MATHEMATICAL MODELS INVOLVING MULTIPLE RESOURCE LIMITATION

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Abstract

A model of the chemostat involving two populations of microorganisms competing for two perfectly substitutable resources is developed and analyzed. A general class of functions is used to describe nutrient uptake, one which allows for the effect that the concentration of each resource has on the amount of the other resource consumed. The model significantly generalizes those previously studied. The dynamics of this model are then compared with the dynamics of the classical growth and two-species competition models, as well as models involving two perfectly complementary resources.

It is not surprising that the above competition for two resources can result in the coexistence of the two competitor populations. However, an example is also given in which the extinction of one population is averted by the introduction of its competitor. Thus, exploitation of common resources promotes diversity in some circumstances. This situation is investigated further and a more general description is given.

A model of single-species growth on two resources is then presented. For a given dilution rate, the medium in the growth vessel is enriched by increasing the input concentration of one of the resources. Enrichment is considered beneficial if the carrying capacity of the environment is increased. Analytic methods are used to determine the effects of enrichment on the asymptotic behaviour of the model for different dilution rates. The existence of a threshold value for the dilution rate is established. For dilution rates below the threshold, enrichment is beneficial, regardless of which resource is used to enrich the environment. When the dilution rate is increased beyond the threshold, it becomes important to consider which resource is used to enrich the environment. For one of the resources it is shown that, while moderate enrichment can be beneficial, sufficient enrichment leads to the extinction of the population. For the other resource, enrichment leads from washout or initial condition dependent outcomes to survival, and is thus beneficial.

The growth model is then extended to include a single predator population. Using the threshold value for the dilution rate established in the growth model, the

effects of enrichment on the asymptotic behaviour of the resultant predator-prey model are investigated. Here, enrichment is considered beneficial if it can lead from washout for some positive initial conditions to survival of both species for any positive initial conditions. For dilution rates below the threshold, enrichment is beneficial, regardless of which resource is used for enrichment. As in the growth model, it becomes important to consider which resource is used to enrich the environment when the dilution rate is above the threshold. For one of the resources, moderate enrichment can be beneficial, while sufficient enrichment leads to a regime in which washout is possible. For the other resource, sufficient enrichment is beneficial.

To my parents

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Now, to the guzzintas ...

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1 Preliminaries

1.1 Introduction

The classical theory of species interaction, attributed to Lotka [32] and Volterra [58], is an extension of the basic logistic model for single-species growth due to Verhulst [57]. The appeal of this theory lies in its generality and simplicity. For example, in the case of competition, it seeks to describe how the numbers of competitors change without indicating the resources upon which competition is based or how these resources are used by the consumer. As it is difficult to estimate the parameters of the classical competition model governing the extent of interaction without actually growing the species together, these models are often more phenomenological than predictive.

In response to these deficiencies, a more mechanistic, resource-based theory has developed (see, for example, [24], [31], [38], [39]). The resources are incorporated into the models to capture consumer-resource interactions as well as interspecific interactions. The resulting mathematical models may be less general and more difficult to analyze. (See, for example, [1], [3], [4], [8], [10], [12], [25], [26], [27], [60], and [65].) However, these models are often predictive, because the parameters can be measured on species grown alone, in advance of competition (see, for example, Hansen and Hubbell [22]). The models we consider involve this resource-based approach.

The chemostat is a laboratory apparatus that was developed to provide a controlled environment in which the growth of microbial populations could be studied under nutrient limitation. (See Novick and Sziliard [39].) It is used for the continuous culture of microorganisms. The apparatus can be thought to consist of three components: a feed vessel, a growth or culture vessel, and a receptacle. (See Figure 1.1.) The feed vessel contains near-optimal levels of all required nutrients with the exception of the nutrients under investigation. These are maintained at growth limiting levels. The contents of the feed vessel are supplied to the culture vessel at a constant rate, while the medium in the culture vessel is removed to the receptacle at the same rate. Thus, constant volume is maintained. The culture vessel, containing one or more populations of microorganisms, is continuously stirred. Thus, nutrients, microorganisms, and byproducts are removed in proportion to their concentrations.

In this thesis we are interested in studying models of population growth and species interaction under chemostat-like conditions. In all of the models it is assumed that there are two resources supplied in growth limiting amounts.

1.2   Thesis Outline

In this thesis we consider models of growth, exploitative competition and predation under chemostat-like conditions. In Chapter 2 we formulate a general model involving two populations of microorganisms competing for two nonreproducing, growth limiting resources in a chemostat, and then focus on perfectly substitutable resources. León and Tumpson [31] considered a model of perfectly substitutable resources in which the amount of each resource consumed is assumed to be independent of the concentration of the other resource. We extend their analysis and then consider a new model involving a class of response functions that takes into consideration the effect that the concentration of each resource has on the amount of the other resource consumed. This new model includes, as a special case, the model studied by Waltman, Hubbell, and Hsu [60] in which Michaelis-Menten functional response for a single resource is generalized to two perfectly substitutable resources. Analytical methods are used to obtain information about the qualitative behaviour of the models. The range of possible dynamics of model I of León and Tumpson [31] and our new model is then compared. The dynamics of these models for perfectly substitutable resources are also compared with the dynamics of the classical growth and two-species competition models as well as models involving two perfectly complementary resources.

One surprising outcome allowed by the competition model is investigated in further detail in the next chapter. Exploitative competition is usually thought of as a factor that reduces the diversity of natural ecosystems. In Chapter 3 we consider a scenario based in a chemostat in which the extinction of a population is averted by the introduction of a population that interacts only by depleting the common pool of resources, thus promoting greater diversity.

In Chapter 4, a model of single-species growth in the chemostat on two nonreproducing, growth limiting, noninhibitory, perfectly substitutable resources is considered. Here, nutrient uptake is specified to be the two-resource generalization of Michaelis-Menten functional response for a single resource studied by Waltman, Hubbell, and Hsu [60]. The medium in the growth vessel is enriched by increasing the input concentration of one of the resources. Analytical methods are used to determine the effects of this enrichment on the asymptotic behaviour of the model for different

dilution rates.

In Chapter 5 we extend the model considered in Chapter 4 to include a predator population. While the prey-resource interaction is described as above, a general class of functions is used to describe the predator-prey interaction. Analytical methods are used to determine the effects of enrichment on the asymptotic behaviour of the resultant four-dimensional model.

1.3   Notation

The following notation is used throughout this thesis.

R denotes the real numbers

$$\mathbf{R}^n = \{(x_1, \ldots, x_n) : x_i \in \mathbf{R}, i = 1, \ldots, n\}$$

$$\mathbf{R}^n_+ = \{(x_1, \ldots, x_n) \in \mathbf{R}^n : x_i \geq 0, i = 1, \ldots, n\}$$

*int***A** denotes the interior of the set **A**

*cl***A** denotes the closure of the set **A**

$\mathcal{O}(X)$ denotes the entire orbit through the point X

$\Omega(X)$ denotes the omega limit set of the orbit through X

$M^s(E)$ denotes the stable manifold of the equilibrium point E

All other notation is either standard or is defined independently for each chapter.
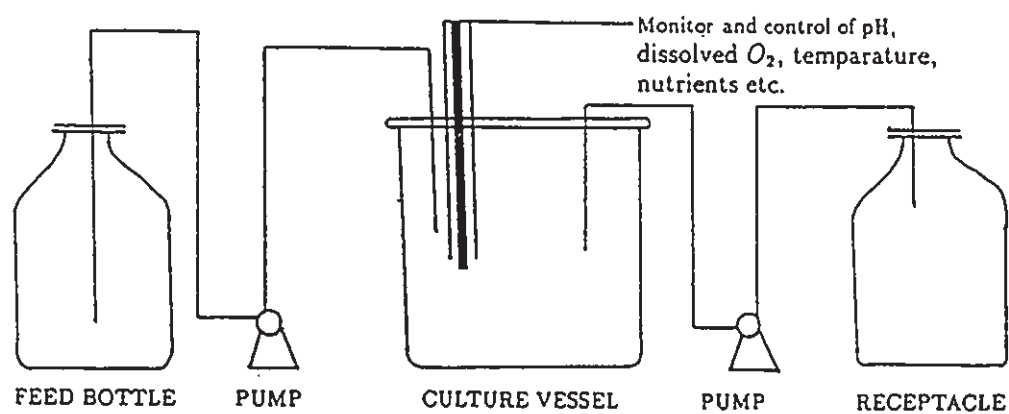
1.4 Figure

Figure 1.1: Schematic Diagram of the Chemostat

2 Exploitative Competition in the Chemostat for Two Perfectly Substitutable Resources

2.1 Introduction

In this chapter we examine a model of competition for multiple resources under chemostat-like conditions. There are many articles devoted to such studies; as a very incomplete sample of these, we mention [1], [3], [4], [12], [15], [23], [26], [27], [31], [36], [41], [49], [53], [54], and [56]. Here we restrict our attention to exploitative competition for two nonreproducing resources. With two resources available, it is important to consider how, once consumed, they are used by the individual competitors. This leads to the classification of resources as perfectly complementary, perfectly substitutable, and imperfectly substitutable (see León and Tumpson [31] and Rapport [42]).

This chapter is organized as follows. First we describe a resource-based model of exploitative, two-species competition in the chemostat for two growth limiting, nonreproducing resources. We have found that many of the characteristics of such a model can be described without restricting one's attention to specific resource types. We then describe the classification of resources provided by León and Tumpson [31] and Rapport [42] and specify the model in the extreme cases.

For the remainder, we consider the perfectly substitutable case. First, as in León and Tumpson [31], we focus on functional responses that are strictly monotone increasing functions of resource concentrations. Implicit in their model is the further assumption that the amount of each resource consumed is independent of the concentration of the other resources. Under the assumption that an interior equilibrium exists, León and Tumpson [31] derive necessary and sufficient conditions for its local asymptotic stability and hence conditions for coexistence of the competitors. In this setting, restricting our attention to nonreproducing resources (in [31] both reproducing and nonreproducing resources are considered), we extend their work by giving a complete global analysis of the three-dimensional subsystems describing the growth of one species on the two resources. We then provide conditions that are necessary and

sufficient to guarantee uniform persistence in the full four-dimensional competition model (i.e., coexistence of both species independent of their initial concentrations). Thus, these conditions are sufficient to guarantee the existence of a coexistence equilibrium. We then extend their model to a more general and more realistic setting, incorporating the possible inhibitory effects that the concentration of one resource may have on the consumption of the other, since the time spent handling one resource may reduce the amount of time available for handling the other resource. The model studied by Waltman, Hubbell, and Hsu [60] is a special case. They specifically generalize the Monod model involving Michaelis-Menten functional response for a single resource to two perfectly substitutable resources. In the general setting, under the assumption that the intrinsic death rate is insignificant compared to the dilution rate, we give a complete global analysis of the three-dimensional subsystems describing the growth of one species on the two resources. Assuming differential death rates in the full four-dimensional competition model, we provide a characterization of those nutrient concentrations that yield coexistence equilibria. We use this characterization to obtain sufficient conditions for the existence of such equilibria and then consider local asymptotic stability. We provide an interesting example in which one species cannot survive in the absence of a competitor but for which there is a locally asymptotically stable coexistence equilibrium in the presence of a competitor. Finally, we provide conditions under which the competition model and the related three dimensional one-species growth models are uniformly persistent.

We conclude the chapter with a discussion in which we summarize our results and then examine the similarities and differences in the range of possible dynamics of our model and the classical model, the perfectly substitutable model studied in [31], and the perfectly complementary model studied in [31] and [12], restricting our attention to noninhibitory resources.

2.2   Two Resource Competition: A General Framework

We discuss exploitative competition in the chemostat for two nonreproducing resources. In the two-competitor case, the dynamical system may be written

$$
\begin{aligned}
S'(t) &= (S^\circ - S(t))\frac{D}{V} - \sum_{i=1}^{2} x_i(t)\mathcal{U}_{S_i}(S(t), R(t)), \\
R'(t) &= (R^\circ - R(t))\frac{D}{V} - \sum_{i=1}^{2} x_i(t)\mathcal{U}_{R_i}(S(t), R(t)), \\
x'_i(t) &= x_i(t)(-\frac{D_i}{V} + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2, \\
&\quad S(0) \geq 0, \ R(0) \geq 0, \ x_i(0) \geq 0, \ i = 1, 2.
\end{aligned}
\tag{2.1}
$$

We identify (S, R, x_1, x_2)-space with $\mathbf{R}_+^4$. Assuming, for convenience, that the volume V of suspension in the culture vessel is one cubic unit, the quantities in (2.1) are described as follows. In these equations, $x_i(t)$ is the biomass of the ith population of microorganisms in the culture vessel at time t, $i = 1$, 2, while $S(t)$ and $R(t)$ represent the concentrations of the two nonreproducing resources in the culture vessel at time t. If only one feed bottle is used, S° and R° are the concentrations of resource S and resource R, respectively, in the feed bottle. The constant D is the input rate from the feed bottle to the culture vessel as well as the washout rate from the culture vessel to the receptacle. Thus constant volume is maintained. We assume that there is perfect mixing in the culture vessel so that nutrients, microorganisms, and byproducts are removed in proportion to their concentrations. The constant D_i denotes the rate at which population x_i is eliminated from competition, either by death or by removal to the receptacle. Therefore, $D_i = D + \epsilon_i$, $\epsilon_i \geq 0$, where ϵ_i is the intrinsic death rate of population x_i, assumed to be a constant.

The functions $\mathcal{U}_{S_i}(S, R)$ and $\mathcal{U}_{R_i}(S, R)$ represent the rate of consumption of resources S and R, respectively, per unit of biomass of population x_i as functions of the concentrations of S and R in the culture vessel. It is generally assumed that

$$
\mathcal{U}_{S_i}, \ \mathcal{U}_{R_i} : \mathbf{R}_+^2 \longrightarrow \mathbf{R}_+,
\tag{2.2}
$$

and that

$$
\mathcal{U}_{S_i}, \ \mathcal{U}_{R_i} \text{ are continuously differentiable almost everywhere.}
\tag{2.3}
$$

It is natural to expect that if the concentration of resource S in the culture vessel is zero, there will be no consumption of resource S. A similar statement holds for resource R. Therefore,

$$\mathcal{U}_{S_i}(0, R) = 0 \text{ for all } R \geq 0,$$

$$(2.4)$$

$$\mathcal{U}_{R_i}(S, 0) = 0 \text{ for all } S \geq 0.$$

In focusing on the consumer-resource interactions, we wish to describe each population's functional response, that is, how the consumption rate of each population changes in response to fluctuations in resource concentrations. We assume that the rate of consumption of each resource is a monotone increasing function of the concentration of that resource. Thus,

$$\frac{\partial}{\partial S}\mathcal{U}_{S_i}(S, R) \geq 0 \text{ for almost all } (S, R) \in int\mathbf{R}_+^2,$$

$$(2.5)$$

$$\frac{\partial}{\partial R}\mathcal{U}_{R_i}(S, R) \geq 0 \text{ for almost all } (S, R) \in int\mathbf{R}_+^2.$$

Why we require (2.5) to hold for almost all $(S, R) \in int\mathbf{R}_+^2$ rather than for all $(S, R) \in int\mathbf{R}_+^2$ will be explained later when we specify the model in the complementary resource case.

The function $\mathcal{G}_i(S, R)$ represents the rate of conversion of nutrient to biomass of population x_i as a function of the concentrations of resources S and R in the culture vessel. The properties of $\mathcal{G}_i(S, R)$ will be discussed later when we discuss the perfectly complementary case and the perfectly substitutable case.

Let $\mathcal{S}_i(S, R)$ denote the rate of conversion of nutrient S to biomass of population x_i. Assuming that the conversion of nutrient to biomass is proportional to the amount of nutrient consumed, the consumption rate of resource S per unit of competitor x_i is of the form

$$\mathcal{U}_{S_i}(S, R) = \frac{\mathcal{S}_i(S, R)}{\xi_i},$$

$$(2.6)$$

where ξ_i is the corresponding growth yield constant. Similarly, the rate of consumption of resource R per unit of competitor x_i is of the form

$$\mathcal{U}_{R_i}(S, R) = \frac{\mathcal{R}_i(S, R)}{\eta_i}, \tag{2.7}$$

where $\mathcal{R}_i(S, R)$ is the rate of conversion of nutrient R to biomass of population x_i and η_i is the corresponding growth yield constant.

An important consideration that arises in the two resource case is how the resources, once consumed, are used by the individual competitors for growth. Rapport [42] and León and Tumpson [31] classify resources in terms of consumer needs. This classification yields a spectrum of resource types and hence a continuum of competitive situations. At opposite extremes are the perfectly complementary and perfectly substitutable resources.

Between these extremes, we have the imperfectly substitutable resources. Although more realistic, this situation is more difficult to study as the nature of the corresponding conversion functions $\mathcal{S}_i(S, R)$, $\mathcal{R}_i(S, R)$ and $\mathcal{G}_i(S, R)$ is less clear. Hence, competitive situations involving the extreme resource types are examined initially. By understanding the similarities and differences we may be able to increase our understanding of the dynamics in the intermediate cases.

Perfectly complementary resources are substances that fulfill different essential needs in terms of growth and so must be taken together by the consumer. These resources must be used in fixed proportions to maintain a given rate of growth. If a higher growth rate is to be attained, it is necessary to increase the consumption rate of both resources. For example, a nitrogen source and a carbon source might be perfectly complementary for a bacterium. Following Butler and Wolkowicz [12], but restricting our attention to noninhibitory resources, we now describe the functions $\mathcal{S}_i(S, R)$, $\mathcal{R}_i(S, R)$ and $\mathcal{G}_i(S, R)$ in the perfectly complementary case.

Let $h_i(S)$ denote the rate of conversion of resource S to biomass of population x_i when resource S alone is limiting. Similarly, let $k_i(R)$ denote the rate of conversion of resource R to biomass of population x_i when resource R alone is limiting. It is assumed that

$$h_i, \; k_i \; : \; \mathbf{R}_+ \longrightarrow \mathbf{R}_+, \tag{2.8}$$

$$h_i, \ k_i \text{ are continuously differentiable,} \qquad (2.9)$$

and that

$$h_i'(S) > 0 \text{ for all } S > 0 \text{ and } k_i'(R) > 0 \text{ for all } R > 0. \qquad (2.10)$$

For given concentrations of resources S and R, say $(\bar{S}, \bar{R})$, only one resource is, in fact, limiting, the one that is in relatively short supply, unless $h_i(\bar{S}) = k_i(\bar{R})$. The other resource, in comparison, can be thought of as being in abundant supply because increasing its concentration would not affect the growth rate. Thus, if resource S is limiting at $(\bar{S}, \bar{R})$, the conversion rate is given by $\mathcal{G}_i(\bar{S}, \bar{R}) = h_i(\bar{S})$. The consumption rate of the limiting resource S is given by $\mathcal{U}_{S_i}(\bar{S}, \bar{R}) = (1/\xi_i)h_i(\bar{S})$, and the rate of consumption of the nonlimiting resource R is $\mathcal{U}_{R_i}(\bar{S}, \bar{R}) = (1/\eta_i)h_i(\bar{S})$. Note that $\mathcal{U}_{R_i}(\bar{S}, \bar{R}) = (\xi_i/\eta_i)\mathcal{U}_{S_i}(\bar{S}, \bar{R})$. That is, the rate of consumption of the nonlimiting resource is proportional to the rate of consumption of the limiting resource, the constant of proportionality being the ratio of the growth yield constants ξ_i and η_i.

Thus, if the resources are perfectly complementary, the rate of conversion of nutrient to biomass of population x_i is given by $\mathcal{G}_i(S, R) = \min\{h_i(S), k_i(R)\}$, the rate of consumption of S is $\mathcal{U}_{S_i}(S, R) = (1/\xi_i)\mathcal{G}_i(S, R)$, and the rate of consumption of R is $\mathcal{U}_{R_i}(S, R) = (1/\eta_i)\mathcal{G}_i(S, R)$. In this case, system (2.1) becomes

$$
\begin{aligned}
S'(t) &= (S^\circ - S(t))\frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i}\min\{h_i(S), k_i(R)\}, \\
R'(t) &= (R^\circ - R(t))\frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i}\min\{h_i(S), k_i(R)\}, \qquad (2.11) \\
x_i'(t) &= x_i(t)(-\frac{D_i}{V} + \min\{h_i(S), k_i(R)\}), \quad i = 1, \ 2,
\end{aligned}
$$

$$S(0) \geq 0, \ R(0) \geq 0, \ x_i(0) \geq 0, \ i = 1, \ 2.$$

Note that at points where $h_i(S) = k_i(R)$, it is unlikely that $\mathcal{U}_{S_i}(S, R), \mathcal{U}_{R_i}(S, R)$, and $\mathcal{G}_i(S, R)$ are differentiable. It is for this reason that we require (2.5) to hold only for almost all $(S, R) \in int\mathbf{R}_+^2$.

This is precisely Model III of León and Tumpson [31] adapted to the chemostat. If $D_i = D$, $i = 1$, 2, that is, the death rate of each population is assumed to be negligible compared to the dilution rate, then (2.11) is precisely the model studied

by Butler and Wolkowicz [12] in the noninhibitory kinetics case. If we further assume that the h_i's and k_i's satisfy Michaelis-Menten dynamics, this is the model studied by Hsu, Cheng and Hubbell [26].

Perfectly substitutable resources are alternative sources of the same essential nutrient. In this case, the rates of consumption of the different resources can be substituted in a fixed ratio to maintain a given growth rate. An example for a bacterium would be two carbon sources or two nitrogen sources.

For the remainder of this chapter we assume that resources S and R of system (2.1) are perfectly substitutable for both populations x_1 and x_2.

2.3 The Model in the Substitutable Case

The model that we consider is

$$
\begin{aligned}
S'(t) &= (S^\circ - S(t))\frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} \mathcal{S}_i(S(t), R(t)), \\
R'(t) &= (R^\circ - R(t))\frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} \mathcal{R}_i(S(t), R(t)), \\
x_i'(t) &= x_i(t)(-\frac{D_i}{V} + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2, \\
S(0) &\geq 0, \ R(0) \geq 0, \ x_i(0) \geq 0, \ i = 1, 2.
\end{aligned}
\tag{2.12}
$$

Since perfectly substitutable resources are alternative sources of the same essential nutrient, the rate of conversion of nutrient to biomass of population x_i is made up of a contribution from the consumption of resource S as well as a contribution from the consumption of resource R. Therefore,

$$
\mathcal{G}_i(S(t), R(t)) = \mathcal{S}_i(S(t), R(t)) + \mathcal{R}_i(S(t), R(t)).
\tag{2.13}
$$

We strengthen hypothesis (2.3) by assuming that

$$
\mathcal{S}_i, \mathcal{R}_i \text{ are continuously differentiable.}
\tag{2.14}
$$

The rate of consumption of each resource is assumed to be a strictly monotone increasing function of the concentration of that resource. Thus, hypothesis (2.5) becomes

$$
\frac{\partial}{\partial S}\mathcal{S}_i(S, R) > 0 \text{ and } \frac{\partial}{\partial R}\mathcal{R}_i(S, R) > 0 \text{ for all } (S, R) \in int\mathbf{R}_+^2.
\tag{2.15}
$$

It should be noted that with two resources available, both serving the same need, it becomes necessary to determine how changes in the concentration of one resource affect the consumption rate of the other. It seems natural to assume that increasing the available amount of one resource might result in a reduction in the amount of the other resource consumed. In Holling terminology [24], the handling time devoted to the processing of a unit of one resource is time no longer available for the processing of the other resource. This is reflected in the assumption that

$$\frac{\partial}{\partial R}\mathcal{S}_i(S,R) \leq 0 \text{ and } \frac{\partial}{\partial S}\mathcal{R}_i(S,R) \leq 0 \quad \text{for all} \quad (S,R) \in \mathbf{R}_+^2. \tag{2.16}$$

By (2.4), (2.6), and (2.7),

$$\mathcal{S}_i(0,R) = 0 \text{ for all } R \geq 0 \quad \text{and} \quad \mathcal{R}_i(S,0) = 0 \text{ for all } S \geq 0. \tag{2.17}$$

Define

$$p_i(S) = \mathcal{S}_i(S,0) \text{ for all } S \geq 0 \quad \text{and} \quad q_i(R) = \mathcal{R}_i(0,R) \text{ for all } R \geq 0. \tag{2.18}$$

That is, $p_i(S)/\xi_i$ is the function describing the uptake of nutrient S in the absence of nutrient R. Similarly, $q_i(R)/\eta_i$ is the function describing the uptake of nutrient R in the absence of nutrient S. We assume that both $p_i(S)$ and $q_i(R)$ are strictly monotone increasing functions.

Further, define λ_i and μ_i so that

$$\mathcal{G}_i(\lambda_i,0)(= p_i(\lambda_i)) = D_i \text{ and } \mathcal{G}_i(0,\mu_i)(= q_i(\mu_i)) = D_i. \tag{2.19}$$

Thus λ_i and μ_i represent the breakeven concentrations for resources S and R, respectively, when none of the other resource is available. By the monotonicity of $p_i(S)$, λ_i is a uniquely defined extended positive real number provided we assume that $\lambda_i = \infty$ if $\mathcal{G}_i(S,0) < D_i$ for all $S \geq 0$. A similar statement can be made for μ_i and $q_i(R)$ provided we assume that $\mu_i = \infty$ if $\mathcal{G}_i(0,R) < D_i$ for all $R \geq 0$.

If the amount of each resource consumed is independent of the concentration of the other resource, that is, if $\mathcal{S}_i(S,R) = p_i(S)$ and $\mathcal{R}_i(S,R) = q_i(R)$ for all $S \geq 0$ and $R \geq 0$, then model (2.12) reduces to Model I of León and Tumpson [31], adapted to the chemostat. However, model (2.12) allows for a more realistic selection of functions

describing resource consumption — functions that take into consideration the possible effects that the availability of one resource has on how much of the other resource is consumed.

With this in mind, we make the following assumptions regarding the functions that describe the rate of conversion of nutrient to biomass, $\mathcal{G}_i(S, R)$. Let

$$m_{S_i} = \lim_{S \to \infty} p_i(S) \quad \text{and} \quad m_{R_i} = \lim_{R \to \infty} q_i(R) \tag{2.20}$$

denote the maximal growth rates of population x_i on resources S and R, respectively, when none of the other resource is available. Assume that one of the resources, say S, is superior in the sense that

$$m_{S_i} \geq m_{Ri}. \tag{2.21}$$

Then it seems reasonable to assume that the more of resource S that is consumed, the better, that is,

$$\frac{\partial \mathcal{G}_i}{\partial S} > 0 \quad \text{for all} \quad (S, R) \in \operatorname{int}\mathbf{R}_+^2. \tag{2.22}$$

However, if the inequality in (2.21) is strict, a critical concentration of S, say S_i^c, is assumed to exist such that

$$\frac{\partial \mathcal{G}_i}{\partial R} > 0 \quad \text{for all} \quad R > 0, 0 < S < S_i^c,$$

$$\tag{2.23}$$

$$\frac{\partial \mathcal{G}_i}{\partial R} < 0 \quad \text{for all} \quad R > 0, S > S_i^c,$$

where S_i^c is related to m_{R_i} in the following manner:

$$\mathcal{G}_i(S_i^c, R) = m_{R_i} \quad \text{for all} \quad R \geq 0. \tag{2.24}$$

Thus when both resources are in *relatively* short supply, increasing the concentration of either resource is beneficial. However, once resource S is plentiful enough that m_{R_i} would be exceeded by consuming only resource S, the presence of resource R would actually become detrimental. In any case, the presence of resource R would never be detrimental enough to decrease $\mathcal{G}_i(S, R)$ below m_{R_i}.

$$\lim_{R \to \infty} \mathcal{G}_i(S, R) = \lim_{R \to \infty} q_i(R) = m_{R_i} \quad \text{for each fixed} \quad S \geq 0. \tag{2.25}$$

It is also assumed that $\mathcal{G}_i(S,R)$ can never increase above m_{S_i}, the maximal growth rate of population x_i on resource S when there is no resource R available, since an abundance of S and no R would be optimal for the growth of population x_i.

$$\lim_{S\to\infty} \mathcal{G}_i(S,R) = \lim_{S\to\infty} p_i(S) = m_{S_i} \quad \text{for each fixed} \quad R \geq 0. \tag{2.26}$$

If, instead, $m_{R_i} > m_{S_i}$, a critical concentration of R, say R_i^c, can be defined in an analogous manner, making the appropriate changes in assumptions (2.22)–(2.26). If $m_{R_i} = m_{S_i}$, define $R_i^c = S_i^c = \infty$.

The following technical lemma summarizes some important consequences of assumptions (2.19)–(2.26). Also see Figure 2.1. An analogous result holds if $m_{R_i} > m_{S_i}$.

Lemma 2.1 (a) *If $m_{S_i} \geq m_{R_i}$, then*

(i) $\mathcal{G}_i(S,R) < m_{R_i}$ *if $R \geq 0$ and $0 \leq S < S_i^c$,*

(ii) $\mathcal{G}_i(S,R) > m_{R_i}$ *if $R \geq 0$ and $S > S_i^c$, and*

(iii) $\mathcal{G}_i(S,R) < m_{S_i}$ *if $R \geq 0$ and $S \geq 0$.*

(b) *If $m_{S_i} \geq m_{R_i}$ and μ_i is finite, then*

(i) $m_{R_i} > D_i$, *and*

(ii) λ_i *is finite and $\lambda_i < S_i^c$.*

(c) *If $m_{S_i} \geq m_{R_i}$ and $\mu_i = \infty$, then either*

(i) $m_{R_i} < D_i$ *and $\lambda_i > S_i^c$ or $\lambda_i = S_i^c = \infty$, or*

(ii) $m_{R_i} = D_i$ *and $\lambda_i = S_i^c \leq \infty$.*

Proof: Recall that $S_i^c = \infty$ if $m_{S_i} = m_{R_i}$.

(a)(i,ii) These follow from (2.22) and (2.24).

(a)(iii) If $m_{S_i} = m_{R_i}$, then the result follows immediately from (a)(i), since $S_i^c = \infty$. Suppose $m_{S_i} > m_{R_i}$. If $0 \leq S \leq S_i^c$, then by (a)(i) and (2.24), $\mathcal{G}_i(S,R) \leq m_{R_i} < m_{S_i}$ for all $R \geq 0$. If $S > S_i^c$, then $\mathcal{G}_i(S,0) \geq \mathcal{G}_i(S,R)$ for all $R \geq 0$ and, by (2.22), $\mathcal{G}_i(S,0) \leq \lim_{S\to\infty} \mathcal{G}_i(S,0) = m_{S_i}$.

(b)(i) $m_{R_i} = \mathcal{G}_i(S_i^c, \mu_i) > \mathcal{G}_i(0, \mu_i) = D_i$.

(b)(ii) See Figure 2.1(a). Since, in (b)(i), $m_{S_i} \geq m_{R_i} > D_i$, it follows that λ_i is finite. If $m_{S_i} = m_{R_i}$, then $S_i^c = \infty$. If $m_{S_i} > m_{R_i}$, then S_i^c is finite and $\mathcal{G}_i(S_i^c, 0) = m_{R_i} > D_i = \mathcal{G}_i(\lambda_i, 0)$.

(c) See Figure 2.1(b) and (c). $\mu_i = \infty$ implies that $\mathcal{G}_i(0, R) < D_i$ for all $R \geq 0$. This implies that $m_{R_i} = \lim_{R \to \infty} \mathcal{G}_i(0, R) \leq D_i$. If $S_i^c = \infty$, then $\mathcal{G}_i(S, 0) < m_{R_i} \leq D_i$ for all $S \geq 0$, and so $\lambda_i = \infty$. If S_i^c is finite, then $\mathcal{G}_i(S_i^c, 0) = m_{R_i} \leq D_i = \mathcal{G}_i(\lambda_i, 0)$. ∎

The functions $\mathcal{S}_i(S, R)$ and $\mathcal{R}_i(S, R)$ in Waltman et al. [60] generalize the familiar Michaelis-Menten prototype of functional response to a single resource and are given by

$$\mathcal{S}_i(S, R) = \frac{m_{S_i} S}{K_{S_i}(1 + S/K_{S_i} + R/K_{R_i})},$$

$$\mathcal{R}_i(S, R) = \frac{m_{R_i} R}{K_{R_i}(1 + S/K_{S_i} + R/K_{R_i})}, \tag{2.27}$$

where m_{S_i}, m_{R_i}, K_{S_i} and K_{R_i} are positive constants, so that

$$\mathcal{G}_i(S, R) = \frac{(m_{S_i}/K_{S_i})S + (m_{R_i}/K_{R_i})R}{1 + S/K_{S_i} + R/K_{R_i}}. \tag{2.28}$$

The functions $\mathcal{S}_i(S, R)$ and $\mathcal{R}_i(S, R)$ in (2.27) satisfy all assumptions (2.14)–(2.18) and $\mathcal{G}_i(S, R)$ in (2.28) satisfies all assumptions (2.13) and (2.19)–(2.26). In fact,

$$\lambda_i = \begin{cases} \dfrac{D_i K_{S_i}}{m_{S_i} - D_i} & \text{if } m_{S_i} > D_i, \\ \infty & \text{otherwise,} \end{cases} \quad \text{and} \quad \mu_i = \begin{cases} \dfrac{D_i K_{R_i}}{m_{R_i} - D_i} & \text{if } m_{R_i} > D_i, \\ \infty & \text{otherwise.} \end{cases} \tag{2.29}$$

Also,

$$\frac{\partial \mathcal{G}_i}{\partial S} = \frac{R(m_{S_i} - m_{R_i}) + m_{S_i} K_{R_i}}{K_{S_i} K_{R_i}(1 + S/K_{S_i} + R/K_{R_i})^2}$$

$$\frac{\partial \mathcal{G}_i}{\partial R} = \frac{S(m_{R_i} - m_{S_i}) + m_{R_i} K_{S_i}}{K_{S_i} K_{R_i}(1 + S/K_{S_i} + R/K_{R_i})^2}. \tag{2.30}$$

If $m_{S_i} > m_{R_i}$, then

$$S_i^c = \frac{m_{R_i} K_{S_i}}{m_{S_i} - m_{R_i}}.$$

If $S_i(S, R) = p_i(S)$ and $R_i(S, R) = q_i(R)$ for all $S \geq 0$ and $R \geq 0$, as in Model I of León and Tumpson [31], then (2.13)–(2.22) hold but (2.23)–(2.26) do not hold. Since $G_i(S, R) = p_i(S) + q_i(R)$, $\partial G_i / \partial R > 0$ for all $R > 0$ and $S > 0$, and $\sup_{(S,R) \in \mathbf{R}_+^2} G_i(S, R) = m_{S_i} + m_{R_i}$ in this case.

2.3.1 The Scaled Version: Some Preliminary Results

It follows immediately from (2.12) that if S^o and R^o are both zero, then neither species survives. Also, if only one of S^o or R^o is zero, say $S^o = 0$ and $R^o \neq 0$, then

$$S'(t) = -S(t)\frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} S_i(S(t), R(t)) \leq -S(t)\frac{D}{V}.$$

Therefore, $S(t) \leq S(0)e^{-\frac{D}{V}t}$, and so for sufficiently large t, (2.12) is approximated by

$$
\begin{aligned}
S'(t) &= 0, \\
R'(t) &= (R^o - R(t))\frac{D}{V} - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} q_i(R(t)), \\
x_i'(t) &= x_i(t)(-\frac{D_i}{V} + q_i(R(t))), \quad i = 1, \, 2,
\end{aligned}
$$

$$S(0) = 0, \; R(0) \geq 0, \; x_i(0) \geq 0, \; i = 1, \, 2.$$

This is the model of exploitative competition in the chemostat for one limiting resource studied by Wolkowicz and Lu [65]. They considered n competitors and allowed both monotone kinetics and inhibitory kinetics. They extended some of the results of Butler and Wolkowicz [10], who restricted $D_i = D$ for $i = 1, ..., n$. Under the additional assumption that q_i assumes the form of Michaelis-Menten kinetics, the model is the Monod model examined by Hsu, Hubbell and Waltman [27] in the case $D_i = D$ for $i = 1, ..., n$ and by Hsu [25] in the differential death rate case. For our purposes, we assume that neither S^o nor R^o is zero.

It will be more convenient to analyze the model after the following substitutions:

$$\bar{t} = t\frac{D}{V}, \ \bar{S} = \frac{S}{S^o}, \ \bar{R} = \frac{R}{R^o},$$

$$\bar{S}_i(\bar{S}, \bar{R}) = \frac{VS_i(S, R)}{D}, \ \bar{\mathcal{R}}_i(\bar{S}, \bar{R}) = \frac{V\mathcal{R}_i(S, R)}{D}, \ \bar{\mathcal{G}}_i(\bar{S}, \bar{R}) = \frac{V\mathcal{G}_i(S, R)}{D}, \quad (2.31)$$

$$\bar{\epsilon}_i = \frac{\epsilon_i}{D}, \ \bar{x}_i = \frac{x_i}{S^o}, \ \bar{\eta}_i = \frac{R^o}{S^o}\eta_i.$$

Removing the bars to simplify notation, we obtain

$$S'(t) \ = \ 1 - S(t) - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} S_i(S(t), R(t)),$$

$$R'(t) \ = \ 1 - R(t) - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} \mathcal{R}_i(S(t), R(t)), \quad (2.32)$$

$$x_i'(t) \ = \ x_i(t)(-D_i + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2,$$

$$S(0) \geq 0, \ R(0) \geq 0, \ x_i(0) \geq 0, \ i = 1, 2.$$

All of the corresponding assumptions hold for this version of the model, so there will be no loss of generality if we study (2.32) instead of (2.12). Our results can be reinterpreted in terms of the unscaled variables using (2.31).

We first note that all solutions of (2.32) are positive and bounded. These are minimum requirements for a reasonable model of the chemostat.

Theorem 2.2 (a) *All solutions $S(t), R(t), x_i(t), i = 1, 2,$ of (2.32) for which $x_i(0) > 0, \ i = 1, 2$ are positive and bounded for $t > 0$.*

(b) *Given any $\delta > 0$, for all solutions $S(t), \ R(t)$ of (2.32), $S(t) < 1 + \delta$ and $R(t) < 1 + \delta$ for all sufficiently large t.*

(c) *If there exists a $t_o \geq 0$ such that $S(t_o) \leq 1$, then $S(t) < 1$ for all $t > t_o$. A similar result holds for $R(t)$.*

Proof: The proof of (a) is similar to the proof given in [10]. In fact, by considering

$$z(t) = S(t) + R(t) + \frac{x_1(t)}{\max\{\xi_1, \eta_1\}} + \frac{x_2(t)}{\max\{\xi_2, \eta_2\}},$$

it can be shown that

$$z(t) \leq \begin{cases} 2 & \text{if } z(0) < 2, \\ z(0) & \text{otherwise.} \end{cases}$$

The proofs of (b) and (c) are immediate from (2.32). ∎

Remark concerning Theorem 2.2:

Suppose

$$\frac{\xi_1}{\eta_1} = \frac{\xi_2}{\eta_2} \tag{2.33}$$

$$D_i = 1, \; i = 1, \, 2, \tag{2.34}$$

and define

$$z(t) = \xi_1 S(t) + \eta_1 R(t) + x_1(t) + \frac{\xi_1}{\xi_2} x_2(t).$$

Then from (2.32), $z'(t) = (\xi_1 + \eta_1) - z(t)$ so that $z(t) = [z(0) - (\xi_1 + \eta_1)]e^{-t} + (\xi_1 + \eta_1)$ and $z(t) \to (\xi_1 + \eta_1)$ as $t \to \infty$. Therefore, under assumptions (2.33) and (2.34), system (2.32) is conservative in the sense that the simplex

$$\{(S, R, x_1, x_2) \in \mathbf{R}_+^4 : \xi_1 S + \eta_1 R + x_1 + \frac{\xi_1}{\xi_2} x_2 = (\xi_1 + \eta_1)\}$$

is a global attractor for (2.32). Although there is some biological merit in assumption (2.33), our analysis does not require (2.33) or (2.34).

Theorem 2.3 *The equilibrium solution $E_o = (1, 1, 0, 0)$ is locally asymptotically stable for (2.32) if $\mathcal{G}_i(1, 1) < D_i$ for $i = 1, 2$, and E_o is unstable if $\mathcal{G}_i(1, 1) > D_i$ for $i = 1$ or 2.*

Proof: See Section 3.3 for the local stability analysis. ∎

The next result concerns competition-independent extinction of a population. It gives conditions under which there is total washout of both competing species.

Theorem 2.4 *Define $\Gamma_\epsilon \equiv \{(S, R) : 0 \leq S \leq 1 + \epsilon, 0 \leq R \leq 1 + \epsilon\}$. Assume that $m_{S_i} \geq m_{R_i}$.*

(a) *If either (μ_i is finite and $\mathcal{G}_i(1, 1) < D_i$) or ($\mu_i = \infty$ and $\lambda_i > 1$), then there exists a $\delta_i > 0$ such that $\max_{(S,R) \in \Gamma_{\delta_i}} \mathcal{G}_i(S, R) < D_i$.*

(b) *If either (μ_i is finite and $\mathcal{G}_i(1,1) < D_i$) or ($\mu_i = \infty$ and $\lambda_i \geq 1$), then $x_i(t) \to 0$ as $t \to \infty$, in (2.32).*

(c) *If $x_i(t) \to 0$ as $t \to \infty$ for $i = 1,2$, then $E_o = (1,1,0,0)$ is globally asymptotically stable for (2.32) with respect to all solutions satisfying $x_i(0) \geq 0$ for $i = 1,2$.*

Proof: (a) Since $m_{S_i} \geq m_{R_i}$, it follows from Lemma 2.1 2(b) that if μ_i is finite, then λ_i is finite. Therefore, it suffices to consider the following three cases:

1. μ_i and λ_i are both finite,
2. $\mu_i = \infty$, but λ_i is finite,
3. $\mu_i = \infty$ and $\lambda_i = \infty$.

Case 1. By hypothesis $\mathcal{G}_i(1,1) < D_i$. By Lemma 2.1 (b)(ii), $\lambda_i < S_i^c$ and so $D_i = \mathcal{G}_i(\lambda_i,0) < \mathcal{G}_i(\lambda_i,1)$. If $\lambda_i \leq 1$, then $D_i < \mathcal{G}_i(\lambda_i,1) \leq \mathcal{G}_i(1,1) < D_i$, a contradiction. It follows that $\lambda_i > 1$. Therefore, $\delta_i > 0$ can be chosen sufficiently small that $S_i^c > 1 + \delta_i$ and, by the continuity of $\mathcal{G}_i$, so that $\mathcal{G}_i(1 + \delta_i, 1 + \delta_i) < D_i$. Therefore, $\max_{(S,R)\in\Gamma_{\delta_i}} \mathcal{G}_i(S,R) = \mathcal{G}_i(1 + \delta_i, 1 + \delta_i) < D_i$.

Case 2. By hypothesis, $\lambda_i > 1$. By Lemma 2.1(c), $\lambda_i \geq S_i^c$, and so either $\lambda_i > 1 \geq S_i^c$ or $\lambda_i \geq S_i^c > 1$. If $\lambda_i > 1 \geq S_i^c$, then $\mathcal{G}_i(1,1) \leq \mathcal{G}_i(1,0) < \mathcal{G}_i(\lambda_i,0) = D_i$ and if $\lambda_i \geq S_i^c > 1$, then $\mathcal{G}_i(1,1) < \mathcal{G}_i(S_i^c,1) = m_{R_i} \leq D_i$. In either case, it follows that $\mathcal{G}_i(1,1) < D_i$, and hence, by the continuity of $\mathcal{G}_i$, there exists $\delta_i > 0$ such that $\mathcal{G}_i(1 + \delta_i, 1 + \delta_i) < D_i$ and $\lambda_i > 1 + \delta_i$. If $\lambda_i > 1 \geq S_i^c$, then $\max_{(S,R)\in\Gamma_{\delta_i}} \mathcal{G}_i(S,R) = \mathcal{G}_i(1 + \delta_i, 0) < \mathcal{G}_i(\lambda_i, 0) = D_i$, and if $\lambda_i \geq S_i^c > 1$, δ_i can be chosen so that $S_i^c > 1 + \delta_i$, and so $\max_{(S,R)\in\Gamma_{\delta_i}} \mathcal{G}_i(S,R) = \mathcal{G}_i(1 + \delta_i, 1 + \delta_i) < D_i$.

Case 3. In this case, since $\mu_i = \infty$ and $\lambda_i = \infty, m_{R_i} \leq m_{S_i} \leq D_i$. Therefore, for any fixed $\delta_i > 0$, if $(\bar{S},\bar{R}) \in \Gamma_{\delta_i}$, then $\mathcal{G}_i(\bar{S},\bar{R}) < \lim_{S\to\infty} \mathcal{G}_i(S,\bar{R}) = m_{S_i} \leq D_i$.

(b) Suppose that either μ_i is finite and $\mathcal{G}_i(1,1) < D_i$, or $\mu_i = \infty$ and $\lambda_i > 1$. Choose $\delta_i > 0$ as in part (a). By Theorem 2.2(b), $S(t) < 1 + \delta_i$ and $R(t) < 1 + \delta_i$ for all sufficiently large t, and so, by (2.32), $x_i'(t) < 0$ for all sufficiently large t. Also, $x_i''(t)$ is bounded below. It follows, by a result of Miller [37], that $x_i'(t) \to 0$ as $t \to \infty$. However, $\limsup_{t\to\infty} \mathcal{G}_i(S(t),R(t)) \leq \max_{(S,R)\in\Gamma_{\delta_i}} \mathcal{G}_i(S,R) < D_i$, and so the only possibility is that $x_i(t) \to 0$ as $t \to \infty$.

Suppose that $\mu_i = \infty$ and $\lambda_i = 1$. Without loss of generality, assume that $i = 1$.

First, consider $m_{R_1} = D_1$. Then $S_1^c = \lambda_1$. By Theorem 2.2(c), either $S(t) > 1$ for all $t \geq 0$ or $S(t) < 1$ for all sufficiently large t.

Suppose $S(t) > 1$ for all $t \geq 0$. Then $S'(t) < 0$ for all $t \geq 0$, so that $S(t) \searrow S^* \geq 1$. If $S^* > 1$, then $S'(t) \leq 1 - S(t) \leq 1 - S^* < 0$, so that $S(t) \to -\infty$ as $t \to \infty$, a contradiction. Therefore, $S(t) \searrow 1$ as $t \to \infty$. Since $S(t) > 1$ for all $t \geq 0$, $\mathcal{G}_1(S(t), R(t)) > D_1$ for all $t \geq 0$ by Lemma 2.1(a)(ii). Then $x_1'(t) > 0$ for all $t \geq 0$, so that $x_1(t) \nearrow x_1^* > 0$. Define $R_{\max} = \sup\{R(t) : t \geq 0\}$. Then $R_{\max} \leq \max\{R(0), 1\}$, so

$$S'(t) \leq 1 - S(t) - \frac{x_1(t)}{\eta_1} S_1(S(t), R(t)) \leq -\frac{x_1(0)}{\eta_1} S_1(1, R_{\max}) < 0,$$

so that $S(t) \to -\infty$ as $t \to \infty$, a contradiction.

Therefore, $S(t) < 1$ for all sufficiently large t. By part 1(a) of Lemma 2.1, $\mathcal{G}_1(S(t), R(t)) < D_1$ for all sufficiently large t, so that $x_1'(t) < 0$ for all sufficiently large t. Therefore, $x_1(t) \searrow x_1^* \geq 0$. Since $x_1''(t)$ is bounded, $x_1'(t) \to 0$ as $t \to \infty$. If $x_1^* > 0$, then $\mathcal{G}_1(S(t), R(t)) \to D_1$ as $t \to \infty$, implying that $S(t) \to 1$ as $t \to \infty$. But then $S'(t) < 0$ for all sufficiently large t. Since $S(t) < 1$ for all sufficiently large t, $S(t)$ cannot decrease to 1. This contradiction implies that $x_1^* = 0$.

Now consider $m_{R_1} < D_1$. Then $S_1^c < \lambda_1 = 1$. Again, either $S(t) > 1$ for all $t \geq 0$ or $S(t) < 1$ for all sufficiently large t.

Suppose $S(t) > 1$ for all $t \geq 0$. As above, $S(t) \searrow 1$ as $t \to \infty$. If $\liminf_{t \to \infty} x_1(t) > 0$, then there exists $\epsilon > 0$ such that $x_1(t) > \epsilon$ for all sufficiently large t. Then

$$S'(t) \leq 1 - S(t) - \frac{x_1(t)}{\eta_1} S_1(S(t), R(t)) \leq -\frac{\epsilon}{\eta_1} S_1(1, R_{\max}) < 0$$

for all sufficiently large t, so $S(t) \to -\infty$ as $t \to \infty$, a contradiction. Therefore, $\liminf_{t \to \infty} x_1(t) = 0$.

Suppose $\limsup_{t \to \infty} x_1(t) = x_1^* > 0$. Then there exist sequences of consecutive local minima $\{\tau_n\}_{n=1}^{\infty}$ and consecutive local maxima $\{\sigma_n\}_{n=1}^{\infty}$ of $x_1(t)$ satisfying $\tau_n \to$

∞, $\sigma_n \to \infty$ as $n \to \infty$, $\tau_n < \sigma_n < \tau_{n+1} < \sigma_{n+1}$,

$$x_1'(\tau_n) = 0 = x_1'(\sigma_n),$$

$$x_1'(t) \geq 0 \quad \text{if} \quad \tau_n < t < \sigma_n,$$
$$x_1'(t) \leq 0 \quad \text{if} \quad \sigma_n < t < \tau_{n+1}.$$

Therefore, since $x_1(t) > 0$ for all $t \geq 0$,

$$
\begin{aligned}
\mathcal{G}_1(S(\tau_n), R(\tau_n)) &= D_1 &= \mathcal{G}_1(S(\sigma_n), R(\sigma_n)), \\
\mathcal{G}_1(S(t), R(t)) &\geq D_1 &\text{if} \quad \tau_n < t < \sigma_n, \\
\mathcal{G}_1(S(t), R(t)) &\leq D_1 &\text{if} \quad \sigma_n < t < \tau_{n+1}.
\end{aligned}
\tag{2.35}
$$

But then $R(\tau_n) = \varphi_1(S(\tau_n))$ for all n. Since $\varphi_1(1) = 0, \varphi_1(S)$ is continuous, and $S(\tau_n) \to 1$ as $n \to \infty$, $R(\tau_n) \to 0$ as $n \to \infty$. Now,

$$R'(\tau_n) = 1 - R(\tau_n) - \frac{x_1(\tau_n)}{\xi_1}\mathcal{R}_1(S(\tau_n), R(\tau_n)) - \frac{x_2(\tau_n)}{\xi_2}\mathcal{R}_2(S(\tau_n), R(\tau_n)).$$

Since $R(\tau_n) \to 0$ as $n \to \infty$, $\mathcal{R}_i(S(\tau_n), R(\tau_n)) \to 0$, $i = 1, 2$, as $n \to \infty$ by (2.17), and since $x_i(t)$ is bounded for all $t \geq 0$, $R'(\tau_n) \to 1$ as $n \to \infty$. Therefore, $S'(\tau_n) < 0$ and $R'(\tau_n) > 0$ for all sufficiently large n, and so there exists an $N > 0$ and an $\epsilon(N) > 0$ such that $\mathcal{G}_1(S(t), R(t)) < \mathcal{G}_1(S(\tau_N), R(\tau_N)) = D_1$ for all $\tau_N < t < \tau_N + \epsilon(N)$, contradicting (2.35). Therefore, $\limsup_{t \to \infty} x_1(t) = 0$, and hence $\lim_{t \to \infty} x_1(t) = 0$.

If $S(t) < 1$ for all sufficiently large t, then the proof of $x_1(t) \to 0$ as $t \to \infty$ is similar to the proof given for $m_{R_1} = D_1$.

(c) Take $Q \in \{(S, R, x_1, x_2) \in \mathbf{R}_+^4 : x_1 > 0, x_2 > 0\}$. Let $\Omega(Q)$ denote the omega limit set of the orbit through Q. By the hypothesis, any $P = (\underline{S}, \underline{R}, \underline{x}_1, \underline{x}_2) \in \Omega(Q)$ satisfies $\underline{x}_1 = 0$ and $\underline{x}_2 = 0$. On $\{(S, R, 0, 0) \in \mathbf{R}_+^4\}$ the system reduces to

$$S'(t) = 1 - S(t),$$
$$R'(t) = 1 - R(t),$$

and hence $S(t) \to 1$ and $R(t) \to 1$. Therefore, $\{E_o\} \in \Omega(Q)$. By Theorem 2.2, $\Omega(Q)$ is a nonempty, compact subset of $\mathbf{R}_+^4$. If $P \in \Omega(Q)$, then the entire trajectory through P is in $\Omega(Q)$. Hence, E_o is the only candidate.∎

Remarks concerning Theorem 2.4:

1. An analogous result holds if $m_{R_i} \geq m_{S_i}$. Just interchange the roles of λ_i and μ_i in the previous theorem.

2. It can be shown that if $\mathcal{S}_i(S, R) = p_i(S)$ and $\mathcal{R}_i(S, R) = q_i(R)$ for all $S \geq 0$ and $R \geq 0$, as in the model of León and Tumpson [31], then $\mathcal{G}_i(1, 1) < D_i$ implies $x_i(t) \to 0$ as $t \to \infty$ regardless of the relative values of m_{S_i}, m_{R_i}, and D_i.

Next we discuss subsistence curves, $\varphi_i(S)$ and $\sigma_i(R)$, in the (S, R)-plane. These are curves that give the concentrations of S and R at which the biomass of population x_i in the culture vessel is neither increasing nor decreasing.

Lemma 2.5 (a) *If λ_i and μ_i are both finite, then there exist C^1 functions $\varphi_i(S)$ and $\sigma_i(R)$ satisfying*

$$\varphi_i : [0, \lambda_i] \longrightarrow [0, \mu_i], \ \sigma_i : [0, \mu_i] \longrightarrow [0, \lambda_i],$$

$$\mathcal{G}_i(S, \varphi_i(S)) = D_i, \ \mathcal{G}_i(\sigma_i(R), R) = D_i,$$

$$\varphi_i'(S) < 0, \ \sigma_i'(R) < 0.$$

(b) *If $m_{S_i} > D_i > m_{R_i}$, and $0 < \lambda_i \leq 1$, then there exist C^1 functions $\varphi_i(S)$ and $\sigma_i(R)$ satisfying*

$$\varphi_i : [\lambda_i, M_i^S] \longrightarrow [0, 1], \ \sigma_i : [0, \varphi_i(M_i^S)] \longrightarrow [\lambda_i, M_i^S],$$

$$\mathcal{G}_i(S, \varphi_i(S)) = D_i, \ \mathcal{G}_i(\sigma_i(R), R) = D_i,$$

$$\varphi_i'(S) > 0, \ \sigma_i'(R) > 0,$$

where

$$M_i^S \equiv \max_{\substack{\lambda_i \leq S \leq 1, \\ \mathcal{G}_i(S, 1) \leq D_i}} S. \tag{2.36}$$

(c) *If $m_{R_i} > D_i > m_{S_i}$, and $0 < \mu_i \leq 1$, then there exist C^1 functions $\varphi_i(S)$ and $\sigma_i(R)$ satisfying*

$$\sigma_i : [\mu_i, M_i^R] \longrightarrow [0, 1], \quad \varphi_i : [0, \sigma_i(M_i^R)] \longrightarrow [\mu_i, M_i^R],$$

$$\mathcal{G}_i(S, \varphi_i(S)) = D_i, \quad \mathcal{G}_i(\sigma_i(R), R) = D_i,$$

$$\varphi_i'(S) > 0, \quad \sigma_i'(R) > 0,$$

where

$$M_i^R \quad \equiv \quad \max_{\substack{\mu_i \leq R \leq 1, \\ \mathcal{G}_i(1,R) \leq D_i}} R. \qquad (2.37)$$

Proof: (a) By Lemma 2.1 and (2.19), $\mathcal{G}_i(S, 0) < D_i$ and $\mathcal{G}_i(S, \mu_i) > D_i$ for each $S \in (0, \lambda_i)$. Therefore, by (2.14), (2.22), and (2.23), to each fixed $S \in (0, \lambda_i)$, there corresponds a unique $R_S \in (0, \mu_i)$ such that $\mathcal{G}_i(S, R_S) = D_i$. Define $\varphi_i : [0, \lambda_i] \longrightarrow [0, \mu_i]$ by setting $\varphi_i(S) = R_S$. Then $\mathcal{G}_i(S, \varphi_i(S)) = D_i$ for all $0 \leq S \leq \lambda_i$. In view of (2.22) and (2.23), by a straightforward application of the Implicit Function Theorem, it follows that $\varphi_i \in C^1$ and $\varphi_i'(S) < 0$ for all $0 < S < \lambda_i$.

In a similar manner, one can define a function $\sigma_i : [0, \mu_i] \longrightarrow [0, \lambda_i]$ such that $\mathcal{G}_i(\sigma_i(R), R) = D_i$ for all $0 \leq R \leq \mu_i$, with $\sigma_i \in C^1$ and $\sigma_i'(R) < 0$ for all $0 < R < \mu_i$.

(b) In this case, by Lemma 2.1(c), $\lambda_i > S_i^c$ and so $\mathcal{G}_i(\lambda_i, 1) < D_i$. Thus, $\mathcal{G}_i(S, 0) > D_i$ and $\mathcal{G}_i(S, 1) < D_i$ for each $S \in (\lambda_i, M_i^S)$. Therefore, by (2.14), (2.22), and (2.23), for each fixed $S \in [\lambda_i, M_i^S]$, there corresponds a unique $R_S \in [0, 1]$ such that $\mathcal{G}_i(S, R_S) = D_i$. Define $\varphi_i : [\lambda_i, M_i^S] \longrightarrow [0, 1]$ by setting $\varphi_i(S) = R_S$. Continue now as in the proof of (a).

(c) The proof is similar to the proof of (b). ∎

Remarks concerning Lemma 2.5:

1. Note that $M_i^S = 1$ if and only if $\mathcal{G}_i(M_i^S, 1) = \mathcal{G}_i(1, 1) \leq D_i$. This implies that $\varphi_i(M_i^S) \leq 1$. Also, $M_i^S < 1$ if and only if $\mathcal{G}_i(1, 1) > \mathcal{G}_i(M_i^S, 1) = D_i$. This implies that $\varphi_i(M_i^S) = 1$.

2. For the functions (2.27) and (2.28), the subsistence curves

$$\varphi_i(S) = \left(1 + S\left(\frac{D_i - m_{S_i}}{D_i K_{S_i}}\right)\right)\left(\frac{D_i K_{R_i}}{m_{R_i} - D_i}\right)$$

and

$$\sigma_i(R) = \left(1 + R\left(\frac{D_i - m_{R_i}}{D_i K_{R_i}}\right)\right)\left(\frac{D_i K_{S_i}}{m_{S_i} - D_i}\right)$$

are both linear functions.

Before proceeding, we discuss the function $\mathcal{G}_i(S, R)$ described above in the context of the classifications given by Rapport [42], León and Tumpson [31], and Tilman [56] and relate the subsistence curves to what they call indifference curves. Assume $m_{S_i} \geq m_{R_i}$. Consider

$$\Phi_i(S, R) \equiv \frac{x_i'}{x_i} = \mathcal{G}_i(S, R) - D_i = C,$$

where C is any constant such that $-D_i < C < m_{S_i} - D_i$. The curve $\Phi_i(S, R) = C$ projected onto the $(\mathcal{S}_i(S, R), \mathcal{R}_i(S, R))$ plane gives an indifference curve, that is, a curve along which any combination of values of $\mathcal{S}_i(S, R)$ and $\mathcal{R}_i(S, R)$ gives the same rate of growth C. By (2.13), these curves are linear and decreasing, precisely as in Figure 1D of [42] and Figure 1(a) of [31]. Since $\Phi_i(S, R) = 0 = \Phi_i(S, \varphi_i(S)) = \Phi_i(\sigma_i(R), R)$, these curves can be projected into the (S, R) plane. Under our assumptions, Figure 2.2 depicts the indifference curves in the (S, R) plane in the case that $m_{S_i} > m_{R_i}$. For $C = m_{R_i} - D_i$, the indifference curve in (S, R)-space is the vertical line $S = S_i^c$. For $C < m_{R_i} - D_i$, the indifference curves are decreasing, and for $C > m_{R_i} - D_i$, they are increasing. If $m_{S_i} = m_{R_i}$, so that $S_i^c = R_i^c = \infty$, then the indifference curves in the (S, R) plane are decreasing. In the special case that the indifference curves in the (S, R) plane are linear, as is the case when $\mathcal{G}_i(S, R)$ is defined by (2.28) (see Remark 2 following Lemma 2.5), then resources S and R are perfectly substitutable in the sense of Tilman [56]. In the classification in [56], the resources S and R are considered perfectly substitutable if S and R, rather than the rates of consumption of S and R, can be substituted in a fixed ratio in order to maintain a given growth rate.

2.3.2 Single Species Growth –
The Three Dimensional Subsystems

There are only two three-dimensional subsystems of (2.32) of interest. Each involves one population of microorganisms consuming the two nonreproducing, perfectly substitutable resources. Due to symmetry, both subsystems exhibit the same set of possible dynamics. Throughout this section, the same notation as in the previous sections is used, but the subscripts are omitted. We examine the system

$$
\begin{aligned}
S'(t) &= 1 - S(t) - \frac{x(t)}{\xi} \mathcal{S}(S(t), R(t)), \\
R'(t) &= 1 - R(t) - \frac{x(t)}{\eta} \mathcal{R}(S(t), R(t)), \\
x'(t) &= x(t)(-d + \mathcal{G}(S(t), R(t))),
\end{aligned}
\tag{2.38}
$$

$$
S(0) \geq 0, \ R(0) \geq 0, \ x(0) \geq 0.
$$

Here, d represents the rate of removal of the microbial population from competition, that is, $d = 1 + \epsilon$, $\epsilon \geq 0$, where ϵ is the intrinsic death rate. The functions $\mathcal{S}(S(t), R(t))$, $\mathcal{R}(S(t), R(t))$, and $\mathcal{G}(S(t), R(t))$ are assumed to satisfy all of the assumptions (2.2)–(2.10) and (2.13)–(2.26).

By Theorem 2.2(a), all solutions $S(t), R(t), x(t)$ of (2.38) for which $x(0) > 0$ are positive and bounded for all $t > 0$. By Theorems 2.3 and 2.4(b), if μ is finite and $\mathcal{G}(1,1) < d$, or if $\mu = \infty$ and $\lambda \geq 1$, then $E_o = (1,1,0)$ is globally asymptotically stable for (2.38) (with respect to solutions for which $x(0) \geq 0$).

Besides $E_o = (1,1,0)$, any other critical points must be one-species survival equilibria. A one-species survival equilibrium of (2.38) is a solution $(\bar{S}, \bar{R}, \bar{x})$ of the system

$$
\begin{aligned}
x\mathcal{S}(S, R) &= \xi(1 - S), \\
x\mathcal{R}(S, R) &= \eta(1 - R), \\
\mathcal{G}(S, R) &= d,
\end{aligned}
\tag{2.39}
$$

with $(\bar{S}, \bar{R}, \bar{x}) \in int\mathbf{R}^3_+$.

Lemma 2.6 *Assume that $m_S \geq m_R$. Suppose that a one-species survival equilibrium $(\bar{S}, \bar{R}, \bar{x})$ of (2.38) exists.*

(a) *If μ is finite, then $0 < \bar{S} < \min\{1, \lambda\}$ and $0 < \bar{R} < \min\{1, \mu\}$.*

(b) *If $\mu = \infty$ and $\lambda \leq 1$, then either*

$$m_R < d, \text{ and so } S^c < \lambda \text{ and } \lambda < \bar{S} < M^S \leq 1, 0 < \bar{R} < \varphi(M^S) \leq 1,$$

or

$$m_R = d, \text{ and so } S^c = \lambda \text{ and } \lambda = \bar{S} < 1, 0 < \bar{R} < 1,$$

where M^S is defined by (2.36).

Proof: First, note that, from (2.39), $\bar{x} > 0$ implies that $0 < \bar{S} < 1$ and $0 < \bar{R} < 1$.

(a) If μ is finite, then, by Lemma 2.1(b)(ii), λ is finite and $\lambda < S^c$. Therefore, $\mathcal{G}(S, R) > \mathcal{G}(S, 0) > \mathcal{G}(\lambda, 0) = d$ for all $S > \lambda, R > 0$; and $\mathcal{G}(S, R) > \mathcal{G}(0, R) > \mathcal{G}(0, \mu) = d$ for all $S > 0, R > \mu$; and so $0 < \bar{S} < \min\{1, \lambda\}$ and $0 < \bar{R} < \min\{1, \mu\}$.

(b) In this case, by Lemma 2.1(c), $S^c \leq \lambda$. First, consider $S^c < \lambda$. Then $\mathcal{G}(S, R) \leq \mathcal{G}(S^c, R) = m_R < d$ for all $0 < S \leq S^c, R > 0$; $\mathcal{G}(S, R) \leq \mathcal{G}(\lambda, R) < \mathcal{G}(\lambda, 0) = d$ for all $S^c < S \leq \lambda, R > 0$; and $\mathcal{G}(S, R) \geq \mathcal{G}(M^S, R) > \mathcal{G}(M^S, \varphi(M^S)) = d$ for all $S \geq M^S, \varphi(M^S) > R > 0$; and so $\lambda < \bar{S} < M^S \leq 1$ and $0 < \bar{R} < \varphi(M^S)$. If, on the other hand, $S^c = \lambda$, then $\mathcal{G}(S^c, R) = d = m_R$ for all $R \geq 0$ and, by Lemma 2.1(a)(i,ii), $\mathcal{G}(S, R) \neq d$ for any $R \geq 0, S \neq S^c$; and so $\lambda = \bar{S} < 1$ and $0 < \bar{R} < 1$. ∎

Theorem 2.7 *Assume that $m_S \geq m_R$.*

(a) *If μ is finite, then a one-species survival equilibrium of (2.38) exists if and only if $\mathcal{G}(1, 1) > d$. When a one-species survival equilibrium exists, it is unique. In particular, if $\lambda < 1$ or $\mu < 1$, then $\mathcal{G}(1, 1) > d$.*

(b) *Suppose $\mu = \infty$.*

(i) *If $\lambda \geq 1$ or $\lambda = \infty$, then (2.38) has no one-species survival equilibrium.*

(ii) *If $m_R = d$, then $\mathcal{G}(1,1) > d$ if and only if $\lambda < 1$, and a one-species survival equilibrium of (2.38) exists if and only if $\mathcal{G}(1,1) > d$. When a one-species survival equilibrium exists, it is unique.*

(iii) *If $m_R < d$, then $\mathcal{G}(1,1) > d$ if and only if $M^S < 1$, and if $\mathcal{G}(1,1) > d$, then (2.38) has at least one one-species survival equilibrium.*

Proof: (a) First we show that if μ is finite and a one-species survival equilibrium $(\bar{S}, \bar{R}, \bar{x})$ exists, then $\mathcal{G}(1,1) > d$. By Lemma 2.6, $0 < \bar{S} < \min\{\lambda, 1\}$ and $0 < \bar{R} < \min\{\mu, 1\}$. By Lemma 2.1(b)(i,ii), $m_R > d$ and $S^c > \lambda > \bar{S}$. If $S^c > 1$, then $d = \mathcal{G}(\bar{S}, \bar{R}) < \mathcal{G}(1, \bar{R}) < \mathcal{G}(1,1)$. If $S^c \leq 1$, then $d < m_R = \mathcal{G}(S^c, 1) \leq \mathcal{G}(1,1)$.

Next we show that if $\mathcal{G}(1,1) > d$, then a one-species survival equilibrium exists. For $S \in (0, \lambda)$, define

$$x_S(S) = \frac{\xi(1-S)}{\mathcal{S}(S, \varphi(S))} \quad \text{and} \quad x_R(S) = \frac{\eta(1 - \varphi(S))}{\mathcal{R}(S, \varphi(S))}, \tag{2.40}$$

where, by Lemma 2.5, $\mathcal{G}(S, \varphi(S)) = d$ for all $0 \leq S \leq \lambda$. If $\mu > 1$, then $\mathcal{G}(0,1) < d$, and since $\mathcal{G}(\lambda, 1) > d$ and $\mathcal{G}(1,1) > d$, there exists a unique $\tilde{S} \in (0, \min\{1, \lambda\})$ such that $\mathcal{G}(\tilde{S}, 1) = d$ and $\varphi(\tilde{S}) = 1$. By Lemma 2.5, $0 < \varphi(S) < \mu$ for $S \in (0, \min\{1, \lambda\})$ if $\mu \leq 1$, and $0 < \varphi(S) < 1$ for $S \in (\tilde{S}, \min\{1, \lambda\})$ if $\mu > 1$. In both cases, by (2.15), (2.16), and Lemma 2.5, $x_S(S)$ is a decreasing function, $x_R(S)$ is an increasing function, and both functions are continuous. There are four cases to consider.

Case 1. $\lambda \leq 1$ and $\mu \leq 1$ (see Figure 2.3(a)).

$$x_S(0) = \infty \qquad \text{and} \quad x_R(0) = \frac{\eta(1-\mu)}{d},$$
$$x_S(\lambda) = \frac{\xi(1-\lambda)}{d} \quad \text{and} \quad x_R(\lambda) = \infty.$$

Case 2. $\lambda > 1$ and $\mu > 1$ (see Figure 2.3(b)).

$$x_S(\tilde{S}) = \frac{\xi(1 - \tilde{S})}{\mathcal{S}(\tilde{S}, 1)} > 0 \quad \text{and} \quad x_R(\tilde{S}) = 0,$$
$$x_S(1) = 0 \qquad \text{and} \quad x_R(1) = \frac{\eta(1 - \varphi(1))}{\mathcal{R}(1, \varphi(1))} > 0.$$

Case 3. $\lambda \leq 1$ and $\mu \geq 1$ (see Figure 2.3(c)).

$$x_S(\tilde{S}) = \frac{\xi(1 - \tilde{S})}{S(\tilde{S}, 1)} > 0 \quad \text{and} \quad x_R(\tilde{S}) = 0,$$

$$x_S(\lambda) = \frac{\xi(1 - \lambda)}{d} \qquad \text{and} \quad x_R(\lambda) = \infty.$$

Case 4. $\lambda \geq 1$ and $\mu \leq 1$ (see Figure 2.3(d)).

$$x_S(0) = \infty \quad \text{and} \quad x_R(0) = \frac{\eta(1 - \mu)}{d},$$

$$x_S(1) = 0 \quad \text{and} \quad x_R(1) = \frac{\eta(1 - \varphi(1))}{\mathcal{R}(1, \varphi(1))}.$$

Therefore, in each case there exists a unique $\hat{S} \in (0, \lambda)$ such that $x_S(\hat{S}) = x_R(\hat{S})$, and hence a unique one-species survival equilibrium, with $\bar{S} = \hat{S}, \bar{R} = \varphi(\hat{S})$, and $\bar{x} = x_S(\hat{S}) = x_R(\hat{S})$.

In particular, since $S^c > \lambda$, if $\lambda < 1$, then $\mathcal{G}(1,1) > \mathcal{G}(\lambda, 1) > d$, and if $\mu < 1$, then $\mathcal{G}(1,1) > \mathcal{G}(0,1) > \mathcal{G}(0, \mu) = d$.

(b)(i) By Theorem 2.4(b), if $\mu = \infty$ and $\lambda \geq 1$, then $x(t) \to 0$ as $t \to \infty$, and so there can be no one-species survival equilibrium.

(b)(ii) If $m_R = d$, then $S^c = \lambda$.

Suppose that $\mathcal{G}(1,1) > d = m_R$. If $\lambda \geq 1$, then $m_R = \mathcal{G}(S^c, 1) = \mathcal{G}(\lambda, 1) \geq \mathcal{G}(1,1) > d = m_R$, a contradiction. It follows that $\lambda < 1$.

Suppose $\lambda < 1$. Then $d = m_R = \mathcal{G}(S^c, 1) = \mathcal{G}(\lambda, 1) < \mathcal{G}(1,1)$, so $\mathcal{G}(1,1) > d$.

Next we show that if $\mathcal{G}(1,1) > d = m_R$, then there exists a unique one-species survival equilibrium. Since $S^c = \lambda$, by Lemma 2.6(b), $\bar{S} = \lambda$, and so $\mathcal{G}(\lambda, R) = d$ for all $R \geq 0$. Therefore, by (2.39), a one-species survival equilibrium exists if and only if R satisfies

$$f(R) \equiv \xi(1 - \lambda)\mathcal{R}(\lambda, R) = \eta(1 - R)S(\lambda, R) \equiv g(R).$$

By (2.15) and (2.16), $f(R)$ is an increasing function and $g(R)$ is a decreasing function on $[0, 1]$, with $f(0) = 0$, $f(1) = \xi(1 - \lambda)\mathcal{R}(\lambda, 1) > 0$, $g(0) = \eta d > 0$, and $g(1) = 0$. (See Figure 2.3(e).) Hence, there exists a unique $\bar{R}$ satisfying $f(\bar{R}) = g(\bar{R})$, and hence

a unique one-species survival equilibrium, $(\lambda, \bar{R}, \tilde{x})$, where

$$\tilde{x} = \frac{\xi(1-\lambda)}{\mathcal{S}(\lambda, \bar{R})} = \frac{\eta(1-\bar{R})}{\mathcal{R}(\lambda, \bar{R})}.$$

Finally, by (b)(i), if a one-species survival equilibrium exists in this case, then $\lambda < 1$, and hence $\mathcal{G}(1,1) > d$.

(b)(iii) If $m_R < d$, then $S^c < \lambda$.

Suppose $m_R < d$ and $\mathcal{G}(1,1) > d$. Since $M^S \leq 1$ and $M^S = 1$ implies that $\mathcal{G}(1,1) \leq d$, it follows that $M^S < 1$.

Suppose $m_R < d$ and $M^S < 1$. Then $\mathcal{G}(1,1) > \mathcal{G}(M^S, 1) = d$.

Next we show that if $m_R < d$ and $\mathcal{G}(1,1) > d$ (and hence $\lambda < M^S < 1$), then at least one one-species survival equilibrium exists. Define $x_S(S)$ and $x_R(S)$ as in (2.40) for $S \in (\lambda, M^S)$, where by Lemma 2.5, $\mathcal{G}(S, \varphi(S)) = d$ for all $S \in [\lambda, M^S]$. Then $\varphi(\lambda) = 0$, $\varphi(M^S) = 1$, and $0 < \varphi(S) < 1$ for all $S \in (\lambda, M^S)$, and so x_S and x_R are continuous for all $S \in (\lambda, M^S)$. Since (see Figure 2.3(f))

$$x_S(\lambda) = \frac{\xi(1-\lambda)}{d} > 0 \quad \text{and} \quad x_R(\lambda) = \infty,$$

$$x_S(M^S) = \frac{\xi(1 - M^S)}{\mathcal{S}(M^S, 1)} > 0 \quad \text{and} \quad x_R(M^S) = 0,$$

there exists at least one point $\hat{S} \in (\lambda, M^S)$ such that $x_S(\hat{S}) = x_R(\hat{S})$. Hence, there exists at least one one-species survival equilibrium, $(\hat{S}, \varphi(\hat{S}), x_S(\hat{S}))$. ∎

Remarks concerning Theorem 2.7:

1. If $m_S < m_R$, an analogous result holds. Just interchange the roles of λ and μ and those of m_S and m_R.

2. If μ is finite, it is possible for $\lambda > 1$, $\mu > 1$, and $\mathcal{G}(1,1) > d$. For example, consider

$$\mathcal{G}(S,R) = \frac{4S + 3R}{1 + S + R}, \quad d = \frac{13}{6}.$$

$\mathcal{G}(1,0) = 2 < d$, and so $\lambda > 1$, $\mathcal{G}(0,1) = 3/2 < d$, and so $\mu > 1$, and $\mathcal{G}(1,1) = 7/3 > d$.

3. If $\mu = \infty$ with $m_R < d$, then $\lambda < 1$ need not imply that $\mathcal{G}(1,1) > d$. Rather, it is possible that $M^S = 1$, and so $\mathcal{G}(1,1) \leq d$. There may or may not be one-species survival equilibria in this case, and multiple one-species survival equilibria are possible. For example, consider

$$\mathcal{G}(S,R) = \frac{4S + R}{1 + S + R}, \quad d = \frac{11}{6}.$$

Then $m_R = 1 < d$, $\mathcal{G}(11/13, 0) = d$, so $\lambda = 11/13 < 1$, but $\mathcal{G}(1,1) = 5/3 < d$.

For a one-species survival equilibrium $(\bar{S}, \bar{R}, \bar{x})$ to exist, by Lemma 2.6(b), $\lambda < \bar{S} < 1$ and $0 < \varphi(\bar{S}) < 1$. Thus $\bar{S} \in (11/13, 1)$, and since $\varphi(S) = (13S - 11)/5, \varphi(\bar{S}) \in (0, 2/5)$. Also, since $\bar{S}$ must satisfy $x_S(\bar{S}) = x_R(\bar{S})$, where $x_S(S)$ and $x_R(S)$ are given in (2.40),

$$\frac{\xi}{\eta} = \frac{4\bar{S}(16 - 13\bar{S})}{(1 - \bar{S})(13\bar{S} - 11)}.$$

Since $\bar{S} \in (11/13, 1)$, it follows that $\xi/\eta > 190.628$ must hold. Therefore, if $\xi/\eta < 190$, then there is no one-species survival equilibrium. However, if $\xi/\eta > 191$, then there is at least one one-species survival equilibrium. In particular, if $\xi = 1/2$ and $\eta = 1/384$, so that $\xi/\eta = 192$, then there are exactly two one-species survival equilibria:

$$(\frac{12}{13}, \frac{1}{5}, \frac{23}{1040}) \text{ and } (\frac{44}{47}, \frac{11}{47}, \frac{153}{8272}).$$

4. Note that if $\mathcal{S}(S,R) = p(S)$ and $\mathcal{R}(S,R) = q(R)$ for all $S \geq 0$ and $R \geq 0$, then, regardless of the relative values of m_S, m_R, and d, a one-species survival equilibrium exists if and only if $\mathcal{G}(1,1) > d$, and if one exists, then it is unique.

Let us denote a one-species survival equilibrium, when it exists, by $E = (\bar{S}, \bar{R}, \bar{x})$. Next we investigate the local stability properties of the equilibria of (2.38) through an examination of the linearized system about each equilibrium.

The eigenvalues of $V_3(1,1,0)$, the variational matrix of (2.38) evaluated at $E_o = (1,1,0)$, are $\alpha_1 = \alpha_2 = -1$ and $\alpha_3 = \mathcal{G}(1,1) - d$. Thus, if $\mathcal{G}(1,1) > d$, then E_o is unstable, and by Theorem 2.7 at least one one-species survival equilibrium

exists. Also, if $\mathcal{G}(1,1) < d$, then E_o is locally asymptotically stable and, provided that $m_R \geq d$ and $m_S \geq d$, no one-species survival equilibrium exists. In fact, by Theorem 2.4, E_o is globally asymptotically stable in this case. However, if $m_R < d$ or $m_S < d$, it is possible for a one-species survival equilibrium to exist even though E_o is locally asymptotically stable. For an example, see Remark 3 following Theorem 2.7.

Let us assume that a one-species survival equilibrium $E = (\bar{S}, \bar{R}, \bar{x})$ exists, and examine the local stability properties of E. The characteristic equation of $V_3(\bar{S}, \bar{R}, \bar{x})$, the variational matrix evaluated at E, is given by $\alpha^3 + A_1\alpha^2 + A_2\alpha + A_3$, where

$$A_1 = 2 + \bar{x}\left(\frac{1}{\xi}\frac{\partial}{\partial S}\mathcal{S}(\bar{S}, \bar{R}) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(\bar{S}, \bar{R})\right), \tag{2.41}$$

$$A_2 = 1 + \bar{x}\left(\frac{1}{\xi}\frac{\partial}{\partial S}\mathcal{S}(\bar{S}, \bar{R}) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(\bar{S}, \bar{R})\right) \tag{2.42}$$

$$+ \bar{x}\left(\frac{1}{\xi}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial S}\mathcal{G}(\bar{S}, \bar{R}) + \frac{1}{\eta}\mathcal{R}(\bar{S}, \bar{R})\frac{\partial}{\partial R}\mathcal{G}(\bar{S}, \bar{R})\right)$$

$$+ \frac{\bar{x}^2}{\xi\eta}\left(\frac{\partial}{\partial S}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial R}\mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial R}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial S}\mathcal{R}(\bar{S}, \bar{R})\right),$$

$$A_3 = \bar{x}\left(\frac{1}{\xi}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial S}\mathcal{G}(\bar{S}, \bar{R}) + \frac{1}{\eta}\mathcal{R}(\bar{S}, \bar{R})\frac{\partial}{\partial R}\mathcal{G}(\bar{S}, \bar{R})\right) \tag{2.43}$$

$$+ \frac{\bar{x}^2}{\xi\eta}d\left(\frac{\partial}{\partial S}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial R}\mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial R}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial S}\mathcal{R}(\bar{S}, \bar{R})\right).$$

If $m_R < d$ or $m_S < d$, the stability of E is, in general, difficult to determine. However, if $m_R \geq d$ and $m_S \geq d$, then by hypotheses (2.13), (2.15), (2.16), (2.22), and (2.23), it follows that

$$\frac{\partial}{\partial S}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial R}\mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial R}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial S}\mathcal{R}(\bar{S}, \bar{R}) > 0. \tag{2.44}$$

Hence, A_1, A_2, and A_3 are all positive so that, by the Routh-Hurwicz Criterion, to determine the stability of E it suffices to determine the sign of $A_1A_2 - A_3$, where $A_1A_2 - A_3$ is given by

$$2 + 3\bar{x}\left(\frac{1}{\xi}\frac{\partial}{\partial S}\mathcal{S}(\bar{S}, \bar{R}) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(\bar{S}, \bar{R})\right) \tag{2.45}$$

$$+ \bar{x}\left(\frac{1}{\xi}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial S}\mathcal{G}(\bar{S}, \bar{R}) + \frac{1}{\eta}\mathcal{R}(\bar{S}, \bar{R})\frac{\partial}{\partial R}\mathcal{G}(\bar{S}, \bar{R})\right)$$

$$+ \quad \bar{x}^2 \frac{1}{\xi} \frac{\partial}{\partial S} \mathcal{S}(\bar{S}, \bar{R}) \left(\frac{1}{\xi} \mathcal{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial S} \mathcal{G}(\bar{S}, \bar{R}) + \frac{1}{\eta} \mathcal{R}(\bar{S}, \bar{R}) \frac{\partial}{\partial R} \mathcal{G}(\bar{S}, \bar{R}) \right)$$

$$+ \quad \bar{x}^2 \frac{1}{\eta} \frac{\partial}{\partial R} \mathcal{R}(\bar{S}, \bar{R}) \left(\frac{1}{\xi} \mathcal{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial S} \mathcal{G}(\bar{S}, \bar{R}) + \frac{1}{\eta} \mathcal{R}(\bar{S}, \bar{R}) \frac{\partial}{\partial R} \mathcal{G}(\bar{S}, \bar{R}) \right)$$

$$+ \quad \bar{x}^2 \left(\frac{1}{\xi} \frac{\partial}{\partial S} \mathcal{S}(\bar{S}, \bar{R}) + \frac{1}{\eta} \frac{\partial}{\partial R} \mathcal{R}(\bar{S}, \bar{R}) \right)^2$$

$$+ \quad \frac{\bar{x}^3}{\xi \eta} \frac{1}{\xi} \frac{\partial}{\partial S} \mathcal{S}(\bar{S}, \bar{R}) \left(\frac{\partial}{\partial S} \mathcal{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial R} \mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial R} \mathcal{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial S} \mathcal{R}(\bar{S}, \bar{R}) \right)$$

$$+ \quad \frac{\bar{x}^3}{\xi \eta} \frac{1}{\eta} \frac{\partial}{\partial R} \mathcal{R}(\bar{S}, \bar{R}) \left(\frac{\partial}{\partial S} \mathcal{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial R} \mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial R} \mathcal{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial S} \mathcal{R}(\bar{S}, \bar{R}) \right)$$

$$+ \quad \frac{\bar{x}^2}{\xi \eta} (2 - d) \left(\frac{\partial}{\partial S} \mathcal{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial R} \mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial R} \mathcal{S}(\bar{S}, \bar{R}) \frac{\partial}{\partial S} \mathcal{R}(\bar{S}, \bar{R}) \right).$$

Assuming that $m_R \geq d$ and $m_S \geq d$, a superficial examination of this expression yields a range of values of the intrinsic death rate ϵ for which $A_1 A_2 - A_3$ is positive and hence E is locally asymptotically stable. In particular, a sufficient condition for the local asymptotic stability of E is $d \leq 2$ (so that $\epsilon \leq 1$). For example, if it is assumed that the intrinsic death rate is insignificant compared to the dilution rate, then $d = 1$, and so E is locally asymptotically stable. Moreover, if, by increasing d, E can lose its stability, it can do so only by means of a Hopf bifurcation, since $A_3 > 0$ implies that no root can equal zero. However, given $p(\alpha) = \alpha^3 + A_1 \alpha^2 + A_2 \alpha + A_3$ with $A_1, A_2,$ and A_3 positive, if $A_1 A_2 - A_3 < 0$, then p has one negative real root and a pair of complex conjugate roots with positive real part. Since, by Theorem 2.7, parts (a) and (b)(ii), E exists only if $\mathcal{G}(1,1) > d$, a Hopf bifurcation can occur only for $2 < d < \mathcal{G}(1,1)$. Therefore, if $m_S \geq d$, $m_R \geq d$, and $\mathcal{G}(1,1) \leq 2$, then no change in stability can occur. Although we have not ruled out the possibility of a Hopf bifurcation, this was not observed in any of the specific examples we studied.

If we assume that $\mathcal{S}(S, R) = p(S)$ and $\mathcal{R}(S, R) = q(R)$ for all $S \geq 0$ and $R \geq 0$, as in Model I of León and Tumpson [31], as long as E exists, $A_1, A_2,$ and A_3 are always positive, and $A_1 A_2 - A_3$ is given by

$$2 \quad + \quad \bar{x} \left\{ 3 \left(\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right) + \frac{p(\bar{S}) p'(\bar{S})}{\xi} + \frac{q(\bar{R}) q'(\bar{R})}{\eta} \right\} \qquad (2.46)$$

$$+ \quad \bar{x}^2 \left\{ \left(\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right)^2 + p(\bar{S}) \left(\frac{p'(\bar{S})}{\xi} \right)^2 + q(\bar{R}) \left(\frac{q'(\bar{R})}{\eta} \right)^2 + \frac{2}{\xi \eta} p'(\bar{S}) q'(\bar{R}) \right\}$$

$$+ \quad \bar{x}^3 \left(\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right) p'(\bar{S}) q'(\bar{R}).$$

Clearly, $A_1 A_2 - A_3$ is also always positive, regardless of the relative values of m_S, m_R, and d. Therefore, by the Routh-Hurwicz Criterion, whenever E exists, it is locally asymptotically stable.

Before examining the global properties of system (2.38), we define the terms persistent and uniformly persistent, as in [17]. Let $f = (f_1, \ldots, f_n)$ be a continuously differentiable function from $\mathbf{R}^n$ to $\mathbf{R}^n$ such that

$$f_i(w) \geq 0 \text{ whenever } w = (w_1, \ldots, w_n) \text{ satisfies } w_i = 0 \text{ and } w_j \geq 0, \ i \neq j.$$

Consider the system

$$w'(t) = f(w(t)), \ w_i(0) \geq 0, \ i = 1, \ldots, n. \tag{2.47}$$

The conditions on f guarantee that (2.47) defines a dynamical system that leaves the positive cone in $\mathbf{R}^n$ positively invariant.

Definition 2.8 *If every solution $w(t) = (w_1(t), \ldots, w_n(t))$ of (2.47) with $w_i(0) > 0$, $i = 1, \ldots, n$, satisfies $\liminf_{t \to \infty} w_i(t) > 0$, $i = 1, \ldots, n$, then system (2.47) is persistent.*

Definition 2.9 *If there exists a number $\delta > 0$ such that every solution $w(t) = (w_1(t), \ldots, w_n(t))$ of (2.47) with $w_i(0) > 0$, $i = 1, \ldots, n$ satisfies $\liminf_{t \to \infty} w_i(t) \geq \delta$, $i = 1, \ldots, n$, then system (2.47) is uniformly persistent.*

Theorem 2.10 *Suppose $\mathcal{G}(1,1) > d$. Then system (2.38) is uniformly persistent with respect to all solutions for which $x(0) > 0$.*

Proof: Identify (S, R, x)-space with $\mathbf{R}^3_+$. Choose $\underline{X} = (S(0), R(0), x(0)) \in int\mathbf{R}^3_+$. By Theorem 2.2(a), $\Omega(\underline{X})$ is a nonempty, compact invariant set with respect to (2.38), and $x(t) > 0$ and bounded. Thus, by (2.14) and (2.17), $S'(t) > 0$ if $S(t)$ is sufficiently

close to zero and $R'(t) > 0$ if $R(t)$ is sufficiently close to zero. Since $S(t)$ and $R(t)$ are also bounded by Theorem 2.2(a), it follows that any point in $\Omega(\underline{X})$ must satisfy $\liminf_{t\to\infty} S(t) > 0$ and $\liminf_{t\to\infty} R(t) > 0$. If we can show that $\liminf_{t\to\infty} x(t) > 0$, then (2.38) is persistent.

Suppose $\{E_o\} \in \Omega(\underline{X})$. Since $\mathcal{G}(1,1) > d$, E_o is an unstable, hyperbolic critical point. From (2.38) it is clear that E_o is globally attracting with respect to solutions initiating in its stable manifold, $M^s(E_o) = \{(S,R,0) \in \mathbf{R}^3_+\}$. Since $\underline{X} \notin M^s(E_o)$, $\{E_o\} \neq \Omega(\underline{X})$. Therefore, by the Butler-McGehee Lemma (see Lemma A1 of [17]), there exists $P \in (M^s(E_o)\backslash\{E_o\}) \cap \Omega(\underline{X})$ and hence $cl\mathcal{O}(P) \subset \Omega(\underline{X})$, where $\mathcal{O}(P)$ denotes the entire orbit through P. But then, as $t \to -\infty$, either $\mathcal{O}(P)$ becomes unbounded or one of the S or R components becomes negative. In either case we have a contradiction, and therefore $\{E_o\} \notin \Omega(\underline{X})$.

Suppose $\liminf_{t\to\infty} x(t) = 0$. Then there exists a point $\tilde{P} = (\underline{S}, \underline{R}, 0) \in \Omega(\underline{X})$, which implies that $cl\mathcal{O}(\tilde{P}) \subset \Omega(\underline{X})$. But then $\{E_o\} \in \Omega(\underline{X})$, a contradiction. Thus $\liminf_{t\to\infty} x(t) > 0$, and so (2.38) is persistent. It now follows from the main result of [8] that system (2.38) is uniformly persistent. ∎

If in (2.38) the intrinsic death rate is assumed to be insignificant compared to the dilution rate, so that $d = 1$, and $m_S \geq 1$ and $m_R \geq 1$, then the results of Theorem 2.10 can be significantly strengthened. We will require the following lemma.

Lemma 2.11 *Assume $d = 1$ in (2.38). The simplex*

$$\mathcal{L} = \{(S,R,x) \in \mathbf{R}^3_+ : \xi S + \eta R + x = \xi + \eta\}$$

is a global attractor for system (2.38).

Proof: Define $z(t) = \xi S(t) + \eta R(t) + x(t)$. Then, since $d = 1$, $z'(t) = (\xi + \eta) - z(t)$, so $z(t) = [z(0) - (\xi + \eta)]e^{-t} + (\xi + \eta)$. ∎

Theorem 2.12 *Assume $d = 1$ in (2.38) .*

(a) *Suppose that $m_S \geq 1$ and $m_R \geq 1$. If $\mathcal{G}(1,1) > 1$, then there exists a unique one-species survival equilibrium E, and E is globally asymptotically stable with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) > 0$.*

(b) *If no one-species survival equilibrium E exists, then E_o is globally asymptotically stable with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) \geq 0$.*

Proof: (a) The existence and uniqueness of the one-species survival equilibrium E is given by Theorem 2.7, parts (a) and (b)(ii).

By Lemma 2.11, the simplex $\mathcal{L}$ is a global attractor, so we restrict our attention to $\mathcal{L}$. Since $\mathcal{L}$ is positively invariant, let $x(t) = \xi(1 - S(t)) + \eta(1 - R(t))$, and consider the system

$$
\begin{aligned}
S'(t) &= 1 - S(t) - \frac{1}{\xi}[\xi(1 - S(t)) + \eta(1 - R(t))]\mathcal{S}(S(t), R(t)), \\
R'(t) &= 1 - R(t) - \frac{1}{\eta}[\xi(1 - S(t)) + \eta(1 - R(t))]\mathcal{R}(S(t), R(t)), \quad (2.48)
\end{aligned}
$$

$$
S(0) \geq 0, R(0) \geq 0, \xi + \eta \geq \xi S(0) + \eta R(0).
$$

There exist precisely two equilibria for system (2.48), $E_o^2 = (1,1)$ and $E^2 = (\bar{S}, \bar{R})$, where the superscript 2 denotes the two-dimensional system (2.48). From the local stability analysis it follows that E^2 is locally asymptotically stable and that E_o^2 is unstable.

Fix $S(t) = 1$ in (2.48) and define

$$
F_1(R(t)) \equiv S'(t) = -\frac{\eta}{\xi}(1 - R(t))\mathcal{S}(1, R(t)).
$$

Then $F_1(1) = 0$, and by (2.2) and (2.16),

$$
\frac{d}{dR}F_1(R) = -\frac{\eta}{\xi}(1 - R)\frac{\partial}{\partial R}\mathcal{S}(1, R) + \frac{\eta}{\xi}\mathcal{S}(1, R) > 0
$$

for all $0 \leq R \leq 1$. Therefore, $S'(t) < 0$ at all points $(1, R)$ where $0 \leq R < 1$.

Fix $S(t) = \bar{S}$ in (2.48), and define

$$
F_2(R(t)) \equiv S'(t) = 1 - \bar{S} - \frac{1}{\xi}[\xi(1 - \bar{S}) + \eta(1 - R(t))]\mathcal{S}(\bar{S}, R(t)).
$$

Then $F_2(\bar{R}) = 0$, and by (2.2) and (2.16),

$$
\frac{d}{dR}F_2(R) = -\frac{1}{\xi}[\xi(1 - \bar{S}) + \eta(1 - R)]\frac{\partial}{\partial R}\mathcal{S}(\bar{S}, R) + \frac{\eta}{\xi}\mathcal{S}(\bar{S}, R) > 0
$$

for all $0 \leq R \leq 1$. Therefore, $S'(t) < 0$ at all points $(\bar{S}, R)$ where $0 \leq R < \bar{R}$, and $S'(t) > 0$ at all points $(\bar{S}, R)$ where $\bar{R} < R \leq 1$.

Similarly, fixing $R(t) = 1$ and $R(t) = \bar{R}$, we obtain the partial vector field shown in Figure 2.4. It is clear that no periodic orbits exist in $\mathcal{L}$. Since $\liminf_{t\to\infty} x(t) > 0$, it follows from the Poincaré-Bendixson Theorem that E^2 is globally asymptotically stable for (2.48) with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$, and $\xi + \eta > \xi S(0) + \eta R(0) > 0$ (i.e., $x(0) \equiv \xi + \eta - \xi S(0) - \eta R(0) > 0$). It follows from Theorem 1.5 of [55] that $E = (\bar{S}, \bar{R}, \bar{x})$, where $\bar{x} = \xi(1 - \bar{S}) + \eta(1 - \bar{R})$, is in the omega limit set of any solution of system (2.38) with $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) > 0$. Since E is locally asymptotically stable for (2.38) with $d = 1$, it follows that it is the only point in the omega limit set, and so it must be globally asymptotically stable for (2.38) with $d = 1$ with respect to all solutions satisfying $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) > 0$.

(b) The proof is similar to the proof of (a). ∎

If in (2.38) $\mathcal{S}(S, R) = p(S)$ and $\mathcal{R}(S, R) = q(R)$ as in Model I of León and Tumpson [31] (with d not necessarily equal to 1), then the results of Theorem 2.10 can again be significantly strengthened, regardless of the relative values of m_S, m_R, and d.

Theorem 2.13 *Assume that $\mathcal{S}(S, R) = p(S)$ and $\mathcal{R}(S, R) = q(R)$ for all $S \geq 0$ and $R \geq 0$.*

(a) *If $\mathcal{G}(1,1) \leq d$, then E_o is globally asymptotically stable for (2.38) with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) \geq 0$.*

(b) *If $\mathcal{G}(1,1) > d$, then there exists a unique one-species survival equilibrium E, and E is globally asymptotically stable for (2.38) with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) > 0$.*

Proof: (b) The proof of existence and uniqueness of the one-species survival equilibrium E is similar to the proof of Theorem 2.7(a). To prove the global stability of this equilibrium, define $L : int\mathbf{R}_+^3 \longrightarrow \mathbf{R}$ by

$$L(S, R, x) = \xi \int_{\bar{S}}^{S} \frac{-p(\bar{S}) + p(\tau)}{p(\tau)} d\tau + \eta \int_{\bar{R}}^{R} \frac{-q(\bar{R}) + q(\tau)}{q(\tau)} d\tau + x - \bar{x} - \bar{x}\ln(\frac{x}{\bar{x}}).$$

Since $p(S)$ and $q(R)$ are continuous on $int\mathbf{R}_+^3$, we have $L \in C^1(int\mathbf{R}_+^3)$. Also, $E = (\bar{S}, \bar{R}, \bar{x})$ is the global minimum of L on $\mathbf{R}_+^3$, and $L(\bar{S}, \bar{R}, \bar{x}) = 0$. The time derivative of L computed along solutions of (2.38) is

$$\dot{L}(S,R,x) = \xi\left(\frac{p(S)-p(\bar{S})}{p(S)}\right)(1-S) + \eta\left(\frac{q(R)-q(\bar{R})}{q(R)}\right)(1-R)$$
$$-\bar{x}(-d+\mathcal{G}(S,R))$$
$$+x(-d+\mathcal{G}(S,R)-(p(S)-p(\bar{S}))-(q(R)-q(\bar{R}))).$$

Noting that

$$\bar{x} = \frac{\xi(1-\bar{S})}{p(\bar{S})} = \frac{\eta(1-\bar{R})}{q(\bar{R})} \text{ and } d = p(\bar{S})+q(\bar{R}),$$

we have

$$\dot{L}(S,R,x) = \xi(p(S)-p(\bar{S}))\left(\frac{1-S}{p(S)} - \frac{1-\bar{S}}{p(\bar{S})}\right)$$
$$+\eta(q(R)-q(\bar{R}))\left(\frac{1-R}{q(R)} - \frac{1-\bar{R}}{q(\bar{R})}\right).$$

For $0 < S < \bar{S}$, $p(S)-p(\bar{S}) < 0$ and $(1-S)/p(S)-(1-\bar{S})/p(\bar{S}) > 0$, whereas for $S > \bar{S}$, $p(S)-p(\bar{S}) > 0$ and $(1-S)/p(S)-(1-\bar{S})/p(\bar{S}) < 0$. A similar result holds for R.

Thus, $\dot{L}(S,R,x) \leq 0$, and so L is a Lyapunov function for (2.38) in $int\mathbf{R}_+^3$. Note that $\dot{L}(S,R,x) = 0$ if and only if $S = \bar{S}$ and $R = \bar{R}$. Hence, by Theorem 2.2(a) and LaSalle's Extension Theorem [30], every solution of (2.38) for which $x(0) > 0$ approaches $\mathcal{M}$, where $\mathcal{M}$ is the largest invariant subset of $\{(S,R,x) \in \mathbf{R}_+^3 : S = \bar{S}, R = \bar{R}, x \geq 0\}$. But then $\mathcal{M} = \{E\}$, a single point, since by Theorem 2.7 the one-species survival equilibrium is unique and since $x \neq \bar{x}$ implies that either $S' \neq 0$ or $R' \neq 0$, $x \neq \bar{x}$ would violate the invariance of $\mathcal{M}$. This completes the proof.

(a) Take

$$L(S,R,x) = \xi\int_1^S \frac{-p(1)+p(\tau)}{p(\tau)}d\tau + \eta\int_1^R \frac{-q(1)+q(\tau)}{q(\tau)}d\tau + x,$$

and argue as in (b). ∎

In the next section we use the information from this section to determine existence and local stability properties of the equilibria of the four dimensional system as well as to determine criteria for uniform persistence of the four dimensional system.

2.3.3 Two-Species Competition –
The Four Dimensional System

We now return to a study of the full four-dimensional system; that is,

$$
\begin{aligned}
S'(t) &= 1 - S(t) - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} \mathcal{S}_i(S(t), R(t)), \\
R'(t) &= 1 - R(t) - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} \mathcal{R}_i(S(t), R(t)), \\
x_i'(t) &= x_i(t)(-D_i + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2,
\end{aligned}
\tag{2.49}
$$

$$
S(0) \geq 0, R(0) \geq 0, x_i(0) \geq 0, i = 1, 2.
$$

Three of the critical points of (2.49) are readily determined and will be denoted

$$
\begin{aligned}
E_o &= (1, 1, 0, 0), \\
E_1 &= (\bar{S}_1, \bar{R}_1, \bar{x}_1, 0), \\
E_2 &= (\bar{S}_2, \bar{R}_2, 0, \bar{x}_2).
\end{aligned}
$$

Conditions for the existence, and in some cases the uniqueness, of equilibria of the form E_i, $i = 1, 2$, are given in Theorem 2.7 (with the appropriate subscripts included and d replaced by D_i).

We first determine the local stability properties of these equilibria of (2.49) through an examination of the linearized system about each equilibrium point.

The eigenvalues of $V_4(1, 1, 0, 0)$, the variational matrix of (2.49) evaluated at $E_o = (1, 1, 0, 0)$, are $\alpha_1 = \alpha_2 = -1$, $\alpha_3 = \mathcal{G}_1(1, 1) - D_1$, and $\alpha_4 = \mathcal{G}_2(1, 1) - D_2$. Thus, if either $\mathcal{G}_1(1, 1) > D_1$ or $\mathcal{G}_2(1, 1) > D_2$, then E_o is unstable, and by Theorem 2.7 at least one one-species survival equilibrium exists. Also, if $\mathcal{G}_1(1, 1) < D_1$ and $\mathcal{G}_2(1, 1) < D_2$, then E_o is locally asymptotically stable and, provided that $m_{S_i} \geq D_i$ and $m_{R_i} \geq D_i$ for $i = 1$ and 2, no one-species survival equilibrium exists. In fact, by Theorem 2.4, E_o is globally asymptotically stable in this case.

Now assume that $\mathcal{G}_1(1, 1) > D_1$, so that $E_1 = (\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$ exists. The characteristic polynomial of $V_4(\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$, the variational matrix of (2.49) evaluated at E_1, is given by

$$
(\alpha - (\mathcal{G}_2(\bar{S}_1, \bar{R}_1) - D_2))(\alpha^3 + A_1\alpha^2 + A_2\alpha + A_3),
$$

where $\alpha^3 + A_1 \alpha^2 + A_2 \alpha + A_3$ is the characteristic polynomial of $V_3(\bar{S}_1, \bar{R}_1, \bar{x}_1)$ given in (2.41)–(2.43) with $\mathcal{S}(S, R) = \mathcal{S}_1(S, R)$, $\mathcal{R}(S, R) = \mathcal{R}_1(S, R)$, $\mathcal{G}(S, R) = \mathcal{G}_1(S, R)$, and $d = D_1$. From this, together with a local stability analysis of the one-species equilibrium in (S, R, x_1)-space, we see that if $m_{S_1} \geq D_1, m_{R_1} \geq D_1, \mathcal{G}_1(1, 1) \leq 2$, and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$, then E_1 is locally asymptotically stable.

In the special case that $\mathcal{S}_1(S, R) = p_1(S)$ and $\mathcal{R}_1(S, R) = q_1(R)$ for all $S \geq 0$ and $R \geq 0$, E_1 exists if and only if $\mathcal{G}_1(1, 1) > D_1$ and is locally asymptotically stable if $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$. A similar result holds for E_2.

If any other equilibria of (2.49) exist, they must be interior equilibria. An interior equilibrium of (2.49) is a solution $E^* = (S^*, R^*, x_1^*, x_2^*)$ of the system

$$\mathcal{G}_1(S, R) = D_1,$$

$$\mathcal{G}_2(S, R) = D_2,$$

(2.50)

together with the system

$$\frac{x_1}{\xi_1} \mathcal{S}_1(S, R) + \frac{x_2}{\xi_2} \mathcal{S}_2(S, R) = 1 - S,$$

$$\frac{x_1}{\eta_1} \mathcal{R}_1(S, R) + \frac{x_2}{\eta_2} \mathcal{R}_2(S, R) = 1 - R,$$

(2.51)

with $(S^*, R^*, x_1^*, x_2^*) \in \text{int} \mathbf{R}_+^4$. As in Lemma 2.6, one can show that S^* and R^* must satisfy the inequalities in Table 2.1. The following theorem is an immediate consequence of Theorem 2.4(b).

Theorem 2.14 *If $(\lambda_i = \infty$ and $\mu_i \geq 1)$ or $(\mu_i = \infty$ and $\lambda_i \geq 1)$ for at least one $i \in \{1, 2\}$, then no interior equilibrium E^* exists.*

Theorem 2.15 (a) *If E^* exists and, for $i = 1$ or $2, m_{S_i} \geq D_i$ and $m_{R_i} \geq D_i$, then E_i exists and is unique.*

(b) *If E^* exists and, for $i = 1$ or 2, $(m_{R_i} < D_i$ and $M_i^S < 1)$ or $(m_{S_i} < D_i$ and $M_i^R < 1)$, then at least one E_i exists.*

Proof: (a) Suppose $m_{S_i} \geq m_{R_i}$. If $m_{R_i} > D_i$, then $0 < S^* < \min\{1, \lambda_i\} < S_i^c$ and $0 < R^* < \min\{1, \mu_i\}$. By (2.22) and (2.23), $D_i = \mathcal{G}_i(S^*, R^*) < \mathcal{G}_i(1, 1)$. Therefore, by Theorem 2.7(a), E_i exists and is unique. If $m_{R_i} = D_i$, then $S_i^c = \lambda_i = S^* < 1$ and $0 < R^* < 1$, so that $D_i = \mathcal{G}_i(S^*, R^*) = \mathcal{G}_i(S^*, 1) < \mathcal{G}_i(1, 1)$. Therefore, by Theorem 2.7(b)(ii), E_i exists and is unique.

The argument is similar when $m_{R_i} \geq m_{S_i} \geq D_i$.

(b) Suppose $m_{R_i} < D_i$. Since E^* exists, $\lambda_i < 1$ and so $D_i < m_{S_i}$. From Table 1, $\lambda_i < S^* < M_i^S$ and $0 < R^* < \varphi_i(M_i^S)$. If $M_i^S < 1$, then $\varphi_i(M_i^S) = 1$, and by (2.22) $D_i = \mathcal{G}_i(S^*, R^*) = \mathcal{G}_i(M_i^S, 1) < \mathcal{G}_i(1, 1)$. Therefore, by Theorem 2.7(b)(iii), at least one E_i exists.

The argument is similar when $m_{S_i} < D_i$ and $M_i^R < 1$. ∎

Remark concerning Theorem 2.15:

As Theorem 2.15(b) would indicate, the cases ($m_{R_i} < D_i$ and $M_i^S = 1$) and ($m_{S_i} < D_i$ and $M_i^R = 1$) are special. In these cases, it is, in fact, possible to construct examples in which one species cannot survive in the absence of competition and yet a locally asymptotically stable coexistence equilibrium exists when a competitor population is present. We now describe one such example.

In this example, population x_1 cannot survive in the absence of competition, but population x_2 can. If we take

$$\mathcal{G}_1(S, R) = \frac{(9/4)S + (1/2)R}{1 + S + R} \text{ and } D_1 = 1,$$

then (as in the example described in Remark 3 concerning Theorem 2.7), provided that $\xi_1/\eta_1 < 119$, no equilibrium of the form E_1 exists. By Theorem 2.12(b), E_o is globally asymptotically stable with respect to (S, R, x_1)-space, and so species x_1 cannot survive in the absence of competition. If we take

$$\mathcal{G}_2(S, R) = \frac{3S + 3R}{1 + S + R} \text{ and } D_2 = \frac{3}{2},$$

then $\mathcal{G}_2(1, 1) = 2 > D_2$, and hence by Theorem 2.7(a), a unique equilibrium of the form E_2 exists. Moreover, E_2 is locally asymptotically stable with respect to (S, R, x_2)-space and is unstable with respect to (S, R, x_1, x_2)-space. In this case, a

coexistence equilibrium, E^*, exists if and only if $S^* = 6/7$, $R^*_* = 1/7$, and

$$x_1^* = \frac{4\xi_1\eta_1(\xi_2 - 36\eta_2)}{3(9\xi_2\eta_1 - 2\xi_1\eta_2)} > 0,$$

$$x_2^* = \frac{2\xi_2\eta_2(162\eta_1 - \xi_1)}{9(9\xi_2\eta_1 - 2\xi_1\eta_2)} > 0.$$

Assuming that $\xi_1/\eta_1 < 119$, then $x_1^* > 0$ and $x_2^* > 0$ if and only if $\xi_2/\eta_2 > 36$. If we wish to assume as well that $\xi_1/\eta_1 = \xi_2/\eta_2$, then this condition becomes $36 < \xi_1/\eta_1 = \xi_2/\eta_2 < 119$. In any case, it can also be shown (using a standard linear analysis involving the Routh-Hurwicz criterion) that whenever E^* lies in the positive cone, it is locally asymptotically stable.

To investigate under what conditions E^* exists in general, we begin with an examination of system (2.51). Note that for fixed values of S and R, a solution (x_1^*, x_2^*) of (2.51) with both x_1^* and x_2^* positive is required. Define

$$\Delta(S, R) = \left(\frac{S_1(S, R)}{\xi_1}\right)\left(\frac{R_2(S, R)}{\eta_2}\right) - \left(\frac{S_2(S, R)}{\xi_2}\right)\left(\frac{R_1(S, R)}{\eta_1}\right) \qquad (2.52)$$

for $(S, R) \in \mathbf{R}_+^2$. It follows from (2.51) and Cramer's rule that

$$x_1^* = \frac{(1/\eta_2)R_2(S, R)(1 - S) - (1/\xi_2)S_2(S, R)(1 - R)}{\Delta(S, R)},$$

$$x_2^* = \frac{(1/\xi_1)S_1(S, R)(1 - R) - (1/\eta_1)R_1(S, R)(1 - S)}{\Delta(S, R)}, \qquad (2.53)$$

provided $\Delta(S, R) \neq 0$. The following lemma is a direct consequence of (2.52) and (2.53).

Lemma 2.16 *Let (x_1^*, x_2^*) be a solution of (2.51) for fixed S, R satisfying $0 < S < 1$ and $0 < R < 1$. Then $x_1^* > 0$ and $x_2^* > 0$ if and only if the numerators of x_1^* and x_2^* as given in (2.53) are nonzero and of the same sign.*

For the remainder of this section we study the existence and stability of E^*. As in the one-species growth model, it is difficult to determine criteria in the case

that $m_{R_i} < D_i$ or $m_{S_i} < D_i$, $i = 1$ or 2. In what follows we assume that $m_{R_i} \geq D_i$ and $m_{S_i} \geq D_i$ for $i = 1$ and 2.

Using Lemma 2.16 we are now able to provide a characterization of the solutions (S^*, R^*) of equations (2.50) that yield an interior equilibrium.

Theorem 2.17   (a) *Suppose* $(m_{R_i} \geq m_{S_i} \geq D_i,\ i = 1$ *and* 2$)$ *or* $(m_{S_2} \geq m_{R_2} > D_2$ *and* $m_{R_1} \geq m_{S_1} \geq D_1)$ *or* $(m_{R_2} > m_{S_2} = D_2$ *and* $m_{S_1} \geq m_{R_1} \geq D_1)$. *Suppose further that there exists a solution* (S^*, R^*) *of* (2.50) *and that* E_i *exists,* $i = 1$ *and* 2, *with* $\bar{S}_1 \neq \bar{S}_2$. *If* λ_i *is finite and* $\varphi_i(0) > 1$, *then let* $\hat{S}_i$ *be the unique solution of the equation* $\varphi_i(S) = 1$; *otherwise, take* $\hat{S}_i = 0$. *Take* $i,\ j \in \{1,2\}$, $i \neq j$. *For* $\bar{S}_i < \bar{S}_j$, *define*

$$I_{ij} = [\bar{S}_i, min\{1, \lambda_i\}] \cap [\hat{S}_j, \bar{S}_j].$$

Then the corresponding solution (x_1^*, x_2^*) *of* (2.51) *satisfies* $x_1^* > 0$ *and* $x_2^* > 0$ *if and only if* $S^* \in intI_{ij}$.

(b) *Suppose* $(m_{S_i} \geq m_{R_i} \geq D_i,\ i = 1$ *and* 2$)$ *or* $(m_{R_2} \geq m_{S_2} > D_2$ *and* $m_{S_1} \geq m_{R_1} \geq D_1)$ *or* $(m_{S_2} > m_{R_2} = D_2$ *and* $m_{R_1} \geq m_{S_1} \geq D_1)$. *Suppose further that there exists a solution* (S^*, R^*) *of* (2.50) *and that* E_i *exists,* $i = 1$ *and* 2, *with* $\bar{R}_1 \neq \bar{R}_2$. *If* μ_i *is finite and* $\sigma_i(0) > 1$, *then let* $\hat{R}_i$ *be the unique solution of the equation* $\sigma_i(R) = 1$; *otherwise, take* $\hat{R}_i = 0$. *Take* $i,\ j \in \{1,2\}$, $i \neq j$. *For* $\bar{R}_i < \bar{R}_j$, *define*

$$I_{ij} = [\bar{R}_i, min\{1, \mu_i\}] \cap [\hat{R}_j, \bar{R}_j].$$

Then the corresponding solution (x_1^*, x_2^*) *of* (2.51) *satisfies* $x_1^* > 0$ *and* $x_2^* > 0$ *if and only if* $R^* \in intI_{ij}$.

(c) *Take* $i,\ j \in \{1,2\}$, $i \neq j$. *Suppose* $m_{S_i} > m_{R_i} = D_i$ *and* $m_{R_j} > m_{S_j} = D_j$. *Suppose further that there exists a solution* (S^*, R^*) *of* (2.50) . *Then the corresponding solution* (x_1^*, x_2^*) *of* (2.51) *satisfies* $x_1^* > 0$ *and* $x_2^* > 0$ *if and only if* $(\lambda_i < \bar{S}_j$ *and* $\mu_j < \bar{R}_i)$ *or* $(\bar{S}_j < \lambda_i$ *and* $\bar{R}_i < \mu_j)$.

Proof: (a) Note that by Theorem 2.15(a), there is no loss of generality in assuming the existence of E_1 and E_2. Suppose first that λ_i and μ_i are all finite, $i = 1$ and 2.

Define

$$\mathcal{N}x_1(S) = \frac{\mathcal{R}_2(S, \varphi_2(S))}{\eta_2}(1 - S) - \frac{S_2(S, \varphi_2(S))}{\xi_2}(1 - \varphi_2(S)), \quad 0 \leq S \leq \lambda_2,$$

and

$$\mathcal{N}x_2(S) = \frac{S_1(S, \varphi_1(S))}{\xi_1}(1 - \varphi_1(S)) - \frac{\mathcal{R}_1(S, \varphi_1(S))}{\eta_1}(1 - S), \quad 0 \leq S \leq \lambda_1.$$

Then $\mathcal{N}x_i(S)$ is the numerator of x_i^* as given in (2.53) with R replaced by $\varphi_j(S)$, where $i, j = 1, 2$ and $i \neq j$. By Lemma 2.5(a) and hypotheses (2.15) and (2.16), $\mathcal{N}x_1(S)$ is a decreasing function of S and $\mathcal{N}x_2(S)$ is an increasing function of S provided $S \leq 1$ and $\varphi_i(S) \leq 1$, $i = 1, 2$.

Recall that at $E_2 = (\bar{S}_2, \bar{R}_2, 0, \bar{x}_2)$, $0 < \bar{S}_2 < \min\{1, \lambda_2\}$, $0 < \bar{R}_2 < \min\{1, \mu_2\}$, and

$$\bar{x}_2 = \frac{\xi_2(1 - \bar{S}_2)}{S_2(\bar{S}_2, \varphi_2(\bar{S}_2))} = \frac{\eta_2(1 - \varphi_2(\bar{S}_2))}{\mathcal{R}_2(\bar{S}_2, \varphi_2(\bar{S}_2))}.$$

Therefore,

$$\mathcal{N}x_1(\bar{S}_2) = \frac{\mathcal{R}_2(\bar{S}_2, \varphi_2(\bar{S}_2))}{\eta_2}(1 - \bar{S}_2) - \frac{S_2(\bar{S}_2, \varphi_2(\bar{S}_2))}{\xi_2}(1 - \varphi_2(\bar{S}_2)) = 0.$$

Similarly, $\mathcal{N}x_2(\bar{S}_1) = 0$.

Note that $\hat{S}_i \in [0, \bar{S}_i)$, since $0 < \varphi_i(\bar{S}_i) = \bar{R}_i < \min\{1, \mu_i\}$ and $0 \leq \varphi_i(S) \leq 1$ for all $S \in [\hat{S}_i, \lambda_i]$.

If $\bar{S}_1 < \bar{S}_2$, then $\varphi_1(S) < 1$ for all $S \in [\bar{S}_1, \min\{1, \lambda_1\}]$ and $\varphi_2(S) \leq 1$ for all $S \in [\hat{S}_2, \min\{1, \lambda_2\}]$. Therefore, $\mathcal{N}x_1(S)$ and $\mathcal{N}x_2(S)$ are both positive for all $S \in intI_{12}$.

If $\bar{S}_2 < \bar{S}_1$, then $\varphi_2(S) < 1$ for all $S \in [\bar{S}_2, \min\{1, \lambda_2\}]$ and $\varphi_1(S) \leq 1$ for all $S \in [\hat{S}_1, \min\{1, \lambda_1\}]$. Therefore, $\mathcal{N}x_1(S)$ and $\mathcal{N}x_2(S)$ are both negative for all $S \in intI_{21}$. Combining this with Lemma 2.16, the result follows.

For the other cases, define $\mathcal{N}x_1(S)$ as follows. In the numerator of x_1^* as given in (2.53), if λ_2 is finite, then define $\mathcal{N}x_1(S)$ as above; otherwise take

$$\mathcal{N}x_1(S) = \frac{\mathcal{R}_2(S, \mu_2)}{\eta_2}(1 - S) - \frac{S_2(S, \mu_2)}{\xi_2}(1 - \mu_2), \quad S \geq 0.$$

Define $\mathcal{N}x_2(S)$ similarly, and proceed as above.

(b) Define $\mathcal{N}x_1(R)$ as follows. In the numerator of x_1^* as given in (2.53), if μ_2 is finite, then let

$$\mathcal{N}x_1(R) = \frac{\mathcal{R}_2(\sigma_2(R), R)}{\eta_2}(1 - \sigma_2(R)) - \frac{\mathcal{S}_2(\sigma_2(R), R)}{\xi_2}(1 - R), \quad 0 \leq R \leq \mu_2;$$

otherwise take

$$\mathcal{N}x_1(R) = \frac{\mathcal{R}_2(\lambda_2, R)}{\eta_2}(1 - \lambda_2) - \frac{\mathcal{S}_2(\lambda_2, R)}{\xi_2}(1 - R), \quad R \geq 0.$$

Define $\mathcal{N}x_2(R)$ similarly, and proceed as in *(a)*.

(c) Proceed as above. ∎

Remarks concerning Theorem 2.17:

1. Note that under the hypotheses of Theorem 2.17, $\bar{S}_1 < \bar{S}_2$ if and only if $\bar{R}_2 < \bar{R}_1$, and $\bar{S}_2 < \bar{S}_1$ if and only if $\bar{R}_1 < \bar{R}_2$.

2. (a) If $\bar{S}_1 < \bar{S}_2$, then either ($\mathcal{N}x_1(S) > 0$ and $\mathcal{N}x_2(S) > 0$ for all $S \in intI_{12}$) or ($\mathcal{N}x_1(R) > 0$ and $\mathcal{N}x_2(R) > 0$ for all $R \in intI_{12}$). Therefore, by Lemma 2.16, $\Delta(S^*, R^*) > 0$ for any solution (S^*, R^*) of (2.50) with $S^* \in intI_{12}$ or $R^* \in intI_{12}$.

   (b) If $\bar{S}_2 < \bar{S}_1$, then either ($\mathcal{N}x_1(S) < 0$ and $\mathcal{N}x_2(S) < 0$ for all $S \in intI_{21}$) or ($\mathcal{N}x_1(R) < 0$ and $\mathcal{N}x_2(R) < 0$ for all $R \in intI_{21}$). Therefore, by Lemma 2.16, $\Delta(S^*, R^*) < 0$ for any solution (S^*, R^*) of (2.50) with $S^* \in intI_{21}$ or $R^* \in intI_{21}$.

The next result links the existence of an interior equilibrium E^* with the stability of the one-species equilibria E_1 and E_2. We will require the following hypotheses:

$$\lambda_i \text{ and } \mu_i \text{ are finite, } i = 1 \text{ and } 2; \text{ and } \varphi_i(S) \text{ is linear, } i = 1 \text{ and } 2; \tag{2.54}$$

$$\lambda_i \text{ or } \mu_i \text{ is infinite, } i = 1 \text{ or } 2. \tag{2.55}$$

Theorem 2.18 *Suppose $m_{S_i} \geq D_i$, $m_{R_i} \geq D_i$, and the E_i exist, $i = 1$ and 2. Suppose further that for $i \in \{1, 2\}$, at least one λ_i is finite and at least one μ_i is finite.*

(a) If $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$, then E^* exists. If (2.54) or (2.55) holds as well, then E^* is unique.

(b) If $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$, then E^* exists. If (2.54) or (2.55) holds as well, then E^* is unique.

(c) If either $(\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2)$ or $(\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2)$, and either (2.54) or (2.55) holds, then E^* does not exist.

Proof: (a) Suppose λ_i and μ_i are finite, $i = 1$ and 2. Without loss of generality, assume that $\bar{S}_1 < \bar{S}_2$. Since $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$, $\varphi_2(\bar{S}_1) > \varphi_1(\bar{S}_1) = \bar{R}_1$. Since $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1$, $\varphi_1(\bar{S}_2) > \varphi_2(\bar{S}_2) = \bar{R}_2 > 0$ and $\lambda_1 > \bar{S}_2$. This implies that a solution (S^*, R^*) of (2.50) exists, with $\bar{S}_1 < S^* < \bar{S}_2$. If $\varphi_2(\bar{S}_1) \leq 1$, then $I_{12} = [\bar{S}_1, \bar{S}_2]$. If $\varphi_2(\bar{S}_1) > 1$, then $I_{12} = [\hat{S}_2, \bar{S}_2]$, where $\hat{S}_2 \in (\bar{S}_1, \bar{S}_2)$ because $\varphi_2(\hat{S}_2) = \bar{R}_2 < 1$. Also, $\varphi_1(S) \leq \bar{R}_1 < 1$ and $\varphi_2(S) \geq 1$ for all $\bar{S}_1 < S < \hat{S}_2$, so φ_1 and φ_2 do not intersect on $[\bar{S}_1, \hat{S}_2]$. Therefore, φ_1 and φ_2 must intersect at some $S^* \in intI_{12}$, so, by Theorem 2.17, E^* exists. If, in addition, φ_1 and φ_2 are linear, then S^* is unique, so that E^u is unique.

In the other cases, the existence of E^* is proved similarly, and its uniqueness is immediate.

(b) Suppose λ_i and μ_i are finite, $i = 1$ and 2. Without loss of generality, assume that $\bar{S}_1 < \bar{S}_2$. Since $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$, it follows that $\varphi_2(\bar{S}_1) < \varphi_1(\bar{S}_1) = \bar{R}_1 < 1$ and $\hat{S}_2 < \bar{S}_1$. Since $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$, either φ_1 is defined at $\bar{S}_2$ (so $\lambda_1 \geq \bar{S}_2$) and $\varphi_1(\bar{S}_2) < \varphi_2(\bar{S}_2) = \bar{R}_2$, or φ_1 is not defined at $\bar{S}_2$ (so $\lambda_1 < \bar{S}_2$). Then $I_{12} = [\bar{S}_1, \bar{S}_2]$ if $\lambda_1 \geq \bar{S}_2$, and $I_{12} = [\bar{S}_1, \lambda_1]$ otherwise. In either case, φ_1 and φ_2 must intersect at some $S^* \in intI_{12}$, so, by Theorem 2.17, E^* exists. If, in addition, φ_1 and φ_2 are linear, then S^* is unique, so E^* is unique.

In the other cases, the existence of E^* is proved similarly, and its uniqueness is immediate.

(c) Consider $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$ and suppose that (2.54) holds. Without loss of generality, assume that $\bar{S}_1 < \bar{S}_2$. Since $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$, $\varphi_1(\bar{S}_2) < \varphi_2(\bar{S}_2) = \bar{R}_2$, and since $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$, $\bar{R}_1 = \varphi_1(\bar{S}_1) < \varphi_2(\bar{S}_1)$. Since φ_1 and φ_2 are linear, $\varphi_1(S) \neq \varphi_2(S)$ for every $S \in intI_{12}$, so, by Theorem 2.17, E^* does not exist.

The other cases, where the linearity hypothesis is not required, are proved similarly. ∎

Remark concerning Theorem 2.18:

From the characteristic polynomial of $V_4(\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$, it follows that if $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$, then E_1 is attracting from the interior, and if $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$, then E_1 is repelling into the interior. A similar result holds for E_2.

Now, assuming that a solution $E^* = (S^*, R^*, x_1^*, x_2^*) \in \mathbf{R}_+^4$ of (2.50)–(2.51) exists, we investigate its stability. Define

$$\nabla(S, R) = \frac{\partial}{\partial S}\mathcal{G}_1(S, R)\frac{\partial}{\partial R}\mathcal{G}_2(S, R) - \frac{\partial}{\partial R}\mathcal{G}_1(S, R)\frac{\partial}{\partial S}\mathcal{G}_2(S, R).$$

Evaluating the variational matrix $V_4(E^*)$, the associated characteristic polynomial is

$$\alpha^4 + B_1\alpha^3 + B_2\alpha^2 + B_3\alpha + B_4. \tag{2.56}$$

If $m_{S_i} < D_i$ or $m_{R_i} < D_i$ for $i = 1$ or 2, it is difficult, in general, to provide even a partial analysis of the roots of (2.56). However, if $m_{S_i} \geq D_i$ and $m_{R_i} \geq D_i$ for $i = 1$ and 2, then some conclusions can be reached. By hypotheses (2.13), (2.15), (2.16), (2.22), and (2.23), it follows that $B_1 > 0$, $B_2 > 0$, and $B_3 > 0$. Also,

$$B_4 = x_1^* x_2^* \nabla(S^*, R^*)\, \triangle(S^*, R^*),$$

where $\triangle(S, R)$ was given in (2.52), and so by the Routh-Hurwicz Criterion, a necessary condition for the local asymptotic stability of E^* is that $\nabla(S^*, R^*)$ and $\triangle(S^*, R^*)$ have the same sign.

Suppose that $m_{S_i} \geq D_i$, $m_{R_i} \geq D_i$, $i = 1$ and 2, $\bar{S}_1 < \bar{S}_2$, and (S^*, R^*) is an isolated solution of (2.50). By Remark 2 following Theorem 2.17, $\triangle(S^*, R^*) > 0$. If $|\varphi_1'(S^*)| < |\varphi_2'(S^*)|$, then, since

$$\varphi_i'(S) = -\frac{\frac{\partial}{\partial S}\mathcal{G}_i(S, R)}{\frac{\partial}{\partial R}\mathcal{G}_i(S, R)},$$

it follows that

$$\frac{\frac{\partial}{\partial S}\mathcal{G}_1(S^*, R^*)}{\frac{\partial}{\partial R}\mathcal{G}_1(S^*, R^*)} < \frac{\frac{\partial}{\partial S}\mathcal{G}_2(S^*, R^*)}{\frac{\partial}{\partial R}\mathcal{G}_2(S^*, R^*)}.$$

After rearranging,

$$\bigtriangledown(S^*, R^*) = \frac{\partial}{\partial S}\mathcal{G}_1(S^*, R^*)\frac{\partial}{\partial R}\mathcal{G}_2(S^*, R^*) - \frac{\partial}{\partial R}\mathcal{G}_1(S^*, R^*)\frac{\partial}{\partial S}\mathcal{G}_2(S^*, R^*) < 0.$$

Therefore, $B_4 < 0$, and E^* is unstable. If $|\varphi_1'(S^*)| > |\varphi_2'(S^*)|$, then

$$\frac{\frac{\partial}{\partial S}\mathcal{G}_1(S^*, R^*)}{\frac{\partial}{\partial R}\mathcal{G}_1(S^*, R^*)} > \frac{\frac{\partial}{\partial S}\mathcal{G}_2(S^*, R^*)}{\frac{\partial}{\partial R}\mathcal{G}_2(S^*, R^*)},$$

so

$$\bigtriangledown(S^*, R^*) = \frac{\partial}{\partial S}\mathcal{G}_1(S^*, R^*)\frac{\partial}{\partial R}\mathcal{G}_2(S^*, R^*) - \frac{\partial}{\partial R}\mathcal{G}_1(S^*, R^*)\frac{\partial}{\partial S}\mathcal{G}_2(S^*, R^*) > 0.$$

Since $\triangle(S^*, R^*) > 0$, then $B_4 > 0$. A similar result holds when $\bar{S}_2 < \bar{S}_1$.

For example, suppose the hypotheses of Theorem 2.18(a) and hypothesis (2.54) hold. Then E^* exists and is unique. If $\bar{S}_1 < \bar{S}_2$, then $|\varphi_1'(S^*)| < |\varphi_2'(S^*)|$, so $\bigtriangledown(S^*, R^*) < 0$ and E^* is unstable. Similarly, if $\bar{S}_2 < \bar{S}_1$, then $|\varphi_2'(S^*)| < |\varphi_1'(S^*)|$, so $\bigtriangledown(S^*, R^*) > 0$ and, since $\triangle(S^*, R^*) < 0$, E^* is unstable.

Suppose the hypotheses of Theorem 2.18(b) and hypothesis (2.54) hold. Then E^* exists and is unique. If $\bar{S}_1 < \bar{S}_2$, then $|\varphi_2'(S^*)| < |\varphi_1'(S^*)|$, so $\bigtriangledown(S^*, R^*) > 0$ and $B_4 > 0$. Similarly, if $\bar{S}_2 < \bar{S}_1$, then $|\varphi_1'(S^*)| < |\varphi_2'(S^*)|$, so $\bigtriangledown(S^*, R^*) < 0$ and $B_4 > 0$.

If $\mathcal{S}_i(S, R) = p_i(S)$ and $\mathcal{R}_i(S, R) = q_i(R)$ for all $S \geq 0$, and $R \geq 0$, $i = 1$, 2, then as shown by León and Tumpson [31], $B_4 > 0$ is a necessary and sufficient condition for all roots of (2.56) to have negative real part, and hence sufficient for the local asymptotic stability of an interior equilibrium. This follows from the fact that, in this case, the characteristic equation of $V_4(E^*)$ satisfies all other conditions of the Routh-Hurwicz Criterion. As in [31],

$$B_4 = \left(\left(\frac{\partial x_1'}{\partial S}\right)_{E^*} \left(\frac{\partial x_2'}{\partial R}\right)_{E^*} - \left(\frac{\partial x_1'}{\partial R}\right)_{E^*} \left(\frac{\partial x_2'}{\partial S}\right)_{E^*} \right)$$
$$\times \left(\frac{p_1(S^*)}{\xi_1} \frac{q_2(R^*)}{\eta_2} - \frac{p_2(S^*)}{\xi_2} \frac{q_1(R^*)}{\eta_1} \right).$$

Therefore, *two species competing for two perfectly substitutable resources will coexist stably at equilibrium if at that point each competitor removes at a higher rate that resource which contributes more to its own rate of growth.*

Finally we study a global property of the model. In the following, let

$$\mathcal{J}_o = \{(S, R, 0, 0) \in \mathbf{R}_+^4\},$$

$$\mathcal{J}_1 = \{(S, R, x_1, x_2) \in \mathbf{R}_+^4 : x_1 > 0, \ x_2 = 0\},$$

$$\mathcal{J}_2 = \{(S, R, x_1, x_2) \in \mathbf{R}_+^4 : x_1 = 0, \ x_2 > 0\}.$$

Theorem 2.19 *Assume that* $\mathcal{G}_i(1,1) > D_i$, $i = 1$ *and 2. Assume also that* E_i *is globally asymptotically stable with respect to all solutions initiating in* $\mathcal{J}_i$ *for* $i = 1$ *and 2 and that* $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ *and* $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$. *Then system (2.49) is uniformly persistent with respect to all solutions for which* $x_1(0) > 0$ *and* $x_2(0) > 0$.

Proof: Since $\mathcal{G}_i(1,1) > D_i$, $i = 1$ and 2, by Theorem 2.7, at least one E_i exists for each $i = 1$ and 2. Identify (S, R, x_1, x_2)-space with $\mathbf{R}_+^4$, and choose $\underline{X} = (S(0), R(0), x_1(0), x_2(0)) \in \mathbf{R}_+^4$. By Theorem 2.2(a), $\Omega(\underline{X})$ is a nonempty, compact, invariant set with respect to (2.49).

By an argument similar to that given in Theorem 2.10, it follows that any point in $\Omega(\underline{X})$ must satisfy $\liminf_{t\to\infty} S(t) > 0$ and $\liminf_{t\to\infty} R(t) > 0$. Therefore, to show that (2.49) is persistent, it remains to show that $\liminf_{t\to\infty} x_i(t) > 0$, $i = 1$, 2.

Note that E_o is globally attracting with respect to all solutions initiating in $\mathcal{J}_o$. By an argument similar to that used in Theorem 2.10, $E_o \notin \Omega(\underline{X})$.

Suppose $\{E_1\} \in \Omega(\underline{X})$. Since $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$, E_1 is an unstable hyperbolic critical point, and therefore $\dim(M^s(E_1)) < 4$. Since $M^s(E_1) \supset \mathcal{J}_1$, $\dim(M^s(E_1)) \geq 3$. Therefore, $M^s(E_1) = \mathcal{J}_1$ and hence does not intersect $int\mathbf{R}_+^4$. This implies that $\{E_1\} \neq \Omega(\underline{X})$. Therefore, by the Butler-McGehee Lemma (see Lemma A1 of [17]), there exists $P \in (M^s(E_1)\backslash\{E_1\}) \cap \Omega(\underline{X})$ and hence $cl\mathcal{O}(P) \subset \Omega(\underline{X})$. But then, as $t \to -\infty$, $\mathcal{O}(P)$ either becomes unbounded or leaves the positive cone or $cl\mathcal{O}(P) \supset \{E_o\}$. In any case, we have a contradiction, and therefore $\{E_1\} \notin \Omega(\underline{X})$. Similarly, $\{E_2\} \notin \Omega(\underline{X})$.

Suppose $\liminf_{t\to\infty} x_i(t) = 0$, $i = 1$ or 2. Then there exists a point $\tilde{P} \in \Omega(\underline{X})$ such that $\tilde{P} \in \mathcal{J}_i$ for some $i \in \{0, 1, 2\}$. Now, $\tilde{P} \in \Omega(\underline{X})$ implies that $cl\mathcal{O}(\tilde{P}) \subset \Omega(\underline{X})$. However, if $\tilde{P} \in \mathcal{J}_i$, then $\{E_i\} \in cl\mathcal{O}(\tilde{P})$, because E_i is globally attracting with respect to all solutions initiating in the set $\mathcal{J}_i$, implying that $\{E_i\} \in \Omega(\underline{X})$, a contradiction.

Thus $\liminf_{t\to\infty} x_i(t) > 0$, $i = 1$, 2, and so (2.49) is persistent. It now follows from the main result of [8] that (2.49) is uniformly persistent. ∎

Remark concerning Theorem 2.19:

Note that since system (2.49) is dissipative and uniformly persistent, there is a compact set in $int\mathbf{R}_+^n$ which is a weak global attractor with respect to $int\mathbf{R}_+^n$. Thus, by Theorem 3.9 of [5], there exists at least one coexistence equilibrium.

Note also that if $m_{S_i} \geq D_i, m_{R_i} \geq D_i$, and $D_i = 1$ for $i = 1$ and 2 or if $S_i(S, R) = p_i(S)$ and $\mathcal{R}_i(S, R) = q_i(R)$ for all $S \geq 0$ and $R \geq 0$, $i = 1$, 2 (regardless of the relative values of m_{S_i}, m_{R_i} and D_i and with D_i not necessarily equal to 1), then by Theorem 2.12(a) and Theorem 2.13(b), respectively, E_i is globally asymptotically stable with respect to all solutions initiating in $\{(S, R, x_1, x_2) \in \mathbf{R}_+^4 : x_i > 0, \ x_j = 0\}$, where $i \neq j \in \{1, 2\}$. Therefore, Theorem 2.19(a) gives necessary and sufficient conditions for uniform persistence in these cases.

2.4 Summary of Results and Discussion

In this section we summarize the results of our analysis in terms of the original unscaled variables, both for model I of León and Tumpson [31] and for model (2.12). We then compare the dynamics with the dynamics of the classical growth and two-species competition models and the corresponding models for perfectly complementary resources. For convenience, we retain the notation of Section 3 for the equilibria E_1, E_2, and E^*. However, it is to be understood that by the scaling (2.31), the S and x_i components of the equilibria of (2.12) should be multiplied by S^o and the R components of the equilibria of (2.12) should be multiplied by R^o. To facilitate the description of the quantities governing the dynamics of (2.12), we assume that the volume V of suspension in the growth vessel is one cubic unit. In (2.12), D, D_1, and D_2 are divided by the actual volume V.

2.4.1 Model I of León and Tumpson Adapted to the Chemostat

We obtain our most complete results when the amount of each resource consumed is assumed to be independent of the concentration of the other resource, that is,

$\mathcal{S}_i(S, R) = p_i(S)$ and $\mathcal{R}_i(S, R) = q_i(R)$, for $i = 1$ and 2. First we consider the one-species growth models (the (S, R, x_i) subsystems of (2.12), $i \in \{1, 2\}$). We show that for each $i \in \{1, 2\}$, x_i avoids extinction if and only if $\mathcal{G}_i(S^o, R^o) > D_i$. In other words, if a species cannot consume enough resource to compensate for the rate D_i at which it is being removed, even if the growth vessel is maintained at the input concentrations S^o and R^o of resources S and R, then that species will become extinct. Otherwise, there exists a unique one-species survival equilibrium that is globally asymptotically stable. Next we consider the two-species competition model in this setting. In Table 2.2, we summarize the criteria for existence of the equilibria in the nonnegative cone, as well as the criteria that guarantee local asymptotic stability of these equilibria. For the two-species competition model, if $\mathcal{G}_i(S^o, R^o) < D_i$ for $i = 1$ and 2, then E_o, the washout equilibrium, is globally asymptotically stable. On the other hand, $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$ is necessary and sufficient for solutions of the two-species competition model to be uniformly persistent, thus ensuring that both species survive in the presence of competition, regardless of the (positive) initial concentrations.

In this setting, we now compare the dynamics of growth on perfectly complementary resources with the dynamics of growth on perfectly substitutable resources. In both cases either the washout equilibrium is globally asymptotically stable and hence the carrying capacity of the environment is zero, or there exists a one-species survival equilibrium that is globally asymptotically stable, and the species component of the equilibrium gives the carrying capacity of the environment. The major difference in the criterion that determines whether the species will survive or wash out is precisely as expected. For perfectly complementary resources, both resources must be above some threshold (see Table 3 of Butler and Wolkowicz [12]), whereas for perfectly substitutable resources, the threshold (see Theorem 2.13) depends on the combined amount of the resources. The classical, or logistic, model due to Verhulst predicts that as long as the initial population is positive, the population size will approach the carrying capacity of the environment, which must be known in advance because it is a parameter in the model that is always assumed to be positive. Thus, an advantage of both of the resource based growth models over the classical model is

that they predict the carrying capacity of the environment.

Using graphical techniques to examine the local stability properties of two-species competition for two resources, Tilman [56] conjectured that *the type of resources for which competition occurs will not lead to major, qualitative differences in the ecological patterns that can result from competition between two species for two resources.* Butler and Wolkowicz [12], who extended the work of León and Tumpson [31], in the perfectly complementary resource case, found that in the case of monotone response functions, each of the outcomes of the classical theory for two-species competition is possible. We show that each of the outcomes for perfectly complementary resources is also possible in the perfectly substitutable case. Competition-independent extinction, an impossibility in the classical model, can occur in the resource-based models. Both for perfectly complementary resources and in the classical model, coexistence always occurs at a globally asymptotically stable critical point. For perfectly substitutable resources in this setting, we are only able to show uniform persistence. (Note that uniform persistence of a system implies that at least one coexistence equilibrium exists.) In fact, multiple interior equilibria are possible, and so coexistence need not always occur at a globally asymptotically stable equilibrium. It is even possible for the outcome to be initial condition dependent in the sense that for certain initial conditions there is coexistence whereas for others there is competitive dominance, that is, one population drives the other population to extinction.

2.4.2 Model (2.12)

While Tilman's conjecture appears to be true for the most part, there seems to be a wider range of possible dynamics in the perfectly substitutable case. What also seems to make a difference is the strategy used for consumption, in particular, whether or not the concentration of each resource affects the amount of the other resource consumed. We extend model I of León and Tumpson to incorporate handling time in the sense of Holling [24] and hence allow the concentration of one resource to act as a competitive inhibitor on the consumption of the other resource (see assumptions (2.16)–(2.26)). Here it becomes important to consider the relative values of m_{S_i} and m_{R_i}, the maximal growth rates on resource S and R, respectively, and D_i, the combined washout and

specific death rate. When the maximal growth rate of population x_i on one resource, say resource S, is larger than the maximal growth rate of population x_i on the other resource, then there is a threshold, S_i^c, for resource S. (See Figure 2.1.) If the concentration of resource S is below this threshold, increasing the concentration of either resource is beneficial to that population. However, once the concentration of resource S is above this threshold, so that the maximal growth rate on resource R is exceeded by consuming only resource S, increasing resource S is beneficial, but the presence of resource R becomes detrimental to that population.

In this setting, we again considered the one-species growth model. As in model I of León and Tumpson, we find that $\mathcal{G}_i(S^o, R^o) > D_i$ is necessary and sufficient for this model to be uniformly persistent, regardless of the relative values of m_{S_i}, m_{R_i} and D_i. If $m_{S_i} \geq D_i$ and $m_{R_i} \geq D_i$, so the rate of removal from competition does not exceed the maximal growth rate for each resource, then if $\mathcal{G}_i(S^o, R^o) < D_i$, the environment is not rich enough to support population x_i, and it is driven to extinction. On the other hand, $\mathcal{G}_i(S^o, R^o) > D_i$ is a necessary and sufficient condition to ensure that a unique one-species survival equilibrium E_i exists. We have only shown that the criteria for the local asymptotic stability of E_i (see Table 2.2) apply under the added assumption that $\mathcal{G}_i(S^o, R^o) \leq 2D$. However, if the intrinsic death rate is assumed to be insignificant compared to the dilution rate ($D_i = D$), then E_i is globally asymptotically stable with respect to the interior of (S, R, x_i)-space.

The growth model exhibits more unusual dynamics when $m_{S_i} < D_i < m_{R_i}$ or $m_{R_i} < D_i < m_{S_i}$. If, in addition, $\mathcal{G}_i(S^o, R^o) \leq D_i$, there may or may not exist a one-species survival equilibrium, and if one exists it need not be unique. In fact, we provide an example (see Remark 3 following Theorem 2.7) in which $m_{R_i} < D_i < m_{S_i}$, and $\mathcal{G}_i(S^o, R^o) < D_i$ so the washout equilibrium is locally asymptotically stable. By treating the ratio of the growth yield constants, ξ_i/η_i, as a bifurcation parameter while fixing all of the other parameters in the model, one can obtain either zero, one, or two one-species survival equilibria. In this example, for at least one one-species survival equilibrium to exist, ξ_i/η_i must be sufficiently large. To see this, consider all concentrations $\bar{S}$, $\bar{R}$ of resources S and R satisfying $\mathcal{G}_i(\bar{S}, \bar{R}) = D_i$. Since the concentration $\bar{S}$ of resource S is above the threshold S_i^c, resource R is detrimental.

One would expect that the faster resource R is depleted the better. If the ratio ξ_i/η_i is too small, then

$$\frac{(R^o - \bar{R})(D/V)}{(S^o - \bar{S})(D/V)} > \frac{(1/\eta_i)\mathcal{R}_i(\bar{S}, \bar{R})}{(1/\xi_i)\mathcal{S}_i(\bar{S}, \bar{R})}, \tag{2.57}$$

and so the ratio of the net supply rate of resource R to that of resource S exceeds the ratio of the consumption rate of resource R to that of resource S. As species x_i cannot deplete resource R quickly enough, no one-species survival equilibrium exists. In this example, if at least one one-species equilibrium exists, then at least one of them is locally asymptotically stable, and so whether the species survives or washes out depends on the initial conditions. Multiple one-species survival equilibria and initial condition dependent survival is not possible in any of the other growth models discussed in this chapter.

We then consider the two-species competition model. If, for each species, either (both breakeven concentrations, λ_i and μ_i, are finite and $\mathcal{G}_i(S^o, R^o) < D_i$) or ($\lambda_i = \infty$ and $\mu_i \geq R^o$) or ($\lambda_i \geq S^o$ and $\mu_i = \infty$), then E_o, the washout equilibrium, is globally asymptotically stable, that is, both species become extinct. On the other hand, we find that if E_1 and E_2 are globally asymptotically stable in their respective three-dimensional subsystems, then a necessary and sufficient condition for the two-species competition model to be uniformly persistent is that $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$. We examine the existence and stability of coexistence equilibria under the assumption that $m_{S_i} \geq D_i$ and $m_{R_i} \geq D_i$ for $i = 1$ and 2. The results in this case are summarized in Table 2.2. (Note that the condition for the local asymptotic stability of E^* only ensures that the constant term in the characteristic equation of the variational matrix of (2.12) evaluated at E^* is positive.) We first show that if a coexistence equilibrium exists, then E_1 and E_2 exist and are unique. We then characterize those resource concentrations that yield coexistence equilibria. Using this characterization, we prove that if E_1 and E_2 exist and either both repel into or both attract from the interior, then at least one coexistence equilibrium exists. We also show that $\mathcal{G}_1(S, R)$ and $\mathcal{G}_2(S, R)$ can be chosen so that these conditions on the stability of E_1 and E_2 yield precisely one coexistence equilibrium. In particular, when the subsistence curves are linear, as in Waltman et. al. [60], we find that if both E_1 and E_2 attract from the interior, then E^* is unique and unstable, and if both E_1 and

E_2 repel into the interior, then E^* is unique and the condition for the local asymptotic stability of E^*, given in Table 2, is satisfied. Also, if E_1 and E_2 exist and one attracts and the other repels with respect to the interior, no coexistence equilibrium exists. However, if the subsistence curves are nonlinear, multiple coexistence equilibria are possible, and, as in model I of León and Tumpson, the outcome of competition may depend on the initial conditions.

As in the growth model, the competition model exhibits more unusual dynamics when $m_{S_i} < D_i < m_{R_i}$ or $m_{R_i} < D_i < m_{S_i}$ for at least one i. We provide an example (see the remark following Theorem 2.15) in which one species is unable to survive in the absence of a competitor even though there exists a locally asymptotically stable coexistence equilibrium when a competitor is present. Thus, in some circumstances it seems that a population can be better off with a competitor than without one. This situation will be examined in further detail in the next chapter.
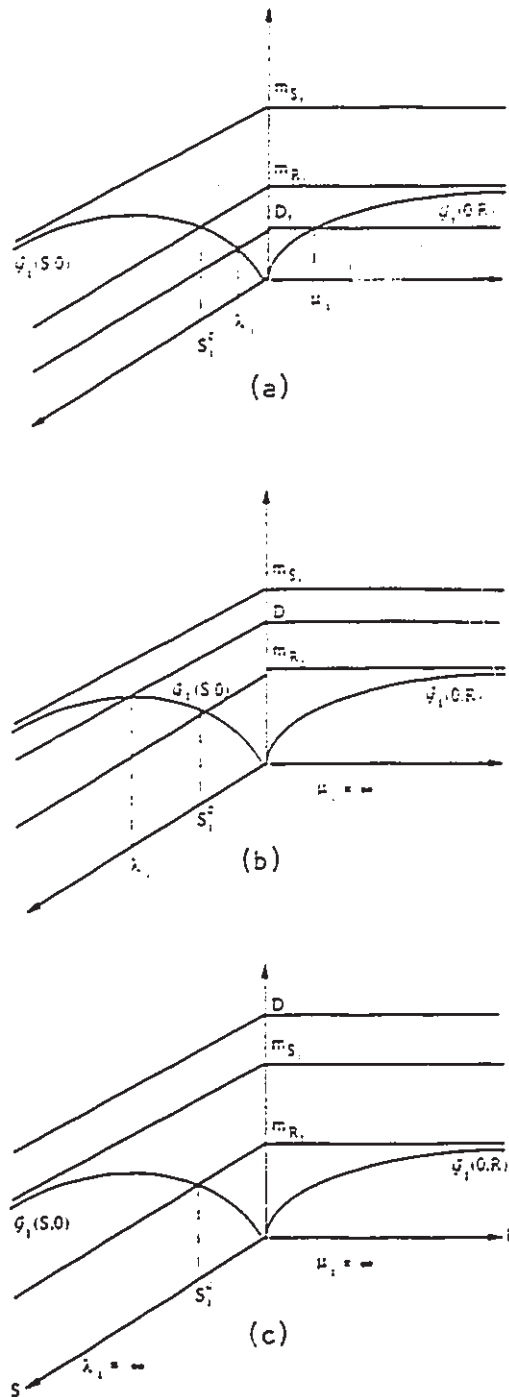
2.5 Figures and Tables

Figure 2.1: Schematic Diagram for Lemma 2.1 (a) $m_{S_i} > m_{R_i} > D_i$; (b) $m_{S_i} > D_i > m_{R_i}$; (c) $D_i > m_{S_i} > m_{R_i}$.
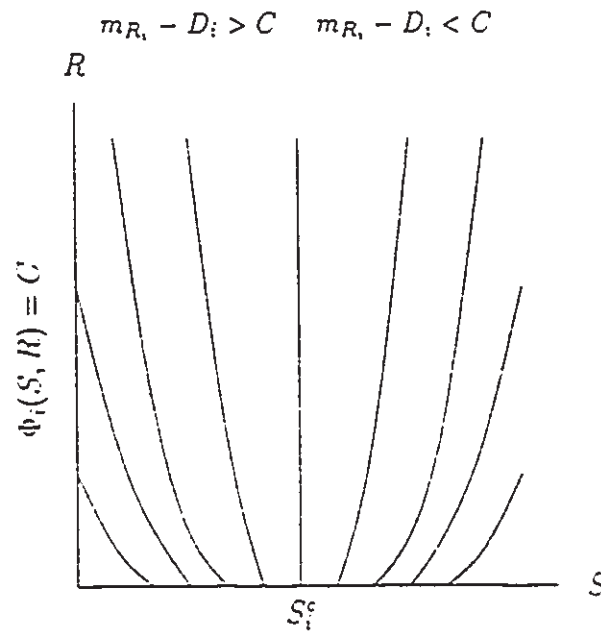
$$m_{R_1} - D_i > C \quad m_{R_1} - D_i < C$$

Figure 2.2: "Indifference" curves in the (S, R) plane and the "subsistence" curve for $m_{S_i} > m_{R_i}$. Since $\Phi_i(S, R) = 0 = \Phi_i(S, \varphi_i(S)) = \Phi_i(\sigma_i(R), R)$, the indifference curve with $C = 0$ gives the subsistence curve.
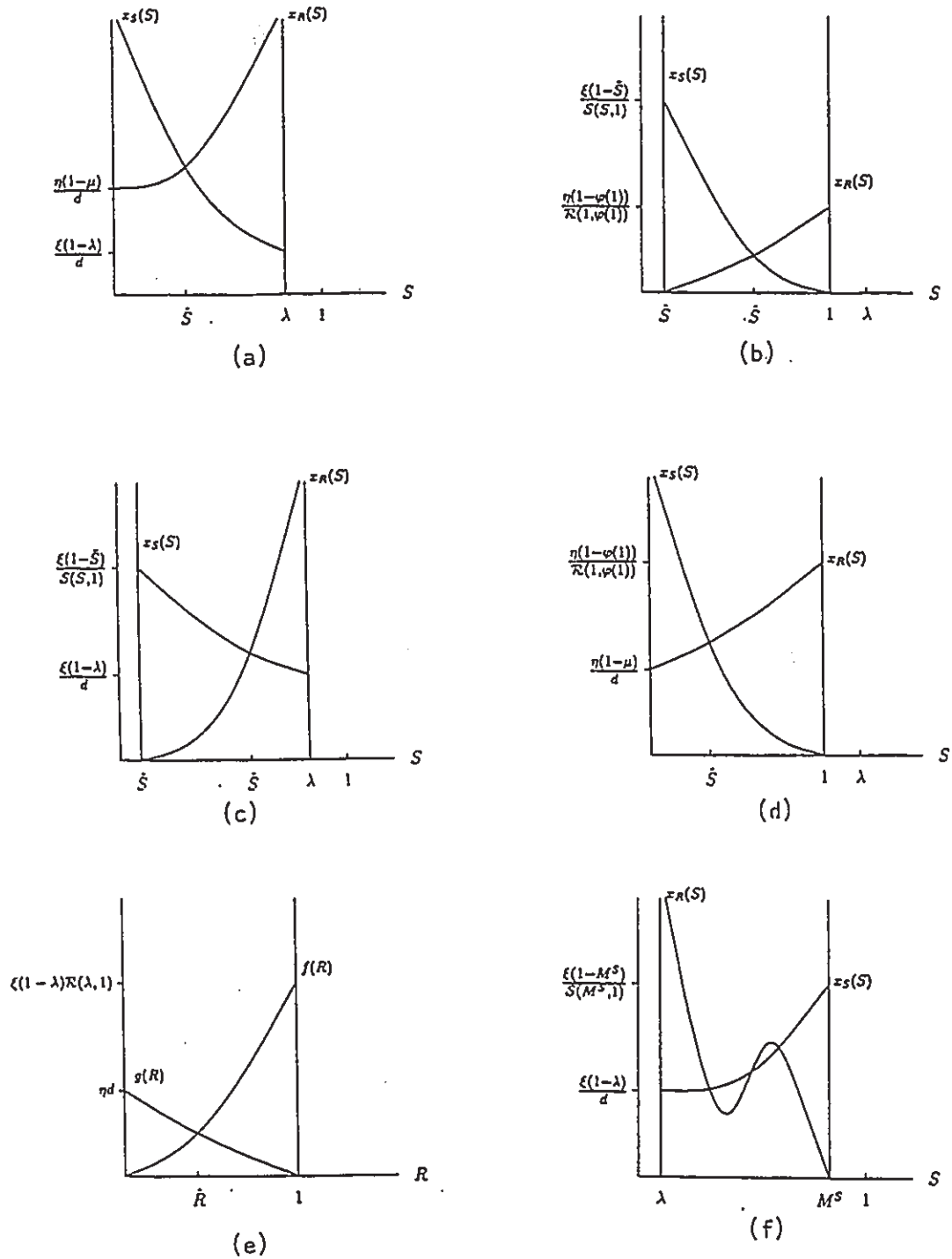
Figure 2.3: Schematic Diagram for Theorem 2.7. For $m_S \geq m_R > d$: (a) $\lambda \leq 1$ and $\mu \leq 1$; (b) $\lambda > 1$ and $\mu > 1$; (c) $\lambda \leq 1$ and $\mu \geq 1$; (d) $\lambda \geq 1$ and $\mu \leq 1$. For $m_S > d \geq m_R$: (e) $m_R = d$; (f) $m_R < d$ and $M^S < 1$.
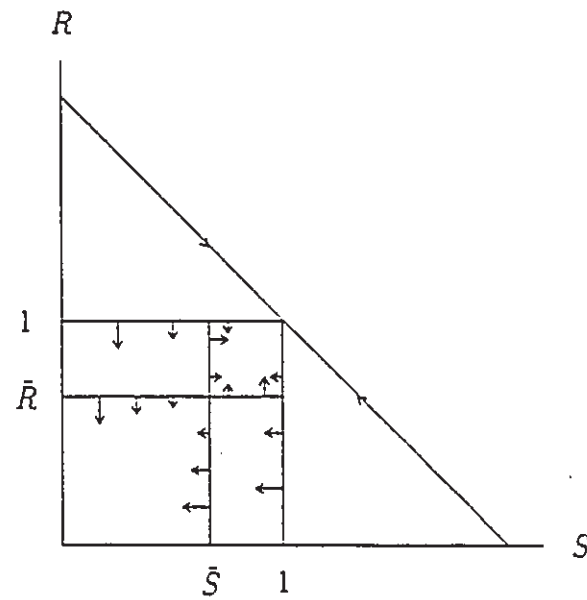
Figure 2.4: Partial Vector Field for Theorem 2.12. Vectors parallel to the S axis indicate the sign of $S'(t)$ along the indicated line. Vectors parallel to the R axis indicate the sign of $R'(t)$ along the indicated line.

$m_{S_i} \geq m_{R_i}$, $i=1,2$	$m_{R_i} > D_i$	$m_{R_i} = D_i$	$m_{R_i} < D_i$
$m_{R_2} > D_2$	$0 < S^* < \min\{1, \lambda_1, \lambda_2\}$ $0 < R^* < \min\{1, \mu_1, \mu_2\}$	$\lambda_1 = S^* < \min\{1, \lambda_2\}$ $0 < R^* < \min\{1, \mu_2\}$	$\lambda_1 < S^* < \min\{\lambda_2, M_1^S\}$ $0 < R^* < \min\{\varphi_1(M_1^S), \mu_2\}$
$m_{R_2} = D_2$	$\lambda_2 = S^* < \min\{1, \lambda_1\}$ $0 < R^* < \min\{1, \mu_1\}$	$\lambda_1 = \lambda_2 = S^* < 1$ $0 < R^* < 1$	$\lambda_1 < \lambda_2 = S^* < M_1^S$ $0 < R^* < \varphi_1(M_1^S)$
$m_{R_2} < D_2$	$\lambda_2 < S^* < \min\{\lambda_1, M_2^S\}$ $0 < R^* < \min\{\varphi_2(M_2^S), \mu_1\}$	$\lambda_2 < \lambda_1 = S^* < M_2^S$ $0 < R^* < \varphi_2(M_2^S)$	$\max\{\lambda_1, \lambda_2\} < S^* < \min\{M_1^S, M_2^S\}$ $0 < R^* < \min\{\varphi_1(M_1^S), \varphi_2(M_2^S)\}$

$m_{S_1} \geq m_{R_1}$ $m_{S_2} < m_{R_2}$	$m_{R_1} > D_1$	$m_{R_1} = D_1$	$m_{R_1} < D_1$
$m_{S_2} > D_2$	$0 < S^* < \min\{1, \lambda_1, \lambda_2\}$ $0 < R^* < \min\{1, \mu_1, \mu_2\}$	$\lambda_1 = S^* < \min\{1, \lambda_2\}$ $0 < R^* < \min\{1, \mu_2\}$	$\lambda_1 < S^* < \min\{\lambda_2, M_1^S\}$ $0 < R^* < \min\{\varphi_1(M_1^S), \mu_2\}$
$m_{S_2} = D_2$	$0 < S^* < \min\{1, \lambda_1\}$ $\mu_2 = R^* < \min\{1, \mu_1\}$	$\lambda_1 = S^* < 1$ $\mu_2 = R^* < 1$	$\lambda_1 < S^* < M_1^S$ $\mu_2 = R^* < \varphi_1(M_1^S)$
$m_{S_2} < D_2$	$0 < S^* < \min\{\sigma_2(M_2^R), \lambda_1\}$ $\mu_2 < R^* < \min\{\mu_1, M_2^R\}$	$\lambda_1 = S^* < \sigma_2(M_2^R)$ $\mu_2 < R^* < M_2^R$	$\lambda_1 < S^* < \min\{M_1^S, \sigma_2(M_2^R)\}$ $\mu_2 < R^* < \min\{\varphi_1(M_1^S), M_2^R\}$

Table 2.1: Necessary conditions for a solution (S^*, R^*) of system (2.50) to be an interior equilibrium of (2.49). If $m_{R_i} > m_{S_i}$ for $i = 1$ and 2, replace λ_i by μ_i, S^* by R^*, M_i^S by M_i^R, $\varphi_i(M_i^S)$ by $\varphi_i(M_i^R)$, and vice versa, in the first portion of the table. If $m_{S_1} < m_{R_1}$ and $m_{S_2} \geq m_{R_2}$, replace 1 by 2 in the second portion of the table.

CRITICAL POINT	EXISTENCE CRITERIA	CRITERIA FOR ASYMPTOTIC STABILITY
E_o	always exists	$\mathcal{G}_1(S^o, R^o) < \frac{D_1}{V}$ and $\mathcal{G}_2(S^o, R^o) < \frac{D_2}{V}$
E_1	$\mathcal{G}_1(S^o, R^o) > \frac{D_1}{V}$	$\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < \frac{D_2}{V}$
E_2	$\mathcal{G}_2(S^o, R^o) > \frac{D_2}{V}$	$\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < \frac{D_1}{V}$
E^* (not necessarily unique)	(i) $\mathcal{G}_1(\bar{S}_2, \varphi_2(\bar{S}_2)) < \frac{D_1}{V}$ and $\mathcal{G}_2(\bar{S}_1, \varphi_1(\bar{S}_1)) < \frac{D_2}{V}$ or (ii) $\mathcal{G}_1(\bar{S}_2, \varphi_2(\bar{S}_2)) > \frac{D_1}{V}$ and $\mathcal{G}_2(\bar{S}_1, \varphi_1(\bar{S}_1)) > \frac{D_2}{V}$	(ii) holds and either $|\varphi_1'(S^*)| > |\varphi_2'(S^*)|$ if $\bar{S}_1 < \bar{S}_2$ or $|\varphi_1'(S^*)| < |\varphi_2'(S^*)|$ if $\bar{S}_1 > \bar{S}_2$

Table 2.2: Summary of Local Stability Analysis of (2.12) $S_i(S, R) = p_i(S)$ for all $R \geq 0$; $\mathcal{R}_i(S, R) = q_i(R)$ for all $S \geq 0$.

3 Competition Can Lead to Diversity

3.1 Introduction

It is well known (see for example [4], [10], [25], [27], [56], [60], [65]) that models of exploitative competition in a chemostat with constant input by n populations of microorganisms for a single, essential, nonreproducing, growth limiting resource predict competitive exclusion. That is, they predict that at most one population avoids extinction. Hence, exploitative competition is usually thought of as a factor that reduces the diversity of natural ecosystems. On the other hand, predation is usually assumed to be one of the factors that promotes diversity (see for example [11], [40], [51], [63], [64]). In fact, Wolkowicz [63] considered a model of a food web in a chemostat in which an arbitrary number of competitor populations compete exploitatively for a single resource and an arbitrary number of predator populations predate on the competitor populations. The model predicts that *invasion* by a competitor population or *removal* of a predator population can cause a drastic reduction in the number of populations in the system.

In this chapter we describe a scenario based in a chemostat in which the introduction of a population that exploits common resources actually promotes *greater* diversity. As in the previous chapter, we consider two populations that interact simply by consuming the same two perfectly substitutable resources. It is not surprising that competition for two resources can result in the coexistence of two competitor populations. What is surprising in the example considered is that one of the populations cannot survive in the absence of its apparent rival. However, survival is assured provided both populations are present initially, regardless of the initial concentrations. This example seems to indicate that exploitation of common resources in some circumstances promotes diversity. A similar situation occurs in Butler and Wolkowicz [12], where competition is for two perfectly complementary resources. Examples are given (see examples 3.9 and 3.11 in [12]) predicting that when both resources are limiting at low concentrations and at least one of the resources is inhibitory at high concentrations, two populations can coexist even though neither one can survive without the other.

3.2 The Model

The model that we consider is precisely model (2.12), discussed in the previous chapter, under the assumption that species-specific death rates are insignificant compared to the dilution rate. We assume for convenience that the volume V in the growth vessel is one cubic unit. Under these assumptions the equations become

$$
\begin{aligned}
S'(t) &= (S^\circ - S(t))D - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} \mathcal{S}_i(S(t), R(t)), \\
R'(t) &= (R^\circ - R(t))D - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} \mathcal{R}_i(S(t), R(t)), \\
x_i'(t) &= x_i(t)(-D + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2,
\end{aligned}
\tag{3.1}
$$

$$
S(0) \geq 0, \ R(0) \geq 0, \ x_i(0) \geq 0, \ i = 1, 2.
$$

The functions $\mathcal{S}_i(S, R)$ and $\mathcal{R}_i(S, R)$ are assumed to satisfy all of hypotheses (2.2) and (2.14)–(2.18), while $\mathcal{G}_i(S, R)$ is assumed to satisfy all of hypotheses (2.13) and (2.19)–(2.26).

3.3 The Main Result

As shown in Chapter 2, $int\mathbf{R}_+^4$ is positively invariant for all solutions of (3.1) and all solutions are bounded.

We maintain the notation of the previous chapter for the equilibria of system (3.1). Therefore, the washout equilibrium is denoted $E_o = (S^\circ, R^\circ, 0, 0)$. When they exist, the one-species survival equilibria are denoted $E_1 = (\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$ and $E_2 = (\bar{S}_2, \bar{R}_2, 0, \bar{x}_2)$ and the coexistence equilibrium is denoted $E^* = (S^*, R^*, x_1^*, x_2^*)$.

Lemmas 2.1, 2.5 and 2.11 as well as Theorems 2.7 and 2.12 will be used to prove the main result of this section. Where necessary, they are used with the obvious modifications so that they can be applied in terms of the original unscaled variables.

Theorem 3.1 *Consider system* (3.1). *Let* $j, k \in \{1, 2\}$ *with* $j \neq k$. *Assume that no one-species survival equilibrium of the form* E_j *exists. Assume also that there is a unique one-species survival equilibrium of the form* E_k *and that* E_k *is globally*

asymptotically stable with respect to the positive cone in (S, R, x_k)-space, but that it is unstable with respect to (S, R, x_1, x_2)-space.

(a) If $x_k(0) = 0$, then $\lim_{t\to\infty} x_j(t) = 0$.

(b) System (3.1) is uniformly persistent with respect to all solutions for which $x_1(0) > 0$ and $x_2(0) > 0$.

Proof: (a) This follows immediately by Theorem 2.12(b).

(b) Define $\underline{X} = (S(0), R(0), x_1(0), x_2(0)) \in int\mathbf{R}_+^4$. Since all solutions of (3.1) are nonnegative and bounded, $\Omega(\underline{X})$ is a nonempty, compact, invariant set contained in the nonnegative cone in (S, R, x_1, x_2)-space.

First we show that $E_o \notin \Omega(\underline{X})$. Suppose $E_o \in \Omega(\underline{X})$. Since $M^s(E_o) = \{(S, R, x_1, x_2) \in \mathbf{R}_+^4 : x_k = 0\}$ and $x_k(0) > 0$, $\Omega(\underline{X}) \neq \{E_o\}$. By the Butler-McGehee Lemma, there exists $P^s \in (M^s(E_o) \setminus \{E_o\}) \cap \Omega(\underline{X})$. However, since $P^s \in \Omega(\underline{X})$, $cl\mathcal{O}(P^s) \in \Omega(\underline{X})$. By Lemma 2.11, $(M^s(E_o) \setminus \{E_o\})$ is two dimensional. Since no equilibrium of the form E_j exists, it follows from the Poincaré-Bendixson Theorem that $cl\mathcal{O}(P^s)$ is either unbounded or leaves the nonnegative cone in (S, R, x_1, x_2)-space, a contradiction.

Next we show that $E_k \notin \Omega(\underline{X})$. Suppose $E_k \in \Omega(\underline{X})$. Since $M^s(E_k) = \{(S, R, x_1, x_2) \in \mathbf{R}_+^4 : x_j = 0, x_k > 0\}$, $\Omega(\underline{X}) \neq \{E_k\}$. By the Butler-McGehee Lemma, there exists $Q^s \in (M^s(E_k) \setminus \{E_k\}) \cap \Omega(\underline{X})$. By Lemma 2.11 and the Poincaré-Bendixson Theorem, $cl\mathcal{O}(Q^s)$ either contains E_o, becomes unbounded, or leaves the nonnegative cone in (S, R, x_1, x_2)-space, a contradiction.

Let $X_0 = (\underline{S}, \underline{R}, \underline{x}_1, \underline{x}_2)$ be a point in $\Omega(\underline{X})$. Then $cl\mathcal{O}(X_0) \subset \Omega(\underline{X})$. If $\underline{x}_k = 0$ and $\underline{x}_j \geq 0$, then $E_o \in \Omega(\underline{X})$, a contradiction, and if $\underline{x}_j = 0$ and $\underline{x}_k > 0$, then $E_k \in \Omega(\underline{X})$, again a contradiction. Thus, $\liminf_{t\to\infty} x_i(t) > 0$, $i = 1, 2$, and so (3.1) is persistent. It now follows from the main result of [8] that system (3.1) is uniformly persistent. ∎

Corollary 3.2 *Consider system (3.1). Let $j, k \in \{1, 2\}$ with $j \neq k$. Assume*

$$\frac{R^o - \hat{R}}{S^o - \hat{S}} > \frac{(1/\eta_j)\mathcal{R}_j(\hat{S}, \hat{R})}{(1/\xi_j)\mathcal{S}_j(\hat{S}, \hat{R})} \text{ for all } \hat{S} \in (0, S^o), \hat{R} \in (0, R^o) \qquad (3.2)$$

$$\text{satisfying } \mathcal{G}_j(\hat{S}, \hat{R}) = D.$$

Assume also that $m_{R_k} > D$, $m_{S_k} > D$, $\mathcal{G}_k(S^o, R^o) > D$, and $\mathcal{G}_j(\bar{S}_k, \bar{R}_k) > D$.

(a) *If $x_k(0) = 0$, then $\lim_{t \to \infty} x_j(t) = 0$.*

(b) *If $x_i(0) > 0$, $i = 1, 2$, then $\liminf_{t \to \infty} x_i(t) > 0$.*

Proof: Condition (3.2) implies that no one-species survival equilibrium of the form E_j exists. By Lemma 2.12(a), the conditions $m_{R_k} > D$, $m_{S_k} > D$, and $\mathcal{G}_k(S^o, R^o) > D$ imply that E_k exists and is globally asymptotically stable with respect to the positive cone in (S, R, x_k)-space. By a standard linear analysis (see Section 2.3.3), $\mathcal{G}_j(\bar{S}_k, \bar{R}_k) > D$ implies that E_k is unstable with respect to (S, R, x_1, x_2)-space. The result now follows immediately from Theorem 3.1. ∎

Surprisingly, then, the exploitation of resources S and R by population x_k helps population x_j. We offer an explanation of this rather curious behaviour in the discussion. The following results are required.

Lemma 3.3 *Consider system (3.1). Let $j, k \in \{1, 2\}$ with $j \neq k$. Assume (3.2) holds. Assume also that $\mathcal{G}_j(\bar{S}_k, \bar{R}_k) > D$. Then $\mathcal{G}_j(S^o, R^o) \leq D$ and $m_{S_j} > D > m_{R_j}$.*

Proof: By (3.2) and (2.38), no one-species survival equilibrium of the form E_j exists. Therefore, by Theorem 2.7, $\mathcal{G}_j(S^o, R^o) \leq D$.

To prove that $m_{S_j} > D > m_{R_j}$ we exclude the following three cases:

1. $D \geq m_{S_j}$ and $D \geq m_{R_j}$,

2. $m_{S_j} > m_{R_j} = D$,

3. $m_{R_j} > D$,

   (a) $D > m_{S_j}$

   (b) $m_{S_j} \geq m_{R_j} > D$,

   (c) $m_{R_j} > m_{S_j} > D$.

Case 1. By Lemma 2.1(a)(iii), $\mathcal{G}_j(S, R) < D$ for all $(S, R) \in \mathbf{R}_+^2$, a contradiction.

Case 2. By Lemma 2.1 parts (a) and (c)(ii), $\mathcal{G}_j(\bar{S}_k, \bar{R}_k) > D$ implies $\lambda_j = S_j^c < \bar{S}_k$. Since $\bar{S}_k < S^o$, it follows from Lemma 2.1(a)(ii) that $\mathcal{G}_j(S^o, R^o) > m_{R_j} = D$, a contradiction.

Case 3(a). In this case, $\mu_j < \infty$ and $\lambda_j = \infty$. Since $\mathcal{G}_j(0, \mu_j) = D$,

$$\lim_{S \to 0+} \frac{R^o - \mu_j}{S^o - S} = \frac{R^o - \mu_j}{S^o}, \text{ and } \lim_{S \to 0+} \frac{(1/\eta_j)\mathcal{R}_j(S, \mu_j)}{(1/\xi_j)\mathcal{S}_j(S, \mu_j)} = \infty,$$

we have a contradiction to (3.2).

Case 3(b). By Lemma 2.1(b)(ii), $\lambda_j < S_j^c$. Note that, by Lemma 2.5(a), $\varphi_j'(S) < 0$ for all $S \in (0, \lambda_j)$.

If $\bar{S}_k < S^o \leq \lambda_j < S_j^c$, then $R^o > \varphi_j(\bar{S}_k) > \varphi_j(S^o)$, so $D = \mathcal{G}_j(S^o, \varphi_j(S^o)) < \mathcal{G}_j(S^o, R^o)$ (by (2.23)). If $\lambda_j < S^o < S_j^c$, then $D < \mathcal{G}_j(S^o, 0) \leq \mathcal{G}_j(S^o, R^o)$ (by (2.23)). If $\lambda_j < S_j^c \leq S^o$, then $\mathcal{G}_j(S^o, R^o) > m_{R_j} > D$ (by Lemma 2.1(a)(iii)).

Case 3(c). The proof in this case is similar to previous one. Simply replace λ_j by μ_j and S_j^c by R_j^c. ∎

Lemma 3.4 *Under the assumptions of Corollary 3.2, there exists precisely one co-existence equilibrium $E^* = (S^*, R^*, x_1^*, x_2^*)$ for system (3.1) and*

$$\frac{(1/\eta_k)\mathcal{R}_k(S^*, R^*)}{(1/\xi_k)\mathcal{S}_k(S^*, R^*)} > \frac{R^o - R^*}{S^o - S^*}. \tag{3.3}$$

Proof: Since system (3.1) is uniformly persistent, at least one coexistence equilibrium E^* exists. By (3.1), $\mathcal{G}_i(S^*, R^*) = D$ for $i = 1, 2$. By Lemma 2.5(a), $\varphi_k'(S) < 0$ for all $S \in (0, \lambda_k)$ and by Lemma 2.5(b), $\varphi_j'(S) > 0$ for all $S \in (\lambda_j, M_j^S)$. Therefore, there is exactly one coexistence equilibrium in this case.

Without loss of generality, assume $k = 1$. Then, by Theorem 2.7(a), E_1 exists and is unique. By Lemma 3.3, $m_{S_2} > D > m_{R_2}$. Note that $0 < S^* < S^o$ and $0 < R^* < R^o$. From (3.1), x_1^* and x_2^* must satisfy

$$x_1^* = \frac{(1/\eta_2)\mathcal{R}_2(S^*, R^*)(1 - S^*) - (1/\xi_2)\mathcal{S}_2(S^*, R^*)(1 - R^*)}{\Delta(S^*, R^*)},$$

$$x_2^* = \frac{(1/\xi_1)\mathcal{S}_1(S^*, R^*)(1 - R^*) - (1/\eta_1)\mathcal{R}_1(S^*, R^*)(1 - S^*)}{\Delta(S^*, R^*)},$$

where $\triangle(S^*, R^*)$ is as in (2.52). Recall that, by Lemma 2.16, the numerators of x_1^* and x_2^* must be nonzero and of the same sign. By (3.2), the numerator of x_1^* is negative, implying that the numerator of x_2^* is negative, and the result follows. The proof for $k = 2$ is similar. ∎

3.4 Discussion

Why should exploitation of resources S and R by population x_k help population x_j? Under the hypotheses of Corollary 3.2, $m_{S_j} > D > m_{R_j}$ by Lemma 3.3. Therefore, the rate at which population x_j is removed from competition by dilution exceeds its maximal growth rate on resource R. As well, there exists a critical concentration S_j^c of resource S beyond which the presence of resource R becomes detrimental to population x_j. Since $\hat{S} > (\lambda_j >)S_j^c$ for all $(\hat{S}, \hat{R})$ satisfying $\mathcal{G}_j(\hat{S}, \hat{R}) = D$, the presence of resource R is detrimental to population x_j when the concentration of resource S is close to any such concentration $\hat{S}$. One would expect that the faster resource R is depleted, the better. However, for all $\hat{S} \in (0, S^o)$, $\hat{R} \in (0, R^o)$ satisfying $\mathcal{G}_j(\hat{S}, \hat{R}) = D$,

$$\frac{(R^o - \hat{R})D}{(S^o - \hat{S})D} > \frac{(1/\eta_j)\mathcal{R}_j(\hat{S}, \hat{R})}{(1/\xi_j)\mathcal{S}_j(\hat{S}, \hat{R})}.$$

Therefore, the ratio of the net supply rate of resource R to that of resource S exceeds the ratio of the consumption rate of resource R by population x_j to that of resource S close to any subsistence concentrations $(\hat{S}, \hat{R})$. Therefore, population x_j cannot deplete resource R quickly enough and so no one-species survival equilibrium of the form E_j exists. In the absence of population x_k, the washout equilibrium E_o is globally attracting and population x_j dies out.

Now, for population x_k, $m_{S_k} > D$ and $m_{R_k} > D$. Since $\mathcal{G}_k(S^o, R^o) > D$, E_o is unstable, and in the absence of population x_j, population x_k would survive at a globally asymptotically stable one-species survival equilibrium $E_k = (\bar{S}_k, \bar{R}_k, \bar{x}_1, \bar{x}_2)$ (where $\bar{x}_j = 0$). At the resource concentrations of this one-species survival equilibrium, $\mathcal{G}_j(\bar{S}_k, \bar{R}_k) > D$. Thus, population x_j would be able to compensate for the rate at which it was being removed from competition by dilution and E_k is unstable with respect to (S, R, x_1, x_2)-space. Also, $\lambda_j < \bar{S}_k < \lambda_k$, and so population x_j would

outcompete population x_k driving it to extinction if no resource R were available. Under these conditions, a unique coexistence equilibrium E^* exists. Since

$$\frac{(1/\eta_k)\mathcal{R}_k(S^*,R^*)}{(1/\xi_k)\mathcal{S}_k(S^*,R^*)} > \frac{(R^\circ - R^*)D}{(S^\circ - S^*)D},$$

we see that at resource concentrations near (S^*, R^*), the ratio of the consumption of resource R by population x_k to that of resource S would exceed the ratio of the net supply rate of resource R to that of resource S. Thus, population x_k would deplete resource R quickly enough so that coexistence is possible.

That the hypotheses of Corollary 3.2 can be easily satisfied is shown in the following example:

$$
\begin{aligned}
S' &= 1 - S - \frac{x_1}{\xi_1}\left(\frac{2.25S}{1+S+R}\right) - \frac{x_2}{\xi_2}\left(\frac{2.1S}{1+S+R}\right), \\
R' &= 1 - R - \frac{x_1}{\eta_1}\left(\frac{0.5R}{1+S+R}\right) - \frac{x_2}{\eta_2}\left(\frac{2.1R}{1+S+R}\right), \\
x_1' &= x_1\left(-1 + \frac{2.25S+0.5R}{1+S+R}\right), \\
x_2' &= x_2\left(-1 + \frac{2.1S+2.1R}{1+S+R}\right).
\end{aligned}
$$

In Corollary 3.2, $j = 1$, $k = 2$, $S^\circ = R^\circ = D = 1$, $m_{S_1} = 2.25 > 1 > 0.5 = m_{R_1}$, $m_{S_2} = 2.1 = m_{R_2} > 1$, $\lambda_1 = 4/5$, $\mu_1 = \infty$, $\lambda_2 = \mu_2 = 10/11$, $\mathcal{G}_1(1,1) = 11/12 < 1$, $\mathcal{G}_2(1,1) = 1.4 > 1$, $S_1^c = 2/7$, $R_1^c = S_2^c = R_2^c = \infty$. Provided ξ_1 and η_1 are chosen so that (3.2) holds, i.e.,

$$\frac{\xi_1}{\eta_1} < \frac{9(20 - 11\sqrt{10})}{40 - 13\sqrt{10}} \approx 119.9210,$$

and ξ_2 and η_2 are chosen so that (3.3) holds, i.e.,

$$\frac{\xi_2}{\eta_2} > \frac{2272}{39} \approx 58.2564,$$

then the hypotheses of Corollary 3.2 are all satisfied by this example. The coexistence equilibrium, $E^* = (64/77, 6/77, x_1^*, x_2^*)$, where

$$x_1^* = \frac{7\xi_1\eta_1(2272\eta_2 - 39\xi_2)}{176(2\xi_1\eta_2 - 9\eta_1\xi_2)} \quad \text{and} \quad x_2^* = \frac{5\xi_2\eta_2(-3408\eta_1 + 13\xi_1)}{176(2\xi_1\eta_2 - 9\eta_1\xi_2)},$$

can be shown to be locally asymptotically stable, and is probably globally asymptotically stable. In the absence of population x_2, population x_1 dies out. However, if both populations x_1 and x_2 are present at some time and in any amount, then both populations persist.

Note that resource R is not inherently detrimental to population x_1. If nothing were changed in the above example except that the dilution rate D were reduced so that $D < m_{R_1}$, then it would not be possible to satisfy the hypotheses of the Corollary. In the absence of population x_2, population x_1 would survive at a globally stable one-species survival equilibrium. In fact, if D is sufficiently small and no x_2 is present, x_1 could survive by consuming resource R exclusively, even if resource S is eliminated. With this in mind, the following scenario is possible. If D is sufficiently small, x_1 could survive with or without x_2. If D is suddenly increased, x_1 could be forced to extinction unless some x_2 is present. (For example, the dilution rate often changes significantly due to spring run off.)

The above example also provides support for the so-called *paradox of enrichment* introduced by Rosenzweig [44] — "Man must be careful in attempting to enrich ecosystems in order to increase its food yield. There is a real chance that such activity may result in a decimation of the food species that are wanted in greater abundance." One could imagine the following scenario. In the above example, fix $\xi_1/\eta_1 < 45/2$ and take $x_2(0) = 0$. If $S^\circ = 1$ and $R^\circ = 0$, then the model predicts that x_1 approaches a positive equilibrium concentration. However, if the environment is enriched by increasing R° above a critical value R_c°, x_1 is no longer able to avoid extinction. This scenario will be investigated in further detail in the next chapter.

4 An examination of the thresholds of enrichment: A resource-based growth model

4.1 Introduction

In [44], Rosenzweig considers six mathematical models of predator-prey interaction. He shows that sufficient enrichment of the environment supporting the prey species can cause destabilization of an otherwise stable coexistence equilibrium. Integrating his equations numerically and using a truncation for the sake of biological reality, he obtains extinction of the predator population. Consequently, he issues the following warning. "Man must be very careful in attempting to enrich an ecosystem in order to increase its food yield. There is a real chance that such activity may result in decimation of the food species that are wanted in greater abundance."

A number of authors have raised objections to Rosenzweig's results. Gilpin [20] and May [35] show that the destabilization of the coexistence equilibrium results in the birth of an asymptotically stable periodic orbit. Freedman [16] shows the destabilization of the equilibrium to be the result of a Hopf bifurcation. Rosenzweig [45, 46] points out that if the amplitude of the periodic orbit is sufficiently large, a random perturbation could result in the extinction of one or both populations when sections of it come close to the axes.

McAllister, LeBrasseur and Parsons [34] suggest that Rosenzweig's results might have better been used to prompt questions concerning the critical values of enrichment and how they relate to the other parameters. They object to the extrapolation of Rosenzweig's mathematical results to natural ecosystems, providing experimental evidence that moderate enrichment can be beneficial. However, there is experimental evidence in support of Rosenzweig's results. (See, for example, [28], [33], [48].)

In most of the work dealing with the paradox of enrichment, two-species models are considered. As a very incomplete sample, we mention [2], [6], [14], [16], [18], [20], [34], [35], [43], [44], [52], [66]. In this paper we deal with a single-species growth model, and show that enrichment of the system via an increase in the availability of

a noninhibitory resource can lead to the extinction of the species. In so doing, we begin to answer some of the questions posed by McAllister et al. [34].

This chapter is organized as follows. First, a resource-based model of single-species growth in the chemostat on two growth limiting, nonreproducing, noninhibitory, perfectly substitutable resources is described. Members of the microbial population are assumed to compete only by decreasing the common pool of resources, so that there is no mutual interference. All species-specific parameters of our model are considered fixed, while the quantities under the control of the experimenter are varied. For a given dilution rate, the environment is enriched by increasing the input concentration of one of the resources. It is then shown that there exists a threshold value for the dilution rate which depends on the maximal growth rate of the species on each of the resources. Provided the dilution rate is below this threshold, enrichment is beneficial in the sense that the carrying capacity of the environment is increased, regardless of which resource is used to enrich the environment. When the dilution rate is increased beyond the threshold, it becomes important to consider which resource is used for enrichment. For one of the resources it is shown that, while moderate enrichment can be beneficial, sufficient enrichment leads to the extinction of the microbial population. For the other resource, enrichment leads from washout or initial condition dependent outcomes to survival, and is thus beneficial. We conclude with a discussion in which we summarize and interpret our results, and indicate the implications for resource management.

In the next chapter the thresholds established here are used to study the effects of enrichment in a resource-based predator-prey model.

4.2   The Model

We consider a model of single-species growth in the chemostat on two essential, nonreproducing, perfectly substitutable resources. It is an example of the one-species growth submodels treated in Chapter 2, and is given by the following system of differential equations:

$$S'(t) = (S^\circ - S(t))D - x(t)\frac{1}{\xi}\mathcal{S}(S(t), R(t)),$$

$$R'(t) = (R^\circ - R(t))D - x(t)\frac{1}{\eta}\mathcal{R}(S(t), R(t)), \qquad (4.1)$$

$$x'(t) = x(t)(-D + \mathcal{G}(S(t), R(t))),$$

$$S(0) \geq 0, \ R(0) \geq 0, \ x(0) \geq 0.$$

We identify (S, R, x)-space with $\mathbf{R}_+^3$. For the purposes of this chapter we restrict our attention to the response functions in Waltman, Hubbell and Hsu [60]. Again, they are a generalization of the familiar Michaelis-Menten prototype of functional response to a single resource, and are given by

$$\mathcal{S}(S, R) = \frac{m_S K_R S}{K_S K_R + K_R S + K_S R},$$

$$\qquad (4.2)$$

$$\mathcal{R}(S, R) = \frac{m_R K_S R}{K_S K_R + K_R S + K_S R}.$$

Thus, the resources are noninhibitory, as the consumption of each resource is a strictly monotone increasing function of the concentration of that resource. Since resources S and R are perfectly substitutable, the rate of conversion of nutrient to biomass of population x, denoted $\mathcal{G}(S, R)$ in (4.1), is made up of a contribution from the consumption of nutrient S as well as a contribution from the consumption of resource R. Therefore,

$$\mathcal{G}(S, R) = \frac{m_S K_R S + m_R K_S R}{K_S K_R + K_R S + K_S R}. \qquad (4.3)$$

System (4.1) is precisely the unscaled version of system (2.38) restricted to the functional responses described above and the assumption that the species-specific death rate is insignificant compared to the dilution rate.

We assume that resource S is superior to resource R in the sense that

$$m_S \geq m_R. \qquad (4.4)$$

When the inequality in (4.4) is strict, the partial derivatives of $\mathcal{G}(S, R)$ satisfy the following conditions:

$$\frac{\partial}{\partial S}\mathcal{G}(S,R) > 0 \quad \text{for all} \quad (S,R) \in int\mathbf{R}_+^2,$$

$$\frac{\partial}{\partial R}\mathcal{G}(S,R) > 0 \quad \text{for all} \quad R > 0, 0 < S < S^c, \tag{4.5}$$

$$\frac{\partial}{\partial R}\mathcal{G}(S,R) < 0 \quad \text{for all} \quad R > 0, S > S^c,$$

where $S^c = \dfrac{m_R K_S}{m_S - m_R}$ is related to m_R in the following manner:

$$\mathcal{G}(S^c, R) = m_R \quad \text{for all} \quad R \geq 0. \tag{4.6}$$

Thus, when both resources are in relatively short supply, increasing the concentration of either resource is beneficial. Once resource S is plentiful enough that m_R would be exceeded by consuming only resource S, the presence of resource R could actually become detrimental. However,

$$\lim_{R \to \infty} \mathcal{G}(S,R) = m_R \quad \text{for each fixed} \quad S \geq 0, \tag{4.7}$$

so that the presence of resource R would never be detrimental enough to decrease $\mathcal{G}(S,R)$ below m_R. Since an abundance of S and no R would be optimal for the growth of population x, m_S can never be exceeded, so that

$$\lim_{S \to \infty} \mathcal{G}(S,R) = m_S \quad \text{for each fixed} \quad R \geq 0.$$

Define

$$\lambda = \begin{cases} \dfrac{K_S D}{m_S - D} & \text{if } m_S > D, \\ \infty & \text{otherwise,} \end{cases} \quad \text{and} \quad \mu = \begin{cases} \dfrac{K_R D}{m_R - D} & \text{if } m_R > D, \\ \infty & \text{otherwise,} \end{cases}$$

where λ is obtained by solving the equation $\mathcal{G}(S,0) = D$ when $m_S > D$ and μ is obtained by solving the equation $\mathcal{G}(0,R) = D$ when $m_R > D$. Thus λ and μ represent the breakeven concentrations for resources S and R, respectively, when none of the other resource is available.

Suppose $m_R \neq D$. Setting $\mathcal{G}(S,R) = D$ and solving for R we obtain

$$\varphi(S) = \begin{cases} \dfrac{\mu}{\lambda}(\lambda - S) \text{ for all } 0 \leq S \leq \lambda & \text{if } m_R > D, \\ \\ \dfrac{\delta}{\lambda}(\lambda - S) \text{ for all } S \geq \lambda & \text{if } m_R < D < m_S, \end{cases} \tag{4.8}$$

so that

$$\mathcal{G}(S, \varphi(S)) = D. \tag{4.9}$$

Then the curve $\varphi(S)$ gives the concentrations of resources S and R at which the biomass of population x is neither increasing nor decreasing. For $m_R = D$, $S^c = \lambda$ and

$$\mathcal{G}(\lambda, R) = D \text{ for all } R \geq 0.$$

Note that if $m_S \leq \Gamma$, then the solutions of the equation $\mathcal{G}(S, R) = D$ lie outside the positive cone in (S, R)-space.

Finally, for notational convenience we define

$$P = \frac{\eta}{\xi} \frac{m_S K_R}{m_R K_S}. \tag{4.10}$$

Note that if the dilution rate is slow enough so that $\lambda < S^o$ ($\mu < R^o$), then species x could survive on resource S (respectively, resource R) alone and the higher S^o (respectively, R^o), the better. (See, for example, [59].) In this respect, neither resource is inherently detrimental.

For system (4.1), the coordinate plane in which species x is absent is invariant. If $S(\bar{t}) = 0$ (respectively, $R(\bar{t}) = 0$) for some $\bar{t}$, then $S'(\bar{t}) = S^o D > 0$ (respectively, $R'(\bar{t}) = R^o D > 0$). From this, and the uniqueness of initial value problems, it follows that $int\mathbf{R}^3_+$ is positively invariant for solutions of (4.1). Further, by considering $z(t) = \xi S(t) + \eta R(t) + x(t)$ it follows from (4.1) that the simplex

$$\mathcal{M} = \{(S, R, x) \in \mathbf{R}^3_+ : \xi S + \eta R + x = \xi S^o + \eta R^o\} \tag{4.11}$$

is a global attractor. Thus, all solutions are positive and bounded.

Besides the washout equilibrium $E_o = (S^o, R^o, 0)$, any other equilibria of (4.1) must be survival equilibria. A survival equilibrium of (4.1) is a solution $\bar{E} = (\bar{S}, \bar{R}, \bar{x})$ of the system

$$x\mathcal{S}(S, R) = \xi(S^o - S)D, \tag{4.12}$$

$$x\mathcal{R}(S, R) = \eta(R^o - R)D, \tag{4.13}$$

$$\mathcal{G}(S, R) = D, \tag{4.14}$$

with $\bar{S} \geq 0$, $\bar{R} \geq 0$ and $\bar{x} > 0$.

4.3   Below the Threshold

First consider the case where the dilution rate, D, is relatively small.

Lemma 4.1 *Consider* (4.1). *Suppose that* $m_S \geq D, m_R \geq D$, *and* $\mathcal{G}(S^\circ, R^\circ) > D$. *The species component of the survival equilibrium, $\bar{x}$, is a strictly increasing function of both S° and R°.*

Proof: Since $\mathcal{G}(S^\circ, R^\circ) > D$ implies that at least one of the inequalities, $m_S \geq D$ or $m_R \geq D$, must be strict, we assume, without loss of generality, that $m_S > D, m_R \geq D$, and $m_S \geq m_R$.

Motivated by equation (4.12), define

$$x_S(S, S^\circ) = \frac{\xi(S^\circ - S)D}{\mathcal{S}(S, \varphi(S))}$$

for $S^\circ \geq 0$ and $0 < S < \min\{\lambda, S^\circ\}$, where $\mathcal{S}(S, R)$ is as in (4.2) and $\varphi(S)$ is as in (4.8). Then

$$\frac{\partial}{\partial S^\circ} x_S(S, S^\circ) = \frac{\xi D}{\mathcal{S}(S, \varphi(S))} > 0 \text{ for all } S \in (0, \min\{\lambda, S^\circ\}).$$

Also,

$$\frac{\partial}{\partial S} x_S(S, S^\circ) = \frac{\xi D(m_S - m_R)[S^2 - S^\circ S^c]}{m_S(m_R - D)S^2}.$$

Since $0 < S < \min\{\lambda, S^\circ\}$ and $\lambda < S^c$, $S^2 < S^\circ S^c$, so

$$\frac{\partial}{\partial S} x_S(S, S^\circ) < 0 \text{ for all } S \in (0, \min\{\lambda, S^\circ\}).$$

Similarly, define

$$x_R(S, R^\circ) = \frac{\eta(R^\circ - \varphi(S))D}{\mathcal{R}(S, \varphi(S))}$$

for $R^\circ \geq 0$ and $0 < S < \min\{\lambda, S^\circ\}$. Then

$$\frac{\partial}{\partial R^\circ} x_R(S, R^\circ) = \frac{\eta D}{\mathcal{R}(S, \varphi(S))} > 0 \text{ for all } S \in (0, \min\{\lambda, S^\circ\}).$$

Also,

$$\frac{\partial}{\partial S} x_R(S, R^\circ) = \eta D \left\{ \frac{R^\circ K_R^2 m_S(m_R - D)}{K_S m_R(m_S - D)^2(\lambda - S)^2} + \frac{K_R}{S^c(m_R - D)} \right\}$$
$$> 0 \text{ for all } S \in (0, \min\{\lambda, S^\circ\}).$$

Define
$$g(S, S^\circ, R^\circ) = x_S(S, S^\circ) - x_R(S, R^\circ).$$

By Lemma 2.6(a) and Theorem 2.7(a), there exists a unique $\bar{S} \in (0, \min\{\lambda, S^\circ\})$ such that $g(\bar{S}, S^\circ, R^\circ) = 0$ for each fixed (S°, R°) such that $\mathcal{G}(S^\circ, R^\circ) > D$. Note that

$$\frac{\partial}{\partial S}g(S, S^\circ R^\circ) < 0, \frac{\partial}{\partial S^\circ}g(S, S^\circ, R^\circ) > 0, \text{ and } \frac{\partial}{\partial R^\circ}g(S, S^\circ, R^\circ) < 0.$$

For fixed R°, $\bar{S}$ increases as S° increases, so $x_R(\bar{S}, R^\circ)$ increases. For fixed S°, $\bar{S}$ decreases as R° increases, so $x_S(\bar{S}, S^\circ)$ increases. The result follows.

When $m_R = D$, define

$$x_S(R, S^\circ) = \frac{\xi(S^\circ - \lambda)D}{S(\lambda, R)} \text{ and } x_R(R, R^\circ) = \frac{\eta(R^\circ - R)D}{\mathcal{K}(\lambda, R)}$$

for $0 < R < R^\circ$ and proceed as above. ∎

Thus, if $m_S \geq D$, $m_R \geq D$, and $\mathcal{G}(S^\circ, R^\circ) > D$, enriching the environment by increasing either S° or R° cannot destroy the global stability of the unique survival equilibrium, $\bar{E}$. Also, identifying the carrying capacity of the environment with the species component of the survival equilibrium, $\bar{x}$, it follows that the carrying capacity is always an increasing function of both S° and R°. Thus, provided the dilution rate is sufficiently slow, enrichment using either resource is always beneficial.

4.4 Above the Threshold

We now consider what happens when the dilution rate D is increased subject to $m_S > D > m_R$. Note that

$$\lambda = \frac{K_S D}{m_S - D} > \frac{K_S m_R}{m_S - m_R} = S^c \qquad (4.15)$$

in this case. For mathematical convenience only, we define

$$\delta = \frac{K_R D}{m_R - D} < 0; \qquad (4.16)$$

δ is not intended to denote a resource concentration. We begin by examining the existence of equilibria of system (4.1) when $m_S > D > m_R$. The washout equilibrium,

$E_o = (S^o, R^o, 0)$, always exists. A standard linear analysis shows that E_o is unstable whenever $\mathcal{G}(S^o, R^o) > D$ and is locally asymptotically stable whenever $\mathcal{G}(S^o, R^o) < D$. (See section 2.3.3.) Any other critical points of (4.1) must be survival equilibria. Note that if a survival equilibrium of the form $\bar{E} = (\bar{S}, \bar{R}, \bar{x})$ exists, then, by (4.12), (4.13), (4.14), (4.8), and the positivity constraint on $\bar{x}$,

$$\lambda < \bar{S} < S^o. \tag{4.17}$$

The following theorem examines the existence of survival equilibria as a function of R^o, the input concentration of resource R. Clearly $S^o > \lambda$ is a necessary condition for the existence of a survival equilibrium.

Theorem 4.2 *Consider system (4.1). Assume $m_S > D > m_R$ and fix $S^o > \lambda$. Define*

$$R_1^o = \varphi(S^o) = \frac{\delta}{\lambda}(\lambda - S^o),$$

$$R_2^o = \begin{cases} -\dfrac{\delta}{\lambda}\dfrac{1}{P}\left(\sqrt{\lambda(1-P)} - \sqrt{S^o}\right)^2 & \text{if} \quad P\dfrac{S^o}{(S^o - \lambda)} < 1, \\[4mm] R_1^o & \text{otherwise,} \end{cases}$$

where P is as in (4.10).

(a) *If $0 \leq R^o < R_1^o$, then there exists a unique survival equilibrium $\bar{E}$ of (4.1).*

(b) *If $R^o > R_2^o$, then no survival equilibrium exists.*

(c) *If $R_1^o < R^o < R_2^o$, then there exist precisely two survival equilibria for system (4.1).*

Proof: Note that $(PS^o)/(S^o - \lambda) < 1$ implies $P < 1$, so R_2^o is well-defined. If $R^o = 0$, then it follows immediately from (4.1) that the unique survival equilibrium is given by $\bar{E} = (\lambda, 0, \xi(S^o - \lambda))$.

If an equilibrium of the form $\bar{E} = (\bar{S}, \bar{R}, \bar{x})$ exists for $R^o > 0$, then it follows from (4.14) that $\bar{R} = \varphi(\bar{S})$, where $\varphi(S)$ is as in (4.8). From (4.12) and (4.13), define

$$x_S(S) \triangleq \frac{\xi(S^o - S)D}{S(S, \varphi(S))} \quad \text{and} \quad x_R(S, R^o) \triangleq \frac{\eta(R^o - \varphi(S))D}{\mathcal{R}(S, \varphi(S))}$$

for $S \geq \lambda$ and $R^\circ \geq 0$. Note that $x_S(\bar{S}) = x_R(\bar{S}, R^\circ)$ where, by (4.17), $\lambda < \bar{S} < S^\circ$. By (4.2), (4.15), and (4.8), $x_S(S) = x_R(S, R^\circ)$ if and only if

$$f(S, R^\circ) \triangleq [R^\circ - \varphi(S)]S = \frac{\delta}{\lambda} \frac{1}{P}(S^\circ - S)(\lambda - S) \triangleq g(S). \qquad (4.18)$$

By (4.16) and (4.8), $f(S, R^\circ)$ and $g(S)$ are parabolas opening downward for each $R^\circ \geq 0$. Fixing R° and setting $f(S, R^\circ) = 0$ we find that $S = 0$ or

$$S = \hat{S}(R^\circ) \triangleq \frac{\lambda}{\delta}(\delta - R^\circ).$$

Note that $\hat{S}(0) = \lambda$, $\hat{S}'(R^\circ) > 0$ and $\hat{S}(R^\circ) \leq S^\circ$ if and only if $R^\circ \leq R_1^\circ$. Also, $g(S) \geq 0$ for all $S \in [\lambda, S^\circ]$. Therefore, to each $R^\circ \in (0, R_1^\circ)$ there corresponds a unique $\bar{S} \in (\lambda, S^\circ)$ such that $f(\bar{S}, R^\circ) = g(\bar{S})$. This proves (a).

Consider $R^\circ = R_1^\circ$. Noting that $\hat{S}(R_1^\circ) = S^\circ$, we find that

$$f(S, R_1^\circ) = g(S) \quad \text{whenever} \quad S = S^\circ \quad \text{or} \quad S = S_1^\circ \triangleq \frac{\lambda}{(1-P)}, \qquad (4.19)$$

where

$$\lambda < \frac{\lambda}{(1-P)} < S^\circ \quad \text{if and only if} \quad P \frac{S^\circ}{(S^\circ - \lambda)} < 1.$$

Since $\frac{\partial}{\partial R^\circ} f(S, R^\circ) = S$, parts (b) and (c) now follow. See Figure 4.1. ∎

Remarks concerning Theorem 4.2:

1. Note that $S^\circ/(S^\circ - \lambda) > 1$ is decreasing in S° for $S^\circ > \lambda$. Therefore, if $P \geq 1$, $R_1^\circ = R_2^\circ$ for all $S^\circ > \lambda$. However, if $P < 1$, then $R_2^\circ = R_1^\circ$ for all $\lambda < S^\circ < S_1^\circ$, while $R_2^\circ > R_1^\circ$ for all $S^\circ > S_1^\circ$. Here, S_1° is as in (4.19).

2. The reader is referred to section 4.6 for a derivation of R_1° and R_2°.

We now examine the global properties of system (4.1). To begin, we show that enriching the environment by increasing the R° leads to the extinction of the population when $m_S > D > m_R$. Theorems 2.10 and 2.12(b) will be used in the proof, with the obvious modifications to the former so that it can be applied in terms of the original unscaled variables.

Theorem 4.3 *Consider system (4.1). Assume $m_S > D > m_R$ and fix $S^o > \lambda$. Let R_1^o and R_2^o be as in Theorem 4.2.*

(a) *If $0 \le R^o < R_1^o$, then there exists a unique survival equilibrium $\bar{E}$ and $\bar{E}$ is globally asymptotically stable with respect to all solutions for which $S(0) \ge 0$, $R(0) \ge 0$, and $x(0) > 0$.*

(b) *If $R^o > R_2^o$, then E_o is globally asymptotically stable with respect to all solutions for which $S(0) \ge 0$, $R(0) \ge 0$, and $x(0) \ge 0$.*

(c) *If $R_1^o < R^o < R_2^o$, then the asymptotic behaviour of system (4.1) is initial condition dependent. Any solution either approaches E^o or approaches a survival equilibrium.*

Proof: (a) The existence and uniqueness of $\bar{E}$ is given by Theorem 4.2(a). We first note that, by (4.8), $\mathcal{G}(S^o, R_1^o) = D$. By (4.5) and (4.15), $\mathcal{G}(S^o, R^o) > D$ for all $0 \le R^o < R_1^o$, so E_o is unstable. Also, by Lemma 2.10, $\liminf_{t \to \infty} x(t) > 0$.

We restrict our attention to the globally attracting simplex $\mathcal{M}$ given in (4.11). Since $\mathcal{M}$ is positively invariant, let $x(t) = \xi(S^o - S(t)) + \eta(R^o - R(t))$ and consider the system

$$S'(t) = (S^o - S(t))D - [(S^o - S(t)) + \frac{\eta}{\xi}(R^o - R(t))]\mathcal{S}(S(t), R(t)),$$

$$R'(t) = (R^o - R(t))D - [\frac{\xi}{\eta}(S^o - S(t)) + (R^o - R(t))]\mathcal{R}(S(t), R(t)), \quad (4.20)$$

$$S(0) \ge 0, \quad R(0) \ge 0, \quad \xi S^o + \eta R^o \ge \xi S(0) + \eta R(0).$$

Since $0 \le R^o < R_1^o$, there are precisely two equilibria for system (4.20), $E_o^2 = (S^o, R^o)$ and $\bar{E}^2 = (\bar{S}, \bar{R})$ where the superscript 2 denotes the two-dimensional system (4.20). Sample isoclines and a partial vector field for (4.20) are shown in Figure 4.2(a). (A derivation of the form of the isoclines can be found in section 4.7.) Noting the direction that solutions must cross the isoclines we conclude that no periodic orbits exist on $\mathcal{M}$. Since $\liminf_{t \to \infty} x(t) > 0$, it follows from the Poincaré-Bendixson Theorem that $\bar{E}^2$ is globally asymptotically stable for system (4.20) with respect to all solutions for which $S(0) \ge 0$, $R(0) \ge 0$, and $\xi(S^o - S(0)) + \eta(R^o - R(0)) > 0$. It follows from

Theorem 1.5 of [55] that $\bar{E} = (\bar{S}, \bar{R}, \bar{x})$, where $\bar{x} = \xi(S^o - \bar{S}) + \eta(R^o - \bar{R})$, is in the omega limit set of any solution of (4.1) with $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) > 0$. Since $\bar{E}$ is locally asymptotically stable, $\bar{E}$ is the only point in the omega limit set and so it must be globally asymptotically stable for (4.1) with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) > 0$.

(b) The result follows from Theorem 4.2(b) and Lemma 2.12(b).

(c) We again restrict our attention to $\mathcal{M}$ and consider system (4.20). Since $R_1^o < R^o < R_2^o$, it follows from Theorem 4.2(c) that there are precisely three equilibria for system (4.20), two of which correspond to interior equilibria of system (4.1). The equilibria will be denoted $E_o^2 = (S^o, R^o)$ and $\bar{E}_i^2 = (\bar{S}_i, \bar{R}_i)$, $i = 1, 2$. The isoclines, equilibria, and a partial vector field for (4.20) are shown in Figure 4.2(b). (The reader is again referred to section 4.7 for a derivation of the form of the isoclines.) Noting the direction that solutions must cross the isoclines we conclude that there can be no periodic orbits. All solutions initiating off the stable manifold of $\bar{E}_2^2$ must eventually enter region I, II or III. By the Poincaré-Bendixson Theorem, those entering regions II and III approach $\bar{E}_1^2$ while those entering region I approach E_o^2. Thus $\bar{E}_1^2$ and E_o^2 are locally asymptotically stable while E_2^2 is a saddle. It follows from Theorem 1.5 of [55] that (S_1, R_1, x_1) and $(S^o, R^o, 0)$ are locally asymptotically stable while (S_2, R_2, x_2) is unstable with two-dimensional stable manifold. (Here $x_i = \xi(S^o - S_i) + \eta(R^o - R_i)$, $i = 1, 2$.) Therefore, whether the species survives or washes out depends on the initial conditions when $R_1^o < R^o < R_2^o$. $\blacksquare$

We are now prepared to offer the following bifurcation analysis of system (4.1) for $m_S > D > m_R$ and fixed $S^o > \lambda$, based on the parameter R^o. There are two cases to consider.

Case 1: $P\dfrac{S^o}{(S^o - \lambda)} \geq 1$.

When $R^o = 0$ the survival equilibrium $\bar{E} = (\lambda, 0, \xi(S^o - \lambda))$ in the $R = 0$ plane is globally asymptotically stable. The critical point E_o, corresponding to total washout, exists and is unstable. As R^o is increased subject to $0 < R^o < R_1^o$, $\bar{E}$ enters the positive cone while maintaining its stability. When $R^o = R_1^o$, $\bar{E}$ and E_o coalesce (see Figure 4.1(a)) and the washout equilibrium is globally asymptotically stable. As

R° is increased above R_1°, $\bar{E}$ leaves the nonnegative cone and loses its stability to E_o, so E_o is globally asymptotically stable for all $R^\circ > R_1^\circ$. Thus, there is a transcritical bifurcation at $R^\circ = R_1^\circ$. See Figure 4.3(a).

Case 2: $P\dfrac{S^\circ}{(S^\circ - \lambda)} < 1$.

For $0 \leq R^\circ < R_1^\circ$, E_o and the survival equilibrium $\bar{E}_1$ behave as above. The second survival equilibrium, $\bar{E}_2$, cannot exist in the nonnegative cone. (See Figure 4.1(b).) When $R^\circ = R_1^\circ$, E_o and $\bar{E}_2$ coalesce. As R° is increased subject to $R_1^\circ < R^\circ < R_2^\circ$, $\bar{E}_2$, a saddle, enters the positive cone. E_o and $\bar{E}_1$ are locally asymptotically stable. Thus we have initial condition dependent outcomes with the stable manifold of $\bar{E}_2$ acting as the separatrix. When $R^\circ = R_2^\circ$, $\bar{E}_1$ and $\bar{E}_2$ coalesce, resulting in a saddle-node. If R° is increased beyond R_2°, $\bar{E}_1$ and $\bar{E}_2$ no longer exist and E_o is globally asymptotically stable. Thus, there is a saddle-node bifurcation at $R^\circ = R_2^\circ$. See Figure 4.3(b). Note the hysteresis effect in Figure 4.3(b). If the input concentration of resource R exceeds R_2°, the biomass in the culture vessel decreases. If the quantity of species is very low, the input concentration must be decreased below R_1° before extinction can be avoided.

The question that remains is how the species component of the survival equilibria are affected by an increase in the input concentration of resource R. Figure 4.4 is the bifurcation diagram for system (4.1) exhibiting the change in $\bar{x}$ as a function of R°. In Figure 4.4(a) we used the parameter values $K_S = K_R = 1$, $m_S = 2.25$, $m_R = 0.5$, $D = 1$, $S^\circ = 1$, $\xi = 70$ and $\eta = 1$. Then

$$P\frac{S^\circ}{(S^\circ - \lambda)} \approx 0.32 < 1.$$

Thus, there are two critical values of R°: $R_1^\circ = 0.5$ and $R_2^\circ \approx 0.7066$. For $0 \leq R^\circ < R_1^\circ$, the carrying capacity of the environment is a decreasing function of R°. For $R_1^\circ < R^\circ < R_2^\circ$, the species component of the locally asymptotically stable survival equilibrium is also a decreasing function of R°. This would indicate that even moderate enrichment is detrimental to the species. However, this is not always the case.

In Figure 4.4(b) we used the following parameter values. The growth parameters are $m_S = 0.145h^{-1}$, $K_S = 1.00\mu M$, $\xi = 25.6$ g dry wt/mol, $m_R = 0.085h^{-1}$, $K_R = 1.00\mu M$, and $\eta = 6.40$ g dry wt/mol. (These values correspond to a facultatively chemolithotrophic *Thiobacilus* species which can grow heterotrophically on acetate (S), autotrophically on thiosulfate (R), and mixotrophically on both. See [21].) Fixing $D = 0.10h^{-1}$, so that $m_S > D > m_R$, we have $\lambda \approx 2.22\mu M$. If $S^o = 20.00\mu M$, then

$$P\frac{S^o}{(S^o - \lambda)} \approx 0.48 < 1.$$

Again, there are two critical values of R^o: $R_1^o \approx 53.33\mu M$ and $R_2^o \approx 78.62\mu M$. For $0 \leq R^o < R_1^o$, the carrying capacity of the environment is an increasing function of R^o. Also, there exists $\hat{R}^o \in (R_1^o, R_2^o)$ such that, for $R_1^o < R^o < \hat{R}^o$, the species component of the locally asymptotically stable survival equilibrium is an increasing function of R^o. It is only when R^o is increased beyond $\hat{R}^o$ that the species component of this equilibrium begins to decrease until, for $R^o > R_2^o$, we have washout. Thus, in some cases, moderate enrichment can be beneficial.

Given the input concentration of resource S and the growth parameters for species x, it is possible to anticipate the response of system (4.1) to moderate enrichment. Consider the function $\bar{S}(R^o)$ satisfying

$$\delta\lambda S^o + [\delta\lambda(P - 1) - \delta S^o - \lambda R^o P]\bar{S}(R^o) - \delta(P - 1)\bar{S}(R^o)^2 = 0.$$

This equation follows from (4.18) and gives the equilibrium concentration of S for a fixed value of R^o. Differentiating with respect to R^o we obtain

$$[\delta\lambda(P - 1) - \delta S^o - \lambda R^o P]\bar{S}'(R^o) - \lambda P\bar{S}(R^o) - 2\delta(P - 1)\bar{S}(R^o)\bar{S}'(R^o) = 0,$$

so

$$\bar{S}'(R^o) = \frac{\lambda P\bar{S}(R^o)}{[\delta\lambda(P - 1) - \delta S^o - \lambda R^o P] - 2\delta(P - 1)\bar{S}(R^o)}.$$

Since $\bar{S}(0) = \lambda$,

$$\bar{S}'(0) = \frac{\lambda^2 P}{-\delta[(S^o - \lambda) + \lambda P]} > 0.$$

Next, consider the function

$$x_S(R^o) = x_S(\bar{S}(R^o)) = \frac{\xi(S^o - \bar{S}(R^o))D}{S(\bar{S}(R^o), \varphi(\bar{S}(R^o))}$$

which gives the equilibrium concentration of species x. The sign of $x'_S(R^\circ)$ is determined by

$$-\xi\bar{S}'(R^\circ)\mathcal{S}(\bar{S}(R^\circ),\varphi(\bar{S}(R^\circ))) - \xi(S^\circ - \bar{S}(R^\circ))D\frac{d}{dR^\circ}\mathcal{S}(\bar{S}(R^\circ),\varphi(\bar{S}(R^\circ))).$$

Note that

$$\frac{d}{dR^\circ}\mathcal{S}(\bar{S}(R^\circ),\varphi(\bar{S}(R^\circ))) = \left(K_R + \varphi(\bar{S}(R^\circ)) + \bar{S}(R^\circ)\frac{\delta}{\lambda}\right)$$
$$\times\frac{m_S K_S K_R \bar{S}'(R^\circ)}{(K_S K_R + K_R \bar{S}(R^\circ) + K_S\varphi(\bar{S}(R^\circ)))^2}.$$

Again, $\bar{S}(0) = \lambda$, so $\varphi(\bar{S}(0)) = 0$ and

$$\frac{d}{dR^\circ}\mathcal{S}(\bar{S}(0),\varphi(\bar{S}(0))) = \frac{m_S K_S}{(K_S + \lambda)^2}\left(1 + \frac{\delta}{K_R}\right)\bar{S}'(0).$$

Therefore,

$$x'_S(0) = -\xi D\bar{S}(0)\left\{D + (S^\circ - \lambda)\frac{m_S K_S}{(K_S + \lambda)^2}\left(1 + \frac{\delta}{K_R}\right)\right\}.$$

Define

$$T = D + (S^\circ - \lambda)\frac{m_S K_S}{(K_S + \lambda)^2}\left(1 + \frac{\delta}{K_R}\right).$$

Then even moderate enrichment will be detrimental in the (S, R, x)-subsystem when $T > 0$, while moderate enrichment will be beneficial when $T < 0$. Note that $T \approx 0.9573964$ for Figure 4.4(a), while $T \approx -16.228829$ for Figure 4.4(b).

We note that when $m_S > D > m_R$, enriching the environment by increasing S°, the input concentration of resource S, is beneficial. This can be seen by viewing R_1° as a function of S°. Fix $S^\circ > \lambda$ and $R^\circ > R_1^\circ(S^\circ)$. Then, by Theorem 4.3(b,c), we have either washout or initial condition dependent outcomes. Note that $R_1^\circ(S^\circ)$ is an increasing function of S° and $\lim_{S^\circ \to \infty} R_1^\circ(S^\circ) = \infty$. By increasing the input concentration of resource S, two values of S° distinguish themselves:

$$S_{R_1}^\circ = \frac{\lambda}{\delta}(\delta - R^\circ),$$

$$
S_{R_2}^o = \begin{cases} -\dfrac{\lambda}{\delta}\left(\sqrt{PR^o} + \sqrt{\delta(P-1)}\right)^2 & \text{if} \quad P\dfrac{(R^o - \delta)}{R^o} < 1, \\[20pt] S_{R_1}^o & \text{otherwise.} \end{cases}
$$

For $S_{R_2}^o < S^o < S_{R_1}^o$, there exist two survival equilibria for system (4.1) and the behaviour of the system is initial condition dependent. Any solution either approaches E_o or approaches a survival equilibrium. When $S^o > S_{R_1}^o$, $R_1^o(S^o) > R^o$. By Theorem 4.3(a) it follows that there exists a unique survival equilibrium $\bar{E}$ and $\bar{E}$ is globally asymptotically stable with respect to all solutions satisfying $S(0) \geq 0$, $R(0) \geq 0$, and $x(0) > 0$. As in Lemma 4.1 it can be shown that the carrying capacity of the environment is an increasing function of S^o once the system enters this regime. (See Figure 4.5.) The reader is referred to section 4.6 for a derivation of $S_{R_1}^o$ and $S_{R_2}^o$.

Finally, we note that if the dilution rate satisfies $D \geq m_S \geq m_R$, then E^o is globally asymptotically stable for system (4.1), regardless of the input concentrations of the resources. This follows from equations (4.2), (4.3) and (4.14), and Lemma 2.12(b).

4.5   Discussion

In this chapter we consider a resource-based model of single-species growth in the chemostat on two growth-limiting, nonreproducing, noninhibitory, perfectly substitutable resources, S and R. We do not allow for mutual interference, so that the members of the microbial population compete only by depleting the common pool of resources. Except for S^o and R^o, the input concentrations of the resources, and D, the input and washout rate, all parameters of the model are fixed. Therefore, all species-specific parameters are fixed while the quantities under the control of the experimenter are varied.

It is important to note that neither resource is inherently detrimental. Resources S and R are alternative sources of the same essential nutrient. Therefore, at least one of these resources must be supplied in sufficient amounts in order for the species to survive. Even if only one of the resources (S or R) is supplied, species

x would survive provided the dilution rate is sufficiently slow. In fact, in this one-resource case, the carrying capacity of the environment (given by the species component of the survival equilibrium) is an increasing function of the input concentration of that resource.

If there are two perfectly substitutable resources, our results seem to indicate that the predictions of a model in which only one resource is assumed to be limiting can be misleading if the two-resource model is to be robust enough to remain valid for reasonable ranges of the parameters. In the two resource case one must consider the relative values of m_S and m_R, the maximal growth rates of species x on resources S and R, respectively, and D. We assume that resource S is superior to resource R in the sense that $m_S \geq m_R$, so that there is a critical value, S^c, for resource S. If the concentration of resource S is below S^c, an increase in the concentration of either resource is beneficial. However, once the concentration of resource S is above this critical value, the presence of resource R actually becomes detrimental.

First, assume that the dilution rate does not exceed the maximal growth rate on either resource, so $m_R \geq D$, and equate enrichment of the environment with an increase in the input concentration of one resource. In this case, $\mathcal{G}(S^o, R^o) > D$ is necessary and sufficient to ensure that a unique survival equilibrium exists and is globally asymptotically stable with respect to the interior of (S, R, x)-space. Moreover, the carrying capacity of the environment is an increasing function of both input concentrations. Thus, provided the input rate is sufficiently slow, enriching the environment by increasing S^o or R^o is beneficial.

If D is increased subject to $m_S > D > m_R$, the scenario changes dramatically. First, equate enrichment of the environment with an increase in the input concentration of resource R. In this case, we identify two critical values of R^o, $R_1^o \leq R_2^o$, where

$$R_1^o < R_2^o \quad \text{if and only if} \quad \frac{\eta}{\xi} \frac{m_S K_R}{m_R K_S} \frac{S^o}{(S^o - \lambda)} < 1.$$

When $0 \leq R^o < R_1^o$ there exists a unique survival equilibrium that is globally asymptotically stable. For $R_1^o < R^o < R_2^o$ the species survives or washes out depending on the initial conditions. Increasing R^o beyond R_2^o leads to extinction. Thus we provide more support that Rosenzweig's [44] warning is valid. We give two examples which

indicate that moderate enrichment via an increase in the input concentration of resource R can be, but is not always, beneficial in the sense that the carrying capacity of the environment is increased. However, enriching the environment by increasing the input concentration of resource S is beneficial. If $R^o > R_1^o$, increasing S^o leads from washout or initial condition dependent outcomes (with washout possible) to survival. Once the system enters this regime, the carrying capacity of the environment is an increasing function of S^o.

Why should increasing the input concentration of resource R lead to extinction when $m_S > D > m_R$? Consider all concentrations $\bar{S}$, $\bar{R}$ of resources S and R satisfying $\mathcal{G}(\bar{S}, \bar{R}) = D$. The concentration $\bar{S}$ of resource S is above the critical value S^c. For any fixed $S > S^c$, the growth rate, given by $\mathcal{G}(S, R)$, is a decreasing function of resource R. One would expect that the faster resource R is depleted, the better. However, when $R^o > R_2^o$,

$$\frac{(R^o - \bar{R})D}{(S^o - \bar{S})D} > \frac{(1/\eta)\mathcal{R}(\bar{S}, \bar{R})}{(1/\xi)\mathcal{S}(\bar{S}, \bar{R})}.$$

Thus, the ratio of the net supply rate of resource R to that of resource S exceeds the ratio of the consumption rate of resource R to that of resource S. As species x cannot deplete resource R quickly enough, no survival equilibrium exists.

More intuitively, resource S is more nourishing than resource R in the sense that the maximal growth rate on resource S is assumed to be higher than on resource R. Thus, resource R can be thought of as junk food. Even though resource R is adequately sustaining when the dilution rate is sufficiently small, it is not nourishing enough when the dilution rate is high because the species cannot grow fast enough on it in this case. Its presence also reduces the consumption of the more nourishing resource S because the species wastes time consuming resource R. Thus, moderate concentrations of resource R can be beneficial (see Figure 4(b)), but sufficiently high concentrations can cause washout.

Perhaps motivated by the methods of Rosenzweig [44], Brauer [6] states that "enrichment of the prey's environment ... may be described mathematically by an increase in the carrying capacity." For dilution rates below the threshold the results of our resource-based study would support this relationship between enrichment of

the prey's environment and the carrying capacity. However, for dilution rates above the threshold, the validity of this relationship depends on the resource used for enrichment. The relationship remains valid for the superior resource. (See Figure 5.) However, it can only hold for moderate enrichment when the inferior resource is used. (See Figures 4(a) and 4(b).)

We stress that we have considered a constant dilution rate D rather than a time-dependent dilution rate $D(t)$. The latter may be more appropriate for species at higher trophic levels, where seasonal fluctuations come into play. We feel that a bifurcation approach using a constant dilution rate may actually be a better approximation for the lower-level microbial species considered here. We are motivated by the shorter generation times typical of such species. (For example, the generation time of the prey species *paramecium aurelia* considered by Luckinbill [33] is approximately 0.26 days.) Usually the dilution rate remains relatively constant within a season, and the time required for the chemostat to equilibrate is relatively short compared to the length of a season.

The importance of single-species microbial population dynamics to ecology is beautifully detailed by Williams [61]. In the same study he asserts that the chemostat provides a good laboratory idealization of nature. Our results may provide important implications for the management of aquatic systems. In managing the microbial populations of such systems, it may be necessary to take into consideration when and how much to enrich. In the summer the natural dilution rate may satisfy $D < m_S$ and $D < m_R$, so enrichment with either resource is beneficial. However, the natural dilution rate is higher during spring run-off. Success with enrichment in the summer can lead to the false conclusion that enriching the environment in the spring will be equally beneficial. In fact, if the dilution rate is so high that $m_S > D > m_R$, it becomes necessary to consider which resource is used for enrichment. When the superior resource is used, enrichment is beneficial. When the inferior resource is used, moderate enrichment can be beneficial, while increasing the nutrient input to the system sufficiently actually leads to washout.

The results in this chapter may also help to explain some of the effects of fertilizer runoff and industrial waste on the microbial populations of certain lakes.

4.6 Appendix A: The Derivation of R_1^o, R_2^o, $S_{R_1}^o$, and $S_{R_2}^o$.

In this section we indicate how the quantities R_1^o, R_2^o, $S_{R_1}^o$, and $S_{R_2}^o$ are derived. In equation (4.18), consider g to be a function of S and S^o. Then

$$f(S, R^o) \triangleq [R^o - \varphi(S)]S = \frac{\delta}{\lambda}\frac{1}{P}(S^o - S)(\lambda - S) \triangleq g(S, S^o). \qquad (4.21)$$

To find R_1^o, fix S^o and increase R^o until the rightmost roots of f and g coincide. This yields the equation

$$\frac{\lambda}{\delta}(\delta - R^o) = S^o,$$

which is then solved for R^o. The quantity $S_{R_1}^o$ is obtained similarly.

Again fixing S^o, R_2^o is the value of R^o for which f and g intersect uniquely in $(\lambda, S^o]$. From (4.21),

$$\delta\lambda S^o + [\delta\lambda(P - 1) - \delta S^o - \lambda R^o P]S - \delta(P - 1)S^2 = 0.$$

In solving this equation for S uniquely, the discriminant must be zero. Thus,

$$(P\lambda)^2(R^o)^2 + 2P\lambda\delta[S^o + \lambda(1 - P)] + \delta^2[S^o + \lambda(P - 1)]^2 = 0.$$

For $P < 1$ this yields

$$R^o = -\frac{\delta}{\lambda}\frac{1}{P}\left(\sqrt{S^o} \pm \sqrt{\lambda(1 - P)}\right)^2.$$

The S value corresponding to $\oplus$ is

$$S = -\sqrt{\frac{\lambda S^o}{(1 - P)}} < 0,$$

which is inadmissible. If

$$R_2^o = -\frac{\delta}{\lambda}\frac{1}{P}\left(\sqrt{S^o} - \sqrt{\lambda(1 - P)}\right)^2,$$

then $S = \sqrt{\lambda S^o/(1 - P)}$, and we have

$$S < S^o \quad \text{if and only if} \quad P\frac{S^o}{(S^o - \lambda)} < 1.$$

Fixing R°, $S^\circ_{R_2}$ is the value of S° for which f and g intersect uniquely in $(\lambda, S^\circ]$. For $P < 1$ this yields

$$S^\circ = -\frac{\lambda}{\delta} \left(\sqrt{PR^\circ} \pm \sqrt{\delta(P-1)} \right)^2.$$

The S value corresponding to $\ominus$ is

$$S = \lambda - \lambda \sqrt{\frac{PR^\circ}{\delta(P-1)}} < \lambda,$$

which is inadmissible. If

$$S^\circ_{R_2} = -\frac{\lambda}{\delta} \left(\sqrt{PR^\circ} + \sqrt{\delta(P-1)} \right)^2,$$

then

$$\varphi(S) = -\delta\sqrt{\frac{PR^\circ}{\delta(P-1)}} < R^\circ \quad \text{if and only if} \quad \frac{P(R^\circ - \delta)}{R^\circ} < 1.$$

4.7   Appendix B: The Isoclines of (4.20)

In this section we examine the general shape of the isoclines for system (4.20). First, consider the case $R^\circ_1 < R^\circ < R^\circ_2$. Since $PS^\circ/(S^\circ - \lambda) < 1$ and $m_S > D > m_R$, it follows from (4.10) that

$$\frac{\eta}{\xi} \frac{m_S K_R}{D K_S} < 1 \quad \text{and} \quad \frac{\xi}{\eta} \frac{m_R K_S}{D K_R} > 1.$$

Setting $S' = 0$ in (4.20) and solving for R we obtain

$$\Phi(S) = K_\Phi \left\{ \frac{S^2 + a_\Phi S + b_\Phi}{S - c_\Phi} \right\},$$

where

$$a_\Phi = -\left\{ \frac{\eta}{\xi} \frac{m_S R^\circ}{D K_S} \lambda + \lambda + S^\circ \right\} < 0,$$

$$b_\Phi = S^\circ \lambda > 0,$$

$$c_\Phi = S^\circ \left(1 - \frac{\eta}{\xi} \frac{m_S K_R}{D K_S} \right)^{-1} > S^\circ, \quad \text{and}$$

$$K_\Phi = \frac{K_R}{\lambda} \left(1 - \frac{\eta}{\xi} \frac{m_S K_R}{D K_S} \right)^{-1} > 0.$$

Similarly, setting $R' = 0$ in (4.20) and solving for S we obtain

$$\Sigma(R) = K_\Sigma \left\{ \frac{R^2 + a_\Sigma R + b_\Sigma}{R - c_\Sigma} \right\},$$

where

$$
\begin{aligned}
a_\Sigma &= -\left\{ \frac{\xi}{\eta} \frac{m_R S^\circ}{DK_R} \delta + \delta + R^\circ \right\}, \\
b_\Sigma &= R^\circ \delta < 0, \\
c_\Sigma &= R^\circ \left(1 - \frac{\xi}{\eta} \frac{m_R K_S}{DK_R} \right)^{-1} < 0, \quad \text{and} \\
K_\Sigma &= \frac{K_S}{\delta} \left(1 - \frac{\xi}{\eta} \frac{m_R K_S}{DK_R} \right)^{-1} > 0.
\end{aligned}
$$

Note that $\Phi(0) = -K_R$ and $\Sigma(0) = -K_S$.

Both $\Phi(S)$ and $\Sigma(R)$ are of the form

$$f(x) = K \frac{x^2 + ax + b}{x - c}, \quad K > 0,$$

so that both functions have slant asymptote with positive slope. For each, the graph is either concave up for $x < c$ and concave down for $x > c$, as in Figure 4.6(a), or concave down for $x < c$ and concave up for $x > c$, as in Figure 4.6(b).

First, consider $\Phi(S)$. The vertical asymptote occurs at $S = c_\Phi > S^\circ$. By Theorem 4.2(c) the points $\bar{E}_i^2 = (\bar{S}_i, \bar{R}_i)$, $i = 1, 2$, and $E_o^2 = (S^\circ, R^\circ)$ lie on $\Phi(S)$. Since the $\bar{E}_i^2$ lie on the line $\varphi(S)$, given by (4.9), and $R^\circ > \varphi(S^\circ) = R_1^\circ$, $\Phi(S)$ must be concave up on the interval $(-\infty, c_\Phi)$, as in Figure 4.6(a). Similarly, the curve $\Sigma(R)$ must be concave down on the interval (c_Σ, ∞), as in Figure 4.6(a), where $c_\Sigma < 0$. Therefore, for $R_1^\circ < R^\circ < R_2^\circ$ the isoclines of (4.20) are as in Figure 4.2(b).

For $0 \leq R^\circ \leq R_1^\circ$, the precise shape of the isoclines cannot be stated, since there is insufficient information to determine the concavity of the corresponding functions $\Phi(S)$ and $\Sigma(R)$. There are nine possible pairings, one of which is depicted in Figure 4.2(a). However, regardless of the concavity, the asymptotic behaviour of system (4.1) for $0 \leq R^\circ < R_1^\circ$ is determined as in Theorem 4.3(a).
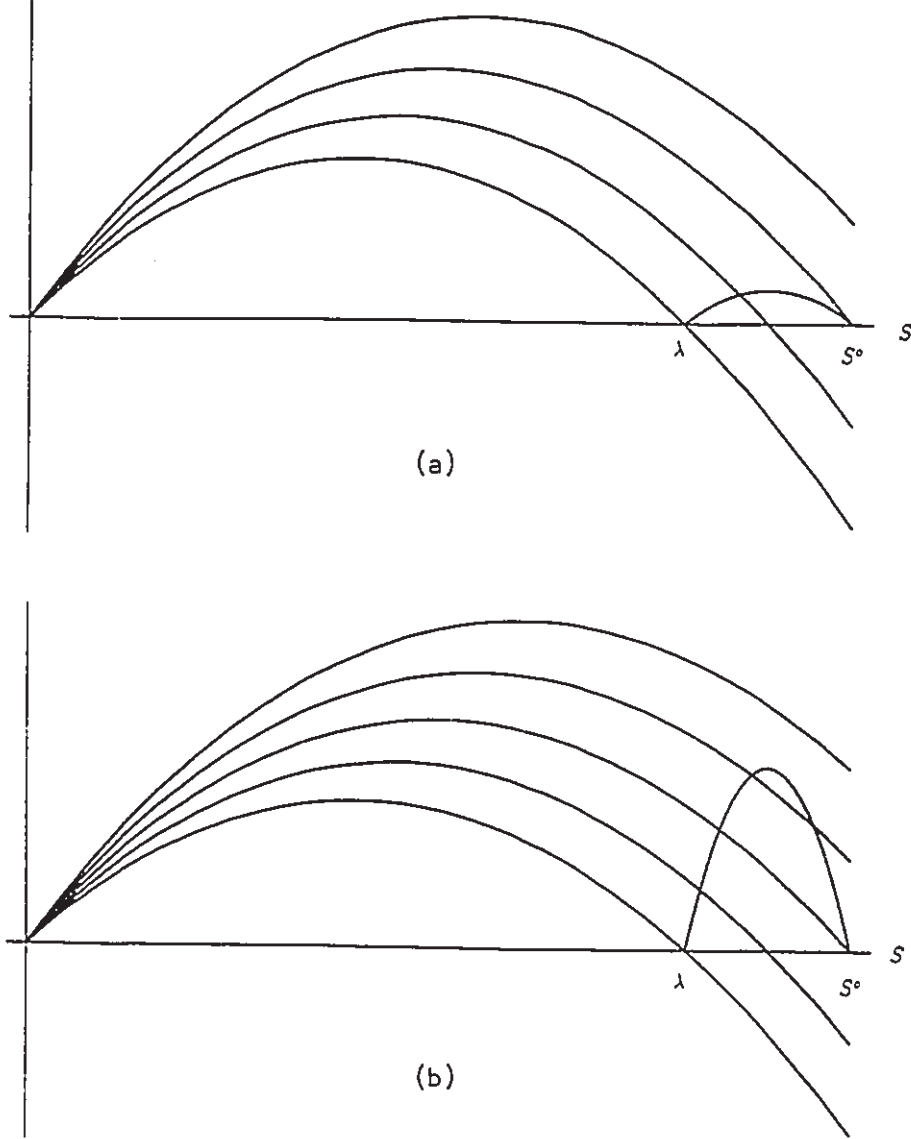
4.8   Figures

Figure 4.1: Schematic Diagram for Theorem 4.2

(a) $PS^\circ/(S^\circ - \lambda) \geq 1$

(b) $PS^\circ/(S^\circ - \lambda) < 1$

In each of (a) and (b), the parabolas with roots 0 and λ correspond to $R^\circ = 0$ while the parabolas with roots 0 and S° correspond to $R^\circ = R_1^\circ$.
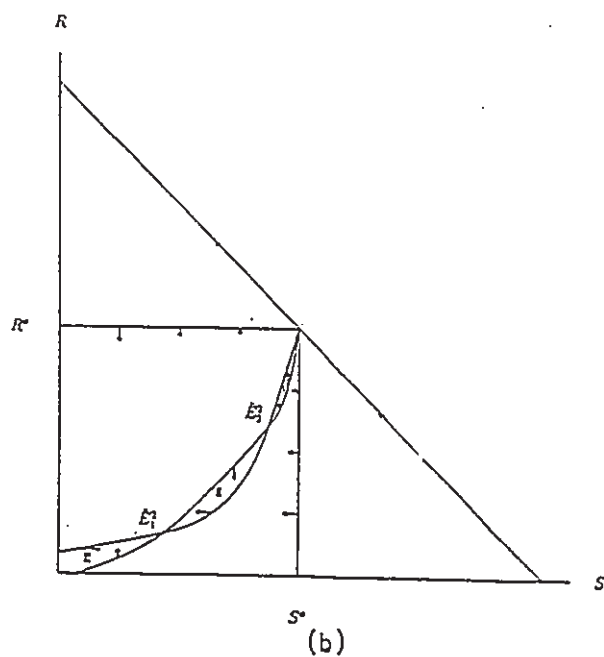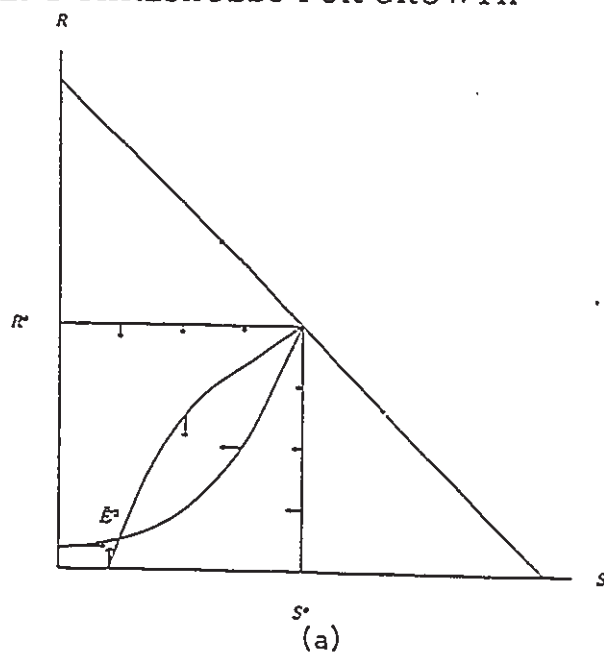
Figure 4.2: Partial vector fields for Theorem 4.3

(a) $0 \leq R^\circ < R_1^\circ$

(b) $R_1^\circ < R^\circ < R_2^\circ$

Vectors parallel to the S axis indicate the sign of $S'(t)$ along the indicated line. Vectors parallel to the R axis indicate the sign of $R'(t)$ along the indicated line.
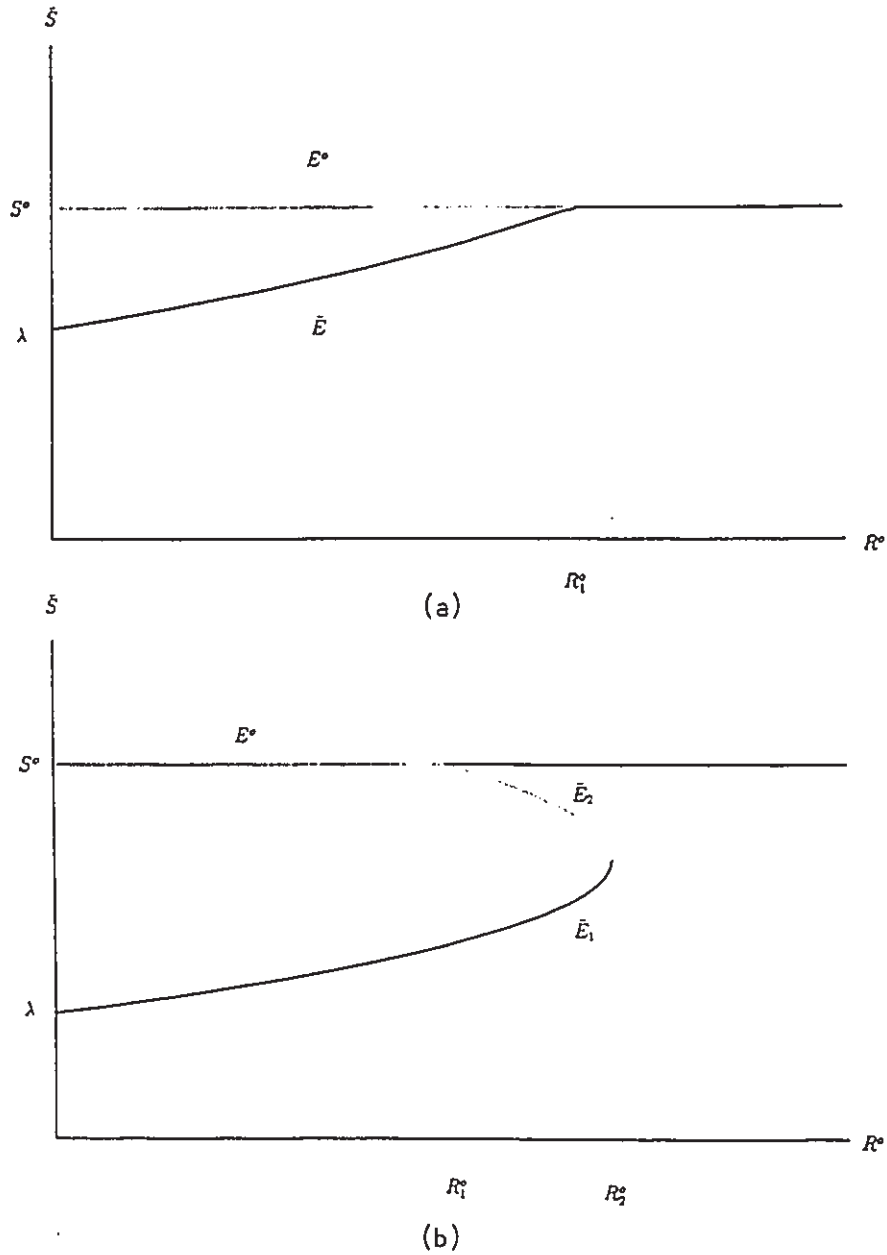
Figure 4.3: Bifurcation Diagrams R^o vs $\bar{S}$ for System (4.1) where $m_S > D > m_R$ and $S^o > \lambda$

(a) $PS^o/(S^o - \lambda) \geq 1$

(b) $PS^o/(S^o - \lambda) < 1$

Note that values of $\bar{S}$ satisfying $\bar{S} < \lambda$ correspond to $\bar{R} < 0$, while values of $\bar{S}$ satisfying $\bar{S} > S^o$ correspond to $\bar{x} < 0$.
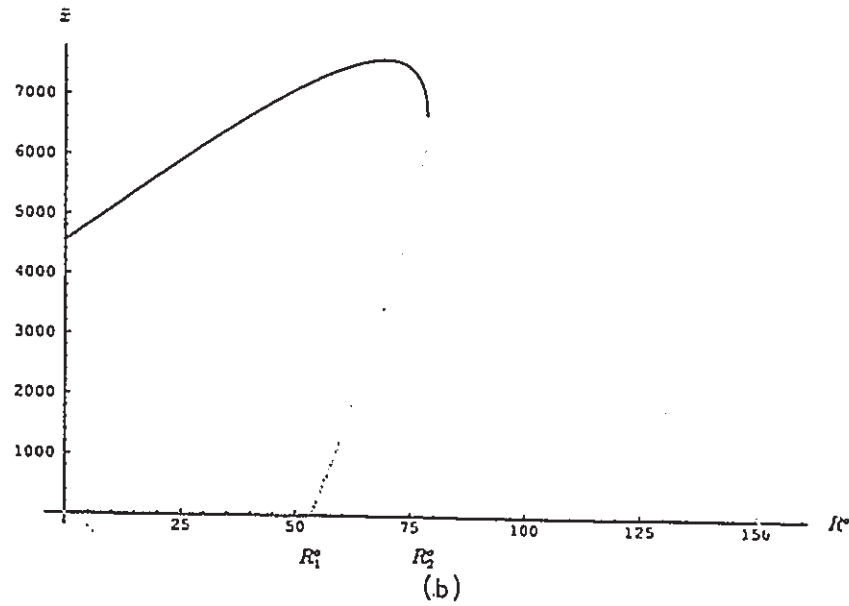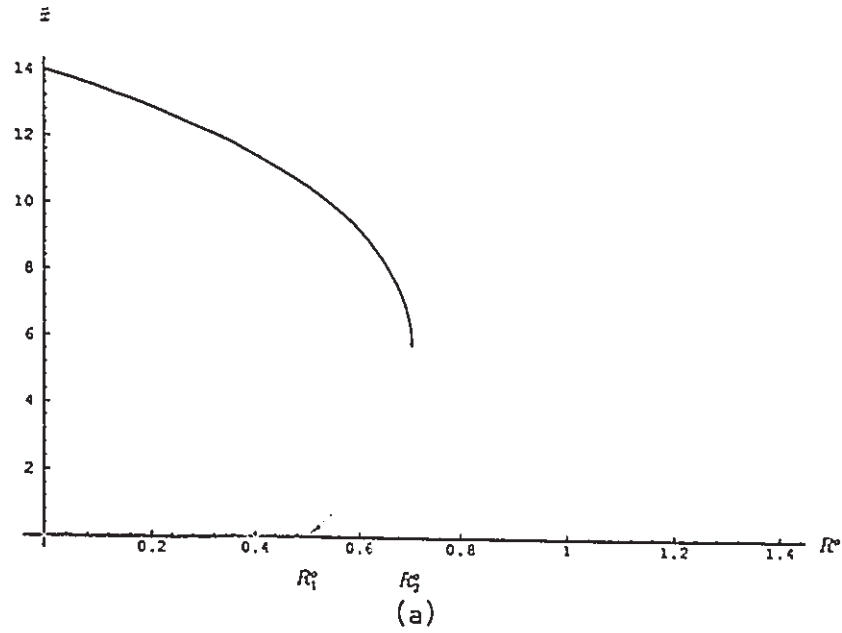
(a)

(b)

Figure 4.4: Bifurcation Diagrams R° vs $\bar{x}$ for System (4.1) where $m_S > D > m_R$ and $S^\circ > \lambda$

(a) $m_S = 2.25$, $K_S = 1.00$, $\xi = 70$, $m_R = 0.5$, $K_R = 1.00$, $\eta = 1$, $D = 1$, $S^\circ = 1$

(b) $m_S = 0.145h^{-1}$, $K_S = 1.00\mu M$, $\xi = 25.6$ g dry wt/mol, $m_R = 0.085h^{-1}$, $K_R = 1.00\mu M$, $\eta = 6.40$ g dry wt/mol $D = 0.10h^{-1}$, $S^\circ = 20.00\mu M$
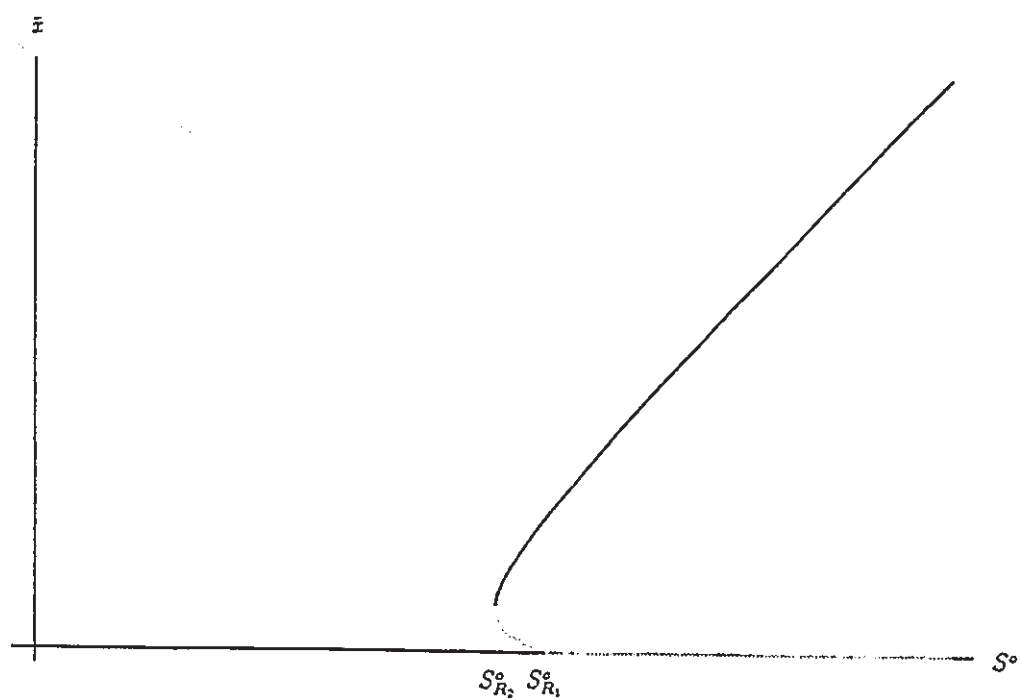
Figure 4.5: Bifurcation Diagram S^o vs $\bar{x}$ for System (4.1) where $m_S > D > m_R$ and $P < 1$
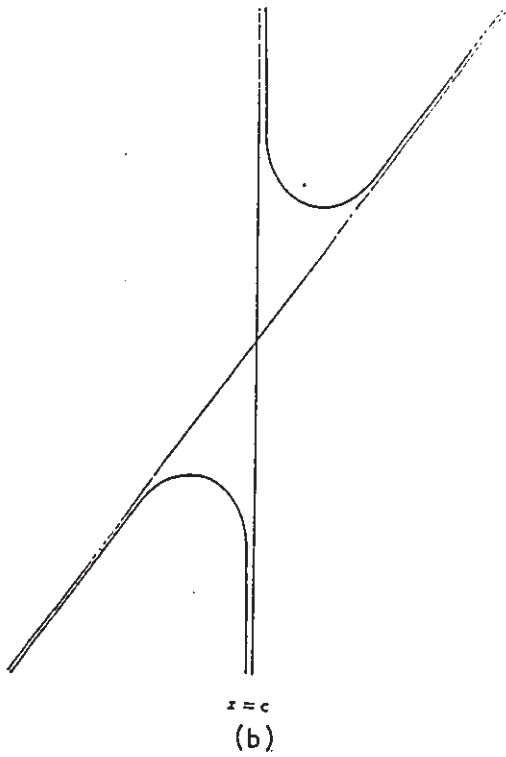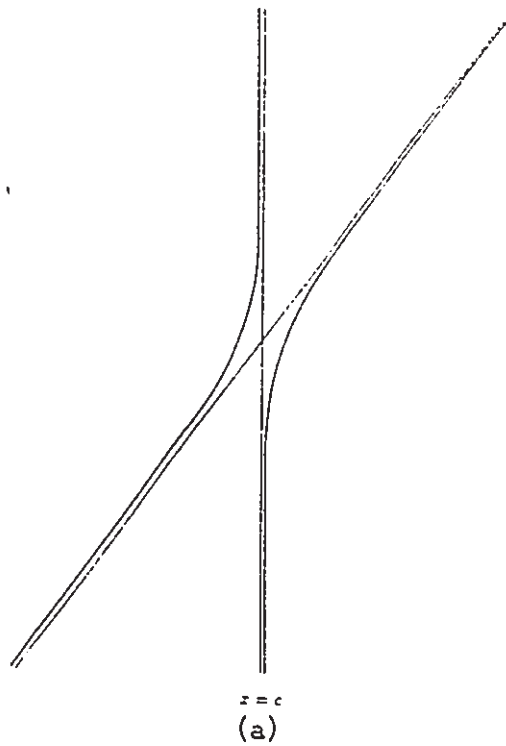
$z = c$

(a)

$z = c$

(b)

Figure 4.6: Schematic Diagram for the Nullclines of System (4.20)

5 An examination of the thresholds of enrichment: A resource-based predator-prey model

5.1 Introduction

In this chapter we extend the model considered in Chapter 4 to include a single predator species. Models of predator-prey interaction involving a single resource have been studied by a number of authors. For example, simple food chains are considered by Canale [13], Gard [19], Jost et al. [29], Saunders and Bazin [47], and Sell [50], and occur as submodels in the systems analyzed by Butler, Hsu and Waltman [9], Butler and Wolkowicz [11], and Wolkowicz [63].

This chapter is organized as follows. First we describe a resource-based model of predator-prey interaction in the chemostat involving two nonreproducing resources which are growth limiting, noninhibitory, and perfectly substitutable for the prey. As in Chapter 4, a generalization of the Michaelis-Menten prototype of functional response to a single resource is used to describe the response of the prey to changes in resource density. However, we allow a general class of functions to describe predator-prey dynamics. Only the quantities under the control of the experimenter are varied; all species-specific parameters of our model are considered fixed.

To begin, we completely characterize those nutrient concentrations that yield coexistence equilibria and show that when a coexistence equilibrium exists, it is unique. We then provide conditions that are necessary and sufficient to guarantee uniform persistence of the model (ie., coexistence of both species independent of their initial concentrations). Thus, these conditions are sufficient to guarantee the existence of a unique coexistence equilibrium.

Using the thresholds established in Chapter 4, we consider the effects of enrichment on the asymptotic behaviour of the model. For the purposes of this chapter, enrichment is considered beneficial if it leads from washout for some positive initial conditions to the survival of both species for any positive initial conditions. For dilution rates below the threshold, enrichment is beneficial, regardless of which resource is used to enrich the environment. As in the growth model, it becomes important to

consider which resource is used to enrich the environment when the dilution rate is above the threshold. For one of the resources, moderate enrichment can be beneficial, while sufficient enrichment leads to a regime in which washout is possible. For the other resource, sufficient enrichment is beneficial.

5.2   The Model

We consider a model of predator-prey interaction in the chemostat involving two non-reproducing resources which are growth limiting, noninhibitory and perfectly substitutable for the prey. The model is an extension of the one considered in Chapter 4, and is given by the following dynamical system:

$$
\begin{aligned}
S'(t) &= (S^\circ - S(t))D - \frac{x(t)}{\xi}\mathcal{S}(S(t), R(t)), \\
R'(t) &= (R^\circ - R(t))D - \frac{x(t)}{\eta}\mathcal{R}(S(t), R(t)), \\
x'(t) &= x(t)(-D + \mathcal{G}(S(t), R(t))) - \frac{y(t)}{\gamma}q(x(t)), \\
y'(t) &= y(t)(-D + q(x(t))),
\end{aligned}
\tag{5.1}
$$

$$
S(0) \geq 0, R(0) \geq 0, x(0) \geq 0, y(0) \geq 0.
$$

We identify (S, R, x, y)-space with $\mathbf{R}_+^4$. In these equations, $y(t)$ is the biomass of the microbial predator population in the culture vessel at time t. We assume that $\mathcal{S}(S, R)$ and $\mathcal{R}(S, R)$ have the form given in (4.2). In the absence of the predator, this model reduces to model (4.1). Therefore, $S(t)$, $R(t)$, $x(t)$, S°, R°, D, ξ, and η have the same biological meaning as in Chapter 4. Also, we assume that resource S is superior to resource R in the sense of equation (4.4).

The function $\frac{1}{\gamma}q(x)$ represents the rate of consumption of species x per unit biomass of the microbial population y as a function of the biomass of species x in the culture vessel. Just as we assumed that the conversion of nutrient S (respectively, R) to biomass of species x is proportional to the amount of nutrient S (respectively, R) consumed, we assume that the biomass of species y produced is proportional to the biomass of species x consumed, with growth yield constant γ. Thus, $q(x)$ represents the rate of conversion of species x to biomass of species y as a function of the biomass

of species x in the culture vessel. We make the following assumptions concerning the function q:

$$q : R_+ \longrightarrow R_+,$$
$$q \text{ is continuously differentiable,}$$
$$q'(x) > 0 \text{ for all } x > 0, \tag{5.2}$$
$$q(0) = 0.$$

Define θ so that

$$q(\theta) = D. \tag{5.3}$$

Thus θ represents the breakeven concentration of prey. By the monotonicity of $q(x)$, this concentration is a uniquely defined extended positive real number provided we assume that $\theta = \infty$ if $q(x) < D$ for all $x \geq 0$.

If one of the resources is not made available to species x, say $R^\circ = 0$, then system (5.1) is approximated for large t by

$$
\begin{aligned}
S'(t) &= (S^\circ - S(t))D - \frac{x(t)}{\xi}p(S(t)), \\
R'(t) &= 0, \\
x'(t) &= x(t)(-D + p(S(t))) - y(t)\frac{1}{\gamma}q(x(t)), \\
y'(t) &= y(t)(-D + q(x(t))),
\end{aligned}
\tag{5.4}
$$

$$S(0) \geq 0, \ R(0) \geq 0, \ x(0) \geq 0, \ y(0) \geq 0,$$

where $p(S)$ satisfies Michaelis-Menten kinetics. This is a model of a simple food chain. It is a special case of the model studied by Gard [19]. When $q(x)$ is also assumed to satisfy Michaelis-Menten kinetics, (5.4) arises in the more complicated context of competing predators studied by Butler, Hsu and Waltman [9]. It was also discussed by Bungay and Bungay [7], and studied by Jost et al. [29] and Sell [50]. Jost et al. [29] also considered the case in which p is assumed to satisfy multiple saturation kinetics. When $q(x) = xh(x)$ is monotone nondecreasing and $p(S)$ is given by any continuously differentiable monotone increasing function with $p(0) = 0$, system (5.4) also occurs as a submodel of the food web examined by Butler and Wolkowicz [11]. We will assume that neither S° nor R° is zero.

5.3 Preliminary Analysis

We first note that all solutions are positive and bounded. These are minimum requirements for a reasonable model of the chemostat.

Theorem 5.1 (a) *All solutions $S(t)$, $R(t)$, $x(t)$, $y(t)$ of (5.1) are nonnegative and bounded for $t > 0$.*

(b) *The 3-dimensional simplex*

$$\mathcal{M} = \{(S, R, x, y) \in \mathbf{R}_+^4 : \gamma\xi S + \gamma\eta R + \gamma x + y = \gamma(\xi S^\circ + \eta R^\circ)\}$$

is a global attractor for (5.1).

Proof: The proof of (a) is similar to the proof given in [10]. For (b), consider

$$z(t) = \gamma\xi S(t) + \gamma\eta R(t) + \gamma x(t) + y(t),$$

and proceed as in the proof of Theorem 2.11. ∎

In fact, the following theorem holds:

Theorem 5.2 (a) *Given $\epsilon > 0$, for all solutions $S(t)$, $R(t)$ of (5.1), $S(t) < S^\circ + \epsilon$ and $R(t) < R^\circ + \epsilon$ for all sufficiently large t.*

(b) *Given $\epsilon > 0$, for all solutions $x(t)$ of (5.1), $x(t) < \xi S^\circ + \eta R^\circ + \epsilon$ for all sufficiently large t.*

(c) *If there exists a $t_o \geq 0$ such that $S(t_o) \leq S^\circ$ ($R(t_o) \leq R^\circ$), then $S(t) < S^\circ$ ($R(t) < R^\circ$) for all $t > t_o$.*

Proof: The proofs of (a) and (c) are immediate from (5.1). For (b), let $\epsilon > 0$ be given. By Theorem 5.1(b), $\mathcal{M}$ is a global attractor for (5.1). Therefore

$$\gamma\{\xi S(t) + \eta R(t) + x(t)\} + y(t) < \gamma\{\xi S^\circ + \eta R^\circ + \epsilon\}$$

for all sufficiently large t. The result now follows immediately from Theorem 5.1(a). ∎

The next theorem concerns the extinction of the populations; it gives conditions under which there is total washout of both microbial species.

Theorem 5.3 *Consider system* (5.1).

(a) *If either* $(m_R > D$ *and* $\mathcal{G}(S^\circ, R^\circ) < D)$ *or* $(m_R \leq D$ *and* $\lambda \geq S^\circ)$, *then* $x(t) \to 0$ *as* $t \to \infty$ *in* (5.1).

(b) *If* $\xi S^\circ + \eta R^\circ < \theta$ *or* $\theta = \infty$, *then* $y(t) \to 0$ *as* $t \to \infty$ *in* (5.1).

(c) *If* $x(t) \to 0$ *as* $t \to \infty$ *in* (5.1), *then* $y(t) \to 0$ *as* $t \to \infty$ *in* (5.1).

(d) *If* $x(t) \to 0$ *and* $y(t) \to 0$ *as* $t \to \infty$, *then* $E_o = (S^\circ, R^\circ, 0, 0)$ *is globally asymptotically stable for* (5.1).

Proof: The proofs of (a) and (d) are similar to the proofs of Theorems 2.4(b) and (c), respectively.

(b) Suppose $\xi S^\circ + \eta R^\circ < \theta < \infty$ and choose $\epsilon > 0$ such that $\xi S^\circ + \eta R^\circ + \epsilon < \theta$. By Theorem 5.2(b), $x(t) < \xi S^\circ + \eta R^\circ + \epsilon$ for all sufficiently large t. Since $q(x) < D$ for $0 \leq x \leq \xi S^\circ + \eta R^\circ + \epsilon$, we have

$$\hat{\epsilon} = \max\{q(x) - D : 0 \leq x \leq \xi S^\circ + \eta R^\circ + \epsilon\} < 0.$$

Therefore,

$$y'(t) = y(t)(-D + q(x(t))) \leq y(t)\hat{\epsilon}$$

implies that $y(t) \to 0$ as $t \to \infty$.

Suppose $\theta = \infty$. Then $q(x) < D$ for all $0 \leq x < \infty$. By Theorem 5.1(a), $x(t)$ is bounded above, so there exists an $x_{\max}$ such that

$$x(t) \leq x_{\max} \text{ for all } t \geq 0.$$

Thus, $y'(t) \leq y(t)\hat{\epsilon}$ for all t, where

$$\hat{\epsilon} = \max\{q(x) - D : 0 \leq x \leq x_{\max}\} < 0.$$

Therefore, $y(t) \to 0$ as $t \to \infty$.

(c) Note that, by (5.1),

$$y(t) = y(0) \exp\{\int_0^t (-D + q(x(\tau)))d\tau\}.$$

Taking the limit as $t \to \infty$, part (c) follows. ∎

5.4   The Main Results

Thus far we have seen two types of equilibria of system (5.1): the washout equilibrium $E_o = (S^o, R^o, 0, 0)$ and prey survival equilibria $\bar{E} = (\bar{S}, \bar{R}, \bar{x}, 0)$. It is clear from (5.1) that E_o always exists. Conditions for the existence and, in some cases, uniqueness of equilibria of the form $\bar{E}$ were given in Theorems 2.7 and 4.2.

We first determine the local stability properties of equilibria of the form E_o and $\bar{E}$ through an examination of the linearized system about each equilibrium point.

The eigenvalues of $V_4(E_o)$, the variational matrix of system (5.1) evaluated at E_o, are $-D$ (of multiplicity three) and $\mathcal{G}(S^o, R^o) - D$. Thus, if $\mathcal{G}(S^o, R^o) > D$, then E_o is unstable and, by Theorem 2.7 parts (a) and (b)(ii) and Theorem 4.2(a), a unique prey survival equilibrium exists. Also, if $\mathcal{G}(S^o, R^o) < D$, then no prey survival equilibria exist, and E_o is locally asymptotically stable. If, in addition, $m_R \geq D$, then E_o is globally asymptotically stable by Theorem 5.3.

Assume that $\mathcal{G}(S^o, R^o) > D$, so $\bar{E}$ exists uniquely. The characteristic polynomial of $V_4(\bar{E})$ is given by

$$(w - (q(\bar{x}) - D))(w^3 + A_1 w^2 + A_2 w + A_3).$$

Here $w^3 + A_1 w^2 + A_2 w + A_3$ is the characteristic polynomial of $V_3(\bar{S}, \bar{R}, \bar{x})$, the variational matrix of the (S, R, x)-subsystem evaluated at the prey survival equilibrium. By Theorem 2.12(a) and Theorem 4.3(a), $\bar{E}$ is globally asymptotically stable with respect to all solutions initiating in $\mathcal{T} = \{(S, R, x, y) \in \mathbf{R}^4_+ : x > 0, y = 0\}$. Therefore, $\bar{E}$ is locally asymptotically stable for (5.1) if $q(\bar{x}) < D$ and unstable if $q(\bar{x}) > D$.

If any other equilibria of (5.1) exist, they must be coexistence equilibria. Such an equilibrium is a solution $E^* = (S^*, R^*, x^*, y^*)$ of the system

$$
\begin{aligned}
xS(S, R) &= \xi(S^o - S)D, & (5.5) \\
xR(S, R) &= \eta(R^o - R)D, & (5.6) \\
x\gamma(-D + \mathcal{G}(S, R)) &= yq(x), & (5.7) \\
q(x) &= D, & (5.8)
\end{aligned}
$$

with $(S^*, R^*, x^*, y^*) \in int\mathbf{R}^4_+$. By (5.8), $x^* = \theta$, where θ is as in (5.3). Therefore, by (5.5), (5.6), and (4.2), $0 < S^* < S^o$ and $0 < R^* < R^o$.

The following theorem is an immediate consequence of Theorem 5.3(a,b).

Theorem 5.4   (a) *If $\mu = \infty$ and $\lambda \geq S^\circ$, then no coexistence equilibrium E^* exists.*

(b) *If $\xi S^\circ + \eta R^\circ < \theta$ or $\theta = \infty$, then no coexistence equilibrium E^* exists.*

Theorem 5.5   (a) *If E^* exists and $m_R \geq D$, then $\bar{E}$ exists and is unique.*

(b) *If E^* exists, $m_R < D$, and $0 \leq R^\circ < R_1^\circ$, then $\bar{E}$ exists and is unique.*

Proof: (a) If $\mathcal{G}(S^\circ, R^\circ) \leq D$, then $\mathcal{G}(S, R) < D$ for all $0 < S < S^\circ$ and $0 < R < R^\circ$, implying $\mathcal{G}(S^*, R^*) < D$ and violating the positivity constraint on y^*. Therefore, $\mathcal{G}(S^\circ, R^\circ) > D$, and the result now follows from Theorem 2.7(a) and (b)(ii).
(b) Since E^* exists, $\lambda < S^\circ$ and so $D < m_S$. The result now follows from Theorem 4.2(a). ∎

We now investigate the conditions under which E^* exists and is unique. From (5.5) and (5.6) we must have

$$\frac{\xi(S^\circ - S)D}{\mathcal{S}(S, R)} = \frac{\eta(R^\circ - R)D}{\mathcal{R}(S, R)}. \tag{5.9}$$

Define

$$\Phi(S) \triangleq \frac{R^\circ P S}{S^\circ + (P - 1)S}, \quad 0 \leq S \leq S^\circ, \tag{5.10}$$

where P is as in (4.10). Then (5.9) is satisfied for $0 < S < S^\circ$ by taking $R = \Phi(S)$. From (5.5) and (5.6) we now have

$$\xi(S^\circ - S)D = \theta \mathcal{S}(S, \Phi(S)),$$

$$\tag{5.11}$$

$$\eta(R^\circ - \Phi(S))D = \theta \mathcal{R}(S, \Phi(S)).$$

Clearly, the two equations are equivalent.

Theorem 5.6 *There exists a unique solution S^* of (5.11) and it satisfies $0 < S^* < S^\circ$ and $0 < \Phi(S^*) < R^\circ$.*

Proof: Define

$$
\begin{aligned}
f(S) &\triangleq K_S K_R S^\circ + [K_S K_R (P-1) + K_R S^\circ + K_S R^\circ P] S + K_R (P-1) S^2 \\
&\triangleq a_0 + a_1 S + a_2 S^2, \\
g_1(S) &\triangleq \xi D (S^\circ - S) f(S), \\
g_2(S) &\triangleq \theta m_S K_R S [S^\circ + (P-1)S].
\end{aligned}
$$

Then (5.10) and (5.11) yield, by (4.2),

$$
g_1(S) = g_2(S). \tag{5.12}
$$

We will examine equation (5.12) for all values of P.

Case 1: $P > 1$.

In this case, $g_2(S)$ is a parabola opening upward with roots at $S = 0$ and $S = S^\circ/(1 - P) < 0$. The function $g_1(S)$ is a cubic satisfying $g_1(S) \to \pm\infty$ as $S \to \mp\infty$, $g_1(S^\circ) = 0$, and $g_1(0) = \xi D K_S K_R S^{\circ 2} > 0$. Note that the quadratic $f(S)$ satisfies a_0, a_1, and $a_2 > 0$. By the Routh-Hurwicz Criterion, the two remaining roots of $g_1(S)$ have negative real part. In fact, $a_1^2 - 4 a_0 a_2 > 0$, so that these roots are negative. It follows that g_1 and g_2 intersect uniquely in $(0, S^\circ)$. Clearly, $0 < S^* < S^\circ$, and

$$
0 < \Phi(S^*) = R^\circ \frac{PS^*}{PS^* + (S^\circ - S^*)} < R^\circ.
$$

Case 2: $P = 1$

In this case, $g_2(S)$ is the line through the origin with positive slope $\theta m_S K_R S^\circ$. The function $g_1(S)$ is a parabola opening upward with roots at $S = S^\circ$ and $S = -K_S K_R S^\circ/(K_R S^\circ + K_S R^\circ) < 0$. Thus, g_1 and g_2 intersect uniquely in $(0, S^\circ)$, and the result follows.

Case 3: $P < 1$

In this case, $g_2(S)$ is a parabola opening downward with roots at $S = 0$ and $S = S^\circ/(1 - P) > S^\circ$. The function $g_1(S)$ is a cubic satisfying $g_1(S) \to \pm\infty$ as $S \to \pm\infty$, $g_1(S^\circ) = 0$, and $g_1(0) = \xi D K_S K_R S^{\circ 2} > 0$. Note that $g_1'(S^\circ) = -\xi D \{ (K_R + R^\circ) K_S P S^\circ + K_R P S^{\circ 2} \} < 0$. Therefore $g_1(S)$ has one negative root and

one positive root beyond S°. This implies that g_1 and g_2 intersect uniquely in $(0, S^\circ)$. The result now follows. ∎

The following is an immediate consequence of (5.5), (5.6), (5.7), (5.8), and Theorem 5.6.

Theorem 5.7 *When a coexistence equilibrium for system* (5.1) *exists, it is unique.*

Lemma 5.8 *Consider system* (5.1).

(a) *If $m_R > D$ and $\mathcal{G}(S^\circ, R^\circ) > D$, then $\varphi(S)$ and $\Phi(S)$ intersect uniquely in $(0, min\{\lambda, S^\circ\})$ at $(\bar{S}, \bar{R})$.*

(b) *If $m_R = D$ and $\mathcal{G}(S^\circ, R^\circ) > D$, then $\Phi(S)$ intersects the line $S = \bar{S}$ at $\bar{R}$.*

(c) *Suppose $m_S > D > m_R$ and $S^\circ > \lambda$.*

   (i) *If $\mathcal{G}(S^\circ, R^\circ) > D$, then $\varphi(S)$ and $\Phi(S)$ intersect uniquely in (λ, S°) at $(\bar{S}, \bar{R})$.*

   (ii) *If $\mathcal{G}(S^\circ, R^\circ) \leq D$, then $\varphi(S)$ and $\Phi(S)$ intersect 0, 1 or 2 times in (λ, S°), depending on the number of prey survival equilibria. Any such intersection occurs at the (S, R) coordinates of a prey survival equilibrium.*

Proof: (a) Since $\mathcal{G}(S^\circ, R^\circ) > D$, $\bar{E} = (\bar{S}, \bar{R}, \bar{x}, 0)$ exists uniquely by Theorem 2.7(a). The quadratic

$$\mu\lambda S^\circ + [\mu\lambda(P - 1) - \mu S^\circ - \lambda R^\circ P]S - \mu(P - 1)S^2 = 0$$

is obtained both by setting $\varphi(S) = \Phi(S)$ and from the equation for $\bar{S}$,

$$\frac{\xi(S^\circ - S)D}{\mathcal{S}(S, \varphi(S))} = \frac{\eta(R^\circ - \varphi(S))D}{\mathcal{R}(S, \varphi(S))},$$

using (4.2) and (4.8). If $S^\circ < \lambda$, note that $\mathcal{G}(S^\circ, R^\circ) > D$ implies $\Phi(S^\circ) = R^\circ > \varphi(S^\circ)$ by (4.5), since $\lambda < S^c$. If $\lambda < S^\circ$, note that $\Phi(\lambda) = R^\circ P\lambda/\{(S^\circ - \lambda) + \lambda P\} > 0 = \varphi(\lambda)$. Since $\Phi(0) = 0 < \mu = \varphi(0)$, the result now follows.

(b) For $m_R = D$ it can be shown that $\bar{S} = \lambda = S^c < S^o$. (See Lemma 2.6(b).) The fact that $\Phi(\lambda) = \bar{R}$ follows from the equation for $\bar{R}$,

$$\frac{\xi D(S^o - \lambda)}{S(\lambda, R)} = \frac{\eta D(R^o - R)}{\mathcal{R}(\lambda, R)},$$

using (4.2).

(c) As in part (a), both the equation for the intersection and the equation for $\bar{S}$ yield

$$\delta\lambda S^o + [\delta\lambda(P - 1) - \delta S^o - \lambda R^o P]S - \delta(P - 1)S^2 = 0.$$

For (i), note that $\mathcal{G}(S^o, R^o) > D$ implies $0 \le R^o = \Phi(S^o) < \varphi(S^o) = R_1^o$ by (4.5), since $S^c < \lambda < S^o$. Therefore, $\bar{E}$ exists uniquely by Theorem 4.2(a) and the result now follows.

For (ii), note that $\mathcal{G}(S^o, R^o) \le D$ implies $R^o \ge R_1^o$ by (4.5). If $P \ge (S^o - \lambda)/S^o$, then $R_2^o = R_1^o$ so that, by Theorem 4.2(b), no prey survival equilibria exist. If $P < (S^o - \lambda)/S^o$, then $R_2^o > R_1^o$. By Theorem 4.2(b,c), there exist 0, 1 or 2 prey survival equilibria, depending on the value of R^o relative to R_1^o and R_2^o. We need only observe that, for $R^o = R_1^o$,

$$\Phi'(S^o) = \frac{R_1^o}{PS^o} > -\frac{\delta}{\lambda} \text{ if and only if } P < \frac{(S^o - \lambda)}{S^o},$$

where $\varphi'(S) = -\delta/\lambda$. $\blacksquare$

Consequently, we have the following theorem.

Theorem 5.9 *If $m_S > D > m_R$ and $R^o > R_2^o$, then no coexistence equilibrium E^* exists.*

Proof: If E^* exists, then $\mathcal{G}(S^*, R^*) > D$, so that $\varphi(S^*) > \Phi(S^*) = R^*$ by (4.5). Since $\Phi(0) = 0$, (4.8) implies that $\varphi(S)$ and $\Phi(S)$ intersect at least once. Thus, by Lemma 5.8(c)(ii), there exists at least one prey survival equilibrium, contradicting Theorem 4.2(b). $\blacksquare$

Theorem 5.6 indicates that there is always a solution $S^* \in (0, S^o)$ of (5.11). However, the corresponding solution y^* of (5.7),

$$y^* = \frac{\gamma\theta}{D}(-D + \mathcal{G}(S^*, R^*)),$$

need not be positive. This is the content of the following theorem.

Theorem 5.10 *Let S^* satisfy (5.11) and let $R^* = \Phi(S^*)$.*

(a) *If $m_R \geq D$, then there exists a coexistence equilibrium $E^* = (S^*, R^*, x^*, y^*)$ for system (5.1) if and only if $\bar{E}$ exists and $\bar{S} < S^* < S^\circ$ and $\bar{R} < R^* < R^\circ$.*

(b) *Suppose $m_S > D > m_R$ and $S^\circ > \lambda$.*

    (i) *If $0 \leq R^\circ < R_1^\circ$, then there exists a coexistence equilibrium $E^* = (S^*, R^*, x^*, y^*)$ for system (5.1) if and only if $\bar{E}$ exists and $\bar{S} < S^* < S^\circ$ and $\bar{R} < R^* < R^\circ$.*

    (ii) *If $R_1^\circ < R^\circ < R_2^\circ$, then there exists a coexistence equilibrium $E^* = (S^*, R^*, x^*, y^*)$ for system (5.1) if and only if $\bar{E}_i$ exists, $i = 1,\ 2$, and $\min\{\bar{S}_1, \bar{S}_2\} < S^* < \max\{\bar{S}_1, \bar{S}_2\}$ and $\min\{\bar{R}_1, \bar{R}_2\} < R^* < \max\{\bar{R}_1, \bar{R}_2\}$.*

Proof: For part (a), the existence of $\bar{E}$ is given by Theorem 2.7 parts (a) and (b)(ii). For part (b)(i), the existence of $\bar{E}$ is given by Theorem 4.2(a). For part (b)(ii), the existence of the $\bar{E}_i$, $i = 1,\ 2$, is given by Theorem 4.2(c).

(a) If $m_R > D$, (5.10), (4.8), and Lemma 5.8(a) imply that

$$\Phi(S) \leq \varphi(S) \text{ for all } 0 \leq S \leq \bar{S} \text{ and } \Phi(S) > \varphi(S) \text{ for all } \bar{S} < S \leq \min\{\lambda, S^\circ\}.$$

By (4.5) and (4.9),

$$\mathcal{G}(S, \Phi(S)) \leq D \text{ for all } 0 \leq S \leq \bar{S} \text{ and } \mathcal{G}(S, \Phi(S)) > D \text{ for all } \bar{S} < S \leq S^\circ,$$

since $S^c > \lambda$. Note that if $\bar{S} < S^*$ and $\bar{R} < R^*$, then

$$
\begin{aligned}
\xi S^\circ + \eta R^\circ \;&>\; \bar{x} \\
&=\; \xi(S^\circ - \bar{S}) + \eta(R^\circ - \bar{R}) \\
&>\; \xi(S^\circ - S^*) + \eta(R^\circ - R^*) \\
&>\; \xi(S^\circ - S^*) + \eta(R^\circ - R^*) - \frac{1}{\gamma} y^* \\
&=\; x^* \\
&=\; \theta.
\end{aligned}
$$

If $m_R = D$, then $S^c = \lambda = \bar{S}$. The result follows immediately from (4.5) since

$$\mathcal{G}(S, R) \leq D \text{ for all } R > 0,\ 0 \leq S \leq \bar{S} \text{ and } \mathcal{G}(S, R) > D \text{ for all } R > 0,\ \bar{S} < S.$$

(b) After noting that $S^c < \lambda$, the proof follows as in (a). ∎

We now present a global property of the model. The terms persistent and uniformly persistent are used here as in [17], and are given in Definitions 2.8 and 2.9 of section 2.3.2. The following notation will be required:

$$\mathcal{T} = \{(S, R, x, y) \in \mathbf{R}_+^4 : x > 0, y = 0\}. \tag{5.13}$$

Theorem 5.11 *Assume* $\mathcal{G}(S^o, R^o) > D$.

(a) *If* $x(0) > 0$, *then* $\liminf_{t \to \infty} x(t) > 0$.

(b) *System (5.1) is uniformly persistent with respect to all solutions for which* $x(0) > 0$ *and* $y(0) > 0$ *if and only if* $q(\bar{x}) > D$.

Proof: Since $\mathcal{G}(S^o, R^o) > D$, E_o is an unstable hyperbolic critical point. By Theorem 2.7(a) and (b)(ii) and Theorem 4.2(a), $\bar{E}$ exists and is globally asymptotically stable with respect to all solutions initiating in $\mathcal{T}$, where $\mathcal{T}$ is as in (5.13). Choose $\underline{X} = (S(0), R(0), x(0), y(0)) \in int\mathbf{R}_+^4$. Since all solutions are positive and bounded, $\Omega(\underline{X})$ is a nonempty, compact, invariant set with respect to (5.1).

Suppose $E_o \in \Omega(\underline{X})$. E_o is globally attracting with respect to all solutions initiating in its stable manifold. Since $M^s(E_o) = \{(S, R, x, y) \in \mathbf{R}_+^4 : x = 0\}$ and $x(0) > 0$, $\Omega(\underline{X}) \neq \{E_o\}$. By the Butler-McGehee Lemma, there exists $Q \in (M^s(E_o) \setminus \{E_o\}) \cap \Omega(\underline{X})$ and hence $cl\mathcal{O}(Q) \subset \Omega(\underline{X})$, where $cl\mathcal{O}(Q)$ denotes the closure of the entire orbit through Q. But then as $t \to -\infty$, $\mathcal{O}(Q)$ either becomes unbounded or leaves the positive cone. In either case we have a contradiction and therefore $\{E_o\} \notin \Omega(\underline{X})$.

For part (a), suppose $\liminf_{t \to \infty} x(t) = 0$. Then there exists a point $\tilde{Q} \in \Omega(\underline{X})$ such that $\tilde{Q} \in M^s(E_o)$. Since $cl\mathcal{O}(\tilde{Q}) \subset \Omega(\underline{X})$, $\{E_o\} \in \Omega(\underline{X})$, a contradiction. Therefore, $\liminf_{t \to \infty} x(t) > 0$.

For part (b), suppose $\{\bar{E}\} \in \Omega(\underline{X})$. Since $q(\bar{x}) > D$, $\bar{E}$ is an unstable hyperbolic critical point. Since $M^s(\bar{E}) = \mathcal{T}$ and $y(0) > 0$, $\Omega(\underline{X}) \neq \{\bar{E}\}$. By the Butler-McGehee Lemma, there exists $Q \in (M^s(\bar{E}) \setminus \{\bar{E}\}) \cap \Omega(\underline{X})$ and hence $cl\mathcal{O}(Q) \subset \Omega(\underline{X})$. But then, as $t \to -\infty$, either $\mathcal{O}(Q)$ becomes unbounded or leaves the positive cone or $cl\mathcal{O}(Q) \supset \{E^o\}$. In any case, we have a contradiction, and therefore $\{\bar{E}\} \notin \Omega(\underline{X})$.

Suppose $\liminf_{t\to\infty} y(t) = 0$. Then there exists a point $\tilde{Q} \in \Omega(\underline{X})$ such that $\tilde{Q} \in M^s(\bar{E})$. Since $cl\mathcal{O}(\tilde{Q}) \subset \Omega(\underline{X})$, $\{\bar{E}\} \in \Omega(\underline{X})$, a contradiction. Therefore, (5.1) is persistent, and it now follows from the main result of [8] that (5.1) is uniformly persistent.

Note that $\bar{E}$ is locally asymptotically stable with respect to (S, R, x, y)-space when $q(\bar{x}) < D$, so that (5.1) is not uniformly persistent. If $q(\bar{x}) = D$, then $\bar{E}$ and E^* coalesce and there is no equilibrium in $int\mathbf{R}^4_+$. It follows as in the remark concerning Theorem 2.19 that (5.1) is not uniformly persistent when $q(\bar{x}) \le D$. ∎

Remark concerning Theorem 5.11

When $m_S > D > m_R$ and $R^o_1 < R^o < R^o_2$, there exist precisely two prey survival equilibria by Theorem 4.2(c). Note that $\mathcal{G}(S^o, R^o) < D$ for all $R^o > R^o_1$. Since E_o is locally asymptotically stable, it follows that there is no result analogous to Theorem 5.11 in this case. Therefore it is possible for a coexistence equilibrium to exist for system (5.1) even though the system is not persistent.

Theorem 5.12 *If $\mathcal{G}(S^o, R^o) > D$, then a coexistence equilibrium of (5.1) exists if and only if $q(\bar{x}) > D$.*

Proof: If $q(\bar{x}) > D$, then, by Theorem 5.11, (5.1) is uniformly persistent with respect to all solutions for which $x(0) > 0$ and $y(0) > 0$. Thus, at least one coexistence equilibrium E^* exists.

Suppose E^* exists. Then, by Theorem 5.10 parts (a) and (b)(i), $\bar{S} < S^*$ and $\bar{R} < R^*$. As shown in the proof of that theorem, $\bar{x} > \theta$. Therefore, $D = q(\theta) < q(\bar{x})$ by (5.2). ∎

Consider $m_R > D$ and fix $S^o < \lambda$. We give the following bifurcation analysis of system (5.1) based on the parameter R^o. For all $0 \le R^o < \varphi(S^o)$, $\mathcal{G}(S^o, R^o) < D$ and, by Theorem 5.3, E_o is globally asymptotically stable for (5.1). Neither $\bar{E}$ nor E^* exists in the nonnegative cone. If R^o is increased to $\varphi(S^o)$, then $\mathcal{G}(S^o, R^o) = D$ and the critical points E_o and $\bar{E}$ coalesce. If R^o is slightly increased, $\bar{E}$ bifurcates into $\mathcal{T} = \{(S, R, x, y) \in \mathbf{R}^4_+ : x > 0, y = 0\}$ and E_o loses its stability. By Theorem 2.12(a), $\bar{E}$ is globally asymptotically stable with respect to all solutions initiating in $\mathcal{T}$. Now,

by Lemma 4.1, the species component of the prey survival equilibrium, $\bar{x}$, is a strictly monotone increasing function of both S^o and R^o. Therefore there exists a unique $\hat{R}^o \in (\varphi(S^o), \infty]$ such that $\bar{x} = \theta$ when $R^o = \hat{R}^o$. For $\varphi(S^o) < R^o < \hat{R}^o$, $q(\bar{x}) < D$, so $\bar{E}$ is locally asymptotically stable for (5.1). If R^o is increased to $\hat{R}^o$, $\bar{E}$ and E^* coalesce. If R^o is increased beyond $\hat{R}^o$, then $q(\bar{x}) > D$, E^* bifurcates into $\{(S, R, x, y) \in \mathbf{R}_+^4 : x > 0, y > 0\}$, $\bar{E}$ becomes unstable, and system (5.1) is uniformly persistent. In this case sufficient enrichment with resource R is beneficial in the sense that it leads from total washout to survival of both species.

For $m_R > D$ and $\lambda \leq S^o$, the initial configuration of the equilibria may differ, but the bifurcation proceeds as above with increasing R^o. Note that a bifurcation analysis can be done based on the parameter S^o with similar outcome. Thus, sufficient enrichment with resource S is also beneficial in this case. Also, for $m_R = D$ we must have $S^o > \lambda = S^c$. Then $\mathcal{G}(S^o, R^o) > D$ for all $R^o \geq 0$ and the series of bifurcations proceeds similarly.

In Chapter 4 it was shown that, for $m_S > D > m_R$, sufficient enrichment with resource R leads to the extinction of species x in the (S, R, x)-subsystem. However, moderate enrichment with resource R may or may not be beneficial there. As a result, tracking the evolution of E^* is more difficult in this case. Some conclusions can nonetheless be reached concerning the effects of enrichment on the asymptotic behaviour of (5.1).

If $0 \leq R^o < R_1^o$, then $\mathcal{G}(S^o, R^o) > D$, and E_o is unstable. Also, there exists a prey survival equilibrium which is globally asymptotically stable with respect to all solutions initiating in $\mathcal{T}$. When $R^o = 0$, the prey survival equilibrium is given by $(\lambda, 0, \xi(S^o - \lambda), 0)$.

Suppose $\xi(S^o - \lambda) > \theta$. Then E^* exists in the nonnegative cone and system (5.1) is uniformly persistent. This remains the case initially as R^o is increased. However, for $R^o > R_1^o$, $\mathcal{G}(S^o, R^o) < D$, so E_o is locally asymptotically stable. Therefore, enrichment with resource R may be detrimental for system (5.1) in the sense that it can lead from survival of both species for any positive initial condition to washout for some positive initial conditions.

Suppose instead that $\xi(S^o - \lambda) < \theta$. Then there is no coexistence equilibrium

in the nonnegative cone and the prey survival equilibrium is locally asymptotically stable. Thus, solutions of the model do not persist. If even moderate enrichment is detrimental in the (S, R, x)-subsystem, this situation cannot be improved. However, suppose moderate enrichment is beneficial in the (S, R, x)-subsystem and there exists $\hat{R}^o \in (0, R_1^o)$ such that $\bar{x} = \theta$ when $R^o = \hat{R}^o$. As R^o is increased beyond $\hat{R}^o$, E^* enters the nonnegative cone and system (5.1) is uniformly persistent. Therefore, moderate enrichment with resource R may be beneficial for system (5.1).

Note that increasing S^o, the input concentration of resource S, is beneficial. As in the previous chapter, this can be seen by viewing R_1^o as a function of S^o. Fix $S^o = \bar{S}^o > \lambda$ and $R^o > R_1^o(\bar{S}^o)$. Then $\mathcal{G}(\bar{S}^o, R^o) < D$, so E_o is locally asymptotically stable for (5.1) and total washout can occur for some positive initial conditions. By (4.5), increasing S^o sufficiently destabilizes E_o, that is, $\mathcal{G}(S^o, R^o) > D$. By Theorem 5.11(a), total washout is then impossible for any positive initial conditions. If $q(\bar{x}) < D$, then increasing S^o further leads to uniform persistence of (5.1). In the (S, R, x)-subsystem, enrichment with resource S leads from washout or initial condition dependent outcome to survival. Once the (S, R, x)-subsystem enters this regime, the carrying capacity of the environment is an increasing function of S^o. Thus, if the environment supporting the prey is sufficiently enriched with resource S we have $\bar{x} > \theta$, so that $q(\bar{x}) > D$.

In what follows we examine the local stability properties of the coexistence equilibrium E^* in the case $m_R \geq D$. Let us assume that $\mathcal{G}(S^o, R^o) > D$ so that $\bar{E}$ exists and is globally asymptotically stable with respect to all solutions initiating in $\mathcal{T}$. Further, assume $q(\bar{x}) > D$ so that E^* exists.

By Theorem 5.1(b) the simplex $\mathcal{M} = \{(S, R, x, y) \in \mathbf{R}_+^4 : \gamma\xi S + \gamma\eta R + \gamma x + y = \gamma(\xi S^o + \eta R^o)\}$ is a global attractor for (5.1), and so we may restrict our attention to $\mathcal{M}$. Since $\mathcal{M}$ is positively invariant, let $y(t) = \gamma\{\xi(S^o - S(t)) + \eta(R^o - R(t)) - x(t)\}$ and consider the system

$$S'(t) = (S^\circ - S(t))D - \frac{x(t)}{\xi}\mathcal{S}(S(t), R(t)),$$

$$R'(t) = (R^\circ - R(t))D - \frac{x(t)}{\eta}\mathcal{R}(S(t), R(t)),$$

$$x'(t) = x(t)(-D + \mathcal{G}(S(t), R(t)) + q(x(t))) \tag{5.14}$$

$$+ (\xi(S(t) - S^\circ) + \eta(R(t) - R^\circ))q(x(t)),$$

$$S(0) \geq 0, R(0) \geq 0, x(0) \geq 0, \xi(S^\circ - S(0)) + \eta(R^\circ - R(0)) - x(0) \geq 0.$$

Both (5.1) and (5.14) will be used in the examination of the local asymptotic stability of E^*. The variational matrix of (5.1) evaluated at E^* will be denoted $V_4(E^*)$. The critical point of (5.14) corresponding to E^* will be denoted E_3^*, while the variational matrix of (5.14) evaluated at E_3^* will be denoted $V_3(E_3^*)$.

From (5.1), $V_4(E^*)$ is given by

$$\begin{pmatrix} -D - \frac{x^*}{\xi}\frac{\partial}{\partial S}\mathcal{S}(S^*, R^*) & -\frac{x^*}{\xi}\frac{\partial}{\partial R}\mathcal{S}(S^*, R^*) & -\frac{1}{\xi}\mathcal{S}(S^*, R^*) & 0 \\ -\frac{x^*}{\eta}\frac{\partial}{\partial S}\mathcal{R}(S^*, R^*) & -D - \frac{x^*}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*, R^*) & -\frac{1}{\eta}\mathcal{R}(S^*, R^*) & 0 \\ x^*\frac{\partial}{\partial S}\mathcal{G}(S^*, R^*) & x^*\frac{\partial}{\partial R}\mathcal{G}(S^*, R^*) & -D + \mathcal{G}(S^*, R^*) - \frac{y^*}{\gamma}q'(x^*) & -\frac{1}{\gamma}q(x^*) \\ 0 & 0 & y^*q'(x^*) & -D + q(x^*) \end{pmatrix}.$$

Noting that $q(x^*) = D$, the characteristic equation of $V_4(E^*)$ is given by $p_4(w) = w^4 + A_1 w^3 + A_2 w^2 + A_3 w + A_4$, where

$$A_1 = y^*\frac{1}{\gamma}q'(x^*) + x^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}\mathcal{S}(S^*, R^*) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*, R^*)\right) \tag{5.15}$$

$$+ 3D - \mathcal{G}(S^*, R^*)$$

$$A_2 = y^*\frac{1}{\gamma}q'(x^*)\left(3D + x^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}\mathcal{S}(S^*, R^*) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*, R^*)\right)\right) \tag{5.16}$$

$$+ D^2 + 2D(D - \mathcal{G}(S^*, R^*)) + 2Dx^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}\mathcal{S}(S^*, R^*) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*, R^*)\right)$$

$$+ \frac{x^{*2}}{\xi\eta}\left(\frac{\partial}{\partial S}\mathcal{S}(S^*, R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*, R^*) - \frac{\partial}{\partial R}\mathcal{S}(S^*, R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*, R^*)\right)$$

$$+ \frac{x^*}{\xi}\left(\mathcal{S}(S^*, R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*, R^*) - \mathcal{R}(S^*, R^*)\frac{\partial}{\partial S}\mathcal{S}(S^*, R^*)\right)$$

$$+\frac{x^*}{\eta}\left(\mathcal{R}(S^*,R^*)\frac{\partial}{\partial R}\mathcal{S}(S^*,R^*)-\mathcal{S}(S^*,R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right),$$

$$A_3 = y^*\frac{1}{\gamma}q'(x^*)\left\{3D^2+2Dx^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}\mathcal{S}(S^*,R^*)+\frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right)\right. \quad (5.17)$$

$$\left.+\frac{x^*}{\xi\eta}\left(\frac{\partial}{\partial S}\mathcal{S}(S^*,R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)-\frac{\partial}{\partial R}\mathcal{S}(S^*,R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*,R^*)\right)\right\}$$

$$+D^2(D-\mathcal{G}(S^*,R^*))+D^2x^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}\mathcal{S}(S^*,R^*)+\frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right)$$

$$+D\frac{x^{*2}}{\xi\eta}\left(\frac{\partial}{\partial S}\mathcal{S}(S^*,R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)-\frac{\partial}{\partial R}\mathcal{S}(S^*,R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*,R^*)\right)$$

$$+D\frac{x^*}{\xi}\left(\mathcal{S}(S^*,R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*,R^*)-\mathcal{R}(S^*,R^*)\frac{\partial}{\partial S}\mathcal{S}(S^*,R^*)\right)$$

$$+D\frac{x^*}{\eta}\left(\mathcal{R}(S^*,R^*)\frac{\partial}{\partial R}\mathcal{S}(S^*,R^*)-\mathcal{S}(S^*,R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right),$$

$$A_4 = y^*D\frac{1}{\gamma}q'(x^*)\left\{D^2+Dx^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}\mathcal{S}(S^*,R^*)+\frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right)\right. \quad (5.18)$$

$$\left.+\frac{x^{*2}}{\xi\eta}\left(\frac{\partial}{\partial S}\mathcal{S}(S^*,R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)-\frac{\partial}{\partial R}\mathcal{S}(S^*,R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*,R^*)\right)\right\}.$$

Since $m_R \geq D$ we have, by (4.2), (4.3), and (4.5),

$$\frac{\partial}{\partial S}\mathcal{S}(S^*,R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)-\frac{\partial}{\partial R}\mathcal{S}(S^*,R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*,R^*)>0. \quad (5.19)$$

For $R^\circ = \hat{R}^\circ$, $\bar{E}$ and E^* coalesce, so $A_4 = 0$. Since $\bar{E}$ is globally asymptotically stable in (S,R,x)-space, $A_1 > 0$, $A_3 > 0$, and $(A_1A_2 - A_3) > 0$. Thus, the three nonzero roots of $p_4(w)$ have negative real part. As R° is slightly increased beyond $\hat{R}^\circ$, E^* bifurcates into the interior of (S,R,x,y)-space. By (5.19), $A_4 > 0$. By the continuity of the roots of the characteristic equation as a function of its coefficients, it follows that $p_4(w)$ satisfies the Routh-Hurwicz Criterion at least initially, that is,

$$A_1 > 0, A_3 > 0, A_3(A_1A_2 - A_3) - A_1^2A_4 > 0, A_4 > 0.$$

Therefore, E^* is initially locally asymptotically stable.

To continue the discussion we turn to (5.14). Noting that $q(x^*) = D$, it follows

from (5.14), $V_3(E_3^*)$ is given by

$$
\begin{pmatrix}
-D - \frac{x^*}{\xi}\frac{\partial}{\partial S}S(S^*,R^*) & -\frac{x^*}{\xi}\frac{\partial}{\partial R}S(S^*,R^*) & -\frac{1}{\xi}S(S^*,R^*) \\[2ex]
-\frac{x^*}{\eta}\frac{\partial}{\partial S}\mathcal{R}(S^*,R^*) & -D - \frac{x^*}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*) & -\frac{1}{\eta}\mathcal{R}(S^*,R^*) \\[2ex]
x^*\frac{\partial}{\partial S}\mathcal{G}(S^*,R^*) + \xi D & x^*\frac{\partial}{\partial R}\mathcal{G}(S^*,R^*) + \eta D & \mathcal{G}(S^*,R^*) - q'(x^*)y^*
\end{pmatrix},
$$

where $y^* = \{\xi(S^o - S^*) + \eta(R^o - R^*) - x^*\}$. The characteristic equation of $V_3(E_3^*)$ is given by $p_3(w) = w^3 + B_1 w^2 + B_2 w + B_3$, where

$$
\begin{aligned}
B_1 &= y^*\frac{1}{\gamma}q'(x^*) + x^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}S(S^*,R^*) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right) \qquad (5.20) \\
&\quad + 2D - \mathcal{G}(S^*,R^*),
\end{aligned}
$$

$$
\begin{aligned}
B_2 &= y^*\frac{1}{\gamma}q'(x^*)\left(2D + x^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}S(S^*,R^*) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right)\right) \qquad (5.21) \\
&\quad + D(D - \mathcal{G}(S^*,R^*)) + Dx^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}S(S^*,R^*) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right) \\
&\quad + \frac{x^{*2}}{\xi\eta}\left(\frac{\partial}{\partial S}S(S^*,R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*) - \frac{\partial}{\partial R}S(S^*,R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*,R^*)\right) \\
&\quad + \frac{x^*}{\xi}\left(S(S^*,R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*,R^*) - \mathcal{R}(S^*,R^*)\frac{\partial}{\partial S}S(S^*,R^*)\right) \\
&\quad + \frac{x^*}{\eta}\left(\mathcal{R}(S^*,R^*)\frac{\partial}{\partial R}S(S^*,R^*) - S(S^*,R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right),
\end{aligned}
$$

$$
\begin{aligned}
B_3 &= y^*\frac{1}{\gamma}q'(x^*)\left\{D^2 + Dx^*\left(\frac{1}{\xi}\frac{\partial}{\partial S}S(S^*,R^*) + \frac{1}{\eta}\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*)\right) \right. \qquad (5.22) \\
&\quad \left. + \frac{x^{*2}}{\xi\eta}\left(\frac{\partial}{\partial S}S(S^*,R^*)\frac{\partial}{\partial R}\mathcal{R}(S^*,R^*) - \frac{\partial}{\partial R}S(S^*,R^*)\frac{\partial}{\partial S}\mathcal{R}(S^*,R^*)\right)\right\}.
\end{aligned}
$$

We first note that, as with A_4, $B_3 > 0$. Also, E^* and E_3^* have the same stability. Therefore, for values of $R^o > \hat{R}^o$ such that E^* is locally asymptotically stable, $p_3(w)$ satisfies the Routh-Hurwicz Criterion. Then $B_1 > 0$, $B_2 > 0$ and $B_1 B_2 - B_3 > 0$. Therefore, if E^* can lose its stability, it can do so only by means of a Hopf bifurcation.

Let $V_3(E_3^*) = [v_{ij}], i, j = 1, \cdots, 3$. The signs of the entries are as follows:

$$\begin{pmatrix} - & + & - \\ + & - & - \\ + & + & ? \end{pmatrix}.$$

Also,

$$B_1 = -(v_{11} + v_{22} + v_{33}),$$

$$B_2 = (v_{11}v_{22} - v_{12}v_{21}) + (v_{11}v_{33} - v_{13}v_{31}) + (v_{22}v_{33} - v_{23}v_{32}),$$

$$B_3 = -|V_3(E_3^*)|,$$

and

$$B_1 B_2 - B_3 = -\ (v_{11} + v_{22} + v_{33})\{(v_{11}v_{33} - v_{13}v_{31}) + (v_{22}v_{33} - v_{23}v_{32})\}$$
$$-\ (v_{11} + v_{22} + \mathcal{G}(S^*, R^*))(v_{11}v_{22} - v_{12}v_{21}).$$

Note that $v_{11}v_{22} - v_{12}v_{21} = (\gamma/(q'(x^*)y^*))B_3 > 0$.

If $\mathcal{G}(S^\circ, R^\circ) \leq 2D$, then $\mathcal{G}(S^*, R^*) + v_{11} + v_{22} < 0$. If, in addition, $v_{33} < 0$, it follows from the signs of the v_{ij} that $B_1 B_2 - B_3 > 0$, and no Hopf bifurcation can occur.

However, a Hopf bifurcation may occur. Consider the system

$$S'(t) = 1 - S(t) - \frac{x(t)}{3}\frac{3S(t)}{1 + S(t) + R(t)},$$

$$R'(t) = R^\circ - R(t) - \frac{x(t)}{2}\frac{2R(t)}{1 + S(t) + R(t)},$$

$$x'(t) = x(t)(-1 + \frac{3S(t) + 2R(t)}{1 + S(t) + R(t)}) - y(t)\frac{3x(t)}{1 + x(t)}, \qquad (5.23)$$

$$y'(t) = y(t)(-1 + \frac{3x(t)}{1 + x(t)}),$$

$$S(0) \geq 0, R(0) \geq 0, x(0) \geq 0, y(0) \geq 0.$$

The symbolic manipulation package MAPLE was used to show that

$$B_1(R^\circ)B_2(R^\circ) - B_3(R^\circ) = 0 \quad \text{when} \quad R^\circ = R_c^\circ \approx 0.2114675777.$$

(The program is included in section 5.6.) Then E^* is locally asymptotically stable for $0 \leq R^o < R_c^o$ and is unstable for $R^o > R_c^o$. At $R^o = R_c^o$, $p_4(E^*)$ can be shown to have two real, negative roots and two pure imaginary roots. The real part of the complex conjugate pair of roots crosses zero transversely at $R^o = R_c^o$ since $(B_1 B_2 - B_3)'(R_c^o) \neq 0$. Thus, the change in stability at $R^o = R_c^o$ is via a Hopf bifurcation. Numerical evidence indicates that it is a supercritical Hopf bifurcation. In Figure 5.1(a), $R^o = 0.1 < R_c^o$ and the solution converges to E^*. In Figure 5.1(b), $R^o = 0.3 > R_c^o$ so that E^* is unstable. This figure seems to depict a stable periodoc orbit. As further evidence, an (x, y) projection for $R^o = 0.3 > R_c^o$ is shown in Figure 5.2.

5.5 Discussion

In this chapter we consider a resource-based model of predator-prey interaction in the chemostat involving two nonreproducing resources, S and R, that are growth limiting, noninhibitory, and perfectly substitutable for the prey. As in the previous chapter, only the parameters under the control of the experimenter are varied. These are S^o and R^o, the input concentrations of the resources, and D, the input and washout rate.

We first examine the question of the existence of a coexistence equilibrium, E^*, for our model. This leads to a complete characterization of those resource concentrations that yield coexistence equilibria. We show that when such an equilibrium exists, it is unique. The condition $\mathcal{G}(S^o, R^o) > D$ is sufficient to guarantee the survival of the prey. Thus, so long as the resources are sufficient to ensure that the prey can consume eno; ;h to more than compensate for the rate D at which it is being washed out, it will survive predation. We find that $\mathcal{G}(S^o, R^o) > D$ and $q(\bar{x}) > D$ is necessary and sufficient for the model to be uniformly persistent, thus ensuring that both species survive, regardless of the (positive) initial conditions. Consequently, when $\mathcal{G}(S^o, R^o) > D$, $q(\bar{x}) > D$ is necessary and sufficient to guarantee the existence of a coexistence equilibrium.

As an investigation of the effects of enrichment on a predator-prey system, this chapter again addresses issues raised by Rosenzweig [44]. Investigations involving a single resource have been carried out by a number of authors. (See, for example, [9],

[11], [13], [19], [29], [47], [50], and [63].) We compare our results in the two-resource case for $m_S \geq D$ and $m_R \geq D$ to those of Butler and Wolkowicz [11] for the (S, x, y) food chain. There, the predator response function, $q(x) = xh(x)$, is continuously differentiable and monotone nondecreasing, and the prey response function, $p(S)$, is any continuously differentiable, monotone increasing function satisfying $p(0) = 0$.

There are three possible steady states in both the one-resource model and the two-resource model: the washout equilibrium E_o, the prey survival equilibrium $\bar{E}$, and the coexistence equilibrium E^*. For given values of D and the input concentration(s), no more than one of these steady states can be locally asymptotically stable. The washout equilibrium is locally asymptotically stable if and only if $\mathcal{G}(S^o, R^o) < D$ for two resources, $p(S^o) < D$ in the one-resource case. The prey survival equilibrium exists if and only if $\mathcal{G}(S^o, R^o) > D$ $(p(S^o) > D)$, and is locally asymptotically stable when $q(\bar{x}) < D$. Though we suspect it is true, we are unable to show, as they do for the one-resource model, that $\bar{E}$ is globally asymptotically stable when it is locally asymptotically stable. Both models are uniformly persistent if and only if $\bar{E}$ exists and $q(\bar{x}) > D$, and this condition is necessary and sufficient for the existence of E^*. For both models, E^* is at least initially locally asymptotically stable, and examples exist in which E^* loses its stability via a Hopf bifurcation. (Here, the bifurcation parameter is the input concentration of one of the resources; in [11], this is only one possible choice for the bifurcation parameter.) In the food chain, then, enrichment is beneficial in the sense that it leads from total washout to the sole survival of the prey, and then to the survival of both species, for any positive initial condition. The progression is the same in the two-resource case for dilution rates below the threshold, regardless of which resource is used for enrichment.

That system (5.23) exhibits a supercritical Hopf bifurcation is consistent with the results of Rosenzweig [44], May [35], Gilpin [20], and Freedman [16]. Rosenzweig [44] examines six models of predator-prey interaction and shows that sufficient enrichment of the environment supporting the prey results in the destabilization of then otherwise stable coexistence equilibrium. May [35] and Gilpin [20] show that the destabilization results in the birth of an asymptotically stable coexistence equilibrium. And Freedman [16] shows the destabilization of the equilibrium to be the

result of a Hopf bifurcation. Wolkowicz [62] proved that depending on the form of the response functions, the Hopf bifurcation could be supercritical or subcritical, and hence there could be more than one periodic orbit.

As was the case for the growth model, it becomes important to consider which resource is used to enrich the environment when the dilution rate is increased beyond the threshold, that is, when $m_S > D > m_R$. First, equate enrichment of the environment with an increase in the input concentration of resource R. Initially (for $R^\circ = 0$), E_o is unstable, so that total washout is impossible when $x(0) > 0$ and $y(0) > 0$. Also, at least the prey species can survive at $\bar{E} = (S^\circ, 0, \xi(S^\circ - \lambda), 0)$. If, in addition, $q(\xi(S^\circ - \lambda)) > D$, then the system is uniformly persistent. Increasing R° beyond R_1° stabilizes E_o, so that washout is possible. Thus, sufficient enrichment with resource R is certainly detrimental. Now, if $q(\xi(S^\circ - \lambda)) < D$, then the system is not uniformly persistent. It may respond well to moderate enrichment provided the carrying capacity of the environment supporting the prey increases sufficiently when R° is increased. If even moderate enrichment is detrimental in the (S, R, x)- subsystem, the situation will not be improved by increasing R°. On the other hand, enriching the environment by increasing the input concentration of resource S is beneficial when $m_S > D > m_R$. If $R^\circ > R_1^\circ$, increasing S° destabilizes E_o, so that washout is impossible when $x(0) > 0$ and $y(0) > 0$. Suppose $q(\bar{x}) < D$ and there exists a unique prey survival equilibrium, that is, $R^\circ < R_1^\circ(S^\circ)$. Then increasing S° sufficiently increases the carrying capacity of the environment supporting the prey beyond θ, so that the predator-prey system is uniformly persistent.

5.6 Appendix: Maple Program

The following maple program was used to verify that system 5.23 exhibits a Hopf bifurcation.

```
d:=1:
so:=1:
ms:=3:
mr:=2:
mx:=3:
ks:=1:
kr:=1:
kx:=1:
xi:=3:
eta:=2:
gam:=1:
theta:=kx*d/(mx-d):
p:=(eta*ms*kr)/(xi*mr*ks):
with(linalg):
ss(s,r):=(ms*kr*s)/(ks*kr+kr*s+ks*r):
rr(s,r):=(mr*ks*r)/(ks*kr+kr*s+ks*r):
q(x):=mx*x/(kx+x):
f1:=(so-s)*d-x*ss(s,r)/xi:
f2:=(ro-r)*d-x*rr(s,r)/eta:
f3:=x*(-d+ss(s,r)+rr(s,r))-(xi*(so-s)+eta*(ro-r)-x)*q(x)/gam:
Phi(s):=ro*p*s/(so+(p-1)*s):
sstar:=solve(subs(r=Phi(s),x=theta,f1)=0,s):
sstar:=sstar[2]:
rstar:=simplify(subs(s=sstar,Phi(s))):
A:=[f1,f2,f3]:
v3:=jacobian(A,[s,r,x]):
poly:=collect(charpoly(v3,a),a):
```

```
det:=coeff(poly,a,2)*coeff(poly,a,1)-coeff(poly,a,0):
detcrit:=simplify(subs(s=sstar,r=rstar,x=theta,det):
rocrit:=fsolve(detcrit=0,ro);
Sstar:=simplify(subs(ro=rocrit,x=theta,sstar):
Rstar:=simplify(subs(ro=rocrit,x=theta,rstar):
Bone(ro):=subs(s=Sstar,r=Rstar,x=theta,coeff(poly,2)):
Btwo(ro):=subs(s=Sstar,r=Rstar,x=theta,coeff(poly,1)):
Bthree(ro):=subs(s=Sstar,r=Rstar,x=theta,coeff(poly,0)):
f(ro):=Bone(ro)*Btwo(ro)-Bthree(ro):
fprime(ro):=diff(f(ro),ro):
transcalc:=simplify(subs(ro=rocrit,fprime(ro)));
```
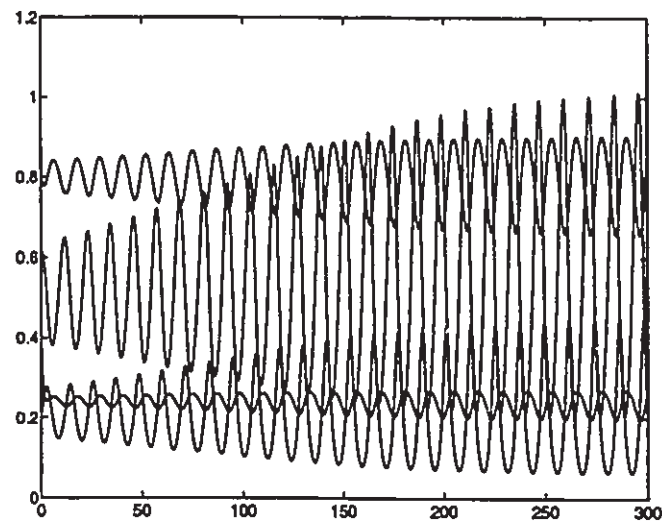
5.7 Figures
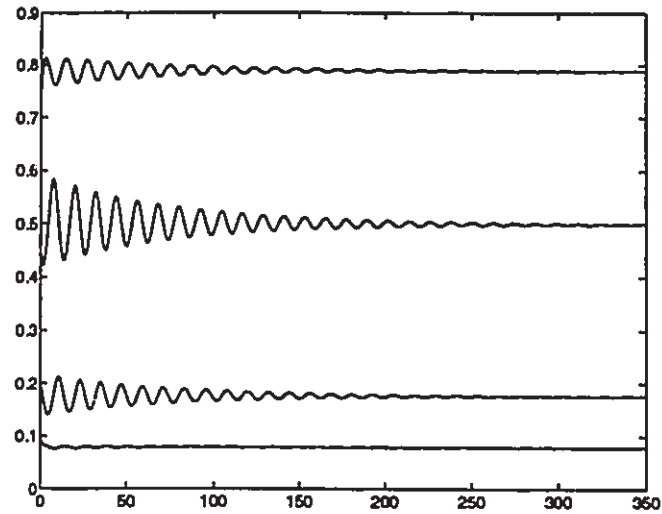
(a)

(b)

Figure 5.1: Numerical simulations of system (5.23).

(a) Time series for $R^o = 0.1 < R_c^o$ and initial condition $(S(0), R(0), x(0), y(0)) = (0.75, 0.1, 0.45, 0.2)$. E^* is asymptotically stable.

(b) Time series for $R^o = 0.3 > R_c^o$ and initial condition $(S(0), R(0), x(0), y(0)) = (0.8, 0.4, 0.6, 0.21)$. E^* is unstable.
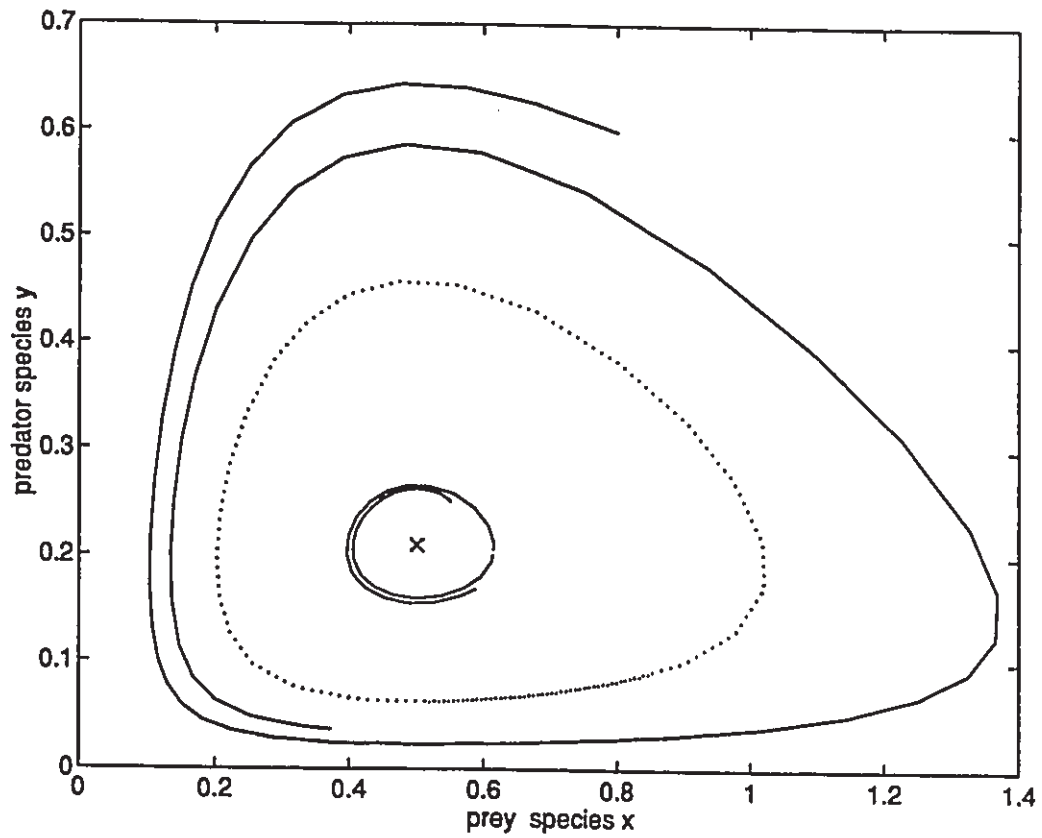
Figure 5.2: Further numerical simulations of system (5.23). (x, y) projection for $R^o = 0.3 > R_c^o$. $(S(0), R(0), x(0), y(0)) = (0.1, 0.7, 0.8, 0.6)$ for the outer orbit while $(S(0), R(0), x(0), y(0)) = (0.8, 0.4, 0.55, 0.25)$ for the inner orbit.

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