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# Mutual Inhibition, Competition, and Periodicity in a Two Species Chemostat-like System

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## ABSTRACT

A model addressing mutual inhibition in a periodic chemostat is presented in this paper. The operating parameters, including the nutrient uptake function, washout rate, and nutrient concentration are allowed to be periodic functions of time, with commensurate periods. It is shown that with mutual inhibition, competitive exclusion always holds in models that would allow coexistence without inhibition. We further show that initial conditions play a crucial role in determining which species survives. Simulations using MATLAB appear to confirm the predictions of the models. Some results from the simulations are presented graphically.

*Keywords:* Periodic Chemostat; Mutual Inhibition; Exploitative Competition.

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## 1. Introduction

Finding criteria for the long term coexistence of species is an important problem in population biology. This long term coexistence, also referred to as permanence or uniform persistence, requires non-extinction as well as non-explosion of species, but allows otherwise arbitrary asymptotic behaviour [8]. Most studies dealing with permanence are centered on models governed by autonomous systems of differential equations. The models predict that when species compete for  $n$  resources available in limiting supply, at most  $n$  species can survive [16]. Thus, for a single limiting resource, the models predict that at most one species can survive. This competition for a single resource is called exploitative competition [4]. In nature, however, only a few resources are usually in limiting supply, but the number of species surviving on those few resources is abundant.

A good place where the predictions of these mathematical models may be tested experimentally is in a laboratory device called a *chemostat*. The chemostat models a very simple lake [15] and is important in ecological studies because the mathematics can be traced and the relevant experiments are possible [4]. It is an important piece of apparatus 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 [2], [3], [4], [5], [6], [7].

Mathematical models of exploitative competition in a well-stirred chemostat operated under constant

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input and dilution rates, with competition for a single essential, non-reproducing, growth limiting nutrient whose concentration varies periodically with time predict competitive exclusion, that is only one competitor population avoids extinction (see for instance [1], [2], [6], [13]). 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, as noted in [2], [4], [6]. 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 [4].

There have been some studies looking at some aspects of periodicity in chemostat models. Butler, Hsu and Watman [5] found that in a model of the chemostat with periodic washout rate, under suitable circumstances, there is coexistence of the competing population. Cushing [17] 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 predators. Zhao and Hutson addressed permanence in Kolmogorov periodic-predator prey models with diffusion with the result that permanence is expected to hold [8]. There have also been some studies involving various aspects of inhibition to the growth of competing species. Most of these studies looked at one of the species producing a toxin or shading. Hsu, and Watman [9] 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 [10]. Hsu et al [11] studied competition in the presence of a lethal external inhibitor, Braselton and Watman, [12] developed a competition model with dynamically allocated inhibitor production, while Jianhua et al [14] addressed the effect of inhibitor on the plasmid bearing and plasmid-free model in the unstirred chemostat. The inhibition included introduction of an external toxin or one of the species producing the toxin. The models addressing inhibition in these models were those of the homogeneous chemostat.

In these studies, no model addressed mutual inhibition in competing species. In this study, we present a model of a 2-species competition with mutual inhibition in a periodically operated chemostat. We shall assume that the chemostat is spatially homogeneous, but all 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 a function of time with its period being commensurate with that of the other parameters. We shall take a Holling Type II function for the nutrient uptake, that is, the function follows Michaelis-Menten kinetics. As long as both species are present, inhibition is also present; that  $x_i$ , being the biomass of species  $i$  ( $i = 1, 2$ ), does not inhibit its own growth, and that overall inhibition effect to  $x_i$  decreases as the biomass of  $x_i$  increases and vice versa. In addition, inhibition to the growth of  $x_i$  increases as  $x_j$ ,  $i = 1, 2$ ,  $j = 1, 2$ ,  $i \neq j$  increases.

In this paper, section 2 presents the model with mutual inhibition as well as some theorems that arise from the model. Section 3 covers discussion of the results and presents an example with plots of the simulated model.

## 2. The Model

The model for competition for a single, essential, growth limiting nutrient with mutual inhibition is described by

$$\begin{aligned} \frac{dS(t)}{dt} &= (S_0(t) - S(t))D_0(t) - \sum_{i=1}^2 x_i(t)P_i(t, S(t))g_i(x_1(t), x_2(t)), \\ \frac{dx_i(t)}{dt} &= x_i(t) \{P_i(t, S(t))g_i(x_1(t), x_2(t)) - D_i(t)\}, \quad i = 1, 2, \\ x_i(0) &= x_{i0} \geq 0, \quad S_0(0) \geq 0, \quad x_i \in \mathbb{R}_+ = [0, \infty), \end{aligned} \quad (2.1)$$

where,

$S(t)$  is nutrient concentration at time  $t$ ,  
 $x_i(t)$  is the biomass of  $i^{th}$  species at time  $t$ ,  
 $P_i(t, S(t))$  is the specific per capita nutrient uptake function of species  $i$ ,  
 $S_0(t)$  is the input nutrient concentration,  
 $D_0(t)$  is the nutrient dilution rate and,  
 $D_i(t)$  is the specific removal rate (washout rate) of species  $i$ ,  
 $g_i(x_1(t), x_2(t))$  represents the degree of inhibition to the growth of species  $i$ .

Here, it is assumed that  $S_0(t), D_0(t)$  and  $D_i(t)$  are all continuous,  $\omega$ -periodic, positive functions and that each  $P_i(t, S) : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+$  is continuous,  $\omega$ -periodic in  $t$  and satisfies:-

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

We further assume that  $g_i(x_1(t), x_2(t))$  is a continuous function for all  $(x_1, x_2) \in \mathbb{R}_+^2$  which satisfies the following conditions **A1**:-

- i)  $g_i(x_1(t), x_2(t)) : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+ \in [0, 1]$
- ii)  $g_i(x_1(t), x_2(t))$  is strictly decreasing in  $x_j$   $i = 1, 2, j = 1, 2, i \neq j$
- iii)  $g_i(x_1(t), x_2(t))$  is strictly increasing in  $x_i$
- iv)  $g_i(x_1(t), x_2(t)) = 1$  for  $x_j = 0, i \neq j$  and for all  $t \geq 0$ .

Condition i) helps to delineate the meaning of  $g_i(x_1(t), x_2(t))$  with  $g_i(x_1(t), x_2(t)) = 0$  being total inhibition to the growth of species  $i$  while  $g_i(x_1(t), x_2(t)) = 1$  being no inhibition at all. Decreasing levels of  $g_i(x_1(t), x_2(t))$  imply greater levels of inhibition to the growth of species  $i$  and vice versa. Conditions ii) and iii) make physical sense because we expect increasing biomass of  $x_i$  to cause a greater inhibition effect on  $x_j, i = 1, 2, j = 1, 2, i \neq j$ , while the overall inhibition effect on  $x_i$  from  $x_j$  will be decreasing. If  $x_j$  is not present, we do not expect any inhibition on  $x_i$  as condition iv) implies.

In the special case when  $g_1(x_1(t), x_2(t)) = g_2(x_1(t), x_2(t)) = 1$ , the system reduces to

$$\begin{aligned} \dot{S}(t) &= (S_0(t) - S(t))D_0(t) - \sum_{i=1}^n x_i(t)P_i(t, S(t)), \\ \dot{x}_i(t) &= x_i(t)(P_i(t, S(t)) - D_i(t)) \quad 1 \leq i \leq n, \end{aligned} \tag{2.2}$$

which is the standard chemostat model without inhibition. A discussion of this case may be found in [2], [4], and [15].

If conditions A1 are satisfied, we have the following results for model (2.1) where, by a solution of (2.1) we mean a differentiable triple  $(S(t), x_1(t), x_2(t)) \in \mathbb{R}_+^3$  that satisfies the system of differential equations (2.1).

**Theorem 2.1.** *The positive  $(S(t), x_1(t), x_2(t))$ -cone is positively invariant for (2.1) as are the surfaces  $x_1 = 0$  and  $x_2 = 0$ . The solutions of the model are uniformly bounded as  $t \rightarrow \infty$  i.e the system is dissipative.*

*Proof.* The solution of system (2.1) is said to be entirely bounded in  $\mathbb{R}$  if,

$$\sup_{t \in \mathbb{R}} |(S(t), x_1(t), x_2(t))| < +\infty. \tag{2.3}$$

We start by showing that  $S(t) > 0$ . Suppose that  $S(t) < 0$ , for all  $t \geq 0$ . Since  $\dot{S}(t) = S_0(t)D_0(t) - S(t)D_0(t) - \sum_{i=1}^2 x_i(t)P_i(t, S(t))g_i(x_1(t), x_2(t))$ , it follows that

$$\dot{S}(t) \geq - \left[ S(t)D_0(t) + \sum_{i=1}^2 x_i(t)P_i(t, S(t))g_i(x_1(t), x_2(t)) \right]$$

and since  $S(t)$  is assumed to be negative,

$$\frac{\dot{S}(t)}{S(t)} \leq - \left[ D_0(t) + \frac{1}{S(t)} \sum_{i=1}^2 x_i(t)P_i(t, S(t))g_i(x_1(t), x_2(t)) \right]$$

or

$$\frac{\dot{S}(t)}{S(t)} \geq D_0(t) + \frac{1}{S(t)} \sum_{i=1}^2 x_i(t)P_i(t, S(t))g_i(x_1(t), x_2(t))$$

meaning

$$S(t) \geq S(0) \exp \int_0^t \left[ D_0(\xi) + \frac{1}{S(\xi)} \sum_{i=1}^2 x_i(\xi)P_i(\xi, S(\xi))g_i(x_1(\xi), x_2(\xi)) \right] d\xi \quad (2.4)$$

Since the quantity on the right of (2.4) is positive for  $S(0) = S_0 > 0$  and for all  $t$ , this contradicts our assumption that  $S(t) < 0$ . This means that  $S(t) > 0$  for all  $t$ .

From the second equation in (2.1), we immediately see that

$$x_i(t) = x_i(0) \exp \left[ \int_0^t (p_i(\xi, S(\xi))g_i(x_1(\xi), x_2(\xi)) - D_i(\xi)) d\xi \right]. \quad (2.5)$$

Thus, for  $x_i(0) \geq 0$  equation (2.5) means  $x_i(t) \geq 0$  for all  $t$ . This completes the proof that the solution  $(S(t), x_1(t), x_2(t))$  of (2.1) is positive.

We now show that the solution is bounded. Let  $V(t) = S(t) + x_1(t) + x_2(t)$ . Clearly,  $V(t)$  is a continuous, positive and  $\omega$ -periodic function. Then, using (2.1), we find

$$\begin{aligned} \dot{V}(t) &= S_0(t)D_0(t) - (S(t)D_0(t) + x_1(t)D_1 + x_2(t)D_2(t)) \\ &\leq S_0(t)D_0(t). \end{aligned} \quad (2.6)$$

This means that

$$V(t) \leq \int_0^t S_0(\xi)D_0(\xi) d\xi < \infty, \text{ for all } t \geq 0 \quad (2.7)$$

and since all solutions are positive, it follows that all solutions are bounded, completing the proof.  $\square$

The theorem below gives conditions that make the species either persistent or extinct.

**Theorem 2.2.** *If  $g_i(x_1(t), x_2(t)) < \frac{D_i(t)}{P_i(t, S(t))}$ , then  $\lim_{t \rightarrow \infty} x_i(t) = 0$ ,  $i = 1, 2$ , and for all  $t \geq 0$ .*

*Proof.* Assume that  $P_i(t, S(t))$  is locally Lipschitz and is strictly increasing for  $S \in R_+$ , and  $P_i(t, 0) = 0$ , for  $t \geq 0$ . From (2.5) we see that for  $g_i(x_1(t), x_2(t)) < \frac{D_i(t)}{P_i(t, S(t))}$ ,

$$x_i(t) = x_i(0) \exp \left[ - \int_0^t (D_i(\xi) - P_i(\xi, S(\xi))g_i(x_1(\xi), x_2(\xi))) d\xi \right]$$

Since  $\lim_{t \rightarrow \infty} x_i(0) \exp \left[ - \int_0^t (D_i(\xi) - P_i(\xi, S(\xi))g_i(x_1(\xi), x_2(\xi)))d\xi \right] = 0$ , it means that  $\lim_{t \rightarrow \infty} x_i(t) = 0, \quad i = 1, 2$ , completing the proof. □

In mutual inhibition, the first few moments of interaction seem to be crucial in determining which species survives the competition and which becomes extinct. Indeed, the initial concentration  $S(0) = S_0$  and the uptake function  $P_i(t, S(t))$  during the first instances of interaction appear to determine which species survives. We assume a Holling Type II (Monod) uptake function which is of the form

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

where  $\mu$  is the intrinsic growth rate and  $\beta$  is a Michaelis-Menten constant.

The relationship between  $P_1(t, S(t))$  and  $P_2(t, S(t))$  and  $S(t)$  will be of one of the following forms:- Figure

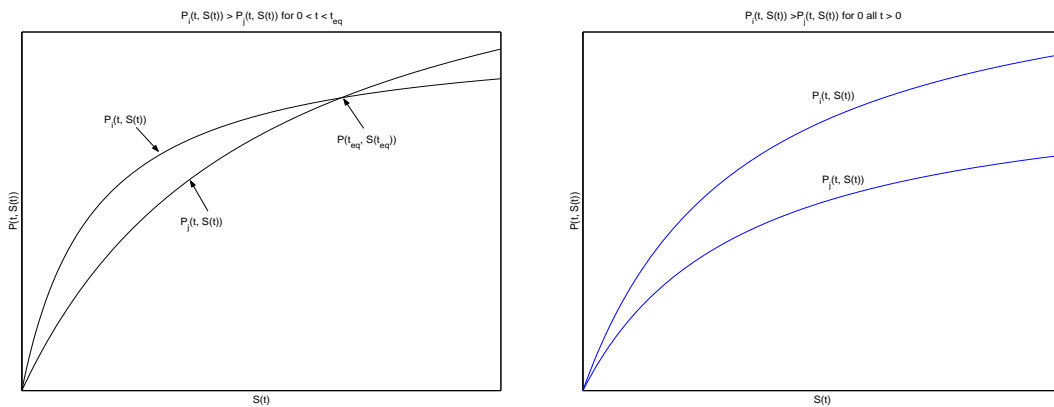


Figure 1: Two possible relationships between the uptake functions of the species

1(i) shows one possible relationship between  $P_1(t, S(t))$  and  $P_2(t, S(t))$  as  $S(t)$  increases where  $P_1(t, S(t)) > P_2(t, S(t))$  for  $0 < t < t_{eq} < \infty$  while Figure 1(ii) shows another possibility for the same relationship where  $P_1(t, S(t)) > P_2(t, S(t))$  for  $0 < t \leq t_{eq} = \infty$ . We easily find  $S(t_{eq}) = \frac{\mu_2 \beta_1 - \mu_1 \beta_2}{\mu_1 - \mu_2}$ . For this type of relationship and if we let  $D_0(t) = D_1(t) = D_2(t) = D(t)$  for simplicity, we have the following result.

**Theorem 2.3.** *i) If  $P_1(t, S(t)) < P_2(t, S(t))$  for  $0 < t < t_{eq}$ , then for  $x_1(0) = x_2(0) > 0, \lim_{t \rightarrow \infty} x_1(t) = 0$  and  $\lim_{t \rightarrow \infty} x_2(t) = x_2^*(t)$  where  $x_2^*(t)$  is the  $\omega$ -periodic solution of the equation*

$$\frac{dx_2(t)}{dt} = x_2(t) \{P_2(t, S(t))g_2(x_1(t), x_2(t)) - D(t)\}, \quad i = 1, 2,$$

*ii) If  $P_1(t, S(t)) > P_2(t, S(t))$  for  $0 < t < t_{eq}$ , then for  $x_1(0) = x_2(0) > 0, \lim_{t \rightarrow \infty} x_1(t) = x_1^*(t)$  and  $\lim_{t \rightarrow \infty} x_2(t) = 0$  where  $x_1^*(t)$  is the  $\omega$ -periodic solution of the equation*

$$\frac{dx_1(t)}{dt} = x_1(t) \{P_1(t, S(t))g_1(x_1(t), x_2(t)) - D(t)\}, \quad i = 1, 2,$$

This theorem states that in a competition with mutual inhibition, the species which has an advantage at the beginning of the interaction wins the competition. It also predicts that there is no persistence in this type of competition. That is the theorem predicts competitive exclusion.

*Proof.* Since  $x_1(0) = x_2(0) > 0$ , it follows that

$$g_1(x_1(0), x_2(0)) = g_2(x_1(0), x_2(0)).$$

From (2.1) we have

$$x_i(t) = x_i(0) \exp \int_0^{t_1} \{P_i(\xi, S(\xi))g_i(x_1(\xi), x_2(\xi)) - D(\xi)\} d\xi \quad i = 1, 2. \quad (2.8)$$

The fact that  $x_1(0) = x_2(0) > 0$ , and  $P_1(t, S(t_0)) < P_2(t, S(t_0))$ , means that

$$x_1(t_1) < x_2(t_1) \quad \text{for } t_1 = t_0 + a < t_{eq}, \quad a > 0 \quad (2.9)$$

The strict monotonicity of  $g_i(x_1(t), x_2(t))$ ,  $i = 1, 2$  that satisfies conditions A1 (more specifically A1 (ii) and (iii)) and (2.9) mean that

$$g_1(x_1(t_1), x_2(t_1)) < g_1(x_1(t_0), x_2(t_0)) = g_2(x_1(t_0), x_2(t_0)) < g_2(x_1(t_1), x_2(t_1)) \quad (2.10)$$

Consequently, (2.10) implies that for  $t_2 = t_1 + a < t_{eq}$ ,  $a > 0$ , we have

$$x_1(t_2) < x_1(t_1) < x_1(t_0)$$

and

$$x_2(t_0) < x_2(t_1) < x_2(t_2).$$

This process may be repeated for  $t_3 = t_2 + a < t_{eq}$ , ...,  $t_n = t_{n-1} + a \leq t_{eq}$ ,  $a > 0$  until  $x_1(t_n) = 0$  and, together with condition A1 (iv), find that  $g_2(0, x_2(t_n)) = 1$ . Once  $x_1(t_n) = 0$ , it follows from Theorem 2.2 in [2] that  $x_1(t) = 0$ , for all  $t \geq t_n$ . This means that species  $x_1$  becomes extinct. When this happens, species  $x_2$  experiences no inhibition to its growth ( $g_2(0, x_2(t_n)) = 1$ ) and Theorem 3.1 in [2] assures that  $\lim_{t \rightarrow \infty} x_2(t) = x_2^*(t)$ . This completes proof of the first part of the theorem.  $\square$

When  $P_1(t, S(t)) > P_2(t, S(t))$  and  $x_1(0) = x_2(0) > 0$ , then  $g_1(x_1(0), x_2(0)) = g_2(x_1(0), x_2(0))$ . An argument similar to that of the first part the theorem completes the proof.

The theorem above is based on the assumption that the initial population sizes of the two species are equal at the beginning of the interaction. In most cases in nature, this is not true. We relax this condition to state the following.

**Theorem 2.4.** *If  $x_1(t)P_1(x_1(t), x_2(t)) < x_2(t)P_2(x_1(t), x_2(t))$  for  $0 < t < t_{eq}$ , then  $\lim_{t \rightarrow \infty} x_2(t) = x_2^*(t)$ ,  $\lim_{t \rightarrow \infty} x_1(t) = 0$ , and if  $x_1(t)P_1(x_1(t), x_2(t)) < x_2(t)P_2(x_1(t), x_2(t))$  for  $0 < t < t_{eq}$  then  $\lim_{t \rightarrow \infty} x_2(t) = 0$  and  $\lim_{t \rightarrow \infty} x_1(t) = x_1^*(t)$  where  $x_i^*(t)$  is the  $\omega$ -periodic solution of the equation  $\frac{dx_i(t)}{dt} = x_i(t) \{P_i(t, S(t))g_i(x_1(t), x_2(t)) - D(t)\}$ ,  $i = 1, 2, .$*

*Proof.* Since  $x_1(t)P_1(x_1(t), x_2(t)) < x_2(t)P_2(x_1(t), x_2(t))$  for  $0 < t < t_{eq}$ , we have by A1 (ii),

$$g_1(x_1(t_0), x_2(t_0))P_1(t_0, S(t_0)) < g_2(x_1(t_0), x_2(t_0))P_2(t_0, S(t_0))$$

and

$$\exp \int_0^t g_1(x_1(\xi), x_2(\xi))P_1(\xi, S(\xi)) - D(\xi) d\xi < \exp \int_0^t (g_2(x_1(\xi), x_2(\xi))P_2(\xi, S(\xi)) - D(\xi)) d\xi.$$

Using comparison theorems, we conclude that

$$\begin{aligned} \lim_{t \rightarrow \infty} x_1(0) \exp \int_0^t (g_1(x_1(\xi), x_2(\xi))P_1(\xi, S(\xi)) - D(\xi)) d\xi \\ < \lim_{t \rightarrow \infty} x_2(0) \exp \int_0^t (g_2(x_1(\xi), x_2(\xi))P_2(\xi, S(\xi)) - D(\xi)) d\xi. \end{aligned}$$

It then follows that for some  $t_n \geq 0$ , we have  $x_1(t_n) < x_2(t_n)$ , which in turn implies that  $g_1(x_1(t_n), x_2(t_n)) < g_2(x_1(t_n), x_2(t_n))$ . Since  $g_i(x_1(t), x_2(t))$ ,  $i = 1, 2$  is strictly monotonic, we can find a  $t_{n+\delta} \geq t_n \geq 0$  such that

$$g_1(x_1(t_{n+\delta}), x_2(t_{n+\delta})) < g_1(x_1(t_n), x_2(t_n)) < g_2(x_1(t_n), x_2(t_n)) < g_2(x_1(t_{n+\delta}), x_2(t_{n+\delta})),$$

from which we conclude that

$$x_1(t_{n+\delta}) < x_1(t_n) < x_2(t_n) < x_2(t_{n+\delta}).$$

Proceeding in a manner similar to the proof of Theorem 3 completes the proof. □

### 3. Results and Discussion

In the absence of mutual inhibition, (2.2) with periodic parameters predict uniform persistence of the two competing species and guarantees the existence of at least one positive periodic solution [2].

Model (2.1) that we have presented predicts that if mutual inhibition is present, competitive exclusion holds. We have shown in Theorem 3 that the species that wins the competition is determined by the initial conditions of the parameters at the beginning of the interaction. In Theorem 4 we have shown that the initial biomass of the species contributes in determining which competitor wins. The key difference in predictions between (2.2) and (2.1) is that while (2.2) predicts persistence for all competing species, (2.1) predicts that only one competitor survives.

It appears that the species that has even a slight advantage at the beginning of the competition capitalizes on that advantage, however small, to inhibit the growth of its competitor and ensure its own survival. In the critical situation where the uptake function and biomass of both species are the same, then the two species may coexist, but are indistinguishable from each other, at least from a modeling point of view. That is, the two species behave as if it were a single species and  $g_1(x_1(t), x_2(t)) = g_2(x_1(t), x_2(t))$ , for all  $t \geq 0$ . An open question arises as to whether choosing different functions to model mutual inhibition would result in different dynamics of (2.1).

**Example.** We use parameters from [2] where the dilution rate is given by  $D(t) = \mu_0 + a \cos(\omega t)$ , and vary the initial nutrient input concentration to fit the requirements of Theorem 3. We then vary the initial biomass concentrations of the competitors to fit the requirements of Theorem 4.

From the simulations, it appears that the hypotheses of both models are satisfied. In fact, we have carried out hundreds of simulations of these models and all of them seem to agree with the predictions of the theorems presented. We used a nutrient uptake function of the form

$$P_i(t, S(t)) = \frac{\mu_i S(t)}{\beta_i + S(t)}$$

Here are some of the figures obtained with the following settings.

The values in the columns satisfy the following requirements:- Figure 2.1k ( $k = a, b, c, d$ ) means the plot is of model (2.1) using parameter settings from column  $k = a, b, c, d$  while figure 2.2k, ( $k = a, b, c, d$ ) means the plot is of model(2.2) using parameter settings from column  $k = a, b, c, d$ .

Clearly, Figure 1a shows that species  $x_2$  wins the competition while Figure 1b shows that species  $x_1$  emerges the winner, where by  $x_i$ ,  $i = 1, 2$  winning the competition we mean that  $\lim_{t \rightarrow \infty} x_i(t) > 0$  and  $\lim_{t \rightarrow \infty} x_j(t) = 0, i = 1, 2, j = 1, 2, i \neq j$ . Figure 2a shows that  $x_1(t)$  loses the competition as predicted by part b of Theorem 2.2 in [2] while 2b shows coexistence of the two competing species. Figures 2c and 2d again show coexistence of the two competing species while Figure 1c shows species  $x_2$  winning the competition while figure 1d shows that  $x_1$  wins the competition. This is consistent with the predictions of the models in this paper.



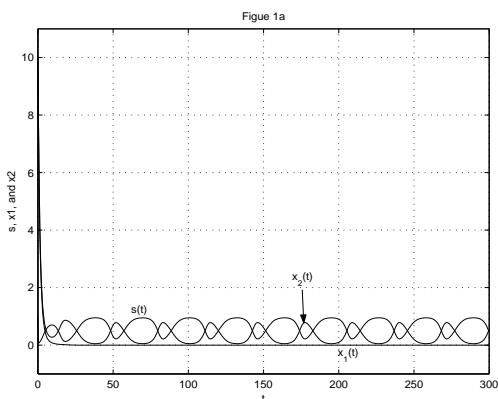


Figure 2

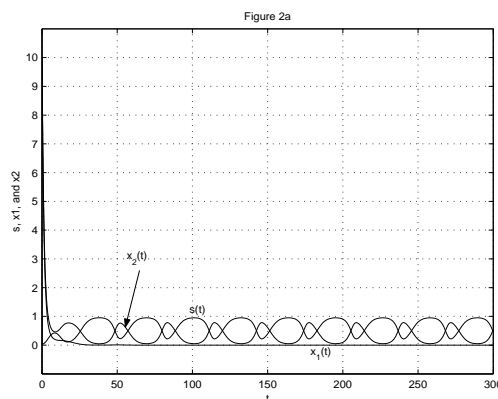


Figure 3

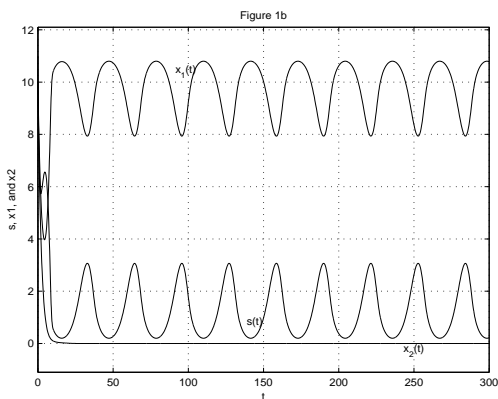


Figure 4

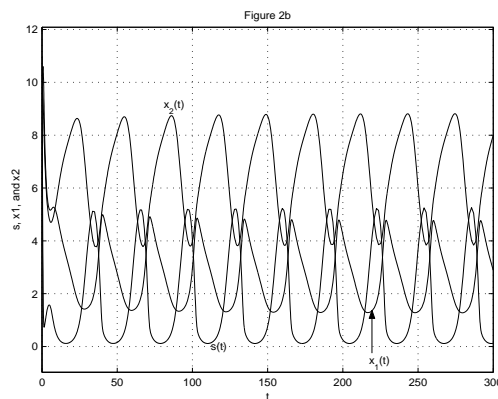


Figure 5

Table 1: Parameter values used in the plots of figure 1 (a – d) and 2(a – d)

Parameter	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>
$\mu_0$	0.4675	0.4675	0.4675	0.4675
$S_0(t)$	1	11	11	11
<i>a</i>	0.3	0.3	0.3	0.3
$\omega$	0.2	0.2	0.2	0.2
$\mu_1$	1	1	1	1
$\beta_1$	1	1	1	1
$\mu_2$	0.7	0.7	0.7	0.7
$\beta_2$	0.3	0.3	0.3	0.3
$x_1(0)$	10	10	7	8
$x_2(0)$	10	10	10	10

Table 2: Relationship between parameters in table 1

column <i>a</i>	$P_1(0, S(0)) < P_2(0, S(0))$	$x_1(0) = x_2(0)$
column <i>b</i>	$P_1(0, S(0)) > P_2(0, S(0))$	$x_1(0) = x_2(0)$
column <i>c</i>	$x_1(0)P_1(0, S(0)) < x_2(0)P_2(0, S(0))$	$x_1(0) \neq x_2(0)$
column <i>d</i>	$x_1(0)P_1(0, S(0)) > x_2(0)P_2(0, S(0))$	$x_1(0) \neq x_2(0)$

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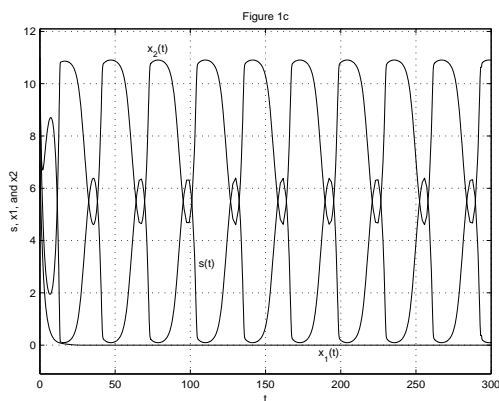


Figure 6

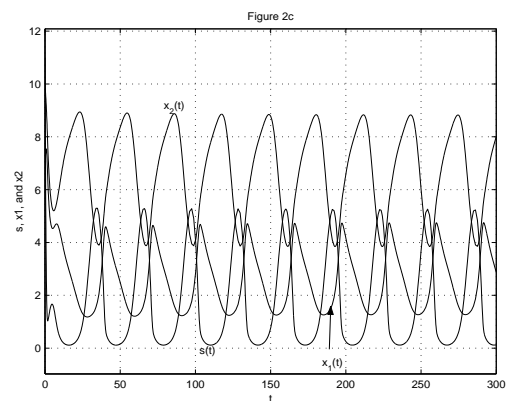


Figure 7

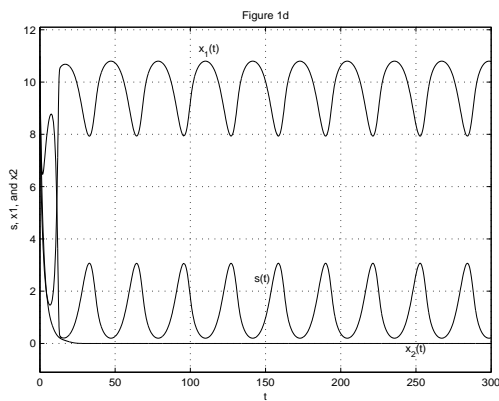


Figure 8

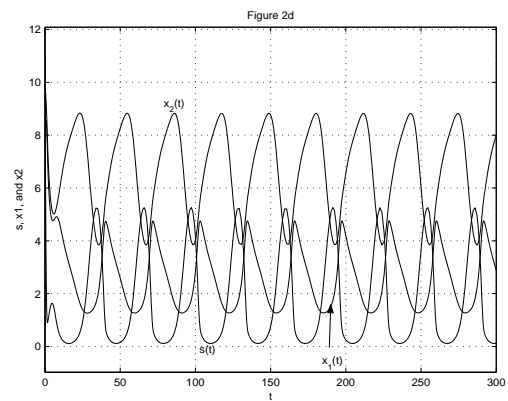


Figure 9

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