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THE UNIVERSITY OF ALBERTA

AN ANALYSIS OF MATHEMATICAL MODELS RELATED TO THE CHEMOSTAT

by

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A THESIS

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submitted by Gail Susan Kohl Wolkowicz

in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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To my mother and the memory of my father

ABSTRACT

A model of the chemostat involving n populations of microorganisms competing for a single, essential, growth-limiting substrate is considered. Instead of assuming the familiar Michaelis-Menten kinetics for nutrient uptake, a general class of functions is used which includes all monotone increasing uptake functions, but also allows uptake functions that describe inhibition by the substrate at high concentrations. The qualitative behaviour of this generalized model is determined analytically. It is shown that the behaviour depends intimately upon certain parameters. Provided that all the parameters are distinct (which is a biologically reasonable assumption), at most one competitor survives. The substrate and the surviving competitor (if one exists), approach limiting values. Thus there is competitive exclusion. However, unlike the standard model, in certain cases the outcome is initial condition dependent.

Next, a model of the chemostat involving two populations of microorganisms competing for two complementary, growth-limiting substrates is considered. Again, a general class of functions is used to describe nutrient uptake. Graphical techniques are developed to analyze the model. In the case of monotone kinetics the results are similar to those of Hsu, Cheng and Hubbell [41] who study this problem assuming Michaelis-Menten kinetics. For monotone kinetics, all dynamics are trivial in the sense that all solutions approach equilibria. However, when at least one of the competitors is inhibited by high concentrations of the substrate, one can easily construct examples for

which there is a stable periodic solution. Surprisingly, if the substrates are inhibitory at high concentrations, there are examples for which coexistence is possible but neither competitor can survive in the absence of its rival.

Finally, a model of the chemostat is considered in which there is predation on the competitors that are competing for a single, essential, growth-limiting nutrient. Here the class of response functions is restricted to be monotone. It is shown that although at most one competitor survives in the absence of predation, the addition of a predator can cause persistence in a strong sense. Under certain circumstances one can also show that there is a globally asymptotically stable interior critical point.

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CHAPTER I

INTRODUCTION

1. THE CHEMOSTAT. The chemostat is a laboratory apparatus used for the continuous culture of microorganisms. The continuous culture technique was mainly developed in order to study microbial growth under nutrient limitation in a controlled environment (see Monod [56] and Novick and Szilard [58]) and the term "chemostat" used in this context was apparently coined by Novick and Szilard.

A good description of the continuous culture technique can be found in Kubitschek [46] and a schematic diagram of a chemostat is given on the following page. Basically one can think of a chemostat as three bottles: a feed bottle, a growth or culture chamber and a collecting vessel. Microorganisms are inoculated into the culture chamber which is well-stirred. It is assumed that all essentials for growth are supplied at near optimal amounts except for the one or ones which the experimenter chooses to supply in growth-limiting amounts. These limiting nutrients are supplied continuously from the feed bottle at a constant input rate and removed at the same rate along with proportional amounts of microorganisms, byproducts, and other growth medium. Thus the volume in the culture chamber is held constant.

The continuous culture technique is used in industry for the economical production of useful microorganisms (see Herbert, Elsworth and Telling [36]) as well as for the simulation of biological waste decomposition or water purification by microorganisms (see Yang and Humphrey [83]). According to Williams [82], the chemostat can be viewed

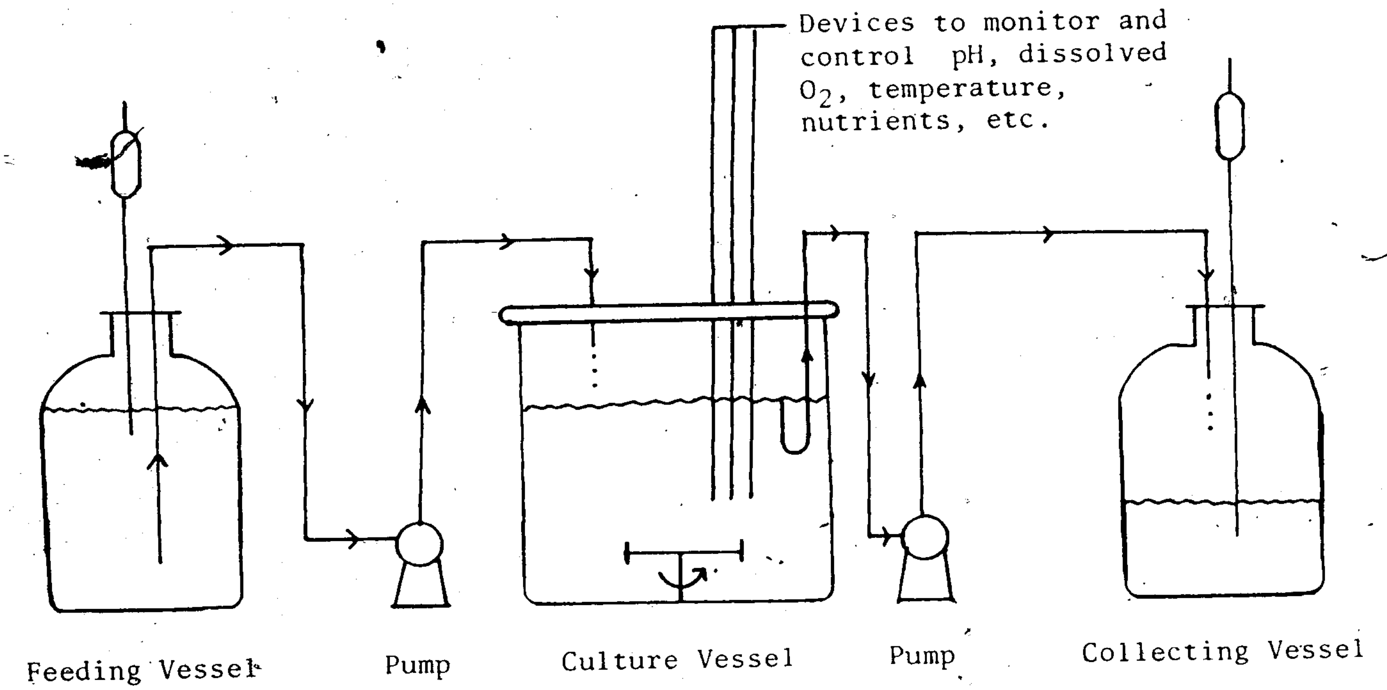


FIGURE 1 Schematic Diagram of a Chemostat

as the best laboratory idealization of nature in the context of population studies. He points out that natural systems are open for the input of energy and other material substances. He interprets the removal rate in terms of the continuous turnover of nutrients in nature and he formally equates the outflow of organisms with non-specific death rates, predation and emigration.

In this thesis we shall be mainly interested in studying how different populations interact under *"chemostat-like"* conditions. The interactions of interest will be exploitative competition for resources and predator-mediated competition.

The classical theory of ecological competition and predator-prey relationships was originated by Lotka [50] and Volterra [80]. This approach is appealing because of its generality and its simplicity. The competition equations studied are basically an extension of the logistic model of single-species growth that dates back to Verhulst [79]. The classical theory is an attempt to describe population dynamics without being specific about which resources are limiting and hence the focus of the competition, and how these limiting resources are utilized by the different competitors. These models are usually phenomenological rather than predictive since it is very difficult to measure the critical parameters used in the theory independently of actually observing the populations in competition. One way to overcome these defects is to develop a more mechanistic, resource-based theory of ecological interactions and such an approach is currently being taken by many researchers. Some of the pioneer work can be attributed to Monod [56] and Holling [38]. Though this approach may result in mathematical models that are less general and more difficult to analyze, the resulting models are often predictive since parameters can frequently be measured independently of the competition (see eg. Hansen and Hubbell [33]). Mathematical modelling of population interactions in a chemostat is certainly an example of this resource-based approach and is the approach taken in this thesis. The models we study involve systems of first order, autonomous differential equations. However, there are models in the literature that involve periodic coefficients and time-delays. For an excellent survey article of previous work done on the mathematical modelling of population interactions under chemostat-like conditions the reader is referred to the article by Waltman, Hubbell and Hsu [81].

2. THESIS OUTLINE. In this thesis we consider three different types of population interactions under chemostat-like conditions. In Chapter II we analyze a modified version of the classical chemostat equations that describe exploitative competition between n populations of microorganisms for a single, essential, growth-limiting substrate. We allow population-resource dynamics to be described by a general class of functions. This class of functions includes all monotone increasing functions as well as functions that describe the inhibition of population growth by the substrate at high concentrations.

In Chapter III we restrict our attention to exploitative competition between two populations. This time, however, the competition is for two complementary resources which are assumed to be growth-limiting. As in Chapter II, general population-resource dynamics are considered.

In Chapter IV we consider a case of predator-mediated competition between two populations for a single, growth-limiting nutrient. Unlike in the first two chapters, in this chapter we restrict the class of functions describing population-resource dynamics to be monotone.

The basic approach used in this thesis is a differential equations, dynamical systems approach. For source texts for the fundamental theory, we refer the reader to [6,16,17,35,52,67].

3. NOTATION. The following notation and abbreviations will be used consistently throughout the thesis:

$\mathbf{R}$ denotes the set of real numbers.

$\mathbf{R}^n = \{(x_1, x_2, \ldots, x_n) : x_i \in \mathbf{R},\ i = 1, \ldots, n\}$.

$\mathbf{R}^n_+ = \{(x_1, x_2, \ldots, x_n) \in \mathbf{R}^n : x_i \geq 0,\ i = 1, \ldots, n\}$.

C^1 denotes the class of continuously differentiable functions.

∂A denotes the boundary of the set A.

int A denotes the interior of the set A.

$c\ell\ A$ denotes the closure of the set A.

$B \setminus A = \{x \in B : x \notin A\}$.

$\emptyset$ denotes the empty set.

Any other notation is either standard in mathematics or is defined independently for each chapter.

4. NUMBERING SYSTEM AND CROSS REFERENCING. Throughout this thesis we use the following system of numbering and cross-referencing. At the top of each page in the left-hand margin, appear the chapter and section numbers or the appendix number. Roman numerals are always used to denote the chapter number. For example, I.4 at the top left of this page means that the discussion on this page is part of Chapter I, Section 4. On the other hand A1.B at the top left of a page means that the page is part of Appendix 1, Subsection B. Each item (Definition, Theorem, Lemma, Corollary, Proposition, Display, Example) is identified by section and item number. Items are numbered consecutively within each section. On the other hand, Tables and Figures are numbered consecutively throughout the thesis and a List of Tables and a List of Figures, indicating page numbers, follow the Table of Contents.

Cross references are of the form "by Theorem III.2.3" for items and "by (IV.5.3)" for displays. The former means "by the theorem which is item 3 of Section 2 in Chapter III" and the latter means "by display 3 of Section 5 in Chapter IV." Note that the theorem which is item 3 of a particular section is not necessarily the third theorem of that section, whereas display 3 of a section is the third display of the section. Whenever we refer to an item (display) within the same chapter, only the section and item (display) numbers are given. For example "by (4.2)" means "by the second display in Section 4 of this chapter."

CHAPTER II

A MATHEMATICAL MODEL OF THE CHEMOSTAT WITH A GENERAL CLASS OF FUNCTIONS DESCRIBING NUTRIENT UPTAKE

1. INTRODUCTION. In this chapter we consider a deterministic model of purely exploitative competition between n populations of microorganisms for a single, essential, growth-limiting nutrient, in a chemostat with constant input and wash-out rate. Our purpose is to show that for any "realistic" functions describing nutrient uptake rates for the competing microorganisms, the principle of competitive exclusion holds. That is to say, at most one population of microorganisms survives. Furthermore, the system always asymptotically approaches an equilibrium state. Our results may be regarded as extending those of Hsu, Hubbell, and Waltman [40] and a result of Armstrong and McGehee [5]. The novelty of this work is that in allowing very general nutrient-uptake functional responses, the competitive outcome becomes, in some cases, initial condition dependent. This is in contrast to the references cited above, but has been noted experimentally and by numerical simulation in the case of nutrient inhibition [1,64,83], of which we give a brief discussion later. For a more detailed account of the chemostat and related experimental results, we refer the reader to [33,40,44,56,58,62,78,81].

This chapter is organized in the following manner. In Section 2 we present the model and some background remarks. Section 3 contains a statement of the main results. However, for clarity of presentation, the proofs of these results are deferred to Section 5. Proofs of the preliminary results and technical lemmas are given in Section 4. We conclude with a discussion and an application in Section 6. A linear analysis of the model is given in Appendix 1.

2. THE MODEL. We shall consider the following model of the chemostat:

$$
\begin{aligned}
&S'(t) = (S^0 - S(t))D - \sum_{i=1}^{n} \frac{x_i(t)p_i(S(t))}{y_i},\\
(2.1)\quad &x_i'(t) = x_i(t)\big(-D + p_i(S(t))\big), \quad i \in I,\\
&S(0) = S_0 \geq 0, \quad x_i(0) = x_{i0} > 0, \quad i \in I,
\end{aligned}
$$

where $I = \{1,\ldots,n\}$.

In these equations, $x_i(t)$ denotes the concentration of the ith population of microorganisms at time t; $S(t)$ denotes the concentration of substrate at time t; $p_i(S)$ is the function that represents the rate of conversion of nutrient to biomass, i.e. the per capita growth rate of the ith population as a function of substrate concentration; y_i is a growth yield constant, and we assume $p_i(S)/y_i$ represents the substrate-uptake function for the ith population; S^0 denotes the concentration of substrate in the feed bottle; D denotes the input rate from the feed bottle containing the substrate and the wash-out rate of substrate, microorganisms and byproducts from the growth chamber. Thus S^0D represents the input rate of substrate concentration.

The system (2.1) describes a chemostat in which n populations of microorganisms compete exploitatively for a single, essential, growth-limiting substrate. It is assumed that the substrate is non-reproducing, the input concentration and the dilution rate are constant, and there is perfect mixing in the growth vessel so that substrate and microorganisms are removed in proportion to their concentrations. The individual death rate of any species is considered insignificant compared to the dilution rate, and it is assumed that growth rates adjust instantaneously to changes in the concentration of substrate. Furthermore we assume that the substrate-uptake rate is proportional to the rate of conversion to biomass. To motivate the conditions that we shall place on the uptake functions $p_i(S)$, we give a brief account of the development of the model.

Volterra, in 1928 [80], appears to have been the first to use a mathematical model to show that under certain conditions, the coexistence of two or more populations competing for the same limiting resource is impossible. In his model, he assumed a linear relationship between the amount of substrate present and the specific growth rate for each of the competing populations; in the context of (2.1) this requires the functions $p_i(S)$ to be linear functions. Monod, in 1942 [56], formulated a model which featured the dependence of microbial growth rate on the concentration of the limiting substrate, as a data-fitting curve which later was interpreted in terms of Michaelis-Menten kinetics. A theoretical derivation of the same model involving a substrate and a single population is given, for example, in [36]. An extension of this basic model to several competing populations was given by Taylor and Williams [72]. In these models there is a saturation effect at higher resource levels; $p_i(S)$ takes the form $(m_iS)/(a_i+S)$, where m_i and a_i are positive constants. A complete global analysis of this model was given by Hsu, Hubbell and Waltman [40] and Hsu [39]. They showed that at most one of the competing populations survives, the one whose "Michaelis-Menten constant" a_i, is smallest in comparison with its intrinsic growth rate, and that the dynamical system has an equilibrium point which is globally stable for solutions with positive initial conditions. This result was confirmed experimentally by Hansen and Hubbell [33]. Armstrong and McGehee [5] extended these theoretical results to models with arbitrary, smooth, monotone increasing uptake functions $p_i(S)$. An example of such functions is given by the Holling type III multiple saturation response of the form $p_i(S) = m_iS^2/(b_i+S)(c_i+S)$, see [44].

A number of authors have pointed out that certain substrates may be growth-limiting at low concentrations and growth-inhibiting at high concentrations; for example there is inhibition of Nitrobacter by nitrite and of Nitrosomonas by ammonia [44]. This results in non-monotone uptake functions. Andrews [1] and Yang and Humphrey [83] discuss several specific models of inhibitory kinetics. Bush and Cook [10] give an analysis of such a model involving one substrate and one population of microorganisms, using a general inhibition function. Aris and Humphrey [2] give an analysis of a model of one substrate and two competing microorganisms, using a specific functional form of inhibitory kinetics proposed by Boon and Laudelout [7], $p_i(S) = m_i/\left(1 + \frac{b_i}{S} + \frac{S}{c_i}\right)$.

With inhibitory kinetics, each competing population of microorganisms has a lower threshold level of substrate below which it cannot grow (irrespective of competition) and an upper threshold level of substrate above which substrate inhibition prevents growth.

Guided by this, we make the following assumptions concerning the functions p_i in our model equations (2.1):

$$p_i : \mathbb{R}_+ \to \mathbb{R}_+ ; \tag{2.2}$$

(2.3) p_i is continuously differentiable;

(2.4) $p_i(0) = 0$;

and there exist uniquely defined positive extended real

(2.5) numbers λ_i and μ_i, with $\lambda_i \leq \mu_i$, such that

$$p_i(S) < D \text{ if } S \notin [\lambda_i, \mu_i],$$

and

$$p_i(S) > D \text{ if } S \in (\lambda_i, \mu_i).$$

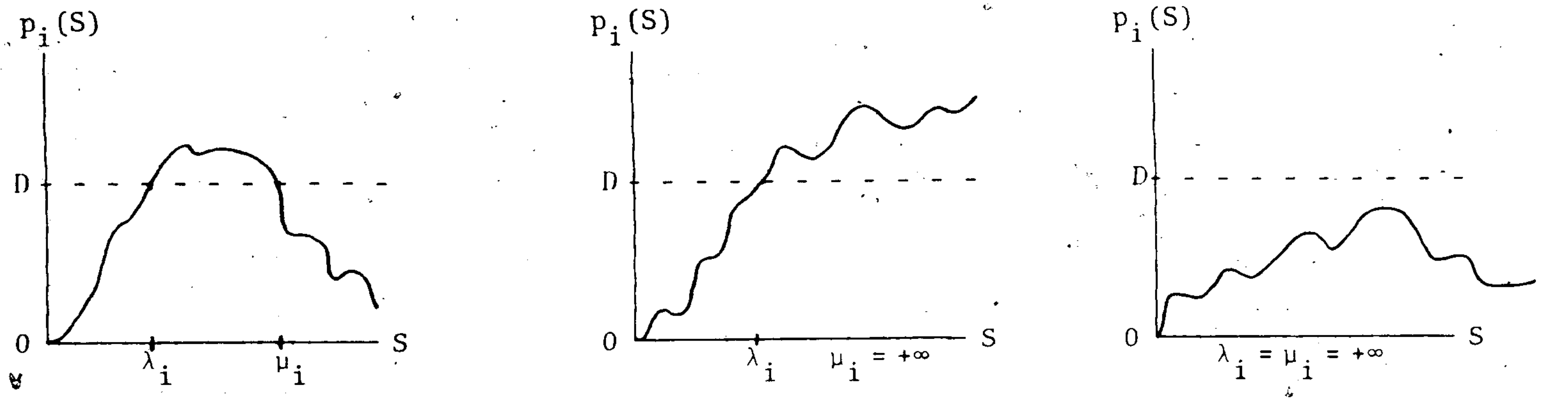
(See Figure 2.)

With inhibition kinetics in mind, λ_i and μ_i represent the break-even concentrations of substrate referred to above. But it should be noted that we allow λ_i and/or μ_i to be equal to $+\infty$ so that our results also apply in the case of any monotone uptake functions and in particular, in the case of Michaelis-Menten kinetics.

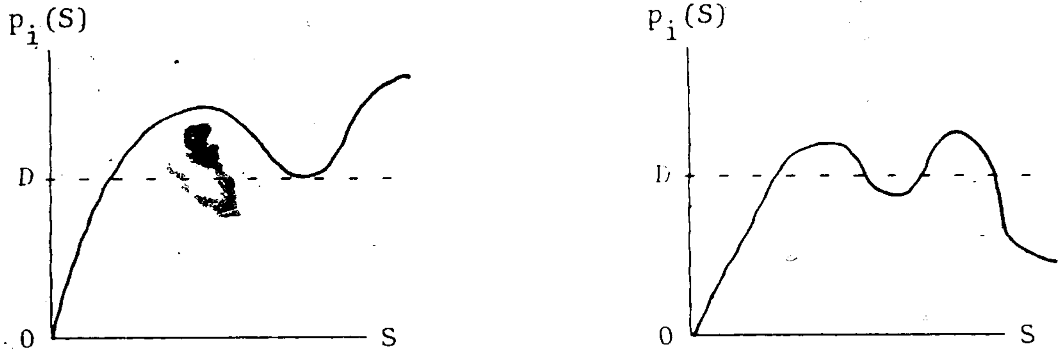
It will be evident from the method of proof that we could consider an even more general class of functions p_i; it is partly for the sake of clarity of our arguments and partly for the sake of biological reality that we impose conditions (2.2) - (2.5) above. Again, for the sake of clarity, we make two further assumptions of a generic nature:

(2.6) If λ_i (or μ_i) is finite, then $p_i'(\lambda_i) \neq 0$ $(p_i'(\mu_i) \neq 0)$.

(2.7) All λ_i, μ_j (other than those which are infinite) are distinct from each other and from S^0.



(a) Acceptable p_i's



(b) Unacceptable p_i's

FIGURE 2 Acceptable and Unacceptable Uptake Functions

Note that in the definition of (2.1), we assume $x_{i0} > 0$ for all $i \in I$. This involves no loss of generality since if $x_{i0} = 0$ for some $i \in I$, then $x_i(t) = 0$ for all $t \geq 0$ and that population can be eliminated from consideration.

3. STATEMENT OF RESULTS. From now on (except in Theorem 3.6 where we relax (2.7)), we assume that the functions p_i satisfy (2.2) - (2.7). First we note that (2.1) has positive, bounded solutions, which is a prerequisite for any reasonable model of the chemostat.

Theorem 3.1. All solutions $S(t)$, $x_i(t)$, $i \in I$, of (2.1) are positive and bounded for $t > 0$.

The next result concerns competition-independent extinction of a population. It states that if the conversion rate of the *i*th organism is less than the dilution rate, for all nutrient densities below the input concentration, then that organism dies out.

Theorem 3.2. If $\lambda_i \geq S^0$ (or $\lambda_i = +\infty$) , then $\lim_{t\to\infty} x_i(t) = 0$ for all solutions of (2.1).

Henceforth, we shall assume that the populations are labelled so that

$$(3.1) \qquad \lambda_1 < \lambda_2 < \dots < \lambda_\nu < S^0 \leq \lambda_j , \qquad \nu + 1 \leq j \leq n ,$$

where $0 \leq \nu \leq n$. As a consequence of Theorem 3.2, x_1 through x_ν are the only competitors that have a chance of surviving. If $\nu = 0$, the system clearly crashes, i.e. all populations of microorganisms become extinct and the substrate concentration converges to S^0.

To describe our results on the competitive outcomes of the system (2.1), the following definitions will be useful.

Let $Q = \bigcup_{i=1}^{\nu} (\lambda_i, \mu_i)$. (If $\nu = 0$, let $Q = \emptyset$.)

From (2.7) and (3.1) it follows that every connected component of Q is an open interval of the form (λ_i, μ_k), where $1 \leq i \leq k$. Evidently, for each j, $1 \leq j \leq \nu$, λ_j and μ_j belong to the closure of exactly one and the same component of Q. Note that if (λ_i, μ_k) is a component of Q, then for any time τ for which $S(\tau) \in (\lambda_i, \mu_k)$, the concentration of at least one population of microorganisms is increasing.

Now we define

$$\Gamma = \{\lambda_i : \lambda_i < S^0\} \cup \{\mu_j : \mu_j < S^0\} . \tag{3.2}$$

It will be convenient to relabel the elements of Γ as $\gamma_1 < \gamma_2 < \ldots < \gamma_k$. Note that $k \leq 2\nu$.

The following results show that solutions of (2.1) always have limiting behaviour.

Theorem 3.3. (a) For any solution of (2.1), $\lim_{t\to\infty} S(t) = \gamma$, where γ is either S^0 or is the endpoint of a component of Q.

(b) A necessary condition for $\lim_{t\to\infty} S(t) = \gamma$, where γ is the endpoint of a component of Q, is that $\gamma \leq S^0$. If $\lim_{t\to\infty} S(t) = \gamma$, where γ is such an endpoint, then $\lim_{t\to\infty} x_i(t) = y_i(S^0 - \gamma)$ if $\gamma = \lambda_i$ or μ_i, and $\lim_{t\to\infty} x_j(t) = 0$ for all other j.

(c) A necessary condition for $\lim_{t\to\infty} S(t) = S^0$ is that $S^0 \notin Q$. If $\lim_{t\to\infty} S(t) = S^0$, then $\lim_{t\to\infty} x_i(t) = 0$ for all i.

In fact, for almost all solutions of (2.1), $\lim_{t\to\infty} S(t) = S^0$ or

λ_i, where λ_i is the left endpoint of a component of Q. More precisely, we have the following theorem, which is the main result of this chapter:

Theorem 3.4. Let Λ denote the set of left endpoints of components of Q, together with S^0, if $S^0 \notin Q$. With the exception of a set of initial conditions of Lebesgue measure zero, all solutions of (2.1) satisfy

$$\lim_{t\to\infty} S(t) = \gamma , \quad \gamma \in \Lambda , \tag{3.3}$$

with the corresponding asymptotic behaviour: $\lim_{t\to\infty} x_i(t) = y_i(S^0 - \lambda_i)$, $\lim_{t\to\infty} x_j(t) = 0$, $j \neq i$, if $\gamma = \lambda_i$; and $\lim_{t\to\infty} x_j(t) = 0$, $j \in I$ if $\gamma = S^0$.

Conversely, for each $\gamma \in \Lambda$, there is an open, nonempty set of initial conditions for which the solutions of (2.1) satisfy (3.3).

Corollary 3.5. If Q is connected, then for all $j \geq 2$, $\lim_{t\to\infty} x_j(t) = 0$. If, in addition, $S^0 \in Q$, then the critical point $(\lambda_1, y_1(S^0 - \lambda_1), 0, \ldots, 0)$ is globally asymptotically stable for (2.1).

Corollary 3.5 applies to all models for which the functions p_i are monotonically increasing (actually only p_1 need be monotonically increasing), as well as those for which either the input concentration or the wash-out rate is sufficiently small.

The exceptional set mentioned in the statement of the above theorem consists of the stable manifolds of the (unstable) critical points $(S, x_1, \ldots, x_n)$ where $S = \mu_k$, $x_k = y_k(S^0 - \mu_k)$, $x_j = 0$, $j \neq k$;

and μ_k is a right endpoint of a component of Q.

In all cases then, at most one competitor survives and the substrate and surviving competitor approach limiting values. Competitive exclusion therefore applies with the proviso that the outcome of the competition may be initial condition dependent.

If for the moment, we relax the generic assumption (2.7), i.e. no longer require that all λ_i and μ_j's be distinct from each other and from S^0, coexistence is possible (at least in a weak sense) as is suggested by the following theorem.

Theorem 3.6. For any solution of (2.1), $\lim_{t\to\infty} S(t) = \gamma$ where either $\gamma = S^0$ or γ is the endpoint of a component of Q. If $\gamma = S^0$, then $\lim_{t\to\infty} x_j(t) = 0$, $j \in I$. Otherwise $\lim_{t\to\infty} \left(\sum_{i\in\Phi} x_i(t)/y_i \right) = S^0 - \gamma$ where $\Phi = \{i : \lambda_i = \gamma \text{ or } \mu_i = \gamma\}$, and $\lim_{t\to\infty} x_j(t) = 0$ if neither λ_j nor μ_j is equal to γ.

4. LEMMAS AND PROOFS OF PRELIMINARY RESULTS.

Proof of Theorem 3.1: Let $z(t) = S(t) + \sum_{i=1}^{n} \frac{x_i(t)}{y_i}$. From (2.1), we have

$$z'(t) = \left(S^0 - z(t)\right)D \tag{4.1}$$

from which we obtain

$$z(t) = S^0(1 - e^{-Dt}) + z_0e^{-Dt} \tag{4.2}$$

where $z_0 = z(0)$. It is clear from (2.1) that the positive $(S,x_1,\ldots,x_n)$ cone is positively invariant. Thus solutions are positive for all $t > 0$ and so, by (4.2), are bounded. □

The following corollary is immediate from (4.2).

Corollary 4.1. The n-dimensional simplex,

$$\mathcal{S} = \{(S,x_1,\ldots,x_n) : S,x_1,\ldots,x_n \geq 0;\ S + \sum_{i=1}^{n} x_i/y_i = S^0\},$$

is a global attractor for (2.1).

Proof of Theorem 3.2: Let $\left(S(t),x_1(t),\ldots,x_n(t)\right)$ be a solution of (2.1). Suppose that $S^0 \leq \lambda_i < \infty$. From Corollary (4.1) it follows that for each $\varepsilon > 0$, there exists $T = T(\varepsilon)$ such that

$$S^0 - \varepsilon/2y_i \leq S(t) + \sum_{j=1}^{n} x_j(t)/y_j \leq S^0 + \varepsilon/2y_i, \quad t \geq T(\varepsilon). \tag{4.3}$$

Since $p_i(S) - D < 0$ for $0 \leq S \leq S^0 - \varepsilon/2y_i$, we have $\delta_i = \max\{p_i(S) - D : 0 \leq S \leq S^0 - \varepsilon/2y_i\} < 0$. If $S(t) \geq S^0 - \varepsilon/2y_i$ for all sufficiently large t, then (4.3) implies that $x_i(t) \leq \varepsilon$ for all large t. If $S(t) \leq S^0 - \varepsilon/2y_i$ for all sufficiently large t, then we have $x_i'(t) \leq \delta_i x_i(t)$ for all large t, and again we shall have $x_i(t) \leq \varepsilon$ if t is large enough. If there is a sequence $t_n \to \infty$ with $S(t_n) = S^0 - \varepsilon/2y_i$, and

$$S(t) \begin{cases} \leq S^0 - \varepsilon/2y_i, & t_{2n} < t < t_{2n+1} \\ \geq S^0 - \varepsilon/2y_i, & t_{2n+1} < t < t_{2n+2} \end{cases}$$

we have $x_i(t) \leq \varepsilon$ on $[t_{2n+1}, t_{2n+2}]$ and $x_i'(t) < 0$ on (t_{2n}, t_{2n+1}), so $x_i(t) \leq \varepsilon$ on (t_{2n}, t_{2n+1}), also. Thus in all cases, we have $x_i(t) \leq \varepsilon$ for all sufficiently large t. It follows that $\lim_{t\to\infty} x_i(t) = 0$.

If $\lambda_i = \infty$, then $p_i(S) - D < 0$ for $0 \leq S < \infty$. By Theorem 3.1 $S(t)$ is bounded above by σ, say and so $\eta_i = \max\{p_i(S) - D : 0 \leq S \leq \sigma\} < 0$. Since $0 \leq S(t) \leq \sigma$, for all t we have $x_i'(t) \leq \eta_i x_i(t)$, and so $\lim_{t\to\infty} x_i(t) = 0$. □

The following lemma describes a condition that guarantees convergence of the substrate to one of the break-even concentrations. An analogous result was proved in [40], based on a result of Miller [54]. Since the proof of our lemma is similar, we shall omit it.

Lemma 4.2. Let $(S(t), x_1(t), \ldots, x_n(t))$ be a solution of (2.1). Suppose that for some i, $x_i(t)$ converges monotonely to $x_i^* > 0$ as

$t \to \infty$. Then $\lim_{t\to\infty} S(t)$ exists and is equal either to λ_i or to μ_i.

In the event that $S(t)$ converges to a limit as $t \to \infty$, then it must be to S^0 or to one of the break-even concentrations, and the population biomasses have appropriate limiting behaviours. This is the content of the next lemma.

Lemma 4.3. Let $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ be a solution of (2.1). Suppose that $\lim_{t\to\infty} S(t) = \gamma$. Then

(a) $\gamma = S^0$ or is the endpoint of a component of Q.

(b) If $\gamma = S^0$, then $\lim_{t\to\infty} x_i(t) = 0$, $i \in I$.

(c) If $\gamma = \lambda_i$ or μ_i, the endpoint of a component of Q, then $\lim_{t\to\infty} x_i(t) = y_i(S^0 - \gamma)$, $\lim_{t\to\infty} x_j(t) = 0$, $j \neq i$.

Proof: (a) From Corollary 4.1, we know that $0 < \gamma \le S^0$. Suppose that (a) does not hold. Then either $\gamma \in (\lambda_i, \mu_i)$ for some i, or there exists $\varepsilon_0 > 0$ such that $[\gamma - \varepsilon_0, \gamma + \varepsilon_0]$ is disjoint from $c\ell(Q)$.

In the former case, $\lambda_i < S(t) < \mu_i$ for t sufficiently large, which implies x_i is monotone increasing. By Lemma 4.2, it follows that $\lim_{t\to\infty} S(t)$ is equal either to λ_i or μ_i, contradicting $\gamma \in (\lambda_i, \mu_i)$.

In the latter case, we shall have $p_i\big(S(t)\big) - D < 0$ for all large t, for all i, so all the $x_i(t)$ are eventually monotone decreasing. If they all decrease to zero, then we have $\lim_{t\to\infty} S(t) = S^0$ by Corollary 4.1; otherwise we may apply Lemma 4.2 and deduce that $\lim_{t\to\infty} S(t) = \lambda_j$ or μ_j for some j. But this contradicts

$[\gamma - \varepsilon_0, \gamma + \varepsilon_0] \cap c\ell(Q) = \emptyset$. Thus (a) must hold.

(b) follows at once from Corollary 4.1.

(c) If $\gamma = \lambda_i$ or μ_i, the endpoint of a component of Q, then for all $j \neq i$, we have $x_j'(t) < 0$ for t sufficiently large. If we had $\lim_{t\to\infty} x_j(t) > 0$, then $\lim_{t\to\infty} S(t) = \lambda_j$ or μ_j by Lemma 4.2, which is a contradiction. Thus $\lim_{t\to\infty} x_j(t) = 0$ for all $j \neq i$. That $\lim_{t\to\infty} x_i(t) = y_i(S^0 - \gamma)$ now follows from Corollary 4.1. □

Recall that the simplex,

$$\mathcal{S} = \{(S, x_1, \dots, x_n) : S, x_1, \dots, x_n \geq 0 ;\; S + \sum_{i=1}^{n} x_i/y_i = S^0\}$$

is globally attracting for the system (2.1) (and therefore positively invariant). Since every bounded trajectory is asymptotic to its omega-limit set it is evident that the dynamics of (2.1) restricted to $\mathcal{S}$ will provide the key to understanding the general behaviour of (2.1). It will be convenient to introduce the following notation for the positively invariant subsimplices of $\mathcal{S}$:

$$\mathcal{S}_H = \{(S, x_1, \dots, x_n) \in \mathcal{S} : x_h > 0 \text{ if and only if } h \in H\}$$

defined for every subset H of I. Note then that $\mathcal{S} = \mathcal{S}_I$. Accordingly we denote the system (2.1) restricted to these subsimplices as:

$$S'(t) = \big(S^0 - S(t)\big)D - \sum_{i=1}^{n} \frac{x_i(t)}{y_i} p_i\big(S(t)\big),$$

$$x_i'(t) = x_i(t)\big(-D + p_i(S(t))\big), \quad i \in I,$$

$$(4.4)_{S_H} \qquad S(0) = S_0 \geq 0, \quad x_i(0) = x_{i0} > 0, \quad i \in H, \quad x_{i0} = 0 \quad i \notin H.$$

$$S_0 + \sum_{i=1}^{n} x_{i0}/y_i = S^0 .$$

We also define $Q_H = \big(\bigcup_{h \in H} (\lambda_h, \mu_h)\big) \cap Q$, the analogue of Q with respect to $(4.4)_{S_H}$.

Note that solutions of $(4.4)_S$ are positive for all $t > 0$ and satisfy,

$$(4.5) \qquad S'(t) + \sum_{i=1}^{n} \frac{x_i'(t)}{y_i} = 0, \quad t > 0 .$$

The next sequence of lemmas is directed at analysing $(4.4)_S$.

We will be mainly concerned with showing that on the positively invariant linear manifold S, the concentration of substrate, $S(t)$, eventually becomes trapped either outside of Q or inside a component of Q between particular values of T, forcing monotonic convergence of the concentration of each competitor, $x_i(t)$, and hence convergence of $S(t)$.

Lemma 4.4. Let $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ be a solution of $(4.4)_S$. Let γ be the endpoint of a component of Q. Suppose there exists $\tau \geq 0$ with $S(\tau) = \gamma$. Then $S'(\tau) > 0$ or $n = 1$ and $S'(\tau) = 0$.

Proof: Since γ is the endpoint of a component of Q, $x_i'(\tau) = 0$ for some i and $x_j'(\tau) < 0$ for all $j \neq i$. The result now follows from (4.5). □

The following lemma is an immediate consequence of Lemma 4.4.

Lemma 4.5. Let $(S(t), x_1(t), \ldots, x_n(t))$ be a solution of $(4.4)_S$ and let (λ_i, μ_j) be a component of Q. Then, for all sufficiently large t, precisely one of the following occurs:

(a) $S(t) < \lambda_i$, or

(b) $\lambda_i \leq S(t) \leq \mu_j$, or

(c) $S(t) > \mu_j$.

[illegible] this point we digress by stating and proving a result for the [illegible]1). We do this here, to emphasize that in this special case [illegible] is fairly straightforward. However, the result is quite g[illegible] and natural from a biological viewpoint. It states that if the co[illegible]tor with the lowest break-even concentration level λ_1, also has it[illegible]rgest break-even concentration level μ_1 (level above which it is in[illegible]ited) greater than the input concentration rate S^0, then there is a [illegible]obally asymptotically stable critical point. This applies in the ca[illegible] that $\mu_1 = +\infty$ and so it generalizes results of Hsu, Hubbell and Wal[illegible]an [illegible]40]. More generally, it applies to all models in which the kinetic growth function p_1 is monotonically increasing.

Theorem 4.6. If $\lambda_1 < S^0 < \mu_1$, then the critical point $E_{\lambda_1} = (\lambda_1, y_1(S^0 - \lambda_1), 0, \ldots, 0)$ is globally asymptotically stable for (2.1).

Proof: First we show that the result holds for $(4.4)_{S_H}$ where $H = I \backslash \Theta$ and Θ is any index set such that $\Theta \subset I \backslash \{1\}$. By Lemma 4.4, if there exists $\tau \geq 0$ such that $S(\tau) = \lambda_1$, then $S'(\tau) > 0$. (In the case that $n = 1$, $S'(\tau) = 0$ and $S(t) \equiv \lambda_1$.) Therefore, on S_H, either $S(t) < \lambda_1$ for all $t \geq 0$ or $\lambda_1 \leq S(t) \leq S^0$ for all large t. In the former case all $x_i(t)$ monotonely decrease. By (4.5), $S(t)$ must monotonely increase. Since $S(t)$ is bounded above it converges and so the result follows by Lemma 4.3(a) and (c). In the latter case, $x_1(t)$ is bounded above and monotonely increasing. Since this implies that it must converge to a positive limit, the result follows for $(4.4)_{S_H}$, by Lemmas 4.2 and 4.3(a) and (c).

To show that the result holds for (2.1), it suffices to show that E_{λ_1} belongs to the omega-limit set, Ω, of any solution $(S(t), x_1(t), \ldots, x_n(t))$ of (2.1), since it is easily verified that E_{λ_1} is locally asymptotically stable for (2.1).

First we show that if $\overline{\lim_{t\to\infty}}\, x_1(t) > 0$ then $E_{\lambda_1} \in \Omega$. Suppose $\overline{\lim_{t\to\infty}}\, x_1(t) > 0$. Then there exists $P = (S, \xi_1, \ldots, \xi_n) \in \Omega$ with $\xi_1 > 0$. By Corollary 4.1, $P \in S_H$, for some $H \subset I$ with $1 \in H$, and so by the proof for $(4.4)_{S_H}$ above, E_{λ_1} belongs to the closure of the orbit through P and hence belongs to Ω.

If we assume $\overline{\lim_{t\to\infty}}\, x_1(t) = 0$, and hence $\lim_{t\to\infty} x_1(t) = 0$, we derive a contradiction as follows. Let $z(t) = S(t) + \sum_{i=1}^{n} x_i(t)/y_i$. By (4.2), $\Omega \subset S$, $\lim_{t\to\infty} z(t) = S^0$ and $\lim_{t\to\infty} z'(t) = 0$. In this case $\underline{\lim}_{t\to\infty} S(t) \leq \lambda_1$ (or $x_1(t)$ increases to a positive limit) and so there exists $t_k \to \infty$ such that for fixed $\bar{\lambda}$ satisfying $\lambda_1 < \bar{\lambda} < \min(\lambda_2, S^0)$, $S(t_k) \leq \bar{\lambda}$ and $\lim_{k\to\infty} S'(t_k) = 0$. Now $x_1'(t_k) = (-D + p_1(S(t_k)))x_1(t_k) \to 0$

as $k \to \infty$, since $\lim_{k\to\infty} x_1(t_k) = 0$, and for $i \geq 2$, $x_i'(t_k) = c_i x_i(t_k)$ where $c_i = -D + p_i\big(S(t_k)\big) \leq -D + p_i\big(S(\overline{\lambda})\big) < 0$. Since $\lim_{k\to\infty} z'(t_k) = 0$, it follows that $\lim_{k\to\infty} x_i'(t_k) = 0$ and therefore $\lim_{k\to\infty} x_i(t_k) = 0$ for $i \geq 2$. Thus $\lim_{k\to\infty} x_i(t_k) = 0$ for all $i \in I$, which implies that $\lim_{k\to\infty} S(t_k) = S^0 > \overline{\lambda}$, a contradiction. Theorem 4.6 now follows. □

Lemma 4.7. Let $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ be any solution of $(4.4)_S$. Let $\gamma \in \Gamma$. Then there do not exist t_1, t_2 with $0 \leq t_1 < t_2$, such that

$$\text{(i)} \quad S(t_1) = S(t_2) = \gamma > S(t), \quad \text{for} \quad t_1 < t < t_2$$

and

$$\text{(ii)} \quad S'(t_1) \leq 0 \leq S'(t_2).$$

Proof: In this proof we adopt the convention that the result of summation over an empty index set is zero.

Recall that $\Gamma = \{\lambda_i : \lambda_i < S^0\} \cup \{\mu_j : \mu_j < S^0\}$, and that the elements of Γ have been relabelled as $\gamma_1 < \gamma_2 < \cdots < \gamma_k < S^0$. The proof will proceed by induction on the index set $\{1,2,\ldots,k\}$.

Let $\gamma = \gamma_1 = \lambda_1$, and suppose that (i) and (ii) hold. Since $S(t_1) = \gamma_1 = \lambda_1$, γ_1 is the endpoint of a component of Q, and so it follows from Lemma 4.4 that $S'(t_1) > 0$, contradicting (i). Therefore the lemma holds for $\gamma = \gamma_1$.

Now suppose the lemma is true for $\gamma = \gamma_m$, for all m with $1 \leq m \leq h-1$, where $2 \leq h \leq k$. Let $\gamma = \gamma_h$ and suppose that (i) and (ii) are satisfied.

Let $a_i = \big(p_i(\gamma_h) - D\big)/y_i$, $i \in I$. Then $\dfrac{x_i'(t_j)}{y_i} = a_i x_i(t_j)$,

$j = 1,2$; $i \in I$, and so (ii) and (4.5) imply that

$$(4.6) \qquad -\sum_{i=1}^{n} a_i x_i(t_1) \le -\sum_{i=1}^{n} a_i x_i(t_2) .$$

Suppose that $\gamma_h = \lambda_\ell$ for some $\ell \ge 2$ (note this implies $n \ge 2$). Define J to be $\{j \in I : \mu_j < \lambda_\ell\}$ and L to be $\{1,\ldots,\ell - 1\}$. Observe that the a_i have the following signs:

$$(4.7) \qquad \begin{aligned} a_i &> 0 , & i &\in L\backslash J \\ a_i &\le 0 , & i &\in (I\backslash L) \cup J \end{aligned}$$

with strict inequality except for $i = \ell$. Rearranging (4.6) gives

$$(4.8) \qquad -\sum_{i\in(I\backslash L)\cup J} a_i\big(x_i(t_1) - x_i(t_2)\big) \le \sum_{i\in(L\backslash J)} a_i\big(x_i(t_1) - x_i(t_2)\big).$$

By (i), $S(t) < \lambda_\ell$ for $t_1 < t < t_2$. The inductive hypothesis gives $S(t) \ge \gamma_{h-1}$, i.e. $S(t) \ge \max(\lambda_{\ell-1} , \max_{i\in J} \mu_i)$, with (by continuity of $S(t)$) strict inequality in some nonempty subinterval U of (t_1,t_2). Thus for $t_1 < t < t_2$, we have

$$p_i\big(S(t)\big) - D \begin{cases} \ge 0 , & i \in L\backslash J \\ \le 0 , & i \in (I\backslash L) \cup J \end{cases}$$

with strict inequality in U, and so

$$(4.9) \qquad \begin{aligned} x_i(t_1) - x_i(t_2) &< 0 , & i &\in L\backslash J . \\ x_i(t_1) - x_i(t_2) &> 0 , & i &\in (I\backslash L) \cup J . \end{aligned}$$

By (4.7) and (4.9), the left-hand side of (4.8) is nonnegative and the right-hand side is nonpositive, which is possible only if all a_i are zero. But only a_ℓ is zero and since $n \geq 2$ in this case, we have a contradiction.

Now suppose that $\gamma_h = \mu_\ell$ for some ℓ. We define $K = \{i \in I : \mu_i < \mu_\ell\}$, $M = \{i \in I : \lambda_i > \mu_\ell\}$, and rearrange (4.6) to give

$$(4.10) \qquad -\sum_{i \in K \cup M} a_i\big(x_i(t_1) - x_i(t_2)\big) \leq \sum_{i \in I \setminus (K \cup M)} a_i\big(x_i(t_1) - x_i(t_2)\big) .$$

A similar argument as before gives a contradiction. Thus the induction is complete, and the lemma is proved. □

Lemma 4.8. Let $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ be a solution of $(4.4)_S$ and let γ_ℓ, $\gamma_{\ell+1}$ be consecutive elements of Γ. Then, for all sufficiently large t, precisely one of the following occurs:

(a) $S(t) < \gamma_\ell$, or

(b) $\gamma_\ell \leq S(t) \leq \gamma_{\ell+1}$, or

(c) $S(t) > \gamma_{\ell+1}$.

Proof: If for all t, $S(t) \notin [\gamma_\ell, \gamma_{\ell+1}]$ then clearly (a) or (c) must hold. Suppose then that $\gamma_\ell \leq S(\tau_0) \leq \gamma_{\ell+1}$ for some τ_0. If $\gamma_\ell \leq S(t) \leq \gamma_{\ell+1}$ for all $t \geq \tau_0$, then (b) holds. If there exists $\bar{\tau}_0 > \tau_0$ such that $S(\bar{\tau}_0) < \gamma_\ell$, then there will exist τ_1 with $\tau_0 \leq \tau_1 \leq \bar{\tau}_0$, such that $S(\tau_1) = \gamma_\ell > S(t)$ for $\tau_1 < t < \bar{\tau}_0$, and $S'(\tau_1) \leq 0$. It follows from Lemma 4.7 that we must have $S(t) < \gamma_\ell$ for all $t > \tau_1$, i.e. (a) holds. If there exist $\bar{\tau}_1 > \tau_0$ such that $S(\bar{\tau}_1) > \gamma_{\ell+1}$, then either $S(t) > \gamma_{\ell+1}$ for all $t > \bar{\tau}_1$, in which case (c) holds, or there exists $\tau_2 > \bar{\tau}_1$ such that $S(\tau_2) = \gamma_{\ell+1}$, and $S'(\tau_2) \leq 0$. By Lemma 4.7 again, we must then have $S(t) < \gamma_{\ell+1}$ for all $t > \tau_1$. By the preceding argument, we will then have (a) or (b) occurring. This proves the lemma. $\square$

Lemma 4.9. Let $(S(t), x_1(t), \ldots, x_n(t))$ be a solution of $(4.4)_S$, let (λ_i, μ_j) be a component of Q, and suppose that $S(t) \in [\lambda_i, \mu_j]$ for all sufficiently large t. Then $\lim_{t\to\infty} S(t)$ exists and is equal to λ_i or to μ_j.

Proof: Let $\Gamma_{ij} = \{\lambda_h : \lambda_i \leq \lambda_h \leq \mu_j\} \cup \{\mu_\ell : \lambda_i \leq \mu_\ell \leq \mu_j\}$. Since (λ_i, μ_j) is a component of Q, we have $\lambda_i < S^0$, and so Γ_{ij} is a nonempty subset of Γ. With the labelling used for Γ, there exist r, s such that $\lambda_i = \gamma_r < \gamma_{r+1} \leq \gamma_s = \mu_j$. By Lemma 4.8, for each interval $[\gamma_\ell, \gamma_{\ell+1}]$, where $r \leq \ell \leq s-1$, $S(t)$ is either eventually in that interval or eventually outside it. Since these intervals decompose $[\lambda_i, \mu_j]$, there is some value of ℓ such that $\gamma_\ell \leq S(t) \leq \gamma_{\ell+1}$ for all sufficiently large t. If $\gamma_\ell = \lambda_{\bar{p}}$, say, then $\gamma_{\ell+1} \leq \mu_{\bar{p}}$ and so $x'_{\bar{p}}(t) \geq 0$ for all sufficiently large t. If $\gamma_\ell = \mu_q$, say, then it cannot be that $\mu_{\bar{q}} < \mu_q$ for all $\bar{q}$ for which $\lambda_i \leq \lambda_{\bar{q}} < \mu_q$; for otherwise (λ_i, γ_ℓ) is a component of Q, a contradiction since, by assumption, (λ_i, μ_j) is a component of Q, and $\gamma_\ell < \mu_j$. Thus there exists $\bar{q}$ such that $\lambda_i \leq \lambda_{\bar{q}} < \mu_q = \gamma_\ell < \gamma_{\ell+1} \leq \mu_{\bar{q}} \leq \mu_j$, and so $x'_{\bar{q}}(t) \geq 0$ for all sufficiently large t. In either event, therefore, there exists p such that $x'_p(t) \geq 0$ for all sufficiently large t. Since solutions of $(4.4)_S$ are bounded, $x_p(t)$ converges monotonely to $x_p^* > 0$ as $t \to \infty$. By Lemma 4.2, $\lim_{t\to\infty} S(t) = \gamma$ (where $\gamma = \lambda_p$ or μ_p).

Now we use Lemma 4.3(a) to deduce that $\gamma = \lambda_i$ or μ_j. □

The next lemma describes the asymptotic behaviour of the system $(4.4)_S$.

Lemma 4.10. Let $(S(t), x_1(t), \ldots, x_n(t))$ be a solution of $(4.4)_S$. Then $\lim_{t\to\infty} S(t)$ exists and is equal to γ, where γ is either S^0 or is the endpoint of a component of Q. If $\gamma = S^0$, then $\lim_{t\to\infty} x_j(t) = 0$, $j \in I$. If $\gamma = \lambda_i$ or μ_i, the endpoint of a component of Q, then $\lim_{t\to\infty} x_i(t) = y_i(S^0 - \gamma)$, $\lim_{t\to\infty} x_j(t) = 0$, $j \neq i$.

Proof: By Lemma 4.5, $S(t)$ is either eventually interior or exterior to the closure of each component of Q. Since Q is the union of its (disjoint) components, either $S(t)$ is eventually in the closure of some component $[\lambda_i, \mu_j]$ or is eventually exterior to $c\ell(Q)$. In the first case, Lemma 4.9 gives the result. In the second case, $x_i(t)$ is eventually decreasing for all i. By (4.5), $S(t)$ is eventually increasing and therefore has a limit as $t \to \infty$. Lemma 4.3 now completes the proof. □

It is evident that we can replace $(4.4)_S$ in Lemma 4.10 by $(4.4)_{S_H}$, where H is any subset of I, provided we also replace Q by $Q_H = \left(\bigcup_{h\in H} (\lambda_h, \mu_h)\right) \cap Q$.

5. PROOFS OF THE MAIN RESULTS. We introduce the following notation for the critical points of (2.1):

$$E_{\lambda_k} = \{(S,x_1,\dots,x_n) : S = \lambda_k ;\ x_k = y_k(S^0 - \lambda_k) ;\ x_\ell = 0\ \ell \neq k\},$$

defined for $\lambda_k < S^0$.

$$E_{\mu_k} = \{(S,x_1,\dots,x_n) : S = \mu_k ;\ x_k = y_k(S^0 - \mu_k) ;\ x_\ell = 0\ \ell \neq k\},$$

defined for $\mu_k < S^0$.

$$E_{S_0} = (S^0,0,\dots,0).$$

We let $\mathcal{E}$ denote the set of all critical points of (2.1), i.e.

$$\mathcal{E} = \left(\bigcup_{\lambda_k<S^0}\left\{E_{\lambda_k}\right\}\right) \cup \left(\bigcup_{\mu_k<S^0}\left\{E_{\mu_k}\right\}\right) \cup \left\{E_{S^0}\right\}.$$

We will also consider the following subsets of $\mathcal{E}$:

$$L = \left\{E_{\lambda_k} : \lambda_k \text{ is a left endpoint of a component of } Q\right\}.$$

$$R = \left\{E_{\mu_k} : \mu_k \text{ is a right endpoint of a component of } Q\right\}.$$

$$\mathcal{E}^* = \begin{cases} \mathcal{E}\setminus(L\cup R\cup\{E_{S^0}\}) & \text{if } S^0 \notin Q, \\ \mathcal{E}\setminus(L\cup R) & \text{if } S^0 \in Q. \end{cases}$$

In order to prove Theorems 3.3 and 3.4 we first establish the local stability of the critical points of (2.1). Since this is obtained fairly routinely from standard linearization procedures, we summarize this result here and relegate the proof to Appendix 1.

Lemma 5.1. All the points in E are hyperbolic critical points (i.e. all the associated eigenvalues of the linearized systems have nonzero real parts). Furthermore,

(i) For the system (2.1), the critical points in L are all asymptotically stable.

(ii) The critical points in R are all unstable, but each has an n-dimensional stable manifold.

(iii) The critical point $(S^0,0,\ldots,0)$ is asymptotically stable iff $S^0 \notin Q$. (Note that $S^0 \in \partial Q$ is excluded by the generic condition (2.7).)

(iv) The critical points in the set E^* are all unstable. The stable manifold of each of these points is entirely contained in the boundary of $\mathbb{R}_+^{n+1}$ (which we identify with $(S,x_1,\ldots,x_n)$-space).

The following lemma will be useful. It can be obtained either by the use of Hartman's Linearization Theorem [35] or by the method of isolating blocks [15], and a proof may be found in Appendix 1 of a paper of Freedman and Waltman [21].

Lemma 5.2. Let P be an isolated hyperbolic critical point in the omega-limit set $\Omega(X)$ of an orbit through X of a dynamical system. Then either $\Omega(X) = \{P\}$, or there exist points P^s and P^u in $\Omega(X)$, with $P^s \in W^s(P)\backslash\{P\}$ and $P^u \in W^u(P)\backslash\{P\}$, where $W^s(P)$ and $W^u(P)$ denote the stable and unstable manifold of P respectively. —

Lemma 5.3. (i) No point of the set E^* is in the omega-limit set of any solution of (2.1).

(ii) If a point of the set $E \setminus E^*$ is in the omega-limit set of some solution of (2.1), then it is the only point in the omega-limit set of that solution.

Proof: Let $(S(t), x_1(t), \dots, x_n(t))$ be a solution of (2.1) and let Ω be its omega-limit set. Suppose that $P \in \Omega \cap E^*$. Then P is of the form E_{λ_ℓ}, E_{μ_ℓ} or E_{S^0}, and $I = \{i \in I : \lambda_i < \lambda_\ell < \mu_i\}$ (resp. $\{i \in I : \lambda_i < \mu_\ell < \mu_i\}$, $\{i \in I : \lambda_i < S^0 < \mu_i\}$) is nonempty. By Lemma 5.1, $W^s(P) \subset \partial \mathbb{R}_+^{n+1}$. Since the trajectory of $(S(t), x_1(t), \dots, x_n(t))$ is contained in int $\mathbb{R}_+^{n+1}$, Lemma 5.2 yields the existence of a point $P^u \in (W^u(P) \setminus \{P\}) \cap \Omega$ and we may assume that P^u and the negative semi-orbit through P^u are as close to P as we wish. Let this negative semi-orbit be denoted $(\overline{S}(t), \overline{x}_1(t), \dots, \overline{x}_n(t))$, $t \le 0$, so that $P^u = (\overline{S}(0), \overline{x}_1(0), \dots, \overline{x}_n(0))$. Define J to be $\{j \in I : \overline{x}_j(0) \neq 0\}$.

If $j \notin I \cup \{\ell\}$ (if $j \notin I$ in the case that $P = E_{S^0}$), then $p_j(\overline{S}(t)) - D < 0$ for $t \le 0$ and so $\overline{x}_j(t)$ is nonincreasing on $(-\infty, 0]$. Since $\overline{x}_j(t) \to 0$ as $t \to -\infty$, it follows that $\overline{x}_j(t) \equiv 0$ on $(-\infty, 0]$ and so $\overline{x}_j(0) = 0$.

On the other hand, there must exist some $j \in I$ with $\overline{x}_j(0) > 0$, otherwise P^u would belong to $W^s(P)$. Hence the trajectory of the solution $(\overline{S}(t), \overline{x}_1(t), \dots, \overline{x}_n(t))$ is in the relative interior of the subsimplex S_J of S. Since $(\lambda_j, \mu_j) \cap (\lambda_\ell, \mu_\ell) \neq \emptyset$ for all $j \in J$ ($S^0 \in (\lambda_j, \mu_j)$ for all $j \in J$ in the case that $P = E_{S^0}$), it follows that Q_J is connected, say $Q_J = (\lambda_m, \mu_M)$. By Lemma 4.10 applied to $(4.4)_{S_J}$, we have

(5.1) $$\overline{S}(t) \to \lambda_m, \quad \mu_M \text{ or } S^0 .$$

(a) Suppose that $P = E_{\lambda_\ell}$.

We may assume that P^u is so close to P that $\overline{S}(t) \in (\lambda_j, \mu_j)$ for all $t \leq 0$, for all $j \in J\setminus\{\ell\}$. We cannot have $\overline{S}(t) > \lambda_\ell$ for any $t \in (-\infty, 0]$, for otherwise there exists $\tau \in (-\infty, 0]$ with $\overline{S}'(\tau) > 0$ and $\overline{S}(\tau) \in (\lambda_j, \mu_j)$ for all $j \in J$, which implies that $\overline{x}_j'(\tau) > 0$, contradicting $\overline{S}' + \sum_{j\in J} \overline{x}_j'/y_j \equiv 0$. Thus $\overline{S}(t) < \lambda_\ell$ for all t . Since $\lambda_m < \lambda_\ell < \mu_M$ (and $S^0 > \lambda_\ell$), we must have $\overline{S}(t) \to \lambda_m$ as $t \to \infty$. By Lemma 4.10 it follows that $E_{\lambda_m} \in \Omega$.

Repeating this argument inductively, we may eventually conclude that $E_{\lambda_i} \in \Omega$, where $E_{\lambda_i} \in L$. By Lemma 5.1, E_{λ_i} is asymptotically stable for (2.1), so $\Omega = \{E_{\lambda_i}\}$, contradicting $E_{\lambda_\ell} \in \Omega$.

(b) Suppose that $P = E_{S^0}$.

By arguments similar to the above, we find that $E_{\lambda_m} \in \Omega$, and obtain a contradiction.

(c) Suppose that $P = E_{\mu_\ell}$.

An argument similar to that used in (a) shows that $\overline{S}(t) > \mu_\ell$ for all t and then (5.1) implies that $\lim_{t\to\infty} \overline{S}(t) = \mu_M$ or S^0 . Repeating this argument inductively, we arrive at the conclusion that either $E_{\mu_j} \in \Omega$ where $E_{\mu_j} \in R$ or $E_{S^0} \in \Omega$. Suppose that $E_{S^0} \in \Omega$. If $E_{S^0} \in E^*$, we are back in case (b) and obtain a contradiction. If $E_{S^0} \notin E^*$, it is asymptotically stable for (2.1), by Lemma 5.1, so that $\Omega = \{E_{S^0}\}$, contradicting $E_{\mu_\ell} \in \Omega$.

Suppose that $E_{\mu_j} \in \Omega$, but $\Omega \neq \{E_{\mu_j}\}$. Then $(W^u(E_{\mu_j})\backslash\{E_{\mu_j}\}) \cap \Omega \neq \emptyset$, by Lemma 5.2. By considering the subsimplex $S_{\{j\}}$, we find that either E_{λ_j} or $E_{S^0} \in \Omega$, and obtain a contradiction by the preceding arguments.

This proves the first assertion of the lemma. If $P \in \Omega$ and $P \in L$, or $P = E_{S^0}$ in the case that $S^0 \not\subset c\ell(Q)$, then P is asymptotically stable and so $\Omega = \{P\}$. If $P \in R$, then $\Omega = \{P\}$. Otherwise we obtain a contradiction as in case (c) discussed above. This proves the second part of the lemma. □

Proof of Theorem 3.3: Since S is globally attracting for (2.1), the omega-limit set Ω, of any solution of (2.1) is a union of trajectories lying entirely in S, where each such trajectory is a solution of $(4.4)_{S_H}$ for some $H \subset I$. By the remark following Lemma 4.10, applied to $(4.4)_{S_H}$ for any $H \subset I$, every solution of $(4.4)_{S_H}$ converges to a point in E. Since the omega-limit set is closed, Ω must contain a point of E. The result follows by Lemma 5.3. □

Proof of Theorem 3.4: Immediate from Theorem 3.3 and Lemma 5.1. □

Corollary 3.5 follows at once from Theorem 3.4.

Theorem 3.6 can be proved using arguments similar to those used to prove Theorem 3.4.

6. DISCUSSION. We have considered a model of purely exploitative competition between n populations in a chemostat for a single, essential, nonreproducing growth-limiting substrate, which may be inhibiting at high concentrations. Our results predict that at most one of the competing populations survives, i.e. there is competitive exclusion. However, the outcome may be initial condition dependent. The global dynamics of the model are in a sense, trivial, in that all solutions have limiting asymptotic behaviour. There are a finite number of locally asymptotically stable equilibria whose domains of attraction partition the (strictly) positive $(S,x_1,x_2,\ldots,x_n)$ cone, their boundaries being comprised of the stable manifolds of some of the unstable equilibria of the system (if all the λ_i and μ_i are finite, there are at most $2n+1$ equilibria, at most $n+1$ of which are asymptotically stable). These results are not surprising. According to Fredrickson [20], there is much experimental evidence that "*pure and simple competitors will not coexist indefinitely in a system that is spatially homogeneous and that is subject to time-invariant external influences,*" which is precisely the case in the biological system we consider.

On the attracting simplex $\mathcal{S}$, we could eliminate S from the model to obtain a system of interactions between the x_i. However, the non-monotone nature of the functions p_i does not allow this system to satisfy the hypotheses of the competition models studied by Armstrong and McGehee [5] or by Hirsch [37]. Our results also contrast with the example given by Nitecki [57] of competition for a single resource, where competitive exclusion does not hold, and the examples of competition for a single reproducing resource (prey) in which coexistence occurs for a variety of models with monotone uptake (predation) responses [3,11,13,45,53,70].

Provided that conditions (2.6) and (2.7) hold, our results are easily extended to models with uptake functions p_i that have an arbitrary number of "break-even" concentrations, instead of the two, (λ_i, μ_i) considered in this paper. If these genericity assumptions are not made, more delicate, but technical, arguments are needed.

We have used the same wash-out rate, D for both substrate and microorganism populations. This is equivalent to assuming that the death rates of the microorganism populations are negligible compared with the wash-out rate. It would be interesting to see if similar results hold for different wash-out rates (or death rates), D_i. Hsu [39] has carried out the analysis for this situation in the case of Michaelis-Menten kinetics.

To illustrate our results, we consider the following (at least, theoretical) application to water purification. Here we are motivated by experimental work of Yang and Humphrey [83]. Suppose that there is one contaminant, say phenol, in the water supply, and that S^0, the input concentration of phenol, is high. Suppose also that certain microorganisms feed on phenol in such a way that it is growth-limiting at low concentrations, but inhibits growth at high concentration (e.g. Pseudomonas putida and Trichosporon cutaneum). Let A denote an acceptable concentration of phenol in the water supply and assume $A << S^0$. Suppose that microorganism 1 is harmless and that $\lambda_1 < A$ but $\mu_1 << S^0$. If the initial concentration of phenol in the water suppl[illegible]tively high, and microorganism 1 is used alone in an atte[illegible]e the phenol level, then it is likely to wash out of the s[illegible]the concentration of phenol would approach the [illegible]acce[illegible]level S^0. On the other hand, suppose that microorganism [illegible] has [illegible] $< \lambda_n < S^0 < \mu_n$. If microorganism n is used alone, $S(t)$ [illegible]ld [illegible]proach the value λ_n, which is again unacceptable. However, i[illegible]uld find microorganisms $2,\ldots,n-1$, so that (λ,μ) intervals ov[illegible]p in such a way as to form a single component of Q, containing S^0 [illegible]hen we would have $\lim_{t\to\infty} S(t) = \lambda_1 < A$, $\lim_{t\to\infty} x_1(t) = y_1(S^0 - \lambda_1)$ and [illegible]m $x_j(t) = 0$, $j > 1$, arriving eventually at a tolerable situ[illegible]on.

CHAPTER III

EXPLOITATIVE COMPETITION IN A CHEMOSTAT FOR TWO COMPLEMENTARY RESOURCES

1. INTRODUCTION. In this chapter we extend the theory of the previous chapter to cover exploitative competition for two resources. However, we restrict our attention to the two competitor situation.

When there is competition for two or more resources it becomes necessary to consider how the resources, once consumed, interact to promote growth. Leon and Tumpson [48] and Rapport [65] use consumer needs to provide a criterion to classify resources. They classify resources as perfectly complementary, perfectly substitutable or imperfectly substitutable.

Perfectly complementary resources are sources of different essential substances which must be taken together because each substance fulfils a different function with respect to growth. For example a carbon source and a nitrogen source might be complementary for a bacterium.

Perfectly substitutable resources, on the other hand, are alternate sources of an essential substance or of essential substances that fulfil the same function. The intermediate case is called imperfectly substitutable.

In this chapter we shall restrict our attention exclusively to perfectly complementary resources S and R. In this context we shall say that a population is S-limited (resp. R-limited) if its per capita consumption rate of R (resp. S) is independent of the concentration of R (resp. S) and depends only on the concentration of S (resp. R).

Leon and Tumpson [48] seem to be the first to have modelled exploitative competition for perfectly complementary resources. They assume that each competitor's functional response is a strictly monotone function of resource concentration. In the two resource, two competitor case they derive conditions for the existence of a locally asymptotically stable interior critical point and hence conditions for the coexistence of two competitors.

Hsu, Cheng and Hubbell [41] derive a model for exploitative competition in a chemostat between two populations for two perfectly complementary resources. They assume that consumption of the resources follows Holling Type II, or equivalently Michaelis-Menten kinetics, generalized to the two resource situation. They give a complete global analysis of their model. They conclude that *"each of the four outcomes of classical Lotka-Volterra two-species competition theory has multiple mechanistic origins in terms of consumer resource interactions."* They also give biological conditions based on parameters in their model that predict the competitive outcome. Their results are also summarized in a survey paper by Waltman et al., [81]. For other related work see [4,29,61,76].

The content of this chapter is organized as follows. In Section 2 we consider the model of Hsu et al. [41]. We point out that their derivation and their arguments apply for any functional responses that are strictly monotone functions of resource concentration. We also give an alternative method of obtaining their results which we shall find useful in Section 3.

In Section 3, we modify the model considered in Section 2 by allowing a more general class of functions to describe consumption and conversion rates, as we did in Chapter II. Again this class will allow us to consider substrates that are growth-limiting at low concentrations as well as at overly high concentrations. After presenting some preliminary results we develop graphical criteria that characterize the set of critical points and show under what circumstances the model permits trivial dynamics only. These graphical criteria are based on the methods developed in Section 2 as well as some concepts from linear programming. Surprisingly enough, using these graphical criteria, we are able to show that the model predicts that there are cases in which, in the absence of a rival each population definitely dies out, whereas when both competitors are present there is a possibility of coexistence. Thus, in some sense the rivals are cooperating. We then show by means of an example that even if we allow only one resource to be inhibitory to only one of the competitors at high concentrations, the model permits an orbitally asymptotically stable periodic orbit. Hence the model predicts that under certain conditions coexistence of the competitors with concentrations in sustained oscillation is possible. In this same example, there is also an unstable periodic orbit associated with a locally asymptotically stable critical point. Thus, there can be initial condition dependent regions of coexistence. In each case, the existence of the periodic orbit is obtained through a Hopf bifurcation. Since the analysis of stability involves computations that would be extremely tedious, they were done using the symbol manipulation language, REDUCE2. The algorithm used is based on the work of Marsden and McCracken [52]. The REDUCE2 program is general enough to be adapted for use to determine whether or not there is a Hopf bifurcation and, if there is, to determine the stability of the bifurcating periodic orbit, in the case of most systems of two first order, autonomous, ordinary differential equations. The program and an explanation of how to adapt it is included in Appendix 3 along with the program results. To illustrate the examples we use computer graphics to generate phase plane portraits. The equations are solved numerically by means of the IMSL double precision algorithm DGEAR.

We conclude the chapter with a discussion in which we summarize our results, compare the difference in dynamics between monotone kinetics and non-monotone-kinetics and consider the merits of other possible ways of modelling this problem.

Some auxiliary results appear in Appendices 2 and 4 as well.

2. THE MODEL - MONOTONE KINETICS. We consider the following model of exploitative competition in a chemostat between two populations of microorganisms for two purely complementary resources:

$$
(2.1)\qquad
\begin{aligned}
S'(t) &= \big(S^0 - S(t)\big)D - \sum_{i=1}^{2} \frac{x_i(t)}{y_{Si}} f_i\big(S(t),R(t)\big)\,,\\
R'(t) &= \big(R^0 - R(t)\big)D - \sum_{i=1}^{2} \frac{x_i(t)}{y_{Ri}} f_i\big(S(t),R(t)\big)\,,\\
x_i'(t) &= x_i(t)\big(-D + f_j(S(t),R(t))\big)\,, \quad i = 1,2\,,\\
S(0) &= S_0 \ge 0, \quad R(0) = R_0 \ge 0, \quad x_i(0) = x_{i0} > 0, \quad i = 1,2.
\end{aligned}
$$

where

$$f_i\big(S(t),R(t)\big) = \min\big(p_i(S(t),q_i(R(t))\big), \quad i = 1,2\,.$$

Here, $S(t)$ and $R(t)$ denote the concentrations of the two nonreproducing, complementary resources at time t and $x_i(t)$ denotes the concentration of the *i*th population of microorganisms at time t. The function $p_i\big(S(t)\big)$ (resp. $q_i\big(R(t)\big)$) represents the per capita growth rate of the *i*th population when resource S is limiting (resp. resource R is limiting) and so $f_i\big(S(t),R(t)\big)$ is the function that represents the rate of conversion of nutrient to biomass for the *i*th population. We take the minimum here because the resources are purely complementary. We are therefore assuming that growth rates adjust instantaneously to changes in the resource concentration. The consumption rate of nutrient is also assumed to be proportional to the rate of conversion to biomass. Thus, $f_i(S,R)/y_{Si}$ (resp. $f_i(S,R)/y_{Ri}$)

represents the consumption rate of resource S (resp. resource R) by the *i*th species where y_{Si} and y_{Ri} are the growth yield factors. If only one feed bottle is used, S^0 and R^0 denote the concentrations of resources S and R respectively in the feed bottle and D denotes the input rate from the feed bottle containing the resources to the growth chamber, as well as the wash-out rate of nutrients, microorganisms and byproducts from the growth chamber to the collection vessel. Thus the volume in the growth chamber remains constant. Here we are assuming, therefore, that the input rate of resource and the dilution rate are constant and that there is perfect mixing in the growth vessel so that nutrient and microorganisms are removed in proportion to their concentration. We are also assuming that individual death rates of either population are insignificant compared to the dilution rate, D.

If the experimenter prefers to use two separate feed bottles, each containing only one resource, and input from each feed bottle to the growth chamber at different rates, say rate D_S from the bottle containing resource S and rate D_R from the bottle containing resource R, then $D = D_S + D_R$, $S^0 = (\bar{S}^0 D_S)/(D_S + D_R)$ and $R^0 = (\bar{R}^0 D_R)/(D_S + D_R)$ where $\bar{S}^0$ and $\bar{R}^0$ represent the concentrations of resources S and R, respectively in each separate feed bottle. Here, D still represents the dilution rate.

We make the following assumptions concerning the functions p_i and q_i in our model:

(2.2) $p_i, q_i : \mathbf{R}_+ \to \mathbf{R}_+$;

(2.3) p_i, q_i are continuously differentiable,

$$(2.4) \qquad p_i(0) = 0, \quad q_i(0) = 0,$$

that is, if there is no nutrient, there is no uptake. Due to assumption (2.3), the functions $f_i(S,R)$ satisfy a Lipschitz condition in S and R on any compact subset of $\mathbf{R}_+ \times \mathbf{R}_+$ and so we have uniqueness of initial value problems and continuous dependence on initial conditions and parameters for system (2.1).

In this section we shall also assume that

$$(2.5) \qquad p_i'(S) > 0 \text{ for } S > 0 \text{ and } q_i'(R) > 0 \text{ for } R > 0,$$

that is, that the kinetics are strictly monotone.

This is precisely model III of Leon and Tumpson [48], adapted to a chemostat in which individual death rates are assumed insignificant compared to the dilution rate. The model applies when the functions p_i and q_i assume the form of the usual prototypes for monotone functional responses, eg. Holling Type I (or Lotka-Volterra kinetics), Holling Type II (or Michaelis-Menten kinetics) and Holling Type III (or multiple saturation dynamics). In the case that all the p_i's and q_i's satisfy Michaelis-Menten dynamics the model is precisely the one studied by Hsu, Cheng and Hubbell [41].

By means of a linear analysis, Leon and Tumpson [48] proved that "*Necessary and sufficient conditions for stable coexistence of two species engaged in exploitative competition for complementary resources*" (at an asymptotically stable equilibrium) "*are that each species must at equilibrium consume a greater fraction of the net rate of supply of its limiting resource than of the net rate of supply of* *its competitor's limiting resource."*

Hsu et al. [41], on the other hand, do a complete global analysis of the model. We summarize their results here. Although they assume the functions p_i and q_i, $i = 1,2$ all satisfy Michaelis-Menten kinetics, their proofs are also valid for strictly monotone functions. However, we give alternative proofs for some of their results. The methods we employ will be useful in a subsequent section where we relax assumption (2.5) in order to allow resources that are inhibitory at high concentrations, as we did in Chapter II. Some of the ideas to be used in these proofs are similar to ones used in the proofs in Chapter II.

We begin by stating some preliminary results. Just as in Chapter II (the proofs are similar as well) the system is as well-behaved as one would expect from the biological problem. More precisely, solutions of (2.1) are positive and bounded. Furthermore the polygonal set

$$(2.6)\qquad M = \left\{(S,R,x_1,x_2) \in \mathbb{R}^4_+ : S + \frac{x_1}{y_{S1}} + \frac{x_2}{y_{R2}} = S^0 \right.$$

$$\left. \text{and } R + \frac{x_1}{y_{R1}} + \frac{x_2}{y_{R2}} = R^0 \right\}$$

is a global attractor for (2.1) and on M solutions satisfy:

$$(2.7)\qquad \begin{gathered} S'(t) + \sum_{i=1}^{2} x_i'(t)/y_{Si} = 0 \\ \text{and} \\ R'(t) + \sum_{i=1}^{2} x_i'(t)/y_{Ri} = 0\,. \end{gathered}$$

At this point we introduce some useful notation:

$$p_i(\lambda_{Si}) = D \quad \text{and} \quad q_i(\lambda_{Ri}) = D \quad i = 1,2 . \tag{2.8}$$

Thus λ_{Si} and λ_{Ri} represent the break-even concentrations for resource S and R respectively, when that resource is limiting. By assumption (2.5) these concentrations are uniquely defined extended positive real numbers provided we assume that $\lambda_{Si} = +\infty$ if $p_i(S) < D$ for all $S \geq 0$ (similarly $\lambda_{Ri} = +\infty$ if $q_i(R) < D$ for all $R \geq 0$).

Following Hsu et al. [41], we define

$$C_i = y_{Si}/y_{Ri} , \quad i = 1,2 .$$

Since the units of $(1/y_{Si})$ are (units of S consumed)/(unit of population i produced), C_i represents the invariant ratio in which R and S are consumed by population i .

Let

$$T_i = \frac{R^0 - \lambda_{Ri}}{S^0 - \lambda_{Si}} \quad i = 1,2 \tag{2.9}$$

and

$$T^* = \frac{R^0 - \lambda_{R2}}{S^0 - \lambda_{S1}} \quad \text{and} \quad T_* = \frac{R^0 - \lambda_{R1}}{S^0 - \lambda_{S2}} . \tag{2.10}$$

As Hsu et al. [41] explain, by comparing T_i and C_i we can determine whether population i is S-limited or R-limited. T_i represents the ratio in which resources R and S are externally regenerated under steady-state consumption pressure from population i in the absence of his competitor. Therefore $T_i > C_i$ implies that population i is S-limited because S is regenerating at a steady state rate slower than R with respect to the required consumption ratio of population i. Similarly $T_i < C_i$ implies that population i is R-limited.

T^* (resp. T_*) represents the ratio of the steady state regeneration rate of R when x_2 (resp. x_1) is alone and that of S when x_1 (resp. x_2) is alone.

To avoid critical points for which the associated matrix of the linearization (the Jacobian) has any real root equal to zero, if the parameters are finite, we assume that

$$(2.11)\quad \begin{cases} \lambda_{S1} \text{ and } \lambda_{S2} \text{ are distinct from each other and from } S^0. \\ \lambda_{R1} \text{ and } \lambda_{R2} \text{ are distinct from each other and from } R^0. \end{cases}$$

and

$$(2.12)\qquad T_* \text{ and } T^* \text{ are distinct from } C_1 \text{ and } C_2.$$

To ensure that the critical points are all isolated we assume that

$$(2.13)\qquad C_1 \neq C_2.$$

So that we can assume that the vector field is continuously differentiable at and in some neighbourhood of each critical point we assume that

$$(2.14)\quad \text{if } (\bar{S},\bar{R},\bar{x}_1,\bar{x}_2) \text{ is a critical point, then } p_i(\bar{S}) \neq q_i(\bar{R}),\ i = 1,2.$$

Assumption (2.14) implies that

(2.15) $$T_i \neq C_i \,, \quad i = 1,2 .$$

Table I contains notation for the possible critical points of (2.1). In Table II we summarize criteria that ensure that these critical points lie in the nonnegative cone, as well as criteria that guarantee local asymptotic stability of these critical points. For completeness the linear analysis is given in A2.A.

We provide a summary of all the possible biological outcomes along with the competition criteria that yield each outcome, in Table III. To prove the results summarized in Table III we proceed as follows. First we note that since M is globally attracting and all solutions are bounded, the omega-limit set of any solution of (2.1) lies entirely in M. We shall show that the dynamics of (2.1) restricted to M are trivial (i.e. all trajectories with initial conditions in M approach some equilibrium in the limit). Next we shall appeal to the local analysis results and do a phase plane analysis in (x_1,x_2)-space to eliminate saddle connections and hence shall show that all solutions of (2.1) asymptotically approach equilibria. Finally, we shall consider the location of the stable manifolds of certain critical points to show that no solution with initial conditions in the positive cone can converge to that critical point.

That the dynamics of (2.1) restricted to M are trivial follows from Hirsch's results [37] on competitive systems adapted to monotone Lipschitzian functions rather than C^1 functions since (2.1) restricted to M is equivalent to system

TABLE I

NOTATION FOR THE CRITICAL POINTS† OF (2.1)

NOTATION	CRITICAL POINT (provided it lies in $\mathbb{R}^4_+$)
E_{S^0,R^0}	$= (S^0, R^0, 0, 0)$
$E_{\lambda_{S1},*}$	$= (\lambda_{S1}, R^0 - C_1(S^0 - \lambda_{S1}), y_{S1}(S^0 - \lambda_{S1}), 0)$
$E_{*,\lambda_{R1}}$	$= (S^0 - (R^0 - \lambda_{R1})/C_1, \lambda_{R1}, y_{R1}(R^0 - \lambda_{R1}), 0)$
$E_{\lambda_{S2},*}$	$= (\lambda_{S2}, R^0 - C_2(S^0 - \lambda_{S2}), 0, y_{S2}(S^0 - \lambda_{S2}))$
$E_{*,\lambda_{R2}}$	$= (S^0 - (R^0 - \lambda_{R2})/C_2, \lambda_{R2}, 0, y_{R2}(R^0 - \lambda_{R2}))$
$E_{\lambda_{S1},\lambda_{R2}}$	$= (\lambda_{S1}, \lambda_{R2}, x_1^*, x_2^*)$
	where $x_1^* = y_{S1}y_{R1}\left(\dfrac{y_{S2}(S^0-\lambda_{S1}) - y_{R2}(R^0-\lambda_{R2})}{y_{R1}y_{S2} - y_{S1}y_{R2}}\right)$
	and $x_2^* = y_{S2}y_{R2}\left(\dfrac{y_{R1}(R^0-\lambda_{R2}) - y_{S1}(S^0-\lambda_{S1})}{y_{R1}y_{S2} - y_{S1}Y_{R2}}\right)$
$E_{\lambda_{S2},\lambda_{R1}}$	$= (\lambda_{S2}, \lambda_{R1}, \hat{x}_1, \hat{x}_2)$
	where $\hat{x}_1 = y_{S1}y_{R1}\left(\dfrac{y_{S2}(S^0-\lambda_{S2}) - y_{R2}(R^0-\lambda_{R1})}{y_{R1}y_{S2} - y_{S1}y_{R2}}\right)$
	and $\hat{x}_2 = y_{S2}y_{R2}\left(\dfrac{y_{R1}(R^0-\lambda_{R1}) - y_{S1}(S^0-\lambda_{S2})}{y_{R1}y_{S2} - y_{S1}y_{R2}}\right)$

---

†under assumption (2.13), i.e. $C_1 \neq C_2$

TABLE II

SUMMARY OF THE LOCAL STABILITY ANALYSIS OF (2.1)

Exploitative Competition Between Two Populations for Two Complementary Resources

Monotone Functional Responses

CRITICAL POINT	CRITERIA FOR EXISTENCE	CRITERIA FOR ASYMPTOTIC STABILITY
E_{S^0,R^0}	always exists	$\lambda_{S1} > S^0$ or $\lambda_{R1} > R^0$ and $\lambda_{S2} > S^0$ or ${}_{R2} > R^0$
$E_{\lambda_{S1},*}$	$\lambda_{S1} < S^0$ and $T_1 > C_1$	$\lambda_{S1} < \lambda_{S2}$ or $T^* < C_1$
$E_{*,\lambda_{R1}}$	$\lambda_{R1} < R^0, \lambda_{S1} < S^0$ and $T_1 < C_1$	$\lambda_{R1} < \lambda_{R2}$ or $(T_* > C_1$ and $\lambda_{S2} < S^0)$
$E_{\lambda_{S2},*}$	$\lambda_{S2} < S^0$ and $T_2 > C_2$	$\lambda_{S1} > \lambda_{S2}$ or $T_* < C_2$
$E_{*,\lambda_{R2}}$	$\lambda_{R2} < R^0, \lambda_{S2} < S^0$ and $T_2 < C_2$	$\lambda_{R1} > \lambda_{R2}$ or $(T_* > C_2$ and $\lambda_{S1} < S^0)$
$E_{\lambda_{S1},\lambda_{R2}}$	$\lambda_{S1} > \lambda_{S2}$ and $\lambda_{R1} < \lambda_{R2}$ and $(C_1 < T^* < C_2$ and $\lambda_{S1} < S^0$ or $C_1 > T^* > C_2$ and $\lambda_{S1} < S^0)$	$C_1 < C_2$
$E_{\lambda_{S2},\lambda_{R1}}$	$\lambda_{S1} < \lambda_{S2}$ and $\lambda_{R1} > \lambda_{R2}$ and $(C_1 < T_* < C_2$ and $\lambda_{S2} < S^0$ or $C_1 > T_* > C_2$ and $\lambda_{S2} < S^0)$	$C_1 > C_2$

TABLE III

CLASSIFICATION OF COMPETITIVE OUTCOMES OF (2.1)

Exploitative Competition Between Two Populations for
Two Complementary Resources

Monotone Functional Responses

BIOLOGICAL OUTCOME		COMPETITION CRITERIA
1. Both populations die out. ((a) $\Rightarrow$ population 1 dies out) ((b) $\Rightarrow$ population 2 dies out) This is competitive-independent extinction.		(a) $\lambda_{S1} > S^0$ or $\lambda_{R1} > R^0$ and (b) $\lambda_{S2} > S^0$ or $\lambda_{R2} > R^0$
2. Population 1 always wins. Population 2 dies out.	and	$\lambda_{S1} < S^0$ and $\lambda_{R1} < R^0$ $\left\{\begin{array}{l} \lambda_{S1} < \lambda_{S2} \text{ and } \lambda_{R1} < \lambda_{R2}, \\ \text{or } \lambda_{S1} < \lambda_{S2}, \lambda_{R1} > \lambda_{R2} \text{ and } T_* > C_1, C_2 \\ \text{or } \lambda_{S1} > \lambda_{S2}, \lambda_{R1} < \lambda_{R2} \text{ and } T^* < C_1, C_2 \\ \text{or } \lambda_{S2} > S^0 \\ \text{or } \lambda_{R2} > R^0 \end{array}\right.$
3. Population 2 always wins. Population 1 dies out.	and	$\lambda_{S2} < S^0$ and $\lambda_{R2} < R^0$ $\left\{\begin{array}{l} \lambda_{S1} > \lambda_{S2} \text{ and } \lambda_{R1} > \lambda_{R2}, \\ \text{or } \lambda_{S1} < \lambda_{S2}, \lambda_{R1} > \lambda_{R2} \text{ and } T_* < C_1, C_2 \\ \text{or } \lambda_{S1} > \lambda_{S2}, \lambda_{R1} < \lambda_{R2} \text{ and } T^* > C_1, C_2 \\ \text{or } \lambda_{S1} > S^0 \\ \text{or } \lambda_{R1} > R^0 \end{array}\right.$

TABLE III (Continued)

CLASSIFICATION OF COMPETITIVE OUTCOMES OF (2.1)

Exploitative Competition Between Two Populations for
Two Complementary Resources

Monotone Functional Responses

BIOLOGICAL OUTCOME		COMPETITION CRITERIA
4. Populations 1 and 2 coexist at a positive equilibrium.	and	$\lambda_{Si} < S^0$ and $\lambda_{Ri} < R^0$, $i = 1,2$ $\lambda_{S1}<\lambda_{S2}, \lambda_{R1}>\lambda_{R2}$ and $C_1 > T_* > C_2$ or $\lambda_{S1}>\lambda_{S2}, \lambda_{R1}<\lambda_{R2}$ and $C_1 < T^* < C_2$
5. One population wins and the other dies out. Initial concentrations determine the outcome. Coexistence only for solutions with initial conditions on the separatrix (a set of measure zero).	and	$\lambda_{Si} < S^0$ and $\lambda_{Ri} < R^0$, $i = 1,2$ $\lambda_{S1}<\lambda_{S2}, \lambda_{R1}>\lambda_{R2}$ and $C_1 < T_* < C_2$ or $\lambda_{S1}>\lambda_{S2}, \lambda_{R1}<\lambda_{R2}$ and $C_1 > T^* > C_2$

$$(2.16)\quad \begin{cases} x_i'(t) = x_i(t)\left(-D + f_i\left(S^0 - \frac{x_1(t)}{y_{S1}} - \frac{x_2(t)}{y_{S2}},\ R^0 - \frac{x_1(t)}{y_{R1}} - \frac{x_2(t)}{y_{2R}}\right)\right), \\ \qquad i = 1,2 \\ x_{i0} > 0 \quad i = 1,2\,; \quad \frac{x_{10}}{y_{S1}} + \frac{x_{20}}{y_{S2}} \le S^0\,; \quad \frac{x_{10}}{y_{R1}} + \frac{x_{20}}{y_{R2}} \le R^0\,; \end{cases}$$

coupled with

$$(2.17)\quad S(t) = S^0 - \frac{x_1(t)}{y_{S1}} - \frac{x_2(t)}{y_{S2}}; \qquad R(t) = R^0 - \frac{x_1(t)}{y_{R1}} - \frac{x_2(t)}{y_{R2}},$$

and (2.16) is a two-dimensional competitive system. Hirsch's results for two-dimensional competitive systems depend on Kamke's comparison theorem which requires only monotone behaviour with respect to the appropriate variables. Viewing the system this way it is not surprising that the biological outcomes of the two resource model can be compared with the outcomes of the classical model of Verhulst [79] for two-species competition with constant carrying capacity. These outcomes with corresponding competitive criteria are compared in Table 4.2 of Waltman, Hubbell and Hsu [81].

We use a more elementary approach, one similar to the approach used in Chapter II, to show that the dynamics are trivial. This approach also gives more information about the behaviour of solutions on the triangle M, and will be employed when we consider non-monotone uptake functions in a later section.

We shall require the following notation:

$$(2.18)\qquad B_i = \{(S,R) : S > \lambda_{Si} \text{ and } R > \lambda_{Ri}\}, \quad i = 1,2.$$

(2.19) $$Q = \bigcup_{i=1}^{2} B_i .$$

(2.20) $$K = \bigcap_{i=1}^{2} B_i .$$

Therefore,

$$f_i(S,R) > D \quad \text{if} \quad (S,R) \in B_i ,$$

$$f_i(S,R) < D \quad \text{if} \quad (S,R) \notin \mathrm{c}\ell\ B_i ,$$

$$\text{and} \quad f_i(S,R) = D \quad \text{if} \quad (S,R) \in \partial B_i .$$

Here Q can be thought of as an analogue of the Q defined in Chapter II and parts (i) and (ii) of the following lemma can be viewed as an analogue of Lemma II.4.4. The lemma is illustrated in Figure 3.

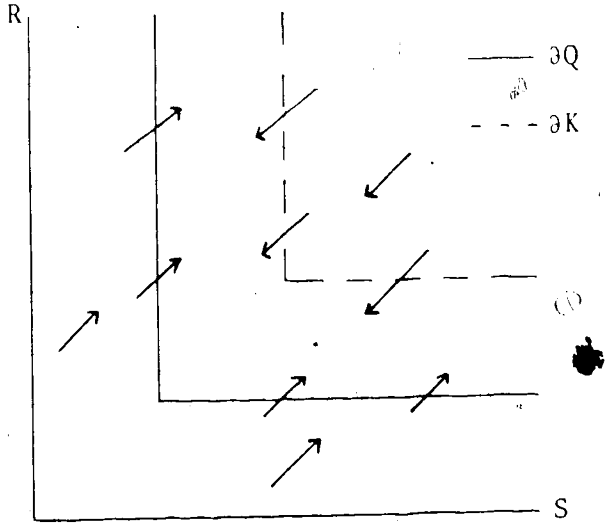
Lemma 2.1. Let $(S(t),R(t),x_1(t),x_2(t))$ be a solution of (2.1) with initial conditions restricted to M. (Note that this still implies that $x_{i0} > 0$, $i = 1,2$.)

(i) If there exists $\tau \geq 0$ with $(S(\tau),R(\tau)) \in \partial Q \setminus \partial K$ then $S'(\tau) > 0$ and $R'(\tau) > 0$.

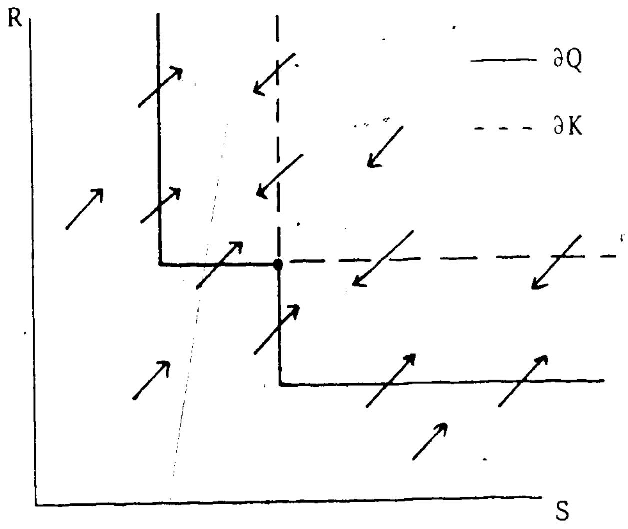
(ii) If there exists $\tau \geq 0$ with $(S(\tau),R(\tau)) \in \partial Q \cap \partial K$ then $(S(\tau),R(\tau),x_1(\tau),x_2(\tau))$ is an equilibrium for (2.1) and so $S'(\tau) = 0 = R'(\tau)$.

(iii) If there exists $\tau \geq 0$ with $(S(\tau),R(\tau)) \in \partial K \setminus \partial Q$ then $S'(\tau) < 0$ and $R'(\tau) < 0$.

(iv) If there exists $\tau \geq 0$ with $(S(\tau),R(\tau)) \in \mathbf{R}_+^4 \setminus \mathrm{c}\ell\ Q$ then



(a) $\lambda_{S1} < \lambda_{S2}$ and $\lambda_{R1} < \lambda_{R2}$
or
$\lambda_{S1} > \lambda_{S2}$ and $\lambda_{R1} > \lambda_{R2}$



(b) $\lambda_{S1} < \lambda_{S2}$ and $\lambda_{R1} > \lambda_{R2}$
or
$\lambda_{S1} > \lambda_{S2}$ and $\lambda_{R1} < \lambda_{R2}$

FIGURE 3 Dynamics on $\mathcal{M}$ are Trivial

$S'(\tau) > 0$ and $R'(\tau) > 0$.

(v) If there exists $\tau \geq 0$ with $(S(\tau),R(\tau)) \in K$ then $S'(\tau) < 0$ and $R'(\tau) < 0$.

Proof: (i) If $(S(\tau),R(\tau)) \in \partial Q \setminus \partial K$, since $x_i'(t) = x_i(t)(-D + f_i(S(t),R(t)))$ $i = 1,2$ either $x_1'(\tau) = 0$ and $x_2'(\tau) < 0$ or $x_1'(\tau) < 0$ and $x_2'(\tau) = 0$. The result follows by (2.7).

(ii) If $(S(\tau),R(\tau)) \in \partial Q \cap \partial K$ then $x_1'(\tau) = x_2'(\tau) = 0$. By (2.7) and (2.13) it follows that $S'(\tau) = R'(\tau) = 0$ and we are at an equilibrium.

(iii), (iv) and (v) are proved similarly. □

The next lemma is the analogue of Lemma II.4.5 and is also illustrated in Figure 3. It follows immediately from Lemma 2.1.

Lemma 2.2. Let $(S(t),R(t),x_1(t),x_2(t))$ be a solution of (2.1) with initial conditions in M. For all sufficiently large t precisely one of the following holds:

(i) $(S(t),R(t)) \in \mathbf{R}_+^4 \setminus c\ell\, Q$,

(ii) $(S(t),R(t)) \in K$,

(iii) $(S(t),R(t)) \in Q \setminus c\ell\, K$,

or (iv) $(S(t),R(t)) \in \partial Q \cap \partial K$.

Theorem 2.3. The dynamics of (2.1) with initial conditions restricted to M are trivial.

Proof: Let $\gamma(t) = (S(t),R(t),x_1(t),x_2(t))$ be a solution of (2.1) with initial conditions in M. Then for all sufficiently large t

precisely one of the options of Lemma 2.2 holds. Recall that on M

$$S(t) + \frac{x_1(t)}{y_{S1}} + \frac{x_2(t)}{y_{S2}} = S^0$$

(2.21) and

$$R(t) + \frac{x_1(t)}{y_{R1}} + \frac{x_2(t)}{y_{R2}} = R^0 .$$

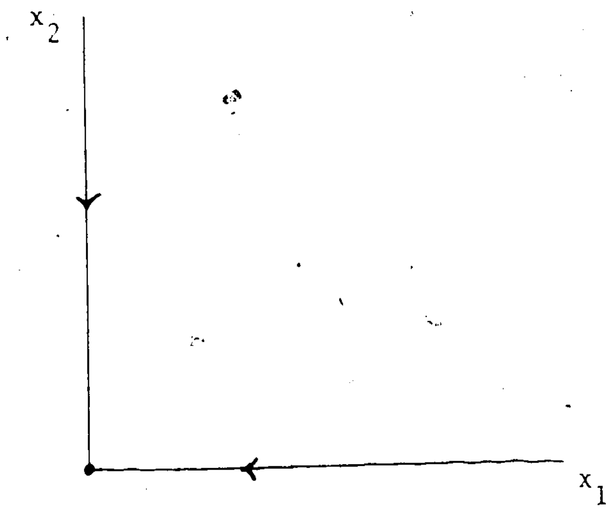
If option (i) holds, i.e. $(S(t),R(t)) \in \mathbb{R}^4_+ \setminus c\ell\, Q$ for all large t, then $x_1'(t) < 0$ and $x_2'(t) < 0$ for all large t since $x_i'(t) = x_i(t)(-D + f_i(S(t),R(t)))$, $x_i(t) > 0$ for all $t \geq 0$ and $S(t) < \min(\lambda_{S1},\lambda_{S2})$ and $R(t) < \min(\lambda_{R1},\lambda_{R2})$ for all large t. Since solutions are bounded, the monotonicity of $x_1(t)$ and $x_2(t)$ for large t implies convergence and hence by (2.21) $S(t)$ and $R(t)$ also converge.

If option (ii) or (iii) holds the proof is similar.

If option (iv) holds the result follows by Lemma 2.1 (ii). □

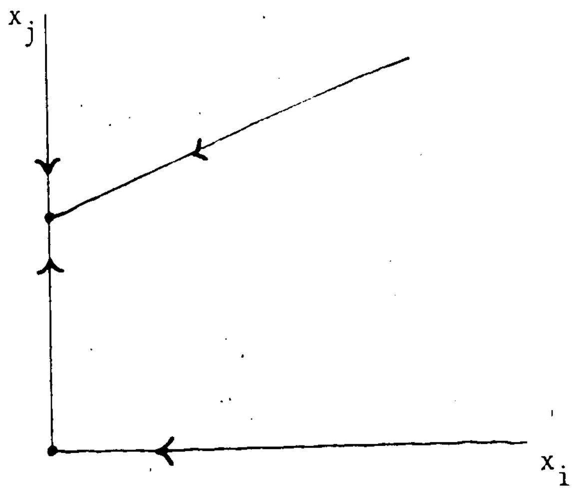
Next we consider system (2.16)-(2.17). This system is equivalent to system (2.1) with initial conditions restricted to M. We do a phase plane analysis of (2.16) in (x_1,x_2)-space based on the information summarized in Table II in order to show that no saddle connections are possible and hence the dynamics of (2.1) are trivial.

If we allow $\lambda_{Si} > S^0$ or $\lambda_{Ri} > R^0$ for $i = 1$ or 2 then there is no equilibrium for which the concentration of x_i is positive and hence there is competition-independent extinction of x_i. See Figure 4 (a-b). Figure 4(a) corresponds to the first biological outcome of Table III. Figure 4(b) corresponds to the second and third biological outcomes.



(a) $\lambda_{Si} > S^0$ and $\lambda_{Ri} > R^0$, $i = 1,2$.

Each population dies out even in the the absence of its competitor.



(b) $\lambda_{Si} > S^0$ or $\lambda_{Ri} > R^0$, $i = 1$ or 2

$\lambda_{Sj} < S^0$ and $\lambda_{Rj} < R^0$, $j = 1$ or 2, $j \neq i$

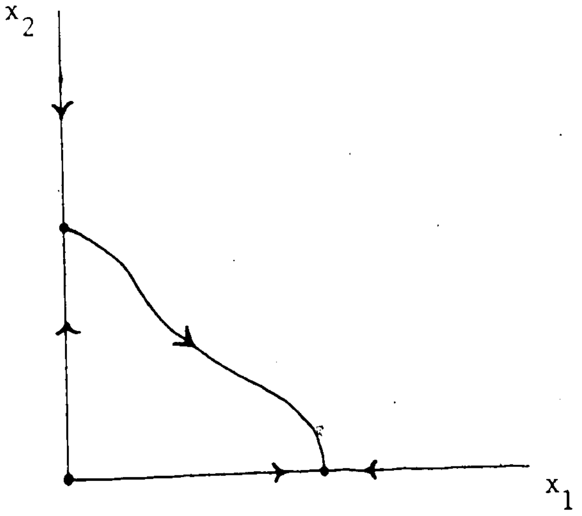
Population x_i dies out even in the absence of its competitor.

FIGURE 4 Competition-Independent Extinction

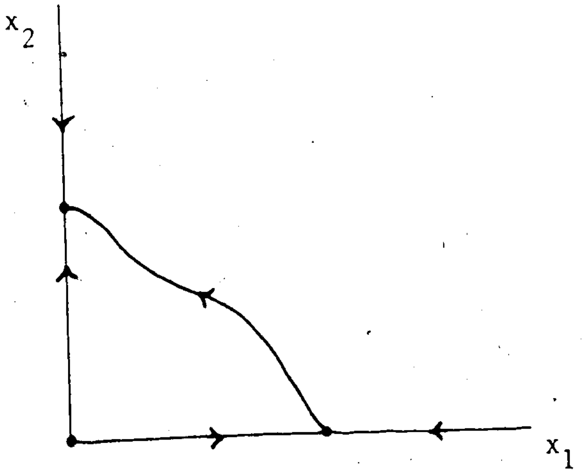
If we assume that $\lambda_{Si} < S^0$ and $\lambda_{Ri} < R^0$, $i = 1,2$ then there are only 4 basic pictures (since we are assuming $C_1 \neq C_2$) (see Figure 5 (a-d)). On M Figure 5(a) corresponds to the second biological outcome of Table III, Figure 5(b) to the third biological outcome, Figure 5(c) to the fourth and Figure 5(d) to the fifth. Clearly there are no saddle connections. We have therefore proved

Theorem 2.4. The dynamics of (2.1) are trivial.

Finally we note that by considering the location of the stable manifolds of the critical points on $\partial \mathbb{R}^4_+$ it follows that for the particular parameter ranges described in Table III, solutions of (2.1) (i.e. solutions with initial conditions in the positive cone) have the same type of asymptotic behaviour as solutions with initial conditions in the relative interior of M. Hence we have shown that Table III applies globally.

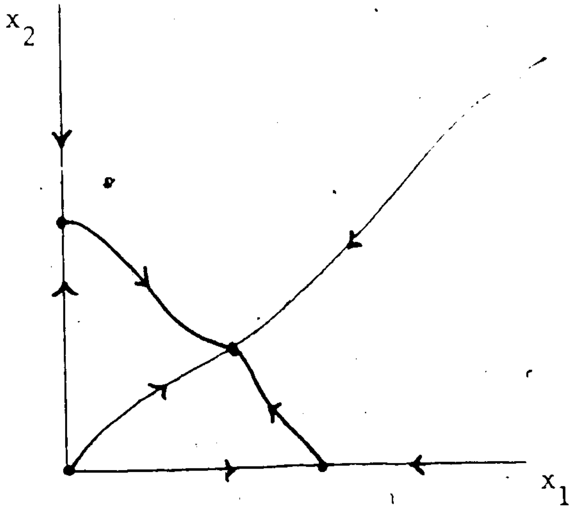


(a) Population 1 always wins.

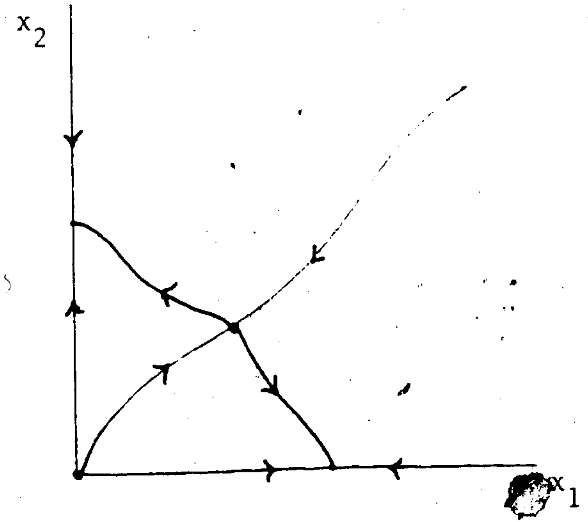


(b) Population 2 always wins.

FIGURE 5 (a-b)



(c) Populations 1 and 2 coexist at a globally asymptotically stable interior equilibrium.



(d) Initial concentrations determine the outcome. One population wins, the other dies out, except for solutions with initial conditions on the separatrix.

FIGURE 5 Phase Portraits in (x_1,x_2)-Space for (2.1) Assuming $\lambda_{Si} < S^0$ and $\lambda_{Ri} < R^0$, $i = 1,2$.

3. THE MODEL - GENERAL KINETICS. We continue to study exploitative competition for two purely complementary resources. This section differs from the previous section in that we now allow the resources to be inhibitory at high concentrations. We make the same basic assumptions we made for model (2.1) of the previous section and use the same notation. In particular, in the previous section we assume that growth rates adjust instantaneously to changes in resource concentration, that functions $p_i(S)$ (resp. $q_i(R)$) represent per capita growth rate of the *i*th population when resource S (resp. resource R) is limiting, and that resource consumption rates and growth rates are proportional. Recall that for complementary resources S and R, a population is considered S-limited if its per capita consumption rate is independent of the concentration of R and is considered R-limited if its per capita consumption rate is independent of the concentration of S. In the context of model (3.1) below, a population can be limited by a resource either because that resource is in short supply or because it is overabundant.

The model we study in this section is:

$$S'(t) = \left(S^0 - S(t)\right)D - \sum_{i=1}^{2} \frac{x_i(t)}{y_{Si}} f_i\left(S(t),R(t)\right),$$

$$R'(t) = \left(R^0 - R(t)\right)D - \sum_{i=1}^{2} \frac{x_i(t)}{y_{Ri}} f_i\left(S(t),R(t)\right)$$

$$(3.1) \qquad x_i'(t) = x_i(t)\left(-D + f_i(S(t),R(t))\right), \quad i = 1,2,$$

$$S(0) = S_0 \geq 0, \quad R(0) = R_0 \geq 0, \quad x_i(0) = x_{i0} > 0,$$

$$i = 1, 2,$$

where

$$f_i(S(t),R(t)) = \min(p_i(S(t)) , q_i(R(t))), \quad i = 1 , 2 ,$$

and

$$p_i \text{ and } q_i \text{ satisfy assumptions } (2.2) - (2.4).$$

It is the same as model (2.1) except that we replace the monotonicity assumptions (2.5) on p_i and q_i by the following assumption.

(3.2) There exist uniquely defined extended positive real numbers λ_{Si}, λ_{Ri}, μ_{Si} and μ_{Ri}, $i = 1 , 2$ with $\lambda_{Si} \leq \mu_{Si}$ and $\lambda_{Ri} \leq \mu_{Ri}$ such that:

$$p_i(S) < D \text{ if } S \notin [\lambda_{Si} , \mu_{Si}] ,$$

$$p_i(S) > D \text{ if } S \in (\lambda_{Si} , \mu_{Si}) ,$$

$$q_i(R) < D \text{ if } R \notin [\lambda_{Ri} , \mu_{Ri}] ,$$

$$q_i(R) > D \text{ if } R \in (\lambda_{Ri} , \mu_{Ri}) .$$

We make the following generic assumptions:

(3.3) If λ_{Si} (resp. λ_{Ri}, μ_{Si}, μ_{Ri}) is finite then

$$p_i'(\lambda_{Si}) \neq 0 \quad (\text{resp. } q_i'(\lambda_{Ri}) \neq 0,\ p_i'(\mu_{Si}) \neq 0,\ q_i'(\mu_{Ri}) \neq 0).$$

If the parameters are finite we assume

$$(3.4) \begin{cases} \lambda_{S1}, \lambda_{S2}, \mu_{S1} \text{ and } \mu_{S2} \text{ are distinct from each other and from } S^0 . \\ \lambda_{R1}, \lambda_{R2}, \mu_{R1} \text{ and } \mu_{R2} \text{ are distinct from each other and from } R^0 . \end{cases}$$

(3.5) If $(\bar{S},\bar{R},\bar{x}_1,\bar{x}_2)$ is a critical point, then $p_i(\bar{S}) \neq q_i(\bar{R})$, $i = 1,2$.

We shall also require the following notation:

(3.6) $\mathcal{B}_i = \{(S,R) : \lambda_{Si} < S < \mu_{Si}$ and $\lambda_{Ri} < R < \mu_{Ri}\}$, $i = 1,2$.

(3.7) $$Q = \bigcup_{i=1}^{2} \mathcal{B}_i .$$

(3.8) $$K = \bigcap_{i=1}^{2} \mathcal{B}_i .$$

Therefore,

$$f_i(S,R) > D \quad \text{if} \quad (S,R) \in \mathcal{B}_i ,$$

$$f_i(S,R) < D \quad \text{if} \quad (S,R) \notin \mathrm{c}\ell\, \mathcal{B}_i ,$$

$$\text{and} \quad f_i(S,R) = D \quad \text{if} \quad (S,R) \in \partial\mathcal{B}_i .$$

Again, as one expects from the biology, solutions of (3.1) are positive and bounded. (The proof is similar to the proof of Theorem II.3.1.) Also, the polygonal set

(3.9) $$M = \left\{(S,R,x_1,x_2) \in \mathbf{R}_+^4 : S + \frac{x_1}{y_{S1}} + \frac{x_2}{y_{S2}} = S^0 \text{ and } R + \frac{x_1}{y_{R1}} + \frac{x_2}{y_{R2}} = R^0\right\}$$

is a global attractor for (3.1) and as in Section 2, on M solutions satisfy:

(3.10) $$S'(t) + \sum_{i=1}^{2} x_i'(t)/y_{Si} = 0$$

and

$$R'(t) + \sum_{i=1}^{2} x_i'(t)/y_{Ri} = 0 .$$

However, even if at high concentrations, only one resource is inhibitory to only one of the competitors, Lemma 2.2 need not hold, and the dynamics need not be trivial. For example, the existence of a nontrivial, orbitally asymptotically stable periodic orbit for model (3.1) is possible. In this case the concentrations of the resources and of the competitors oscillate indefinitely.

Before we consider examples that illustrate this oscillatory behaviour, we give a table of useful notation (see Table IV), a table of notation for the critical points (see Table V) and a table summarizing criteria for the existence and stability of these critical points (see Table VI). We then give sufficient conditions that guarantee that the dynamics of (3.1) are trivial.

To ensure that the vector field at, and in a neighbourhood of, each critical point is C^1 we made assumption (3.5). In terms of the notation in Table IV, assumption (3.5) implies that

(3.11) T_i, W_i, V_i and U_i are all distinct from C_i, $i = 1,2$.

We also assume that

(3.12) $$C_1 \neq C_2$$

and

(3.13) T_*, T^*, W_*, W^*, V_*, V^*, U_* and U^* are distinct from C_1 and C_2.

This ensures that the critical points are isolated and together with assumptions (3.3) and (3.4) ensures that for each critical point, none of the eigenvalues of the associated matrix of the linearization equals zero.

TABLE IV

USEFUL NOTATION FOR (3.1)

$$C_i = y_{Si}/y_{Ri}, \qquad i = 1,2,$$

$$T_i = \frac{R^0-\lambda_{Ri}}{S^0-\lambda_{Si}}, \qquad i = 1,2, \qquad T^* = \frac{R^0-\lambda_{R2}}{S^0-\lambda_{S1}}, \qquad T_* = \frac{R^0-\lambda_{R1}}{S^0-\lambda_{S2}}$$

$$V_i = \frac{R^0-\mu_{Ri}}{S^0-\mu_{Si}}, \qquad i = 1,2, \qquad V^* = \frac{R^0-\mu_{R2}}{S^0-\mu_{S1}}, \qquad V_* = \frac{R^0-\mu_{R1}}{S^0-\mu_{S2}}$$

$$U_i = \frac{R^0-\lambda_{Ri}}{S^0-\mu_{Si}}, \qquad i = 1,2, \qquad U^* = \frac{R^0-\lambda_{R2}}{S^0-\mu_{S1}}, \qquad U_* = \frac{R^0-\lambda_{R1}}{S^0-\mu_{S2}}$$

$$W_i = \frac{R^0-\mu_{Ri}}{S^0-\lambda_{Si}}, \qquad i = 1,2, \qquad W^* = \frac{R^0-\mu_{R2}}{S^0-\lambda_{S1}}, \qquad W_* = \frac{R^0-\mu_{R1}}{S^0-\lambda_{S2}}$$

TABLE V

NOTATION FOR THE CRITICAL POINTS OF (3.1)

NOTATION		†CRITICAL POINT (provided it lies in $\mathbb{R}^4_+$)
$E_{\mu_{S1},*}$	=	$(\mu_{S1}, R^0 - C_1(S^0-\mu_{S1}), y_{S1}(S^0-\mu_{S1}), 0)$
$E_{*,\mu_{R1}}$	=	$(S^0 - (R^0-\mu_{R1})/C_1, \mu_{R1}, y_{R1}(R^0-\mu_{R1}), 0)$
$E_{\mu_{S2},*}$	=	$(\mu_{S2}, R^0 - C_2(S^0-\mu_{S2}), 0, y_{S2}(S^0-\mu_{S2}))$
$E_{*,\mu_{R2}}$	=	$(S^0 - (R^0-\mu_{R2})/C_2, \mu_{R2}, 0, y_{R2}(R^0-\mu_{R2}))$
$E_{\gamma,\eta}$	=	$(\gamma, \eta, x_1^*, x_2^*)$

$$\text{where} \quad x_1^* = y_{S1}y_{R1}\left(\frac{y_{S2}(S^0-\gamma) - y_{R2}(R^0-\eta)}{y_{R1}y_{S2} - y_{S1}y_{R2}}\right),$$

$$x_2^* = y_{S2}y_{R2}\left(\frac{y_{R1}(R^0-\eta) - y_{S1}(S^0-\gamma)}{y_{R1}y_{S2} - y_{S1}y_{R2}}\right),$$

and $\gamma, \eta = \lambda_{S1}, \lambda_{R2};\ \lambda_{S2}, \lambda_{R1};\ \mu_{S1}, \lambda_{R2};\ \mu_{S2}, \lambda_{R1};$
$\lambda_{S1}, \mu_{R2};\ \lambda_{S2}, \mu_{R1};\ \mu_{S1}, \mu_{R2};\ \mu_{S2}, \mu_{R1}.$

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†E_{S^0,R^0}, $E_{\lambda_{S1},*}$, $E_{*,\lambda_{R1}}$, $E_{\lambda_{S2},*}$ and $E_{*,\lambda_{R2}}$ as defined in Table I are also critical points of (3.1) provided they lie in $\mathbb{R}^4_+$.

TABLE VI

EXISTENCE AND STABILITY CRITERIA FOR CRITICAL POINTS OF (3.1)

CRITICAL POINT	CRITERIA FOR EXISTENCE	CRITERIA FOR ASYMPTOTIC STABILITY
E_{S^0,R^0}	always exists	$(\lambda_{S1} > S^0$ or $\lambda_{R1} > R^0$ or $\mu_{S1} < S^0$ or $\mu_{R1} < R^0)$ and $(\lambda_{S2} > S^0$ or $\lambda_{R2} > R^0$ or $\mu_{S2} < S^0$ or $\mu_{R2} < R^0)$
$E_{\lambda_{S1},*}$	$\lambda_{S1} < S^0$, $T_1 > C_1$ and $W_1 < C_1$	$\lambda_{S1} < \lambda_{S2}$ or $\lambda_{S1} > \mu_{S2}$ or $T^* < C_1$ or $W^* > C_1$
$E_{*,\lambda_{R1}}$	$\lambda_{R1} < R^0$, $\lambda_{S1} < S^0$ and $T_1 < C_1$ and if $\mu_{S1} < S^0$ then $C_1 < U_1$	$\lambda_{R1} < \lambda_{R2}$ or $\lambda_{R1} > \mu_{R2}$ or $(C_1 < T_*$ and $\lambda_{S2} < S^0)$ or $\lambda_{S2} > S^0$ or $(C_1 > U_*$ and $\mu_{S2} < S^0)$
$E_{\lambda_{S2},*}$	$\lambda_{S2} < S^0$, $T_2 > C_2$ and $W_2 < C_2$	$\lambda_{S2} < \lambda_{S1}$ or $\lambda_{S2} > \mu_{S1}$ or $T_* < C_2$ or $W_* > C_2$
$E_{*,\lambda_{R2}}$	$\lambda_{R2} < R^0$, $\lambda_{S2} < S^0$ and $T_2 < C_2$ and if $\mu_{S2} < S^0$ then $C_2 < U_2$	$\lambda_{R2} < \lambda_{R1}$ or $\lambda_{R2} > \mu_{R1}$ or $(C_2 < T^*$ and $\lambda_{S1} < S^0)$ or $\lambda_{S1} > S^0$ or $(C_2 > U^*$ and $\mu_{S1} < S^0)$

TABLE VI-(Continued)

EXISTENCE AND STABILITY CRITERIA FOR CRITICAL POINTS OF (3.1)

CRITICAL POINT	CRITERIA FOR EXISTENCE	CRITERIA FOR ASYMPTOTIC STABILITY
$E_{\mu_{S1},*}$	$\mu_{S1} < S^0$, $V_1 < C_1$ and $U_1 > C_1$	always unstable
$E_{*,\mu_{R1}}$	$\mu_{R1} < R^0$, $\lambda_{S1} < S^0$ and $W_1 < C_1$ and if $\mu_{S1} < S^0$ then $C_1 < V_1$	always unstable
$E_{\mu_{S2},*}$	$\mu_{S2} < S^0$, $V_2 < C_2$ and $U_2 > C_2$	always unstable
$E_{*,\mu_{R2}}$	$\mu_{R2} < R^0$, $\lambda_{S2} < S^0$ and $W_2 < C_2$ and if $\mu_{S2} < S^0$ then $C_2 < V_2$	always unstable
$E_{\lambda_{S1},\lambda_{R2}}$	$(\lambda_{S2}<\lambda_{S1}<\mu_{S2})$ and $(\lambda_{R1}<\lambda_{R2}<\mu_{R1})$ and $\begin{pmatrix} C_1 < T^* < C_2 & \text{and} & \lambda_{S1} < S^0 \\ & \text{or} & \\ C_1 > T^* > C_2 & \text{and} & \lambda_{S1} < S^0 \end{pmatrix}$	$C_1 < C_2$
$E_{\lambda_{S2},\lambda_{R1}}$	$(\lambda_{S1}<\lambda_{S2}<\mu_{S1})$ and $(\lambda_{R2}<\lambda_{R1}<\mu_{R2})$ and $\begin{pmatrix} C_1 < T_* < C_2 & \text{and} & \lambda_{S2} < S^0 \\ & \text{or} & \\ C_1 > T_* > C_2 & \text{and} & \lambda_{S2} < S^0 \end{pmatrix}$	$C_1 > C_2$
$E_{\mu_{S1},\lambda_{R2}}$	$(\lambda_{S2}<\mu_{S1}<\mu_{S2})$ and $(\lambda_{R1}<\lambda_{R2}<\mu_{R1})$ and $\begin{pmatrix} C_1 < U^* < C_2 & \text{and} & \mu_{S1} < S^0 \\ & \text{or} & \\ C_1 > U^* > C_2 & \text{and} & \mu_{S1} < S^0 \end{pmatrix}$	$**$

TABLE VI (Continued)

EXISTENCE AND STABILITY CRITERIA FOR CRITICAL POINTS OF (3.1)

CRITICAL POINT	CRITERIA FOR EXISTENCE	CRITERIA FOR ASYMPTOTIC STABILITY
$E_{\mu_{S2},\lambda_{R1}}$	$(\lambda_{S1}<\mu_{S2}<\mu_{S1})$ and $(\lambda_{R2}<\lambda_{R1}<\mu_{R2})$ and $\begin{pmatrix} C_1 < U_* < C_2 & \text{and} & \mu_{S2} < S^0 \\ & \text{or} & \\ C_1 > U_* > C_2 & \text{and} & \mu_{S2} < S^0 \end{pmatrix}$	**
$E_{\lambda_{S1},\mu_{R2}}$	$(\lambda_{S2}<\lambda_{S1}<\lambda_{S2})$ and $(\lambda_{R1}<\mu_{R2}<\mu_{R1})$ and $\begin{pmatrix} C_1 < W^* < C_2 & \text{and} & \lambda_{S1} < S^0 \\ & \text{or} & \\ C_1 > W^* > C_2 & \text{and} & \lambda_{S1} < S^0 \end{pmatrix}$	**
$E_{\lambda_{S2},\mu_{R1}}$	$(\lambda_{S1}<\lambda_{S2}<\mu_{S1})$ and $(\lambda_{R2}<\mu_{R1}<\mu_{R2})$ and $\begin{pmatrix} C_1 < W_* < C_2 & \text{and} & \lambda_{S2} < S^0 \\ & \text{or} & \\ C_1 > W_* > C_2 & \text{and} & \lambda_{S2} < S^0 \end{pmatrix}$	**
$E_{\mu_{S1},\mu_{R2}}$	$(\lambda_{S2}<\mu_{S1}<\mu_{S2})$ and $(\lambda_{R1}<\mu_{R2}<\mu_{R1})$ and $\begin{pmatrix} C_1 < V^* < C_2 & \text{and} & \mu_{S1} < S^0 \\ & \text{or} & \\ C_1 > V^* > C_2 & \text{and} & \mu_{S1} < S^0 \end{pmatrix}$	always unstable†
$E_{\mu_{S2},\mu_{R1}}$	$(\lambda_{S1}<\mu_{S2}<\mu_{S1})$ and $(\lambda_{R2}<\mu_{R1}<\mu_{R2})$ and $\begin{pmatrix} C_1 < V_* < C_2 & \text{and} & \mu_{S2} < S^0 \\ & \text{or} & \\ C_1 > V_* > C_2 & \text{and} & \mu_{S2} < S^0 \end{pmatrix}$	always unstable†

** Stability depends on the sign of the real part of the roots of the characteristic equation:

$$\xi^2 - \xi\left(x_1^* \frac{\partial f_1}{\partial x_1} + x_2^* \frac{\partial f_2}{\partial x_2}\right) + x_1^* x_2^* \left(\frac{\partial f_1}{\partial x_1}\frac{\partial f_2}{\partial x_2} - \frac{\partial f_1}{\partial x_2}\frac{\partial f_2}{\partial x_1}\right) = 0$$

evaluated at the critical point.

† by phase plane analysis in (S,R)-space using Lemma 2.1.

Next we develop simple graphical criteria that, when satisfied, ensure that the dynamics are trivial. We adapt certain concepts and terminology frequently used in linear programming (see eg. Luenberger [51]). We also apply the techniques used in Section 2. In particular, Lemma 2.1 (see below) also holds for model (3.1) subject to considerations of feasibility, provided we replace Q by $\mathcal{Q}$ and K by $\mathcal{K}$.

We shall refer to M as the *feasible region.*

Definition 3.1. We define the *feasible region projected on* (S,R)*-space*, which we denote by F, as the set

$$(3.14)\qquad F = \left\{(S,R) \in \mathbf{R}^2_+ : S + \frac{x_1}{y_{S1}} + \frac{x_2}{y_{S2}} = S^0, \right.$$

$$\left. R + \frac{x_1}{y_{R1}} + \frac{x_2}{y_{R2}} = R^0, \quad x_1 \geq 0, \quad x_2 \geq 0 \right\}.$$

F is therefore the projection of M on (S,R)-space. Since we are assuming $C_1 \neq C_2$, for each pair $(\hat{S},\hat{R})$ with $\hat{S} \geq 0$ and $\hat{R} \geq 0$ there is at most one pair $(\hat{x}_1,\hat{x}_2)$ such that $(\hat{S},\hat{R},\hat{x}_1,\hat{x}_2) \in F$.

We point out here, that if $\big(S(t),R(t),x_1(t),x_2(t)\big)$ is a solution of (3.1) with initial conditions in M, then $\big(S(t),R(t)\big) \in F$ for all $t \geq 0$. Thus Lemma 2.1 only applies to points $\big(S(\tau),R(\tau)\big) \in F$ and therefore Figure 3 (in Section 2) is actually only valid for points in F.

Again adopting the terminology of linear programming, we give

Definition 3.2. A *basic feasible solution of* M is a point

$(S,R,x_1,x_2) \in M$ with at least two components equal to zero.

Definition 3.3. A *basic feasible solution of* F is a point (S,R) such that (S,R,x_1,x_2) is a basic feasible solution of M.

We generate the $C_2^4 = 6$ possible basic feasible solutions of M and therefore of F in Appendix 4 and we summarize the results in Table VII.

It is well known from the theory of linear programming that M is precisely the closed convex hull of the set of all basic feasible solutions of M and so F is the closed convex hull of all basic feasible solutions of F. See Figure 6 for examples of F.

It is interesting to note that the feasible region depends only on the yield factors y_{Si} and y_{Ri} and the concentrations S^0 and R^0 of S and R in the feed bottle. Since S^0 and R^0 are easily controlled by the experimenter the shape of the feasible region can be controlled and as we shall see this implies that the experimenter has a lot of control over which critical points lie in the feasible region.

Using this idea of the feasible region, we are able to graphically determine whether a critical point exists or not. In order to do this we need the following notation. For each $i = 1,2$, that portion of ∂F which corresponds to the portion of ∂M along which $x_i = 0$ we call F_i. We also define

$$G = \partial B_1 \cap \partial B_2 \cap \text{int } F. \tag{3.15}$$

Lemma 3.4. (i) The set of all critical points in $\mathbb{R}_+^4$ is the set of all points in M for which the projection onto (S,R)-space belongs to the set $(\partial B_1 \cap F_2) \cup (\partial B_2 \cap F_1) \cup \{(S^0,R^0)\} \cup G$.

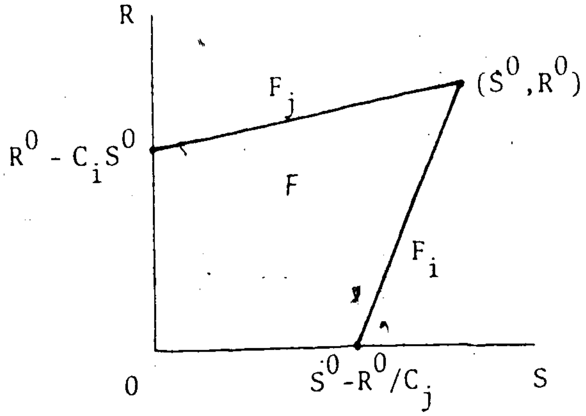
TABLE VII

BASIC FEASIBLE SOLUTIONS

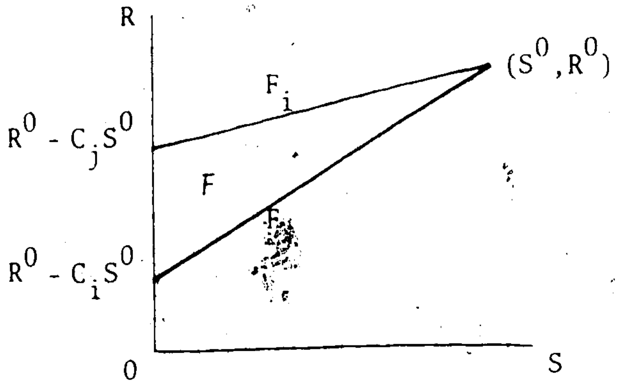
BASIC FEASIBLE SOLUTIONS OF M	BASIC FEASIBLE SOLUTIONS OF F	CRITERIA FOR EXISTENCE
$(S^0,R^0,0,0)$	(S^0,R^0)	always exists
$(0,R^0-C_1S^0,y_{S1}S^0,0)$	$(0,R^0-C_1S^0)$	$R^0/S^0 \geq C_1$
$(S^0-R^0/C_1,0,y_{R1},0)$	$(S^0-R^0/C_1,0)$	$R^0/S^0 \leq C_1$
$(0,R^0-C_2S^0,0,y_{S2}S^0)$	$(0,R^0-C_2S^0)$	$R^0/S^0 \geq C_2$
$(S^0-R^0/C_2,0,y_{R2}R^0,0)$	$(S^0-R^0/C_2,0)$	$R^0/S^0 \leq C_2$
$(0,0,\dagger,\Delta)$	$(0,0)$	$C_1 \leq R^0/S^0 \leq C_2$ or $C_2 \leq R^0/S^0 \leq C_1$

$\dagger = y_{S1}y_{R1}(y_{S2}S^0 - y_{R2}R^0)/(y_{S2}y_{R1} - y_{S1}y_{R2})$

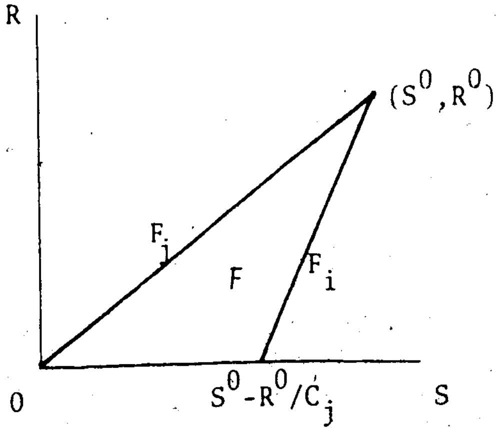
$\Delta = y_{S2}y_{R2}(y_{R1}R^0 - y_{S1}S^0)/(y_{S2}y_{R1} - y_{S1}y_{R2})$



(a) $C_i < R^0/S^0 < C_j$, $i = 1$ or 2, $j = 1$ or 2, $i \neq j$



(b) $R^0/S^0 > C_i > C_j$, $i = 1$ or 2, $j = 1$ or 2, $i \neq j$



(c) $C_i = R^0/S^0 < C_j$

FIGURE 6 Examples of the Feasible Region Projected on (S,R)-Space, F

(ii) The set of all interior critical points in $\mathbf{R}_+^4$ is the set of all points in M for which the projection onto (S,R)-space belongs to the set G.

(iii) The set of all boundary critical points in $\mathbf{R}_+^4$ is the set of all points in M for which the projection onto (S,R)-space belongs to the set

$$(\partial B_1 \cap F_2) \cup (\partial B_2 \cap F_1) \cup \{(S^0,R^0)\}.$$

<u>Proof:</u> The proof is obvious (and the result holds even if $C_1 = C_2$ in which case more than one point of M may correspond to a point in F and so the critical points would not be isolated). □

The application of Lemma 3.4 is illustrated in Figure 7. Although, in Table VI we see that there are seventeen possible critical points, from this lemma it follows that for any particular example there can be no more than nine critical points (see Figure 7(d)) and even as few as one critical point (see Figure 7(c)).

We are now ready to give a sufficient condition that ensures that the dynamics of (3.1) are trivial.

<u>Theorem 3.5.</u> If

$$(3.16) \quad G \cap \{(\lambda_{S1},\mu_{R2}), (\lambda_{S2},\mu_{R1}), (\mu_{S1},\lambda_{R2}), (\mu_{S2},\lambda_{R1})\} = \emptyset$$

then the dynamics of (3.1) are trivial.

(See Figure 7(a),(b) and (c) for examples of when this theorem applies. Note also that at most two of the four points in brackets in (3.16) can intersect G in any particular example.)

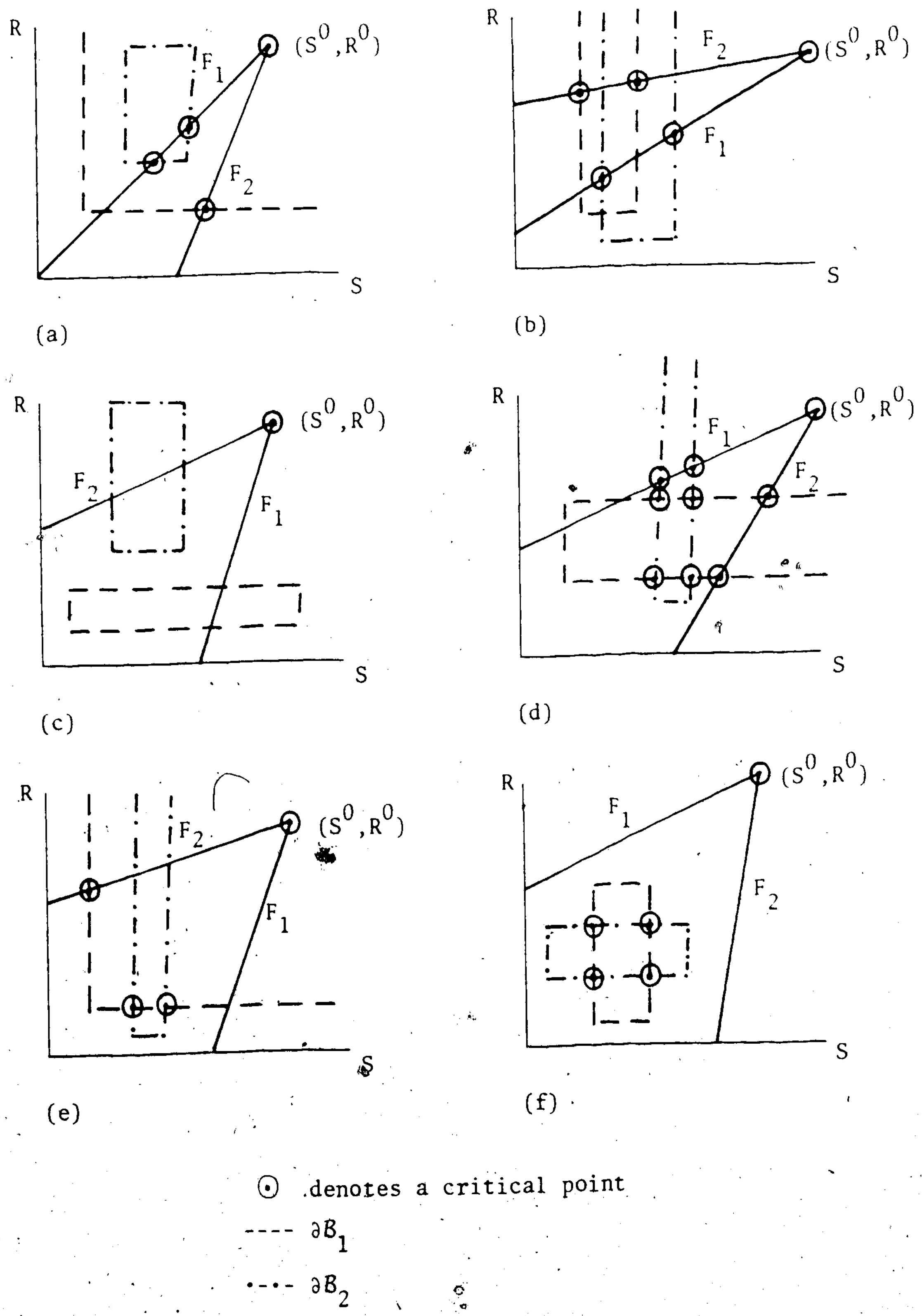


FIGURE 7 Examples of the Graphical Method of Determining Critical Points

Proof: By the generic assumptions (3.3)-(3.5) and (3.11)-(3.13) it follows that the critical points are isolated, the vector field is C^1 at and in a neighbourhood of each critical point and the matrix of the linearization associated with each critical point never has an eigenvalue equal to zero.

First we show that the dynamics of (3.1) restricted to M are trivial. Note that (3.1) restricted to M is equivalent to the two dimensional system (2.16)-(2.17). Hypothesis (3.16) implies that the only candidates for interior critical points are of the form

$$(3.17) \qquad E_{\lambda_{Si},\lambda_{Rj}} \quad \text{and} \quad E_{\mu_{Sk},\mu_{R\ell}}$$

where $i,j,k,\ell = 1$ or 2 and $i \neq j$, $k \neq \ell$. In this case Lemma 2.1 can be used to show that Lemma 2.2 holds provided we replace Q and K by Q and K respectively. That the dynamics of (3.1) restricted to M are trivial now follows by a proof similar to the proof of Theorem 2.3.

To show that the dynamics of (3.1) are trivial, since M is globally attracting, and all solutions are bounded it suffices to show that the phase portrait of system (2.16) (in (x_1,x_2)-space) contains no saddle connections. If $G = \emptyset$, i.e. there are no interior critical points of (2.16) then clearly there can be no saddle connections since a saddle connection must contain a critical point in its interior. If $G \neq \emptyset$, the only interior critical points of (3.1) are of the form in (3.17) and hence system (2.16) can have at most two interior critical points. By index theory if both interior critical points of

(2.16) are a saddle points (or if there is a unique interior critical point, and it is a saddle point) then there are no saddle connections. To prove that the dynamics on M are trivial we showed that the competitor concentrations converge monotonely. The same method can be used to show that if we reverse time competitor concentrations either converge monotonely or leave $\mathbf{R}_+^4$. Therefore, under assumption (3.16), no interior critical point of (2.16) is a spiral. Since solutions in (x_1,x_2)-space are eventually monotone both in positive and in negative time, by the Poincaré-Bendixson Theorem and the generic nature of the critical points, there cannot be a unique unstable or a stable node inside a saddle connection and by index theory there cannot be precisely two nodes inside a saddle connection. Thus there can be no interior critical point(s) inside a saddle connection of (2.16) and so there can be no saddle connections. Therefore the dynamics of (3.1) are trivial. $\square$

As an immediate consequence of the previous two theorems we obtain the following result concerning the extinction of both competitors. The corollary is illustrated in Figure 8.

Corollary 3.6. If (i) $G = \emptyset$,

(ii) $\partial B_1 \cap F_2 = \emptyset$,

and (iii) $\partial B_2 \cap F_1 = \emptyset$,

then the critical point E_{S^0,R^0} is globally asymptotically stable for (3.1).

Proof: By Lemma 3.4, E_{S^0,R^0} is the only critical point of (3.1).

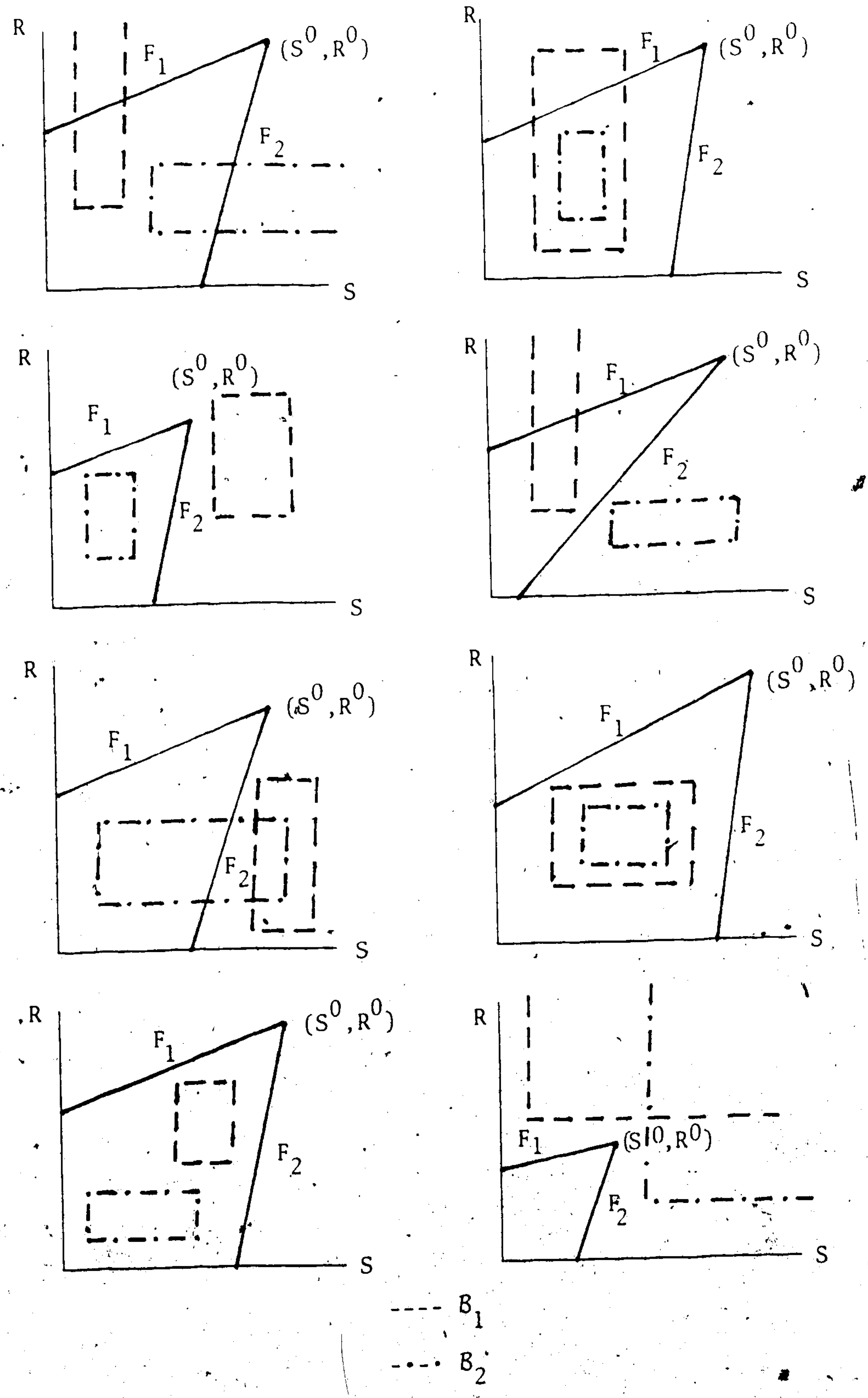


FIGURE 8 Examples of Competition-Independent Extinction

The result is immediate from Theorem 3.5 and the fact that all solutions are bounded.

□

Other immediate consequences of Lemma 3.4 and Theorem 3.5 are the following results concerning competition-independent extinction.

Corollary 3.7. Let $(S(t), R(t), x_1(t), x_2(t))$ be a solution of (3.1). If $B_i \cap F = \emptyset$, then $\lim_{t\to\infty} x_i(t) = 0$, $i = 1,2$.

Corollary 3.8. Let $(S(t), R(t), x_1(t), x_2(t))$ be a solution of (3.1). Assume $i, j = 1,2$, $i \neq j$, and $x_{j0} = 0$. (Therefore, $x_j(t) = 0$, for all t.) If $B_i \cap F_j = \emptyset$, then $\lim_{t\to\infty} x_i(t) = 0$.

This leads to a surprising result that seems to indicate that at times, the competitors are actually cooperating. There are situations in which in the absence of a rival each population would die out, but when a rival is present there is a possibility of coexistence. This is demonstrated in the following example and illustrated in Figure 9.

Example 3.9. Let

$$\lambda_{S1} = 2 \quad \lambda_{S2} = 3 \quad \mu_{S1} = 5 \quad \mu_{S2} = \infty$$

$$\lambda_{R1} = 4 \quad \lambda_{R2} = 2 \quad \mu_{R1} = \infty \quad \mu_{R2} = 9$$

$$S^0 = 20 \quad R^0 = 30 \quad D = 1$$

$$y_{S1} = 2 \quad y_{S2} = 1 \quad y_{R1} = 1 \quad y_{R2} = 1$$

If x_i is absent (i.e. $x_{i0} = 0$), then $\lim_{t\to\infty} x_j = 0$ where $i,j = 1,2$ and $i \neq j$. This follows from Corollary 3.8 (see Figure 9) since there are no critical points on the boundary except E_{S^0,R^0}. However,

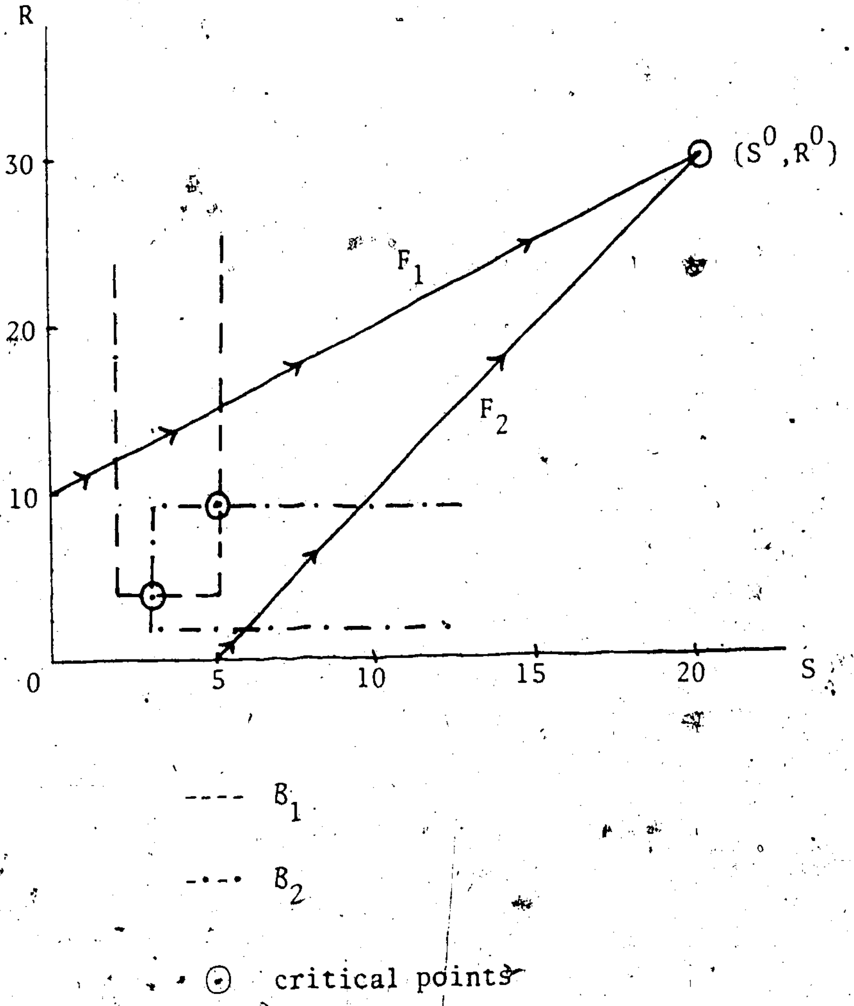


FIGURE 9 Cooperative Coexistence

the interior critical point $E_{\lambda_{S2},\lambda_{R1}}$ is asymptotically stable (see Table VI) since

$$1 = C_2 < T_* = \frac{26}{17} < C_1 = 2$$

and so there are initial conditions for which there is coexistence. This coexistence must in some sense be due to cooperation.

By Theorem 3.5 it follows that a necessary condition for (3.1) to have nontrivial dynamics is that there exist a critical point of the form given in (3.17), i.e. a critical point at which one competitor is S-limited and the other is R-limited and one competitor is limited because a resource is in short supply whereas the other is limited because a resource is overabundant and thus inhibitory.

We consider two examples that illustrate that (3.1) can have nontrivial dynamics. The functions in both examples are chosen purely for their mathematical convenience rather than for any biological significance.

In the first example, only one resource is inhibitory to only one population at high concentrations, in particular resource S is inhibitory to population 2 at high concentrations. All the other kinetics are monotone with microbial responses modelled by Michaelis-Menten kinetics.

Example 3.10. Let,

$$p_1(S) = \frac{5S}{8+S}$$

$$p_2(S) = 1 + \frac{(S - 4)(6 - S)}{24(A_1S^2 + 7/12\ S + 1)} = \frac{(24A_1 - 1)S^2 + 4S}{24A_1S^2 + 14S + 24}$$

$$q_1(R) = \frac{10R}{4 + 9R}$$

$$q_2(R) = \frac{5.1R}{8.2 + R}$$

$$D = 1,\quad S^0 = 40,\quad R^0 = 30,$$

$$y_{S1} = 1,\quad y_{S2} = 1,\quad y_{R1} = 2,\quad y_{R2} = 1$$

Here,

$$\lambda_{S1} = 2,\quad \lambda_{S2} = 4,\quad \lambda_{R1} = 4,\quad \lambda_{R2} = 2,$$

$$\mu_{S1} = \infty,\quad \mu_{S2} = 6,\quad \mu_{R1} = \infty,\quad \mu_{R2} = \infty.$$

CRITICAL POINTS	LOCAL STABILITY
$E_{S^0,R^0} = (40,30,0,0)$	unstable
$E_{\lambda_{S1},*} = (2,11,38,0)$	asymptotically stable
$E_{\lambda_{S2},\lambda_{R1}} = (4,4,20,16)$	unstable
$E_{\mu_{S2},\lambda_{R1}} = (6,4,16,18)$	asymptotically stable if $A_1 > 1/12$, unstable if $A_1 < 1/12$, Hopf bifurcation at $A_1 = 1/12$.

In this example, as A_1 decreases through $1/12$ the critical point $E_{\mu_{S2},\lambda_{R1}}$ changes its stability. For $A_1 > 1/12$, $E_{\mu_{S2},\lambda_{R1}}$ is asymptotically stable whereas for $A_1 < 1/12$, $E_{\mu_{S2},\lambda_{R1}}$ is unstable. This change in stability occurs via a Hopf bifurcation. The resulting periodic orbits appear for values of $A_1 < 1/12$ and are orbitally asymptotically stable.

The calculations to show that there is a Hopf bifurcation at $A_1 = 1/12$ and that the resulting periodic orbits exist for $A_1 < 1/12$ and are asymptotically stable are usually very tedious if done by hand. Instead they were done by means of the symbol manipulation language REDUCE2 according to the method described in Marsden and McCracken [52, Section 4]. The REDUCE2 program is given in Appendix 3.A and the results for Example 3.10 are given in Appendix 3.B.

The feasible set in (S,R)-space, $\mathcal{B}_1$ and $\mathcal{B}_2$ are shown in Figure 10. The next series of graphs are also in (S,R)-space. In Figure 11 we show sample solutions for $A_1 = 0.08 < 1/12$. The solutions in Figure 11 that are depicted by dotted lines were found by integrating backward in time whereas all other solutions were integrated forward in time. However, all arrows indicate the evolution of solutions for positive time. In Figure 12 we focus on the critical point $E_{\mu_{S2},\lambda_{R1}}$ and the asymptotically stable periodic orbit surrounding $E_{\mu_{S2},\lambda_{R1}}$ and we show two solutions, one winding in towards the periodic orbit from the outside and one winding out towards the periodic orbit from the inside. Figure 13 is in (x_1,x_2)-space. Here again we focus on the critical point $E_{\mu_{S2},\lambda_{R1}}$ and show the periodic orbit with trajectories winding toward it.

It is interesting to note that in this example there is a range of choices of A_1 for which the critical point $E_{\lambda_{S1},*}$ is asymptotically

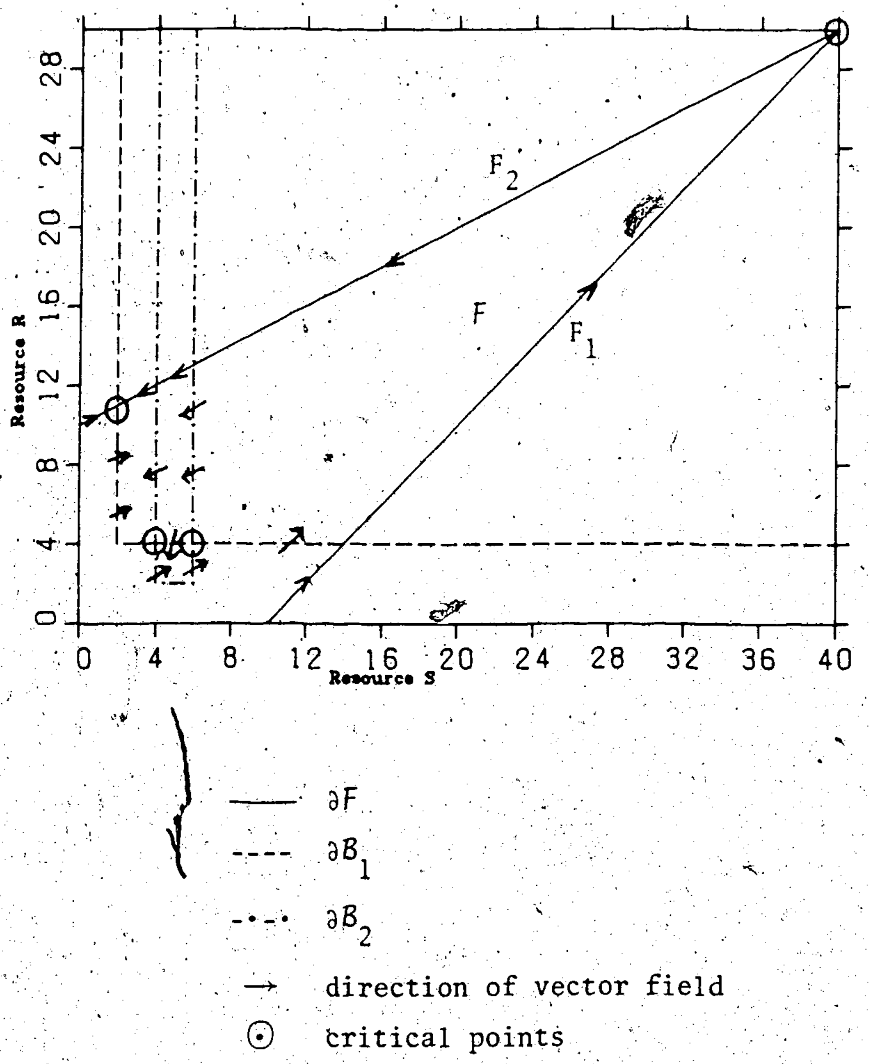


FIGURE 10 F, B_1 and B_2 for Example 3.10

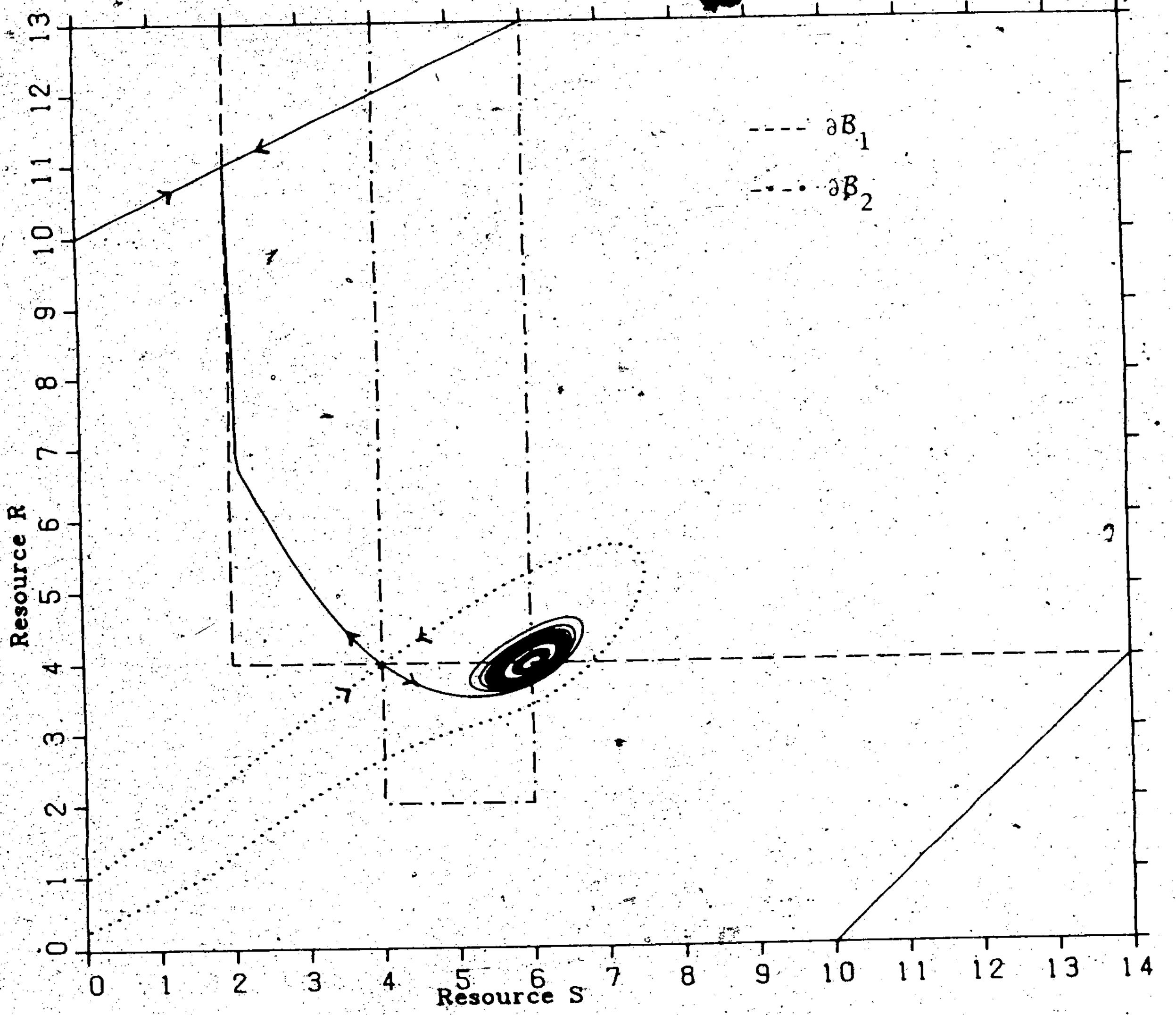


FIGURE 11 Sample Trajectories of Example 3.10; $A_1 = .08 < 1/12$

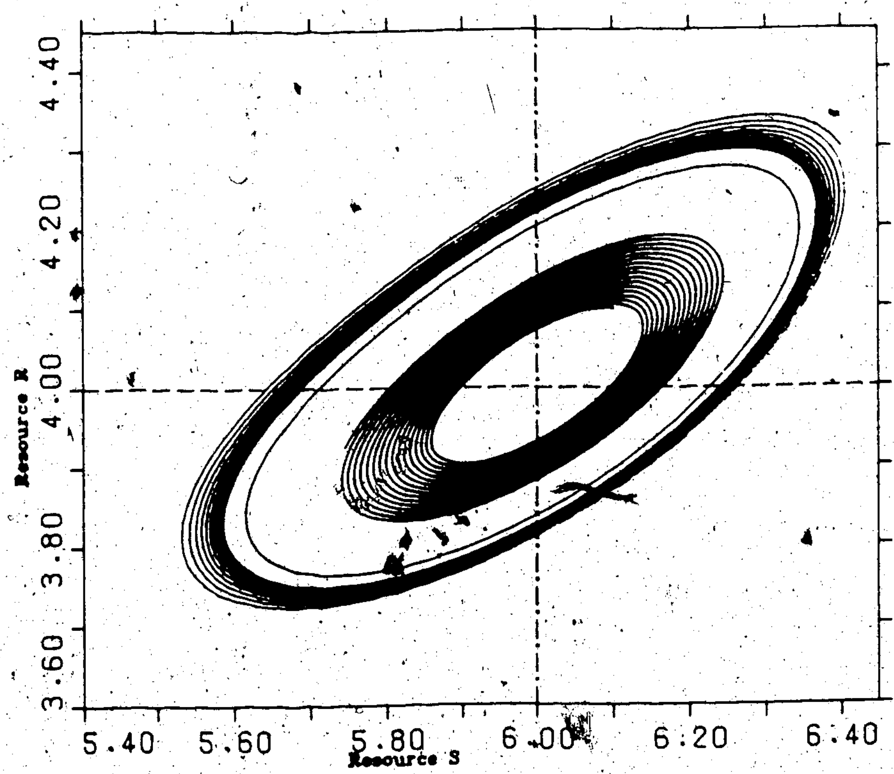


FIGURE 12 The Stable Periodic Orbit of Example 3.10 in (S,R)-Space

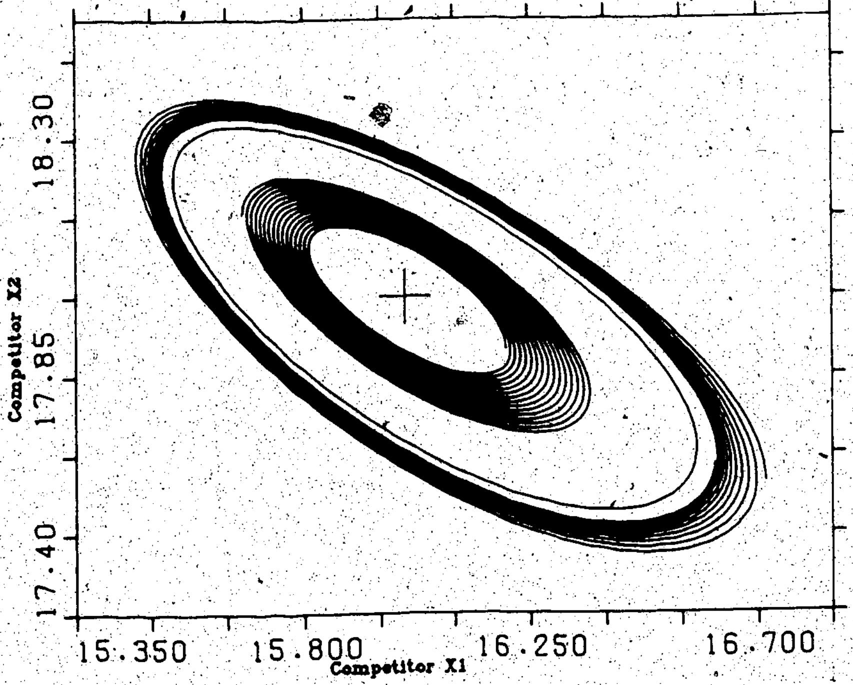


FIGURE 13 The Stable Periodic Orbit of Example 3.10 in (x_1,x_2)-Space

stable and for these same parameters there is a stable periodic orbit. Therefore there are at least two distinct biological outcomes possible.

That there is a Hopf bifurcation and that the bifurcating periodic orbit is asymptotically stable is actually independent of the choice of the functions $p_1(S)$ and $q_2(R)$ provided that for $p_1(S)$, $\lambda_{S1} < 6 < \mu_{S1}$ and for $q_2(R)$, $\lambda_{R2} < 4 < \mu_{R2}$, thus ensuring that $E_{\mu_{S2},\lambda_{R1}}$ is an equilibrium point and that the vector field in a neighbourhood of $E_{\mu_{S2},\lambda_{R1}}$ is analytic. This is because the Hopf bifurcation is a local phenomenon. However, it is interesting to note that in this example there are points at which the vector field is not differentiable. The choice of the functions $p_1(S)$ and $q_2(R)$ can affect how close a point at which the vector field is not differentiable is to an equilibrium point. This can influence the size of the parameter range $A_1 < 1/12$ for which a periodic orbit exists. In our example as A_1 decreases the amplitude of the bifurcating periodic orbit increases. As A_1 continues to decrease the amplitude of the periodic orbit continues to increase and it may approach a point where the vector field is not differentiable. If A_1 is decreased even more the orbit could disappear. That this can actually happen is demonstrated in Figure 14. We keep everything the same as before (including $A_1 = .08$) except that we replace $p_1(S)$ by

$$p_1(S) = \frac{1.004\ S}{.008 + S} .$$

For this choice of $p_1(S)$, $E_{\mu_{S2},\lambda_{R1}}$ is still a critical point. With the previous choice for $p_1(S)$ there is a periodic orbit (see

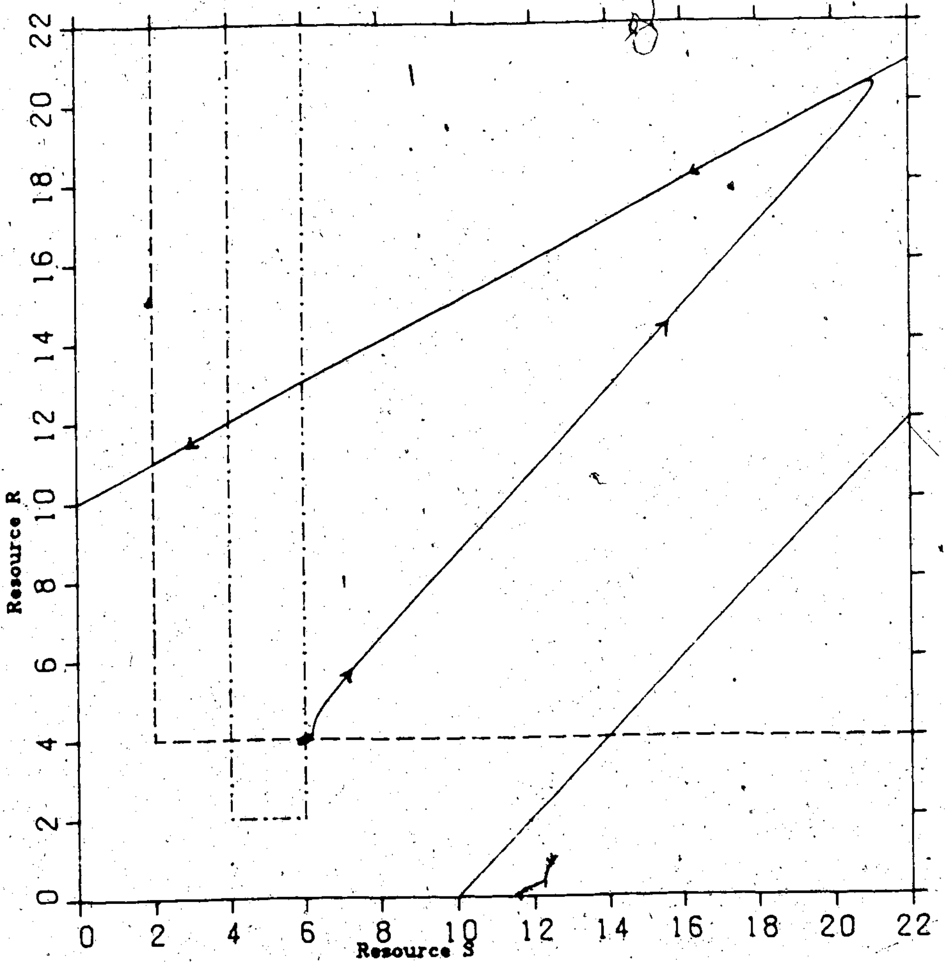


FIGURE 14 Discontinuity in the Vector Field - Periodic Orbit Disappears

Figures 11-13). However, for this choice of the function $p_1(S)$ there is a discontinuity in the vector field at (approximately) the point (6.0, 4.10914) and this is apparently close enough to $E_{\mu_{S2},\lambda_{R1}}$ so that there is no longer a periodic orbit for $A_1 = .08$. (Figure 14 is in (S,R)-space. The initial conditions for the substrate are (6.05,4.05). Instead of cycling out to a periodic orbit, the solution escapes and converges to (2,11).)

In the second example both resources are inhibitory to both populations at high concentrations. In this example we can adjust the parameters to obtain simultaneous Hopf bifurcations about two distinct interior equilibria, one super critical and the other subcritical. Therefore there can be both stable and unstable periodic orbits. In this way we again show that there can be two independent regimes of coexistence for the same value of the bifurcation parameter. Also, as in Example 3.9 this example depicts a case where both competitors wash out when their rival is absent but can otherwise coexist given certain initial conditions.

<u>Example 3.11</u>. Let,

$$p_1(S) = 1 + \frac{(S-2)(8-S)}{16(.0625S^2 + .125S + 1)}$$

$$p_2(S) = 1 + \frac{(S-4)(6-S)}{24(A_1S^2 + 10S + 1)}$$

$$q_1(R) = 1 + \frac{(R-4)(6-R)}{24(.075R^2 + 7.625R + 1)}$$

$$q_2(R) = 1 + \frac{(R-2)(8-R)}{16(.125R^2 + .1R + 1)},$$

$$D = 1, \quad S^0 = 32, \quad R^0 = 24$$

$$y_{S1} = 1, \quad y_{S2} = 1, \quad y_{R1} = 2, \quad y_{R2} = 1$$

Here,

$$\lambda_{S1} = 2, \quad \lambda_{S2} = 4, \quad \lambda_{R1} = 4, \quad \lambda_{R2} = 2,$$

$$\mu_{S1} = 8, \quad \mu_{S2} = 6, \quad \mu_{R1} = 6, \quad \mu_{R2} = 8$$

CRITICAL POINTS	LOCAL STABILITY
$E_{S^0,R^0} = (32,24,0,0)$	asymptotically stable
$E_{\lambda_{S2},\lambda_{R1}} = (4,4,16,12)$	unstable
$E_{\mu_{S2},\mu_{R1}} = (6,6,16,10)$	unstable
$E_{\lambda_{S2},\mu_{R1}} = (4,6,20,8)$	asymptotically stable if $A_1 < 9/8$, unstable if $A_1 > 9/8$, Hopf bifurcation at $A_1 = 9/8$.
$E_{\mu_{S2},\lambda_{R1}} = (6,4,12,14)$	asymptotically stable if $A_1 > 9/8$, unstable if $A_1 < 9/8$, Hopf bifurcation at $A_1 = 9/8$.

As in the previous example the computations to show the existence of a Hopf bifurcation and the stability of bifurcating orbits were done using the REDUCE2 program in Appendix 3.A. The program results for this example can be found in Appendix 3.C.

There is a simultaneous Hopf bifurcation of the critical points $E_{\mu_{S2},\lambda_{R1}}$ and $E_{\lambda_{S2},\mu_{R1}}$ as A_1 passes through 9/8. For $E_{\mu_{S2},\lambda_{R1}}$, as in the previous example, the critical point loses stability as A_1 decreases through the critical value and the bifurcating periodic orbit appears for values of $A_1 < 9/8$ and is asymptotically stable. On the other hand, $E_{\lambda_{S2},\mu_{R1}}$ goes from unstable to asymptotically stable as A_1 decreases below 9/8 and the associated periodic orbit is unstable and exists for $A_1 < 9/8$. From this we see that there is a range of parameters ($A_1 < 9/8$) for which there is an asymptotically stable interior critical point surrounded by an unstable periodic orbit and for the same value of A_1 an orbitally asymptotically stable periodic orbit. Thus there are at least two different possibilities for coexistence and the outcome is initial condition dependent. This was not possible in the monotone kinetics case. Recall that in that case the dynamics are always trivial and there is at most one interior critical point which is either globally asymptotically stable or unstable.

The dynamics for this example are illustrated in the figures that follow. The first series of graphs are in (S,R)-space. Figure 15 shows F, B_1 and B_2. Figure 16 ((a) and (b)) depicts sample trajectories for $A_1 = 1.1 < 9/8$. (As for Figure 11, the dotted line was found by integrating backward in time. However all arrows indicate evolution of solutions for positive time.) In Figure 17 (respectively Figure 19) we focus on the critical point $E_{\lambda_{S2},\mu_{R1}}$ (respectively

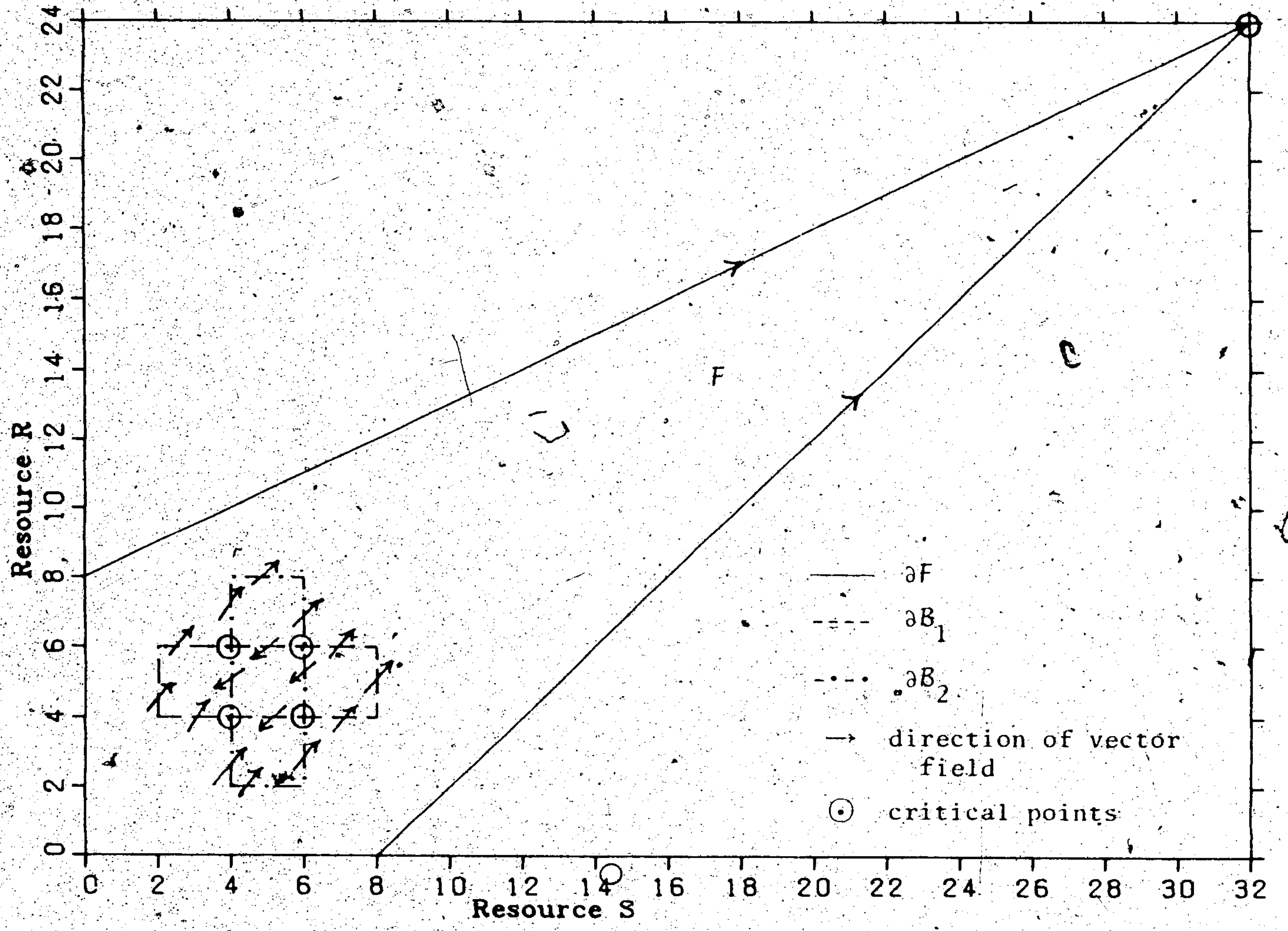


FIGURE 15 F , B_1 and B_2 for Example 3.11

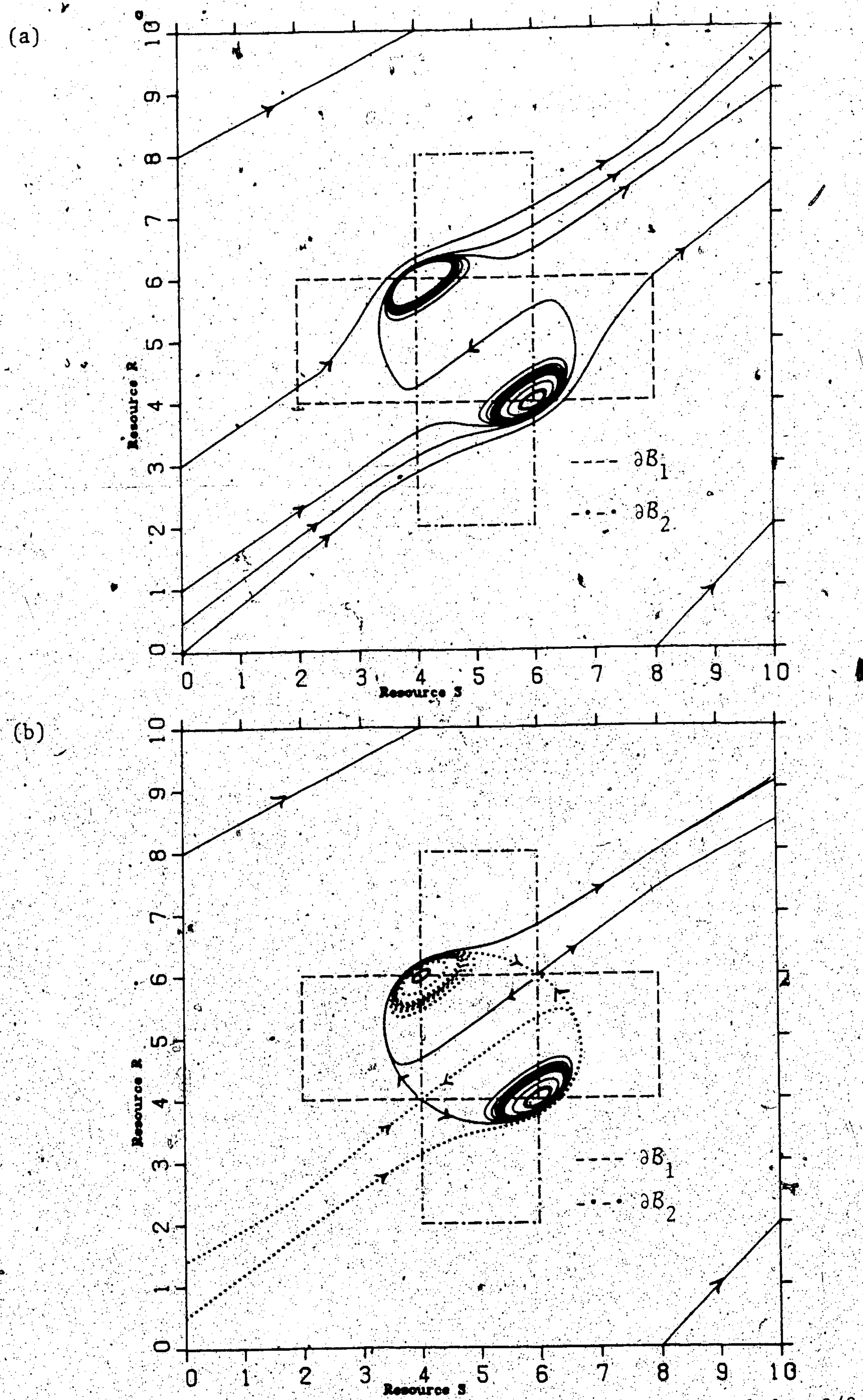


FIGURE 16 Sample Trajectories of Example 3.11; $A_1 = 1.1 < 9/8$

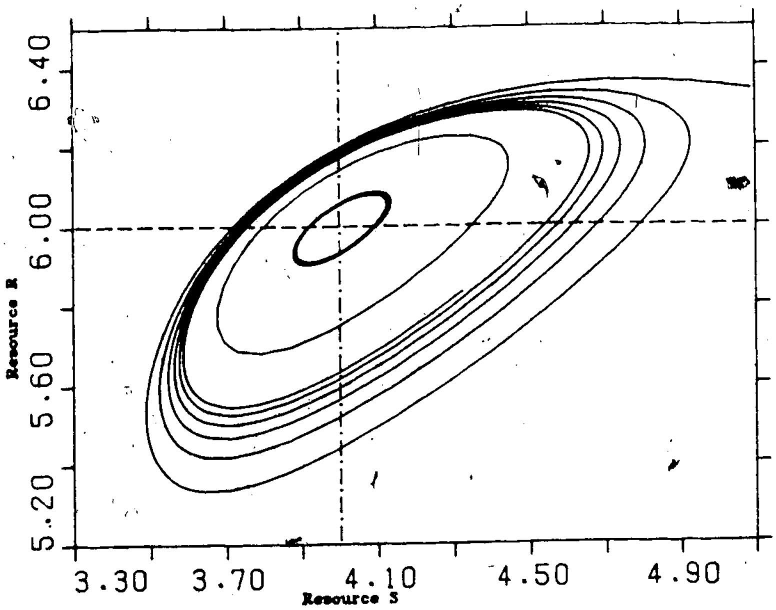


FIGURE 17 The Unstable Periodic Orbit of Example 3.11 in (S,R)-Space

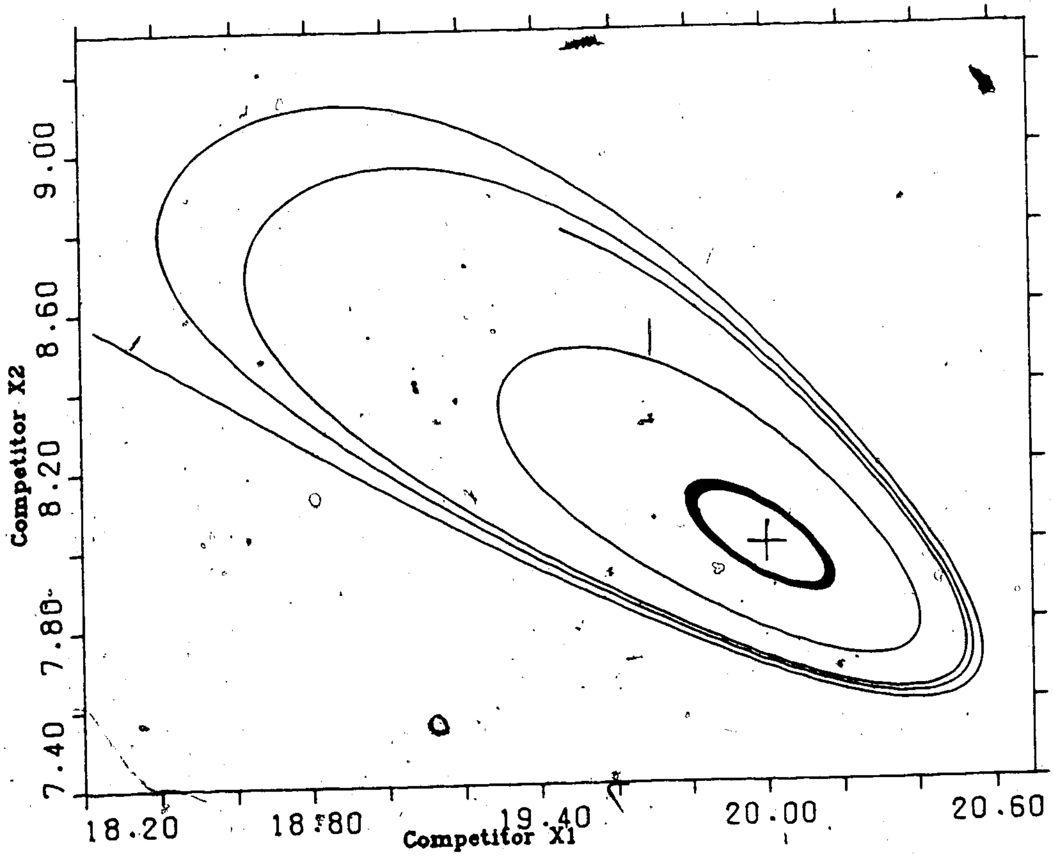


FIGURE 18 The Unstable Periodic Orbit of Example 3.11 in (x_1,x_2)-Space

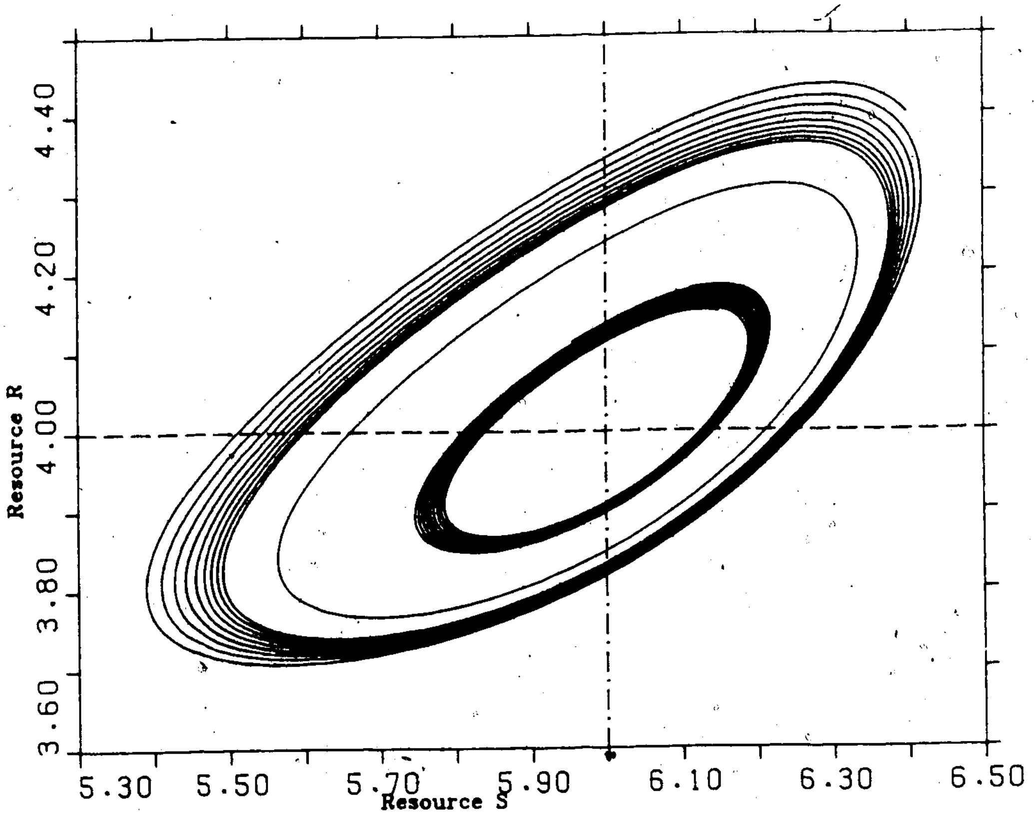


FIGURE 19 The Stable Periodic Orbit of Example 3.11 in (S,R)-Space

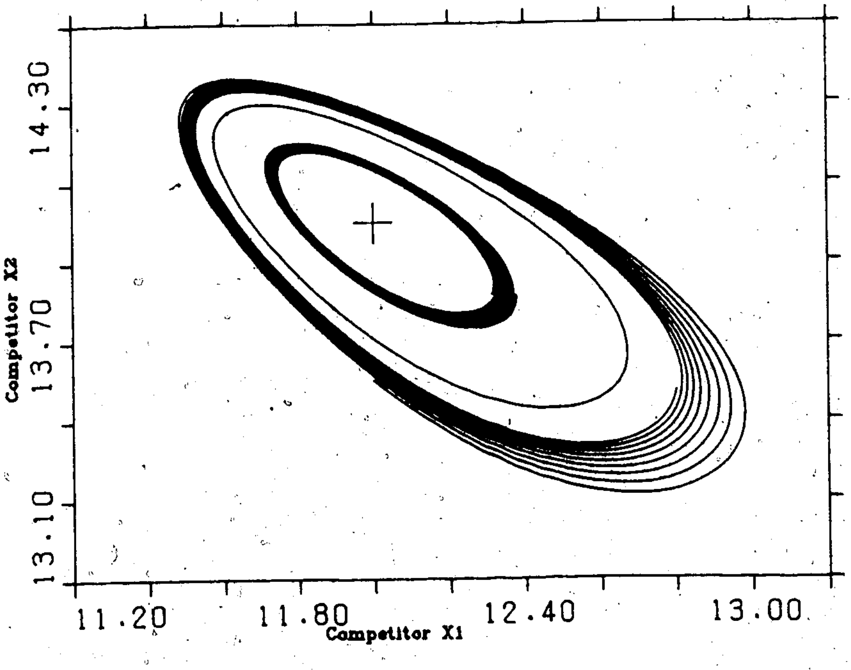


FIGURE 20 The Stable Periodic Orbit of Example 3.11 in (x_1,x_2)-Space

$E_{\mu_{S2}, \lambda_{R1}^*}$) and the associated unstable (respectively stable) periodic orbit in (S,R)-space. Finally, in Figures 18 and 20 we again focus on these same critical points, but this time in (x_1, x_2)-space.

4. DISCUSSION. In this chapter we showed that if one models exploitative competition for two complementary resources in a chemostat with microbial responses modelled by general monotone kinetics one obtains the same qualitative results as Hsu, Cheng and Hubbell [41] did for microbial responses modelled by Holling Type II dynamics. However, we use a different technique which can be applied with some success in the non-monotone case.

In the monotone case, we show that the dynamics are always trivial and that there are only five possible distinct biological outcomes. We summarize these results in Table III and in each case give criteria that guarantee each outcome.

In the non-monotone case, which can arise if a resource is inhibitory at high concentrations, we give graphical criteria for the existence of critical points. We give sufficient conditions which are also graphical which ensure that the dynamics of the model are trivial. However, we show that the model permits nontrivial periodic solutions which may be either unstable or orbitally asymptotically stable (see Examples 3.10 and 3.11). This is only possible however if there is an interior critical point at which each resource is limiting to a different competitor population and one resource is limiting because it is in short supply whereas the other resource is limiting because it is overabundant. We have therefore shown that sustained oscillations are possible in a chemostat with nonreproducing nutrients and constant nutrient input rate. It has already been shown in [11,13,45,53,70] that for a reproducing resource (prey) or by Hale and Somolinos [32] for a periodically fluctuating nutrient that oscillatory behaviour in a chemostat is possible.

It should be pointed out that the model with non-monotone kinetics cannot be reduced to a competitive model in the sense of Hirsch [37], as it can be with monotone kinetics. In the non-monotone case, under generic assumptions, up to nine distinct critical points are possible whereas in the monotone case at most four distinct critical points are possible. This leads to a wealth of different possible biological outcomes even when the dynamics are trivial. There is actually the possibility that in the absence of its rival, a population dies out, whereas in the presence of its rival there is (depending on the initial conditions), a possibility of coexistence. Thus in some sense the competitors are cooperating (see Example 3.9). There is also another situation in which the competitors clearly do not compete. This is in the case that the resources are both overabundant and hence inhibitory to both competitors. The fact that the other population is consuming can only be of help.

An advantage of explicitly modelling the resources is that the model is predictive and the predictions are made based on parameters that can be measured independent of competition, with each competitor limited by only one resource at a time. A disadvantage is that to simplify the mathematics certain assumptions were made that need not hold. For example, it was assumed that the individual death rates of each competitor population are insignificant when compared to the wash-out rate. It might be appropriate in many cases to consider differential death rates. Also most nutrients are probably imperfectly substitutable rather than perfectly complementary. It might also be the case that the per capita growth rate is not proportional to the consumption rate as in the models of Tilman [73,74,75,76] or that the mechanism for inhibition of complementary resources may not lead to a model in which $f_i(S(t),R(t)) = \min(p_i(S(t)),q_i(R(t)))$. In the context of simple enzyme catalyzed reactions, a reaction can be considered to have two time consuming parts. The first is the binding of the substrate with the enzyme and the second is the actual reaction formation of the product. There is evidence, according to Dixon and Webb [18] and Palmer [60], that inhibition by high substrate concentrations (in the context of enzyme catalyzed reactions) in some cases may be due to the specificity of certain enzymes. Many enzymes have two or more groups and in an effective enzyme-substrate molecule complex a single substrate molecule must be combined with all these groups. However, it might be the case that a substrate molecule may combine with only one of these groups if the other groups are combined with other substrate molecules thus forming an ineffective complex. In this case a reaction cannot take place until some of the substrate molecules dissociate away. When the substrate concentration is high the chance of forming ineffective complexes increases. Thus the inhibition can come into the enzyme-substrate complex formation only. The analogous concepts for microbial growth might be search time and processing time of nutrient and the analogous mechanism for inhibition might be that at high resource concentrations the resource might form clumps too large for the the microorganisms to handle. The microorganisms might have to wait until a clump dissociates in order to absorb it. If these mechanisms which affect only substrate-enzyme complex formation or analogously search time are responsible for the inhibition then there is reason to assume that $f_i\big(S(t),R(t)\big) = \min\big(p_i(S(t),q_i(R(t))\big)$. However, if reaction time or analogously processing time is slowed by high concentration of substrate a different model might have to be considered. There is also experimental evidence to indicate that some microorganisms employ such strategies as luxury consumption and that there is probably a time delay between absorption of nutrient and conversion to biomass. Neither of these possibilities is taken into account in our model.

As a next step it would be interesting to consider the "Principle of Competitive Exclusion" in this context and determine whether or not it is possible for more than 2 competitors to survive if limited by only two resources.

Before concluding this chapter, we wish to point out that just as in the single resource case studied in Chapter II, in the two resource case, qualitative outcomes depend on the relative values of the break-even concentrations and on the concentration of nutrient in the feed bottle. In the single resource case, the qualitative outcome is independent of the growth yield factors. However, in the two resource case the growth yield factors play a significant role in determining the qualitative outcome since their ratios C_1 and C_2 play an important part in determining both the position of the feasible set and the local stability of critical points.

Finally, with respect to the application to water purification given in Chapter II, it would be important to be aware whether or not the contaminant is a complementary resource and if it is to know whether or not its complement is ever limiting since our results show that this could influence the predicted outcome significantly. This is likely to be important for perfectly and imperfectly substitutable resources as well.

CHAPTER IV

PREDATOR-MEDIATED COMPETITION

1. INTRODUCTION. In this chapter we consider a mathematical model of a chemostat describing two competitors competing for a single, essential, growth-limiting substrate and a predator predating on the superior competitor. (Recall that in Chapter II we showed that in the absence of a predator the inferior competitor is always eliminated by the competition.) Besides this food web we shall also study the food chain that results when the inferior competitor is omitted from the model.

As in the previous chapters, we allow a general class of functions to describe microbial-nutrient dynamics in order to see what can be said in general about such food webs and food chains. However, unlike in the previous chapters, in this chapter we restrict the class of functions to be monotone nondecreasing. Thus we allow saturation but not inhibition at high concentrations of either substrate or prey.

Three prototypes for monotone functional responses are Lotka-Volterra (linear), Michaelis-Menten (concave), and multiple saturation (sigmoidal). We shall see that even among these three prototypes there will be qualitative differences in the dynamic behaviour of the model. However, we shall find that there is a certain structural behaviour that is common to all models involving monotone kinetics. Hopefully this will be helpful to experimenters who wish to gain insight into the basic mechanisms underlying microbial interactions, in particular those who wish to determine the most appropriate function describing growth and feeding dynamics of a given class of microorganisms.

The work in this chapter is an attempt to unify the mathematical work already done on this problem as well as to present new results. The novelty is that many of the results are of a global nature and are for general monotone functions. We do however, give results for specific prototypes where appropriate.

We shall address the related ecological question of whether or not the invasion by a predator can reverse the outcome of competition. The answer may depend upon whether one interprets our results purely deterministically or whether one allows for stochastic influences. Our results also help to confirm the current ecological thinking, based on much experimental evidence, (see for example Slobodkin [69] and Paine [59]) that predation is often responsible for the diversity in ecosystems. Paine postulates that *"Local species diversity is directly related to the efficiency with which predators prevent monopolization of the major environmental requisites by one species."*

A central concept in our discussion is the notion of *persistence*. Following Freedman and Waltman [22], we give the following formal definition:

Definition 1.1. Let

$$w'(t) = f(w(t)) \tag{1.1}$$

be a system of differential equations where f is a vector-valued function in $w = (w_1, \ldots, w_n) \in \mathbb{R}^n$. Then (1.1) is said to *persist* if $w_i(0) > 0$ for all $i = 1,\ldots,n$ implies that $\underline{\lim}_{t\to\infty} w_i(t) > 0$ for all $i = 1,\ldots,n$.

For other definitions of persistence see [8,21,23,28,31,34,42,53].

This chapter is organized in the following manner. In Section 2 we set down the mathematical model of the food web that we wish to study and we outline the underlying assumptions. An equivalent nondimensional version of this model is given in Section 3 where we also define several important parameters and introduce notation for the critical points of this system. It is this nondimensional version of the model that we actually analyze. In Section 4 we introduce notation for the three dimensional subsystems that result if one of the competitors or the predator is omitted.

Sections 5 through 9 contain mathematical results. We state and prove preliminary results in Section 5. In Section 6 we show that under certain conditions there is a chain of transference of global stability from one critical point to another as certain parameters are decreased. (So [71] gives a similar result for the classical Lotka-Volterra food chain.) Before we give an example to show that this sequence of transference of global stability can be interrupted by the appearance of a stable limit cycle (see Section 9), we consider the food chain that results if the inferior rival is eliminated from the model in Section 7, and we determine conditions that ensure persistence of the entire food web in Section 8. The persistence of the entire food web can be considered predator-mediated, since in the absence of the predator at least one of the competitors always becomes extinct. This predator-mediated coexistence is highlighted in the example in Section 9 where we also show that invasion by a predator can in some sense reverse the outcome of pure competition.

We conclude the chapter with Section 10 in which we summarize our results, interpret them with respect to the original model described in Section 2, and finally consider the ecological ramifications. For completeness we summarize the local stability analysis of the food web in Appendix 5.A and of the food chain in Appendix 5.B. Part of this linear analysis has already appeared in the literature (see for example Canale [14] and Saunders and Bazin [66]).

Throughout this chapter we shall use the following notation:

$\mathcal{O}(P)$ will denote the orbit of a dynamical system, that passes through the point P and $\mathcal{O}^+(P)$ and $\mathcal{O}^-(P)$ will denote the positive and negative semi-orbit through P, respectively.

If E is an equilibrium point of a dynamical system, then $W^s(E)$ and $W^u(E)$ will denote the stable and unstable manifolds of E respectively (provided they exist).

2. THE MODEL - A FOOD WEB. We shall consider the following model of predator-mediated competition in the chemostat:

$$\begin{aligned}
&S'(t) = \big(S^0 - S(t)\big)D - \sum_{i=1}^{2} \frac{x_i(t)p_i\big(S(t)\big)}{y_i}\,,\\
&x_1'(t) = x_1(t)\big(-D + p_1(S(t))\big) - y(t)q\big(x_1(t)\big)/z\,,\\
(2.1)\quad &x_2'(t) = x_2(t)\big(-D + p_2(S(t))\big)\,,\\
&y'(t) = y(t)\big(-D + q(x_1(t))\big)\,,\\
&S(0) = S_0 \geq 0,\ \ x_i(0) = x_{i0} \geq 0,\ \ i = 1,2,\ \ y(0) = y_0 \geq 0\,.
\end{aligned}$$

In these equations $y(t)$ denotes the concentration of the predator population of microorganisms at time t. In the absence of the predator (i.e. $y(t) = 0$ for all t) this model reduces to the model (II.2.1) with $n = 2$. Therefore $x_i(t)$, $S(t)$, $p_i(S)$, S^0, D and y_i have the same biological meaning as in Chapter II. However, in this model $x_1(t)$ is viewed as both a prey population and a competitor population. Here, $q(x_1)$ denotes the per capita growth rate of the predator population as a function of the prey concentration; z is the growth yield factor for the predator population feeding on the prey; and we assume that $q(x_1)/z$ represents the prey-uptake function for the predator.

We make the following assumptions concerning the functions p_i and q in the model equations (2.1):

$$(2.2)\qquad p_i\,,\ \ q : \mathbb{R}_+ \to \mathbb{R}_+\,;$$

(2.3) p_i , q are continuously differentiable;

(2.4) $p_1'(S) > 0$ for all $S \in \mathbb{R}_+$;

(2.5) $p_2'(S) \geq 0$ for all $S \in \mathbb{R}_+$;

(2.6) $q'(x_1) \geq 0$ for all $x_1 \in \mathbb{R}_+$;

(2.7) $p_i(0) = 0, \quad q(0) = 0$.

It will also be convenient to denote $q(x_1)$ as

(2.8) $$q(x_1) = x_1 h(x_1) .$$

Note that since q is (continuously) differentiable it follows that $\lim_{x \to 0} h(x) = q'(0)$, and so we define $h(0) = q'(0)$.

The system (2.1) describes a chemostat set up as in Chapter II with nonreproducing substrate, constant input and dilution rate, perfect mixing in the growth vessel, insignificant death rates compared to dilution rate, and instantaneous adjustment of growth rates to changes in the concentration of nutrient. Furthermore, just as we assume that the substrate-uptake rate is proportional to the rate of conversion to competitor biomass, we assume that the prey-uptake rate is proportional to the rate of conversion to predator biomass. In this model two populations compete solely for an essential, growth-limiting substrate. Also a predator population predates on the competitor population that would be the sole survivor provided the predator population were absent.

This model is similar to the models studied by Jost et al [43]. However in their model of a food web they allow the predator to predate on both competitors. In all of their models they use Michaelis-Menten kinetics to describe nutrient uptake and competitor (prey) growth. In the food chain that results when the second competitor is absent, they consider two different models, one with Michaelis-Menten kinetics describing predator-prey dynamics and the other with multiple saturation kinetics. Their experimental results seem to indicate that the latter model is more satisfactory. In the food web they derive a more complicated functional response for the predator that takes food preference into consideration but that reduces to multiple saturation dynamics when one competitor is absent.

Freedman and Waltman [22] consider a general Kolmogorov model of three interacting predator-prey populations. They derive persistence criteria for this general model and then illustrate their results in special cases. In particular, under certain conditions their system can be interpreted as two rival populations with a predator predating on either one or both of the rival populations.

The food chain that results when the second competitor is eliminated from the model (2.1) was also studied by Butler, Hsu and Waltman [12], Bungay and Bungay [9] and Sell [68], among others. They all consider a model in which all functional responses are modelled by Michaelis-Menten type dynamics. Experiments [27] seem to show that this is quite reasonable for *soluble organic nutrient - heterotrophic bacteria - holozoic protozoa* food chains. Canale [14] also considers M'Kendrick and Pai's [55] model (i.e. Lotka-Volterra dynamics). The food chain with very general dynamics is also studied by Saunders and Bazin [66] and by Gard [24,27].

3. THE NONDIMENSIONAL VERSION OF THE MODEL. It will be more convenient to analyze the model after the following substitutions are performed:

$$\bar{t} = tD; \quad \bar{S} = S/S^0; \quad \bar{x}_i = x_i/y_i S^0 \quad i = 1,2; \quad \bar{y} = y/S^0 y_1 z . \tag{3.1}$$

$$\bar{p}_i(\bar{S}) = p_i(S)/D \quad i = 1,2 . \tag{3.2}$$

$$\bar{q}(\bar{x}_1) = q(x_1)/D \quad \text{(and so} \quad \bar{h}(\bar{x}_1) = y_1 S^0 h(x_1)/D) \tag{3.3}$$

Omitting the bars, in order to simplify the notation, the nondimensional version of model (2.1) can be written:

$$\begin{aligned} S'(t) &= \big(1 - S(t)\big) - \sum_{i=1}^{2} x_i(t) p_i\big(S(t)\big), \\ x_1'(t) &= x_1(t)\big(-1 + p_1(S(t))\big) - y(t) q(x_1(t)), \\ x_2'(t) &= x_2(t)\big(-1 + p_2(S(t))\big), \\ y'(t) &= y(t)\big(-1 + q(x_1(t))\big), \\ S_0 &\geq 0, \quad x_{i0} \geq 0 \quad i = 1,2, \quad y_0 \geq 0 . \end{aligned} \tag{3.4}$$

All the assumptions (2.2) - (2.8) hold for this nondimensional version of the system (2.1). Therefore, there will be no loss of generality if we study system (3.4) instead of (2.1) and we can always reinterpret our results in terms of the unscaled variables by the appropriate application of (3.1) - (3.3).

By the monotonicity assumptions (2.4) - (2.6) it follows that there exist uniquely defined positive extended real numbers λ_i and δ such that:

$$
\begin{aligned}
&p_i(S) < 1 \quad \text{if} \quad S < \lambda_i\,, \\
&p_i(S) > 1 \quad \text{if} \quad S > \lambda_i\,, \\
&q(x_1) < 1 \quad \text{if} \quad x_1 < \delta\,, \\
\text{and} \quad &q(x_1) > 1 \quad \text{if} \quad x_1 > \delta\,,
\end{aligned} \tag{3.5}
$$

provided we make the following assumption of a generic nature:

(3.6) If λ_2 (or δ) is finite, then $p_2'(\lambda_2) > 0$ $(q'(\delta) > 0)$.

Assume also that

(3.7) all λ_i, δ (other than those which are infinite) are distinct from each other and from 1, and

$$\lambda_1 < \lambda_2 \quad \text{if} \quad \lambda_1 < \infty\,. \tag{3.8}$$

Then λ_i and δ represent the break-even concentrations of substrate and prey, respectively. Also in the absence of the predator x_1 drives x_2 to extinction.

The critical points of the system (3.4) will be denoted:

$E_1 = (1,0,0,0)$

$E_{\lambda_1} = (\lambda_1, 1-\lambda_1, 0, 0)$

$E_{\lambda_2} = (\lambda_2, 0, 1-\lambda_2, 0)$

$E_{S^*} = (S^*, \delta, 0, y^*)$ where $y^* = \delta(-1 + p_1(S^*))$ and S^* satisfies $1 - S^* = \delta p_1(S^*)$.

$\hat{E}_{\lambda_2} = (\lambda_2, \delta, \hat{x}_2, \hat{y})$ where $\hat{x}_2 = 1 - \lambda_2 - \delta p_1(\lambda_2)$ and $\hat{y} = \delta(-1 + p_1(\lambda_2))$

and will be assumed to be critical points if and only if all their components are nonnegative. Therefore E_{λ_1} (resp. E_{λ_2}) is a critical point provided $\lambda_1 \leq 1$ $(\lambda_2 \leq 1)$ and $\hat{E}_{\lambda_2}$ is a critical point provided $\hat{x}_2 = 1 - \lambda_2 - \delta p_1(\lambda_2) \geq 0$. In particular, this implies that $\lambda_2 + \delta < 1$. E_{S*} is a critical point provided $S^* \geq 0$ is well-defined and $y^* \geq 0$. S^* is defined by the equation $1 - S^* = \delta p_1(S^*)$. If we plot the functions $1 - S$ and $\delta p_1(S)$ on the same graph (see Figure 21), since $p_1(0) = 0$ and $p_1(S)$ strictly increases it follows that there is a unique point S^* that satisfies the equation $1 - S = \delta p_1(S)$ and this point lies between 0 and 1. In order for $y^* \geq 0$ we require $S^* \geq \lambda_1$. But the solution of $1 - S = \delta p_1(S)$ is less than λ_1 if and only if $1 - \lambda_1 < 1 - S = \delta p_1(S) < \delta p_1(\lambda_1) = \delta$, i.e. $1 - \lambda_1 < \delta$. Thus, E_{S*} is a critical point provided that $\lambda_1 + \delta \leq 1$. Actually, since in this case $S^* \geq \lambda_1$, it follows that $1 - S^* = \delta p_1(S^*) \geq \delta$ and so when E_{S*} is a critical point $\lambda_1 \leq S^* \leq 1 - \delta$.

See Table VIII for a summary of the critical points and the parameter ranges in which they appear in the nonnegative cone. For convenience we shall identify the nonnegative (S, x_1, x_2, y) cone with $\mathbf{R}^4_+$.

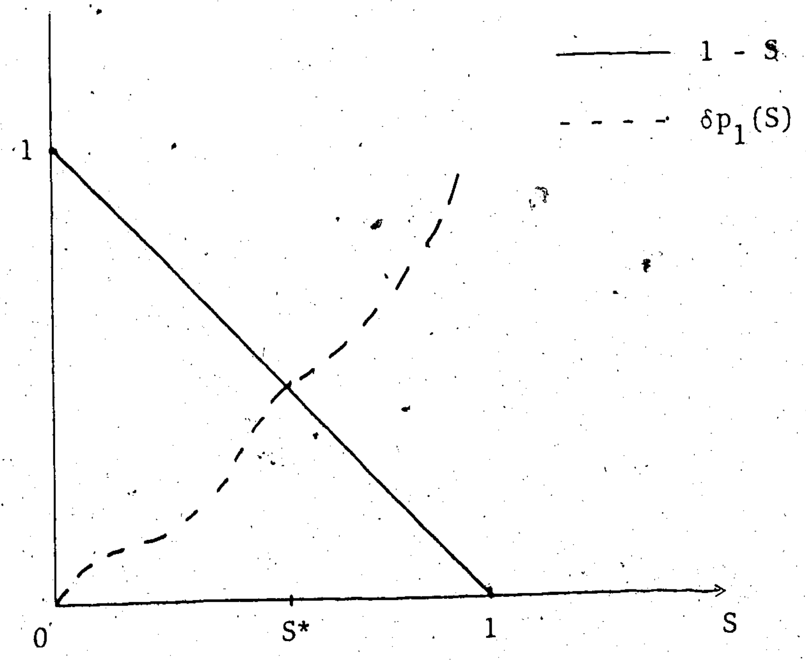


FIGURE 21 Position of S*

	$\lambda_1 > 1$	$\lambda_1 \leq 1$ $\lambda_1 + \delta > 1$	$1-\lambda_2-\delta p_1(\lambda_2)<0$ $\lambda_1 + \delta \leq 1$	$1-\lambda_2-\delta p_1(\lambda_2)\geq 0$
E_1	yes	yes	yes	yes
E_{λ_1}	no	yes	yes	yes
E_{λ_2}	no	no if $\lambda_2 > 1$ yes if $\lambda_2 \leq 1$	no if $\lambda_2 > 1$ yes if $\lambda_2 \leq 1$	yes
E_{S*}	no	no	yes	yes
$\hat{E}_{\lambda_2}$	no	no	no	yes

TABLE VIII Critical Points in Nonnegative Cone

4. THREE-DIMENSIONAL SUBSYSTEMS. In this section we shall consider the three dimensional subsystems that result if one of the competitors or the predator is absent from the system.

If the predator is absent, i.e. $y_0 = 0$, then system (3.4) reduces to:

$$\begin{aligned} & S'(t) = \big(1-S(t)\big) - \sum_{i=1}^{2} x_i(t)p_i\big(S(t)\big), \\ (4.1)\qquad & x_i'(t) = x_i(t)\big(-1 + p_i(S(t))\big), \quad i = 1,2 \\ & S_0 \geq 0 \text{ and } x_{i0} > 0 \quad i = 1,2 . \end{aligned}$$

But this is the same as model (II.2.1) with $n = 2$ and so all the results of Chapter II apply, in particular Theorem II.3.4 and Corollary II.3.5.

If competitor x_1 is absent, i.e. $x_{10} = 0$, then (3.4) reduces to:

$$\begin{aligned} & S'(t) = \big(1 - S(t)\big) - x_2(t)p_2\big(S(t)\big), \\ & x_2'(t) = x_2(t)\big(-1 + p_2(S(t))\big), \\ (4.2)\qquad & y'(t) = -y(t), \\ & S_0 \geq 0, \quad x_{20} > 0, \text{ and } y_0 > 0 . \end{aligned}$$

Since the y equation decouples it is clear that $\lim_{t\to\infty} y(t) = 0$ and so the model has the same form as model (II.2.1) with $n = 1$.

If competitor x_2 is absent then (3.4) has the form:

$$\left.\begin{aligned} S'(t) &= \big(1 - S(t)\big) - x_1(t)p_1\big(S(t)\big)\,, \\ x_1'(t) &= x_1(t)\big(-1 + p_1(S(t))\big) - y(t)q\big(x_1(t)\big)\,, \\ y'(t) &= y(t)\big(-1 + q(x_1(t))\big)\,, \end{aligned}\right\} \qquad (4.3)$$

$$S_0 \geq 0, \quad x_{10} \geq 0 \quad \text{and} \quad y_0 \geq 0\,.$$

The critical points of this system will be denoted by: $E_1^3 = (1,0,0)$, $E_{\lambda_1}^3 = (\lambda_1, 1-\lambda_1, 0)$, and $E_{S^*}^3 = (S^*, \delta, y^*)$ where $y^* = \delta\big(-1+p_1(S^*)\big)$ and S^* satisfies $1 - S^* = \delta p_1(S^*)$ and will be considered critical points if and only if all the components are nonnegative.

System (4.3) describes a food chain where y eats x_1 which in turn eats S. It will be studied in more detail in Section 8 and a linear analysis can be found in Appendix 5.B.

For notational convenience we shall identify the nonnegative (S,x_1,y) cone with $\mathbf{R}_+^3$.

5. PRELIMINARY RESULTS. As for the models in the previous chapters, the solutions of model (3.4) are well-behaved.

Theorem 5.1. All solutions $S(t)$, $x_1(t)$, $x_2(t)$ and $y(t)$ of (3.4) for which $x_{i0} > 0$, $i = 1,2$ and $y_0 > 0$ are positive and bounded for $t > 0$.

The proof is similar to the proof of Theorem II.3.1.

Theorem 5.2. The simplex

$$L = \left\{(S,x_1,x_2,y) : S,x_1,x_2,y \geq 0; \quad S + \sum_{i=1}^{2} x_i + y = 1\right\}$$

is a global attractor for (3.4).

Proof: Adding the equations in (3.4) and solving the resulting differential equation, it follows that for any solution of (3.4):

$$S(t) + \sum_{i=1}^{2} x_i(t) + y(t) = 1 + e^{-t}\left(S_0 + \sum_{i=1}^{2} x_{i0} + y_0 - 1\right). \tag{5.1}$$

□

It is evident that for all solutions of (3.4), $\underline{\lim}_{t\to\infty} S(t) > 0$.

Just as in Chapter II, it will be useful to consider the subsimplices L_H of L:

$$L_H = \{(S,x_1,x_2,y) \in L : x_i = 0,\ i \notin H\} \tag{5.2}$$

where $H \subset \{1,2\}$. Thus $L = L_{\{1,2\}}$.

The next two results concern extinction of a population due to insufficient nutrient. The extinction is independent of either competition or predation.

Theorem 5.3. For all solutions of (3.4) :

(i) if $\lambda_i \geq 1$ (or $\lambda_i = +\infty$), then $\lim_{t\to\infty} x_i(t) = 0$;

(ii) if $\delta \geq 1$ (or $\delta = +\infty$), then $\lim_{t\to\infty} y(t) = 0$;

(iii) if $\lim_{t\to\infty} x_1(t) = 0$ then $\lim_{t\to\infty} y(t) = 0$.

Proof: The proof of (i) and (ii) is similar to the proof of Theorem II.3.2 and (iii) follows by integrating $y'(t)/y(t) = -1 + q(x_1(t))$ and taking the limit as $t \to \infty$. $\square$

6. TRANSFER OF GLOBAL STABILITY. In this section we show that there is a hierarchy of critical points and that under certain conditions global stability transfers from one critical point to another as various parameters are decreased. This is a prototype for the general case. In this instance, the global behaviour at each stage resides in a single equilibrium point.

Note that when $\lambda_1 > 1$, then E_1 is the only critical point in the nonnegative (S, x_1, x_2, y) cone, $\mathbb{R}_+^4$, and when $\lambda_1 = 1$, E_1 and E_{λ_1} coalesce.

Theorem 6.1. If $\lambda_1 \geq 1$, then E_1 is globally asymptotically stable for (3.4).

Proof: Since $\lambda_2 > \lambda_1 \geq 1$, the result follows immediately from Theorems 5.2 and 5.3. □

Now we shall maintain $\lambda_1 + \delta > 1$, but allow λ_1 to decrease below 1. We shall show that as E_{λ_1} appears in $\mathbb{R}_+^4$ there is a transfer of global stability from E_1 to E_{λ_1}, and E_{λ_1} remains globally asymptotically stable provided $1 - \delta < \lambda_1 < 1$. In this parameter range E_1, E_{λ_1}, and if $\lambda_2 \leq 1$, E_{λ_2}, are the only equilibria in $\mathbb{R}_+^4$. In order to prove this we shall use the following lemma.

Lemma 6.2. Assume $\lambda_1 < 1$. Then for any solution of (3.4) for which $x_{10} > 0$, $\overline{\lim_{t\to\infty}}\, x_1(t) > 0$.

Proof: Suppose $\lim_{t\to\infty} x_1(t) = 0$. By Theorem 4.3 (iii), $\underline{\lim_{t\to\infty}}\, y(t) = 0$. If $\lambda_2 \geq 1$, then $\lim_{t\to\infty} x_2(t) = 0$ and $\lim_{t\to\infty} S(t) = 1$. If $\lambda_2 < 1$, then

$\lim_{t\to\infty} x_2(t) = 1 - \lambda_2$ and $\lim_{t\to\infty} S(t) = \lambda_2$. In either case $\lim_{t\to\infty} S(t) > \lambda_1$ exists. But $x_1'(t) = x_1(t)\big(-1 + p_1(S(t)) - y(t)h(x_1(t))\big)$, and so $x_1'(t) > 0$ for sufficiently large t, contradicting $\lim_{t\to\infty} x_1(t) = 0$. Therefore $\overline{\lim_{t\to\infty}}\, x_1(t) > 0$. □

<u>Theorem 6.3</u>. If $1 - \delta < \lambda_1 < 1$, then E_{λ_1} is globally asymptotically stable for (3.4) with respect to all solutions with initial conditions satisfying $x_{10} > 0$.

<u>Proof</u>: Let $\big(S(t), x_1(t), x_2(t), y(t)\big)$ be a solution of (3.4) and let Ω denote its omega-limit set. Since $1 - \delta < \lambda_1 < 1$, E_{λ_1} is locally asymptotically stable for (3.4) (see A5.A). Therefore $E_{\lambda_1} \in \Omega$ implies $\Omega = \{E_{\lambda_1}\}$. By Lemma 6.2, $\overline{\lim_{t\to\infty}}\, x_1(t) > 0$, and so there exists $P = (\bar S, \bar x$ [illegible] $\bar y) \in \Omega$ with $\bar x_1 > 0$. Let $\bar\gamma(t) = \big(\bar S(t), \bar x_1(t), \bar x_2(t), \bar y(t)\big)$, [illegible] P, be the solution of (3.4) through P and denote its o[illegible]). Since $c\ell\, O(P) \subset \Omega$, if $\bar y = 0$ then $E_{\lambda_1} \in \Omega$ by [illegible] (II.3.5). If $\bar y \neq 0$, by the preceding argument it suff[illegible]o show that $\lim_{t\to\infty} \bar y(t) = 0$.

[illegible] sume $\delta < 1$ or the result follows by Theorem 5.3 (ii). Define ε su[illegible]hat $1 - \delta + \varepsilon = \lambda_1$. Then $\varepsilon > 0$. Since $P \in \Omega$ and $\Omega \subset L$ by [illegible]) and Theorem 5.2,

$$(\bar S + \bar x_1 + \bar x_2 + \bar y)(t) = 1 \quad \text{for all } t \geq 0, \text{ and} \tag{6.1}$$

$$(\bar S + \bar x_1 + \bar x_2 + \bar y)'(t) = 0 \quad \text{for all } t \geq 0. \tag{6.2}$$

If $\overline{\lim_{t\to\infty}}\, \bar S(t) < \lambda_1$, then $\lim_{t\to\infty} \bar x_1(t) = 0$ contradicting Lemma 6.2.

But $\overline{\lim_{t\to\infty}}\, \bar{S}(t) \ge \lambda_1$ implies that $\bar{S}(t) > \lambda_1$ for all large t or there exists $\tau \ge 0$ such that $\lambda_1 \ge \bar{S}(\tau) \ge \lambda_1 - \varepsilon/2$. By (6.1) $\bar{x}_1(\tau) \le 1 - \bar{S}(\tau) \le 1 - (\lambda_1 - \varepsilon/2) = \delta - \varepsilon/2$. But then $\bar{y}'(\tau) \le \bar{y}(\tau)\big(-1 + q(\delta - \varepsilon/2)\big) < 0$. $\bar{S}(\tau) \le \lambda_1$ implies $\bar{x}_1'(\tau) \le 0$ and $\bar{x}_2'(\tau) \le 0$. Therefore, by (6.2) $\bar{S}'(\tau) > 0$ and so $\bar{S}(\tau) \ge \lambda_1 - \varepsilon/2$ for all $t \ge \tau$. In any case it follows that $\bar{S}(t) \ge \lambda_1 - \varepsilon/2$ for all sufficiently large t and so $\bar{x}_1(t) \le \delta - \varepsilon/2$ for all large t. This implies $\lim_{t\to\infty} \bar{y}(t) = 0$. The result follows. □

Next we shall assume that λ_2 is sufficiently large so that $\hat{x}_2 = 1 - \lambda_2 - \delta p_1(\lambda_2) < 0$. This is equivalent to $S^* < \lambda_2$. However, we shall allow the sum $\lambda_1 + \delta$ to decrease. When $\lambda_1 + \delta = 1$ then E_{λ_1} and E_{S^*} coalesce, i.e. $S^* = \lambda_1$ and $y^* = 0$. Therefore condition (A5.A.3), (i.e. $y^*(\delta q'(\delta) - 1)/\delta + \delta p_1'(S^*) > 0$) holds, since $p_1'(\lambda_1) > 0$ by (2.4). By the continuity of the roots of the characteristic equation as a function of its coefficients, it follows that as the sum $\lambda_1 + \delta$ decreases below 1, E_{S^*} is at least initially locally asymptotically stable (see (A5.A.2) and (A5.A.3)). At the same time E_{λ_1} loses not only its global stability but also its local stability since $1 - \lambda_1 > \delta$ implies that the eigenvalue $-1 + q(1 - \lambda_1)$ is positive (see A5.A.c).

In what follows we shall see that in certain special cases E_{S^*} picks up the global stability lost by E_{λ_1} and maintains it provided $\lambda_1 + \delta < 1$ and $1 - \lambda_2 - \delta p_1(\lambda_2) < 0$. In this case, if we allow λ_2 and/or δ to decrease, once $1 - \lambda_2 - \delta p_1(\lambda_2) = 0$, E_{S^*} and $\hat{E}_{\lambda_2}$ coalesce. As these parameters decrease further, E_{S^*} loses its local stability since then $S^* > \lambda_2$, and there is a transfer of global stability to $\hat{E}_{\lambda_2}$. That this nice sequential transfer of global stability from one critical point to another is not always the case with general monotone kinetics will be demonstrated by an example in Section 9.

In order to prove the global stability results, we will use LaSalle's extension theorem [47] which we shall state here for the general system of differential equations

$$x' = f(x) . \tag{6.3}$$

Here $f(x)$ is a vector-valued function, continuous in x for $x \in c\ell\, G$ where G is an open subset of $\mathbf{R}^n$. Before we state the theorem we require the following definition. Let V be a continuously differentiable function mapping $\mathbf{R}^n$ to $\mathbf{R}$. Then we say V is a *Lyapunov function* in G for (6.3) if, the trajectory derivative with respect to (6.3), $\dot{V} = \operatorname{grad} V \cdot f \leq 0$ on G.

Theorem 6.4 (LaSalle's Extension Theorem). If V is a Lyapunov function in G for (6.3), then each bounded orbit $\gamma \subseteq G$ approaches M where M is the largest invariant subset of $\{x \in c\ell\, G : \dot{V}(x) = 0\}$.

The following Theorem shows that in the special case that predation is described by a linear function of prey concentration (i.e. $q(x_1) = x_1/\delta$) and substrate uptake by each competitor either by linear (i.e. $p_i(S) = S/\lambda_i$) or by Michaelis-Menten $(p_i(S) = m_i S/(\delta(m_i - 1) + S))$ kinetics, global stability transfers from E_{λ_1} to E_{S^*} as $\lambda_1 + \delta$ decreases below 1 and is maintained by E_{S^*} in the parameter range $\lambda_1 + \delta < 1$ and $1 - \lambda_2 - \delta p_1(\lambda_2) < 0$.

Theorem 6.5. Assume that $\lambda_1 + \delta < 1$. If $x_{20} \geq 0$, assume that $1 - \lambda_2 - \delta p_1(\lambda_2) < 0$. Let $q(x_1)$ be linear, i.e. $q(x_1) = x_1/\delta$ and assume that each $p_i(S)$ $i = 1,2$ is either linear, i.e. $p_i(S) = S/\lambda_i$ or Michaelis-Menten, i.e. $p_i(S) = m_i S/(\lambda_i(m_i - 1) + S)$. Then E_{S^*} is globally asymptotically stable for (3.4) with respect to all solutions for which $x_{10} > 0$ and $y_0 \geq 0$.

Proof: Define the function $V : \text{int}\, \mathbb{R}_+^4 \to \mathbb{R}$ by

$$(6.4) \qquad V(S,x_1,x_2,y) = S - S^* - S^* \ln \frac{S}{S^*} + k_1 \left[x_1 - \delta - \delta \ln \frac{x_1}{\delta} \right] + k_2 x_2 + k_1 \left[y - y^* - y^* \ln \frac{y}{y^*} \right],$$

where the constants $k_1, k_2 \in \mathbb{R}$ are assumed to satisfy

$$(6.5) \qquad \delta(S^* - S)p_1(S)/S + k_1(\delta(-1 + p_1(S)) - y^*) = 0, \quad \text{for all } S > 0,$$

and if $x_{20} > 0$,

$$(6.6) \qquad (S^* - S)p_2(S)/S + k_2(-1 + p_2(S)) \leq 0, \quad \text{for all } S > 0.$$

If such constants k_1 and k_2 exist, then the time derivative of V computed along solutions of system (3.4) is

$$\begin{aligned}
\dot{V}(S,x_1,x_2,y) &= \left(1-\frac{S}{S^*}\right)S' + k_1\left(1-\frac{\delta}{x_1}\right)x_1' + k_2x_2' + k_1\left(1-\frac{y^*}{y}\right)y' \\
&= x_1\big(\delta(S^*-S)p_1(S)/S + k_1(\delta(-1+p_1(S)) - y^*)\big)/\delta \\
&\qquad + x_2\,\big((S^*-S)p_2(S)/S + k_2(-1+p_2(S))\big) \\
&\qquad + (S-S^*)(1-S)/S - k_1\big(\delta(-1+p_1(S)) - y^*\big) \\
&= x_2\,\big((S^*-S)p_2(S)/S + k_2(-1+p_2(S))\big) \\
&\qquad + (S-S^*)\big(1-S-\delta p_1(S)\big)/S, \quad \text{by} \quad (6.5) \\
&\le 0,
\end{aligned}$$

since $1 - S^* - \delta p_1(S^*) = 0$ and either $x_{20} = 0$ and so $x_2(t) = 0$ for all t or the coefficient of the x_2 term is nonnegative by (6.6). Thus, if k_1 and k_2 exist such that (6.5) and (6.6) hold, then V is a Lyapunov function for (3.4) in the int $\mathbf{R}^4_+$. By Theorems 5.1 and 6.4 every solution of (3.4) for which $x_{10} > 0$ and $y_0 > 0$ approaches H where H is the largest invariant set in $\{(S,x_1,x_2,y) \in \mathbf{R}^4_+ : S = S^*,\ x_2 = 0,\ x_1 \ge 0,\ y \ge 0\}$. But then $H = \{E_{S^*}\}$, since $S = S^*$ and $x_2 = 0$ imply that $S' = 1 - S^* - x_1p_1(S^*) = 0$. Therefore, $x_1 = \delta$ and by Theorem 5.2, $y = y^*$.

The result follows provided we can show that there exist constants k_1 and k_2 such that (6.5) and (6.6) hold. If $p_1(S) = S/\lambda_1$ then take $k_1 = 1$. Then (6.5) becomes,

$$\delta(S^*-S)/\lambda_1 + \big(\delta(-1+S/\lambda_1) - \delta(-1+S^*/\lambda_1)\big) = 0 .$$

If $p_1(S) = m_1S/\big(\lambda_1(m_1-1)+S\big)$ take $k_1 = \big((m_1-1)\lambda_1 + S^*\big)/\big(\lambda_1(m_1-1)\big)$.

In this case (6.5) becomes,

$$\frac{\delta(S^*-S)m_1}{\lambda_1(m_1-1)+S} + \frac{\big((m_1-1)\lambda_1+S^*\big)}{\lambda_1(m_1-1)}\left(\delta\left(-1+\frac{m_1S}{\lambda_1(m_1-1)+S}\right) - \delta\left(-1+\frac{m_1S^*}{\lambda_1(m_1-1)+S^*}\right)\right)$$

$$= \frac{\delta(S^*-S)m_1}{\lambda_1(m_1-1)+S} + \frac{\delta\big((m_1-1)\lambda_1+S^*\big)}{\lambda_1(m_1-1)}\left(\frac{m_1S\big(\lambda_1(m_1-1)+S^*\big) - m_1S^*\big(\lambda_1(m_1-1)+S\big)}{\big(\lambda_1(m_1-1)+S\big)\big(\lambda_1(m_1-1)+S^*\big)}\right)$$

$$= \frac{\delta(S^*-S)m_1}{\lambda_1(m_1-1)+S} + \frac{\delta m_1\lambda_1(m_1-1)(S-S^*)}{\lambda_1(m_1-1)\big(\lambda_1(m_1-1)+S\big)}$$

$$= 0 .$$

If $p_2(S) = S/\lambda_2$, let $k_2 = 1$. Then (6.6) becomes,

$$(S^*-S)/\lambda_2 + (-1+S/\lambda_2) = (S^*-\lambda_2)/\lambda_2 < 0$$

since $1-\lambda_2-\delta p_1(\lambda_2) < 0$ implies that $S^* < \lambda_2$. If $p_2(S) = m_2S/\big(\lambda_2(m_2-1)+S\big)$, let $k_2 = m_2/(m_2-1)$. Then (6.6) becomes,

$$\frac{(S^*-S)m_2}{\lambda_2(m_2-1)+S} + \left(\frac{m_2}{m_2-1}\right)\left(-1+\frac{m_2S}{\lambda_2(m_2-1)+S}\right)$$

$$= \frac{(S^*-S)m_2}{\lambda_2(m_2-1)+S} + \frac{m_2}{m_2-1}\left(\frac{(S-\lambda_2)(m_2-1)}{\lambda_2(m_2-1)+S}\right)$$

$$= \frac{m_2(S^*-\lambda_2)}{\lambda_2(m_2-1)+S} < 0 .$$

□

The next theorem also concerns the transfer of global stability under the assumptions that predation is linear and substrate uptake is either linear or Michaelis-Menten. In this case stability passes from E_{S*} to $\hat{E}_{\lambda_2}$ as $1 - \lambda_2 - \delta p_1(\lambda_2)$ increases above zero and $\hat{E}_{\lambda_2}$ appears in the positive (S,x_1,x_2,y) cone and $\hat{E}_{\lambda_2}$ remains globally stable provided $1 - \lambda_2 - \delta p_1(\lambda_2) > 0$. (Recall that when $1 - \lambda_2 - \delta p_1(\lambda_2) = 0$, E_{S*} and $\hat{E}_{\lambda_2}$ coalesce.)

Theorem 6.6. Assume that $1 - \lambda_2 - \delta p_1(\lambda_2) > 0$. Let $q(x_1) = x_1/\delta$ and assume that for each $i = 1,2$ either $p_i(S) = S/\lambda_i$ or $p_i(S) = m_i S/\big(\lambda_i(m_i - 1) + S\big)$. Then $\hat{E}_{\lambda_2}$ is globally asymptotically stable with respect to solutions of (3.4) for which $x_{i0} > 0$, $i = 1,2$ and $y_0 > 0$. (Recall that $\hat{E}_{\lambda_2} = (\lambda_2, \delta, \hat{x}_2, \hat{y})$ where $\hat{x}_2 = 1 - \lambda_2 - \delta p_1(\lambda_2)$ and $\hat{y} = \delta\big(-1 + p_1(\lambda_2)\big)$.)

Proof: Define the function $V : \operatorname{int} \mathbb{R}^4_+ \to \mathbb{R}$ by

$$(6.7)\qquad V(S,x_1,x_2,y) = S - \lambda_2 - \lambda_2 \ln \frac{S}{\lambda_2} + k_1\left(x_1 - \delta - \delta \ln \frac{x_1}{\delta}\right) + k_2\left(x_2 - \hat{x}_2 - \hat{x}_2 \ln \frac{x_2}{\hat{x}_2}\right) + k_1\left(y - \hat{y} - \hat{y} \ln \frac{y}{\hat{y}}\right),$$

where the constants k_1 and k_2 are assumed to satisfy

$$(6.8)\qquad \delta(\lambda_2 - S)p_1(S)/S + k_1\big(\delta(-1 + p_1(S)) - \hat{y}\big) = 0, \quad \text{for all } S > 0,$$

and

$$(6.9)\qquad (\lambda_2 - S)p_2(S)/S + k_2\big(-1 + p_2(S)\big) = 0, \quad \text{for all } S > 0.$$

Provided that such constants exist, the time derivative of V along solutions of (3.4) is

$$\begin{aligned}
\dot{V}(S,x_1,x_2,y) &= \left(1-\frac{\lambda_2}{S}\right)S' + k_1\left(1-\frac{\delta}{x_1}\right)x_1' + k_2\left(1-\frac{\hat{x}_2}{x_2}\right)x_2' + k_1\left(1-\frac{\hat{y}}{y}\right)y' \\
&= x_1\big((\lambda_2 - S)p_1(S)/S + k_1(\delta(-1+p_1(S)) - \hat{y})/\delta\big) \\
&\quad + x_2\big((\lambda_2 - S)p_2(S)/S + k_2(-1+p_2(S))\big) \\
&\quad + (S-\lambda_2)(1-S)/S - k_1\delta\big(-1+p_1(S)\big) - k_2\hat{x}_2\big(-1+p_2(S)\big) + k_1\hat{y} \\
&= (S-\lambda_2)(1-S)/S - \delta p_1(S)(S-\lambda_2)/S - \hat{x}_2 p_2(S)(S-\lambda_2)/S\,, \\
&\qquad \text{by (6.8) and (6.9)}, \\
&= (S-\lambda_2)\big(1 - S - \delta p_1(S) - \hat{x}_2 p_2(S)\big)/S \\
&\le 0\,.
\end{aligned}$$

Therefore if k_1 and k_2 exist such that (6.8) and (6.9) hold, V is a Lyapunov function for (3.4) in int $\mathbb{R}_+^4$ and so Theorems 5.1 and 6.4 imply that every solution of (3.4) with $x_{i0} > 0$ $i = 1,2$ and $y_0 > 0$ approaches H where H is the largest invariant set in $G = \{(S,x_1,x_2,y) \in \mathbb{R}_+^4 : S = \lambda_2,\ x_i \geq 0\ i = 1,2 \text{ and } y \geq 0\}$. Now $S = \lambda_2$ implies that $S' = 0$ and $x_2' = 0$. But then x_2 is constant and so since $S' = 1 - \lambda_2 - x_1p_1(\lambda_2) - x_2 = 0$ it follows that x_1 is constant. Therefore $x_1' = 0$ which implies that $x_1 = 0$ or $-1 + p_1(\lambda_2) - yh(x_1) = 0$. If $x_1 = 0$, then $x_2 = 1 - \lambda_2$ and $y = 0$ since $S + x_1 + x_2 + y = 1$ by Theorem 5.2. If $x_1 \neq 0$, then $y = \big(-1 + p_1(\lambda_2)\big)/h(x_1)$ a constant and so $x_1 = \delta$ and $x_2 = 1 - \lambda_2 - \delta p_1(\lambda_2)$. Therefore $G = \{E_{\lambda_2}\} \cup \{\hat{E}_{\lambda_2}\}$. However E_{λ_2} is locally unstable and has the 3-dimensional stable manifold

$$W^s(E_{\lambda_2}) = \{(S,x_1,x_2,y) : x_1 = 0,\ x_2 > 0,\ y \geq 0,\ S \geq 0\}$$

and so no trajectory with $x_{i0} > 0 \quad i = 1,2$ and $y_0 > 0$ can approach E_{λ_2}. Hence $\hat{E}_{\lambda_2}$ is globally asymptotically stable for (3.4) provided $x_{i0} > 0 \quad i = 1,2$ and $y_0 > 0$.

The result follows provided we can show that there exist constants k_1 and k_2 such that (6.8) and (6.9) hold.

If $p_1(S) = S/\lambda_1$ let $k_1 = 1$.

If $p_1(S) = m_1S/(\lambda_1(m_1-1)+S)$ let $k_1 = ((m_1-1)\lambda_1+\lambda_2)/(\lambda_1(m_1-1))$.

If $p_2(S) = S/\lambda_2$ let $k_2 = 1$.

If $p_2(S) = m_2S/(\lambda_2(m_2-1)+S)$ let $k_2 = m_2/(m_2-1)$.

□

Sufficient conditions for the global stability of critical points of (3.4) are summarized in Table IX. That this orderly transfer of global stability from one critical point to another (as various parameters are varied, making conditions favourable enough for a new population to survive) is not always the case for general monotone dynamics, will be illustrated in Example 9.1. First we shall see what can be said for general monotone dynamics. Before we consider the entire food web (3.4) in Section 8, we consider a simple food chain in the next section. This food chain is interesting in its own right, and we shall need some information concerning it in order to analyze the food web.

Critical Point	*Conditions for Global Stability
E_1	$\lambda_1 > 1$
E_{λ_1}	$\lambda_1 < 1$, $\lambda_1 + \delta > 1$
E_{S*}	$\lambda_1 + \delta < 1$, $1 - \lambda_1 - \delta p_1(\lambda_2) < 0$
$\hat{E}_{\lambda_2}$	$1 - \lambda_1 - \delta p_1(\lambda_2) > 0$

*q assumed to be Lotka-Volterra

p_i assumed to be either Lotka-Volterra or Michaelis-Menten for each $i = 1,2$.

TABLE IX Sufficient Conditions for Global Stability of Critical Points of (3.4)

7. A SIMPLE FOOD CHAIN. We first encountered the following food chain in Section 4 (see system (4.3)) where we considered the three dimensional subsystems of the food web (3.4).

$$\begin{aligned} S'(t) &= 1 - S(t) - x(t)\,p\big(S(t)\big)\,, \\ x'(t) &= x(t)\big(-1 + p(S(t))\big) - y(t)q\big(x(t)\big)\,, \\ y'(t) &= y(t)\big(-1 + q(x(t))\big)\,, \end{aligned} \tag{7.1}$$

$$S_0\,,\ x_0\,,\ \text{and}\ \ y_0 \geq 0\,.$$

We drop the subscript 1 here (except for λ_1), since there is no ambiguity, and we use the notation for the critical points (E_1^3, $E_{\lambda_1}^3$, and E_{S*}^3) introduced for system (4.3).

System (7.1) has been studied by others (eg. [12,19,27,44,68,77]). Except for Butler, Hsu, and Waltman [12] and Gard [27] most of the previous work has concerned local stability analysis, numerical solutions or experimental results. The local analysis is summarized in A5.B.

Note that all the results in Sections 5 and 6 apply to (7.1) with the obvious modifications. In particular, there is a transference of global stability from E_1^3 to $E_{\lambda_1}^3$ as λ_1 decreases below 1 and at least a transference of local stability from $E_{\lambda_1}^3$ to E_{S*}^3 as $\lambda_1 + \delta$ decreases below 1. We conjecture that E_{S*}^3 is globally asymptotically stable as long as it is locally asymptotically stable and that if it loses its stability it does so via a Hopf bifurcation in which the bifurcating periodic orbit picks up the global stability.

In the special case that the functional response q is

Lotka-Volterra and p satisfies either Lotka-Volterra or Michaelis-Menten kinetics, by Corollary 6.6, E^3_{S*} is globally asymptotically stable provided $\lambda_1 + \delta < 1$.

Assuming the functional responses p and q both satisfy Michaelis-Menten kinetics, Butler et al. [12] use the Poincaré criterion (see eg. Coppel [17]) to show that E^3_{S*} is globally asymptotically stable whenever it is locally asymptotically stable. Since E^3_{S*} is at least initially asymptotically stable as $\lambda_1 + \delta$ decreases below 1, this implies that in this case, there is a transfer of global stability from $E^3_{\lambda_1}$ to E^3_{S*}. They also show that if E^3_{S*} is ever unstable then there is at least one periodic orbit surrounding it. They conjecture that if E^3_{S*} is unstable then the limit cycle is unique and hence must be a global attractor with respect to noncritical orbits with positive initial conditions. Though they do not comment, by their method of proof they actually show that if E^3_{S*} loses stability by decreasing $\lambda_1 + \delta$ appropriately, then the inequality in (A5.B.2) must be reversed and so at least initially there is a unique periodic orbit which is globally attracting with respect to noncritical orbits with positive initial conditions. In this case, then, there is a transfer of global stability from E^3_{S*} to a bifurcating periodic orbit (as $\lambda_1 + \delta$ decreases).

Gard [27] on the other hand, considers a more general model than (7.1) which reduces to (7.1) if the function $g(x)$ in his model is taken to be $1 - x$ and the parameters a,b,c and d in his model are all equal to 1. In this case Gard obtains a weaker form of persistence of (7.1), namely that provided the initial conditions are positive and

$\lambda_1 + \delta < 1$, then $\overline{\lim}_{t\to\infty}$ of each component of the solution is positive. He also shows that there is a unique interior equilibrium and if the equilibrium is unstable there is a nontrivial periodic orbit with trajectory in $L_{\{1\}} \cap \mathbf{R}^3_+$.

In this section we strengthen Gard's result for (7.1) by showing $\underline{\lim}_{t\to\infty}$ of each component of the solution is positive using a technique similar to the one used to prove Theorem 2.1 in Freedman and Waltman [22]. We also prove several results about (7.1) which will be used in Section 8 to show persistence of (3.4). These results are interesting in themselves since they concern the eventual behaviour of solutions of (7.1). Then we investigate the properties of periodic orbits if they exist. Finally we apply the Poincaré criterion to (7.1) to determine results for global stability of E^3_{S*}.

Theorem 7.1. Let $\gamma(t) = \big(S(t), x(t), y(t)\big)$ be a solution of (7.1). Then

(i) $\underline{\lim}_{t\to\infty} S(t) > 0$.

(ii) if $\lambda_1 < 1$ and $x_0 > 0$, $\underline{\lim}_{t\to\infty} x(t) > 0$.

(iii) if $\lambda_1 + \delta < 1$ and $x_0, y_0 > 0$, $\underline{\lim}_{t\to\infty} y(t) > 0$.

Proof: (i) is obvious.

(ii) Let Ω denote the omega-limit set of $\gamma(t)$. By Theorem 5.1 $\Omega \subset \mathbf{R}^3_+$ is compact.

Assume $\lambda_1 < 1$ and $x_0 > 0$. Suppose $E^3_1 \in \Omega$. Since $\lambda_1 < 1$, E^3_1 is an unstable hyperbolic critical point (see (A5.B)) with stable manifold $W^s(E^3_1) = \{(S,x,y) : S \geq 0,\ x = 0,\ y \geq 0\}$. Since $\gamma(0) \notin W^s(E_1)$, $\Omega \neq \{E^3_1\}$. By Theorem II.5.2, there exists

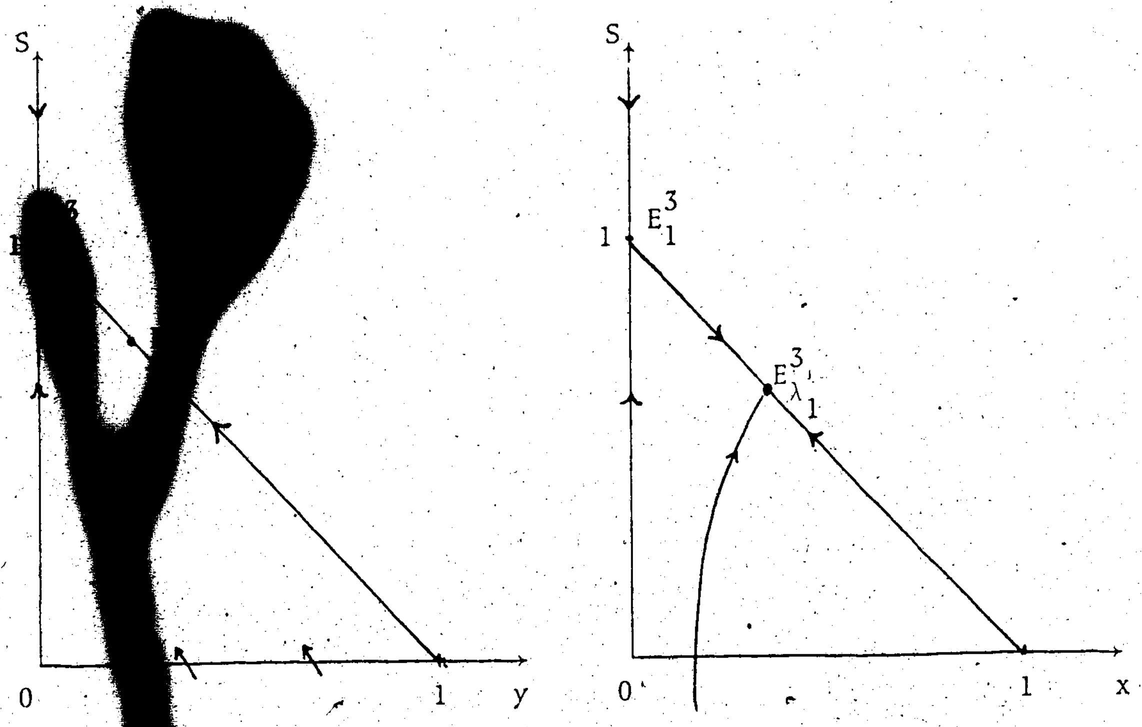
$P^s \in \left(W^s(E_1^3)\setminus\{E_1^3\}\right) \cap \Omega$. By Theorem 5.2, $P^s \in \Omega \subset \mathcal{L}_{\{1\}}$, a positively invariant set. But then (see Figure (22(a))) $\mathcal{O}^-(P^s) \not\subset \mathbb{R}^3_+$, a contradiction since $P^s \in \Omega$ implies that $c\ell\left(\mathcal{O}(P^s)\right) \subset \Omega \subset \mathbb{R}^3_+$. Therefore $E_1^3 \notin \Omega$.

Suppose $\lambda_1 < 1$, $x_0 > 0$ and $\underline{\lim}_{t\to\infty}\, x(t) = 0$. Then there exists $P = (\bar{S},0,\bar{y}) \in \Omega$ and so $c\ell\left(\mathcal{O}(P)\right) \subset \Omega$. By Theorem 5.3 (iii), $E_1^3 \in \Omega$, a contradiction. Therefore $\underline{\lim}_{t\to\infty}\, x(t) > 0$.

(iii) Suppose $\lambda_1 + \delta < 1$, $x_0, y_0 > 0$. By a similar argument to the one used above to show $E_1^3 \notin \Omega$, it can be shown that $E^3_{\lambda_1} \notin \Omega$. Assume $\underline{\lim}_{t\to\infty}\, y(t) = 0$. Then there exists $Q = (\tilde{S},\tilde{x},0) \in \Omega$ where $\tilde{x} > 0$ since $\underline{\lim}_{t\to\infty}\, x(t) > 0$ by (ii). By Corollary II.3.5, $E^3_{\lambda_1} \in c\ell\left(\mathcal{O}(Q)\right) \subset \Omega$, a contradiction. Therefore $\underline{\lim}_{t\to\infty}\, y(t) > 0$.

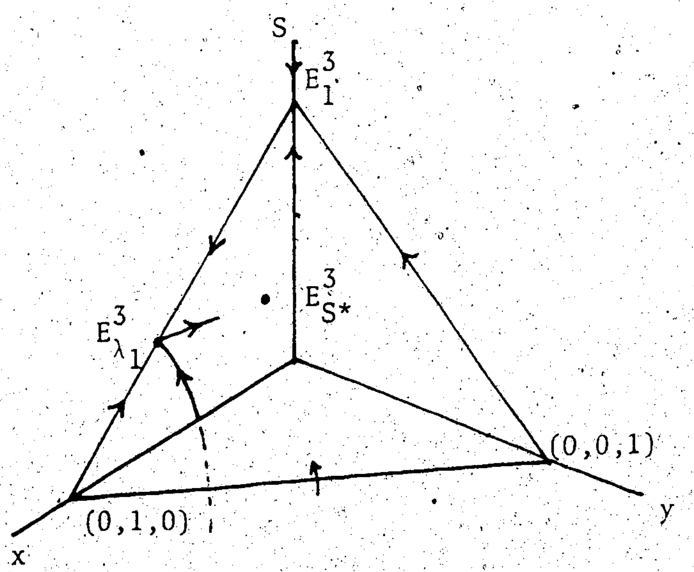
□

We have therefore shown that no matter how tenacious the predator, provided the substrate concentration is sufficient for the prey to survive in pure competition, it will survive predation in the sense that its concentration remains bounded away from zero for all positive time. To avoid extinction of the predator, however, the predator must be efficient enough, i.e. $\lambda_1 + \delta < 1$. In this case the food chain persists. On the other hand it is possible to show that the more efficient the predator (i.e. the closer δ is to zero), the smaller the prey concentration is *"on the average"* and even though the prey concentration is bounded away from zero, the closer that bound is to zero. This is basically the content of the next lemma in which we clarify what we mean by *"on the average."* We shall also require this



(a) $x \equiv 0$, $\lambda_1 < 1$

(b) $y \equiv 0$



(c) $E_{S*}^3 \in \text{int}\ \mathbb{R}_+^3$ and may be stable or unstable

FIGURE 22 Phase Portraits of (7.1) for $\lambda_1 + \delta < 1$

lemma and the following as technical lemmas for our discussion of persistence of the food web in Section 8. However, before stating the next lemma we introduce the following parametrization of (7.1):

$$(7.2)_\delta \qquad \begin{aligned} S'(t) &= 1 - S(t) - x(t)p\big(S(t)\big) , \\ x'(t) &= x(t)\big(-1 + p(S(t))\big) - y(t)q_\delta\big(x(t)\big) , \\ y'(t) &= y(t)\big(-1 + q_\delta(x(t))\big) , \\ &S_0 ,\ x_0 \text{ and } y_0 \ge 0 . \end{aligned}$$

We assume that the function q_δ satisfies all the usual assumptions on q (i.e. (2.2)-(2.3); (2.6)-(2.8); and (3.5)-(3.7)). In addition we assume that

$$(7.3) \qquad \lim_{\delta\to 0^+} q_\delta(\varepsilon) = +\infty \quad \text{for every fixed } \varepsilon > 0 .$$

We show that if q satisfies Lotka-Volterra, Michaelis-Menten or multiple saturation kinetics then q can be parametrized in this way. In these examples $\delta \to 0^+$ is equivalent to the maximum growth rate tending to $+\infty$.

If q is Lotka-Volterra then $q(x) = \eta x$ for some positive constant $\eta(\delta) > 0$. Then $q_\delta(x) = x/\delta$, since then $q_\delta(\delta) = 1$. But for any fixed $\varepsilon > 0$, $\lim_{\delta\to 0^+} q_\delta(\varepsilon) = \lim_{\delta\to 0^+} \varepsilon/\delta = +\infty$.

If q satisfies Michaelis-Menten kinetics, then $q(x) = \frac{\eta x}{a+x}$ where $\eta(\delta)$ and a are positive constants. Then $q_\delta(x) = \frac{(a+\delta)x}{\delta(a+x)}$ and so for $\varepsilon > 0$ fixed, $\lim_{\delta\to 0^+} q_\delta(\varepsilon) = \lim_{\delta\to 0^+} \frac{(a+\delta)\varepsilon}{\delta(a+\varepsilon)} = +\infty$.

If q satisfies multiple saturation kinetics, (e.g. $q(x) = (\eta x^2)/((K+x)(L+x))$ where $\eta(\delta)$, K and L are positive constants), then $q_\delta(x) = ((K+\delta)(L+\delta)x^2)/(\delta^2(K+x)(L+x))$ and so for $\varepsilon > 0$ fixed, $\lim_{\delta \to 0^+} q_\delta(\varepsilon) = \lim_{\delta \to 0^+} ((K+\delta)(L+\delta)\varepsilon^2)/(\delta^2(K+\varepsilon)(L+\varepsilon)) = +\infty$.

Lemma 7.2. Let $\varepsilon > 0$ be given. Assume that $\lambda_1 + \delta < 1$. Let $(S(t), x(t), y(t))$ be any fixed solution of $(7.2)_\delta$ for which $x_0 > 0$ and $y_0 > 0$. Choose $\ell > 0$, $L > 1$ and $\overline{T} \geq 0$ such that $\ell < y(t) < L$ for all $t \geq \overline{T}$ where ℓ and $\overline{T}$ depend on δ and the solution. (This is possible by Theorems 5.1, 5.2 and 7.1.) Select any $T > \ell n(L/\ell)$ and any $s \geq \max(T, \overline{T})$. Define $A = \{t \in [s-T, s] : x(s) \geq \varepsilon\}$, $a = \mu(A)$, the Lebesgue measure of A, and $\alpha = \frac{1}{T}\mu(A)$. Then $\alpha < 2/q_\delta(\varepsilon)$.

Proof: Define A^c to be $[s-T, s] \setminus A$.

If $t \in A$, then $y'(t)/y(t) \geq -1 + q_\delta(\varepsilon)$.

If $t \in A^c$ then $y'(t)/y(t) \geq -1$.

Integrating the y equation from $s-T$ to s yields:

$$\ell n(y(s)/y(s-T)) \geq \int_A (-1 + q_\delta(\varepsilon))d\mu + \int_{A^c} -1\, d\mu$$

$$= (-1 + q_\delta(\varepsilon))a - (T - a)$$

$$= T(\alpha q_\delta(\varepsilon) - 1).$$

Therefore $\alpha < 2/q_\delta(\varepsilon)$ since otherwise

$$\ell n(L/\ell) \geq \ell n(y(s)/y(s-T)) \geq T,$$

a contradiction. $\square$

We can also show that if $\delta > 0$ is sufficiently small then *"on the average"* the S-component of any solution eventually remains close to one. This is made rigorous in the following lemma.

Lemma 7.3. Choose ε such that $0 < \varepsilon < 1/4$ and choose $L > 1$. Let $M = \max(L, p(L))$. Assume $\delta > 0$ is sufficiently small so that $\lambda_1 + \delta < 1$ and $q_\delta(\varepsilon) > 4(1 + M/\varepsilon k)/\sqrt{\varepsilon}$. Let $(S(t), x(t), y(t))$ be any fixed solution of $(7.2)_\delta$ for which $x_0 > 0$ and $y_0 > 0$. Choose $\ell > 0$ and $\bar{T} > 0$ so that

$$\ell \leq y(t) \leq L\,,$$

$$0 \leq S(t) \leq L\,, \text{ and}$$

$$0 \leq x(t) \leq L$$

for all $t \geq \bar{T}$. Select

$$T > \max\left(\ell n(L\backslash\ell), 2/\varepsilon, \bar{T}\right)$$

such that

$$S(t) < 1 + \varepsilon M \quad \text{for all } t \geq T\,.$$

For any $s \geq T$, define

$$B = \{t \in [s-T, s] : S(t) \leq 1 - (1+k)\,\varepsilon M\} \quad \text{where} \quad k + 1 = 1/\sqrt{\varepsilon}\,,$$

$$b = \mu(B) \quad \text{and} \quad \beta = \frac{1}{T}\,\mu(B)\,.$$

Then $\beta < 6\sqrt{\varepsilon}$.

Proof: Define

$$A = \{t \in [s-T,s] : x(t) \geq \varepsilon\},$$

$$a = \mu(A) \quad \text{and} \quad \alpha = \frac{1}{T}\mu(A).$$

Let B^c denote $[s-T,s] \setminus B$. Then $[s-T,s] = \bigcup_{i=1}^{n} G_i$ where

$$G_1 = B \cap A^c \quad (\text{and so } \mu(G_1) \geq b-a),$$

$$G_2 = B \cap A \quad (\text{and so } \mu(G_2) \leq a),$$

$$G_3 = B^c \cap A^c \quad (\text{and so } \mu(G_3) \leq T),$$

$$G_4 = B^c \cap A \quad (\text{and so } \mu(G_4) \leq a).$$

Then,

$$S'(t) \geq 1 - \big(1-(1+k)\varepsilon M\big) - \varepsilon M = \varepsilon kM \quad \text{for} \quad t \in G_1,$$

$$S'(t) \geq 1 - \big(1-(1+k)\varepsilon M\big) - M^2 \geq -M^2 \quad \text{for} \quad t \in G_2,$$

$$S'(t) \geq 1 - (1+\varepsilon M) - \varepsilon M \geq -2\varepsilon M \quad \text{for} \quad t \in G_3,$$

and $$S'(t) \geq 1 - (1+\varepsilon M) - M^2 = -\varepsilon M - M^2 \quad \text{for} \quad t \in G_4,$$

since s is chosen sufficiently large.

Integrating the S equation from $s-T$ to s yields

$$M \geq S(s) - S(s-T) \geq \varepsilon kM(b-a) - M^2 a - 2\varepsilon MT - (\varepsilon M + M^2)a.$$

Therefore,

$$b \leq a(1+1/k) + (1 + 2Ma + 2\varepsilon T)/\varepsilon k\ , \quad \text{or}$$

$$\beta \leq 2\alpha + 1/T\varepsilon k + 2M\alpha/\varepsilon k + 2/k, \quad \text{since}\quad k > 1 \quad \text{if}\quad 0 < \varepsilon < 1/4$$

$$\leq 6\sqrt{\varepsilon}$$

since $T > 2/\varepsilon$ by selection and for $0 < \varepsilon < 1/4$, $k > 1/2\sqrt{\varepsilon}$ which implies that $1/T\varepsilon k < \sqrt{\varepsilon}$ and $2/k < 4\sqrt{\varepsilon}$. Also, $2\alpha(1+M/\varepsilon k) < \sqrt{\varepsilon}$ by Lemma 7.2 since $q_\delta(\varepsilon) > 4(1+M/\varepsilon k)/\sqrt{\varepsilon}$. □

Since by Theorem 5.2, $S + x + y \to 1$, it is evident that if the hypotheses of the preceding Lemma hold then *"on the average"* the y-component of any solution eventually remains close to zero provided $\delta > 0$ is sufficiently small.

Next we use a phase portrait analysis to determine some properties of periodic orbits for (7.1) when they exist. In order to do this we note that by Lemma 5.2 the simplex

$$L_{\{1\}} = \{(S,x,y) : S,x,y \geq 0\ ;\ S + x + y = 1\}$$

is positively invariant and globally attracting for (7.1). Since the omega-limit set of any solution of (7.1) lies in $L_{\{1\}}$ it will be useful to consider (7.1) restricted to $L_{\{1\}}$:

$$(7.4)_{L_{\{1\}}}\qquad \begin{aligned} S'(t) &= 1 - S(t) - x(t)p\big(S(t)\big)\ , \\ x'(t) &= x(t)\big(-1 + p(S(t))\big) - y(t)q\big(x(t)\big)\ , \\ y'(t) &= y(t)\big(-1 + q(x(t))\big)\ , \\ S_0 + x_0 + y_0 &= 1,\ \ S_0,x_0,y_0 \geq 0\ . \end{aligned}$$

This system is equivalent to the two dimensional system obtained by substituting $x(t) = 1 - S(t) - y(t) \geq 0$:

$$S'(t) = 1 - S(t) - \big(1 - S(t) - y(t)\big)p\big(S(t)\big) = f_1(S,y),$$

$$(7.5) \qquad y'(t) = y(t)\big(-1 + q(1 - S(t) - y(t))\big) = f_2(S,y),$$

$$S_0, \ y_0 \geq 0 \ \text{ and } \ S_0 + y_0 \leq 1.$$

The phase portrait for (7.5) in the case that $\lambda_1 + \delta < 1$ is given in Figure 23. The equations of the substrate and predator isoclines are

$$(7.6) \qquad y(t) = \frac{-\big(1 - S(t)\big)\big(1 - p(S(t))\big)}{p\big(S(t)\big)} \quad \text{and} \quad 1 - S(t) - y(t) = \delta$$

respectively. It is now possible to prove

<u>Theorem 7.4</u>. Assume $\lambda_1 + \delta < 1$. Then, any nontrivial periodic solution $\big(S(t),x(t),y(t)\big)$ of (7.1) (or $\big(S(t),y(t)\big)$ of (7.2)) satisfies:

$$(7.7) \qquad \lambda_1 < S(t) < 1,$$

$$(7.8) \qquad 0 < x(t) < 1 - \lambda_1,$$

$$(7.9) \qquad 0 < y(t) < 1 - (\lambda_1 + \delta).$$

<u>Proof</u>: By Theorem 5.2 the omega-limit set of any solution of (7.1) lies entirely in the simplex $L_{\{1\}}$. Thus any periodic orbit of (7.1) lies entirely in $L_{\{1\}}$ since the omega-limit set of any periodic orbit is the periodic orbit itself. Thus it suffices to consider

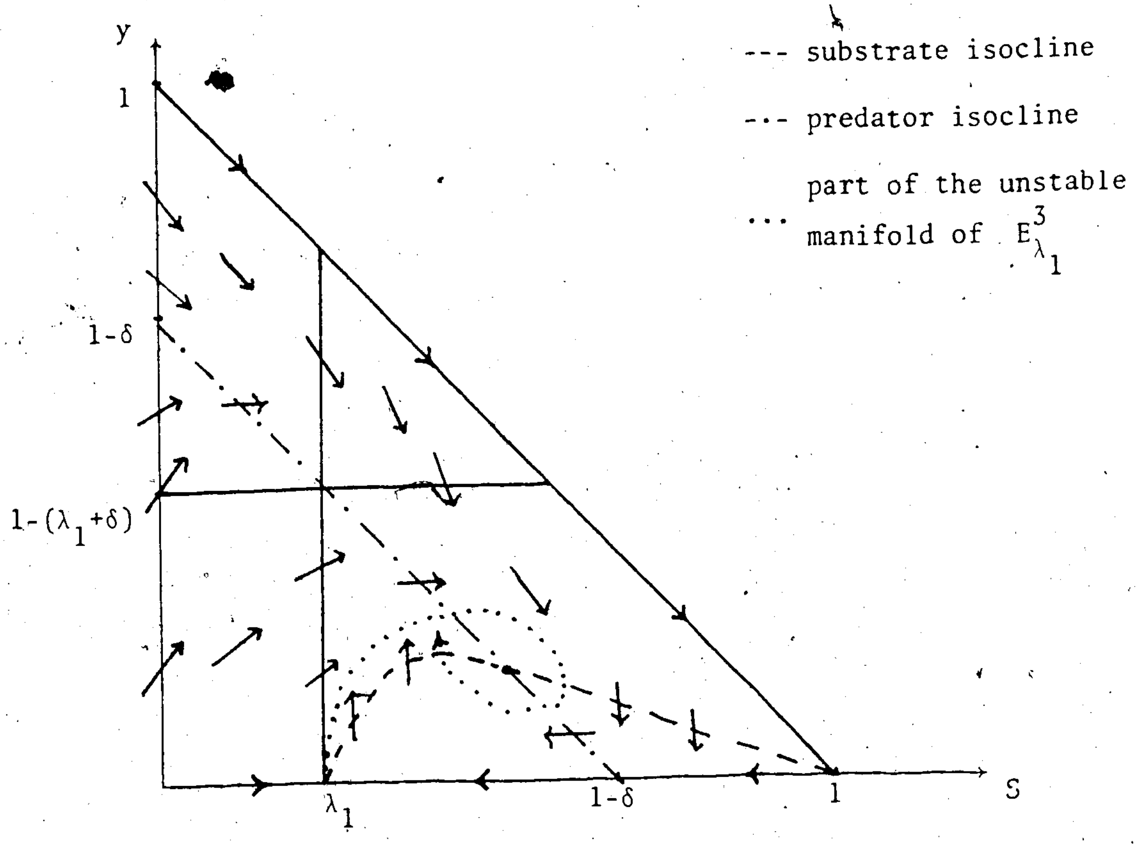


FIGURE 23 Phase Portrait of (7.5) for $\lambda_1 + \delta < 1$.

Any periodic orbit must lie inside the region marked out by the dotted line (part of the unstable manifold of $E^3_{\lambda_1}$).

$(7.4)_{L_{\{1\}}}$ or equivalently (7.5). But this is a 2-dimensional system (refer to Figure 23).

Assume $\gamma(t) = (S(t), y(t))$ is a nontrivial periodic solution of (7.5) and $x(t) = 1 - S(t) - y(t)$. For all $\tau \geq 0$ such that $S(\tau) \leq \lambda_1$,

$$S'(\tau) \geq 1 - S(\tau) - (1 - S(\tau) - y(\tau))p(\lambda_1) = y(\tau) > 0 .$$

(Note $y(\tau) \neq 0$ since otherwise $\gamma(t) = E^3_{\lambda_1}$, contradicting γ is a nontrivial periodic orbit.) Therefore on $\gamma(t)$, $S(t) > \lambda_1$ for all t.

For all $\tau \geq 0$ such that $y(\tau) \geq 1 - (\lambda_1 + \delta)$ and $S(\tau) > \lambda_1$,

$$y'(\tau) = y(\tau)(-1 + q(1 - S(\tau) - y(\tau))) < 0$$

since $1 - S(\tau) - y(\tau) < 1 - \lambda_1 - (1 - (\lambda_1 + \delta)) = \delta$. Therefore on $\gamma(t)$, $y(t) < 1 - (\lambda_1 + \delta)$ for all t.

That $S(t) < 1$, $0 < x(t) < 1 - \lambda_1$ and $y(t) > 0$ on $\gamma(t)$ for all t now follows, since $\gamma \subset L_{\{1\}}$ and the S-axis and the line $y + S = 1$ are invariant.

□

We are now ready to apply the Poincaré criterion to determine more information about the existence and stability of periodic orbits for (7.5) and hence (7.1).

Lemma 7.5. Let $(S(t), y(t))$ be an arbitrary periodic orbit of (7.5) with period ω. If we assume h is differentiable and we define

$$\Delta = \int_0^\omega \frac{\partial f_1}{\partial S}(S(t), y(t)) + \frac{\partial f_2}{\partial y}(S(t), y(t))dt ,$$

then

$$(7.10) \qquad \Delta = -\int_0^{\omega} x(t)\big(p'(S(t)) + y(t)h'(x(t))\big)dt ,$$

where $x(t) = 1 - S(t) - y(t) \geq 0$.

<u>Proof</u>: $$\Delta = \int_0^{\omega}\Bigg\{\Big[\big(-1 + p(S(t))\big) - x(t)p'\big(S(t)\big)\Big] + \Big[\big(-1 + q(x(t))\big) - y(t)q'\big(x(t)\big)\Big]\Bigg\}dt$$

$$= \int_0^{\omega}\Bigg\{\Bigg[\bigg(\frac{x'(t)}{x(t)} + y(t)h\big(x(t)\big)\bigg) - x(t)p'\big(S(t)\big)\Bigg] + \Bigg[\frac{y'(t)}{y(t)} - y(t)\big(h(x(t) - x(t)h'(x(t))\big)\Bigg]\Bigg\}dt$$

$$= -\int_0^{\omega} x(t)\big(p'(S(t)) + y(t)h'(x(t))\big)dt$$

since $\int_0^{\omega} \frac{x'(t)}{x(t)}dt = \int_0^{\omega}\frac{y'(t)}{y(t)}dt = 0$ since $x(t)$ and $y(t)$ are periodic of period ω. □

<u>Theorem 7.6</u>. Assume that h is differentiable and that E^3_{S*} is locally asymptotically stable. Suppose also that $p'\big(S(t)\big) + y(t)h'\big(x(t)\big) > 0$ whenever $0 < x(t) < 1 - \lambda_1$, $0 \leq y(t) < 1 - (\lambda_1 + \delta)$, and $\lambda_1 < S(t) < 1$. Then E^3_{S*} is globally asymptotically stable with respect to solutions of (7.1) which satisfy $x_0, y_0 > 0$ and $S_0 \geq 0$.

<u>Proof</u>: Recall that by Theorem 5.2 the omega-limit set of any solution of (7.1) lies entirely in the positively invariant simplex $L_{\{1\}}$

and note that if $(S(t),y(t))$ is a solution of (7.5) then $(S(t),x(t),y(t))$ is a solution of (7.1) where $x(t) = 1 - S(t) - y(t)$. Also by Theorem 7.1 any solution of (7.1) for which x_0, $y_0 > 0$ and $S_0 \geq 0$, persists, and so any solution of (7.5) for which $y_0 > 0$, $S_0 \geq 0$ and $S_0 + y_0 < 1$, persists.

To show that E^3_{S*} is globally asymptotically stable for (7.1) with respect to solutions for which x_0, y_0 and $S_0 \geq 0$, it suffices to show that (S^*,y^*) is globally asymptotically stable with respect to solutions of (7.5) for which $y_0 > 0$, $S_0 \geq 0$ and $S_0 + y_0 < 1$. This follows because the omega-limit set, Ω of any solution of (7.1) with x_0, $y_0 > 0$ and $S_0 \geq 0$ must contain only points of the form $\bar{P} = (\bar{S},\bar{x},\bar{y})$ where $\bar{S},\bar{x},\bar{y} > 0$ and $\bar{S} + \bar{x} + \bar{y} = 1$. The solution of (7.2) through the associated point $\bar{P}_1 = (\bar{S},\bar{y})$ converges to (S^*,y^*) if it is globally asymptotically stable. Therefore the orbit through $\bar{P}$, $\mathcal{O}(\bar{P})$, converges to E^3_{S*}. Since $c\ell(\mathcal{O}(\bar{P})) \subset \Omega$, $E^3_{S*} \in \Omega$. But then, E^3_{S*} asymptotically stable implies $\Omega = \{E^3_{S*}\}$.

Let $(S(t),y(t))$ be a nontrivial periodic solution of (7.2) with period $\omega > 0$. Let $x(t) = 1 - S(t) - y(t)$. Then $(S(t),x(t),y(t))$ is a nontrivial periodic solution of (7.1). By Theorem 7.4 and the hypothesis of this theorem, $p'(S(t)) + y(t)h'(x(t)) > 0$ and $x(t) > 0$ for $0 < t < \omega$. Therefore by (7.10) of Lemma 7.5, $\Delta < 0$. Applying the Poincaré criterion it follows that all nontrivial period solutions of (7.2) are asymptotically stable. Since (7.5) is a 2-dimensional system and since the only interior critical point is asymptotically stable, in order for a nontrivial periodic solution to exist, there must exist at least one unstable periodic solution. Thus, no nontrivial periodic orbit exists. By the Poincaré-Bendixson Theorem it follows that (S^*,y^*) is globally asymptotically stable and the result follows. ☐

Corollary 7.7. Assume that h is differentiable. Provided $\lambda_1 + \delta < 1$ is sufficiently close to 1, $E^3_{S^*}$ is globally asymptotically stable with respect to (7.1) for solutions satisfying $x_0, y_0 > 0$ and $S_0 \geq 0$.

Proof: Recall that $E^3_{S^*}$ is locally asymptotically stable for $\lambda_1 + \delta < 1$ provided $\lambda_1 + \delta$ is sufficiently close to 1. (This was shown in Section 6 for system (3.4).) If $h'(x(t)) \geq 0$, then $p'(S(t)) + y(t)h'(x(t)) > 0$. If $h'(x(t)) < 0$, but we assume $y(t) < 1 - (\lambda_1 + \delta)$, then

$$p'(S(t)) + y(t)h'(x(t)) > p'(S(t)) + (1 - (\lambda_1 + \delta))h'(x(t)) > 0$$

if $\lambda_1 + \delta$ sufficiently close to 1. The result follows by Theorem 7.6. ☐

Corollary 7.8. Assume $\lambda_1 + \delta < 1$. If h is differentiable and

$$h'(x(t)) \geq 0 \quad \text{for all} \quad 0 < x(t) < 1 - \lambda_1, \tag{7.11}$$

then $E^3_{S^*}$ is globally asymptotically stable with respect to solutions of (7.1) for which $x_0, y_0 > 0$ and $S_0 \geq 0$.

Proof: Since

$$q'(x(t)) = h(x(t)) + x(t)h'(x(t)), \tag{7.12}$$

by (7.11), $q'(x(t)) - h(x(t)) \geq 0$ for all $0 < x(t) < 1 - \lambda_1$. In particular this holds for $x(t) = \delta$ since $\delta < 1 - \lambda_1$. Therefore $\delta q'(\delta) - \delta h(\delta) = \delta q'(\delta) - 1 \geq 0$. This implies that condition (A5.B.2) holds. Thus E^3_{S*} is locally asymptotically stable for (7.1). The result follows by Theorem 7.6. □

Corollary 7.9. Assume $\lambda_1 + \delta < 1$. Assume also that h is differentiable and q is twice differentiable. If q is convex for $0 \leq x(t) \leq \delta$, then E^3_{S*} is locally asymptotically stable. If q is convex for $0 \leq x(t) \leq 1 - \lambda_1$, then E^3_{S*} is globally asymptotically stable with respect to solutions of (7.1) for which $x_0, y_0 > 0$ and $S_0 \geq 0$. In particular if

$$q(x) = x/\delta, \quad \text{or} \tag{7.13}$$

$$q(x) = \frac{\mu x^2}{(x+K)(x+L)} \quad \text{where} \quad K,L > 0, \quad \mu = \frac{(K+\delta)(L+\delta)}{\delta^2} \quad \text{and} \tag{7.14}$$

$$1 - \lambda_1 \leq \sqrt{KL}$$

then E^3_{S*} is globally asymptotically stable with respect to solutions of (7.1) for which $x_0, y_0 > 0$ and $S_0 \geq 0$. If we replace $1 - \lambda_1 \leq \sqrt{KL}$ by $\delta \leq \sqrt{KL}$ in (8.14) then E^3_{S*} is at least locally asymptotically stable.

Proof: By (7.9) $h'(x(t)) = (q'(x(t)) - h(x(t)))/x(t)$ provided $x(t) \neq 0$. But then the sign of $h'(x(t))$ depends on the sign of

$$r(x(t)) = x(t)q'(x(t)) - q(x(t)) \quad \text{for} \quad x(t) > 0. \tag{7.15}$$

Now,

$$r'\big(x(t)\big) = x(t)q''\big(x(t)\big) . \tag{7.16}$$

Since $r(0) = 0$, if q is convex for $0 < x(t) \le \delta$, then by (7.16) r is nondecreasing from 0 to δ and so by (7.16) $\delta q'(\delta) - 1 > 0$. This implies that condition (A5.B.2) holds and E^3_{S*} is locally asymptotically stable. If q is convex for $0 \le x(t) \le 1 - \lambda_1$, then similarly $r\big(x(t)\big) \ge 0$ for $0 \le x(t) \le 1 - \lambda_1$ and hence $h'\big(x(t)\big) \ge 0$ there. The global stability of E^3_{S*} follows immediately by Theorem 7.6.

If $q(x) = x/\delta$ then $q(x)$ is twice differentiable and convex for all x.

If q satisfies (7.14), then

$$h'(x) = \frac{\mu(KL-x^2)}{(K+x)^2(K+L)^2} ,$$

and so $h'\big(x(t)\big) \ge 0$ for $0 \le x(t) \le 1 - \lambda_1$ if $1 - \lambda_1 \le \sqrt{KL}$. The global stability of E^3_{S*} follows by Theorem 7.6. If we replace $1 - \lambda_1 \le \sqrt{KL}$ by $\delta \le \sqrt{KL}$, then $h'(\delta) \ge 0$. Thus,

$$\delta q'(\delta) - 1 = \delta\big(h(\delta) + \delta h'(\delta)\big) - 1 = \delta h'(\delta) \ge 0 .$$

Therefore (A5.B.2) holds, implying local asymptotic stability of E^3_{S*}.

□

Equation (7.14) describes a multiple saturation growth function and has been studied in this context by Jost et al. [43,44] and by Saunders and Bazin [66].

Theorem 7.11. Assume $\lambda_1 + \delta < 1$ and that h is differentiable. If E^3_{S*} is unstable then there exists a nontrivial periodic solution of (7.1). If the Δ of Lemma 7.5 is negative for every nontrivial periodic solution of (7.1) then the periodic orbit is unique and hence globally orbitally asymptotically stable with respect to solutions of (7.1) for which $x_0, y_0 > 0$ and $S_0 \geq 0$.

Proof: The proof is similar to the proof of Theorem 7.6. □

The hypotheses of Theorem 7.11 hold for the model studied by Butler et al. [12]. As mentioned previously they consider the case when both the functional responses p and q satisfy Michaelis-Menten kinetics. In particular, if $p(S) = \frac{mS}{\lambda_1(m-1)+S}$ and $q(x) = \frac{\mu x}{\delta(\mu-1)+x}$ where $m, \mu > 1$, then they show that E^3_{S*} is unstable if

$$\frac{y^*}{\mu\delta} - \frac{\lambda_1 m(m-1)\delta}{(\lambda_1(m-1)+S^*)^2} > 0\,. \tag{7.15}$$

They also show that Δ can be written as the sum of the left-hand side of (7.15) and something negative. Therefore if E^3_{S*} destabilizes by decreasing δ then at least initially Theorem 7.11 applies.

8. PERSISTENCE OF THE FOOD WEB. We again focus our attention on the food web described by model (3.4). In Section 6, we showed that in the special case that the predation response function is Lotka-Volterra and each competitor response function is either Lotka-Volterra or Michaelis-Menten, then $\hat{E}_{\lambda_2}$ is globally asymptotically stable for (3.4) with respect to solutions with positive initial conditions, provided that $\hat{E}_{\lambda_2}$ lies in the positive cone. This is an example of persistence of (3.4). (Refer to Definition 1.1 for the formal definition of persistence.) In this section we show that under less restrictive conditions on the functions p_i, $i = 1,2$ and q (motivated by results on the food chain in Section 7), system (3.4) persists.

We begin with the results that require the fewest restrictions on the functions p_i, $i = 1,2$ and q. If not otherwise stated, the only assumptions on these functions are those given in Sections 2 and 3.

Lemma 8.1. For any solution of (3.4):

(i) if $\lambda_1 < 1$ and $x_{10} > 0$, then $\varliminf_{t\to\infty} x_1(t) > 0$;

(ii) if $\lambda_1 + \delta < 1$ and $x_{10}, y_0 > 0$, then $\varliminf_{t\to\infty} y(t) > 0$.

Proof: Let $\gamma(t) = (S(t), x_1(t), x_2(t), y(t))$ be a solution of (3.4) and let Ω denote the omega-limit set of $\gamma(t)$.

(i) Assume $\lambda_1 < 1$ and $x_{10} > 0$. Suppose $\varliminf_{t\to\infty} x_1(t) = 0$. Then there exists $\bar{P} = (\bar{S}, 0, \bar{x}_2, \bar{y}) \in \Omega$, and by Theorem 5.2, $\bar{S} + \bar{x}_2 + \bar{y} = 1$. By Theorem 5.1, Ω is compact and contained in $\mathbb{R}^4_+$. From (4.2) it follows that

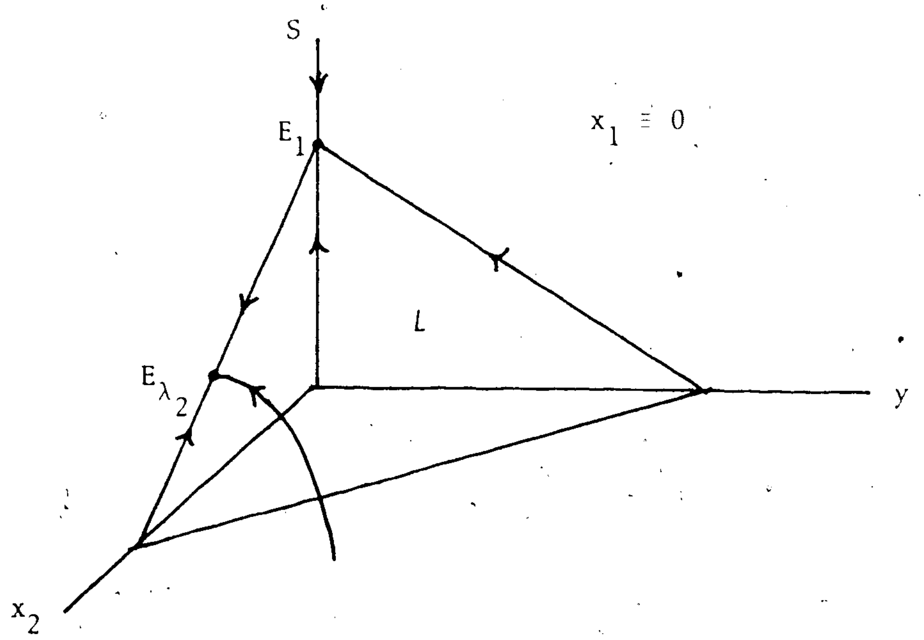
(8.1) at least one of E_{λ_1} or E_{λ_2} (if $\lambda_2 < 1$) $\in \Omega$.

Suppose $E_1 \in \Omega$. $\Omega \neq \{E_1\}$ since by Lemma 6.2, $\overline{\lim}_{t\to\infty} x_1(t) > 0$. Since E_1 is hyperbolic (see (A5.A)), by Lemma II.5.2, there exists $P^S \in (W^S(E_1)\setminus\{E_1\}) \cap \Omega$. But $W^S(E_1) = \{(S,x_1,x_2,y) \in \mathbf{R}^4_+ : x_1 = 0$ and if $\lambda_2 < 1$ then $x_2 = 0\}$. Thus $P^S \in \{(S,x_1,x_2,y) \in L : x_1 = 0$ and if $\lambda_2 < 1$ then $x_2 = 0$ and $y > 0\}$. If $\lambda_2 \geq 1$, by Theorem 5.3 (i), $\lim_{t\to\infty} x_2(t) = 0$ and so there is no loss of generality if we assume $\lambda_2 < 1$. But then $O^-(P^S) \not\subset \mathbf{R}^4_+$. Since $P^S \in \Omega$ implies that $c\ell(O(P^S)) \subset \Omega$, we have derived a contradiction. Therefore $E_1 \notin \Omega$.

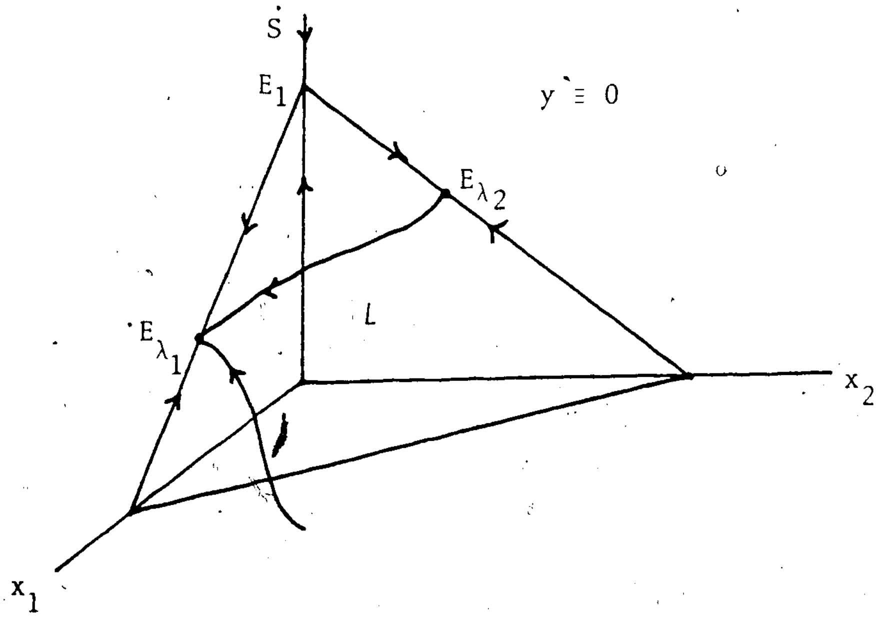
Suppose $\lambda_2 < 1$ and $E_{\lambda_2} \in \Omega$. $\{E_{\lambda_2}\} \neq \Omega$ since $\overline{\lim}_{t\to\infty} x_1(t) > 0$. Since E_{λ_2} is hyperbolic, by Lemma II.5.2, there exists $Q^S \in (W^S(E_{\lambda_2})\setminus\{E_{\lambda_2}\}) \cap \Omega$. Since $W^S(E_{\lambda_2}) = \{(S,x_1,x_2,y) \in \mathbf{R}^4_+ : x_1 = 0, x_2 > 0\}$ (see Figure 24(a)) and $\Omega \subset L$, $Q^S \in \{(S,x_1,x_2,y) \in L : x_1 = 0, x_2 > 0\}$, a two-dimensional positively invariant set. By the Poincaré-Bendixson Theorem, either $E_1 \in \Omega$ or $O^-(Q^S) \not\subset \mathbf{R}^4_+$. But both alternatives are impossible. Therefore $E_{\lambda_2} \notin \Omega$. Hence, by (8.1) $\underline{\lim}_{t\to\infty} x_1(t) > 0$.

(ii) Assume $\lambda_1 + \delta < 1$ and $x_{10}, y_0 > 0$. Suppose $\lim_{t\to\infty} y(t) = 0$. Then the system reduces to the chemostat model (4.1). Since $x_{10} > 0$, $\lim_{t\to\infty} S(t) = \lambda_1$, $\lim_{t\to\infty} x_1(t) = 1 - \lambda_1$ and $\lim_{t\to\infty} x_2(t) = 0$ by Corollary II.3.5. But $1 - \lambda_1 > \delta$ and so, since $y_0 > 0$, $y'(t) > 0$ for all sufficiently large t. Therefore

$$\lim_{t\to\infty} y(t) \neq 0. \tag{8.2}$$



(a) $W^s(E_{\lambda_2}) = \{(S,x_1,x_2,y) \in \mathbb{R}^4_+ : x_1 = 0,\ x_2 > 0\}$ $(\lambda_2 > 1)$



(b) $W^s(E_{\lambda_1}) = \{(S,x_1,x_2,y) \in \mathbb{R}^4_+ : x_1 > 0,\ y = 0\}$ $(\lambda_2 < 1)$

FIGURE 24 Stable Manifolds

If $\lambda_2 \geq 1$, by Theorem 5.3(i), $\lim_{t\to\infty} x_2(t) = 0$ and so the result follows by Theorem 7.1. Therefore, assume $\lambda_2 < 1$. Suppose $\underline{\lim}_{t\to\infty} y(t) = 0$. Then there exists $\bar{P} = (\bar{S},\bar{x}_1,\bar{x}_2,0) \in \Omega$ with $\bar{S} + \bar{x}_1 + \bar{x}_2 = 1$. $\bar{P} \in \Omega$ implies that $c\ell\, \mathcal{O}(\bar{P}) \subset \Omega$ and so at least one of E_1, E_{λ_1}, or $E_{\lambda_2} \in \Omega$. But by part (i), $\underline{\lim}_{t\to\infty} x_1(t) > 0$ and so $E_1 \notin \Omega$ and $E_{\lambda_2} \notin \Omega$. Suppose $E_{\lambda_1} \in \Omega$. By (8.2) $\lim_{t\to\infty} y(t) \neq 0$. Therefore $\{E_{\lambda_1}\} \neq \Omega$. Since E_{λ_1} is hyperbolic (see A5.A), by Lemma II.5.2, there exists $P^s \in \left(W^s(E_{\lambda_1})\setminus\{E_{\lambda_1}\}\right) \cap \Omega$ where (see Figure 24(b)) $W^s(E_{\lambda_1}) = \{(S,x_1,x_2,y) \in \mathbf{R}^4_+ : x_1 > 0,\ y = 0\}$. Since $P^s \in \Omega \subset L$, $P^s \in \{(S,x_1,x_2,y) \in L : x_1 > 0,\ y = 0\}$. Now either E_1 or $E_{\lambda_2} \in c\ell\, \mathcal{O}^-(P^s)$ or $c\ell\, \mathcal{O}^-(P^s) \not\subset \mathbf{R}^4_+$. None of these alternatives is possible. Hence $\underline{\lim}_{t\to\infty} y(t) > 0$. □

Part (i) of this lemma tells us that provided the concentration of substrate in the feed bottle is high enough to enable x_1 to survive in the absence of competition and predation, if the system is viewed purely deterministically, x_1 will survive the competition of any inferior competitor (i.e. $\lambda_1 < \lambda_2$), even in the presence of a predator that predates soley on x_1. Thus, viewed deterministically, the introduction of a predator cannot reverse the outcome of the competition. We comment further on this in the discussion in Section 10.

It is evident from Theorems 6.1 and 6.3 that a necessary condition for persistence of (3.4) is that $\lambda_1 + \delta < 1$. This condition is certainly not sufficient since E_{S*} is locally asymptotically stable if, as well, $\lambda_1 + \delta$ is sufficiently close to 1. The next few results deal with sufficient conditions for persistence of (3.4).

Lemma 8.2. Let $\gamma(t) = \big(S(t),x_1(t),x_2(t),y(t)\big)$ be any solution of (3.4) such that $x_{i0} > 0$ $i = 1,2$, $y_0 > 0$ and $\underline{\lim}_{t\to\infty} x_2(t) > 0$. Then $\underline{\lim}_{t\to\infty} S(t) > 0$, $\underline{\lim}_{t\to\infty} x_1(t) > 0$ and $\underline{\lim}_{t\to\infty} y(t) > 0$.

Proof: Let Ω denote the omega-limit set of $\gamma(t)$. First we show that $E_{\lambda_2} \notin \Omega$. Suppose $E_{\lambda_2} \in \Omega$. $\{E_{\lambda_2}\} \neq \Omega$ since E_{λ_2} is always unstable (see (A5.A.b)) and since $x_{10} > 0, \gamma(0) \notin W^s(E_{\lambda_2})$ (the stable manifold of E_{λ_2} - see Figure 24(a)). Therefore by Lemma II.5.2 there exists $P^s \in \big(W^s(E_{\lambda_2})\setminus\{E_{\lambda_2}\}\big) \cap \Omega$. But $\Omega \subset L$ and so

$P^s \in \{(S,x_1,x_2,y) : x_1 = 0,\ x_2 > 0,\ S + x_1 + x_2 + y = 1\}$. But then either $E_1 \in c\ell\big(\mathcal{O}^-(P^s)\big)$ or $E_{\lambda_1} \in c\ell\big(\mathcal{O}^-(P^s)\big)$ or $c\ell\big(\mathcal{O}^-(P^s)\big) \not\subset \mathbf{R}^4_+$. But $c\ell\big(\mathcal{O}(P^s)\big) \subset \Omega$. Since $\underline{\lim}_{t\to\infty} x_2(t) > 0$ and $\Omega \subset \mathbf{R}^4_+$, we have a contradiction. Therefore $E_{\lambda_2} \notin \Omega$.

Suppose $\underline{\lim}_{t\to\infty} x_1(t) = 0$. Then there exists a point $\bar{P} = (\bar{S},0,\bar{x}_2,\bar{y}) \in \Omega$. Since $c\ell\big(\mathcal{O}(\bar{P})\big) \subset \Omega \subset L$ it follows that either E_1 or $E_{\lambda_2} \in \Omega$. $E_1 \notin \Omega$ since $\underline{\lim}_{t\to\infty} x_2(t) > 0$ and we just showed $E_{\lambda_2} \notin \Omega$. This contradiction implies $\underline{\lim}_{t\to\infty} x_1(t) > 0$.

That $\underline{\lim}_{t\to\infty} y(t) > 0$ follows similarly.

□

Theorem 8.3. Assume $\lambda_2 < 1$. Assume also that $q\big(x(t)\big) = q_\delta\big(x(t)\big)$ where $\lim_{\delta\to 0^+} q_\delta(\varepsilon) = +\infty$ for any fixed $\varepsilon > 0$. Provided $\delta > 0$ is sufficiently close to zero, it follows that $\underline{\lim}_{t\to\infty} x_2(t) > 0$ for any solution of (3.4) for which $S_0 \geq 0$, x_{i0}, $y_0 > 0$ $i = 1,2$ and hence system (3.4) persists.

Proof: Define

$$\bar{\varepsilon} = p_2(\lambda_2 + (1 - \lambda_2)/2) - 1 . \tag{8.4}$$

Then $\bar{\varepsilon} > 0$ since $\lambda_2 < 1$. Choose $L > 1$ and let $M = \max(L, p(L))$. Select $\varepsilon > 0$ such that

$$\varepsilon < \min\left[\frac{1}{4}, \left(\frac{1 - \lambda_2}{4M}\right)^2, \left(\frac{\bar{\varepsilon}}{6(1 + \bar{\varepsilon})}\right)^2\right] . \tag{8.5}$$

Choose $\delta > 0$ sufficiently small so that

$$\lambda_1 + \delta < 1 \quad \text{and} \quad q_\delta(\varepsilon) > 4(1 + M/\varepsilon k)/\sqrt{\varepsilon} . \tag{8.6}$$

Let $\gamma(t) = (S(t), x_1(t), x_2(t), y(t))$ be a fixed solution of (3.4) for which $S_0 \geq 0$ and $x_{i0}, y_0 > 0$ $i = 1,2$. Assume $\underline{\lim}_{t\to\infty} x_2(t) = 0$. Then there exists a sequence $\{t_n\}$ with $t_n \to \infty$ as $n \to \infty$ such that $x_2(t_n) \to 0$ and $x_2(t_n) < x_2(t)$ for all $t < t_n$. Since all solutions are bounded, without loss of generality, we assume that $\gamma(t_n) \to \bar{P} = (\bar{S}, \bar{x}_1, 0, \bar{y})$ (passing to a subsequence and relabelling if necessary). Let $\bar{\gamma}(t) = (\bar{S}(t), \bar{x}_1(t), 0, \bar{y}(t))$ denote the solution of (3.4) through $\bar{P}$. Since $\lambda_1 + \delta < 1$, by Lemma 8.1 $\bar{x}_1(0) > 0$ and $\bar{y}(0) > 0$.

Choose $\ell > 0$ and $\bar{T} \geq 0$ with respect to the solution $\bar{\gamma}(t)$ so that

$$\ell \leq \bar{y}(t) \leq L ,$$

for all $t \geq \bar{T}$. Select

$$T > \max\,[2/\varepsilon\,,\ \ell n(L/\ell)\,,\ \bar{T}]\,, \tag{8.7}$$

such that

$$\bar{S}(t) < 1 + \varepsilon M \quad \text{for all} \quad t \geq T\,.$$

Since the functions on the right-hand side of (3.4) are C^1 and autonomous and since all solutions are bounded, it follows by continuous dependence on initial conditions that there exists $\bar{\delta} > 0$ such that $\rho(\gamma(\tau)\,,\bar{\gamma}(\tau)) < \bar{\delta}$ implies that $\rho(\gamma(t)\,,\bar{\gamma}(t)) < \sqrt{\varepsilon}\,M$ for all $t \in [\tau - T,\tau]$ where $\bar{\delta}$ depends on T but not on τ. Here the metric ρ is defined by $\rho(a,b) = \sum_{i=1}^{4} |a_i - b_i|$ if $a = (a_1,a_2,a_3,a_4)$ and $b = (b_1,b_2,b_3,b_4)$. Since $\gamma(t_n) \to \bar{P}$, there exists $\bar{N} > 0$ such that $\rho(\gamma(t_n),\bar{P}) < \bar{\delta}$ provided $n \geq \bar{N}$. Since the system (3.4) is autonomous, there is no loss of generality if we assume $\bar{P} = \bar{\gamma}(t_N)$ for any $N \geq \bar{N}$, fixed. Therefore, $\rho(\gamma(t_N),\bar{\gamma}(t_N)) < \bar{\delta}$ and so $\rho(\gamma(t),\bar{\gamma}(t)) < \sqrt{\varepsilon}\,M$ for all $t \in [t_N - T,t_N]$. Therefore, by the definition of ρ

$$|S(t) - \bar{S}(t)| < \sqrt{\varepsilon}\,M \quad \text{for all} \quad t \in [t_N - T,t_N]\,. \tag{8.8}$$

Define,

$$B = \{t \in [t_N - T,t_N] : S(t) \leq 1 - 2\sqrt{\varepsilon}\,M\}\,,$$

$$G = \{t \in [t_N - T,t_N] : \bar{S}(t) \leq 1 - \sqrt{\varepsilon}\,M\}\,,$$

$$\beta = \frac{1}{T}\,\mu(B) \quad \text{and} \quad \gamma = \frac{1}{T}\,\mu(G)\,.$$

Then by Lemma 7.3, $\gamma \le 6\sqrt{\varepsilon}$ provided $t_N > T$. Since $t_n \to \infty$ as $n \to \infty$ and the only restriction on N is that $N \ge \bar{N}$, there is no loss of generality if we assume $t_N > T$. By (8.8) $B \subset G$ and so

$$\beta \le \gamma \le 6\sqrt{\varepsilon}\,. \tag{8.9}$$

Also, if $\tilde{t} \in [t_N - T, t_N] \setminus B$, defined to be B^c, then

$$\begin{aligned} S(\tilde{t}) &> 1 - 2\sqrt{\varepsilon}\, M \\ &\ge 1 - 2\left(\frac{1-\lambda_2}{4M}\right) M \quad \text{by (8.5)} \\ &= \lambda_2 + (1-\lambda_2)/2\,. \end{aligned}$$

Therefore, by (8.4)

$$-1 + p_2\big(S(t)\big) \ge \bar{\varepsilon} \quad \text{for all } t \in B^c\,. \tag{8.10}$$

Integrating the x_2 equation from $t_N - T$ to t_N yields

$$x_2(t_N) = x_2(t_N - T)\exp\left(\int_{t_{N-T}}^{t_N} \big(-1 + p_2(S(v))\big)dv\right),$$

which implies that

$$\int_{t_N - T}^{t_N} \big(-1 + p_2(S(v))\big)dv < 0 \tag{8.11}$$

since by construction of the sequence $\{t_n\}$, $x_2(t_N - T) > x_2(t_N)$.

However,

$$\int_{t_N-T}^{t_N} \left(-1 + p_2(S(v))\right)dv = \int_B \left(-1 + p_2(S(v))\right)d\mu + \int_{B^c} \left(-1 + p_2(S(v))\right)d\mu$$

$$\geq (-1)\mu(B) + \bar{\varepsilon}\left(T - \mu(B)\right) \quad \text{by} \quad (8.10)$$

$$= T\left(\bar{\varepsilon} - \beta(1 + \bar{\varepsilon})\right)$$

$$\geq T\left(\bar{\varepsilon} - 6\sqrt{\varepsilon}\ (1 + \bar{\varepsilon})\right) \quad \text{by} \quad (8.6) \quad \text{and} \quad (8.9)$$

$$> T\left(\bar{\varepsilon} - 6\left(\frac{\bar{\varepsilon}}{6(1 + \bar{\varepsilon})}\right)(1 + \bar{\varepsilon})\right) \quad \text{by} \quad (8.5)$$

$$= 0$$

contradicting (8.11). Therefore, provided $\delta > 0$ is sufficiently close to zero so that (8.6) holds, $\underline{\lim}_{t\to\infty}\, x_2(t) > 0$.

That system (3.4) persists now follows immediately from Lemma 8.2.

□

One can actually show that $S(t) + x_2(t)$ is *"on the average"* as close to 1 as we like if q can be parametrized as in the hypothesis of the previous theorem and $\delta > 0$ is chosen sufficiently close to zero. The proof is similar to the proof of Lemma 7.3. From this we infer that as δ tends to zero both the $\underline{\lim}_{t\to\infty}\, x_1(t)$ and $\underline{\lim}_{t\to\infty}\, y(t)$ tend to zero. We shall comment further on the ecological implications of this in the discussion in Section 10.

Theorem 8.4. Assume $1 - \lambda_2 - \delta p_1(\lambda_2) > 0$. If E_{S*} is globally asymptotically stable for (3.4) with respect to solutions for which $x_{10} > 0$, $x_{20} = 0$ and $y_0 > 0$, then system (3.4) persists with respect to solutions for which $x_{i0} > 0$ $i = 1,2$, $y_0 > 0$.

Proof: Let $\gamma(t) = \big(S(t), x_1(t), x_2(t), y(t)\big)$ be a solution of (3.4) for which $x_{i0}, y > 0 \quad i = 1,2$ and let Ω denote the associated omega-limit set. Since $1 - \lambda_2 - \delta p_1(\lambda_2) > 0$ implies that $\lambda_1 + \delta < 1$, by Lemma 8.2 it suffices to show that $\varliminf_{t\to\infty} x_2(t) > 0$.

Suppose $\varliminf_{t\to\infty} x_2(t) = 0$. Then there exists $\bar{P} = (\bar{S}, \bar{x}_1, 0, \bar{y}) \in \Omega$, where $\bar{x}_1, \bar{y} > 0$ by Lemma 8.2, and $c\ell\big(\mathcal{O}(\bar{P})\big) \subset \Omega$. Note that $1 - \lambda_2 - \delta p_1(\lambda_2) > 0$ implies that $S^* > \lambda_2$ and so by (A5.A.2) E_{S^*} is unstable. Therefore $\{E_{S^*}\} \neq \Omega$ since $\gamma(0) \notin W^s(E_{S^*}) = \{(S, x_1, x_2, y) : x_1 > 0,\ x_2 = 0,\ y > 0,\ S \geq 0\}$ because $x_{20} > 0$. Suppose $\bar{P} = E_{S^*}$. Since E_{S^*} is hyperbolic and $\{E_{S^*}\} \neq \Omega$, by Lemma II.5.2 there exists $P^s \in \big(W^s(E_{S^*}) \backslash \{E_{S^*}\}\big) \cap \Omega$. Therefore, without loss of generality, assume $\bar{P} \neq E_{S^*}$. Since $\bar{P} \subset L$ and $\bar{x}_1, \bar{y} > 0$, the closure of the negative semi-orbit through $\bar{P}$ either contains E_1, E_{λ_1}, E_{λ_2} or it is not contained in $\mathbf{R}^4_+$. But $\varliminf_{t\to\infty} y(t) > 0$ and $\Omega \subset \mathbf{R}^4_+$ and so none of these alternatives is possible. This contradiction yields the result. □

In Section 7 we derived several sufficient conditions for the global stability of $E^3_{S^*}$ with respect to (7.1). Under these conditions, the above Theorem applies and so provided that $\hat{E}_{\lambda_2}$ lies in the positive cone, i.e. $1 - \lambda_2 - \delta p_1(\lambda_2) > 0$, it follows that system (3.4) persists. This is summarized in

Corollary 8.5. Assume $1 - \lambda_2 - \delta p_1(\lambda_2) > 0$. Suppose that one of the following alternatives holds:

(i) h is differentiable and $\lambda_1 + \delta$ is sufficiently close to 1, or

(ii) h is differentiable and $h'(x) \geq 0$ for all

$0 < x < 1 - \lambda_1$, or

(iii) q is twice differentiable and convex for $0 < x < 1 - \lambda_1$, for example if q satisfies (7.13) or (7.14).

Then system (3.4) persists with respect to all solutions for which $x_{i0} > 0$, $i = 1,2$, and $y_0 > 0$.

Proof: E_{S*} is globally asymptotically stable for (3.4) with respect to solutions for which $x_{10} > 0$, $x_{20} = 0$, $y_0 > 0$ if and only if E_{S*}^3 is globally asymptotically stable for (7.1) with respect to solutions for which $x_0, y_0 > 0$. The corollary therefore follows directly by Theorem 8.4 and Corollaries 7.7, 7.8 and 7.9. □

By Theorem 5.2 it is possible to eliminate $\overset{\circ}{S}$ from model (3.4) to obtain a three-dimensional Kolmogorov model that could be interpreted as two competitors and a predator with the predator predating on one of the competitors. In [22], Freedman and Waltman derive persistence criteria for general Kolmogorov models describing three interacting predator-prey populations as long as it can be shown that there are no nontrivial periodic orbits on the bounding coordinate planes. Our results contrast with theirs, since in our more restricted context, we are able to derive persistence criteria without having to exclude the possibility of periodic orbits. See in particular Theorem 8.3 and the example in the following section.

9. AN EXAMPLE. That the orderly transfer of global stability from one critical point to another, as described in Section 6 (see Table IX), is not always the case for the food web (3.4) will be illustrated by means of an example. Recall that E_{S*} is always locally asymptotically stable when it first enters the nonnegative cone (i.e. just as the sum $\lambda_1 + \delta$ is decreased below 1). In the following example, as δ is decreased further, E_{S*} loses its stability via a Hopf bifurcation before $\hat{E}_{\lambda_2}$ appears and $\hat{E}_{\lambda_2}$ is unstable as it enters $\mathbb{R}^4_+$. If δ is decreased sufficiently there is predator-mediated persistence and not only does the otherwise inferior competitor survive, but it survives at a higher concentration than that of its rival.

<u>Example 9.1</u>. In this example we assume that p_1 is Lotka-Volterra and q is Michaelis-Menten. More specifically, let

(9.1) $$p_1(S) = 4S \quad (\text{i.e. } \lambda_1 = 1/4)$$

and

(9.2) $$q(x_1) = x_1(\delta+2\alpha)/\big(\delta(2\alpha+x_1)\big), \text{ where } \alpha = (\sqrt{13}-2)/12 \approx .1338 .$$

We also fix

(9.3) $$\lambda_2 = 67/100 .$$

Then, provided

(9.4) $\delta > 33/268 \approx 0.1$[illegible] $(\text{i.e. } 1 - \lambda_2 - \delta p_1(\lambda_2) < 0)$

$\hat{E}_{\lambda_2}$ does not lie in $\mathbb{R}^4_+$, but provided

$$(9.5) \qquad \delta \le 3/4 \quad (\text{i.e. } \lambda_1 + \delta \le 1)$$

E_{S*} does lie in $\mathbf{R}^4_+$. For this example

$$(9.6) \qquad S^* = \lambda_1/(\lambda_1 + \delta) = 1/(1+4\delta)$$

and so if both (9.4) and (9.5) hold, $S^* < \lambda_2$. Therefore, by (A5.A.3) the local stability of E_{S*} depends on the sign of

$$(9.7) \qquad y^*\big(\delta q'(\delta) - 1\big)/\delta + \delta p_1'(S^*) .$$

If (9.7) is positive, E_{S*} is locally asymptotically stable and if (9.7) is negative, then E_{S*} is unstable. With p_1 and q satisfying (9.1) and (9.2), (9.7) equals $\big(\delta(16\delta^2 + 32\alpha\delta + 8\alpha - 3)\big)/\big((1+4\delta)(2\alpha+\delta)\big)$. Thus the sign of (9.7) depends on the sign of $g(\delta) = 16\delta^2 + 32\alpha\delta + 8\alpha - 3$. Since $\alpha > 0$, $g(\delta)$ is a strictly increasing function of δ. Noting that $g(\alpha) = 0$, it follows that E_{S*} is locally asymptotically stable for $\delta > \alpha$ and is unstable for $\delta < \alpha$. For $\delta = \alpha$ both (9.4) and (9.5) are satisfied and so E_{S*} loses its stability before $\hat{E}_{\lambda_2}$ appears in the nonnegative cone. At $\alpha = \delta$, the characteristic equation (see (A5.A.1)) has two real, negative roots and two pure imaginary roots. Since

$$\left(\frac{d\,\mathrm{Re}(\lambda)}{d\delta}\right)_{\delta=\alpha} = -\frac{1}{2}\frac{d}{d\delta}\left(y^*(\delta q'(\delta) - 1)/\delta + \delta p_1'(S^*)\right)_{\delta=\alpha}$$

$$= \frac{-32\alpha}{3(1+4\alpha)}$$

$$\ne 0 .$$

(where $\mathrm{Re}(\lambda)$ denotes the real part of the roots of the quadratic expression in (A5.A.1)), the real part of the complex conjugate pair of roots crosses zero transversely at $\delta = \alpha$ and so the change in stability at $\delta = \alpha$ is via a Hopf bifurcation. Numerical results seem to indicate that the bifurcating periodic orbits exist for $\delta < \alpha$ and are stable.

Figures 25 and 26 illustrate this Hopf bifurcation in the case that

$$(9.8) \qquad p_2(S) = 150S/(67 + 50S) .$$

In both figures we take

$$(9.9) \qquad S_0 = 0.4, \quad x_{10} = 0.3, \quad x_{20} = 0.2 \text{ and } y_0 = 0.1 .$$

In Figure 25 $\delta = 0.3 > \alpha$. The solution converges to E_{S*}. In Figure 26 $\delta = 0.13 < \alpha$ and so δ satisfies (9.4) and (9.5). Therefore $\hat{E}_{\lambda_2} \notin \mathbf{R}^4_+$ and E_{S*} is unstable. This figure seems to depict a stable periodic solution.

Figures 27 and 28 also depict solutions with $p_2(S)$ defined by (9.8) and initial conditions (9.9). In Figure [illegible], $\delta = .12$ and so $\hat{E}_{\lambda_2} \in \mathbf{R}^4_+$, but δ is close to the value at which $\hat{E}_{\lambda_2}$ and E_{S*} coalesce. Clearly $\hat{E}_{\lambda_2}$ is unstable.

[illegible] the final graph, Figure 28, we reduce δ even further, to $\delta = 0.014$. For this value of δ we obtain persistence. Note that not only does x_2 survive, but it survives at higher concentrations than its rival, x_1. Also, a good deal of the time the concentrations of x_1 and y are very close to zero. Thus each of these populations is in danger of a small stochastic event causing extinction in finite time.

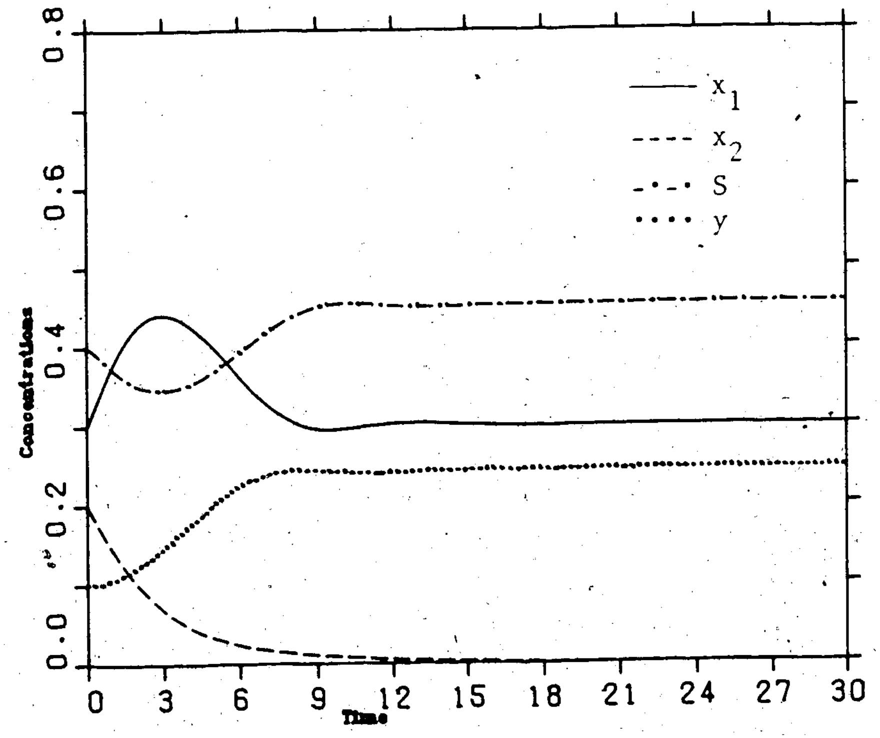


FIGURE 25 E_{S*} is Asymptotically Stable ($\delta = 0.3 > \alpha$)

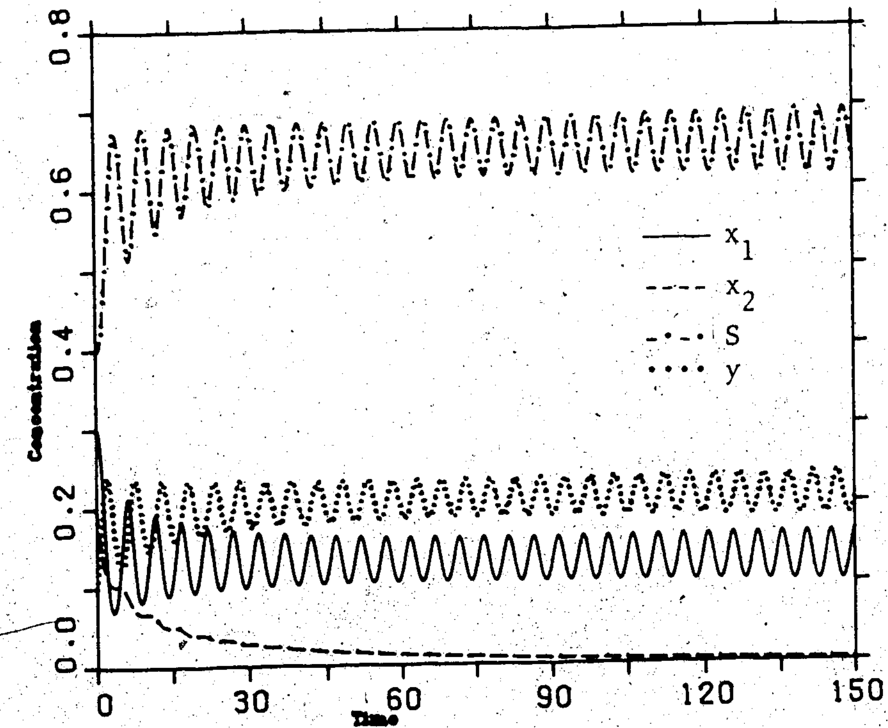


FIGURE 26 E_{S*} is Unstable and $\hat{E}_{\lambda_2} \notin \mathbb{R}^4_+$ ($\delta = 0.13 < \alpha$)

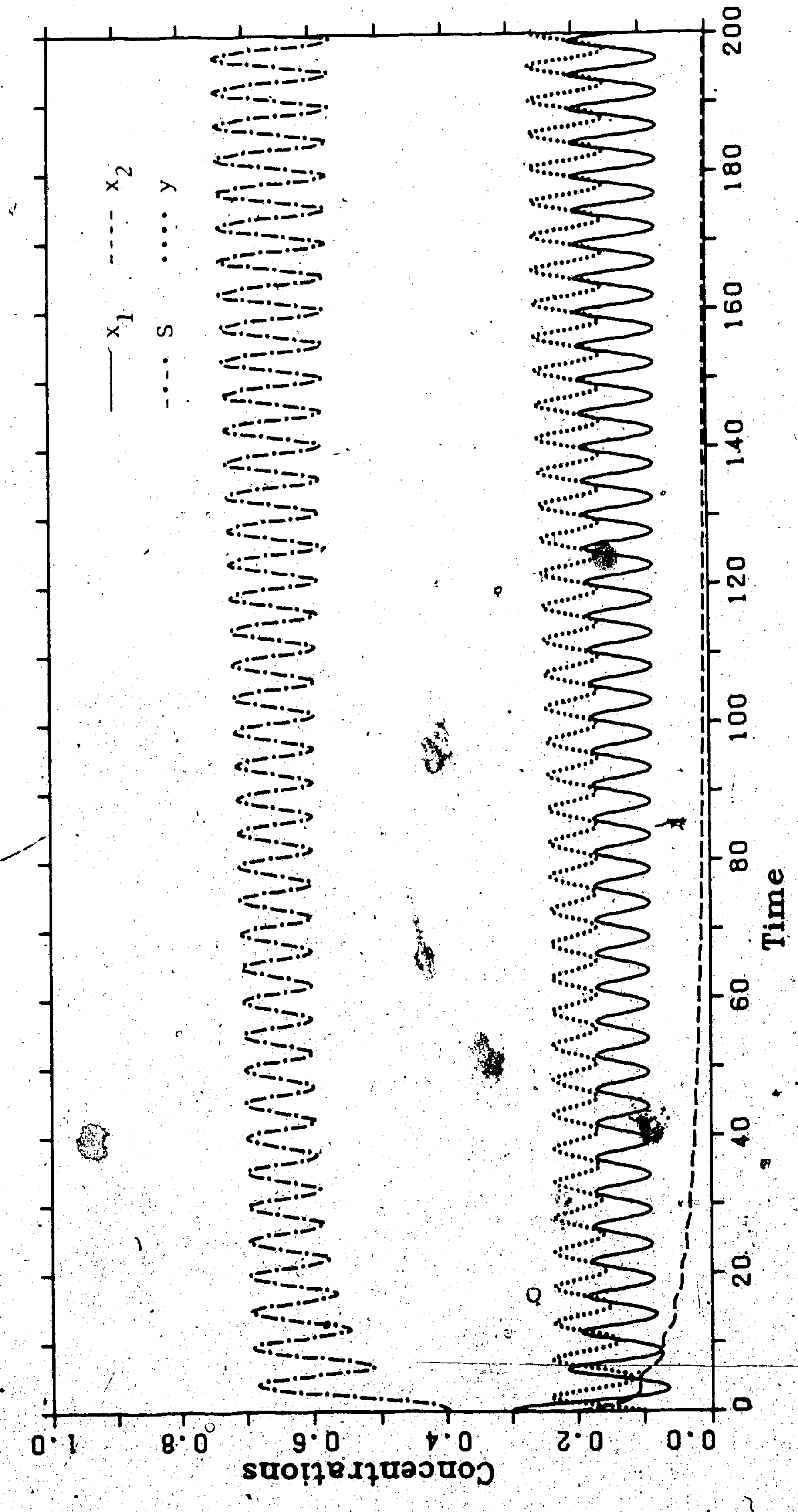


FIGURE 27 $\hat{E}_{\lambda_2} \in \mathbb{R}^4_+$ but is Unstable (δ = 0.12)

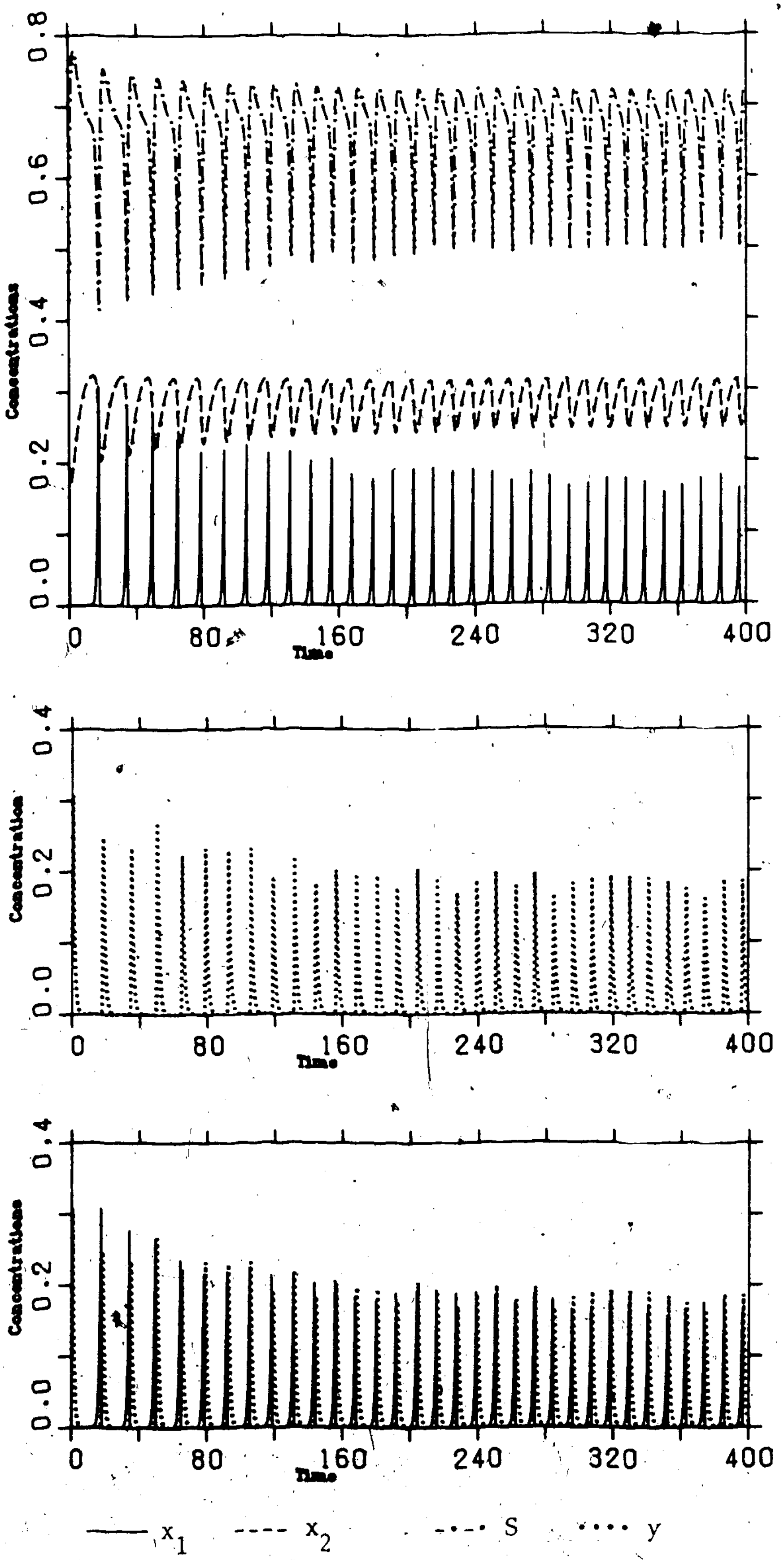


FIGURE 28 Predator - Mediated Persistence ($\delta = 0.014$)

10. DISCUSSION. This chapter is mainly concerned with the qualitative behaviour that can result when a predator invades a chemostat in which two populations of microorganisms are competing for a single, essential, growth-limiting nutrient. We are also interested in the 3-dimensional food chain that results when the competitor that is inferior in the absence of predation is eliminated. For the most part we consider general monotone dynamics for microbial-nutrient dynamics. We are however, motivated by results obtained by considering three common prototypes for monotone functional responses: Lotka-Volterra, Michaelis-Menten, and multiple saturation.

In general we can summarize the results of this chapter as follows. As various parameters are decreased, the model exhibits a sequence of different stages of global behaviour. At each stage, conditions have become sufficiently favourable for a new population to survive. Eventually the model predicts persistence of the entire food web.

We obtain our most complete results in the case that a Lotka-Volterra response function is used to describe prey utilization by the predator and each response function describing competitor-substrate interaction is of either Lotka-Volterra or Michaelis-Menten form. In this case there is an unbroken chain of transference of global stability from one critical point to another as certain parameters decrease. At each new link in the chain conditions become favourable enough for a new population to survive. The specific conditions for global stability of each critical point are summarized in Table IX.

For the next set of results we allow a general monotone response function to describe each competitor's utilization of substrate. Instead of restricting our attention to Lotka-Volterra kinetics for the predator response function $q(x_1)$, we assume either that $q(x_1)$ is convex for $0 < x_1 < 1 - \lambda_1$ or $q(x_1) = x_1 h(x_1)$ where $h(x_1)$ is monotone nondecreasing for $0 < x_1 < 1 - \lambda_1$. These assumptions allow for Lotka-Volterra response functions as well as for multiple saturation response functions if we restrict certain parameters appropriately (see (7.14)). Under these assumptions we still obtain the same transference of global stability from E_1 to E_{λ_1} to E_{S*} at the same critical values of the parameters, and as before E_{S*} remains globally asymptotically stable if $\lambda_1 + \delta < 1$ and $1 - \lambda_1 - \delta p_1(\lambda_2) < 0$. Though we conjecture that for the parameter range $1 - \lambda_1 - \delta p_1(\lambda_2) > 0$, $\hat{E}_{\lambda_2}$ is as above, globally asymptotically stable, we are only able to prove that for this parameter range, $\hat{E}_{\lambda_2}$ is locally asymptotically stable and that the entire food web persists.

If we relax the assumptions on the functional responses further to allow quite general monotone kinetics, there is still a transference of global stability from E_1 to E_{λ_1} to E_{S*} as described above. However, the chain can be broken at this point. In particular, it is possible for there to exist $\varepsilon > 0$ such that E_{S*} is globally asymptotically stable if $1 - \varepsilon < \lambda_1 + \delta < 1$ and $1 - \lambda_1 - \delta p_1(\lambda_2) < 0$, but is unstable if $\lambda_1 + \delta < 1 - \varepsilon$ even though $1 - \lambda_1 - \delta p_1(\lambda_2) < 0$. In Example 9.1, for example, E_{S*} loses stability via a Hopf bifurcation and the stability is picked up by the bifurcating periodic orbit that sits in (S,x_1,y) space. Also, in this example $\hat{E}_{\lambda_2}$ is initially unstable as it appears in the nonnegative (S,x_1,x_2,y) cone. Although the chain of transference of global stability from critical point to critical point can be broken, it is still always the case that the (S,x_1,y) food chain persists if $\lambda_1 + \delta < 1$ and the entire (S,x_1,x_2,y) food web persists if $\lambda_2 < 1$, the predation response function can be parametrized appropriately with respect to δ (see (7.3)), and $\delta > 0$ is sufficiently small. (Note that this parametrization is possible for all three of the prototypes of monotone response functions.)

If we interpret the thresholds λ_1, $\lambda_1 + \delta$, and $1 - \lambda_1 - \delta p_1(\lambda_2)$ in terms of their counterparts for the unscaled model, we gain insight into the biology of the situation. Decreasing a λ_i can be achieved either by increasing S^0, the concentration of nutrient in the feed bottle, by decreasing D, the dilution rate or by selecting a competitor that is more efficient at low concentrations of substrate. Decreasing δ can be achieved by increasing S^0, by decreasing D or by selecting a predator that is more efficient at low concentrations of the prey. However, δ can also be decreased by selecting a prey with larger growth yield constant y_1. Thus, according to the predictions of this model, there are a number of ways that an experimenter can make adjustments in order to influence the outcome of the microbial interactions in a chemostat. Also, he should be able to predict the outcome in advance, based on the measurement of certain parameters and the measurement of these parameters can be achieved by studying the interactions between pairs (i.e. competitor-substrate pairs or the predator-prey pair). Therefore, the predictions of this model can be tested in the laboratory in a way analogous to that used by Hansen and Hubbell [33] to verify the predictions of the model analyzed by Hsu, Hubbell and Waltman [40].

Recall that in Chapter II we showed that in the absence of a predator, one competitor always outcompetes his rival (i.e. there is at most one survivor). This model evidently confirms current ecological thinking that predation can be responsible for diversity in ecosystems. Levin [49] explains that, "*two species can coexist at a stable equilibrium if each is limited by an independent combination of predation and resource limitation, since then two independent factors are serving to limit two species.*" Paine [59] gives experimental results that actually show that the removal of one predator, Pisaster, resulted in a collapse from a 15 species to an 8 species food web. It would be interesting to investigate whether mathematically it is possible to show that the invasion by one predator can cause persistence of many competing populations. This would involve modelling predator preferences and strategies and it was to avoid this complication that in our model the predator predates on only one of the competitors.

What can be said about the possibility of invasion by a predator actually causing reversal in the outcome of competition between two rivals, in the sense that the competitor that is inferior in the absence of the predator survives and the otherwise superior competitor is driven to extinction? On first thought our model would appear to predict that this is impossible. We have shown that the competitor that wins in pure competition continues to survive even in the presence of a predator. However, if we look more closely we realize that in the course of proving persistence of the food web, we showed that the closer the predator's break-even concentration is to zero, the closer the average value of the concentration of the competitor that wins in pure competition, $x_1(t)$ (and of the predator, $y(t)$) are to zero. Although our model is completely deterministic, a more sophisticated attempt at modelling the situation might wish to take into account stochastic effects, in which case a small random event might cause extinction of $x_1(t)$ in finite time. Under these circumstances it is conceivable that there would be a reversal of the outcome of the competition. If by *reversal* of the outcome we mean only that the loser in pure competition survives at a *more abundant concentration* on the average than his rival in the presence of a predator and we do not require the rival population to be forced to extinction then our model predicts that *reversal* is indeed possible. This is illustrated in Figure 28. It is also easy to construct examples in which the interior equilibrium $\hat{E}_{\lambda_2}$ is asymptotically stable and the equilibrium value of x_2 is larger than the equilibrium value of x_1.

With respect to Rosensweig's paradox of enrichment [63], it is also noteworthy that this model predicts that the more the environment is enriched by increasing the concentration of substrate in the feed bottle, the more diverse the ecosystem that persists, even though, as Saunders and Bazin [66] point out, enrichment can cause all the equilibria to destabilize.

As for the models in the preceding chapters, we have assumed that the specific death rates of the microbial populations are negligible compared with the washout rate. In this context as well, it would be interesting to study a model which allows for significantly different death rates.

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APPENDIX 1

LINEAR ANALYSIS OF THE SIMPLE CHEMOSTAT MODEL (II.2.1) - GENERAL KINETICS

The matrix of the linearization $V(S, x_1, x_2, \dots, x_n)$ is:

$$\begin{bmatrix} -D - \sum_{i=1}^{n} \frac{x_i p_i'(S)}{y_i}, & -\frac{p_1(S)}{y_1}, & \dots, & \frac{-p_{n-1}(S)}{y_{n-1}}, & \frac{-p_n(S)}{y_n} \\ x_1 p_1'(S), & -D + p_1(S), & \dots, & 0, & 0 \\ x_2 p_2'(S), & 0, & \dots & 0, & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ x_{n-1} p_{n-1}'(S), & 0, & \dots, & -D + p_{n-1}(S), & 0 \\ x_n p_n'(S), & 0, & \dots, & 0, & -D + p_n(S) \end{bmatrix}$$

Since at any equilibrium point at most one x_i is nonzero this matrix is quite sparce and so the signs of the real part of the roots of the variational equation (evaluated at any of the equilibria) are easy to determine. For example for the critical point $(S^*, x_1^*, x_2^*, \dots, x_n^*) = (\lambda_1, y_1(S^0 - \lambda_1), 0, \dots, 0)$, $(n-1)$ of the roots equal: $-D + p_i(\lambda_1) < 0$, $i = 2, \dots, n$. The remaining 2 roots satisfy [illegible] quadratic:

$$\mu^2 + \mu\left(D + \frac{x_1^* p_1'(\lambda_1)}{y_1}\right) + x_1^* p_1'(\lambda_1) + \frac{D}{y_1} = 0.$$

Since the coefficients of this quadratic are positive the roots have negative real part and so this critical point is locally asymptotically stable.

The analysis for the other critical points is similar.

APPENDIX 2

LINEAR ANALYSIS OF COMPLEMENTARY RESOURCE MODELS

A. LINEAR ANALYSIS - MONOTONE KINETICS MODEL (III.2.1)

By III.2.6, M is globally attracting. For the linear analysis it is therefore sufficient to consider the following system:

$$\text{(A2.A.1)} \qquad x_i' = x_i\left(-D + f_i\left(S^0 - \frac{x_1}{y_{S1}} - \frac{x_2}{y_{S2}}, R^0 - \frac{x_1}{y_{R1}} - \frac{x_2}{y_{R2}}\right)\right), \quad i = 1,2 .$$

The variational matrix is:

$$\text{(A2.A.2)} \qquad V = \begin{bmatrix} -D + f_1(S,R) + x_1 \dfrac{\partial f_1}{\partial x_1} & x_1 \dfrac{\partial f_1}{\partial x_2} \\ x_2 \dfrac{\partial f_2}{\partial x_1} & -D + f_2(S,R) + x_2 \dfrac{\partial f_2}{\partial x_2} \end{bmatrix}$$

where $S = S^0 - \dfrac{x_1}{y_{S1}} - \dfrac{x_2}{y_{S2}}$ and $R = R^0 - \dfrac{x_1}{y_{R1}} - \dfrac{x_2}{y_{R2}}$.

a. $$V(E_{S^0,R^0}) = \begin{bmatrix} -D + f_1(S^0,R^0) & 0 \\ 0 & -D + f_2(S^0,R^0) \end{bmatrix} .$$

Therefore the eigenvalues are: $\eta_1 = -D + \min(p_1(S^0), q_1(R^0))$,

$\eta_2 = -D + \min(p_2(S^0), q_2(R^0))$.

E_{S^0,R^0} is locally asymptotically stable if $(\lambda_{S1} > S^0$ or $\lambda_{R1} > R^0)$ and $(\lambda_{S2} > S^0$ or $\lambda_{R2} > R^0)$.

E_{S^0,R^0} is unstable if $(\lambda_{S1} < S^0$ and $\lambda_{R1} < R^0)$ or

$(\lambda_{S2} < S^0$ and $\lambda_{R2} < R^0)$.

E_{S^0,R^0} can therefore have a 1 or 2 dimensional, unstable manifold.

b. $E_{\lambda_{S1},*}$ exists distinct from E_{S^0,R^0} iff $\lambda_{S1} < S^0$ and $T_1 \geq C_1$.

$$V(E_{\lambda_{S1},*}) = \begin{bmatrix} -D + f_1\big(\lambda_{S1}, R^0 - C_1(S^0 - \lambda_{S1})\big) + y_{S1}(S^0 - \lambda_{S1}) \dfrac{\partial f_1}{\partial x_1} & ** \\ 0 & -D + f_2\big(\lambda_{S1}, R^0 - C_1(S^0 - \lambda_{S1})\big) \end{bmatrix}$$

Therefore the eigenvalues are: $\eta_1 = y_{S1}(S^0 - \lambda_{S1}) \dfrac{\partial f_1}{\partial x_1} < 0$

$$\eta_2 = -D + \min\big(p_2(\lambda_{S1}), q_2(R^0 - C_1(S^0 - \lambda_{S1}))\big)$$

$E_{\lambda_{S1},*}$ is locally asymptotically stable if $\lambda_{S1} < \lambda_{S2}$, or $T^* < C_1$ and

is unstable if $\lambda_{S1} > \lambda_{S2}$ and $T^* > C_1$.

$E_{\lambda_{S1},*}$ always has at least a 3-dimensional stable manifold.

c. The analysis for $E_{*,\lambda_{R1}}$, $E_{\lambda_{S2},*}$ and $E_{*,\lambda_{R2}}$ is similar and the stability results are summarized in Table II in (III.2).

d. $E_{\lambda_{S1},\lambda_{R2}}$ exists in the positive cone provided

$$\lambda_{R1} < \lambda_{R2} \text{ and } \lambda_{S1} > \lambda_{S2}$$

$$\text{and} \quad \left\{ \begin{array}{l} C_1 < C_2 \quad \text{and} \quad C_1 < T^* < C_2 \\ \qquad\quad \text{or} \\ C_1 > C_2 \quad \text{and} \quad C_1 > T^* > C_2 . \end{array} \right.$$

$$V(E_{\lambda_{S1},\lambda_{R2}}) = \begin{bmatrix} x_1^* \dfrac{\partial f_1}{\partial x_1} & x_1^* \dfrac{\partial f_1}{\partial x_2} \\ x_2^* \dfrac{\partial f_2}{\partial x_1} & x_2^* \dfrac{\partial f_2}{\partial x_2} \end{bmatrix} .$$

The characteristic equation is:

$$\eta^2 + \eta\left(\frac{x_1^*}{y_{S1}} p_1'(\lambda_{S1}) + \frac{x_2^*}{y_{R2}} q_2'(\lambda_2)\right) + x_1^* x_2^* p_1'(\lambda_{S1}) q_2'(\lambda_{R2}) \left(\frac{1}{y_{S1} y_{R2}} - \frac{1}{y_{S2} y_{R1}}\right)$$

$$= 0$$

$E_{\lambda_{S1},\lambda_{R2}}$ is locally asymptotically stable if $C_1 < C_2$ (all roots are negative and real), and

is unstable if $C_1 > C_2$ (three negative roots and one positive root).

e. The analysis is similar for $E_{\lambda_{S2},\lambda_{R1}}$ and the stability results are summarized in Table II in (III.2).

B. LINEAR ANALYSIS - GENERAL KINETICS MODEL (III.3.1)

The analysis is similar to the non-monotone case and the results are summarized in Table VI in (III.3).

APPENDIX 3

REDUCE2 PROGRAM AND ITS APPLICATION

A. REDUCE2 PROGRAM

```
   1    COMMENT...FILE HOPF.W
   2          Given a system of two first order autonomous differential
   3    equations we can determine whether or not there is a Hopf
   4    Bifurcation by using the symbol manipulation language REDUCE2 in the
   5    following way:
   6
   7          First create files:     SCRATCH              POLYW
   8                                  CANONICALFOR         POLYW1
   9                                                       INVERSEW
  10                                                       BIFSTABW
  11
  12          If these files already exist then make sure they are empty
  13          . The definition of the system to be analysed must be in a file.
  14    For the 2 resource and 2 competitor problem in a chemostat this
  15    appears in the file named DATA. See this file for particulars on
  16    how to enter the definition of the system properly.
  17          The program is started by  EX *REDUCE2 in MTS mode.
  18    Once in REDUCE2 type IN FILENAME; where FILENAME is the file
  19    containing the problem definition (e.g. IN DATA;).Next type IN POLY;
  20    From now on the program prompts you.
  21          You will need files:  POLY
  22                                INVERSE
  23                                TRANSFORM
  24                                BIFSTAB
  25          The output appears in :POLYW
  26                                  POLYW1
  27                                  INVERSEW
  28                                  CANONICALFOR
  29                                  BIFSTABW
End of file
   1    COMMENT...-FILE DATA (FOR EXAMPLE III.3.11)
   2          IN ORDER TO DETERMINE WHETHER THERE IS A HOPF BIFURCATION AND
   3                   IF THERE IS, TO DETERMINE THE STABILITY OF THE
   4                   BIFURCATING PERIODIC ORBIT;
   5    OUT SCRATCH;
   6    COMMENT...
   7          REPLACE LINES 22 THROUGH 56 WITH THE DEFINITION OF THE SYSTEM
   8                   IN TERMS OF THE VARIABLES S AND R.
   9          HERE LINES 22 THROUGH 56 REPRESENT A CHEMOSTAT MODEL OF 2
  10                   COMPETITORS COMPETING FOR 2 COMPLEMENTARY RESOURCES.
  11                   S AND R. ALL RESOURCES ARE INHIBITORY AT HIGH
  12                   CONCENTRATIONS.
  13          THE DEFINING EQUATIONS MUST BE OF THE FORM
  14                   DS:=SOME FUNCTION OF S,R AND A1.
  15                   DR:=SOME FUNCTION OF S,R AND A1
  16          A1 IS THE BIFURCATION PARAMETER. HOWEVER ONE CAN LEAVE
  17                   OTHER VARIABLES UNDEFINED AS WELL IN ORDER TO
  18                   DETERMINE IF THERE ARE PARAMETER COMBINATIONS
  19                   THAT GIVE A HOPF BIFURCATION.
  20          IT IS ASSUMED THAT THE CRITICAL POINT IS (S,R)=(0,0);
  21    OFF NAT; OFF ALLFAC;
  22    COMMENT...S,R DENOTE CONCENTRATIONS OF NUTRIENTS
  23              X1,X2 DENOTE CONCENTRATIONS OF COMPETITOR POPULATIONS
  24              F1,F2 DENOTE THE FUNCTIONAL RESPONSES
  25              DS (RESP. DR) DENOTES THE FIRST DERIVATIVE OF S (RESP. R)
  26                   WITH RESPECT TO T;
  27    COMMENT...THE CRITICAL POINT BEFORE TRANSLATION IS (TS,RT);
  28    TS:=6;
  29    RT:=4;
  30    DS:=((SO-S-TS)*D)-(X1*F1/YS1)-(X2*F2/YS2);
```

A3.A

```
DR:=((RO-R-RT)*D)-(X1*F1/YR1)-(X2*F2/YR2);
X1:=(((RO-R-RT)/YS2)-((SO-S-TS)/YR2))/((1/(YS2*YR1))-(1/(YS1*YR2)));
X2:=(((SO-S-TS)/YR1)-((RO-R-RT)/YS1))/((1/(YS2*YR1))-(1/(YS1*YR2)));
COMMENT...BOTH RESOURCES INHIBITORY KINETICS;
F1:=D+(D*(R+RT-LR1)*(MR1-R-RT)/(LR1*MR1*((AR1*((R+RT)**2))
+(BR1*(R+RT))+1)));
F2:=D+(D*(S+TS-LS2)*(MS2-S-TS)/(LS2*MS2*((A1*((S+TS)**2))
+(BS2*(S+TS))+1)));
COMMENT...WE DEFINE THE PARAMETERS USED IN THE MODEL EXCEPT A1
          WHICH WE USE AS THE BIFURCATION PARAMETER AND
          WHICHEVER OTHER PARAMETERS MIGHT AFFECT WHETHER OR
          NOT THERE IS A HOPF BIFURCATION;
LS2:=4;
MS2:=6;
LR1:=4;
MR1:=6;
YS1:=1;
YS2:=1;
YR1:=2;
YR2:=1;
AR1:=3/4;
BR1:=61/8;
BS2:=10;
SO:=32;
RO:=24;
D:=1;
SHUT SCRATCH;
COMMENT...TYPE IN POLY FOLLOWED BY A SEMICOLON NEXT;
END;
End of file
      COMMENT...FILE POLY
              TO FIND THE CHARACTERISTIC POLYNOMIAL IN ORDER TO SEE
           IF THERE IS SOME VALUE OF A1 THAT GIVES PURE IMAGINARY
           EIGENVALUES. IF THERE IS WE ASSIGN A1 THAT VALUE AND
           CHECK TRANSVERSALITY, I.E. THAT DRGAMWRTA1 IS NONZERO
           IEIG IS THE PURE IMAGINARY EIGENVALUE (POSITIVE);
      OUT SCRATCH;
      OFF NAT;
      OFF ALLFAC;
      FACTOR GAMMA;
      MATRIX M(2,2),ID(2,2),MEIG(2,2);
      COMMENT...M IS THE VARIATIONAL MATRIX;
      M:=MAT((DF(DS,S),DF(DS,R)),(DF(DR,S),DF(DR,R)));
      S:=0;
      R:=0;
      ID:=MAT((1,0),(0,1));
      M;
      MEIG:=M-GAMMA*ID;
      COMMENT...CHARPOLY IS THE CHARACTERISTIC POLYNOMIAL;
      CHARPOLY:=DET(MEIG);
      COEFF(CHARPOLY,GAMMA,C);
      COMMENT...ASSUMING THE DISCRIMINANT IS NEGATIVE, RGAM IS THE REAL
            PART OF THE ROOT OF THE CHARACTERISTIC POLYNOMIAL;
      RGAM:=(-C1)/(2*C2);
      COMMENT...DRGAMWRTA1 IS THE DERIVATIVE OF RGAM WITH RESPECT TO A1;
      DRGAMWRTA1:=DF(RGAM,A1);
      ON RAT;
      ON GCD;
      SHUT SCRATCH;
      OUT POLYW;
```

```
M;
RGAM;
DRGAMWRTA1;
CHARPOLY;
SHUT POLYW;
OUT T;
CHARPOLY;
COMMENT...TYPE N
          IF POSSIBLE ASSIGN A1 BASED ON CHARPOLY SO THAT THE
COEFFICIENT OF THE LINEAR TERM EQUALS ZERO AND THE CONSTANT
IS POSITIVE. IF THIS IS NOT POSSIBLE THERE IS NO VALUE OF A1
THAT GIVES A HOPF BIFURCATION FOR THIS SET OF PARAMETERS.
          ONCE A1 IS ASSIGNED TYPE RGAMWRTA1 TO CHECK
TRANSVERSALITY.
          TYPE CONT TO CONTINUE OR STOP;
PAUSE;
CHARPOLY;
COEFF(CHARPOLY,GAMMA,CC);
IEIG:=CCO**(1/2);
COMMENT...TYPE N
          EVALUATE IEIG BY USE OF A CALCULATOR OR OTHERWISE AND THEN
     ASSIGN THAT VALUE TO IEIG. IEIG IS MODULUS OF THE PURE
     IMAGINARY EIGENVALUE.
          TYPE CONT;
PAUSE;
OUT POLYW1;
DS;
DR;
A1;
RGAM;
COMMENT...RGAM SHOULD EQUAL ZERO;
DRGAMWRTA1;
COMMENT...DRGAMWRTA1 SHOULD BE NONZERO;
CHARPOLY;
IEIG;
SHUT POLYW1;
OUT T;
OFF NAT;
OFF GCD;
OFF RAT;
COMMENT...FIND EIGENVECTORS NEXT TO TRANSFORM TO CANONICAL
     FORM BY TYPING IN INVERSE;
END;
End of file
COMMENT...FILE INVERSE
          TO FIND THE EIGENVECTORS ASSOCIATED WITH THE PURE
    IMAGINARY ROOT AND HENCE THE MATRIX THAT TRANSFORMS THE
    SYSTEM TO CANONICALFORM;
COMMENT...IF DIVIDE BY ZERO MESSAGE SET V2:=VV2. IF A SECOND
     DIVIDE BY ZERO MESSAGE APPEARS SET V2 TO ANYTHING E.G. 0;
OUT SCRATCH;
U1:=1;
V2:=(-U1*( M(2,1)+(M(2,1)*M(2,2)/M(1,1))))/
((((IEIG**2)+M(2,2)**2)/IEIG)-(M(1,2)*M(2,1)*M(2,2)/(M(1,1)*IEIG)));
SHUT SCRATCH;
OUT T;
VV2:=(U1*M(2,1)*IEIG*(M(1,1)+M(2,2)))/
   ((M(1,2)*M(2,2)*M(2,1))-(M(1,1)*((IEIG**2)+M(2,2)**2)));
V1:=(IEIG*U1/M(1,1))-(M(1,2)*V2/M(1,1));
U2:=(M(2,1)*U1/M(1,1))-(V2/(IEIG*M(1,1)))
```

```
      *((M(1,2)*M(2,1))-(M(1,1)*M(2,2)));
    COMMENT...THE COLUMNS OF COMPRISE OF THE EIGENVECTORS OF M
         ASSOCIATED WITH THE EIGENVALUES PLUS AND MINUS IEIG;
    V:=MAT((U1,V1),(U2,V2));
    OUT INVERSEW;
    V;
    VINV:=1/V;
    M;
    VINV*M*V;
    COMMENT...VINV*M*V SHOULD HAVE DIAGONAL ELEMENTS EQUAL TO ZERO
         AND OFF DIAGONAL ELEMENTS EQUAL TO PLUS AND MINUS IEIG;
    SHUT INVERSEW;
    COMMENT...CHECK IF TRANSFORM TO CANONICAL FORM WORKS;
    OUT T;
    VINV*M*V;
    COMMENT...VINV*M*V SHOULD HAVE DIAGONAL ELEMENTS EQUAL TO ZERO
         AND OFF DIAGONAL ELEMENTS EQUAL TO PLUS AND MINUS IEIG;
    COMMENT...TYPE IN TRANSFORM NEXT TO TRANSFORM TO CANONICAL FORM;
    END;
End of file
    COMMENT...FILE TRANSFORM
              TRANSFORMS THE SYSTEM TO CANONICAL FORM AND PUTS OUTPUT
         IN A FILE NAMED CANONICALFOR;
    OUT SCRATCH;
    OFF NAT;
    OFF ALLFAC;
    CLEAR R,S;
    MATRIX X(2,1),DN(2,1),N(2,1);
    DX:=MAT((DS),(DR));
    DN:=VINV*DX;
    N:=MAT((N1),(N2));
    X:=V*N;
    S:=X(1,1);
    R:=X(2,1);
    SHUT SCRATCH;
    OUT CANONICALFOR;
    IEIG;
    DN;
    SHUT CANONICALFOR;
    OUT T;
    COMMENT...EDIT FILE CANONICALFOR AS FOLLOWS -
              DELETE ALL LINES BUT THE ONE DEFINING IEIG AND THE
         ELEMENTS OF DN.  REPLACE MAT(1,1) BY DN1 AND MAT(2,1)
         BY DN2.
              SIMPLIFY DN1 AND DN2 BY OMITTING ALL TERMS HIGHER THAN
         THIRD ORDER FROM THE NUMERATOR AND HIGHER THAN CONSTANT
         FROM THE DENOMINATOR.
              PUT IN THE MISSING SEMICOLONS AT THE END OF IEIG AND
         EACH ELEMENT OF DN.
              THIS IS LESS EXPENSIVE AND PREVENTS OVERFLOW.
              THEN EX *REDUCE2 AGAIN AND TYPE IN CANONICALFOR
         FOLLOWED BY IN BIFSTAB;
    END;
End of file
    COMMENT... FILE BIFSTAB
         TO FIND THE STABILITY OF THE BIFURCATING PERIODIC ORBIT.
         TO BE USED IN CONJUNCTION WITH CANONICALFOR ONCE IT IS EDITED.
         TYPE IN CANONICALFOR BEFORE TYPING IN BIFSTAB.
         RESULTS APPEAR IN FILE NAMED BIFSTABW;
    OUT SCRATCH;
```

```
OFF ALLFAC;
D1F11:=DF(DN1,N1,2);
N1:=0;
N2:=0;
F1F11:=D1F11;
CLEAR D1F11,N1,N2;
D1F12:=DF(DN1,N1,1,N2,1);
N1:=0;
N2:=0;
F1F12:=D1F12;
CLEAR  D1F12,N1,N2;
D1F22:=DF(DN1,N2,2);
N1:=0;
N2:=0;
F1F22:=D1F22;
CLEAR D1F22,N1,N2;
D2F11:=DF(DN2,N1,2);
N1:=0;
N2:=0;
F2F11:=D2F11;
CLEAR D2F11,N1,N2;
D2F12:=DF(DN2,N1,1,N2,1);
N1:=0;
N2:=0;
F2F12:=D2F12;
CLEAR D2F12,N1,N2;
D2F22:=DF(DN2,N2,2);
N1:=0;
N2:=0;
F2F22:=D2F22;
CLEAR D2F22,N1,N2;
D1F111:=DF(DN1,N1,3);
N1:=0;
N2:=0;
F1F111:=D1F111;
CLEAR D1F111,N1,N2;
D1F122:=DF(DN1,N1,1,N2,2);
N1:=0;
N2:=0;
F1F122:=D1F122;
CLEAR D1F122,N1,N2;
D2F112:=DF(DN2,N1,2,N2,1);
N1:=0;
N2:=0;
F2F112:=D2F112;
CLEAR D2F112,N1,N2;
F2F222:=DF(DN2,N2,3);
N1:=0;
N2:=0;
F2F222;
DV3:=(F1F111+F1F122+F2F112+F2F222)+((1/IEIG)*(-(F1F11*F1F12)
         +(F2F22*F2F12)+(F2F11*F2F12)-(F1F22*F1F12)
         +(F1F11*F2F11)-(F1F22*F2F22)));
DDV3:=(3*DV3*PI)/(4*IEIG);
SHUT SCRATCH;
OUT BIFSTABW;
COMMENT ..DDV3 IS THE EVALUATION OF THE FORMULA (4.2) ON PAGE
       126 OF MARSDEN AND McCRACKEN [52]. THE STABILITY OF THE
       BIFURCATING PERIODIC ORBIT DEPENDS ON THE SIGN OF DDV3;
F1F11;
```

```
        F1F12;
        F1F22;
        F2F11;
        F2F12;
        F2F22;
        F1F111;
        F1F122;
        F2F112;
        F2F222;
        DV3;
        DDV3;
        SHUT BIFSTABW;
        END;
End of file
```

B. DATA AND BIFURCATION ANALYSIS FOR EXAMPLE (III.3.10)

a. Data.

```
 1   COMMENT . . .FILE DATA (FOR EXAMPLE III 3 10)
 2         IN ORDER TO DETERMINE WHETHER THERE IS A HOPF BIFURCATION AND
 3                  IF THERE IS, TO DETERMINE THE STABILITY OF THE
 4                  BIFURCATING PERIODIC ORBIT;
 5   OUT SCRATCH;
 6   COMMENT
 7         REPLACE LINES 22 THROUGH 55 WITH THE DEFINITION OF THE SYSTEM
 8                  IN TERMS OF THE VARIABLES S AND R
 9         HERE LINES 22 THROUGH 55 REPRESENT A CHEMOSTAT MODEL OF 2
10                  COMPETITORS COMPETING FOR 2 COMPLEMENTARY RESOURCES,
11                  S AND R. ONLY ONE SUBSTRATE IS INHIBITORY TO ONLY
12                  COMPETITOR AT HIGH CONCENTRATIONS
13         THE DEFINING EQUATIONS MUST BE OF THE FORM
14                  DS:=SOME FUNCTION OF S,R AND A1
15                  DR:=SOME FUNCTION OF S,R AND A1
16         A1 IS THE BIFURCATION PARAMETER. HOWEVER ONE CAN LEAVE
17                  OTHER VARIABLES UNDEFINED AS WELL IN ORDER TO
18                  DETERMINE IF THERE ARE PARAMETER COMBINATIONS
19                  THAT GIVE A HOPF BIFURCATION
20         IT IS ASSUMED THAT THE CRITICAL POINT IS (S,R)=(0,0);
21   OFF NAT; OFF ALLFAC;
22   COMMENT . . .S,R DENOTE CONCENTRATIONS OF NUTRIENTS
23               X1,X2 DENOTE CONCENTRATIONS OF COMPETITOR POPULATIONS
24               F1,F2 DENOTE THE FUNCTIONAL RESPONSES
25               DS (RESP. DR) DENOTES THE FIRST DERIVATIVE OF S (RESP. R)
26                    WITH RESPECT TO T;
27   COMMENT . . .THE CRITICAL POINT BEFORE TRANSLATION IS (TS,RT);
28   TS:=6;
29   RT:=4;
30   DS:=((SO-S-TS)*D)-(X1*F1/YS1)-(X2*F2/YS2);
31   DR:=((RO-R-RT)*D)-(X1*F1/YR1)-(X2*F2/YR2);
32   X1:=(((RO-R-RT)/YS2)-((SO-S-TS)/YR2))/((1/(YS2*YR1))-(1/(YS1*YR2)));
33   X2:=(((SO-S-TS)/YR1)-((RO-R-RT)/YS1))/((1/(YS2*YR1))-(1/(YS1*YR2)));
34   COMMENT . . .MICHAELIS-MENTEN KINETICS;
35   F1:=(D*AR1*(R+RT))/(LR1*(AR1-1)+R+RT);
36   COMMENT . . .INHIBITION KINETICS;
37   F2:=D+(D*(S+TS-LS2)*(MS2-S-TS)/(LS2*MS2*((A1*((S+TS)**2))
38   +(BS2*(S+TS))+1)));
39   COMMENT . . .WE DEFINE THE PARAMETERS USED IN THE MODEL EXCEPT A1
40                WHICH WE USE AS THE BIFURCATION PARAMETER AND
41                WHICHEVER OTHER PARAMETERS MIGHT AFFECT WHETHER OR
42                NOT THERE IS A HOPF BIFURCATION;
43   LS2:=4;
44   MS2:=6;
45   LR1:=4;
46   MR1:=6;
47   YS1:=1;
48   YS2:=1;
49   YR1:=2;
50   YR2:=1;
51   AR1:=10/9;
52   BS2:=7/12;
53   SO:=40;
54   RO:=30;
55   D:=1;
56   SHUT SCRATCH;
57   COMMENT . . . TYPE IN POLY FOLLOWED BY A SEMICOLON NEXT;
58   END;
End of file
```

b. Bifurcation analysis for the critical point E_{S2}, μ_{R1}

```
M  (Variational Matrix)

MAT(1,1)  := 1/(24*A1 + 3)
MAT(1,2)  := ( - 2)/5
MAT(2,1)  := 1/(24*A1 + 3)
MAT(2,2)  := ( - 1)/5

RGAM=( - 12*A1 + 1)/(120*A1 + 15)

DRGAMWRTA1=( - 4)/(192*A1**2 + 48*A1 + 3)

CHARPOLY=GAMMA**2 + GAMMA*(24*A1 - 2)/(120*A1 + 15)
              + 1/(120*A1 + 15)

A1=1/12  (Bifurcation value)

RGAM=0
COMMENT...RGAM SHOULD EQUAL ZERO;

DRGAMWRTA1=( - 12)/25
COMMENT...DRGAMWRTA1 SHOULD BE NONZERO;

CHARPOLY=GAMMA**2 + 1/25

IEIG=1/5  (Pure imaginary eigenvalue)

V  (Matrix of the transformation)

MAT(1,1)  := 1
MAT(1,2)  := 1
MAT(2,1)  := 1
MAT(2,2)  := 0

VINV:=1/V  (The inverse of the matrix of the transformation)

VINV(1,1)  := 0
VINV(1,2)  := 1
VINV(2,1)  := 1
VINV(2,2)  := ( -1)

M  (Variational matrix)

MAT(1,1)  := 1/5
MAT(1,2)  := ( - 2)/5
MAT(2,1)  := 1/5
MAT(2,2)  := ( - 1)/5

VINV*M*V  (The transformed variational matrix)

MAT(1,1)  := 0
MAT(1,2)  := 1/5
MAT(2,1)  := ( - 1)/5
MAT(2,2)  := 0

COMMENT...VINV*M*V SHOULD HAVE DIAGONAL ELEMENTS EQUAL TO ZERO
     AND OFF DIAGONAL ELEMENTS EQUAL TO PLUS AND MINUS IEIG;

(The transformed system -  omitting higher order terms)

DN1  := (  + 88*N1**3 + 290*N1**2*N2 + 660*N1**2 + 242*N1*N2**2
```

```
                + 1640*N1*N2 + 40*N2**3 + 800*N2**2 + 1440*N2)/(7200)

      DN2 := ( - 8*N1**3 + 3*N1**2*N2 - 152*N1**2  + 11*N1*N2**2
             - 62*N1*N2 - 720*N1)/(3600)

      COMMENT...DDV3 IS THE EVALUATION OF THE FORMULA (4.2) ON PAGE
            126 OF MARSDEN AND McCRACKEN [52]. THE STABILITY OF THE
            BIFURCATING PERIODIC ORBIT DEPENDS ON THE SIGN OF DDV3;

      F1F11=11/60
      F1F12=41/180
      F1F22=2/9
      F2F11=( - 19)/225
      F2F12=( - 31)/1800
      F2F22=0
      F1F111=11/150
      F1F122=121/1800
      F2F112=1/600
      F2F222=0

      DV3=( - 21049)/54000

      DDV3=( - 21049*PI)/14400 (Indicates stability of the periodic
                                 orbit)
End of file
```

C. BIFURCATION ANALYSIS FOR EXAMPLE (III.3.11)

a. The bifurcation analysis for the critical point $E_{\mu_{S2},\lambda_{R1}}$ follows. (The data for this example is given in file DATA in Appendix 3.A.).

```
M  (Variational Matrix)

MAT(1,1) = 7/(216*A1 + 366)
MAT(1,2) = ( - 2)/87
MAT(2,1) = 7/(216*A1 + 366)
MAT(2,2) = ( - 1)/87

RGAM=( - 24*A1 + 27)/(4176*A1 + 7076)

DRGAMWRTA1=( - 21)/(1296*A1**2 + 4392*A1 + 3721)

CHARPOLY=GAMMA**2 + GAMMA*(24*A1 - 27)/(2088*A1 + 3538)
                 + 7/(18792*A1 + 31842)

A1=9/8  (Bifurcation value)

RGAM=0
COMMENT...RGAM SHOULD EQUAL ZERO;

DRGAMWRTA1=( - 12)/5887
COMMENT...DRGAMWRTA1 SHOULD BE NONZERO OR TRANSVERSALITY VIOLATED;

CHARPOLY=GAMMA**2 + 1/7569

IEIG=1/87 (Pure imaginary eigenvalue)

V (Matrix of the transformation)

MAT(1,1) = 1
MAT(1,2) = 1
MAT(2,1) = 1
MAT(2,2) = 0

VINV=1/V (The inverse of the matrix of the transformation)

VINV(1,1) = 0
VINV(1,2) = 1
VINV(2,1) = 1
VINV(2,2) = ( -1)

M (Variational matrix)

MAT(1,1) = 1/87
MAT(1,2) = ( - 2)/87
MAT(2,1) = 1/87
MAT(2,2) = ( - 1)/87

VINV*M*V  (The transformed variational matrix)

MAT(1,1) = 0
MAT(1,2) = 1/87
MAT(2,1) = ( - 1)/87
MAT(2,2) = 0

COMMENT...VINV*M*V SHOULD HAVE DIAGONAL ELEMENTS EQUAL TO ZERO
    AND OFF DIAGONAL ELEMENTS EQUAL TO PLUS AND MINUS IEIG;

(The transformed system - omitting higher order terms)

DN1=( 2148*N1**3  + 3348*N1**2*N2 + 9844*N1**2  + 2360*N1*N2**2
```

```
 + 12164*N1*N2 + 348*N2**3 + 5568*N2**2 + 9744*N2)/(3*( 282576))

DN2=(  + 1020*N1**3+ 476*N1**2*N2 + 2616*N1**2 + 18*N1*N2**3
 + 268*N1*N2**2 - 632*N1*N2 - 9744*N1)/(3*(282576))

COMMENT...DDV3 IS THE EVALUATION OF THE FORMULA (4.2) ON PAGE
       126 OF MARSDEN AND McCRACKEN [52]. THE STABILITY OF THE
       BIFURCATING PERIODIC ORBIT DEPENDS ON THE SIGN OF DDV3;

F1F11=2461/105966
F1F12=3041/211932
F1F22=5/609
F2F11=109/17661
F2F12=( - 79)/105966
F2F22=0
F1F111=179/11774
F1F122=295/52983
F2F112=17/15138
F2F222=0

DV3=( - 2949797)/258133176

DDV3=( - 2949797*PI)/3956064 (Indicates stability of periodic
                              orbit)
End of file
```

b. The bifurcation analysis for the critical point $E_{\lambda_{S2},\mu_{R1}}$ follows. (The data for this case is the same as in file DATA in Appendix 3.A except that TS = 4 and RT = 6.)

```
M (Variational matrix)

MAT(1,1) = ( - 2)/(48*A1 + 123)
MAT(1,2) = 4/177
MAT(2,1) = ( - 2)/(48*A1 + 123)
MAT(2,2) = 2/177

RGAM=(16*A1 - 18)/(2832*A1 + 7257)

DRGAMWRTA1=16/(768*A1**2 + 3936*A1 + 5043)

CHARPOLY=GAMMA**2 + GAMMA*( - 32*A1 + 36)/(2832*A1 + 7257)
                  + 4/(8496*A1 + 21771)

A1=9/8  (Bifurcation value)

RGAM=0
COMMENT...RGAM SHOULD EQUAL ZERO;

DRGAMWRTA1=16/10443
COMMENT...DRGAMWRTA1 SHOULD BE NONZERO;

CHARPOLY=GAMMA**2 + 4/31329

IEIG=2/177 (Pure imaginary eigenvalue)

V (Matrix of the transformation)

MAT(1,1) = 1
MAT(1,2) = ( -1)
MAT(2,1) = 1
MAT(2,2) = 0

VINV=1/V (The inverse of the matrix of the transformation)

VINV(1,1) = 0
VINV(1,2) = 1
VINV(2,1) = ( -1)
VINV(2,2) = 1

M (Variational matrix)

MAT(1,1) = ( - 2)/177
MAT(1,2) = 4/177
MAT(2,1) = ( - 2)/177
MAT(2,2) = 2/177

VINV*M*V (The transformed variational matrix)

MAT(1,1) = 0
MAT(1,2) = 2/177
MAT(2,1) = ( - 2)/177
MAT(2,2) = 0

COMMENT...VINV*M*V SHOULD HAVE DIAGONAL ELEMENTS EQUAL TO ZERO
      AND OFF DIAGONAL ELEMENTS EQUAL TO PLUS AND MINUS IEIG;

(The transformed system - omitting higher order terms)

DN1= (  2344*N1**3 - 2546*N1**2*N2 + 11532*N1**2  + 1264*N1*N2**2
```

```
 - 9408*N1*N2 - 590*N2**3 + 3540*N2**2 + 9440*N2)/(835440)

DN2= ( - 1700*N1**3  + 1104*N1**2*N2 - 7760*N1**2  + 124*N1*N2**2
 + 2096*N1*N2 - 9440*N1)/(835440)

COMMENT...DDV3 IS THE EVALUATION OF THE FORMULA (4.2) ON PAGE
      126 OF MARSDEN AND McCRACKEN [52]. THE STABILITY OF THE
      BIFURCATING PERIODIC ORBIT DEPENDS ON THE SIGN OF DDV3;

F1F11=961/34810
F1F12=( - 196)/17405
F1F22=1/118
F2F11=( - 194)/10443
F2F12=131/52215
F2F22=0
F1F111=293/17405
F1F122=158/52215
F2F112=46/17450
F2F222=0

DV3=275717/30806850

DDV3=(827154*PI)/1392400  (Indicates instability of periodic
                           orbit)

End of file
```

APPENDIX 4

BASIC FEASIBLE SOLUTIONS OF M

We consider the following system of 2 linear equations in 4 unknowns $(S, R, x_1$ and $x_2)$:

$$S + \frac{x_1}{y_{S1}} + \frac{x_2}{y_{S2}} = S^0$$

$$R + \frac{x_1}{y_{R1}} + \frac{x_2}{y_{R2}} = R^0$$

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

Since the rank of this system is 2 there are $C_2^4 = 6$ possible basic feasible solutions of M and hence of F. We generate these solutions by the method of pivoting used in linear programming (see Luenberger [51, Chapter 3]). (Recall that we are assuming $C_1 \neq C_2$.)

We start with S and R in the basis.

(I)

$$\begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline S & 1 & 0 & 1/y_{S1} & 1/y_{S2} & S^0 \\ R & 0 & 1 & 1/y_{R1} & 1/y_{R2} & R^0 \\ \hline \end{array}$$

Corresponding basic feasible solution: $(S^0, R^0, 0, 0)$.

If $R^0/S^0 \geq C_1$ then we replace S in the basis of Tableau I by x_1 (i.e. pivot on the $(S - x_1)$ element, $1/y_{S1}$, of Tableau I).

(II)

$$\begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline x_1 & y_{S1} & 0 & 1 & y_{S1}/y_{S2} & y_{S1}S^0 \\ R & -y_{S1}/y_{R1} & 1 & 0 & * & R^0-C_1S^0 \\ \hline \end{array}$$

Corresponding basic feasible solution: $(0,R^0-C_1S^0,y_{S1}S^0,0)$.

$* = (y_{R1}y_{S2} - y_{S1}y_{R2})/(y_{R1}y_{R2}y_{S2})$.

If $R^0/S^0 \leq C_1$ then pivot on the $(R-x_1)$ element of Tableau I.

(III)

$$\begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline S & 1 & -y_{R1}/y_{S1} & 0 & * & S^0-R^0/C_1 \\ x_1 & 0 & y_{R1} & 1 & y_{R1}/y_{R2} & y_{R1}R^0 \\ \hline \end{array}$$

Corresponding basic feasible solution: $(S^0-R^0/C_1,0,y_{R1}R^0,0)$

$* = (y_{S1}y_{R2} - y_{R1}y_{S2})/y_{S1}y_{S2}y_{R2}$.

If $R^0/S^0 \geq C_2$ then pivot on the $(S-x_2)$ element of Tableau I.

(IV)

$$\begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline x_2 & y_{S2} & 0 & y_{S2}/y_{S1} & 1 & y_{S2}S^0 \\ R & -y_{S2}/y_{R2} & 1 & * & 0 & R^0-C_2S^0 \\ \hline \end{array}$$

Corresponding basic feasible solution: $(0,R^0-C_2S^0,0,y_{S2}S^0)$

$* = (y_{S1}y_{R2} - y_{S2}y_{R1})/y_{S1}y_{R1}y_{R2}$.

If $R^0/S^0 \leq C_2$ then pivot on the $(R-x_2)$ element of Tableau I.

(V)

$$\begin{array}{c|cccc|c} & S & R & x_1 & x_2 & \\ \hline S & 1 & -y_{R2}/y_{S2} & * & 0 & S^0-R^0/C_2 \\ x_2 & 0 & y_{R2} & y_{R2}/y_{R1} & 1 & y_{R2}R^0 \\ \hline \end{array}$$

Corresponding basic feasible solution: $(S^0-R^0/C_2,0,y_{R2}R^0,0)$

$* = (y_{S2}y_{R1} - y_{S1}y_{R2})/y_{S1}y_{S2}y_{R1}$.

A4

If $C_1 \leq R^0/S^0 \leq C_2$ or $C_1 \geq R^0/S^0 \geq C_2$ then pivot on the $(R-x_2)$ element of Tableau II to obtain the basic feasible solution

$$\left(0,0,y_{S1}y_{R1}(y_{S2}S^0-y_{R2}R^0)/(y_{S2}y_{R1}-y_{S1}y_{R2}),y_{S2}y_{R2}(y_{R1}R^0-y_{S1}S^0)/(y_{S2}y_{R1}-y_{S1}y_{R2})\right)$$

APPENDIX 5

LINEAR ANALYSIS OF THE FOOD WEB AND FOOD CHAIN MODELS

A. LINEAR ANALYSIS - FOOD WEB MODEL (IV.3.4)

The variational matrix is:

$$V(S,x_1,x_2,y) = \begin{bmatrix} -1-x_1p_1'(S)-x_2p_2'(S) & -p_1(S) & -p_2(S) & 0 \\ x_1p_1'(S) & -1+p_1(S)-yq'(x_1) & 0 & -q(x_1) \\ x_2p_2'(S) & 0 & -1+p_2(S) & 0 \\ 0 & yq'(x_1) & 0 & -1+q(x_1) \end{bmatrix}.$$

We consider the local stability of each of the eigenvalues E_1, E_{λ_1}, E_{λ_2}, E_{S*}, E_{λ_2}.

a.

$$V(1,0,0,0) = \begin{bmatrix} -1 & -p_1(1) & -p_2(1) & 0 \\ 0 & -1+p_1(1) & 0 & 0 \\ 0 & 0 & -1+p_2(1) & 0 \\ 0 & 0 & 0 & -1 \end{bmatrix}$$

The eigenvalues of the variational equation at the critical point E_1 are: -1, -1, $-1+p_1(1)$ and $-1+p_2(1)$. It follows that E_1 is locally asymptotically stable provided $\lambda_1 > 1$ and $\lambda_2 > 1$, that is, provided there is not enough substrate to support either competitor (see Theorem IV.5.3). If either $\lambda_2 < 1$ or $\lambda_1 < 1$ then E_1 is unstable.

b.

$$V(\lambda_2,0,1-\lambda_2,0) = \begin{bmatrix} -1-(1-\lambda_2)p_2'(\lambda_2) & -p_1(\lambda_2) & -1 & 0 \\ 0 & -1+p_1(\lambda_2) & 0 & 0 \\ (1-\lambda_2)p_2'(\lambda_2) & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 \end{bmatrix}$$

Clearly -1 is an eigenvalue of the variational equation at the critical point E_{λ_2}. We can therefore eliminate the last row and column and consider the remaining 3×3 matrix which we shall call $V(\lambda_2,0,1-\lambda_2)$. Then expanding $V(\lambda_2,0,1-\lambda_2) - \mu I$ along the second column it follows that the remaining three eigenvalues are: -1, $-1+p_1(\lambda_2)$ and $-(1-\lambda_2)p_2'(\lambda_2)$. It follows that E_{λ_2} is always unstable since $-1+p_1(\lambda_2) > 0$.

Assume $\lambda_1 < 1$. Then E_{λ_1} is in the nonnegative (S,x_1,x_2,y) cone.

c.

$$V(\lambda_1,1-\lambda_1,0,0) = \begin{bmatrix} -1-(1-\lambda_1)p_1'(\lambda_1) & -1 & -p_2(\lambda_1) & 0 \\ (1-\lambda_1)p_1'(\lambda_1) & 0 & 0 & -q(1-\lambda_1) \\ 0 & 0 & -1+p_2(\lambda_1) & 0 \\ 0 & 0 & 0 & -1+q(1-\lambda_1) \end{bmatrix}$$

Expanding $V(\lambda_1,1-\lambda_1,0,0) - \lambda I$ along the first column it follows that the eigenvalues of E_{λ_1} are: -1, $-(1-\lambda_1)p_1'(\lambda_1)$, $-1+p_2(\lambda_1)$ and $-1+q(1-\lambda_1)$. Provided $\lambda_1 < 1$ by assumption, (IV.2.4) it follows that $-(1-\lambda_1)p_1'(\lambda_1) < 0$. Provided $1-\lambda_1 < \delta$ it follows that $-1+q(1-\lambda_1) < 0$. Since $\lambda_1 < \lambda_2$, $-1+p_2(\lambda_1) < 0$. Therefore E_{λ_1} is asymptotically stable provided $1-\delta < \lambda_1 < 1$ and is unstable if $\lambda_1 + \delta < 1$.

d.

$$V(S^*,\delta,0,y^*) = \begin{bmatrix} -1-\delta p_1'(S^*) & -p_1(S^*) & -p_2(S^*) & 0 \\ \delta p_1'(S^*) & -1+p_1(S^*)-y^*q'(\delta) & 0 & -q(\delta) \\ 0 & 0 & -1+p_2(S^*) & 0 \\ 0 & y^*q'(\delta) & 0 & 0 \end{bmatrix}.$$

If we interchange the last two rows and the last two columns we do not change the eigenvalues:

Let

$$\tilde{V} = \begin{bmatrix} -1- p_1'(S^*) & -p_1(S^*) & 0 & -p_2(S^*) \\ p_1'(S^*) & -1+p_1(S^*)-y^*q'(\delta) & -1 & 0 \\ 0 & y^*q'(\delta) & 0 & 0 \\ 0 & 0 & 0 & -1+p_2(S^*) \end{bmatrix}$$

Expanding $\tilde{V} - \lambda I$ along the last row and factoring out $(\mu+1)$ the characteristic equation is:

(A5.A.1) $$(-1+p_2(S^*)-\lambda)(\lambda+1)[\lambda^2+\lambda(y^*(\delta q'(\delta)-1)/\delta+\delta p_1'(S^*)) + y^*q'(\delta)(1+ p_1'(S^*))] = 0$$

We only consider this critical point when $y^* \geq 0$, i.e. $S^* \geq \lambda_1$, since otherwise it does not lie in the nonnegative cone.

Then by the Routh-Hurwitz criteria (see Eg. [30]) E_{S*} is asymptotically stable provided that

(A5.A.2) (i) $S^* < \lambda_2$, and

(A5.A.3) (ii) $y^*(\delta q'(\delta) - 1)/\delta + \delta p_1'(S^*) > 0$.

If the inequality in (i) and (ii) is reversed then E_{S*} is unstable.

Note that,

$$\delta q'(\delta) - 1 = \delta^2 h'(\delta) ,$$

so that (ii) is equivalent to

(A5.A.3)' $$\text{(ii)}' \quad y^* h'(\delta) + p_1'(S^*) > 0 .$$

e. $$V(\lambda_2,\delta,\hat{x}_2,\hat{y}) = \begin{bmatrix} -1-\delta p_1'(\lambda_2)-\hat{x}_2 p_2'(\lambda_2) & -p_1(\lambda_2) & -1 & 0 \\ \delta p_1'(\lambda_2) & -1+p_1(\lambda_2)-\hat{y}q'(\delta) & 0 & -1 \\ \hat{x}_2 p_2'(\lambda_2) & 0 & 0 & 0 \\ 0 & \hat{y}q'(\delta) & 0 & 0 \end{bmatrix} .$$

The characteristic equation is:

(A5.A.4) $$\begin{aligned} &(\mu+1)\big(\mu^3+\mu^2[\hat{y}(\delta q'(\delta)-1)/\delta + \delta p_1'(\lambda_2) + \hat{x}_2 p_2'(\lambda_2)] \\ &\quad + \mu[\hat{x}_2 \hat{y} p_2'(\lambda_2)(\delta q'(\delta)-1)/\delta + \hat{y}q'(\delta)(1+\delta p_1'(\lambda_2))] \\ &\quad + \hat{x}_2 \hat{y} q'(\delta) p_2'(\lambda_2)\big) = 0 \end{aligned}$$

We assume that $\hat{x} = 1 - \lambda_2 - \delta p_1(\lambda_2) \geq 0$, otherwise $\hat{E}_{\lambda_2}$ does not lie in the nonnegative cone. We denote the coefficients in the characteristic equation:

(A5.A.5) $$C_0 = \hat{x}_2 \hat{y} q'(\delta) p_2'(\lambda_2) ,$$

(A5.A.6) $$C_1 = \hat{x}_2 \hat{y} p_2'(\lambda_2)\big(\delta q'(\delta) - 1\big)/\delta + \hat{y}q'(\delta)\big(1 + \delta p_1'(\lambda_2)\big)$$

(A5.A.7) $$C_2 = \hat{y}\big(\delta q'(\delta) - 1\big)/\delta + \delta p_1'(\lambda_2) + \hat{x}_2 p_2'(\lambda_2) .$$

By the Routh-Hurwitz criteria, $\hat{E}_{\lambda_2}$ is locally asymptotically stable provided

(A5.A.8) (i) $C_0 > 0$, $C_1 > 0$ and $C_2 > 0$, and

(A5.A.9) (ii) $\Delta_2 = C_2C_1 - C_0 > 0$,

and is unstable if any inequality in (i) or (ii) is reversed. Suppose all the components of $\hat{E}_{\lambda_2}$ are positive and that $\delta q'(\delta) \geq 1$. Then condition (A5.A.5) holds and condition (A5.A.9) can be written,

$$\begin{aligned}\Delta_2 &= C_2\left(C_1-\hat{y}q'(\delta)\right) + \hat{y}q'(\delta)\left(C_2-\hat{x}_2p_2'(\lambda_2)\right) + \hat{x}_2\hat{y}q'(\delta)p_2'(\lambda_2) - C_0\\ &= C_2\left(C_1-\hat{y}q'(\delta)\right) + \hat{y}q'(\delta)\left(C_2-\hat{x}_2p_2'(\lambda_2)\right)\\ &> 0, \text{ provided } \delta q'(\delta) \geq 1 .\end{aligned}$$

Therefore, provided $\hat{E}_{\lambda_2}$ lies in the positive (S,x_1,x_2,y) cone and $\delta q'(\delta) \geq 1$ then $\hat{E}_{\lambda_2}$ is locally asymptotically stable. In particular, this applies if $q(x_1)$ is Lotka-Volterra i.e. $q(x_1) = x_1/\delta$ since then $\delta q'(\delta) = 1$. However, if $q(x_1)$ satisfies Michaelis-Menten kinetics, i.e. $q(x_1) = \mu x_1/\ \delta(\mu-1)+x_1$ where $\mu > 1$, then $\delta q'(\delta) = (\mu-1)/\mu < 1$.

Note also that E_{S*} and $\hat{E}_{\lambda_2}$ coalesce when $\hat{x}_2 = 1 - \lambda_2 - \delta p_1(\lambda_2) = 0$. At $\hat{x}_2 = 0$, $\Delta = C_1C_2$ since $C_0 > 0$. In this case $C_1 > 0$ and C_2 reduces to the expression in condition (A5.A.3) for the asymptotic stability of E_{S*}. Therefore if condition (A5.A.3) for local asymptotic stability of E_{S*} holds as E_{S*} and $\hat{E}_{\lambda_2}$ coalesce, then $\hat{E}_{\lambda_2}$ is at least initially locally asymptotically stable. On the other hand if there has been a Hopf bifurcation of E_{S*} previous to the coalescence of E_{S*} and $\hat{E}_{\lambda_2}$, then $\hat{E}_{\lambda_2}$ is at least initially unstable.

B. LINEAR ANALYSIS - FOOD CHAIN MODEL (IV.4.3)

The matrix of the associated linear system is

$$V(S,x_1,y) = \begin{bmatrix} -1-x_1p_1'(S) & -p_1(S) & 0 \\ x_1p_1'(S) & -1+p_1(S)-yq'(x_1) & -q(x_1) \\ 0 & yq'(x_1) & -1+q(x_1) \end{bmatrix}.$$

We consider the stability of each of the eigenvalues E_1^3, $E_{\lambda_1}^3$, E_{S*}^3.

The eigenvalues of E_1^3 are: -1, -1 and $-1+p_1(1)$.

The eigenvalues of $E_{\lambda_1}^3$ are: -1, $-(1-\lambda_1)p_1'(\lambda_1)$ and $-1+q(1-\lambda_1)$.

The eigenvalues of E_{S*}^3 satisfy the characteristic equation:

$$(\mathrm{A5.B.1}) \quad (\mu+1)[\mu^2+\mu\big(y^*q'(\delta)-p_1(S^*)+1+\delta p_1'(S^*)\big)+y^*q'(\delta) + \delta y^*p_1'(S^*)q'(\delta)] = 0,$$

and so E_{S*}^3 is asymptotically stable provided

$$(\mathrm{A5.B.2}) \qquad y^*\big(\delta q'(\delta)-1\big)/\delta + \delta p_1'(S^*) > 0$$

and is unstable if the inequality is reversed.