

# INAUGURAL-DISSERTATION

zur

Erlangung der Doktorwürde

der

Naturwissenschaftlich-Mathematischen Gesamtfakultät

der

RUPRECHT-KARLS-UNIVERSITÄT

HEIDELBERG

vorgelegt von

**Diplom-Mathematikerin Adela Tambulea**

aus Cluj-Napoca, Rumänien

Tag der mündlichen Prüfung: **23. 12. 2005**



# Competition and Persistence of Microorganisms in the Gradostat

Gutachter: **Prof. Dr. Dr. h. c. mult. Willi Jäger**

**Prof. Dr. Dr. h. c. Hans Georg Bock**





## Abstract

In the present thesis we give some answers to the question of which species of microorganisms can coexist and which can not in a spacial heterogeneous environment, called a **gradostat**. The dynamics of  $m$  species in  $n$  gradostat vessels is described by a system of  $n \times m$  ordinary differential equations. Using the results on the coexistence of two species, with the aid of the method of lower and upper solutions for systems with quasimonotone reaction terms, we are able to give general sufficient conditions for the persistence of  $n$  species in  $m$  vessels.

For the case of 3 species, we are able to improve these conditions and construct a positively invariant region corresponding to each species concentration remaining strictly positive. For this we first look for conditions a species would need to fulfill in order to survive when introduced into a gradostat already containing two species at two-species persistent equilibrium concentration levels. Moreover, through a bifurcation analysis we can partially describe the region in the parameter space corresponding to persistence, and give numerous numerical examples of coexistence when our sufficient persistence conditions are fulfilled.

## Zusammenfassung

In der vorliegenden Arbeit geben wir ein paar Antworten auf die Frage welche Mikroorganismen in einer räumlich heterogenen Umgebung, genannt **Gradostat**, koexistieren können und welche nicht. Die Dynamik von  $m$  Spezies in  $n$  Gradostat-Gefäßen wird beschrieben durch ein System von  $n \times m$  gewöhnlichen Differentialgleichungen. Aufbauend auf den Ergebnissen für Koexistenz von zwei Spezies, unter Zuhilfenahme der Methode der unteren und oberen Lösungen für Systeme mit quasimonotonen Reaktionstermen, sind wir in der Lage allgemein ausreichende Bedingungen für die Persistenz von  $n$  Spezies in  $m$  Gefäßen zu finden.

Für den Fall von 3 Spezies können wir diese Bedingungen verbessern und ein positiv invariantes Gebiet erzeugen, in dem die Konzentration jeder Spezies strikt positiv bleibt. Dafür suchen wir zunächst Bedingungen die eine Spezies erfüllen müsste um in einem Gradostat zu Überleben, in welchem sich bereits zwei Spezies mit Konzentrationen entsprechend einem strikt positiven Zwei-Spezies Gleichgewicht befinden. Außerdem können wir durch eine Verzweigungsanalyse teilweise das Persistenz-Gebiet im Parameter-Raum beschreiben und zahlreiche numerischen Beispielen für Koexistenz finden, in denen unsere ausreichenden Bedingungen für die Persistenz erfüllt sind.



## Acknowledgements

The work at this thesis has been partially financed by SFB 359 *Reaktive Strömungen, Diffusion und Transport*.

There are a lot of people I would like to thank for a variety of reasons.

Firstly, 'Thank you' Prof. Jäger, for the chance of working in applied mathematics, for proposing this topic, for all your ideas and suggestions, and for supporting me not only on a scientific level.

'Thank you' to my colleagues and - hopefully still for a long time - friends, for much of what I have learned during the past few years.

Finally 'Thank you' to my family and friends, wherever they are, and, most important of all, 'Thank you!' Christoph for everything.

Adela

Heidelberg, 11 October 2005



# Contents

<b>Introduction</b>	<b>1</b>
1. Competition and coexistence . . . . .	1
2. Industry and experiments . . . . .	3
3. Mathematical introduction . . . . .	4
4. Outline of the thesis . . . . .	6
 <b>1 The Gradostat</b>	 <b>9</b>
1.1 The model . . . . .	9
1.2 No competition . . . . .	14
1.3 Two species . . . . .	14
1.4 Three species . . . . .	17
1.5 $m$ species . . . . .	19
 <b>2 Persistence Results for the Gradostat</b>	 <b>21</b>
2.1 The system . . . . .	21
2.2 Definition of persistence . . . . .	22
2.3 A pair of lower and upper solutions . . . . .	23
2.4 A measure for the "fitness" of each competitor . . . . .	23
2.5 One species: bifurcation diagrams . . . . .	27
2.6 Competition . . . . .	37
2.7 Two species: persistence and existence of positive equilibria . . . . .	43
2.8 Two species: bifurcation diagrams . . . . .	46
2.9 Notes and discussions . . . . .	58
 <b>3 Three species</b>	 <b>59</b>
3.1 The system . . . . .	59
3.2 Invasion of a persistent two-species system . . . . .	63
3.3 Further invariant regions . . . . .	68

3.4	Some examples . . . . .	77
3.5	Bifurcation diagrams . . . . .	84
3.6	Three-species persistence . . . . .	107
3.7	The number of vessels . . . . .	112
3.8	Notes and comments . . . . .	116
<b>Conclusions</b>		<b>116</b>
<b>Appendix</b>		<b>121</b>
<b>A</b>	<b>Lower and upper solutions and quasimonotone functions</b>	<b>121</b>
A.1	Quasimonotone reaction terms . . . . .	121
A.2	Lower and upper solutions . . . . .	122
A.3	Monotone schemes . . . . .	124
A.4	Existence comparison theorems for the time dependent problem . . . . .	128
A.5	Lower and upper solutions and existence comparison theorems for the steady state problem . . . . .	131
A.6	Stability and asymptotic behavior of solutions . . . . .	135
A.7	Notes and discussions. Bibliographical comments . . . . .	139
<b>B</b>	<b>Bifurcation from Simple Eigenvalues</b>	<b>141</b>
B.1	M. Crandall and P. Rabinowitz ([CR1], [CR2]) . . . . .	141
B.2	E. N. Dancer ([Dan]) . . . . .	142
<b>C</b>	<b>Further Tools</b>	<b>143</b>
C.1	Quasipositive matrices . . . . .	143
C.2	Differential inequalities . . . . .	144
C.3	Monotone systems . . . . .	146
<b>D</b>	<b>Numerical tools</b>	<b>149</b>
D.1	Continuation of solutions . . . . .	149
D.2	Detection of bifurcation points and branch switching . . . . .	151
D.3	Operating diagrams . . . . .	152
<b>References</b>		<b>153</b>

# Introduction

The questions of which species survive and which do not in a certain environment is an intriguing one in ecology. In the present work we give some answers to this question by taking a look at the possibility of persistence as well as invadability of a community in the gradostat, which is a laboratory system with the aid of which we can study the effect of spacial heterogeneity on the outcome of *competition*.

## 1. Competition and coexistence

Microbial populations interact between one another in a number of different ways. Different species inhabiting a common environment are said to *compete purely* and *simply* when there is no other interaction among them and competition occurs for a single nutrient, for which the limited availability exerts a dynamical effect on the growth of each of the species involved. Even though simple and pure competition is not realistic enough to represent an actual ecosystem, it has been widely studied as a consequence of Hardin's ([Har1]) "competitive exclusion principle" which states that only one population should eventually persist on one resource, contested later by Hutchinson ([Hut]) in his "paradox of the plankton" according to which, even though positive equilibria might really correspond to the persistence of only one species, equilibria "should not be expected due to temporal variations in the prevailing conditions". In addition to Hutchinson's hypothesis of temporal heterogeneity as a cause for coexistence, Richerson et al. ([RAG]) suggest that the diversity is due rather to spacial heterogeneity, as they observed formation of patches allowing the simultaneous exploitation of a habitat by many species.

An important tool for studying exploitative competition is the *chemostat*, a basic piece of laboratory apparatus. It consists of a culture vessel into which growth medium is continuously added from a reservoir, together with nutrients, and from which a mixture containing the medium, microorganisms, and unused nutrients are continuously removed. The input contains all nutrients necessary for growth in excess of demand, except for one, which has a growth limiting effect. Experiments in an ideal chemostat ([HH], [Jan]) having time-invariant inputs, for a given set of conditions (all growth affecting factors like input concentration, dilution rate, temperature, pH, etc.), confirmed Hardin's principle for simple and pure competition for a not biologically renewable resource (i.e. not "produced" within the environment by a population not involved in the competition, for example a growing prey population). These led to the development of mathematical theories by, among others, Hsu,

and Waltman ([Hsu], [HHW]), according to which the competitive exclusion holds for an homogeneous - spatially and temporally - environment.

Coexistence in the chemostat in an homogeneous environment has been shown to occur for example for biologically renewable resources by Butler, Hsu and Waltman ([BHW], [Koc]): a prey-predator model in which pure and simple competitors (for the same prey), members a food chain or food web, can coexist in an oscillatory state (limit cycle). Another situation in which coexistence occurs is the presence of an inhibitor, produced by one of the species as an anticompetitor agent, or as an external toxin (pollutant) introduced together with the nutrient and either having a lethal effect on some species or affecting its nutrient uptake (or its growth) while being taken up by some other species without any ill effect (detoxification). In this case as well coexistence can occur in the form of oscillations. For a survey of models for competition in the presence of inhibition see Hsu and Waltman ([HW]).

Regarding the temporal heterogeneity, Butler, Hsu, Waltman, Smith showed coexistence (again as oscillations) in a number of theoretical studies in which the environment has been modeled as a periodically run chemostat: for example by changing the pH, the dilution rate or the input nutrient concentration in a cyclic mode ([HS1], [Smi3], [DS]).

For a spatial heterogeneous environment, with constant inputs, models for chemostats with wall attachment for example, have resulted in coexistence as a stable state ([BF]).

Spatial heterogeneities can also be created using interconnected reactors connected in both directions, known under the name of *gradostats*. The purpose of a gradostat is to create an environment with a nutrient gradient, as growth along nutrient gradients occurs in abundance in nature, for example in the case of growth along the banks of a stream or along a seacoast. By supplying seawater to one end and freshwater to the other end, a gradostat can be used to simulate an estuary. Flow in both directions can be regulated to represent tides. Cooper and Copeland ([CC]) used an experimental model very similar to the gradostat to study the effect of pollution on the structure of an estuarine planktonic community.

In a loose sense the apparatus generates a discrete gradient, and if there is no consumption, the nutrient concentrations will arrange themselves as discrete points along a linear gradient. The study of only one species in a gradostat by Tang ([Tan]) has suggested that it is easier for a species to survive in a gradostat than it is in the chemostat. Pure and simple competition between two species in two-vessel gradostats has been numerically and theoretically investigated by Jäger, So, Tang, and Waltman in a number of studies ([JSTW], [HS3]) which have shown that coexistence as a steady state is possible. Moreover, when Monod kinetics is assumed for the uptake of nutrient, the positive steady state can be shown to be unique and a global attractor. The case of two species in  $n$  vessels connected together in a wide variety of ways and using arbitrary monotone uptake functions has also been studied by Smith, Tang and Waltman ([STW]). Coexistence occurs again as a steady state,



although its uniqueness was no longer shown. Coexistence occurs provided that each population can successfully invade its rival's single-population equilibrium. In [HS3], a matrix of inter-vessel communications is constructed with the aid of which an unstable positive rest point exists.

Further insight into the dynamics of two species in  $n$  vessels comes with [Smi4] where Smith looks at the distribution of concentrations of each species at equilibria. As the equilibria cannot be explicitly calculated, the problem is approached by considering a continuum limit as the number of vessels approaches infinity.

In [JST] Jäger, Smith, and Tang showed that coexistence for all the species is not possible when the number of vessels is smaller than the number of species. Otherwise very little has been rigorously established concerning competition between more than two species in a gradostat.

The main aim of this work is to obtain persistence results for more than two species. For the competition of three species in  $n$  vessels we are able to give a quite detailed description of the dynamics, followed by numerous numerical examples which agree with our analytical predictions.

## 2. Industry and experiments

The literature corresponds to papers in mathematical as well as biological and chemical engineering journals. Other common names for the chemostat are "continuous culture" or "continuously stirred tank reactor".

From the engineering point of view as well as in industrial applications, the interest in the dynamics of competition is mainly due to the fact that contamination and mutations of a species transform initially pure cultures into mixed cultures. If a mixed culture is to be used in a continuous mode, the main questions are whether the interacting species can coexist and if it is possible to design reactors and operate them in such a way that coexistence (or, in some applications, washout) of certain species can occur.

The chemostat plays a central role, for example, in certain fermentation processes, particularly in the commercial production of metabolic byproducts by genetically altered organisms, like the production of insulin.

Another example is the biological treatment of industrial hazardous and toxic wastes. There are organic substances which cannot serve as energy sources for microorganisms, unless another organic substance is introduced into the environment which induces the production

of certain enzymes necessary for the decomposition or degradation of the organic waste. For example *p*-xylene can be metabolized only in the presence of toluene. We can have then a situation where a waste contains a number of pollutants which need to be cometabolized and a different microbial strain is needed for treating each of the polluting substances while a single additional substance can play the role of the substrate. The treatment could then be achieved in a pure and simple competition situation in a properly designed reactor or reactor configuration.

Further examples come from antibiotic production. It is common for one strain of bacteria to be affected by an antibiotic while another is resistant. The antibiotic acts as an inhibitor and we look for operating conditions such that the nonresistant strain can eliminate the resistant one due to competition. If it can't the antibiotic is not effective.

For the gradostat, the experimental data is rather scarce. In [CG] a 3-vessel gradostat with a phosphate gradient is used to study the effect of spatial heterogeneity on the spatial distribution of *Pseudomonas* sp., an heterotrophic aquatic bacterium. The observed distributions partially agree with theoretical predictions, obtained from the mathematical model.

In practice, for the gradostat, one does not use a large number of interconnected reactors, as they are difficult to operate and have a high cost. Difficulties come from the fact that the proper organisms and the nutrient must be selected so that they can grow under the operating circumstances. The reactor must be operated at a dilution rate that allows no growth on the walls but at the same time does not induce washout. The feed vessel must not contain substances from which the organisms can synthesize the limiting nutrient. If the organism mutates during the experiment, the experiment is invalid, so careful checks must be run to determine that what is grown is actually what was introduced in the reactor. The measurements must be very exact, as species have been noticed to recover even after long times at very low concentrations, sometimes below preset measurable levels.

Many theoretical models have been proposed to deal with the effect of space on population dynamics and interactions, but most of them are difficult to translate into experimental setups, due to their abstract nature. Kareiva ([Kar]) stressed out the existence of a large gap between theory and experimentation.

### 3. Mathematical introduction

The equations of population biology, in general, and those for the chemostat and gradostat, in particular, provide an interesting class of nonlinear systems of differential equations that are worthy of study for their mathematical properties. The theory of cooperative and

competitive dynamical systems, has been motivated, at least in part, by problems in population biology. The theory of persistence in dynamical systems grew directly from such considerations.

In describing the theoretical aspects of competition in the gradostat, in the present work we consider a widely accepted nutrient uptake term, usually attributed to Monod, that appears in enzyme kinetics as the Michaelis-Menten model. However, for models for the gradostat the mathematics frequently allows for more general nonlinearities and often little is gained by the Monod assumption. We still assume Monod kinetics in order to have a definite uptake term for simulation reasons.

Most of the deterministic models in population biology make use of the theory of dynamical systems, and that includes models described by ordinary differential equations, functional differential equations, or reaction-diffusion equations. The "language" of dynamical systems is used throughout this work.

In general, competition equations have a rather simple solution behaviour compared to predator prey equations for example. Usually, all orbits corresponding to nonnegative data tend to an equilibrium.

Chemostats have a certain conservation property which requires some mathematics to treat properly. It is widely used and is actually fundamental for the definition of an ideal chemostat. The mathematics can be found in a paper of Thieme ([Thi]).

The aim of this work is the analytical derivation of persistence results for competition in the gradostat as well as invadability of a certain community. In literature, the persistence results for the gradostat are reduced to the dynamics of one species and the competition of two species. The analysis makes extensive use of the theory of monotone dynamical systems. For more than two competitors however, the equations no longer give rise to monotone dynamical systems.

We want to see what happens in the gradostat for more than two species. Our approach is by taking a look at different regions of the parameter space and constructing invariant regions.

We apply intensively a quite new machinery, namely the method of lower and upper solutions by using some general properties of systems with quasimonotone reaction terms. Looking at the literature it can be seen that quasimonotonicity is a widely spread property in models describing population growth. The monotonicity property of the quasimonotone reaction terms reduces the finding of a solution of a nonlinear system of equations to finding iteratively a sequence of solutions of linear problems. This sequence will converge towards a solution of the nonlinear problem, with an initial iteration given by a pair of lower and

upper solutions. The method is constructive and allows the possibility of obtaining comparison results and thus persistence without too much information on the  $\omega$ -limit set of the solution.

For each of the situations considered, a bifurcation analysis is carried out and coexistence is obtained by varying a parameter. By continuing certain equilibria, numerical computation results are presented which suggest that coexistence equilibria exist under the sufficient conditions we find analytically.

## 4. Outline of the thesis

The main tool of this thesis, namely the method of lower and upper solutions for systems of ordinary differential equations with quasimonotone reaction terms, has been moved to *Appendix A*. We present all the theorems together with proofs, following the presentation of Pao for parabolic equations ([Pao3]). Even though the material is not necessarily new, we were not able to find it in a single source or with complete proofs.

In *Chapter 1* we describe the basic apparatus together with the model and some basic features. We also give a short overview of the main theorems in literature.

In *Chapter 2* we apply the method of lower and upper solutions for one species and two species and are able to give slightly different proofs to some well known theorems, namely in **Theorem 2.4.1** for one species, and **Theorem 2.7.1** for two species, by using the method of lower and upper solutions. We also present some features observed from numerical simulations. In *Section 2.6* we obtain some results on the persistence as well as invadability conditions for the competition of  $m$  species in  $n$  vessels, for general  $m$  and  $n$ : in **Theorem 2.6.2** we give sufficient conditions for the persistence of all  $m$  species, in **Theorem 2.6.6**, we give sufficient conditions for the washout of certain species, and in **Theorem 2.6.7**, sufficient conditions for the invadability of a  $m$ -species persistent system. Unfortunately, we were not able to find any numerical examples of persistence of more than two species when the persistence conditions of **Theorem 2.6.2** are fulfilled, moreover, from all our simulations it looks like persistence occurs when the parameters fulfill some much weaker conditions.

In *Chapter 3*, for the case of three species, we improve the persistence and invadability conditions found in Chapter 2, by applying the results on the dynamics of two species. We first look for a species which is able to invade a two-species persistent equilibrium by constructing invariant sets. In **Theorem 3.2.2** we give general invadability conditions and in *Section 3.3* we construct different invariant regions for which we can apply Theorem 3.2.2. In *Section 3.5*, through a bifurcation analysis we also obtain a branch of equilibria corresponding to the coexistence of all three species and present the results of extensive

numerical investigations in this direction. In **Section 3.6** we find sufficient conditions for the persistence of all three species to occur.

We have tried to make this work as mathematically self-contained as possible. For the different tools and the theorems frequently used or mentioned, like the Perron-Frobenius Theory, we give a short presentation in the appendices. In **Appendix D** we shortly present the numerical tools used in the simulations.



# 1

## The Gradostat

In this chapter we shortly present some of the results existing in the literature for the gradostat. As we have already mentioned in the Introduction, these are restricted to the competition of maximum two species, except of some papers presenting the outcomes of numerical simulations. Some of the results will apply for the general gradostat with  $n$  vessels.

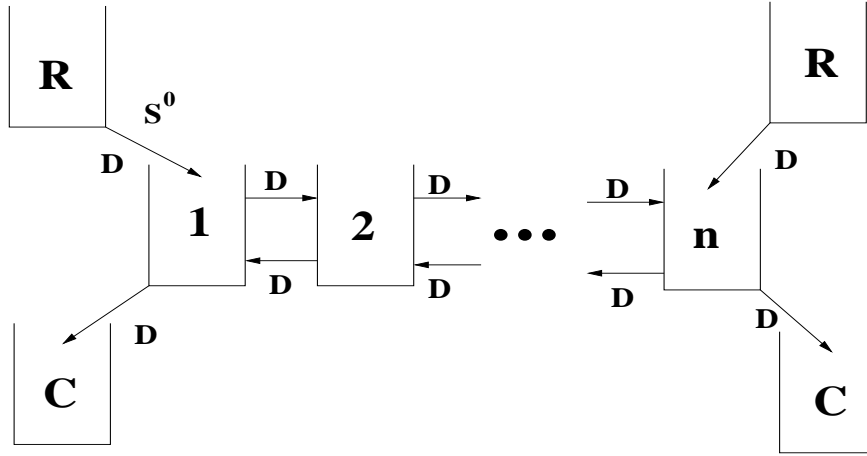
We will present the theorems without proofs. To some of them we will come back in the following chapters giving slightly different proofs than the ones in literature.

### 1.1 The model

As originally designed by Lovitt and Wimpenny ([LW1], [LW2]), the gradostat was linearly connected, namely the contents of vessel  $i$  are transmitted only to vessels  $i - 1$  and  $i + 1$ . In Figure 1.1.1 we give a schematic representation of such a device.

The basic properties of the system are that the flow rates and the volumes are kept constant: the flow rates between the vessels as well as the flow rates in and out of the gradostat are all equal to the dilution  $D$ . The nutrient is supplied into the first vessel, and in order to keep the volumes constant, we have input of medium without nutrient in the last vessel.

The growth of the microorganisms can be described by equations similar to the ones for the chemostat. We study the case of pure competition for a single limiting nutrient with the help of a  $n \cdot m$  system, with  $n$  the number of vessels and  $m$  the number of species of microorganisms. The growth will assume Michaelis-Menten kinetics of uptake of nutrient by the microorganisms.



**Figure 1.1.1.: Schematic representation of the gradostat with  $n$  vessels.**  $R$  denotes reservoir,  $C$  denotes collection, and  $D$  dilution rate. (Reproduced from [STW]).

For each  $1 \leq j \leq m$  the vector  $u^j(t) = (u_1^j(t), \dots, u_n^j(t))$  denotes the concentration of species  $j$  at time  $t$ , with  $u_i^j(t)$  the concentration of species  $j$  in vessel  $i$  for  $1 \leq i \leq n$ . For the nutrient, we denote with  $S_i(t)$ , the concentration in vessel  $i$  at time  $t$ . The equations take the form:

$$\left\{ \begin{array}{l} S_i'(t) = (S_{i-1}(t) - 2S_i(t) + S_{i+1}(t))D - \sum_{k=1}^n \frac{u_i^k(t)}{\gamma_k} f_k(S_i(t)), \\ u_i^{j'}(t) = (u_{i-1}^j(t) - 2u_i^j(t) + u_{i+1}^j(t))D + \frac{u_i^j(t)}{\gamma_j} f_j(S_i(t)), \\ i = 1, \dots, n, j = 1, \dots, m \\ S_0 = S^0, S_{n+1} = u_0 = u_{n+1} = 0, \\ S_i(t_0) \geq 0, u_i^j(t_0) \geq 0; \end{array} \right. \quad (1.1.1)$$

$$f_j(S) = \frac{m_j S}{a_j + S} = \text{Michaelis-Menten kinetics}$$

where

$$' = \frac{d}{dt},$$

$S^0$  = concentration of nutrient supply in the first vessel,



$\gamma_j =$  yield constant; converts units of concentration of biomass  
 into units of concentration of nutrient,  
 $m_j =$  maximum concentration rate for species  $j$ ,  
 $a_j =$  half-saturation constant for species  $j$ .

Since we are interested in competition, we assume that the  $f_j$ s are different from each other, namely the parameters  $a_j$  and  $m_j$  are different for different values of  $j$ .

The quantities  $S^0$  and  $D$  are under the control of the experimenter. Since the parameters  $a_j$  have units of concentration, if we measure all concentrations in units of  $S^0$ ,  $S^0$  can be scaled out of the system. For the parameters  $m_j$  we have as unit  $1/t$ , the same as for  $D$ , and with an appropriate change of time scale, we can scale  $D$  out of the system. The conversion factors  $\gamma_j$  will be incorporated into  $u^j$ , and we obtain the new scaled system:

$$\left\{ \begin{array}{l} S'_i(t) = S_{i-1}(t) - 2S_i(t) + S_{i+1}(t) - \sum_{k=1}^n u_i^k(t) f_k(S_i(t)), \\ u_i^{j'}(t) = u_{i-1}^j(t) - 2u_i^j(t) + u_{i+1}^j(t) + u_i^j(t) f_j(S_i(t)), \\ i = 1, \dots, n, j = 1, \dots, m \\ S_0 = S^0, S_{n+1} = u_0 = u_{n+1} = 0, \\ S_i(t_0) \geq 0, u_i^j(t_0) \geq 0, \end{array} \right. \quad (1.1.2)$$

where the parameters  $m_j$  and  $a_j$  have different biological meaning as the ones in (1.1.1).

We next write system (1.1.2) in vector form:

$$\left\{ \begin{array}{l} S'(t) = e_0 + AS(t) - \sum_{k=1}^n u^k(t) F_k(S(t)), \\ u^{j'}(t) = [A + F_j(S(t))] u^j(t), \\ j = 1, \dots, m \\ S(t_0) \geq 0, u^j(t_0) \geq 0, \end{array} \right. \quad (1.1.3)$$

where

$$e_0 = (1, 0, \dots, 0) \in \mathbf{R}^n,$$

$$A = \begin{bmatrix} -2 & 1 & 0 & \cdots & 0 & 0 \\ 1 & -2 & 1 & \cdots & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & \cdots & 1 & -2 \end{bmatrix},$$

and

$$F_j(S) = \begin{bmatrix} f_j(S_1) & 0 & \cdots & 0 \\ 0 & f_j(S_2) & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & \cdots & f_j(S_n) \end{bmatrix}.$$

An important property of matrix  $A$ , and, consequently  $A + F_j(S)$ , is that they are irreducible, quasipositive (with positive off-diagonal elements) and symmetric. Moreover, all eigenvalues of  $A$  are negative.

Denote with  $s(M) = \max\{Re(\lambda) : \lambda \text{ is an eigenvalue of } M\}$ , called the *stability modulus* for a matrix  $M$ . Thus  $s(A) < 0$ .

Note that the positive cone  $\mathbf{R}_+^m$  is positively invariant under the solution map of (1.1.3). Moreover we have the following conservation principle holding:

**Lemma 1.1.1**

*Solutions of (1.1.3) for nonnegative initial data exist, are nonnegative and bounded for  $t \geq t_0$  and*

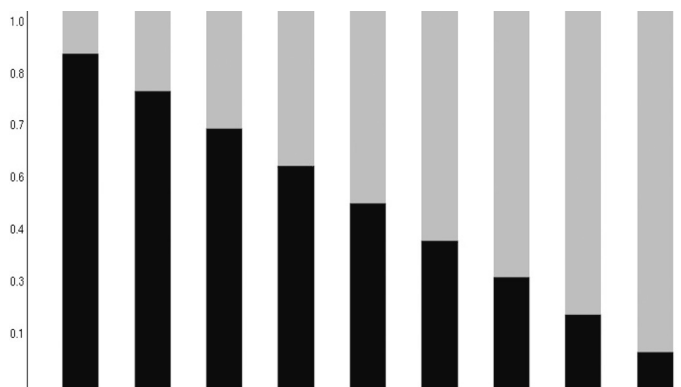
$$\lim_{t \rightarrow \infty} [S(t) + \sum_j u^j(t)] = z,$$

where  $z > 0$  is the unique solution of

$$Az + e_0 = 0.$$

**Proof:** The proof is basically the same as the proof in [STW] for the case of two species.  $\square$ .

We have actually that  $z$  is the steady-state distribution of nutrient in the gradostat in the absence of microorganisms ( $u^j = 0$  for all  $j$ ). We can easily calculate that  $z_i = 1 - i/(n+1)$  for  $1 \leq i \leq n$  giving a linear gradient, fact which justifies the name "gradostat" for our device. In Figure 1.1.2. we represent the equilibrium distribution  $z$  for the gradostat with 9 vessels.



**Figure 1.1.2.: Equilibrium distribution** of nutrient concentration in the absence of microorganisms for a gradostat with 9 vessels and all vessels having equal volumes.

As in [JSTW], the set

$$\Omega = \{u \in \mathbf{R}_+^{nm} : \sum_j u^j \leq z\}$$

is positively invariant for (1.1.3) and the omega limit set of any trajectory is nonempty, compact, connected and contained in  $\Omega$ . Since every trajectory is asymptotic to its omega limit set, it is sufficient to consider the flow on the omega limit set of (1.1.3), where the trajectories satisfy

$$\begin{cases} u^{j'}(t) = [A + F_j(z - \sum_k u^k(t))] u^j(t), \\ j = 1, \dots, m \\ u^j(t_0) \geq 0. \end{cases} \quad (1.1.4)$$

We will refer to system (1.1.4) as "the reduced system". For a rigorous proof for the fact that the asymptotic behavior of the two systems is the same there is a classical result by Markus in [Mar], which gives conditions under which the solutions of asymptotically autonomous differential equations have the same asymptotic behavior as the solutions of associated limit equations. Further results, together with examples, can be found in a paper of Thieme [Thi].

As a consequence of the irreducibility and quasipositivity of matrix  $A$  we have the following result corresponding to the one for two species in [JSTW] which says that a species occupies **all** vessels or **none** of the vessels:

**Lemma 1.1.2**

If  $u(t)$  satisfies (1.1.4) and  $u_i^j(t_0) > 0$  for some  $i$ , then  $u^j(t) > 0$  for all  $t > t_0$ .

## 1.2 No competition

When we have only one species in the gradostat, [Tan] gives a Lyapunov function for (1.1.4) and each trajectory of the system tends to a critical point, which in turn, is a solution of a system of algebraic equations.

(1.1.4) generates a strongly monotone dynamical system in the interior of  $[0, z]$  which is positively invariant. We can then use a comparison argument to prove the following theorem:

**Theorem 1.2.1** ([Tan], [SW])

*If  $s[A + F_j(z)] \leq 0$ , then  $\lim_{t \rightarrow \infty} u^j(t) = 0$  for every initial data in  $[0, z]$ . If  $s[A + F_j(z)] > 0$ , then there exists a unique equilibrium  $\hat{u}^j$ ,  $\hat{u}^j > 0$  and  $\lim_{t \rightarrow \infty} u^j(t) = \hat{u}^j$  for every nontrivial initial data in  $[0, z]$ .*

The proofs in [Tan], [SW] are slightly different from each other.

## 1.3 Two species

In order for coexistence to be possible, we assume each species is able to survive alone in the gradostat. We have the following possible equilibria:

$$E_0 = (0, 0), \quad \hat{E}^1 = (\hat{u}^1, 0), \quad \hat{E}^2 = (0, \hat{u}^2),$$

and

$$E^* > 0.$$

For two vectors  $x = (x^1, x^2)$  and  $y = (y^1, y^2) \in \mathbf{R}^{2n}$ , define the partial order relation

$$x \leq_k y \quad \Leftrightarrow \quad x^1 \leq y^1 \text{ and } x^2 \geq y^2.$$

We will also use  $x <_k y$  when  $x^1 < y^1$  and  $x^2 > y^2$ . The notation  $\leq_k$  is attributed to Kamke ([Kam]). For more results on differential inequalities and monotone systems see [Mül], [BW2], as well as [Smi1] and [Smi2] (Appendix C).

Denote with  $\pi(u_0, t)$  the solution of (1.1.4) corresponding to initial data  $u_0$ . As noted in [JSTW] and [STW], (1.1.4) generates a strongly monotone, with regard to  $\leq_k$ , dynamical

system in the interior of  $\Omega$ . Moreover, if  $u_0$  and  $v_0$  belong to  $\Omega$  and either  $u_0 > 0$  or  $v_0 > 0$  with  $u_0 <_k v_0$ , then  $\pi(u_0, t) <_k \pi(v_0, t)$  for all  $t > t_0$ . Another useful result is the following lemma from [STW]:

**Lemma 1.3.1** ([STW])

If  $u_0 \in \Omega$  satisfies

$$([A + F_1(z - u_0^1 - u_0^2)] u_0^1, [A + F_2(z - u_0^1 - u_0^2)] u_0^2) \leq_k 0,$$

then for  $t_0 \leq t_1 \leq t_2$  we have

$$\pi(u_0, t_2) \leq_k \pi(u_0, t_1) \leq_k u_0.$$

Moreover,  $\pi(u_0, t)$  converges to an equilibrium of (1.1.4) as  $t \rightarrow \infty$ . A similar conclusion holds with inequalities reversed.

We have the following necessary conditions for coexistence: if  $f_1(s) > f_2(s)$  for all  $0 < s < \max z_i$  then species 1 is the superior competitor in every vessel and coexistence is not possible, fact proven in [STW]. Thus coexistence is not possible unless the functions  $f_1$  and  $f_2$  intersect at some positive value  $s^*$ , which means that

$$m_1 > m_2 \Rightarrow \frac{m_1}{a_1} < \frac{m_2}{a_2}$$

and

$$m_1 < m_2 \Rightarrow \frac{m_1}{a_1} > \frac{m_2}{a_2}$$

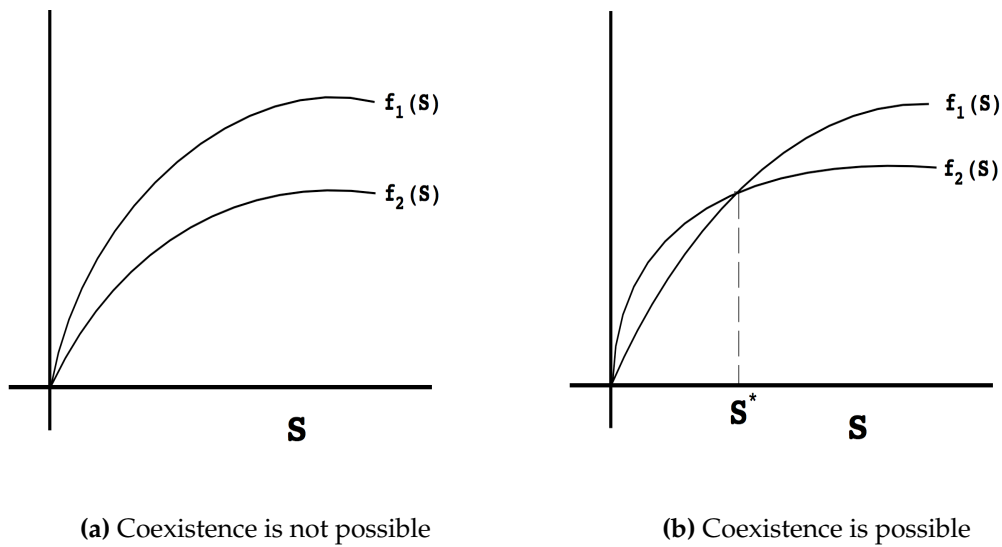


Figure 1.3.1.: Positional configurations of specific growth rate curves.

**Theorem 1.3.2 ([STW])**

Suppose that  $\hat{E}^1$  and  $\hat{E}^2$  exist and

$$s[A + F_1(z - \hat{u}^2)] > 0, \quad s[A + F_2(z - \hat{u}^1)] > 0.$$

Then there exist rest points (which may coincide)

$$E^* > 0, \quad E^{**} > 0$$

of (1.1.4) belonging to  $\Omega$  and satisfying

$$\hat{E}^2 <_k E^{**} \leq_k E^* <_k \hat{E}^1.$$

The set

$$O := [E^{**}, E^*]_K \cap \Omega$$

attracts all orbits corresponding to initial data  $u_0 \in \Omega$  satisfying  $u_0 > 0$ . If  $E^* = E^{**}$  then  $E^*$  attracts all orbits as before. Moreover, there exists an open and dense subset of  $\Omega$  consisting of points  $u_0$  for which  $\pi(u_0, t)$  approaches a rest point in  $O$  as  $t \rightarrow \infty$ . Both  $E^*$  and  $E^{**}$  have the property that the stability modulus of the Jacobian of (1.1.4) at these points is nonpositive. We also have that  $E^*$  attracts all orbits corresponding to initial data  $u_0 \in [\hat{E}^2, E^*]_K \cap \Omega$  and  $u_0 > 0$ , and  $E^{**}$  attracts all orbits corresponding to initial data  $u_0 \in [E^{**}, \hat{E}^1]_K \cap \Omega$  and  $u_0 > 0$ .

In the case of two species in two vessels ([JSTW]), the positive equilibrium is unique and a global attractor in the interior of  $\Omega$ . As in the case of one species, we can build a Lyapunov function for (1.1.4) which gives us convergence to an equilibrium for each trajectory starting from points in  $[0, z]^2$  ([EOEL]).

Since the conditions in Theorem 1.3.2 are only sufficient conditions for coexistence, we take a look at what happens when one or both are not fulfilled.

**Theorem 1.3.3 ([SW])**

Suppose that  $\hat{E}^1$  and  $\hat{E}^2$  exist and that

$$s_1 := s[A + F_1(z - \hat{u}^2)] \neq 0,$$

$$s_2 := s[A + F_2(z - \hat{u}^1)] \neq 0.$$

(a) If  $s_1 > 0$  and  $s_2 < 0$ , then either:

- (i)  $\hat{E}^2$  attracts all solutions  $u(t)$  with  $u^2(0) \neq 0$ ; or
- (ii) there exists a positive rest point  $E^*$ ,  $\hat{E}^2 <_k E^* <_k \hat{E}^1$ , that attracts all solutions satisfying  $E^* \leq_k u(0) \leq_k \hat{E}^1$  for which  $u^2(0) \neq 0$ , and  $s(J^*) \leq 0$  with  $J^*$  the Jacobian of (1.1.4) at  $E^*$ . If  $s(J^*) < 0$  then there exists another positive rest point  $E_\#$  such that  $\hat{E}^2 <_k E_\# <_k E^*$  and  $s(J_\#) \geq 0$ .

(b) The case  $s_2 > 0$  and  $s_1 < 0$ , is similar to (a).

(c) If  $s_1 < 0$  and  $s_2 < 0$  then there exists a positive rest point  $E_{\#}$  such that  $s(J_{\#}) \geq 0$ ,  $\hat{E}^2 <_k E_{\#} <_k \hat{E}^1$ . If  $s(J_{\#}) > 0$  then there exist rest points  $E_{\blacksquare}$  and  $E_{\blacktriangle}$ :

$$\hat{E}^2 \leq_k E_{\blacktriangle} <_k E_{\#} <_k E_{\blacksquare} \leq_k \hat{E}^1,$$

where equality may hold in either the first or last inequalities. The rest point  $E_{\blacktriangle}$  attracts all solutions satisfying  $E_{\blacktriangle} \leq_k u_0 \leq_k E_{\#}$  except  $E_{\#}$ ;  $E_{\blacksquare}$  attracts all solutions satisfying  $E_{\#} \leq_k u_0 \leq_k E_{\blacksquare}$  except  $E_{\#}$ . Both  $s(J_{E_{\blacktriangle}}) \leq 0$  and  $s(J_{E_{\blacksquare}}) \leq 0$ .

## 1.4 Three species

The possible equilibria this time are

$$E_0 = (0, 0, 0), \quad \hat{E}^1 = (\hat{u}^1, 0, 0), \quad \hat{E}^2 = (0, \hat{u}^2, 0), \quad \hat{E}^3 = (0, 0, \hat{u}^3),$$

$$E_{1,2}^* = (u_{(1,2)}^{*1}, u_{(1,2)}^{*2}, 0), \quad E_{1,3}^* = (u_{(1,3)}^{*1}, 0, u_{(1,3)}^{*3}), \quad E_{2,3}^* = (0, u_{(2,3)}^{*2}, u_{(2,3)}^{*3}),$$

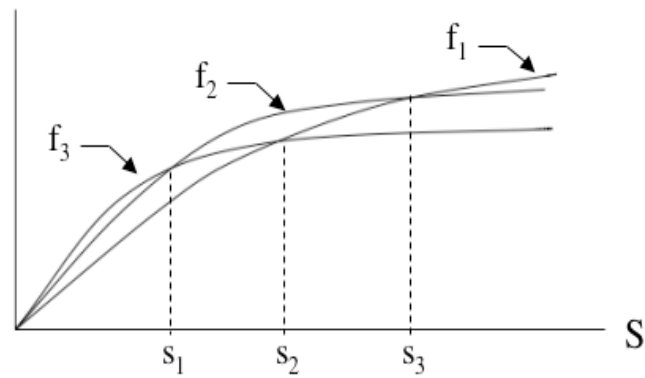
and

$$\tilde{E} > 0,$$

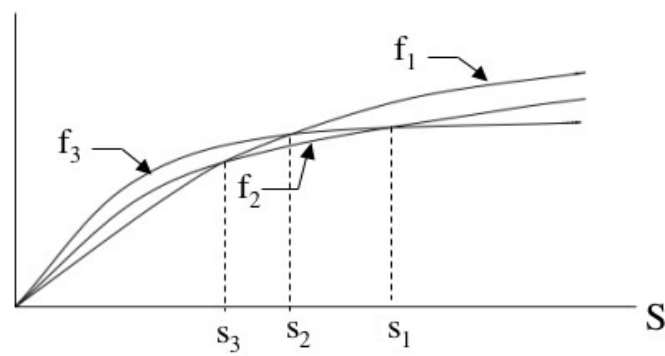
where  $E_{j,k}^*$  with  $j \neq k$  represent the two-species equilibria corresponding to the coexistence of species  $j$  and  $k$ , for which however, we do not have uniqueness.

Which of the possible equilibria can actually occur, depends also on how the growth rate curves  $f_j(s)$ ,  $j = 1, 2, 3$  are related. As for the case of two species, it can be shown that a necessary condition for coexistence of all three species is that all of the three specific growth rate curves cross each other. Assume  $m_1 > m_2 > m_3$ . Then the pairwise crossing occurs as follows:

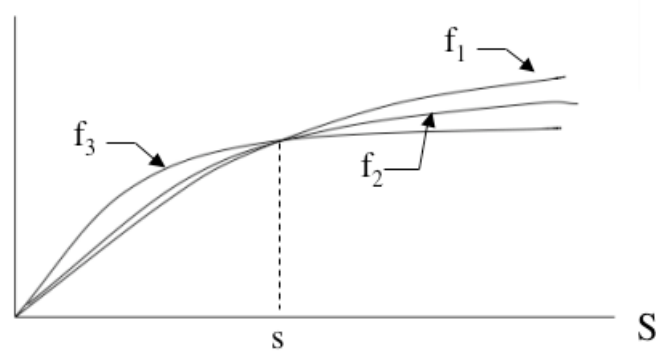
$$\begin{aligned} f_1(s_3) = f_2(s_3) \quad \text{at} \quad s_3 = \frac{m_2 a_1 - m_1 a_2}{m_1 - m_2} \quad \text{for} \quad \frac{m_1}{a_1} < \frac{m_2}{a_2}, \\ f_1(s_2) = f_3(s_2) \quad \text{at} \quad s_2 = \frac{m_3 a_1 - m_1 a_3}{m_1 - m_3} \quad \text{for} \quad \frac{m_1}{a_1} < \frac{m_3}{a_3}, \\ f_2(s_1) = f_3(s_1) \quad \text{at} \quad s_1 = \frac{m_3 a_2 - m_2 a_3}{m_2 - m_3} \quad \text{for} \quad \frac{m_2}{a_2} < \frac{m_3}{a_3}. \end{aligned}$$



(a)



(b)



(c)

Figure 1.4.1.: Positional configurations of specific growth rate curves for three species when pairwise crossing occurs.



For the case (a) of Figure 1.4.1 to occur, we need  $f_2(s_2) > f_1(s_2) = f_3(s_2)$  and thus

$$m_3a_1 - m_1a_3 + m_2a_3 < m_2a_1 - m_1a_2 + m_3a_2.$$

For (b) to occur we need the above inequalities reversed, and for (c),  $f_2(s) > f_1(s) = f_3(s)$  and thus

$$m_3a_1 - m_1a_3 + m_2a_3 = m_2a_1 - m_1a_2 + m_3a_2.$$

In case (b) species 2 never has the advantage over its competitors and we expect that the outcome of the competition can not correspond to any of the situations for which species 2 survives. Numerical simulations mentioned in [CB] indicate such a behavior, concluding that if three species are to coexist in the gradostat, the growth rate curves must relate to each other in a way depicted in Figure 1.1.4.(a).

In the same article, namely [CB], the results of extensive numerical investigations are presented for the case of 3 species in 3 vessels, concluding that "coexistence of three species in three vessels is impossible, except possibly for some discrete values of the operating parameters". We will come back to this affirmation in section 3.7.

## 1.5 $m$ species

We can come up with similar conditions to the ones found in the previous section regarding the growth rate curves also for the gradostat with more than 3 species.

Otherwise, besides some numerical simulations, the results for competition of more than two species in the gradostat are reduced to [JST] according to which for  $m$  species to survive, the number of vessels has to be at least  $m$ : when the number of vessels  $n$  is such that  $n < m$ , it is shown that the region in the parameter space corresponding to all  $m$  species coexisting as a steady state has measure zero. In addition, there exist trajectories which originate from the interior of the state space and eventually approach a boundary equilibrium point, so the system does not exhibit any type of persistence.

In the following chapters we will look for persistence conditions for more than two species and present numerous numerical examples describing the competition and the possibility of coexistence for three species in the gradostat.



# 2

## Persistence Results for the Gradostat

### 2.1 The system

We saw in chapter 1 that there exist very few results for the gradostat with  $m$  species in  $n$  vessels for  $n > 2$ . In this chapter we will use the methods described in Appendix A to get some results on the persistence of  $n$  species. We will refer to the theorems and definitions in Appendix A without listing them here.

Consider again the scaled reduced system describing competition of  $m$  species in a  $n$ -vessel gradostat:

$$\begin{aligned} u_i^{j'} &= u_{i-1}^j - 2u_i^j + u_{i+1}^j + f_j(z_i - \sum_{k=1}^m u_i^k) u_i^j, \\ u_0^j &= u_{n+1}^j = 0, \end{aligned} \tag{2.1.1}$$

$$u_i^j(t_0) \geq 0,$$

$$1 \leq i \leq n, 1 \leq j \leq m,$$

or, equivalently, (2.1.1) in the vector form:

$$\begin{aligned} u^{j'} &= [A + F_j(z - \sum_{k=1}^m u^k)] u^j, \\ u^j(t_0) &\geq 0, \end{aligned} \tag{2.1.2}$$

$$1 \leq j \leq m,$$

with  $\Omega = \{u \geq 0 \mid \sum_{j=1}^m u_i^j \leq z_i, 1 \leq i \leq n\}$ .

It is easy to see that the reaction functions of (2.1.1)

$$h_i^j(u) = u_{i-1}^j - 2u_i^j + u_{i+1}^j + f_j(z_i - \sum_{k=1}^m u_i^k) u_i^j,$$

for  $1 \leq i \leq n$ ,  $1 \leq j \leq m$ , satisfy the hypothesis (H1) and (H2) in Appendix A, with the index sets:

$$\begin{aligned} I^{\uparrow ij}(h) &= \\ &= \{(l, k) \in \{1, \dots, m\} \times \{1, \dots, n\} \setminus \{(j, i)\} \mid h_i^j \text{ is monotone nondecreasing in } u_i^l\} \\ &= \{(j, i-1), (j, i+1)\}, \end{aligned}$$

the *nondecreasing index set* of  $h_i^j$  (with respect to  $\Omega$ ), and

$$\begin{aligned} I^{\downarrow ij}(h) &= \\ &= \{(l, k) \in \{1, \dots, m\} \times \{1, \dots, n\} \setminus \{(j, i)\} \mid h_i^j \text{ is monotone nonincreasing in } u_i^l\} \\ &= \{(k, i) \mid 1 \leq i \leq n, 1 \leq j \leq m \text{ and } k \neq j\}, \end{aligned}$$

the *nonincreasing index set* of  $h_i^j$  (with respect to  $\Omega$ ).

## 2.2 Definition of persistence

**Definition 2.2.1** (Persistence of one species) A component  $u^j$ ,  $1 \leq j \leq m$ , of a solution  $u(t)$  of problem (2.1.2), defined for all  $t \geq t_0$ , is called persistent if for  $u^j(t_0) > 0$  there exists a continuous  $\eta > 0$  such that

$$u^j(t) \geq \eta \tag{2.2.1}$$

for all  $t \geq t_0$ . In this case we also call species  $j$  persistent.

If each component  $u^j$ ,  $1 \leq j \leq m$  is persistent, then (2.1.2) is called persistent. Note, that in order to be able to even consider persistence for (2.1.2), each species has to start with positive concentrations.

In the present chapter, as well as in the following one, we will be looking for conditions on the parameters that will give us persistence, first for one species, and then, of course, for  $n > 1$ .

## 2.3 A pair of lower and upper solutions

As mentioned in Appendix A, since we have positive initial data,  $\underline{u} \equiv 0$  is always a lower solution for (2.1.2), independently of the choice of  $\bar{u}$ . An obvious choice for a pair of (time-independent) lower and upper solutions will be

$$(\underline{u}^j, \bar{u}^j) = (0, z),$$

with  $z$  defined in Chapter 1.

For  $z$ , we have  $Az + e_1 = 0$ , hence

$$\bar{u}^{j'} = z' = 0 \geq [A + F_j(z - \bar{u}^j - \sum_{\substack{k=1, m \\ k \neq j}} \underline{u}^k)] \bar{u}^j = [A + F_j(z - z - 0)] z = Az = -e_1.$$

With this pair of lower and upper solutions, from Theorem A.5.6 we have:

### Proposition 2.3.1

(2.1.2) has a unique solution  $u = (u^1, \dots, u^m)$  with

$$0 \leq u^j(t) \leq z, \quad 1 \leq j \leq m,$$

for all  $t > t_0$ , provided that it was true at  $t = t_0$ .

## 2.4 A measure for the "fitness" of each competitor

Denote

$$A_j := A + F_j(z - x),$$

with  $x$  some positive vector.  $A_j$  is an irreducible matrix with nonnegative off-diagonal elements.

Let  $s[X]$  be the stability modulus of a matrix  $X$ :

$$s[X] = \max\{\operatorname{Re} \lambda \mid \lambda \text{ eigenvalue of } X\}.$$

For  $A_j$  we have (see Appendix C):

**(sa)**  $s[A_j]$  is an eigenvalue with algebraic multiplicity 1;

**(sb)**  $\operatorname{Re} \lambda < s[A_j]$  for all  $\lambda$  eigenvalue of  $A_j$  and  $\lambda \neq s[A_j]$ ;

**(sc)** there exists an eigenvector  $\phi_s^j[A_j]$  associated to  $s[A_j]$ :

$$A \cdot \phi_s^j[A_j] = s[A_j] \cdot \phi_s^j[A_j]$$

and  $\phi_s^j[A_j] > 0$ ;

**(sd)** for a matrix  $B \geq A_j$ ,  $B \neq A$ , we have  $s[B] > s[A_j]$ .

As for the case of the gradostat with 2 species, we want to use the stability modulus of some irreducible quasipositive matrix of type  $A_j$ , to relate positive real numbers to each of the competitors. In the case of 2 species,  $s[A + F_j(z)]$ ,  $j = 1, 2$  measures the "fitness" of species  $j$  without competition, and  $s[A + F_j(z - \hat{u}^k)]$ ,  $k \neq j$  measures the "fitness" of species  $j$  in the competition situation, where  $\hat{u}^k$  is the single species equilibrium solution for species  $k$ .

We want to find similar measures for the case of  $m$  species. We will use the positivity of the associated eigenvectors in order to obtain  $\eta$ -functions in (2.2.1).

Assume that we have just one species:  $m = 1$ , or equivalently, all other species have zero initial conditions.

The system takes then the form ( $j = 1$ ):

$$u_i^{j'} = u_{i-1}^j - 2u_i^j + u_{i+1}^j + f_j(z_i - u_i^j)u_i^j, \quad (2.4.1)$$

$$u_i^j(t_0) > 0,$$

$$1 \leq i \leq n,$$

or, in the vector form:

$$u^{j'} = [A + F_j(z - u^j)] u^j, \quad (2.4.2)$$

$$u^j(t_0) \geq 0,$$

with  $u^j \leq z$ .

Since the functions  $h_i^j(u) = u_{i-1}^j - 2u_i^j + u_{i+1}^j + f_j(z_i - u_i^j)u_i^j$ ,  $i = 1, \dots, n$  do not depend on  $u_i^k$ ,  $k \neq j$ ,  $i = 1, \dots, n$ , we see that  $h_i^j$  are quasimonotone nondecreasing (fact which does not hold in the competition case, i.e.  $m > 1$ ). Hence we can use the results we obtained in

Appendix A on the uniqueness and stability of the steady state solution of a problem with quasimonotone nondecreasing reaction functions.

**Theorem 2.4.1** (Single species persistence)

In (2.1.2) let  $u_0^j > 0$  and  $u_0^k \equiv 0, k \neq j$ . Then the following hold:

(i) If

$$s[A + F_j(z)] \leq 0 \quad (2.4.3)$$

then species  $j$  is not persistent: we have  $0 \leq u^j(t) \leq \gamma(t) \cdot \phi_s^j[A + F_j(z)]$  if  $0 < u_0^j \leq \gamma(t_0) \cdot \phi_s^j[A + F_j(z)] \leq z$ , where the function  $\gamma : \mathbb{R}^+ \rightarrow \mathbb{R}^+$  satisfies  $\gamma(t_0) > 0$ ,  $\gamma' < 0$  and  $\lim_{t \rightarrow \infty} \gamma(t) = 0$ .

(ii) If

$$s[A + F_j(z)] > 0 \quad (2.4.4)$$

then species  $j$  is persistent.

**Proof:** (i) Let  $s[A + F_j(z)] \leq 0$  and assume species  $j$  persistent, that means that there exists a continuous function  $\eta^j > 0, \eta^j \in \mathbb{R}_+^n$  such that  $u^j(t) \geq \eta^j$ , for all  $t \geq t_0$ .

For an  $\bar{\eta}$ , with  $0 < \bar{\eta} < \eta^j$ , we have  $f_j(z_i - \bar{\eta}_i) < f_j(z_i), 1 \leq i \leq n$  and hence  $F_j(z - \bar{\eta}) < F_j(z)$  and from (sd) we get that

$$s[A + F_j(z - \bar{\eta})] < s[A + F_j(z)] \leq 0.$$

Take

$$\underline{u}^j = 0$$

and

$$\bar{u}^j = \gamma(t) \cdot \phi_s^j[A + F_j(z)]$$

(and  $\underline{u}_k = \bar{u}_k = 0$  for  $k \neq j$ ). The function  $\gamma : \mathbb{R}^+ \rightarrow \mathbb{R}^+$  will be defined later.

Next,  $(\underline{u}_j, \bar{u}_j)$  is a pair of lower and upper solutions:  $\underline{u}_j$  is clearly a lower solution, and for  $\bar{u}_j$  we have

$$\begin{aligned} \bar{u}_j' &= \gamma'(t) \cdot \phi_s^j[A + F_j(z)] \\ &\geq (A + F_j(z - \gamma(t) \cdot \phi_s^j[A + F_j(z)])) \cdot \gamma(t) \cdot \phi_s^j[A + F_j(z)]. \end{aligned} \quad (2.4.5)$$

Define now the function  $\gamma$  to be the function

$$\gamma(t) \stackrel{\text{def}}{=} \tilde{\gamma} \cdot e^{s[A + F_j(z - \bar{\eta})] \cdot t},$$

with  $\tilde{\gamma} > 0$  so that  $u_0^j \leq \gamma(t) \cdot \phi_s^j[A + F_j(z)] \leq z$ .

With this choice for  $\gamma$ , (2.4.5) takes the form:

$$\begin{aligned}
& \tilde{\gamma} \cdot e^{s[A + F_j(z - \bar{\eta})]} \cdot t \cdot s[A + F_j(z - \bar{\eta})] \cdot \phi_s^j[A + F_j(z)] \\
& \geq \left[ F_j(z - \gamma(t) \cdot \phi_s^j[A + F_j(z)]) - F_j(z) \right] \cdot \phi_s^j[A + F_j(z)] \cdot \tilde{\gamma} \cdot e^{s[A + F_j(z - \bar{\eta})]} \cdot t \\
& \quad + F_j(z) \cdot \phi_s^j[A + F_j(z)] \cdot \tilde{\gamma} \cdot e^{s[A + F_j(z - \bar{\eta})]} \cdot t \\
& \Leftrightarrow s[A + F_j(z - \bar{\eta})] \cdot \phi_s^j[A + F_j(z)] \\
& \geq \left[ F_j(z - \gamma(t) \cdot \phi_s^j[A + F_j(z)]) - F_j(z) \right] \cdot \phi_s^j[A + F_j(z)] \\
& \quad + s[A + F_j(z)] \cdot \phi_s^j[A + F_j(z)] \\
& \Leftrightarrow \underbrace{[-s[A + F_j(z)] + s[A + F_j(z - \bar{\eta})]]}_{>0} \cdot \underbrace{\phi_s^j[A + F_j(z)]}_{>0} \\
& \geq \underbrace{\left[ F_j(z - \gamma(t) \cdot \phi_s^j[A + F_j(z)]) - F_j(z) \right]}_{<0} \cdot \underbrace{\phi_s^j[A + F_j(z)]}_{>0}. \tag{2.4.6}
\end{aligned}$$

The last inequality is satisfied and therefore  $\bar{u}^j$  is an upper solution.

By our choice of  $\bar{\eta}$  and  $\tilde{\gamma}$  there must be a  $\bar{t} < \infty$  such that  $\bar{u}^j(\bar{t}) < \eta^j$ , a contradiction. Thus species  $j$  is not persistent.

**(ii)** Let  $s[A + F_j(z)] > 0$ .

Now take

$$\underline{u}^j = \tilde{\gamma} \cdot \phi_s^j[A + F_j(z)],$$

and

$$\bar{u}^j = z,$$

with  $\tilde{\gamma}$  a positive constant so that  $\tilde{\gamma} \cdot \phi_s^j[A + F_j(z)] < z$ . For  $\underline{u}^j$  we have

$$\begin{aligned}
\underline{u}_j' = 0 & \leq (A + F_j(z - \tilde{\gamma} \cdot \phi_s^j[A + F_j(z)])) \cdot \tilde{\gamma} \cdot \phi_s^j[A + F_j(z)] \\
& \Leftrightarrow 0 \leq \left[ F_j(z - \gamma(t) \cdot \phi_s^j[A + F_j(z)]) - F_j(z) \right] \cdot \phi_s^j[A + F_j(z)] \\
& \quad + s[A + F_j(z)] \cdot \phi_s^j[A + F_j(z)]
\end{aligned}$$

The last inequality is satisfied for  $\tilde{\gamma}$  small enough and thus  $\underline{u}^j$  is a lower solution and we have

$$0 < \underline{u}^j \leq u(t) \leq z$$



for all  $t > t_0$  provided that it was true at  $t = t_0$ . By taking  $\eta := \underline{u}^j$ , species  $j$  is persistent.  $\square$

**Theorem 2.4.2** (Existence of positive single species equilibrium solutions)

If  $s[A + F_j(z)] > 0$ , then the steady state system of problem (2.4.2)

$$[A + F_j(z - u^j)] \cdot u^j = 0, \quad (2.4.7)$$

has at least one positive solution  $\xi^j$  satisfying  $0 < \xi^j \leq z$ .

**Proof:** The pair of lower and upper solutions  $(\underline{u}^j, \bar{u}^j)$  in the proof of Theorem 2.4.1 is also a pair of lower and upper solutions for (2.4.7), with  $\tilde{\gamma}$  small enough, since both  $\underline{u}^j$  and  $\bar{u}^j$  are time independent. Thus, the theorem follows from Theorem A.5.4.  $\square$

**Theorem 2.4.3** (Uniqueness of positive single species steady state solutions)

If  $s[A + F_j(z)] > 0$  the positive steady state solution  $\xi^j$  found in Theorem 2.4.2 is the unique positive steady state solution of (2.4.2) and it is stable.

**Proof:** As we noted in the beginning of this section, the functions

$$h_i^j(u) = u_{i-1}^j - 2u_i^j + u_{i+1}^j + f_j(z_i - u_i^j)u_i^j,$$

$i = 1, \dots, n$  are quasimonotone nondecreasing.

We check whether (H3) from Appendix A holds:

Let  $\gamma > 1$  a constant. Then we have  $z^i - u_i^j \leq z^i - \gamma u_i^j$ ,  $i = 1, \dots, n$  and thus  $h_i^j(\gamma u) \leq \gamma h_i^j(u)$  and is not an identity if  $u_j \neq 0$ . We have then that (H3) holds in  $\langle \underline{u}, \bar{u} \rangle$ , with  $(\underline{u}, \bar{u})$  the pair of coupled time-independent lower and upper solutions found in the proof of Theorem 2.4.1(ii). Since  $\underline{u}^j = \tilde{\gamma} \cdot \phi_s^j[A + F_j(z)]$  can be made very small (by decreasing  $\tilde{\gamma}$ ), (H3) holds in  $\langle 0, z \rangle$  as long as  $u_j$  has positive initial values. By Theorem A.5.8 the positive steady state solution  $\xi^j$  is unique in  $\langle 0, z \rangle$ , for  $u_0^j \geq 0$ ,  $u_0^j \neq 0$ ,  $u_0^j \leq z$ .

From Theorem A.6.5 we get that any solution  $u^j$  of (2.4.2) with  $u_0^j \in \langle 0, z \rangle$ ,  $u_0^j \neq 0$ , converges to  $\xi^j$  as  $t \rightarrow \infty$ .  $\square$

## 2.5 One species: bifurcation diagrams

In the previous section we obtained sufficient conditions for the existence, uniqueness and stability of the single-species steady state solution. From a practical point of view, it would

be interesting to give similar conditions in terms of the different parameters of the system. Such conditions could be achieved via a bifurcation analysis of the solution of the system

$$[A + F_j(z - u^j)] \cdot u^j = 0, \quad (2.5.1)$$

with  $u^j \leq z$ .

The parameters that an experimenter can control in operating a gradostat, are the input concentration of nutrient,  $S^0$ , the dilution rate,  $D$ , and the volume of the vessels.

However, we are working with the scaled system (2.4.2), and the analysis can be carried out easier if we consider one of the species-dependent parameters,  $m_j$ ,  $a_j$ , as the bifurcation parameter. We choose to vary  $m_j$ , keeping  $a_j$  fixed (otherwise, for the full system the more natural choice for the bifurcation parameter would be  $D$ ; see [Tan] for a  $D$ -bifurcation analysis for the full one-species system).

Before we go on, we give here the following theorem:

**Theorem 2.5.1** (Theorem A.1.2 in [Tan])

*Each trajectory of (2.5.1) tends to a critical point.*

The theorem is proved with the aid of the Lyapunov function

$$V(u) = \sum_{i=1}^n \left( (u_i^{j^2} - u_i^j u_{i+1}^j) - \int_0^{u_i^j} \frac{m_j(z^i - u_i^j)}{a_j + z^i - u_i^j} \cdot s \, ds \right).$$

Following [STW], we write

$$f_j(S) = m_j \cdot \tilde{f}_j(S),$$

and

$$F_j(x) = m_j \cdot \tilde{F}_j(x),$$

for the vector form, where  $\tilde{f}_j(S) = S/(a_j + S)$ , and the system can be written in the form

$$[A + m_j \cdot \tilde{F}_j(z - u^j)] \cdot u^j = 0, \quad (2.5.2)$$

In the following, since we have just one species, we omit the index  $j$ .

**Lemma 2.5.2**

*Let  $m_1$  and  $m_2$  be two values for the parameter  $m$  such that  $0 < m_1 < m_2$ . If  $u_1 > 0$  is the solution of (2.5.2) corresponding to  $m_1$  and  $u_2$ , the solution corresponding to  $m_2$  then  $u_1 < u_2$ .*

**Proof:** For  $u_1$  we have

$$0 = u_1' = [A + m_1 \cdot \tilde{F}(z - u_1)]u_1 < [A + m_2 \cdot \tilde{F}(z - u_1)]u_1,$$

which means that  $u_1$  is a lower solution for (2.5.2) with  $m = m_2$ . By Theorem A.5.4 there exists a solution  $u_2$  of (2.5.2) with  $m = m_2$  such that  $u_2 \in \langle u_1, z \rangle$ , and  $u_2 < u_1$ .  $\square$

Let

$$\Lambda_m = \{(m, u_s) \mid u_s \text{ satisfies (2.4.7) corresponding to } m\} \subseteq \mathbb{R}^+ \times \mathbb{R}_+^n.$$

Clearly,  $s[A + m\tilde{F}(z)]$  strictly increases with  $m$ : from a negative value for small  $m$ , corresponding to species not strong enough to survive in the gradostat, to infinity, as  $m$  increases without bound, and there exists a unique critical value  $m^*$  (by Perron-Frobenius theory) such that

$$s[A + m^*\tilde{F}(z)] = 0.$$

By Theorem 2.4.3, once  $m$  'passes' the value  $m^*$ , the corresponding species is strong enough to survive in the gradostat, and the positive steady state  $\xi$  exists and it is (globally and asymptotically) stable for positive initial data. We have then the following theorem (corresponding to Theorem A.1.8 in [Tan] with  $D$  the bifurcation parameter):

### Theorem 2.5.3

There exists a number  $m^*(a, n) > 0$  such that we have the following for the solution set  $\Sigma$  :

- (i) if  $m \leq m^*$  then  $\Sigma = \{0\}$ ,
- (ii) if  $m > m^*$  then  $\Sigma = \{0, \xi\}$ ,
- (iii)  $(m^*, \infty) \times \langle 0, z \rangle \rightarrow \langle 0, z \rangle : m \mapsto \xi(m)$  is a strongly increasing  $\mathbf{C}^2$  map, and

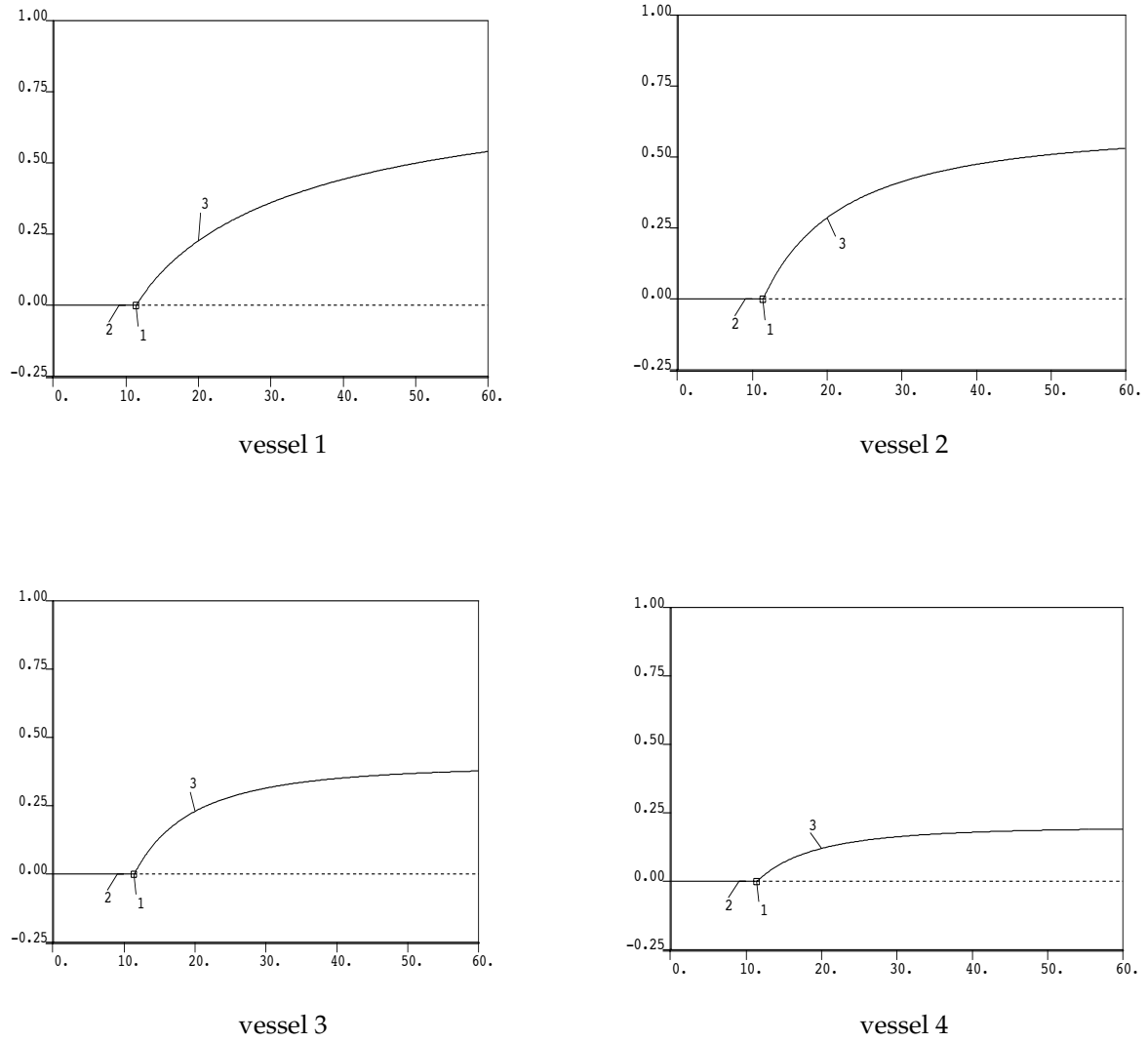
$$\lim_{m \rightarrow m^*, m > 0} \xi(m) = 0, \quad \lim_{m \rightarrow \infty} \xi(m) = z,$$

- (iv) if  $m \leq m^*$ ,  $0$  is (globally and asymptotically) stable,
- (v) if  $m > m^*$ ,  $0$  is unstable and  $\xi$  is (globally and asymptotically) stable.

We can now divide the set  $\Lambda_m$  into two branches:

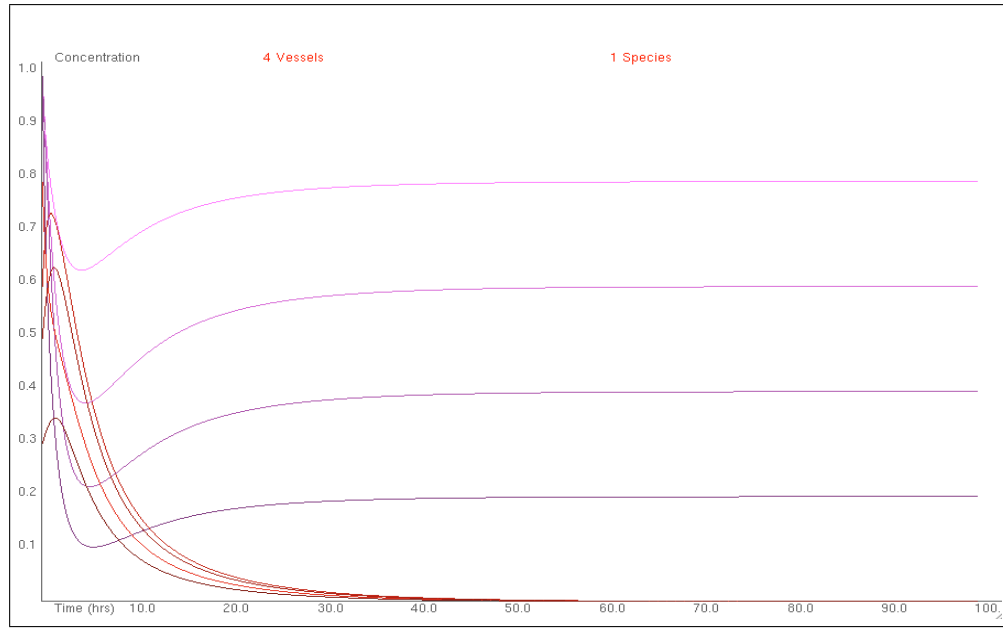
$$\Lambda_m = Q_{m_0} \cup Q_{m_+},$$

where  $Q_{m_0} = \{(m, u_s) \mid u_s = 0\}$  corresponds to  $\mathbf{0}$  being the stable steady state, and  $Q_{m_+} = \{(m, u_s) \mid u_s = \hat{u} > 0\}$  corresponds to the steady state staying positive.

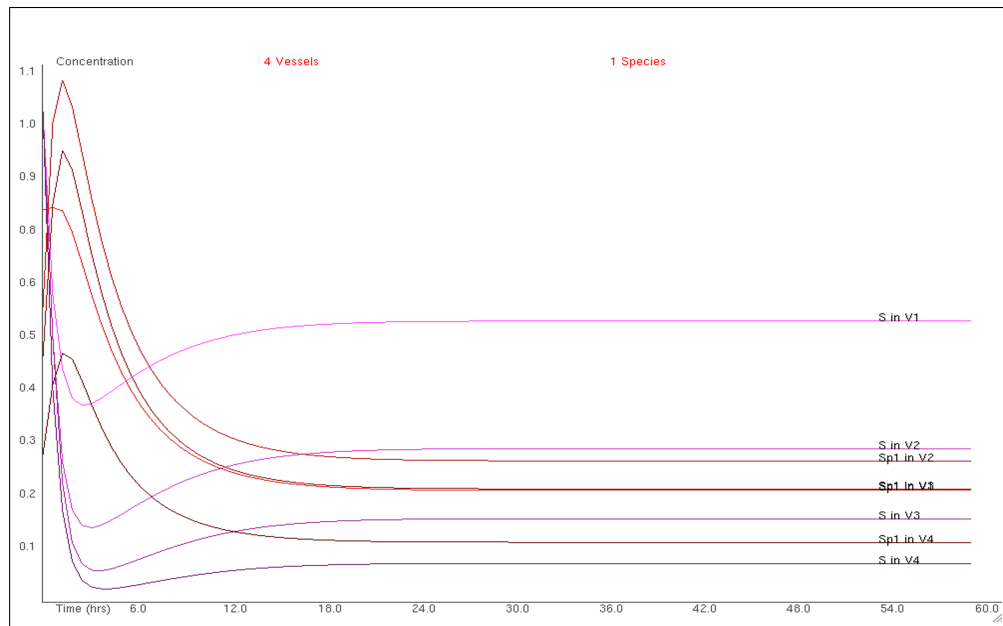


**Figure 2.5.1. Bifurcation diagram for 1 species in 4 vessels for  $a = 15$ .** We plot equilibrium concentration in each vessel vs. parameter  $m$ . **Label 1** - the bifurcation value:  $m_1 = m^* = 11.38960$ ; **label 2** - a species that is not strong enough to survive:  $m_2 = 9$ ; **label 3** - a species that survives:  $m_3 = 20$ .

For the different values for  $m$  labeled in Figure 2.5.1, we give in Figure 2.5.2 and 2.5.3 the plots of the solution of system (2.5.1)- we plot concentration vs.time.



**Figure 2.5.2** Label 2:  $m_2 = 9$ ;  $u_2 = (0, 0, 0, 0)$



**Figure 2.5.3.** Label 3:  $m_3 = 20$ ;  
 $u_3 = (0.2272965, 0.2874113, 0.2301828, 0.1214191)$

Now fix the parameter  $m$  and consider  $a$  as the bifurcation parameter. Note that this time the functions  $f$  and  $h$  are monotone decreasing in  $a$ : for  $0 < a_1 < a_2$  with  $a_1$  and  $a_2$  two values for the parameter  $a$  such that the steady state solutions of (2.5.1),  $u_1$  and  $u_2$ , corresponding

to  $a_1$  and  $a_2$ , respectively, are positive, then they satisfy  $u_1 > u_2 > 0$ . Thus we can state a similar lemma to Lemma 2.5.2:

**Lemma 2.5.4**

Let  $a_1$  and  $a_2$  be two values for the parameter  $a$  such that  $0 < a_1 < a_2$ . If  $u_1 > 0$  is the solution of (2.5.2) corresponding to  $a_1$  and  $u_2$ , the solution corresponding to  $a_2$  then  $u_1 > u_2$ .

We have this time that  $s[A + F(z)]$  strictly decreases with  $a$ : from a negative value for  $a$  large corresponding to species not strong enough to survive in the gradostat, to infinity, as  $a$  decreases towards zero, and there exists a unique critical value  $a^*$  such that

$$s[A + F(z)] = 0.$$

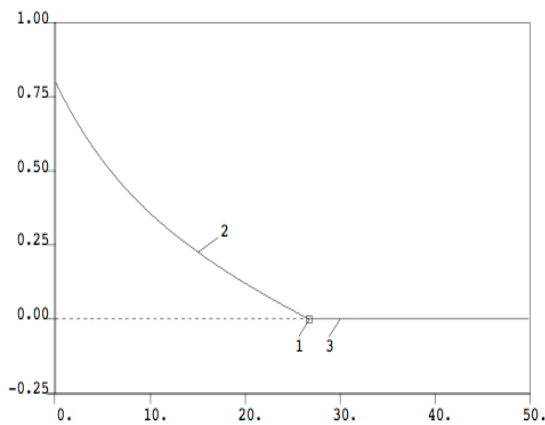
By Theorem 2.4.3 once more,  $a^*$  is the threshold value under which the corresponding species is strong enough to survive in the gradostat, and the positive steady state  $\xi$  exists and it is (globally and asymptotically) stable for positive initial data. We have then a similar theorem to Theorem 2.5.3 (that we do not state any more), that allows us to split the set

$$\Lambda_a = \{(a, u_s) \mid u_s \text{ satisfies (2.4.7) corresponding to } a\} \subseteq \mathbb{R}^+ \times \mathbb{R}_+^n$$

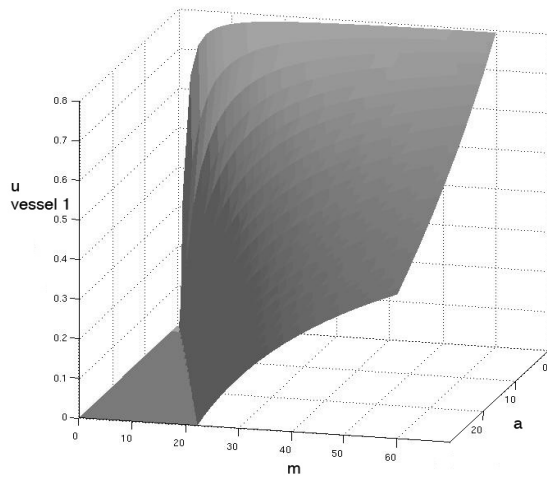
into two branches:

$$\Lambda_a = Q_{a_0} \cup Q_{a_+},$$

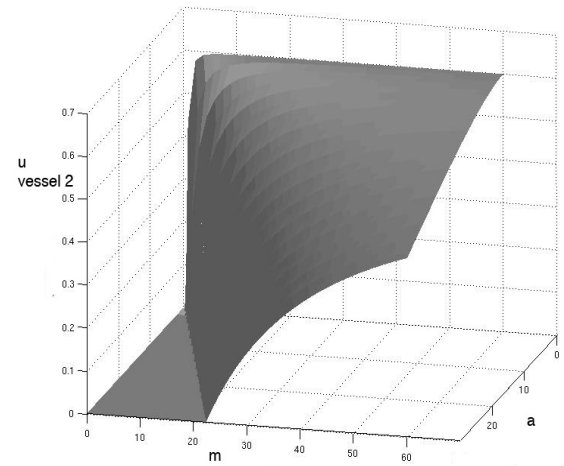
where  $Q_{a_0} = \{(a, u_s) \mid u_s = 0\}$  corresponds to  $\mathbf{0}$  being the stable steady state, and  $Q_{a_+} = \{(a, u_s) \mid u_s = \hat{u} > 0\}$  corresponds to the steady state staying positive.



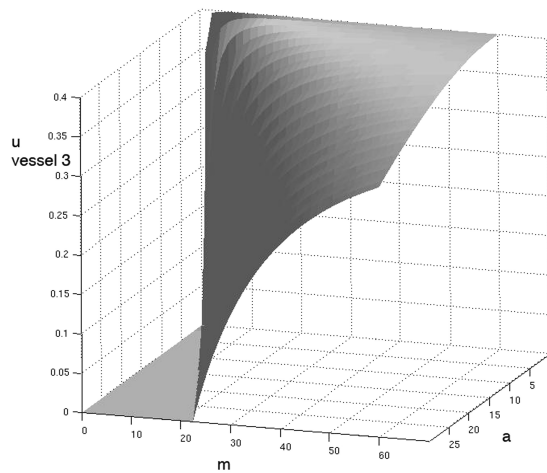
**Figure 2.5.4. Bifurcation diagram for 1 species in 4 vessels for  $m = 20$ .** We plot equilibrium concentration in vessel 1 vs. parameter  $a$ . **Label 1** - the bifurcation value:  $a_1 = a^* = 26.79317129$ ; **label 2**:  $a_2 = 15$ ; **label 3**:  $a_3 = 30$ .



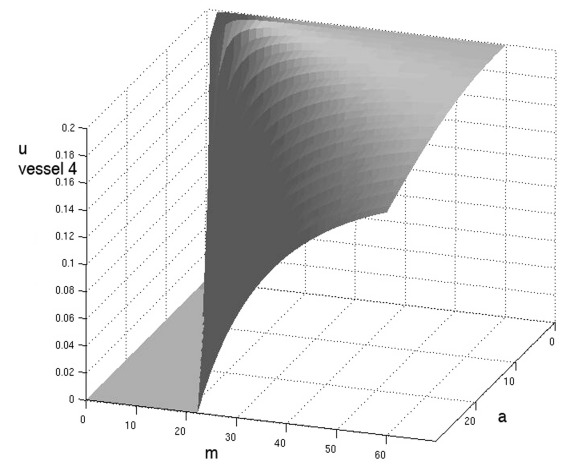
vessel 1



vessel 2

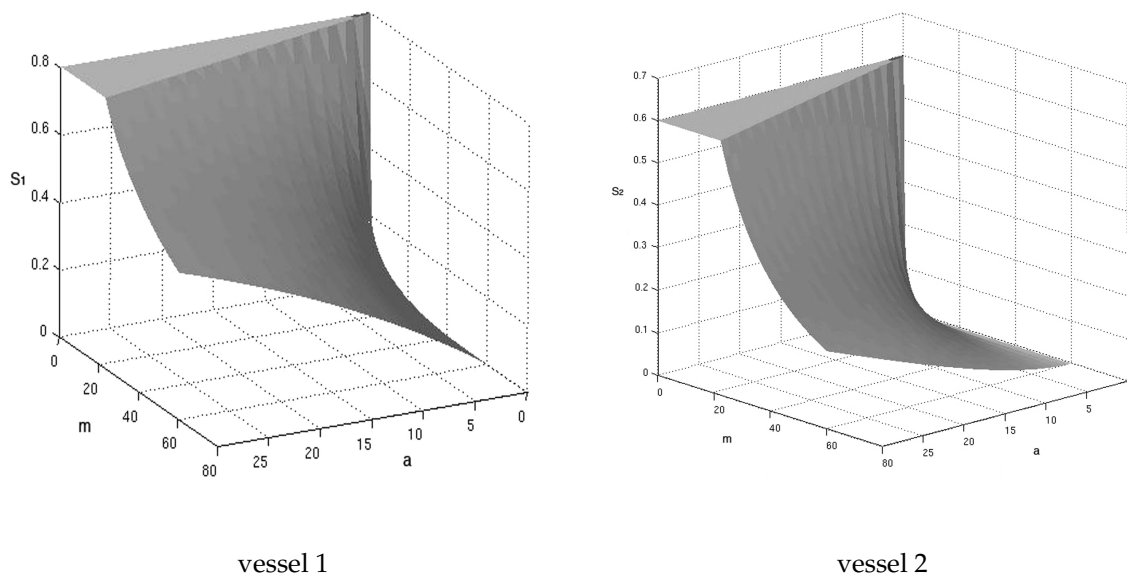


vessel 3



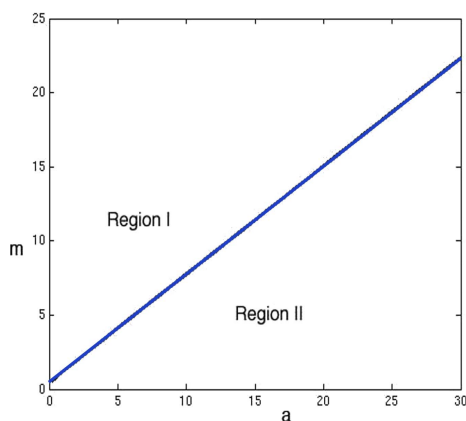
vessel 4

**Figure 2.5.5.** Two parameter bifurcation diagram for 1 species in 4 vessels. We plot equilibrium concentration in each vessel vs. both parameters  $a$  and  $m$ .



**Figure 2.5.6.** Two parameter bifurcation diagram for 1 species in 4 vessels. We plot equilibrium concentration of nutrient (i.e.  $z - u$ ) in vessel 1 and 2 vs. both parameters  $a$  and  $m$ .

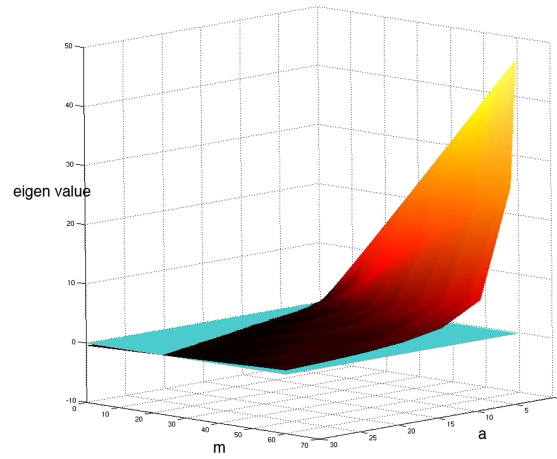
In Figure 2.5.7 we plot  $m^*$  as a function of  $a$  and we obtain a so called *operating diagram* for the gradostat with 1 species in 4 vessels: if the parameters  $a$  and  $m$  are chosen in region II the species dies out, and if they are chosen in region I, the species survives. Note that  $m^*$  increases with  $a$  increasing. As the name says, operating diagrams actually stands for bifurcation diagrams corresponding to the variation of the operating parameters  $S^0$  or  $D$ . Since we have scaled these out of our system, we keep the name also for variation of the species specific parameters.



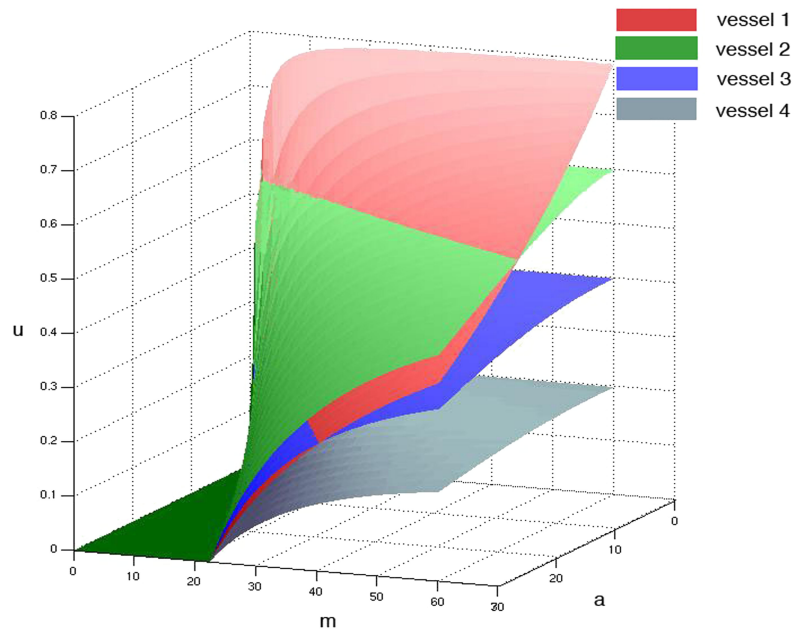
**Figure 2.5.7.** An operating diagram for the gradostat with 1 species in 4 vessels: if the parameters  $a$  and  $m$  are chosen in region I the species survives, and if they are chosen in region II, the species dies out.



In Figure 2.5.8 we plot our measure for the "fitness" of the species i.e.  $s[A + F(z)]$  vs. both  $m$  and  $a$ . Note that for  $m < m^*$ ,  $s[A + F(z)]$  takes negative values very close to zero.



**Figure 2.5.8.** The eigenvalue  $s[A + F(z)]$  vs. the parameters  $m$  and  $a$ .

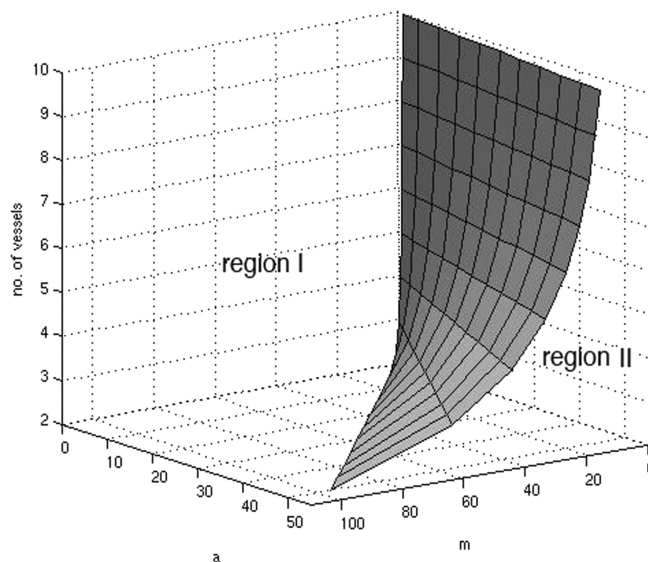


**Figure 2.5.9.** Two parameter bifurcation diagram for 1 species in 4 vessels. We plot the equilibrium species-concentration in all 4 vessels vs. the two parameters  $m$  and  $a$ .

In Figure 2.5.9 we put the 4 different plots from Figure 2.5.4 together to visualize the distribution of species-concentration at equilibrium in the 4 different vessels. As noted in [Tan] and [Smi4], when  $m$  is larger than  $m^*$  but still close to  $m^*$ , which means that the species is strong enough to survive but still quite weak, the species grows best at approximately the middle of the gradostat - this is because even though the left-end vessel is closest to the substrate "source", since it receives migration from only one other vessel, dilution dominates growth due to uptake and migration. As the species grows stronger, the dilution effect decreases and the effect of the amount of available nutrient increases. Thus the maximum concentration-vessel shifts to the left, and for strong enough species it stays in the left-end vessel, where it is closest to the source.

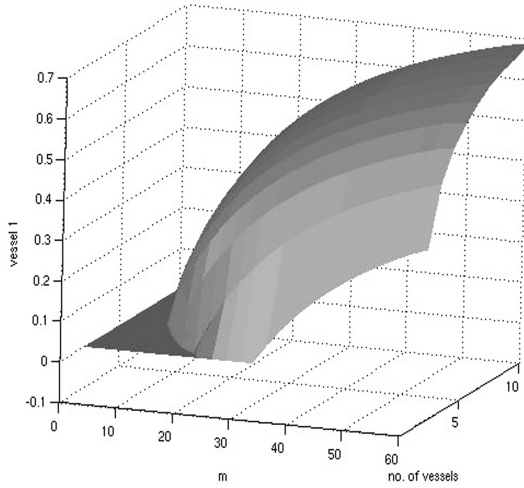
We have been able to visualize the dependence of the species-concentration, the eigenvalue  $s[A + F(z)]$ , and the nutrient concentration on the system's parameters. It remains to see how they depend on  $n$ , the number of vessels.

As noted in [Tan] it is more difficult for a species to survive in the chemostat (in one vessel) than it is in two vessels. In the gradostat also, for a fixed  $a$ , the value of  $m^*$  decreases with the number of vessels increasing: in Figure 2.5.10 we give an operating diagram for one species in up to 10 vessels.



**Figure 2.5.10.** An operating diagram for the gradostat for the no. of vessels between 2 and 10: if the parameters  $a$  and  $m$  are chosen in region I the species survives, and if they are chosen in region II, the species dies out. Note that the size of region II decreases with the no. of vessels increasing.

In Figure 2.5.11 we give a bifurcation diagram for the equilibrium concentration in the first vessel where we fixed the parameter  $a$  and varied  $m$  and the number of vessels  $n$ .



**Figure 2.5.11.** A bifurcation diagram: the equilibrium concentration in the first vessel for  $a = 15$ , vs.  $n$  and  $m$ , with  $n$  varying from 2 to 10.

## 2.6 Competition

We consider now the question of coexistence and persistence of several species in the gradostat and for this we come back to the system (2.1.2).

We have obtained  $s[A + F_j(z)]$  as a first measure of the "fitness" of species  $j$ : if

$$s[A + F_j(z)] > 0,$$

the species is "fit" enough to survive in the gradostat in the absence of competition. It is obvious that survivability is more difficult in the presence of other competitors, so each species needs to be at least as "fit" as in the no-competition situation:

### Proposition 2.6.1

*In the case of  $m$  species competing, let each species start with positive concentrations, and consider one species, say  $j$ ,  $1 \leq j \leq m$ , such that  $s[A + F_j(z)] \leq 0$ . Then species  $j$  is not persistent. That means that any equilibrium solution of (2.1.2),  $\tilde{u} = (\tilde{u}^1, \dots, \tilde{u}^j, \dots, \tilde{u}^m)$ , is of the form*

$$\tilde{u} = (\tilde{u}^1, \dots, \underbrace{0}_{\text{position } j}, \dots, \tilde{u}^m), \text{ with } \tilde{u}^k \geq 0, \text{ for } 1 \leq k \leq m, k \neq j.$$

**Proof:** Choose  $\underline{u}^k = 0$  and  $\bar{u}^k = z$ , for  $1 \leq k \leq m, k \neq j$ , and  $(\underline{u}^j, \bar{u}^j)$  as in the proof of Theorem 2.4.1(i). The proposition follows then immediately.  $\square$

**Remark:** The statement in Prop. 2.5.1 is valid for any number of species for which  $s[A + F_\bullet(z)] \leq 0$ . Therefore, to have a chance of finding strictly positive values for  $\tilde{u}^j$ , in the following we consider  $s[A + F_j(z)] > 0$  for all  $1 \leq j \leq m$ .

**Theorem 2.6.2** (Persistence of several species)

For all  $1 \leq j \leq m$ , let  $\xi^j$  be a time independent upper solution of the steady state problem

$$\begin{aligned} [A + F_j(z - u^j)] \cdot u^j &= 0, \\ u_0^j &> 0. \end{aligned} \quad (2.6.1)$$

Let

$$\theta^j \stackrel{\text{def}}{=} z - \sum_{k \neq j} \xi^k \quad (2.6.2)$$

for all  $1 \leq j \leq m$ , where

$$z - \xi^j > 0, \quad (2.6.3)$$

Suppose that at  $t = t_0$  we have

$$0 < u_0^j \leq \xi^j, \quad (2.6.4)$$

and

$$\sum_{j=1}^m u_0^j \leq z, \quad (2.6.5)$$

for all  $1 \leq j \leq m$ . Moreover, suppose

$$s[A + F_j(\theta^j)] > 0, \text{ for } 1 \leq j \leq m. \quad (2.6.6)$$

Then, for all  $j$ , it is possible to find time independent lower solutions  $\underline{u}^j > 0$ , such that  $\underline{u}^j \leq u^j(t) \leq \xi^j$ , for all  $t > t_0$ , provided that this was true at  $t = t_0$ . This means that all  $m$  species are persistent.

**Proof:** Choose

$$\underline{u}^j := \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)] > 0,$$

with  $\tilde{\gamma}^j$  positive constants, and

$$\bar{u}^j := \xi^j,$$

for  $1 \leq j \leq m$ . We will show that  $(\underline{u}^j, \bar{u}^j)$  is a pair of lower and upper solutions. First, for  $\underline{u}^j$ , we have

$$\begin{aligned} \underline{u}^{j'} &\leq \left[ A + F_j(z - \underline{u}^j - \sum_{k \neq j} \bar{u}^k) \right] \cdot \underline{u}^j \\ \Leftrightarrow 0 &\leq \left[ A + F_j(z - \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)] - \sum_{k \neq j} \xi^k) \right] \cdot \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)] \\ \Leftrightarrow 0 &\leq [A + F_j(\theta^j)] \cdot \phi_s^j[A + F_j(\theta^j)] + [F_j(\theta^j - \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)]) - F_j(\theta^j)] \cdot \phi_s^j[A + F_j(\theta^j)] \\ \Leftrightarrow 0 &\leq \underbrace{s[A + F_j(\theta^j)] \cdot \phi_s^j[A + F_j(\theta^j)]}_{>0} + [F_j(\theta^j - \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)]) - F_j(\theta^j)] \cdot \phi_s^j[A + F_j(\theta^j)]. \end{aligned}$$

The last inequality is satisfied for  $\tilde{\gamma}^j$  chosen small enough and thus  $\underline{u}^j$  is a lower solution.

Now, for  $\bar{u}^j$  we have

$$\begin{aligned}\bar{u}^{j'} &\geq \left[ A + F_j(z - \bar{u}^j - \sum_{k \neq j} \bar{u}^k) \right] \cdot \bar{u}^j \\ \Leftrightarrow 0 &\leq \left[ A + F_j(z - \xi^j - \sum_{k \neq j} \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)]) \right] \cdot \xi^j.\end{aligned}\quad (2.6.7)$$

We choose  $\tilde{\gamma}^j$  small enough so that  $z - \xi^j - \sum_{k \neq j} \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)] \geq 0$  (we have already assumed that  $z - \xi^j > 0$ ).

Since  $\xi^j$  is an upper solution for (2.6.1), we have

$$\begin{aligned}[A + F_j(z - \xi^j)]\xi^j &\leq 0 \\ \Rightarrow -A \cdot \xi^j &\geq F_j(z - \xi^j) \cdot \xi^j \geq F_j(z - \xi^j - \sum_{k \neq j} \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)]) \cdot \xi^j\end{aligned}$$

and the last inequality in (2.6.7) is satisfied and thus  $\bar{u}^j$  is an upper solution.  $\square$

Note that the equilibrium solution of (2.5.1) is also a time independent upper solution, which can be chosen independently of a time independent lower solution. Thus, persistence of a species  $j$  happens if  $s[A + F_j(z - \sum_{k \neq j} \hat{u}^k)] > 0$ , with  $\hat{u}^j$  the single species equilibrium of species  $j$ .

**Remark 2.6.3** For (2.1.2),  $(\underline{u}, \bar{u})$ , with  $\underline{u} \equiv 0$  and  $\bar{u}^j = \hat{u}^j$  for  $1 \leq j \leq m$ , is a pair of lower and upper solutions.

**Proof:** Since  $[A + F_j(z - \hat{u}^j)]\hat{u}^j = 0$  for all  $1 \leq j \leq m$ , the remark follows immediately.  $\square$

It is interesting to see that  $\hat{u}^j$  is an upper solution, independently of the number of species competing and/or persisting in the gradostat. This shows that the single species equilibrium concentration is the highest concentration that the species can achieve in the gradostat, fact which is actually expected, since in a competition situation there is less nutrient available than in the no competition one.

On the other hand, such an affirmation is not necessarily true for coexistence-equilibria, regardless of the number of competitors:

**Remark 2.6.4** Assume  $k$  species coexisting in the gradostat and let  $\bar{u}^j > 0$ ,  $1 \leq j \leq k$ , denote a coexistence-equilibrium. For  $k > 1$ ,  $\bar{u}^j$  will not necessarily be upper solutions for the system describing competition of  $m$  species in the gradostat, for any  $m > k$ .

**Proof:** Let species  $1, \dots, k$  coexist.

Let  $\underline{u}^j$ ,  $1 \leq j \leq m$  be lower solutions, and  $\bar{u}^j = \hat{u}^j$  for  $k < j \leq m$ .

For  $\tilde{u}^j$ ,  $1 \leq j \leq k$ , we have

$$[A + F_j(z - \sum_{l=1}^k \tilde{u}^l)]\tilde{u}^j = 0.$$

We check whether  $\tilde{u}^j$  are upper solutions:

$$\tilde{u}^{j'} = 0 \stackrel{?}{\geq} [A + F_j(z - \tilde{u}^j - \sum_{\substack{l=1 \\ l \neq j}}^m \underline{u}^l)]\tilde{u}^j.$$

For the inequality to hold, we would need  $\sum_{l=1, l \neq j}^m \underline{u}^l \geq \sum_{l=1, l \neq j}^k \tilde{u}^l$ ,  $1 \leq j \leq m$ , which does not necessarily hold since  $\underline{u}^j$  are small.  $\square$

**Corollary 2.6.5** (Existence of positive steady state solutions)

*Under the conditions of Theorem 2.6.2, (2.1.2) has at least one positive steady state solution.*

**Proof:** This follows immediately since in Theorem 2.6.2 we have used time independent lower and upper solutions.  $\square$

**Remark** At this point, for the one-species problem we were able to show that the positive steady state solution was unique and stable for positive initial values. The proof was based on the fact that the one-species reaction function was quasimonotone nondecreasing. Unfortunately, the nondecreasing hypothesis no longer holds for the competition reaction terms. Uniqueness of the positive steady state solution and the global behavior of the competition system remain open problems.

A biological interpretation of Theorem 2.6.2 would be that  $m$  species can coexist in the gradostat if each of them is able to survive on the amount of nutrient left in the system by the rest of the species, each present at its no-competition equilibrium level. These were exactly the conditions obtained for the persistence of two species in the gradostat.

We have obtained conditions for persistence of (2.1.2) and for the existence of at least one equilibrium point inside the positive cone. We also have conditions for the system to tend to the boundary of the positive cone, in the case of one or more species not being able to survive alone in the gradostat. We want to see now when the system tends to the boundary even though each species can survive in the gradostat by itself, that means we look for conditions that give us no persistence for one or more species but this time due to competition. Since, from Theorem 2.6.2, a species  $j$  is persistent if  $s[A + F_j(z - \sum_{k \neq j} \xi^k)] > 0$ , we want to see what happens if this inequality does not hold.

**Theorem 2.6.6** (Extinction of "bad" competitors)

Consider the sets  $P$ ,  $B$ , and  $U$  such that  $P \cup B \cup U = \{1, \dots, m\}$  and  $P \cap B = P \cap U = B \cap U = \emptyset$ .

With the same notations as in Theorem 2.6.2, for  $j \in P$  suppose that

$$s[A + F_j(\theta^j)] > 0, \text{ for } 1 \leq j \leq m. \quad (2.6.8)$$

Define now

$$v \stackrel{\text{def}}{=} z - \sum_{j \in P} \underline{u}^j \quad (2.6.9)$$

with

$$\underline{u}^j := \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)], \quad j \in P.$$

For  $j \in B$ , assume

$$s[A + F_j(v)] \leq 0, \quad (2.6.10)$$

and for  $j \in U$ ,

$$s[A + F_j(v)] > 0 \geq s[A + F_j(\theta^j)]. \quad (2.6.11)$$

Let (2.6.2) to (2.6.5) hold for  $1 \leq j \leq m$ .

Then there exists a pair of lower and upper solutions  $(\underline{u}, \bar{u})$  such that:

(a) For  $j \in P$ , we have

$$0 < \underline{u}^j = \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)] \leq u^j(t) \leq \xi^j,$$

for all  $t > t_0$ , provided that it was true at  $t = t_0$ , which means that all  $P$ -species are persistent.

(b) For  $j \in B$ , we have

$$0 \leq u^j(t) \leq \bar{u}^j(t) \leq \xi^j$$

for all  $t > t_0$ , provided that it was true at  $t = t_0$ , where  $\bar{u}^j(t) > 0$  and  $\bar{u}^j(t)$  decays exponentially to zero, which means that all  $B$ -species are not persistent.

(c) For  $j \in U$ , we have

$$0 \leq u^j(t) \leq \xi^j,$$

for all  $t > t_0$ , provided that it was true at  $t = t_0$ .

**Proof:** Define:

$$\underline{u}^j = \begin{cases} \tilde{\gamma}^j \cdot \phi_s^j[A + F_j(\theta^j)] & : j \in P \\ 0 & : j \in B \cup U, \end{cases} \quad (2.6.12)$$

and

$$\bar{u}^j = \begin{cases} \xi^j & : j \in P \cup U \\ \gamma^j(t) \cdot \phi_s^j[A + F_j(v)] & : j \in B, \end{cases} \quad (2.6.13)$$

with

$$\gamma^j(t) \stackrel{\text{def}}{=} \tilde{\gamma}^j \cdot e^{s[A + F_j(v)] \cdot t},$$

for  $j \in B$  and  $\tilde{\gamma}^j$ , for  $j \in P \cap B$ , fulfill the same conditions as the positive constants chosen in the proof of Theorem 2.6.2.

We first prove that  $(\underline{u}^j, \bar{u}^j)$  is a pair of lower and upper solutions for  $j \in B$ . The function  $\underline{u}^j \equiv 0$  is obviously a subsolution, and for  $\bar{u}^j$ , we have:

$$\begin{aligned} \bar{u}^{j'} &\geq \left[ A + F_j(z - \bar{u}^j - \sum_{k \neq j} \underline{u}^k) \right] \cdot \bar{u}^j \\ \Leftrightarrow &\tilde{\gamma}^j \cdot s[A + F_j(v)] \cdot e^{s[A + F_j(v)] \cdot t} \cdot \phi_s^j[A + F_j(v)] \\ &\geq \left[ A + F_j \left( z - \tilde{\gamma}^j \cdot e^{s[A + F_j(v)] \cdot t} \cdot \phi_s^j[A + F_j(v)] - \sum_{k \in P} \tilde{\gamma}^k \cdot \phi_s^k[A + F_k(\theta^k)] \right) \right] \\ &\quad \cdot \tilde{\gamma}^j \cdot e^{s[A + F_j(v)] \cdot t} \cdot \phi_s^j[A + F_j(v)] \\ \Leftrightarrow &s[A + F_j(v)] \cdot \phi_s^j[A + F_j(v)] \\ &\geq \left[ A + F_j \left( v - \tilde{\gamma}^j \cdot e^{s[A + F_j(v)] \cdot t} \cdot \phi_s^j[A + F_j(v)] \right) \right] \cdot \phi_s^j[A + F_j(v)] \\ \Leftrightarrow &F_j(v) \cdot \phi_s^j[A + F_j(v)] \geq F_j \left( v - \tilde{\gamma}^j \cdot e^{s[A + F_j(v)] \cdot t} \cdot \phi_s^j[A + F_j(v)] \right) \cdot \phi_s^j[A + F_j(v)]. \end{aligned}$$

The last inequality is satisfied, with  $\tilde{\gamma}^j$ , for  $j \in P \cap B$ , chosen small enough so that

$$z - \tilde{\gamma}^j \cdot e^{s[A + F_j(v)] \cdot t} \cdot \phi_s^j[A + F_j(v)] - \sum_{k \in P} \tilde{\gamma}^k \cdot \phi_s^k[A + F_k(\theta^k)] \geq 0,$$

and thus the functions  $\bar{u}^j$  are upper solutions for  $j \in B$ .

The proof that  $(\underline{u}^j, \bar{u}^j)$  is a pair of lower and upper solutions for  $j \in U$  is trivial, and for  $j \in U$ , the proof is as in the proof of Theorem 2.6.2.  $\square$

**Proposition 2.6.7** (Invasion of a persistent equilibrium)

Consider  $m$  species persistent in the gradostat and let  $(\tilde{u}^1, \dots, \tilde{u}^m)$ ,  $\tilde{u}^j > 0$  for all  $1 \leq j \leq m$ , denote a coexistence equilibrium. We introduce a  $m + 1$ -th species in the system.

If

$$s[A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] > \max_{1 \leq i \leq n} (f_{m+1}(z - \sum_{j=1}^m \tilde{u}^j) - f_{m+1}(z - \sum_{j=1}^m \hat{u}^j)),$$

then species  $m + 1$  is persistent.



**Proof:** For  $1 \leq j \leq m$ , choose  $(\underline{u}^j, \bar{u}^j) = (0, \hat{u}^j)$ , as lower and upper solutions. Choose then  $\bar{u}^{m+1} = \hat{u}^{m+1}$  which is an upper solution, and

$$\underline{u}^{m+1} = \tilde{\gamma}^{m+1} \cdot \phi_s^{m+1} [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)].$$

For  $\underline{u}^{m+1}$  we have:

$$\begin{aligned} \underline{u}^{m+1'} &= 0 \\ &\leq \left[ A + F_{m+1} \left( z - \tilde{\gamma}^{m+1} \cdot \phi_s^{m+1} [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] - \sum_{j=1}^m \hat{u}^j \right) \right] \cdot \\ &\quad \cdot \tilde{\gamma}^{m+1} \cdot \phi_s^{m+1} [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] \\ \Leftrightarrow 0 &\leq \left[ F_{m+1} \left( z - \tilde{\gamma}^{m+1} \cdot \phi_s^{m+1} [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] - \sum_{j=1}^m \hat{u}^j \right) - F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j) \right] \cdot \\ &\quad \cdot \phi_s^{m+1} [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] + \left[ A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j) \right] \cdot \phi_s^{m+1} [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] \\ \Leftrightarrow 0 &\leq \left[ F_{m+1} \left( z - \tilde{\gamma}^{m+1} \cdot \phi_s^{m+1} [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] - \sum_{j=1}^m \hat{u}^j \right) - F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j) \right] \cdot \\ &\quad \cdot \phi_s^{m+1} [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] + s [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] \cdot \phi_s^{m+1} [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] \end{aligned}$$

and the last inequality is true if

$$s [A + F_{m+1}(z - \sum_{j=1}^m \tilde{u}^j)] > \max_{1 \leq i \leq n} (f_{m+1}(z_i - \sum_{j=1}^m \tilde{u}_i^j) - f_{m+1}(z_i - \sum_{j=1}^m \hat{u}_i^j)),$$

and  $\tilde{\gamma}^{m+1}$  small enough.  $\square$

## 2.7 Two species: persistence and existence of positive equilibria

In the following we consider the competition of two species in  $n$  vessels. We have then the system

$$\begin{aligned} u^{1'} &= [A + F_1(z - u^1 - u^2)] u^1, \\ u^{2'} &= [A + F_2(z - u^1 - u^2)] u^2, \\ u^1(t_0) &\geq 0, \quad u^2(t_0) \geq 0, \end{aligned} \tag{2.7.1}$$

in  $\Omega = \{u \geq 0 \mid u^1 + u^2 \leq z\}$ , and the corresponding steady state system:

$$\begin{aligned} [A + F_1(z - u^1 - u^2)] u^1 &= 0, \\ [A + F_2(z - u^1 - u^2)] u^2 &= 0. \end{aligned} \quad (2.7.2)$$

Using Remark 2.6.3, Theorem 2.6.2 takes then the form:

### Theorem 2.7.1

Consider that both  $s[A + F_1(z)] > 0$  and  $s[A + F_2(z)] > 0$  and thus both single species equilibria  $\hat{E}_1 = (\hat{u}^1, 0)$  and  $\hat{E}_2 = (0, \hat{u}^2)$  exist.

Suppose that

$$\begin{aligned} s[A + F_1(z - \hat{u}^2)] &> 0, \\ s[A + F_2(z - \hat{u}^1)] &> 0. \end{aligned} \quad (2.7.3)$$

Then both species are persistent: it is possible to find time independent lower solutions  $\underline{u}^1$  and  $\underline{u}^2$  such that  $\underline{u}^1 \leq u^1(t) \leq \hat{u}^1$  and  $\underline{u}^2 \leq u^2(t) \leq \hat{u}^2$  for all  $t \leq t_0$ , provided it was true at  $t = t_0$ .

The lower solutions in this case are the same as the ones found in the proof of Theorem 2.6.2, namely

$$\begin{aligned} \underline{u}^1 &= \tilde{\gamma}^1 \dot{\phi}_s^1[A + F_1(z - \hat{u}^2)] > 0, \\ \underline{u}^2 &= \tilde{\gamma}^2 \dot{\phi}_s^2[A + F_2(z - \hat{u}^1)] > 0, \end{aligned}$$

with  $\phi_s^1[A + F_1(z - \hat{u}^2)]$ , the eigenvector corresponding to  $s[A + F_1(z - \hat{u}^2)]$  and  $\phi_s^2[A + F_2(z - \hat{u}^1)]$ , the eigenvector corresponding to  $s[A + F_2(z - \hat{u}^1)]$ , and  $\tilde{\gamma}^1$  and  $\tilde{\gamma}^2$  positive constants.

From the iteration process (A.5.7), namely

$$\begin{aligned} \underline{u}^{(0)} &= \underline{u}, \\ \bar{u}^{(0)} &= \bar{u}, \end{aligned}$$

$k \geq 1$ :

$$\begin{aligned} M_1 \underline{u}^{1,(k)} &= [A + F_1(z - \underline{u}^{1,(k-1)} - \bar{u}^{2,(k-1)})] \cdot \underline{u}^{1,(k-1)} + M_1 \underline{u}^{1,(k-1)}, \\ M_2 \underline{u}^{2,(k)} &= [A + F_2(z - \bar{u}^{1,(k-1)} - \underline{u}^{2,(k-1)})] \cdot \underline{u}^{2,(k-1)} + M_2 \underline{u}^{2,(k-1)}, \end{aligned} \quad (2.7.4)$$

$$\begin{aligned} M_1 \bar{u}^{1,(k)} &= [A + F_1(z - \bar{u}^{1,(k-1)} - \underline{u}^{2,(k-1)})] \cdot \bar{u}^{1,(k-1)} + M_1 \bar{u}^{1,(k-1)}, \\ M_2 \bar{u}^{2,(k)} &= [A + F_2(z - \underline{u}^{1,(k-1)} - \bar{u}^{2,(k-1)})] \cdot \bar{u}^{2,(k-1)} + M_2 \bar{u}^{2,(k-1)}, \end{aligned}$$

$$u^{(k)}(t_0) = u_0,$$

we obtain the two sequences  $\{\underline{u}^{(k)}\}$  and  $\{\bar{u}^{(k)}\}$  with the property

$$\underline{u} \leq \underline{u}^{(k)} \leq \underline{u}^{(k+1)} \leq u_{\min} \leq u_{\max} \leq \bar{u}^{(k+1)} \leq \bar{u}^{(k)} \leq \bar{u}$$

for every  $k$ , with  $(\underline{u}^{1,(k)}, \underline{u}^{2,(k)})$  and  $(\bar{u}^{1,(k)}, \bar{u}^{2,(k)})$  coupled lower and upper solutions for each  $k$ , where

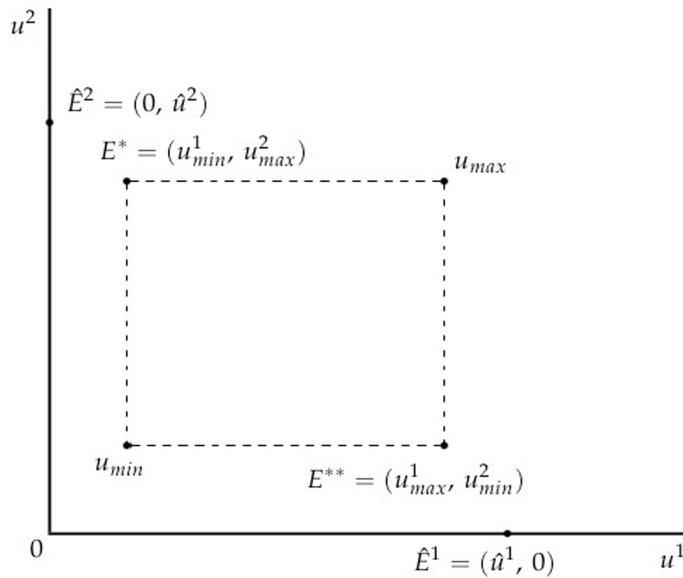
$$u_{\min}(t) = \lim_{k \rightarrow \infty} \underline{u}^{(k)}(t), \quad u_{\max}(t) = \lim_{k \rightarrow \infty} \bar{u}^{(k)}(t).$$

We have that  $u_{\min}$  and  $u_{\max}$  satisfy the relations

$$\begin{aligned} u_{\min}^1 &= [A + F_1(z - u_{\min}^1 - u_{\max}^2)] u_{\min}^1, \\ u_{\min}^2 &= [A + F_2(z - u_{\max}^1 - u_{\min}^2)] u_{\min}^2, \end{aligned}$$

$$\begin{aligned} u_{\max}^1 &= [A + F_1(z - u_{\max}^1 - u_{\min}^2)] u_{\max}^1, \\ u_{\max}^2 &= [A + F_2(z - u_{\min}^1 - u_{\max}^2)] u_{\max}^2, \end{aligned}$$

and thus,  $(u_{\min}^1, u_{\max}^2)$  and  $(u_{\max}^1, u_{\min}^2)$  are solutions of the steady state system (2.7.2). Denote with  $E^* = (u_{\min}^1, u_{\max}^2)$  and  $E^{**} = (u_{\max}^1, u_{\min}^2)$  the two steady states.



**Figure 2.7.1.** The two equilibria  $E^*$  and  $E^{**}$  together with the single species equilibria  $\hat{E}^1$  and  $\hat{E}^2$ . Each axis represents a copy of  $\mathbb{R}^n$ .

Applying Theorem A.5.5 in our case, we obtain that any solution  $u$  of (2.7.2) in the sector  $\langle \underline{u}, \bar{u} \rangle$  is necessarily in the sector  $\langle u_{\min}, u_{\max} \rangle$ .

Thus, the positive equilibria  $E^*$  and  $E^{**}$  are the same as the equilibria obtained in [STW], Th. 5.5 (see Theorem 1.3.2). We have then that the set

$$O = ([u_{min}^1, u_{max}^1] \times [u_{min}^2, u_{max}^2]) \cap \Omega$$

attracts (almost) all orbits corresponding to initial data  $u_0 \in \Omega$  with  $u_0 > 0$ : there exists an open and dense subset of  $\Omega$  consisting of points  $u_0$  for which the solution of (2.7.2) approaches an equilibrium point in  $O$  as  $t \rightarrow \infty$ . Moreover,  $E^*$  attracts all orbits with initial data in  $(0, u_{min}^1] \times [u_{max}^2, \hat{u}^2]$ , with  $u_0^1 > 0$ , and  $E^{**}$  attracts all orbits with initial data in  $[u_{max}^1, \hat{u}^1] \times (0, u_{min}^2]$  with  $u_0^2 > 0$ .

As mentioned in section 2.4, the reaction functions in the system for more than 1 species are no longer quasimonotone nondecreasing (which was the case for a single species) and thus the results in Appendix A for the uniqueness of the positive steady state can no longer be used. Of course, if we could show that  $u_{min} = u_{max}$ , uniqueness would follow automatically with  $E^* = E^{**}$  as a global attractor. This was the case for 2 species in 2 vessels, but for more than 2 vessels, there are no analytic results regarding uniqueness of the positive steady state.

Numerically however, in every simulation it looks like the positive steady states are unique: for initial data with  $u_0^1$  slightly smaller or even equal to  $\hat{u}^1$  and small  $u_0^2 > 0$  we obtained the same steady states as for initial data with small, positive  $u_0^1$  and  $u_0^2$  slightly smaller than  $\hat{u}^2$ .

## 2.8 Two species: bifurcation diagrams

In the previous section we were able to obtain with the help of the tools described in Appendix A, sufficient conditions for the persistence of 2 species in a  $n$  vessel gradostat and the existence of positive equilibria.

As in section 2.5 and following the results from [STW], we next take a look at system (2.7.2) with  $m_2$  as a bifurcation parameter (keeping all other parameters fixed). We assume throughout this section that  $s[A + F_1(z)] > 0$  so that species 1 survives alone in the gradostat and look for "types of species" (in terms of the species-dependent parameters) that can 'invade' the equilibrium  $\hat{u}^1$ .

Let  $\Lambda_2 = \{(m_2, u) : u \in \Omega \text{ satisfies (2.7.2) corresponding to } m_2\}$ .

Denote with

$$\hat{Q}_1 = \{(m_2, \hat{u}^1, 0) : m_2 \geq 0\},$$

the branch of the solution set corresponding to the equilibrium  $\hat{E}^1$ .

Since  $s[A + m_2 \tilde{F}_2(z)]$  increases from negative values to infinity with  $m_2$  increasing (Lemma 2.5.2), there exists a unique value  $\hat{m}_2$  such that  $s[A + \hat{m}_2 \tilde{F}_2(z)] = 0$ , and  $\hat{m}_2$  is the threshold value for  $m_2$  above which  $\hat{E}^2$  exists (Theorem 2.5.3). We obtain the branch

$$\hat{Q}_2 = \{(m_2, 0, \hat{u}^2(m_2)) : m_2 > \hat{m}_2\},$$

corresponding to the equilibrium  $\hat{E}^2$ . From Lemma 2.5.2 we have that the value of  $\hat{u}^2(m_2)$  increases with  $m_2 > \hat{m}_2$  increasing.

The sufficient conditions for the coexistence of the two species were

$$\begin{aligned} s[A + F_1(z - \hat{u}^2(m_2))] &> 0, \\ s[A + m_2 \tilde{F}_2(z - \hat{u}^1)] &> 0. \end{aligned}$$

According to Perron-Frobenius Theorem there exists a unique positive  $m_2^{**}$  such that

$$s[A + m_2^{**} \tilde{F}_2(z - \hat{u}^1)] = 0,$$

with  $\hat{m}_2 < m_2^{**}$ , and for  $m_2 > m_2^{**}$  we have that  $s[A + F_1(z - \hat{u}^2(m_2))] > 0$  holds and  $\hat{E}^1$  is unstable.

Next, since  $\hat{u}^2$  is strictly increasing in  $m_2$  with  $\hat{u}^2$  decreasing to 0 with  $m_2$  decreasing towards  $\hat{m}_2$ , we have that  $s[A + F_1(z - \hat{u}^2(m_2))]$  is strictly decreasing in  $m_2$  and tends to  $s[A + F_1(z)]$  as  $m_2$  tends to  $\hat{m}_2$ .

In [STW] it is shown that there exists a unique positive  $m_2^*$  such that

$$s[A + F_1(z - \hat{u}^2(m_2^*))] = 0$$

with  $\hat{m}_2 < m_2^*$ , and for  $\hat{m}_2 < m_2 < m_2^*$ ,  $\hat{E}^2(m_2)$  is unstable and asymptotically stable for  $m_2 > m_2^*$ , justifying the decomposition of  $\hat{Q}_2$  into an unstable and stable branch:

$$\begin{aligned} \hat{Q}_2 &= \hat{Q}_2^u \cup \hat{Q}_2^s, \\ \hat{Q}_2^u &= \{(m_2, 0, \hat{u}_2(m_2)) : \hat{m}_2 < m_2 < m_2^*\}, \\ \hat{Q}_2^s &= \{(m_2, 0, \hat{u}_2(m_2)) : m_2 > m_2^*\}. \end{aligned}$$

**Theorem 2.8.1** (Theorem 6.1. in [STW])

There exists an unbounded connected subset  $S^+$  of  $\Lambda_2$  bifurcating from  $\hat{Q}_1$  at  $(m_2^{**}, \hat{u}^1, 0)$  and joining  $\hat{Q}_2^s$  at  $(m_2^*, 0, \hat{u}^2(m_2^*))$ :

(a)  $(m_2^{**}, \hat{u}^1, 0) \in S^+$  and  $(m_2, u^1, u^2) \in S^+$  with  $u^2 = 0$  implies  $m_2 = m_2^{**}$  and  $u^1 = \hat{u}^1$ .

(b) There exists a neighborhood  $W_1^+$  of  $(m_2^{**}, \hat{u}^1, 0)$  in  $\mathbb{R}_+ \times \mathbb{R}_+^{2n}$  such that

$$W_1^+ \cap S^+ = \{(m_2^{**}(s), \hat{u}^1(s), \hat{u}^2(s)) : 0 \leq s \leq \delta\},$$

where  $m_2^{**}(s)$ ,  $\hat{u}^1(s)$ ,  $\hat{u}^2(s)$  are smooth functions satisfying

$$\begin{aligned} m_2^{**}(s) &= m_2^{**} + \kappa s + o(s), \\ \hat{u}^1(s) &= \hat{u}^1 + s\hat{w}_1 + o(s), \quad s \rightarrow 0_+, \\ \hat{u}^2(s) &= s\hat{w}_2 + o(s), \end{aligned} \tag{2.8.1}$$

where  $(\hat{w}_1, \hat{w}_2)$  with  $\hat{w}_1 < 0$  and  $\hat{w}_2 > 0$  is a normalized null vector of the Jacobian of (2.7.2) at  $\hat{E}^1$  corresponding to  $m_2^{**}$ .

(c)  $Q_2^s \subseteq S^+$  and  $Q_2^s \cap S^+ = \emptyset$ . If  $(m_2, u^1, u^2) \in S^+$  and  $u^1 = 0$ , then  $(m_2, u^1, u^2) \in Q_2^s$ .

(d) There exists a neighborhood  $W_2^+$  of  $(m_2^*, 0, \hat{u}^2)$  in  $\mathbb{R}_+ \times \mathbb{R}_+^{2n}$  such that

$$W_2^+ \cap S^+ = \{(m_2^*(s), \hat{u}^1(s), \hat{u}^2(s)) : 0 \leq s \leq \delta\} \cup \{(m_2, 0, \hat{u}^2) : m_2^* < m_2 < m_2^* + s\},$$

where  $m_2^*(s)$ ,  $\hat{u}^1(s)$ ,  $\hat{u}^2(s)$  are smooth functions satisfying

$$\begin{aligned} m_2^*(s) &= m_2^* + \eta s + o(s), \\ \hat{u}^1(s) &= s\hat{v}_1 + o(s), \quad s \rightarrow 0_+, \\ \hat{u}^2(s) &= \hat{u}^2(s)(m_2^*) + s\hat{v}_2 + o(s), \end{aligned} \tag{2.8.2}$$

where  $(\hat{v}_1, \hat{v}_2)$  with  $\hat{v}_1 > 0$  and  $\hat{v}_2 < 0$  is a normalized null vector of the Jacobian of (2.7.2) at  $\hat{E}^2(m_2^*)$ .

(e) There exists  $\bar{m}_2 \geq m_2^*$  such that for  $m_2 > \bar{m}_2$ , the solution set is

$$\Sigma = \{E_0 = (0, 0), \hat{E}^1, \hat{E}^2(m_2)\}$$

and  $\hat{E}^2$  is the attractor for all solutions of (2.7.1) with  $u_0 > 0$ .

The variational matrix of (2.7.1) takes the form

$$J = \begin{bmatrix} A + F_1(z - u^1 - u^2) - D_1 & -D_1 \\ -D_2 & A + F_2(z - u^1 - u^2) - D_2 \end{bmatrix},$$

where

$$\begin{aligned} D_1 &= \text{diag}(u_1^1 f_1'(z_1 - u_1^1 - u_1^2), \dots, u_n^1 f_1'(z_n - u_n^1 - u_n^2)), \\ D_2 &= \text{diag}(u_1^2 f_2'(z_1 - u_1^1 - u_1^2), \dots, u_n^2 f_2'(z_n - u_n^1 - u_n^2)). \end{aligned}$$

At  $\hat{E}^1$   $J$  is of the form

$$J(\hat{E}^1) = \begin{bmatrix} A + F_1(z - \hat{u}^1) - D_1 & -D_1 \\ 0 & A + F_2(z - \hat{u}^1) \end{bmatrix},$$

and has  $\hat{s}_1 = s[A + F_2(z - \hat{u}^1)] > 0$  as a simple eigenvalue with the corresponding eigenvector  $(\hat{w}_1, \hat{w}_2)$  satisfying

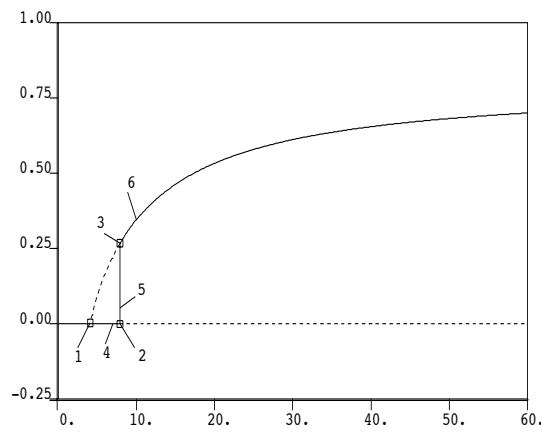
$$\begin{aligned} [A + F_1(z - \hat{u}^1) - D_1]\hat{w}_1 - D_1\hat{w}_2 &= \hat{s}_1\hat{w}_1, \\ [A + F_2(z - \hat{u}^1)]\hat{w}_2 &= \hat{s}_1\hat{w}_2, \end{aligned}$$

where, by Perron-Frobenius Theorem, we can choose  $\hat{w}_2 > 0$ . We can then determine  $\hat{w}_1$  from  $\hat{w}_1 = [A + F_1(z - \hat{u}^1) - D_1 - \hat{s}_1 I]^{-1} D_1 \hat{w}_2 < 0$ . At  $m_2^{**}$  we have  $\hat{s}_1 = 0$  and we obtain the null vector in Theorem 2.8.1 (b). Similarly,  $J(\hat{E}^2)$  has  $\hat{s}_2 = s[A + F_1(z - \hat{u}^2)] > 0$  as a simple eigenvalue with the corresponding eigenvector  $(\hat{v}_1, \hat{v}_2)$  satisfying  $\hat{v}_1 > 0$  and  $\hat{v}_2 = [A + F_2(z - \hat{u}^2) - D_2 - \hat{s}_2 I]^{-1} D_2 \hat{v}_1 < 0$ . At  $m_2^*$  we have  $\hat{s}_2 = 0$  and we obtain the null vector in Theorem 2.8.1 (d).

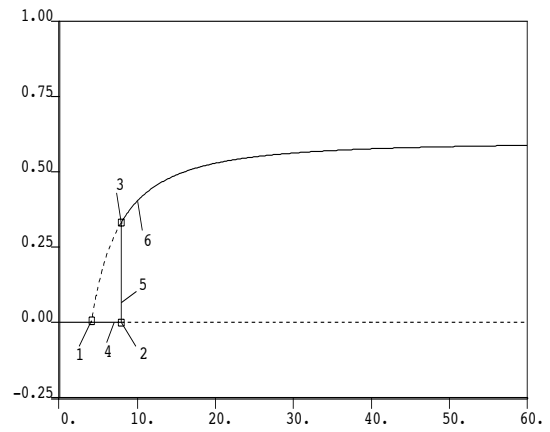
To visualize the results described above for competition between two species, numerical simulations were carried out on the gradostat with four vessels.

We fixed the first species to be the species described by  $m_1 = 30$  and  $a_1 = 20$ . For species 2 we fixed parameter  $a_2 = 5$ . We are interested in finding values for  $m_2$  such that the two species can coexist.

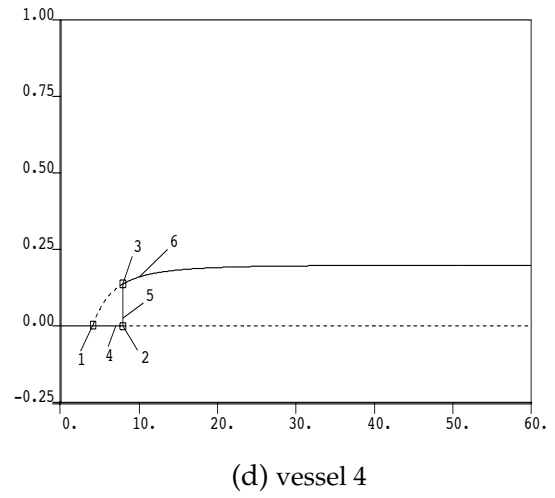
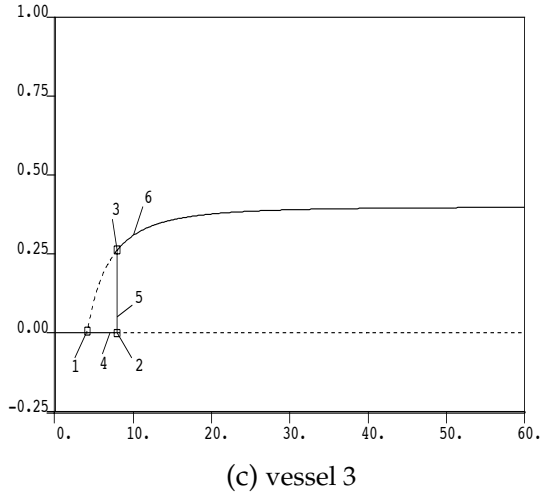
In Figure 2.8.1 and Figure 2.8.2 we give the bifurcation diagrams for the two species in each vessel, with the parameter  $m_2$  varying between 0 and 60.



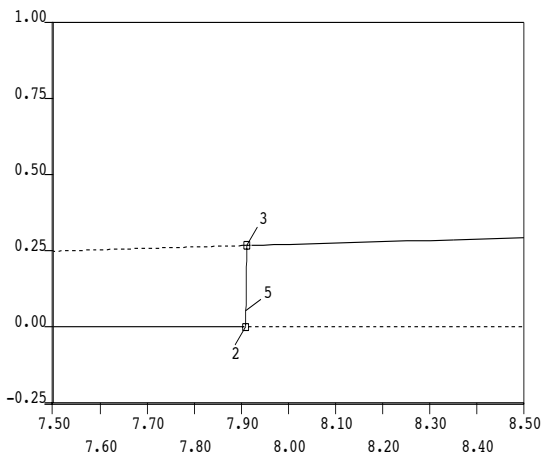
(a) vessel 1



(b) vessel 2

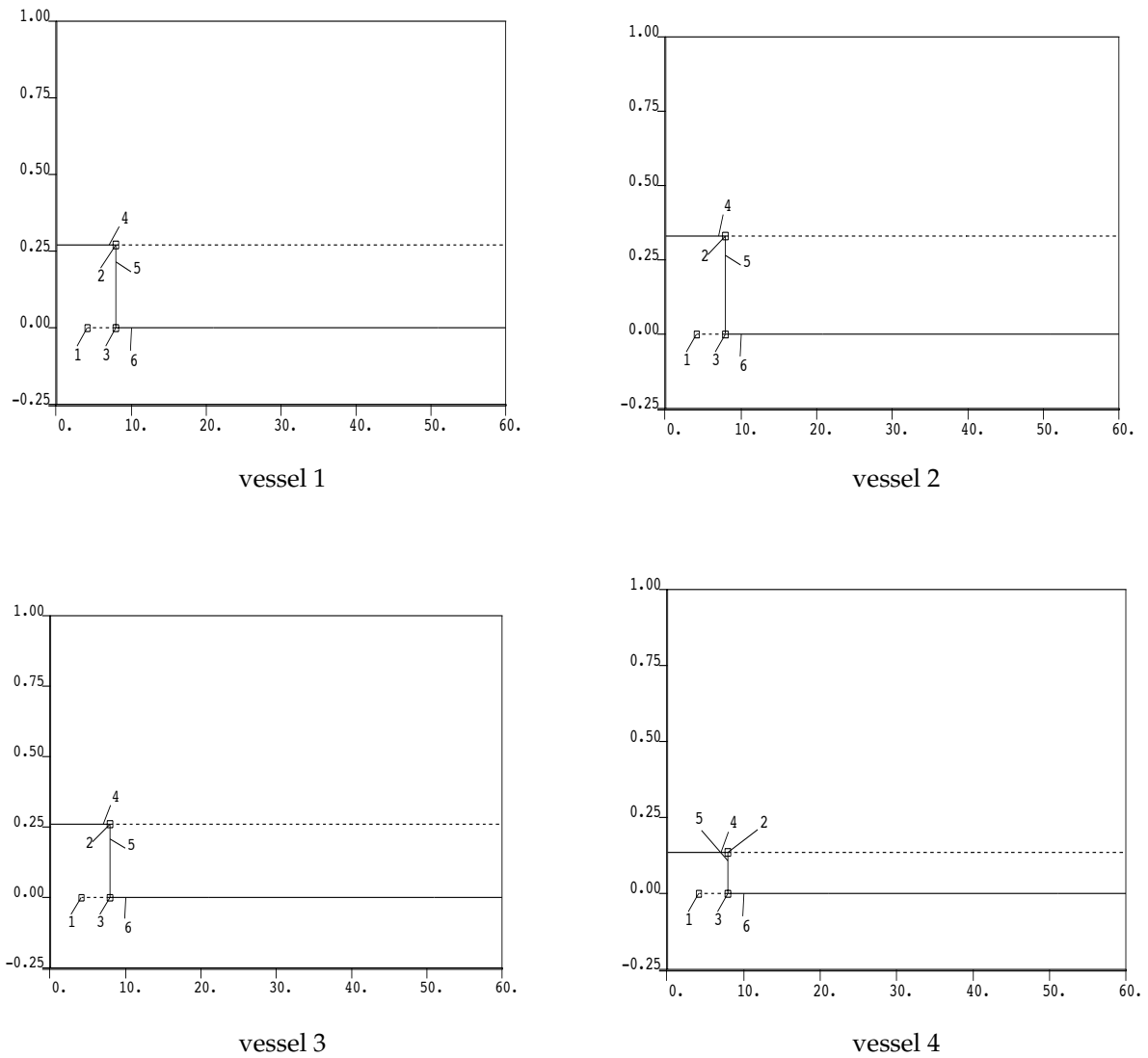


**Figure 2.8.1. (a)-(d): Bifurcation diagram for 2 species in 4 vessels for  $m_1 = 30$ ,  $a_1 = 20$  and  $a_2 = 5$ .** We plot equilibrium concentrations of species 1 in each vessel vs. parameter  $m_2$ . **Label 1** - the bifurcation value:  $\hat{m}_2 = 4.086064$  above which species 2 is able to survive alone in the gradostat ; **label 2** - the bifurcation value  $m_2^{**} = 7.909584$  above which  $\hat{E}^1$  is unstable ; **label 3** - the bifurcation value  $m_2^* = 7.911823$  above which  $\hat{E}^2$  is stable. **Coexistence holds for  $m_2$  between  $m_2^{**}$  and  $m_2^*$ .** **Label 4** -  $m_2 = 7.0$ : species 2 is not strong enough to survive and  $\hat{E}^1$  attracts all orbits with positive initial data -  $\hat{u}^1 = (2.706689E - 01, 3.319689E - 01, 2.615669E - 01, 1.372240E - 01)$ ,  $\hat{u}^2 = 0$ ; **label 5** -  $m_2 = 7.91$ : the two species coexist and there exists a unique positive equilibrium  $E^*$  with  $u^{1*} = (2.170917E - 01, 2.661089E - 01, 2.095885E - 01, 1.099382E - 01)$  and  $u^{2*} = (5.309547E - 02, 6.595205E - 02, 5.227480E - 02, 2.748093E - 02)$ ; **label 6** -  $m_2 = 10.0$ : species 1 is not strong enough to survive and  $\hat{E}^2$  attracts all orbits with positive initial data -  $\hat{u}^1 = 0$ ,  $\hat{u}^2 = (3.461917E - 01, 4.043192E - 01, 3.101712E - 01, 1.612821E - 01)$ . The solid line corresponds to stable equilibria, and the dotted line, to unstable equilibria.



**Figure 2.8.1. (e) Species 2 in vessel 1: detail**

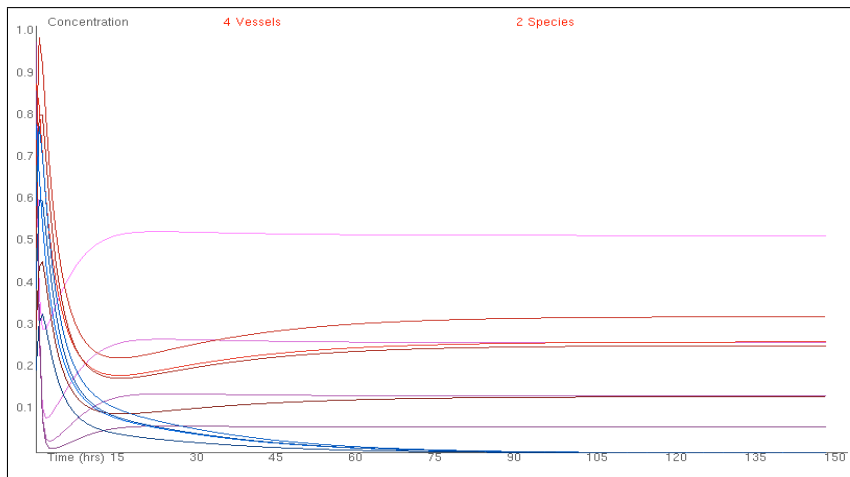




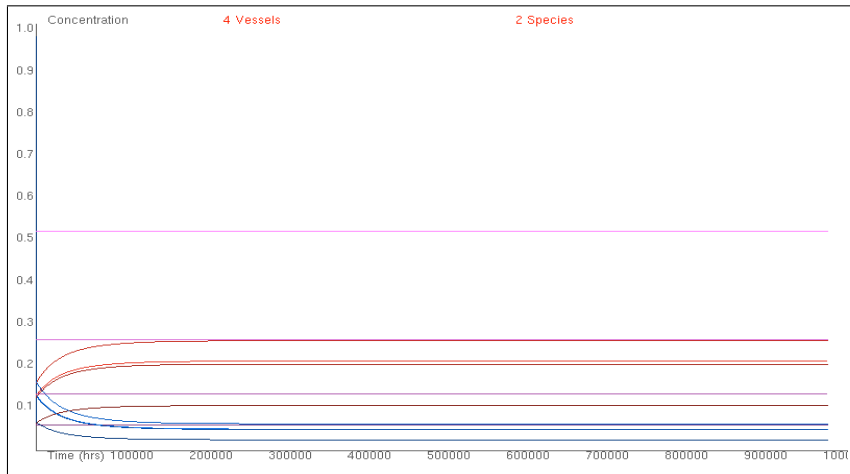
**Figure 2.8.2.** Bifurcation diagram for 2 species in 4 vessels for  $m_1 = 30$ ,  $a_1 = 20$  and  $a_2 = 5$ . We plot equilibrium concentrations of species 1 in each vessel vs. parameter  $m_2$ . The labels are as in Figure 2.8.1.

For the points represented by labels 4, 5, and 6 we plot in Figure 2.8.3 to Figure 2.8.5 the solutions of the system (2.7.1).

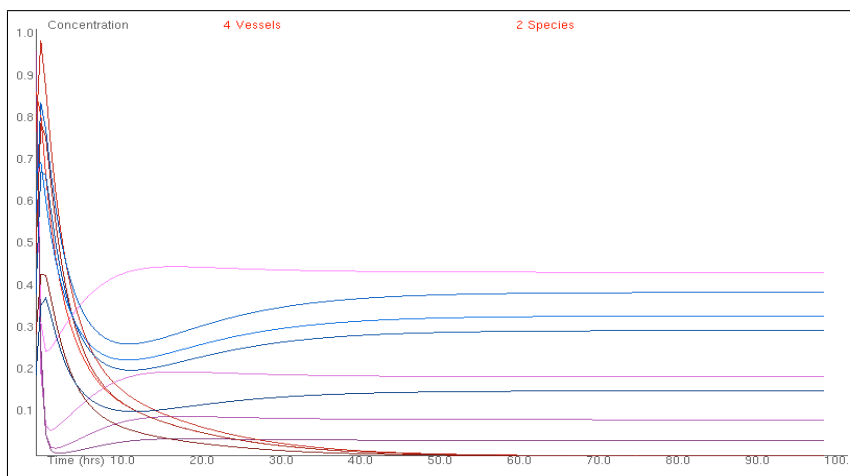
In Figure 2.8.6 we give the bifurcation diagram for vessel 1 and plot the equilibrium concentrations of the two species together in order to better visualize the different branches of the solution set.



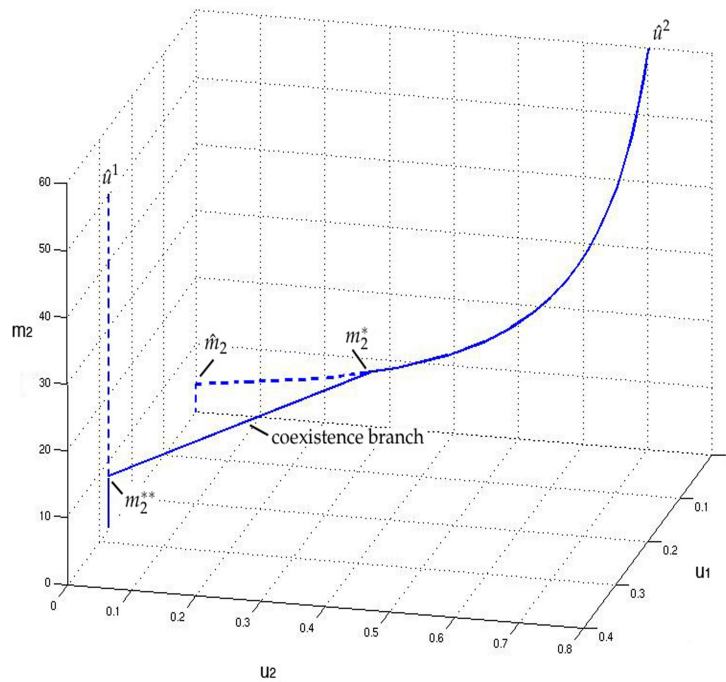
**Figure 2.8.3.** Label 4:  $m_2 = 7$ ;  $u^2 = 0$ .



**Figure 2.8.4.** Label 5:  $m_2 = 7.9$ ; both species survive.



**Figure 2.8.5.** Label 6:  $m_2 = 10$ ;  $u^1 = 0$ .



**Figure 2.8.6.** Bifurcation diagram for 2 species in 4 vessels for  $m_1 = 30$ ,  $a_1 = 20$  and  $a_2 = 5$ . We plot equilibrium concentrations of both species in vessel 1 vs. parameter  $m_2$ .

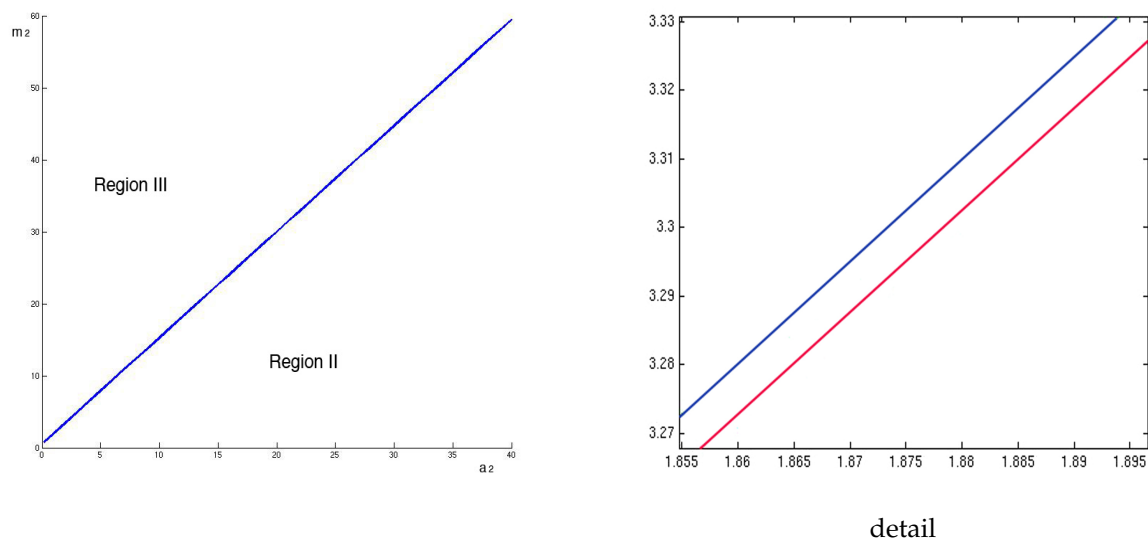
As remarked in [STW], in Theorem 2.8.1 (b) and (d), the coefficients  $\kappa$  and  $\eta$  could be both positive as well as negative, and we can have both  $m_2^{**} < m_2^*$  and  $m_2^{**} > m_2^*$ . If  $\kappa > 0$ , (2.8.1) corresponds to a (supercritical) asymptotically stable branch, and if  $\kappa < 0$ , the branch is unstable (subcritical). Moreover, if  $m_2^{**} > m_2^*$ ,  $\hat{E}^1$  and  $\hat{E}^2$  are both stable and the sufficient conditions we found for coexistence are never met (for the same  $m_2$ ), even though Theorem 2.8.1 gives the existence of a positive equilibrium.

For the gradostat with two vessels however, it must be that  $m_2^{**} < m_2^*$  and the positive equilibrium does not exist for  $m_2$  outside the interval  $(m_2^{**}, m_2^*)$ .

All the simulations we carried out gave  $m_2^{**} < m_2^*$  also for  $n > 2$  and bifurcation diagrams as in Figures 2.8.1., 2.8. 2., and 2.8.6. For the rest of this chapter we make the conjecture that  $m_2^{**} < m_2^*$ , or rather, study the competition of only such species for which this happens (from the examples presented we can see that there exist such species and so far we have no evidence of any "pair" of species for which  $m_2^{**} > m_2^*$ ).

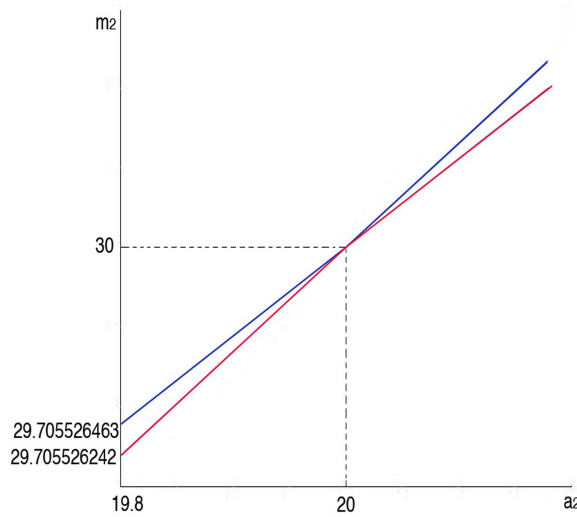
Following this remarks, in Figure 2.8.7 we plot an "operating diagram" which gives us the different species - in terms of  $a_2$  and  $m_2$  - that are able to coexist in the gradostat with 4

vessels together with species 1 given by  $a_1 = 20$  and  $m_1 = 30$ : for each value for  $a_2$  we plot the coexistence interval  $(m_2^{**}(a_2), m_2^*(a_2))$ .

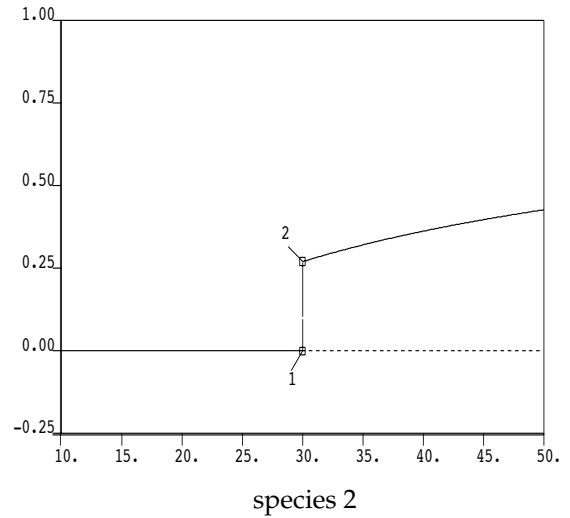
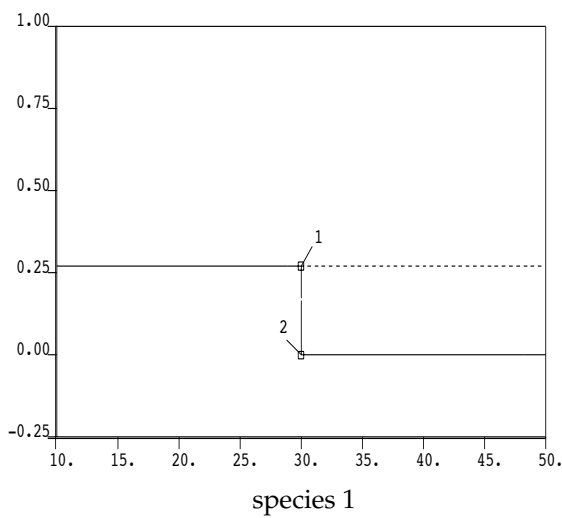


**Figure 2.8.7.** An “operating diagram” for the gradostat with 4 vessels: we plot the three different regions corresponding to the three different types of behavior of a species in competition with the species given by  $a_1 = 20$  and  $m_1 = 30$ . For each value of  $a_2$  we obtain the interval  $(m_2^{**}, m_2^*)$  of coexistence (**Region I**). For  $m_2 < m_2^{**}$  (**Region II**) species 2 dies out, and for  $m_2 > m_2^*$  (**Region III**) species 1 dies out.

Observe that the coexistence interval  $(m_2^{**}, m_2^*)$  may be degenerated: if, for example,  $a_1 = a_2$ , we have that  $m_2^{**} = m_2^*$  and the coexistence equilibria form a line segment joining  $\hat{E}^1$  to  $\hat{E}^2$  - a structurally unstable situation, as coexistence happens only on the ‘border’ between the two single species attractors. In Figure 2.8.8. we give the portion of the plot in Figure 2.8.7. with  $a_2$  around  $a_2 = a_1$  and in Figure 2.8.9 we give the corresponding bifurcation diagrams.

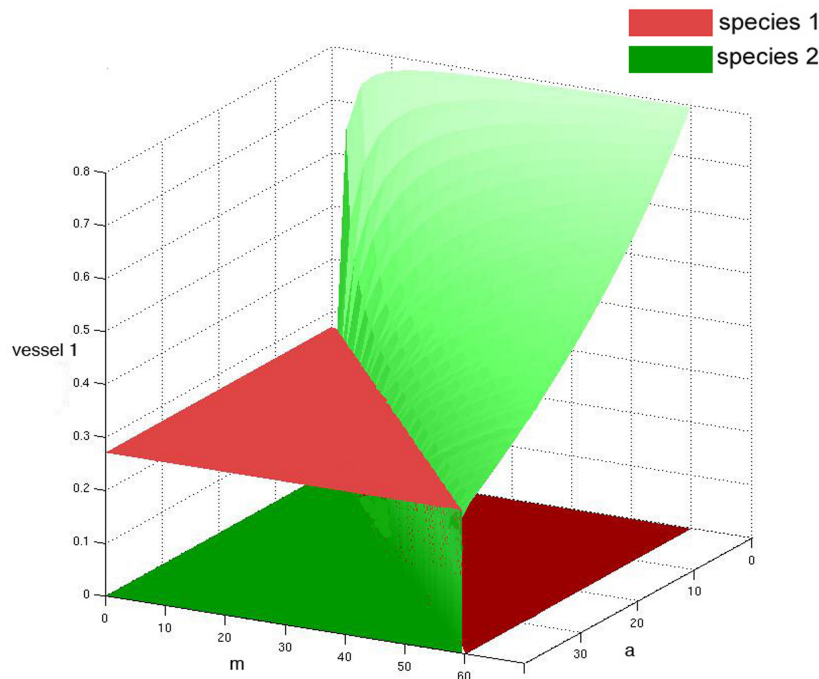


**Figure 2.8.8.** A detail of the operating diagram for  $m_1 = 30$ , and  $a_1 = 20$ . The size of the coexistence interval decreases as  $a_2$  increases towards  $a_1$  and increases as  $a_2$  grows beyond  $a_1$ . In  $a_2 = a_1$  the interval degenerates to one point.



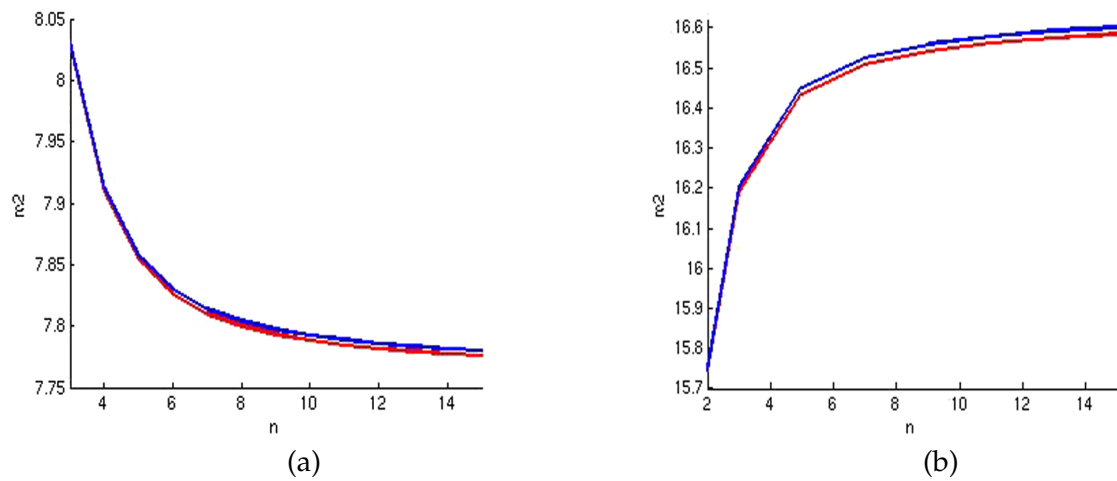
**Figure 2.8.9.** Bifurcation diagrams for  $a_1 = a_2 = 20$ , and  $m_1 = 30$ . We plot the equilibrium concentrations of the two species in the first vessel. The coexistence equilibria form a line segment joining  $\hat{E}^1$  to  $\hat{E}^2$

In Figure 2.8.10 we plot the bifurcation diagram with  $a_1$  and  $m_1$  as above and both  $a_2$  and  $m_2$  as bifurcation parameters.

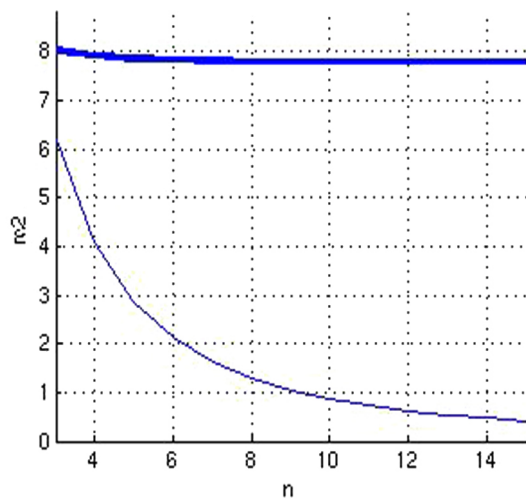


**Figure 2.8.10.** Two parameter bifurcation diagram for 2 species in 4 vessels for  $m_1 = 30$ ,  $a_1 = 20$ . We plot equilibrium concentrations of both species in vessel 1 vs. parameters  $a_2$  and  $m_2$ .

We can see from Figure 2.8.7 to Figure 2.8.10 that the size of the coexistence interval  $(m_2^{**}, m_2^*)$  is very small. In the case of a single species in the gradostat, surviving was becoming "easier" as the number of vessels increased. We obtained the same result for competition, and namely, the size of the coexistence interval increases as  $n$  increases. From the simulations it looks like the size of  $(m_2^{**}, m_2^*)$  approaches a certain constant as  $n$  is large. Moreover, for  $a_1 > a_2$  both  $m_2^{**}$  and  $m_2^*$  decrease towards some constant values, and for  $a_1 < a_2$ ,  $m_2^{**}$  and  $m_2^*$  increase towards some constant values. We give in Figure 2.8.11 two examples that picture this behavior.



**Figure 2.8.11.** The coexistence interval:  $(m_2^{**}, m_2^*)$  for different number of vessels. The interval widens as  $n$  increases. **(a):**  $a_1 = 20, m_1 = 30, a_2 = 5$ . **(b):**  $a_1 = 2, m_1 = 7, a_2 = 5$ .



**Figure 2.8.12.** For the species in Figure 2.8.10. (a) we plot together with the coexistence interval - the upper line - also the different values for  $\hat{m}_2$  - the lower line.

## 2.9 Notes and discussions

In this chapter we have applied the method described in Appendix A in order to obtain persistence results for  $m$  species competing in the gradostat. The main theorem, Theorem 2.6.2, gives sufficient conditions for persistence for a general  $m$ .

For  $m = 1$  - Section 2.4, and  $m = 2$  - Section 2.7, the corresponding theorems, namely Theorem 2.4.1, respectively Theorem 2.7.1, are equivalent to the ones already existing in the literature (see chapter 1). When the sufficient persistence conditions are fulfilled, we are able to find numerous examples for the persistence of one and two species, and by a bifurcation analysis, with various parameters as bifurcation parameters, we can give a quite detailed description of the region in the parameter space for which persistence occurs: for  $m = 1$  - Section 2.5, and for  $m = 2$  - Section 2.8.

For  $m > 2$  however, we were not able to find any numerical examples of  $m$ -species persistence when the persistence conditions (2.6.6) were fulfilled. As we will discuss it in the beginning of the next chapter, we expect these persistence conditions to be too strong, such that, from a bifurcation analysis point of view, when the varying parameters are such that the corresponding conditions in (2.6.6) are fulfilled, we have already "missed" the  $m$ -species persistence region.

In the next chapter we consider the case of three species, and by applying the results for two species, we improve the corresponding (2.6.6) in order to obtain sufficient conditions for the persistence of all three species, for which we also find numerous numerical examples.



# 3

## Three species

### 3.1 The system

For the case of three species in the gradostat with  $n$  vessels ( $n \geq 3$ ), the system takes the form:

$$\begin{aligned} u^{1'} &= [A + F_1(z - u^1 - u^2 - u^3)] u^1, \\ u^{2'} &= [A + F_2(z - u^1 - u^2 - u^3)] u^2, \\ u^{3'} &= [A + F_3(z - u^1 - u^2 - u^3)] u^3, \\ u^1(t_0) &\geq 0, \quad u^2(t_0) \geq 0, \quad u^3(t_0) \geq 0, \end{aligned} \tag{3.1.1}$$

in  $\Omega = \{u = (u^1, u^2, u^3) \in \mathbf{R}_+^{3n} \mid u^1 + u^2 + u^3 \leq z\}$ , and the corresponding steady state system:

$$\begin{aligned} [A + F_1(z - u^1 - u^2 - u^3)] u^1 &= 0, \\ [A + F_2(z - u^1 - u^2 - u^3)] u^2 &= 0, \\ [A + F_3(z - u^1 - u^2 - u^3)] u^3 &= 0. \end{aligned} \tag{3.1.2}$$

For the gradostat with two species we obtained, with the help of Theorem 2.6.2, sufficient conditions for coexistence.

For three species, a set of sufficient conditions for persistence given by Theorem 2.6.2 would be

$$\begin{aligned} s[A + F_1(z - \hat{u}^2 - \hat{u}^3)] &> 0, \\ s[A + F_2(z - \hat{u}^1 - \hat{u}^3)] &> 0, \\ s[A + F_3(z - \hat{u}^1 - \hat{u}^2)] &> 0, \end{aligned} \tag{3.1.3}$$

with  $\hat{u}^1, \hat{u}^2, \hat{u}^3$  the single species equilibria.

When (3.1.3) hold, the system with  $0 < u_0^j \leq \hat{u}^j$ ,  $j = 1, 2, 3$ , and  $\sum_{j=1}^3 u_0^j \leq z$ , is persistent: there exist positive constants  $\tilde{\gamma}^1, \tilde{\gamma}^2, \tilde{\gamma}^3$ , such that

$$0 < \tilde{\gamma}^j \cdot \phi_s^j \leq u^j(t) \leq \hat{u}^j,$$

for all  $j = 1, 2, 3$ , with  $\phi_s^j$  the positive (by Perron-Frobenius Theory) eigenvector corresponding to  $s[A + F_j(z - \sum_{k \neq j} \hat{u}^k)]$ .

The possible steady states of system (3.1.1) are  $E_0 = (0, 0, 0)$ , then the single species equilibria, namely

$$\hat{E}^1 = (\hat{u}^1, 0, 0), \hat{E}^2 = (0, \hat{u}^2, 0), \hat{E}^3 = (0, 0, \hat{u}^3),$$

the equilibria corresponding to two species surviving and the third dying out, namely  $E_{1,2}^* = (u^1, u^2, 0)$  with  $u^1, u^2 > 0$ , corresponding to species 1 and 2 coexisting,  $E_{1,3}^* = (u^1, 0, u^3)$  with  $u^1, u^3 > 0$ , corresponding to species 1 and 3 coexisting, and  $E_{2,3}^* = (0, u^2, u^3)$  with  $u^2, u^3 > 0$ , corresponding to species 2 and 3 coexisting, and a positive equilibrium  $\tilde{E} = (\tilde{u}^1, \tilde{u}^2, \tilde{u}^3)$  with  $\tilde{u}^1, \tilde{u}^2, \tilde{u}^3 > 0$ . We saw in the previous chapter that the two-species equilibria may be not unique.

As in the case of two species, we study the system (3.1.1) via a bifurcation analysis of the solution of (3.1.2). For this we fix the parameters for the first two species, namely  $a_1, m_1, a_2, m_2$ , as well as  $a_3$  for the third species, and take  $m_3$  as the bifurcation parameter. We assume that each species is able to survive by itself in the gradostat:  $s[A + F_j(z)] > 0$  for all  $j$ .

We are of course interested in the persistence of the whole system, but the system is now larger, as well as the number of parameters, thus whether there exist values for  $m_3$  such that all three species survive, highly depends on 'where' exactly we fixed the values for the parameters corresponding to the first two species.

To make our task slightly easier, we look for values for  $m_3$  such that the third species is able to successfully invade an already established equilibrium corresponding to the coexistence of the first two species. That means we choose two species that are able to coexist:  $a_1, m_1, a_2, m_2$  are such that

$$\begin{aligned} s[A + F_1(z - \hat{u}^2)] &> 0, \\ s[A + F_2(z - \hat{u}^1)] &> 0, \end{aligned} \tag{3.1.4}$$

operate the gradostat until they reach an equilibrium, and then look for a third species (in terms of  $a_3$  and  $m_3$ ) such that if introduced in the gradostat, it is able to survive. We are first interested only in the possibility of persistence for the third species and allow one or both of the first two to die out.

We can see that the eigenvalues in (3.1.3) are no longer eigenvalues of the variational matrix of (3.1.1) at any of the possible equilibrium points, as it was the case for two species. Thus, values for  $m_3$  such that

$$s[A + F_3(z - \hat{u}^1 - \hat{u}^2)] = 0$$

are not necessarily bifurcation values.

Let  $\Lambda_3 = \{(m_3, u) : u \in \Omega \text{ satisfies (3.1.2) corresponding to } m_2\}$ . Denote with

$$Q_{1,2}^* = \{(m_3, u^{*1}, u^{*2}, 0) : m_2 \geq 0\},$$

the branch of the solution set corresponding to a possible equilibrium  $E_{1,2}^*$ . We are interested in the bifurcation of solutions of (3.1.2) from the branch  $Q_{1,2}^*$  of  $\Lambda_3$ . Since  $E_{1,2}^*$  may not be unique, the introduction of a third species however could only perturb the system such that it approaches one of the other possible  $u^1 \times u^2$  equilibria, and the branch emanating from the  $Q_{1,2}^*$  at  $E_{1,2}^*$  (when such a branch exists) corresponds to some other branch in the  $u^1 \times u^2$  hyperplane.

We will later see that we can find values for  $m_3$  such that the third species persists in the form of convergence to a positive (in the last  $n$  components) steady state. This means that there exists a value for  $m_3 = \tilde{m}_3$  and a point  $(u^{*1}(\tilde{m}_3), u^{*2}(\tilde{m}_3), 0)$  in the  $u^1 \times u^2$  hyperplane on one of the possible  $Q_{1,2}^*$ -type branches such that  $(\tilde{m}_3, u^{*1}(\tilde{m}_3), u^{*2}(\tilde{m}_3), 0)$  is a bifurcation point of  $\Lambda_3$  with respect to the branch  $Q_{1,2}^*$ , with  $(u^{*1}(m_3), u^{*2}(m_3), 0)$  one of the possible two species equilibria.

It is easy to check that for every two-species equilibrium  $E_{1,2}^* = (u^{*1}, u^{*2}, 0)$ , the eigenvalue  $s[A + F_3(z - u^{*1} - u^{*2})]$  is an eigenvalue of  $J(E_{1,2}^*)$ , the variational matrix of (3.1.1) at this point, and that for  $m_3 = \tilde{m}_3$ , where

$$s[A + F_3(z - u^{*1}(\tilde{m}_3) - u^{*2}(\tilde{m}_3))] = 0,$$

$J(E_{1,2}^*)$  has 0 as a simple eigenvalue as long as the stability modulus of the variational matrix of (2.7.1) at  $(u^{*1}, u^{*2})$  is strictly smaller than zero. For each  $E_{1,2}^*$  there exists a unique such  $\tilde{m}_3$ .

We write  $F_3(x) = m_3 \tilde{F}_3(x)$ , for  $x \in \mathbf{R}_+^n$ . Clearly,  $s[A + m_3 \tilde{F}_3(z - u^{*1} - u^{*2})]$  strictly increases from negative values for  $m_3$  near zero to infinity as  $m_3$  increases. Thus, for  $m_3 > \tilde{m}_3$  we have that  $s[A + m_3 \tilde{F}_3(z - u^{*1} - u^{*2})] > 0$  and  $J(E_{1,2}^*)$  has a positive eigenvalue which makes  $E_{1,2}^*$  unstable.

For  $\bar{u}^j$  an upper solution for  $u^j$ , if  $m_3$  is such that

$$s[A + m_3 \tilde{F}_3(z - \bar{u}^1 - \bar{u}^2)] > 0, \quad (3.1.5)$$

every two-species equilibrium is unstable, as

$$s[A + m_3 \tilde{F}_3(z - \bar{u}^1 - \bar{u}^2)] \leq s[A + m_3 \tilde{F}_3(z - u^{*1} - u^{*2})].$$

We saw in Theorem 2.6.2, that in case (3.1.5) holds, the third species is persistent ( for appropriate initial values) and there exists an equilibrium of the form  $(\bar{u}^1, \bar{u}^2, \bar{u}^3)$  with  $\bar{u}^1, \bar{u}^2 \geq 0$  and  $\bar{u}^3 > 0$ .

We expect that persistence holds even for a weaker condition than (3.1.5), and namely, that every  $E_{1,2}^*$  equilibrium has a positive eigenvalue, which is fulfilled if

$$s[A + m_3 \tilde{F}_3(z - \tilde{u}^{*1} - \tilde{u}^{*2})] > 0 \quad (3.1.6)$$

where  $\tilde{E}_{1,2}^* = (\tilde{u}^{*1}, \tilde{u}^{*2}, 0)$  with

$$k := \tilde{u}^{*1} + \tilde{u}^{*2} = \max\{u^{*1} + u^{*2} : (u^{*1}, u^{*2}, 0) \text{ solution of (3.1.2)}\},$$

$k \in \mathbf{R}_+^n$ . Since for every equilibrium  $E_{1,2}^* = (u^{*1}, u^{*2}, 0)$  we have that

$$u_{(1,2)min}^1 \leq u^{*1} \leq u_{(1,2)max}^1 \text{ and } u_{(1,2)min}^2 \leq u^{*2} \leq u_{(1,2)max}^2,$$

with  $u_{(1,2)min}$  and  $u_{(1,2)max}$  the limits of the two sequences given by (2.7.4), for the competition of species 1 and 2 ( $u_0^3 = 0$ ), we obtain that

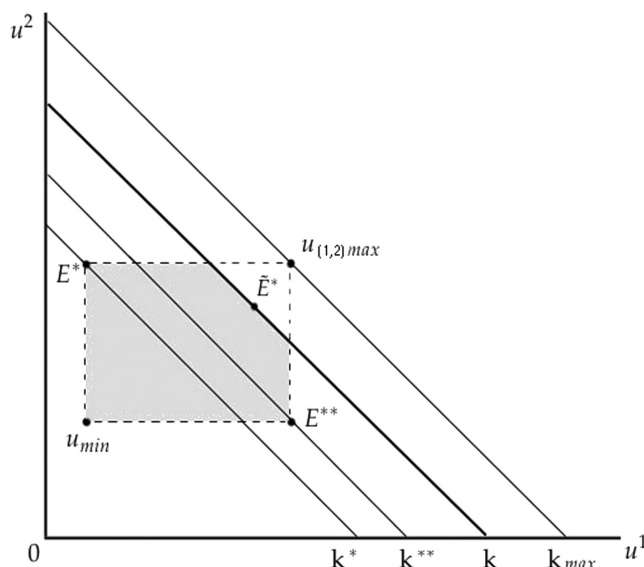
$$\max\{k^*, k^{**}\} \leq k \leq k_{max},$$

where  $k^* = u_{(1,2)min}^1 + u_{(1,2)max}^2$ ,  $k^{**} = u_{(1,2)max}^1 + u_{(1,2)min}^2$ , and  $k_{max} = u_{(1,2)max}^1 + u_{(1,2)max}^2$ .

When  $E_{1,2}^*$  is unique, we have  $k^* = k^{**} = k = k_{max}$  and  $E_{1,2}^* = (u_{(1,2)max}^1, u_{(1,2)max}^2, 0)$ . When  $u_{min} \neq u_{max}$ , we have  $k_{max} > k^*$  and  $k_{max} > k^{**}$ , and thus

$$s[A + F_i(z - k_{max})] < s[A + F_i(z - k^*)] = 0, \quad i = 1, 2$$

and  $(u_{(1,2)max}^1, u_{(1,2)max}^2, 0)$  is not a solution of (3.1.2).



**Figure 3.1.1.** The attracting hypercube in the  $u^1 \times u^2$  hyperplane.

For the system with  $u_0^3 = 0$ , the set

$$O = ([u_{(1,2)min}^1, u_{(1,2)max}^1] \times [u_{(1,2)min}^2, u_{(1,2)max}^2]) \times \{0\} \cap \Omega$$

attracts (almost) all orbits with initial values  $(u_0^1, u_0^2, 0) \in \Omega$ ,  $u_0^1, u_0^2 > 0$ . Since for all two-species equilibria  $(u^{*1}, u^{*2}, 0)$  we have that  $u^{*1} + u^{*2} \leq k$ , the omega limit set of (3.1.1), for trajectories with  $u_0^1 > 0$ ,  $u_0^2 > 0$  and  $u_0^3 = 0$ , is included in

$$O \subset O_{k_{max}},$$

$$O_{k_{max}} := \{(u^1, u^2, 0) \in \Omega : u^1 > 0, u^2 > 0, u^1 + u^2 \leq k_{max}\}.$$

Denote with with

$$O_k := \{(u^1, u^2, 0) \in \Omega : u^1 > 0, u^2 > 0, u^1 + u^2 \leq k\}.$$

## 3.2 Invasion of a persistent two-species system

**Definition 3.2.1** (Invariant region) ([Smo]) A closed subset  $\Gamma \subset \mathbf{R}^n$  is called a (positively) invariant region under the flow of

$$\begin{aligned} \frac{du}{dt} &= f(u, t), u \in U \subset \mathbf{R}^n, t \in \mathbf{R}_+, \\ u(t_0) &= u_0, \end{aligned} \tag{3.2.1}$$

if every solution  $u(t)$  of (3.2.1) having its initial value in  $\Gamma$ , satisfies  $u(t) \in \Gamma$  for all  $t \geq t_0$ ,  $t \in I$ , with  $I$  the maximal interval of existence of solution  $u$ .

Invariant regions will be made up of intersections like

$$\Gamma = \bigcap_{i=1}^m \{u \in : G_i(u) \leq 0\},$$

where  $G_i$  are smooth real-valued functions defined on open subsets of  $U$ , and for each  $i$ , the gradient  $dG_i$  does not vanish.

If there is a solution  $u$  of (3.2.1) with initial values in  $\Gamma$  which is not in  $\Gamma$  for all  $t > t_0$ , then there is a function  $G_i$ , a time  $\bar{t} > t_0$ , such that for  $t < \bar{t}$  we have  $G_i \circ u(t) \leq 0$  and for any  $\epsilon > 0$ , there is a  $t'$  with  $\bar{t} < t' < \bar{t} + \epsilon$ , such that  $G_i \circ u(t') > 0$ . Thus, if

$$G_i \circ u(t) < 0 \text{ for } t_0 \leq t < \bar{t}$$

and

$$G_i \circ u(\bar{t}) = 0$$

imply that

$$\frac{\partial(G_i \circ u)}{\partial t} < 0 \text{ at } \bar{t}, \quad (3.2.2)$$

then  $\Gamma$  must be invariant.

It can be shown that any intersection of invariant regions is an invariant region and an omega-limit set is an invariant region.

Following [Smo], a set  $\Gamma$  is an invariant set for the gradostat system if and only if the flow doesn't point outside  $\Gamma$  on  $\partial\Gamma$ . Thus, any sector  $\langle \underline{u}, \bar{u} \rangle$  with  $\underline{u}, \bar{u}$ , a pair of lower and upper solutions for (3.1.1), is an invariant region.

We saw earlier that every single-species equilibrium concentration  $\hat{u}^j$  is an upper solution for  $u^j$ , for all  $j = 1, \dots, m$ , for any number of species  $m$ , and hence  $P = \prod_{j=1}^m [0, \hat{u}^j] \subset \mathbf{R}_+^{nm}$  is an invariant region for the gradostat with  $m$  species in  $n$  vessels.

In particular, the sets  $\Omega$  and  $O$  are (positively) invariant regions.

Before we go on we make the following remark:

**Remark (I):** Fix  $u^3 = u^3(t) \in [0, z]$ , and consider  $(u^1(u^3), u^2(u^3))$ , the solution of

$$\begin{aligned} u^1(u^3)' &= [A + F_1(z - u^1(u^3) - u^2(u^3) - u^3)]u^1(u^3), \\ u^2(u^3)' &= [A + F_2(z - u^1(u^3) - u^2(u^3) - u^3)]u^2(u^3), \\ u_0^i(u^3) &> 0, \quad i = 1, 2, \end{aligned}$$

with  $u^i \in [0, z - u^3]$ ,  $i = 1, 2$ . Since both  $F_i(z - u^1 - u^2 - u^3)$ ,  $i = 1, 2$  are monotone decreasing in  $u^3$ , we have

$$\begin{aligned} \frac{d(u^1(v^3) + u^2(v^3))}{dt}(t) &= \\ &= [A + F_1(z - u^1(v^3)(t) - u^2(v^3)(t) - v^3(t))]u^1(v^3)(t) + \\ &\quad + [A + F_2(z - u^1(v^3)(t) - u^2(v^3)(t) - v^3(t))]u^2(v^3)(t) \geq \quad (3.2.3) \\ &\geq [A + F_1(z - u^1(v^3)(t) - u^2(v^3)(t) - u^3(t))]u^1(v^3)(t) + \\ &\quad + [A + F_2(z - u^1(v^3)(t) - u^2(v^3)(t) - u^3(t))]u^2(v^3)(t), \end{aligned}$$

for  $u^3 > v^3$ , and thus  $u^1(v^3) + u^2(v^3)$  is an upper solution for  $u^1 + u^2$  when  $u^3 > v^3$ . In particular,  $u^1(0) + u^2(0)$  is an upper solution for  $u^1(u^3) + u^2(u^3)$ , for all  $u^3 > 0$ .

### Theorem 3.2.2

For system (3.1.1) with  $n \geq 3$  assume

$$s[A + F_3(z - \hat{u}^1)] > 0, \quad (3.2.4)$$

and

$$s[A + F_3(z - \hat{u}^2)] > 0. \quad (3.2.5)$$

Consider  $Y \subset \{(u^1, u^2, u^3) \in \Omega : u^3 = 0\}$  an invariant set for (3.1.1) with  $u^3 = 0$ . Denote with  $K = \max\{u^1 + u^2 : (u^1, u^2, u^3) \in Y\}$ . If

$$s[A + F_3(z - K)] > 0 \quad (3.2.6)$$

holds, then we can find initial data for which species 3 is persistent.

In this case there exists an equilibrium solution of (3.1.1),  $\tilde{u} \in P$  with  $\tilde{u}^3 > 0$ .

**Proof:** By Perron-Frobenius Theorem, the matrix  $A + F_3(z - K)$  has a positive eigenvector  $\phi^3 > 0$  corresponding to  $s[A + F_3(z - K)]$ . Consider  $u_0 \in P$ ,  $u_0 > 0$ , with  $(u_0^1, u_0^2, 0) \in Y$ .

For  $u^1, u^2 > 0$ , if (3.2.6) holds, we have

$$\begin{aligned} [A + F_3(z - u^1 - u^2 - \bar{\gamma}^3 \cdot \phi^3)] \cdot \bar{\gamma}^3 \cdot \phi^3 &= \\ &= [A + F_3(z - K)] \cdot \bar{\gamma}^3 \cdot \phi^3 + [F_3(z - u^1 - u^2 - \bar{\gamma}^3 \cdot \phi^3) - F_3(z - K)] \cdot \bar{\gamma}^3 \cdot \phi^3 \\ &= \underbrace{s[A + F_3(z - K)] \cdot \bar{\gamma}^3 \cdot \phi^3}_{>0} + [F_3(z - u^1 - u^2 - \bar{\gamma}^3 \cdot \phi^3) - F_3(z - K)] \cdot \bar{\gamma}^3 \cdot \phi^3 \geq 0 \end{aligned}$$

$$\Leftrightarrow s[A + F_3(z - K)] \cdot \phi^3 + [F_3(z - u^1 - u^2 - \bar{\gamma}^3 \cdot \phi^3) - F_3(z - K)] \cdot \phi^3 \geq 0.$$

The last inequality holds for  $\bar{\gamma}^3$  small enough since, from Remark (I),  $u^1 + u^2 \leq K$  for all  $t$ , as long as  $u^1 \neq 0$ ,  $u^2 \neq 0$ . Since we allow species 1 or/and 2 to die out of the gradostat, we

also have to consider the hyperplanes  $u^1 = 0$  and  $u^2 = 0$ , both being themselves invariant sets for (3.1.1).

For  $u^1 = 0$ , we can have that there exist initial data  $u_0$  and  $i \in \{1, \dots, n\}$  with  $K_i < \hat{u}_i^3$  and  $u_i^2(t) > K_i$  for some time  $t$ . However this can only happen if the trajectory through  $u_0$  reaches the hyperplane  $u^1 = 0$  in finite time, and we have that the set

$$\{u \in \Omega : u^1 = 0, u^2 \leq \hat{u}^2, u^3 \leq \hat{u}^3\}$$

is invariant for (3.1.1). A similar affirmation holds for  $u^2 = 0$ .

For  $u^1 = 0$ , since (3.2.5) holds, we have from Theorem 2.6.2, that there exists a  $\tilde{\gamma}^3 > 0$  such that  $\tilde{\gamma}^3 \cdot \tilde{\phi}^3 > 0$  is a lower solution for  $u^3$  with  $\tilde{\phi}^3$  the positive eigenvector corresponding to  $s[A + F_3(z - \hat{u}^2)] > 0$ , and thus

$$[A + F_3(z - u^2 - \tilde{\gamma}^3 \cdot \tilde{\phi}^3)] \cdot \tilde{\gamma}^3 \cdot \tilde{\phi}^3 \geq 0,$$

for all  $0 \leq u^2 \leq \hat{u}^2$ .

Similarly, for  $u^2 = 0$ , since (3.2.4) holds, we have from Theorem 2.6.2, that there exists a  $\hat{\gamma}^3 > 0$  such that  $\hat{\gamma}^3 \cdot \hat{\phi}^3 > 0$  is a lower solution for  $u^3$  with  $\hat{\phi}^3$  the positive eigenvector corresponding to  $s[A + F_3(z - \hat{u}^1)] > 0$ , and thus

$$[A + F_3(z - u^1 - \hat{\gamma}^3 \cdot \hat{\phi}^3)] \cdot \hat{\gamma}^3 \cdot \hat{\phi}^3 \geq 0,$$

for all  $0 \leq u^1 \leq \hat{u}^1$ .

For both  $u^1 = 0$  and  $u^2 = 0$ , from Theorem 2.4.1, there exists a  $\gamma^0 > 0$  such that  $\gamma^0 \cdot \phi^0$ , with  $\phi^0 > 0$  the positive eigenvector corresponding to  $s[A + F_3(z)] > 0$ , is a lower solution for  $u^3$ .

Take

$$\phi_{Y,i}^3 := \min\{\bar{\gamma}^3 \cdot \phi_i^3, \tilde{\gamma}^3 \cdot \tilde{\phi}_i^3, \hat{\gamma}^3 \cdot \hat{\phi}_i^3, \gamma^0 \cdot \phi_i^0\} > 0,$$

for  $i = 1, \dots, n$ , and we have that

$$[A + F_3(z - u^1 - u^2 - \phi_Y^3)] \cdot \phi_Y^3 \geq 0$$

holds for all  $0 < u^1, u^2$  with  $u^1 + u^2 \leq K$  as well as for  $u^1 = 0$  or  $u^2 = 0$ .

Thus we have showed that for  $u_0 \in P$ ,  $u_0 > 0$ , with  $(u_0^1, u_0^2) \in Y$ , and  $u_0^3 \geq \phi_Y^3$ , species 3 is persistent and the solution of (3.1.1) takes values in

$$\begin{aligned} & \{(u^1, u^2, u^3) \in P : u > 0, u^1 + u^2 \leq K, u^3 \geq \phi_Y^3\} \cup \\ & \cup \{(u^1, u^2, u^3) \in P, u^1 = 0, u^3 \geq \phi_Y^3\} \cup \{(u^1, u^2, u^3) \in P, u^2 = 0, u^3 \geq \phi_Y^3\}. \end{aligned} \quad (3.2.7)$$

□



Note that the persistence condition for species 3 given by Theorem 2.6.2 is a special case of Theorem 3.2.1. The invariant set  $Y$  for Theorem 2.6.2 is given by the invariant region  $< \underline{u}^1, \bar{u}^1 > \times < \underline{u}^2, \bar{u}^2 > \times \{0\}$  and in this case  $K$  is reached in  $(\bar{u}^1, \bar{u}^2, 0)$  which makes condition (2.6.6) equivalent to (3.2.6).

### Proposition 3.2.3

For system (3.1.1) with  $n \geq 3$  assume that (3.1.4), (3.2.4) and (3.2.5) hold. Denote with  $Y_l$  the sector

$$Y_l = < \underline{u}_{(1,2)}^{1,(l)}, \bar{u}_{(1,2)}^{1,(l)} > \times < \underline{u}_{(1,2)}^{2,(l)}, \bar{u}_{(1,2)}^{2,(l)} >, \quad l \geq 0,$$

given by the  $l$ -iteration of the process (2.7.4), with  $(\underline{u}_{(1,2)}^{1,(0)}, \underline{u}_{(1,2)}^{2,(0)})$  the lower solution given in the proof of Theorem 2.6.2, and  $(\bar{u}_{(1,2)}^{1,(0)}, \bar{u}_{(1,2)}^{2,(0)}) = (\hat{u}^1, \hat{u}^2)$ . If, for a  $l \geq 0$ , we have

$$s[A + F_3(z - \bar{u}_{(1,2)}^{1,(l)} - \bar{u}_{(1,2)}^{2,(l)})] > 0, \quad (3.2.8)$$

then we can find initial data for which species 3 is persistent.

In this case, there exists at least one equilibrium solution  $\tilde{u}$  of (3.1.1), with  $\tilde{u}^3 > 0$ .

**Proof:** Proposition 3.2.2 is an application of Theorem 3.2.1 since for every  $l \geq 0$  we have that  $(\underline{u}_{(1,2)}^{(l)}, \bar{u}_{(1,2)}^{(l)})$  is a pair of coupled lower and upper solutions and thus every sector  $Y_l$  is an invariant region for (3.1.1).  $\square$

The difficulty in applying Theorem 3.2.1 lies in finding such an invariant region  $Y$  for (3.1.1). The easiest choice is, as shown in Proposition 3.2.2, the sequence of regions given by the iteration process (2.7.4), in the case species 1 and 2 coexist.

It is obvious that the smaller the values for  $K$  are, the "easier" it is for species 3 to verify condition (3.2.6) - note that (3.2.6) is just a sufficient condition for persistence. Thus, the smallest the invariant region  $Y$  is, the smallest the values for  $m_3$  satisfying (3.2.6) get, and thus closer to the expected bifurcation value for  $m_3$  above which species 3 is persistent.

The "smallest" invariant region  $Y$  given by the iteration process (2.7.4) is obviously  $O$ , and in this case, for initial values as described in the proof of Theorem 3.2.1, the solution of (3.1.1) is such that  $(u^1, u^2) \in O_{k_{\max}} \cup \{u^1 = 0\} \cup \{u^2 = 0\}$ , and (3.2.6) is given by

$$s[A + F_3(z - k_{\max})] > 0. \quad (3.2.9)$$

In case the two-species equilibrium corresponding to the coexistence of species 1 and 2 is unique,  $O$  degenerates to one point. In this case, if

$$s[A + F_3(z - k - \epsilon)] > 0, \quad (3.2.10)$$

with  $\epsilon$  small positive constants, species 3 is persistent for initial data such that

$$(u_0^1, u_0^2) \in Y_{l_\epsilon}, \text{ with } Y_{l_\epsilon} \text{ such that } \bar{u}_{(1,2)}^{1, (l_\epsilon)} + \bar{u}_{(1,2)}^{2, (l_\epsilon)} = k + \epsilon.$$

When  $\epsilon \rightarrow 0$ , a biological interpretation of Proposition 3.2.2 with  $Y_{l_\epsilon}$  and condition (3.2.10) would be: assume species 1 and 2 are able to coexist in the gradostat in the form of a unique equilibrium. We operate the gradostat until the two species reach (or are  $\epsilon$ -close to) their equilibrium concentration - say time  $T$  - and then introduce into the system a third species. If this third species would be able to survive alone on the amount of nutrient present in the gradostat at time  $T$  (its parameters are such that (3.2.10) holds), then it will be persistent, and we have:

#### Corollary 3.2.4

When  $s[A + F_3(z - k)] \geq \eta$  with  $\eta > 0$ , there exists an equilibrium solution of (3.1.1),  $\tilde{E}$ , with  $\tilde{u}^3 > 0$ .

### 3.3 Further invariant regions

In the present section we extend the analysis from the previous section by looking for different possible invariant regions of the type described in Theorem 3.2.1 and for corresponding persistence conditions for species 3.

We assume that (3.1.4) hold, namely that species 1 and 2 are able to coexist.

We saw that for initial data in  $O$ ,

$$s[A + F_3(z - k_{\max})] > 0 \tag{3.3.1}$$

is a sufficient condition for species 3 to survive and the solution of (3.1.1) is such that  $(u^1, u^2, 0) \in O_{k_{\max}}$  as long as  $u^1, u^2 \geq 0$ .

We will take a closer look at the set  $O_{k_{\max}}$ .

**A:** Assume  $u_{(1,2)\min} \neq u_{(1,2)\max}$ . Since  $O$  attracts (almost) all orbits with initial values  $(u_0^1, u_0^2, 0) \in \Omega$ ,  $u_0^1, u_0^2 > 0$  and  $O \subset O_{k_{\max}}$ , we have that for each point

$$(u_0^1, u_0^2, 0) \in \{(u^1, u^2, 0) \in \Omega : u^1, u^2 > 0, u^1 + u^2 \leq k_{\max}\},$$

there exists a  $T \geq t_0$  such that the solution  $u(t)$  of (3.1.1) with initial value  $(u_0^1, u_0^2, 0)$ , remains in  $O_{k_{\max}}$  for all  $t \geq T$  and

$$[A + F_1(z - k_{\max})]u^1(t) + [A + F_2(z - k_{\max})]u^2(t) \leq 0,$$

for  $u^1(t) + u^2(t) = k_{max}$ , for  $t \geq T$ .

Moreover, for each point

$$(u_0^1, u_0^2, 0) \in \{(u^1, u^2, 0) \in \Omega : u^1, u^2 > 0, u^1 + u^2 \geq k_{max}\},$$

there exists a  $T \geq t_0$  such that the solution  $u(t)$  of (3.1.1) with initial value  $(u_0^1, u_0^2, 0)$ , enters  $O_{k_{max}}$  and remains in  $O_{k_{max}}$  for all  $t \geq T$  and

$$[A + F_1(z - k_{max})]u^1(t) + [A + F_2(z - k_{max})]u^2(t) \leq 0, \quad (3.3.2)$$

for  $u^1(t) + u^2(t) = k_{max}$ .

From Remark (I), we have that for any  $u_0$  with  $u_0^1 + u_0^2 \leq k_{max}$ ,  $u_0^1 > 0$ ,  $u_0^2 > 0$ , and  $u_0^3 \geq 0$ , there exists a  $T \geq t_0$  such that the solution  $u(t)$  of (3.1.1) with initial value  $u_0$ , remains in

$$Q_{k_{max}} := \{u \in \Omega : u^1 + u^2 \leq k_{max}, u^1 > 0, u^2 > 0, \text{ and } u^3 \geq 0\}$$

for all  $t \geq T$  since, from (3.2.6) and (3.3.2) we have

$$\begin{aligned} & [A + F_1(z - k_{max} - u^3(t))]u^1(t) + [A + F_2(z - k_{max} - u^3(t))]u^2(t) \leq \\ & \leq [A + F_1(z - k_{max})]u^1(t) + [A + F_2(z - k_{max})]u^2(t) \leq 0, \end{aligned} \quad (3.3.3)$$

for  $u^1(t) + u^2(t) = k_{max}$ , and for all  $u^3 \geq 0$ , and thus any possible equilibrium solution  $u^*$  with  $u^{*1}, u^{*2} > 0, u^{*3} \geq 0$  is in  $Q_{k_{max}} \cap P$ .

Since we allow species 1 and/or 2 to die out of the gradostat, we also consider the hyperplanes  $u^1 = 0$  and  $u^2 = 0$ .

For  $u_1 = 0$ , from section 2.6, a sufficient condition for species 3 to be persistent is

$$s[A + F_3(z - \hat{u}^2)] > 0. \quad (3.3.4)$$

If the system parameters are such that species 2 and 3 can coexist, namely there exist equilibria of the type  $E_{2,3}^* = (0, u^{*2}, u^{*3})$  with  $u^{*2}, u^{*3} > 0$ , we have that  $u^{*2} < u_{(2,3)max}^2$ , with  $u_{(2,3)max}$  the limit of the decreasing sequence given by (2.7.4) for the competition of species 2 and 3. Thus  $u_{(2,3)max}^2$  is the largest value that  $u^2$  can reach when there exists a coexistence equilibrium for species 2 and 3.

A similar affirmation holds when  $u^2 = 0$ .

**B:** Assume  $k_{max,j} < \hat{u}_j^2$  for some  $j \in J \subseteq \{1, \dots, n\}$ . Assume that there exists a stable equilibrium  $E_{2,3}^* = (0, u^{*2}, u^{*3})$ , with  $u_i^{*2} > k_{max,i}$  for some  $i \in I \subseteq J \subseteq \{1, \dots, n\}$ . Note that  $I \neq \{1, \dots, n\}$ , as, if  $u^{*2} > k_{max}$ , then

$$0 > s[A + F_2(z - k_{max})] > s[A + F_2(z - u^{*2})],$$

and we have a contradiction with  $s[A + F_2(z - u^{*2} - u^{*3})] = 0$ , since  $u^{*3} > 0$ .

Since  $k_{\max} > u_{(1,2)\max}^2$ , we have that  $O \subset \{(u^1, u^2, 0) \in \Omega : u^1, u^2 > 0, u^2 \leq k_{\max}\}$ , and for every point  $u_0 = (u_0^1, k_{\max}, 0)$  with  $u_0^1 > 0$ , there exists a time  $T \geq t_0$ , such that  $u(t)$ , the solution of (3.1.1) with initial value  $u_0$ , remains in  $O \subset \{(u^1, u^2, 0) \in \Omega : u^1, u^2 > 0, u^2 \leq k_{\max}\}$  for all  $t \geq T$ , and

$$[A + F_2(z - u^1(t) - k_{\max})]k_{\max} \leq 0,$$

with  $u^1(t) > 0$ .

Consider  $\hat{w} = (\hat{w}^1, \hat{w}^2)$ , the eigenvector of the variational matrix  $J_{1,2}(\hat{E}^1)$  of (2.7.1), corresponding to the competition of species 1 and 2, at the equilibrium  $\hat{E}^1$ . We saw in section 2.8. that  $\hat{w}^1 < 0$  and  $\hat{w}^2 > 0$ . We also have that  $\hat{v} = (\hat{v}^1, \hat{v}^2)$ , the eigenvector of  $J_{1,2}(\hat{E}^2)$ , is such that  $\hat{v}^1 > 0$  and  $\hat{v}^2 < 0$ .

In [STW] (Theorem 5.5) it was shown that the sets

$$H_r = \{(u^1, u^2, 0) \in \Omega \cap P : (u^1, u^2) \in [(0, \hat{u}^2) + r \cdot \hat{v}, (\hat{u}^1, 0) + r \cdot \hat{w}]_K\} \quad (3.3.5)$$

with  $r > 0$  small enough constants, are positively invariant with respect to (3.1.1).

For a fixed, small  $r$ , denote with  $S_r^1$  the  $\leq_K$ -monotone orbit through  $(\hat{u}^1, 0, 0) + r \cdot (\hat{w}, 0)$  and  $(E^{**}, 0)$ , and with  $S_r^2$  the  $\leq_K$ -monotone orbit through  $(0, \hat{u}^2, 0) + r \cdot (\hat{v}, 0)$  and  $(E^*, 0)$ .

Since  $u_{(1,2)\max,i}^2 < k_{\max,i} < \hat{u}_i^2$  for  $i \in I$ , for  $r$  small enough, we have that  $S_{r,i}^2$  intersects  $\{(u_i^1, k_{\max,i}, 0) \in \Omega : u_i^1 > 0\}$ , thus there exists a  $q > 0$  with  $(q, k_{\max,i}) \in S_{r,i}^2$ , and, from the  $\leq_K$ -monotonicity of (3.1.1) with  $u^3 = 0$ , we have

$$k_{\max,i-1} - 2k_{\max,i} - k_{\max,i+1} + f_2(z - k_{\max,i} - u_{i,0}^1)k_{\max,i} \leq 0, \quad (3.3.6)$$

for all  $q \leq u_{i,0}^1$  that means  $u_i^{2'}$  points inside  $\{(u^1, u^2, 0) \in \Omega : u^1, u^2 > 0, u^1 \geq q, u^2 \leq k_{\max}\}$ .

As  $u_i^{*2} > k_{\max,i}$ , there exists a  $\eta > 0$  and a  $T \geq t_0$  such that on the hyperplane  $u^1 = 0$  we have

$$k_{\max,i-1} - 2k_{\max,i} - k_{\max,i+1} + f_2(z - k_{\max,i} - \eta)k_{\max,i} > 0, \quad (3.3.7)$$

and the solution  $\tilde{u}(t)$  of (3.1.1) with  $\tilde{u}^1 = 0$ ,  $\tilde{u}_i^2(T) = k_{\max,i}$  and  $\tilde{u}_i^3(T) = \eta$  is such that  $\tilde{u}_i^2(t) > k_{\max,i}$  for all  $t > T$ .

From (3.3.5), we can see that we need  $\eta < q$ .

Assume that  $s[A + F_2(z - \hat{u}^3)] > 0$ . As all trajectories on the hyperplane  $u^1 = 0$  starting at positive  $(u_0^1, u_0^2) > 0$  approach an equilibrium point situated in

$$O_{(2,3)} := \{0\} \times ([u_{(2,3)\min}^2, u_{(2,3)\max}^2] \times [u_{(2,3)\min}^3, u_{(2,3)\max}^3]) \cap \Omega,$$

if  $\eta < q$ , then all solutions  $u(t)$  of (3.1.1) starting at points  $u_0$  with  $(k_{\max,i}, \eta) \leq_k (u_{i,0}^2, u_{i,0}^3)$  and  $u_{i,0}^2 > k_{\max,i}$  are such that  $u_i^2(t) > k_{\max,i}$  for all  $t > t_0$ , and thus  $u_{(2,3)\max_i}^2 > k_{\max,i}$ .

For points  $u_0$  with  $u_{i,0}^2 < k_{\max,i}$  and  $q \leq u_{i,0}^3$ , from (3.3.5) we have that all solutions  $u(t)$  of (3.1.1) starting at  $u_0$  are such that  $u_i^2(t) < k_{\max,i}$  for all  $t > t_0$ , and thus  $u_{(2,3)\min_i}^2 < k_{\max,i}$ , and it follows that  $u_{(2,3)\min_i}^2 < u_{(2,3)\max_i}^2$  and  $u_{(2,3)\min} \neq u_{(2,3)\max}$ .

In Figure 3.3.1. we depict schematically the reasoning above.

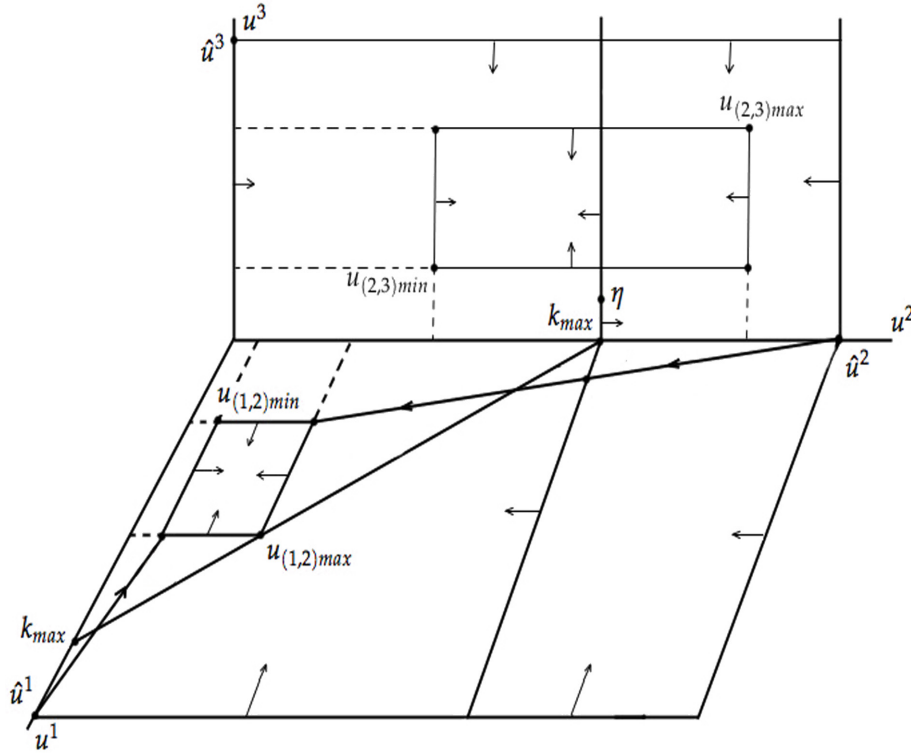


Figure 3.3.1.

**Remark (II):** If the system parameters are such that the coexistence equilibrium of species 2 and 3 with  $u^1 = 0$  is unique, we have that  $(u^{*2}, u^{*3}) = u_{(2,3)\min} = u_{(2,3)\max}$ , and thus there exists no  $\eta$  such that (3.3.6) holds, and

$$u^{*2} \leq k. \quad (3.3.8)$$

This will be actually the case for all the examples we will present in the next sections, as all the positive two-species equilibria we have found in simulations seem to be unique.

Similar remarks hold on  $u^2 = 0$ .

**C:** For a fixed, small  $r > 0$ , let  $S^1 := S_r^1$  and  $S^2 := S_r^2$ . From the  $\leq_K$ -monotonicity of (3.1.1) with  $u^3 = 0$  we obtain then that for the region  $\mathcal{S}_0 = \mathcal{S} \cap \{u^3 = 0\}$  with

$$\begin{aligned} \mathcal{S} = & \{u \in P : (u^1, u^2) \in H_r, 0 \leq u^1 \leq u_{(1,2)min}^1, u^2 \leq x \text{ with } (u^1, x) \in S^2\} \cup \\ & \cup \{u \in P : (u^1, u^2) \in H_r, 0 \leq u^2 \leq u_{(1,2)min}^2, u^2 \leq x \text{ with } (x, u^2) \in S^1\} \cup \\ & \cup \{u \in P : u^1 \leq u_{(1,2)max}^1, u^2 \leq u_{(1,2)max}^2\}, \end{aligned}$$

all orbits with  $u^3 = 0$  starting from points in  $\mathcal{S}_0$  stay inside  $\mathcal{S}_0$  or are tangent to  $S^1$  or  $S^2$ . Moreover, for  $r \rightarrow 0$ , we have that  $(\hat{u}^1, 0) \in cl(S_r^1)$  and  $(0, \hat{u}^2) \in cl(S_r^2)$ .

When the the two-species equilibrium  $E_{1,2}^*$  is unique,  $S^1 \cap S^2 = \{E_{1,2}^*\}$  and  $O = \{E_{1,2}^*\}$ , and  $S^1 \cup S^2$  is connected.

**D:** Consider (3.1.1) and  $u^3 = 0$ .

We have

$$u_{(1,2)max}^1{}' = [A + F_1(z - k_{max})]u_{(1,2)max}^1 \geq [A + F_1(z - u_{(1,2)max}^1 - u^2)]u_{(1,2)max}^1,$$

and the inequality holds for all  $u^2 \geq u_{(1,2)max}^2$ . Thus the vector field of (3.1.1) with  $u_0^3 = 0$  points inside (or stays tangent to)  $\{u \in P : u^1 = u_{(1,2)max}^1, u^2 \geq u_{(1,2)max}^2, u^3 = 0\}$ .

Analogously, we have

$$u_{(1,2)max}^2{}' = [A + F_2(z - k_{max})]u_{(1,2)max}^2 \geq [A + F_2(z - u^2 - u_{(1,2)max}^2)]u_{(1,2)max}^2,$$

and the inequality holds for all  $u^1 \geq u_{(1,2)max}^1$ . Thus the vector field of (3.1.1) with  $u_0^3 = 0$  points inside (or stays tangent to)  $\{u \in P : u^1 \geq u_{(1,2)max}^1, u^2 = u_{(1,2)max}^2, u^3 = 0\}$ .

**E:** Assume  $O_{k_{max}}$  is not invariant. That means that there exists a  $v = (v^1, v^2, 0) \neq u_{(1,2)max}$  with  $v^1 + v^2 = k_{max}$  such that the vector field of (3.1.1) with  $u_0^3 = 0$  does not point inside  $O_{k_{max}}$  at  $v$ : there exists  $i \in \{1, \dots, n\}$  such that  $v_i^1{}' + v_i^2{}' > 0$ , namely

$$[A + F_1(z - k_{max})]_i v_i^1 + [A + F_2(z - k_{max})]_i v_i^2 > 0. \quad (3.3.9)$$

Since  $O \subseteq O_{k_{max}}$  and  $O$  is an attractor, there exists at least one  $w = (w^1, w^2, 0)$  with  $w^1 + w^2 = k_{max}$  such that the vector field of (3.1.1) with  $u_0^3 = 0$  points inside  $O_{k_{max}}$  at  $w$  or stays tangent to  $\partial O_{k_{max}}$ :  $w^1{}' + w^2{}' \leq 0$  ( $u_{(1,2)max}$  is such a point). From (3.3.8) we have then

$$\begin{aligned} & [A + F_1(z - k_{max})]_i (k_{max,i} - v_i^2) > -[A + F_2(z - k_{max})]_i v_i^2 \\ \Leftrightarrow & \underbrace{[A + F_1(z - k_{max})]_i w_i^1 + [A + F_1(z - k_{max})]_i w_i^2 - [A + F_1(z - k_{max})]_i v_i^2}_{= w_i^1{}' \leq -w_i^2{}'} > \\ & > -[A + F_2(z - k_{max})]_i v_i^2 \\ \Rightarrow & -[A + F_2(z - k_{max})]_i w_i^2 + [A + F_1(z - k_{max})]_i w_i^2 - [A + F_1(z - k_{max})]_i v_i^2 > \\ & > -[A + F_2(z - k_{max})]_i v_i^2 \\ \Rightarrow & f_1(z_i - k_{max,i})(w_i^2 - v_i^2) > f_2(z_i - k_{max,i})(w_i^2 - v_i^2). \end{aligned}$$

Analogously, from

$$[A + F_2(z - k_{\max})]_i (k_{\max,i} - v_i^1) > -[A + F_1(z - k_{\max})]_i v_i^1,$$

we obtain

$$f_1(z_i - k_{\max,i})(v_i^1 - w_i^1) > f_2(z_i - k_{\max,i})(v_i^1 - w_i^1).$$

We have then the following two situations:

**(a)** If  $f_1(z_i - k_{\max,i}) < f_2(z_i - k_{\max,i})$  then  $(v_i^1, v_i^2) \leq_K (w_i^1, w_i^2)$  and in particular

$$(v_i^1, v_i^2) \leq_K (u_{(1,2)\max,i}^1, u_{(1,2)\max,i}^2).$$

In this case, for all  $(u_i^1, u_i^2) \leq_K (v_i^1, v_i^2)$  we have  $u_i^{1'} + u_i^{2'} > 0$  and for all  $(u_i^1, u_i^2, 0)$  with  $u^1 + u^2 = k_{\max}$  for which  $u_i^{1'} + u_i^{2'} \leq 0$  we have  $(v_i^1, v_i^2) \leq_K (u_i^1, u_i^2)$ .

Thus, for all  $(u_{(1,2)\max,i}^1, u_{(1,2)\max,i}^2) \leq_K (u^1, u^2)$  with  $u^1 + u^2 = k_{\max}$  we have  $u_i^{1'} + u_i^{2'} \leq 0$ . It follows immediately that the vector field of (3.1.1) with  $u_0^3 = 0$  points inside (or stays tangent to)  $\{u \in P : u_i^1 + u_i^2 = k_{\max,i}, (u_{(1,2)\max,i}^1, u_{(1,2)\max,i}^2) \leq_K (u_i^1, u_i^2), u^3 = 0\}$ .

From **D** we can then conclude that the set

$$D_i = \{u \in P : u^1, u^2 \neq 0, u_i^1 + u_i^2 \leq k_{\max,i}, (u_{(1,2)\max,i}^1, u_{(1,2)\max,i}^2) \leq_K (u_i^1, u_i^2), u^3 = 0\} \cup \\ \cup \{u \in P : u_i^1 = u_{(1,2)\max,i}^1, u_{(1,2)\max,i}^2 \leq u_i^2 \leq \hat{u}_i^2, u^3 = 0\}$$

is such that the vector field of (3.1.1) points inside  $D_i$ .

**(b)** If  $f_1(z_i - k_{\max,i}) > f_2(z_i - k_{\max,i})$  then  $(w_i^1, w_i^2) \leq_K (v_i^1, v_i^2)$  and in particular

$$(u_{(1,2)\max,i}^1, u_{(1,2)\max,i}^2) \leq_K (v_i^1, v_i^2).$$

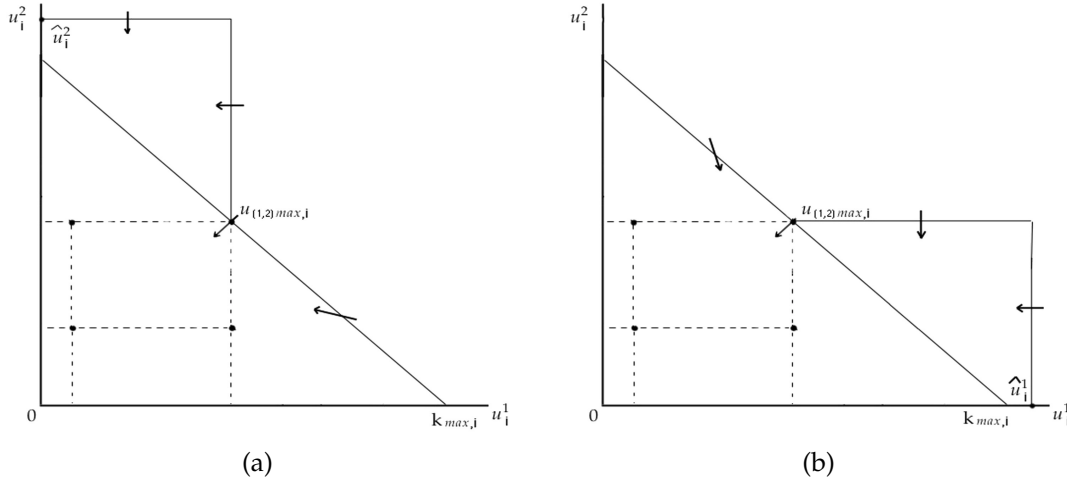
In this case, for all  $(v_i^1, v_i^2) \leq_K (u_i^1, u_i^2)$  we have  $u_i^{1'} + u_i^{2'} > 0$  and for all  $(u_i^1, u_i^2, 0)$  with  $u^1 + u^2 = k_{\max}$  for which  $u_i^{1'} + u_i^{2'} \leq 0$  we have  $(u_i^1, u_i^2) \leq_K (v_i^1, v_i^2)$ .

Thus, for all  $(u^1, u^2) \leq_K (u_{(1,2)\max,i}^1, u_{(1,2)\max,i}^2)$  with  $u^1 + u^2 = k_{\max}$  we have  $u_i^{1'} + u_i^{2'} \leq 0$  and the vector field of (3.1.1) with  $u_0^3 = 0$  points inside (or stays tangent to)

$\{u \in P : u_i^1 + u_i^2 = k_{\max,i}, (u_i^1, u_i^2) \leq_K (u_{(1,2)\max,i}^1, u_{(1,2)\max,i}^2), u^3 = 0\}$ . From **D** we have again that the set

$$D_i = \{u \in P : u^1, u^2 \neq 0, u_i^1 + u_i^2 \leq k_{\max,i}, (u_i^1, u_i^2) \leq_K (u_{(1,2)\max,i}^1, u_{(1,2)\max,i}^2), u^3 = 0\} \cup \\ \cup \{u \in P : u_{(1,2)\max,i}^1 \leq u_i^1 \leq \hat{u}_i^1, u_i^2 = u_{(1,2)\max,i}^2, u^3 = 0\}$$

is such that the vector field of (3.1.1) points inside  $D_i$ .



**Figure 3.3.2. The sets  $D_i$ :**

(a)  $f_1(z_i - k_{max,i}) < f_2(z_i - k_{max,i})$  and (b)  $f_1(z_i - k_{max,i}) > f_2(z_i - k_{max,i})$ .

When the two-species equilibrium solution corresponding to the coexistence of species 1 and 2 is unique, namely  $k_{max} = k$ , we have

$$\begin{aligned} [A + F_1(z - k)]u^{*1} &= 0, \\ [A + F_2(z - k)]u^{*2} &= 0. \end{aligned}$$

For  $v$  and  $w$  as above,

$$\begin{aligned} [A + F_1(z - k)]_i (k_i - w_i^2) &\leq -[A + F_2(z - k)]_i w_i^2 \\ \Leftrightarrow \underbrace{[A + F_1(z - k)]_i u_i^{*1}}_{= u_i^{*1'}} + [A + F_1(z - k)]_i u_i^{*2} - [A + F_1(z - k)]_i w_i^2 &\leq \\ &\leq -[A + F_2(z - k)]_i w_i^2 \\ \Leftrightarrow -[A + F_2(z - k)]_i u_i^{*2} + [A + F_1(z - k)]_i u_i^{*2} - [A + F_1(z - k)]_i w_i^2 &\leq \\ &\leq -[A + F_2(z - k)]_i w_i^2 \\ \Rightarrow f_1(z_i - k_i)(u_i^{*2} - w_i^2) &\leq f_2(z_i - k_i)(u_i^{*2} - w_i^2), \end{aligned}$$

and from **D** we obtain that  $w = (u^{*1}, u^{*2}, 0)$ .

Consider initial data for (3.1.1) such that  $u_0 \in D \cap P$ , where  $D = \prod_{i=1}^n D_i$ . Assume  $l > 0$  is such that  $Y_l$  given in Proposition 3.2.2 is the smallest such invariant rectangle with  $u_0 \in Y_l$ . Denote with  $\underline{u}_l^1$ ,  $\underline{u}_l^2$ ,  $\bar{u}_l^1$ , and  $\bar{u}_l^2$  the vectors for which  $Y_l = [\underline{u}_l^1, \bar{u}_l^1] \times [\underline{u}_l^2, \bar{u}_l^2] \times \{0\}$ .

Next we build the following vector:



$$\omega_{l,i} = \begin{cases} u_{(1,2)max,i}^1 + \bar{u}_{(1,2)}^{1,(l)} & : f_1(z_i - k_{max,i}) < f_2(z_i - k_{max,i}) \\ u_{(1,2)max,i}^2 + \bar{u}_{(1,2)}^{2,(l)} & : f_1(z_i - k_{max,i}) > f_2(z_i - k_{max,i}), \end{cases} \quad (3.3.10)$$

for  $i = 1, \dots, n$ , and we have that

$$k_{max} = u_{(1,2)max}^1 + u_{(1,2)max}^2 \leq \omega_r \leq \bar{u}_{(1,2)}^{1,(l)} + \bar{u}_{(1,2)}^{2,(l)} = K_l.$$

We can now prove the following proposition:

**Proposition 3.3.1**

For system (3.1.1) with  $n \geq 3$  assume that (3.1.4), (3.2.4) and (3.2.5) hold. For initial data  $u_0$  such that  $u_0 > 0$  and  $(u_0^1, u_0^2, 0) \in Y_l \cap D \cap P$ , with  $Y_l$  the smallest such invariant rectangle, if

$$s[A + F_3(z - \omega_l)] > 0, \quad (3.3.11)$$

then we can find initial data for species 3 such that it is persistent.

The advantage Proposition 3.3.1 brings with regard to Proposition 3.2.2, is that, even though the allowed initial-data-region for  $u^1$  and  $u^2$  is smaller, condition (3.3.11) is weaker than (3.2.8) (this follows immediately from (3.3.10)).

**F:** From **C** we have that the set  $\mathcal{S}_0$ , for a fixed  $r > 0$ , is such that the vector field of (3.1.1) points inside  $\mathcal{S}_0$  or stays tangent to  $\mathcal{S}_0$ . If  $O_{k_{max}}$  is not invariant, we saw that if  $i \in \{1, \dots, n\}$  is such that there exists a  $v = (v^1, v^2, 0) \neq u_{(1,2)max}$  with  $v^1 + v^2 = k_{max}$  with  $v_i^{1'} + v_i^{2'} > 0$ , then the vector field of (3.1.1) points inside the set  $\mathcal{S}_0 \cap D$ , with  $D$  given in **E**.

For a fixed  $r > 0$ , denote with

$$w_1 = \max\{u^1 + u^2 : (u^1, u^2, 0) \in S^1\},$$

and with

$$w_2 = \max\{u^1 + u^2 : (u^1, u^2, 0) \in S^2\}.$$

We build the vector  $\omega$  with:

$$\omega_i = \begin{cases} \max\{k_{max,i}, w_{2,i}\} & : f_1(z_i - k_{max,i}) < f_2(z_i - k_{max,i}) \\ \max\{k_{max,i}, w_{1,i}\} & : f_1(z_i - k_{max,i}) > f_2(z_i - k_{max,i}), \end{cases}$$

for  $i \in \{1, \dots, n\}$ , and we have that  $\max\{u^1 + u^2 : u \in \mathcal{S}_0 \cap D\} \leq \omega$ .

Note that when  $\mathcal{S}_0 \cap D \subset O_{k_{\max}}$ , we have that  $\omega = k_{\max}$ . Moreover, for  $Y_l$  with  $l > 0$  large enough, if  $k_{\max} > k$ ,  $\max\{u^1 + u^2, (u^1, u^2, 0) \in Y_l \cap S^i\} < k_{\max}$ , with  $i = 1, 2$ .

**Proposition 3.3.2**

For system (3.1.1) with  $n \geq 3$  assume that (3.1.4), (3.2.4) and (3.2.5) hold. For initial data  $u_0$  such that  $u_0 > 0$  and  $(u_0^1, u_0^2, 0) \in \mathcal{S}_0 \cap D$ , if

$$s[A + F_3(z - \omega)] > 0,$$

then we can find initial data for species 3 such that it is persistent.

Moreover, if  $(u_0^1, u_0^2, 0) \in Y_l \cap \mathcal{S}_0 \cap D$  for  $l$  large enough, and  $k_{\max} \neq k$ ,

$$s[A + F_3(z - k_{\max})] > 0,$$

is a sufficient condition for the persistence of species 3, for appropriate  $u_0^3$ .

When the two-species equilibrium corresponding to the coexistence of species 1 and 2 is unique, namely  $k_{\max} = k$ , we have that none of the following can hold:

$$k < \hat{u}^1 \quad \text{or} \quad k > \hat{u}^1,$$

as  $s[A + F_1(z - k)] = s[A + F_1(z - \hat{u}^1)] = 0$ , and

$$k < \hat{u}^2 \quad \text{or} \quad k > \hat{u}^2,$$

as  $s[A + F_2(z - k)] = s[A + F_2(z - \hat{u}^2)] = 0$ .

In this case, there always exists a  $i \in \{1, \dots, n\}$  such that

$$\max\{u_i^1 + u_i^2 : (u^1, u^2, 0) \in S^j\} > k_i$$

with  $j = 1$  or  $2$ .

**Proposition 3.3.3**

For system (3.1.1) with  $n \geq 3$  assume (3.1.4), (3.2.4) and (3.2.5) hold and that  $k_{\max} = k$ . Then, if

$$s[A + F_3(z - k)] > 0,$$

we can find initial data  $u_0 > 0$  such that species 3 is persistent.

**Proof:** For a fixed small  $r > 0$ , denote with  $w_1^l = \max\{u^1 + u^2 : (u^1, u^2, 0) \in Y_l \cap S^1\}$  and  $w_2^l = \max\{u^1 + u^2 : (u^1, u^2, 0) \in Y_l \cap S^2\}$ , and we build the vector

$$\omega_{l,i} = \begin{cases} \max\{k_i, w_{2,i}^l\} & : f_1(z_i - k_{\max,i}) < f_2(z_i - k_{\max,i}) \\ \max\{k_i, w_{1,i}^l\} & : f_1(z_i - k_{\max,i}) > f_2(z_i - k_{\max,i}), \end{cases}$$

for  $i \in \{1, \dots, n\}$ . From **C** and **E**, for initial data such that

$$(u_0^1, u_0^2, 0) \in Y_l \cap \mathcal{S}_0 \cap D,$$

we have that  $\max\{u^1 + u^2\} \geq \omega_l$ .

Consider  $\phi^3 > 0$  the eigenvector associated to  $s[A + F_3(z - k)] > 0$ , and take

$$\underline{u}^3 = \gamma^3 \cdot \phi^3 > 0$$

with  $\gamma^3$  a positive constant such that  $\gamma^3 \cdot \phi^3 \geq \omega_l - k$ . From (3.2.3), for a fixed  $u^3 \geq \underline{u}^3$ , we have that  $u^1(u^3)(t) + u^2(u^3)(t) \leq k$ , for all  $t$ . Thus, if  $\underline{u}^3$  is a lower solution for  $u^3$  corresponding to the solution of (3.1.1), we have that the solution of (3.1.1) is such that  $u^1(t) + u^2(t) \leq k$  for all initial data with  $u_0^3 \geq \underline{u}^3$ .

$$\begin{aligned} & [A + F_3(z - u^1 - u^2 - \gamma^3 \cdot \phi^3)] \cdot \gamma^3 \cdot \phi^3 = \\ & = [A + F_3(z - k)] \cdot \gamma^3 \cdot \phi^3 + [F_3(z - u^1 - u^2 - \gamma^3 \cdot \phi^3) - F_3(z - k)] \cdot \gamma^3 \cdot \phi^3 \\ & = \underbrace{s[A + F_3(z - k)]}_{>0} \cdot \gamma^3 \cdot \phi^3 + [F_3(z - u^1 - u^2 - \gamma^3 \cdot \phi^3) - F_3(z - K)] \cdot \gamma^3 \cdot \phi^3 \geq 0 \end{aligned}$$

$$\Leftrightarrow s[A + F_3(z - k)] \cdot \phi^3 + [F_3(z - u^1 - u^2 - \gamma^3 \cdot \phi^3) - F_3(z - k)] \cdot \phi^3 \geq 0.$$

The last inequality holds for small enough  $\omega_l$  which corresponds to a small enough  $Y_l$ , and for  $u^1 + u^2 \leq k$ . Thus, for initial conditions such that  $(u_0^1, u_0^2, 0) \in Y_l \cap \mathcal{S}^2 \cap D$  and  $u_0^3 \geq \underline{u}^3$ , we have that the solution of (3.1.1) is such that  $u^1(t) + u^2(t) \leq k$  and  $u^3(t) > 0$  for all  $t$ .  $\square$

### 3.4 Some examples

In this section we come back to the remark in **C**. In all our simulations, the two-species equilibria, when they exist, seem to be unique, and we have that  $\mathcal{S}$  is an invariant set. To illustrate this fact, we present here, as example, the dynamics of (3.1.1) with  $n = 4$  and with parameters

$$\begin{aligned} m_1 &= 30; & a_1 &= 20; \\ m_2 &= 7.91; & a_2 &= 5; \\ m_3 &= 44.72297534; & a_3 &= 30, \end{aligned} \tag{3.4.1}$$

for various initial data.

The single-species equilibria:

$$\begin{aligned}\hat{u}^1 &\simeq (0.27066891994, 0.33196890647, 0.26156692065, 0.13722402374); \\ \hat{u}^2 &\simeq (0.26814416439, 0.33236453212, 0.26301176787, 0.13818029367); \\ \hat{u}^3 &\simeq (0.27095081213, 0.33190903698, 0.26139111872, 0.13710946726),\end{aligned}$$

The two-species equilibrium:

$$\begin{aligned}u^{*1} &\simeq (0.21708890273, 0.26610542059, 0.20958574735, 0.10993673265); \\ u^{*2} &\simeq (0.053098263052, 0.065955519062, 0.052277541573, 0.027482372352),\end{aligned}$$

and thus  $k = k_{max} \simeq (0.270187165782, 0.332060939652, 0.261863288923, 0.137419105002)$ .

The three-species equilibrium:

$$\begin{aligned}\tilde{u}^1 &\simeq (0.10788525398, 0.13224474933, 0.10415641976, 0.054634487155); \\ \tilde{u}^2 &\simeq (0.064432302660, 0.080034033703, 0.063436365047, 0.33348560429); \\ \tilde{u}^3 &\simeq (0.097870108208, 0.11978131275, 0.094271125969, 0.049436800312).\end{aligned}$$

In the following examples we have  $S^1 := S_r^1$  and  $S^2 := S_r^2$ , with  $r = 1.0E - 8$ .

## I. Two species

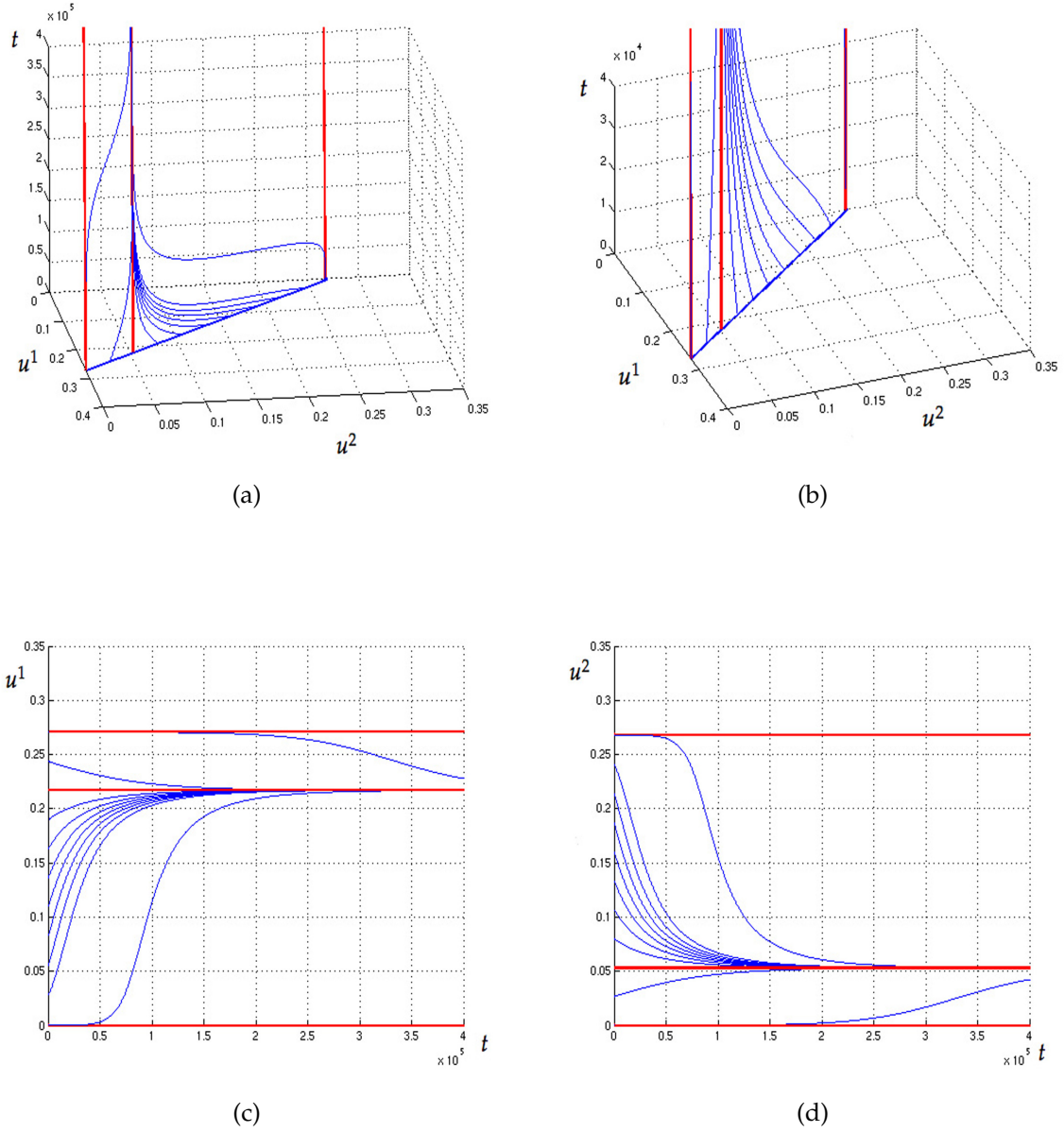
In Figure 3.4.1 we plot some trajectories of (2.7.1) with parameters (3.4.1), for initial values in  $\{(u^1, u^2) \in S^1 \cup S^2\}$ .

In Figure 3.4.2 we plot some trajectories starting from initial values arbitrarily in  $\Omega$ . In this case, for any of the initial values we have chosen, for large enough time the trajectories converge "along"  $S^1 \cup S^2$  towards a unique equilibrium.

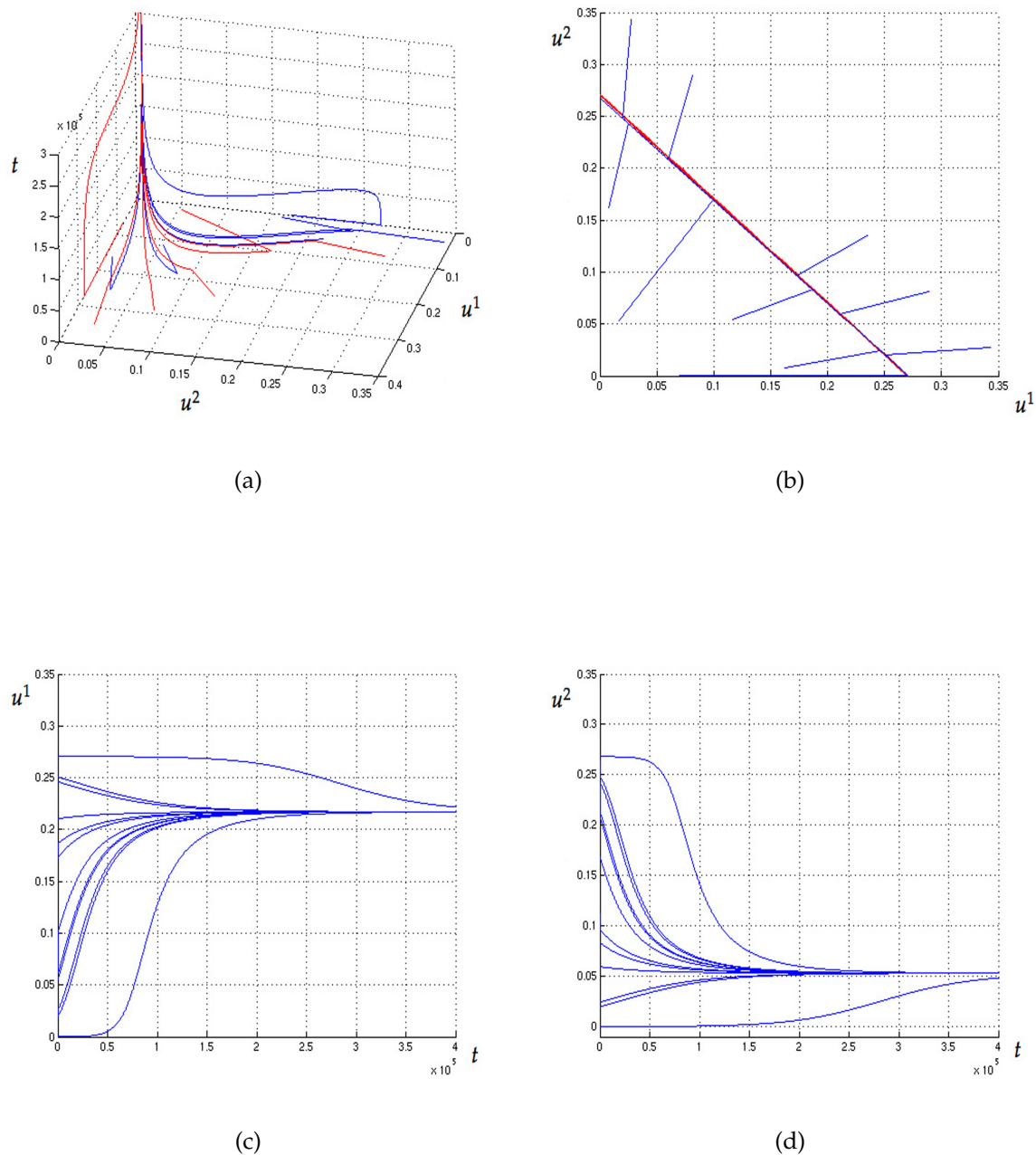
## II. Three species

For the parameters (3.4.1) we have  $s[A + F_3(z - k_{max})] \simeq 2.605905E - 10 > 0$ .

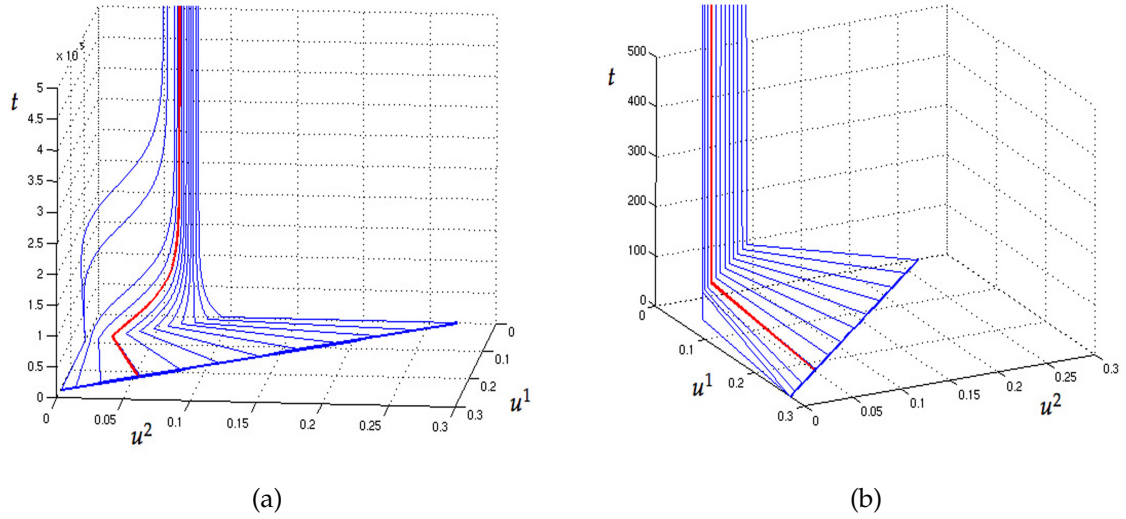
In this case we plot several trajectories of (3.1.1) for initial data such that  $(u_0^1, u_0^2) \in S^1 \cup S^2$ . As can be seen in Figure 3.4.3 - Figure 3.4.8, all plotted solutions converge towards the unique equilibrium along  $S^1 \cup S^2$ .



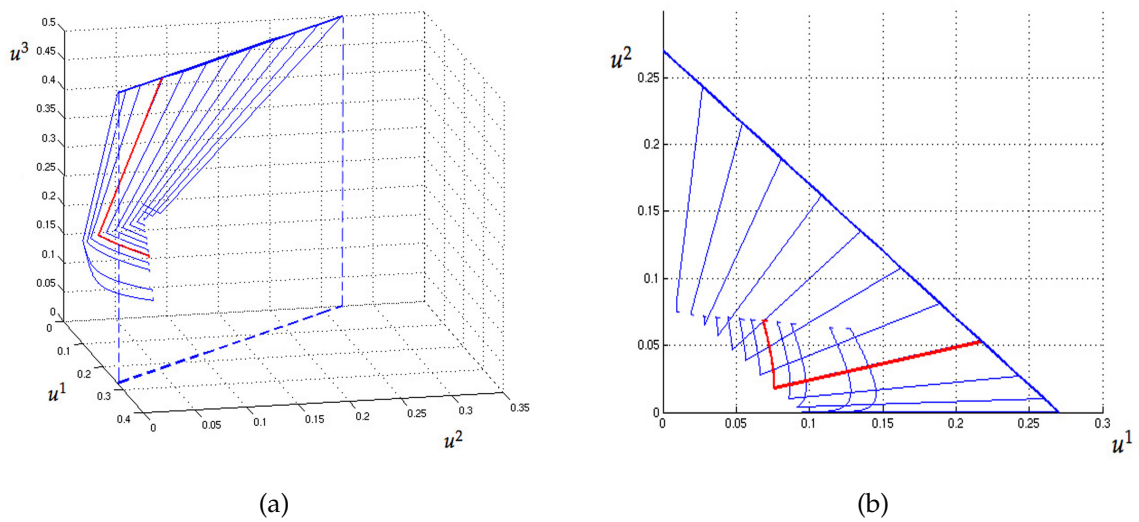
**Figure 3.4.1.** The solution of (2.7.1) - corresponding to the first vessel - with parameters given in (3.4.1), for initial values on  $S^1 \cup S^2$ . The trajectories colored in red correspond to the three possible equilibrium solutions of the system:  $(\hat{u}^1, 0)$  - for  $u_0^2 = 0$ ,  $(0, \hat{u}^2)$  - for  $u_0^1 = 0$ , and  $(u^{*1}, u^{*2}) > 0$ . For all the considered initial values with  $u_0 > 0$ , the trajectories approach  $u^*$ , for  $t \rightarrow \infty$ .  
**(a):** We plot  $(u_1^1(t), u_1^2(t))$  vs. time. **(b):** The same trajectories as in (a), for small  $t$ . **(c):**  $u_1^1(t)$  vs.  $t$  for the different values for  $u_{0,1}^1$ . **(d):**  $u_1^2(t)$  vs.  $t$  for the different values of  $u_{0,1}^2$ .



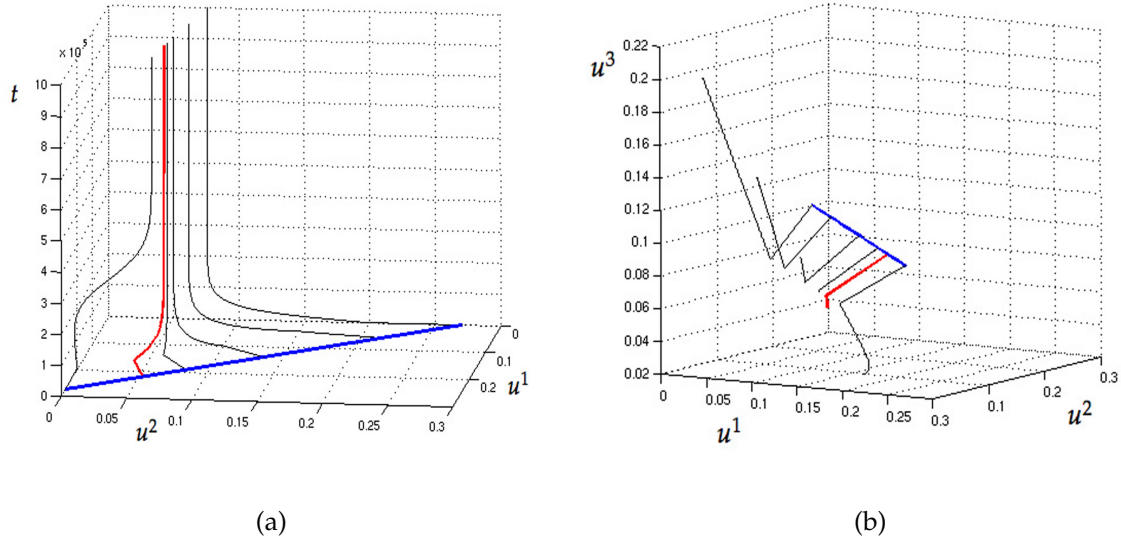
**Figure 3.4.2.** The solution of (2.7.1) - corresponding to the first vessel - with parameters given in (3.4.1), for initial values in  $\Omega$ . For all the considered initial values, the trajectories approach  $u^*$ , for  $t \rightarrow \infty$ , along  $S^1 \cup S^2$ , and all orbits starting in  $\mathcal{S}$  remain in  $\mathcal{S}$  for all time. **(a):** We plot  $(u_1^1(t), u_1^2(t))$  vs. time. **(b):** The orbits corresponding to some of the trajectories in (a) - we plot  $u_1^1$  vs.  $u_1^2$ . **(c):**  $u_1^1(t)$  vs.  $t$  for the different values for  $u_{0,1}^1$ . **(d):**  $u_1^2(t)$  vs.  $t$  for the different values of  $u_{0,1}^2$ .



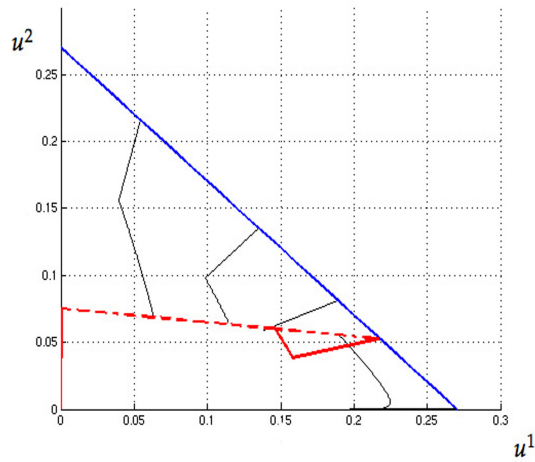
**Figure 3.4.3.** The solution of (3.1.1) - corresponding to the first vessel - with parameters given in (3.4.1), for initial values with  $(u_0^1, u_0^2) \in S^1 \cup S^2$  and  $u_0^3 = 0.5$ . The trajectory colored in red corresponds to  $(u_0^1, u_0^2) = (u^{*1}, u^{*2})$ . For all the considered initial values, the trajectories remain in  $\mathcal{S}$  and approach  $\tilde{u}$  for  $t \rightarrow \infty$ . **(a):** We plot  $(u_1^1(t), u_1^2(t))$  vs. time. **(b):** The same as in (a), for small  $t$ .



**Figure 3.4.4.** **(a):** The orbits  $(u_1^1, u_1^2, u_1^3)$  for the same initial data as in Figure 3.4.3. **(b):** The projections on the  $(u_1^1, u_1^2)$ -plane for the orbits in (a).



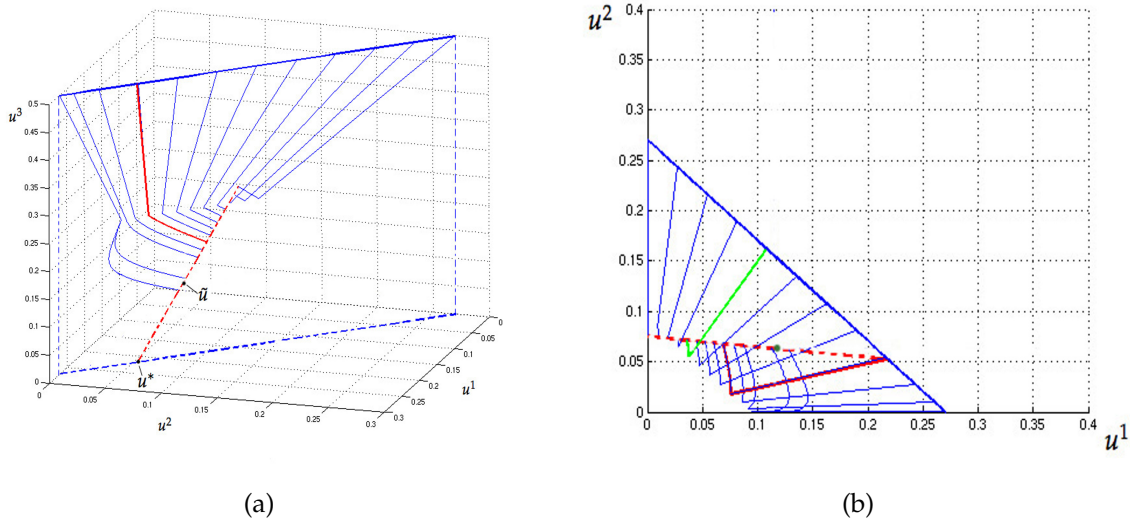
**Figure 3.4.5.** The solution of (3.1.1) - corresponding to the first vessel - with parameters given in (3.4.1), for initial values with  $(u_0^1, u_0^2) \in S^1 \cup S^2$  and  $u_0^3 = 0.1$ . The trajectory colored in red corresponds to  $(u_0^1, u_0^2) = (u^{*1}, u^{*2})$ . For all the considered initial values, the trajectories remain in  $\mathcal{S}$  and approach  $\tilde{u}$  for  $t \rightarrow \infty$ . **(a):** We plot  $(u_1^1(t), u_1^2(t))$  vs. time. **(b):** The orbits  $(u_1^1, u_1^2, u_1^3)$  for the trajectories in (a).



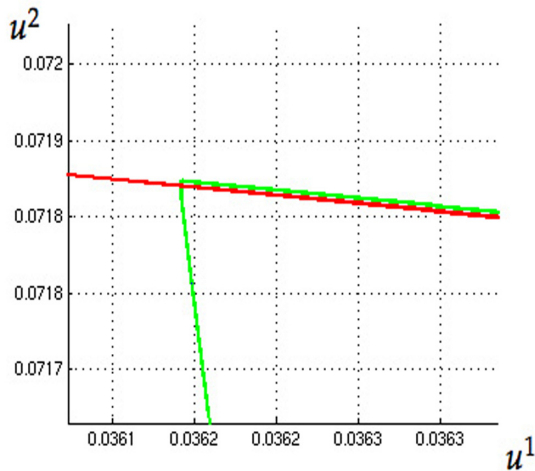
**Figure 3.4.6.** The projections on the  $(u_1^1, u_1^2)$ -plane for the orbits in Figure 3.4.5(b).



In all our simulations it looks like the three-species equilibria, when they exist, are unique. To illustrate this, for the initial values  $u_0$  in Figure 3.4.4, we consider the solution  $\pi(u_0, t)$  for very large  $t$ . As can be seen in Figure 3.4.7, each trajectory approaches a curve through the two-species equilibrium  $u^*$  corresponding to the coexistence of species 1 and 2, and through  $\tilde{u}$  the three-species coexistence equilibrium, and then converges along this curve, this time very "slowly", towards  $\tilde{u}$  - Figure 3.4.8.



**Figure 3.4.7. (a):** The orbits  $(u_1^1, u_1^2, u_1^3)$  for the same initial data as in Figure 3.4.4. After large enough  $t$ , each orbit approaches the equilibrium  $\tilde{u}$  along a curve through the two-species equilibrium  $u^*$  corresponding to the coexistence of species 1 and 2, and through  $\tilde{u}$  the three-species coexistence equilibrium, - here, the dotted red line **(b):** The projections on the  $(u_1^1, u_1^2)$ -plane for the orbits in (a) .



**Figure 3.4.8.** The orbit colored in green in Figure 3.4.7(b) approaches the equilibrium  $\tilde{u}$  along the curve through  $\tilde{u}$  and  $u^*$ .

### 3.5 Bifurcation diagrams

We now come back to the bifurcation analysis we have started in the beginning of the chapter. Let (3.1.4) hold.

First, remark that since  $O$  attracts all orbits with initial values  $(u_0^1, u_0^2, 0) \in \Omega$ , with  $u_0^1, u_0^2 > 0$ , we have that  $O \subseteq Y$ , for every invariant region  $Y$  in Theorem 3.2.1 with  $Y \not\subseteq O$ . Thus, any condition (3.2.6) implies

$$s[A + m_3 \tilde{F}_3(z - u^{*1} - u^{*2})] > 0, \quad (3.5.1)$$

with  $E_{1,2}^* = (u^{*1}, u^{*2}, 0)$  any two-species equilibrium corresponding to the coexistence of species 1 and 2. In particular, (3.1.6) holds.

The variational matrix of (3.1.1) is of the form

$$J = \begin{bmatrix} A_1 - D_1 & -D_1 & -D_1 \\ -D_2 & A_2 - D_2 & -D_2 \\ -D_3 & -D_3 & A_3 - D_3 \end{bmatrix},$$

where

$$\begin{aligned} A_1 &= A + F_1(z - u^1 - u^2 - u^3) \\ A_2 &= A + F_2(z - u^1 - u^2 - u^3) \\ A_3 &= A + F_3(z - u^1 - u^2 - u^3), \end{aligned}$$

and

$$\begin{aligned} D_1 &= \text{diag}(u_1^1 f_1'(z_1 - u_1^1 - u_1^2 - u_1^3), \dots, u_n^1 f_1'(z_n - u_n^1 - u_n^2 - u_n^3)), \\ D_2 &= \text{diag}(u_1^2 f_2'(z_1 - u_1^1 - u_1^2 - u_1^3), \dots, u_n^2 f_2'(z_n - u_n^1 - u_n^2 - u_n^3)), \\ D_3 &= \text{diag}(u_1^3 f_3'(z_1 - u_1^1 - u_1^2 - u_1^3), \dots, u_n^3 f_3'(z_n - u_n^1 - u_n^2 - u_n^3)). \end{aligned}$$

At  $E_{1,2}^*$ ,  $J$  takes the form

$$J(E_{1,2}^*) = \begin{bmatrix} A + F_1(z - u^{*1} - u^{*2}) - D_1 & -D_1 & -D_1 \\ -D_2 & A + F_2(z - u^{*1} - u^{*2}) - D_2 & -D_2 \\ 0 & 0 & A + F_3(z - u^{*1} - u^{*2}) \end{bmatrix},$$

and has  $\tilde{s}_3 = s[A + F_3(z - u^{*1} - u^{*2})]$  as a simple eigenvalue with the corresponding eigenvector  $(\tilde{w}_1, \tilde{w}_2, \tilde{w}_3)$  satisfying

$$\begin{aligned} [A + F_1(z - u^{*1} - u^{*2}) - D_1 - \tilde{s}_3 I] \tilde{w}_1 &= D_1 \tilde{w}_2 + D_1 \tilde{w}_3, \\ -D_2 \tilde{w}_1 + [A + F_2(z - u^{*1} - u^{*2}) - D_2 - \tilde{s}_3 I] \tilde{w}_2 &= D_2 \tilde{w}_3, \\ [A + F_3(z - u^{*1} - u^{*2})] \tilde{w}_3 &= \tilde{s}_3 \tilde{w}_3, \end{aligned}$$

where, by Perron-Frobenius Theorem, we can choose  $\tilde{w}_3 > 0$ . When (3.5.1) holds, since  $[A + F_1(z - u^{*1} - u^{*2}) - D_1 - \tilde{s}_3 I]^{-1} < 0$  and  $[A + F_2(z - u^{*1} - u^{*2}) - D_2 - \tilde{s}_3 I]^{-1} < 0$  we have that if  $\tilde{w}_2 \geq 0$  then  $\tilde{w}_1 < 0$ , and if  $\tilde{w}_1 \geq 0$  then  $\tilde{w}_2 < 0$ , and they can not be both positive.

From [STW] we have that the stability modulus  $s_3$  of the variational matrix of (2.7.1) at  $(u^{*1}, u^{*2})$  is such that  $s_3 \leq 0$ . Moreover, when:

**C1:** The two species equilibria, when they exist, are unique.

holds, we have that  $s_3 < 0$ .

Let  $\tilde{m}_3$  be the unique value for  $m_3$  with

$$s[A + \tilde{m}_3 \tilde{F}_3(z - k)] = 0, \quad (3.5.2)$$

and we have that for  $m_3 > \tilde{m}_3$ ,  $E_{1,2}^* = (u^{*1}, u^{*2}, 0)$  with  $u^{*1} + u^{*2} = k$ , is unstable.

### Theorem 3.5.1

For (3.1.1) with  $n \geq 3$ , let (3.1.4), (3.2.4) and (3.2.5) hold and assume  $s_3 \neq 0$ . Then there exists a branch  $S_3^*$  of  $\Lambda_3$  bifurcating at  $(\tilde{m}_3, u^{*1}, u^{*2}, 0)$  from  $Q_{1,2}^*$ , the branch of the solution set corresponding to the equilibrium  $E_{1,2}^*$ . Moreover, there exists a neighborhood  $\tilde{W}_3$  of  $(\tilde{m}_3, u^{*1}, u^{*2}, 0)$  in  $\mathbb{R}_+ \times \mathbb{R}_+^{3n}$  such that

$$\tilde{W}_3 \cap S_3^* = \{(\tilde{m}_3(s), u^{*1}(s), u^{*2}(s), \tilde{u}^3(s)) : 0 \leq s \leq \delta\},$$

where  $\tilde{m}_3(s), u^{*1}(s), u^{*2}(s), \tilde{u}^3(s)$  are smooth functions satisfying

$$\begin{aligned} \tilde{m}_3(s) &= \tilde{m}_3 + \tilde{\kappa}s + o(s), \\ u^{*1}(s) &= u^{*1} + s\tilde{w}_1 + o(s), \quad s \rightarrow 0_+, \\ u^{*2}(s) &= u^{*2} + s\tilde{w}_2 + o(s) \\ \tilde{u}^3(s) &= s\tilde{w}_3 + o(s), \end{aligned} \quad (3.5.3)$$

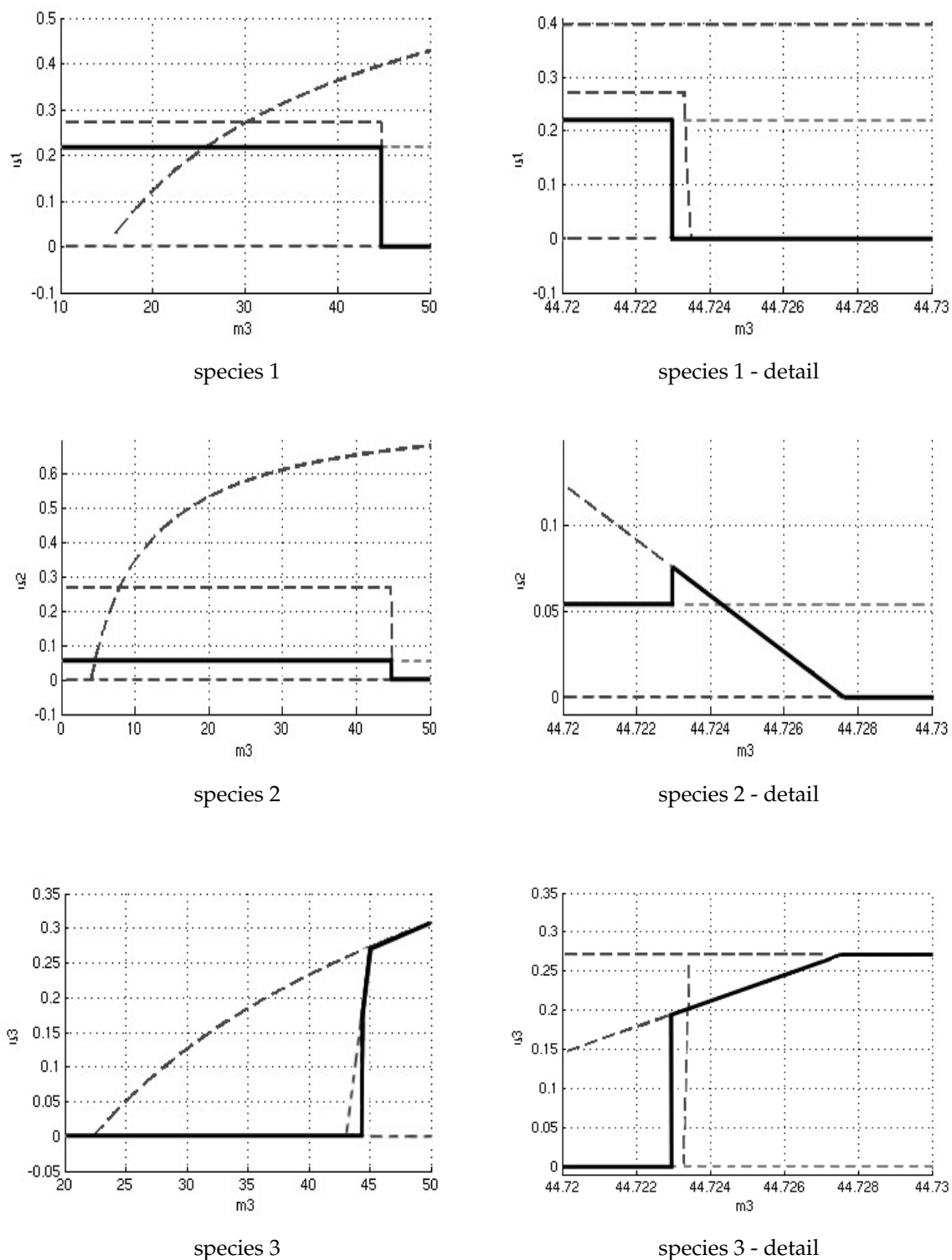
where  $\tilde{w}$  with  $\tilde{w}_3 > 0$  is a normalized null vector of the Jacobian of (3.1.1) at  $E_{1,2}^*$  corresponding to  $\tilde{m}_3$ . For  $s$  small enough,  $S_3^*$  corresponds to positive equilibria.

**Proof:** Since  $J$ , the variational matrix of (3.1.1) at  $E_{1,2}^*$ , has 0 as a simple eigenvalue for  $m_3 = \tilde{m}_3$ , the theorem follows from [CR1], Th. 1.7. (see Appendix B).  $\square$

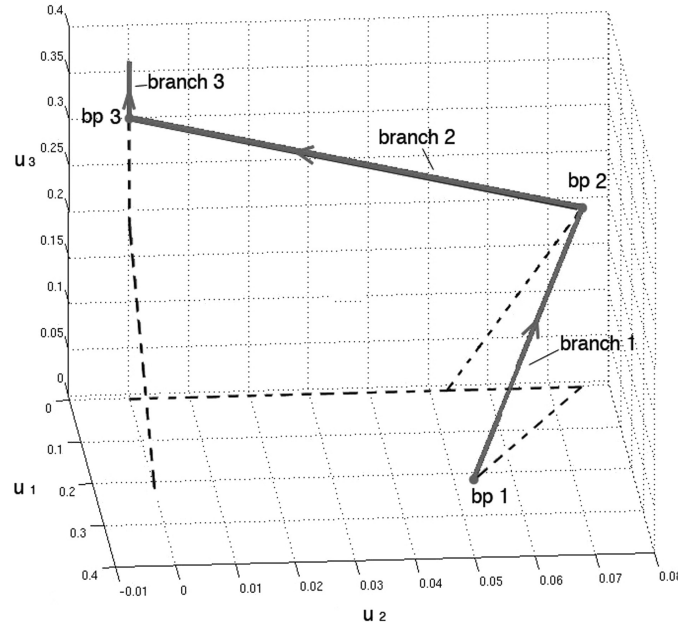
For the null vector  $\tilde{w}$  in Theorem 3.5.1 we have  $\tilde{w}_1 = M\tilde{w}_2$  with  $M$  a matrix such that  $M < 0$ .

When **C1** holds, we saw in the last paragraph of 3.1, that, when (3.5.1) is fulfilled, we can find initial data for which  $u^3$  is persistent. In this case, when  $\tilde{\kappa}$  in (3.5.3) is positive, the branch in (3.5.3) is stable and corresponds to equilibria  $\tilde{u}$  with  $\tilde{u}^3 > 0$ , and, for  $s$  small enough,  $\tilde{u}^1, \tilde{u}^2 > 0$ .

In Figure 3.5.1 we give the bifurcation diagrams of (3.1.1) with the parameters  $a_1, m_1, a_2, m_2$  and  $a_3$  given in (3.4.1) and  $m_3$  as the bifurcation parameter.



**Figure 3.5.1.** Bifurcation diagrams for (3.1.1) - corresponding to the first vessel - with parameters given in (3.4.1) and  $m_3$  as bifurcation parameter. Interrupted lines represent unstable equilibria.



**Figure 3.5.2.** Bifurcation diagram for (3.1.1) - corresponding to the first vessel - with parameters given in (3.4.1) and  $m_3$  as bifurcation parameter. We plot the equilibria  $(\tilde{u}_1^1(m_3), \tilde{u}_1^2(m_3), \tilde{u}_1^3(m_3))$ . Arrows indicate the direction of growth of  $m_3$ . Interrupted lines represent projections.

In Figure 3.5.2, "bp 1" is reached for  $m_3 = \tilde{m}_3$ , where the branch  $S^+$  ("branch 1") appears, corresponding to three-species-coexistence equilibria (and persistence of (3.1.1)). In this case (parameters given by (3.4.1)),  $S^+$  emanates from the  $u^1 \times u^2$  hyperplane at  $E_{1,2}^*$  and joins the  $u^2 \times u^3$  hyperplane on the two-species-coexistence branch  $Q_{2,3}^*$  ("branch 2"), corresponding to the coexistence of species 2 and 3, for  $m_3 = m_3^*$  ("bp 2"), with

$$s[A + F_1(z - u_{(2,3)}^{*1}(m_3^*) - u_{(2,3)}^{*2}(m_3^*))] = 0,$$

where  $u_{(2,3)}^*(m_3^*)$  represents the two-species equilibrium for species 2 and 3 corresponding to  $m_3^*$ .

For fixed  $a_1, m_1, a_2, m_2$  and  $a_3$  (such that (3.1.4) hold), we make the following notations:

1. Assume that for  $u_2 = 0$ , the coexistence of species 1 and 3 holds for  $m_3 \in (\underline{m}_{(1,3)}, \overline{m}_{(1,3)})$ .
2. Assume that for  $u_1 = 0$ , the coexistence of species 2 and 3 holds for  $m_3 \in (\underline{m}_{(2,3)}, \overline{m}_{(2,3)})$ .

According to Theorem 3.8.1 such intervals exist, but they can be degenerate, for example if  $a_1 = a_3$  or  $a_2 = a_3$ .

For the example in Figure 3.5.2 we have:

$$\underline{m}_{(2,3)} < \tilde{m}_3 < m_3^* < \underline{m}_{(1,3)} < \overline{m}_{(1,3)} < \overline{m}_{(2,3)},$$

for  $m_3 < \tilde{m}_3$ ,  $E_{1,2}^*$  attracts all trajectories with positive initial data, for  $\tilde{m}_3 < m_3 < m_3^*$ , there exists a three-species-coexistence equilibrium  $\tilde{E}(m_3)$  and all equilibria on the boundary of the positive cone in  $\mathbb{R}^{3n}$  are unstable; for  $m_3^* < m_3 < \overline{m}_{(2,3)}$ ,  $E_{2,3}^*(m_3)$  attracts all trajectories with positive initial data, and for  $m_3 > \overline{m}_{(2,3)}$ , the attractor is  $\hat{E}^3(m_3)$ .

Let  $\overline{m}_3$  be such that  $\overline{m}_3 \tilde{f}_3(S) > \max\{f_1(S), f_2(S)\}$  for all scalar  $S > 0$ . Then for all  $m_3 \geq \overline{m}_3$  we have  $\overline{m}_3 \tilde{F}_3(u) > \max\{F_1(u), F_2(u)\}$  for all vectors  $u \geq 0$ ,  $u \neq 0$ . It follows that for  $m_3 \geq \overline{m}_3$

$$\begin{aligned} [A + m_3 \tilde{F}_3(z - u^{*1} - u^{*2})]u^{*1} &> [A + F_1(z - u^{*1} - u^{*2})]u^{*1} = 0, \\ [A + m_3 \tilde{F}_3(z - u^{*1} - u^{*2})]u^{*2} &> [A + F_2(z - u^{*1} - u^{*2})]u^{*2} = 0, \end{aligned}$$

and thus

$$[A + m_3 \tilde{F}_3(z - u^{*1} - u^{*2})](u^{*1} + u^{*2}) > 0,$$

and  $u^{*1} + u^{*2}$  is a lower solution for the no-competition system (3.4.2) corresponding to species 3, and  $u^{*1} + u^{*2} < \hat{u}^3(m_3)$ .

Since  $\overline{m}_3 \tilde{f}_3(S) > \max\{f_1(S), f_2(S)\}$  for all  $S > 0$ , coexistence is not possible. We have

$$\begin{aligned} s[A + F_1(z - \hat{u}^3(m_3))] &< s[A + F_1(z - u^{*1} + u^{*2})] = 0, \\ s[A + F_2(z - \hat{u}^3(m_3))] &< s[A + F_2(z - u^{*1} + u^{*2})] = 0, \end{aligned}$$

for all  $m_3 \geq \overline{m}_3$ , and thus we have that

$$\begin{aligned} \overline{m}_3 &> m_{(1,3)} \quad \text{with} \quad s[A + F_1(z - \hat{u}^3(m_{(1,3)}))] = 0, \\ \overline{m}_3 &> m_{(2,3)} \quad \text{with} \quad s[A + F_2(z - \hat{u}^3(m_{(2,3)}))] = 0. \end{aligned}$$

In particular, we have established the following proposition:

**Proposition 3.5.2**

There exists a  $\overline{m}_3 \geq \max\{m_{(1,3)}, m_{(2,3)}\}$  such that for  $m_3 > \overline{m}_3$ , the solution set is

$$\Sigma = \{E_0 = (0, 0, 0), \hat{E}^1, \hat{E}^2, \hat{E}^3(m_3), E_{1,2}^*\},$$

and  $\hat{E}^3(m_3)$  is the attractor for all solutions of (3.1.1) with positive initial data.

In all our examples we have  $m_{(1,3)} = \bar{m}_{(1,3)}$  and  $m_{(2,3)} = \bar{m}_{(2,3)}$ .

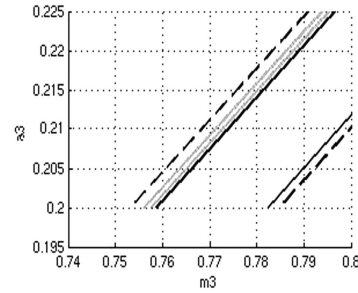
In Figure 3.5.3 we plot the above intervals for  $m_3$  for different values of  $a_3$  and in Figures 3.5.4 to 3.5.6 we give some of the corresponding bifurcation diagrams.

Line types:

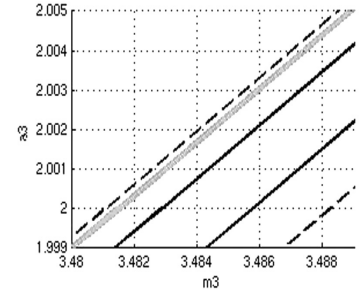
---  $\rightarrow [\underline{m}_{(1,3)}, \bar{m}_{(1,3)}]$

—  $\rightarrow [\underline{m}_{(2,3)}, \bar{m}_{(2,3)}]$

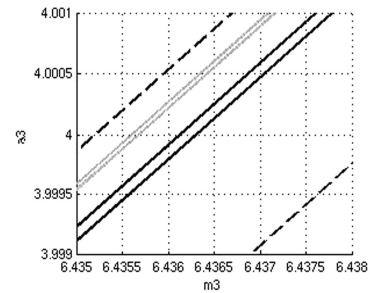
—  $\rightarrow [\tilde{m}_3, m_3^*]$



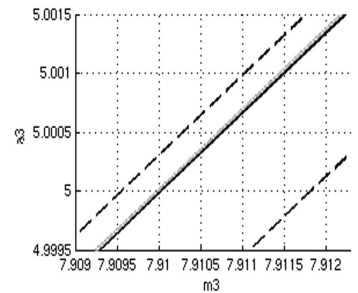
$a_3 = 0.2$



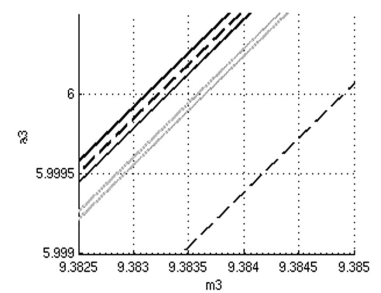
$a_3 = 2$



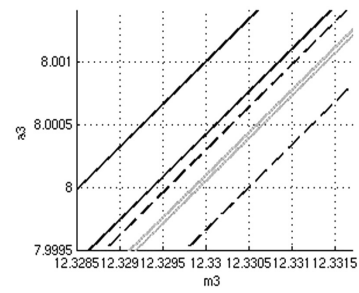
$a_3 = 4$



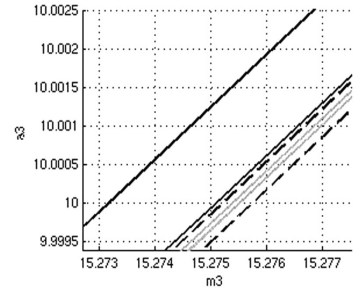
$a_3 = 5$  - degenerate interval



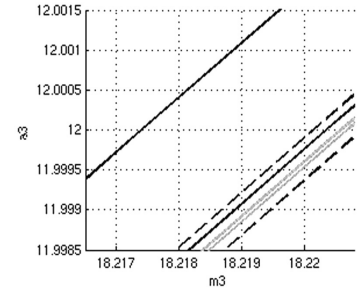
$a_3 = 6$



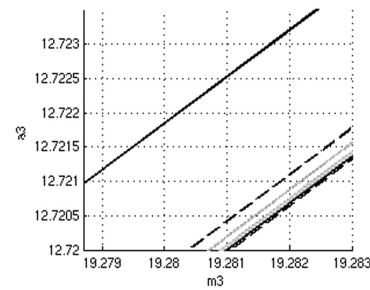
$a_3 = 8$



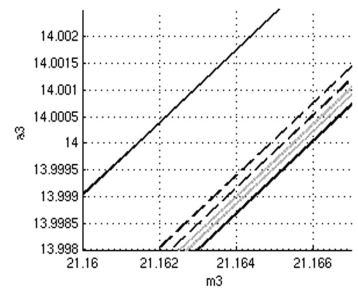
$a_3 = 10$



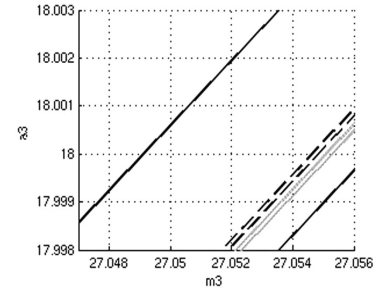
$a_3 = 12$



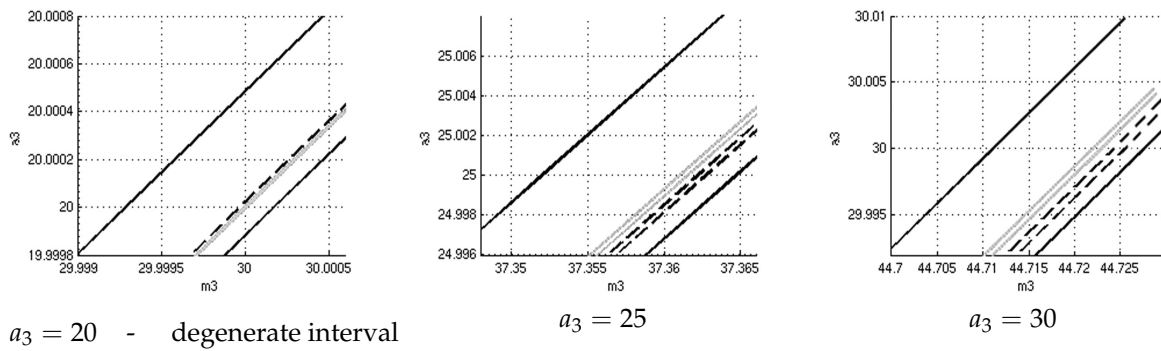
$a_3 = 12.7214372$  - each two species can coexist



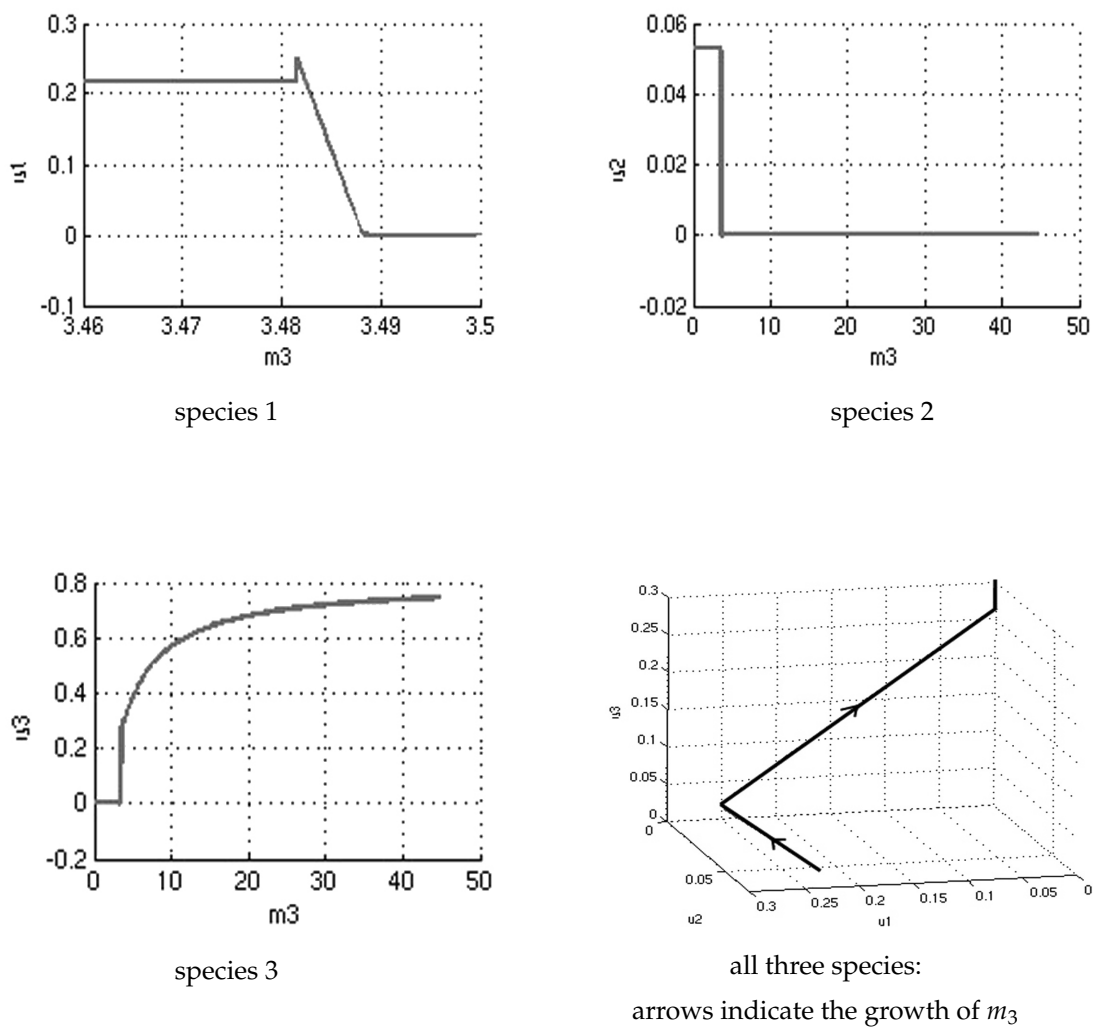
$a_3 = 14$



$a_3 = 18$

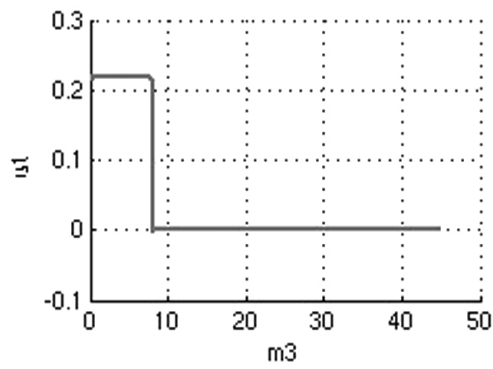


**Figure 3.5.3.** The intervals  $[\underline{m}_{(1,3)}, \bar{m}_{(1,3)}]$ ,  $[\underline{m}_{(2,3)}, \bar{m}_{(2,3)}]$ ,  $[\tilde{m}_3, m_3^*]$  for  $a_1, m_1, a_2, m_2$  given in (3.4.1) and different values for  $a_3$ .

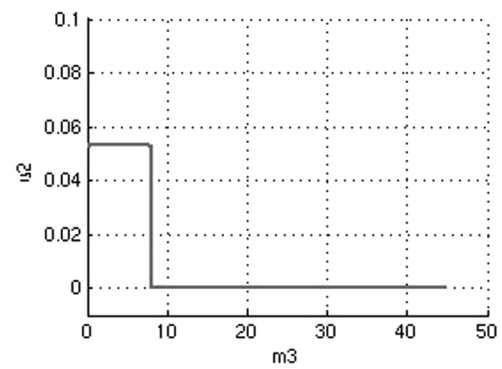


**Figure 3.5.4.** Bifurcation diagrams for (3.1.1) - corresponding to the first vessel - for  $a_1, m_1, a_2, m_2$  given in (3.4.1),  $a_3 = 2$ , and  $m_3$  as bifurcation parameter.

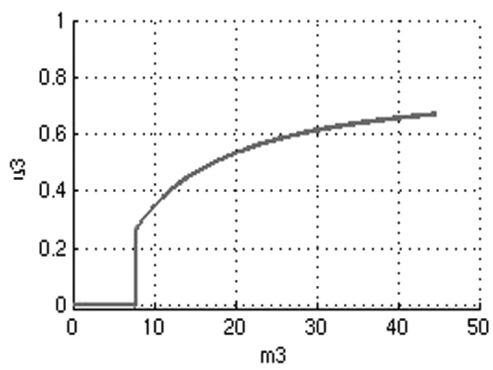




species 1

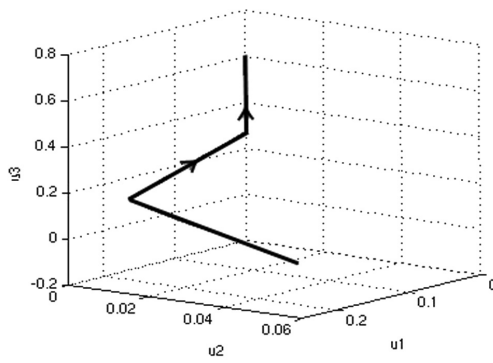
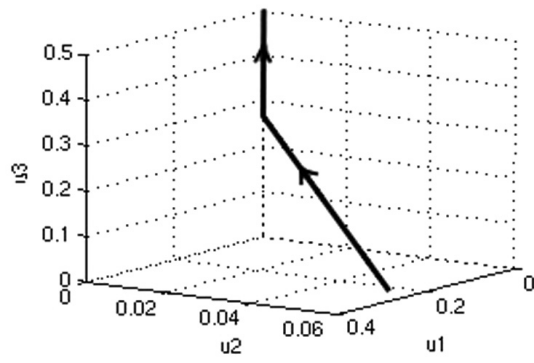
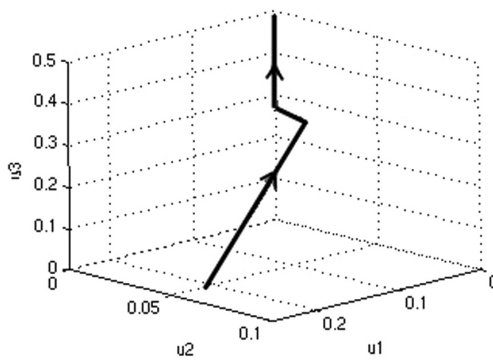


species 2



species 3

**Figure 3.5.5.** Bifurcation diagrams for (3.1.1) - corresponding to the first vessel - for  $a_1, m_1, a_2, m_2$  given in (3.4.1),  $a_3 = a_2$ , and  $m_3$  as bifurcation parameter. The interval  $[\tilde{m}_3, m_3^*]$  is degenerate.

 $a_3 = 8$  $a_3 = 12.7214372$  $a_3 = 14$ 

**Figure 3.5.6.** Bifurcation diagrams for (3.1.1) - corresponding to the first vessel - for  $a_1, m_1, a_2, m_2$  given in (3.4.1), and different values for  $a_3$ .

In Table 3.5.1 we give the different values for  $\underline{m}_{(1,3)}$ ,  $\overline{m}_{(1,3)}$ ,  $\underline{m}_{(2,3)}$ ,  $\overline{m}_{(2,3)}$ ,  $\tilde{m}_3$ ,  $m_3^*$ :

$a_3$	$\underline{m}_{(1,3)}$	$\overline{m}_{(1,3)}$	$\underline{m}_{(2,3)}$	$\overline{m}_{(2,3)}$	$\tilde{m}_3$	$m_3^*$
0.2	0.753216	0.784836	0.7588000	0.782476	0.75763324413	0.75765980648
2	3.481101	3.488242	3.4828880	3.485770	3.48160180210	3.48160233500
3	4.959600	4.964167	4.9609790	4.961896	4.96008931200	4.96008942140
4	6.435208	6.438359	6.4361310	6.436309	6.43567732060	6.43567733570
5	7.909555	7.911823	7.9100000	7.910000	7.91000000000	7.91000000000
5.5	8.646458	8.648401	8.6466610	8.646694	8.64689050710	8.64689050890
6	9.383301	9.384911	9.3831960	9.383320	9.38365754990	9.38365755500
8	12.32957	12.33051	12.328540	12.32939	12.3299359520	12.3299359800
10	15.2752	15.27573	15.273160	15.27508	15.2755013960	15.2755014380
11	16.74786	16.74825	16.745320	16.74784	16.7481347820	16.7481348270
12	18.22046	18.22074	18.217410	18.22057	18.2207009170	18.2207009630
12.7214372	19.28280	19.28303	19.279399	19.28303	19.2830318550	19.2830318890
14	21.16550	21.16564	21.161440	21.16595	21.1656877600	21.1656877900
18	27.05524	27.05525	27.049140	27.05651	27.0553019260	27.0553019280
20	30.00000	30.00000	29.999288	30.000174	30.0000000000	30.0000000000
25	37.36172	37.36177	37.352050	37.36472	37.3615628000	37.3615653100
30	44.72328	44.72347	44.711070	44.72761	44.7229753160	44.7229753670

From the relative positions of the intervals  $[\underline{m}_{(1,3)}, \overline{m}_{(1,3)}]$ ,  $[\underline{m}_{(2,3)}, \overline{m}_{(2,3)}]$ ,  $[\tilde{m}_3, m_3^*]$  in Figure 3.5.3, we can see that two-species coexistence for each of the possible three pairs of species, for  $m_3 \in [\tilde{m}_3, m_3^*]$ , occurs only in the case

$$\overline{m}_{(1,3)} = \overline{m}_{(2,3)}$$

which holds for  $a_3 \simeq 12.7214372$ . In this case, the branch  $S_3^*$  bifurcating at  $E_{1,2}^*$  from the  $u^1 \times u^2$  hyperplane, joins the  $u^3$  axis for  $m^3 = m_3^* = \overline{m}_{(1,3)} = \overline{m}_{(2,3)}$ .

In every other case we have:

1. If  $\overline{m}_{(1,3)} > \overline{m}_{(2,3)}$ , then

$$[\tilde{m}_3, m_3^*] \subset [\underline{m}_{(1,3)}, \overline{m}_{(1,3)}] \quad \text{and} \quad [\tilde{m}_3, m_3^*] \cap [\underline{m}_{(2,3)}, \overline{m}_{(2,3)}] = \emptyset.$$

2. If  $\overline{m}_{(1,3)} < \overline{m}_{(2,3)}$ , then

$$[\tilde{m}_3, m_3^*] \subset [\underline{m}_{(2,3)}, \overline{m}_{(2,3)}] \quad \text{and} \quad [\tilde{m}_3, m_3^*] \cap [\underline{m}_{(1,3)}, \overline{m}_{(1,3)}] = \emptyset.$$

In this case, the branch  $S_3^*$  bifurcating at  $E_{1,2}^*$  from the  $u^1 \times u^2$  hyperplane, joins the two-species-coexistence branch of species 3 and the species corresponding to  $\max\{\bar{m}_{(1,3)}, \bar{m}_{(2,3)}\}$ . As  $m_3$  grows further we "move" along this branch for  $m_3^* < m_3 < \max\{\bar{m}_{(1,3)}, \bar{m}_{(2,3)}\}$ , until we reach the  $u^3$  axis at  $\max\{\bar{m}_{(1,3)}, \bar{m}_{(2,3)}\}$ .

At  $\hat{E}^3$ , the variational matrix  $J$  of (3.1.1) takes the form

$$J(\hat{E}^3) = \begin{bmatrix} A + F_1(z - \hat{u}^3) & 0 & 0 \\ 0 & A + F_2(z - \hat{u}^3) & 0 \\ -D_3 & -D_3 & A + F_3(z - \hat{u}^3) - D_3 \end{bmatrix},$$

with  $s[A + F_3(z - \hat{u}^3) - D_3] < 0$  and thus  $s[J(\hat{E}^3)] < 0$  if and only if both  $s[A + F_1(z - \hat{u}^3)] < 0$  and  $s[A + F_2(z - \hat{u}^3)] < 0$ , and  $J(\hat{E}^3)$  has a positive eigenvalue when either  $s[A + F_1(z - \hat{u}^3)] > 0$  or  $s[A + F_2(z - \hat{u}^3)] > 0$ . Denote with  $\hat{m}_3 = \max\{m_{(1,3)}, m_{(2,3)}\}$  and with  $\hat{Q}_{3,s} = \{(m_3, 0, 0, \hat{u}^3(m_3)) : m_3 \geq \hat{m}_3\}$ . It is obvious that (3.2.4) and (3.2.5) hold at  $\hat{m}_3$ .

**(1):** Assume  $\hat{m}_3 = m_{(1,3)} > m_{(2,3)}$ . Hence

$$\begin{aligned} s[A + F_1(z - \hat{u}^3(\hat{m}_3))] &= 0 \quad \text{and} \quad s[A + F_1(z - \hat{u}^3(m_3))] > 0 \quad \text{for} \quad m_3 < \hat{m}_3, \\ s[A + F_2(z - \hat{u}^3(m_3))] &< 0 \quad \text{for} \quad m_3 \in (m_{(2,3)}, \hat{m}_3]. \end{aligned} \quad (3.5.4)$$

For a null vector  $w = (w_1, w_2, w_3)$  of  $J(\hat{E}^3(\hat{m}_3))$  we have:

$$\begin{aligned} (A + F_1(z - \hat{u}^3)) \cdot w_1 &= 0, \\ (A + F_2(z - \hat{u}^3)) \cdot w_2 &= 0, \\ -D_3 \cdot w_1 - D_3 \cdot w_2 + (A + F_3(z - \hat{u}^3) - D_3) \cdot w_3 &= 0. \end{aligned}$$

From (3.5.5) and the Perron-Frobenius theory we have that  $w_1 > 0$ ,  $w_2 = 0$  and, since  $s[A + F_3(z - \hat{u}^3) - D_3] > 0$ , we have that  $-(A + F_3(z - \hat{u}^3) - D_3)^{-1} > 0$  and thus  $w_3 = (A + F_3(z - \hat{u}^3) - D_3)^{-1} \cdot D_3 \cdot w_1 < 0$ .

**(2):** Assume  $\hat{m}_3 = m_{(2,3)} > m_{(1,3)}$ . Then, as above, we obtain that a null vector  $w = (w_1, w_2, w_3)$  of  $J(\hat{E}^3(\hat{m}_3))$  is such that  $w_1 = 0$ ,  $w_2 > 0$ , and  $w_3 < 0$ .

**(3):** If  $\hat{m}_3 = m_{(1,3)} = m_{(2,3)}$ , then a null vector  $w = (w_1, w_2, w_3)$  of  $J(\hat{E}^3(\hat{m}_3))$  is such that  $w_1 > 0$ ,  $w_2 > 0$ , and  $w_3 < 0$ , but zero is no longer a simple eigenvalue of  $J(\hat{E}^3(\hat{m}_3))$ .

The following theorem follows immediately, from [CR1], Th.1.7.:

**Theorem 3.5.3**

For (3.1.1) with  $n \geq 3$ , let (3.1.4) hold and  $m_{(1,3)} \neq m_{(2,3)}$ . There exists a branch  $\hat{S}$  of  $\Lambda_3$  bifurcating at  $(\hat{m}_3, 0, 0, \hat{u}^3(\hat{m}_3))$  from

$$\hat{Q}_3 = \{(m_3, 0, 0, \hat{u}^3(m_3)) : m_3 > 0 \text{ such that } s[A + m_3 \tilde{F}_3(z)] > 0\},$$

the branch corresponding to the equilibrium  $\hat{E}^3$ . Moreover, there exists a neighborhood  $\hat{W}_3$  of  $(\hat{m}_3, 0, 0, \hat{u}^3(\hat{m}_3))$  in  $\mathbb{R}_+ \times \mathbb{R}_+^{3n}$  such that

$$\hat{W}_3 \cap \hat{S} = \{(\hat{m}_3(s), u^1(s), u^2(s), u^3(s)) : 0 \leq s < \delta\},$$

where  $\hat{m}_3(s), u^1(s), u^2(s), u^3(s)$  are smooth functions satisfying

$$\begin{aligned} \hat{m}_3(s) &= \hat{m}_3 + \hat{\kappa}s + o(s), \\ u^1(s) &= s\hat{w}_1 + o(s), \quad s \rightarrow 0_+, \\ u^2(s) &= s\hat{w}_2 + o(s), \\ u^3(s) &= \hat{u}^3 + s\hat{w}_3 + o(s), \end{aligned} \tag{3.5.5}$$

where  $\hat{w}$  is a null vector of the Jacobian of (3.1.1) at  $\hat{E}^3(\hat{m}_3)$ .

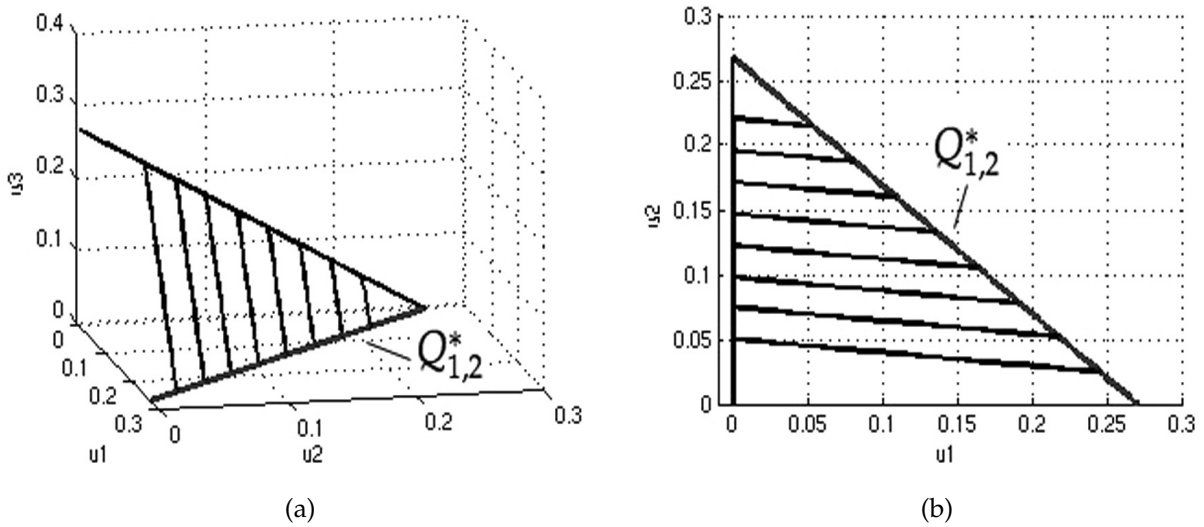
If  $\hat{\kappa} < 0$  then (3.5.6) is stable. If  $m_{(1,3)} > m_{(2,3)}$ , then, for  $s < \delta$ ,

$$(\hat{m}_3(s), u^1(s), u^2(s), u^3(s)) \in Q_{1,3}^*,$$

the branch of the solution set corresponding to the equilibrium  $E_{1,3}^*$ . If  $m_{(2,3)} > m_{(1,3)}$ , then, for  $s < \delta$ ,

$$(\hat{m}_3(s), u^1(s), u^2(s), u^3(s)) \in Q_{2,3}^*,$$

the branch of the solution set corresponding to the equilibrium  $E_{2,3}^*$ .



**Figure 3.5.7. (a):** The bifurcation branches  $(u_1^1, u_1^2, u_1^3)$  for (3.1.1) with parameters  $a_1, m_1, a_2, a_3$  given in (3.4.1), different values for  $m_2$ , and  $m_3$  as bifurcation parameter. **(b):** The projections on the  $(u_1^1, u_1^2)$ -plane for the branches in (a).

In Figure 3.5.7 we plot the bifurcation diagrams corresponding to the continuation, with  $a_3$  given in (3.4.1) and  $m_3$  as bifurcation parameter, of different two-species equilibria  $E_{1,2}^*(m_2)$  situated on the branch  $Q_{1,2}^*$  of coexistence for species 1 and 2, with  $a_1, m_1, a_2$  given in (3.4.1) and different values for  $m_2$ .

For  $\hat{m}_3 = m_{(1,3)} = m_{(2,3)}$  when, as we saw,  $\dim N(J(\hat{E}^3(\hat{m}_3))) = 2$ , we can obtain a similar theorem by applying Theorem 8.D in [Zei] and in this case, for the bifurcating solution we have

$$\begin{aligned} u^1(s) &= sw_1 + o(s), \quad s \rightarrow 0_+, \\ u^2(s) &= sw_2 + o(s), \\ u^3(s) &= \hat{u}^3 + sw_3 + o(s), \end{aligned}$$

with  $u^1(s), u^2(s), u^3(s)$  smooth functions,  $0 \leq s < \delta$ , and

$$w = \alpha\phi_1 + \beta\phi_2$$

where  $\phi_1$  and  $\phi_2$  are two linearly independent null vectors of  $J(\hat{E}^3(\hat{m}_3))$  and  $\alpha$  and  $\beta$  are not both zero. We can choose, for example,  $\phi_1$  as the direction of the  $\hat{Q}^3$  at  $\hat{m}_3$  and  $\phi_2 \perp \phi_1$ , and  $\alpha$  and  $\beta$  will be given by the *Algebraic Bifurcation Equation* - see [Kel1].

Following [STW], for each fixed  $u^3 \in [0, z]$  let

$$\begin{aligned} H_{u^3} = \{(u^1, u^2) \in [0, z - u^3]^2 : [A + F_1(z - u^1 - u^2 - u^3)]u^1 = 0, \\ [A + F_2(z - u^1 - u^2 - u^3)]u^2 = 0\}. \end{aligned}$$

We have:

$$H_{u^3} = \{(0, 0)\}, \text{ or}$$

$$H_{u^3} = \{(0, 0), (u^1, u^2)\}, u^1 + u^2 > 0.$$

From [SW] we have the following possibilities:

**(a)**  $H_{u^3} = \{(0, 0)\}$ , which holds if and only if

$$\begin{aligned} s[A + F_1(z - u^3)] &\leq 0, \text{ and} \\ s[A + F_2(z - u^3)] &\leq 0. \end{aligned}$$

**(b)**  $H_{u^3} = \{(0, 0), (u^*(u^3), 0)\}$  with  $u^*(u^3) > 0$  unique, which holds if and only if

$$\begin{aligned} s[A + F_1(z - u^3)] &> 0, \text{ and} \\ s[A + F_2(z - u^3)] &\leq 0. \end{aligned}$$

In this case, the map

$$u^{*1}(u^3) = \begin{cases} 0 & : H_{u^3} = \{(0, 0)\}, \\ u^{*2}(u^3) & : (u^{*1}(u^3), 0) \in H_{u^3}, \end{cases}$$

is continuous, decreasing in  $u^3$  and smooth in a neighborhood of  $u^3 = 0$  in  $[0, z]$  (from [STW]).

(c)  $H_{u^3} = \{(0, 0), (0, u^{*2}(u^3))\}$  with  $u^{*2}(u^3) > 0$  unique, which holds if and only if

$$\begin{aligned} s[A + F_1(z - u^3)] &\leq 0, \text{ and} \\ s[A + F_2(z - u^3)] &> 0. \end{aligned}$$

In this case, the map

$$u^{*2}(u^3) = \begin{cases} 0 & : H_{u^3} = \{(0, 0)\}, \\ u^{*2}(u^3) & : (0, u^{*2}(u^3)) \in H_{u^3}, \end{cases}$$

is continuous, decreasing in  $u^3$  and smooth in a neighborhood of  $u^3 = 0$  in  $[0, z]$ .

(d)  $H_{u^3} = \{(0, 0), (u^{*1}(u^3), 0), (0, u^{*2}(u^3))\}$ , and we have that both

$$\begin{aligned} s[A + F_1(z - u^3)] &> 0, \text{ and} \\ s[A + F_2(z - u^3)] &> 0, \end{aligned}$$

hold, and one and only one of

$$\begin{aligned} s[A + F_1(z - u^{*2}(u^3) - u^3)] &\leq 0, \text{ and} \\ s[A + F_2(z - u^{*1}(u^3) - u^3)] &\leq 0 \end{aligned}$$

holds.

(e)  $H_{u^3} = \{(0, 0), (u^{*1}(u^3), 0), (0, u^{*2}(u^3)), (\tilde{u}^1(u^3), \tilde{u}^2(u^3))\}$  with  $\tilde{u}^1(u^3), \tilde{u}^2(u^3) > 0$ .

A sufficient condition for  $(\tilde{u}^1(u^3), \tilde{u}^2(u^3)) \in H_{u^3}$  is

$$\{(u^{*1}(u^3), 0), (0, u^{*2}(u^3))\} \subset H_{u^3}$$

with

$$\begin{aligned} s[A + F_1(z - u^{*2}(u^3) - u^3)] &> 0, \text{ and} \\ s[A + F_2(z - u^{*1}(u^3) - u^3)] &> 0. \end{aligned}$$

Conversely, if  $(\tilde{u}^1(u^3), \tilde{u}^2(u^3)) \in H_{u^3}$ , then  $\{(u^{*1}(u^3), 0), (0, u^{*2}(u^3))\} \subset H_{u^3}$ .

We saw in 3.5 that for  $m_3 \geq 0$ , we have  $u^3(m_3) \in [0, z]$ ,  $\lim_{m_3 \rightarrow \infty} u^3(m_3) = z$  and, if  $m_3^1 < m_3^2$  such that  $u^3(m_3^1), u^3(m_3^2) > 0$  then  $u^3(m_3^1) < u^3(m_3^2)$ .

Denote with  $v_1 := u^3(m_{(1,3)})$  and  $v_2 := u^3(m_{(2,3)})$ . Hence

$$\begin{aligned} u^{*1}(u^3) &> 0 \text{ for } u^3 < v_1, \\ u^{*2}(u^3) &> 0 \text{ for } u^3 < v_2, \end{aligned}$$

and for  $u^3 > \max\{v_1, v_2\}$ , we have  $H_{u^3} = \{(0, 0)\}$ .

**(1):** If  $m_{(1,3)} > m_{(2,3)}$ , then  $v_1 > v_2$ . For  $v_2 < u^3 < v_1$ , we have  $H_{u^3} = \{(0, 0), (u^{*1}(u^3), 0)\}$  and

$$s[A + F_2(z - u^3 - u^{*1}(u^3))] < 0,$$

and, at  $v_2$ :

$$s[A + F_1(z - v_2)] > 0, \quad s[A + F_2(z - v_2 - u^{*1}(v_2))] < 0.$$

At  $u^3 = 0$ ,  $s[A + F_2(z - \hat{u}^1)] > 0$ , and from the continuity of  $s$  and the continuity of  $u^{*1}(u^3)$  for  $u^3 \in [0, z]$ , we have that there exists a  $v_1^* < v_2$  such that

$$s[A + F_2(z - v_1^* - u^{*1}(v_1^*))] = 0$$

and

$$s[A + F_2(z - u^3 - u^{*1}(u^3))] > 0$$

for  $u^3 > v_1^*$ . In this case  $J((u^{*1}(v_1^*), 0, v_1^*))$  has a zero eigenvalue.

For a  $\epsilon > 0$ , we have at  $u^3 = v_2 - \epsilon$ :

$$v_2 - \epsilon + u^{*2}(v_2 - \epsilon) < v_1 \quad \Leftrightarrow \quad u^{*2}(v_2 - \epsilon) < v_1 - v_2 + \epsilon$$

which holds for  $\epsilon$  small enough since  $v_1 > v_2$  and  $u^{*2}(v_2) = 0$ . Thus

$$s[A + F_1(z - u^{*2}(v_2 - \epsilon) - (v_2 - \epsilon))] > s[A + F_1(z - v_1)] = 0,$$

and for  $u^3 \geq v_2^* = v_2 - \epsilon$ , the branch  $Q_{2,3}^*$  is unstable.

If the Jacobian of (2.7.1), corresponding to species 1 and 3, has no zero eigenvalue at  $(u^{*1}(v_1^*), v_1^*)$ , which is true when **C1** holds, we have a similar theorem to Theorem 3.5.1 at  $(u^{*1}(v_1^*), 0, v_1^*)$ :

#### Theorem 3.5.4

Assume that the Jacobian of (2.7.1), corresponding to species 1 and 3, has no zero eigenvalue at  $(u^{*1}(v_1^*), v_1^*)$ . Then there exists a branch  $S_1^*$  of  $\Lambda_3$  bifurcating at  $(\check{m}_3, u^{*1}(v_1^*), 0, v_1^*)$  from  $Q_{1,3}^*$ , with  $v_1^* = u^3(\check{m}_3)$ . Moreover, there exists a neighborhood  $U_3$  of  $(\check{m}_3, u^{*1}(v_1^*), 0, v_1^*)$  in  $\mathbb{R}_+ \times \mathbb{R}_+^{3n}$ , such that

$$U_3 \cap S_1^* = \{(\check{m}_3(s), u^1(s), u^2(s), u^3(s)) : 0 \leq s \leq \delta\},$$

where  $\check{m}_3(s)$ ,  $u^1(s)$ ,  $u^2(s)$ ,  $u^3(s)$  are smooth functions satisfying

$$\begin{aligned}\check{m}_3(s) &= \check{m}_3 + \check{\kappa}s + o(s), \\ u^1(s) &= u^{*1}(v_1^*) + s \cdot \check{w}_1(v_1^*) + o(s), \quad s \rightarrow 0_+, \\ u^2(s) &= s \cdot \check{w}_2(v_1^*) + o(s), \\ u^3(s) &= v_1^* + s \cdot \check{w}_3(v_1^*) + o(s),\end{aligned}\tag{3.5.6}$$

where  $\check{w}(v_1^*)$  with  $\check{w}_2 > 0$  is a normalized null vector of the Jacobian of (3.1.1) at  $(u^{*1}(v_1^*), 0, v_1^*)$ . For  $s$  small enough,  $S_1^*$  corresponds to positive equilibria.

Denote with  $Q_{1,3}^s$  the stable portion of  $Q_{1,3}^*$  corresponding to  $u^3 > v_1^*$ . We have that

$$\{(u^{*1}(u^3), 0, u^3) \in Q_{1,3}^* : u^3 \geq v_1^*\} \subseteq Q_{1,3}^s.$$

We construct the map

$$\tilde{k}_1(u^3) = \begin{cases} 0 & : & u^3 \geq v_1, \\ u^{*1}(u^3) & : & (u^{*1}(u^3), 0, u^3) \in Q_{1,3}^s \\ \tilde{u}^1(u^3) + \tilde{u}^2(u^3) & : & (\tilde{u}^1(u^3)(s), \tilde{u}^2(u^3)(s), u^3) > 0, \quad 0 \leq u^3 \leq q \\ & & \text{corresponding to the branch } S_3^* \text{ in Th.3.5.1} \end{cases}$$

such that  $\tilde{k}_1(u^3)$ ,  $u^3 \in [0, z)$  continuous, with  $q \leq v_1^* < v_2$  small enough (the continuity at  $v_1$  follows from the continuity of  $u^{*1}$ ), and  $\tilde{k}_1(0) = k^* = u^{*1} + u^{*2}$ , with  $(u^{*1}, u^{*2}, 0) \in Q_{1,2}^*$ . Since we assumed that  $s_3 < 0$  in Theorem 3.5.1, from the continuity of  $s_3$  and from the implicit function theorem, we obtain that  $\tilde{k}_1(u^3)$  is smooth in a neighborhood of  $u^3 = 0$ .

If  $(u^1, u^2) \in [0, z - u^3]^2$  with  $u^1, u^2 \geq 0$  and  $u^1, u^2 \neq 0$  are such that

$$\begin{aligned}[A + F_1(z - u^1 - u^2 - u^3)]u^1 &= 0, \\ [A + F_2(z - u^1 - u^2 - u^3)]u^2 &= 0,\end{aligned}$$

from the Perron-Frobenius theory we have that  $u^1, u^2 > 0$ . Thus  $u_i^3 = z_i$  for any  $i$  implies that  $u^1 = 0$  and  $u^2 = 0$  and  $\tilde{k}_1(u^3)$  is defined for all  $u^3 \in [0, z]$ .

Consider  $u^3$  as the solution of

$$[A + m_3 \tilde{F}_3(z - \tilde{k}_1(u^3) - u^3)]u^3 = 0.\tag{3.5.7}$$

We rewrite this as a fixed point equation:

$$\mathcal{A}(u^3, m_3) = m_3[-A^{-1} \tilde{F}_3(z - \tilde{k}_1(u^3) - u^3)]u^3 = u^3.\tag{3.5.8}$$



We extend the map  $\mathcal{A}(u^3, m_3)$  to  $\mathbb{R}_+^n \times \mathbb{R}_+$ . As in [STW], for  $u \in \mathbb{R}_+^n$ , write  $u \wedge z$  for the vector whose  $i$ th component is  $\min\{u_i, z_i\}$ . Then define  $\mathcal{A} : \mathbb{R}_+^n \times \mathbb{R}_+ \rightarrow \mathbb{R}_+^n$  as

$$\mathcal{A}(u^3, m_3) = [A + m_3 \tilde{F}_3(z - \tilde{k}_1(u^3 \wedge z) - u^3 \wedge z)]u^3 = 0,$$

and  $\mathcal{A}$  is continuous, and  $\mathcal{A}(u^3, 0) = 0$  and  $\mathcal{A}(0, m_3) = 0$  for  $u^3 \in \mathbb{R}_+^n, m_3 \geq 0$ . Since  $\tilde{k}_1(u^3)$  is smooth at 0,  $\mathcal{A}$  is smooth at  $(0, m^3)$  for each  $m^3$ . We can write

$$\mathcal{A}(u^3, m_3) = m_3 Lu^3 + H(u^3, m_3),$$

where

$$Lu^3 = -A^{-1} \tilde{F}_3(z - k)u^3,$$

$$H(u^3, m_3) = m_3 A^{-1} [\tilde{F}_3(z - k) - \tilde{F}_3(z - \tilde{k}_1(u^3) - u^3)]u^3,$$

with

$$H(u^3, m_3) = o(\|u^3\|) \quad \text{as} \quad \|u^3\| \rightarrow 0,$$

uniformly for  $m_3$  on bounded sets, and  $L$  a positive linear operator.

We can apply Th.2. in [Dan] with

$$c_k(L) = \{\lambda \geq 0 : \text{there exists } u^3 \geq 0, u^3 \neq 0, \text{ such that } \lambda Lu^3 = u^3\} = \{\tilde{m}_3\},$$

with  $\tilde{m}_3$  in Theorem 3.5.1, as

$$\lambda Lu^3 = u^3 \Leftrightarrow \lambda [-A^{-1} \tilde{F}_3(z - k)]u^3 = u^3, \quad u^3 \neq 0$$

which implies  $u^3 > 0$  and  $s[A + \lambda \tilde{F}_3(z - k)] = 0$ . Hence, according to Th.2 of [Dan],

$$D_k(\mathcal{A}) = \{(0, \tilde{m}_3)\} \cup \{(u^3, m_3) \in \mathbb{R}_+^n \times \mathbb{R}_+ : u^3 = \mathcal{A}(u^3, m_3), u^3 \neq 0\}$$

contains an unbounded connected subset  $T$  such that  $(0, \tilde{m}_3) \in T$ . As in [STW] it can be shown that  $T \subseteq [0, z] \times \mathbb{R}_+$ , and

$$S^+ = \{(m_3, u^1(u^3), u^2(u^3), u^3) \in T, \text{ with } u^1(u^3) + u^2(u^3) = \tilde{k}_1(u^3)\}$$

is unbounded, connected and  $(\tilde{m}_3, u^{*1}, u^{*2}, 0) \in S^+$  where  $u^{*1} + u^{*2} = k^*$ . Moreover,  $Q_{1,3}^s \subset S^+$  and  $\{(m_3, u^1(u^3), u^2(u^3), u^3) : u^3 \geq v_1\} \subset S^+$ .

Note that  $S^+ \cap \{(m_3, u^1, u^2, u^3) : 0 \leq u^3 \leq q, \text{ and } u^3 \geq v_2\} \subset \Lambda_3$  corresponding to solutions of (3.1.1).

In case the continuous  $\tilde{k}_3(u^3)$  for  $q \leq u^3 \leq v_2$  corresponds to  $H_{u^3}$ , then  $S^+ \subset \Lambda_3$ , and thus  $\Lambda_3$  contains an unbounded, connected branch bifurcating at  $(\tilde{m}_3, u^{*1}, u^{*2}, 0)$  from  $Q_{1,2}^*$  and joining  $Q_{1,3}^*$  for a value of  $m_3$  for which  $0 < u_{(1,3)}^{*3}(m_3) \leq v_2$ . This holds in all our simulations, as the following are all true:

**C2:** For a fixed  $u^i > 0, i = 1, 2, 3$ , if the two-species system

$$[A + F_j(z - u^1 - u^2 - u^3)]u^j = 0, \quad j \neq i$$

has a positive solution, then it is unique. We have **C2**  $\Rightarrow$  **C1**.

**C3:** There exists a unique  $0 < v_1^* < v_2$  such that  $s[A + F_2(z - v_1^* - u^{*1}(v_1^*))] = 0$  and the Jacobian of (2.7.1) corresponding to species 1 and 3 has no zero eigenvalue at  $(u^{*1}(v_1^*), v_1^*)$ .

**C4:** For all  $0 \leq u^3 < v_2$ ,  $s[A + F_1(z - u^{*2}(u^3) - u^3)] > 0$ .

Moreover, for a fixed  $u^3 \geq 0$ , we have found  $(\tilde{u}^1(u^3), \tilde{u}^2(u^3)) > 0$  in  $H_{u^3}$  only when both  $s[A + F_1(z - u^{*2}(u^3) - u^3)] > 0$  and  $s[A + F_2(z - u^{*1}(u^3) - u^3)] > 0$ , namely for  $u^3 < v_1^*$ . In this case,  $\tilde{k}_3(u^3)$  takes the form:

$$\tilde{k}_3(u^3) = \begin{cases} 0, & \text{for } u^3 \geq v_1, \\ u^{*1}(u^3), & \text{with } u^{*1}(u^3) > 0 \text{ unique, for } v_1^* \leq u^3 < v_1, \\ \tilde{u}^1(u^3) + \tilde{u}^2(u^3), & \text{with } \tilde{u}^1(u^3), \tilde{u}^2(u^3) > 0 \text{ unique, for } u^3 < v_1^*. \end{cases}$$

The continuity of  $\tilde{k}_3(u^3)$  at  $u^3 = v_1$  follows from the continuity of  $u^{*1}(u^3)$ .

Consider the closed set

$$\mathcal{C} = \{u^3 \in [0, z] : s[A + F_1(z - u^{*2}(u^3) - u^3)] \leq 0 \text{ and } s[A + F_2(z - u^{*1}(u^3) - u^3)] > 0\}.$$

At  $u^3 = v_1^*$ , take  $u_n^3$ , a sequence converging to a  $v \in \mathcal{C}$  with  $0 < (\tilde{u}^1(u_n^3), \tilde{u}^2(u_n^3)) \in H_{u_n^3}$ , for all  $n$ . Assume we can find a subsequence we relabel as  $(\tilde{u}^1(u_n^3), \tilde{u}^2(u_n^3))$  converging to a  $w > 0$ . Since we have

$$\begin{aligned} [A + F_1(z - \tilde{u}^1(u_n^3) - \tilde{u}^2(u_n^3) - u_n^3)]\tilde{u}^1(u_n^3) &= 0, \\ [A + F_2(z - \tilde{u}^1(u_n^3) - \tilde{u}^2(u_n^3) - u_n^3)]\tilde{u}^2(u_n^3) &= 0, \end{aligned}$$

passing to the limit we get

$$\begin{aligned} [A + F_1(z - w_1 - w_2 - v)]w_1 &= 0, \\ [A + F_2(z - w_1 - w_2 - v)]w_2 &= 0, \end{aligned}$$

with, from Perron-Frobenius theory,  $w_1, w_2 > 0$ , and thus  $w \in H_v$  which contradicts  $v \in \mathcal{C}$ . Hence  $\tilde{k}_3(u^3)$  is continuous. As in (3.2.3), it can also be shown that  $\tilde{k}_3(u^3)$  is decreasing in  $u^3$ .

From Theorem 3.5.4, we have that for a  $p > 0$ ,  $\tilde{k}_3(u^3)$ , with  $v_1^* - p \leq u^3 \leq v_1^*$  is given by the branch (3.5.7), and thus  $\Lambda_3$  contains an unbounded, connected branch bifurcating at  $(\check{m}_3, u^{*1}, u^{*2}, 0)$  from  $Q_{1,2}^*$  and joining  $Q_{1,3}^*$  at  $m^3 = \check{m}_3$  with  $u^3(\check{m}_3) = v_1^*$ .

In Figure 3.5.8 we give a schematic representation of the reasoning above.

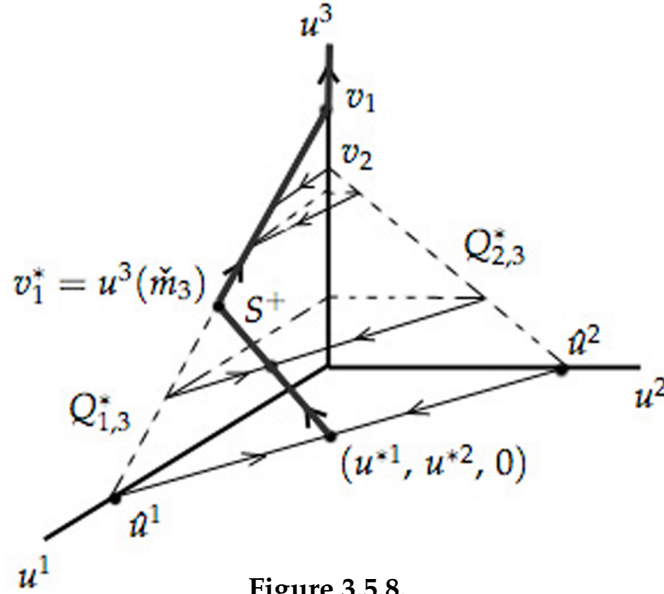


Figure 3.5.8.

In our examples, this situation occurs in Figure 3.5.4 and 3.5.6, with  $a_3 = 2$  and, respectively,  $a_3 = 8$ .

When in Theorem 3.5.4  $\check{\kappa} < 0$ , from **C2** we have that for  $p > 0$ ,  $\tilde{k}_3(u^3)$ , with  $v_1^* - p \leq u^3 \leq v_1^*$  is given by the branch (3.5.7), even when there exist positive  $(\hat{u}^1(u^3), \hat{u}^2(u^3))$  in  $H_{u^3}$  for  $u^3 > v_1^*$ , which will correspond to a different branch. In this case, the continuity of  $\tilde{k}_3(u^3)$  at  $v_1^*$  follows from the continuity of the functions in (3.5.7).

**(2):** If  $m_{(1,3)} < m_{(2,3)}$ , then  $v_1 < v_2$ . This situation is similar. It occurs for the examples in Figure 3.5.2 together with 3.5.7 with different values for  $m_2$ , and in Figure 3.5.7, with  $a_3 = 14$ . In Figure 3.5.9 we plot again the bifurcation diagram for (3.4.1), with  $m_3$  as bifurcation parameter, and, to illustrate the corresponding **C3** and **C4**, we also plot the branches corresponding to  $u^{*1}(u^3)$  and  $u^{*2}(u^3)$ , for  $u^3 \geq 0$ .

**(3):** If  $m_{(1,3)} = m_{(2,3)}$ , then  $v_1 = v_2 = v$ . This situation occurs in Figure 3.5.6 for  $a_3 \simeq 12.7214372$ , for which we have the following holding:

**C5:** For all  $0 \leq u^3 < v$ ,

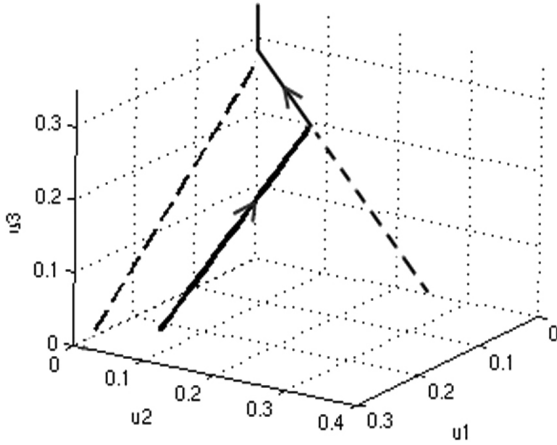
$$s[A + F_1(z - u^{*2}(u^3) - u^3)] > 0,$$

$$s[A + F_2(z - u^{*1}(u^3) - u^3)] > 0.$$

and thus, there exists a  $(\tilde{u}^1(u^3), \tilde{u}^2(u^3)) > 0$  in  $H_{u^3}$  for all  $0 \leq u^3 < v$ . When the latter is unique, the function

$$\tilde{k}_3(u^3) = \begin{cases} 0, & \text{for } u^3 \geq v, \\ \tilde{u}^1(u^3) + \tilde{u}^2(u^3), & \text{with } \tilde{u}^1(u^3), \tilde{u}^2(u^3) > 0 \text{ unique, for } u^3 < v, \end{cases}$$

is well defined and continuity follows immediately. Moreover,  $\tilde{k}_3(u^3)$  is decreasing in  $u^3$ ,  $\tilde{k}_3(0) = k$  and  $\tilde{k}_3(u^3)$  is smooth in a neighborhood of zero. Thus, as in (1),  $\Lambda_3$  contains an unbounded, connected branch bifurcating at  $(\tilde{m}_3, u^{*1}, u^{*2}, 0)$  from  $Q_{1,2}^*$  and joining  $\hat{Q}_3$  at  $m^3 = m_{(1,3)} = m_{(2,3)}$ , with  $\hat{Q}_3$  the branch corresponding to species 3 alone in the gradostat.



**Figure 3.5.9.** Bifurcation diagram for (3.1.1) - corresponding to the first vessel - with parameters given in (3.4.1) and  $m_3$  as bifurcation parameter. The interrupted lines plot the unstable branches corresponding to  $u^{*1}(u^3)$  and  $u^{*2}(u^3)$ , for  $u^3 \geq 0$ .

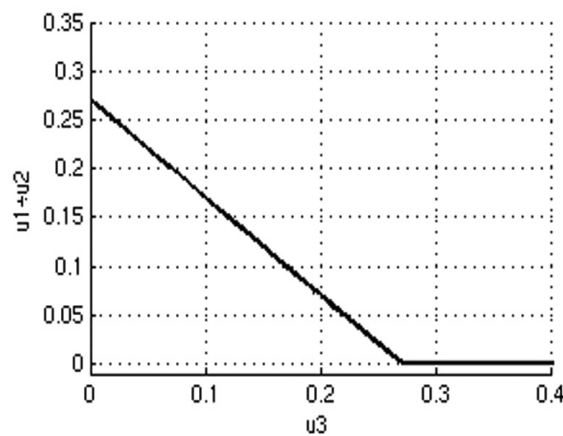
For a fixed  $u^3 > 0$ , we have that if

$$s[A + F_1(z - u^{*2}(u^3) - u^3)] > 0,$$

$$s[A + F_2(z - u^{*1}(u^3) - u^3)] > 0,$$

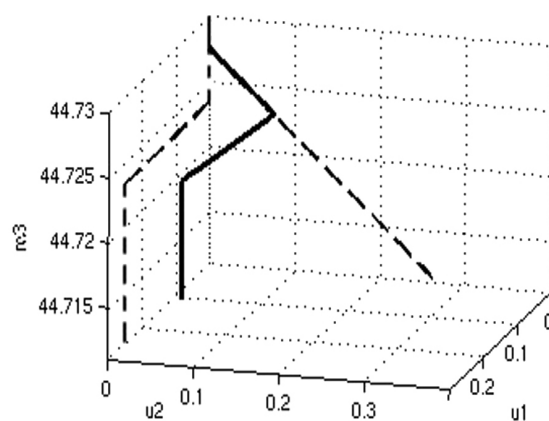
there exists a positive equilibrium solution  $(\tilde{u}^1(u^3), \tilde{u}^2(u^3)) > 0$  in  $H_{u^3}$ . For system (3.1.1), the two smooth local branches in (3.5.3) and (3.5.6) represent coexistence of all three species, and we saw that when  $\check{\kappa} < 0$  in (3.5.6) and C2, C3 and C4 (or C5) hold, we can find three-species coexistence equilibria  $\tilde{E}$  for each value of  $m_3$  in some interval containing  $\tilde{m}_3$ . This interval however, may degenerate to one point, if, for example,  $a_1 = a_3$  or  $a_2 = a_3$  in which case three-species coexistence occurs only for  $u^3 = \tilde{m}_3$  and the three-species equilibria form a line segment joining  $E_{1,2}^*$  to  $\hat{Q}_3$ .

In Figure 3.5.10 we plot  $\tilde{k}_3(u^3)$  for (3.4.1).



**Figure 3.5.10.** The continuous function  $\tilde{k}_3(u^3)$  - corresponding to the first vessel - for (3.4.1).

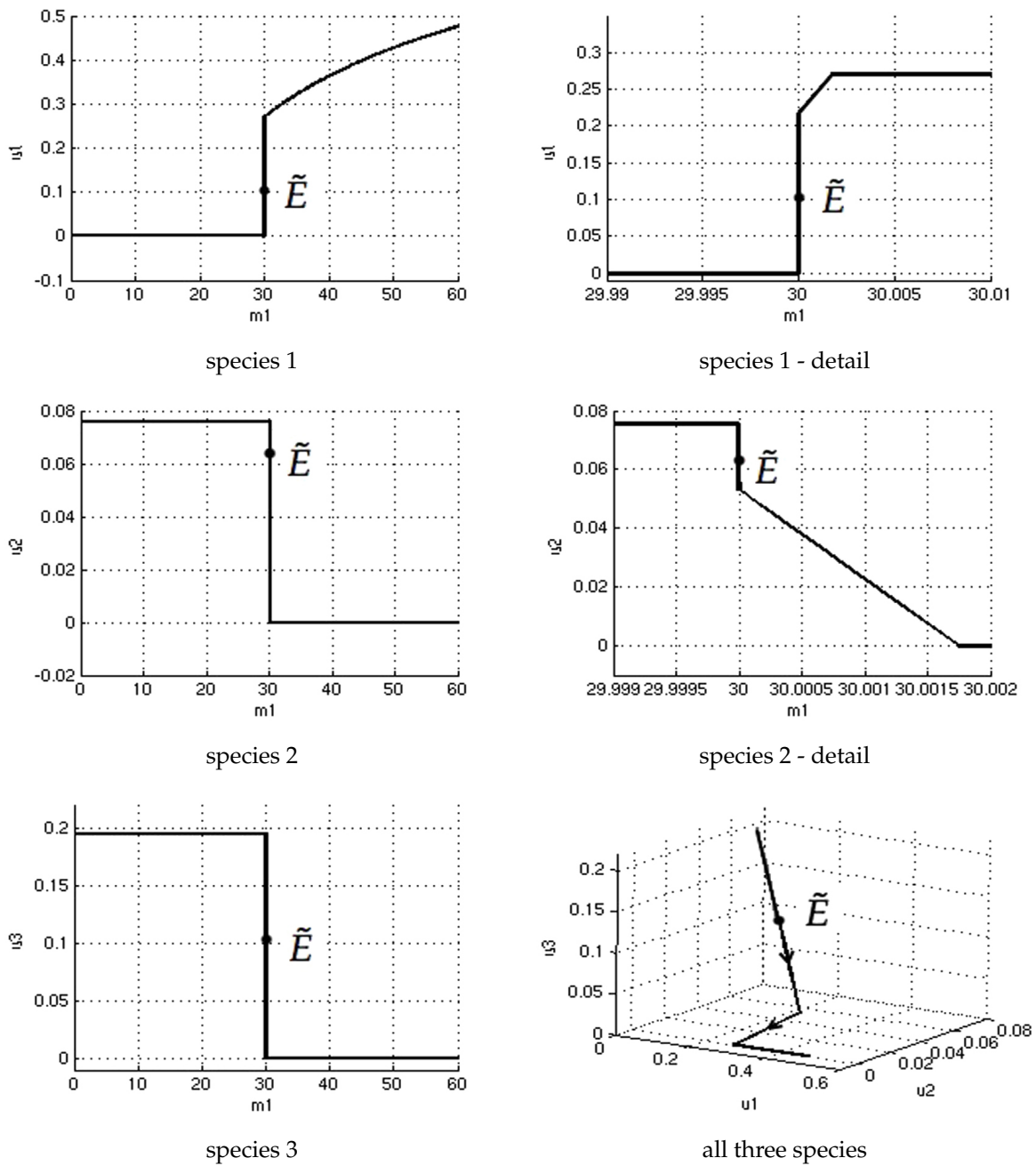
**Remark:** Note that when  $m_{(1,3)} > m_{(2,3)}$ , when  $\check{\kappa} < 0$  in (3.5.6) and C2, C3 and C4 hold, the branch  $S^+ \cap \{u^1 = 0, u^3 > 0\} = \emptyset$  and thus, condition (3.2.4) is not necessary for the persistence of species 3. Moreover, for (3.4.1) with, for example,  $a_3 = 2$ , if  $m_3$  is such that (3.2.4) is fulfilled, then there no longer exists a three-species coexistence equilibrium. Similarly, when  $m_{(1,3)} < m_{(2,3)}$ , then under the same conditions as above, (3.2.5) is not necessary for the persistence of species 3, and, for (3.4.1) with, for example,  $a_3 = 30$ , if  $m_3$  is such that (3.2.5) is fulfilled, then there no longer exists a three-species coexistence equilibrium. In Figure 3.5.11, we plot  $(m_3, u^1(m_3), u^2(m_3))$  for  $(m_3, u^1(m_3), u^2(m_3), u^3(m_3)) \in S^+$ .



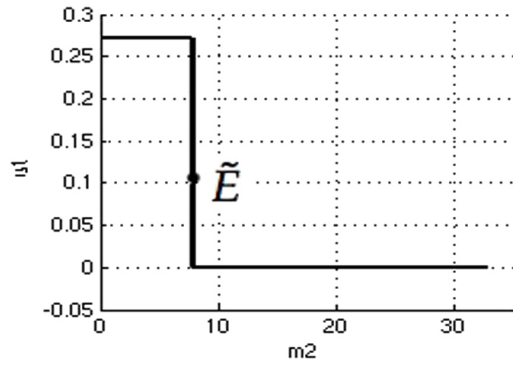
**Figure 3.5.11.** Bifurcation diagram for (3.1.1) - corresponding to the first vessel - with parameters given in (3.4.1) and  $m_3$  as bifurcation parameter. We plot  $(m_3, u^1(m_3), u^2(m_3))$  for  $(m_3, u^1(m_3), u^2(m_3), u^3(m_3)) \in S^+$ . The interrupted lines plot the unstable branches corresponding to  $u^{*1}(m_3)$  and  $u^{*2}(m_3)$ , for  $m_3 \geq m_{(2,3)}$ .

When  $m_{(1,3)} = m_{(2,3)}$  however, for  $m_3$  such that the three-species coexistence equilibrium exists, both (3.2.4) and (3.2.5) hold.

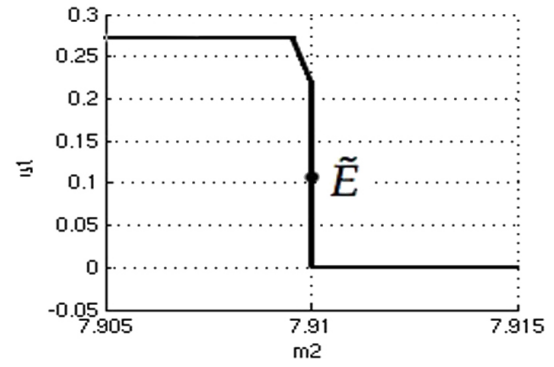
In Figure 3.5.12 and 3.5.13 we give the bifurcation diagrams for (3.1.1) with (3.4.1) corresponding to the continuation of the three-species coexistence equilibrium  $\tilde{E}$ , given in the beginning of section 3.4, with  $m_1$  and  $m_2$  as continuation parameters.



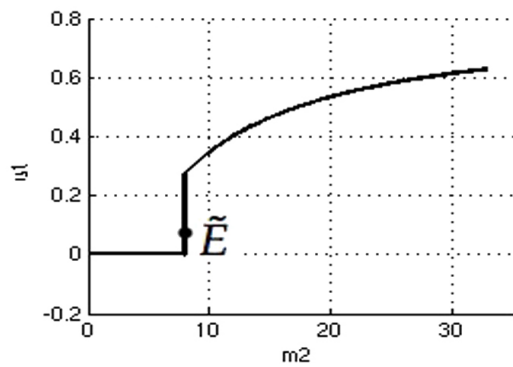
**Figure 3.5.12.** Bifurcation diagrams for (3.1.1) - corresponding to the first vessel - with parameters given in (3.4.1) and  $m_1$  as bifurcation parameter.



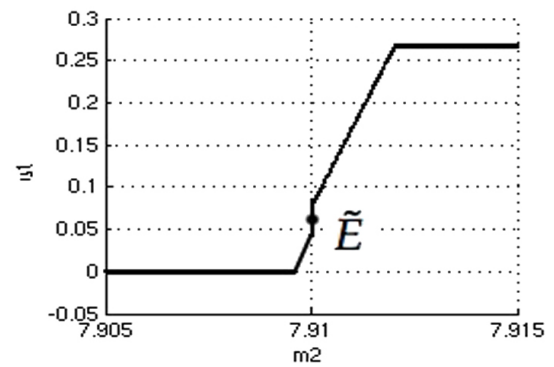
species 1



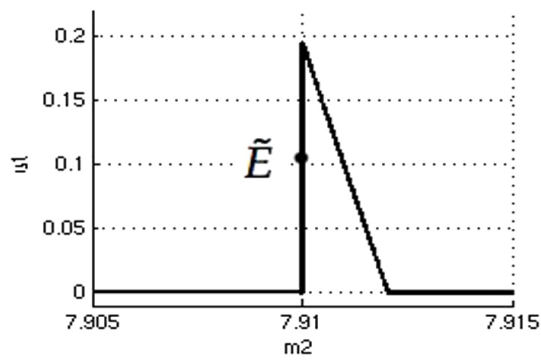
species 1 - detail



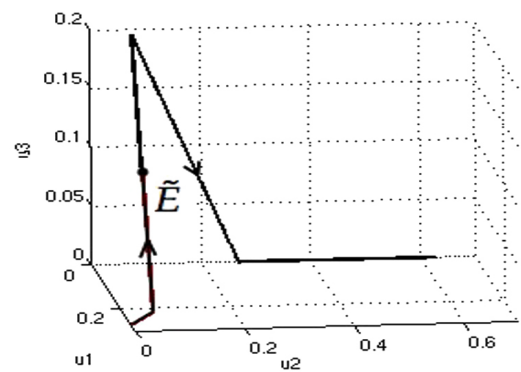
species 2



species 2 - detail



species 3

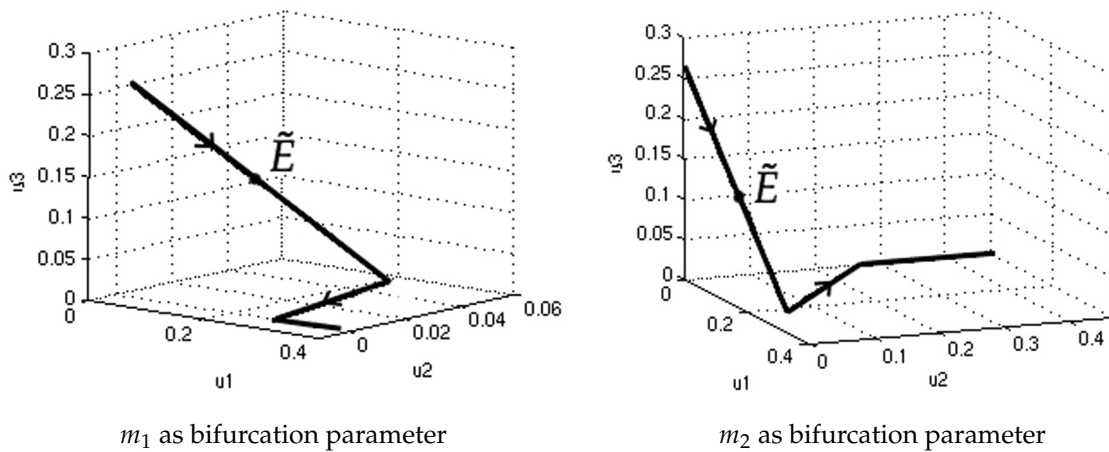


all three species

**Figure 3.5.13.** Bifurcation diagrams for (3.1.1) - corresponding to the first vessel - with parameters given in (3.4.1) and  $m_2$  as bifurcation parameter.

For  $m_1$  and  $m_2$  as bifurcation parameters we observe basically the same behavior as for  $m_3$ , namely, the respective branch corresponding to three-species coexistence equilibria connects  $Q_{1,2}^*$  and  $Q_{2,3}^*$  and it contains no point on the  $u^1 \times u^3$  hyperplane with both  $u^1 > 0$  and  $u^2 > 0$ .

The same holds also when  $m_{(1,3)} = m_{(2,3)}$ , for example for (3.4.1) with  $a_3 = 12.7214372$ , namely the respective branch corresponding to three-species coexistence equilibria connects  $Q_{1,2}^*$  and  $Q_{2,3}^*$  for both  $m_1$  and, respectively  $m_2$  as bifurcation parameters - fact illustrated in Figure 3.5.14.



**Figure 3.5.14.** Bifurcation diagrams for (3.1.1) - corresponding to the first vessel - with parameters given in (3.4.1) and  $a_3 = 12.7214372$ , with  $m_1$  and  $m_2$  as bifurcation parameters.

Note that since  $\tilde{E}$  for  $a_3 \simeq 12.7214372$  is a three-species equilibrium corresponding to parameters for which each two-species system is persistent, by varying  $m_1$  or  $m_2$ , we obtain further three-species equilibria corresponding to parameters for which each two-species system is persistent. Actually this was the only way we were able to find, numerically, three-species equilibria corresponding to each two species coexisting, namely, starting from values for  $a_3$  such that  $m_{(1,3)} = m_{(2,3)}$ .



### 3.6 Three-species persistence

Assume **C1** holds.

Let species 1 and 2 and species 2 and 3 coexist, and assume species 1 and 3 are not able to coexist, and denote with  $k_1 = u_{(2,3)}^{*2} + u_{(2,3)}^{*3}$  and  $k_2 = u_{(1,3)}^{*1} + u_{(1,3)}^{*3}$ .

Starting from the results in 3.3 **C - F**, define the vectors

$$\eta_{1,i} = \begin{cases} 0, & \text{if } u_{(2,3),i}^2 < u_{(1,2),i}^2, \\ 0, & \text{if } u_{(2,3),i}^2 < u_{(1,2),i}^2, \text{ and } f_2(z_i - k_{2,3,i}) \geq f_3(z_i - k_{2,3,i}), \\ v, & \text{if } u_{(2,3),i}^2 < u_{(1,2),i}^2, \text{ and } f_2(z_i - k_{2,3,i}) < f_3(z_i - k_{2,3,i}), \\ & \text{where } (0, k_{2,3,i}, v) \in S_{2,3,i}^2, \end{cases} \quad (3.6.1)$$

and

$$\eta_{3,i} = \begin{cases} 0, & \text{if } u_{(2,3),i}^2 < u_{(1,2),i}^2, \\ 0, & \text{if } u_{(2,3),i}^2 > u_{(1,2),i}^2, \text{ and } f_1(z_i - k_{1,2,i}) \geq f_2(z_i - k_{1,2,i}), \\ w, & \text{if } u_{(2,3),i}^2 > u_{(1,2),i}^2, \text{ and } f_1(z_i - k_{1,2,i}) < f_2(z_i - k_{1,2,i}), \\ & \text{where } (w, k_{1,2,i}, 0) \in S_{1,2,i}^2, \end{cases} \quad (3.6.2)$$

for  $i = 1, \dots, n$ . We have that  $\eta_1, \eta_2 \geq 0$  and  $\eta_1, \eta_2 \neq 0$  and both having some components equal to zero.

For the vector field on  $u^1 + u^2 = k_{1,2}$  we have

$$\begin{aligned} & [A + F_1(z - k_{1,2} - u^3)]u^1 + [A + F_2(z - k_{1,2} - u^3)]u^2 \leq \\ & \leq [A + F_1(z - k_{1,2} - \underline{u}^3)]u^1 + [A + F_2(z - k_{1,2} - \underline{u}^3)]u^2 < \\ & < [A + M_{1,2}(z - k_{1,2} - \underline{u}^3)]k_{1,2} \leq 0 \end{aligned}$$

where  $M_{1,2}(x)$  for some vector  $x$  is the diagonal matrix with  $M_{1,2,i}(x) = \max\{f_1(x_i), f_2(x_i)\}$ , and the last inequality holds if we can find  $\underline{u}^3 \geq \eta_3$ . A similar affirmation holds for the vector field on  $u^2 + u^3 = k_{2,3}$ .

We look for strictly positive lower solutions for  $u^1$  and  $u^3$  such that  $u^1 \geq \eta_1$  and  $u^3 \geq \eta_3$ .

Let  $\gamma_1$  be a positive constant such that  $\underline{u}^1 := \gamma_1 \cdot \phi_1 \geq \eta_1$ , with  $\phi_1$  a positive vector to be chosen later. We have

$$[A + F_1(z - k_{2,3} - \gamma_1 \cdot \phi_1)]\gamma_1 \cdot \phi_1 \geq 0,$$

and thus  $\underline{u}^1$  is a lower solution for  $u^1$  for  $\gamma_1$  small enough when

$$s[A + F_1(z - k_{2,3} - \eta_1)] > 0, \quad (3.6.3)$$

with  $\phi_1$  the positive eigenvector associated to  $s[A + F_1(z - k_{2,3} - \eta_1)]$  (from 3.3 **C - F**).

Similarly, for a small enough positive constant  $\gamma_3$ ,  $\underline{u}^3 := \gamma_3 \cdot \phi_3 \geq \eta_3$  is a lower solution for  $u^3$  when

$$s[A + F_3(z - k_{1,2} - \eta_3)] > 0, \quad (3.6.4)$$

with  $\phi_3$  the positive eigenvector associated to  $s[A + F_3(z - k_{1,2} - \eta_3)]$ .

We have that (3.6.3) and (3.6.4) are sufficient conditions for species 1 and, respectively 3, to be persistent, for appropriate initial data. Note that (3.6.3) and (3.6.4) are slightly stronger conditions than

$$s[A + F_1(z - k_{2,3})] > 0, \quad (3.6.5)$$

and

$$s[A + F_3(z - k_{1,2})] > 0, \quad (3.6.6)$$

for which species 1 and 3 are persistent in all our simulations. In all the simulations we have that the vector  $\eta_1$  and  $\eta_3$  are so small that  $\underline{u}_1 = \tilde{\gamma}_1 \cdot \tilde{\phi}_1 \geq \eta_1$ , with  $\tilde{\gamma}_1$  small enough, is a lower solution for  $u_1$  when (3.6.5) holds and  $\tilde{\phi}_1$  is the positive eigenvector associated to  $s[A + F_1(z - k_{2,3})]$ , and  $\underline{u}_3 = \tilde{\gamma}_3 \cdot \tilde{\phi}_3 \geq \eta_3$ , with  $\tilde{\gamma}_3$  small enough, is a lower solution for  $u_3$  when (3.6.6) holds and  $\tilde{\phi}_3$  is the positive eigenvector associated to  $s[A + F_3(z - k_{1,2})]$ .

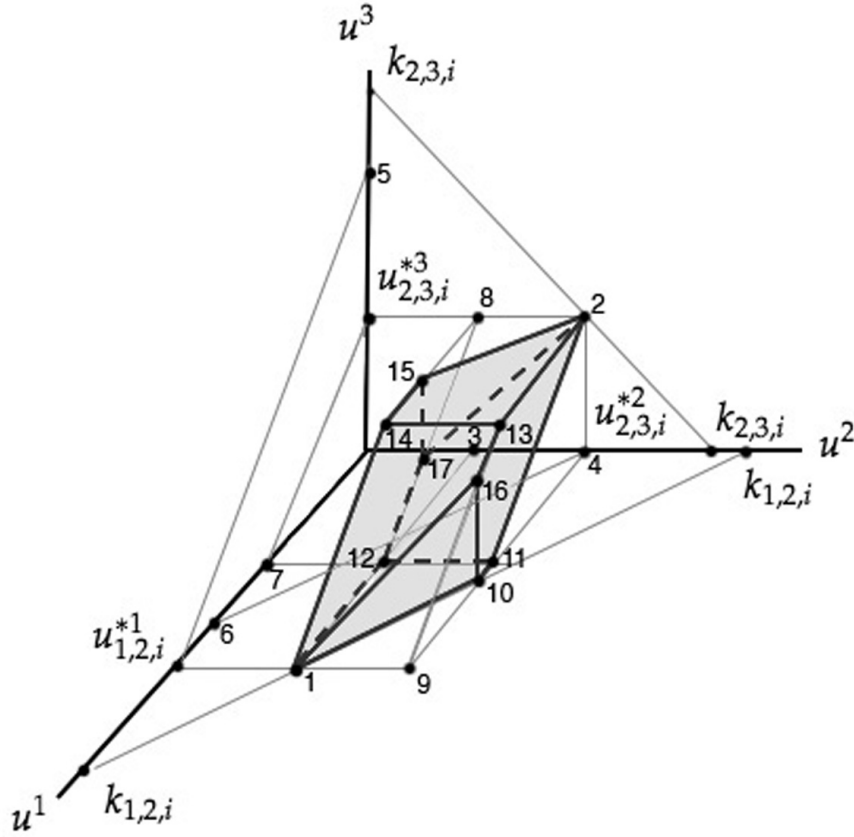
Consider the set  $\Delta \in \Omega$  defined by:

$$\begin{aligned} \eta_1 &\leq \underline{u}_1 \leq u_1 \leq u_{(1,2)}^*, \\ \min\{u_{(1,2),i}^*, u_{(2,3),i}^*\} &\leq u_i^2 \leq \max\{u_{(1,2),i}^*, u_{(2,3),i}^*\}, \quad i = 1, \dots, n, \\ \eta_3 &\leq \underline{u}_3 \leq u_3 \leq u_{(2,3)}^*, \\ u_{(2,3)}^* &\leq u^1 + u^2 \leq k_{1,2}, \\ u_{(1,2)}^* &\leq u^2 + u^3 \leq k_{2,3}, \\ \min\{u_{(1,2),i}^*, u_{(2,3),i}^*\} &\leq u_i^1 + u_i^3 \leq \max\{u_{(1,2),i}^*, u_{(2,3),i}^*\}, \quad i = 1, \dots, n, \end{aligned}$$

with  $\underline{u}_1$  and  $\underline{u}_3$  as above.

We will show that  $\Delta$  is an invariant set for (3.1.1).

In Figure 3.6.1 we depict schematically a possible  $\Delta_i$ , when  $u_{(1,2),i}^* < u_{(2,3),i}^*$  and  $k_{2,3,i} < k_{1,2,i}$ .



**Figure 3.6.1.** A schematic representation of a possible invariant region for (3.1.1): - corresponding to  $u_{(1,2),i}^{*2} < u_{(2,3),i}^{*2}$  and  $k_{2,3,i} < k_{1,2,i}$ .  $\Delta_i$  is given by the shaded region intersected with  $u_i^1 \geq \underline{u}_i^1$  and  $u_i^3 \geq \underline{u}_i^3$ . The labeled points are given by:

$$\begin{aligned}
 1 &= Q_{1,2,i}^* = (u_{(1,2),i}^{*1}, u_{(1,2),i}^{*2}, 0) \\
 2 &= Q_{1,2,i}^* = (0, u_{(2,3),i}^{*2}, u_{(2,3),i}^{*3}) \\
 3 &= (0, u_{(1,2),i}^{*2}, 0) \\
 4 &= ((0, , u_{(2,3),i}^{*2}) \\
 5 &= (0, 0, , u_{(1,2),i}^{*1}) \\
 6 &= (u_{(2,3),i}^{*2}, 0, 0) \\
 7 &= (u_{(2,3),i}^{*3}, 0, 0) \\
 8 &= (0, u_{(1,2),i}^{*2}, u_{(2,3),i}^{*3}) \\
 9 &= (u_{(1,2),i}^{*1}, u_{(2,3),i}^{*2}, 0) \\
 10 &= (u_{1,2,i} - u_{(2,3),i}^{*2}, u_{(2,3),i}^{*2}, 0) \\
 11 &= (u_{(2,3),i}^{*3}, u_{(2,3),i}^{*2}, 0) \\
 12 &= (u_{(2,3),i}^{*3}, u_{(1,2),i}^{*2}, 0) \\
 13 &= (u_{(1,2),i}^{*1} - u_{(2,3),i}^{*3}, u_{(2,3),i}^{*2}, u_{(2,3),i}^{*3}) \\
 14 &= (u_{(1,2),i}^{*1} - u_{(2,3),i}^{*3}, u_{(1,2),i}^{*2}, u_{(2,3),i}^{*3}) \\
 15 &= (u_{(2,3),i}^{*2} - u_{(1,2),i}^{*2}, u_{(2,3),i}^{*2}, u_{(2,3),i}^{*3}) \\
 16 &= (k_{1,2,i} - u_{(2,3),i}^{*2}, u_{(2,3),i}^{*2}, u_{(2,3),i}^{*2} - u_{(1,2),i}^{*2}) \\
 17 &= (u_{(2,3),i}^{*2} - u_{(1,2),i}^{*2}, u_{(1,2),i}^{*2}, u_{(2,3),i}^{*3} - u_{(2,3),i}^{*2} + u_{(1,2),i}^{*2})
 \end{aligned}$$

For  $u_{(1,2)}^{*1}$  we have

$$\begin{aligned} [A + F_1(z - u_{(1,2)}^{*1} - u^2 - u^3)]u_{(1,2)}^{*1} &\leq \\ [A + F_1(z - u_{(1,2)}^{*1} - u_{(1,2)}^{*2})]u_{(1,2)}^{*1} &= 0, \end{aligned}$$

and  $u_{(1,2)}^{*1}$  is an upper solution for  $u^1$ . Similarly,  $u_{(2,3)}^{*3}$  is an upper solution for  $u^3$ .

With our choice for  $\underline{u}^1$  and  $\underline{u}^3$  we have that  $u^1 + u^2 \leq k_{1,2}$  and  $u^2 + u^3 \leq k_{2,3}$

For  $i \in \{1, \dots, n\}$  assume  $u_{(1,2),i}^{*2} < u_{(2,3),i}^{*2}$ .

For  $u_{(1,2),i}^{*2}$ , if  $u_{(1,2),i}^{*1} > u_{(2,3),i}^{*3}$  we have

$$\begin{aligned} [A + F_2(z - u_{(1,2)}^{*2} - u^1 - u^3)]_i u_{(1,2),i}^{*1} &\geq \\ \geq [A + F_2(z - u_{(1,2)}^{*2} - u_{(1,2)}^{*1})]_i u_{(1,2),i}^{*1} &= 0, \end{aligned}$$

and  $u_{(1,2),i}^{*2}$  is a lower solution for  $u_i^2$ . If  $u_{(1,2),i}^{*1} < u_{(2,3),i}^{*3}$  we have

$$\begin{aligned} [A + F_2(z - u_{(1,2)}^{*2} - u^1 - u^3)]_i u_{(1,2),i}^{*1} &\geq \\ \geq [A + F_2(z - u_{(1,2)}^{*2} - u_{(2,3)}^{*3})]_i u_{(1,2),i}^{*1} &> 0, \end{aligned}$$

since  $u_{(1,2),i}^{*2} + u_{(2,3),i}^{*3} < k_{2,3,i}$ , and  $u_{(1,2),i}^{*2}$  is a lower solution for  $u_i^2$ .

The fact that  $u_{(2,3),i}^{*2}$  is an upper solution for  $u_i^2$  follows similarly.

For the vector field on  $u^1 + u^2 = u_{(2,3)}^{*2}$  we have

$$\begin{aligned} &[A + F_1(z - u_{(2,3)}^{*2} - u^3)]_i u_i^1 + [A + F_2(z - u_{(2,3)}^{*2} - u^3)]_i u_i^2 \geq \\ &\geq [A + F_1(z - u_{(2,3)}^{*2} - u_{(2,3)}^{*2})]_i \underline{u}_i^1 + [A + F_2(z - u_{(2,3)}^{*2} - u_{(2,3)}^{*2})]_i u_{(1,2),i}^{*2} \geq \\ &\geq [A + F_1(z - k_{2,3} - \underline{u}^1)]_i \underline{u}_i^1 + [A + F_2(z - k_{2,3})]_i u_{(1,2),i}^{*2}, \end{aligned}$$

with  $[A + F_1(z - k_{2,3} - \underline{u}^1)]_i \underline{u}_i^1 \geq 0$  from our choice of  $\underline{u}^1$ . If  $k_{2,3,i} \geq k_{1,2,i}$  then

$$[A + F_2(z - k_{2,3})]_i u_{(1,2),i}^{*2} \geq [A + F_2(z - k_{1,2})]_i u_{(1,2),i}^{*2} = 0,$$

and if  $k_{2,3,i} < k_{1,2,i}$ , then

$$[A + F_2(z - k_{2,3})]_i u_{(1,2),i}^{*2} > 0$$

from the results for the two-species systems. Thus the vector field of (3.1.1) points inside  $\Delta_i$  on  $u^1 + u^2 = u_{(2,3)}^{*2}$ .

We can similarly show that the vector field of (3.1.1) points inside  $\Delta_i$  on  $u^2 + u^3 = u_{(1,2)}^{*2}$ .

On  $u_i^1 + u_i^2 = \max\{u_{(1,2),i}^{*1}, u_{(2,3),i}^{*3}\}$ , if  $u_{(1,2),i}^{*1} < u_{(2,3),i}^{*3}$ , we have

$$\begin{aligned} &[A + F_1(z - u_{(2,3)}^{*3} - u^2)]_i u_i^1 + [A + F_3(z - u_{(2,3)}^{*3} - u^2)]_i u_i^3 \leq \\ &\leq [F_1(z - u_{(2,3)}^{*3} - u_{(1,2)}^{*1})]_i (u_{(1,2),i}^{*1} - \eta_{1,i}) + [A + F_3(z - u_{(2,3)}^{*3} - u_{(1,2)}^{*2})]_i u_{(2,3),i}^{*3} \leq \\ &\leq [A + F_1(z - k_{1,2})]_i (u_{(1,2),i}^{*1} - \eta_{1,i}) + [A + F_3(z - u_{(2,3)}^{*3} - u_{(1,2)}^{*2})]_i u_{(2,3),i}^{*3} \leq \\ &\leq -[A + F_1(z - k_{1,2})]_i \eta_{1,i} [A + F_3(z - u_{(2,3)}^{*3} - u_{(1,2)}^{*2})]_i u_{(2,3),i}^{*3} < 0 \end{aligned}$$

since  $k_{1,2,i} < u_{(2,3),i}^{*3} - u_{(1,2),i}^{*2} < k_{2,3,i}$ .

If  $u_{(1,2),i}^{*1} > u_{(2,3),i}^{*3}$ , we have

$$\begin{aligned} & [A + F_1(z - u_{(1,2)}^{*1} - u^2)]_i u_i^1 + [A + F_3(z - u_{(1,2)}^{*1} - u^2)]_i u_i^3 \leq \\ & \leq [F_1(z - u_{(1,2)}^{*1} - u_{(1,2)}^{*2})]_i (u_{(1,2),i}^{*1} - \eta_{1,i}) + [A + F_3(z - u_{(1,2)}^{*1} - u_{(1,2)}^{*2})]_i u_{(2,3),i}^{*3} = \\ & = [A + F_1(z - k_{1,2})]_i (u_{(1,2),i}^{*1} - \eta_{1,i}) + [A + F_3(z - k_{1,2})]_i u_{(2,3),i}^{*3} \leq \\ & \leq -[A + F_1(z - k_{1,2})]_i \eta_{1,i} + [A + F_3(z - k_{1,2})]_i u_{(2,3),i}^{*3} < 0, \end{aligned}$$

and thus the vector field of (3.1.1) points inside  $\Delta_i$  on  $u_i^1 + u_i^2 = \max\{u_{(1,2),i}^{*1}, u_{(2,3),i}^{*3}\}$ .

In a similar way we obtain that the vector field of (3.1.1) points inside  $\Delta_i$  on  $u_i^1 + u_i^2 = \min\{u_{(1,2),i}^{*1}, u_{(2,3),i}^{*3}\}$ .

When  $u_{(1,2),i}^{*2} > u_{(2,3),i}^{*2}$  analogous reasonings apply, and we have showed that  $\Delta_i$  is an invariant region for (3.1.1), and we have the following theorems holding:

### Theorem 3.6.1

Assume **C1** holds. Consider the system (3.1.1) with  $n \geq 3$  and parameters such that each species is able to survive alone in the gradostat. Assume species 1 and 2 and species 2 and 3 coexist, and species 1 and 3 do not coexist.

If (3.6.3) and (3.6.4) hold, then all three species are persistent for appropriate initial data.

### Theorem 3.6.2

Assume the hypothesis of Theorem 3.6.1 hold. If there exists an equilibrium  $\tilde{E}$  corresponding to the persistence of all three species, then  $\tilde{E} \in \Delta$ .

From the simulations it looks like the equilibrium  $\tilde{E}$  is unique and attracts all orbits corresponding to large enough positive initial data. As an analogy to the case of two species, trajectories starting from  $r \cdot v$  and  $q \cdot w$ , with  $r$  and  $q$  small positive constants and  $v$  and  $w$  the eigenvectors corresponding to the positive stability moduli of the Jacobian of (3.1.1) at  $Q_{1,2}^*$  and, respectively,  $Q_{2,3}^*$ , will both tend to  $\tilde{E}$  and the corresponding orbits  $S_{1,2}$  and  $S_{2,3}$  with  $S_{1,2} \cup S_{2,3}$  connected, will determine a "curve" connecting  $Q_{1,2}^*$  and  $Q_{2,3}^*$  on which  $\tilde{E}$  is situated: this is the curve we have observed in Figure 3.4.7 and 3.4.8.

Now assume that each two species can coexist, and in addition to (3.6.3) and (3.9.49), assume

$$s[A + F_2(z - k_{1,3} - \eta_2)] > 0, \quad (3.6.7)$$

with  $k_{1,3} = u_{(1,3)}^{*1} + u_{(1,3)}^{*1}$  and  $\eta_2$  built as in (3.6.1) and (3.6.2). In this case, just as for species 1 and 3, we can find a lower solution  $\underline{u}^2$  for  $u^2$  with  $\underline{u}^2 = \gamma_2 \cdot \phi_2 \geq \eta_2$  with  $\gamma_2$  a small enough

positive constant, and  $\phi_2$  the positive eigenvector associated to  $s[A + F_2(z - k_{1,3} - \eta_2)]$ , such that for  $u_0^2 \geq \underline{u}^2$ , the solution of (3.1.1) is such that  $u^1 + u^3 \leq k_{1,3}$ .

### Theorem 3.6.3

*Assume C1 holds. Consider the system (3.1.1) with  $n \geq 3$  and parameters such that each two species can coexist.*

*If (3.6.3), (3.6.4), and (3.6.7) hold, then all three species are persistent for appropriate initial data.*

Remark that Theorem 2.6.2 for  $m = 3$  applies only when each two species coexist, and in this case conditions (2.6.6) are stronger than (3.6.3), (3.6.4), and (3.6.7), namely, the region in the parameter space for which (2.6.6) hold is a subset of the region in the parameter space corresponding to (3.6.3), (3.6.4), and (3.6.7).

In both cases we have consider in this section, namely species 1 and 3 can not coexist and, respectively, species 1 and 3 can coexist, we have obtained sufficient conditions for persistence of the whole system. Even though we were able to improve the conditions given by Theorem 2.6.2, our conditions (3.6.3), (3.6.4), and (3.6.7) are still slightly stronger than what we have observed from simulations. However, while for conditions (2.6.6) we were not able to find examples and thus show that the region in the parameter space for which (2.6.6) holds is nonempty, it looks like every example of three-species coexistence we have found, with  $\tilde{E}$  "far enough away" from the boundary of the positive cone, fulfills (3.6.3), (3.6.4), and, when each two species coexist, (3.6.7).

## 3.7 The number of vessels

As we mentioned in chapter 1, in [CB] it is "shown" numerically that coexistence of three species as a steady state in three interconnected chemostats is impossible. Chang and Baltzis study all possible alternate configurations for the three vessels (not just the gradostat for which the vessels are linearly interconnected) by looking at the possible equilibria that arise in different domains of the operating parameter space. They build so called operating diagrams by varying the input concentration of nutrient  $S^0$  and the dilution rate  $D$ . The search in the  $S^0 \times D$  domain was as detailed as using a grid size of 0.01 in both directions.

We were able to find many examples of three species coexisting, as a steady state, in the gradostat with three vessels for corresponding domains in the species-specific parameter space, but for the scaled system.

For example we fix

$$\begin{aligned} a_1 &= 20, & m_1 &= 30; \\ a_2 &= 5, \\ a_3 &= 30 \end{aligned} \tag{3.7.1}$$

for which

$$m_2 \in [8.0301175727, 8.030998659] \quad \text{and we fix } m_2 = 8.0305$$

and then

$$m_3 \in [44.642960922, 44.642960935] \quad \text{and we fix } m_3 = 44.642960928.$$

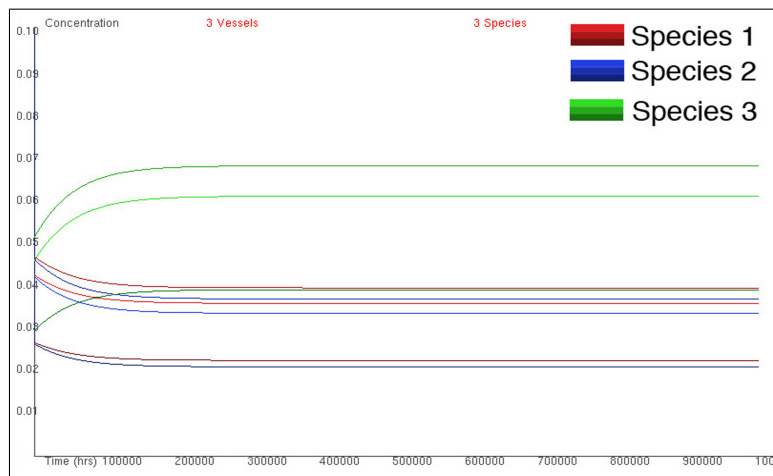
For this choice of parameters we plot in Figure 3.7.1 the solution of (1.1.4).

We can see in (3.7.1) that the coexistence interval for  $m_3$  is very small, and an explanation for the failure in finding coexisting equilibria in [CB] is the choice of a too coarse grid.

It is not clear, even though mathematically we have been able to find coexistence of three species in three vessels, whether biologically such a small coexistence interval makes sense. In order to take a look at what biologically the outcome would be, we perturb the value for  $m_3$ : we solve system (1.1.4) with (3.7.1) and

$$\bar{m}_3 := m_3(1 - d - 2dr)$$

with  $d$  a disturbance factor and  $r \in [0, 1]$  randomly generated at each time step.

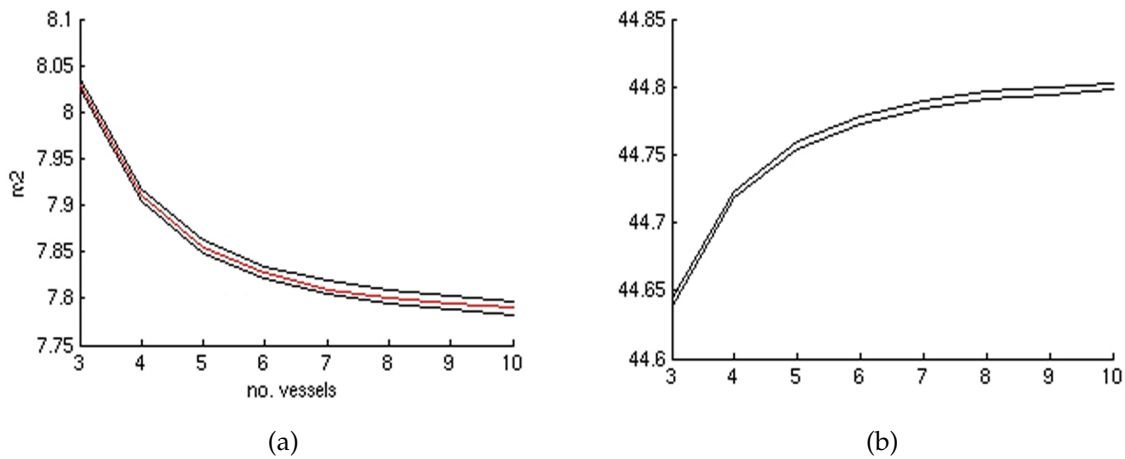


**Figure 3.7.1.** The solution of (1.1.4) with parameters given in (3.7.1).

Thus  $\bar{m}_3 \in [m_3 - dm_3, m_3 + dm_3]$ . In Figure 3.7.3 we plot the solution for a small disturbance factor, namely  $d = 0.001$ , and in Figure 3.7.4, for  $d = 0.1$ . In order to make the simulation more realistic, we also introduced a "low-life" limit: whenever a species reaches a concentration lower than the "low-life" limit, we consider it washed out of the gradostat, namely it no longer grows. In both cases persistence of all three species still occurs. It is interesting to see that a species is able to recover even if it stays at a very low concentration for a long time.

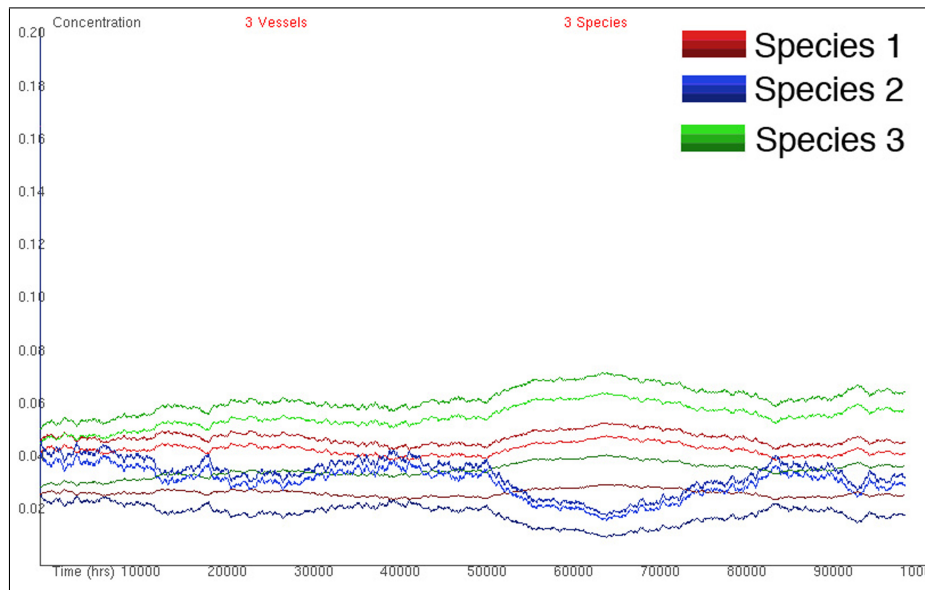
The same actually happens - persistence in the perturbed situation- even for three species in two vessels, where persistence in the unperturbed system occurs only on a line segment connecting two equilibria on the boundary of the positive cone, namely for discrete values for the parameters.

As for the case of two species, we also have the coexistence interval growing with the number of vessels increasing, and this time as well, approaching some constant size. However, as we can see from Figure 3.7.2, the interval stays small.

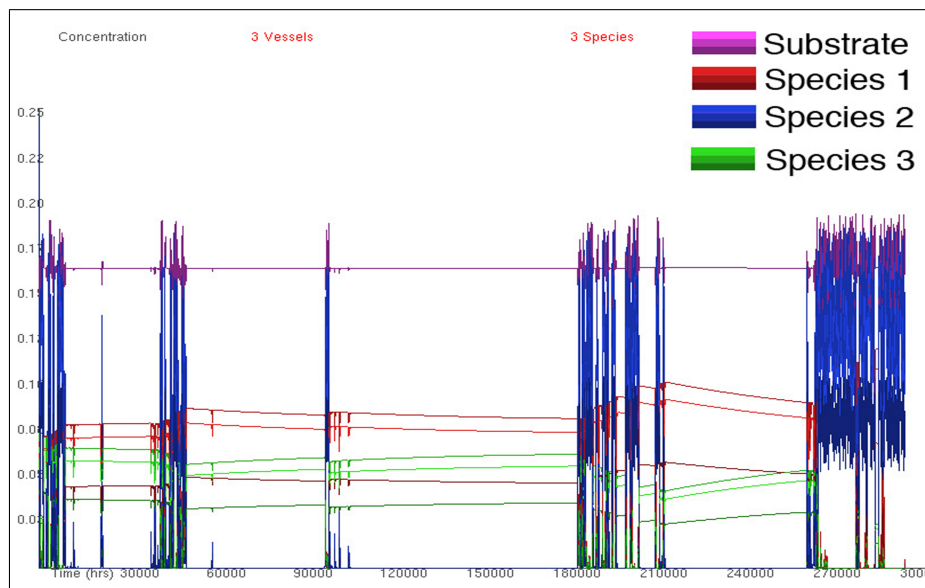


**Figure 3.7.2.** The coexistence interval grows as the number of vessels increases and approaches some constant size. **(a)** The coexistence interval for  $m_2$  corresponding to the coexistence of species 1 and 2. **(b)** The coexistence interval for  $m_3$  corresponding to the coexistence of all three species: we continue the two-species equilibria corresponding to values for  $m_2$  on the red line in (a).





**Figure 3.7.3.** The solution of (1.1.4) with parameters given in (3.7.1) and perturbed  $m_3$  with  $d = 0.001$ .



**Figure 3.7.4.** The solution of (1.1.3) with parameters given in (3.7.1) and perturbed  $m_3$  with  $d = 0.1$ .

### 3.8 Notes and comments

In the present chapter, for the case of three competing species, we have applied the features of the dynamics of the system for two species in order to improve the sufficient persistence conditions given by Theorem 2.6.2. We start from various invariant regions for the two-species system obtained with the help of the lower and upper solution method, the monotonicity of the dynamical system, and some geometrical arguments in Section 3.3 (in Section 3.4 we illustrate some of the possible such regions). We then studied the dynamics of the three-species system by first looking for sufficient persistence conditions for a species when introduced into the gradostat already containing two species present at two-species persistence concentration values (invadability). This was done by a mixture of bifurcation analysis arguments together with the method of lower and upper solutions. The results thus obtained were then in Section 3.6 extended in order to build an invariant region corresponding to all three species concentrations remaining strictly positive.

At this point, for the two species case, starting from the invariant region determined by the pair of coupled lower and upper solutions, we were able to build an iterative process resulting into contracting invariant regions with the corresponding two-species equilibria situated in the smallest such invariant region. Since for three species our invariant region is no longer determined by the sector generated by the pair of coupled lower and upper solutions, the methods in Appendix A no longer apply.

For the invariant  $\Delta$ , the pair of lower and upper solutions is "coupled" with "lower-and-upper-solution-like" conditions for the sums of each two species concentrations: if  $h_i^j$  denotes the right-hand side of system (3.1.1), we have that each  $h_i^j$  is monotone decreasing in  $\sum_{k \neq j} u_i^k$ . It would be interesting to see whether we can build similar processes as the ones described in Appendix A, this time using also the "lower-and-upper-solution-like" conditions for the sums. This would give us contracting  $\Delta$ -like invariant regions and obtain a method which would apply also for  $m > 3$ , provided we can find initial  $\Delta$ -like invariant regions, which, as we have seen in this chapter, is not trivial.

# Conclusions

It has been our aim in this work to check under what conditions several competitors can coexist on a single resource in the gradostat. We were able to give conditions for persistence as well as invadability of a persistent community.

We proposed two different approaches in analyzing our system. The first approach is the construction of invariant regions that keep the solution "away" from zero, with the aid of the features of a system with quasimonotone reaction terms. Thanks to the special form of the variational matrices, with the aid of Perron-Frobenius theory, we could associate positive vectors to each species and thus construct positive lower solutions. For the case of one species (Theorem 2.4.1) and two species (Theorem 2.7.1) the persistence conditions we obtained were the same as the ones in literature. In Section 2.6 (Theorem 2.6.2) we were able to find sufficient conditions for the coexistence of an arbitrary number of species. From [JST], when the number of vessels is smaller than the number of species, we have that the persistence conditions are fulfilled only for a region in the parameter space having measure zero. The question is then "how many vessels do we need such that  $n$  species can persist?". We could see that for three species coexistence can already occur in three vessels (we give an example in Section 3.7).

Using the monotonicity of the dynamical system describing the competition of two species, for three species, in Chapter 3 we were able to improve the general persistence conditions of Theorem 2.6.2. We first considered the question of invadability of a persistent two-species community by a third species. Since the reaction terms corresponding to the third species are decreasing in the sum of the corresponding first two species concentrations, in Section 3.3 we looked for invariant regions for the first two species. As the invariant rectangles given by a pair of coupled lower and upper solutions were resulting into quite strong persistence conditions in Theorem 2.6.2, we looked for slightly different invariant regions with the aid of which we could relax the conditions the third species had to fulfill in order to survive. In Section 3.3 we find several invariant regions for the first two species with corresponding persistence conditions for the third species. Even though the "best" conditions for which we could rigorously prove persistence were slightly stronger than what we have noticed from simulations, in Section 3.6 we were able to construct an invariant region in which all three species were persistent.

The second approach consisted in the continuation of certain equilibria when varying a species-specific parameter and looking for bifurcation conditions with the aid of which we

obtained branches corresponding to persistence. For three species, as above, in Section 3.5 we looked for parameter values for a third species for which invadability occurs by continuing the equilibria corresponding to the coexistence of two species. We obtained a branch of three-species equilibria, and depending on the relative positions of certain coexistence regions in the parameter space, we looked at "where" the three-species branch joined again the boundary of the positive cone. Unfortunately we could not determine the stability of the persistence branch, but, when some further conditions were fulfilled, the region in the parameter space for which the three-species branch existed included the region in the parameter space for which we could show three-species persistence in Section 3.6.

A quite unexpected feature of the system for three species, was that persistence could occur also when not each two species coexisted (we give examples in Section 3.5), fact which brought a further improvement to Theorem 2.6.2.

Together with the analysis, we have presented numerous examples illustrating the different features of the behavior of the dynamical system. As the number of species increases, the dynamics becomes more and more complicated, and to the three species system we devoted a whole chapter. However the theory is not complete. The asymptotic behavior of solutions and the stability and uniqueness are still a challenging problem. As the analysis was "guided" by the observations following extensive numerical investigations, and all persistence examples for three species were found through the continuation of two-species equilibria, whether three-species persistence can occur when we have coexistence for only one (out of three) possible combination of two species, remains an open question.

As has been noted repeatedly, the main difficulty we have encountered throughout this work was the possible non-uniqueness of the positive rest point even for the gradostat with two species in more than two vessels. However, no example of non-uniqueness is known, on the contrary, from all the simulations it looks like the positive equilibrium is unique. Many of the results for three species were possible only assuming the uniqueness of the two-species equilibrium. Sufficient conditions for the uniqueness would greatly simplify the main results.

Obviously, in nature one is concerned with greater number of competitors. Obtaining the models is quite straightforward: we just need to add new equations, but the widely used techniques for the analysis, namely monotone dynamics, fail when the number of competitors exceeds two. New techniques are needed to handle this problem and in the present work we show how, by using the quasimonotonicity of the reaction terms, invariant regions can be built to prove persistence.

To conclude with, we ask the question how extensive is the parameter region where coexistence occurs, and how stable is the behavior under small perturbations which are expected

to occur in nature, or even in a laboratory? Throughout this work we were able to partially answer this question, but as the number of species increases so does the number of the parameters, and exploring the entire parameter space is not possible. Operating diagrams, or as in this work, one or two parameter diagrams with the aid of which we obtain regions in the parameter space corresponding to coexistence, remain the most easily to obtain answers.



# A

## Lower and upper solutions and quasimonotone functions

### A.1 Quasimonotone reaction terms

**Definition A.1.1** (Quasimonotonicity) Let  $D_T \subset \mathbf{R}$ ,  $D_u \subset \mathbf{R}^N$ . Let  $H \subset D_T \times D_u$  be a given set. Consider a function  $h = (h_1, \dots, h_N)$ ,  $h_i : H \subset D_T \times D_u \rightarrow \mathbf{R}$ ,  $(t, u) \mapsto h_i(t, u)$ ,  $u = (u_1, \dots, u_N)$ . The component  $h_i$  is called monotone nondecreasing in  $u_j$  with respect to  $H$  if for all  $(t, \tilde{u}) \in H$ ,  $\tilde{u} = (u_1, \dots, \tilde{u}_j, \dots, u_N)$  and  $(t, u) \in H$ ,  $u = (u_1, \dots, u_j, \dots, u_N)$ , with  $\tilde{u}_j \geq u_j$ , we have

$$h_i(t, u) \geq h_i(t, \tilde{u}). \quad (\text{A.1.1})$$

It is called monotone nonincreasing in  $u_j$  with respect to  $H$  if

$$h_i(t, u) \leq h_i(t, \tilde{u}). \quad (\text{A.1.2})$$

for all such  $(t, u)$  and  $(t, \tilde{u})$ .

The component  $h_i$  is called quasimonotone nondecreasing with respect to  $H$  if for any couple  $i, j \in \{1, \dots, N\}$ ,  $i \neq j$ ,

- (i)  $h_i$  is monotone nondecreasing in  $u_j$  with respect to  $H$  or  $h_i$  is monotone nonincreasing in  $u_j$  with respect to  $H$ , and
- (ii) there is a positive constant  $M_i$  such that

$$\bar{h}_i(t, u) \stackrel{\text{def}}{=} h_i(t, u) + M_i u_i \quad (\text{A.1.3})$$

is monotone nondecreasing in  $u_i$  with respect to  $H$ .

The function  $h$  is called quasimonotone with respect to  $H$  if each component  $h_i$  is quasimonotone.

Following the notations from [Kir], we write a vector  $u$  in the split form

$$u = (u_i, , u^{\uparrow i}, u^{\downarrow i})$$

and rewrite the functions  $h_i$  as

$$h_i(t, u) = h(t, u_i, , u^{\uparrow i}, u^{\downarrow i})$$

for  $i = 1, \dots, N$ , where  $u^{\uparrow i}$  is the vector consisting of all components  $u_k$  of  $u$ , with index  $k$  in the index set

$$I_H^{\uparrow i}(h) \stackrel{\text{def}}{=} \{j \in \{1, \dots, N\} \setminus \{i\} \mid h_i \text{ is monotone nondecreasing in } u_j\},$$

called the *nondecreasing index set* of  $h_i$  (with respect to  $H$ ), and, similarly,  $u^{\downarrow i}$  is the vector consisting of all components  $u_k$  of  $u$ , with index  $k$  in the index set

$$I_H^{\downarrow i}(h) \stackrel{\text{def}}{=} \{j \in \{1, \dots, N\} \setminus \{i\} \mid h_i \text{ is monotone nonincreasing in } u_j\},$$

called the *nonincreasing index set* of  $h_i$  (with respect to  $H$ ).

Clearly, if  $h_i$  is quasimonotone, we have  $\{i\} \cup I_H^{\uparrow i}(h) \cup I_H^{\downarrow i}(h) = \{1, \dots, N\}$ .

We say that  $h_i$  is *monotone nondecreasing* in  $u^{\uparrow i}$  and *monotone nonincreasing* in  $u^{\downarrow i}$  with respect to  $H$ .  $u^{\uparrow i}$  will be called the *nondecreasing subvector* of  $h_i$ , and  $u^{\downarrow i}$ , the *nonincreasing subvector* of  $h_i$ , with respect to  $H$ . When  $I_H^{\uparrow i}(h) = \emptyset$  or  $I_H^{\downarrow i}(h) = \emptyset$ ,  $h_i$  is said to be *quasimonotone non-increasing* and *quasimonotone nondecreasing*, respectively. Note that the split form of  $u$  varies with respect to  $i$  and is determined by the quasimonotone property of  $h_i$ .

**Remark:** In [Pao3], the definition of quasimonotonicity consists only of the condition (i), (ii) appearing as an extra condition that function  $h$  has to fulfill.

## A.2 Lower and upper solutions

Consider a domain  $\Omega \subset \mathbf{R}^N$ , and the functions  $h_i : \mathbf{R}^+ \times \Omega \rightarrow \mathbf{R}^N$ ,  $i = 1, \dots, N$ ,  $h_i$  continuous on  $\mathbf{R}^+ \times \Omega$ . Let  $u_i$ ,  $i = 1, \dots, N$  denote the population densities for  $N$  different species. The equations describing the dynamics of each species  $u_i$  are assumed to have the form:

$$\begin{aligned} u_i' &= h_i(t, u_1, \dots, u_N), \\ u_i(t_0) &= u_{i,0}, \\ i &= 1, \dots, N. \end{aligned} \tag{A.2.1}$$



**H 1: (Quasimonotonicity)** Assume that the reaction function  $h = (h_1, \dots, h_N)$  is quasimonotone with respect to a  $T \subset \mathbf{R}^+ \times \Omega$ . If  $u_i = 0$  then let

$$h_i(t, u_1, \dots, u_i, \dots, u_N) \geq 0$$

for all  $(t, u) \in T$ .

Using the split form for  $h_i$ , the system (A.2.1) may be written in the form:

$$\begin{aligned} u_i' &= h_i(t, u_i, u^{\uparrow i}, u^{\downarrow i}), \\ u_i(t_0) &= u_{i,0}, \\ i &= 1, \dots, N. \end{aligned} \tag{A.2.2}$$

**Definition A.2.1** (Lower and upper solutions) A pair of  $C^1$  vector functions  $\underline{u} = (\underline{u}_1, \dots, \underline{u}_N)$  and  $\bar{u} = (\bar{u}_1, \dots, \bar{u}_N)$  are called coupled lower and upper solutions for (A.2.1) if

(i)  $\underline{u} \leq \bar{u}$ ,

(ii) for each  $\underline{u}_i$  the inequality

$$\underline{u}_i' \leq h_i(t, u_1, \dots, \underline{u}_i, \dots, u_N) \tag{A.2.3}$$

holds for all  $u_j, j \neq i$  with  $\underline{u}_j \leq u_j \leq \bar{u}_j$ ,

(iii) for each  $\bar{u}_i$  the inequality

$$\bar{u}_i' \geq h_i(t, u_1, \dots, \bar{u}_i, \dots, u_N) \tag{A.2.4}$$

holds for all  $u_j, j \neq i$  with  $\underline{u}_j \leq u_j \leq \bar{u}_j$ ,

(iv)  $\underline{u}(t_0) \leq u(t_0) \leq \bar{u}(t_0)$ .

Note that in some literature lower and upper solutions are called sub- and supersolutions or subfunctions and superfunctions.

**Remark:** Using the split form for  $h_i$ , we can obtain sufficient conditions to satisfy (ii) and (iii) in definition (A.2.1):

$$\underline{u}_i' \leq h_i(t, \underline{u}_i, \underline{u}^{\uparrow i}, \bar{u}^{\downarrow i}) \tag{A.2.5}$$

is a sufficient condition for (ii), and

$$\bar{u}_i' \geq h_i(t, \bar{u}_i, \bar{u}^{\uparrow i}, \underline{u}^{\downarrow i}) \tag{A.2.6}$$

is a sufficient condition for (iii).

We can see from the definition that lower and upper solutions are, in general, coupled, unless  $h$  is quasimonotone nondecreasing. For a give pair of coupled lower and upper solutions,  $\underline{u}$  and  $\bar{u}$ , we define the sector

$$\langle \underline{u}, \bar{u} \rangle = \{(t, u) \mid \underline{u}(t) \leq u(t) \leq \bar{u}(t)\},$$

and consider (H1), the quasimonotonicity assumption for  $h$ , with this choice of  $T$ .

### A.3 Monotone schemes

Define the functions  $H_i$  by

$$H_i(t, u) = h_i(t, u) + M_i u_i,$$

or, equivalently,

$$H_i(t, u_i, , u^{\uparrow i}, u^{\downarrow i}) = h_i(t, u_i, , u^{\uparrow i}, u^{\downarrow i}) + M_i u_i,$$

where  $M_i$  are the positive constants that appear in (A.1.3), in the definition of quasimonotonicity, and hence  $H_i$  are monotone nondecreasing in  $u_i$ .

#### Lemma A.3.1

If  $h = (h_1, \dots, h_N)$  is quasimonotone in  $\langle \underline{u}, \bar{u} \rangle$  then for any  $u, v \in \langle \underline{u}, \bar{u} \rangle$  with  $u \geq v$

$$H_i(t, u_i, , u^{\uparrow i}, v^{\downarrow i}) - H_i(t, v_i, , v^{\uparrow i}, u^{\downarrow i}) \geq 0. \quad (\text{A.3.1})$$

**Proof:** For any  $u, v \in \langle \underline{u}, \bar{u} \rangle$ , write

$$\begin{aligned} & H_i(t, u_i, , u^{\uparrow i}, v^{\downarrow i}) - H_i(t, v_i, , v^{\uparrow i}, u^{\downarrow i}) = \\ &= [M_i(u_i - v_i) + h_i(t, u_i, , u^{\uparrow i}, v^{\downarrow i}) - h_i(t, v_i, , u^{\uparrow i}, v^{\downarrow i})] \\ &+ [h_i(t, v_i, , u^{\uparrow i}, v^{\downarrow i}) - h_i(t, v_i, , v^{\uparrow i}, v^{\downarrow i})] \\ &+ [h_i(t, v_i, , v^{\uparrow i}, v^{\downarrow i}) - h_i(t, v_i, , v^{\uparrow i}, u^{\downarrow i})]. \end{aligned}$$

By condition (ii) in the definition of quasimonotonicity we have  $M_i(u_i - v_i) + h_i(t, u_i, , u^{\uparrow i}, v^{\downarrow i}) - h_i(t, v_i, , u^{\uparrow i}, v^{\downarrow i}) \geq 0$ . The remaining two terms are also nonnegative, in view of the quasimonotonicity property of  $h$ .  $\square$

With our choice for  $H_i$ , the system (A.2.1) is equivalent to

$$\begin{aligned} u_i' + M_i u_i &= H_i(t, u_i, , u^{\uparrow i}, u^{\downarrow i}), \\ u_i(t_0) &= u_{i0}, \\ i &= 1, \dots, N. \end{aligned} \quad (\text{A.3.2})$$

Starting from an initial iteration  $\underline{u}^{(0)} = \underline{u}$ ,  $\bar{u}^{(0)} = \bar{u}$ , we construct two sequences  $\{\underline{u}^{(k)}\} = \{\underline{u}_1^{(k)}, \dots, \underline{u}_N^{(k)}\}$ ,  $\{\bar{u}^{(k)}\} = \{\bar{u}_1^{(k)}, \dots, \bar{u}_N^{(k)}\}$  from the iteration process

$$\begin{aligned} \underline{u}_i^{(k)'} + M_i \underline{u}_i^{(k)} &= H_i(t, \underline{u}_i^{(k-1)}, \underline{u}^{(k-1)\uparrow i}, \bar{u}^{(k-1)\downarrow i}), \\ \bar{u}_i^{(k)'} + M_i \bar{u}_i^{(k)} &= H_i(t, \bar{u}_i^{(k-1)}, \bar{u}^{(k-1)\uparrow i}, \underline{u}^{(k-1)\downarrow i}), \\ i &= 1, \dots, N, \end{aligned} \quad (\text{A.3.3})$$

with the initial conditions

$$\begin{aligned} \underline{u}_i^{(k)}(t_0) &= \bar{u}_i^{(k)}(t_0) = u_{i,0} \\ i &= 1, \dots, N. \end{aligned} \quad (\text{A.3.4})$$

For each  $k$  the right-hand side of the two systems for  $\underline{u}_i^{(k)}$  and  $\bar{u}_i^{(k)}$  is known and the sequences  $\{\underline{u}_i^{(k)}\}$  and  $\{\bar{u}_i^{(k)}\}$  are well defined (for each  $k$  the two systems have unique solutions). They will be referred to as lower and upper sequences. In order to prove the monotone property of these two sequences, we need the following lemma:

**Lemma A.3.2** (Positivity)

Suppose that  $f : \mathbf{R} \times D \rightarrow \mathbf{R}^N$ ,  $D \subset \mathbf{R}^N$ , has the property that solutions of the initial value problem

$$\begin{aligned} u' &= f(t, u) \\ u(t_0) &= u_0 \geq 0 \end{aligned}$$

are unique and, for all  $i$ ,  $f_i(t, u) \geq 0$  whenever  $u \geq 0$  satisfies  $u_i = 0$ . Then  $u(t) \geq 0$  for all  $t \geq t_0$  for which it is defined.

The proof of this lemma can be found, for example, in [Smith&Waltman] (Proposition B.1).

An analogous condition on  $f_i$ , with inequalities reversed, ensures that  $u(t) \leq 0$  for all  $t \geq t_0$ , provided that  $u(t_0) \leq 0$ . We will refer to it as the *negativity lemma*.

**Lemma A.3.3**

The lower and upper sequences  $\{\underline{u}_i^{(k)}\}$  and  $\{\bar{u}_i^{(k)}\}$  possess the monotone property

$$\underline{u} \leq \underline{u}^{(k)} \leq \underline{u}^{(k+1)} \leq \bar{u}^{(k+1)} \leq \bar{u}^{(k)} \leq \bar{u} \quad (\text{A.3.5})$$

for every  $k$ , and  $\underline{u}_i^{(k)}$  and  $\bar{u}_i^{(k)}$  are coupled lower and upper solutions for each  $k$ .

**Proof:** Let  $\omega_i = \bar{u}_i^{(0)} - \bar{u}_i^{(1)} = \bar{u}_i - \bar{u}_i^{(1)}$ ,  $i = 1, \dots, N$ . Then  $\omega_i$  will satisfy the relation

$$\begin{aligned} \omega_i' + M_i \omega_i &= \bar{u}_i' - h_i(t, \bar{u}_i, \bar{u}^{\uparrow i}, \underline{u}^{\downarrow i}) \geq 0 \\ \omega_i(t_0) &= \bar{u}_i(t_0) - u_{i,0} \geq 0 \end{aligned}$$

which implies that  $\omega_i \geq 0$ . This shows that  $\bar{u}_i^{(1)} \leq \bar{u}_i^{(0)}$  for  $i = 1, \dots, N$ . A similar argument gives  $\underline{u}_i^{(1)} \leq \underline{u}_i^{(0)}$ .

Let  $\omega_i^{(1)} = \bar{u}_i^{(1)} - \underline{u}_i^{(1)} = \bar{u}_i - \bar{u}_i^{(1)}$ . From Lemma A.3.1

$$\omega_i^{(1)'} + M_i \omega_i^{(1)} = H_i(t, \bar{u}_i^{(0)}, \bar{u}^{(0)\uparrow i}, \underline{u}^{(0)\downarrow i}) - H_i(t, \underline{u}_i^{(0)}, \underline{u}^{(0)\uparrow i}, \bar{u}^{(0)\downarrow i}) \geq 0$$

for  $i = 1, \dots, N$ . Since  $\omega_i^{(1)}(t_0) = 0$ , it follows that  $\omega_i^{(1)} \geq 0$ .

So far we have showed that  $\underline{u} \leq \underline{u}^{(1)} \leq \bar{u}^{(1)} \leq \bar{u}$ .

Assume, by induction, that

$$\underline{u}^{(k-1)} \leq \underline{u}^{(k)} \leq \bar{u}^{(k)} \leq \bar{u}^{(k-1)}. \quad (\text{A.3.6})$$

Then the functions  $u$  and  $v$  given by

$$\begin{aligned} u &= (\bar{u}^{(k-1)}, \bar{u}^{(k-1)\uparrow i}, \underline{u}^{(k)\downarrow i}) \\ v &= (\bar{u}^{(k)}, \bar{u}^{(k)\uparrow i}, \underline{u}^{(k-1)\downarrow i}) \end{aligned}$$

are in  $\langle \underline{u}, \bar{u} \rangle$  and  $u \geq v$ .

In view of Lemma A.3.1 the function  $\bar{\omega}^{(k)} = \bar{u}^{(k)} - \bar{u}^{(k+1)}$  satisfies the relation

$$\bar{\omega}_i^{(k)'} + M_i \bar{\omega}_i^{(k)} = H_i(t, \bar{u}_i^{(k-1)}, \bar{u}^{(k-1)\uparrow i}, \underline{u}^{(k-1)\downarrow i}) - H_i(t, \bar{u}_i^{(k)}, \bar{u}^{(k)\uparrow i}, \underline{u}^{(k)\downarrow i}) \geq 0.$$

It follows from  $\bar{\omega}^{(k)}(t_0) = 0$  and the positivity lemma that  $\bar{u}^{(k)} \geq \bar{u}^{(k-1)}$ .

Similarly, using (A.3.3) and (A.3.4), the functions  $\underline{\omega}^{(k)} = \underline{u}^{(k+1)} - \underline{u}^{(k)}$  and  $\bar{\omega}^{(k)} = \bar{u}^{(k+1)} - \underline{u}^{(k+1)}$  satisfy the respective equations

$$\begin{aligned} \underline{\omega}_i^{(k)'} + M_i \underline{\omega}_i^{(k)} &= H_i(t, \underline{u}_i^{(k)}, \underline{u}^{(k)\uparrow i}, \bar{u}^{(k)\downarrow i}) - H_i(t, \underline{u}_i^{(k-1)}, \underline{u}^{(k-1)\uparrow i}, \bar{u}^{(k-1)\downarrow i}) \\ \bar{\omega}_i^{(k)'} + M_i \bar{\omega}_i^{(k)} &= H_i(t, \bar{u}_i^{(k)}, \bar{u}^{(k)\uparrow i}, \underline{u}^{(k)\downarrow i}) - H_i(t, \bar{u}_i^{(k-1)}, \bar{u}^{(k-1)\uparrow i}, \underline{u}^{(k-1)\downarrow i}) \end{aligned} \quad (\text{A.3.7})$$

with the conditions  $\underline{\omega}^{(k)}(t_0) = \bar{\omega}^{(k)}(t_0) = 0$ . From (A.3.6) and Lemma A.3.1, the right-hand sides of (A.3.7) for both equations are nonnegative and from the positivity lemma we have that  $\underline{\omega}^{(k)} \geq 0$  and  $\bar{\omega}^{(k)} \geq 0$ . This proves the relation (A.3.6) when  $k$  is replaced by  $k + 1$ . From the principle of induction, (A.3.5) follows.

Relations (A.3.1), (A.3.3) and (A.3.5), imply that for each  $k$

$$\begin{aligned} \bar{u}_i^{(k)'} + M_i \bar{u}_i^{(k)} &= H_i(t, \bar{u}_i^{(k-1)}, \bar{u}^{(k-1)\uparrow i}, \underline{u}^{(k-1)\downarrow i}) \geq H_i(t, \bar{u}_i^{(k)}, \bar{u}^{(k)\uparrow i}, \underline{u}^{(k)\downarrow i}) \\ \underline{u}_i^{(k)'} + M_i \underline{u}_i^{(k)} &= H_i(t, \underline{u}_i^{(k-1)}, \underline{u}^{(k-1)\uparrow i}, \bar{u}^{(k-1)\downarrow i}) \leq H_i(t, \underline{u}_i^{(k)}, \underline{u}^{(k)\uparrow i}, \bar{u}^{(k)\downarrow i}). \end{aligned}$$

Hence

$$\begin{aligned} \bar{u}_i^{(k)'} &\geq h_i(t, \bar{u}_i^{(k)}, \bar{u}^{(k)\uparrow i}, \underline{u}^{(k)\downarrow i}) \\ \underline{u}_i^{(k)'} &\leq h_i(t, \underline{u}_i^{(k)}, \underline{u}^{(k)\uparrow i}, \bar{u}^{(k)\downarrow i}). \end{aligned}$$

From  $\underline{u}^{(k)}(t_0) = \bar{u}^{(k)}(t_0) = u_{i,0}$ , it follows that  $\underline{u}^{(k)}$  and  $\bar{u}^{(k)}$  are coupled lower and upper solutions.  $\square$

**Lemma A.3.4**

The pointwise and componentwise limits

$$\lim_{k \rightarrow \infty} \underline{u}^{(k)}(t) = u_{\min}(t), \quad \lim_{k \rightarrow \infty} \bar{u}^{(k)}(t) = u_{\max}(t) \quad (\text{A.3.8})$$

exist and satisfy the relation

$$\underline{u} \leq \underline{u}^{(k)} \leq \underline{u}^{(k+1)} \leq u_{\min} \leq u_{\max} \leq \bar{u}^{(k+1)} \leq \bar{u}^{(k)} \leq \bar{u}. \quad (\text{A.3.9})$$

**Proof:** By Lemma A.3.3 the sequence  $\{\underline{u}^{(k)}\}$  is monotone nondecreasing and is bounded from above and the sequence  $\{\bar{u}^{(k)}\}$  is monotone nonincreasing and bounded from below. Hence the pointwise (and componentwise) limits exist and are denoted as in (A.3.8). Moreover, by (A.3.5), the relation (A.3.9) holds.  $\square$

We have found so far the limits  $u_{\min}$  and  $u_{\max}$  which will be called *minimal quasisolution* and, respectively, *maximal quasisolution*. We want to see now under which conditions these two limits are equal.

**Theorem A.3.5**

Let  $\underline{u}$  and  $\bar{u}$  be a pair of bounded coupled lower and upper solutions for (A.2.1), with  $h$  satisfying (H1) in  $\langle \underline{u}, \bar{u} \rangle$ . Assume that the following hypothesis holds:

**H2:** For all  $i$ , the functions  $h_i$  satisfy the Lipschitz condition:

$$|h_i(t, u) - h_i(t, v)| \leq m_i(t) \sum_{j=1}^N |u_j - v_j|, \quad (\text{A.3.10})$$

for all  $t$  and all  $u, v \in \langle \underline{u}, \bar{u} \rangle$ , with  $u \geq v$ , and  $m_i$  bounded functions.

Then

$$u_{\min} \equiv u_{\max}, \quad (\text{A.3.11})$$

which means that the sequences  $\{\underline{u}^{(k)}\}$  and  $\{\bar{u}^{(k)}\}$  have the same limit.

**Proof:** From (A.3.8) and since  $H_i$  are continuous, we have the pointwise limits

$$\begin{aligned} \lim_{k \rightarrow \infty} H_i(t, \underline{u}_i^{(k)}, \underline{u}^{(k)\uparrow i}, \bar{u}^{(k)\downarrow i}) &= H_i(t, u_{\min_i}, u_{\min}^{\uparrow i}, u_{\max}^{\downarrow i}) \\ \lim_{k \rightarrow \infty} H_i(t, \bar{u}_i^{(k)}, \bar{u}^{(k)\uparrow i}, \underline{u}^{(k)\downarrow i}) &= H_i(t, u_{\min_i}, u_{\max}^{\uparrow i}, u_{\min}^{\downarrow i}) \end{aligned} \quad (\text{A.3.12})$$

By taking the integral representation for:

$$\begin{aligned} \underline{u}_i^{(k)'} &= M_i(\underline{u}_i^{(k-1)} - \underline{u}_i^{(k)}) + h_i(t, \underline{u}_i^{(k-1)}, \underline{u}^{(k-1)\uparrow i}, \bar{u}^{(k-1)\downarrow i}) \\ \bar{u}_i^{(k)'} &= M_i(\bar{u}_i^{(k-1)} - \bar{u}_i^{(k)}) + h_i(t, \bar{u}_i^{(k-1)}, \bar{u}^{(k-1)\uparrow i}, \underline{u}^{(k-1)\downarrow i}) \end{aligned} \quad (\text{A.3.13})$$

and then using the dominated convergence theorem, with the aid of (A.3.12), we obtain

$$\begin{aligned} \underline{u}_{\min_i}' &= h_i(t, u_{\min_i}, u_{\min_i}^{\uparrow i}, u_{\max}^{\downarrow i}) \\ \bar{u}_{\max_i}' &= h_i(t, u_{\min_i}, u_{\max}^{\uparrow i}, u_{\min}^{\downarrow i}). \end{aligned} \quad (\text{A.3.14})$$

Define now the modified functions  $\hat{h}_i$  such that  $\hat{h}_i(t, u) = h_i(t, u)$  for  $u \in \langle \underline{u}, \bar{u} \rangle$  and  $\hat{h}_i$  uniformly bounded and satisfying a global Lipschitz condition, for all  $i = 1, \dots, N$ .

Consider the  $2N$  system

$$\begin{aligned} v_i' &= \hat{h}_i(t, v_i, v^{\uparrow i}, w^{\downarrow i}) \\ w_i' &= \hat{h}_i(t, w_i, w^{\uparrow i}, v^{\downarrow i}) \\ v_i(t_0) &= w_i(t_0) = u_{i,0} \\ i &= 1, \dots, N. \end{aligned} \quad (\text{A.3.15})$$

By taking the  $2N$  vector  $u$ :

$$(u_1, \dots, u_N) = (v_1, \dots, v_N), \quad (u_{N+1}, \dots, u_{2N}) = (w_1, \dots, w_N),$$

we can write the system (A.3.15) in the form

$$\begin{aligned} u_i' &= \hat{h}_i(t, u_i, u^{\uparrow i}, u^{\downarrow i}) \\ u_i(t_0) &= u_{i,0} \\ i &= 1, \dots, 2N. \end{aligned} \quad (\text{A.3.16})$$

Since  $\hat{h}_i$  are global Lipschitz in  $u$ , the system (A.3.15) has a unique solution  $(v^*, w^*)$ . By the symmetry of the system,  $(w^*, v^*)$  is also a solution, and since the solution is unique, we have that  $(v^*, w^*) = (v^*, w^*)$ , and hence,  $w^* = v^*$ .

From (A.3.14)  $(u_{\min}, u_{\max})$  is also a solution of (A.3.15) and it follows again from the uniqueness of the solution of (A.3.15) that  $u_{\min} = u_{\max} = v^*$ .

We had that  $\hat{h}_i(t, u) = h_i(t, u)$  for  $u \in \langle \underline{u}, \bar{u} \rangle$  and therefore  $u_{\min} = u_{\max} = u^*$  is the unique solution of (A.2.1) in  $\langle \underline{u}, \bar{u} \rangle$ .  $\square$

## A.4 Existence comparison theorems for the time dependent problem

The basic requirements in the construction of the two monotone schemes for system (A.2.1) in the preceeding section were the quasipositivity of the reaction terms and the existence of

a pair of coupled lower and upper solutions. We showed that if, in addition, the reaction functions satisfy a Lipschitz condition in the sector  $\langle \underline{u}, \bar{u} \rangle$ , the pointwise limits of the two monotone sequences coincide and verify the equations in the system (A.2.1).

We will see next that the existence of a pair of coupled lower and upper solutions  $(\underline{u}, \bar{u})$  for (A.2.1) with quasipositive reaction terms is sufficient to assure the existence of at least one solution of (A.2.1) lying pointwise in the sector  $\langle \underline{u}, \bar{u} \rangle$ .

**Theorem A.4.1**

Let  $(\underline{u}, \bar{u})$  be a pair of bounded coupled lower and upper solutions for (A.2.1). Assume (H1) in  $\langle \underline{u}, \bar{u} \rangle$  and that  $\underline{u}(t_0) \leq u_0 \leq \bar{u}(t_0)$ . Then there exists at least one solution  $u$  of (A.2.1) such that

$$\underline{u} \leq u \leq \bar{u}. \quad (\text{A.4.1})$$

**Proof:** Consider the subspace  $T$  of the continuous functions  $v : \mathbf{R}^+ \rightarrow \mathbf{R}^N, v \in \langle \underline{u}, \bar{u} \rangle$ .

Define the operator  $\mathcal{T} : T \rightarrow \mathbf{C}(\mathbf{R}^+, \mathbf{R}^N)$  by  $v \mapsto \omega_v$ , where  $\omega_v$  is the unique solution of the linear system

$$\begin{aligned} \omega_{v_i}' + M_i \omega_{v_i} &= H_i(t, v) \\ \omega_{v_i}(t_0) &= u_{i,0} \\ i &= 1, \dots, N, \end{aligned} \quad (\text{A.4.2})$$

and  $\omega_{v_i} \in \mathbf{C}^1(\mathbf{R}^+, \mathbf{R}^N)$ .

We show first that  $\mathcal{T} : T \rightarrow T$ . For this we have to prove that  $\omega_v \geq \underline{u}$  and  $\omega_v \leq \bar{u}$ . We have

$$\begin{aligned} (\omega_{v_i} - \underline{u}_i)' + M_i(\omega_{v_i} - \underline{u}_i) &\geq H_i(t, v) - H_i(t, \underline{u}_i, \underline{u}^{\uparrow i}, \bar{u}^{\downarrow i}) \geq 0, \\ \omega_{v_i}(t_0) - \underline{u}_i(t_0) &\geq 0 \end{aligned}$$

since  $\underline{u}$  lower solution, which means

$$\begin{aligned} \underline{u}_i' &\leq H_i(t, \underline{u}_i, \underline{u}^{\uparrow i}, \bar{u}^{\downarrow i}), \\ \underline{u}_i(t_0) &\leq u_{i,0}, \end{aligned}$$

and hence  $\omega_v - \underline{u} \geq 0$ .

For  $\bar{u} - \omega_v$  we have

$$\begin{aligned} (\bar{u}_i - \omega_{v_i})' + M_i(\bar{u}_i - \omega_{v_i}) &\geq H_i(t, \bar{u}_i, \bar{u}^{\uparrow i}, \underline{u}^{\downarrow i}) - H_i(t, v) \geq 0, \\ \bar{u}_i(t_0) - \omega_{v_i}(t_0) &\geq 0 \end{aligned}$$

since  $\bar{u}$  upper solution, which means

$$\begin{aligned} \bar{u}_i' &\geq H_i(t, \bar{u}_i, \bar{u}^{\uparrow i}, \underline{u}^{\downarrow i}), \\ \bar{u}_i(t_0) &\geq u_{i,0}, \end{aligned}$$

and hence  $\bar{u} - \omega_v \geq 0$ .

$\mathcal{T}$  can be shown to be continuous. Moreover, using the integral representation of a solution of (A.4.2), since the lower and upper solutions are both bounded, the family of functions  $\omega_v$ ,  $v \in T$  can be shown to be equicontinuous and uniformly bounded. Hence, by the Arzela-Ascoli theorem, this family is a precompact set of  $T$ .

Since  $T$  is obviously convex, by Schauder's fixed point theorem, the operator  $\mathcal{T}$  has at least one fixed point  $u$  in  $T$ . The fact that  $\mathcal{T}$  maps  $\mathbf{C}(\mathbf{R}^+)$  into  $\mathbf{C}^1(\mathbf{R}^+)$  ensures that  $u \in \mathbf{C}^1(\mathbf{R}^+)$  is a solution of (A.2.1).

Thus we have found a solution  $u$  of (A.2.1) which satisfies  $\underline{u} \leq u \leq \bar{u}$ .  $\square$

Since the quasisolutions  $u_{min}$  and  $u_{max}$  are themselves (bounded) lower and upper solutions for (A.2.1), Theorem A.4.1. implies that there exists at least one solution  $u$  in  $\langle u_{min}, u_{max} \rangle$ . We show that in fact every solution of (A.2.1) in  $\langle \underline{u}, \bar{u} \rangle$  is actually in  $\langle u_{min}, u_{max} \rangle$ .

#### Theorem A.4.2

Let the hypotheses of Theorem A.4.1 hold, and let  $u_{min}$ , and  $u_{max}$  be the limits in (A.3.8). Then any solution  $u$  of (A.2.1) in  $\langle \underline{u}, \bar{u} \rangle$  is necessarily in  $\langle u_{min}, u_{max} \rangle$ :

$$\underline{u} \leq u_{min} \leq u \leq u_{max} \leq \bar{u}. \quad (\text{A.4.3})$$

**Proof:** From Lemma A.3.3 for each  $k$  we have that  $(\underline{u}^{(k)}, \bar{u}^{(k)})$  is a pair of coupled lower and upper solutions for (A.2.1).

For the functions  $\omega_i = \bar{u}_i^{(1)} - u_i$ , by Lemma (A.3.1), we have

$$\omega_i' + M_i \omega_i = H_i(\bar{u}_i, \bar{u}^{\uparrow i}, \underline{u}^{\downarrow i}) - H_i(u_i, u^{\uparrow i}, u^{\downarrow i}) \geq 0,$$

thus  $u_i \leq \bar{u}_i^{(1)}$ , for  $i = 1, \dots, N$ .

Similarly, we get  $u \geq \underline{u}^{(1)}$ , for  $i = 1, \dots, N$ , which leads to

$$\underline{u}^{(1)} \leq u \leq \bar{u}^{(1)}.$$

Assume, by induction, that

$$\underline{u}^{(k)} \leq u \leq \bar{u}^{(k)}. \quad (\text{A.4.4})$$

Then, by Lemma A.3.1, the functions  $\omega_i^{(k)} = \bar{u}_i^{(k+1)} - u_i$  satisfy

$$\omega_i^{(k)'} + M_i \omega_i^{(k)} = H_i(\bar{u}_i^{(k)}, \bar{u}^{(k)\uparrow i}, \underline{u}^{(k)\downarrow i}) - H_i(u_i, u^{\uparrow i}, u^{\downarrow i}) \geq 0,$$

thus we have again that  $u \leq \bar{u}^{(k+1)}$ . An analogous argument gives  $u \geq \underline{u}^{(k+1)}$ , and thus, by induction, (A.4.4) holds for each  $k$ . Letting  $k \rightarrow \infty$  in (A.2.4), we get  $u_{min} \leq u \leq u_{max}$ .  $\square$



In Theorem A.3.5 we showed that if  $h$  fulfills (H2), the limits  $u_{min}$  and  $u_{max}$  coincide, and  $u^* = u_{min} = u_{max}$  is the unique solution of (A.2.1) in the sector  $\langle \underline{u}^{(k)}, \bar{u}^{(k)} \rangle$ :

**Theorem A.4.3**

Assume the hypothesis of Theorem A.4.1 hold, and in addition, let (H2) be satisfied. Then  $u^* = u_{min} = u_{max}$  is the unique solution of (A.2.1) in the sector  $\langle \underline{u}^{(k)}, \bar{u}^{(k)} \rangle$ .

**Remark:** We have shown that when (H1) and (H2) hold, the system (A.2.1) has a unique solution in  $\langle \underline{u}, \bar{u} \rangle$ . However this uniqueness result is ensured only with respect to the given pair of coupled lower and upper solutions, and it does not rule out the possibility of other solutions outside the sector  $\langle \underline{u}, \bar{u} \rangle$ .

Note that by our second assumption in (H1),  $\underline{u} \equiv 0$  is always a lower solution independently of our choice of  $\bar{u}$ , this implies that for nonnegative initial conditions, a solution will stay nonnegative for all time.

## A.5 Lower and upper solutions and existence comparison theorems for the steady state problem

We consider now the steady state problem for (A.2.1):

$$\begin{aligned} 0 &= h_i(u_1, \dots, u_N), \\ i &= 1, \dots, N, \end{aligned} \tag{A.5.1}$$

with  $h$  independent of  $t$ , or, using the split form for  $h_i$

$$\begin{aligned} 0 &= h_i(u_i, u^{\uparrow i}, u^{\downarrow i}), \\ i &= 1, \dots, N. \end{aligned} \tag{A.5.2}$$

We assume that for each  $i$ ,  $h_i$  is quasimonotone in  $\langle \underline{u}, \bar{u} \rangle$ , with  $\underline{u}$  and  $\bar{u}$  given by:

**Definition A.5.1** (Time-independent lower and upper solutions) A pair of continuous vector functions  $\underline{u} = (u_1, \dots, u_N)$  and  $\bar{u} = (\bar{u}_1, \dots, \bar{u}_N)$  are called coupled time-independent lower and upper solutions for (A.5.1) if

(i)  $\underline{u} \leq \bar{u}$ ,

(ii) for each  $\underline{u}_i$  the inequality

$$0 \leq h_i(u_1, \dots, \underline{u}_i, \dots, u_N) \quad (\text{A.5.3})$$

holds for all  $u_j, j \neq i$  with  $\underline{u}_j \leq u_j \leq \bar{u}_j$ ,

(iii) for each  $\bar{u}_i$  the inequality

$$0 \geq h_i(u_1, \dots, \bar{u}_i, \dots, u_N) \quad (\text{A.5.4})$$

holds for all  $u_j, j \neq i$  with  $\underline{u}_j \leq u_j \leq \bar{u}_j$ ,

**Remark:** Using the split form for  $h_i$ , since  $h_i$  are quasimonotone, we can obtain sufficient conditions to satisfy (ii) and (iii) in definition (A.5.1):

$$0 \leq h_i(\underline{u}_i, \underline{u}^{\uparrow i}, \bar{u}^{\downarrow i}) \quad (\text{A.5.5})$$

is a sufficient condition for (ii), and

$$0 \geq h_i(\bar{u}_i, \bar{u}^{\uparrow i}, \underline{u}^{\downarrow i}) \quad (\text{A.5.6})$$

is a sufficient condition for (iii).

To prove existence of solutions for the time-independent problem (A.5.1), assume we can find a pair of coupled time-independent lower and upper solutions  $(\underline{u}, \bar{u})$ , and using them as initial iterations, we can construct two sequences  $\{\underline{u}^{(k)}\} \equiv \{\underline{u}_1^{(k)}, \dots, \underline{u}_N^{(k)}\}$  and  $\{\bar{u}^{(k)}\} \equiv \{\bar{u}_1^{(k)}, \dots, \bar{u}_N^{(k)}\}$  from the iteration process

$$\begin{aligned} \underline{u}_i^{(0)} &= \underline{u}_i \\ \bar{u}_i^{(0)} &= \bar{u}_i \\ M_i \underline{u}_i^{(k)} &= H_i(\underline{u}_i, \underline{u}_i^{(k-1)\uparrow i}, \bar{u}_i^{(k-1)\downarrow i}) \\ M_i \bar{u}_i^{(k)} &= H_i(\bar{u}_i, \bar{u}_i^{(k-1)\uparrow i}, \underline{u}_i^{(k-1)\downarrow i}) \\ i &= 1, \dots, N. \end{aligned} \quad (\text{A.5.7})$$

Clearly these two sequences are well defined. In the same manner as for the time-dependent problem we can prove the following results:

**Lemma A.5.2**

The two sequences  $\{\underline{u}^{(k)}\}$  and  $\{\bar{u}^{(k)}\}$  given by (A.5.7) posses the monotone property

$$\underline{u} \leq \underline{u}^{(k)} \leq \underline{u}^{(k+1)} \leq \bar{u}^{(k+1)} \leq \bar{u}^{(k)} \leq \bar{u} \quad (\text{A.5.8})$$

for every  $k$ , and  $\underline{u}_i^{(k)}$  and  $\bar{u}_i^{(k)}$  are coupled lower and upper solutions for each  $k$ .

**Lemma A.5.3**

The pointwise and componentwise limits

$$\lim_{k \rightarrow \infty} \underline{u}^{(k)}(t) = u_{\min}(t), \quad \lim_{k \rightarrow \infty} \bar{u}^{(k)}(t) = u_{\max}(t) \quad (\text{A.5.9})$$

exist and satisfy the relation

$$\underline{u} \leq \underline{u}^{(k)} \leq \underline{u}^{(k+1)} \leq u_{\min} \leq u_{\max} \leq \bar{u}^{(k+1)} \leq \bar{u}^{(k)} \leq \bar{u}. \quad (\text{A.5.10})$$

We can see that the limits  $u_{\min}$  and  $u_{\max}$  satisfy the relations

$$\begin{aligned} \underline{u}_{\min_i} &= h_i(t, u_{\min_i}, u_{\min}^{\uparrow i}, u_{\max}^{\downarrow i}) \\ \bar{u}_{\max_i} &= h_i(t, u_{\min_i}, u_{\max}^{\uparrow i}, u_{\min}^{\downarrow i}) \\ i &= 1, \dots, N. \end{aligned} \quad (\text{A.5.11})$$

It is clear that if  $h$  is quasimonotone nondecreasing in  $\langle \underline{u}, \bar{u} \rangle$ , then both  $u_{\min}$  and  $u_{\max}$  are solutions of (A.5.1). In this case  $u_{\min}$  and  $u_{\max}$  are called *minimal solution* and respectively *maximal solution* of (A.5.1).

Note as well, that for quasimonotone nondecreasing  $h$ , any solution of (A.5.1) is both a lower and an upper solution for (A.5.1).

**Theorem A.5.4**

Let  $(\underline{u}, \bar{u})$  be a pair of bounded coupled time-independent lower and upper solutions for (A.2.1). Assume (H1) in  $\langle \underline{u}, \bar{u} \rangle$ . Then there exists at least one solution  $u$  of (A.5.1) such that

$$\underline{u} \leq u \leq \bar{u}. \quad (\text{A.5.12})$$

**Theorem A.5.5**

Let the hypotheses of Theorem A.5.4 hold, and let  $u_{\min}$ , and  $u_{\max}$  be the limits in (A.5.9). Then any solution  $u$  of (A.5.1) in  $\langle \underline{u}, \bar{u} \rangle$  is necessarily in  $\langle u_{\min}, u_{\max} \rangle$ :

$$\underline{u} \leq u_{\min} \leq u \leq u_{\max} \leq \bar{u}. \quad (\text{A.5.13})$$

If  $h$  is quasimonotone nondecreasing in  $\langle \underline{u}, \bar{u} \rangle$ , then both  $u_{\min}$  and  $u_{\max}$  are solutions of (A.5.1).

When  $h_i$  in (A.2.1) are time independent, any coupled time-independent lower and upper solutions of (A.5.1) are also coupled lower and upper solutions for (A.2.1) provided that  $u_0 \in \langle \underline{u}, \bar{u} \rangle$ . When in addition,  $h$  is quasipositive nondecreasing, any equilibrium solution will be both a lower and an upper solution for (A.2.1).

With this observation and applying Theorem A.4.1 we have the following invariance property for (A.5.1):

**Theorem A.5.6**

Let the conditions in Theorem A.4.1 be satisfied and the functions  $h$ ,  $\underline{u}$  and  $\bar{u}$  independent of  $t$ . Then any solution  $u$  of (A.2.1) remains in  $\langle \underline{u}, \bar{u} \rangle$  for all time, provided it was true at  $t_0$ . If in addition  $h$  satisfies (H2), this solution is unique.

We can see from Theorem A.5.5 that if  $\underline{u}$  is nonnegative nontrivial lower solution then a solution of (A.5.1) stays positive for all time, provided it was true at  $t_0$ .

We next show the uniqueness of a positive solution in  $\langle \underline{u}, \bar{u} \rangle$  when  $h$  is quasimonotone nondecreasing satisfying the condition

$$\text{H3:} \quad h_i(\gamma u) \leq \gamma h_i(u), \quad \text{for } u \geq 0, \gamma > 1, \quad i = 1, \dots, N.$$

**Lemma A.5.7**

Let  $\underline{u}$  and  $\bar{u}$  be any lower and upper solutions of (A.5.1) such that  $0 \leq \underline{u} \leq b\bar{u}$ , for some  $b > 1$  and  $\underline{u}_i \not\equiv 0$  for all  $i$ . Let  $h$  be quasimonotone nondecreasing and satisfy (H2) in  $\langle \underline{u}, b\bar{u} \rangle$ . Assume (H3) holds and is not an identity for each  $i$ . Then  $\underline{u} \leq \bar{u}$ .

**Proof:** Let  $v_\gamma = \gamma \bar{u}$  for  $\gamma \in (1, b]$ .

From (H3) we get

$$\begin{aligned} h_i(v_\gamma) &= h_i(\gamma \bar{u}) \leq \gamma h_i(\bar{u}) \leq 0 \\ i &= 1, \dots, N. \end{aligned} \tag{A.5.14}$$

Thus  $v_\gamma$  is a positive upper solution for (A.5.1), since  $h$  is quasimonotone nondecreasing.

We next show that  $\underline{u} \leq v_\gamma$ , for every  $\gamma \in (1, b]$ . Suppose this were not true. Then let  $\underline{\gamma}$  be the smallest constant in  $(1, b]$  such that  $\underline{u} \leq v_\gamma$  for  $\underline{\gamma} \leq \gamma \leq b$ , that is

$$\underline{\gamma} = \inf \{ \gamma \mid \underline{u} \leq v_\gamma \} > 1.$$

Let  $\underline{v} = v_{\underline{\gamma}}$ . From (A.3.10) we get then

$$0 \geq h_i(\underline{v}_i, \underline{v}^{\uparrow i}) - h_i(\underline{u}_i, \underline{u}^{\uparrow i}) \geq -m_i(\underline{v}_i - \underline{u}_i).$$

Then either  $\underline{v}_i = \underline{u}_i$  or  $\underline{v}_i > \underline{u}_i$ . Assume  $\underline{v}_i = \underline{u}_i$  for some  $i = \underline{i}$ , then from  $\underline{v} \geq \underline{u}$  we get

$$0 \leq h_i(\underline{u}_i, \underline{u}^{\uparrow i}) \leq h_i(\underline{v}_i, \underline{v}^{\uparrow i}) \leq 0$$

when  $i = \underline{i}$ , which shows that  $\underline{v}_i$  satisfies the equation

$$h_i(\underline{v}_i, \underline{v}^{\uparrow i}) = 0$$

when  $i = \underline{i}$ . Since  $\underline{v}_i = \underline{\gamma} \bar{u}_i$  we get

$$0 = h_i(\underline{\gamma} \bar{u}) \leq \underline{\gamma} h_i(\bar{u})$$

and the last inequality is not an identity for  $i = \bar{i}$ . This is a contradiction with the fact that  $\bar{u}$  is an upper solution, and thus  $\underline{u} \leq \gamma \bar{u}$  for every  $\gamma \in (0, b]$ . Letting  $\gamma \rightarrow 1$  we get  $\underline{u} \leq \bar{u}$ .  $\square$

We can now prove the theorem:

**Theorem A.5.8**

Let  $\underline{u}$  and  $\bar{u}$  be coupled lower and upper solutions of (A.5.1) such that  $0 \leq \underline{u}$ , and  $\underline{u}_i \not\equiv 0$  for all  $i$ . Let  $h$  be quasimonotone nondecreasing and satisfy (H2) in  $\langle \underline{u}, \bar{u} \rangle$ . Assume (H3) holds and is not an identity for each  $i$ . Then (A.5.1) has exactly one positive solution  $u \in \langle \underline{u}, \bar{u} \rangle$ .

**Proof:** We have showed in Theorems A.5.4 and A.5.5 that problem (A.5.1) has a minimal solution  $u_{min}$  and a maximal solution  $u_{max}$  such that  $0 \leq u_{min} \leq u_{max}$  and any solution  $u \in \langle \underline{u}, \bar{u} \rangle$  satisfies  $u_{min} \leq u \leq u_{max}$ .

If we can show that  $u_{min} \geq u_{max}$  then the uniqueness of  $u$  follows.

Let  $b > 1$  sufficiently large such that  $u_{max} \leq b u_{min}$ . Define now the modified function  $\hat{h}(u)$  such that  $\hat{h}(u) = h(u)$  for  $u \in \langle \underline{u}, \bar{u} \rangle$  and  $\hat{h}(u)$  is quasimonotone nondecreasing and satisfies (A.3.10) in  $\langle \underline{u}, b u_{min} \rangle$ . Both  $u_{min}$  and  $u_{max}$  are solutions of (A.5.1) with  $h$  replaced by  $\hat{h}$ , since  $\underline{u} \leq u_{min} \leq u_{max} \leq b u_{min}$ .

Since  $\hat{h}$  is quasimonotone nondecreasing, every solution of the modified problem is a lower solution as well as an upper solution and we may consider  $u_{min}$  as an upper solution and  $u_{max}$  as a lower solution. Since  $0 \leq u_{max} \leq b u_{min}$ , it follows from Lemma A.5.7 that  $u_{max} \leq u_{min}$  and thus  $u_{max} = u_{min}$ . The uniqueness of the positive solution of (A.5.1) in  $\langle \underline{u}, \bar{u} \rangle$  follows.  $\square$

## A.6 Stability and asymptotic behavior of solutions

The existence-comparison theorems in the previous sections can be used to study the asymptotic behavior of the time dependent solution and the stability or instability of a steady state solution.

Consider the system (A.2.1) and the corresponding steady-state system (A.5.1) where  $h$  is independent of  $t$ . Assume  $h$  is quasimonotone and that there exist coupled lower and upper solutions  $(\underline{u}_s, \bar{u}_s)$  to the system A.5.1. Then by Theorem A.5.6, for any  $u_0 \in \langle \underline{u}_s, \bar{u}_s \rangle$ , problem (A.2.1) has a solution in  $\langle \underline{u}_s, \bar{u}_s \rangle$ , for all  $t \geq t_0$ .

Suppose  $h$  is nondecreasing in  $\langle \underline{u}_s, \bar{u}_s \rangle$ . According to the paragraph following Lemma A.5.3, problem (A.5.1) has a minimal solution  $u_{s,min}$  and a maximal solution  $u_{s,max}$  in  $\langle \underline{u}_s, \bar{u}_s \rangle$ .

To study the asymptotic behavior of the time dependent solution of (A.2.1), we consider two solutions of (A.2.1),  $\underline{u}$  and  $\bar{u}$  starting with the initial values  $u_0 = \underline{u}_s$  and  $u_0 = \bar{u}_s$ , respectively. In order to be able to consider the two solutions  $\underline{u}$  and  $\bar{u}$ , we need them to be unique, thus we assume that function  $h$  satisfies the Lipschitz condition (H2).

**Definition A.6.1** A steady state solution  $u_s$  of (A.5.1) is said to be *stable* if given any  $\epsilon > 0$ , there exists  $\delta > 0$  such that

$$|u(t) - u_s(t)| = \sum_{i=1}^N |u_i(t) - u_{s_i}(t)| < \epsilon,$$

for all  $t > t_0$ , whenever

$$|u_0 - u_{s_0}| = \sum_{i=1}^N |u_{0,i} - u_{s_{0,i}}| < \delta,$$

where  $u$  is the solution of (A.2.1). If in addition,

$$\lim_{t \rightarrow \infty} |u(t) - u_s(t)| = 0,$$

then  $u_s$  is said to be *asymptotically stable*. The solution  $u_s$  is said to be *unstable* if it is not stable.

For an asymptotically stable steady state solution  $u_s$ , the set of initial values  $u_0$  for which the corresponding solution  $u$  of (A.2.1) converges to  $u_s$  is called the *domain of attraction* of  $u_s$ . In particular, if the solution of (A.2.1) converges to  $u_s$  for any  $u_0$ , then  $u_s$  is said to be *globally asymptotically stable*.

As an application to the positivity lemma we have:

**Lemma A.6.2**

Consider  $f : \mathbf{R} \times D \rightarrow \mathbf{R}^N$ ,  $D \subset \mathbf{R}^N$ , and  $f$  linear:

$$f_i(t, u) = \sum_{j=1}^N c_{ij}(t) u_j,$$

for  $i = 1, \dots, N$ , with  $c_{ij}$  continuous and  $c_{ij} \geq 0$  for all  $j \neq i$ . Then the unique solution of the linear system

$$\begin{aligned} u_i'(t) &= f_i(t, u) \\ u_i(t_0) &\geq 0 \end{aligned}$$

stays nonnegative for all time.

This is useful in obtaining the following monotonicity properties for  $\underline{u}$  and  $\bar{u}$ .

**Lemma A.6.3**

Let  $h$  quasimonotone nondecreasing in  $\langle \underline{u}_s, \bar{u}_s \rangle$ , and let  $\underline{U}$  and  $\bar{U}$  be the solutions of (A.2.1) with  $u_0 = \underline{u}_s$  and  $u_0 = \bar{u}_s$ , respectively.

Then

$$\underline{U}' \geq 0, \quad \bar{U}' \leq 0, \quad \text{and} \quad \underline{U} \leq \bar{U}. \quad (\text{A.6.1})$$

The limits

$$\lim_{t \rightarrow \infty} \underline{U}(t) = \underline{U}_s(t), \quad \lim_{t \rightarrow \infty} \bar{U}(t) = \bar{U}_s(t) \quad (\text{A.6.2})$$

exist and  $\underline{U}_s \leq \bar{U}_s$ .

**Proof:** Let  $\delta > 0$  and let  $\omega(t) = \bar{U}(t) - \bar{U}(t + \delta)$ . We have  $\omega(t_0) = \bar{u}_s - \bar{U}(\delta) \geq 0$  and, using the mean value theorem

$$\begin{aligned} \omega_i'(t) &= h_i(\bar{U}_i(t), \bar{U}(t)^{\uparrow i}) - h_i(\bar{U}_i(t + \delta), \bar{U}(t + \delta)^{\uparrow i}) = \\ &= \sum_{j=1}^N \left( \frac{\partial h_i}{\partial u_j}(\xi_j) \right) \omega_j \end{aligned}$$

where  $\xi_j$  is some intermediate value between  $\bar{U}(t)$  and  $\bar{U}(t + \delta)$ .

We had that  $h$  is quasimonotone nondecreasing, hence

$$\frac{\partial h_i}{\partial u_j} \geq 0$$

for all  $j \neq i$ . Thus  $\bar{U}_i(t + \delta) \leq \bar{U}_i(t)$  and  $\bar{U}' \leq 0$ . Similarly we get  $\underline{U}' \geq 0$ .

Now let  $\omega = \bar{U} - \underline{U}$ . We have  $\omega(t_0) = \bar{u}_s - \underline{u}_s \geq 0$  and

$$\begin{aligned} \omega_i' &= h_i(\bar{U}_i, \bar{U}^{\uparrow i}) - h_i(\underline{U}_i, \underline{U}^{\uparrow i}) = \\ &= \sum_{j=1}^N \left( \frac{\partial h_i}{\partial u_j}(\xi_j) \right) \omega_j \geq 0, \end{aligned}$$

where  $\xi_j$  is some intermediate value between  $\bar{U}$  and  $\underline{U}$ . Thus  $\underline{U} \leq \bar{U}$ . It follows that the limits in (A.6.2) exist and  $\underline{U}_s \leq \bar{U}_s$ .  $\square$

We can now prove:

**Theorem A.6.4**

Let  $\underline{u}_s$  and  $\bar{u}_s$  be coupled lower and upper solutions of (A.5.1) and let  $h$  a quasipositive nondecreasing  $\mathbf{C}^1$  function in  $\langle \underline{u}_s, \bar{u}_s \rangle$ . Then the solutions  $\underline{U}$  and  $\bar{U}$  of (A.2.1) converge monotonically to the respective solutions  $\underline{U}_s$  and  $\bar{U}_s$  of (A.5.1) with  $\underline{U}_s \leq \bar{U}_s$ . For any solution  $u_s \in \langle \underline{u}_s, \bar{u}_s \rangle$  we have  $\underline{U}_s \leq u_s \leq \bar{U}_s$ .

**Proof:** Let  $\omega_i$  be the equilibrium solution ( $\omega_i' = 0$ ) of the linear system

$$\begin{aligned}\omega_i' + c_i \omega_i &= c_i \bar{U}_{s_i} + h_i(\bar{U}_s) \\ i &= 1, \dots, N,\end{aligned}$$

where  $c_i > 0$  is a constant. Let  $W_i = \bar{U}_i - \omega_i$ . Then  $W_i$  satisfies

$$\begin{aligned}W_i' + c_i W_i &= c_i(\bar{U}_i - \bar{U}_{s_i}) + h_i(\bar{U}) - h_i(\bar{U}_s) \\ i &= 1, \dots, N.\end{aligned}$$

From (A.6.2) we have that  $c_i(\bar{U}_i - \bar{U}_{s_i}) + h_i(\bar{U}) - h_i(\bar{U}_s) \rightarrow 0$  as  $t \rightarrow \infty$  and thus  $W_i \rightarrow 0$  as  $t \rightarrow \infty$ , which shows that  $\bar{U}_s = \omega$ , and  $\bar{U}_s$  is a solution of (A.5.1). In a similar way we can show that  $\bar{U}_s$  is as well a solution of (A.5.1).

Suppose  $u_s$  is any other solution of (A.5.1) in  $\langle \underline{u}_s, \bar{u}_s \rangle$ . Since  $h$  is quasimonotone nondecreasing in  $\langle \underline{u}_s, \bar{u}_s \rangle$ , the two pairs  $(\underline{u}_s, u_s)$  and  $(u_s, \bar{u}_s)$  are both pairs of coupled time-independent lower and upper solutions. Since  $\underline{U}_s \leq \bar{U}_s$  with respect to any pair of coupled time-independent lower and upper solutions, we get  $\underline{U}_s \leq u_s \leq \bar{U}_s$ .  $\square$

From Theorem A.6.4 we get that the solutions  $\underline{U}_s$  and  $\bar{U}_s$  coincide with the minimal and, respectively, the maximal solutions  $u_{s,min}$  and  $u_{s,max}$  of (A.5.1). Hence the problem (A.5.1) has a unique solution in  $\langle \underline{u}_s, \bar{u}_s \rangle$  if and only if  $\underline{U}_s = \bar{U}_s$ :

### Theorem A.6.5

Let the hypothesis of Theorem A.6.4 hold. If the solution  $u_s$  of (A.5.1) is unique in  $\langle \underline{u}_s, \bar{u}_s \rangle$ , then for any  $u_0 \in \langle \underline{u}_s, \bar{u}_s \rangle$  the solution  $u$  of (A.2.1) converges to  $u_s$  as  $t \rightarrow \infty$ .

**Proof:** Let  $\omega_i = \bar{U}_i - u_i$ . Then  $\omega(t_0) = \bar{u}_s - u_0 \geq 0$  and

$$\begin{aligned}\omega_i' &= h_i(\bar{U}_i, \bar{U}^{\uparrow i}) - h_i(u_i, u^{\uparrow i}) = \\ &= \sum_{j=1}^N \left( \frac{\partial h_i}{\partial u_j}(\xi_j) \right) \omega_j \geq 0,\end{aligned}$$

where  $\xi_j$  is some intermediate value between  $\bar{U}$  and  $u$ . Thus  $\omega_i \geq 0$  and  $u \leq \bar{U}$ . A similar argument gives  $u \geq \underline{U}$ , and we have

$$\underline{U} \leq u \leq \bar{U}.$$

When the solution  $u_s$  of (A.5.1) is unique in  $\langle \underline{u}_s, \bar{u}_s \rangle$ , both time-dependent solutions  $\underline{U}$  and  $\bar{U}$  of (A.2.1) converge to  $u_s$  as  $t \rightarrow \infty$ . Hence  $u$  converges to  $u_s$  as  $t \rightarrow \infty$ .  $\square$



## A.7 Notes and discussions. Bibliographical comments

In the present appendix, the method of lower and upper solutions and its associated monotone iteration, were introduced for the time dependent problem as well as the steady-state problem, both with quasimonotone reaction terms. We use the results in this appendix to study the gradostat model, which fulfills the quasimonotonicity hypothesis. Since we are presenting the analysis for a system describing some dynamics of biological species concentration, we introduced the positivity hypothesis in (H1) which ensured the nonnegativity of the solutions.

With the aid of the monotone iterations we were able to obtain existence comparison results for both time dependent and steady state problems. When the reaction functions fulfilled an additional condition, namely (H2), we were also able to show uniqueness of the time dependent solution. Uniqueness for the steady state solution though, we could prove only for the case of quasimonotone nondecreasing reaction terms, with the additional condition (H3). In this case, the unique steady state solution proved to be asymptotically stable in the sector where uniqueness could be shown.

For the gradostat model, the quasimonotone nondecreasing hypothesis is fulfilled only in the case of no competition. Thus we are left with some open problems, which, unfortunately, is also the case for the gradostat model.

The theory presented here follows mainly the one from [Pao3] and [Kir] for parabolic and elliptic boundary value problems. In [Pao3] the definition for lower and upper solutions are given in the form (A.2.5) and (A.2.6) and, respectively, (A.5.5) and (A.5.6). The notations for the split form for the different vectors, follows [Kir]. In [Kir] though, the monotone schemes are obtained from slightly different iterative processes and the condition on  $h_i$  that ensures uniqueness is slightly relaxed.

The method of lower and upper solutions and the construction of monotone sequences for proving existence of minimal and maximal solutions for steady state problems was used as early as 1920s by Müller ([Mül]) for ODEs and, a little later, by Nagumo ([Nag1], [Nag2]), for both ODEs and PDEs. For a while, the basic idea was constructing monotone sequences starting from some initial iterations, but without the notion of lower and upper solutions. In the 1970s, Amman ([Amm]) and Sattinger ([Sat]) formalized the properties of lower and upper solutions, constructing monotone sequences for elliptic boundary value problems and, respectively, parabolic value problems. Their results were extended by Pao ([Pao1]) to parabolic boundary value problems with nonlinear boundary conditions.

The book by Pao contains a huge reference list with quite detailed bibliographical comments. The same book presents applications of the method to different problems from bi-

ology (and not only), for example to some prey-predator models, some epidemic problems with diffusion etc.

The results on the existence, uniqueness, and/or positivity of solutions for systems of ordinary differential equations are standard, and can be found in various books ([Har2] , [HS2], [Ama]).

# B

## Bifurcation from Simple Eigenvalues

In this Appendix we list two theorems we have used for our bifurcation analysis in chapters 2 and 3.

### B.1 M. Crandall and P. Rabinowitz ([CR1], [CR2])

Let  $X$  and  $Y$  be Banach spaces and let  $F : \mathbf{R} \times X \rightarrow Y$  be twice continuously Frechet differentiable. Consider  $F(\lambda, x) = 0$  the equilibrium equation of

$$\frac{dx}{dt} = F(\lambda, x). \quad (\text{B.1.1})$$

Let  $F_x$ ,  $F_\lambda$  and  $F_{\lambda x}$  denote the derivatives of  $F$  with respect to  $x$  and  $\lambda$ . With  $N(A)$  and  $R(A)$  we denote the null space and respectively the range of a linear mapping  $A$ .

**Definition B.1.1** Let  $T$  and  $K \in B(X, Y)$  the set of bounded linear maps from  $X$  to  $Y$ . Then  $\mu \in \mathbf{R}$  is a  $K$ -simple eigenvalue of  $T$  if

$$\dim N(T - \mu K) = \text{codim } R(T - \mu K) = 1,$$

and, if  $N(T - \mu K) = \text{span}\{x_0\}$ ,

$$Kx_0 \notin R(T - \mu K).$$

Suppose that  $F(\bar{\lambda}, 0) = 0$  and that  $F_x(\bar{\lambda}, 0)$  is an isomorphism of  $X$  into  $Y$ . Then we can describe the solutions of (B.1.1) near  $(\bar{\lambda}, 0)$  where 0 is a simple eigenvalue of  $F_x(\bar{\lambda}, 0)$ . In fact we can continue the curve of solutions uniquely and smoothly through  $(\bar{\lambda}, 0)$ . Moreover, [CR2] studies the existence of secondary bifurcations, and in [CR2] it is shown that the shape of the curve and the eigenvalues of  $F_x$  near zero along the curve are related.

**Theorem B.1.2**

Let  $F(\lambda, 0) = 0$  for all  $\lambda \in \mathcal{T}$  with  $\bar{\lambda} \in \mathcal{T}$ . Let  $N(F_x(\bar{\lambda}, 0)) = \text{span}\{x_0\}$  be one dimensional and  $\text{codim } R(F_x(\bar{\lambda}, 0)) = 1$ . Let  $F_{\lambda x}(\bar{\lambda}, 0)x_0 \notin R(F_x(\bar{\lambda}, 0))$ . If  $Z$  is a complement of  $\text{span}\{x_0\}$  in  $X$ , then the solutions of  $F(\lambda, x) = 0$  near  $(\bar{\lambda}, 0)$  form a curve  $(\lambda(s), x(s)) = (\bar{\lambda} + \tau(s), sx_0 + z(s))$ , where  $s \rightarrow (\tau(s), z(s)) \in \mathbf{R} \times Z$  is a continuously differentiable function near  $s = 0$  and  $\tau(0) = \tau'(0) = 0, z(0) = z'(0) = 0$ . Moreover, if  $F$  is  $k$ -times continuously differentiable, so are  $\tau(s)$  and  $z(s)$ .

**B.2 E. N. Dancer ([Dan])**

Assume that the non-linear mapping  $A : K \times [0, \infty) \rightarrow E$  with  $E$  a Banach space and  $K$  a cone in  $E$ , is *positive*, i.e.  $A(K \times [0, \infty)) \subseteq K$ , that it is  *$K$ -completely continuous*, i.e. it is continuous and maps bounded subsets of  $K \times [0, \infty)$  to precompact sets of  $E$ . Assume  $A(x, 0) = 0$  for  $x \in K$ ,  $A(0, \lambda) = 0$  for  $\lambda \in [0, \infty)$  and  $A = \lambda B + F$ , where  $B : E_K \rightarrow E$  is a linear operator on  $E_K = \{x - y : x, y \in K\}$ , for each  $\nu \geq 0$ ,  $F : K \times [0, \infty) \rightarrow E$  satisfies  $\|F(x, \lambda)\| = o(\|x\|)$  as  $\|x\| \rightarrow 0$  (and  $x \in K$ ) uniformly in  $\lambda$  in some neighborhood of  $\nu$ .

Define

$$r_K := \lim_{n \rightarrow \infty} (\|B^n\|_K)^{1/n}.$$

Then if  $B$  is a  $K$ -completely continuous positive linear operator on  $E_K$  and  $r_K(B) > 0$ , then there exists a  $x \in K$  such that  $\|x\| = 1$  and  $Bx = r_K(B)x$ .

**Theorem B.2.1**

If  $A$  satisfies the assumptions above and  $r_K(B) > 0$ , then there exists an unbounded connected subset  $T$  of

$$\mathcal{D}_K(A) := \{(x, \lambda) \in K \times [0, \infty) : x = A(x, \lambda), x \neq 0\} \cup (\{0\} \times c_K(B)),$$

with

$$c_K(B) := \{\lambda \in [0, \infty) : \text{there exists a } x \in K \text{ with } \|x\| = 1 \text{ and } x = \lambda Bx\},$$

such that  $(0, r_K(B)^{-1}) \in T$ .

# C

## Further Tools

In this Appendix we collect a number of results that we have used or mentioned throughout the previous chapters involving mainly matrices and inequalities. We follow the presentation in [SW].

### C.1 Quasipositive matrices

For the matrices that have appeared throughout this work the basic properties were irreducibility and quasipositivity. A general reference on matrices is [LT] or [BP] for nonnegative matrices.

- The *stability modulus* of a matrix  $A$ , denoted by  $s(A)$ , is

$$s(A) = \max\{\operatorname{Re}\lambda \mid \lambda \in \sigma(A)\}.$$

- The *spectral radius* of a matrix, denoted by  $\mu(A)$ , is

$$\mu(A) = \max\{|\lambda| \mid \lambda \in \sigma(A)\}.$$

**Theorem C.1.1** (Perron-Frobenius)

*If the  $n \times n$  matrix  $A$  is nonnegative, then*

- (i)  $\mu(A)$  is an eigenvalue; and
- (ii) there is a nonnegative eigenvector  $v$  associated with  $\mu(A)$ .

**Theorem C.1.2**

If the  $n \times n$  matrix  $A$  is irreducible and has nonnegative off-diagonal elements (quasi-positive), then:

- (i)  $s$  is an eigenvalue with algebraic multiplicity 1;
- (ii)  $\operatorname{Re}(\lambda) < s(A)$  for  $\lambda \in \sigma(A)$ ,  $\lambda \neq s(A)$ ;
- (iii) there is a positive eigenvector  $v$  associated with  $s$ ;
- (iv) any nonnegative eigenvector of  $A$  is a positive multiple of  $v$ ;
- (iiv) if  $B$  is a  $n \times n$  matrix s.t.  $B \geq A$  and  $B \neq A$ , then  $s(B) > s(A)$ .

**Theorem C.1.3**

Let  $A$  quasi-positive and irreducible. Then

- (i) if  $s(A) < 0$  then  $-A^{-1} > 0$ ; and
- (ii) if  $s(A) > 0$  and  $r > 0$  then  $Ax + r = 0$  has no solution  $x$ ,  $x > 0$ .

**Lemma C.1.4**

Let  $A = (a_{ij})$  be quasi-positive and irreducible. Suppose that

$$\sum_{j=1}^n a_{ij} \leq 0$$

for each  $i$  and strict inequality holds for some  $i$ . Then  $s(A) < 0$  and  $-A^{-1} > 0$ .

## C.2 Differential inequalities

The main results in the present section as well as the following one can be found in [Kam], [Mül], [Smi1] and [Smi2].

- We write  $(b, d) \leq_k (a, c)$  if  $b \leq a$  and  $d \geq c$ ; if both inequalities are strict, we write  $(b, d) <_k (a, c)$ .
- Let  $f : \mathbf{R} \times D \rightarrow \mathbf{R}^n$ , where  $D$  is an open subset of  $\mathbf{R}^n$ , be a vector valued function  $f = (f_1, \dots, f_n)$ . The function  $f$  is of type  $K$  in  $D$  if, for each  $i$  and all  $t$ ,  $f_i(t, a) \leq f_i(t, b)$  for any two points  $a$  and  $b$  in  $D$  satisfying  $a \leq b$  and  $a_i = b_i$ .

**Theorem C.2.1**

Let  $f$  be continuous on  $\mathbf{R} \times D$  and of type  $K$ . Let  $x(t)$  be a solution of

$$x' = f(t, x), \quad (\text{C.2.1})$$

defined on  $[a, b]$ . If  $z(t)$  is a continuous function on  $[a, b]$  satisfying

$$z' \leq f(t, z) \quad (\text{C.2.2})$$

on  $(a, b)$  with  $z(a) \leq x(a)$ , then

$$z(t) \leq x(t)$$

for all  $t$  in  $[a, b]$ . The affirmation is valid also if both inequalities are reversed.

We call a domain  $D$   $p$ -convex if  $tx + (1 - t)y \in D$  for all  $t \in [0, 1]$  and  $x, y \in D$  with  $x \leq y$ .

**Corollary C.2.2**

Let  $f(t, x)$  and  $(\partial f / \partial x)(t, x)$  be continuous on  $\mathbf{R} \times D$ , where  $D$  is a  $p$ -convex subset of  $\mathbf{R}^n$ . Let

$$\frac{\partial f_i}{\partial x_j}(t, x) \geq 0, \quad i \neq j, \quad (t, x) \in D \quad (\text{C.2.3})$$

hold. If  $y(t)$  and  $z(t)$  are two solutions of (C.2.1) defined for  $t \geq t_0$  satisfying  $y(t_0) \leq z(t_0)$ , then  $y(t) \leq z(t)$  for all  $t \geq t_0$ .

- If (C.2.3) holds, (C.2.1) is called *cooperative*. If the reversed inequalities hold, (C.2.1) is called *competitive*.
- Take the system

$$\begin{aligned} x' &= F(t, x, y), \\ y' &= G(t, x, y) \end{aligned} \quad (\text{C.2.4})$$

where  $x, y \in \mathbf{R}^n$ ,  $H = (F, G) : \mathbf{R} \times D \rightarrow \mathbf{R}^{2n}$ , and  $D \subset \mathbf{R}^{2n}$  is open. The function  $H$  is said to be of *generalized type  $K$*  in  $D$  if

- (a) for each  $i$ ,  $1 \leq i \leq n$ ,  $F_i(t, a, c) \geq F_i(t, b, d)$  whenever  $(b, d) <_k (a, c)$ ,  $t \in \mathbf{R}$  and  $a_i = b_i$ ; and
- (b) for each  $j$ ,  $n + 1 \leq j \leq 2n$ ,  $G_j(t, a, c) \leq G_j(t, b, d)$  whenever  $(b, d) <_k (a, c)$ ,  $t \in \mathbf{R}$  and  $c_j = d_j$ .

**Theorem C.2.3**

Let  $H$  be continuous on  $\mathbf{R} \times D$  and suppose that  $H$  is of generalized type  $K$  in  $D$ . Let  $(x(t), y(t))$  be a solution of (C.2.1) on a interval  $[a, b]$ . If  $(u(t), v(t))$  is continuous on  $[a, b]$  and satisfies

$$\begin{aligned} u' &\leq F(t, u, v), \\ v' &\geq G(t, u, v), \end{aligned}$$

on  $(a, b)$  and if  $(u(a), v(a)) \leq_k (x(a), y(a))$ , then  $(u(t), v(t)) \leq_k (x(t), y(t))$  for all  $t \in [a, b]$ .

**Corollary C.2.4**

Let  $H$  be continuous and have a continuous derivatives with respect to  $(x, y)$  in  $\mathbf{R} \times D$ , where  $D$  is a convex subset of  $\mathbf{R}^{2n}$ . Assume that:

$$\begin{aligned} \frac{\partial F_i}{\partial x_j} &\geq 0, \quad \frac{\partial G_i}{\partial y_j} \geq 0, \quad i \neq j; \\ \frac{\partial F_i}{\partial y_j} &\leq 0, \quad \frac{\partial G_i}{\partial x_j} \leq 0, \quad \text{all } i, j. \end{aligned} \tag{C.2.5}$$

Let  $(x(t), y(t))$  and  $(u(t), v(t))$  be solutions of (C.2.4) defined for all  $t \geq t_0$  satisfying  $(x(t_0), y(t_0)) \leq_k (u(t_0), v(t_0))$ . Then  $(x(t), y(t)) \leq_k (u(t), v(t))$  for all  $t \geq t_0$ .

**Proposition C.2.5**

Suppose that  $f$  in (C.2.1) has the property that solutions of initial value problems  $x(t_0) = x_0 \geq 0$  are unique and, for all  $i$ ,  $f_i(t, x) \geq 0$  whenever  $x \geq 0$  satisfies  $x_i = 0$ . Then  $x(t) \geq 0$  for all  $t \geq t_0$  for which it is defined, provided that  $x(t_0) \geq 0$ .

## C.3 Monotone systems

Let  $\pi(x, t)$  denote the dynamical system generated by the autonomous system of differential equations

$$x' = f(x), \tag{C.3.1}$$

where  $f$  is continuously differentiable on a subset  $D \subset \mathbf{R}$ .

- A dynamical system will be called a *monotone dynamical system* with respect to  $\leq_k$  if  $\pi(x, t) \leq_k \pi(y, t)$  for all  $t \geq 0$  whenever  $x \leq_k y$ .
- $\pi$  is called *strongly monotone* with respect to  $\leq_k$  if  $x \leq_k y$  and  $x \neq y$  implies that  $\pi(x, t) <_k \pi(y, t)$ .



We assume  $D$  convex.

**Theorem C.3.1 (1)** *If (A.3.1) is cooperative in  $D$ , then  $\pi$  is a monotone dynamical system with respect to  $\leq$  in  $D$ .*

**(2)** *If (A.3.1) is cooperative and irreducible in  $D$ , then  $\pi$  is a strongly monotone dynamical system with respect to  $\leq$  in  $D$ .*

**(3)** *If (A.3.1) has the form (C.2.4) where  $F$  and  $G$  are independent of  $t$  and (C.2.5) holds in  $D$ , then  $\pi$  is a monotone dynamical system with respect to  $\leq_k$  in  $D$ .*

**(4)** *If, in addition, the Jacobian matrix is irreducible at every point of  $D$ , then  $\pi$  is a strongly monotone dynamical system with respect to  $\leq_k$  in  $D$ .*

**Theorem C.3.2**

*Let  $\gamma^+(x)$  be an orbit of the monotone dynamical system (A.3.1) which has compact closure in  $D$ . Then either of the following conditions is sufficient for  $\omega(x)$  to be a rest point:*

**(a)**  $0 \leq_k f(x) \leq_k 0$ ;

**(b)**  $x <_k \pi(x, T) <_k x$  for some  $T > 0$ .



# D

## Numerical tools

In this work we have two types of numerical examples, where we plot either the solution of (1.1.2) or (1.1.4), or bifurcation diagrams.

For the solution plots we have used the LSODE package, implemented for the gradostat system by Christoph Kindl. LSODE is a package of sub-routines for the numerical solution of the initial value problem for systems of first order ordinary differential equations. The package is suitable for either stiff or nonstiff systems. LSODE contains two variable-order, variable-step (with interpolatory step-changing) integration methods. The first is the implicit Adams or nonstiff method, of orders one through twelve. The second is the backward differentiation or stiff method (or BDF method, or Gear's method), of orders one through five.

For the bifurcation diagrams we have used the package AUTO, version 2000. For a full description of AUTO, see [DK], and Keller ([Kel1] and [Kel2]) for a description of the numerical methods. AUTO2000 can be downloaded from <http://www.ama.caltech.edu/redrod/auto2000/distribution/>.

We shortly present here Keller's continuation method and the implementation into AUTO, following [DKK].

### D.1 Continuation of solutions

We take a look at equations of the form

$$u'(t) = f(u, \lambda), \quad f, u \in \mathbf{R}^n, \quad \lambda \in \mathbf{R}. \quad (\text{D.1.1})$$

A first step in the bifurcation analysis consists in determining the stationary solution branches  $(u(s), \lambda(s))$  for

$$f(u, \lambda) = 0, \quad (\text{D.1.2})$$

with  $s$  denoting some parametrization, for  $f$  sufficiently smooth. Denote with  $x = (u, \lambda)$ , and  $x(s)$  a solution branch of  $f(x) = 0$ .

A solution  $x_0 = x(s_0)$  is called regular if  $f'_x = f'_x(x_0)$  has rank  $n$ . A segment of a solution branch is regular if  $x(s)$  is regular along the segment. We have that a unique branch of solutions passes through a regular solution.

A solution  $x_0 = x(s_0)$  is called a simple singular point if  $f'_x = f'_x(x_0)$  has rank  $n - 1$ , and in terms of the parameter formulation,  $(u_0, \lambda_0)$  is a simple singular point iff either one of the following holds:

- (1)  $\dim(N(f'_u)) = 1, \quad f'_\lambda \in R(f'_u),$
- (2)  $\dim(N(f'_u)) = 2, \quad f'_\lambda \notin R(f'_u).$

We consider  $\lambda$  as the continuation parameter. Suppose we have a solution  $(u_0, \lambda_0)$  of (D.1.1) and the direction vector  $\dot{u}_0$ . To find the solution  $u_1$  at a value of  $\lambda = \lambda_1 = \lambda_0 + \Delta\lambda$ , we use Newton's method.

From differentiating  $f(u(s), \lambda(s)) = 0$  we have  $f'_u \dot{u}(s) + f'_\lambda \dot{\lambda}(s) = 0$ . We can choose a parametrization such that

$$\|\dot{u}\|^2 + \dot{\lambda}^2 = 1$$

called the arclength parametrization, with the approximate formulation

$$f(u_1, \lambda_1) = 0, \quad (u_1 - u_0)^* \dot{u}_0 + (\lambda_1 - \lambda_0) \dot{\lambda}_0 - \Delta s = 0,$$

called the pseudoarclength continuation. Newton's method is now

$$\begin{pmatrix} f'_u & f'_\lambda \\ \dot{u}_0^* & \dot{\lambda}_0 \end{pmatrix} \begin{pmatrix} \Delta u_1^{(k)} \\ \Delta \lambda_1^{(k)} \end{pmatrix} = - \begin{pmatrix} f(u_1^{(k)}, \lambda_1^{(k)}) \\ (u_1^{(k)} - u_0)^* \dot{u}_0 + (\lambda_1^{(k)} - \lambda_0) \dot{\lambda}_0 - \Delta s \end{pmatrix}.$$

After convergence of the Newton iterations, the new direction  $\dot{u}_1$  can be obtained with only one extra back substitution

$$f'_u \dot{u}_1 + f'_\lambda \dot{\lambda} = 0, \quad \dot{u}_0^* \dot{u}_1 + \dot{\lambda}_0 \dot{\lambda}_1 = 1.$$

The orientation of the branch is preserved if  $\Delta s$  is small enough. We then rescale the direction vector so that  $\|\dot{u}_1\|^2 + \dot{\lambda}_1^2 = 1$ .

In AUTO it is assumed that a regular solution  $(u_0, \lambda_0)$  is known for some particular value  $\lambda_0$ . For the gradostat system we always begin with the zero steady state for zero values for the continuation parameter. It can be easily shown that the direction  $(\dot{u}_0, \dot{\lambda}_0)$  of the branch at a regular starting point coincides with the normalized null vector of the  $n \times n + 1$  dimensional matrix  $(f_u(u_0, \lambda_0) | f_\lambda(u_0, \lambda_0))$ . From the starting point the branch is traced out in a stepwise manner using pseudoarclength continuation. Assuming  $(u_{j-1}, \lambda_{j-1})$  and  $(\dot{u}_{j-1}, \dot{\lambda}_{j-1})$  have been computed, the next solution  $(u_j, \lambda_j)$  is determined by

$$f(u_j, \lambda_j) = 0, \quad (u_j - u_{j-1})^* \dot{u}_{j-1} + (\lambda_j - \lambda_{j-1}) \dot{\lambda}_{j-1} - \Delta s = 0,$$

with  $\Delta s$  the step size along the branch. The direction vector  $(\dot{u}_{j-1}, \dot{\lambda}_{j-1})$  can be computed as mentioned above followed by a rescaling so that  $\dot{u}_{j-1}^* \dot{u}_{j-1} + \dot{\lambda}_{j-1}^2 = 1$ . We can choose the step size  $\Delta s$  to be fixed or adaptive: if Newton's method converges rapidly, then the step size is increased, and if it converges slowly or fails to converge, the step size is halved. If a selected maximum step size is reached, then  $\Delta s$  will not exceed that value, and if the selected minimum step size is reached, nonconvergence is signaled. Convergence criteria can also be selected, as convergence occurs when

$$\frac{|\Delta \lambda|}{1 + |\lambda|} < \epsilon_\lambda \quad \text{and} \quad \frac{\|\Delta u\|_\infty}{1 + \|u\|_\infty} < \epsilon_u,$$

with  $\epsilon_u$  the convergence criterion for the solution components, and  $\epsilon_\lambda$  the convergence criterion for the parameter.

## D.2 Detection of bifurcation points and branch switching

Let  $F(x, s) = \begin{pmatrix} f(x) \\ (x - x_0)^* \dot{x}_0 - s \end{pmatrix}$  with  $x_0$  a singular point. Then  $F_x^0 = F_x(x_0, s_0) = F_x(x_0) = \begin{pmatrix} f_x^0 \\ \dot{x}_0^* \end{pmatrix}$ . Assume  $N(f_x^0) = \text{span}\{\phi_1, \phi_2\}$ . We choose  $\phi_0 = \dot{x}_0$  for the first null vector of  $f_x^0$ , and the second null vector  $\phi_2$  such that  $\phi_2^* \phi_1 = 0$ . Thus  $F_x^0 = \begin{pmatrix} f_x^0 \\ \phi_1^* \end{pmatrix}$ . We have

### Theorem D.2.1

Let  $x(s)$  be a smooth solution branch of  $F(x, s) = 0$  where  $F : \mathbf{R}^{n+1} \times \mathbf{R} \rightarrow \mathbf{R}^{n+1}$  is  $\mathbf{C}^1$ . Assume  $\det F_x(x(s), s)$  changes sign at  $s = s_0$ . Then  $x(s_0)$  is a bifurcation point.

For a proof, see [Kel2].

In AUTO, the determinant of  $F_x$  is monitored along  $x(s) = (u(s), \lambda(s))$  and points where the determinant changes sign are located by the secant iteration scheme:

$$s^{(k+1)} = s^{(k)} - \frac{s^{(k)} - s^{(k-1)}}{\det F_x(s^{(k)}) - \det F_x(s^{(k-1)})} \det F_x(s^{(k)}).$$

The relative arclength convergence for detection of bifurcation points can also be selected.

After the computation of a given branch is completed, branch switching at potential bifurcation points is attempted, by the orthogonal direction method, as  $\phi_2 \perp \phi_1$ , with

$$\begin{aligned} f(x_1) &= 0, \\ (x_1 - x_0)^* \phi_2 - \Delta s &= 0. \end{aligned}$$

The computation of the basic branch, as well as of a bifurcating branch is stopped if  $\lambda$  or  $u$  reach some preset limits, if a specified number of steps is reached or if the procedure doesn't converge.

### D.3 Operating diagrams

After the bifurcation points are detected they can be used as starting points for tracing bifurcation curves in a two-parameter diagram by changing a second parameter simultaneously.

Unfortunately AUTO does not do two-parameter continuation of transcritical bifurcation points. What one can do however is to consider the second parameter as a variable and add one more equation to the system: since at a transcritical bifurcation point we have a zero eigenvalue for the Jacobian, the transcritical bifurcation curve can be traced by doing one-parameter continuation of the solution of the system

$$\begin{aligned} f(u, \lambda_1, \lambda_2) &= 0, \\ \det f_u(u, \lambda_1, \lambda_2) &= 0. \end{aligned}$$

For more details on computing operating diagrams see [Pav].

# References

- [Alt] H. W. Alt. *Lineare Funktionalanalysis*. Springer, Heidelberg, 2002.
- [Ama] H. Amann. *Gewöhnliche Differentialgleichungen*. Walter de Gruyter, Berlin, New York, 1995.
- [Amm] H. Amman. "On the Existence of Positive Solutions of Nonlinear Elliptic Boundary Value Problems". *Indiana Univ. Math. J.*, (21):125–146, 1971.
- [BDL] S. R. Bernfeld, R. D. Driver, and V. Lakshmikantham. "Uniqueness for ordinary differential equations". *Math. Syst. Theory*, (9):359–367, 1975-76.
- [BF] B. C. Baltzis and A. G. Fredrickson. "Competition of two microbial populations for a single resource in a chemostat when one of them exhibits wall attachment". *Biotechnology and Bioengineering*, (25):2419–2439, 1983.
- [BFW] G. Butler, H. I. Freedman, and P. Waltman. "Uniformly Persistent Systems". *Proceedings of the Mathematical Society*, 96(3):425–430, March 1986.
- [BHW] G.J. Butler, S.B. Hsu, and P. Waltman. "Coexistence of competing predators in a chemostat". *Mathematical Biology*, (10):61–68, 1983.
- [BP] A. Berman and R. J. Plemmons. *Nonnegative Matrices in the Mathematical Sciences*. Academic Press, New York, 1979.
- [BW1] B. C. Baltzis and Ming Wu. "Steady State Coexistence of Three Pure and Simple Competitors in a Four-Membered Reactor Network". *Mathematical Biosciences*, (123):174–165, 1994.
- [BW2] L. P. Burton and W. M. Whyburn. "Minimax solutions of ordinary differential systems". *Proceedings of the American Mathematical Society*, (3):794–803, 1952.
- [BW3] G. Butler and P. Waltman. "Persistence in Dynamical Systems". *J. of Differential Equations*, (63):255–263, 1986.
- [CB] S.-W. Chang and B. C. Baltzis. "Impossibility of Coexistence of Three Pure and Simple Competitors in Configurations of Three Interconnected Chemostats". *Biotechnology and Bioengineering*, 33:460–470, 1989.
- [CC] D. C. Cooper and B. J. Copeland. "Responses of continuous-series estuarine microsystems to point-source input variations". *Ecol. Monogr.*, (43):213–236, 1973.

- [CG] C. T. Codeco and J. P. Grover. "Population dynamics of pseudomonas sp. along a spatial gradient of phosphate: an experimental approach for spatial ecology". *Braz J Biol.*, (4):637–44, 2000.
- [CR1] M. G. Crandall and P. H. Rabinowitz. "Bifurcation from Simple Eigenvalues". *Journal of Functional Analysis*, (8):321–340, 1971.
- [CR2] M. G. Crandall and P. H. Rabinowitz. "Bifurcation, Perturbation of Simple Eigenvalues, and Linearized Stability". *Archive for Rational Mechanics and Analysis*, 52(2):161–180, June 1973.
- [Dan] E. N. Dancer. "Global Solution Branches for Positive Mappings". *Archive for Rational Mechanics and Analysis*, 52(2):161–180, June 1973.
- [DK] E. Doedel and J. P. Kernevez. "AUTO: Software for continuation and bifurcation problems in ordinary differential equations". *Applied Mathematics Report*, 1986.
- [DKK] E. Doedel, H. Keller, and J. P. Kernevez. "Numerical Analysis and Control of Bifurcation Problems (I) Bifurcation in Finite Dimensions". *International J. of Bifurcation and Chaos*, 1(3):493–520, 1991.
- [DL] K. Deimling and V. Lakshmikantham. "Quasi-solutions and their role in the qualitative theory of differential equations". *Nonlinear Anal., Theory Methods Appl.*, (4):657–663, 1980.
- [DS] B. H. Davison and G. Stephanopoulos. "Effect of pH oscillations on a competing mixed culture". *Biotechnology and Bioengineering*, (28):1127–1137, 1986.
- [EOAEL] H. El-Owaidey, A. A. Ammar, and O. A. El-Leithy. "Competition in the Gradostat for the Case of Three Vessels and Three Populations". *Tamkang Journal of Mathematics*, 21(2):143–158, 1990.
- [EOEL] H. El-Owaidey and O. A. El-Leithy. "Theoretical Studies on Extinction in the Gradostat". *Mathematical Biosciences*, (101):1–26, 1990.
- [Har1] G. Hardin. "The competitive exclusion principle". *Science*, (131):1292–1297, 1960.
- [Har2] P. Hartman. *Ordinary Differential Equations*. John Wiley Press, New York, 1964.
- [Her1] R. A. Herbert. "Bidirectional compound chemostats: Applications of compound diffusion-linked chemostats in microbial ecology". In J. W. T. Wimpenny, editor, *CRC Handbook of Laboratory Model Systems for Microbial Ecosystems*, volume 1, pages 99–115. CRC Press, Boca Raton, FL, 1988.
- [Her2] G. Herzog. "On quasimonotone increasing systems of ordinary differential equations". *Port. Math.*, (1):35–43, 2000.



- [Her3] G. Herzog. "Quasimonotonicity". *Nonlinear Anal., Theory Methods Appl.*, (47):2213–2224, 2001.
- [HG] K. P. Hadeler and D. Glas. "Quasimonotone Systems and Convergence to Equilibrium in a Population Genetic Model". *J. Math. Anal. Appl.*, (95):297–303, 1983.
- [HH] S. R. Hansen and S. P. Hubbell. "Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes". *Science*, (207):1491–1493, 1980.
- [HHW] S. B. Hsu, S. P. Hubbell, and P. Waltman. "A mathematical theory for single-nutrient competition in continuous cultures of microorganisms". *SIAM Journal on Applied Mathematics*, (32):366–383, 1977.
- [HL1] G. Herzog and R. Lemmert. "Intermediate value theorems for quasimonotone increasing mappings". *Numer. Funct. Anal. Optimization*, (20):901–908, 1999.
- [HL2] G. Herzog and R. Lemmert. "On maximal and minimal solutions for  $x(t) = f(t, x(t), x(h(t)))$ ,  $x(0) = x_0$ ". *Ann. Soc. Math. Pol., Ser. I, Commentat. Math.*, (40):93–102, 2000.
- [HL3] G. Herzog and R. Lemmert. "One-sided estimates for quasimonotone increasing functions". *Bull. Aust. Math. Soc.*, (3):383–392, 2003.
- [HS1] J. K. Hale and A. S. Somolinos. "Competition for fluctuating nutrient". *Journal of Mathematical Biology*, (18):255–280, 1983.
- [HS2] M. W. Hirsch and S. Smale. *Differential Equations, Dynamical Systems, and Linear Algebra*. Academic Press, New York, 1974.
- [HS3] J. Hofbauer and J. W.-H. So. "Competition in the Gradostat: the Global Stability Problem". *Nonlinear Analysis, Theory, Methods and Applications*, 22(8):1017–1031, 1994.
- [Hsu] S. B. Hsu. "Limiting Behavior for Competing Species". *SIAM Journal on Applied Mathematics*, (34):760–763, 1978.
- [Hut] G. E. Hutchinson. "The paradox of the plankton". *American Naturalist*, (95):137–144, 1961.
- [HW] S.-B. Hsu and P. Waltman. "A Survey of Mathematical Models of Competition with inhibitor". *Mathematical Biosciences*, (187):53–91, 2004.
- [Jan] H. W. Jannasch. "Enrichments of aquatic bacteria in continuous culture". *Arch. Mikrobiol.*, (59):165–173, 1967.

- [JL] T. Jankowski and V. Lakshmikantham. "Monotone iterations for differential equations with a parameter". *J. Appl. Math. Stochastic Anal.*, 3(10):273–278, 1997.
- [JST] W. Jaeger, H. Smith, and B. Tang. "Generic failure of persistence and equilibrium coexistence in a model of m-species competition in a n-vessel gradostat when  $m > n$ ". In S. Busenberg and M. Martinelli, editors, *Lecture Notes in Biomathematics 92: Differential Equations Models in Biology, Epidemiology and Ecology*, pages 200–209, Springer-Verlag, NY, 1990.
- [JSTW] W. Jaeger, J. W.-H. So, B. Tang, and P. Waltman. "Competition in the gradostat". *Journal of Mathematical Biology*, (25):23–42, 1987.
- [Kam] E. Kamke. "Zür Theorie der Systems Gewöhnlicher Differentialgleichungen II". *Acta Mathematica*, (58):57–85, 1932.
- [Kar] P. Kareiva. "Population dynamics in spatially complex environments: Theory and data". *Phil. Trans. R. Soc. London B*, (330):175–190, 1990.
- [Kel1] H. B. Keller. "Numerical solutions of bifurcation and nonlinear eigenvalue problems". In P. H. Rabinowitz, editor, *Applications of Bifurcation Theory*, pages 359–384. Academic Press, 1977.
- [Kel2] H. B. Keller. *Lectures on numerical methods in bifurcation problems*. Springer-Verlag, Indian Institute of Science, Bangalore, 1987.
- [Kir] M. Kirkilionis. *Mathematical Theorey of Horizontal Planktonic Distributions*. PhD thesis, Ruprecht-Karls-Universität Heidelberg, 1995.
- [Koc] A.L. Koch. "Competitive coexistence of two predators utilizing the same prey under constant environmental conditions". *Journal of Theoretical Biology*, (44):387–95, 1974.
- [Lak] V. Lakshmikanham. "Existence and comparison results for differential equations". *Int. Conf. Differ. Equat., Los Angeles 1974*, pages 459–473, 1975.
- [LL] V. Lakshmikanham and G. Ladas. "Asymptotic equilibrium of ordinary differential systems". *Appl. Analysis*, (5):33–39, 1975.
- [LT] P. Lancaster and M. Tismenetsky. *The Theory of Matrices*. Academic Press, Orlando, FL, 1985.
- [LW1] R. W. Lovitt and J. W. T. Wimpenny. "The Gradostat: A tool for investigating microbial growth and interactions in solute gradients". *Society of General Microbiology Quarterly*, 6(80), 1979.

- [LW2] R. W. Lovitt and J. W. T. Wimpenny. "The Gradostat: A bidirectional compound chemostat and its applications in microbiological research". *Journal of General Microbiology*, (127):261–8, 1981.
- [Mar] L. Markus. "Asymptotically autonomous differential systems". In *Contributions to the Theory of Nonlinear Oscillations*, volume 3, pages 17–29. Princeton University Press, Princeton, NJ, 1953.
- [Mon] J. Monod. *Recherches sur la croissance des cultures bacteriennes*. Hermann, Paris, 1942.
- [Mül] M. Müller. "Über das Fundamental Theorem in der Theorie der Gewöhnlichen Differential Gleichungen". *Math. Z.*, (26):619–645, 1926.
- [Mur] J. D. Murray. *Mathematical Biology*. Springer-Verlag, Heidelberg, 1993.
- [Nag1] M. Nagumo. "Über das Randwertproblem der Nichtlinearen Gewöhnlichen Differentialgleichung Zweiter Ordnung". *Proc. Phys.-Math. Soc. Japan*, (24):845–851, 1942.
- [Nag2] M. Nagumo. "On Principally Linear Elliptic Differential Equations of the Second Order". *Osaka Math. J.*, (6):207–229, 1954.
- [Pao1] C. V. Pao. "Positive Solutions of a Nonlinear Boundary Value Problem of Parabolic Type". *J. Differential Equations*, (22):145–163, 1976.
- [Pao2] C. V. Pao. "Coexistence and Stability of a Competition-diffusion System in Population Dynamics". *J. Math. Anal. Appl.*, (83):54–76, 1981.
- [Pao3] C. V. Pao. *Nonlinear Parabolic and Elliptic Equations*. Plenum Press, New York, 1992.
- [Pav] S. Pavlou. "Computing operating diagrams of bioreactors". *Journal of Biotechnology*, (71):7–16, 1999.
- [RAG] P. Richerson, R. Armstrong, and C. R. Goldman. "Contemporaneous Disequilibrium, a New Hypothesis to Explain the Paradox of the Plankton". *Proc. Natl. Acad. Sci. U. S. A.*, 4(67):1710–1714, 1970.
- [Sat] D. H. Sattinger. "Monotone Methods in Nonlinear Elliptic and Parabolic Boundary Value Problems". *Indiana Univ. Math. J.*, (21):979–1000, 1972.
- [Smi1] H. L. Smith. "Competing sub-communities of mutualists and a generalized Kamke theorem". *SIAM Journal on Mathematical Analysis*, (4):856–74, 1986a.
- [Smi2] H. L. Smith. "Systems of ordinary differential equations which generate an order preserving flow: A survey of results". *SIAM Review*, (30):87–113, 1988.

- [Smi3] H. L. Smith. "Equilibrium distribution of species among vessels of a gradostat: A singular perturbation approach". *Journal of Mathematical Biology*, (30):31–48, 1991.
- [Smi4] H. L. Smith. "Equilibrium distribution of species among vessels of a gradostat". *J. Math. Biology*, (30):31–48, 1991b.
- [Smo] J. Smoller. *Shock-Waves and Reaction-Diffusion Equations*. Springer-Verlag, New York, 2nd edition edition, 1994.
- [STW] H. L. Smith, B. Tang, and P. Waltman. "Competition in an n-vessel Gradostat". *SIAM J. Appl. Math. Anal.*, (5):1451–71, 1991.
- [SW] H. L. Smith and P. Waltman. *The theory of the chemostat : dynamics of microbial competition*. Cambridge University Press, New York, 1995.
- [Tan] B. Tang. "Mathematical Investigations of Growth of Microorganisms in the Gradostat". *J. Math. Biol.*, (23):319–339, 1986.
- [Thi] H. R. Thieme. "Convergence results and a Poincare-Bendixon trichotomy for asymptotically autonomous differential equations". *Journal of Mathematical Biology*, (30):755–763, 1992.
- [Zei] E. Zeidler. *Nonlinear Functional Analysis and its Applications*, volume I. Springer, 1986.