To my father, Willard S. Keeran; my mother, Kathleen Frost; and my Aunt, Gertrude Roughen
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This work examines coexistence in a chemostat equipped with a feedback-mediated diluter function. For a system with two organisms and a single growth limiting nutrient, diluter functions are designed which produce orbits of circular and elliptical shapes. By further modifying the feedback function, an individual orbit may be made asymptotically stable or a series of orbits may be produced with alternating stability. For a system of three organisms, a single growth limiting nutrient, and an affine feedback function, a perturbation method is used to establish restrictions on growth functions which yield coexistence of all three species. The local bifurcation analysis is presented and the criterion for stability of the bifurcating periodic solutions is obtained. Numerical results for a feedback function which is affine in three variables is presented and initial findings for bifurcation from a line of equilibria are discussed.
CHAPTER 1
INTRODUCTION

A chemostat is a laboratory apparatus used to grow microorganisms. In its most basic form it consists of a culturing vessel or container with an inlet and an outlet. The nutrients or substrates for the organisms are present in a solution which is delivered to the vessel through the inlet. Depending on the purpose of the chemostat, this influent may be mixed, using a mechanical stirrer, with the suspension of microbes present in the container. Excess liquid containing waste, nutrients, and organisms leaves the vessel through the outlet and at a rate equal to that of the influent. Under normal operating conditions, the volume as well as the temperature, pH, etc., remains constant. As we shall soon see, many combinations of nutrients, organisms, and influent rates, to name a few variations, are possible and add theoretical complexities to the basic system. The importance of the chemostat transcends its use as a means of culturing bacteria and fungi. In the pharmaceutical industry, bioengineered organisms grown in chemostats are harvested for enzymes such as human insulin. In the agricultural industry, the chemostat is used in the production of dairy items such as yogurt and cheese, while in waste treatment, it is used in the removal of heavy metals from water. From an ecological standpoint, the chemostat serves as an experimental platform for the modeling of the interactions of microbes in a simple ecosystem. Thus for both practical and theoretical purposes, a mathematical understanding of the chemostat in its many configurations is important.

1.1 Model of a Basic Chemostat

To introduce the mathematical description of the chemostat, we begin by considering a simple, well-stirred bioreactor of constant volume $V$ inoculated with two organisms whose only interactions are competition for nutrients and whose concentrations are denoted by $x_1(t)$ and $x_2(t)$. The chemostat will have a flow rate, $F$, (the rate, volume per unit time, at which the influent enters and the effluent exists the reaction vessel) and a single growth-limiting substrate whose concentration in the vessel is given by
$S(t)$ and whose concentration in the influent has a constant value of $S_0$. A substrate is growth-limiting if all other essential nutrients are present in excess and the rate of growth for the microorganism depends solely on this single nutrient. In the absence of consumption by microorganisms, the rate of change of the total quantity of substrate would be represented by

$$
(VS)' = FS_0 - FS(t).
$$

Since the volume of the chemostat remains constant, we may divide through by $V$ in the above equation and write

$$
S' = DS_0 - DS(t)
$$

where $D = F/V$ and is referred to as the diluter rate. In the development below, the volume of the chemostat will be scaled out of all rate equations using a similar method.

The dependence of the growth of the microbes on $S$ is represented by introducing uptake-functions, $f_i(S(t))$, which give the rate of ingestion of the limiting substrate by organism $x_i(t)$ as a function of $S$. The form of these functions can vary greatly and they may be simple linear rates or much more complex mappings; in general, however, it is assumed that $f_i(0) = 0$ or in other words that uptake does not occur in the absence of the substrate. Associated with the uptake functions, are the yield functions, $\gamma_i(S(t))$, which give the rate of conversion of nutrients to biomass. The forms of these functions are also variable and in the simplest case are assumed to be constant. Combining the above, the rate of growth or increase in organism $x_i(t)$ is given by $x_i(t)f_i(S(t))\gamma_i(S(t))$. In addition to growth, the chemostat model can be varied to include a microbial death rate which in its most basic form is given by $-\mu_i x_i(t)$ with $\mu_i$ a constant; in this exposition, however, we will consider the death rate to be insignificant when compared to the "washout rate", $-Dx_i(t)$, which results from microbes leaving the vessel in the effluent. As with the microbes, the substrate concentration is affected by several influences. The substrate enters the reaction vessel at a concentration $S_0$ with a diluter rate $D$, is consumed by the organisms at rates $x_1(t)f_1(S(t))$ and $x_2(t)f_2(S(t))$, and leaves the chemostat at a
concentration $S(t)$ and at a diluter rate $D$. From this discussion, it is readily deduced that the system of equations describing the time dependent rate of change of the variables $x_1(t), x_2(t),$ and $S(t)$ is given by

$$
\dot{x}_1(t) = x_1(t)f_1(S(t))\gamma_1(S(t)) - Dx_1(t),
$$

$$
\dot{x}_2(t) = x_2(t)f_2(S(t))\gamma_2(S(t)) - Dx_2(t),
$$

$$
\dot{S}(t) = DS_0 - x_1(t)f_1(S(t)) - x_2(t)f_2(S(t)) - DS(t).
$$

Quite often it is convenient to redefine variables so that the resulting system of ODEs has a less-complicated structure; this technique is referred to as rescaling. To demonstrate this technique we use the above system and assume that the $\gamma_i$'s are constant. Rewriting the above system using this simplification and not explicitly denoting the dependence of the other variables on $t$ we obtain

$$
\dot{x}_1 = x_1 f_1(S)\gamma_1 - Dx_1,
$$

$$
\dot{x}_2 = x_2 f_2(S)\gamma_2 - Dx_2,
$$

$$
\dot{S} = DS_0 - x_1 f_1(S) - x_2 f_2(S) - DS.
$$

If we perform the following substitutions: $S = S_0 s$, $x_i = S_0 \gamma_i X_i$, and $\gamma_i f_i(S_0 s) = F_i(s)$ into the above system and then simplify we obtain

$$
\dot{X}_1 = X_1 (F_1(s) - D),
$$

$$
\dot{X}_2 = X_2 (F_2(s) - D),
$$

$$
\dot{s} = (1-s)D - X_1 F_1(s) - X_2 F_2(s).
$$

In this report, all chemostat systems will be appropriately rescaled in order to facilitate computations.
1.2 Coexistence and Systems of Greater Complexity

Since the initial analysis of the chemostat over fifty years ago [33], the basic model introduced above has been greatly varied to reflect the natural differences and complexities found in microorganisms and their ecosystems. A common theme which resonates from this large body of research is that of coexistence of multiple organisms. A fundamental result, known as competitive exclusion [21], states that if a chemostat contains a single growth-limiting nutrient, a fixed diluter value, and multiple organisms, then at most one of the organisms will survive and the others will be driven to extinction. Since natural ecosystems display species diversity, much effort has been expended in modifying basic chemostat models in order to understand the factors which contribute to this diversity.

Perhaps the simplest way to achieve this coexistence is through the introduction of multiple nutrients which are chosen in such a way that each organism has a "preference" for a different substrate [4, 23, 30, 43]. Two nutrients are called "substitutable" if an organism will grow in the presence of each individually or "complementary" if both are required for growth. Leon and Tumpson [30] established equilibrium conditions for two organisms with monotonically increasing kinetics in the cases of both substitutable and complementary nutrients. Hsu, et al., [23] examined the system parameters required for the coexistence of two organisms with Michaelis-Menten growth functions and complementary resources. Butler and Wolkowicz studied non-monotonic kinetics for systems of two organisms and using growth inhibition at high substrate concentrations found conditions which produced periodic orbits and conditions in which one organism could not survive without the presence of the other.

Since naturally occurring temporal variations in environmental conditions may effect coexistence, much effort has been expended to understand and model these influences [6, 17, 22, 37, 38, 49]. Butler, et. al., [6] examined a system with two organisms, Michaelis-Menten growth functions, and a periodic diluter rate and found conditions under which a periodic orbit was obtained. Hsu [22] performed numerical studies on
systems with Michaelis-Menten growth functions and oscillatory nutrient concentration and obtained coexistence results. Smith [38] expanded the work of Hsu and was able to analytically establish the conditions for coexistence of two organisms. Hale and Somolinos [17] examined systems with monotonically increasing and bounded yet non Michaelis-Menten growth functions and discovered the existence of periodic orbits. With minimal conditions on continuous growth functions, Rao and Roxin [37] used a time dependent nutrient concentration to produce systems in which $n$ organisms can coexist. In a somewhat recent paper Wolkowicz and Zhao [49] have combined the periodicity of the diluter and substrate concentration to obtain, under certain conditions, coexistence of an arbitrary number of organisms.

Two additional mechanisms for achieving coexistence in a system with a single growth limiting nutrient are variable yields and the unstirred chemostat. For a system of two organisms, one of which exhibited a variable yield (i.e., a yield which is a function of the substrate concentration), Pilyugin and Waltman [35] provided numerical evidence of coexistence through oscillatory growth. The variable yield question was further studied in Arino, et. al., [1] where a necessary condition for strong coexistence was established and where a coexistence result for three organisms was numerically demonstrated. Reflecting the fact that in most ecosystems nutrients and biological organisms are not "homogeneously" distributed, Hsu, et. al., [24] studied an unstirred chemostat and demonstrated uniform persistence of two organisms. Pilyugin and Waltman [34] analyzed a model of an unstirred chemostat with two organisms and periodic input and washout; they established conditions under which coexistence or competitive exclusion were possible.

1.3 Feedback-Mediated Coexistence

A new approach to the coexistence problem has been the use of a feedback-mediated diluter function [11–13, 15, 27, 42]. This technique has gained popularity due to recent advances in technology which has made possible "near real-time" determination of
substrate and species concentrations. Using affine feedback in a model with monotonic growth functions, DeLeenheer and Smith [11] were able to create a globally attracting equilibrium for a system with two organisms and a single substrate. This technique, however, could not be extended to a larger number of species. The above results, including the inability of three species to coexist, were extended by Gouze and Robledo [15] to a system with non-monotonic growth functions. Taking into consideration the effects of time delays in the model of De Leenheer and Smith [11], Tagashira and Hara [42] demonstrated the existence of a periodic orbit even in the absence of an interior equilibrium.

1.4 Present Research

The use of feedback to provide for coexistence in the chemostat was the motivation for the present research. The specific goal of this study was to produce a system with a single growth-limiting nutrient, a feedback-mediated diluter function, and in which the coexistence of three or more organisms was possible. The overall approach was to first develop a system for two species which exhibited an asymptotically stable periodic orbit and then introducing a third species, obtain a bifurcation which transformed the above orbit into one which was three dimensional and asymptotically stable.

To this end, the research initially focused on systems of two organisms and the development of diluter functions to produce stable orbits of known shape [28]. We were able to develop nonlinear diluter functions which produced both circular and elliptic orbits for systems of two organisms whose growth functions were subjected to quite minimal constraints. By further modifying the diluter function it was possible to choose a particular orbit and make it asymptotically stable. Finally, we were able to design diluter functions that guaranteed the simultaneous existence of a finite number of elliptical orbits with alternating stability.

The diluter functions used to produce orbits of known shape were quite complex and this complexity made the analysis of bifurcations from these orbits a less viable option. As a result, a second approach was developed which used an affine diluter function in
two variables and a bifurcation from a Hopf-generated periodic orbit present in one of the coordinate planes. Using a perturbation technique (which did not require a geometric description of the Hopf orbit) employed by Smith [39] and under appropriate restrictions on growth functions, it was possible after some extensive, computer-aided calculations to prove that affine feedback systems could produce an asymptotically stable periodic orbit for three organisms [27].

Although the above results demonstrated coexistence, the perturbation technique yielded orbits of small amplitude in which the concentration of one of the organisms was arbitrarily small. To circumvent this, additional linear diluter functions were designed which, in numerical simulations, suggest the existence of a asymptotically stable periodic orbits throughout positive octant (the octant formed by the concentrations of the three species). In addition, the above research indicated the importance of bifurcation from a line of equilibria for a system of three organisms. As a result, some preliminary analysis was performed for such a bifurcation with a system possessing linear growth functions.

1.5 Some Preliminary Concepts

In order to assist the reader who may not be familiar with key concepts needed later in the document, this section is included as an abridged introduction to these topics.

1.5.1 Poincaré-Lindstedt Method

Central to proof of the coexistence of three organisms is the Poincaré-Lindstedt Method (PLM) [44]. The method is designed to work for a system of ODEs with a periodic solution and a scalar parameter; if the parameter is changed by some small positive quantity, then the perturbed system may or may not have a periodic solution. If such a solution does exist the PLM is designed to detect it. To this end, the method assumes that if the perturbation is slight then the new periodic solution will be very close to the original solution and the new period will vary slightly from the old one. As described below, the method relies upon a power series expansion of the new solution and
the theoretical justification for this approach and in particular for the convergence of the
power series is based on the following Poincaré expansion theorem (Theorem 9.2 in [44])

**Theorem 1.** Consider the initial value problem
\[ \dot{x}(t) = f(t, x, \varepsilon), \quad x(t_0) = \mu \]
with \( |t - t_0| \leq h, \ x \in D \subset \mathbb{R}^n, \ 0 \leq \varepsilon \leq \varepsilon_0, \text{ and } 0 \leq \mu \leq \mu_0. \) If \( f(t, x, \varepsilon) \) is continuous with respect to \( t, x, \) and \( \varepsilon \) and can be expanded in a convergent power series with respect to \( x \) and \( \varepsilon \) for \( ||x|| \leq \rho, \ 0 \leq \varepsilon \leq \varepsilon_0, \) then \( x(t) \) can be expanded in a convergent power series with respect to \( \varepsilon \) and \( \mu \) in a neighborhood of \( \varepsilon = \mu = 0, \) convergent on a time-scale 1.

To understand the method we consider the system \( \dot{x}(t) = f(t, x, \varepsilon) \) where the derivative is with respect to \( t \) and assume that for \( \varepsilon = 0 \) there exists a periodic solution \( \phi(t) \) with period \( T. \) If the parameter \( \varepsilon \) is perturbed to a small positive number, we assume there exists a new periodic solution to the altered system and represent it by
\[ \tilde{\phi}(t) = \phi(t) + \varepsilon \phi_1(t) + \varepsilon^2 \phi_2(t) + \cdots. \]
We also introduce a new variable \( \tau = \omega t \) with \( \omega = 1 + \varepsilon \omega_1 + \varepsilon^2 \omega_2 + \cdots. \) Placing the time variable substitution into the original system we obtain
\[ \omega \frac{d}{d\tau} x(\tau/\omega) = \tilde{f}(\tau/\omega, x(\tau/\omega), \varepsilon). \]
Replacing \( x(\tau/\omega) \) with \( \tilde{\phi}(\tau/\omega) \) in the above equation, we separately collect the terms of power \( \varepsilon^0, \varepsilon^1, \) etc., and successively determine the components \( \omega_i \) and \( \phi_i \) by solving each equality and requiring all solutions to be periodic with period \( \omega T. \) If a periodic solution does not exist for the perturbed system, then for at least one of the \( \varepsilon^n, \) a periodic solution will not exist for the associated equality; otherwise, an approximation to the new periodic solution will be obtained.

### 1.5.2 Bifurcation from a Simple Eigenvalue

In Chapter 3 the coexistence result for three organisms is obtained by bifurcating from a Hopf orbit in the \( x, y \) plane to a locally stable periodic orbit in the positive first octant. A tool needed in the justification for the existence of such a three dimensional limit cycle is provided by the following theorem (Theorem 1.7 in [9])

**Theorem 2.** Let \( V \) be a neighborhood of \( 0 \) in \( \mathbb{R}^2 \) (the \( y, z \) plane) and \( \tilde{F} : V \times (-1, 1) \to \mathbb{R}^2 \) have the properties
1. \( \tilde{F}(0, \eta) = 0 \) for \( |\eta| < 1, \)
2. The partial derivatives \( \bar{F}_\eta, \bar{F}_{(y,z)}, \) and \( \bar{F}_{\eta(y,z)} \) exist and are continuous,

3. \( N(\bar{F}_{(y,z)}(0,0)) \) is one dimensional.

4. \( \bar{F}_{\eta(y,z)}(0,0)u \not\in \text{R}(\bar{F}_{(y,z)}(0,0)), \) where \( N(\bar{F}_{(y,z)}(0,0)) = \text{span}\{u\}. \)

If \( Z \) is any element in \( \mathbb{R}^2 \) which is not in \( N(\bar{F}_{(y,z)}(0,0)) \), then there exists a neighborhood \( U \) of \( (0,0) \) in \( \mathbb{R}^2 \times \mathbb{R} \), an interval \( (-a,a) \), and continuous functions \( \phi : (-a,a) \rightarrow \mathbb{R}, \psi : (-a,a) \rightarrow Z \) such that \( \phi(0) = 0, \psi(0) = 0, \) and \( F^{-1}(0) \cap U = \{(su + s\psi(s), \phi(s)) : |s| < a\} \cup \{(0,\eta) : (0,\eta) \in U\}. \)

To summarize the approach in Chapter 3, a point on the planar Hopf orbit will be chosen and the variables translated so that this point is the new origin for a three dimensional system with a scalar bifurcation variable \( \eta \). Next a Poincaré map is defined with the origin as a fixed point and the function \( \bar{F} \) is defined to represent a displacement from this fixed point. The function \( \bar{F} \) will be shown to satisfy the four conditions of the theorem and hence we establish the existence of a branch of solutions of \( \bar{F}^{-1}(0) \) which are a function of a new scalar variable \( s \). This branch of solutions correspond to fixed points of the Poincaré map and thus defines a set of periodic orbits which exist in the first octant. The stability of these orbits will be determined by other procedures.

1.5.3 Liapunov Functions and the LaSalle Invariance Principle

In the study of dynamical systems it is of interest to determine the stability of equilibrium points and to gather some information on the basin of attraction of those rest points which are asymptotically stable. Such analysis is sometimes possible using Liapunov functions and the LaSalle’s invariance principle. The present discourse on these techniques is based upon the book by Hale and Kocak [16].

For the sake of this presentation, we assume there exists a two dimensional system of ODEs given by \( \dot{x} = f(x) \) and that \( x = 0 \) is an isolated equilibrium for this system. Let \( U \) be a neighborhood of \( 0 \) which contains no other rest points; a function \( V(x) : U \rightarrow \mathbb{R} \) is called positive-definite on \( U \) if \( V(0) = 0 \) and \( V(x) > 0 \) for all \( x \in U \) with \( x \neq 0 \). Under
certain conditions these positive-definite functions can be used to determine the stability of the origin as is noted by the following theorem due to Liapunov (Theorem 9.12 in [16])

**Theorem 3.** Let $\mathbf{x} = 0$ be an equilibrium point of $\mathbf{x} = f(\mathbf{x})$ and $V$ be a positive-definite $C^1$ function on $U$

1. If $\dot{V}(\mathbf{x}) \leq 0$ for $\mathbf{x} \in U \setminus \{\mathbf{0}\}$, then $\mathbf{0}$ is stable.
2. If $\dot{V}(\mathbf{x}) < 0$ for $\mathbf{x} \in U \setminus \{\mathbf{0}\}$, then $\mathbf{0}$ is asymptotically stable.
3. If $\dot{V}(\mathbf{x}) > 0$ for $\mathbf{x} \in U \setminus \{\mathbf{0}\}$, then $\mathbf{0}$ is unstable.

A function $V(\mathbf{x})$ is called a Liapunov function if it satisfies the first condition above and is called strictly Liapunov if it satisfies the second condition. While in theory Liapunov functions are useful in analyzing the stability of equilibria, the difficulty lies in the fact that there is no method to derive such a function $V(\mathbf{x})$ for an arbitrary system of ODEs.

Closely related to the concept of Liapunov functions is LaSalle’s invariance principle. The principle is useful in defining, under certain conditions, $\omega$-limit sets and basins of attractions for systems of ODE’s. The general statement of the result is given by the following theorem (Theorem 9.22 in [16])

**Theorem 4.** Let $V$ be a real-valued function and let $U \equiv \{\mathbf{x} \in \mathbb{R}^2 : V(\mathbf{x}) < k\}$, where $k$ is a real number. Suppose further that $V$ is continuous on the closure $\bar{U}$ of $U$ and is $C^1$ on $U$ with $\dot{V}(\mathbf{x}) \leq 0$ for $\mathbf{x} \in U$. Consider the subset $S$ of $U$ defined by $S \equiv \{\mathbf{x} \in \bar{U} : \dot{V}(\mathbf{x}) = 0\}$ and let $M$ be the largest invariant set in $S$. Then every positive orbit that starts in $U$ and remains bounded has its $\omega$-limit set in $M$.

While the function $V$ used in the above theorem need not be a Liapunov function, it is clear that if $V$ is a Liapunov function for an equilibrium point $\bar{x}$ and if $\bar{x}$ is the only rest point contained in $U$, then $V$ satisfies the conditions for the function used in Theorem 4.

Of practical use in the analysis of rest points is the following corollary to the above theorem (Corollary 9.24 in [16])
Corollary 1. If, in addition, every positive orbit is bounded and $V$ is positive definite for $x \in U \backslash \{0\}$, then $M = \{0\}$, that is the origin is asymptotically stable and all of $U$ belongs to its basin of attraction.

In Section 2.3 these concepts will play a pivotal role in applying a result from control theory to the stabilization of elliptical orbits.
CHAPTER 2
CIRCULAR AND ELLIPTICAL ORBITS

In this chapter we discuss the design of elliptical and circular orbits for a system of two organisms and a single growth-limiting nutrient.

2.1 Model of the Feedback-Mediated Chemostat

We begin with a set of equations which represent the chemostat described in the introduction and which have been rescaled so that the feed concentration and yield coefficients are all equal to one:

\[
\begin{align*}
\dot{S} &= (1 - S)D(x, y) - xf(S) - yg(S), \\
\dot{x} &= x(f(S) - D(x, y)), \\
\dot{y} &= y(g(S) - D(x, y)),
\end{align*}
\]

where \( S \) is the concentration of growth limiting nutrient; \( x \) and \( y \) are the concentrations of the organisms; \( D(x, y) \) is the dilution rate which is a function of \( x \) and \( y \); and \( f(S) \) and \( g(S) \) are the growth functions for organisms \( x \) and \( y \) respectively and both functions are at least \( C^2 \). We assume that the state variables \( x, y, \) and \( S \) are all greater than or equal to zero. We also assume that the growth functions are equal to zero when the substrate concentration is zero and are equal at some intermediate substrate concentration \( S \in (0, 1) \). Finally, we assume that the growth functions satisfy the inequality \((f(S) - g(S))(S - \bar{S}) > 0\) for \( S \in (0, 1), \, S \neq \bar{S} \). \(^1\)

In order to reduce the number of equations representing the system, we define a new variable \( z = 1 - S - x - y \) and using Equation 2-1 and the time dependence of \( x \) and \( y \) obtain the equation \( \dot{z} = -D(x(t), y(t))z \). The solutions of this equation are given by \( z(t) = z(0)e^{-\int_0^t D(x(s), y(s)) ds} \) and they clearly converge to zero as long as \( \int_0^{+\infty} D(x(t), y(t)) dt = +\infty \). In particular, this will happen if \( D(x(t), y(t)) > 0 \) is bounded

\[\text{Importantly, we do not assume that the growth functions } f \text{ and } g \text{ are monotonically increasing.}\]
away from zero. The set \( \{ z = 0 \} \) is an exponentially attracting invariant set for system given by Equation 2–1. In what follows, we restrict the analysis to the dynamics on this set. As a result, we substitute \( S = 1 - x - y \) into Equation 2–1, and obtain the so-called limiting system

\[
\begin{align*}
\dot{x} &= x(f(1 - x - y) - D(x, y)), \\
\dot{y} &= y(g(1 - x - y) - D(x, y)), \\
\end{align*}
\] (2–2)

where \( D(x, y) \) is strictly positive. Since \( 1 - S = x + y \geq 0 \), the state space for this system is the triangular region in the \( xy \) plane with vertices \((0, 0)\), \((1, 0)\), and \((0, 1)\). The intersection of this triangle with the line \( 1 - \bar{S} = x + y \) provides a segment which must contain all nontrivial equilibria (if they exist).

In the subsequent sections, we will present several different constructions for the feedback function \( D(x, y) \) that produce both stable and unstable periodic solutions of Equation 2–2. Here, we present a formal justification that the stability of such periodic solutions under the dynamics of the full system given by Equation 2–1 remains the same. Suppose that \((x(t), y(t))\) is a periodic solution of Equation 2–2 of period \( T > 0 \) with Floquet multipliers \( \mu_1 = 1 \) and \( \mu_2 \neq 1 \). Then \((x(t), y(t), 0)\) is a \( T \)-periodic solution of the system

\[
\begin{align*}
\dot{x} &= x(f(1 - x - y - z) - D(x, y)), \\
\dot{y} &= y(g(1 - x - y - z) - D(x, y)), \\
\dot{z} &= -D(x, y)z, \\
\end{align*}
\] (2–3)

which is equivalent to Equation 2–1. The variational system of Equation 2–3 along \((x(t), y(t), 0)\) is given by

\[
\dot{\phi} = \begin{pmatrix}
M(t) & -x(t)f'(1 - x(t) - y(t)) \\
-y(t)g'(1 - x(t) - y(t)) & -D(x(t), y(t)) \\
0 & 0
\end{pmatrix} \phi, \phi(0) = I_3,
\]

where \( M(t) \) is the \( 2 \times 2 \) matrix of the variational system of Equation 2–2 along \((x(t), y(t))\). Consequently, the Floquet multipliers of \((x(t), y(t), 0)\) are \( \mu_1 = 1 \), \( \mu_2 \neq 1 \), and \( \mu_3 = \)
\exp(- \int_0^T D(x(t), y(t)) \, dt) < 1. In both cases, the stability of the corresponding periodic solution is determined by \( \mu_2 \).

### 2.2 Dilution Function for Circular and Elliptic Orbits

The main focus of this section is the construction of dilution rates which control the shape, number, and stability of periodic orbits for the given chemostat system. The following theorem establishes the basic results for orbits of prescribed shape.

**Theorem 5.** Let \( f, g \) be \( C^n \) (\( n \geq 2 \)) smooth and suppose that there exists \( \bar{S} \in (0, 1) \) such that \( f(\bar{S}) = g(\bar{S}), f'(\bar{S}) \neq g'(\bar{S}), \) and \( f(S) \neq g(S) \) for all \( S \in (0, 1) \setminus \{ \bar{S} \} \). Then there exists a non-empty elliptic domain \( \Omega \subset \{(x, y) : 0 < x, y < x + y < 1\} \) and a \( C^{n-1} \) smooth function \( D : \Omega \to (0, \infty) \) such that

- The domain \( \Omega \) is invariant under the flow of the system given by Equation 2–2 with \( D = D(x, y) \);
- The system given by Equation 2–2 with \( D = D(x, y) \) is conservative in \( \Omega \);
- The point \( \left( \frac{1-\bar{S}}{2}, \frac{1-\bar{S}}{2} \right) \in \Omega \) is the only equilibrium of Equation 2–2 in \( \Omega \), any other point of \( \Omega \) belongs to an elliptic periodic orbit. One of the elliptic orbits is a circle.

The proof proceeds in several stages. First, we construct a smooth dilution rate which produces a circular periodic orbit. Second, we show that all orbits interior to the circle are elliptic periodic orbits and that the only equilibrium occurs at \( \left( \frac{1-\bar{S}}{2}, \frac{1-\bar{S}}{2} \right) \). The region \( \Omega \) is then defined and the properties of the orbits in \( \Omega \) are shown to be identical to those of the orbits in the interior of the circle. Once these properties are established, the invariance of \( \Omega \) and the conservative nature of system given by Equation 2–2 on \( \Omega \) follow naturally.

**Proof of Theorem 5.** We begin by introducing a new coordinate system defined by \( z = x + y, w = x - y \). In the new variables, the system given by Equation 2–2 becomes

\begin{align*}
\dot{z} &= zF(z) + wG(z) - zD(z, w), \\
\dot{w} &= zG(z) + wF(z) - wD(z, w),
\end{align*}

(2–4)

where

\[ F(z) = \frac{f(1-z) + g(1-z)}{2}, \quad G(z) = \frac{f(1-z) - g(1-z)}{2}. \]
The triangular state space in the new coordinates is formed by the intersection of the lines \( w = z, w = -z, \) and \( z = 1 \) and the segment containing possible nontrivial equilibria is on the line \( z = 1 - \bar{S} = \lambda. \)

2.2.1 Construction of \( D(z, w) \)

We assume the existence of a circular periodic orbit given algebraically by \((w - w_0)^2 + (z - z_0)^2 = r^2\) and determine the necessary dilution rate. Differentiating both sides of this equation with respect to time yields

\[
(w - w_0)\dot{w} + (z - z_0)\dot{z} = 0,
\]

and substituting from the transformed system provides

\[
(w - w_0)(zG(z) + wF(z) - wD(z, w)) + (z - z_0)(zF(z) + wG(z) - zD(z, w)) = 0. \tag{2–5}
\]

For any \( T \)-periodic solution \((z(t), w(t))\) of Equation 2–4 in the region \( z > 0, -z < w < z, \)

we can define \( \alpha(t) = w(t)/z(t) \in (-1, 1) \) so that

\[
\dot{\alpha} = (1 - \alpha^2)G(z).
\]

Integrating over the period, we obtain

\[
0 = \int_0^T \frac{\dot{\alpha}(t)}{1 - \alpha^2(t)} dt = \int_0^T G(z(t)) dt.
\]

Therefore, any nontrivial periodic orbit of Equation 2–4 must contain points where \( G(z) < 0 \) and \( G(z) > 0. \) For instance, if the periodic orbit is a circle, it must intersect the line \( z = \lambda \) at two distinct points. To find these points we substitute \( z = \lambda \) and \( w = w^* \) into Equation 2–5 and obtain

\[
(f(1 - \lambda) - D(\lambda, w^*))(\lambda - z_0) + w^*(w^* - w_0)) = 0.
\]

If \( w^* \) is such that \( f(1 - \lambda) - D(\lambda, w^*) = 0, \) then \( g(1 - \lambda) - D(\lambda, w^*) = 0 \) and there is an equilibrium at the intersection of the circle and the line \( z = \lambda \) so that the orbit is no
longer periodic. Hence we must have

\[ \lambda(\lambda - z_0) + w^*(w^* - w_0) = 0, \]
\[ f(1 - \lambda) - D(\lambda, w^*) \neq 0. \]

Solving for \( w^* \), we find \( w^* = \frac{w_0 \pm \sqrt{w_0^2 - 4\lambda(\lambda - z_0)}}{2} \). Substituting \((\lambda, w^*)\) into the equation for the circle and rearranging gives

\[ \left( -w_0 \pm \sqrt{w_0^2 - 4\lambda(\lambda - z_0)} \right)^2 = r^2 - (\lambda - z_0)^2 = \text{Const}. \]

This equation is consistent if and only if \( w_0 = 0 \) or \( \sqrt{w_0^2 - 4\lambda(\lambda - z_0)} = 0 \). If the radical is equal to zero, this implies that the line \( z = \lambda \) intersects the circle at only one point which is a contradiction; thus \( w_0 = 0 \) and \( w^* = \frac{\pm\sqrt{-4\lambda(\lambda - z_0)}}{2} \).

The fact that \( w_0 = 0 \) immediately leads to several constraints on the circular orbit. First, since \( w^* \) is real and \( \lambda \) is real and positive, this implies \( z_0 > \lambda \) or that the center of the circle, \((z_0, 0)\), lies to the right of the line \( z = \lambda \). Using this fact and considering that the circle must intersect the line \( z = \lambda \) twice while not intersecting the line \( z = 1 \) implies \( \lambda < z_0 < \frac{1}{2}(1 + \lambda) \). In addition, there are several constraints on the radius of the circle. Since the circle may not intersect the line \( z = 1 \), this implies \( r < 1 - z_0 \); since the circle may not intersect the line \( z = 0 \), this implies \( r < z_0 \). The fact that the circle may not intersect the lines \( w = \pm z \) provides the restriction: \( r < \frac{\sqrt{3}z_0}{2} \).

Returning to equation Equation 2–5, we substitute \( w_0 = 0 \) and solve for \( D(z, w) \) to obtain for all \((z, w)\) on the circle

\[ D(z, w) = \frac{(z - z_0)(zF(z) + wG(z)) + w(zG(z) + wF(z))}{r^2 - z_0^2 + z_0 z} \]

or by defining the formal expression

\[ \tilde{G}(z) = \frac{(2z - z_0)}{r^2 + z_0(z - z_0)} G(z), \]
the equation for $D$ becomes

$$D(z, w) = F(z) + w\tilde{G}(z). \quad (2-6)$$

Substituting the dilution rate Equation 2–6 into Equation 2–4, we obtain the system

$$\begin{align*}
\dot{z} &= w(G(z) - z\tilde{G}(z)), \\
\dot{w} &= zG(z) + w^2\tilde{G}(z),
\end{align*} \quad (2-7)$$

For the function $D(z, w)$ to be a feasible dilution rate for the chemostat model, it must be smooth, strictly positive, and not produce any equilibria on the circle.

### 2.2.2 Feasibility and Smoothness of $D(z, w)$

In determining the smoothness of the dilution rate $D(z, w)$, we note that $F(z)$ and $G(z)$ are as smooth as the growth functions $f(S)$ and $g(S)$ which by assumption are $C^n$. Examining the denominator of the expression $\tilde{G}(z)$ we find that a first degree zero exists at the point $z^* = \frac{z_0 - r^2}{z_0}$. For the dilution rate to remain smooth, the function $G(z)$ must also have at least a first degree zero at $z^*$. By assumption, the growth functions intersect only at one point in $(0, 1]$, so that the only zero of $G(z)$ occurs at $z = \lambda$. Thus a criterion for smoothness is that $z^* = \lambda$ which implies $r = \sqrt{z_0(z_0 - \lambda)}$. The value of $\tilde{G}(\lambda)$ is then determined from l’Hospital’s rule,

$$\tilde{G}(z) = \begin{cases} 
\frac{(2z - z_0)}{r^2 + z_0(z - z_0)} G(z), & z \neq \lambda, \\
\frac{(2\lambda - z_0)}{z_0} G'(), & z = \lambda.
\end{cases}$$

By the definitions of $\tilde{G}(z)$, $G(z)$, $F(z)$, and Equation 2–6, the function $D(z, w)$ is $C^{n-1}$.

To ensure that the dilution rate $D$ remains positive on the circle, we begin by fixing an $h$ with $0 < h < \min(\lambda, 1 - \lambda)$ and such that $[z_0 - r, z_0 + r] \subset [\lambda - h, \lambda + h]$; by continuity of $F$ and $\tilde{G}$, there exist positive constants $m_1$ and $m_2$ such that $F(z) \geq m_1$ and $|\tilde{G}(z)| \leq m_2$ for $z \in [\lambda - h, \lambda + h]$. Using the definition of $D$ given by Equation 2–6 and the fact that $|w| \leq r$ on the circle, we establish the following inequality

$$D(z, w) = F(z) + w\tilde{G}(z) \geq m_1 - rm_2.$$
Thus by choosing \( 0 < r < \min(h, \frac{m_1}{m_2}) \) the dilution rate will remain positive for all points on the circular orbit.

Finally, we must ensure that our choice of the dilution rate does not produce equilibria on the invariant circle. It was previously noted that equilibria can only occur on the line \( z = \lambda \) so that the only candidate points on the circle would be \((\lambda, w^*) = (\lambda, \pm \sqrt{-4\lambda(\lambda-z_0)})\). These points are equilibria if and only if \( D(\lambda, w^*) = f(1 - \lambda) = g(1 - \lambda) \) which implies that \( w^* \hat{G}(\lambda) = 0 \). In particular, if \( w^* \neq 0 \), then \( \hat{G}(\lambda) = 0 \). Hence, our choice of \( D \) produces no equilibria on the circle if and only \( G'(\lambda) \neq 0 \) (equivalently, \( f'(1 - \lambda) \neq g'(1 - \lambda) \)).

Summarizing the results, we find the dilution rate defined by Equation 2–6 will produce a circular periodic orbit provided that the following constraints are satisfied:

1. the circle is centered at \((z_0, 0)\), and \( \lambda < z_0 < \frac{1}{2}(1 + \lambda) \);
2. the radius of the circle is \( r = \sqrt{z_0(z_0 - \lambda)} \), and \( r < \min\left(1 - z_0, \frac{\sqrt{z_0}}{2}, \frac{m_1}{m_2}, h\right) \);
3. \( f'(\bar{S}) \neq g'(\bar{S}) \).

Note that the second condition can always be satisfied by choosing \( z_0 \) sufficiently close to \( \lambda \).

It is important to note that the dilution rate \( D(z, w) \) was constructed on a circle and that its sign and continuity are yet undetermined at other points of the state space. However, the special form of Equation 2–6 and the above arguments imply that the function \( D(z, w) \) is both smooth and positive at all points interior to the circular periodic orbit. Beyond the circle, the sign of the function may change since the inequality \( |w| \leq r \) no longer holds. The region in the state space where the function \( D \) is positive depends on the particular growth functions involved. If the dilution rate becomes negative in some domain, it must be modified via a continuous, positive extension. It can be shown that there exists a Lipschitz extension of \( D(z, w) \) into the entire state space and simulations using such extensions will be presented at the end of this chapter.
The domain $\Omega$ can now be defined as the disk $(z - z_0)^2 + w^2 \leq r^2$. Since the boundary of $\Omega$ is a periodic orbit, the set $\Omega$ is invariant under the flow of Equation 2–7. In what follows, we will show that the invariant domain $\Omega$ can be further extended to include a larger elliptical region.

2.2.3 Conservative System in $\Omega$.

Having established the existence of a circular periodic orbit, we will now show that all orbits in the interior of the circle are elliptical. Since the vector field of Equation 2–7 has a special symmetry with respect to the $z$ axis ($\dot{z}$ is an odd function of $w$ and $\dot{w}$ is an even function of $w$), it is clear that all interior orbits are closed. To prove that these orbits are ellipses, we begin by rewriting system Equation 2–7 in the form

$$
\begin{align*}
    \dot{z} &= \frac{G(z)}{r^2 + z_0(z - z_0)}(r^2 - z_0^2 + 2z_0 - 2z^2)w, \\
    \dot{w} &= \frac{G(z)}{r^2 + z_0(z - z_0)}(z(r^2 - z_0^2) + z_0 z^2 + w^2(z_0 - 2z)).
\end{align*}
$$

From the condition $(f(S) - g(S))(S - \bar{S}) > 0$ for $S \in (0,1), \ S \neq \bar{S}$ stated in Section 2.1, we have that $f'(\bar{S}) - g'(\bar{S}) \geq 0$. In addition, we require that $f'(\bar{S}) \neq g'(\bar{S})$. Hence, we have that $G'(\lambda) < 0$ and the expression $\frac{G(z)}{r^2 + z_0(z - z_0)} = \frac{G(z)}{z_0(z - \lambda)}$ is strictly negative in $\Omega$. As a result, the phase portrait of the above system is identical (by reversing the direction of the flow) to that of the system

$$
\begin{align*}
    \dot{z} &= (r^2 - z_0^2 + 2z_0 - 2z^2)w, \\
    \dot{w} &= z(r^2 - z_0^2) + z_0 z^2 + w^2(z_0 - 2z).
\end{align*}
$$

We observe that the new system given by Equation 2–8 retains the same symmetry with respect to the $z$-axis. Hence all elliptical orbits (if any) must be symmetric about the $z$-axis. With this in mind, we seek elliptical orbits of the form

$$
\frac{(z - \hat{z})^2}{a^2} + \frac{w^2}{b^2} = 1.
$$

(2–9)
Taking the derivative of this equation with respect to time and substituting the equations for \( \dot{z} \) and \( \dot{w} \) from Equation 2–8 yields

\[
\frac{w(z - \hat{z})}{a^2} (r^2 - z_0^2 + 2zz_0 - 2z^2) + \frac{w}{b^2} (z(r^2 - z_0^2) + z^2z_0 + w^2(z_0 - 2z)) = 0.
\]

By performing the substitution \( w^2 = b^2(1 - \frac{(z - \hat{z})^2}{a^2}) \) and rearranging the above equation as a polynomial in \( z \) we obtain

\[ P_3z^3 + P_2z^2 + P_1z + P_0 = 0, \]

where

\[
\begin{align*}
P_3 &= 0, \\
P_2 &= \frac{b^2}{a^2}(z_0 - 2\hat{z}) + z_0, \\
P_1 &= \frac{b^2}{a^2}(r^2 - z_0^2 + 2\hat{z}^2 - 2a^2) + r^2 - z_0^2, \\
P_0 &= \frac{b^2}{a^2}(-\hat{z}r^2 + \hat{z}z_0^2 + a^2z_0 - \hat{z}^2z_0).
\end{align*}
\]

In order for the ellipse to be invariant, all the coefficients in the above expression must be zero. Setting \( P_2 \) and \( P_0 \) equal to zero, we obtain the constraints

\[
1 + \frac{a^2}{b^2} - 2\frac{\hat{z}}{z_0} = 0, \quad \hat{z}(z_0^2 - r^2) = z_0(\hat{z}^2 - a^2).
\]

We also note that \( P_2 = P_0 = 0 \) implies that \( P_1 = 0 \), so that the constraint \( P_1 = 0 \) is redundant. From these equations we obtain the expressions for both semi-axes of the ellipse

\[
a^2 = \hat{z}(\hat{z} - \lambda), \quad b^2 = \frac{z_0\hat{z}(\hat{z} - \lambda)}{2\hat{z} - z_0},
\]

where both \( a \) and \( b \) are functions of \( \hat{z} \). These functions impose additional constraints on \( \hat{z} \), namely that \( \hat{z} > \lambda \) and \( \hat{z} > z_0/2 \). In addition, if \( \hat{z} \to \lambda^+ \), then both functions approach zero while \( a \) and \( b \) approach \( r \) as \( \hat{z} \to z_0^- \). This implies that each point in the interior of the circle lies on one such ellipse with the point \((\lambda, 0)\) being the only equilibrium in this region.
We can use the constructed $D(z, w)$ on the exterior of the circle as long as the function remains positive and we define this region of the state space as $\Omega$ (alternatively if we desire a closed set, we can define $\Omega$ to be the set of all points in and on the largest elliptical orbit in the state space). By an extension of the above arguments, it is evident that any orbit lying entirely in $\Omega$ will be elliptical (with the circle being a "symmetric" ellipse).

A numerical example illustrating the conservative flow of Equation 2–1 for an appropriate choice of $D(z, w)$ is presented in Figure 2-1. The details of the system are given in the figure legend.

### 2.3 Stabilizing Elliptical Orbits

We now wish to modify the dilution rate so that the circular orbit (or any elliptical orbit in $\Omega$) is asymptotically stable. We begin by considering a theorem [28] which provides a technique for the stabilization of invariant level sets of conservative systems.

As a background to the theorem, consider a system

$$\dot{x} = f(x),$$  \hspace{1cm} (2–10)

where $x \in U$, an open set of $\mathbb{R}^n$, and $f$ is smooth. We assume that the system given by Equation 2–10 is conservative, that is, there exists a smooth function $V : U \to \mathbb{R}$ such that $\nabla V \neq 0$ almost everywhere in $U$, and $\langle \nabla V, f \rangle = 0$, for all $x \in U$ (such $V$ is also referred to as the first integral). In particular, we have that $\dot{V} = 0$ along solutions of Equation 2–10, and $V$ is a conserved quantity. We will impose two additional assumptions on $V$:

1. $V$ is bounded below. Without loss of generality we therefore assume $V \geq 0$ in $U$ (by simply adding a constant to $V$ if it takes negative values).

2. $V$ is proper, i.e. $V^{-1}([0, K]) := \{x \in U | V(x) \in [0, K]\}$ is a compact set in $U$ for all $K \geq 0$.

These assumptions imply that all forward solutions of Equation 2–10 are bounded and hence defined for all $t \geq 0$. 

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Consider the following controlled version of system given by Equation 2–10:

\[
\dot{x} = f(x) + u(y)g(x), \\
y = V(x),
\]

where \(y \in \mathbb{R}^+, \ u : \mathbb{R}^+ \to \mathbb{R},\) and \(g : U \to \mathbb{R}^n\) is a smooth vector field which satisfies the weak transversality condition: \(\langle g(x), \nabla V(x) \rangle \geq 0\) in \(U\) and \(\langle g(x), \nabla V(x) \rangle > 0\) almost everywhere in \(U\).

Now we pick an arbitrary level set \(V_C := \{x \in U | V(x) = C\}\) of \(V\), where \(C > 0\). We wish to find a feedback control \(u(y)\) which transforms the level set \(V_C\) into an attractor. Note that the proposed feedback control \(u(y)\) only uses the information given by the current value of the function \(V\), and not by the entire state \(x\). The statement of the theorem [28] is as follows.

**Theorem 6.** Suppose that \(u : \mathbb{R}^+ \to \mathbb{R}\) is such that

\[
u(y)(C - y) > 0, \ \forall y \neq C. \quad (2-12)
\]

Let \(B = \{x \in U | \langle g(x), \nabla V(x) \rangle = 0\}\), and suppose that

1. The largest invariant subset in \(V_C \cup B\) is \(V_C \cup B_\omega\) for some compact set \(B_\omega\) such that \(V_C \cap B_\omega = \emptyset\).
2. For all \(x \in U \setminus B_\omega\), \(\omega(x) \cap B_\omega = \emptyset\).

Then for any \(x \in U \setminus B_\omega\), \(\omega(x) \subset V_C\).

We wish to use Theorem 6 and modify the dilution rate so that a given elliptical orbit of Equation 2–4 is locally asymptotically stable. We begin by designating the set of all orbits in \(\Omega\) by \(E\) and defining the elements, \(E(a, b, \hat{z})\), in this set as

\[
E(a, b, \hat{z}) = \{(z, w) \in \Omega | \frac{(z - \hat{z})^2}{a^2} + \frac{w^2}{b^2} = 1\}.
\]

The desired result is summarized below.

**Theorem 7.** Given the system represented by Equation 2–4 with the dilution rate Equation 2–6, any ellipse \(E(a, b, \hat{z}) \in E\) can be made globally asymptotically stable by defining a
new dilution rate

\[
D(z, w) = F(z) + w\tilde{G}(z) - \alpha\left(z\frac{\partial V}{\partial z}(z, w) + w\frac{\partial V}{\partial w}(z, w)\right)(C - V(z, w)),
\]

where

\[
V(z, w) = (z - \hat{z}(z, w))^2 + \left(\frac{a(z, w)}{b(z, w)}\right)^2 w^2,
\]

\[
\hat{z}(z, w) = \frac{z_0(w^2 - z^2)}{2w^2 - z_0(2z - \lambda)},
\]

\[a(z, w) = a(\hat{z}) \text{ and } b(z, w) = b(\hat{z}) \text{ are as previously defined, } \alpha \in \mathbb{R}^+ \text{ is sufficiently small,}
\]

and \(C = a^2(\hat{z})\).

Proof of Theorem 7. We consider Equation 2-4 to be the system referenced in the

Theorem 6 and seek an appropriate function \(V(z, w)\). Any point \((z, w)\) in \(\Omega\) belongs to

an elliptical orbit of the form Equation 2-9. Since \(a\) and \(b\) were previously shown to be

functions of \(\hat{z}\), these relations can be used to express \(\hat{z}\) as a function of \((z, w)\). Specifically,

we substitute the expressions

\[a^2 = \hat{z}(\hat{z} - \lambda), \quad b^2 = \frac{z_0\hat{z}(\hat{z} - \lambda)}{2\hat{z} - z_0},
\]

into Equation 2-9, and solve for \(\hat{z}\) to obtain

\[\hat{z}(z, w) = \frac{z_0(w^2 - z^2)}{2w^2 - z_0(2z - \lambda)}.
\]

This equation demonstrates that both \(a = a(\hat{z})\) and \(b = b(\hat{z})\) can be treated as functions of

the state variables. Motivated by the result of Theorem 6, we define the function

\[V(z, w) = (z - \hat{z}(z, w))^2 + \left(\frac{a(z, w)}{b(z, w)}\right)^2 w^2.
\]

For a given point \((z, w) \in \Omega\), the constant \(C = a^2(\hat{z})\) can be chosen to define a level curve,

\(V_C\), which is the elliptical orbit \(E(a, b, \hat{z})\) and it follows that on this ellipse \(\nabla V(z, w)\).
\((\dot{z}, \dot{w})^T = 0\) so that \(E(a, b, \dot{z})\) remains invariant under the new system. We also calculate
\[
\frac{\partial V}{\partial z} = \frac{2z_0(w^2(-2z + z_0) + zz_0(z - \lambda))(2w^2(z_0 - \lambda) - z_0(2z^2 - 2z\lambda + \lambda^2))}{(2w^2 + z_0(\lambda - 2z))^3},
\] (2–14)
\[
\frac{\partial V}{\partial w} = \frac{2wz_0(2z(z - z_0) + z_0\lambda)(2w^2(z_0 - \lambda) - z_0(2z^2 - 2z\lambda + \lambda^2))}{(2w^2 + z_0(\lambda - 2z))^3},
\] (2–15)
and conclude that \(\nabla V(z, w) \neq (0, 0)\) almost everywhere in \(\Omega\). In addition, we have that \(V(z, w) \geq 0\) for \((z, w) \in \Omega\), and \(V(z, w)\) is proper.

For the second function associated with Theorem 6 we choose
\[
g(z, w) = \begin{pmatrix} z \\ w \end{pmatrix} \left( z \frac{\partial V}{\partial z}(z, w) + w \frac{\partial V}{\partial w}(z, w) \right)
\]
and it is clear that
\[
\langle g, \nabla V \rangle = \left( z \frac{\partial V}{\partial z}(z, w) + w \frac{\partial V}{\partial w}(z, w) \right)^2 \geq 0
\]
for all \(x \in U\). To determine the set \(B\) where \(\langle g, \nabla V \rangle = 0\), we set
\[
z \frac{\partial V}{\partial z}(z, w) + w \frac{\partial V}{\partial w}(z, w) = 0.
\]
Substituting the expressions (2–14) and (2–15) for \(\frac{\partial V}{\partial z}\) and \(\frac{\partial V}{\partial w}\) respectively and simplifying, we find that
\[
z \frac{\partial V}{\partial z}(z, w) + w \frac{\partial V}{\partial w}(z, w) =
\frac{2(w^2 - z^2)z_0^2(z - \lambda)(-2w^2(z_0 - \lambda) + z_0(2z^2 - 2z\lambda + \lambda^2))}{(2w^2 + z_0(\lambda - 2z))^3}.
\] (2–16)
Expression (2–16) equals zero if one of the following holds: either \(w = \pm z\), or \(z = \lambda\), or
\[
-2w^2(z_0 - \lambda) + z_0(2z^2 - 2z\lambda + \lambda^2) = 0.
\] (2–17)
Solving the above equation for \(w^2\), we obtain
\[
w^2 = \frac{z_0(z^2 + (z - \lambda)^2)}{2(z_0 - \lambda)}.
\]
Using condition 2 on page 27, namely that $\sqrt{z_0(z_0 - \lambda)} < z_0/\sqrt{2}$, we replace (2–17) with the inequality

$$w^2 > z^2 + (z - \lambda)^2 \geq z^2,$$

and conclude that (2–17) defines a curve that lies outside of the sector $-z \leq w \leq z$. Since the domain $\Omega$ is contained in the interior of the sector $-z \leq w \leq z$, it does not intersect the boundary of this sector $w = \pm z$ and it does not intersect the curve defined by equation (2–17). We conclude that the set $B$ consists of all points in $\Omega$ where $z = \lambda$. Substituting $z = \lambda$ into Equation 2–6, we find that $\dot{z} = - w \lambda \tilde{G}(\lambda)$. Therefore, the largest invariant set $B_\omega$ in $B$ is the equilibrium $(\lambda, 0)$, which is clearly disjoint with any nontrivial ellipse $E(a, b, \hat{z})$.

To apply the result of Theorem 6, we need to verify that $B_\omega$ does not contain limit points of any forward solution starting outside of $B_\omega$. We will do so by showing that $B_\omega$ is asymptotically stable in reverse time. We observe that when time is reversed, the function $V(z, w)$ becomes a Liapunov function inside the ellipse $E(a, b, \hat{z})$ which serves as a neighborhood of $B_\omega$ where $\dot{V} \leq 0$. Since $B_\omega$ is the only invariant set in $B = \{(z, w) \in \text{Int} E(a, b, \hat{z}) | \dot{V} = 0\}$, we apply the LaSalle’s invariance principle and conclude that any solution starting inside $E(a, b, \hat{z})$ converges to $B_\omega$ in reverse time. Therefore, $B_\omega$ cannot contain limit points of any forward solution starting outside of $B_\omega$.

Now we apply the result of Theorem 6 and conclude that all forward solutions in $\Omega$ except the equilibrium $B_\omega$ have their $\omega$-limit sets in $\mathcal{V}_C = E(a, b, \hat{z})$.

Finally, we remark that $\alpha > 0$ must be sufficiently small so that the expression Equation 2–13 defines a positive dilution rate in $\Omega$.

2.4 Nested Orbits of Alternating Stability

As a final result, we design a dilution rate which produces a finite number of elliptical orbits with alternating stability. The number and selection of ellipses in $\Omega$ to be stabilized is determined by the appropriate modification of Equation 2–6. The following theorem formalizes our assertion.
Theorem 8. Suppose that $\lambda < \hat{z}_1 < \hat{z}_2 < \cdots < \hat{z}_k$ and consider the corresponding ellipses $E_i = E(a_i, b_i, \hat{z}_i) \in E$ for $i = 1, 2, \ldots, k$. Let $\alpha > 0$ and define a new dilution rate for system given by Equation 2–4 by

$$D(z, w) = F(z) + w\tilde{G}(z) + H(z, w)$$

where

$$H(z, w) = \alpha(z - \lambda) \prod_{i=1}^{k} \left( \frac{(z - \hat{z}_i)^2}{a_i^2} + \frac{w^2}{b_i^2} - 1 \right).\quad (2–18)$$

Then the ellipses $\{E_1, \ldots, E_k\}$ are the only periodic orbits in $\Omega$. Moreover, the stability of the ellipses alternates with $E_k$ (the largest) being stable. If $k = 0$, then all orbits in $\Omega$ converge to $(z_0, 0)$.

Proof of Theorem 8. Since the function $H(z, w)$ is zero at all points contained on the ellipses $E_i$, these ellipses remain periodic orbits. Consider a new ellipse $E_0(a_0, b_0, \hat{z}_0)$ which is a member of $E$ but which is not an element of the set $\{E_1, \ldots, E_k\}$ and define a new function by

$$V(z, w) = \frac{(z - \hat{z}_0)^2}{a_0^2} + \frac{w^2}{b_0^2} - 1.$$ 

Differentiating $V(z, w)$ with respect to $t$ we find

$$\dot{V} = \nabla V \cdot (\dot{z}, \dot{w})^T = -(z \frac{\partial V}{\partial z} + w \frac{\partial V}{\partial z})H,$$

that is,

$$\dot{V}(z, w) = -2\alpha(z - \lambda) \left( \frac{z(z - \hat{z}_0)}{a_0^2} + \frac{w^2}{b_0^2} \right) \prod_{i=1}^{k} \left( \frac{(z - z_i)^2}{a_i^2} + \frac{w^2}{b_i^2} - 1 \right).$$

For all $(z, w) \in E_0(a_0, b_0, \hat{z}_0)$, we have

$$\frac{z(z - \hat{z}_0)}{a_0^2} + \frac{w^2}{b_0^2} = \frac{(z - \hat{z}_0)^2}{a_0^2} + \frac{w^2}{b_0^2} + \frac{\hat{z}_0(z - \hat{z}_0)}{a_0^2}$$

$$= 1 + \frac{\hat{z}_0(z - \hat{z}_0)}{a_0^2} = 1 + \frac{\hat{z}_0(z - \hat{z}_0)}{\hat{z}_0(\hat{z}_0 - \lambda)} = \frac{z - \lambda}{\hat{z}_0 - \lambda},$$

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where we used the fact that $a_0^2 = \dot{z}_0 (\dot{z}_0 - \lambda)$. Consequently on $E_0$,

$$\dot{V}(z, w) = -2a (z - \lambda)^2 \prod_{i=1}^{k} \left( \frac{(z - z_i)^2}{a_i^2} + \frac{w^2}{b_i^2} - 1 \right). \quad (2–19)$$

In expression Equation 2–19, each term of the form

$$\frac{(z - z_i)^2}{a_i^2} + \frac{w^2}{b_i^2} - 1$$

is positive (negative) for $(z, w) \in E_0$ if and only if $E_i \subset E_0$ $(E_0 \subset E_i)$. Therefore, with the exception of two points $(\lambda, \pm w)$ on $E_0$ where $\dot{V}(z, w) = 0$, the sign of $\dot{V}(z, w)$ is negative (positive) if an even (odd) number of ellipses $E_i$ lie outside of $E_0$. If $\dot{V}(z, w)$ is negative, then Equation 2–19 implies that all orbits traverse $E_0$ from the exterior to the interior while the opposite is true for positive valued $\dot{V}(z, w)$; since the sign of $\dot{V}(z, w)$ is constant for all $E_0$ between $E_i$ and $E_{i+1}$, the alternating stabilities of these ellipses is established. The largest ellipse $E_k$ is always stable.

If $k = 0$, then $\dot{V}(z, w) = -2a (\frac{(z - \lambda)^2}{z_0 - \lambda} < 0$ for any $E_0 \in E$ (again, excluding the points with $z = \lambda$) and thus the equilibrium point $(z_0, 0)$ is globally attracting in $\Omega$. □

A numerical example illustrating the flow of Equation 2–1 where $D(z, w)$ is chosen to stabilize two elliptical orbits is given in Figure 2-2. The system details are stated in the figure legend.

### 2.5 Lipschitz Extensions of $D(z, w)$

Most of the analysis performed in this chapter has been in a region $\Omega$ contained in the triangular state space. The function $D(z, w)$ developed in the previous sections is well defined and positive in $\Omega$ but since $\Omega$ may not encompass the entire phase plane, Lipschitz continuous, positive extensions of $D(z, w)$ may be required to insure uniqueness of solutions for all possible initial conditions. The purpose of this section is to introduce some of these extensions and through simulations to demonstrate how these extensions affect the behavior of solutions outside of $\Omega$. 

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2.5.1 Theoretical Considerations

We begin with several definitions needed to introduce the concept of a radial extension of a diluter function and to prove the nontrivial fact that such extensions are indeed Lipschitz. Modifications of this extension are given and they are also shown to be Lipschitz. Finally, these extensions are used in simulations for a given set of growth functions.

Definition 1. Consider any domain \( \Omega' \) such that \( \Omega \subset \Omega' \) and let \( \pi : \Omega' \to \Omega \). We say that \( \pi \) is a projection of \( \Omega' \) onto \( \Omega \) if \( \pi(x) = x \) for all \( x \in \Omega \).

Definition 2. For any function \( f : \Omega \to \mathbb{R} \), we define its \( \pi \)-extension to \( \Omega' \) as \( f^{\pi} : \Omega' \to \mathbb{R} \) so that \( f^{\pi} = f(\pi(x)) \).

Definition 3. Let \( \Omega \) be a compact convex domain in \( \mathbb{R}^2 \). Let \( O \) be a point in the interior of \( \Omega \). Define the radial projection of \( \mathbb{R}^2 \) onto \( \Omega \) as follows: if \( X \in \Omega \) then \( \pi(X) = X \), if \( X \notin \Omega \) then \( \pi(X) \) is the point of intersection of the segment \([O,X]\) with \( \partial \Omega \).

Definition 4. A function \( f \) is Lipschitz on \( X \) if there exists an \( L > 0 \) such that \( |f(x) - f(y)| < L|x - y| \) for all \( x, y \in X \). A function \( f \) is locally Lipschitz on \( X \) if for all \( x \in X \) there exists an open set \( U \subset X \) with \( x \in U \) and such that \( f \) is Lipschitz on \( U \).

(Note, if \( f \) is locally Lipschitz on \( X \) and \( X \) is compact, then \( f \) is Lipschitz on \( X \).)

If \( f \) is Lipschitz on a compact and connected domain \( D \) and if \( \pi(x) \) is a Lipschitz projection onto this same domain, then it is easy to show that the composition function \( f^{\pi} \) is also Lipschitz on \( D \). Since we know by previous results that the diluter function \( D(z,w) \) given by Equation 2–6 is at least \( C^1 \) in \( \Omega \), it is therefore Lipschitz in this domain; thus in order to prove that the extension \( D(\pi(z,w)) \) is Lipschitz simply requires the proof that \( \pi(x) \) is Lipschitz on the triangular state space. This fact is proved in the following lemmas and corollaries.

Lemma 1. The radial projection \( \pi(X) \) is well-defined.

Proof of Lemma 1. Suppose there exists two distinct points \( X_1, X_2 \in [O,X] \cap \partial \Omega \). Without loss of generality, let \( X_1 \in [O,X_2] \). Since \( O \) is an interior point, there exists a real number
$R > 0$ such that the ball $B_R(O) \subset \Omega$ (see Figure 2-3). The convexity of $\Omega$ implies that for any $Y \in B_R(O)$, the entire segment $[Y, X_2]$ lies in $\Omega$. Using similar triangles, we find that $\Omega$ contains the entire ball $B_r(X_1)$ where $r = R|X_1 - X_2|/|O - X_2|$ so that $X_1$ must be an interior point. This contradicts the assumption that $X_1 \in \partial \Omega$.

**Corollary 2.** For any $X \in \partial \Omega$, there exists a cone $C$ with the vertex at $X$ such that $C$ has a nonempty interior and for sufficiently small $\delta > 0$, $\text{Int}(C) \cap B_\delta(X) = C^+ \cup C^-$ where $C^+ \subset \text{Int}(\Omega)$ and $C^- \cap \Omega = \emptyset$. Without loss of generality, we may assume that the boundary of $C$ forms a constant angle $\alpha > 0$ with the segment $[O, X]$, that is, $C$ is rotationally symmetric about $[O, X]$.

**Proof of Corollary 2.** Choose any point $X$ on $\partial \Omega$. We can find $\delta$ sufficiently small so that (with the exception of points on $\partial \Omega$) $B_\delta$ is partitioned into two parts by the boundary of $\Omega$. Now consider Figure 2-4 and suppose that there exists a point $Y \in \partial \Omega$ which lies in $C^-$. The segment $[O, Y]$ contains at least two boundary points of $\Omega$ and thus contradicts Lemma 1. A similar argument holds for $C^+$. Hence by contradiction the result is established.

**Lemma 2.** The radial projection $\pi(X)$ is Lipschitz on any compact, convex domain containing $\Omega$.

**Proof of Lemma 2.** The proof will proceed in three steps. First we show that $\pi(X)$ is everywhere continuous; next we prove that if $\pi(X)$ is Lipschitz on the boundary of a ball centered at $O$ and containing $\Omega$, then it is Lipschitz in the entire ball. Finally, we show that the radial extension is Lipschitz on the boundary of any such ball.

We begin by establishing that $\pi(X)$ is continuous. Clearly the function is continuous in the interior of $\Omega$ since it is the identity function in this region. Next, consider a fixed point $X$ which is not in the interior of $\Omega$ and let $\{X_n\}$ be a sequence of points such that $|X - X_n| < \frac{1}{n}$. Referencing Figure 2-6, define $A_n$ and $B_n$ to be the respective points of intersection of the ray $O\bar{X}$ with the cones $C^+$ and $C^-$. For sufficiently large $n$, $\pi(X_n)$ will
always lie between \( A_n \) and \( B_n \) and as \( n \to \infty \), these points of intersection converge to \( \pi(X) \). Hence by the squeeze theorem, the radial projection is continuous.

For the second part of the proof we define \( \mathcal{B}_R(O) \) as a ball of radius \( R \) centered at \( O \) and which contains \( \Omega \); we assume that \( \pi(X) \) is Lipschitz on \( \partial \mathcal{B}_R(O) \) with Lipschitz constant \( M \). It is clear that the radial projection is Lipschitz on \( \Omega \) with Lipschitz constant 1. Let \( d \) be the distance between \( O \) and \( \partial \Omega \) and define a second ball of radius \( r < \frac{d}{2} \) centered at \( O \) and such that this ball is contained in the interior of \( \Omega \) (see Figure 2-5). First consider two points \( X' \) and \( Y' \) in the annular region defined by the two balls (panel A, Figure 2-5). Let \( X \) and \( X'' \) be the respective points of intersection of the ray \( \vec{OX}' \) with the balls \( \partial \mathcal{B}_R(O) \) and \( \partial \mathcal{B}_r(O) \) and define the points \( Y \) and \( Y'' \) in a similar manner. It is clear that \( |X'' - Y''| < |X' - Y'| \) and using similar triangles we obtain \( |X - Y| = \frac{R|X'' - Y''|}{r} \).

Hence

\[
|\pi(X') - \pi(Y')| = |\pi(X) - \pi(Y)| \leq M|X - Y| = M \frac{R|X'' - Y''|}{r} < M \frac{R|X' - Y'|}{r}.
\]

Next, let \( X' \) be as defined above and suppose \( Y' \in \mathcal{B}_r(O) \) (panel B, Figure 2-5). The following inequalities follow

\[
|\pi(X') - \pi(Y')| \leq |\pi(X') - Y''| + |Y'' - Y'| < M \frac{R|X' - Y'|}{r} + |Y'' - Y'|
\]

\[
< M \frac{R|X' - Y'|}{r} + M \frac{R|Y'' - Y'|}{r} + |Y'' - Y'| < M \frac{R|X' - Y'|}{r} + M \frac{R|X' - Y'|}{r} + |X' - Y'|
\]

\[
= (\frac{2MR}{r} + 1)|X' - Y'|.
\]

Thus by combining the above we see that the radial extension is Lipschitz on \( B_R(O) \) with a Lipschitz constant of \( \frac{2MR}{r} + 1 \).

In the final part of the proof we demonstrate that \( \pi(X) \) is Lipschitz on \( \partial \mathcal{B}_R(O) \). We proceed by contradiction and assume that the radial projection is not Lipschitz on the boundary; then there exists sequences of points \( \{X_n\}, \{Y_n\} \) contained in \( \partial \mathcal{B}_R(O) \) such that

\[
\lim_{n \to \infty} \frac{|\pi(X_n) - \pi(Y_n)|}{|X_n - Y_n|} = +\infty.
\]
Since $\Omega$ is bounded, this implies that $|X_n - Y_n| \to 0$. Due to the compactness of boundary, by passing to subsequences (if necessary) we may assume that there exists $X \in \partial B_R(O)$ such that $X_n \to X$ and
\[
\lim_{n \to \infty} \frac{|\pi(X_n) - \pi(X)|}{|X_n - X|} = +\infty.
\]
Now consider Figure 2-6 which represents the plane containing $O, X,$ and $X_n$. Since $X_n \to X$, we have $\theta_n \to 0$. The points $A_n$ and $B_n$ denote the intersections of the segment $[O, X_n]$ with the boundary of $C^+$ and $C^-$ respectively. Let
\[
r = |O - \pi(X)|, \quad a_n = |A_n - \pi(X)|, \quad b_n = |B_n - \pi(X)|.
\]
It is clear that
\[
|\pi(X_n) - \pi(X)| \leq \max(a_n, b_n).
\]
Solving the corresponding triangles, we find that
\[
a_n = \frac{r \sin(\theta_n)}{\sin(\alpha + \theta_n)}, \quad b_n = \frac{r \sin(\theta_n)}{\sin(\alpha - \theta_n)}.
\]
It follows that $a_n \leq b_n$ and $|\pi(X_n) - \pi(X)| \leq b_n$. We also have that $|X_n - X| = R\sqrt{2 - 2\cos(\theta_n)}$, which implies the inequality
\[
\frac{|\pi(X_n) - \pi(X)|}{|X_n - X|} \leq \frac{r \sin(\theta_n)}{R \sin(\alpha - \theta_n) \sqrt{2 - 2\cos(\theta_n)}}.
\]
The existence of the limit
\[
\lim_{\theta_n \to 0} \frac{r \sin(\theta_n)}{R \sin(\alpha - \theta_n) \sqrt{2 - 2\cos(\theta_n)}} = \frac{r}{R \sin(\alpha)} < +\infty
\]
contradicts the original assertion and we conclude that $\pi(X)$ is Lipschitz on $\partial B_R(O)$ and thus Lipschitz on $B_R(O)$.

Since any compact, convex domain containing $\Omega$ can be placed in a sufficiently large ball centered at $O$, the result follows.
**Corollary 3.** In the chemostat problem, $\Omega$ is an ellipse and hence both convex and compact. Thus the radial extension of the dilution rate into the region of the phase plane exterior to $\Omega$ produces a positive Lipschitz function and the extended system exhibits uniqueness of solutions.

In addition to the basic radial extension, we will derive two other Lipschitz extensions of $D(z, w)$ which are based on the projection $\pi(X)$.

**Definition 5.** Let $O$ be an interior point of $\Omega$ as defined above and let $X$ be an arbitrary point in the state space. We define the continuous function $R(X)$ by

$$R(X) = \begin{cases} \frac{|X-O|}{|\pi(X)-O|}, & X \neq O, \\ 1, & X = O. \end{cases}$$

It is clear from the definition that $R(X) = 1$ for all $X \in \Omega$ and that for $X \notin \Omega$, $R(X)$ increases linearly as we proceed along the ray $O\overline{X}$. An important property of this function is stated below.

**Lemma 3.** On a compact, convex domain $\Omega$, the function $\bar{R}(X) = 1/R(X)$ is Lipschitz.

**Proof of Lemma 3.** We begin as in the proof of Lemma 2. Let $R$ be a positive sufficiently large real number so that $\Omega \subset B_R(O)$ and let $S = \partial B_R(O)$. It suffices to show that $\bar{R}(X)$ is Lipschitz on $S$. For $X \in S$ we have

$$\bar{R}(X) = |\pi(X) - O|/|X - O| = |\pi(X) - O|/R.$$  

The function $F(X) = |X - O|$ is Lipschitz since by the triangle inequalities we have

$$|X - O| < |X - Y| + |Y - O|$$

and

$$|Y - O| < |X - Y| + |X - O|$$

which implies

$$|F(X) - F(Y)| = ||X - O| - |Y - O|| < |X - Y|.$$  

Thus $\bar{R}(X)$ is the composition of two Lipschitz functions and hence is Lipschitz.

Let $M$ be the maximum value of $R(X)$ on the state space. Using the inequalities

$$|R(X) - R(Y)| = |R(X)R(Y)||1/R(X) - 1/R(Y)| < M^2|1/R(X) - 1/R(Y)| < M^2 K |X - Y|$$

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(where \( K \) is the Lipschitz constant of \( \tilde{R}(X) \)) the following corollary results:

**Corollary 4.** On a compact, convex domain \( \Omega \), the function \( R(X) \) is Lipschitz.

We are now in a position to define the new Lipschitz extensions of the dilution function. Let \( \bar{D}(z, w) \) be the extended diluter function described in Corollary 3, then

**Definition 6.** \( \bar{D}_1(X) = \bar{D}(X)R(X) \),

**Definition 7.** \( \bar{D}_2(X) = \bar{D}(X)/R(X) \).

Since the product of two bounded Lipschitz functions is Lipschitz, it follows that the functions \( \bar{D}_i(X) \) are Lipschitz.

### 2.5.2 Simulations

For the simulations using the above extensions, the two growth functions were selected to be \( f(S) = \frac{2S}{1+S} \) and \( g(S) = \frac{4S}{2.5+S} \). Based upon these, \( \tilde{S} \) was calculated to have a value of 0.5 and the value of \( z_0 \) was chosen as 0.6; hence using the diluter function given by Equation 2–6, the system given by Equation 3–1 produced a circular orbit in \( \Omega \) with a center at \((z, w) = (0.6, 0)\) and with a radius of value \( \sqrt{0.06} \). While the region \( \Omega \) extended beyond this circular orbit, for the present purpose, the radial projection function \( \pi(X) \) was chosen so that all points in the exterior of this circular orbit were projected onto the circle.

Three simulations were run with equilibria results summarized in Table 2-1 and select trajectories shown in Figure 2-7 (Note, some trajectories were simulated with negative time to demonstrate the approximate locations of stable manifolds). The function \( \bar{D}(z, w) \) (panel A) produced a stable node on the line \( z = w \) with a basin of attraction in a part of the region \( w > 0 \) defined by the stable manifolds of the equilibrium at \((0.5000, 0.2821)\). For all interior points which are neither in this basin nor in \( \Omega \) it appears that the circular orbit is an attracting limit cycle. In the second simulation the extended diluter function \( \bar{D}_1(z, w) \) was used. For this function there were no equilibria on \( z = \pm w \) and the origin was a stable node; the orbits in panel B suggest that the origin attracts all trajectories which are not in or on the circular orbit. The final simulation used the extension \( \bar{D}_2(z, w) \).
This diluter function also produced a stable node on the line $z = w$ and the numerical results suggest that this point attracts all trajectories which are not in $\Omega$.

As demonstrated by these simulations, the fate of trajectories lying outside of the chosen $\Omega$ is dependent on the extension of the diluter function and that the state space is very sensitive to small changes in these functions. While numerical methods with specific growth functions have demonstrated that it is possible to design a diluter function which makes $\Omega$ attracting in the entire state space, it is still an open question as to whether or not this is possible for arbitrary growth functions.

![Family of nested elliptical orbits in the region $\Omega$. The feedback control $D(z, w)$ was constructed following the steps of the proof of Theorem 5. The growth functions are $f(s) = \frac{2s}{s+1/2}$ and $g(s) = \frac{3s}{s+1}$ respectively. Their graphs intersect at the common value $\lambda = 1/2$. Representative elliptical orbits are shown in solid. The circular orbit (dashed) has parameters $r = 0.2$ and $z_0 = \frac{5+\sqrt{11}}{20} \approx 0.57$. The numerical integration was performed using Mathematica.](image)

Figure 2-1. Family of nested elliptical orbits in the region $\Omega$. The feedback control $D(z, w)$ was constructed following the steps of the proof of Theorem 5. The growth functions are $f(s) = \frac{2s}{s+1/2}$ and $g(s) = \frac{3s}{s+1}$ respectively. Their graphs intersect at the common value $\lambda = 1/2$. Representative elliptical orbits are shown in solid. The circular orbit (dashed) has parameters $r = 0.2$ and $z_0 = \frac{5+\sqrt{11}}{20} \approx 0.57$. The numerical integration was performed using Mathematica.
Figure 2-2. Numerical example illustrating the result of Theorem 8. The growth functions are the same as in Figure 2-1. The initial feedback control $D(z, w)$ was modified by adding a function $H(z, w)$ of the form Equation 2–18 with $\alpha = 0.01$, $k = 3$, $\hat{z}_1 = 0.52$, $\hat{z}_2 = 0.55$, and $\hat{z}_3 = 0.59$. The corresponding invariant ellipses are shown by dashed curves. The largest and the smallest ellipses are stable while the intermediate ellipse is unstable. Representative orbits starting at $(z, 0)$ with $z \in \{0.55, 0.69, 0.73, 0.95\}$ are drawn with solid curves. The numerical integration was performed using Mathematica.

Figure 2-3. Illustration of the boundary region described in the proof of Lemma 1.
Figure 2-4. Illustration of the region described in the proof of Corollary 3.

Figure 2-5. Illustration for the function $\pi(X)$ Lipschitz on $B_R(O)$. A) $Y'$ in the annular region between the two balls. B) $Y'$ in the ball $B_r(O)$. 
Figure 2-6. Illustration of the region described in the proof of Lemma 2.

Table 2-1. Equilibria external to Ω.

<table>
<thead>
<tr>
<th></th>
<th>$\bar{D}(z, w)$</th>
<th>$\bar{D}_1(z, w)$</th>
<th>$\bar{D}_2(z, w)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Origin</td>
<td>unstable node</td>
<td>stable node</td>
<td>unstable node</td>
</tr>
<tr>
<td>$z = w$</td>
<td>stable node</td>
<td>none</td>
<td>stable node</td>
</tr>
<tr>
<td></td>
<td>$(0.5743,0.5743)$</td>
<td></td>
<td>$(0.9355,0.9355)$</td>
</tr>
<tr>
<td>$z = -w$</td>
<td>saddle</td>
<td>none</td>
<td>saddle</td>
</tr>
<tr>
<td></td>
<td>$(0.6193,-0.6193)$</td>
<td></td>
<td>$(0.9295, -0.9295)$</td>
</tr>
<tr>
<td>Internal</td>
<td>saddle</td>
<td>saddle</td>
<td>saddle</td>
</tr>
<tr>
<td></td>
<td>$(0.5000,0.2821)$</td>
<td>$(0.5000,-0.2318)$</td>
<td>$(0.5000, 0.2295)$</td>
</tr>
</tbody>
</table>
Figure 2-7. Simulations for different Lipschitz extensions of the diluter function. A) The basic radial extension $\bar{D}(z, w)$ is employed. B) The extension $\bar{D}_1(z, w)$ is used. C) The extension $\bar{D}_1(z, w)$ is used.
CHAPTER 3
COEXISTENCE FOR THREE SPECIES

In this chapter we discuss the coexistence of three organisms in a chemostat with a single growth-limiting nutrient and a linear feedback-mediated diluter function.

3.1 Model of the Chemostat with Three Species

For the coexistence of three species we will consider the following chemostat model:

\[
\begin{align*}
\dot{S} &= D(x, y)(1 - S) - x f(S) - y g(S) - z h(S), \\
\dot{x} &= x(f(S) - D(x, y)), \\
\dot{y} &= y(g(S) - D(x, y)), \\
\dot{z} &= z(h(S) - D(x, y)), \\
\end{align*}
\]

(3–1)

where

\[
(S, x, y, z) \in T := \{(S, x, y, z) \in \mathbb{R}^4_+ | S + x + y + z \leq 1\},
\]

with \(D(x, y) = -k_1 x - k_2 y + E\) where \(k_1, k_2,\) and \(E\) are nonnegative constants to be specified later and \(f, g, h\) are Michaelis-Menten growth functions given by:

\[
\begin{align*}
    f(S) &= \frac{m_1 S}{a_1 + S}, \\
    g(S) &= \frac{m_2 S}{a_2 + S}, \\
    h(S) &= \frac{m_3 S}{a_3 + S}. \\
\end{align*}
\]

(3–2)

We assume that there exists unique substrate concentrations \(\bar{S}\) and \(\hat{S}\) such that \(0 < \bar{S}, \hat{S} < 1; f(\bar{S}) = g(\bar{S}); g'(\bar{S}) > f'(\bar{S})\) and \(f(\hat{S}) = h(\hat{S})\). For this system the set \(T\) is clearly forward invariant and hence the system given by Equation 3–1 is well-posed. We introduce the variable \(V = S + x + y + z\) and use a reduction argument to study the system

\[
\begin{align*}
\dot{x} &= x(f(1 - x - y - z) - D(x, y)), \\
\dot{y} &= y(g(1 - x - y - z) - D(x, y)), \\
\dot{z} &= z(h(1 - x - y - z) - D(x, y)). \\
\end{align*}
\]

(3–3)
3.2 Coexistence Theorem

The main result to be derived is given by the following theorem.

**Theorem 9.** For a system given by Equation 3–3 with $D(x, y)$ given above and where $k_1 = f'(\bar{S}) + \kappa = \bar{k}_1 + \kappa$ and $k_2 = g'(\bar{S}) = \bar{k}_2$, then for $\dot{S}$ sufficiently close to $S$ and $\kappa$ a sufficiently small positive number, there exists a locally asymptotically stable periodic orbit in the interior of the first orthant if $h'(\bar{S}) < f'(\bar{S})$ or $h'(\bar{S}) > g'(\bar{S})$, while an unstable periodic orbit results for $f'(\bar{S}) < h'(\bar{S}) < g'(\bar{S})$.

The basic idea of the proof is to first obtain a periodic Hopf orbit in the $xy$ plane and then to bifurcate from this orbit to a limit cycle in the first octant. While this statement of intent is concise, the actual methodology is quite tedious and lengthy. To guide the reader, we first outline the approach and then fill in the necessary details to complete the proof.

The development begins with a limiting system for two organisms obtained from Equation 3–1 by setting $z = 0$, with growth functions $f(S)$ and $g(S)$, and a diluter rate $D(x, y)$ as described above. By Theorem 4.2 and Corollary 4.3 [27], for sufficiently small positive $\kappa$ there exists an asymptotically stable Hopf orbit in the $x, y$ plane. This orbit is approximated by a perturbation technique and the system is then expanded for $z \geq 0$ with the growth function for the third organism given by $h(S, \eta)$ where $\eta$ is the second bifurcation parameter and $h(\bar{S}, 0) = f(\bar{S})$. Next we determine a neutral stability condition for the Hopf orbit with respect to the third organism and establish a neutral stability curve by obtaining a relation between $\eta$ and the Poincaré-Lindstedt perturbation parameter $\varepsilon$. We define a Poincaré map in a plane parallel to the $yz$ coordinate plane and for the fixed point corresponding to the Hopf orbit test the conditions for a bifurcation from a simple eigenvalue. This bifurcation result provides the existence of parametric family of periodic orbits in the first octant yet does not provide information on the stability of these orbits. We express the new orbits as an expansion in the parameter $s$. We also expand $\eta$ as a function of the parameter $s$, $\eta = \eta^* + \eta_1 s + O(s^2)$, and demonstrate
that the stability of the orbits are determined by the sign of \( \eta_1 \). To find this sign we substitute the \( s \)-based parameter expansions into the neutral stability equation and calculate its derivative with respect to \( s \) at \( s = 0 \). By combining like-terms of \( \varepsilon \) in the resulting equations an expression for \( \eta_1 \) is found. Finally, the dependence of the sign of \( \eta_1 \) on the relative positions of the growth functions is determined. As a concluding note, due to the complexity of the perturbation calculations, we used the symbolic capabilities of Mathematica [46] at several steps in the following proof.

3.3 Proof of the Coexistence Theorem

3.3.1 Planar Hopf Orbit and its Asymptotic Expansion

Proof. We begin by establishing the existence of a periodic Hopf orbit in the \( x, y \) plane and approximating the orbit using a perturbation technique. From the initial assumptions on the system given by Equation 3–1 there exists an equilibrium point \( (\bar{x}, \bar{y}, 0) \) in the \( x, y \) coordinate plane; hence at this point, \( \bar{S} = 1 - \bar{x} - \bar{y} \) and the equilibrium condition requires that \( f(\bar{S}) = g(\bar{S}) \). Using the definition of the growth functions this last equation may be rewritten as

\[
\frac{m_1 \bar{S}}{a_1 + \bar{S}} = \frac{m_2 \bar{S}}{a_2 + \bar{S}}
\]

which upon cross-multiplication and rearrangement gives

\[
\bar{S}(\bar{S}(m_2 - m_1) + (m_2 a_1 - m_1 a_2)) = 0.
\]

This equation is solved to yield the nonzero solution \( \bar{S} = \frac{m_1 a_2 - m_2 a_1}{m_2 - m_1} \). Since

\[
\bar{k}_1 = f'(\bar{S}) = \frac{m_1 a_1}{(a_1 + \bar{S})^2}
\]

the expression for \( \bar{S} \) can be substituted into the above equation and simplified to yield \( \bar{k}_1 = \frac{a_1 (m_2 - m_1)^2}{m_1 (a_2 - a_1)^2} \); by similar means we find \( \bar{k}_2 = \frac{a_2 (m_2 - m_1)^2}{m_2 (a_2 - a_1)^2} \). Next, we define \( \bar{D} = f(\bar{S}) \) and again using the expression for \( \bar{S} \) calculate

\[
\bar{D} = \frac{m_1 \bar{S}}{a_1 + \bar{S}} = \frac{m_1 a_2 - m_2 a_1}{a_2 - a_1}.
\]
Finally the values of \(\bar{x}\) and \(\bar{y}\) are determined in terms of the system parameters by simultaneously solving the equations

\[
\bar{S} = 1 - \bar{x} - \bar{y},
\]
\[
\bar{D} = E - \bar{k}_1 \bar{x} - \bar{k}_2 \bar{y}
\]

with the result is given by

\[
\bar{x} = \frac{\bar{k}_2(1 - \bar{S}) - E + \bar{D}}{\bar{k}_2 - \bar{k}_1},
\]
\[
\bar{y} = \frac{E - \bar{D} - \bar{k}_1(1 - \bar{S})}{\bar{k}_2 - \bar{k}_1}.
\]

For the system given by Equation 3–1 with \(z = 0\) and the conditions given in the statement of Theorem 9, the following theorem and its corollary [27] provides the existence of the Hopf orbit for sufficiently small positive values of the bifurcation parameter \(\kappa\):

**Theorem 10.** Fix \(E \in I\), and let \(\mathcal{N}\) be a (sufficiently small) open neighborhood of \((f'(S), g'(S))\). Assume that \(f(S)\) and \(g(S)\) are of Michaelis-Menten type. Fixing \(k_2 = g'(\bar{S})\), a supercritical Hopf bifurcation occurs on the \(xy\) plane at the interior steady state of system given by Equation 3–1 when \(k_1\) passes through \(f'(\bar{S})\). There exists a \(\delta > 0\) such that for all \(k_1 \in (f'(\bar{S}), f'(\bar{S}) + \delta)\), the system given by Equation 3–1 has an asymptotically stable periodic solution in the \(x, y\) plane with a Floquet multiplier in \((0, 1)\).

**Corollary 5.** Under the conditions of Theorem 10, the system given by Equation 3–1 has a steady state on the boundary of \(T\) on the \(x, y\) plane which undergoes a supercritical Hopf bifurcation when \(k_1\) passes through \(f'(\bar{S})\). There exists a \(\delta > 0\) such that for all \(k_1 \in (f'(\bar{S}), f'(\bar{S}) + \delta)\), Equation 3–1 has an asymptotically stable periodic solution in the \(x, y\) plane having two Floquet multipliers inside the unit circle.
An approximation to this Hopf orbit is obtained by first varying the parameter $\kappa$ which shifts the original equilibrium $(\bar{x}, \bar{y})$ (for $\kappa = 0$) to the point $(\hat{x}, \hat{y})$, where

$$
\hat{x} = \frac{k_2(1 - \bar{S}) - E + \bar{D})}{k_2 - k_1},
$$

$$
\hat{y} = \frac{E - \bar{D} - k_1(1 - \bar{S})}{k_2 - k_1}.
$$

Next, this new system and its equilibrium are perturbed as follows

$$
x = \hat{x} + x_1 \varepsilon + x_2 \varepsilon^2 + x_3 \varepsilon^3 + \cdots,
$$

$$
y = \hat{y} + y_1 \varepsilon + y_2 \varepsilon^2 + y_3 \varepsilon^3 + \cdots,
$$

$$
\omega = \omega_0 + \omega_1 \varepsilon + \omega_2 \varepsilon^2 + \omega_3 \varepsilon^3 + \cdots,
$$

$$
\kappa = \kappa_1 \varepsilon + \kappa_2 \varepsilon^2 + \kappa_3 \varepsilon^3 + \cdots.
$$

Substituting the above perturbed variables into the system and rescaling the time $t = \omega \tau$, we obtain a sequence of equations by collecting and equating powers of $\varepsilon$. The $\varepsilon^0$ terms correspond to equilibrium and vanish. The $\varepsilon^1$ terms yield

$$
\begin{pmatrix}
\dot{x}_1 \\
\dot{y}_1
\end{pmatrix} =
\begin{pmatrix}
0 & \omega_0 \bar{x} (\bar{k}_2 - \bar{k}_1) \\
-\omega_0 \bar{y} (\bar{k}_2 - \bar{k}_1) & 0
\end{pmatrix}
\begin{pmatrix}
x_1 \\
y_1
\end{pmatrix}.
$$

In order for this system to have a solution of period $2\pi$ we choose $\omega_0$ so that $\omega_0 = (\sqrt{\bar{x} \bar{y} (\bar{k}_2 - \bar{k}_1)})^{-1}$. Utilizing this new value, a fundamental matrix solution for the above is given by

$$
\Psi(\tau) =
\begin{pmatrix}
\sqrt{\frac{\bar{x}}{\bar{y}}} \cos \tau & \sqrt{\frac{\bar{x}}{\bar{y}}} \sin \tau \\
-\sin \tau & \cos \tau
\end{pmatrix}.
$$

We are free to choose an arbitrary initial value for $(x_1, y_1)$ and choose one such that

$$
\begin{pmatrix}
x_1 \\
y_1
\end{pmatrix} =
\begin{pmatrix}
\sqrt{\frac{\bar{x}}{\bar{y}}} \cos \tau \\
-\sin \tau
\end{pmatrix}.
$$
The $\varepsilon^2$ terms are of the form

$$\begin{pmatrix} \dot{x}_2 \\ \dot{y}_2 \end{pmatrix} = \begin{pmatrix} 0 & \omega_0 \bar{x}(\bar{k}_2 - \bar{k}_1) \\ -\omega_0 \bar{y}(\bar{k}_2 - \bar{k}_1) & 0 \end{pmatrix} \begin{pmatrix} x_2 \\ y_2 \end{pmatrix} + \begin{pmatrix} f_1(\omega_1, \kappa_1, x_1, y_1) \\ f_2(\omega_1, \kappa_1, x_1, y_1) \end{pmatrix},$$

where $f_i$ are quadratic functions of $x_1$ and $y_1$ with nontrivial coefficients. In order for the $x_2$ and $y_2$ to be $2\pi$ periodic, the following secularity condition must be satisfied

$$\begin{pmatrix} 0 \\ 0 \end{pmatrix} = \int_0^{2\pi} \Psi^{-1}(\tau) \begin{pmatrix} f_1(\omega_1, \kappa_1, x_1, y_1) \\ f_2(\omega_1, \kappa_1, x_1, y_1) \end{pmatrix} d\tau.$$

After integrating and simplifying, the first component of this vector equation is given by

$$0 = \kappa_1 \omega_0 \bar{x}.$$

We know $\omega_0$ and $\bar{x}$ are nonzero; thus we have $\kappa_1 = 0$. Placing this value of $\kappa_1$ into the second component of the secularity condition gives

$$0 = \frac{2\omega_1 p_1}{\omega_0}.$$

This condition implies $\omega_1 = 0$. Thus we may modify the expansions of $\omega$ and $\kappa$ as follows

$$\omega = \omega_0 + \omega_2 \varepsilon^2 + \omega_3 \varepsilon^3 + \cdots,$$

$$\kappa = \kappa_2 \varepsilon^2 + \kappa_3 \varepsilon^3 + \cdots$$

and write the parameterization of the Hopf orbit as

$$x(t, \varepsilon) = \tilde{x}(\tau, \varepsilon) = \dot{x} + \varepsilon \sqrt{\frac{x}{y}} \cos(\tau) + \varepsilon^2 x_2(\tau) + \cdots,$$

$$y(t, \varepsilon) = \tilde{y}(\tau, \varepsilon) = \dot{y} - \varepsilon \sin(\tau) + \varepsilon^2 y_2(\tau) + \cdots.$$

In addition to the $\varepsilon^1$ terms, the constant terms of the functions $x_2(\tau)$ and $y_2(\tau)$ will also be required in the next step of method. The general form for these functions is given
by
\[
\begin{pmatrix}
  x_2 \\
  y_2
\end{pmatrix}
= \Psi(\tau) \begin{pmatrix}
  p_2 \\
  q_2
\end{pmatrix} + \int_0^\tau \Psi^{-1}(s) \begin{pmatrix}
  f_1(\omega_1, k_1, x_1, y_1) \\
  f_2(\omega_1, k_1, x_1, y_1)
\end{pmatrix} ds.
\]

The constant terms are obtained as follows
\[
\begin{pmatrix}
  c_{x_2} \\
  c_{y_2}
\end{pmatrix}
= \frac{1}{2\pi} \int_0^{2\pi} \Psi(\tau) \left( \int_0^\tau \Psi^{-1}(s) \begin{pmatrix}
  f_1(\omega_1, k_1, x_1, y_1) \\
  f_2(\omega_1, k_1, x_1, y_1)
\end{pmatrix} ds \right) d\tau.
\]

Performing this calculation we find
\[
\begin{pmatrix}
  c_{x_2} \\
  c_{y_2}
\end{pmatrix}
= \begin{pmatrix}
  -(\bar{x} + \bar{y})k_2^2 \left( 2\sqrt{a_2m_2(k_2 - k_1)} \right)^{-1} \\
  (\bar{x} + \bar{y})k_1^2 \left( 2\sqrt{a_1m_1(k_2 - k_1)} \right)^{-1}
\end{pmatrix}.
\]

### 3.3.2 Neutral Stability

We now consider the system represented by Equation 3–3 and note that the Hopf orbit obtained in the previous section exists in the present system when \( z = 0 \). The focus of this section is to determine the conditions for the neutral stability of this orbit with respect to the third species. Following the development in Smith [39], by examining the variational equation of Equation 3–3, the neutral stability condition can be expressed by
\[
G(\varepsilon) = \frac{1}{2\pi} \int_0^{2\pi} \frac{m_3(1 - \bar{x}(\tau, \varepsilon) - \bar{y}(\tau, \varepsilon))}{a_3 + 1 - \bar{x}(\tau, \varepsilon) - \bar{y}(\tau, \varepsilon)} - E + k_1\bar{x}(\tau, \varepsilon) + \bar{k}_2\bar{y}(\tau, \varepsilon) d\tau = 0.
\]

Expanding the integrand with respect to \( \varepsilon \), to within \( o(\varepsilon^2) \) the above equation becomes
\[
G(\varepsilon) = \frac{1}{2\pi} \int_0^{2\pi} \frac{(m_3 - \bar{D})\bar{S} - a_3\bar{D}}{a_3 + \bar{S}} + \\
\varepsilon \left( \frac{m_3a_3}{(a_3 + \bar{S})^2} - \bar{k}_2 \right) \sin \tau + \sqrt{\frac{x}{y}} \left( \frac{-m_3a_3}{(a_3 + \bar{S})^2} - \bar{k}_1 \right) \cos \tau + \\
\varepsilon^2 \left( \frac{m_3a_3}{(a_3 + \bar{S})^3} \right) \left( -\frac{\bar{x}}{\bar{y}} \cos^2 \tau + 2\sqrt{\frac{x}{y}} (\sin \tau \cos \tau) - \sin^2 \tau \right) + \bar{k}_1x_2 + \bar{k}_2y_2 - \frac{m_3a_3(x_2 + y_2)}{(a_3 + \bar{S})^2} d\tau.
\]
Performing the integration and rewriting the result in terms of the growth functions we obtain

\[ G(\varepsilon) = \frac{\bar{S}(m_3 - m_1)(\bar{S} - \hat{S})}{(a_3 + \bar{S})(a_1 + \bar{S})} + \varepsilon^2 \left( \frac{(\bar{x} + \bar{y})}{4\bar{y}(k_2 - k_1)} \right) \left( h''(\bar{S})(g'(\bar{S}) - f'(\bar{S})) + \right. \\
\left. + g''(\bar{S})(h'(\bar{S}) - f'(\bar{S})) + f''(\bar{S})(g'(\bar{S}) - h'(\bar{S})) \right) + o(\varepsilon^2). \]

Based on the \( \varepsilon^0 \) term in \( G(\varepsilon) \) we define \( \eta = \bar{S} - \hat{S} \). From the fact that \( f(\hat{S}) = h(\hat{S}) \), it is possible to define \( m_3 \) as a function of \( \eta \) and write

\[ m_3(\eta) = \frac{m_1(a_3 + \bar{S})}{a_1 + \bar{S}} = \frac{m_1(a_3 + \bar{S} - \eta)}{a_1 + \bar{S} - \eta}. \]

Since we assumed that \( m_3(0) \neq m_1 \), the continuity argument implies that the sign of \( (m_3(\eta) - m_1) \) remains constant in some neighborhood of \( \eta = 0 \). The \( \varepsilon^0 \) term can therefore be rewritten as

\[ \frac{\bar{S}(m_3(\eta) - m_1)\eta}{(a_3 + \bar{S})(a_1 + \bar{S})} \]

and we note that the sign of this expression changes as \( \eta \) passes through zero.

We define a new function

\[ H(\varepsilon, \eta) = \frac{1}{2\pi} \int_0^{2\pi} m_3(\eta)(1 - \bar{x}(\tau, \varepsilon) - \bar{y}(\tau, \varepsilon)) \frac{a_3 + 1 - \bar{x}(\tau, \varepsilon) - \bar{y}(\tau, \varepsilon)}{a_3 + \bar{S}(a_1 + \bar{S})} - E + k_1\bar{x}(\tau, \varepsilon) + \bar{k}_2\bar{y}(\tau, \varepsilon) \, d\tau \]

and recognize that \( H(\varepsilon, \eta) = 0 \) gives the neutral stability criteria. Using the previous results and definitions, the following are derived

\[ H(0, 0) = 0, \]
\[ \frac{\partial H}{\partial \varepsilon}(0, 0) = 0, \]
\[ \frac{\partial H}{\partial \eta}(0, 0) = \frac{\bar{S}(m_3(0) - m_1)}{(a_3 + \bar{S})(a_1 + \bar{S})}. \]

From the Implicit Function Theorem \( \eta \) can be defined as a function of \( \varepsilon, \eta(\varepsilon) \), in some neighborhood of \( \varepsilon = 0 \) with \( \eta(0) = 0 \). By implicit differentiation the following results are
\[
\frac{\partial \eta}{\partial \varepsilon}(0) = -\frac{\partial H}{\partial \varepsilon}(0, 0) = 0,
\]
\[
\frac{\partial^2 \eta}{\partial \varepsilon^2}(0) = -\frac{\partial^2 H}{\partial \varepsilon \partial \eta}(0, 0) = \left( \frac{a_1 m_3(0)(\bar{x} + \bar{y})}{2 \bar{y} h(\bar{S}) f'(\bar{S})(a_1 - a_3)(g'(\bar{S}) - f'(\bar{S}))} \right) \left( \bar{h}''(\bar{S})(g'(\bar{S}) - f'(\bar{S})) + g''(\bar{S})(\bar{h}'(\bar{S}) - f'(\bar{S})) + f''(\bar{S})(g'(\bar{S}) - \bar{h}'(\bar{S})) \right).
\]

where \(\bar{h}(S)\) is the growth function with \(m_3 = m_3(0)\). Summarizing, the neutral stability criterion near \(\varepsilon = 0\) can be expressed as \(H(\varepsilon, \eta(\varepsilon)) = 0\) where \(\eta(\varepsilon) = \frac{\partial^2 \eta}{\partial \varepsilon^2}(0) \varepsilon^2 + O(\varepsilon^3) \approx \frac{\partial^2 \eta}{\partial \varepsilon^2}(0) \varepsilon^2\).

### 3.3.3 Bifurcation Result

The next step in the technique is to obtain a parametric family of periodic orbits which bifurcate from the planar Hopf orbit into the positive orthant. We begin by modifying the third equality in Equation 3–3 to reflect its dependence on \(\eta\)

\[
\dot{z} = z \left( \frac{m_3(\eta)(1 - x - y - z)}{a_3 + (1 - x - y - z)} - E + k_1 x + k_2 y \right)
\]

and assume that \(k_1\) and all other parameters are fixed. Letting \(x(t) = p(t)\) correspond to the Hopf periodic orbit of the above system with \(z = 0\), it is noted that the orbit is asymptotically stable in the \(xy\) plane. By the appropriate translation of variables the Hopf orbit has the form \(p(0) = 0\) and \(p'(0) = (p_1'(0), 0)\). Next, \(\phi(t, (x, y, z); \eta)\) is defined as a solution to the above system in the translated coordinates with \(\phi(0, (x, y, z); \eta) = (x, y, z)\).

A Poincaré map \(P\) is established in a neighborhood \(U\) of \(0\) in the plane \(H = \{x = 0\}\) where \(P\) maps \(U\) into \(V\), with \(V\) another neighborhood of \(0\) in \(H\). Corresponding to \(P\) is a smooth function \(\tau(y, z; \eta)\) which gives the first return time for any point in \(U\) to \(V\).

It follows that \(\tau(0, 0; \eta) = \tau_0\), the period of the Hopf orbit \(p(t)\). Thus \(P(y, z; \eta)\) may be regarded as a projection of \(\phi(\tau(y, z; \eta), 0, y, z; \eta)\) onto the \(yz\) plane with \(P(0, 0; \eta) = (0, 0)\).

We define the displacement map \(\bar{F}: U \times \mathbb{R} \to H\) by \(\bar{F}(y, z; \eta) = (y, z) - P(y, z; \eta)\) and note that periodic solutions to Equation 3–3 will be zeros of \(\bar{F}\). Expressing the component
functions of $P$ as $P_1$ and $P_2$ and using the invariance of the $xy$ plane for the above system we may write $P_2(y,0;\eta) = 0$ so that the Jacobian of the Poincaré map is given by

$$D_{(y,z)}P(0,0;\eta) = \begin{pmatrix} \frac{\partial P_1}{\partial y}(0,0;\eta) & \frac{\partial P_1}{\partial z}(0,0;\eta) \\ \frac{\partial P_2}{\partial z}(0,0;\eta) & 0 \end{pmatrix}.$$  

Note that since $p(t)$ is asymptotically stable and independent of $\eta$, the inequality $0 < \frac{\partial P_1}{\partial y}(0,0;\eta) < 1$ holds for all $\eta$. Expressing the component functions of $\phi$ as $\phi_1, \phi_2,$ and $\phi_3$, gives $P_2(0, z; \eta) = \phi_3(\tau(0, z; \eta), 0, 0, z; \eta)$, and taking derivatives yields

$$\frac{\partial P_2}{\partial z}(0,0;\eta) = \frac{\partial \phi_3}{\partial \tau}(\tau(0,0;\eta), 0,0,0;\eta) \cdot \frac{\partial \tau}{\partial z}(0,0;\eta) + \frac{\partial \phi_3}{\partial z}(\tau(0,0;\eta), 0,0,0;\eta)$$

and since $\phi_3(t,0,0,0;\eta) \equiv 0$, the above simplifies to

$$\frac{\partial P_2}{\partial z}(0,0;\eta) = \frac{\partial \phi_3}{\partial \tau}(\tau(0,0;\eta), 0,0,0;\eta).$$

Expressing the third equality in Equation 3–3 as $\dot{z} = \tilde{G}(x,y,z;\eta)$ and integrating the variational equation of the system along $p(t)$, we find

$$\frac{\partial \phi_3}{\partial z}(\tau(0,0;\eta), 0,0,0;\eta) = e^{\int_0^{\eta_0} \frac{\partial \phi_3}{\partial z}(p_1(s),p_2(s),0;\eta)ds}.$$  

If $\eta$ is an element of the neutral stability curve, then the integral evaluates to zero and $\frac{\partial P_2}{\partial z}(0,0;\eta) = 1$.

Next we seek a particular branch of solutions of $\tilde{F}(y,z;\eta) = 0$ (i.e., a collection of periodic solutions) and begin by noting

$$D_{(y,z)}\tilde{F}(0,0;\eta) = \begin{pmatrix} 1 - \frac{\partial P_1}{\partial y}(0,0;\eta) & -\frac{\partial P_1}{\partial z}(0,0;\eta) \\ 0 & 1 - \frac{\partial P_2}{\partial z}(0,0;\eta) \end{pmatrix}.$$  

For $\eta = \eta^*$ ($\eta^*$ an element of the neutral stability curve) the above Jacobian becomes

$$D_{(y,z)}\tilde{F}(0,0;\eta^*) = \begin{pmatrix} 1 - \frac{\partial P_1}{\partial y}(0,0;\eta^*) & -\frac{\partial P_1}{\partial z}(0,0;\eta^*) \\ 0 & 0 \end{pmatrix}.$$
which has a one-dimensional null space spanned by the vector
\[
u = \left( \frac{\frac{\partial P_1}{\partial y}(0,0;\eta^*)}{1-\frac{\partial P_2}{\partial y}(0,0;\eta^*)}, \right)^T.
\]
Observing that the column space of \(D_{(y,z)}\bar{F}(0,0;\eta^*)\) has dimension one, we seek to verify the condition
\[
D_{(y,z)}\bar{F}(0,0;\eta^*)\nu \not\in \text{Range } D_{(y,z)}\bar{F}(0,0;\eta^*). \tag{3–6}
\]
Since the range of \(D_{(y,z)}\bar{F}(0,0;\eta^*)\) is of the form \((a,0)^T\) with \(a \in \mathbb{R}\), the bifurcation condition is satisfied if the second element of the column vector \(D_{(y,z)}\eta\bar{F}(0,0;\eta^*)\nu\) is nonzero. Calculating we find that since \(\frac{\partial P_1}{\partial y}(0,0;\eta)\) is independent of \(\eta\)
\[
D_{(y,z)}\eta\bar{F}(0,0;\eta^*)\nu = \begin{pmatrix}
0 & -\frac{\partial^2 P_1}{\partial z \partial \eta}(0,0;\eta^*) \\
0 & -\frac{\partial^2 P_2}{\partial z \partial \eta}(0,0;\eta^*)
\end{pmatrix} \nu = -\begin{pmatrix}
\frac{\partial^2 P_1}{\partial z \partial \eta}(0,0;\eta^*) \\
\frac{\partial^2 P_2}{\partial z \partial \eta}(0,0;\eta^*)
\end{pmatrix}
\]
so that the bifurcation condition of Theorem 2 is satisfied if \(\frac{\partial^2 P_2}{\partial z \partial \eta}(0,0;\eta^*) \neq 0\). Combining equations Equation 3–4, Equation 3–5 and the observation following Equation 3–5 provides the equation
\[
\frac{\partial^2 P_2}{\partial z \partial \eta}(0,0;\eta^*) = \int_0^{\tau_0} \frac{\partial^2 \tilde{G}}{\partial z \partial \eta}(\mathbf{p}_1(r), \mathbf{p}_2(r), 0; \eta^*) \, dr = m'_3(\eta^*) \int_0^{\tau_0} \frac{S(r)}{a_3 + S(r)} \, dr
\]
where \(S(r) = 1 - p_1(r) - p_2(r)\). Note that \(S(r)\) is strictly positive and since \(m'_3(\eta^*) = \frac{m_1(a_3-a_1)}{(a_1+S-\eta^*)^2} \neq 0\), (it is assumed \(a_1 \neq a_3\)), this implies \(\frac{\partial^2 P_2}{\partial z \partial \eta}(0,0;\eta^*) \neq 0\) so that Equation 3–6 is satisfied.

This development verifies the conditions 1, 3, and 4 of Theorem 2 given in Section 1.5.2; the continuity conditions in 2 readily follow from standard theorems on ODEs. Hence we have proved the existence of a branch of solutions of \(F(y,z;\eta) = 0\) of the form
\[
\begin{pmatrix} y \\ z \end{pmatrix} = s\nu + o(s),
\]
\[
\eta = \eta^* + s\eta_1 + o(s) \tag{3–7}
\]
where $s$ is a real scalar.

### 3.3.4 Expansion for the Bifurcating Orbit

In order to determine the stability of the periodic solutions resulting from this branch, it is necessary to study the interactions of the terms $\eta_1$, $\frac{\partial^2 \eta}{\partial \varepsilon^2}(0)$, and $\frac{\bar{S}(m_3(0)-m_1)\eta}{(a_1+S)(a_3+S)}$. Near the origin of the $\varepsilon, \eta$ plane, the curve $\eta(\varepsilon) = \frac{\partial^2 \eta}{\partial \varepsilon^2}(0)\varepsilon^2$ approximates the neutral stability curve and locally partitions the plane into a region of stability and instability with respect to the third organism for the planar Hopf orbit. The relative positions of the stable and unstable regions can be determined by the quantity $\frac{\bar{S}(m_3(0)-m_1)\eta}{(a_1+S)(a_3+S)}$ since it governs the sign of $G(\varepsilon)$ at $\varepsilon = 0$. As the parameter $s$ increases from zero, the bifurcating orbits advance into the first octant and $\eta$ increases if $\eta_1$ is positive and decreases otherwise. Therefore, once the relative positions of the stable and unstable regions are known, the direction that $\eta$ travels from the neutral stability curve as $s$ is varied will determine the stability of Hopf orbit and therefore of the bifurcating orbits since they are opposite [10]. Thus the problem is understood once the sign of $\eta_1$ is determined (see Figures 3-1 and 3-2).

To find the sign of $\eta_1$, we begin by representing the branch of periodic solutions as an expansion in $s$ as follows

$$
\eta = \eta^* + s\eta_1 + \cdots,
$$

$$
x(t) = x_0(t) + sx_1(t) + \cdots,
$$

$$
y(t) = y_0(t) + sy_1(t) + \cdots,
$$

$$
z(t) = sz_1(t) + \cdots
$$

(3-8)

where $(x_0(t), y_0(t))$ are time translates of the Hopf periodic solution to Equation 3-3 which satisfy $y_0'(0) = 0$. We use the previous results obtained in the bifurcation discussion by translating the origin to the point $(x_0(0), y_0(0), 0)$. For the orbits described by Equation 3-8 we require $(y(0), z(0)) \in H = \{ x = x_0(0) \}$ so that the periods are given by

$$
\tau = \tau(y(0), z(0); \eta) \equiv \tau(s).
$$

Since the orbits are all periodic, from Equation 3-3 it is
deduced that
\[
g(s) \equiv \int_0^{\tau(s)} \left\{ \frac{m_3(\eta)}{a_3 + (1 - x(t) - y(t) - z(t))} - E + k_1x(t) + \bar{k}_2y(t) \right\} dt \equiv 0.
\]

Differentiating \(g(s)\) with respect to \(s\) at \(s = 0\) gives
\[
0 = \left( \frac{m_3(\eta^*)}{a_3 + (1 - x_0(\tau(0)) - y_0(\tau(0)))} - E + k_1x_0(\tau(0)) + \bar{k}_2y_0(\tau(0)) \right) \frac{d\tau}{ds}(0) + \\
\int_0^{\tau(0)} \left\{ -\frac{a_3m_3(\eta^*)(x_1(t) + y_1(t) + z_1(t))}{(a_3 + (1 - x_0(t) - y_0(t)))^2} + k_1x_1(t) + \bar{k}_2y_1(t) \right\} dt + \\
\int_0^{\tau(0)} \eta_1m_3'(\eta^*)(1 - x_0(t) - y_0(t)) \frac{dt}{a_3 + (1 - x_0(t) - y_0(t))} dt. \tag{3–9}
\]

This equation will be used to calculate the sign of \(\eta_1\).

Recalling the definition of \(\tau(y, z; \eta)\), we observe that the period of the planar Hopf orbit is independent of the value of \(\eta\); thus \(\frac{d\tau}{d\eta}(y_0(0), 0; \eta^*) = 0\) and using the chain rule we calculate
\[
\frac{d\tau}{ds}(0) = \frac{\partial\tau}{\partial y}(y_0(0), 0; \eta^*)y_1(0) + \frac{\partial\tau}{\partial z}(y_0(0), 0; \eta^*)z_1(0).
\]

Because the Poincaré map is defined in the plane \(x = x_0(0)\) with the fixed point at \(y = y_0(0)\) and \(z = 0\) corresponding to the Hopf orbit, the bifurcation result given in Equation 3–7 is used to conclude that \(y_1(0) = \frac{\partial P_1(y_0(0), 0; \eta^*)}{1 - \frac{\partial P_1}{\partial (y_0(0), 0; \eta^*)}}\) and \(z_1(0) = 1\). Since
\[
P_1(y, z; \eta) = \phi_2(\tau(y, z; \eta), x_0(0), y, z; \eta),
\]
by taking derivatives the following equation results
\[
\frac{\partial P_1}{\partial z}(y_0(0), 0; \eta^*) = \frac{\partial \phi_2}{\partial \tau}(\tau(0), x_0(0), y_0(0), 0; \eta^*) \frac{\partial \tau}{\partial z}(y_0(0), 0; \eta^*) + \frac{\partial \phi_2}{\partial z}(\tau(0), x_0(0), y_0(0), 0; \eta^*);
\]

the point \((x_0(0), y_0(0), 0)\) was defined so that \(0 = y_0(0) = \frac{\partial \phi_2}{\partial \tau}(\tau(0), x_0(0), y_0(0), 0; \eta^*)\) and thus
\[
\frac{\partial P_1}{\partial z}(y_0(0), 0; \eta^*) = \frac{\partial \phi_2}{\partial z}(\tau(0), x_0(0), y_0(0), 0; \eta^*).
\]

A similar calculation yields
\[
1 - \frac{\partial P_1}{\partial y}(y_0(0), 0; \eta^*) = 1 - \frac{\partial \phi_2}{\partial y}(\tau(0), x_0(0), y_0(0), 0; \eta^*)
\]
and so
\[ y_1(0) = \frac{\frac{\partial \phi_2}{\partial z}(\tau(0), x_0(0), y_0(0), 0; \eta^*)}{1 - \frac{\partial \phi_2}{\partial y}(\tau(0), x_0(0), y_0(0), 0; \eta^*)}. \]

By definition \( \phi_1(\tau(y, z; \eta), x_0(0), y, z; \eta) \equiv x_0(0) \), so by differentiating this expression with respect to \( y \) and evaluating at \( s = 0 \) we find
\[ \frac{\partial \phi_1}{\partial t}(\tau(0), x_0(0), y_0(0), 0; \eta^*) \frac{\partial \tau}{\partial y}(y_0(0), 0; \eta^*) + \frac{\partial \phi_1}{\partial y}(\tau(0), x_0(0), y_0(0), 0; \eta^*) = 0 \]
or upon rearrangement and suppressing dependent variables
\[ \frac{\partial \tau}{\partial y}(y_0(0), 0; \eta^*) = -\frac{\frac{\partial \phi_1}{\partial y}(\tau(0), x_0(0), y_0(0), 0; \eta^*)}{\frac{\partial \phi_1}{\partial t}(\tau(0), x_0(0), y_0(0), 0; \eta^*)}. \]

A similar approach also yields
\[ \frac{\partial \tau}{\partial z}(y_0(0), 0; \eta^*) = -\frac{\frac{\partial \phi_1}{\partial z}(\tau(0), x_0(0), y_0(0), 0; \eta^*)}{\frac{\partial \phi_1}{\partial t}(\tau(0), x_0(0), y_0(0), 0; \eta^*)}. \]

Thus by combining all of the above and displaying only the time dependence we obtain
\[ \frac{d\tau}{ds}(0) = -\left( \frac{\frac{\partial \phi_1}{\partial y}(\tau_0)}{\frac{\partial \phi_1}{\partial t}(\tau_0)} \right) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau_0)}{1 - \frac{\partial \phi_2}{\partial y}(\tau_0)} \right) - \frac{\frac{\partial \phi_1}{\partial t}(\tau_0)}{\frac{\partial \phi_1}{\partial t}(\tau_0)}. \] (3–10)

Next we need to calculate the expansions of \( x(t), y(t), \) and \( z(t) \) in Equation 3–8.

Beginning with
\[ x(t) = \phi_1(t, x(0), y(0), z(0); \eta) \]
and rewriting in terms of the expanded variables gives
\[ x(t) = \phi_1(t, x_0(0), y_0(0) + s y_1(0) + \cdots, s z_1(0) + \cdots; \eta^* + s \eta_1 + \cdots) \]
\[ x(t) = \phi_1(t, x_0(0), y_0(0) + s \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau(0), x_0(0), y_0(0), 0; \eta^*)}{1 - \frac{\partial \phi_2}{\partial y}(\tau(0), x_0(0), y_0(0), 0; \eta^*)} \right) + \cdots, s + \cdots; \eta^* + s \eta_1 + \cdots). \]

Performing a Taylor series expansion of the above about \( s = 0 \) provides the equation
\[ x(t) = x_0(t) + s \left( \frac{\partial \phi_1}{\partial y}(t, x_0(0), y_0(0), 0; \eta^*) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau(0), x_0(0), y_0(0), 0; \eta^*)}{1 - \frac{\partial \phi_2}{\partial y}(\tau(0), x_0(0), y_0(0), 0; \eta^*)} \right) + \cdots, s + \cdots; \eta^* + s \eta_1 + \cdots \right) + o(s). \]
A similar expansion for the remaining two variables yields

\[ y(t) = y_0(t) + s \left( \frac{\partial \phi_2}{\partial y}(t, x_0(0), y_0(0), 0; \eta^*) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau(0), x_0(0), y_0(0), 0; \eta^*)}{1 - \frac{\partial \phi_2}{\partial y}(\tau(0), x_0(0), y_0(0), 0; \eta^*)} \right) + \frac{\partial \phi_2}{\partial z}(t, x_0(0), y_0(0), 0; \eta^*) \right) + o(s), \]

\[ z(t) = s \left( \frac{\partial \phi_3}{\partial z}(t, x_0(0), y_0(0), 0; \eta^*) \right) + o(s). \]

From the above series expansions we find the following expressions in which all variables except \( t \) have been suppressed for ease of notation

\[
x_1(t) = \frac{\partial \phi_1}{\partial y}(t) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau_0)}{1 - \frac{\partial \phi_2}{\partial y}(\tau_0)} \right) + \frac{\partial \phi_1}{\partial z}(t),
\]
\[
y_1(t) = \frac{\partial \phi_2}{\partial y}(t) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau_0)}{1 - \frac{\partial \phi_2}{\partial y}(\tau_0)} \right) + \frac{\partial \phi_2}{\partial z}(t),
\]
\[
z_1(t) = \frac{\partial \phi_3}{\partial z}(t). \tag{3–11}
\]

Substituting Equation 3–10 and Equation 3–11 into Equation 3–9 yields

\[
0 = - \left( \frac{m_3(\eta^*)(1 - x_0(\tau_0) - y_0(\tau_0))}{a_3 + (1 - x_0(\tau_0) - y_0(\tau_0))} - E + k_1 x_0(\tau_0) + \bar{k}_2 y_0(\tau_0) \right) \times
\]
\[
\left( \left( \frac{\frac{\partial \phi_1}{\partial y}(\tau_0)}{1 - \frac{\partial \phi_2}{\partial y}(\tau_0)} \right) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau_0)}{1 - \frac{\partial \phi_2}{\partial y}(\tau_0)} \right) + \frac{\partial \phi_1}{\partial z}(\tau_0) \right) + \]
\[
- \int_0^{\tau(0)} a_3 m_3(\eta^*) \left( \frac{\partial \phi_1}{\partial y}(t) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau_0)}{1 - \frac{\partial \phi_2}{\partial y}(\tau_0)} \right) + \frac{\partial \phi_1}{\partial z}(t) \right) + \bar{k}_2 \left( \frac{\partial \phi_2}{\partial y}(t) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau_0)}{1 - \frac{\partial \phi_2}{\partial y}(\tau_0)} \right) \right) + \bar{k}_2 \frac{\partial \phi_2}{\partial z}(t) \right) dt + \]
\[
\int_0^{\tau(0)} k_1 \left( \frac{\partial \phi_1}{\partial y}(t) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau_0)}{1 - \frac{\partial \phi_2}{\partial y}(\tau_0)} \right) + \frac{\partial \phi_1}{\partial z}(t) \right) + \bar{k}_2 \left( \frac{\partial \phi_2}{\partial y}(t) \left( \frac{\frac{\partial \phi_2}{\partial z}(\tau_0)}{1 - \frac{\partial \phi_2}{\partial y}(\tau_0)} \right) \right) + \bar{k}_2 \frac{\partial \phi_2}{\partial z}(t) \right) dt + \]
\[
\int_0^{\tau(0)} \eta_1 m_3(\eta^*)(1 - x_0(t) - y_0(t)) \left( \frac{\partial \phi_2}{\partial y}(t) \right) \left( \frac{\partial \phi_2}{\partial z}(\tau_0) \right) \right) dt.
\]

We simplify this expression by multiplying through by \( (1 - \frac{\partial \phi_1}{\partial y}(\tau_0)) \frac{\partial \phi_2}{\partial z}(\tau_0) \) and rearrange to obtain

\[
0 = - \left( \frac{m_3(\eta^*)(1 - x_0(\tau_0) - y_0(\tau_0))}{a_3 + (1 - x_0(\tau_0) - y_0(\tau_0))} - E + k_1 x_0(\tau_0) + \bar{k}_2 y_0(\tau_0) \right) \times
\]
(\((\frac{\partial \phi_1}{\partial y}(\tau_0))(\frac{\partial \phi_2}{\partial z}(\tau_0)) + (\frac{\partial \phi_1}{\partial z}(\tau_0))(1 - \frac{\partial \phi_2}{\partial y}(\tau_0))\) +

\(-\left(1 - \frac{\partial \phi_2}{\partial y}(\tau_0)\right)\frac{\partial \phi_1}{\partial t}(\tau_0)\int_0^{\tau(0)} a_3 m_3(\eta^*)(\frac{\partial \phi_1}{\partial z}(t) + \frac{\partial \phi_2}{\partial y}(t) + \frac{\partial \phi_1}{\partial z}(\tau_0))\right) dt +

\(-\frac{\partial \phi_1}{\partial t}(\tau_0)\int_0^{\tau(0)} a_3 m_3(\eta^*)(\frac{\partial \phi_1}{\partial y}(t) + \frac{\partial \phi_2}{\partial y}(t) + \frac{\partial \phi_1}{\partial z}(\tau_0))\right) dt +

\(\left(1 - \frac{\partial \phi_2}{\partial y}(\tau_0)\right)\left(\frac{\partial \phi_1}{\partial t}(\tau_0)\right)\int_0^{\tau(0)} k_1\left(\frac{\partial \phi_1}{\partial z}(t)\right) + k_2\left(\frac{\partial \phi_2}{\partial y}(t)\right) dt +

\(\frac{\partial \phi_1}{\partial t}(\tau_0)\int_0^{\tau(0)} k_1\left(\frac{\partial \phi_1}{\partial y}(t)\right)\left(\frac{\partial \phi_2}{\partial z}(\tau_0)\right) + k_2\left(\frac{\partial \phi_2}{\partial y}(t)\right)\left(\frac{\partial \phi_2}{\partial z}(\tau_0)\right) dt +

\(\left(1 - \frac{\partial \phi_2}{\partial y}(\tau_0)\right)\left(\frac{\partial \phi_1}{\partial t}(\tau_0)\right)\int_0^{\tau(0)} \eta_1 m_3'(\eta^*)(1 - x_0(t) - y_0(t))\right) dt. (3-12)

3.3.5 Additional Expansions

In order to use Equation 3–12 to determine the sign of \(\eta_1\), the following perturbation expansions are required (note \(x_0(t)\) and \(y_0(t)\) are chosen so that \(y_0'(0) = 0\):

\[\eta^* = \frac{1}{2}\varepsilon^2 N + \ldots,\]

\[x_0(t) = \bar{x} + \varepsilon \sqrt{\frac{\bar{x}}{\bar{y}}} \sin\left(\frac{t}{\omega_0}\right) + \ldots,\]

\[y_0(t) = \bar{y} + \varepsilon \cos\left(\frac{t}{\omega_0}\right) + \ldots,\]

\[\frac{\partial \phi_1}{\partial t}(\tau_0) = \frac{\partial \phi_1}{\partial t}(0) = x_0(0) = \varepsilon \sqrt{\frac{\bar{x}}{\bar{y}}} \left(\frac{1}{\omega_0}\right) + \ldots,\]

\[\frac{\partial \phi_1}{\partial y}(t) = \psi_0(t) + \varepsilon \psi_1(t) + \ldots,\]

\[\frac{\partial \phi_1}{\partial z}(t) = \gamma_0(t) + \varepsilon \gamma_1(t) + \ldots,\]

\[\frac{\partial \phi_2}{\partial y}(t) = \delta_0(t) + \varepsilon \delta_1(t) + \ldots,\]

\[\frac{\partial \phi_2}{\partial z}(t) = \rho_0(t) + \varepsilon \rho_1(t) + \ldots,\]

\[\frac{\partial \phi_3}{\partial z}(t) = 1 + \varepsilon \left(\omega_0(k_2 - \bar{k}'(\bar{S})) \sin\left(\frac{t}{\omega_0}\right) + \ldots\right).\]
\[ \omega_0(\bar{h}'(\bar{S}) - \bar{k}_1)\sqrt{\frac{x}{y}} \cos \left( \frac{t}{\omega_0} \right) + \omega_0(\bar{k}_1 - \bar{h}'(\bar{S}))\sqrt{\frac{x}{y}} \right) + \cdots \]  

(3–13)

where the constant \( N \) is given by

\[ N = \left( \frac{a_1 m_3(0)(x + y)}{2gh(\bar{S})f'(\bar{S})(a_1 - a_3)(g'(\bar{S}) - f'(\bar{S}))} \right) \left( \bar{h}''(\bar{S})(g'(\bar{S}) - f'(\bar{S})) + \bar{g}''(\bar{S})(\bar{h}'(\bar{S}) - f'(\bar{S})) + \bar{f}''(\bar{S})(g'(\bar{S}) - \bar{h}'(\bar{S})) \right). \]

Note that the expansion for \( \frac{\partial \phi_3}{\partial z}(t) \) results from taking the partial derivative with respect to \( z \) of a term in the variational equation for system Equation 3–3:

\[ \frac{d}{dt} \left( \frac{\partial \phi_3}{\partial z}(t) \right) = \frac{\partial \phi_3}{\partial z}(t) \left( \frac{m_3(1 - x_0(t) - y_0(t))}{a_3 + 1 - x_0(t) - y_0(t)} - E + k_1 x_0(t) + \bar{k}_2 y_0(t) \right) \]

where \( \phi_3(0) = 0 \) and \( \frac{\partial \phi_3}{\partial z}(0) = 1 \). After substituting the expansions for \( x_0(t), y_0(t), \) and \( k_1 \) and solving the above differential equation we find

\[ \frac{\partial \phi_3}{\partial z}(t) = e^{\left( \omega_0(\bar{k}_2 - h'(\bar{S})) \sin \left( \frac{t}{\omega_0} \right) + \omega_0(h'(\bar{S}) - \bar{k}_1)\sqrt{\frac{x}{y}} \cos \left( \frac{t}{\omega_0} \right) + \omega_0(\bar{k}_1 - h'(\bar{S}))\sqrt{\frac{x}{y}} \right)} \]

which simplifies to within \( O(\varepsilon^3) \) as

\[ \frac{\partial \phi_3}{\partial z}(t) = 1 + e^{\left( \omega_0(\bar{k}_2 - h'(\bar{S})) \sin \left( \frac{t}{\omega_0} \right) + \omega_0(h'(\bar{S}) - \bar{k}_1)\sqrt{\frac{x}{y}} \cos \left( \frac{t}{\omega_0} \right) + \omega_0(\bar{k}_1 - h'(\bar{S}))\sqrt{\frac{x}{y}} \right)}. \]

To evaluate the integrals in Equation 3–12, we must perform some calculations on certain quantities in the expansions given by Equation 3–13. First the functions \( \psi_0(t), \delta_0(t), \gamma_0(t), \) and \( \rho_0(t) \) must be determined. Considering \( (\phi_1(t), \phi_2(t), \phi_3(t)) \) as a solution to the system given by Equation 3–3 and taking the derivative of the first two equations with respect to \( y \) gives

\[ \frac{d}{dt} \left( \frac{\partial \phi_1}{\partial y}(t) \right) = \frac{\partial \phi_1}{\partial y}(t) \left( \frac{m_1(1 - \phi_1(t) - \phi_2(t) - \phi_3(t))}{a_1 + (1 - \phi_1(t) - \phi_2(t) - \phi_3(t))} - E + k_1 \phi_1(t) + \bar{k}_2 \phi_2(t) \right) + \]

\[ \phi_1(t) \left( - \frac{m_1 a_1 (\frac{\partial \phi_1}{\partial y}(t) + \frac{\partial \phi_2}{\partial y}(t) + \frac{\partial \phi_3}{\partial y}(t))}{(a_1 + (1 - \phi_1(t) - \phi_2(t) - \phi_3(t)))^2} + k_1 \frac{\partial \phi_1}{\partial y}(t) + \bar{k}_2 \frac{\partial \phi_2}{\partial y}(t) \right), \]

\[ \frac{d}{dt} \left( \frac{\partial \phi_2}{\partial y}(t) \right) = \frac{\partial \phi_2}{\partial y}(t) \left( \frac{m_2(1 - \phi_1(t) - \phi_2(t) - \phi_3(t))}{a_2 + (1 - \phi_1(t) - \phi_2(t) - \phi_3(t))} - E + k_1 \phi_1(t) + \bar{k}_2 \phi_2(t) \right) + \]

\[ \frac{\partial \phi_2}{\partial y}(t) \left( - \frac{m_2 a_2 (\frac{\partial \phi_1}{\partial y}(t) + \frac{\partial \phi_2}{\partial y}(t) + \frac{\partial \phi_3}{\partial y}(t))}{(a_2 + (1 - \phi_1(t) - \phi_2(t) - \phi_3(t)))^2} + k_1 \frac{\partial \phi_1}{\partial y}(t) + \bar{k}_2 \frac{\partial \phi_2}{\partial y}(t) \right), \]

\[ \phi_2(t) \left( - \frac{m_2 a_2 (\frac{\partial \phi_1}{\partial y}(t) + \frac{\partial \phi_2}{\partial y}(t) + \frac{\partial \phi_3}{\partial y}(t))}{(a_2 + (1 - \phi_1(t) - \phi_2(t) - \phi_3(t)))^2} + k_1 \frac{\partial \phi_1}{\partial y}(t) + \bar{k}_2 \frac{\partial \phi_2}{\partial y}(t) \right). \]
\[ \phi_2(t) \left( - \frac{m_2a_2(\partial \phi_1(t)) + \partial \phi_2(t) + \partial \phi_2(t)}{(a_2 + (1 - \phi_1(t) - \phi_2(t) - \phi_3(t)))^2} + k_1 \frac{\partial \phi_1(t)}{\partial y} + k_2 \frac{\partial \phi_2(t)}{\partial y} \right). \]

Letting \( \phi_1(t) = x_0(t), \phi_2(t) = y_0(t), \phi_3(t) = 0 \), substituting from Equation 3–13, and collecting the \( \varepsilon^0 \) terms gives the system

\[
\begin{align*}
\psi'_0(t) &= \psi_0(t) \left( \frac{m_1(1 - \bar{x} - \bar{y})}{a_1 + (1 - \bar{x} - \bar{y})} - E + \bar{k}_1 \bar{x} + \bar{k}_2 \bar{y} \right) + \bar{x} \left( - \frac{m_1a_1(\psi_0(t) + \delta_0(t))}{(a_1 + (1 - \bar{x} - \bar{y}))^2} + \bar{k}_1 \psi_0(t) + \bar{k}_2 \delta_0(t) \right), \\
\delta'_0(t) &= \delta_0(t) \left( \frac{m_2(1 - \bar{x} - \bar{y})}{a_2 + (1 - \bar{x} - \bar{y})} - E + \bar{k}_1 \bar{x} + \bar{k}_2 \bar{y} \right) + \bar{y} \left( - \frac{m_2a_2(\psi_0(t) + \delta_0(t))}{(a_2 + (1 - \bar{x} - \bar{y}))^2} + \bar{k}_1 \psi_0(t) + \bar{k}_2 \delta_0(t) \right)
\end{align*}
\]

which simplifies to

\[
\begin{align*}
\psi'_0(t) &= \bar{x}(\bar{k}_2 - \bar{k}_1)\delta_0(t) \\
\delta'_0(t) &= -\bar{y}(\bar{k}_2 - \bar{k}_1)\psi_0(t)
\end{align*}
\]

Since \( \phi_1(0, x_0(0), y_0(0), 0; \eta) = x_0(0) \) and \( \phi_2(0, x_0(0), y_0(0), 0; \eta) = y_0(0) \), this implies \( \frac{\partial \phi_1}{\partial y}(0) = 0 \) and \( \frac{\partial \phi_2}{\partial y}(0) = 1 \) so that we conclude \( \psi_0(0) = 0 \) and \( \delta_0(0) = 1 \). Thus the above system may be written as

\[
\begin{pmatrix}
\psi'_0(t) \\
\delta'_0(t)
\end{pmatrix} =
\begin{pmatrix}
0 & \bar{x}(\bar{k}_2 - \bar{k}_1) \\
-\bar{y}(\bar{k}_2 - \bar{k}_1) & 0
\end{pmatrix}
\begin{pmatrix}
\psi_0(t) \\
\delta_0(t)
\end{pmatrix},
\begin{pmatrix}
\psi_0(0) \\
\delta_0(0)
\end{pmatrix} =
\begin{pmatrix}
0 \\
1
\end{pmatrix}
\]

with the solution given by

\[
\begin{pmatrix}
\psi_0(t) \\
\delta_0(t)
\end{pmatrix} =
\begin{pmatrix}
\sqrt{\frac{\bar{x}}{\bar{y}}} \sin \left( \frac{t}{\omega_0} \right) \\
\cos \left( \frac{t}{\omega_0} \right)
\end{pmatrix}.
\]

Similarly, taking the derivative with respect to \( z \) of the first two equations of system Equation 3–3, substituting the \( \varepsilon \) expansions, using \( \frac{\partial \phi_1}{\partial z} = 1 + O(\varepsilon) \), and collecting the \( \varepsilon^0 \) terms gives the following system

\[
\begin{pmatrix}
\gamma'_0(t) \\
\rho'_0(t)
\end{pmatrix} =
\begin{pmatrix}
0 & \bar{x}(\bar{k}_2 - \bar{k}_1) \\
-\bar{y}(\bar{k}_2 - \bar{k}_1) & 0
\end{pmatrix}
\begin{pmatrix}
\gamma_0(t) \\
\rho_0(t)
\end{pmatrix} -
\begin{pmatrix}
\bar{x} \bar{k}_1 \\
\bar{y} \bar{k}_2
\end{pmatrix},
\begin{pmatrix}
\gamma_0(0) \\
\rho_0(0)
\end{pmatrix} =
\begin{pmatrix}
0 \\
0
\end{pmatrix}
\]

which has the solution
\[
\begin{pmatrix}
\gamma_0(t) \\
\rho_0(t)
\end{pmatrix} = \frac{1}{\bar{k}_2 - \bar{k}_1} \begin{pmatrix}
\bar{k}_2 \cos\left(\frac{\bar{\omega} t}{\omega_0}\right) - \bar{k}_1 \sqrt{\frac{x}{y}} \sin\left(\frac{\bar{\omega} t}{\omega_0}\right) \\
\bar{k}_1 - \bar{k}_2 \cos\left(\frac{\bar{\omega} t}{\omega_0}\right) - \bar{k}_2 \sqrt{\frac{x}{y}} \sin\left(\frac{\bar{\omega} t}{\omega_0}\right)
\end{pmatrix}.
\]

(3-14)

Additionally we must compute certain quantities involving \(\psi_1(t), \delta_1(t), \gamma_1(t)\) and \(\rho_1(t)\).

Proceeding as above we collect the \(\varepsilon^1\) terms of the expansions and find

\[
\begin{pmatrix}
\psi'_1(t) \\
\delta'_1(t)
\end{pmatrix} = \begin{pmatrix}
0 & \bar{x}(\bar{k}_2 - \bar{k}_1) \\
-\bar{y}(\bar{k}_2 - \bar{k}_1) & 0
\end{pmatrix} \begin{pmatrix}
\psi_1(t) \\
\delta_1(t)
\end{pmatrix} + \begin{pmatrix}
\begin{pmatrix}
0 \\
0
\end{pmatrix}
\begin{pmatrix}
0 \\
0
\end{pmatrix}
\begin{pmatrix}
0 \\
0
\end{pmatrix}
\begin{pmatrix}
0 \\
0
\end{pmatrix}
\begin{pmatrix}
0 \\
0
\end{pmatrix}
\begin{pmatrix}
0 \\
0
\end{pmatrix}
\begin{pmatrix}
0 \\
0
\end{pmatrix}
\begin{pmatrix}
0 \\
0
\end{pmatrix}
\end{pmatrix}
\begin{pmatrix}
\psi_1(0) \\
\delta_1(0)
\end{pmatrix} = \begin{pmatrix}
0 \\
0
\end{pmatrix}
\]

where

\[
\begin{align*}
\alpha_1 &= \frac{f(\bar{S}) - m_1 - 2\bar{x}\bar{k}_1 + \bar{k}_1(a_1 + \bar{S})}{a_1 + \bar{S}}, \\
\alpha_2 &= \frac{f(\bar{S}) - m_1 - 2\bar{x}\bar{k}_1 + \bar{k}_2(a_1 + \bar{S})}{a_1 + \bar{S}}, \\
\alpha_3 &= \frac{-2\bar{x}\bar{k}_1 + (\bar{k}_2 - \bar{k}_1)(a_1 + \bar{S})}{a_1 + \bar{S}}, \\
\alpha_4 &= \frac{-2\bar{x}\bar{k}_1}{a_1 + \bar{S}}, \\
\alpha_5 &= \frac{-2\bar{y}\bar{k}_2}{a_2 + \bar{S}}, \\
\alpha_6 &= \frac{-2\bar{y}\bar{k}_2 - (\bar{k}_2 - \bar{k}_1)(a_2 + \bar{S})}{a_2 + \bar{S}}, \\
\alpha_7 &= \frac{g(\bar{S}) - m_2 - 2\bar{y}\bar{k}_2 + \bar{k}_1(a_2 + \bar{S})}{a_2 + \bar{S}}, \\
\alpha_8 &= \frac{g(\bar{S}) - m_2 - 2\bar{y}\bar{k}_2 + \bar{k}_2(a_2 + \bar{S})}{a_2 + \bar{S}}.
\end{align*}
\]

The above system can be written as

\[
\begin{pmatrix}
\psi'_1(t) \\
\delta'_1(t)
\end{pmatrix} = A \begin{pmatrix}
\psi_1(t) \\
\delta_1(t)
\end{pmatrix} + D(t)
\]

Letting \(\Phi(t)\) be the fundamental matrix for the homogeneous problem, then the following equations are developed

\[
\begin{pmatrix}
\psi_1(\tau_0) \\
\delta_1(\tau_0)
\end{pmatrix} = \Phi(\tau_0) \int_0^{\tau_0} \Phi(t)^{-1} D(t) \, dt,
\]

66
\[
\int_0^{2\pi\omega_0} \left( \psi_1(t) \right) dt = \int_0^{2\pi\omega_0} \Phi(t) \left( \int_0^t \Phi(s)^{-1} D(s) \, ds \right) dt.
\]

which when solved yields \( \psi_1(\tau_0) = \delta_1(\tau_0) = 0 \) and

\[
\int_0^{2\pi\omega_0} \left( \psi_1(t) \right) dt = \begin{pmatrix} \omega_0^2 \pi (\bar{x} + \bar{y}) g''(\bar{S}) \sqrt{\frac{\pi}{\bar{y}}} \\ -\omega_0^2 \pi (\bar{x} + \bar{y}) f''(\bar{S}) \sqrt{\frac{\pi}{\bar{y}}} \end{pmatrix}.
\]

The system obtained for \( \gamma_1(t) \) and \( \rho_1(t) \) is given by

\[
\begin{pmatrix} \gamma'_1(t) \\ \rho'_1(t) \end{pmatrix} = \begin{pmatrix} 0 & \bar{x}(\bar{k}_2 - \bar{k}_1) \\ -\bar{y}(\bar{k}_2 - \bar{k}_1) & 0 \end{pmatrix} \begin{pmatrix} \gamma_1(t) \\ \rho_1(t) \end{pmatrix} + \begin{pmatrix} \frac{\sqrt{\frac{\pi}{\bar{y}}} \pi \bar{k}_1 \bar{k}_2 \bar{y} \bar{y}'(\bar{S}) - \omega_0 \bar{x} \bar{k}_1(\bar{k}_2 - \bar{k}_1) \cos(\frac{\tau}{\omega_0}) - \omega_0 \bar{x} \bar{k}_1(\bar{k}_1 - \bar{k}_1(\bar{S}'(\bar{S})) \sqrt{\frac{\pi}{\bar{y}}})} \\ \frac{\sqrt{\frac{\pi}{\bar{y}}} \pi \bar{k}_1 \bar{k}_2 \bar{y} \bar{y}'(\bar{S}) - \omega_0 \bar{y} \bar{k}_2 (\bar{k}_2 - \bar{k}_1) \cos(\frac{\tau}{\omega_0}) - \omega_0 \bar{y} \bar{k}_2 (\bar{k}_1 - \bar{k}_1(\bar{S}'(\bar{S})) \sqrt{\frac{\pi}{\bar{y}}})} \end{pmatrix} + \frac{1}{k_2 - k_1} \begin{pmatrix} \alpha_1 \sqrt{\frac{\pi}{\bar{y}}} \sin(\frac{\tau}{\omega_0}) + \alpha_2 \cos(\frac{\tau}{\omega_0}) & \alpha_3 \sqrt{\frac{\pi}{\bar{y}}} \sin(\frac{\tau}{\omega_0}) + \alpha_4 \cos(\frac{\tau}{\omega_0}) \\ \alpha_5 \sqrt{\frac{\pi}{\bar{y}}} \sin(\frac{\tau}{\omega_0}) + \alpha_6 \cos(\frac{\tau}{\omega_0}) & \alpha_7 \sqrt{\frac{\pi}{\bar{y}}} \sin(\frac{\tau}{\omega_0}) + \alpha_8 \cos(\frac{\tau}{\omega_0}) \end{pmatrix} \times \begin{pmatrix} \bar{k}_2 \cos(\frac{\tau}{\omega_0}) - \bar{k}_2 - \bar{k}_2 \sqrt{\frac{\pi}{\bar{y}}} \sin(\frac{\tau}{\omega_0}) \\ \bar{k}_1 - \bar{k}_1 \cos(\frac{\tau}{\omega_0}) - \bar{k}_2 \sqrt{\frac{\pi}{\bar{y}}} \sin(\frac{\tau}{\omega_0}) \end{pmatrix}, \quad \begin{pmatrix} \gamma_1(0) \\ \rho_1(0) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}.
\]

Proceeding as above we obtain the result

\[
\rho_1(\tau_0) = -\omega_0 \pi \bar{h}'(\bar{S}).
\]

As a final preparatory step, we note that the displacement function \( V(y) = P_1(y, 0) - y \) has the property that \( V(0) = V'(0) = V''(0) = 0 \) [32]. Hence, its Taylor expansion has the form \( V(y) = \frac{1}{3!} V''(0) y^3 + \cdots \) (Note that the dependence of \( V \) on the bifurcation parameter
has been suppressed). The above implies
\[ 1 - \frac{\partial \phi_2}{\partial y}(\tau_0) = 1 - \frac{\partial P_1}{\partial y}(y, 0) = -\frac{1}{2!} V''(0)y^2 + \cdots = -\frac{1}{2!} V''(0)\varepsilon^2 + \cdots \]
where \(y\) has been replaced by \(\varepsilon\) since they agree to the first order. (Recall the fixed point of the Poincaré map corresponds to \((0, 0)\).) This gives
\[ 1 - \frac{\partial \phi_2}{\partial y}(\tau_0) = \bar{N}\varepsilon^2 + O(\varepsilon^3) \]
where \(\bar{N} = -\frac{1}{2!} V''(0) > 0\).

3.3.6 Sign of \(\eta_1\)

Having performed all of the above calculations, we are finally in a position to solve Equation 3–12 for \(\eta_1\). We begin by expanding this equation with respect to \(\varepsilon\), performing the integrations, simplifying, collecting the like powers of \(\varepsilon\), and equating their coefficients to zero. The result of these operations will be an expression for \(\eta_1\) in terms of the system variables, the growth functions, and their derivatives.

To aid in the simplification of Equation 3–12, we perform some preliminary computations. Based upon Equation 3–13 and the discussion at the end on section 3.3.5 the following equality holds
\[ \left(1 - \frac{\partial \phi_2}{\partial y}(\tau_0)\right)\left(\frac{\partial \phi_1}{\partial t}(\tau_0)\right) = \bar{N}\frac{\bar{x}}{\bar{y}}\varepsilon^3 + O(\varepsilon^4). \]  
(3–15)

Using the definition of \(m_3(\eta)\) and \(\eta^*\), one can easily derive the expansions
\[ m_3(\eta^*) = \frac{m_1(a_3 + \bar{S} - \eta^*)}{a_1 + \bar{S} - \eta^*} = \frac{m_1(a_3 + \bar{S})}{a_1 + \bar{S}} + O(\varepsilon^2) = m_3(0) + O(\varepsilon^2), \]
\[ m'_3(\eta^*) = \frac{m_1(a_3 - a_1)}{(a_1 + \bar{S} - \eta^*)^2} = \frac{m_1(a_3 - a_1)}{(a_1 + \bar{S})^2} + O(\varepsilon^2). \]  
(3–16)

For the first term of Equation 3–12, using Equation 3–13 and Equation 3–16 the first factor can be expanded as
\[ \frac{m_3(\eta^*)(1 - x_0(\tau_0) - y_0(\tau_0))}{a_3 + (1 - x_0(\tau_0) - y_0(\tau_0))} - E + k_1x_0(\tau_0) + k_2y_0(\tau_0) = \]
\[ \varepsilon^0 \left( \frac{\bar{m}_3(1 - \bar{x} - \bar{y})}{a_3 + (1 - \bar{x} - \bar{y}) - E + \bar{k}_1 \bar{x} + \bar{k}_2 \bar{y}} \right) + \varepsilon^1 \left( \frac{\bar{m}_3(1 - \bar{x} - \bar{y})}{(a_3 + (1 - \bar{x} - \bar{y}))^2} \right) + \bar{m}_3 + \bar{k}_2 + \mathcal{O}(\varepsilon^2). \]

From the development of \( h(S) \), if \( m_3(\eta) = \bar{m}_3 \), then \( h(\bar{S}) = f(\bar{S}) \) so that the \( \varepsilon^0 \) term vanishes in the above expression. For the second factor, we deduce from section 3.3.5 that \( \psi_0(\tau_0) = \rho_0(\tau_0) = \gamma_0(\tau_0) = \psi_1(\tau_0) = 0 \) and upon expansion obtain

\[ \begin{align*}
\frac{\partial \phi_1}{\partial y}(\tau_0) & \left( \frac{\partial \phi_2}{\partial z}(\tau_0) \right) = \varepsilon^0(\psi_0(\tau_0)\rho_0(\tau_0)) + \varepsilon^1(\psi_0(\tau_0)\rho_1(\tau_0) + \psi_1(\tau_0)\rho_0(\tau_0)) + \\
\frac{\partial \phi_1}{\partial z}(\tau_0) & \left( 1 - \frac{\partial \phi_2}{\partial y}(\tau_0) \right) = (\varepsilon^0\gamma_0(\tau_0) + \varepsilon^1\gamma_1(\tau_0) + \mathcal{O}(\varepsilon^2))(\varepsilon^2 N + \mathcal{O}(\varepsilon^3)) = \mathcal{O}(\varepsilon^3).
\end{align*} \]

Combining all of this information, the first term is found to be of order \( \mathcal{O}(\varepsilon^4) \).

For the second term of Equation 3–12, the numerator of the integrand can be expanded as

\[ a_3(\varepsilon^0 m_3 + \mathcal{O}(\varepsilon^2))(\varepsilon^0 \gamma_0(t) + \varepsilon^1 \gamma_1(t) + \varepsilon^0 \rho_0(t) + \varepsilon^1 \rho_1(t) + 1 + \\
\varepsilon^1(\omega_0(\bar{k}_2 - \bar{h}'(\bar{S})) \sin \left( \frac{t}{\omega_0} \right) + \omega_0(\bar{h}'(\bar{S}) - \bar{k}_1) \sqrt{\frac{x}{y}} \cos \left( \frac{t}{\omega_0} \right)) \]

and the denominator can be written as

\[ \varepsilon^0 \left( \frac{1}{(a_3 + 1 - \bar{x} - \bar{y})^2} \right) + \varepsilon^1 \left( \frac{2}{(a_3 + 1 - \bar{x} - \bar{y})^3} \right) \left( \sqrt{\frac{x}{y}} \sin \left( \frac{t}{\omega_0} \right) + \cos \left( \frac{t}{\omega_0} \right) \right) + \mathcal{O}(\varepsilon^2). \]

Combining these expressions with Equation 3–15 yields for the second term of Equation 3–12

\[ \left( \frac{N}{\omega_0} \sqrt{\frac{x}{y}} \int_0^{2\pi a_0} \frac{a_3 m_3(\gamma_0(t) + \rho_0(t) + 1)}{(a_3 + 1 - \bar{x} - \bar{y})^2} dt \right) \varepsilon^3 + \mathcal{O}(\varepsilon^4). \]

From Equation 3–14 it is clear that \( \gamma_0(t) + \rho_0(t) + 1 \) will integrate to zero so the above expression is of order \( \mathcal{O}(\varepsilon^4) \).

The numerator of the integrand in the third term can be written as

\[ a_3(\varepsilon^0 m_3 + \mathcal{O}(\varepsilon^2))(\varepsilon^0 \psi_0(t) + \varepsilon^1 \psi_1(t) + \varepsilon^0 \delta_0(t) + \varepsilon^1 \delta_1(t) + \mathcal{O}(\varepsilon^2))(\varepsilon^1 \rho_1(\tau_0) + \varepsilon^2 \rho_2(\tau_0) + \mathcal{O}(\varepsilon^3)) \]
while the denominator may be expanded as

\[
\varepsilon^0 \frac{1}{(a_3 + 1 - \bar{x} - \bar{y})^2} + \varepsilon^1 \frac{2}{(a_3 + 1 - \bar{x} - \bar{y})^3} \left( \sqrt{\frac{\bar{x}}{\bar{y}}} \sin \left( \frac{t}{\omega_0} \right) + \cos \left( \frac{t}{\omega_0} \right) \right) + O(\varepsilon^2).
\]

Combining this information, the integrand can be expressed as

\[
\varepsilon^1 \frac{a_3 \bar{m}_3 \rho_1(\tau_0)(\psi_0(t) + \delta_0(t))}{(a_3 + 1 - \bar{x} - \bar{y})^2} + \varepsilon^2 \frac{a_3 \bar{m}_3 \rho_2(\tau_0)(\psi_0(t) + \delta_0(t))}{(a_3 + 1 - \bar{x} - \bar{y})^2} + \varepsilon^2 \left( \frac{2a_3 \bar{m}_3 \rho_1(\tau_0)(\psi_0(t) + \delta_0(t))}{(a_3 + 1 - \bar{x} - \bar{y})^3} \left( \sqrt{\frac{\bar{x}}{\bar{y}}} \sin \left( \frac{t}{\omega_0} \right) + \cos \left( \frac{t}{\omega_0} \right) \right) + \frac{a_3 \bar{m}_3 \rho_1(\tau_0)(\psi_1(t) + \delta_1(t))}{(a_3 + 1 - \bar{x} - \bar{y})^2} \right) + O(\varepsilon^3).
\]

It is clear that the first two terms will integrate to zero, while the remaining \(\varepsilon^2\) term can be written as

\[
\varepsilon^2 \left( \frac{2a_3 \bar{m}_3 \rho_1(\tau_0)}{(a_3 + 1 - \bar{x} - \bar{y})^3} \left( \sqrt{\frac{\bar{x}}{\bar{y}}} \sin \left( \frac{t}{\omega_0} \right) + \cos \left( \frac{t}{\omega_0} \right) \right)^2 + \frac{a_3 \bar{m}_3 \rho_1(\tau_0)(\psi_1(t) + \delta_1(t))}{(a_3 + 1 - \bar{x} - \bar{y})^2} \right).
\]

After integration and using Equation 3–13, the third term is given by

\[
-\varepsilon^3 \left[ \frac{2a_3 \bar{m}_3 \rho_1(\tau_0)}{(a_3 + 1 - \bar{x} - \bar{y})^3} \sqrt{\frac{\bar{x}}{\bar{y}}} \left( \frac{\bar{x}}{\bar{y}} + 1 \right) + \sqrt{\frac{\bar{x}}{\bar{y}}} \omega_0 (a_3 + 1 - \bar{x} - \bar{y})^2 \int_0^{\pi(0)} (\psi_1(t) + \delta_1(t)) dt \right] + O(\varepsilon^4).
\]

In the fourth term, we note that for the integral, the coefficient of \(\varepsilon^0\) is given by

\[
\int_0^{2\pi \omega_0} \bar{k}_1 \gamma_0(t) + \bar{k}_2 \rho_0(t) \ dt.
\]

From Equation 3–14, it is evident that this integral is equal to zero, so that using Equation 3–15, the fourth term is of order \(O(\varepsilon^4)\).

For the fifth term of Equation 3–12, the integrand can be expanded as

\[
[(\varepsilon^0 \bar{k}_1 + \varepsilon^2 \bar{k}_2 + O(\varepsilon^3))(\varepsilon^0 \psi_0(t) + \varepsilon^1 \psi_1(t) + \varepsilon^2 \psi_2(t) + O(\varepsilon^3)) + \bar{k}_2 (\varepsilon^0 \delta_0(t) + \varepsilon^1 \delta_1(t) + \varepsilon^2 \delta_2(t) + O(\varepsilon^3))] (\varepsilon^1 \rho_1(\tau_0) + \varepsilon^2 \rho_2(\tau_0) + O(\varepsilon^3))
\]

which reduces to

\[
\varepsilon^1 [(\bar{k}_1 \psi_0(t) + \bar{k}_2 \delta_0(t)) \rho_1(\tau_0) + \varepsilon^2 [(\bar{k}_1 \psi_0(t) + \bar{k}_2 \delta_0(t)) \rho_2(\tau_0) + (\bar{k}_1 \psi_1(t) + \bar{k}_2 \delta_1(t)) \rho_1(\tau_0)].
\]
Each expression which involves \( \psi_0(t) \) or \( \delta_0(t) \) integrates to zero so using Equation 3–13, this term can be expressed as

\[
\varepsilon^3 \sqrt{\frac{x}{y}} \left( \frac{p_1(\tau_0)}{\omega_0} \right) \int_0^{2\pi \omega_0} k_1 \psi_1(t) + k_2 \delta_1(t) \, dt + O(\varepsilon^4).
\]

Analyzing the final term, we expand the integral as

\[
\int_0^{\tau(0)} \frac{(1 - x_0(t) - y_0(t))}{a_3 + (1 - x_0(t) - y_0(t))} \, dt = \int_0^{2\pi \omega_0} \frac{(1 - \bar{x} - \bar{y})}{a_3 + (1 - \bar{x} - \bar{y})} \, dt + O(\varepsilon^1) = \frac{2\pi \omega_0 h(\bar{S})}{m_3} + O(\varepsilon^1).
\]

Combining this with Equation 3–15 and Equation 3–16 the last term may be written as

\[
\eta_1 \sqrt{\frac{x}{y}} \left( \frac{2\pi m_1 \bar{N} h(\bar{S})(a_3 - a_1)}{m_3(a_1 + S)^2} \right) \varepsilon^3 + O(\varepsilon^4) = \eta_1 \sqrt{\frac{x}{y}} \left( \frac{2\pi \bar{N} f'(\bar{S}) h(\bar{S})(a_3 - a_1)}{a_1 m_3} \right) \varepsilon^3 + O(\varepsilon^4).
\]

We conclude that all the \( \varepsilon^k \) terms with \( k = 0, 1, 2 \) in Equation 3–12 are zero. Setting the coefficient of the \( \varepsilon^3 \) term equal to zero yields

\[
0 = \eta_1 \sqrt{\frac{x}{y}} \left( \frac{2\pi \bar{N} f'(\bar{S}) h(\bar{S})(a_3 - a_1)}{a_1 m_3} \right) + \sqrt{\frac{x}{y}} \left( \frac{\rho_1(\tau_0)}{\omega_0} \right) \int_0^{2\pi \omega_0} k_1 \psi_1(t) + k_2 \delta_1(t) \, dt
\]

\[
- \frac{2\pi a_3 m_3 \rho_1(\tau_0)}{(a_3 + S)^3} \sqrt{\frac{x}{y}} \left( \frac{\bar{x}}{\bar{y}} + 1 \right) + - \sqrt{\frac{x}{y}} \frac{a_3 m_3 \rho_1(\tau_0)}{\omega_0(a_3 + S)^2} \int_0^{2\pi \omega_0} \psi_1(t) + \delta_1(t) \, dt.
\]

Rearranging this equation, evaluating integrals, and substituting we obtain

\[
\eta_1 = \rho_1(\tau_0) \left( \frac{m_1}{N} \right) \left( \frac{a_1(\bar{x} + \bar{y})}{2\bar{y}h(\bar{S}) f'(\bar{S})(a_1 - a_3)(g'(\bar{S}) - f'(\bar{S}))} \right) \left( \bar{h}''(\bar{S})(g'(\bar{S}) - f'(\bar{S})) + g''(\bar{S})(f'(\bar{S}) - \bar{h}'(\bar{S})) + f''(\bar{S})(\bar{h}'(\bar{S}) - g'(\bar{S})) \right).
\]

### 3.3.7 Stability of Bifurcating Orbits

As we explained previously, the stability of the bifurcating orbits is determined by the signs of \( \eta_1 \), \( \frac{\partial^2 \bar{S}}{\partial \bar{x} \partial \bar{y}}(0) \), and \( \frac{\bar{S}(m_3 - m_1) \rho_1}{(a_1 + S)(a_3 + S)} \). By defining

\[
P = \frac{a_1(\bar{x} + \bar{y})}{2\bar{y}h(\bar{S}) f'(\bar{S})(a_1 - a_3)(g'(\bar{S}) - f'(\bar{S}))}
\]

\[
Q = \bar{h}''(\bar{S})(g'(\bar{S}) - f'(\bar{S})) + g''(\bar{S})(f'(\bar{S}) - \bar{h}'(\bar{S})) + f''(\bar{S})(\bar{h}'(\bar{S}) - g'(\bar{S}))
\]

\[
71
\]
\[
\frac{\partial^2 \eta}{\partial \varepsilon^2}(0) = m_3 PQ \\
\eta_1 = \rho_1(\tau_0) \left( \frac{m_1}{N} \right) PQ.
\] (3–17)

We observe from the statement of the problem as well as the definition of the growth functions that \( P \) has the same sign as \((a_1 - a_3)\) and since \( \rho_1(\tau_0) \) is strictly negative, the two terms in Equation 3–17 are of opposite sign.

Having established the above identities we wish to examine \( Q \) and to determine the sign of this quantity as a function of \( a_3 \). Using the fact that \( f(\bar{S}) = g(\bar{S}) = h(\bar{S}) \) when \( \eta = 0 \), it follows that \( a_3 = a_i \) gives \( m_3(0) = m_i \) for \( i \in \{1, 2\} \). Thus \( a_3 = a_1 \) implies \( \bar{h}(S) = f(S) \) and \( a_3 = a_2 \) implies \( \bar{h}(S) = g(S) \) (recall \( \bar{h}(S) \) is the growth function with \( m_3 = m_3(0) \)), so that in either case, \( Q = 0 \). Using the definitions of the uptake functions it is possible to express \( Q \) as a third degree polynomial in \( a_3 \) as follows

\[
Q = \left( \frac{2m_1m_2(a_2 - a_1)}{(a_1 + \bar{S})^3(a_2 + \bar{S})^3(a_3 + \bar{S})^3} \right) \times \\
\left( (m_2 - m_1)^2 \bar{S}^2 a_3^2 + \bar{S}[(m_1a_2 - m_2a_1) + m_1a_1 - m_2a_2]a_3^2 + \\
(m_2 - m_1)\bar{S}^2[(m_2 - m_1)(a_1 + a_2)^2 + m_1a_1^2 - m_2a_2^2]a_3 + a_1a_2\bar{S}^3(m_2 - m_1)^2 \right).
\]

Since, as previously discussed, \( a_2 > a_1 \), the term \( \frac{2m_1m_2(a_2 - a_1)}{(a_1 + \bar{S})^3(a_2 + \bar{S})^3(a_3 + \bar{S})^3} \) is positive, which means that the constant term in the polynomial as well as the coefficient of \( a_3^3 \) are both positive. This implies \( Q \) has one negative root and the two positive roots given by \( a_1 \) and \( a_2 \). From this information it is possible to deduce that \( Q > 0 \) for \( a_3 \in (0, a_1) \cup (a_2, +\infty) \) and \( Q < 0 \) for \( a_3 \in (a_1, a_2) \).

We are now in a position to determine how the interactions of the three growth functions affect the bifurcation. First, Table I is constructed based upon the results derived above. From the information in this table as well as the locally quadratic nature of \( G(\varepsilon) \) it is possible to construct the graphs of the neutral stability curves (Figure 3-2).
where $U$ represents the region of instability for the planar Hopf orbit, $S$ represents the region of stability for the planar Hopf orbit, and the arrow points in the direction of the change of $\eta$ as the value of $s$ becomes positive in the expansion $\eta = \eta^* + s\eta_1 + O(s^2)$. These graphs demonstrate that for $a_3 < a_1$ or $a_2 < a_3$, the Hopf orbit loses its stability and the bifurcating orbit in the first octant becomes asymptotically stable. The opposite is true for the case $a_1 < a_3 < a_2$.

Figure 3-3 indicates the relative positions of the growth functions as the value of $a_3$ is varied. Recall that $g'(\bar{S}) > f'(\bar{S})$ implies that $f(S) > g(S)$ for $S \in (0, \bar{S})$. Combining the information presented in Figures 3-2 and 3-3, we observe that a stable periodic orbit in the first octant results from a bifurcation when $h'(\bar{S})$ is either greater than or less than both $f'(\bar{S})$ and $g'(\bar{S})$ while the bifurcating orbit is unstable otherwise. This concludes the proof of Theorem 9.

### 3.4 Coexistence and a Diluter Function of Three Variables

A natural extension of the above studies is to investigate the question of coexistence when the diluter function is affine in all three variables $x, y,$ and $z$. A motivation for the introduction of a third variable is given by the following calculations.

We begin with the system Equation 3–1 and modify the diluter function so that

$$D(x, y, z) = -k_1x - \bar{k}_2y - \bar{k}_3z + E$$

where $\bar{k}_3 = h(\bar{S})$ and all other constants are as previously described. For $k_1 = \bar{k}_1$, there exists a line of equilibria for the new system which is formed by the intersection of the planes $\bar{S} = 1 - x - y - z$ and $f(\bar{S}) = D(x, y, z) = E - \bar{k}_1x - \bar{k}_2y - \bar{k}_3z$.

A vector parallel to the line is given by the cross products of the normal vectors to the above planes: $\langle 1, 1, 1 \rangle \times \langle \bar{k}_1, \bar{k}_2, \bar{k}_3 \rangle = \langle \bar{k}_3 - \bar{k}_2, \bar{k}_1 - \bar{k}_3, \bar{k}_2 - \bar{k}_1 \rangle$; thus the line of equilibria may be represented parametrically by $x = \bar{x} + (\bar{k}_3 - \bar{k}_2)t$, $y = \bar{y} + (\bar{k}_1 - \bar{k}_3)t$, and $z = (\bar{k}_2 - \bar{k}_1)t$. It is interesting to note that $\langle \bar{k}_3 - \bar{k}_2, \bar{k}_1 - \bar{k}_3, \bar{k}_2 - \bar{k}_1 \rangle \cdot \langle f''(\bar{S}), g''(\bar{S}), h''(\bar{S}) \rangle$ is identical to the quantity $Q$ defined in Section 3.3.7. Hence it may be reasonable to assume that the above line of equilibria (and hence the new expression for the diluter function) plays a key role in the coexistence result.
To further explore these connections and to test the feasibility of bifurcating from a line of equilibria, a numerical study was performed on a system where the growth functions were given by

\[
f(S) = \frac{1.4S}{0.2 + S}, \quad g(S) = \frac{2.5S}{0.75 + S}, \quad h(S) = \frac{m_3(\eta)S}{0.1 + S} \quad (m_3(0) = 1.2).\]

Based on these functions, we find that to within four significant figures \(\bar{S} = 0.5000\), \(\bar{k}_1 = f'(0.5000) = 0.5714\), \(\bar{k}_2 = g'(0.5000) = 1.200\), and \(\bar{k}_3 = h'(0.5000) = 0.3333\). Hence choosing \(E = 1.450\), we write the diluter function as \(D = 1.45 - (\kappa + 0.5714)x - 1.2y - 0.3333z\) where \(|\kappa| \ll 1\). The purpose of this study is to perturb the system by varying \(m_3\) and \(\kappa\) so that the line of equilibria vanishes and then to check for the existence of asymptotically stable limit cycles by studying trajectories in the first octant. The system was analyzed for discrete values of \(m_3 \in [1.19900, 1.20090]\) and \(\kappa \in [-0.0134, 0.0186]\). The results suggest that for \(m_3 > 1.2\), the equilibrium point in the \(y, z\) plane is an attractor for orbits with initial values in the interior of the first octant; for \(m_3 < 1.2\) and \(\kappa < 0\) the equilibrium in the \(x, y\) plane is the attractor; and locally stable periodic orbits can exist when \(m_3 < 1.2\) and \(\kappa > 0\). The dependence of the orbits on \(\kappa\) and \(m_3\) is exhibited in Figures 3-4 and 3-5. In Figure 3-4, \(\kappa = 0.0101\) and \(m_3\) is varied while in Figure 3-5, \(\kappa\) is perturbed while \(m_3\) has a constant value of 1.19970. In both cases it appears possible to generate a family of periodic orbits which traverses part of the first octant from the \(x, y\) plane to the \(y, z\) plane.

Table 3-1. Signs of essential quantities as functions of \(a_3\).

<table>
<thead>
<tr>
<th>(a_3)</th>
<th>(a_1)</th>
<th>(a_2)</th>
<th>(a_3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\eta_1)</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>(\frac{\partial^2 \eta}{\partial \varepsilon^2}(0))</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>(\frac{\bar{S}(\bar{m}_3-m_1)}{(a_1+S)(a_3+S)})</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>
Figure 3-1. Transcritical bifurcation into the first octant. A) Stable orbit. B) Unstable orbit.

Figure 3-2. Stability of the Hopf Orbit as a function of $a_3$. A) $a_3 < a_1$. B) $a_1 < a_3 < a_2$. C) $a_2 < a_3$.

Figure 3-3. Relative positions of the growth functions as determined by $a_3$. A) $a_3 < a_1$. B) $a_1 < a_3 < a_2$. C) $a_2 < a_3$. 
Figure 3-4. Periodic Orbits as a function of $m_3$.

Figure 3-5. Periodic Orbits as a function of $\kappa$. 
CHAPTER 4
LINEAR GROWTH FUNCTIONS AND A LINE OF EQUILIBRIA

The simulations from Chapter 3 suggest that for a diluter function which is affine in all three variables it is possible to bifurcate from a line of equilibria and obtain coexistence by means of periodic orbits. In this chapter, we will begin a preliminary exploration of this idea and present the results to date of this continuing research. Many fundamental questions remain open and these will be noted as they arise.

4.1 First Integrals and Level Surfaces

We begin with the system Equation 3-1 and simplify the equalities by replacing the Michaelis-Menten growth functions $f(S)$, $g(S)$, and $h(S)$ with linear approximations which intersect at a nonzero substrate concentration $\bar{S}$. Hence we define

$$f(S) = 1 + \bar{k}_1(S - \bar{S}),$$
$$g(S) = 1 + \bar{k}_2(S - \bar{S}),$$
$$h(S) = 1 + \bar{k}_3(S - \bar{S})$$

and rewrite the system equations of as

$$\dot{x} = x(1 + \bar{k}_1(1 - \bar{S} - x - y - z) - E + k_1x + k_2y + k_3z),$$
$$\dot{y} = y(1 + \bar{k}_2(1 - \bar{S} - x - y - z) - E + k_1x + k_2y + k_3z),$$
$$\dot{z} = z(1 + \bar{k}_3(1 - \bar{S} - x - y - z) - E + k_1x + k_2y + k_3z)$$

where the constants $k_i$ are nonnegative and where we assume that $k_2 > k_1$ and $\bar{k}_2 > \bar{k}_1$. Note that the coordinate planes remain invariant so that the solutions of interest are constrained to lie in the first octant and its associated planar boundaries. The system admits a line of equilibria $L$ which is the intersection of the planes $x + y + z = 1 - \bar{S}$ and $k_1x + k_2y + k_3z = E - 1$ (this assumes of course that the above planes are distinct and nonparallel). The directional vector for $L$ is calculated from the cross product

$$\langle 1, 1, 1 \rangle \times \langle k_1, k_2, k_3 \rangle$$

and is equal to $\langle k_3 - k_2, k_1 - k_3, k_2 - k_1 \rangle$. Presently we will require
that this line intersects the first octant in one of two possible ways: it intersects the first quadrant of both the \(x, y\) and \(y, z\) coordinate planes or it intersects the first quadrant of both the \(x, z\) and \(y, z\) coordinate planes. The following lemma gives necessary and sufficient conditions for these intersection properties.

**Lemma 4.** The line \(L\) intersects the first octant and the first quadrant of both the \(x, y\) and \(y, z\) coordinate planes if and only if \(k_3 < k_2, k_2(1 - \bar{S}) > E - 1, \) and both \(k_1(1 - \bar{S})\) and \(k_3(1 - \bar{S})\) are less than \(E - 1\). The line \(L\) intersects the first octant and the first quadrant of both the \(x, z\) and \(y, z\) coordinate planes if and only if \(k_3 < k_1 < k_2\) and \(k_2(1 - \bar{S}) > k_1(1 - \bar{S}) > E - 1 > k_3(1 - \bar{S})\) or \(k_2 < k_3\) and \(k_3(1 - \bar{S}) > E - 1 > k_2(1 - \bar{S}) > k_1(1 - \bar{S})\).

**Proof of Lemma 4.** We define \((x_a, y_a, 0), (0, y_b, z_b),\) and \((x_c, 0, z_c)\) to be the respective points of intersection (where appropriate) of \(L\) with the \(x, y\); \(y, z\); and \(x, z\) coordinate planes. It is clear that the line \(L\) will intersect the first octant and the first quadrants of the appropriate coordinate planes if and only if the corresponding variables \(x_a, x_c, y_a, y_b, z_b\) and \(z_c\) are all positive. At these points, the system of equations

\[
x + y + z = 1 - \bar{S},
\]

\[
k_1x + k_2y + k_3z = E - 1
\]

must be solved simultaneously (note \(1 - \bar{S}\) and \(E - 1\) are positive quantities).

Performing the substitutions and solving for the variables in the case of intersection with the \(x, y\) and \(y, z\) coordinate planes yields

\[
x_a = \frac{k_2(1 - \bar{S}) - (E - 1)}{k_2 - k_1}, \quad y_a = \frac{(E - 1) - k_1(1 - \bar{S})}{k_2 - k_1}
\]

\[
y_b = \frac{(E - 1) - k_3(1 - \bar{S})}{k_2 - k_3}, \quad z_b = \frac{k_2(1 - \bar{S}) - (E - 1)}{k_2 - k_3}
\]

It is easily checked that the assumptions \(k_3 < k_2, k_2(1 - \bar{S}) > E - 1, \) and both \(k_1(1 - \bar{S})\) and \(k_3(1 - \bar{S})\) are less than \(E - 1\) imply that \(x_a, y_a, y_b,\) and \(z_b\) are all positive. Using the assumption \(k_2 > k_1,\) we find \(x_a > 0\) implies \(k_2(1 - \bar{S}) - (E - 1) > 0;\) (given
\[ k_2(1 - \bar{S}) - (E - 1) > 0 \] \( z_b > 0 \) implies \( k_3 < k_2 \); and (given \( k_3 < k_2 \)) \( y_a \) and \( y_b \) are positive imply \( k_1(1 - \bar{S}) \) and \( k_3(1 - \bar{S}) \) respectively are less than \( E - 1 \).

Similarly the intersection of \( L \) with the \( x, z \) and \( y, z \) coordinate planes yield the equations

\[
y_b = \frac{(E - 1) - k_3(1 - \bar{S})}{k_2 - k_3}, \quad z_b = \frac{k_2(1 - \bar{S}) - (E - 1)}{k_2 - k_3}
\]
\[
x_c = \frac{k_3(1 - \bar{S}) - (E - 1)}{k_3 - k_1}, \quad z_c = \frac{(E - 1) - k_1(1 - \bar{S})}{k_3 - k_1}.
\]

Again, one can readily check that the assumptions \( k_3 < k_1 < k_2 \) and \( k_2(1 - \bar{S}) > k_1(1 - \bar{S}) > E - 1 > k_3(1 - \bar{S}) \) or \( k_2 < k_3 \) and \( k_3(1 - \bar{S}) > E - 1 > k_2(1 - \bar{S}) > k_1(1 - \bar{S}) \) imply that \( x_c, y_b, z_b, \) and \( z_c \) are greater than zero. Now assume \( k_3 < k_2 \). The assumption that the variables \( y_b \) and \( z_b \) are greater than zero imply \( k_3(1 - \bar{S}) < E - 1 \) and \( E - 1 < k_2(1 - \bar{S}) \) respectively; (given \( k_3(1 - \bar{S}) < E - 1 \)) \( x_c > 0 \) implies \( k_1 > k_3 \); and (given \( k_1 > k_3 \)) \( z_c \) is positive requires that \( k_1(1 - \bar{S}) > E - 1 \). For \( k_3 > k_2 \), \( y_b \) and \( z_b \) are greater than zero imply \( k_3(1 - \bar{S}) > E - 1 \) and \( E - 1 > k_2(1 - \bar{S}) \) respectively. Since \( k_1 < k_2 \), the condition \( E - 1 > k_2(1 - \bar{S}) \) automatically gives \( E - 1 > k_2(1 - \bar{S}) > k_1(1 - \bar{S}) \).

The elements of the directional vector of \( L \) are nontrivial as noted in Section 3.4 and appear again in a first integral of the linear system. A first integral is a nonconstant function whose level surfaces are invariant for the solutions of an ODE; hence the gradient of the function is orthogonal to the tangent vector of the trajectory at each point on a level surface. We shall examine two particular cases for the linear system: Case I, \( k_i = \bar{k}_i \) for \( i \in \{1, 2, 3\} \) and Case II, \( k_i = \tilde{k}_i \) for \( i \in \{1, 2\} \) and \( k_3 = 0 \). In both cases, the function \( V(x, y, z) = x^{k_3 - k_2}y^{k_1 - k_3}z^{k_2 - k_1} \) is a first integral as is verified by computing

\[
\dot{V}(x, y, x) = \nabla V(x, y, z) \cdot \langle \dot{x}, \dot{y}, \dot{z} \rangle = 0.
\]

As is readily observed, the exponents in \( V \) are the elements of the directional vector for Case I.

The existence of the first integral implies that the first octant is foliated by the invariant manifolds that are the level surfaces of \( V \). We will separately consider the
intersections of these level surfaces with the line of equilibria for Case I and II and characterize certain elements of the corresponding state space.

4.2 Case I Levels Surfaces

For Case I, the behavior of solutions is quite simple and is described in the following Theorem and Lemma.

**Theorem 11.** For Case I, every first octant level surface of $V$ intersects the line of equilibria exactly once.

**Proof of Theorem 11.** We begin the proof with the following parameterization of the line of equilibria. Recalling that for Case I, $k_1 = \bar{k}_1$, $k_2 = \bar{k}_2$, and $k_3 = \bar{k}_3$, we have

$$x(r) = x_0 + (\bar{k}_3 - \bar{k}_2)r,$$
$$y(r) = y_0 + (\bar{k}_1 - \bar{k}_3)r,$$
$$z(r) = z_0 + (\bar{k}_2 - \bar{k}_1)r$$

where $(x_0, y_0, z_0)$ is a first octant point on the line and $r$ is a scalar variable. Next the three possible modes of intersections outlined in Lemma 4 are considered in turn. Initially we assume that $L$ intersects the first quadrants of the $x, y$ and $y, z$ coordinate planes so that $\bar{k}_3 < \bar{k}_2$ and define $r_0 < r_1$, $z(r_0) = 0$ and $x(r_1) = 0$. Next we examine the component functions of $V(x(r), y(r), z(r))$ for $r \in (r_0, r_1)$. The exponent of the term $x(r)^{\bar{k}_3 - \bar{k}_2}$ is negative so that this function is continuous and increasing as $r : r_0 \to r_1$; its value is a finite positive number for $r = r_0$ and approaches $+\infty$ as $r \to r_1^-$. Since $y(r) > 0$ for $r \in [r_0, r_1]$, the function $y(r)^{k_1 - k_3}$ is clearly continuous and bounded on this interval. Since we assume that $\bar{k}_2 > \bar{k}_1$, the function $z(r)^{\bar{k}_2 - k_1}$ is continuous, bounded, and increasing on $r \in (r_0, r_1)$ with a minimum value of zero at $r = r_0$. Combining these facts we see that $V(x(r), y(r), z(r))$ is continuous on $(r_0, r_1)$, it approaches zero as $r \to r_0^+$ and it approaches positive infinity as $r \to r_1^-$. Hence, by the intermediate value theorem, for any $C > 0$ there exists a $\bar{r} \in (r_0, r_1)$ such that $V(x(\bar{r}), y(\bar{r}), z(\bar{r})) = C$. 
For the second mode we assume that $L$ intersects the first quadrants of the $x,z$ and $y,z$ coordinate planes and that $\bar{k}_3 < \bar{k}_1 < \bar{k}_2$. We define $r_0 < r_1$, $y(r_0) = 0$, and $x(r_1) = 0$ and again examine the component functions of $V$. As before $x(r)^{\bar{k}_3 - \bar{k}_2}$ is continuous on $(r_0, r_1)$, bounded below by $x(r_0)^{\bar{k}_3 - \bar{k}_2}$ and increases to $+\infty$ as $r \to r_1^-$. Since $\bar{k}_1 - \bar{k}_3 > 0$, the function $y(r)^{\bar{k}_1 - \bar{k}_3}$ is a continuous, bounded function on the interval of interest with $y(r_0)^{\bar{k}_1 - \bar{k}_3} = 0$; likewise $z(r)^{\bar{k}_2 - \bar{k}_1}$ is a continuous, bounded, nonzero function on $[r_0, r_1)$. Thus by again invoking the intermediate value theorem for the function $V$, it is clear that each level surface intersects the line of equilibria.

For the final mode, we assume that $L$ intersects the first quadrants of the $x,z$ and $y,z$ coordinate planes and that $\bar{k}_2 < \bar{k}_3$ with $r_0 < r_1$, $y(r_0) = 0$, and $x(r_1) = 0$. For this case, all of the component functions of $V$ are continuous on $(r_0, r_1)$; $x(r)^{\bar{k}_3 - \bar{k}_2}$ attains a finite maximum at $r = r_0$ and is zero at $r = r_1$; $y(r)^{\bar{k}_1 - \bar{k}_3}$ attains a finite minimum at $r = r_1$ and approaches positive infinity as $r \to r_1^+$; $z(r)^{\bar{k}_2 - \bar{k}_1}$ is bounded in the first octant. Hence by previous arguments, it follows that the function $V$ can assume any positive value so that the intersection result again holds.

To prove that the intersection is unique we calculate the derivative of $V(x(r), y(r), z(r))$ with respect to $r$ and find

$$\frac{d}{dr} V = V \left( \frac{(\bar{k}_3 - \bar{k}_2)^2}{x_0 + (\bar{k}_3 - \bar{k}_2)r} + \frac{(\bar{k}_1 - \bar{k}_3)^2}{y_0 + (\bar{k}_1 - \bar{k}_3)r} + \frac{(\bar{k}_1 - \bar{k}_3)^2}{z_0 + (\bar{k}_2 - \bar{k}_1)r} \right)$$

which is clearly a positive number on the interval of interest. Thus the function $V$ is strictly increasing with respect to $r$ which implies that each point on the line of equilibria can be contained in at most one level set of $V$. 

Lemma 5. For Case I, every non-equilibrium, first octant solution is periodic.

Proof of Lemma 5. We begin by defining the function

$$U(x, y, z) = \int_{x_0}^{x} \frac{s - x_0}{s} \, ds + \int_{y_0}^{y} \frac{s - y_0}{s} \, ds + \int_{z_0}^{z} \frac{s - z_0}{s} \, ds$$
where \((x_0, y_0, z_0)\) is a first octant equilibrium. A direct calculation provides \(\dot{U}(x, y, x) = \nabla U(x, y, z) \cdot (\dot{x}, \dot{y}, \dot{z}) = 0\) so that the function \(U\) is a first integral. It is clear that the level sets of \(U^{-1}(K), K > 0\) are topological spheres so that all positive solutions are bounded. By the previous discussion we conclude that the level sets of \(V^{-1}(C), C > 0\) are topological planes.

Next we choose some point \((\tilde{x}, \tilde{y}, \tilde{z})\) and define \(V(\tilde{x}, \tilde{y}, \tilde{z}) = \tilde{C}\) as the level surface containing this point. Choose the equilibrium point \((x_0, y_0, z_0)\) so that it is in the set \(V = \tilde{C}\) and define the function \(U\) using this point. We note that the set \(U^{-1}(0)\) is the singleton \(\{(x_0, y_0, z_0)\}\) and let \(U(\tilde{x}, \tilde{y}, \tilde{z}) = \tilde{K} > 0\). By the definition of the first integral, the general solution to the ODE system which contains \((\tilde{x}, \tilde{y}, \tilde{z})\) must lie in the set \(U^{-1}(\tilde{K}) \cap V^{-1}(\tilde{C})\) which is a closed curve on the level surface \(V = \tilde{C}\). By the previous remarks, this curve contains no equilibria. Hence by the Poincaré-Bendixon Theorem, the curve is a periodic orbit.

4.3 Case II Level Surfaces

For Case II, the behavior of solutions on level surfaces is less well understood. Our development will concentrate on determining how a given level surface intersects \(L\) and the stability of the resulting internal equilibria. We limit our discussion to lines of equilibria which intersect the \(x, y\) and \(y, z\) coordinate planes.

We parameterize \(L\) as follows

\[
\begin{align*}
x_0 &= x^* - \tilde{k}_2 r, \\
y_0 &= y^* + \tilde{k}_1 r, \\
z_0 &= z^* + (\tilde{k}_2 - \tilde{k}_1) r
\end{align*}
\]

where \(r\) is a scalar variable with domain \([0, \frac{k_2(1-S)-(E-1)}{k_2(k_2-k_1)}]\) and where \((x^*, y^*, z^*)\) is the point of intersection of the line with the \(x, y\) coordinate plane \((r = 0)\) so that

\[
x^* = \frac{\tilde{k}_2(1 - S) - (E - 1)}{k_2 - k_1},
\]
\begin{align*}
y^* &= \frac{(E - 1) - \bar{k}_1(1 - \bar{S})}{\bar{k}_2 - \bar{k}_1}, \\
z^* &= 0.
\end{align*}

The point of intersection of the line with the \( y, z \) coordinate plane is denoted by \((\hat{x}, \hat{y}, \hat{z})\), occurs when \( r = \frac{\bar{k}_2(1 - \bar{S}) - (E - 1)}{\bar{k}_2(\bar{k}_2 - \bar{k}_1)} \), and has component values
\[
\begin{align*}
\hat{x} &= 0, \\
\hat{y} &= \frac{E - 1}{\bar{k}_2}, \\
\hat{z} &= \frac{\bar{k}_2(1 - \bar{S}) - (E - 1)}{\bar{k}_2}.
\end{align*}
\]

The nonzero eigenvalues of the Jacobian matrix at \((x^*, y^*, z^*)\) are given by
\[
\lambda = \pm \sqrt{x^*y^*(\bar{k}_2 - \bar{k}_1)}i
\]
so that this point is a center for the planar system and all orbits are periodic. For the point \((\hat{x}, \hat{y}, \hat{z})\) the nonzero eigenvalues are given by
\[
\lambda = \frac{1}{2} \left( -\bar{k}_3 \hat{z} \pm \sqrt{(\bar{k}_3 \hat{z})^2 - 4\hat{y}\hat{z}\bar{k}_2(\bar{k}_2 - \bar{k}_3)} \right).
\]

We note that for \( \bar{k}_3 > \bar{k}_2 \), one of the eigenvalues is positive and one is negative. The discriminant is an increasing function of \( \bar{k}_3 \) and is zero when \((\bar{k}_3 \hat{z})^2 = 4\hat{y}\hat{z}\bar{k}_2(\bar{k}_2 - \bar{k}_3)\).

Solving the resulting quadratic in \( \bar{k}_3 \) yields
\[
\bar{k}_3 = \frac{2\bar{k}_2}{\hat{z}} \left( -\hat{y} \pm \sqrt{\hat{y}^2 + \hat{y}\hat{z}} \right).
\]

Combining this information we deduce that complex eigenvalues with negative real components exist for \( 0 < \bar{k}_3 < \frac{2\bar{k}_2}{\hat{z}}(-\hat{y} + \sqrt{\hat{y}^2 + \hat{y}\hat{z}}) \); two negative real eigenvalues exist for \( \frac{2\bar{k}_2}{\hat{z}}(-\hat{y} \pm \sqrt{\hat{y}^2 + \hat{y}\hat{z}}) < \bar{k}_3 < \bar{k}_2 \); and there exists one positive real and one negative real eigenvalue for \( \bar{k}_2 < \bar{k}_3 \).

Next we examine the trace and determinant of the Jacobian matrix along the line of equilibrium. It is clear that every level set of \( V \) can be represented in the following form
\[
\left( \begin{array}{c} x \\ x_0 \end{array} \right)^{k_3-k_2} \left( \begin{array}{c} y \\ y_0 \end{array} \right)^{k_1-k_3} \left( \begin{array}{c} z \\ z_0 \end{array} \right)^{k_2-k_1} = 1
\]

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and that this equation can be solved for \( z \) with the result
\[
z = z_0 \left( \frac{x}{x_0} \right)^{\frac{k_2-k_3}{k_2-k_1}} \left( \frac{y}{y_0} \right)^{\frac{k_3-k_1}{k_2-k_1}}.
\]

Using this expression, the original system in three variables can be reduced to the following
\[
\begin{align*}
\dot{x} &= x \left( (\bar{k}_2 - \bar{k}_1)(y - y_0) - \bar{k}_1 z_0 \left( \frac{x}{x_0} \right)^p \left( \frac{y}{y_0} \right)^{1-p} - 1 \right), \\
\dot{y} &= y \left( (\bar{k}_1 - \bar{k}_2)(x - x_0) - \bar{k}_2 z_0 \left( \frac{x}{x_0} \right)^p \left( \frac{y}{y_0} \right)^{1-p} - 1 \right)
\end{align*}
\]

with the Jacobian at \((x_0, y_0, z_0)\) given by
\[
J = \begin{pmatrix}
-\frac{z_0k_1(k_2-k_3)}{k_2-k_1} & (y_0(\bar{k}_2 - \bar{k}_1))^2 - z_0\bar{k}_1(\bar{k}_3 - \bar{k}_1)\left( \frac{x_0}{y_0(k_2-k_1)} \right) \\
(-x_0(\bar{k}_2 - \bar{k}_1)^2 - z_0\bar{k}_2(\bar{k}_2 - \bar{k}_3))\left( \frac{y_0}{x_0(k_2-k_1)} \right) & -\frac{z_0k_2(k_3-k_1)}{k_2-k_1}
\end{pmatrix}
\]

The trace of the Jacobian is equal to \(-\bar{k}_3z_0\) and
\[
\det J = x_0y_0(\bar{k}_2 - \bar{k}_1)^2 - \bar{k}_3z_0(\bar{k}_1x_0 + \bar{k}_2y_0) + z_0(\bar{k}_1^2x_0 + \bar{k}_2^2y_0).
\]

Using the parameterization of the line of equilibria given above, the determinant may be rewritten as
\[
\det J(r) = (\bar{k}_2 - \bar{k}_1)(\bar{k}_1\bar{k}_2(1 - \bar{S}) - \bar{k}_3(E - 1))r - (\bar{k}_1(1 - \bar{S}) - (E - 1))(\bar{k}_2(1 - \bar{S}) - (E - 1)).
\]

We note that the geometry of the line of equilibrium requires that \( \bar{k}_2(1 - \bar{S}) > E - 1 > \bar{k}_1(1 - \bar{S}) \) so that the constant term is positive; we also note that for a fixed \( r \) the determinant is a decreasing function of \( \bar{k}_3 \). At the point \((x^*, y^*, z^*)\) \((r = 0)\) we know from the above discussion that the determinant is positive. For the point \((\hat{x}, \hat{y}, \hat{z})\) the resulting determinant is given by
\[
\det J = \frac{(\bar{k}_2 - \bar{k}_3)(\bar{k}_2(1 - \bar{S}) - (E - 1))(E - 1)}{\bar{k}_2}.
\]

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This determinant is positive for \( \bar{k}_3 < \bar{k}_2 \), zero for \( \bar{k}_3 = \bar{k}_2 \), and negative for \( \bar{k}_3 > \bar{k}_2 \).

Interpreting this result, for \( \bar{k}_3 < \bar{k}_2 \) all first octant points on the line of equilibria are locally stable; for \( \bar{k}_3 > \bar{k}_2 \) there exist both locally stable and unstable points on the line.

For a fixed \( \bar{k}_3 \) greater than \( \bar{k}_2 \), the continuity of \( Det J(r) \) implies that there exists an \( \bar{r} \in [0, \frac{\bar{k}_2(1-S)-(E-1)}{\bar{k}_2(\bar{k}_2-\bar{k}_1)}] \) such that \( Det J(\bar{r}) = 0 \), \( Det J(r) > 0 \) for \( r \in [0, \bar{r}) \), and \( Det J(r) < 0 \) for \( r \in (\bar{r}, \frac{\bar{k}_2(1-S)-(E-1)}{\bar{k}_2(\bar{k}_2-\bar{k}_1)}) \); the value of \( \bar{r} \) is readily calculated with

\[
\bar{r} = \frac{(\bar{k}_1(1-S)-(E-1))(\bar{k}_2(1-S)-(E-1))}{\bar{k}_1 \bar{k}_2(1-S)-\bar{k}_3(E-1)}.
\]

Next we investigate the relationship (in terms of numbers of intersections) between the line of equilibria and the level sets of the function \( V = x^{\bar{k}_3-\bar{k}_2}y^{\bar{k}_1-\bar{k}_3}z^{\bar{k}_2-\bar{k}_1} \). We know that \( V \) is positive in the first octant and consider \( V(r) \) to be the function restricted to coordinates on the line of equilibria. To determine whether \( V(r) \) is monotonically increasing with respect to \( r \), we consider the term

\[
\frac{V(r)'}{V(r)} = \left( \frac{1}{r(x^* - \bar{k}_2r)(y^* + \bar{k}_1r)} \right) \left( \frac{\bar{k}_1 \bar{k}_2(1-S)-(E-1)) r - (\bar{k}_1(1-S)-(E-1))(\bar{k}_2(1-S)-(E-1))}{(\bar{k}_2 - \bar{k}_1)} \right)
\]

which after rearrangement and consulting the above discussion can be written as

\[
\frac{V(r)'}{V(r)} = \left( \frac{1}{(\bar{k}_2 - \bar{k}_1)r(x^* - \bar{k}_2r)(y^* + \bar{k}_1r)} \right) Det J(r).
\]

From this equation we deduce that the sign of \( V'(r) \) is the same as the sign of \( Det J(r) \).

Now consider the case \( \bar{k}_3 < \bar{k}_2 \), we know that for \( r \in (0, \frac{\bar{k}_2(1-S)-(E-1)}{\bar{k}_2(\bar{k}_2-\bar{k}_1)}) \), \( Det J(r) > 0 \) so that \( V(r) \) is monotonically increasing and therefore each level surface can intersect the line of equilibria at most once. By using the technique in the Case I analysis, it is readily established that for \( r \) in the above domain, \( V(r) \) can assume any positive value so that each level surface must intersect the line in exactly one point.
For $\bar{k}_3 > \bar{k}_2$ and with previously introduced notation, we find that $V(0) = V(\frac{\bar{k}_2(1-S)-(E-1)}{\bar{k}_2(\bar{k}_2-\bar{k}_1)}) = 0$, $V'(\bar{r}) = 0$, $V'(r) > 0$ for $r \in (0, \bar{r})$, and $V'(r) < 0$ for $r \in (\bar{r}, \frac{\bar{k}_2(1-S)-(E-1)}{\bar{k}_2(\bar{k}_2-\bar{k}_1)})$. This implies that $V(r)$ attains a local max at $r = \bar{r}$ and it is easily found that

$$V(\bar{r}) = \left( \frac{\bar{k}_2 - \bar{k}_1}{E - 1} \right)^{\bar{k}_2 - \bar{k}_1} \left( \frac{\bar{k}_3 - \bar{k}_2}{-(\bar{k}_1(1-S)-(E-1))} \right)^{\bar{k}_3 - \bar{k}_2} \left( \frac{\bar{k}_3 - \bar{k}_1}{\bar{k}_2(1-S)-(E-1)} \right)^{\bar{k}_1 - \bar{k}_3}.$$ 

Hence any level surface $V(x, y, z) = C > V(\bar{r})$ does not intersect the line of equilibria. Furthermore it follows that the level surface $V(x, y, z) = V(\bar{r})$ intersects the line exactly once, and for $0 < V(x, y, z) < V(\bar{r})$ the level surface has at least two intersections with the line. In fact these surfaces intersect the line exactly twice; if more than two intersections occurred this would imply at least two points in the domain of $r$ where $V'(r) = 0$ which is a contradiction.

Combining all of the above information we obtain the following theorem.

**Theorem 12.** For Case II with $\bar{k}_3 < \bar{k}_2$, each level surface of $V$ intersects the line of equilibria exactly once. Furthermore, each equilibria is locally asymptotically stable in its respective level surface. For $\bar{k}_3 > \bar{k}_2$, there exists three possible cases. For $V(r) = C > V(\bar{r})$, the level surface does not intersect the line of equilibria and there are no internal equilibria on the surface; for $V(r) = V(\bar{r})$, the level surface intersects the line of equilibria exactly once and the internal equilibrium has one negative and one zero eigenvalue; for $0 < V(r) < V(\bar{r})$, the level surface intersects the line of equilibria exactly twice, say for $r$ values $r_1$ and $r_2$ with $r_1 < r_2$; the equilibrium at $r_1$ is locally stable while the equilibria at $r_2$ is a saddle point.

The above results are just the first step in the study of bifurcations from a line of equilibria. Current research focuses on quadratic and higher approximations of growth functions as well as the fate of trajectories when the line is broken.
CHAPTER 5
CONCLUSIONS AND FUTURE RESEARCH

The research results presented in this dissertation have focused on coexistence of two or three organisms in a feedback-mediated chemostat. For two organisms with transversally intersecting growth functions, we have demonstrated not only that coexistence can occur, but that the diluter function may be designed so that a circular or elliptic asymptotically stable periodic orbit results. This result is unique since in general only the existence of a periodic orbit can be established and its resulting shape only approximated. Furthermore, by additional modifications of the diluter function, embedded elliptical orbits of alternating stability may be designed. The applied significance of these results will be realized as technological progress will allow "real-time" analysis of organism and substrate concentrations. In the meantime, research or at least numeric studies into the affect of delays on the above periodic orbits could yield information on the "robustness" of such solutions.

For the case of three organisms, the coexistence results were not as general. Using a linear feedback diluter function of two variables it was demonstrated that for Michaelis-Menten growth functions which intersect transversally that coexistence was possible. While this result is significant, it did not provide general criteria of feedback-mediated coexistence for three organisms with arbitrary growth functions. In addition, the periodic solutions which were obtained were "arbitrarily close" to one of the coordinate planes. Numerical studies suggest that the addition of a third variable to the feedback function eliminates this problem and results in orbits which traverse the first octant. Further research is needed to analytically establish this observation.

An initial investigation into bifurcation from a line of equilibria has yielded some interesting results for linear growth functions but additional work is needed to determine necessary conditions to insure that such bifurcations result in periodic orbits.
The use of feedback in the chemostat is a new area of research and it is hoped that the findings contained in this dissertation will advance this field and provide new topics for further investigation.
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BIOGRAPHICAL SKETCH

Willard S. Keeran was born in Savannah, Georgia in 1959. He received a Bachelor of Science degree in chemistry from the University of Georgia in 1981. He received both a Master of Science degree in 2004 and a Ph.D. in mathematics in 2007 from the University of Florida.