PREDATOR MEDIATED COMPETITION IN THE CHEMOSTAT

PREDATOR MEDIATED COMPETITON : PREDATOR FEEDING ON TWO DIFFERENT TROPHIC LEVELS

By

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A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree
Master of Science

McMaster University
January 1992

MASTER OF SCIENCE (1992) MCMASTER UNIVERSITY
(Mathematics) Hamilton, Ontario

TITLE: Predator Mediated Competiton : Predator Feeding on Two Different Trophic Levels

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NUMBER OF PAGES: vi, 75

I would like to dedicate
this thesis to the loving
memory of my late uncle,
Evangelos Daoussis.

Acknowlegements

I would like to extend both my gratitute and my appreciation to my supervisor, Dr. G.S.K. Wolkowicz for her patience and tireless efforts in guiding my research, and for introducing me to the area of Mathematical Ecology early in my undergraduate career.

I would also like to thank my father, Jerry Daoussis, and my uncle, Steve Daoussis, for their love, support and encouragement throughout my academic endeavors.

I would also like to thank Vicki Ringelberg for her love and understanding over the past few years and a special thank you to her mother, Mrs. Francis Ringelberg whose love and support rivaled my own mother's.

Finally my thanks go to Sean Milosevic-Hill for his expert typing and to Chan Ping Shing for his invaluable help in latexing this thesis.

This research was supported by the Natural Sciences Engineering Research Council and McMaster University.

Abstract

We consider a model of the chemostat in which three competitor populations compete for a single, essential, growth-limiting nutrient. As well, the least efficient competitor population also acts as a predator on the most efficient competitor population. Bifurcation methods are used to obtain information about the qualitative behaviour of the model. A complete description of the global stability is given for the case when Lotka-Volterra response functions describe both competitor-nutrient and predator-prey interactions. For certain parameter values, the model predicts coexistence of the three species. The model also shows that the elimination of the predator population or the elimination of a competitor population can cause the system to collapse from three species to one.

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Chapter 1

Introduction

1.1 Introduction and Thesis Outline

What accounts for the diversity of ecosystems? This is an interesting question. There is considerable theoretical and experimental evidence that supports the notion that predation can be one of the factors responsible for the diversity displayed by natural ecosystems. We refer the reader to [3], [5], [6], [7], [17], [18], [20], [22], [24] as a short but incomplete survey of both experimental evidence and predictions of mathematical models. Throughout the study of this question, the chemostat has played an integral part. Simply put, the chemostat is a laboratory apparatus used for the continuous culture of organisms. For a detailed description of the chemostat and its importance in ecology, see Waltman [21] and the references found therein.

In this thesis we consider a model of a chemostat in which three competitor populations compete for a single, essential, growth-limiting nutrient. As well, the least efficient competitor population also acts as a predator on the most efficient competitor population. We shall refer to this model as the four dimensional model or the three species model. We also consider the subsystems that result when one of the competitor populations is absent. In particular, if the predator is absent, or if the competitor that is predated upon is absent, then the model reduces to a three dimensional model of pure competition. If, on the other hand, the competitor that is not predated upon is absent, the model reduces to a three dimensional model of a food web in which the predator feeds on two different trophic levels. In all of our models of the chemostat we assume that the growth vessel is perfectly mixed, thus there is no spatial variation in the concentration of nutrient or species population. Nutrient is supplied at a constant rate and removed at the same rate. We also assume the death rates of the populations are insignificant compared to the dilution rate.

In this context it is known that in the absence of any predator, the model predicts that at most one competitor population will survive ([1], [4], [23]). The surviving population is the one that can maintain itself on the lowest concentration of nutrient. The behaviour of this competitive chemostat when invaded by a predator that feeds only on one trophic level has also been studied ([5], [9], [10], [19]). In fact, this food web can be persistent. In our model, we allow the predator to feed on two different trophic levels. We also show that this system can persist under favourable conditions. Thus our results, just as the results mentioned above, tend to support Paine's conjecture that predation is one of the factors contributing to the diversity of ecosystems.

In addition, our results also lend support to the idea that competition may also account for the complexity of these systems. In particular, under the same conditions that support the persistence of the entire four dimensional model, removal of the competitor that is not predated upon can also result in the extinction of the other competitor, the one that is predated upon. If we view our three species food web model as a model resulting from a two species food web, in which one of the populations is being driven to extinction by its predator, being invaded by a population that competes for nutrient but is not predated upon by either competitor, the coexistence of the three species can be attributed to competition rather than to predation.

This thesis is organized in the following way. In Chapter 2 we give the mathematical description of the model along with the necessary assumptions. In addition, we give a non-dimensional version of the model (introducing the constant γ, which results from scaling), and introduce notation for the critical points. Finally, we give a description of the three subsystems that arise when one population is absent. Chapters 3 and 4 contain the mathematical analysis and results for the model and its corresponding three-dimensional food web (resulting from the omition of the second most efficient competitor, the one with no predator). The analysis is carried out on the non-dimensional versions of the model. In Chapter 3 we consider the full four dimensional system. The chapter begins with preliminary results, followed by a complete description of the transfer of global stability for particular prototypes of uptake functions, and concludes with the persistence arguments. In Chapter 4, we consider the two species food web with the predator that feeds on two different trophic levels, the other competitor and the nutrient. We begin by assuming the scaling constant, $\gamma = 1$. We give some global results. For example, we examine properties of periodic orbits, when they exist. The rest of the chapter is devoted to the technical complications that arise when $\gamma \neq 1$. We conclude with Chapter 5 in which we summarize and discuss our results. Appendices A and B contain the table and figures. Appendices C and D contain respectively, the local stability analysis for the four dimensional model and the three dimensional food web. For the relevant mathematical background needed for the analysis of this dynamical system see [2], [8], [12], [15].

1.2 Notation

The following notation is used throughout this thesis.

$\Re$ denotes the real numbers

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

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

$int\Re^n_+$ denotes the interior of $\Re^n_+$

clA denotes the closure of the set A

$\mathcal{O}^+(X)$ denotes the positive semi-orbit through the point X

$\mathcal{O}^-(X)$ denotes the negative semi-orbit through the point X

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

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

$W^s(X)$ denotes the stable manifold of the critical point X

$W^u(X)$ denotes the unstable manifold of the critical point X

All other notation in this thesis is either standard or is defined in the text of the thesis.

Chapter 2

Predator Mediated Competition : Predator Feeding On Two Different Trophic Levels

2.1 The Model

We shall discuss a model of predator-mediated competition in the chemostat described by the following system of ordinary differential equations:

$$\begin{aligned}
S'(t) &= (S^o - S(t))D - \frac{x_1(t)p_1(S(t))}{\eta_1} - \frac{x_2(t)p_2(S(t))}{\eta_2} - \frac{y(t)p_3(S(t))}{\eta_3} \\
x_1'(t) &= x_1(t)(-D + p_1(S(t))) - \frac{y(t)q(x_1(t))}{z} \\
x_2'(t) &= x_2(t)(-D + p_2(S(t))) \\
y'(t) &= y(t)(-D + p_3(S(t)) + q(x_1(t))) \\
S(0) &= S_0 \geq 0,\ x_i(0) = x_{i0} \geq 0,\ i = 1, 2,\ y(0) = y_0 \geq 0.
\end{aligned} \tag{2.1}$$

In these equations (assuming for convenience that the volume of the culture vessel is one cubic unit), $S(t)$ represents the concentration of substrate at time t; $x_i(t)$ $i = 1, 2$ and $y(t)$ represent populations of microorganisms at time t. All populations of microorganisms are assumed to compete for resource $S(t)$. However, $y(t)$

can also be considered a predator population, since besides consuming $S(t)$, it predates on $x_1(t)$. $p_i(S)$ is a function describing the rate of conversion of nutrient to biomass; η_i is a growth yield constant, and we assume $\frac{p_i(S)}{\eta_i}$ is the rate of consumption of nutrient S for the respective populations; $q(x_1)$ is a function describing the rate of conversion of prey x_1 to biomass $y(t)$, (i.e. the per capita growth rate of the predator population as a function of the prey population); z is the growth yield constant for the predator population feeding on the prey; $\frac{q(x_1)}{z}$ is assumed to denote the prey-uptake function for the predator; S^o denotes the concentration of substrate in the feed bottle; assume insignificant death rates of the three populations as compared to the dilution rate, and furthermore; D denotes both the input rate of substrate from the feed bottle to the growth chamber and the wash-out rate of substrate, population members and byproducts from the growth chamber to a receptacle container. Hence S^oD denotes the rate of input of substrate concentration from the feed bottle to the growth chamber.

The above system describes a chemostat in which three populations of microorganisms compete for a single, essential, nonreproducing, growth-limiting substrate. In addition, one of the three competitor populations is also a predator population which predates on the competitor population that would be the sole survivor in the absence of the predator. The growth vessel is assumed to be perfectly stirred, and hence there are no spatial variations in the concentration of nutrient or the concentration of the populations. The substrate-uptake (the prey-uptake) is assumed to be proportional to the rate of conversion to competitor biomass (predator biomass).

We make the following assumptions concerning the functions $p_i(S), i = 1, 2, 3$ and $q(x_1)$ in system (2.1) :

$$p_i, q : \Re_+ \rightarrow \Re_+; \tag{2.2}$$

$$p_i, q \text{ are continously differentiable ;} \tag{2.3}$$

$$p_1'(S) > 0 \text{ for all } S \in \Re_+; \tag{2.4}$$

$$p_i'(S) \geq 0 \text{ for all } S \in \Re_+ \ i = 2, 3; \tag{2.5}$$

$$q'(x_1) \geq 0 \text{ for all } x_1 \in \Re_+; \tag{2.6}$$

$$p_i(0) = 0, \ q(0) = 0. \tag{2.7}$$

2.2 The Scaled Model

The following substitutions will help simplify the analysis of system (2.1) :

$$\bar{t} = tD;\ \bar{S} = \frac{S}{S^o};\ \bar{x}_i = \frac{x_i}{\eta_i S^o}\ \text{i} = 1,2; \tag{2.8}$$

$$\bar{y} = \frac{y}{\eta_1 S^o z};\ \bar{p}_i(\bar{S}) = \frac{p_i(S)}{D}\ \text{i=1,2,3}; \tag{2.9}$$

$$\bar{q}(x_1) = \frac{q(x_1)}{D};\ \gamma = \frac{\eta_2}{\eta_1 z}. \tag{2.10}$$

Omitting the bars, to simplify the notation, the scaled version of system (2.1) can be written as follows :

$$\begin{aligned}
S'(t) &= (1 - S(t)) - x_1(t)p_1(S(t)) \ - x_2(t)p_2(S(t)) - \frac{y(t)p_3(S(t))}{\gamma} \\
x_1'(t) &= x_1(t)(-1 + p_1(S(t))) - y(t)q(x_1(t)) \\
x_2'(t) &= x_2(-1 + p_2(S(t))) \\
y'(t) &= y(t)(-1 + p_3(S(t)) + q(x_1(t))) \\
S_0 &\geq 0, x_{i0} \geq 0 \text{ i=1,2, } y_0 \geq 0.
\end{aligned} \tag{2.11}$$

There is no loss of generality if we analyze system (2.11) instead of system (2.1), since all assumption (2.2) - (2.7) hold for this scaled version of the model, and our findings and results can easily be reinterpreted in terms of system (2.1) by the appropriate usage of (2.8) - (2.10). It follows, from assumptions (2.4) - (2.7), that there exist uniquely defined positive extended real numbers λ_i and δ such that:

$$\begin{aligned}
&p_i(S) < 1 \text{ if } S < \lambda_i, \\
&p_i(S) > 1 \text{ if } S > \lambda_i, \\
&q(x_1) < 1 \text{ if } x_1 < \delta, \\
&q(x_1) > 1 \text{ if } x_1 > \delta.
\end{aligned} \tag{2.12}$$

Hence λ_i and δ denote the break-even concentrations of nutrient and prey, respectively. We make the following assumption of a technical nature : if λ_i, $(i = 1,2,3)$ (or δ) is finite, then $p_i'(\lambda_i) > 0$ $(q'(\delta) > 0)$.

We also assume that λ_i, δ are distinct from 1 and from each other whenever they are finite, and

$$\lambda_1 < \lambda_2 < \lambda_3 \text{ if } \lambda_1, \lambda_2 < \infty. \tag{2.13}$$

The critical points of system (2.11)when they exist will be denoted as :

$$\begin{aligned} E_0 &= (1,0,0,0) \\ E_{\lambda_1} &= (\lambda_1, 1-\lambda_1, 0, 0) \\ E_{\lambda_2} &= (\lambda_2, 0, 1-\lambda_2, 0) \\ E_{\lambda_3} &= (\lambda_3, 0, 0, \gamma(1-\lambda_3)) \\ E_{S^*} &= (S^*, x_1^*, 0, y^*) \end{aligned}$$

where $y^* = \frac{x_1^*(-1+p_1(S^*))}{(1-p_3(S^*))}$, $x_1^* = q^{-1}(1-p_3(S^*))$ and S^* must satisfy $1-S^* = x_1^* p_1(S^*) + \frac{y^* p_3(S^*)}{\gamma}$, and

$$\tilde{E}_{\lambda_2} = (\lambda_2, \tilde{x}_1, \tilde{x}_2, \tilde{y})$$

where $\tilde{x}_1 = q^{-1}(1-p_3(\lambda_2))$, $\tilde{y} = \frac{\tilde{x}_1(-1+p_1(\lambda_2))}{(1-p_3(\lambda_2))}$ and $\tilde{x}_2 = 1-\lambda_2-\tilde{x}_1 p_1(\lambda_2) - \frac{\tilde{y} p_3(\lambda_2)}{\gamma}$.

We say that a critical point exists if and only if all of its components are nonnegative. Hence, E_{λ_i} exists provided that $\lambda_i \leq 1$ for $i = 1,2,3$. $\tilde{E}_{\lambda_2}$ exists provided that $\tilde{x}_2 = 1-\lambda_2-\tilde{x}_1 p_1(\lambda_2) - \frac{\tilde{y} p_3(\lambda_2)}{\gamma} \geq 0$. In particular, if $\gamma = 1$ and $q(x_1) = \frac{x_1}{\delta}$, this implies that $\lambda_2 + \delta \leq 1$. E_{S^*} exists provided $\lambda_1 \leq S^* \leq \lambda_3$ satisfies the equation $1-S^* = x_1^* p_1(S^*) + \frac{y^* p_3(S^*)}{\gamma}$. The question of existence and/or uniqueness of S^* will be addressed in later chapters.

2.3 Three Dimensional Subsystems

We will examine the three dimensional subsystems of system (2.11) that result from the absence of one of the competitors or the predator in that system. If the predator, $y(t)$, is absent (that is $y_0 = 0$ in system (2.11)) then (2.11) becomes:

$$S'(t) = 1 - S(t) - x_1(t)p_1(S(t)) - x_2(t)p_2(S(t))$$

$$\begin{aligned} x_i'(t) &= x_i(t)(-1+p_i(S(t))),\ i=1,2. \\ S_0 &\geq 0 \text{ and } x_{i0} > 0 \text{ for } i=1,2. \end{aligned} \tag{2.14}$$

This is the model studied by Butler et al. [4] restricted to two competitors. Thus the results in [4] apply to subsystem (2.14). In particular, if $\lambda_1 < 1$ and $\lambda_1 < \lambda_2$, then x_1 drives x_2 to extinction.

If competitor x_1 is absent (that is $x_{10} = 0$ in system (2.11)), then (2.11) becomes:

$$\begin{aligned} S'(t) &= 1 - S(t) - x_2(t)p_2(S(t)) - y(t)p_3(S(t)) \\ x_2'(t) &= x_2(t)(-1+p_2(S(t))) \\ y'(t) &= y(t)(-1+p_3(S(t))) \\ S_0 &\geq 0, x_{20} > 0, \text{ and } y_0 > 0. \end{aligned} \tag{2.15}$$

This subsystem is identical to subsystem (2.14) above, with $y(t)$ no longer behaving as both predator and competitor but as a competitor only. Note that in subsystem (2.15), x_2 plays the role of x_1 and y plays the role of x_2 in subsystem (2.14).

Finally, if x_2 is absent (that is $x_{20} = 0$), then (2.11) becomes the food web

$$\begin{aligned} S'(t) &= 1 - S(t) - x_1(t)p_1(S(t)) - \frac{y(t)p_3(S(t))}{\gamma} \\ x_1'(t) &= x_1(t)(-1+p_1(S(t))) - y(t)q(x_1(t)) \\ y'(t) &= y(t)(-1+p_3(S(t)) + q(x_1(t))) \\ S_0 &\geq 0, x_{10} \geq 0, \text{ and } y_0 \geq 0. \end{aligned} \tag{2.16}$$

This food web is different from the one considered by Butler and Wolkowicz [5], Gard ([9], [10]) and Saunders and Bazin [19], since it also allows the predator to feed on the nutrient. The critical points of subsystem (2.16) when they exist will be denoted by :

$$E_0^3 = (1,0,0)$$

$$\begin{aligned} E^3_{\lambda_1} &= (\lambda_1, 1-\lambda_1, 0) \\ E^3_{\lambda_3} &= (\lambda_3, 0, \gamma(1-\lambda_3)) \\ E^3_{S^*} &= (S^*, x_1^*, y^*) \end{aligned}$$

where $x_1^* = q^{-1}(1 - p_3(S^*))$, and $y^* = \frac{x_1^*(-1+p_1(S^*))}{(1-p_3(S^*))}$ and S^* must satisfy $1 - S^* = x_1^* p_1(S^*) + \frac{y^* p_3(S^*)}{\gamma}$. As before, a critical point will be said to exist only if its components are nonnegative. Subsystem (2.16) will be examined in more detail in the following chapters and a linear analysis can be found in Appendix D.1.

Chapter 3

Global Dynamics of the Four Dimensional System

3.1 Preliminary Results

As is with any other reasonable model of the chemostat, the solutions of system (2.11) are well behaved which is the content of our first theorem.

Theorem 3.1 *All solutions $S(t)$, $x_1(t)$, $x_2(t)$ and $y(t)$ of (2.11) for which $x_{i0} > 0$ $i = 1, 2$ and $y_0 > 0$ are* a) *positive and* b) *bounded for $t > 0$.*

Proof of a): If $S(0) = 0$ then $S'(0) = 1 > 0$. Suppose there exists a first $t_1 > 0$ such that $S(t_1) = 0$ and $S(t) > 0$ for $0 < t < t_1$. Then $S'(t_1) \leq 0$. But by (2.11), $S'(t_1) = 1 > 0$, a contradiction.

Next, $x_i(t) > 0$ for $i = 1, 2$ and all $t > 0$ since the boundary face where $x_i \equiv 0$ $i = 1, 2$ is invariant and hence by uniqueness of solutions, it cannot be reached in finite time by any trajectory originating in the interior of $\Re^4_+$. Similiarly $y(t) > 0$.■

Proof of b): First assume $0 < \gamma \leq 1$ and let $z(t) = S(t) + x_1(t) + x_2(t) + y(t)$. Adding the equations in (2.11) we obtain:

$$z'(t) = (1 - z(t)) + y(t)p_3(S(t))(1 - \frac{1}{\gamma})$$

$$\leq \; 1 - z(t)$$

This is a differential inequality for $z(t)$ with solution given by:

$$z(t) \; \leq \; 1 + (z(0) - 1)e^{-t}.$$

Hence, $\limsup_{t\to\infty} z(t) \leq 1$. That is, $z(t)$ is bounded. By part (a), all solutions are positive and hence $S(t)$, $x_1(t)$, $x_2(t)$ and $y(t)$ are bounded in the case where $0 < \gamma \leq 1$. Next, assume $\gamma > 1$ and let $z_0(t) = \gamma S(t) + x_1(t) + x_2(t) + y(t)$. Rewriting the first equation in (2.11) as:

$$\gamma S'(t) = \gamma(1 - S(t)) - \gamma x_1(t)p_1(S(t)) - \gamma x_2(t)p_2(S(t)) - y(t)p_3(S(t))$$

and adding this equation and the remaining three equations in (2.11) we obtain:

$$\begin{aligned} z_0'(t) &= \gamma - z_0(t) + (1-\gamma)x_1(t)p_1(S(t)) \; + (1-\gamma)x_2(t)p_2(S(t)) \\ &< \gamma - z_0(t). \end{aligned}$$

This is a differential inequality for $z_0(t)$ with solution given by:

$$z_0(t) \; < \; \gamma + (z_0(0) - \gamma)e^{-t}.$$

Hence, $\limsup_{t\to\infty} z_0(t) \leq \gamma$. That is, $z_0(t)$ is bounded. By part (a), all solutions are positive and hence $S(t)$, $x_1(t)$,$x_2(t)$ and $y(t)$ are bounded in the case where $\gamma > 1$. ■

Theorem 3.2 *If $\gamma = 1$, then the simplex*

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

is a global attractor for (2.11).

Proof: For $\gamma = 1$, adding the equations in (2.11) and letting

$$z(t) = S(t) + \sum_{i=1}^{2} x_i(t) + y(t)$$

we have

$$z'(t) = 1 - z(t).$$

Solving the differential equation above results in

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

Thus as $t \to \infty$,

$$S(t) + \sum_{i=1}^{2} x_i(t) + y(t) \to 1. \blacksquare$$

The next theorem is concerned with extinction of a population due to insufficient nutrient. The extinction is independent of competition and/or predation. We will first require the following propositions.

Proposition 3.1 *Given any $\epsilon > 0$, for all solutions of (2.11), $S(t) < 1 + \epsilon$ for all sufficiently large t.*

Proof: From (2.11) and Theorem (3.1) we have

$$\begin{aligned} S'(t) &= 1 - S(t) - \sum_{i=1}^{2} x_i(t)p_i(S(t)) - \frac{y(t)p_3(S(t))}{\gamma} \\ &\leq 1 - S(t) \end{aligned}$$

which implies that for all sufficiently large t

$$\begin{aligned} S(t) &\leq 1 + (S_0 - 1)e^{-t} \\ &< 1 + \epsilon. \blacksquare \end{aligned}$$

Proposition 3.2 *If there exists a $t_0 \geq 0$ such that $S(t_0) < 1$ then $S(t) < 1$ for all $t \geq t_0$.*

Proof: Suppose that there exists a first $t_1 > t_0$ such that $S(t_1) = 1$ and $S(t) < 1$ for $t_0 \leq t < t_1$. Then $S'(t_1) \geq 0$. But from (2.11) and Theorem (3.1) we have

$$\begin{aligned} S'(t_1) &= 1 - S(t_1) - \sum_{i=1}^{2} x_i(t_1)\, p_i(S(t_1)) - \frac{y(t_1)p_3(S(t_1))}{\gamma} \\ &= -\sum_{i=1}^{2} x_i(t_1)p_i(1) \; - \frac{y(t_1)p_3(1)}{\gamma} < 0 \end{aligned}$$

which is a contradiction. ∎

In addition to Propositions (3.1) and (3.2) we will need the following lemma due to Miller [16].

Lemma 3.1 *Let $w(t) \in C^2(t_0, \infty)$, $w(t) \geq 0$ and $K > 0$.*

(i) *If $w'(t) \geq 0$, $w(t)$ is bounded and $w''(t) \leq K$ for every $t \geq t_0$, then $w'(t) \to 0$ as $t \to \infty$.*

(ii) *If $w'(t) \leq 0$, $w''(t) \geq -K > -\infty$ for every $t \geq t_0$, then $w'(t) \to 0$ as $t \to \infty$.*

Theorem 3.3 *For all solutions of system (2.11) :*

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

(ii) *If $\lambda_3 > 1$ and $\lim_{t\to\infty} x_1(t) = 0$ then $\lim_{t\to\infty} y(t) = 0$.*

Proof (i): If $1 < \lambda_i$, then $p_i(1) < 1$ for $i = 1, 2$. Hence by the continuity of $p_i(S)$, there exists $\epsilon > 0$ such that $p_i(1 + \epsilon) < 1$. By Proposition (3.1), $S(t) < 1 + \epsilon$ for all sufficiently large t. Since all solutions are positive and bounded, $x_i'(t) < 0$ for all sufficiently large t. Hence, by Lemma (3.1),

$$x_i'(t) \to 0 \text{ as } t \to \infty.$$

However,

$$\limsup_{t\to\infty} p_i(S(t)) \leq p_i(1 + \epsilon) < 1.$$

Hence from (2.11) it follows that $x_i(t) \to 0$ as $t \to \infty$. ∎

Proof (ii): If $1 < \lambda_3$, then $p_3(1) < 1$. Hence by the continuity of $p_3(S(t))$, there exists $\epsilon > 0$ such that $p_3(1 + \epsilon) < 1$. By Proposition (3.1), $S(t) < 1 + \epsilon$ for all sufficiently large t. Thus $p_3(S(t)) < 1$, which implies that $p_3(S(t)) \leq 1 - \epsilon_1$ for some $\epsilon_1 > 0$ for all sufficiently large t. Since $\lim_{t\to\infty} x_1(t) = 0$, then for large enough t we have $q(x_1(t)) = \frac{\epsilon_1}{2}$. Thus for sufficiently large t, $p_3(S(t)) + q(x_1(t)) < 1$. Hence $y'(t) < 0$ for all sufficiently large t. By Lemma (3.1),

$$y'(t) \to 0 \text{ as } t \to \infty.$$

From (2.11) it follows that $y(t) \to 0$ as $t \to \infty$.■

Remark : If $\gamma = 1$ then Theorem (3.3) can be strengthened to include the case when $\lambda_i = 1$ for $i = 1, 2, 3$.

3.2 Global Stability Results

When $\gamma = 1$ and Lotka-Volterra response functions are considered in the model (2.11), we show that as various parameters are allowed to decrease, there is a transfer of global stability from one critical point to another. Unfortunely, if γ is not equal to 1 and/or the mechanics of the model are something other than Lotka-Volterra (i.e. Michaelis-Menten), then the complete global behaviour of the model becomes difficult to describe. This is partially due to the fact that in these instances the existence of the critical point E_{S^*} and whether or not it is unique when it exists, (i.e. unique in the sense that it is the only equilibrium having the prey and predator populations positive and the remaining competitor population zero), becomes increasingly difficult to deal with. As a result, our findings in this section are confined mostly to the special case when $\gamma = 1$ and the dynamics are Lotka-Volterra. However, in Chapter 3 where we discuss the behaviour of subsystem (2.16), we do address these questions and offer some insight into these problems and how they effect the dynamics of (2.16). We state our first global result without any assumptions on the response functions of (2.11) or the value of γ. For $\lambda_1 > 1$, E_0 is the only critical point in the nonnegative (S, x_1, x_2, y)-cone and when $\lambda_1 = 1$, E_0 and E_{λ_1} coalesce.

Theorem 3.4 *If $\lambda_1 > 1$ then E_0 is globally asymptotically stable for (2.11).*

Proof: Let

$$P \in \{(S, x_1, x_2, y) \in \Re^4_+ : x_i, y > 0\}.$$

If $R = (\bar{S}, \bar{x}_1, \bar{x}_2, \bar{y}) \in \Omega(P)$ then by Theorem (3.3), $\bar{x}_i = 0$ for $i = 1, 2$ and $\bar{y} = 0$. On the subspace $\{(S, 0, 0, 0) \in \Re^4_+\}$ system (2.11) reduces to,

$$S'(t) = 1 - S(t).$$

Hence $S(t) \to 1$. Since if $R \in \Omega(P)$ the entire trajectory through R is in $\Omega(P)$ and since $\Omega(P)$ is closed, $\{E_0\} \in \Omega(P)$. Since $\lambda_1 > 1$, E_0 is locally asymptotically stable. Therefore $\Omega(P) = \{E_0\}$. Thus if $\lambda_1 > 1$, then E_0 is globally asymptotically stable for (2.11). ■

Next we let $1 - p_3(1) - q(1 - \lambda_1) > 0$, which implies $\lambda_1 + \delta > 1$. We allow $\lambda_1 < 1$. By the continuity of the roots of the characteristic equation as a function of its coefficients, as λ_1 decreases below 1 there is a transfer of stability from E_0 to E_{λ_1}, and E_{λ_1} is at least initially locally stable regardless of the value of γ.

For the remainder of this chapter we assume that $\gamma = 1$. Under this condition, if $1 - p_3(1) - q(1 - \lambda_1) > 0$ then as λ_1 decreases below 1 there is a transfer of global stability from E_0 to E_{λ_1}, and E_{λ_1} remains globally asymptotically stable provided $1 - p_3(1) - q(1 - \lambda_1) > 0$ and $\lambda_1 < 1$. To show this we require the following lemma.

Lemma 3.2 *If* $\lambda_1 < 1 < \lambda_3$, *then for any solution of (2.11) with* $x_{10} > 0$ $\limsup_{t\to\infty} x_1(t) > 0$.

Proof: Let $\lambda_1 < 1 < \lambda_3$ and $x_{10} > 0$. Suppose $\lim_{t\to\infty} x_1(t) = 0$. Then by Theorem (3.3), $\lim_{t\to\infty} y(t) = 0$. So if $\lambda_2 \geq 1$, then by Theorems (3.2) and (3.3) $\lim_{t\to\infty} x_2(t) = 0$ and $\lim_{t\to\infty} S(t) = 1$, and if $\lambda_2 < 1$, then $\lim_{t\to\infty} x_2(t) = 1 - \lambda_2$ and $\lim_{t\to\infty} S(t) = \lambda_2$. Thus regardless of the value of λ_2, $\lim_{t\to\infty} S(t) \geq \lambda_1$. However, from (2.11) we have, $x_1'(t) = x_1(t)(-1 + p_1(S(t))) - y(t)q(x_1(t))$. For all sufficiently large t, $x_1'(t) > 0$. This implies that $\lim_{t\to\infty} x_1(t) \neq 0$. A contradiction. Thus if $\lambda_1 < 1$ and $x_{10} > 0$, then $\limsup_{t\to\infty} x_1(t) > 0$. ■

Theorem 3.5 *If* $1 - p_3(1) - q(1 - \lambda_1) > 0$ *and* $\lambda_1 < 1$ *then* E_{λ_1} *is globally asymptotically stable for (2.11) with respect to all solutions satisfying* $x_{10} > 0$.

Proof: First note that $\lambda_3 > 1$ since $p_3(1) < 1$, and so we can always choose $\xi > 0$ such that $\lambda_3 > 1 + \xi$. Let $P = (S(t), x_1(t), x_2(t), y(t))$ be a solution of (2.11) with $x_{i0} > 0$ $i = 1, 2$, and let $\Omega(P)$ denote its omega limit set. E_{λ_1} is locally asymptotically stable since $\lambda_1 < 1$ and $1 - p_3(1) - q(1 - \lambda_1) > 0$ implies $1 - p_3(\lambda_1) - q(1 - \lambda_1) > 0$. Hence, it is enough to show that $E_{\lambda_1} \in \Omega(P)$, since this implies $\{E_{\lambda_1}\} = \Omega(P)$. Since $x_{i0} > 0$ $i = 1, 2$, and $\lambda_1 < 1$, by Lemma (3.2) $\limsup_{t\to\infty} x_1(t) > 0$. By definition of $\Omega(P)$, there exists $R = (\bar{S}, \bar{x_1}, \bar{x_2}, \bar{y}) \in \Omega(P)$ such that $\bar{x}_i > 0$ for $i = 1, 2$. Define the trajectory $\bar{\gamma}(t) = (\bar{S}(t), \bar{x}_1(t), \bar{x}_2(t), \bar{y}(t))$ with $\bar{\gamma}(0) = R$. If $\bar{y}(0) = 0$, then the system reduces to the three-dimensional chemostat and hence the result follows (see [4]). If $\bar{y}(0) \neq 0$ then it sufficies to show that $\lim_{t\to\infty} \bar{y}(t) = 0$.

Since $1 - p_3(1) - q(1 - \lambda_1) > 0$ then $\lambda_1 + \delta > 1$. Define $\epsilon > 0$ such that $1 - \delta + \epsilon = \lambda_1$. Since $R \in \Omega(P)$, then by Theorem (3.2),

$$(\bar{S}(t) + \bar{x}_1(t) + \bar{x}_2(t) + \bar{y}(t)) = 1 \text{ for all } t \geq 0 \tag{3.1}$$

$$(\bar{S}(t) + \bar{x}_1(t) + \bar{x}_2(t) + \bar{y}(t))' = 0 \text{ for all } t \geq 0. \tag{3.2}$$

If, $\limsup_{t\to\infty} \bar{S}(t) < \lambda_1$, then there exists $T > 0$, such that $\bar{S}(T) < \lambda_1$ for all $t \geq T$. This implies that

$$\begin{aligned} \bar{x}_1'(T) &= \bar{x}_1(T)(-1 + p_3(\bar{S}(T))) - \bar{y}(T)q(\bar{x}_1(T)) \\ &\leq \bar{x}_1(T)(-1 + p_3(\bar{S}(T))) < 0. \end{aligned}$$

That is, $\bar{x}_1'(t) < 0$ for all $t \geq T$, and hence by Lemma (3.1), $\lim_{t\to\infty} x_1'(t) = 0$. By the continuity of p_1, $\limsup_{t\to\infty} p_1(\bar{S}(t)) < 1$. This implies that $\lim_{t\to\infty} x_1(t) = 0$, which is a contradiction. Thus, $\limsup_{t\to\infty} \bar{S}(t) \geq \lambda_1$, and so either, $\bar{S}(t) > \lambda_1$ for large enough t or, there exists $\tau > 0$ such that $\lambda_1 \geq \bar{S}(\tau) \geq \lambda_1 - \frac{\epsilon}{2}$. In the latter case , from (3.1) we have

$$\bar{x}_1(\tau) \leq 1 - \bar{S}(\tau) \leq 1 - \lambda_1 + \frac{\epsilon}{2}$$

thus,

$$\begin{aligned} \bar{y}'(\tau) &\leq \bar{y}(\tau)(-1 + p_3(\bar{S}(\tau)) + q(1 - \lambda_1 + \frac{\epsilon}{2})) \\ &\leq \bar{y}(\tau)(-1 + p_3(\lambda_1) + q(1 - \lambda_1 + \frac{\epsilon}{2})). \end{aligned}$$

But by the continuity of $q(x_1)$, the above inequality implies that $\bar{y}'(\tau) < 0$. Also, since $\bar{S}(\tau) \leq \lambda_1$,

$$\begin{aligned}\bar{x}_1'(\tau) &= \bar{x}_1(\tau)(-1 + p_1(\bar{S}(\tau))) - \bar{y}(\tau)q(\bar{x}_1(\tau)) \\ &\leq \bar{x}_1(\tau)(-1 + p_1(\bar{S}(\tau))) \leq 0\end{aligned}$$

and,

$$\bar{x}_2'(\tau) = \bar{x}_2(\tau)(-1 + p_2(\bar{S}(\tau))) \leq 0.$$

Since $\bar{x}_i'(\tau) \leq 0$ and $\bar{y}'(\tau) < 0$, then from (3.2) we obtian $\bar{S}'(\tau) > 0$ and so $\bar{S}(t) \geq \lambda_1 - \frac{\epsilon}{2}$ for all $t \geq \tau$. In either case, $\bar{S}(t) \geq \lambda_1 - \frac{\epsilon}{2}$ for large enough t, which implies that $\bar{x}_1(t) \leq \delta - \frac{\epsilon}{2}$ for large enough t. By Proposition (3.1) and since $\lambda_3 > 1$ we can choose $\xi > 0$ such that for large t,

$$\lambda_3 > 1 + \xi > \bar{S}(t) \geq \lambda_1 - \frac{\epsilon}{2}.$$

But then for large enough t we have,

$$\begin{aligned}\bar{y}'(t) &= \bar{y}(t)(-1 + p_3(\bar{S}(t)) + q(\bar{x}_1(t)) \\ &\leq \bar{y}(t)(-1 + p_3(1 + \xi) + q(1 - \lambda_1 + \frac{\epsilon}{2})).\end{aligned}$$

By the continuity of $p_3(S(t))$ and $q(x_1)$, the above inequality implies that $\bar{y}'(t) < 0$ for large t, and hence by Lemma (3.1), $\lim_{t\to\infty} \bar{y}'(t) = 0$. This implies that $\lim_{t\to\infty} \bar{y}(t) = 0$, as desired. ■

Remark: For general monotone response functions, we see that from the local analysis of (2.11), (see Appendix C.1) if $1 - p_3(\lambda_1) - q(1 - \lambda_1) > 0$ then as λ_1 decreases below 1, there is a transfer of local stability from E_0 to E_{λ_1}. However, we are only able to show that the transfer of global stability from E_0 to E_{λ_1} occurs when λ_1 decreases below 1 and $1 - p_3(1) - q(1 - \lambda_1) > 0$. In particular instances when the functions $p_i(S(t))$ and $q(x_1(t))$ are of a specific form (i.e. Lotka-Volterra) the condition $1 - p_3(1) - q(1 - \lambda_1) > 0$ in Theorem (3.5) can be relaxed to the local asymptotic stability condition $1 - p_3(\lambda_1) - q(1 - \lambda_1) > 0$ and still give global asymptotic stability of E_{λ_1}, (for local stability analysis of (2.11) see Appendix C.2.).

To continue to extract global stability information for system (2.11) we shall assume that

$$p_i(S) = \frac{S}{\lambda_i},\ i = 1, 2, 3 \text{ and } q(x_1) = \frac{x_1}{\delta}$$

and also that λ_2 is sufficiently large such that

$$\tilde{x}_2 = 1 - \lambda_2 - \frac{\lambda_2 \delta}{\lambda_1 \lambda_3}(\lambda_3 - \lambda_1) < 0, \text{ i.e. } S^* < \lambda_2.$$

In this case, where Lotka-Volterra response functions are considered, when $\lambda_1 < 1$ and $1 - p_3(\lambda_1) - q(1 - \lambda_1) > 0$, by previous remark, E_{λ_1} is globally asymptotically stable. If we allow $1 - p_3(\lambda_1) - q(1 - \lambda_1)$ to decrease, then when

$$1 - p_3(\lambda_1) - q(1 - \lambda_1) = 0,$$

E_{λ_1} and E_{S^*} coalesce. That is to say, $S^* = \lambda_1$ and $y^* = 0$. Hence by the continuity of the roots of the characteristic equation as a function of its coefficients, once $1 - p_3(\lambda_1) - q(1 - \lambda_1)$ is allowed to decrease, it decreases below 0 (i.e. $S^* > \lambda_1$) and E_{S^*} is at least initially locally asymptotically stable. Simultaneously, since the eigenvalue $-1 + p_3(\lambda_1) + q(1 - \lambda_1)$ is positive, E_{λ_1} becomes unstable.

The following theorem shows that under these circumstances E_{S^*} picks up the global stability lost by E_{λ_1}, and remains globally asymptotically stable provided

$$1 - p_3(\lambda_1) - q(1 - \lambda_1) < 0$$

and

$$\tilde{x}_2 = 1 - \lambda_2 - \frac{\lambda_2 \delta}{\lambda_1 \lambda 3}(\lambda_3 - \lambda_1) < 0.$$

At this point if λ_2 and/or δ are allowed to decrease, when

$$1 - \lambda_2 - \frac{\lambda_2 \delta}{\lambda_1 \lambda_3}(\lambda_3 - \lambda_1) = 0,$$

then E_{S^*} and $\tilde{E}_{\lambda_2}$ coalesce. In this case $S^* = \lambda_2$. As $1 - \lambda_2 - \frac{\lambda_2 \delta}{\lambda_1 \lambda_3}(\lambda_3 - \lambda_1)$ becomes positive (i.e. $S^* > \lambda_2$), there is a transfer of global stability from E_{S^*} to $\tilde{E}_{\lambda_2}$. $\tilde{E}_{\lambda_2}$ remains globally asymptotically stable provided

$$1 - \lambda_2 - \frac{\lambda_2 \delta}{\lambda_1 \lambda_3}(\lambda_3 - \lambda_1) > 0$$

and hence $\lambda_2 < 1$.

To show the above global results, we will require LaSalle's Extension theorem, which we state below.

For a system of differential equations given by

$$x'(t) = f(x(t)), \tag{3.3}$$

where $f : G^* \subset \Re^n \rightarrow \Re$ is a continous function, we have

Theorem 3.6 *Assume V is a Lyapunov function for (3.3) on some subset $G \subset G^*$. Let $\mathcal{S}$= $\{x \in \bar{G} \cap G^* : \dot{V}(x) = 0\}$ and let M be the largest invariant subset of $\mathcal{S}$. Then every bounded trajectory of (3.3) that remains in G for $t \geq 0$ approaches M as $t \rightarrow \infty$.*

Theorem 3.7 *Let $q(x_1)$ and $p_i(S)$ for $i = 1, 2, 3$ be linear, i.e. $q(x_1) = \frac{x_1}{\delta}$ and $p_i(S) = \frac{S}{\lambda_i}$ for $i = 1, 2, 3$. If $\lambda_1 < S^* < \lambda_2$, then E_{S^*} is globally asymptotically stable for system (2.11) with respect to all solutions for which $S_0 \geq 0$, $x_{20} \geq 0$, and x_{10}, $y_0 > 0$.*

Proof : Define the function $V : int\Re^4_+ \rightarrow \Re$ by

$$\begin{aligned} V(S, x_1, x_2, y) &= S - S^* - S^* \ln(\frac{S}{S^*}) + \{x_1 - x_1^* - x_1^* \ln(\frac{x_1}{x_1^*})\} \\ &+ x_2 + \{y - y^* - y^* \ln(\frac{y}{y^*})\}, \end{aligned}$$

The time derivative of V calculated along solutions of system (2.11) is

$$\begin{aligned} \dot{V}(S, x_1, x_2, y) &= (1 - \frac{S^*}{S})S' + (1 - \frac{x_1^*}{x_1})x_1' + x_2' \\ &+ (1 - \frac{y^*}{y})y' \\ &= (\frac{S - S^*}{S})(1 - S) + x_1(-1 + \frac{S^*}{\lambda_1} - \frac{y^*}{\delta}) \\ &+ x_2(\frac{S^* - \lambda_2}{\lambda_2}) + y(-1 + \frac{S^*}{\lambda_3} + \frac{x_1^*}{\delta}) \\ &- x_1^*(-1 + \frac{S}{\lambda_1}) - y^*(-1 + \frac{S}{\lambda_3}) \end{aligned}$$

substituting $x_1^* = \delta(1 - \frac{S^*}{\lambda_3})$ and $y^* = \delta(-1 + \frac{S^*}{\lambda_1})$,

$$\begin{aligned}
&= (\frac{S-S^*}{S})(1-S) + x_2(\frac{S^*-\lambda_2}{\lambda_2}) \\
&- \delta(1-\frac{S^*}{\lambda_3})(-1+\frac{S}{\lambda_1}) - \delta(-1+\frac{S^*}{\lambda_1})(-1+\frac{S}{\lambda_3}) \\
&= (\frac{S-S^*}{S})(1-S) + x_2(\frac{S^*-\lambda_2}{\lambda_2}) \\
&- \frac{\delta}{\lambda_1\lambda_3}(S-S^*)(\lambda_3-\lambda_1) \\
&= (\frac{S-S^*}{S})\{1-S-\frac{S\delta}{\lambda_1\lambda_3}(\lambda_3-\lambda_1)\} \\
&+ x_2(\frac{S^*-\lambda_2}{\lambda_2}) \leq 0,
\end{aligned}$$

since if $S > S^*$ then this implies that $1 - S - \frac{S\delta}{\lambda_1\lambda_3}(\lambda_3 - \lambda_1) < 0$, or if $S < S^*$, then $1 - S - \frac{S\delta}{\lambda_1\lambda_3}(\lambda_3 - \lambda_1) > 0$, and by hypothesis $S^* < \lambda_2$. Moreover,

$$\dot{V}(S, x_1, x_2, y) = 0 \text{ if and only if } S = S^*, \text{ and } x_2 = 0.$$

Hence V is a Lyapunov function for (2.11) in the $int\Re^4_+$. Since all solutions are positive and bounded, then by LaSalle's Extension Theorem, every solution of (2.11) for which S_0, $x_{20} > 0$, approaches $\mathcal{M}$, where $\mathcal{M}$ is the largest invariant subset of

$$\mathcal{S} = \{(S, x_1, x_2, y) \in int\Re^4_+ : \dot{V}(S, x_1, x_2, y) = 0\}.$$

Since $S = S^*$ then $S' = 0$, and since $x_2 = 0$ then $S' = 1 - S^* - x_1(t)p_1(S^*) - y(t)p_3(S^*) = 0$ which implies

$$y(t) = \frac{1-S^*}{p_3(S^*)} - x_1(t)\frac{p_1(S^*)}{p_3(S^*)}.$$

Assume $x_1(t)$ is not a constant. Then differentiating the above expression gives

$$y'(t) = -x_1'(t)\frac{p_1(S^*)}{p_3(S^*)}.$$

Substituting these expressions for $y(t)$ and $y'(t)$ into the equations for $x_1'(t)$ and $y'(t)$ in (2.11) we have

$$x_1'(t) = x_1(t)(-1 + p_1(S^*)) - \{\frac{1-S^*}{p_3(S^*)} - x_1(t)\frac{p_1(S^*)}{p_3(S^*)}\}q(x_1(t))$$

and

$$x_1'(t) = -\{\frac{1-S^*}{p_1(S^*)} - x_1(t)\}(-1 + p_3(S^*) + q(x_1(t))).$$

Substituting $p_i(S) = \frac{S}{\lambda_i}$ for $i = 1, 2, 3$ and $q(x_1) = \frac{x_1}{\delta}$ and equating the two expressions for $x_1'(t)$ we obtain a quadratic in $x_1(t)$ given by

$$x_1^2(t)\frac{(\lambda_3-\lambda_1)}{\lambda_1\delta} + x_1(t)(\lambda_3-\lambda_1)\{\frac{S^*}{\lambda_1\lambda_3} - \frac{(1-S^*)}{S^*\delta}\} + \frac{\lambda_1}{S^*\lambda_3}(1-S^*)(S^*-\lambda_3) = 0.$$

Hence x_1 must be a constant. This implies that y is also a constant. Therefore $x_1' = 0$ and $y' = 0$. If $x_1 = 0$ and y is constant then this implies that $y = 0$ by setting $y' = 0$ in (2.11). But then by setting $S' = 0$ we have $0 = S^* = 1 - S^* \neq 0$ (since $S^* < 1$), a contradiction. Next, when $x_1 \neq 0$ and y is constant, this implies that $y = \delta(-1 + p_1(S^*)) \equiv y^*$ by setting $x_1' = 0$ in (2.11). Setting $y' = 0$, we have $x_1 = \delta(1 - p_3(S^*)) \equiv x_1^*$.

If $\lambda_1 < S^* < \lambda_2$, then $\mathcal{S} = \mathcal{M} = \{E_{S^*}\}$, hence E_{S^*} is globally asymptotically stable. ∎

Theorem 3.8 *Let $q(x_1)$ and $p_i(S)$ for $i = 1, 2, 3$ be linear, i.e. $q(x_1) = \frac{x_1}{\delta}$ and $p_i(S) = \frac{S}{\lambda_i}$ for $i = 1, 2, 3$. If $\lambda_2 < S^*$, then $\tilde{E}_{\lambda_2}$ is globally asymptotically stable for system (2.11) with respect to all solutions for which $S_0 \geq 0$, and x_{i0}, $y_0 > 0$ for $i = 1, 2$.*

Proof : Define the function $V : int\Re_+^4 \rightarrow \Re_+^4$ by

$$\begin{aligned} V(S, x_1, x_2, y) &= S - \tilde{S} - \tilde{S}\ln(\frac{S}{\tilde{S}}) + \{x_1 - \tilde{x}_1 - \tilde{x}_1\ln(\frac{x_1}{\tilde{x}_1})\} \\ &+ \{x_2 - \tilde{x}_2 - \tilde{x}_2\ln(\frac{x_2}{\tilde{x}_2})\} + \{y - \tilde{y} - \tilde{y}\ln(\frac{y}{\tilde{y}})\} \end{aligned}$$

The time derivative calculated along solutions of system (2.11) is

$$\begin{aligned} \dot{V}(S, x_1, x_2, y) &= (1 - \frac{\tilde{S}}{S})S' + (1 - \frac{\tilde{x}_1}{x_1})x_1' \\ &+ (1 - \frac{\tilde{x}_2}{x_2})x_2' + (1 - \frac{\tilde{y}}{y})y' \\ &= (\frac{S-\lambda_2}{S})(1-S) + x_1(\frac{\lambda_2}{\lambda_1} - 1 - \frac{\tilde{y}}{\delta}) \end{aligned}$$

$$
\begin{aligned}
&+ \quad y(\frac{\lambda_2}{\lambda_3} - 1 + \frac{\tilde{x}_1}{\delta}) - \tilde{x}_1(-1 + \frac{S}{\lambda_1}) \\
&- \quad \tilde{x}_2(-1 + \frac{S}{\lambda_2}) - \tilde{y}(-1 + \frac{S}{\lambda_3})
\end{aligned}
$$

substituting $\tilde{x}_1 = \delta(1 - \frac{\lambda_2}{\lambda_3})$, $\tilde{x}_2 = 1 - \lambda_2 - \frac{\lambda_2\delta}{\lambda_1\lambda_3}(\lambda_3 - \lambda_1)$ and $\tilde{y} = \delta(-1 + \frac{\lambda_2}{\lambda_1})$,

$$
\begin{aligned}
&= \quad (\frac{S - \lambda_2}{S})(1 - S) - \tilde{x}_1(-1 + \frac{S}{\lambda_1}) \\
&- \quad \tilde{x}_2(-1 + \frac{S}{\lambda_2}) - \tilde{y}(-1 + \frac{S}{\lambda_3}) \\
&= \quad (\frac{S - \lambda_2}{S})(1 - S) - \delta(\frac{\lambda_3 - \lambda_2}{\lambda_3})(\frac{S - \lambda_1}{\lambda_1}) \\
&- \quad (1 - \lambda_2 - \frac{\delta\lambda_2}{\lambda_1\lambda_3}(\lambda_3 - \lambda_1))(\frac{S - \lambda_3}{\lambda_2}) \\
&- \quad \delta(\frac{\lambda_2 - \lambda_1}{\lambda_1})(\frac{S - \lambda_3}{\lambda_3}) \\
&= \quad (\frac{S - \lambda_2}{S})(1 - S) - (\frac{1 - \lambda_2}{\lambda_2})(S - \lambda_2) \\
&- \quad \frac{\delta}{\lambda_1\lambda_3}\{(\lambda_3 - \lambda_2)(S - \lambda_1) \\
&- \quad (\lambda_3 - \lambda_1)(S - \lambda_2) + (\lambda_2 - \lambda_1)(S - \lambda_3)\} \\
&= \quad -\frac{1}{S\lambda_2}(S - \lambda_2)^2 \leq 0.
\end{aligned}
$$

Hence V is a Lyapunov function for (2.11) in the $int\Re^4_+$. Since all solutions are positive and bounded, then by LaSalle's Extension Theorem, every solution of (2.11) for which $S_0 \geq 0$, x_{i0}, $y_0 > 0$, approaches $\mathcal{M}$, where $\mathcal{M}$ is the largest invariant subset of

$$\mathcal{S} = \{(S, x_1, x_2, y) \in int\Re^4_+ \; : \; \dot{V}(S, x_1, x_2, y) = 0 \; \}.$$

Since $S = \lambda_2$ then $S' = 0$ and $x_2' = 0$ which implies x_2 is a constant, and moreover $S' = 1 - \lambda_2 - x_1(t)p_1(\lambda_2) - x_2 - y(t)p_3(\lambda_2) = 0$ which implies

$$y(t) = (\frac{1 - \lambda_2 - x_2}{p_3(\lambda_2)}) - x_1(t)\frac{p_1(\lambda_2)}{p_3(\lambda_2)}.$$

Assume $x_1(t)$ is not a constant, then differentiating the above expression we have

$$y'(t) = -x'(t)\frac{p_1(\lambda_2)}{p_3(\lambda_2)}.$$

Substituting the above expressions for $y(t)$ and $y'(t)$ into the equations for $x_1'(t)$ and $y'(t)$ in (2.11) we have

$$x_1'(t) = x_1(t)(-1 + p_1(\lambda_2)) - \{\frac{1 - \lambda_2 - x_2}{p_3(\lambda_2)} - x_1(t)\frac{p_1(\lambda_2)}{p_3(\lambda_2)}\}q(x_1(t))$$

and

$$x_1'(t) = -\{\frac{1 - \lambda_2 - x_2}{p_1(\lambda_2)} - x_1(t)\}(-1 + p_3(\lambda_2) + q(x_1(t))).$$

Since $p_i(S) = \frac{S}{\lambda_i}$ for $i = 1, 2, 3$ and $q(x_1) = \frac{x_1}{\delta}$ then equating the two expressions for $x_1(t)$ and solving, we obtain a quadratic in $x_1(t)$ given by

$$x_1^2(t)\frac{(\lambda_3 - \lambda_1)}{\lambda_1 \delta} + x_1(t)(\lambda_3 - \lambda_1)\{\frac{\lambda_2}{\lambda_1 \lambda_3} - \frac{1 - \lambda_2 - x_2}{\lambda_2 \delta}\} - \frac{\lambda_2(1 - \lambda_2 - x_2)}{\lambda_2 \lambda_3}(\lambda_3 - \lambda_2) = 0.$$

Hence x_1 must be a constant, which implies y is also a constant. Therefore $x_1' = 0$ and $y' = 0$. If $x_1 = 0$ and y is constant then this implies that $y = 0$ by setting $y' = 0$ in (2.11). Then $x_2 = 1 - \lambda_2$ by setting $S' = 0$ in (2.11). If $x_1 \neq 0$ and y constant, then this implies that $y = \delta(-1 + p_1(\lambda_2)) \equiv \tilde{y}$ by setting $x_1' = 0$. $x_1 = \delta(1 - p_3(\lambda_2)) \equiv \tilde{x}_1$ by setting $y' = 0$ which implies by setting $S' = 0$, that $x_2 = 1 - \lambda_2 - \delta(p_1(\lambda_2) - p_3(\lambda_2)) \equiv \tilde{x}_2$. Hence $\mathcal{S} = \{E_{\lambda_2}\} \cup \{\tilde{E}_{\lambda_2}\}$. But E_{λ_2} is locally unstable and has stable manifold

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

Since $\mathcal{W}^s(E_{\lambda_2})$ does not interest $int\Re^4_+$, then $\tilde{E}_{\lambda_2}$ is globally asymptotically stable. ∎

In the next chapter we examine the food web described by subsystem (2.16) in order to illustrate that the orderly transfer of global stability from one critical point to another is not always the case for general monotone dynamics.

3.3 Persistence

In this section we discuss the persistence of system (2.11). We begin with the definition of persistence as given by Freedman and Waltman [8].

Definition 3.1 *Let $x'(t) = f(x(t))$ be a system of differential equations, where f is a continuous vector valued function in $x = (x_1, ..., x_n) \in \Re^n$. Then the system of differential equations is said to* persist *if $x_i(0) > 0$ for $i = 1, ..., n$ implies that*

$$\liminf_{t \to \infty} x_i(t) > 0 \ for \ i = 1, ..., n.$$

In section 2 of this chapter, we have shown that when $\gamma = 1$, $p_i(S) = \frac{S}{\lambda_i}$ for $i = 1, 2, 3$ and $q(x_1) = \frac{x_1}{\delta}$ then $\tilde{E}_{\lambda_2}$ is globally asymptotically stable for (2.11) with respect to solutions with positive initial conditions, provided that $\lambda_2 < S^*$. This is an example of persistence of (2.11). In this section we show that (2.11) can persist under less restrictive conditions on $p_i(S)$ $i = 1, 2, 3$ and $q(x_1)$. For the remainder of this section, unless otherwise stated, we assume that $p_i(S)$ $i = 1, 2, 3$ and $q(x_1)$ satisfy only the assumptions of section (2.2).

Before we state and prove our results of this section, we give the statement of the Butler-McGehee Lemma (whose proof may be found in Freedman and Waltman [8]), that we will use extensively in proving our results. First we give the definition of hyperbolic critical point (Arrowsmith and Place [2]).

Definition 3.2 *A critical point of a dynamical system is said to be* hyperbolic *if no eigenvalue of the linearization of the dynamical system, about the critical point, has zero real part.*

Lemma 3.3 *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 exists points P^s and P^u satisfying $P^s \in W^s(P) \setminus \{P\}$ and $P^u \in W^u(P) \setminus \{P\}$, where $W^s(P)$ and $W^u(P)$ denote the stable and unstable manifolds of P respectively.*

Lemma 3.4 *For any solution of (2.11):*

(i) *If $\lambda_1 < 1$, $x_{i0} > 0$ for $i = 1, 2$, then* $\liminf_{t\to\infty} x_1(t) > 0$.

(ii) *If $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$, $x_{i0} > 0$ for $i = 1, 2$ and $y_0 > 0$, then* $\liminf_{t\to\infty} y(t) > 0$.

Proof : Let $\Gamma(t) = (S(t), x_1(t), x_2(t), y(t))$ be any solution of system (2.11) and let Ω denote the omega-limit set of $\Gamma(t)$.

(i) : Assume $\lambda_1 < 1$, and suppose $\liminf_{t\to\infty} x_1(t) = 0$ with $x_{i0} > 0$ for $i = 1, 2$, and $y_0 \geq 0$. Since solutions are positive and bounded, by Theorem (3.1), $\Omega \subset \Re^4_+$ is non-empty and compact. Then there must exist $\bar{R} = (\bar{S}, 0, \bar{x}_2, \bar{y}) \in \Omega$ and by Theorem (3.2), $\bar{S} + \bar{x}_2 + \bar{y} = 1$. Hence from (2.15) either

$$E_0 \text{ or } E_{\lambda_2} \text{ (if } \lambda_2 < 1) \text{ or } E_{\lambda_3} \text{ (if } \lambda_3 < 1) \in \Omega.$$

Suppose $E_0 \in \Omega$. Then $\Omega \neq \{E_0\}$, since $\lambda_1 < 1$ implies E_0 is an unstable hyperbolic critical point with stable manifold $W^s(E_0) = \{(S, x_1, x_2, y) \in \Re^4_+ \ : \ x_1 = 0,\ x_2 = 0 \text{ (if } \lambda_2 < 1\text{), and } y = 0 \text{ (if } \lambda_3 < 1) \ \}$, and since $x_{10} > 0$, $\Gamma(0) \notin W^s(E_0)$. By Lemma (3.3), there exists $R^s \in (W^s(E_0) \setminus \{E_0\}) \cap \Omega$. Since $\Omega \subset \mathcal{S}$, then $R^s \in \{(S, x_1, x_2, y) \in \mathcal{S} \ : \ x_1 = 0 \text{ and } x_2 = 0 \text{ (if } \lambda_2 < 1\text{) and } y = 0 \text{ (if } \lambda_3 < 1) \ \}$. If $\lambda_2 \geq 1$, then by Theorem (3.3) we have $\lim_{t \to \infty} x_2(t) = 0$. Thus there is no loss of generality if we assume $\lambda_2 < 1$. If $\lambda_3 \geq 1$, then R^s is an element of a two-dimensional, positively invariant set and hence by the Poincaré-Bendixson Theorem, either $E_{\lambda_3} \in cl\mathcal{O}^-(R^s)$ or $cl\mathcal{O}^-(R^s) \not\subset \Re^4_+$ or $\mathcal{O}^-(R^s)$ becomes unbounded. But since $R^s \in \Omega$ then $cl\mathcal{O}(R^s) \subset \Omega \subset \Re^4_+$, and since $\lambda_3 \geq 1$ implies $E_{\lambda_3} \notin \Re^4_+$, and since all solutions are bounded, then neither choice is possible, hence a contradiction. If $\lambda_3 < 1$, then we must have $cl\mathcal{O}^-(R^s) \not\subset \Re^4_+$ or $\mathcal{O}^-(R^s)$ becomes unbounded. But as above, this is a contradiction. Therefore $E_0 \notin \Omega$.

Next assume $\lambda_3 < 1$ and $E_{\lambda_3} \in \Omega$. E_{λ_3} is an unstable hyperbolic critical point with stable manifold, $W^s(E_{\lambda_3}) =$

$$\begin{cases} \{(S, x_1, x_2, y) \in \Re^4_+ \ : \ x_2 = 0,\ x_1 > 0,\ y > 0 \ \} \\ \qquad \text{if } -1 + p_1(\lambda_3) - (1 - \lambda_3)q'(0) < 0 \\ \text{or} \\ \{(S, x_1, x_2, y) \in \Re^4_+ \ : \ x_1 = x_2 = 0,\ y > 0 \ \} \\ \qquad \text{if } -1 + p_1(\lambda_3) - (1 - \lambda_3)q'(0) > 0 \end{cases}$$

In either case, since $x_{20} > 0$, then $\Gamma(0) \notin W^s(E_{\lambda_3})$ and thus $\Omega \neq \{E_{\lambda_3}\}$. By Lemma (3.3), there exists $Q^s \in (W^s(E_{\lambda_3}) \setminus \{E_{\lambda_3}\}) \cap \Omega$. If $-1 + p_1(\lambda_3) - (1 - \lambda_3)q'(0) < 0$, then since $\Omega \subset \mathcal{S}$, we have

$$Q^s \in \{(S, x_1, x_2, y) \in \mathcal{S} \ : \ x_2 = 0,\ x_1 > 0,\ y > 0 \ \},$$

which is a two-dimensional, positively invariant set. Hence, by the Poincaré-Bendixson Theorem, either $E_0 \in cl\mathcal{O}^-(Q^s)$ or $cl\mathcal{O}^-(Q^s) \not\subset \Re^4_+$. But as before $cl\mathcal{O}(Q^s) \subset \Omega \subset \Re^4_+$, and from above $E_0 \notin \Omega$. Thus neither choice is possible, and hence $E_{\lambda_3} \notin \Omega$. If $-1 + p_1(\lambda_3) - (1 - \lambda_3)q'(0) > 0$ then since $\Omega \subset \mathcal{S}$ we have

$$Q^s \in \{(S, x_1, x_2, y) \in \mathcal{S} \ : \ x_1 = x_2 = 0,\ y > 0 \ \},$$

thus by the Poincaré-Bendixson Theorem either $cl\mathcal{O}^-(Q^s) \not\subset \Re^4_+$ or $\mathcal{O}^-(Q^s)$ becomes unbounded. As above this is a contradiction, therefore $E_{\lambda_3} \notin \Omega$.

Next assume $\lambda_2 < 1$ and $E_{\lambda_2} \in \Omega$. However $\Omega \neq \{E_{\lambda_2}\}$ since E_{λ_2} is an unstable hyperbolic critical point with stable manifold $W^s(E_{\lambda_2}) = \{(S, x_1, x_2, y) \in \Re^4_+ \ : \ x_1 = 0, \ x_2 > 0 \ \}$, thus since $x_{10} > 0$, $\Gamma(0) \notin W^s(E_{\lambda_2})$. By Lemma (3.3) there exists $P^s \in (W^s(E_{\lambda_2}) \setminus \{E_{\lambda_2}\}) \cap \Omega$. Since $\Omega \subset \mathcal{S}$, then

$$P^s \in \{(S, x_1, x_2, y) \in \mathcal{S} \ : \ x_1 = 0, \ x_2 > 0 \ \},$$

which is a two-dimensional, positively invariant set. By the Poincaré-Bendixson Theorem, either $E_0 \in cl\mathcal{O}^-(P^s)$ or $E_{\lambda_3} \in cl\mathcal{O}^-(P^s)$ (if $\lambda_3 < 1$) or $cl\mathcal{O}^-(P^s) \not\subset \Re^4_+$. But from above E_0, $E_{\lambda_3} \notin \Omega$ and as before $cl\mathcal{O}^-(P^s) \subset \Omega$, a contradiction. Therefore $E_{\lambda_2} \notin \Omega$.

Hence, since E_0, E_{λ_2}, $E_{\lambda_3} \notin \Omega$ then $\liminf_{t\to\infty} x_1(t) > 0$. ■

(ii) : Assume $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$ and $x_{i0} > 0$ for $i = 1,2$ and $y_0 > 0$. Let $\lim_{t\to\infty} y(t) = 0$. Then system (2.11) reduces to the familiar two competitor chemostat (2.14),

$$\begin{aligned} S'(t) &= 1 - S(t) - x_1(t)p_1(S(t)) \ - x_2(t)p_2(S(t)) \\ x_i'(t) &= x_i(t)(-1 + p_i(S(t))), \ i = 1,2. \\ S_0 &\geq 0 \text{ and } x_{i0} > 0 \text{ for } i = 1,2. \end{aligned}$$

Since $\lambda_1 < 1$ and $x_{10} > 0$ it follows that

$$\lim_{t\to\infty} S(t) = \lambda_1, \ \lim_{t\to\infty} x_1(t) = 1 - \lambda_1 \text{ and } \lim_{t\to\infty} x_2 = 0.$$

But since $y_0 > 0$ and $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$, then $y'(t) > 0$ for large enough t. That is $\lim_{t\to\infty} y(t) \neq 0$.

First assume $\lambda_2 \geq 1$, then by Theorem (3.3) $\lim_{t\to\infty} x_2(t) = 0$ and system (2.11) reduces to subsystem (2.16)

$$S'(t) \ = \ 1 - S(t) - x_1(t)p_1(S(t)) \ - y(t)p_3(S(t))$$

$$\begin{aligned} x_1'(t) &= x_1(t)(-1+p_1(S(t))) - y(t)q(x_1(t)) \\ y'(t) &= y(t)(-1+p_3(S(t))+q(x_1(t))) \\ S_0 &\geq 0, x_{10}>0, \text{ and } y_0>0. \end{aligned}$$

Lemma 3.5 *For any solution of the above subsystem :*

(i) If $\lambda_1 < 1 < \lambda_3$ and $x_{10} > 0$ then $\liminf_{t\to\infty} x_1(t) > 0$.

(ii) If $-1 + p_3(\lambda_1) + q(1-\lambda_1) > 0$, $\lambda_3 > 1$ and $x_{10} > 0$, $y_0 > 0$ then $\liminf_{t\to\infty} y(t) > 0$.

For now we will assume the lemma holds and continue with the proof of Lemma (3.4). The proof of Lemma (3.5) will follow this proof.

If $\lambda_2 \geq 1$, then by Lemma (3.5) we have $\liminf_{t\to\infty} y(t) > 0$. Hence assume $\lambda_2 < 1$. Suppose $\liminf_{t\to\infty} y(t) = 0$, then there must exist a point $\bar{P} = (\bar{S}, \bar{x}_1, \bar{x}_2, 0) \in \Omega$ with $\bar{S}+\bar{x}_1+\bar{x}_2 = 1$ and since $\bar{P} \in \Omega$, Ω compact then at least one of E_0, E_{λ_1}, $E_{\lambda_2} \in \Omega$. But since $\lambda_1 < 1$, then by part (i), $\liminf_{t\to\infty} x_1(t) > 0$ and so E_0, $E_{\lambda_2} \notin \Omega$.

Suppose $E_{\lambda_1} \in \Omega$. From above $\lim_{t\to\infty} y(t) \neq 0$ and thus $\Omega \neq \{E_{\lambda_1}\}$. E_{λ_1} is an unstable hyperbolic critical point with stable manifold $W^s(E_{\lambda_1}) = \{(S, x_1, x_2, y) \in \Re^4_+ \ : \ x_1 > 0, \ y = 0\ \}$. By Lemma (3.3) there exists $P^s \in (W^s(E_{\lambda_1}) \setminus \{E_{\lambda_1}\} \cap \Omega$. Since $\Omega \subset \mathcal{S}$ then $P^s \in \{(S, x_1, x_2, y) \in \mathcal{S} \ : \ x_1 > 0, \ y = 0\ \}$, which is a two-dimensional, positively invariant set. By the Poincaré-Bendixson Theorem, either E_0, $E_{\lambda_2} \in cl\mathcal{O}^-(P^s)$ or $cl\mathcal{O}^-(P^s) \not\subset \Re^4_+$. As before none of these choices is possible. Thus $E_{\lambda_1} \notin \Omega$ and hence $\liminf_{t\to\infty} y(t) > 0$. ■

Proof of Lemma (3.5) : Let $\Gamma(t) = (S(t), x_1(t), x_2(t), y(t))$ be any solution of (2.16) and Ω its omega-limit set.

(i) : Assume $\lambda_1 < 1 < \lambda_3$ and $x_{10} > 0$. Suppose $E_0^3 \in \Omega$. Since $\lambda_1 < 1 < \lambda_3$ then E_0^3 is an unstable hyperbolic critical point with stable manifold $W^s(E_0^3) = \{(S, x_1, y) \in \Re^3_+ \ : \ x_1 = 0, \ y > 0\ \}$. Since $x_{10} > 0$ then $\Gamma(0) \notin W^s(E_0^3)$ and hence $\Omega \neq \{E_0^3\}$. By Lemma (3.3) there exists $P^s \in (W^s(E_0^3) \setminus \{E_0^3\}) \cap \Omega$. But $\Omega \subset \mathcal{S}^3$, thus $P^s \in \{(S, x_1, y) \in \mathcal{S}^3 \ : \ x_1 = 0, \ y > 0\ \}$, which is a two-dimensional, positively invariant set. By the Poincaré-Bendixson Theorem, either $E_{\lambda_3}^3 \in \Omega$ or $cl\mathcal{O}^-(P^s) \not\subset \Re^3_+$ or $\mathcal{O}^-(P^s)$ becomes unbounded. But $\lambda_3 > 1$ implies $E_{\lambda_3}^3 \notin \Re^3_+$ and

since $cl\mathcal{O}(P^s) \subset \Omega \subset \Re^3_+$, and all solutions are bounded, we have a contradiction. Therefore $E^3_0 \notin \Omega$.

Suppose $\lambda_1 < 1 < \lambda_3$, $x_{10} > 0$ and $\liminf_{t\to\infty} x_1(t) = 0$. Then there must exist $\bar{P} = (\bar{S}, 0, \bar{y}) \in \Omega$. But this implies that either $E^3_0 \in \Omega$ or $E^3_{\lambda_3} \in \Omega$. This is a contradiction. Therefore $\liminf_{t\to\infty} x_1(t) > 0$. ■

(ii) : Next assume $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$ and $x_{10},\ y_0 > 0$. Suppose $E^3_{\lambda_1} \in \Omega$. Since $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$, then $E^3_{\lambda_1}$ is an unstable hyperbolic critical point with stable manifold $W^s(E^3_{\lambda_1}) = \{(S, x_1, y) \in \Re^3_+ \ :\ x_1 > 0,\ y = 0\ \}$. Since $y_0 > 0$ then $\Gamma(0) \notin W^s(E^3_{\lambda_1})$ and hence $\Omega \neq \{E^3_{\lambda_1}\}$. By Lemmma (3.3) there exists $R^s \in (W^s(E^3_{\lambda_1})\backslash\{E^3_{\lambda_1}\})\cap\Omega$. But $\Omega \subset S^3$ and thus $R^s \in \{(S, x_1, y) \in \Re^3_+ \ :\ x_1 > 0,\ y = 0\ \}$. By the Poincaré-Bendixson Theorem, either $E^3_0 \in \Omega$ or $cl\mathcal{O}^-(R^s) \not\subset \Re^3_+$. But neither choice is possible and therefore $E^3_{\lambda_1} \notin \Omega$.

Assume $\liminf_{t\to\infty} y(t) = 0$, then there must exist a point $\bar{R} = (\bar{S}, \bar{x}_1, 0) \in \Omega$. But $\lambda_1 < 1$ and $x_{10} > 0$ implies by part (i) that $\liminf_{t\to\infty} x_1(t) > 0$. Thus $E^3_{\lambda_1} \in cl\mathcal{O}(\bar{R}) \subset \Omega$, which is a contradiction. Therefore $\liminf_{t\to\infty} y(t) > 0$.■

Part (i) of Lemma (3.4) shows that regardless how aggressive the predator is, provided that the concentration of the substrate is sufficient for the prey to survive in pure competition, it will always survive predation. However, part (ii) shows that in order for the predator to survive, it must be sufficient. On the other hand, Lemma (3.5) suggests that when considering subsystem (2.16) on its own, survivability of the prey does not solely depend on the concentration of substrate as was the case above for system (2.11). In Chapter 4, where we discuss the behaviour of subsystem (2.16) in more detail, we show that in fact that under favourable conditions the predator can drive the prey to extinction.

It is clear from Lemma (3.4) that a necessary condition for persistence of system (2.11) is that $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$. However this is not a sufficient condition, for instance if the hypotheses of Theorem (3.7) are satisfied then E_{S^*} is globally asymptotically stable. The next two results deal with sufficient conditions for persistence of (2.11).

Lemma 3.6 *Let* $\Gamma(t) = (S(t), x_1(t), x_2(t), y(t))$ *be any solution of system (2.11) with* $x_{i0} > 0$ $i = 1, 2$, $y_0 > 0$ *and* $\liminf_{t\to\infty} x_2(t) > 0$. *Then* $\liminf_{t\to\infty} S(t) > 0$, $\liminf_{t\to\infty} x_1(t) > 0$ *and* $\liminf_{t\to\infty} y(t) > 0$.

Proof : Let Ω denote the omega-limit set of $\Gamma(t)$, and assume $E_{\lambda_2} \in \Omega$. However, $\Omega \neq \{E_{\lambda_2}\}$ since E_{λ_2} is an unstable hyperbolic critical point with stable manifold $W^s(E_{\lambda_2}) = \{(S, x_1, x_2, y) \in \Re^4_+ \ : \ x_1 = 0, \ x_2 > 0\ \}$, thus since $x_{10} > 0$ then $\Gamma(0) \notin W^s(E_{\lambda_2})$. By Lemma (3.3) there exists $P^s \in (W^s(E_{\lambda_2}) \setminus \{E_{\lambda_2}\}) \cap \Omega$, but since $\Omega \subset \mathcal{S}$, then $P^s \in \{(S, x_1, x_2, y) \in \mathcal{S} \ : \ x_1 = 0, \ x_2 > 0\ \}$. Hence by the Poincaré-Bendixson Theorem, either $E_0 \in \Omega$ or $E_{\lambda_3} \in \Omega$ or $cl\mathcal{O}^-(P^s) \not\subset \Re^4_+$. But since $\liminf_{t\to\infty} x_2(t) > 0$ then $E_0, \ E_{\lambda_3} \notin \Omega$ and since $cl\mathcal{O}(P^s) \subset \Omega \subset \Re^4_+$ we have a contradiction. Therefore $E_{\lambda_2} \notin \Omega$.

Suppose $\liminf_{t\to\infty} x_1(t) = 0$, then there exists a point $\bar{R} = (\bar{S}, 0, \bar{x}_2, \bar{y}) \in \Omega$. Since $cl\mathcal{O}(\bar{R}) \subset \Omega \subset \mathcal{S}$ then either $E_0 \in \Omega$ or $E_{\lambda_2} \in \Omega$ or $E_{\lambda_3} \in \Omega$. But $E_0, \ E_{\lambda_3} \notin \Omega$ since $\liminf_{t\to\infty} x_2(t) > 0$ and from above $E_{\lambda_2} \notin \Omega$. Hence a contradiction and thus $\liminf_{t\to\infty} x_1(t) > 0$.

Similarly, suppose $\liminf_{t\to\infty} y(t) = 0$. Then there exists a point $\bar{Q} = (\bar{S}, \bar{x}_1, \bar{x}_2, 0) \in \Omega$. Since $cl\mathcal{O}(\bar{Q}) \subset \Omega \subset \mathcal{S}$ then either $E_0 \in \Omega$ or $E_{\lambda_1} \in \Omega$ or $E_{\lambda_2} \in \Omega$. But $E_0, \ E_{\lambda_1} \notin \Omega$ since $\liminf_{t\to\infty} x_2(t) > 0$ and from above $E_{\lambda_2} \notin \Omega$. Hence a contradiction and thus $\liminf_{t\to\infty} y(t) > 0$. ■

Theorem 3.9 *Assume* $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$. *If* E_{S^*} *exists with* $S^* > \lambda_2$ *and* E_{S^*} *is globally asymptotically stable for system (2.11) with respect to solutions for which* $x_{10} > 0$, $x_{20} = 0$, *and* $y_0 > 0$, *then system (2.11) is persistent.*

Proof : Let $\Gamma(t) = (S(t), x_1(t), x_2(t), y(t))$ be any solution of system (2.11) with $x_{i0} > 0$ $i = 1, 2$ and $y_0 > 0$. Let Ω denote its omega-limit set. Since $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$, by Lemma (3.6), it is enough to show that $\liminf_{t\to\infty} x_2(t) > 0$.

Suppose $\liminf_{t\to\infty} x_2(t) = 0$. Then, by Lemma (3.4) there must exist a point $\bar{P} = (\bar{S}, \bar{x}_1, 0, \bar{y}) \in \Omega$, where $\bar{x}_1, \ \bar{y} > 0$. Suppose $\bar{P} = E_{S^*}$. Since $S^* > \lambda_2$, then E_{S^*} is an unstable hyperbolic critical point with stable manifold $W^s(E_{S^*}) = \{(S, x_1, x_2, y) \in \Re^4_+ \ : \ x_1 > 0, \ x_2 = 0 \text{ and } y > 0\ \}$. Because $x_{20} > 0$, then $\Gamma(0) \notin W^s(E_{S^*})$ and thus $\Omega \neq \{E_{S^*}\}$. By Lemma (3.3) there exists $P^s \in (W^s(E_{S^*}) \setminus \{E_{S^*}\}) \cap \Omega$. But

$\Omega \subset \mathcal{S}$ and hence $P^s \in \{(S, x_1, x_2, y) \in \mathcal{S} : \; x_1 > 0, \; x_2 = 0 \text{ and } y > 0 \}$. Therefore, $cl\mathcal{O}^-(P^s)$ either contains E_0, E_{λ_1}, E_{λ_3} or it escapes $\Re^4_+$. But $\Omega \subset \Re^4_+$ and by Lemma (3.4) $\liminf_{t\to\infty} x_1(t) > 0$ and $\liminf_{t\to\infty} y(t) > 0$. Thus none of the above choices are possible. Hence, $\liminf_{t\to\infty} x_2(t) > 0$ and the result now follows by Lemma (3.6).■

Chapter 4

The 3-Dimensional Food Web

4.1 The Food Web

Recall that we first saw the food web in section 3 of Chapter 2 when we discussed the three dimensional subsystems of system (2.11).

$$\begin{aligned} S'(t) &= 1 - S(t) - x_1(t)p_1(S(t)) - \frac{y(t)p_3(S(t))}{\gamma} \\ x_1'(t) &= x_1(t)(-1 + p_1(S(t))) - y(t)q(x_1(t)) \\ y'(t) &= y(t)(-1 + p_3(S(t)) + q(x_1(t))) \\ S_0 &\geq 0, \; x_{10} \geq 0, \text{ and } y_0 \geq 0. \end{aligned} \tag{4.1}$$

We use the same notation for the critical points of the above subsystem as introduced in Chapter 2 (i.e. E_0^3, $E_{\lambda_1}^3$, $E_{S^*}^3$ and $E_{\lambda_3}^3$). A local analysis of (4.1) may be found in Appendix D.1. We define $q(x_1) = x_1 h(x_1)$ and since q is differentiable, we have $\lim_{x_1 \to 0} h(x_1) = q'(0)$. Thus we define $h(0) = q'(0)$. Finally, all the results of Chapter 3 apply here. Specifically, Theorems (3.1) - (3.5) and Theorems (3.7) and (3.8), with the appropriate changes. In particular, all solutions are positive and bounded, and when $\gamma = 1$, the simplex

$$\mathcal{S}^3 = \{(S, x_1, y) \; : \; S, x_1, y \geq 0; \; S + x_1 + y = 1\}$$

is a global attractor for (4.1). Moreover, when $p_1(S) = \frac{S}{\lambda_1}$, $p_3(S) = \frac{S}{\lambda_3}$, and $q(x_1) = \frac{x_1}{\delta}$ ($\gamma = 1$) there is an orderly transfer of global stability from one critical point to another, i.e.

$$E_0^3 \to E_{\lambda_1}^3 \to E_{S^*}^3 \to E_{\lambda_3}^3$$

as certain parameters are decreased. We summarize this transfer in the following Theorem.

Theorem 4.1 *Let $p_i(S) = \frac{S}{\lambda_i}$ for $i = 1, 2, 3$, $q(x_1) = \frac{x_1}{\delta}$ and $\gamma = 1$.*

(i) : *If $\lambda_1 < 1$ and $-1 + p_3(\lambda_1) + q(1 - \lambda_1) < 0$ (i.e. $S^* < \lambda_1 < 1$), then $E_{\lambda_1}^3$ is globally asymptotically stable for (4.3) with respect to all solutions for which $S_0 \geq 0$, $y_0 \geq 0$ and $x_{10} > 0$.*

(ii) : *If $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$ and $-1 + p_1(\lambda_3) - (1 - \lambda_3)q'(0) > 0$ (i.e. $\lambda_1 < S^* < \lambda_3$), then $E_{S^*}^3$ is globally asymptotically stable for (4.3) with respect to all solutions for which $S_0 \geq 0$, $y_0 > 0$ and $x_{10} > 0$.*

(iii) : *If $-1 + p_1(\lambda_3) - (1 - \lambda_3)q'(0) < 0$ (i.e. $\lambda_3 < S^*$), then $E_{\lambda_3}^3$ is globally asymptotically stable for (4.3) with respect to all solutions for which $S_0 \geq 0$, $x_{10} \geq 0$ and $y_0 > 0$.*

We omit the proof of this Theorem since it is similar to the proofs of Theorems (3.7) and (3.8) with the appropriate changes.

Notice that under the conditions of Theorem (4.1), the food web (4.3) does not persist. In particular, if $-1 + p_1(\lambda_3) - (1 - \lambda_3)q'(0) < 0$ (which implies $\lambda_3 < 1$) then the predator drives the prey to extinction. Thus the presence of the second competitor population, i.e. x_2, in system (2.11) is necessary for the persistence of (2.11).

4.2 Properties of Periodic Orbits

In this section, we give a numerical example to show that it is possible for periodic orbits to exist in subsystem (4.1). We examine the properties of such periodic orbits when $\gamma = 1$. Since the simplex $\mathcal{S}^3$ is a global attractor, any periodic orbit would lie entirely in $\mathcal{S}^3$ and hence we can restrict our attention to the positively invariant set $\mathcal{S}^3$. Thus we consider the system

$$\begin{aligned} S'(t) &= 1 - S(t) - x_1(t)p_1(S(t)) - y(t)p_3(S(t)) \\ x_1'(t) &= x_1(t)(-1 + p_1(S(t))) - y(t)q(x_1(t)) \\ y'(t) &= y(t)(-1 + p_3(S(t)) + q(x_1(t))) \\ S_0, x_{10}, y_0 &\geq 0, \text{ and } S_0 + x_{10} + y_0 = 1. \end{aligned}$$

Since $\mathcal{S}^3$ is positively invariant, there is no loss of generality if we replace $x_1(t)$ with $x_1(t) = 1 - S(t) + y(t)$. Then the above is equivalent to

$$\begin{aligned} S'(t) &= 1 - S(t) - (1 - S(t) - y(t))p_1(S(t)) - y(t)p_3(S(t)) \\ y'(t) &= y(t)(-1 + p_3(S(t)) + q(1 - S(t) - y(t))) \\ S_0, y_0 &\geq 0, \text{ and } S_0 + y_0 \leq 1. \end{aligned} \tag{4.2}$$

Theorm 4.2 *Assume $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$. Then any nontrivial periodic solution of (4.1) (or of (4.2)) must satisfy :*

$$\lambda_1 < S(t) < 1$$
$$0 < x_1(t) < 1 - \lambda_1$$
$$0 < y(t) < 1 - \lambda_1 - q^{-1}(1 - \lambda_1).$$

Proof : Let $\Gamma(t) = (S(t), y(t))$ be any nontrivial periodic solution of (4.2) and $x_1(t) = 1 - S(t) - y(t)$. For any $t \geq 0$, such that $S(t) \leq \lambda_1$ we have

$$\begin{aligned} S'(t) &\geq 1 - S(t) - (1 - S(t) - y(t))p_1(\lambda_1) - y(t)p_3(\lambda_1) \\ &= y(t)(1 - p_3(\lambda_1)) \geq 0. \end{aligned}$$

Now, $y(t) \neq 0$ for every $t \geq 0$, since otherwise $S(t) = \lambda_1$ which implies that $\Gamma(t) = E^3_{\lambda_1}$ which is a contradiction since we assumed that $\Gamma(t)$ was a nontrivial periodic solution. Thus for every $t \geq 0$, $S'(t) > 0$ which is a contradiction. Hence, for every $t \geq 0$

$$S(t) > \lambda_1 \text{ on } \Gamma(t).$$

Similiarly, for every $t \geq 0$, such that $y(t) \geq 1 - \lambda_1 - q^{-1}(1 - p_3(\lambda_1))$ and $S(t) > \lambda_1$ we have

$$\begin{aligned} 1 - S(t) - y(t) &< 1 - \lambda_1 - (1 - \lambda_1 - q^{-1}(1 - p_3(\lambda_1)) \\ &= q^{-1}(1 - p_3(\lambda_1)) \end{aligned}$$

which implies

$$\begin{aligned} y'(t) &< y(t)(-1 + p_3(S(t)) + (1 - p_3(\lambda_1)) \\ &= y(t)(p_3(S(t)) - p_3(\lambda_1)) \geq 0. \end{aligned}$$

As before, $y(t) \neq 0$ which implies $y'(t) > 0$, a contradiction. Hence, for every $t \geq 0$

$$y(t) < 1 - \lambda_1 - q^{-1}(1 - p_3(\lambda_1)) \text{ on } \Gamma(t).$$

Since $\Gamma(t)$ is contained in $\mathcal{S}^3$ and $x_1(t) = 1 - S(t) - y(t)$, it follows that $S(t) < 1$, $y(t) > 0$ and $0 < x_1(t) < 1 - \lambda_1$. ■

Next we use the Poincaré criterion to determine the stability of the periodic orbits of subsystem (4.2) when they exist.

Lemma 4.1 *Let $(S(t), y(t))$ be an arbitrary periodic solution of (4.2) with period T. Assume $h(x_1(t))$ is differentiable and define*

$$\triangle = \int_0^T \{\tfrac{\partial f_1}{\partial S}(S(t), y(t)) + \tfrac{\partial f_2}{\partial y}(S(t), y(t))\} dt.$$

Then

$$\triangle = -\int_0^T \{x_1(t)p_1'(S(t)) + y(t)p_3'(S(t)) + x_1(t)y(t)h'(x_1(t))\} dt \quad ,$$

where

$$x_1(t) = 1 - S(t) - y(t) \geq 0$$
$$f_1(S(t), y(t)) = 1 - S(t) - (1 - S(t) - y(t))p_1(S(t)) - y(t)p_3(S(t))$$
$$f_2(S(t), y(t)) = y(t)(-1 + p_3(S(t)) + q(1 - S(t) - y(t)).$$

Proof :

$$\begin{aligned} \triangle &= \int_0^T \{-1 + p_1(S(t)) - x_1(t)p_1'(S(t)) - y(t)p_3'(S(t))\} \\ &+ \{-1 + p_3(S(t)) + q(x_1(t)) - y(t)q'(x_1(t))\} dt \end{aligned}$$

$$= \int_0^T \{\frac{x_1'(t)}{x_1(t)} + y(t)h(x_1(t)) - x_1(t)p_1'(S(t)) - y(t)p_3'(S(t))\}$$
$$+ \{\frac{y'(t)}{y(t)} - y(t)(h(x_1(t)) + x_1(t)h'(x_1(t)))\}dt$$
$$= -\int_0^T \{x_1(t)p_1'(S(t)) + y(t)p_3'(S(t)) + x_1(t)y(t)h'(x_1(t))\}dt$$

since,

$$\int_0^T \frac{x_1'(t)}{x_1(t)}dt = \int_0^T \frac{y'(t)}{y(t)}dt = 0.\blacksquare$$

Theorem 4.3 *Assume $h(x_1(t))$ is differentiable, $\lambda_3 > 1$, and $E^3_{S^*}$ exists and is locally asymptotically stable. Suppose that*

$$x_1(t)p_1'(S(t)) + y(t)p_3'(S(t)) + x_1(t)y(t)h'(x_1(t)) > 0$$

where

$$\lambda_1 < S(t) < 1,\ 0 < x_1(t) < 1 - \lambda_1,\ \textit{and } 0 < y(t) < 1 - \lambda_1 - q^{-1}(1 - p_3(\lambda_1)).$$

Then, $E^3_{S^*}$ is globally asymptotically stable with respect to all solutions of (4.1) which satisfy S_0, $x_{10}, y_0 > 0$.

Proof : To show $E^3_{S^*} = (S^*, x_1^*, y^*)$ is globally asymptotically stable, it sufficies to show that (S^*, y^*) is globally asymptotically stable with respect to solutions of (4.2) for which S_0, $y_0 > 0$ and $S_0 + y_0 < 1$. This is true because the omega-limit set, Ω, of any solution of (4.1) ($\gamma = 1$) must contain points of the form $Q = (S, x_1, y)$, where $S + x_1 + y = 1$. The trajectory through the point $Q = (S, y)$ converges to (S^*, y^*) if it is globally asymptotically stable. Hence, the orbit through Q, denoted $\mathcal{O}(Q)$, converges to $E^3_{S^*}$, since $cl\mathcal{O}(Q)$ is contained in Ω and $E^3_{S^*} \in \Omega$. But then, since $E^3_{S^*}$ is locally asymptotically stable, $\Omega = \{E^3_{S^*}\}$.

Let $(S(t), y(t))$ be any nontrivial periodic solution of (4.2), with period $T > 0$. Since $x_1(t) = 1 - S(t) - y(t)$, then $(S(t), x_1(t), y(t))$ is a nontrivial periodic solution of (4.1). By the hypothesis of this theorem, $\Delta < 0$, (as defined in Lemma (4.1)). Hence, by the Poincaré criterion, all nontrivial periodic solutions are locally asymptotically stable. Since (S^*, y^*) is the only interior equilibrium point of (4.2) and is locally asymptotically stable by hypothesis, then in order for a nontrivial periodic solution to exist, there must be at least one that is unstable from inside. This is a contradiction. Hence no nontrivial periodic orbits exist. By the Poincaré-Bendixson Theorem, (S^*, y^*) is globally asymptotically stable.■

Recall that when $1 = p_3(\lambda_1)+q(1-\lambda_1)$ then $E^3_{\lambda_1}$ and $E^3_{S^*}$ coalesce, i.e. $S^* = \lambda_1$. If $A_3 > 0$ and $A_1A_2 - A_3 > 0$, where A_i for $i = 1,2,3$ are defined as in Appendix D.1., then $E^3_{S^*}$ is locally asymptotically stable (for example if $p_i(S)$, $i = 1,2,3$, and $q(x_1)$ are Lotka-Volterra response functions). By the continuity of the roots of the characteristic equation as a function of its coefficients, as $p_3(\lambda_1) + q(1 - \lambda_1)$ becomes greater than 1, and $\lambda_3 > 1$, $E^3_{S^*}$ is at least initially locally asymptotically stable. At the same time $E^3_{\lambda_1}$ becomes unstable. The following Corollaries show that in certain special cases $E^3_{S^*}$ can pick up the global stability lost by $E^3_{\lambda_1}$.

Corollary 4.1 *Assume $h(x_1(t))$ is differentiable, $\lambda_3 > 1$, and $p_3(\lambda_1) + q(1 - \lambda_1) < 1$ but is sufficiently close to 1. Then, if $E^3_{S^*}$ is locally asymptotically stable, it is globally asymptotically stable with respect to (4.1) ($\gamma = 1$) for solutions satisfying x_{10}, $y_0 > 0$ and $S_0 \geq 0$.*

Proof : By the above remark, $E^3_{S^*}$ is locally asymptotically stable provided $p_3(\lambda_1) + q(1 - \lambda_1)$ is sufficiently close to 1. Since h is differentiable, if $h'(x_1(t)) \geq 0$ we have

$$x_1(t)p_1'(S(t)) + y(t)p_3'(S(t)) + x_1(t)y(t)h'(x_1(t)) > 0.$$

If $h'(x_1(t)) < 0$ and $y(t) < 1 - \lambda_1 - q^{-1}(1 - p_3(\lambda_1))$ then we have

$$x_1(t)p_1'(S(t)) + y(t)p_3'(S(t)) + x_1(t)y(t)h'(x_1(t)) >$$
$$x_1(t)p_1'(S(t)) + y(t)p_3'(S(t)) + x_1(t)(1 - \lambda_1 - q^{-1}(1 - p_3(\lambda_1)))h'(x_1(t)) > 0$$

provided $p_3(\lambda_1) + q(1 - \lambda_1)$ is sufficiently close to 1. In either case, $E^3_{S^*}$ is globally asymptotically stable by Theorem (4.3).■

Corollary 4.2 *Assume $-1 + p_3(\lambda_1) + q(1 - \lambda_1) > 0$, $\lambda_3 > 1$ and $h(x_1(t))$ is differentiable. Let $p_1(S(t)) = \frac{S(t)}{\lambda_1}$ and $p_3(S(t)) = \frac{S(t)}{\lambda_3}$. If*

(i) $h'(x_1(t)) \geq 0$ *for* $0 < x_1(t) < 1 - \lambda_1$

or,

(ii) $q(x_1(t))$ *is twice differentiable, and convex for* $0 \leq x_1(t) \leq 1-\lambda_1$ *then* $E^3_{S^*}$ *is globally asymptotically stable with respect to solutions of (4.1)* ($\gamma = 1$) *for which* x_{10}, $y_0 > 0$ *and* $S_0 \geq 0$.

Proof (i): First assume that $h(x_1(t))$ is differentiable for $0 < x_1(t) < 1-\lambda_1$, then since

$$q'(x_1(t)) = h(x_1(t)) + x_1(t)h'(x_1(t)),$$

we have $x_1(t)q'(x_1(t)) - q(x_1(t)) = x_1^2(t)h'(x_1(t)) \geq 0$. Thus $E^3_{S^*}$ is locally asymptotically stable since the characteristic equation of $E^3_{S^*}$ has positive coefficients and $A_1A_2 - A_3 > 0$ where A_1, A_2, and A_3 are the coefficients of the quadratic term, the linear term , and the constant term respectively, in the characteristic equation. The result now follows by Theorem (4.3).

(ii): Secondly, assume $q(x_1(t))$ is twice differentiable, and convex for $0 \leq x_1(t) \leq 1-\lambda_1$ then

$$h'(x_1(t)) = \frac{q'(x_1(t)) - h(x_1(t))}{x_1(t)}, \text{ provided } x_1(t) \neq 0.$$

Thus the sign of $h'(x_1(t))$ depends on the sign of

$$N(x_1(t)) = x_1(t)q'(x_1(t)) - q(x_1(t)) \text{ for } x_1(t) > 0.$$

Which implies

$$N'(x_1(t)) = x_1(t)q''(x_1(t)).$$

Since $N(0) = 0$ and $q(x_1(t))$ is convex for $0 \leq x_1(t) \leq 1-\lambda_1$, then $N(x_1(t))$ is nondecreasing from 0 to $1-\lambda_1$. Therefore $N(x_1(t)) \geq 0$ for $0 \leq x_1(t) \leq 1-\lambda_1$, which implies $h'(x_1(t) \geq 0$ for $0 \leq x_1(t) \leq 1-\lambda_1$. The global stability of $E^3_{S^*}$ now follows by Theorem (4.3).■

Remark : Notice that Corollaries (4.1) and (4.2) in conjunction with Theorem (3.9) imply that system (4.3) persists.

Theorem 4.4 *Assume* $-1 + p_3(\lambda_1) + q(1-\lambda_1) > 0$, $\lambda_3 > 1$, *and* $h(x_1(t))$ *is differentiable. If* $E^3_{S^*}$ *exists and is unstable, then there exists a nontrivial periodic solution of (4.1)* ($\gamma = 1$). *If in addition* $\Delta < 0$ *(in Lemma (4.1)), then there exists a unique* *nontrivial periodic orbit that is globally asymptotically stable with respect to solutions of (4.1) for which x_{10}, $y_0 > 0$ and $S_0 \geq 0$.*

Proof : Let $\Gamma(t) = (S(t), y(t))$ be any solution of subsystem (4.2) with $x_1(t) = 1 - S(t) - y(t)$ and $S_0 \geq 0$, $y_0 > 0$. Denote the omega-limit set of $\Gamma(t)$ by Ω, and the corresponding critical points by E_0^2, $E_{S^*}^2$ and $E_{\lambda_3}^2$. Since all solutions are positive and bounded, $\Omega \subset \Re_+^2$ is compact. Also, since $\lambda_3 > 1$, $E_{\lambda_3}^2$ is not in the non-negative (S, y)-plane.

Suppose $E_0^2 \in \Omega$. Then $\Omega \neq \{E_0^2\}$, since $\lambda_1 < 1$ implies that E_0^2 is an unstable isolated hyperbolic critical point with stable manifold given by $W^s(E_0^2) = \{(S, y) \in \Re_+^2 \ : \ y = 0, \ S \geq 0 \ \}$ and since $y_0 > 0$, $\Gamma(0) \notin W^s(E_0^2)$. By Lemma (3.3), there exists $P^s \in (W^s(E_0^2) \setminus \{E_0^2\}) \cap \Omega$, i.e. $P^s \in \{(S, y) \in \mathcal{S}^3 \ : \ y = 0, \ S \geq 0 \ \}$. Hence, $cl\mathcal{O}^-(P^s) \not\subset \Re_+^2$ or $\mathcal{O}^-(P^s)$ becomes unbounded. But this is a contradiction. Therefore $E_0^2 \notin \Omega$.

Note that there is no critical point on the $S \equiv 0$ face. Since $E_{S^*}^2$ is unstable by hypothesis, and $E_0^2 \notin \Omega$, by the Poincaré-Bendixson Theorem, there must exist a nontrivial periodic orbit.

By hypothesis we have $\Delta < 0$, hence by the Poincaré criterion all nontrivial periodic solutions are locally asymptotically stable. Since $E_{S^*}^2$ is the only interior equilibrium of (4.2) in the non-negative cone and it is unstable, then for more than one nontrivial periodic solution to exist, there must be at least one that is unstable from the inside. But this is a contradiction. Hence there exists a unique nontrivial periodic solution which is globally asymptotically stable by the Poincaré-Bendixson Theorem.■

4.3 A Numerical Example

In this section we give an example that shows that the orderly transfer of global stability from one critical point to another in subsystem (4.1) with $\gamma = 1$ (and consequently of system (2.11), i.e. Theorems (3.7) and (3.8)), is not always the case. This example demonstrates that using δ as the bifurcation parameter, it is possible to have $E^3_{S^*}$ lose its stability by means of a Hopf bifurcation before $E^3_{\lambda_3}$ even enters the non-negative cone (i.e. $\lambda_3 > 1$).

In subsystem (4.1) let $p_1(S) = \frac{S}{\lambda_1}$, $p_3(S) = \frac{S}{\lambda_3}$ and $q(x_1) = \frac{mx_1}{\delta(m-1)+x_1}$, where $m > 1$. Hence $E^3_{S^*}$ is given by

$$S^* = \frac{-C+\sqrt{C^2+4\lambda_3(m-1)}}{2}$$
$$x_1^* = \frac{\delta(m-1)(1-\frac{S^*}{\lambda_3})}{(m-1)+\frac{S^*}{\lambda_3}}$$
$$y^* = \frac{\delta(m-1)(-1+\frac{S^*}{\lambda_1})}{(m-1)+\frac{S^*}{\lambda_3}}$$

where ,

$$C = \frac{\delta}{\lambda_1}(m-1)(\lambda_3-\lambda_1) + \lambda_3(m-1) - 1.$$

Let $\lambda_1 = 0.25$, $\lambda_3 = 3$,$m = 8$ and $K \approx 0.827922029$. Then $-1+p_3(\lambda_1)+q(1-\lambda_1) > 0$ for $0 < \delta < K$ (i.e. $E^3_{\lambda_1}$ is unstable) and $-1 + p_1(\lambda_3) - (1 - \lambda_3)q'(0) > 0$ for $\delta > 0$. If $\delta \approx 0.059246187975 \equiv \delta_0$, then $S^* \approx 0.82712713$ (i.e. $\lambda_1 < S^* < \lambda_3$), $x_1^* \approx 0.04128537084$, $y^* \approx 0.1315874928$ and,

$$A_1A_2 - A_3 = 0 \text{ and } A_i > 0 \text{ for } i = 1,2,3$$

where A_i, $i = 1,2,3$, are respectively the coefficients of μ^2, μ and the constant term in the characteristic equation of the associated variational matrix of $E^3_{S^*}$. The coefficient μ^3 is equal to 1. Moreover, if $0 < \delta < K$, then $A_i > 0$ for $i = 1,2,3$ and

$$\text{if } 0 < \delta < \delta_0 \text{ then } A_1A_2 - A_3 < 0,$$
$$\text{if } \delta_0 < \delta < K \text{ then } A_1A_2 - A_3 > 0.$$

Thus the real part of the complex conjugate pair of eigenvalues crosses zero transversely at $\delta = \delta_0$ and so the change in stability at $\delta = \delta_0$ is through a Hopf bifurcation.

Figures 1 and 2 illustrate this Hopf bifurcation. In both cases $S_0 = 0.5$, $x_{10} = y_0 = 0.25$ and $\delta = 0.05$. $E^3_{S^*}$ is unstable and $E^3_{\lambda_3}$ is not in $\Re^3_+$. These figures seem to depict a stable periodic orbit.

4.4 Analysis of Food Web for $\gamma \neq 1$

In this section we consider subsystem (4.1) for $\gamma \neq 1$. The substrate and prey uptake functions are given by Lotka-Volterra functions. More specifically we consider the system

$$\begin{aligned}
S'(t) &= 1 - S(t) - x_1(t)\frac{S(t)}{\lambda_1} - \frac{y(t)S(t)}{\gamma\lambda_3} \\
x_1'(t) &= x_1(t)(-1 + \frac{S(t)}{\lambda_1}) - y(t)\frac{x_1(t)}{\delta} \\
y'(t) &= y(t)(-1 + \frac{S(t)}{\lambda_3} + \frac{x_1(t)}{\delta}) \\
S_0 &\geq 0, x_{10} \geq 0, \text{ and } y_0 \geq 0
\end{aligned} \tag{4.3}$$

where $\gamma \neq 1$. Notice that for this system solutions are still positive and bounded. When $\lambda_1 > 1$, by Theorem (3.4), E_0^3 is globally asymptotically stable. Also note that Theorem (3.3) holds for this system. However, the simplex $\mathcal{S}^3$ is no longer a global attractor (i.e. $(S + x_1 + y)(t) \neq 1$).

4.4.1 Case $\gamma < 1$

The first thing we do is determine conditions for the existence and/or uniqueness of the interior equilibrium $E_{S^*}^3$. From the local analysis of subsystem (4.3) in Appendix D.2. we have

$$S^* = \frac{-b_1 \pm \sqrt{b_1^2 + b_2}}{b_3}$$

where b_i for $i = 1, 2, 3$ are defined as in Appendix D.2. Since $\gamma < 1$ then b_2, $b_3 > 0$ and thus $|b_1| < \sqrt{b_1^2 + b_2}$. Hence, since we must have $S^* > 0$, then $S^* = \frac{-b_1+\sqrt{b_1^2+b_2}}{b_3}$. Also for $E_{S^*}^3$ to be in the non-negative cone we must have $\lambda_1 < S^* < \lambda_3$. Thus when $E_{S^*}^3$ exists it is unique.

Notice that $b_1 + b_3\lambda_1 = (\frac{1}{\gamma\lambda_3} - \frac{1}{\lambda_3}) + (\frac{1}{\lambda_1} - \frac{1}{\lambda_3}) + \frac{1}{\delta} > 0$ and that $b_1 + b_3\lambda_3 = \frac{1}{\lambda_1}(\frac{2\lambda_3-\lambda_1}{\gamma\lambda_3} - 1) + \frac{1}{\delta} > 0$. Thus simple algebraic manipulation gives

$$\lambda_1 < S^* \text{ if and only if } -1 + \tfrac{\lambda_1}{\lambda_3} + \tfrac{(1-\lambda_1)}{\delta} > 0,$$
$$S^* < \lambda_3 \text{ if and only if } -1 + \tfrac{\lambda_3}{\lambda_1} - \tfrac{\gamma(1-\lambda_3)}{\delta} > 0.$$

The local analysis of subsystem (4.3) is summarized in the following proposition.

Proposition 4.1 (a) : *If* $S^* < \lambda_1 < 1$ *then* $E^3_{\lambda_1}$ *is locally asymptotically stable and* E^3_0 *is unstable. If* $\lambda_3 < 1$, *then* $E^3_{\lambda_3}$ *is in* $\Re^3_+$ *and is unstable.*
(b) : *If* $\lambda_1 < S^* < \lambda_3$, $\lambda_1 < 1$ *and* $A_1A_2 - A_3 > 0$ *with* $A_3 > 0$ *then* $E^3_{S^*}$ *is locally asymptotically stable. (A_i for $i = 1, 2, 3$ are defined as in Appendix D.1.).* E^3_0, $E^3_{\lambda_1}$ *are unstable. If* $\lambda_3 < 1$, *then* $E^3_{\lambda_3}$ *is in* $\Re^3_+$ *and is unstable.*
(c) : *If* $\lambda_3 < S^*$ *then* $E^3_{\lambda_3}$ *is locally asymptotically stable.* E^3_0, $E^3_{\lambda_1}$ *are unstable.*

Theorem 4.5 *If* $\lambda_1 < 1$ *and* $-1+\frac{\lambda_1}{\gamma\lambda_3}+\frac{(1-\lambda_1)}{\delta} < 0$, *then* $E^3_{\lambda_1}$ *is globally asymptotically stable for subsystem (4.3) with respect to all solutions for which* S_0, $x_{10} > 0$ *and* $y_0 \geq 0$.

Proof : First note that $\lambda_1 < 1$ and $-1 + \frac{\lambda_1}{\gamma\lambda_3} + \frac{(1-\lambda_1}{\delta} < 0$ implies $E^3_{\lambda_1}$ is locally asymptotically stable. Define the function $V : int\Re^3_+ \to \Re$ by

$$\begin{aligned} V(S,x_1,y) &= S-\lambda_1-\lambda_1\ln(\frac{S}{\lambda_1}) \\ &+ \{x_1-(1-\lambda_1)-(1-\lambda_1)\ln(\frac{x_1}{1-\lambda_1})\}+y. \end{aligned}$$

The time derivative calculated along solutions of subsystem (4.3) is

$$\begin{aligned} \dot V(S,x_1,y) &= (1-\frac{\lambda_1}{S})S'+(1-\frac{1-\lambda_1}{x_1})x_1'+y' \\ &= \frac{(S-\lambda_1)}{S}(1-S)-(1-\lambda_1)(-1+\frac{S}{\lambda_1}) \\ &+ y\{-1+\frac{\lambda_1}{\gamma\lambda_3}+\frac{(1-\lambda_1)}{\delta}+(1-\frac{1}{\gamma})\frac{S}{\lambda_3}\} \\ &= -\frac{(S-\lambda_1)^2}{S\lambda_1} \\ &+ y\{-1+\frac{\lambda_1}{\gamma\lambda_3}+\frac{(1-\lambda_1)}{\delta}+(1-\frac{1}{\gamma})S\} \leq 0. \end{aligned}$$

Hence $\dot V(S,x_1,y) = 0$ if and only if $S = \lambda_1$ and $y = 0$. Since S is constant then $S' = 0$, which implies that $x_1 = 1 - \lambda_1$ (since $y = 0$). Thus V is a Lyapunov function for (4.3) in the $int\Re^3_+$ and since all solutions are positive and bounded, by LaSalle's

Extension Theorem, every solution of (4.3) for which S_0, $y_0 > 0$, approaches M, where M is the largest invariant subset of

$$\mathcal{S} = \{(S, x_1, y) \in int\Re^3_+ \ : \ \dot{V}(S, x_1, y) = 0 \ \}.$$

If $\lambda_1 < 1$ and $-1 + \frac{\lambda_1}{\gamma\lambda_3} + \frac{(1-\lambda_1)}{\delta} > 0$ then $\mathcal{S} = \mathcal{M} = \{E^3_{\lambda_1}\}$. Hence $E^3_{\lambda_1}$ is globally asymptotically stable.■

At this point, Lyapunov functions of the form used in the proof of the above theorem are no longer adequate to continue to extract global information for subsystem (4.3). This along with the fact that there no longer is a simplex that could serve as a global attractor for solutions of (4.3) make it difficult to obtain any more global results. However, note that for γ sufficiently close to zero, $E^3_{\lambda_3}$ is always unstable. But before we conclude this subsection for the case $\gamma < 1$ we give a numerical example demonstrating that periodic solutions can occur via a Hopf bifurcation.

Example : Let $\lambda_1 = 0.25$, $\lambda_3 = 3.0$ and $\delta = 0.1$ in subsystem (4.3). For $0 < \gamma < 1$ we have $-1 + \frac{\lambda_1}{\lambda_3} + \frac{(1-\lambda_1)}{\delta} > 0$ and $-1 + \frac{\lambda_3}{\lambda_1} - \frac{\gamma(1-\lambda_3)}{\delta} > 0$. Let $\gamma \approx 0.05145044175 \equiv \gamma_0$ then $S^* \approx 0.5029206281$, $x_1^* \approx 0.08323597907$ and $y^* \approx 0.1011682512$. Moreover

$$A_1A_2 - A_3 = 0 \text{ and } A_i > 0 \text{ for } i = 1, 2, 3$$

where A_i for $i = 1, 2, 3$ are as defined in Appendix D.2. Also for $0 < \gamma < 1$, $A_i > 0$ for $i = 1, 2, 3$ and

$$\text{if } 0 < \gamma < \gamma_0 \text{ then } A_1A_2 - A_3 < 0,$$
$$\text{if } \gamma_0 < \gamma < 1 \text{ then } A_1A_2 - A_3 > 0.$$

Thus the real part of the complex conjugate pair of eigenvalues crosses zero transversely at $\gamma = \gamma_0$ and so the change in stability at $\gamma = \gamma_0$ is through a Hopf bifurcation.

Figures 3 and 4 illustrate this Hopf bifurcation. In both cases $S_0 = 0.7$, $x_{10} = 0.1$, $y_0 = 0.05$ and $\gamma = 0.01$. $E^3_{S^*}$ is unstable and $E^3_{\lambda_3}$ is not in $\Re^3_+$. These figures seem to depict a stable periodic orbit.

4.4.2 Case $\gamma > 1$

As in the case for $\gamma < 1$ we first determine when $E^3_{S^*}$ exists and when it exists whether or not it is unique in the sense that it is the only equilibrium having all three species positive. S^* as above is again given by $S^* = \frac{-b_1 \pm \sqrt{b_1^2 + b_2}}{b_3}$. Notice that for $\gamma > 1$, we have b_2, $b_3 < 0$. The discriminant $b_1^2 + b_2$ can be positive, negative or zero depending on the choice of values for the parameters λ_1, λ_3, δ and γ. That is, S^* may not exist, or it may exist and be unique, or there might be two distinct values of S^*. Figures 5 to 14 illustrate these possible outcomes. Table 1 gives the parameter values used for each figure along with the local asymptotic stability of each critical point. From these numerical illustrations, it is clear that any qualitative conclusions regarding the global stability of $E^3_{\lambda_1}$, $E^3_{S^*}$ and $E^3_{\lambda_3}$ is difficult to make without some additional information about the values of the parameters. Note that in Figures 7 to 9, S^* changes from not existing, to existing and being unique, to having two distinct values, and there is no change in the local stability of the remaining critical points.
Also note that from the local analysis of $E^3_{S^*}$, when $\gamma > 1$, then the interior critical point(s) is (are) locally asymptotically stable when it (they) is (are) in the non-negative cone (i.e $\lambda_1 < S^*_{1,2} < \lambda_3$) and when $A_3 > 0$. We conclude this section by stating our only global result when $\gamma > 1$.

Theorem 4.6 *If $-1 + \frac{\gamma\lambda_3}{\lambda_1} - \frac{\gamma(1-\lambda_3)}{\delta} < 0$, then $E^3_{\lambda_3}$ is globally asymptotically stable for subsystem (4.3) with respect to all solutions for which S_0, $y_0 > 0$ and $x_{10} \geq 0$.*

Proof: First note that $-1 + \frac{\gamma\lambda_3}{\lambda_1} - \frac{\gamma(1-\lambda_3)}{\delta} < 0$ implies that $E^3_{\lambda_3}$ is locally asymptotically stable. Define the function $V \ : \ int\Re^3_+ \to \Re$ by

$$\begin{aligned} V(S, x_1, y) &= \gamma\{S - \lambda_3 - \lambda_3 \ln(\frac{S}{\lambda_3})\} + x_1 \\ &+ \{y - \gamma(1-\lambda_3) - \gamma(1-\lambda_3)\ln(\frac{y}{\gamma(1-\lambda_3)})\}. \end{aligned}$$

The time derivative calculated along solutions of (4.3) is

$$\dot{V}(S, x_1, y) = \gamma(1 - \frac{\lambda_3}{S})S' + x_1' + (1 - \frac{\gamma(1-\lambda_3)}{y})y'$$

$$\begin{aligned}
&= \frac{(S-\lambda_3)}{S}(1-S) - \gamma(1-\lambda_3)(-1+\frac{S}{\lambda_3}) \\
&+ x_1\{-1+\frac{\gamma\lambda_3}{\lambda_1} - \frac{\gamma(1-\lambda_3)}{\delta} + (1-\gamma)\frac{S}{\lambda_1}\} \\
&= -\frac{(S-\lambda_3)^2}{S\lambda_3} \\
&+ x_1\{-1+\frac{\gamma\lambda_3}{\lambda_1} - \frac{\gamma(1-\lambda_3)}{\delta} + (1-\gamma)\frac{S}{\lambda_1}\} \leq 0.
\end{aligned}$$

Hence $\dot{V}(S, x_1, y) = 0$ if and only if $S = \lambda_3$ and $x_1 = 0$. Since S is constant then $S' = 0$ implies that $y = \gamma(1-\lambda_3)$ (since $x_1 = 0$). Thus V is a Lyapunov function for (4.3) in the $int\Re^3_+$ and since all solutions are positive and bounded, then by LaSalle's Extension Theorem, every solution of (4.3) for which S_0, $x_{10} > 0$ approaches $\mathcal{M}$, where $\mathcal{M}$ is the largest invariant subset of

$$\mathcal{S} = \{(S, x_1, y) \in \Re^3_+ \ : \ \dot{V}(S, x_1, y) = 0 \ \}.$$

If $-1 + \frac{\gamma\lambda_3}{\lambda_1} - \frac{\gamma(1-\lambda_3)}{\delta} < 0$ then $\mathcal{S} = \mathcal{M} = \{E^3_{\lambda_3}\}$. Hence $E^3_{\lambda_3}$ is globally asymptotically stable.■

Chapter 5

Summary and Discussion

In this thesis we have been concerned with how a chemostat with two competitors that compete for the nutrient is effected by the invasion of a predator who feeds on two trophic levels (i.e. on the nutrient as well as on one of the competitors). We also consider the behaviour of the resulting three-dimensional subsystem that results when the inferior competitor (i.e. inferior with respect to the two-dimensional competitive chemostat) is removed.

First, we consider the four-dimensional system with $\gamma = 1$. We obtain the complete global behaviour of the model when Lotka-Volterra response functions are used to describe predator-prey and competitor-substrate interactions. In this case there is a transfer of global stability from one critical point to another as various parameters are decreased. At each stage of this transfer, conditions become sufficient such that a new population survives. However, if we change the predator-prey response function from a Lotka-Volterra to a Michaelis-Menten response function, then the orderly transfer of global stability from one critical point to another is interrupted. Under these circumstances for certain parameter values we have the birth of a periodic orbit via a Hopf bifurcation. Even in the case when the functional responses are described by general monotone dynamics there still is a transfer of global stability from E_0 to E_{λ_1}, but further description of the global behaviour becomes complicated by the unknown existence and/or uniqueness of E_{S^*}. However, when E_{S^*} is known to exist, then the system is shown to persist under certain favourable conditions.

As in the model studied by Butler et al. [5] where they considered a chemostat with two competitor populations competing for a single, essential growth-limiting nutrient and a predator feeding on the more aggressive competitor, here too, at least in the case when $\gamma = 1$, if any competitor survived it was the one with the lowest break-even concentration. If the competitor with the second lowest break-even concentration was to survive it had to do so in the presence of the predator.

Secondly, in contrast to the four-dimensional system with $\gamma = 1$, the subsystem obtained by eliminating the inferior competitor need not persist, even in the case where Lotka-Volterra response functions describe predator-prey and competitor-nutrient interactions. However we still have an orderly transfer of global stability from one critical point to another in this case. By allowimg $\gamma \neq 1$ (i.e. $0 < \gamma < 1$) in this subsystem we can interrupt this orderly transfer of stability even when the predator-prey uptake function is still described by Lotka-Volterra kinetics. In passing, it should be noted that when the break-even concentration of the predator with respect to the nutrient is sufficiently large (i.e. $\lambda_3 > 1$), then the subsystem for $\gamma = 1$ can persist.

There are several examples in the literature of competitive coexistence resulting from the invasion of a single predator or several predators (see [3] [5] [6] [7] [17] [18] [20]). Our four-dimensional model falls into this category. Thus our model tends to lend support to the notion that predation is one of the factors that accounts for the complexity and diversity observed in ecological systems. Paine [18] gives experimental evidence that the removal of a single predator in a fifteen species food web caused a collapse to an eight species food web. Similiarly, in our four-dimensional model if we remove the predator, the system collapses from three species to one. The surviving population is the one that can sustain itself on the lowest concenration of nutrient. However, if instead of removing the predator we remove the inferior competitor (i.e. inferior with respect to the two-dimensional chemostat) we again observe a collapse in the system from three species to one. But in this case, the predator is the sole survivor. Hence, we can also view our model as one resulting from the invasion of a competitor in the three-dimensional predator-mediated subsystem. Thus our model also supports the notion of a competitor being responsible in part for the diversity of ecosystems.

It is known that in the competitive chemostat at most one population can survive ([1], [4], [23]). The surviving population is the one with the lowest break-even concentration. When considering the outcome of a two competitor chemostat that has been invaded by a predator that feeds on two distinct trophic levels, we have shown (when $\gamma = 1$) that no matter how aggressive the predator is, the predator cannot drive the prey to extinction. Next, consider the two competitor chemostat with the competitor with the largest break-even concentration, faced with starvation, predating on the other competitor. In this case, the least efficient competitor, who now is also the predator, can drive the best competitor (i.e. prey) to extinction. Finally, it has been shown that in the predator-mediated food web, with the predator feeding solely on the prey, the predator cannot drive the prey to extinction without causing its own extinction (see [5], [9], [10], [19]). However, in our food web model (4.3) ($\gamma = 1$) we have shown that the predator feeding on two different trophic levels can drive the prey to extinction and then sustain itself on nutrient.

Appendix A

Table

A.1 Table 1 : Local Analysis ($\gamma > 1$)

Fig.	Parameters				Equilibria				
	λ_1	λ_3	δ	γ	E_0^3	$E_{\lambda_1}^3$	$E_{S_1^*}^3$	$E_{S_2^*}^3$	$E_{\lambda_3}^3$
5	.6	1.5	.4	5	uns.	uns.	a.s.	NIPC	NIPC
6	.6	1.5	.8	50	uns.	a.s.	NIPC	NIPC	NIPC
7	.2	.7	.5	10	uns.	uns.	DNE	DNE	a.s.
8	.2	.7	.5	*	uns.	uns.	$A_3 = 0$, $S_1^* = S_2^*$		a.s.
9	.2	.7	.5	4.3	uns.	uns.	a.s.	uns.	a.s.
10	.2	.7	.5	2	uns.	uns.	a.s.	NIPC	uns.
11	.4	.5	5	10	uns.	a.s.	NIPC	uns.	a.s.
12	.4	.5	5	1.5	uns.	a.s.	NIPC	NIPC	uns.
13	.7	.8	.5	2	uns.	uns.	NIPC	NIPC	a.s.
14	.7	.75	3	3	uns.	uns.	NIPC	NIPC	a.s.

*=4.615702185

NIPC = Not In Positive Cone

DNE = Does Not Exist

uns. = unstable

a.s. = asymptotically stable

Appendix B

Figures

B.1 Figure Captions

Figure 1 : $E^3_{S^*}$ is unstable and $E^3_{\lambda_3} \notin \Re^3_+$ ($\delta = 0.05 < \delta_0$).

Figure 2 : Phase portrait : Nutrient vs. Predator ($\delta = 0.05 < \delta_0$).

Figure 3 : $E^3_{S^*}$ is unstable and $E^3_{\lambda_3} \notin \Re^3_+$ ($\gamma = 0.01 < \gamma_0$).

Figure 4 : Phase portrait : Nutrient vs. Predator ($\gamma = 0.01 < \gamma_0$).

Figure 5 : $E^3_{S_1^*} \in \Re^3_+$ and $E^3_{S_2^*} \notin \Re^3_+$ ($\lambda_1 < S_1^* < 1 < \lambda_3 < S_2^*$).

Figure 6 : $E^3_{S_1^*}$ and $E^3_{S_2^*} \notin \Re^3_+$ ($S_1^* < \lambda_1 < 1 < \lambda_3 < S_2^*$).

Figure 7 : S_1^* and S_2^* do not exist.

Figure 8 : $E^3_{S_1^*} = E^3_{S_2^*} \in \Re^3_+$ ($\lambda_1 < S_1^* = S_2^* < \lambda_3 < 1$).

Figure 9 : $E^3_{S_1^*}$ and $E^3_{S_2^*} \in \Re^3_+$ ($\lambda_1 < S_1^* < S_2^* < \lambda_3 < 1$).

Figure 10 : $E^3_{S_1^*} \in \Re^3_+$ and $E^3_{S_2^*} \notin \Re^3_+$ ($\lambda_1 < S_1^* < \lambda_3 < 1 < S_2^*$).

Figure 11 : $E^3_{S_1^*} \notin \Re^3_+$ and $E^3_{S_2^*} \in \Re^3_+$ ($S_1^* < \lambda_1 < S_2^* < \lambda_3 < 1$).

Figure 12 : $E^3_{S_1^*}$ and $E^3_{S_2^*} \notin \Re^3_+$ ($S_1^* < \lambda_1 < \lambda_3 < S_2^* < 1$).

Figure 13 : $E^3_{S_1^*}$ and $E^3_{S_2^*} \notin \Re^3_+$ ($\lambda_1 < \lambda_3 < 1 < S_1^* < S_2^*$).

Figure 14 : $E^3_{S_1^*}$ and $E^3_{S_2^*} \notin \Re^3_+$ ($S_1^* < S_2^* < \lambda_1 < \lambda_3 < 1$).

B.2 Figures

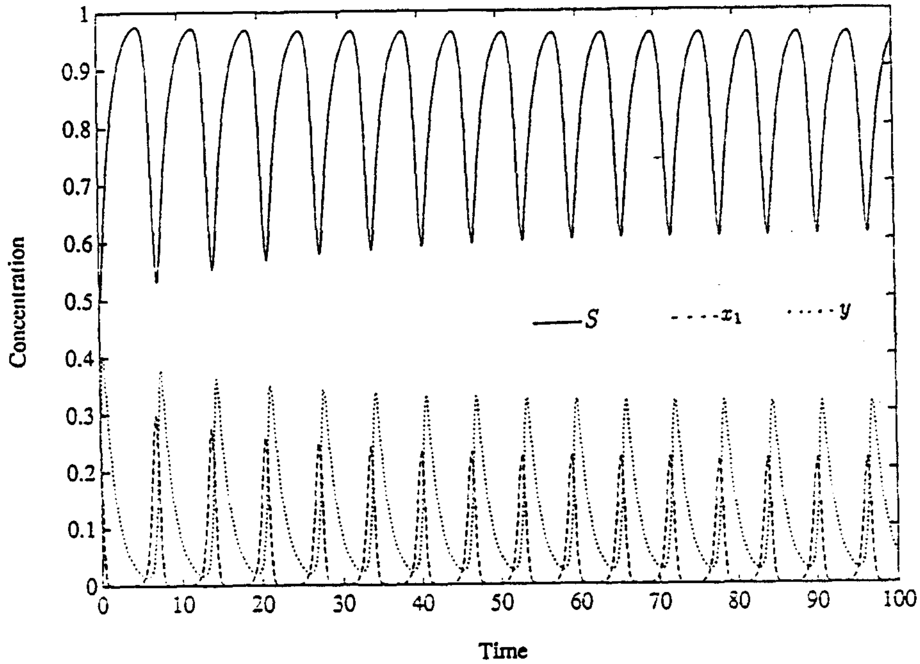

Concentration
Time
S
x_1
y

Fig. 1

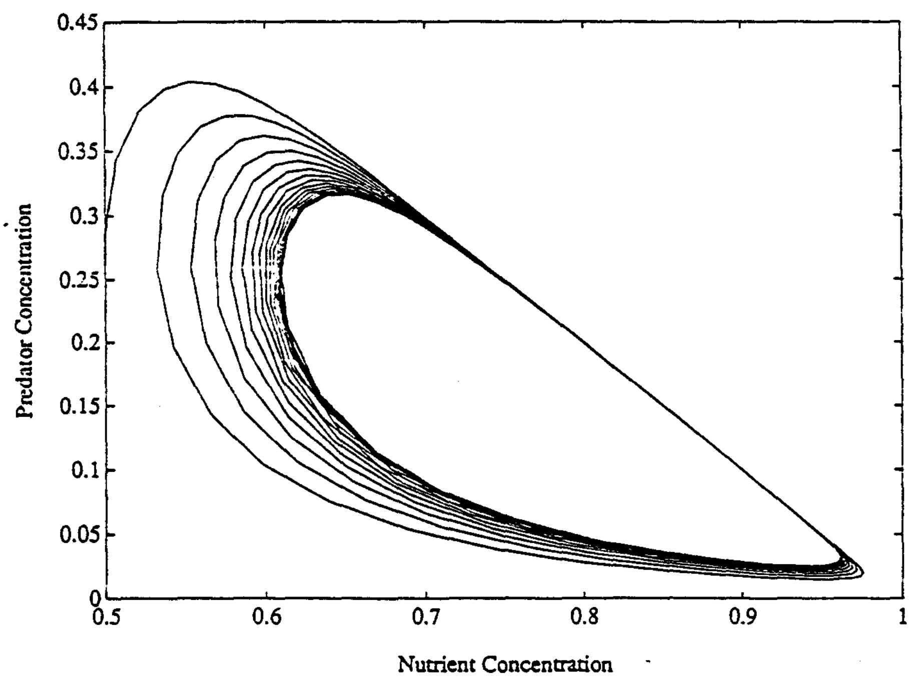

Predator Concentration
Nutrient Concentration

Fig. 2

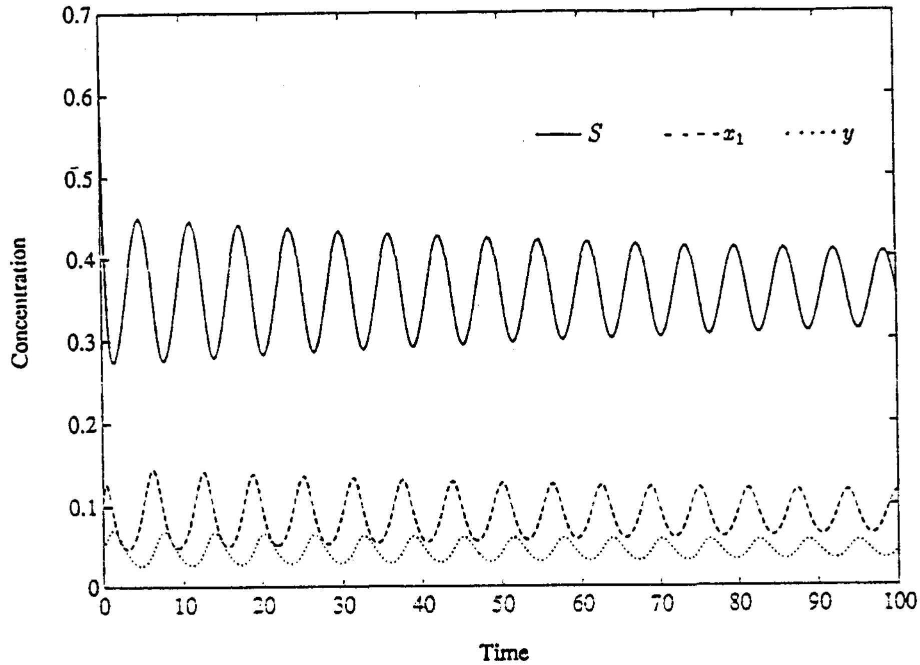

S
x_1
y
Concentration
Time
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
10
20
30
40
50
60
70
80
90
100

Fig. 3

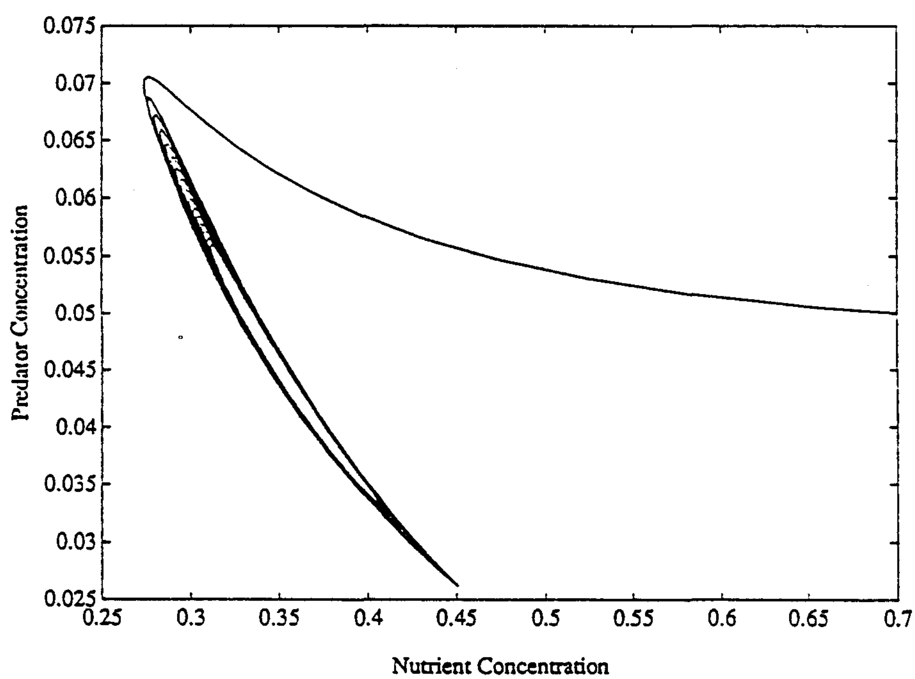

Predator Concentration
Nutrient Concentration
0.075
0.07
0.065
0.06
0.055
0.05
0.045
0.04
0.035
0.03
0.025
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7

Fig. 4

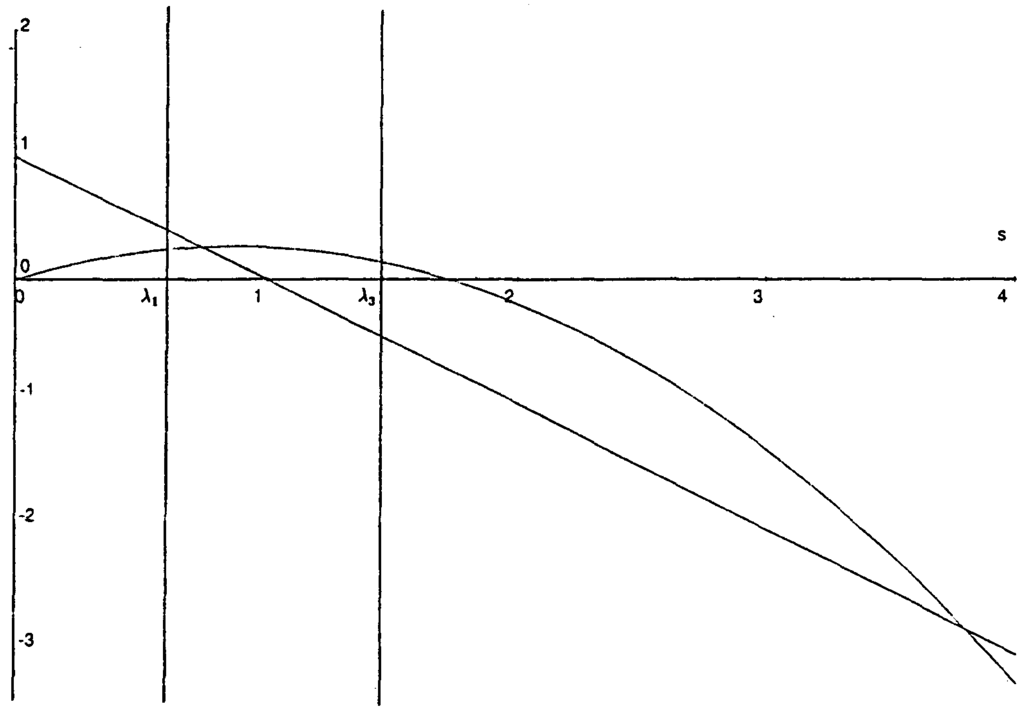

2
1
0
-1
-2
-3
s
0
λ_1
1
λ_3
2
3
4

Fig. 5

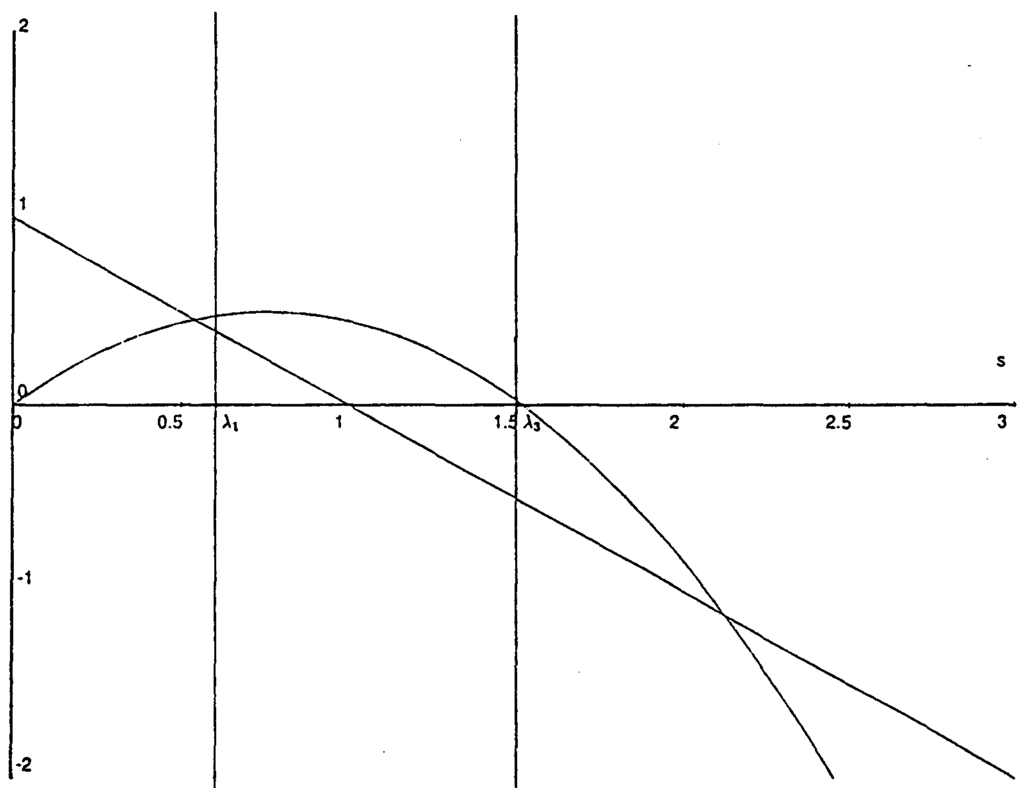
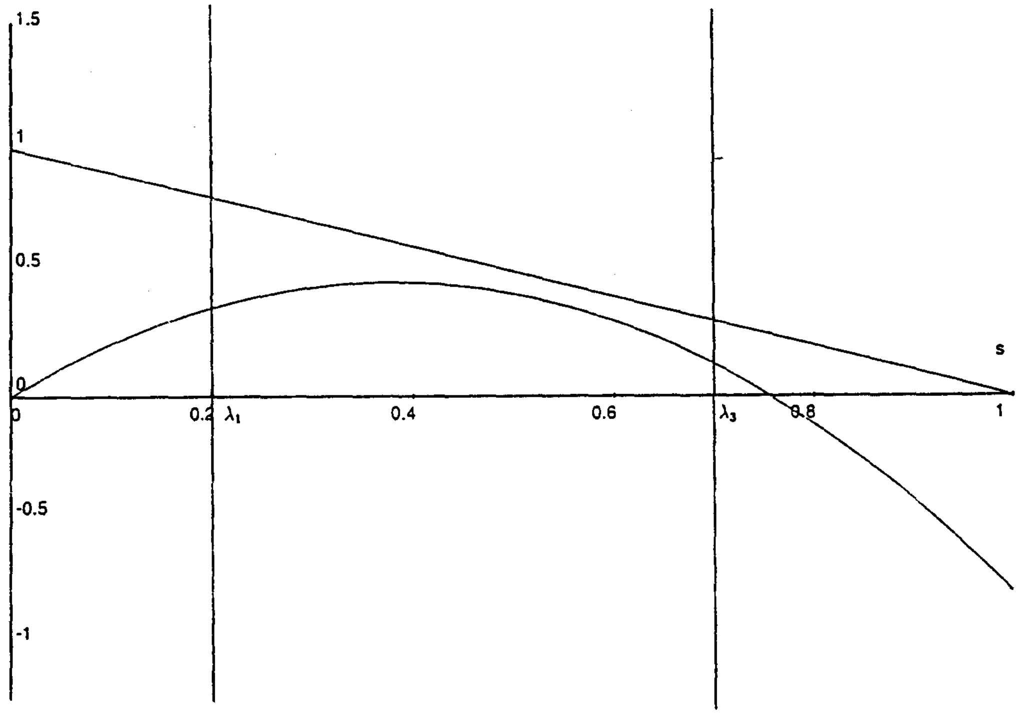

2
1
0
-1
-2
s
0
0.5
λ_1
1
1.5
λ_3
2
2.5
3

Fig. 6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1
0.5
0
-0.5
-1
s
0
0.2
λ_1
0.4
0.6
λ_3
0.8
1

Fig. 7

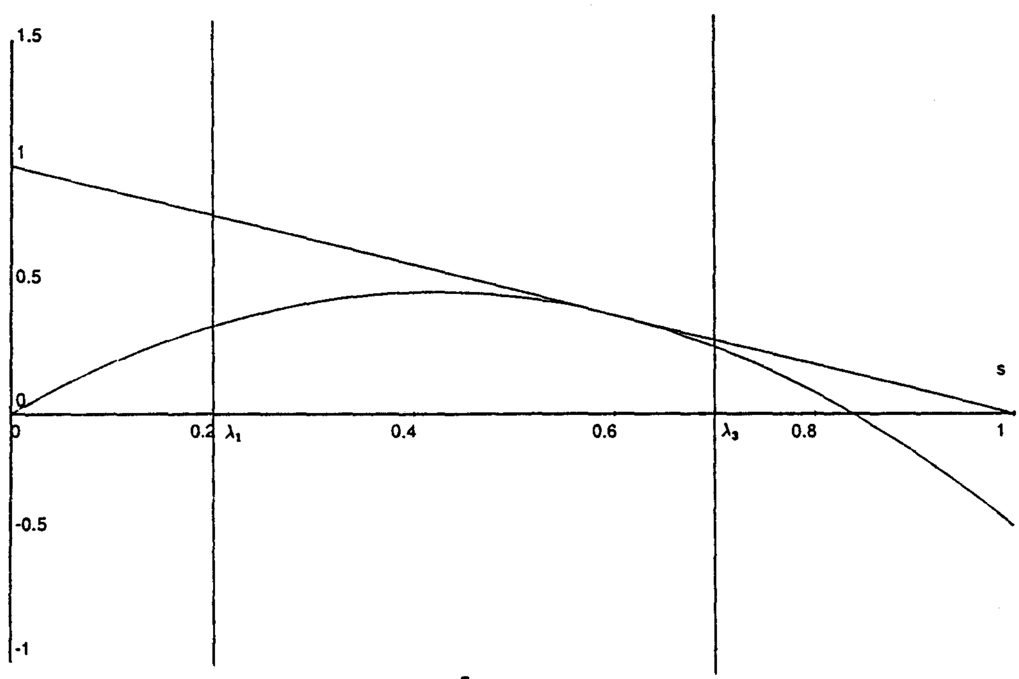
1.5
1
0.5
0
-0.5
-1
s
0
0.2
λ_1
0.4
0.6
λ_3
0.8
1

Fig. 8

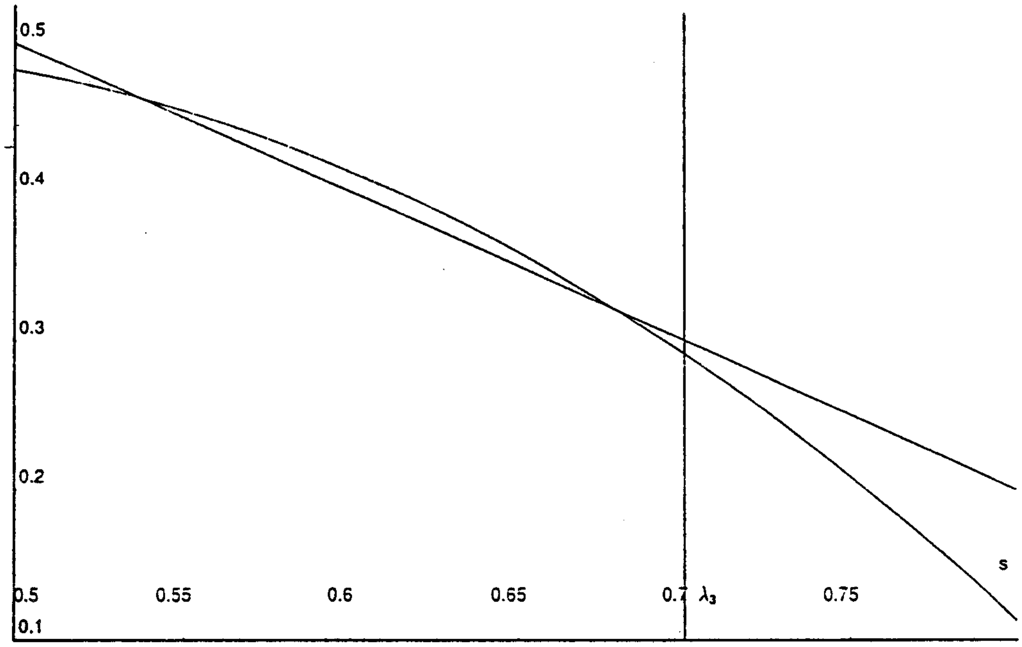
0.5
0.4
0.3
0.2
0.5
0.55
0.6
0.65
0.7
λ_3
0.75
s
0.1

Fig. 9

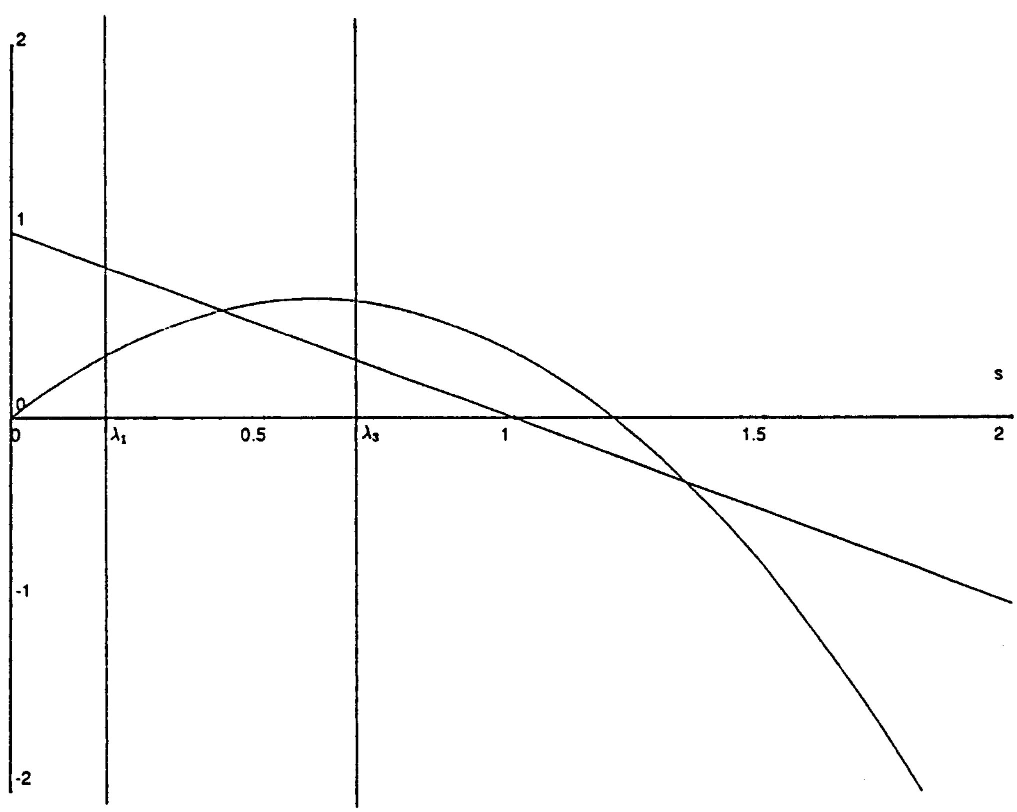
2
1
0
-1
-2
0
λ_1
0.5
λ_3
1
1.5
2
s

Fig. 10

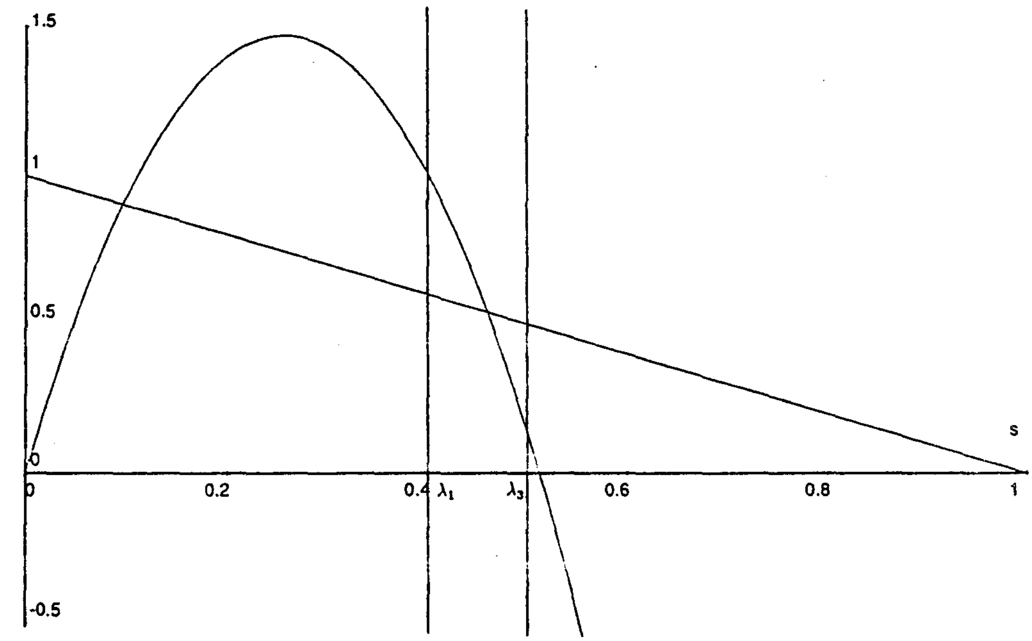
1.5
1
0.5
0
-0.5
0
0.2
0.4
λ_1
λ_3
0.6
0.8
1
s

Fig. 11

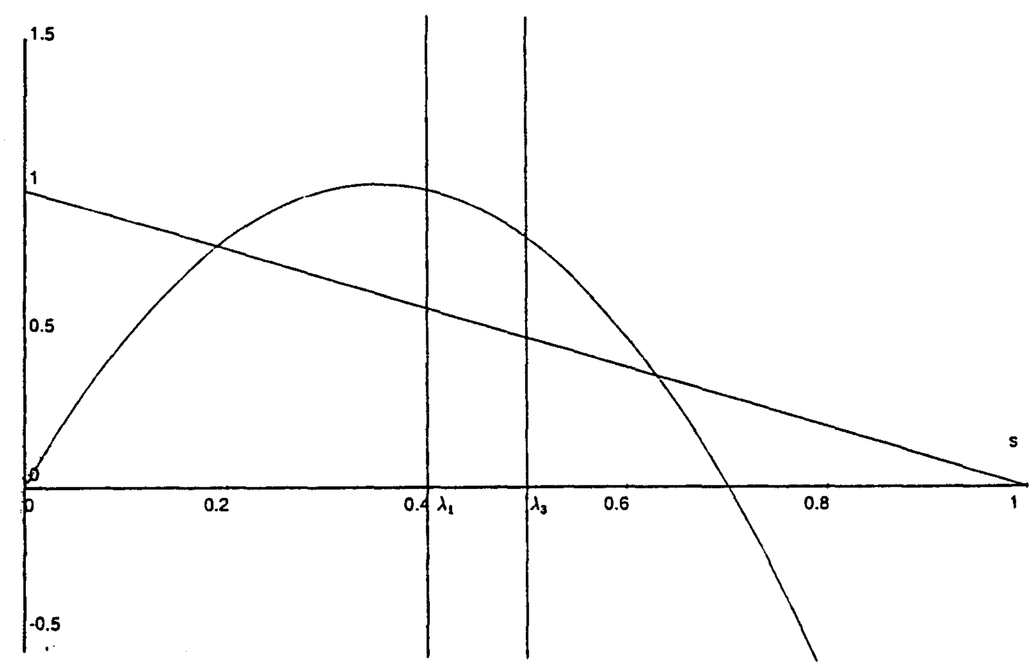
1.5
1
0.5
0
-0.5
0
0.2
0.4
λ_1
λ_3
0.6
0.8
1
s

Fig. 12

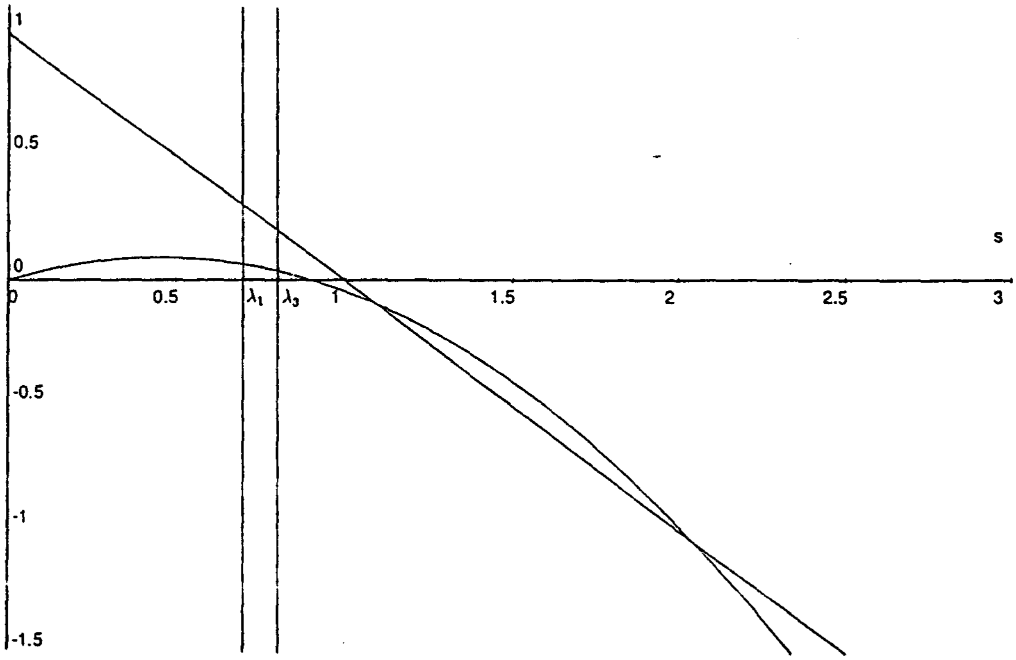
1
0.5
0
-0.5
-1
-1.5
s
0
0.5
λ_1
λ_3
1
1.5
2
2.5
3

Fig. 13

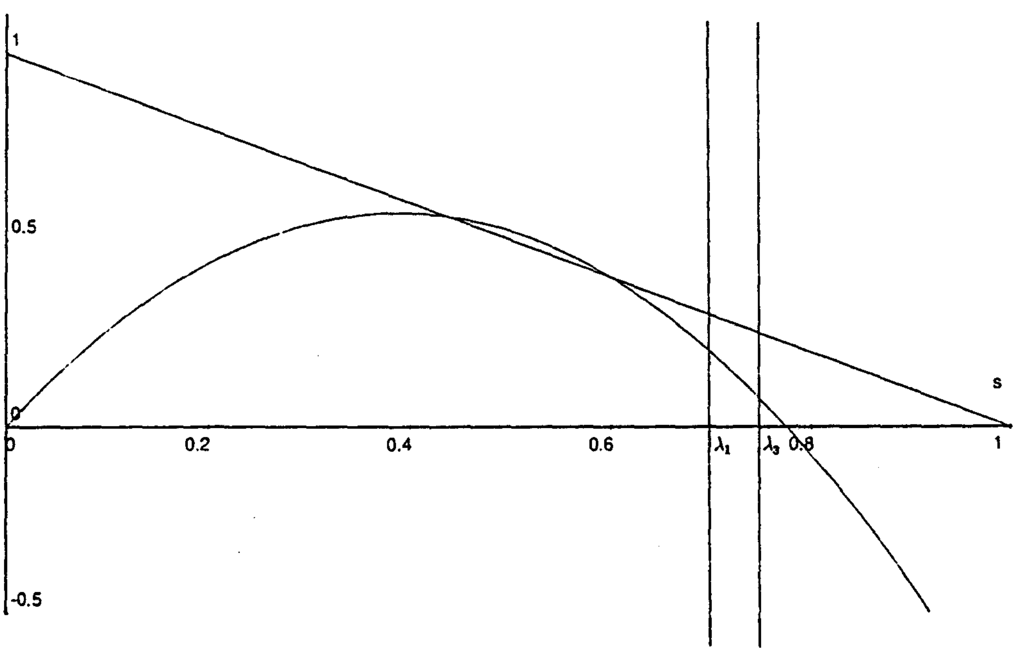
1
0.5
0
-0.5
s
0
0.2
0.4
0.6
λ_1
λ_3
0.8
1

Fig. 14

Appendix C

Linear Analysis of The Four Dimensional System (2.11)

C.1 Linear Analysis for General Response Functions

The variational matrix is:

$$V(S, x_1, x_2, y) =$$

$$\begin{pmatrix} D & -p_1(S) & -p_2(S) & -\frac{p_3(S)}{\gamma} \\ x_1 p_1'(S) & -1 + p_1(S) - yq'(x_1) & 0 & -q(x_1) \\ x_2 p_2'(S) & 0 & -1 + p_2(S) & 0 \\ yp_3'(S) & yq'(x_1) & 0 & -1 + p_3(S) + q(x_1) \end{pmatrix}$$

where $D = -1 - \sum_{i=1}^{2} x_i p_i'(S) - \frac{yp_3'(S)}{\gamma}$.

In the following sections we examine the local stability of each of the critical points $E_0, E_{\lambda_1}, E_{\lambda_2}, E_{\lambda_3}, E_{S^*} and \tilde{E}_{\lambda_2}$.

a.)

$$V(1, 0, 0, 0) =$$

$$\begin{pmatrix} -1 & -p_1(1) & -p_2(1) & -\frac{p_3(1)}{\gamma} \\ 0 & -1+p_1(1) & 0 & 0 \\ 0 & 0 & -1+p_2(1) & 0 \\ 0 & 0 & 0 & -1+p_3(1) \end{pmatrix}$$

Hence, the eigenvalues of the characteristic equation at E_0 are:

$$-1, -1+p_1(1), -1+p_2(1), -1+p_3(1).$$

It follows that E_0 is locally asymptotically stable provided that $\lambda_i > 1$ for $i = 1, 2, 3$ ($i.e. 1 < \lambda_1 < \lambda_2 < \lambda_3$). If for some λ_i, $\lambda_i < 1$ then E_0 is unstable.

b.)

$$V(\lambda_2, 0, 1-\lambda_2, 0) \;=$$

$$\begin{pmatrix} -1-(1-\lambda_2)p_2'(\lambda_2) & -p_1(\lambda_2) & -1 & -\frac{p_3(\lambda_2)}{\gamma} \\ 0 & -1+p_1(\lambda_2) & 0 & 0 \\ (1-\lambda_2)p_2'(\lambda_2) & 0 & 0 & 0 \\ 0 & 0 & 0 & -1+p_3(\lambda_2) \end{pmatrix}$$

Expanding $det(V - I_4\mu)$ along the fourth column we have, $det(V - I_4\mu) = 0$ if and only if:

$$\begin{gathered}(-1+p_3(\lambda_2)-\mu)(-1+p_1(\lambda_2)-\mu) \\ (\mu^2 + (1+(1-\lambda_2)p_2'(\lambda_2))\mu \; + (1-\lambda_2)p_2'(\lambda_2)) = 0 \quad .\end{gathered}$$

Hence, the eigenvalues of the characteristic equation at E_{λ_2} are:

$$-1, -(1-\lambda_2)p_2'(\lambda_2), -1+p_1(\lambda_2), -1+p_3(\lambda_2).$$

Since $-1+p_1(\lambda_2) > 0$, it follows that E_{λ_2} is always unstable.

Next, assume $\lambda_1 < 1$ so that E_{λ_1} is in the nonnegative (S, x_1, x_2, y)-cone.

c.)

$$V(\lambda_1, 1-\lambda_1, 0, 0) \;=$$

$$\begin{pmatrix} -1-(1-\lambda_1)p_1'(\lambda_1) & -1 & -p_2(\lambda_1) & -\frac{p_3(\lambda_1)}{\gamma} \\ (1-\lambda_1)p_1'(\lambda_1) & 0 & 0 & -q(1-\lambda_1) \\ 0 & 0 & -1+p_2(\lambda_1) & 0 \\ 0 & 0 & 0 & -1+p_3(\lambda_1)+q(1-\lambda_1) \end{pmatrix}$$

Expanding $det(V - I_4\mu)$ along the first column we have $det(V - I_4\mu) = 0$ if and only if:

$$(-1+p_2(\lambda_1)-\mu)(-1+p_3(\lambda_1)+\ q(1-\lambda_1)-\mu)$$
$$(\mu^2+(1+(1-\lambda_1)p_1'(\lambda_1))\mu+\ (1-\lambda_1)p_1'(\lambda_1))=0.$$

Hence, the eigenvalues of the characteristic equation at E_{λ_1} are:

$$-1, -(1-\lambda_1)p_1'(\lambda_1), -1+p_2(\lambda_1), -1+p_3(\lambda_1)+q(1-\lambda_1).$$

Since $\lambda_1 < \lambda_2 < \lambda_3$ and by monotinicity assumption (2.4) it follows that $-(1-\lambda_1)p_1'(\lambda_1) < 0$ and $-1+p_2(\lambda_1) < 0$. Thus, E_{λ_1} is locally asymptotically stable provided that $-1+p_3(\lambda_1)+q(1-\lambda_1) < 0$ and unstable if $-1+p_3(\lambda_1)+q(1-\lambda_1) > 0$.

Next, assume $\lambda_3 < 1$ so that E_{λ_3} is in the nonnegative (S, x_1, x_2, y)-cone.

d.)

$$V(\lambda_3, 0, 0, \gamma(1-\lambda_3)) =$$

$$\begin{pmatrix} -1-(1-\lambda_3)p_3'(\lambda_3) & -p_1(\lambda_3) & -p_2(\lambda_3) & -\frac{1}{\gamma} \\ 0 & -1+p_1(\lambda_3)-\gamma(1-\lambda_3)q(0) & 0 & 0 \\ 0 & 0 & -1+p_2(\lambda_3) & 0 \\ \gamma(1-\lambda_3)p_3'(\lambda_3) & \gamma(1-\lambda_3)q'(0) & 0 & 0 \end{pmatrix}$$

Expanding $det(V - I_4\mu)$ along the first column we have $det(V - I_4\mu) = 0$ if and only if:

$$(-1+p_2(\lambda_3)-\mu)(-1+p_1(\lambda_3)-\ \gamma(1-\lambda_3)q'(0)-\mu)$$
$$(\mu^2+(1+(1-\lambda_3)p_3'(\lambda_3))\mu\ +(1-\lambda_3)p_3'(\lambda_3))=0.$$

Hence, the eigenvalues of the characteristic equation at E_{λ_3} are:

$$-1, -(1-\lambda_3)p_3'(\lambda_3), -1+p_2(\lambda_3), -1+p_1(\lambda_3)-\gamma(1-\lambda_3)q'(0).$$

Since $-1+p_2(\lambda_3)>0$, it follows that E_{λ_3} is always unstable.

e.)

$$V(S^*, x_1^*, 0, y^*) =$$

$$\begin{pmatrix} -1-x_1^*p_1'(S^*)-\frac{y^*p_3'(S^*)}{\gamma} & -p_1(S^*) & -p_2(S^*) & -\frac{p_3(S^*)}{\gamma} \\ x_1^*p_1'(S^*) & -1+p_1(S^*)-y^*q'(x_1^*) & 0 & -q(x_1^*) \\ 0 & 0 & -1+p_2(S^*) & 0 \\ y^*p_3'(S^*) & y^*q'(x_1^*) & 0 & 0 \end{pmatrix}$$

Interchanging last two rows and last two columns of V gives

$$V(S^*, x_1^*, 0, y^*) =$$

$$\begin{pmatrix} -1-x_1^*p_1'(S^*)-\frac{y^*p_3'(S^*)}{\gamma} & -p_1(S^*) & -\frac{p_3(S^*)}{\gamma} & -p_2(S^*) \\ x_1^*p_1'(S^*) & -1+p_1(S^*)-y^*q'(x_1^*) & -q(x_1^*) & 0 \\ y^*p_3'(S^*) & y^*q'(x_1^*) & 0 & 0 \\ 0 & 0 & 0 & -1+p_2(S^*) \end{pmatrix}$$

Expanding $det(V-I_4\mu)$ along the last row we have $det(V-I_4\mu)=0$ if and only if:

$$\begin{aligned}(-1+p_2(S^*)-\mu)\{\mu^3+\mu^2((1-p_1(S^*)+y^*q'(x_1^*))+(1+x_1^*p_1'(S^*)+\tfrac{y^*p_3'(S^*)}{\gamma}))\\ +\mu((1-p_1(S^*)+y^*q'(x_1^*))(1+x_1^*p_1'(S^*)+\tfrac{y^*p_3'(S^*)}{\gamma})\\ +x_1^*p_1(S^*)p_1'(S^*)+\tfrac{y^*p_3(S^*)p_3'(S^*)}{\gamma}+y^*q(x_1^*)q'(x_1^*))\\ +\tfrac{y^*p_3(S^*)p_3'(S^*)(1-p_1(S^*)+y^*q'(x_1^*))}{\gamma}\\ +y^*q(x_1^*)q'(x_1^*)(1+x_1^*p_1'(S^*)+\tfrac{y^*p_3'(S^*)}{\gamma})\\ -y^*p_1(S^*)p_3'(S^*)q(x_1^*)+\tfrac{x_1^*y^*p_1'(S^*)p_3(S^*)q'(x_1^*)}{\gamma}\}=0.\end{aligned}$$

We assume $S^* \geq 0$ exists and $x_1^*, y^* \geq 0$, (i.e. $\lambda_1 \leq S^* \leq \lambda_3$), otherwise E_{S^*} does not lie in the nonnegative cone. Denote the coefficients in the characteristic equation by:

$$\begin{aligned}
a_3 &= \frac{y^* p_3(S^*) p_3'(S^*)\ (1 - p_1(S^*) + y^* q'(x_1^*))}{\gamma} + y^* q(x_1^*) q'(x_1^*)\ (1 + x_1^* p_1'(S^*) + \frac{y^* q'(x_1^*)}{\gamma}) \\
&- \ y^* p_1(S^*) p_3'(S^*) q(x_1^*)\ + \frac{x_1^* y^* p_1'(S^*) p_3(s^*)\ q'(x_1^*)}{\gamma} \\
a_2 &= (1 - p_1(S^*) + y^* q'(x_1^*))\ (1 + x_1^* p_1'(S^*) + \frac{y^* p_3'(S^*)}{\gamma}) \\
&+ \ x_1^* p_1(S^*) p_1'(S^*)\ + \frac{y^* p_3(S^*) p_3'(S^*)}{\gamma}\ + y^* q(x_1^*) q'(x_1^*) \\
a_1 &= (1 - p_1(S^*) + y^* q'(x_1^*))\ + (1 + x_1^* p_1'(S^*) + \frac{y^* p_3'(S^*)}{\gamma}) \\
a_0 &= 1
\end{aligned}$$

By the Routh-Hurwitz criteria, E_{S^*} is locally asymptotically stable provided

$$\begin{array}{rl}
(i) & S^* < \lambda_2 \\
(ii) & a_0 > 0,\ a_1 > 0,\ \text{and } a_3 > 0 \\
(iii) & a_1 a_2 - a_3 a_0 > 0,
\end{array}$$

and is unstable if any inequality in (i), (ii) or (iii) is changed.Note that $a_1 a_2 - a_3 a_0 > 0$ if and only if $a_2 > 0$.

f.)

$$V(\lambda_2, \tilde{x}_1, \tilde{x}_2, \tilde{y}) \ =$$

$$\begin{pmatrix}
-1 - \sum_{i=1}^{2} \tilde{x}_i p_i'(\lambda_2)\ -\frac{\tilde{y} p_3'(\lambda_2)}{\gamma} & -p_1(\lambda_2) & -1 & -\frac{p_3(\lambda_2)}{\gamma} \\
\tilde{x}_1 p_1'(\lambda_2) & -1 + p_1(\lambda_2) - \tilde{y} q'(\tilde{x}_1) & 0 & -q(\tilde{x}_1) \\
\tilde{x}_2 p_2'(\lambda_2) & 0 & 0 & 0 \\
\tilde{y} p_3'(\lambda_2) & \tilde{y} q'(\tilde{x}_1) & 0 & 0
\end{pmatrix}$$

Expanding $det(V - I_4 \mu)$ along the third row we have $det(V - I_4 \mu) = 0$ if and only if:

$$\tilde{x}_2 p_2'(\lambda_2) det M_{31} - \mu det M_{33} = 0$$

where,

$$M_{31} = \begin{pmatrix} -p_1(\lambda_2) & -1 & -\frac{p_3(\lambda_2)}{\gamma} \\ -1 + p_1(\lambda_2) - \tilde{y}q'(\tilde{x}_1) - \mu & 0 & -q(\tilde{x}_1) \\ \tilde{y}q'(\tilde{x}_1) & 0 & -\mu \end{pmatrix}$$

and

$$M_{33} = \begin{pmatrix} -1 - \sum_{i=1}^{2} \tilde{x}_i p_i'(\lambda_2) - \frac{\tilde{y}p_3'(\lambda_2)}{\gamma} - \mu & -p_1(\lambda_2) & -\frac{p_3(\lambda_2)}{\gamma} \\ \tilde{x}_1 p_1'(\lambda_2) & -1 + p_1(\lambda_2) - \tilde{y}q'(\tilde{x}_1) - \mu & -q(\tilde{x}_1) \\ \tilde{y}p_3'(\lambda_2) & \tilde{y}q'(\tilde{x}_1) & -\mu \end{pmatrix}$$

which implies,

$$det(M_{31}) = \tilde{y}q(\tilde{x}_1)q'(\tilde{x}_1) - \mu\ (-1 + p_1(\lambda_2) - \tilde{y}q'(\tilde{x}_1) - \mu)$$

and,

$$\begin{aligned} -det M_{33} &= \mu^3 + \mu^2\{(1 - p_1(\lambda_2) + \tilde{y}\ q'(\tilde{x}_1)) + (1 + \sum_{i=1}^{2} \tilde{x}_i p_i'\ (\lambda_2) + \frac{\tilde{y}p_3'(\lambda_2)}{\gamma}\} \\ &+ \mu\{(1 - p_1(\lambda_2) + \tilde{y}q'(\tilde{x}_1)\ (1 + \sum_{i=1}^{2} \tilde{x}_i p_i'(\lambda_2)\ + \frac{\tilde{y}p_3'(\lambda_2)}{\gamma}) \\ &+ \tilde{x}_1 p_1(\lambda_2) p_1'(\lambda_2)\ + \frac{\tilde{y}p_3(\lambda_2)p_3'(\lambda_2)}{\gamma}\ + \tilde{y}q(\tilde{x}_1)q'(\tilde{x}_1)\} \\ &+ \frac{\tilde{y}p_3(\lambda_2)p_3'(\lambda_2)}{\gamma}\ (1 - p_1(\lambda_2) + \tilde{y}q'(\tilde{x}_1)) \\ &+ \tilde{y}q(\tilde{x}_1)q'(\tilde{x}_1)\ (1 + \sum_{i=1}^{2} \tilde{x}_i p_i'(\lambda_2) + \frac{\tilde{y}p_3'(\lambda_2)}{\gamma}) \\ &+ \frac{\tilde{x}_1 \tilde{y} p_1'(\lambda_2)\ p_3(\lambda_2) q'(\tilde{x}_1)}{\gamma} \\ &- \tilde{y}p_1(\lambda_2)p_3'(\lambda_2)\ q(\tilde{x}_1). \end{aligned}$$

Hence,

$$\tilde{x}_2 p_2'(\lambda_2) det M_{31} - \mu det M_{33} = 0$$

if and only if

$$\mu^4 + \mu^3\{(1 - p_1(\lambda_2) + \tilde{y}\ q'(\tilde{x}_1)) + (1 + \sum_{i=1}^{2} \tilde{x}_i\ p_i'(\lambda_2) + \frac{\tilde{y}\ p_3'(\lambda_2)}{\gamma}\}$$
$$+\mu^2\{(1 - p_1(\lambda_2) + \tilde{y}\ q'(\tilde{x}_1))(1 + \sum_{i=1}^{2} \tilde{x}_i\ p_i'(\lambda_2) + \frac{\tilde{y}\ p_3'(\lambda_2)}{\gamma}) + \tilde{x}_1\ p_1(\lambda_2)p_1'(\lambda_2)$$
$$+\frac{\tilde{y}p_3(\lambda_2)p_3'(\lambda_2)}{\gamma} + \tilde{y}q(\tilde{x}_1)q'(\tilde{x}_1) + \tilde{x}_2 p_2'(\lambda_2)\}$$
$$+\mu\{\frac{\tilde{y}p_3(\lambda_2)p_3'\ (\lambda_2)}{\gamma}(1 - p_1(\lambda_2) + \tilde{y}\ q'(\tilde{x}_1)) + \tilde{y}q(\tilde{x}_1)\ q'(\tilde{x}_1)(1 + \sum_{i=1}^{2} \tilde{x}_i\ p_i'(\lambda_2) + \frac{\tilde{y}p_3'\ (\lambda_2)}{\gamma})$$
$$+\frac{\tilde{x}_1\tilde{y}p_1'(\lambda_2)\ p_3(\lambda_2)q'(\tilde{x}_1)}{\gamma} + \tilde{x}_2p_2'(\lambda_2)(1 - p_1(\lambda_2) + \tilde{y}q'(\tilde{x}_1)) - \tilde{y}p_1(\lambda_2)\ p_3'(\lambda_2)q(\tilde{x}_1)\}$$
$$+\tilde{x}_2\tilde{y}p_2'(\lambda_2)\ q(\tilde{x}_1)q'(\tilde{x}_1) = 0$$

We assume that $\tilde{x}_2 \geq 0$, otherwise $\tilde{E}_{\ \lambda_2}$ does not lie in the nonnegative cone. Denote the coefficients in the characteristic equation by:

$$\begin{aligned}
a_4 &= \tilde{x}_2\tilde{y}p_2'(\lambda_2)\ q(\tilde{x}_2)q'(\tilde{x}_2) \\
a_3 &= \frac{\tilde{y}p_3(\lambda_2)\ p_3'(\lambda_3)}{\gamma}(1 - p_1(\lambda_2) + \tilde{y}q'(\tilde{x}_1)) \\
&\quad +\tilde{y}q(\tilde{x}_1)q'(\tilde{x}_1)\ (1 + \sum_{i=1}^{2} \tilde{x}_i p_i'(\lambda_2) + \frac{\tilde{y}p_3'(\lambda_2)}{\gamma}) + \frac{\tilde{x}_1\tilde{y}p_1'(\lambda_2)\ p_3(\lambda_2)q'(\tilde{x}_1)}{\gamma} \\
&\quad +\tilde{x}_2p_2'(\lambda_2)\ (1 - p_1(\lambda_2) + \tilde{y}q'(\tilde{x}_1)) - \tilde{y}p_1(\lambda_2)p_3'(\lambda_2)\ q(\tilde{x}_1) \\
a_2 &= (1 - p_1(\lambda_2) + \tilde{y}q'(\tilde{x}_1))\ (1 + \sum_{i=1}^{2} \tilde{x}_i p_i'(\lambda_2) + \frac{\tilde{y}p_3'(\lambda_2)}{\gamma}) \\
&\quad +\tilde{x}_1p_1(\lambda_2)p_1'(\lambda_2) + \frac{\tilde{y}p_3(\lambda_2)p_3'\ (\lambda_2)}{\gamma} + \tilde{y}q(\tilde{x}_1)\ q'(\tilde{x}_1) + \tilde{x}_2p_2'(\lambda_2) \\
a_1 &= (1 - p_1(\lambda_2) + \tilde{y}q'(\tilde{x}_1)) + (1 + \sum_{i=1}^{2} \tilde{x}_i p_i'(\lambda_2) + \frac{\tilde{y}p_3'(\lambda_2)}{\gamma}) \\
a_0 &= 1
\end{aligned}$$

By the Routh-Hurwitz criteria, $\tilde{E}_{\lambda_2}$ is locally asymptotically stable provided

$$(i) \qquad a_0 > 0,\ a_1 > 0,\ \text{and}\ a_4 > 0$$

$$(ii) \qquad a_1a_2 - a_3a_0 > 0$$
$$(iii) \qquad a_3(a_1a_2 - a_3a_0) - a_4a_1^2 > 0$$

and is unstable if any inequality in $(i),(ii)$ or (iii) is changed. Note that condition (ii) is true if and only if $a_2 > 0$ which in turn implies that condition (iii) is true if and only if $a_3 > 0$. Note also that E_{S^*} and $\tilde{E}_{\lambda_2}$ coalesce when $\tilde{x}_2 = 0$. In this case the conditions for local asymptotic stability for $\tilde{E}_{\lambda_2}$ and E_{S^*} are the same. Hence if the conditions for local asymptotic stability of E_{S^*} hold as E_{S^*} and $\tilde{E}_{\lambda_2}$ coalesce, then $\tilde{E}_{\lambda_2}$ is at least initially locally asymptotically stable.

C.2 Linear Analysis for Lotka-Volterra Response Functions

If $p_i(S) = \frac{S}{\lambda_i}$, $i = 1, 2, 3$ and $q(x_1) = \frac{x_1}{\delta}$, $\gamma = 1$, then the local asymptotic stability analysis of the critical points of system (1.11) is simplified to the following:

The eigenvalues of E_0 are:

$$-1, \quad -1 + \frac{S}{\lambda_i} \text{ for } i = 1, 2, 3.$$

Hence, E_0 is locally asymptotically stable if $\lambda_i > 1$ for $i = 1, 2, 3$.
The eigenvalues of E_{λ_2} are:

$$-1, \quad -\frac{(1-\lambda_2)}{\lambda_2}, \quad -1 + \frac{\lambda_2}{\lambda_1}, \quad -1 + \frac{\lambda_2}{\lambda_3}.$$

Hence, E_{λ_2} is always unstable since $\lambda_1 < \lambda_2$.
The eigenvalues of E_{λ_3} are:

$$-1, \quad -\frac{(1-\lambda_3)}{\lambda_3}, \quad -1 + \frac{\lambda_3}{\lambda_1} - \frac{(1-\lambda_3)}{\delta}, \quad -1 + \frac{\lambda_3}{\lambda_2}.$$

Hence, E_{λ_3} is always unstable since $\lambda_2 < \lambda_3$.
The eigenvalues of E_{λ_1} are:

$$-1, \quad -\frac{(1-\lambda_1)}{\lambda_1}, \quad -1 + \frac{\lambda_1}{\lambda_2}, \quad -1 + \frac{\lambda_1}{\lambda_3} + \frac{1-\lambda_1}{\delta}.$$

Hence, E_{λ_1} is locally asymptotically stable if $\lambda_1 < 1$ (i.e. E_{λ_1} lies in the nonnegative cone), and $-1 + \frac{\lambda_1}{\lambda_3} + \frac{1-\lambda_1}{\delta} < 0$.
For E_{S^*} we have:

$$S^* = \frac{\lambda_1\lambda_3}{\lambda_1\lambda_3 + \delta(\lambda_3 - \lambda_1)}, \; x_1^* = \delta(1 - \frac{S^*}{\lambda_3}), \; y^* = \delta(-1 + \frac{S^*}{\lambda_1}) \text{ and } x_2^* = 0.$$

Thus E_{S^*} is unique and lies in the nonnegative cone provided $\lambda_1 \leq S^* \leq \lambda_3$. The corresponding charateristic equation is given by:

$$\begin{gathered}(-1 + \tfrac{S^*}{\lambda_2} - \mu)\{\mu^3 + \mu^2(1 + \tfrac{x_1^*}{\lambda_1} + \tfrac{y^*}{\lambda_3}) \\ +\mu(\tfrac{x_1^* S^*}{\lambda_1^2} + \tfrac{y^* S^*}{\lambda_3^2} + \tfrac{x_1^* y^*}{\delta^2}) + \tfrac{x_1^* y^*}{\delta^2}(1 + \tfrac{x_1^*}{\lambda_1} + \tfrac{y^*}{\lambda_3})\} = 0.\end{gathered}$$

Hence, by Routh-Hurwitz criteria, E_{S^*} is locally asymptotically stable if $S^* < \lambda_2$.
For $\tilde{E}_{\lambda_2}$ we have:

$$\tilde{S} = \lambda_2, \; \tilde{x}_1 = \delta(1 - \frac{\lambda_2}{\lambda_3}), \; \tilde{x}_2 = 1 - \lambda_2 - \delta\lambda_2\frac{(\lambda_3 - \lambda_1)}{\lambda_1\lambda_3}, \text{ and } \tilde{y} = \delta(-1 + \frac{\lambda_2}{\lambda_1}).$$

Thus $\tilde{E}_{\lambda_2}$ is unique and lies in the nonnegative cone provided $\tilde{x}_2 \geq 0$. The corresponding charateristic equation is given by:

$$\begin{gathered}\mu^4 + \mu^3(1 + \tfrac{\tilde{x}_1}{\lambda_1} + \tfrac{\tilde{x}_2}{\lambda_2} + \tfrac{\tilde{y}}{\lambda_3}) + \mu^2(\tfrac{\tilde{x}_1\lambda_2}{\lambda_1^2} + \tfrac{\tilde{y}\lambda_2}{\lambda_3^2} + \tfrac{\tilde{x}}{\lambda_2} + \tfrac{\tilde{y}\tilde{x}_1}{\delta^2}) \\ +\mu(1 + \tfrac{\tilde{x}_1}{\lambda_1} + \tfrac{\tilde{x}_2}{\lambda_2} + \tfrac{\tilde{y}}{\lambda_3}) + \tfrac{\tilde{x}_1\tilde{x}_2\tilde{y}}{\delta^2\lambda_2} = 0.\end{gathered}$$

Hence, by the Routh-Hurwitz criteria $\tilde{E}_{\lambda_2}$ is locally asymptotically stable provided it exists (i.e. $\tilde{x}_2 \geq 0$).
Finally note that simple algebraic manipulations give us:

$$\begin{gathered}\lambda_1 < S^* \text{ if and only if } -1 + \tfrac{\lambda_1}{\lambda_3} + \tfrac{(1-\lambda_1)}{\delta} > 0, \\ S^* < \lambda_2 \text{ if and only if } \tilde{x}_2 = 1 - \lambda_2 - \delta\lambda_2\tfrac{(\lambda_3-\lambda_1)}{\lambda_1\lambda_3} < 0, \\ S^* < \lambda_3 \text{ if and only if } -1 + \tfrac{\lambda_3}{\lambda_1} - \tfrac{(1-\lambda_3)}{\delta} > 0.\end{gathered}$$

Appendix D

Linear Analysis of Food Web (4.1)

D.1 Linear Analysis for General Response Functions

The variational matrix is :

$$V(S,x_1,y) =$$

$$\begin{pmatrix} -1-x_1p_1'(S)-\frac{y}{\gamma}p_3'(S) & -p_1(S) & -\frac{1}{\gamma}p_3(S) \\ x_1p_1'(S) & -1+p_1(S)-yq'(x_1) & -q(x_1) \\ yp_3'(S) & yq'(x_1) & -1+p_3(S)+q(x_1) \end{pmatrix}$$

The eigenvalues of E_0^3 are:

$$-1, \ -1+p_1(1), \ -1+p_3(1).$$

Hence, E_0^3 is locally asymptotically stable if $1 < \lambda_1 < \lambda_3$.
The eigenvalues of $E_{\lambda_1}^3$ are:

$$-1, \ -(1-\lambda_1)p_1'(\lambda_1), \ -1+p_3(\lambda_1)+q(1-\lambda_1).$$

Hence, $E_{\lambda_1}^3$ is locally asymptotically stable if $\lambda_1 < 1$ (i.e. $E_{\lambda_1}^3$ lies in the non-negative cone), and $-1+p_3(\lambda_1)+q(1-\lambda_1) < 0$.
For $E_{S^*}^3$ we have:

$$x_1^* = q^{-1}(1-p_3(S^*)), \ y^* = \frac{x_1^*(-1+p_1(S^*))}{(1-p_3(S^*))}$$

where S^* must satisfy

$$1 - S^* = x_1^* p_1(S^*) + \frac{y^* p_3(S^*)}{\gamma}.$$

Thus $E^3_{S^*}$ (which may or may not be unique in this case) lies in the non-negative cone provided it exists and $\lambda_1 < S^* < \lambda_3$. The corresponding characteristic equation is given by

$$\mu^3 + A_1\mu^2 + A_2\mu + A_3 = 0$$

where,

$$\begin{aligned}
A_1 &= (1 - p_1(S^*) + y^* q'(x_1^*)) + (1 + x_1^* p_1'(S^*) + \frac{y^* p_3'(S^*)}{\gamma}) \\
A_2 &= (1 - p_1(S^*) + y^* q'(x_1^*))(1 + x_1^* p_1'(S^*) + \frac{y^* p_3'(S^*)}{\gamma}) \\
&+ x_1^* p_1(S^*) p_1'(S^*) + \frac{y^* p_3(S^*) p_3'(S^*)}{\gamma} + y^* q(x_1^*) q'(x_1^*) \\
A_3 &= \frac{y^* p_3(S^*) p_3'(S^*)(1 - p_1(S^*) + y^* q'(x_1^*))}{\gamma} - y^* p_1(S^*) p_3'(S^*) q(x_1^*) \\
&+ y^* q(x_1^*) q'(x_1^*)(1 + x_1^* p_1'(S^*) + \frac{y^* p_3'(S^*)}{\gamma}) + \frac{x_1^* y^* p_1'(S^*) p_3(S^*) q'(x_1^*)}{\gamma}.
\end{aligned}$$

Hence, by the Routh-Hurwitz criteria, $E^3_{S^*}$ is locally asymptotically stable if $A_i > 0$ for $i = 1, 2, 3$ and $A_1A_2 - A_3 > 0$.

The eigenvalues of $E^3_{\lambda_3}$ are:

$$-1, \; -(1 - \lambda_3)p_3'(\lambda_3), \; -1 + p_1(\lambda_3) - \gamma(1 - \lambda_3)q'(0).$$

Hence, $E^3_{\lambda_3}$ is locally asymptotically stable if $\lambda_3 < 1$ (i.e. $E^3_{\lambda_3}$ lies in the non-negative cone), and $-1 + p_1(\lambda_3) - \gamma(1 - \lambda_3)q'(0) < 0$.

D.2 Linear Analysis for Lotka-Volterra Response Functions

If $p_1(S) = \frac{S}{\lambda_1}$, $p_3(S) = \frac{S}{\lambda_3}$ and $q(x_1) = \frac{x_1}{\delta}$ then the local analysis for $E^3_{S^*}$ is simplified considerably. That is,

$$x_1^* = \delta(1 - \frac{S^*}{\lambda_3}), \; y^* = \delta(-1 + \frac{S^*}{\lambda_1})$$

and S^* must satisfy

$$1 - S^* = \frac{\delta}{\gamma\lambda_1\lambda_3}\{(1-\gamma)S^{*^2} + (\gamma\lambda_3 - \lambda_1)S^*\}.$$

This implies that

$$S^* = \frac{-b_1 \pm \sqrt{b_1^2 + b_2}}{b_3}$$

where,

$$\begin{aligned} b_1 &= \frac{1}{\lambda_1} - \frac{1}{\gamma\lambda_3} + \frac{1}{\delta} \\ b_2 &= \frac{4(1-\gamma)}{\gamma\delta\lambda_1\lambda_3} \\ b_3 &= \frac{2(1-\gamma)}{\gamma\lambda_1\lambda_3} \end{aligned}$$

Also the Routh-Hurwitz criteria simplifies to showing that

$$A_1A_2 - A_3 = (1 + \frac{x_1^*}{\lambda_1} + \frac{y^*}{\gamma\lambda_3})(\frac{S^*x_1^*}{\lambda_1^2} + \frac{S^*y^*}{\gamma\lambda_3^2}) - \frac{x_1^*y^*S^*}{\delta\lambda_1\lambda_3}(\frac{1}{\gamma} - 1)$$

is strictly greater than zero and

$$A_3 = \frac{x_1^*y^*}{\delta^2}(1 + \frac{x_1^*}{\lambda_1} + \frac{y^*}{\gamma\lambda_3} + \frac{S^*\delta}{\lambda_1\lambda_3}(\frac{1}{\gamma} - 1))$$

is also strictly greater than zero.

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