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Mathematical analysis of a food chain model

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Abstract
An ODE-system modelling a generalist predator, specialist predator and prey food chain is studied. The biological feasibility of the model and the existence of a global attractor is proven for certain parameter ranges. Investigating the attractor, both analytically and numerically, reveals a diverse long-term behaviour of the species which critically depends on the parameters in the system. An extension of the model for several prey species is also proposed.

Zusammenfassung
Eine Nahrungskette, bestehend aus zwei Jägerspezies mit unterschiedlichem Jagdverhalten und einer Beutespezies, wird mittels eines GDGL-Systems modelliert. Die biologische Relevanz des Modells, wie auch die Existenz eines globalen Attraktors für gewisse Parameterregionen, werden bewiesen. Das Studium des Attraktors zeigt ein vielfältiges Langzeitverhalten auf, welches entscheidend von den Modellparametern abhängt. Eine Erweiterung des Modells für mehrere Beutespezies wird ebenfalls präsentiert.

Contents

1 Introduction

Understanding and predicting the dynamics of a population has always been of interest and relevance to mankind. A reliable prediction of the change in livestock numbers by next spring is as important to a farmer, as a good approximation of the amount of bacteria in a Petri dish the following morning is to a biochemist, or the spread of a virus on the globe is to the World Health Organisation. Studying such population dynamics dates back many centuries. In the twelfth century the following population growth problem was posed (translated from Latin, see [Bacaër, 2011]):

> *A certain man had one pair of rabbits together in a certain enclosed place. One wishes to know how many are created from the pair in one year when it is the nature of them in a single month to bear another pair and in the second month those born to bear also.*

While the above problem is very simple to solve from a modern mathematical point of view, it nonetheless entails everything that is necessary to pose a problem in population dynamics: A current or **initial state** of the system (*here:* one pair of rabbits) and a **model** dictating the dynamics of the system (*here:* the breeding habits of the rabbits). Furthermore, it also entails a **problem** that has to be solved (*here:* One wishes to...). This problem often involves determining future (or past) states of the system, given the initial state and the dynamics induced by the model. It was Leonardo of Pisa, better known as Fibonacci, who solved the above riddle in 1202 using the sequence that bears his name nowadays, the Fibonacci sequence:

$$1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, 233, 377, ...$$

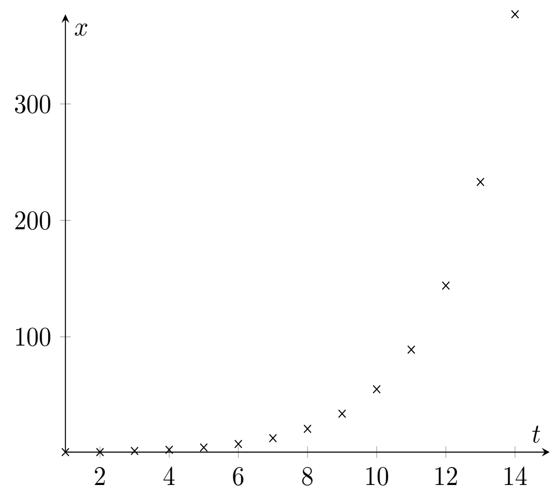
The sequence (i.e. the number of rabbit pairs) grows geometrically and is unbounded (see Figure 1.0.1a). The time increment in the above problem is discrete (one month) and hence it is called a *time-discrete* problem. Due to the significant contributions of Leibniz and Newton to differential calculus in the 17th and 18th centuries (see e.g. [Leibniz, 1684] and [Newton, 1687]) the *time-continuous* counterpart to geometrical growth could be studied mathematically: exponential growth. In the context of population dynamics this was studied by Euler and Malthus (cf. [Turchin, 2001], [Bacaër, 2011]), among others. The ordinary differential equation (ODE) modelling exponential growth reads

$$\dot{x}(t) = rx(t),$$

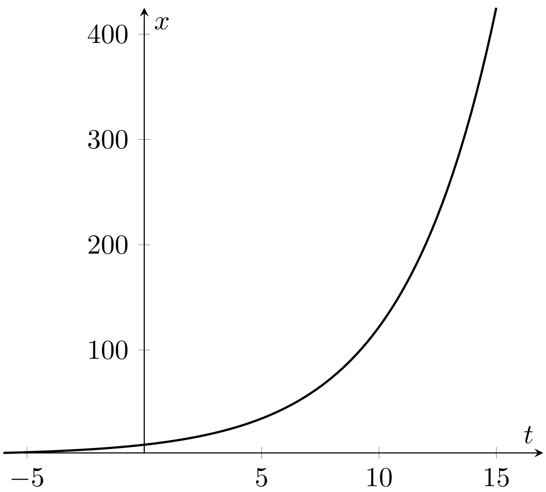
where $t \in \mathbb{R}$ is the continuous time variable and $r > 0$ is the growth rate parameter of the species considered. For any initial state $x_0 > 0$, the solution of this ordinary differential equation is given by

$$x(t) = x_0 e^{rt}. \tag{1.0.1}$$

It was Euler himself (see [Euler, 1763], [Euler, 1767]), as well as Süssmilch and Malthus (see [Süssmilch, 1761], [Malthus, 1798]) who noted that the drawback of



(a) Geometric growth



(b) Exponential growth

Figure 1.0.1: The number of individuals grows rapidly.

both geometric and exponential growth models is, that they predict too large numbers of individuals after fairly short times (see Figure 1.0.1). In particular, an environment with limited space and a maximal capacity for food (recall the *enclosed space* in the rabbit problem) could not possibly sustain such large numbers. Severe overpopulation and hence migration, famine or even starvation would be consequences. This problem is coined the *Malthusian catastrophe*.
Another phenomenon that is likely to be observed due to overpopulation is an increase of *intraspecific competition*. More precisely, individuals of the same species will compete for resources, instead of cooperating. In the mid 19th century it was Verhulst who proposed a model that included this aspect of competition and rectified the drawback of exponential population growth models (see [Verhulst, 1845] and [Verhulst, 1847]). The Verhulst logistic equation reads

$$\dot{x}(t) = rx(t)\left(1 - \frac{x(t)}{K}\right),$$

where $K > 0$ is the carrying capacity parameter of the environment. The solution to an initial value problem corresponding to the above equation with initial state $x_0 > 0$, is given by

$$x(t) = \frac{x_0 e^{rt}}{1 + \frac{x_0}{K}\left(e^{rt} - 1\right)} \tag{1.0.2}$$

Two solutions for different initial states $x_0 > 0$ are shown in Figure 1.0.2. The population with initial state $x_0 = \frac{K}{4}$ increases and tends towards the carrying capacity K of the environment, as t tends to infinity. The second population (red line) has an initial size of $x_0 = 2K$ (i.e. the environment is overpopulated) and the intraspecific competition results in a *decrease* in the number of individuals until once more the carrying capacity K is reached (asymptotically, as t tends to infinity).

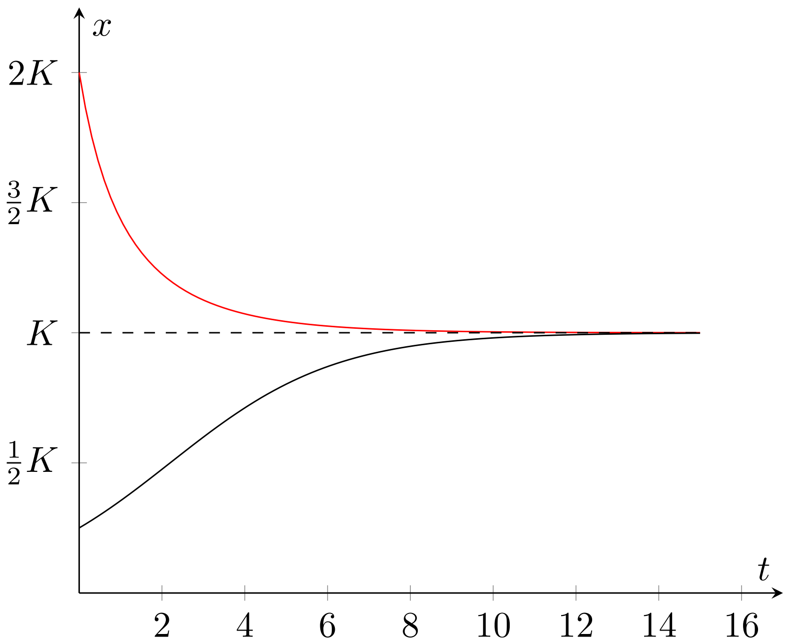


Figure 1.0.2: Solutions of the Verhulst logistic equation with $x_0 = \frac{K}{4}$ (black) and $x_0 = 2K$ (red).

The models discussed so far always refer to a single species and are one-dimensional. However, when modelling a population's dynamics, not only its intraspecific properties are of importance, but also its interspecific aspects, such as competition with other species or predation of one species by another. This leads to higher-dimensional models that consist of *systems* of ordinary differential equations. A specific system of this type, is the Lotka-Volterra predator-prey system. It reads:

$$\dot{x}(t) = ax(t) - bx(t)y(t)$$
$$\dot{y}(t) = -cy(t) + dx(t)y(t)$$

with the positive parameters a, b, c and d. The equations model a prey species x that grows exponentially and is preyed upon by the predator species y. The species y dies out exponentially fast if it lacks food. The interactive behaviour of the species is assumed to be similar to the mass-action principle. The central question answered by Lotka and Volterra in the early 20th century (see [Lotka, 1920], [Volterra, 1926]) was whether coexistence of the species is possible (according to the model dynamics) and what this coexistence looks like. Indeed, the answer was that, depending on the value of the parameters, one of three long-term behaviours may be observed:

- Only the x-species survives (sole survivor)
- The x- and y-species survive, converging to a point of coexistence (equilibrium state) as time tends to infinity
- Both species coexist and as time tends to infinity, their population sizes oscillate periodically over time (asymptotically stable periodic solution)

The last point in particular was a novelty, as it implies that oscillating population sizes (as observed in ecological systems at that time) may well be a natural phenomenon, caused by the laws of predation. The Lotka-Volterra model introduced above is considered to be a milestone in ecology and serves as a standard textbook example to this very day (see e.g. [Aulbach, 1997], [Hirsch et al., 2004], [Britton, 2012]).
In the middle of the 20th century Holling suggested that the interaction of species may be modelled more accurately, in particular, by taking into account a *saturation* of the predator in the case of sufficient prey. This leads to a class of *functional responses* of which Holling suggested several himself (see e.g. [Holling, 1959], [Holling, 1965], [Leslie and Gower, 1960], [Beddington, 1975], [DeAngelis et al., 1975]). Among these is the Holling functional response of type II, which was coupled with the Verhulst logistic equation and the Lotka-Volterra model to obtain the following rescaled version of the model equations (we omit writing the explicit dependence of the variables x and y on the time t):

$$\begin{aligned}\dot{x} &= x(1-x) - \frac{xy}{x+\alpha}\\ \dot{y} &= -\beta y + \gamma\frac{xy}{x+\alpha}\end{aligned}$$

The above model equations are known as the Rosenzweig-MacArthur model (see [Rosenzweig and MacArthur, 1963]).
The field of population dynamics and mathematical ecology (also termed population ecology) has branched into several directions since the introduction of predator-prey models. One of these directions is based on the concepts of *food chains* and *food webs*. In ecological systems (for short: ecosystems) food webs and food chains are used to characterise the interactions of species within the system. A web usually consists of several chains and in turn the species in the chains may be divided into different trophic levels. Depending on the environment one is considering, these trophic levels may vary in their number and meaning. A common choice is found in [Odum and Barrett, 1971] where producers and consumers are divided up into the following five trophic levels:

- **Level 1:** Primary producers - plants and algae
- **Level 2:** Primary consumers - herbivores
- **Level 3:** Secondary consumers - carnivores that prey upon herbivores
- **Level 4:** Tertiary consumers - carnivores that prey upon carnivores
- **Level 5:** Apex predators

The order of the levels is defined in such a way, that species from a higher trophic level will generally prey on species in a lower trophic level. An apex predator (e.g. wolf, killer whale, alligator, human) is generally not preyed upon. A specific food web is visualised in Figure 1.0.3.

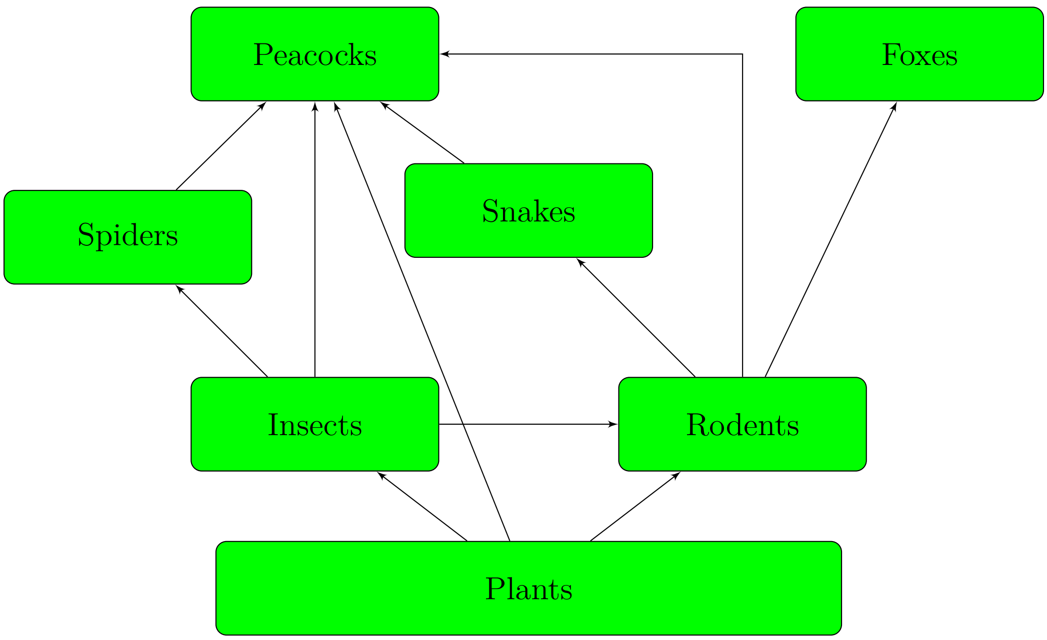
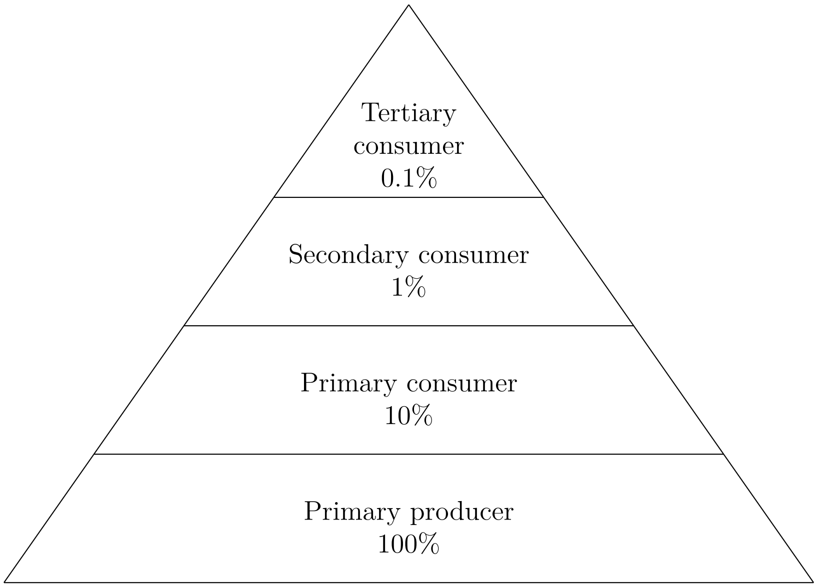
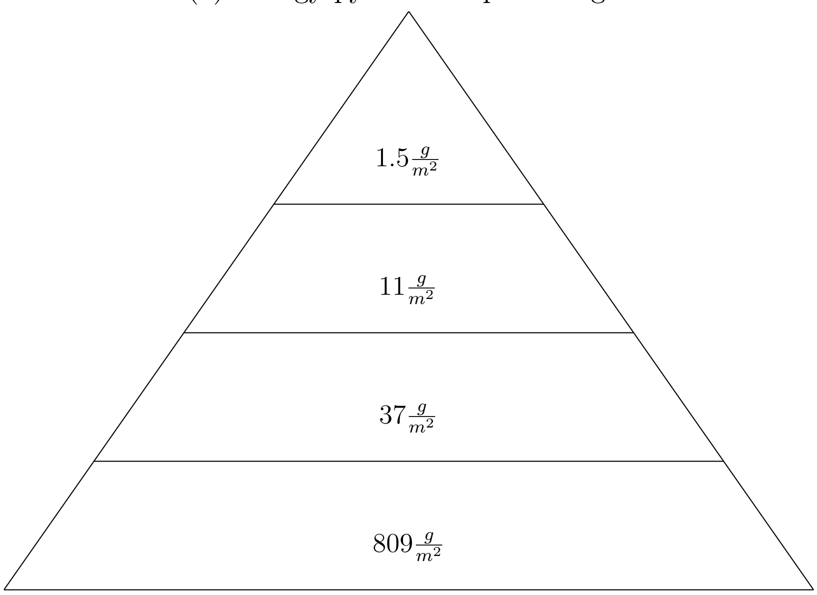


Figure 1.0.3: A food web, consisting of four trophic levels, including various food chains

For a given ecosystem an ecological (energy) pyramid can be constructed to visualise the amount of energy, biomass or individuals necessary to support the next trophic level (see Figure 1.0.4). The lifespan of a species in a low trophic level is usually short, but the species reproduces frequently. As one moves up the trophic levels, the opposite is usually true: a slow reproduction rate and few individuals, but long average lifespans. The loss of energy in consecutive levels (approximately only an average of 10% of the energy of the previous level is transferred to the next level, see [Odum and Barrett, 1971], [Pauly and Christensen, 1995]) results in the pyramid-like structure, as fewer individuals (or biomass or energy respectively) are present compared to the previous trophic level. This is an essential aspect of an ecosystem, which should be captured by any mathematical model. In particular such a model should include, if possible, all species of the ecosystem or at least the species that are *most relevant* for the evolution of the system. Numerous systems of this sort have been suggested and analysed in the past decades. As previously mentioned, the field of population ecology has branched into several sub-branches. These are related to mathematical modelling devices, such as ODE-systems with or without time-delays (cf. [Levin, 1974], [May and Leonard, 1975], [MacDonald, 1976], [Kuang, 1993], [Thieme, 1993], [Kuznetsov and Rinaldi, 1996], [Smith, 2011], [Müller and Kuttler, 2015], [Schmitt et al., 2016] among many others), partial differential equations (cf. [Fisher, 1937], [Levin, 1986], [Holmes et al., 1994], [Diekmann and Heesterbeek, 2000], [Gambino et al., 2014] for example) or stochastic differential equations (cf. [Mao et al., 2002], [Mao et al., 2005], [Capasso and Bakstein, 2015] for example).



(a) Energy pyramid in percentage.



(b) Biomass density pyramid in $\frac{g}{m^2}$ - sample data from [Odum and Barrett, 1971].

Figure 1.0.4: Ecological energy and biomass density pyramids

In this thesis we consider a food chain, modelled by a n-dimensional ($n \in \mathbb{N}$ and $n \geq 3$) first order ODE-system, which we call a **generalist predator-specialist predator-prey food chain**, for short **GSP food chain**. The model equations (in their non-dimensionalised form) read:

$$\begin{aligned}
\dot{\mathbf{x}}(t) &= F(\mathbf{x}(t), y(t), z(t)) \\
\dot{y}(t) &= \left(-b + \frac{cx_{n-2}(t)}{x_{n-2}(t)+d} - \frac{z(t)}{y(t)+e}\right) y(t) \\
\dot{z}(t) &= \left(f - \frac{g}{y(t)+h}\right) z^2(t)
\end{aligned} \tag{1.0.3}$$

Here $t \in \mathbb{R}$ is the continuous time variable, the variable $\mathbf{x} = (x_1, ..., x_{n-2})^T \in \mathbb{R}^{n-2}$ is a vector of length $n-2$ and the variables y, $z \in \mathbb{R}$ are scalars. The parameters b, c, d, e, f, g, h are assumed to be positive and the vector field F is at least Lipschitz continuous on the phase space. The variables $\mathbf{x}$, y and z represent the *species densities* of the n different species in the environment of the GSP food chain that is being modelled.

In a GSP food chain the two upper trophic levels are occupied by *special types* of predator populations, namely a generalist predator (with density z) in the top level and a specialist predator (with density y) in the second topmost level. The remaining $n-2$ species in the lower trophic levels are represented by the species density vector $\mathbf{x}$. In Figure 1.0.5 the hierarchy and interactions between the species in the GSP food chain (described below) are depicted.

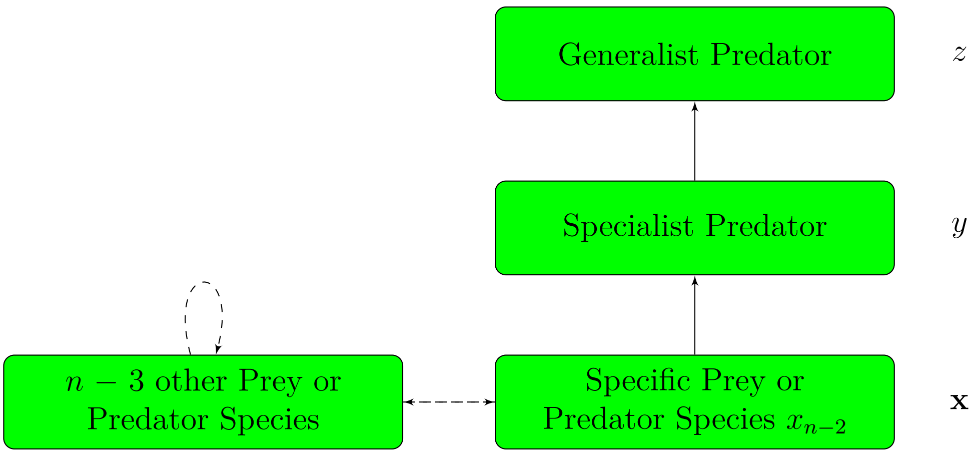


Figure 1.0.5: Scheme of a n-dimensional GSP food chain

Since a *generalist predator* (e.g. omnivores) has a very diverse diet, it *can choose from a wide variety of food.* In particular, it will prey on many different species, including the specialist predator species (the upper solid arrow in Figure 1.0.5). A generalist predator is often not limited by the availability of food, but rather by the availability of a mate, as it belongs to the highest trophic levels, in general. Quite the opposite is true for a specialist predator. A *specialist predator* has a rather limited diet. It mainly preys on a very specific kind of prey and is not very flexible in its choice of food. It is, in particular, *strongly dependent on the availability of its primary food source.* Thus specialist predators can be said to be 'picky with their

food'. This motivates that among the $n-2$ species in the lower trophic levels there is *exactly one* prey species (denoted by x_{n-2} in Figure 1.0.5) the specialist predator preys on. The interaction among the $n-2$ species in the lower trophic levels is not specified further *a priori* (see the dashed arrows Figure 1.0.5). For a detailed motivation and derivation of the model equations see sections 2.1 and 3.1, as well as Appendix C.1.
In this thesis we use concepts and methods from the mathematical theory of dynamical systems, including attractor theory, linear stability analysis, centre manifold reduction and bifurcation theory, to study the dynamics of such GSP food chain models. This requires delicate *a prori* estimates for the underlying first-order ODE system (1.0.3).

In chapter 2 a specific three-dimensional GSP food chain model that was proposed in [Upadhyay and Iyengar, 1998] and discussed to some extent in [Aziz-Alaoui, 2002], [Letellier and Aziz-Alaoui, 2002] and [Parshad et al., 2015] is analysed.
In section 2.1 the model equations of this three-dimensional GSP food chain model are motivated in detail (see subsections 2.1.1 and 2.1.2). A rescaling argument from [Letellier and Aziz-Alaoui, 2002] then leads to the model equations as we study them (see equation (2.1.3)). The section is completed by proving that the model guarantees that for non-negative initial species densities, the corresponding densities stay non-negative in the future (see subsection 2.1.3). Of course, negative species densities would not make sense from a biological point of view.
The second section of chapter 2 deals with exploding densities. In more mathematical terms we prove that the solutions of the ODE-model do not blow up in finite time (see Proposition 2.2.1 in subsection 2.2.4) or as time tends to infinity (see Proposition 2.2.2 in subsection 2.2.5) under certain assumptions on the parameters of the model. In particular, the GSP food chain model generates a semiflow Φ on the non-negative octant of the corresponding phase space (see Corollary 2.2.3). This result answers a question that has been controversially discussed in previous works (cf. [Aziz-Alaoui, 2002] and [Parshad et al., 2015] and Appendix B). Namely, existence of the solution of that model corresponding to any initial state in the phase space for all future time values is shown. Finally, in subsection 2.2.6, we derive certain bounds for those solutions.
These bounds are then used in section 2.3 to prove the existence of a global attractor $\mathcal{A}$ under the same parameter assumptions for which the semiflow Φ is proven to exist (see Theorem 2.3.1 in subsection 2.3.5). The attractor's existence is proven constructively.
Section 2.4 is devoted to the characterisation of the global attractor $\mathcal{A}$. By employing different techniques, such as the analysis of the equilibria, bifurcation theory (subsection 2.4.1) and a method involving the time average of one of the solution's components (subsection 2.4.2), local and global results concerning the dynamics of the system are obtained. These techniques help to determine the structure of the attractor $\mathcal{A}$ in different parameter regions. Depending on the parameter region, the model has up to five biologically feasible equilibria, namely an equilibrium of

extinction, an equilibrium of sole survival of the prey species, an equilibrium of coexistence of the prey species and the specialist predator species and two equilibria of coexistence of all three species. The central result of this section is Theorem 2.4.1 in subsection 2.4.2. It summarises the previous results and gives conditions (on the parameters) for the extinction and persistence of different species in the ecosystem. Section 2.4 concludes with subsection 2.4.3 in which the equilibria of coexistence of all three species of the GSP food chain model are studied. For one type of these equilibria the occurrence of a Hopf bifurcation along the corresponding branch of equilibria is shown (see Proposition 2.4.1). The consequence of this is, that for parameter values close to the Hopf bifurcation point, the three species may either tend to a stable state of coexistence or to a limit cycle of coexistence as time tends to infinity.

A biological interpretation and discussion of the parameter restrictions and corresponding results obtained in the previous sections are tackled in section 2.5. Furthermore, numerical results are presented which confirm and visualise the analytical results of this thesis (also compare to [Letellier and Aziz-Alaoui, 2002], [Letellier et al., 2002], [Rai and Upadhyay, 2004]). The numerical results are provided for two biologically relevant points in the parameter space (subsection 2.5.2). Furthermore, in subsection 2.5.3 the numerical treatment goes beyond the scope of the analytical results. It reveals the existence of a Shilnikov homoclinic bifurcation occurring in the system, implying the onset of chaotic dynamics. In particular, several windows of period doubling cascades are found.

In chapter 3 a GSP food chain of arbitrary length $n \in \mathbb{N}$ (with $n \geq 3$), as depicted in Figure 1.0.5, is considered. To the best of our knowledge such models have not been discussed in the literature before. The question arises under which assumptions do the results from the three-dimensional model carry over to the general case.

This question is pursued in section 3.1. Two biologically meaningful and important assumptions on the dynamics of the general GSP food chain model are introduced. These suffice to show the biological feasibility, as well as boundedness of the solutions as time tends to infinity (see subsections 3.1.1 and 3.1.2 and Theorem 3.1.1). In subsection 3.1.3 a short discussion follows, on how the global results in section 2.4, and in particular the technique applied to prove them, may be generalised to the n-dimensional case.

In the second section of chapter 3, specific n-dimensional GSP food chain models are considered. In subsection 3.2.1 it is shown that there exist n-dimensional GSP food chain models (with $n > 3$) which fulfil the two assumptions required in the previous section (see Corollary 3.2.2). In subsection 3.2.2 a GSP food *web* model is briefly studied for which similar results hold by applying the theory developed above.

Finally, in chapter 4 we present an outlook on further open problems concerning GSP food chain models, as well as GSP food web models (and the corresponding dynamics), that arise on grounds of this thesis. In particular, two GSP food web models are presented that no longer fit into the framework introduced before.

2 The 3-dimensional model

In this chapter we introduce a three-species predator-prey model, corresponding to a food chain consisting of one generalist predator species, one specialist predator species and one prey species (section 2.1). We analyse the generated dynamics of this GSP food chain model. By proving that under certain parameter conditions the solutions of the model with non-negative initial species densities do not have negative species densities for any future time (see section 2.1) and are bounded as time tends to infinity (see section 2.2), we show that the model equations induce a semiflow Φ on the given phase space (see Corollary 2.2.3). In the consecutive section 2.3 the existence of a global attractor $\mathcal{A}$ of Φ is shown (see Theorem 2.3.1). Furthermore, the dynamics of the system are discussed by characterising the global attractor (see Theorem 2.4.1), including bifurcation theory and centre manifold reduction among others (section 2.4). In section 2.5 a biological interpretation of the obtained results, as well as a visualisation and numerical results regarding the GSP food chain model, are presented and discussed.

2.1 The model

In this section we motivate the three-dimensional GSP food chain model equations from both an ecological and a mathematical point of view and then derive a rescaled version of the system equations (see subsections 2.1.1 and 2.1.2). Furthermore, in subsection 2.1.3 we establish that solutions of the system with non-negative initial conditions, also are non-negative in all their components for all future times, which is vital for the biological feasibility of solutions.

2.1.1 Biological motivation

As discussed above, we consider GSP food chains. Such food chains in particular consist of a *generalist predator species* and a *specialist predator species*. While a generalist predator has a very diverse diet, the diet of a specialist predator is limited. In fact, the survival of a specialist predator species will, in general, be highly dependent on the availability of its specific (favourite) food. A generalist predator species on the other hand will generally have plenty of food available, while the survival of its species is far more dependent on the availability of a mate. These fundamentally different characteristics of predator species motivate, that a differentiation of predator types is necessary when modelling the evolution of their respective population sizes, i.e. the population dynamics. The respective rates of reproduction of the two predator species are dependent on very different parameters, namely the availability of a *mate* in case of the generalist predator species and the availability of *food* in case of the specialist predator species. This food is the third species we include in the GSP food chain we consider, i.e. a *prey species*. We additionally assume that the generalist predator species preys on the specialist predator species, thus crating a food chain as shown in Figure 2.1.1. Two examples

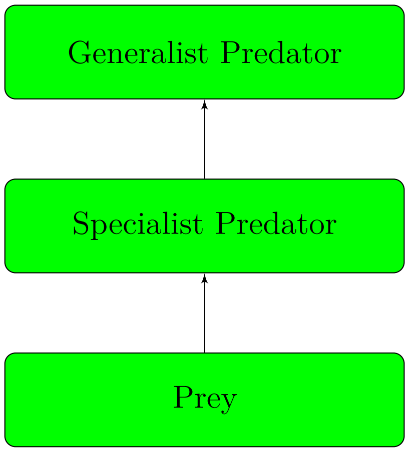


Figure 2.1.1: Scheme of a three-dimensional GSP food chain

of GSP food chains are the triples peacock-snake-rodent (see [Upadhyay and Iyengar, 1998] and [Letellier and Aziz-Alaoui, 2002]) and spider-insect-plantation (see [Hassell and May, 1986] and [Upadhyay et al., 2001]). Both these triples are food chains in the food web in Figure 1.0.3. In the first example, the peacock is the generalist predator species (belonging to the trophic level 4), the snake is the specialist predator species (trophic level 3) and the rodents are the prey species (trophic level 2). Such a food chain occurs in India, for example.

2.1.2 The model equations

We turn to the question how to find a mathematical model that describes the population dynamics of a GSP food chain as introduced above. Denoting the (time-dependent) density of the prey species with $\tilde{x}(\tilde{t})$, the density of the specialist predator species with $\tilde{y}(\tilde{t})$ and the density of the generalist predator species with $\tilde{z}(\tilde{t})$, we supply the model equations first (as derived in [Upadhyay and Iyengar, 1998]) and then motivate the various terms included. The model consists of a set of first-order ordinary differential equations (ODEs), which depend on a continuous time variable $\tilde{t} \in \mathbb{R}$ (we do not always emphasise this dependence explicitly):

$$\begin{aligned} \dot{\tilde{x}} &= a_1\tilde{x} - b_1\tilde{x}^2 - \frac{\omega_0\tilde{x}\tilde{y}}{\tilde{x}+d_0} \\ \dot{\tilde{y}} &= -a_2\tilde{y} + \frac{\omega_1\tilde{x}\tilde{y}}{\tilde{x}+d_1} - \frac{\omega_2\tilde{y}\tilde{z}}{\tilde{y}+d_2} \\ \dot{\tilde{z}} &= c_0\tilde{z}^2 - \frac{\omega_3\tilde{z}^2}{\tilde{y}+d_3} \end{aligned} \tag{2.1.1}$$

In system (2.1.1) the parameter $a_1 > 0$ is the birth (or growth) rate of the prey species. Hence the term $a_1\tilde{x}$ models the growth of the prey species. In order for the prey numbers (or density) not to explode in absence of any predators, a carrying capacity or limiting term is included: The parameter $b_1 > 0$ regulates the death rate due to intraspecific competition among the individuals of species $\tilde{x}$ (strictly speaking of the species modelled by $\tilde{x}$), modelled by the term $-b_1\tilde{x}^2$. This first part of the equation, i.e.

$$\dot{\tilde{x}} = a_1\tilde{x} - b_1\tilde{x}^2,$$

is known as the Verhulst logistic growth equation (see [Verhulst, 1845], [Verhulst, 1847], [Kot, 2001]). The final term of the first equation, i.e.

$$-\frac{\omega_0\tilde{x}\tilde{y}}{\tilde{x}+d_0},$$

models the interaction of the prey species with the specialist predator species. This interactive term is known as a Holling functional response of type II (see e.g. [Holling, 1959], [Holling, 1965]). Here $\omega_0 > 0$ is the 'maximum feeding rate' of $\tilde{y}$ on $\tilde{x}$, i.e. if there is abundant prey available then the parameter ω_0 measures the maximum per capita intake of food by the specialist predator species. The value of $d_0 > 0$ resembles the protection that the prey species may experience due to the environment or similar circumstances. For larger values of d_0 the prey is less exposed to the predator.
The second equation of system (2.1.1) determines the evolution of the population of the specialist predator species density:

$$\dot{\tilde{y}} = -a_2\tilde{y} + \frac{\omega_1\tilde{x}\tilde{y}}{\tilde{x}+d_1} - \frac{\omega_2\tilde{y}\tilde{z}}{\tilde{y}+d_2}.$$

The parameter a_2 measures the death rate of $\tilde{y}$ in absence of prey. Note that this term was included since a specialist predator is strongly dependent on the availability of its prey, and is assumed to die out without it. The term $\frac{\omega_1\tilde{x}\tilde{y}}{\tilde{x}+d_1}$ represents that availability and moreover it models the growth of the specialist predator species density dependent on the density (i.e. abundance) of the prey species. The structure of the term is the same as in the first equation of the system (except for the opposite sign as it represents the corresponding growth of $\tilde{y}$ - i.e. the energy transferred from the lower trophic level of the prey species to the trophic level of the specialist predator species). In a similar fashion the term

$$-\frac{\omega_2\tilde{y}\tilde{z}}{\tilde{y}+d_2}$$

models the predation of the generalist predator species $\tilde{z}$ on the specialist predator species $\tilde{y}$. The protection parameter d_2 is the value of $\tilde{y}$ at which the per capita removal rate of $\tilde{y}$ is $\frac{\omega_2}{2}$ (cf. e.g. [Aziz-Alaoui, 2002]). Once again positivity of the parameters is assumed, i.e. $\omega_1, \omega_2, d_1, d_2 > 0$.
Finally the third equation of (2.1.1) models the evolution of the generalist predator species:

$$\dot{\tilde{z}} = c_0\tilde{z}^2 - \frac{\omega_3\tilde{z}^2}{\tilde{y}+d_3}.$$

Here $c_0 > 0$ describes the growth rate of the generalist predator species by reproduction. The predator is assumed *to reproduce rarely* (compared to the other species) and hence the quantity c_0 is small. Recall that for the generalist predator species the limiting factor of reproducing is the availability of a mate. We model this using the term $c_0\tilde{z}^2$, as it is assumed that two individuals of the generalist predator species need to meet (similar to the mass action principle) before they reproduce. This motivates the *quadratic* term $\tilde{z}^2$. This approach (or assumption) includes both the fact that species in a higher trophic level reproduce less often and are not as abundant as species in lower levels. The last term, namely

$$-\frac{\omega_3\tilde{z}^2}{\tilde{y}+d_3},$$

models the decrease of the generalist predator species density due to scarcity of one of its resources - the specialist predator species. This approach is known as a modified version of a Leslie-Gower scheme ([Leslie and Gower, 1960], [May, 1973], [Upadhyay and Iyengar, 1998]). The growth rate of $\tilde{z}$ diminishes with decreasing availability of the favourite prey $\tilde{y}$. Here $\omega_3 > 0$ and $d_3 > 0$ once again are parameters that control and determine the maximal removal rate and protection respectively.
The model equations (2.1.1) contain the twelve different parameters

$$a_1, a_2, b_1, c_0, d_0, d_1, d_2, d_3, \omega_0, \omega_1, \omega_2, \omega_3.$$

All these parameters are assumed to be positive in order for them to be biologically meaningful. For several GSP food chains, including the aforementioned peacock-snake-rodent model, data has been collected and evaluated ([Jørgensen, 1979], [Hanski et al., 1991], [Upadhyay and Iyengar, 1998]) to some extent, resulting in a good indication, which parameter ranges are biologically meaningful and reasonable to consider. A sample set of such parameters is

$$\begin{array}{llll} a_1 = 2, & a_2 = 1, & b_1 = 0.06, & c_0 = 0.03, \\ d_0 = 10, & d_1 = 10, & d_2 = 10, & d_3 = 20, \\ \omega_0 = 1, & \omega_1 = 2, & \omega_2 = 0.405, & \omega_3 = 1. \end{array} \tag{2.1.2}$$

In order to simplify notation and reduce the number of parameters, system (2.1.1) may be rescaled (see [Letellier and Aziz-Alaoui, 2002] and Appendix C.1) by defining new variables $x, y, z \in \mathbb{R}$. The rescaled system reads (depending on the rescaled time variable $t \in \mathbb{R}$)

$$\begin{aligned} \dot{x}(t) &= x(t)(1 - x(t)) - \frac{x(t)y(t)}{x(t)+a} \\ \dot{y}(t) &= -by(t) + \frac{cx(t)y(t)}{x(t)+d} - \frac{y(t)z(t)}{y(t)+e} \\ \dot{z}(t) &= fz^2(t) - \frac{gz^2(t)}{y(t)+h} \end{aligned} \tag{2.1.3}$$

where $a, b, c, d, e, f, g, h > 0$ are positive parameters. By the rescaling, our sample parameter set in (2.1.2) translates to

$$\begin{aligned} &a = \tfrac{3}{10}, \quad &b = \tfrac{1}{2}, \quad &c = 1, \quad &d = \tfrac{3}{10}, \\ &e = \tfrac{3}{20}, \quad &f = \tfrac{400}{81}, \quad &g = \tfrac{200}{81}, \quad &h = \tfrac{3}{10}. \end{aligned} \tag{2.1.4}$$

For convenience and notations sake we rewrite (2.1.3) in a slightly different manner (not indicating the explicit dependence of x, y, z on t):

$$\left.\begin{aligned} \dot{x} &= \left(1 - x - \tfrac{y}{x+a}\right) x \\ \dot{y} &= \left(-b + \tfrac{cx}{x+d} - \tfrac{z}{y+e}\right) y \\ \dot{z} &= \left(f - \tfrac{g}{y+h}\right) z^2 \end{aligned}\right\} = \begin{pmatrix} v_1(x,y,z) \\ v_2(x,y,z) \\ v_3(x,y,z) \end{pmatrix} =: v(x,y,z) \tag{2.1.5}$$

The above system of ordinary differential equations (ODE-system) is in the form in which we want to study it.

2.1.3 Solutions and non-negativity

A question that arises naturally when modelling population dynamics is: are solutions of the mathematical model biologically relevant and feasible? First and foremost this *feasibility* requires that the model that is being considered predicts *non-negative* species numbers and densities for all future times. In this subsection we investigate this for our model in (2.1.5).
In more mathematical terms we ask: How do the dynamics generated by solutions of the initial value problems with initial conditions in $\mathbb{R}^3$ and the vector field v in system (2.1.5) look on some phase space $X \subset \mathbb{R}^3$?
Since we are interested in the biologically relevant dynamics (i.e. non-negative species densities) we want to restrict our analysis to an appropriate subset $X \subset \mathbb{R}^3$ (equipped with the standard inner product $\langle \cdot, \cdot \rangle$ and the induced Euclidean norm $\| \cdot \|$ and metric $d(\cdot, \cdot)$). This motivates the following

Definition 2.1.1.
The sets

$$\mathcal{O}_0^+ := \{(x,y,z) \in \mathbb{R}^3 \,|\, x \geq 0,\ y \geq 0,\ z \geq 0\}$$

$$\mathcal{O}^+ := \{(x,y,z) \in \mathbb{R}^3 \,|\, x > 0,\ y > 0,\ z > 0\}$$

are defined as the ***non-negative octant*** *and* ***positive octant*** *respectively.*
A ***solution*** *s of the initial value problem (IVP) given by system* (2.1.5) *and initial conditions*

$$s_0 = (x_0, y_0, z_0)^T = (x(0), y(0), z(0))^T \in \mathcal{O}_0^+$$

is denoted by

$$s := s(t) = (x(t), y(t), z(t))^T.$$

The maximal existence interval of s is denoted by $I_M \subset \mathbb{R}$.
The maximal right (or positive) existence interval of s is denoted by $I \subset [0, \infty)$.

Remark 2.1.1.

- The existence and uniqueness of any solution s and the corresponding existence intervals $I \subsetneq I_M$ are guaranteed by combining the Picard-Lindelöf Theorem and the theorem on the maximal existence interval (see e.g. [Amann, 1990], [Aulbach, 1997], [Sell and You, 2002]), for the locally Lipschitz vector field

$$v \in C_{Lip}(\mathcal{O}_0^+, \mathbb{R}^3).$$

  Such a solution s is also differentiable (and therefore also continuous) on I_M by construction.

- Note that above we choose $t_0 = 0$ to be the initial time of the IVP. This is no restriction on the initial time, since for any given initial time $t_0 \in \mathbb{R}$ we may define a new time variable $\widehat{t} := t - t_0$ and work with this variable instead. The vector field v remains unchanged under such a translation, as it does not depend explicitly on the time variable t, i.e. v is autonomous (cf. [Guckenheimer and Holmes, 1983]). Thus, without loss of generality and for simplicity's sake, we only consider solutions s for initial time $t_0 = 0$ and corresponding initial state $s_0 = s(0) \in \mathcal{O}_0^+$ in this thesis.

- We emphasise that a solution s (as a function of t) and the corresponding *phase curve* or *solution curve* in the phase space may be identified with each other in a natural way. Indeed, any initial state s_0 and the corresponding (continuous) solution s define a (continuous) curve

$$\gamma_{s_0} : I_M \to \mathbb{R}^3,$$

  parametrised in $t \in I_M$, which is tangent to the vector field v in the phase space (cf. [Guckenheimer and Holmes, 1983], [Wiggins, 1990]). Accordingly, when no ambiguity may occur, the terms *solution* and *phase curve* are used in an interchangeable manner. We often use the term solution when emphasising that s is a function of t, while we use the term phase curve for the emphasis of geometrical properties and implications (in the phase space). The *positive phase curve* $\gamma_{s_0}^+$ is given by the phase curve to a solution s, restricted to the maximal right existence interval $I \subset [0, \infty)$ of s, i.e. the curve

$$\gamma_{s_0}^+ : I \to \mathbb{R}^3.$$

  The uniqueness of solutions implies that two phase curves to solutions cannot intersect each other (in the phase space) for any $t \in \mathbb{R}$, unless they are identical.

We would like to restrict our analysis of the dynamics generated by system (2.1.5) to the phase space $X = \mathcal{O}_0^+$ (see Figure 2.1.2) and thus to the solutions s as defined above. For this we need to ensure that the phase curve corresponding to a solution s does not leave $\mathcal{O}_0^+$ (forwards or backwards in time) while it exists. To ensure this we define the following property:

Definition 2.1.2.
A subset $K \subset \mathcal{O}_0^+$ is said to have ***the property (I1)*** *under the dynamics generated by* (2.1.5)*, if for all $s_0 \in K \subset \mathcal{O}_0^+$ the corresponding solution s (from Definition 2.1.1) satisfies*

$$s(t) \in K \qquad \forall\, t \in I_M.$$

Remark 2.1.2.
Several remarks concerning the above definition are in order:

- The property *(I1)* of a set $K \subset \mathcal{O}_0^+$ is equivalent to the the set

  $$s(I_M) := \{s(t) \,:\, t \in I_M\},$$

  being a subset of K for any solution s with $s_0 \in K$. In graphical or geometrical terms this implies that any phase curve γ_{s_0} with $s_0 \in K$ is (completely) contained in K. In particular, no phase curve can enter or leave a set K with property *(I1)*. More precisely it holds that

  $$\begin{aligned} K \cap \gamma_{s_0}(I_M) &= \gamma_{s_0}(I_M) \qquad && \text{if} \quad s_0 \in K \\ K \cap \gamma_{s_0}(I_M) &= \emptyset && \text{if} \quad s_0 \notin K \end{aligned}$$

- The property *(I1)* may also be termed *finite invariance* or *pre-invariance* (cf. [Aulbach, 1997]), as it requires a phase curve corresponding to a solution s with $s_0 \in K$, to be completely contained in K *while it exists*. Furthermore, if a set K has the property *(I1)* and for any solution s with $s_0 \in K$ it holds that the solutions exist for all time-values $t \geq 0$, i.e.

  $$[0, \infty) \subset I_M,$$

  then the set K is also *positive invariant*. Likewise, if $(-\infty, 0] \subset I_M$ holds, then K is *negative invariant* and if $I_M = \mathbb{R}$ for all such solutions, then K is even *invariant*.

- Any finite union and any finite intersection of sets with property *(I1)* once more has property *(I1)*.

In the subsequent lemmas we will prove that $\mathcal{O}_0^+$ as well as various subsets of $\mathcal{O}_0^+$ (including the boundary $\partial\mathcal{O}_0^+$ of $\mathcal{O}_0^+$) have property *(I1)*.

Lemma 2.1.1.
The boundary $\partial\mathcal{O}_0^+$ of $\mathcal{O}_0^+$ is given by

$$\partial\mathcal{O}_0^+ = \mathcal{O}_0^+ \backslash \mathcal{O}^+ = \bigcup_{i=1}^{7} O_i$$

where the sets $O_i \neq \emptyset$ (with $i \in \{1, ..., 7\}$) are defined as follows:

$$\begin{aligned} &O_1 = \{(0,0,0)^T\}, \\ &O_2 = \mathbb{R}^+ \times \{0\} \times \{0\}, \qquad O_3 = \{0\} \times \mathbb{R}^+ \times \{0\}, \qquad O_4 = \{0\} \times \{0\} \times \mathbb{R}^+ \\ &O_5 = \mathbb{R}^+ \times \mathbb{R}^+ \times \{0\}, \qquad O_6 = \mathbb{R}^+ \times \{0\} \times \mathbb{R}^+, \qquad O_7 = \{0\} \times \mathbb{R}^+ \times \mathbb{R}^+. \end{aligned}$$

Moreover the family $(O_i)_{i \in \{1,...,7\}}$ forms a partition of $\partial\mathcal{O}_0^+$.

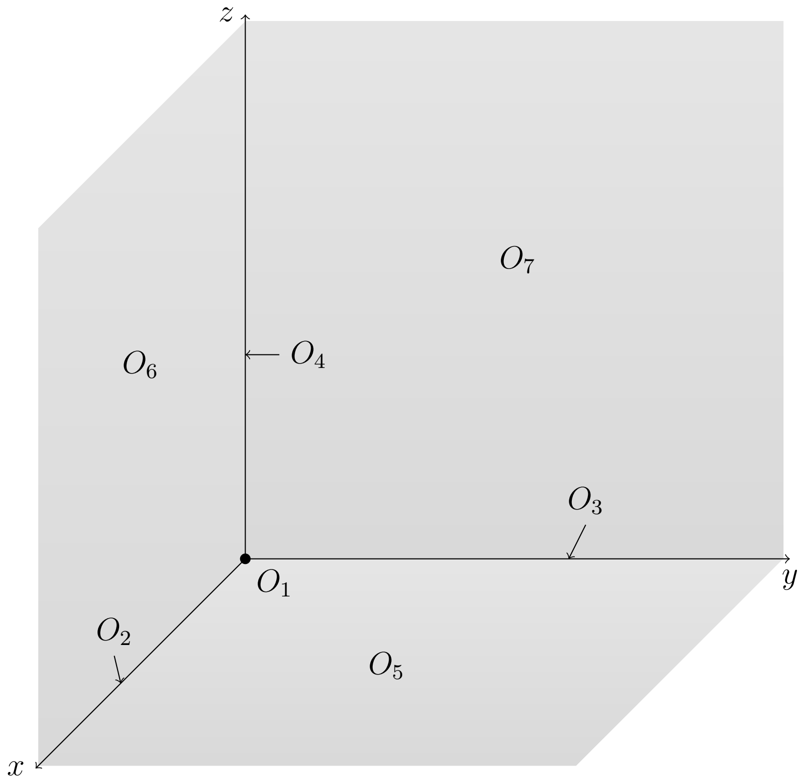


Figure 2.1.2: The set $\mathcal{O}_0^+$ and the subsets O_i from Lemma 2.1.1.

Proof.
The set $\mathcal{O}^+$ is the interior of $\mathcal{O}_0^+$. Furthermore $\mathcal{O}_0^+$ is closed (in $\mathbb{R}^3$) and hence

$$\partial\mathcal{O}_0^+ = \mathcal{O}_0^+ \backslash \mathcal{O}^+.$$

By the definition of $\mathcal{O}_0^+$, $\mathcal{O}^+$ and the sets O_i we obtain (see Figure 2.1.2)

$$\partial\mathcal{O}_0^+ = \mathcal{O}_0^+ \backslash \mathcal{O}^+ = \bigcup_{i=1}^{7} O_i$$

Furthermore, the family $(O_i)_{i\in\{1,...,7\}}$ forms a partition of $\partial\mathcal{O}_0^+$ since $O_i \neq \emptyset$ for any $i \in \{1,...,7\}$ and

$$O_i \cap O_j = \emptyset \qquad \forall\, i,j \in \{1,...,7\}, i \neq j. \qquad \square$$

In other words: the boundary $\partial\mathcal{O}_0^+$ consists of the origin O_1 as well as the three positive semi-axes O_2, O_3, O_4 of the (Cartesian) coordinate axes (in $\mathbb{R}^3$) and the three positive 'quarter' planes O_5, O_6, O_7 of the coordinate planes (in $\mathbb{R}^3$). We use the above result to prove the following

Lemma 2.1.2.
The sets O_i with $i \in \{1,2,3,4\}$ all have property (I1) from Definition 2.1.2.

Proof.
We will show the claim consecutively for the various sets.

- Consider $O_1 = \{(0,0,0)^T\}$. Let s be any solution such that $s_0 \in O_1$. We claim that s is given by
$$s(t) = (0,0,0)^T \qquad \forall\, t \in \mathbb{R}.$$
We check this by computing
$$s(0) = (0,0,0)^T = s_0$$
and
$$v(s(t)) = v(0,0,0) = (0,0,0)^T = (\dot{x}(t), \dot{y}(t), \dot{z}(t))^T = \dot{s}(t) \qquad \forall\, t \in \mathbb{R}.$$
Hence s is a solution and since it is unique it is the only solution. In particular we have
$$s_0 \in O_1 \quad \Rightarrow \quad s(t) \in O_1 \qquad \forall\, t \in I_M,$$
i.e. O_1 has property *(I1)*.

- Consider $O_2 = \mathbb{R}^+ \times \{0\} \times \{0\}$, i.e. the positive x-axis (in $\mathbb{R}^3$). We claim that for fixed (but arbitrary) $s_0 = (x_0, 0, 0) \in O_2$ the corresponding *unique* solution
$$s(t) = (x(t), y(t), z(t))^T \qquad \forall\, t \in I_M.$$
has the form
$$s(t) = (x(t), 0, 0)^T \qquad \forall\, t \in I_M.$$
Indeed such a solution fulfils the initial value condition
$$s(0) = (x(0), 0, 0)^T = (x_0, 0, 0)^T = s_0 \in O_2$$
and solves the system of differential equations in (2.1.5) for all time values $t \in I_M$
$$v(s(t)) = ([1 - x(t)]x(t), 0, 0)^T = (\dot{x}(t), \dot{y}(t), \dot{z}(t))^T = \dot{s}(t).$$
Thus any solution s with $s_0 \in O_2$ has the form
$$s(t) = (x(t), y(t), z(t))^T = (x(t), 0, 0)^T \qquad \forall\, t \in I_M.$$
Hence - in order to show $s(t) \in O_2$ for all $t \in I_M$ - it remains to show that
$$x(t) > 0 \qquad \forall\, t \in I_M.$$
We assume that the above does not hold, i.e.
$$\exists\, \tau \in I_M \,:\, x(\tau) \leq 0.$$

However $x(0) > 0$ (since $s_0 \in O_2$) and x is continuous (in t) implying that the intermediate value theorem holds and yields

$$\exists\, T \in [\min\{0,\tau\}, \max\{0,\tau\}] \subset I_M \,:\, x(T) = 0.$$

For the time T we now have

$$s(T) = (0,0,0) \in O_1.$$

This however is a contradiction since O_1 has property *(I1)* (and thus the uniqueness of the solution s with $s_0 \in O_1$ is violated). Hence O_2 also fulfils property *(I1)*.

- Considering the sets O_3 and O_4 we see that an analogous argument to the one for O_2 yields the property *(I1)* of these sets. □

Furthermore we can now prove

Lemma 2.1.3.
The sets O_5, O_6 and O_7 as well as the boundary set $\partial\mathcal{O}_0^+$ as defined in Lemma 2.1.1 have property (I1) under the dynamics generated by system (2.1.5).

Proof.
Once more we can consider the sets consecutively. Note that a likewise argument to the one in the previous proof yields the property *(I1)* of the sets O_i (with $i \in \{5,6,7\}$ - see the shaded sets in Figure 2.1.2). However, we present a geometrical approach instead:

- Consider the set $O_5 = \mathbb{R}^+ \times \mathbb{R}^+ \times \{0\}$. This set is a (relatively open) 'quarter' plane and a normal vector to it (i.e. to any point in O_5) is given by

$$n = \lambda \cdot \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix} \qquad \lambda \in \mathbb{R}\backslash\{0\}$$

From (2.1.5) we obtain that in O_5 (in particular for $z = 0$) it holds that

$$\langle n, v(x,y,z)\rangle = \lambda \left(f - \frac{g}{y+h} \right) \underbrace{z^2}_{=0} = 0.$$

This implies that the vector field v is tangent to O_5 *at any point in the plane* and hence the phase curve γ_{s_0} to any solution s with $s_0 \in O_5$ can only escape from O_5 via the relative boundary relbdd(O_5), see Figure 2.1.3. This boundary however is given by

$$\text{relbdd}(O_5) = O_1 \cup O_2 \cup O_3$$

which is a union of sets with property *(I1)* by Lemma 2.1.2. Hence the phase curve to s cannot enter any of these sets (this would be a contradiction to the

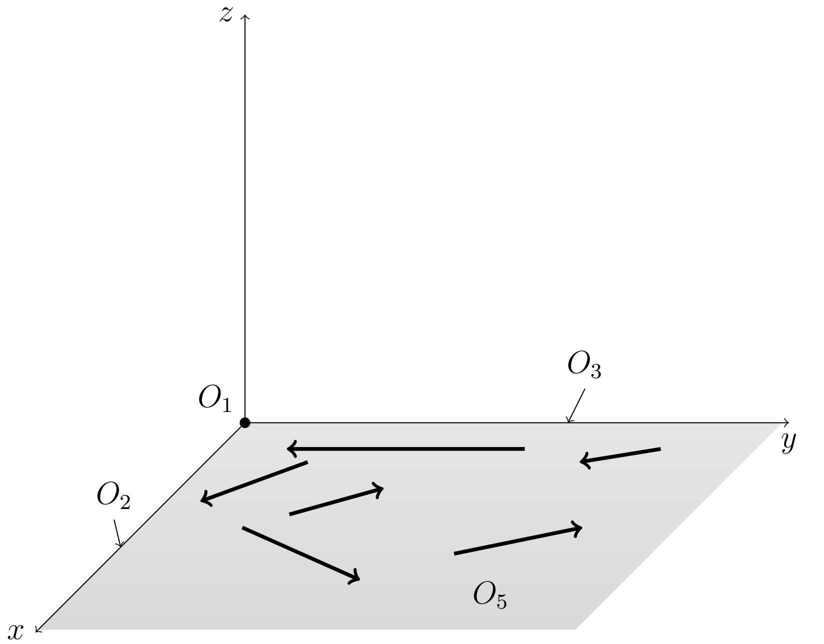


Figure 2.1.3: Schematic figure of a vector field *tangent* to the set $O_5 \subset \mathcal{O}_0^+$.

property *(I1)* of the sets O_i with $i \in \{1, 2, 3\}$). Thus the curve is completely contained in O_5 while it exists, i.e.

$$s(t) \in O_5 \qquad \forall\, t \in I_M,$$

proving the set O_5 has property *(I1)*.

- We can proceed likewise to above for the other sets O_6 and O_7 noting that for O_6 (with normal vector $n = \lambda \cdot (0, 1, 0)^T$ and $y = 0$) it holds that

$$\langle n, v(x, y, z)\rangle = \lambda \left(-b + \frac{cx}{x+d} - \frac{y}{z+e}\right) \underbrace{y}_{=0} = 0$$

and for O_7 (with normal vector $n = \lambda \cdot (1, 0, 0)^T$ and $x = 0$) we obtain

$$\langle n, v(x, y, z)\rangle = \lambda \left(1 - x - \frac{y}{x+a}\right) \underbrace{x}_{=0} = 0$$

and the relative boundaries of O_6 and O_7 are also made up of unions of the sets O_1, O_2, O_3, O_4 which all have the property *(I1)*. The same argument as for the set O_5 yields property *(I1)* for O_6 and O_7 respectively.

- We now consider $\partial\mathcal{O}_0^+$. By Lemma 2.1.1 we have

$$\partial\mathcal{O}_0^+ = \bigcup_{i=1}^{7} O_i$$

and since all the sets O_i with $i \in \{1, ..., 7\}$ have property *(I1)* (see above and Lemma 2.1.2) the set $\partial\mathcal{O}_0^+$ also has property *(I1)* as a union of sets with property *(I1)*. □

Using the above result, we show

Lemma 2.1.4.
The set $\mathcal{O}_0^+$ has property (I1) under the dynamics generated by system (2.1.5)*. I.e. for any solution s (with $s_0 \in \mathcal{O}_0^+$) we have*

$$s(t) \in \mathcal{O}_0^+ \qquad \forall\, t \in I_M$$

and $x(t) \geq 0$, $y(t) \geq 0$ and $z(t) \geq 0$ for all $t \in I_M$.

Proof.
We provide a proof by contradiction. Indeed, if $\mathcal{O}_0^+$ does not have property *(I1)*, then there exists some solution s (with $s_0 \in \mathcal{O}_0^+$) and

$$\exists\, \tau \in I_M \;:\; s(\tau) \notin \mathcal{O}_0^+. \tag{2.1.6}$$

Since $s(0) = s_0 \in \mathcal{O}_0^+$ we have $\tau \neq 0$ and the continuity of s infers that the phase curve γ_{s_0} corresponding to s intersects the boundary $\partial\mathcal{O}_0^+$ of $\mathcal{O}_0^+$ at some time in between the times zero and τ, i.e.

$$\exists\, T \in [\min\{0, \tau\}, \max\{0, \tau\}] \subset I_M \;:\; s(T) \in \partial\mathcal{O}_0^+.$$

However the boundary $\partial\mathcal{O}_0^+$ has property *(I1)* by Lemma 2.1.3 and is a subset of $\mathcal{O}_0^+$. Coupled with the uniqueness of s (on I_M) this implies that the corresponding phase curve γ_{s_0} is contained in $\partial\mathcal{O}_0^+ \subset \mathcal{O}_0^+$ for all $t \in I_M$. This is a contradiction to the assumption in (2.1.6). Hence $\mathcal{O}_0^+$ has property *(I1)*. Note that this implies

$$s(t) \in \mathcal{O}_0^+ \qquad \forall\, t \in I_M$$

and therefore $x(t) \geq 0$, $y(t) \geq 0$ and $z(t) \geq 0$ for all $t \in I_M$. □

Remark 2.1.3.
The above result implies that choosing $\mathcal{O}_0^+$ as a phase space X for the dynamics generated by system (2.1.5) is in fact sensible. The lemma ensures that any solution s stays non-negative in every component while it exists (i.e. for all $t \in I_M$). As each component of s represents a population density of a species this is a vital property of the system with respect to biological relevance and meaningfulness. Thus the mathematical model we study generates solutions which are *biologically feasible.*

We can in fact even show a little bit more:

Lemma 2.1.5.
The set $\mathcal{O}^+$ has property (I1) under the dynamics generated by system (2.1.5)*. Furthermore, any s fulfils*

$$\begin{aligned} x_0 > 0 \quad &\Rightarrow \quad x(t) > 0 \quad \forall\, t \in I_M, \\ y_0 > 0 \quad &\Rightarrow \quad y(t) > 0 \quad \forall\, t \in I_M, \\ z_0 > 0 \quad &\Rightarrow \quad z(t) > 0 \quad \forall\, t \in I_M. \end{aligned}$$

Proof.
Let s be an arbitrary solution with $s_0 \in \mathcal{O}^+$. By Lemma 2.1.4 we know that

$$s(t) \in \mathcal{O}_0^+ \qquad \forall\, t \in I_M.$$

Furthermore, the boundary $\partial\mathcal{O}_0^+ = \mathcal{O}_0^+ \backslash \mathcal{O}^+$ has property *(I1)* by Lemma 2.1.3 and hence assuming that the phase curve γ_{s_0} corresponding to s is in the boundary $\partial\mathcal{O}_0^+$ for any time $t \in I_M$, then

$$s(t) \in \partial\mathcal{O}_0^+ \qquad \forall\, t \in I_M,$$

i.e. the curve is completely contained in the boundary (for all $t \in I_M$). This however is a contradiction since s is unique and the corresponding phase curve is not in the boundary at $t = 0 \in I_M$ by assumption ($s_0 \in \mathcal{O}^+$ and $\mathcal{O}^+ \cap \partial\mathcal{O}_0^+ = \emptyset$). Therefore we have

$$s(t) \in \mathcal{O}_0^+ \backslash \partial\mathcal{O}_0^+ = \mathcal{O}^+ \qquad \forall\, t \in I_M,$$

proving the first part of the claim.
We now consider a solution s with $x_0 > 0$. The set of feasible initial conditions s_0 is given by

$$\{(x, y, z) \in \mathcal{O}_0^+ \,:\, x > 0\} = \mathcal{O}^+ \cup O_2 \cup O_5 \cup O_6$$

and thus has property *(I1)* as a union of sets with property *(I1)* (see Lemmas 2.1.2 and 2.1.3 and the first part of this proof). Hence s (and the phase curve respectively) fulfils

$$s(t) \in \{(x, y, z) \in \mathcal{O}_0^+ \,:\, x > 0\} \qquad \forall\, t \in I_M,$$

which is equivalent to

$$x(t) > 0 \quad \forall\, t \in I_M.$$

Analogously we may prove the remaining two implications for the y- and z-component of s. □

Remark 2.1.4.
The lemma implies that a solution s with $s_0 \in \mathcal{O}^+$ is positive in every component for all $t \in I_M$. We call such an s a **positive** solution. Furthermore, by the above we also have

$$\begin{aligned} x_0 = 0 \quad &\Rightarrow \quad x(t) = 0 \quad \forall\, t \in I_M, \\ y_0 = 0 \quad &\Rightarrow \quad y(t) = 0 \quad \forall\, t \in I_M, \\ z_0 = 0 \quad &\Rightarrow \quad z(t) = 0 \quad \forall\, t \in I_M. \end{aligned} \tag{2.1.7}$$

Having established, that any solution s remains in $\mathcal{O}_0^+$ (in the sense that the corresponding phase curve is a subset of $\mathcal{O}_0^+$) while it exists, the question arises under which restrictions on the parameters of (2.1.5) these solutions s exist *for all* time values $t \in \mathbb{R}$ or at least for all non-negative time values, i.e. for all $t \geq 0$. Differently put: we want to investigate the maximal existence interval I_M of solutions s. In fact we cannot expect the solutions to exist for all negative time values. This becomes clear by the following

Lemma 2.1.6.
The solution s to the IVP given by (2.1.5) and $s_0 = (x_0, 0, 0)$ with $x_0 > 1$ has the maximal existence interval

$$I_M = \left(\ln\left(1 - \tfrac{1}{x_0}\right), \infty\right)$$

for any parameters $a, b, c, d, e, f, g, h > 0$.

Proof.
We consider the solution s to the IVP given by (2.1.5) and $s_0 = (x_0, 0, 0)$ with $x_0 > 1$. Since $y_0 = 0 = z_0$ the Lemmas 2.1.2 and 2.1.3 yield $y(t) = 0 = z(t)$ for all $t \in I_M$. Hence finding the solution s reduces to solving the initial value problem

$$\dot{x}(t) = x(t)\,(1 - x(t)) \qquad x(0) = x_0.$$

The above ODE is the (Verhulst) logistic equation. For arbitrary $x_0 > 1$ it is solved by

$$x(t) = \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)}.$$

Indeed

$$x(0) = \frac{x_0 \exp(0)}{1 + x_0(\exp(0) - 1)} = x_0$$

and

$$\begin{aligned}
\frac{d}{dt}x(t) &= \frac{x_0 \exp(t)[1 + x_0(\exp(t) - 1)] - x_0 \exp(t)(x_0 \exp(t))}{[1 + x_0(\exp(t) - 1)]^2} \\
&= \frac{x_0 \exp(t)(1 - x_0)}{[1 + x_0(\exp(t) - 1)]^2} \\
&= \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} \cdot \frac{1 - x_0}{1 + x_0(\exp(t) - 1)} \\
&= x(t) \cdot \frac{1 + x_0(\exp(t) - 1) - x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} \\
&= x(t)(1 - x(t)),
\end{aligned}$$

which shows that

$$s(t) = \left(\frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)}, 0, 0\right)^T$$

is the unique solution of the given IVP. Now s is not defined if and only if

$$1 + x_0(\exp(t) - 1) = 0 \quad \Leftrightarrow \quad \exp(t) - 1 = -\frac{1}{x_0} \quad \Leftrightarrow \quad t = \ln\left(1 - \tfrac{1}{x_0}\right) < 0.$$

Hence the maximal existence interval of s is $I_M = \left(\ln\left(1 - \tfrac{1}{x_0}\right), \infty\right)$, see Figure 2.1.4. □

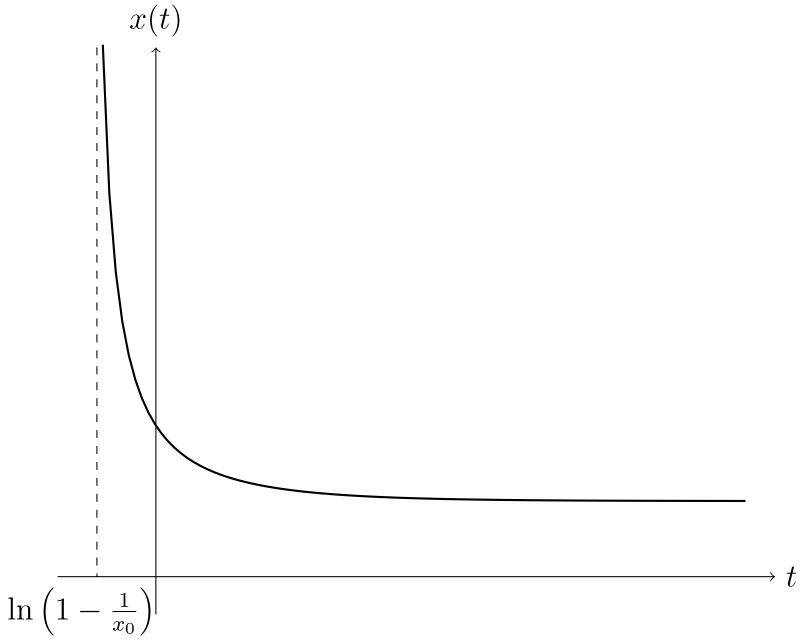


Figure 2.1.4: For the initial condition $s_0 = (x_0, 0, 0)$ and $x_0 > 1$ the first component of the solution s diverges as $t \to \ln\left(1 - \frac{1}{x_0}\right)$.

By the above result we see that not all solutions s exist for all $t < 0$. In fact, using that

$$\ln\left(1 - \frac{1}{x_0}\right) \to \ln(1) = 0 \quad \text{as} \quad x_0 \to \infty$$

we can find solutions that blow up (backward in time) after an arbitrary short time by choosing x_0 sufficiently large. For this reason we restrict our analysis to the maximal *right* existence interval $I \subset [0, \infty)$ of solutions s in this thesis. Likewise we restrict ourselves to *positive* phase curves $\gamma^+_{s_0}$ in the following considerations. From a biological point of view this means that we study the evolution of an initial state s_0 of the food chain for *future times* of the initial time $t_0 = 0$.
In the subsequent considerations we show that under certain parameter restrictions we can ensure that solutions s exist for all time values $t \geq 0$. In particular, the dynamics generated by system (2.1.5) define a semiflow on $\mathcal{O}^+_0$ (see Corollary 2.2.3).

2.2 Boundedness of solutions

The aim of this section is to prove that all solutions s are bounded as time tends to infinity, if we impose certain conditions on the parameters in system (2.1.5). We first show that the solutions exist for all $t \geq 0$ (see subsections 2.2.1 to 2.2.4) and then prove that they are also bounded for $t \to \infty$ (subsection 2.2.5), even uniformly with respect to bounded subsets (subsection 2.2.6). The approach entails a consecutive consideration of the solutions' x-, y- and z-components.

2.2.1 Boundedness of the first two components

We first show the boundedness of the x-component (of s) on I.

Lemma 2.2.1.
Any solution s has the property

$$0 \leq x(t) \leq \max\{1, x_0\} =: x_M(x_0) = x_M \qquad \forall\, t \in I. \tag{2.2.1}$$

Proof.
Let any solution s be given (as defined in Definition 2.1.1). From Lemma 2.1.4 we know that $x(t) \geq 0$ and $y(t) \geq 0$ for all $t \in I$ and hence we may estimate the first equation in (2.1.5) as follows

$$\dot{x}(t) = x(t)\left(1 - x(t) - \frac{y(t)}{x(t) + a}\right) \leq x(t)(1 - x(t))$$

for any $t \in I$. This differential inequality is the key to proving the claim. Comparison (cf. [Arnold, 1979], [Walter, 1990], [Aziz-Alaoui, 2002]) of the above to the solution of the IVP given by (the logistic equation [Kot, 2001])

$$\dot{\xi}(t) = \xi(t)\,(1 - \xi(t)) \qquad \xi(0) = x(0) = x_0$$

yields (see the proof of Lemma 2.1.6)

$$x(t) \leq \xi(t) = \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} \qquad \forall\, t \in I. \tag{2.2.2}$$

Consider the following cases:

- Assume $x_0 = 0$ then (2.2.2) yields

$$x(t) \leq \xi(t) = \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} = 0 \leq \max\{1, x_0\} \qquad \forall\, t \in I.$$

- Assume $0 < x_0 \leq 1$ then (2.2.2) yields

$$x(t) \leq \xi(t) = \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} = \frac{1}{\underbrace{\left(\frac{1}{x_0} - 1\right)}_{\geq 0} \exp(-t) + 1} \leq 1 \leq \max\{1, x_0\}$$

  for any $t \in I$, proving (2.2.1) holds.

- Assume $x_0 > 1$. For any $t \in I \subset [0, \infty)$ it holds that $\exp(-t) \leq 1$ and hence we have

$$1 = x_0 + \underbrace{1 - x_0}_{<0} \leq x_0 + (1 - x_0)\exp(-t).$$

Dividing by the term $x_0 + (1 - x_0)\exp(-t) > 0$ in the above, yields

$$\frac{1}{x_0 + (1 - x_0)\exp(-t)} \leq 1 \qquad \forall\, t \in I.$$

Multiplying by $x_0 > 1$ yields

$$\frac{x_0}{x_0 + (1 - x_0)\exp(-t)} \leq x_0 \qquad \forall\, t \in I. \tag{2.2.3}$$

Furthermore using

$$\frac{x_0}{x_0 + (1 - x_0)\exp(-t)} = \frac{x_0 \exp(t)}{x_0 \exp(t) + 1 - x_0} = \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} = \xi(t)$$

we obtain from (2.2.3) that

$$\xi(t) = \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} \leq x_0 \qquad \forall\, t \in I.$$

Hence combining this with (2.2.2) we obtain

$$x(t) \leq \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} \leq x_0 \leq \max\{1, x_0\} \qquad \forall\, t \in I. \qquad \square$$

Remark 2.2.1.
Note that we will omit denoting the dependence of $x_M(x_0)$ on x_0 (or s_0 respectively) explicitly in general and merely write x_M instead. Only where the dependence is deliberately emphasised, will we add the argument x_0.

We turn to proving the boundedness of solutions in their second component on I. For this we need the following lemma (cf. [Aziz-Alaoui, 2002]).

Lemma 2.2.2.
Let ϕ be a differentiable function satisfying the differential inequality

$$\frac{d\phi(t)}{dt} + k_1\phi(t) \leq k_2$$

for $t \in I$, where $(k_1, k_2) \in \mathbb{R}^2$, $k_1 \neq 0$ and $I \subset [0, \infty)$ is an interval. Then for all $t \in I$ it holds that

$$\phi(t) \leq \frac{k_2}{k_1} - \left[\frac{k_2}{k_1} - \phi(0)\right] \exp(-k_1 t).$$

Proof.
Let ϕ be a differentiable function satisfying the differential inequality

$$\frac{d\phi(t)}{dt} + k_1\phi(t) \leq k_2 \qquad \forall\, t \in I,$$

where $(k_1, k_2) \in \mathbb{R}^2$, $k_1 \neq 0$ and $I \subset [0, \infty)$ is an interval. Gathering all terms on one side and multiplying the above by $\exp(k_1 t) > 0$, yields

$$\left(\frac{d\phi(t)}{dt} + k_1\phi(t) - k_2\right)\exp(k_1 t) \leq 0 \qquad \forall\, t \in I.$$

This is equivalent to writing

$$\frac{d}{dt}\left(\left[\phi(t) - \frac{k_2}{k_1}\right]\exp(k_1 t)\right) \leq 0$$

implying that the function $[\phi(t) - \frac{k_2}{k_1}]\exp(k_1 t)$ is non-increasing for $t \in I$. Hence for any $t \in I \subset [0, \infty)$ we have

$$\left[\phi(t) - \frac{k_2}{k_1}\right]\exp(k_1 t) \leq \left[\phi(0) - \frac{k_2}{k_1}\right]\underbrace{\exp(k_1 \cdot 0)}_{=1}$$

Simple algebraic manipulations yield the desired result

$$\phi(t) \leq \frac{k_2}{k_1} - \left[\frac{k_2}{k_1} - \phi(0)\right]\exp(-k_1 t) \qquad \forall\, t \in I. \qquad \square$$

With this auxiliary lemma and restricting the parameters in system (2.1.5) by $a = d$ and $\frac{g}{f} - h > 0$, we can now prove (cf. [Aziz-Alaoui, 2002], [Aziz-Alaoui and Okiye, 2003])

Lemma 2.2.3.
In equations (2.1.5) *assume $a = d$ and $\frac{g}{f} - h > 0$. Then for any solution s it holds that*

$$x(t) + \frac{y(t)}{c} < x_M + \frac{y_0}{c} + \frac{1}{4b} \tag{2.2.4}$$

for all $t \in I$. Furthermore, for any s we have

$$\begin{aligned} 0 \leq y(t) &< cx_M + y_0 + \frac{c}{4b} \\ &< cx_M + y_0 + \frac{c}{4b} + \frac{g}{f} - h =: y_M(x_0, y_0) = y_M \qquad \forall\, t \in I. \end{aligned}$$

Proof.
Let $a = d$ and and $\frac{g}{f} - h > 0$ hold in system (2.1.5) and any solution s be given. We define the function $\phi(t) := x(t) + \frac{y(t)}{c}$ and compute

$$\begin{aligned} \frac{d\phi(t)}{dt} &= \dot{x}(t) + \frac{\dot{y}(t)}{c} \\ &= x(1-x) - \frac{xy}{x+a} - \frac{b}{c}y + \frac{1}{c}\frac{cxy}{x+a} - \frac{1}{c}\frac{yz}{y+e} \qquad (2.2.5) \\ &= x(1-x) - \frac{b}{c}y - \underbrace{\frac{1}{c}\frac{yz}{y+e}}_{\geq 0} \\ &\leq x(1-x) - \frac{b}{c}y, \end{aligned}$$

where the inequality holds since $y(t) \geq 0$ and $z(t) \geq 0$ for any $t \in I$ by Lemma 2.1.4. Inserting a 'zero' yields

$$\frac{d\phi}{dt} \leq x(1-x) + bx - b\underbrace{\left(x + \tfrac{y}{c}\right)}_{=\phi}$$

which may be rewritten as

$$\frac{d\phi(t)}{dt} + b\phi(t) \leq x(1-x) + bx \qquad \forall\, t \in I.$$

Since $\max_{x\in[0,\infty)} x(1-x) = \frac{1}{4}$ and using Lemma 2.2.1 we obtain for all $t \in I$:

$$\frac{d\phi(t)}{dt} + b\phi(t) \leq x(1-x) + bx \leq \frac{1}{4} + bx_M \leq \frac{1}{4} + b\left(x_M + \frac{y_0}{c}\right).$$

Now ϕ is differentiable on I (since s is a solution of an IVP) and hence fulfils all the assumptions of Lemma 2.2.2 with

$$k_1 = b > 0 \quad \text{and} \quad k_2 = \frac{1}{4} + b\left(x_M + \frac{y_0}{c}\right).$$

Applying the lemma yields

$$\phi(t) \leq x_M + \frac{y_0}{c} + \frac{1}{4b} - \left[x_M + \frac{y_0}{c} + \frac{1}{4b} - \phi(0)\right]\exp(-bt)$$

for all $t \in I$. Using that

$$\phi(0) = x_0 + \frac{y_0}{c} \leq x_M + \frac{y_0}{c} < x_M + \frac{y_0}{c} + \frac{1}{4b}$$

holds, we obtain

$$\phi(t) \leq x_M + \frac{y_0}{c} + \frac{1}{4b} - \underbrace{\left[x_M + \frac{y_0}{c} + \frac{1}{4b} - \phi(0)\right]}_{>0}\underbrace{\exp(-bt)}_{>0} < x_M + \frac{y_0}{c} + \frac{1}{4b}$$

for all $t \in I$. This proves the first claim of the lemma.
By solving (2.2.4) for $y(t)$ and noting that $\frac{g}{f} - h > 0$ and $x(t) \geq 0$ and $y(t) \geq 0$ for all $t \in I$ (Lemma 2.1.4) we obtain

$$\begin{aligned} 0 \leq y(t) < c\left(x_M + \frac{y_0}{c} + \frac{1}{4b} - x(t)\right) &\leq cx_M + y_0 + \frac{c}{4b} \\ &< cx_M + y_0 + \frac{c}{4b} + \frac{g}{f} - h \qquad \forall\, t \in I, \end{aligned}$$

which proves the second claim of the lemma. □

Remark 2.2.2.
Concerning the restrictions on the parameters we remark:

- Considering the estimate (2.2.5) in the above proof more closely, we see that the restriction $a \leq d$ would in fact be sufficient since we still obtain

$$\frac{d\phi(t)}{dt} = x(1-x) - \frac{b}{c}y - \underbrace{\left(\frac{xy}{x+a} - \frac{xy}{x+d}\right)}_{>0} - \frac{1}{c}\frac{yz}{y+e} \leq x(1-x) - \frac{b}{c}y.$$

  Nonetheless, we will assume that $a = d$ for the further considerations, as it is a common assumption for ecological predator-prey systems (cf. [Holling, 1965], [Kuznetsov, 1995] for example). A biological interpretation of the above condition is provided in subsection 2.5.1.

- Note that the restriction $\frac{g}{f} - h > 0$ is in fact not necessary to prove the existence of a bound y_M as above. One can simply choose the *stricter* bound

$$\widetilde{y}_M = cx_M + y_0 + \frac{c}{4b},$$

  by omitting the last line of the proof. However, since we will need and use the restriction $\frac{g}{f} - h > 0$ in any case (this will become apparent just now - see Lemma 2.2.4), we define this looser bound in favour of simpler estimates and better readability later on in this thesis.

By the above remark and Lemmas 2.2.1 and 2.2.3 we obtain that under the assumption $a = d$ (which we assume to hold from now on, unless stated otherwise) for any solution s we have

$$0 \leq x(t) \leq x_M = x_M(x_0) < \infty$$
$$0 \leq y(t) \leq y_M = y_M(x_0, y_0) < \infty$$

for all $t \in I$. In other words, the first two components of a solution s are bounded by constants (for any time value in $I \subset [0, \infty)$), that (only) depend on the initial conditions x_0 and y_0. Hence, only the the z-component of a solution s can blow up in finite future time or be unbounded as time tends to infinity.

2.2.2 Blow-up

The results from above motivate the following

Definition 2.2.1.
*A solution s is said to **blow up** or **explode** (in finite future time) if there exists a finite $T^{**} > 0$ such that*

$$\limsup_{t \nearrow T^{**}} z(t) = \infty.$$

By this the maximal right existence interval of s is given by $I = [0, T^{**})$.

We first consider a case for which a blow-up is guaranteed (cf. [Aziz-Alaoui, 2002], [Parshad et al., 2015]):

Lemma 2.2.4.
Let $f - \frac{g}{h} > 0$ and a solution s be given. If $z_0 > 0$ then s will blow up.

Proof.
Let $f - \frac{g}{h} > 0$ hold in (2.1.5) and a solution s with $z_0 > 0$ be given. Note that this implies $z(t) > 0$ for all $t \in I$ (Lemma 2.1.5). Furthermore, for any $t \in I$ we estimate

$$\dot{z}(t) = \left(f - \frac{g}{y(t) + h}\right) z^2(t) \geq \left(f - \frac{g}{h}\right) z^2(t).$$

Dividing by $z^2(t) > 0$ and integrating from zero to $t \in I$ results in

$$-\frac{1}{z(t)} + \frac{1}{z_0} \geq \left(f - \frac{g}{h}\right) t.$$

Solving this for $z(t)$ yields

$$z(t) \geq \frac{1}{\frac{1}{z_0} - \left(f - \frac{g}{h}\right) t}$$

for any $t \in I$ (a result we may also obtain by comparison in the above differential inequality, cf. [Walter, 1990]). However, the right-hand side of the above fulfils

$$\frac{1}{\frac{1}{z_0} - \left(f - \frac{g}{h}\right) t} \to \infty \quad \text{as} \quad t \to \frac{1}{z_0 \left(f - \frac{g}{h}\right)} =: T^* > 0.$$

Hence there exists a $T^{**} \in (0, T^*]$ such that

$$\limsup_{t \to T^{**}} z(t) = \infty. \qquad \square$$

The above lemma motivates imposing the following restriction on the parameters

$$f - \frac{g}{h} < 0, \tag{2.2.6}$$

which is in fact equivalent to the condition $\frac{g}{f} - h > 0$ imposed in Lemma 2.2.3. Throughout the rest of this text we assume this condition holds, unless stated otherwise. A biological interpretation of the condition is given in subsection 2.5.1. Furthermore, for any solution s we obtain (by Lemma 2.1.3) the implication

$$z_0 = 0 \quad \Rightarrow \quad z(t) = 0 \quad \forall\, t \in I \tag{2.2.7}$$

and hence if $z_0 = 0$ the z-component does not blow up and the corresponding maximal right existence interval of s is given by $I = [0, \infty)$. In a similar manner for any solution s it holds that

$$y_0 = 0 \quad \Rightarrow \quad y(t) = 0 \quad \forall\, t \in I$$

which in turn implies (by (2.2.6))

$$\dot{z}(t) = \left(f - \frac{g}{h}\right) z^2(t) \leq 0 \quad \forall\, t \in I \quad \Rightarrow \quad z(t) \leq z_0 \quad \forall\, t \in I \tag{2.2.8}$$

and hence the z-component does not blow up and $I = [0, \infty)$. Thus we have shown

Corollary 2.2.1.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold.

- *For any solution s with $y_0 = 0$, it holds that*

$$z(t) \leq z_0 \qquad \forall\, t \in I = [0, \infty).$$

- *For any solution s with $z_0 = 0$, it holds that*

$$z(t) = z_0 = 0 \qquad \forall\, t \in I = [0, \infty).$$

Having considered the cases $y_0 = 0$ and $z_0 = 0$ we assume $y_0 > 0$ and $z_0 > 0$ to hold, which implies $y(t) > 0$ and $z(t) > 0$ for any $t \in I$ (Lemma 2.1.5). Hence, we still need to consider solutions s with the following restrictions on the parameters in (2.1.5) and the initial values $s_0 \in \mathcal{O}_0^+$:

- $a = d$
- $f - \frac{g}{h} < 0$
- $y_0 > 0$ (implying $y(t) > 0$ for all $t \in I$)
- $z_0 > 0$ (implying $z(t) > 0$ for all $t \in I$)

Before considering the issue of the blow-up we show the following auxiliary

Lemma 2.2.5.
Let a solution s be given and define

$$z_* := \max \left\{ \left(-b + \frac{c x_M}{x_M + d} \right) (y_M + e)\, , 0 \right\} \geq 0.$$

If s fulfils $y_0 > 0$ and $z_0 > 0$, then for any $t \in I$ such that $z(t) > z_*$ it holds that $\dot{y}(t) < 0$.

Proof.
Let any solution s with $y_0 > 0$ and $z_0 > 0$ be given and observe that since $y(t) > 0$ for any $t \in I$ holds, the second equation in (2.1.5) yields

$$\begin{aligned} \dot{y}(t) < 0 \quad &\Leftrightarrow \quad -b + \frac{c x(t)}{x(t) + d} - \frac{z(t)}{y(t) + e} < 0 \\ &\Leftrightarrow \quad z(t) > \left(-b + \frac{c x(t)}{x(t) + d} \right) (y(t) + e)\, . \end{aligned}$$

Furthermore, since the first two components of s are both bounded by zero from below and x_M and y_M from above respectively on I, we obtain for any $t \in I$

$$\begin{aligned} \left(-b + \frac{c x(t)}{x(t) + d} \right) \underbrace{(y(t) + e)}_{>0} &\leq \left(-b + \frac{c x_M}{x_M + d} \right) (y(t) + e) \\ &\leq \max \left\{ \left(-b + \frac{c x_M}{x_M + d} \right) (y_M + e)\, , 0 \right\} = z_* \end{aligned}$$

where the first inequality holds due to the fact that $\frac{cx}{x+d}$ is monotonically increasing in x on $[0, \infty)$. Combining the above yields that if $z(t) > z_*$ (for any $t \in I$) then $\dot{y}(t) < 0$, or differently put

$$(\forall\, t \in I : z(t) > z_*) \quad \Rightarrow \quad \dot{y}(t) < 0. \qquad \square$$

Having proven the lemma we now consider blow-up solutions.

2.2.3 Monotone blow-up property

The aim of this subsection is to prove Lemma 2.2.6 (see below). In order to achieve this we first prove several auxiliary lemmas and eventually, at the end of this subsection, Lemma 2.2.6.

Lemma 2.2.6 (Monotone blow-up)**.**
Let s be a solution with $y_0 > 0$ and $z_0 > 0$ that blows up (at the time $T^{**} > 0$). Then there exists a $T_0 \in [0, T^{**})$ such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in [T_0, T^{**}).$$

Remark 2.2.3.
Note that for any such solution s (recall $z_0 > 0$ holds) we have $z(t) > 0$ for any $t \in I$. Therefore considering the third equation of (2.1.5) one obtains

$$\begin{aligned} \dot{z}(t) > 0 \quad &\Leftrightarrow \quad y(t) > \frac{g}{f} - h \\ \dot{z}(t) = 0 \quad &\Leftrightarrow \quad y(t) = \frac{g}{f} - h \\ \dot{z}(t) < 0 \quad &\Leftrightarrow \quad y(t) < \frac{g}{f} - h \end{aligned} \tag{2.2.9}$$

for any $t \in I$. Hence the claim of the above lemma is equivalent to saying that there exists a $T_0 \in [0, T^{**})$ such that z is strictly monotonically increasing on $[T_0, T^{**})$. This motivates the expression 'monotone blow-up property' (of s), see Figure 2.2.1.

As mentioned beforehand, prior to proving Lemma 2.2.6 we first state and prove several auxiliary lemmas.

Lemma 2.2.7.
Let s be a solution with $y_0 > 0$ and $z_0 > 0$ that blows up and fulfils $z_* = 0$. Then it holds that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in [0, T^{**}).$$

Proof.
Let s be a solution with $y_0 > 0$ and $z_0 > 0$ that blows up and fulfils $z_* = 0$. Since $z_* = 0$ we obtain from the definition in Lemma 2.2.5 that

$$-b + \frac{cx_M}{x_M + d} \leq 0.$$

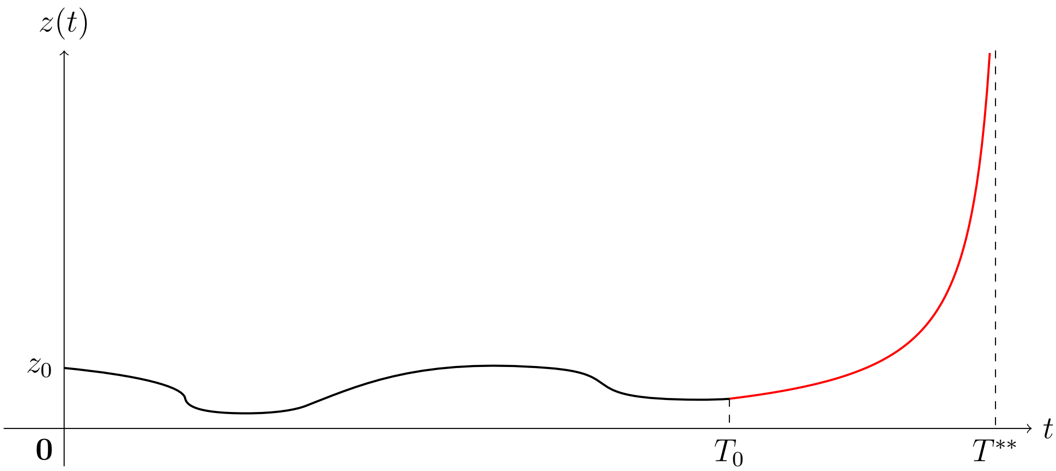


Figure 2.2.1: The monotone blow-up property of solutions s. The third component of s is strictly monotonically increasing on $[T_0, T^{**})$.

In particular for any $t \in [0, T^{**})$:

$$\dot{y}(t) = y(t)\left(-b + \frac{cx(t)}{x(t)+d} - \frac{z(t)}{y(t)+e}\right) \leq y(t)\Big(\underbrace{-b + \frac{cx_M}{x_M+d}}_{\leq 0} - \underbrace{\frac{z(t)}{y(t)+e}}_{<0}\Big) < 0,$$

i.e. in short

$$\dot{y}(t) < 0 \qquad \forall\, t \in [0, T^{**}). \tag{2.2.10}$$

Using this we now provide a proof by contradiction. Assume there exists a $T_0 \in [0, T^{**})$ such that $y(T_0) \leq \frac{g}{f} - h$. By (2.2.10) this implies that

$$y(t) \leq \frac{g}{f} - h \qquad \forall\, t \in [T_0, T^{**}).$$

This in turn implies (by (2.2.9)) that

$$\dot{z}(t) \leq 0 \qquad \forall\, t \in [T_0, T^{**}).$$

Hence

$$z(t) \leq z(T_0) \qquad \forall\, t \in [T_0, T^{**}).$$

This however is a contradiction to s blowing up. Therefore our assumption was wrong and

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in [0, T^{**}).$$ □

We now consider the case $z_* > 0$.

Lemma 2.2.8.
Let s be a solution with $y_0 > 0$ and $z_0 > 0$ such that it blows up and fulfils $z_* > 0$ and there exists a $T_0 \in [0, T^{**})$ such that $y(T_0) \leq \frac{g}{f} - h$. Then there exists a $\widehat{T} \in [T_0, T^{**})$ such that

$$z(\widehat{T}) \leq z_*.$$

Proof.
Let s be a solution with $y_0 > 0$ and $z_0 > 0$ such that it blows up and fulfils $z_* > 0$ and there exists a $T_0 \in [0, T^{**})$ such that $y(T_0) \leq \frac{g}{f} - h$. Once again we provide a proof by contradiction and hence we assume that

$$z(t) > z_* \qquad \forall\, t \in [T_0, T^{**}).$$

Thus, by Lemma 2.2.5 we know that

$$\dot{y}(t) < 0 \qquad \forall\, t \in [T_0, T^{**}).$$

Since by assumption $y(T_0) \leq \frac{g}{f} - h$ we obtain

$$y(t) \leq \frac{g}{f} - h \qquad \forall\, t \in [T_0, T^{**}).$$

This in turn implies (by (2.2.9)) that

$$\dot{z}(t) \leq 0 \qquad \forall\, t \in [T_0, T^{**}).$$

Hence

$$z(t) \leq z(T_0) \qquad \forall\, t \in [T_0, T^{**}).$$

This however is a contradiction to s blowing up. Therefore our assumption was wrong and there exists a $\widehat{T} \in [T_0, T^{**})$ such that

$$z(\widehat{T}) \leq z_*. \qquad \square$$

We will use this previous lemma to show the next one.

Lemma 2.2.9.
Let s be a solution with $y_0 > 0$ and $z_0 > 0$ such that it blows up and fulfils $z_* > 0$ and there exists a $T_0 \in [0, T^{**})$ such that $y(T_0) \leq \frac{g}{f} - h$. Then there exists a $\widehat{T} \in [T_0, T^{**})$ such that

$$-\frac{1}{z(t)} < (T^{**} - \widehat{T})f - \frac{1}{z_*} \qquad \forall\, t \in [\widehat{T}, T^{**}).$$

Proof.
Let s be a solution with $y_0 > 0$ and $z_0 > 0$ such that it blows up and fulfils $z_* > 0$ and there exists a $T_0 \in [0, T^{**})$ such that $y(T_0) \leq \frac{g}{f} - h$. Hence the conditions of Lemma 2.2.8 are met and in particular there exists a $\widehat{T} \in [T_0, T^{**})$ such that

$$z(\widehat{T}) \leq z_*.$$

We show that this $\widehat{T}$ suffices to also fulfil our current claim. Consider the following estimate of the third line of our ODE-system (2.1.5):

$$\dot{z}(t) = \left(f - \frac{g}{y(t) + h}\right) z^2(t) < f z^2(t).$$

Since $z(t) > 0$ this is equivalent to

$$\frac{\dot{z}(t)}{z^2(t)} < f.$$

Integration from $\widehat{T} \in [T_0, T^{**})$ to $t \in [\widehat{T}, T^{**})$ now yields

$$\int_{\widehat{T}}^{t} \frac{\dot{z}(\tau)}{z^2(\tau)} d\tau < \int_{\widehat{T}}^{t} f d\tau$$

which is equivalent to

$$-\frac{1}{z(t)} + \frac{1}{z(\widehat{T})} < (t - \widehat{T})f \qquad \forall\, t \in [\widehat{T}, T^{**}).$$

Subtracting $\frac{1}{z(\widehat{T})} > 0$ on both sides yields

$$-\frac{1}{z(t)} < (t - \widehat{T})f - \frac{1}{z(\widehat{T})} \qquad \forall\, t \in [\widehat{T}, T^{**}) \tag{2.2.11}$$

Finally, since $t < T^{**}$ and $0 < z(\widehat{T}) \leq z_*$ (by the choice of $\widehat{T}$) we obtain

$$(t - \widehat{T})f - \frac{1}{z(\widehat{T})} < (T^{**} - \widehat{T})f - \frac{1}{z_*} \qquad \forall\, t \in [\widehat{T}, T^{**})$$

and hence applying this in (2.2.11) results in

$$-\frac{1}{z(t)} < (T^{**} - \widehat{T})f - \frac{1}{z_*} \qquad \forall\, t \in [\widehat{T}, T^{**}).$$ □

With these result we now turn to proving Lemma 2.2.6.

Proof of Lemma 2.2.6.
Let s be a solution with $y_0 > 0$ and $z_0 > 0$ that blows up.

Case 1: $z_* = 0$
The conditions of Lemma 2.2.7 are met and choosing $T_0 = 0$ yields the claim.

Case 2: $z_* > 0$
We provide a proof by contradiction. Therefore we assume the opposite of the claim, that is

$$\forall\, T_0 \in [0, T^{**}) \;\; \exists\, \widetilde{T} \in [T_0, T^{**}) : y(\widetilde{T}) \leq \frac{g}{f} - h.$$

Using this property we choose a sufficiently large $T_0 \in [0, T^{**})$ such that

$$T^{**} - T_0 < \frac{1}{2fz_*} \quad \text{and} \quad y(T_0) = y(\widetilde{T}) \leq \frac{g}{f} - h$$

hold. For this T_0 the conditions of Lemma 2.2.9 are met and in particular we conclude that there exists a $\widehat{T} \in [T_0, T^{**})$ such that

$$-\frac{1}{z(t)} < (T^{**} - \widehat{T})f - \frac{1}{z_*} \qquad \forall\, t \in [\widehat{T}, T^{**}).$$

Since $[\widehat{T}, T^{**}) \subset [T_0, T^{**})$ we have $T^{**} - \widehat{T} \leq T^{**} - T_0$. Applying this to the above yields

$$-\frac{1}{z(t)} < (T^{**} - T_0)f - \frac{1}{z_*} \qquad \forall\, t \in [\widehat{T}, T^{**}).$$

For our choice of T_0 we may further estimate for any $t \in [\widehat{T}, T^{**})$

$$-\frac{1}{z(t)} < (T^{**} - T_0)f - \frac{1}{z_*} < \frac{1}{2fz_*}f - \frac{1}{z_*} = -\frac{1}{2z_*}.$$

Rewriting this and noting that $\frac{1}{2z_*} > 0$ yields

$$z(t) < 2z_* \qquad \forall\, t \in [\widehat{T}, T^{**}).$$

This however is a contradiction to the blow-up property of s. In particular our assumption was wrong and there exists a $T_0 \in [0, T^{**})$ such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in [T_0, T^{**}).$$ □

We have now proven that Lemma 2.2.6 holds and by the remark on said lemma we know that this is equivalent to the z-component (of any exploding solution) increasing monotonically on some subinterval $[T_0, T^{**}) \subset [0, T^{**}) = I$, recall Figure 2.2.1.

2.2.4 Non-blow-up

In this subsection we prove, that in fact **no** solution s may blow-up under the assumptions $a = d$ and $f - \frac{g}{h} < 0$.

Proposition 2.2.1.
Let $a = d$ and $f - \frac{g}{h} < 0$ and any solution s be given. Then s does not blow up (in finite future time) and thus the positive existence interval of s is $I = [0, \infty)$.

Proof.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold in (2.1.5) and any solution s be given. If $y_0 = 0$ or $z_0 = 0$ then the solution s cannot explode by Corollary 2.2.1.
For the other cases we again provide a proof by contradiction: Hence we are left with solutions s that fulfil $y_0 > 0$ and $z_0 > 0$ and assume that such a solution s blows up. In particular s fulfils the conditions of Lemma 2.2.6. Therefore we know that there exists a $T_0 \in [0, T^{**})$ such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in [T_0, T^{**}). \tag{2.2.12}$$

We now consider the solution for $t \in [T_0, T^{**})$. From the third line of the given ODE-system in (2.1.5) we see

$$0 < z(t) = \frac{\dot{z}(t)}{z(t)} \cdot \underbrace{\frac{1}{f - \frac{g}{y(t)+h}}}_{>0 \text{ by } (2.2.12)}, \tag{2.2.13}$$

for $t \in [T_0, T^{**})$, recalling that $z(t) > 0$ for any $t \in I$ since $z_0 > 0$ (Lemma 2.1.5). Substituting this into the second equation of (2.1.5) yields

$$\dot{y}(t) = y(t)\left[-b + \frac{cx(t)}{x(t)+d} - \frac{\dot{z}(t)}{z(t)} \cdot \frac{1}{f - \frac{g}{y(t)+h}} \cdot \frac{1}{y(t)+e}\right] \qquad \forall\, t \in [T_0, T^{**}).$$

Dividing by $y(t) > 0$ and estimating the term $\frac{cx(t)}{x(t)+d}$ as before yields

$$\begin{aligned}\frac{\dot{y}(t)}{y(t)} &= -b + \frac{cx(t)}{x(t)+d} - \frac{\dot{z}(t)}{z(t)} \frac{1}{f - \frac{g}{y(t)+h}} \frac{1}{y(t)+e} \\ &\leq -b + \frac{cx_M}{x_M+d} - \frac{\dot{z}(t)}{z(t)} \frac{1}{f - \frac{g}{y(t)+h}} \frac{1}{y(t)+e}\end{aligned}$$

for $t \in [T_0, T^{**})$. Since equation (2.2.12) holds on $[T_0, T^{**}) \subset I$ and y is bounded by $y_M > \frac{g}{f} - h$ on I, we obtain

$$\begin{aligned}\frac{\dot{y}(t)}{y(t)} &\leq -b + \frac{cx_M}{x_M+d} - \overbrace{\frac{\dot{z}(t)}{z(t)} \underbrace{\frac{1}{f - \frac{g}{y(t)+h}}}_{>0 \text{ by } (2.2.12)}}^{>0 \text{ by } (2.2.13)} \frac{1}{y(t)+e} \\ &\leq -b + \frac{cx_M}{x_M+d} - \frac{\dot{z}(t)}{z(t)} \underbrace{\frac{1}{f - \frac{g}{y_M+h}}}_{>0} \frac{1}{y_M+e}\end{aligned}$$

for $t \in [T_0, T^{**})$. For the sake of readability we define

$$\begin{aligned}\alpha &:= -b + \frac{cx_M}{x_M+d} \\ \beta &:= \frac{1}{f - \frac{g}{y_M+h}} \cdot \frac{1}{y_M+e} > 0\end{aligned}$$

which allows us to write the previous estimate as follows

$$\frac{\dot{y}(t)}{y(t)} \leq \alpha - \beta \frac{\dot{z}(t)}{z(t)} \qquad \forall\, t \in [T_0, T^{**}).$$

Integrating both sides from T_0 to $t \in [T_0, T^{**})$ yields

$$\int_{T_0}^{t} \frac{\dot{y}(\tau)}{y(\tau)} d\tau \leq \int_{T_0}^{t} \alpha - \beta \frac{\dot{z}(\tau)}{z(\tau)} d\tau$$

$$\Leftrightarrow \qquad [\ln(y(\tau))]_{\tau=T_0}^{\tau=t} \leq \alpha(t - T_0) - \beta \left[\ln(z(\tau))\right]_{\tau=T_0}^{\tau=t}$$

This may also be written as

$$\ln\left(\frac{y(t)}{y(T_0)}\right) \leq \alpha(t - T_0) - \beta \ln\left(\frac{z(t)}{z(T_0)}\right) = \alpha(t - T_0) + \ln\left(\left(\frac{z(T_0)}{z(t)}\right)^{\beta}\right).$$

Applying the exponential function on both sides of the equation yields

$$\frac{y(t)}{y(T_0)} \leq \exp(\alpha(t - T_0)) \left(\frac{z(T_0)}{z(t)}\right)^{\beta}.$$

Furthermore, multiplying by $y(T_0) > 0$ results in

$$y(t) \leq y(T_0) \exp(\alpha(t - T_0)) \left(\frac{z(T_0)}{z(t)}\right)^{\beta} \qquad \forall\, t \in [T_0, T^{**}). \tag{2.2.14}$$

Rewriting this we obtain (note $\beta > 0$)

$$z(t) \leq z(T_0) \sqrt[\beta]{\frac{y(T_0)}{y(t)} \exp(\alpha(t - T_0))} \qquad \forall\, t \in [T_0, T^{**}).$$

Using (2.2.12) and the boundedness of the y-component by y_M allows the estimate

$$z(t) < z(T_0) \sqrt[\beta]{\frac{y_M}{\frac{g}{f} - h} \exp(\alpha(t - T_0))} \qquad \forall\, t \in [T_0, T^{**}). \tag{2.2.15}$$

We now consider two cases, dependent on the sign of α.

i) If $\alpha \leq 0$ then $\exp(\alpha(t - T_0)) \leq 1$ for any $t \in [T_0, T^{**})$. This allows us to estimate (2.2.15) as follows

$$\begin{aligned} z(t) &< z(T_0) \sqrt[\beta]{\frac{y_M}{\frac{g}{f} - h} \exp(\alpha(t - T_0))} \\ &\leq z(T_0) \sqrt[\beta]{\frac{y_M}{\frac{g}{f} - h}} < \infty \qquad \forall\, t \in [T_0, T^{**}). \end{aligned}$$

This however is a contradiction to s blowing up.

ii) If $\alpha > 0$ then $\exp(\alpha(t - T_0)) \leq \exp(\alpha(T^{**} - T_0))$ for any $t \in [T_0, T^{**})$. This allows us to estimate (2.2.15) as follows

$$\begin{aligned} z(t) &< z(T_0) \sqrt[\beta]{\frac{y_M}{\frac{g}{f} - h} \exp(\alpha(t - T_0))} \\ &\leq z(T_0) \sqrt[\beta]{\frac{y_M}{\frac{g}{f} - h} \exp(\alpha(T^{**} - T_0))} < \infty \qquad \forall\, t \in [T_0, T^{**}). \end{aligned}$$

This however is a contradiction to s blowing up. □

The proposition proves that under the given restrictions on the parameters no solution s can blow up in finite time, contradicting the claim in [Parshad et al., 2015] and [Parshad et al., 2016b]. We discuss this controversy concerning blow-up of solutions (which arose in [Aziz-Alaoui, 2002] and [Parshad et al., 2015]) in Appendix B. By the above the maximal right existence interval of any such solution s is in fact given by $I = [0, \infty)$.
Note that as a consequence of the above proof we obtain an estimate for the y- or z-component of a solution s when imposing certain conditions on s and the parameters:

Corollary 2.2.2.
Let $a = d$ and $f - \frac{g}{h} < 0$ and any solution s be given with $y_0 > 0$ and $z_0 > 0$. Furthermore let an interval $I_0 \subset [0, \infty)$ with $\min I_0 = T_0 \geq 0$ exist such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in I_0.$$

Then it holds that

$$y(t) \leq y(T_0) \exp(\alpha(t - T_0)) \left(\frac{z(T_0)}{z(t)} \right)^{\beta} \qquad \forall\, t \in I_0,$$

where

$$\begin{aligned} \alpha &:= -b + \frac{c x_M}{x_M + d}, \\ \beta &:= \frac{1}{\left(f - \frac{g}{y_M + h}\right)(y_M + e)} > 0. \end{aligned}$$

Proof.
The proof works analogously to the derivation of equation (2.2.14) from (2.2.12) in the proof of Proposition 2.2.1 by replacing the interval $[T_0, T^{**})$ with any interval I_0 fulfilling $\min I_0 = T_0 \geq 0$. □

Remark 2.2.4.
Note that the interval I_0 in the above corollary may in particular be closed, i.e. $I_0 = [T_0, T^{**}]$, or unbounded, i.e. $I_0 = [T_0, \infty)$. This will prove useful later.

Another important consequence of the result in Proposition 2.2.1 is that the dynamics generated by system (2.1.5) define a semiflow on $\mathcal{O}_0^+$ (for the definition see Appendix A).

Corollary 2.2.3.
Assume $a = d$ *and* $f - \frac{g}{h} < 0$ *holds in* (2.1.5)*. Then the map*

$$\begin{aligned} \Phi : \mathbb{R}_0^+ \times \mathcal{O}_0^+ &\to \mathcal{O}_0^+ \\ (t, s_0) &\mapsto s(t) \end{aligned}$$

is a semiflow on $\mathcal{O}_0^+$*, where the solution* s *(with* $s_0 \in \mathcal{O}_0^+$*) is defined in Definition 2.1.1.*

Proof.
The metric space we consider is $(\mathcal{O}_0^+, \mathrm{d})$ (with the Euclidean metric d). The map Φ is given by setting $\Phi(t, s_0) = s(t)$, where s is the solution of the initial value problem given by $s_0 \in \mathcal{O}_0^+$ and the system (2.1.5). Since we have proven that any such solution s is defined for all $t \geq 0$ (Proposition 2.2.1) and maps into $\mathcal{O}_0^+$ (Lemma 2.1.4) we indeed have

$$\Phi : \mathbb{R}_0^+ \times \mathcal{O}_0^+ \to \mathcal{O}_0^+.$$

The fact that the map fulfils all the other required properties (identity, continuity, semiflow) is an immediate consequence of the fact that Φ is obtained from solutions of initial value problems corresponding to an autonomous vector field v (see e.g. [Amann, 1990], [Sell and You, 2002]). □

Hence the *dynamics on* $\mathcal{O}_0^+$ *generated by system* (2.1.5) can be identified with the semiflow Φ on $\mathcal{O}_0^+$. In particular, via $\Phi(t, s_0) = s(t)$ for any $s_0 \in \mathcal{O}_0^+$, we are able to formulate results in terms of the flow or of solutions interchangeably. For example we can identify a solution s for $t \in I$ (and hence the corresponding positive phase curve $\gamma_{s_0}^+$) with the positive orbit through a point $s_0 \in \mathcal{O}_0^+$, since

$$s(I) = \{s(t) \, : \, t \geq 0\} = \{\Phi(t, s_0) \, : \, t \geq 0\} = \Gamma_{s_0}^+.$$

The existence of the semiflow Φ also implies that the sets $\mathcal{O}_0^+$ and $\mathcal{O}^+$ are *positive invariant* under Φ, since both sets have property *(I1)*. We will make use of this in subsequent considerations.

2.2.5 Boundedness

Having proven that solutions s do not explode in *finite future time* the question arises whether the same holds true for *infinite future time* (i.e. as $t \to \infty$). From Lemma 2.2.1 and Lemma 2.2.3 we know that the first two components of s are bounded for all $t \geq 0$ from above and below and hence once again an explosion of s as time tends to infinity may only occur in the z-component. I.e. we ask whether a solution s exists such that

$$\limsup_{t \to \infty} z(t) = \infty.$$

In fact, we prove that **no** such solution exists under the parameter assumptions from above, i.e. $a = d$ and $f - \frac{g}{h} < 0$ (which we assume to hold throughout this subsection as well). We will show this by proving that any such solution s is bounded by a *time-independent* bound for all $t \geq 0$ (see Proposition 2.2.2 and Corollary 2.2.5 at the end of this subsection). Analogously to the blow-up we commence the discussion by considering special cases (concerning the initial conditions s_0) and then turn to the remaining (general) case.

The special cases

We remind the reader that for the particular cases $y_0 = 0$ and $z_0 = 0$ we obtained bounds on the z-component in Corollary 2.2.1. Next we consider the cases $x_0 = 0$ and $z_* = 0$ (where z_* is defined as in Lemma 2.2.5).

Lemma 2.2.10.
Let s be a solution such that $x_0 = 0$ or $z_* = 0$ (or both) holds. Then the y-component of s is non-increasing for any $t \geq 0$, i.e.

$$\dot{y}(t) \leq 0 \qquad \forall\, t \geq 0.$$

Proof.
Let s be a solution such that $x_0 = 0$ or $z_* = 0$ (or both).

- If $x_0 = 0$ then $x(t) = 0$ for all $t \geq 0$ (by Lemmas 2.1.2 and 2.1.3). This allows us to conclude for any $t \geq 0$ that

$$\dot{y}(t) = y(t)\left(-b + \frac{cx(t)}{x(t)+d} - \frac{z(t)}{y(t)+e}\right) = y(t)\underbrace{\left(-b - \frac{z(t)}{y(t)+e}\right)}_{\leq 0} \leq 0.$$

- If $z_* = 0$ we have

$$-b + \frac{cx_M}{x_M + d} \leq 0$$

  and hence - using $x(t) \leq x_M$ for any $t \geq 0$ (Lemma 2.2.1) - it holds that for all $t \geq 0$

$$\begin{aligned}\dot{y}(t) &= y(t)\left(-b + \frac{cx(t)}{x(t)+d} - \frac{z(t)}{y(t)+e}\right)\\ &\leq y(t)\underbrace{\left(-b + \frac{cx_M}{x_M+d} - \frac{z(t)}{y(t)+e}\right)}_{\leq 0} \leq 0.\end{aligned}$$ □

This allows us to prove

Lemma 2.2.11.
Let s be a solution such that $y_0 \leq \frac{g}{f} - h$ and $x_0 = 0$ or $z_* = 0$ (or both), then it holds that

$$z(t) \leq z_0 \qquad \forall\, t \geq 0.$$

Proof.
Let s be a solution such that $y_0 \le \frac{g}{f} - h$ and $x_0 = 0$ or $z_* = 0$ (or both). By Lemma 2.2.10 the y-component is monotonically decreasing on $I = [0, \infty)$ and hence

$$y(t) \le y_0 \le \frac{g}{f} - h$$

for all $t \ge 0$. This in turn implies (by the third equation of system (2.1.5)) that

$$\dot{z}(t) \le 0 \qquad \forall\, t \ge 0$$

and therefore

$$z(t) \le z_0 \qquad \forall\, t \ge 0. \qquad \square$$

The case $y_0 > \frac{g}{f} - h$ is a bit more work:

Lemma 2.2.12.
Let s be a solution such that $y_0 > \frac{g}{f} - h$ and $x_0 = 0$ or $z_* = 0$ (or both), then it holds that

$$z(t) \le z_0 \left(\frac{y_0}{\frac{g}{f} - h} \right)^{\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \forall\, t \ge 0.$$

Proof.
Let s be a solution such that $y_0 > \frac{g}{f} - h$ and $x_0 = 0$ or $z_* = 0$ (or both). If $z_0 = 0$ we immediately obtain (from Corollary 2.2.1) that

$$z(t) = 0 = z_0 \left(\frac{y_0}{\frac{g}{f} - h} \right)^{\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \forall\, t \ge 0.$$

Hence we additionally assume $z_0 > 0$ for s, implying

$$z(t) > 0 \qquad \forall\, t \ge 0.$$

Let $I_L = [0, T_L) \subset [0, \infty)$ be the maximal (positive) interval such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in I_L. \tag{2.2.16}$$

Note that such an interval I_L exists and is non-empty, since $y(0) = y_0 > \frac{g}{f} - h$ and y is continuous for any $t \ge 0$ (since s is so too). Applying Corollary 2.2.2 (with $I_0 = I_L$ and $T_0 = 0$) now yields

$$y(t) \le y_0 \exp(\alpha t) \left(\frac{z_0}{z(t)} \right)^{\beta} \qquad \forall\, t \in I_L, \tag{2.2.17}$$

where

$$\alpha = -b + \frac{c x_M}{x_M + d} \overset{z_*=0}{\le} 0 \quad \text{and} \quad \beta = \frac{1}{\left(f - \frac{g}{y_M + h}\right)(y_M + e)} > 0.$$

Solving (2.2.17) for $z(t)$ yields

$$z(t) \leq z_0 \sqrt[\beta]{\frac{y_0}{y(t)} \exp(\alpha t)} \qquad \forall\, t \in I_L,$$

and estimating the above using $\alpha \leq 0$ and (2.2.16) results in

$$z(t) \leq z_0 \sqrt[\beta]{\frac{y_0}{y(t)} \exp(\alpha t)} < z_0 \sqrt[\beta]{\frac{y_0}{\frac{g}{f} - h}} \qquad \forall\, t \in I_L = [0, T_L). \tag{2.2.18}$$

i) If $I_L = [0, \infty)$ then

$$z(t) < z_0 \sqrt[\beta]{\frac{y_0}{\frac{g}{f} - h}} \qquad \forall\, t \geq 0.$$

ii) If $|I_L| < \infty$, i.e. $T_L < \infty$, then

$$y(T_L) \leq \frac{g}{f} - h,$$

since I_L was chosen to be maximal. Furthermore, from Lemma 2.2.10 we know that y is monotonically decreasing on $I = [0, \infty)$ and therefore the above implies

$$y(t) \leq \frac{g}{f} - h \qquad \forall\, t \geq T_L.$$

This in turn results in

$$\dot{z}(t) \leq 0 \qquad \forall\, t \geq T_L.$$

Therefore it holds that

$$z(t) \leq z(T_L) \qquad \forall\, t \geq T_L. \tag{2.2.19}$$

We now need an estimate for $z(T_L)$. Observe that z is continuous in t and (2.2.18) holds, yielding

$$z(T_L) = \lim_{t \nearrow T_L} z(t) \leq z_0 \sqrt[\beta]{\frac{y_0}{\frac{g}{f} - h}}.$$

Therefore (2.2.19) becomes

$$z(t) \leq z(T_L) \leq z_0 \sqrt[\beta]{\frac{y_0}{\frac{g}{f} - h}} \qquad \forall\, t \geq T_L.$$

and combining this with (2.2.18) results in

$$z(t) \leq z_0 \sqrt[\beta]{\frac{y_0}{\frac{g}{f} - h}} \qquad \forall\, t \geq 0.$$

Recalling the definition of $\beta > 0$ we finally obtain for any $t \geq 0$ that

$$z(t) \leq z_0 \sqrt[\beta]{\frac{y_0}{\frac{g}{f} - h}} = z_0 \left(\frac{y_0}{\frac{g}{f} - h}\right)^{\frac{1}{\beta}} = z_0 \left(\frac{y_0}{\frac{g}{f} - h}\right)^{\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \square$$

Having found bounds on the z-component in the special cases we now turn to the general case.

The general case

We restrict ourselves to (the remaining) solutions s with the following initial conditions:

- $x_0 > 0$ (implying $x(t) > 0$ for all $t \geq 0$)
- $y_0 > 0$ (implying $y(t) > 0$ for all $t \geq 0$)
- $z_0 > 0$ (implying $z(t) > 0$ for all $t \geq 0$)
- $z_* > 0$

Observing that

$$x_0 > 0 \wedge y_0 > 0 \wedge z_0 > 0 \quad \Leftrightarrow \quad s_0 \in \mathcal{O}^+$$

holds, the above conditions on the solutions may simply be written as $s_0 \in \mathcal{O}^+$ and $z_* > 0$. In order to show that such a solution s is bounded as time tends to infinity, we divide the positive octant $\mathcal{O}^+ \subset \mathcal{O}_0^+$ using two planes that partition $\mathcal{O}^+$ into four sets $\Omega_1, \Omega_2, \Omega_3, \Omega_4$ (see Figure 2.2.2). We then show that the positive phase curve $\gamma_{s_0}^+$ corresponding to s is bounded in any of these four sets for any $t \geq 0$.

Definition 2.2.2.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. We define

$$\Omega_1 := \left\{ (x, y, z) \in \mathcal{O}^+ \,:\, y \leq \frac{g}{f} - h,\, z < 2z_* \right\}$$
$$\Omega_2 := \left\{ (x, y, z) \in \mathcal{O}^+ \,:\, y > \frac{g}{f} - h,\, z < 2z_* \right\}$$
$$\Omega_3 := \left\{ (x, y, z) \in \mathcal{O}^+ \,:\, y > \frac{g}{f} - h,\, z \geq 2z_* \right\}$$
$$\Omega_4 := \left\{ (x, y, z) \in \mathcal{O}^+ \,:\, y \leq \frac{g}{f} - h,\, z \geq 2z_* \right\}$$

In particular we have

$$\mathcal{O}^+ = \Omega_1 \,\dot{\cup}\, \Omega_2 \,\dot{\cup}\, \Omega_3 \,\dot{\cup}\, \Omega_4 = \bigcup_{i=1}^{4} \Omega_i,$$

i.e. the sets Ω_i form a partition of $\mathcal{O}^+$.

Remark 2.2.5.
Since we assumed $\frac{g}{f} - h > 0$ and $z_* > 0$ to hold, we see that

$$\Omega_1, \Omega_2, \Omega_3, \Omega_4 \neq \emptyset$$

for any such solution s. The two planes given by $y = \frac{g}{f} - h$ and $z = 2z_*$ define the sets Ω_i. For a visualisation, see Figure 2.2.2.

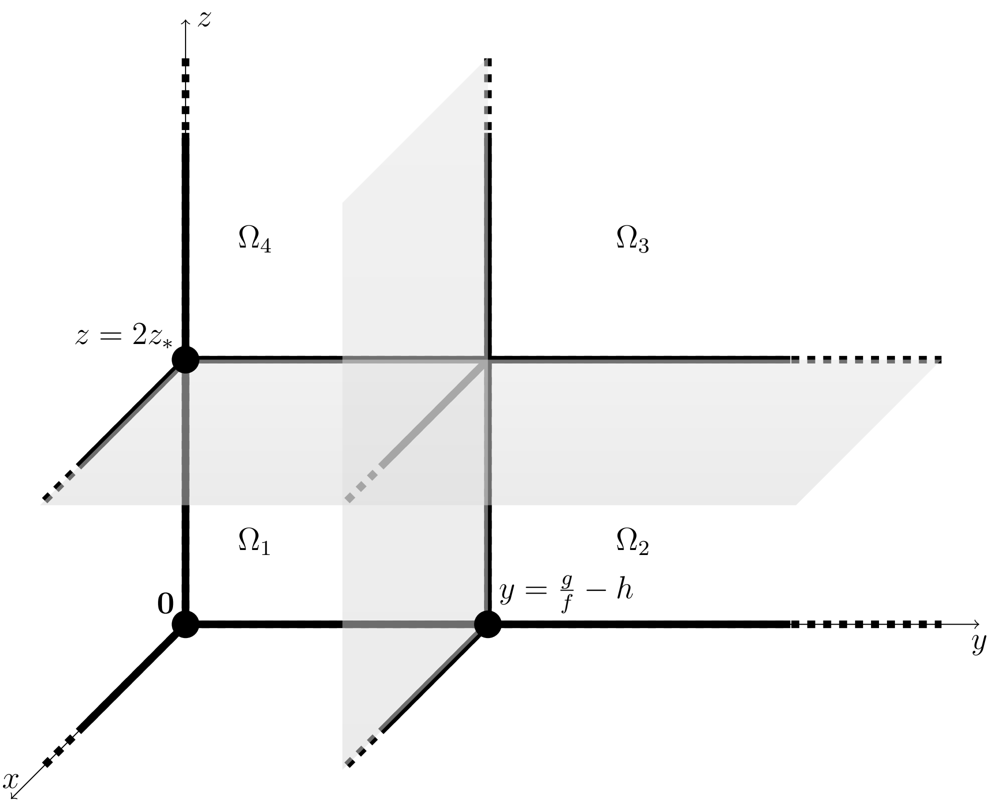


Figure 2.2.2: The sets $\Omega_1, \Omega_2, \Omega_3, \Omega_4$ form a partition of $\mathcal{O}^+$.

By the the property positive invariance of $\mathcal{O}^+$ we see

$$s_0 \in \mathcal{O}^+ \quad \Rightarrow \quad s(t) \in \mathcal{O}^+ = \bigcup_{i=1}^{4} \Omega_i \qquad \forall\, t \geq 0.$$

Therefore a positive phase curve $\gamma_{s_0}^+$ to a solution s that commences in $\mathcal{O}^+$ (i.e. $\gamma_{s_0}^+(0) = s(0) = s_0 \in \mathcal{O}^+$) *will be completely contained in $\mathcal{O}^+$ for all future times*, i.e.

$$\gamma_{s_0}^+(I) \subset \mathcal{O}^+,$$

and hence also in exactly one of the disjoint Ω_i for any time $t \geq 0$, where $i \in \{1, 2, 3, 4\}$. Thus it suffices to show that this positive phase curve is bounded (by a time-independent bound) while in any of the Ω_i, to conclude that the corresponding solution is bounded as $t \to \infty$. In the following we will prove several auxiliary results and then put these together to prove the boundedness of the respective $\gamma_{s_0}^+$ and hence the corresponding solutions s fulfilling $s_0 \in \mathcal{O}^+$ and $z_* > 0$.

Lemma 2.2.13.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. For any $t \geq 0$ such that $s(t) \in \Omega_1 \cup \Omega_2$ it holds that

$$z(t) < 2z_*.$$

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$ and any $t \geq 0$ such that $s(t) \in \Omega_1 \cup \Omega_2$ be given. Since $s(t) \in \Omega_1 \cup \Omega_2$ we have - by definition of Ω_1 and Ω_2 - that

$$z(t) < 2z_*. \qquad \square$$

We now turn to the sets Ω_3 and Ω_4 which are trickier to handle than Ω_1 and Ω_2.

The set Ω_3

To control solutions (and the corresponding positive phase curves) in Ω_3 we first show that any such positive phase curves cannot be contained in Ω_3 indefinitely, but much rather leave Ω_3 after a finite time $T_M > 0$, which we define in the following

Lemma 2.2.14.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Then it holds that

$$T_M := \frac{1}{\alpha} \ln \left(\frac{y_M}{\frac{g}{f} - h} \right) > 0,$$

where $\alpha > 0$ is defined as in Corollary 2.2.2, i.e. T_M is positive.

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Note that by the definition of z_* in Lemma 2.2.5 we see that $z_* > 0$ implies

$$z_* = \max \left\{ \left(-b + \frac{c x_M}{x_M + d} \right) (y_M + e), 0 \right\} = \left(-b + \frac{c x_M}{x_M + d} \right) (y_M + e).$$

Hence we obtain

$$0 < z_* = \underbrace{\left(-b + \frac{c x_M}{x_M + d} \right)}_{= \alpha \text{ from Corollary 2.2.2}} (y_M + e) = \alpha \underbrace{(y_M + e)}_{>0},$$

and therefore $\alpha > 0$. We conclude (using $y_M > \frac{g}{f} - h$) that

$$T_M = \underbrace{\frac{1}{\alpha}}_{>0} \underbrace{\ln \left(\frac{y_M}{\frac{g}{f} - h} \right)}_{>0} > 0. \qquad \square$$

We now show that T_M is in fact the required time that we are looking for:

Lemma 2.2.15.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Furthermore let a $T_3 \geq 0$ exist such that $s(T_3) \in \Omega_3$. Then there exists a $t \in [T_3, T_3 + T_M]$ such that $s(t) \notin \Omega_3$, where T_M is defined as in Lemma 2.2.14.

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$ and let a $T_3 \geq 0$ exist such that $s(T_3) \in \Omega_3$. We set $I_3 := [T_3, T_3 + T_M]$ and see $|I_3| > 0$ by Lemma 2.2.14. We now provide a proof by contradiction, i.e. we assume that

$$s(t) \in \Omega_3 \qquad \forall\, t \in I_3.$$

Hence for all $t \in I_3$ we have $z(t) \geq 2z_*$ and $x(t) \leq x_M$ and $y(t) \leq y_M$ (by Lemmas 2.2.1 and 2.2.3 respectively), which allows us to estimate

$$\begin{aligned}\dot{y}(t) &= y(t)\left(-b + \frac{cx(t)}{x(t)+d} - \frac{z(t)}{y(t)+e}\right)\\ &\leq y(t)\left(-b + \frac{cx_M}{x_M+d} - \frac{2z_*}{y_M+e}\right).\end{aligned}$$

Since $z_* > 0$ we have $z_* = \left(-b + \frac{cx_M}{x_M+d}\right)(y_M + e)$ and using this in the above yields

$$\begin{aligned}\dot{y}(t) &\leq y(t)\left(-b + \frac{cx_M}{x_M+d} - 2\left(-b + \frac{cx_M}{x_M+d}\right)\right)\\ &= -y(t)\underbrace{\left(-b + \frac{cx_M}{x_M+d}\right)}_{=\alpha \text{ from Corollary 2.2.2}}\\ &= -\alpha y(t) \end{aligned}\tag{2.2.20}$$

for all $t \in I_3$. From (2.2.20) we obtain

$$\frac{\dot{y}(t)}{y(t)} \leq -\alpha \qquad \forall\, t \in I_3$$

and integrating from $T_3 \in I_3$ to $T_3 + T_M \in I_3$ yields

$$[\ln(y(\tau))]_{\tau=T_3}^{\tau=T_3+T_M} \leq -\alpha(T_3 + T_M - T_3) = -\alpha T_M.$$

Using the definition of T_M from Lemma 2.2.14 this may be rewritten as

$$\ln\left(\frac{y(T_3+T_M)}{y(T_3)}\right) \leq -\alpha\frac{1}{\alpha}\ln\left(\frac{y_M}{\frac{g}{f}-h}\right) = \ln\left(\frac{\frac{g}{f}-h}{y_M}\right).$$

Solving this for $y(T_3 + T_M)$ results in

$$y(T_3+T_M) \leq y(T_3)\frac{\frac{g}{f}-h}{y_M}.$$

Since s is bounded by y_M in the y-component for all $t \geq 0$ it holds that $y(T_3) \leq y_M$ and therefore we estimate further:

$$y(T_3+T_M) \leq y(T_3)\frac{\frac{g}{f}-h}{y_M} \leq \frac{g}{f} - h.$$

This however implies $s(T_3 + T_M) \notin \Omega_3$, which is a contradiction to our assumption, since $T_3 + T_M \in I_3$. □

An immediate consequence of the above result is that any positive phase curve to a solution s (as defined in the above lemma) cannot stay in Ω_3 for any time *interval* longer than the value T_M (although the curve may of course *return* to Ω_3 at a later time - i.e. for a larger time-value -, but also then it can stay for no longer than T_M). We will use this to show that such a positive phase curve is also bounded in its z-component while in Ω_3 (and $t \geq 0$ as always), since it only has a finite time to increase while there. For this we consider the two cases of a positive phase curve *commencing* in Ω_3 (i.e. $s_0 \in \Omega_3$) and a positive phase curve *entering* Ω_3. We start with the case $s_0 \in \Omega_3$:

Lemma 2.2.16.
Let s be a solution that fulfils $s_0 \in \Omega_3 \subset \mathcal{O}^+$ and $z_* > 0$. The third component of s is bounded by

$$z(t) < z_0 \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}$$

while the corresponding positive phase curve to s is still in Ω_3.

Proof.
Let s be a solution that fulfils $s_0 \in \Omega_3$ and $z_* > 0$. The expression '*while the corresponding positive phase curve to s is still in Ω_3*' is specified as follows by defining the interval I_3: Let $I_3 \subset [0, \infty)$ with $\min I_3 = 0$ be the maximal (positive) interval such that

$$s(t) \in \Omega_3 \qquad \forall\, t \in I_3.$$

Note that $I_3 \neq \emptyset$ since $s_0 \in \Omega_3$ (and hence is well-defined). By Lemma 2.2.15 (with $T_3 = 0$) we know that

$$\exists\, t \in [0, T_M] \,:\, s(t) \notin \Omega_3$$

and hence $|I_3| \leq T_M < \infty$. Furthermore, $s(t) \in \Omega_3$ for all $t \in I_3$ implies

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in I_3. \tag{2.2.21}$$

Therefore, Corollary 2.2.2 applies (with $I_0 = I_3$ and $T_0 = 0$), yielding

$$y(t) \leq y_0 \exp(\alpha t) \left(\frac{z_0}{z(t)} \right)^{\beta} \qquad \forall\, t \in I_3.$$

From this we obtain the following estimate for the z-component (note $\beta > 0$)

$$z(t) \leq z_0 \sqrt[\beta]{\frac{y_0}{y(t)} \exp(\alpha t)} \qquad \forall\, t \in I_3.$$

Since $|I_3| \leq T_M$ for any $t \in I_3$ we obtain $t \leq T_M$. Using this and noting once more that $z_* > 0$ implies $\alpha > 0$ yields

$$z(t) \leq z_0 \sqrt[\beta]{\frac{y_0}{y(t)} \exp(\alpha t)} \leq z_0 \sqrt[\beta]{\frac{y_0}{y(t)} \exp(\alpha T_M)} \qquad \forall\, t \in I_3.$$

Furthermore, since (2.2.21) holds and y is bounded by y_M for any $t \geq 0$ we may estimate

$$z(t) \leq z_0 \sqrt[\beta]{\frac{y_0}{y(t)} \exp(\alpha T_M)} < z_0 \sqrt[\beta]{\frac{y_M}{\frac{g}{f} - h} \exp(\alpha T_M)} \qquad \forall\, t \in I_3.$$

Finally using the definitions of T_M and $\beta > 0$ yields

$$\begin{aligned} z(t) &< z_0 \sqrt[\beta]{\frac{y_M}{\frac{g}{f} - h} \exp\left(\alpha \frac{1}{\alpha} \ln\left(\frac{y_M}{\frac{g}{f} - h}\right)\right)} \\ &= z_0 \sqrt[\beta]{\left(\frac{y_M}{\frac{g}{f} - h}\right)^2} \\ &= z_0 \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \forall\, t \in I_3. \end{aligned}$$

□

The above shows that a solution s fulfilling the conditions of the previous lemma (in particular $s_0 \in \Omega_3$) is bounded while the corresponding positive phase curve remains in Ω_3. However, such a positive phase curve may leave and *re-enter* Ω_3 for larger time values, or the curve may not commence in Ω_3 and only *enter* Ω_3 for a time value larger than zero. Hence we consider positive phase curves (and hence solutions s) that (re-)enter Ω_3 in finite time.
Note that for any subset $M \subset \mathcal{O}_0^+$ a positive phase curve to a solution s *can only enter* M *via the boundary* ∂M *of* M (s is continuous in t and therefore the corresponding positive phase curve cannot 'simply jump into M', without crossing ∂M in the complete space $(\mathcal{O}_0^+, \mathrm{d})$).
Bearing this in mind we consider the boundary $\partial\Omega_3$ of Ω_3 (for any given solution s with $s_0 \in \mathcal{O}^+$ and $z_* > 0$). It may be split into three sets as follows

$$\partial\Omega_3 = B_0 \,\dot\cup\, B_2 \,\dot\cup\, B_4,$$

where

$$\begin{aligned} B_0 &:= \left\{(x,y,z) \in \mathcal{O}_0^+ \,:\, x = 0,\ y \geq \frac{g}{f} - h,\ z \geq 2z_*\right\} \subset O_7 \\ B_2 &:= \left\{(x,y,z) \in \mathcal{O}^+ \,:\, y > \frac{g}{f} - h,\ z = 2z_*\right\} \subset \Omega_3 \\ B_4 &:= \left\{(x,y,z) \in \mathcal{O}^+ \,:\, y = \frac{g}{f} - h,\ z \geq 2z_*\right\} \subset \Omega_4. \end{aligned}$$

See Figure 2.2.3 for a visualisation of these *common boundary parts*.
We show that a positive phase curve to a solution s as above can in fact only enter the set Ω_3 via the common boundary part of Ω_2 and Ω_3, i.e. the set B_2. We first show

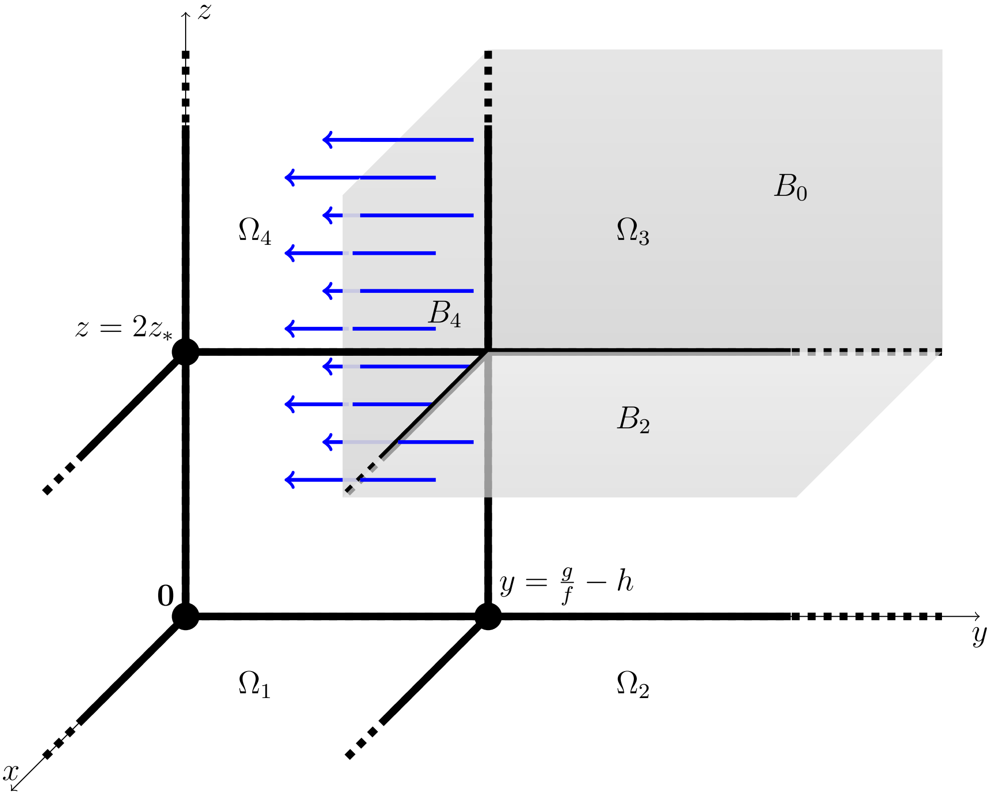


Figure 2.2.3: The subsets B_0, B_2 and B_4 of $\partial\Omega_3$. On B_4 the vector field v points into $\Omega_1 \cup \Omega_4$ (blue arrows).

Lemma 2.2.17.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. For any $t \geq 0$ the corresponding positive phase curve cannot enter Ω_3 via the common boundary part of Ω_3 and O_7 (defined in Lemma 2.1.1), i.e. via the set $B_0 \subset O_7$.

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. By Lemma 2.1.5 the solution (and hence the positive phase curve) fulfils

$$s(t) \in \mathcal{O}^+ \qquad \forall\, t \geq 0.$$

Since $\mathcal{O}^+ \cap O_7 = \emptyset$ and $B_0 \subset O_7$ we also have $\mathcal{O}^+ \cap B_0 = \emptyset$ and hence

$$s(t) \notin B_0 \qquad \forall\, t \geq 0.$$

This implies that the positive phase curve does not enter the boundary set B_0 for any $t \geq 0$ and in particular cannot enter Ω_3 via the boundary B_0. □

We see that since O_7 has property *(I1)* the positive phase curve to s will not enter Ω_3 via B_0. The only two options left are entering via the common boundary parts of Ω_3 with either Ω_2 or Ω_4, i.e. the sets B_2 and B_4. We claim that the second option can in fact never occur.

Lemma 2.2.18.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. For any $t \geq 0$ the corresponding positive phase curve cannot enter Ω_3 via the common boundary part of Ω_3 and Ω_4, i.e. via the set

$$B_4 = (\partial\Omega_3 \cap \partial\Omega_4)\backslash O_7 = \left\{(x, y, z) \in \mathcal{O}^+ \,:\, y = \frac{g}{f} - h,\, z \geq 2z_*\right\} \subset \Omega_4.$$

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. The set B_4 is a half plane and the common boundary part of Ω_3 and Ω_4, fulfils

$$B_4 \subset \Omega_4 \quad \text{and} \quad B_4 \cap \Omega_3 = \emptyset.$$

We now consider the vector field v on B_4 and show that that v *points into* $\Omega_1 \cup \Omega_4$ (observe the blue arrows in Figure 2.2.3). For this we define the set

$$\widehat{B}_4 := \operatorname{relint}(B_4) = \left\{(x, y, z) \in \mathcal{O}^+ \,:\, y = \frac{g}{f} - h,\, z > 2z_*\right\} \subset \Omega_4,$$

being the relative interior of B_4. The outer normal vector (with respect to Ω_4) for any point in $\widehat{B}_4$ is given by the vector $n = (0, 1, 0)^T$. In particular for any time $t \geq 0$ such that $s(t) \in \widehat{B}_4 \subset \Omega_4$ we obtain

$$\langle n, v(s(t))\rangle = \left\langle \begin{pmatrix} 0 \\ 1 \\ 0 \end{pmatrix}, \begin{pmatrix} \dot{x}(t) \\ \dot{y}(t) \\ \dot{z}(t) \end{pmatrix} \right\rangle = \dot{y}(t)$$

and since $s(t) \in \widehat{B}_4$ we have

$$z(t) > 2z_* > z_*$$

which allows us to apply Lemma 2.2.5, yielding

$$\langle n, v(s(t))\rangle = \dot{y}(t) < 0. \tag{2.2.22}$$

Hence on $\widehat{B}_4$ the semiflow Φ generated by v is transverse (to $\widehat{B}_4$) and moreover, since the value of the inner product in (2.2.22) is negative, the vector field v points strictly into the *interior* of the set Ω_4 (the interior exists since $\frac{g}{f} - h > 0$). This implies that the positive phase curve corresponding to s (being tangent to v by definition) cannot enter Ω_3 via the boundary part $\widehat{B}_4$, but rather moves (with respect to the time forward parametrisation of the curve) into the interior of Ω_4.
We still need to consider the case

$$s(t) \in B_4\backslash\widehat{B}_4 \quad \text{for some} \quad t \geq 0.$$

Then $y(t) = \frac{g}{f} - h$ and

$$z(t) = 2z_* > z_*$$

and Lemma 2.2.5 yields $\dot{y}(t) < 0$. This implies that the solution decreases in its y-component at time $t \geq 0$ and the positive phase curve corresponding to s does not enter Ω_3 via $B_4 \backslash \widehat{B}_4$ either. Note that at this particular time t the positive phase curve could also leave Ω_4 and enter Ω_1 instead. But in either case it cannot enter Ω_3. Once again consider Figure 2.2.3. □

As a consequence of this we obtain

Corollary 2.2.4.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. For any $t \geq 0$ the positive phase curve corresponding to s can only enter Ω_3 via the common boundary part of Ω_2 and Ω_3, i.e. the set

$$B_2 = \left\{ (x, y, z) \in \mathcal{O}^+ \ : \ y > \frac{g}{f} - h, \ z = 2z_* \right\} \subset \Omega_3.$$

Furthermore if the positive phase curve enters Ω_3 then there exists a corresponding entrance time $T_3 \geq 0$ such that $s(T_3) \in B_2 \subset \partial\Omega_3 \subset \Omega_3$ and $z(T_3) = 2z_*$.

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Since s is continuous for all $t \geq 0$ the positive phase curve can only enter the set Ω_3 via the boundary of Ω_3, i.e. the set

$$\partial\Omega_3 = B_0 \,\dot{\cup}\, B_2 \,\dot{\cup}\, B_4.$$

However, by Lemmas 2.2.17 and 2.2.18 the curve cannot enter Ω_3 via B_0 or B_4 and therefore $\gamma_{s_0}^+$ may only enter via the *remaining part of the boundary*, namely the set B_2. Hence if the positive phase curve enters Ω_3 (for a finite time) it necessarily intersects the boundary part B_2 (see Figure 2.2.4). Since s is continuous and $B_2 \subset \Omega_3$ this implies that there exists a corresponding entrance time $T_3 \geq 0$ such that

$$s(T_3) \in B_2 \subset \Omega_3,$$

which implies $z(T_3) = 2z_*$. □

Remark 2.2.6.
Note that the entrance time T_3 is (only) well-defined, since $B_2 \subset \Omega_3$. Else (i.e. if the boundary part considered is not part of the set considered) it might happen that no such entrance time exists.

We can now determine an estimate on the z-component of any solution s while the positive phase curve of s is in Ω_3.

Lemma 2.2.19.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Furthermore assume that the positive phase curve corresponding to s enters the set Ω_3. Then the third component of s is bounded by

$$z(t) < 2z_* \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}$$

while the positive phase curve is still in Ω_3.

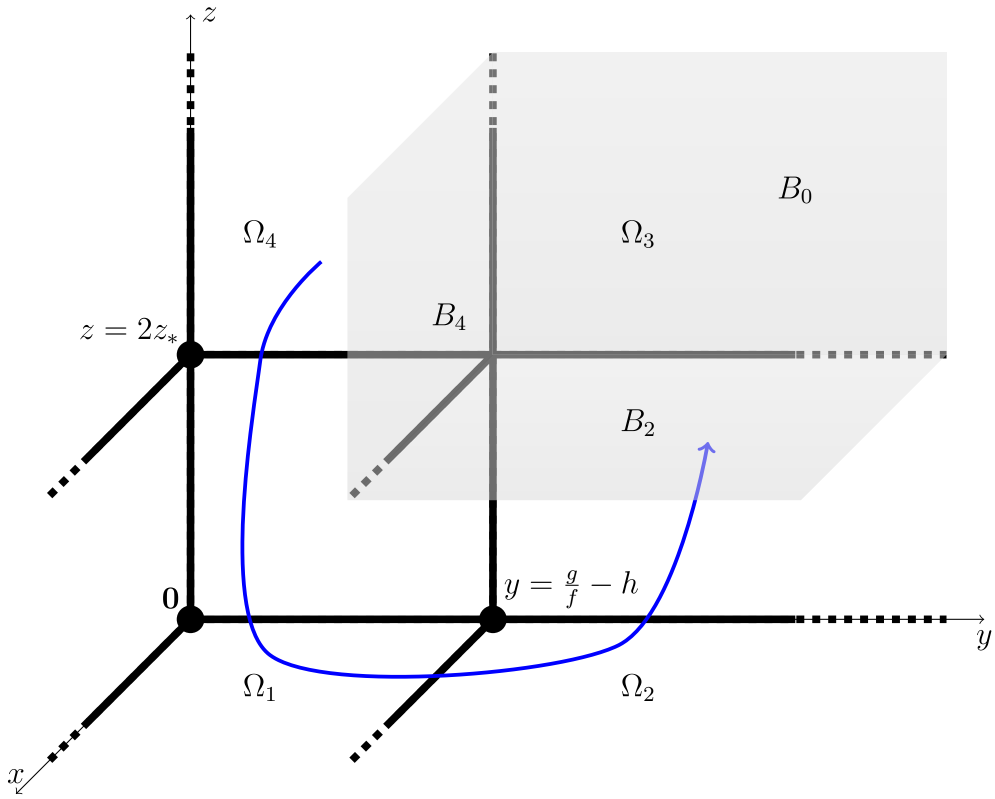


Figure 2.2.4: A positive phase curve can only enter the set Ω_3 via the set B_2.

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Furthermore assume that the positive phase curve corresponding to s enters the set Ω_3. By Corollary 2.2.4 we know that there exists a corresponding entrance time $T_3 \geq 0$ such that

$$s(T_3) \in B_2 \subset \Omega_3 \quad \text{and} \quad z(T_3) = 2z_*. \tag{2.2.23}$$

The rest of the proof is very similar to the proof of Lemma 2.2.16. Let $I_3 \subset [0, \infty)$ with $\min I_3 = T_3$ be the maximal (positive) interval such that

$$s(t) \in \Omega_3 \qquad \forall\, t \in I_3.$$

Note that $I_3 \neq \emptyset$ since $s(T_3) \in \Omega_3$ (and hence is well-defined). By Lemma 2.2.15 we know that

$$\exists\, t \in [T_3, T_3 + T_M] \,:\, s(t) \notin \Omega_3$$

and hence $|I_3| \leq T_M < \infty$. Furthermore $s(t) \in \Omega_3$ for all $t \in I_3$ implies

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in I_3. \tag{2.2.24}$$

Therefore Corollary 2.2.2 applies (with $I_0 = I_3$ and $T_0 = T_3$), yielding

$$y(t) \leq y(T_3) \exp(\alpha(t - T_3)) \left(\frac{z(T_3)}{z(t)}\right)^{\beta} \qquad \forall\, t \in I_3.$$

From this we obtain the following estimate for the z-component (note $\beta > 0$)

$$z(t) \leq z(T_3) \sqrt[\beta]{\frac{y(T_3)}{y(t)} \exp(\alpha(t - T_3))} \qquad \forall\, t \in I_3.$$

Since $|I_3| \leq T_M$ holds for any $t \in I_3$ we obtain

$$T_3 \leq t \leq T_3 + T_M \quad \forall\, t \in I_3,$$

which is equivalent to

$$0 \leq t - T_3 \leq T_M \quad \forall\, t \in I_3.$$

Using this (and recalling that $z_* > 0$ implies $\alpha > 0$) yields

$$z(t) \leq z(T_3) \sqrt[\beta]{\frac{y(T_3)}{y(t)} \exp(\alpha(t - T_3))} \leq z(T_3) \sqrt[\beta]{\frac{y(T_3)}{y(t)} \exp(\alpha T_M)} \qquad \forall\, t \in I_3.$$

Furthermore since (2.2.24) holds and $y(t) \leq y_M$ for any $t \geq 0$ we have

$$z(t) \leq z(T_3) \sqrt[\beta]{\frac{y(T_3)}{y(t)} \exp(\alpha T_M)} < z(T_3) \sqrt[\beta]{\frac{y_M}{\frac{g}{f} - h} \exp(\alpha T_M)} \qquad \forall\, t \in I_3.$$

Finally since $z(T_3) = 2z_*$ (by (2.2.23)) and using the definitions of T_M and $\beta > 0$, we conclude for any $t \in I_3$ that

$$z(t) < z(T_3) \sqrt[\beta]{\frac{y_M}{\frac{g}{f} - h} \exp(\alpha T_M)} = 2z_* \sqrt[\beta]{\left(\frac{y_M}{\frac{g}{f} - h}\right)^2} = 2z_* \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}$$

□

By combining the previous results we now obtain

Lemma 2.2.20.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. For any $t \geq 0$ such that $s(t) \in \Omega_3$ it holds that

$$z(t) < \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}.$$

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$ and let any $t \geq 0$ such that $s(t) \in \Omega_3$ be given. Since $s(t) \in \Omega_3$ either

- the positive phase curve corresponding to solution s was contained in Ω_3 for the entire time interval $[0, t]$, i.e. $s_0 \in \Omega_3$,

or

- the positive phase curve corresponding to solution s entered the set Ω_3 at some entrance time $T_3 \in (0, t]$ such that $s([T_3, t]) \in \Omega_3$, see Corollary 2.2.4.

In the first case Lemma 2.2.16 yields

$$z(t) < z_0 \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)},$$

while in the second case Lemma 2.2.19 yields

$$z(t) < 2z_* \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}.$$

Combining these two results we obtain

$$z(t) < \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}. \qquad \square$$

This proves that a solution is bounded while it (i.e. the positive phase curve corresponding to s) is in Ω_3. Note that the two key aspects of the dynamics that led to this conclusion were:

- A positive phase curve corresponding to s cannot stay in Ω_3 longer than the time T_M.
- A positive phase curve corresponding to s can only (re-)enter Ω_3 'from below', i.e. via the common boundary part of Ω_2 and Ω_3, recall the set B_2 in Figure 2.2.3.

Using Corollary 2.2.2, this essentially allowed us to determine an upper bound on the z-component of a solution s above which z cannot increase (for any $t \geq 0$) in the finite time T_M. Before turning to the remaining set Ω_4 we prove a specific estimate, which we will need subsequently.

Lemma 2.2.21.
For any solution s (i.e. for any $s_0 \in \mathcal{O}_0^+$) the following estimate holds:

$$\left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \geq 1.$$

Proof.
Let s be an arbitrary solution with $s_0 \in \mathcal{O}_0^+$. Since $y_M > \frac{g}{f} - h$ we have $f - \frac{g}{y_M + h} > 0$. Thus

$$\underbrace{\left(\frac{y_M}{\frac{g}{f} - h} \right)}_{>1}^{\overbrace{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}^{>0}} > 1. \qquad \square$$

This allows us to show

Lemma 2.2.22.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. For any $t \geq 0$ such that $s(t) \in \Omega_1 \cup \Omega_2 \cup \Omega_3 = \mathcal{O}^+ \backslash \Omega_4$ it holds that

$$z(t) < \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}.$$

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$ and let any $t \geq 0$ such that $s(t) \in \Omega_1 \cup \Omega_2 \cup \Omega_3$ be given. If $s(t) \in \Omega_1 \cup \Omega_2$ we may combine the results of Lemmas 2.2.13 and 2.2.21 to obtain

$$z(t) < 2z_* \leq \max\{z_0, 2z_*\} \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}.$$

If $s(t) \in \Omega_3$ Lemma 2.2.20 yields the result immediately. □

This concludes the considerations concerning the set Ω_3.

The set Ω_4

We now turn to positive phase curves (i.e. solutions s) that are in Ω_4 for some time $t \geq 0$. The key observation which will help us, is that the vector field v is non-increasing in z-direction in Ω_4. Once again we split the considerations into positive phase curves *commencing* in Ω_4 (i.e. $s_0 \in \Omega_4$) and positive phase curves that *(re-)enter* Ω_4.

Lemma 2.2.23.
Let s be a solution that fulfils $s_0 \in \Omega_4 \subset \mathcal{O}^+$ and $z_* > 0$. The third component of s is bounded by

$$z(t) \leq z_0$$

while s is still in Ω_4.

Proof.
Let s be a solution that fulfils $s_0 \in \Omega_4$ and $z_* > 0$. Let $I_4 \subset [0, \infty)$ with $\min I_4 = 0$ be the maximal (positive) interval such that

$$s(t) \in \Omega_4 \qquad \forall\, t \in I_4. \tag{2.2.25}$$

Note that $I_4 \neq \emptyset$ since $s_0 \in \Omega_4$ (and hence is well-defined). Furthermore (2.2.25) implies that

$$y(t) \leq \frac{g}{f} - h \qquad \forall\, t \in I_4$$

and therefore also

$$\dot{z}(t) = \left(f - \frac{g}{y(t)+h}\right) z^2(t) \leq 0 \qquad \forall\, t \in I_4.$$

Hence z is monotonically decreasing on I_4 and thus we obtain

$$z(t) \leq z_0 \qquad \forall\, t \in I_4. \qquad \square$$

We now turn to positive phase curves that (re-)enter Ω_4 and once again consider the boundary of Ω_4 (see Figure 2.2.5) via which positive phase curves must enter Ω_4.

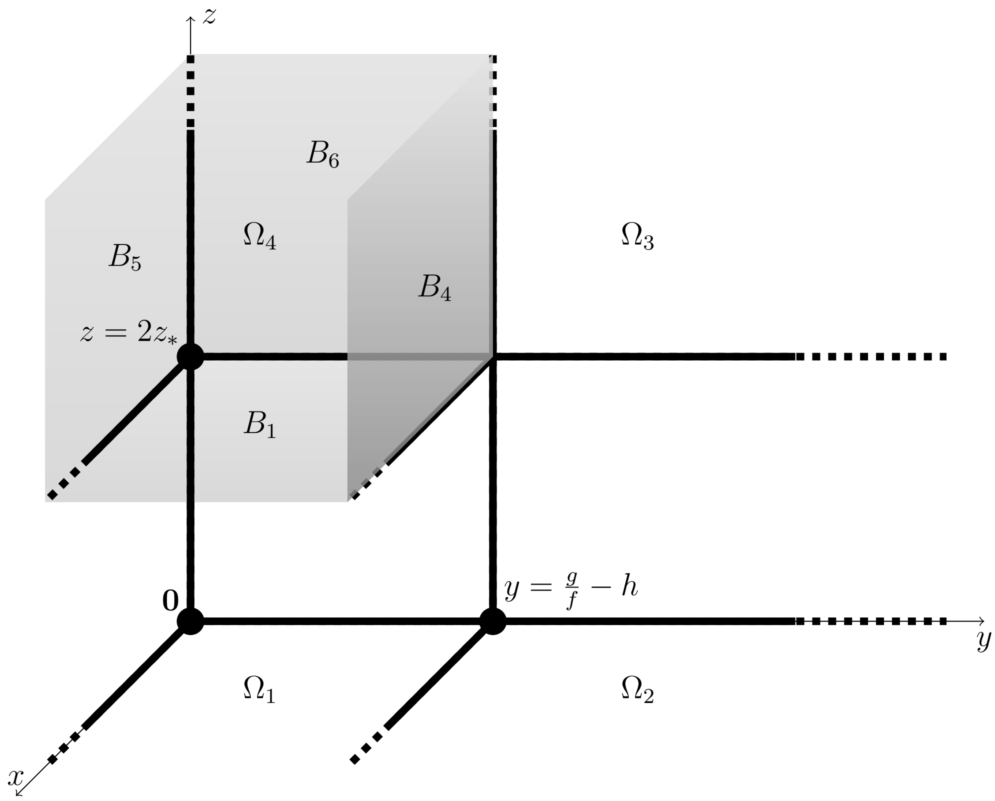


Figure 2.2.5: The subsets B_1, B_4, B_5 and B_6 of $\partial\Omega_4$.

Lemma 2.2.24.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. For any $t \geq 0$ the positive phase curve corresponding to the solution s can only enter Ω_4 via the common boundary parts of Ω_4 with either Ω_1 or Ω_3, i.e. the sets

$$B_1 = \left\{(x,y,z) \in \mathcal{O}^+ \,:\, y \leq \frac{g}{f} - h,\, z = 2z_*\right\} \subset \Omega_4,$$

$$B_4 = \left\{(x,y,z) \in \mathcal{O}^+ \,:\, y = \frac{g}{f} - h,\, z \geq 2z_*\right\} \subset \Omega_4.$$

Furthermore if the positive phase curve enters Ω_4 then there exists a corresponding entrance time $T_4 > 0$ such that $s(T_4) \in B_1 \cup B_4 \subset \partial\Omega_4 \subset \Omega_4$.

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Since s is continuous its positive phase curve can only enter Ω_4 via the boundary of Ω_4. The boundary of Ω_4 consists of the sets B_1, B_4 and

$$B_5 := \left\{(x,y,z) \in \mathcal{O}_0^+ \;:\; y = 0,\, z \geq 2z_*\right\} \subset O_4 \cup O_6$$
$$B_6 := \left\{(x,y,z) \in \mathcal{O}_0^+ \;:\; x = 0,\, y \leq \frac{g}{f} - h,\, z \geq 2z_*\right\} \subset O_4 \cup O_7.$$

However, B_5 and B_6 are subsets of the sets $O_4 \cup O_6$ and $O_4 \cup O_7$, which both have property *(I1)* respectively. Therefore, Since

$$(O_4 \cup O_6) \cap \mathcal{O}^+ = \emptyset \quad \text{and} \quad (O_4 \cup O_7) \cap \mathcal{O}^+ = \emptyset$$

holds, the positive phase curve of the solution s (with $s_0 \in \mathcal{O}^+$) can enter neither B_5 nor B_6 in finite time (Lemma 2.1.5). Hence the curve can only enter Ω_4 by crossing a point in the remaining part of the boundary, namely $B_1 \cup B_4$ (see Figure 2.2.5). Since s is continuous and $B_1 \cup B_4 \subset \Omega_4$ this implies that if s enters Ω_4 there exists a corresponding entrance time $T_4 \geq 0$ such that

$$s(T_4) \in B_1 \cup B_4 \subset \partial\Omega_4 \subset \Omega_4. \qquad \square$$

Using the above result we can determine a bound on the z-component of s at the entrance time T_4.

Lemma 2.2.25.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Furthermore assume that the positive phase curve corresponding to s enters the set Ω_4 at some entrance time $T_4 > 0$. Then the z-component of s fulfils

$$z(T_4) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}.$$

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Furthermore assume that the positive phase curve corresponding to s enters the set Ω_4 at some entrance time $T_4 > 0$ (the time T_4 is well-defined by Lemma 2.2.24). Then the continuity of s implies that there exists a sufficiently small $\varepsilon > 0$ such that

$$s(t_i) \notin \Omega_4 \qquad \forall\, t_i \in [T_4 - \varepsilon, T_4) =: I_\varepsilon \subset I.$$

Otherwise the positive phase curve would have entered Ω_4 at an earlier time and not left it since, implying that T_4 is not an entrance time. We now choose a sequence $(t_i)_{i\in\mathbb{N}}$ with $t_i \in I_\varepsilon \subset I$ and $t_i \nearrow T_4$ as $i \to \infty$. Since $s(t) \in \mathcal{O}^+$ for all $t \geq 0$ (see Lemma 2.1.5) this implies

$$s(t_i) \in \mathcal{O}^+ \backslash \Omega_4 \qquad \forall\, t_i \in I_\varepsilon.$$

Therefore Lemma 2.2.22 yields

$$z(t_i) < \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \forall\, t_i \in I_\varepsilon. \tag{2.2.26}$$

Furthermore, since s (and hence the z-component) is continuous it holds that

$$z(T_4) = \lim_{t \to T_4} z(t) = \lim_{t_i \nearrow T_4} z(t) = \lim_{i \to \infty} z(t_i).$$

Thus, by (2.2.26) we have

$$z(T_4) = \lim_{i \to \infty} z(t_i) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}. \qquad \square$$

We now show that also those positive phase curves entering Ω_4 are bounded in their third component.

Lemma 2.2.26.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Furthermore assume that the positive phase curve corresponding to s enters the set Ω_4 at some entrance time $T_4 > 0$. Then the third component of s is bounded by

$$z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}$$

while the positive phase curve is still in Ω_4.

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Furthermore assume that the positive phase curve corresponding to s enters the set Ω_4 at some entrance time $T_4 > 0$. By Lemma 2.2.25 we know that

$$z(T_4) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}.$$

Furthermore let $I_4 \subset [0, \infty)$ with $\min I_4 = T_4$ be the maximal (positive) interval such that

$$s(t) \in \Omega_4 \qquad \forall\, t \in I_4. \tag{2.2.27}$$

Note that $I_4 \neq \emptyset$ since $s(T_4) \in \Omega_4$. Furthermore (2.2.27) implies that

$$y(t) \leq \frac{g}{f} - h \qquad \forall\, t \in I_4$$

and therefore also

$$\dot{z}(t) = \left(f - \frac{g}{y(t)+h}\right) z^2(t) \leq 0 \qquad \forall\, t \in I_4.$$

Thus z is monotonically decreasing on I_4 and hence

$$z(t) \leq z(T_4) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M+e)} \qquad \forall\, t \in I_4. \qquad \square$$

We now combine the previous results to obtain

Lemma 2.2.27.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. For any $t \geq 0$ such that $s(t) \in \Omega_4$ it holds that

$$z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M+e)}.$$

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$ and let any $t \geq 0$ such that $s(t) \in \Omega_4$ be given. Since $s(t) \in \Omega_4$ either

- the positive phase curve corresponding to solution s was contained in Ω_4 for the entire time interval $[0, t]$, i.e. $s_0 \in \Omega_4$,

or

- the positive phase curve corresponding to solution s entered the set Ω_4 at some entrance time $T_4 \in (0, t]$ such that $s([T_4, t]) \in \Omega_4$, see Lemma 2.2.24.

In the first case the results of Lemmas 2.2.21 and 2.2.23 yield

$$z(t) \leq z_0 \leq z_0 \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M+e)},$$

while in the second case Lemma 2.2.26 yields

$$z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M+e)}.$$

Combining these two results we obtain

$$z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M+e)}. \qquad \square$$

Finally, we prove the boundedness of solutions (for $t \geq 0$) fulfilling $s_0 \in \mathcal{O}^+$ and $z_* > 0$.

Lemma 2.2.28.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. It holds that

$$z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \forall\, t \geq 0.$$

Proof.
Let s be a solution that fulfils $s_0 \in \mathcal{O}^+$ and $z_* > 0$. Since $\mathcal{O}^+$ has property *(I1)* for all $t \geq 0$, we have

$$s(t) \in \mathcal{O}^+ = \Omega_1 \cup \Omega_2 \cup \Omega_3 \cup \Omega_4 \qquad \forall\, t \geq 0.$$

I.e. the positive phase curve corresponding to the solution is in one of the sets Ω_i for any $t \geq 0$. In particular combining Lemmas 2.2.22 and 2.2.27 we immediately obtain that for any $t \geq 0$ such that $s(t) \in \mathcal{O}^+$(which in fact is any $t \geq 0$ as argued just now) it holds that

$$z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}. \qquad \square$$

Thus we have shown that solutions s fulfilling $s_0 \in \mathcal{O}^+$ and $z_* > 0$ are bounded (by a time-independent bound) for all $t \geq 0$ and hence will not diverge as time tends to infinity.

Boundedness

Combining the results from the special and the general cases from above, we summarise our result in

Proposition 2.2.2.
Let $a = d$ and $f - \frac{g}{h} < 0$ and any solution s be given. Then s is bounded for all $t \geq 0$. The bounds on the first two components of s are given by

$$\begin{aligned} 0 &\leq x(t) \leq x_M(x_0) = \max\{1, x_0\} \\ 0 &\leq y(t) \leq y_M(x_0, y_0) = c \max\{1, x_0\} + y_0 + \frac{c}{4b} + \frac{g}{f} - h \end{aligned}$$

for all $t \geq 0$. The bound on the third component of s depends on the initial conditions $s_0 \in \mathcal{O}_0^+$ in the following way:

i) If $s_0 \in \mathcal{O}^+$ and $z_* > 0$ holds then

$$0 \leq z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \forall\, t \geq 0.$$

ii) If $y_0 > \frac{g}{f} - h$ *and* $x_0 = 0$ *or* $z_* = 0$ *(or both) holds then*

$$0 \leq z(t) \leq z_0 \left(\frac{y_0}{\frac{g}{f} - h} \right)^{\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \forall\, t \geq 0.$$

iii) Else (i.e. if $s_0 \in \mathcal{O}_0^+$ *does not fulfil the conditions in i) or ii)) it holds that*

$$0 \leq z(t) \leq z_0 \qquad \forall\, t \geq 0.$$

Proof.
Let $a = d$ and $f - \frac{g}{h} < 0$ and any solution s be given. This solution is bounded in the first two components by

$$\begin{aligned} 0 &\leq x(t) \leq x_M(x_0) = \max\{1, x_0\} \\ 0 &\leq y(t) \leq y_M(x_0, y_0) = c \max\{1, x_0\} + y_0 + \frac{c}{4b} + \frac{g}{f} - h \end{aligned}$$

for all $t \geq 0$ (Lemmas 2.2.1 and 2.2.3). Furthermore, the z-component is bounded by zero from below for all $t \geq 0$. We now show that s is also bounded from above in the third component for all $t \geq 0$, by proving that *i*), *ii*) and *iii*) from above hold.

i) If $s_0 \in \mathcal{O}^+$ and $z_* > 0$ holds then the conditions of Lemma 2.2.28 are met and we obtain

$$z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \forall\, t \geq 0.$$

ii) If $y_0 > \frac{g}{f} - h$ and $x_0 = 0$ or $z_* = 0$ (or both) holds, then Lemma 2.2.12 applies and we obtain

$$z(t) \leq z_0 \left(\frac{y_0}{\frac{g}{f} - h} \right)^{\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \qquad \forall\, t \geq 0.$$

iii) We now consider the case(s) such that $s_0 \in \mathcal{O}_0^+$ does not fulfil the conditions in *i*) or *ii*).

If $y_0 \leq \frac{g}{f} - h$ and $x_0 = 0$ or $z_* = 0$ (or both) then Lemma 2.2.11 applies and

$$z(t) \leq z_0 \qquad \forall\, t \geq 0.$$

If $y_0 = 0$ or $z_0 = 0$ then Corollary 2.2.1 applies and

$$z(t) \leq z_0 \qquad \forall\, t \geq 0.$$

□

A consequence of the above is that we can construct a bound z_M on the z-component of solutions for all $t \geq 0$ and use this bound to show that these solutions do not blow up as time tends to infinity.

Corollary 2.2.5.
Let $a = d$ and $f - \frac{g}{h} < 0$ and any solution s be given. Then this solution does not blow up as time tends to infinity and in particular

$$\limsup_{t\to\infty} z(t) < \infty$$

Moreover, for any $t \geq 0$ it holds that

$$0 \leq z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M+e)} =: z_M(x_0, y_0, z_0) = z_M.$$

Proof.
Let $a = d$ and $f - \frac{g}{h} < 0$ and any solution s be given. We consider the same cases for the initial conditions as those in Proposition 2.2.2.

- If $z_* > 0$ and $s_0 \in \mathcal{O}^+$ then Proposition 2.2.2 yields

  $$z(t) \leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M+e)} = z_M$$

  for all $t \geq 0$.

- If $y_0 > \frac{g}{f} - h$ and $x_0 = 0$ or $z_* = 0$ (or both) then by Proposition 2.2.2 we obtain

  $$z(t) \leq z_0 \left(\frac{y_0}{\frac{g}{f} - h} \right)^{\left(f - \frac{g}{y_M+h}\right)(y_M+e)}$$

  for all $t \geq 0$. Since $y_M > \frac{g}{f} - h$ and $z_0 \leq \max\{z_0, 2z_*\}$ we may estimate

  $$\begin{aligned} z(t) &\leq z_0 \left(\frac{y_0}{\frac{g}{f} - h} \right)^{\overbrace{\left(f - \frac{g}{y_M+h}\right)(y_M+e)}^{>0}} \\ &\leq z_0 \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M+e)} \\ &\leq \max\{z_0, 2z_*\} \left(\frac{y_M}{\frac{g}{f} - h} \right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M+e)} = z_M \end{aligned}$$

  for all $t \geq 0$.

- For any other $s_0 \in \mathcal{O}_0^+$ we obtain

$$z(t) \leq z_0 \qquad \forall\, t \geq 0$$

as shown in Proposition 2.2.2. Using Lemma 2.2.21 we immediately obtain

$$\begin{aligned} z(t) &\leq z_0 \\ &\leq \max\{z_0, 2z_*\} \\ &\leq \max\{z_0, 2z_*\} \underbrace{\left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}}_{\geq 1} = z_M \end{aligned}$$

for any $t \geq 0$.

This proves the boundedness of the z-component by the constant $z_M \geq 0$ for all $t \geq 0$. By this we conclude

$$\limsup_{t \to \infty} z(t) \leq z_M < \infty. \qquad \square$$

Having shown that any solution s does not explode in finite time or as time tends to infinity, the question arises, what these solutions do instead. Their *long-term behaviour* is of interest. In fact, in section 2.3 we will prove the existence of an attractor $\mathcal{A}$ (as defined in Appendix A) of the semiflow Φ on $\mathcal{O}_0^+$. In this regard, bounded subsets $B \subset \mathcal{O}_0^+$ play an important role. More precisely, we will show that for all $t \geq 0$ *uniform bounds* on the components of solutions s with $s_0 \in B$ can be found, for a given bounded subset $B \subset \mathcal{O}_0^+$.

2.2.6 Uniform bounds

We once again assume $a = d$ and $f - \frac{g}{f} < 0$ to hold for the parameters in (2.1.5) throughout this subsection. As mentioned above, we will deal with bounded subsets $B \subset \mathcal{O}_0^+$ frequently in this subsection. For this reason we introduce some notation in the following

Lemma 2.2.29.
Let any bounded subset $B \subset \mathcal{O}_0^+$ be given. We set

$$\overline{x_B} := \max_{s_0 \in \overline{B}} x_0 \qquad \overline{y_B} := \max_{s_0 \in \overline{B}} y_0 \qquad \overline{z_B} := \max_{s_0 \in \overline{B}} z_0,$$

where $\overline{B}$ is the closure of B in $\mathcal{O}_0^+$. Then for any $s_0 = (x_0, y_0, z_0) \in B$ it holds that

$$x_0 \leq \overline{x_B} \qquad y_0 \leq \overline{y_B} \qquad z_0 \leq \overline{z_B}.$$

Proof.
Let any bounded subset $B \subset \mathcal{O}_0^+$ be given. We remark that the projection onto the first component, i.e. the map

$$\psi : \mathcal{O}_0^+ \to \mathbb{R}_0^+$$
$$s_0 \mapsto x_0$$

is continuous in s_0 on $\mathcal{O}_0^+$. Since B is bounded the closure of B (in $\mathcal{O}_0^+$) - i.e. $\overline{B}$ - is compact and hence the expression

$$\overline{x_B} := \max_{s_0 \in \overline{B}} x_0$$

is well-defined (i.e. the maximum is attained and finite) by the Weierstraß extreme value theorem. Furthermore, for any $s_0 \in B \subset \overline{B}$ we obtain

$$x_0 \overset{s_0 \in \overline{B}}{\leq} \max_{\widehat{s}_0 \in \overline{B}} \widehat{x}_0 = \overline{x_B}.$$

Analogous arguments for the other two components yield the claim. □

The terms $\overline{x_B}, \overline{y_B}, \overline{z_B}$ are upper bounds on the three components of the initial condition $s_0 \in B$. They will prove useful in finding *uniform bounds* (with respect to bounded subsets). We obtain the first such bound on the x-component (for all $t \geq 0$) in the following

Lemma 2.2.30.
Let any bounded subset $B \subset \mathcal{O}_0^+$ be given. We set

$$x_M(B) := \max\{1, \overline{x_B}\} = x_M(\overline{x_B}) > 0,$$

where $x_M(x_0)$ and $\overline{x_B}$ are defined as in Lemmas 2.2.1 and 2.2.29 respectively. Then any solution s with $s_0 \in B$ fulfils

$$0 \leq x(t) \leq x_M(x_0) \leq x_M(B) \qquad \forall\, t \geq 0.$$

Proof.
Let any bounded subset $B \subset \mathcal{O}_0^+$ and solution s with $s_0 \in B$ be given. By Lemmas 2.2.1 and 2.2.29 it holds that

$$\begin{aligned} 0 \leq x(t) \leq x_M(x_0) &= \max\{1, x_0\} \\ &\leq \max\{1, \overline{x_B}\} = x_M(\overline{x_B}) = x_M(B) \qquad \forall\, t \geq 0. \end{aligned}$$ □

Remark 2.2.7.
The bound $x_M(B)$ from the above lemma is *uniform* in the sense that the bound does not explicitly depend on the specific $s_0 \in B$, but rather - given a bounded subset $B \subset \mathcal{O}_0^+$ - is the same for *any* $s_0 \in B$.

We will now construct such uniform bounds on the other two components of solutions as well.

Lemma 2.2.31.
Let any bounded subset $B \subset \mathcal{O}_0^+$ be given. We set

$$y_M(B) := c\max\{1, \overline{x_B}\} + \overline{y_B} + \frac{c}{4b} + \frac{g}{f} - h = y_M(\overline{x_B}, \overline{y_B}) > 0,$$

where $y_M(x_0, y_0)$ and $\overline{x_B}$ and $\overline{y_B}$ are defined as in Lemmas 2.2.3 and 2.2.29 respectively. Then any solution s with $s_0 \in B$ fulfils

$$0 \leq y(t) \leq y_M(x_0, y_0) \leq y_M(B) \qquad \forall\, t \geq 0.$$

Proof.
Let any bounded subset $B \subset \mathcal{O}_0^+$ and solution s with $s_0 \in B$ be given. By Lemmas 2.2.3 and 2.2.29 the following estimate holds for any $t \geq 0$:

$$\begin{aligned} 0 \leq y(t) \leq y_M(x_0, y_0) &= c\max\{1, x_0\} + y_0 + \frac{c}{4b} + \frac{g}{f} - h \\ &\leq c\max\{1, \overline{x_B}\} + \overline{y_B} + \frac{c}{4b} + \frac{g}{f} - h \\ &= y_M(\overline{x_B}, \overline{y_B}) = y_M(B) \end{aligned}$$ □

We show a similar result on the z-component of solutions. To this end we use the bound z_M from Corollary 2.2.5 likewise to the use of x_M and y_M in the preceding proofs. This will prove to be more technical, and hence - for the sake of readability - we split up the process into several auxiliary lemmas. Consider

$$z_M = z_M(x_0, y_0, z_0) = \max\{z_0, 2z_*(x_0, y_0)\} \left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)}$$

from Corollary 2.2.5. We investigate the various terms of z_M separately and then plug the results together (see Lemma 2.2.35), yielding an uniform bound $z_M(B)$ on the z-component for all $t \geq 0$ and a given bounded subset $B \subset \mathcal{O}_0^+$. We commence with

Lemma 2.2.32.
Let any bounded subset $B \subset \mathcal{O}_0^+$ be given. Then for any $s_0 \in B$ it holds that

$$\max\{z_0, 2z_*(x_0, y_0)\} \leq \max\{\overline{z_B}, 2z_*(\overline{x_B}, \overline{y_B})\},$$

where $\overline{x_B}, \overline{y_B}, \overline{z_B}$ are defined as in Lemma 2.2.29.

Proof.
Let any bounded subset $B \subset \mathcal{O}_0^+$ and an arbitrary $s_0 \in B$ be given. Recall the

definition of z_* from Lemma 2.2.5:

$$\begin{aligned} z_*(x_0, y_0) &= \max\left\{\left(-b + \frac{c x_M(x_0)}{x_M(x_0) + d}\right)(y_M(x_0, y_0) + e), 0\right\} \\ &= \max\left\{\left(-b + \frac{c\max\{1, x_0\}}{\max\{1, x_0\} + d}\right)\left(c\max\{1, x_0\} + y_0 + \frac{c}{4b} + \frac{g}{f} - h + e\right), 0\right\} \end{aligned}$$

Since $x_0 \leq \overline{x_B}$ and $y_0 \leq \overline{y_B}$ (see Lemma 2.2.29) and $\frac{cx}{x+d}$ is monotonically increasing for $x \geq 0$ we obtain the following estimate (compare to the proof of Lemma 2.2.5)

$$\begin{aligned} z_*(x_0, y_0) &= \max\left\{\left(-b + \frac{c\max\{1, x_0\}}{\max\{1, x_0\} + d}\right)\left(c\max\{1, x_0\} + y_0 + \frac{c}{4b} + \frac{g}{f} - h + e\right), 0\right\} \\ &\leq \max\left\{\left(-b + \frac{c\max\{1, \overline{x_B}\}}{\max\{1, \overline{x_B}\} + d}\right)\left(c\max\{1, \overline{x_B}\} + \overline{y_B} + \frac{c}{4b} + \frac{g}{f} - h + e\right), 0\right\} \\ &= z_*(\overline{x_B}, \overline{y_B}). \end{aligned}$$

Together with $z_0 \leq \overline{z_B}$ (see Lemma 2.2.29) this yields

$$\max\{z_0, 2z_*(x_0, y_0)\} \leq \max\{z_0, 2z_*(\overline{x_B}, \overline{y_B})\} \leq \max\{\overline{z_B}, 2z_*(\overline{x_B}, \overline{y_B})\}. \qquad \square$$

Next we show

Lemma 2.2.33.
Let any bounded subset $B \subset \mathcal{O}_0^+$ be given. Then for any $s_0 \in B$ it holds that

$$\left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M(x_0, y_0) + e)} \leq \left(\left(\frac{y_M}{\frac{g}{f} - h}\right)^{\left(f - \frac{g}{y_M + h}\right)}\right)^{2(y_M(\overline{x_B}, \overline{y_B}) + e)},$$

where $\overline{x_B}$ and $\overline{y_B}$ are defined as in Lemma 2.2.29.

Proof.
Let any bounded subset $B \subset \mathcal{O}_0^+$ and an arbitrary $s_0 \in B$ be given. Recall from Lemma 2.2.21 that

$$\left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M + h}\right)(y_M + e)} \geq 1.$$

Since $2(y_M + e) \geq 0$ and $y_M > \frac{g}{f} - h > 0$ this implies

$$\left(\frac{y_M}{\frac{g}{f} - h}\right)^{\left(f - \frac{g}{y_M + h}\right)} \geq 1.$$

From this we obtain the following estimate, bearing in mind that it holds that $y_M(x_0, y_0) \leq y_M(\overline{x_B}, \overline{y_B})$ (see Lemma 2.2.31),

$$\left(\frac{y_M}{\frac{g}{f} - h}\right)^{2\left(f - \frac{g}{y_M+h}\right)(y_M(x_0,y_0)+e)} = \underbrace{\left(\left(\frac{y_M}{\frac{g}{f} - h}\right)^{\left(f - \frac{g}{y_M+h}\right)}\right)}_{\geq 1}^{2(y_M(x_0,y_0)+e)}$$
$$\leq \left(\left(\frac{y_M}{\frac{g}{f} - h}\right)^{\left(f - \frac{g}{y_M+h}\right)}\right)^{2(y_M(\overline{x_B},\overline{y_B})+e)}. \qquad \square$$

The third auxiliary lemma we need is

Lemma 2.2.34.
Let any bounded subset $B \subset \mathcal{O}_0^+$ be given. Then for any $s_0 \in B$ it holds that

$$\left(\frac{y_M}{\frac{g}{f} - h}\right)^{\left(f - \frac{g}{y_M+h}\right)} \leq \left(\frac{y_M(\overline{x_B}, \overline{y_B})}{\frac{g}{f} - h}\right)^f$$

where $\overline{x_B}$ and $\overline{y_B}$ are defined as in Lemma 2.2.29.

Proof.
Let any bounded subset $B \subset \mathcal{O}_0^+$ and an arbitrary $s_0 \in B$ be given. Note that the following equivalence holds:

$$y_M = cx_M + y_0 + \frac{c}{4b} + \frac{g}{f} - h > \frac{g}{f} - h \quad \Leftrightarrow \quad f - \frac{g}{y_M + h} > 0.$$

Using this and $y_M(x_0, y_0) \leq y_M(\overline{x_B}, \overline{y_B})$ (see Lemma 2.2.31), the following estimate holds

$$\underbrace{\left(\frac{y_M}{\frac{g}{f} - h}\right)}_{>1}^{\overbrace{\left(f - \frac{g}{y_M+h}\right)}^{>0}} \leq \left(\frac{y_M(x_0, y_0)}{\frac{g}{f} - h}\right)^f \leq \left(\frac{y_M(\overline{x_B}, \overline{y_B})}{\frac{g}{f} - h}\right)^f. \qquad \square$$

Finally, we can also introduce the uniform bound $z_M(B)$ in

Lemma 2.2.35.
Let any bounded subset $B \subset \mathcal{O}_0^+$ be given. We set

$$z_M(B) := \max\{\overline{z_B}, 2z_*(\overline{x_B}, \overline{y_B})\} \left(\frac{y_M(\overline{x_B}, \overline{y_B})}{\frac{g}{f} - h}\right)^{2f(y_M(\overline{x_B},\overline{y_B})+e)} < \infty,$$

where $y_M(x_0, y_0)$, $z_*(x_0, y_0)$, $\overline{x_B}$, $\overline{y_B}$ and $\overline{z_B}$ are defined as in Lemmas 2.2.3, 2.2.5 and 2.2.29 respectively. Then any solution s with $s_0 \in B$ fulfils

$$0 \leq z(t) \leq z_M(x_0, y_0, z_0) \leq z_M(B) \qquad \forall\, t \geq 0.$$

Proof.
Let any bounded subset $B \subset \mathcal{O}_0^+$ and solution s with $s_0 \in B$ be given. By Corollary 2.2.5 it holds that

$$0 \leq z(t) \leq z_M(x_0, y_0, z_0) \qquad \forall\, t \geq 0.$$

We may estimate z_M as follows, using the results of Lemmas 2.2.32, 2.2.33 and 2.2.34 in that order for the inequalities:

$$\begin{aligned}
z_M(x_0,y_0,z_0) &= \underbrace{\max\{z_0, 2z_*(x_0,y_0)\}}_{\geq 0} \overbrace{\left(\frac{y_M}{\frac{g}{f}-h}\right)^{2\left(f-\frac{g}{y_M+h}\right)(y_M+e)}}^{\geq 1} \\
&\leq \max\{\overline{z_B}, 2z_*(\overline{x_B},\overline{y_B})\} \left(\frac{y_M}{\frac{g}{f}-h}\right)^{2\left(f-\frac{g}{y_M+h}\right)(y_M+e)} \\
&\leq \max\{\overline{z_B}, 2z_*(\overline{x_B},\overline{y_B})\} \left(\left(\frac{y_M}{\frac{g}{f}-h}\right)^{\left(f-\frac{g}{y_M+h}\right)}\right)^{2(y_M(\overline{x_B},\overline{y_B})+e)} \\
&\leq \max\{\overline{z_B}, 2z_*(\overline{x_B},\overline{y_B})\} \left(\frac{y_M(\overline{x_B},\overline{y_B})}{\frac{g}{f}-h}\right)^{2f(y_M(\overline{x_B},\overline{y_B})+e)} \qquad = z_M(B)
\end{aligned}$$

Hence we immediately obtain

$$0 \leq z(t) \leq z_M(x_0,y_0,z_0) \leq z_M(B) \qquad \forall\, t \geq 0. \qquad \square$$

Lemmas 2.2.30, 2.2.31 and 2.2.35 yield the uniform bounds $x_M(B)$, $y_M(B)$ and $z_M(B)$ on the three components of the solutions for all $t \geq 0$ and a given bounded subset $B \subset \mathcal{O}_0^+$. We use these bounds in the next section when turning to the issue of the existence of a (global) attractor of the semiflow Φ.

2.3 Attractor - Existence

As mentioned above, in this section we investigate the long-term behaviour of solutions s (i.e. we study their behaviour for $t \to \infty$) and show that their (positive) orbits are uniformly attracted by a set $\mathcal{A}$, being the global attractor (for the definition see Appendix A) of the semiflow Φ on the phase space $X = \mathcal{O}_0^+$. In subsection 2.3.4 we construct a set $\mathcal{B}$, which is absorbing in $\mathcal{O}_0^+$ (with respect to bounded subsets of $\mathcal{O}_0^+$, also see Appendix A) and then prove the existence of the global attractor $\mathcal{A}$ (see Theorem 2.3.1 in subsection 2.3.5) under the known parameter conditions

$$a = d \quad \text{and} \quad f - \frac{g}{h} < 0.$$

We once again impose these two restrictions on our parameters throughout this section. In order to show that the aforementioned set $\mathcal{B}$ in fact exists we construct it.

Showing that this set is absorbing in $\mathcal{O}_0^+$ is a rather lengthy and technical argument and therefore this process is split up in a step-by-step construction in the following subsections 2.3.1 to 2.3.3.

2.3.1 The set $\mathcal{Q}$

In this subsection we construct a set $\mathcal{Q} \subset \mathcal{O}_0^+$ that will help us to control solutions in their x-component, in the sense that $\mathcal{Q}$ will be (uniformly) absorbing in $\mathcal{O}_0^+$ and bounded in both positive and negative x-direction.

Lemma 2.3.1.
Let any solution s be given. Then it holds that

$$\begin{aligned} x_0 = 0 \quad &\Rightarrow \quad x(t) = 0 \\ x_0 > 0 \quad &\Rightarrow \quad x(t) \leq \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} = \frac{1}{\left(\frac{1}{x_0} - 1\right)\exp(-t) + 1} \end{aligned}$$

for all $t \geq 0$.

Proof.
Let any solution s be given. If $x_0 = 0$ then (by 2.1.7) we obtain

$$x_0 = 0 \quad \Rightarrow \quad x(t) = 0 \qquad \forall\, t \geq 0.$$

If $x_0 > 0$ we may estimate the first equation of (2.1.5) for any $t \geq 0$ as follows

$$\dot{x}(t) = x(t)\left(1 - x(t) - \frac{y(t)}{x(t) + a}\right) \leq x(t)\left(1 - x(t)\right).$$

Comparison of the above to the solution of the initial value problem (see the proof of Lemma 2.2.1)

$$\dot{\xi}(t) = \xi(t)\left(1 - \xi(t)\right) \qquad \xi(0) = x(0) = x_0$$

yields

$$x(t) \leq \xi(t) = \frac{x_0 \exp(t)}{1 + x_0(\exp(t) - 1)} = \frac{1}{\left(\frac{1}{x_0} - 1\right)\exp(-t) + 1} \qquad \forall\, t \geq 0. \qquad \square$$

Using the above result we prove

Lemma 2.3.2.
Let any $\varepsilon > 0$ be given. The set

$$\mathcal{Q} := \left\{(x, y, z) \in \mathcal{O}_0^+ \,:\, x \leq 1 + \varepsilon\right\}$$

is positive invariant under the dynamics on $\mathcal{O}_0^+$ generated by system (2.1.5).

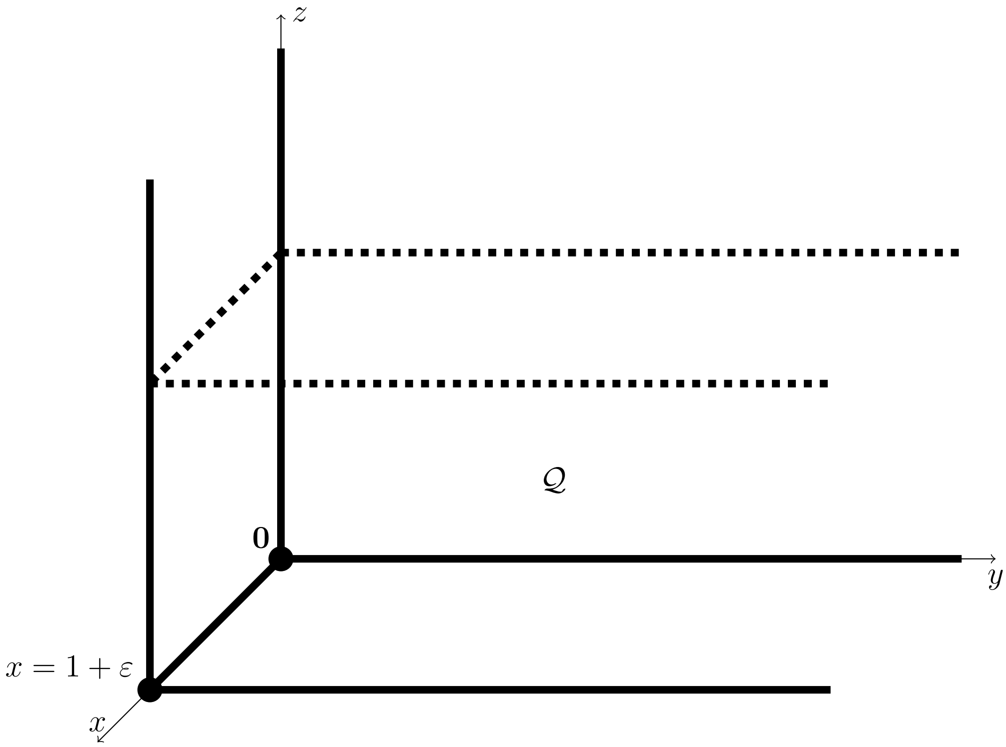


Figure 2.3.1: The set $\mathcal{Q}$ from Lemma 2.3.2.

Proof.
Let any $\varepsilon > 0$ be given and consider the non-empty set

$$\emptyset \neq \mathcal{Q} := \Big\{(x, y, z) \in \mathcal{O}_0^+ \, : \, x \leq 1 + \varepsilon\Big\} \subset \mathcal{O}_0^+.$$

For a visualisation of $\mathcal{Q}$ see Figure 2.3.1. In order to prove that $\mathcal{Q}$ is positive invariant under the dynamics on $\mathcal{O}_0^+$ generated by system (2.1.5) (given by solutions s and the semiflow Φ respectively - see Corollary 2.2.3), we need to show that

$$\Phi(t, \mathcal{Q}) \subset \mathcal{Q} \qquad \forall\, t \geq 0.$$

Since for fixed $t \geq 0$ it holds that

$$\Phi(t, \mathcal{Q}) = \{\Phi(t, s_0) \, : \, s_0 \in \mathcal{Q}\} = \{s(t) \, : \, s_0 \in \mathcal{Q}\},$$

the positive invariance of $\mathcal{Q}$ is equivalent to

$$\forall\, s_0 \in \mathcal{Q} \quad \Rightarrow \quad s(t) \in \mathcal{Q} \qquad \forall\, t \geq 0,$$

i.e. for any given $s_0 \in \mathcal{Q}$ the corresponding solution s fulfils $s(t) \in \mathcal{Q}$ for all $t \geq 0$. Since $\mathcal{O}_0^+$ has property *(I1)* for all $t \geq 0$, the above simplifies to showing (for corresponding solutions s) that

$$\forall\, s_0 \in \mathcal{Q} \quad \Rightarrow \quad x(t) \leq 1 + \varepsilon \qquad \forall\, t \geq 0. \tag{2.3.1}$$

We show that (2.3.1) holds by considering three different cases:

- Let $s_0 \in \mathcal{Q}$ be given such that $x_0 = 0$. Then
$$x(t) = 0 \leq 1 + \varepsilon \qquad \forall\, t \geq 0$$
and (2.3.1) is fulfilled.

- Let $s_0 \in \mathcal{Q}$ be given such that $0 < x_0 \leq 1$. Then Lemma 2.3.1 yields
$$x(t) \leq \frac{1}{\underbrace{\left(\frac{1}{x_0} - 1\right)}_{\geq 0} \exp(-t) + 1} \leq 1 < 1 + \varepsilon$$
for all $t \geq 0$ and (2.3.1) is fulfilled.

- Let $s_0 \in \mathcal{Q}$ be given such that $1 < x_0 \leq 1 + \varepsilon$. We consider the function
$$\xi(t) := \frac{1}{\left(\frac{1}{x_0} - 1\right) \exp(-t) + 1}.$$
more closely and observe for any $t \geq 0$
$$\begin{aligned}
\frac{d}{dt}\xi(t) &= \frac{d}{dt}\left(\frac{1}{\left(\frac{1}{x_0} - 1\right) \exp(-t) + 1}\right) \\
&= (-1)\left(\left(\frac{1}{x_0} - 1\right) \exp(-t) + 1\right)^{-2} \left(\frac{1}{x_0} - 1\right) \exp(-t)(-1) \\
&= \frac{\left(\frac{1}{x_0} - 1\right) \exp(-t)}{\left(\left(\frac{1}{x_0} - 1\right) \exp(-t) + 1\right)^2}.
\end{aligned}$$
Since $1 < x_0 \leq 1 + \varepsilon$ it holds that $\frac{1}{x_0} - 1 < 0$ and therefore
$$\frac{d}{dt}\xi(t) = \frac{\overbrace{\left(\frac{1}{x_0} - 1\right)}^{<0} \exp(-t)}{\left(\left(\frac{1}{x_0} - 1\right) \exp(-t) + 1\right)^2} < 0.$$
In particular ξ is monotonically decreasing for all $t \geq 0$ and furthermore fulfils
$$\xi(0) = \frac{1}{\left(\frac{1}{x_0} - 1\right) \exp(0) + 1} = \frac{1}{\frac{1}{x_0} - 1 + 1} = x_0 \leq 1 + \varepsilon.$$
Therefore
$$\xi(t) \leq 1 + \varepsilon \qquad \forall\, t \geq 0.$$
Using this, Lemma 2.3.1 yields
$$x(t) \leq \frac{1}{\left(\frac{1}{x_0} - 1\right) \exp(-t) + 1} = \xi(t) \leq 1 + \varepsilon \qquad \forall\, t \geq 0. \qquad \square$$

We show next, that the positive phase curve to any solution s will enter the set $\mathcal{Q}$ from the previous lemma by a finite time $T_{\mathcal{Q}}$.

Lemma 2.3.3.
Let $\varepsilon > 0$ be given and set

$$T_{\mathcal{Q}}(s_0) = T_{\mathcal{Q}} := \begin{cases} \ln\left(\frac{(1+\varepsilon)(x_0-1)}{\varepsilon x_0}\right) & \textit{if} \quad x_0 > 1+\varepsilon \\ 0 & \textit{if} \quad x_0 \leq 1+\varepsilon \end{cases}$$

Then $T_{\mathcal{Q}} > 0$ if $x_0 > 1+\varepsilon$ and $T_{\mathcal{Q}}$ is continuous in s_0 on $\mathcal{O}_0^+$, i.e.

$$T_{\mathcal{Q}} \in C^0(\mathcal{O}_0^+, \mathbb{R}_0^+).$$

Proof.
Let $\varepsilon > 0$ be given and set

$$T_{\mathcal{Q}} := \begin{cases} \ln\left(\frac{(1+\varepsilon)(x_0-1)}{\varepsilon x_0}\right) & \text{if} \quad x_0 > 1+\varepsilon \\ 0 & \text{if} \quad x_0 \leq 1+\varepsilon \end{cases}$$

Let $x_0 > 1+\varepsilon$, then $T_{\mathcal{Q}}$ is strictly positive, since

$$\begin{aligned} 1+\varepsilon < x_0 \quad &\Leftrightarrow \quad 1+\varepsilon+\varepsilon x_0 < x_0 + \varepsilon x_0 \\ &\Leftrightarrow \quad \varepsilon x_0 < (1+\varepsilon)x_0 - 1 - \varepsilon \\ &\Leftrightarrow \quad \varepsilon x_0 < (1+\varepsilon)(x_0-1) \\ &\Leftrightarrow \quad 1 < \frac{(1+\varepsilon)(x_0-1)}{\varepsilon x_0} \\ &\Leftrightarrow \quad 0 < \ln\left(\frac{(1+\varepsilon)(x_0-1)}{\varepsilon x_0}\right) = T_{\mathcal{Q}}. \end{aligned}$$

It remains to be shown that $T_{\mathcal{Q}}$ is continuous in s_0 on $\mathcal{O}_0^+$. Since $T_{\mathcal{Q}}$ is independent of y_0 and z_0, it is continuous in s_0 on $\mathcal{O}_0^+$ if it is continuous in x_0 on $\mathbb{R}_0^+$. Note that $T_{\mathcal{Q}}$ is continuous in x_0 on the intervals $[0, 1+\varepsilon)$ and $(1+\varepsilon, \infty)$ as a composition of continuous functions and it remains to show that it is continuous at $x_0 = 1+\varepsilon$. This is the case since

$$\begin{aligned} \lim_{x_0 \searrow 1+\varepsilon} T_{\mathcal{Q}}(x_0, y_0, z_0) &= \ln\left(\frac{(1+\varepsilon)(1+\varepsilon-1)}{\varepsilon(1+\varepsilon)}\right) \\ &= \ln(1) = 0 = T_{\mathcal{Q}}(1+\varepsilon) = \lim_{x_0 \nearrow 1+\varepsilon} T_{\mathcal{Q}}(x_0, y_0, z_0). \end{aligned}$$

Thus $T_{\mathcal{Q}}$ is continuous in $s_0 = (x_0, y_0, z_0)$ on $\mathcal{O}_0^+$, i.e. $T_{\mathcal{Q}} \in C^0(\mathcal{O}_0^+, \mathbb{R})$. □

The above allows us to show

Lemma 2.3.4.
Let any $\varepsilon > 0$ and any solution s be given. Then it holds that

$$s(t) \in \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}(s_0) \geq 0,$$

where $T_{\mathcal{Q}}(s_0)$ is defined as in Lemma 2.3.3.

Proof.
Let any $\varepsilon > 0$ and any solution s be given. This solution fulfils $s(t) \in \mathcal{O}_0^+$ for all $t \geq 0$.

- If $x_0 \leq 1+\varepsilon$ then $s_0 \in \mathcal{Q}$. Furthermore, $\mathcal{Q}$ is positive invariant by Lemma 2.3.2, implying
$$s(t) \in \mathcal{Q} \qquad \forall\, t \geq 0 = T_{\mathcal{Q}}.$$

- Let $x_0 > 1+\varepsilon$. Since by Lemma 2.3.3 we have $T_{\mathcal{Q}} > 0$, Lemma 2.3.1 applies for $t = T_{\mathcal{Q}}$, i.e.
$$x(T_{\mathcal{Q}}) \leq \frac{1}{\left(\frac{1}{x_0}-1\right)\exp(-T_{\mathcal{Q}})+1}.$$
We compute
$$\begin{aligned} x(T_{\mathcal{Q}}) &\leq \frac{1}{\left(\frac{1}{x_0}-1\right)\exp\left(-\ln\left(\frac{(1+\varepsilon)(x_0-1)}{\varepsilon x_0}\right)\right)+1} \\ &= \frac{1}{\left(\frac{1-x_0}{x_0}\right)\frac{\varepsilon x_0}{(1+\varepsilon)(x_0-1)}+1} \\ &= \frac{1}{-\frac{\varepsilon}{(1+\varepsilon)}+1} \\ &= 1+\varepsilon. \end{aligned}$$
Therefore $x(T_{\mathcal{Q}}) \leq 1+\varepsilon$ and $s(T_{\mathcal{Q}}) \in \mathcal{Q}$. Since $\mathcal{Q}$ is positive invariant (Lemma 2.3.2) we obtain
$$s(t) \in \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}.$$ □

The above lemma states that the positive phase curve corresponding to any solution s is contained in the set $\mathcal{Q}$ for all time values than $T_{\mathcal{Q}}$, see Figure 2.3.2. Note that the time $T_{\mathcal{Q}}(s_0)$ is dependent on the initial condition s_0 and hence we have shown that $\mathcal{Q}$ is 'pointwise absorbing' in $\mathcal{O}_0^+$, which is unfortunately not yet sufficient. However, the particular dependence of $T_{\mathcal{Q}}$ on s_0 as well as the uniform bounds from subsection 2.2.6 will prove useful to show that $\mathcal{Q}$ is also (uniformly) absorbing with respect to bounded subsets $B \subset \mathcal{O}_0^+$.

Lemma 2.3.5.
Let any $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given and define
$$T_{\mathcal{Q}}(B) := \max_{s_0 \in \overline{B}} T_{\mathcal{Q}}(s_0) = \begin{cases} \ln\left(\frac{(1+\varepsilon)\left(1-(\overline{x_B})^{-1}\right)}{\varepsilon}\right) & \text{if} \quad B \not\subset \mathcal{Q} \\ 0 & \text{if} \quad B \subset \mathcal{Q}, \end{cases}$$
where $\overline{x_B}$, $\mathcal{Q}$ and $T_{\mathcal{Q}}(s_0)$ are defined as in Lemmas 2.2.29, 2.3.2 and 2.3.3 respectively. Then it holds that $T_{\mathcal{Q}}(B) \geq 0$.

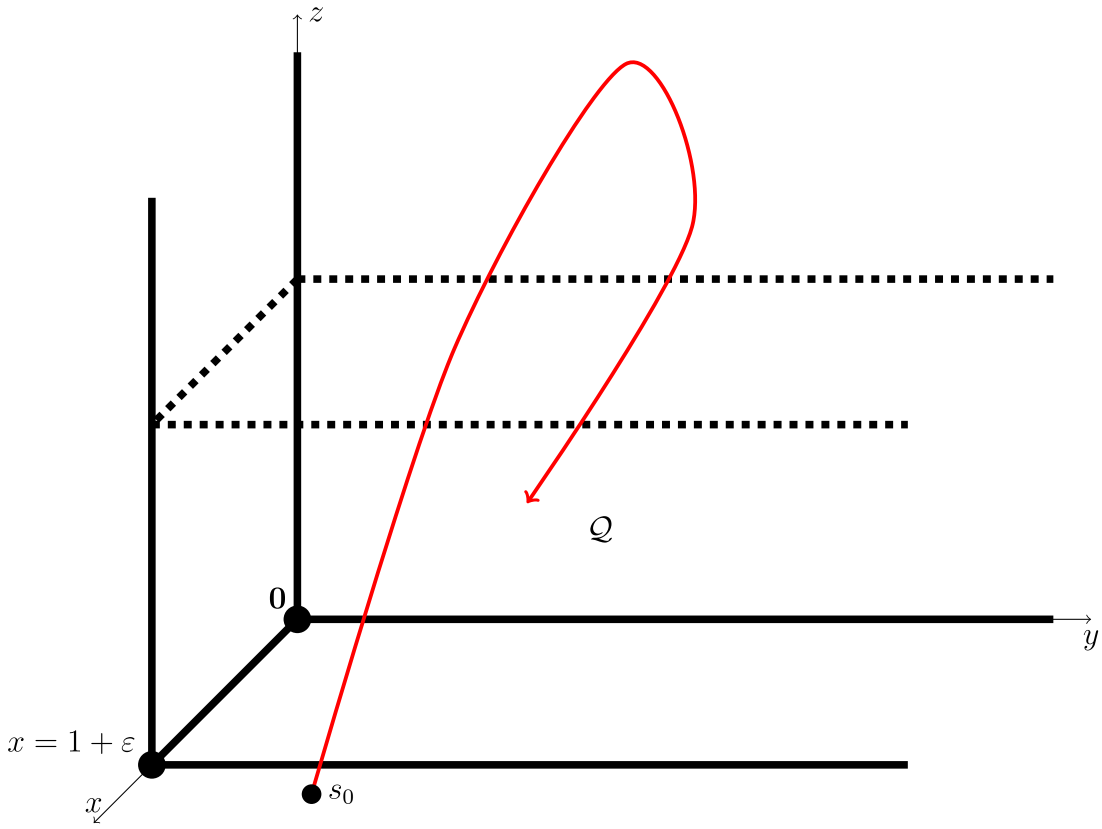


Figure 2.3.2: The set $\mathcal{Q}$ is 'pointwise absorbing', i.e. the positive phase curve of a solution s (with $s_0 \in \mathcal{O}_0^+$) is contained in $\mathcal{Q}$ for all $t \geq T_{\mathcal{Q}}(s_0)$.

Proof.
Let any $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given. We show that $T_{\mathcal{Q}}(B)$ is well-defined (i.e. the maximum is attained and is finite):

- Assume $B \subset \mathcal{Q}$ holds. Since $\mathcal{Q}$ is closed in $\mathcal{O}_0^+$, we have $\overline{B} \subset \mathcal{Q}$ as well. In particular $s_0 \in \overline{B} \subset \mathcal{Q}$ implies $x_0 \leq 1 + \varepsilon$ and therefore (by the definition of $T_{\mathcal{Q}}(s_0)$ in Lemma 2.3.4)

$$T_{\mathcal{Q}}(B) = \max_{s_0 \in \overline{B}} T_{\mathcal{Q}}(s_0) = 0.$$

- If on the other hand $B \not\subset \mathcal{Q}$ then

$$\exists\, \widehat{s}_0 \in B \,:\, \widehat{x}_0 > 1 + \varepsilon$$

and therefore

$$\overline{x_B} = \max_{s_0 \in \overline{B}} x_0 \geq \widehat{x}_0 > 1 + \varepsilon > 0.$$

Due to the monotonicity of the natural logarithm and the fact that $T_{\mathcal{Q}} > 0$ for

$x_0 > 1 + \varepsilon$ (see Lemma 2.3.3) we obtain

$$\begin{aligned} T_{\mathcal{Q}}(B) &= \max_{s_0 \in \overline{B}} T_{\mathcal{Q}}(s_0) \\ &= \max_{s_0 \in \overline{B}} \ln\left(\frac{(1+\varepsilon)(x_0-1)}{\varepsilon x_0}\right) \\ &= \max_{s_0 \in \overline{B} \setminus \mathcal{Q}} \ln\left(\frac{(1+\varepsilon)(1-\frac{1}{x_0})}{\varepsilon}\right) \\ &= \ln\left(\frac{(1+\varepsilon)\left(1-\frac{1}{\overline{x_B}}\right)}{\varepsilon}\right) = \ln\left(\frac{(1+\varepsilon)\left(1-(\overline{x_B})^{-1}\right)}{\varepsilon}\right). \end{aligned}$$

The above proves that $T_{\mathcal{Q}}(B)$ is well-defined. Furthermore, since $T_{\mathcal{Q}}(s_0) \geq 0$ for any $s_0 \in \mathcal{O}_0^+$ we have

$$T_{\mathcal{Q}}(B) = \max_{s_0 \in \overline{B}} \underbrace{T_{\mathcal{Q}}(s_0)}_{\geq 0} \geq 0. \qquad \square$$

The definition of $T_{\mathcal{Q}}(B)$ allows us to prove the following

Lemma 2.3.6.
Let any $\varepsilon > 0$ be given. Then the set $\mathcal{Q}$ is absorbing in $\mathcal{O}_0^+$ under the dynamics on $\mathcal{O}_0^+$ generated by system (2.1.5). More precisely, for any given bounded subset $B \subset \mathcal{O}_0^+$ and for $T_{\mathcal{Q}}(B) \geq 0$ it holds that

$$\Phi(t, B) \subset \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}(B).$$

which is equivalent to

$$\forall\, s_0 \in B \quad \Rightarrow \quad s(t) \in \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}(B).$$

Here $T_{\mathcal{Q}}(B)$ is defined as in Lemma 2.3.5.

Proof.
Let any $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given.

Case 1: If $B \subset \mathcal{Q}$ then $T_{\mathcal{Q}}(B) = 0$ and it is necessary to show

$$\Phi(t, B) \subset \mathcal{Q} \qquad \forall\, t \geq 0. \tag{2.3.2}$$

Since $B \subset \mathcal{Q}$ and $\mathcal{Q}$ is positive invariant (Lemma 2.3.2) we directly obtain

$$\Phi(t, B) \subset \Phi(t, \mathcal{Q}) \subset \mathcal{Q} \qquad \forall\, t \geq 0.$$

Case 2: If $B \not\subset \mathcal{Q}$ then

$$T_{\mathcal{Q}}(B) = \ln\left(\frac{(1+\varepsilon)\left(1-(\overline{x_B})^{-1}\right)}{\varepsilon}\right) \geq 0$$

and it is necessary to show

$$\forall\, s_0 \in B \quad \Rightarrow \quad s(t) \in \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}(B). \tag{2.3.3}$$

i) For any solution s with $s_0 \in B$ and $s_0 \in \mathcal{Q}$ it holds that $x_0 \leq 1+\varepsilon$. Hence, using Lemma 2.3.4 we obtain

$$s(t) \in \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}(s_0) = 0.$$

Since $T_{\mathcal{Q}}(B) \geq 0 = T_{\mathcal{Q}}(s_0)$ we conclude for any solution s with $s_0 \in B$ and $s_0 \in \mathcal{Q}$ that

$$s(t) \in \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}(B) \geq 0.$$

ii) For any solution s with $s_0 \in B$ and $s_0 \notin \mathcal{Q}$. It holds that $x_0 > 1+\varepsilon$ (and $\overline{x_B} > 0$). Hence, using Lemma 2.3.4 we obtain

$$s(t) \in \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}(s_0).$$

By Lemma 2.3.5 it holds that

$$T_{\mathcal{Q}}(B) = \max_{s_0 \in \overline{B}} T_{\mathcal{Q}}(s_0) \geq T_{\mathcal{Q}}(s_0)$$

and we conclude that for any solution s with $s_0 \in B$ and $s_0 \notin \mathcal{Q}$ it holds that

$$s(t) \in \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}(B) \geq T_{\mathcal{Q}}(s_0).$$

Combining the results of *i*) and *ii*) yields that (2.3.3) holds. □

Remark 2.3.1.
Note that the essence of the above results is that we can choose a (uniform) absorbance time $T_{\mathcal{Q}}(B)$ for any bounded subset B by setting

$$T_{\mathcal{Q}}(B) = \max_{s_0 \in \overline{B}} T_{\mathcal{Q}}(s_0).$$

The particular structure of $T_{\mathcal{Q}}$ (continuity on $\mathcal{O}_0^+$ - Lemma 2.3.3) allows this.

The above result proves that $\mathcal{Q}$ is absorbing in $\mathcal{O}_0^+$. However, $\mathcal{Q}$ is clearly **not** bounded (recall Figure 2.3.1). Nonetheless, we obtain a time $T_{\mathcal{Q}}(B) \geq 0$ such that any solution s commencing in a bounded subset $B \subset \mathcal{O}_0^+$ is bounded in the x-component (by zero from below and $1+\varepsilon$ from above) for times larger than $T_{\mathcal{Q}}(B)$.

2.3.2 The set $\mathcal{P}$

We proceed in a similar manner to above, to determine a subset $\mathcal{P}$ of $\mathcal{Q}$ such that the y-component of a solution s is bounded (by a bound given by $\mathcal{P}$) after some time $T_{\mathcal{P}}(B) \geq T_{\mathcal{Q}}(B)$ for any bounded subset $B \subset \mathcal{O}_0^+$ and initial conditions $s_0 \in B$.

Lemma 2.3.7.
Let any $\varepsilon > 0$ be given. The set

$$\mathcal{P} := \left\{(x,y,z) \in \mathcal{O}_0^+ \,:\, x \leq 1+\varepsilon\,,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c}\right\} \subset \mathcal{Q} \subset \mathcal{O}_0^+$$

is positive invariant under the dynamics on $\mathcal{O}_0^+$ generated by system (2.1.5).

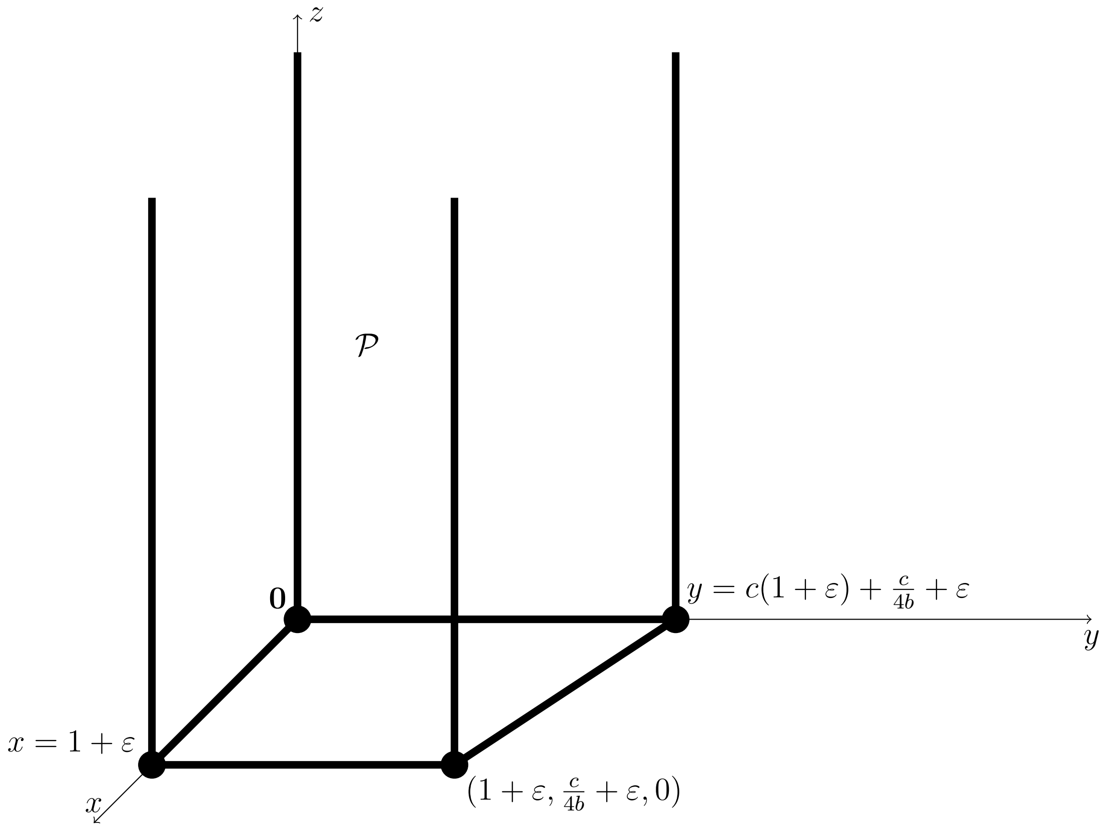


Figure 2.3.3: The set $\mathcal{P} \subset \mathcal{O}_0^+$ is a semi-infinite prism.

Proof.
Let any $\varepsilon > 0$ be given and consider the non-empty set (see Figure 2.3.3)

$$\emptyset \neq \mathcal{P} := \left\{ (x,y,z) \in \mathcal{O}_0^+ \,:\, x \leq 1+\varepsilon\,,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} \right\} \subset \mathcal{Q}.$$

In order to prove that $\mathcal{P}$ is positive invariant, we need to show that

$$\Phi(t,\mathcal{P}) \subset \mathcal{P} \qquad \forall\, t \geq 0$$

which is equivalent to

$$\forall\, s_0 \in \mathcal{P} \quad \Rightarrow \quad s(t) \in \mathcal{P} \qquad \forall\, t \geq 0. \tag{2.3.4}$$

Let s be any solution such that $s_0 \in \mathcal{P}$. Since $\mathcal{O}_0^+$ has property *(I1)* for all $t \geq 0$ and $\mathcal{Q}$ is positive invariant (Lemma 2.3.2), we have

$$\begin{aligned} 0 &\leq x(t) \leq 1 + \varepsilon \\ 0 &\leq y(t) \\ 0 &\leq z(t) \end{aligned}$$

for all $t \geq 0$ and proving that (2.3.4) holds, simplifies to showing

$$\forall\, s_0 \in \mathcal{P} \quad \Rightarrow \quad x(t) + \frac{y(t)}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} \qquad \forall\, t \geq 0. \tag{2.3.5}$$

This is achieved in an identical manner to the proof of Lemma 2.2.3. We define the function $\phi(t) := x(t) + \frac{y(t)}{c}$ and compute

$$\begin{aligned}\frac{d\phi(t)}{dt} &= \dot{x}(t) + \frac{\dot{y}(t)}{c} \\ &= x(1-x) - \frac{xy}{x+a} - \frac{b}{c}y + \frac{1}{c}\frac{cxy}{x+a} - \frac{1}{c}\frac{yz}{y+e} \\ &\leq x(1-x) - \frac{b}{c}y,\end{aligned}$$

where the inequality holds since $y(t) \geq 0$ and $z(t) \geq 0$ for any $t \geq 0$. Inserting a 'zero' yields

$$\frac{d\phi}{dt} \leq x(1-x) + bx - b\underbrace{\left(x + \tfrac{y}{c}\right)}_{=\phi}$$

which may be rewritten as

$$\frac{d\phi(t)}{dt} + b\phi(t) \leq x(1-x) + bx.$$

Since $\max_{x\in[0,\infty)} x(1-x) = \frac{1}{4}$ and $x(t) \leq 1+\varepsilon$ we obtain for all $t \geq 0$:

$$\frac{d\phi(t)}{dt} + b\phi(t) \leq \frac{1}{4} + b(1+\varepsilon) < \frac{1}{4} + b(1+\varepsilon) + \frac{b\varepsilon}{c}.$$

Now ϕ fulfils all the assumptions of Lemma 2.2.2 for $t \geq 0$ with

$$k_1 = b > 0 \quad \text{and} \quad k_2 = \frac{1}{4} + b(1+\varepsilon) + \frac{b\varepsilon}{c}.$$

Applying the lemma yields

$$\phi(t) \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} - \left[1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} - \phi(0)\right]\exp(-bt)$$

for all $t \geq 0$. Now since $s_0 \in \mathcal{P}$ it follows that

$$\phi(0) = x_0 + \frac{y_0}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c}$$

holds and we obtain

$$\phi(t) \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} - \underbrace{\left[1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} - \phi(0)\right]}_{\geq 0}\exp(-bt) \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c}$$

for all $t \geq 0$. This however implies that (2.3.5) holds and hence $\mathcal{P}$ is positive invariant. $\square$

We now turn to show that $\mathcal{P}$ is even absorbing in $\mathcal{O}_0^+$. We commence by proving the following

Lemma 2.3.8.
Let any $\varepsilon > 0$ and any solution s be given. It holds that

$$\exists\, T \in [T_{\mathcal{Q}}(s_0), T_{\mathcal{P}}(s_0)] \;:\; y(T) \leq \frac{c}{4b} + \varepsilon$$

where $T_{\mathcal{Q}}(s_0)$ is defined as in Lemma 2.3.3 and

$$T_{\mathcal{P}}(s_0) = T_{\mathcal{P}} := T_{\mathcal{Q}}(s_0) + \frac{c}{\varepsilon b}\left(x_M(x_0) + \frac{y_0}{c} + \frac{1}{4b}\right) > 0.$$

Proof.
Let any $\varepsilon > 0$ and any solution s be given. We remark that

$$T_{\mathcal{P}}(s_0) = T_{\mathcal{Q}}(s_0) + \frac{c}{\varepsilon b}\left(x_M(x_0) + \frac{y_0}{c} + \frac{1}{4b}\right) \geq T_{\mathcal{Q}} + \underbrace{\frac{c}{4\varepsilon b^2}}_{>0} > T_{\mathcal{Q}} \geq 0$$

and hence the interval $[T_{\mathcal{Q}}, T_{\mathcal{P}}]$ is non-empty and has an interior. We now provide a proof by contradiction and hence assume that

$$y(t) > \frac{c}{4b} + \varepsilon \qquad \forall\, t \in [T_{\mathcal{Q}}, T_{\mathcal{P}}].$$

Using this and by once again defining $\phi(t) := x(t) + \frac{y(t)}{c}$ we then obtain the following estimate for all $t \in [T_{\mathcal{Q}}, T_{\mathcal{P}}]$

$$\begin{aligned}
\frac{d}{dt}\phi(t) &= \dot{x} + \frac{\dot{y}}{c} \\
&\leq x(1-x) - \frac{b}{c}y \\
&\leq \frac{1}{4} - \frac{b}{c}y \\
&< \frac{1}{4} - \frac{b}{c}\left(\frac{c}{4b} + \varepsilon\right) \\
&= -\frac{\varepsilon b}{c}.
\end{aligned}$$

Integrating the above from $T_{\mathcal{Q}}$ to $T_{\mathcal{P}}$ yields

$$\begin{aligned}
\int_{T_{\mathcal{Q}}}^{T_{\mathcal{P}}} \frac{d}{dt}\phi(t)dt < -\int_{T_{\mathcal{Q}}}^{T_{\mathcal{P}}} \frac{\varepsilon b}{c} dt \quad &\Leftrightarrow \quad \phi(T_{\mathcal{P}}) - \phi(T_{\mathcal{Q}}) < -\frac{\varepsilon b}{c}(T_{\mathcal{P}} - T_{\mathcal{Q}}) \\
&\Leftrightarrow \quad \phi(T_{\mathcal{P}}) < \phi(T_{\mathcal{Q}}) - \frac{\varepsilon b}{c}(T_{\mathcal{P}} - T_{\mathcal{Q}})
\end{aligned}$$

where the first equivalence holds due to the fundamental theorem of calculus. By Lemma 2.2.3 we know that $\phi(t) \leq x_M + \frac{y_0}{c} + \frac{1}{4b}$ for any $t \geq 0$ and in particular for $t = T_{\mathcal{Q}} \geq 0$. Hence

$$\phi(T_{\mathcal{P}}) < \phi(T_{\mathcal{Q}}) - \frac{\varepsilon b}{c}(T_{\mathcal{P}} - T_{\mathcal{Q}}) \leq x_M + \frac{y_0}{c} + \frac{1}{4b} - \frac{\varepsilon b}{c}(T_{\mathcal{P}} - T_{\mathcal{Q}})$$

Inserting the definition of $T_{\mathcal{P}}$ yields

$$\begin{aligned}\phi(T_{\mathcal{P}}) &< x_M + \frac{y_0}{c} + \frac{1}{4b} - \frac{\varepsilon b}{c}\left(T_{\mathcal{Q}} + \frac{c}{\varepsilon b}\left(x_M + \frac{y_0}{c} + \frac{1}{4b}\right) - T_{\mathcal{Q}}\right) \\ &= x_M + \frac{y_0}{c} + \frac{1}{4b} - \left(x_M + \frac{y_0}{c} + \frac{1}{4b}\right) \\ &= 0\end{aligned}$$

Hence using the non-negativity of s in its components we obtain

$$0 > \phi(T_{\mathcal{P}}) = \underbrace{x(T_{\mathcal{P}})}_{\geq 0} + \underbrace{\frac{y(T_{\mathcal{P}})}{c}}_{\geq 0} \geq 0,$$

a contradiction. Hence our assumption was wrong and

$$\exists\, T \in [T_{\mathcal{Q}}, T_{\mathcal{P}}] \,:\, y(T) \leq \frac{c}{4b} + \varepsilon. \qquad \square$$

This result allows us to prove

Lemma 2.3.9.
Let any $\varepsilon > 0$ and any solution s be given. Then it holds that

$$s(t) \in \mathcal{P} \qquad \forall\, t \geq T_{\mathcal{P}}(s_0) > 0,$$

where $T_{\mathcal{P}}(s_0)$ is defined as in Lemma 2.3.8. Furthermore, it holds that

$$y(t) \leq c\,(1 + \varepsilon) + \frac{c}{4b} + \varepsilon \qquad \forall\, t \geq T_{\mathcal{P}}.$$

Proof.
Let any $\varepsilon > 0$ and any solution s be given. By Lemma 2.3.8

$$\exists\, T \in [T_{\mathcal{Q}}, T_{\mathcal{P}}] \,:\, y(T) \leq \frac{c}{4b} + \varepsilon.$$

Since $T \geq T_{\mathcal{Q}}$ holds, Lemma 2.3.4 yields $s(T) \in \mathcal{Q}$ and in particular $x(T) \leq 1 + \varepsilon$. Hence

$$x(T) + \frac{y(T)}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c},$$

i.e. $s(T) \in \mathcal{P}$. Since $\mathcal{P}$ is positive invariant (Lemma 2.3.7) we obtain that

$$s(t) \in \mathcal{P} \qquad \forall\, t \geq T$$

and since $T \leq T_{\mathcal{P}}$, also

$$s(t) \in \mathcal{P} \qquad \forall\, t \geq T_{\mathcal{P}}$$

which proves the first claim of the lemma. This is equivalent to

$$x(t) + \frac{y(t)}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} \qquad \forall\, t \geq T_{\mathcal{P}}$$

and solving for $y(t)$ yields

$$y(t) \leq c\,(1+\varepsilon) + \frac{c}{4b} + \varepsilon - \underbrace{cx(t)}_{\geq 0} \leq c\,(1+\varepsilon) + \frac{c}{4b} + \varepsilon \qquad \forall\, t \geq T_{\mathcal{P}}. \qquad \square$$

Thus we have shown that the set $\mathcal{P}$ is also 'pointwise absorbing', see Figure 2.3.4. We introduce the (uniform) absorbance time in the following, using the uniform bounds on the y-component we derived in Lemma 2.2.31.

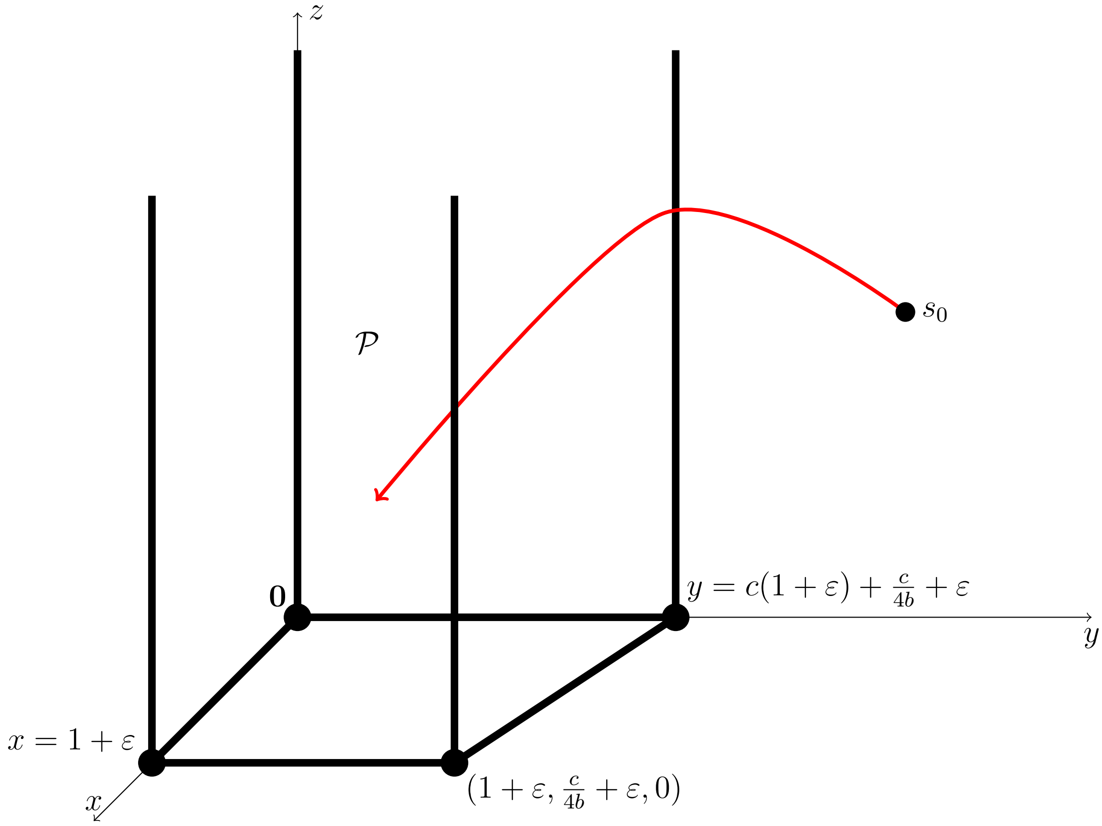


Figure 2.3.4: The set $\mathcal{P}$ is 'pointwise absorbing', see Lemma 2.3.9.

Lemma 2.3.10.
Let any $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given and define

$$T_{\mathcal{P}}(B) := T_{\mathcal{Q}}(B) + \frac{y_M(B)}{\varepsilon b},$$

where $y_M(B)$ and $T_{\mathcal{Q}}(B)$ are defined as in Lemmas 2.2.31 and 2.3.6 respectively. Then for any $s_0 \in B$ it holds that

$$T_{\mathcal{P}}(s_0) < T_{\mathcal{P}}(B),$$

where $T_{\mathcal{P}}(s_0)$ is defined as in Lemma 2.3.8.

Proof.
Let any $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given. We choose an arbitrary $s_0 \in B$ and recall the definition of $T_{\mathcal{P}}(s_0)$ from Lemma 2.3.8:

$$T_{\mathcal{P}}(s_0) = T_{\mathcal{Q}}(s_0) + \frac{c}{\varepsilon b}\left(x_M(x_0) + \frac{y_0}{c} + \frac{1}{4b}\right).$$

From the definition of $T_{\mathcal{Q}}(B)$ in Lemma 2.3.5 we immediately obtain

$$T_{\mathcal{Q}}(B) = \max_{\widehat{s}_0 \in \overline{B}} T_{\mathcal{Q}}(\widehat{s}_0) \geq T_{\mathcal{Q}}(s_0).$$

Combining this with the fact that

$$x_M(x_0) = \max\{1, x_0\} \leq \max\{1, \overline{x_B}\} \quad \text{and} \quad y_0 \leq \overline{y_B}$$

- see Lemmas 2.2.29 and 2.2.30 -, yields

$$\begin{aligned}
T_{\mathcal{P}}(s_0) &= T_{\mathcal{Q}}(s_0) + \frac{c}{\varepsilon b}\left(x_M(x_0) + \frac{y_0}{c} + \frac{1}{4b}\right) \\
&\leq T_{\mathcal{Q}}(B) + \frac{c}{\varepsilon b}\left(\max\{1, x_0\} + \frac{y_0}{c} + \frac{1}{4b}\right) \\
&\leq T_{\mathcal{Q}}(B) + \frac{c}{\varepsilon b}\left(\max\{1, \overline{x_B}\} + \frac{\overline{y_B}}{c} + \frac{1}{4b}\right) \\
&< T_{\mathcal{Q}}(B) + \frac{c}{\varepsilon b}\left(\max\{1, \overline{x_B}\} + \frac{\overline{y_B}}{c} + \frac{1}{4b} + \frac{\frac{g}{f} - h}{c}\right) \\
&= T_{\mathcal{Q}}(B) + \frac{y_M(B)}{\varepsilon b} = T_{\mathcal{P}}(B)
\end{aligned}$$

□

We can now show that also $\mathcal{P}$ is absorbing in $\mathcal{O}_0^+$.

Lemma 2.3.11.
Let any $\varepsilon > 0$ be given. Then the set $\mathcal{P}$ is absorbing in $\mathcal{O}_0^+$ under the dynamics on $\mathcal{O}_0^+$ generated by system (2.1.5). More precisely, for any given bounded subset $B \subset \mathcal{O}_0^+$ and for $T_{\mathcal{P}}(B) \geq 0$ it holds that

$$\Phi(t, B) \subset \mathcal{P} \qquad \forall\, t \geq T_{\mathcal{P}}(B).$$

which is equivalent to

$$\forall\, s_0 \in B \quad \Rightarrow \quad s(t) \in \mathcal{P} \qquad \forall\, t \geq T_{\mathcal{P}}(B).$$

Here $T_{\mathcal{P}}(B)$ is defined as in Lemma 2.3.10.

Proof.
Let any $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given. We show that $T_{\mathcal{P}}(B)$ fulfils

$$\forall\, s_0 \in B \quad \Rightarrow \quad s(t) \in \mathcal{P} \qquad \forall\, t \geq T_{\mathcal{P}}(B).$$

Let an arbitrary solution s such that $s_0 \in B$ be given. By Lemma 2.3.9 we have

$$s(t) \in \mathcal{P} \qquad \forall\, t \geq T_{\mathcal{P}}(s_0) \geq 0,$$

and combining this with $T_{\mathcal{P}}(B) \geq T_{\mathcal{P}}(s_0)$ from Lemma 2.3.10 yields

$$s(t) \in \mathcal{P} \qquad \forall\, t \geq T_{\mathcal{P}}(B) \geq 0.$$

Since $s_0 \in B$ was chosen arbitrarily the proof is complete. □

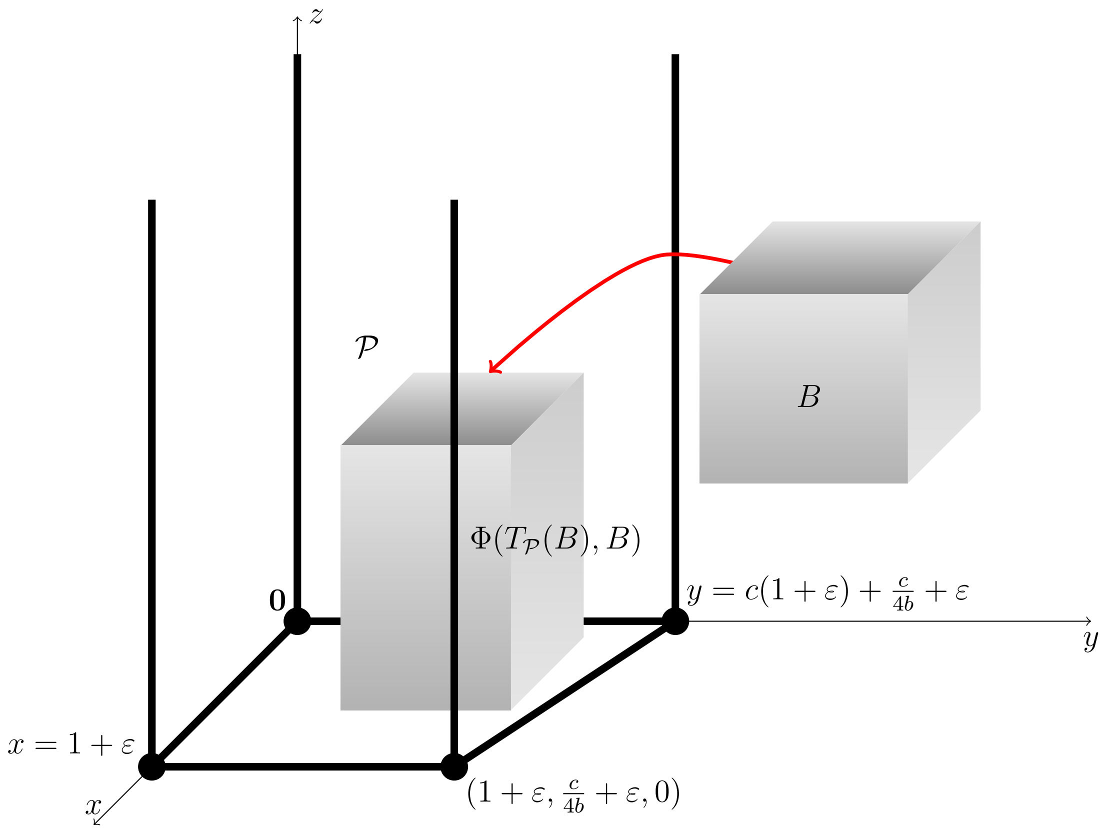


Figure 2.3.5: The set $\mathcal{P}$ (uniformly) absorbs the bounded set B by the time $T_{\mathcal{P}}(B)$.

This proves that $\mathcal{P}$ is absorbing in $\mathcal{O}_0^+$, see Figure 2.3.5. However, the set $\mathcal{P}$ is **not** bounded and hence not a candidate for the non-empty, bounded and absorbing set $\mathcal{B}$ we are looking for. However, $\mathcal{P}$ is only unbounded in 'one direction', namely the positive z-direction (recall Figure 2.3.5). In the following subsection we will construct a third set $\mathcal{R} \subset \mathcal{P} \subset \mathcal{Q}$ which will then allow us to rectify this final drawback of $\mathcal{P}$ and from $\mathcal{R}$ determine the set $\mathcal{B}$ we require.

2.3.3 The set $\mathcal{R}$

We commence with the following

Definition 2.3.1.
Let any $\varepsilon > 0$ *be given. We define*

$$\mathcal{R} := \left\{(x, y, z) \in \mathcal{O}_0^+ \,:\, x \leq 1 + \varepsilon\,,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c}\,,\, z \leq \widehat{z} + \varepsilon\right\} \subset \mathcal{P}$$

where

$$\widehat{z} := \max\left\{\left(-b + \frac{c(1+\varepsilon)}{1+\varepsilon+d}\right)\left(c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + e\right), 0\right\} \geq 0.$$

Remark 2.3.2.
Note that $\mathcal{R} \neq \emptyset$ since $\widehat{z} + \varepsilon > 0$. Furthermore we have $\mathcal{R} \subset \mathcal{P} \subset \mathcal{Q} \subset \mathcal{O}_0^+$ by definition. A visualisation of the set $\mathcal{R}$ may be found in Figure 2.3.6.

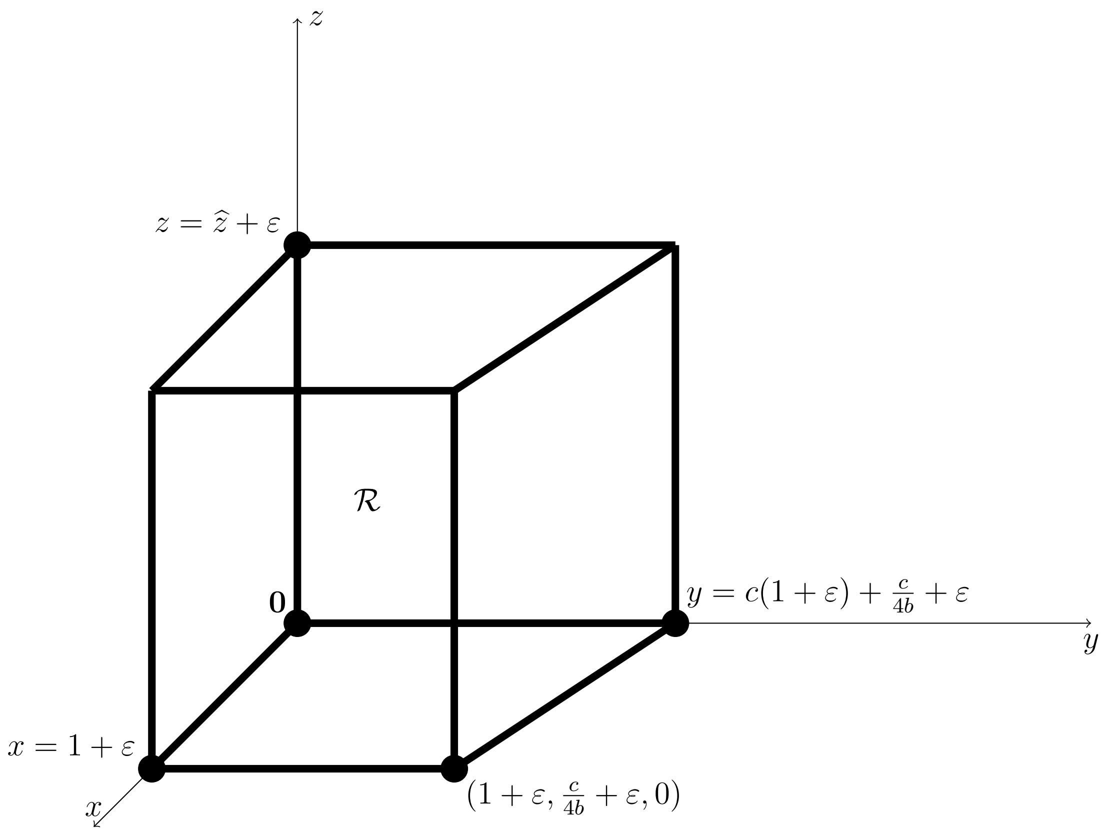


Figure 2.3.6: The set $\mathcal{R} \subset \mathcal{P} \subset \mathcal{Q} \subset \mathcal{O}_0^+$.

Our goal of this subsection is to prove the following result (the proof may be found at the end of this subsection):

Lemma 2.3.12.
For sufficiently small $\varepsilon > 0$ *and any bounded subset* $B \subset \mathcal{O}_0^+$ *there exists a* $T_{\mathcal{R}}(B) > 0$ *such that for any solution* s *with* $s_0 \in B$ *it holds that*

$$\exists T \in [0, T_{\mathcal{R}}(B)] \, : \, s(T) \in \mathcal{R}.$$

Remark 2.3.3.
Once we have proven the above result we will know that for any bounded set $B \subset \mathcal{O}_0^+$ there exists a time $T_{\mathcal{R}}(B)$ such that the positive phase curve corresponding to any solution s with $s_0 \in B$ was in $\mathcal{R}$ *at least once* (i.e. either it commenced in $\mathcal{R}$ or entered it) by the time $T_{\mathcal{R}}(B)$. However, the set $\mathcal{R}$ will **not** be positive invariant in general. Hence such a positive phase curve may leave $\mathcal{R}$ again (for future time values). Nonetheless, the set $\mathcal{R}$ will still suffice to define the absorbing set $\mathcal{B}$ in $\mathcal{O}_0^+$ we are looking for (see Definition 2.3.3).

In order to show that Lemma 2.3.12 holds we will once more proceed stepwise and at the end of this subsection plug the results together to prove the claim.

The case $\frac{1}{2}\left(\frac{g}{f} - h\right) > c + \frac{c}{4b}$

We will first prove the result for the case that the restriction

$$\frac{1}{2}\left(\frac{g}{f} - h\right) > c + \frac{c}{4b}$$

holds for the respective parameters in (2.1.5). In this case we have:

Lemma 2.3.13.
Let $\frac{1}{2}\left(\frac{g}{f} - h\right) > c + \frac{c}{4b}$ *and* $\varepsilon \in \left(0, \frac{\frac{1}{2}\left(\frac{g}{f}-h\right)-c-\frac{c}{4b}}{c+1}\right)$ *and any solution* s *be given and define*

$$T_{\mathcal{R}}(s_0) = T_{\mathcal{R}} := T_{\mathcal{P}}(s_0) + \frac{\frac{g}{f} + h}{(g - hf)(\widehat{z} + \varepsilon)^2} z_M(x_0, y_0, z_0) + \varepsilon.$$

where $z_M(x_0, y_0, z_0) \geq 0$ *and* $T_{\mathcal{P}}(s_0)$ *are defined as in Corollary 2.2.5 and Lemma 2.3.8 respectively. It holds that* $T_{\mathcal{R}} > T_{\mathcal{P}} > 0$.

Proof.
Let $\frac{1}{2}\left(\frac{g}{f} - h\right) > c + \frac{c}{4b}$ and $\varepsilon \in \left(0, \frac{\frac{1}{2}\left(\frac{g}{f}-h\right)-c-\frac{c}{4b}}{c+1}\right)$ and any solution s be given. We first remark that since

$$\frac{1}{2}\left(\frac{g}{f} - h\right) > c + \frac{c}{4b} \quad \Leftrightarrow \quad \frac{1}{2}\left(\frac{g}{f} - h\right) - c - \frac{c}{4b} > 0$$

we have

$$\varepsilon \in \left(0, \frac{\frac{1}{2}\left(\frac{g}{f} - h\right) - c - \frac{c}{4b}}{c + 1}\right) \neq \emptyset.$$

Furthermore, our assumption on the parameters f, g, h implies

$$f - \frac{g}{h} < 0 \quad \Leftrightarrow \quad g - hf > 0$$

and hence by using $z_M(x_0, y_0, z_0) \geq 0$ (see Corollary 2.2.5) and $T_{\mathcal{P}}(s_0) > 0$ (see Lemma 2.3.8) we obtain

$$T_{\mathcal{R}} = T_{\mathcal{P}}(s_0) + \underbrace{\frac{\frac{g}{f} + h}{(g - hf)(\widehat{z} + \varepsilon)^2} z_M(x_0, y_0, z_0) + \varepsilon}_{>0} > T_{\mathcal{P}}(s_0) > 0. \qquad \square$$

We show that under the above parameter conditions the positive phase curve to a solution s was in the set $\mathcal{R}$ after the time $T_{\mathcal{R}}(s_0)$, however does not necessarily stay in $\mathcal{R}$ for all $t \geq T_{\mathcal{R}}$, see Figure 2.3.7.

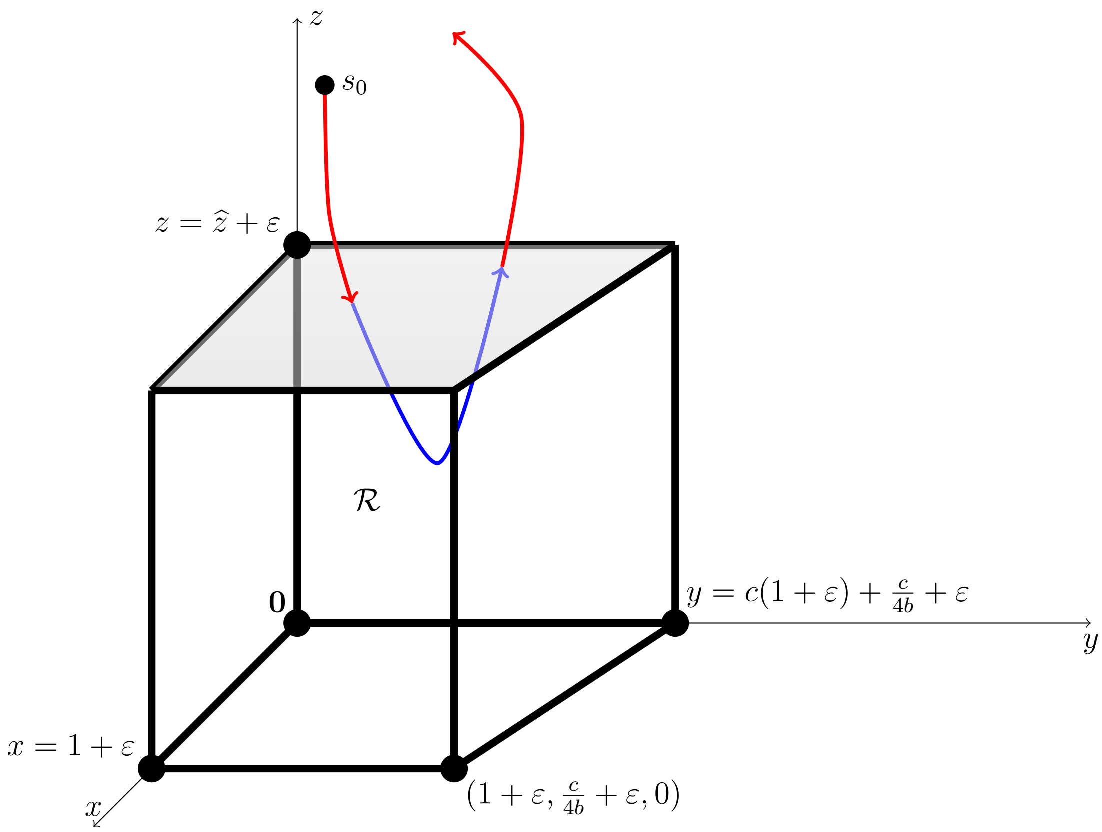


Figure 2.3.7: The positive phase curve is in the set $\mathcal{R}$ for some time $T \in [T_{\mathcal{P}}, T_{\mathcal{R}}]$ (depicted in blue).

Lemma 2.3.14.
Let $\frac{1}{2}\left(\frac{g}{f} - h\right) > c + \frac{c}{4b}$ *and* $\varepsilon \in \left(0, \frac{\frac{1}{2}\left(\frac{g}{f} - h\right) - c - \frac{c}{4b}}{c+1}\right)$ *and any solution* s *be given. Then it holds that*

$$\exists T \in [T_{\mathcal{P}}(s_0), T_{\mathcal{R}}(s_0)] \,:\, s(T) \in \mathcal{R}$$

where $T_{\mathcal{P}}(s_0)$ *and* $T_{\mathcal{R}}(s_0)$ *are defined as in Lemmas 2.3.8 and 2.3.13 respectively.*

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) > c + \frac{c}{4b}$ and $\varepsilon \in \left(0, \frac{\frac{1}{2}\left(\frac{g}{f}-h\right)-c-\frac{c}{4b}}{c+1}\right)$ and any solution s be given. Since $T_{\mathcal{R}} > T_{\mathcal{P}}$ (by Lemma 2.3.13) the interval $[T_{\mathcal{P}}, T_{\mathcal{R}}]$ is non-empty and has an interior. Also note that Lemma 2.3.9 yields

$$s(t) \in \mathcal{P} \qquad \forall\, t \geq T_{\mathcal{P}},$$

i.e. for any $t \geq T_{\mathcal{P}}$ we have

$$\begin{aligned} &0 \leq x(t) \leq 1+\varepsilon \\ &0 \leq x(t) + \frac{y(t)}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} \\ &0 \leq z(t). \end{aligned} \tag{2.3.6}$$

Hence - in order to prove the claim - it remains to be shown that

$$\exists\, T \in [T_{\mathcal{P}}, T_{\mathcal{R}}] \,:\, z(T) \leq \widehat{z} + \varepsilon.$$

We show this via a proof by contradiction, and therefore assume

$$z(t) > \widehat{z} + \varepsilon > 0 \qquad \forall\, t \in [T_{\mathcal{P}}, T_{\mathcal{R}}] \tag{2.3.7}$$

to hold. Considering the third equation of (2.1.5) and using (2.3.6) yields

$$\dot{z}(t) = \left(f - \frac{g}{y(t)+h}\right) z^2(t) \leq \left(f - \frac{g}{c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + h}\right) z^2(t) \tag{2.3.8}$$

for all $t \in [T_{\mathcal{P}}, T_{\mathcal{R}}]$. Now using the following equivalence

$$\begin{aligned} \varepsilon < \frac{\frac{1}{2}\left(\frac{g}{f}-h\right) - c - \frac{c}{4b}}{c+1} \quad &\Leftrightarrow \quad \varepsilon c + \varepsilon < \frac{1}{2}\left(\frac{g}{f} - h\right) - c - \frac{c}{4b} \\ &\Leftrightarrow \quad c(1+\varepsilon) + \frac{c}{4b} + \varepsilon < \underbrace{\frac{1}{2}\left(\frac{g}{f} - h\right)}_{>0} \end{aligned}$$

we may estimate (2.3.8) further

$$\begin{aligned} \dot{z}(t) &\leq \left(f - \frac{g}{c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + h}\right) z^2(t) \\ &\leq \left(f - \frac{g}{\frac{1}{2}\left(\frac{g}{f} - h\right) + h}\right) z^2(t) = \left(f - \frac{2g}{\frac{g}{f} + h}\right) z^2(t) = \frac{hf - g}{\frac{g}{f} + h} z^2(t) \end{aligned}$$

for all $t \in [T_{\mathcal{P}}, T_{\mathcal{R}}]$. Since

$$f - \frac{g}{h} < 0 \quad \Leftrightarrow \quad hf - g < 0$$

and using our assumption in (2.3.7), we obtain

$$\dot{z}(t) \leq \underbrace{\frac{hf-g}{\frac{g}{f}+h}}_{<0} z^2(t) < \frac{hf-g}{\frac{g}{f}+h}(\widehat{z}+\varepsilon)^2$$

for all $t \in [T_{\mathcal{P}}, T_{\mathcal{R}}]$. Integrating the above from $T_{\mathcal{P}}$ to $T_{\mathcal{R}}$ yields

$$\begin{aligned} & \int_{T_{\mathcal{P}}}^{T_{\mathcal{R}}} \frac{d}{dt} z(t) dt < \int_{T_{\mathcal{P}}}^{T_{\mathcal{R}}} \frac{hf-g}{\frac{g}{f}+h}(\widehat{z}+\varepsilon)^2 dt \\ \Leftrightarrow \quad & z(T_{\mathcal{R}}) - z(T_{\mathcal{P}}) < \frac{hf-g}{\frac{g}{f}+h}(\widehat{z}+\varepsilon)^2 (T_{\mathcal{R}} - T_{\mathcal{P}}) \\ \Leftrightarrow \quad & z(T_{\mathcal{R}}) < z(T_{\mathcal{P}}) + \frac{hf-g}{\frac{g}{f}+h}(\widehat{z}+\varepsilon)^2 (T_{\mathcal{R}} - T_{\mathcal{P}}) \end{aligned}$$

Inserting the definition of $T_{\mathcal{R}}$ in the above, yields

$$\begin{aligned} z(T_{\mathcal{R}}) &< z(T_{\mathcal{P}}) + \frac{hf-g}{\frac{g}{f}+h}(\widehat{z}+\varepsilon)^2 \left(T_{\mathcal{P}} + \frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2} z_M + \varepsilon - T_{\mathcal{P}} \right) \\ &= z(T_{\mathcal{P}}) + \frac{hf-g}{g-hf} z_M + \underbrace{\frac{hf-g}{\frac{g}{f}+h}}_{<0}(\widehat{z}+\varepsilon)^2 \varepsilon \\ &< z(T_{\mathcal{P}}) + \frac{hf-g}{g-hf} z_M \\ &= z(T_{\mathcal{P}}) - z_M. \end{aligned}$$

Furthermore recall that by Corollary 2.2.5 we have $z(t) \leq z_M$ for any $t \geq 0$ and in particular for $t = T_{\mathcal{P}} > 0$. Hence

$$z(T_{\mathcal{R}}) < z(T_{\mathcal{P}}) - z_M \leq z_M - z_M = 0.$$

This however is a contradiction to the non-negativity of the z-component of s (Lemma 2.1.4). □

We now define the uniform absorbance time $T_{\mathcal{R}}(B)$ we require.

Lemma 2.3.15.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) > c + \frac{c}{4b}$ *and* $\varepsilon \in \left(0, \frac{\frac{1}{2}\left(\frac{g}{f}-h\right)-c-\frac{c}{4b}}{c+1}\right)$ *and any bounded subset* $B \subset \mathcal{O}_0^+$ *be given. We define*

$$T_{\mathcal{R}}(B) := T_{\mathcal{P}}(B) + \frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2} z_M(B) + \varepsilon,$$

where $z_M(B)$ *and* $T_{\mathcal{P}}(B)$ *are defined as in Lemmas 2.2.35 and 2.3.11 respectively. Then for any* $s_0 \in B$ *it holds that*

$$T_{\mathcal{R}}(s_0) \leq T_{\mathcal{R}}(B),$$

where $T_{\mathcal{R}}(s_0)$ *is defined as in Lemma 2.3.13.*

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right)>c+\frac{c}{4b}$ and $\varepsilon\in\left(0,\frac{\frac{1}{2}\left(\frac{g}{f}-h\right)-c-\frac{c}{4b}}{c+1}\right)$ and any bounded subset $B\subset\mathcal{O}_0^+$ be given. We choose an arbitrary $s_0\in B$ and recall the definition of $T_{\mathcal{R}}(s_0)$ from Lemma 2.3.13:

$$T_{\mathcal{R}}(s_0)=T_{\mathcal{P}}(s_0)+\frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2}z_M(x_0,y_0,z_0)+\varepsilon.$$

Note that from Lemma 2.3.10 we have $T_{\mathcal{P}}(s_0)\le T_{\mathcal{P}}(B)$ and from Lemma 2.2.35 we have $z_M(x_0,y_0,z_0)\le z_M(B)$. Using these results yields

$$\begin{aligned}T_{\mathcal{R}}(s_0)&=T_{\mathcal{P}}(s_0)+\frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2}z_M(x_0,y_0,z_0)+\varepsilon\\&\le T_{\mathcal{P}}(B)+\frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2}z_M(B)+\varepsilon\\&=T_{\mathcal{R}}(B).\end{aligned}$$
□

Recall that the goal of this section is to prove Lemma 2.3.12. We do this for the above parameter assumptions.

Lemma 2.3.16.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right)>c+\frac{c}{4b}$ *and* $\varepsilon\in\left(0,\frac{\frac{1}{2}\left(\frac{g}{f}-h\right)-c-\frac{c}{4b}}{c+1}\right)$ *and any bounded subset* $B\subset\mathcal{O}_0^+$ *be given. Then for any solution* s *with* $s_0\in B$ *it holds that*

$$\exists T\in[0,T_{\mathcal{R}}(B)]\,:\,s(T)\in\mathcal{R},$$

where $T_{\mathcal{R}}(B)>0$ *is defined as in Lemma 2.3.15.*

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right)>c+\frac{c}{4b}$ and $\varepsilon\in\left(0,\frac{\frac{1}{2}\left(\frac{g}{f}-h\right)-c-\frac{c}{4b}}{c+1}\right)$ and any bounded subset $B\subset\mathcal{O}_0^+$ be given. Furthermore, let s be a solution with $s_0\in B$. Since the conditions of Lemma 2.3.14 are met, we have that

$$\exists T\in[T_{\mathcal{P}},T_{\mathcal{R}}]\subset[0,T_{\mathcal{R}}]\,:\,s(T)\in\mathcal{R}.$$

By Lemma 2.3.15 we obtain $T_{\mathcal{R}}=T_{\mathcal{R}}(s_0)\le T_{\mathcal{R}}(B)$ and hence

$$[0,T_{\mathcal{R}}]\subset[0,T_{\mathcal{R}}(B)],$$

yielding

$$\exists T\in[T_{\mathcal{P}},T_{\mathcal{R}}]\subset[0,T_{\mathcal{R}}(B)]\,:\,s(T)\in\mathcal{R}$$

and thus the claim holds true since s (with $s_0\in B$) was chosen arbitrarily. □

This proves Lemma 2.3.12 for the restriction $\frac{1}{2}\left(\frac{g}{f}-h\right)>c+\frac{c}{4b}$.

The case $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c + \frac{c}{4b}$

We now consider the other case, i.e. let the parameters fulfil

$$\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c + \frac{c}{4b}.$$

We commence by defining some auxiliary sets.

Definition 2.3.2.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c + \frac{c}{4b}$ and $\varepsilon > 0$ hold. We define

$$\Lambda_1 := \Big\{(x,y,z) \in \mathcal{O}_0^+ \,:\, x \leq 1+\varepsilon \,,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} \,, \\ y > \frac{1}{2}\left(\frac{g}{f}-h\right) \,,\, z > \widehat{z} + \varepsilon\Big\} \subset \mathcal{P}$$

and

$$\Lambda_2 := \Big\{(x,y,z) \in \mathcal{O}_0^+ \,:\, x \leq 1+\varepsilon \,,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c} \,, \\ y \leq \frac{1}{2}\left(\frac{g}{f}-h\right) \,,\, z > \widehat{z} + \varepsilon\Big\} \subset \mathcal{P}$$

Remark 2.3.4.
We remark that the set Λ_1 is non-empty, since

$$\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c + \frac{c}{4b} < c(1+\varepsilon) + \frac{c}{4b} + \frac{\varepsilon}{c}$$

and hence there exists a $y > 0$ such that

$$\frac{1}{2}\left(\frac{g}{f}-h\right) < y \leq c(1+\varepsilon) + \frac{c}{4b} + \frac{\varepsilon}{c}.$$

Furthermore Λ_2 is non-empty since $\frac{g}{f} - h > 0$ and hence there exists a $y > 0$ such that

$$0 < y \leq \frac{1}{2}\left(\frac{g}{f}-h\right) \leq c + \frac{c}{4b} < c(1+\varepsilon) + \frac{c}{4b} + \frac{\varepsilon}{c}.$$

The sets $\mathcal{R}$, Λ_1 and Λ_2 are a partition of $\mathcal{P}$, i.e.

$$\mathcal{P} = \mathcal{R} \,\dot{\cup}\, \Lambda_1 \,\dot{\cup}\, \Lambda_2,$$

see Figure 2.3.8.

Using the above definition of the sets Λ_1 and Λ_2 we prove the claim of Lemma 2.3.12 step by step. Note that some similarity of the results we are about to prove and those from the previous sections may be observed. In particular the auxiliary sets Λ_1 and Λ_2 from above have a similar function as the auxiliary sets Ω_3 and Ω_4 from Definition 2.2.2. The decisive difference is that Λ_1, Λ_2 are independent of the initial conditions (as opposed to Ω_3 and Ω_4).

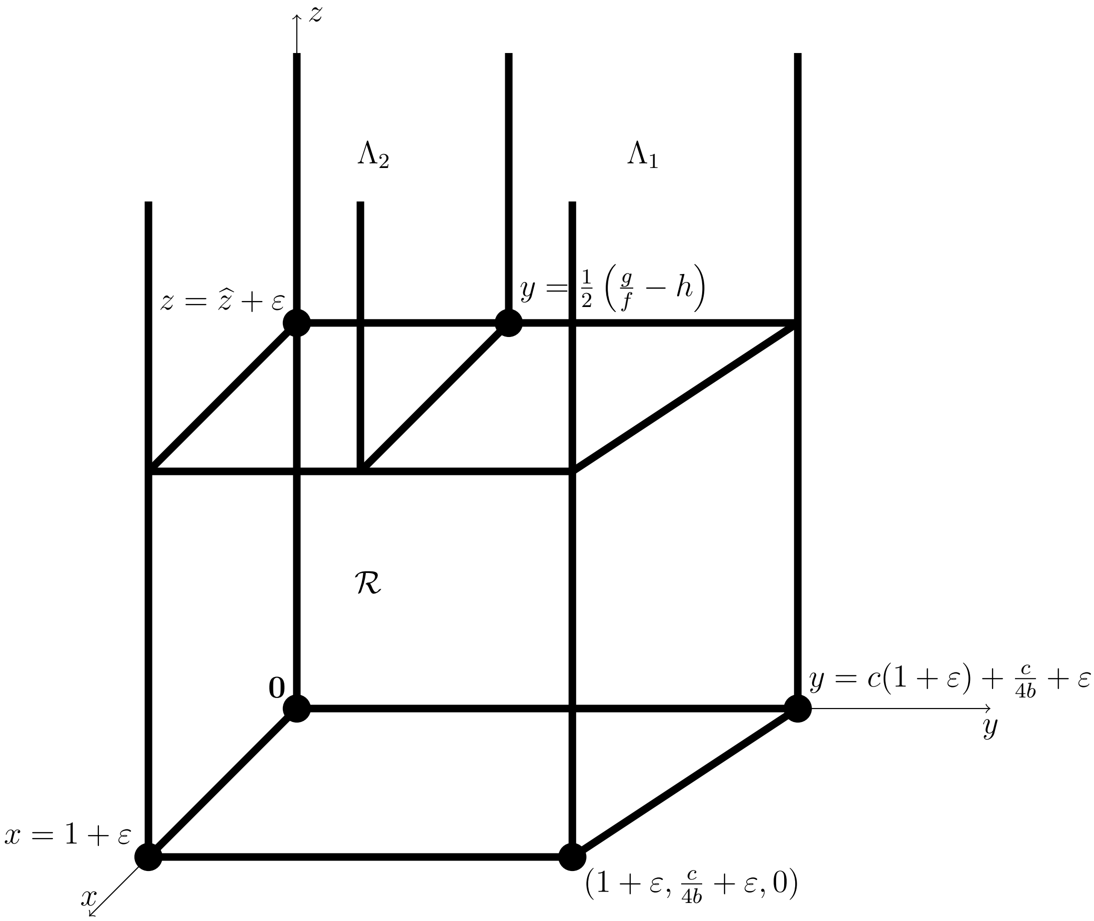


Figure 2.3.8: The sets $\mathcal{R}$, Λ_1 and Λ_2.

The set Λ_1

We will consider the set Λ_1 first.

Lemma 2.3.17.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \le c+\frac{c}{4b}$ and $\varepsilon>0$. Furthermore, let any solution s be given. We set

$$T_{\Lambda_1}(s_0) = T_{\Lambda_1} := T_{\mathcal{P}}(s_0) + \frac{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}{\varepsilon}\left(\frac{2\left[c(1+\varepsilon)+\frac{c}{4b}+\varepsilon\right]}{\frac{g}{f}-h}\right)$$

where $T_{\mathcal{P}}(s_0)$ is defined as in Lemma 2.3.8 and claim $T_{\Lambda_1} > T_{\mathcal{P}} > 0$.

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \le c+\frac{c}{4b}$ and $\varepsilon>0$. Furthermore, let any solution s be given. Since $\frac{g}{f}-h>0$ this allows us to estimate

$$T_{\Lambda_1} = T_{\mathcal{P}} + \underbrace{\frac{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}{\varepsilon}}_{>0}\underbrace{\left(\frac{2\left[c(1+\varepsilon)+\frac{c}{4b}+\varepsilon\right]}{\frac{g}{f}-h}\right)}_{>0} > T_{\mathcal{P}} > 0$$

where the positivity of $T_{\mathcal{P}}$ was proven in Lemma 2.3.8. $\square$

Before using the time T_{Λ_1} we show the following auxiliary

Lemma 2.3.18.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c+\frac{c}{4b}$ and $\varepsilon > 0$. Furthermore, let any solution s and any time $t \geq 0$ be given such that

$$\dot{y}(t) \leq y(t)\left(-b+\frac{c(1+\varepsilon)}{1+\varepsilon+d}-\frac{\widehat{z}+\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right).$$

Then it holds that

$$\dot{y}(t) \leq y(t)\underbrace{\left(\frac{-\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)}_{<0}.$$

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c+\frac{c}{4b}$ and $\varepsilon > 0$. Furthermore, let any solution s and any time $t \geq 0$ be given such that

$$\dot{y}(t) \leq y(t)\left(-b+\frac{c(1+\varepsilon)}{1+\varepsilon+d}-\frac{\widehat{z}+\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right) \tag{2.3.9}$$

Recall the definition

$$\widehat{z} := \max\left\{\left(-b+\frac{c(1+\varepsilon)}{1+\varepsilon+d}\right)\left(c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e\right), 0\right\} \geq 0$$

and consider two different cases:

- If $\widehat{z}=0$ then
$$-b+\frac{c(1+\varepsilon)}{1+\varepsilon+d} \leq 0$$
and therefore (2.3.9) may be estimated as follows (recall $\widehat{z}=0$):
$$\begin{aligned}\dot{y}(t) &\leq y(t)\left(-b+\frac{c(1+\varepsilon)}{1+\varepsilon+d}-\frac{\widehat{z}+\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)\\ &\leq y(t)\left(\frac{-\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)\end{aligned}$$
for $t \geq 0$.

- If on the other hand $\widehat{z} > 0$ then
$$\widehat{z} = \left(-b+\frac{c(1+\varepsilon)}{1+\varepsilon+d}\right)\left(c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e\right)$$

and therefore (2.3.9) simplifies to

$$\begin{aligned}\dot{y}(t) &\leq y(t)\left(-b + \frac{c(1+\varepsilon)}{1+\varepsilon+d} - \frac{\widehat{z}+\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)\\ &= y(t)\left(\frac{-\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)\end{aligned}$$

for $t \geq 0$. □

We use the above and T_{Λ_1} to prove

Lemma 2.3.19.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c + \frac{c}{4b}$ *and* $\varepsilon > 0$. *Furthermore, let any solution* s *be given. Then it holds that*

$$\exists\, T \in [T_{\mathcal{P}}(s_0), T_{\Lambda_1}(s_0)] \;:\; s(T) \in \mathcal{R} \cup \Lambda_2 = \mathcal{P}\backslash\Lambda_1,$$

where $T_{\mathcal{P}}(s_0)$ *and* $T_{\Lambda_1}(s_0)$ *are defined as in Lemmas 2.3.8 and 2.3.17 respectively.*

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c + \frac{c}{4b}$ and $\varepsilon > 0$. Furthermore, let any solution s be given. Note that due to the fact that $T_{\Lambda_1} > T_{\mathcal{P}}$ (from Lemma 2.3.17) the interval $[T_{\mathcal{P}}, T_{\Lambda_1}]$ is non-empty and has an interior. Furthermore, by Lemma 2.3.9 we have $s(t) \in \mathcal{P}$ for all $t \geq T_{\mathcal{P}}$. In particular

$$s(t) \in \mathcal{P} \qquad \forall\, t \in [T_{\mathcal{P}}, T_{\Lambda_1}].$$

Since

$$\mathcal{P} = \mathcal{R}\,\dot{\cup}\,\Lambda_1\,\dot{\cup}\,\Lambda_2$$

the claim of the lemma holds true, unless it holds that

$$s(t) \in \Lambda_1 \qquad \forall\, t \in [T_{\mathcal{P}}, T_{\Lambda_1}]. \tag{2.3.10}$$

We show that (2.3.10) in fact cannot hold, by assuming it does and concluding a contradiction. Since $s(t) \in \mathcal{P}$ for any $t \in [T_{\mathcal{P}}, T_{\Lambda_1}]$ we estimate

$$\begin{aligned}\dot{y}(t) &= y(t)\left(-b + \frac{cx(t)}{x(t)+d} - \frac{z(t)}{y(t)+e}\right)\\ &\leq y(t)\left(-b + \frac{c(1+\varepsilon)}{1+\varepsilon+d} - \frac{z(t)}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)\end{aligned}$$

for any $t \in [T_{\mathcal{P}}, T_{\Lambda_1}]$. Furthermore, (2.3.10) implies $z(t) > \widehat{z}+\varepsilon$ for all $t \in [T_{\mathcal{P}}, T_{\Lambda_1}]$ and hence we may estimate the above further to obtain

$$\dot{y}(t) \leq y(t)\left(-b + \frac{c(1+\varepsilon)}{1+\varepsilon+d} - \frac{\widehat{z}+\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)$$

for all $t \in [T_{\mathcal{P}}, T_{\Lambda_1}]$. Applying Lemma 2.3.18 yields

$$\dot{y}(t) \leq y(t) \left(\frac{-\varepsilon}{c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + e} \right) \qquad \forall\, t \in [T_{\mathcal{P}}, T_{\Lambda_1}].$$

Furthermore, since we assumed (2.3.10) to hold, we have

$$y(t) > \frac{1}{2} \left(\frac{g}{f} - h \right) \qquad \forall\, t \in [T_{\mathcal{P}}, T_{\Lambda_1}],$$

by the definition of Λ_1, whence

$$\dot{y}(t) \leq y(t) \underbrace{\left(\frac{-\varepsilon}{c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + e} \right)}_{<0} < \frac{1}{2} \left(\frac{g}{f} - h \right) \left(\frac{-\varepsilon}{c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + e} \right)$$

for any $t \in [T_{\mathcal{P}}, T_{\Lambda_1}]$. Integration of the above from $T_{\mathcal{P}}$ to T_{Λ_1} yields

$$\begin{aligned} & y(T_{\Lambda_1}) - y(T_{\mathcal{P}}) < \frac{1}{2} \left(\frac{g}{f} - h \right) \left(\frac{-\varepsilon}{c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + e} \right) [T_{\Lambda_1} - T_{\mathcal{P}}] \\ \Leftrightarrow \quad & y(T_{\Lambda_1}) < y(T_{\mathcal{P}}) + \frac{1}{2} \left(\frac{g}{f} - h \right) \left(\frac{-\varepsilon}{c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + e} \right) [T_{\Lambda_1} - T_{\mathcal{P}}]. \end{aligned}$$

Inserting the definition of T_{Λ_1} yields

$$\begin{aligned} y(T_{\Lambda_1}) &< y(T_{\mathcal{P}}) + \frac{1}{2} \left(\frac{g}{f} - h \right) \left(\frac{-\varepsilon}{c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + e} \right) \cdot \\ &\qquad \left[T_{\mathcal{P}} + \frac{c(1+\varepsilon) + \frac{c}{4b} + \varepsilon + e}{\varepsilon} \left(\frac{2\left[c(1+\varepsilon) + \frac{c}{4b} + \varepsilon\right]}{\frac{g}{f} - h} \right) - T_{\mathcal{P}} \right] \\ &= y(T_{\mathcal{P}}) - \frac{1}{2} \left(\frac{g}{f} - h \right) \left(\frac{2\left[c(1+\varepsilon) + \frac{c}{4b} + \varepsilon\right]}{\frac{g}{f} - h} \right) \\ &= y(T_{\mathcal{P}}) - \left[c(1+\varepsilon) + \frac{c}{4b} + \varepsilon \right]. \end{aligned}$$

By Lemma 2.3.9 we have $y(T_{\mathcal{P}}) \leq c(1+\varepsilon) + \frac{c}{4b} + \varepsilon$ and hence

$$\begin{aligned} y(T_{\Lambda_1}) &< y(T_{\mathcal{P}}) - \left[c(1+\varepsilon) + \frac{c}{4b} + \varepsilon \right] \\ &\leq c(1+\varepsilon) + \frac{c}{4b} + \varepsilon - \left[c(1+\varepsilon) + \frac{c}{4b} + \varepsilon \right] = 0 \end{aligned}$$

which is a contradiction to the non-negativity of the y-component of s. Hence (2.3.10) cannot hold and the proof is complete. □

The above result implies that the positive phase curve to any solution s is sure to have been in $\mathcal{R} \cup \Lambda_2$ by the time T_{Λ_1}. In order to show that such a curve is in $\mathcal{R}$ we need to prove that it leaves Λ_2 and does not enter Λ_1 again. This motivates

Lemma 2.3.20.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c + \frac{c}{4b}$ *and* $\varepsilon > 0$*. Furthermore, let* s *be any solution. Then for any* $t \geq 0$ *the positive phase curve corresponding to the solution* s *cannot enter* Λ_1 *via the common boundary part of* Λ_1 *and* Λ_2*, i.e. the set*

$$B_\Lambda := \Big\{(x,y,z) \in \mathcal{O}_0^+ \,:\, x \leq 1+\varepsilon\,,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c}\,, \\ y = \frac{1}{2}\left(\frac{g}{f}-h\right)\,,\, z > \widehat{z} + \varepsilon\Big\} \subset \Lambda_2.$$

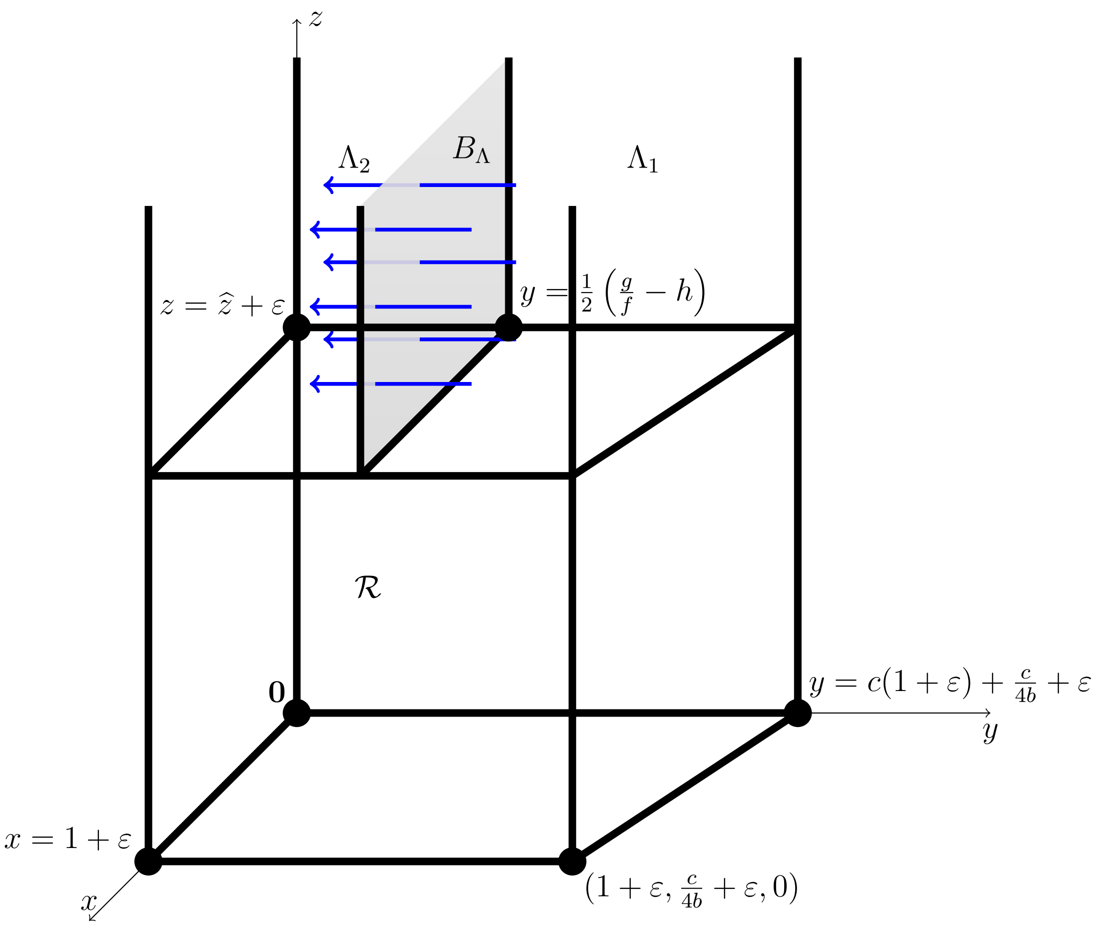


Figure 2.3.9: The vector field (blue arrows) on B_Λ points into $\mathcal{R} \cup \Lambda_2$.

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c + \frac{c}{4b}$ and $\varepsilon > 0$. Furthermore, let s be any solution. To show that the above claim holds true we show that the y-component of s is strictly decreasing if $s(t) \in B_\Lambda$ for any $t \geq 0$. Since $\mathcal{P}$ is positive invariant, this implies that the vector field on B_Λ (and thus the positive phase curve) points *into* $\mathcal{R} \cup \Lambda_2$ (see Figure 2.3.9). Hence, let $s(t) \in B_\Lambda$ for any $t \geq 0$. Then we obtain the following estimate (also

compare to the proof of Lemma 2.3.18):

$$\begin{aligned}
\dot{y}(t) &= y(t)\left(-b + \frac{cx(t)}{x(t)+d} - \frac{z(t)}{y(t)+e}\right)\\
&\le y(t)\left(-b + \frac{c(1+\varepsilon)}{1+\varepsilon+d} - \frac{z(t)}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)\\
&\le y(t)\left(-b + \frac{c(1+\varepsilon)}{1+\varepsilon+d} - \frac{\widehat{z}+\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)\\
&\le y(t)\left(\frac{-\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)\\
&= \underbrace{\frac{1}{2}\left(\frac{g}{f}-h\right)}_{>0}\underbrace{\left(\frac{-\varepsilon}{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}\right)}_{<0} < 0
\end{aligned}$$

Since $B_\Lambda \subset \Lambda_2$ this implies that no positive phase curve can enter the set Λ_1 via the common boundary part B_Λ of Λ_1 and Λ_2. □

Remark 2.3.5.
We highlight the similarity between the above result and that of Lemma 2.2.18. Indeed, in both cases a specific half plane B_Λ (or B_4 respectively) separates the sets Λ_1 and Λ_2 (or Ω_3 and Ω_4 respectively) and no positive phase curve to a solution s can enter Λ_1 (or Ω_4) via B_Λ (or B_4).

The times $T_{\mathcal{R}}(s_0)$ and $T_{\mathcal{R}}(B)$

We define the time $T_{\mathcal{R}}(s_0)$ required to ensure that a corresponding positive phase curve to a solution s was in the set $\mathcal{R}$ at least once.

Lemma 2.3.21.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \le c + \frac{c}{4b}$ and $\varepsilon > 0$. Furthermore, let any solution s be given. We set

$$T_{\mathcal{R}}(s_0) = T_{\mathcal{R}} := T_{\Lambda_1}(s_0) + \frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2} z_M(x_0,y_0,z_0) + \varepsilon$$

where $T_{\Lambda_1}(s_0)$ and $z_M(x_0,y_0,z_0)$ are defined as in Lemma 2.3.17 and Corollary 2.2.5 respectively. We claim that $T_{\mathcal{R}} > T_{\Lambda_1} > T_{\mathcal{P}} > 0$ holds.

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \le c + \frac{c}{4b}$ and $\varepsilon > 0$. Furthermore, let any solution s be given. We have

$$f - \frac{g}{h} < 0 \quad \Leftrightarrow \quad g - hf > 0$$

and hence by using $z_M(x_0,y_0,z_0) \ge 0$ (see Corollary 2.2.5) and $T_{\Lambda_1}(s_0) > T_{\mathcal{P}}(s_0) > 0$ (see Lemma 2.3.17) we obtain

$$T_{\mathcal{R}} := T_{\Lambda_1}(s_0) + \underbrace{\frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2} z_M(x_0,y_0,z_0) + \varepsilon}_{>0} > T_{\Lambda_1}(s_0) > T_{\mathcal{P}}(s_0) > 0. \quad \square$$

Similar to the previous arguments we show that $T_{\mathcal{R}}$ has the property we asserted it does.

Lemma 2.3.22.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c+\frac{c}{4b}$ and $\varepsilon > 0$. Furthermore, let any solution s be given. Then it holds that

$$\exists\, T \in [T_{\mathcal{P}}(s_0), T_{\mathcal{R}}(s_0)] \,:\, s(T) \in \mathcal{R}$$

where $T_{\mathcal{P}}(s_0)$ and $T_{\mathcal{R}}(s_0)$ are defined as in Lemmas 2.3.8 and 2.3.21 respectively.

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c+\frac{c}{4b}$ and $\varepsilon > 0$. Furthermore, let any solution s be given. Note that by Lemma 2.3.21 we have $T_{\mathcal{R}} > T_{\mathcal{P}}$ and hence the interval $[T_{\mathcal{P}}, T_{\mathcal{R}}]$ is non-empty and has an interior. We provide a proof by contradiction, i.e. we assume

$$s(t) \notin \mathcal{R} \qquad \forall\, t \in [T_{\mathcal{P}}, T_{\mathcal{R}}]. \tag{2.3.11}$$

By Lemma 2.3.9 we have $s(t) \in \mathcal{P}$ for all $t \geq T_{\mathcal{P}}$. In particular

$$s(t) \in \mathcal{P} \qquad \forall\, t \in [T_{\mathcal{P}}, T_{\mathcal{R}}]$$

and since

$$\mathcal{P} = \mathcal{R} \,\dot{\cup}\, \Lambda_1 \,\dot{\cup}\, \Lambda_2$$

the assumption in (2.3.11) is equivalent to

$$s(t) \in \Lambda_1 \,\dot{\cup}\, \Lambda_2 \qquad \forall\, t \in [T_{\mathcal{P}}, T_{\mathcal{R}}]. \tag{2.3.12}$$

By Lemma 2.3.19 there exists a $\widetilde{T} \in [T_{\mathcal{P}}, T_{\Lambda_1}] \subsetneq [T_{\mathcal{P}}, T_{\mathcal{R}}]$ such that $s(\widetilde{T}) \in \mathcal{R} \cup \Lambda_2$. Since (2.3.12) holds this implies

$$\exists\, \widetilde{T} \in [T_{\mathcal{P}}, T_{\Lambda_1}] \subset [T_{\mathcal{P}}, T_{\mathcal{R}}] \,:\, s(\widetilde{T}) \in \Lambda_2, \tag{2.3.13}$$

i.e. at this time $\widetilde{T}$ the positive phase curve corresponding to solution s is in Λ_2. By Lemma 2.3.20 the positive phase curve cannot enter Λ_1 via the common boundary part of Λ_1 and Λ_2, i.e. the set B_{Λ}, for any $t \in [\widetilde{T}, T_{\mathcal{R}}] \subset [0, \infty)$, and hence the curve must stay in Λ_2 for $[\widetilde{T}, T_{\mathcal{R}}]$. Differently put: Combining Lemma 2.3.20 with (2.3.12) and (2.3.13) yields

$$s(t) \in \Lambda_2 \qquad \forall\, t \in [\widetilde{T}, T_{\mathcal{R}}], \tag{2.3.14}$$

which we will now lead to a contradiction. Note $\widetilde{T} \leq T_{\Lambda_1} < T_{\mathcal{R}}$ implies that the interval $[\widetilde{T}, T_{\mathcal{R}}]$ is non-empty and has an interior. Furthermore, by (2.3.14) we have

$$y(t) \leq \frac{1}{2}\left(\frac{g}{f}-h\right) \quad \text{and} \quad z(t) > \widehat{z}+\varepsilon > 0$$

for all $t \in [\widetilde{T}, T_{\mathcal{R}}]$. This allows us to estimate the change of the z-component of s (given by the third equation in (2.1.5)) as follows

$$\begin{aligned}
\dot{z}(t) &= \left(f - \frac{g}{y(t)+h}\right) z^2(t) \\
&\leq \left(f - \frac{g}{\frac{1}{2}\left(\frac{g}{f} - h\right) + h}\right) z^2(t) \\
&= \underbrace{\frac{hf-g}{\frac{g}{f}+h}}_{<0} z^2(t) \\
&< \frac{hf-g}{\frac{g}{f}+h} (\widehat{z}+\varepsilon)^2 \\
&< 0
\end{aligned}$$

for all $t \in [\widetilde{T}, T_{\mathcal{R}}]$. Integrating the above from $\widetilde{T}$ to $T_{\mathcal{R}}$ yields

$$\begin{aligned}
& \int_{\widetilde{T}}^{T_{\mathcal{R}}} \frac{d}{dt} z(t) dt < \int_{\widetilde{T}}^{T_{\mathcal{R}}} \frac{hf-g}{\frac{g}{f}+h} (\widehat{z}+\varepsilon)^2 dt \\
\Leftrightarrow \quad & z(T_{\mathcal{R}}) - z(\widetilde{T}) < \frac{hf-g}{\frac{g}{f}+h} (\widehat{z}+\varepsilon)^2 (T_{\mathcal{R}} - \widetilde{T}) \\
\Leftrightarrow \quad & z(T_{\mathcal{R}}) < z(\widetilde{T}) + \frac{hf-g}{\frac{g}{f}+h} (\widehat{z}+\varepsilon)^2 (T_{\mathcal{R}} - \widetilde{T})
\end{aligned}$$

Inserting the definition of $T_{\mathcal{R}}$ in the above and recalling that $\widetilde{T} \in [T_{\mathcal{P}}, T_{\Lambda_1}]$ yields

$$\begin{aligned}
z(T_{\mathcal{R}}) &< z(\widetilde{T}) + \frac{hf-g}{\frac{g}{f}+h} (\widehat{z}+\varepsilon)^2 \left(T_{\Lambda_1} + \frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2} z_M + \varepsilon - \widetilde{T}\right) \\
&= z(\widetilde{T}) + \frac{hf-g}{g-hf} z_M + \underbrace{\frac{hf-g}{\frac{g}{f}+h}}_{<0} (\widehat{z}+\varepsilon)^2 \underbrace{\left(T_{\Lambda_1} + \varepsilon - \widetilde{T}\right)}_{>0} \\
&< z(\widetilde{T}) - z_M.
\end{aligned}$$

Furthermore, recall that by Corollary 2.2.5 we have $z(t) \leq z_M$ for any $t \geq 0$ and in particular for $t = \widetilde{T} > 0$. Hence

$$z(T_{\mathcal{R}}) < z(\widetilde{T}) - z_M \leq z_M - z_M = 0,$$

which is a contradiction to the non-negativity of the z-component of s. Hence (2.3.11) is false and the assertion of the lemma holds true. □

We now define the absorbance time $T_{\mathcal{R}}(B)$.

Lemma 2.3.23.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c+\frac{c}{4b}$ *and* $\varepsilon > 0$ *and any bounded subset* $B \subset \mathcal{O}_0^+$ *be given. We define*

$$T_{\mathcal{R}}(B) := T_{\Lambda_1}(B) + \frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2} z_M(B) + \varepsilon,$$

where $z_M(B)$ *is defined as in Lemma 2.2.35 and* $T_{\Lambda_1}(B)$ *is given by*

$$T_{\Lambda_1}(B) := T_{\mathcal{P}}(B) + \frac{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}{\varepsilon}\left(\frac{2\left[c(1+\varepsilon)+\frac{c}{4b}+\varepsilon\right]}{\frac{g}{f}-h}\right),$$

with $T_{\mathcal{P}}(B)$ *defined in Lemma 2.3.10. Then for any* $s_0 \in B$ *it holds that*

$$T_{\mathcal{R}}(s_0) \leq T_{\mathcal{R}}(B),$$

where $T_{\mathcal{R}}(s_0)$ *is defined as in Lemma 2.3.21.*

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c+\frac{c}{4b}$ and $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given. We choose an arbitrary $s_0 \in B$. Since Lemma 2.3.10 yields $T_{\mathcal{P}}(s_0) \leq T_{\mathcal{P}}(B)$, we estimate $T_{\Lambda_1}(s_0)$ from Lemma 2.3.17 as follows:

$$\begin{aligned} T_{\Lambda_1}(s_0) &= T_{\mathcal{P}}(s_0) + \frac{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}{\varepsilon}\left(\frac{2\left[c(1+\varepsilon)+\frac{c}{4b}+\varepsilon\right]}{\frac{g}{f}-h}\right) \\ &\leq T_{\mathcal{P}}(B) + \frac{c(1+\varepsilon)+\frac{c}{4b}+\varepsilon+e}{\varepsilon}\left(\frac{2\left[c(1+\varepsilon)+\frac{c}{4b}+\varepsilon\right]}{\frac{g}{f}-h}\right) = T_{\Lambda_1}(B) \end{aligned}$$

Using this and the fact that $z_M(x_0, y_0, z_0) \leq z_M(B)$ (see Lemma 2.2.35), we estimate $T_{\mathcal{R}}(s_0)$ from Lemma 2.3.21 in the following way:

$$\begin{aligned} T_{\mathcal{R}}(s_0) &= T_{\Lambda_1}(s_0) + \frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2} z_M(x_0, y_0, z_0) + \varepsilon \\ &\leq T_{\Lambda_1}(B) + \frac{\frac{g}{f}+h}{(g-hf)(\widehat{z}+\varepsilon)^2} z_M(B) + \varepsilon \\ &= T_{\mathcal{R}}(B). \end{aligned}$$

□

Finally, we prove Lemma 2.3.12 for the above parameter assumptions.

Lemma 2.3.24.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c+\frac{c}{4b}$ *and* $\varepsilon > 0$ *and any bounded subset* $B \subset \mathcal{O}_0^+$ *be given. Then for any solution* s *with* $s_0 \in B$ *it holds that*

$$\exists\, T \in [0, T_{\mathcal{R}}(B)] \, : \, s(T) \in \mathcal{R},$$

where $T_{\mathcal{R}}(B) > 0$ *is defined as in Lemma 2.3.23.*

Proof.
Let $\frac{1}{2}\left(\frac{g}{f}-h\right) \leq c+\frac{c}{4b}$ and $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given. Furthermore, let s be a solution with $s_0 \in B$. Since the conditions of Lemma 2.3.22 are fulfilled, we have that

$$\exists\, T \in [T_{\mathcal{P}}, T_{\mathcal{R}}] \subset [0, T_{\mathcal{R}}] \,:\, s(T) \in \mathcal{R}.$$

By Lemma 2.3.23 we obtain $T_{\mathcal{R}} = T_{\mathcal{R}}(s_0) \leq T_{\mathcal{R}}(B)$ and hence

$$[0, T_{\mathcal{R}}] \subset [0, T_{\mathcal{R}}(B)].$$

This yields

$$\exists\, T \in [0, T_{\mathcal{R}}] \subset [0, T_{\mathcal{R}}(B)] \,:\, s(T) \in \mathcal{R}$$

and thus the claim holds true since s (with $s_0 \in B$) was chosen arbitrarily. $\square$

This allows us to complete this subsection by proving Lemma 2.3.12:

Proof of Lemma 2.3.12.
Let $\varepsilon > 0$, any bounded subset $B \subset \mathcal{O}_0^+$ and any solution s with $s_0 \in B$ be given.

- If $c+\frac{c}{4b} < \frac{1}{2}\left(\frac{g}{f}-h\right)$ then for $\varepsilon \in \left(0, \frac{\frac{1}{2}\left(\frac{g}{f}-h\right)-c-\frac{c}{4b}}{c+1}\right)$ Lemma 2.3.16 yields the claim with $T_{\mathcal{R}}(B) > 0$ defined as in Lemma 2.3.15.
- If $c+\frac{c}{4b} \geq \frac{1}{2}\left(\frac{g}{f}-h\right)$ then for any $\varepsilon > 0$ Lemma 2.3.24 yields the claim with $T_{\mathcal{R}}(B) > 0$ defined as in Lemma 2.3.23. $\square$

This concludes this subsection and we define the absorbing set $\mathcal{B}$ in $\mathcal{O}_0^+$.

2.3.4 The set $\mathcal{B}$

Consider

Definition 2.3.3.
Let $\varepsilon > 0$ be given. Then for the semiflow Φ on $\mathcal{O}_0^+$ generated by system (2.1.5) we define

$$\mathcal{B} := \bigcup_{t \geq 0} \Phi(t, \mathcal{R}),$$

where $\mathcal{R}$ is defined as in Definition 2.3.1.

Remark 2.3.6.
Note that $\mathcal{B}$ is non-empty since

$$\emptyset \neq \mathcal{R} = \Phi(0, \mathcal{R}) \subset \bigcup_{t \geq 0} \Phi(t, \mathcal{R}) = \mathcal{B}.$$

The set $\mathcal{B}$ is the union of all positive orbits (of the semiflow Φ on $\mathcal{O}_0^+$) through points in $\mathcal{R}$, or in formula

$$\mathcal{B} = \bigcup_{t \geq 0} \Phi(t, \mathcal{R}) = \bigcup_{t \geq 0} \{\Phi(t, s_0) \,:\, s_0 \in \mathcal{R}\} = \{\Phi(t, s_0) \,:\, s_0 \in \mathcal{R}\,,\, t \geq 0\} = \bigcup_{s_0 \in \mathcal{R}} \Gamma_{s_0}^+.$$

As a union of positive orbits $\mathcal{B}$ is also positive invariant (we formally prove this in Lemma 2.3.25 below).

We derive several properties of the set $\mathcal{B}$ which will prove useful later.

Lemma 2.3.25.
Let $\varepsilon > 0$ be given. Then the set $\mathcal{B}$ as defined in Definition 2.3.3 is positive invariant under the dynamics on $\mathcal{O}_0^+$ generated by (2.1.5).

Proof.
Let $\varepsilon > 0$ be given. We need to prove that the set $\mathcal{B}$ fulfils

$$\Phi(t, \mathcal{B}) \subset \mathcal{B} \qquad \forall\, t \geq 0.$$

An equivalent statement to this is

$$\forall\, s_0 \in \mathcal{B} \quad \Rightarrow \quad s(t) = \Phi(t, s_0) \in \mathcal{B} \qquad \forall\, t \geq 0.$$

We show that this second statement holds. Indeed, let any solution s with $s_0 \in \mathcal{B}$ be given. The following equivalence holds

$$s_0 \in \mathcal{B} \quad \Leftrightarrow \quad s_0 \in \bigcup_{t \geq 0} \Phi(t, \mathcal{R}) \quad \Leftrightarrow \quad \exists\, \widehat{T} \geq 0 \text{ and } \widehat{s}_0 \in \mathcal{R} \,:\, \Phi(\widehat{T}, \widehat{s}_0) = s_0.$$

Hence, using the semiflow property, we obtain for any $t \geq 0$ that

$$s(t) = \Phi(t, s_0) = \Phi(t, \Phi(\widehat{T}, \widehat{s}_0)) = \Phi(t + \widehat{T}, \widehat{s}_0) \in \bigcup_{\tau \geq 0} \Phi(\tau, \widehat{s}_0) \subset \bigcup_{\tau \geq 0} \Phi(\tau, \mathcal{R}) = \mathcal{B},$$

which proves the positive invariance of $\mathcal{B}$. □

Next we show that $\mathcal{B}$ is in fact (uniformly) absorbing in $\mathcal{O}_0^+$.

Lemma 2.3.26.
Let $\varepsilon > 0$ sufficiently small be given. Then the set $\mathcal{B}$ as defined in Definition 2.3.3 uniformly absorbs bounded subsets B of $\mathcal{O}_0^+$ under the dynamics on $\mathcal{O}_0^+$ generated by system (2.1.5) (being the semiflow Φ on $\mathcal{O}_0^+$), i.e. for any bounded subset $B \subset \mathcal{O}_0^+$ there exists a $T(B) \geq 0$ such that

$$\Phi(t, B) \subset \mathcal{B} \qquad \forall\, t \geq T(B).$$

Proof.
Let $\varepsilon > 0$ be given. In order to prove the claim we show that for any bounded subset $B \subset \mathcal{O}_0^+$ there exists a (uniform) time $T(B) \geq 0$ such that for any solution s with $s_0 \in B$ it holds that

$$s(t) \in \mathcal{B} \qquad \forall\, t \geq T(B). \tag{2.3.15}$$

Consider any bounded subset $B \subset \mathcal{O}_0^+$ and any solution s with $s_0 \in B$. By Lemma 2.3.12 we have that for sufficiently small $\varepsilon > 0$ there exists a $T_{\mathcal{R}}(B) > 0$ that fulfils

$$\exists\, T \in [0, T_{\mathcal{R}}(B)] \,:\, s(T) \in \mathcal{R} \subset \mathcal{B}.$$

Since $s(T) \in \mathcal{B}$ and $\mathcal{B}$ is positive invariant (Lemma 2.3.25) we in fact have

$$s(t) \in \mathcal{B} \qquad \forall\, t \geq T$$

and since $T \leq T_{\mathcal{R}}(B)$ we even obtain that

$$s(t) \in \mathcal{B} \qquad \forall\, t \geq T_{\mathcal{R}}(B).$$

Hence, setting $T(B) = T_{\mathcal{R}}(B)$ yields (2.3.15) and therefore the claim. □

We now show that $\mathcal{B}$ is bounded. To achieve this we introduce an auxiliary set $\mathcal{C}$ (in which $\mathcal{B}$ is contained), see Figure 2.3.10.

Lemma 2.3.27.
Let $\varepsilon > 0$ be given. Define the set

$$\mathcal{C} := \left\{ (x, y, z) \in \mathcal{O}_0^+ \,:\, x \leq 1 + \varepsilon\,,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c}\,,\, z \leq z_{\mathcal{R}} \right\} \subset \mathcal{P}$$

with $z_{\mathcal{R}} := z_M(\mathcal{R})$ from Lemma 2.2.35 for the bounded set $B = \mathcal{R}$. Then $\mathcal{C}$ is non-empty, bounded and closed in $\mathcal{O}_0^+ \subset \mathbb{R}^3$.

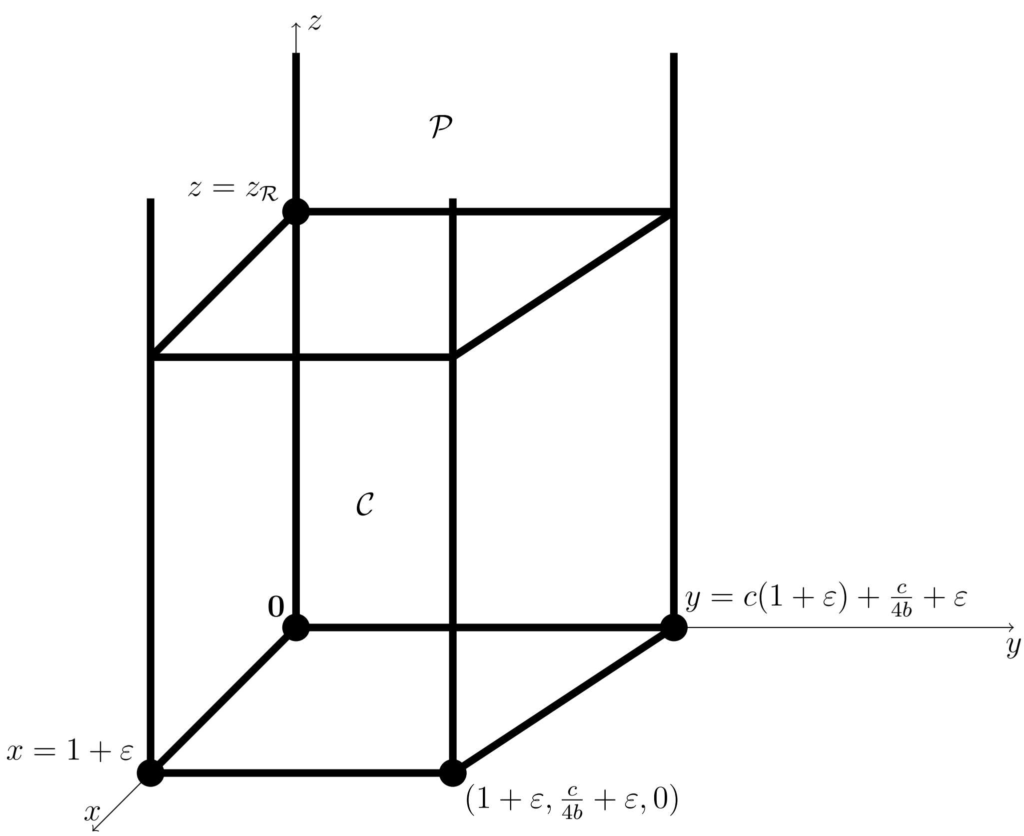


Figure 2.3.10: The set $\mathcal{C} \subset \mathcal{P}$.

Proof.
Let $\varepsilon > 0$ be given. The set $\mathcal{C}$ is non-empty and bounded, since considering Lemma 2.2.35 for the bounded set $B = \mathcal{R}$, we see that

$$0 \leq z_{\mathcal{R}} = z_M(\mathcal{R}) < \infty.$$

Furthermore, $\mathcal{C}$ is closed in $\mathcal{O}_0^+$, since the compliment, i.e. $\mathcal{O}_0^+ \backslash \mathcal{C}$, is open in $\mathcal{O}_0^+$. □

We use the above result to prove that $\mathcal{B}$ is bounded.

Lemma 2.3.28.
Let $\varepsilon > 0$ be given. Then the sets $\mathcal{B}$ and $\mathcal{C}$ - as defined in Definition 2.3.3 and Lemma 2.3.27 respectively - fulfil $\mathcal{B} \subset \mathcal{C}$. In particular $\mathcal{B}$ is bounded.

Proof.
Let $\varepsilon > 0$ be given. Recall from Remark 2.3.6 that

$$\begin{aligned} \mathcal{B} = \bigcup_{t \geq 0} \Phi(t, \mathcal{R}) = \bigcup_{t \geq 0} \{\Phi(t, s_0) \,:\, s_0 \in \mathcal{R}\} \\ = \{\Phi(t, s_0) \,:\, s_0 \in \mathcal{R}\,,\, t \geq 0\} = \{s(t) \,:\, s_0 \in \mathcal{R}\,,\, t \geq 0\}\,. \end{aligned}$$

Hence in order to prove $\mathcal{B} \subset \mathcal{C}$, it suffices to show that

$$\forall\, s_0 \in \mathcal{R} \quad \Rightarrow \quad s(t) \in \mathcal{C} \quad \forall\, t \geq 0,$$

i.e. the positive phase curve to any solution s with initial condition $s_0 \in \mathcal{R}$ is contained in $\mathcal{C}$ for all non-negative times. Let s be an arbitrary solution with $s_0 \in \mathcal{R}$. Since $\mathcal{R} \subset \mathcal{P}$ and $\mathcal{P}$ is positive invariant (Lemma 2.3.7) we immediately obtain

$$s(t) \in \mathcal{P} \qquad \forall\, t \geq 0.$$

Since $\mathcal{C} \subset \mathcal{P}$ (recall Lemma 2.3.27 and Figure 2.3.10), we see that the claim holds true if s fulfils

$$z(t) \leq z_{\mathcal{R}} \qquad \forall\, t \geq 0.$$

This however holds by applying Lemma 2.2.35 to the bounded set $B = \mathcal{R}$, yielding

$$z(t) \leq z_M(\mathcal{R}) = z_{\mathcal{R}} \qquad \forall\, t \geq 0.$$

Hence

$$s(t) \in \mathcal{P} \quad \forall\, t \geq 0 \quad \text{and} \quad z(t) \leq z_{\mathcal{R}} \quad \forall\, t \geq 0$$

which is equivalent to

$$s(t) \in \mathcal{C} \qquad \forall\, t \geq 0.$$

This proves that $\mathcal{B} \subset \mathcal{C}$ and since $\mathcal{C}$ is bounded (Lemma 2.3.27) so is $\mathcal{B}$. □

Before finally proving the existence of the global attractor $\mathcal{A}$ there is one last result we need.

Lemma 2.3.29.
Let a sufficiently small $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given. We claim that under the dynamics on $\mathcal{O}_0^+$ generated by system (2.1.5) *the set*

$$\bigcup_{t \geq T(B)} \Phi(t, B)$$

is relatively compact in $\mathcal{O}_0^+ \subset \mathbb{R}^3$, where $T(B)$ is defined as in Lemma 2.3.26. In particular, the semiflow Φ on $\mathcal{O}_0^+$ is uniformly compact for large t (defined in Appendix A).

Proof.
Let a sufficiently small $\varepsilon > 0$ and any bounded subset $B \subset \mathcal{O}_0^+$ be given. By Lemma 2.3.26 we have the existence of a $T(B) \geq 0$ such that

$$\Phi(t, B) \subset \mathcal{B} \qquad \forall\, t \geq T(B).$$

This implies

$$\bigcup_{t \geq T(B)} \Phi(t, B) \subset \mathcal{B}.$$

Taking the closure (in $\mathcal{O}_0^+$) and recalling that $\mathcal{B} \subset \mathcal{C}$ (by Lemma 2.3.28) now yields

$$\overline{\bigcup_{t \geq T(B)} \Phi(t, B)} \subset \overline{\mathcal{B}} \subset \overline{\mathcal{C}} = \mathcal{C} \subset \mathcal{O}_0^+,$$

where the equality holds since $\mathcal{C}$ is closed (in $\mathcal{O}_0^+$) - see Lemma 2.3.27. Since $\mathcal{C}$ is bounded, the set

$$\overline{\bigcup_{t \geq T(B)} \Phi(t, B)}$$

is a closed and bounded set in $\mathcal{O}_0^+ \subset \mathbb{R}^3$ and hence compact in $\mathcal{O}_0^+$. Therefore the set

$$\bigcup_{t \geq T(B)} \Phi(t, B)$$

is relatively compact in $\mathcal{O}_0^+ \subset \mathbb{R}^3$. This implies that the semiflow Φ on $\mathcal{O}_0^+$ is uniformly compact for large t (in particular for $t \geq T(B)$ - see Appendix A). □

This result allows us to prove the existence of the global attractor $\mathcal{A}$.

2.3.5 The attractor $\mathcal{A}$

We establish the existence of a set $\mathcal{A}$, being the global attractor of the semiflow Φ on $\mathcal{O}_0^+$:

Theorem 2.3.1.
For the equations in (2.1.5) *assume $a = d$ and $f - \frac{g}{h} < 0$. For Φ on $\mathcal{O}_0^+$ the set*

$$\mathcal{A} = \omega(\mathcal{B})$$

is the global attractor of $\mathcal{O}_0^+$ (i.e. of the the dynamics on $\mathcal{O}_0^+$ generated by system (2.1.5)*). Here $\mathcal{B}$ is defined as in Definition 2.3.3 and $\omega(\mathcal{B})$ denotes the ω-limit set of $\mathcal{B}$.*

Proof.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold in (2.1.5) and consider the metric space $(\mathcal{O}_0^+, \mathrm{d})$. We prove the existence of the attractor by using the theorem in [Temam, 1997] (see Appendix A). The semiflow Φ on $\mathcal{O}_0^+$ (see Corollary 2.2.3) is uniformly compact for large t by Lemma 2.3.29. Next we choose $U = \mathcal{O}_0^+$ as our open set (in $\mathcal{O}_0^+$). By Lemma 2.3.26 the set $\mathcal{B}$ is absorbing in $\mathcal{O}_0^+$. Hence all the conditions of the theorem in Appendix A are met and the set

$$\mathcal{A} = \omega(\mathcal{B}) \neq \emptyset$$

is an attractor in U. Since we have chosen $U = \mathcal{O}_0^+$, we in fact obtain that $\mathcal{A}$ is the *global* attractor of the dynamics on $\mathcal{O}_0^+$ generated by system (2.1.5). □

2.4 Attractor - Characterisation

Having established the existence of the global attractor $\mathcal{A}$ in Theorem 2.3.1, it is natural to ask how the set $\mathcal{A}$ actually looks. How complicated is its structure and how may it be characterised? In order to gain a sound understanding of the attractor and its properties, we try to describe it as completely as possible for various parameter regions of the parameter space. There are general properties of attractors, which also apply to the set $\mathcal{A}$, and hence yield a more detailed characterisation of the attractor.

- It holds that $\mathcal{A} \subset \mathcal{B}$ (since $\mathcal{B}$ absorbs bounded sets) and hence also $\mathcal{A} \subset \mathcal{C}$ for any $\varepsilon > 0$.
- The attractor $\mathcal{A}$ is connected since $\mathcal{O}_0^+$ is connected (see e.g. [Temam, 1997], [Gobbino and Sardella, 1997]).
- The set $\mathcal{A}$ is maximal among the bounded functional invariant sets of $\mathcal{O}_0^+$ (see e.g. [Hale, 1988], [Temam, 1997]). I.e. any bounded invariant set of (2.1.5) is (completely) contained in $\mathcal{A}$.
- By the previous point any bounded orbit $\Gamma_b \in \mathcal{O}_0^+$ of (2.1.5) is completely contained in $\mathcal{A}$. In particular any equilibrium point $p^* \in \mathcal{O}_0^+$ and any periodic, heteroclinic and homoclinic orbit in $\mathcal{O}_0^+$ is a subset of $\mathcal{A}$.

We may now exploit the above properties of the global attractor to determine the set $\mathcal{A}$ more explicitly. A question that arises in this context is what dimension $\mathcal{A}$ has. In fact, an attractor may theoretically be anything from a simple single point (dimension zero) to a very complicated set with fractal dimension (cf. [Grassberger and Procaccia, 1983], [Leonov et al., 2016]). A good first indication of the *minimal* dimension and geometrical properties of the attractor is given by the number of equilibria of the system, as well as their position in phase space. In fact we will see that - dependent on the parameters a and b - we may characterise $\mathcal{A}$ quite well by considering the equilibria of system (2.1.5). This is investigated below in subsection 2.4.1.

In subsection 2.4.2 global results on the solutions are proven, allowing the precise characterisation of the global attractor for several parameter regions (in parameter space), see Theorem 2.4.1. In particular the result addresses the problem of persistence and extinction of a species in the GSP food chain. This is of relevance, since the loss of biodiversity in an ecosystem (caused for example by the extinction of a species in the ecosystem), may have an effect on the performance of the ecosystem (cf. [Naeem et al., 1994], [Smith et al., 2003]). Furthermore, the change of the attractor is caused by various bifurcations occurring, which are studied throughout this section. In particular the stability properties of both the equilibria of coexistence of all species, as well as the occurrence of a Hopf bifurcaton along a branch of one of these equilibria, is shown analytically in subsection 2.4.3.

2.4.1 Analysis of equilibria I

The equilibria of (2.1.5) and their properties have already been studied to some extent (cf. [Letellier and Aziz-Alaoui, 2002], [Aziz-Alaoui, 2002]). We nonetheless investigate them, thus extending results from the aforementioned works as well as adding new results which help to characterise the attractor $\mathcal{A}$. In the analysis we pay specific attention to how the parameters a and b influence the properties of the equilibria and hence the structure of $\mathcal{A}$. Only those equilibria fulfilling $p_i^* \in \mathcal{O}_0^+$, i.e. those in the non-negative octant, will be of biological relevance. They are the equilibrium states of system (2.1.5) in $\mathcal{O}_0^+$, i.e. the points $p_i^* \in \mathcal{O}_0^+$ satisfying the algebraic equations

$$v(p_i^*) = v(x_i^*, y_i^*, z_i^*) = (0, 0, 0)^T.$$

The solution to these equations are summarised in Table 1, bearing in mind that all parameters are positive and we still assume they satisfy $a = d$ and $f - \frac{g}{h} < 0$ (including the rest of this section). For a detailed derivation of the equilibria see Appendix C.2.1.

From a biological point of view p_0^* (the origin) is the point of extinction of all species, p_1^* is the point of a sole survivor - the prey species -, p_2^* is the point of coexistence of the specialist predator and the prey species and finally $p_{3\pm}^*$ are points of coexistence of all three species. Table 1 gives precise restrictions on the parameters for which the points are real (i.e. in $\mathbb{R}^3$) and in the non-negative octant $\mathcal{O}_0^+$. While the conditions on the points p_0^*, p_1^* and p_2^* are fairly straightforward, the conditions for p_{3+}^* and p_{3-}^* are more involved. However, there is a simple geometric interpretation of the conditions, using the concept of nullclines ([Rosenzweig and MacArthur, 1963], [Simonyi and Kaszás, 1968], [Albrecht et al., 1974]).

For the equilibrium p_2^* this geometric approach is well understood and documented in the literature ([Kuznetsov, 1995], [Kot, 2001], [Smith, 2008]) and reads as follows: Since $z = 0$ for p_2^*, we consider (a projection onto) the positive x-y-quadrant, as well as the straight line and parabola defined by

$$x = \frac{ab}{c - b} \quad \text{and} \quad y = (1 - x)(x + a)$$

Equilibrium Point ($v(p_i^*) = (0,0,0)^T$)	Existence ($p_i^* \in \mathbb{R}^3$)	Non-Negativity ($p_i^* \in \mathcal{O}_0^+$)
$p_0^* = \begin{pmatrix} x_0^* \\ y_0^* \\ z_0^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$	-	-
$p_1^* = \begin{pmatrix} x_1^* \\ y_1^* \\ z_1^* \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}$	-	-
$p_2^* = \begin{pmatrix} x_2^* \\ y_2^* \\ z_2^* \end{pmatrix} = \begin{pmatrix} \frac{ab}{c-b} \\ (1-x_2^*)(x_2^*+a) \\ 0 \end{pmatrix}$	$b \neq c$	$b \leq \frac{c}{a+1}$
$p_{3+}^* = \begin{pmatrix} x_{3+}^* \\ y_{3+}^* \\ z_{3+}^* \end{pmatrix} = \begin{pmatrix} \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} \\ \frac{g}{f} - h \\ \left(h - \frac{g}{f} - e\right)\left(b - \frac{cx_{3+}^*}{x_{3+}^*+a}\right) \end{pmatrix}$	$a \geq 2\sqrt{\frac{g}{f} - h} - 1$	$(0 < a \leq 1 \vee a > \frac{g}{f} - h) \wedge b \leq \frac{cx_{3+}^*}{x_{3+}^*+a}$
$p_{3-}^* = \begin{pmatrix} x_{3-}^* \\ y_{3-}^* \\ z_{3-}^* \end{pmatrix} = \begin{pmatrix} \frac{1-a}{2} - \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} \\ \frac{g}{f} - h \\ \left(h - \frac{g}{f} - e\right)\left(b - \frac{cx_{3-}^*}{x_{3-}^*+a}\right) \end{pmatrix}$	$a \geq 2\sqrt{\frac{g}{f} - h} - 1$	$0 < a \leq 1 \wedge a < \frac{g}{f} - h \wedge b \leq \frac{cx_{3-}^*}{x_{3-}^*+a}$

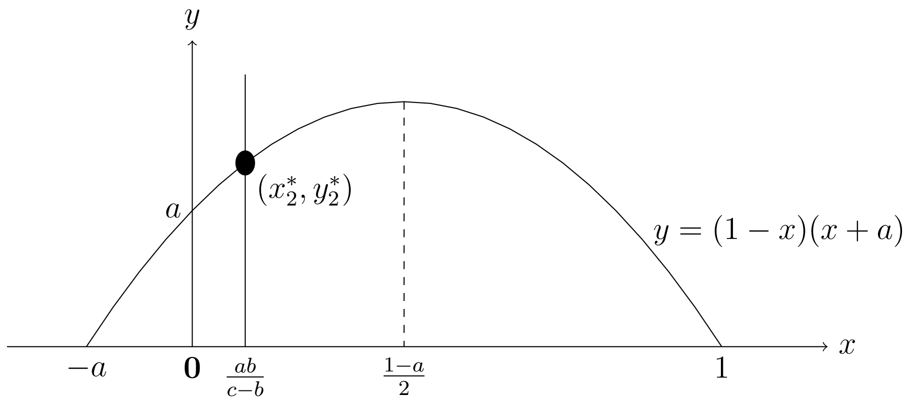
Table 1: Parameter-dependent conditions on the biologically meaningful equilibria

respectively (see Figure 2.4.1). The point of intersection (x_2^*, y_2^*) of the line and the parabola defines the first two components of p_2^* and thus the equilibrium point $p_2^* = (x_2^*, y_2^*, 0)^T$, see Figure 2.4.1c. The point wanders from left to right along the parabola (compare Figures 2.4.1a and 2.4.1b) for increasing values of b. It leaves the positive quadrant (or octant respectively) and is no longer biologically relevant once $b > \frac{c}{a+1}$, which agrees with the conditions in Table 1.
We can interpret the conditions on p_{3+}^* and p_{3-}^* in Table 1 in a similar manner to above. Consider (a projection onto) the positive x-y-quadrant as well as the straight line and parabola defined by

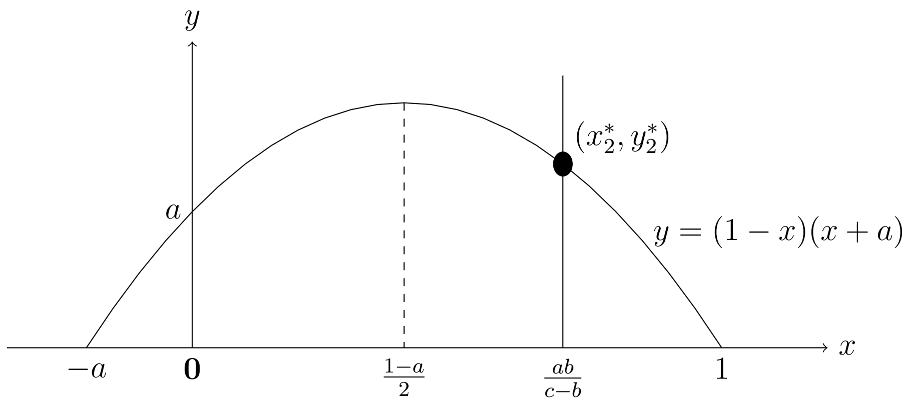
$$y = \frac{g}{f} - h \quad \text{and} \quad y = (1-x)(x+a)$$

respectively, see Figure 2.4.2.
The line may have zero, one or two points of intersection with the parabola in the positive quadrant (see the various cases in Figures 2.4.2 and 2.4.3). This is determined by the the conditions in Table 1. The intersection points determine *the first two* components $x_{3\pm}^*$ and $y_{3\pm}^*$ of the equilibria $p_{3\pm}^* = (x_{3\pm}^*, y_{3\pm}^*, z_{3\pm}^*)^T$. Thus if any intersections exist, the *sign* of the third component $z_{3\pm}^*$ determines whether the equilibria are in $\mathcal{O}_0^+$ or not. In fact, the conditions that ensure that the final component of the equilibria $p_{3\pm}^*$ is non-negative are listed in Table 1 and read

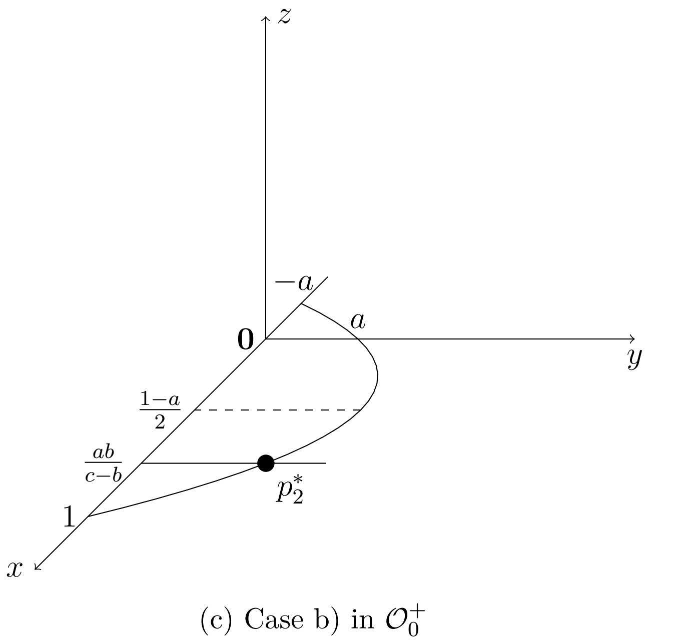
$$b \leq \frac{cx_{3+}^*}{x_{3+}^*+a} =: b_{3+}^* \quad \text{and} \quad b \leq \frac{cx_{3-}^*}{x_{3-}^*+a} =: b_{3-}^* \tag{2.4.1}$$



(a) Case $x_2^* < \frac{1-a}{2}$ and $a < 1$, i.e. small $b > 0$



(b) Case $\frac{1-a}{2} < x_2^* < 1$ and $a < 1$, i.e. larger b



(c) Case b) in $\mathcal{O}_0^+$

Figure 2.4.1: The nullclines defining the equilibrium p_2^*.

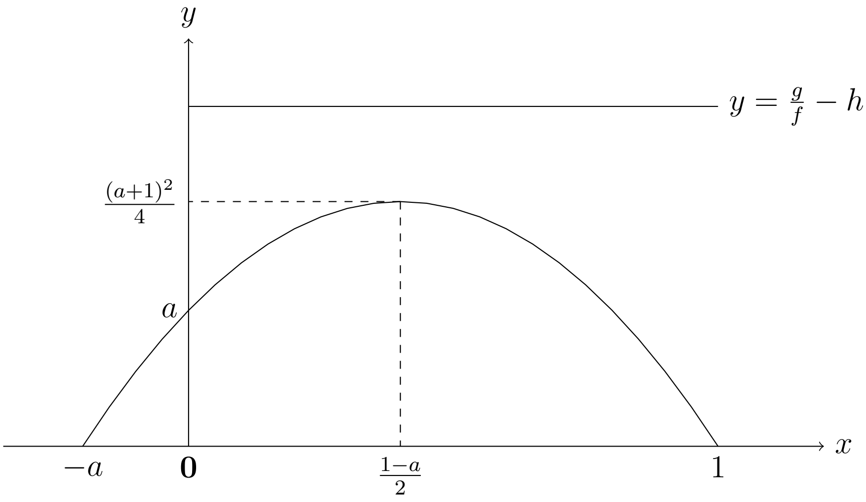
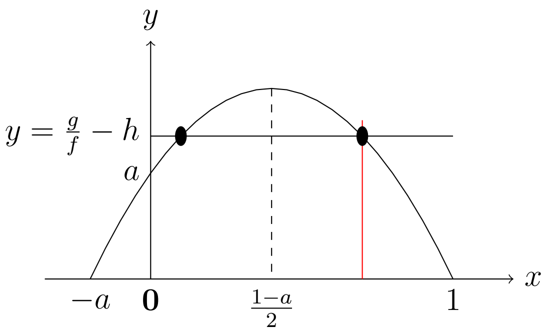
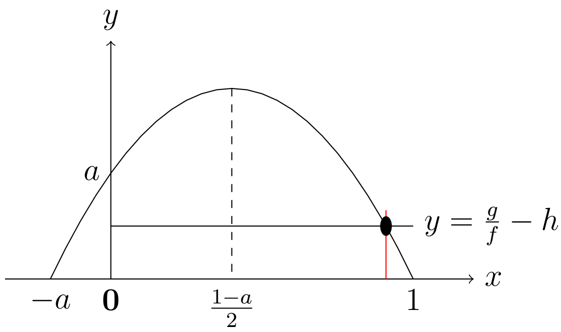


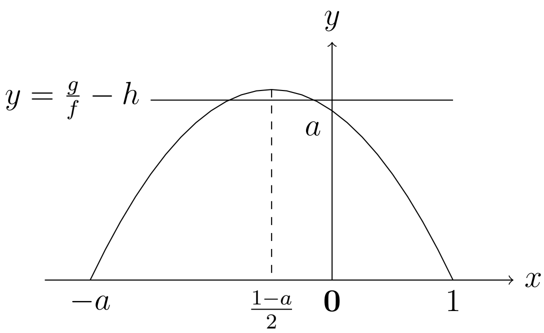
Figure 2.4.2: Case $a < 2\sqrt{\frac{g}{f} - h} - 1$ or equivalently $\frac{(a+1)^2}{4} < \frac{g}{f} - h$



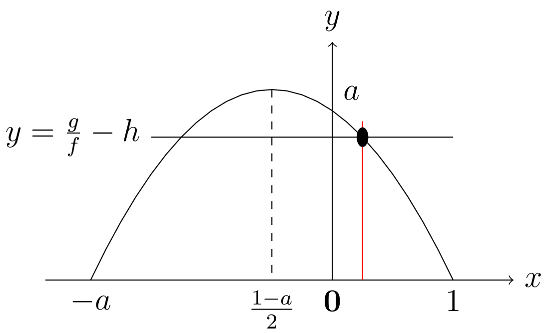
(a) Case $a \leq 1$ and $a < \frac{g}{f} - h$



(b) Case $a \leq 1$ and $a > \frac{g}{f} - h$



(c) Case $a > 1$ and $a < \frac{g}{f} - h$



(d) Case $a > 1$ and $a > \frac{g}{f} - h$

Figure 2.4.3: Visualisation of the conditions in Table 1 if $a \geq 2\sqrt{\frac{g}{f} - h} - 1$ holds.

respectively. There is a simple geometric interpretation in terms of the nullclines defining p_2^* and $p_{3\pm}^*$ of the above results. Equality holds in (2.4.1) when both straight lines and the parabola, i.e. all three nullclines given by

$$x = \frac{ab}{c-d} \quad \text{and} \quad y = \frac{g}{f} - h \quad \text{and} \quad y = (1-x)(x+a),$$

intersect, see Figure 2.4.4. If all three intersect, the respective equilibria p_2^* and

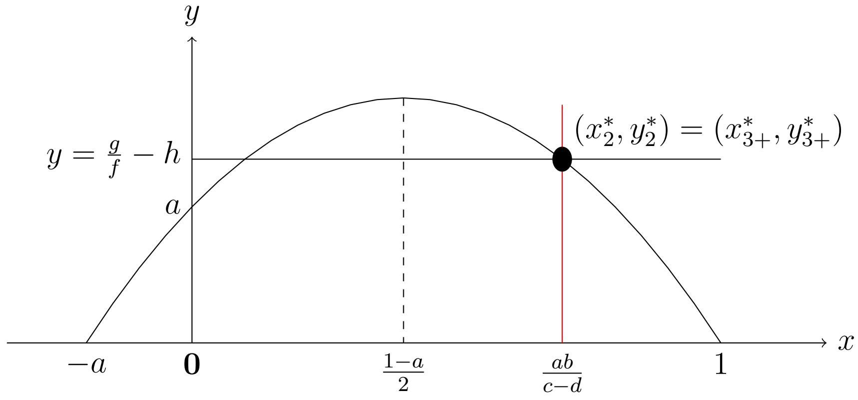


Figure 2.4.4: The case $b = b_{3+}^* = \frac{cx_{3+}^*}{x_{3+}^*+a}$ or equivalently $x_{3+}^* = \frac{ab}{c-b} = x_2^*$

either p_{3+}^* or p_{3-}^* coincide (see Lemma 2.4.1 below), thus fulfilling $z_2^* = z_{3\pm}^* = 0$ and

$$b = b_{3+}^* \qquad \text{or} \qquad b = b_{3-}^*$$

respectively. Furthermore, p_{3+}^* is in $\mathcal{O}_0^+$ for all $b \in (0, b_{3+}^*)$. Indeed, note that only the *third* component of p_{3+}^* depends on b and is positive for $b \in (0, b_{3+}^*)$, implying that all the components of the equilibrium are non-negative for $b \in (0, b_{3+}^*)$. Hence the equilibrium is in $\mathcal{O}_0^+$ for $b = b_{3+}^*$ where it coincides with p_2^* and in the non-negative octant for all $b \in (0, b_{3+}^*)$. The same holds true for the equilibrium p_{3-}^* and the value b_{3-}^*. The equilibria $p_{3\pm}^*$ are also called the *interior equilibria*, as they may be in the positive octant $\mathcal{O}^+$, i.e. the interior of the phase space $\mathcal{O}_0^+$. From Figures 2.4.3 and 2.4.4 we obtain the following implications by considering the nullclines of p_2^* (observe the intersection of the vertical red lines and the parabola in the figures, which moves to the left for decreasing values of $b \in (0, b_{3+}^*)$):

$$p_{3+}^* \in \mathcal{O}_0^+ \quad \Rightarrow \quad y_2^* \geq \frac{g}{f} - h \quad \vee \quad x_2^* \leq \frac{1-a}{2}. \tag{2.4.2}$$

$$p_{3+}^* \notin \mathcal{O}_0^+ \quad \Rightarrow \quad y_2^* < \frac{g}{f} - h \tag{2.4.3}$$

Furthermore, there is a fixed order (with respect to biological feasibility), by which the equilibria may be sorted. We elaborate on this in the following

Lemma 2.4.1.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold in system (2.1.5). For the equilibria p_i^* (listed in Table 1) of the semiflow Φ induced by (2.1.5) on $\mathcal{O}_0^+$ the following implications hold:

$$p_{3-}^* \in \mathcal{O}_0^+ \quad \overset{1)}{\Rightarrow} \quad p_{3+}^* \in \mathcal{O}_0^+ \quad \overset{2)}{\Rightarrow} \quad p_2^* \in \mathcal{O}_0^+ \quad \overset{3)}{\Rightarrow} \quad p_0^* \in \mathcal{O}_0^+ \wedge p_1^* \in \mathcal{O}_0^+$$

Furthermore

- *The points* p_1^* *and* p_2^* *coincide in* $\mathcal{O}_0^+$ *for* $b = \frac{c}{a+1}$.
- *The points* p_2^* *and* p_{3+}^* *coincide in* $\mathcal{O}_0^+$ *for* $b = b_{3+}^*$.
- *The points* p_2^* *and* p_{3-}^* *coincide in* $\mathcal{O}_0^+$ *for* $b = b_{3-}^*$.

Proof.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold in system (2.1.5) and consider the equilibria p_i^* (listed in Table 1). We prove the three implications first.

1) Assume $p_{3-}^* \in \mathcal{O}_0^+$. By Table 1 the following conditions hold:

$$a \geq 2\sqrt{\tfrac{g}{f} - h} - 1 \quad \wedge \quad 0 < a \leq 1 \quad \wedge \quad a < \frac{g}{f} - h \quad \wedge \quad b \leq \frac{cx_{3-}^*}{x_{3-}^* + a}. \tag{2.4.4}$$

Since

$$0 \leq x_{3-}^* = \frac{1-a}{2} - \underbrace{\sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h}}_{\geq 0} \leq \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} = x_{3+}^*$$

we have

$$b \leq \frac{cx_{3-}^*}{x_{3-}^* + a} \quad \Rightarrow \quad b \leq \frac{cx_{3+}^*}{x_{3+}^* + a}.$$

Thus, from Table 1 and (2.4.4) we immediately see that $p_{3+}^* \in \mathcal{O}_0^+$.

2) Assume $p_{3+}^* \in \mathcal{O}_0^+$. By Table 1 the following conditions hold:

$$a \geq 2\sqrt{\tfrac{g}{f} - h} - 1 \quad \wedge \quad \left(0 < a \leq 1 \quad \vee \quad a > \frac{g}{f} - h\right) \quad \wedge \quad b \leq \frac{cx_{3+}^*}{x_{3+}^* + a}.$$

We show from the above that $x_{3+}^* \leq 1$ holds, since

$$\begin{array}{rcl} & f - \frac{g}{h} & \leq & 0 \\ \Leftrightarrow & -\frac{g}{f} + h & \leq & 0 \\ \Leftrightarrow & \frac{(a+1)^2}{4} - \frac{g}{f} + h & \leq & \frac{(a+1)^2}{4} \\ \Leftrightarrow & \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} & \leq & \frac{a+1}{2} \\ \Leftrightarrow & \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} & \leq & 1 \\ \Leftrightarrow & x_{3+}^* & \leq & 1 \end{array}$$

Thus we may estimate

$$b \leq \frac{cx_{3+}^*}{x_{3+}^* + a} \leq \frac{c}{1+a} < c,$$

which implies $p_2^* \in \mathcal{O}_0^+$ by Table 1.

3) Since p_0^* and p_1^* are always contained in $\mathcal{O}_0^+$, regardless of the parameter-values, this implication is trivially fulfilled.

Furthermore, we show that certain equilibria coincide for specific parameter values.

- Let $b = \frac{c}{a+1}$ which is equivalent to $c = b(a+1)$ and consider

$$p_2^* = \begin{pmatrix} x_2^* \\ y_2^* \\ z_2^* \end{pmatrix} = \begin{pmatrix} \frac{ab}{c-b} \\ (1-x_2^*)(x_2^*+a) \\ 0 \end{pmatrix} = \begin{pmatrix} \frac{ab}{b(a+1)-b} \\ (1-x_2^*)(x_2^*+a) \\ 0 \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix} = p_1^*.$$

- Let $b = \frac{cx_{3+}^*}{x_{3+}^*+a}$, which is equivalent to $x_{3+}^* = \frac{ab}{c-b} = x_2^*$ and consider

$$p_{3+}^* = \begin{pmatrix} x_{3+}^* \\ y_{3+}^* \\ z_{3+}^* \end{pmatrix} = \begin{pmatrix} \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} \\ \frac{g}{f} - h \\ \left(h - \frac{g}{f} - e\right)\left(b - \frac{cx_{3+}^*}{x_{3+}^*+a}\right) \end{pmatrix} = \begin{pmatrix} \frac{ab}{c-b} \\ \frac{g}{f} - h \\ 0 \end{pmatrix} = \begin{pmatrix} x_2^* \\ \frac{g}{f} - h \\ z_2^* \end{pmatrix}$$

Hence the claim holds true if

$$y_{3+}^* = \frac{g}{f} - h \overset{!}{=} (1-x_2^*)(x_2^*+a) = y_2^*.$$

Since

$$x_2^* = \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h}$$

we in fact obtain

$$\begin{aligned} y_2^* &= (1-x_2^*)(x_2^*+a) \\ &= \left(\frac{1+a}{2} - \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h}\right)\left(\frac{1+a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h}\right) \\ &= \left(\frac{1+a}{2}\right)^2 - \frac{(a+1)^2}{4} + \frac{g}{f} - h \\ &= \frac{g}{f} - h, \end{aligned}$$

thus proving $y_{3+}^* = y_2^*$ and hence $p_{3+}^* = p_2^*$.

- We need to show $p_{3-}^* = p_2^*$ for $b = b_{3-}^*$. Analogous computations as in the previous point immediately yield the result. □

Remark 2.4.1.
Using the symbol ⊳ to indicate that the biological feasibility of the previous equilibrium implies the biological feasibility of the next equilibrium we obtain the following order from the above result

$$p_{3-}^* \rhd p_{3+}^* \rhd p_2^* \rhd p_0^* \wedge p_1^*.$$

A (biological) interpretation of the above chain is that whenever there exist states of coexistence of order n of the species (i.e. equilibria with n non-zero entries, $n \in \{1, 2, 3\}$), there are also biologically relevant equilibria of all orders k, with $k \in \{0, ..., n-1\}$.

We observe that any number from two to five equilibria may be found in $\mathcal{O}_0^+$, dependent on $a > 0$ and $b > 0$. While three of the equilibria are confined to the boundary of $\mathcal{O}_0^+$, two of them (p_{3+}^* and p_{3-}^*) may be in the positive octant $\mathcal{O}^+$. Considering that all these points are part of the set $\mathcal{A}$ and that $\mathcal{A}$ is connected, it is clear that - at least for certain parameter regions - the attractor may have a more involved structure. We will investigate this structure step by step, by determining various local and global properties of the equilibria. We commence by considering the dynamics in the boundary of $\mathcal{O}_0^+$, i.e. those cases for which at least one species is assumed to not be present (e.g. extinct) in the ecosystem initially.

Lemma 2.4.2.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold and any solution s with $s_0 \in \partial\mathcal{O}_0^+ = \mathcal{O}_0^+ \backslash \mathcal{O}^+$ be given. The dynamics in the boundary of $\mathcal{O}_0^+$ are characterised as follows:

- *If $x_0 = 0$ then $s(t) \to p_0^*$ as $t \to \infty$.*
- *If $y_0 = 0$ and $x_0 > 0$ then $s(t) \to p_1^*$ as $t \to \infty$.*
- *If $z_0 = 0$ and $x_0 > 0$ and $y_0 > 0$ and $s_0 \neq p_2^*$ then*
  - *it holds that $s(t) \to p_1^*$ as $t \to \infty$ if $b \geq \frac{c}{a+1}$.*
  - *it holds that $s(t) \to p_2^*$ as $t \to \infty$ if $\frac{c(1-a)}{1+a} \leq b < \frac{c}{a+1}$.*
  - *it holds that $s(t) \to \Gamma_{per}^*$ as $t \to \infty$ if $b < \frac{c(1-a)}{1+a}$ and $a < 1$ (Remark 2.4.2).*

Here p_0^*, p_1^* and p_2^* are the equilibria from Table 1 and Γ_{per}^* is a unique periodic orbit contained in the set $O_5 = \mathbb{R}^+ \times \mathbb{R}^+ \times \{0\}$ (see Lemma 2.1.1). In all cases it holds that

$$\lim_{t\to\infty} z(t) = 0.$$

Proof.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold and any solution s with $s_0 \in \partial\mathcal{O}_0^+ = \mathcal{O}_0^+ \backslash \mathcal{O}^+$ be given.

- Let $x_0 = 0 = x_0^*$. Then $x(t) = 0$ for all $t \geq 0$ and the equation governing the change in the y-component of s reduces to

  $$\dot{y}(t) = y(t)\left(-b - \frac{z(t)}{y(t) + e}\right),$$

  allowing the following estimate

  $$\dot{y}(t) \leq -by(t).$$

Integration yields

$$y(t) \leq y_0 \exp(-bt) \qquad \forall\, t \geq 0.$$

Since on the other hand $y(t) \geq 0$ for all $t \geq 0$ (Lemma 2.1.4), we obtain

$$0 \leq \lim_{t\to\infty} y(t) \leq \lim_{t\to\infty} y_0 \exp(-bt) = 0,$$

i.e. $y(t) \to 0 = y_0^*$ as $t \to \infty$. By the above we have that for any given $\varepsilon > 0$ there exists a time $T \geq 0$ such that

$$y(t) < \varepsilon \qquad \forall\, t \geq T.$$

For the $\dot{z}$-equation in (2.1.5) this implies

$$\dot{z}(t) = \left(f - \frac{g}{y(t)+h}\right) z^2(t) \leq \left(f - \frac{g}{\varepsilon + h}\right) z^2(t) \qquad \forall\, t \geq T.$$

Since $f - \frac{g}{h} < 0$, any $\varepsilon > 0$ chosen sufficiently small fulfils

$$f - \frac{g}{\varepsilon + h} < 0$$

and hence for $z_0 > 0$ (else $z(t) = 0 = z_0^*$ for all $t \geq 0$)

$$\dot{z}(t) \leq \underbrace{\left(f - \frac{g}{\varepsilon+h}\right)}_{<0} z^2(t) < 0 \qquad \forall\, t \geq T.$$

Dividing by $z^2(t) > 0$ and integration from $T \geq 0$ to $t \geq T$ yields

$$z(t) \leq \frac{1}{\frac{1}{z(T)} - \underbrace{\left(f - \frac{g}{\varepsilon+h}\right)}_{<0}(t-T)} \qquad \forall\, t \geq T \geq 0.$$

Since on the other hand $z(t) \geq 0$ for all $t \geq 0$ (Lemma 2.1.4), we obtain

$$0 \leq \lim_{t\to\infty} z(t) \leq \lim_{t\to\infty} \frac{1}{\frac{1}{z(T)} - \left(f - \frac{g}{\varepsilon+h}\right)(t-T)} = 0,$$

i.e. $z(t) \to 0 = z_0^*$ as $t \to \infty$. Thus we have shown for $x_0 = 0$, that

$$s(t) \to (0,0,0)^T = p_0^* \qquad \text{as} \qquad t \to \infty.$$

- Let $y_0 = 0 = y_1^*$ and $x_0 > 0$. This implies that $y(t) = 0$ for all $t \geq 0$. Hence the first and third equation in system (2.1.5) reduce to

$$\begin{aligned} \dot{x} &= x(1-x) \\ \dot{z} &= \left(f - \frac{g}{h}\right) z^2, \end{aligned}$$

of which we already know the respective solutions (recall Lemmas 2.2.4 and 2.3.1 and note that the case $z_0 = 0$ yields $z(t) = 0 = z_1^*$ for all $t \geq 0$ and is thus not considered):

$$x(t) = \frac{1}{\left(\frac{1}{x_0} - 1\right)\exp(-t) + 1}$$
$$z(t) = \frac{1}{\frac{1}{z_0} - \left(f - \frac{g}{h}\right)t}$$

Hence, we obtain

$$\lim_{t\to\infty} x(t) = \lim_{t\to\infty} \frac{1}{\left(\frac{1}{x_0} - 1\right)\exp(-t) + 1} = 1 = x_1^*$$

and

$$\lim_{t\to\infty} z(t) = \lim_{t\to\infty} \frac{1}{\frac{1}{z_0} - \underbrace{\left(f - \frac{g}{h}\right)}_{<0} t} = 0 = z_1^*.$$

Thus we have shown for $y_0 = 0$ and $x_0 > 0$, that

$$s(t) \to (1, 0, 0)^T = p_1^* \qquad \text{as} \qquad t \to \infty.$$

- If $z_0 = 0$ and $x_0 > 0$ and $y_0 > 0$ and $s_0 \neq p_2^*$, then $z(t) = 0$ for all $t \geq 0$ and the model equations in (2.1.5) that need to be analysed reduce to

$$\dot{x} = x\left(1 - x - \frac{y}{x+a}\right)$$
$$\dot{y} = y\left(-b + \frac{cx}{x+a}\right)$$

which are the classical equations for a two-species predator-prey model with Holling functional response type II. These equations have been thoroughly studied and the proof of the claim may for example be found in [Cheng, 1981], [Muratori and Rinaldi, 1989] and [Feo and Rinaldi, 1997].

Since all the limit sets p_0^*, p_1^*, p_2^* and Γ_{per}^* are contained in the non-negative x-y-quadrant we have

$$\lim_{t\to\infty} z(t) = 0.$$

□

Remark 2.4.2.
The expression $s(t) \to \Gamma_{per}^*$ stands for the convergence of the solution s to the set Γ_{per}^* in the sense of orbital (asymptotic) stability (with $t \to \infty$).

Having established how the dynamics in the boundary $\partial\mathcal{O}_0^+$ unfold, we now ask the same question with respect to the interior of $\mathcal{O}_0^+$, i.e. the positive octant $\mathcal{O}^+$. To this extent we remark the following on the notion of stability of an equilibrium.

Remark 2.4.3.
Since we have been considering the phase space $X = \mathcal{O}_0^+$ for the semiflow Φ we will also restrict stability properties to this set. In particular, when considering an equilibrium p_i^* of the semiflow Φ on $\mathcal{O}_0^+$ we will say that it is (asymptotically) stable, if it is (asymptotically) stable in some neighbourhood $N_\varepsilon(p_i^*)$ of the equilibrium intersected with $\mathcal{O}_0^+$. In this way we capture the behaviour of the biologically relevant solutions only, which is a common restriction (cf. [Muratori and Rinaldi, 1989]). If the above holds for any neighbourhood $N_\varepsilon(p_i^*)$, i.e. for arbitrary large $\varepsilon > 0$, then we call the equilibrium globally asymptotically stable.
Furthermore, we will say that an equilibrium p_i^* of the semiflow Φ is **globally (asymptotically) stable in** $\mathcal{O}^+$, if it is (asymptotically) stable for *any* neighbourhood $N_\varepsilon(p_i^*)$ of p_i^* *intersected with the positive octant* $\mathcal{O}^+$. In particular, any solution s with $s_0 \in \mathcal{O}^+$ will converge to the equilibrium p_i^* as $t \to \infty$.

Note that also points in the boundary of $\mathcal{O}_0^+$ may be globally asymptotically stable in $\mathcal{O}^+$, although the points themselves are not contained in $\mathcal{O}^+$. Indeed, we will observe precisely this in the stability analysis of the equilibria (see Lemma 2.4.4).
We commence with the standard technique (generally known as Lyapunov's indirect method [Wiggins, 1990]) of linearising the vector field $v(x, y, z)$ and computing the eigenvalues of the Jacobian matrix evaluated at the various equilibria (compare to [Aziz-Alaoui, 2002]). The Jacobian of v is given by

$$\mathrm{Dv}(x,y,z) = \begin{pmatrix} 1 - 2x - \frac{ay}{(x+a)^2} & -\frac{x}{x+a} & 0 \\ \frac{acy}{(x+a)^2} & -b + \frac{cx}{x+a} - \frac{ez}{(y+e)^2} & -\frac{y}{y+e} \\ 0 & \frac{gz^2}{(y+h)^2} & 2z\left(f - \frac{g}{y+h}\right) \end{pmatrix} \tag{2.4.5}$$

Our first result is the following claim.

Lemma 2.4.3.
The equilibrium p_0^* of the semiflow Φ is unstable for any parameters $a > 0$ and $b > 0$.

Proof.
Inserting the equilibrium $p_0^* = (0,0,0)^T$ into (2.4.5) yields

$$\mathrm{Dv}(0,0,0) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -b & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

of which the eigenvalues are $\lambda_1 = 1$, $\lambda_2 = -b$ and $\lambda_3 = 0$. Since $\mathrm{Re}(\lambda_1) = 1 > 0$ the equilibrium is unstable by Lyapunov's indirect method. The associated local unstable manifold $W^u_{loc}(p_0^*)$ is tangent to the eigenvector corresponding to λ_1, which is the standard unit vector $(1,0,0)^T$, see Figure 2.4.5. □

Remark 2.4.4.
Note that p_0^* is also non-hyperbolic, since $\mathrm{Re}(\lambda_3) = 0$. Hence we can determine the stability properties of p_0^* on the corresponding (non-trivial) local centre manifold

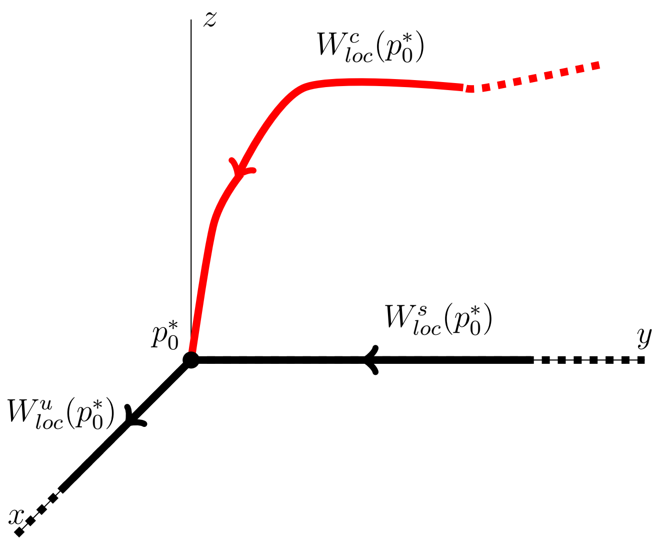


Figure 2.4.5: Schematic figure of the invariant local manifolds to the equilibrium p^*_0.

$W^c_{loc}(p^*_0)$ by the tangent space approximation ([Guckenheimer and Holmes, 1983], [Wiggins, 1990]). The eigenvectors corresponding to the eigenvalues $\lambda_1, \lambda_2, \lambda_3$ are simply the standard unit vectors. Hence we know by the centre manifold theorem that there exists a function h such that on $W^c_{loc}(p^*_0)$ we can express the non-centre variables x, y in terms of the centre variable z in the following way:

$$\begin{pmatrix} x \\ y \end{pmatrix} = h(z) = \begin{pmatrix} 0 \\ 0 \end{pmatrix} + \begin{pmatrix} \mathcal{O}(z^2) \\ \mathcal{O}(z^2) \end{pmatrix} \quad \text{as} \quad z \to 0.$$

Therefore $y = y(z) = \mathcal{O}(z^2)$ for $z \to 0$ on the centre manifold and in particular

$$y(z) \to 0 \qquad \text{as} \qquad z \searrow 0.$$

Hence, for any $z > 0$ sufficiently close to zero (we restrict ourselves to non-negative values of z - i.e. biologically relevant values - in the reduced system as well), one obtains

$$y(z) < \underbrace{\frac{g}{f} - h}_{>0}.$$

For the dynamics on the centre manifold close to $z = 0$ and $z > 0$ this implies

$$\dot{z} = \left(f - \frac{g}{y(z) + h} \right) z^2 < \left(f - \frac{g}{\frac{g}{f} - h + h} \right) z^2 = 0.$$

Thus $\dot{z} < 0$ holds for $z > 0$ sufficiently close to $z = 0$ and this equilibrium is asymptotically stable for the reduced system, see Figure 2.4.6. Therefore the equilibrium p^*_0 has a stable centre component, see the red curve in Figure 2.4.5.

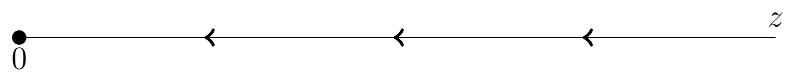


Figure 2.4.6: On the centre manifold $W^c_{loc}(p_0^*)$ it holds that $\dot{z} < 0$ for small $z > 0$.

The above analysis gives insight to more involved aspects of the dynamics close to an equilibrium, induced by the non-hyperbolicity of the point. In fact, along the local centre manifold $W^c_{loc}(p_0^*)$ solution curves move *towards* p_0^*. The centre manifold reduction approach will be of significance as we analyse the other equilibria. The next one being the point of a sole survivor, i.e. $p_1^* = (1,0,0)^T$:

Lemma 2.4.4.
The equilibrium p_1^* of the semiflow Φ is asymptotically stable if $b > \frac{c}{a+1}$ and unstable if $b < \frac{c}{a+1}$.

Proof.
Inserting the equilibrium $p_1^* = (1,0,0)^T$ into (2.4.5) yields

$$\mathrm{Dv}(1,0,0) = \begin{pmatrix} -1 & -\frac{1}{1+a} & 0 \\ 0 & -b + \frac{c}{a+1} & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

of which the eigenvalues are $\lambda_1 = -1$, $\lambda_2 = -b + \frac{c}{a+1}$ and $\lambda_3 = 0$.

- If $b < \frac{c}{a+1}$ then $\mathrm{Re}(\lambda_2) = -b + \frac{c}{a+1} > 0$ and p_1^* is unstable by Lyapunov's indirect method.
- If $b > \frac{c}{a+1}$ then $\mathrm{Re}(\lambda_1) = -1 < 0$ and $\mathrm{Re}(\lambda_2) = -b + \frac{c}{a+1} < 0$ and hence p_1^* is possibly asymptotically stable, since the unstable eigenspace is trivial. Furthermore $\mathrm{Re}(\lambda_3) = 0$ holds, implying that the equilibrium is non-hyperbolic and a stability analysis on the local centre manifold $W^c_{loc}(p_1^*)$ will determine the stability properties of p_1^*. Performing a centre manifold reduction (see Appendix C.3.1) with the new variables (ξ, ν, ω) - with ω being the centre variable -, yields the following equation for the change of ω:

$$\dot{\omega} = \left(f - \frac{g}{[1+a+c-b(a+1)]\nu + h} \right) \omega^2.$$

  By the same arguments as in Remark 2.4.4, i.e. applying the tangent space approximation

$$\begin{pmatrix} \xi \\ \nu \end{pmatrix} = h(\omega) = \begin{pmatrix} 0 \\ 0 \end{pmatrix} + \begin{pmatrix} \mathcal{O}(\omega^2) \\ \mathcal{O}(\omega^2) \end{pmatrix} \quad \text{as} \quad \omega \to 0,$$

  we obtain

$$\dot{\omega} = \left(f - \frac{g}{[1+a+c-b(a+1)]\nu(\omega) + h} \right) \omega^2 < \left(f - \frac{g}{\frac{g}{f} - h + h} \right) \omega^2 = 0$$

for the dynamics of the reduced system and $\omega > 0$ sufficiently small, see Figure 2.4.7. Hence the equilibrium $\omega = 0$ (of the reduced system) is asymptotically stable (for $\omega > 0$) and therefore the equilibrium p_1^* is asymptotically stable as well, see Figure 2.4.8.

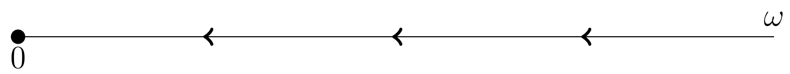


Figure 2.4.7: On the centre manifold $W^c_{loc}(p_1^*)$ it holds that $\dot{\omega} < 0$ for small $\omega > 0$.

□

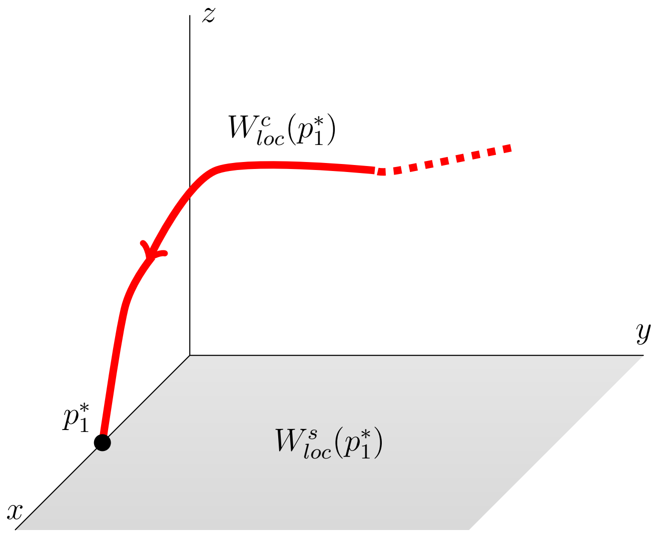


Figure 2.4.8: Schematic figure of the two invariant local manifolds of the equilibrium p_1^*.

Having proven some local results on the equilibria (in particular for the case $b > \frac{c}{a+1}$), we show the first global result for these parameter values and in fact precisely characterise the global attractor $\mathcal{A}$. Before doing so, a simple auxiliary result is proven:

Lemma 2.4.5.
Let $b > \frac{c}{a+1}$ hold and $\varepsilon > 0$ be given. For any sufficiently small $\varepsilon > 0$, the expression

$$K_1 := -b + \frac{c(1+\varepsilon)}{a+1+\varepsilon}$$

fulfils $K_1 < 0$.

Proof.
Let $b > \frac{c}{a+1}$ hold and $\varepsilon > 0$ be given. We consider the term

$$K_1 := -b + \frac{c(1+\varepsilon)}{a+1+\varepsilon}.$$

It holds that

$$K_1 \overset{!}{<} 0 \quad \Leftrightarrow \quad -b(a+1+\varepsilon) + c(1+\varepsilon) < 0 \quad \Leftrightarrow \quad (1+\varepsilon)(-b+c) < ab \tag{2.4.6}$$

We prove that (2.4.6) holds for any sufficiently small $\varepsilon > 0$.

- If $b < c$, then (2.4.6) may be rewritten as

$$1 + \varepsilon < \frac{ab}{c-b} \quad \Leftrightarrow \quad \varepsilon < \frac{ab}{c-b} - 1.$$

  Since

$$b > \frac{c}{a+1} \quad \Leftrightarrow \quad ab > c - b \quad \Leftrightarrow \quad \frac{ab}{c-b} > 1$$

  we can choose any positive $\varepsilon \in \left(0, \frac{ab}{c-b} - 1\right)$ to fulfil (2.4.6).

- If $b = c$, then (2.4.6) holds for any $\varepsilon > 0$ since

$$ab > 0 = (1+\varepsilon)\underbrace{(c-b)}_{=0}.$$

- If $b > c$, then (2.4.6) may be rewritten as

$$1 + \varepsilon > \frac{ab}{c-b} \quad \Leftrightarrow \quad \varepsilon > \frac{ab}{c-b} - 1.$$

  However, now

$$\frac{ab}{\underbrace{c-b}_{<0}} < 0$$

  and therefore any $\varepsilon > 0$ suffices for (2.4.6) to hold.

In particular for sufficiently small $\varepsilon > 0$ we have $K_1 < 0$. □

We use the above result in the proof of the following

Lemma 2.4.6.
Let $b > \frac{c}{a+1}$ hold, then

$$\mathcal{A} = [0,1] \times \{0\} \times \{0\}$$

is the global attractor of the semiflow Φ in $\mathcal{O}_0^+$. Furthermore, the equilibrium p_1^* is globally asymptotically stable in $\mathcal{O}^+$.

Proof.
Let $b > \frac{c}{a+1}$ (and $f - \frac{g}{h} < 0$ and $a = d$, as always) hold. Furthermore, let any bounded subset $B \subset \mathcal{O}_0^+$ be given. We show that for sufficiently small $\varepsilon > 0$ the set

$$\mathcal{B} = \Big\{(x, y, z) \in \mathcal{O}_0^+ \,:\, 0 \leq x \leq 1 + \varepsilon,\, 0 \leq y \leq \varepsilon,\, 0 \leq z \leq \varepsilon\Big\}$$

is uniformly absorbing (in $\mathcal{O}_0^+$). We do this by considering any solution s with $s_0 \in B$ and constructing a uniform absorbance time $T_{\mathcal{B}}(B) > 0$ such that

$$s(t) \in \mathcal{B} \qquad \forall\, t \geq T_{\mathcal{B}}(B).$$

x-coordinate:
By Lemma 2.3.6 we have

$$s(t) \in \mathcal{Q} \qquad \forall\, t \geq T_{\mathcal{Q}}(B),$$

implying

$$0 \leq x(t) \leq 1 + \varepsilon \qquad \forall\, t \geq T_{\mathcal{Q}}(B). \tag{2.4.7}$$

y-coordinate:
If $y_0 = 0$, then

$$y(t) = 0 \leq \varepsilon \qquad \forall\, t \geq 0.$$

Now assume $y_0 > 0$ (implying $y(t) > 0$ for any $t \geq 0$). For any $t \geq T_{\mathcal{Q}}(B)$ the inequality in (2.4.7) allows the estimate

$$\dot{y}(t) = \left(-b + \frac{cx(t)}{a + x(t)} - \frac{z(t)}{y(t) + e}\right) y(t) \leq \underbrace{\left(-b + \frac{c(1+\varepsilon)}{a + 1 + \varepsilon}\right)}_{=:K_1} y(t).$$

For any sufficiently small $\varepsilon > 0$ Lemma 2.4.5 yields $K_1 < 0$. Separation of variables and integration from $T_{\mathcal{Q}}(B)$ to $t \geq T_{\mathcal{Q}}(B)$ of the above, as well as recalling the uniform bound $y_M(B) \geq 0$ from Lemma 2.2.31 yields

$$y(t) \leq y(T_{\mathcal{Q}}(B)) \exp\left[K_1(t - T_{\mathcal{Q}}(B))\right] \leq y_M(B) \exp\left[K_1(t - T_{\mathcal{Q}}(B))\right] \qquad \forall\, t \geq T_{\mathcal{Q}}(B).$$

By solving

$$y(t) \leq y_M(B) \exp\left[K_1(t - T_{\mathcal{Q}}(B))\right] \overset{!}{\leq} \varepsilon$$

for t one obtains a sufficiently large time $T_\varepsilon(B) \geq T_{\mathcal{Q}}(B)$, such that

$$y(t) \leq \varepsilon \qquad \forall\, t \geq T_\varepsilon(B).$$

This time is given by

$$T_\varepsilon(B) := T_{\mathcal{Q}}(B) + \begin{cases} \frac{1}{K_1} \ln\left(\frac{\varepsilon}{y_M(B)}\right) & \text{if} \quad y_M(B) > \varepsilon \\ 0 & \text{if} \quad y_M(B) \leq \varepsilon. \end{cases}$$

Hence for any $t \geq T_\varepsilon(B)$ and sufficiently small $\varepsilon > 0$ it holds that

$$x(t) \leq 1 + \varepsilon \quad \text{and} \quad y(t) \leq \varepsilon. \tag{2.4.8}$$

z-coordinate:
If $z_0 = 0$, then

$$z(t) = 0 \leq \varepsilon \qquad \forall\, t \geq 0.$$

Now assume $z_0 > 0$ (implying $z(t) > 0$ for any $t \geq 0$). For any $t \geq T_\varepsilon(B)$ the results in (2.4.8) allow the estimate

$$\dot{z}(t) = \left(f - \frac{g}{y(t) + h}\right) z^2(t) \leq \underbrace{\left(f - \frac{g}{\varepsilon + h}\right)}_{=:K_2} z^2(t).$$

Since $f - \frac{g}{h} < 0$ we have $K_2 < 0$ for sufficiently small $\varepsilon > 0$. Separating variables and integrating the above from $T_\varepsilon(B)$ to any $t > T_\varepsilon(B) \geq 0$ yields

$$z(t) \leq \frac{1}{\underbrace{\frac{1}{z(T_\varepsilon(B))} - K_2(t - T_\varepsilon(B))}_{>0}} \qquad \forall\, t \geq T_\varepsilon(B).$$

Recalling that $z(t) \leq z_M(B)$ for any $t \geq 0$ (by Lemma 2.2.35), yields

$$z(t) \leq \frac{1}{\frac{1}{z(T_\varepsilon(B))} - K_2(t - T_\varepsilon(B))} \leq \frac{1}{\frac{1}{z_M(B)} - K_2(t - T_\varepsilon(B))} \qquad \forall\, t \geq T_\varepsilon(B).$$

Thus, analogously to above, by solving

$$\frac{1}{\frac{1}{z_M(B)} - K_2(t - T_\varepsilon(B))} \overset{!}{\leq} \varepsilon$$

for t, we once again determine a $T_\mathcal{B}(B) \geq T_\varepsilon(B)$ such that

$$z(t) \leq \varepsilon \qquad \forall\, t \geq T_\mathcal{B}(B).$$

The time $T_\mathcal{B}(B) \geq 0$ is given by

$$T_\mathcal{B}(B) := T_\varepsilon(B) + \begin{cases} \frac{1}{K_2}\left(\frac{1}{z_M(B)} - \frac{1}{\varepsilon}\right) & \text{if} \quad z_M(B) > \varepsilon \\ 0 & \text{if} \quad z_M(B) \leq \varepsilon. \end{cases}$$

Thus we obtain the statement we wanted to prove

$$s(t) \in \mathcal{B} \qquad \forall\, t \geq T_\mathcal{B}(B).$$

Since $\varepsilon > 0$ may be chosen arbitrarily small and the global attractor $\mathcal{A}$ is closed and fulfils $\mathcal{A} \subset \mathcal{B}$ we have

$$\mathcal{A} \subset \{(x, y, z) \in \mathcal{O}_0^+ \,:\, 0 \leq x \leq 1,\, y = 0,\, z = 0\}. \tag{2.4.9}$$

However, on the other hand we know that the equilibria p_0^* and p_1^* are contained in $\mathcal{A}$. Furthermore, $\mathcal{A}$ is connected and by (2.4.9) the only connection of the two aforementioned equilibria is the line segment $(0,1) \times \{0\} \times \{0\}$. Thus

$$\mathcal{A} \supset \{(x,y,z) \in \mathcal{O}_0^+ \, : \, 0 \leq x \leq 1, \, y=0, \, z=0\},$$

implying

$$\mathcal{A} = \{(x,y,z) \in \mathcal{O}_0^+ \, : \, 0 \leq x \leq 1, \, y=0, \, z=0\} = [0,1] \times \{0\} \times \{0\}.$$

Since the only limit points in the attractor are the equilibria p_0^* and p_1^* and p_0^* is unstable, it follows that p_1^* is globally asymptotically stable in $\mathcal{O}^+$ (cf. [Freedman and Waltman, 1977]). □

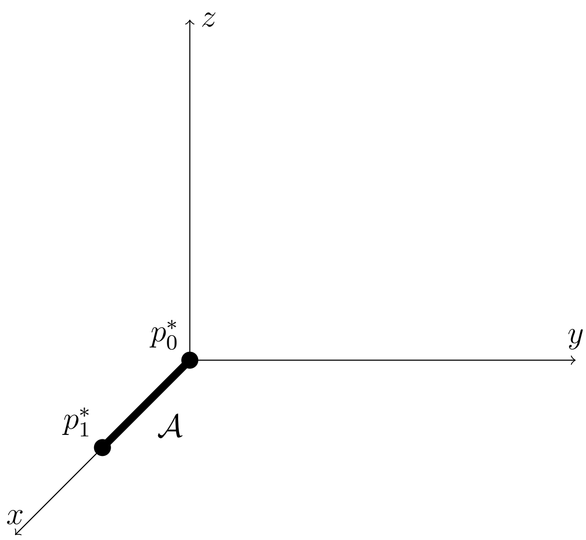


Figure 2.4.9: The attractor $\mathcal{A}$ for $b > \frac{c}{a+1}$

Remark 2.4.5.
The above result is a complete characterisation of the global attractor $\mathcal{A}$ for $b > \frac{c}{a+1}$:

- From a geometric point of view this implies that that for $b > \frac{c}{a+1}$ the set $\mathcal{A}$ is given by two equilibria and the connecting heteroclinic orbit of these equilibria - see Figure 2.4.9. Since the equilibria do not coincide, $\mathcal{A}$ has dimension one.
- A biological interpretation is that for $b > \frac{c}{a+1}$ both the specialist predator species and generalist predator species will become extinct as time tends to infinity (also see subsection 2.5.2).

Furthermore, for $b = \frac{c}{a+1}$ the equilibria p_1^* and p_2^* coincide (Lemma 2.4.1) where p_1^* loses its stability (Lemma 2.4.4) and a transcritical bifurcation occurs along the branch of equilibria corresponding to p_1^*, i.e. $\left(\frac{c}{a+1}, p_1^*\right)$ is a transcritical bifurcation point. The equilibrium p_1^* turns unstable as b is decreased below the value $\frac{c}{a+1}$

and the point p_2^* becomes asymptotically stable (due to the principle of exchange of stability [Guckenheimer and Holmes, 1983]). The stability properties of p_2^* are provided in the following

Lemma 2.4.7.
The equilibrium $p_2^* \in \mathcal{O}_0^+$ of the semiflow Φ is

- *asymptotically stable if $\frac{c(1-a)}{a+1} < b < \frac{c}{a+1}$ and $p_{3+}^* \notin \mathcal{O}_0^+$.*
- *unstable if $b < \frac{c(1-a)}{a+1}$ or $p_{3+}^* \in \mathcal{O}^+$.*

For $b = \frac{c(1-a)}{a+1}$ a subcritical Hopf bifurcation occurs (restricted to the x-y-plane) along the branch of equilibria corresponding to p_2^*, i.e. the point $\left(\frac{c(1-a)}{a+1}, p_2^*\right) \in \mathbb{R}^+ \times \mathcal{O}_0^+$ is a Hopf bifurcation point.

Proof.
Assume $b < \frac{c}{a+1}$ to hold. Inserting the equilibrium $p_2^* = (x_2^*, y_2^*, 0)^T \in \mathcal{O}_0^+$ into the Jacobian in (2.4.5) yields

$$\mathrm{Dv}(p_2^*) = \begin{pmatrix} \frac{x_2^*(1-a-2x_2^*)}{a+x_2^*} & -\frac{x_2^*}{x_2^*+a} & 0 \\ \frac{ac(1-x_2^*)}{a+x_2^*} & 0 & -\frac{y_2^*}{y_2^*+e} \\ 0 & 0 & 0 \end{pmatrix}$$

of which one of the eigenvalues is given by $\lambda_3 = 0$ and the corresponding eigenvector is the unit vector $(0, 0, 1)^T$. The other two eigenvalues of $\mathrm{Dv}(p_2^*)$ are given by the eigenvalues of the submatrix

$$\begin{pmatrix} \frac{x_2^*(1-a-2x_2^*)}{a+x_2^*} & -\frac{x_2^*}{x_2^*+a} \\ \frac{ac(1-x_2^*)}{a+x_2^*} & 0 \end{pmatrix},$$

which is in fact the same Jacobian matrix as for the classical two-dimensional predator-prey model with Holling functional response type II, also called the Rosenzweig-MacArthur model (cf. [Rosenzweig and MacArthur, 1963], [Muratori and Rinaldi, 1989], [Jones et al., 2009]). Accordingly the eigenvalues are identical and the analysis (see [Kot, 2001], [Aziz-Alaoui, 2002], [Smith, 2008] and Appendix C.3.2) - for example using the trace-determinant criterion - yields that:

- $\mathrm{Re}(\lambda_{1/2}) > 0$ for $b < \frac{c(1-a)}{a+1}$, whence the equilibrium p_2^* is unstable by Lyapunov's indirect method
- $\mathrm{Re}(\lambda_{1/2}) = 0$ and $\mathrm{Im}(\lambda_{1/2}) \neq 0$ for $b = \frac{c(1-a)}{a+1}$ and a subcritical Hopf bifurcation occurs (restricted to the positive invariant x-y-plane) along the branch of equilibria corresponding to p_2^* ([Kuznetsov, 1995]). The stability of the bifurcating periodic orbit depends on whether the vector field is increasing or decreasing in z-direction close to the equilibrium, which in turn depends on whether $p_{3+}^* \in \mathcal{O}_0^+$, see the centre manifold reduction below.

- $\mathrm{Re}(\lambda_{1/2}) < 0$ for $\frac{c(1-a)}{a+1} < b$, i.e. the equilibrium p_2^* is possibly (asymptotically) stable, dependent on the other eigenvalue of $\mathrm{Dv}(p_2^*)$, namely $\lambda_3 = 0$.

From the above we see, that the only case left to consider is $\frac{c(1-a)}{a+1} < b$, which we assume to hold for the rest of the proof. In fact, since $\mathrm{Re}(\lambda_3) = 0$ the equilibrium p_2^* is non-hyperbolic and hence we perform a centre manifold reduction. The reduction (see Appendix C.3.2) with the new variables (ξ, ν, ω) - with ω being the centre variable -, yields the following $\dot{\omega}$-equation

$$\dot{\omega} = \left(f - \frac{g}{\xi + \nu + C\omega + y_2^* + h} \right) \omega^2,$$

where $C > 0$ for $b > \frac{c(1-a)}{a+1}$. Once more, the tangent space approximation yields

$$\begin{pmatrix} \xi(\omega) \\ \nu(\omega) \end{pmatrix} = h(\omega) = \begin{pmatrix} 0 \\ 0 \end{pmatrix} + \begin{pmatrix} \mathcal{O}(\omega^2) \\ \mathcal{O}(\omega^2) \end{pmatrix} \quad \text{as} \quad \omega \to 0.$$

Thus we have

$$0 \leq \xi(\omega) + \nu(\omega) + C\omega = C\omega + \mathcal{O}(\omega^2) \quad \text{as} \quad \omega \to 0 \tag{2.4.10}$$

with $C > 0$ on the local centre manifold $W^c_{loc}(p_2^*)$. We now consider two different cases:

- If $p_{3+}^* \in \mathcal{O}^+$ then by (2.4.2) we obtain

$$y_2^* \geq \frac{g}{f} - h \quad \vee \quad x_2^* = \frac{ab}{c-b} \leq \frac{1-a}{2} \quad \Leftrightarrow \quad b \leq \frac{c(1-a)}{a+1},$$

  The second case has been excluded since $\frac{c(1-a)}{a+1} < b$ was assumed. If on the other hand $y_2^* \geq \frac{g}{f} - h$ holds, then the dynamics on the centre manifold for small $\omega > 0$ may be estimated as follows (using the positivity in (2.4.10)):

$$\begin{aligned} \dot{\omega} &= \left(f - \frac{g}{\xi + \nu + C\omega + y_2^* + h} \right) \omega^2 \\ &\geq \left(f - \frac{g}{\xi + \nu + C\omega + \frac{g}{f} - h + h} \right) \omega^2 \\ &= \left(f - \frac{g}{\xi + \nu + C\omega + \frac{g}{f}} \right) \omega^2 \\ &> \left(f - \frac{g}{\frac{g}{f}} \right) \omega^2 \\ &= 0 \end{aligned}$$

  Thus the equilibrium $\omega = 0$ (of the reduced system, i.e. on the centre manifold) is unstable and hence p_2^* is unstable in this case, see Figure 2.4.10.

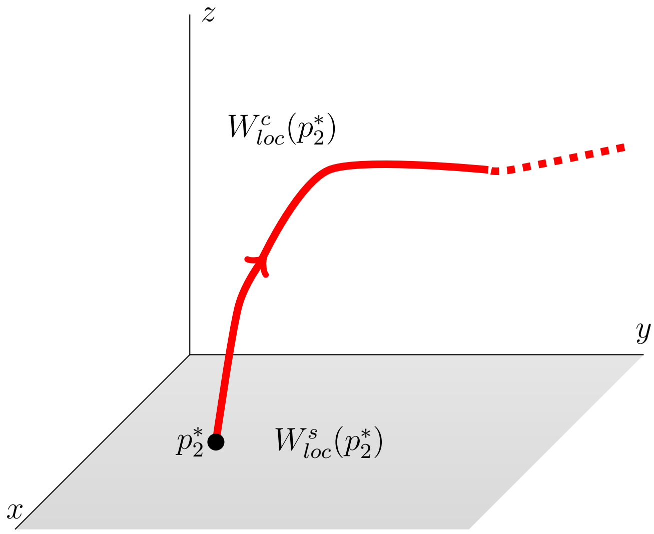


Figure 2.4.10: If $\frac{c(1-a)}{a+1} < b$ and $p_{3+}^* \in \mathcal{O}^+$, the equilibrium p_2^* is unstable due to the dynamics on the local centre manifold $W^c_{loc}(p_2^*)$.

- If $p_{3+}^* \notin \mathcal{O}_0^+$ then by (2.4.3) we know that $y_2^* < \frac{g}{f} - h$. Hence for a sufficiently small $\varepsilon > 0$ it holds that
$$y_2^* < \frac{g}{f} - h - \varepsilon.$$
Using (2.4.10) we see that for such an $\varepsilon > 0$ and any sufficiently small $\omega > 0$ it holds that
$$0 \le \xi(\omega) + \nu(\omega) + C\omega \le \varepsilon$$
is valid on $W^c_{loc}(p_2^*)$. Thus close to $\omega = 0$ (with $\omega > 0$) the following estimate holds
$$\begin{aligned} \dot{\omega} &= \left(f - \frac{g}{\xi + \nu + C\omega + y_2^* + h}\right)\omega^2 \\ &\le \left(f - \frac{g}{\varepsilon + y_2^* + h}\right)\omega^2 \\ &< \left(f - \frac{g}{\varepsilon + \frac{g}{f} - h - \varepsilon + h}\right)\omega^2 \\ &= \left(f - \frac{g}{\frac{g}{f}}\right)\omega^2 \\ &= 0. \end{aligned}$$
Therefore the equilibrium $\omega = 0$ on the local centre manifold $W^c_{loc}(p_2^*)$ is asymptotically stable (in our sense, i.e. for $\omega > 0$) and hence p_2^* is asymptotically stable, see Figure 2.4.11. □

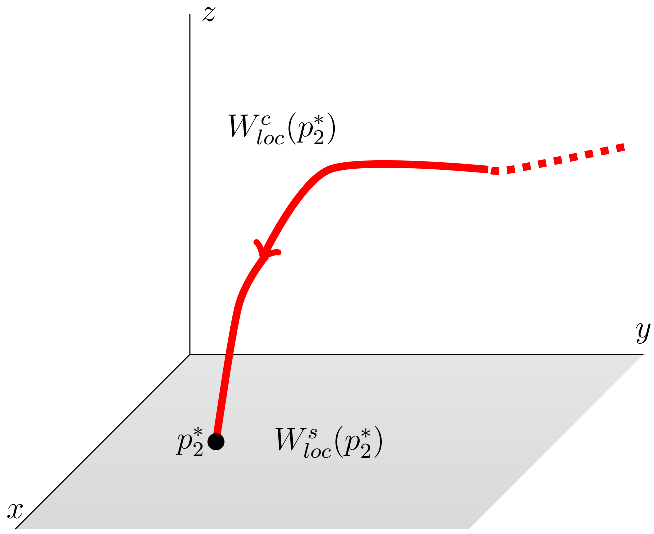


Figure 2.4.11: If $\frac{c(1-a)}{a+1} < b$ and $p^*_{3+} \notin \mathcal{O}^+_0$, the equilibrium p_2^* is stable due to the dynamics on the local centre manifold $W^c_{loc}(p_2^*)$.

Remark 2.4.6.
In geometrical terms the above result may be understood as follows: The equilibrium p_2^* is locally asymptotically stable while both the periodic orbit Γ^*_{per} in the x-y-plane created by the subcritical Hopf bifurcation does not exist (i.e. $b > \frac{c(1-a)}{a+1}$) and the equilibrium p^*_{3+} is not biologically relevant (i.e. $p^*_{3+} \notin \mathcal{O}^+_0$). Recall that the equilibria p_2^* and p^*_{3+} coincide for

$$b^*_{3+} = \frac{cx^*_{3+}}{x^*_{3+} + a}$$

by Lemma 2.4.1, provided $x^*_{3+} \in \mathbb{R}$. Furthermore,

$$\begin{aligned} p^*_{3+} &\in \mathcal{O}^+_0 \quad \forall\, b \in (0, b^*_{3+}] \\ p^*_{3+} &\notin \mathcal{O}^+_0 \quad \forall\, b \in (b^*_{3+}, \infty) \end{aligned}$$

holds (recall Figure 2.4.4). A transcritical bifurcation occurs along the branch of equilibria corresponding to p_2^* (and p^*_{3+}) for $b = b^*_{3+}$, i.e. $\left(b^*_{3+}, p_2^*\right)$ is a transcritical bifurcation point. By the above results, p_2^* is unstable for $b < b^*_{3+}$ and asymptotically stable for $b^*_{3+} < b$ (b close to b^*_{3+}).

Two (of many) questions that arise naturally from the above are:

- For which parameter values is p_2^* *globally* asymptotically stable in $\mathcal{O}^+$?
- Do the periodic orbit Γ^*_{per} or equilibrium p^*_{3+} inherit the stability properties of p_2^* when they bifurcate with p_2^* and if so, are they *globally* (orbitally) asymptotically stable in $\mathcal{O}^+$ for some parameter values?

In Lemma 2.4.6 we proved a global result concerning the semiflow Φ and the corresponding global attractor $\mathcal{A} \subset \mathcal{O}^+_0$. In the following subsection we attain more results of the same kind, giving answers to the questions listed above and characterising $\mathcal{A}$ for various parameter regions.

2.4.2 Global results

As always we assume $a = d$ and $f - \frac{g}{h} < 0$ to hold in this subsection. The goal of this subsection is to present global results with respect to the dynamics induced by the semiflow Φ on $\mathcal{O}_0^+$. A central tool in proving these results is an observation which we present in the following

Lemma 2.4.8.
Let $T > 0$ and a function $u \in \mathcal{C}^0([0,T], \mathbb{R}^+)$ be given. Furthermore, let constants $C_1, C_2 > 0$ exist such that

$$0 < \frac{1}{T}\int_0^T u(t)dt \le C_1 \tag{2.4.11}$$

$$0 < \frac{1}{T}\int_0^T \frac{1}{u(t)}dt \le C_2. \tag{2.4.12}$$

Then it holds that

$$C_1 \cdot C_2 \ge 1. \tag{2.4.13}$$

If either of the inequalities (2.4.11) *and* (2.4.12) *is strict, then so is* (2.4.13).

Proof.
Let $T > 0$ and a function $u \in \mathcal{C}^0([0,T], \mathbb{R}^+)$ be given. Note that since u is positive and continuous for all $t \in [0,T]$, we have

$$\frac{1}{u} \in \mathcal{C}^0\left([0,T], \mathbb{R}^+\right),$$

i.e. the function $\frac{1}{u}$ is defined, continuous and positive on $[0,T]$ as well. Since u and $\frac{1}{u}$ are both continuous on $[0,T]$ they are also integrable on that interval. We will need this throughout the proof. Indeed, the integrals in (2.4.11) and (2.4.12) are well-defined due to the integrability of u and $\frac{1}{u}$. We assume that constants $C_1, C_2 > 0$ exist such that

$$0 < \frac{1}{T}\int_0^T u(t)dt \le C_1$$

$$0 < \frac{1}{T}\int_0^T \frac{1}{u(t)}dt \le C_2.$$

Multiplying by $T > 0$ and taking the square root on both sides yields

$$0 < \left(\int_0^T u(t)dt\right)^{\frac{1}{2}} \le (C_1 T)^{\frac{1}{2}}$$

$$0 < \left(\int_0^T \frac{1}{u(t)}dt\right)^{\frac{1}{2}} \le (C_2 T)^{\frac{1}{2}}.$$

By using the identities (recall u is positive)

$$u(t) = \left(\sqrt{u(t)}\right)^2 \quad \text{and} \quad \frac{1}{u(t)} = \left(\frac{1}{\sqrt{u(t)}}\right)^2,$$

we may rewrite the above as follows

$$0 < \left(\int_0^T \left(\sqrt{u(t)}\right)^2 dt\right)^{\frac{1}{2}} \leq (C_1 T)^{\frac{1}{2}} \tag{2.4.14}$$

$$0 < \left(\int_0^T \left(\frac{1}{\sqrt{u(t)}}\right)^2 dt\right)^{\frac{1}{2}} \leq (C_2 T)^{\frac{1}{2}}. \tag{2.4.15}$$

Taking the product of the left-hand side and right-hand side of (2.4.14) and (2.4.15) yields

$$0 < \left(\int_0^T \left(\sqrt{u(t)}\right)^2 dt\right)^{\frac{1}{2}} \cdot \left(\int_0^T \left(\frac{1}{\sqrt{u(t)}}\right)^2 dt\right)^{\frac{1}{2}} \leq (C_1 T)^{\frac{1}{2}} \cdot (C_2 T)^{\frac{1}{2}} = (C_1 C_2)^{\frac{1}{2}} T.$$

We may now apply Hölder's inequality to the left-hand side of the above, with the Hölder conjugates fulfilling $\frac{1}{2} + \frac{1}{2} = 1$. This results in

$$\begin{aligned}
(C_1 C_2)^{\frac{1}{2}} T &\geq \left(\int_0^T \left(\sqrt{u(t)}\right)^2 dt\right)^{\frac{1}{2}} \cdot \left(\int_0^T \left(\frac{1}{\sqrt{u(t)}}\right)^2 dt\right)^{\frac{1}{2}} \\
&\geq \int_0^T \sqrt{u(t)} \frac{1}{\sqrt{u(t)}} dt \\
&= \int_0^T 1 dt \\
&= T
\end{aligned}$$

Dividing by $T > 0$ on both sides yields

$$(C_1 C_2)^{\frac{1}{2}} \geq 1$$

and by squaring both sides we obtain the claim

$$C_1 \cdot C_2 \geq 1.$$

The second part of the claim is obtained by replacing the appropriate inequalities with strict inequalities in the above proof. □

Remark 2.4.7.
By additionally assuming that u is not constant on $[0,T]$ we may also improve the above result to a strict inequality in (2.4.13). This is true since equality in Hölder's inequality only holds if the two functions considered are linearly dependent almost everywhere. In the above case this translates to the existence of some constant $C \in \mathbb{R}$, such that

$$\sqrt{u(t)} = C\frac{1}{\sqrt{u(t)}}$$

for all $t \in [0,T]$ (since u is continuous). However, this is equivalent to

$$u(t) = C \qquad \forall\, t \in [0,T].$$

Thus if u is not constant, Hölder's inequality is truly an inequality and we may estimate

$$\left(\int_0^T \left(\sqrt{u(t)}\right)^2 dt\right)^{\frac{1}{2}} \cdot \left(\int_0^T \left(\frac{1}{\sqrt{u(t)}}\right)^2 dt\right)^{\frac{1}{2}} > \int_0^T \sqrt{u(t)}\frac{1}{\sqrt{u(t)}}dt$$

in the above proof.

While the above result has an abstract character as it stands, we will in fact be able to use it several times to prove various global results on $\mathcal{A}$, we are seeking. The key task is to find integral estimates of the same form as in equations (2.4.11) and (2.4.12) for an appropriate function u. We will obtain results for periodic solutions s_p of (2.1.5), extending them to any solution s with $s_0 \in \mathcal{O}^+$ subsequently.

Periodic solutions

The first estimate of the kind we require is given in the following

Lemma 2.4.9.
Let s_p be any periodic solution with $s_0 \in \mathcal{O}^+$ and period $T > 0$. The solution $s_p(t) = (x(t), y(t), z(t))^T$ fulfils

$$\frac{1}{T}\int_0^T \frac{dt}{y(t)+h} = \frac{f}{g}.$$

Proof.
Let s_p be any periodic solution with $s_0 \in \mathcal{O}^+$ and period $T > 0$. Since $s_0 \in \mathcal{O}^+$ we know that s_p is positive in all its components for $t \geq 0$ (Lemma 2.1.5). Furthermore, since s_p is periodic we have $s_p(0) = s_p(T)$ and in particular the third component fulfils $z_0 = z(0) = z(T)$. Consider the third equation of (2.1.5):

$$\dot{z}(t) = \left(f - \frac{g}{y(t)+h}\right) z^2(t).$$

Dividing by $z^2(t) > 0$ and integrating from zero to $T > 0$ yields

$$\int_0^T f - \frac{g}{y(t)+h}dt = \int_0^T \frac{\dot{z}(t)}{z^2(t)}dt \quad \Leftrightarrow \quad fT - g\int_0^T \frac{dt}{y(t)+h} = \underbrace{-\frac{1}{z(T)} + \frac{1}{z_0}}_{=0}$$

$$\Leftrightarrow \quad g\int_0^T \frac{dt}{y(t)+h} = fT$$

$$\Leftrightarrow \quad \frac{1}{T}\int_0^T \frac{dt}{y(t)+h} = \frac{f}{g}. \qquad \square$$

In a similar manner we may prove

Lemma 2.4.10.
Let s_p be any periodic solution with $s_0 \in \mathcal{O}^+$ and period $T > 0$. The solution $s_p(t) = (x(t), y(t), z(t))^T$ fulfils

$$\frac{1}{T}\int_0^T y(t) + h\,dt \leq \frac{(a+1)^2}{4} + h.$$

Proof.
Let s_p be any periodic solution with $s_0 \in \mathcal{O}^+$ and period $T > 0$. Since $s_0 \in \mathcal{O}^+$ we know that s_p is positive in all its components for $t \geq 0$ (Lemma 2.1.5). Furthermore, since s_p is periodic we have $s_p(0) = s_p(T)$ and in particular the first component fulfils $x_0 = x(0) = x(T)$. Consider the $\dot{x}$-equation (for the sake of readability we drop the dependence on t in the notation):

$$\dot{x} = x(1-x) - \frac{xy}{x+a}.$$

Multiplying by $x + a$ and dividing by $x > 0$ yields

$$\frac{\dot{x}(x+a)}{x} = (1-x)(x+a) - y.$$

This is equivalent to

$$\dot{x} + a\frac{\dot{x}}{x} + y = (1-x)(x+a).$$

Since

$$\max_{x\in\mathbb{R}}(1-x)(x+a) = \frac{(1+a)^2}{4}$$

holds (also see Figure 2.4.2), we obtain

$$\dot{x} + a\frac{\dot{x}}{x} + y = (1-x)(x+a) \leq \frac{(1+a)^2}{4}.$$

Integrating the above from zero to $T > 0$ yields

$$x(T) - x_0 + a\ln\left(\frac{x(T)}{x_0}\right) + \int_0^T y(t)dt \leq \int_0^T \frac{(1+a)^2}{4}dt.$$

Since $x_0 = x(0) = x(T)$ this simplifies to

$$\int_0^T y(t)dt \leq \frac{(1+a)^2}{4}T.$$

Adding hT on both sides, results in

$$\int_0^T y(t)dt + hT = \int_0^T y(t) + h\,dt \leq \left(\frac{(1+a)^2}{4} + h\right)T.$$

Dividing by $T > 0$ yields the result:

$$\frac{1}{T}\int_0^T y(t) + h\,dt \leq \frac{(a+1)^2}{4} + h. \qquad \square$$

Applying Lemma 2.4.8 to the results of the two previous lemmas allows us to prove

Lemma 2.4.11.
Let s_p be any periodic solution with $s_0 \in \mathcal{O}^+$ and period $T > 0$. Then the parameters in (2.1.5) *fulfil*

$$\frac{g}{f} - h \leq \frac{(a+1)^2}{4}.$$

Proof.
Let s_p be any periodic solution with $s_0 \in \mathcal{O}^+$ and period $T > 0$. By Lemmas 2.4.9 and 2.4.10 it holds that

$$\frac{1}{T}\int_0^T y(t) + h\,dt \leq \frac{(a+1)^2}{4} + h.$$
$$\frac{1}{T}\int_0^T \frac{1}{y(t)+h}\,dt = \frac{f}{g}$$

Since s is continuous on $[0, T]$ and positive in every component (by $s_0 \in \mathcal{O}^+$), it holds that

$$y + h \in \mathcal{C}^0([0, T], \mathbb{R}^+).$$

Thus, Lemma 2.4.8 applies to the function $y + h$ (with the above estimates), yielding

$$\left(\frac{(a+1)^2}{4} + h\right)\frac{f}{g} \geq 1.$$

This is equivalent to the claim:

$$\frac{(a+1)^2}{4} \geq \frac{g}{f} - h. \qquad \square$$

Note that the above result supplies a *necessary* condition for periodic solutions of (2.1.5) to exist. Likewise it also yields a *sufficient* condition for the non-existence of periodic solutions or orbits:

Corollary 2.4.1.
Assume that

$$\frac{g}{f} - h > \frac{(a+1)^2}{4}$$

holds and let s be a solution with $s_0 \in \mathcal{O}^+$. Then s is not periodic. In particular, any periodic orbit Γ_{per} of the semiflow Φ on $\mathcal{O}_0^+$ is contained in the boundary $\partial\mathcal{O}_0^+$ of $\mathcal{O}_0^+$.

Proof.
Assume that

$$\frac{g}{f} - h > \frac{(a+1)^2}{4} \tag{2.4.16}$$

holds and let s be a solution with $s_0 \in \mathcal{O}^+$. Assuming that s is periodic immediately implies that

$$\frac{g}{f} - h \leq \frac{(a+1)^2}{4}$$

holds by Lemma 2.4.11, which is a contradiction to the parameter assumption in (2.4.16). Hence s is not periodic and no periodic solution exists in $\mathcal{O}^+$. Furthermore, the fact that $\mathcal{O}^+$ and $\partial\mathcal{O}_0^+$ has property *(I1)* for all $t \geq 0$ and fulfil

$$\mathcal{O}_0^+ = \mathcal{O}^+ \,\dot{\cup}\, \partial\mathcal{O}_0^+,$$

implies that any periodic orbit Γ_{per} of the semiflow Φ on $\mathcal{O}_0^+$ fulfils

$$\Gamma_{per} \subset \partial\mathcal{O}_0^+. \qquad \square$$

Remark 2.4.8.
Note that the condition

$$\frac{g}{f} - h > \frac{(a+1)^2}{4}$$

is equivalent to

$$a < 2\sqrt{\frac{g}{f} - h} - 1.$$

We have encountered this condition previously already - recall Figure 2.4.2 for example. It is the condition for which the two equilibria $p_{3\pm}^*$ are not real (see Table 1). Hence the above corollary may also be read as:

If the equilibria $p_{3\pm}^*$ are not real-valued, no periodic solution s_p with $s_0 \in \mathcal{O}^+$ exists.

We also emphasise the **generality of the method** we used above. More precisely, Lemma 2.4.8 is not restricted to the semiflow Φ induced by (2.1.5). For an arbitrary semiflow $\widehat{\Phi}$ on a subset of $\mathbb{R}^n$ the decisive question is whether one can find a $T > 0$ and a corresponding function

$$u \in \mathcal{C}^0\left([0,T], \mathbb{R}^+\right)$$

(for example a component of $\widehat{\Phi}$) fulfilling estimates (2.4.11) and (2.4.12), i.e. that the function u and its reciprocal have a bounded mean. If so, Lemma 2.4.8 yields necessary parameter conditions for such a function to exist. In turn this allows the exclusion of certain properties of u, such as periodicity (as shown above), if the parameter conditions are not met. In fact, periodic functions u are a natural point to start at, when searching for such estimates (recall the proofs of Lemmas 2.4.9 and 2.4.10 and cf. [Volterra, 1927], [Freedman and Waltman, 1977], [Ruan and Freedman, 1991]). However, they are not the only type of functions that may be studied with this method (as we will see in the rest of this subsection).
In addition to this, note that the estimates (2.4.11) and (2.4.12) only have to hold for a *single* $T > 0$ and that the *dimension* of the phase space may be an arbitrary value $n \in \mathbb{N}$, i.e. this method is not restricted to two or three-dimensional space. Other mathematical models of ecosystems may prove to be a good field of application of this method, as we show in subsections 3.1.3 and 3.2.1 in this thesis for example.

The results and proofs of Lemma 2.4.11 and Corollary 2.4.1 give a good idea about how we will go about to prove more global results on the dynamics of the semiflow Φ. We will generalise the results in two ways:

- A broader spectrum of parameters is covered.
- The results extend to more solutions than just periodic solutions, thus allowing a better characterisation of the global attractor $\mathcal{A}$.

Persistence and extinction

For this purpose (especially regarding the second aspect of the above list) we introduce the following

Definition 2.4.1.
The x-species in the GSP food chain model (2.1.5) *is said to* ***persist*** *if for all solutions s with $s_0 \in \mathcal{O}^+$ it holds that*

$$\limsup_{t\to\infty} x(t) > 0.$$

The x-species in the GSP food chain model (2.1.5) *is said to* ***become extinct*** *if for all solutions s with $s_0 \in \mathcal{O}^+$ it holds that*

$$\limsup_{t\to\infty} x(t) = 0.$$

The definitions for the y- and z-species are analogous.

Remark 2.4.9.
The above definition (cf. [Gard, 1980], [Thieme, 2003]) ensures that if a species persists, it survives for *any* positive initial species density of all species (i.e. $s_0 \in \mathcal{O}^+$).

The definition of extinction can be understood accordingly. We emphasise that neither condition has to hold, since a species may fulfil

$$\limsup_{t\to\infty} x(t) = 0$$

for certain initial values s_0 while it survives for others.

Similarly to above we will now prove two estimates which we then use to apply Lemma 2.4.8:

Lemma 2.4.12.
Let s be a solution with $s_0 \in \mathcal{O}^+$ and assume that

$$\limsup_{t\to\infty} z(t) > 0$$

holds. Then for any $\varepsilon > 0$ there exists an arbitrarily large $T > 0$ such that

$$\frac{1}{T}\int_0^T \frac{1}{y(t)+h}dt < \frac{f}{g} + \varepsilon.$$

Proof.
Let s be a solution with $s_0 \in \mathcal{O}^+$ and assume that

$$\limsup_{t\to\infty} z(t) > 0$$

holds. As done before, dividing by $z^2(t) > 0$ and integrating from zero to $t > 0$ the third equation of (2.1.5) becomes

$$-\frac{1}{z(t)} + \frac{1}{z_0} = ft - g\int_0^t \frac{d\tau}{y(\tau)+h}.$$

This is equivalent to

$$\frac{1}{t}\int_0^t \frac{d\tau}{y(\tau)+h} = \frac{f}{g} + \frac{1}{gt}\left(\frac{1}{z(t)} - \frac{1}{z_0}\right). \tag{2.4.17}$$

We now consider the term

$$\frac{1}{gt}\left(\frac{1}{z(t)} - \frac{1}{z_0}\right)$$

for large t. Since $\limsup_{t\to\infty} z(t) > 0$ we know that there exists a time sequence $(t_i)_{i\in\mathbb{N}}$ with $t_i \to \infty$ as $i \to \infty$ such that

$$\underbrace{\frac{1}{gt_i}}_{\to 0}\underbrace{\left(\frac{1}{z(t_i)} - \frac{1}{z_0}\right)}_{\not\to\pm\infty} \to 0 \quad \text{as} \quad i \to \infty.$$

Consequently, for any given $\varepsilon > 0$ we can find an arbitrarily large $i \in \mathbb{N}$ and corresponding time $t_i =: T$ from the aforementioned sequence such that

$$\frac{1}{gT}\left(\frac{1}{z(T)} - \frac{1}{z_0}\right) < \varepsilon.$$

Inserting $t = T$ in (2.4.17) yields the claim

$$\frac{1}{T}\int_0^T \frac{d\tau}{y(\tau)+h} = \frac{f}{g} + \frac{1}{gT}\left(\frac{1}{z(T)} - \frac{1}{z_0}\right) < \frac{f}{g} + \varepsilon. \qquad \square$$

The next lemma yields another estimate we will use

Lemma 2.4.13.
Let s be a solution with $s_0 \in \mathcal{O}^+$. Then for any $\varepsilon > 0$ there exists a $\widetilde{T} > 0$ such that

$$\frac{1}{T}\int_0^T y(t) + h\,dt < \frac{c}{4b} + h + \varepsilon \qquad \forall\, T \geq \widetilde{T}.$$

Proof.
Let s be a solution with $s_0 \in \mathcal{O}^+$. It holds that

$$\dot{x} + \frac{\dot{y}}{c} = x(1-x) - \frac{b}{c}y - \underbrace{\frac{1}{c}\frac{yz}{y+e}}_{>0} < x(1-x) - \frac{b}{c}y$$

for any $t \geq 0$. Solving for y and adding the term h on both sides of the inequality yields

$$y + h < \frac{c}{b}x(1-x) - \frac{c}{b}\left(\dot{x} + \frac{\dot{y}}{c}\right) + h.$$

Furthermore $x(1-x) \leq \frac{1}{4}$ holds for all $x \in \mathbb{R}$ and thus

$$y + h < \frac{c}{4b} + h - \frac{c}{b}\left(\dot{x} + \frac{\dot{y}}{c}\right).$$

Integration of the above from zero to $T > 0$ yields

$$\int_0^T y(t) + h\,dt < \left(\frac{c}{4b} + h\right)T - \frac{c}{b}\left(x(T) - x_0 + \frac{y(T) - y_0}{c}\right).$$

Dividing by $T > 0$ results in

$$\frac{1}{T}\int_0^T y(t) + h\,dt < \frac{c}{4b} + h + \frac{c}{bT}\left(x_0 - x(T) + \frac{y_0 - y(T)}{c}\right).$$

Since $x(T), y(T) > 0$ holds, we have

$$\frac{1}{T}\int_0^t y(t) + h\,dt < \frac{c}{4b} + h + \frac{c}{bT}\left(x_0 + \frac{y_0}{c}\right).$$

Since for any given $\varepsilon > 0$ we can choose a sufficiently large $\widetilde{T} > 0$ such that

$$\frac{c}{bT}\left(x_0 + \frac{y_0}{c}\right) < \varepsilon \qquad \forall T \geq \widetilde{T}$$

the claim of the lemma holds:

$$\frac{1}{T}\int_0^T y(t) + h\,dt < \frac{c}{4b} + h + \frac{c}{bT}\left(x_0 + \frac{y_0}{c}\right) < \frac{c}{4b} + h + \varepsilon \qquad \forall T \geq \widetilde{T}. \qquad \square$$

Combining the two previous results we now obtain

Lemma 2.4.14.
A sufficient condition for the z-species of the GSP food chain model in (2.1.5) *to become extinct is*

$$\frac{c}{4b} < \frac{g}{f} - h.$$

In particular, a necessary condition for persistence of z is given by

$$\frac{g}{f} - h \leq \frac{c}{4b} \quad \Leftrightarrow \quad b \leq \frac{c}{4\left(\frac{g}{f} - h\right)}.$$

Proof.
Let

$$\frac{c}{4b} < \frac{g}{f} - h$$

hold for the parameters in (2.1.5) and assume the assertion is false. In particular, assume that there exists a solution s with $s_0 \in \mathcal{O}^+$ such that

$$\limsup_{t\to\infty} z(t) > 0.$$

This is the only possible case since $z(t) > 0$ for all $t \geq 0$ by Lemma 2.1.5. The solution s fulfils the conditions of Lemma 2.4.12 and 2.4.13 and hence for any given $\varepsilon > 0$ there exists a (sufficiently large) $T > 0$ such that

$$\frac{1}{T}\int_0^T y(t) + h\,dt < \frac{c}{4b} + h + \varepsilon$$
$$\frac{1}{T}\int_0^T \frac{1}{y(t) + h}dt < \frac{f}{g} + \varepsilon$$

holds. Therefore we can apply Lemma 2.4.8 and obtain

$$\left(\frac{c}{4b} + h + \varepsilon\right)\left(\frac{f}{g} + \varepsilon\right) > 1$$

for all $\varepsilon > 0$. Multiplying by $\frac{g}{f} > 0$ on both sides yields

$$\frac{c}{4b} + h + \varepsilon + \frac{\varepsilon g}{f}\left(\frac{c}{4b} + h + \varepsilon\right) > \frac{g}{f}$$

which is in turn equivalent to

$$\frac{c}{4b} > \frac{g}{f} - h - \varepsilon \left[1 + \frac{g}{f} \left(\frac{c}{4b} + h + \varepsilon \right) \right]$$

for all $\varepsilon > 0$. Since $\varepsilon > 0$ can be chosen arbitrarily small ($\varepsilon \searrow 0$), the above implies

$$\frac{c}{4b} \geq \frac{g}{f} - h,$$

which is a contradiction to our parameter assumption and thus the first claim of the lemma is proven. The fact that the above condition is necessary for persistence of z is an immediate consequence of the above result, i.e. else there are solutions (in fact all) that fulfil $\limsup_{t\to\infty} z(t) = 0$. □

The above result enables us to conclude that the global attractor $\mathcal{A}$ is planar while $\frac{c}{4b} < \frac{g}{f} - h$ holds (thus improving the result of Theorem 7 in [Aziz-Alaoui, 2002]):

Lemma 2.4.15.
Let the condition $\frac{c}{4b} < \frac{g}{f} - h$ hold for the parameters in (2.1.5)*. Then the global attractor $\mathcal{A}$ of the semiflow Φ fulfils*

$$\mathcal{A} \subset \left\{ (x, y, z) \in \mathcal{O}_0^+ \,:\, x \leq 1 + \varepsilon,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c},\, z = 0 \right\},$$

with $\varepsilon > 0$. Therefore $\mathcal{A}$ has at most dimension two and is planar.

Proof.
Let the condition $\frac{c}{4b} < \frac{g}{f} - h$ hold for the parameters in (2.1.5) and let any solution s with $s_0 \in \mathcal{O}_0^+$ be given. If $s_0 \in \partial\mathcal{O}_0^+$ then by Lemma 2.4.2 we have

$$\lim_{t\to\infty} z(t) = 0.$$

If $s_0 \in \mathcal{O}^+$ then by Lemma 2.4.14 we have

$$\limsup_{t\to\infty} z(t) = 0.$$

Since $z(t) > 0$ for all $t \geq 0$ we in fact obtain

$$\liminf_{t\to\infty} z(t) = \lim_{t\to\infty} z(t) = \limsup_{t\to\infty} z(t) = 0.$$

Thus any solution s with $s_0 \in \mathcal{O}_0^+$ fulfils

$$\lim_{t\to\infty} z(t) = 0$$

and hence the global attractor (which exists by Theorem 2.3.1) is a subset of the set

$$\mathbb{R}_0^+ \times \mathbb{R}_0^+ \times \{0\}.$$

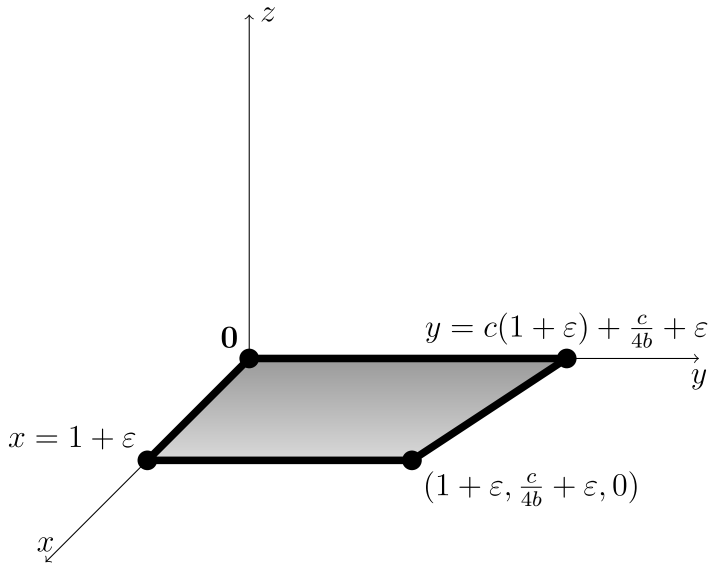


Figure 2.4.12: For $\frac{c}{4b} < \frac{g}{f} - h$ the attractor $\mathcal{A}$ is a subset of the shaded, planar region.

Thus $\mathcal{A}$ is at most planar and has dimension two or less. Furthermore $\mathcal{A}$ fulfils

$$\mathcal{A} \subset \mathcal{C},$$

where the set $\mathcal{C}$ was defined in Lemma 2.3.27 for some $\varepsilon > 0$. Intersecting the two supersets of $\mathcal{A}$ yields

$$\begin{aligned}\mathcal{A} &\subset \mathcal{C} \cap \left(\mathbb{R}_0^+ \times \mathbb{R}_0^+ \times \{0\}\right)\\ &= \left\{(x, y, z) \in \mathcal{O}_0^+ \,:\, x \leq 1 + \varepsilon,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c},\, z = 0\right\}. \qquad \square\end{aligned}$$

Remark 2.4.10.
The set in which the attractor $\mathcal{A}$ is contained for $\frac{c}{4b} < \frac{g}{f} - h$ is depicted in Figure 2.4.12. Dependent on how many equilibria are present in $\mathcal{O}_0^+$ the attractor may have dimension two or reduce to dimension one again, if

$$b \geq \frac{c}{4\left(\frac{g}{f} - h\right)} > \frac{c}{a+1}$$

holds additionally (recall Lemma 2.4.6 and the corresponding Figure 2.4.9). Next we prove that the attractor $\mathcal{A}$ is planar under several other parameter conditions. To this end, we first show a property of the prey species.

Strong persistence of the prey species

We will show that the prey species density modelled by x fulfils:

Lemma 2.4.16.
Let any solution s with $s_0 \in \mathcal{O}^+$ be given. Then s is bounded away from zero in the first component for any time $t \geq 0$, i.e. there exists a $x_m(s_0) = x_m > 0$ such that

$$x(t) \geq x_m \qquad \forall\, t \geq 0.$$

We will show that the above claim holds using several auxiliary results and then proving Lemma 2.4.16 at the end of this subsection. We introduce

Definition 2.4.2.
For $b \leq \frac{c}{a+1}$ we define the non-empty sets

$$\mathcal{S}_1 := \left\{ (x, y, z) \in \mathcal{O}^+ \; : \; x > \frac{x_2^*}{2} = \frac{ab}{2(c-b)} \right\}$$
$$\mathcal{S}_2 := \left\{ (x, y, z) \in \mathcal{O}^+ \; : \; x \leq \frac{x_2^*}{2},\, y > \frac{a}{2} \right\}$$
$$\mathcal{S}_3 := \left\{ (x, y, z) \in \mathcal{O}^+ \; : \; x \leq \frac{x_2^*}{2},\, y \leq \frac{a}{2} \right\}$$

They form a partition of $\mathcal{O}^+$, i.e.

$$\mathcal{O}^+ = \mathcal{S}_1 \,\dot{\cup}\, \mathcal{S}_2 \,\dot{\cup}\, \mathcal{S}_3.$$

Remark 2.4.11.
Note that since $a > 0$ it holds that

$$b \leq \frac{c}{a+1} < c$$

and hence

$$0 < \frac{x_2^*}{2} = \frac{ab}{2(c-b)} \leq \frac{1}{2}.$$

Thus, the sets $\mathcal{S}_1$, $\mathcal{S}_2$ and $\mathcal{S}_3$ are indeed non-empty, have an interior and form a partition of $\mathcal{O}^+$. For a visualisation see Figure 2.4.13.

Notice the similarity of the above definition and Definition 2.2.2. We will use a similar technique for the sets $\mathcal{S}_1$, $\mathcal{S}_2$ and $\mathcal{S}_3$ as we applied to the set Ω_1 to Ω_4 from Definition 2.2.2 We consider the positive phase curve in the disjoint sets $\mathcal{S}_i$. Using the above partition of $\mathcal{O}^+$ we show

Lemma 2.4.17.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M \leq \frac{a}{2}$. Then the first component of s fulfils

$$x(t) \geq \max\left\{ x_0, \frac{x_2^*}{2} \right\} \qquad \forall\, t \geq 0$$

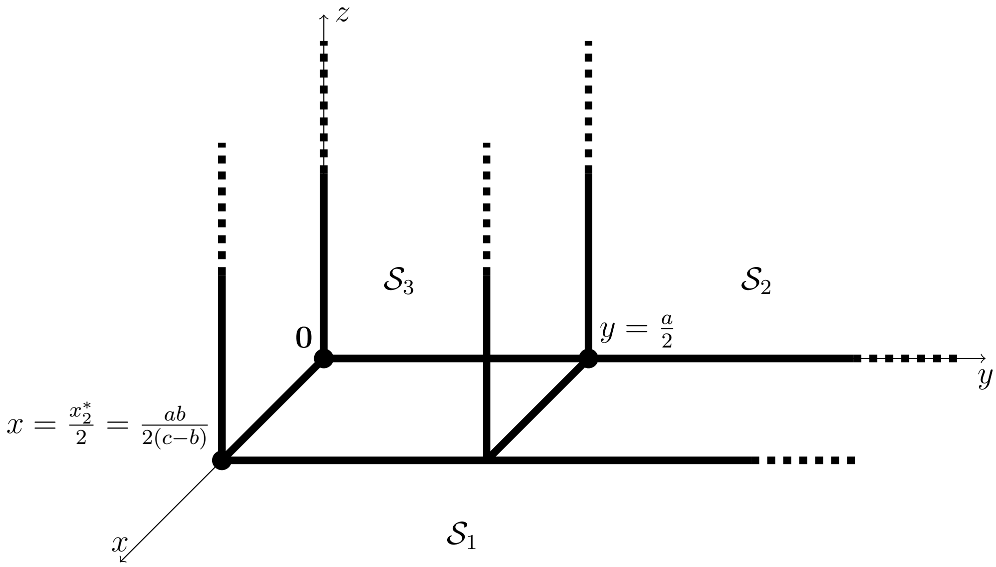


Figure 2.4.13: The sets $\mathcal{S}_1$, $\mathcal{S}_2$ and $\mathcal{S}_3$ in $\mathcal{O}^+$.

Proof.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M \leq \frac{a}{2}$. Since

$$y(t) \leq y_M \leq \frac{a}{2} \qquad \forall\, t \geq 0$$

by Lemma 2.2.3, it holds that $s(t) \in \mathcal{S}_1 \cup \mathcal{S}_3$ for all $t \geq 0$.

- If $s(t) \in \mathcal{S}_1$ for any $t \geq 0$ it fulfils

$$x(t) > \frac{x_2^*}{2}$$

  by the definition of $\mathcal{S}_1$.

- The following estimate holds in $\mathcal{S}_3$:

$$\begin{aligned}\dot{x} &= x(1-x) - \frac{xy}{x+a} \\ &\geq x(1-x) - \frac{\frac{a}{2}x}{x+a} \\ &= \frac{x}{x+a}\left((1-x)(x+a) - \frac{a}{2}\right)\end{aligned}$$

  Since in $\mathcal{S}_3$ it holds that $0 \leq x \leq \frac{x_2^*}{2} \leq \frac{1}{2}$ we can use

$$\min_{x\in\left[0,\frac{1}{2}\right]}\left((1-x)(x+a) - \frac{a}{2}\right) = \min_{x\in\left[0,\frac{1}{2}\right]}\left(-x^2 + (1-a)x + \frac{a}{2}\right) = \min\left\{\frac{1}{4}, \frac{a}{2}\right\} > 0,$$

  to obtain

$$\dot{x} \geq \frac{x}{x+a}\left((1-x)(x+a) - \frac{a}{2}\right) > \frac{x}{x+a} \cdot \min\left\{\frac{1}{4}, \frac{a}{2}\right\} > 0. \tag{2.4.18}$$

Thus the vector field is *strictly increasing in x-direction* in $\mathcal{S}_3$. This includes the boundary between $\mathcal{S}_1$ and $\mathcal{S}_3$ (see the green arrows in Figure 2.4.14, the projection merely simplifies the visualisation). Hence the solution s will not enter $\mathcal{S}_3$ via this boundary. Since

$$s(t) \in \mathcal{S}_1 \cup \mathcal{S}_3 \qquad \forall\, t \geq 0$$

holds, we either have $s(t) \in \mathcal{S}_1$ for all $t \geq 0$ or $s_0 \in \mathcal{S}_3$. The first case we already dealt with above. In the second case we know by (2.4.18) that the vector field is strictly increasing in x-direction in $\mathcal{S}_3$, and therefore for the first component of s we have

$$x(t) \geq x_0,$$

for any $t \geq 0$ such that $s(t) \in \mathcal{S}_3$.

Combining the above results we obtain

$$x(t) \geq \max\left\{x_0, \frac{x_2^*}{2}\right\} \qquad \forall\, t \geq 0. \qquad \square$$

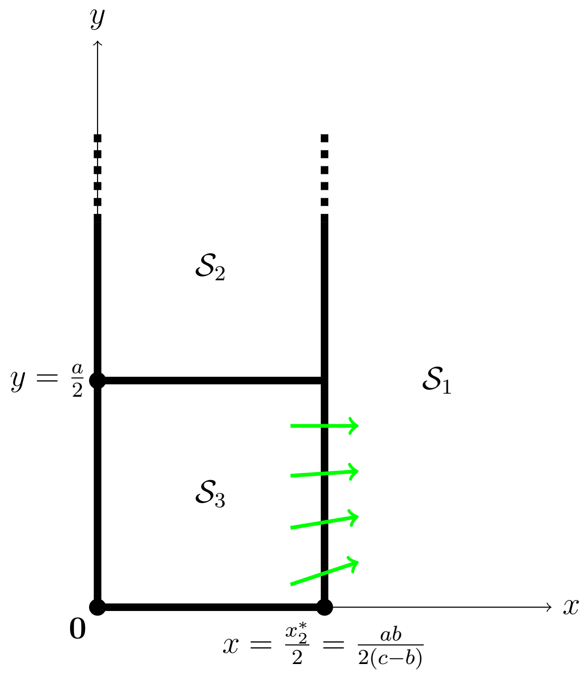


Figure 2.4.14: An x-y-plane projection of the sets $\mathcal{S}_1$, $\mathcal{S}_2$ and $\mathcal{S}_3$ and the direction of the vector field on the common boundary of $\mathcal{S}_1$ and $\mathcal{S}_3$.

We now consider the case $y_M > \frac{a}{2}$, which will prove to be more technical. We introduce the time $T_{\mathcal{S}_2}$ in the following

Lemma 2.4.18.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. Define the time

$$T_{\mathcal{S}_2} := \frac{1}{K_{\mathcal{S}}} \ln\left(\frac{a}{2y_M}\right),$$

where

$$K_{\mathcal{S}} := -b + \frac{c\frac{x_2^*}{2}}{\frac{x_2^*}{2} + a} = -b + \frac{cx_2^*}{x_2^* + 2a}.$$

Then it holds that $K_{\mathcal{S}} < 0$ and $T_{\mathcal{S}_2} > 0$.

Proof.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. Consider the following equivalence for $x > 0$ (using $c - b > 0$)

$$-b + \frac{cx}{x+a} \overset{!}{<} 0 \quad \Leftrightarrow \quad cx < b(x+a) \quad \Leftrightarrow \quad x < \frac{ab}{c-b} = x_2^*.$$

Since $0 < \frac{x_2^*}{2} = \frac{ab}{2(c-b)} < \frac{ab}{c-b} = x_2^*$ the above implies

$$K_{\mathcal{S}} := -b + \frac{c\frac{x_2^*}{2}}{\frac{x_2^*}{2} + a} < 0.$$

Furthermore we have

$$y_M > \frac{a}{2} \quad \Leftrightarrow \quad 1 > \frac{a}{2y_M},$$

implying

$$T_{\mathcal{S}_2} = \underbrace{\frac{1}{K_{\mathcal{S}}}}_{<0} \underbrace{\ln\left(\frac{a}{2y_M}\right)}_{<0} > 0.$$ □

We make use of the above result to prove

Lemma 2.4.19.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. The maximal length of a time interval for which s is contained in $\mathcal{S}_2$ is at most $T_{\mathcal{S}_2}$ (from Lemma 2.4.18), i.e. for any $T \geq 0$ there exists a $t \in [T, T + T_{\mathcal{S}_2}]$ such that $s(t) \notin \mathcal{S}_2$.

Proof.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. We provide a proof by contradiction, and hence we assume there exists a $T \geq 0$ such that

$$s(t) \in \mathcal{S}_2 \qquad \forall\, t \in [T, T + T_{\mathcal{S}_2}].$$

By the definition of $\mathcal{S}_2$ the above implies for all $t \in [T, T + T_{\mathcal{S}_2}]$ that

$$y(t) > \frac{a}{2} \quad \text{and} \quad x(t) \leq \frac{x_2^*}{2}.$$

Using the above and considering the $\dot{y}$-equation in (2.1.5) we conclude that for all $t \in [T, T + T_{\mathcal{S}_2}]$ it holds that

$$\frac{\dot{y}}{y} = -b + \frac{cx}{x+a} - \frac{z}{y+e} \leq -b + \frac{c\frac{x_2^*}{2}}{\frac{x_2^*}{2} + a} = K_{\mathcal{S}},$$

where $K_{\mathcal{S}}$ is defined in Lemma 2.4.18. Integrating the above from T to $T + T_{\mathcal{S}_2}$ and inserting the definition of $T_{\mathcal{S}_2} > 0$ yields

$$\int_T^{T+T_{\mathcal{S}_2}} \frac{\dot{y}(\tau)}{y(\tau)} d\tau = \ln\left(\frac{y(T+T_{\mathcal{S}_2})}{y(T)}\right) \leq K_{\mathcal{S}}(T + T_{\mathcal{S}_2} - T) = K_{\mathcal{S}} T_{\mathcal{S}_2} = \ln\left(\frac{a}{2y_M}\right).$$

Applying the exponential function and multiplying by $y(T) > 0$ on both sides of the above inequality yields

$$y(T + T_{\mathcal{S}_2}) \leq \frac{ay(T)}{2y_M}.$$

Since $y(T) \leq y_M$ for any $T \geq 0$ (see Lemma 2.2.3), the above yields

$$y(T + T_{\mathcal{S}_2}) \leq \frac{ay(T)}{2Y_M} \leq \frac{ay_M}{2y_M} = \frac{a}{2}.$$

This however is a contradiction to $y(t) > \frac{a}{2}$ for all $t \in [T, T + T_{\mathcal{S}_2}]$. □

The next auxiliary result we prove is

Lemma 2.4.20.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. For any $t \geq 0$ the positive phase curve corresponding to s can only enter the set $\mathcal{S}_2$ via the common boundary part of $\mathcal{S}_1$ and $\mathcal{S}_2$. In particular any solution (curve) entering $\mathcal{S}_2$ fulfils $x(t) = \frac{x_2^*}{2}$ at the entrance time $t \geq 0$.

Proof.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. We want to show that s may only enter $\mathcal{S}_2$ via the common boundary part of $\mathcal{S}_1$ and $\mathcal{S}_2$. We show this by proving that s cannot enter $\mathcal{S}_2$ via any *other part* of the boundary of $\mathcal{S}_2$. Indeed, since

$$s_0 \in \mathcal{O}^+ \qquad \Rightarrow \qquad s(t) \in \mathcal{O}^+ \quad \forall\, t \geq 0,$$

the positive phase curve to s cannot enter $\mathcal{S}_2$ via any common boundary part with the coordinate planes. The positive phase curve to s does not enter them for any finite time. The only boundary part remaining is the common boundary part of $\mathcal{S}_2$ and $\mathcal{S}_3$. We call this set

$$B_{\mathcal{S}} := \left\{(x,y,z) \in \mathcal{O}^+ \,:\, x \leq \frac{x_2^*}{2},\, y = \frac{a}{2}\right\},$$

see Figure 2.4.15.

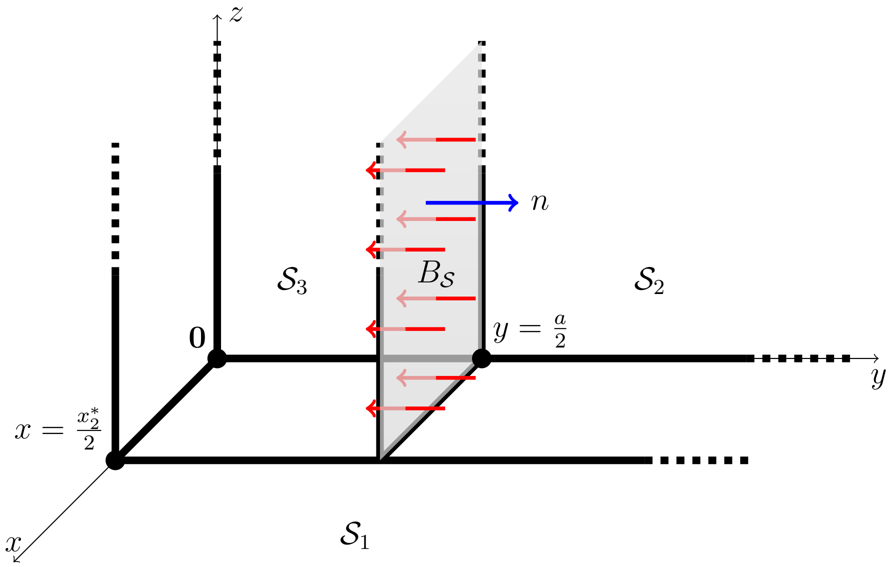


Figure 2.4.15: The common boundary part $B_{\mathcal{S}}$, the normal vector n (blue) and the schematic vector field (red).

Here it holds that

$$x \leq \frac{x_2^*}{2} \quad \text{and} \quad y = \frac{a}{2}.$$

Thus we can use the normal vector $n = (0, 1, 0)^T$ of the common boundary part $B_{\mathcal{S}}$ (see Figure 2.4.15) to obtain

$$\begin{aligned} \left\langle \begin{pmatrix} 0 \\ 1 \\ 0 \end{pmatrix}, \begin{pmatrix} \dot{x} \\ \dot{y} \\ \dot{z} \end{pmatrix} \right\rangle = \dot{y} &= \left(-b + \frac{cx}{x+a} - \frac{z}{y+e} \right) y \\ &\leq \left(-b + \frac{cx}{x+a} \right) y \\ &= \left(-b + \frac{cx}{x+a} \right) \frac{a}{2} \\ &\leq \underbrace{\left(-b + \frac{c\frac{x_2^*}{2}}{\frac{x_2^*}{2} + a} \right)}_{=K_{\mathcal{S}}<0 \text{ from Lemma 2.4.18}} \frac{a}{2} = K_{\mathcal{S}} \frac{a}{2} < 0. \end{aligned}$$

Hence the vector field v points out of $\mathcal{S}_2$ in the set $B_{\mathcal{S}}$ (see the red arrows in Figure 2.4.15) and no positive phase curve can enter $\mathcal{S}_2$ via this boundary part. Therefore, the only remaining boundary part is the common boundary of $\mathcal{S}_1$ and $\mathcal{S}_2$ where $x = \frac{x_2^*}{2}$ holds. □

The two previous lemmas allow us to prove

Lemma 2.4.21.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. There is a positive

minimal value that the first component of s can attain while in $\mathcal{S}_2$. More precisely, for any $t \geq 0$ such that $s(t) \in \mathcal{S}_2$ it holds that

$$x(t) > \min\left\{x_0, \frac{x_2^*}{2}\right\}\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}} > 0$$

Proof.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. By Lemma 2.4.19 the positive phase curve to s cannot be in $\mathcal{S}_2$ longer than the time $T_{\mathcal{S}_2}$. We determine the maximal decrease of the first component of s in this time span. In $\mathcal{S}_2$ it holds that

$$\dot{x} = \underbrace{x(1-x)}_{>0} - \frac{xy}{x+a} > -\frac{xy}{x+a} > -\frac{y_M}{a}x \tag{2.4.19}$$

Now if the positive phase curve corresponding to s is in $\mathcal{S}_2$ then it either commenced in $\mathcal{S}_2$ (i.e. $s_0 \in \mathcal{S}_2$) or entered it via the common boundary of $\mathcal{S}_1$ and $\mathcal{S}_2$ (see Lemma 2.4.20, in particular $x(T_E) = \frac{x_2^*}{2}$ at the entrance time $T_E \geq 0$).

- In the first case (i.e. $s_0 \in \mathcal{S}_2$) separation of variables and integration of (2.4.19) from zero to $t \in [0, T_{\mathcal{S}_2}]$ yields

$$\ln\left(\frac{x(t)}{x_0}\right) > -\frac{y_M}{a}t \geq -\frac{y_M}{a}T_{\mathcal{S}_2} = -\frac{y_M}{a}\frac{1}{K_{\mathcal{S}}}\ln\left(\frac{a}{2y_M}\right) = \ln\left(\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}}\right)$$

  Solving the above for $x(t)$ yields that for any $t \in [0, T_{\mathcal{S}_2}]$ it holds that

$$x(t) > x_0\left(\frac{2y_M}{a}\right)^{\frac{aK_{\mathcal{S}}}{y_M}}$$

- In the second case we have an entrance time $T_E \geq 0$ for which $x(T_E) = \frac{x_2^*}{2}$ holds. The positive phase curve of s leaves the set $\mathcal{S}$ for some time t in the interval $[T_E, T_E + T_{\mathcal{S}_2}]$. Once more we can approximate the maximal decay of the first component by separation of variables and integration of (2.4.19) from T_E to $t \in [T_E, T_E + T_{\mathcal{S}_2}]$:

$$\ln\left(\frac{x(t)}{x(T_E)}\right) > -\frac{y_M}{a}(t - T_E) \geq -\frac{y_M}{a}T_{\mathcal{S}_2} = \ln\left(\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}}\right).$$

  We solve the above for $x(t)$ recalling that $x(T_E) = \frac{x_2^*}{2}$ obtaining for any $t \in [T_E, T_E + T_{\mathcal{S}_2}]$ that

$$x(t) > \frac{x_2^*}{2}\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}}$$

Combining the above results we obtain that for any $t \geq 0$ such that $s(t) \in \mathcal{S}_2$ it holds that

$$x(t) > \min\left\{x_0, \frac{x_2^*}{2}\right\}\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}}.$$

□

The above allows us to 'control' the x-component of a solution s if its positive phase curve is in $\mathcal{S}_2$. We now need to do the same for the sets $\mathcal{S}_1$ and $\mathcal{S}_3$, which will prove less technical.

Lemma 2.4.22.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. There is a positive minimal value that the first component of s can attain while in $\mathcal{S}_3$. More precisely, for any $t \geq 0$ such that $s(t) \in \mathcal{S}_3$ it holds that

$$x(t) \geq \min\left\{x_0, \frac{x_2^*}{2}\right\}\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}} > 0$$

Proof.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. Recall that by (2.4.18) the following estimate holds in $\mathcal{S}_3$:

$$\dot{x} \geq \frac{x}{x+a}\left((1-x)(x+a) - \frac{a}{2}\right) > \frac{x}{x+a} \cdot \min\left\{\frac{1}{4}, \frac{a}{2}\right\} > 0.$$

Thus while the positive phase curve corresponding to s is in $\mathcal{S}_3$ the first component of s is monotonically increasing. In particular the minimal value that the first component of s can attain in $\mathcal{S}_3$ is either the initial value x_0 if $s_0 \in \mathcal{S}_3$ or the entrance value.

- For $s_0 \in \mathcal{S}_3$ we obtain $x(t) \geq x_0$ while $s(t) \in \mathcal{S}_3$. Since $y_M > \frac{a}{2}$ and $K_{\mathcal{S}} < 0$ it holds that

$$0 < \left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}} = \underbrace{\left(\frac{a}{2y_M}\right)}_{<1}^{\overbrace{-\frac{y_M}{aK_{\mathcal{S}}}}^{>0}} < 1$$

  allowing the estimate

$$x(t) \geq x_0 \geq x_0\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}}$$

- Now consider the case that s enters $\mathcal{S}_3$. From Figure 2.4.14 we see that s may only enter $\mathcal{S}_3$ via the common boundary of $\mathcal{S}_2$ and $\mathcal{S}_3$, i.e. the set $B_{\mathcal{S}}$ (see Figure 2.4.15). Thus, the previous Lemma 2.4.21 yields the minimal entrance value and lower bound to the first component of s while in $\mathcal{S}_3$:

$$x(t) \geq \min\left\{x_0, \frac{x_2^*}{2}\right\}\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}}.$$

Combining the above results we obtain that for any $t \geq 0$ such that $s(t) \in \mathcal{S}_3$ it holds that

$$x(t) \geq \min\left\{x_0, \frac{x_2^*}{2}\right\}\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}}.$$

□

The estimate for the set $\mathcal{S}_1$ is very simple:

Lemma 2.4.23.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. There is a minimal positive value that the first component of s can attain while in $\mathcal{S}_1$. More precisely, for any $t \geq 0$ such that $s(t) \in \mathcal{S}_1$ it holds that

$$x(t) > \min\left\{x_0, \frac{x_2^*}{2}\right\}\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}} > 0$$

Proof.
Let $b \leq \frac{c}{a+1}$ and s be a solution such that $s_0 \in \mathcal{O}^+$ and $y_M > \frac{a}{2}$. If $s(t) \in \mathcal{S}_1$ for some $t \geq 0$ then by definition of $\mathcal{S}_1$ it holds that $x(t) > \frac{x_2^*}{2}$. Since $y_M > \frac{a}{2}$ and $K_{\mathcal{S}} < 0$ it holds that

$$0 < \left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}} = \underbrace{\left(\frac{a}{2y_M}\right)}_{<1}^{\overbrace{-\frac{y_M}{aK_{\mathcal{S}}}}^{>0}} < 1$$

allowing the estimate

$$x(t) > \frac{x_2^*}{2} \geq \min\left\{x_0, \frac{x_2^*}{2}\right\}\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}}$$

for any $t \geq 0$ such that $s(t) \in \mathcal{S}_1$. □

The above results now enables us to prove the claim of Lemma 2.4.16.

Proof of Lemma 2.4.16.
Let any solution s with $s_0 \in \mathcal{O}^+$ be given. If $b > \frac{c}{a+1}$ then by Lemma 2.4.6 the equilibrium p_1^* is globally asymptotically stable in $\mathcal{O}^+$ (in the sense of Remark 2.4.3) and hence

$$\lim_{t\to\infty} x(t) = x_1^* = 1.$$

Thus

$$\liminf_{t\to\infty} x(t) = 1 > 0,$$

yielding the claim for $b > \frac{c}{a+1}$.
If $b \leq \frac{c}{a+1}$ and any solution s with $s_0 \in \mathcal{O}^+$ is given, then:

- Assume $y_M \leq \frac{a}{2}$ then by Lemma 2.4.17 we have

$$x(t) \geq \max\left\{x_0, \frac{x_2^*}{2}\right\} \qquad \forall\, t \geq 0.$$

- Assume $y_M > \frac{a}{2}$ and note that since $s_0 \in \mathcal{O}^+$ we have

$$s(t) \in \mathcal{O}^+ = \mathcal{S}_1 \,\dot{\cup}\, \mathcal{S}_2 \,\dot{\cup}\, \mathcal{S}_3 \quad \forall\, t \geq 0.$$

In particular the positive phase curve corresponding to s is contained in either of the three sets $\mathcal{S}_1$, $\mathcal{S}_2$ and $\mathcal{S}_3$. Thus combining Lemmas 2.4.21, 2.4.22 and 2.4.23 yields

$$x(t) \geq \min\left\{x_0, \frac{x_2^*}{2}\right\}\left(\frac{2y_M}{a}\right)^{\frac{y_M}{aK_{\mathcal{S}}}} \quad \forall\, t \geq 0. \qquad \square$$

Remark 2.4.12.
Note that the result of Lemma 2.4.16 implies that for any solution s with $s_0 \in \mathcal{O}^+$ we have

$$\limsup_{t\to\infty} x(t) \geq x_m(s_0) > 0.$$

Hence the x-species persists (compare to Definition 2.4.1). Moreover, the result even implies that

$$\liminf_{t\to\infty} x(t) \geq x_m(s_0) > 0.$$

This property is known as **strong persistence** of the species x in a food chain (cf. [Muratori and Rinaldi, 1992] for example).

Estimates

The strong persistence property of the x-species allows us to prove estimates similar to the one in Lemma 2.4.13:

Lemma 2.4.24.
Let s be a solution with $s_0 \in \mathcal{O}^+$. Then for any $\varepsilon > 0$ there exists a $\widetilde{T} > 0$ such that

$$\frac{1}{T}\int_0^T y(t) + h\,dt < \frac{(a+1)^2}{4} + h + \varepsilon \qquad \forall\, T \geq \widetilde{T}.$$

Furthermore, if $a > 1$ then for any $\varepsilon > 0$ there exists a $\widetilde{T} > 0$ such that

$$\frac{1}{T}\int_0^T y(t) + h\,dt < a + h + \varepsilon \qquad \forall\, T \geq \widetilde{T}.$$

Proof.
Let s be a solution with $s_0 \in \mathcal{O}^+$. It holds that

$$\dot{x} = x(1-x) - \frac{xy}{x+a} \quad \Leftrightarrow \quad \frac{\dot{x}(x+a)}{x} = (1-x)(x+a) - y$$
$$\Leftrightarrow \quad y = (1-x)(x+a) - \left[\dot{x} + \frac{\dot{x}}{x}a\right]$$

Recall that $\max_{x\in\mathbb{R}}(1-x)(x+a) = \frac{(1+a)^2}{4}$ (see Figure 2.4.2) and hence

$$y = (1-x)(x+a) - \left[\dot{x} + \frac{\dot{x}}{x}a\right] \leq \frac{(1+a)^2}{4} - \left[\dot{x} + \frac{\dot{x}}{x}a\right] \qquad (2.4.20)$$

Adding the term h on both sides results in

$$y + h \leq \frac{(a+1)^2}{4} + h - \left[\dot{x} + \frac{\dot{x}}{x} a\right].$$

Integration of the above from zero to $T > 0$ yields

$$\int_0^T y(t) + h \, dt \leq \left(\frac{(a+1)^2}{4} + h\right) T - \left[x(T) - x_0 + \ln\left(\frac{x(T)}{x_0}\right)\right].$$

By dividing by $T > 0$ we obtain

$$\frac{1}{T}\int_0^T y(t) + h \, dt \leq \frac{(a+1)^2}{4} + h - \frac{1}{T}\left[x(T) - x_0 + \ln\left(\frac{x(T)}{x_0}\right)\right]. \tag{2.4.21}$$

Since by Lemmas 2.2.1 and 2.4.16 we have

$$0 < x_m(s_0) \leq x(t) \leq x_M(s_0) \qquad \forall\, t \geq 0$$

we can in particular estimate for $t = T$, that

$$x_m - x_0 + \ln\left(\frac{x_m}{x_0}\right) \leq x(T) - x_0 + \ln\left(\frac{x(T)}{x_0}\right) \leq x_M - x_0 + \ln\left(\frac{x_M}{x_0}\right)$$

Thus the middle term in the above inequality is bounded by constants (which are independent of T) from above and below for any $T \geq 0$. In particular for any given $\varepsilon > 0$ there exists a (sufficiently large) $\widetilde{T} \geq 0$ such that

$$\frac{1}{T}\left|x(T) - x_0 + \ln\left(\tfrac{x(T)}{x_0}\right)\right| < \varepsilon \qquad \forall\, T \geq \widetilde{T}.$$

For estimate (2.4.21) this implies

$$\begin{aligned}\frac{1}{T}\int_0^T y(t) + h \, dt &\leq \frac{(a+1)^2}{4} + h - \frac{1}{T}\left[x(T) - x_0 + \ln\left(\frac{x(T)}{x_0}\right)\right] \\ &\leq \frac{(a+1)^2}{4} + h + \frac{1}{T}\left|x(T) - x_0 + \ln\left(\tfrac{x(T)}{x_0}\right)\right| \\ &< \frac{(a+1)^2}{4} + h + \varepsilon\end{aligned}$$

for all $T \geq \widetilde{T}$, thus proving the first part of the lemma. Now we additionally assume that $a > 1$. This implies

$$\max_{x \geq 0}(1 - x)(x + a) = a$$

- see Figure 2.4.16 -, allowing us to modify the estimate (2.4.20) as follows:

$$y = (1 - x)(x + a) - \left[\dot{x} + \frac{\dot{x}}{x} a\right] \leq a - \left[\dot{x} + \frac{\dot{x}}{x} a\right].$$

Following the same line of argumentation as above we obtain

$$\frac{1}{T}\int_0^T y(t) + h \, dt < a + h + \varepsilon \qquad \forall\, T \geq \widetilde{T}.$$

□

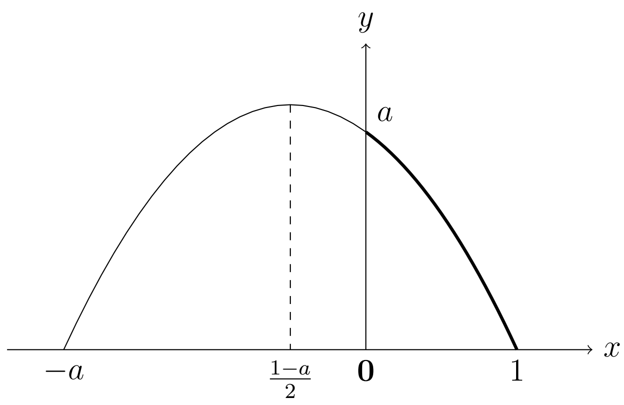


Figure 2.4.16: For $a > 1$ it holds that $\max_{x\geq 0}(1-x)(x+a) = a$.

The above yields further sufficient conditions under which the z-species will become extinct.

Lemma 2.4.25.
A sufficient condition for the z-species of the GSP food chain model in (2.1.5) *to become extinct is*

$$\frac{(a+1)^2}{4} < \frac{g}{f} - h.$$

and additionally if $a > 1$ then

$$a < \frac{g}{f} - h$$

is sufficient. In particular, a necessary condition for persistence of z is given by

$$\frac{g}{f} - h \leq \frac{(a+1)^2}{4} \quad \Leftrightarrow \quad a \geq 2\sqrt{\frac{g}{f} - h} - 1.$$

Proof.
Let

$$\frac{(a+1)^2}{4} < \frac{g}{f} - h$$

hold for the parameters in (2.1.5) and assume the assertion is false. In particular, assume that there exists a solution s with $s_0 \in \mathcal{O}^+$ such that

$$\limsup_{t\to\infty} z(t) > 0.$$

Note that this is the only possible case since $z(t) > 0$ for any $t \geq 0$ by Lemma 2.1.5. The solution s fulfils the conditions of Lemma 2.4.12 and 2.4.24 and hence for any given $\varepsilon > 0$ there exists a (sufficiently large) $T > 0$ such that

$$\frac{1}{T}\int_0^T y(t) + h\,dt < \frac{(a+1)^2}{4} + h + \varepsilon$$
$$\frac{1}{T}\int_0^T \frac{1}{y(t)+h}dt < \frac{f}{g} + \varepsilon$$

holds. Therefore we can apply Lemma 2.4.8 and obtain

$$\left(\frac{(a+1)^2}{4}+h+\varepsilon\right)\left(\frac{f}{g}+\varepsilon\right)>1$$

for all $\varepsilon > 0$. Multiplying by $\frac{g}{f} > 0$ on both sides, yields

$$\frac{(a+1)^2}{4}+h+\varepsilon+\frac{\varepsilon g}{f}\left(\frac{(a+1)^2}{4}+h+\varepsilon\right)>\frac{g}{f}$$

which is in turn equivalent to

$$\frac{(a+1)^2}{4}>\frac{g}{f}-h-\varepsilon\left[1+\frac{g}{f}\left(\frac{(a+1)^2}{4}+h+\varepsilon\right)\right]$$

for all $\varepsilon > 0$. Since $\varepsilon > 0$ can be chosen arbitrarily small ($\varepsilon \searrow 0$), the above implies

$$\frac{(a+1)^2}{4}\geq\frac{g}{f}-h,$$

which is a contradiction to our parameter assumption and thus the first claim of the lemma is proven. The case $a > 1$ is treated in an analogous way. Since $f - \frac{g}{h} < 0$ it holds that

$$\frac{g}{f}-h\leq\frac{(a+1)^2}{4} \quad\Leftrightarrow\quad a\geq 2\sqrt{\frac{g}{f}-h}-1.$$

Therefore the above condition is a necessary one for persistence of z, since else there are solutions (in fact all) that fulfil $\limsup_{t\to\infty} z(t) = 0$. □

Remark 2.4.13.
Note that this result is a generalisation of Corollary 2.4.1 because we have shown that under the condition

$$\frac{(a+1)^2}{4}<\frac{g}{f}-h$$

any solution s with $s_0 \in \mathcal{O}^+$ fulfils

$$\limsup_{t\to\infty} z(t)=0,$$

which in particular implies that s cannot be periodic.

Characterising the global attractor $\mathcal{A}$

Thus we have the following result, characterising $\mathcal{A}$:

Theorem 2.4.1.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold for the parameters in (2.1.5) *and consider the corresponding semiflow Φ on $\mathcal{O}_0^+$. Then the global attractor $\mathcal{A}$ of Φ has the following properties:*

i) If $b > \frac{c}{a+1}$ *then*

$$\mathcal{A} = [0,1] \times \{0\} \times \{0\}$$

and thus $\mathcal{A}$ *has dimension one. The equilibrium* p_1^* *is globally asymptotically stable in* $\mathcal{O}^+$*. A biological interpretation of this is that the* y*-species and the* z*-species become extinct and the* x*-species is the sole survivor (except if its initial density is zero, i.e.* $x_0 = 0$*).*

ii) If any one of the following conditions holds

- $\frac{c}{4\left(\frac{g}{f}-h\right)} < b$
- $\frac{(a+1)^2}{4} < \frac{g}{f} - h$
- $1 < a < \frac{g}{f} - h$

then $\mathcal{A}$ *fulfils*

$$\mathcal{A} \subset \left\{(x,y,z) \in \mathcal{O}_0^+ \,:\, x \leq 1+\varepsilon,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c},\, z = 0\right\},$$

for any $\varepsilon > 0$*. In particular* $\mathcal{A}$ *has at most dimension two and is planar. A biological interpretation of this is that the* z*-species becomes extinct.*

If additionally to one of the above conditions it holds that

$$\frac{c(1-a)}{a+1} < b < \frac{c}{a+1},$$

then the equilibrium p_2^* *is globally asymptotically stable in* $\mathcal{O}^+$*. A biological interpretation of this is that the* x*-species and* y*-species tend to a state of coexistence, if both their initial densities are non-zero, i.e.* $x_0 \neq 0 \neq y_0$*.*

Proof.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold for the parameters in (2.1.5) and consider the corresponding semiflow Φ on $\mathcal{O}_0^+$. By Theorem 2.3.1 the global attractor $\mathcal{A}$ exists. We show the above claim for this global attractor $\mathcal{A}$ of Φ:

i) This is the result of Lemma 2.4.6 and the subsequent remark.

ii) The case

$$\frac{c}{4\left(\frac{g}{f}-h\right)} < b \qquad \Leftrightarrow \qquad \frac{c}{4b} < \frac{g}{f} - h$$

was considered in Lemma 2.4.15. For the other two cases we have shown in Lemma 2.4.25 that

$$\limsup_{t\to\infty} z(t) = 0$$

and hence also

$$\lim_{t\to\infty} z(t) = 0.$$

By analogous arguments to the proof of Lemma 2.4.15 we obtain the claim.

If we additionally assume that

$$\frac{c(1-a)}{a+1} < b < \frac{c}{a+1}$$

holds, then the only limit points in the non-negative x-y-quadrant (and thus also in the *planar* attractor) are the equilibria p_0^*, p_1^* and p_2^* (see Lemma 2.4.2). Since p_0^* and p_1^* are unstable (Lemmas 2.4.3 and 2.4.4), it follows that p_2^* (which is already locally asymptotically stable by Lemma 2.4.7) is globally asymptotically stable in $\mathcal{O}^+$ (in the sense of Remark 2.4.3). □

Remark 2.4.14.
In the subsequent remarks to Lemmas 2.4.6 and 2.4.15 we visualised the attractor set $\mathcal{A}$ for the respective parameter values (Figures 2.4.9 and 2.4.12). Indeed, for any one of the three conditions in case *ii*) of Theorem 2.4.1 the attractor is contained in the set depicted in Figure 2.4.12. If additionally the condition

$$\frac{c(1-a)}{a+1} < b < \frac{c}{a+1}$$

holds, we may characterise the set $\mathcal{A}$ further. Indeed, we know that the equilibrium p_2^* is globally asymptotically stable in $\mathcal{O}^+$, i.e. any solution s with $s_0 \in \mathcal{O}^+$ has the property

$$\lim_{t\to\infty} s(t) \to p_2^*.$$

Since we have also covered all the cases in the boundary of $\mathcal{O}_0^+$ in Lemma 2.4.2 we characterise $\mathcal{A}$ precisely. It consists of the equilibria p_0^*, p_1^* and p_2^* and the heteroclinic orbits connecting p_0^* and p_1^* and p_1^* and p_2^* respectively, see Figure 2.4.17. There can be no heteroclinic connection between p_0^* and p_2^*, since p_0^* only has a single unstable direction (the centre direction on $W^c_{loc}(p_0^*)$ is weakly stable by Lemma 2.4.3 and the subsequent Figure 2.4.5) causing the heteroclinic orbit with p_1^*. If on the other hand the condition

$$b < \frac{c(1-a)}{a+1}$$

holds, then we know by Lemma 2.4.2 that there is an additional periodic orbit Γ^*_{per} in the positive x-y-quadrant, which must also be at least part of $\mathcal{A}$ - see Figure 2.4.18. Furthermore, $\mathcal{A}$ is still connected.

It is worth noting that the conditions

$$\frac{(a+1)^2}{4} < \frac{g}{f} - h \qquad \text{and} \qquad 1 < a < \frac{g}{f} - h$$

are both sharp sufficient conditions for $p_{3+}^* \notin \mathcal{O}_0^+$ (recall Table 1). The question arises whether

$$b > b_{3+}^* = \frac{c x_{3+}^*}{x_{3+}^* + a},$$

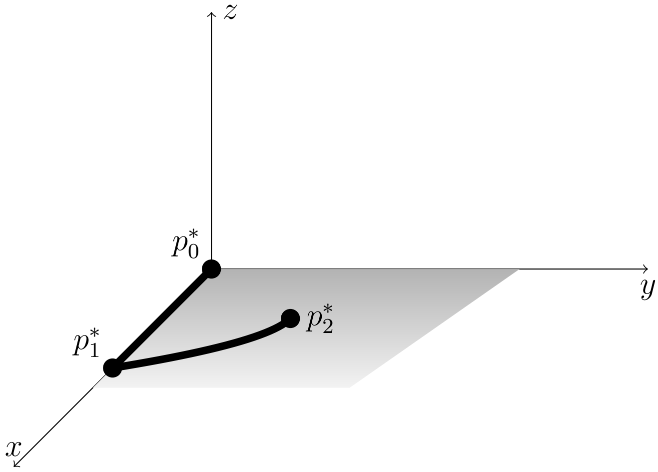


Figure 2.4.17: The planar attractor $\mathcal{A}$ for case $ii)$ in Theorem 2.4.1 and $\frac{c(1-a)}{a+1} < b < \frac{c}{a+1}$.

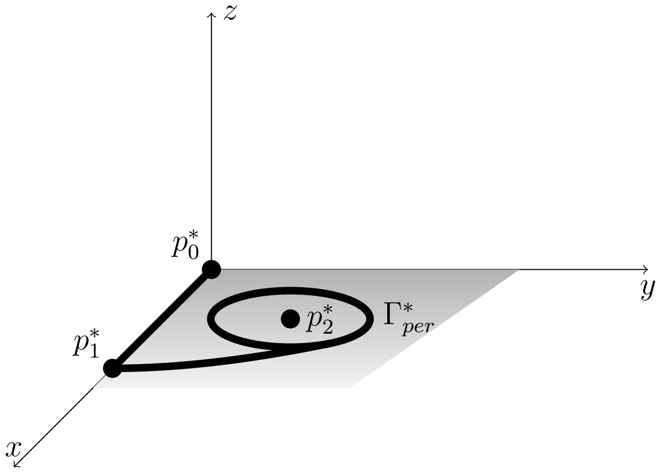


Figure 2.4.18: A subset of the planar attractor $\mathcal{A}$ for case $ii)$ in Theorem 2.4.1 and $b < \frac{c(1-a)}{a+1}$.

being the third condition for which $p_{3+}^* \notin \mathcal{O}_0^+$ holds (see Table 1), is also a sufficient condition for the extinction of the z-species and a planar attractor $\mathcal{A}$. This leads to the following

Conjecture 2.4.1.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold for the parameters in (2.1.5) *and consider the corresponding semiflow Φ on $\mathcal{O}_0^+$. If the equilibrium p_{3+}^* fulfils $p_{3+}^* \notin \mathcal{O}_0^+$, then the global attractor $\mathcal{A}$ of Φ is planar and fulfils*

$$\mathcal{A} \subset \left\{(x, y, z) \in \mathcal{O}_0^+ \,:\, x \leq 1 + \varepsilon,\, x + \frac{y}{c} \leq 1 + \varepsilon + \frac{1}{4b} + \frac{\varepsilon}{c},\, z = 0\right\}$$

for an $\varepsilon > 0$. If on the contrary $p_{3+}^* \in \mathcal{O}^+$ holds, then $\mathcal{A}$ cannot be planar.

Remark 2.4.15.
Note that the second part of the conjecture is true since $p^*_{3+} \in \mathcal{O}^+$ implies that the additional equilibrium is in the positive octant. I.e. at least the four equilibria p^*_0, p^*_1, p^*_2 and p^*_{3+} are contained in the attractor and additionally $\mathcal{A}$ is connected. Since these points do not lie in one plane, the set $\mathcal{A}$ cannot be planar (see Figure 2.4.19).

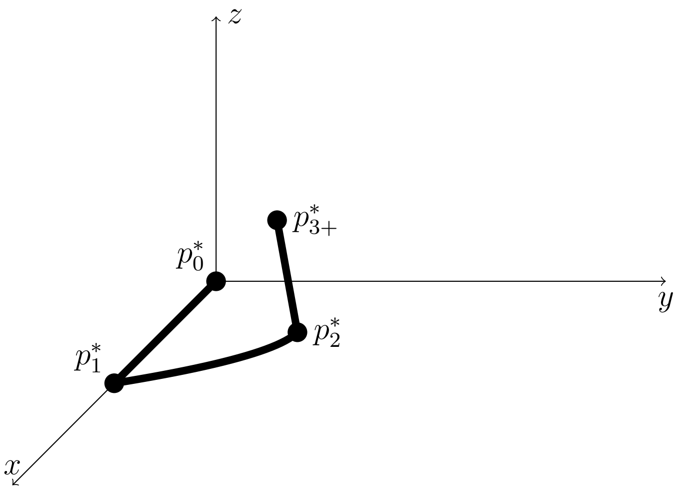


Figure 2.4.19: The case $p^*_{3+} \in \mathcal{O}^+$: The attractor $\mathcal{A}$ is a superset of the depicted set.

Concerning the first part of the conjecture, we have that $p^*_{3+} \notin \mathcal{O}^+_0$ if any of the following conditions hold (see Table 1):

- $a < 2\sqrt{\frac{g}{f} - h} - 1$ which is equivalent to

$$\frac{(1+a)^2}{4} < \frac{g}{f} - h$$

- $1 < a < \frac{g}{f} - h$
- $b > b^*_{3+} = \frac{cx^*_{3+}}{x^*_{3+}+a}$

If either of the first two conditions are fulfilled, then Theorem 2.4.1 immediately yields the claim. The third condition, i.e. $b > b^*_{3+}$, needs to be considered more closely:

Wanting to apply the same technique as in the previous cases, we obtain the following

Lemma 2.4.26.
Let $b \leq \frac{c}{a+1}$ and any solution s with $s_0 \in \mathcal{O}^+$ be given. Assume that for any given $\varepsilon > 0$ there exists a $\widetilde{T} > 0$ such that

$$\frac{1}{T}\int_0^T y(t) + h\,dt \leq y^*_2 + h + \varepsilon = (1 - x^*_2)(x^*_2 + a) + h + \varepsilon \qquad \forall\, T \geq \widetilde{T}, \quad (2.4.22)$$

then a sufficient condition for the z-species of the GSP food chain model in (2.1.5) *to become extinct is*

$$b > b_{3+}^*.$$

Proof.
Let

$$\frac{cx_{3+}^*}{cx_{3+}^* + a} < b \leq \frac{c}{a+1} < c$$

and any solution s with $s_0 \in \mathcal{O}^+$ be given. Assume that for any given $\varepsilon > 0$ there exists a $\widetilde{T} > 0$ such that

$$\frac{1}{T}\int_0^T y(t) + h \, dt \leq y_2^* + h + \varepsilon \qquad \forall\, T \geq \widetilde{T}.$$

We assume that the assertion of the lemma is false. In particular, assume that there exists a solution s with $s_0 \in \mathcal{O}^+$ such that

$$\limsup_{t\to\infty} z(t) > 0.$$

Note that this is the only possible case since $z(t) > 0$ for any $t \geq 0$ by Lemma 2.1.5. The solution s fulfils the conditions of Lemma 2.4.12 as well. Hence for any given $\varepsilon > 0$ there exists a (sufficiently large) $T > 0$ such that

$$\begin{aligned}\frac{1}{T}\int_0^T y(t) + h \, dt &\leq y_2^* + h + \varepsilon\\ \frac{1}{T}\int_0^T \frac{1}{y(t)+h} dt &< \frac{f}{g} + \varepsilon\end{aligned}$$

holds. Therefore we can apply Lemma 2.4.8 and obtain

$$(y_2^* + h + \varepsilon)\left(\frac{f}{g} + \varepsilon\right) > 1$$

for all $\varepsilon > 0$. Multiplying by $\frac{g}{f} > 0$ on both sides, yields

$$y_2^* + h + \varepsilon + \frac{\varepsilon g}{f}\left(\frac{(a+1)^2}{4} + h + \varepsilon\right) > \frac{g}{f}$$

which is in turn equivalent to

$$y_2^* > \frac{g}{f} - h - \varepsilon\left[1 + \frac{g}{f}\left(\frac{(a+1)^2}{4} + h + \varepsilon\right)\right]$$

for all $\varepsilon > 0$. Since $\varepsilon > 0$ can be chosen arbitrarily small ($\varepsilon \searrow 0$), the above implies

$$y_2^* \geq \frac{g}{f} - h.$$

This is equivalent to (since $b < c$)

$$
\begin{aligned}
y_2^* \geq \frac{g}{f} - h \quad &\Leftrightarrow \quad (1 - x_2^*)(x_2^* + a) \geq \frac{g}{f} - h \\
&\Leftrightarrow \quad -(x_2^*)^2 + (1-a)x_2^* + a \geq \frac{g}{f} - h \\
&\Leftrightarrow \quad -(x_2^*)^2 + (1-a)x_2^* + a - \frac{(1-a)^2}{4} + \frac{(1-a)^2}{4} \geq \frac{g}{f} - h \\
&\Leftrightarrow \quad -(x_2^*)^2 + (1-a)x_2^* - \frac{(1-a)^2}{4} + \frac{(1+a)^2}{4} \geq \frac{g}{f} - h \\
&\Leftrightarrow \quad -\left(x_2^* - \frac{1-a}{2}\right)^2 + \frac{(1+a)^2}{4} \geq \frac{g}{f} - h \\
&\Leftrightarrow \quad \left(x_2^* - \frac{1-a}{2}\right)^2 \leq \frac{(1+a)^2}{4} - \frac{g}{f} + h \\
&\Leftrightarrow \quad x_2^* - \frac{1-a}{2} \leq \sqrt{\frac{(1+a)^2}{4} - \frac{g}{f} + h} \\
&\Leftrightarrow \quad x_2^* \leq \frac{1-a}{2} + \sqrt{\frac{(1+a)^2}{4} - \frac{g}{f} + h} = x_{3+}^*
\end{aligned}
$$

Thus we have

$$\frac{ab}{c-b} = x_2^* \leq x_{3+}^*$$

which we may solve for b yielding

$$b \leq \frac{cx_{3+}^*}{cx_{3+}^* + a} = b_{3+}^*.$$

This is a contradiction to our parameter assumption and thus the claim of the lemma is proven. □

Remark 2.4.16.
Note that the assumption of the previous lemma is very strong. In fact the integral estimate in equation (2.4.22) is of the same kind as those in Lemmas 2.4.12, 2.4.13 and 2.4.24. Unfortunately we have not been able to find sufficient estimates to show that (2.4.22) indeed holds. However, consider the following reasoning:
By Lemma 2.4.2 the planar equilibrium p_2^* is asymptotically stable in the positive x-y quadrant for

$$b \in \left(b_{3+}^*, \frac{c}{a+1}\right).$$

Thus, for these b-values the inequality (2.4.22) holds for solutions with $z_0 = 0$ (since then $\lim_{t\to\infty} y(t) = y_2^*$). The asymptotic stability of p_2^* may be proven, by employing a strict Lyapunov function (see e.g. [Cheng et al., 1982], [Aulbach, 1997]). Extending this Lyapunov function to phase *space* and incorporating the dynamics of the generalist predator species is the aim (similar to [Chiu and Hsu, 1998], [Hsu, 2005] for example). The local asymptotic stability of p_2^* (see Lemma 2.4.7) allows the construction of a strict Lyapunov function *locally*, i.e. in a neighbourhood of p_2^*. Extending it to a global Lyapunov function is difficult. This final - yet missing - step would yield the global result, but depends strongly on the coupling of the variables x, y and z.

As mentioned in the subsequent remark to Conjecture 2.4.1 the nature of the attractor $\mathcal{A}$ changes if $p_{3+}^* \in \mathcal{O}^+$, since the additional equilibrium inside the positive octant is necessarily part of the attractor and thus $\mathcal{A}$ not planar (recall Figure 2.4.19). In fact the equilibrium p_{3+}^* and its properties play an important role in understanding the nature of the set $\mathcal{A}$ and thus studying p_{3+}^* is subject of the next subsection.

2.4.3 Analysis of equilibria II

In this subsection we investigate the (interior) equilibria of coexistence p_{3+}^* and p_{3-}^* and their respective stability properties. As always we assume $a = d$ and $f - \frac{g}{h} < 0$ to hold for the parameters in (2.1.5).

The equilibrium p_{3+}^*

Since we are only interested in the biologically relevant cases, we will in fact assume $p_{3+}^* \in \mathcal{O}_0^+$, i.e. that the equilibrium is in the non-negative octant. From Table 1 we see that this is equivalent to the conditions

$$a \geq 2\sqrt{\tfrac{g}{f} - h} - 1 \quad \wedge \quad \left(0 < a \leq 1 \quad \vee \quad a > \frac{g}{f} - h\right) \quad \wedge \quad b \leq \frac{cx_{3+}^*}{x_{3+}^* + a} = b_{3+}^*,$$

which we assume to hold in this subsection. In particular this implies that a branch of equilibria corresponding to p_{3+}^* exists for $b \in (0, b_{3+}^*)$, along which a bifurcation may occur (as we show below). By Lemma 2.4.1 we know that

$$p_2^* = p_{3+}^* \quad \text{for} \quad b = b_{3+}^*,$$

i.e. the equilibria coincide for the value $b = b_{3+}^*$. A transcritical bifurcation occurs and p_2^* is unstable for $0 < b < b_{3+}^*$ (see Lemma 2.4.7 and the subsequent remark). For all values of b strictly less than b_{3+}^* the equilibrium p_{3+}^* is then indeed contained in the *positive* octant, i.e.

$$\forall\, b \in \left(0, b_{3+}^*\right) : \; p_{3+}^* \in \mathcal{O}^+.$$

We will restrict ourselves to this case $0 < b < b_{3+}^*$. The question arises whether the equilibrium $p_{3+}^* \in \mathcal{O}^+$ inherits the stability properties of p_2^*, i.e. whether it is asymptotically stable for $b < b_{3+}^*$. As an answer to this question we will prove the following result in this subsection:

Proposition 2.4.1.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold and furthermore assume that $p_{3+}^* \in \mathcal{O}^+$.
If $a = 2\sqrt{\frac{g}{f} - h} - 1$ holds, then p_{3+}^* is unstable for all $b \in \left(0, b_{3+}^*\right)$.

If $a > 2\sqrt{\frac{g}{f} - h} - 1$, *then there exists a minimal* $\widehat{b} \in \left(-\infty, b^*_{3+}\right)$, *such that* p^*_{3+} *is (locally) asymptotically stable and hyperbolic for all* $b \in \left(\widehat{b}, b^*_{3+}\right)$.

- *If* $\widehat{b} \leq 0$ *then the equilibrium is asymptotically stable and hyperbolic for all* $b > 0$ *(i.e. for all biologically relevant parameters).*
- *If* $\widehat{b} > 0$ *then a Hopf bifurcation occurs for* $b = \widehat{b}$ *along the branch of equilibria corresponding to* p^*_{3+}, *i.e.*

$$\left(\widehat{b}, p^*_{3+}\right) \in \left(0, b^*_{3+}\right) \times \mathcal{O}^+_0$$

is a Hopf bifurcation point. Furthermore, p^*_{3+} *is unstable and hyperbolic for all* $b \in \left(0, \widehat{b}\right)$.

The (both necessary and sufficient) conditions such that $\widehat{b} > 0$ *holds may be found in Lemmas 2.4.36 and 2.4.37.*

Remark 2.4.17.
More concisely, the above proposition states that either p^*_{3+} is asymptotically stable for all values of $b \in \left(0, b^*_{3+}\right)$ or the equilibrium turns unstable for some $\widehat{b} \in \left(0, b^*_{3+}\right)$ via a Hopf bifurcation and remains unstable for all $b \in \left(0, \widehat{b}\right)$.
The statement in Proposition 2.4.1 will turn out to be the result of an eigenvalue analysis and employing Lyapunov's indirect method, as well as the Routh-Hurwitz criteria. This analysis, however, is not straightforward and is therefore split up into several parts below, yielding the proof of Proposition 2.4.1 at the end of this subsection. We consider the Jacobian $\mathrm{D}v(x, y, z)$ of the vector field v (see equation (2.4.5)) evaluated at the equilibrium p^*_{3+} (for the derivation see Appendix C.2.2):

$$J := \mathrm{D}v(p^*_{3+}) = \begin{pmatrix} 1 - 2x - \frac{ay}{(x+a)^2} & -\frac{x}{x+a} & 0 \\ \frac{acy}{(x+a)^2} & -b + \frac{cx}{x+a} - \frac{ez}{(y+e)^2} & -\frac{y}{y+e} \\ 0 & \frac{gz^2}{(y+h)^2} & 2z\left(f - \frac{g}{y+h}\right) \end{pmatrix}\Bigg|_{(x,y,z)=\left(x^*_{3+}, y^*_{3+}, z^*_{3+}\right)}$$

$$= \begin{pmatrix} \frac{-x^*_{3+} \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x^*_{3+} + a} & -\frac{x^*_{3+}}{x^*_{3+} + a} & 0 \\ \frac{ac(1 - x^*_{3+})}{x^*_{3+} + a} & \left(b^*_{3+} - b\right)\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right) & -\frac{y^*_{3+}}{y^*_{3+} + e} \\ 0 & \frac{f^2}{g}\left(h - \frac{g}{f} - e\right)^2 \left(b - b^*_{3+}\right)^2 & 0 \end{pmatrix} \tag{2.4.23}$$

We will use the standard notation for matrix entries for J, i.e.

$$J = \begin{pmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ j_{31} & j_{32} & j_{33} \end{pmatrix} = \mathrm{D}v(p^*_{3+}).$$

We wish to determine the eigenvalues of J. Throughout the rest of this subsection we will call these (not necessarily different) eigenvalues λ_1, λ_2 and λ_3 respectively. The characteristic polynomial

$$\begin{aligned}\chi_J(\xi) &= \left|\begin{pmatrix} j_{11}-\xi & j_{12} & 0 \\ j_{21} & j_{22}-\xi & j_{23} \\ 0 & j_{32} & -\xi \end{pmatrix}\right| \\ &= (j_{11}-\xi)(j_{22}-\xi)(-\xi) - j_{32}j_{23}(j_{11}-\xi) - j_{21}j_{12}(-\xi) \\ &= -\xi^3 + (j_{11}+j_{22})\xi^2 + (j_{32}j_{23}+j_{21}j_{12}-j_{11}j_{22})\xi - j_{11}j_{32}j_{23} \end{aligned} \tag{2.4.24}$$

associated with J is of degree three. Therefore χ_J has a real root, i.e. at least one eigenvalue of J will be real-valued, while the other two eigenvalues are either complex conjugates (c.c.) or also both real-valued (being a consequence of the Fundamental Theorem of Algebra). Considering Proposition 2.4.1 we see that we need to differentiate between two different cases for the parameter a. We consider the shorter case, the equality, first:

Lemma 2.4.27.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a = 2\sqrt{\frac{g}{f} - h} - 1$, then for any $b \in \left(0, b^*_{3+}\right)$ the equilibrium is unstable.

Proof.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a = 2\sqrt{\frac{g}{f} - h} - 1$ hold and any $b \in \left(0, b^*_{3+}\right)$ be given. Note that the parameter assumption is equivalent to

$$a = 2\sqrt{\frac{g}{f} - h} - 1 \qquad \Leftrightarrow \qquad (a+1)^2 = 4\left(\frac{g}{f} - h\right).$$

Thus the Jacobian J in equation (2.4.23) simplifies to

$$J = \mathrm{Dv}(p^*_{3+}) = \begin{pmatrix} 0 & * & 0 \\ * & \left(b^*_{3+} - b\right)\left(\frac{\frac{g}{f}-h}{\frac{g}{f}-h+e}\right) & * \\ 0 & * & 0 \end{pmatrix},$$

where the $*$ stands for some entry in J (which we do not need to know precisely). We now consider the trace of the matrix J and observe that for any $b \in \left(0, b^*_{3+}\right)$ it holds that

$$\mathrm{tr}(J) = \underbrace{\left(b^*_{3+} - b\right)}_{>0} \underbrace{\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right)}_{>0} > 0.$$

On the other hand, since the trace is the sum of the real parts of the eigenvalues of J we obtain

$$\mathrm{tr}(J) = \mathrm{Re}(\lambda_1) + \mathrm{Re}(\lambda_2) + \mathrm{Re}(\lambda_3) > 0,$$

which implies that at least one of the eigenvalues has a positive real part and hence by Lyapunov's indirect method, the equilibrium p^*_{3+} is unstable. □

This result takes care of the case where $a = 2\sqrt{\frac{g}{f} - h} - 1$, and we now turn to the other case. In order to prove that Proposition 2.4.1 holds, we will show various results in the following, namely:

- properties regarding the matrix J (Lemmas 2.4.28, 2.4.30, 2.4.33, 2.4.35)
- properties regarding the eigenvalues $\lambda_{2/3}$ crossing the imaginary axis (Lemmas 2.4.32, 2.4.34 and Corollary 2.4.2)
- conditions under which the eigenvalues cross the imaginary axis (Lemma 2.4.36, 2.4.37 and Corollary 2.4.3)

Combined, these results will conclude in the proof of the proposition. We first prove the following statement concerning the determinant of J.

Lemma 2.4.28.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$, then for any $b \in \left(0, b^*_{3+}\right)$ the matrix J from equation (2.4.23) *fulfils*

$$\det(J) = -j_{11}j_{32}j_{23} = \lambda_1 \cdot \lambda_2 \cdot \lambda_3 < 0.$$

Also the determinant of J is differentiable and strictly monotonically increasing in b on $\left(0, b^*_{3+}\right)$.

Proof.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ hold and any $b \in \left(0, b^*_{3+}\right)$ be given. The determinant of J is strictly negative since

$$\det(J) = -\underbrace{\left(\frac{x^*_{3+} \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x^*_{3+} + a}\right)}_{>0} \underbrace{\left(\frac{y^*_{3+}}{y^*_{3+} + e}\right)}_{>0} \underbrace{\left(\frac{f^2}{g}\left(h - \frac{g}{f} - e\right)^2 \left(b - b^*_{3+}\right)^2\right)}_{>0} < 0.$$

Since the first two terms of the above product are independent of b, we see that $\det(J)$ is differentiable (even on $\mathbb{R}$) and as $b \in \left(0, b^*_{3+}\right)$ is increased $\det(J)$ is strictly monotonically increasing and converges to zero as $b \to b^*_{3+}$. □

In order to use the above result we need the following auxiliary

Lemma 2.4.29.
Let $p^*_{3+} \in \mathcal{O}^+_0$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ hold. Then the following estimate is true

$$b^*_{3+} = \frac{cx^*_{3+}}{x^*_{3+} + a} > \frac{c(1-a)}{a+1}.$$

In particular the bifurcation value b^*_{3+} for which the transcritical bifurcation of p^*_2 and p^*_{3+} (see Lemma 2.4.1) is strictly larger than the bifurcation value $\frac{c(1-a)}{a+1}$ for which the planar Hopf bifurcation of p^*_2 (see Lemma 2.4.7) occurs.

Proof.
Let $p^*_{3+} \in \mathcal{O}^+_0$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ hold. We consider the following two cases:

- If $a > 1$, then using $x^*_{3+} \geq 0$, we immediately obtain

$$b^*_{3+} = \frac{cx^*_{3+}}{x^*_{3+} + a} \geq 0 > \frac{c\overbrace{(1-a)}^{<0}}{a+1}.$$

- If $a \leq 1$ then, using the definition of x^*_{3+}, we obtain

$$x^*_{3+} = \frac{1-a}{2} + \underbrace{\sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h}}_{>0} > \frac{1-a}{2} \geq 0.$$

  Thus monotonicity yields

$$b^*_{3+} = \frac{cx^*_{3+}}{x^*_{3+} + a} > \frac{c\left(\frac{1-a}{2}\right)}{\frac{1-a}{2} + a} = \frac{c(1-a)}{1-a+2a} = \frac{c(1-a)}{a+1}. \qquad \square$$

We use the two previous results to prove

Lemma 2.4.30.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ hold. There exists a minimal $\widehat{b} \in \left(-\infty, b^*_{3+}\right)$, such that the eigenvalues $\lambda_1, \lambda_2, \lambda_3$ all have negative real part for all $b \in \left(\widehat{b}, b^*_{3+}\right)$ and in particular p^*_{3+} is asymptotically stable and hyperbolic for all $b \in \left(\widehat{b}, b^*_{3+}\right)$.

Proof.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ hold. Recall that for $b = b^*_{3+} > 0$ the equilibria p^*_2 and p^*_{3+} coincide and a transcritical bifurcation occurs (see Lemma 2.4.1). Thus the Jacobians

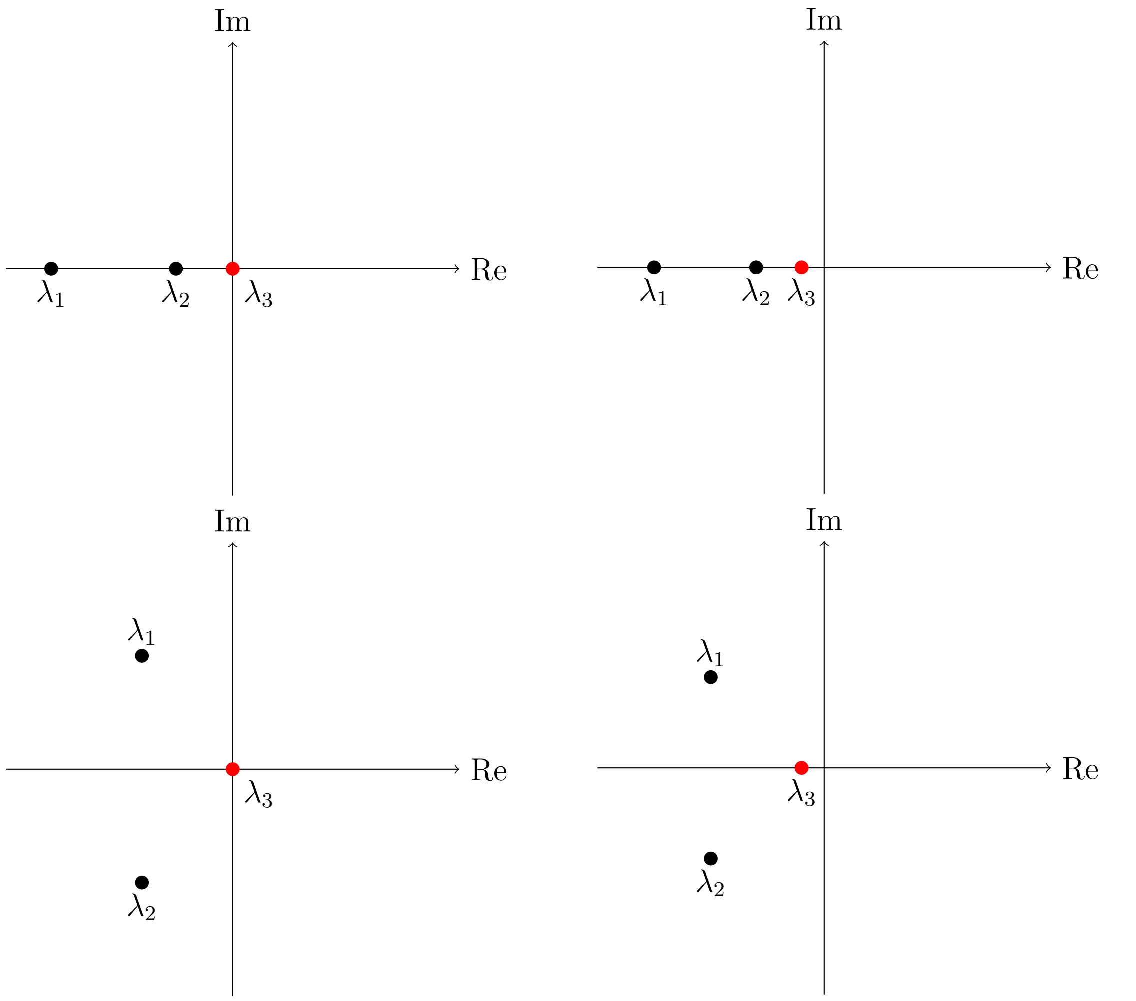
$$\mathrm{Dv}(p^*_2) = \begin{pmatrix} \frac{x^*_2(1-a-2x^*_2)}{a+x^*_2} & -\frac{x^*_2}{x^*_2+a} & 0 \\ \frac{ac(1-x^*_2)}{a+x^*_2} & 0 & -\frac{y^*_2}{y^*_2+e} \\ 0 & 0 & 0 \end{pmatrix} = \mathrm{Dv}(p^*_{3+}) = J$$

also coincide and have the same three eigenvalues λ_1, λ_2 and λ_3. From Lemma 2.4.29 we know that

$$b = b^*_{3+} > \frac{c(1-a)}{a+1}$$

and hence from the proof of Lemma 2.4.7 we obtain that the eigenvalues of J fulfil

$$\mathrm{Re}(\lambda_{1/2}) < 0 \quad \wedge \quad \lambda_3 = 0 \qquad \text{for} \qquad b = b^*_{3+},$$



(a) The case $b = b^*_{3+}$ - one zero eigenvalue.

(b) The case $b \in (\widehat{b}, b^*_{3+})$ - all eigenvalues have negative real part.

Figure 2.4.20: Constellations of λ_1, λ_2, λ_3 in the complex plane $\mathbb{C}$ for $b \in \left(\widehat{b}, b^*_{3+}\right]$.

also see Figure 2.4.20a. Since the eigenvalues depend continuously on b (cf. [Marden, 1949], [Ortega, 1972]), we obtain that for any $b < b^*_{3+}$ sufficiently close to b^*_{3+} it still holds that

$$\mathrm{Re}(\lambda_{1/2}) < 0.$$

Furthermore, since by Lemma 2.4.28 the determinant of J is strictly negative for all $b \in \left(0, b^*_{3+}\right)$, we obtain that for any $b < b^*_{3+}$ sufficiently close to b^*_{3+} we also have

$$\mathrm{Re}(\lambda_3) < 0,$$

see Figure 2.4.20b. Thus there exists an interval $\widehat{I} \subset \left(-\infty, b^*_{3+}\right)$ such that

$$\mathrm{Re}(\lambda_{1/2/3}) < 0 \qquad \forall\, b \in \widehat{I}.$$

Due to the continuous dependence of the eigenvalues on b, this interval $\widehat{I}$ can be extended to the left until one of the eigenvalues has zero real part for some $\widehat{b} \in \left(-\infty, b^*_{3+}\right)$, or else we set $\widehat{b} = -\infty$, thus yielding a maximal interval

$$\widehat{I} = \left(\widehat{b}, b^*_{3+}\right)$$

for this minimal $\widehat{b}$. By construction, the eigenvalues all have negative real part for all $b \in \left(\widehat{b}, b^*_{3+}\right)$. Thus the equilibrium p^*_{3+} is hyperbolic and asymptotically stable for this parameter range. □

Recall that one of the eigenvalues of J is always real-valued. *Without loss of generality we name the real-valued eigenvalue* λ_1, i.e. $\text{Im}(\lambda_1) = 0$. We prove several properties of the eigenvalues that are a consequence of the above results.

Lemma 2.4.31.
Let $p^*_{3+} \in \mathcal{O}^+$ *and* $a > 2\sqrt{\frac{g}{f} - h} - 1$ *hold. Then for all* $b \in \left(0, b^*_{3+}\right)$ *it holds that*

i) $\text{Re}(\lambda_1) < 0$ *and* $\text{Im}(\lambda_1) = 0$

ii) if $\text{Re}(\lambda_2) = 0$ *or* $\text{Re}(\lambda_3) = 0$ *then* $\lambda_2 = \overline{\lambda_3}$ *(c.c.) and* $\text{Im}(\lambda_{2/3}) \neq 0$.

iii) if $\text{Im}(\lambda_2) = 0$ *or* $\text{Im}(\lambda_3) = 0$ *then* $\text{Re}(\lambda_{2/3}) \neq 0$.

Proof.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ hold and any $b \in \left(0, b^*_{3+}\right)$ be given.

i) Since without loss of generality λ_1 was assumed to be the real-valued eigenvalue it holds that $\text{Im}(\lambda_1) = 0$. By Lemma 2.4.30 we know that the real-part of all three eigenvalues of J is strictly negative for some $b \in (0, b^*_{3+})$. Assuming that $\text{Re}(\lambda_1) \geq 0$ for some $b \in (0, b^*_{3+})$ implies that the eigenvalue *crosses* the imaginary axis for some $b \in (0, b^*_{3+})$ (due to the continuous dependence on b) and thus $\lambda_1 = 0$ holds for this b-value. This however is a contradiction to the negativity of the determinant proven in Lemma 2.4.28, i.e. for any $b \in (0, b^*_{3+})$ it holds that:
$$\det(J) = \lambda_1 \cdot \lambda_2 \cdot \lambda_3 < 0.$$
Therefore $\text{Re}(\lambda_1) < 0$ for all $b \in (0, b^*_{3+})$.

ii) Assume - without loss of generality - that $\text{Re}(\lambda_2) = 0$ holds. If we further assume, that $\text{Im}(\lambda_2) = 0$ then in fact $\lambda_2 = 0$, thus contradicting
$$\det(J) = \lambda_1 \cdot \lambda_2 \cdot \lambda_3 < 0.$$
Hence $\text{Im}(\lambda_2) \neq 0$. However, then there is a complex conjugate to the eigenvalue λ_2 and since λ_1 is real-valued, we have $\lambda_2 = \overline{\lambda_3}$ (complex conjugate) and $\text{Im}(\lambda_{2/3}) \neq 0$.

iii) Assume - without loss of generality - that $\mathrm{Im}(\lambda_2) = 0$. Since λ_1 is also real-valued, the third eigenvalue cannot be complex, since it has no complex conjugate. Hence all three eigenvalues are real-valued. However, if any of them would be identically zero, the determinant of J would also be zero, a contradiction. Hence $\mathrm{Re}(\lambda_{2/3}) \neq 0$ holds. □

From the result of Lemma 2.4.30 the question arises in which cases the eigenvalues of J have a negative real part *for all* $b \in \left(0, b_{3+}^*\right)$. This is equivalent to asking under which conditions on the parameters it holds that $\widehat{b} \leq 0$. We will see that the eigenvalues may in fact cross the imaginary axis in some cases (see Corollary 2.4.3). We consider this crossing more closely:

Lemma 2.4.32.
Let $p_{3+}^* \in \mathcal{O}^+$ *and* $a > 2\sqrt{\frac{g}{f} - h} - 1$ *hold and assume that* $\mathrm{Re}(\lambda_2) = 0$ *or* $\mathrm{Re}(\lambda_3) = 0$ *for some* $\widehat{b}_h \in \left(0, b_{3+}^*\right)$. *Then it holds that* $\lambda_2 = \overline{\lambda_3}$ *and*

$$\mathrm{Im}(\lambda_2)(b) = \sqrt{\frac{j_{11}j_{21}j_{12}}{j_{22}} - j_{11}^2} > 0 \qquad \textit{for} \qquad b = \widehat{b}_h,$$

using the notation introduced for the entries in J. *Furthermore, the above expression* $\mathrm{Im}(\lambda_2)$ *is differentiable and strictly monotonically increasing in* b *on* $\left(0, b_{3+}^*\right)$.

Proof.
Let $p_{3+}^* \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ hold and assume without loss of generality that $\mathrm{Re}(\lambda_2) = 0$ for some $\widehat{b}_h \in \left(0, b_{3+}^*\right)$. By Lemma 2.4.31 it holds that $\lambda_2 = \overline{\lambda_3}$ and hence

$$\lambda_2 = i\,\mathrm{Im}(\lambda_2) = -\lambda_3.$$

We now determine $\mathrm{Im}(\lambda_2)$. For this, we consider the characteristic polynomial χ_J of J. Note that by the above the polynomial can be written as

$$\chi_J(\xi) = \gamma(\xi - \lambda_1)(\xi - \lambda_2)(\xi - \lambda_3) = \gamma(\xi - \lambda_1)(\xi^2 + \mathrm{Im}^2(\lambda_2)),$$

with $\gamma \in \mathbb{R}\backslash\{0\}$. Expanding the above yields

$$\chi_J(\xi) = \gamma\xi^3 - \gamma\lambda_1\xi^2 + \gamma\,\mathrm{Im}^2(\lambda_2)\xi - \gamma\lambda_1\,\mathrm{Im}^2(\lambda_2). \tag{2.4.25}$$

On the other hand the characteristic polynomial is given by (2.4.24):

$$\chi_J(\xi) = -\xi^3 + (j_{11} + j_{22})\xi^2 + (j_{32}j_{23} + j_{21}j_{12} - j_{11}j_{22})\xi - j_{11}j_{32}j_{23}.$$

Thus, comparing coefficients with (2.4.25) yields the following system of equations

$$\begin{aligned} \gamma &= -1 \\ -\gamma\lambda_1 &= j_{11} + j_{22} \\ \gamma\,\mathrm{Im}^2(\lambda_2) &= j_{32}j_{23} + j_{21}j_{12} - j_{11}j_{22} \\ -\gamma\lambda_1\,\mathrm{Im}^2(\lambda_2) &= -j_{11}j_{32}j_{23} \end{aligned}$$

Using the first equation, the other three simplify to

$$\begin{aligned} \lambda_1 &= j_{11} + j_{22} \\ -\operatorname{Im}^2(\lambda_2) &= j_{32}j_{23} + j_{21}j_{12} - j_{11}j_{22} \\ \lambda_1 \operatorname{Im}^2(\lambda_2) &= -j_{11}j_{32}j_{23} \end{aligned} \tag{2.4.26}$$

By the assumptions we have that

$$j_{11} = -\frac{x_{3+}^* \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x_{3+}^* + a} < 0$$

and dividing by $-j_{11} > 0$ in the third line of (2.4.26) yields

$$j_{32}j_{23} = -\frac{\lambda_1 \operatorname{Im}^2(\lambda_2)}{j_{11}}.$$

Substituting this into the second line of (2.4.26) yields

$$-\operatorname{Im}^2(\lambda_2) = -\frac{\lambda_1 \operatorname{Im}^2(\lambda_2)}{j_{11}} + j_{21}j_{12} - j_{11}j_{22},$$

which is equivalent to

$$\operatorname{Im}^2(\lambda_2)\left(\frac{\lambda_1 - j_{11}}{j_{11}}\right) = j_{21}j_{12} - j_{11}j_{22}.$$

Rewriting the first equation of (2.4.26) as $\lambda_1 - j_{11} = j_{22}$, the above simplifies to

$$\operatorname{Im}^2(\lambda_2)\frac{j_{22}}{j_{11}} = j_{21}j_{12} - j_{11}j_{22}. \tag{2.4.27}$$

Since for any $b \in \left(0, b_{3+}^*\right)$ and thus in particular for $\widehat{b}_h$, it holds that

$$j_{22} = \underbrace{\left(b_{3+}^* - b\right)}_{>0} \underbrace{\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right)}_{>0} > 0, \tag{2.4.28}$$

we may reformulate (2.4.27) as

$$0 < \operatorname{Im}^2(\lambda_2) = \frac{j_{11}j_{21}j_{12}}{j_{22}} - j_{11}^2.$$

Thus, taking the square root on both sides yields the next part of the claim

$$\operatorname{Im}(\lambda_2) = \sqrt{\frac{j_{11}j_{21}j_{12}}{j_{22}} - j_{11}^2} > 0.$$

Finally, note that in the above expression the term j_{22} is the only component of J that depends on the parameter b (see (2.4.23)). From (2.4.28) we see that j_{22} is strictly monotonically decreasing in b on $\left(0, b_{3+}^*\right)$. Since $j_{11}j_{21}j_{12} > 0$ and

$$\mathrm{Im}(\lambda_2) = \sqrt{\frac{j_{11}j_{21}j_{12}}{j_{22}} - j_{11}^2}$$

depends inversely on the square root of j_{22} we in fact obtain that the above expression is differentiable and strictly monotonically increasing in b on $\left(0, b_{3+}^*\right)$. □

Next we prove a result on the trace of J, namely

Lemma 2.4.33.
Let $p_{3+}^* \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$, then for any $b \in \left(0, b_{3+}^*\right)$ the trace of the matrix J from equation (2.4.23)*, i.e.*

$$\mathrm{tr}(J) = j_{11} + j_{22} = \lambda_1 + \lambda_2 + \lambda_3 = \mathrm{Re}(\lambda_1) + \mathrm{Re}(\lambda_2) + \mathrm{Re}(\lambda_3),$$

is differentiable and strictly monotonically decreasing in b on $\left(0, b_{3+}^*\right)$.

Proof.
Let $p_{3+}^* \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$. The trace of J is given by

$$\mathrm{tr}(J) = \frac{-x_{3+}^* \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x_{3+}^* + a} + \left(b_{3+}^* - b\right) \underbrace{\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right)}_{>0}.$$

Since the first term in the above sum is independent of b we immediately see that the trace is differentiable and strictly monotonically decreasing in b on $\left(0, b_{3+}^*\right)$. □

The above results allow us to show that if the eigenvalues of J are on the imaginary axis for some $\widehat{b}_h \in \left(0, b_{3+}^*\right)$, then this $\widehat{b}_h$ is unique.

Lemma 2.4.34.
Let $p_{3+}^* \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ and assume that $\mathrm{Re}(\lambda_2) = 0$ or $\mathrm{Re}(\lambda_3) = 0$ for some $\widehat{b}_h \in \left(0, b_{3+}^*\right)$. Then $\widehat{b}_h$ is the unique b-value in $\left(0, b_{3+}^*\right)$ with this property.

Proof.
Let $p_{3+}^* \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ and assume that $\mathrm{Re}(\lambda_2) = 0$ or $\mathrm{Re}(\lambda_3) = 0$ for some $\widehat{b}_h \in \left(0, b_{3+}^*\right)$. We now provide a proof by contradiction of the lemma, by assuming that $\widehat{b}_h$ is not unique. More precisely, without loss of generality assume

$$\exists\, \widetilde{b} \in (0, \widehat{b}_h) \subset (0, b_{3+}^*) \;:\; \mathrm{Re}(\widetilde{\lambda_2}) = 0 \,\vee\, \mathrm{Re}(\widetilde{\lambda_3}) = 0,$$

where for $b = \widetilde{b}$ the eigenvalues of J are denoted by $\widetilde{\lambda_1}$, $\widetilde{\lambda_2}$ and $\widetilde{\lambda_3}$. We now consider the eigenvalues λ_1, λ_2, λ_3, $\widetilde{\lambda_1}$, $\widetilde{\lambda_2}$ and $\widetilde{\lambda_3}$. Recall from Lemma 2.4.31 that we have

$$\begin{array}{ccc} \lambda_1 < 0 & \text{and} & \widetilde{\lambda_1} < 0 \\ \operatorname{Re}(\lambda_2) = 0 = \operatorname{Re}(\lambda_3) & \text{and} & \operatorname{Re}(\widetilde{\lambda_2}) = 0 = \operatorname{Re}(\widetilde{\lambda_3}) \\ \operatorname{Im}(\lambda_2) = -\operatorname{Im}(\lambda_3) & \text{and} & \operatorname{Im}(\widetilde{\lambda_2}) = -\operatorname{Im}(\widetilde{\lambda_3}) \end{array}$$

Considering Lemma 2.4.32, we see that since $0 < \widetilde{b} < \widehat{b}_h < b^*_{3+}$, we can use the monotonicity property of the imaginary part to obtain

$$\begin{aligned} 0 < \operatorname{Im}^2(\widetilde{\lambda_2}) < \operatorname{Im}^2(\lambda_2) \quad &\Leftrightarrow \quad 0 < -\operatorname{Im}(\widetilde{\lambda_2})\operatorname{Im}(\widetilde{\lambda_3}) < -\operatorname{Im}(\lambda_2)\operatorname{Im}(\lambda_3) \\ &\Leftrightarrow \quad 0 < i\operatorname{Im}(\widetilde{\lambda_2}) i\operatorname{Im}(\widetilde{\lambda_3}) < i\operatorname{Im}(\lambda_2) i\operatorname{Im}(\lambda_3) \\ &\Leftrightarrow \quad 0 < \widetilde{\lambda_2}\widetilde{\lambda_3} < \lambda_2\lambda_3. \end{aligned} \tag{2.4.29}$$

Furthermore, recall that the determinant is negative and also strictly monotonically increasing on $(0, b^*_{3+})$ in b (see Lemma 2.4.28), whence

$$\det(J)(\widetilde{b}) < \det(J)(\widehat{b}_h) < 0 \quad \Leftrightarrow \quad \widetilde{\lambda_1}\widetilde{\lambda_2}\widetilde{\lambda_3} < \lambda_1\lambda_2\lambda_3 < 0. \tag{2.4.30}$$

Comparing equations (2.4.29) and (2.4.30) and recalling that $\lambda_1, \widetilde{\lambda_1} < 0$ we see that

$$\widetilde{\lambda_1} < \lambda_1 < 0 \tag{2.4.31}$$

necessarily holds. On the other hand, by the monotonicity property of the trace of J (see Lemma 2.4.33) it holds that

$$\operatorname{tr}(J)(\widehat{b}_h) < \operatorname{tr}(J)(\widetilde{b}) \quad \Leftrightarrow \quad \lambda_1 + \lambda_2 + \lambda_3 < \widetilde{\lambda_1} + \widetilde{\lambda_2} + \widetilde{\lambda_3}.$$

which is equivalent to

$$\operatorname{Re}(\lambda_1) + \underbrace{\operatorname{Re}(\lambda_2)}_{=0} + \underbrace{\operatorname{Re}(\lambda_3)}_{=0} < \operatorname{Re}(\widetilde{\lambda_1}) + \underbrace{\operatorname{Re}(\widetilde{\lambda_2})}_{=0} + \underbrace{\operatorname{Re}(\widetilde{\lambda_3})}_{=0} \quad \Leftrightarrow \quad \lambda_1 < \widetilde{\lambda_1}.$$

This is a contradiction to equation (2.4.31). Thus our assumption was false and $\widehat{b}_h$ is indeed unique in $(0, b^*_{3+})$. □

Remark 2.4.18.
Recall that for the value $\widehat{b} \in (-\infty, b^*_{3+})$ from Lemma 2.4.30 the eigenvalues λ_2 and λ_3 of J are on the imaginary axis, i.e. by construction it holds that $\operatorname{Re}(\lambda_2) = 0 = \operatorname{Re}(\lambda_3)$. Thus, if $\widehat{b} > 0$, then

$$\widehat{b}_h = \widehat{b},$$

since $\widehat{b}_h$ is the *unique* value in $(0, b^*_{3+}) \subset (-\infty, b^*_{3+})$ with this property.

The question that arises naturally from the previous result is what the eigenvalues do for $0 < b < \widehat{b}_h$. Do they *cross* the imaginary axis (implying that a Hopf bifurcation occurs along the branch of equilibria corresponding to p^*_{3+}) and remain on the right-hand side of the imaginary axis for all $b \in (0, \widehat{b}_h)$ or do they *turn around* and have a negative real part again for all $b \in (0, \widehat{b}_h)$? The answer is given in the following

Lemma 2.4.35.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ and assume there exists a $\widehat{b}_h > 0$ as defined in Lemma 2.4.34. Then it holds that the eigenvalues λ_2, λ_3 both have positive real part for all $b \in \left(0, \widehat{b}_h\right)$. Moreover, p^*_{3+} is hyperbolic and unstable for all $b \in \left(0, \widehat{b}_h\right)$.

Proof.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ and assume there exists a $\widehat{b}_h > 0$ as defined in Lemma 2.4.34. By Lemma 2.4.31 it holds that for $b = \widehat{b}_h$ the eigenvalues of J fulfil

$$\lambda_1 < 0 \quad \wedge \quad \operatorname{Re}(\lambda_2) = 0 = \operatorname{Re}(\lambda_3) \quad \wedge \quad \operatorname{Im}(\lambda_2) = -\operatorname{Im}(\lambda_3). \tag{2.4.32}$$

We want to show that the eigenvalues cross the imaginary axis, i.e.

$$\frac{d}{db}\operatorname{Re}(\lambda_{2/3})(\widehat{b}_h) < 0,$$

see Figure 2.4.21). Due to the continuity of the eigenvalues in b and since λ_2 and λ_3 are complex conjugates for $b = \widehat{b}_h$, we know that

$$\lambda_2 = \overline{\lambda_3} \qquad \forall\, b \in (\widehat{b}_h - \varepsilon, \widehat{b}_h + \varepsilon) =: I_\varepsilon \subset \left(0, \widehat{b}_h\right)$$

for sufficiently small $\varepsilon > 0$. Thus for all $b \in I_\varepsilon$ the determinant of J fulfils

$$\det(J) = \lambda_1 \cdot \lambda_2 \cdot \lambda_3 = \lambda_1 \cdot \left(\operatorname{Re}^2(\lambda_2) + \operatorname{Im}^2(\lambda_2)\right).$$

Since $\det(J)$ is strictly monotonically increasing in b on $(0, b^*_{3+})$ by Lemma 2.4.28, the above line yields that for any $b \in I_\varepsilon$

$$\begin{aligned}
0 < \frac{d}{db}\det(J) &= \frac{d}{db}\lambda_1\left(\operatorname{Re}^2(\lambda_2) + \operatorname{Im}^2(\lambda_2)\right) \\
&= \left(\operatorname{Re}^2(\lambda_2) + \operatorname{Im}^2(\lambda_2)\right)\frac{d}{db}\lambda_1 + \lambda_1\frac{d}{db}\left(\operatorname{Re}^2(\lambda_2) + \operatorname{Im}^2(\lambda_2)\right) \\
&= \left(\operatorname{Re}^2(\lambda_2) + \operatorname{Im}^2(\lambda_2)\right)\frac{d}{db}\lambda_1 + 2\lambda_1\left(\operatorname{Re}(\lambda_2)\frac{d}{db}\operatorname{Re}(\lambda_2) + \operatorname{Im}(\lambda_2)\frac{d}{db}\operatorname{Im}(\lambda_2)\right)
\end{aligned}$$

Note that the determinant is differentiable (in b) on $(0, b^*_{3+})$ by Lemma 2.4.28. Furthermore, the eigenvalues and their components are differentiable in b on I_ε. Indeed, the eigenvalues all have multiplicity one (i.e. they are simple) and the coefficients of the characteristic polynomial χ_J (see equation (2.4.24)) are $\mathcal{C}^\infty$ in b.

Applying the implicit function theorem yields the asserted differentiability ([Lax, 2007]). The above can be rewritten as

$$2\lambda_1\left(\operatorname{Re}(\lambda_2)\frac{d}{db}\operatorname{Re}(\lambda_2)+\operatorname{Im}(\lambda_2)\frac{d}{db}\operatorname{Im}(\lambda_2)\right) > -\left(\operatorname{Re}^2(\lambda_2)+\operatorname{Im}^2(\lambda_2)\right)\frac{d}{db}\lambda_1.$$

In particular for $b=\widehat{b}_h\in I_\varepsilon$ and by (2.4.32), the above reduces to

$$2\lambda_1\operatorname{Im}(\lambda_2)\frac{d}{db}\operatorname{Im}(\lambda_2) > -\operatorname{Im}^2(\lambda_2)\frac{d}{db}\lambda_1.$$

We compare the signs of terms on the left- and right-hand side. Recall from Lemma 2.4.32, that for $b=\widehat{b}_h$ the expression $\operatorname{Im}(\lambda_2)$ is strictly positive and strictly monotonically increasing in b, i.e.

$$\operatorname{Im}(\lambda_2)>0 \quad\wedge\quad \frac{d}{db}\operatorname{Im}(\lambda_2)>0.$$

Thus we obtain (dividing by $\operatorname{Im}(\lambda_2)>0$ and also using (2.4.32))

$$\underbrace{2\cdot\underbrace{\lambda_1}_{<0}\cdot\underbrace{\frac{d}{db}\operatorname{Im}(\lambda_2)}_{>0}}_{<0} > \underbrace{-\operatorname{Im}(\lambda_2)}_{<0}\cdot\frac{d}{db}\lambda_1$$

for $b=\widehat{b}_h$. Hence the sign on the right-hand side of the above equation needs to be negative and therefore we conclude

$$\frac{d}{db}\lambda_1>0 \quad\text{for}\quad b=\widehat{b}_h. \tag{2.4.33}$$

On the other hand, since $\lambda_2=\overline{\lambda_3}$ for all $b\in I_\varepsilon$ it holds that

$$\operatorname{tr}(J)=\lambda_1+2\operatorname{Re}(\lambda_2).$$

Since the trace is monotonically decreasing for all $b\in(0,b^*_{3+})\supset I_\varepsilon$ by Lemma 2.4.33, we have

$$0>\frac{d}{db}\operatorname{tr}(J)=\frac{d}{db}\lambda_1+2\frac{d}{db}\operatorname{Re}(\lambda_2)$$

for $b\in I_\varepsilon$. In particular for $b=\widehat{b}_h\in I_\varepsilon$ it holds that (using (2.4.33))

$$0<\frac{d}{db}\lambda_1<-2\frac{d}{db}\operatorname{Re}(\lambda_2).$$

Thus, comparing signs yields

$$\frac{d}{db}\operatorname{Re}(\lambda_2)(\widehat{b}_h)<0,$$

implying that for any $b < \widehat{b}_h$ sufficiently close to $\widehat{b}_h$ it holds that

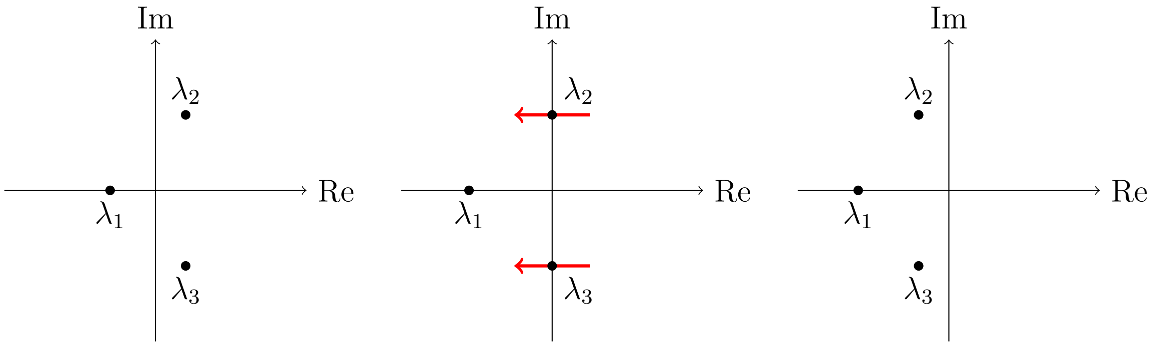
$$0 < \mathrm{Re}(\lambda_2) = \mathrm{Re}(\lambda_3),$$

see Figure 2.4.21. Since we have shown in Lemma 2.4.34 that $\widehat{b}_h$ is the *unique* value in $(0, b^*_{3+})$ such that $\mathrm{Re}(\lambda_2) = 0$ or $\mathrm{Re}(\lambda_3) = 0$, the continuous dependence of the eigenvalues on b yields

$$\mathrm{Re}(\lambda_{2/3}) > 0 \qquad \forall\, b \in (0, \widehat{b}_h).$$

Lyapunov's indirect method yields that p^*_{3+} is unstable for all these values of b and since $\lambda_1 < 0$ it also holds that all eigenvalues have non-zero real part, implying that p^*_{3+} is also hyperbolic for all $b \in (0, \widehat{b}_h)$. □

Thus the eigenvalues indeed cross the imaginary axis as b is decreased below $\widehat{b}_h$, see Figure 2.4.21. From this we immediately obtain



(a) $0 < b < \widehat{b}_h$ (b) $b = \widehat{b}_h$ (c) $\widehat{b}_h < b < b^*_{3+}$

Figure 2.4.21: The eigenvalues $\lambda_{2/3}$ *cross* the imaginary axis for $b = \widehat{b}_h \in (0, b^*_{3+})$.

Corollary 2.4.2.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ and assume there exists a $\widehat{b}_h > 0$ as defined in Lemma 2.4.34. Then a Hopf bifurcation occurs along the branch of equilibria corresponding to p^*_{3+} for $b = \widehat{b}_h$.

Proof.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ and assume there exists a $\widehat{b}_h > 0$ as defined in Lemma 2.4.34. By Lemma 2.4.31 and the proof of Lemma 2.4.35 the eigenvalues of J fulfil

$$\mathrm{Re}(\lambda_2) = 0 = \mathrm{Re}(\lambda_3) \quad \wedge \quad \mathrm{Im}(\lambda_{2/3}) \neq 0 \quad \wedge \quad \frac{d}{db}\mathrm{Re}(\lambda_{2/3}) < 0$$

for $b = \widehat{b}_h$. Since p^*_{3+} is an equilibrium point we conclude that $(\widehat{b}_h, p^*_{3+})$ is a Hopf bifurcation point and thus a Hopf bifurcation occurs along the branch of equilibria corresponding to p^*_{3+} for $b = \widehat{b}_h$ (cf. [Guckenheimer and Holmes, 1983]). □

So far we have not yet determined whether such a $\widehat{b}_h \in (0, b^*_{3+})$ as introduced in the previous results indeed *exists*. In other words: are there biologically relevant parameter values for which the eigenvalues do indeed cross the imaginary axis? The exact conditions for this happening are obtained from the Routh-Hurwitz criterion (see [Hurwitz, 1895], [Kot, 2001]). More precisely, all the roots of the characteristic polynomial

$$\chi_J(\xi) = -\xi^3 + (j_{11} + j_{22})\xi^2 + (j_{32}j_{23} + j_{21}j_{12} - j_{11}j_{22})\xi - j_{11}j_{32}j_{23}$$

from (2.4.24) have negative real part if and only if all of the following three conditions hold

$$j_{11}j_{32}j_{23} > 0 \tag{2.4.34}$$

$$-(j_{11} + j_{22}) > 0 \tag{2.4.35}$$

$$(j_{11} + j_{22})(j_{32}j_{23} + j_{21}j_{12} - j_{11}j_{22}) > j_{11}j_{32}j_{23}. \tag{2.4.36}$$

Note that the first condition is fulfilled for any $b \in (0, b^*_{3+})$, since

$$j_{11}j_{32}j_{23} = -\det(J) > 0$$

by Lemma 2.4.28. Moreover, the condition (2.4.35) is equivalent to

$$-(j_{11} + j_{22}) = -\operatorname{tr}(J) > 0.$$

We prove

Lemma 2.4.36.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$. If the parameters additionally fulfil

$$(a+1)^2 < c^2 \left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e} \right)^2 + 4\left(\frac{g}{f} - h \right) \tag{2.4.37}$$

then there exists a unique $\widehat{b}_t \in (0, b^*_{3+})$ such that

$$-\operatorname{tr}(J) \le 0 \qquad \forall\, b \in (0, \widehat{b}_t).$$

Else, i.e. if (2.4.37) *does not hold, then*

$$-\operatorname{tr}(J) > 0 \qquad \forall\, b \in (0, b^*_{3+})$$

and thus condition (2.4.35) *holds for all $b \in (0, b^*_{3+})$.*

Proof.
Let $p^*_{3+} \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$. Considering the expression

$$\Theta(b) := -\operatorname{tr}(J)(b) = \frac{x^*_{3+} \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x^*_{3+} + a} - \left(b^*_{3+} - b\right) \underbrace{\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e} \right)}_{>0}$$

we observe that it is linear in b with positive slope and thus also continuous and strictly monotonically increasing in b on $\mathbb{R}$. Moreover, for $b = b^*_{3+}$ the expression simplifies to

$$\Theta(b^*_{3+}) = \frac{x^*_{3+} \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x^*_{3+} + a} > 0.$$

Thus, determining whether $\Theta(b) \leq 0$ holds for some $\widehat{b}_t \in (0, b^*_{3+})$ is equivalent to determining the sign of the Θ-axis intercept of the *linear* function Θ, see Figure 2.4.22.

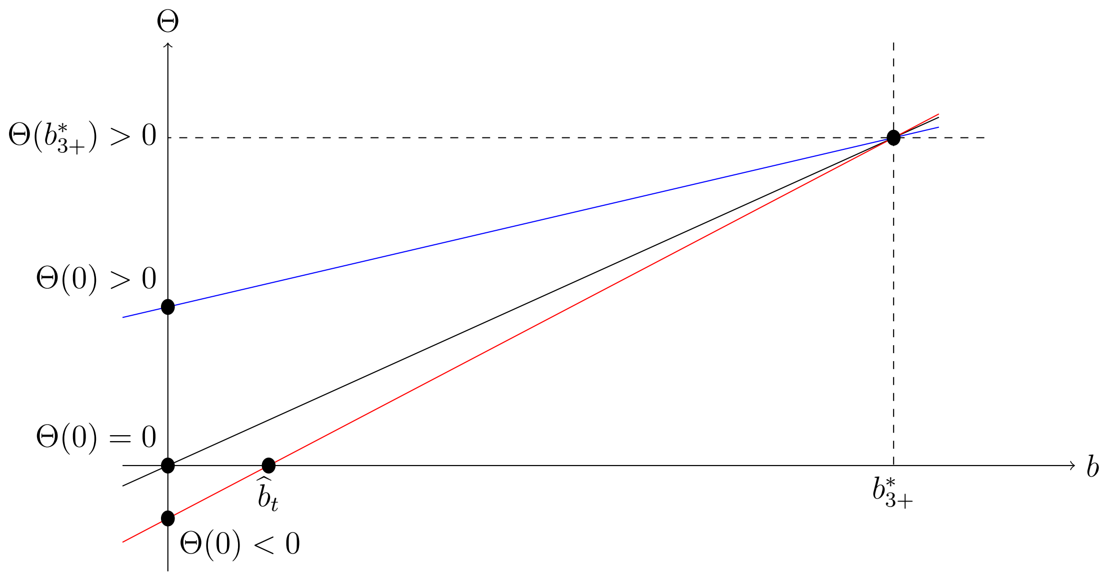


Figure 2.4.22: The root $\widehat{b}_t$ is positive, if and only if $\Theta(0) < 0$.

The intercept is negative if

$$\Theta(0) = \frac{x^*_{3+} \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x^*_{3+} + a} - b^*_{3+}\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right) < 0.$$

Since by definition $b^*_{3+} := \frac{cx^*_{3+}}{x^*_{3+}+a}$ we may rewrite the above as follows

$$\frac{x^*_{3+} \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)} - cx^*_{3+}\left(\frac{\frac{g}{f}-h}{\frac{g}{f}-h+e}\right)}{x^*_{3+} + a} < 0.$$

Observe that $x^*_{3+} > 0$ and the denominator of the above expression is strictly positive for all $b \in (0, b^*_{3+})$ and hence the above simplifies to solving

$$\sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)} - c\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right) < 0.$$

Simple algebraic manipulations and observing that both terms in the above difference are positive yields

$$(a+1)^2 < c^2 \left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e} \right)^2 + 4 \left(\frac{g}{f} - h \right),$$

which is in fact condition (2.4.37). Thus $\Theta(0) < 0$ holds if and only if (2.4.37) holds. Since $\Theta(b^*_{3+}) > 0$ the continuity of Θ and the intermediate value theorem yield

$$\exists\, \widehat{b}_t \in (0, b^*_{3+}) \,:\, \Theta(\widehat{b}_t) = 0,$$

see Figure 2.4.22. Since the function Θ is monotonically increasing and continuous in b, this $\widehat{b}_t$ is unique (even on $\mathbb{R}$). Hence, if condition (2.4.37) holds, there exists a unique $\widehat{b}_t \in (0, b^*_{3+})$ such that

$$\Theta(b) = -\operatorname{tr}(J)(b) \leq 0 \qquad \forall\, b \in (0, \widehat{b}_t),$$

yielding the first claim. Else, i.e. if $\Theta(0) \geq 0$, the function $\Theta = -\operatorname{tr}(J)$ has *no* positive b-axis intercept and since it is continuous it is positive for all $b \in (0, b^*_{3+})$, thus yielding the second part of the claim. □

Remark 2.4.19.
We remark that the conditions on the parameters in the previous lemma, i.e. the restrictions

$$a > 2\sqrt{\frac{g}{f} - h} - 1 \qquad \Leftrightarrow \qquad 4\left(\frac{g}{f} - h\right) < (a+1)^2$$

and (2.4.37), in fact only yield a narrow parameter range for which the trace actually may turn positive, namely

$$4\left(\frac{g}{f} - h\right) < (a+1)^2 < c^2 \left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e} \right)^2 + 4 \left(\frac{g}{f} - h \right).$$

Equivalently, this may be written as

$$0 < (a+1)^2 - 4\left(\frac{g}{f} - h\right) < c^2 \left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e} \right)^2.$$

If on the other hand

$$(a+1)^2 - 4\left(\frac{g}{f} - h\right) \geq c^2 \left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e} \right)^2 > 0,$$

then the condition $a > 2\sqrt{\frac{g}{f} - h} - 1$ and (2.4.35) is satisfied for all $b \in (0, b^*_{3+})$.

Next we consider the third Routh-Hurwitz condition (2.4.36). For this we first remark that by setting $\gamma := \frac{f^2}{g}\left(h - \frac{g}{f} - e\right)^2$ and since $y^*_{3+} = \frac{g}{f} - h$, the following holds for the entries j_{22} and j_{32} in J:

$$j_{22} = \left(b^*_{3+} - b\right)\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right) = \left(b^*_{3+} - b\right)\overbrace{\left(\frac{y^*_{3+}}{y^*_{3+} + e}\right)}^{=-j_{23}} = -j_{23}\left(b^*_{3+} - b\right) = j_{23}\left(b - b^*_{3+}\right)$$

$$j_{32} = \frac{f^2}{g}\left(h - \frac{g}{f} - e\right)^2\left(b - b^*_{3+}\right)^2 = \gamma\left(b - b^*_{3+}\right)^2.$$

Thus condition (2.4.36) is equivalent to

$$\begin{aligned}
&(j_{11} + j_{22})(j_{32}j_{23} + j_{21}j_{12} - j_{11}j_{22}) > j_{11}j_{32}j_{23} \\
\Leftrightarrow\quad & j_{22}(j_{32}j_{23} + j_{21}j_{12} - j_{11}j_{22}) > j_{11}(j_{11}j_{22} - j_{21}j_{12}) \\
\Leftrightarrow\quad & j_{23}\left(b - b^*_{3+}\right)\left(\gamma\left(b - b^*_{3+}\right)^2 j_{23} + j_{21}j_{12} + j_{11}j_{23}\left(b^*_{3+} - b\right)\right) > j_{11}(j_{11}j_{23}\left(b - b^*_{3+}\right) - j_{21}j_{12})
\end{aligned}$$

Considering the above expression, we define a function θ of b as follows:

$$\theta(b) := j_{23}\left(b - b^*_{3+}\right)\left(\gamma\left(b - b^*_{3+}\right)^2 j_{23} + j_{21}j_{12} + j_{11}j_{23}\left(b^*_{3+} - b\right)\right) - j_{11}(j_{11}j_{23}\left(b - b^*_{3+}\right) - j_{21}j_{12}).$$

Hence by construction, (2.4.36) holds for some b if and only if $\theta(b) > 0$. Thus determining whether (2.4.36) holds reduces to determining the sign and thus the roots of the polynomial θ on $(0, b^*_{3+})$, which in fact is the core idea of the proof of the following Lemma 2.4.37. The expanded form of θ is given by

$$\begin{aligned}
\theta(b) = \gamma j_{23}^2 b^3 &+ \left(-3\gamma j_{23}^2 b^*_{3+} - j_{11}j_{23}^2\right) b^2 \\
&+ \left(3\gamma j_{23}^2\left(b^*_{3+}\right)^2 + 2j_{11}j_{23}^2 b^*_{3+} + j_{21}j_{12}j_{23} - j_{11}^2 j_{23}\right) b \\
&- \gamma j_{23}^2 (b^*_{3+})^3 - j_{21}j_{12}j_{23}b^*_{3+} + j_{11}j_{23}b^*_{3+}(j_{11} - j_{23}b^*_{3+}) + j_{11}j_{21}j_{12}
\end{aligned} \tag{2.4.38}$$

Using this, we prove

Lemma 2.4.37.
Let $p^*_{3+} \in \mathcal{O}^+$ and

$$(a+1)^2 - 4\left(\frac{g}{f} - h\right) \geq c^2\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right)^2$$

hold and consider the polynomial θ defined above (see (2.4.38)). If the parameters additionally fulfil one of the following conditions

i) $\theta(0) < 0$

ii) $\theta(0) = 0$ *and* $\theta'(0) < 0$

iii) $\theta(0) = 0$ *and* $\theta'(0) = 0$ *and* $\theta''(0) < 0$

then there exists a unique $\widehat{b}_r \in (0, b^*_{3+})$ *such that the condition* (2.4.36) *is not fulfilled for all* $b \in (0, \widehat{b}_r)$.
Else, if i), ii) and iii) do not hold, then condition (2.4.36) *holds for all* $b \in (0, b^*_{3+})$.

Proof.
Let $p^*_{3+} \in \mathcal{O}^+$ and

$$(a+1)^2 - 4\left(\frac{g}{f} - h\right) \geq c^2 \left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right)^2$$

hold. The above in particular implies that condition (2.4.35) holds for all $b \in (0, b^*_{3+})$, see the subsequent remark on Lemma 2.4.36. Thus the sign of $\mathrm{Re}(\lambda_{2/3})$ solely depends on whether the *third* Routh-Hurwitz condition in (2.4.36) holds, i.e. on the sign of θ. Furthermore, recall that by Lemma 2.4.35 we know that if the eigenvalues are on the imaginary axis for some $\widehat{b}_h \in (0, b^*_{3+})$ they indeed cross the axis and do not intersect or touch it again for any

$$b \in (0, b^*_{3+}) \backslash \{\widehat{b}_h\}.$$

This implies that if there exists a root $\widehat{b}_r \in (0, b^*_{3+})$ of θ then it is unique (with $\widehat{b}_r = \widehat{b}_h$) and

$$\theta(b) \leq 0 \qquad \forall\, b \in (0, \widehat{b}_r). \tag{2.4.39}$$

Thus the question whether condition (2.4.36) holds on $(0, b^*_{3+})$ *reduces to determining whether* θ *has a root in* $(0, b^*_{3+})$. We answer this question below. Note that θ is positive for $b = b^*_{3+}$ since

$$\theta(b^*_{3+}) = \underbrace{j_{11}}_{<0} \cdot \underbrace{j_{21}}_{>0} \cdot \underbrace{j_{12}}_{<0} > 0$$

i) Let $\theta(0) < 0$, then by the intermediate value theorem there must be a root $\widehat{b}_r$ of θ located in $(0, b^*_{3+})$, see the black curve in Figure 2.4.23.

ii) Let $\theta(0) = 0$ and $\theta'(0) < 0$. Then the slope of θ is negative for $b = 0$ (see the red curve in Figure 2.4.23) and in particular for $\varepsilon > 0$ sufficiently small it holds that

$$\theta(\varepsilon) < 0,$$

once more implying by the intermediate value theorem that there must be a root $\widehat{b}_r$ of θ located in $(0, b^*_{3+})$.

iii) Let $\theta(0) = 0$ and $\theta'(0) = 0$ and $\theta''(0) < 0$. Then θ has a root and is strictly concave at $b = 0$ (see the blue curve in Figure 2.4.23). In particular for $\varepsilon > 0$ sufficiently small it holds that

$$\theta(\varepsilon) < 0,$$

once more implying by the intermediate value theorem that there must be a root $\widehat{b}_r$ of θ located in $(0, b^*_{3+})$.

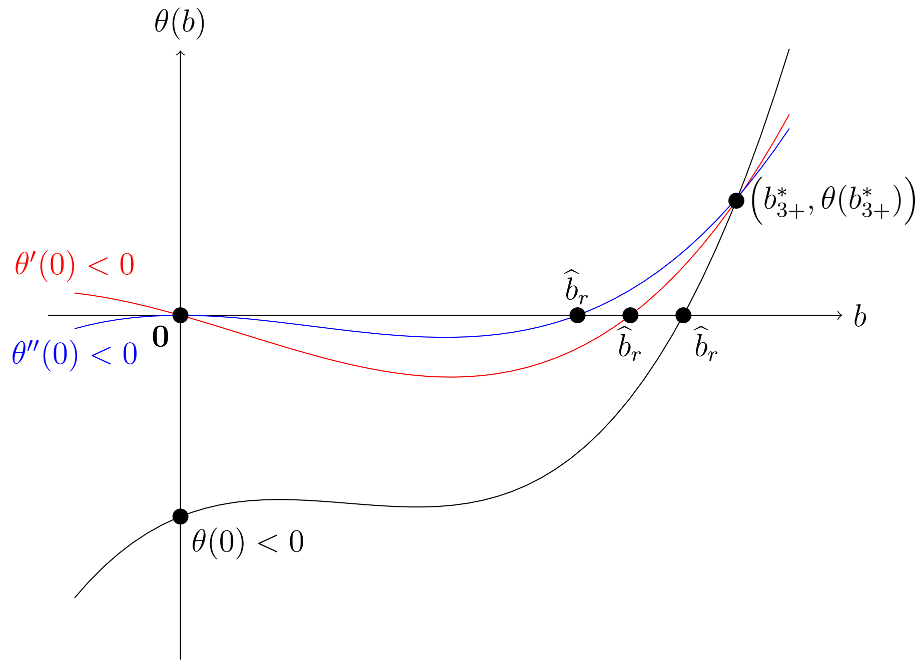


Figure 2.4.23: The unique root $\widehat{b}_r \in (0, b^*_{3+})$ of the respective polynomials θ.

This proves the first part of the lemma. We now assume that the above conditions do not hold.

- If $\theta(0) > 0$ then due to the continuity of θ for a sufficiently small $\varepsilon > 0$ it holds that
$$\theta(b) > 0 \qquad \forall\, b \in (0, \varepsilon). \tag{2.4.40}$$
Assuming that $\theta(b) > 0$ for all $b \in (0, b^*_{3+})$ does not hold, implies that θ has a root in $(0, b^*_{3+})$, in turn implying that (2.4.39) holds, which is a contradiction to (2.4.40).

- Likewise, if $\theta(0) = 0$ and $\theta'(0) > 0$, then θ is strictly increasing in a vicinity of $b = 0$ and hence (2.4.40) holds for a sufficiently small $\varepsilon > 0$. By the same argument as above we obtain the claim.

- Similarly, if $\theta(0) = 0$, $\theta'(0) = 0$ and $\theta''(0) > 0$, then the function is strictly convex at $b = 0$ and (2.4.40) holds for a sufficiently small $\varepsilon > 0$. We may use the same argument as previously to obtain the claim.

- Finally, if $\theta(0) = 0$, $\theta'(0) = 0$ and $\theta''(0) = 0$, then
$$\theta'''(0) = \gamma j_{23}^2 > 0$$
determines the local behaviour at $b = 0$. Since this is strictly positive we once more obtain that θ is strictly increasing in a vicinity of $b = 0$ and hence by the arguments from above, the claim holds. □

Remark 2.4.20.
Note that the conditions in the previous lemma, in fact are conditions on the *coefficients* of θ (recall (2.4.38)), since

$$\begin{aligned}
\theta(0) < 0 \quad &\Leftrightarrow \quad -\gamma j_{23}^2 (b_{3+}^*)^3 - j_{21} j_{12} j_{23} b_{3+}^* + j_{11} j_{23} b_{3+}^* (j_{11} - j_{23} b_{3+}^*) + j_{11} j_{21} j_{12} < 0 \\
&\Leftrightarrow \quad -\gamma j_{23}^2 (b_{3+}^*)^3 + \left(j_{11} j_{23} b_{3+}^* + j_{21} j_{12}\right)\left(j_{11} - j_{23} b_{3+}^*\right) < 0
\end{aligned}$$

$$\begin{aligned}
\theta'(0) < 0 \quad &\Leftrightarrow \quad 3\gamma j_{23}^2 \left(b_{3+}^*\right)^2 + 2 j_{11} j_{23}^2 b_{3+}^* + j_{21} j_{12} j_{23} - j_{11}^2 j_{23} < 0 \\
&\Leftrightarrow \quad 3\gamma j_{23} \left(b_{3+}^*\right)^2 + 2 j_{11} j_{23} b_{3+}^* + j_{21} j_{12} - j_{11}^2 > 0
\end{aligned}$$

$$\begin{aligned}
\theta''(0) < 0 \quad &\Leftrightarrow \quad -3\gamma j_{23}^2 b_{3+}^* - j_{11} j_{23}^2 < 0 \\
&\Leftrightarrow \quad -3\gamma b_{3+}^* - j_{11} < 0
\end{aligned}$$

These are conditions on the parameters a, c, e, f, g, h which are easily verified, if required. For example, using the definition of j_{11}, $b_{3+}^* > 0$ and γ, we obtain

$$\begin{aligned}
\theta''(0) < 0 \quad &\Leftrightarrow \quad -3\gamma j_{23}^2 b_{3+}^* - j_{11} j_{23}^2 < 0 \\
&\Leftrightarrow \quad -3\gamma b_{3+}^* - j_{11} < 0 \\
&\Leftrightarrow \quad -j_{11} < 3\gamma b_{3+}^* \\
&\Leftrightarrow \quad \frac{b_{3+}^*}{c} \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)} < 3\gamma b_{3+}^* \\
&\Leftrightarrow \quad \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)} < \frac{3cf^2}{g}\left(h - \frac{g}{f} - e\right)^2 \\
&\Leftrightarrow \quad (a+1)^2 < \frac{9c^2 f^4}{g^2}\left(h - \frac{g}{f} - e\right)^4 + 4\left(\frac{g}{f} - h\right)
\end{aligned}$$

Likewise, the conditions $\theta(0) < 0$ and $\theta'(0) < 0$ may be written in terms of the parameters of (2.1.5) - excluding the bifurcation parameter b.

This nearly completes the considerations of the equilibrium p_{3+}^*, as we now immediately conclude

Corollary 2.4.3.
Let $p_{3+}^* \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ hold. If either the conditions of Lemma 2.4.36 or Lemma 2.4.37 are met, then there exists a unique $\widehat{b} \in (0, b_{3+}^*)$ such that $(\widehat{b}, p_{3+}^*)$ is a Hopf bifurcation point and p_{3+}^* is unstable and hyperbolic for all $b \in (0, \widehat{b})$.

Proof.
Let $p_{3+}^* \in \mathcal{O}^+$ and $a > 2\sqrt{\frac{g}{f} - h} - 1$ hold.

- If the conditions of Lemma 2.4.36 are met, then by the same lemma, the second Routh-Hurwitz condition is violated for some $\widehat{b}_t \in (0, b_{3+}^*)$. Note that it might happen, that the third condition (2.4.36) is *also* violated for some $\widehat{b}_r \in (0, b^*_{3+})$. We then set

$$\widehat{b} := \max\{\widehat{b}_t, \widehat{b}_r\},$$

which ensures that *at least one* Routh-Hurwitz condition is violated for all $b > 0$ less than $\widehat{b}$ and *none* are violated for $b \in (\widehat{b}, b^*_{3+})$. Thus $\widehat{b}$ is a b-value for which the eigenvalues cross the imaginary axis. This value, however, is unique in $(0, b^*_{3+})$ by Lemma 2.4.34. Thus Corollary 2.4.2 and Lemma 2.4.35 yield the existence of the Hopf bifurcation along the branch of equilibria corresponding to p_{3+} for $b = \widehat{b} = \widehat{b}_h$ (by the uniqueness of $\widehat{b}_h$) and the claimed stability and hyperbolicity properties of p^*_{3+} hold.

- If the conditions of Lemma 2.4.37 are met then only the third Routh-Hurwitz criterion can and in fact is violated for some $\widehat{b}_r \in (0, b^*_{3+})$ by Lemma 2.4.37. Thus setting $\widehat{b} = \widehat{b}_r$ and arguing as in the previous point yields the claim. □

This allows us to prove Proposition 2.4.1:

Proof of Proposition 2.4.1.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold and furthermore assume that $p^*_{3+} \in \mathcal{O}^+$.

- If $a = 2\sqrt{\frac{g}{f} - h} - 1$ holds, then Lemma 2.4.27 yields that the equilibrium is unstable for any $b \in (0, b^*_{3+})$.

- Now assume $a > 2\sqrt{\frac{g}{f} - h} - 1$ holds. By Lemma 2.4.30 we know that the asserted $\widehat{b} \in (-\infty, b^*_{3+})$ exists. Corollary 2.4.3 supplies the sufficient conditions such that $\widehat{b} > 0$. These conditions are also necessary since otherwise (see Lemmas 2.4.36 and 2.4.37) all three of the Routh-Hurwitz criteria hold for all $b \in (0, b^*_{3+})$ and thus all three eigenvalues λ_1, λ_2, λ_3 have negative real part for all $b \in (0, b^*_{3+})$, implying that neither a Hopf bifurcation may occur, nor can the equilibrium turn unstable, i.e. $\widehat{b} \leq 0$. □

Thus we have shown that the point of coexistence p^*_{3+} is locally asymptotically stable for some values of $b \in (0, b^*_{3+})$, but may turn unstable via a Hopf bifurcation for values below a certain threshold $\widehat{b}$. We remark that the above proof of the existence of the Hopf bifrucation point bears similarity to that in [Liu, 1994], where the Routh-Hurwitz criteria are also used to obtain a condition for the existence of a Hopf bifurcation point. An open question that the result in Proposition 2.4.1 poses, is which type or rather *direction* the Hopf bifurcation has. Is it sub- or supercritcal? This is determined by the second non-degeneracy condition, which may in principle be checked by using normal form theory for example. Also what do the potential periodic solutions created by the Hopf bifurcation represent from a biological point of view? Among others, these questions will be addressed using numerical tools in section 2.5 below.

The equilibrium p_{3-}^*

Recall from Table 1 and Lemma 2.4.1 that under certain parameter conditions - which we assume to hold true for the moment - there may be a second interior equilibrium p_{3-}^* in the positive octant $\mathcal{O}^+$. Like the equilibrium p_{3+}^* this equilibrium enters the biologically relevant part of phase space (i.e. the set $\mathcal{O}_0^+$) via a transcritical bifurcation with the equilibrium p_2^* for the bifurcation value

$$b = b_{3-}^* = \frac{cx_{3-}^*}{x_{3-}^* + a}.$$

The stability properties of p_{3-}^* are more easily determined than those of p_{3+}^* - recall Proposition 2.4.1. In fact, the equilibrium is always unstable. We prove this in

Proposition 2.4.2.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold and furthermore assume that $p_{3-}^* \in \mathcal{O}^+$. Then the equilibrium is unstable for any $b \in (0, b_{3-}^*)$.

Proof.
Let $a = d$ and $f - \frac{g}{h} < 0$ hold and furthermore assume that $p_{3-}^* \in \mathcal{O}^+$. Since $p_{3-}^* \in \mathcal{O}^+$, it holds that $b \in (0, b_{3-}^*)$ - see Table 1. The Jacobian of the vector field v from (2.1.5) evaluated at the equilibrium p_{3-}^* is given by

$$\mathrm{Dv}(p_{3-}^*) = \begin{pmatrix} \frac{x_{3-}^* \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x_{3-}^* + a} & -\frac{x_{3-}^*}{x_{3-}^* + a} & 0 \\ \frac{ac(1 - x_{3-}^*)}{x_{3-}^* + a} & \left(b_{3-}^* - b\right)\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right) & -\frac{y_{3-}^*}{y_{3-}^* + e} \\ 0 & \frac{f^2}{g}\left(h - \frac{g}{f} - e\right)^2\left(b - b_{3-}^*\right)^2 & 0 \end{pmatrix}$$

Considering the trace of $\mathrm{Dv}(p_{3-}^*)$, we observe that it is always strictly positive for all $b \in (0, b_{3-}^*)$:

$$\mathrm{tr}(\mathrm{Dv}(p_{3-}^*)) = \underbrace{\frac{x_{3-}^* \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x_{3-}^* + a}}_{\geq 0} + \underbrace{\left(b_{3-}^* - b\right)}_{>0}\underbrace{\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right)}_{>0} > 0$$

Since the trace of the matrix $\mathrm{Dv}(p_{3-}^*)$ is equal to the sum of the real parts of the eigenvalues of $\mathrm{Dv}(p_{3-}^*)$, we immediately conclude that for any $b \in (0, b_{3-}^*)$ at least one eigenvalue of $\mathrm{Dv}(p_{3-}^*)$ has a strictly positive real part. Hence by Lyapunov's indirect method the equilibrium p_{3-}^* is unstable for all $b \in (0, b_{3-}^*)$. □

2.5 Numerical results and biological interpretation

Having established the existence of the semiflow Φ, as well as the nature of the attractor $\mathcal{A}$ for various parameter regions in the previous sections, we turn to the visualisation and interpretation of these results. More precisely, in subsection 2.5.1 we investigate the various restrictions on the parameters which we have imposed. We also interpret the attained results, from a biological point of view in subsection 2.5.2. Moreover, we present numerical results, being computed solutions s of system (2.1.5), and visualise them by plotting their corresponding positive phase curves in the phase space $\mathcal{O}_0^+$ in subsections 2.5.2 and 2.5.3. Several bifurcations occurring in the system (some of which have already been proven to occur by analytical means in the sections above) are also investigated numerically in these subsections.

2.5.1 Restrictions of parameters

Recall that the two parameter restrictions we imposed throughout most parts this thesis are

$$a = d \qquad \text{and} \qquad f - \frac{g}{h} < 0.$$

These two restrictions were sufficient for the solutions s not to blow up in finite time nor as $t \to \infty$ (recall Propositions 2.2.1 and 2.2.2). In addition to this they guaranteed the existence of the attractor $\mathcal{A}$ (see Theorem 2.3.1).

- As mentioned in the subsequent remark to Lemma 2.2.3, the restriction

  $$a = d$$

  is a common assumption for predator-prey models which are modelled with a Holling functional response of type II. The assumption implies that the availability of the prey species x for the specialist predator species y, represented by the term

  $$\frac{xy}{x+d} = \frac{xy}{x+a}$$

  in (2.1.5), is - up to the factor c - equal to the quantity by which the prey is diminished by the specialist predator, represented by the term

  $$-c \cdot \frac{xy}{x+a}\,.$$

  This is commonly interpreted as follows: When the predator species preys on the prey species, it gains the same energy that the prey species loses up to a factor c. As mentioned in Remark 2.2.2 even the assumption $a \leq d$ is sufficient for the result to hold, which, from a biological point of view, means that the specialist predator species cannot gain more energy from the prey species, than the prey species loses itself (or eat *more* food than it kills). If on the other hand $a > d$, then the specialist predator species could potentially gain more energy from the prey that it kills, than the prey species loses itself, which seems contradictory to the idea that energy is conserved or even dissipates as one moves up the trophic levels in a food chain. Thus the assumption $a \leq d$ seems sensible and even necessary from a biological point of view. In particular, the restriction $a = d$ is a biologically meaningful hypothesis.

- The restriction
$$f - \frac{g}{h} < 0$$
can equivalently be considered in the original parameters from (2.1.1). Here it reads
$$\frac{a_1^2}{b_1\omega_0\omega_2}\left(c_0 - \frac{\omega_3}{d_3}\right) < 0$$
and since all parameters are assumed to be strictly positive, this simplifies to
$$c_0 - \frac{\omega_3}{d_3} < 0.$$
In this form the assumption has been made in previous works (cf. e.g. [Aziz-Alaoui, 2002], [Letellier et al., 2002]). It implies that the reproduction rate c_0 of the generalist predator species (modelled by z) may not exceed the rate of loss the generalist predator species experiences due to lack of one of its food sources, namely the specialist predator species y. On the one hand, the species modelled by z is assumed to *reproduce rarely*, which motivates that c_0 should in fact be a small quantity. On the other hand, z models a *generalist* predator, which implies that the lack of a single food source - such as y - should not be too much of a problem for the predator, i.e. $\frac{\omega_3}{d_3}$ is also a relatively small quantity. Thus the imposed condition is indeed a restriction on the variety of generalist predator species that may be modelled in this way. Alternatively one can understand the quantity $\frac{g}{f} - h > 0$ as a *threshold value*. If the specialist predator species density is below this value, the generalist predator species cannot increase in numbers and vice versa (recall the equivalence in (2.2.9)). Thus if this threshold value is negative, the generalist predator species always reproduces. I.e. if we consider the opposite condition
$$f - \frac{g}{h} \geq 0 \qquad \Leftrightarrow \qquad c_0 - \frac{\omega_3}{d_3} \geq 0,$$
we see that this would imply that the generalist predator species density explodes, regardless of other limiting effects of the environment (recall Lemma 2.2.4). This seems unreasonable from a biological point of view and is a possible drawback or limitation of the model equations. It gives rise to the idea that the inequality $f - \frac{g}{h} < 0$ has to hold for the model to be biologically feasible.

Thus a biological interpretation of the results in Propositions 2.2.1 and 2.2.2 and Theorem 2.3.1 may be summed up as follows:

Under the two assumptions that

- *the specialist predator gains no more energy than the prey loses when the two species interact,*
- *the generalist predator does not reproduce faster than it diminishes due to the lack of availability of the specialist predator as food source,*

the population densities of the GSP food chain species (modelled by (2.1.5)*) are confined to finite numbers for all future times and converge to a set $\mathcal{A}$ (the attractor) as $t \to \infty$.*

We now turn to investigating the parameter b. Recall that this was the primary bifurcation parameter we varied in section 2.4. The nature of the attractor $\mathcal{A}$ and the dynamics were fundamentally different for various values of the parameter b (recall Theorem 2.4.1, Conjecture 2.4.1 and Proposition 2.4.1). In the original parameters from (2.1.1) the parameter reads

$$b = \frac{a_2}{a_1},$$

where a_2 was the death rate of the specialist predator species and a_1 the birth rate of the prey species. Thus:

Decreasing b implies either a decrease in the mortality rate of the specialist predator species (modelled by y) or an increase in the birth rate of the prey species (modelled by x), or both.

We bear this in mind when interpreting the results we obtained.

2.5.2 Interpretation and visualisation of the results

The aim of this subsection is to interpret and visualise the results of Theorem 2.4.1. We first remark on the numerical methods used to obtain an approximate solution (and thus the positive phase curve) for the visualisation.
The software MATLAB [MATLAB, 2015] was used to obtain the results. For more details on the source code see Appendix D. We emphasise that, unless stated otherwise, all solutions were obtained with the ode45-solver, using:

- a maximal step size of $\hat{t} = 10^{-4}$
- the time interval $I = [0, 2000]$
- the initial conditions $s_0 = (x_0, y_0, z_0)^T = (0.9, 0.3, 0.1)^T$

The choice of the initial conditions reflects the idea that the lower trophic levels are generally more populated, while higher trophic levels are scarcely populated (recall the energy pyramid in Figure 1.0.4). I.e. the initial conditions were chosen so that they reflect a potentially 'normal' state of the ecosystem.
Moreover, two points in parameter space were used for the simulations. For one, the **standard parameters** from (2.1.4) were used, which we list again here, for convenience sake:

$$\begin{aligned} a &= \tfrac{3}{10}, \qquad c = 1, \qquad d = \tfrac{3}{10}, \qquad e = \tfrac{3}{20} \\ f &= \tfrac{400}{81}, \qquad g = \tfrac{200}{81}, \qquad h = \tfrac{3}{10}. \end{aligned} \tag{2.5.1}$$

Note that we omitted the value $b = \frac{1}{2}$ since b is the bifurcation parameter and is varied. We also introduce a set of **non-standard parameters**:

$$\begin{aligned} a &= \tfrac{3}{10}, \qquad c = 1, \qquad d = \tfrac{3}{10}, \qquad e = \tfrac{3}{20} \\ f &= \tfrac{400}{81}, \qquad g = \tfrac{200}{81}, \qquad h = \tfrac{1}{20}. \end{aligned} \tag{2.5.2}$$

The only difference to the biologically relevant standard parameters is the value of h. The choice was made on the basis of trying to keep the parameters *comparable* to the standard parameters, but nonetheless observing a different behaviour of solutions in phase space.

Non-standard parameters

We first consider Theorem 2.4.1 for the non-standard parameters in (2.5.2). The conditions

$$a = \frac{3}{10} = d \qquad \text{and} \qquad f - \frac{g}{h} = \frac{400}{81} - \frac{\frac{200}{81}}{\frac{1}{20}} = -\frac{3600}{81} = -\frac{400}{9} < 0$$

are both fulfilled by these parameters. Furthermore, it holds that

$$\begin{aligned} \frac{c}{a+1} &= \frac{1}{\frac{3}{10}+1} = \frac{10}{13} \approx 0.7629 \\ \frac{c(1-a)}{a+1} &= \frac{1-\frac{3}{10}}{\frac{3}{10}+1} = \frac{7}{13} \approx 0.5385 \\ \frac{(a+1)^2}{4} &= \frac{\left(\frac{3}{10}+1\right)^2}{4} = \frac{169}{400} < \frac{180}{400} = \frac{9}{20} = \frac{1}{2} - \frac{1}{20} = \frac{g}{f} - h \end{aligned} \tag{2.5.3}$$

Considering Theorem 2.4.1 *i*) we see that for

$$b = \frac{8}{10} > \frac{10}{13} = \frac{c}{a+1}$$

it holds that the global attractor is given by

$$\mathcal{A} = [0,1] \times \{0\} \times \{0\}$$

and the equilibrium $p_1^* = (1,0,0)^T$ is globally asymptotically stable in $\mathcal{O}^+$ (more precisely, except if $x_0 = 0$) - recall Figure 2.4.9. Using $b = 0.8$ and the parameters in (2.5.2) we obtain Figure 2.5.1 for the initial condition $s_0 = (0.9, 0.3, 0.1)^T$. We remark

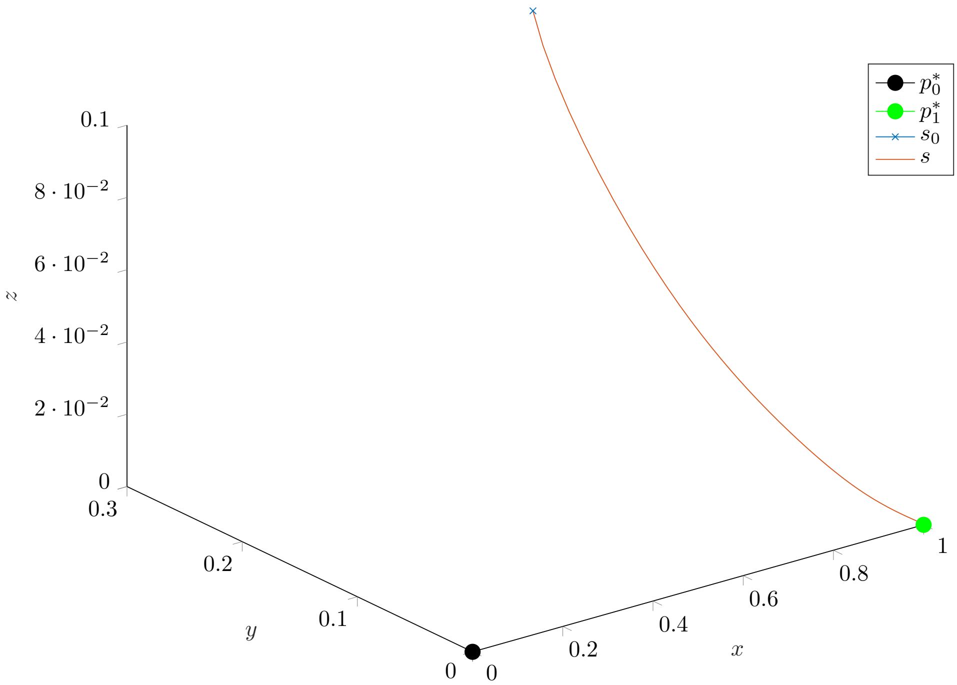


Figure 2.5.1: The equilibrium p_1^* is globally asymptotically stable in $\mathcal{O}^+$ for $b = 0.8$

that using a single initial condition is not necessarily particularly significant, when visualising a global attractor, such as $\mathcal{A}$. However, in order to be able to compare the results as we vary the bifurcation parameter b, we have chosen to always use the same, single initial condition. Recalling the biological meaning of the parameter b from above, we conclude that the case $b > \frac{c}{a+1}$ may be interpreted as follows:

For low birth rates of the prey species or high death rates of the specialist predator species, both the specialist and the generalist predator species become extinct, while the prey species is the sole survivor and its density tends towards the carrying capacity of the ecosystem (rescaled to the value 1 here), as $t \to \infty$. Hence the prey species provides insufficient amounts of energy to sustain a predator species over long time periods.

Decreasing the bifurcation parameter to $b = \frac{7}{10}$ we observe, using (2.5.3), that

$$\frac{c(1-a)}{a+1} = \frac{7}{13} < \frac{7}{10} < \frac{10}{13} = \frac{c}{a+1}$$

holds. Since the condition

$$\frac{(a+1)^2}{4} < \frac{g}{f} - h \tag{2.5.4}$$

is also fulfilled (see (2.5.3)), the result of Theorem 2.4.1 *ii*) holds. Hence the equilibrium p_2^* is globally asymptotically stable in $\mathcal{O}^+$ (more precisely, for $x_0 \neq 0 \neq y_0$) - recall Figure 2.4.17. The numerical simulation of this case yields Figure 2.5.2.

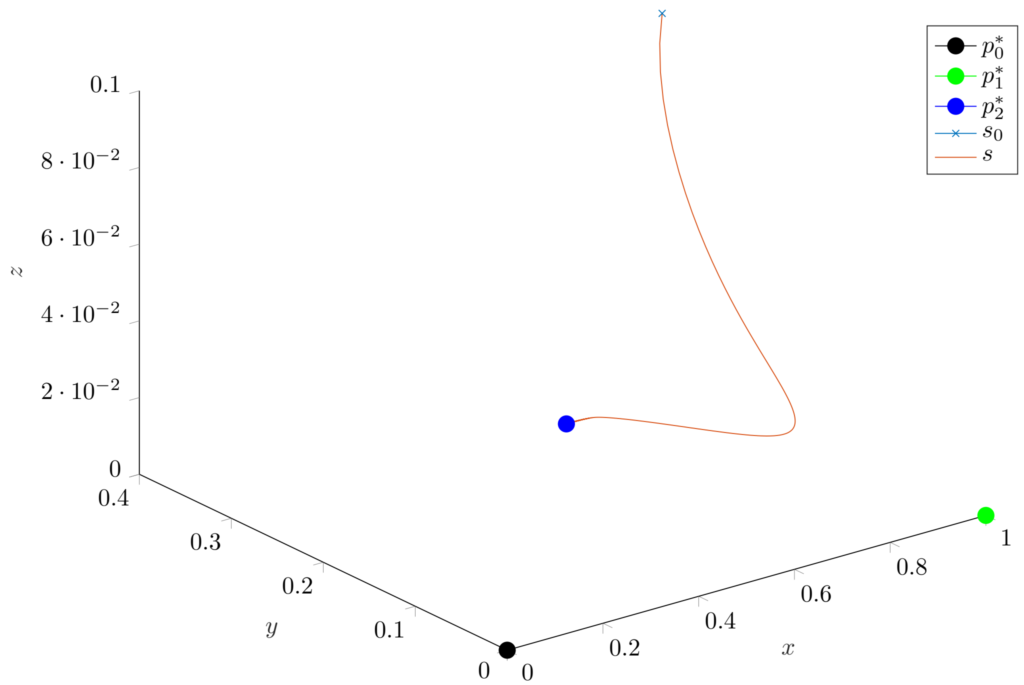


Figure 2.5.2: The equilibrium p_2^* is globally asymptotically stable in $\mathcal{O}^+$ for $b = 0.7$

For $b = \frac{6}{10}$ it still holds that

$$\frac{c(1-a)}{a+1} = \frac{7}{13} < \frac{6}{10} < \frac{10}{13} = \frac{c}{a+1} \tag{2.5.5}$$

and hence the same situation as above arises, see Figure 2.5.3. Interpreting the above result, requires considering the condition (2.5.4). Recalling the nullclines in Figure 2.4.2, we observe that the inequality (2.5.4) expresses that the *maximal* density value $\frac{(a+1)^2}{4}$ for which the specialist predator species density still increases is smaller than the threshold value $\frac{g}{f} - h > 0$ for which the generalist predator species density increases (thus leading to the extinction of the z-species). In this case, the attractor $\mathcal{A}$ is planar. This allows the following biological interpretation:

> *If the maximal density value for which the specialist predator species density increases is less than the (minimal) threshold density value $\frac{g}{f} - h$ for which the generalist predator species density increases, the generalist predator species becomes extinct.*

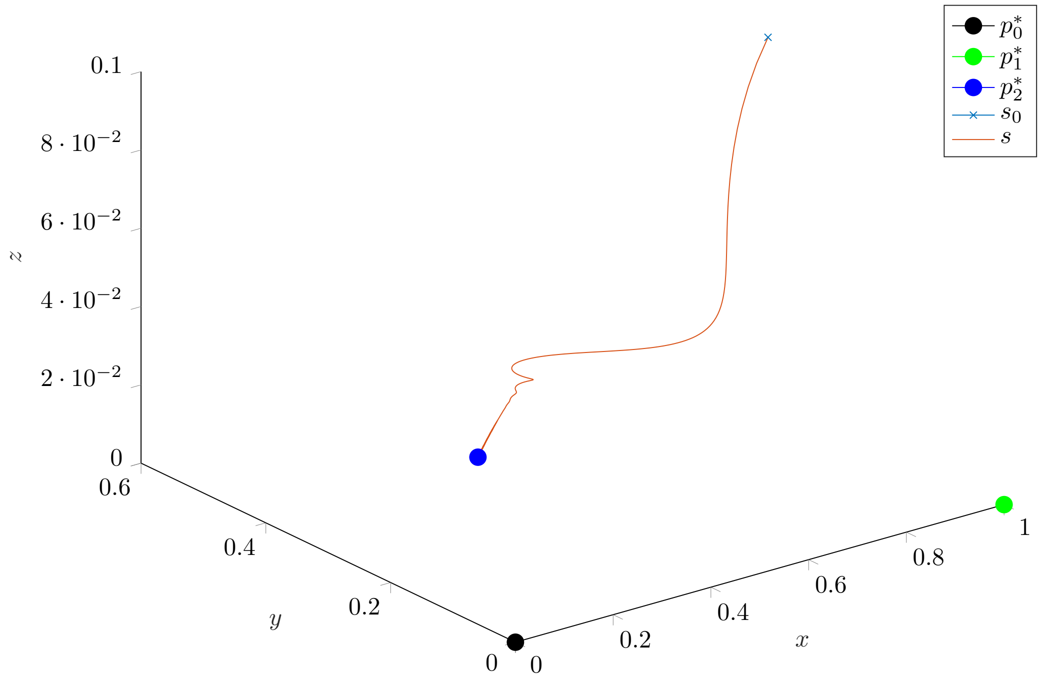


Figure 2.5.3: The equilibrium p_2^* is globally asymptotically stable in $\mathcal{O}^+$ for $b = 0.6$

Condition (2.5.4) relates the sizes of the parameter a (associated with the prey species) and the parameters f, g and h (associated with the generalist predator species). In particular this shows that:

Parameters or changes of parameters in the lowest trophic level may have an influence on the population dynamics in the highest trophic level and vice versa.

This shows that although the $\dot{x}$-equation and $\dot{z}$-equation in (2.1.5) are not directly coupled, their induced species dynamics still influence each other. Note that in the above interpretation we have not yet included the role of the bifurcation parameter b. We will do this after considering the cases $b = \frac{1}{2}$ and $b = \frac{2}{5}$. In both cases it holds that

$$\frac{2}{5} < \frac{1}{2} < \frac{7}{13} = \frac{c(1-a)}{a+1}.$$

Hence the equilibrium p_2^* is no longer globally asymptotically stable in $\mathcal{O}^+$, but rather a periodic orbit Γ_{per}^* in the positive x-y quadrant exists (recall Lemma 2.4.2). Since the periodic orbit Γ_{per}^* is bounded, it is also part of the attractor $\mathcal{A}$, recall Figure 2.4.18. A subcritical Hopf bifurcation occurs for

$$b = \frac{c(1-a)}{a+1} = \frac{7}{13}$$

along the branch of equilibria corresponding to p_2^* (see Figure 2.5.4), creating the orbit Γ_{per}^*. Figures 2.5.5 and 2.5.6 show the numerical results for $b = \frac{1}{2}$ and $b = \frac{2}{5}$.

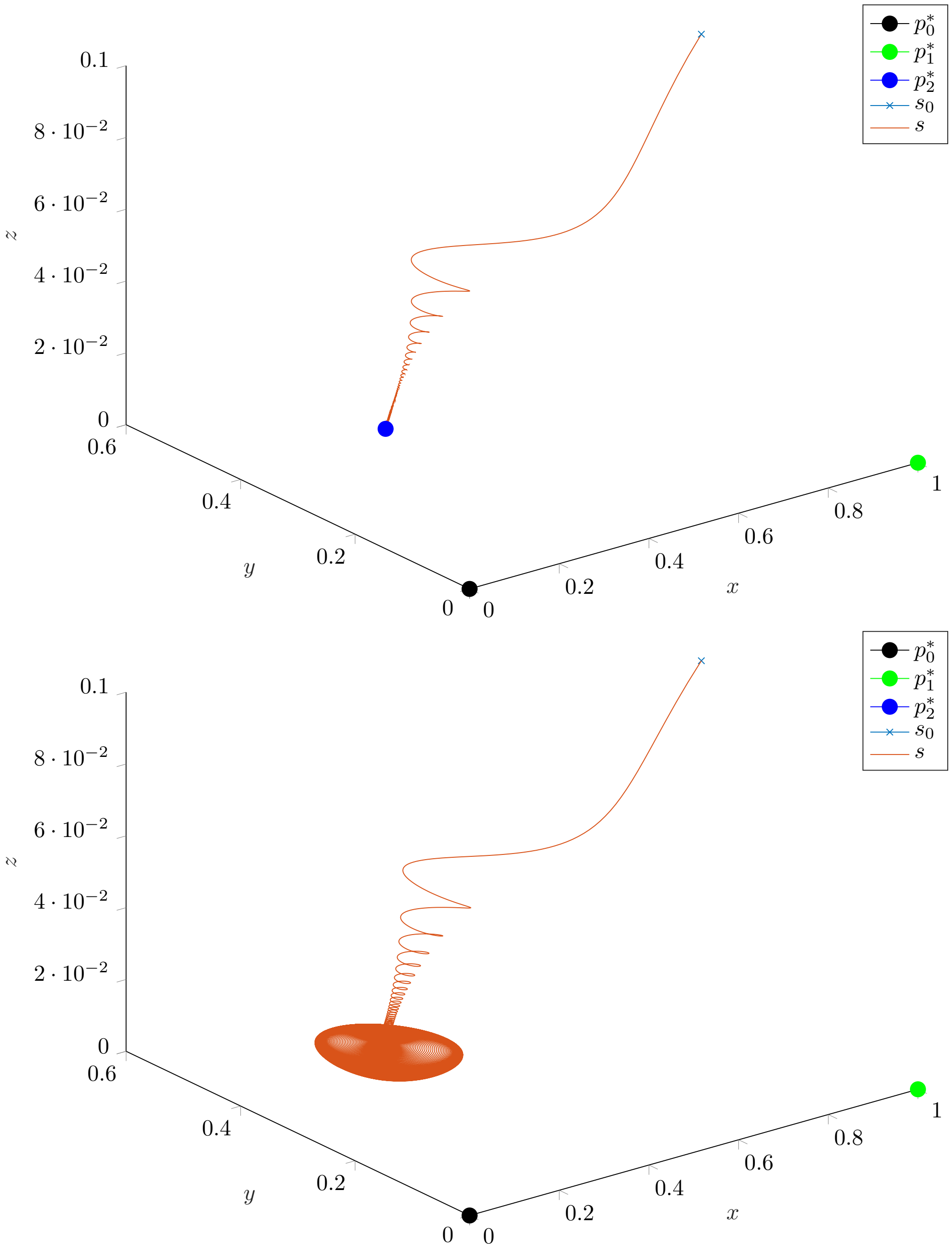


Figure 2.5.4: The cases $b = 0.54$ (top) and $b = 0.53$ (bottom), close to the Hopf bifurcation value $b = \frac{7}{13} \approx 0.5385$

We observe that the periodic orbit Γ^*_{per} seems to inherit the stability properties of p_2^* for $b < \frac{c(1-a)}{a+1}$. This is the case since Γ^*_{per} is orbitally stable in the positive x-y quadrant (recall Lemma 2.4.2) and the attractor is still planar (since (2.5.4) still holds), but the equilibrium p_2^* has turned unstable. From a biological point of view this means that *if the condition* (2.5.4) *holds*:

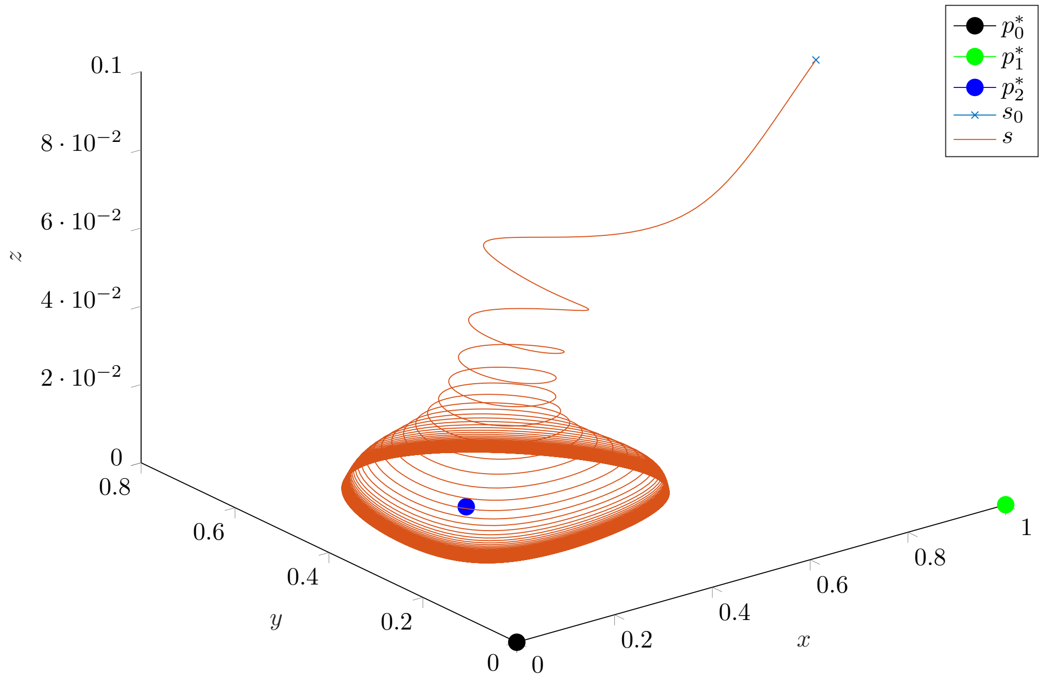


Figure 2.5.5: For $b = 0.5$ The positive phase curve converges to the periodic orbit Γ^*_{per} as $t \to \infty$

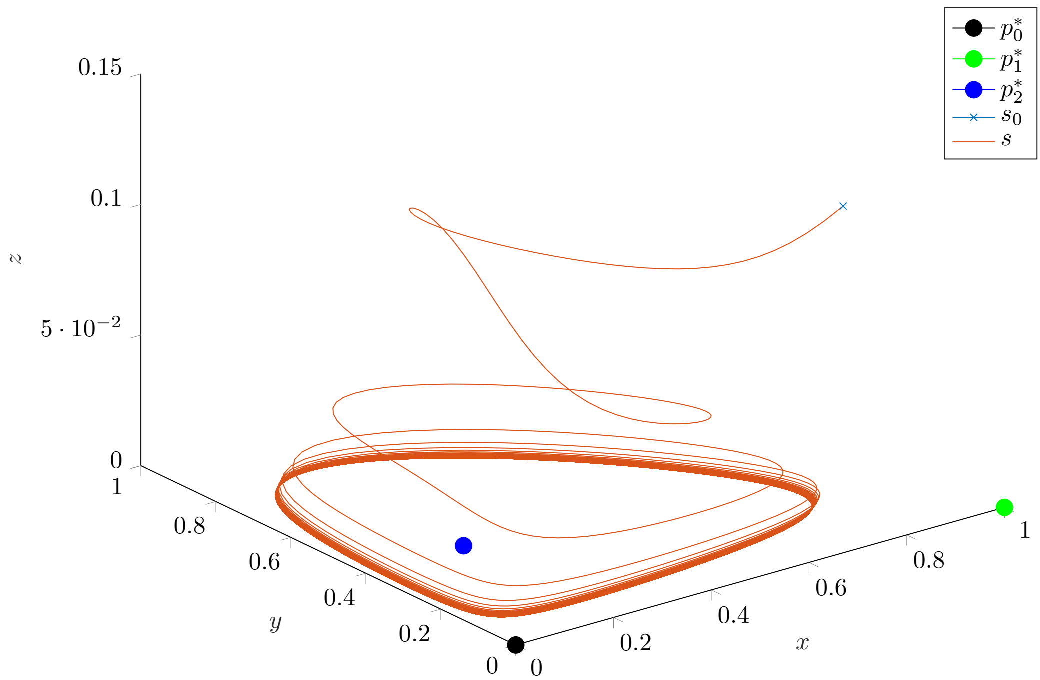


Figure 2.5.6: For $b = 0.4$ The positive phase curve converges to the periodic orbit Γ^*_{per} as $t \to \infty$

For mid-range birth rates of the prey species and death rates of the specialist predator species (see (2.5.5)*), the generalist predator species becomes extinct, while the prey and specialist predator species tend towards a stable equilibrium of coexistence, as* $t \to \infty$*.*
For high birth rates of the prey species or low death rates of the specialist predator species, the prey and specialist predator species tend to coexist in stable cycles, while the generalist predator species still becomes extinct.

Decreasing the parameter b further does not have any effect on the qualitative behaviour of the system, see Figure 2.5.7 for $b = 0.2$ for example. We see that the orbitally stable limit cycle Γ^*_{per} still exists. It merely grows in size (compare the scaling of the x- and y-axis in Figures 2.5.6 and 2.5.7), i.e. the population densities of the prey and the specialist predator species vary more (over time) as $b \to 0$. The reason for this is that as b tends to zero the specialist predator species density does not diminish quickly (the death rate a_2 of the specialist predator is low) and has food in abundance (the birth rate a_1 of the prey species is high). Very low species densities of a population may also be considered as critical, since - at least from a statistical point of view - extinction becomes more likely. In light of this argument, the limit cycle in Figure 2.5.7 does not necessarily reflect a stable long term-behaviour as $b \to 0$. Hence:

For very small values of b *the specialist predator species can populate the ecosystem to such an extreme, that it can nearly extinguish the entire prey species before coming close to extinction itself shortly thereafter.*

This also explains the shape of the limit cycle Γ^*_{per} and the direction in which the cycle oscillates.
We emphasise that since condition (2.5.4) holds, the attractor $\mathcal{A}$ is planar by Theorem 2.4.1 and the generalist predator species becomes extinct for any choice of the bifurcation parameter b. In particular, the limit of any solution must lie in the positive x-y quadrant. This suggests, that the long-term behaviour of the system is mainly driven by the specialist predator and prey species, i.e. the first two equations in (2.1.5), namely

$$\dot{x} = x\left(1 - x - \frac{y}{x+a}\right)$$
$$\dot{y} = y\left(-b + \frac{cx}{x+a}\right).$$

This subsystem has been studied thoroughly (see e.g. [Muratori and Rinaldi, 1989], [Feo and Rinaldi, 1997]). In particular the existence and stability properties of the periodic orbit Γ^*_{per} has been established analytically for $b < \frac{c(1-a)}{a+1}$ (cf. [May, 1972], [Cheng, 1981]). The numerical computations (recall Figures 2.5.5, 2.5.6 and 2.5.7)

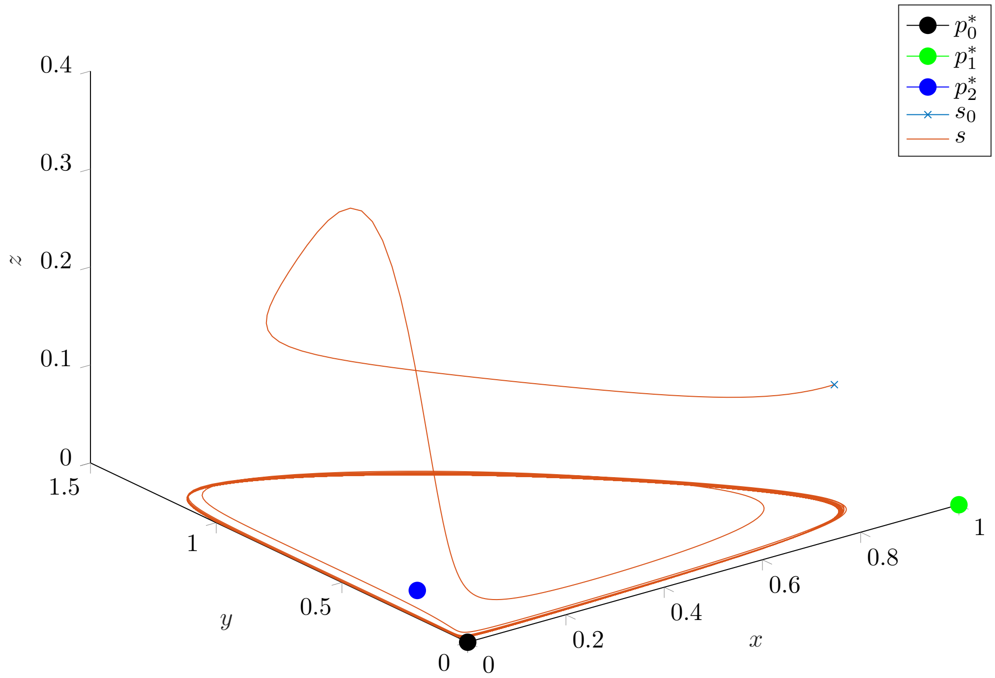


Figure 2.5.7: For $b = 0.2$ the positive phase curve approaches the periodic orbit Γ^*_{per} as $t \to \infty$

suggest that this stability property of Γ^*_{per} also extends to the three-dimensional system (2.1.5). Note that it is, however, possible to choose a point in $\mathcal{O}^+$ on the *one-dimensional centre manifold* $W^c_{loc}(p_2^*)$ of p_2^* in which case the solution s with this point as initial condition will converge to p_2^* as $t \to \infty$ (observe the spirals around $W^c_{loc}(p_2^*)$ in Figure 2.5.5 and recall Figure 2.4.11). We conclude that for parameter ranges that cause the top predator species to become extinct (see Theorem 2.4.1), the long-term dynamics of the system are similar to those of the two-dimensional subsystem, but not identical. The non-standard parameters from (2.5.2) represent such a case and a stability and bifurcation diagram of the above results may be constructed, see Figure 2.5.8.

We observe that there is always one stable set in the bifurcation diagram. An interpretation of this is:

The GSP food chain model predicts that an extinction of the top generalist predator species does not destabilise the population of the lower trophic levels of the ecosystem, but rather that either the prey species is a sole survivor or the prey and specialist predator species coexist (either tending towards an equilibrium p_i^* or periodic motions on Γ^*_{per} asymptotically, as $t \to \infty$).

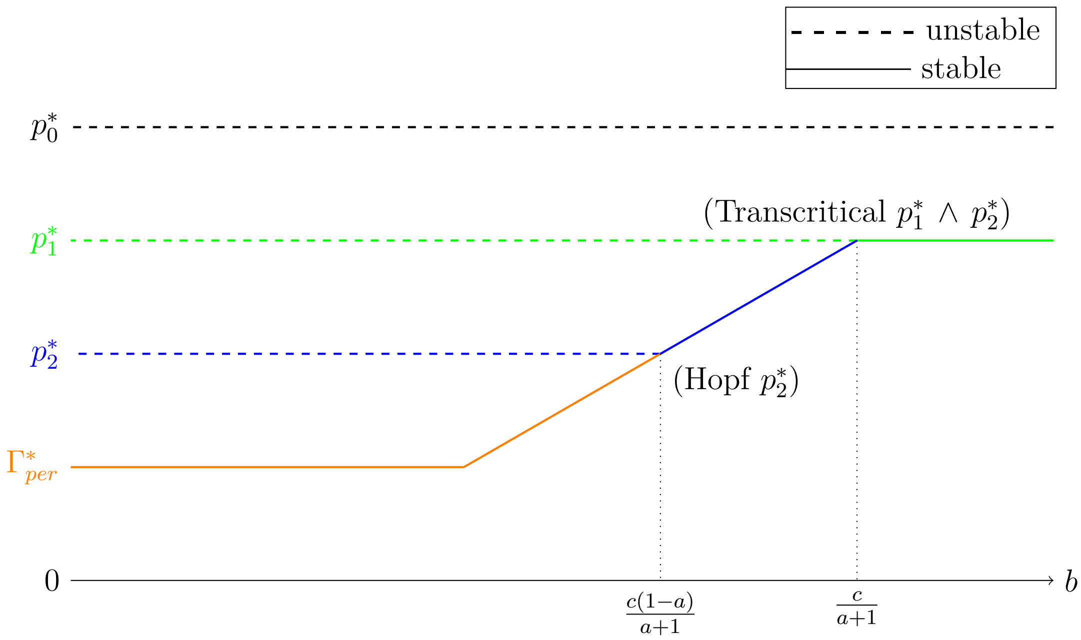


Figure 2.5.8: A stability and bifurcation diagram for the bifurcation parameter b and the non-standard parameters in (2.5.2)

Standard parameters

We turn to study the case of the standard parameters given in (2.5.1). They fulfil

$$a = \frac{3}{10} = d \qquad \text{and} \qquad f - \frac{g}{h} = \frac{400}{81} - \frac{\frac{200}{81}}{\frac{3}{10}} = -\frac{800}{81} < 0,$$

i.e. the two basic assumptions we made throughout the majority of this thesis hold. Thus Theorem 2.4.1 i) holds for

$$b > \frac{c}{a+1} = \frac{10}{13} \approx 0.7629.$$

In particular, for $b = 0.8$ the equilibrium p_1^* is globally asymptotically stable in $\mathcal{O}^+$ - see Figure 2.5.9. We now decrease the value of the bifurcation parameter to $b = 0.75$. Considering the three conditions in Theorem 2.4.1 ii) we observe that none of them hold, since

$$\begin{aligned} \frac{(a+1)^2}{4} &= \frac{169}{400} > \frac{80}{400} = \frac{1}{2} - \frac{3}{10} = \frac{g}{f} - h \\ 1 &> \frac{3}{10} = a \\ \frac{c}{4\left(\frac{g}{f} - h\right)} &= \frac{1}{4 \cdot \frac{1}{5}} = \frac{5}{4} > \frac{3}{4} = b \end{aligned} \qquad (2.5.6)$$

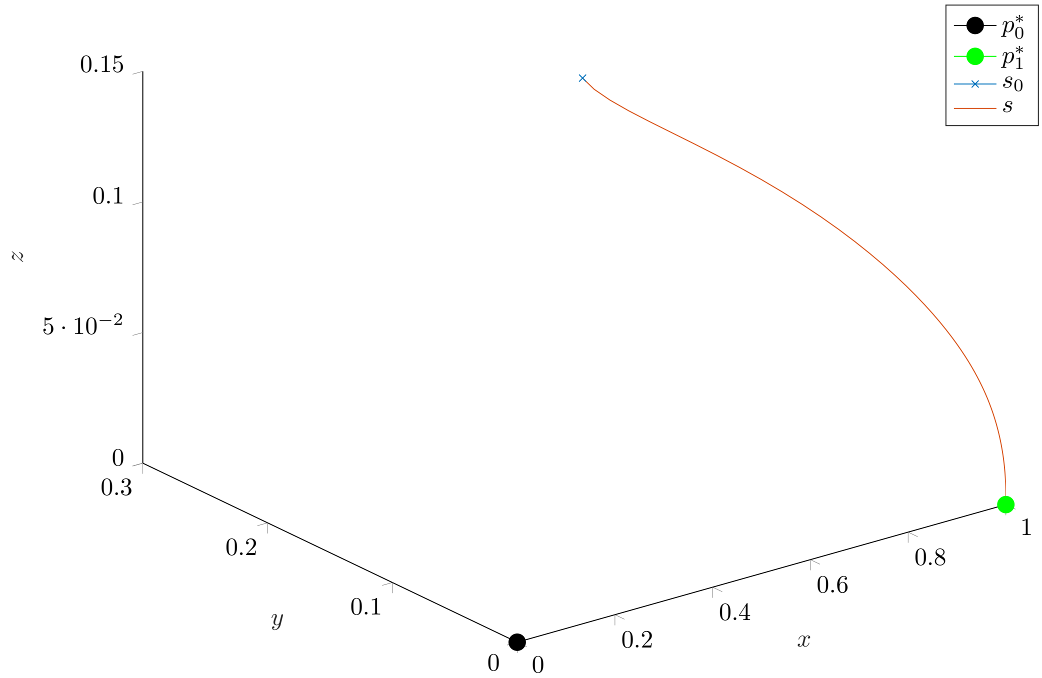


Figure 2.5.9: The equilibrium p_1^* is globally asymptotically stable in $\mathcal{O}^+$ for $b = 0.8$

Considering Table 1 we conclude from the first two lines of (2.5.6) that $p_{3+}^* \in \mathcal{O}_0^+$ if and only if

$$b \leq b_{3+}^* = \frac{cx_{3+}^*}{x_{3+}^* + a}$$

We compute the value of b_{3+}^* as

$$x_{3+}^* = \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} = \frac{7}{20} - \sqrt{\frac{89}{400}} = \frac{7+\sqrt{89}}{20}$$

$$\Rightarrow \quad b_{3+}^* = \frac{cx_{3+}^*}{x_{3+}^* + a} = \frac{\frac{7+\sqrt{89}}{20}}{\frac{7+\sqrt{89}}{20} + \frac{3}{10}} = \frac{1+3\sqrt{89}}{40} \approx 0.7325$$

Thus for the parameter range

$$b \in \left(b_{3+}^*, \frac{c}{a+1}\right) = \left(\frac{1+3\sqrt{89}}{40}, \frac{10}{13}\right) \approx (0.7325, 0.7629)$$

neither Theorem 2.4.1 holds, nor is the equilibrium p_{3+}^* in the non-negative octant. This is the case we consider in Conjecture 2.4.1, in which we suggested that the attractor $\mathcal{A}$ remains planar. Since $b = 0.75$ is in the above range, we can check this hypothesis for the standard parameter and the initial condition we use for the computations, i.e. $s_0 = (0.9, 0.3, 0.1)^T$. The result may be found in Figure 2.5.10. Observe that the phase curve moves into a small neighbourhood of the equilibrium p_1^*, before it converges to p_2^* as $t \to \infty$. We give a biological interpretation of the above cases in the following:

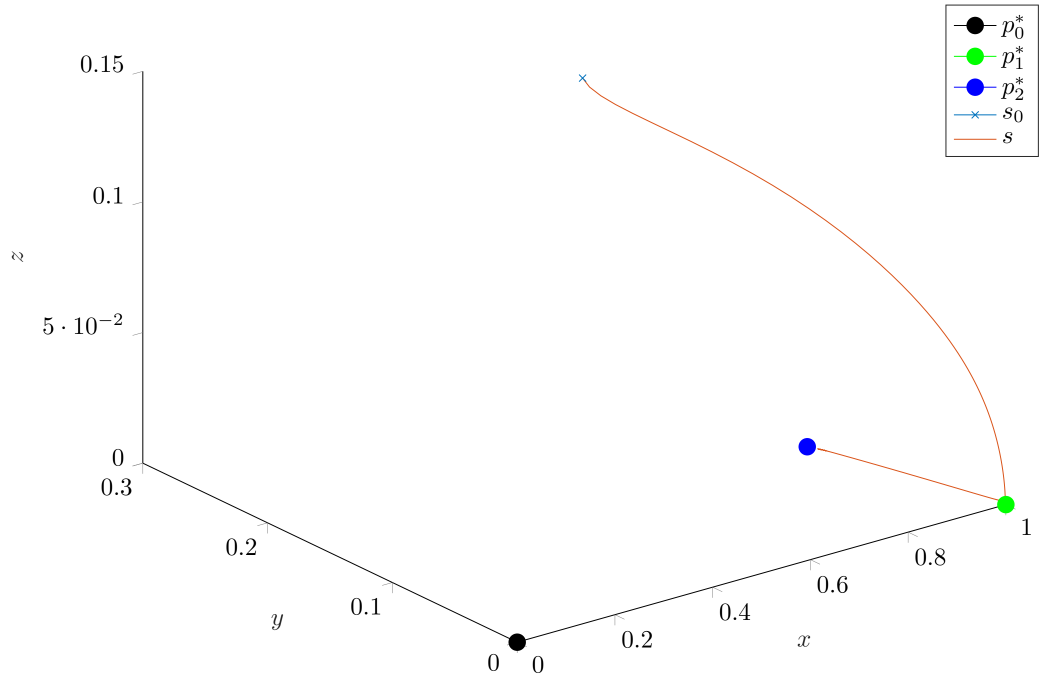


Figure 2.5.10: For $b = 0.75$ the positive phase curve converges to equilibrium p_2^* as $t \to \infty$

For low birth rates of the prey species or high death rates of the specialist predator species (i.e. comparatively large b-values, $b \geq b_{3+}^*$), the generalist predator species and possibly the specialist predator species (if $b \geq \frac{c}{a+1}$) become extinct, while the prey species survives. The ecosystem tends towards the state of sole survival or coexistence of the two species in the lower trophic levels, as $t \to \infty$.

For values of the bifurcation parameter $b > 0$ below b_{3+}^* a fourth equilibrium is present in the non-negative octant (due to the transcritical bifurcation of p_2^* and p_{3+}^* - recall Lemma 2.4.1). Since the first line of (2.5.6) implies that

$$a > 2\sqrt{\frac{g}{f} - h} - 1$$

holds, Proposition 2.4.1 also holds, i.e. there exists some interval $(\widehat{b}, b_{3+}^*)$ such that the equilibrium p_{3+}^* is locally asymptotically stable. Consider Figure 2.5.11 for the value $b = 0.7$. Note that it is not clear *a priori* if $\widehat{b} < 0.7$, i.e. whether Proposition 2.4.1 indeed holds for $b = 0.7$. We can determine the value of $\widehat{b}$ by Lemmas 2.4.36 and 2.4.37, and in particular whether $\widehat{b}$ is positive. If it is, a Hopf bifurcation occurs along the branch of equilibria corresponding to p_{3+}^* at $b = \widehat{b}$ and the equilibria are

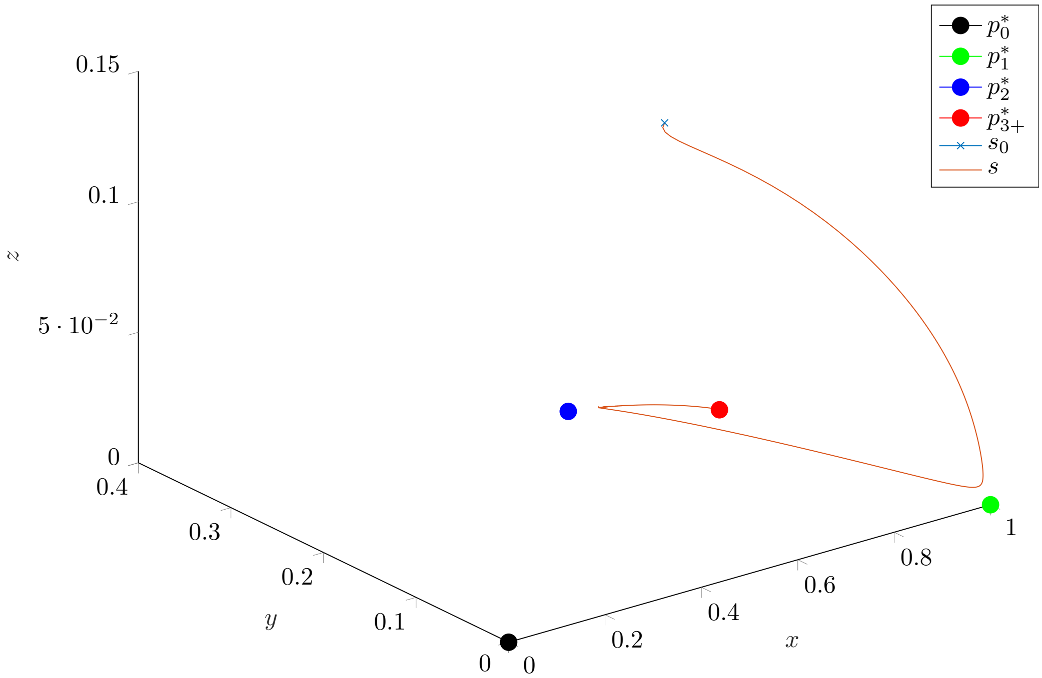


Figure 2.5.11: For $b = 0.7$ the solution converges to the asymptotically stable equilibrium p_{3+}^* as $t \to \infty$

unstable for all $b \in (0, \widehat{b})$. Observe that since

$$(a+1)^2 = \frac{169}{100} > \frac{144}{100} = \frac{16}{25} + \frac{4}{5} = c^2 \left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e} \right)^2 + 4 \left(\frac{g}{f} - h \right)$$

holds for the standard parameters (2.5.1), the conditions of Lemma 2.4.36 are *not* met. Thus we check the conditions of Lemma 2.4.37 next. By the subsequent remark on the lemma this is equivalent to determining the coefficients of the polynomial θ introduced in (2.4.38). We compute these numerically (rounding to four decimal places) and obtain

$$\theta(0) \approx -0.2246 \qquad \theta'(0) \approx 0.5983$$
$$\theta''(0) \approx -0.6425 \qquad \theta'''(0) \approx 0.395$$

In particular it holds that $\theta(0) < 0$ and the criteria of Lemma 2.4.37 are met, i.e. $\widehat{b} > 0$. From the proof of Lemma 2.4.37 we know that the precise value $\widehat{b}$ is now given by the unique zero of the polynomial θ located in

$$\left(0, b_{3+}^*\right) = \left(0, \frac{1 + 3\sqrt{89}}{40}\right) \approx (0, 0.7325).$$

Since we have the coefficients of θ we can determine the roots by using Cardano's formula or numerically (rounding to four decimal places). They are given by

$$\widehat{b} \approx 0.6451 \qquad \text{and} \qquad b_{\pm} \approx 0.4907 + 0.8003i.$$

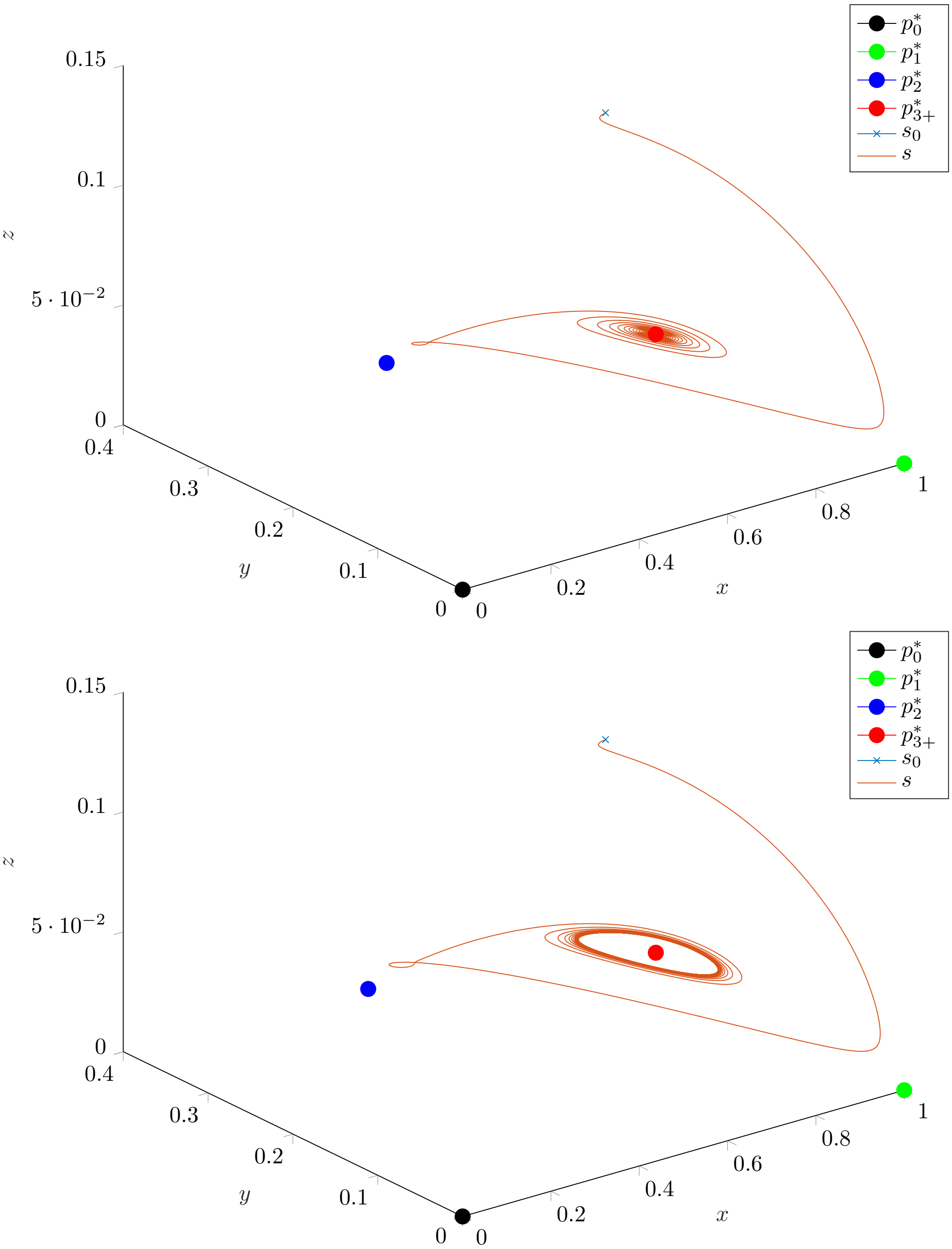


Figure 2.5.12: The cases $b = 0.65$ (top) and $b = 0.64$ (bottom), close to the Hopf bifurcation value $\widehat{b} \approx 0.6451$

We see that θ indeed has a unique root in the interval $\left(0, b_{3+}^*\right) \approx (0, 0.7325)$. As mentioned, $\widehat{b}$ is the value for which the Hopf bifurcation of p_{3+}^* occurs. We can also observe this in the numerical simulations of the cases $b = 0.65 > \widehat{b}$ and $b = 0.64 < \widehat{b}$ (see Figure 2.5.12). The figure shows that for $b > \widehat{b}$ the equilibrium p_{3+}^* is a stable spiral (i.e. the associated Jacobian J has two complex conjugated eigenvalues and a negative real-valued eigenvalue), while for $b < \widehat{b}$ the equilibrium is no longer stable. Instead there is an orbitally stable periodic orbit Γ_1^* which the positive phase curve approaches as t increases. Thus the Hopf bifurcation is *subcritical* for these parameter values, i.e. the periodic orbit Γ_1^* created by the Hopf bifurcation exists for $b < \widehat{b}$ and b sufficiently close to $\widehat{b}$. We remark that the result in Proposition 2.4.1 was merely a *local* result. Thus the global attractor $\mathcal{A}$ is potentially larger than the equilibria, the periodic orbit Γ_1^* and the respective connecting orbits. A biological interpretation of the above is:

> *For mid-range birth rates of the prey species and death rates of the specialist predator species (more precisely for $b \in (\widehat{b}, b_{3+}^*)$), all three species survive and tend toward a single point of coexistence, at least if the respective initial state is not too far away from the point of coexistence.*
> *For high birth rates of the prey species or low death rates of the specialist predator species (i.e. $b < \widehat{b}$), the three species tend to coexist in stable cycles.*

From the above results we can once more construct a stability and bifurcation diagram of the parameter ranges we have discussed so far, see Figure 2.5.13.

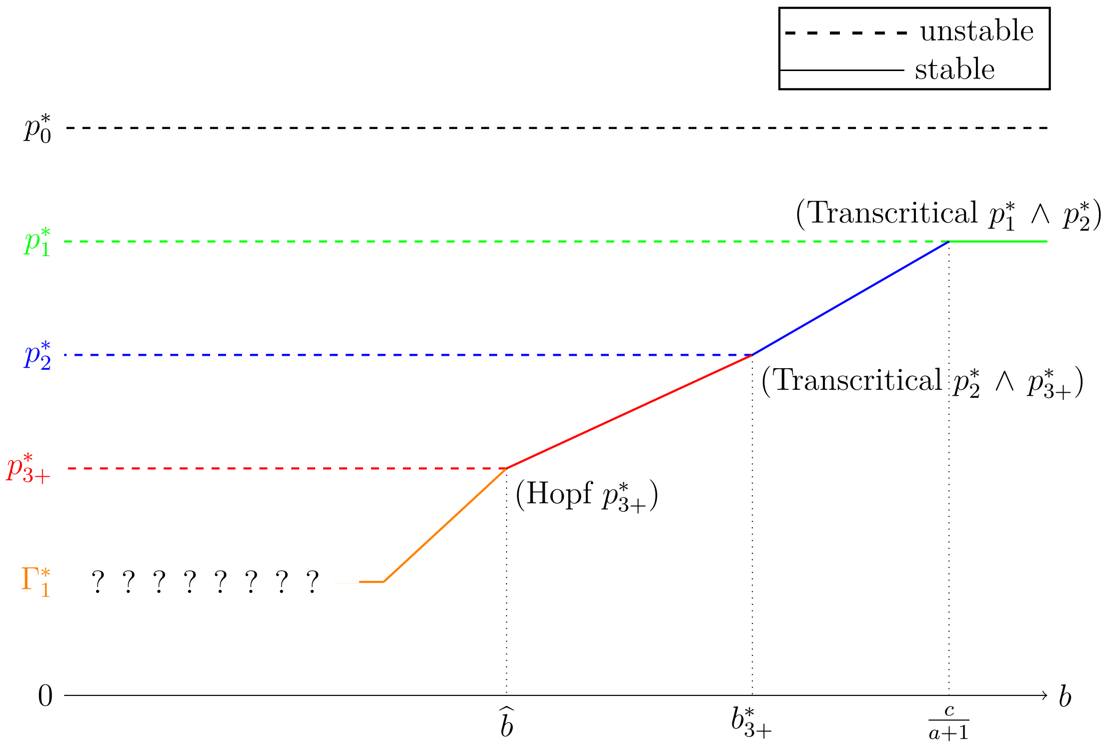


Figure 2.5.13: Stability and bifurcation diagram for the bifurcation parameter $b \in [\widehat{b}, \infty)$ and the standard parameters in (2.5.1)

A question that arises naturally from the bifurcation diagram, is whether the orbitally stable limit cycle continues to exist (and be stable) for all $b \in (0, \widehat{b})$ - similar to the case for the non-standard parameters (recall Figures 2.5.7 and 2.5.8). Differently put: do the dynamics experience any change, when the bifurcation parameter b is decreased further (indicated by the question marks in Figure 2.5.13)? To investigate this we consider the case $b = 0.6$ in Figure 2.5.14. We observe that the limit cycle

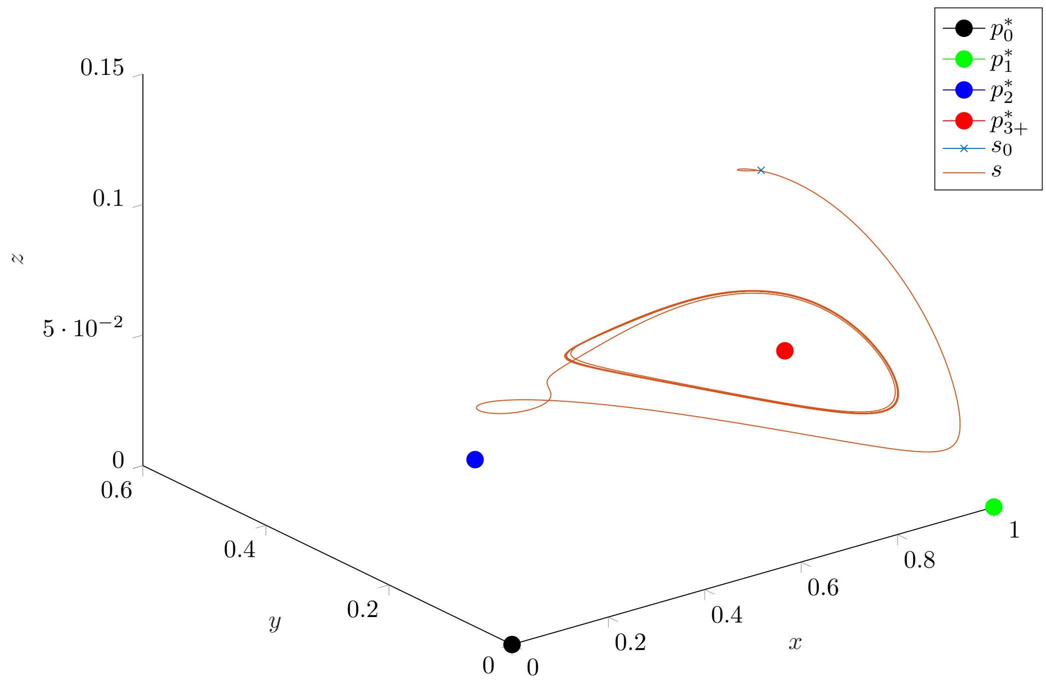


Figure 2.5.14: The limit cycle Γ_1^* deforms for $b = 0.6$

Γ_1^* is still present but has deformed itself (the radius has increased). Decreasing the parameter to $b = 0.55$ clearly shows that the system has 'more to offer' than in the case of the non-standard parameters - see Figure 2.5.15. The limit cycle now has a double loop which is a strong indication of a period doubling bifurcation occurring for some $b \in (0.55, 0.6)$. This and other numerical results will be subject of the next subsection.

2.5.3 Further numerical results

In this subsection we present numerical results that go beyond the scope of the analytical results we have proven above. We emphasise that numerical simulations regarding the dynamics of system (2.1.5) have already been undertaken, e.g. in [Letellier and Aziz-Alaoui, 2002], [Aziz-Alaoui, 2002], [Letellier et al., 2002], [Rai and Upadhyay, 2004], [Parshad et al., 2015] and [Parshad et al., 2016b], for certain parameter ranges and the subsequent results we provide, elaborate and extend these results.

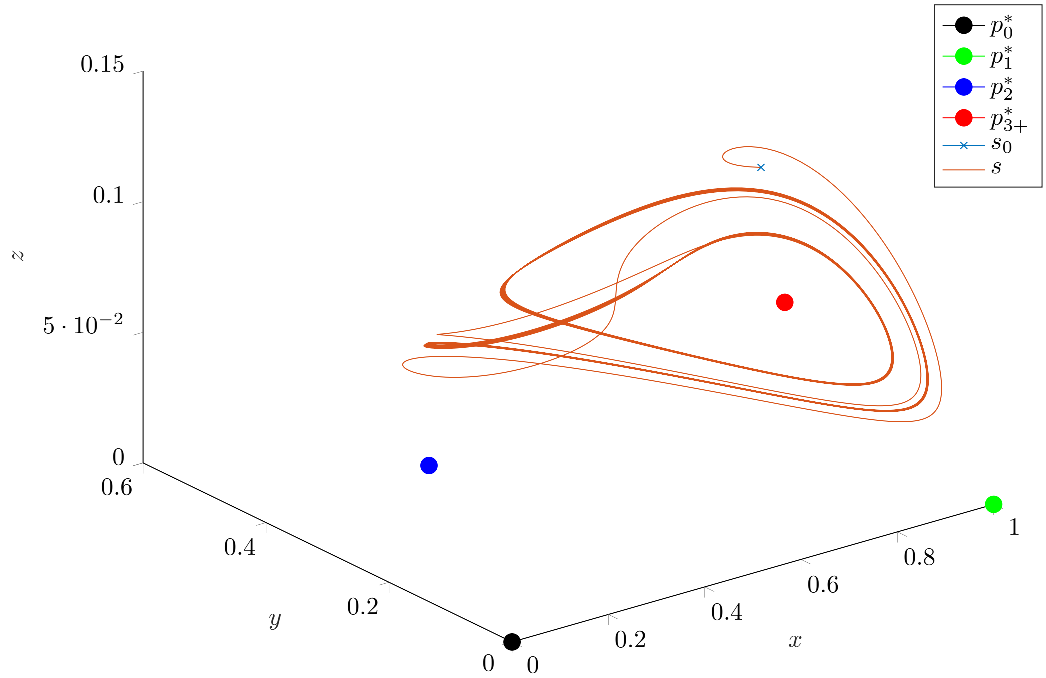


Figure 2.5.15: The limit cycle has a double loop for $b = 0.55$

Period doubling bifurcation and strange attractor

Recall from the last subsection that for the standard parameters (2.5.1) and $b = 0.55$ we obtained Figure 2.5.15. Comparing this to Figure 2.5.14 suggests that a period doubling bifurcation occurs for some $b \in (0.55, 0.6)$. More precisely, a periodic orbit with twice the original period emerges from the periodic orbit Γ_1^* (cf. [Guckenheimer and Holmes, 1983]). Since we are decreasing the b-value the bifurcation is subcritical (also sometimes know as period-halving bifurcation). In order to narrow down the range for which the bifurcation occurs we considered the cases $b = 0.565$ and $b = 0.57$ for which the difference in the limit cycles is still clearly distinguishable, see Figure 2.5.16. The thick bands around the orbit result from the fact that the positive phase curve corresponding to s only slowly settles down onto the actual limit cycle. By iterative bisection of the parameter interval $[0.565, 0.57]$ one may determine a more precise value for the bifurcation value at which the period doubling bifurcation occurs, cf. [Letellier and Aziz-Alaoui, 2002].

We, however, turn to the question of what happens to the limit cycle of twice the period if b is again decreased. The result is that yet *another* subcritical period doubling bifurcation is observed. Consider Figure 2.5.17 for the parameter $b = 0.547$. In the figure we only show the phase curve for the time interval $[1000, 2000]$, i.e. we discard the first half of the computed solution s (with the same initial condition s_0 as above), also see [Letellier and Aziz-Alaoui, 2002]. Hence the thick bands from Figure 2.5.16 do not feature in Figure 2.5.17. This method allows us to visualise the *long-term behaviour* of the solutions more easily. We observe a periodic orbit with four loops as limit cycle. This suggests that another period doubling bifurcation

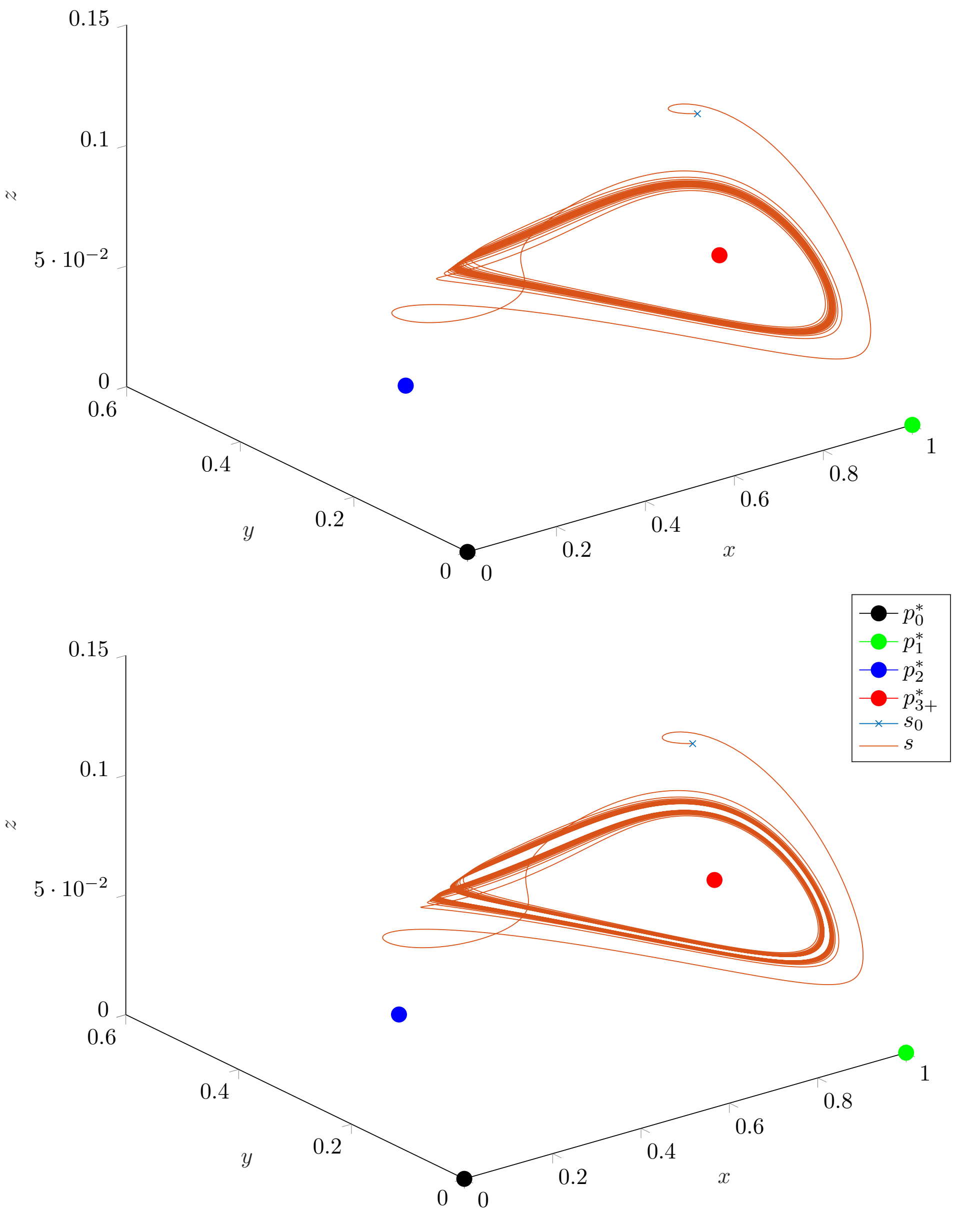


Figure 2.5.16: The cases $b = 0.57$ (top) and $b = 0.565$ (bottom), close to the period doubling bifurcation value

occurred in the interval $b \in (0.547, 0.55)$. Decreasing b further reveals that more and more subcritical period doubling bifurcations occur (see Figure 2.5.18 showing the solution s on the time interval $[1000, 2000]$ for $b = 0.545$). In the literature this is known as a *periodic doubling cascade* (see e.g. [Kuznetsov, 1995], [Perko, 2001]). It is observed for several systems that such a cascade often leads to strange attractors including fractal sets and chaotic dynamics (cf. [Hale and Kocak, 1991], [Strogatz, 1994]). This has been observed for some food chain models before as well (see [Hastings and Powell, 1991], [Klebanoff and Hastings, 1994], [Gross et al., 2005]

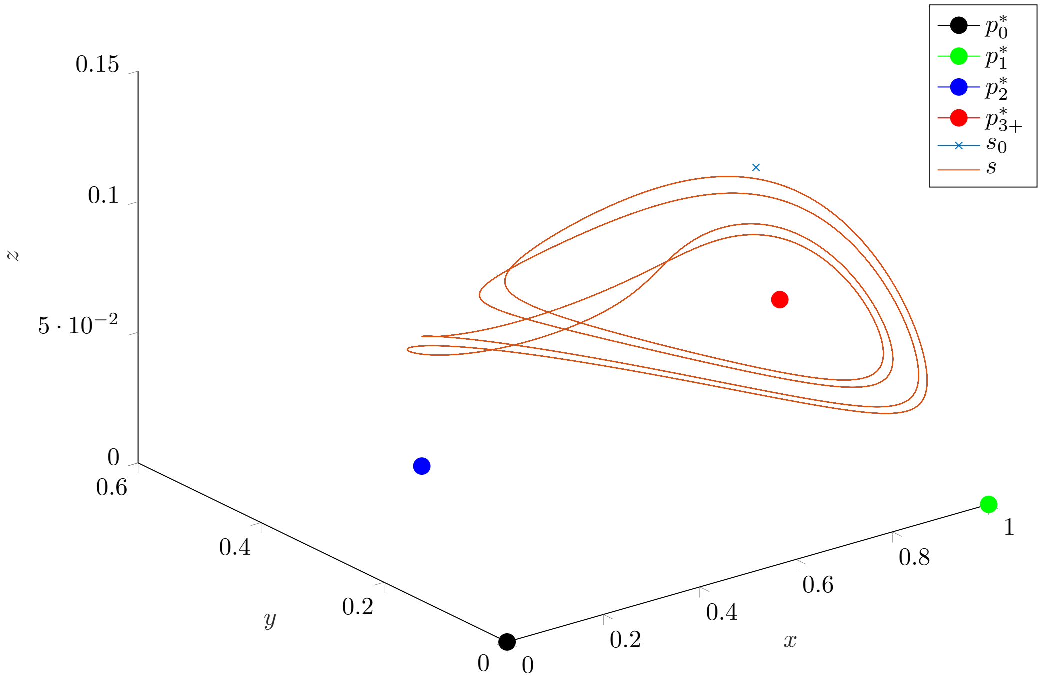


Figure 2.5.17: The limit cycle has four loops for $b = 0.547$

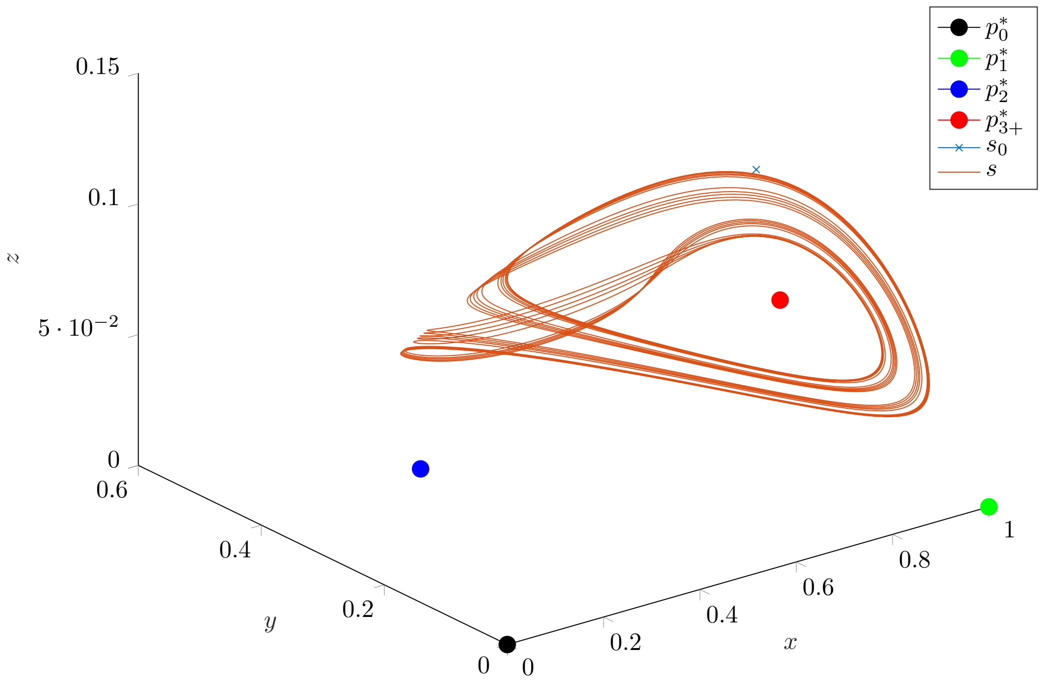


Figure 2.5.18: The limit cycle has multiple loops for $b = 0.545$

for example). Below we will briefly comment on the matter with respect to the GSP food chain model.
As we decrease the bifurcation parameter b further and the period doubling cascade

unravels, the set on which the solution s settles down on for large times becomes less and less discernible as a periodic solution (see Figure 2.5.19 for $b \in [0.5425, 0.543]$ and large time intervals).

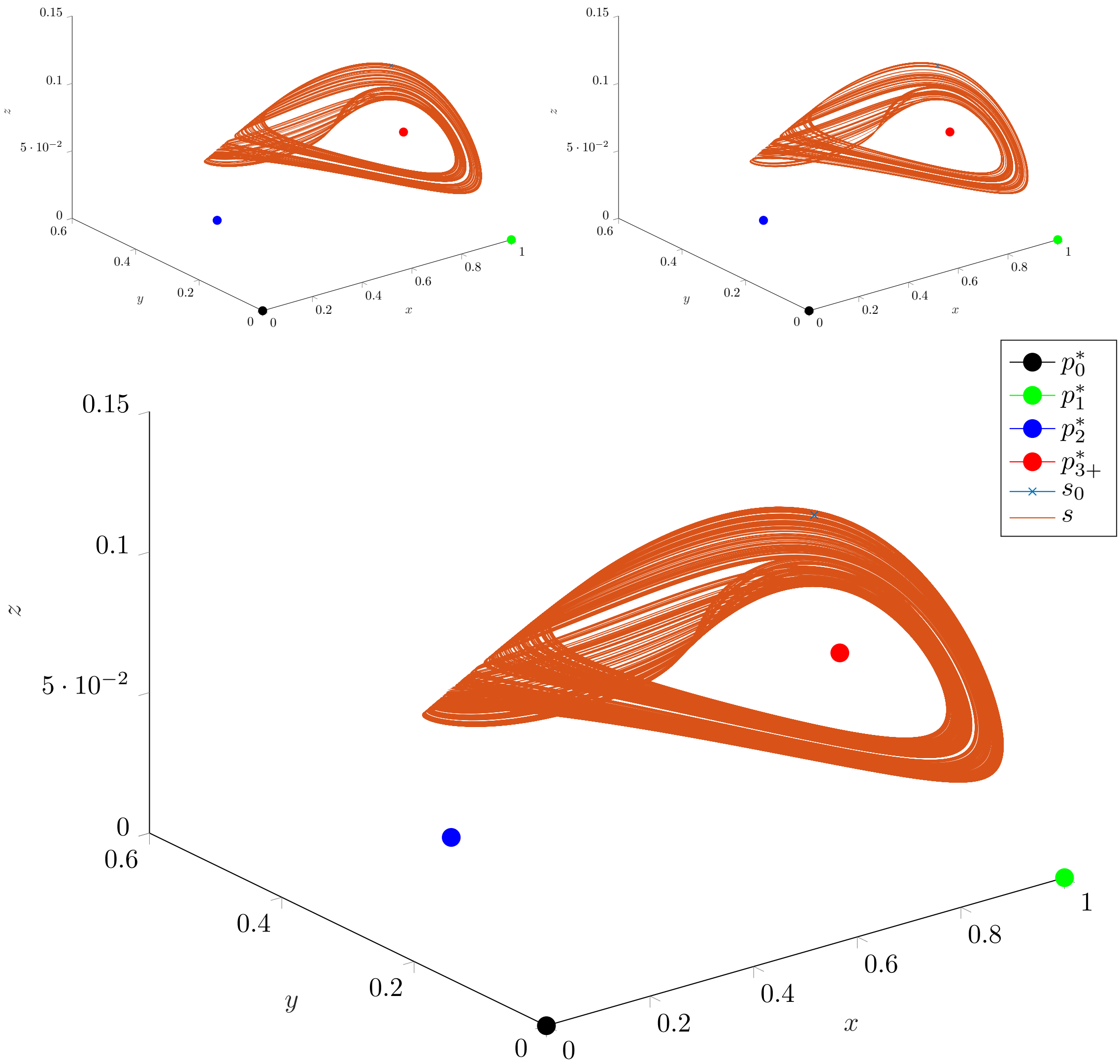


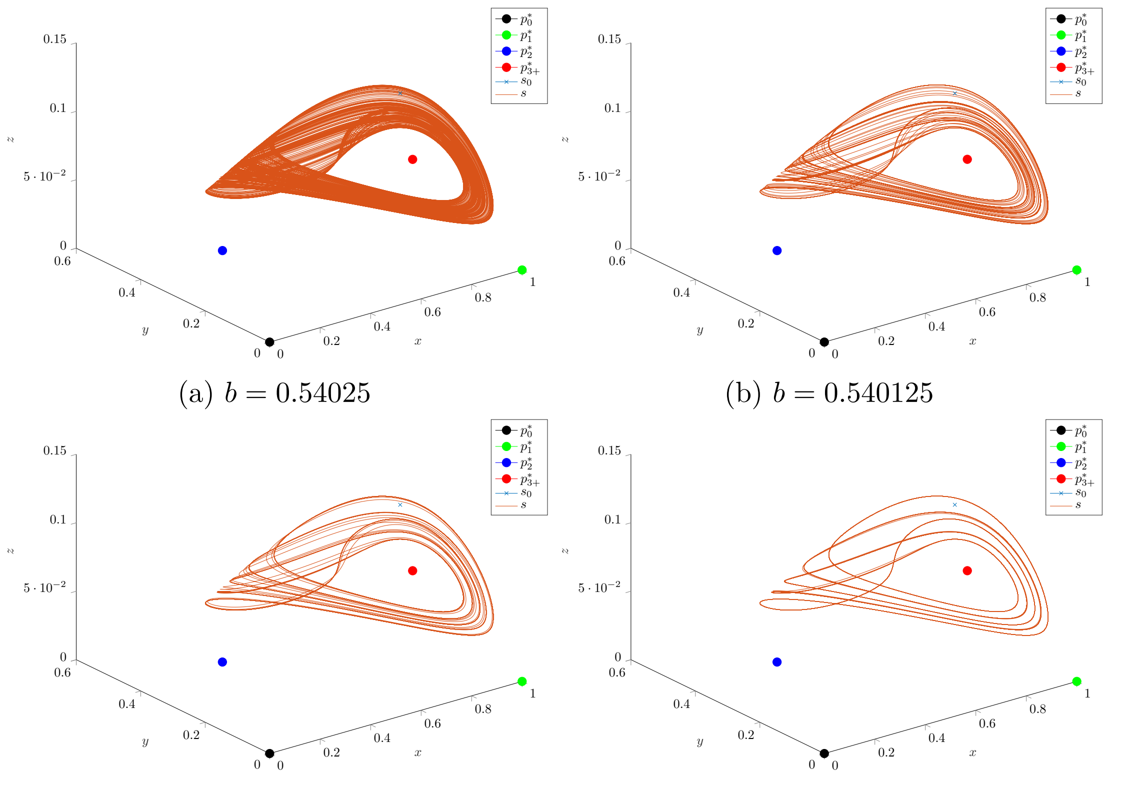
Figure 2.5.19: The cases $b = 0.543$ and $b = 0.54275$ on a time interval $[1000, 8000]$ (top) and the case $b = 0.5425$ on a time interval $[1000, 12000]$ (bottom), showing the strange attractor

This is an indication that the attractor $\mathcal{A}$ is a *strange attractor* (the term originating from [Ruelle and Takens, 1971]) for some parameter ranges. In particular, the set $\mathcal{A}$ might have a fractal dimension and the dynamics of the system - and in particular on the attractor - might be chaotic. This second aspect concerning chaotic behaviour will be discussed below. A strange attractor that is created by a period doubling cascade may be destroyed by exactly such a cascade again (e.g. the Hénon attractor, see [Sander and Yorke, 2011]) as the bifurcation parameter is decreased further.

However the period-doubling bifurcations involved are now supercritical and the period of the loops halves. Decreasing the bifurcation parameter b we observe that the positive phase curve indeed settles down on a limit cycle again as time tends to infinity (see Figure 2.5.20).

Observe that the parameter range $b \in [0.54, 0.54025]$ in which this reverse cascade occurs is very narrow. This implies that a small perturbation of the bifurcation parameter may already have a large effect on the dynamics of the system. Moreover, the strange attractor is created and destroyed in the narrow range of $b \in [0.54, 0.547]$ (recall Figures 2.5.17 to 2.5.20). From a biological point of view, such instabilities of the system may indicate that the ecosystem undergoes a fundamental change in this specific parameter regime. An interpretation of this is:

When varying the parameter b for mid-range values, transient regimes of very complex behaviour (the strange attractor) occur, that separate different stable configurations of coexistence and population dynamics of the ecosystems (the limit cycles at the respective ends of the cascades).



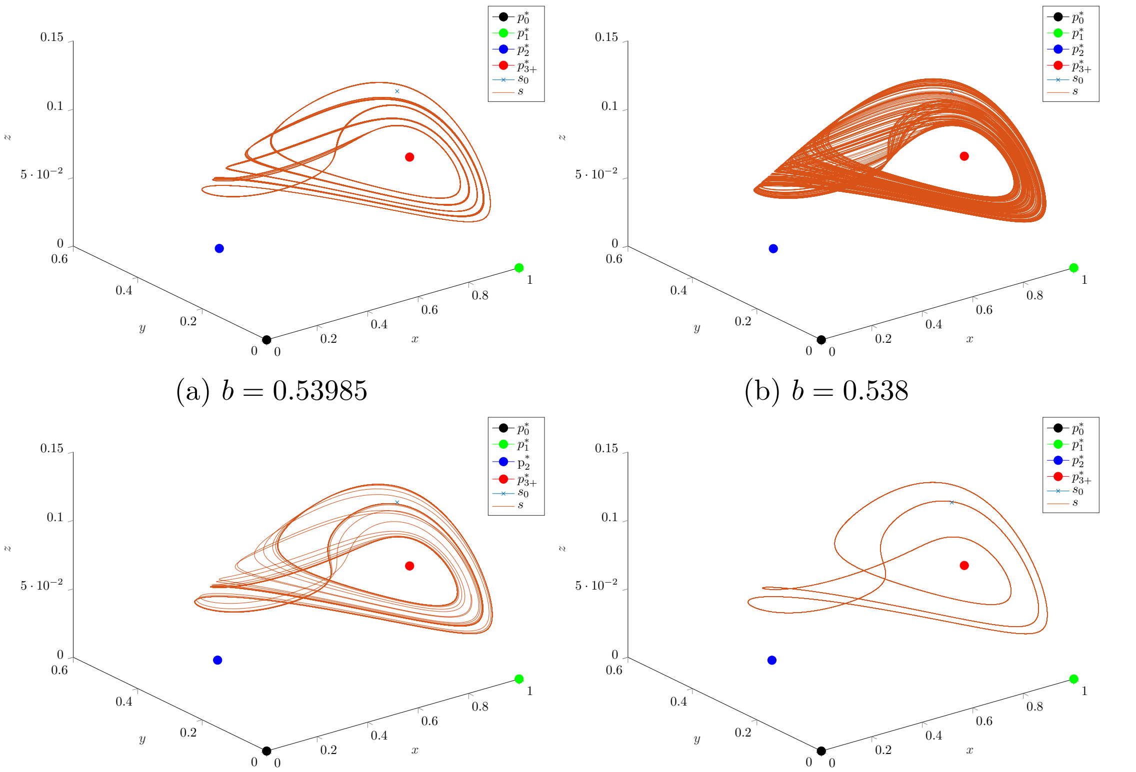
(a) $b = 0.54025$ (b) $b = 0.540125$

(c) $b = 0.540075$ (d) $b = 0.54$

Figure 2.5.20: Solutions on the time interval $[1000, 8000]$, showing the destruction of the strange attractor via a cascade of supercritical period doubling bifurcations.

It has been suggested in the literature that the above mentioned (chaotic) transient regimes may be caused by breakouts of epidemics for example, usually resulting in a different but still stable configuration of the ecosystem at the end of the epidemic (cf. [Aziz-Alaoui, 2002]).

Continuing to decrease the bifurcation parameter b further we observe that the limit cycle prevails for a while before the phenomenon we just described *repeats itself*. I.e. once more a strange attractor is created and destroyed by two period doubling cascades in a narrow parameter range or transient regime, see Figure 2.5.21.



(a) $b = 0.53985$ (b) $b = 0.538$

(c) $b = 0.535$ (d) $b = 0.534$

Figure 2.5.21: Solutions on the time interval $[1000, 8000]$, showing the construction and destruction of the strange attractor in the window $b \in [0.535, 0.53985]$.

In literature such parameter intervals (or transient regimes) have been coined *windows* in parameter space (see e.g. [Kuznetsov, 1995]). Two opposing period doubling cascades create and destroy a strange attractor in several windows of the range in which the bifurcation parameter b is varied. For our parameter settings we have observed several such windows, see Table 2. The long-term dynamics on these strange attractors are not particularly straightforward. For example no periodic motion is evidently identifiable, although the attractor results from a bifurcation of periodic orbits. It is much rather a seemingly *chaotic* behaviour, which is observed at the end of period-doubling cascades (cf. [Hale and Kocak, 1991]).

Approximate window intervals	Visualisation
$[0.54, 0.57]$	Figures 2.5.16 to 2.5.20
$[0.534, 0.53985]$	Figure 2.5.21
$[0.5243, 0.532]$	Appendix D
$[0.5091, 0.5243]$	Appendix D
$[0.4751, 0.501]$	Appendix D
$[0.466, 0.475]$	Appendix D

Table 2: Six period-doubling cascade windows for the standard parameters (2.5.1)

Chaotic dynamics and Shilnikov homoclinic bifurcation

We suppose that in some window the underlying reason the dynamics are chaotic, and the period doubling bifurcations occur, is a global bifurcation occurring within the same parameter range of the parameter b we have considered. More precisely, we study the occurrence of a *Shilnikov homoclinic bifurcation* (see [Shilnikov, 1965]) occurring in the parameter window $b \in [0.4751, 0.501]$ (recall Table 2). The two key conditions for such a bifurcation to occur are:

- The existence of a saddle-focus equilibrium p^*
- The existence of a homoclinic orbit $\Gamma_{hom}(p^*)$ to the equilibrium p^*

Using numerical tools we discuss whether these conditions hold. For the dynamics induced by system (2.1.5) we have determined the equilibria (recall Table 1) and are able to handle them well, analytically and numerically. The equilibrium we will consider is p^*_{3+}. Finding a homoclinic orbit to an equilibrium analytically or even numerically is difficult in general. However, [Letellier and Aziz-Alaoui, 2002] have found numerical evidence for the existence of such an orbit for system (2.1.5), albeit for different parameter values than ours in (2.5.1). This gives reason to the conjecture that homoclinic orbits might exist (or persist) for other parameter values as well - including ours. In fact, using the very coarse purely adaptive step size in our numerical scheme we obtain Figure 2.5.22. We have used the standard parameters from (2.5.1) as well as $b = 0.5$ for the simulation. The initial condition is given by

$$s_0 = \begin{pmatrix} 0.8212772953202039 \\ 0.2 \\ 0.0815160196451393 \end{pmatrix}$$

which is in a small neighbourhood of p^*_{3+} since

$$\|s_0 - p^*_{3+}\| = 4.396160620943584 \cdot 10^{-4}.$$

The figure shows a positive phase curve to a solution s (on the time interval $[0, 180]$) that spirals away from the equilibrium p^*_{3+} along (i.e. close to) the local unstable

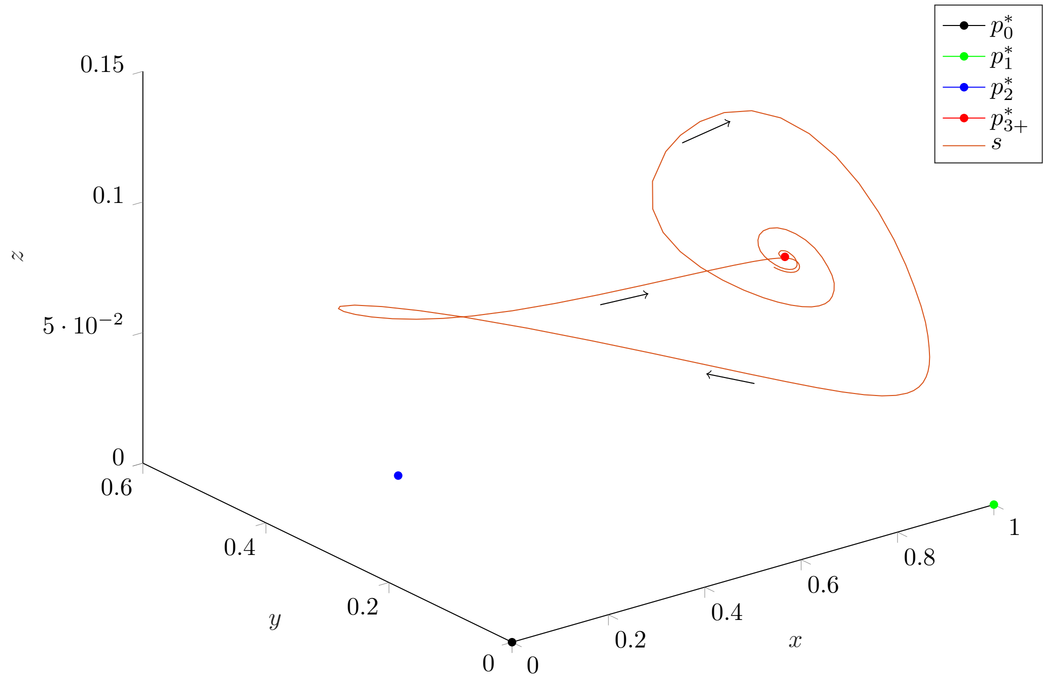


Figure 2.5.22: The positive phase curve s revisits the neighbourhood of equilibrium p_{3+}^* for $b = 0.5$

manifold $W_{loc}^u(p_{3+}^*)$ and then returns to a neighbourhood of p_{3+}^* along the local stable manifold $W_{loc}^s(p_{3+}^*)$ of p_{3+}^*. This *characterises* the saddle-focus equilibrium point (often also considered backwards in time, i.e. a one-dimensional unstable manifold and reinjection of the phase curve via the spiralling on the stable two dimensional manifold - cf. [Wiggins, 1990] for example). By this characterisation it is necessary for the eigenvalues of the Jacobian J (evaluated at p_{3+}^*) to have a negative real-valued eigenvalue λ_1 and two complex-conjugated eigenvalues $\lambda_{2/3}$ with positive real part. For $b = 0.5$ these eigenvalues are approximately

$$\begin{aligned} \lambda_1 &\approx -0.649495399683059 \\ \lambda_+ = \lambda_2 &\approx 0.045647676256243 + 0.194160274641232i \\ \lambda_- = \lambda_3 &\approx 0.045647676256243 - 0.194160274641232i, \end{aligned}$$

i.e. they fulfil the above criterion and p_{3+}^* is indeed a saddle-focus equilibrium. The corresponding approximate eigenvectors $w_1, w_\pm$ are given by

$$w_1 = \begin{pmatrix} 0.998375978636216 \\ -0.056681579460958 \\ 0.005709976531338 \end{pmatrix} \tag{2.5.7}$$

$$w_\pm = \begin{pmatrix} -0.652220281778129 \pm 0.171887689016383i \\ 0.701503947225430 \\ 0.052666139390298 \mp 0.224012982192389i \end{pmatrix}$$

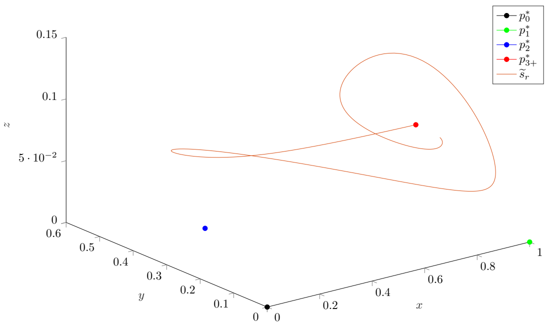
From the eigenvalues we determine the *saddle-index* δ of p^*_{3+} (cf. [Wiggins, 1990] or [Glendinning, 1994] for example), being the quantity

$$\delta = \frac{-\operatorname{Re}(\lambda_{2/3})}{\lambda_1} \approx \frac{-0.045647676256243}{-0.649495399683059} \approx 0.070452982797700 < 1. \tag{2.5.8}$$

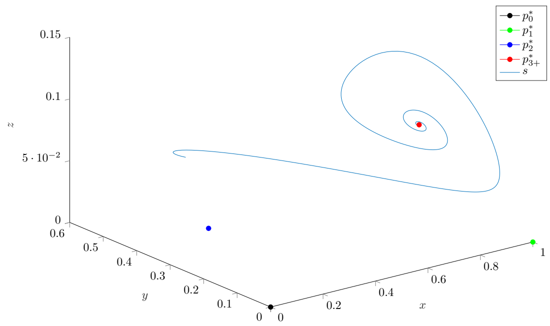
The Shilnikov bifurcation exhibits an especially interesting behaviour if $\delta < 1$, as is the case here. In particular Shilnikov showed that the dynamics on a specific return map associated to the homoclinic orbit $\Gamma_{hom}(p^*)$ 'are topologically conjugate to a full shift on two symbols' (as [Wiggins, 1990] puts it) or, in the words of [Guckenheimer and Holmes, 1983], a 'countable infinity of horseshoes is present'. Both statements reflect the same point that the flow close to the homoclinic orbit may be put into relation (via a conjugacy) to a map that is known to exhibit chaotic behaviour (the Shift map and the Smale Horseshoe map respectively). Shilnikov proved the existence of countably many periodic orbits in a neighbourhood of $\Gamma_{hom}(p^*)$. The onset of these complex and chaotic dynamics causes a sequence of period doubling (and halving) bifurcations and saddle-node bifurcations to occur as the homoclinic orbit breaks (when the bifurcation parameter is varied). This explains the occurrence of the period doubling cascades we observed in the window $[0.4751, 0.501]$ when varying the parameter b (recall Table 2). The homoclinic orbit $\Gamma_{hom}(p^*)$ breaks for a b-value close to $b = 0.5$. The saddle-node bifurcations have not been investigated and observed numerically (however they have been observed numerically for other parameter regions, see [Letellier and Aziz-Alaoui, 2002]).
So far the above numerical evidence with regard to the existence of such a homoclinic orbit $\Gamma^*_{hom}(p^*_{3+})$ is rather weak, especially since a very coarse numerical scheme was used. A method that is particularly useful in this scenario is *reverting the direction of time*, i.e. considering the dynamics induced by the vector field $-v$ instead of v from (2.1.5) (cf. [Parker and Chua, 1989], [Deng, 2017]). Doing so, causes the one-dimensional local stable manifold $W^s_{loc}(p^*_{3+})$ of p^*_{3+} (of the original *time-forward* system) associated with λ_1 to be the local unstable manifold $\widetilde{W}^u_{loc}(p^*_{3+})$ of the *time-reversed* system. Hence in the time-reversed system the equilibrium p^*_{3+} now has a one-dimensional local unstable manifold $\widetilde{W}^u_{loc}(p^*_{3+})$. For a given $b > 0$, we choose a point

$$s_0 = p^*_{3+} - 10^{-3} \cdot (1, 0, 0)^T$$

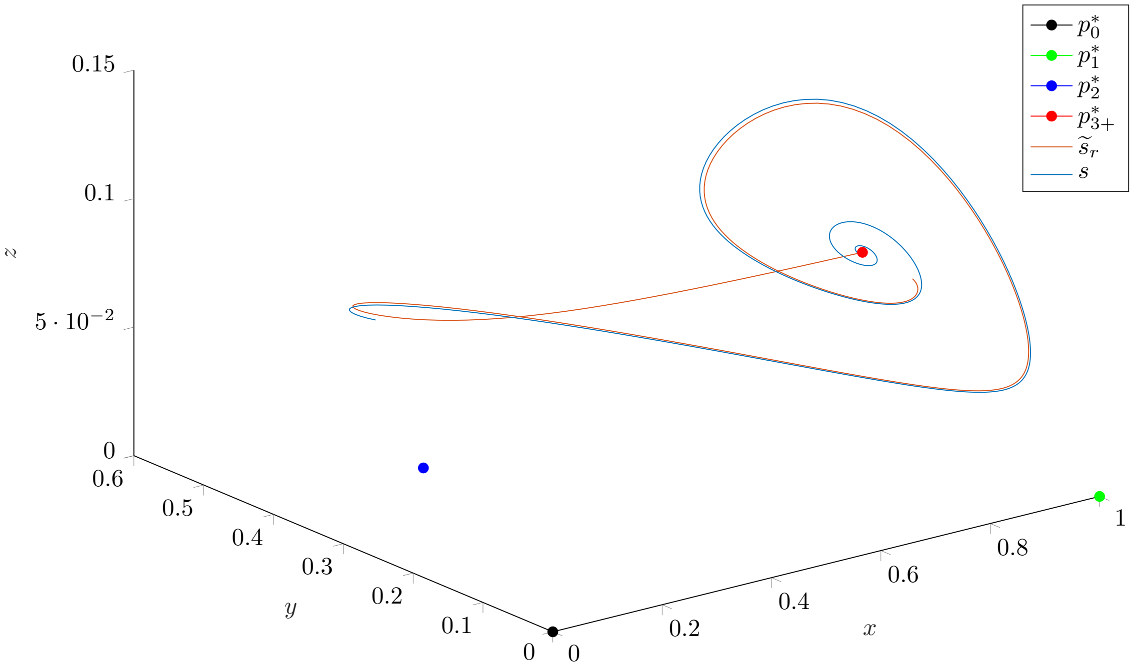
close to the equilibrium p^*_{3+} as the initial condition. The choice of this particular initial condition is based on the observation that the eigenvector w_1 associated with λ_1 (recall (2.5.7)) has the largest entry in the first component by a factor of more than 17, motivating that the eigendirection (given by w_1) may be roughly approximated by the unit vector $(1, 0, 0)^T$. Since such an eigendirection gives a first order approximation to a one-dimensional local (un)stable manifold of an equilibrium, the choice of s_0 above is made so that the initial state is in a small vicinity of the one-dimensional local unstable manifold $\widetilde{W}^u_{loc}(p^*_{3+})$ we are computing.
We now observe the positive phase curve to the solution $\widetilde{s}_r$ (with s_0 from above) in the time-reversed system. By slightly varying the parameter b (bisecting method)



(a) Approximating the unstable manifold $\widetilde{W}^u_{loc}(p^*_{3+})$ of p^*_{3+} for time-reversed system



(b) A solution on the unstable manifold $W^u_{loc}(p^*_{3+})$ of p^*_{3+} for time-forward system



(c) Combining the positive phase curves

Figure 2.5.23: Solutions on the unstable manifolds of the time-forward and time-reversed system for $b = 0.49964510020384728$.

we have forced the positive phase curve of $\widetilde{s}_r$ back into a neighbourhood of the local stable manifold $\widetilde{W}^s_{loc}(p^*_{3+})$ of the time-reversed system. This leads to Figure 2.5.23a for

$$b = 0.49964510020384728 \in [0.4751, 0.501],$$

with maximal step size 10^{-4} and time interval $[0, 70]$. The solution $\widetilde{s}_r$ moves away from the equilibrium in the direction of the eigenvector w_1 corresponding to λ_1, but turns around and commences to spiral in on the equilibrium p^*_{3+} again. Note that this behaviour is difficult to capture from a numerical point of view, due to the hyperbolicity properties of the flow. More precisely, the saddle-index value δ is very small, i.e. the expansion in the unstable eigendirection (caused by the eigenvalue λ_1

of the time-reversed system) is greater than the contraction caused by the eigenvalues $\lambda_{2/3}$. In this case by a factor of more than ten, since the saddle-index

$$\delta \approx 0.07 << 1$$

measures precisely this ratio, see (2.5.8). This causes a strong expansion rate in the unstable direction to oppose a relatively weak attraction rate in the vicinity of the equilibrium p^*_{3+}, making the positive phase curve corresponding to the solution $\widetilde{s}_r$ likely to move away from p^*_{3+}. Likewise we can obtain a solution s in the time-forward

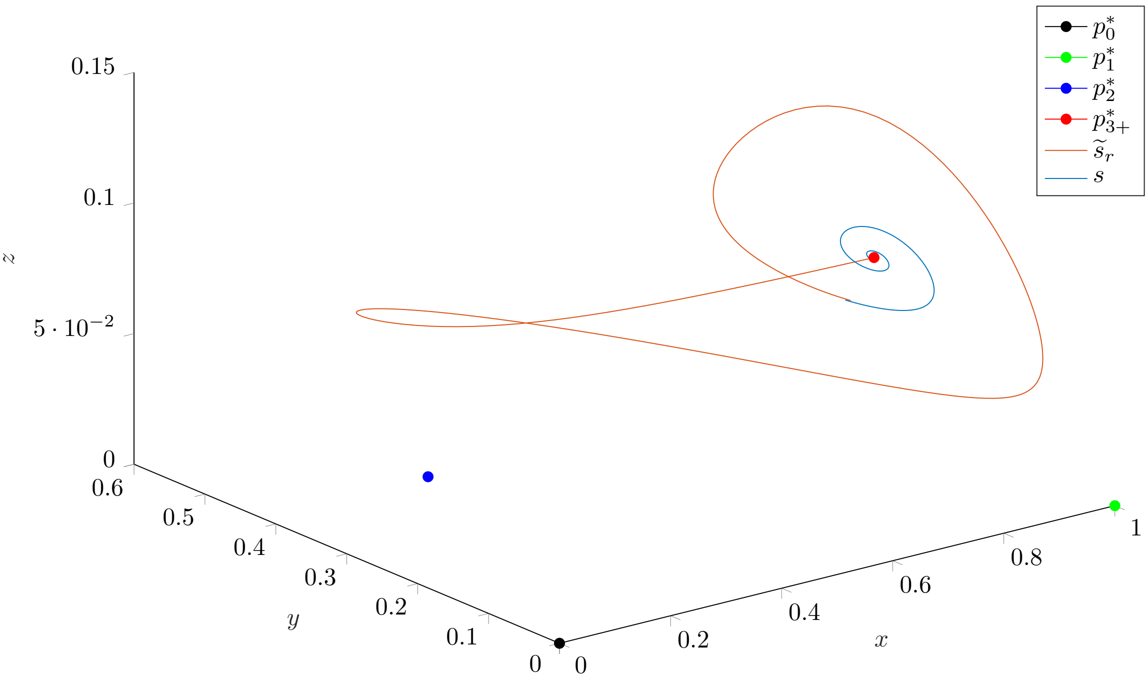
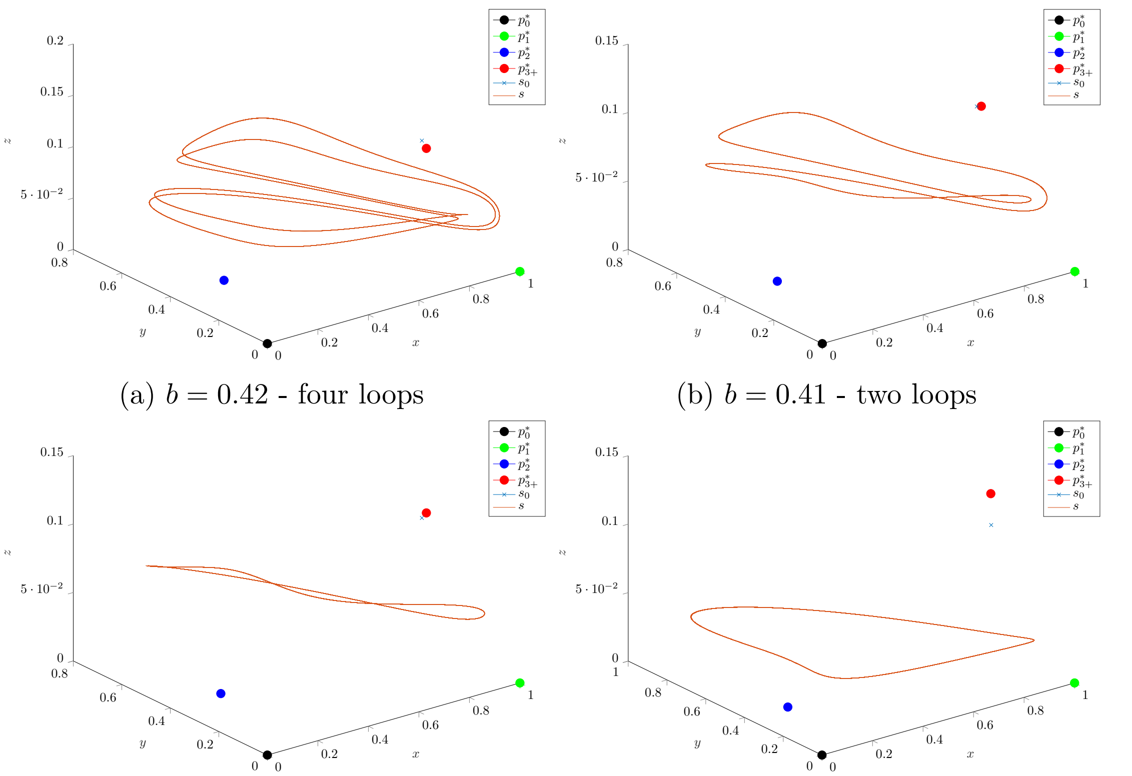


Figure 2.5.24: Constructing a homoclinic orbit $\Gamma_{hom}(p^*_{3+})$ using stable and unstable manifolds for $b = 0.49964510020384728$

system, in which case the corresponding positive phase curve spirals outwards from the equilibrium p^*_{3+}, see Figure 2.5.23b (on the time interval $[0, 220]$). Combining two solutions $\widetilde{s}_r$ and s that intersect, creates a homoclinic orbit $\Gamma_{hom}(p^*_{3+})$, since they are intersections of the local stable manifold $W^s_{loc}(p^*_{3+})$ (being the local unstable manifold $\widetilde{W}^u_{loc}(p^*_{3+})$ of the time-reversed system) and the local unstable manifold $W^u_{loc}(p^*_{3+})$ of p^*_{3+}, see Figure 2.5.24. We remark that the intersection of our solutions $\widetilde{s}_r$ and s is not particularly smooth, due to numerical limitations. However, using finer numerical schemes, more computational resources and small perturbances of the parameter b, a better approximation of the solutions and in particular of the local stable and unstable manifolds and positive phase curves thereon would be achieved. In turn this would yield a better approximation of the homoclinic orbit $\Gamma_{hom}(p^*_{3+})$. This supplies further numerical evidence (cf. [Rai and Upadhyay, 2004]) that the homoclinic orbit we are looking for indeed exists for the standard parameters we have chosen to work with. Since the equilibrium p^*_{3+} is indeed a saddle-focus and the saddle-index fulfils $\delta < 1$, the onset of complex and chaotic behaviour of the ecosystem for $b \approx 0.5$ is caused by the global Shilnikov homoclinic bifurcation.

Leaving the chaotic regime

The final point we make, is that the complex and chaotic dynamics of the system do not persist for all sufficiently small $b > 0$. In fact for the standard parameters a numerical simulation yields that - similar to the build-up of the first period-doubling cascade commencing for $b \approx 0.57$ (recall Figure 2.5.16) - the *final* cascade leading to a simple period orbit with a single loop occurs in the range $[0.35, 0.42]$, see Figure 2.5.25.



(a) $b = 0.42$ - four loops

(b) $b = 0.41$ - two loops

(c) $b = 0.4$ - single loop

(d) $b = 0.35$ - single loop

Figure 2.5.25: Positive phase curves on the time interval $[1000, 8000]$, showing the final period doubling cascade for $b \in [0.35, 0.42]$.

Below this value the asymptotic behaviour is very similar to the case of the non-standard parameters: a single periodic orbit Γ_1^* is the limit cycle of solutions s as $t \to \infty$, see Figure 2.5.26 and compare to Figure 2.5.7.
The difference is that the limit cycle Γ_1^* is not contained in the x-y-plane, as was the case for the non-standard parameters, but much rather it is situated slightly 'above' the plane. This means that the generalist predator species density (i.e. the quantity

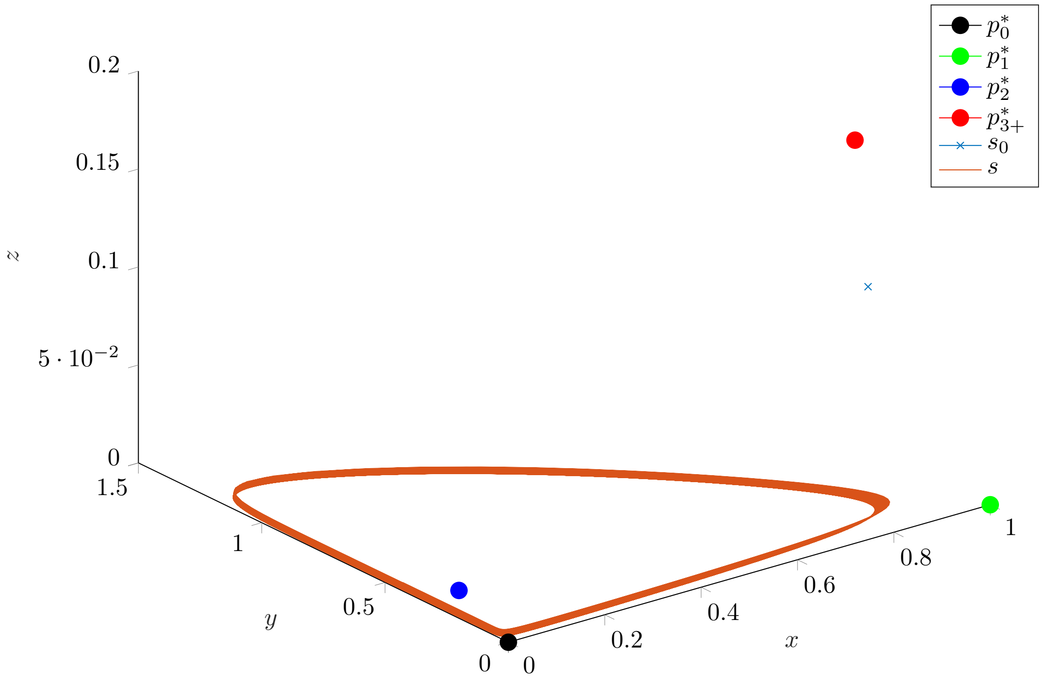


Figure 2.5.26: The positive phase curve approaches the periodic orbit Γ_1^* on the time interval $[1000, 8000]$ for $b = 0.2$

z) does not tend to zero but persists at a low average value, which is very sensible from a biological point of view, recalling the definition of a generalist predator.

For low values of the parameter b the dynamics of the ecosystem tend to a cyclic motion in which all the three species persist. The average density value of the generalist predator species is low in this case.

With this remark we conclude the presentation of numerical results and the analytical study of the three-dimensional GSP food chain model in this chapter. The above results are promising in the sense that proving the existence of the homoclinic orbit $\Gamma_{hom}(p_{3+}^*)$ analytically, and thus the occurrence of the Shilnikov homoclinic bifurcation, seems plausible and poses an interesting topic of study in future works. Further numerical observations we made during the simulations, such as the existence of a *heteroclinic orbit* connecting the equilibria p_2^* and p_{3+}^* for various parameters of b, give reason to investigating the dynamics induced by (2.1.5) further. Studying the dynamics for the case that the (unstable) second interior equilibrium p_{3-}^* is biologically feasible, is also interesting, as the equilibrium must be part of the global attractor $\mathcal{A}$, thus possibly altering the nature of the attractor. However, we will turn to the question how to *generalise* the GSP food chain model to any arbitrary length $n \in \mathbb{N}$, as well as how to generalise the results from above (where possible), in the next chapter.

3 N-dimensional generalisation

Not all food chains merely consist of three species or three trophic levels, recall Figures 1.0.3 and 1.0.4 for example. In fact, food chain lengths vary, depending on the specific properties of the ecosystem that is being considered, such as the size of the environment, for example (cf. [Schoener, 1989], [Vander Zanden et al., 1999]). To capture the evolution and dynamics of longer chains, it is natural to adjust the model equations accordingly. From a mathematical point of view extending and generalising food chain models is achieved by including more general interaction terms of the species in the model equations, as well as modelling more different species. We provide such a generalisation of the equations of the three-dimensional GSP food chain model introduced in chapter 2 in section 3.1 below (see (3.1.1)) and discuss some of the results from the three-dimensional model which carry over to the general model. In section 3.2 we then apply the generalised results to two ODE-systems (see (3.2.1) and (3.2.4)) which fit into the framework of the general GSP food chain model introduced beforehand.

3.1 The generalised model

As mentioned above, we want to generalise the three-dimensional GSP food chain model. To this end we will extend the food chain (and hence the model equations) to a chain of arbitrary length $n \in \mathbb{N}$ ($n \geq 3$), with $n-2$ prey and/or predator species $\mathbf{x}$ interacting in the lower trophic levels, see Figure 3.1.1. Since the intermediate predator species y remains a *specialist* predator it will still only prey on a *single* species x_{n-2} of the $n-2$ species in the lower trophic level.

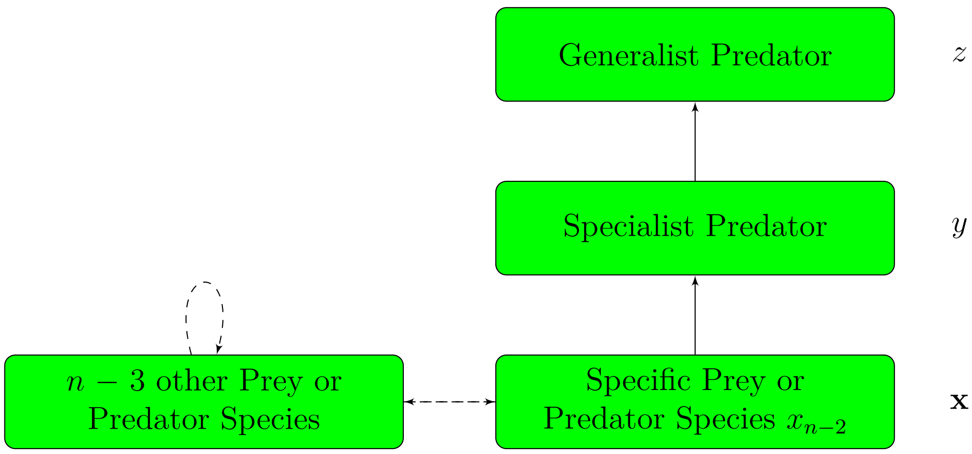


Figure 3.1.1: Scheme of a n-dimensional GSP food chain

3.1.1 The model equations and solutions

The above discussion suggests the following generalisation of the model equations in (2.1.5) for a given $n \in \mathbb{N}$ with $n \geq 3$ (omitting the explicit dependency of $\mathbf{x}$, y, z on

t in the notation):

$$\left.\begin{aligned} \dot{\mathbf{x}} &= F(\mathbf{x}, y, z) \\ \dot{y} &= \left(-b + \tfrac{cx_{n-2}}{x_{n-2}+d} - \tfrac{z}{y+e}\right) y \\ \dot{z} &= \left(f - \tfrac{g}{y+h}\right) z^2 \end{aligned}\right\} =: \widehat{v}(\mathbf{x}, y, z), \tag{3.1.1}$$

where $\mathbf{x} = (x_1, ..., x_{n-2})^T \in \mathbb{R}^{n-2}$ is a vector of length $n-2$ and the variables $y, z \in \mathbb{R}$ are scalars. The parameters $b, c, d, e, f, g, h > 0$ are still assumed to be positive. The vector field F determines the interactions of the $n-2$ species in the lowest trophic level (recall Figure 3.1.1). It can be chosen far more generally (than in (2.1.5)), however, we will impose certain conditions on F below. Note that for the choice

$$F(\mathbf{x}, y, z) = F(x_1, y, z) = (1 - x_1)x_1 - \frac{x_1 y}{x_1 + a}$$

with $a > 0$ we obtain the original three-dimensional system (2.1.5). Thus the n-dimensional system (3.1.1) is indeed a *generalisation* of the three-dimensional GSP food chain model. This gives rise to the question which of the results obtained for the three-dimensional model (see chapter 2) also hold for this generalisation. Or differently put: which properties of the three-dimensional system were essential to obtain the results and which conditions do we have to impose on the model in (3.1.1) to obtain comparable results? Investigating and answering this question is the essence of this section.
The first thing we consider is the biological feasibility of the n-dimensional GSP food chain model. Since we are still considering an ecosystem, non-negative species densities are important for biologically meaningful population dynamics induced by (3.1.1). Similar to Definition 2.1.1 this motivates

Definition 3.1.1.
We define the index set $\mathcal{I} := \{1, ..., n-2\}$ and the sets

$$\widehat{\mathcal{O}}_0^+ := \{(\mathbf{x}, y, z) \in \mathbb{R}^n \,|\, y \geq 0,\ z \geq 0,\ x_i \geq 0 \ \text{for all}\ i \in \mathcal{I}\}$$

$$\widehat{\mathcal{O}}^+ := \{(\mathbf{x}, y, z) \in \mathbb{R}^n \,|\, y > 0,\ z > 0,\ x_i > 0 \ \text{for all}\ i \in \mathcal{I}\}$$

as the ***non-negative orthant*** *and the* ***positive orthant*** *respectively.*
Furthermore, a ***solution*** *$\widehat{s}$ of the initial value problem given by system (3.1.1) and initial conditions*

$$\widehat{s}_0 = (\mathbf{x}(0), y(0), z(0))^T \in \widehat{\mathcal{O}}_0^+$$

is denoted by

$$\widehat{s} := \widehat{s}(t) = (\mathbf{x}(t), y(t), z(t))^T.$$

The maximal existence interval of $\widehat{s}$ is denoted by $\widehat{I}_M \subset \mathbb{R}$.
The maximal right (or positive) existence interval of $\widehat{s}$ is denoted by $\widehat{I} \subset [0, \infty)$.

Remark 3.1.1.
In order to ensure the existence and uniqueness of $\widehat{s}$ and $\widehat{I}_M$ we impose the smoothness condition

$$F \in \mathcal{C}_{Lip}\left(\widehat{\mathcal{O}}_0^+, \mathbb{R}^{n-2}\right),$$

on the vector field F in (3.1.1) for the following discussion, which in turn implies

$$\widehat{v} \in \mathcal{C}_{Lip}\left(\widehat{\mathcal{O}}_0^+, \mathbb{R}^{n}\right).$$

This allows the application of the Picard-Lindelöf Theorem and the theorem on the maximal existence interval, providing the existence and uniqueness of the solutions $\widehat{s}$ on their maximal existence intervals $\widehat{I}_M$. Since the vector field is also autonomous, using $t_0 = 0$ as initial time is also no restriction (recall the Remark 2.1.1).

Recall that *property (I1)* of the phase space X (see Definition 2.1.2) played an important role in the three-dimensional case (Lemmas 2.1.1 to 2.1.5). It ensured that the positive octant $\mathcal{O}_0^+ \subset \mathbb{R}^3$ could be chosen as the phase space on which the semiflow Φ acts, similar to an invariance property. Likewise we introduce the property for an n-dimensional chain:

Definition 3.1.2.
A subset $K \subset \widehat{\mathcal{O}}_0^+$ is said to have ***the property*** $(\widehat{I}1)$ *under the dynamics generated by* (3.1.1)*, if for all $\widehat{s}_0 \in K \subset \widehat{\mathcal{O}}_0^+$ the corresponding solution $\widehat{s}$ satisfies*

$$\widehat{s}(t) \in K \qquad \forall\, t \in \widehat{I}_M.$$

In order to ensure that $\widehat{\mathcal{O}}_0^+$ has property $(\widehat{I}1)$ (and thus can be chosen as phase space X) we impose a restriction on system (3.1.1). We want the boundary of $\widehat{\mathcal{O}}_0^+$ to have the property $(\widehat{I}1)$. A sufficient assumption is given by

Assumption (*(H1)*)**.**
Assume that for any $i \in \mathcal{I}$ the sets

$$\begin{aligned} \mathcal{H}_i &:= \left\{(\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \mid x_i = 0\right\} \\ \mathcal{H}_{n-1} &:= \left\{(\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \mid y = 0\right\} \\ \mathcal{H}_n &:= \left\{(\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \mid z = 0\right\} \end{aligned}$$

have the property $(\widehat{I}1)$ in the sense of Definition 3.1.2. We call this assumption (H1).

From a geometrical point of view the assumption may be interpreted as follows: the boundary $\partial\widehat{\mathcal{O}}_0^+$ of the non-negative orthant $\widehat{\mathcal{O}}_0^+$ consists of the n hyperplanes $\mathcal{H}_i \subset \widehat{\mathcal{O}}_0^+ \subset \mathbb{R}^n$ (with $i \in \{1, ..., n\}$), i.e.

$$\partial\widehat{\mathcal{O}}_0^+ = \bigcup_{i \in \{1,\dots,n\}} \mathcal{H}_i,$$

see Figure 3.1.2. These boundary subsets are assumed to be have property $(\widehat{I}1)$ (similar to [Amann, 1990]).

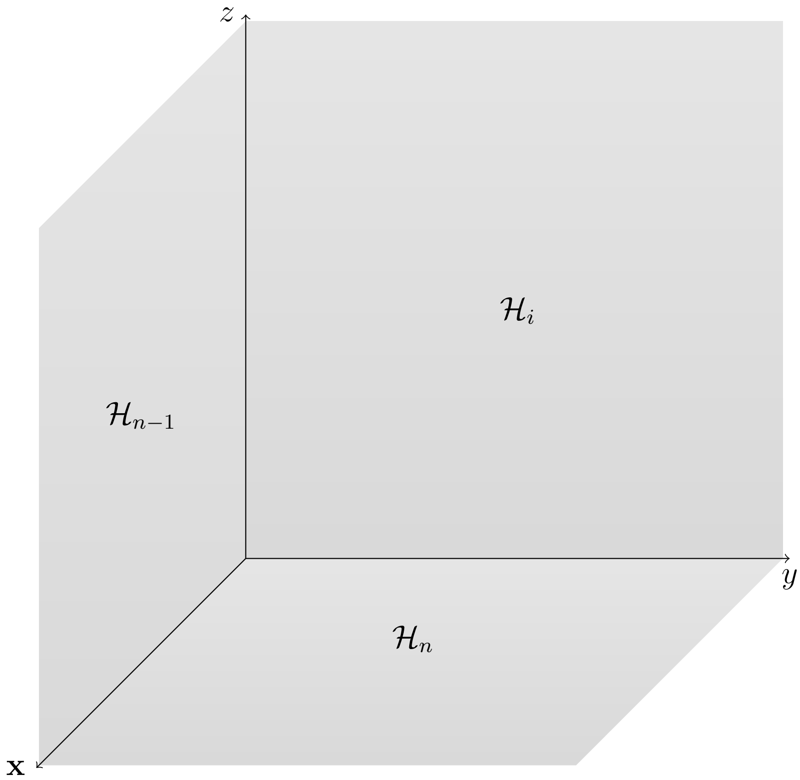


Figure 3.1.2: Schematic figure of the hyperplanes $\mathcal{H}_i$ with $i \in \{1, ..., n\}$ forming the boundary of $\widehat{\mathcal{O}}_0^+$.

Considering the $\dot{y}$- and $\dot{z}$-equation in (3.1.1) we observe that they are unchanged compared to those in the three-dimensional system (2.1.5). In particular this implies

$$\begin{aligned} y = 0 \quad &\Rightarrow \quad \dot{y} = 0 \quad \Rightarrow \quad y(t) = 0 \quad \forall\, t \in \widehat{I}_M \\ z = 0 \quad &\Rightarrow \quad \dot{z} = 0 \quad \Rightarrow \quad z(t) = 0 \quad \forall\, t \in \widehat{I}_M \end{aligned}$$

and hence it is in fact even sufficient to make the weaker assumption that the $\mathcal{H}_i$ (with $i \in \mathcal{I}$) have property $(\widehat{I}1)$, since the property $(\widehat{I}1)$ of $\mathcal{H}_{n-1}$ and $\mathcal{H}_n$ may be deduced from this (recall the proof of Lemma 2.1.3). For simplicity's and readabilities sake we choose to keep assumption *(H1)* as it is. The assumption allows us to prove the following

Lemma 3.1.1.
Assume (H1) to hold, then the boundary set $\partial\widehat{\mathcal{O}}_0^+$ and the sets $\widehat{\mathcal{O}}^+$ and $\widehat{\mathcal{O}}_0^+$ have property $(\widehat{I}1)$.

Proof.
Let assumption *(H1)* hold.

- We have

$$\partial\widehat{\mathcal{O}}_0^+ = \bigcup_{i\in\{1,\ldots,n\}} \mathcal{H}_i$$

and hence $\partial\widehat{\mathcal{O}}_0^+$ is a union of sets with property $(\widehat{I}1)$ and as such also has property $(\widehat{I}1)$ itself.

- Let any solution $\widehat{s}$ with $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$ be given. Assuming the phase curve of $\widehat{s}$ leaves the positive orthant in past or future time, the continuity of $\widehat{s}$ implies that the phase curve necessarily intersects the boundary $\partial\widehat{\mathcal{O}}_0^+$ (for some time in $\widehat{I}_M$). The boundary however has property $(\widehat{I}1)$, implying that $\widehat{s}$ fulfils

$$\widehat{s}(t) \in \partial\widehat{\mathcal{O}}_0^+ \qquad \forall\, t \in \widehat{I}_M,$$

which is a contradiction to $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$, since $\widehat{s}$ is unique and $\partial\widehat{\mathcal{O}}_0^+ \cap \widehat{\mathcal{O}}^+ = \emptyset$ holds. Thus

$$\widehat{s} \in \widehat{\mathcal{O}}^+ \qquad \forall\, t \in \widehat{I}_M,$$

i.e. $\widehat{\mathcal{O}}^+$ has property $(\widehat{I}1)$ (also compare to the proofs of Lemmas 2.1.4 and 2.1.5).

- Since

$$\widehat{\mathcal{O}}_0^+ = \partial\widehat{\mathcal{O}}_0^+ \cup \widehat{\mathcal{O}}^+$$

holds, the non-negative orthant $\widehat{\mathcal{O}}_0^+$ also has property $(\widehat{I}1)$ as a union of two sets with property $(\widehat{I}1)$. □

Hence under assumption *(H1)* we can choose $X = \widehat{\mathcal{O}}_0^+$ as the phase space on which the dynamics induced by (3.1.1) evolve. Thus, all the components of a solution $\widehat{s}$ are non-negative for all $t \in \widehat{I}_M$, i.e. the species densities remain non-negative, which is vital when modelling population dynamics. The assumption *(H1)* also implies that for any solution $\widehat{s}$ and any $i \in \mathcal{I}$ we have

$$\begin{aligned} x_i(0) > 0 &\quad \overset{(H1)}{\Rightarrow} \quad x_i(t) > 0 \quad \forall\, t \in \widehat{I}_M \\ y(0) > 0 &\quad \overset{(H1)}{\Rightarrow} \quad y(t) > 0 \quad \forall\, t \in \widehat{I}_M \\ z(0) > 0 &\quad \overset{(H1)}{\Rightarrow} \quad z(t) > 0 \quad \forall\, t \in \widehat{I}_M \end{aligned} \tag{3.1.2}$$

i.e. a positive component of a solution stays positive, while the corresponding solution exists.

3.1.2 Boundedness of solutions

Apart from the non-negativity of solutions, we also want to ensure their boundedness for all future times, i.e. that they do not blow-up in any component in finite future or as time tends to infinity ($t \to \infty$). For this reason we once again restrict the discussion to the positive existence interval $\widehat{I}$. Since the $\dot{z}$-equation is unchanged, the result of Lemma 2.2.4 still holds, i.e. if the parameters fulfil $f - \frac{g}{h} > 0$ then any solution $\widehat{s}$ with $z_0 > 0$ will blow-up in the z-component after a finite time $T^* > 0$. Thus we once again impose the restriction

$$f - \frac{g}{h} < 0$$

on the parameters, which is equivalent to

$$\frac{g}{f} - h > 0.$$

We introduce a second assumption on (3.1.1), or more precisely on solutions $\widehat{s}$ and their bounds (compare to Lemmas 2.2.1 and 2.2.3):

Assumption (*(H2)*).
Let any solution $\widehat{s}$ (with $\widehat{s}_0 \in \widehat{\mathcal{O}}_0^+$) be given. Assume there exist constants

$$\widehat{x}_M = \widehat{x}_M(\widehat{s}_0) > 0 \quad \textit{and} \quad \widehat{y}_M = \widehat{y}_M(\widehat{s}_0) > \frac{g}{f} - h > 0$$

such that

$$\begin{aligned} 0 &\le x_i(t) \le \widehat{x}_M \qquad \forall\, i \in \mathcal{I} \\ 0 &\le y(t) \le \widehat{y}_M \end{aligned}$$

holds for all $t \in \widehat{I}$. We call this assumption (H2).

Remark 3.1.2.
The above assumption is equivalent to saying that the first $n-1$ components of a solution $\widehat{s}$ are bounded for all times in the maximal right existence interval $\widehat{I}$ of $\widehat{s}$. Note that the inequality

$$\widehat{y}_M > \frac{g}{f} - h > 0$$

is no restriction since any given upper bound $\widehat{y}_B$ on the y-component can be increased until it fulfils the above inequality (still remaining an upper bound), for example by setting

$$\widehat{y}_M := \max\left\{\widehat{y}_B, 2\left(\frac{g}{f} - h\right)\right\} > \frac{g}{f} - h > 0.$$

We also remark that the two assumptions *(H1)* and *(H2)* are fulfilled by the three-dimensional system introduced in chapter 2. The assumptions are biologically meaningful hypotheses:

- The first assumption implies that a species with zero species density at some point in time should also have zero species density for all other times (invariance of the coordinate hyperplanes). This is a necessary assumption since otherwise a species could reappear 'by itself' in the ecosystem although, it is or has become extinct. This is not reasonable, unless effects such as migration are included in the considerations. The model equations (i.e. the vector field $\widehat{v}$ and in particular also F in (3.1.1)) should reflect and induce such a behaviour, thus motivating *(H1)*.

- The second assumption *(H2)* implies that the first $n-1$ species have a bounded species density for all future times, i.e. none of these species increase to arbitrary large densities. This is sensible from a biological point of view, since an ecosystem limits a species abundance in some way. Limiting factors may for example be the availability of nutrition, mates or space. The mathematical model (and in particular the vector field) should capture this behaviour.

If assumption *(H2)* holds then a solution can only diverge in its final component (both in finite and asymptotically as $t \to \infty$). This is analogous to the three-dimensional case from chapter 2. Using assumptions *(H1)* and *(H2)* we will also conclude the boundedness of the z-component for all $t \geq 0$ (i.e. that also the generalist predator species does not multiply to arbitrary large numbers) in an analogous way. In the following we present these results in their generalised version, omitting explicit proofs in some cases, but highlighting the parallels and differences to the three-dimensional case instead then.

Semiflow $\widehat{\Phi}$

The aim of this subsection is to show that no finite future time blow-up (of the z-component of any solution $\widehat{s}$) may occur under our assumptions. More precisely, we show

Proposition 3.1.1.
Let $f - \frac{g}{h} < 0$ as well as any solution $\widehat{s}$ be given. Under the assumptions (H1) and (H2) the solution $\widehat{s}$ does not blow up in finite future time.

This is the analogous result to Proposition 2.2.1 and we will in fact prove it in the same manner. To this end we state the generalisation of Lemma 2.2.5 and prove it:

Lemma 3.1.2.
Let $f - \frac{g}{h} < 0$ as well as any solution $\widehat{s}$ be given. Assume (H1) and (H2) to hold and define

$$\widehat{z}_* := \max\left\{\left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d}\right)(\widehat{y}_M + e)\,, 0\right\} \geq 0.$$

If $\widehat{s}$ fulfils $y_0 > 0$ and $z_0 > 0$, then for any $t \in \widehat{I}$ such that $z(t) > \widehat{z}_*$ it holds that $\dot{y}(t) < 0$.

Proof.
Let $f - \frac{g}{h} < 0$ as well as any solution $\widehat{s}$ with $y_0 > 0$ and $z_0 > 0$ be given. Assume *(H1)* and *(H2)* to hold. By (3.1.2) we have

$$y(t) > 0 \qquad \forall\, t \in \widehat{I}.$$

Thus we obtain the following equivalence from the $\dot{y}$-equation in (3.1.1):

$$\begin{aligned} \dot{y}(t) < 0 \quad &\Leftrightarrow \quad -b + \frac{cx_{n-2}(t)}{x_{n-2}(t) + d} - \frac{z(t)}{y(t) + e} < 0 \\ &\Leftrightarrow \quad z(t) > \left(-b + \frac{cx_{n-2}(t)}{x_{n-2}(t) + d}\right)(y(t) + e)\,. \end{aligned}$$

Furthermore, using *(H2)*, it holds that for any $t \in \widehat{I}$

$$\left(-b + \frac{cx_{n-2}(t)}{x_{n-2}(t)+d}\right) \underbrace{(y(t)+e)}_{>0} \leq \left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d}\right)(y(t)+e)$$

$$\leq \max\left\{\left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d}\right)(\widehat{y}_M + e), 0\right\} = \widehat{z}_*$$

Combining the above yields that if $z(t) > \widehat{z}_*$ for any $t \in \widehat{I}$, then $\dot{y}(t) < 0$ holds. Or differently put

$$\left(\forall\, t \in \widehat{I} : z(t) > \widehat{z}_*\right) \quad \Rightarrow \quad \dot{y}(t) < 0. \qquad \square$$

Likewise we want a generalisation of the monotone blow-up Lemma 2.2.6 to hold:

Lemma 3.1.3.
Let $f - \frac{g}{h} < 0$ and a solution $\widehat{s}$ with $y_0 > 0$ and $z_0 > 0$ be given. Assume that (H1) and (H2) hold and that $\widehat{s}$ blows up (for the finite time $T^{**} > 0$). Then there exists a $T_0 \in [0, T^{**})$ such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in [T_0, T^{**}).$$

In particular it holds that

$$\dot{z}(t) > 0 \qquad \forall\, t \in [T_0, T^{**}).$$

Proof.
Recall that the proof of Lemma 2.2.6 entailed proving the auxiliary Lemmas 2.2.7 to 2.2.9. Using *(H1)* and *(H2)*, all these proofs (including the one of Lemma 2.2.6) work identically for the n-dimensional case, by merely replacing the terms

$$s \qquad x(t) \qquad x_M \qquad z_*$$

by their respective generalised versions:

$$\widehat{s} \qquad x_{n-2}(t) \qquad \widehat{x}_M \qquad \widehat{z}_*$$

The essential point why these proofs carry over analogously is that the coupling between the $\dot{y}$-equation and $\dot{z}$-equation is the same in both the three-dimensional and the n-dimensional system. Considering the $\dot{z}$-equation in (3.1.1) and $z_0 > 0$, we observe that the following equivalence holds (for any $t \in \widehat{I}$)

$$y(t) > \frac{g}{f} - h \qquad \Leftrightarrow \qquad \dot{z}(t) > 0. \qquad \square$$

Thus, under the above assumptions, the monotone blow-up property of the z-component also holds for solutions $\widehat{s}$ (with $y_0 > 0$ and $z_0 > 0$). We show the counterpart to Corollary 2.2.2 next:

Lemma 3.1.4.
Let $f - \frac{g}{h} < 0$ and a solution $\widehat{s}$ with $y_0 > 0$ and $z_0 > 0$ be given. Assume that (H1) and (H2) hold and furthermore let an interval $\widehat{I}_0 \subset [0, \infty)$ with $\min \widehat{I}_0 = T_0 \geq 0$ exist such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in \widehat{I}_0.$$

Then it holds that

$$y(t) \leq y(T_0) \exp(\widehat{\alpha}(t - T_0)) \left(\frac{z(T_0)}{z(t)}\right)^{\widehat{\beta}} \qquad \forall\, t \in \widehat{I}_0,$$

where

$$\begin{aligned}\widehat{\alpha} &:= -b + \frac{c\widehat{x}_M}{\widehat{x}_M + d},\\ \widehat{\beta} &:= \frac{1}{\left(f - \frac{g}{\widehat{y}_M + h}\right)(\widehat{y}_M + e)} > 0.\end{aligned}$$

Proof.
Let $f - \frac{g}{h} < 0$ and a solution $\widehat{s}$ with $y_0 > 0$ and $z_0 > 0$ be given. Assume that *(H1)* and *(H2)* hold and furthermore let an interval $\widehat{I}_0 \subset [0, \infty)$ with $\min \widehat{I}_0 = T_0 \geq 0$ exist such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in \widehat{I}_0. \tag{3.1.3}$$

We consider the solution for $t \in \widehat{I}_0$. From the third equation in (3.1.1) we obtain

$$0 < z(t) = \frac{\dot{z}(t)}{z(t)} \cdot \underbrace{\frac{1}{f - \frac{g}{y(t) + h}}}_{>0 \text{ by } (3.1.3)}, \tag{3.1.4}$$

for $t \in \widehat{I}_0$, recalling that $z(t) > 0$ for any $t \in \widehat{I}$ (by (3.1.2) using *(H1)*). Substituting this into the second equation of (3.1.1) yields

$$\dot{y}(t) = y(t) \left[-b + \frac{cx_{n-2}(t)}{x_{n-2}(t) + d} - \frac{\dot{z}(t)}{z(t)} \frac{1}{f - \frac{g}{y(t)+h}} \frac{1}{y(t) + e}\right] \qquad \forall\, t \in \widehat{I}_0.$$

Dividing by $y(t) > 0$ and using $x_{n-2}(t) \leq \widehat{x}_M$ for any all $t \in \widehat{I}_0$ (using *(H2)*), yields

$$\begin{aligned}\frac{\dot{y}(t)}{y(t)} &= -b + \frac{cx_{n-2}(t)}{x_{n-2}(t) + d} - \frac{\dot{z}(t)}{z(t)} \frac{1}{f - \frac{g}{y(t)+h}} \frac{1}{y(t) + e}\\ &\leq -b + \frac{c\widehat{x}_M}{\widehat{x}_M + d} - \frac{\dot{z}(t)}{z(t)} \frac{1}{f - \frac{g}{y(t)+h}} \frac{1}{y(t) + e}\end{aligned}$$

for $t \in \widehat{I}_0$. Since equation (3.1.3) holds on $\widehat{I}_0$ and y is bounded by $\widehat{y}_M > \frac{g}{f} - h$ for all $t \in \widehat{I} \supset \widehat{I}_0$ (by *(H2)*), we obtain

$$\begin{aligned}
\frac{\dot{y}(t)}{y(t)} &\leq -b + \frac{c\widehat{x}_M}{\widehat{x}_M + d} - \overbrace{\frac{\dot{z}(t)}{z(t)} \underbrace{\frac{1}{f - \frac{g}{y(t)+h}}}_{>0 \text{ by } (3.1.3)}}^{>0 \text{ by } (3.1.4)} \frac{1}{y(t)+e} \\
&\leq -b + \frac{c\widehat{x}_M}{\widehat{x}_M + d} - \frac{\dot{z}(t)}{z(t)} \underbrace{\frac{1}{f - \frac{g}{\widehat{y}_M+h}}}_{>0} \frac{1}{\widehat{y}_M + e}
\end{aligned}$$

for $t \in \widehat{I}_0$. For the sake of readability we define

$$\begin{aligned}
\widehat{\alpha} &:= -b + \frac{c\widehat{x}_M}{\widehat{x}_M + d}, \\
\widehat{\beta} &:= \frac{1}{\left(f - \frac{g}{\widehat{y}_M+h}\right)(\widehat{y}_M + e)} > 0.
\end{aligned}$$

which allows us to write the previous estimate as follows

$$\frac{\dot{y}(t)}{y(t)} \leq \widehat{\alpha} - \widehat{\beta}\frac{\dot{z}(t)}{z(t)} \qquad \forall\, t \in \widehat{I}_0.$$

Integrating both sides from $T_0 \in \widehat{I}_0$ to $t \in \widehat{I}_0$ yields

$$\int_{T_0}^{t} \frac{\dot{y}(\tau)}{y(\tau)} d\tau \leq \int_{T_0}^{t} \widehat{\alpha} - \widehat{\beta}\frac{\dot{z}(\tau)}{z(\tau)} d\tau$$

$$\Leftrightarrow \qquad [\ln(y(\tau))]_{\tau=T_0}^{\tau=t} \leq \widehat{\alpha}(t - T_0) - \widehat{\beta}\,[\ln(z(\tau))]_{\tau=T_0}^{\tau=t}$$

This may also be written as

$$\ln\left(\frac{y(t)}{y(T_0)}\right) \leq \widehat{\alpha}(t - T_0) - \widehat{\beta}\ln\left(\frac{z(t)}{z(T_0)}\right) = \widehat{\alpha}(t - T_0) + \ln\left(\left(\frac{z(T_0)}{z(t)}\right)^{\widehat{\beta}}\right).$$

Applying the exponential function on both sides of the equation yields

$$\frac{y(t)}{y(T_0)} \leq \exp(\widehat{\alpha}(t - T_0))\left(\frac{z(T_0)}{z(t)}\right)^{\widehat{\beta}}.$$

Furthermore, multiplying by $y(T_0) > 0$ results in the claim

$$y(t) \leq y(T_0)\exp(\widehat{\alpha}(t - T_0))\left(\frac{z(T_0)}{z(t)}\right)^{\widehat{\beta}} \qquad \forall\, t \in \widehat{I}_0. \qquad \square$$

We use the above to prove Proposition 3.1.1, i.e. that under our assumptions no solution $\widehat{s}$ blows up in finite time:

Proof of Proposition 3.1.1.
Let $f - \frac{g}{h} < 0$ as well as any solution $\widehat{s}$ be given. Furthermore assume that *(H1)* and *(H2)* hold. The assumption in *(H2)* implies that the first $n-1$ component of $\widehat{s}$ are bounded for all $t \in \widehat{I}$ and a blow-up can only occur in the final component, the z-component. We consider this for three different cases.

- Let $y_0 = 0$, then *(H1)* implies that $y(t) = 0$ for all $t \in \widehat{I}$. Thus the $\dot{z}$-equation in (3.1.1) simplifies to

$$\dot{z}(t) = \underbrace{\left(f - \frac{g}{h}\right)}_{<0} z^2(t) \leq 0.$$

  Hence the final component of $\widehat{s}$ is non-increasing on $\widehat{I}$, implying $z(t) \leq z_0$ for all $t \in \widehat{I}$ and thus the z-component of $\widehat{s}$ does not blow up.

- Let $z_0 = 0$ then *(H1)* implies that $z(t) = 0$ for all $t \in \widehat{I}$ and $\widehat{s}$ only has bounded components for all $t \in \widehat{I}$.

- Let $y_0 > 0$ and $z_0 > 0$ hold for $\widehat{s}$. We provide a proof by contradiction, i.e. we assume that $\widehat{s}$ blows up in a finite time $T^{**} > 0$. Thus the conditions of Lemma 3.1.3 are met and there exists a $T_0 \in [0, T^{**})$ such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in [T_0, T^{**}).$$

  In turn, this implies that for $\widehat{I}_0 = [T_0, T^{**})$ the conditions of Lemma 3.1.4 are met and hence

$$y(t) \leq y(T_0) \exp(\widehat{\alpha}(t - T_0)) \left(\frac{z(T_0)}{z(t)}\right)^{\widehat{\beta}} \qquad \forall\, t \in [T_0, T^{**})$$

  holds. The rest of the proof works analogously to that of Proposition 2.2.1. We reformulate the above to obtain an estimate on the z-component (note $\widehat{\beta} > 0$):

$$z(t) \leq z(T_0) \sqrt[\widehat{\beta}]{\frac{y(T_0)}{y(t)} \exp(\widehat{\alpha}(t - T_0))} \qquad \forall\, t \in [T_0, T^{**}).$$

  Using $y(t) > \frac{g}{f} - h$ for all $t \in [T_0, T^{**})$ and the boundedness of the y-component by $\widehat{y}_M$ for all $t \in \widehat{I}$ (from *(H2)*) allows the estimate

$$z(t) < z(T_0) \sqrt[\widehat{\beta}]{\frac{\widehat{y}_M}{\frac{g}{f} - h} \exp(\widehat{\alpha}(t - T_0))} \qquad \forall\, t \in [T_0, T^{**}). \tag{3.1.5}$$

  We now consider two cases, dependent on the sign of $\widehat{\alpha}$.

i) If $\widehat{\alpha} \leq 0$ then $\exp(\widehat{\alpha}(t - T_0)) \leq 1$ for any $t \in [T_0, T^{**})$. This allows us to estimate (3.1.5) as follows

$$\begin{aligned} z(t) &< z(T_0) \sqrt[\widehat{\beta}]{\frac{\widehat{y}_M}{\frac{g}{f} - h} \exp(\widehat{\alpha}(t - T_0))} \\ &\leq z(T_0) \sqrt[\widehat{\beta}]{\frac{\widehat{y}_M}{\frac{g}{f} - h}} < \infty \qquad \forall\, t \in [T_0, T^{**}). \end{aligned}$$

This however is a contradiction to $\widehat{s}$ blowing up.

ii) If $\widehat{\alpha} > 0$ then $\exp(\widehat{\alpha}(t - T_0)) \leq \exp(\widehat{\alpha}(T^{**} - T_0))$ for any $t \in [T_0, T^{**})$. This allows us to estimate (3.1.5) as follows

$$\begin{aligned} z(t) &< z(T_0) \sqrt[\widehat{\beta}]{\frac{\widehat{y}_M}{\frac{g}{f} - h} \exp(\widehat{\alpha}(t - T_0))} \\ &\leq z(T_0) \sqrt[\widehat{\beta}]{\frac{\widehat{y}_M}{\frac{g}{f} - h} \exp(\widehat{\alpha}(T^{**} - T_0))} < \infty \qquad \forall\, t \in [T_0, T^{**}). \end{aligned}$$

This however is a contradiction to $\widehat{s}$ blowing up. □

Hence under the assumptions of Proposition 3.1.1 any solution $\widehat{s}$ indeed does not blow up and the mathematical model generates biologically feasible and bounded solutions. In particular the maximal positive existence interval of $\widehat{s}$ is in fact given by $\widehat{I} = [0, \infty)$, i.e. the solution is defined for all $t \geq 0$. This allows us to show that the model equations induce a semiflow on $\widehat{\mathcal{O}}_0^+$ (compare to Corollary 2.2.3).

Corollary 3.1.1.
Let $f - \frac{g}{h} < 0$ hold and assume that (H1) and (H2) hold for any solution $\widehat{s}$. Then the map

$$\begin{aligned} \widehat{\Phi} : \mathbb{R}_0^+ \times \widehat{\mathcal{O}}_0^+ &\to \widehat{\mathcal{O}}_0^+ \\ (t, \widehat{s}_0) &\mapsto \widehat{s}(t) \end{aligned}$$

defines a semiflow on $\widehat{\mathcal{O}}_0^+$.

Proof.
The metric space we consider is $(\widehat{\mathcal{O}}_0^+, \mathrm{d})$ (with the Euclidean metric d on $\mathbb{R}^n$). The rest of the proof is analogous to that of Corollary 2.2.3. □

The reason why we can use analogous proofs to the three-dimensional system in many cases is because the 'main ingredients' (i.e. the essential properties of the dynamics induced by (2.1.5)) we used in the proofs were the property $(\widehat{I}1)$ and positivity (due to *(H1)*), the boundedness of the first components (due to *(H2)*) and the structure of the $\dot{y}$- and $\dot{z}$-equations, which remained the same in (2.1.5) and (3.1.1). This allowed us to conclude counterpart results such as above for the n-dimensional case. It will allow us to show that under our assumptions solutions $\widehat{s}$ are also bounded as $t \to \infty$, compare to subsection 2.2.5.

Boundedness

We show

Theorem 3.1.1.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ be given. Assume that (H1) and (H2) hold. Then $\widehat{s}$ does not blow up in finite future time and is bounded as time tends to infinity. In particular it holds that

$$\limsup_{t\to\infty} z(t) < \infty.$$

Proving the theorem works in a similar way to the procedure in subsection 2.2.5. We first recall

Corollary 3.1.2.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 = 0$ or $z_0 = 0$ (or both) be given. Assume that (H1) and (H2) hold. Then

$$z(t) \leq z_0 \qquad \forall\, t \geq 0.$$

Proof.
We showed this in the first two bullets in the proof of Proposition 3.1.1. □

We now turn to the case $\widehat{z}_* = 0$ (compare to Lemmas 2.2.10 to 2.2.12).

Lemma 3.1.5.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $\widehat{z}_* = 0$ be given. Assume that (H1) and (H2) hold. Then

$$\dot{y}(t) \leq 0 \qquad \forall\, t \geq 0.$$

Proof.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $\widehat{z}_* = 0$ be given. Assume that *(H1)* and *(H2)* hold. Since $\widehat{z}_* = 0$ holds, we have

$$-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d} \leq 0. \tag{3.1.6}$$

Hence, using $x_{n-2}(t) \leq \widehat{x}_M$ for any $t \geq 0$ (by *(H2)*), it holds that for all $t \geq 0$

$$\begin{aligned}\dot{y}(t) &= y(t)\left(-b + \frac{cx_{n-2}(t)}{x_{n-2}(t) + d} - \frac{z(t)}{y(t) + e}\right) \\ &\leq y(t)\underbrace{\left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d} - \frac{z(t)}{y(t) + e}\right)}_{\leq 0 \text{ by } (3.1.6)} \leq 0.\end{aligned}$$

□

Thus we can prove

Lemma 3.1.6.
Let $f - \frac{g}{h} < 0$ *and any solution* $\widehat{s}$ *with* $y_0 \leq \frac{g}{f} - h$ *and* $\widehat{z}_* = 0$ *be given. Assume that (H1) and (H2) hold. Then it holds that*

$$z(t) \leq z_0 \qquad \forall\, t \geq 0.$$

Proof.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 \leq \frac{g}{f} - h$ and $\widehat{z}_* = 0$ be given. Assume that *(H1)* and *(H2)* hold. By Lemma 3.1.5 the y-component is non-increasing on $\widehat{I} = [0, \infty)$ and hence

$$y(t) \leq y_0 \leq \frac{g}{f} - h$$

for all $t \geq 0$. This in turn implies (by the third equation of system (3.1.1)) that

$$\dot{z}(t) \leq 0 \qquad \forall\, t \geq 0$$

and therefore

$$z(t) \leq z_0 \qquad \forall\, t \geq 0. \qquad \square$$

The case $y_0 > \frac{g}{f} - h$ is slightly more work:

Lemma 3.1.7.
Let $f - \frac{g}{h} < 0$ *and any solution* $\widehat{s}$ *with* $y_0 > \frac{g}{f} - h$ *and* $\widehat{z}_* = 0$ *be given. Assume that (H1) and (H2) hold. Then there exists a* $C = C(s_0) \geq 0$ *such that*

$$z(t) \leq C < \infty \qquad \forall\, t \geq 0.$$

Proof.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > \frac{g}{f} - h$ and $\widehat{z}_* = 0$ be given. Assume that *(H1)* and *(H2)* hold. If $z_0 = 0$ we obtain

$$z(t) = 0 \qquad \forall\, t \geq 0.$$

Setting $C = 0$ in this case, yields the claim. Thus we additionally assume $z_0 > 0$ for $\widehat{s}$ implying

$$z(t) > 0 \qquad \forall\, t \geq 0.$$

Let $\widehat{I}_L = [0, T_L) \subset [0, \infty)$ be the maximal (positive) interval such that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in \widehat{I}_L. \tag{3.1.7}$$

Note that such an interval $\widehat{I}_L$ exists and is non-empty, since $y_0 = y(0) > \frac{g}{f} - h$ and y is continuous for any $t \geq 0$ (since $\widehat{s}$ is continuous). Applying Lemma 3.1.4 (with $\widehat{I}_0 = \widehat{I}_L$ and $T_0 = 0$) now yields

$$y(t) \leq y_0 \exp(\widehat{\alpha} t) \left(\frac{z_0}{z(t)} \right)^{\widehat{\beta}} \qquad \forall\, t \in \widehat{I}_L,$$

with $\widehat{\alpha} \leq 0$ (since $\widehat{z}_* = 0$) and $\widehat{\beta} > 0$. Solving the above for $z(t)$ yields

$$z(t) \leq z_0 \sqrt[\widehat{\beta}]{\frac{y_0}{y(t)} \exp(\widehat{\alpha} t)} \qquad \forall\, t \in \widehat{I}_L.$$

Estimating the above using $\widehat{\alpha} \leq 0$ and (3.1.7) results in

$$z(t) \leq z_0 \sqrt[\widehat{\beta}]{\frac{y_0}{y(t)} \exp(\widehat{\alpha} t)} < z_0 \sqrt[\widehat{\beta}]{\frac{y_0}{\frac{g}{f} - h}} \qquad \forall\, t \in \widehat{I}_L = [0, T_L). \tag{3.1.8}$$

i) If $\widehat{I}_L = [0, \infty)$ then

$$z(t) < z_0 \sqrt[\widehat{\beta}]{\frac{y_0}{\frac{g}{f} - h}} < \infty \qquad \forall\, t \geq 0$$

and the z-component is evidently bounded by a constant for all $t \geq 0$.

ii) If $|\widehat{I}_L| < \infty$, i.e. $T_L < \infty$, then

$$y(T_L) \leq \frac{g}{f} - h,$$

since $\widehat{I}_L$ was chosen to be maximal. Furthermore, from Lemma 3.1.5 we know that y is non-increasing on $[0, \infty)$ and therefore the above implies

$$y(t) \leq \frac{g}{f} - h \qquad \forall\, t \geq T_L.$$

This in turn results in

$$\dot{z}(t) \leq 0 \qquad \forall\, t \geq T_L.$$

Therefore it holds that

$$z(t) \leq z(T_L) \qquad \forall\, t \geq T_L.$$

Thus combining the above and (3.1.8) and setting

$$C := \max \left\{ z(T_L), z_0 \sqrt[\widehat{\beta}]{\frac{y_0}{\frac{g}{f} - h}} \right\} < \infty$$

yields

$$z(t) \leq C \qquad \forall\, t \geq 0$$

in this case and hence the proof is complete. □

We can now restrict the following considerations to solutions $\widehat{s}$ that fulfil $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$. As always we will also assume $f - \frac{g}{h} < 0$ and *(H1)* and *(H2)* to hold. Such solutions are confined to a subset $\widehat{\Omega} \subset \widehat{\mathcal{O}}_0^+$, which we define in the following

Lemma 3.1.8.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume that (H1) and (H2) hold. For the set

$$\widehat{\Omega} := \left\{ (\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \,:\, 0 < y \leq \widehat{y}_M,\, 0 < z,\, x_i \leq \widehat{x}_M \text{ for all } i \in \mathcal{I} \right\}$$

it holds that

$$\widehat{s}(t) \in \widehat{\Omega} \qquad \forall\, t \geq 0.$$

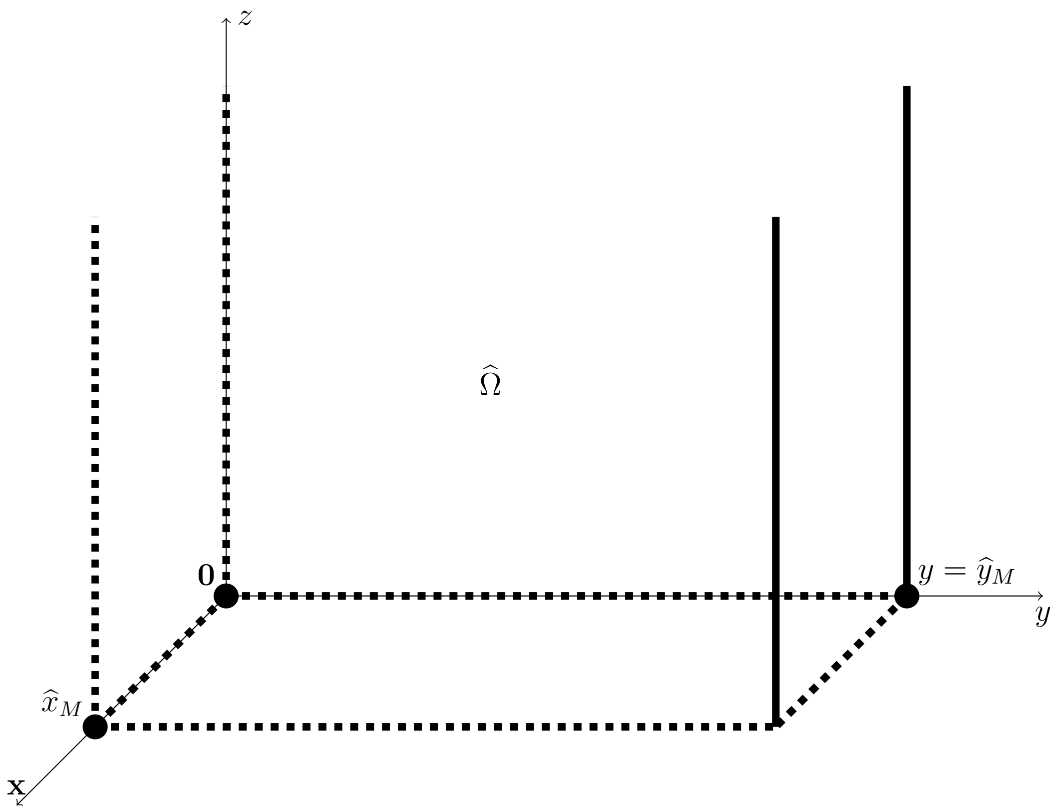


Figure 3.1.3: Schematic figure of the set $\widehat{\Omega} \subset \widehat{\mathcal{O}}_0^+ \subset \mathbb{R}^n$ (Note: $\mathbf{x} \in \mathbb{R}^{n-2}$).

Proof.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume that *(H1)* and *(H2)* hold. We show that $\widehat{s}$ is contained in the set $\widehat{\Omega}$ defined above (see Figure 3.1.3) for all $t \geq 0$, by consecutively considering each component of $\widehat{s}$. By assumption *(H2)* the solution fulfils

$$0 \leq x_i(t) \leq \widehat{x}_M \qquad \forall\, t \geq 0$$

and for all $i \in \mathcal{I}$. By the same assumption we have

$$y(t) \leq \widehat{y}_M \qquad \forall\, t \geq 0.$$

Additionally, (3.1.2) and $y_0 > 0$ implies that the y-component of $\widehat{s}$ is strictly positive for all $t \geq 0$. Finally, by the same argument we also have

$$z_0 > 0 \qquad \Rightarrow \qquad z(t) > 0 \quad \forall\, t \geq 0$$

and hence we indeed have

$$\widehat{s}(t) \in \widehat{\Omega} \qquad \forall\, t \geq 0. \qquad \square$$

We partition the set $\widehat{\Omega}$ into four subsets by inserting two hyperplanes defined by $y = \frac{g}{f} - h$ and $z = 2\widehat{z}_*$ respectively (compare to Definition 2.2.2), which will prove useful in showing the boundedness of $\widehat{s}$:

Definition 3.1.3.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume that (H1) and (H2) hold. We define

$$\widehat{\Omega}_1 := \left\{ (\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \;:\; y \leq \frac{g}{f} - h,\; z < 2\widehat{z}_* \right\} \cap \widehat{\Omega}$$

$$\widehat{\Omega}_2 := \left\{ (\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \;:\; y > \frac{g}{f} - h,\; z < 2\widehat{z}_* \right\} \cap \widehat{\Omega}$$

$$\widehat{\Omega}_3 := \left\{ (\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \;:\; y > \frac{g}{f} - h,\; z \geq 2\widehat{z}_* \right\} \cap \widehat{\Omega}$$

$$\widehat{\Omega}_4 := \left\{ (\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \;:\; y \leq \frac{g}{f} - h,\; z \geq 2\widehat{z}_* \right\} \cap \widehat{\Omega}$$

In particular we have

$$\widehat{\Omega} = \widehat{\Omega}_1 \,\dot{\cup}\, \widehat{\Omega}_2 \,\dot{\cup}\, \widehat{\Omega}_3 \,\dot{\cup}\, \widehat{\Omega}_4 = \bigcup_{i=1}^{4} \widehat{\Omega}_i,$$

i.e. the sets $\widehat{\Omega}_i$ form a partition of $\widehat{\Omega}$ (defined in Lemma 3.1.8).

The above-defined sets are visualised in Figure 3.1.4. Note that since $\widehat{z}_* > 0$ and $\widehat{y}_M > \frac{g}{f} - h$ (due to assumption *(H2)*) hold, the sets $\widehat{\Omega}_i$ (with $i \in \{1, 2, 3, 4\}$) are non-empty. By Lemma 3.1.8 we know that any solution $\widehat{s}$ we are considering (or rather its positive phase curve) is contained in the set $\widehat{\Omega}$ for all $t \geq 0$ and therefore also in exactly one of the four partitions $\widehat{\Omega}_i$ for any $t \geq 0$. We discuss how to prove that such a $\widehat{s}$ is also bounded in the z-component as time tends to infinity by considering the behaviour of the solution (and its respective positive phase curve) in the four partitions.

- **The case** $\widehat{\Omega}_1$ and $\widehat{\Omega}_2$: These two sets are *bounded* by $2\widehat{z}_*$ in the z-direction and hence any solution $\widehat{s}$ as defined in Lemma 3.1.8 is bounded for all $t \geq 0$ while it is in these sets, i.e.

$$\left(\forall\, t \geq 0 \;:\; \widehat{s}(t) \in \widehat{\Omega}_1 \cup \widehat{\Omega}_2\right) \quad \Rightarrow \quad \widehat{s}(t) \leq 2\widehat{z}_*$$

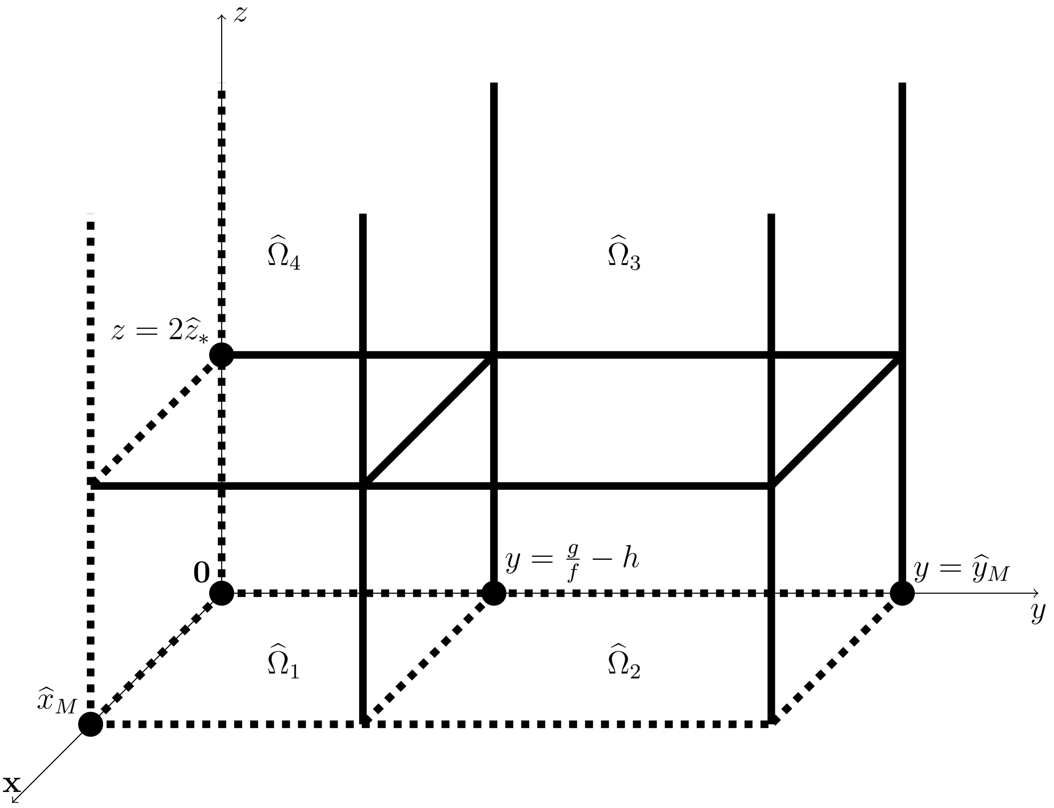


Figure 3.1.4: The sets $\widehat{\Omega}_1$, $\widehat{\Omega}_2$, $\widehat{\Omega}_3$, $\widehat{\Omega}_4$ form a partition of $\widehat{\Omega} \subset \widehat{\mathcal{O}}_0^+$.

- **The case $\widehat{\Omega}_4$:** By definition it holds that

$$y \leq \frac{g}{f} - h$$

in $\widehat{\Omega}_4$. Thus if a solution $\widehat{s}$ fulfils $\widehat{s}(t) \in \widehat{\Omega}_4$ for some $t \geq 0$, then it also fulfils $\dot{z}(t) \leq 0$ for this t (due to the last line of (3.1.1)). I.e. the z-component of a solution is *non-increasing* while the solution is in the set $\widehat{\Omega}_4$. Differently put, the vector field in $\widehat{\Omega}_4$ is non-increasing in z-direction. Thus a solution $\widehat{s}$ is bounded in $\widehat{\Omega}_4$, in the sense that it cannot increase in the z-component there. Furthermore,

$$z > 2\widehat{z}_*$$

holds in $\widehat{\Omega}_4$ by construction. Thus, Lemma 3.1.2 yields that the vector field in $\widehat{\Omega}_4$ is strictly decreasing in y-direction as well. This results in a vector field as depicted schematically in Figure 3.1.5.

Hence we conclude:

Corollary 3.1.3.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume that (H1) and (H2) hold. Furthermore assume that

$$\widehat{s}(t) \in \widehat{\Omega}_1 \cup \widehat{\Omega}_2 \cup \widehat{\Omega}_4 \qquad \forall\, t \geq 0.$$

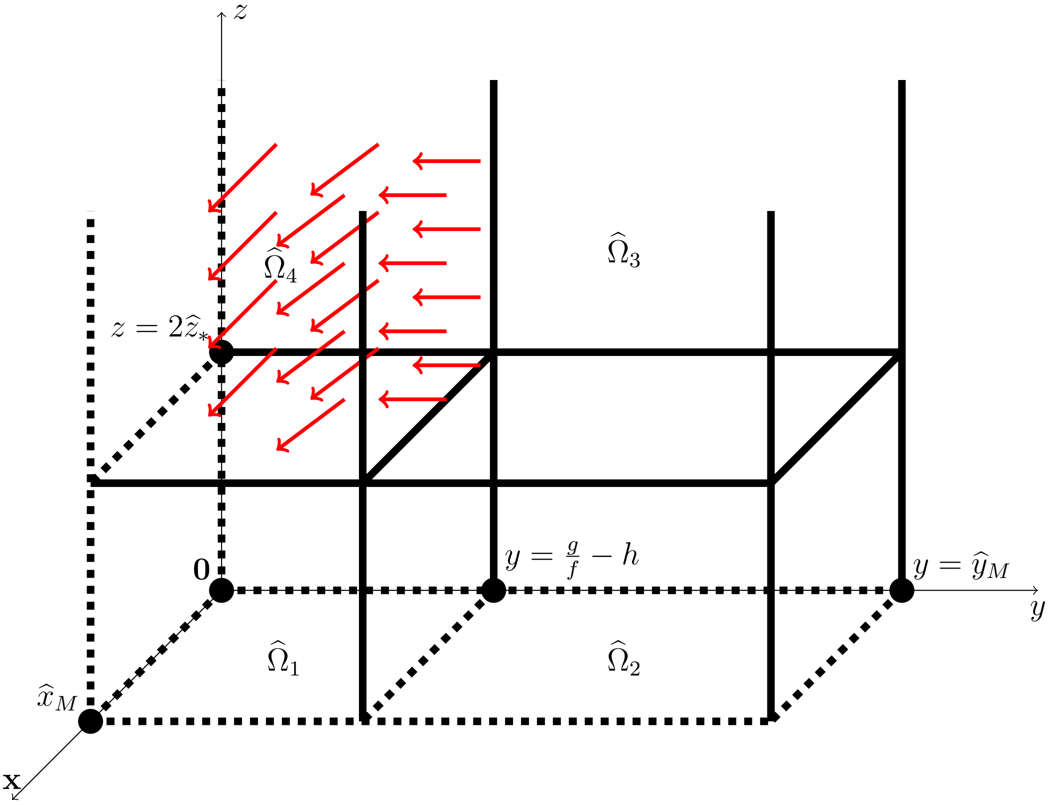


Figure 3.1.5: Schematic figure of the vector field (red arrows) in $\widehat{\Omega}_4$. It is non-increasing in both y- and z-direction.

Then $\widehat{s}$ does not blow up in finite future time and is bounded as time tends to infinity. In particular it holds that

$$\limsup_{t\to\infty} z(t) < \infty.$$

As a consequence of the above corollary, it is clear that if a solution $\widehat{s}$ should diverge as $t \to \infty$, then this necessarily has to involve the set $\widehat{\Omega}_3$, as it is the only set where the z-component of $\widehat{s}$ could possibly increase without bound. We will show that any solution $\widehat{s}$ will leave the set $\widehat{\Omega}_3$ after a finite time $\widehat{T}_M > 0$ (possibly re-entering it later), compare to Lemmas 2.2.14 and 2.2.15.

Lemma 3.1.9.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume that (H1) and (H2) hold. Then it holds that

$$\widehat{T}_M := \frac{1}{\widehat{\alpha}} \ln\left(\frac{\widehat{y}_M}{\frac{g}{f} - h}\right) > 0,$$

where $\widehat{\alpha} > 0$ is defined as in Lemma 3.1.4.

Proof.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume

that *(H1)* and *(H2)* hold. By the definition of $\widehat{z}_*$ in Lemma 3.1.2 we see that $\widehat{z}_* > 0$ implies

$$\widehat{z}_* = \left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d}\right)(\widehat{y}_M + e).$$

Thus we obtain

$$0 < \widehat{z}_* = \underbrace{\left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d}\right)}_{=\widehat{\alpha} \text{ from Lemma 3.1.4}}(\widehat{y}_M + e) = \widehat{\alpha}\,\underbrace{(\widehat{y}_M + e)}_{>0},$$

and therefore $\widehat{\alpha} > 0$. We conclude (using $\widehat{y}_M > \frac{g}{f} - h$) that

$$\widehat{T}_M = \underbrace{\frac{1}{\widehat{\alpha}}}_{>0}\underbrace{\ln\left(\frac{\widehat{y}_M}{\frac{g}{f} - h}\right)}_{>0} > 0. \qquad \square$$

We now show that $\widehat{T}_M$ is in fact sufficiently large.

Lemma 3.1.10.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume that (H1) and (H2) hold. Furthermore let a $T_3 \geq 0$ exist such that $\widehat{s}(T_3) \in \widehat{\Omega}_3$. Then there exists a $t \in [T_3, T_3 + \widehat{T}_M]$ such that $\widehat{s}(t) \notin \widehat{\Omega}_3$.

Proof.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume that *(H1)* and *(H2)* hold. Furthermore, let a $T_3 \geq 0$ exist such that $\widehat{s}(T_3) \in \widehat{\Omega}_3$. We set $\widehat{I}_3 := [T_3, T_3 + \widehat{T}_M]$ and see $|\widehat{I}_3| > 0$ by Lemma 3.1.9. We now provide a proof by contradiction, i.e. we assume that

$$\widehat{s}(t) \in \widehat{\Omega}_3 \qquad \forall\, t \in \widehat{I}_3.$$

Hence for all $t \in \widehat{I}_3$ we have $z(t) \geq 2\widehat{z}_*$ and by *(H2)* it also holds that $x_{n-2}(t) \leq \widehat{x}_M$ and $y(t) \leq \widehat{y}_M$. This allows the estimate

$$\begin{aligned}\dot{y}(t) &= y(t)\left(-b + \frac{cx_{n-2}(t)}{x_{n-2}(t) + d} - \frac{z(t)}{y(t) + e}\right)\\ &\leq y(t)\left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d} - \frac{2\widehat{z}_*}{\widehat{y}_M + e}\right).\end{aligned}$$

Since $\widehat{z}_* > 0$ we have $\widehat{z}_* = \left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d}\right)(\widehat{y}_M + e)$ and using this in the above yields

$$\begin{aligned}\dot{y}(t) &\leq y(t)\left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d} - 2\left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d}\right)\right)\\ &= -y(t)\underbrace{\left(-b + \frac{c\widehat{x}_M}{\widehat{x}_M + d}\right)}_{=\widehat{\alpha}}\\ &= -\widehat{\alpha}y(t)\end{aligned}$$

for all $t \in \widehat{I}_3$. Dividing by $y(t) > 0$ above, we obtain

$$\frac{\dot{y}(t)}{y(t)} \leq -\widehat{\alpha} \qquad \forall\, t \in \widehat{I}_3$$

and integrating from $T_3 \in \widehat{I}_3$ to $T_3 + \widehat{T}_M \in \widehat{I}_3$ yields

$$[\ln(y(\tau))]_{\tau=T_3}^{\tau=T_3+\widehat{T}_M} \leq -\widehat{\alpha}(T_3 + \widehat{T}_M - T_3) = -\widehat{\alpha}\widehat{T}_M.$$

Using the definition of $\widehat{T}_M$ from Lemma 3.1.9 this may be rewritten as

$$\ln\left(\frac{y(T_3+\widehat{T}_M)}{y(T_3)}\right) \leq -\widehat{\alpha}\frac{1}{\widehat{\alpha}}\ln\left(\frac{\widehat{y}_M}{\frac{g}{f}-h}\right) = \ln\left(\frac{\frac{g}{f}-h}{\widehat{y}_M}\right).$$

Solving this for $y(T_3 + \widehat{T}_M)$ results in

$$y(T_3+\widehat{T}_M) \leq y(T_3)\frac{\frac{g}{f}-h}{\widehat{y}_M}.$$

Since $\widehat{s}$ is bounded by $\widehat{y}_M$ in the y-component for all $t \geq 0$ it holds that $y(T_3) \leq \widehat{y}_M$ and therefore we estimate further:

$$y(T_3+\widehat{T}_M) \leq y(T_3)\frac{\frac{g}{f}-h}{\widehat{y}_M} \leq \frac{g}{f} - h.$$

This however implies $\widehat{s}(T_3+\widehat{T}_M) \notin \widehat{\Omega}_3$, which is a contradiction to our assumption. □

The above result implies that the z-component of solutions cannot grow arbitrarily, as we prove in:

Lemma 3.1.11.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume that (H1) and (H2) hold. Then $\widehat{s}$ does not blow up in finite future time and is bounded as time tends to infinity. In particular it holds that

$$\limsup_{t\to\infty} z(t) < \infty.$$

Proof.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ with $y_0 > 0$, $z_0 > 0$ and $\widehat{z}_* > 0$ be given. Assume that *(H1)* and *(H2)* hold. Since *(H2)* and Proposition 3.1.1 hold, $\widehat{s}$ cannot blow up in finite future time and only blow up in the z-component as time tends to infinity. We prove that this is not possible. Recall that by Lemma 3.1.8 the positive phase curve corresponding to $\widehat{s}$ is contained in the set $\widehat{\Omega}$ for all $t \geq 0$. We partitioned this set into four subsets (recall Definition 3.1.3 and Figure 3.1.4). Assume that

$$\widehat{s}(t) \notin \widehat{\Omega}_3 \qquad \forall\, t \geq 0,$$

then $\widehat{s}$ is confined to the sets $\widehat{\Omega}_1$, $\widehat{\Omega}_2$ and $\widehat{\Omega}_4$, where it cannot diverge as time tends to infinity as it is bounded, by Corollary 3.1.3 and we are done. Hence we can assume

$$\exists\, T_3 \geq 0 \,:\, \widehat{s}(T_3) \in \widehat{\Omega}_3.$$

Thus Lemma 3.1.10 applies and we know that $\widehat{s}$ will have left the set $\widehat{\Omega}_3$ at least for one time point in the time interval $[T_3, T_3 + \widehat{T}_M]$. Once the solution has left $\widehat{\Omega}_3$ it is either contained in $\widehat{\Omega}_1 \cup \widehat{\Omega}_2 \cup \widehat{\Omega}_4$ for all future times (in which case Corollary 3.1.3 holds once more) or the positive phase curve is *reinjected* into $\widehat{\Omega}_3$ for some $\widehat{T}_R > T_3 > 0$. We consider this reinjection more closely. Since

$$\widehat{s}(t) \in \widehat{\Omega} \qquad \forall\, t \geq 0$$

holds, this reinjection occurs via the common boundary of $\widehat{\Omega}_3$ with one of the other $\widehat{\Omega}_i$, with $i \in \{1, 2, 4\}$. However, recall that the vector field is pointing out of $\widehat{\Omega}_3$ on the common boundary with $\widehat{\Omega}_1$ and $\widehat{\Omega}_4$ (since there $z \geq 2\widehat{z}_* > \widehat{z}_*$, see Lemma 3.1.2 and Figures 3.1.5 and 3.1.6). Thus $\widehat{s}$ can only be reinjected into $\widehat{\Omega}_3$, via the remaining common boundary with $\widehat{\Omega}_2$ (see the blue phase curve and grey region in Figure 3.1.6), i.e. the set (hypersurface)

$$\widehat{\Omega}_B = \left\{ (\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \,:\, y > \frac{g}{f} - h,\, z = 2\widehat{z}_* \right\} \cap \widehat{\Omega} \subset \widehat{\Omega}_3.$$

This implies that for the reinjection time $\widehat{T}_R$ it holds that $z(\widehat{T}_R) = 2\widehat{z}_*$. I.e. the z-component always has the same value when $\widehat{s}$ is reinjected into $\widehat{\Omega}_3$, independent of the fact at which point in $\widehat{\Omega}_B$ or time point $\widehat{T}_R \in (0, \infty)$ the reinjection occurs. Furthermore, the implication

$$\widehat{\Omega}_B \subset \widehat{\Omega}_3 \qquad \Rightarrow \qquad \widehat{s}(\widehat{T}_R) \in \widehat{\Omega}_3$$

is true and hence Lemma 3.1.10 applies to the time interval $[\widehat{T}_R, \widehat{T}_R + \widehat{T}_M]$, in which the solution $\widehat{s}$ will leave the set $\widehat{\Omega}_3$ again. The scenario from above repeats and either the solution does not return to the set $\widehat{\Omega}_3$ or it has to drop to or below the value $2\widehat{z}_*$ in its z-component again, in order to be reinjected into $\widehat{\Omega}_3$ via $\widehat{\Omega}_B$. Now while the solution is in $\widehat{\Omega}_3$ (we call this time interval $\widehat{I}_\Omega$ with $\min \widehat{I}_\Omega = \widehat{T}_R$ and $|\widehat{I}_\Omega| \leq \widehat{T}_M$) we have

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in \widehat{I}_\Omega \tag{3.1.9}$$

by the definition of $\widehat{\Omega}_3$. Thus Lemma 3.1.4 applies and we obtain

$$y(t) \leq y(\widehat{T}_R) \exp(\widehat{\alpha}(t - \widehat{T}_R)) \left(\frac{z(\widehat{T}_R)}{z(t)} \right)^{\widehat{\beta}} \qquad \forall\, t \in \widehat{I}_\Omega.$$

This can be rewritten as

$$z(t) \leq z(\widehat{T}_R) \sqrt[\widehat{\beta}]{\frac{y(\widehat{T}_R)}{y(t)} \exp(\widehat{\alpha}(t - \widehat{T}_R))} \qquad \forall\, t \in \widehat{I}_\Omega.$$

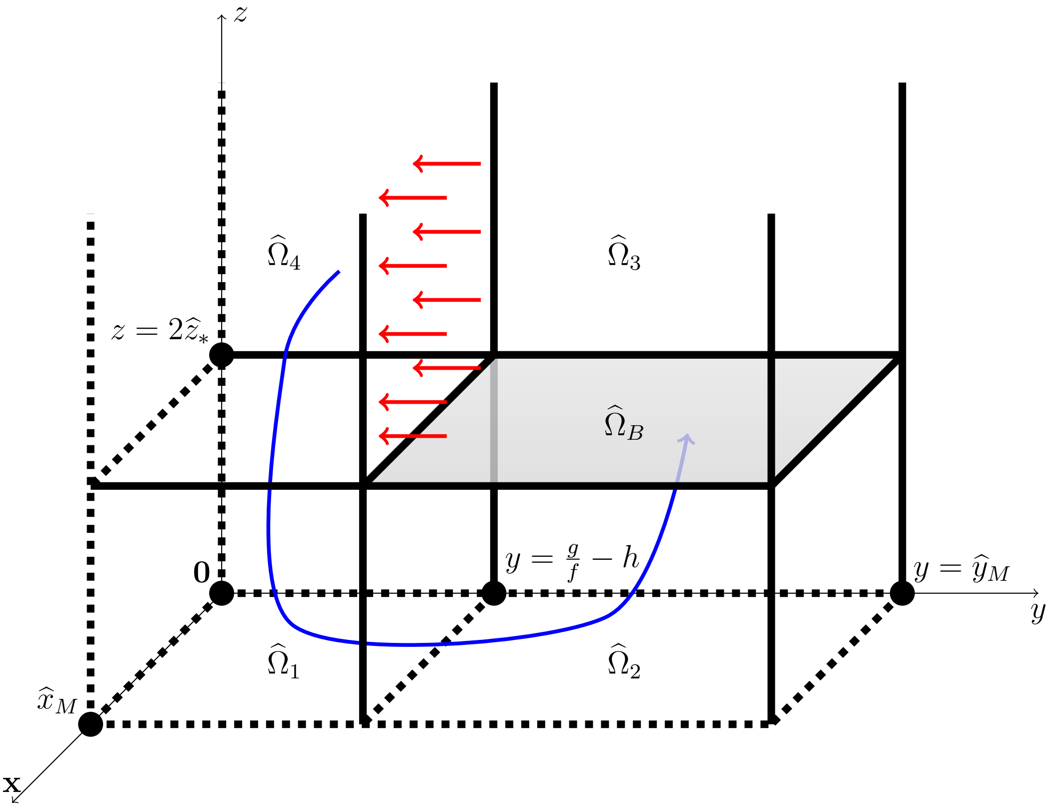


Figure 3.1.6: A solution $\widehat{s}$ (blue) can only enter the set $\widehat{\Omega}_3$ via the common boundary $\widehat{\Omega}_B$ of $\widehat{\Omega}_2$ and $\widehat{\Omega}_3$.

Recall that $z(\widehat{T}_R) = 2\widehat{z}_*$ and since the y-component is bounded by $\widehat{y}_M$ for all $t \geq 0$, we have $y(\widehat{T}_R) \leq \widehat{y}_M$. Thus the above implies

$$z(t) \leq 2\widehat{z}_* \sqrt[\widehat{\beta}]{\frac{\widehat{y}_M}{y(t)} \exp(\widehat{\alpha}(t - \widehat{T}_R))} \qquad \forall t \in \widehat{I}_\Omega.$$

Using $\widehat{I}_\Omega \subset [\widehat{T}_R, \widehat{T}_R + \widehat{T}_M]$ (by construction of the interval), $\widehat{\alpha} > 0$ (since $\widehat{z}_* > 0$) and (3.1.9) we obtain

$$z(t) \leq 2\widehat{z}_* \sqrt[\widehat{\beta}]{\frac{\widehat{y}_M}{y(t)} \exp(\widehat{\alpha}(t - \widehat{T}_R))} \leq 2\widehat{z}_* \sqrt[\widehat{\beta}]{\frac{\widehat{y}_M}{\frac{g}{f} - h} \exp(\widehat{\alpha}(\widehat{T}_R + \widehat{T}_M - \widehat{T}_R))} \qquad \forall t \in \widehat{I}_\Omega.$$

Which, recalling the definition of $\widehat{T}_M$, simplifies to

$$z(t) \leq 2\widehat{z}_* \sqrt[\widehat{\beta}]{\left(\frac{\widehat{y}_M}{\frac{g}{f} - h}\right)^2} \qquad \forall t \in \widehat{I}_\Omega. \tag{3.1.10}$$

This is a bound on the solution while in $\widehat{\Omega}_3$ that only depends on the initial conditions $\widehat{s}_0$ and holds for arbitrarily large $\widehat{T}_R > 0$, i.e. for an *arbitrarily late* reinjection time.

In particular there can be no divergent subsequence $(t_i)_{i\in\mathbb{N}}$ of time points $t_i > 0$ such that

$$z(t_i) \to \infty \qquad \text{as} \quad i \to \infty,$$

i.e. we have

$$\limsup_{t\to\infty} z(t) \neq \infty.$$

Hence, the final component of $\widehat{s}$ is bounded by the above value in 3.1.10 while in $\widehat{\Omega}_3$ for any $t \geq 0$ and bounded in the set $\widehat{\Omega}_1 \cup \widehat{\Omega}_2 \cup \widehat{\Omega}_4$ by Corollary 3.1.3. We have thus found a time-independent bound on the z-component of $\widehat{s}$, implying

$$\limsup_{t\to\infty} z(t) < \infty$$

and that $\widehat{s}$ does not blow up as time tends to infinity. □

The proof of Theorem 3.1.1 is now merely plugging together the above results:

Proof of Theorem 3.1.1.
Let $f - \frac{g}{h} < 0$ and any solution $\widehat{s}$ be given. Assume that *(H1)* and *(H2)* hold. Since *(H2)* and Proposition 3.1.1 hold, it only remains to show that $\widehat{s}$ does not diverge in the final component. We study several cases

- If $y_0 = 0$ or $z_0 = 0$ then Corollary 3.1.2 yields the claim.
- If $\widehat{z}_* = 0$ then Lemmas 3.1.6 and 3.1.7 yield the result.
- If $y_0 > 0$ and $z_0 > 0$ and $\widehat{z}_* > 0$ then we obtain the claim from Lemma 3.1.11. □

Thus we have proven that the solutions are bounded for all $t \geq 0$ and indeed as $t \to \infty$. Naturally this gives rise to the question how the dynamics and the long-term behaviour of solutions looks. The asymptotic behaviour could once more settle down on an attractor $\mathcal{A}$ as $t \to \infty$, for example. In order to clarify this, more assumptions on the vector field F in (3.1.1) would be required to be made. Assumptions implying the existence of uniform bounds (and contraction rates) on the various species densities would be one possibility (recall the three-dimensional case). Under these conditions the similar structures of the food chain models promise similar results. However, we will not venture in this direction. Much rather, we investigate and present how the method for obtaining global results from subsection 2.4.2 can be applied to the n-dimensional model.

3.1.3 Global results

Recall from subsection 2.4.2 that the central tool we used to obtain global results was Lemma 2.4.8. For the sake of convenience and readability we state the lemma again below:

Lemma (Lemma 2.4.8)**.**
Let $T > 0$ *and a function* $u \in \mathcal{C}^0([0,T], \mathbb{R}^+)$ *be given. Furthermore, let constants* $C_1, C_2 > 0$ *exist such that*

$$0 < \frac{1}{T}\int_0^T u(t)dt \leq C_1 \tag{3.1.11}$$

$$0 < \frac{1}{T}\int_0^T \frac{1}{u(t)}dt \leq C_2. \tag{3.1.12}$$

Then it holds that

$$C_1 \cdot C_2 \geq 1. \tag{3.1.13}$$

If either of the inequalities (3.1.11) *and* (3.1.12) *is strict, then so is* (3.1.13)*.*

The lemma allowed us to restrict the parameter space for which certain solutions (such as periodic ones) could exist in $\mathcal{O}^+ \subset \mathbb{R}^3$. In a similar manner, the method is applicable to the dynamics of the n-dimensional system (3.1.1) on $\widehat{\mathcal{O}}^+$. For this, it is decisive to obtain estimates of the same type as (3.1.11) and (3.1.12). We will restrict ourselves to periodic solutions in this case. The first result is identical to that of Lemma 2.4.9:

Lemma 3.1.12.
Let $f - \frac{g}{h} < 0$ *and any periodic solution* $\widehat{s}$ *with* $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$ *and period* $T > 0$ *be given. Assume that (H1) and (H2) hold. Then* $\widehat{s} = (\mathbf{x}(t), y(t), z(t))^T$ *fulfils*

$$\frac{1}{T}\int_0^T \frac{dt}{y(t)+h} = \frac{f}{g}.$$

Proof.
The proof is analogous to that of Lemma 2.4.9, using the fact that $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$ along with the assumptions *(H1)* and *(H2)* yield the positivity of all the components of $\widehat{s}$ for all $t \geq 0$. □

Before we obtain an estimate for $y + h$, we need one more consideration. Recall that the bound $\widehat{y}_M$ on the y-component of a solution $\widehat{s}$ from assumption *(H2)* was assumed to fulfil $\widehat{y}_M > \frac{g}{f} - h$. This proved convenient for several estimates in the previous subsection. However, as mentioned in the subsequent remark to assumption *(H2)*, the 'restriction'

$$\widehat{y}_M > \frac{g}{f} - h$$

is in fact none and we can work with any given bound $\widehat{y}_B$ on the y-component instead, since the following implication holds true:

$$y(t) \leq \widehat{y}_B \quad \forall\, t \in \widehat{I} \qquad \Rightarrow \qquad y(t) \leq \max\left\{\widehat{y}_B, 2\left(\frac{g}{f} - h\right)\right\} = \widehat{y}_M \quad \forall\, t \in \widehat{I}.$$

I.e. the assumption in the above implication (which we call *(H2')* - see below) implies the existence of such a bound $\widehat{y}_M$, i.e.

$$\textit{(H2')} \qquad \Rightarrow \qquad \textit{(H2)}.$$

Thus all of the above results also hold if we assume *(H2')* to hold instead of *(H2)*:

Assumption (*(H2')*)**.**
Let any solution $\widehat{s}$ (with $\widehat{s}_0 \in \widehat{\mathcal{O}}_0^+$) be given. Assume there exist constants

$$\widehat{x}_M = \widehat{x}_M(\widehat{s}_0) > 0 \quad \textit{and} \quad \widehat{y}_B = \widehat{y}_B(\widehat{s}_0) > 0$$

such that

$$\begin{aligned} &0 \le x_i(t) \le \widehat{x}_M \qquad \forall\, i \in \mathcal{I} \\ &0 \le y(t) \le \widehat{y}_B \end{aligned}$$

holds for all $t \in \widehat{I}$. We call this assumption (H2').

Using the new assumption, we now show a counterpart to Lemma 2.4.10:

Lemma 3.1.13.
Let $f - \frac{g}{h} < 0$ and any periodic solution $\widehat{s}$ with $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$ and period $T > 0$ be given. Assume that (H1) and (H2') hold. The solution $\widehat{s}(t) = (\mathbf{x}(t), y(t), z(t))^T$ fulfils

$$\frac{1}{T}\int_0^T y(t) + h\, dt \le \widehat{y}_B + h.$$

Proof.
Let $f - \frac{g}{h} < 0$ and any periodic solution $\widehat{s}$ with $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$ and period $T > 0$ be given. Assume that *(H1)* and *(H2')* hold. By Theorem 3.1.1 the $\widehat{s}$ is bounded (in all components) for all $t \ge 0$ and using *(H2')* it holds that

$$y(t) + h \le \widehat{y}_B + h \qquad \forall\, t \ge 0.$$

In particular, integrating the above from zero to $T > 0$ and dividing by T yields the claim

$$\frac{1}{T}\int_0^T y(t) + h\, dt \le \frac{1}{T}\int_0^T \widehat{y}_B + h\, dt = \widehat{y}_B + h. \qquad \square$$

Thus we can now apply Lemma 2.4.8 to obtain

Lemma 3.1.14.
Let $f - \frac{g}{h} < 0$ and any periodic solution $\widehat{s}$ with $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$ and period $T > 0$ be given. Assume that (H1) and (H2') hold. Then it holds that

$$\frac{g}{f} - h \le \widehat{y}_B.$$

Conversely, if

$$\frac{g}{f} - h > \widehat{y}_B$$

holds, then $\widehat{s}$ cannot be periodic.

Proof.
Let $f - \frac{g}{h} < 0$ and any periodic solution $\widehat{s}$ with $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$ and period $T > 0$ be given. Assume that *(H1)* and *(H2')* hold. By Lemmas 3.1.12 and 3.1.13 it holds that

$$\frac{1}{T}\int_0^T y(t) + h \, dt \leq \widehat{y}_B + h.$$
$$\frac{1}{T}\int_0^T \frac{1}{y(t)+h} \, dt = \frac{f}{g}$$

Since $\widehat{s}$ is continuous on $[0, T]$ and positive in every component (by $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$ and (3.1.2)), it holds that

$$y + h \in \mathcal{C}^0([0,T], \mathbb{R}^+).$$

Thus, Lemma 2.4.8 applies to the function $y + h$ (with the above estimates), yielding

$$(\widehat{y}_B + h)\,\frac{f}{g} \geq 1.$$

This is equivalent to the claim:

$$\widehat{y}_B \geq \frac{g}{f} - h. \tag{3.1.14}$$

Conversely, assuming that

$$\frac{g}{f} - h > \widehat{y}_B$$

holds and still assuming that $\widehat{s}$ is periodic, leads to a contradiction since we have just proven that this implies (3.1.14) to hold. □

Remark 3.1.3.
Thus the above result implies that if the solution $\widehat{s}$ (with $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$) is bounded by $\widehat{y}_B < \frac{g}{f} - h$ in the y-component, it is not periodic. In chapter 2 in subsection 2.4.2 we saw that such bounds $\widehat{y}_B$ exist for the three-dimensional GSP food chain model (see Lemma 2.4.10 for example). They significantly depend on the specific vector field F in (3.1.1) and the interaction of the specialist predator species (modelled by y) with the species modelled by x_i (with $i \in \mathcal{I}$). I.e. how the change in the $n-2$ prey species limits the growth and maximal density of the specialist predator species. Note that if the bound $\widehat{y}_B$ is independent of the initial conditions $\widehat{s}_0$ (such as in chapter 2), we can *restrict the set in parameter space* for which a solution $\widehat{s}$ may be periodic. In this sense, the result is *global*, as it rules out the existence of periodic solutions in $\widehat{\mathcal{O}}^+$ for various choices of the parameters - regardless of the initial conditions.
We also remark that the above method is not restricted to periodic solutions, but may in principle be applied to any solution $\widehat{s}$, provided the right estimates are found (recall subsection 2.4.2).

With these remarks we conclude this section and now consider a few biologically meaningful choices for the vector field F in (3.1.1) and apply the theory developed above.

3.2 Specific GSP food chain models

In this section we consider a n-dimensional GSP food chain model (see subsection 3.2.1) and a GSP food web model (see subsection 3.2.2) and check whether the hypotheses *(H1)* and *(H2')* from above are fulfilled for the dynamics induced by these models.

3.2.1 The n-d food chain

We discuss the canonical extension of the GSP food chain from (2.1.5). The extension is called canonical, as it is a common way to extend food chains (cf. [Gard and Hallam, 1979], [Gard, 1980]), by extending the chain of predator (and possibly prey) species, i.e. the middle part of the chain. In our case we elongate the chain by assuming we have $n-2$ specialist predator species and still one prey and one generalist predator species (for a given $n \in \mathbb{N}$ with $n \geq 3$). A scheme of this extension is provided in Figure 3.2.1. The corresponding model equations (omitting the explicit

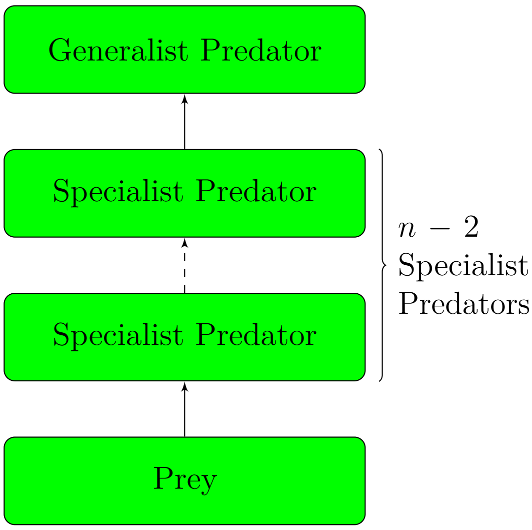


Figure 3.2.1: Scheme of the canonical n-dimensional GSP food chain, see (3.2.1)

dependency of x_i, y, z on t in the notation) are given by

$$\begin{aligned}
\dot{x}_1 &= \left(1 - x_1 - \frac{x_2}{x_1 + a_1}\right) x_1 \\
\dot{x}_i &= \left(-b_i + \frac{c_i x_{i-1}}{x_{i-1} + d_i} - \frac{x_{i+1}}{x_i + a_i}\right) x_i \\
\dot{x}_{n-2} &= \left(-b_{n-2} + \frac{c_{n-2} x_{n-3}}{x_{n-3} + d_{n-2}} - \frac{y}{x_{n-2} + a_{n-2}}\right) x_{n-2} \\
\dot{y} &= \left(-b_{n-1} + \frac{c_{n-1} x_{n-2}}{x_{n-2} + d_{n-1}} - \frac{z}{y + a_{n-1}}\right) y \\
\dot{z} &= \left(f - \frac{g}{y + h}\right) z^2
\end{aligned} \tag{3.2.1}$$

where $i \in \{2, ..., n-3\}$, i.e. the chain has length n. Furthermore the parameters a_i, b_i, c_i, d_i, f, g, h are all assumed to be positive. Thus the system (3.2.1) has the same form as the n-dimensional model in (3.1.1) with

$$F(\mathbf{x}, y, z) = \begin{pmatrix} \left(1 - x_1 - \frac{x_2}{x_1+a_1}\right) x_1 \\ \left(-b_i + \frac{c_i x_{i-1}}{x_{i-1}+d_i} - \frac{x_{i+1}}{x_i+a_i}\right) x_i \\ \left(-b_{n-2} + \frac{c_{n-2}x_{n-3}}{x_{n-3}+d_{n-2}} - \frac{y}{x_{n-2}+a_{n-2}}\right) x_{n-2} \end{pmatrix}$$

and

$$b = b_{n-1} \qquad c = c_{n-1} \qquad d = d_{n-1} \qquad e = a_{n-1}.$$

We will therefore also use the same notation as in the previous chapter. In particular the phase space $\widehat{\mathcal{O}}_0^+$ and solutions $\widehat{s}$ are denoted as in Definition 3.1.1. We remark that

$$F \in \mathcal{C}_{Lip}\left(\widehat{\mathcal{O}}_0^+, \mathbb{R}^{n-2}\right)$$

holds and therefore the solutions we consider exist on their respective existence intervals and are unique and sufficiently smooth. We check whether the conditions of Theorem 3.1.1 are met, and thus whether it holds that all solutions $\widehat{s}$ (with $\widehat{s}_0 \in \widehat{\mathcal{O}}_0^+$) are bounded in every component for all $t \geq 0$ and as $t \to \infty$. For this we assume $f - \frac{g}{h} < 0$ and need to check if the assumptions *(H1)* and *(H2)* hold. We first show that *(H1)* holds.

Lemma 3.2.1.
For $i \in \{1, ..., n-2\}$ the sets

$$\mathcal{H}_i := \left\{(\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \,|\, x_i = 0\right\}$$
$$\mathcal{H}_{n-1} := \left\{(\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \,|\, y = 0\right\}$$
$$\mathcal{H}_n := \left\{(\mathbf{x}, y, z) \in \widehat{\mathcal{O}}_0^+ \,|\, z = 0\right\}$$

have property $(\widehat{I}1)$ *as defined in Definition 3.1.2 under the dynamics generated by* (3.2.1). *In particular assumption (H1) holds for the dynamics generated by* (3.2.1).

Proof.
Note that from the vector field in (3.2.1) we see that for all $i \in \{1, ..., n-2\}$ it holds that

$$\begin{aligned} x_i = 0 \quad &\Rightarrow \quad \dot{x}_i = 0 \\ y = 0 \quad &\Rightarrow \quad \dot{y} = 0 \\ z = 0 \quad &\Rightarrow \quad \dot{z} = 0 \end{aligned}$$

Hence all the coordinate hyperplanes of $\mathbb{R}^n$ have property $(\widehat{I}1)$, since the vector field $\widehat{v}$ is tangential to the planes by the above and the planes have no boundary. Thus all intersections of these coordinate hyperplanes also have property $(\widehat{I}1)$ and in particular the boundary $\partial\mathcal{H}_i$ of any $\mathcal{H}_i$ with $i \in \{1, ..., n\}$ (recall Figure 3.1.2). Hence for any solution $\widehat{s}$ with $\widehat{s}_0 \in \mathcal{H}_i$ (and $i \in \{1, ..., n\}$) it holds that

$$\widehat{s}(t) \in \mathcal{H}_i \qquad \forall\, t \in \widehat{I}_M$$

since otherwise the (continuous) phase curve of $\widehat{s}$ would necessarily have to intersect the boundary of $\mathcal{H}_i$ (a contradiction to the property $(\widehat{I}1)$ of $\partial\mathcal{H}_i$) or be contained completely in this boundary (in which case it does not leave $\mathcal{H}_i$, since $\mathcal{H}_i$ is closed and hence $\partial\mathcal{H}_i \subset \mathcal{H}_i$). This is in fact the generalised version of the argument we used in Lemma 2.1.3. Thus the property $(\widehat{I}1)$ claim holds. □

Having shown that *(H1)* holds we also know that Lemma 3.1.1 holds, i.e. that the phase space $\widehat{\mathcal{O}}_0^+$ and the positive orthant $\widehat{\mathcal{O}}^+$ also have property $(\widehat{I}1)$. We now show that the solutions $\widehat{s}$ are also bounded for all $t \geq 0$, by proving that *(H2)* holds. We commence with

Lemma 3.2.2.
Let any solution $\widehat{s}$ be given, then the first component of the solution fulfils

$$0 \leq x_1(t) \leq \max\{1, x_1(0)\} \qquad \forall\, t \in \widehat{I}.$$

Proof.
Let any solutions $\widehat{s}$ be given. Since property $(\widehat{I}1)$ holds for $\widehat{\mathcal{O}}_0^+$ by Lemma 3.1.1, we know that all components are non-negative for all $t \in \widehat{I}$. The rest of the proof is analogous to the proof of Lemma 2.2.1 using the following estimate on the first line of (3.2.1):

$$\dot{x}_1(t) = (1 - x_1(t))x_1(t) - \frac{x_1(t)x_2(t)}{x_1(t) + a_1} \leq (1 - x_1(t))x_1(t) \qquad \forall\, t \in \widehat{I}. \qquad \square$$

Finding bounds on the $n-2$ specialist predator species densities (for $t \in \widehat{I}$) will prove more technical, however similar in manner to the proof of Lemma 2.2.3. In fact, we will also restrict the parameters a_i and d_i and apply the auxiliary Lemma 2.2.2, albeit to a different function $\widehat{\phi}$ (than the function ϕ in the proof of Lemma 2.2.3).

Lemma 3.2.3.
In equations (3.2.1) *assume $a_{i-1} \leq d_i$ to hold for all $i \in \{2, ..., n-1\} =: \mathcal{J}$. Furthermore define the function*

$$\widehat{\phi}(t) := x_1(t) + \sum_{i=2}^{n-2} \gamma_i x_i(t) + \gamma_{n-1} y(t),$$

where for any $i \in \mathcal{J}$ we set

$$\gamma_i := \left(\prod_{k=2}^{i} c_k\right)^{-1} = \frac{1}{c_2 \cdot \ldots \cdot c_i} > 0$$

Then for any solution $\widehat{s}$ *with* $\widehat{s}_0 \in \widehat{\mathcal{O}}_0^+$ *it holds that*

$$\widehat{\phi}(t) < \beta_0 + \frac{1}{4b_m}, \tag{3.2.2}$$

for all $t \in \widehat{I}$*, where*

$$b_m := \min_{i \in \mathcal{J}} b_i > 0 \quad \textit{and} \quad \beta_0 := \max\{1, x_1(0)\} + \sum_{i=2}^{n-2} \gamma_i x_i(0) + \gamma_{n-1} y(0) > 0.$$

Proof.
In equations (3.2.1) assume $a_{i-1} \leq d_i$ to hold for all $i \in \{2, ..., n-1\} =: \mathcal{J}$. Let a corresponding solution $\widehat{s}$ be given. For the above defined function $\widehat{\phi}$ we have that

$$\frac{d}{dt}\widehat{\phi}(t) = \dot{x}_1(t) + \sum_{i=2}^{n-2} \gamma_i \dot{x}_i(t) + \gamma_{n-1}\dot{y}(t).$$

Dropping the explicit dependence on t in the notation we observe

$$\begin{aligned}
\frac{d}{dt}\widehat{\phi} &= \dot{x}_1 + \sum_{i=2}^{n-2} \gamma_i \dot{x}_i + \gamma_{n-1}\dot{y} \\
&= \left(1 - x_1 - \frac{x_2}{x_1 + a_1}\right) x_1 + \underbrace{\gamma_2}_{=\frac{1}{c_2}} \left(-b_2 + \frac{c_2 x_1}{x_1 + d_2} - \frac{x_3}{x_2 + a_2}\right) x_2 + \sum_{i=3}^{n-2} \gamma_i \dot{x}_i + \gamma_{n-1}\dot{y} \\
&= (1 - x_1)x_1 - \gamma_2 b_2 x_2 - \frac{x_1 x_2}{x_1 + a_1} + \frac{x_1 x_2}{x_1 + d_2} - \frac{\gamma_2 x_2 x_3}{x_2 + a_2} + \sum_{i=3}^{n-2} \gamma_i \dot{x}_i + \gamma_{n-1}\dot{y} \\
&= (1 - x_1)x_1 - \gamma_2 b_2 x_2 + x_1 x_2 \underbrace{\left(\frac{a_1 - d_2}{(x_1 + a_1)(x_1 + d_2)}\right)}_{\leq 0 \text{ since } a_1 \leq d_2} - \frac{\gamma_2 x_2 x_3}{x_2 + a_2} + \sum_{i=3}^{n-2} \gamma_i \dot{x}_i + \gamma_{n-1}\dot{y} \\
&\leq (1 - x_1)x_1 - \gamma_2 b_2 x_2 - \frac{\gamma_2 x_2 x_3}{x_2 + a_2} + \sum_{i=3}^{n-2} \gamma_i \dot{x}_i + \gamma_{n-1}\dot{y}
\end{aligned}$$

We can use the same method as above to obtain estimates for all the remaining $\dot{x}_i$-terms in the sum (i.e. for $i \in \{3, ..., n-2\}$):

$$\begin{aligned}
\frac{d}{dt}\widehat{\phi} &\leq (1 - x_1)x_1 - \gamma_2 b_2 x_2 - \frac{\gamma_2 x_2 x_3}{x_2 + a_2} + \sum_{i=3}^{n-2} \gamma_i \dot{x}_i + \gamma_{n-1}\dot{y} \\
&\leq (1 - x_1)x_1 - \gamma_2 b_2 x_2 - \gamma_3 b_3 x_3 - \frac{\gamma_3 x_3 x_4}{x_3 + a_3} + \sum_{i=4}^{n-2} \gamma_i \dot{x}_i + \gamma_{n-1}\dot{y} \\
&\leq ... \\
&\leq (1 - x_1)x_1 - \sum_{i=2}^{n-2} \gamma_i b_i x_i - \frac{\gamma_{n-2} x_{n-2} y}{x_{n-2} + a_{n-2}} + \gamma_{n-1}\dot{y}
\end{aligned}$$

$$
\begin{aligned}
&= (1-x_1)x_1 - \sum_{i=2}^{n-2} \gamma_i b_i x_i - \frac{\gamma_{n-2}x_{n-2}y}{x_{n-2}+a_{n-2}} + \gamma_{n-1}\left(- b_{n-1} + \frac{c_{n-1}x_{n-2}}{x_{n-2}+d_{n-1}} - \underbrace{\frac{z}{y+a_{n-1}}}_{\leq 0} \right) y \\
&\leq (1-x_1)x_1 - \sum_{i=2}^{n-2} \gamma_i b_i x_i - \gamma_{n-1}b_{n-1}y - \frac{\gamma_{n-2}x_{n-2}y}{x_{n-2}+a_{n-2}} + \gamma_{n-1}\frac{c_{n-1}x_{n-2}y}{x_{n-2}+d_{n-1}} \\
&\leq (1-x_1)x_1 - \sum_{i=2}^{n-2} \gamma_i b_i x_i - \gamma_{n-1}b_{n-1}y + \gamma_{n-2}x_{n-2}y \underbrace{\left(\frac{a_{n-2}-d_{n-1}}{(x_{n-2}+a_{n-2})(x_{n-2}+d_{n-1})} \right)}_{\leq 0} \\
&\leq (1-x_1)x_1 - \sum_{i=2}^{n-2} \gamma_i b_i x_i - \gamma_{n-1}b_{n-1}y \\
&\leq (1-x_1)x_1 - b_m \left(\sum_{i=2}^{n-2} \gamma_i x_i + \gamma_{n-1} y \right)
\end{aligned}
$$

We add a 'zero' to the above estimate:

$$
\begin{aligned}
\frac{d}{dt}\widehat{\phi} &\leq (1-x_1)x_1 - b_m \left(\sum_{i=2}^{n-2} \gamma_i x_i + \gamma_{n-1} y \right) + b_m x_1 - b_m x_1 \\
&= (1-x_1)x_1 + b_m x_1 - b_m \widehat{\phi}
\end{aligned}
$$

This is equivalent to

$$
\frac{d}{dt}\widehat{\phi}(t) + b_m\widehat{\phi}(t) \leq (1-x_1(t))x_1(t) + b_m x_1(t) \qquad \forall\, t \in \widehat{I}. \tag{3.2.3}
$$

Using the estimate

$$
\max_{x_1\in\mathbb{R}} (1-x_1)x_1 = \frac{1}{4}
$$

as well as the fact that by Lemma 3.2.2 we have

$$
x_1(t) \leq \max\{1, x_1(0)\} \leq \max\{1, x_1(0)\} + \sum_{i=2}^{n-2} \gamma_i x_i(0) + \gamma_{n-1} y(0) = \beta_0,
$$

we conclude from (3.2.3) that

$$
\frac{d}{dt}\widehat{\phi}(t) + b_m\widehat{\phi}(t) \leq (1-x_1(t))x_1(t) + b_m x_1(t) \leq \frac{1}{4} + b_m\beta_0 \qquad \forall\, t \in \widehat{I}.
$$

We can now apply Lemma 2.2.2 with $k_1 = b_m > 0$ and $k_2 = \frac{1}{4} + b_m\beta_0$, i.e.

$$
\widehat{\phi}(t) \leq \frac{1}{4b_m} + \beta_0 - \left[\frac{1}{4b_m} + \beta_0 - \widehat{\phi}(0) \right] \exp(-b_m t)
$$

holds for all $t \in \widehat{I}$. Since

$$
\beta_0 - \widehat{\phi}(0) = \max\{1, x_1(0)\} + \sum_{i=2}^{n-2} \gamma_i x_i(0) + \gamma_{n-1} y(0) - \left(x_1(0) + \sum_{i=2}^{n-2} \gamma_i x_i(0) + \gamma_{n-1} y(0) \right)
$$

$$= \max\{1, x_1(0)\} - x_1(0) \geq 0$$

holds, we obtain the claim by the following estimate:

$$\widehat{\phi}(t) \leq \frac{1}{4b_m} + \beta_0 - \underbrace{\left[\frac{1}{4b_m} + \beta_0 - \widehat{\phi}(0)\right] \exp(-b_m t)}_{>0} < \frac{1}{4b_m} + \beta_0$$

for all $t \in \widehat{I}$. □

As an immediate consequence of the above result we obtain

Corollary 3.2.1.
Let $a_{i-1} \leq d_i$ hold for all $i \in \mathcal{J}$ and any solution $\widehat{s}$ be given. Then for all $t \in \widehat{I}$ and all $i \in \{2, ..., n-2\}$ it holds that

$$0 \leq x_i(t) < \frac{\beta_0 + \frac{1}{4b_m}}{\gamma_i}$$
$$0 \leq y(t) < \frac{\beta_0 + \frac{1}{4b_m}}{\gamma_{n-1}}.$$

Proof.
Let $a_{i-1} \leq d_i$ hold for all $i \in \mathcal{J}$ and any solution $\widehat{s}$ be given. Since $\widehat{\mathcal{O}}_0^+$ has property $(\widehat{I}1)$ by Lemma 3.1.1, the components of $\widehat{s}$ are all non-negative for all $t \in \widehat{I}$. Furthermore the conditions of Lemma 3.2.3 are met and in particular

$$x_1(t) + \sum_{k=2}^{n-2} \gamma_k x_k(t) + \gamma_{n-1} y(t) < \beta_0 + \frac{1}{4b_m} \qquad \forall\, t \in \widehat{I}.$$

Solving this for any $x_i(t)$ with $i \in \{2, ..., n-2\}$ yields

$$\gamma_i x_i(t) < \beta_0 + \frac{1}{4b_m} - x_1(t) - \sum_{k=2}^{i-1} \gamma_k x_k(t) - \sum_{k=i+1}^{n-2} \gamma_k x_k(t) - \gamma_{n-1} y(t) \leq \beta_0 + \frac{1}{4b_m}.$$

Dividing by $\gamma_i > 0$ in the above inequality, yields

$$x_i(t) < \frac{\beta_0 + \frac{1}{4b_m}}{\gamma_i} \qquad \forall\, t \in \widehat{I}$$

and all $i \in \{2, ..., n-2\}$. Analogously, solving for $y(t)$ above and dividing by $\gamma_{n-1} > 0$ instead yields

$$y(t) < \frac{\beta_0 + \frac{1}{4b_m}}{\gamma_{n-1}} \qquad \forall\, t \in \widehat{I}.$$ □

Thus assumption *(H2)* also holds for the dynamics generated by (3.2.1):

Lemma 3.2.4.
Let $a_{i-1} \leq d_i$ hold for all $i \in \mathcal{J}$ and any solution $\widehat{s}$ be given. Then it holds that

$$\begin{aligned} &0 \leq x_i(t) \leq \widehat{x}_M \qquad \forall\, i \in \{1, ..., n-2\} \\ &0 \leq y(t) \leq \widehat{y}_B \end{aligned}$$

for all $t \in \widehat{I}$, where

$$\begin{aligned} \widehat{x}_M &:= \max_{i \in \{2,\dots,n-2\}} \left\{ 1, x_1(0), \frac{\beta_0 + \frac{1}{4b_m}}{\gamma_i} \right\} > 0 \\ \widehat{y}_B &:= \frac{\beta_0 + \frac{1}{4b_m}}{\gamma_{n-1}} > 0 \end{aligned}$$

in particular the assumption (H2') is fulfilled. Assuming $\frac{g}{f} - h > 0$ for the parameters implies that (H2) holds.

Proof.
Let $a_{i-1} \leq d_i$ hold for all $i \in \mathcal{J}$ and any solution $\widehat{s}$ be given. Combining the results of Lemma 3.2.2 and Corollary 3.2.1 we obtain for any $i \in \{1, ..., n-2\}$ that

$$0 \leq x_i(t) \leq \max_{i \in \{2,\dots,n-2\}} \left\{ 1, x_1(0), \frac{\beta_0 + \frac{1}{4b_m}}{\gamma_i} \right\} = \widehat{x}_M \qquad \forall\, t \in \widehat{I}.$$

Furthermore by Corollary 3.2.1 we immediately obtain

$$0 \leq y(t) \leq \frac{\beta_0 + \frac{1}{4b_m}}{\gamma_{n-1}} = \widehat{y}_B \qquad \forall\, t \in \widehat{I}.$$

Thus the assumption *(H2')* is fulfilled with the bounds $\widehat{x}_M > 0$ and $\widehat{y}_B > 0$. Additionally assuming $\frac{g}{f} - h > 0$ to hold and defining

$$\widehat{y}_M := \widehat{y}_B + \frac{g}{f} - h > \frac{g}{f} - h > 0$$

implies that *(H2)* holds. □

Thus we have that Theorem 3.1.1 holds under the above conditions (compare to Corollary 2.2.5), i.e.

Corollary 3.2.2.
Let $f - \frac{g}{h} < 0$ and $a_{i-1} \leq d_i$ hold for all $i \in \mathcal{J}$. Then any solution $\widehat{s}$ (of 3.2.1) does not blow up for any $t \geq 0$ and is bounded as $t \to \infty$.

Proof.
Let $f - \frac{g}{h} < 0$ and $a_{i-1} \leq d_i$ hold for all $i \in \mathcal{J}$. Furthermore let any solution $\widehat{s}$ (of 3.2.1) be given. By Lemmas 3.2.1 and 3.2.4 the assumptions *(H1)* and *(H2)* are fulfilled and thus Theorem 3.1.1 yields the claim. □

Thus we have shown that (3.2.1) induces a semiflow $\widehat{\Phi}$ with bounded solutions $\widehat{s}$. The long-term behaviour may be investigated in a similar manner to the three-dimensional case (also proving the existence of an attractor $\mathcal{A}$), due to the similar structures of the specialist predator equations in (2.1.5) and (3.2.1). These structures allow corresponding estimates. This will not be discussed further here. Much rather we remark that by the above results we can conclude

Corollary 3.2.3.
Let $f - \frac{g}{h} < 0$ and $a_{i-1} \leq d_i$ hold for all $i \in \mathcal{J}$. Then any solution $\widehat{s}$ with $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$ and

$$\widehat{y}_B = \frac{\beta_0 + \frac{1}{4b_m}}{\gamma_{n-1}} < \frac{g}{f} - h$$

is not periodic.

Proof.
This is an immediate consequence of Lemma 3.1.14 and the fact that assumptions *(H1)* and *(H2')* hold. □

Remark 3.2.1.
The condition

$$\frac{\beta_0 + \frac{1}{4b_m}}{\gamma_{n-1}} < \frac{g}{f} - h$$

in the above result may be interpreted as a condition on the initial conditions and is equivalent to (recalling the definition of β_0 in Lemma 3.2.3):

$$\beta_0 = \max\{1, x_1(0)\} + \sum_{i=2}^{n-2} \gamma_i x_i(0) + \gamma_{n-1} y(0) < \gamma_{n-1} \left(\frac{g}{f} - h \right) - \frac{1}{4b_m}$$

Any solution $\widehat{s}$ with initial conditions that fulfil the above inequality (and $\widehat{s}_0 \in \widehat{\mathcal{O}}^+$) is not periodic. The above inequality defines a set in $\widehat{\mathcal{O}}^+$, where no periodic solution can exist (not even only partially, i.e. only a subset of a periodic orbit). Note however, that the right-hand side of the above inequality need not necessarily be positive, i.e. such a regime must not always exist (in the positive orthant $\widehat{\mathcal{O}}^+$).

With this result we conclude the discussion of the dynamics induced by (3.2.1), i.e. the n-dimensional canonical extension of the GSP food chain system (2.1.5). Naturally there are many more aspects of the system that may be considered (recall the three-dimensional results), which remains to be discussed in other works.

3.2.2 A food web

Another sensible generalisation of the three-dimensional GSP food chain model in (2.1.5) is given by extending the *chain* to a *web*. A simple extension would be the idea that the prey species is also preyed upon by the generalist predator species, see Figure 3.2.2. In the peacock-snake-rodent model this would mean that the peacocks

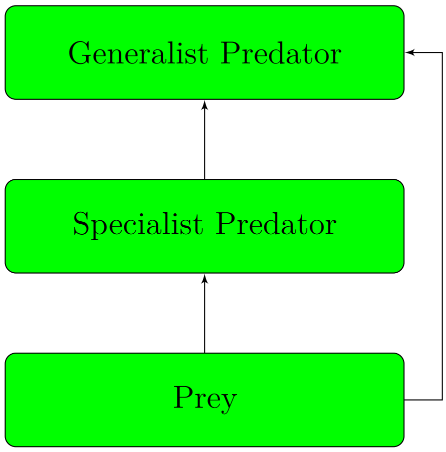


Figure 3.2.2: Scheme of a three-dimensional GSP food web, see (3.2.4)

also feed on the rodents. This indeed occurs in nature in this particular case, since peacocks eat mice for example.
Equations, i.e. a set of ODEs, that reflect the above interactions are given by

$$\begin{aligned}\dot{x} &= \left(1 - x - \frac{y}{x+a_1} - \frac{z}{x+a_2}\right)x \\ \dot{y} &= \left(-b + \frac{cx}{x+d} - \frac{z}{y+e}\right)y \\ \dot{z} &= \left(f - \frac{g}{y+h}\right)z^2\end{aligned} \tag{3.2.4}$$

where the parameter a_1, a_2, b, c, d, e, f, g, h are once more assumed to be positive. Comparing (3.2.4) to (2.1.5), we observe that they differ in the first equation by the term

$$-\frac{xz}{x+a_2}$$

being the interaction term between the prey species and the generalist predator species. Note that we did not change the generalist predator equation, since the assumption that the *availability of a mate* is the limiting factor for reproduction implies that more food, and in particular abundance of the prey species as an additional resource, should not have an influence on the change of the generalist predators species density. If at all, the reproduction rate f might be higher, i.e. the parameter value of f increase, compared to the parameter values in (2.1.4) for the model (2.1.5). In biological terms this would mean: mice do not make a significant contribution to a peacocks diet, however they do feed on them. A mathematical model for which the change of the generalist predator density (i.e. the $\dot{z}$-equation) is altered, is presented in chapter 4. Note that (3.2.4) has the same structure as (3.1.1), with

$$F(\mathbf{x}, y, z) = \left(1 - x - \frac{y}{x+a_1} - \frac{z}{x+a_2}\right)x \qquad \text{and} \qquad F \in \mathcal{C}_{Lip}(\widehat{\mathcal{O}}_0^+, \mathbb{R}).$$

Furthermore, the dynamics induced by (3.2.4) also fulfil assumptions *(H1)* and *(H2)* for $f - \frac{g}{h} < 0$ and $a_1 \leq d$. Indeed, observe that we once more have

$$\begin{aligned} x = 0 \quad &\Rightarrow \quad \dot{x} = 0 \\ y = 0 \quad &\Rightarrow \quad \dot{y} = 0 \\ z = 0 \quad &\Rightarrow \quad \dot{z} = 0 \end{aligned}$$

for (3.2.4), implying that property $(\widehat{I}1)$ holds for the (Cartesian) coordinate planes in $\mathbb{R}^3$, in turn implying that *(H1)* holds (recall the proof of Lemma 3.2.1 for example). Also the first equation of (3.2.4) allows the estimate

$$\dot{x} = \left(1 - x - \frac{y}{x + a_1} - \frac{z}{x + a_2}\right) x \leq \left(1 - x - \frac{y}{x + a_1}\right) x \leq x(1 - x),$$

for any $t \in \widehat{I}$. This estimate may be used to prove the boundedness of solutions in their first two components for $t \in \widehat{I}$ (and thus that *(H2)* holds), by mimicking the proofs of Lemmas 2.2.1 and 2.2.3 or Lemmas 3.2.2 and 3.2.3 respectively. Thus we once more obtain

Corollary 3.2.4.
Let $f - \frac{g}{h} < 0$ and $a_1 \leq d$ hold in (3.2.4). Then any solution $\widehat{s}$ of (3.2.4) is bounded (in $\widehat{\mathcal{O}}_0^+ \subset \mathbb{R}^3$) for all $t \geq 0$ and as $t \to \infty$.

Proof.
As argued above, for $f - \frac{g}{h} < 0$ and $a_1 \leq d$ the assumptions *(H1)* and *(H2)* are fulfilled for the dynamics generated by (3.2.4) and hence Theorem 3.1.1 applies, yielding the result. □

These results make further considerations of the system (3.2.4) in future works on food webs sensible and interesting. With this we conclude our considerations on n-dimensional GSP food chain models.

4 Outlook

In the final chapter we present several open problems which arise on grounds of this thesis. Moreover two GSP food *web* models are presented, which no longer fit into the framework (i.e. the equations 3.1.1) of above.

4.1 Open problems

The results from the previous chapters provide reasons to study further open problems with respect to GSP food chain models, which arise on grounds of this thesis:

- Concerning the global attractor $\mathcal{A}$ of the semiflow Φ (recall Theorem 2.3.1) the question whether $\mathcal{A}$ is planar if $p^*_{3+} \notin \mathcal{O}_0^+$, i.e. when no equilibrium of coexistence of all three species is biologically feasible, is addressed in *Conjecture 2.4.1.* Recall that the conjecture was proven to hold for all but one parameter range of the bifurcation parameter b. For this range $\left(b^*_{3+}, \frac{c}{a+1}\right)$ the problem remains open.

- Recall that for the three-dimensional GSP food chain model in chapter 2, numerical evidence of a *Shilnikov Homoclinic bifurcation* occurring was presented. An analytical proof of this, i.e. the existence of a saddle-focus equilibrium p^* and a corresponding homoclinic orbit $\Gamma_{hom}(p^*)$, would confirm the existence of chaotic dynamics in the system for some parameter regions. Also numerically and analytically investigating the period-doubling bifurcations and saddle-node bifurcations caused by the Shilnikov Homoclinic bifurcation promises more insights on the details of the systems dynamics.

- The bifurcation analysis of the three-dimensional system focused on the parameter b. However, the system in (2.1.5) entails a total of eight parameters, implying, that *further bifurcations* with respect to the other parameters as well as bifurcations of co-dimension larger than one, may be observed in the system.

- With regard to the n-dimensional GSP food chain models in chapter 3 it is immediate to ask the following: Under which conditions does a *global attractor* exist for the semiflow $\widehat{\Phi}$? Can a general assumption *(H3)*, similar to *(H1)* and *(H2)* in chapter 3.2, be made to carry over the results from the three-dimensional case to the n-dimensional case? The existence of the attractor would in turn give rise to the question how the attractor may be characterised.

- By applying Lemma 2.4.8 to the GSP food chain models (both the three-dimensional and the n-dimensional version), we proved results on the necessary and sufficient conditions of the persistence and extinction of a species. Applying the same lemma to *other systems*, in particular those modelling population dynamics, promises concluding similar results.

- Dependent on the specific ecosystem that is being modelled by the GSP food chain, *adapting the model equations* to reflect the evolution of the system more precisely may be necessary. One possibility is to extend the chain to a web, as briefly commented on in subsection 3.2.2 and below. Other possibilities have been suggested and studied to some degree as well. Among these is adding a spatial aspect in terms of diffusion of the species (see [Parshad et al., 2015]), using a different functional response term for the species involved ([Upadhyay et al., 2013], [Ali et al., 2016], [Parshad et al., 2016a]) and including new effects, such as considering a polluted environment ([Misra and Babu, 2016]).

4.2 GSP food webs

In subsection 3.2.2 a GSP food chain model was extended in such a way that it became a GSP food *web* model. This is a natural approach to extend a food chain model. Indeed, recall that the term GSP food chain model was motivated by the fact that a generalist predator, a specialist predator and a prey species were modelled (in (2.1.5)). In particular, the generalist predator species has a diverse diet and feeds on *many different* species, apart from the prey species, see Figure 4.2.1. We create a GSP food web model by adding additional (prey) species and denoting their densities with p.

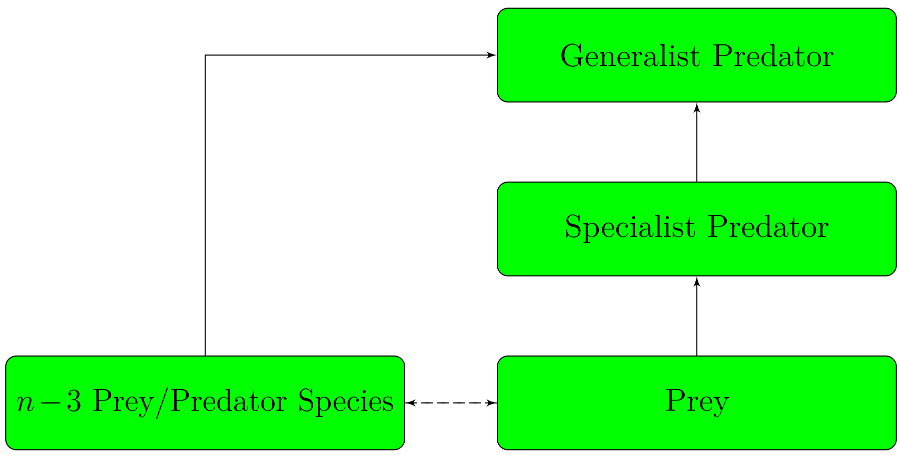


Figure 4.2.1: Scheme of the generalist predator - specialist predator - multiple prey species model, see (4.2.1) and (4.2.2)

To this extent we suggest two different ODE models (see (4.2.1) and (4.2.2)). The first model reads

$$\begin{aligned}\dot{p} &= \left(k - p - \frac{z}{p + a_2}\right) p \\ \dot{x} &= \left(1 - x - \frac{y}{x + a_1}\right) x \\ \dot{y} &= \left(-b + \frac{cx}{x + d} - \frac{z}{y + e}\right) y \end{aligned} \tag{4.2.1}$$

$$\dot{z} = \left(f - \frac{g_1}{y + h_1} - \frac{g_2}{p + h_2} \right) z^2,$$

where the parameters a_1, a_2, b, c, d, e, f, g_1, g_2, h_1, h_2 and k are assumed to be positive parameters. The additional one-dimensional $\dot{p}$-equation now models the change of other species densities, including the predation of the generalist predator species on these other species. The growth of these species (represented by $\dot{p}$) is once more modelled by a logistic equation with a carrying capacity $k > 0$ of the ecosystem. The interaction term

$$-\frac{pz}{p + a_2}$$

of z and p may be interpreted identically to that of the other species. Note that the $\dot{z}$-equation has also changed (compared to (2.1.5)) since the assumption that all the other prey species are scarce (i.e. p close to zero), should decrease the reproduction of the generalist predator species, motivating the extra term

$$-\frac{g_2 z^2}{p + h_2}$$

in the fourth equation. The equation in (4.2.1) do no longer fit in the n-dimensional GSP food chain model from (3.1.1), as the generalist predator equation has been altered. Hence the theory we have developed in this thesis does not apply *a priori*. However, from the previous considerations (recall Lemma 2.2.4) it is immediate that

$$f - \frac{g_1}{h_1} - \frac{g_2}{h_2} < 0$$

is a necessary restriction on the parameters for solutions of (4.2.1) not to blow up in finite time in the z-component. Whether this is already sufficient to obtain a semiflow on the non-negative orthant of $\mathbb{R}^4$ (compare to Corollary 2.2.3 for example) remains to be investigated.

A second set of equations we propose to model the extension of the GSP food chain model to a GSP food web model as shown in Figure 4.2.1 is given by

$$\begin{aligned}
\dot{p} &= \left(k - p - \frac{z}{p + a_2} \right) p \\
\dot{x} &= \left(1 - x - \frac{y}{x + a_1} \right) x \\
\dot{y} &= \left(-b + \frac{c_1 x}{x + d_2} - \frac{z}{y + e} \right) y \qquad (4.2.2) \\
\dot{z} &= \left(\frac{c_2 p}{p + d_2} - \frac{gz}{y + h} \right) z,
\end{aligned}$$

where the parameters are once again assumed to be positive. Here the generalist predator species is more dependent on the prey species (modelled by p), i.e. the predator's primary limitation to reproduction is no longer only the availability of a mate, but also the availability of enough food. This is modelled by the interaction term

$$\frac{c_2 p z}{p + d_2}$$

in the $\dot{z}$-equation. Note that in this term the z is no longer quadratic, possibly causing a fundamentally different evolution of the generalist predator species. Once again the change in the $\dot{z}$-equation is the reason why the model in (4.2.2) does no longer belong to the GSP food chain model class from (3.1.1). This calls for further studies of GSP food web models.

A Definitions and Theorems

Definition.
Let (X, d_x) and (Y, d_y) be metric spaces. We define the function spaces

$$C^0(X, Y) := \{\textit{Continuous functions } f : X \to Y\}$$

and

$$C_{Lip}(X, Y) := \{\textit{(locally) Lipschitz continuous functions } f : X \to Y\} \subset C^0(X, Y).$$

Definition.
Let (X, d) be a metric space. A map $\Phi : \mathbb{R}_0^+ \times X \to X$ is called a (time-continuous) ***semiflow*** *(or semi-dynamical system) on X if the following properties hold for Φ:*

i) Identity property: $\Phi(0, x) = x$ for all $x \in X$

ii) Continuity in time-component: $\Phi(\cdot, x) : \mathbb{R}_0^+ \to X$ is continuous.

iii) Continuity in space-component: $\Phi(t, \cdot) : X \to X$ is continuous.

iv) Semiflow property: $\Phi(\tau, \Phi(t, x)) = \Phi(\tau + t, x)$ for all $\tau, t \in \mathbb{R}_0^+$ and $x \in X$.

If the map may be extended such that $\Phi : \mathbb{R} \times X \to X$ and the above properties hold for all $t, \tau \in \mathbb{R}$, then Φ is a flow map that generates a (time-continuous) ***dynamical system*** *(X, Φ) on X.*

Definition.
Let Φ be a semiflow on X. Then the ***positive orbit*** *through $x \in X$ is given by the set*

$$\Gamma_x^+ := \{\Phi(t, x) \,:\, t \geq 0\}.$$

Definition.
Let Φ be a semiflow on X. Then a set $M \subset X$ is called ***positive invariant*** *if*

$$\Phi(t, M) \subset M \qquad \forall\, t \geq 0,$$

where

$$\Phi(t, M) := \{\Phi(t, x) \,:\, x \in M\}.$$

Definition.
Let Φ be a semiflow on X and $M \subset X$. Then the ***ω-limit set*** *of M is defined as*

$$\omega(M) = \bigcap_{\tau \geq 0} \overline{\bigcup_{t \geq \tau} \Phi(t, M)}.$$

Definition.
Let Φ be a semiflow on X and $N, M \subset X$ with N bounded. The set M ***uniformly attracts*** *the set N if*

$$\lim_{t\to\infty} \operatorname{dist}(\Phi(t, N), M) = 0,$$

where (for the given metric d) we define

$$\operatorname{dist}(N, M) := \sup_{x\in N} \inf_{y\in M} d(x, y).$$

Definition.
Let Φ be a semiflow on X. Then the set $\mathcal{A} \subset U \subset X$ (U open) is said to be an ***attractor*** *of the semiflow Φ in U provided that:*

- *$\mathcal{A}$ is non-empty and compact*
- *$\mathcal{A}$ fulfils $\Phi(t, \mathcal{A}) = \mathcal{A}$ for all $t \geq 0$*
- *$\mathcal{A}$ uniformly attracts any bounded subset $B \subset U$*

The attractor is called ***global attractor*** *if $U = X$.*

Definition.
Let Φ be a semiflow on X. Then the set $\mathcal{B} \subset U \subset X$ (U open) is said to be (uniformly) ***absorbing in*** *U provided that for any bounded set $B \subset U$ there exists an* ***absorbance time*** *$T(B) \geq 0$ such that*

$$\Phi(t, B) \subset \mathcal{B} \qquad \forall\, t \geq T(B).$$

Definition.
Let Φ be a semiflow on X. Then Φ is said to be ***uniformly compact for large*** *t provided that for any bounded subset $B \subset X$ there exists a time $T(B) \geq 0$ such that the set*

$$\bigcup_{t\geq T(B)} \Phi(t, B)$$

is relatively compact in X.

Using the above definitions allows us to state the following theorem (adapted) from [Temam, 1997]

Theorem.
Let (X, d) be a metric space and Φ be a semiflow on X. Assume that Φ is uniformly compact for large t. Furthermore assume there exists an open set $U \subset X$ and a bounded set $\mathcal{B} \subset U$ such that $\mathcal{B}$ is absorbing in U. Then the set

$$\mathcal{A} = \omega(\mathcal{B}) \neq \emptyset$$

is an attractor of U. The set $\mathcal{A}$ is the maximal attractor in U (for the inclusion relation).

B Concerning blow-up

In [Parshad et al., 2015] and [Parshad et al., 2016b] it is argued that solutions s of system (2.1.5) and related systems exist that *blow up* (in finite future time), even under the restrictions we have imposed on the parameters in Proposition 2.2.1 or severer ones. This is of course contradictory (to the result in Proposition 2.2.1) and requires a thorough analysis. Indeed, we will consider the proof of Theorem 2.1 in [Parshad et al., 2015] and the (identical) proofs of Theorem 3.1 in [Parshad et al., 2015] and Theorem 2.3 in [Parshad et al., 2016b] in the following and show where they fail.

B.1 Blow-up times

We consider the proof of Theorem 2.1 in [Parshad et al., 2015]. Essential to the argument are the blow-up times considered, in particular the time $T^{**} := \frac{1}{\delta|r_1(0)|} > 0$. In the proof (towards the end) the solution to the initial value problem (IVP) given by the initial conditions $r_1(0) > 0$ and the differential equation

$$\frac{dr_1}{dt} = \frac{\delta}{2} r_1^2(t)$$

- with $\delta > 0$ - is considered. The solution is given by

$$r_1(t) = \frac{1}{\frac{1}{r_1(0)} - \frac{\delta}{2}t}.$$

This solution blows up at the time

$$T^{***} = \frac{2}{\delta|r_1(0)|} = 2T^{**}$$

and r_1 is used as a subsolution of the z-component of the solution s of the original system (2.1.5). However, r_1 is only surely a subsolution while estimate (12) in [Parshad et al., 2015], i.e.

$$c - \frac{w_3}{v_1(t) + D_3} \geq \frac{\delta}{2} \tag{B.1.1}$$

holds, using the notation in [Parshad et al., 2015] (in the notation of system (2.1.5) we have $c = f$, $w_3 = g$, $D_3 = h$ and v_1 is a subsolution to the y-component of the solution s). By the proof provided the inequality (B.1.1) is only guaranteed to hold for all

$$t \in \left[0, \frac{1}{2\delta|r_1(0)|}\right] = \left[0, \frac{T^{**}}{2}\right] \subsetneq [0, 2T^{**}] = [0, T^{***}].$$

Hence the problem that arises in the proof is that r_1 is only surely a subsolution of the z-component of the solution s on the interval $\left[0, \frac{T^{**}}{2}\right]$ which does not contain the blow-up time $T^{***} = 2T^{**}$ of r_1. Or differently put: *The blow-up time of the solution r_1 is larger than the time for which r_1 can be guaranteed to be a subsolution of the z-component of a solution s.*

B.2 The $\dot{y}$-equation

We consider the proofs of Theorem 3.1 in [Parshad et al., 2015] and Theorem 2.3 in [Parshad et al., 2016b]. Note that in both cases the proofs are the same and we therefore only argue the case for Theorem 2.3 in [Parshad et al., 2016b]. We also point out that the system considered is not identical to the one in (2.1.5), however the proof is independent of the differences in the structures of the systems provided in [Parshad et al., 2016b] and (2.1.5), i.e. we consider the following system of differential equations

$$\begin{aligned} \dot{x} &= \left(1 - x - \frac{y}{x+d}\right) x \\ \dot{y} &= \left(-b + \frac{cx}{x+d} - \frac{z}{y+e}\right) y \\ \dot{z} &= \left(f - \frac{g}{y+h}\right) z^2 \end{aligned} \tag{B.2.1}$$

and solutions s of the initial value problem (IVP) corresponding to (B.2.1) and positive initial conditions, i.e. with $s_0 \in \mathcal{O}^+ = \mathbb{R}^3_+$ and maximal positive existence interval I, as done in [Parshad et al., 2016b]. Note that we use the notation as given in (2.1.5). In terms of the notation in [Parshad et al., 2016b] we have

$$d = a, \qquad f = p, \qquad g = q, \qquad h = r.$$

Considering the claim and proof of Theorem 2.3 in [Parshad et al., 2016b] we observe that both are independent of the initial value x_0 of a solution s and the size of the (positive) parameters involved. In particular the blow-up is claimed to occur, *regardless of the size of* x_0 *and restrictions on the parameters.* Thus the claim must also hold if the parameters fulfil

$$-b + c < 0$$

which we assume to hold from now on. Furthermore we restrict the parameters in (B.2.1) to $f - \frac{g}{h} < 0$. These restrictions allow us to show

Lemma B.2.1.
Let $-b + c < 0$ *and* $f - \frac{g}{h} < 0$ *hold for the parameters in* (B.2.1). *Furthermore let any solution* s *with* $s_0 \in \mathcal{O}^+$ *be given. It holds that*

$$\dot{y}(t) < 0 \qquad \forall\, t \in I$$

and hence also

$$y(t) \leq y_0 \qquad \forall\, t \in I.$$

Proof.
Let $-b + c < 0$ and $f - \frac{g}{h} < 0$ hold for the parameters in (B.2.1). Furthermore let

any solution s with $s_0 \in \mathcal{O}^+$ be given. The following estimate holds for s and any $t \in I$:

$$-b + \frac{cx(t)}{x(t)+d} = -b + \frac{c}{1 + \underbrace{\frac{d}{x(t)}}_{>0}} < -b + c =: -\gamma < 0.$$

Using this estimate and since we know that $y(t) > 0$ for all $t \in I$ we obtain

$$\dot{y}(t) = \underbrace{\left(-b + \frac{cx(t)}{x(t)+d}\right)}_{<-\gamma} y(t) - \underbrace{\frac{y(t)z(t)}{y(t)+e}}_{\leq 0} \leq -\gamma y(t) < 0$$

for all $t \in I$. In particular the y-component of s is strictly monotonically decreasing on I. This also implies

$$y(t) \leq y_0 \qquad \forall\, t \in I. \qquad \square$$

This result allows us to show

Lemma B.2.2.
Let $-b+c<0$ and $f - \frac{g}{h} < 0$ hold for the parameters in (B.2.1)*. Furthermore let any solution s with $s_0 \in \mathcal{O}^+$ be given. Also assume that s blows up at the finite time $T^{**} > 0$, i.e.*

$$\limsup_{t \nearrow T^{**}} z(t) = \infty.$$

Then it holds that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in I = [0, T^{**})$$

and furthermore

$$\dot{z}(t) > 0 \qquad \forall\, t \in I.$$

Moreover, for any $K \in \mathbb{R}$ there exists a $T_K \in [0, T^{**})$ such that

$$z(t) > K \qquad \forall\, t \in [T_K, T^{**}).$$

Proof.
Let $-b+c<0$ and $f - \frac{g}{h} < 0$ hold for the parameters in (B.2.1). Furthermore let any solution s with $s_0 \in \mathcal{O}^+$ be given. Also assume that s blows up at the finite time $T^{**} > 0$, i.e.

$$\limsup_{t \nearrow T^{**}} z(t) = \infty.$$

We prove that

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in I = [0, T^{**})$$

holds by assuming the contrary, i.e. that there exists a $T_0 \in I$ such that $y(T_0) \leq \frac{g}{f} - h$. Since y is strictly monotonically decreasing (by Lemma B.2.1) we obtain

$$y(t) \leq \frac{g}{f} - h \qquad \forall\, t \in [T_0, T^{**}). \tag{B.2.2}$$

Considering the $\dot{z}$-equation in (B.2.1) we see that (since $z(t) > 0$ for all $t \in I$)

$$\begin{aligned}
\dot{z}(t) > 0 \quad &\Leftrightarrow \quad f - \frac{g}{y(t)+h} > 0 \quad &\Leftrightarrow \quad y(t) > \frac{g}{f} - h \\
\dot{z}(t) = 0 \quad &\Leftrightarrow \quad f - \frac{g}{y(t)+h} = 0 \quad &\Leftrightarrow \quad y(t) = \frac{g}{f} - h \\
\dot{z}(t) < 0 \quad &\Leftrightarrow \quad f - \frac{g}{y(t)+h} < 0 \quad &\Leftrightarrow \quad y(t) < \frac{g}{f} - h
\end{aligned}$$

for any $t \in I$. Hence (B.2.2) implies

$$\dot{z}(t) \leq 0 \quad \forall\, t \in [T_0, T^{**}) \quad \Rightarrow \quad z(t) \leq z(T_0) < \infty \quad \forall\, t \in [T_0, T^{**}).$$

This however is a contradiction to s blowing up at $T^{**} > 0$, since then

$$\limsup_{t \nearrow T^{**}} z(t) \leq z(T_0) < \infty.$$

We conclude that in fact

$$y(t) > \frac{g}{f} - h \qquad \forall\, t \in I$$

must hold. Considering the $\dot{z}$-equation in (B.2.1) we observe that this implies

$$\dot{z}(t) > 0 \qquad \forall\, t \in I,$$

i.e. the z-component is strictly monotonically increasing on I. Finally, since

$$\limsup_{t \nearrow T^{**}} z(t) = \infty,$$

there exists a monotonically increasing sequence $(t_i)_{i \in \mathbb{N}}$ with $t_i \in [0, T^{**})$ for any $i \in \mathbb{N}$ and $t_i \to T^{**}$ as $i \to \infty$ such that

$$z(t_i) \to \infty \quad \text{as} \quad t_i \to T^{**}.$$

Hence for any given $K \in \mathbb{R}$ we can choose a (sufficiently large) $t_i =: T_K \in I$ of the sequence such that $z(T_K) > K$. Since z is strictly monotonically increasing we have

$$z(t) \geq z(T_K) > K \qquad \forall\, t \in [T_K, T^{**}),$$

thus proving the final claim of the lemma. □

Remark B.2.1.
Note the similarity of the above result and the monotone blow-up property of solutions s in Lemma 2.2.6.

Having established the above results we now consider the claim of Theorem 2.3 in [Parshad et al., 2016b]. The mean by which the claim is proven is by showing that for a solution s with sufficiently large initial values $y_0, z_0 > 0$ the function

$$\psi(t) := \frac{1}{z(t)} = \frac{1}{z_0} - ft + g \int_0^t \frac{d\tau}{y(\tau) + h}$$

vanishes at a time $T^{**} > 0$, i.e. $\psi(T^{**}) = 0$. We claim and show that this is not the case by showing

Lemma B.2.3.
Let $-b+c<0$ *and* $f-\frac{g}{h}<0$ *hold for the parameters in* (B.2.1)*. Furthermore let any solution* s *with* $s_0 \in \mathcal{O}^+$ *be given. Then for any* $T^{**}>0$ *it holds that*

$$\liminf_{t\nearrow T^{**}} \psi(t) > 0,$$

where

$$\psi(t) = \frac{1}{z(t)} = \frac{1}{z_0} - ft + g\int_0^t \frac{d\tau}{y(\tau)+h}.$$

Proof.
Let $-b+c<0$ and $f-\frac{g}{h}<0$ hold for the parameters in (B.2.1). Furthermore let any solution s with $s_0 \in \mathcal{O}^+$ be given. We provide a proof by contradiction, i.e. we assume that there exists a $T^{**}>0$ such that

$$\liminf_{t\nearrow T^{**}} \psi(t) \le 0.$$

Recalling that $z(t)>0$ for all $t\in I=[0,T^{**})$ and the fact that $\psi(t)=\frac{1}{z(t)}$, we obtain

$$\liminf_{t\nearrow T^{**}} \psi(t) = \liminf_{t\nearrow T^{**}} \underbrace{\frac{1}{z(t)}}_{>0} \ge 0.$$

Hence the only case that remains to be considered is the case

$$\liminf_{t\nearrow T^{**}} \psi(t) = 0,$$

which is equivalent to the z-component of s blowing up at the finite time $T^{**}>0$, since - by the positivity of z - it holds that

$$\liminf_{t\nearrow T^{**}} \frac{1}{z(t)} = 0 \quad \Leftrightarrow \quad \limsup_{t\nearrow T^{**}} z(t) = \infty.$$

Hence s fulfils all the conditions of Lemma B.2.2. In particular the y-component of s fulfils

$$y(t) > \frac{g}{f} - h > 0 \qquad \forall\, t\in[0,T^{**}).$$

Thus the third equation of (B.2.1) may be written as

$$z(t) = \frac{\dot z(t)}{z(t)} \underbrace{\frac{1}{f-\frac{g}{y(t)+h}}}_{>0} \qquad \forall\, t\in[0,T^{**}).$$

Substituting this into the second equation of (B.2.1) yields

$$\begin{aligned}\dot y(t) &= y(t)\left(-b+\frac{cx(t)}{x(t)+d} - \frac{\dot z(t)}{z(t)}\frac{1}{f-\frac{g}{y(t)+h}}\frac{1}{y(t)+e}\right)\\ &\le y(t)\left(-\gamma - \frac{\dot z(t)}{z(t)}\frac{1}{f-\frac{g}{y(t)+h}}\frac{1}{y(t)+e}\right)\end{aligned}$$

for all $t \in [0, T^{**})$, where $\gamma = b - c > 0$ is used as in the proof of Lemma B.2.1. Dividing by $y(t) > 0$ and multiplying by $f - \frac{g}{y(t)+h} > 0$ in the above yields

$$\frac{\dot{y}(t)}{y(t)}\left(f - \frac{g}{y(t)+h}\right) \leq -\gamma\left(f - \frac{g}{y(t)+h}\right) - \frac{\dot{z}(t)}{z(t)}\frac{1}{y(t)+e}$$

for any $t \in [0, T^{**})$. Rearranging the terms and dividing by $\gamma = b - c > 0$ we obtain

$$-f + \frac{g}{y(t)+h} \geq \frac{1}{\gamma}\frac{\dot{y}(t)}{y(t)}\left(f - \frac{g}{y(t)+h}\right) + \frac{1}{\gamma}\frac{\dot{z}(t)}{z(t)}\frac{1}{y(t)+e}.$$

Since $\dot{y}(t) < 0$ and $y(t) \leq y_0$ for all $t \in I$ (Lemma B.2.1) and $\dot{z}(t) > 0$ for all $t \in I$ (Lemma B.2.2) the following estimate holds on $I = [0, T^{**})$:

$$\begin{aligned}-f + \frac{g}{y(t)+h} &\geq \frac{1}{\gamma}\frac{\overbrace{\dot{y}(t)}^{<0}}{y(t)}\overbrace{\left(f - \frac{g}{y(t)+h}\right)}^{>0} + \frac{1}{\gamma}\frac{\overbrace{\dot{z}(t)}^{>0}}{z(t)}\frac{1}{y(t)+e}\\ &\geq \frac{1}{\gamma}\frac{\dot{y}(t)}{y(t)}\left(f - \frac{g}{y_0+h}\right) + \frac{1}{\gamma}\frac{\dot{z}(t)}{z(t)}\frac{1}{y_0+e}\end{aligned}$$

Integrating the above from zero to $t \in I$ yields

$$\int_0^t -f + \frac{g}{y(\tau)+h}d\tau \geq \frac{1}{\gamma}\left(f - \frac{g}{y_0+h}\right)\int_0^t \frac{\dot{y}(\tau)}{y(\tau)}d\tau + \frac{1}{\gamma}\frac{1}{y_0+e}\int_0^t \frac{\dot{z}(\tau)}{z(\tau)}d\tau,$$

which is equivalent to

$$-ft + \int_0^t \frac{g}{y(\tau)+h}d\tau \geq \frac{1}{\gamma}\left(f - \frac{g}{y_0+h}\right)\ln\left(\frac{y(t)}{y_0}\right) + \frac{1}{\gamma(y_0+e)}\ln\left(\frac{z(t)}{z_0}\right).$$

Adding $\frac{1}{z_0}$ on both sides of the inequality and using the definition of $\psi(t)$, we obtain

$$\begin{aligned}\psi(t) = \frac{1}{z_0} - ft + \int_0^t \frac{g}{y(\tau)+h}d\tau \geq\\ \frac{1}{z_0} + \frac{1}{\gamma}\left(f - \frac{g}{y_0+h}\right)\ln\left(\frac{y(t)}{y_0}\right) + \frac{1}{\gamma(y_0+e)}\ln\left(\frac{z(t)}{z_0}\right)\end{aligned}$$

for any $t \in [0, T^{**})$. Since $y_0 \geq y(t) > \frac{g}{f} - h > 0$ on I we can estimate the above as follows for any $t \in I$:

$$\begin{aligned}\psi(t) &\geq \frac{1}{z_0} + \frac{1}{\gamma}\left(f - \frac{g}{y_0+h}\right)\ln\left(\frac{y(t)}{y_0}\right) + \frac{1}{\gamma(y_0+e)}\ln\left(\frac{z(t)}{z_0}\right)\\ &> \underbrace{\frac{1}{z_0} + \frac{1}{\gamma}\left(f - \frac{g}{y_0+h}\right)\ln\left(\frac{\frac{g}{f}-h}{y_0}\right)}_{=:\alpha} + \underbrace{\frac{1}{\gamma(y_0+e)}}_{=:\beta>0}\ln\left(\frac{z(t)}{z_0}\right).\end{aligned}$$

For any given $C > 0$ we now set

$$K := z_0 \exp\left(\frac{C - \alpha}{\beta}\right) > 0.$$

By Lemma B.2.2 we can now find a $T_K \in [0, T^{**})$ such that $z(t) > K$ for all $t \in [T_K, T^{**}) \subset I$. Hence for $t \in [T_K, T^{**})$ we may estimate

$$\psi(t) > \alpha + \beta \ln\left(\frac{z(t)}{z_0}\right) > \alpha + \beta \ln\left(\frac{K}{z_0}\right) = \alpha + \beta \ln\left(\exp\left(\frac{C - \alpha}{\beta}\right)\right) = C > 0.$$

Hence

$$\psi(t) > C > 0 \qquad \forall\, t \in [T_K, T^{**}),$$

which is a contradiction to

$$\liminf_{t \nearrow T^{**}} \psi(t) = 0,$$

since for any sequence $(t_i)_{i\in\mathbb{N}}$ with $t_i \in [T_K, T^{**})$ for all $i \in \mathbb{N}$ we obtain

$$\psi(t_i) \geq C > 0 \quad \forall\, i \in \mathbb{N} \quad \Rightarrow \quad \liminf_{t \nearrow T^{**}} \psi(t) \geq C > 0.$$

Hence our assumption was incorrect and indeed for any $T^{**} > 0$ it holds that

$$\liminf_{t \nearrow T^{**}} \psi(t) > 0. \qquad \square$$

The above result implies that the function ψ in fact *cannot* vanish for any $T^{**} > 0$ under the parameter restrictions

$$-b + c < 0 \quad \text{and} \quad f - \frac{g}{h} < 0.$$

The same result may be obtained in an identical manner to above when loosening the restriction $-b + c < 0$ to $-b + \frac{c}{1+d} < 0$ and imposing $x_0 \in (0, 1]$ instead. Indeed, for a solution s such that $x_0 \in (0, 1]$ we have (see e.g. Lemma 2.2.1)

$$x(t) \in (0, 1] \qquad \forall\, t \in I.$$

Thus it holds that for s and any $t \in I$:

$$-b + \frac{cx(t)}{x(t) + d} = -b + \frac{c}{1 + \underbrace{\frac{d}{x(t)}}_{\geq d}} \leq -b + \frac{c}{1 + d} =: -\gamma_2 < 0,$$

which may then be used in the $\dot{y}$-equation of (B.2.1) to obtain the monotonicity of the y-component of a solution (see Lemma B.2.1). In particular the claim of Theorem 2.3 in [Parshad et al., 2016b] does *not hold* independently of the initial condition x_0 and the parameters involved.

Remark B.2.2.
Considering the proof of Theorem 2.3 in [Parshad et al., 2016b], one observes that an essential point in the proof is the existence of

$$T^* = \frac{2}{z_0 f} \in (0, \delta)$$

for some sufficiently large $z_0 > 0$ and a $\delta > 0$ provided by the expression

$$\frac{1}{t}\int_0^t \frac{d\tau}{y(\tau) + h} < \frac{f}{2g} \qquad \forall\, t \in (0, \delta) \tag{B.2.3}$$

for sufficiently large $y_0 > 0$. We point out that the y-component of the solution may (and for system (B.2.1) it in fact *does*) depend on the z-component and hence also on z_0 (and likewise on x_0 and y_0). This in turn implies that the δ in (B.2.3) is *not* independent of z_0 (and x_0, y_0), i.e. $\delta = \delta(x_0, y_0, z_0) = \delta(s_0)$. Therefore,

$$T^* = \frac{2}{z_0 f} \in (0, \delta(x_0, y_0, z_0))$$

need not be fulfilled for any $z_0 > 0$, provided that

$$\delta(s_0) \leq \frac{2}{z_0 f} \qquad \forall\, s_0 \in \mathcal{O}^+$$

This is determined by the dependence of the solutions y-component on z_0. Hence the exact structure of the $\dot{y}$-equation in (2.1.5) *would have to be included in the proof.* This then yields conditions (such as restrictions on the parameters) for solutions to indeed blow up (one well-known restriction is $f - \frac{g}{h} > 0$). But for a general $\dot{y}$-equation and no further restrictions the assertion is wrong (as shown in the above lemma for system (B.2.1) or consider e.g. $\dot{y} = -y\frac{\dot{z}}{z}$). Note that in equation (2.2.14) we have been able to determine a dependence of the y-component on z_0 (for the case $T_0 = 0$). This is the decisive inequality that allowed us to show that solutions do not blow up in all the cases claimed in [Parshad et al., 2016b].

C Additional computations

C.1 Non-Dimensionalisation

Here we present the rescaling of the original system (2.1.1)

$$\begin{aligned}
\dot{\tilde{x}} &= a_1\tilde{x} - b_1\tilde{x}^2 - \frac{\omega_0\tilde{x}\tilde{y}}{\tilde{x}+d_0} \\
\dot{\tilde{y}} &= -a_2\tilde{y} + \frac{\omega_1\tilde{x}\tilde{y}}{\tilde{x}+d_1} - \frac{\omega_2\tilde{y}\tilde{z}}{\tilde{y}+d_2} \\
\dot{\tilde{z}} &= c_0\tilde{z}^2 - \frac{\omega_3\tilde{z}^2}{\tilde{y}+d_3}
\end{aligned} \tag{C.1.1}$$

by defining the following new variables (also see [Letellier and Aziz-Alaoui, 2002])

$$\begin{aligned}
x(t) &= \frac{b_1}{a_1}\tilde{x}(\tilde{t}), \\
y(t) &= \frac{b_1\omega_0}{a_1^2}\tilde{y}(\tilde{t}), \\
z(t) &= \frac{b_1\omega_0\omega_2}{a_1^3}\tilde{z}(\tilde{t}), \\
t &= a_1\tilde{t}
\end{aligned}$$

and rewriting the old equations in terms of x, y, z and t. For the first equation of (C.1.1) this yields

$$\begin{aligned}
\dot{x} &= \frac{dx(t)}{dt} \\
&= \frac{b_1}{a_1}\frac{d\tilde{x}(\tilde{t})}{dt} \\
&= \frac{b_1}{a_1}\frac{d\tilde{x}(\tilde{t})}{d\tilde{t}}\frac{d\tilde{t}}{dt} \\
&= \frac{b_1}{a_1}\frac{d\tilde{x}(\tilde{t})}{d\tilde{t}}\frac{1}{a_1} \\
&= \frac{b_1}{a_1^2}\dot{\tilde{x}}(\tilde{t}) \\
&= \frac{b_1}{a_1^2}\left(a_1\tilde{x} - b_1\tilde{x}^2 - \frac{\omega_0\tilde{x}\tilde{y}}{\tilde{x}+d_0}\right) \\
&= \frac{b_1}{a_1^2}\left(a_1\frac{a_1}{b_1}x - b_1\frac{a_1^2}{b_1^2}x^2 - \frac{\omega_0\frac{a_1}{b_1}\frac{a_1^2}{b_1\omega_0}xy}{\frac{a_1}{b_1}x + d_0}\right) \\
&= x(1-x) - \frac{xy}{x + \frac{b_1}{a_1}d_0} \\
&= x(1-x) - \frac{xy}{x+a}
\end{aligned}$$

with $a := \frac{b_1 d_0}{a_1}$. Similarly for the second equation of (C.1.1) we obtain

$$\begin{aligned}
\dot{y} &= \frac{b_1\omega_0}{a_1^2}\frac{d\tilde{y}(\tilde{t})}{d\tilde{t}}\frac{d\tilde{t}}{dt} \\
&= \frac{b_1\omega_0}{a_1^3}\dot{\tilde{y}}(\tilde{t}) \\
&= \frac{b_1\omega_0}{a_1^3}\left(-a_2\tilde{y} + \frac{\omega_1\tilde{x}\tilde{y}}{\tilde{x}+d_1} - \frac{\omega_2\tilde{y}\tilde{z}}{\tilde{y}+d_2}\right) \\
&= \frac{b_1\omega_0}{a_1^3}\left(-a_2\frac{a_1^2}{b_1\omega_0}y + \frac{\omega_1\frac{a_1}{b_1}\frac{a_1^2}{b_1\omega_0}xy}{\frac{a_1}{b_1}x+d_1} - \frac{\omega_2\frac{a_1^2}{b_1\omega_0}\frac{a_1^3}{b_1\omega_0\omega_2}yz}{\frac{a_1^2}{b_1\omega_0}y+d_2}\right) \\
&= -\frac{a_2}{a_1}y + \frac{\frac{\omega_1}{b_1}xy}{\frac{a_1}{b_1}x+d_1} - \frac{\frac{a_1^2}{b_1\omega_0}yz}{\frac{a_1^2}{b_1\omega_0}y+d_2} \\
&= -\frac{a_2}{a_1}y + \frac{\frac{\omega_1}{a_1}xy}{x+d_1\frac{b_1}{a_1}} - \frac{yz}{y+\frac{b_1\omega_0}{a_1^2}d_2} \\
&= -by + \frac{cxy}{x+d} - \frac{yz}{y+e}
\end{aligned}$$

with

$$b := \frac{a_2}{a_1}, \quad c := \frac{\omega_1}{a_1}, \quad d := \frac{b_1 d_1}{a_1}, \quad e := \frac{b_1 d_2 \omega_0}{a_1^2}.$$

Finally, the equation for the generalist predator density in (C.1.1) transforms to

$$\begin{aligned}
\dot{z} &= \frac{b_1\omega_0\omega_2}{a_1^3}\frac{d\tilde{z}(\tilde{t})}{d\tilde{t}}\frac{d\tilde{t}}{dt} \\
&= \frac{b_1\omega_0\omega_2}{a_1^4}\dot{\tilde{z}}(\tilde{t}) \\
&= \frac{b_1\omega_0\omega_2}{a_1^4}\left(c_0\tilde{z}^2 - \frac{\omega_3\tilde{z}^2}{\tilde{y}+d_3}\right) \\
&= \frac{b_1\omega_0\omega_2}{a_1^4}\left(c_0\frac{a_1^6}{b_1^2\omega_0^2\omega_2^2}z^2 - \frac{\omega_3\frac{a_1^6}{b_1^2\omega_0^2\omega_2^2}z^2}{\frac{a_1^2}{b_1\omega_0}y+d_3}\right) \\
&= \frac{c_0 a_1^2}{b_1\omega_0\omega_2}z^2 - \frac{\frac{\omega_3 a_1^2}{b_1\omega_0\omega_2}z^2}{\frac{a_1^2}{b_1\omega_0}y+d_3} \\
&= \frac{c_0 a_1^2}{b_1\omega_0\omega_2}z^2 - \frac{\frac{\omega_3}{\omega_2}z^2}{y+\frac{b_1\omega_0}{a_1^2}d_3} \\
&= fz^2 - \frac{gz^2}{y+h}
\end{aligned}$$

with

$$f := \frac{c_0 a_1^2}{b_1\omega_0\omega_2}, \quad g := \frac{\omega_3}{\omega_2}, \quad h := \frac{b_1 d_3 \omega_0}{a_1^2}.$$

Thus the rescaled system reads

$$\begin{aligned}\dot{x} &= x(1-x) - \frac{xy}{x+a}\\ \dot{y} &= -by + \frac{cxy}{x+d} - \frac{yz}{y+e}\\ \dot{z} &= fz^2 - \frac{gz^2}{y+h}\end{aligned}$$

C.2 Equilibria

In this section we gather various calculations involving the equilibria of the system (2.1.5).

C.2.1 Computation of equilibria

Here we present a detailed derivation of the equilibria of the semiflow Φ induced by (2.1.5). Only the equilibria $p_i^* \in \mathcal{O}_0^+$ will be of biological relevance to the system dynamics. We also assume that $f - \frac{g}{h} < 0$ holds. Consider the equations

$$v(x,y,z) = 0 \quad \Leftrightarrow \quad \begin{aligned}\left(1 - x - \tfrac{y}{x+a}\right)x &= 0,\\ \left(-b + \tfrac{cx}{x+d} - \tfrac{z}{y+e}\right)y &= 0,\\ \left(f - \tfrac{g}{y+h}\right)z^2 &= 0.\end{aligned} \tag{C.2.1}$$

Quite a few different cases need to be considered here.

Case 1: $x = 0$
We commence by assuming $x = 0$. Then the two remaining equations in (C.2.1) read

$$0 = \left(-b - \frac{z}{y+e}\right)y, \tag{C.2.2}$$

$$0 = \left(f - \frac{g}{y+h}\right)z^2. \tag{C.2.3}$$

1a) If $y = 0$ as well, we are left with

$$0 = \left(f - \frac{g}{h}\right)z^2$$

which is only solved by $z = 0$, since we assumed, that $f - \frac{g}{h} < 0$. Hence the first equilibrium is given by $p_0^* = (0,0,0)^T \in \mathcal{O}_0^+$, i.e. the origin.

1b) If $y \neq 0$ then from (C.2.2) one obtains

$$-b - \frac{z}{y+e} = 0 \quad \Leftrightarrow \quad z = -b(y+e).$$

Substituting this into (C.2.3) yields

$$0 = \left(f - \frac{g}{y+h}\right)(-b(y+e))^2$$

which is solved by $y = -e < 0$ or $y = \frac{g}{f} - h > 0$. The point $(0, -e, 0)^T$ however, does not lie in $\mathcal{O}_0^+$ and is thus not relevant for us. The point

$$\begin{pmatrix} x \\ y \\ z \end{pmatrix} = \begin{pmatrix} 0 \\ \frac{g}{f} - h \\ -b\left(\frac{g}{f} - h + e\right) \end{pmatrix} = \begin{pmatrix} 0 \\ \frac{g}{f} - h \\ b\left(h - \frac{g}{f} - e\right) \end{pmatrix}$$

is also not feasible (in a biological sense), since $z = h - \frac{g}{f} - e < h - \frac{g}{f} < 0$ by assumption. Hence the third component is negative and the equilibrium is not a point in $\mathcal{O}_0^+$. Thus the only feasible point for $x = 0$ is the origin, i.e. p_0^*.

Case 2: $x \neq 0$
We now assume $x \neq 0$ for (C.2.1) and seek solutions for

$$1 - x - \frac{y}{x+a} = 0 \quad \Leftrightarrow \quad (1-x)(a+x) = y.$$

2a) Now if $z = 0$ the third equation of (C.2.1) is fulfilled and with the above the second equation of (C.2.1) simplifies to

$$(1-x)(x+a)\left(-b + \frac{cx}{x+d}\right) = 0$$

which is fulfilled for $x = 1$, $x = -a < 0$ and $x = \frac{bd}{c-b}$ (with $b \neq c$). The first value yields the equilibrium $p_1^* = (1, 0, 0)^T \in \mathcal{O}_0^+$. The second value is not feasible, as $(-a, 0, 0)^T$ does not lie in the non-negative octant. Finally, the third equilibrium reads (for $b \neq c$)

$$p_2^* = \begin{pmatrix} x_2^* \\ y_2^* \\ z_2^* \end{pmatrix} = \begin{pmatrix} \frac{bd}{c-b} \\ (1 - x_2^*)(x_2^* + a) \\ 0 \end{pmatrix} = \begin{pmatrix} \frac{bd}{c-b} \\ \left(1 - \frac{bd}{c-b}\right)\left(a + \frac{bd}{c-b}\right) \\ 0 \end{pmatrix}.$$

Here the feasibility of the equilibrium depends on the parameters of the system. More precisely, in order for $x_2^* \geq 0$ we need

$$\frac{bd}{c-b} \geq 0 \quad \Leftrightarrow \quad c > b.$$

The second component, i.e. y_2^*, is non-negative if

$$1 - \frac{bd}{c-b} \geq 0 \quad \Leftrightarrow \quad c - b \geq bd \quad \Leftrightarrow \quad \frac{c}{d+1} \geq b.$$

Note that this condition implies $c > b$ (since $d > 0$) and hence

$$p_2^* \in \mathcal{O}_0^+ \quad \Leftrightarrow \quad b \leq \frac{c}{d+1}.$$

2b) We now assume that $z \neq 0$ then the third equation of (C.2.1) implies $y_3^* = \frac{g}{f} - h > 0$. Furthermore for $x \neq 0$ we have

$$(1-x)(x+a) = y \quad \text{and} \quad -b + \frac{cx}{x+d} - \frac{z}{y+e} = 0.$$

Plucking these together yields values of two further equilibria. For the x-component one computes

$$(1-x)(x+a) = \tfrac{g}{f} - h \quad \Leftrightarrow \quad x^2 + (a-1)x - a - h + \tfrac{g}{f} = 0$$

which is solved by

$$x_{3\pm}^* = \frac{1 - a \pm \sqrt{(a-1)^2 - 4\left(\frac{g}{f} - h - a\right)}}{2} = \frac{1-a}{2} \pm \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h}.$$

For the z-component we obtain

$$-b + \frac{cx}{x+d} - \frac{z}{y+e} = 0 \quad \Leftrightarrow \quad z = -(y+e)\left(b - \frac{cx}{x+d}\right)$$

and substituting $x_{3\pm}^*$ and y_3^* yields

$$z_{3\pm}^* = \left(h - \frac{g}{f} - e\right)\left(b - \frac{cx_{3\pm}^*}{x_{3\pm}^* + d}\right).$$

Hence the equilibria read

$$p_{3\pm}^* = \begin{pmatrix} x_{3\pm}^* \\ y_3^* \\ z_{3\pm}^* \end{pmatrix} = \begin{pmatrix} \frac{1-a}{2} \pm \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} \\ \frac{g}{f} - h \\ \left(h - \frac{g}{f} - e\right)\left(b - \frac{cx_{3\pm}^*}{x_{3\pm}^*+d}\right) \end{pmatrix}.$$

It is not immediately clear whether the points $p_{3\pm}^*$ are feasible, i.e. if $p_{3\pm}^* \in \mathcal{O}_0^+$. First of all we need to check, that the point is actually real-valued. We have

$$\operatorname{Im}(p_{3\pm}^*) = 0 \quad \Leftrightarrow \quad \frac{(a+1)^2}{4} - \frac{g}{f} + h \geq 0 \quad \Leftrightarrow \quad a \geq 2\sqrt{\tfrac{g}{f} - h} - 1 \quad \text{(C.2.4)}$$

which yields a necessary and sufficient condition (in terms of $a > 0$) for the equilibrium to be real-valued. We still need, that $p_{3\pm}^*$ is non-negative. For $y_3^* = \frac{g}{f} - h > 0$ this is always fulfilled. For the first component we consider x_{3+}^* and x_{3-}^* separately. For x_{3+}^* we see that if $0 < a \leq 1$, then evidently $x_{3+}^* > 0$ if it is real-valued (see (C.2.4)). For $a > 1$ we compute

$$\begin{array}{rccc} x_{3+}^* = & \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} & \geq & 0 \\ \Leftrightarrow & \sqrt{\frac{(a-1)^2}{4} + a - \frac{g}{f} + h} & \geq & \frac{a-1}{2} \\ \Leftrightarrow & \frac{(a-1)^2}{4} + a - \frac{g}{f} + h & \geq & \frac{(a-1)^2}{4} \\ \Leftrightarrow & a & \geq & \frac{g}{f} - h \end{array}$$

which implies that if (C.2.4) holds

$$x^*_{3+} \geq 0 \quad \Leftrightarrow \quad 0 < a \leq 1 \quad \text{or} \quad a \geq \frac{g}{f} - h.$$

For x^*_{3-} on the other hand we see that if $a > 1$ then $x^*_{3-} < 0$ and for $0 < a \leq 1$ we obtain

$$\begin{array}{rcl} \frac{1-a}{2} - \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} & \geq & 0 \\ \Leftrightarrow \quad -\sqrt{\frac{(a-1)^2}{4} + a - \frac{g}{f} + h} & \geq & \frac{a-1}{2} \\ \Leftrightarrow \quad \frac{(a-1)^2}{4} + a - \frac{g}{f} + h & \leq & \frac{(a-1)^2}{4} \\ \Leftrightarrow \quad a & \leq & \frac{g}{f} - h \end{array}$$

yielding (if (C.2.4) holds)

$$x^*_{3-} \geq 0 \quad \Leftrightarrow \quad 0 < a \leq 1 \quad \text{and} \quad a \leq \frac{g}{f} - h.$$

Finally we need $z^*_{3\pm} = \left(h - \frac{g}{f} - e\right)\left(b - \frac{cx^*_{3\pm}}{x^*_{3\pm}+d}\right) \geq 0$. Since $h - \frac{g}{f} - e < 0$ this condition reduces to

$$z^*_{3\pm} \geq 0 \quad \Leftrightarrow \quad b - \frac{cx^*_{3\pm}}{x^*_{3\pm} + d} \leq 0 \quad \Leftrightarrow \quad b \leq \frac{cx^*_{3\pm}}{x^*_{3\pm} + d}.$$

Note that in order for a $b > 0$ to exist, such that

$$b \leq \frac{cx^*_{3\pm}}{x^*_{3\pm} + d}$$

can hold, we need $x^*_{3\pm} > 0$. In particular, if $a = \frac{g}{f} - h$ then

$$x^*_{3+} = \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} = \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - a} = \frac{1-a}{2} + \sqrt{\frac{(a-1)^2}{4}} = 0$$

Thus we exclude the case $a = \frac{g}{f} - h$. This concludes the derivation of the biologically meaningful equilibria of the system. We sum up the results in Table 3, bearing in mind that $\frac{g}{f} - h > 0$.

C.2.2 Computing $J = \mathrm{Dv}(p^*_{3+})$

We consider the Jacobian $\mathrm{Dv}(x, y, z)$ of the vector field v (see equation (2.4.5)) evaluated at the equilibrium p^*_{3+}:

$$J := \mathrm{Dv}(p^*_{3+}) = \left.\begin{pmatrix} 1 - 2x - \frac{ay}{(x+a)^2} & -\frac{x}{x+a} & 0 \\ \frac{acy}{(x+a)^2} & -b + \frac{cx}{x+a} - \frac{ez}{(y+e)^2} & -\frac{y}{y+e} \\ 0 & \frac{gz^2}{(y+h)^2} & 2z\left(f - \frac{g}{y+h}\right) \end{pmatrix}\right|_{(x,y,z)=\left(x^*_{3+},y^*_{3+},z^*_{3+}\right)}$$

Point	Existence ($p_i^* \in \mathbb{R}^3$)	Non-Negativity ($p_i^* \in \mathcal{O}_0^+$)
$p_0^* = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$	-	-
$p_1^* = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}$	-	-
$p_2^* = \begin{pmatrix} \frac{bd}{c-b} \\ (1-x_2^*)(x_2^*+a) \\ 0 \end{pmatrix}$	$b \neq c$	$b \leq \frac{c}{d+1}$
$p_{3+}^* = \begin{pmatrix} \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} \\ \frac{g}{f} - h \\ \left(h - \frac{g}{f} - e\right)\left(b - \frac{cx_{3+}^*}{x_{3+}^*+d}\right) \end{pmatrix}$	$a \geq 2\sqrt{\frac{g}{f} - h} - 1$	$(0 < a \leq 1 \vee a > \frac{g}{f} - h) \wedge b \leq \frac{cx_{3+}^*}{x_{3+}^*+d}$
$p_{3-}^* = \begin{pmatrix} \frac{1-a}{2} - \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} \\ \frac{g}{f} - h \\ \left(h - \frac{g}{f} - e\right)\left(b - \frac{cx_{3-}^*}{x_{3-}^*+d}\right) \end{pmatrix}$	$a \geq 2\sqrt{\frac{g}{f} - h} - 1$	$0 < a \leq 1 \wedge a < \frac{g}{f} - h \wedge b \leq \frac{cx_{3-}^*}{x_{3-}^*+d}$

Table 3: Existence conditions on the equilibrium points

We use

$$p_{3+}^* = \begin{pmatrix} x_{3+}^* \\ y_{3+}^* \\ z_{3+}^* \end{pmatrix} = \begin{pmatrix} \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} \\ \frac{g}{f} - h \\ \left(h - \frac{g}{f} - e\right)\left(b - \frac{cx_{3+}^*}{x_{3+}^*+a}\right) \end{pmatrix} = \begin{pmatrix} \frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h} \\ \frac{g}{f} - h \\ \left(h - \frac{g}{f} - e\right)\left(b - b_{3+}^*\right) \end{pmatrix}$$

to obtain an explicit expression for

$$J = \begin{pmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ j_{31} & j_{32} & j_{33} \end{pmatrix} = \mathrm{Dv}(p_{3+}^*).$$

Evidently it holds that $j_{13} = j_{31} = 0$. Furthermore, since $y_{3+}^* = \frac{g}{f} - h$ we have

$$j_{33} = 2z_{3+}^* \underbrace{\left(f - \frac{g}{y_{3+}^* + h}\right)}_{=0} = 0.$$

Next we compute

$$j_{32} = \frac{g(z_{3+}^*)^2}{(y_{3+}^* + h)^2} = \frac{g}{\frac{g^2}{f^2}}(z_{3+}^*)^2 = \frac{f^2}{g}(z_{3+}^*)^2 = \frac{f^2}{g}\left(h - \frac{g}{f} - e\right)^2 \left(b - b_{3+}^*\right)^2.$$

We determine an explicit expression for the entry j_{22} of J as follows

$$
\begin{aligned}
j_{22} &= -b + \overbrace{\frac{cx^*_{3+}}{x^*_{3+} + a}}^{=b^*_{3+}} - \frac{ez^*_{3+}}{(y^*_{3+} + e)^2} \\
&= -b + b^*_{3+} - \frac{e\left(h - \frac{g}{f} - e\right)\left(b - b^*_{3+}\right)}{\left(\frac{g}{f} - h + e\right)^2} \\
&= -b + b^*_{3+} + \frac{e\left(b - b^*_{3+}\right)}{\frac{g}{f} - h + e} \\
&= \left(b^*_{3+} - b\right)\left(1 - \frac{e}{\frac{g}{f} - h + e}\right) \\
&= \left(b^*_{3+} - b\right)\left(\frac{\frac{g}{f} - h}{\frac{g}{f} - h + e}\right)
\end{aligned}
$$

Recall from the derivation of the equilibrium point p^*_{3+} that its components fulfil $y^*_{3+} = (1 - x^*_{3+})(x^*_{3+} + a)$. This allows us to write

$$
j_{21} = \frac{acy^*_{3+}}{(x^*_{3+} + a)^2} = \frac{ac(1 - x^*_{3+})(x^*_{3+} + a)}{(x^*_{3+} + a)^2} = \frac{ac(1 - x^*_{3+})}{x^*_{3+} + a}.
$$

Finally, by using $y^*_{3+} = (1 - x^*_{3+})(x^*_{3+} + a)$ once more, we obtain

$$
\begin{aligned}
j_{11} &= 1 - 2x^*_{3+} - \frac{ay^*_{3+}}{(x^*_{3+} + a)^2} \\
&= 1 - 2x^*_{3+} - \frac{a(1 - x^*_{3+})(x^*_{3+} + a)}{(x^*_{3+} + a)^2} \\
&= \frac{(x^*_{3+} + a)(1 - 2x^*_{3+}) - a(1 - x^*_{3+})}{x^*_{3+} + a} \\
&= \frac{x^*_{3+}(1 - a - 2x^*_{3+})}{x^*_{3+} + a} \\
&= \frac{x^*_{3+}\left(1 - a - 2\left(\frac{1-a}{2} + \sqrt{\frac{(a+1)^2}{4} - \frac{g}{f} + h}\right)\right)}{x^*_{3+} + a} \\
&= \frac{-x^*_{3+} \cdot \sqrt{(a+1)^2 - 4\left(\frac{g}{f} - h\right)}}{x^*_{3+} + a}
\end{aligned}
$$

We gather all the expressions from above to obtain

$$J = \mathrm{Dv}(p^*_{3+}) = \begin{pmatrix} \frac{-x^*_{3+}\cdot\sqrt{(a+1)^2-4\left(\frac{g}{f}-h\right)}}{x^*_{3+}+a} & -\frac{x^*_{3+}}{x^*_{3+}+a} & 0 \\ \frac{ac(1-x^*_{3+})}{x^*_{3+}+a} & \left(b^*_{3+}-b\right)\left(\frac{\frac{g}{f}-h}{\frac{g}{f}-h+e}\right) & -\frac{y^*_{3+}}{y^*_{3+}+e} \\ 0 & \frac{f^2}{g}\left(h-\frac{g}{f}-e\right)^2\left(b-b^*_{3+}\right)^2 & 0 \end{pmatrix}$$

C.3 Centre manifold reductions

We provide the centre manifold reductions omitted in the proofs of Lemmas 2.4.4 and 2.4.7. Recall that we assumed $a = d$ and $f - \frac{g}{h} < 0$ to hold throughout the section, which we also assume to hold here.

C.3.1 Centre manifold reduction for p^*_1

We provide the computations for the centre manifold reduction from the proof of Lemma 2.4.4. Recall that $b > \frac{c}{a+1}$ was assumed to hold in the proof. Translating the equilibrium $p^*_1 = (1,0,0)^T$ to the origin by means of setting $\widetilde{x} = x - 1$ yields

$$\begin{aligned} \dot{\widetilde{x}} &= -(\widetilde{x}+1)\widetilde{x} - \frac{(\widetilde{x}+1)y}{\widetilde{x}+1+a} \\ \dot{y} &= \left(-b + \frac{c(\widetilde{x}+1)}{\widetilde{x}+1+a} - \frac{yz}{y+e}\right) y \\ \dot{z} &= \left(f - \frac{g}{y+h}\right) z^2 \end{aligned} \tag{C.3.1}$$

We call the right-hand side $\widetilde{v}$. The linearisation of $\widetilde{v}$ evaluated at the shifted equilibrium (i.e. in the origin) is given by

$$\mathrm{D}\widetilde{\mathrm{v}}(0,0,0) = \begin{pmatrix} -1 & -\frac{1}{1+a} & 0 \\ 0 & -b+\frac{c}{a+1} & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

of which the eigenvalues are $\lambda_1 = -1$, $\lambda_2 = -b + \frac{c}{a+1}$ and $\lambda_3 = 0$ and the respective eigenvectors are

$$v_1 = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}, \qquad v_2 = \begin{pmatrix} -1 \\ 1+a+c-b(a+1) \\ 0 \end{pmatrix}, \qquad v_3 = \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}.$$

The next step is to determine the Jordan normal form of $\mathrm{D}\widetilde{\mathrm{v}}(0,0,0)$. The required transformation matrix $S \in \mathbb{R}^{3\times 3}$ consists of the three eigenvectors v_1, v_2 and v_3, i.e.

$$S = \begin{pmatrix} 1 & -1 & 0 \\ 0 & 1+a+c-b(a+1) & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

The change of coordinates is now given by

$$\begin{pmatrix} \widetilde{x} \\ y \\ z \end{pmatrix} = S \begin{pmatrix} \xi \\ \nu \\ \omega \end{pmatrix} = \begin{pmatrix} \xi - \nu \\ [1+a+c-b(a+1)]\nu \\ \omega \end{pmatrix}.$$

Hence the variable ω is the centre variable (associated to the eigenvalues $\lambda_3 = 0$). The dynamics of the transformed system of (C.3.1) are given by

$$\begin{aligned} \begin{pmatrix} \dot{\xi} \\ \dot{\nu} \\ \dot{\omega} \end{pmatrix} &= \widehat{v}(\xi, \nu, \omega) := S^{-1}\widetilde{v}(\widetilde{x}, y, z) \\ &= S^{-1}\widetilde{v}\left(S \begin{pmatrix} \xi \\ \nu \\ \omega \end{pmatrix} \right) = S^{-1}\widetilde{v}(\xi - \nu, [1+a+c-b(a+1)]\nu, \omega) \end{aligned}$$

Computing this last expression explicitly, yields the rather unhandy expression

$$S^{-1}\widetilde{v}(\xi - \nu, [1+a+c-b(a+1)]\nu, \omega) =$$

$$\begin{pmatrix} 1 & \frac{1}{1+a+c-b(a+1)} & 0 \\ 0 & \frac{1}{1+a+c-b(a+1)} & 0 \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} -(\xi-\nu+1)(\xi-\nu) - \frac{(\xi-\nu+1)[1+a+c-b(a+1)]\nu}{\xi-\nu+1+a} \\ \left(-b + \frac{c(\xi-\nu+1)}{\xi-\nu+1+a} - \frac{[1+a+c-b(a+1)]\nu\omega}{[1+a+c-b(a+1)]\nu+e}\right)[1+a+c-b(a+1)]\nu \\ \left(f - \frac{g}{[1+a+c-b(a+1)]\nu+h}\right)\omega^2 \end{pmatrix}$$

From the above equality we see that the third line of $\widehat{v}$ and therefore the dynamics on the local centre manifold are governed by

$$\dot{\omega} = \left(f - \frac{g}{[1+a+c-b(a+1)]\nu + h}\right)\omega^2,$$

which corresponds to the claim in the proof of Lemma 2.4.4.

C.3.2 Centre manifold reduction for p_2^*

Analogously to the above case we want to determine the centre manifold reduction that was omitted in the proof of Lemma 2.4.7. Recall that $\frac{c(1-a)}{a+1} < b < \frac{c}{a+1}$ was assumed to hold in that part of the proof. Translating the equilibrium $p_2^* = (x_2^*, y_2^*, 0)^T$ to the origin by means of setting $\widetilde{x} = x - x_2^*$ and $\widetilde{y} = y - y_2^*$ yields

$$\begin{aligned} \dot{\widetilde{x}} &= (\widetilde{x} + x_2^*)(1 - \widetilde{x} - x_2^*) - \frac{(\widetilde{x} + x_2^*)(\widetilde{y} + y_2^*)}{\widetilde{x} + x_2^* + a} \\ \dot{\widetilde{y}} &= \left(-b + \frac{c(\widetilde{x} + x_2^*)}{\widetilde{x} + x_2^* + a} - \frac{(\widetilde{y} + y_2^*)z}{\widetilde{y} + y_2^* + e}\right)(\widetilde{y} + y_2^*) \\ \dot{z} &= \left(f - \frac{g}{\widetilde{y} + y_2^* + h}\right)z^2 \end{aligned} \tag{C.3.2}$$

We call the right-hand side $\widetilde{v}$. The linearisation of $\widetilde{v}$ evaluated at the shifted equilibrium (i.e. in the origin) is given by

$$\mathrm{D}\widetilde{\mathrm{v}}(0,0,0) = \begin{pmatrix} \frac{x_2^*(1-a-2x_2^*)}{a+x_2^*} & -\frac{x_2^*}{x_2^*+a} & 0 \\ \frac{ac(1-x_2^*)}{a+x_2^*} & 0 & -\frac{y_2^*}{y_2^*+e} \\ 0 & 0 & 0 \end{pmatrix}$$

of which one eigenvalue is $\lambda_3 = 0$ and the corresponding eigenvector reads

$$v_3 = \begin{pmatrix} \frac{(a+x_2^*)^2}{ac(y_2^*+e)} \\ \\ \frac{(1-a-2x_2^*)(a+x_2^*)^2}{ac(y_2^*+e)} \\ \\ 1 \end{pmatrix}$$

The other two eigenvalues can be determined by considering the submatrix

$$J_2 = \begin{pmatrix} \frac{x_2^*(1-a-2x_2^*)}{a+x_2^*} & -\frac{x_2^*}{x_2^*+a} \\ \frac{ac(1-x_2^*)}{a+x_2^*} & 0 \end{pmatrix}$$

of $\mathrm{D}\widetilde{\mathrm{v}}(0,0,0)$. Note that for a matrix of the form

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & 0 \end{pmatrix}$$

with $a_{11}, a_{12} \in \mathbb{R}$ and $a_{21} \neq 0$ the trace and determinant are given by

$$\operatorname{tr}(A) = a_{11} \quad \text{and} \quad \det(A) = -a_{12}a_{21}.$$

Using the trace-determinant criterion, the eigenvalues $\mu_{1/2}$ and the corresponding eigenvectors $w_{1/2}$ of A are given by

$$\mu_{1/2} = \frac{1}{2}\left(\operatorname{tr}(A) \pm \sqrt{\operatorname{tr}^2(A) - 4\det(A)}\right) = \frac{1}{2}\left(a_{11} \pm \sqrt{a_{11}^2 + 4a_{12}a_{21}}\right)$$

$$w_{1/2} = \begin{pmatrix} \frac{a_{11} \pm \sqrt{a_{11}^2+4a_{12}a_{21}}}{2a_{21}} \\ 1 \end{pmatrix} = \begin{pmatrix} \frac{\mu_{1/2}}{a_{21}} \\ 1 \end{pmatrix}$$

We apply this to the matrix J_2. First note that $0 < x_2^* = \frac{ab}{c-b} < 1$ since $b < \frac{c}{a+1}$ and hence

$$\frac{ac(1-x_2^*)}{a+x_2^*} > 0.$$

Furthermore we have

$$\operatorname{tr}(J_2) = \frac{x_2^*(1-a-2x_2^*)}{a+x_2^*} \quad \text{and} \quad \det(J_2) = \frac{acx_2^*(1-x_2^*)}{(a+x_2^*)^2}.$$

Thus setting

$$\Delta := \mathrm{tr}^2(J_2) - 4\det(J_2) = \frac{(x_2^*(1-a-2x_2^*))^2 - 4acx_2^*(1-x_2^*)}{(a+x_2^*)^2}$$

yields the following eigenvalues and eigenvectors of J_2:

$$\mu_{1/2} = \frac{1}{2}\left(\frac{x_2^*(1-a-2x_2^*)}{a+x_2^*} \pm \sqrt{\Delta}\right)$$
$$w_{1/2} = \begin{pmatrix} \frac{-x_2^*(1-a-2x_2^*)\pm(a+x_2^*)\sqrt{\Delta}}{2ac(1-x_2^*)} \\ 1 \end{pmatrix} = \begin{pmatrix} \frac{\mu_{1/2}(a+x_2^*)}{ac(1-x_2^*)} \\ 1 \end{pmatrix}.$$

For the matrix $\mathrm{D}\tilde{\mathrm{v}}(0,0,0)$ the eigenvalues $\lambda_{1/2}$ and the corresponding eigenvectors $v_{1/2}$ turn out to be

$$\lambda_{1/2} = \frac{1}{2}\left(\frac{x_2^*(1-a-2x_2^*)}{a+x_2^*} \pm \sqrt{\Delta}\right)$$
$$v_{1/2} = \begin{pmatrix} \frac{\lambda_{1/2}(a+x_2^*)}{ac(1-x_2^*)} \\ 1 \\ 0 \end{pmatrix}.$$

Thus the transformation matrix S required to determine the Jordan normal form of $\mathrm{D}\tilde{\mathrm{v}}(0,0,0)$ is given by

$$S = \begin{pmatrix} \frac{\lambda_1(a+x_2^*)}{ac(1-x_2^*)} & \frac{\lambda_2(a+x_2^*)}{ac(1-x_2^*)} & \frac{(a+x_2^*)^2}{ac(y_2^*+e)} \\ 1 & 1 & \frac{(1-a-2x_2^*)(a+x_2^*)^2}{ac(y_2^*+e)} \\ 0 & 0 & 1 \end{pmatrix} = \begin{pmatrix} s_{11} & s_{12} & s_{13} \\ 1 & 1 & s_{23} \\ 0 & 0 & 1 \end{pmatrix}$$

Accordingly, the change of coordinates reads

$$\begin{pmatrix} \tilde{x} \\ \tilde{y} \\ z \end{pmatrix} = S \begin{pmatrix} \xi \\ \nu \\ \omega \end{pmatrix} = \begin{pmatrix} s_{11}\xi + s_{12}\nu + s_{13}\omega \\ \xi + \nu + s_{23}\omega \\ \omega \end{pmatrix}.$$

Hence the variable ω is the centre variable (corresponding to the eigenvalue $\lambda_3 = 0$). We remark that since

$$0 < 1 - a - 2x_2^* \quad \Leftrightarrow \quad \frac{2ab}{c-b} < 1 - a \quad \Leftrightarrow \quad \frac{c(1-a)}{a+1} < b$$

we have

$$s_{23} = \frac{\overbrace{(1-a-2x_2^*)}^{>0}\overbrace{(a+x_2^*)^2}^{>0}}{\underbrace{ac(y_2^*+e)}_{>0}} > 0. \tag{C.3.3}$$

The dynamics of the transformed system of (C.3.2) are given by

$$\begin{pmatrix} \dot{\xi} \\ \dot{\nu} \\ \dot{\omega} \end{pmatrix} = \widehat{v}(\xi, \nu, \omega) := S^{-1}\widetilde{v}(\widetilde{x}, \widetilde{y}, z)$$
$$= S^{-1}\widetilde{v}(s_{11}\xi + s_{12}\nu + s_{13}\omega, \xi + \nu + s_{23}\omega, \omega)$$

The matrix S is invertible, since it consist of three linearly independent, possibly generalised eigenvectors v_1, v_2, v_3. The inverse of S has the structure

$$S^{-1} = \begin{pmatrix} * & * & * \\ * & * & * \\ 0 & 0 & 1 \end{pmatrix},$$

where $*$ denotes entries we do not need to compute explicitly. Thus we obtain

$$S^{-1}\widetilde{v}(s_{11}\xi + s_{12}\nu + s_{13}\omega, \xi + \nu + s_{23}\omega, \omega) = \begin{pmatrix} * & * & * \\ * & * & * \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} * \\ * \\ \left(f - \frac{g}{\xi+\nu+s_{23}\omega+y_2^*+h}\right)\omega^2 \end{pmatrix}$$

From the above equality we see that the third line of $\widehat{v}$ and therefore the dynamics on the local centre manifold are governed by

$$\dot{\omega} = \left(f - \frac{g}{\xi + \nu + C\omega + y_2^* + h}\right)\omega^2,$$

where $C = s_{23} > 0$ for $b > \frac{c(1-a)}{a+1}$ by (C.3.3). This proves the claim in the proof of Lemma 2.4.4.

D Numerical computations

We comment on the numerical methods by which the results of subsection 2.5 were obtained.

D.1 The code

In this subsection we present the code with which the numerical simulations were run. The computations were performed in MATLAB [MATLAB, 2015] using the code presented in Listing 1.

```
function [] = DAecosys(s,ti,tf,x0,y0,z0,b,varargin)

%Variables:
%s: maximal step size (if s=0 the solver is adaptive)
%ti: initial time
%tf: final time
%x0,y0,z0: initial value
%b: value of the parameter b
%varargin: if non-empty it contains the other 7 parameter
    values in the order (a,c,d,e,f,g,h)

%Setting and checking the parameters

if tf-ti<=0 %Ensuring that the time interval is positive
        X=['The final time must be chosen strictly larger
            than the initial time!'];
        error(X)
end

l=length(varargin);

if l==0 %The standard parameters are used
        a=0.3; c=1; d=0.3; e=0.15; f=400/81; g=200/81; h
            =0.3;
elseif l~=7 %Checking the length of the parameter vector
        X=['Parameter vector must have length 0 or 7.
            Currently it has length ', num2str(l), '.'];
        error(X)
else %The alternative parameters are used
        a=varargin{1}; c=varargin{2}; d=varargin{3}; e=
            varargin{4}; f=varargin{5}; g=varargin{6}; h=
            varargin{7};
end

```

```
29 %The vector field
30 v = @(t,x) [x(1)*(1-x(1))-(x(1)*x(2))/(x(1)+a);-b*x(2)+(c*x
     (1)*x(2))/(x(1)+d)-(x(2)*x(3))/(x(2)+e);f*(x(3))^2-(g*(x
     (3))^2)/(x(2)+h)];
31
32 %The solver
33 if s<0 %Ensuring that the step size is non-negative
34         X=['The step size s may not be negative! s=',
              num2str(s), '.'];
35         error(X)
36 elseif s==0 %If s=0, the solver is adaptive
37         [t,sol] = ode45(v, [ti tf],[x0,y0,z0]);
38 else
39         options = odeset('MaxStep',s);
40         [t,sol] = ode45(v, [ti tf],[x0,y0,z0],options);
41 end
```

Listing 1: The MATLAB code

The input values of the function DAecosys are:

- The maximum step size s, the (adaptive) solver can choose.
- The respective initial and final times ti and tf. The solution is computed on the interval [ti, tf].
- The initial values x0, y0, z0, being $s_0 = (x_0, y_0, z_0)^T$.
- The parameter b, being the $b > 0$ of the vector field given in (2.1.5).
- The argument varargin, which is an optional input of the other seven parameters a, c, d, e, f, g, h (in that order) in (2.1.5).

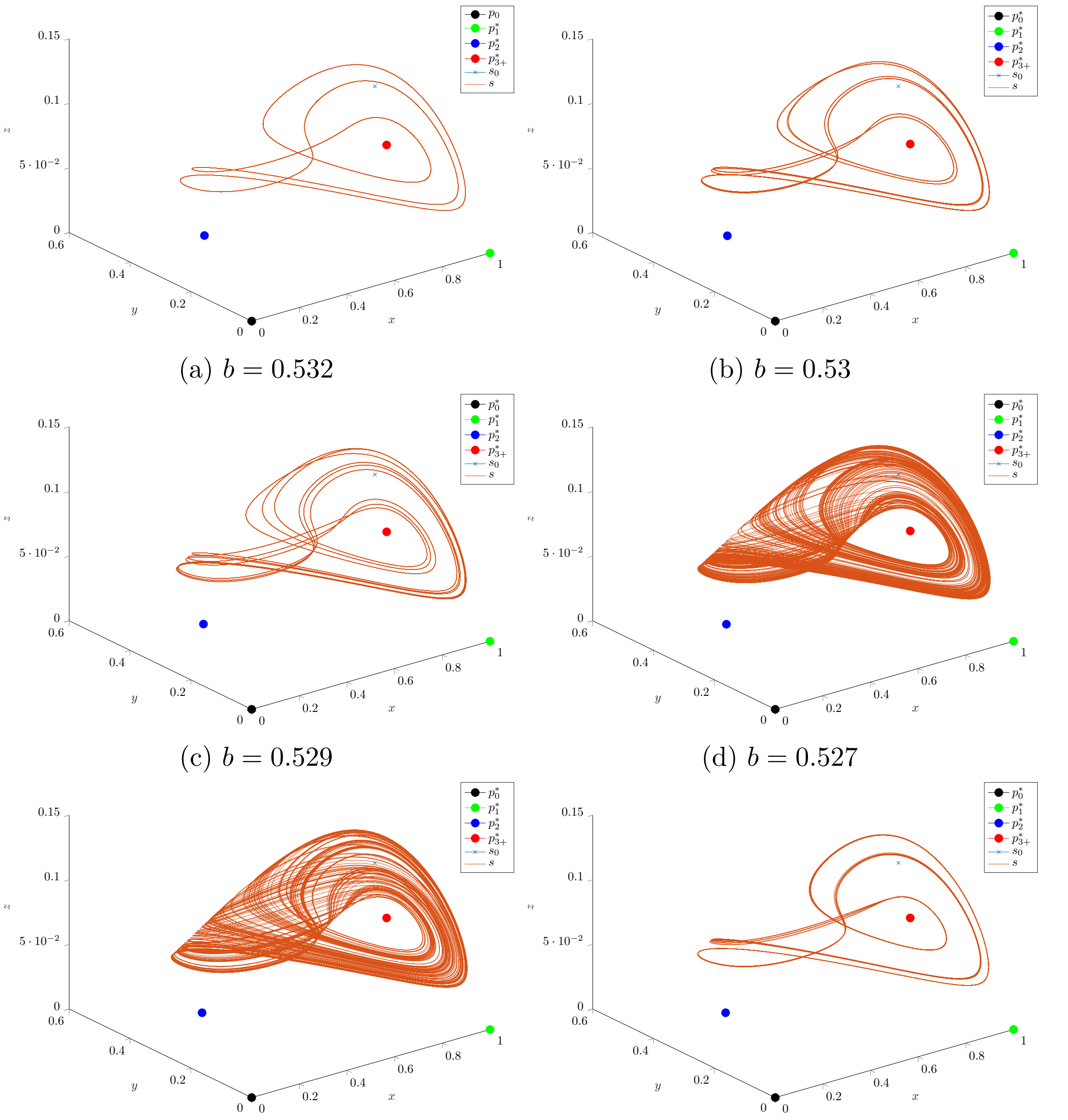
We remark, that if the parameter vector varargin is empty, then the standard parameters from (2.5.1) are used (see line 21).
The key ingredient of the program is the integrated ODE-solver ode45 (see lines 37 and 40 in Listing 1). It uses an *adaptive* step size. However, the maximal step size s can be controlled by the option 'MaxStep'. If s is chosen to be zero, the solver is purely adaptive and the step size is controlled by the internal implementation only.
A sample for calling the function is given by

```
DAecosys(10^-4,0,2000,0.9,0.3,0.1,0.7)
```

Here the solution is computed on the time interval $I = [0, 2000]$ for $b = 0.7$ and the initial conditions $s_0 = (0.9, 0.3, 0.1)^T$ using a maximal step size of 10^{-4}. The result of this was presented in Figure 2.5.11. We remark that for readabilities sake of Listing 1, we did not include the command lines how the plots (such as Figure 2.5.11) were created in the listing.

D.2 Visualisation

We present the additional figures of the windows of period-doubling cascades from Table 2 in section 2.5. In Figure D.2.1 the window for the approximate range $b \in [0.5243, 0.532]$ is depicted.



(a) $b = 0.532$ (b) $b = 0.53$

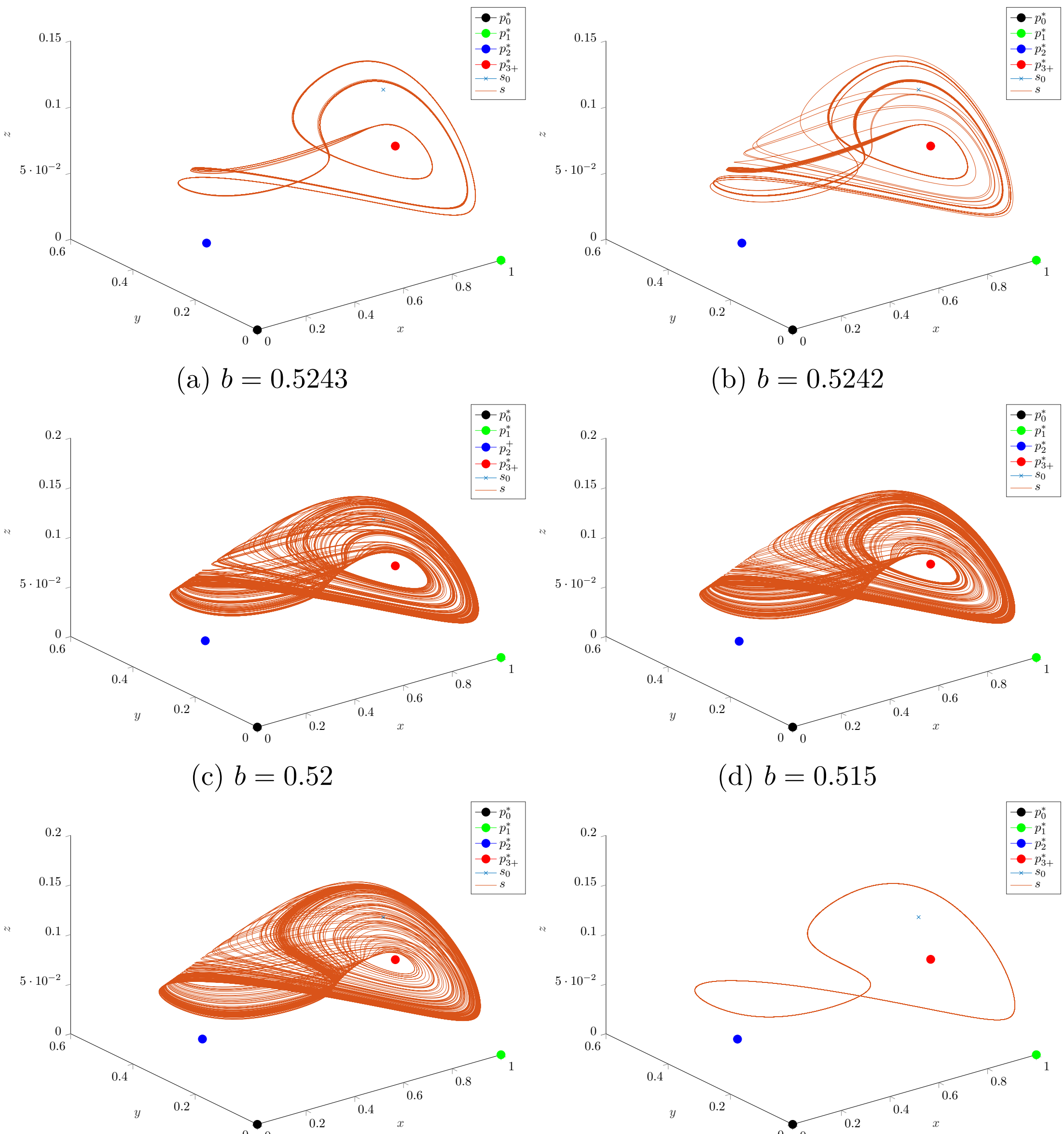
(c) $b = 0.529$ (d) $b = 0.527$

(e) $b = 0.5244$ (f) $b = 0.5243$

Figure D.2.1: Solutions on the time interval $[1000, 8000]$, showing the construction and destruction of the strange attractor in the window $b \in [0.5243, 0.532]$.

In Figure D.2.2 one can observe the phenomenon again in the approximate range $b \in [0.5091, 0.5243]$. Observe that the periodic orbit for $b = 0.5091$ only has a single loop, i.e. the period-halving cascade completely reverses somewhere in the range

[0.5091, 0.51] in this case. For the further windows [0.4751, 0.501] and [0.466, 0.475], see Figures D.2.3 and D.2.4.

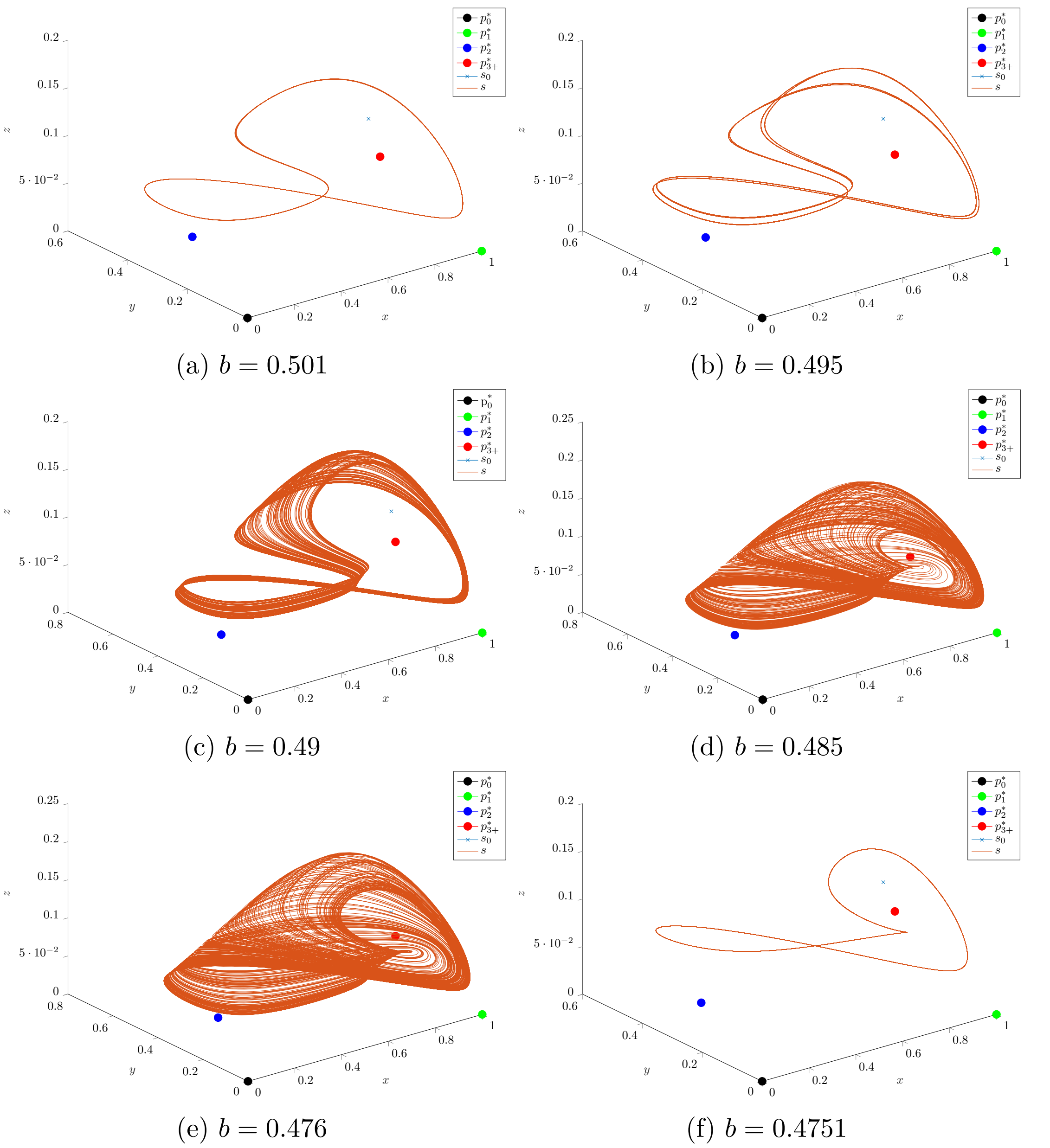


(a) $b = 0.5243$ (b) $b = 0.5242$

(c) $b = 0.52$ (d) $b = 0.515$

(e) $b = 0.51$ (f) $b = 0.5091$

Figure D.2.2: Solutions on the time interval [1000, 8000], showing the construction and destruction of the strange attractor in the window $b \in [0.5091, 0.5243]$.

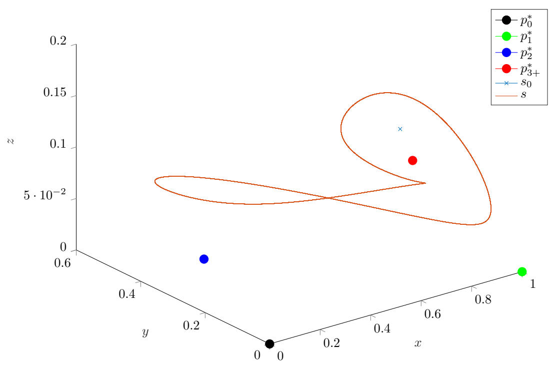


(a) $b = 0.501$ (b) $b = 0.495$

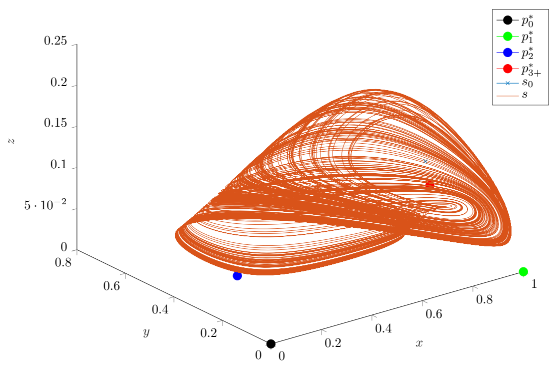
(c) $b = 0.49$ (d) $b = 0.485$

(e) $b = 0.476$ (f) $b = 0.4751$

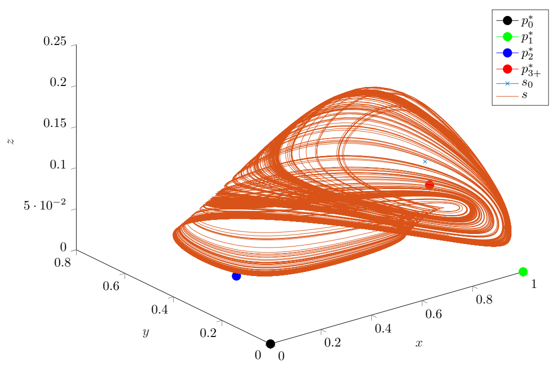
Figure D.2.3: Solutions on the time interval $[1000, 8000]$, showing the construction and destruction of the strange attractor in the window $b \in [0.4751, 0.501]$.



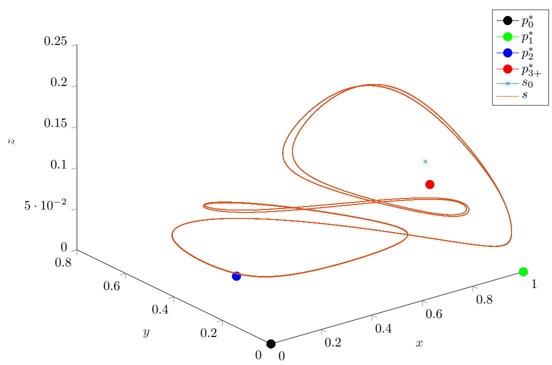
(a) $b = 0.475$



(b) $b = 0.47$



(c) $b = 0.468$



(d) $b = 0.466$

Figure D.2.4: Solutions on the time interval $[1000, 8000]$, showing the construction and destruction of the strange attractor in the window $b \in [0.466, 0.475]$.

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