Periodicity in a Chemostat with a Periodic Substrate Input and Allelopathic Growth Inhibition

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Abstract

We present a periodic chemostat with allelopathic growth inhibition. The operating parameters including the nutrient uptake function, washout rate and nutrient concentration are allowed to be periodic functions of time, with commensurate periods. We show that competitive exclusion always holds in a periodic chemostat with allelopathic growth inhibition. We find that the species with the smallest break-even concentration survives the competition for a single growth-limiting nutrient independent of the initial conditions. Using Matlab software, we carry out numerical simulations to confirm the theoretical findings.

Key words: Periodic Chemostat; Allelopathic Growth Inhibition; Exploitative Competition; Competitive Exclusion.

1 Introduction

A fundamental problem in population biology concerns the long-term survival of all competing species for a single growth-limiting nutrient. From the biological perspective, this long-term survival is well known as permanent coexistence which guarantees non-extinction of species as well as all species do not grow indefinitely, however allows an arbitrary asymptotic behaviour [21]. Many applications of permanent coexistence are focussed on models with autonomous systems of differential equations. These models predict that when the number (r) of limited resources are competed by species, then only r competing species may avoid extinction [1]. The competition for a single, limited resource is known as exploitative competition [22]. Though, it is common in nature that a few available resources are limited and the size of species depending on limited resources is large.

A favorable area where experimental predictions can be made from these mathematical models is in a laboratory apparatus known as a *chemostat*. The chemostat models a very simple lake [13] and is important in ecological studies because the mathematics can be traced and the relevant experiments are possible [22]. It is an important piece of device for studying interaction between species competing for a nutrient largely because most parameters that affect the interaction are under the control of the experimenter, see for instance [4, 5, 14, 17, 19, 22].

Mathematical models of exploitative competition in a well-stirred chemostat operated under constant input and dilution rates, with competition for a single essential, non-reproducing, growth-limiting nutrient predict competitive exclusion, that is only one competitor population avoids extinction, see for instance [3, 5, 7, 8, 17, 18]. That is, in temporally homogeneous (constant operating parameters) and spatially homogeneous (well-stirred chemostat) environment, the model predicts competitive exclusion. If the homogeneity conditions are relaxed and the parameters allowed to be periodic, the models predict that coexistence of the competing species can occur, see for instance [4, 19, 22]. Relaxation of these conditions is plausible because real environments are far from being homogeneous, either in space or time. In addition to the day/night variability, there are seasonal effects as well as random effects caused by the variable weather patterns [22].

There have been some studies looking at some aspects of periodicity in chemostat models. Butler, Hsu and Waltman [4] found that in a model of the chemostat with periodic washout rate, under suitable circumstances, there is coexistence of the competing population. Cushing [6] looked at periodic two predator one prey interactions and the time sharing of a resource niche and found that there is a possibility of stable coexistence of the predator prey models with diffusion with the result that permanence is expected to hold [21]. In all of these studies, where periodicity is introduced in the chemostat model, none has addressed any form of allelopathic inhibition. Also, there have been some studies involving various aspects of inhibition to the growth of competing species. Hsu and Waltman [11] looked at a model of the effect of anti-competitor toxins on plasmid-bearing, plasmid-free competition, and also addressed competition in the chemostat when one competitor produces a toxin [9]. Hsu et al [10] studied competition in the presence of a lethal external inhibitor, Braselton and Waltman [2] developed a competition model with dynamically allocated inhibitor production, while Jianhua et al [20] addressed the effect of inhibitor on the plasmid-bearing and plasmid-free model in the unstirred chemostat. These mathematical models of allelopathic inhibition in the chemostat were operated under constant input and dilution rates.

In this study, we present a model of two species competition with allelopathic growth inhibition in a periodically operated chemostat. We shall assume that the chemostat is spatially homogeneous, but allow the parameters in the model including nutrient input concentration, dilution rate as well as the species specific removal rates are periodic with their periods being commensurate. The species specific nutrient uptake is assumed to be a monotone increasing function of the nutrient concentration, but allowed to be periodic as function of time with its period being commensurate with that of other parameters. We shall use a Holling Type II function for the nutrient uptake, that is, the function follows Michaelis-Menten kinetics. We shall introduce a parameter that represents the fraction of the growth-rate devoted to toxin production. A function that account for the allelopathic inhibitory effects on the growth of non-toxic competitor is also introduced.

This paper is organized as follows. In section 2, we present the model incorporating both periodicity and allelopathic growth inhibition. In Section 3, we show the positivity and boundedness of the solution. In Section 4, we establish the competition-independent extinction of the single species. In Section 5, we describe an outcome in which both species become extinct. In Section 6, we demonstrate that there will be a self-extinction of the toxin producing species. In Section 7, we determine the break-even concentration of the nutrient. Section 8 deals with the conditions for competitive exclusion while numerical simulations are found in Section 9. Finally, we conclude with a brief discussion in Section 10.

2 The Model

The model incorporating both periodicity and allelopathic growth inhibition takes the following form:

$$\begin{aligned}
\dot{S}(t) &= (S^0(t)-S(t))D_0(t) - x_1(t)g_1(t,S(t))h(p) - x_2g_2(t,S(t)),\\
\dot{x_1}(t) &= x_1(t)\{g_1(t,S(t))h(p) - D_1(t)\},\\
\dot{x_2}(t) &= x_2(t)\{(1-k)g_2(t,S(t)) - D_2(t)\},\\
\dot{p}(t) &= kg_2(t,S(t))x_2(t) - D_2(t)p(t),
\end{aligned} \tag{1}$$

with $S(0)\geq 0$, $x_1(0)\geq 0$, $x_2(0)\geq 0$, $p(0)\geq 0$, for $0\leq t<\infty$,
where,

$S(t)$ is the nutrient concentration at time t,
$x_1(t)$ is the density of the species affected by the toxin at time t,
$x_2(t)$ is the density of the species producing the toxin at time t,
$p(t)$ is the concentration of the toxin at time t,
$S^0(t)$ is the input nutrient concentration at time t,
$D_0(t)$ is the nutrient dilution rate,
$D_i(t)$ is the specific removal rate or the washout rate of the i^{th} species,
$g_i(t,S(t))$ is the specific per capita nutrient uptake function of the i^{th} species,
$h(p)$ represents the degree of inhibition of the toxin to the growth-rate of species x_1,
k represents the fraction of the growth-rate of species x_2 allocated to toxin production,
$D_2(t)p(t)$ represents the washout rate of the toxin.

Here, it is assumed that $S^0(t), D_0(t), D_i(t)$ are all continuous, ω-periodic, positive functions and that each $g_i(t,S):\mathbb{R}_+^2\to\mathbb{R}_+$ is continuous, ω-periodic in t and satisfies:-

(i) $g_i(t,S)$ is locally Lipschitz in S,

(ii) $g_i(t,0)=0$ for $t\geq 0$ and for any $t\geq 0$, $g(t,S)$ is strictly increasing for $S\in\mathbb{R}_+$.

The relationship between $g_1(t,S(t))$ and $g_2(t,S(t))$ and $S(t)$ is of the following form:-

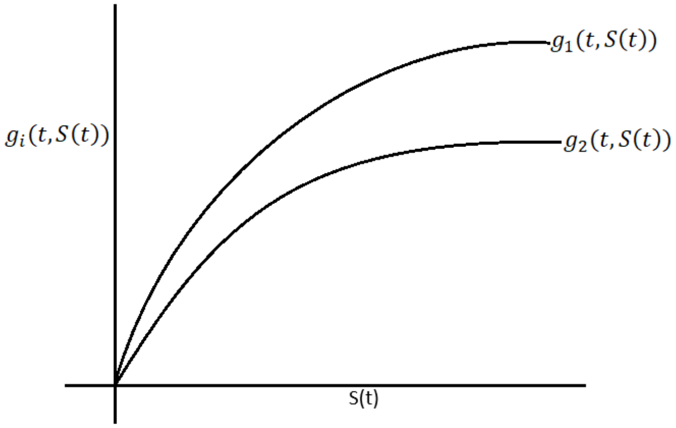

Figure 1: Relationship between the uptake functions of the species.

We assume that the inhibiting function of toxin $h(p)$ satisfies the following conditions:-

(i)

$$h(0) = 1, \quad h(p) \geq 0;$$

(ii)

$$h'(p) < 0, \quad p > 0. \tag{2}$$

Equation (2)(i) helps to delineate the meaning of $h(p)$ with $h(0) = 1$ being no inhibition at all to the growth-rate of the species x_1 while $h(p) = 0$ being a total inhibition to the growth-rate of species x_1. A decrease in the value of the inhibition function $h(p)$ implies high concentration of toxin in the environment. In Equation (2)(ii), $h'(p) < 0$ makes a physical sense because we expect that high concentration of toxin in the environment to cause a greater inhibition to growth-rate of species x_1. If the toxin p is not present in the environment, then we do not expect any inhibition to the growth-rate of species x_1 as $h(0) = 1$ implies. A reasonable function describing $h(p)$ as suggested in [12] is given by

$$h(p) = e^{-\gamma p}, \tag{3}$$

where $\gamma > 0$ is a measure of the inhibiting effect of toxin, while $p := p(t)$ is the concentration of toxin at time t. Clearly $h(p)$ in Equation (3) verifies all the conditions in Equation (2).

Some resources are needed to account for the metabolic burden and this must come at some cost to the organism's reproductive abilities. When $k = 0$, we have a system asymptotic to the standard periodic chemostat, while when $k = 1$, we have all uptake devoted to toxin production and none to growth and thus extinction of species x_2. These two extremes help to delineate the meaning of k. Thus, we assume the parameter $k \in (0, 1)$ is a constant that represents the fraction of the growth-rate of species x_2 allocated to toxin production.

We see that in the special case if there is no production of the toxin; that is, $k = 0$, and $p(t) = 0$ for all $t \geq 0$, then the system in Equation (1) reduces to

$$\begin{aligned} \dot{S} &= (S^0(t) - S)D_0(t) - x_1 g_1(t, S) - x_2 g_2(t, S), \\ \dot{x_1} &= x_1\{g_1(t, S) - D_1(t)\}, \\ \dot{x_2} &= x_2\{g_2(t, S) - D_2(t)\}, \end{aligned} \tag{4}$$

which is a standard periodic chemostat model without allelopathic growth inhibition. A more detailed discussion of the standard periodic chemostat model can be found in [15, 16, 19, 22]. In addition, when $S^0(t) = S^0$, $g_i(t, S) = g_i(S)$, $D_0(t) = D_i(t) = D$, $i = 1, 2$, the system in Equation (1) can be written as

$$\begin{aligned} \dot{S} &= (S^0 - S)D - x_1 g_1(S)h(p) - x_2 g_2(S), \\ \dot{x_1} &= x_1\{g_1(S)h(p) - D\}, \\ \dot{x_2} &= x_2\{(1 - k)g_2(S) - D\}, \\ \dot{p} &= k g_2(S)x_2 - Dp, \end{aligned} \tag{5}$$

which is the chemostat model with allelopathic growth inhibition without periodicity. A more detailed discussion of the chemostat model with allelopathic growth inhibition can be found in [12].

3 Positivity and Boundedness of the solution

Since a general prerequisite of any chemostat-like model is positivity and boundedness of its solution, we first show that for a given non-negative initial condition, the solution of Equation (1) remains positive and bounded for all $t \geq 0$. This information is given in Proposition 1.

Proposition 1. *For every positive initial condition* $(S(0), x_1(0), x_2(0), p(0)) \in \mathbb{R}^4_+$, *the solution* $(S(t), x_1(t), x_2(t), p(t))$ *of Equation* (1) *is positive and bounded for all* $t \geq 0$.

Proof. We begin by showing that $S(t)$ is positive. Suppose for a while that $S(t)$ is not positive for all $t \geq 0$. By the continuity of $S(t)$ and the fact that $S(0) > 0$, then $S(t) < 0$ implies that there exists a point t_0 with $S(t_0) = 0$ and $S(t) > 0$ for all $0 \leq t \leq t_0$. For $0 \leq t \leq t_0$, we see from the first equation in Equation (1) that,

$$\dot{S}(t) > -\Big[S(t)D_0(t) + x_1(t)g_1(t, S(t))h(p) + x_2(t)g_2(t, S(t))\Big].$$

Substituting

$$g_i(t, S(t)) = \frac{\mu_i S(t)}{a_i + S(t)}, \quad i = 1, 2,$$

and integrating from 0 to t_0, then it follows that

$$S(t_0) > S(0)\exp\left[\int_0^{t_0}\left(-D_0(\xi) - \frac{\mu_1 x_1(\xi)}{a_1 + S(\xi)}h(p) - \frac{\mu_2 x_2(\xi)}{a_2 + S(\xi)}\right)\mathrm{d}\xi\right] > 0. \tag{6}$$

This leads to a contradiction and hence it implies that $S(t) > 0$ for all $t \geq 0$.

From the second and third equations in Equation (1), we see that

$$\begin{aligned} x_1(t) &= x_1(0)\exp\left[\int_0^t (g_1(\xi, S(\xi))h(p) - D_1(\xi))\mathrm{d}\xi\right], \\ x_2(t) &= x_2(0)\exp\left[\int_0^t ((1-k)g_2(\xi, S(\xi)) - D_2(\xi))\mathrm{d}\xi\right]. \end{aligned} \tag{7}$$

Since $x_i(0) \geq 0$, then Equation (7) implies that $x_i(t) \geq 0$ for all $t \geq 0$, $i = 1, 2$.
For the fourth equation of Equation (1), we have;

$$\begin{aligned} \dot{p}(t) &= kg_2(t, S(t))x_2(t) - D_2(t)p(t) \\ &> -D_2(t)p(t), \end{aligned} \tag{8}$$

which on integration we obtain

$$p(t) > p(0)\exp\left[-\int_0^t D_2(\xi)\mathrm{d}\xi\right] > 0. \tag{9}$$

Since $p(0) \geq 0$, then it implies that $p(t) \geq 0$ for all $t \geq 0$. This completes the proof that the solution $(S(t), x_1(t), x_2(t), p(t))$ of Equation (1) is positive for all $t \geq 0$.

Next, we show that the solution of Equation (1) is bounded. By adding all equations in Equation (1), one gets

$$S^0(t)D_0(t) - \overline{D}(t)V(t) \leq \dot{V}(t) \leq S^0(t)D_0(t) - \underline{D}(t)V(t), \quad \forall t \geq 0, \tag{10}$$

where

$$V(t) := S(t) + x_1(t) + x_2(t) + p(t);$$

$$\underline{D}(t) := D_{min}(t) = min\Big\{D_0(t), D_1(t), D_2(t)\Big\};$$

and

$$\overline{D}(t) := D_{max}(t) = max\Big\{D_0(t), D_1(t), D_2(t)\Big\}.$$

Upon integrating the inequalities in (10), we obtain,

$$V(t) \leq \frac{1}{\underline{D}(t)}\left\{S^0(t)D_0(t) - \frac{d}{dt}\left(\frac{S^0(t)D_0(t)}{\underline{D}(t)}\right) - \frac{d^2}{dt^2}\left(\frac{S^0(t)D_0(t)}{\underline{D}(t)}\right) - ....\right\} + \varepsilon_1(t) \tag{11}$$

$$V(t) \geq \frac{1}{\overline{D}(t)}\left\{S^0(t)D_0(t) - \frac{d}{dt}\left(\frac{S^0(t)D_0(t)}{\overline{D}(t)}\right) - \frac{d^2}{dt^2}\left(\frac{S^0(t)D_0(t)}{\overline{D}(t)}\right) - ....\right\} + \varepsilon_2(t), \tag{12}$$

where

$$\varepsilon_1(t) := \left\{ V(0) - \frac{1}{\underline{D}(0)} \left\{ S^0(0)D_0(0) - \frac{\dot{S}^0(0)D_0(0)}{\underline{D}(0)} - ... \right\} \right\} \exp\left[- \int_0^t \underline{D}(\xi)\mathrm{d}\xi \right] \quad (13)$$

and

$$\varepsilon_2(t) := \left\{ V(0) - \frac{1}{\overline{D}(0)} \left\{ S^0(0)D_0(0) - \frac{\dot{S}^0(0)D_0(0)}{\overline{D}(0)} - ... \right\} \right\} \exp\left[- \int_0^t \overline{D}(\xi)\mathrm{d}\xi \right]. \quad (14)$$

Clearly, we see that as $t \to \infty$, $\varepsilon_i(t) \to 0$ exponentially for $i \in \{1, 2\}$. This leads to the following well-defined numbers $\alpha = \liminf\limits_{t\to\infty} V(t)$ and $\beta = \limsup\limits_{t\to\infty} V(t)$. Therefore, we obtain

$$Q(t) \leq \alpha \leq \beta \leq P(t), \quad (15)$$

where

$$P(t) := \left\{ \frac{S^0(t)D_0(t)}{\underline{D}(t)} - \frac{1}{\underline{D}(t)} \frac{d}{dt} \left(\frac{S^0(t)D_0(t)}{(\underline{D}(t)} \right) - ... \right\}, \quad (16)$$

and

$$Q(t) := \left\{ \frac{S^0(t)D_0(t)}{\overline{D}(t)} - \frac{1}{\overline{D}(t)} \frac{d}{dt} \left(\frac{S^0(t)D_0(t)}{(\overline{D}(t))} \right) - ... \right\}. \quad (17)$$

This shows that $V(t)$ is bounded and all positive solutions of the System (1) are also bounded, completing the proof. $\square$

4 Competition-independent extinction of single species

We show that competition-independent extinction occurs for any population x_i with $g_i(t, S(t)) < D_i(t)$ for all $t \geq 0$.

Lemma 1 simply means that if the death rate is higher than the growth rate, then the species will go to extinction as a result of high death rate rather than by cause of competition for the nutrient.

Lemma 1. *(1) If* $g_1(t, S(t)) < D_1(t)$*, then it follows* $\lim_{t\to\infty} x_1(t) = 0$ *for all* $t \geq 0$.

(2) If $g_2(t, S(t)) < D_2(t)$*, then it follows* $\lim_{t\to\infty} x_2(t) = \lim_{t\to\infty} p(t) = 0$ *for all* $t \geq 0$.

Proof (1)**.** For $0 < S(t) < S^0(t)$, from the second equation in System (1) and noting that $h(p) = e^{-\gamma p} < 1$ for $\gamma, p > 0$, we have

$$\dot{x_1}(t) = x_1(t)\{g_1(t, S(t))h(p) - D_1(t)\} \leq x_1(t)\{g_1(t, S(t)) - D_1(t)\},$$

which, upon integration from 0 to t yields,

$$x_1(t) \leq x_1(0) \exp\left[\int_0^t (g_1(\xi, S(\xi)) - D_1(\xi))\mathrm{d}\xi \right].$$

Assuming that $g_1(t, S(t))$ is locally Lipschitz and is strictly increasing for $S \in \mathbb{R}_+$, $g_1(t, 0) = 0$, for $t \geq 0$, then from $g_1(t, S(t)) < D_1(t)$, it follows that

$$x_1(t) \leq x_1(0) \exp\left[-\int_0^t (D_1(\xi) - g_1(\xi, S(\xi)))\mathrm{d}\xi\right],$$

which gives:-

$$\lim_{t\to\infty} x_1(t) \leq \lim_{t\to\infty} x_1(0) \exp\left[-\int_0^t (D_1(\xi) - g_1(\xi, S(\xi)))\mathrm{d}\xi\right] = 0.$$

Proof (2). For $0 < S(t) < S^0(t)$, from the last two equations in System (1), we have

$$\begin{aligned}
\frac{d}{dt}(x_2(t) + p(t)) &= x_2(t)g_2(t, S(t)) - (x_2(t) + p(t))D_2(t) \\
&\leq x_2(t)g_2(t, S(t)) + p(t)g_2(t, S(t)) - (x_2(t) + p(t))D_2(t) \\
&= (x_2(t) + p(t))[g_2(t, S(t)) - D_2(t)],
\end{aligned}$$

which, upon integration from 0 to t yields,

$$x_2(t) + p(t) \leq (x_2(0) + p(0)) \exp\left[\int_0^t (g_2(\xi, S(\xi)) - D_2(\xi))\mathrm{d}\xi\right].$$

Assuming that $g_2(t, S(t))$ is locally Lipschitz and is strictly increasing for $S \in \mathbb{R}_+$, $g_2(t, 0) = 0$, for $t \geq 0$, then from $g_2(t, S(t)) < D_2(t)$ and by the continuity of $x_2(t)$ and $p(t)$ on $0 \leq t < \infty$, it follows that $\lim_{t\to\infty}[x_2(t)+p(t)] = 0$, which in turn implies that $\lim_{t\to\infty} x_2(t) = \lim_{t\to\infty} p(t) = 0$. This completes the proof of Lemma 1. $\square$

5 Inadequacy of environment for a species

We describe an outcome in which all populations are eliminated from the chemostat due to the inadequacy of the nutrient supply.

Proposition 2 simply confirms the biological intuition that if the amount of nutrient in the system falls below a level required by the species for survival, then there will be an asymptotic extinction. This extinction is not as a result of competition, but due to the fact that the chemostat-like aquatic ecosystem is an inadequate environment for any of the populations to survive.

Proposition 2. *For all positive initial conditions of Equation* (1)*, if*

(i) $g_1(t, S(t)) < D_1(t)$*; and*

(ii) $g_2(t, S(t)) < D_2(t)$*,*

for all $t \geq 0$*, then it follows* $\lim_{t\to\infty}(S(t), x_1(t), x_2(t), p(t)) = (S^0(t), 0, 0, 0)$.

Proof. Lemma 1 implies that when $g_i(t, S(t)) < D_i(t)$ then $\lim_{t\to\infty} x_i(t) = 0$, for $i \in \{1, 2\}$. From Inequality (11) and since $x_i \to 0$ as $t \to \infty$, it follows that $\lim_{t\to\infty} S(t) = S^0(t)$. Thus, we have $\lim_{t\to\infty}(S(t), x_1(t), x_2(t), p(t)) = (S^0(t), 0, 0, 0)$. $\square$

6 Asymptotic behaviour of the species producing a toxin

We demonstrate that if a species devotes to toxin production, it will get extinct. Let's consider Equation (1). We define $z := p - \frac{k}{1-k}x_2$ which essentially reflects the amount of toxin in terms of the amount of the toxin producing species.

Lemma 2 is a conservation law that changes the System (1) from a four dimensional to three dimensional.

Lemma 2. *Let* $z := p - \frac{k}{1-k}x_2$*. Then the omega limit set of any solution of the initial value problem in Equation* (1) *lies in the plane* $z = 0$.

Proof. If $z := p - \frac{k}{1-k}x_2$, then it follows from Equation (1) that

$$\begin{aligned}\dot{z} &= kg_2(t,S)x_2 - D_2(t)p - kg_2(t,S)x_2 + \frac{k}{1-k}x_2 D_2(t) \\ &= -(p - \frac{k}{1-k}x_2)D_2(t) \\ &= -zD_2(t),\end{aligned}$$

which, upon integration from 0 to t yields,

$$z(t) = z(0)\exp\left[\int_0^t -D_2(\xi)\mathrm{d}\xi\right].$$

Since $D_2(t)$ is a positive and continuous function, $z(t) \to 0$ exponentially as $t \to \infty$. This completes the proof of Lemma 2. □

Lemma 2 simply implies that if there is no fraction of the nutrient consumption devoted to toxin production, then the toxin will be absent in the chemostat. In addition, if the fraction of the nutrient consumption devoted to toxin production is equal to one, then there will be a self-extinction of the toxin producing species. This is seen by noting that

$$x_2(t) = \frac{(1-k)}{k}p(t)$$

which tends to zero as $k \to 1$.

In what follows, we define relative values of the break-even concentration of the nutrient that will determine the outcome of the competition.

7 Break-even concentration

We obtain the break-even concentration for population x_i on nutrient S by setting

$$\dot{x}_i = 0, \quad i = 1, 2, \tag{18}$$

and solving for S. We first simplify the model in Equation (1) by a reduction of system of equations. Let

$$z := p - \frac{k}{1-k}x_2.$$

Substituting $h(p) = e^{-\gamma p}$ in Equation (1) yields the system

$$\begin{aligned} \dot{z} &= -zD_2(t), \\ \dot{S} &= (S^0(t) - S)D_0(t) - x_1 g_1(t, S)e^{-\gamma(z + \frac{k}{1-k}x_2)} - x_2 g_2(t, S), \\ \dot{x_1} &= x_1\{g_1(t, S)e^{-\gamma(z+\frac{k}{1-k}x_2)} - D_1(t)\}, \\ \dot{x_2} &= x_2\{(1 - k)g_2(t, S) - D_2(t)\}. \end{aligned} \tag{19}$$

Hence in view of the Lemma 2, trajectories which form the positive omega limit set of any solution of Equation (19) are the solutions of

$$\begin{aligned} \dot{S} &= (S^0(t) - S)D_0(t) - x_1 g_1(t, S)e^{-\frac{\gamma k}{1-k}x_2} - x_2 g_2(t, S), \\ \dot{x_1} &= x_1\{g_1(t, S)e^{-\frac{\gamma k}{1-k}x_2} - D_1(t)\}, \\ \dot{x_2} &= x_2\{(1 - k)g_2(t, S) - D_2(t)\}. \end{aligned} \tag{20}$$

We turn now to determine the important parameters that will describe the global asymptotic behaviour of the System (20). Assuming that the species-specific death rates are relatively small and insignificant as compared to the washout rate of the chemostat, we can allow $D_0(t) = D_1(t) = D_2(t) = D(t)$ for simplicity and the only interesting cases will therefore be

$$g_i(t, S(t)) > D(t), \quad i = 1, 2,$$

for all $t \geq 0$. Let $\langle D \rangle$ denote the mean value of a positive continuous function $D(t)$, i.e.

$$\langle D \rangle = \frac{1}{t}\int_0^t D(s)ds.$$

If we let

$$g_i(S) := \frac{\mu_i S}{a_i + S}, \quad i = 1, 2,$$

then the minimum amount of the nutrient necessary to ensure nonnegative growth of the populations can be defined by $\lambda_1,\ \lambda_2,\ \lambda_2^+$ as the unique positive solutions of the following system of equations:

$$\begin{aligned} \frac{\mu_1 \lambda_1}{a_1 + \lambda_1} &= \langle D \rangle, \\ \frac{\mu_2 \lambda_2}{a_2 + \lambda_2} &= \langle D \rangle, \\ \frac{\mu_2 \lambda_2^+}{a_2 + \lambda_2^+} &= \frac{\langle D \rangle}{1 - k}. \end{aligned} \tag{21}$$

The parameter values λ_1, λ_2 and λ_2^+ represent the break-even concentration of the nutrient and play an important role in determining competitive ability of the populations. From Equation

(21), we see that λ_2, λ_2^+ involve only the parameters for the x_2-population. Since if the x_2-population washes out of the chemostat, no toxin is produced, then there will be no minimum value of the toxin. Also, we note from Equation (21) that

$$\begin{aligned}\lambda_2 &= \frac{a_2\langle D\rangle}{\mu_2 - \langle D\rangle},\\ \lambda_2^+ &= \frac{a_2\langle D\rangle}{(1-k)\mu_2 - \langle D\rangle},\end{aligned} \tag{22}$$

from which for $0 < k < 1$, it then easily follows that $(1-k)\mu_2 < \mu_2$. Thus, λ_2 and λ_2^+ are related as follows:-

$$\lambda_2 < \lambda_2^+. \tag{23}$$

This Inequality (23) indicates that species x_2 will require more energy for its growth when a fraction of the nutrient consumption is devoted to toxin production than if no fraction of the nutrient consumption is devoted to toxin production.

8 Competitive Exclusion

We obtain conditions for the single species to go to extinction as a result of the competition for the same growth-limiting nutrient.

To understand the global dynamics of the single species growth model in the periodic chemostat, we consider the following two dimensional system:

$$\begin{aligned}\dot{S}(t) &= (S^0(t) - S(t))D_0(t) - x(t)g(t, S(t)),\\ \dot{x}(t) &= x(t)\{g(t, S(t)) - D_1(t)\},\\ x(0) &= x_0 \geq 0, \;\; S(0) \;=\; S_0 \geq 0.\end{aligned} \tag{24}$$

Here, $x(t)$ represents the density of the species at time t, $S(t)$ denotes the growth-limiting essential nutrient concentration in the water external to the plant cells at time t, $g(t, S(t))$ represents the specific per capita nutrient uptake function of the species, $S^0(t)$ is the periodic inflow concentration of the essential nutrient at time t, $D_0(t)$ is the nutrient dilution rate or the rate at which the nutrient enters the aquatic system, and $D_1(t)$ represents the specific removal rate of the species. We assume that $S^0(t), D_0(t), D_1(t)$ are continuous, ω-periodic, positive functions and that $g(t, S) : \mathbb{R}_+^2 \to \mathbb{R}_+$ is continuous, ω-periodic in t and satisfies:-

(i) $g(t, S)$ is locally Lipschitz in S,

(ii) $g(t, 0) = 0$ for $t \geq 0$ and for any $t \geq 0$, $g(t, S)$ is strictly increasing for $S \in \mathbb{R}_+$.

Let $D(t) : \mathbb{R}_+ \to \mathbb{R}_+$ be a continuous, ω-periodic and positive function. Then, the linear periodic equation

$$\dot{V}(t) = S^0(t)D_0(t) - V(t)D(t), \;\; V(0) \geq 0, \tag{25}$$

admits a unique positive global attractive ω-periodic solution $V^*(t)$, which can be given as

$$V^*(t) = e^{-\int_0^t D(\tau)d\tau}\left[\frac{\int_0^\omega e^{\int_0^\tau D(\theta)d\theta}S^0(\tau)D_0(\tau)d\tau}{e^{\int_0^\omega D(\tau)d\tau}-1} + \int_0^t e^{\int_0^\tau D(\theta)d\theta}S^0(\tau)D_0(\tau)d\tau\right].$$

Let $\underline{D}(t) = min\{D_0(t), D_1(t)\}$ and $\overline{D}(t) = max\{D_0(t), D_1(t)\}$. Then, $\underline{D}(t)$ and $\overline{D}(t)$: $\mathbb{R}_+ \to \mathbb{R}_+$ are continuous, ω-periodic and positive functions. Let $V_1^*(t)$ and $V_2^*(t)$ be unique positive ω-periodic solutions of Equation (25) with $D(t)$ replaced with $\underline{D}(t)$ and $\overline{D}(t)$ respectively. By comparison theorem and global attractivity of $V_i^*(t)$, $1 \le i \le 2$, it easily follows that $V_2^*(t) \le V_1^*(t)$, $\forall t \ge 0$.

Lemma 3 will be useful in the proof of Proposition 3 to show that the remaining species x and its nutrient S have limiting periodic behaviour.

Lemma 3. *Let* $D_0(t) = D_1(t)$, $t \in [0, \omega]$. *If*

$$\int_0^\omega (g(t, V_1^*(t)) - D_1(t))dt > 0,$$

then Equation (24) *has a unique positive global attractive ω-periodic solution* $(S^*(t), x^*(t))$.

Proof. In Equation (24), take $g(t, S(t)) = P(t, S(t))$. It then follows from the similar arguments as those in [19, Theorem 2.2] that $\lim_{t\to\infty}(S(t), x(t)) = (S^*(t), x^*(t))$. ☐

Proposition 3 simply means that if one species is a better competitor for every level of the nutrient, then the other species will become extinct.

Proposition 3. *(a) Let $0 < \lambda_1 < \lambda_2^+ < S^0(t)$. If $g_1(t, S(t)) > g_2(t, S(t))$ for $0 < S(t) < S^0(t)$, then for $S(0) > 0, x_1(0) > 0, x_2(0) > 0$, it follows $x_2(t) \to 0$, $S(t) \to S_1^*(t)$, $x_1(t) \to x_1^*(t)$ as $t \to \infty$, where $S_1^*(t)$ and $x_1^*(t)$ are respectively the ω-periodic solutions of the equations*

$$\begin{aligned} \dot{S}(t) &= (S^0(t) - S(t))D(t) - x_1(t)g_1(t, S(t)), \\ \dot{x_1}(t) &= x_1(t)\{g_1(t, S(t)) - D(t)\}. \end{aligned}$$

(b) Let $0 < \lambda_2^+ < \lambda_1 < S^0(t)$. If $g_2(t, S(t)) > g_1(t, S(t))$ for $0 < S(t) < S^0(t)$, then for $S(0) > 0, x_1(0) > 0, x_2(0) > 0$, it follows $x_1(t) \to 0$, $S(t) \to S_2^*(t)$, $x_2(t) \to x_2^*(t)$ as $t \to \infty$, where $S_2^*(t)$ and $x_2^*(t)$ are respectively the ω-periodic solutions of the inequalities

$$\begin{aligned} \dot{S}(t) &\le (S^0(t) - S(t))D(t) - x_2(t)g_2(t, S(t)), \\ \dot{x_2}(t) &\le x_2(t)\{g_2(t, S(t)) - D(t)\}. \end{aligned}$$

Proof (a)**.** For $0 < S(t) < S^0(t)$, from the second and third equations in the System (20) and noting that $0 < k < 1$ and $e^{-\frac{\gamma k}{1-k}x_2(t)} < 1$ for $\gamma, k, x_2(t) > 0$, we have

$$\begin{aligned} \dot{x_1}(t) &= x_1(t)\{g_1(t, S(t))e^{-\frac{\gamma k}{1-k}x_2(t)} - D(t)\} \le x_1(t)\{g_1(t, S(t)) - D(t)\}, \\ \dot{x_2}(t) &= x_2(t)\{(1-k)g_2(t, S(t)) - D(t)\} \le x_2(t)\{g_2(t, S(t)) - D(t)\}, \end{aligned} \tag{26}$$

from which it follows that

$$\frac{\dot{x_2}(t)}{x_2(t)} - \frac{\dot{x_1}(t)}{x_1(t)} \leq [g_2(t,S(t)) - g_1(t,S(t))]. \tag{27}$$

Since $g_1(t,S(t)) > g_2(t,S(t))$ for $0 < S(t) < S^0(t)$, then by substituting

$$g_i(t,S(t)) = \frac{\mu_i S(t)}{a_i + S(t)}, \;\; i \in \{1,2\},$$

and letting

$$\delta_1 := \max_{0<S(t)<S^0(t)} \left[\frac{\mu_2}{a_2 + S(t)} - \frac{\mu_1}{a_1 + S(t)}\right] < 0,$$

we obtain that

$$\begin{aligned}\frac{\dot{x_2}(t)}{x_2(t)} - \frac{\dot{x_1}(t)}{x_1(t)} &\leq S(t)\left[\frac{\mu_2}{a_2 + S(t)} - \frac{\mu_1}{a_1 + S(t)}\right] \\ &\leq \left(\inf_{0\leq t<\infty} S(t)\right)(\delta_1). \qquad (28)\end{aligned}$$

Now, supposing that

$$\inf_{0\leq t<\infty} S(t) = \delta_2 > 0,$$

then we can let $\delta = \delta_1\delta_2$ so that

$$\frac{\dot{x_2}(t)}{x_2(t)} - \frac{\dot{x_1}(t)}{x_1(t)} \leq \delta < 0, \tag{29}$$

which, upon integration from 0 to t and taking exponentials on both sides yields

$$x_2(t) \leq \psi_0 x_1(t) e^{\delta t},$$

for some $\psi_0 > 0$ depending upon the initial conditions. Since $x_1(t)$ is positive and bounded and δ is negative, $\lim_{t\to\infty} x_2(t) = 0$. By substituting $x_2 = 0$ into System (20), we have

$$\begin{aligned}\dot{S}(t) &= (S^0(t) - S(t))D(t) - x_1(t)g_1(t,S(t)), \\ \dot{x_1}(t) &= x_1(t)\{g_1(t,S(t)) - D(t)\}. \qquad (30)\end{aligned}$$

Hence, it follows from Lemma 3 that $\lim_{t\to\infty} S(t) = S_1^*(t)$, and $\lim_{t\to\infty} x_1(t) = x_1^*(t)$.

Proof (b). Since $g_2(t,S(t)) > g_1(t,S(t))$ for $0 < S(t) < S^0(t)$, similar arguments as in the proof of (a) establishes that $\lim_{t\to\infty} x_1(t) = 0$. By substituting $x_1 = 0$ into System (20), we get

$$\begin{aligned}\dot{S}(t) &= (S^0(t) - S(t))D(t) - x_2(t)g_2(t,S(t)), \\ \dot{x_2}(t) &= x_2(t)\{(1-k)g_2(t,S(t)) - D(t)\}, \qquad (31)\end{aligned}$$

from which by the positivity of solutions, and using the fact that $k \in (0,1)$, we have

$$\begin{aligned}\frac{dS(t)}{dt} &\leq (S^0(t) - S(t))D(t) - x_2(t)g_2(t, S(t)),\\ \frac{dx_2(t)}{dt} &\leq x_2(t)\{g_2(t, S(t)) - D(t)\}.\end{aligned} \tag{32}$$

Now, if we let $(\widehat{S}(t), \widehat{x_2}(t))$ be the unique solution of the following auxiliary problem

$$\begin{aligned}\frac{d\widehat{S}(t)}{dt} &= (S^0(t) - \widehat{S}(t))D(t) - \widehat{x_2}(t)g_2(t, \widehat{S}(t)),\\ \frac{d\widehat{x_2}(t)}{dt} &= \widehat{x_2}(t)\{g_2(t, \widehat{S}(t)) - D(t)\},\\ \widehat{x}(0) &= x(0) \geq 0, \;\; \widehat{S}(0) = S(0) \geq 0.\end{aligned} \tag{33}$$

By applying comparison theorem, we have from Equation (32) and Equation (33) that

$$(S(t), x_2(t)) \leq (\widehat{S}(t), \widehat{x_2}(t)), \;\; \forall t \geq 0. \tag{34}$$

It then follows from Lemma 3 that

$$\lim_{t\to\infty}(S(t), x_2(t)) \leq \lim_{t\to\infty}(\widehat{S}(t), \widehat{x_2}(t)) = (S_2^*(t), x_2^*(t)).$$

This completes the proof of the proposition. $\square$

Proposition 3 above shows that one competitor always wins the competition and coexistence is not possible. This differs with the result of the periodic chemostat without inhibition as demonstrated for instance in [19].

9 Numerical results

We illustrate the global behaviour of the reduced system (20) by some graphical results. The numerical results are obtained by using the adaptive **MatLab** solver ode45 applied to the reduced system (20) considering a nutrient uptake function of the Michaelis-Menten form

$$g_i(t, S(t)) = \frac{\mu_i S(t)}{a_i + S(t)}, \;\; i = 1, 2,$$

and a nutrient supply of the type

$$S^0(t) = \tilde{S}^0 + \eta + 2\eta\frac{(T_1 - T_2)}{T_p} + \sum_{n=1}^{\infty} \frac{4\eta}{n\pi} \cos\Big(\frac{n\pi}{T_p}(T_1 + T_2)\Big) \sin\Big(\frac{n\pi}{T_p}(T_1 - T_2)\Big) \cos\frac{2\pi nt}{T_p},$$

with parameters which are described in Tables 1 and 2. The parameter values are hypothetical and do not necessarily have a biological meaning.

Table 1: Parameter values used in the plots of Figures 3 and 4

Parameter	**Value used in Figure 3**	**Value used in Figure 4**
$\tilde{S}^0$	1	1
η	3	2
T_1	2	1
T_2	4	3
T_p	6	4
n	11	9
$D_0(t)$	1	1
$D_1(t)$	0.8425	0.9725
$D_2(t)$	0.9865	1.2885
$S(0)$	1	1
$x_1(0)$	2	2
$x_2(0)$	2	2
μ_1	1	1
μ_2	1	1
a_1	1	1
a_2	1	1
λ_1	0.2	5
λ_2^+	0.5	6
k	0.5	0.5
γ	1	1

We present numerical simulations of the reduced system (20) that reflect the condition

$$g_i(t, S(t)) < D_i(t), \quad \text{for } \ i \in \{1, 2\},$$

where the level of nutrient available in the chemostat is either sufficient for both species to survive or it is insufficient resulting to extinction which is independent of any population interactions. The parameter values in Table 1 satisfy that

$$g_1(t, \lambda_1) < D_1(t), \quad g_2(t, \lambda_2^+) < D_2(t), \quad \text{with } \ max(S^0(t)) < \lambda_1, \lambda_2^+ < min(S^0(t)).$$

Figure 3 shows that despite the growth rates of the species x_1 and x_2 require lower levels of the nutrient S than the input nutrient supply $S^0(t)$, both species become extinct because of the high death rates.

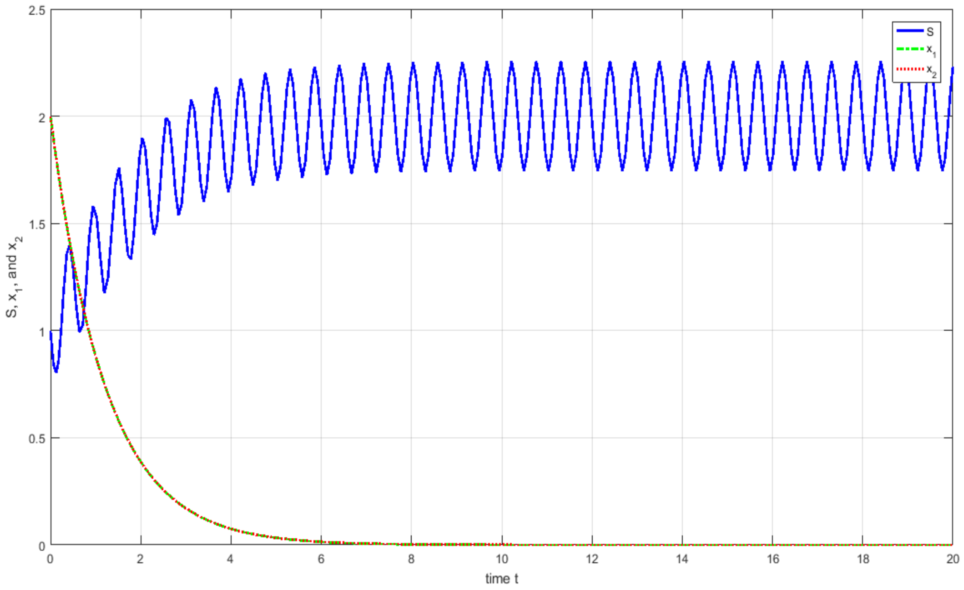

Figure 3: Simulation for $g_1(t,\lambda_1) < D_1(t)$ and $g_2(t,\lambda_2^+) < D_2(t)$, where $\lambda_1, \lambda_2^+ < min(S^0(t))$.

Figure 4 represents the extinction of both species because the growth rates of the species x_1 and x_2 require higher levels of the nutrient S than the input nutrient supply $S^0(t)$.

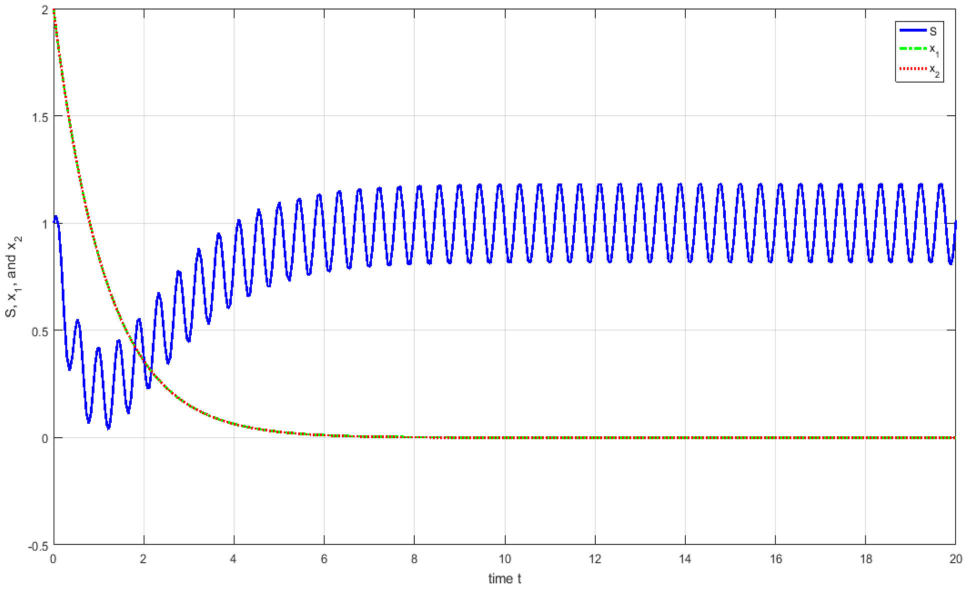

Figure 4: Simulation for $g_1(t,\lambda_1) < D_1(t)$ and $g_2(t,\lambda_2^+) < D_2(t)$, where $\lambda_1, \lambda_2^+ > max(S^0(t))$.

We present numerical simulations of the reduced system (20) where competition is the agent of elimination. The following parameter values satisfy the requirements that

$$g_1(t,\lambda_1) > g_2(t,\lambda_2^+), \quad \text{where} \quad 0 < \lambda_1 < \lambda_2^+ < min(S^0(t)),$$

and

$$g_2(t, \lambda_2^+) > g_1(t, \lambda_1), \quad \text{where} \quad 0 < \lambda_2^+ < \lambda_1 < min(S^0(t)).$$

Table 2: Parameter values used in the plots of Figures 5 and 6

Parameter	Value used in Figure 5	Value used in Figure 6
$\tilde{S}^0$	3	2
η	2	2
T_1	1	1
T_2	3	3
T_p	4	4
n	9	9
$D_0(t)$	1	1
$D_1(t)$	0.4525	0.8895
$D_2(t)$	0.2005	0.5025
$S(0)$	3	2
$x_1(0)$	3	1
$x_2(0)$	2	1
μ_1	6	1
μ_2	8.5	1
a_1	1.4	0.01
a_2	0.7	0.02
λ_1	0.14	3/53
λ_2^+	0.07	3/49
k	0.5	0.5
γ	1	0.15

Figure 5 shows that species x_2 wins the competition while Figure 6 shows that species x_1 emerges the winner. In these two cases, despite the growth rates of the species x_1 and x_2 require lower levels of the nutrient S than the input nutrient supply $S^0(t)$, the species with the least requirements of the nutrient wins the competition.

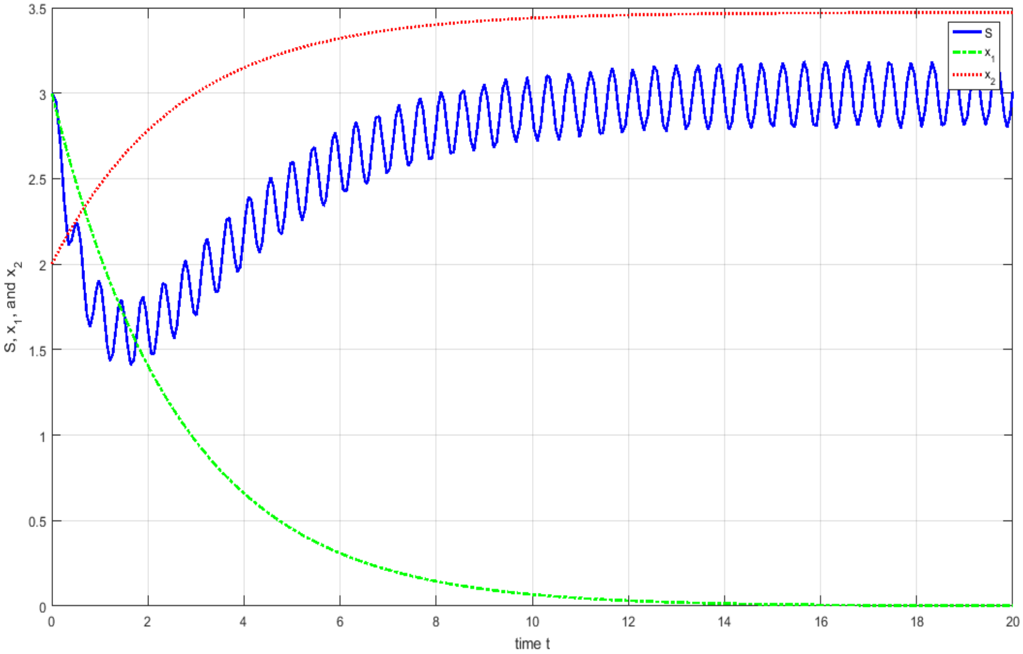

Figure 5: Simulation for $g_2(t, \lambda_2^+) > g_1(t, \lambda_1)$, where $0 < \lambda_2^+ < \lambda_1 < min(S^0(t))$.

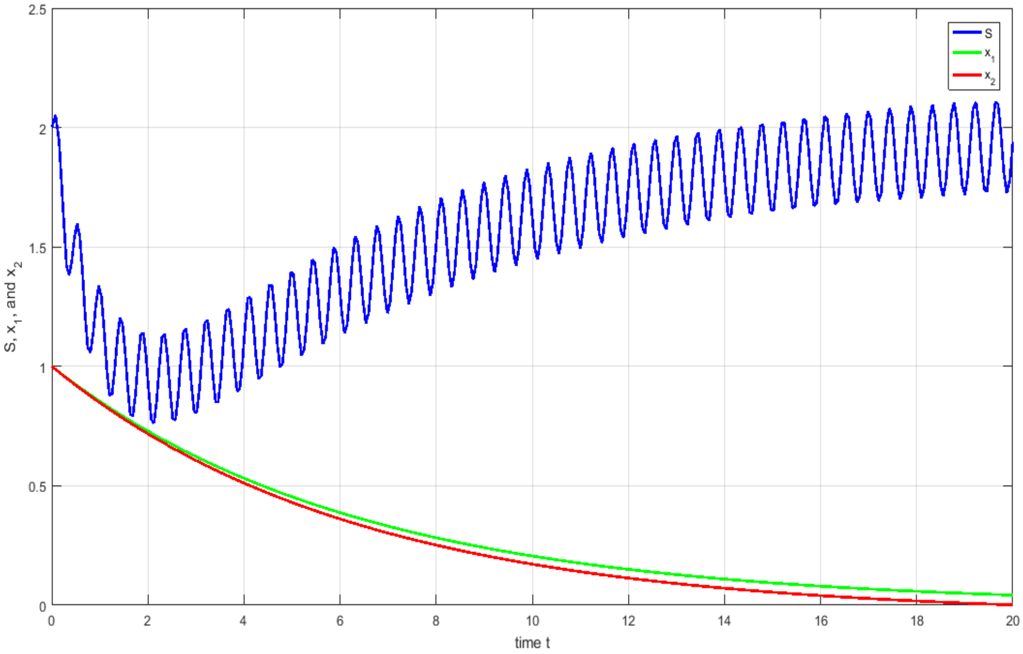

Figure 6: Simulation for $g_1(t, \lambda_1) > g_2(t, \lambda_2^+)$, where $0 < \lambda_1 < \lambda_2^+ < min(S^0(t))$.

10 Conclusion

By using both analytical and numerical results, we have shown that competitive exclusion always holds in a two species periodic chemostat-like model with allelopathic growth inhibition. We have found that the species with the smallest break-even concentration survives the competition for a single growth-limiting nutrient independent of the initial conditions.

This study can be improved by incorporating discrete time delays to account for the lag in the conversion of nutrient consumed to viable biomass.

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