

**MATHEMATICAL ANALYSIS OF ALLELOPATHY AND RESOURCE  
COMPETITION MODELS**

by

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## ABSTRACT

### MATHEMATICAL ANALYSIS OF ALLELOPATHY AND RESOURCE COMPETITION MODELS

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Mathematical population models of nutrient recycling and allelopathy are presented. The chemostat limited-resource model forms the basis for each of the models, amended with the dynamics of nutrient recycling and allelopathy. Nutrient recycling considers the explicit mortality of the population as providing additional recycled nutrient available to the remaining organisms. Also considered is allelopathy in which one population produces a poison to increase the mortality of another population. In this study we explore allelopathy in which the poison producer increases toxicity as the nutrients are limited. In addition to the chemostat model, we also consider the associated gradostat, two chemostat devices in series. Local analysis and numerical simulations are presented for each of the models along with global results where available.

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## CHAPTER 1

### INTRODUCTION

The chemostat, also known as a continuous culture or continuously stirred tank reactor, is a laboratory device designed for experimentation on microorganism populations in a vessel. Used to model a primitive lake, see Figure (1.1), the chemostat enables the limitation of a necessary nutrient consumed by the organism. Several variants have been considered, all derived from the simple chemostat which consists of a constant inflow into the vessel and a matching outflow. This mass balance combined with the assumption that the medium contained within the vessel remains continuously stirred allows for a model of the experiment to consist of a system of ordinary differential equations. Typical experiments, and models of such experiments, employ the inflow to supply nutrients to a population of organisms contained within the vessel with the constant washout rate, or dilution rate, removing both organisms and nutrient. The relationship between the available resource and resulting population growth is typically seen as nonlinear [12]. Although the representation of this nonlinearity in models leads to mathematical difficulty, the study of the chemostat and its variations has provided higher order models capable of being analyzed globally in the sense of a dynamical system [16, 15, 14, 35]. This coupled with the ability to build such devices has enabled the chemostat to take a central role in mathematical ecology. Many variants on the simple chemostat model have been analyzed including competition of species for common resources and the role of chemical inhibition, both internally and externally produced, on such competition [2, 14, 15]. Several extensions to the chemostat are presented here with concentration on the ideas of nutrient recycling and allelopathy. Nutrient recycling considers the explicit death of a



Figure 1.1. A lake to be described by the chemostat.

microorganism and the resulting availability of the dead organism as additional resources for the remaining population [3, 23, 26]. That is, a dead organism becomes part of the available resource pool. Allelopathy is the production of a chemical by one species of microorganism to increase the mortality of a competitor. Several models exist representing allelopathic bacteria and the allelopathy has also been exhibited in species of algae [2, 9, 19, 14, 15, 22]. Considered here is allelopathy in which the toxicity increases as the toxin producer becomes limited in nutrient [1]. The mathematical terms for modeling and biological basis for each variation will be presented along with the models. Before continuing to the advanced models, it is necessary to present the elementary results for the simple chemostat model. A derivation and analysis of the model can be found in [28] and references contained therein.

### 1.1 The Simple Chemostat

As stated above, the chemostat is used to model a primitive lake with one inflow and one outflow (See Fig 1.1). The simple chemostat models the growth of a single population and one limited resource. The model for growth of a single microbial

population in a chemostat takes the following form

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 (\mu_1(R) - D), \\ \frac{dR}{dt} &= D (R_{in} - R) - \mu_1(R) q_1 N_1.\end{aligned}\tag{1.1}$$

Here we consider a constant a dilution rate of  $D$  with  $R_{in}$  being the concentration of the limiting nutrient supplied in the inflowing medium. The variable  $N_1$  represents the population density of the microorganism which has a growth rate depending on the nutrient concentration  $R$ . The function  $\mu_1(R)$  is bounded and increasing with  $\mu_1(0) = 0$ ,  $0 \leq \mu_1(R) \leq \mu_1^{max} < \infty$ , and  $d\mu_1/dR > 0$ . For growth functions the well-known Monod [24] functions are used:  $\mu_1(R) = \mu_1^{max} R / (k_1 + R)$ , where  $\mu_1^{max}$  is the maximal growth rate as  $R \rightarrow \infty$ , and  $k_1$  is the half-saturation constant, the nutrient concentration supporting growth at half the maximal rate. Both  $\mu_1^{max}$  and  $k_1$  are measured experimentally and the functions are used based on experimental evidence, not based on the underlying physiology. The parameter  $q_1$  is assumed constant and represents the efficiency at which the organism harvests nutrient for population growth. To be biologically relevant, it must be the case that  $R(0) \geq 0$  and  $N_1 > 0$ . The constants  $R_{in}$ ,  $D$  and  $q_1$  are typically scaled out of the system via the following substitutions  $\hat{N}_1 = q_1 N_1 / R_{in}$ ,  $\hat{R} = R / R_{in}$ ,  $\hat{t} = D t$ ,  $\hat{\mu}_1^{max} = \mu_1^{max} / D$  and  $\hat{k}_1 = k_1 / R_{in}$ . System (1.1) becomes

$$\begin{aligned}\frac{d\hat{N}_1}{d\hat{t}} &= \hat{N}_1 (\hat{\mu}_1(\hat{R}) - 1), \\ \frac{d\hat{R}}{d\hat{t}} &= 1 - \hat{R} - \hat{\mu}_1(\hat{R}) \hat{N}_1,\end{aligned}\tag{1.2}$$

where  $\hat{\mu}_1(\hat{R}) = \frac{\hat{\mu}_1^{max} \hat{R}}{\hat{k}_1 + \hat{R}}$ . Dropping the hats we obtain the system of interest

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 (\mu_1(R) - 1), \\ \frac{dR}{dt} &= 1 - R - \mu_1(R) N_1.\end{aligned}\tag{1.3}$$

An important feature of the chemostat is the relationship between the equilibria of the system and the global behavior of any trajectory given positive initial conditions. System (1.3) has two rest points

$$E_0 = (0, 1), \quad E_1 = (N_1^*, R^*),$$

where  $R^* = \mu_1^{-1}(1)$  and  $N_1^* = 1 - R^*$ . If  $\mu_1^{max} < 1$  then certainly  $\frac{dN_1}{dt} < 0$  and therefore  $\lim_{t \rightarrow \infty} N_1(t) = 0$ . That is, if species  $N_1$  is to persist it must be the case that  $\mu_1^{max} > 1$ . Biologically speaking, the maximal growth rate must be larger than the washout rate for the microbial population to continue. Under the assumption  $\mu_1^{max} > 1$ , we can state the following theorem.

**Theorem 1.1.1.** *If  $R^* < 1$  then all trajectories of System (1.3) with positive initial conditions converge to  $E_1$ . If  $R^* > 1$  the convergence is to  $E_0$ .*

The result is interesting since it precisely matches the intuition, and also results of experimentation, of the underlying biology. That is, in the simple chemostat the microbial population will survive and reach its equilibrium if sufficient resources are available. In absence of such resources, the population will die out.

## 1.2 Competition in the Simple Chemostat

The introduction of a second microbial population into the vessel results in competition between the populations for the common limited resource. In addition to the variables necessary for the single species chemostat of the previous section, additional parameters and a new variable for the second species must be appended to the model (See Fig. 1.2). The addition of a second microbial population into the vessel leads to

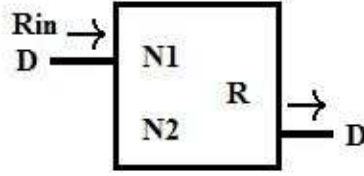


Figure 1.2. Chemostat operating diagram.

a model of the following form

$$\begin{aligned}
 \frac{dN_1}{dt} &= N_1 (\mu_1(R) - D), \\
 \frac{dN_2}{dt} &= N_2 (\mu_2(R) - D), \\
 \frac{dR}{dt} &= D (R_{in} - R) - \mu_1(R) q_1 N_1 - \mu_2(R) q_2 N_2.
 \end{aligned} \tag{1.4}$$

Here  $N_1$ ,  $R$  and the parameters are defined as before with the new variable  $N_2$  being the concentration of a competing species. The growth of  $N_2$  will be according to the function  $\mu_2(R)$ , again chosen to be the Monod function with maximal growth  $\mu_2^{max}$ , half-saturation constant  $k_2$  and nutrient uptake efficiency  $q_2$ . Similar scaling to the one species case can be had:  $\hat{N}_1 = q_1 N_1 / R_{in}$ ,  $\hat{N}_2 = q_2 N_2 / R_{in}$ ,  $\hat{R} = R / R_{in}$ ,  $\hat{t} = D t$ ,  $\hat{\mu}_i^{max} = \mu_i^{max} / D$  and  $\hat{k}_i = k_i / R_{in}$ . System (1.4) then becomes

$$\begin{aligned}
 \frac{d\hat{N}_1}{d\hat{t}} &= \hat{N}_1 (\hat{\mu}_1(\hat{R}) - 1), \\
 \frac{d\hat{N}_2}{d\hat{t}} &= \hat{N}_2 (\hat{\mu}_2(\hat{R}) - 1), \\
 \frac{d\hat{R}}{d\hat{t}} &= 1 - \hat{R} - \hat{\mu}_1(\hat{R}) \hat{N}_1 - \hat{\mu}_2(\hat{R}) \hat{N}_2,
 \end{aligned} \tag{1.5}$$

where  $\hat{\mu}_i(\hat{R}) = \frac{\hat{\mu}_i^{max} \hat{R}}{\hat{k}_i + \hat{R}}$ . Again dropping the hats we obtain the following system of interest

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 (\mu_1(R) - 1), \\ \frac{dN_2}{dt} &= N_2 (\mu_2(R) - 1), \\ \frac{dR}{dt} &= 1 - R - \mu_1(R) N_1 - \mu_2(R) N_2. \end{aligned} \tag{1.6}$$

There are four equilibria for System (1.6)

$$E_0 = (0, 0, 1), \quad E_1 = (N_{(1)}^*, 0, R_{(1)}^*), \quad E_2 = (0, N_{(2)}^*, R_{(2)}^*), \quad E_3 = (N_1^*, N_2^*, R^*),$$

where  $R_{(1)}^* = \mu_1^{-1}(1)$ ,  $R_{(2)}^* = \mu_2^{-1}(1)$ ,  $N_{(1)}^* = 1 - R_{(1)}^*$  and  $N_{(2)}^* = 1 - R_{(2)}^*$ .

The equilibrium  $E_3$  is a special case as its existence requires  $R_{(1)}^* = R_{(2)}^*$ . That is, there is a balance between the competing species in as much as the resources needed to reach equilibrium. Meeting this strict condition should be rare and would be based on experimental measurements as stated above. Moreover, the analysis of the nonlinear system is accomplished by analyzing the linearization. Due to these difficulties and approximations this so called ‘‘knife-edge’’ case is not typically analyzed and will be omitted here.

It is assumed that  $\mu_i^{max} > 1$  for  $i = 1, 2$  in order to produce interesting dynamics, that is neither species will become extinct due to washout. In the same manner as the single population chemostat, the asymptotic outcome for any trajectory can be determined by the parameters alone as seen in the next theorem

**Theorem 1.2.1.** *If  $R_{(1)}^* < R_{(2)}^*$  and  $R_{(1)}^* < 1$  then all trajectories of System (1.6) with positive initial conditions will converge to  $E_1$ . If  $R_{(2)}^* < R_{(1)}^*$  and  $R_{(2)}^* < 1$  then all trajectories converge to  $E_2$ . If  $R_{(1)}^* > 1$  and  $R_{(2)}^* > 1$  then all trajectories converge to  $E_0$ .*

Dynamics of this type are referred to as competitive exclusion, in as much as one competitor will out compete its rival when competition is for a common resource. The

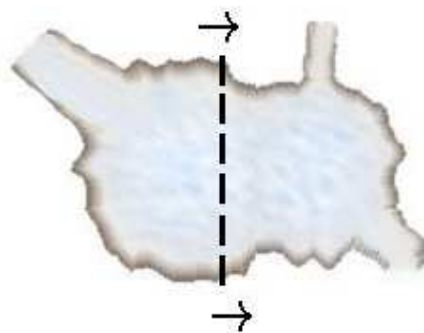


Figure 1.3. Lake system to be described by the gradostat.

preceding theorem reduces the dynamics of competition in the chemostat between viable competitors to the determination of which competitor requires the least resources to reach equilibrium.

The simple chemostat and the competition within form the basis for the models that follow. By modifying these basic models, new models containing the effects of nutrient recycling and allelopathy are studied. In Chapter 2 the simple chemostat model is changed to incorporate nutrient recycling. Competition in the nutrient recycling chemostat is studied in Chapter 3. Chapter 4 introduces allelopathy into the nutrient recycling chemostat. In addition to the study of new models for the chemostat, we also study in Chapter 5 the effects of nutrient recycling when two chemostat devices are connected in series, a device known as the gradostat. The series of chemostat vessels models the dynamics of lake systems (See Fig 1.3). The gradostat incorporates not only the growth of the species, but also the movement of the species between the vessels. In Chapter 6, allelopathy is added to the nutrient recycling gradostat.

The study here addresses the new models in the same spirit as the basic models, that is, to use the parameters of the system to determine the asymptotic outcome of trajectories initiating with positive initial conditions. The nutrient recycling chemostat models presented above have the ability to be analyzed globally. The addition of the



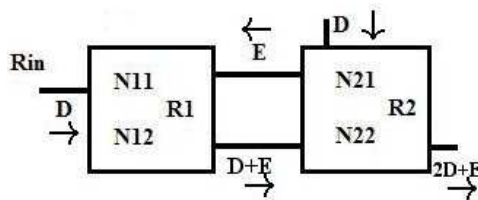


Figure 1.4. The gradostat diagram.

allelopathy removes the conservative property for the dynamical system and hence only local results are presented. The dynamics of the gradostat require the tracking of each population and resource inside of both vessels, doubling the order of the system (See Fig. 1.4). The high order of these models leaves global analysis lacking standard tools. Several variations of the gradostat exist, with the dynamics of the simple system being able to be analyzed globally [18]. Essential to the analysis is monotone semi-flow theory, which is not applicable to the gradostat model if nutrient recycling is included [30]. In cases where the global theory is lacking, numerical simulations are presented to provide global asymptotic conjectures. Numerical values of the required parameters were based on phosphorus-limited algae [10, 11], with the exception of the allelopathic dynamics as these parameters are lacking. The necessary parameters were assigned to arbitrary but plausible values.

## CHAPTER 2

### NUTRIENT RECYCLING IN THE CHEMOSTAT

#### 2.1 Introduction

In this chapter we explore the role of explicit mortality and nutrient recycling in the single population chemostat described by System (1.1). Included in the growth function for the microbial population is a mortality rate with the dead population becoming a resource which can be harvested by the remaining population. We investigate what role, if any, the nutrient recycling will play in the asymptotic outcomes of the experiment. Additionally, the outcome is compared to the existing theory of the simple chemostat presented in the previous chapter.

#### 2.2 The Nutrient Recycling Chemostat Model

To model the effect of nutrient recycling and explicit mortality, we alter System (1.1) by changing  $\frac{dN_1}{dt}$  to include a mortality rate  $m_1$  in the growth function. Additionally,  $\frac{dR}{dt}$  is manipulated to include additional resources arriving from the dead population,  $m_1 N_1$  at rate  $q_1$ , that is, at a rate equal to the nutrient contained in the dead population. These modifications, with the remaining parameters and variables defined as in System (1.1), result in the following model

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 (\mu_1(R) - m_1 - D), \\ \frac{dR}{dt} &= D (R_{in} - R) - (\mu_1(R) - m_1) q_1 N_1.\end{aligned}\tag{2.1}$$

The model can be scaled for mathematical ease by the following substitutions

$$\begin{aligned}\hat{N}_1 &= q_1 N_1 / R_{in}, & \hat{R} &= R / R_{in}, & \hat{k}_1 &= k_1 / R_{in}, \\ \hat{m}_1 &= m_1 / D, & \hat{\mu}_1^{max} &= \mu_1^{max} / D, & \hat{t} &= D t.\end{aligned}$$

Applying the substitutions results in the following system

$$\begin{aligned}\frac{d\hat{N}_1}{d\hat{t}} &= \hat{N}_1 (\hat{\mu}_1(\hat{R}) - \hat{m}_1 - 1), \\ \frac{d\hat{R}}{d\hat{t}} &= 1 - \hat{R} - (\hat{\mu}_1(\hat{R}) - \hat{m}_1) \hat{N}_1,\end{aligned}\tag{2.2}$$

where  $\hat{\mu}_1(\hat{R}) = \frac{\hat{\mu}_1^{max} \hat{R}}{\hat{k}_1 + \hat{R}}$ . Dropping the hats for the remainder of the analysis leaves us with the following system of interest:

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 (\mu_1(R) - m_1 - 1), \\ \frac{dR}{dt} &= 1 - R - (\mu_1(R) - m_1) N_1,\end{aligned}\tag{2.3}$$

Define  $\Sigma = 1 - N_1 - R$ . Then,  $\Sigma' = -N_1' - R' = -1 + N_1 + R = -\Sigma$  where  $'$  denotes the  $t$  derivative. The equation  $\Sigma'(t) = -\Sigma(t)$  has solution  $\Sigma(t) = \Sigma(0)e^{-t}$ . Hence  $\lim_{t \rightarrow \infty} \Sigma(t) = 0$ , that is  $\lim_{t \rightarrow \infty} [N_1(t) + R(t)] = 1$ . From this we see that System (2.3) is dissipative, additionally the set  $\Delta = \{(N_1, R) | N_1 + R \leq 1\}$  is positively invariant.

### 2.3 Equilibria and Local Analysis

To investigate the existence of equilibria for the system we will proceed in two cases:  $N_1 = 0$  and  $N_1 \neq 0$ . In the case  $N_1 = 0$ , to have equilibrium we must satisfy

$$\frac{dR}{dt} = 1 - R = 0.$$

Since  $D > 0$ , the only possible equilibrium value for  $R$  is  $R = 1$ . Therefore we can define our first equilibrium  $E_0 = (0, 1)$ .

In the case  $N_1 \neq 0$ , to have  $\frac{dN_1}{dt} = 0$  the following must be satisfied

$$\mu_1(R) - m_1 - 1 = 0.$$

Only one value of  $R$  will satisfy this condition,  $R_{(1)}^* = \mu_1^{-1}(m_1 + 1)$ . Using this value, to satisfy  $\frac{dR}{dt} = 0$  we must have

$$\frac{dR}{dt} = 1 - R_{(1)}^* - (\mu_1(R_{(1)}^*) - m_1) N_1 = 0.$$

Solving for  $N_1$ , we have

$$N_1 = \frac{(1 - R_{(1)}^*)}{(\mu_1(R_{(1)}^*) - m_1)} = 1 - R_{(1)}^*.$$

Therefore the value  $N_{(1)}^* = 1 - R_{(1)}^*$  enables us to define the second equilibrium  $E_1 = (R_{(1)}^*, N_{(1)}^*)$ . It is important to note that in order for the equilibrium  $E_1$  to be logical, we must have that  $1 > R_{(1)}^*$ . Further, a condition for extinction of the species  $N_1$  is  $\mu_1^{max} < m_1 + D$ . If this condition is met,  $\frac{dN_1}{dt} < 0$  for all values of  $N_1$  and  $R$ . Therefore, the maximum growth rate must be larger than the sum of the death rate and washout rate if Species  $N_1$  is to survive. The Jacobian of the system (2.3) is

$$J(N_1, R) = \begin{pmatrix} \mu_1(R) - m_1 - 1 & \frac{d\mu_1}{dR} N_1 \\ -(\mu_1(R) - m_1) & -1 - \frac{d\mu_1}{dR} N_1 \end{pmatrix}. \quad (2.4)$$

**Theorem 2.3.1.** *The equilibrium  $E_0$  is locally asymptotically stable if and only if  $1 < R_{(1)}^*$ .*

*Proof.* For the equilibrium  $E_0$ , the local stability is determined by the eigenvalues of

$$J(E_0) = \begin{pmatrix} \mu_1(1) - m_1 - 1 & 0 \\ -(\mu_1(1) - m_1) & -1 \end{pmatrix}.$$

The eigenvalues of  $J(E_0)$  are  $\lambda_1 = \mu_1(1) - m_1 - D$  and  $\lambda_2 = -1$ . Therefore  $E_0$  is locally asymptotically stable if  $\mu_1(1) < m_1 + D$ , that is if  $1 < R_{(1)}^*$ .  $\square$

**Theorem 2.3.2.** *The equilibrium  $E_1$  is locally asymptotically stable if and only if  $1 > R_{(1)}^*$ .*

*Proof.* For the equilibrium  $E_1$ , the local stability is determined by the eigenvalues of

$$J(E_1) = \begin{pmatrix} \mu_1(R_{(1)}^*) - m_1 - 1 & \frac{d\mu_1}{dR}|_{R=R_{(1)}^*} N_{(1)}^* \\ -(\mu_1(R_{(1)}^*) - m_1) & -1 - \frac{d\mu_1}{dR}|_{R=R_{(1)}^*} N_{(1)}^* \end{pmatrix}.$$

The characteristic polynomial of  $J(E_1)$  is

$$P(\lambda) = \lambda^2 + \lambda\left(1 + \frac{d\mu_1}{dR}|_{R=R_{(1)}^*} N_{(1)}^*\right) + \frac{d\mu_1}{dR}|_{R=R_{(1)}^*} N_{(1)}^*.$$

Hence  $\lambda_1 = \frac{d\mu_1}{dR}|_{R=R_{(1)}^*} N_{(1)}^*$  and  $\lambda_2 = -1$  are the eigenvalues of  $J(E_1)$ . Therefore since  $\mu_1(R)$  is an increasing function,  $E_1$  is locally asymptotically stable if and only if  $N_{(1)}^* > 0$ . That is, when  $E_1$  exists it is locally asymptotically stable.  $\square$

## 2.4 Global Analysis

In this section we show that the conditions for local stability of the equilibria  $E_0$  and  $E_1$  are in fact global for any initial values taken from the interior of the positive cone  $\Delta$ . Any trajectories initiating on the  $N_1 = 0$  boundary of  $\Delta$  will attract to the equilibrium  $E_0$  as evident in the following Theorem.

**Theorem 2.4.1.** *Given an initial condition  $(0, R_0)$ , the solution  $(N_1(t), R(t))$  approaches  $E_0$ .*

*Proof.* With the initial value  $(0, R_0)$ , we have  $\frac{dN_1}{dt}|_{(0, R_0)} = 0$  and  $\frac{dR}{dt}|_{(0, R_0)} = 1 - R_0$ . If  $R < 1$ , then  $\frac{dR}{dt} > 0$ . Similarly,  $\frac{dR}{dt} < 0$  when  $R > 1$ . Hence, any trajectory initiating on the boundary  $N_1 = 0$  will remain on the boundary and converge to  $E_0$ .  $\square$

**Theorem 2.4.2.** *There are no periodic solutions to System (2.3) on the set  $\Delta$ .*

*Proof.* If we define the functions  $\frac{dN_1}{dt} = F(N_1, R)$  and  $\frac{dR}{dt} = G(N_1, R)$  along with the function  $\beta(N_1, R) = \frac{1}{N_1}$ , then we can apply Dulac's Criterion. Here,

$$\frac{\partial(\beta F)}{\partial N_1} + \frac{\partial(\beta G)}{\partial R} = -\frac{1}{N_1} - \frac{d\mu_1}{dR}.$$

Therefore, since  $N_1 > 0$  and  $\mu_1(R)$  is a monotonically increasing function, we have  $\frac{\partial(\beta F)}{\partial N_1} + \frac{\partial(\beta G)}{\partial R} < 0$  and therefore no periodic solutions to System (2.3) exist.  $\square$

To proceed, we recall the set  $\Delta = \{(N_1, R) | N_1 + R \leq 1\}$ . As seen previously, this set is positively invariant.

**Theorem 2.4.3.** *If  $1 < R_{(1)}^*$ , then  $E_0$  attracts any trajectory initiating in  $\Delta$ .*

*Proof.* Under the condition  $1 < R_{(1)}^*$ ,  $E_0$  is the only equilibrium in  $\Delta$  and is stable. Therefore applying the Poincare-Bendixson Theory, since  $\Delta$  contains no periodic orbits the  $\omega$ -limit set for any trajectory initiating in  $\Delta$  is  $E_0$  alone.  $\square$

**Theorem 2.4.4.** *If  $1 > R_{(1)}^*$ , then  $E_1$  attracts any trajectory initiating in  $\Delta$  such that  $N_1(0) \neq 0$ . If  $N_1(0) = 0$ , then solutions attract to  $E_0$ .*

*Proof.* Under the condition  $1 > R_{(1)}^*$ , both  $E_0$  and  $E_1$  exist in  $\Delta$  with  $E_1$  locally stable and  $E_0$  a saddle with stable manifold being the  $R$ -axis. Again applying the Poincare-Bendixson Theory, since  $\Delta$  contains no periodic orbits and hence the  $\omega$ -limit set for any trajectory initiating in  $\Delta$  must be an equilibrium. Since the  $R$ -axis is an invariant set  $\omega$ -limit set can only consist of  $E_0$ , hence any trajectory initiating there will tend to  $E_0$ . For any other trajectory with initial condition in  $\Delta$ , the  $\omega$ -limit set must be  $E_1$  alone as  $E_0$  is unstable.  $\square$

## 2.5 Numerical Simulations

In this section we present two sets of simulations of System (2.1) as verification of the attraction conditions presented in the previous section. Each set is obtained using the **Mathematica** solver **NDSolve** with parameter values:  $q_1 = 10^{-9}$ ,  $k_1 = 0.005$ ,  $\mu_1^{max} = 0.7$ ,  $m_1 = 0.4$  and  $D = 0.2$ .

The first set of simulations reflects the condition  $1 < R_{(1)}^*$ , after appropriate scaling, by choosing  $R_{in} = 0.01$ . In Fig. (2.5), several trajectories are shown together, with

varying initial conditions. Here the resources available are insufficient for the population to reach equilibrium and each trajectory tends to the equilibrium  $E_0$  as predicted by Theorem 2.4.3.

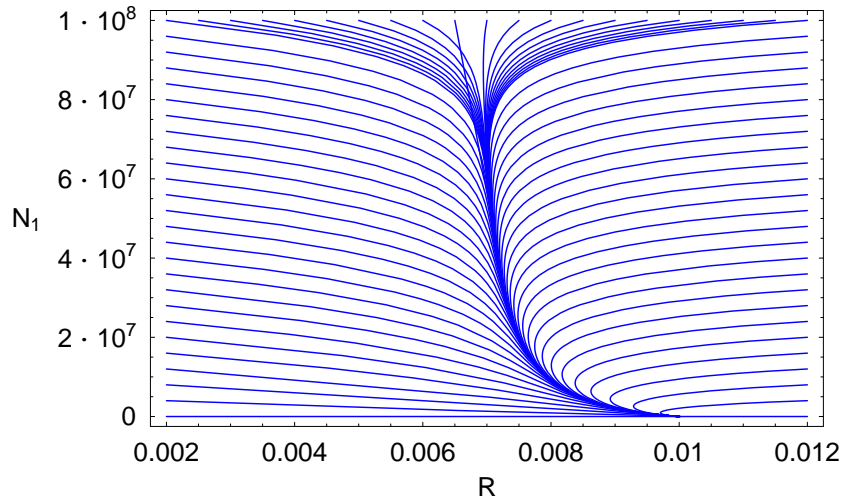


Figure 2.1.  $E_0$  attracts all solutions,  $E_1$  is infeasible.

The second set of simulations uses the inflowing nutrient level  $R_{in} = 0.1$  to satisfy  $1 > R_{(1)}^*$ , after appropriate scaling. Trajectories with differing initial values, in particular nonzero  $N_1$  values, are displayed in Fig. (2.5). In this case sufficient resources are available to reach equilibrium and the solutions tend to  $E_1$  as predicted in Theorem 2.4.4.

## 2.6 Discussion

The model described by System (2.1) introduces an explicit death rate for the microbial population contained in the chemostat vessel. In addition, the dead population is recycled into available nutrient which can be reclaimed by the population or simply wash out of the experiment. Theorems 2.4.3 and 2.4.4 indicate that the inclusion of these

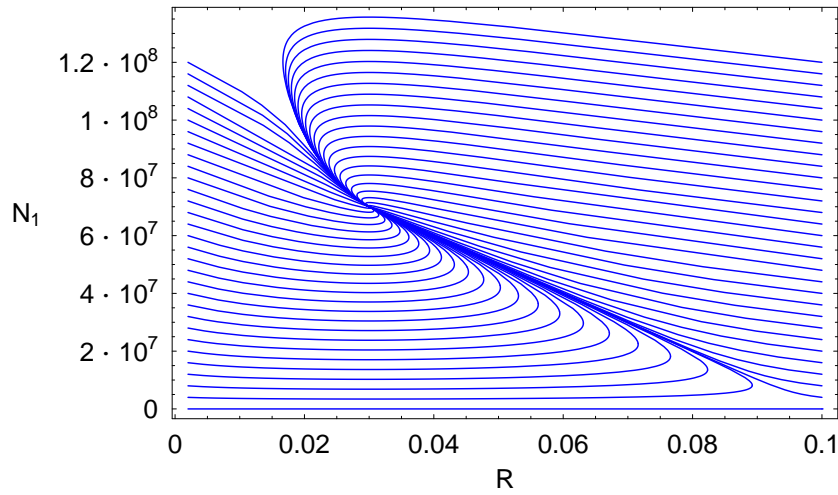


Figure 2.2.  $E_1$  attracts solutions for  $N_1(0) \neq 0$ ,  $E_0$  attracts for  $N_1(0) = 0$ .

terms results in a model that matches the conclusions of the simple chemostat theory. That is, if the equilibrium resources for a population are available, i.e.  $R_{(1)}^* < 1$ , the population persists and tends to the nontrivial equilibrium. If sufficient resources are not available, the population contained in the vessel will become extinct.



## CHAPTER 3

### COMPETITION AND NUTRIENT RECYCLING IN THE CHEMOSTAT

#### 3.1 Introduction

In the previous chapter the role of explicit mortality and nutrient recycling was examined for the single population chemostat. A population in the vessel reached equilibrium if sufficient resources were available and perished if resources were limited. We now investigate effect of the recycling on the competition between two populations.

#### 3.2 The Nutrient Recycling Competition Model

Amending the competition in the simple chemostat model to include the nutrient recycling terms as described in the previous chapter leads to the following model

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 (\mu_1(R) - m_1 - D), \\ \frac{dN_2}{dt} &= N_2 (\mu_2(R) - m_2 - D), \\ \frac{dR}{dt} &= D (R_{in} - R) - (\mu_1(R) - m_1) q_1 N_1 - (\mu_2(R) - m_2) q_2 N_2.\end{aligned}\tag{3.1}$$

System (3.1) includes mortality rates  $m_1$  and  $m_2$  in the growth function for the populations  $N_1$  and  $N_2$ . As in the single species case the dead population is recycled into nutrient available for growth of either population. The idea of explicit death rate in the competition has previously been considered by considering differing washout rates for the two species [35]. Coupling the terms  $m_1 + 1$  and  $m_2 + 1$  would allow the analysis of explicit death rate. The inclusion of nutrient recycling terms in  $\frac{dR}{dt}$  leave us with overall nutrient uptake functions which are not necessarily positive, i.e.  $(\mu_1(R) - m_1)$ .

In an effort to ease calculation complexity and increase overall clarity of the presentation, it is convenient to rescale the variables in System (3.1) in the following way

$$\begin{aligned}\hat{N}_i &= q_i N_i / R_{in}, & \hat{\mu}_i^{max} &= \mu_i^{max} / D, & \hat{k}_i &= k_i / R_{in}, & \hat{m}_i &= m_i / D, & i &= 1, 2 \\ \hat{R} &= R / R_{in}, & \hat{t} &= D t.\end{aligned}$$

Making the substitutions System (3.1) becomes

$$\begin{aligned}\frac{d\hat{N}_1}{d\hat{t}} &= \hat{N}_1 (\hat{\mu}_1(\hat{R}) - \hat{m}_1 - 1), \\ \frac{d\hat{N}_2}{d\hat{t}} &= \hat{N}_2 (\hat{\mu}_2(\hat{R}) - \hat{m}_2 - 1), \\ \frac{d\hat{R}}{d\hat{t}} &= 1 - \hat{R} - (\hat{\mu}_1(\hat{R}) - \hat{m}_1) \hat{N}_1 - (\hat{\mu}_2(\hat{R}) - \hat{m}_2) \hat{N}_2,\end{aligned}\tag{3.2}$$

where  $\hat{\mu}_i(\hat{R}) = \frac{\hat{\mu}_i^{max} \hat{R}}{\hat{k}_i + \hat{R}}$ . Dropping the hats we obtain the following system of interest

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 (\mu_1(R) - m_1 - 1), \\ \frac{dN_2}{dt} &= N_2 (\mu_2(R) - m_2 - 1), \\ \frac{dR}{dt} &= 1 - R - (\mu_1(R) - m_1) N_1 - (\mu_2(R) - m_2) N_2.\end{aligned}\tag{3.3}$$

The problem described by System (3.3) is well posed, since the first quadrant is positively invariant, which is consistent with the biological interpretation of the model. The solutions to System (3.3) with nonnegative initial values are bounded, a fact proved in a later section.

In order to analyze the behavior of System (3.3) we need to establish the existence and stability of the equilibria and then examine the global dynamics.

### 3.2.1 Equilibria and Local Stability Analysis

To investigate the existence of equilibria for System (3.3) we consider the following four cases:

(a) Let  $N_1 = N_2 = 0$ . In this case, we need only satisfy  $1 - R = 0$  for equilibrium.

Therefore we have the first equilibrium  $E_0 = (0, 0, 1)$ .

(b) Let  $N_1 \neq 0$  and  $N_2 = 0$ . In this case the following equations must be satisfied:

$$\begin{aligned}\mu_1(R) &= m_1 + 1, \\ 1 - R &= (\mu_1(R) - m_1) N_1.\end{aligned}$$

Solving the above equations, we obtain the equilibrium  $E_1 = (N_{(1)}^*, 0, R_{(1)}^*)$ , where

$$\begin{aligned}R_{(1)}^* &= \mu_1^{-1}(m_1 + 1), \\ N_{(1)}^* &= 1 - R_{(1)}^*.\end{aligned}\tag{3.4}$$

(c) Let  $N_1 = 0$  and  $N_2 \neq 0$ . Under this condition, for an equilibrium to exist we need to satisfy the following equations

$$\begin{aligned}\mu_2(R) &= m_2 + 1, \\ 1 - R &= (\mu_2(R) - m_2) N_2.\end{aligned}$$

Solving the equations leads to the equilibrium  $E_2 = (0, N_{(2)}^*, R_{(2)}^*)$  where

$$\begin{aligned}R_{(2)}^* &= \mu_2^{-1}(m_2 + 1), \\ N_{(2)}^* &= 1 - R_{(2)}^*.\end{aligned}\tag{3.5}$$

(d) Let  $N_1 \neq 0$  and  $N_2 \neq 0$ . Under this assumption the following must be satisfied:

$$\begin{aligned}\mu_1(R) &= m_1 + 1, \\ \mu_2(R) &= m_2 + 1, \\ 1 - R &= (\mu_2(R) - m_2) N_2 + (\mu_1(R) - m_1) N_1.\end{aligned}$$

The solution to this system yields an interior equilibrium  $E_3 = (N_1^*, N_2^*, R^*)$  where  $R^* = \mu_2^{-1}(m_2 + 1) = \mu_1^{-1}(m_1 + 1)$  and the values of  $N_1$  and  $N_2$  satisfy  $N_1^* + N_2^* = 1 - R^*$ . One should note the strict requirements for the parameter set along with the non-unique equilibrium values for  $N_1$  and  $N_2$  differs significantly from the other

equilibria  $E_0$ ,  $E_1$  and  $E_2$ . These differences reflect the underlying biology. That is, in order for the coexistence equilibrium  $E_3$  to exist the resource requirements for the two species must be in perfect balance. In a biological sense this so called "knife-edge balance" should be seen as an exceptional case and hence further analysis of  $E_3$  will be omitted [28].

The following proposition lists the necessary conditions on the parameters of System (3.3) for the existence of the four equilibria.

**Proposition 1.** *For the equilibria of System (3.3) the following four cases hold:*

- (a)  $E_0$  always exists.
- (b) If  $\mu_1^{max} > m_1 + 1$ , then  $E_1$  exists.
- (c) If  $\mu_2^{max} > m_2 + 1$ , then  $E_2$  exists.
- (d) If both  $\mu_1^{max} > m_1 + 1$  and  $\mu_2^{max} > m_2 + 1$ , then  $E_3$  exists.

The condition  $\mu_1^{max} > m_1 + 1$  simply implies that the maximum growth rate must be larger than the sum of the death rate and washout rate for persistence of  $N_1$  to be feasible. In a similar manner, survival of species  $N_2$  requires  $\mu_2^{max} > m_2 + 1$ .

We now turn to analyzing the local stability of each equilibrium. The Jacobian of System (3.3) is

$$J(N_1, N_2, R) = \begin{pmatrix} \mu_1(R) - m_1 - 1 & 0 & -\frac{d\mu_1}{dR} N_1 \\ 0 & \mu_2(R) - m_2 - 1 & -\frac{d\mu_2}{dR} N_2 \\ -(\mu_1(R) - m_1) & -(\mu_2(R) - m_2) & -1 \end{pmatrix}. \quad (3.6)$$

**Theorem 3.2.1.** *The equilibrium  $E_0$  is locally asymptotically stable if and only if  $\mu_1(1) < m_1 + 1$  and  $\mu_2(1) < m_2 + 1$ .*

*Proof.* For the equilibrium  $E_0$ , the local stability is determined by the eigenvalues of

$$J(E_0) = = \begin{pmatrix} \mu_1(1) - m_1 - 1 & 0 & 0 \\ 0 & \mu_2(R) - m_2 - 1 & 0 \\ -(\mu_1(R) - m_1) & -(\mu_2(R) - m_2) & -1 \end{pmatrix}.$$

Using the characteristic polynomial of  $J(E_0)$  we find the following eigenvalues

$$\begin{aligned} \lambda_1 &= -1, & \lambda_2 &= \mu_1(1) - m_1 - 1, \\ \lambda_3 &= \mu_2(1) - m_2 - 1, & \lambda_4 &= \mu_2(1) - m_2^{\min} - 1. \end{aligned}$$

Therefore,  $E_0$  is locally asymptotically stable if and only if  $\mu_1(1) < m_1 + 1$  and  $\mu_2(1) < m_2 + 1$ .  $\square$

**Theorem 3.2.2.** *The equilibrium  $E_1$  is locally asymptotically stable if and only if  $R_{(1)}^* < R_{(2)}^*$ .*

*Proof.* For the equilibrium  $E_1$ , the local stability is determined by the eigenvalues of

$$J(E_1) = \begin{pmatrix} 0 & 0 & -\frac{d\mu_1}{dR} \Big|_{R=R_{(1)}^*} N_{(1)}^* \\ 0 & \mu_2(R_{(1)}^*) - m_2 - 1 & 0 \\ -1 & -(\mu_2(R_{(1)}^*) - m_2) & -1 \end{pmatrix}.$$

Using the characteristic polynomial of  $J(E_1)$  we find the following eigenvalues

$$\lambda_1 = -1, \quad \lambda_2 = -\frac{d\mu_1}{dR} \Big|_{R=R_{(1)}^*} N_{(1)}^*, \quad \lambda_3 = \mu_2(R_{(1)}^*) - m_2 - 1.$$

Therefore the eigenvalues of  $J(E_1)$  are negative if and only if  $\mu_2(R_{(1)}^*) < m_2 + 1$ . That is, if and only if  $R_{(1)}^* < R_{(2)}^*$ .  $\square$

**Theorem 3.2.3.** *The equilibrium  $E_2$  is locally asymptotically stable if and only if  $R_{(2)}^* < R_{(1)}^*$ .*

*Proof.* For the equilibrium  $E_2$ , the local stability is determined by the eigenvalues of

$$J(E_2) = \begin{pmatrix} \mu_1(R_{(2)}^*) - m_1 - 1 & 0 & 0 \\ 0 & 0 & -\frac{d\mu_2}{dR}\big|_{R=R_{(2)}^*} N_{(2)}^* \\ -(\mu_1(R_{(2)}^*) - m_1) & -1 & -1 \end{pmatrix}.$$

Using the characteristic polynomial of  $J(E_2)$  we find the following eigenvalues

$$\lambda_1 = -1, \quad \lambda_2 = -N_{(2)}^* \frac{d\mu_2}{dR}\big|_{R=R_{(2)}^*}, \quad \lambda_3 = \mu_1(R_{(2)}^*) - m_1 - 1.$$

Therefore the eigenvalues of  $J(E_2)$  are negative if and only if  $\mu_1(R_{(2)}^*) < m_1 + 1$ . That is, if and only if  $R_{(2)}^* < R_{(1)}^*$ . □

### 3.2.2 Global Analysis

To proceed with further analysis we reduce the order of System (3.3) so as to apply known 2-dimensional theory. Define  $\Sigma = 1 - N_1 - N_2 - R$ . Then,

$$\begin{aligned} \frac{d\Sigma}{dt} &= -1 + N_1 + N_2 + R \\ &= -\Sigma. \end{aligned} \tag{3.7}$$

From this we can see that  $\Sigma(t) \rightarrow 0$  as  $t \rightarrow \infty$ . Hence, asymptotically, we have that  $N_1 + N_2 + R = 1$ . Since each of the variables  $N_1, N_2, R$  is positive, each of  $N_1, N_2$  and  $R$  is bounded, which ensures boundedness of any solution to System (3.3). In fact, System (3.3) is dissipative to the set  $\Delta_0 = \{(N_1, N_2, R) | N_1 + N_2 + R \leq 1\}$ .

Using the  $\Sigma$  as defined above, we can rewrite System (3.3) in the following way

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 (\mu_1(1 - N_1 - N_2 - \Sigma) - m_1 - 1), \\ \frac{dN_2}{dt} &= N_2 (\mu_2(1 - N_1 - N_2 - \Sigma) - m_2 - 1), \\ \frac{d\Sigma}{dt} &= -\Sigma. \end{aligned} \tag{3.8}$$

The positively invariant, dissipative set for System (3.8) is  $\Delta = \{(N_1, N_2, \Sigma) | N_1 + N_2 + \Sigma \leq 1\}$ . The asymptotic behavior of System (3.8) can be determined by investigating the asymptotic outcomes when  $\Sigma(t) \rightarrow 0$  as seen in the following system

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 (\mu_1(1 - N_1 - N_2) - m_1 - 1), \\ \frac{dN_2}{dt} &= N_2 (\mu_2(1 - N_1 - N_2) - m_2 - 1).\end{aligned}\tag{3.9}$$

System (3.9) is positively invariant on and dissipative to the set  $\Omega = \{(N_1, N_2) | N_1 + N_2 \leq 1\}$ . Following the theory for asymptotically autonomous systems, Appendix F of [28] and reproduced in Appendix A, System (3.8) will have the same asymptotic outcomes as System (3.9) with  $\Sigma = 0$  if conditions (H1)-(H5) are met. (H1) holds since  $\Sigma = [-1]\Sigma$  and the eigenvalue of  $A = [-1]$  is certainly negative. These remaining conditions require full analysis of System (3.9).

### 3.2.3 Analysis of System (3.9)

There are four steady states of System (3.9):  $\overline{E}_0 = (0, 0)$ ,  $\overline{E}_1 = (\overline{N}_{(1)}^*, 0)$  where  $\overline{N}_{(1)}^* = 1 - \mu_1^{-1}(m_1 + 1)$ ,  $\overline{E}_2 = (0, \overline{N}_{(2)}^*)$  where  $\overline{N}_{(2)}^* = 1 - \mu_2^{-1}(m_2 + 1)$  and a coexistence equilibrium  $\overline{E}_3 = (\overline{N}_1^*, \overline{N}_2^*)$  which requires  $\mu_1^{-1}(m_1 + 1) = \mu_2^{-1}(m_2 + 1)$  in order to exist. To be logical the values  $\overline{N}_{(1)}^*$  and  $\overline{N}_{(2)}^*$  must be positive, hence  $\overline{E}_1$  exists when  $\mu_1^{-1}(m_1 + 1) < 1$  and  $\overline{E}_2$  exists when  $\mu_2^{-1}(m_2 + 1) < 1$ . As before,  $\overline{E}_3$  is an exceptional case and that parameter group will be omitted.

The local stability of the equilibria of System (3.9) is determined by the eigenvalues of  $J(\overline{N}_1, \overline{N}_2) =$

$$\begin{pmatrix} \mu_1(1 - \overline{N}_1 - \overline{N}_2) - m_1 - 1 - \frac{d\mu_1}{dN_1}\overline{N}_1 & -\frac{d\mu_1}{dN_2}\overline{N}_1 \\ -\frac{d\mu_2}{dN_1}\overline{N}_2 & \mu_2(1 - \overline{N}_1 - \overline{N}_2) - m_2 - 1 - \frac{d\mu_2}{dN_2}\overline{N}_2 \end{pmatrix}.\tag{3.10}$$

**Theorem 3.2.4.** *The equilibrium  $\overline{E}_0$  is locally asymptotically stable if and only if  $\mu_1^{-1}(m_1 + 1) > 1$  and  $\mu_2^{-1}(m_2 + 1) > 1$ .*

*Proof.* For the equilibrium  $\overline{E}_0$ , the local stability is determined by the eigenvalues of

$$J(\overline{E}_0) = \begin{pmatrix} \mu_1(1) - m_1 - 1 & 0 \\ 0 & \mu_2(1) - m_2 - 1 \end{pmatrix}.$$

which are easily found to be

$$\lambda_1 = \mu_1(1) - m_1 - 1, \quad \lambda_2 = \mu_2(1) - m_2 - 1.$$

Therefore the eigenvalues of  $J(\overline{E}_0)$  are negative if and only if  $\mu_1(1) < m_1 + 1$  and  $\mu_2(1) < m_2 + 1$ . That is, if and only if  $\mu_1^{-1}(m_1 + 1) > 1$  and  $\mu_2^{-1}(m_2 + 1) > 1$ . □

**Theorem 3.2.5.** *The equilibrium  $\overline{E}_1$  is locally asymptotically stable if and only if  $\mu_1^{-1}(m_1 + 1) < \mu_2^{-1}(m_2 + 1)$ .*

*Proof.* For the equilibrium  $\overline{E}_1$ , the local stability is determined by the eigenvalues of

$$J(\overline{E}_1) = \begin{pmatrix} \mu_1(1 - \overline{N}_{(1)}^*) - m_1 - 1 - \frac{d\mu_1}{d\overline{N}_1} \Big|_{1 - \overline{N}_{(1)}^*} \overline{N}_{(1)}^* & - \frac{d\mu_1}{d\overline{N}_2} \Big|_{1 - \overline{N}_{(1)}^*} \overline{N}_{(1)}^* \\ 0 & \mu_2(1 - \overline{N}_{(1)}^*) - m_2 - 1 \end{pmatrix}.$$

Using the characteristic polynomial of  $J(\overline{E}_1)$  we find the following eigenvalues

$$\lambda_1 = - \frac{d\mu_1}{d\overline{N}_1} \Big|_{1 - \overline{N}_{(1)}^*} \overline{N}_{(1)}^*, \quad \lambda_2 = \mu_2(1 - \overline{N}_{(1)}^*) - m_2 - 1.$$

Therefore the eigenvalues of  $J(\overline{E}_1)$  are negative if and only if

$$\mu_1^{-1}(m_1 + 1) < \mu_2^{-1}(m_2 + 1).$$
□

**Theorem 3.2.6.** *The equilibrium  $\overline{E}_2$  is locally asymptotically stable if and only if  $\mu_2^{-1}(m_2 + 1) < \mu_1^{-1}(m_1 + 1)$ .*



*Proof.* For the equilibrium  $\overline{E}_2$ , the local stability is determined by the eigenvalues of

$$J(\overline{E}_2) = \begin{pmatrix} \mu_1(1 - \overline{N}_{(2)}^*) - m_1 - 1 & 0 \\ -\frac{d\mu_2}{dN_1}\Big|_{1-\overline{N}_{(2)}^*} \overline{N}_{(2)}^* & \mu_2(1 - \overline{N}_{(2)}^*) - m_2 - 1 - \frac{d\mu_2}{dN_2}\Big|_{1-\overline{N}_{(2)}^*} \overline{N}_{(2)}^* \end{pmatrix}.$$

Using the characteristic polynomial of  $J(\overline{E}_2)$  we find the following eigenvalues

$$\lambda_1 = -\frac{d\mu_2}{dN_2}\Big|_{1-\overline{N}_{(2)}^*} \overline{N}_{(2)}^*, \quad \lambda_2 = \mu_1(1 - \overline{N}_{(2)}^*) - m_1 - 1.$$

Therefore the eigenvalues of  $J(\overline{E}_2)$  are negative if and only if  $\mu_2^{-1}(m_2 + 1) < \mu_1^{-1}(m_1 + 1)$ .  $\square$

The previous theorems give conditions on the parameters for the local stability for the equilibria  $\overline{E}_0$ ,  $\overline{E}_1$ , and  $\overline{E}_2$ . These conditions not only determine the local stability, but are also conditions for global stability for the three equilibria in question. The proofs of this result is not provided here since the analysis is reduced to that of the previous chapter.

### 3.2.3.1 Reduction of Order

We now continue the reduction of System (3.8) to System (3.9). Again, we follow the theory in [28] and the five conditions listed therein. Condition (H1) will always hold as previously stated above. In the analysis of System (3.9) we saw that with the exception of the omitted parameter range, namely  $\mu_2^{-1}(m_2 + 1) = \mu_1^{-1}(m_1 + 1)$ , there will always be a finite number of equilibria, each of which is hyperbolic. Hence (H2) will hold for all of the interesting parameter sets.

The analysis continues by separating the parameters into three cases:

- (A)  $1 < \mu_1^{-1}(m_1 + 1)$  and  $1 < \mu_2^{-1}(m_2 + 1)$
- (B)  $\mu_1^{-1}(m_1 + 1) < 1$  and  $\mu_1^{-1}(m_1 + 1) < \mu_2^{-1}(m_2 + 1)$
- (C)  $\mu_2^{-1}(m_2 + 1) < 1$  and  $\mu_2^{-1}(m_2 + 1) < \mu_1^{-1}(m_1 + 1)$

### 3.2.3.2 Parameter Range $1 < \mu_1^{-1}(m_1 + 1)$ and $1 < \mu_2^{-1}(m_2 + 1)$

**Theorem 3.2.7.** *The equilibrium  $E_0$  of System (3.3) is globally asymptotically stable if and only if  $1 < \mu_1^{-1}(m_1 + 1)$  and  $1 < \mu_2^{-1}(m_2 + 1)$ .*

*Proof.* In this parameter range, the analysis of System (3.9) showed that  $\overline{E}_0$  is locally asymptotically stable with  $\overline{E}_2$  and  $\overline{E}_2$  failing to exist. Therefore with the stable manifold of  $\overline{E}_0$  having dimension 2 and no other equilibria being feasible, (H3) holds. Because  $\overline{E}_0$  is locally stable, it cannot be part of any chain of equilibria and therefore (H5) is also satisfied.

It remains to show that  $\Omega$  is the stable manifold for  $\overline{E}_0$ . We already have that System (3.9) is dissipative to  $\Omega$  and certainly the  $\omega$ -limit set must contain  $\overline{E}_0$ . By Poincare-Bendixson theorem, the  $\omega$ -limit set must either be a rest point or a periodic orbit. A limit cycle requires an unstable equilibrium to be enclosed, which is certainly false. Hence the  $\omega$ -limit must be a rest point, in fact since there is only one such point must be  $\overline{E}_0$ . Therefore all trajectories on  $\Omega$  converge to  $\overline{E}_0$ , that is, the stable manifold for  $\overline{E}_0$  is  $\Omega$ . Therefore (H4) is satisfied and under the parameter range (A) any trajectory of System (3.8) will be such that the  $N_1$  and  $N_2$  coordinates will converge to a rest point of System (3.9) with  $\Sigma = 0$ . With the parameter set (A),  $\overline{E}_0$  is globally stable and therefore all trajectories must converge to  $(0, 0, 1)$ , that is  $E_0$  is globally asymptotically stable for System (3.3).  $\square$

### 3.2.3.3 Parameter Range $\mu_1^{-1}(m_1 + 1) < 1$ and $\mu_1^{-1}(m_1 + 1) < \mu_2^{-1}(m_2 + 1)$

**Theorem 3.2.8.** *The equilibrium  $E_1$  of System (3.3) attracts all solutions with initial conditions in the interior of the positive cone if and only if  $\mu_1^{-1}(m_1 + 1) < 1$  and  $\mu_1^{-1}(m_1 + 1) < \mu_2^{-1}(m_2 + 1)$ .*

*Proof.* In this parameter range, the analysis of System (3.9) showed that  $\overline{E}_1$  is locally asymptotically stable with  $\overline{E}_2$  and  $\overline{E}_0$  unstable. Based on the eigenvalue calculations, one of  $\overline{E}_2$  or  $\overline{E}_0$  has stable manifold dimension 1, with the other having stable manifold dimension 0. Therefore (H3) is satisfied. The equilibrium  $\overline{E}_1$  cannot be part of any chain of equilibria, with the same being true for the equilibrium with dimension 0. The remaining equilibrium cannot be linked to itself and therefore no chain of equilibria exists. We already have that System (3.9) is dissipative to  $\Omega$  and certainly the  $\omega$ -limit set must contain  $\overline{E}_1$ . By Poincare-Bendixson theorem, the  $\omega$ -limit set must either be a rest point or a periodic orbit. A limit cycle requires an unstable equilibrium to be enclosed, which again is false. Hence the  $\omega$ -limit set must be a rest point. For trajectories initiating on the  $N_2$ -axis for System (3.9), the problem is reduced to that of the previous chapter. That is the convergence will be to the equilibrium which has stable manifold dimension 1. Therefore trajectories initiating in the interior of the positive cone initiate in the unstable manifolds of both equilibria  $E_0$  and  $E_2$ . Hence, the Butler-McGehee Theorem states that the equilibrium with stable manifold dimension 1 cannot be in the  $\omega$ -limit set and therefore the  $\omega$ -limit set must consist of  $\overline{E}_1$  alone. Thus  $\Omega$  is the union of the stable manifold of  $\overline{E}_1$  and the stable manifold of the equilibrium of the stable manifold with dimension 1. Therefore, condition (H4) is satisfied. Hence under the parameter set (B) any trajectory of System (3.8) will be such that the  $N_1$  and  $N_2$  coordinates will converge to a rest point of System (3.9) with  $\Sigma = 0$ . Specifically, trajectories will converge to equilibrium  $E_1$  of System (3.9) unless initiated on the boundary  $N_1 = 0$  with convergence then to  $E_0$ . □

### 3.2.3.4 Parameter Range $\mu_2^{-1}(m_2 + 1) < 1$ and $\mu_2^{-1}(m_2 + 1) < \mu_1^{-1}(m_1 + 1)$

**Theorem 3.2.9.** *The equilibrium  $E_2$  of System (3.3) attracts all solutions with initial conditions in the interior of the positive cone if and only if  $\mu_2^{-1}(m_2 + 1) < 1$  and  $\mu_2^{-1}(m_2 + 1) < \mu_1^{-1}(m_1 + 1)$ .*

*Proof.* In this parameter range, the analysis of System (3.9) showed that  $\overline{E}_2$  is locally asymptotically stable with  $\overline{E}_1$  and  $\overline{E}_0$  unstable. Based on the eigenvalue calculations, one of  $\overline{E}_1$  or  $\overline{E}_0$  has stable manifold dimension 1, with the other having stable manifold dimension 0. Therefore (H3) is satisfied. The equilibrium  $\overline{E}_2$  cannot be part of any chain of equilibria, with the same being true for the equilibrium with dimension 0. The remaining equilibrium cannot be linked to itself and therefore no chain of equilibria exists. We already have that System (3.9) is dissipative to  $\Omega$  and certainly the  $\omega$ -limit set must contain  $\overline{E}_2$ . By Poincare-Bendixson theorem, the  $\omega$ -limit set must either be a rest point or a periodic orbit. A limit cycle requires an unstable equilibrium to be enclosed, which again is false. Hence the  $\omega$ -limit set must be a rest point. For trajectories initiating on the  $N_1$ -axis for System (3.9), the problem is reduced to that of the previous chapter. That is the convergence will be to the equilibrium which has stable manifold dimension-1. Therefore trajectories initiating in the interior of the positive cone initiate in the unstable manifolds of both equilibria  $E_0$  and  $E_1$ . Hence, the Butler-McGehee Theorem states that the equilibrium with stable manifold dimension-1 cannot be in the  $\omega$ -limit set and therefore the  $\omega$ -limit set must consist of  $\overline{E}_2$  alone. Thus  $\Omega$  is the union of the stable manifold of  $\overline{E}_2$  and the stable manifold of the equilibrium of the stable manifold with dimension-1. Therefore, condition (H4) is satisfied. Hence under the parameter set (B) any trajectory of System (3.8) will be such that the  $N_1$  and  $N_2$  coordinates will converge to a rest point of System (3.9) with  $\Sigma = 0$ . Specifically, trajectories will

converge to equilibrium  $E_2$  of System (3.9) unless initiated on the boundary  $N_1 = 0$  with convergence then to  $E_0$ .  $\square$

### 3.3 Numerical Simulations

In this section we present simulations of System (3.1) as verification of the attraction conditions presented in the previous section. Each set is obtained using the **Mathematica** solver **NDSolve** with parameter values:  $R_{in} = 0.1$ ,  $q_1 = 10^{-9}$ ,  $q_2 = 10^{-9}$ ,  $k = 0.1$ ,  $k_1 = 0.001$ ,  $m_1 = 0.2$ ,  $D = 0.2$ ,  $k_2 = 0.001$  and  $m_2 = 0.2$ .

The first set of simulations reflects the parameters fitting the range  $\mu_1^{-1}(m_1 + 1) < 1$  and  $\mu_1^{-1}(m_1 + 1) < \mu_2^{-1}(m_2 + 1)$ , when appropriately scaled, by choosing  $\alpha = 10^{-11}$ ,  $\mu_1^{max} = 0.7$ , and  $\mu_2^{max} = 0.5$ . In Fig. (3.3) the  $N_1$ - $N_2$  coordinates of several trajectories with differing initial values are plotted. Here the Species  $N_1$  is a better competitor, requiring fewer resources to reach equilibrium. Each of the trajectories tends to the equilibrium  $E_1$ .

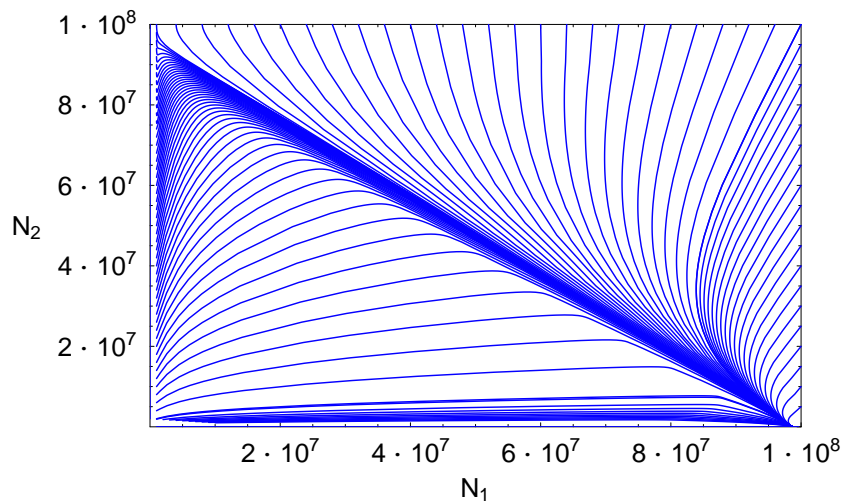


Figure 3.1.  $E_1$  attracts all solutions.

The second set of simulations chooses  $\alpha = 10^{-10}$ ,  $\mu_1^{max} = 0.4$  and  $\mu_2^{max} = 0.7$  to satisfy the parameter range  $\mu_2^{-1}(m_2 + 1) < 1$  and  $\mu_2^{-1}(m_2 + 1) < \mu_1^{-1}(m_1 + 1)$ . In Fig. (3.3) the  $N_1$ - $N_2$  coordinates of several trajectories are plotted, each with a different initial population for  $N_1$  and  $N_2$ . In this parameter range  $N_2$  is a better competitor since fewer resources are required to reach equilibrium. The trajectories converge to  $E_2$  as predicted by Theorem (3.2.9).

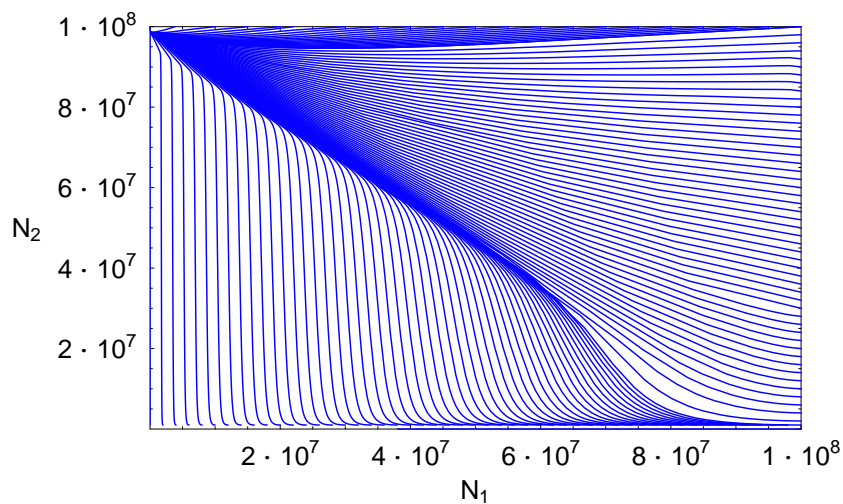


Figure 3.2.  $E_2$  attracts solutions.

### 3.4 Discussion

The model described by System (3.1) introduces nutrient recycling for each population in a competition chemostat. Four steady states were identified, with the “knife-edge” case excluded. The remaining equilibria are also the asymptotic outcomes for any initial trajectory. The inclusion of the nutrient recycling into the model is compatible with the existing chemostat theory as evident by Theorems 3.2.8 and 3.2.9. That is, given viable

competitors, competitive exclusion will hold. In the competition the superior competitor will be determined by requiring the least resources to achieve equilibrium.

## CHAPTER 4

### NUTRIENT RECYCLING AND ALLELOPATHY IN THE CHEMOSTAT

#### 4.1 Introduction

The model presented in this chapter is derived from the nutrient recycling model of competition presented in the previous chapter by appending an equation for dynamics of the poison, which is produced by one competitor and induces mortality in the other. The addition of the poison dynamic removes the conservative property from the resulting dynamical system, limiting the ability to reduce the order as seen in the previous chapter.

#### 4.2 The Chemostat Model of Nutrient Recycling and Allelopathy

The model has the following form

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 (\mu_1(R) - m_1 - D), \\ \frac{dN_2}{dt} &= N_2 (\mu_2(R) - m_2(P) - D), \\ \frac{dR}{dt} &= D (R_{in} - R) - (\mu_1(R) - m_1) q_1 N_1 - (\mu_2(R) - m_2(P)) q_2 N_2, \\ \frac{dP}{dt} &= \alpha (\mu_1^{max} - \mu_1(R)) N_1 - (D + K) P.\end{aligned}\tag{4.1}$$

Here,  $N_1$ ,  $N_2$  again represent population densities of the competing species, with species 1 producing the toxin, while species 2 is susceptible to it. Both species suffer mortality at per capita rates  $m_i$ . For species 1, which produces the poison,  $m_1$  is a positive constant, while for species 2, which suffers mortality from the poison,  $m_2(P)$  is an increasing function of poison concentration  $P$ , with  $0 \leq m_2^{min} \leq m_2(P) \leq \infty$ ,  $m_2(0) = m_2^{min}$ , and  $dm_2/dP > 0$ .



Poison dynamics represent a balance between production by species 1, dilution, and decay. Poison production is proportion to the density of species 1, but also increases when this population is nutrient-limited, leading to the term  $\alpha (\mu_1^{max} - \mu_1(R)) N_1$ , where  $\alpha$  is a positive constant. This assumption is suggested by the observation that some algae become more toxic when nutrient-limited [1]. Poison concentration decreases due to dilution, and decays with a first-order positive rate constant  $K$ .

Much analysis can be completed with only the positive monotonic increasing assumptions on the function  $m_2(P)$ , but an explicit function are needed for numerical simulations. For mortality of species 2 in relation to poison concentration,  $m_2(P) = \gamma P + m_2^{min}$ , where  $\gamma = \mu_2^{max}/(2k_2)$ .

In an effort to ease calculation complexity and increase overall clarity of the presentation, it is convenient to rescale the variables in System (4.1) in the following way

$$\hat{N}_1 = q_1 N_1 / R_{in}, \quad \hat{N}_2 = q_2 N_2 / R_{in}, \quad \hat{R} = R / R_{in}, \quad \hat{P} = q_1 P / (\alpha R_{in}),$$

$$\hat{t} = D t, \quad \hat{\mu}_i^{max} = \mu_i^{max} / D, \quad \hat{k}_i = k_i / R_{in},$$

$$\hat{m}_1 = m_1 / D, \quad \hat{K} = K / D, \quad \hat{m}_2^{min} = m_2^{min} / D.$$

System (4.1) then becomes

$$\begin{aligned} \frac{d\hat{N}_1}{d\hat{t}} &= \hat{N}_1 (\hat{\mu}_1(\hat{R}) - \hat{m}_1 - 1), \\ \frac{d\hat{N}_2}{d\hat{t}} &= \hat{N}_2 (\hat{\mu}_2(\hat{R}) - \hat{m}_2(\hat{P}) - 1), \\ \frac{d\hat{R}}{d\hat{t}} &= 1 - \hat{R} - (\hat{\mu}_1(\hat{R}) - \hat{m}_1) \hat{N}_1 - (\hat{\mu}_2(\hat{R}) - \hat{m}_2(\hat{P})) \hat{N}_2, \\ \frac{d\hat{P}}{d\hat{t}} &= (\hat{\mu}_1^{max} - \hat{\mu}_1(\hat{R})) \hat{N}_1 - (1 + \hat{K}) \hat{P}. \end{aligned} \tag{4.2}$$

where  $\hat{\mu}_i(\hat{R}) = \frac{\hat{\mu}_i^{max} \hat{R}}{\hat{k}_i + \hat{R}}$  and  $\hat{m}_2(\hat{P}) = \frac{\hat{\mu}_2^{max} \alpha \hat{P}}{2\hat{k}_2 q_1} - \hat{m}_2^{min}$ . Dropping the hats we obtain the following system of interest

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 (\mu_1(R) - m_1 - 1), \\ \frac{dN_2}{dt} &= N_2 (\mu_2(R) - m_2(P) - 1), \\ \frac{dR}{dt} &= 1 - R - (\mu_1(R) - m_1) N_1 - (\mu_2(R) - m_2(P)) N_2, \\ \frac{dP}{dt} &= (\mu_1^{max} - \mu_1(R)) N_1 - (1 + K) P. \end{aligned} \tag{4.3}$$

The problem described by System (4.3) is well posed since the first quadrant is positively invariant, which is consistent with the biological interpretation of the model. Define  $\Sigma = \frac{1}{(K+1)} - N_1 - N_2 - R - P$ . Then,

$$\begin{aligned} \frac{d\Sigma}{dt} &= -1 + (1 - (\mu_1^{max} - \mu_1(R))) N_1 + N_2 + R + (1 + K) P, \\ &\leq -(1 + K) \Sigma \end{aligned} \tag{4.4}$$

From this we can see that  $\Sigma(t) \rightarrow 0$  as  $t \rightarrow \infty$ . Hence, asymptotically we have that  $N_1 + N_2 + R + P = \frac{1}{K+1}$ . Since each of the variables  $N_1, N_2, R$  is positive, each of  $N_1, N_2, R$  and  $P$  is bounded, which ensures boundedness of any solution to System (4.3).

In order to analyze the behavior of System (4.3) we establish the existence and stability of the equilibria and then examine the global dynamics via numerical simulations.

### 4.3 Equilibria and Local Analysis

To investigate the existence of equilibria for System (4.3) we consider the following four cases:

- (a) Let  $N_1 = 0$  and  $N_2 = 0$ . In this case, since  $K > 0$ , the only possible equilibrium is  $E_0 = (0, 0, 1, 0)$ .

(b) Let  $N_1 \neq 0$  and  $N_2 = 0$ . In this case the following three equations must be satisfied

$$\begin{aligned}\mu_1(R) &= m_1 + 1, \\ 1 - R &= (\mu_1(R) - m_1) N_1, \\ (\mu_1^{max} - \mu_1(R)) N_1 &= (1 + K) P.\end{aligned}$$

Solving the above equations, we obtain the equilibrium  $E_1 = (N_{(1)}^*, 0, R_{(1)}^*, P_{(1)}^*)$

where

$$\begin{aligned}R_{(1)}^* &= \mu_1^{-1}(m_1 + 1), \\ N_{(1)}^* &= 1 - R_{(1)}^*, \\ P_{(1)}^* &= N_{(1)}^* \frac{(\mu_1^{max} - \mu_1(R_{(1)}^*))}{1 + K}.\end{aligned}\tag{4.5}$$

(c) Let  $N_1 = 0$  and  $N_2 \neq 0$ . Under this condition, for an equilibrium to exist we need

$P = 0$  and the following equations must be satisfied

$$\begin{aligned}\mu_2(R) &= m_2(P) + 1, \\ 1 - R &= (\mu_2(R) - m_2(P)) N_2.\end{aligned}$$

Solving the equations leads to the equilibrium  $E_2 = (0, N_{(2)}^*, R_{(2)}^*, 0)$  where

$$\begin{aligned}R_{(2)}^* &= \mu_2^{-1}(m_2^{min} + 1), \\ N_{(2)}^* &= 1 - R_{(2)}^*.\end{aligned}\tag{4.6}$$

(d) Let  $N_1 \neq 0$  and  $N_2 \neq 0$ . Under this assumption the following must be satisfied

$$\begin{aligned}\mu_1(R) &= m_1 + 1, \\ \mu_2(R) &= m_2(P) + 1, \\ P(1 + K) &= (\mu_1^{max} - \mu_1(R)) N_1, \\ 1 - R &= (\mu_2(R) - m_2(P)) N_2 + (\mu_1(R) - m_1) N_1.\end{aligned}$$

The solution to this system yields the interior equilibrium  $E_3 = (N_1^*, N_2^*, R^*, P^*)$  where

$$\begin{aligned} N_1^* &= \frac{P^*(1+K)}{(\mu_1^{max} - \mu_1(R^*))}, \\ N_2^* &= \frac{1 - R^* - (\mu_1(R^*) - m_1) N_1^*}{(\mu_2(R^*) - m_2(P^*))}, \\ R^* &= R_{(1)}^*, \\ P^* &= m_2^{-1}(\mu_2(R^*) - 1). \end{aligned} \tag{4.7}$$

The following proposition lists necessary conditions on the parameters of System (4.3) for the existence of the four equilibria.

**Proposition 2.** *For the equilibria of System (4.3) the following four cases hold:*

- (a)  $E_0$  always exists.
- (b) If  $\mu_1^{max} > m_1 + 1$ , then  $E_1$  exists.
- (c) If  $\mu_2^{max} > m_2^{min} + 1$ , then  $E_2$  exists.
- (d) If both  $\mu_1^{max} > m_1 + 1$  and  $\mu_2^{max} > m_2^{min} + 1$ , then  $E_3$  exists.

The condition  $\mu_1^{max} > m_1 + 1$  simply requires the maximum growth rate to be larger than the sum of the death rate and washout rate for persistence of  $N_1$  to be feasible. In a similar manner, survival of species  $N_2$  requires  $\mu_2^{max} > m_2^{min} + 1$ .

We now turn to the local stability analysis for each of the four equilibria. The Jacobian of System (4.3) is

$$J(N_1, N_2, R, P) = \begin{pmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{pmatrix}, \tag{4.8}$$

where

$$\begin{aligned}
a_{11} &= \mu_1(R) - m_1 - 1, & a_{12} &= 0, \\
a_{13} &= \frac{d\mu_1}{dR}N_1, & a_{14} &= 0, \\
a_{21} &= 0, & a_{22} &= \mu_2(R) - m_2(P) - 1, \\
a_{23} &= \frac{d\mu_2}{dR}N_2, & a_{24} &= -\frac{dm_2}{dP}N_2, \\
a_{31} &= -(\mu_1(R) - m_1), & a_{32} &= -(\mu_2(R) - m_2(P)), \\
a_{33} &= -1 - \frac{d\mu_1}{dR}N_1 - \frac{d\mu_2}{dR}N_2, & a_{34} &= \frac{dm_2}{dP}N_2, \\
a_{41} &= (\mu_1^{max} - \mu_1(R)), & a_{42} &= 0, \\
a_{43} &= -\frac{d\mu_1}{dR}N_1, & a_{44} &= -(1 + K).
\end{aligned}$$

**Theorem 4.3.1.** *The equilibrium  $E_0$  is locally asymptotically stable if and only if  $\mu_1(1) < m_1 + 1$  and  $\mu_2(1) < m_2^{min} + 1$ .*

*Proof.* For the equilibrium  $E_0$ , the local stability is determined by the eigenvalues of

$$J(E_0) = \begin{pmatrix} \mu_1(1) - m_1 - 1 & 0 & 0 & 0 \\ 0 & \mu_2(1) - m_2^{min} - 1 & 0 & 0 \\ -(\mu_1(1) - m_1) & -(\mu_2(1) - m_2^{min}) & -1 & 0 \\ \alpha(\mu_1^{max} - \mu_1(1)) & 0 & 0 & -(1 + K) \end{pmatrix}.$$

Using the characteristic polynomial of  $J(E_0)$  we find the following eigenvalues

$$\begin{aligned}
\lambda_1 &= -1, & \lambda_2 &= -1 - K, \\
\lambda_3 &= \mu_1(1) - m_1 - 1, & \lambda_4 &= \mu_2(1) - m_2^{min} - 1.
\end{aligned}$$

Therefore,  $E_0$  is locally asymptotically stable if and only if  $\mu_1(1) < m_1 + 1$  and  $\mu_2(1) < m_2^{min} + 1$ .  $\square$

**Theorem 4.3.2.** *The equilibrium  $E_1$  is locally asymptotically stable if and only if  $\mu_2(R_{(1)}^*) < m_2(P_{(1)}^*) + 1$ .*

*Proof.* For the equilibrium  $E_1$ , the local stability is determined by the eigenvalues of  $J(E_1) =$

$$\begin{pmatrix} \mu_1(R_{(1)}^*) - m_1 - 1 & 0 & \frac{d\mu_1}{dR} \Big|_{R=R_{(1)}^*} N_{(1)}^* & 0 \\ 0 & \mu_2(R_{(1)}^*) - m_2(P_{(1)}^*) - 1 & 0 & 0 \\ -(\mu_1(R_{(1)}^*) - m_1) & -(\mu_2(R_{(1)}^*) - m_2(P_{(1)}^*)) & -1 - \frac{d\mu_1}{dR} \Big|_{R=R_{(1)}^*} N_{(1)}^* & 0 \\ (\mu_1^{max} - \mu_1(R_{(1)}^*)) & 0 & -\frac{d\mu_1}{dR} \Big|_{R=R_{(1)}^*} N_{(1)}^* & -(1+K) \end{pmatrix}.$$

Using the characteristic polynomial of  $J(E_1)$  we find the following eigenvalues

$$\begin{aligned} \lambda_1 &= -1, & \lambda_2 &= -1 - K, \\ \lambda_3 &= \mu_2(R_{(1)}^*) - m_2(P_{(1)}^*) - 1, & \lambda_4 &= -N_{(1)}^* \frac{d\mu_1}{dR} \Big|_{R=R_{(1)}^*}. \end{aligned}$$

Therefore the eigenvalues of  $J(E_1)$  are negative if and only if  $\mu_2(R_{(1)}^*) < m_2(P_{(1)}^*) + 1$ .  $\square$

**Theorem 4.3.3.** *The equilibrium  $E_2$  is locally asymptotically stable if and only if  $\mu_1(R_{(2)}^*) < m_1 + 1$ .*

*Proof.* For the equilibrium  $E_2$ , the local stability is determined by the eigenvalues of  $J(E_2) =$

$$\begin{pmatrix} \mu_1(R_{(2)}^*) - m_1 - 1 & 0 & 0 & 0 \\ 0 & \mu_2(R_{(2)}^*) - m_2^{min} - 1 & \frac{d\mu_2}{dR} \Big|_{R=R_{(2)}^*} N_{(2)}^* & -\frac{dm_2}{dP} \Big|_{P=0} N_{(2)}^* \\ -(\mu_1(R_{(2)}^*) - m_1) & -(\mu_2(R_{(2)}^*) - m_2^{min}) & -1 - \frac{d\mu_2}{dR} \Big|_{R=R_{(2)}^*} N_{(2)}^* & \frac{dm_2}{dP} \Big|_{P=0} N_{(2)}^* \\ (\mu_1^{max} - \mu_1(R_{(2)}^*)) & 0 & 0 & -(1+K) \end{pmatrix}.$$

Using the characteristic polynomial of  $J(E_2)$  we find the following eigenvalues

$$\begin{aligned}\lambda_1 &= -1, & \lambda_2 &= -1 - K, \\ \lambda_3 &= \mu_1(R_{(2)}^*) - m_1 - 1, & \lambda_4 &= -N_{(2)}^* \left. \frac{d\mu_2}{dR} \right|_{R=R_{(2)}^*}.\end{aligned}$$

Therefore the eigenvalues of  $J(E_2)$  are negative if and only if  $\mu_1(R_{(2)}^*) < m_1 + 1$ .  $\square$

**Theorem 4.3.4.** *When the equilibrium  $E_3$  exists, it is unstable.*

*Proof.* For the equilibrium  $E_3$ , the local stability is determined by the eigenvalues of  $J(E_3) =$

$$\begin{pmatrix} \mu_1(R^*) - m_1 - 1 & 0 & \left. \frac{d\mu_1}{dR} \right|_{R=R^*} N_1^* & 0 \\ 0 & \mu_2(R^*) - m_2(P^*) - 1 & \left. \frac{d\mu_2}{dR} \right|_{R=R^*} N_2^* & -\left. \frac{dm_2}{dP} \right|_{P=P^*} N_2^* \\ -(\mu_1(R^*) - m_1) & -(\mu_2(R^*) - m_2(P^*)) & -1 - \left. \frac{d\mu_1}{dR} \right|_{R=R^*} N_1^* - \left. \frac{d\mu_2}{dR} \right|_{R=R^*} N_2^* & \left. \frac{dm_2}{dP} \right|_{P=P^*} N_2^* \\ (\mu_1^{max} - \mu_1(R^*)) & 0 & -\left. \frac{d\mu_1}{dR} \right|_{R=R^*} N_1^* & -(1 + K) \end{pmatrix}.$$

Here, the characteristic polynomial has the form

$$P(\lambda) = \lambda^4 + c_3\lambda^3 + c_2\lambda^2 + c_1\lambda + c_0. \quad (4.9)$$

One should note that a necessary condition for all roots of Equation (4.9) to be negative or to have negative real parts is  $c_i > 0$  for each  $i = 0, \dots, 3$ . On a closer inspection,

$$c_0 = \left. \frac{dm_2}{dP} \right|_{P=P^*} \left. \frac{d\mu_1}{dR} \right|_{R=R^*} \mu_1(R) N_1 N_2 - \left. \frac{dm_2}{dP} \right|_{P=P^*} \left. \frac{d\mu_1}{dR} \right|_{R=R^*} \mu_1^{max} N_1 N_2 < 0,$$

since  $\mu_1^{max} > \mu_1(R)$  for all  $R$ . Hence,  $E_3$  must have eigenvalues with nonnegative real part.  $\square$

The local stability conditions for the equilibria for System (4.3) is summarized in Table 4.3. One should notice that the conditions for local stability of  $E_0$  given in Theorem 4.3.1 are equivalent to  $1 < R_{(1)}^*$  and  $1 < R_{(2)}^*$ . Additionally, the condition

Table 4.1. Local Stability Conditions for the Four Equilibria

Equilibrium	Local Stability Conditions
$E_0$	$\mu_1(1) < m_1 + 1$ and $\mu_2(1) < m_2^{min} + 1$
$E_1$	$\mu_2(R_{(1)}^*) < m_2(P_{(1)}^*) + 1$
$E_2$	$\mu_1(R_{(2)}^*) < m_1 + 1$
$E_3$	Always unstable

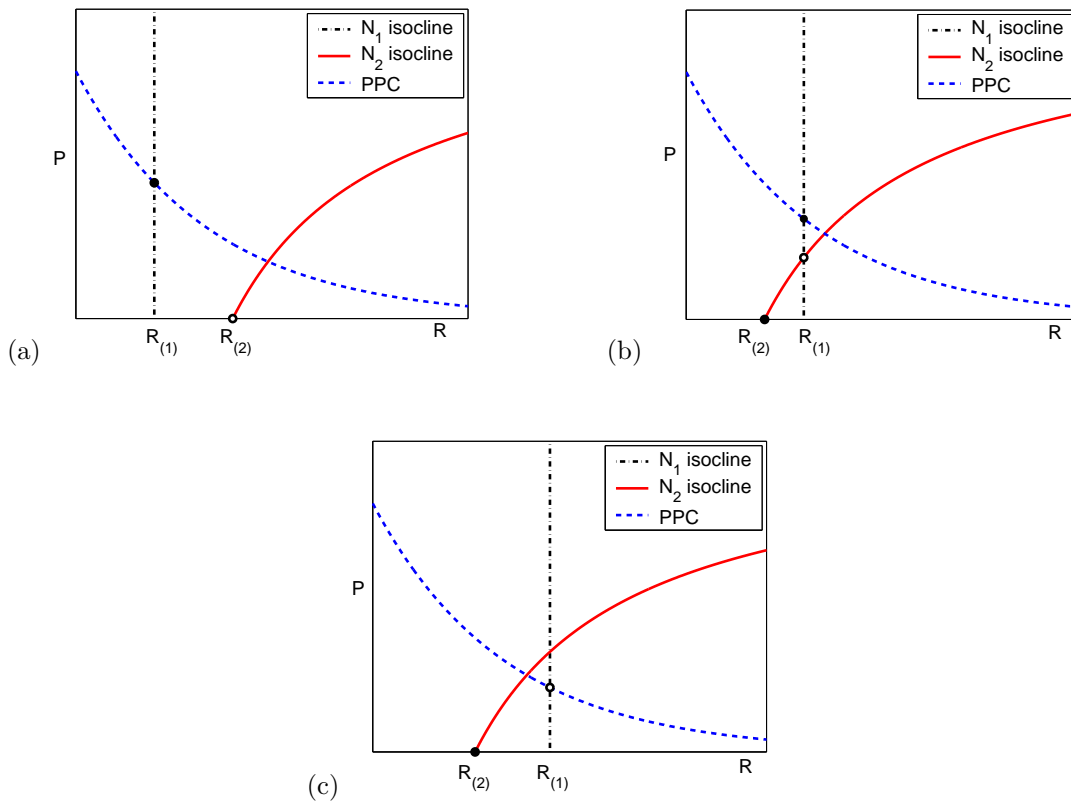


Figure 4.1. Behavior of isoclines: (a) The toxic species is the superior competitor for the resource with  $E_1$  stable,  $E_2$  unstable,  $E_3$  does not exist; (b) The non-toxic species is the superior competitor for the resource, and the toxic species produces sufficient poison to exclude the non-toxic species with  $E_1$  stable,  $E_2$  stable,  $E_3$  unstable; and (c) The non-toxic species is the superior competitor for the resource, and the toxic species does not produce sufficient poison to exclude the non-toxic species with  $E_1$  unstable,  $E_2$  stable,  $E_3$  infeasible .



Table 4.2. Parameter Relationship to Local Stability

Parameter Subset	Local Stability
$A_0$	$E_0$ stable; $E_1, E_2, E_3$ unstable.
$A_1$	$E_1$ stable; $E_0, E_2, E_3$ unstable.
$A_2$	$E_2$ stable; $E_0, E_1, E_3$ unstable.
$A_3$	$E_1$ and $E_2$ stable; $E_0$ and $E_3$ unstable.

$\mu_2(R_{(1)}^*) < m_2(P_{(1)}^*) + 1$  presented in Theorem 4.3.2 for local stability of  $E_1$  will always hold when  $R_{(1)}^* < R_{(2)}^*$ . To discuss the behavior of System (4.3), we now partition the possible parameters into four sets:

$$A_0 : 1 < R_{(1)}^* \text{ and } 1 < R_{(2)}^*$$

$$A_1 : R_{(1)}^* < R_{(2)}^* < 1 \text{ or } R_{(1)}^* < 1 < R_{(2)}^*$$

$$A_2 : \mu_2^{-1}(m_2(P_{(1)}^*) + 1) < R_{(1)}^* < 1 \text{ or } \mu_2^{-1}(m_2(P_{(1)}^*) + 1) < 1 < R_{(1)}^*$$

$$A_3 : R_{(2)}^* < R_{(1)}^* < \mu_2^{-1}(m_2(P_{(1)}^*) + 1) \text{ and } R_{(2)}^* < R_{(1)}^* < 1.$$

The relationship between these parameter sets and the local stability of the equilibria to System (4.3) is listed in Table 4.3.

To further discuss the behavior of trajectories initiating in the interior, we now define the poison production constraint (PPC) as  $P = \frac{(\mu_1^{max} - \mu_1(R))}{1 + K} N_{(1)}^*$ . For a given value of  $R$ , a sustainable poison level cannot exceed the PPC as  $N_{(1)}^*$  is an upper bound for any possible equilibrium. It is important to note that  $N_1$ -isocline is dependent on  $R$  alone, while the  $N_2$ -isocline is dependent on both  $R$  and  $P$ . In terms of the isoclines, the equilibrium  $E_2$  can only occur on the  $N_2$ -isocline when  $P = 0$  while  $E_1$  can only occur when the  $N_1$ -isocline intersects the PPC defined above. The intersection of the  $N_1$ -isocline and  $N_2$ -isocline would be required for  $E_3$ , however from the previous analysis it is unstable (See Figs. 4.1(a), 4.1(b), and 4.1(c)).

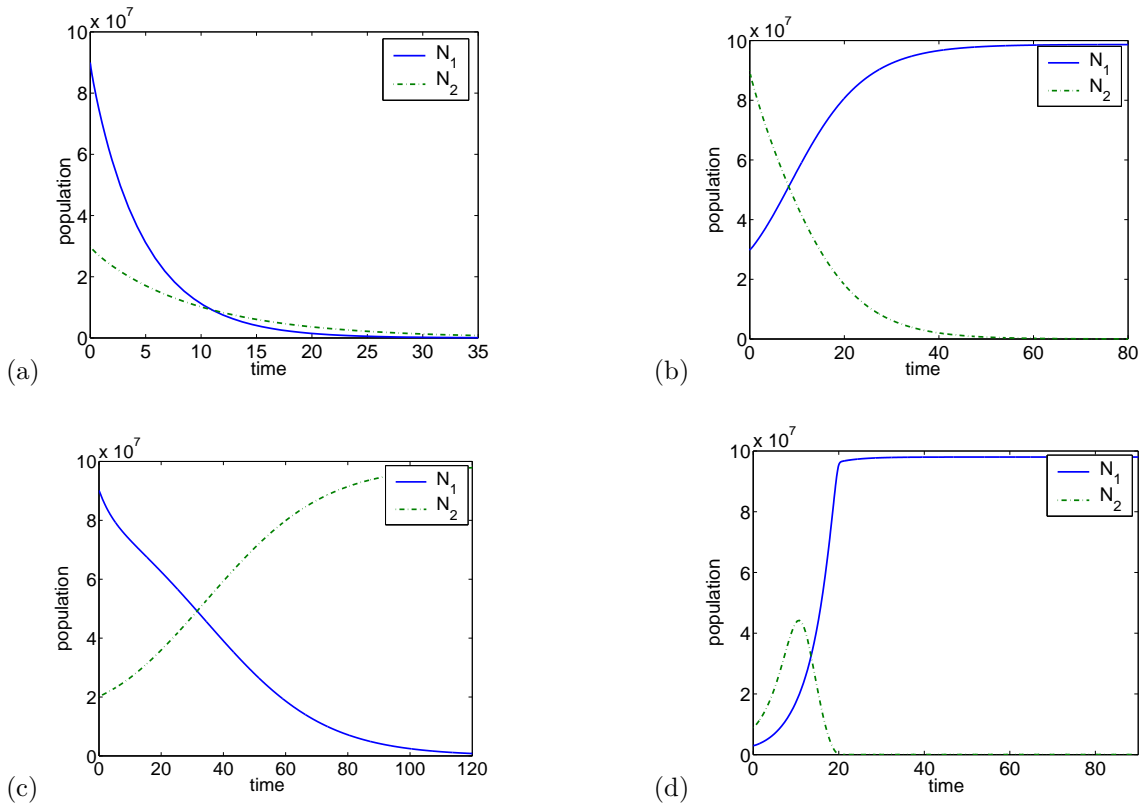


Figure 4.2. (a) Parameter range  $A_0$ , tending to  $E_0$ , (b) Parameter range  $A_1$ , tending to  $E_1$ , (c) Parameter range  $A_2$ , tending to  $E_2$ , (d) Simulation of parameter range  $A_3$  where  $N_1$  overcomes competitive disadvantage with poison production.

#### 4.4 Numerical Simulations

In this section simulations of System (4.1) are presented as a numerical prediction of the global behavior. The simulations are conducted with the parameters meeting the ranges  $A_0$ ,  $A_1$ ,  $A_2$  and  $A_3$  defined in the previous section (when appropriately scaled). The first set of simulations (Fig. 4.2) are obtained by using the adaptive **MatLab** solver `ode45` applied to System (4.1), a second set of visualizations are obtained using **Mathematica**. The following parameters were used in each simulation:  $q_1 = 10^{-9}$ ,  $q_2 = 10^{-9}$ ,  $k_1 = 0.001$ ,  $K = 0.1$ ,  $k_2 = 0.001$ ,  $D = 0.2$ .

For the simulation of the parameter scenario  $A_0$ , i.e.,  $1 < R_{(1)}^*$  and  $1 < R_{(2)}^*$ , a value of  $R_{in} = 0.001$  is used along with  $\alpha = 10^{-11}$ ,  $\mu_1^{max} = 0.3$ ,  $m_1 = 0.3$ ,  $\mu_2^{max} = 0.3$ ,  $m_2^{min} = 0.2$ . With the growth rates of  $N_1$  and  $N_2$  requiring higher levels of  $R$  than  $R_{in}$  to reach equilibrium, both species perish (See Fig. 4.2(a)).

In the remaining simulations, a value of  $R_{in} = 0.1$  is used for the concentration of the limiting nutrient supplied in the inflowing medium.

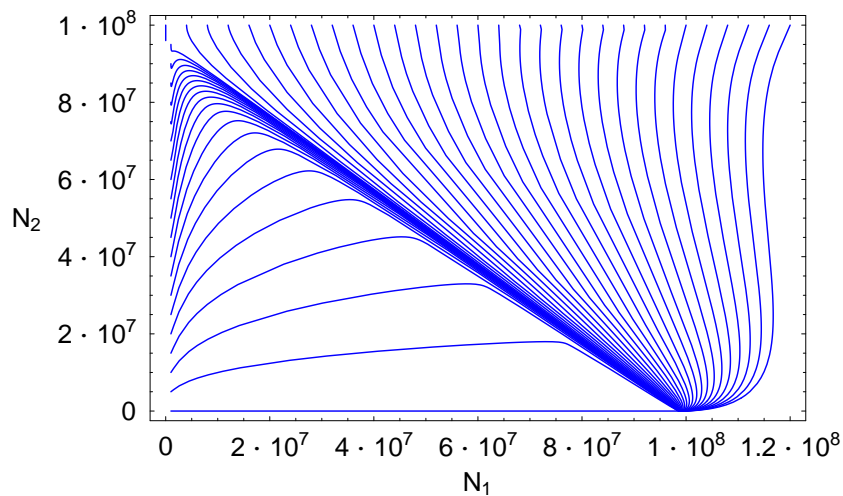


Figure 4.3.  $E_1$  is stable attractor,  $E_2$  and  $E_3$  are unstable.

In Fig. 4.2(b) the parameters  $\alpha = 10^{-11}$ ,  $\mu_1^{max} = 0.7$ ,  $m_1 = 0.2$ ,  $\mu_2^{max} = 0.5$ ,  $m_2^{min} = 0.2$  are used to meet the parameter range  $A_1$ , i.e.,  $R_{(1)}^* < R_{(2)}^* < 1$ . A visualization of the  $N_1$  and  $N_2$  components of several simulations using these parameters, each with different initial values of  $N_1$  and  $N_2$ , is displayed in Fig. 4.3. In this case, the trajectories tend to  $E_1$ , which is an expected result, since  $N_1$  would be the stronger competitor in a chemostat without nutrient recycling and poison production.

In Fig. 4.2(c), the parameters are selected as  $\alpha = 10^{-10}$ ,  $\mu_1^{max} = 0.6$ ,  $m_1 = 0.2$ ,  $\mu_2^{max} = 0.7$ ,  $m_2^{min} = 0.2$ , to meet the parameter range in  $A_2$ , i.e.,  $\mu_2^{-1}(m_2(P_{(1)}^*) + 1) <$

$R_{(1)}^* < 1$ . In this case, the trajectory approaches  $E_2$ , since now  $N_2$  would be the stronger competitor in a chemostat with poison level constant at its maximum. The  $N_1$  and  $N_2$  components of several simulations using these parameters, each with differing initial values of  $N_1$  and  $N_2$ , is displayed in Fig. 4.4.

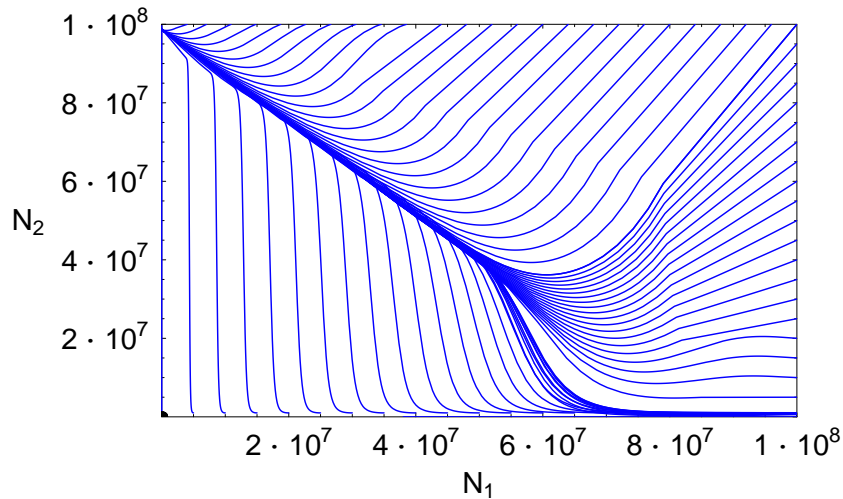


Figure 4.4.  $E_2$  is stable attractor,  $E_1$  and  $E_3$  are unstable.

Of a particular interest is the case  $A_3$ , i.e.,  $R_{(2)}^* < R_{(1)}^* < 1$  and  $R_{(1)}^* < \mu_2^{-1}(m_2(P_{(1)}^*) + 1)$  demonstrated in Fig. 4.2(d). Here, the parameters in System 4.1 are selected as  $\alpha = 10^{-7}$ ,  $\mu_1^{max} = 0.6$ ,  $m_1 = 0.2$ ,  $\mu_2^{max} = 0.7$ ,  $m_2^{min} = 0.2$ . In the standard chemostat,  $N_2$  would be a stronger competitor than  $N_1$ . However, the poison production in the model presented enables  $N_1$  to eliminate  $N_2$ , as seen in Fig. 4.2(d). It should be noted that a different choice of initial populations of  $N_1$  and  $N_2$  affect the outcome of the simulation in Fig. 4.2(d). In Fig. 4.5, several trajectories with the same parameters as in Fig. 4.2(d) are plotted together with varying initial populations. Each of the trajectories will tend to either  $E_1$  or  $E_2$  in this bistable case, resulting in exclusion of one of the species, depending on initial conditions.

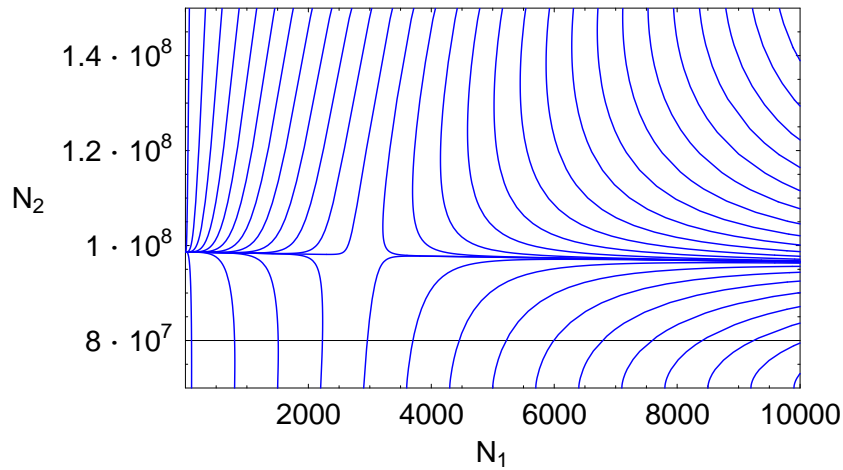


Figure 4.5.  $E_1$  and  $E_2$  are stable attractors,  $E_3$  is unstable.

#### 4.5 Discussion

The inclusion of the alleopathic dynamics into System (4.1) produces results which vary slightly from the simple chemostat theory. Four steady states were identified, but the coexistence equilibrium is feasible not in a “knife-edge” parameter restriction but in fact across a range of parameter values. However as seen in Theorem 4.3.4, the coexistence equilibrium will always be unstable with its existence conditional on the stability of the other non-trivial boundary equilibria. The numerical simulations indicate that the model is consistent with existing theory in as much as competitive exclusion holds in the competition. In the model presented, the bi-stability of the boundary equilibria  $E_1$  and  $E_2$  indicates that established populations are not susceptible to invasion by another species. This differs from the simple chemostat case in which the dominant competitor is determined by its resource requirement alone.

## CHAPTER 5

### NUTRIENT RECYCLING IN THE GRADOSTAT

#### 5.1 Introduction

In this chapter we introduce a gradostat competition model including the concept of nutrient recycling introduced in the previous chapters. Recall the gradostat is two or more chemostat devices connected in series. The focus in this chapter is on a gradostat model of two chemostat devices as described in Chapter 3. A derivation and further definition of the simple gradostat with an extension to  $n$  vessels can be found in [27]. The model here is derived from the operating diagram found in Fig. 5.1. In the series the first vessel has one external inflow, one outflow being an inflow into the second chamber, and one inflow from the second chamber. The second vessel has an additional external inflow and an external outflow. The nutrient arrives to the inflow of the first vessel at a rate  $R_{in}$  as in the chemostat case, with no additional external nutrient arriving in the second chamber. The lateral exchange between the vessels, moving both nutrient and organisms, occurs at differing rates,  $D + E$  from vessel 1 into vessel 2 and  $E$  returning from vessel 2 into vessel 1. Inside the vessels are two species of population,  $N_1$  and  $N_2$ . To track the population existing in each vessel an additional subscript will be added so that  $N_{ij}$   $i = 1, 2; j = 1, 2$  indicates the concentration of species  $i$  in vessel  $j$ . Additionally,

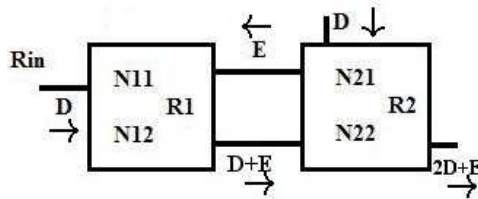


Figure 5.1. The gradostat diagram.

$R_i$  is the concentration of the nutrient in vessel  $i$ . The model including nutrient recycling takes the following form

$$\begin{aligned}
\frac{dN_{11}}{dt} &= (\mu_1(R_1) - m_1 - (D + E))N_{11} + EN_{12}, \\
\frac{dN_{21}}{dt} &= (\mu_2(R_1) - m_2 - (D + E))N_{21} + EN_{22}, \\
\frac{dN_{12}}{dt} &= (\mu_1(R_2) - m_1 - (2D + E))N_{12} + (D + E)N_{11}, \\
\frac{dN_{22}}{dt} &= (\mu_2(R_2) - m_2 - (2D + E))N_{22} + (D + E)N_{21}, \\
\frac{dR_1}{dt} &= DR_{in} + ER_2 - (D + E)R_1 - (\mu_1(R_1) - m_1)q_1N_{11} - (\mu_2(R_1) - m_2)q_2N_{21}, \\
\frac{dR_2}{dt} &= (D + E)R_1 - (E + 2D)R_2 - (\mu_1(R_2) - m_1)q_1N_{12} - (\mu_2(R_2) - m_2)q_2N_{22}.
\end{aligned} \tag{5.1}$$

To ease computation we make the following scaling changes

$$\begin{aligned}
\hat{N}_{11} &= \frac{q_1 N_{11}}{R_{in}}, & \hat{N}_{21} &= \frac{q_2 N_{21}}{R_{in}}, & \hat{N}_{12} &= \frac{q_1 N_{12}}{R_{in}}, & \hat{N}_{22} &= \frac{q_2 N_{22}}{R_{in}}, \\
\hat{R}_1 &= \frac{R_1}{R_{in}}, & \hat{R}_2 &= \frac{R_2}{R_{in}}, & \hat{t} &= Dt, & \hat{m}_1 &= \frac{m_1}{D}, \\
\hat{D} &= \frac{E}{D}, & \hat{K} &= \frac{K}{D}, & \hat{\mu}_i^{max} &= \frac{\mu_i^{max}}{D}, & \hat{k}_i &= \frac{k_i}{R_{in}}, \\
\hat{m}_2^{min} &= \frac{m_2}{D}.
\end{aligned}$$

We also define the following

$$\hat{\mu}_i(\hat{R}) = \frac{\hat{\mu}_i^{max} \hat{R}}{\hat{k}_i + \hat{R}}.$$

After the substitutions and dropping the hats, System (5.1) becomes

$$\begin{aligned}
\frac{dN_{11}}{dt} &= (\mu_1(R_1) - m_1 - (1 + D)) N_{11} + DN_{12}, \\
\frac{dN_{12}}{dt} &= (\mu_1(R_2) - m_1 - (2 + D)) N_{12} + (1 + D)N_{11}, \\
\frac{dN_{21}}{dt} &= (\mu_2(R_1) - m_2 - (1 + D)) N_{21} + DN_{22}, \\
\frac{dN_{22}}{dt} &= (\mu_2(R_2) - m_2 - (2 + D)) N_{22} + (1 + D)N_{21}, \\
\frac{dR_1}{dt} &= 1 - (1 + D)R_1 + DR_2 - (\mu_1(R_1) - m_1)N_{11} - (\mu_2(R_1) - m_2)N_{21}, \\
\frac{dR_2}{dt} &= (1 + D)R_1 - (2 + D)R_2 - (\mu_1(R_2) - m_1)N_{12} - (\mu_2(R_2) - m_2)N_{22}.
\end{aligned} \tag{5.2}$$

## 5.2 Equilibria of the System

To investigate equilibria, we reduce the order of System (5.2). First define

$$\Sigma_1 = N_{11} + N_{21} + R_1; \quad \Sigma_2 = N_{12} + N_{22} + R_2.$$

Then,

$$\Sigma_1' = 1 - (1 + D)\Sigma_1 + D\Sigma_2,$$

$$\Sigma_2' = -(2 + D)\Sigma_2 + (1 + D)\Sigma_1.$$

The solution to this differential system is given by

$$z(t) = M(t)M(0)^{-1}z(0) + \int_0^t M(t)M(s)^{-1}b ds,$$

where

$$z(t) = \begin{bmatrix} \Sigma_1 \\ \Sigma_2 \end{bmatrix}, \quad M(t) = \begin{bmatrix} e^{-t} & -\frac{D}{1+D}e^{-2(1+D)t} \\ e^{-t} & e^{-2(1+D)t} \end{bmatrix}, \quad b = \begin{bmatrix} 1 \\ 0 \end{bmatrix}.$$



The solution  $z(t)$  is such that

$$\lim_{t \rightarrow \infty} z(t) = \begin{bmatrix} \frac{2+D}{2+2D} \\ \frac{1}{2} \end{bmatrix}.$$

That is,

$$\begin{aligned} \frac{2+D}{2+2D} &= N_{11} + N_{21} + R_1, \\ \frac{1}{2} &= N_{12} + N_{22} + R_2. \end{aligned}$$

Therefore, the asymptotic behavior of the resource level  $R_1$  is dependent only on the behavior of  $N_{11}$  and  $N_{21}$ . Similarly, the behavior of  $R_2$  depends only on  $N_{12}$  and  $N_{22}$ .

Hence, the system (5.2) reduces to the following

$$\begin{aligned} \frac{dN_{11}}{dt} &= \left( \mu_1 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right) - m_1 - (1+D) \right) N_{11} + DN_{12}, \\ \frac{dN_{12}}{dt} &= \left( \mu_1 \left( \frac{1}{2} - N_{12} - N_{22} \right) - m_1 - (2+D) \right) N_{12} + (1+D)N_{11}, \\ \frac{dN_{21}}{dt} &= \left( \mu_2 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right) - m_2 - (1+D) \right) N_{21} + DN_{22}, \\ \frac{dN_{22}}{dt} &= \left( \mu_2 \left( \frac{1}{2} - N_{12} - N_{22} \right) - m_2 - (2+D) \right) N_{22} + (1+D)N_{21}. \end{aligned} \tag{5.3}$$

By inspection we can see that  $E_0 = (0, 0, 0, 0)$  will be an equilibrium for the system (5.3).

It is important to note at this time that the equations  $\frac{dN_{11}}{dt} = 0$ ,  $\frac{dN_{12}}{dt} = 0$ ,  $\frac{dN_{21}}{dt} = 0$  and  $\frac{dN_{22}}{dt} = 0$  lead to the following conditions on the equilibria of the system (5.3)

$$N_{11} = 0 \iff N_{12} = 0,$$

$$N_{21} = 0 \iff N_{22} = 0.$$

We now consider the case  $N_{21} = N_{22} = 0$ . Here system (5.3) becomes

$$\begin{aligned} \frac{dN_{11}}{dt} &= \left( \mu_1 \left( \frac{2+D}{2+2D} - N_{11} \right) - m_1 - (1+D) \right) N_{11} + DN_{12}, \\ \frac{dN_{12}}{dt} &= \left( \mu_1 \left( \frac{1}{2} - N_{12} \right) - m_1 - (2+D) \right) N_{12} + (1+D)N_{11}. \end{aligned} \tag{5.4}$$

Equation (5.4) leads us to see that  $N_{11}$  and  $N_{12}$  will be at equilibrium when the following equation is satisfied

$$\left( \mu_1 \left( \frac{2+D}{2+2D} - N_{11} \right) - m_1 - (1+D) \right) \left( \mu_1 \left( \frac{1}{2} - N_{12} \right) - m_1 - (2+D) \right) = D(1+D). \quad (5.5)$$

**Theorem 5.2.1.** *If  $N_{11}^{*(1)}$  and  $N_{12}^{*(1)}$  satisfy (5.5), then these values are unique.*

*Proof.* Suppose that  $N_{11}^{*(1)}, N_{12}^{*(1)}$  and  $\tilde{N}_{11}^{*(1)}, \tilde{N}_{12}^{*(1)}$  satisfy (5.5) and without loss of generality assume  $N_{11}^{*(1)} \leq \tilde{N}_{11}^{*(1)}$ . Then since  $\mu_1$  is a decreasing function with respect to  $N_{11}$ , we have:

$$\left( \mu_1 \left( \frac{2+D}{2+2D} - \tilde{N}_{11}^{*(1)} \right) - m_1 - (1+D) \right) < \left( \mu_1 \left( \frac{2+D}{2+2D} - N_{11}^{*(1)} \right) - m_1 - (1+D) \right).$$

If  $\frac{dN_{11}}{dt} = 0$  in (5.4), we must have

$$\begin{aligned} N_{12}^{*(1)} &= \frac{\left( \mu_1 \left( \frac{2+D}{2+2D} - N_{11}^{*(1)} \right) - m_1 - (1+D) \right)}{-D} N_{11}^{*(1)}, \\ &\leq \frac{\left( \mu_1 \left( \frac{2+D}{2+2D} - \tilde{N}_{11}^{*(1)} \right) - m_1 - (1+D) \right)}{-D} \tilde{N}_{11}^{*(1)}, \\ &= \tilde{N}_{12}^{*(1)}. \end{aligned}$$

Hence,  $N_{11}^{*(1)} \leq \tilde{N}_{11}^{*(1)}$  and  $N_{12}^{*(1)} \leq \tilde{N}_{12}^{*(1)}$ . However, in order to satisfy (5.5) it must be that  $N_{11}^{*(1)} = \tilde{N}_{11}^{*(1)}$  and  $N_{12}^{*(1)} = \tilde{N}_{12}^{*(1)}$ .  $\square$

Thus we have an equilibrium  $E_1 = (N_{11}^{*(1)}, N_{12}^{*(1)}, 0, 0)$  which exists when there exists  $N_{11}^{*(1)}$  and  $N_{12}^{*(1)}$  that satisfy (5.5). By inspection we can see that one solution to (5.5) is

$$N_{11}^{*(1)} = \frac{2+D}{2+2D} - \mu_1^{-1}(m_1 + 1), N_{12}^{*(1)} = \frac{1}{2} - \mu_1^{-1}(m_1 + 1).$$

Hence being the unique solution we have determined  $E_1$ . We now turn to the case  $N_{11} = N_{12} = 0$ . Here system (5.1) reduces to

$$\begin{aligned} \frac{dN_{21}}{dt} &= \left( \mu_2 \left( \frac{2+D}{2+2D} - N_{21} \right) - m_2 - (1+D) \right) N_{21} + DN_{22}, \\ \frac{dN_{22}}{dt} &= \left( \mu_2 \left( \frac{1}{2} - N_{22} \right) - m_2 - (2+D) \right) N_{22} + (1+D)N_{21}. \end{aligned} \quad (5.6)$$

Similar to the previous case, at equilibrium the following equation must be satisfied

$$\left( \mu_2 \left( \frac{2+D}{2+2D} - N_{21} \right) - m_2 - (1+D) \right) \left( \mu_2 \left( \frac{1}{2} - N_{22} \right) - m_2 - (2+D) \right) = D(1+D). \quad (5.7)$$

**Theorem 5.2.2.** *If  $N_{21}^{*(2)}$  and  $N_{22}^{*(2)}$  satisfy (5.7), then these values are unique.*

The proof of Theorem 5.2.2 is omitted as it is much the same as Thm 5.2.1. We therefore have an equilibrium  $E_2 = (0, 0, N_{21}^{*(2)}, N_{22}^{*(2)})$  of system (5.3) which exists when  $N_{21}^{*(2)}$  and  $N_{22}^{*(2)}$  satisfying (5.7) exist. By inspection we can see that one solution to (5.7) is

$$N_{21}^{*(2)} = \frac{2+D}{2+2D} - \mu_2^{-1}(m_2+1), N_{22}^{*(2)} = \frac{1}{2} - \mu_2^{-1}(m_2+1).$$

Hence being the unique solution we have determined  $E_2$ . Next, we investigate the case where each of  $N_{11}$ ,  $N_{12}$ ,  $N_{21}$  and  $N_{22}$  is nonzero. Here, we must satisfy both the equations

$$\left( \mu_1 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right) - m_1 - (1+D) \right) \left( \mu_1 \left( \frac{1}{2} - N_{12} - N_{22} \right) - m_1 - (2+D) \right) = D(1+D), \quad (5.8)$$

and

$$\left( \mu_2 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right) - m_2 - (1+D) \right) \left( \mu_2 \left( \frac{1}{2} - N_{12} - N_{22} \right) - m_2 - (2+D) \right) = D(1+D). \quad (5.9)$$

Thus we have an equilibrium  $E_3 = (N_{11}^*, N_{12}^*, N_{21}^*, N_{22}^*)$  existing when  $N_{11}^*$ ,  $N_{12}^*$ ,  $N_{21}^*$  and  $N_{22}^*$  satisfy (5.8) and (5.9). Further, the satisfaction of these equations implies that both  $E_1$  and  $E_2$  exist and  $E_3$  satisfies the uniqueness arguments for solutions to equations (5.5) and (5.7). Table 5.1 summarizes the equilibria for System (5.3) and the conditions for existence of such equilibria.

Table 5.1. Existence Conditions for the Equilibria of System (5.3)

	Existence equation to be satisfied
$E_0$	Always
$E_1$	$\left(\mu_1 \left(\frac{2+D}{2+2D} - N_{11}\right) - m_1 - (1+D)\right) \left(\mu_1 \left(\frac{1}{2} - N_{12}\right) - m_1 - (2+D)\right) = D(1+D)$
$E_2$	$\left(\mu_2 \left(\frac{2+D}{2+2D} - N_{21}\right) - m_2 - (1+D)\right) \left(\mu_2 \left(\frac{1}{2} - N_{22}\right) - m_2 - (2+D)\right) = D(1+D)$
$E_3$	$\left(\mu_1 \left(\frac{2+D}{2+2D} - N_{11} - N_{21}\right) - m_1 - (1+D)\right) \left(\mu_1 \left(\frac{1}{2} - N_{12} - N_{22}\right) - m_1 - (2+D)\right) = D(1+D)$ $\left(\mu_2 \left(\frac{2+D}{2+2D} - N_{11} - N_{21}\right) - m_2 - (1+D)\right) \left(\mu_2 \left(\frac{1}{2} - N_{12} - N_{22}\right) - m_2 - (2+D)\right) = D(1+D)$

### 5.3 Local Stability Analysis

With the equilibria found we proceed to find conditions for the local stability for each. The Jacobian of the system (5.3) is

$$J(N_{11}, N_{12}, N_{21}, N_{22}) = \begin{pmatrix} \alpha_1 - \beta_1 - \gamma_1 & D & -\beta_7 & 0 \\ (1+D) & \alpha_2 - \beta_2 - \gamma_2 & 0 & -\beta_8 \\ -\beta_5 & 0 & \alpha_3 - \beta_3 - \gamma_3 & D \\ 0 & -\beta_6 & (1+D) & \alpha_4 - \beta_4 - \gamma_4 \end{pmatrix}, \quad (5.10)$$

where

$$\begin{aligned}
\alpha_1 &= \mu_1 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right), & \alpha_2 &= \mu_1 \left( \frac{1}{2} - N_{12} - N_{22} \right), \\
\alpha_3 &= \mu_2 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right), & \alpha_4 &= \mu_2 \left( \frac{1}{2} - N_{12} - N_{22} \right), \\
\beta_1 &= -\frac{d\mu_1}{dN_{11}} N_{11}, & \beta_2 &= -\frac{d\mu_1}{dN_{12}} N_{12}, \\
\beta_3 &= -\frac{d\mu_2}{dN_{21}} N_{21}, & \beta_4 &= -\frac{d\mu_2}{dN_{22}} N_{22}, \\
\beta_5 &= -\frac{d\mu_1}{dN_{11}} N_{21}, & \beta_6 &= -\frac{d\mu_2}{dN_{12}} N_{22}, \\
\beta_7 &= -\frac{d\mu_1}{dN_{21}} N_{11}, & \beta_8 &= -\frac{d\mu_1}{dN_{22}} N_{12}, \\
\gamma_1 &= m_1 + (1 + D), & \gamma_2 &= m_1 + (2 + D), \\
\gamma_3 &= m_2 + (1 + D), & \gamma_4 &= m_2 + (2 + D).
\end{aligned}$$

One should note that each of  $\alpha_i$ ,  $\gamma_i$  and  $\beta_j$  is positive for  $i = 1, \dots, 4$  and  $j = 1, \dots, 8$ . Also, in the case  $N_{11} = N_{12} = 0$  we have  $\beta_1 = \beta_2 = \beta_7 = \beta_8 = 0$  and in the case  $N_{21} = N_{22} = 0$  we have  $\beta_3 = \beta_4 = \beta_5 = \beta_6 = 0$ . Upon calculation, one can see that  $\beta_1 = \beta_7$ ,  $\beta_3 = \beta_5$ ,  $\beta_2 = \beta_8$  and  $\beta_4 = \beta_6$ . From  $\frac{dN_{11}}{dt}$  it is true that  $\alpha_1 - \gamma_1 < 0$  at both  $E_1$  and  $E_3$  since  $N_{11}$  and  $N_{12}$  are nonzero. Similarly,  $\alpha_2 - \gamma_2 < 0$  at  $E_1$  and  $E_3$ ,  $\alpha_3 - \gamma_3 < 0$  at  $E_2$  and  $E_3$ , and  $\alpha_4 - \gamma_4 < 0$  at  $E_2$  and  $E_3$ .

Conditions for the local stability of the equilibria are outlined in the following theorems.

**Theorem 5.3.1.** *The equilibrium  $E_0$  is locally asymptotically stable if when evaluated at  $E_0$  the following conditions hold*

1.  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$ ,
2.  $\alpha_1 - \gamma_1 + \alpha_2 - \gamma_2 < 0$ ,
3.  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) > D(1 + D)$ ,
4.  $\alpha_3 - \gamma_3 + \alpha_4 - \gamma_4 < 0$ .

*Proof.* For the equilibrium  $E_0$ , the local stability is determined by the eigenvalues of

$$J(E_0) = \begin{pmatrix} \alpha_1 - \gamma_1 & D & 0 & 0 \\ (1 + D) & \alpha_2 - \gamma_2 & 0 & 0 \\ 0 & 0 & \alpha_3 - \gamma_3 & D \\ 0 & 0 & (1 + D) & \alpha_4 - \gamma_4 \end{pmatrix}$$

Here the eigenvalues are

$$\lambda_{1,2} = \frac{(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2) \pm \sqrt{((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D)}}{2},$$

$$\lambda_{3,4} = \frac{(\alpha_3 - \gamma_3) + (\alpha_4 - \gamma_4) \pm \sqrt{((\alpha_3 - \gamma_3) - (\alpha_4 - \gamma_4))^2 + 4D(1 + D)}}{2}.$$

Inspection of the radicals above leads us to see that  $J(E_0)$  has real eigenvalues. We now determine conditions which will ensure these eigenvalues are negative. Consider

$$((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D) = (\alpha_1 - \gamma_1)^2 + (\alpha_2 - \gamma_2)^2 - 2(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) + 4D(1 + D).$$

If we assume  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$ , we have

$$((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D) < ((\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2))^2.$$

Therefore if  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$ ,  $\lambda_1$  and  $\lambda_2$  have the same sign which is determined by the expression  $(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2)$ . Hence to ensure negative eigenvalues we must have  $(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2) < 0$ . Now, when  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$  it must be the case that  $(\alpha_1 - \gamma_1)$  and  $(\alpha_2 - \gamma_2)$  have the same sign. Therefore, to ensure negative eigenvalues we must have  $(\alpha_1 - \gamma_1) < 0$  and  $(\alpha_2 - \gamma_2) < 0$ .

Furthermore if we assume  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) < D(1 + D)$ , then it follows that

$$((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D) > ((\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2))^2,$$

which will lead to  $\lambda_1$  and  $\lambda_2$  having opposite signs. Hence, if  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) < D(1 + D)$  then  $E_0$  is not locally stable. Using similar analysis, we can find that if  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) > D(1 + D)$  and  $\alpha_3 - \gamma_3 < 0$  and  $\alpha_4 - \gamma_4 < 0$  then  $\lambda_3$  and  $\lambda_4$  will both be negative. In addition, if  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) < D(1 + D)$  then  $\lambda_3$  and  $\lambda_4$  will have opposite signs.  $\square$

**Theorem 5.3.2.** *The equilibrium  $E_1$  is locally asymptotically stable if when evaluated at  $E_1$  the following conditions hold*

1.  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) > D(1 + D)$ ,
2.  $\alpha_3 - \gamma_3 + \alpha_4 - \gamma_4 < 0$ .

*Proof.* For the equilibrium  $E_1$ , the local stability is determined by the eigenvalues of

$$J(E_1) = \begin{pmatrix} \alpha_1 - \beta_1 - \gamma_1 & D & -\beta_1 & 0 \\ (1 + D) & \alpha_2 - \beta_2 - \gamma_2 & 0 & -\beta_2 \\ 0 & 0 & \alpha_3 - \gamma_3 & D \\ 0 & 0 & (1 + D) & \alpha_4 - \gamma_4 \end{pmatrix}.$$

Here the eigenvalues are

$$\lambda_{1,2} = \frac{(\alpha_1 - \beta_1 - \gamma_1) + (\alpha_2 - \beta_2 - \gamma_2) \pm \sqrt{((\alpha_1 - \beta_1 - \gamma_1) - (\alpha_2 - \beta_2 - \gamma_2))^2 + 4D(1 + D)}}{2},$$

$$\lambda_{3,4} = \frac{(\alpha_3 - \gamma_3) + (\alpha_4 - \gamma_4) \pm \sqrt{((\alpha_3 - \gamma_3) - (\alpha_4 - \gamma_4))^2 + 4D(1 + D)}}{2}.$$

Using similar reasoning to that of the  $E_0$  case, if  $(\alpha_1 - \beta_1 - \gamma_1)(\alpha_2 - \beta_2 - \gamma_2) > D(1 + D)$  then  $\lambda_1$  and  $\lambda_2$  have the same sign determined by the sign of  $(\alpha_1 - \beta_1 - \gamma_1) + (\alpha_2 - \beta_2 - \gamma_2)$ . Each of  $(\alpha_1 - \beta_1 - \gamma_1) < 0$ ,  $(\alpha_2 - \beta_2 - \gamma_2) < 0$  and  $(\alpha_1 - \beta_1 - \gamma_1)(\alpha_2 - \beta_2 - \gamma_2) > D(1 + D)$  hold since  $(\alpha_1 - \gamma_1) < 0$ ,  $(\alpha_2 - \gamma_2) < 0$  and (5.8) is equivalent to  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) = D(1 + D)$  when evaluated at  $E_1$ . Therefore  $\lambda_1$  and  $\lambda_2$  will be negative. Furthermore, if  $(\alpha_1 - \beta_1 - \gamma_1)(\alpha_2 - \beta_2 - \gamma_2) < D(1 + D)$  then  $\lambda_1$  and  $\lambda_2$  have opposite signs. Similarly, if  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) > D(1 + D)$ ,  $\alpha_3 - \gamma_3 < 0$ ,  $\alpha_4 - \gamma_4 < 0$  then  $\lambda_3$  and  $\lambda_4$  will both be negative. Also, if  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) < D(1 + D)$  then  $\lambda_3$  and  $\lambda_4$  will have opposite signs.  $\square$

**Theorem 5.3.3.** *The equilibrium  $E_2$  is locally asymptotically stable if when evaluated at  $E_2$  the following conditions hold*

1.  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$ ,
2.  $\alpha_1 - \gamma_1 + \alpha_2 - \gamma_2 < 0$ ,

*Proof.* For the equilibrium  $E_2$ , the local stability is determined by the eigenvalues of

$$J(E_2) = \begin{pmatrix} \alpha_1 - \gamma_1 & D & 0 & 0 \\ (1 + D) & \alpha_2 - \gamma_2 & 0 & 0 \\ -\beta_3 & 0 & \alpha_3 - \beta_3 - \gamma_3 & D \\ 0 & -\beta_4 & (1 + D) & \alpha_4 - \beta_4 - \gamma_4 \end{pmatrix}.$$

Here the eigenvalues are

$$\lambda_{1,2} = \frac{(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2) \pm \sqrt{((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D)}}{2},$$

$$\lambda_{3,4} = \frac{(\alpha_3 - \beta_3 - \gamma_3) + (\alpha_4 - \beta_4 - \gamma_4) \pm \sqrt{((\alpha_3 - \beta_3 - \gamma_3) - (\alpha_4 - \beta_4 - \gamma_4))^2 + 4D(1 + D)}}{2}.$$

As in the previous cases, if  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$  then  $\lambda_1$  and  $\lambda_2$  have the same sign determined by the sign of  $(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2)$ . Hence if  $(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2) < 0$  then  $\lambda_1$  and  $\lambda_2$  will be negative. Furthermore, if  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) < D(1 + D)$  then  $\lambda_1$  and  $\lambda_2$  have opposite signs. Similarly, if  $(\alpha_3 - \beta_3 - \gamma_3)(\alpha_4 - \beta_4 - \gamma_4) > D(1 + D)$  and  $\alpha_3 - \beta_3 - \gamma_3 + \alpha_4 - \beta_4 - \gamma_4 < 0$  then  $\lambda_3$  and  $\lambda_4$  will both be negative. This will always be the case as  $(\alpha_3 - \beta_3)(\alpha_4 - \beta_4) = D(1 + D)$ ,  $\alpha_3 - \beta_3 < 0$  and  $\alpha_4 - \beta_4 < 0$ .  $\square$

**Theorem 5.3.4.** *The equilibrium  $E_3$  is locally asymptotically stable when it exists.*

*Proof.* For the equilibrium  $E_3$ , the local stability is determined by the eigenvalues of

$$J(E_3) = \begin{pmatrix} \alpha_1 - \beta_1 - \gamma_1 & D & -\beta_1 & 0 \\ (1 + D) & \alpha_2 - \beta_2 - \gamma_2 & 0 & -\beta_2 \\ -\beta_3 & 0 & \alpha_3 - \beta_3 - \gamma_3 & D \\ 0 & -\beta_4 & (1 + D) & \alpha_4 - \beta_4 - \gamma_4 \end{pmatrix}.$$

Applying Theorem B.0.2 found in Appendix B, it is sufficient to calculate the principal minors  $d_1, d_2, d_3, d_4$  of the matrix

$$J(\hat{E}_3) = \begin{pmatrix} \alpha_1 - \beta_1 - \gamma_1 & D & \beta_1 & 0 \\ (1 + D) & \alpha_2 - \beta_2 - \gamma_2 & 0 & \beta_2 \\ \beta_3 & 0 & \alpha_3 - \beta_3 - \gamma_3 & D \\ 0 & \beta_4 & (1 + D) & \alpha_4 - \beta_4 - \gamma_4 \end{pmatrix}.$$



It is then necessary and sufficient for  $d_1 < 0$ ,  $d_2 > 0$ ,  $d_3 < 0$ ,  $d_4 > 0$  to ensure all eigenvalues have negative real part. Here,  $d_1 = \alpha_1 - \beta_1 - \gamma_1$ . It is true that  $d_1 < 0$  since  $\alpha_1 - \gamma_1 < 0$  at any equilibrium with nonzero  $N_{11}$  and  $N_{12}$  values. Similarly, the coexistence equilibrium implies the inequality  $(\alpha_i - \gamma_i) < 0$  holds for  $i = 2, 3, 4$ . Next,  $d_2 = (\alpha_1 - \beta_1 - \gamma_1)(\alpha_2 - \beta_2 - \gamma_2) - D(1 + D)$ . We note that each of  $(\alpha_1 - \gamma_1)$  and  $(\alpha_2 - \gamma_2)$  is negative and  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) = D(1 + D)$  from (5.8). Hence  $(\alpha_1 - \beta_1 - \gamma_1)(\alpha_2 - \beta_2 - \gamma_2) > D(1 + D)$  and therefore  $d_2 > 0$ . For the next principal minor,  $d_3$  reduces to

$$d_3 = -\beta_1\beta_3(\alpha_2 - \beta_2 - \gamma_2) + (\alpha_3 - \beta_3 - \gamma_3)(\alpha_2 - \beta_2 - \gamma_2)(\alpha_1 - \beta_1 - \gamma_1) \\ - (\alpha_3 - \beta_3 - \gamma_3)D(1 + D).$$

Distributing and canceling  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) = D(1 + D)$  leaves us with

$$d_3 = (\alpha_3 - \gamma_3)(-\beta_1(\alpha_2 - \beta_2 - \gamma_2)) + (\alpha_3 - \beta_3 - \gamma_3)(-\beta_2(\alpha_1 - \gamma_1)).$$

Hence since each term is negative,  $d_3 < 0$ . Finally, the calculation of  $d_4$  is

$$d_4 = (\alpha_1 - \beta_1 - \gamma_1)(\alpha_2 - \beta_2 - \gamma_2)(\alpha_3 - \beta_3 - \gamma_3)(\alpha_4 - \beta_4 - \gamma_4) \\ + \beta_1\beta_2\beta_3\beta_4 - \beta_1\beta_3(\alpha_2 - \beta_2 - \gamma_2)(\alpha_4 - \beta_4 - \gamma_4) - (D + (1 + D)^2) \\ - \beta_2\beta_4(\alpha_3 - \beta_3 - \gamma_3)(\alpha_1 - \beta_1 - \gamma_1).$$

Again distribution and cancellation lead to

$$d_4 = -\beta_3(\alpha_4 - \gamma_4)D(1 + D) - \beta_4(\alpha_3 - \gamma_3)D(1 + D) + \beta_3\beta_4D(1 + D) \\ - \beta_1(\alpha_2 - \gamma_2)D(1 + D) + \beta_1\beta_4(\alpha_2 - \gamma_2)(\alpha_3 - \gamma_3) - \beta_2(\alpha_1 - \gamma_1)D(1 + D) \\ \beta_2\beta_3(\alpha_1 - \gamma_1)(\alpha_4 - \gamma_4) + \beta_1\beta_2D(1 + D).$$

Each term is positive and hence  $d_4 > 0$ . Therefore, all eigenvalues of the matrix  $J(E_3)$  are negative when the equilibrium  $E_3$  exists.  $\square$

An important relationship between the existence of the equilibrium  $E_3$  and the stability conditions for  $E_1$  and  $E_2$  can now be seen. The existence conditions for equilibrium

$E_3$  require satisfying both (5.8) and (5.9). Hence the existence of  $E_3$  requires violation of both condition 1 of Theorem (5.3.2) and condition 1 of Theorem (5.3.3). That is, it is necessary for both  $E_1$  and  $E_2$  to be unstable for  $E_3$  to exist.

#### 5.4 Numerical Simulations

In this section simulations of System (5.1) are presented as a numerical verification of the local results for  $E_0$ ,  $E_1$  and  $E_2$  above. The simulations are conducted with the parameters meeting the ranges defined in the previous section (when appropriately scaled). The simulations are obtained by using the adaptive **MatLab** solver `ode45` applied to System (5.1). The following parameters were used in each simulation:  $q_1 = 10^{-9}$ ,  $q_2 = 10^{-9}$ ,  $D = 0.2$ ,  $E = 0.2$ .

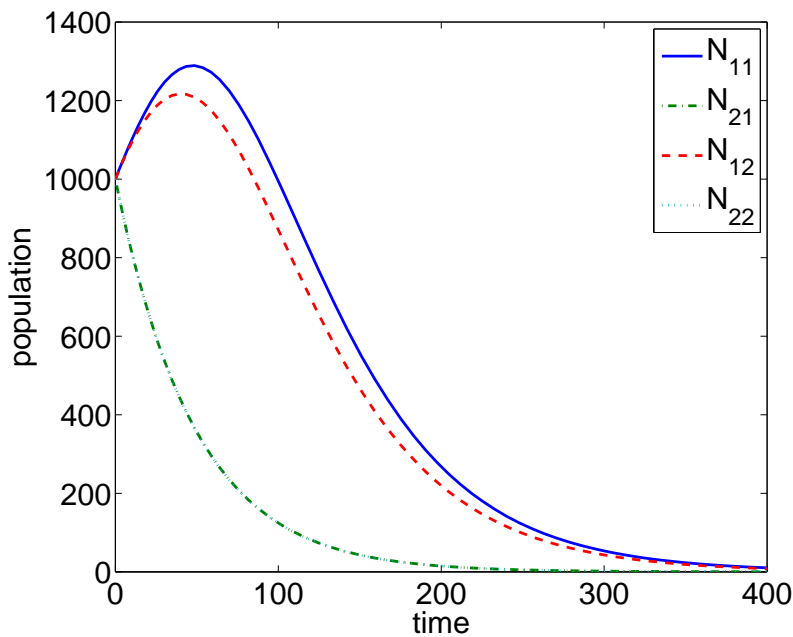


Figure 5.2.  $E_0$  locally stable, both species perish.

The simulation in Fig (5.2) displays the range corresponding to Theorem (5.3.1). The parameters used here are:  $R_{in} = 0.01, \mu_1^{max} = 0.1, \mu_2^{max} = 0.2, m_1 = 0.01, m_2^{min} = 0.01, k_1 = 0.03, k_2 = 0.03$ . The available nutrients are insufficient for either population to reach equilibrium. Both populations perish in the first vessel, which in turn will eliminate the populations in the second vessel.

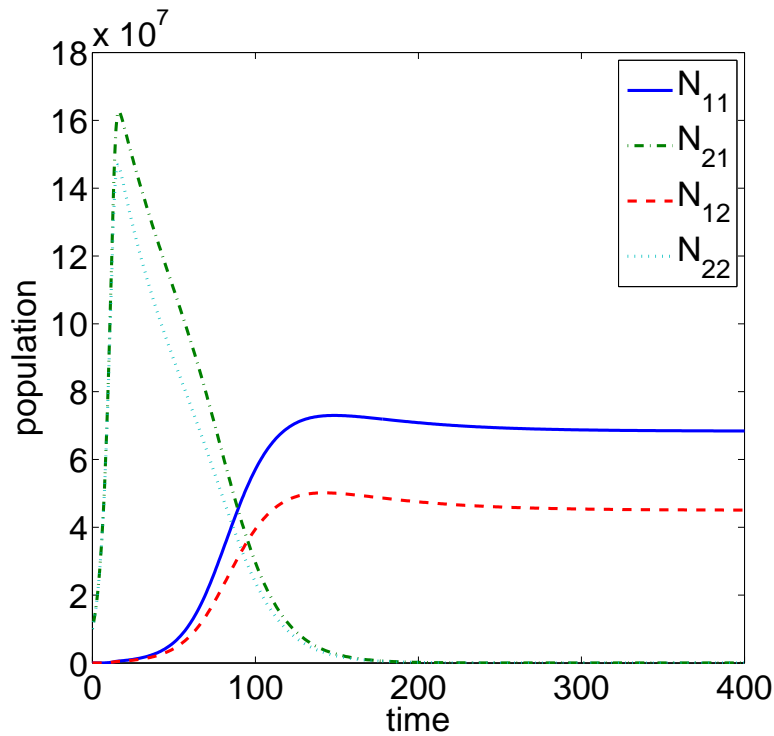


Figure 5.3.  $E_1$  locally stable, Species 1 persists.

In Fig (5.3) presents a simulation matching the conditions of Theorem (5.3.2). Here the parameters used are:  $R_{in} = 0.1, \mu_1^{max} = 0.7, \mu_2^{max} = 0.4, m_1 = 0.01, m_2^{min} = 0.01, k_1 = 0.03, k_2 = 0.001$ . Despite the initial surge of the species  $N_2$ , the equilibrium  $E_1$  is attractive. The species 1 is a superior competitor and eliminates the second species from both vessels. Also seen in Fig (5.3) is  $N_{11} \geq N_{12}$  as equilibrium is approached.

Since all nutrient arriving in vessel 2 must first pass through vessel 1, it is expected for the first vessel to have a larger population.

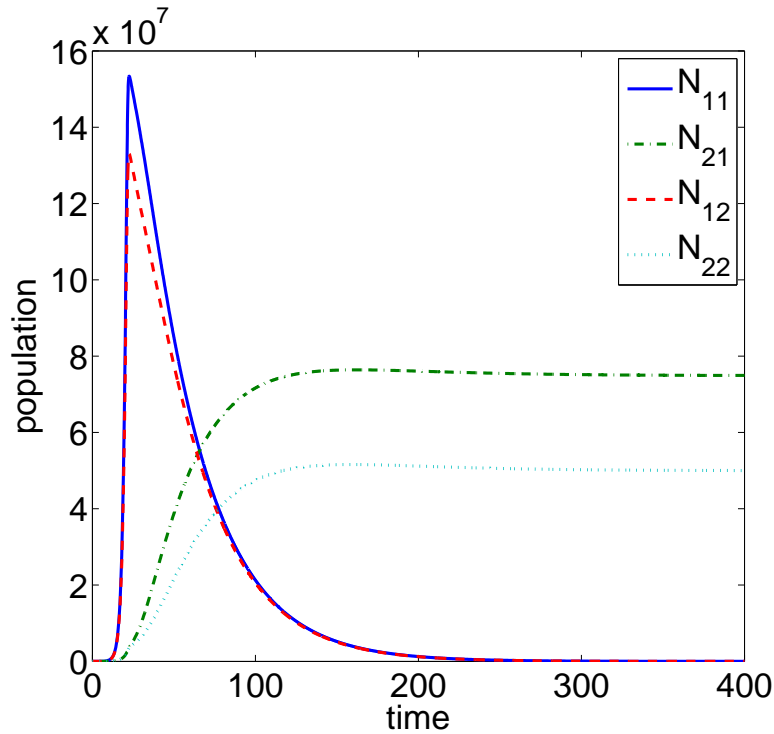


Figure 5.4.  $E_2$  locally stable, Species 2 persists.

In Fig (5.4) presents a simulation matching the conditions of Theorem (5.3.3). Here the parameters used are:  $R_{in} = 0.1, \mu_1^{max} = 0.7, \mu_2^{max} = 0.4, m_1 = 0.1, m_2^{min} = 0.1, k_1 = 0.03, k_2 = 0.03$ . Despite the initial surge of the species  $N_1$ , the equilibrium  $E_2$  is attractive. Here the second species is able to eliminate the first species in both vessels.

## 5.5 Discussion

Four steady states were found for the model defined by System (5.1). Most interesting was the coexistence equilibrium with a stability condition which was absent from the chemostat models presented in previous chapters. Interesting parameters in the

model are the transfer rates  $D$  and  $E$ . If the value of  $E$  is taken too small the gradostat essentially becomes a chemostat in the first vessel [29]. Hence competitive exclusion will hold unless  $E$  is sufficiently large. With appropriate transfer rates, coexistence of the populations is possible in the model. Additional investigation is necessary to determine which conditions for the local stability are in fact global results. Global results for the standard gradostat stem from so called  $K$ -monotone system arguments. In the analysis, the monotonicity of the system stems from the cooperative or competitive nature of the dynamics. The inclusion of nutrient recycling eliminates these methods from consideration, as the competing species do not simply harvest the nutrient but in fact can themselves increase the nutrient [30]. Local stability conditions for each equilibrium were found, along with the result that coexistence requires instability of the equilibria  $E_1$  and  $E_2$ . Numerical simulations with attractiveness of  $E_0$ ,  $E_1$  and  $E_2$  were presented. Although we have shown the theoretical existence of the equilibrium  $E_3$ , no parameter set has yet been found which demonstrates this equilibrium.

## CHAPTER 6

### NUTRIENT RECYCLING AND ALLELOPATHY IN THE GRADOSTAT

#### 6.1 Introduction

In this chapter the study of allelopathy from Chapter 4 is combined with the nutrient recycling gradostat presented in Chapter 5. As in the nutrient recycling gradostat, the latest model contains two populations in competition for a common resource. The competitor  $N_1$  produces a poison which increases the mortality of  $N_2$ . To track the population existing in each vessel an additional subscript will be added so that  $N_{ij}$   $i = 1, 2; j = 1, 2$  indicates the concentration of species  $i$  in vessel  $j$ . The toxicity is assumed to behave as in Chapter 4, that is it will increase as nutrients become limited. In the same way that organisms and nutrient can move between the vessels, poison concentration also moves from vessel 1 into vessel 2 at rate  $D + E$  and from vessel 2 into vessel 1 as rate  $D$ .

#### 6.2 The Gradostat Model of Nutrient Recycling and Allelopathy

To model the poison concentration in each vessel two variables  $P_1$  and  $P_2$  are appended to the model described in System (5.1) representing the concentration of poison

in vessel 1 and 2 respectively. Including the alleopathic terms into the gradostat model results in the system

$$\begin{aligned}
\frac{dN_{11}}{dt} &= (\mu_1(R_1) - m_1 - (D + E)) N_{11} + EN_{12}, \\
\frac{dN_{12}}{dt} &= (\mu_1(R_2) - m_1 - (2D + E)) N_{12} + (D + E)N_{11}, \\
\frac{dN_{21}}{dt} &= (\mu_2(R_1) - m_2(P_1) - (D + E)) N_{21} + EN_{22}, \\
\frac{dN_{22}}{dt} &= (\mu_2(R_2) - m_2(P_2) - (2D + E)) N_{22} + (D + E)N_{21}, \\
\frac{dR_1}{dt} &= DR_{in} - (D + E)R_1 + ER_2 - (\mu_1(R_1) - m_1)q_1N_{11} - (\mu_2(R_1) - m_2(P_1))q_2N_{21}, \\
\frac{dR_2}{dt} &= (D + E)R_1 - (2D + E)R_2 - (\mu_1(R_2) - m_1)q_1N_{12} - (\mu_2(R_2) - m_2(P_2))q_2N_{22}, \\
\frac{dP_1}{dt} &= \alpha(\mu_1^{max} - \mu_1(R_1)) N_{11} - (D + E + K) P_1 + EP_2, \\
\frac{dP_2}{dt} &= \alpha(\mu_1^{max} - \mu_1(R_2)) N_{12} + (D + E)P_1 - (2D + E + K) P_2.
\end{aligned} \tag{6.1}$$

The effects of this poison are incorporated into the mortality rate  $m_2$  for the poison susceptible species. The population of susceptible species in the first vessel,  $N_{12}$ , now decreases at rate  $m_2(P_1)$ . The susceptible species in the second vessel,  $N_{22}$ , decreases at rate  $m_2(P_2)$ . As in the chemostat case the poison is produced at rate  $\alpha(\mu_1^{max} - \mu_1(R_i))N_{1i}$  in vessels  $i = 1, 2$ . To ease computation we make the following scaling changes

$$\begin{aligned}
\hat{N}_{11} &= \frac{q_1 N_{11}}{R_{in}}, & \hat{N}_{21} &= \frac{q_2 N_{21}}{R_{in}}, & \hat{N}_{12} &= \frac{q_1 N_{12}}{R_{in}}, & \hat{N}_{22} &= \frac{q_2 N_{22}}{R_{in}}, \\
\hat{R}_1 &= \frac{R_1}{R_{in}}, & \hat{R}_2 &= \frac{R_2}{R_{in}}, & \hat{P}_1 &= \frac{q_1 P_1}{\alpha R_{in}}, & \hat{P}_2 &= \frac{q_1 P_2}{\alpha R_{in}}, \\
\hat{t} &= Dt, & \hat{m}_1 &= \frac{m_1}{D}, & \hat{D} &= \frac{E}{D}, & \hat{K} &= \frac{K}{D}, \\
\hat{\mu}_i^{max} &= \frac{\mu_i^{max}}{D}, & \hat{k}_i &= \frac{k_i}{R_{in}}, & \hat{m}_2^{min} &= \frac{m_2^{min}}{D}.
\end{aligned}$$

We also define the following scaled functions

$$\hat{\mu}_i(\hat{R}) = \frac{\hat{\mu}_i^{max} \hat{R}}{\hat{k}_i + \hat{R}}, \quad \hat{m}_2(\hat{P}) = \frac{\hat{\mu}_2^{max} \alpha}{2\hat{k}_i q_1} \hat{P} - \hat{m}_2^{min}.$$

After the substitutions and dropping the hats, System (6.1) becomes

$$\begin{aligned} \frac{dN_{11}}{dt} &= (\mu_1(R_1) - m_1 - (1 + D)) N_{11} + DN_{12}, \\ \frac{dN_{12}}{dt} &= (\mu_1(R_2) - m_1 - (2 + D)) N_{12} + (1 + D)N_{11}, \\ \frac{dN_{21}}{dt} &= (\mu_2(R_1) - m_2(P_1) - (1 + D)) N_{21} + DN_{22}, \\ \frac{dN_{22}}{dt} &= (\mu_2(R_2) - m_2(P_2) - (2 + D)) N_{22} + (1 + D)N_{21}, \\ \frac{dR_1}{dt} &= 1 - (1 + D)R_1 + DR_2 - (\mu_1(R_1) - m_1)N_{11} - (\mu_2(R_1) - m_2(P_1))N_{21}, \\ \frac{dR_2}{dt} &= (1 + D)R_1 - (2 + D)R_2 - (\mu_1(R_2) - m_1)N_{12} - (\mu_2(R_2) - m_2(P_2))N_{22}, \\ \frac{dP_1}{dt} &= (\mu_1^{max} - \mu_1(R_1))N_{11} - (1 + D + K) P_1 + DP_2, \\ \frac{dP_2}{dt} &= (\mu_1^{max} - \mu_1(R_2))N_{12} + (1 + D)P_1 - (2 + D + K) P_2. \end{aligned} \tag{6.2}$$

A reduction of order can be made on system (6.2) eliminating the resources from consideration in the analysis. Define

$$\Sigma_1 = N_{11} + N_{21} + R_1, \quad \Sigma_2 = N_{12} + N_{22} + R_2.$$

Then

$$\Sigma_1' = 1 - (1 + D)\Sigma_1 + D\Sigma_2,$$

$$\Sigma_2' = -(2 + D)\Sigma_2 + (1 + D)\Sigma_1.$$

The solution to this differential system is given by

$$z(t) = M(t)M(0)^{-1}z(0) + \int_0^t M(t)M(s)^{-1}b ds,$$



where

$$z(t) = \begin{bmatrix} \Sigma_1 \\ \Sigma_2 \end{bmatrix}, \quad M(t) = \begin{bmatrix} e^{-t} & -\frac{D}{1+D}e^{-2(1+D)t} \\ e^{-t} & e^{-2(1+D)t} \end{bmatrix}, \quad b = \begin{bmatrix} 1 \\ 0 \end{bmatrix}.$$

The solution  $z(t)$  satisfies

$$\lim_{t \rightarrow \infty} z(t) = \begin{bmatrix} \frac{2+D}{2+2D} \\ \frac{1}{2} \end{bmatrix}.$$

That is

$$\begin{aligned} \frac{2+D}{2+2D} &= N_{11} + N_{21} + R_1, \\ \frac{1}{2} &= N_{12} + N_{22} + R_2. \end{aligned}$$

Therefore, the asymptotic behavior of the resource level  $R_1$  is dependent only on the behavior of  $N_{11}$  and  $N_{21}$ . Similarly, the behavior of  $R_2$  depends only on  $N_{12}$  and  $N_{22}$ .

Hence, the system (6.2) reduces to

$$\begin{aligned} \frac{dN_{11}}{dt} &= \left( \mu_1 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right) - m_1 - (1+D) \right) N_{11} + DN_{12}, \\ \frac{dN_{12}}{dt} &= \left( \mu_1 \left( \frac{1}{2} - N_{12} - N_{22} \right) - m_1 - (2+D) \right) N_{12} + (1+D)N_{11}, \\ \frac{dN_{21}}{dt} &= \left( \mu_2 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right) - m_2(P_1) - (1+D) \right) N_{21} + DN_{22}, \\ \frac{dN_{22}}{dt} &= \left( \mu_2 \left( \frac{1}{2} - N_{12} - N_{22} \right) - m_2(P_2) - (2+D) \right) N_{22} + (1+D)N_{21}, \\ \frac{dP_1}{dt} &= \left( \mu_1^{max} - \mu_1 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right) \right) N_{11} - (1+D+K)P_1 + DP_2, \\ \frac{dP_2}{dt} &= \left( \mu_1^{max} - \mu_1 \left( \frac{1}{2} - N_{12} - N_{22} \right) \right) N_{12} + (1+D)P_1 - (2+D+K)P_2. \end{aligned} \tag{6.3}$$

### 6.3 Equilibria

To investigate the existence of equilibria for the system we proceed in four cases:

$N_{11} = 0$  and  $N_{21} = 0$ ;  $N_{11} = 0$  and  $N_{21} \neq 0$ ;  $N_{11} \neq 0$  and  $N_{21} = 0$ ; and  $N_{11} \neq 0$  and

$N_{21} \neq 0$ . It is important to note at this time that the equations  $\frac{dN_{11}}{dt} = 0$ ,  $\frac{dN_{12}}{dt} = 0$ ,  $\frac{dN_{21}}{dt} = 0$  and  $\frac{dN_{22}}{dt} = 0$  lead to the following conditions on the equilibria of System (6.3)

$$\begin{aligned} N_{11} = 0 &\iff N_{12} = 0, \\ N_{21} = 0 &\iff N_{22} = 0. \end{aligned}$$

Biologically, this implies that if a species is present in either of the vessels then it is present in both vessels.

We begin identifying the equilibrium states by considering the case  $N_{11} = N_{12} = N_{21} = N_{22} = 0$ . Here we assume that the vessels are absent of both species. In this case, System (6.3) reduces to

$$\begin{aligned} \frac{dP_1}{dt} &= -(1 + D + K) P_1 + D P_2, \\ \frac{dP_2}{dt} &= (1 + D) P_1 - (2 + D + K) P_2. \end{aligned} \tag{6.4}$$

The only values of  $P_1$  and  $P_2$  satisfying  $\frac{dP_1}{dt} = 0$  and  $\frac{dP_2}{dt} = 0$  are  $P_1 = 0$  and  $P_2 = 0$ . Therefore we can define  $E_0 = (0, 0, 0, 0, 0, 0)$  as an equilibrium of system (6.3). Next, we consider the case  $N_{21} = N_{22} = 0$ . Here system (6.3) becomes

$$\begin{aligned} \frac{dN_{11}}{dt} &= \left( \mu_1 \left( \frac{2 + D}{2 + 2D} - N_{11} \right) - m_1 - (1 + D) \right) N_{11} + D N_{12}, \\ \frac{dN_{12}}{dt} &= \left( \mu_1 \left( \frac{1}{2} - N_{12} \right) - m_1 - (2 + D) \right) N_{12} + (1 + D) N_{11}, \\ \frac{dP_1}{dt} &= \left( \mu_1^{max} - \mu_1 \left( \frac{2 + D}{2 + 2D} - N_{11} \right) \right) N_{11} - (1 + D + K) P_1 + D P_2, \\ \frac{dP_2}{dt} &= \left( \mu_1^{max} - \mu_1 \left( \frac{1}{2} - N_{12} \right) \right) N_{12} + (1 + D) P_1 - (2 + D + K) P_2. \end{aligned} \tag{6.5}$$

The first two equations lead us to see that  $N_{11}$  and  $N_{12}$  will be at equilibrium when the following equation is satisfied

$$\left( \mu_1 \left( \frac{2 + D}{2 + 2D} - N_{11} \right) - m_1 - (1 + D) \right) \left( \mu_1 \left( \frac{1}{2} - N_{12} \right) - m_1 - (2 + D) \right) = D(1 + D). \tag{6.6}$$

**Theorem 6.3.1.** *If  $N_{11}^{*(1)}$  and  $N_{12}^{*(1)}$  satisfy (6.6), then these values are unique.*

*Proof.* Suppose that  $N_{11}^{*(1)}, N_{12}^{*(1)}$  and  $\tilde{N}_{11}^{*(1)}, \tilde{N}_{12}^{*(1)}$  satisfy (6.6) and without loss of generality assume  $N_{11}^{*(1)} \leq \tilde{N}_{11}^{*(1)}$ . Then since  $\mu_1$  is a decreasing function with respect to  $N_{11}$ , we have

$$\left( \mu_1 \left( \frac{2+D}{2+2D} - \tilde{N}_{11}^{*(1)} \right) - m_1 - (1+D) \right) < \left( \mu_1 \left( \frac{2+D}{2+2D} - N_{11}^{*(1)} \right) - m_1 - (1+D) \right).$$

If  $\frac{dN_{11}}{dt} = 0$  in (6.5), we must have

$$\begin{aligned} N_{12}^{*(1)} &= \frac{\left( \mu_1 \left( \frac{2+D}{2+2D} - N_{11}^{*(1)} \right) - m_1 - (1+D) \right)}{-D} N_{11}^{*(1)}, \\ &\leq \frac{\left( \mu_1 \left( \frac{2+D}{2+2D} - \tilde{N}_{11}^{*(1)} \right) - m_1 - (1+D) \right)}{-D} \tilde{N}_{11}^{*(1)}, \\ &= \tilde{N}_{12}^{*(1)}. \end{aligned}$$

Hence,  $N_{11}^{*(1)} \leq \tilde{N}_{11}^{*(1)}$  and  $N_{12}^{*(1)} \leq \tilde{N}_{12}^{*(1)}$ . However, in order to satisfy (6.6) it must be that  $N_{11}^{*(1)} = \tilde{N}_{11}^{*(1)}$  and  $N_{12}^{*(1)} = \tilde{N}_{12}^{*(1)}$ .  $\square$

With values of  $N_{11}^{*(1)}$  and  $N_{12}^{*(1)}$  satisfying (6.6), the equations  $\frac{dP_1}{dt} = 0$  and  $\frac{dP_2}{dt} = 0$  will hold with the values

$$\begin{aligned} P_1^{*(1)} &= \frac{(2+D+K)W_1^* + DW_2^*}{(1+K)(2+2D+K)}, \\ P_2^{*(1)} &= \frac{(1+D)W_1^* + (1+D+K)W_2^*}{(1+K)(2+2D+K)}, \end{aligned}$$

where

$$\begin{aligned} W_1^* &= (\mu_1^{max} - \mu_1 \left( \frac{2+D}{2+2D} - N_{11}^{*(1)} \right)) N_{11}^{*(1)}, \\ W_2^* &= (\mu_1^{max} - \mu_1 \left( \frac{1}{2} - N_{12}^{*(1)} \right)) N_{12}^{*(1)}. \end{aligned}$$

Thus we have an equilibrium  $E_1 = (N_{11}^{*(1)}, N_{12}^{*(1)}, 0, 0, P_1^{*(1)}, P_2^{*(1)})$  which exists when there exists  $N_{11}^{*(1)}$  and  $N_{12}^{*(1)}$  which satisfy (6.6). Similar to the previous chapter, (6.6) has a solution

$$N_{11}^{*(1)} = \frac{2+D}{2+2D} - \mu_1^{-1}(m_1+1), N_{12}^{*(1)} = \frac{1}{2} - \mu_1^{-1}(m_1+1).$$

Hence being the unique solution we have determined  $E_1$ .

We now turn to the case  $N_{11} = N_{12} = 0$ . Here system (6.3) reduces to

$$\begin{aligned} \frac{dN_{21}}{dt} &= \left( \mu_2 \left( \frac{2+D}{2+2D} - N_{21} \right) - m_2(P_1) - (1+D) \right) N_{21} + DN_{22}, \\ \frac{dN_{22}}{dt} &= \left( \mu_2 \left( \frac{1}{2} - N_{22} \right) - m_2(P_2) - (2+D) \right) N_{22} + (1+D)N_{21}, \\ \frac{dP_1}{dt} &= -(1+D+K)P_1 + DP_2, \\ \frac{dP_2}{dt} &= (1+D)P_1 - (2+D+K)P_2. \end{aligned} \tag{6.7}$$

Similar to the previous case, at equilibrium the following equation must be satisfied

$$\left( \mu_2 \left( \frac{2+D}{2+2D} - N_{21} \right) - m_2^{min} - (1+D) \right) \left( \mu_2 \left( \frac{1}{2} - N_{22} \right) - m_2^{min} - (2+D) \right) = D(1+D). \tag{6.8}$$

**Theorem 6.3.2.** *If  $N_{21}^{*(2)}$  and  $N_{22}^{*(2)}$  satisfy (6.8), then these values are unique.*

The proof of Theorem 6.3.2 is omitted as it is much the same as Theorem 6.3.1. For equilibrium values of  $P_1$  and  $P_2$ , the equations for  $\frac{dP_1}{dt} = 0$  and  $\frac{dP_2}{dt} = 0$  are solved as in the  $E_0$  case; that is,  $P_1^{*(2)} = 0$  and  $P_2^{*(2)} = 0$ . Thus we have an equilibrium  $E_2 = (0, 0, N_{21}^{*(2)}, N_{22}^{*(2)}, 0, 0)$  to system (6.3) which exists when there exists  $N_{21}^{*(2)}$  and  $N_{22}^{*(2)}$  satisfying (6.8). With poison levels being zero we can see that one solution to (5.7) is

$$N_{21}^{*(2)} = \frac{2+D}{2+2D} - \mu_2^{-1}(m_2^{min}+1), N_{22}^{*(2)} = \frac{1}{2} - \mu_2^{-1}(m_2^{min}+1).$$

Hence being the unique solution we have determined  $E_2$ .

Finally we investigate the case where each of  $N_{11}$ ,  $N_{12}$ ,  $N_{21}$  and  $N_{22}$  is nonzero. The equilibrium values of  $P_1$  and  $P_2$  can be found in terms of the other variables. From system (6.3), at equilibrium we must satisfy the following

$$\begin{aligned} (\mu_1^{max} - \mu_1 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right)) N_{11} - (1 + D + K)P_1 + DP_2 &= 0, \\ (\mu_1^{max} - \mu_1 \left( \frac{1}{2} - N_{12} - N_{22} \right)) N_{12} + (1 + D)P_1 - (2 + D + K)P_2 &= 0. \end{aligned}$$

Solving these equations we have the equilibrium values

$$\begin{aligned} P_1^* &= \frac{-(2 + D + K)W_1^* - DW_2^*}{2 + 2D + 3K + 2DK + K^2}, \\ P_2^* &= \frac{-(1 + D)W_1^* - (1 + D + K)W_2^*}{2 + 2D + 3K + 2DK + K^2}, \end{aligned}$$

where

$$\begin{aligned} W_1^* &= (\mu_1^{max} - \mu_1 \left( \frac{2 + D}{2 + 2D} - N_{11}^* - N_{21}^* \right)) N_{11}^*, \\ W_2^* &= (\mu_1^{max} - \mu_1 \left( \frac{1}{2} - N_{12}^* - N_{22}^* \right)) N_{12}^*. \end{aligned}$$

Therefore, we can find equilibrium values for the last two equations in system (6.3) so long as we have values for  $N_{ij}$  which satisfy equilibrium of the first four equations of system (6.3). Similar to the two previous cases, the existence of these values depends directly on satisfying equations involving the variables  $N_{ij}$ . Here, we must satisfy the equations

$$\left( \mu_1 \left( \frac{2 + D}{2 + 2D} - N_{11} - N_{21} \right) - m_1 - (1 + D) \right) \left( \mu_1 \left( \frac{1}{2} - N_{12} - N_{22} \right) - m_1 - (2 + D) \right) = D(1 + D), \quad (6.9)$$

and

$$\begin{aligned} \left( \mu_2 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right) - m_2(P_1^*) - (1 + D) \right) \left( \mu_2 \left( \frac{1}{2} - N_{12} - N_{22} \right) - m_2(P_2^*) - (2 + D) \right) \\ = D(1 + D). \end{aligned} \quad (6.10)$$

Thus we have an equilibrium  $E_3 = (N_{11}^*, N_{12}^*, N_{21}^*, N_{22}^*, P_1^*, P_2^*)$  existing when  $N_{11}^*$ ,  $N_{12}^*$ ,  $N_{21}^*$  and  $N_{22}^*$  satisfy (6.9) and (6.10). As in the previous chapter it is the case that  $N_{11}^{*(1)} = N_{11}^* + N_{21}^*$  and  $N_{12}^{*(1)} = N_{12}^* + N_{22}^*$ , but it is not true that similar conditions relating the parameters hold for  $N_{21}^*$ ,  $N_{22}^*$ ,  $P_1^*$  and  $P_2^*$  since the levels of poison at equilibrium  $E_1$  and  $E_3$  are unequal.

## 6.4 Local Stability Analysis

We now turn to the local stability of each equilibrium. The Jacobian of the system (6.3) is

$$J(N_{11}, N_{12}, N_{21}, N_{22}, P_1, P_2) = \begin{pmatrix} \alpha_1 - \beta_1 - \gamma_1 & D & -\beta_7 & 0 & 0 & 0 \\ (1+D) & \alpha_2 - \beta_2 - \gamma_2 & 0 & -\beta_8 & 0 & 0 \\ -\beta_5 & 0 & \alpha_3 - \beta_3 - \gamma_3 & D & -\delta_1 & 0 \\ 0 & -\beta_6 & (1+D) & \alpha_4 - \beta_4 - \gamma_4 & 0 & -\delta_2 \\ -\alpha_1 + \beta_1 & 0 & \beta_7 & 0 & -(1+D+K) & D \\ 0 & -\alpha_2 + \beta_2 & 0 & \beta_8 & (1+D) & -(2+D+K) \end{pmatrix}, \quad (6.11)$$

where

$$\begin{aligned} \alpha_1 &= \mu_1 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right), & \alpha_2 &= \mu_1 \left( \frac{1}{2} - N_{12} - N_{22} \right), \\ \alpha_3 &= \mu_2 \left( \frac{2+D}{2+2D} - N_{11} - N_{21} \right), & \alpha_4 &= \mu_2 \left( \frac{1}{2} - N_{12} - N_{22} \right), \\ \beta_1 &= -\frac{d\mu_1}{dN_{11}} N_{11}, & \beta_2 &= -\frac{d\mu_1}{dN_{12}} N_{12}, \\ \beta_3 &= -\frac{d\mu_2}{dN_{21}} N_{21}, & \beta_4 &= -\frac{d\mu_2}{dN_{22}} N_{22}, \\ \beta_5 &= -\frac{d\mu_1}{dN_{11}} N_{21}, & \beta_6 &= -\frac{d\mu_2}{dN_{12}} N_{22}, \\ \beta_7 &= -\frac{d\mu_1}{dN_{21}} N_{11}, & \beta_8 &= -\frac{d\mu_1}{dN_{22}} N_{12}, \\ \gamma_1 &= m_1 + (1+D), & \gamma_2 &= m_1 + (2+D), \\ \gamma_3 &= m_2(P_1) + (1+D), & \gamma_4 &= m_2(P_2) + (2+D), \\ \delta_1 &= \frac{dm_2}{dP_1} N_{21}, & \delta_2 &= \frac{dm_2}{dP_2} N_{22}. \end{aligned}$$

One should note that each of  $\alpha_i$ ,  $\gamma_i$ ,  $\beta_j$  and  $\delta_k$  is positive. Also, in the case  $N_{11} = N_{12} = 0$  we have  $\beta_1 = \beta_2 = \beta_7 = \beta_8 = 0$  and in the case  $N_{21} = N_{22} = 0$  we have  $\beta_3 = \beta_4 = \beta_5 = \beta_6 = \delta_1 = \delta_2 = 0$ . Upon calculation, one can see that  $\beta_1 = \beta_7$ ,  $\beta_3 = \beta_5$ ,  $\beta_2 = \beta_8$  and  $\beta_4 = \beta_6$ . From  $\frac{dN_{11}}{dt}$  it is true that  $\alpha_1 - \gamma_1 < 0$  at both  $E_1$  and  $E_3$  since  $N_{11}$  and  $N_{12}$  are

nonzero. Similarly,  $\alpha_2 - \gamma_2 < 0$  at  $E_1$  and  $E_3$ ,  $\alpha_3 - \gamma_3 < 0$  at  $E_2$  and  $E_3$ , and  $\alpha_4 - \gamma_4 < 0$  at  $E_2$  and  $E_3$ .

**Theorem 6.4.1.** *The equilibrium  $E_0$  is locally asymptotically stable if when evaluated at  $E_0$  the following conditions hold*

1.  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$ ,
2.  $\alpha_1 - \gamma_1 + \alpha_2 - \gamma_2 < 0$ ,
3.  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) > D(1 + D)$ ,
4.  $\alpha_3 - \gamma_3 + \alpha_4 - \gamma_4 < 0$ .

*Proof.* For the equilibrium  $E_0$ , the local stability is determined by the eigenvalues of

$$J(E_0) = \begin{pmatrix} \alpha_1 - \gamma_1 & D & 0 & 0 & 0 & 0 \\ (1 + D) & \alpha_2 - \gamma_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \alpha_3 - \gamma_3 & D & 0 & 0 \\ 0 & 0 & (1 + D) & \alpha_4 - \gamma_4 & 0 & 0 \\ -\alpha_1 & 0 & 0 & 0 & -(1 + D + K) & D \\ 0 & -\alpha_2 & 0 & 0 & (1 + D) & -(2 + D + K) \end{pmatrix}.$$

Here the eigenvalues are

$$\begin{aligned} \lambda_1 &= -(1 + K); \quad \lambda_2 = -(2 + 2D + K), \\ \lambda_{3,4} &= \frac{(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2) \pm \sqrt{((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D)}}{2}, \\ \lambda_{5,6} &= \frac{(\alpha_3 - \gamma_3) + (\alpha_4 - \gamma_4) \pm \sqrt{((\alpha_3 - \gamma_3) - (\alpha_4 - \gamma_4))^2 + 4D(1 + D)}}{2}. \end{aligned}$$

From above, we can see that  $J(E_0)$  has real eigenvalues. We can now determine conditions which will ensure these eigenvalues are negative. Consider now that

$$((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D) = (\alpha_1 - \gamma_1)^2 + (\alpha_2 - \gamma_2)^2 - 2(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) + 4D(1 + D).$$

If we assume  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$ , we have

$$((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D) < ((\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2))^2.$$

Therefore if  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$ ,  $\lambda_3$  and  $\lambda_4$  have the same sign which is determined by the expression  $(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2)$ . Hence to ensure negative eigenvalues we must have  $(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2) < 0$ . Now, when  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$  it must be the case that  $(\alpha_1 - \gamma_1)$  and  $(\alpha_2 - \gamma_2)$  have the same sign. Therefore, to ensure negative eigenvalues we must have  $(\alpha_1 - \gamma_1) < 0$  and  $(\alpha_2 - \gamma_2) < 0$ .

If we assume  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) < D(1 + D)$ , then it follows that

$$((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D) > ((\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2))^2,$$

which will lead to  $\lambda_3$  and  $\lambda_4$  having opposite signs. Hence, if  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) < D(1 + D)$  then  $E_0$  is not locally stable. Using similar analysis, we can find that if  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) > D(1 + D)$  and  $\alpha_3 - \gamma_3 < 0$  and  $\alpha_4 - \gamma_4 < 0$  then  $\lambda_5$  and  $\lambda_6$  will both be negative. Furthermore, if  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) < D(1 + D)$  then  $\lambda_5$  and  $\lambda_6$  will have opposite signs.  $\square$

**Theorem 6.4.2.** *The equilibrium  $E_1$  is locally asymptotically stable when evaluated at  $E_1$  the following conditions hold*

1.  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) > D(1 + D)$ ,
2.  $\alpha_3 - \gamma_3 + \alpha_4 - \gamma_4 < 0$ .

*Proof.* For the equilibrium  $E_1$ , the local stability is determined by the eigenvalues of

$$J(E_1) = \begin{pmatrix} \alpha_1 - \beta_1 - \gamma_1 & D & -\beta_7 & 0 & 0 & 0 \\ (1 + D) & \alpha_2 - \beta_2 - \gamma_2 & 0 & -\beta_8 & 0 & 0 \\ 0 & 0 & \alpha_3 - \gamma_3 & D & 0 & 0 \\ 0 & 0 & (1 + D) & \alpha_4 - \gamma_4 & 0 & 0 \\ -\alpha_1 + \beta_1 & 0 & \beta_7 & 0 & -(1 + D + K) & D \\ 0 & -\alpha_2 + \beta_2 & 0 & \beta_8 & (1 + D) & -(2 + D + K) \end{pmatrix}.$$



Here the eigenvalues are

$$\lambda_1 = -(1 + K); \lambda_2 = -(2 + 2D + K),$$

$$\lambda_{3,4} = \frac{(\alpha_1 - \beta_1 - \gamma_1) + (\alpha_2 - \beta_2 - \gamma_2) \pm \sqrt{((\alpha_1 - \beta_1 - \gamma_1) - (\alpha_2 - \beta_2 - \gamma_2))^2 + 4D(1 + D)}}{2},$$

$$\lambda_{5,6} = \frac{(\alpha_3 - \gamma_3) + (\alpha_4 - \gamma_4) \pm \sqrt{((\alpha_3 - \gamma_3) - (\alpha_4 - \gamma_4))^2 + 4D(1 + D)}}{2}.$$

Using similar reasoning to that of the  $E_0$  case, if  $(\alpha - \beta_1 - \gamma_1)(\alpha_2 - \beta_2 - \gamma_2) > D(1 + D)$  then  $\lambda_3$  and  $\lambda_4$  have the same sign determined by the sign of  $(\alpha_1 - \beta_1 - \gamma_1) + (\alpha_2 - \beta_2 - \gamma_2)$ . Each of  $(\alpha_1 - \beta_1 - \gamma_1) < 0$ ,  $(\alpha_2 - \beta_2 - \gamma_2) < 0$  and  $(\alpha - \beta_1 - \gamma_1)(\alpha_2 - \beta_2 - \gamma_2) > D(1 + D)$  hold since  $(\alpha_1 - \gamma_1) < 0$ ,  $(\alpha_2 - \gamma_2) < 0$  and  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) = D(1 + D)$  when evaluated at  $E_1$ . Furthermore, if  $(\alpha - \beta_1 - \gamma_1)(\alpha_2 - \beta_2 - \gamma_2) < D(1 + D)$  then  $\lambda_3$  and  $\lambda_4$  have opposite signs. Similarly, if  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) > D(1 + D)$ ,  $\alpha_3 - \gamma_3 < 0$ ,  $\alpha_4 - \gamma_4 < 0$  then  $\lambda_5$  and  $\lambda_6$  will both be negative. Also, if  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) < D(1 + D)$  then  $\lambda_5$  and  $\lambda_6$  will have opposite signs.  $\square$

**Theorem 6.4.3.** *The equilibrium  $E_2$  is locally asymptotically stable if when if when evaluated at  $E_2$  the following conditions hold:*

1.  $(\alpha_1 - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$ ,
2.  $\alpha_1 - \gamma_1 + \alpha_2 - \gamma_2 < 0$ ,

*Proof.* For the equilibrium  $E_2$ , the local stability is determined by the eigenvalues of

$$J(E_2) = \begin{pmatrix} \alpha_1 - \gamma_1 & D & 0 & 0 & 0 & 0 \\ (1 + D) & \alpha_2 - \gamma_2 & 0 & 0 & 0 & 0 \\ -\beta_5 & 0 & \alpha_3 - \beta_3 - \gamma_3 & D & -\delta_1 & 0 \\ 0 & -\beta_6 & (1 + D) & \alpha_4 - \beta_4 - \gamma_4 & 0 & -\delta_2 \\ -\alpha_1 & 0 & 0 & 0 & -(1 + D + K) & D \\ 0 & -\alpha_2 & 0 & 0 & (1 + D) & -(2 + D + K) \end{pmatrix}.$$

Here the eigenvalues are

$$\lambda_1 = -(1 + K); \lambda_2 = -(2 + 2D + K),$$

$$\lambda_{3,4} = \frac{(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2) \pm \sqrt{((\alpha_1 - \gamma_1) - (\alpha_2 - \gamma_2))^2 + 4D(1 + D)}}{2},$$

$$\lambda_{5,6} = \frac{(\alpha_3 - \beta_3 - \gamma_3) + (\alpha_4 - \beta_4 - \gamma_4) \pm \sqrt{((\alpha_3 - \beta_3 - \gamma_3) - (\alpha_4 - \beta_4 - \gamma_4))^2 + 4D(1 + D)}}{2}.$$

As in the previous cases, if  $(\alpha - \gamma_1)(\alpha_2 - \gamma_2) > D(1 + D)$  then  $\lambda_3$  and  $\lambda_4$  have the same sign determined by the sign of  $(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2)$ . Hence if  $(\alpha_1 - \gamma_1) + (\alpha_2 - \gamma_2) < 0$  then  $\lambda_3$  and  $\lambda_4$  will be negative. Furthermore, if  $(\alpha - \gamma_1)(\alpha_2 - \gamma_2) < D(1 + D)$  then  $\lambda_3$  and  $\lambda_4$  have opposite signs. Similarly, if  $(\alpha_3 - \beta_3 - \gamma_3)(\alpha_4 - \beta_4 - \gamma_4) > D(1 + D)$  and  $\alpha_3 - \beta_3 - \gamma_3 + \alpha_4 - \beta_4 - \gamma_4 < 0$  then  $\lambda_5$  and  $\lambda_6$  will both be negative. This will always be the case since at  $E_2$  we have  $(\alpha_3 - \gamma_3)(\alpha_4 - \gamma_4) = D(1 + D)$ ,  $\alpha_3 - \gamma_3 < 0$  and  $\alpha_4 - \gamma_4 < 0$ . Also, if  $(\alpha_3 - \beta_3 - \gamma_3)(\alpha_4 - \beta_4 - \gamma_4) < D(1 + D)$  then  $\lambda_5$  and  $\lambda_6$  will have opposite signs.

□

**Theorem 6.4.4.** *The equilibrium  $E_3$  is locally asymptotically stable if when evaluated at  $E_3$  the following conditions hold*

1.  $|\alpha_1 - \gamma_1| \geq D$
2.  $|\alpha_2 - \gamma_2| \geq (1 + D)$
3.  $|\alpha_3 - \gamma_3| \geq D + \delta_1$
4.  $|\alpha_4 - \gamma_4| \geq 1 + D + \delta_2$
5.  $1 + K \geq |-\alpha_1 + \beta_1| + \beta_1$
6.  $1 + K \geq |-\alpha_2 + \beta_2| + \beta_2$

*Proof.* For the equilibrium  $E_3$ , the local stability is determined by the eigenvalues of

$$J(E_3) = \begin{pmatrix} \alpha_1 - \beta_1 - \gamma_1 & D & -\beta_1 & 0 & 0 & 0 \\ (1 + D) & \alpha_2 - \beta_2 - \gamma_2 & 0 & -\beta_2 & 0 & 0 \\ -\beta_3 & 0 & \alpha_3 - \beta_3 - \gamma_3 & D & -\delta_1 & 0 \\ 0 & -\beta_4 & (1 + D) & \alpha_4 - \beta_4 - \gamma_4 & 0 & -\delta_2 \\ -\alpha_1 + \beta_1 & 0 & \beta_1 & 0 & -(1 + D + K) & D \\ 0 & -\alpha_2 + \beta_2 & 0 & \beta_2 & (1 + D) & -(2 + D + K) \end{pmatrix}.$$

One should note that each of the diagonal elements is negative when the system is at equilibrium. Hence, applying the Gershgorin Circle Theorem we find that the eigenvalues of  $J(E_3)$  will have negative real part if the following conditions hold:

1.  $|\alpha_1 - \beta_1 - \gamma_1| \geq D + \beta_1$
2.  $|\alpha_2 - \beta_2 - \gamma_2| \geq 1 + D + \beta_2$
3.  $|\alpha_3 - \beta_3 - \gamma_3| \geq D + \beta_3 + \delta_1$
4.  $|\alpha_4 - \beta_4 - \gamma_4| \geq 1 + D + \beta_4 + \delta_2$
5.  $1 + D + K \geq |-\alpha_1 + \beta_1| + \beta_1 + D$
6.  $2 + D + K \geq |-\alpha_2 + \beta_2| + \beta_2 + 1 + D$

Each of  $\alpha_1 - \beta_1 - \gamma_1$ ,  $\alpha_2 - \beta_2 - \gamma_2$ ,  $\alpha_3 - \beta_3 - \gamma_3$  and  $\alpha_4 - \beta_4 - \gamma_4$  is negative and hence the first four conditions can be reduced. The sign of  $-\alpha_1 + \beta_1$  and  $-\alpha_2 + \beta_2$  is not necessarily negative, but in that case the last two conditions can be reduced to  $1 + K \geq \alpha_1$  and  $1 + K \geq \alpha_2$ .  $\square$

## 6.5 Numerical Simulations

In this section we present numerical simulations of System (6.1) as verification of the attraction conditions presented in the previous section. Each simulation is obtained

using the **Matlab** solver **ode45** with parameter values:  $q_1 = 10^{-9}$ ,  $q_2 = 10^{-9}$ ,  $k_1 = 0.03$ ,  $k_2 = 0.03$ ,  $D = 0.2$ ,  $E = 0.2$ ,  $K = 0.1$ ,  $m_1 = 0.01$ ,  $m_2^{min} = 0.01$ .

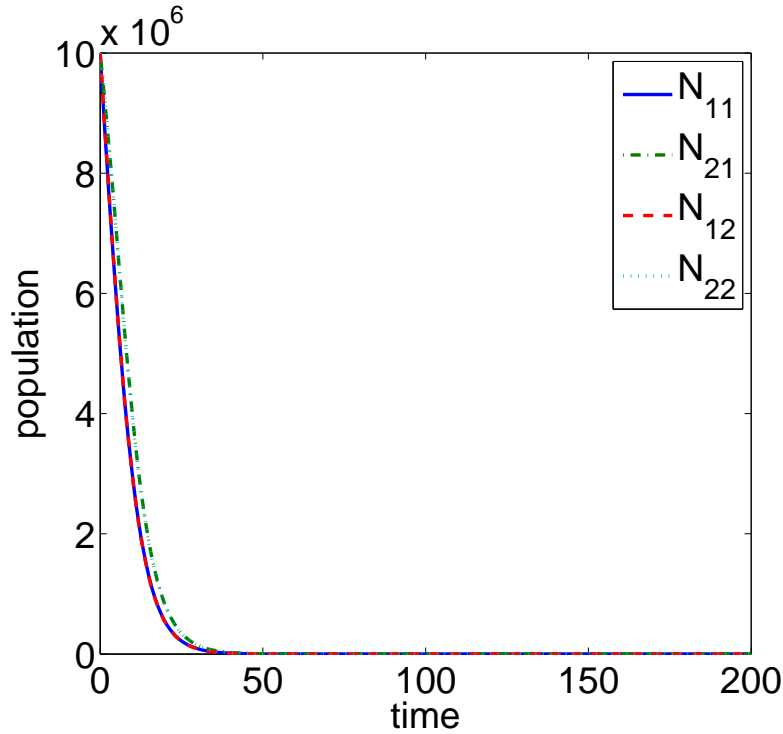


Figure 6.1.  $E_0$  is locally stable, both species perish.

In Figure (6.1) the parameters  $R_{in} = 0.01$ ,  $\mu_1^{max} = 0.1$ ,  $\mu_2^{max} = 0.2$ ,  $m_1 = 0.01$ ,  $m_2^{min} = 0.01$ , and  $\alpha = 10^{-13}$  were used in the simulation. Each of the four populations  $N_{11}$ ,  $N_{12}$ ,  $N_{21}$  and  $N_{22}$  are plotted against time. With the chosen parameters the nutrient level is insufficient for either species to reach equilibrium. Both species perish and the trajectories tend to  $E_0$ .

The parameters  $R_{in} = 0.1$ ,  $\mu_1^{max} = 0.7$ ,  $\mu_2^{max} = 0.4$  and  $\alpha = 10^{-13}$  were used in Figure (6.2). With the parameters chosen in this way the poison producer dominates the susceptible. The second species is eliminated from both vessels and the trajectory tends to the equilibrium  $E_1$ .

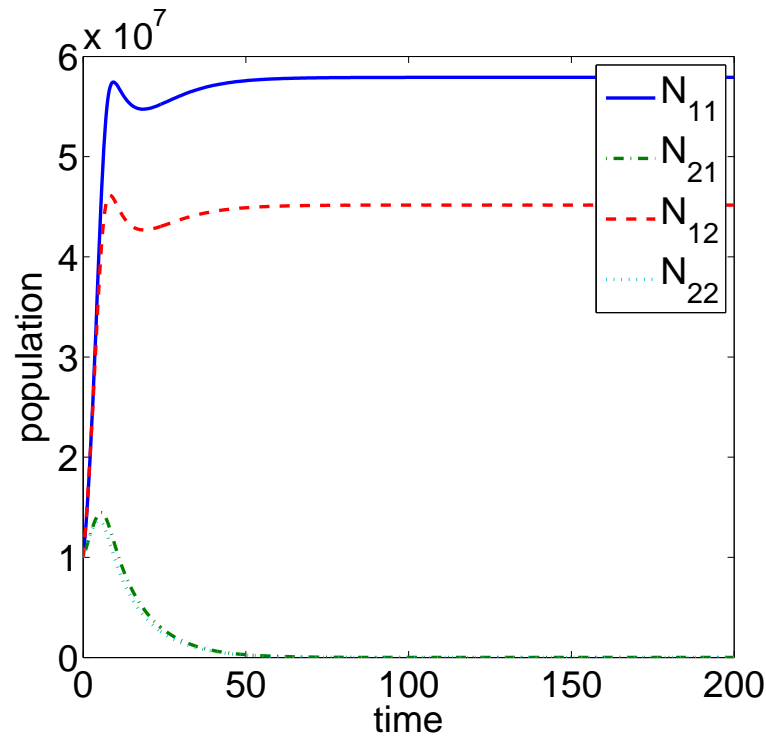


Figure 6.2.  $E_1$  is locally stable.

Figure (6.3) demonstrates the local stability of  $E_2$  by choosing parameters  $R_{in} = 0.3$ ,  $\mu_1^{max} = 0.4$ ,  $\mu_2^{max} = 0.5$ ,  $m_1 = 0.01$ ,  $m_2^{min} = 0.01$ ,  $\alpha = 10^{-13}$ . The trajectory tends to  $E_2$  as species 2 is a better competitor and eliminates the poison producer from the competition.

Figure (6.4) presents an interesting case where in the simple chemostat the poison susceptible species  $N_2$  would be a superior competitor, but fails to win the competition when poison is introduced by its competitor. Here the parameters  $R_{in} = 0.3$ ,  $\mu_1^{max} = 0.5$ ,  $\mu_2^{max} = 0.54$ ,  $m_1 = 0.01$ ,  $m_2^{min} = 0.01$  and  $\alpha = 10^{-10}$ . As in Chapter 4 the additional advantage of the poison production enables the poison producer to eliminate the poison susceptible.

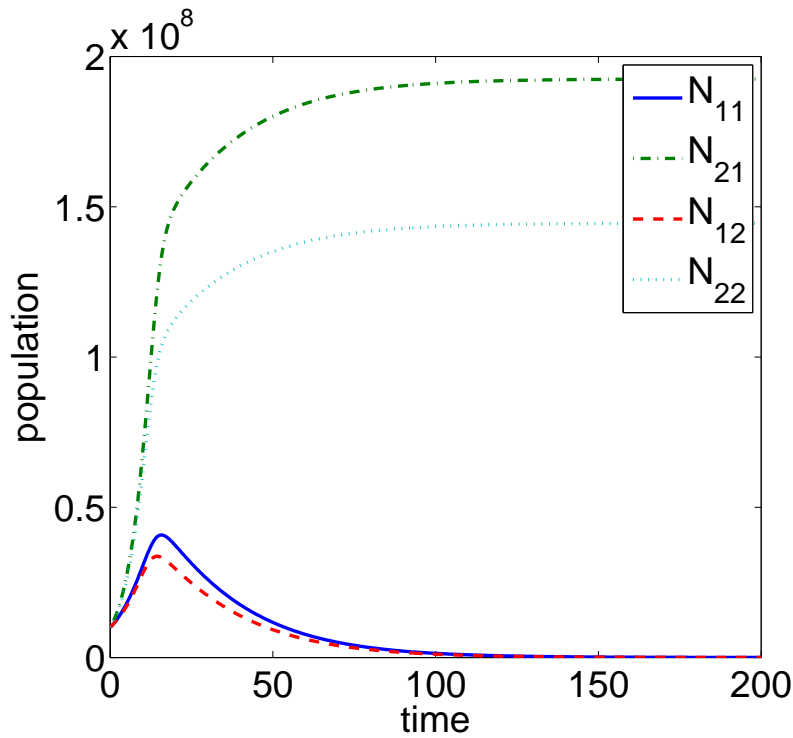


Figure 6.3.  $E_2$  is locally stable.

## 6.6 Discussion

The model presented in (6.1) incorporates the allelopathy of Chapter 4 into the nutrient recycling gradostat presented in Chapter 5. Similar to the chemostat case, the effect of the poison in the system lead to the same results as in the nutrient recycling case with a shift of parameters enabling the poison producer to win the competition when being an inferior competitor in the chemostat. System (6.1) was shown to have four steady states. For the boundary equilibria  $E_1$  and  $E_2$  conditions were found which ensure local stability. Numerical simulations were presented for choices of parameters to demonstrate the attractiveness of the equilibria. Theoretical results indicate that coexistence is possible for at least some parameter ranges, however the relationship between the stability of  $E_3$  and the boundary equilibria  $E_1$  and  $E_2$  being unstable does not necessarily hold. This is in part due to the differing levels of  $P_1$  and  $P_2$  required at  $E_1$  and  $E_3$ . The effect

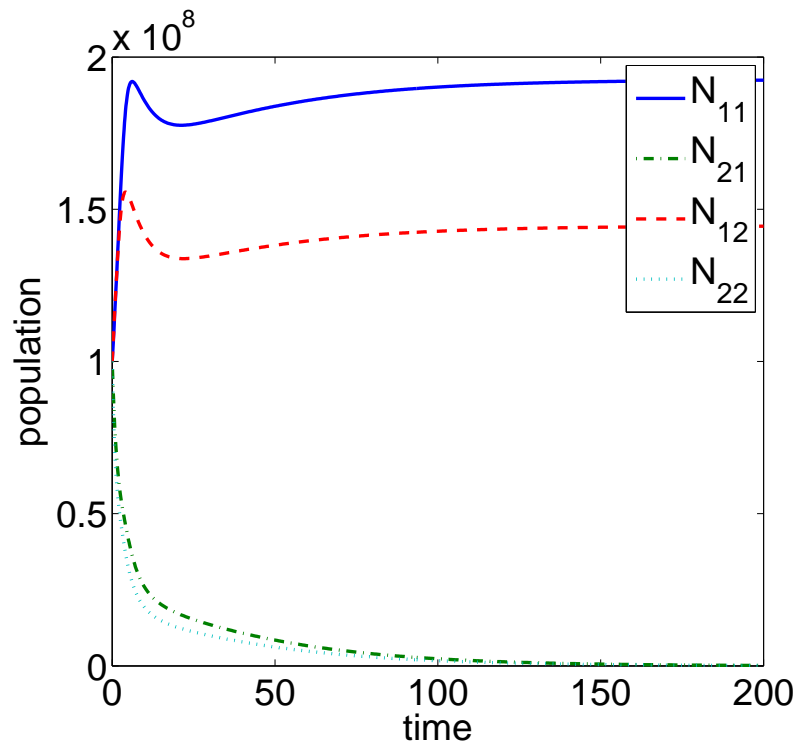


Figure 6.4.  $E_1$  is locally stable.

of the poison is apparent, as seen in Figure (6.4). In this case, species 2 would win the competition in the gradostat model in Chapter 5, but the poison production increases the advantage of the producer.

## CHAPTER 7

### CONCLUSION

Several models and background of resource competition are presented in the previous chapters. The models take the form of chemostat and gradostat models modified appropriately to include the new dynamics of nutrient recycling and alleopathy. The nutrient recycling models incorporate explicit mortality into the chemostat models, similar to previously analyzed models. Different in the models presented in this study is the recycling of dead organisms into available nutrient. In Chapters 2 and 3 the effect of nutrient recycling in the chemostat is studied. In these cases the mass balance is preserved, allowing for global analysis in each model (via reduction of order in the competition case). The theoretical results are consistent with the previous theory of the simple chemostat. That is, the steady states are determined by the parameters of the system and the asymptotic outcome of an trajectory with positive initial conditions can be determined by the resource requirements,  $R^*$  values, of the species contained in the chemostat. The theoretical results are confirmed by numerical simulations with convergence to the equilibrium associated with the population requiring the least nutrient to reach equilibrium regardless of the initial populations. In Chapter 5 the nutrient recycling is implemented into the gradostat model. Again the steady states are analyzed, but only locally. Conditions on the parameters are presented which insure the stability of the equilibria, with instability of the boundary equilibria being required for the existence of the interior equilibrium. Furthermore, existence of the interior equilibrium is sufficient for its stability.



Chapter 4 introduces a particular allelopathy into the chemostat model. The allelopathic models considered are similar to previously analyzed models with two biologically important differences: the rate of poison production increases as the growth rate of the toxic species decreases, and poison production has no explicit cost. These assumptions on the dynamics of the toxin production is biologically observed in at least some species of algae. The growth of algae often requires nitrogen or phosphorus as a nutrient while the toxin produced contains little of this nutrient. Instead the toxin contains organic carbon which can be produced via photosynthesis even when limited amounts of nitrogen or phosphorus are available. [25] Four steady states for the model were identified, with the coexistence equilibrium being feasible not in a non-generic restriction but in fact across a range of parameter values. The interior equilibria is unstable when it exists, with bistability for the nontrivial boundary equilibria. Numerical solutions in this case indicate that one species will become extinct with the outcome depending on initial conditions. In Chapter 6 the allelopathy was incorporated into the nutrient recycling gradostat described in Chapter 5. Again four steady states are found and analyzed locally. Similar to the chemostat, the addition of allelopathy into the gradostat model increases the producers ability to eliminate its competitor. A theoretical coexistence is found along with conditions on parameters ensuring its stability.

**APPENDIX A**  
**CONVERGENCE THEOREM FOR ASYMPTOTICALLY**  
**AUTONOMOUS SYSTEMS**

This appendix reproduces a theorem which appear in Appendix F of [28]. The theorem justifies the reduction of order used in the previous chapters. In reducing the order of a differential system we wish to determine the  $\omega$ -limit set of a higher order system by considering only the  $\omega$ -limit set of a lower order system to which the original is asymptotic. This result is desirable, however not true in general [33]. The theorem contains five conditions which when properly met ensure that reduction can be had. The proof is advanced and not reproduced here but can be found in the reference along with some examples of its application. Consider two systems of ordinary differential equations of the form

$$z' = Az, \quad y' = f(y, z), \quad (\text{A.1})$$

and

$$x' = f(x, 0), \quad (\text{A.2})$$

where

$$z \in \mathbb{R}, \quad (y, z) \in \mathcal{D} \subset \mathbb{R}^n \times \mathbb{R}^m, \quad x \in \Omega = \{x | (x, 0) \in \mathcal{D}\} \subset \mathbb{R}^n.$$

It will be assumed that  $f$  is continuously differentiable,  $\mathcal{D}$  is positively invariant for (A.1), and (A.1) is dissipative in the sense that there is a compact subset of  $\mathcal{D}$  into which every solution eventually enters and remains. The following additional hypothesis will be used.

(H1) All of the eigenvalues of  $A$  have negative real parts.

(H2) Equation (A.2) has a finite number of rest points in  $\Omega$ , each of which is hyperbolic for (A.2). Denote these rest points by  $x_1, x_2, \dots, x_p$ .

(H3) The dimension of the stable manifold of  $x_i$  is  $n$  for  $1 \leq i \leq r$ , and the dimension of the stable manifold of  $x_j$  is less than  $n$  for  $j = r + 1, \dots, p$ . In symbols,  $\dim(M^+(x_i)) = n$ ,  $i = 1, \dots, r$ ;  $\dim(M^+(x_j)) < n$  for  $j = r + 1, \dots, p$ .

(H4)  $\Omega = \bigcup_{i=1}^p M^+(x_i)$ .

(H5) Equation (A.2) does not possess a cycle of rest points.

**Theorem A.0.1.** *Let (H1)-(H5) hold and let  $(y(t), z(t))$  be a solution of (A.1). Then, for some  $i$ ,  $\lim_{t \rightarrow \infty} (y(t), z(t)) = (x_i, 0)$ . In other words,  $\mathcal{D} \subset \bigcup_{i=1}^p \Lambda^+(x_i, 0)$ , where  $\Lambda^+(x_i, 0)$  is the stable manifold for (A.1). Furthermore,  $\bigcup_{i=1}^p \Lambda^+(x_i, 0)$  has Lebesgue measure zero.*

**APPENDIX B**  
**A MATRIX EIGENVALUE THEOREM**

In this section a theorem is reproduced which proves necessary and sufficient conditions for a particular matrix to have negative eigenvalues. In the theorem, found in Appendix A of [28],  $s(A) = \max\{\operatorname{Re} \lambda \mid \lambda \text{ eigenvalue of } A\}$  is shown to be negative given appropriate matrix  $A$ .

**Theorem B.0.2.** *Let*

$$A = \begin{pmatrix} B & C \\ D & E \end{pmatrix}$$

where  $B$  and  $E$  are square matrices of dimension  $k$  and  $l$  (respectively) with nonnegative off-diagonal elements,  $D \geq 0$  and  $C \geq 0$ , and where  $A$  is irreducible. Let  $\hat{A}$  be defined by

$$\hat{A} = \begin{pmatrix} B & -C \\ -D & E \end{pmatrix}.$$

Then  $s(A) < 0$  if and only if  $(-1)^k d_k > 0$ ,  $k = 1, 2, \dots, n$ , where  $d_k$  is the  $k$ th principal minor of  $\hat{A}$ .

## REFERENCES

- [1] A. Barreiro, C. Guisande, I. Maneiro, T. P. Lien, C. Legrand, T. Tamminen, S. Lehtinen, P. Uronen, E. Granali, Relative importance of the different negative effects of the toxic haptophyte *Prymnesium parvum* on *Rhodomonas salina* and *Brachionus plicatilis*, *Aquat. Microb. Ecol.* **38** (2005) 259-267.
- [2] J. P. Braselton, P. Waltman, A competition model with dynamically allocated inhibitor production, *Math. Biosci.* **173** (2001) 55-84.
- [3] G. Bratbak, F. Thingstad, M. Heldal, Viruses and the microbial loop, *Microbial Ecology* **28** (1994) 209.
- [4] R. M. Callaway, W. M. Ridenour, Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers Ecol. Environ.* **2** (8) (2004) 436-443.
- [5] J. M. Chase, M. A. Leibold, *Ecological Niches*, University of Chicago Press, 2001.
- [6] M. J. DeFreitas, A. G. Frederickson, Inhibition as a factor in the maintenance of the diversity of microbial ecosystems, *J. Gen. Microbiol.* **106** (1978) 307-320.
- [7] B. Dubey, J. Husain, A model for the allelopathic effect on two competing species, *Ecol. Model.* **129** (2000) 195-207.
- [8] J. J. Elser, E. R. Marzolf, C. R. Goldman, Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. *Can. J. Fish. Aqu. Sci.* **47** (1990) 1468-1477.
- [9] G. O. Fistarol, C. Legrand, E. Granali, Allelopathic effect of *Prymnesium parvum* on a natural plankton community, *Mar. Ecol. Prog. Ser.* **255** (2003) 115-125.
- [10] J. P. Grover, Phosphorus-dependent growth kinetics of 11 species of freshwater algae, *Limnol. Oceanogr.* **34** (1989) 341-348.

- [11] J. P. Grover, Resource competition in a variable environment: phytoplankton growing according to Monod's model, *Am. Nat.* **136** (1990) 771-789 .
- [12] J. P. Grover, *Resource Competition*, Chapman & Hall, London, 1997.
- [13] R. D. Holt, J. P. Grover, G. D. Tilman, Simple rules for interspecific dominance in systems with exploitative and apparent competition, *Am. Nat.* **144** (1994) 741-771.
- [14] S. B. Hsu, P. Waltman, Competition in the chemostat when one competitor produces a toxin, *Japan J. Indust. Appl. Math.* **15** (1998) 471-490.
- [15] S. B. Hsu, P. Waltman, A survey of mathematical models of competition with an inhibitor, *Math. Biosci.* **187** (2004) 53-91.
- [16] S. B. Hsu, Y.-S. Li, P. Waltman, Competition in the presence of a lethal external inhibitor, *Math. Biosci.* **167** (2000) 177-199.
- [17] F. D. Hulot, J. Huisman, Allelopathic interactions between phytoplankton species: the roles of heterotrophic bacteria and mixing intensity, *Limnol. Oceanogr.* **49** (4, part 2) (2004) 1424-1434.
- [18] W. Jager, J.W.H. So, B. Tang, P. Waltman, Competition in the gradostat, *J. Math. Biol.* **25** (1987) 23-42.
- [19] J. Kubanek, M. K. Hicks, J. Naar, T. A. Villareal, Does the red tide dinoflagellate *Karenia brevis* use allelopathy to outcompete other phytoplankton? *Limnol. Oceanogr.* **50** (3) (2005) 883-895.
- [20] R. E. Lenski, S. E. Hattingh, Coexistence of two competitors on one resource and one inhibitor: a chemostat model based on bacteria and antibiotics, *J. Theor. Biol.* **122** (1986) 83-93.
- [21] R. E. Lenski, M. A. Riley, Chemical warfare from an ecological perspective, *Proc. Nat. Acad. Sci. USA* **99** (2) (2002) 5565-558.
- [22] B. R. Levin, Frequency-dependent selection in bacterial populations, *Phil. Trans. R. Soc. Lond.* **B 319** (1988) 459-472.



- [23] M. Llabres, S. Agust, Picophytoplankton cell death induced by UV radiation: evidence for oceanic Atlantic communities, *Limnology and Oceanography* **51** (2006) 2129.
- [24] J. Monod, La technique de culture continue, theorie et applications, *Ann. Inst. Pasteur* **79** (1950) 390-410.
- [25] M. Murata, T. Yasumoto, The structure elucidation and biological activities of high molecular weight algal toxins: maitotoxin, prymnesins and zooxanthellatoxins, *Nat. Prod. Rep.* **17** (2000) 293-314.
- [26] M. A. Riley, J. E. Wertz, Bacteriocins: evolution, ecology, and application, *Annual Review of Microbiology* **56** (2002) 117-137.
- [27] H. L. Smith and P. Waltman, The Gradostat: A Model of Competition Along a Nutrient Gradient, *Microbial Ecology* **22** (1991) 207-226.
- [28] H. L. Smith and P. Waltman, *The Theory of the Chemostat: Dynamics of Microbial Competition*, Cambridge University, Cambridge 1995.
- [29] H. L. Smith, B. Tang, Competition in the gradostat: the role of the communication rate, *J. Math. Biol.* **27** (1989) 139-165.
- [30] H. L. Smith, personal communication.
- [31] R. W. Sterner, J. J. Elser, *Ecological Stoichiometry*, Princeton University Press, 2002.
- [32] B. Tang, G.S.K. Wolkowicz, Mathematical models of microbial growth and competition in the chemostat regulated by cell-bound extracellular enzymes, *J. Math. Biol.* **31** (1992) 1-23.
- [33] H. R. Thieme, Asymptotically autonomous differential equations in the plane, *Rocky Mountain Journal of Mathematics*, **24** (1994) 351-380.
- [34] D. Tilman, S. S. Kilham, P. Kilham, Phytoplankton community ecology: the role of limiting nutrients, *Annu. Rev. Ecol. Syst.* **13** (1982) 349-372.

- [35] G.S.K. Wolkowicz, Z. Lu, Global Dynamics of a Mathematical Model of Competition in the Chemostat: General Response Functions and Differential Death Rates, *SIAM J. Appl. Math.* **52** (1992) 222-233.

## **BIOGRAPHICAL STATEMENT**

Ian Pablo Martines was born in Alaska in 1977 and raised in rural West Texas. He began college at The University of Texas-Permian Basin, choosing the major of Computer Science with a minor of Geology. A keen academic advisor switched the minor to Mathematics, a change which seemed meaningless at the time but was life changing. He graduated in 2000 from Southwest Texas State University, now Texas State-San Marcos, with a degree in Computer Science. Ian then went on to earn a Master's degree in 2004 from Texas Tech University in Mathematics under the supervision of Edward Allen. He completed his Ph.D. in Mathematics at The University of Texas at Arlington under the direction of Hristo Kojouharov.