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

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Declaration

This thesis is my orignal work and has not been presented for any award in any other institution.

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This thesis has been submitted for examination with our approval as University supervisors.

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Dedication

∼∼To my wife Jane, and daughter Skylar ∼∼

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List of Symbols

Unless otherwise specified, the symbols used in this study will have the following meaning:-

	Symbol	Meaning
1.	$\uplus$	bag union
2.	$\forall$	For all
3.	$\subset$	Subset of
4.	$\rightarrow$	Maps to
5.	$\in$	an element of
6.	$\bigcup_{a \leq i \leq b}$	Generalized union of all sets from a to b
7.	$\gamma^{+}(U)$	Positive orbit or positive trajectory

Other symbols used are defined as they appear in this study.

Abstract

In this study we develop a model that addresses competition in a periodic chemostat-like system with mutual growth inhibition. A periodic Kolmogorov system of ordinary differential equations that describes mutual inhibition for two-species competiting for a single, essential nutrient in a chemostat-like system is developed, and its dynamics studied. We then present a model of the general chemostat with mutual inhibition, where global behavior of the solutions of this model are discussed and we show that for two species competing for a single nutrient available in limiting supply, at most one species will survive. Mutual inhibition in the periodic chemostat where the operating parameters including the nutrient uptake function, washout rate, and nutrient concentration are allowed to be periodic functions of time, with commensurate periods is also studied. it is assumed that the chemostat is spatially homogeneous, but all the parameters in the model are periodic. 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. Each species does not inhibit its own growth, and that overall inhibition effect of a species decreases as its biomass increases and vice versa. In addition, inhibition to the growth of a given species is increased by the presence and growth of its competitor. We describe periodic nutrient input and dilution rates that make persistence of both species possible in the system without inhibition and then show that this persistence does not hold in the mutually inhibiting periodic chemostat-like system.

We introduce a function that accounts for mutual inhibition effects of the species involved in the competition. First, we consider mutual inhibition in the ordinary chemostat and use stability theories to study the global behaviour of the solutions of the model. For two species competing for a single nutrient available in limiting supply, we show that at most one species survives.

To account for realistic periodic variations, we use a cosine Fourier series to introduce periodic parameters in the ordinary chemostat then apply a threshold result on the global dynamics of the scalar asymptotically periodic Kolmogorov equation to a growth model of two species. The theory of asymptotically periodic semiflows and comparison methods are used to demonstrate uniform persistence of all the species and that the full dynamical system admits at least one positive, periodic solution.

Applying comparison theorems, we show that with mutual inhibition, competitive exclusion always holds in models that would allow coexistence without inhibition. Furthermore we demostrate that initial conditions play a crucial role in determining which species survives. Using MATLAB, we get numerical solutions that confirm the predictions of the models.

This thesis is organized as follows:- In Chapter 2 we give an overview of the progress made regarding chemostat models and identify gaps that exist in the current models. We also give some important results that will be useful in the proof of our theorems in subsequent chapters.

In Chapter 1, we introduce the chemostat while in Chapter 3 we present a model of the general chemostat with mutual inhibition and discuss the global behaviour of this chemostat. We also give some numerical results for the model of this section. In Chapter 4 we use Fourier series to describe the nutrient input concentration and washout (dilution) rates. This introduces periodicity in the chemostat and we apply the theory of asymptotically periodic semiflows and the comparison method is used to determine criteria that guarantee the existence of a positive solution for the full system.

Then in Chapter 5 we discuss a model for competition in the periodic chemostat with mutual inhibition. We find that with mutual inhibition, coexistence is not possible. This finding differs with other findings of the periodic chemostat in the sense that without mutual inhibition, coexistence is possible.

It is in Chapter 6 that we give a conclusion and a discussion of our findings. In this Chapter, we also give suggestions for further study and open questions that arise out of this thesis. Further, open questions that have not been addressed in our study have been given.

Definition of Terms

The following terms will have the given meaning in this study.

1. A solution $x(t, t_0, x_0)$ of a system of differential equations $x' = f(t, x)$ is *bounded* if there exists a $\beta > 0$ such that $|x(t, t_0, x_0)| < \beta$ for all $t \geq t_0$ where β may depend on each solution.
2. The solutions of $x' = f(t, x)$ are *equi-bounded*, if for any $\alpha > 0$ and any $t_0 \in I$, there exists a $\beta(t_0, \alpha) > 0$ such that $|x_0| \leq \alpha$ implies $|x(t, t_0, x_0)| < \beta(t_0, \alpha)$ for all $t \geq t_0$.
3. The solutions of $x' = f(t, x)$ are *uniformly bounded*, if the β in Definition 2 above is independent of t_0.
4. The solutions of $x' = f(t, x)$ are *ultimately bounded for bound B*, if there exists a $B > 0$ and a $T > 0$ such that for every solution $x(t, t_0, x_0)$ of $x' = f(t, x)$, $|x(t, t_0, x_0)| < B$ for all $t \geq t_0 + T$ where B is independent of the particular solution while T may depend on each solution.
5. The solutions of $x' = f(t, x)$ are *uniformly ultimately bounded*, if the T in Definition 4 above is independent on t_0.
6. Let $x(t)$ be a solution of the vector differential equation $x' = f(t, x)$ which is defined for all $t \geq t_0$. The solution is said to be *stable* if for each $\epsilon > 0$ there is a corresponding $\delta = \delta(\epsilon) > 0$ such that any solution $\bar{x}(t)$ of $x' = f(t, x)$ which satisfies the inequality $|\bar{x}(t_0) - x(t_0)| < \delta$ exists and satisfies the inequality $|\bar{x}(t) - x(t)| < \epsilon$ for all $t \geq t_0$.
7. The solution $x(t)$ in 6 above is *asymptotically stable* if in addition the requirements in Definition 6, we have $|\bar{x}(t) - s(t)| \to 0$ as $t \to \infty$ whenever $|\bar{x}(t_0) - x(t_0)|$ is sufficiently small.
8. The solution $x(t)$ of $x' = f(t, x)$ is said to be *uniformly stable* if for each $\epsilon > 0$ there

is a corresponding $\delta = \delta(\epsilon) > 0$ such that any solution $\bar{x}(t)$ of $x' = f(t, x)$ which satisfies the inequality $|\bar{x}(t_1) - x(t_1)| < \delta$ for some $t_1 \geq t_0$ exists and satisfies the inequality $|\bar{x}(t) - x(t)| < \epsilon$ for all $t \geq t_1$.

9. The solution $x(t)$ in Definition 8 is said to be *uniformly asymptotically stable* if in addition to the conditions in Definition 8, there is a $\delta_0 > 0$, and for each $\epsilon > 0$ there is a corresponding $T = T(\epsilon) > 0$ such that if $|\bar{x}(t_1) - x(t_1)| < \delta_0$ for some $t_1 \geq t_0$ then $|\bar{x}(t) - x(t)| < \epsilon$ for all $t \geq t_1 + T$.

10. Let π be a continuous dynamical system. Given a point x, the set $\{\pi(x, t), t > 0\}$ is called the *positive orbit or positive trajectory* through the point and is denoted by $\gamma^+(x)$.

List of Symbols

Unless otherwise specified, the symbols used in this study will have the following meaning:-

	Symbol	Meaning
1.	$\uplus$	bag union
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Chapter 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. Many studies dealing with permanence are centered on models governed by autonomous systems of differential equations. The models predict that when species compete for $n \geq 1$ resources available in limiting supply, at most n species can survive. 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. In nature, however, only a few resources are usually in limiting supply, but the number of species surviving on those few resources is abundant. For a detailed discussion of permanence and exploitative competition, see for instance [4], [42] and [43]. A good place where the predictions of these mathematical models may be tested experimentally is in a laboratory device called a *chemostat* that we now discuss.

1.1 The Chemostat

Basically, the chemostat contains three chambers where the first chamber contains the nutrient, the second contains the competing species and the third is for collecting the overflow as shown in Schematic Figure 1.1.

The nutrient from Chamber A is pumped into chamber B where it is assumed that purely exploitative competition takes place [21]. The overflow chamber (Chamber C) collects waste, which is a mixture of nutrients and species. It is from this waste that the washout rate (death rate) of the species is determined. The chemostat is an important piece of apparatus for studying

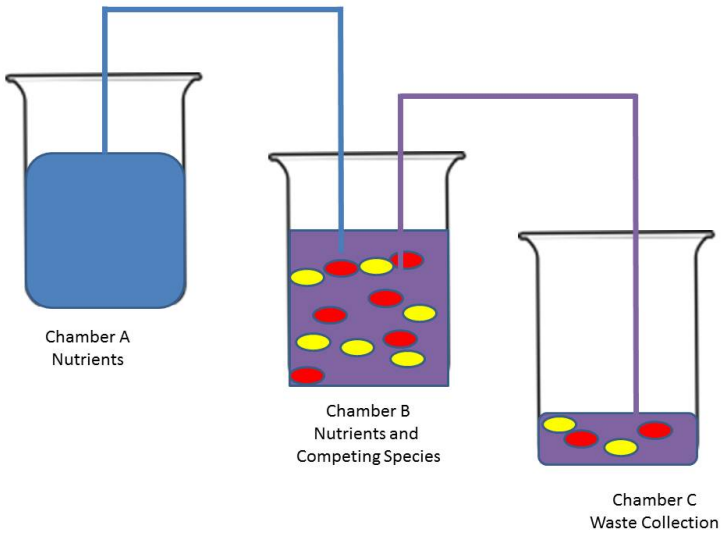

Figure 1.1: Schematic diagram of a Chemostat

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 ([7], [8], [32], [34], [36] and [42]). Mathematically, we are interested in understanding the dynamics of the interaction between the nutrient supplied and the competing species. For this purpose, we describe the interaction using a system of ordinary differential equations.

1.1.1 Chemostat Equations

Consider two species of biomass densities x_1 and x_2 competing for a nutrient of concentration S. The nutrient continuously decreases as long as the species are present. The rate of change of the nutrient is:-

$$\textit{Rate of Change of nutrient} = \textit{Nutrient Input - Washout - Consumption by species}, \qquad (1.1)$$

where the washout is any loss of the nutrient either through conversion to other products (e.g. decay), removal as waste, or loss through other ways other than consumption by the species.

If we let $S(t)$ be the nutrient concentration at any time t, and if there are no species present, i.e. there is no consumption of the nutrient, then the rate of change is directly proportional to input and washout. If the input concentration of the nutrient is represented by a constant S^0, then the relationship may be written as

$$\dot{S}(t) = (S^0 - S(t))D, \tag{1.2}$$

where D is a constant of proportionality.

If μ is the maximum specific growth rate of the species with biomass x, then the growth rate of that species is described by

$$\textit{growth rate of the species} = \frac{\mu x S}{K + S}, \tag{1.3}$$

where K is a constant reffered to as half saturation constant.

The consumption of the nutrient is directly proportional to the biomass of the species present. Thus, the consumption term in Equation (1.1) for species x is described as follows:

$$\textit{Consumption by species} = \frac{\mu c x S}{K + S} \tag{1.4}$$

where c is a constant of proportionality and is actually the content of the nutrient in the species.

From equations (1.3) and (1.4), relationship (1.1) may be represented as

$$\dot{S}(t) = (S^0 - S(t))D - \frac{\mu c x(t) S(t)}{K + S(t)} \tag{1.5}$$

Here, μ is known as the maximum specific growth rate of the species.

Turning to the species, we know that the rate of change of the species is the relationship

$$\textit{Rate of change of species} = \textit{Growth rate - Death rate (Washout)} \tag{1.6}$$

From equation (1.4) we get the growth rate. The washout (Mortality) rate is in proportion to the amount of species present at any time. Thus

$$\textit{washout} = x(t)D, \tag{1.7}$$

again D being a constant of proportionality and is infact the death rate of the species.

From equations (1.4) and (1.7), equation (1.6) is written as

$$\dot{x}(t) = (\frac{\mu S(t)}{K + S(t)} - D)x_i(t) \tag{1.8}$$

We now consider a system where two species with amounts $x_1(t)$ and $x_2(t)$ respectively are competing for the same nutrient. The nutrient is being consumed by the two species at the same time, and the consumption term in Equation (1.5) changes to accommodate the second species. The entire system is then represented by

$$\begin{aligned}
\dot{S}(t) &= (S^0 - S(t))D_0 - \frac{\mu_1 c_1 x_1(t) S(t)}{K_1 + S(t)} - \frac{\mu_2 c_2 x_2(t) S(t)}{K_2 + S(t)}, \\
\dot{x_1}(t) &= x_1(t)\left(\frac{\mu_1 S(t)}{K_1 + S(t)} - D_1\right), \\
\dot{x_2}(t) &= x_2(t)\left(\frac{\mu_2 S(t)}{K_2 + S(t)} - D_2\right),
\end{aligned} \tag{1.9}$$

where $\mu_i, \ \ i = 1, 2$ is the maximum specific growth rate of species i, $K_i, \ \ i = 1, 2$ is called the

half saturation constant for nutrient in species i, D_i is the death rate for species i, c_i, is the amount of nutrient content in species i, D_0 is the systems turnover rate. Model (1.9) is referred to as the standard chemostat model. All the governing parameters can be measured in a Chemostat thus making it plausible to compare experimental and mathematical predictions.

Chemostat models have applications in biotechnology where they model the commercial bio-reactor used to manufacture products with genetically altered organisms [5], in waste water treatment [23] and as a model of a very simple lake [30].

Interesting dynamics are introduced when inhibition is introduced in the chemostat. There are several ways that inhibition may occur. Sometimes, inhibition is caused by competition for light. In a forest, trees form a canopy that prevents light from reaching the shrubs at the floor. In this case the growth of species x_i is affected by shading as outlined below.

1.1.2 Effects of Shading

Consider the species growth which is limited by light availability only. Its model is given by

$$\dot{x}_i = x_i \left\{ \frac{\mu_i I}{I + K_i} - D_i \right\}, i = 1, 2,$$

where I is the incident irradiance assumed to be constant, the growth rate is a saturating function of incident irradiance, described by a Monod function with maximum growth rate μ_i and half saturation constant K_i. $D_i, i = 1, 2$ is the washout rate due to respiration, grazing, sedimentation or dilution [33].

The incident light is determined by incoming light, attenuated according to Lambert-Beer's

law (Litchman and Klausmeier [28]) given by

$$I = I_0 e^{-(\alpha_1 x_1 + \alpha_2 x_2)},$$

where I_0 is the intensity of incoming light while $\alpha_i, i = 1, 2$ is the light attenuation coefficient of species i.

The increase in biomass leads to a decrease in the incident light experienced by the species growing below the biomass. Each species is able to increase when the light is above its minimum resource requirement I_i^*, given by

$$I_i^* = \frac{K_i}{R_i - 1},$$

where $R_i = \frac{\mu_i}{D_i}$ is the ratio of the maximum growth rate to the loss rate.

According to competition theory, under constant conditions, the species with the lowest I^* displaces all others by reducing the incident light below the break-even light level I^* of the other species [28]: that is, the model predicts competitive exclusion. However, in nature there are many instances where co-existence is commonplace. It might be possible that this coexistence could be explained by other factors like seasonality.

An interesting study is that of phytoplankton. Here, competition for light indicates that any changes in the amount of phytoplankton species changes the amount of light available, and that species biomass concentration below certain values may allow co-existence while at other values, it may lead to competitive exclusion. This is well explained in Huisman and Weissing [25] and takes the following approach.

Consider a water column of one unit area and two competing phytoplankton species. Let ξ be the depth of the water column, where ξ runs from 0 (top) to z (bottom). Let $x_i(\xi, t)$ denote the population density of species i at depth ξ and time t. Then [6] and [25] have proposed the

following model for changes in the species population

$$\frac{\partial x_i}{\partial t}(\xi,t) = (\mathrm{P}_i(I(\xi,t)) - D_i)x_i(\xi,t) - \frac{\partial J_i}{\partial \xi}(\xi,t), \tag{1.10}$$

where

$\mathrm{P}_i(I(\xi,t)) =$ Net specific growth rate of species i as a function of light intensity $I(\xi,t)$,

$J_i(\xi,t) =$ net flux of species i,

$\frac{\partial J_i}{\partial \xi} =$ net change of the phytoplankton population density caused by local transport processes,

$D_i =$ loss of phytoplankton through all other processes.

If the phytoplankton transport is governed by turbulent diffusion, then the net flux $J_i(\xi,t)$ of species i at depth ξ is proportional to its local population density gradient

$$J_i(\xi,t) = -\varphi_i(\xi)\frac{\partial x_i}{\partial(\xi)}(\xi,t), \quad i = 1,2,$$

where $\varphi(\xi)$ is known as the turbulent diffusion coefficient, also called vertical eddy diffusivity [26].

If the water column is closed, then the boundary conditions are

$$\frac{\partial x_i}{\partial \xi}(0,t) = \frac{\partial x_i}{\partial \xi}(z,t) = 0.$$

The population size per unit surface area of each species i, denoted by X_i, is given by

$$X_i = \int_0^z x_i(\xi,t)d\xi, \quad i = 1,2.$$

This means the population size per unit surface area of species i changes with time according

to

$$\frac{dX_i}{dt} = \int_0^z \frac{\partial x_i}{\partial t}(\xi, t)d\xi = \int_0^z (P_i(I(\xi, t)) - D_i)x_i(\xi, t)ds, \quad i = 1, 2.$$

The flux terms cancel out because the boundary conditions are closed.

The light intensity at each depth is given by Lambert-Beer's law

$$\frac{\partial I}{\partial \xi}(\xi, t) = -K(\xi, t)I(\xi, t), \tag{1.11}$$

Where $K(\xi, t)$, consists of all components that absorb light including the water itself and the phytoplankton species, that is

$$K(\xi, t) = K_{bg} + \sum_{j=1}^{2} \alpha_j x_j(\xi, t), \tag{1.12}$$

with K_{bg} being the background turbidity that summarizes light absorption by all nonphytoplankton components, and α_j is the light attenuation coefficient of phytoplankton species i.

Substituting (1.12) into (1.11) and integrating over depth gives the light intensity at depth ξ and time t as

$$I(\xi, t) = I_{in}\exp\left(-\left\{\int_0^{\xi}\left[\sum_{j=1}^{2}\alpha_j x_j(\sigma, t) + K_{bg}\right]d\sigma\right\}\right). \tag{1.13}$$

This equation simply says that the light intensity at any particular depth depends on the incident light intensity, I_{in}, and on the total light attenuation by the phytoplankton and the background turbidity above that depth. A change in any of the population densities of the phytoplankton species causes a concomitant change in the light gradient, see for example Huisman, et al [25] where simulations of this model may be found.

Inhibition by shading occurs in a situation that is not spatially homogeneous. In case of spatial homogeneity, Equation (1.10) does not hold. In addition, if one species is inhibiting the growth

of the other through shading, then it is not possible for the other species to reciprocate. Hence, we cannot have mutual inhibition in this situation. To the best of our knowledge, the models in existence today do not address mutual inhibition in Chemostat-like systems. In this study, we consider the possible dynamics when competition involves mutual inhibition. Such situations are prevalent in nature as stated earlier.

1.1.3 Mutual Inhibition

Models that address inhibition in the chemostat have assumed that the inhibition is caused by the production of a toxin by one of the competitors. It is well known that growth inhibition does not necessarily come from a toxin. It may be caused by the growth habits of the organism, shading, weight of one species being placed on the other species, coiling of one species on the other, and various other ways.

It is common knowledge that weeds can smother, and eventually kill trees by their cumulative weight, shading, and growth habit (eg strangulation by vines). In Southeast Asia and the Pacific, the 'mile-a-minute' vine, *mikania cordata*, commonly smothers newly planted trees and is a major reason for expensive and frequent weeding operations [14].

Farmers have to undertake expensive weeding processes for their crops to prevent growth inhibition of their crops that is caused by either shading or competition for limited nutrients [14]. The Bindweed (*Polygonum Convolvulus*) for example has slender stems that spread over the ground until they encounter some other plants upon which it twines to the point of near strangulation! Shrubs are often used to choke weeds out of existence by providing cover that shades the weed.

Some models have been developed that study the effect of one of the species producing a toxin that inhibits growth of the other species (see for instance [5],[21], [22], [23], [38]) and

have discussed the existence of solutions from several perspectives. All the papers discussing competition with inhibition assume that one of the species produces the toxin that inhibits the growth of the other. Others, dealing with shading, assume one of the species causes shading to the other species, thus inhibiting their growth. Some authors such as [28] have developed models that look at effects of self shading in a chemostat. All the authors have assumed constant input and dilution rates.

We are not aware of any model that takes into account the mutual inhibition effect in scenarios such as the ones described above. Mutual inhibition caused by growth habits of the species present and not by production of a toxin has so far not been discussed. Furthermore, models that assume that there is no energy required by one species to inhibit the growth of the other have not, to our knowledge, not been addressed. One of the reasons why no such model has been developed is that though the idea seems simple: when one population increases the growth rate of the others should diminish (or at least not increase), the modeling is difficult to carry out in complete generality [30]. It is this lack of an appropriate model that this study will seek to address.

In order to prove some theorems in subsequent chapters, we shall need results on periodic semiflows to show uniform persistence and existence of periodic coexistence states in infinite-dimensional periodic semiflow under a general abstract setting.

1.2 Periodic Semiflows

Let X be a complete metric space with metric d. Then $T(t) : X \to X, \ \ t \geq 0$ is an $\omega-$periodic semiflow on X if there is an $\omega > 0$ such that $T(t)x$ is continuous in $(t, x) \in [0, \infty) \times X, \ \ T(0) = I$ and $T(t + \omega) = T(t)T(\omega) \ \ \forall t \geq 0$. A point x_0 corresponds to an $\omega-$periodic orbit if $T(t + \omega)x_0 = T(t)x_0 \ \ \forall t \geq 0$ and every $\omega > 0$. For an $\omega-$periodic semiflow, these x_0 coincide with the fixed points of its associated Poincaré map $T(\omega)$.

Let X_0 and ∂X_0 be open and closed subsets of X, respectively, such that $X_0 \cup \partial X_0 = \phi$, $X = X_0 \uplus \partial X_0$, $T(t) : X \to X$, $t \geq 0$, be an $\omega-$periodic semiflow with $T(t)X_0 \subset X_0$, $t \geq 0$; that is, X_0 is a positively invariant subset of X for $T(t)$.

1.2.1 Definition. *The periodic semiflow $T(t)$ is said to be uniformly persistent with respect to $(X_0, \partial X_0)$ if there exists $\eta > 0$ such that for any $x \in X_0$, $\liminf_{t\to\infty} d(T(t)x, \partial X_0) \geq \eta$.*

The following Lemma due to Zhao [41] gives an equivalence result between the uniform persistence of a periodic semiflow $T(t)$ and that of its associated discrete semi-dynamical system $\{\Phi^n\}$ defined by $\Phi = T(\omega)$.The reader is reffered to [41] for the proof.

Lemma 1.1. *Let $T(t)$ be an $\omega-$periodic semiflow on X with $T(t)X_0 \subset X_0$, $t \geq 0$. Assume that $\Phi = T(\omega)$ satisfies the following conditions:*

(1) Φ is point dissipative in X;

(2) Φ is compact, or alternatively, Φ is asymptotically smooth and the positive trajectory $\gamma^+(U)$ is strongly bounded in X_0 if U is strongly bounded in X_0.

Then the uniform persistence of Φ with respect to $(X_0, \partial X_0)$ implies that of $T(t) : X \to X$, $t \geq 0$. More precisely, Φ admits a global attractor $A_0 \subset X_0$ relative to strongly bounded sets in X_0 such that the compact set $A_0^* = \bigcup_{0\leq t\leq\omega} T(t)A_0 \subset X_0$ attracts any strongly bounded sets in X_0; that is, for any bounded subset U of X_0 with $d(U, \partial X_0) = \inf_{x\in U} d(x, \partial X_0) > 0$, $\lim_{t\to\infty} \overline{d}(T(t)U, A_0^*) = 0$, where $\overline{d}(T(t)U, A_0^*) = \sup_{x\in T(t)} d(x, A_0^*)$.

The result is on the existence of coexistence state for the discrete semi-dynamical system $\{\Phi^n\}_{n=1}^{\infty}$ defined by $\Phi : X \to X$ with $\Phi(X_0) \subset X_0$. A point $x_0 \in X$ is called a coexistence state of $\{\Phi^n\}_{n=1}^{\infty}$ if x_0 is a fixed point of Φ in X_0; that is, $x_0 \in X_0$ and $\Phi(x_0) = x_0$. See [41] and references therein for more details on discrete semi-flows.

Lemma 1.2. *Let $\Phi : X \to X$ be a continuous map with $\Phi(X_0) \subset X_0$. Assume that*

(1) $\Phi : X \to X$ *is point dissipative;*

(2) Φ *is compact; or alternatively,* Φ *is* $\alpha-$ *condensing and* $\gamma^+(U)$ *is strongly bounded in* X_0 *if* U *is strongly bounded in* X_0*;*

(3) Φ *is uniformly persistent with respect to* $(X_0, \partial X_0)$.

Then there exists a global attractor A_0 for Φ in X_0 relative to strongly bounded sets in X_0, and Φ has a coexistence state $x_0 \in A_0$.

The following result on uniform boundedness will be useful in the proof of the boundedness of periodic solutions. Its proof may be found in [40].

Let

$$\dot{x} = f(t, x), \quad f(t + \omega, x) = f(t, x), \tag{1.14}$$

be a periodic system of equations with period $\omega > 0$ where $f(t, x) \in C(I \times \mathbb{R}^n, \mathbb{R}^n)$

Lemma 1.3. *Assume that the solution of (1.14) is unique for an initial value problem. If the solutions of (1.14) are ultimately bounded on a set B, then the solution of (1.14) are uniformly bounded. This implies that the solution of (1.14) are uniformly ultimately bounded.*

Chapter 2 Literature Review and Preliminaries

In this chapter, we give an overview of what is known about chemostat-like models with inhibition. We also give some general results of selected studies of chemostat models as well as some preliminary results that we will use to prove some of our findings in subsequent chapters. We start with the spatially homogeneous chemostat.

2.1 Introduction

In this study, we assume that the two competing species have equal access to the nutrients. These nutrients are available in excess supply except for one nutrient, S, that is available in limiting supply. Our focus is on this one nutrient, where we study its effect on the survival of the micro-organisms in competition for it. We further assume that the nutrient is growth limiting in the sense that if it were not present, the species would not survive. The micro-organisms take up this nutrient and use it to reproduce - that is the micro-organisms convert the nutrient into additional micro-organisms. The rate of conversion of nutrient into micro-organism is governed by many factors, which are determined by experiments. In literature, this rate is represented by a *consumption term*, with the most widely used terms being Lotka-Voltera and Michaelis-Menten [37]. The nutrient needs to be available in sufficient quantities to ensure survival of the species. Even if there was only one species, the nutrient needs to be sufficient to make it survive.

2.2 Assumptions and Predictions of Chemostat Models

Mathematical models of exploitative competition in a well-stirred chemostat operated under constant input and dilution rates predict competitive exclusion. Competitive exclusion means that only one competitor population avoids extinction (see for instance [6], [8], [20], [36]). That is, in temporally homogeneous (constant operating parameters) and spatially homogeneous (well-stirred chemostat) environment, the model predicts competitive exclusion. Exploitative competition refers to competition for a single essential, non-reproducing, growth limiting nutrient [31].

Standard chemostat models assume that the competition is purely exploitative and the competition is only through the consumption of the nutrient (see for instance [21]). The models are built on the assumption that competing species do not inhibit the growth of each other during the competition. However, it is known that in nature, micro-organisms produce inhibitors against their rivals. Chao and Levin [9], demonstrated that the outcome of competition between *E. Coli* that produces the toxin and the sensitive *E. Coli* was frequency dependent. They found that the E. Coli producing the toxin will be at an advantage only if the bacteria is fairly common. Hsu and Waltman [21], characterized the outcome of plasmid-free and plasmid bearing competition in terms of relevant parameters in hyperbolic cases and used the perturbation of a globally stable steady state for a sufficiently small plasmid loss rate to prove the global asymptotic behaviour of the solutions. They also considered a model of a competition where the plasmid bearing organism produced a toxin at some cost to its reproductive abilities in [23]. Braselton and Waltman [5], analyzed a model that allowed the amount of resource devoted to inhibitor production to depend on the state of the system. In their case, the inhibitor was dynamically allocated. They found that if the stronger competitor spends too much resources on producing the toxin, the weaker competitor may actually win the competition.

2.3 Periodicity in a Chemostat

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 [8], [36], [42]. 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 variable weather patterns [42]. Consider a situation of a fresh water lake that receives its nutrients mainly from streams draining the watershed. As seasons change, stream drainage patterns change contributing to variations in the supply of nutrients. This is particularly true in many fresh water lakes of East Africa. In some cases, the lake vegetation is fed on by beetles that are their natural biological control. The beetles' rate of reproduction and rate of feeding on the vegetation is positively correlated to the temperature of the season (see for instance [13]). During warmer seasons, the nutrient supply is low while in the colder seasons, the opposite is true [31]. Thus the input concentration should be periodic.

With periodic coefficients, Model (1.9) becomes:-

$$\begin{aligned} \dot{S}(t) &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^{2} \frac{\mu_i(t)c_i x_i(t)S(t)}{K_i + S(t)}, \\ \dot{x}_i(t) &= \left(\frac{\mu_i(t)c_i x_i(t)S(t)}{K_i + S(t)} - D_i(t) \right) x_i(t) \\ & S(0) > 0, \quad x_i(0) = x_{i0}, \quad i = 1, 2. \end{aligned} \tag{2.1}$$

where $x_i(t)$, denotes the density of the i^{th} species or biomass at time t, $S(t)$ denotes the nutrient concentration in the water external to the plant cells at time t, $S^0(t)$ is the periodic inflow concentrations at time t, c_i is the content (or concentration) of the nutrient in the tissue of species i, $D_0(t)$ is the rate at which the nutrient leaves the aquatic system, and $D_i(t)$ is the specific

removal and death rate of the i^{th} species at time t

Let us assume that $S^0(t)$ has period $T_p > 0$. Then $D_i(t)$, and $\mu_i(t)$, $i = 1, 2$ need to have periods that are commensurate to that of $S^0(t)$. The outflow rate $D_0(t)$ is also periodic with the same period as that of $S^0(t)$. The seasonal nutrient input concentration is of a form illustrated in Figure 2.3 [31].

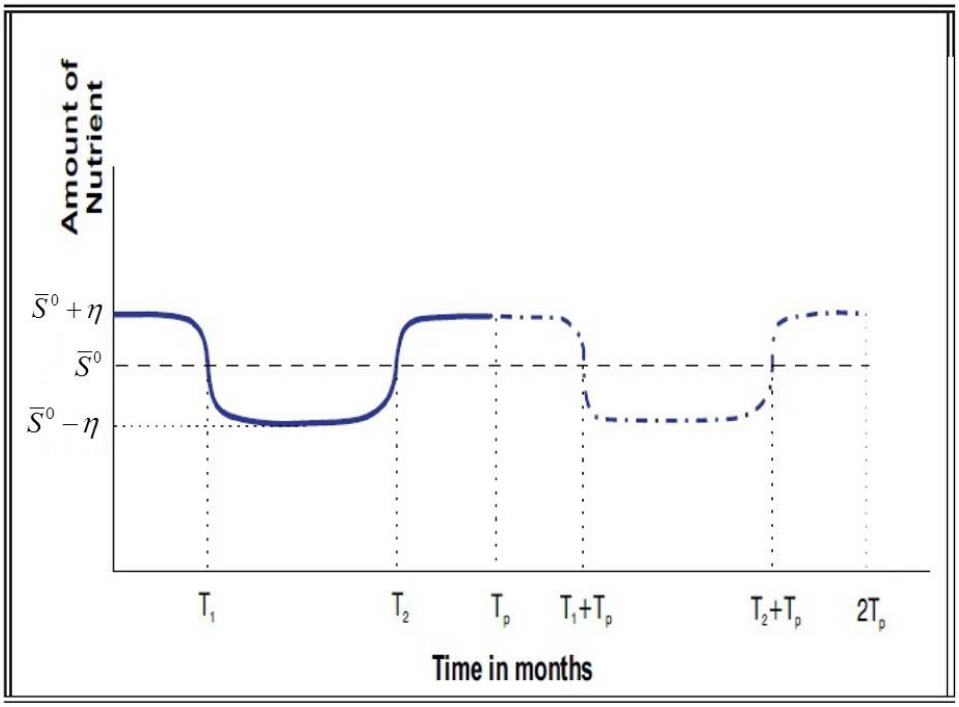

Figure 2.1: Variation of Nutrient Concentration with Time

The nutrient input concentration S^0 is periodic and oscillates about a mean value $\tilde{S^0}$ with an amplitude of η. The amplitude η is assumed to be small compared to $\tilde{S^0}$. Note that $S^0 = \tilde{S^0}$ at time T_1 and T_2 only. A model with this type of nutrient input is discussed in detail in Chapter 4.

The idea of having periodic coefficients in chemostat models is not new. Butler, Hsu and Waltman [7] found that in a model of the chemostat with periodic washout rate, under suitable circumstances, there is coexistence of the competing population. Cushing [12] 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 [43]. Chemostat models become even more interesting when inhibition to the growth of competing species is included.

2.4 Inhibition in the Chemostat

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 Waltman[23] 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 [21]. Hsu et al [22]studied competition in the presence of a lethal external inhibitor, Braselton and Waltman, [5] developed a competition model with dynamically allocated inhibitor production, while Jianhua et al [39] 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. Hsu and Waltman [21] characterized the outcome of plasmid-free and plasmid bearing competition in terms of relevant parameters in hyperbolic cases and used the perturbation of a globally stable steady state for a sufficiently small plasmid loss rate to prove the global asymptotic behaviour of the solutions. They also considered a model of a competition where the plasmid bearing organism produced a toxin at some cost to its reproductive abilities in [23]. Braselton and Waltman [5] analyzed a model that allowed the amount of resource devoted to inhibitor production to depend on the state of the system. In their case, the inhibitor was dynamically allocated. The models addressing inhibition in these models were those of the homogeneous chemostat.

We now look at requirements that must be met for a single species to survive.

2.5 Single Population Growth

Consider the n-dimensional Kolmogorov periodic system

$$\dot{x} = xF_0(t, x), \tag{2.2}$$

where $x = (x_1, x_2, ..., x_n) \in \mathbb{R}^n_+$. We assume that $F_0 = (F_{01}, F_{02}, ..., F_{0n}) : \mathbb{R}^{n+1} \to \mathbb{R}^n$ is continuous and locally Lipschitz in x uniformly for $t \in [0, \omega]$. Further let F_0 be $\omega-$periodic with respect to t ($\omega > 0$), and that the solution $\phi_0(t, x)$ of (2.2) with $\phi_0(0, x) = x$ exists uniquely on $[0, \infty)$. Let $S = \phi_0(\omega, .) : \mathbb{R}^n_+ \to \mathbb{R}^n_+$. Define $S^m(x) := \phi_0(m\omega, x), \forall x \in \mathbb{R}^n_+, m \geq 0$. Lemma 2.1 gives conditions that will make the solution of 2.2 to be positive.

Lemma 2.1. *If for some* $1 \leq i \leq n$,

$$x^*(t) = (x_1^*(t), ..., x_{i-1}^*(t), 0, x_{i+1}^*(t), ..., x_n^*(t))$$

is an $\omega-$*periodic solution of (2.2) with* $x_j^*(0) \geq 0, \forall 1 \leq j \leq n, \ j \neq i$, *and* $x^*(t)$ *satisfies* $\int_0^\omega F_{0i}(t, x^*(t))dt > 0$ *then there exists a* $\delta > 0$ *such that*

$$\limsup_{m\to\infty} d(S^m(x), x^*(0)) \geq \delta, \forall x \in \textit{int}(\mathbb{R}^n_+).$$

Also consider the n-dimensional non autonomous Kolmogorov system

$$\dot{x} = xF(t, x) \ \ 1 \leq i \leq n, \tag{2.3}$$

where $x = (x_1, x_2, ..., x_n) \in \mathbb{R}^n_+$. We assume that $F = (F_1, F_2, ..., F_n) : \mathbb{R}^{n+1} \to \mathbb{R}^n$ is continuous and locally Lipschitz in x. For $s \geq 0$, let $\phi_0(t, s, x) = x_0$ and $\phi(s, s, x) = x$ respectively. Define $T_m := \phi(m\omega, 0, x), \ T(t)x := \phi_0(t, 0, x)$ and $S(x) := T(\omega)x, \forall m \geq$

$0,\ t \geq 0,\ x \in \mathbb{R}^n_+$. Then we have the following lemma showing that solutions of 2.3 are positive.

Lemma 2.2. *Assume that* $\lim_{t\to\infty} |F(t,x) - F_0(t,x)| = 0$ *uniformly for x in any bounded subset of* $\mathbb{R}^n_+$*, and that solutions of (2.2) and (2.3) are uniformly bounded in* $\mathbb{R}^n_+$*. If for some* $1 \leq i \leq n$*,*

$$x^*(t) = (x_1^*(t), ..., x_{i-1}^*(t), 0, x_{i+1}^*(t), ..., x_n^*(t))$$

is an $\omega-$*periodic solution of (2.2) with* $x_j^*(0) \geq 0, \forall 1 \leq j \leq n,\ j \neq i$*, and* $x^*(t)$ *satisfies* $\int_0^\omega F_{0i}(t, x^*(t))dt > 0$ *then*

$$\tilde{W}^s(x^*(0)) \cap \mathit{int}(\mathbb{R}^n_+) = \emptyset$$

where

$$\tilde{W}^s(x^*(0)) = \{x \in \mathbb{R}^n_+ : \lim_{m\to\infty} T_m(x) = x^*(0)\}.$$

Consider equations (2.2) and (2.3) with $n = 1$. This will represent a single population growth model.

2.5.1 Conditions for Persistence of Species

Assume that

A1 $\lim_{t\to\infty} |F(t,x) - F_0(t,x)| = 0$ uniformly for x in any bounded subset of $\mathbb{R}^n_+$, and there exists $K > 0$ such that $F(t,x) \leq 0,$ for $t \geq 0$ and $x \geq K$;

A2 For any $t \geq 0,\ F_0(t,x)$ is strictly decreasing for x, and there exists $K_0 > 0$ such that $F_0(t,K_0) \leq 0,$ for $t \geq 0$ and $x \geq K_0$.

We have the following threshold dynamics for the asymptotically periodic equation (2.3) with $n = 1$.

Lemma 2.3. *Assume that A1 and A2 hold.*

(a) *If* $\int_0^\omega F_0(t,0)dt \leq 0$, *then* $\lim_{t\to\infty} \phi(t,0,x) = 0, \quad \forall x \in \mathbb{R}_+$;

(b) $\int_0^\omega F_0(t,0)dt > 0$ *then* $\lim_{t\to\infty}(\phi(t,0,x) - x^*(t)) = 0, \quad \forall x \in \mathbb{R}_+\backslash\{0\}$, *where* $x^*(t)$ *is the unique positive* $\omega-$*periodic solution of the periodic Kolmogorov equation (2.2) with* $n = 1$.

The proofs of these lemmas can be found in [36].

As an example, for $n = 1$ we have the Kolmogorov equation on single species population growth

$$\frac{dx}{dt} = xF(t,x), \quad x \in \mathbb{R}_+ = [0,\infty), \tag{2.4}$$

and the Kolmogorov periodic equation on single species population growth

$$\frac{dx}{dt} = xF_0(t,x), \tag{2.5}$$

where $F(t,x) : \mathbb{R}^2_+ \to \mathbb{R}$ is continuous and locally Lipschitz in x while $F_0(t,x) : \mathbb{R}^2_+ \to \mathbb{R}$ is continuous, ω-periodic in t (with $\omega > 0$), and also locally Lipschitz in x uniformly for t$\in [0,\omega]$.

Let $\phi(t,s,x)$ with $t > 0$ be the unique solution of (2.4) with the initial condition $\phi(s,s,x) = x$.

Assume that conditions A1 and A2 hold, then Lemma 2.3 may be summarized as:-

$$\text{If} \int_0^\omega F_0(t,0)dt \begin{cases} \leq 0, & \text{there is extinction of the species;} \\ > 0, & \text{the species in System (2.5) is persistent.} \end{cases}$$

In other words, the growth rate of the species needs to be positive for it to survive. If this species is dependent on the availability of a certain nutrient, then the nutrient must be available in such quantities as to make the growth of this species to be positive.

For two species x_1 and x_2 competing for the nutrient, we have the following model that

describes the interaction between the nutrient S and the species.

2.6 Two Species Competition in the Chemostat

The model for two species competing in the chemostat is given by

$$\begin{aligned} \dot{S} &= (S^0 - S)D_0 - \sum_{i=1}^{2} P_i(S)x_i, \\ \dot{x}_i &= x_i(P_i(S) - D_i), \quad i = 1, 2. \end{aligned} \tag{2.6}$$

where $P_i(S)$ is the nutrient uptake function, or the rate at which the nutrient is converted to micro-organisms, D_i is the washout rate or death rate.

For the spatially homogeneous chemostat that is also temporary homogeneous, the death rates of the species are the same as the washout rate of the nutrient. Equations (2.6) may therefore be written as

$$\begin{aligned} \dot{S} &= (S^0 - S)D - \sum_{i=1}^{2} P_i(S)x_i, \\ \dot{x}_i &= x_i(P_i(S) - D), \quad i = 1, 2. \end{aligned} \tag{2.7}$$

It can be shown that for the two species competing for a single nutrient, at most one species will survive (see for instance [8], [30], [20], [32], [37], [42]). If the nutrient is not enough, then both species will not survive as indicated by Lemma 2.3.

Models (2.6) and (2.7) assume that there is no inhibition of the competing species. In some cases, inhibition in the chemostat does take place and some authors have looked at some aspects of inhibition as indicated in the following section.

2.7 Competition with Inhibition

Sometimes, competition between two species is mitigated by the presence of an external inhibitor. Such inhibitors may be introduced into the chemostat, or one of the species might produce toxins that inhibit the growth of competing species. In a situation when one of the competitors is producing a toxin that inhibits the growth of the competitor, the competition model is given by (see for instance [23]):-

$$\begin{aligned} \dot{S} &= (S^0 - S)D - \sum_{i=1}^{2} P_i(S)x_i, \\ \dot{x}_1 &= x_1[P_1(S) - D - f], \\ \dot{x}_2 &= x_2[(1-k)P_2(S) - D], \\ \dot{f} &= kP_2(S)x_2 - Df, \end{aligned} \tag{2.8}$$

where S^0 is the input concentration, D the washout rate, $P_i(S)$ is the uptake function, $f := f(t)$ is the concentration of the toxin present at time t, with x_2 being the toxin producing organism and x_1 being the toxin sensitive organism. System (2.8) may be scaled by setting

$$\overline{S} = \frac{S}{S^0}, \;\; \overline{x}_1 = \frac{x_1}{S^0}, \;\; \overline{x}_2 = \frac{x_2}{S^0}, \;\; \overline{P} = \frac{P}{S^0}, \tau = Dt, \;\; \overline{m}_i = \frac{m_i}{D}, \;\; \overline{a}_i = \frac{a_i}{S^0}, \;\; ' = \frac{d}{d\tau}.$$

Dropping the bars for notational brevity and with this scaling, System (2.8) becomes

$$\begin{aligned} S' &= 1 - S - \sum_{i=1}^{2} P_i(S)x_i, \\ x_1' &= x_1[P_1(S) - 1 - f], \\ x_2' &= x_2[(1-k)P_2(S) - 1], \\ f' &= kP_2(S)x_2 - f, \end{aligned} \tag{2.9}$$

Hsu and Waltman ([21], [23]) have studied this model by analyzing the stability of its equilibrium points and concluded that the desirable organism is a better competitor without producing an inhibitor, and therefore the selective medium may not be important. Further, if x_2 spends too much consumption in producing the inhibitor, x_1 wins in spite of the inhibition. The analysis also found that the inferior competitor can succeed by producing an inhibitor, but only if the initial conditions are suitable. This raises the question:- "what if both species are producing an inhibitor?" This is a question that we will address in Chapter 3 of this thesis.

An improvement of the Model (2.9) is proposed by Braselton and Waltman [5] where the inhibitor is dynamically allocated. They introduced a function $k(x_1, x_2)$ that represents the fraction of potential growth devoted to producing the toxin. The model takes the form

$$\begin{aligned} \dot{S} &= (S^0 - S)D - \sum_{i=1}^{2} P_i(S)x_i, \\ \dot{x}_1 &= x_1(P_1(S) - D - \gamma f), \\ \dot{x}_2 &= x_2((1 - k(x_1, x_2))P_2(S) - D), \\ \dot{f} &= k(x_1, x_2)P_2(S)x_2 - Df, \end{aligned} \tag{2.10}$$

where S^0, S, P, and D are as defined in (2.8). The function $k(x_1, x_2)$ is assumed to be smooth and the interaction between the toxin producing species and the sensitive species (sensitive to the toxin) is of a mass action form. After appropriate non-dimensionalization, the following system of differential equations was obtained:

$$
\begin{aligned}
\dot{S} &= 1 - S - \sum_{i=1}^{2} P_i(S)x_i, \\
\dot{x}_1 &= x_1(P_1(S) - 1 - \gamma f), \\
\dot{x}_2 &= x_2((1 - k(x_1, x_2))P_2(S) - 1), \\
\dot{f} &= k(x_1, x_2)P_2(S)x_2 - f.
\end{aligned} \tag{2.11}
$$

Two types of the function $k(x_1, x_2)$ were used to describe the inhibition. They are given thus:

$$k(x_1, x_2) = \frac{\alpha x_2}{\beta + x_1 + x_2}, \tag{2.12}$$

$$k(x_1, x_2) = \frac{\alpha x_1}{\beta + x_1 + x_2}, \tag{2.13}$$

where (2.12) is monotone increasing in x_2 while (2.13) is monotone increasing in x_1. The constant $\alpha > 0$ may be regarded as a fitting parameter while $\beta > 0$ is an inhibition constant. For Equation (2.12), if x_2 is large, it devotes more of its resources to producing the toxin. If x_1 is not present, the production of the toxin is essentially constant. In Equation (2.13) if x_1 is large, x_2 increase the toxin production since it is already losing the competition and facing extinction - a desperation strategy. This strategy has the advantage that if there is no competition, no energy is wasted on toxin production. Braselton and Waltman [5] studied the rest points and showed that modifying the assumption that production of an allelopathic agent occurs as a constant fraction of the nutrient uptake to the assumption that the production can be dynamically allocated as a function of the state of the system can produce a very different outcome than the expected bi-stable attractors.

In 2.11, we see that only one of the species produces a toxin. The toxin produced by species x_i inhibited the growth of species x_j, $i, j = 1, 2$, $i \neq j$. The toxin production came at a cost to x_i. Supposing the inhibition is a result of growth habits of a species and not production of a

toxin, and the growth habit does not come at a cost to the inhibiting species, will the dynamics of Model (2.6) be the same? What if the inhibition is mutual? Chapter 3 of our study answers these questions.

Apart from mutual inhibition in the chemostat, it is possible for the parameters to be periodic. The model with periodic coefficients is sometimes reffered to as periodic chemostat. We will be interested in mutual inhibition in the periodic chemostat and it is therefore necessary to mention the requirements of the uptake function in the periodic chemostat.

2.8 Growth in a Periodic Chemostat

In the chemostat, the growth of n-species competing for a single nutrient is generally given by

$$\begin{aligned} \dot{S}(t) &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^{n} x_i(t)P_i(t, S(t)), \\ \dot{x}_i(t) &= x_i(t)(P_i(t, S(t)) - D_i(t)) \;\; 1 \leq i \leq n, \end{aligned} \tag{2.14}$$

where $S(t)$ is nutrient concentration at time t, $S^0(t)$ is the input nutrient concentration, $D_0(t)$ is the nutrient dilution rate, $x_i(t)$ 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 and $D_i(t)$ is the specific removal rate (washout rate) of species i.

Model (2.14) is different from (2.6) in that (2.14) assumes $S^0(t), D_0(t)$ and $D_i(t)$ are all continuous, ω-periodic, positive functions and that each $P_i(t, S) : \mathbb{R}^2_+ \to \mathbb{R}_+$ is continuous, ω-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 $S \in \mathbb{R}_+$.

The uptake function $P_i(t, S(t))$ is a Michaelis-Menten type of function that is also referred to as a Holling Type II uptake function. This is the type of function used in this study and is described thus:

$$P_i(t, S(t)) = P_i(S(t)) = \frac{m_i S(t)}{\gamma(a_i + S(t))} \quad i = 1, 2 \tag{2.15}$$

where m_i is called the species specific growth rate of competitor i, a_i is the Michaelis-Menten (or half-saturation) constant, while γ is the yield constant (see for instance [30]). The yield constant represents the number of micro-organisms produced after consumption of one unit of the nutrient. The nutrient consumption rate increases at a decreasing rate with nutrient density until it becomes constant at satiation. Holling Type II functional responses are typical of micro-organisms that specialize on one or a few nutrients.

With appropriate choice of parameters, chemostat models that incorporate periodic coefficients predict coexistence of the competing species. As an example, [7] used bifurcation techniques to show that for the model

$$\begin{aligned} \dot{S}(t) &= (S^0 - S(t))D(t) - \left(\frac{m_1}{y_1}\right)\frac{S(t)x_1(t)}{a_1 + S(t)} - \left(\frac{m_2}{y_2}\right)\frac{S(t)x_2(t)}{a_2 + S(t)}, \\ \dot{x}_i(t) &= x_i(t)\left(\frac{m_i S(t)}{a_i + S(t)} - D(t)\right), \quad i = 1, 2, \\ & \quad x_i(0) \geq 0, \quad S(0) \geq 0, \end{aligned} \tag{2.16}$$

where $S^0, S(t)$, and $D(t)$ are as defined in Equation 2.14, y_i is the yield constant, m_i is the intrinsic growth rate while a_i is the Michaelis-Menten constant, for the i^{th} competitor, a necessary condition for both competitors to go extinct is that

$$\frac{m_i}{a_i + 1} \leq 1, \quad i = 1, 2.$$

Here, D_i is assumed to have a mean value of 1. This extinction occurs regardless of the competition. If we define $\lambda_i := \frac{a_i}{m_i - 1}$ and let m_1 and a_1 be given such that $0 < \lambda_1 < 1$, it can be shown that there exists $\sigma = \sigma(m_1, a_1)$ such that for any $a_2 > \sigma$, m_2 which is taken to be a bifurcation parameter can be chosen such that $\lambda_1 < \lambda_2$ and Equation (2.16) possesses an ω-periodic solution $(S(t), x_1(t), x_2(t))$ (see for instance [7]).

Periodicity in the chemostat may be introduced by a periodic function either in the nutrient input concentration, washout (or death) rate, or in the nutrient uptake function. Wolkowicz and Zhao ([36]) introduced periodicity in the chemostat by using a simple cosine function to describe nutrient input and dilution rates. They obtained results similar to those of [7].

In all these studies where periodicity is introduced in the chemostat, none has addressed any form of inhibition. In addition, the functions used to introduce periodicity do not mimic what is observed in nature closely. It is for this reason that we introduce periodicity in Model (2.14) through a Cosine Fourier Series in chapter 4.

2.9 Statement of the Problem

While situations where mutual inhibition to the growth of a competitor as a result of the natural growth of the two competing species exists in chemostat-like systems, there is no mathematical model that addresses such a situation.

2.10 Objectives of the study

The broad objective of this study is to develop and analyze a chemostat-like model where mutual inhibition is caused by the natural growth habits of the two species competing for a single growth limiting nutrient.

Specific Objectives

The specific objectives are as follows:

(1) To develop a periodic Kolmogorov system of Ordinary Differential Equations that describe mutual inhibition in a two-species chemostat-like system, where the two species are competing for a single essential nutrient.

(2) To study the dynamics of the model developed in (1).

(3) To describe periodic nutrient input and dilution rates that make persistence of the two competing species possible.

(4) To find out if persistence found in (3) will hold in the mutually inhibiting periodic chemostat-like system.

2.11 Methods of Study

This study combines both analytic and numerical methods to dicuss mutual inhibition in a chemostat. We shall use the following:

(1) Global asymptotic stability theorems to analyze the various rest points present in the dynamical system describing mutual inhibition in chemostat-like systems.

(2) Introduce periodicity in the chemostat by using a Fourier series.

(3) Apply the theory of asymptotically periodic semiflows and comparison methods and demonstrate that uniform persistence of the competing species is possible.

(4) Describe mutual inhibition in the periodic chemostat and use comparison theorems to show that competitive exclusion always holds.

(5) Finally use Matlab to numerically solve the given models and present graphical simulations of the results.

Chapter 3 Mutual Inhibition in a Chemostat

3.1 Introduction: Mutual Inhibition

Mutual inhibition is a form of direct competition between populations of two species in which both actively inhibit the growth of each other [2]. It is a different type of competition from the indirect competition that comes about through the nutrient.

In this chapter, we discuss a chemostat-like model with mutual inhibition. We then analyze the stability of rest points of the model.

3.2 The Model

The model for competition for single, essential growth limiting nutrient with mutual inhibition is described as follows:-

$$\begin{aligned} \dot{S} &= (S^0 - S(t))D - \sum_{i=1}^{2} x_i(t) P_i(S(t)) g_i(x_1(t), x_2(t)), \\ \dot{x_i} &= x_i(t) \left\{ P_i(S(t)) g_i(x_1(t), x_2(t)) - D \right\}, \quad i = 1, 2, \\ & \qquad x_i(0) = x_{i0} \geq 0, \quad S(0) \geq 0, \quad x_i(t) \in \mathbb{R}_+ = [0, \infty), \end{aligned} \tag{3.1}$$

where $g_i(x_1(t), x_2(t))$ represents the degree of inhibition to the growth of species i and other variables are as defined in Section 1.1.

3.2.1 Conditions for Inhibition Function - B1

We assume that $g_i(x_1(t), x_2(t))$ is a continuous function in $(x_1, x_2) \in \mathbb{R}^2_+$ and satisfies the following conditions **B1**:-

(i) $g_i(x_1(t), x_2(t)) : \mathbb{R}^2_+ \to \mathbb{R}_+ \in [0, 1]$;

(ii) $g_i(x_1(t), x_2(t))$ is strictly increasing in x_i and strictly decreasing in $x_j \;\; i, j = 1, 2, \;\; i \neq j$;

(iii) $g_i(x_1(t), x_2(t)) \approx 1$ for $x_j = 0, \quad i \neq j$ and for all $t \geq 0$.

Condition B1(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. A decrease in the value of $g_i(x_1(t), x_2(t))$ implies greater levels of inhibition to the growth of species i and vice versa. Condition B1(ii) makes physical sense because we expect increasing biomass of x_i to cause a greater inhibition effect on $x_j, i \neq j$, 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 B1(iii) implies.

A reasonable function describing $g_i(x_1(t), x_2(t))$ as suggested in [27] is given by

$$g_i(x_1(t), x_2(t)) = \frac{\alpha_i x_i}{\beta_i + x_i + x_j}, \quad i, j = 1, 2, \quad i \neq j. \tag{3.2}$$

Clearly $g_i(x_1(t), x_2(t))$ satisfies Condition B1. The positive constant α_i is the inhibition constant and is a measure of how effective the inhibition is. The constant $\beta_i > 0$ may also be interpreted as the degree of self-inhibition in species x_i. It is the density required to produce half of the maximum inhibition. For example, in a forest where trees are tall, the branches at the top cause shading of the branches below which makes the leaves of those branches at the bottom to start

yellowing and hence reducing the total biomass, that could be interpreted as inhibition to the increase in biomass. In this study, we assume that β_i is small to maintain a stricter ratio dependence as required by Condition B1. We choose α_i and β_i in such a way that $g_i(x_1(t), x_2(t)) \in [0, 1]$ and $g_i(x_1(t), x_2(t)) \approx 1$ for $x_j = 0, \quad i \neq j$ for all $t \geq 0$. Without loss of generality, for $x_i > 0$ and $x_j \geq 0$, we can choose $\alpha_i = 1$ and $\beta_i = 0$ so that the inhibition function is described by

$$g_i(x_1(t), x_2(t)) = \frac{x_i}{x_i + x_j}, \quad i = 1, 2, \quad j = 1, 2, \quad i \neq j. \tag{3.3}$$

Clearly, this function satisfies all the requirements in Condition B1. Specifically,

$g_i(x_1(t), x_2(t)) = 1$ for $x_j = 0, \quad i \neq j$ and for all $t \geq 0$.

The relationship between the density of the two competing species and their inhibition ability is summarized in Figure 3.1:-

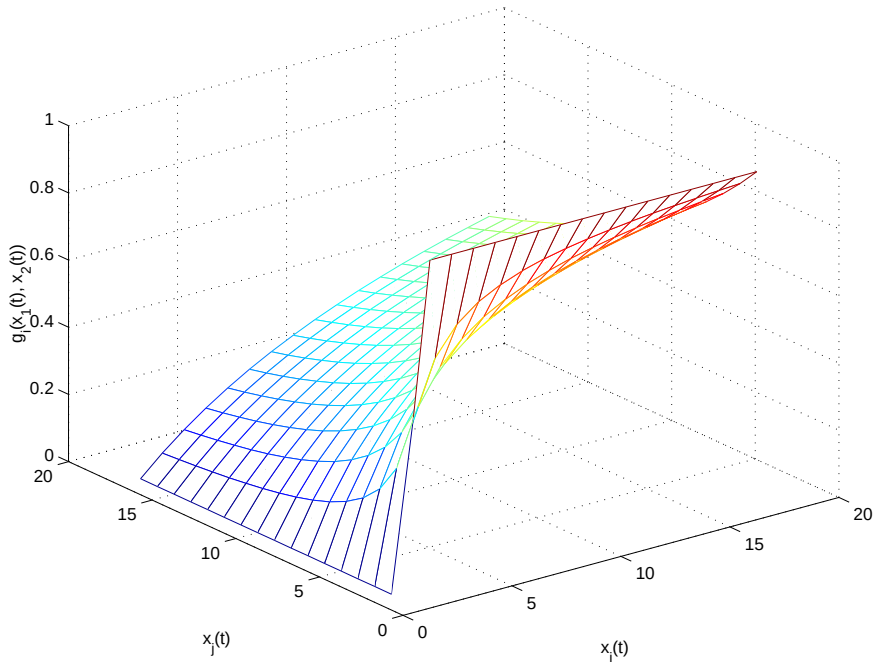

Figure 3.1: Relationship between density of Competing Species and Inhibition

Clearly, as $x_i(t)$ increases $g_i(x_1(t), x_2(t))$ increases and as $x_j(t)$ increases $g_i(x_1(t), x_2(t))$ decreases.

Equation (3.1) is a more basic model of the chemostat as other models developed so far may be obtained from it by choosing $g_i(x_1(t), x_2(t))$ appropriately. For example, if we let $g_1(x_1(t), x_2(t)) = g_2(x_1(t), x_2(t)) = 1$, the Equation(3.1) reduces to Equation (2.6) which is the standard chemostat model without inhibition. A discussion of this case may be found for instance in [30], [36] and [42].

The uptake function is assumed to be a Holling type II function of the form

$$P(S(t)) = \frac{mS(t)}{a + S(t)}, \tag{3.4}$$

where m is the maximal growth rate and a is the Michaelis-Menten constant [30].

With the explicit functions in (3.2) and (3.4), the system in Equation (3.1) may be written as

$$\begin{aligned} \dot{S} &= (S^0 - S(t))D - \sum_{i=1}^{2} x_i \frac{m_i S(t)}{(a_i + S(t))} \frac{\alpha_i x_i}{(\beta_i + x_i + x_j)}, \\ \dot{x_i} &= x_i(t) \left\{ \frac{m_i S(t)}{(a_i + S(t))} \frac{\alpha_i x_i}{(\beta_i + x_i + x_j)} - D \right\}, \quad i = 1, 2, \quad i \neq j, \\ & \quad x_i(0) = x_{i0} \geq 0, \quad S(0) \geq 0. \end{aligned} \tag{3.5}$$

To simplify the analysis of Equation (3.5), we reduce the number of parameters by non-dimensionalizing it using the following dimensionless quantities:-

$$\bar{S} = \frac{S}{S^0}, \quad \bar{x_i} = \frac{x_i}{S^0}, \quad \bar{m_i} = \frac{m_i}{D}, \quad \bar{\beta_i} = \frac{\beta_i}{S^0}, \quad \bar{a_i} = \frac{a_i}{S^0}, \quad \tau = Dt, \quad ' = \frac{d}{d\tau}. \tag{3.6}$$

Using Equation (3.6) in Equation (3.5) and dropping the bars for purposes of notational brevity, we obtain

$$\begin{aligned} \dot{S} &= 1 - S - \sum_{i=1}^{2} x_i P_i(S(t)) g_i(x_1, x_2), \\ \dot{x_i} &= x_i \left\{ P_i(S(t)) g_i(x_1, x_2) - 1 \right\}, \quad i = 1, 2. \end{aligned} \tag{3.7}$$

where the dot here refers to the derivative with respect to τ. The dynamics of (3.7) are qualitatively the same as those of (3.1) and hence we study (3.7) for convenience.

3.3 Analysis of the Model

We look at the boundary rest point and the positive interior rest points. The nature of the parameters in (3.7) are such that the positive cone $(S(t), x_1(t), x_2(t))$ is positively invariant. This means that if the Equation is given positive initial conditions then the two components of the solution remain positive for all finite time. If we let $z(t) := S(t) + x_1(t) + x_2(t)$ then we clearly see that $\dot{z} = 1 - z(t)$, and $\dot{z} \leq -z(t)$. The fact that each component of $z(t)$ is non-negative and by the variation of constants formula, $\dot{z} = 1 - z(t)$ satisfies

$$\lim_{t \to \infty} z(t) = 1,$$

we have that each component of the solution is bounded and there is no explosion in the growth of the competing species. In order to understand the dynamics of (3.7), we need to find the rest points for the Equation. These rest points are the solutions of the following system of equations:-

$$\begin{aligned} 1 - S - x_1 P_1(S) g_1(x_1, x_2) - x_2 P_2(S) g_2(x_1, x_2) &= 0, \\ x_1 \left\{ P_1(S) g_1(x_1, x_2) - 1 \right\} &= 0, \\ x_2 \left\{ P_2(S) g_2(x_1, x_2) - 1 \right\} &= 0. \end{aligned} \tag{3.8}$$

Proposition 3.1. *The boundary rest point* $(1,0,0)$ *always exists and is globally asymptotically stable.*

This rest point represents the state where the nutrient is present but with no species to consume it. The proposition states that if the species are not present, then the nutrient will always be present.

Proof. The variational matrix of Equation (3.7) is given by

$$\begin{bmatrix} -1-x_1P_1'g_1-x_2P_2'g_2 & -P_1g_1-x_1P_1g_{1x_1}-x_2P_2g_{2x_1} & -P_2g_2-x_1P_1g_{1x_2}-x_2P_2g_{2x_2} \\ x_1P_1'g_1 & -1+P_1g_1+x_1P_1g_{1x_1} & x_1P_1g_{1x_2} \\ x_2P_2'g_2 & x_2P_2g_{2x_1} & -1+P_2g_2+x_2P_2g_{2x_2} \end{bmatrix} \tag{3.9}$$

where, for brevity, we have used $x_i := x_i(t)$, $P_i := P_i(S)$, $P_i' = \frac{dP_i(S)}{dS}$, $g_i = g_i(x_1(t),x_2(t))$ and $g_{ix_j} = \frac{\partial}{\partial x_j}g_i(x_1(t),x_2(t))$, $i,j=1,2$.

From (3.2), we see that $g_i(0,0)=0, g_{ix_i}=\frac{\alpha_i}{\beta_i}$ and $g_{ix_j}=0$, $i,j=1,2, i\neq j$. These values give one of the solutions of (3.8) as $(S,x_1,x_2)=(1,0,0)$. By the Existence and Uniqueness Theorem, this is always a solution of Equation (3.8). Substituting the rest point $(1,0,0)$ in (3.9) we see that the variational matrix has -1 as an eigenvalue of multiplicity 3. Thus the rest point (1,0,0) is asymptotically stable which concludes the proof.

□

Theorem 3.2. *Let*

$$g_1(x_1(t),x_2(t)) = \frac{1}{P_1(S(t))} \text{ and } S(t)>0.$$

Then there is a boundary rest point $(1-x_1^*,x_1^*,0)$ *with* $x_1^*=\frac{\beta_1}{\alpha_1-1}$ *that is globally asymptotically*

stable provided that

$$\frac{a_1 m_1(\alpha_1 - 1)^2}{\alpha_1(m_1 - 1)^2} < \beta_1 < (\alpha_1 - 1)$$

and unstable otherwise.

Proof. If $g_1(x_1(t), x_2(t)) = \frac{1}{P_1(S(t))}$, then (3.8) becomes

$$\begin{aligned} 1 - S - x_1 - x_2 P_2(S) g_2(x_1, x_2) &= 0, \\ 0x_1 &= 0, \\ x_2 \left\{ P_2(S) g_2(x_1, x_2) - 1 \right\} &= 0. \end{aligned}$$

Clearly, x_1 is an arbitrary constant and we let $x_1 = x_1^* \neq 0$. It then follows that one of the solutions of (3.8) is $(S, x_1, x_2) = ((1 - x_1^*), x_1^*, 0)$. x_1 is a boundary rest point if we take $x_2 = 0$. Given that at this rest point $x_2 = 0$, we have the inhibition term defined as

$$g_1(x_1^*(t), 0) = \frac{\alpha_1 x_1^*}{\beta_1 + x_1^*} = 1$$

for β_1 small and in adherence to Condition **B1**(iii). This implies that $\alpha_1 x_1^* = \beta_1 + x_1^*$ or

$$x_1^* = \frac{\beta_1}{\alpha_1 - 1}. \tag{3.10}$$

It follows from the first equation in (3.8) that $S = 1 - x_1^* = 1 - \frac{\beta_1}{\alpha_1 - 1}$ or

$$S = \frac{\alpha_1 - (\beta_1 + 1)}{\alpha_1 - 1} \tag{3.11}$$

where we require $\alpha_1 > \beta_1 + 1$ to ensure that S is non negative.

Equations (3.10) and (3.11) mean that the rest point

$$\left(\frac{\alpha_1-(\beta_1+1)}{\alpha_1-1},\frac{\beta_1}{\alpha_1-1},0\right)$$

exists.

Using the triple $((1-x_1^*),x_1^*,0)$ and condition B1(iii) in (3.9) the variation matrix becomes;

$$\begin{bmatrix} -1-x_1^*P_1' & -1-x_1^*g_{1x_1^*} & -x_1^*P_1g_{1x_2^*} \\ x_1^*P_1' & x_1^*g_{1x_1^*} & x_1^*g_{1x_2^*} \\ 0 & 0 & -1 \end{bmatrix}$$

whose eigenvalues are $(\lambda_1,\lambda_2,\lambda_3)=(-1,-1,\xi_1)$ where $\xi_1=x_1^*g_{1x_1^*}-x_1^*P_1'$. The point $((1-x_1^*),x_1^*,0)$ is globally asymptotically stable provided $\xi_1<0$; that is, $x_1^*g_{1x_1^*}-x_1^*P_1'<0$ which requires

$$g_{1x_1^*}<P_1'. \tag{3.12}$$

Now, from Equations (3.2) and (3.4) we find

$$\begin{aligned} g_{ix_i}(x_1(t),x_2(t)) &= \frac{\alpha_i(\beta_i+x_j(t))}{(\beta_i+x_i(t)+x_j(t))^2}, \\ g_{ix_j}(x_1(t),x_2(t)) &= \frac{-\alpha_i x_i(t)}{(\beta_i+x_i(t)+x_j(t))^2}, \\ P_i'(S(t)) &= \frac{m_ia_i}{(a_i+S(t))^2}, \quad i,j=1,2. \end{aligned} \tag{3.13}$$

Clearly,

$$g_{1x_1}(x_1^*(t),0)=\frac{(\alpha_1-1)^2}{\alpha_1\beta_1}. \tag{3.14}$$

We note that at the rest point, since $g_1(x_1(t),0)=1$ and $g_1(x_1^*(t),x_2^*(t))=\frac{1}{P_1(S(t))}$ it will follow

that $P_1(S) = 1$. This means that $\frac{m_1 S}{a_1+S} = 1$ and $S(m_1 - 1) = a_1$ or

$$S = \frac{a_1}{m_1 - 1}.$$

Clearly, from Equation (3.4), $P_1'(S) = \frac{m_1 a_1}{(a_1+S)^2}$ and at the rest point, this becomes

$$P_1'(S) = \frac{(m_1 - 1)^2}{a_1 m_1} \tag{3.15}$$

Combining equations (3.12), (3.14) and (3.15), the global asymptotic stability of the rest point is guaranteed if

$$\frac{(\alpha_1 - 1)^2}{\alpha_1 \beta_1} < \frac{(m_1 - 1)^2}{(a_1 m_1)}$$

or

$$\frac{a_1 m_1 (\alpha_1 - 1)^2}{\alpha_1 (m_1 - 1)^2} < \beta_1.$$

For positivity, we require $\alpha_1 - 1 > \beta_1$ which implies that

$$\frac{a_1 m_1 (\alpha_1 - 1)^2}{\alpha_1 (m_1 - 1)^2} < \beta_1 < (\alpha_1 - 1)$$

which completes the proof.

□

Corollary 3.3. *Let*

$$g_2(x_1^*(t), x_2^*(t)) = \frac{1}{P_2(S(t))}.$$

Then the rest point

$$\left(\frac{\alpha_2 - (\beta_2 + 1)}{\alpha_2 - 1}, 0, \frac{\beta_2}{\alpha_2 - 1} \right)$$

exists and is globally asymptotically stable if

$$\frac{a_2 m_2 (\alpha_2 - 1)^2}{\alpha_2 (m_2 - 1)^2} < \beta_2$$

and unstable otherwise.

Conjecture 3.4. *When*

$$g_1(x_1^*(t), x_2^*(t)) = \frac{1}{P_1(S(t))} \text{ and } g_2(x_1^*(t), x_2^*(t)) = \frac{1}{P_2(S(t))},$$

Equation (3.7) does not admit an interior rest point.

Conjecture 3.4 simply implies that with mutual inhibition, coexistence of the two competing species is not possible. This result agrees with earlier studies that concluded coexistence is not possible in the spatially homogeneous chemostat without inhibition. These conclusions may be found for instance in [30]and [20].

3.4 Numerical Results

To demonstrate Conjecture 3.4, we present numerical results in three steps. The first result represented by Figure 3.2 represents competition when $g_2(x_1^*(t), x_2^*(t))P_2(S(t))$ is *slightly* greater than $g_1(x_1^*(t), x_2^*(t))P_1(S(t))$. Then Figure 3.3 is the numerical result when $g_2(x_1^*(t), x_2^*(t))P_2(S(t)) = g_1(x_1^*(t), x_2^*(t))P_1(S(t)) = 1$ and Figure 3.4 is the result when $g_2(x_1^*(t), x_2^*(t))P_2(S(t))$ is *slightly* less than $g_1(x_1^*(t), x_2^*(t))P_1(S(t))$.

These numerical results are obtained using the following parameter values in Equation (3.7)

Table 3.1: Parameter values used in the plots of Figures 3.2, 3.3 and 3.4

Parameter	a_1	α_1	β_1	m_1	a_2	α_2	β_2	m_2	x_{10}	x_{20}	S^0
Figure 3.2	$\frac{1}{11}$	1.68312234	0.0002	1.296317	$\frac{3}{110}$	1.71213833	0.0001	1.2	$\frac{5}{11}$	$\frac{5}{11}$	1
Figure 3.3	$\frac{1}{11}$	1.68312234	0.0002	1.296318	$\frac{3}{110}$	1.71213833	0.0001	1.2	$\frac{5}{11}$	$\frac{5}{11}$	1
Figure 3.4	$\frac{1}{11}$	1.68312234	0.0002	1.296319	$\frac{3}{110}$	1.71213833	0.0001	1.2	$\frac{5}{11}$	$\frac{5}{11}$	1

We note that there is a very slight difference in the parameter values for Figures 3.2, 3.3

and 3.4. Basically all the values are the same except for m_1 which increases successively by 0.000001. In Figure 3.2, x_2 wins the competition while in Figure 3.4, x_1 wins. This is consistent

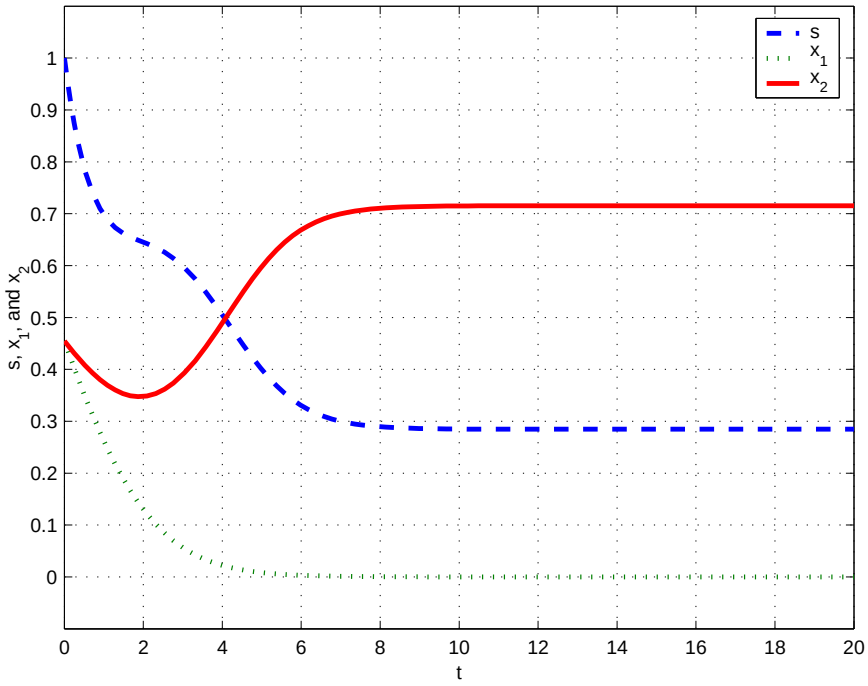

Figure 3.2: Competition with $g_1(x_1^*(t), x_2^*(t))P_1(S(t))$ *slightly* less than $g_2(x_1^*(t), x_2^*(t))P_2(S(t))$.

with Theorem 3.2.

In Figure 3.3, there is no winner and both species become extinct in the long run. This remains the case however much the nutrient input concentration is increased. The lack of coexistence between the two species implies lack of an interior rest point.

The result in Theorem 3.4 is consistent with previous studies involving the chemostat where, with constant operating parameters, coexistence is not possible. The fact that there is no coexistence even when nutrient concentration is increased suggests that for coexistence to occur, some change in the nature of parameters needs to be implemented. We set about changing the nature of these parameters in the next chapter.

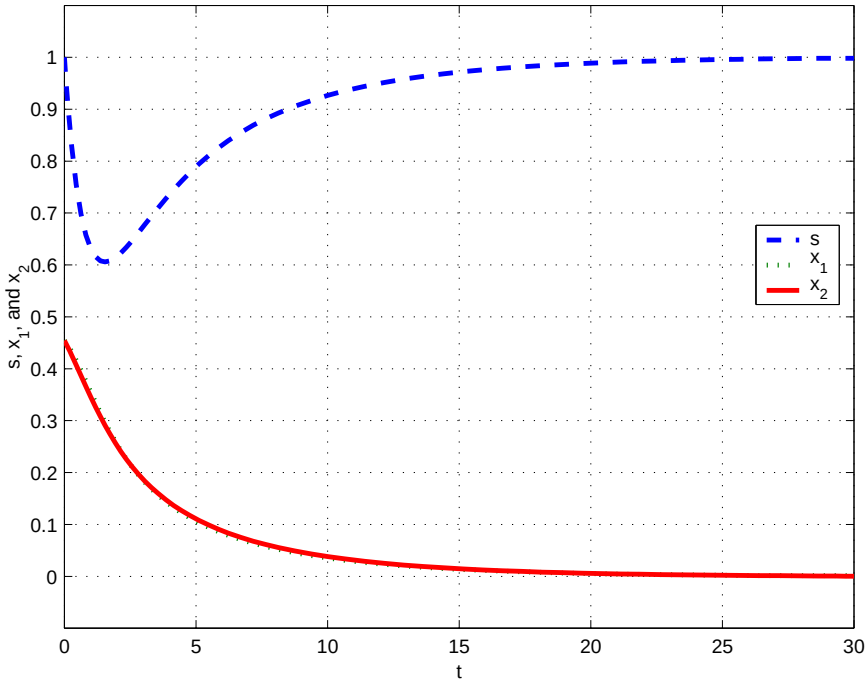

Figure 3.3: Competition with $g_1(x_1^*(t), x_2^*(t))P_1(S(t)) = g_2(x_1^*(t), x_2^*(t))P_2(S(t)) = 1$.

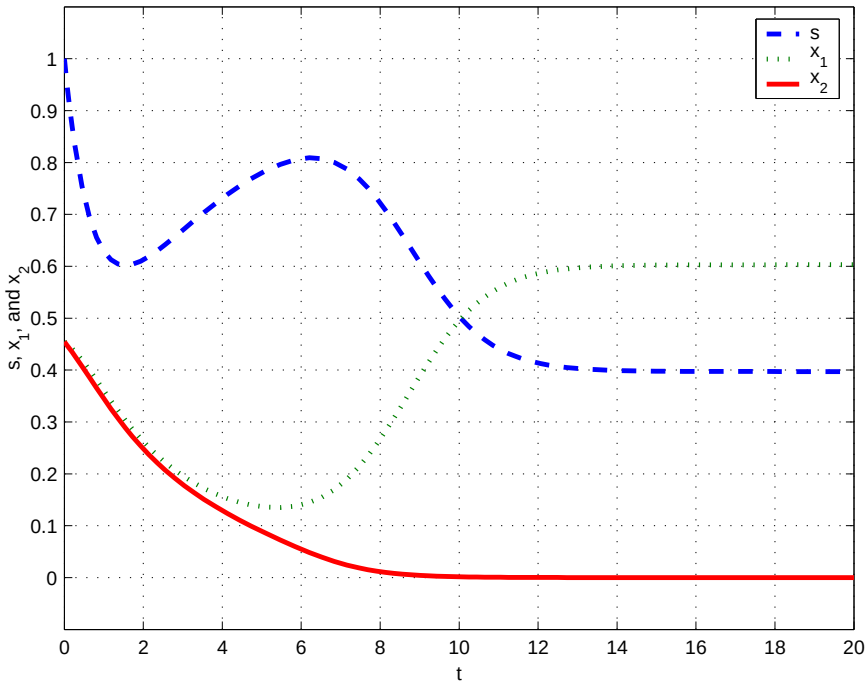

Figure 3.4: Competition with $g_1(x_1^*(t), x_2^*(t))P_1(S(t))$ *slightly* greater than $g_2(x_1^*(t), x_2^*(t))P_2(S(t))$.

Chapter 4 The Periodic Chemostat-like System

4.1 Introduction

In this chapter, we consider the chemostat-like model where nutrient supply, specific death rates and species-specific nutrient uptake function are assumed to be periodic with commensurate periods. We assume a periodic input function envisaged by [31] but use a different way of introducing this periodicity. In this study, we describe nutrient uptake function and washout rate using a Fourier series type of function. This type of series mimics nature more closely because, at least in the tropics, the warm season is generally warm for prolonged periods of time. The cold season is also cold for prolonged periods of time. Hence a Fourier series is more appropriate for modeling systems that may be affected by temperatures. We show that the system using Fourier series results in the persistence of the competing species, hence agreeing with previous studies.

We now present the model of a chemostat-like system with periodic coefficients.

4.2 The Model

The model incorporating periodic coefficients takes the following form:

$$\begin{aligned}
\dot{S}(t) &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^{2} c_i P_i(t, (S(t)x_i(t))), \\
\dot{x}_i(t) &= (P_i(t, S(t)) - D_i(t))x_i(t) \qquad (4.1) \\
& S(0) = S^0 > 0, \quad x_i(0) = x_{i0}, \quad i = 1, 2.
\end{aligned}$$

where $x_i(t)$, denotes the density of the i^{th} species or biomass at time t, $S(t)$ denotes the nutrient concentration in the water external to the plant cells at time t, $S^0(t)$ is the periodic inflow concentrations at time t, c_i is the content (or concentration) of the nutrient in the plant tissue of species i. Here, $D_0(t)$ is the rate at which the nutrient enters and leaves the aquatic system, and $D_i(t)$ is the specific removal and death rate of the i^{th} species at time t. The function

$$P_i(t, S(t)) := \frac{m_i(t)S(t)}{a_i + S(t)},$$

is similar to a Holling type II function (see for instance [27]), describes the per capita nutrient uptake rate of the i^{th} species. The variable $m_i(t)$ is the maximal specific growth rate of the i^{th} species at time t, a_i is the half saturation constant for nutrient-limited growth for the i^{th} species. The model structure of Equation (4.1) that originates from the chemostat theory is suitable for modeling aquatic systems, since all the parameters involved in it can be measured in the field see ([20], [33], [34]).

Let $S^0(t)$ represent the periodic input concentration, which fluctuates about a mean value, $\tilde{S^0}$. Then, we may define the nutrient input concentration as

$$S^0(t) = \begin{cases} \tilde{S}^0 + \eta, & 0 \le t \le T_1; \\ \tilde{S}^0 - \eta, & T_1 \le t \le T_2; \\ \tilde{S}^0 + \eta, & T_2 \le t \le T_p. \end{cases} \qquad (4.2)$$

The period is T_p, which could be measured in weeks or months and $\eta > 0$ indicates the deviation from the mean value $\tilde{S}^0$. The nutrient concentration is below the mean between T_1 and T_2 where T denotes time. Since $S^0(t)$ as depicted in Figure 2.3 on Page 16 is even, it can be represented by a Fourier series of the form,

$$S^0(t) = \tilde{S}^0 + \eta + 2\eta\frac{(T_1 - T_2)}{T_p} + \alpha(t), \tag{4.3}$$

where

$$\alpha(t) = \sum_{n=1}^{\infty} \frac{4\eta}{n\pi}\cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right)\sin\left(\frac{n\pi}{T_p}(T_1 - T_2)\right)\cos\frac{2\pi nt}{T_p}. \tag{4.4}$$

From Equation (4.4) we observe that $|\alpha(t)| \leq \frac{4\eta}{\pi}$. The nutrient supplied at any instant satisfies the inequality

$$S^0(t) - |\alpha(t)| \leq S^0(t) \leq S^0(t) + |\alpha(t)|\,.$$

We know for practical purposes that $S^0(t) > \frac{4\eta}{\pi}$. This condition means that the amplitude of nutrient fluctuation about $\tilde{S}^0$ must be small in comparison to $S^0(t)$. Also,

$$D_0(t) = \tilde{D}_0 + \eta_0 + 2\eta_0\frac{(T_1 - T_2)}{T_p} + \alpha_0(t), \tag{4.5}$$

where $\tilde{D}_0$ is the mean inflow rate, η_0 indicates the deviation from the mean value $\tilde{D}_0$, and $\alpha_0(t)$ is similar to $\alpha(t)$ in (4.4) with η replaced by η_0. We can understand the relationship between the periodicity of $S^0(t)$ and that of the death rate $D_i(t)$ of species x_i by observing what happens in nature. Generally, the death rate of species from nutrient deficiency decreases when the nutrient increases and vice-versa. It is therefore natural to expect the variation of the death rate from the mean to decrease when the deviation of the nutrient from the mean input increases. This suggest

that the death rate $D_i(t)$ of species x_i should deviate from the mean death rate, $\tilde{D_{i0}}$, as follows:-

$$D_i(t) = \begin{cases} \tilde{D}_{i0} - \eta_i, & 0 \leq t \leq T_1; \\ \tilde{D}_{i0} + \eta_i, & T_1 \leq t \leq T_2; \\ \tilde{D}_{i0} - \eta_i, & T_2 \leq t \leq T_p \end{cases} \tag{4.6}$$

$i = 1, 2$ where $\eta_i > 0$, are non-negative constants and $\alpha_i(t)$ is similar to $\alpha(t)$ in (4.4) with η replaced by $-\eta_i$. Thus,

$$D_i(t) = \tilde{D}_{i0} - \eta_i - 2\eta_i \frac{(T_1 - T_2)}{T_p} + \alpha_i(t), \tag{4.7}$$

where, without loss of generality, we have assumed that the period of $D_0(t)$ and $D_i(t)$ are the same.

In most of the previous analytical studies of the periodic chemostat, the powerful theory of monotone dynamical systems was applied to limiting systems obtained using certain conservation principles. However, the theory of monotone dynamical systems can only be applied in this context to study the competition between at most two species. Also, in order to apply a conservation law to obtain the limiting systems, it is necessary to assume that all the removal rates are equal, thus ignoring all the species-specific death rates and only considering the dilution rate.

Here, we apply the theory of asymptotically periodic semiflows and a comparison method as given in [11] to determine criteria that guarantee the existence of at least one positive periodic solution for the full system and the uniform persistence of all the interacting species.

4.3 Analysis of the Model

If we let $\overline{x}_i(t) = c_i x_i(t)$ and ignore the bars for notational brevity, Equation (4.1) becomes

$$\begin{aligned} \dot{S}(t) &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^{2} P_i(t, S(t))x_i(t), \\ \dot{x}_i(t) &= (P_i(t, S(t)) - D_i(t))x_i(t) \\ & S(0) > 0, \quad x_i(0) = x_{i0}, \quad i = 1, 2. \end{aligned} \tag{4.8}$$

Throughout this study, we identify the unique solution of Equation (4.8) by the set

$$(S(t), x_1(t), x_2(t)) \in \mathbb{R}^3_+, \quad S \geq 0, \quad x_i \geq 0, \quad 1 \leq i \leq 2,$$

where $\mathbb{R}^3_+$ is a real 3-dimensional non-negative vector space. By asserting that $(S(t), x_1(t), x_2(t))$ is positive, we mean that each component of the solution is positive for all $t > 0$.

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

$$\dot{V}(t) = S^0(t)D_0(t) - D(t)V(t), \quad V(0) \geq 0, \tag{4.9}$$

has a unique positive $\omega-$periodic solution $V^*(t)$ such that every solution $V(t)$ of (4.9) with $V(0) \geq 0$ satisfies

$$\lim_{t\to\infty}(V(t) - V^*(t)) = 0.$$

Indeed, $V^*(t)$ is given by

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

Let $\overline{D}(t) = \max\{D_0(t), D_1(t), D_2(t)\}$ and $\underline{D}(t) = \min\{D_0(t), D_1(t), D_2(t)\}$. Clearly $\overline{D}(t)$ and $\underline{D}(t) : \mathbb{R}_+ \to \mathbb{R}_+$ are continuous, ω-periodic and positive functions. Let $V_1^*(t)$ and $V_2^*(t)$ be the unique positive ω-periodic solutions of (4.9) with $D(t)$ replaced by $\underline{D}(t)$ and $\overline{D}(t)$ respectively. By the comparison theorem and the global attractivity of $V_i^*(t)$, it easily follows that $V_2^*(t) \leq V_1^*(t), \forall t \geq 0$.

This leads to the following result.

Theorem 4.1. *Assume that*

(1) $\int_0^\omega (P_i(t, V_1^*(t)) - D_i(t))dt > 0, \quad i = 1, 2;$

(2) $\int_0^\omega (P_i(t, V_2^*(t) - x_j^*(t)) - D_i(t))dt > 0, \quad i, j = 1, 2, j \neq i$ *where* $x_j^*(t)$ *is the unique positive* ω*-periodic solution of the scalar periodic equation*

$\dot{x}_j = x_j(P_j(t, V_1^*(t) - x_j) - D_j(t)).$

Then Equation (4.8) admits a positive ω*-periodic solution, and there exists* $\alpha > 0$ *and* $\eta > 0$ *such that any solution* $(S(t), x_1(t), x_2(t))$ *of (4.8) satisfies*

$0 < \alpha \leq \liminf_{t\to\infty} \ x_i(t) \leq \limsup_{t\to\infty} \ x_i(t) \leq \eta, \quad i = 1, 2.$

Proof. We first show that the solution to Equation (4.8) is positive.

Lemma 2.3(b), implies that the periodic equation

$$x_i(P_i(t, V_1^*(t) - x_i) - D_i(t)), \quad i = 1, 2,$$

admits a unique $\omega-$periodic solution $x_i(t)$ that is globally attractive in $\mathbb{R}_+\backslash 0$. We further claim that $V_1^*(t) > x_i^*(t), \forall \ t \in [0, \omega]$. Indeed, let $x_i^*(t_1) = \max_{0\leq t\leq\omega} x_i^*(t), \quad t_1 \in [0, \omega], \quad i = 1, 2$. Then $\dot{x}_i^*(t_1) = 0$, and hence

$$P(t_1, V^*(t_1) - x_i^*(t_1)) = D_1(t_1) > 0.$$

Since $P(t_1, s)$ is strictly increasing for $s \in \mathbb{R}$, $V_1^*(t_1) > x_i^*(t_1)$. Let $y(t) = V_1^*(t) - x_1^*(t)$. Then $y(t)$ satisfies the periodic differential equation

$$\dot{y} = S^0(t)D_0(t) - \underline{D}(t)V_1^*(t) - (V_1^*(t) - y)(P(t, y) - D_1(t)). \tag{4.10}$$

Since $y(t_1) > 0$ and

$$\dot{y}|_{y=0} = S^0(t)D_0(t) + (D_1(t) - \underline{D}(t))V_1^*(t) \geq S^0(t)D_0(t) > 0,$$

if follows that $y(t) > 0, \quad \forall t \geq t_1$. Thus, the $\omega-$periodicity of $y(t)$ implies that $y(t) > 0, \quad \forall t \geq 0$, that is , $V_1^*(t) > x_1^*(t), \quad \forall \ \ t \geq 0$.

For any $(S^0, x_0) := (S(0), x_1(0), x_2(0)) \in \mathbb{R}^3_+$ with $x_i(0) > 0, \quad i = 1, 2$, let $(S(t), x(t)) = (S(t), x_1(t), x_2(t))$ be the unique solution of (4.8) on the maximal interval of existence $[0, t_+)$. Since $\dot{S}(t)|_{s=0} = S^0(t)D_0(t) > 0$, it follows that $S(t) > 0$, and $x(t) > 0, \forall \ \ t \in [0, t_+)$.

We now show that the solution is bounded.
Let $V(t) := S(t) + x_1(t) + x_2(t)$. Then

$$S^0(t)D_0(t) - \overline{D}(t)V(t) \leq \dot{V}(t) \leq S^0(t)D_0(t) - \underline{D}(t)V(t).$$

Therefore, by the comparison theorem, we get

$$\underline{V}(t) \leq V(t) \leq \overline{V}(t), \quad \forall t \in [0, t_+), \tag{4.11}$$

where $\overline{V}(t)$ is the unique solution of the linear $\omega-$periodic equation

$$\dot{V} = S^0(t)D_0 - \underline{D}(t)V(t)$$

with $\overline{V}(0) = V(0)$, and $\underline{V}(t)$ is the unique solution of the linear $\omega-$periodic equation

$$\dot{V} = S^0(t)D_0 - \overline{D}(t)V(t)$$

with $\underline{V}(0) = V(0)$. The global existence of $\overline{V}(t)$ on $[0, \infty)$ implies that $t_+ = \infty$. Since $\lim_{t\to\infty}(\overline{V} - V_1^*(t)) = 0$, $V(t)$ and hence $S(t)$ and $x(t)$ are ultimately bounded; that is, Equation (4.8) is point dissipative on $\mathbb{R}^3_+$. Therefore, for all $t \geq 0, \quad i = 1, 2,$

$$\dot{x}_i(t) = x_i(t)\left(P_i(t, V(t) - \sum_{j=1}^{2} x_j(t)) - D_i(t)\right) \leq x_i(t)(P_i(t, V(t)) - D_i(t)).$$

By the comparison theorem, it follows that

$$x_i(t) \leq \overline{x}_i(t), \quad \forall t \geq 0, \quad i = 1, 2 \tag{4.12}$$

where $\overline{x}_i(t)$ is the unique solution of the non autonomous equation

$$\dot{x}_i(t) = x_i(t)(P_i(t, \overline{V}(t) - x_i(t)) - D_i(t)), \quad \overline{x}_i(0) = x_i(0) > 0, \quad i = 1, 2. \tag{4.13}$$

Since $\lim_{t\to\infty}(\overline{V}(t) - V_1^*(t)) = 0$, we get

$$\lim_{t\to\infty}(P_i(t, \overline{V}(t) - x_i) - P_i(t, V_1^*(t) - x_i)) = 0$$

uniformly for x_i in any bounded subset of $\mathbb{R}_+$. Since

$$\int_0^\omega (P_i(t, V_1^*(t)) - D_i(t))dt > 0,$$

by Lemma 2.3 part (b) we have that

$$\lim_{t\to\infty}(\overline{x}_i(t) - x_i^*(t)) \geq 0, \quad i = 1, 2, \tag{4.14}$$

By (4.11) and (4.12), it then follows that for any $i = 1, 2,$ and $t \geq 0$,

$$\dot{x}_i(t) = x_i(t) \left(P_i(t, V(t) - \sum_{j=1}^{2} x_j(t)) - D_i(t) \right) \geq x_i(t) \left(P_i(t, \underline{V}(t) - \overline{x}_j(t) - x_i(t)) - D_i(t) \right), \tag{4.15}$$

$$i, j = 1, 2, \quad i \neq j$$

and hence, by the comparison theorem,

$$x_i(t) \geq \underline{x}_i(t), \quad t \geq 0, \quad i = 1, 2, \tag{4.16}$$

where $\underline{x}_i(t)$ is the unique solution of the non autonomous equation

$$\dot{x}_i(t) = x_i(t)(P_i(t, \underline{V}(t) - x_j(t) - x_i(t)) - D_i(t)), \quad i, j = 1, 2 \ \ i \neq j \tag{4.17}$$

with $\underline{x}_i(0) = x_i(0) > 0, \quad i = 1, 2$. Since $\lim_{t \to \infty} (\underline{V}(t) - V_2^*(t)) = 0$, we have

$$\lim_{t \to \infty} \left(P_i(t, \underline{V}(t) - x_j^*(t) - x_i(t)) - P_i(t, V_2^*(t) - x_j^*(t) - x_i(t)) \right) = 0, \quad i, j = 1, 2, \quad i \neq j \tag{4.18}$$

uniformly for x_i in any bounded subset of $\mathbb{R}_+$. Since

$$\int_0^\omega (P_i(t, V_2^*(t)) - x_j(t)) - D_i(t)) dt > 0, \quad i, j = 1, 2, \quad i \neq j$$

by Lemma 2.3 part (b) we have that

$$\lim_{t \to \infty} (\underline{x}_i(t) - x_i^*(t) \leq 0, \quad i = 1, 2. \tag{4.19}$$

where $\underline{x}_i^*(t), \quad i = 1, 2,$ is the unique positive $\omega-$periodic solution of the periodic equation

$$\dot{x}_i(t) = x_i(t)(P_i(t, V_2^*(t) - x_j^*(t) - x_i(t)) - D_i(t)), \quad i, j = 1, 2, \quad i \neq j \tag{4.20}$$

By (4.12),(4.14), (4.16), and (4.19), it then follows that

$$\liminf_{t\to\infty}(x_i(t)-\underline{x}_i^*(t)\geq 0\geq \limsup_{t\to\infty}(x_i(t)-\overline{x}_i^*(t)),\quad i=1,2. \tag{4.21}$$

Clearly, (4.21) implies that there exists $\alpha>0$ and $\eta>0$ such that any solution $(S(t),x(t))$ of (4.8) with $S(0)\geq 0$ and $x_i(0)>0,\quad i=1,2$ satisfies

$$0<\alpha\leq \liminf_{t\to\infty}(x_i(t)\leq \limsup_{t\to\infty} x_i(t)\leq \eta,\quad i=1,2.$$

We now prove the existence of a positive $\omega-$periodic solution to equation (4.8).
Let $X:=\mathbb{R}^3_+$,

$$X_0:=\left\{(S(t),x_1(t),x_2(t))\in\mathbb{R}^3_+ : x_i>0,\forall 1\leq i\leq 2\right\},$$

and

$$\partial X_0:=\left\{(S(t),x_1(t),x_2(t))\in\mathbb{R}^3_+ : x_i>0, \text{for some } \ 1\leq i\leq 2\right\}.$$

Then, $X=X_0\cup\partial X_0$. For any $y=(S^0,x_0)\in X$, Equation (4.8) has a unique solution, $\phi(t,y)$, with $\phi(0,y)=y$. The map $T(t)=\phi(t,.):X\to X$ is a periodic semiflow [41] and $T(t)X_0\subset X_0,\forall t\geq 0$. We also know that $T(t)$ is point dissipative; that is ultimately bounded in X and uniformly persistent with respect to $(X_0.\partial X_0)$, in the sense that there exists $\varpi>0$ such that for any $y\in X_0$, $\liminf_{t\to\infty} d(T(t)y,\partial X_0)\geq 0$. Let $Q:=T(\omega):X\to X$ be the Poincare map associated with Equation (4.8). Then by Lemma 1.3 on page 12, the ultimate boundedness of solutions of a periodic system of ordinary differential equations implies the uniform boundedness of solutions, and hence $Q:X\to X$ is compact. Therefore, by Lemma 1.2 on page 12, Q admits a fixed point $y_0\in X_0$ and hence $\phi(t,y_0)$ is a periodic solution of Equation (4.8). Let $y_0=(S^0,x_1(0),x_2(0))\in X_0$. Then $S^0\geq 0;\ \ x_1(0)>0,x_2(0)>0$. It then follows that $\phi(t,y_0)=(S(t),x_1(t),x_2(t))$ satisfies $S(t)>0$ and $x_1(t)>0,x_2(t)>0$. Consequently, $\phi(t,y_0)$ is a positive $\omega-$ periodic solution of (4.8).

□

Note that should $D_0(t) = D_1(t) = D_2(t)$ for $t \in [0, \omega]$, then $V_1^*(t) = V_2^*(t), x_1^*(t) = x_2^*(t)$ and we have the following corollary:

Corollary 4.2. *Let $D_0(t) = D_1(t)$, for $t \in [0, \omega]$*

a) *If $\int_0^\omega (P(t, V_1^*(t)) - D_1(t))dt > 0$, Equation (4.8) admits a unique, positive, periodic solution $(S^*(t), x_1(t)) = (V_1^*(t) - x_1(t), x_1^*(t))$ and any solution $(S(t), x(t))$ of (4.8) with $S(0) \geq 0$ and $x(0) > 0$ satisfies $\lim_{t\to\infty}(S(t) - S^*(t)) = 0$ and $\lim_{t\to\infty}(x(t) - x^*(t)) = 0$.*

b) *If $\int_0^\omega (P(t, V_1^*(t)) - D_1(t))dt \leq 0$, then any solution $(S(t), x(t))$ of (4.8) with $S(0) \geq 0$ and $x(0) \geq 0$ satisfies $\lim_{t\to\infty}(S(t) - V_1^*(t)) = 0$ and $\lim_{t\to\infty} x_i(t) = 0$.*

4.4 Numerical Results

In our model, the nutrient supply and specific death rates are assumed to be periodic with commensurate periods. The nutrient input concentration is described by (4.3) and (4.4). We use the following Fourier series to describe the nutrient input function:-

$$S^0(t) = \tilde{S}^0 + \eta + 2\eta\frac{(T_1 - T_2)}{T_p} + \sum_{n=1}^{\infty}\frac{4\eta}{n\pi}\cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right)\sin\left(\frac{n\pi}{T_p}(T_1 - T_2)\right)\cos\frac{2\pi nt}{T_p}. \tag{4.22}$$

As an example, if we set $\tilde{S}^0 = 11, n = 9$ we obtain the Figure 4.4 that describes the input nutrient concentrations.

Clearly, Figure 4.4 approximates that envisaged by Figure 2.3 on Page 16. The level of accuracy of the function may be increased by adding more harmonics to the function, that is

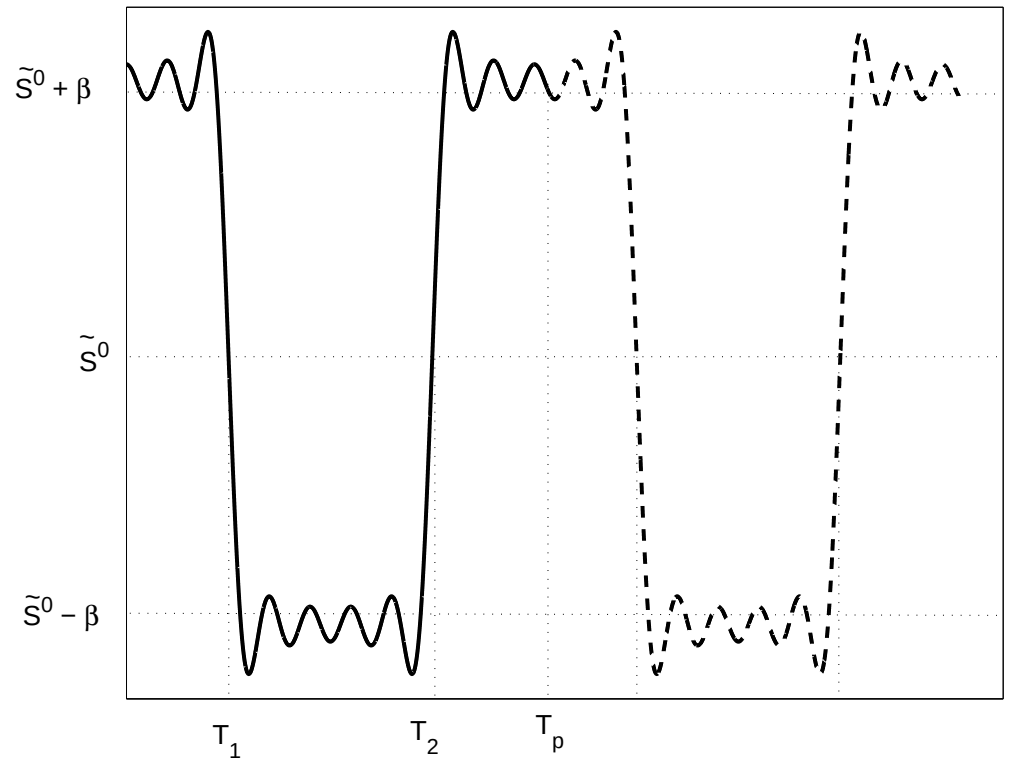

Figure 4.1: Nutrient Input as described by Equation (4.22)

making n to be as large as we desire.

It is reasonable to take input nutrient supply of the form

$$D^0(t) = \tilde{D}_0 - \eta_0 - 2\eta_0 \frac{(T_1 - T_2)}{T_p} - \sum_{n=1}^{\infty} \frac{4\eta_0}{n\pi} \cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right) \sin\left(\frac{n\pi}{T_p}(T_1 - T_2)\right) \cos\frac{2\pi nt}{T_p}. \tag{4.23}$$

so that the nutrient supply and death rates have commensurate period.

For practical purposes, the fluctuations of the nutrient supply must not be very large, and specifically, we choose $S^0(t)$ so that it is non-negative, that is

$$\tilde{S}^0 \geq \left| \eta + 2\eta \frac{(T_1 - T_2)}{T_p} + \sum_{n=1}^{\infty} \frac{4\eta}{n\pi} \cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right) \sin\left(\frac{n\pi}{T_p}(T_1 - T_2)\right) \cos\frac{2\pi nt}{T_p} \right|.$$

For simplicity, we let

$$D_0(t) = D_1(t) = D_2(t) = \tilde{D}_0 - \eta_0 - 2\eta_0\frac{(T_1 - T_2)}{T_p} \quad - \quad \sum_{n=1}^{\infty}\frac{4\eta_0}{n\pi}\cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right) \sin\left(\frac{n\pi}{T_p}(T_1 - T_2)\right)\cos\frac{2\pi nt}{T_p}.$$

Equation (4.8) is then explicitly given by

$$\begin{aligned}
\dot{S}(t) &= (\tilde{S}^0 + \eta + 2\eta\frac{(T_1 - T_2)}{T_p} + \sum_{n=1}^{\infty}\frac{4\eta}{n\pi}\cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right)\sin\left(\frac{n\pi}{T_p}(T_1 - T_2)\right) \\
&\quad \cos\frac{2\pi nt}{T_p} - S(t))(\tilde{D}_0 - \eta_0 - 2\eta_0\frac{(T_1 - T_2)}{T_p} - \sum_{n=1}^{\infty}\frac{4\eta_0}{n\pi}\cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right) \\
&\quad \sin\left(\frac{n\pi}{T_p}(T_1 - T_2)\right)\cos\frac{2\pi nt}{T_p}) - \frac{x_1 m_1 S(t)}{a_1 + S(t)} - \frac{x_2 m_2 S(t)}{a_2 + S(t)} \\
\dot{x}_1(t) &= \frac{x_1 m_1 S(t)}{a_1 + S(t)} - (\tilde{D}_0 - \eta_0 - 2\eta_0\frac{(T_1 - T_2)}{T_p} - \sum_{n=1}^{\infty}\frac{4\eta_0}{n\pi}\cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right) \\
&\quad \sin\left(\frac{n\pi}{T_p}(T_1 - T_2)\right)\cos\frac{2\pi nt}{T_p})x_1(t) \\
\dot{x}_2(t) &= \frac{x_2 m_2 S(t)}{a_2 + S(t)} - (\tilde{D}_0 - \eta_0 - 2\eta_0\frac{(T_1 - T_2)}{T_p} - \sum_{n=1}^{\infty}\frac{4\eta_0}{n\pi}\cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right) \\
&\quad \sin\left(\frac{n\pi}{T_p}(T_1 - T_2)\right)\cos\frac{2\pi nt}{T_p})x_2(t)
\end{aligned} \tag{4.24}$$

The model in Equation 4.24 has numerical results shown in Figure 4.2 using parameters in Table **??**.

Table 4.1: Parameter values used in Equation (4.24) for Figure 4.2

Parameter	$\tilde{D}_0$	η	$\tilde{S}^0$	T_1	m_1	a_1	m_2	a_2	$x_1(0)$	$x_2(0)$	n	T_2	T_p
Value	0.4675	2	11	1	1	1	0.7	0.4	10	10	9	3	4

These parameters satisfy Theorem 4.1 and Figure 4.2 is a time plot of the system of Equations in (4.24).

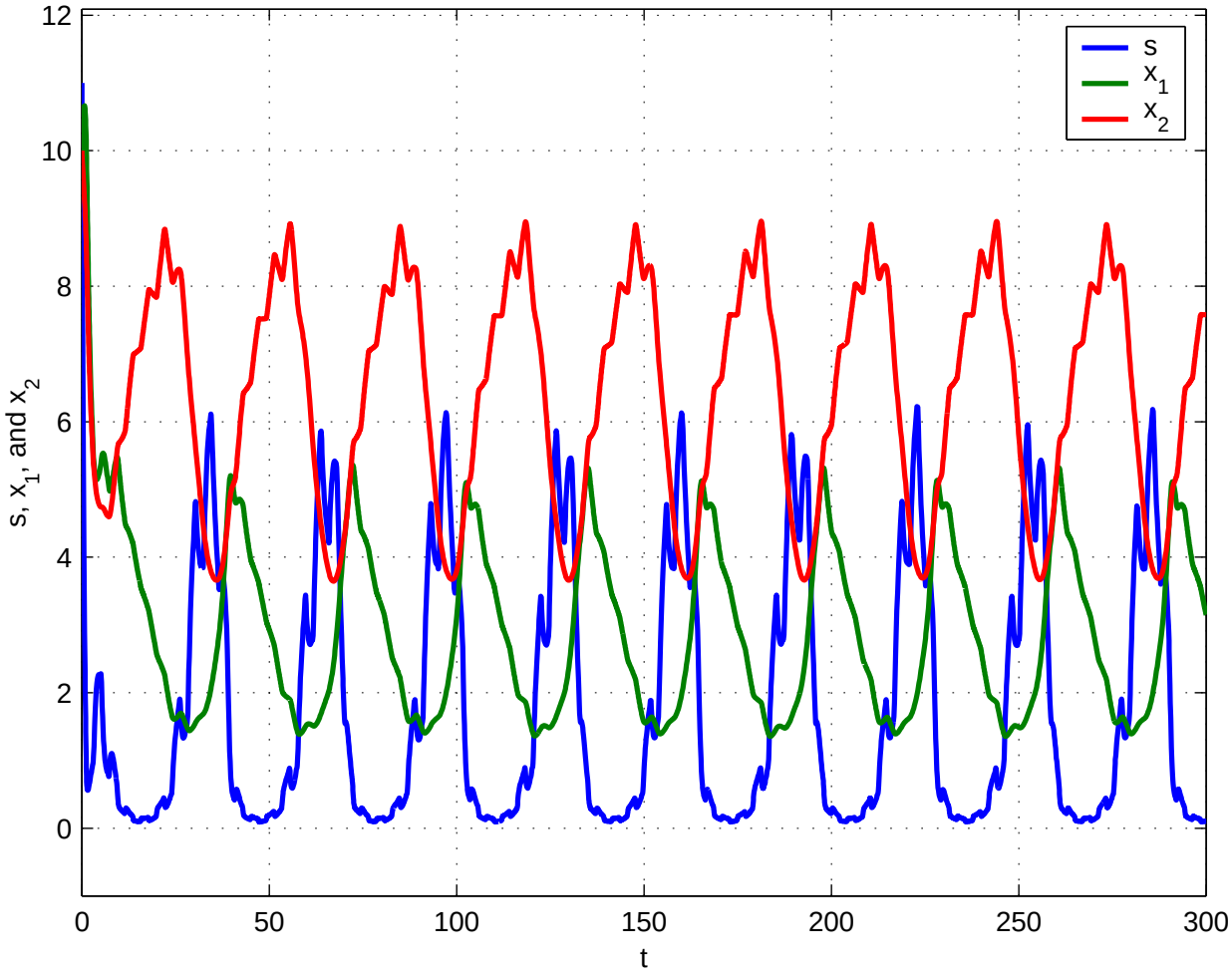

Figure 4.2: Time Plot for Equation (4.24)

The figure shows a more realistic existence of each of the competing species as well as the nutrient. As is observed in nature, there are some perturbations in the species at all times. This is reasonable given that deaths occur at all times even when the population is increasing. It is also naturally observed that there will be small increases in population when the general trend is a decline in species population.

The numerical results above are confirmed by the 3-D plot of $S(t), x_1(t), x_2(t)$ in Figure 4.3.

We can clearly see from figures 4.2 and 4.3 that the solutions of (4.24) remains in the positive interior of (S, x_1, x_2), meaning that $(S(t), x_1(t), x_2(t)) \in \text{int}\mathbb{R}^3_+, \quad 0 \leq t < \infty$. This behaviour is

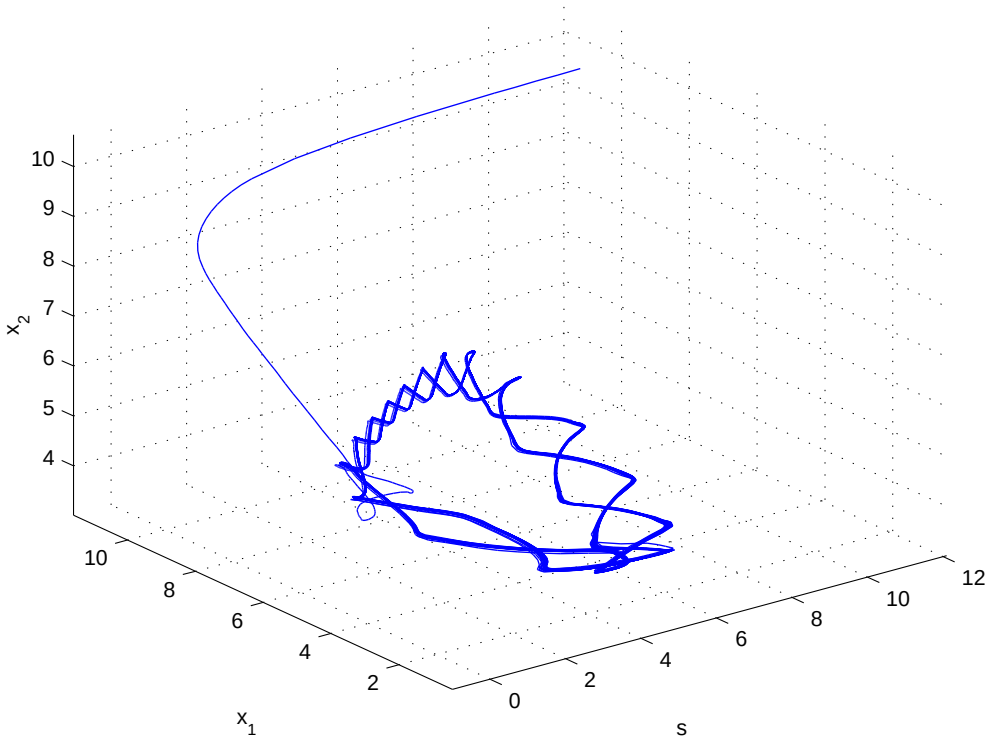

Figure 4.3: 3-D Plot for Equation (4.24)

consistent with what we have determined analytically.

The fact that both competing species do not explode (grow without bound) and do not become extinct is clearly demonstrated by the following 2-D time plot in Figure 4.4 showing x_1 against x_2. These results are important because models with non-periodic coefficients consistently predict competitive exclusion while we observe that in nature, species competing for a nutrient often coexist.

For purposes of comparison, further numerical results from Equation 4.8 are shown in Chapter 5 because the predictions of the Equation and that of Equation 4.1 that includes mutual inhibition differ.

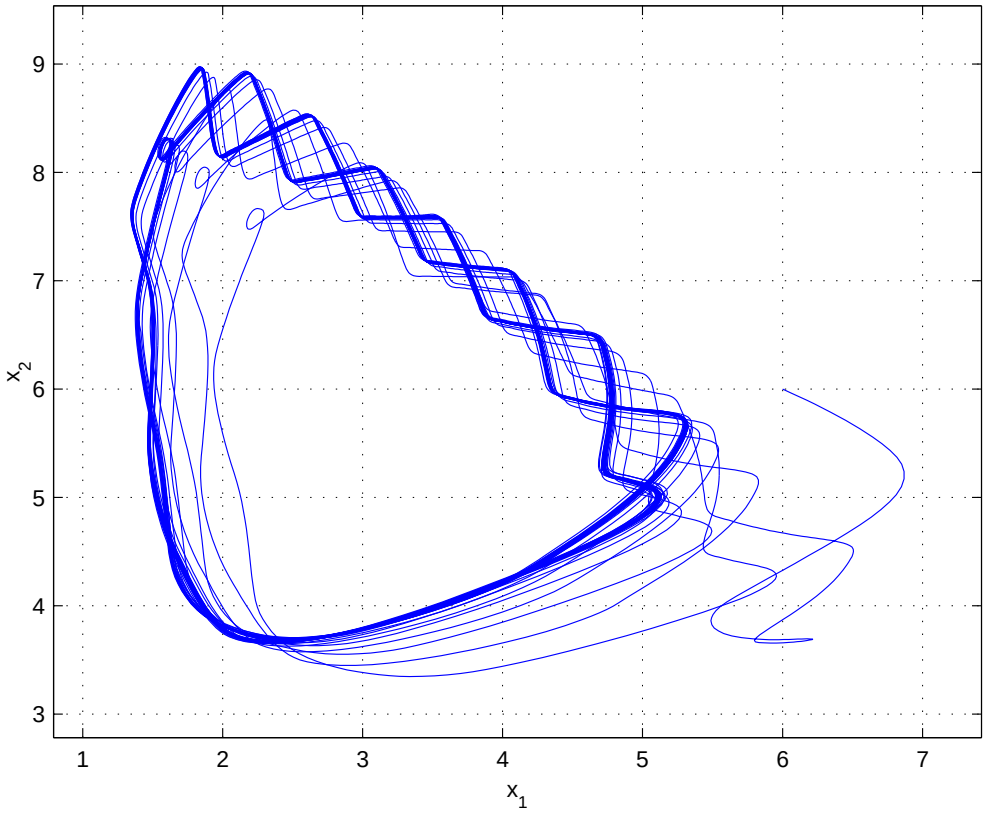

Figure 4.4: Long term relationship between x_1 and x_2

Chapter 5 Mutual Inhibition in a Periodic Chemostat

5.1 Introduction

In this chapter, we present a model of mutual inhibition in the periodic chemostat. The parameters used in this chapter are similar to those used in chapter 4 where nutrient supply, specific death rates, as well as species specific nutrient uptake functions are periodic. We use comparison theorems to show that with mutual inhibition, co-existence of the competing species is not possible.

5.2 The Model

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

$$\begin{aligned} \dot{S} &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^{2} x_i(t)P_i(t,S(t))g_i(x_1(t),x_2(t)), \\ \dot{x_i} &= x_i(t)\left\{P_i(t,S(t))g_i(x_1(t),x_2(t)) - D_i(t)\right\}, \quad i=1,2, \\ & \quad x_i(0) = x_{i0} \geq 0, \quad S(0) \geq 0,. \end{aligned} \tag{5.1}$$

where the parameters $S(t), x_i(t), P_i(t,S(t)), S^0(t)$ and $D_i(t)$ are as defined in Section 4.2 on page 42 while $g_i(x_1(t),x_2(t))$ is as defined in Section 3.2 in page 30.

We note that this is a more general periodic chemostat model than those discussed earlier. We see that 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

$$\begin{aligned} \dot{S}(t) &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^{2} x_i(t)P_i(t, S(t)), \\ \dot{x}_i(t) &= x_i(t)(P_i(t, S(t)) - D_i(t)) \quad 1 \leq i \leq 2, \end{aligned} \tag{5.2}$$

which is the standard periodic chemostat model without inhibition. A discussion of this case may be found in Chapter 4. A more detailed discussion of the standard periodic chemostat model may be found in [36] and [42].

5.3 Analysis of the Model

If Conditions B1 on page 31 are satisfied, we have the following results for Equation (5.1) where, by a solution of (5.1) we mean a differentiable triple $(S(t), x_1(t), x_2(t)) \in \mathbb{R}^3_+$ that satisfies the system of differential equations (5.1).

Theorem 5.1. *The positive $(S(t), x_1(t), x_2(t))$-cone is positively invariant for (5.1) as are the surfaces $x_1 = 0$ and $x_2 = 0$. The solution of the model is uniformly bounded as $t \to \infty$ i.e. the system is dissipative.*

Proof. The solution of Equation (5.1) is said to be entirely bounded in $\mathbb{R}$ if,

$$\sup_{t \in R} \mid (S(t), x_1(t), x_2(t)) \mid < +\infty. \tag{5.3}$$

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

$$S(t) \geq S(0)\exp\left[\int_0^t D_0(\xi) + \frac{1}{S(\xi)}\sum_{i=1}^{2} x_i(\xi)P_i(\xi, S(\xi))g_i(x_1(\xi), x_2(\xi))d\xi\right] \tag{5.4}$$

Since the quantity on the right of (5.4) is positive for $S(0) > 0$ and for all t, this contradicts our assumption that $S(t) < 0$. This means that $S(t) > 0$ for all $t \geq 0$.

From the second equation in (5.1), we immediately see that

$$x_i(t) = x_i(0)\exp\left[\int_0^t (P_i(\xi, S(\xi))g_i(x_1(\xi), x_2(\xi)) - D_i(\xi))d\xi\right]. \tag{5.5}$$

Thus, for $x_i(0) \geq 0$, Equation (5.5) means $x_i(t) \geq 0$ for all $t \geq 0$. This completes the proof that the solution $(S(t), x_1(t), x_2(t))$ of (5.1) is positive.

We now show that the solution is bounded. Let $V(t) = S(t) + x_1(t) + x_2(t)$. Since by Lemma **??** $S(t)$ and $x_i(t)$ $i = 1, 2$ are continuous, positive and ω-periodic, it follows that $V(t)$ is a continuous, positive and ω-periodic function. Then, using (5.1), we find

$$\dot{V}(t) = S^0(t)D_0(t) - (S(t)D_0(t) + x_1(t)D_1 + x_2(t)D_2(t)) \leq S^0(t)D_0(t). \tag{5.6}$$

Practically, the nutrient input concentration $S^0(t) < \infty$ and the nutrient washout rate $D_0(t)$ is bounded as shown on Page 44. Thus we expect that $S^0(t)D_0(t) < \infty$. Since $V(t) \leq S^0(t)D_0(t)$ it follows that

$$V(t) \leq \int_0^t S^0(\xi)D_0(\xi)d\xi < \infty, \text{ for all } t \geq 0. \tag{5.7}$$

The fact that $V(t) = S(t) + x_1(t) + x_2(t) < \infty$, implies each component $S(t), x_1(t)$ and $x_2(t)$ of $V(t)$ must have an upper bound. This means that

$$\sup_{t \in R} \mid (S(t), x_1(t), x_2(t)) \mid < +\infty.$$

Since each component $S(t), x_1(t)$ and $x_2(t)$ of $V(t)$ is non-negative, it follows that the solution $(S(t), x_1(t), x_2(t))$ is bounded, completing the proof.

□

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

Theorem 5.2. *If* $g_i(x_1(t), x_2(t)) < \frac{D_i(t)}{P_i(t,S(t))}$, *then* $\lim_{t\to\infty} x_i(t) = 0, \quad i = 1, 2,$ *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 (5.5) 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 $\lim_{t\to\infty} x_i(0) \exp\left[-\int_0^t (D_i(\xi) - P_i(\xi, S(\xi))g_i(x_1(\xi), x_2(\xi)))d\xi\right] = 0$, it means that $\lim_{t\to\infty} x_i(t) = 0, \quad i = 1, 2$, completing the proof.

□

The biological interpretation of Theorem 5.2 is that if the degree of inhibition of species x_i is very high, then the species will become extinct as a result of the inhibition rather that due to competition for the nutrient.

If the degree of inhibition does not cause extinction, then the first few moments of interaction between species x_1 and x_2 seem to be crucial in determining which species survives the competition and which becomes extinct. Indeed, the initial concentration S^0 and the uptake function $P_i(t, S(t))$ during the first instances of interaction appear to determine which species survives.

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:-

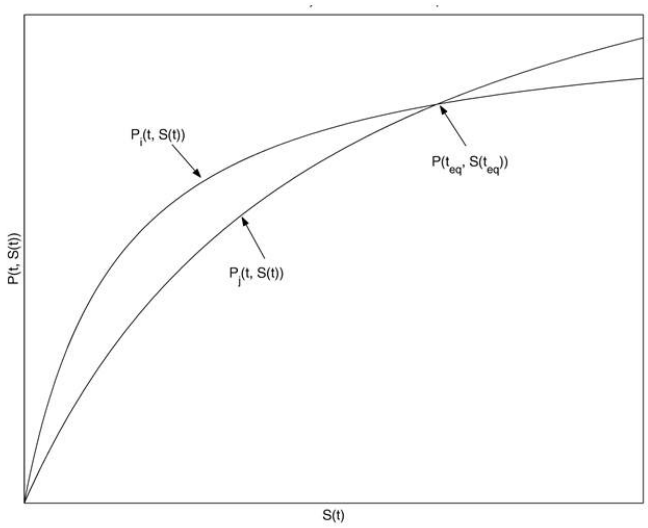

Figure 5.1: $P_i(t, S(t)) > P_j(t, S(t))$ for $0 < t < t_{eq} < \infty$

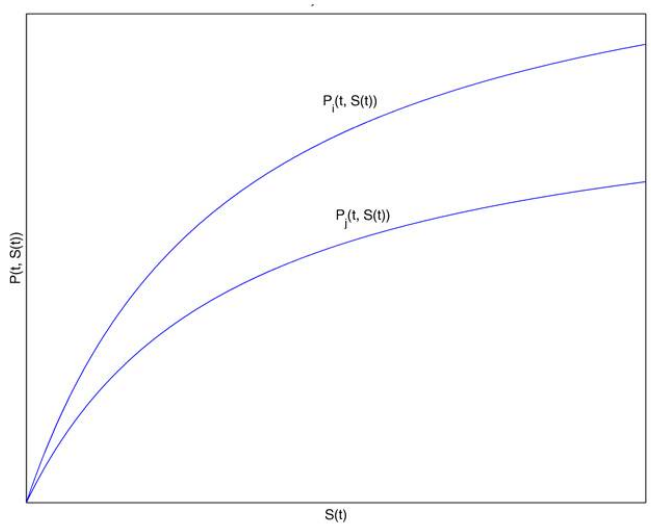

Figure 5.2: $P_i(t, S(t)) > P_j(t, S(t))$ for all $t > 0$

Figure 5.1 shows one possible relationship between $P_1(t, S(t))$ and $P_2(t, S(t))$ as $S(t)$ increases where $P_i(t, S(t)) > P_j(t, S(t))$ for $0 < t < t_{eq} < \infty$ while Figure 5.2 shows another pos-

sibility where $P_i(t, S(t)) > P_j(t, S(t))$ for $0 < t \leq t_{eq} = \infty$. We easily find $S(t_{eq}) = \frac{m_j a_i - m_i a_j}{m_i - m_j}$. 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 results.

Theorem 5.3. *If* $P_i(t, S(t)) < P_j(t, S(t))$ *for* $0 < t < t_{eq}$, *then for* $x_i(0) = x_j(0) > 0$, $\lim_{t\to\infty} x_i(t) = 0$ *and* $\lim_{t\to\infty} x_j(t) = x_j^*(t)$ *where* $x_j^*(t)$ *is the* ω*-periodic solution of the equation*

$$\dot{x}_j(t) = x_j(t)\left\{P_j(t, S(t))g_j(x_i(t), x_j(t)) - D(t)\right\}, \quad j = 1, 2,$$

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. The theorem predicts competitive exclusion.

Proof. Since $x_i(0) = x_j(0) > 0$, it follows that

$$g_i(x_i(0), x_j(0)) = g_j(x_i(0), x_j(0)).$$

From (5.1) we have

$$x_i(t) = x_i(0)\exp\int_0^{t_1}\left\{P_i(\xi, S(\xi))g_i(x_i(\xi), x_j(\xi)) - D(\xi)\right\}d\xi, \quad i = 1, 2. \tag{5.8}$$

By the fact that $x_i(0) = x_j(0) > 0$, and $P_i(t, S(t_0)) < P_j(t, S(t_0))$ for $0 < t_0 < t_{eq}$, it follows from Equation 5.8 that

$$x_i(t_1) < x_j(t_1) \text{ for } 0 < t_0 < t_1 = t_0 + a < t_{eq}, \quad a > 0 \tag{5.9}$$

The strict monotonicity of $g_i(x_i(t), x_j(t)), i = 1, 2$, that satisfies Conditions B1 (more specif-

ically B1 (ii) and (iii)) and (5.9) mean that

$$g_i(x_i(t_1), x_j(t_1)) < g_i(x_i(t_0), x_j(t_0)) = g_j(x_i(t_0), x_j(t_0)) < g_j(x_i(t_1), x_j(t_1)) \tag{5.10}$$

Consequently, (5.10) implies that for $t_2 = t_1 + a < t_{eq}, \;\; a > 0$, we have

$$x_i(t_2) < x_i(t_1) < x_i(t_0),$$

and

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

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 $x_i(t_n) = 0$ and, together with Condition B1 (iii), find that $g_j(0, x_j(t_n)) = 1$. Once $x_i(t_n) = 0$, it follows from Theorem 4.1 (ii) that $x_i(t) = 0$, for all $t \geq t_n$. This means that species x_i becomes extinct. When this happens, species x_j experiences no inhibition to its growth and $g_j(0, x_j(t_n)) = 1$. Theorem 4.1 assures that $\lim_{t\to\infty} x_j(t) = x_j^*(t)$. This completes 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 5.4. *If* $x_i(t)P_i(t, S(t)) < x_j(t)P_j(t, S(t))$ *for* $0 < t < t_{eq}$, *then* $\lim_{t\to\infty} x_j(t) \neq x_j^*(t)$, $\lim_{t\to\infty} x_i(t) = 0$, *where* $x_i^*(t)$ *is the* ω*-periodic solution of the equation*
$\dot{x}_i(t) = x_i(t)\left\{P_i(t, S(t))g_i(x_1(t), x_2(t)) - D(t)\right\}, \;\; i = 1, 2, .$

Proof. Since $x_i(t)P_i(t, S(t)) < x_j(t)P_j(t, S(t))$ for $0 < t < t_{eq}$ and $x_i(0) \neq x_j(0)$, we have by Condition B1 (ii),

$$g_i(x_1(t_0), x_2(t_0))P_i(t_0, S(t_0)) < g_j(x_1(t_0), x_2(t_0))P_j(t_0, S(t_0))$$

and

$$\exp\int_0^t g_i(x_1(\xi),x_2(\xi))P_i(\xi,S(\xi))-D(\xi))d\xi < \exp\int_0^t (g_j(x_1(\xi),x_2(\xi))P_j(\xi,S(\xi))-D(\xi))d\xi.$$

Using comparison theorems, we conclude that

$$\lim_{t\to\infty} x_i(0)\exp\int_0^t (g_i(x_1(\xi),x_2(\xi))P_i(\xi,S(\xi))-D(\xi))d\xi$$

$$< \lim_{t\to\infty} x_j(0)\exp\int_0^t (g_j(x_1(\xi),x_2(\xi))P_j(\xi,S(\xi))-D(\xi))d\xi.$$

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

$$g_i(x_1(t_{n+\delta}),x_2(t_{n+\delta})) < g_i(x_1(t_n),x_2(t_n)) < g_j(x_1(t_n),x_2(t_n)) < g_j(x_1(t_{n+\delta}),x_2(t_{n+\delta})),$$

from which we conclude that

$$x_i(t_{n+\delta}) < x_i(t_n) < x_j(t_n) < x_j(t_{n+\delta}).$$

Proceeding in a manner similar to the proof of Theorem 5.3 completes the proof. □

These theorems mean that one competitor always wins the competition and that coexistence is not possible. This differs with the results of the periodic chemostat without inhibition as demonstrated in Chapter 4 where coexistence was proved. The numerical results that follow support these findings.

5.4 Numerical Results

We use parameters from Table 4.1 and vary the initial nutrient input concentration and the maximum specific growth rate to fit the requirements of Theorem 5.3. We then vary the initial biomass concentrations of the competitors to fit the requirements of Theorem 5.4. The parameters that are varied are given in the tables that preceed the figures.

From the simulations, we see that the hypotheses of both models are satisfied. In fact, we have carried out hundreds of simulations of these models and all of them agree with the predictions of the theorems presented.

The following values satisfy the requirement that

$$P_1(0, S(0)) < P_2(0, S(0)), x_1(0) = x_2(0).$$

Table 5.1: Parameters satisfying $P_1(0, S(0)) < P_2(0, S(0)), x_1(0) = x_2(0)$

Parameter	D_0	α_1	β_1	m_1	a_2	α_2	β_2	m_2	x_{10}	x_{20}	S^0
	0.4675	1	0.0000	1.1701	0.3	1	0.0001	0.3	10	10	1

Figure 5.3 represents the results of Equation (5.1). It satisfies the requirements of part (b) of Theorem 4.1 by the fact that $P_1(0, S(0)) < P_2(0, S(0)), x_1(0) = x_2(0)$. Figure 5.4 represents the numerical results of Equation 4.8. Both figures are generated using the same parameters. Clearly, both Figure 5.3 and 5.4 show species x_2 winning the competition while Figure 5.5 shows that species x_1 emerges the winner, where by $x_i, \ \ i = 1, 2$ winning the competition we mean that $\lim_{t\to\infty} x_i(t) > 0$ and $\lim_{t\to\infty} x_j(t) = 0, \ \ i, j = 1, 2, i \neq j$. In this case, the nutrient is not sufficient to sustain the two competing species, and the species with the higher ability to utilize the available nutrient ultimately wins the competition.

Figure 5.5 is a numerical simulation of Equation 5.1 with $P_1(0, S(0)) > P_2(0, S(0)), x_1(0) =$

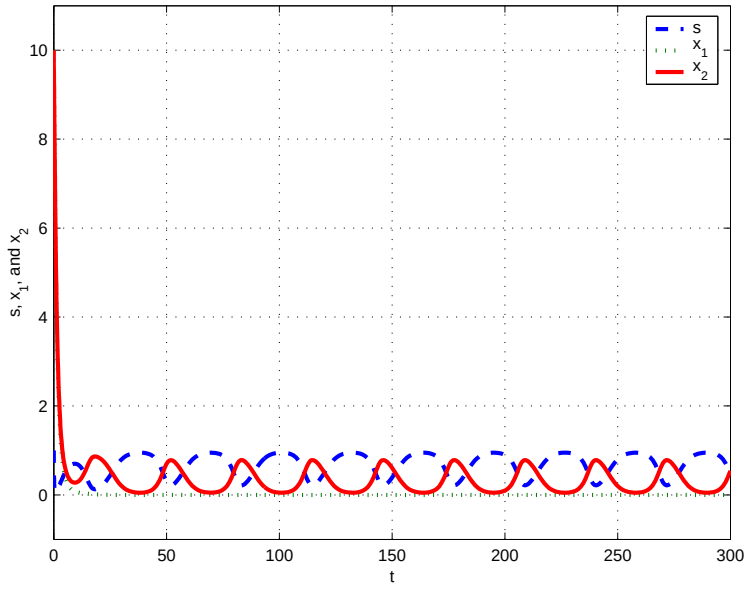

Figure 5.3: Competition for model 5.1 with $P_1(0, S(0)) < P_2(0, S(0)), x_1(0) = x_2(0)$

$x_2(0)$. This is achieved by the following parameters:

Table 5.2: Parameters satisfying $P_1(0, S(0)) > P_2(0, S(0)), x_1(0) = x_2(0)$

Parameter	D_0	α_1	β_1	m_1	a_2	α_2	β_2	m_2	x_{10}	x_{20}	S^0
	0.4675	1	0.0000	1.1701	0.3	1	0.0001	0.3	10	10	11

Here, the nutrient is enough to sustain both species but nevertheless, x_1 wins the competition as predicted by Theorem 5.3. The winning species, x_1 wins as a result of its ability to inhibit the growth of its competitor, x_2 rather than its superiority in the ability to utilize nutrient uptake. This is demonstrated by a simulation of Equation 4.8 using the same parameters as those of Figure 5.5. The simulation is presented in Figure 5.6.

Figure 5.6 clearly shows that the two competing species co-exist with $\lim_{t\to\infty}(x_1(t)) \neq 0$ and $\lim_{t\to\infty}(x_2(t)) \neq 0$. This is consistent with predictions of Theorem 4.1.

One explanation for the difference in the results of Equation 5.1 and 4.8 as demonstrated in Figures 5.5 and 5.6 is that with mutual inhibition, species x_1 that has an uptake advantage at the beginning of the competition capitalizes on this advantage to increase its biomass. The increase in biomass is in turn used to inhibit the growth of its competitor and eventually strangles it. So

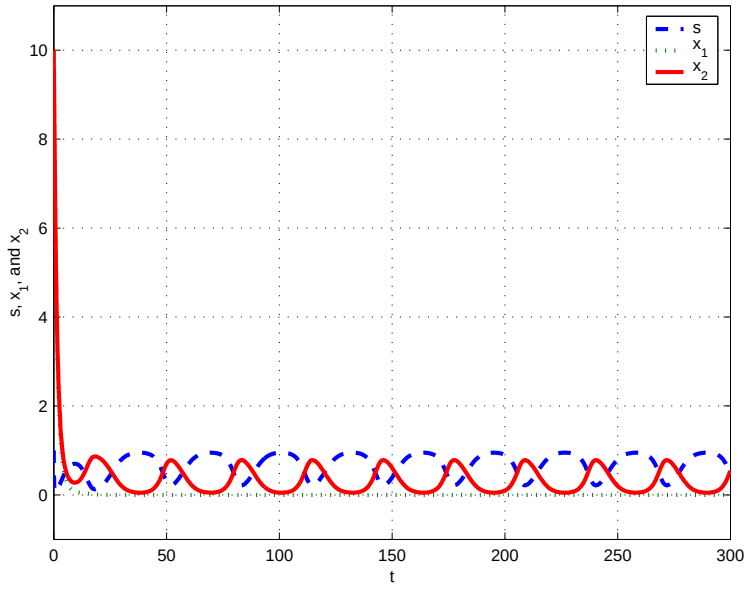

Figure 5.4: Competition for Model in Equation (4.8) with $P_1(0, S(0)) < P_2(0, S(0)), x_1(0) = x_2(0)$

long as $x_1(0) = x_2(0)$ and $P_1(0, S(0)) > P_2(0, S(0))$, x_1 always wins the competition. More generally, if $x_i(0) = x_j(0)$ and $P_i(0, S(0)) > P_j(0, S(0))$, x_i always wins the competition.

A fighting chance is handed to the weaker competitor (in this case x_2) by relaxing the condition that $x_1(0) = x_2(0)$. In this case, the initial biomass of the species and its ability to utilize the nutrient determines what species wins the competition. If the biomass of x_2 is higher than that of x_1, then it may win the competition as shown in Figure 5.7. The figure is obtained by using the following parameters.

Table 5.3: Parameters satisfying $x_1 P_1(0, S(0)) < x_2 P_2(0, S(0)), x_1(0) \neq x_2(0)$

Parameter	D_0	α_1	β_1	m_1	a_2	α_2	β_2	m_2	x_{10}	x_{20}	S^0
	0.4675	1	0.0000	1.1701	0.3	1	0.0001	0.3	7	10	11

The parameters used in the simulations in Figures 5.7 and 5.8 give x_1 a higher ability to utilize the nutrient making it a better competitor. We have maintained this situation throughout these simulations as a control measure in checking the validity of the Theorems 4.1 in Chapter 4 and Theorems 5.3 and 5.4 in Chapter 5. In Figure 5.7, x_2 wins the competition despite it being an inferior competitor. The winning is attributable to its increased ability to inhibit the

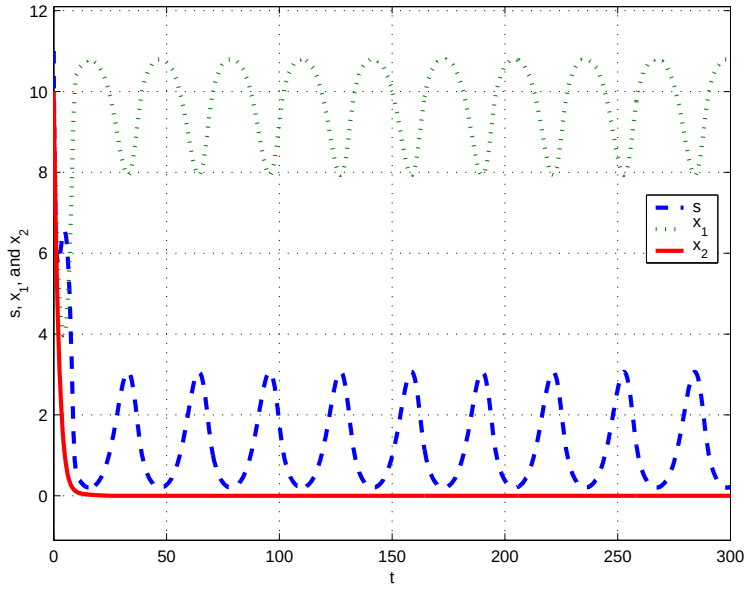

Figure 5.5: Competition for Model in Equation 5.1 with $P_1(0, S(0)) > P_2(0, S(0)), x_1(0) = x_2(0)$

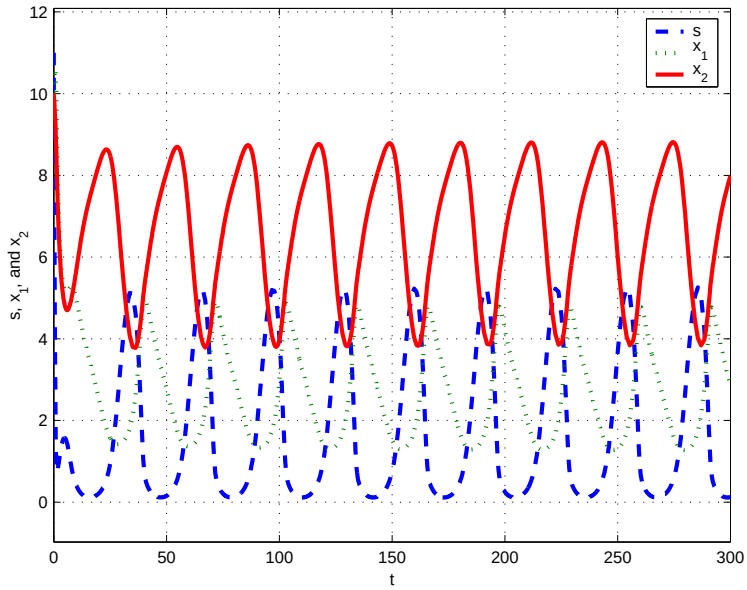

Figure 5.6: Competition for Model in Equation (4.8) with $P_1(0, S(0)) > P_2(0, S(0)), x_1(0) = x_2(0)$

growth of x_1 rather than the utilization of the nutrient. This is confirmed by Figure 5.8, where without inhibition, the two species co-exist. Both simulations have been generated using the same parameters.

We conclude that with mutual inhibition, the initial biomass of the competing species is important in determining which species survives. More specifically, if we allow $P_i(0, S(0)) =$

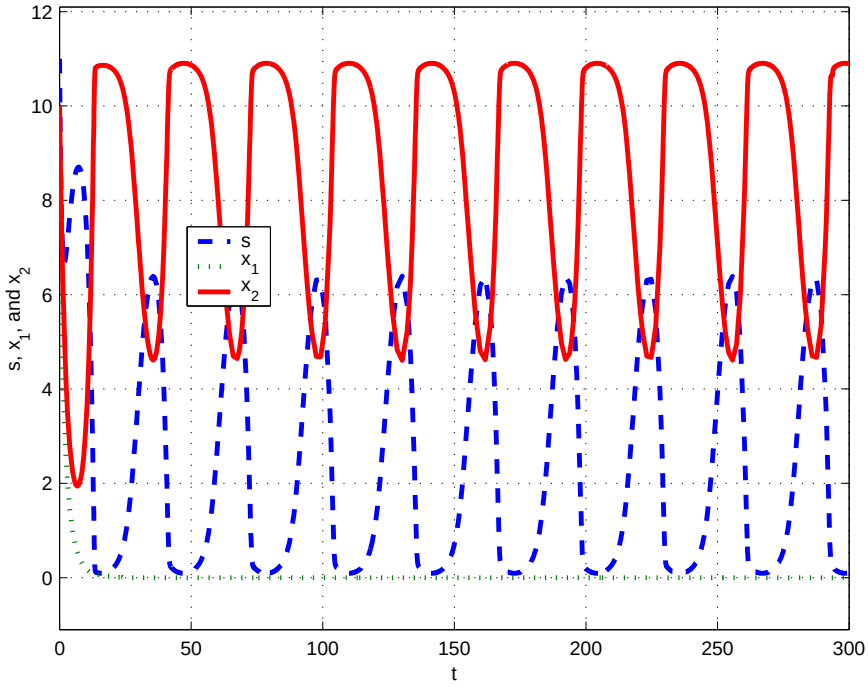

Figure 5.7: Competition for Model in Equation (5.1) with $x_1(0)P_1(0, S(0)) < x_2(0)P_2(0, S(0)), \quad x_1(0) \neq x_2(0)$

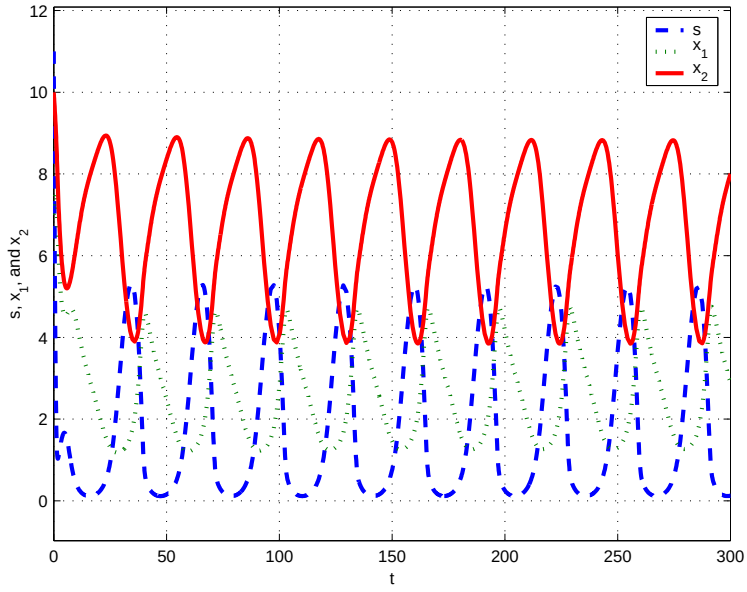

Figure 5.8: Competition for Model in Equation (5.1) with $x_1(0)P_1(0, S(0)) < x_2(0)P_2(0, S(0)), \quad x_1(0) \neq x_2(0)$

$P_j(0, S(0))$ and $x_i(0) > x_j(0)$, then x_i will always win the competition.

In order to confirm that it is not the biomass of a given species alone that determines which species wins the competition, we repeat the simulation with $x_1(0) < x_2(0)$ as in the simulations

above (where x_2 wins the competition) but choose the initial biomass of the species in such a way that $x_1(0)P_1(0, S(0)) > x_2(0)P_2(0, S(0))$. This is achieved using the following parameters.

Table 5.4: Parameters satisfying $x_1(0)P_1(0, S(0)) > x_2(0)P_2(0, S(0)), x_1(0) \neq x_2(0)$

Parameter	m_0	α_1	β_1	m_1	a_2	α_2	β_2	m_2	x_{10}	x_{20}	S^0
	0.4675	1	0.0000	1.1701	0.3	1	0.0001	0.3	8	10	11

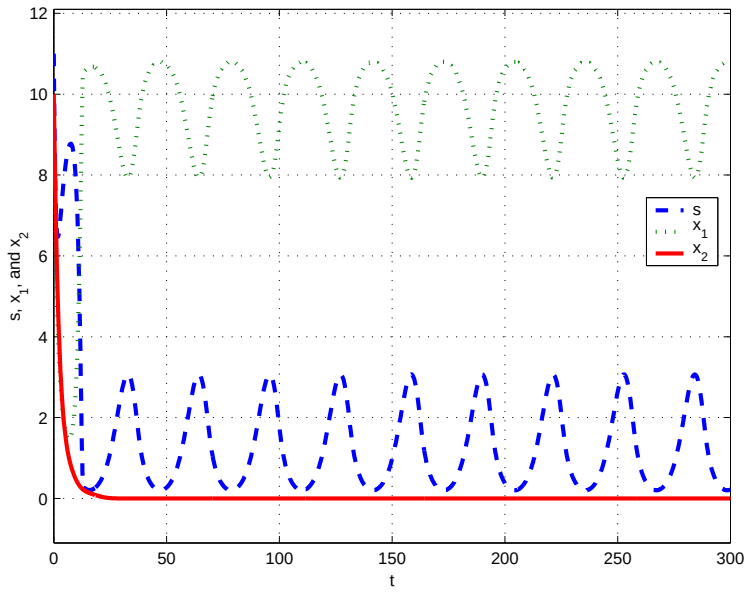

Figure 5.9: Competition for Model in Equation (5.1) with $x_1(0)P_1(0, S(0)) > x_2(0)P_2(0, S(0)), \quad x_1(0) \neq x_2(0)$

Figure 5.9 shows that despite the biomass of $x_1(0)$ being less that of $x_2(0)$, x_1 wins the competition. The fact that x_1 is a better competitor (it is able to utilize the nutrient more efficiently than x_2), it is able to reproduce more quickly and hence increase its ability to inhibit the growth of x_2. The increased biomass of x_1 eventually leads to the extinction of x_2.

Again, the fact that it is inhibition that is playing a key role in determining the winner is confirmed by Figure 5.10. The figure shows that without inhibition, the two species co-exist.

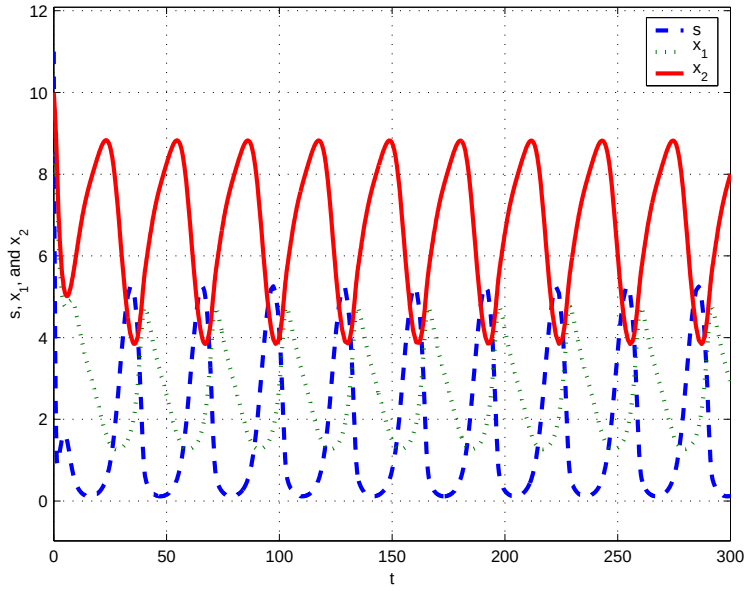

Figure 5.10: Competition for Model in Equation (4.8) with $x_1(0)P_1(0, S(0)) > x_2(0)P_2(0, S(0)), \quad x_1(0) \neq x_2(0)$

Clearly, with mutual inhibition, one species always wins the competition for chemostat models with periodic coefficients. The increase in biomass density of one species inhibits the growth of its competitor and leads to the extinction of that of its competitor. This outcome is predicted by the theorems in this chapter and confirmed by the numerical results. We have given simulations of both Equation 5.1 and 4.8 in this chapter for purposes of emphasizing the difference between their results. The parameters used in these simulations are explicitly given for each figure. This makes reproducing the results easy.

Chapter 6 Conclusion, Applications and Recommendations

In this chapter, we present a summary of what we have found and discuss in some detail the results of the other chapters and how they relate to each other.

6.1 Conclusion

In Chapter 3, we have shown that in the presence of mutual inhibition, at most one species will survive the competition for a single nutrient available in limiting supply. The species that survives is determined by the relationship between the first derivatives of inhibition function and the nutrient uptake function, which are continuous functions of time. The equations in 3.1 described mutual inhibition in a 2-species chemostat-like system. Using Theorem 3.2 we showed the relationship that must exist between the parameters in the model for the boundary rest points to be globally asymptotically stable. In Theorem 3.4 we proved that the model of a chemostat-like system with mutual inhibition does not admit any interior rest point. The lack of an interior rest point means that coexistence of the two competing species is not possible. In Chapter 4, we introduced periodicity in a two-species chemostat-like system and showed that coexistence of the two competing species is possible. The periodicity was introduced by means of a Fourier series function which enabled us to more accurately duplicate periodic nutrient supply as observed in nature. It also enabled us to model dilution rates more realistically. Theorem 4.1 gave the condition that must be satisfied by the nutrient input and dilution rates to make persistence of the two competing species possible.

In Chapter 5, Equation (5.1) that we have presented predicts that if mutual inhibition is present, competitive exclusion holds. We have shown in Theorem 5.3 that the species that wins the competition is determined by the initial conditions of the parameters at the beginning of the interaction. In Theorem 5.4 we have shown that the initial biomass of the species contributes in determining which competitor wins. The species that has an advantage at the beginning of the interaction wins the competition. The advantage comes from two parameters: the initial biomass of the competing species and the efficiency of converting the nutrient into additional biomass. This efficiency is represented by the nutrient uptake function. If the biomass of the two competing species is the same at the beginning of the interaction, the species that is able to convert nutrient to biomass more efficiently wins the competition. If a superior competitor (the one that is more efficient in converting nutrient to biomass) is at a slight disadvantage at the beginning, it might be able to counteract the inhibition effect from its competitor by quickly utilizing the nutrient and converting it to biomass, and increase the inhibition effect against its competitor. But this will be possible only if the product of the biomass and uptake is greater than that of its competitor.

The key difference in predictions between (4.8) and (5.1) is that while (4.8) predicts persistence for all competing species, (5.1) predicts that only one competitor survives. An open question arises as to whether choosing different functions to model mutual inhibition would result in different dynamics of (5.1).

6.2 Applications

The study of chemostat-like models may find many applications in nature. For a start, the models presented in this study are of interest for further research by students and scientists working in, for example, waste water treatment. The general nature of the models presented mean they can

be modified to address specific cases in wide areas of study where competition for resources is involved.

The models may also find applications in continuously stirred tank reactors (CSTR) where they may be used to optimize feasible and reliable bioprocess systems in order to treat hydrocarbon-rich industrial wastewater.

The chemostat-like model with mutual inhibition may help explain why plants such as the Field Bindweed (*Convolvulus arvensis*) intertwines and topples native species [14].

Specifically, the models may find applications in the following areas:-

1. Biotechnology - modeling the commercial bio-reactor used to manufacture products with genetically altered organisms - e.g. Mutual inhibition among postmitotic neurons regulates robustness of brain wiring in Drosophila.
2. Farming e.g. The ability of plants to take nitrogen from the air and fix it in the plant depends on the presence of mutually inhibiting species of Rhizobium
3. Waste water treatment - Easily biodegradable pollutants and Telepthalic acid inhibit each other under anaerobic conditions causing low removal efficiency of both from effluent.
4. Modeling a simple lake - Eurasian water milfoil prevents algae blooms while high densities of algae limits the growth of milfoil.
5. Help explain why some parasitic plants kill off their hosts - tall trees in a forest form a canopy that prevents growth of other plants below, but some of those plants twine up the trees to near strangulation.

6.3 Suggestions for Further Study

With mutual inhibition, chemostat models with periodic parameters predict competitive exclusion. We have used a Holling Type II uptake function. Further studies may be needed to find out whether the predictions hold with different types of functions describing nutrient uptake. The following are suggestions that future studies may look at:-

1. Do the predictions of the chemostat models with mutual inhibition hold if we assume a Lotka-Voltera uptake function?
2. Do other types of uptake functions result in different dynamics of the chemostat model with mutual inhibition?
3. Is there a possibility of the appearance of qualitatively different solutions to the system as the parameters in the inhibition function are varied (emergence of bifurcations)?
4. As shown in this study, the behaviour of the dynamical system is dependent on initial conditions. Is it possible that certain changes in the inhibition function may lead to deterministic chaos?
5. The models presented in this study have assumed that the competing species reproduce immediately after consumption of the nutrient. This is not very realistic in nature. Will the dynamics of the system change if delays are introduced into the system?

The models presented in this study open up exciting opportunities for further research. The models are more basic than those previously presented. The models discussed previously in other studies are just special cases of those presented here.

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Appendix A: Article in International Journal of Applied Mathematics and Computation.

Appendix B: Article in International Journal of Modern Engineering Research.

Appendix C: Accepted Article in American Journal of Mathematics and Mathematical Sciences