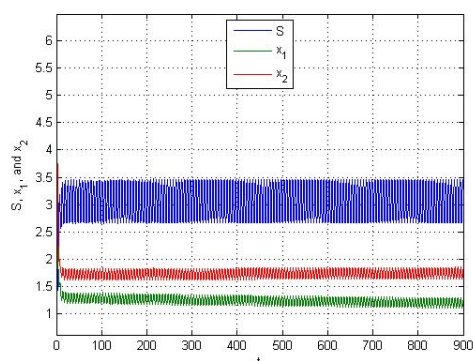


Figure 3: Graph of periodic nutrient input varied using Fourier series

## 4 Conclusion

When using the sine function the amplitudes of the nutrient and species are much larger than would normally be expected in natural environments. Larger variations run the risk of destabilizing the equilibrium point and causing coexistence to be difficult to maintain. Notably, nutrient variations predicted by the system with the sine function are about twice those predicted by the system with Fourier series. The fluctuations for the species predicted by the system with the sine function are almost ten times more than those predicted by the system without Fourier series.

Clearly system 2.1 gives a robustly more appropriate model of the observed natural environment.

## References

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