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Reaction-diffusion-ODE systems: de-novo formation of irregular patterns and model reduction

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Related publications

- S. Härting, A. Marciniak-Czochra, and I. Takagi. Stable patterns with jump discontinuity in systems with turing instability and hysteresis. *submitted*, 2015. arXiv: 1506.00881.
- A. Marciniak-Czochra, S. Härting, G. Karch, and K. Suzuki. Dynamical spike solutions in a nonlocal model of pattern formation. *Preprint*, 2013. arXiv:1307.6236

To My Parents And My Godfather

Abstract

Classical models of pattern formation in *systems* of reaction-diffusion equations are based on diffusion-driven instability (DDI) of constant stationary solutions. The destabilisation may lead to emergence of stable, regular *Turing patterns* formed around the destabilised equilibrium. In this thesis it is shown that coupling reaction-diffusion equations with ordinary differential equations may lead to *de-novo* formation of *far from equilibrium* steady states. In particular, conditions for so called (ε_0, A)-stability (resp. stability in *epi-graph*-topology) are given, yielding from bistability and hysteresis effects in the null sets of nonlinearities.
A model exhibiting coexistence of Turing-type destabilisation and stable far from equilibrium steady states, is proposed. It is shown, under suitable conditions, that DDI and (in)stability can be derived from so called quasi-stationary model reduction. Moreover, similar to a result for ordinary differential equations, proved by Tikhonov, the dynamical behaviour of the reduced and the unreduced model are similar. It is shown that the spectral properties of the operators resulting from linearisation of the unreduced system, determining the long-term behaviour around a steady state, are reflected in the spectral properties of the operators resulting from linearisation of the reduced system. The given conditions are satisfied by a larger range of classical models, as illustrated by application to a degenerate version of the Lengyel-Epstein model.
The dynamical behaviour of reaction-diffusion equations for large diffusion and on finite time intervals is essentially reflected by their so called shadow systems. In this thesis, existence and stability of steady states with jump-type discontinuity is investigated and compared for this reduction. The results show that, in case of static patterns, not only the short-term behaviour, but also the long-term behaviour of the reduced system is reflected in the unreduced system. Moreover, a result showing Turing-type destabilisation for such shadow systems, given in a joint-paper, is generalised.
Finally, such shadow systems are reduced by application of a quasi-stationary model reduction leading to a *scalar* integro-differential equation. It is shown that the quasi-stationary model reduction is regular in the sense of Turing-type destabilisation and dynamical behaviour on finite time intervals. Hence, reaction-diffusion-ODE models may be reduced to scalar integro-differential equations in order to investigate the qualitative behaviour around homogeneous steady states and the qualitative behaviour on finite time intervals. A hypothesis is that the long-term behaviour is similar, but a proof is missing.
The result shows that a link between reaction-diffusion-ODE systems and scalar integro-differential equations exists and that the mechanisms of pattern formation may be investigated based on the reduction.

Zusammenfassung

Klassische mathematische Modelle zur Beschreibung von Musterbildungsprozessen basieren auf Turing Instabilität: ein örtlich homogener stationärer Zustand wird durch die zusätzliche Betrachtung von Diffusion destabilisiert. Diese Destabilisierung kann, unter entsprechenden Annahmen, zur Konvergenz gegen stationäre Zustände in der Nähe des Ursprungszustands (Turing Muster) führen. In der vorliegenden Arbeit wird gezeigt, dass die Kopplung von Reaktionsdiffusionsgleichungen mit gewöhnlichen Differenzialgleichungen zu einer neuartigen de-novo Bildung von Mustern mit Sprung-Unstetigkeiten führen kann. Es werden Bedingungen für sogenannte (ε_0, A)-Stabilität (auch: Stabilität in der Epigraphtopologie) gezeigt. Die Stabilität basiert auf Bistabilität und hysteretischen Effekten in der Nullstellenmenge der Nichtlinearitäten. Es wird ein Modell vorgestellt, das beides, Turing Destabilisierung und Existenz von (ε_0, A)-stabilen stationären Lösungen, die sich nicht in der Nähe des Ursprungszustands befinden, aufweist.
Des Weiteren wird gezeigt, dass es unter entsprechenden Voraussetzungen möglich ist, die Koexistenz von Turing Destabilisierung und Hysteresis auf Grundlage einer quasi-stationären Reduktion des Modells festzustellen. Ähnlich zur Tikhonov-Reduktion für gewöhnliche Differenzialgleichungen wird gezeigt, dass das dynamische Verhalten der Lösungen der Reaktionsdiffusionsgleichungen anhand des quasi-stationären Modells untersucht werden kann. Es wird gezeigt, dass die spektralen Eigenschaften, die das Langzeitverhalten um eine stationäre Lösung determinieren, ähnlich sind. Die in dieser Arbeit gezeigten Bedingungen für die Regularität in diesem Sinne werden von einer größeren Klasse von Gleichungen erfüllt, wie am Beispiel des Lengyel-Epstein Modells gezeigt wird.
In dieser Arbeit werden Existenz und Stabilität von stationären Lösungen mit Sprung-Unstetigkeiten für Shadowsysteme untersucht und mit Existenz und Stabiliät der ursprünglichen Systeme verglichen. Es zeigt sich, dass, im Falle stationärer Muster, nicht nur das Kurzzeitverhalten, sondern auch das Langzeitverhalten wiedergespiegelt wird. Des Weiteren wird ein Ergebnis aus einer gemeinsamen Veröffentlichung über Turing Destabilisierung in Shadowsystemen verallgemeinert.
Zuletzt wird gezeigt, dass eine quasi-stationäre Reduktion auf Shadowsysteme angewendet werden kann. Diese Reduktion ist regulär im Sinne der Turing Destabilisierung und auf endlichen Zeitintervallen. Für die resultierende skalare Integro-Differenzialgleichung wird gezeigt, dass sie eine Turing Instabilität aufweist und es werden Ergebnisse über das dynamische Verhalten präsentiert. Zusammenfassend wird gezeigt, dass das qualitative Verhalten von Lösungen bestimmter Reaktionsdiffusionsgleichungen auf Grundlage einer Reduktion zu skalaren Integro-Differenzialgleichung untersucht werden kann.

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Contents

1 Introduction

A huge variety of (de-novo) pattern formation can be observed in nature, such as symmetry breaking of mouse embryonic stem cell clusters [vdBBJB$^+$14], formation of vegetation on sand dunes [DW15], development of phenotypes of fruit flies [LJ89], extremity-formation in sea anemones [GM72], or stripe formation in zebra-fish [QP02]. Patterns have been observed in chemical reactions as well [LE91]. For a general survey, see [Mur02]. Recently, pattern formation processes have been used for the description of human diseases or human development, such as several types of cancer [FMV02], as well as in neurogenesis [LM10].
In this thesis, we describe two aspects of pattern formation using local properties of spatially homogeneous and spatially inhomogeneous equilibria: The first is destabilisation of a previous state of the system leading to a dynamically non-constant behaviour. The second is stability of the arising pattern. A third, non-local, property is the temporal connection of both local properties by the dynamical behaviour of the considered concentration or substance. We consider Turing-type destabilisation of spatially homogeneous stationary solutions, also called spatially homogeneous steady states. Moreover, we investigate stable patterns exhibiting hysteresis effects. Turing-type destabilisation means that a steady state is stable if inter- and intra-compartmental interaction is considered to be spatially local (i.e. no spatial interaction is considered), but is unstable if spatial interaction, such as diffusion, is considered. In general, Turing-destabilisation is a local phenomenon and does not answer questions about the dynamical behaviour after destabilisation. However, dynamical behaviour has been investigated for particular systems of reaction-diffusion equations considering nonlinear dynamics, for example in [GM72, HN15]. In a system with hysteresis, the output of a system does not solely depend on the input, but also on the history of the system. Depending on the history, the response to an input may be different. Here, different branches of steady states, which are not close to each other, are connected by the solution since it is continuous. The hysteretic effect takes place at the transition layer connecting the states. An example for sharp layers is a sharp gradient in morphogen concentration in drosophila, [MSHS07, AFZM15]. Especially, if properties (such as expression of a particular gene) are binary, sharp transition layers are important in order to not artificially introduce additional states through modelling. Two of the most common mathematical models used to describe pattern formation processes in developmental biology are reaction-diffusion equations and structured population models.

In [Tur52], Turing proposes activator-inhibitor models to model *de-novo* pattern formation. He shows that reaction-diffusion equations (RDE) consisting of one activator, i.e. $\partial f/\partial u > 0$, and one inhibitor, i.e. $\partial g/\partial v < 0$, such as

$$\begin{aligned} \frac{\partial}{\partial t}u(x,t) &= d_u \Delta_x u(x,t) + f(u(x,t), v(x,t)), && x \in I, t > 0, \\ \frac{\partial}{\partial t}v(x,t) &= d_v \Delta_x v(x,t) + g(u(x,t), v(x,t)), && x \in I, t > 0, \\ (u(0), v(0)) &\in C^2(\overline{I})^2, \\ \partial_n u, \partial_n v &= 0, && x \in \partial I, t > 0, \end{aligned} \tag{1.1}$$

with $d_u, d_v \geq 0$ and I being the spatial domain, can model spontaneous destabilisation of a spatially homogeneous steady state. The key idea is the combination of instability with respect to spatially inhomogeneous perturbation and stability with respect to spatially homogeneous perturbation.
Under structured population models in their simplest form, we understand systems of type

$$\begin{aligned} \frac{\partial}{\partial t}u(s,t) &= F(u(s,t), \int_{\Omega} G(u(\tau,t),\tau)d\tau), && s \in \overline{I}, t > 0, \\ u(0) &\in C(\overline{I}). \end{aligned} \tag{1.2}$$

Models of type (1.2) are also known to exhibit stable spatially inhomogeneous stationary solutions, [LP14], reflecting a distribution which is stable under certain environmental conditions. Exempli gratia, consider a population whose members have different types of genes and are not interacting or competing for space or nutrients. It is reasonable to assume that every sub-population tends to a steady state. However, considering inter-type interaction, such as competition for space or nutrients, these steady states may be destabilised and a different pattern may be established. An example for a change of stability through interaction, the ‘competitive exclusion’, is proposed for biology, see [Har60]. The same principle can also be shown by modelling competition systems of ordinary-differential equations (ODEs), see [Mur02]. Hence, structured population models may be interpreted as models of *de-novo* pattern formation as well. An important, even distinguishing, difference is that steady states of scalar reaction-diffusion equations have different stability properties. Considered with space-independent right-hand side and supplemented with homogeneous Neumann boundary conditions on a convex domain, the patterns are stable only if they are spatially homogeneous, see [Ni11], Theorem 2.6. This is not necessarily the case for models of type (1.2).

In this work, we focus on the following two aspects:

1. Consider a reaction-diffusion-ODE system,

$$
\begin{aligned}
\frac{\partial}{\partial t}u(x,t) &= f(u(x,t),v(x,t)), && x\in \overline{I}, t>0\\
\frac{\partial}{\partial t}v(x,t) &= D\Delta_x v(x,t) + g(u(x,t),v(x,t)), && x\in I, t>0\\
(u(0),v(0)) &\in (C(\overline{I})\times C^2(\overline{I})),
\end{aligned}
\tag{1.3}
$$

   supplemented with homogeneous Neumann boundary conditions for v. Can this system exhibit coexistence of Turing-type destabilisation and hysteresis, i.e. a spatially homogeneous steady state is destabilised due to introduction of diffusion and the solution converges towards a stable steady state with jump-type discontinuities? Moreover, do reaction-diffusion-ODE systems exhibit other patterns than reaction-diffusion systems?

2. In which sense are mathematical pattern formation processes in systems of type (1.3) linked to the formation of stable structure distribution in structured population models, i.e. systems of type (1.2)? Even though it may be scalar, does an integro-differential-type system reflect the qualitative properties a reaction-diffusion-ODE system? In particular, does such system exist for reaction-diffusion-ODE models in item 1.?

Modelling de-novo pattern formation with systems of reaction-diffusion equations has received intensive attention during the last decades, see e.g. [GM72, MM04, MWB+12, VE09] and references therein. In his seminal paper [Tur52], Turing proposes a linear system of reaction-diffusion equations whose spatially homogeneous steady state is stable with respect to spatially homogeneous perturbations, but unstable with respect to spatially inhomogeneous perturbations. In his paper, Turing shows that a system consisting of a slowly diffusing activator and a fast diffusing inhibitor is sufficient to observe this type of instability. Moreover, he suggests that this observation might not be limited to linear reaction-diffusion equations: it might be a ruling principle for more *general activator-inhibitor type* models. Depending on the type of the system, the solution may converge to a spatially inhomogeneous steady state. This phenomenon, *de-novo* formation of patterns, can be observed in a sea anemone like creature called hydra, see [GM72]. Hydras have axial body shape and the ends of the body are of different type. Hydra's so-called head has up to dozens of 'fibre like' tentacles used to collect nutrients. So-called feet lack such tentacles and are not used to collect nutrients. In [GM72], in order to explain the mechanism of head or foot formation, Gierer and Meinhardt postulate existence of a so-called 'positional value' determining the type of extremities. Assuming existence of such positional value, e.g. a chemical substance, the authors proposed a reaction-diffusion model for hydra's de-novo pattern formation. The model is based on Turing's

idea and exhibits regular patterns. For example, it has steady states corresponding to a positional value decreasing from one end of an interval to the other, reflecting a head-foot configuration. However, the model cannot explain the so-called ‘grafting experiment’: if a sufficient amount of ‘head cells’ of a hydra is transplanted to another position on the body (not to the foot), a head grows at this position while the original head regenerates, [Bro09]. This results in a hydra having two (or more) heads, presumably giving the polyp its name. The Gierer-Meinhardt model has been in the focus of discussion and investigation during the last four decades as a theoretical model for head and foot formation in hydra, e.g. in [Tak79, NW06, KW08, WW04, HY15]. In such activator-inhibitor models, the diffusion coefficient of the activator must be, by several orders of magnitude, smaller than the diffusion coefficient of the inhibitor. However, diffusion coefficients of diffusive substances in biological or chemical systems diffuse at similar rates or at least at rates which do not differ by orders of magnitude. This leaves open the question of applicability of the theoretically motivated Gierer-Meinhardt model and other systems consisting of reaction-diffusion equations only.
In [KCDB90], de Kepper et al give the first known experimental validation of Turing’s idea of pattern formation in activator-inhibitor systems of diffusive components. They consider a chemical reaction of activator-inhibitor type where both species diffuse at similar rates if there is no further interaction. The authors perform the experiment in a gel reactor which can be understood as binding to an almost non-diffusive substance. In [LE91], Lengyel and Epstein model these findings using a system of two reaction-diffusion equations. Since the molecules are not interacting if they are bound, the non-diffusive species does not act as activator, but as regulator of the diffusion coefficient of the activator. This is also shown by the authors of [KGM$^+$15] for the model in [LE91]. The drawback of this approach is that it appears that the resulting patterns are two times continuously differentiable and highly regular. For the Gierer-Meinhardt model in one-dimensional spatial domain, non-symmetric patterns of a distribution of spikes with two possible heights can be constructed, see [WW04]. However, these regular spikes appear to be unstable as numerical investigations of a Lyapunov-Schmidt reduction of a certain Gierer-Meinhardt model in [WW04] suggest. Moreover, the spikes are not irregularly distributed. For other models, stable patterns seem to be periodic or the position of irregularities predefined, [Tak79, NF87, NT90, HL99]. Consequently, de-novo formation of regular patterns can be described, but modelling of hydra’s grafting experiment remains an open question.
On the other hand, in [MC03], Marciniak-Czochra considered the case of an immobile activator, such as cells on a macroscopic scale producing growth factors. This results in a system of reaction-diffusion equations coupled to ordinary differential equations. Marciniak-Czochra shows that for an immobile activator (ODE) and diffusive inhibitor (RDE), diffusion-driven instability (DDI) can occur. In [Här11], based on the approach in [NF87], we construct

discontinuous steady states to a specific model of this type. In [MCKS13], the authors show analytically that these steady states are unstable. Numerical investigations of solutions in [HMC14] imply grow-up of solutions, i.e. blow up as time tends to infinity. Therefore, examples for reaction-diffusion-ODE models exhibiting diffusion-driven instability and grow-up can be found in these papers.
On the other hand, in [MCK06], Marciniak-Czochra presents a reaction-diffusion-ODE model which does not exhibit diffusion-driven instability, but shows a hysteresis-type pattern in numerical simulations. Stability of such patterns for another systems without diffusion-driven instability is shown by Köthe [Köt13] using a model-tailored approach.

We are interested in generalising conditions for stability of steady states with *jump-type* discontinuities. For a system with cross-diffusion, stability of steady states with jump-type discontinuities has been investigated in [Wei83] by Weinberger. We use the same topology and similar strategy of proof to obtain stability for steady states of more general reaction-diffusion-ODE systems. It is important to notice that both, diffusion-driven instability and stability of steady states with jump-type discontinuity are local properties. Consequently, we present a model with coexistence of diffusion-driven instability and hysteresis. Moreover, we show that a degenerated version of the model proposed in [LE91] exhibits this property as well. The jump-type discontinuities can be distributed irregularly. Hence, we are confident that our model can serve as a prototype model for coexistence of *de-novo* pattern formation and manipulation of patterns such as in the grafting experiment of hydra. However, the model's drawback is that in numerical simulations for very irregular ('high frequency') initial perturbation of the constant steady state, we observe that the arising pattern is irregular as well, and that its shape is similar to the shape of the initial conditions. On the other hand, patterns are not irregularly distributed for regular ('low-frequency') initial perturbations. The solution does not assume values of steady states of the kinetic system. Moreover, the arising pattern varies as the value of the diffusion coefficient varies and the jump-type discontinuities do not move. To be precise, we can arbitrarily reduce the measure of the domain on which they may move. Our conjecture is that the pattern observed in numerical simulations may be a Turing destabilisation induced pre-pattern. Then, the pre-pattern is followed by a 'hardening' of the pattern once it is point-wise sufficiently far away from the destabilised spatially homogeneous steady state. However, this is just a heuristic description.
The model in this thesis is different from the model with arbitrary small diffusion coefficient of the activator, i.e. diffusing u in (1.3). In [Rei14], Reichelt considers homogenisation for periodic coefficients of the right-hand side for a system of reaction-diffusion equations. The diffusion coefficient of the activator U as well as the coefficients depend on a scaling parameter. Let f, g, d_v in model (1.1) be independent from the scaling parameter, but assume that d_u tends towards zero. Reichelt's result implies that the solution converges towards the solution

of the limit system, i.e. the system for diffusion coefficient being equal to zero. Now, one is tempted to assume that the behaviour of reaction-diffusion-ODE systems may be merely an approximation of the behaviour of the corresponding system of reaction-diffusion equations for small diffusion coefficient. However, this argument is not unconditionally valid. Solutions converge uniformly on any finite time interval, but uniform convergence on $(0, \infty)$ cannot be proved in such generality since stability properties change.

In this thesis, we show that spatially inhomogeneous steady states with irregularly distributed jump-type discontinuities are stable. Simulations suggest that, even if very weak diffusion is introduced to the ODE-compartment, the dynamical behaviour changes qualitatively. The solution converges towards very regular, periodic Turing patterns. Therefore, our hypothesis is that the stability properties of patterns and the richness of patterns changes fundamentally in this limit. Mathematically speaking, the hypothesis is that for all stable (for $d_u = 0$) jump-type steady states, approximating sequences of steady states exist as d_u tends towards zero, but they are not necessarily stable.

In Turing-type models, it is uncommon to incorporate integral operators. However, for reaction-diffusion equations, linear integro-operators such as Hilbert-Schmidt-type operators are added to the diffusion operator, see e.g. [AC12] and references therein.
However, application of homogenisation techniques to cell population models with diffusive substances between cells can lead to systems of reaction-diffusion equations, in certain cases coupled to ordinary differential equations, see [MCP08]. As Turing already supposed in [Tur52], activators and inhibitors do not necessarily need to be modelled using reaction-diffusion equations. As mentioned above, non-local spatial operators may facilitate activation and inhibition by the same compartment at another spatial position. In structured population models, it is a popular approach to incorporate integral-operators in order to represent immediate interaction, e.g. in [LP14]. Classical models consider linear integral operators, such as Hilbert-Schmidt operators in order to model consumption of nutrients or in order to prevent a population from growing above its environmental capacity.In this dissertation, we investigate the question whether the qualitative properties *of* pattern formation in reaction-diffusion-models, is preserved under reduction to an integro-differential equations. If this is the case, RDEs can be investigated with the help of the reduced system. Particularly, this aspect is devoted to the investigation of links between systems of reaction-diffusion equations coupled to ordinary differential equations, such as (1.3), and structured population models of integro-differential type, i.e. systems of type (1.2). First, we consider quasi-steady state reduction of compartments described by ordinary differential equations. Then, we apply a so-called 'shadow system' approximation. Finally, the compartment of the shadow system which is described by an integro-differential equation is assumed to be in its steady state. We show that, under certain conditions on the nonlinearities, all these limits are regular in the

sense of existence of steady states and dynamical behaviour. Moreover, the first two are stable in the sense of stability-preservation of steady states. In particular, we consider

1. quasi-steady state approximation for reaction-diffusion-ODE models, where an ODE-compartment is in its steady state,
2. a shadow-system approximation for reaction-diffusion-ODE models, leading to a system of ordinary differential equations coupled to an integro-differential equation,
3. quasi-steady state approximation for the shadow-system, where the integro-differential equation is assumed to be in its steady state. This leads to a nonlinear *scalar* integro-differential equation.

The first two reductions are shown to be regular in the sense of stability-preservation. Concerning the last reduction, preservation of stability is analytically unknown, but numerical approximations suggest it.
Throughout this work, we assume twice continuously differentiable kinetic terms and assume that solutions are uniformly bounded on the time-interval $(0, \infty)$ in $L^\infty(\Omega)$-topology, where Ω denotes the spatial domain. We are interested in the question whether

- Turing-type instability,
- existence and stability of qualitatively similar steady states,
- dynamical behaviour on finite time intervals,

are invariant under the previously described reductions. Under certain conditions on the right-hand side, a system and its quasi-steady state approximation can be rewritten as a system with fewer compartments, having exactly the same steady states. In [Tik52][1], Tikhonov shows for the *kinetic* (ODE) system that the solution of the unreduced system converges almost uniformly towards the solution of the quasi-steady state reduction on any finite time interval in the so-called Tikhonov limit. Since Tikhonov's result holds for finite time, it does not imply 'transfer of stability', only of instability. We extend this result to reaction-diffusion-ODE systems. Hence, instability is invariant under quasi-steady state approximation if the equation for the reduced component has a unique global attractor for any given value of the other components. In [Hop66], Hoppenstaedt extends Tikhonov's result to the time interval $\mathbb{R}_+$ if the solution is close to an exponentially stable steady state. We give an alternative proof for this, considering the spectrum directly. We consider the spectra of the linearised operators of the reduced and the unreduced system and show that they converge towards each other under

[1] The paper is in Russian and is usually referred to within this context. The result can be found in [BL14].

Tikhonov reduction. Consequently, under suitable conditions, Turing-type instability of the quasi-steady state approximation implies Turing-type instability of the unreduced system for sufficiently fast reaction of the reduced component. We show invariance of stability of spatially inhomogeneous steady states under quasi-steady state reduction under stricter conditions only. In particular, we restrict it to one RDE coupled to two ODEs. The investigations are based on stability investigations undertaken in order to construct the model with coexistence of DDI and hysteresis. The next reduction, a shadow-system approximation, leads to consideration of systems of type

$$\frac{\partial}{\partial t}u(t,x) = f(u(t,x), v(t,x)), \qquad x \in \overline{\Omega}, t > 0, \tag{1.4}$$

$$\frac{\partial}{\partial t}\xi(t) = \int_{\Omega} g(u(t,x), \xi(t))dx, \qquad t > 0, \tag{1.5}$$

$$(u(0), \xi(0)) \in (C(\overline{\Omega}) \times \mathbb{R}), \tag{1.6}$$

arising as limit system for arbitrarily large diffusion coefficient of v in model (1.3) (now substituted by ξ). The limit, first proposed by Keener in [Kee78] for the stationary problem of systems of reaction-diffusion equations, i.e. for $d_u, d_v > 0$ in (1.3), has been in the focus of research for several decades, see for example [NTY01] or, for a survey, [Ni11] and references therein. However, the shadow systems, i.e. the dynamical problem, can exhibit *very* different behaviour from the original system. In [LN09], the authors show for a particular system that, under certain conditions, the original system has a global solution and the shadow system has not. Whereas this limit is studied for diffusive u, we study the case of non-diffusive u. We investigate, analogously to the quasi-steady state approximation, whether the properties of these steady states are reflected by steady states of the shadow system. We generalise findings in [MCHKS13] concerning Turing-type instability (in this context called 'integro-driven instability') and show that coinciding conditions for Turing-type instability exist. Furthermore, we investigate existence and stability of spatially inhomogeneous steady states and compare them to the conditions for reaction-diffusion-ODE systems. The investigation is restricted to few components and shows that common conditions for existence and stability of steady states of reaction-diffusion-ODE systems and their shadow systems exist. The dynamical behaviour under reduction is addressed in [MCHKS13], where almost uniform convergence on any finite time interval is shown. The result has been generalised by Bobrowski in [Bob15]. Patterns of shadow-systems presented in this work are qualitatively different from patterns of shadow systems of reaction-diffusion systems. Spatially non-monotone steady states of shadow systems of reaction-diffusion systems are unstable, as shown in [NPY01]. In this work, we show that steady states of shadow systems of reaction-diffusion-ODE systems with

multiple jump-points can be stable. Hence, they are non-monotone *and* stable. This leads to an additional result for reaction-diffusion-ODE systems: Combined with the result of [Bob15] respectively [MCHKS13], breakdown of patterns in case of introduction of small diffusion to u in (1.3) appears analytically plausible for large diffusion coefficient of the inhibitor.
Finally, we apply a quasi-steady state approximation to compartment ξ in system (1.4)-(1.5) and show that Turing-type instability is preserved under reduction assuming suitable conditions. Moreover, we show that the solution of the unreduced system converges almost uniformly on any finite time interval towards the solution of the quasi-steady state approximation.
The quasi-steady state approximation is a scalar structured population model of type (1.2). Hence, Turing-type instability and dynamical behaviour (on any finite time interval) of the solution of the reduced model qualitatively reflects that of the solution of the unreduced model. For parameters sufficiently large/small (i.e. 'close to the limit'), Turing-type instability can be deduced from the reduced system. Moreover, investigation of the dynamical behaviour of a scalar integro-differential equation may be easier than investigation of the dynamical behaviour of the solution of the reaction-diffusion-ODE model. Reaction-diffusion equations may, under suitable conditions on different time-scales and strength of diffusion, behave similar to structured population models.
We apply all reductions to the system proposed in order to investigate the first aspect of this work. The model satisfies all conditions for the Tikhonov-type results with and without spatial operators and for regularity of the shadow limit. We investigate the dynamical behaviour the reduced system, showing that the solution cannot decay for suitable initial conditions, but decays on parts of the spatial domain. This strengthens numerical investigations showing that the Turing-type destabilisation and the stable steady states with jump-type discontinuity may be connected in time by the dynamical behaviour.

1.1 Outline of the thesis

In **chapter 2**, we give a brief overview of the used notation. *We recommend to read this chapter consisting of two pages before reading the other chapters.*

In **chapter 3**, we investigate reaction-diffusion-ODE systems and prove existence of steady states with jump-type discontinuities on one-dimensional spatial domain in Lemma 3.6. In Theorem 3.9, we give general conditions for stability of discontinuous steady states in so-called (ε_0, A)-topology as defined in Definition 3.8. More precise, 'hands-on', conditions are given in Lemma 3.10. The (ε_0, A)-topology has been introduced before by Weinberger in [Wei83]. Moreover, we reintroduce the notion of diffusion-driven instability as generalised by Marciniak-Czochra for reaction-diffusion-ODE systems in [MC03]. Finally, in Section 3.6 we present a system, (3.92)-(3.94), of one reaction-diffusion equation coupled to one

ordinary differential equations exhibiting both local properties: diffusion-driven instability and existence of stable steady states with jump-type discontinuities. The results about this system are summarised in Theorem 3.21. Moreover, we show that the so-called 'Epstein model', (3.166)-(3.169), exhibits coexistence of diffusion-driven instability (DDI) and hysteresis as well. Since these analytical findings are valid only in the neighbourhoods of the destabilised spatially homogeneous steady state and the stable spatially inhomogeneous steady states, the dynamical behaviour remains unknown. Hence, we present numerical results in Subsection 3.6.3 showing that, indeed, the solution converges towards a spatially inhomogeneous steady state with jump-type discontinuity and not towards the stable trivial steady state.
Both systems investigated in Section 3.6 arise as quasi-steady state approximations of systems of two ordinary differential equations coupled to one reaction-diffusion equation. Several ideas have been published in [HMCT15]. However, some of them are generalised in this thesis.

In **chapter 4**, we investigate whether diffusion-driven instability and stability of discontinuous steady states is invariant under quasi-steady state approximation. We extend Tikhonov's result for ordinary differential equations, [Tik52], in Lemma 4.2 by showing that stability of steady states is invariant as well. Hence, DDI is invariant. Moreover, in Lemma 4.5, we show that a Tikhonov-type result holds true for reaction-diffusion-ODE systems on any finite time interval. In Lemma 4.7, we show that under certain conditions, stability of steady states of the unreduced reaction-diffusion-ODE system can be deduced from stability of steady states of the quasi-steady state approximation. However, we investigate the case that a system consisting of two ODEs coupled to one RDE is reduced to a system of one ODE and one RDE. We limit investigation due to the vast technical effort rather than due to counterexamples. In Subsection 4.5, we apply these findings to the examples investigated in Subsection 3.6. The findings are illustrated by numerical results in Subsection 4.5.3.

In **chapter 5**, we investigate the so-called 'shadow system'. In [MCHKS13], it was shown for reaction-diffusion-ODE systems that the solution converges almost uniformly on any finite time interval towards the solution of the shadow system as the diffusion coefficient tends towards infinity. The result by Bobrowski is stated as Proposition 5.1. Shadow systems are systems of type (1.4)-(1.6). Hence, we define integro-driven instability as analogy to DDI in Definition 5.2. Due to our result in [MCHKS13] and Bobrowski's Theorem 5.1, instability of steady states of the shadow-system implies instability of steady states of the reaction-diffusion-ODE system. Hence, we give conditions for instability of spatially homogeneous steady states in Lemma 5.3. Since the kinetic system of a reaction-diffusion-ODE system and its shadow system coincide, integro-driven instability follows. In Section 5.4, we investigate existence of steady states of shadow-systems and show in Corollary 5.4 that existence of a steady state of the shadow system implies existence of steady states of the reaction-diffusion-ODE system in a neighbourhood of the steady state. Moreover, stability conditions for steady states of shadow-systems are given in Lemma 5.6 and Theorem 5.8. Since stability conditions resemble those for reaction-diffusion-ODE systems, sufficiently regular right-hand side of the kinetic system allows to deduce existence of stable discontinuous steady states of the reaction-diffusion-ODE system. In Section 5.7, we apply the results to the example systems and illustrate the findings with numerical approximations in Subsection 5.7.3.

In **chapter 6**, we investigate system (6.12) which results from a quasi-steady state approximation of (1.4)-(1.6), where $\int_\Omega g(u(x,t),\xi(t))dx = 0$ is assumed. Again, a Tikhonov-type results holds true for this class of systems, as shown in Lemma 6.2. Existence for the example system is shown in Lemma 6.1. Moreover, systems of this type can exhibit integro-driven instability, see Lemma 6.3. System (6.25)-(6.26) exhibits integro-driven instability as shown in Corollary 6.4. For the scalar integro-differential equation, we show that the solution stays strictly positive in L^∞-topology and provide a lower limit in Theorem 6.7. Hence, this result holds true on any finite time interval for the solution of the reaction-diffusion-ODE system for sufficiently large diffusion and sufficiently fast reaction of certain compartments. This is summarised in Theorem 6.9.

2 Important preliminaries and notation

In this section, we give an overview over some of the used notation and important preliminaries. $\Omega \subset \mathbb{R}^n$ denotes a convex, bounded domain. $I = (a,b)$ denotes a bounded interval.
In case of compartments of systems of equations, we use capital letters for compartments if considering them to be vector-valued, i.e. $U = (u_1, ..., u_{\dim(U)})$ and analogously for $V, W, \Xi, U^\delta, V^\delta, W^\delta, \Xi^\delta$. *$U_i$ does not describe a component of U, but different, possibly vector-valued Us.* Lower case letters for compartments describe scalar compartments, i.e. $u, v, w, \xi, u^\delta, v^\delta, w^\delta, \xi^\delta$.
Steady states which are not necessarily spatially homogeneous, i.e. can be spatially inhomogeneous, are denoted $\tilde{\cdot}$, e.g. $\tilde{U}, \tilde{v}$. Spatially homogeneous steady states are denoted $\bar{\cdot}$, e.g. $\overline{U}, \overline{v}$. If proving a result for generic systems, we assume throughout this manuscript that all solutions are uniformly bounded, i.e. $\|U\|_{L^\infty(0,T;L^\infty(I))} < \infty$ respectively $\|U\|_{L^\infty(0,T;L^\infty(\Omega))} < \infty$, where $T = \infty$ if not specified differently. We assume that all zero-order-terms f, g, h are *twice continuously differentiable* on the closure of the set of values assumed by the solution. f, g, h can be both, vector-valued and scalar. Whether they are vector-valued or not, can be seen from whether vector valued compartments are used or not.
By *classical initial conditions*, we mean $u(t=0) \in C(\overline{I})$ or $u(t=0) \in C(\overline{\Omega})$, if the dynamics of $u(t,x)$ is described by an ordinary differential equation in each $x \in I$ respectively $x \in \Omega$. Moreover, we mean by *classical initial conditions* that $u(t=0) \in C^2(\overline{I})$ or $u(t=0) \in C^2(\overline{\Omega})$ if the dynamics of $u(t)$ is described by a reaction-diffusion equation.
For functions $f(U,V,W), g(U,V,W), h(U,V,W)$, we define the matrix
$\nabla_U f(A,B,C) := (\partial f_j(u_1, ..u_n, v_1, ..v_m)/\partial u_i(A,B,C))_{ij}$, sometimes also denoted $\nabla_U f|_{(A,B,C)}$. $\nabla_V f(A,B,C)$, $\nabla_W f(A,B,C), \nabla_U g(U,V,W), ...$ are defined analogously. In case of scalar u,v or w and $f(u,v,w)$, the notation $\partial_1 f(a,b,c)$ is equal to $\partial f(u,v,w)/\partial u(a,b,c)$. Symbols $\partial_2 f(a,b,c)$ and $\partial_3 f(a,b,c)$ are defined analogously. The Laplace operator is denoted Δ or Δ_x, while $\nabla_x u(x)$ denotes the Jacobian matrix with respect to the spatial variable. D_1, D, if used as coefficients of Δ, denote non-negative constants if the corresponding compartment is scalar and diagonal matrices with non-negative entries if the corresponding compartment is vector-valued. If the compartment is vector-valued $D_1, D > 0$ means that all entries of the main diagonal are positive. A non-exhaustive list of symbols is given at the end of the thesis. Throughout the thesis, we assume that the following assumption is satisfied by all

compartments. Under *kinetic system* of a system of type (1.3), we understand the ordinary differential equation resulting when setting all diffusion coefficients equal to zero. We call the right-hand side of the kinetic system *zero-order term* or *kinetic term*. Under *jump-type steady states* or *steady states with jump-discontinuity*, we understand steady states constructed in Lemma 3.17.

Assumption 2.1.

1. *$U = (u_i)_i$, $V = (v_i)_i$, $W = (w_i)_i$, $\Xi = (\xi_i)$,.. are uniformly bounded, i.e. there exist constants $U_{\min}, U_{\max}, V_{\min}, V_{\max} \in \mathbb{R}$, such that*

$$-\infty < U_{\min} \leq \min_{1\leq i \leq \dim(U)} \inf_{(t,x)\in\mathbb{R}_{\geq 0}\times I} u_i(t,x) \leq \max_{1\leq i \leq \dim(U)} \sup_{(t,x)\in\mathbb{R}_{\geq 0}\times I} u_i(t,x) \leq U_{\max} < \infty,$$
$$-\infty < V_{\min} \leq \min_{1\leq i \leq \dim(V)} \inf_{(t,x)\in\mathbb{R}_{\geq 0}\times I} v_i(t,x) \leq \max_{1\leq i \leq \dim(V)} \sup_{(t,x)\in\mathbb{R}_{\geq 0}\times I} v_i(t,x) \leq V_{\max} < \infty.$$

   and for W, $\Xi, u, v, w, \xi, u^\delta$, .. analogously.

2. *f, g, h are twice continuously differentiable in all increments on the set of assumed values of their increments.*

3. *Initial functions are classical initial conditions.*

3 Reaction-diffusion-ODE systems

In this chapter, we present results on systems of type

$$\begin{aligned} \frac{\partial U}{\partial t}(x,t) &= f(U(x,t),V(x,t)), && x \in \overline{I}, t > 0, \\ \frac{\partial V}{\partial t}(x,t) &= D\Delta V + g(U(x,t),V(x,t)), && x \in I, t > 0, \\ (U(0),V(0)) &\in (C(\overline{I})^{\dim(U)} \times C^2(\overline{I})^{\dim(V)}), \end{aligned} \tag{3.1}$$

supplemented with homogeneous Neumann boundary conditions for V, i.e.

$$\partial_n v_i(x,t) = 0, \quad x \in \partial I, t > 0, \tag{3.2}$$

for $V = (v_1, ...v_{\dim(V)})$. In general, U and V can be vector-valued. When giving specific conditions for stability of steady states, we restrict analysis to scalar V and U being either scalar or (in chapter 4) of low dimension, i.e. $U = (u_1, u_2)$. *If U respectively V are scalar, we denote them u respectively v.* First, we are concerned with so called *de-novo pattern formation*. It means that

1. there exists a stable steady state $(\overline{U}, \overline{V})$ of the kinetic system ($D = 0$) of (3.1), which becomes unstable if diffusion is introduced, i.e. for $D > 0$, and

2. there exists a stable spatially inhomogeneous steady state of (3.1)-(3.2) for $D > 0$, which we call *stable pattern*.

For scalar u and v, Marciniak-Czochra et al give sufficient conditions on instability of both spatially homogeneous and spatially inhomogeneous steady states of systems of type (3.1)-(3.2) in [MCKS13]. In [KBHG12], the authors give sufficient conditions for a spatially homogeneous steady state to be unstable for $D > 0$. The conditions are similar to the concept of 'unstable subsystems' for diffusive U and V in [ASY12], meaning that the matrix $(\partial_{u_j} f_i|_{(\overline{U},\overline{V})})_{ij}$ has an eigenvalue with positive real part. In case of systems of one ordinary differential equation coupled to one reaction-diffusion equation, it is well known that auto-catalysis of the non-diffusive component, i.e. $\partial_u f|_{(\overline{u},\overline{v})} > 0$, is necessary since the system has to satisfy the so called 'compensation condition', $\partial_u f|_{(\overline{u},\overline{v})} + \partial_v g|_{(\overline{u},\overline{v})} < 0$, due to stability with respect to homogeneous perturbations. We recall these results and give conditions for stability of spatially inhomogeneous steady states of systems of type (3.1)-(3.2), assuming that $U = u$ and $V = v$ are scalar (for $U = (u_1, u_2)$, see chapter 4) and I is a bounded interval. Unfortunately, the use of a Sobolev-type estimate yields a restriction of the proof to one-dimensional spatial domain. It is unknown to us whether the restriction on dimension can be weakened or not, but numerical investigations of an example system suggest that there exist stable steady in higher dimension. Also, stability in L^2-topology, which is weaker than the topology used for one-dimensional spatial domain, can be deduced from the proof.

3.1 Existence of solutions to reaction-diffusion-ODE systems

For classical initial conditions $(U(0), V(0)) \in (C^\alpha(I)^{\dim(U)} \times C^{2+\alpha}(I)^{\dim(V)})$, local existence of classical solutions of the same spatial regularity yields from Assumption 2.1 (2.), see [Rot84]. If, in addition, the local solution satisfies Assumption 2.1 (1.), it can be extended onto the time interval $\mathbb{R}_{\geq 0}$. Even though Assumption 2.1(1.) is rather strong, a violation of this condition can lead to nonexistence of classical solutions, such as blow-up in finite time, see e.g. [Bal77]. An example for grow-up (blow-up as time tends to infinity) has been given in [MCKS15], where the authors show grow-up of solutions to the Grey-Scott model with trivial diffusion coefficient of the compartment u. The Grey-Scott model has uniformly bounded solutions for positive diffusion coefficient of the activator.

3.2 Diffusion-driven instability

In [Tur52], Turing introduced the notion of diffusion-driven instability for linear systems of two reaction-diffusion equations,

$$\frac{\partial u}{\partial t} = D_1 \Delta u + f(u, v), \qquad x \in I, t > 0, \tag{3.3}$$

$$\frac{\partial v}{\partial t} = D \Delta v + g(u, v), \qquad x \in I, t > 0, \tag{3.4}$$

$$(u(0), v(0)) \in C^2(I)^2, \tag{3.5}$$

$$\partial_n u = \partial_n v = 0, \qquad x \in \partial I, t > 0. \tag{3.6}$$

Turing defines diffusion-driven instability as the property of a system of type (3.3)-(3.6) having a homogeneous steady state which is

1. stable with respect to homogeneous perturbation, i.e. is a stable steady state for $D_1 = D = 0$,

2. unstable with respect to inhomogeneous perturbation, i.e. is an unstable steady state for some $D_1, D > 0$.

We follow the definition in [MC03], where Marciniak-Czochra adapts the notion of DDI for some diffusion coefficients being trivial. She gives the following definition:

Definition 3.1. *A system of type* (3.3)-(3.6) *exhibits* ***diffusion-driven instability*** *if there exists a homogeneous steady state which is*

- *stable for* $D_1 = D = 0$,
- *unstable for some* ($D_1 > 0$ *and* $D \geq 0$) *or* ($D_1 \geq 0$ *and* $D > 0$).

This weakening of the notion of diffusion-driven instability facilitates modelling of immobile or non-diffusive substances. The solution to the resulting system of ordinary differential equations describes their concentration. Examples are cells, see [MRJ+12, Ham12] and references therein, or chemically 'immobilised' molecules. Such 'pinned' molecules were shown to facilitate formation of a Turing type pattern in a gel reactor, [KCDB90]. However, the result in [KCDB90] actually considers the case D_1 small, but positive and $0 < D$ large.
Recently, this type of diffusion-driven instability has drawn further attention, [KGM+15, KBHG12, Rei14]. In [KBHG12], the authors consider homogeneous steady states $(\overline{U}, \overline{V})$ of a system of type (3.1) with $D_1 = 0$ and show that if the spectrum of $\nabla_U f = (\partial_{u_j} f_i|_{(\overline{U},\overline{V})})_{ij}$ contains an eigenvalue with positive real part, then this steady state is unstable for all $D > 0$.
We will recall the result that a system of one ordinary differential equation and one reaction-diffusion equation exhibits diffusion-driven instability only if $\partial_u f|_{(\overline{u},\overline{v})} > 0$ is satisfied. This is a direct consequence of Theorem 3.9 which shows that $\partial_u f|_{(\overline{u},\overline{v})} < 0$ implies stability for $\partial_v g|_{(\overline{u},\overline{v})} < 0$ and $(\partial_u f \partial_v g - \partial_v f \partial_u g)|_{(\overline{u},\overline{v})} > 0$.
First, we investigate destabilisation of spatially homogeneous steady states and state a reformulation of a lemma in [KBHG12] for matrices,

Lemma 3.2 ([KBHG12])**.** *Given a quadratic block matrix of type*

$$M_k = \begin{pmatrix} A & B \\ C & D - k^2 \operatorname{id}_{\mathbb{R}^m} \end{pmatrix}, \tag{3.7}$$

where $k \in \mathbb{R}, A \in \mathbb{R}^{n,n}, B \in \mathbb{R}^{n,m}, C \in \mathbb{R}^m, D \in \mathbb{R}^{m,m}$ *and* $\operatorname{id}_{\mathbb{R}^m}$ *is the identity on* $\mathbb{R}^m$. *There exists an injective mapping from the spectrum* $\sigma(A)$ *of* A *into the spectrum* $\sigma(M_k)$ *of* M_k,

$$\begin{aligned} c : \sigma(A) &\to \sigma(M_k), \\ \lambda &\mapsto c(\lambda)_k, \end{aligned}$$

such that for all $\lambda \in \sigma(A)$*, it holds that* $c(\lambda)_k \to \lambda$ *as* $k \to \infty$*. For all* $\lambda_k \in \sigma(M_k) \setminus c(\sigma(A))$*, it holds* $\mathrm{Re}(\lambda_k) \to -\infty$ *as* $k \to \infty$*.*

Proof. See [KBHG12], section 2. □

We apply Lemma 3.2 to system (3.1)-(3.2):

Lemma 3.3. *Consider system* (3.1)-(3.2)*. Denote the linearisation of the kinetic system around a constant steady state* $(\overline{U}, \overline{V})$ *by*

$$\mathcal{A} = \begin{pmatrix} \nabla_U f|_{(\overline{U},\overline{V})} & \nabla_V f|_{(\overline{U},\overline{V})} \\ \nabla_U g|_{(\overline{U},\overline{V})} & \nabla_V g|_{(\overline{U},\overline{V})} \end{pmatrix},$$

where $\nabla_U f|_{(\overline{U},\overline{V})} = (\partial_{u_j} f_i|_{(\overline{u},\overline{v})})_{ij}$ *and* $\nabla_U g|_{(\overline{U},\overline{V})}, \nabla_V f|_{(\overline{U},\overline{V})}, \nabla_V g|_{(\overline{U},\overline{V})}$ *analogously. Consider the operator* $\mathcal{L}$*, defined by*

$$\mathcal{L} : \begin{pmatrix} \varphi \\ \psi \end{pmatrix} \mapsto \begin{pmatrix} \nabla_U f|_{(\overline{U},\overline{V})}\varphi + \nabla_V f|_{(\overline{U},\overline{V})}\psi \\ \nabla_U g|_{(\overline{U},\overline{V})}\varphi + \nabla_V g|_{(\overline{U},\overline{V})}\psi + D\Delta\psi \end{pmatrix},$$

as operator in $(L^p(I))^{\dim(\varphi)+\dim(\psi)}$ *with domain* $(L^p(I))^{\dim(\varphi)} \times (W^{2,p}(I))^{\dim(\psi)}$*. If* $\nabla_U f$ *has an eigenvalue with positive real part and no eigenvalue with trivial real part, the steady state* $(\overline{U}, \overline{V})$ *is unstable.*

Proof. Linear combinations of vectors multiplied by eigenfunctions of the weak Laplace operator with homogeneous Neumann boundary conditions, denoted $\Delta_{w,N}$, form an orthonormal basis of $(L^p(I))^{\dim(\varphi)+\dim(\psi)}$ which is L^p-dense in the domain.Therefore, it is possible to investigate the eigenvalue problem

$$\begin{pmatrix} \nabla_U f|_{(\overline{U},\overline{V})} & \nabla_V f|_{(\overline{U},\overline{V})} \\ \nabla_U g|_{(\overline{U},\overline{V})} & \nabla_V g|_{(\overline{U},\overline{V})} - D\lambda_k \end{pmatrix} \begin{pmatrix} e_1 \\ e_2 \end{pmatrix} = \lambda \begin{pmatrix} e_1 \\ e_2 \end{pmatrix}, \tag{3.8}$$

for any eigenvalue-eigenfunction pair (λ_k, ψ_k) of $\Delta_{w,N}$ in $L^p(I)$. A solution (λ, c) yields the following solution to the eigenvalue problem (3.8),

$$\left(\lambda, \begin{pmatrix} c_1\psi_k \\ c_2\psi_k \end{pmatrix}\right). \tag{3.9}$$

Since $\nabla_u f$ has an eigenvalue with positive real part and no eigenvalue with trivial real part, application of Lemma 3.2 yields existence of a k^*, such that the matrix in (3.8) has at least one eigenvalue with positive real part and no eigenvalue with trivial real part for all $k > k^*$. Consequently, the Hartman-Grobman theorem can be applied for initial conditions $(c_1\psi_k, c_2\psi_k)$, leading to nonlinear instability. □

Additionally, necessary conditions for DDI is stability under absence of diffusion. Under absence of diffusion, the system is a nonlinear system of ordinary differential equations and the Hartman-Grobman theorem can be applied if all eigenvalues have non-trivial real part. From this, the following well known fact follows: A system of one ordinary differential equation coupled to one reaction-diffusion equation exhibits diffusion-driven instability at a steady state $(\overline{u}, \overline{v})$ if the Jacobian matrix of the kinetic system has only eigenvalues with negative real part and the non-diffusive substance, described by the ODE, is auto-catalytic, i.e. $\partial_u f|_{(\overline{u},\overline{v})} > 0$ holds.

Lemma 3.4. *Consider a system of type,*

$$\frac{\partial u}{\partial t} = f(u,v), \qquad x \in \overline{I}, t > 0, \tag{3.10}$$

$$\frac{\partial v}{\partial t} = D\Delta v + g(u,v), \qquad x \in I, t > 0, \tag{3.11}$$

$$(u(x,0), v(x,0)) \in (C(\overline{I}) \times C^2(\overline{I})), \tag{3.12}$$

$$\partial_n v = 0, \qquad x \in \partial I, t > 0. \tag{3.13}$$

System (3.10)-(3.13) *exhibits diffusion-driven instability at a constant steady state* $(\overline{u}, \overline{v})$ *if*

$$\left.\frac{\partial f}{\partial u}\right|_{(\overline{u},\overline{v})} > 0 \text{ and } \left.\left(\frac{\partial f}{\partial u}\frac{\partial g}{\partial v} - \frac{\partial f}{\partial v}\frac{\partial g}{\partial u}\right)\right|_{(\overline{u},\overline{v})} > 0 \text{ and } \left.\left(\frac{\partial f}{\partial u} + \frac{\partial g}{\partial v}\right)\right|_{(\overline{u},\overline{v})} < 0, \tag{3.14}$$

hold, where the derivatives are evaluated at the steady state $(\overline{u}, \overline{v})$*. If one of the two last inequalities is reversed (i.e. excluding the case of assuming value zero), no DDI occurs.*

Remark 3.5. *In Theorem 3.9 and Lemma 3.10, we prove that any weak steady state* $(\tilde{u}, \tilde{v})$ *of class* $BV(\overline{I}) \times \{\tilde{v} \in C^1(I) \,|\, \tilde{v}'' \in BV(\overline{I})\}$ *is stable if* $\frac{\partial f}{\partial u}|_{(\tilde{u},\tilde{v})}, \frac{\partial g}{\partial v}|_{(\tilde{u},\tilde{v})} \leq c < 0$ *and* $(\frac{\partial f}{\partial u}\frac{\partial g}{\partial v} - \frac{\partial f}{\partial v}\frac{\partial g}{\partial u})|_{(\tilde{u},\tilde{v})} \geq c > 0$ *hold for all* $x \in \overline{I}$*, where the derivatives are evaluated at the steady state.*

Proof. In case of homogeneous perturbations (φ, ψ), it holds $\Delta\psi = 0$. Therefore, the spectrum of the linearised operator considered on the subset of spatially constant functions coincides with the spectrum of the kinetic system. Consequently, according to the Hartman-Grobman theorem, the second and third condition are necessary and sufficient for stability with respect to homogeneous perturbations, see e.g. [Tes12]. In case of spatially inhomogeneous perturbation, application of Lemma 3.2 yields linear instability. Nonlinear instability can be conducted on a Hartman-Grobman type result for systems of reaction-diffusion equations, see e.g. [Smo83], which covers the case of trivial diffusion coefficients.

□

In case of vector-valued U, DDI can also occur if the spectrum of $\nabla_U f|_{(\overline{U},\overline{V})}$ consists only of eigenvalues with negative real part, as it was shown by examples in e.g. [KBHG12, MC03]. However, in this work, we restrict analysis to systems with DDI caused by 'unstable systems' in the sense of [ASY12], i.e. we exclude the case that all elements of spectrum of $\nabla_U f|_{(\overline{U},\overline{V})}$ have negative real part. Hence, we exclude the case in which only a finite number of eigenvalues has positive real part, see Lemma 3.2.

3.3 Existence of irregular steady states

In this section we show existence of infinitely many weak steady states on a finite interval. All constructed steady states have representatives in $BV(\overline{I}) \times C^1(\overline{I})$. It is important to note that this method provides weak steady states which do not necessarily have representatives in $C(\overline{I}) \times C^2(\overline{I})$. The construction method resembles the so called shooting method used to approximate solutions to one-dimensional boundary value problems numerically. The result states that it is sufficient to find two branches of solutions to the steady state equation of the ODE subsystem for which the kinetics term of the steady state equation of the reaction-diffusion subsystem has different a sign. Moreover, under these conditions, a system of ordinary differential equations coupled to one reaction-diffusion equation exhibits infinitely many steady states of this type. The proof is based on the multiple shooting method and the basic idea has been applied to a specific system of one ordinary differential equation coupled to one specific reaction-diffusion equation in [MTH80]. Another specific model has been investigated by Köthe in [Köt13] based on potentials, resembling the theory of oscillators, but with nonlinear kinetics. We generalise the idea in [MTH80] to cover a class of systems of ordinary differential equations coupled to one reaction-diffusion equation with homogeneous Neumann boundary conditions.

Lemma 3.6. *Consider a system of type*

$$\begin{aligned} 0 &= f(U(x), v(x)), && x \in [0,1], \\ Dv''(x) &= -g(U(x), v(x)), && x \in (0,1), \\ v'(0) &= v'(1) = 0, \end{aligned} \tag{3.15}$$

where v is scalar, U can be vector-valued and f is continuous. Assume that there exists $v^* \in \mathbb{R}$, such that

$$f(U, v^*) = 0, \tag{3.16}$$

has two solutions $U^-(v^*)$ *and* $U^+(v^*)$ *satisfying*

$$g(U^-(v^*), v^*) < 0 < g(U^+(v^*), v^*). \tag{3.17}$$

Moreover, assume that there exists an $\varepsilon > 0$*, such that*

1. *there exists an 'implicit' relation with continuous branches,*

$$U^-(v) \text{ and } U^+(v), \tag{3.18}$$

   satisfying $f(U^+(v), v) = 0 = f(U^-(v), v)$ *on* $[v^* - \varepsilon, v^* + \varepsilon]$*,*

2. *g is continuous on*

$$\left[\min_{v\in[v^*-\varepsilon,v^*+\varepsilon]} U^+(v), \max_{v\in[v^*-\varepsilon,v^*+\varepsilon]} U^+(v)\right] \times [v^* - \varepsilon, v^* + \varepsilon],$$

   and

$$\left[\min_{v\in[v^*-\varepsilon,v^*+\varepsilon]} U^-(v), \max_{v\in[v^*-\varepsilon,v^*+\varepsilon]} U^-(v)\right] \times [v^* - \varepsilon, v^* + \varepsilon].$$

Then there exist infinitely many weak solutions of (3.15) *which have representatives in* $\mathrm{BV}[0,1]^{\dim(U)} \times C^1[0,1]$.

Remark 3.7. *If* $f, g \in C^1$ *and* $\det(\nabla_U f|_{(U^-(v^*),v^*)}) \neq 0 \neq \det(\nabla_U f|_{(U^+(v^*),v^*)})$*, then items 1. and 2. are satisfied.*

Proof. The proof is illustrated in Figure 3.1. First, we assume $D = 1$ and prove that there exists $x_m > 0$, such that for all $0 < x^* \leq x_m$ there exists a solution of (3.15) on a domain $I = (0, x^*)$. For arbitrary $D > 0$, rescaling the spatial variable yields existence of $x_m > 0$ such that for all $x^* \leq x_m/\sqrt{D}$ there exists a solution of (3.15) for $I = (0, x^*)$. By a mirroring argument, this solution can be extended onto domain $I = (0, 2x^*)$ satisfying periodic Dirichlet boundary conditions and homogeneous Neumann boundary conditions. Choosing $x^* = 1/(2n)$ for sufficiently large n, this can be extended periodically onto $I = (0, 1/\sqrt{D})$.

Since $g(U^+(v), v)$ and $g(U^-(v), v)$ are continuous on $[v^* - \varepsilon, v^* + \varepsilon]$, there exist strictly positive $\varepsilon_2 < \varepsilon$ and $c, C < \infty$, such that

$$0 < c \leq g\left(U^+(v), v\right), -g\left(U^-(v), v\right) \leq C < \infty, \tag{3.19}$$

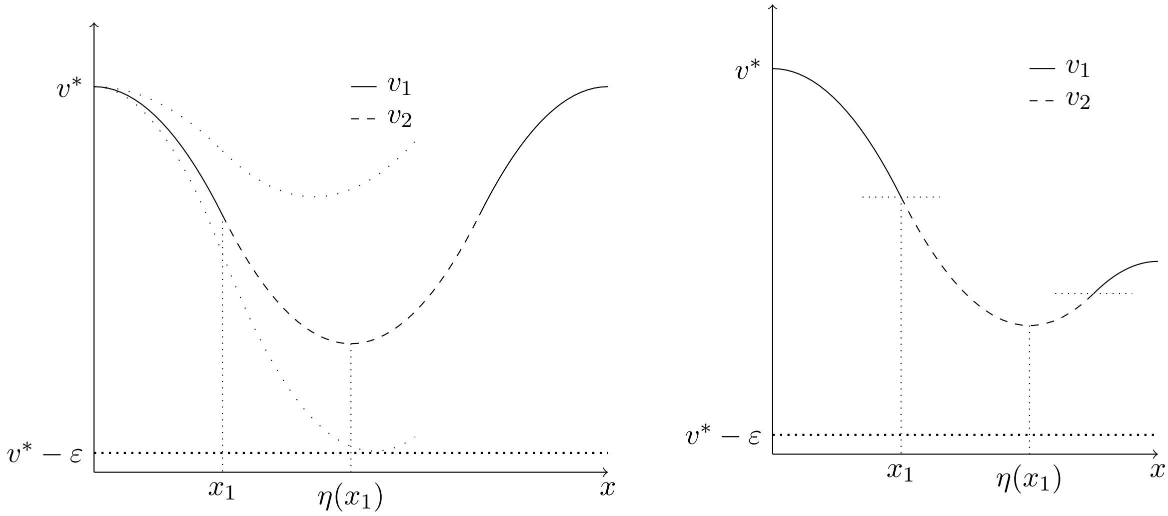

Figure 3.1: Illustration of the proof of Lemma 3.6. The loosely dotted line represents the bounds following from (3.19). Left: Construction of periodic steady states. Right: Construction of non-periodic steady states.

holds for all $v \in [v^* - \varepsilon_2, v^* + \varepsilon_2]$. Consider problem

$$v_1''(x) = -g(U^+(v_1(x)), v_1(x)), \qquad x_0 < x, \tag{3.20}$$

with initial values $(v_1(x_0), v_1'(x_0)) \in ((v^* - \varepsilon_2, v^* + \varepsilon_2) \times (-\varepsilon, \varepsilon))$. For any solution of (3.20) with sufficiently small $0 < \tilde{x}$, the mapping $x_1 \mapsto (v(x_1), v'(x_1))$ is continuous on $[0, \tilde{x}]$. For sufficiently small x_1, , inequality (3.19) implies that

$$\begin{aligned} v_1'(x_0) - C(x_1 - x_0) \le v_1'(x_1) &\le v_1'(x_0) - c(x_1 - x_0), \\ v_1(x_0) + v_1'(x_0)(x_1 - x_0) - \frac{C}{2}(x_1 - x_0)^2 \le v_1(x_1), & \\ &\le v_1(x_0) + v_1'(x_0)(x_1 - x_0) - \frac{c}{2}(x_1 - x_0)^2, \end{aligned} \tag{3.21}$$

hold. Hence, for $x_0 = 0$ and $v_1'(0) = 0$ and $v_1(0) \in (v^*, v^* + \varepsilon_2)$ and $x_1^2 < 2\varepsilon_2/(C + C^2/c)$, the estimates

$$C\sqrt{\frac{2\varepsilon_2}{C(1+\frac{C}{c})}} \le v_1'(x_1) \le -cx_1 \le 0, \tag{3.22}$$

$$v^* - \frac{C}{2}\frac{2\varepsilon_2}{C(1+\frac{C}{c})} \le v_1(x_1) \le v^* + \varepsilon_2, \tag{3.23}$$

hold. Consider problem

$$v_2''(x) = -g(U^-(v_2(x)), v_2(x))), \qquad x_1 < x, \tag{3.24}$$

with initial values $(v_2(x_1), v_2'(x_1)) = (v_1(x_1), v_1'(x_1))$. Due to (3.19) and condition (2.) and an analogous reasoning to (3.21), there exist solutions to (3.24) and a mapping

$$\eta : x_1 \mapsto (v_2(x_1), v_2'(x_1)) \mapsto \min\{x \in \mathbb{R} | v_2'(x) = 0 \wedge x \geq x_1\}, \tag{3.25}$$

which is continuous on the set of initial conditions defined by (3.21). It satisfies

$$\frac{c}{C+c} x_1 \leq \eta(x_1) \leq x_1 \frac{C+c}{c} \leq \sqrt{\frac{2\varepsilon_2}{C(1+\frac{C}{c})}} \frac{C+c}{c}. \tag{3.26}$$

It holds $\eta(x_1) \searrow x_1$ as $v'(x_1) \to 0$. Additionally, it holds $v'(x_1) \to 0$ as $x_1 \to 0$. Consequently, for all $x_2 > 0$ sufficiently small, there exists a weak solution of (3.15) for $D = 1$ on $I = (0, x_2)$. Now, there are different ways to proceed:

1. Periodic steady states: It is possible to extend this weak solution onto the set $(0, 2x_2)$ by defining a solution $v(x_2 + x) = v(x_2 - x)$. For arbitrary $I = (0, \tilde{x}_x)$, $\tilde{x}_x < 2x_2$, we constructed a solution. This solution satisfies

   a) homogeneous Neumann boundary conditions,

   b) periodic Dirichlet boundary conditions,

   on $I = (0, 1/(\sqrt{D}n))$ for sufficiently large n. Consequently, it can be extended periodically onto $(0, 1/\sqrt{D})$ satisfying homogeneous Neumann boundary conditions.

2. 'Irregular' steady states: Defining a problem for v_3 and v_4 analogously to v_2 and v_1 respectively (note the exchange in order), but with initial conditions $(v_3(0), v_3'(0)) = (v_2(\eta(x_1)), v_2'(\eta(x_1))$ leads to a non-periodic solution satisfying homogeneous Neumann-boundary conditions on some domain $(0, \tilde{x})$. If the solution assumes values not in $[v^* - \varepsilon, v^* + \varepsilon]$, the mirroring argument in item (1) can be used instead of irregular extension. Analogously to item (1), a solution on $I = (0, 1/\sqrt{D})$ is constructed for sufficiently large n.

By rescaling $\hat{x} = x/\sqrt{D}$, we obtain, for arbitrary $D > 0$, existence of weak solutions to problem (3.15). □

3.4 (ε_0, A)-stability for reaction-diffusion-ODE systems

In this section, we introduce (ε_0, A)-stability according to [Wei83] and give conditions for stability of steady states of systems of type (3.1)-(3.2) in this topology.
For $I = (0, 1)$, the neighbourhood basis in $BV(\overline{I})$ of a function of bounded variation, denoted $\tilde{U}$, with values in $[U_{\min}, U_{\max}]^{\dim(U)}$ is defined as

$$N_{\varepsilon,U_{\min},U_{\max}}(\tilde{U}) = \{u \in BV(\overline{I}, [U_{\min}, U_{\max}]^{\dim(U)}) \mid \text{there exists } R \subset I \text{ such that } \|U - \tilde{U}\|^2_{L^\infty(R)} < \varepsilon^2 \text{ and } \operatorname{meas}(I \setminus R) < \varepsilon^4\}.$$

We are particularly interested in the situation where the initial function $U(x, 0)$ is *close* to a steady state $\tilde{U}$ with finitely many jump-type discontinuities, but $U(x, 0)$ is continuous on $\overline{I}$. If we assume $(U(x, 0), V(x, 0)) = (U_0(x), V_0(x)) \in (C(\overline{I})^{\dim(U)} \times C^2(\overline{I})^{\dim(V)})$, then the solution $(U(x, t), V(x, t))$ of the initial-boundary value problem is continuous for $t > 0$ due to Assumption 2.1. If the steady state $\tilde{U}$ is 'stable', then $U(x, t)$ is expected to converge or at least stay close to a spatially discontinuous function. Therefore, the uniform norm is not appropriate to measure the closeness, see Figure 2.1. On the other hand, in case of stability in $L^p(I)$ for $p < \infty$, very small 'spike'-like perturbations are admissible and may persist causing the solution to be unstable in $L^\infty(I)$ and changing qualitative characteristics of the solution. Using this topology, we want to exclude the case of uncontrolled emergence of spikes within most parts of the domain. Note that the (ε_0, A)-neighbourhood of a function includes patterns with spikes arbitrarily close to the discontinuities. Even though a proof of non-occurrence of such spikes is missing, numerical observations imply that no spikes occur close to the jump-points. It turns out that $N_{\varepsilon,U_{\min},U_{\max}}(\tilde{U})$ provides us with a reasonable topology for our purposes.
Following [Wei83], (ε_0, A)-stability in this topology is defined as

Definition 3.8 ((ε_0, A)-stability)**.** *A stationary solution* $(\tilde{U}, \tilde{V})$ *of system* (3.1)-(3.2) *is said to be* (ε_0, A)*-stable for positive constants* ε_0 *and* A *if the initial functions* (U_0, V_0) *satisfy*

$$\|U_0 - \tilde{U}\|^2_{L^\infty(R)} + \|V_0 - \tilde{V}\|^2_{H^1(I)} < \varepsilon^2, \tag{3.27}$$

for some $R \subset I$ *with* $\operatorname{meas}(I \setminus R) < \varepsilon^4$*, and* $\varepsilon \in (0, \varepsilon_0)$*, then*

$$\|U(\cdot, t) - \tilde{U}\|^2_{L^\infty(R)} + \|V(\cdot, t) - \tilde{V}\|^2_{H^1(I)} < A\varepsilon^2. \tag{3.28}$$

for all $t > 0$.

Illustration 3.2 shows that the idea of the topology is very close to measurement of concentrations by the human eye: The solution is L^∞-close to the steady state on a subdomain R of the domain which has almost the same measure as I, but it is not controlled around the transition layers, i.e. on $I \setminus R$. However, it must not blow-up or grow-up. We showed that it is possible to construct infinitely many steady states which are not isolated in $L^p(I)$-topology and have jump-type discontinuities. Hence, the topology can be applied.

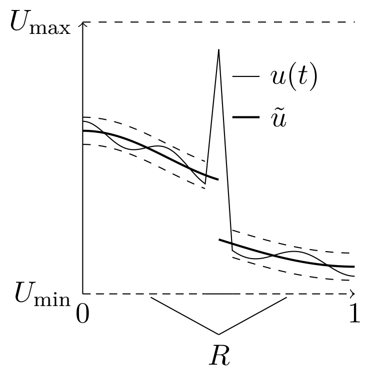

Figure 3.2: Illustration of the (ε_0, A)-topology applied to problem (3.1) for scalar u. A discontinuous steady state and global existence of classical solutions is assumed. $\tilde{u}$ represents the steady state while $u(t)$ represents the solution for some t.

3.5 Conditions for (ε_0, A)-stability

It is important to note that for systems of type (3.3)-(3.6) for vector-valued compartments U^{D_1} and V^{D_1}, the limit $D_1 \to 0$ is not necessarily regular in the sense of stability of steady states. In [NF87], the authors construct steady states $(\tilde{U}^0, \tilde{V}^0)$ with jump type discontinuity for $D_1 = 0$, $D > 0$. Using a perturbation approach, they construct infinitely many steady states $(\tilde{V}^{D_1}, \tilde{V}^{D_1})$ of class C^2 for $D_1 = \varepsilon$, $D > 0$. These steady states are $L^p(I)$-close ($p < \infty$) to $(\tilde{U}^0, \tilde{V}^0)$. In other words, for every steady state $(\tilde{U}^0, \tilde{V}^0)$ with jump-type discontinuities, there exists a sequence of steady states $(\tilde{U}^{D_1}, \tilde{V}^{D_1})$ converging towards it in $L^p(I)$ as D_1 tends to zero. However, in [NF87], for $D_1 > 0$, stability of steady states with hysteresis depends highly on the position of the transition layer and on the type of nonlinearities on the set of values assumed on the transition layer. This is not the case for $D_1 = 0$, since the transition layer is of jump-type. Our conditions for stability are based on point-wise evaluation of the Jacobian matrix on the subdomain on which the steady state is continuous. In section 3.3, we constructed steady states with arbitrary position of the jump-type discontinuities for $D_1 = 0$ and under rather weak conditions. The authors of [NF87] showed that stability depends on

the position of the transition layer for $D_1 > 0$. Consequently, there exist infinitely many stable steady states $(\tilde{U}^0, \tilde{V}^0)$, for which none of the elements of the approximating sequence $(\tilde{U}^{D_1}, \tilde{V}^{D_1})$ is stable. Therefore, we investigate conditions for stability of steady states with or without jump-type discontinuity of system (3.1)-(3.2). We do not exclude the case that kinetic terms f, g depend continuously differentiable on x.
Definition 3.8 allows us to give conditions for (ε_0, A)-stability of possibly discontinuous steady states. Since the proof follows the same lines, we first give general conditions for (ε_0, A)-stability of steady states of systems of ordinary differential equations coupled to reaction-diffusion equations. We suspect that the conditions can be weakened, but for more technical conditions, the possibility of a reasonable biological interpretation is unlikely. We first state the theorem in the most general version. The proof is similar to [Wei83] for a particular system, but is a generalisation.

Theorem 3.9 (Stability theorem).
Let $I \subset \mathbb{R}$ be bounded. Under Assumption 2.1, consider system

$$\begin{aligned} \frac{\partial U}{\partial t} &= f(U, V, x), && x \in \overline{I}, t > 0, \\ \frac{\partial V}{\partial t} &= D \frac{\partial^2}{\partial x^2} V + g(U, V, x), && x \in I, t > 0, \end{aligned}$$

supplemented with homogeneous Neumann boundary conditions for V and classical initial conditions $(U(x,0), V(x,0)) \in (C(\overline{I})^{\dim(U)} \times C^2(\overline{I})^{\dim(V)})$. Moreover, assume that f, g are twice continuously differentiable in all variables.
Let $(\tilde{U}, \tilde{V})$ be a weak steady state with finitely many discontinuities of $\tilde{U}$ in x. Denote the Jacobian matrix of the kinetic system at the steady state by

$$\mathcal{B}(x) = \begin{pmatrix} \nabla_U f(x) & \nabla_V f(x) \\ \nabla_U g(x) & \nabla_V g(x) \end{pmatrix}, \tag{3.29}$$

where $\nabla_U f(x) = (\partial_{u_j} f_i|_{(\tilde{U}, \tilde{V})}(x))_{ij}$ and $\nabla_V f, \nabla_U g, \nabla_V g$ are defined analogously. If

1. *the spectrum of the operator*

$$\mathcal{L} : \begin{pmatrix} \varphi \\ \psi \end{pmatrix} \to \mathcal{B}(x) \begin{pmatrix} \varphi \\ \psi \end{pmatrix} + D \begin{pmatrix} 0 \\ \frac{\partial^2 \psi}{\partial x^2} \end{pmatrix}, \tag{3.30}$$

considered as operator in $(L^2(I))^{(\dim(\varphi)+\dim(\psi))}$ with domain $(L^2(I))^{\dim(\varphi)} \times (W_N^{2,2}(I))^{\dim(\psi)}$, is contained in $\{\lambda \in \mathbb{C} |\, \mathrm{Re}\, \lambda \le c < 0\}$. The space $W_N^{2,2}(I)$ is the subspace of $W^{2,2}(I)$ whose elements satisfy homogeneous Neumann boundary conditions.

2. *for all $x \in \overline{I}$, the spectrum of $\nabla_U f(x)$ is contained in the left complex half-plane,*

$$\bigcup_{x\in\overline{I}} \mathrm{Re}(\sigma(\nabla_U f(x)) \subset (-\infty, -c), \tag{3.31}$$

for some $c > 0$, and

3. *for all $x \in I$, $\nabla_V g(x)$ is negative definite,*

then $(\tilde{U}, \tilde{V})$ is (ε_0, A)-stable for a pair (ε_0, A) with $0 < \varepsilon_0, A < \infty$.

For scalar u and v, more precise conditions can be found:

Corrolary 3.10. *Consider scalar u and v and let $(\tilde{u}, \tilde{v})$ be a jump-type steady state. Assume that for all $x \in I$,*

$$\frac{\partial f}{\partial u}|_{(\tilde{u},\tilde{v})}(x) \le c < 0, \tag{3.32}$$

$$\frac{\partial g}{\partial v}|_{(\tilde{u},\tilde{v})}(x) \le c < 0, \tag{3.33}$$

$$(\frac{\partial f}{\partial u}\frac{\partial g}{\partial v} - \frac{\partial f}{\partial v}\frac{\partial g}{\partial u})|_{(\tilde{u},\tilde{v})}(x) \ge c > 0, \tag{3.34}$$

hold. Then the conditions of Theorem 3.9 are satisfied.

Remark 3.11. *Stability conditions for vector-valued $U = (u_1, u_2)$ are shown in chapter 4. There, the case of different time scales for different components is investigated, similar to the Tikhonov reduction for ordinary differential equations.*

Proof of Theorem 3.9.
Define $\varphi(t) := U(t) - \tilde{U}, \psi(t) := V(t) - \tilde{V}$, $\varphi_0 = \varphi(0), \psi_0 = \psi(0)$. We write the differential equations for the perturbation of the steady state as

$$\frac{\partial}{\partial t}\begin{pmatrix}\varphi\\ \psi\end{pmatrix} = \mathcal{L}\begin{pmatrix}\varphi\\ \psi\end{pmatrix} + \begin{pmatrix}\varrho\\ \sigma\end{pmatrix}, \tag{3.35}$$

where $\mathcal{L}$ denotes the operator resulting from a linearisation around $(\tilde{U}, \tilde{V})$,

$$\mathcal{L} : \begin{pmatrix}\varphi\\ \psi\end{pmatrix} \to \begin{pmatrix}\nabla_U f \cdot \varphi + \nabla_V f \cdot \psi\\ D\Delta\psi + \nabla_U g \cdot \varphi + \nabla_V g \cdot \psi\end{pmatrix}. \tag{3.36}$$

A proof that $\mathcal{L}$ is a sectorial operator is deferred to Lemma 3.12 and was provided by Izumi

Takagi[1]. Now, condition (1.) implies that there exists a $k > 0$ such that

$$\left\| e^{\mathcal{L}} \begin{pmatrix} \varphi \\ \psi \end{pmatrix} \right\|_{L^2(I)^2} \leq ce^{-kt} \left(\|\varphi\|_{L^2(I)} + \|\psi\|_{L^2(I)} \right), \tag{3.37}$$

holds.

Hence,

$$\begin{aligned} \|\varphi(t)\|_2^2 + \|\psi(t)\|_2^2 \leq c\Big(& (\|\varphi_0\|_2^2 + \|\psi_0\|_2^2)e^{-kt} \\ & + \int\limits_0^t (\|\varrho(s)\|_2^2 + \|\sigma(s)\|_2^2)e^{-k(t-s)} ds \Big), \end{aligned} \tag{3.38}$$

holds. Furthermore, because of condition (2.), it holds:

$$|\varphi(x,t)| \leq |\varphi_0(x)|e^{-kt} + \int\limits_0^t (|\psi(x,s)| + |\varrho(x,s)|)e^{k(t-s)} ds, \tag{3.39}$$

$$\|\varphi(t)\|_2^2 \leq c \left(\|\varphi_0\|_2^2 e^{-2kt} + \int\limits_0^t (\|\psi(s)\|_2^2 + \|\varrho(s)\|_2^2)e^{k(t-s)} ds \right). \tag{3.40}$$

Since for all $x \in R$, the real part of the spectrum of $\nabla_U f$ is contained in $(-\infty, -c)$, it holds that on the subset $R \subset I$ which does not contain discontinuities of $\tilde{u}$,

$$\begin{aligned} \|\varphi\|_{L^\infty(R)} &\leq \|\varphi_0\|_{L^\infty(R)} e^{-kt} + c \int\limits_0^t (\|\varphi\|_{L^\infty(R)}^2 + \|\psi\|_\infty^2 + \|\psi\|_\infty) e^{-k(t-s)} ds, \\ \|\varphi\|_{L^\infty(R)}^2 &\leq c \left(\|\varphi_0\|_{L^\infty(R)}^2 e^{-2kt} + \int\limits_0^t ((\|\varphi\|_{L^\infty(R)}^2 + \|\psi\|_\infty^2)^2 + \|\psi\|_\infty^2) e^{-k(t-s)} ds \right), \\ &\leq c \left(\|\varphi_0\|_{L^\infty(R)}^2 e^{-2kt} + \int\limits_0^t ((\|\varphi\|_{L^\infty(R)}^2 + \|\psi\|_{H^1}^2)^2 + \|\psi\|_{H^1}^2) e^{-k(t-s)} ds \right), \\ &\leq c \left(\|\varphi_0\|_{L^\infty(R)}^2 e^{-2kt} + \sup_{s\in(0,t)} (\|\varphi\|_{L^\infty(R)}^2 + \|\psi\|_{H^1}^2)^2 + \int\limits_0^t \|\psi\|_{H^1}^2 e^{-k(t-s)} ds \right). \end{aligned} \tag{3.41}$$

Further, we are interested in estimating $\|\psi\|_{H^1}^2$. For this purpose, we rewrite the second equation of (3.35) as

$$\frac{\partial \psi}{\partial t} - D\frac{\partial^2 \psi}{\partial x^2} = \nabla_U g \varphi + \nabla_V g \psi + \sigma(t). \tag{3.42}$$

[1] Tohoku University, Japan

Testing (3.42) with $\psi^T e^{ks}$ yields

$$\begin{aligned}\frac{1}{2}\int_0^t \left(\frac{\partial\|\psi\|_2^2}{\partial t} + D\|\nabla\psi\|_2^2\right) e^{ks} ds \\ = \int_0^t \int_I \left(\psi^T \nabla_U g\varphi + \psi^T \nabla_V g\psi + \psi^T \sigma(t)\right) dx e^{ks} ds,\end{aligned} \tag{3.43}$$

$$\begin{aligned}\int_0^t \left(-\frac{k}{2}\|\psi\|_2^2 + D\|\nabla\psi\|_2^2\right) e^{ks} ds + \left[\frac{1}{2}\|\psi(s)\|_2^2 e^{ks}\right]_{s=0}^{s=t} \\ = \int_0^t \int_I \left(\psi^T \nabla_U g\varphi + \psi^T \nabla_V g\psi + \psi^T \sigma(t)\right) dx e^{ks} ds.\end{aligned} \tag{3.44}$$

Testing (3.42) with $\partial\psi^T/\partial t\, e^{ks}$, we obtain due to condition (3.) that

$$\begin{aligned}&\int_0^t \left(\left\|\frac{\partial\psi}{\partial t}\right\|_2^2 + \frac{D}{2}\frac{\partial\|\nabla\psi\|_2^2}{\partial t}\right) e^{ks} ds \\ &= \int_0^t \int_I \left(\frac{\partial\psi^T}{\partial t}\nabla_U g\varphi + \frac{1}{2}\frac{\partial(\psi^T \nabla_V g\psi)}{\partial t} + \frac{\partial\psi^T}{\partial t}\sigma(t)\right) dx e^{ks} ds, \\ &\int_0^t \left(\left\|\frac{\partial\psi}{\partial t}\right\|_2^2 - \frac{Dk}{2}\|\nabla\psi\|_2^2\right) e^{ks} ds + \left[\frac{D}{2}\|\nabla\psi(s)\|_2^2 e^{ks}\right]_{s=0}^{s=t} \\ &= \int_0^t \int_I \left(\frac{\partial\psi}{\partial t}\nabla_U g\varphi + \frac{k}{2}\left|\psi^T \nabla_V g\psi\right| + \frac{\partial\psi}{\partial t}\sigma(t)\right) dx e^{ks} ds - \left[\int_I \frac{1}{2}\left|\psi^T \nabla_V g\psi\right| e^{ks}\right]_{s=0}^{s=t}\end{aligned} \tag{3.45}$$

The terms involving $\partial\psi/\partial t$ are rather hard to handle. To obtain an estimate independent of $\partial\psi/\partial t$, we consider the right-hand side of (3.45) with the following two estimates for arbitrary $c^* > 0$:

$$|\frac{\partial\psi^T}{\partial t}\nabla_U g\varphi| \le \frac{c^*}{2}\left(\frac{\partial\psi}{\partial t}\right)^2 + \frac{1}{2c^*}(\nabla_U g\varphi)^2, \tag{3.46}$$

and

$$\begin{aligned}|\frac{\partial\psi^T}{\partial t}\sigma(t)| &\le \left(\frac{c^*}{2} + \frac{c^*}{8} + \frac{c^*}{2} + \frac{c^*}{8}\right)\left(\frac{\partial\psi}{\partial t}\right)^2 + \frac{1}{2c^*}\sigma(t)^2, \\ &\le \frac{5}{4}c^*\left(\frac{\partial\psi}{\partial t}\right)^2 + \frac{c}{2c^*}(\varphi^4 + \psi^4).\end{aligned} \tag{3.47}$$

Using (3.46), (3.47), estimating (3.45) further, leads to

$$\begin{aligned}\int_0^t \left(-\frac{Dk}{2}\|\psi\|_2^2 e^{ks}\right) ds + \left[\frac{D}{2}\|\nabla\psi(s)\|_2^2 e^{ks}\right]_{s=0}^{s=t} \leq \left(\frac{7}{4}c^* - 1\right)\int_0^t \left\|\frac{\partial\psi}{\partial t}\right\|_2^2 e^{ks} ds \\ + \frac{1}{2c^*}\int_0^t \left(\int_I (\nabla_U g\varphi)^2 + c(\varphi^4 + \psi^4)\right) e^{ks} ds \\ + \int_0^t \int_I \frac{k}{2}|\psi^T \nabla_V g\psi| dx e^{ks} ds - \frac{k}{2}\left[\left|\psi^T \nabla_V g\psi\right| e^{ks}\right]_{s=0}^{s=t}.\end{aligned} \tag{3.48}$$

For $c^* = 4/7$, we obtain an estimate independent of $\|\partial\psi/\partial t\|_2$.
Multiplying (3.44) by $k/2$, adding it to (3.48), choosing $c^* = 4/7$ and using the estimate

$$|\sigma\psi| \leq c(|\varphi|^2 + |\psi^2|)|\psi| \leq c(|\varphi|^4 + |\psi|^4 + |\psi|^2), \tag{3.49}$$

yield an estimate of the type

$$\begin{aligned}\|\psi(t)\|_{H^1}^2 \leq c\Bigg((\|\varphi_0\|_2^2 + \|\psi_0\|_{H^1}^2)e^{-kt} \\ + \int_0^t \left((\|\varphi(s)\|_4^4 + \|\psi(s)\|_4^4) + \|\varphi(s)\|_2^2 + \|\psi(s)\|_2^2\right) e^{-k(t-s)} ds\Bigg).\end{aligned} \tag{3.50}$$

The estimate on H^1-norm allows to estimate (3.41). But first, taking $U_{\min} \leq U \leq U_{\max}$ and $V_{\min} \leq V \leq V_{\max}$ and $f, g \in C^2$ into account, the Taylor expansion yields (note boundedness of solutions and regularity of f, g) that

$$|\varrho(x)| \leq c(|\varphi(x)|^2 + |\psi(x)|^2), \tag{3.51}$$

$$|\sigma(x)| \leq c(|\varphi(x)|^2 + |\psi(x)|^2), \tag{3.52}$$

holds, hence

$$\begin{aligned}\|\varrho(t)\|_2^2, \|\sigma(t)\|_2^2 \leq c\left(\|\varphi\|_4^4 + \|\psi\|_4^4\right), \\ \|\varrho(t)\|_1, \|\sigma(t)\|_1 \leq c\left(\|\varphi\|_2^2 + \|\psi\|_2^2\right).\end{aligned} \tag{3.53}$$

holds.

Applying the first estimate of (3.53) to (3.38) yields

$$\begin{aligned}\int_0^t \|\psi\|_2^2 e^{-k(t-s)}ds &\le c\Big(\int_0^t (\|\varphi_0\|_2^2 + \|\psi_0\|_2^2)e^{-ks} \\ &\quad + \int_0^s (\|\sigma(\tau)\|_2^2 + \|\varrho(\tau)\|_2^2)e^{-k(s-\tau)}d\tau e^{-k(t-s)}ds\Big), \\ &\le c\Big(\int_0^t (\|\varphi_0\|_2^2 + \|\psi_0\|_2^2)e^{-ks} \\ &\quad + \int_0^s (\|\varphi(\tau)\|_4^4 + \|\psi(\tau)\|_4^4)e^{-k(s-\tau)}d\tau e^{-k(t-s)}ds\Big), \\ &\le c\Big((\|\varphi_0\|_2^2 + \|\psi_0\|_{H^1}^2) \\ &\quad + \int_0^t \int_0^s (\|\varphi(\tau)\|_4^4 + \|\psi(\tau)\|_4^4)e^{-k(s-\tau)}d\tau e^{-k(t-s)}ds\Big).\end{aligned}$$

Now, see that

$$\|\varphi\|_p^p \le \|\varphi\|_{L^\infty(R)}^p + |U_{\max} - U_{\min}|_{\max}^p \, \mu(I \setminus R). \tag{3.54}$$

Applying (3.54) and Sobolev inequalities to (3.50) yields

$$\begin{aligned}\|\psi(t)\|_{H^1}^2 &\le c\Big(\left(\|\varphi_0\|_{L^\infty(R)}^2 + \|\psi_0\|_{H^1}^2\right)e^{-kt} \\ &\quad + \int_0^t \left(\|\varphi(s)\|_{L^\infty(R)}^2 + \|\psi(s)\|_{H^1}^2\right)^2 e^{-k(t-s)}ds + \mu(I \setminus R)\Big). \\ &\le c\Big(\left(\|\varphi_0\|_{L^\infty(R)}^2 + \|\psi_0\|_{H^1}^2\right)e^{-kt} \\ &\quad + \Big(\sup_{s\in(0,t)}\left(\|\varphi(s)\|_{L^\infty(R)}^2 + \|\psi(s)\|_{H^1}^2\right)\Big)^2 + \mu(I \setminus R)\Big).\end{aligned} \tag{3.55}$$

Using this estimate for $\|\psi\|_{H^1}^2$, we obtain from (3.41) that

$$\|\varphi\|_{L^\infty(R)}^2 \le c\Big((\|\varphi_0\|_{L^\infty(R)}^2 + \|\psi_0\|_{H^1}^2) + \Big(\sup_{s\in(0,t)}(\|\varphi\|_{L^\infty(R)}^2 + \|\psi\|_{H^1}^2)\Big)^2 + \mu(I \setminus R)\Big), \tag{3.56}$$

holds.

Combining the estimates for $\|\varphi(t)\|^2_{L^\infty(R)}$ and $\|\psi(t)\|^2_{H^1}$, we obtain

$$\|\varphi(t)\|^2_{L^\infty(R)} + \|\psi(t)\|^2_{H^1} \le C\Big((\|\varphi_0\|^2_{L^\infty(R)} + \|\psi_0\|^2_{H^1}) + \Big(\sup_{s\in(0,t)} \Big(\|\varphi(s)\|^2_{L^\infty(R)} + \|\psi(s)\|^2_{H^1} \Big) \Big)^2 + \mu(I\setminus R) \Big). \tag{3.57}$$

Choosing $A > \max(C, 1)$ and ε_0 such that

$$1 + A^2\varepsilon_0^2 + \varepsilon_0^2 < \frac{A}{C}, \tag{3.58}$$

allows to estimate for all $0 < \varepsilon \le \varepsilon_0$, hence

$$\|\varphi(0)\|^2_{L^\infty(R)} + \|\psi(0)\|^2_{H^1} < \varepsilon^2 \quad \Rightarrow \quad \forall_{t>0} \|\varphi(t)\|^2_{L^\infty(R)} + \|\psi(t)\|^2_{H^1} < A\varepsilon^2, \tag{3.59}$$

holds. We proved (ε_0, A)-stability. □

Lemma 3.12. *(Provided by Izumi Takagi)*
Under the assumptions of Theorem 3.9, the operator $\mathcal{L}$, defined in Theorem 3.9, is sectorial.

Proof. Define $n = \dim(\varphi)$ and $m = \dim(\psi)$ and $N = n+m$. It is clear that $L^2(I)^n \times W^{2,2}_N(I)^m$ lies dense in $L^2(I)^N$ due to the Rellich embedding theorems. The numerical range is bounded:

$$\left| \mathrm{Re}\left(\mathcal{L}\begin{pmatrix}\varphi\\ \psi\end{pmatrix}, \begin{pmatrix}\varphi\\ \psi\end{pmatrix} \right) \right| \le |(\nabla_U f\varphi + \nabla_V f\psi, \varphi)_{L^2(I)}| + |(\nabla_U g\varphi + \nabla_V g\psi, \psi)_{L^2(I)}| \tag{3.60}$$

$$+ |D(\psi', \psi')_{L^2(I)}|, \tag{3.61}$$

Due to Assumption 2.1, all entries of $\nabla_U f, \nabla_V f, \nabla_U g, \nabla_V g$, considered as x-dependent matrices, are in $L^\infty(I)$. Hence, there exists a constant C, such that we can estimate further by

$$\le C \left(\|\varphi\|^2_{L^2(I)^n} + \|\psi\|^2_{L^2(I)^m} + \|\psi'\|^2_{L^2(I)^m} \right) \tag{3.62}$$

The imaginary part of the numerical range can be estimated analogously. Hence, the numerical range is contained in some set $[-C, C] \times i[-C, C]$ for some $C < \infty$. It is left to prove that there exists a $\lambda_0 > 0$ such that range of $\lambda_0 \,\mathrm{id} - \mathcal{L}$ is $L^2(I)^N$.
Due to Assumption 2.1, $(\nabla_U f - \lambda \,\mathrm{id})$ is invertible for sufficiently large λ. Hence, problem

$$(\mathcal{L} - \lambda \,\mathrm{id}) \begin{pmatrix}\varphi\\ \psi\end{pmatrix} = \begin{pmatrix} f\\ g\end{pmatrix}, \tag{3.63}$$

can be reformulated as

$$\varphi = (\nabla_U f - \lambda\,\mathrm{id})^{-1}(f - \nabla_V f\psi) \tag{3.64}$$

$$\nabla_U g(\nabla_U f - \lambda\,\mathrm{id})^{-1}(f - \nabla_V f\psi) + (D\Delta_x + \nabla_V g - \lambda\,\mathrm{id})\psi = g. \tag{3.65}$$

The operator in the second summand of the left-hand side of (3.65) is invertible for λ sufficiently large. Moreover, its inverse is compact on $L^2(I)^m$. Now, see that

$$\|\nabla_U g(\nabla_U f - \lambda\,\mathrm{id})\|_\infty = |\lambda|^{-1}\left\|\nabla_U g(\mathrm{id} - \lambda^{-1}\nabla_U f)\right\|_\infty = O(\lambda^{-1}), \tag{3.66}$$

as λ tends to ∞. Hence, for sufficiently large λ, the operator on the left-hand side of (3.65) is invertible and the inverse is compact on $L^2(I)^m$. Now, since the inverse is a bounded operator from $L^2(I)^m$ into the domain of $\mathcal{L}$, we can show that the range of $\mathcal{L} - \lambda\,\mathrm{id}$ is closed for sufficiently large λ. This shows that the range of $\mathcal{L} - \lambda\,\mathrm{id}$ is $L^2(I)^N$. We obtained that the operator $\mathcal{L}$ is sectorial. □

Proof of Corollary 3.10. In the following proof, c denotes a strictly positive generic constant. We investigate the spectrum of the operator resulting from linearisation around the steady state $(\tilde{u}, \tilde{v})$.
Define

$$\mathcal{L} : \begin{pmatrix} \varphi \\ \psi \end{pmatrix} \mapsto \begin{pmatrix} \frac{\partial f}{\partial u}|_{(\tilde{u},\tilde{v})}(x)\varphi + \frac{\partial f}{\partial v}|_{(\tilde{u},\tilde{v})}(x)\psi \\ \frac{\partial g}{\partial u}|_{(\tilde{u},\tilde{v})}(x)\varphi + \frac{\partial g}{\partial v}|_{(\tilde{u},\tilde{v})}(x)\psi \end{pmatrix} =: \begin{pmatrix} b_{11}(x)\varphi + b_{12}(x)\psi \\ b_{21}(x)\varphi + b_{22}(x)\psi \end{pmatrix} \tag{3.67}$$

We investigate the eigenvalue problem

$$(\mathcal{L} - \lambda)\begin{pmatrix} \varphi \\ \psi \end{pmatrix} + \begin{pmatrix} 0 \\ D\Delta\psi \end{pmatrix} = 0. \tag{3.68}$$

For $\lambda \notin \bigcup_{x\in\overline{\Omega}}(b_{11}(x)) \subset (-\infty, -c)$, we obtain

$$\varphi = -\frac{b_{12}}{b_{11} - \lambda}\psi. \tag{3.69}$$

Inserting this into the equation for ψ, we obtain

$$\left(-\frac{b_{21}b_{12}}{b_{11} - \lambda} + b_{22} - \lambda\right)\psi + D\Delta\psi = 0. \tag{3.70}$$

Testing this expression formally with ψ, yields

$$\int\limits_I \left(-\frac{b_{21}b_{12}}{b_{11} - \lambda} + b_{22} - \lambda\right)\psi^2 dx = D\int\limits_I (\nabla_x\psi)^2 dx. \tag{3.71}$$

Defining $\lambda = \lambda_1 + i\lambda_2$, the imaginary part of the equation reads

$$-i\lambda_2 \int_I \left(\frac{b_{12}b_{21}}{|b_{11}-\lambda|^2} + 1 \right) \psi^2 dx = 0. \tag{3.72}$$

It follows that λ_2 is uniformly bounded. Moreover, for $b_{11}b_{22} \geq 0$, it follows that $\lambda_2 = 0$ or $\psi = 0$. In case of $\lambda_2 = 0$, (3.71) reads

$$\int_I \underbrace{(b_{11}-\lambda_1)^{-1} \left(\lambda_1^2 - (b_{11}+b_{22})\,\lambda_1 + (b_{11}b_{22} - b_{12}b_{21}) \right)}_{A_1(x,\lambda_1)} \psi^2 dx = \int_I (\nabla_x \psi)^2 dx, \tag{3.73}$$

where $A_1(x, \lambda_1)$ is strictly negative for $-c \leq \lambda_1$. Consequently, $\psi = 0$.
In case of $b_{11}b_{22} < 0$, consider the real part of (3.71), which reads

$$\int_I \underbrace{\left(-\frac{(b_{12}b_{21})(b_{11}-\lambda_1)}{|b_{11}-\lambda|^2} + b_{22} - \lambda_1 \right)}_{A_2(x,\lambda_1,\lambda_2)} \psi^2 dx = D \int_I (\nabla_x \psi)^2 dx. \tag{3.74}$$

Again, $A_2(x, \lambda_1, \lambda_2)$ is strictly negative for $-c \leq \lambda_1$ for some $0 < c$ and $\psi = 0$ follows. Summarising, there exist $c_1, c_2 > 0$ such that the resolvent set of the operator $\mathcal{L}$ contains the set

$$\{\lambda \in \mathbb{C} |\, \mathrm{Re}(\lambda) > -c_1 \text{ or } |\,\mathrm{Im}(\lambda)| > c_2\}. \tag{3.75}$$

□

3.6 Application to example models

3.6.1 A receptor-based model

Derivation of the model

In [MC03], Marciniak-Czochra considered a model of type

$$\frac{\partial}{\partial t} u = -\mu_1 u - buw + dv + m_1 u^2, \qquad (x,t) \in \overline{I} \times (0,T), \tag{3.76}$$

$$\frac{\partial}{\partial t} v = -\mu_2 v + buw - dv, \qquad (x,t) \in \overline{I} \times (0,T), \tag{3.77}$$

$$\frac{\partial}{\partial t} w = D\Delta w - \mu_3 w - buw + dv + m_2 u^2, \qquad (x,t) \in I \times (0,T), \tag{3.78}$$

$$(u(x,0), v(x,0), w(x,0)) \in (C(\overline{I})^2 \times C^2(\overline{I})), \tag{3.79}$$

$$\partial_n w = 0, \qquad (x,t) \in \partial I \times (0,T), \tag{3.80}$$

to model pattern formation in hydra.
Model (3.76)-(3.80) exhibits diffusion-driven instability. Numerical investigations performed in [MC03] show blow-up in finite time. We modify the right-hand side of the model to obtain uniformly bounded solutions,

$$\frac{\partial}{\partial t}u = -\mu_1 u - buw + dv + m_1\frac{u^2}{1+ku^2}, \qquad (x,t) \in \overline{I} \times (0,T), \tag{3.81}$$

$$\frac{\partial}{\partial t}v = -\mu_2 v + buw - dv, \qquad (x,t) \in \overline{I} \times (0,T), \tag{3.82}$$

$$\frac{\partial}{\partial t}w = D\Delta w - \mu_3 w - buw + dv + m_2\frac{u^2}{1+ku^2}, \qquad (x,t) \in I \times (0,T), \tag{3.83}$$

$$\partial_n w = 0, \qquad (x,t) \in \partial I \times (0,T), \tag{3.84}$$

supplemented with classical initial conditions. We consider the so called 'quasi-steady state' approximation, a differential-algebraic equation arising from setting $\delta = 0$ in

$$\frac{\partial}{\partial t}u = -\mu_1 u - buw + dv + m_1\frac{u^2}{1+ku^2}, \qquad (x,t) \in \overline{I} \times (0,T), \tag{3.85}$$

$$\delta\frac{\partial}{\partial t}v = -\mu_2 v + buw - dv, \qquad (x,t) \in \overline{I} \times (0,T), \tag{3.86}$$

$$\frac{\partial}{\partial t}w = D\Delta w - \mu_3 w - buw + dv + m_2\frac{u^2}{1+ku^2}, \qquad (x,t) \in I \times (0,T), \tag{3.87}$$

$$\partial_n w = 0, \qquad (x,t) \in \partial I \times (0,T), \tag{3.88}$$

supplemented with classical initial conditions. We consider the case $\delta = 0$ to be an approximation for δ small, if (3.86) has a unique solution $v(u,w)$ for $\delta = 0$. Later, we show that $\delta = 0$ can be considered to be a suitable approximation. For $\delta = 0$, we obtain the following system:

$$\frac{\partial}{\partial t}u = -\mu_1 u - \left(1 - \frac{d}{\mu_2 + d}\right) buw + m_1\frac{u^2}{1+ku^2}, \qquad (x,t) \in \overline{I} \times (0,T), \tag{3.89}$$

$$\frac{\partial}{\partial t}w = D\Delta w - \mu_3 w - \left(1 - \frac{d}{\mu_2 + d}\right) buw + m_2\frac{u^2}{1+ku^2}, \qquad (x,t) \in I \times (0,T), \tag{3.90}$$

$$(u(x,0), w(x,0)) \in (C(\overline{I}) \times C^2(\overline{I})), \tag{3.91}$$

supplemented with homogeneous Neumann boundary conditions for w. Substituting $\hat{u} = (1 - \frac{d}{d+\mu_2})\frac{b}{\mu_1}u$, $\hat{w} = (1 - \frac{d}{d+\mu_2})\frac{b}{\mu_1}w$ and $\hat{t} = \frac{t}{\mu_1}$, we obtain the rescaled quasi-steady state approximation,

$$\begin{aligned}
\frac{\partial}{\partial \hat{t}}\hat{u} =& -\hat{u} - \hat{u}\hat{w} + \hat{m}_1 \frac{\hat{u}^2}{1+\hat{k}\hat{u}^2}, && (x,t) \in \overline{I} \times (0, \mu_1 T), && (3.92)\\
\frac{\partial}{\partial \hat{t}}\hat{w} =& D\Delta\hat{w} - \hat{\mu}\hat{w} - \hat{u}\hat{w} + \hat{m}_2 \frac{\hat{u}^2}{1+\hat{k}\hat{u}^2}, && (x,t) \in I \times (0, \mu_1 T), && (3.93)\\
\partial_n \hat{w} =& 0, && (x,t) \in \partial I \times (0, \mu_1 T), && (3.94)\\
(\hat{u}(0,x), \hat{w}(0,x)) \in& (C(\overline{I}) \times C^2(\overline{I})). && && (3.95)
\end{aligned}$$

For simplicity, we drop the notation $\hat{\cdot}$ in the following and define

$$f_r(u,w) = -u - uw + m_1 \frac{u^2}{1+ku^2}, \tag{3.96}$$

$$g_r(u,w) = -\mu w - uw + m_2 \frac{u^2}{1+ku^2}. \tag{3.97}$$

In this chapter, we focus on investigation of (3.92)-(3.94) and show in chapter 4 that (in)stability as well as existence of steady states of system (3.85)-(3.88) for small δ can be derived from system (3.92)-(3.94).

Remark 3.13. *Note that for $\mu_1 = 0$, μ_1 can be replaced by μ_2 for rescaling, resulting in a system of type*

$$\begin{aligned}
\frac{\partial}{\partial \hat{t}}u =& -\hat{u}\hat{w} + \hat{m}_1 \frac{\hat{u}^2}{1+\hat{k}\hat{u}^2},\\
\frac{\partial}{\partial \hat{t}}w =& D\Delta\hat{w} - \hat{w} - \hat{u}\hat{w} + \hat{m}_2 \frac{\hat{u}^2}{1+\hat{k}\hat{u}^2}.
\end{aligned} \tag{3.98}$$

In case of $d = 0$, (3.85) and (3.87) do not depend on v and a reduction is therefore not necessary.

Existence and boundedness of solutions

In this section we show that model (3.92)-(3.94) satisfies Assumption 2.1, i.e. the solution is uniformly bounded and the right-hand side is twice continuously differentiable. Regularity of the right-hand side can be seen directly. It is left to prove uniform boundedness:

Lemma 3.14. *System (3.92)-(3.94) has a unique solution of class $C^1(0,T;C(\overline{I}) \times C^2(\overline{I}))$. Moreover, for all non-negative initial conditions and $\varepsilon > 0$, there exist $0 \le t^* < \infty$ such that for all $t \ge t^*$ and all $x \in \overline{I}$ it holds that*

$$0 \le u(x,t) \le \frac{1}{2k}\left(m_1 + \sqrt{m_1^2 - 4k}\right) + \varepsilon, \tag{3.99}$$

$$0 \le w(x,t) \le \frac{m_2}{2k^2 m_1 \mu}\left(m_1 + \sqrt{m_1^2 - 4k}\right)^2 + \varepsilon. \tag{3.100}$$

Proof. Existence of a unique local-in-time solution yields from regularity of the right-hand side, see [Rot84]. For $0 \leq u, w$, it holds that

$$-(1+w)u \leq \frac{\partial}{\partial t} u \leq \underbrace{(-1 + m_1 \frac{u}{1+ku^2})}_{A(u)} u, \tag{3.101}$$

and $A(u) < 0$ for $u > (m_1 + \sqrt{-4k + m_1^2})/(2k)$.
Consequently, it holds for some $t^* \geq 0$ that

$$D\Delta w - (\mu + u)w \leq \frac{\partial}{\partial t} w \leq D\Delta w - w\mu + \frac{\left(m_1 + \sqrt{-4k + m_1^2}\right)^2 m_2}{2k^2 m_1}. \tag{3.102}$$

Consequently, for all $\varepsilon > 0$, there exists a $t^* \geq 0$, such that it holds for all $t \geq t^*$ that

$$0 \leq u(x,t) \leq \frac{1}{2k}\left(m_1 + \sqrt{-4k + m_1^2}\right) + \varepsilon, \tag{3.103}$$

$$0 \leq w(x,t) \leq \frac{m_2}{2k^2 m_1 \mu}\left(m_1 + \sqrt{-4k + m_1^2}\right)^2 + \varepsilon. \tag{3.104}$$

□

Existence of steady states

First, note that all steady states satisfy the following equation

$$0 = -(1+w)u + m_1 \frac{u^2}{1+ku^2}, \qquad x \in \bar{I}, \tag{3.105}$$

$$0 = D\Delta w - (\mu + u)w + m_2 \frac{u^2}{1+ku^2}, \qquad x \in I, \tag{3.106}$$

$$\partial_n w = 0, \qquad x \in \partial I. \tag{3.107}$$

Equation (3.105) is equivalent to

$$(u = 0) \ \text{ or } \ \left(-(1+w)(1+ku^2) + m_1 u = 0\right), \tag{3.108}$$

hence (3.105) has the following solutions:

$$u_0(w) := 0, \tag{3.109}$$

$$u_-(w) := \frac{1}{2k(1+w)}\left(m_1 - \sqrt{m_1^2 - 4k(1+w)^2}\right), \tag{3.110}$$

$$u_+(w) := \frac{1}{2k(1+w)}\left(m_1 + \sqrt{m_1^2 - 4k(1+w)^2}\right). \tag{3.111}$$

In Lemma 3.20, we show that stability of steady states depends highly on the branch. Therefore, we define the different branches,

Definition 3.15 (branches of steady states)**.**
We say that a piece-wise continuous steady state $(\tilde{u}(x), \tilde{w}(x))$ *of system* (3.92)-(3.95) *is of class* u_+ *(resp.* u_- *or* u_0*) at* $x \in I$ *if*

$$\tilde{u}(x) = u_+(\tilde{w}(x)), \text{(resp. } u_-(\tilde{w}(x)) \text{ or } u_0(\tilde{w}(x))\text{)}, \tag{3.112}$$

holds.

We summarise and note that we can distinguish branches u_- and u_+ by a simpler criterion:

Lemma 3.16.
The solution $u^*(w)$ *of* $-(1+w)u + m_1u^2/(1+ku^2) = 0$ *has three branches,*

$$u_0(w) = 0, \tag{3.113}$$
$$u_\pm(w) = \frac{1}{k}\left(\frac{m_1}{2(1+w)} \pm \sqrt{\left(\frac{m_1}{2(1+w)}\right)^2 - k}\right). \tag{3.114}$$

For $u \neq 0$ *and* $0 \leq w \leq w_r := m_1/(2\sqrt{k}) - 1$*,*

1. $u^*(w) = u_+(w)$ *if and only if* $\frac{d}{dw}u^*(w) \leq 0$*,*
2. $u^*(w) = u_-(w)$ *if and only if* $\frac{d}{dw}u^*(w) \geq 0$

hold.

Proof. Deriving,

$$u_+(w) = \frac{1}{k}\left(\frac{m_1}{2(1+w)} + \sqrt{\left(\frac{m_1}{2(1+w)}\right)^2 - k}\right), \tag{3.115}$$

locally with respect to w implies $\frac{d}{dw}u_+(w) < 0$. Combining this with

$$u_+(w)u_-(w) = \frac{1}{k}, \tag{3.116}$$

yields

$$\frac{d}{dw}u_-(w) > 0. \tag{3.117}$$

□

Using this characterisation, we can prove existence of spatially homogeneous steady states and classify them:

Lemma 3.17 (Existence of steady states)**.**

1. *For arbitrary parameters,*

$$(\overline{u}, \overline{w}) = (0,0), \tag{3.118}$$

   is a spatially homogeneous steady state of model (3.92)-(3.95)*.*

2. *Let $m_1 < m_2$ and*

$$\mu > \frac{1}{m_1}\left(\frac{2m_2 - m_1}{m_1} + 2\sqrt{\left(\frac{m_2}{m_1}\right)^2 - \frac{m_2}{m_1}}\right), \tag{3.119}$$

   hold. Then exists a strictly positive k^*, such that for all $k < k^*$ exist exactly two strictly positive homogeneous steady states of model (3.92)-(3.95)*.*
   If $k < \min(k^*, ((m_2 - m_1)(m_1\mu))^2)$, then both strictly positive homogeneous steady states are of class u_-.

3. *For $2\sqrt{k} < m_1 < m_2$ there exist infinitely many weak steady states $(\tilde{u}, \tilde{w}) \in (BV(\overline{I}) \times C^1(\overline{I}))$ of model* (3.92)-(3.95) *which are for all $x \in \overline{I}$ of class u_+ or u_0.*

Proof. Proof of Items 1. and 2. Item 1. can be seen immediately by inserting $(u, w) = (0, 0)$ into (3.92)-(3.95). To obtain nontrivial spatially homogeneous steady states, see that a solution (u, w) is a spatially homogeneous steady state only if

$$\frac{\partial u}{\partial t} = f_r(u,w) = -(1+w)u + m_1\frac{u^2}{1+ku^2} = 0, \tag{3.120}$$

holds. Solving $f_r(u, w) = 0$ yields $u = 0$ or

$$\frac{u}{1+ku^2} = \frac{1}{m_1}(1+w). \tag{3.121}$$

Inserting (3.121) into

$$\frac{\partial w}{\partial t} = g_r(u,w) = -(\mu+u)w + m_2\frac{u^2}{1+ku^2} = 0, \tag{3.122}$$

and solving for w yields

$$w_{f_r,g_r}(u) = \frac{m_2}{m_1} \frac{u}{\mu + (1 - \frac{m_2}{m_1})u}. \tag{3.123}$$

Note that $w_{f_r,g_r}(u)$ is k-independent.
The nullclines of f_r and g_r for $u \neq 0$ are described by

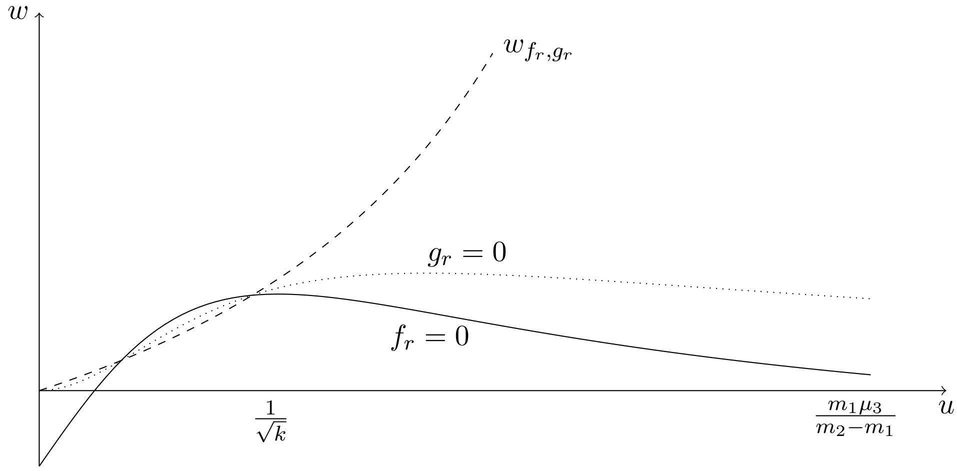

Figure 3.3: Nullclines of f_r and g_r and w_{f_r,g_r} for parameters $m_1 = 1.44, m_2 = 2, \mu_2 = 4.2, k = 0.1$.

$$w_{f_r=0}(u) := -1 + m_1 \frac{u}{1 + ku^2}, \tag{3.124}$$

$$w_{g_r=0}(u) := \frac{m_2}{\mu + u} \frac{u^2}{1 + ku^2}. \tag{3.125}$$

If there exists $u > 0$, such that $w_{f_r=0}(u) = w_{f_r,g_r}(u)$, then $(u, w_{f_r,g_r}(u))$ is a homogeneous steady state.
Note that $w_{f_r=0}(u)$ has a unique positive maximum at $u = 1/\sqrt{k}$, is strictly concave on $[0, \sqrt{3}/\sqrt{k})$, strictly convex on $(\sqrt{3}/\sqrt{k}, \infty)$ and satisfies

$$\lim_{u \searrow 0} w_{f_r=0}(u) = \lim_{u \nearrow \infty} w_{f_r=0}(u) = -1. \tag{3.126}$$

Recall $m_1 < m_2$. Defining $l(u) := m_2 u^2/(\mu + u)$,

$$l(u) - w_{g_r=0}(u) = \frac{m_2}{\mu + u} \left(1 - \frac{1}{1 + ku^2}\right) u^2, \tag{3.127}$$

$$l(u) - w_{g_r=0}(u) > 0, \tag{3.128}$$

$$\lim_{k \to 0} \|l - w_{g_r=0}\|_{L^\infty([0,c])} = 0, \tag{3.129}$$

holds on any finite interval $(0,c]$. Moreover $w_{f_r,g_r}(u)$ is strictly increasing and continuous on $\mathbb{R}_{\geq 0} \setminus \{(m_1\mu)/(m_2-m_1)\}$, non-negative and convex on $[0,(m_1\mu)/(m_2-m_1))$, negative on $((m_1\mu)/(m_2-m_1),\infty)$ and satisfies

$$\lim_{u \nearrow \frac{m_1\mu}{m_2-m_1}} w_{f_r,g_r}(u) = \infty, \tag{3.130}$$

$$\lim_{u \searrow \frac{m_1\mu}{m_2-m_1}} w_{f_r,g_r}(u) = -\infty. \tag{3.131}$$

Furthermore, it holds that

$$w_{f_r,g_r}(0) = w_{g_r=0}(0) = 0, \tag{3.132}$$

$$\frac{dw_{g_r=0}}{du}(0) = 0 < \frac{dw_{f_r,g_r}}{du}(0). \tag{3.133}$$

It follows that $w_{g_r=0}(\varepsilon) < w_{f_r,g_r}(\varepsilon)$ holds for ε small.
Combining this fact with (3.130), the uniform boundedness of $w_{g_r=0}$ and the strict convexity of w_{f_r,g_r} on $(0,(m_1\mu)/(m_2-m_1))$, it follows that if and only if $(u,l(u))$ and $(u,w_{f_r,g_r}(u))$ intersect twice on $(0,(m_1\mu)/(m_2-m_1)) \times (0,\infty)$, there exists k_1^* such that for all $k < k_1^*$, it holds that $(u,w_{f_r=0}(u))$ and $(u,w_{f_r,g_r}(u))$ intersect twice.
We solve

$$l(u) = \frac{m_2u^2}{\mu+u} = \frac{m_2}{m_1}\frac{u}{\mu+(1-\frac{m_2}{m_1})u} = w_{f_r,g_r}(u), \tag{3.134}$$

for u and obtain the following solutions for $u \neq 0$:

$$u_\pm = \frac{m_1\mu-1}{2(m_2-m_1)} \pm \sqrt{\left(\frac{m_1\mu-1}{2(m_2-m_1)}\right)^2 - \frac{\mu}{(m_2-m_1)}}. \tag{3.135}$$

Inequality $u_\pm > 0$ holds if and only if

$$\mu > \frac{1}{m_1}, \tag{3.136}$$

and

$$\left(\frac{m_1\mu-1}{2(m_2-m_1)}\right)^2 > \frac{\mu}{(m_2-m_1)}, \tag{3.137}$$

hold. If (3.136) is satisfied, (3.137) is equivalent to

$$\mu^2 + 2\frac{(m_1-2m_2)}{m_1^2}\mu + \frac{1}{m_1^2} > 0. \tag{3.138}$$

Recall $m_2 > m_1$. Inequality (3.138) is satisfied if and only if

$$\mu < \frac{1}{m_1}\left(\frac{2m_2 - m_1}{m_1} - 2\sqrt{\left(\frac{m_2}{m_1}\right)^2 - \frac{m_2}{m_1}}\right), \tag{3.139}$$

or

$$\mu > \frac{1}{m_1}\left(\frac{2m_2 - m_1}{m_1} + 2\sqrt{\left(\frac{m_2}{m_1}\right)^2 - \frac{m_2}{m_1}}\right), \tag{3.140}$$

hold. Note that

$$\left(\frac{m_2}{m_1}\right)^2 - \frac{m_2}{m_1} > 0,$$

holds. Inequality (3.139) is never satisfied, because

$$\frac{1}{m_1}\left(\frac{2m_2 - m_1}{m_1} - 2\sqrt{\left(\frac{m_2}{m_1}\right)^2 - \frac{m_2}{m_1}}\right) < \frac{1}{m_1}, \tag{3.141}$$

implies $\mu < 1/m_1$ if (3.139) holds. Hence, it contradicts (3.136).
Since $m_2 > m_1$,

$$\frac{2m_2 - m_1}{m_1} + 2\sqrt{\left(\frac{m_2}{m_1}\right)^2 - \frac{m_2}{m_1}} > 1, \tag{3.142}$$

holds. It follows for

$$\mu > \frac{1}{m_1}\left(\frac{2m_2 - m_1}{m_1} + 2\sqrt{\left(\frac{m_2}{m_1}\right)^2 - \frac{m_2}{m_1}}\right), \tag{3.143}$$

$$m_2 > m_1, \tag{3.144}$$

that $(u, l(u))$ and $(u, w_{f,g}(u))$ intersect twice on $(0, (m_1\mu_2)/(m_2 - m_1)) \times (0, \infty)$. It follows existence of two homogeneous steady states for sufficiently small k.
To prove that both steady states are of type u_-, we use the fact that the steady state component u is bounded by $(m_1\mu)/(m_2 - m_1)$.
Since $w_{f_r=0}(u) = -1 + m_1 u/(1 + ku^2)$ is strictly increasing on $(0, 1/\sqrt{k})$,

$$\frac{dw(u)}{du}(u^*) > 0, \tag{3.145}$$

holds at any steady state u^* for $\sqrt{k} < (m_2 - m_1)/(m_1\mu)$.
By the characterisation Lemma 3.16, both spatially homogeneous steady states are of type $(u_-(w), w)$ for $k < ((m_2 - m_1)/(m_1\mu))^2$.

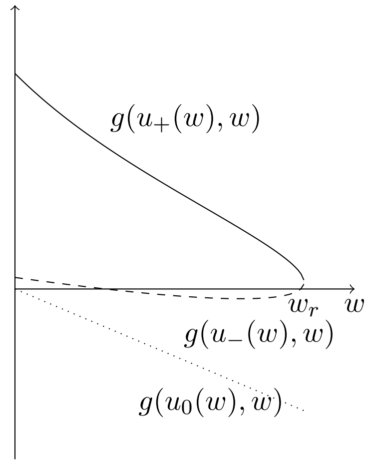

Figure 3.4: Illustration of the right-hand side of $-\partial^2 w/\partial x^2 = g_r(u, w)$ for different branches of the solution $u^*(w)$ of $\partial u/\partial t = f_r(u, w) = 0$. The parameters for illustration are $D = 1, m_1 = 1.44, m_2 = 2, \mu = 4.2$. We can observe that all nontrivial homogeneous steady states are of type u_-.

Proof of Item 3.
Item (3.) is a direct consequence of Lemma 3.6 and the following Auxiliary Lemma.

Auxiliary Lemma 3.18.
Assume $2\sqrt{k} < m_1 < m_2$ and $w \in (0, w_r)$, where w_r is defined as in Lemma 3.16. Then,

$$g_r(u_0(w), w) < 0, \tag{3.146}$$

holds, where g_r is defined in (3.97)*. If there exist two positive spatially homogeneous steady states of type u_-, then*

$$g_r(u_+(w), w) > 0, \tag{3.147}$$

holds.

Proof of Auxiliary Lemma. For $w = 0$,

$$g_r(u_\pm(0), 0) = m_2 \frac{u_\pm(0)^2}{1 + k u_\pm(0)^2} > 0, \tag{3.148}$$

holds. Moreover, $g_r(u_+(w), w)$ is strictly decreasing since derivation with respect to w yields

$$\begin{aligned}\frac{d}{dw} g_r(u_+(w), w) = &-\frac{(1+w)m_1^2 + 2k(1+w)^3 m_1 \mu_3}{2k(1+w)^3 m_1} \\ &- \frac{m_1^3 + 4k(1+w)^3\,(m_2 - m_1)}{2k(1+w)^3 m_1 \sqrt{\frac{-4k(1+w)^2 + m_1^2}{(1+w)^2}}}, \\ &< 0,\end{aligned} \tag{3.149}$$

for $w \geq 0$.

If there exist two spatially homogeneous steady states of type u_-, then $g(u_-(w_r), w_r) = g(u_+(w_r), w_r) > 0$ holds due to the fact that $g(u_-(0), 0) > 0$ holds, because $g(u_-(w), w)$ has exactly two roots of order one. Then, inequality (3.149) and $u_+(w_r) = u_-(w_r)$ yield (3.147). Inequality (3.146) follows immediately from the fact that

$$g_r(0, w) = -\mu w < 0, \tag{3.150}$$

holds for $w \in (0, w_r)$. □

Stability of steady states

To check if the conditions of Theorem 3.9 respectively Lemma 3.10 are satisfied, we need to investigate the signs of the entries of the Jacobian matrix of the kinetic system and the sign of its determinant.

Lemma 3.19. *Consider a system of type*

$$\frac{\partial}{\partial t} u = f(u, w), \qquad x \in \overline{I}, \tag{3.151}$$

$$\frac{\partial}{\partial t} w = D\Delta w + g(u, w), \qquad x \in I, \tag{3.152}$$

$$\partial_n w = 0, \qquad x \in \partial I, \tag{3.153}$$

$$(u(0,x), w(0,x)) \in (C(\overline{I}) \times C^2(\overline{I})) \tag{3.154}$$

Denote the Jacobian matrix of the kinetic system, evaluated at (u, w) as $\mathcal{B}(u, w)$ and let $u^*(w)$ be defined implicitly by $f(u, w) = 0$, where we assume that $|\partial_u f|_{(u^*(w), w)}| \geq c > 0$ holds. Then

$$\det(\mathcal{B}(u^*(w), w)) = -\partial_2 f(u^*(w), w) \frac{d}{dw} g(u^*(w), w) \left(\frac{d}{dw} u^*(w)\right)^{-1}, \tag{3.155}$$

holds, where $\partial_2 f(a, b) := \frac{\partial f(u,w)}{\partial w}(a, b)$.

Proof. Define $\partial_1 f(a,b), \partial_1 g(a,b), \partial_2 g(a,b)$ analogously to $\partial_2 f(a,b)$. First, note that

$$\begin{aligned}
&\frac{d}{dw} g(u^*(w),w) = \frac{du^*(w)}{dw}\partial_1 g(u^*(w),w) + \partial_2 g(u^*(w),w),\\
&\frac{d}{dw} g(u^*(w),w)\frac{dw^*(u)}{du} - \partial_2 g(u^*(w),w)\frac{dw^*(u)}{du} = \partial_1 g(u^*(w),w),
\end{aligned} \tag{3.156}$$

holds, where $w^*(u)$ is defined as the local inverse of $u^*(w)$. Inserting this into the determinant, we obtain

$$\begin{aligned}
\det \mathcal{B}(u^*(w),w) &= \partial_1 f(u^*(w),w)\partial_2 g(u^*(w),w) - \partial_2 f(u^*(w),w)\partial_1 g(u^*(w),w),\\
&= \partial_1 f(u^*(w),w)\partial_2 g(u^*(w),w) + \partial_2 f(u^*(w),w)\partial_2 g(u^*(w),w)\frac{dw^*(u)}{du}\\
&\quad - \partial_2 f(u^*(w),w)\frac{d}{dw}g(u^*(w),w)\frac{dw^*(u)}{du},\\
&= \partial_2 g(u^*(w),w)\left(\partial_1 f(u^*(w),w) + \frac{dw^*(u)}{du}\partial_2 f(u^*(w),w)\right)\\
&\quad - \partial_2 f(u^*(w),w)\frac{d}{dw}g(u^*(w),w)\frac{dw^*(u)}{du},\\
&= \partial_2 g(u^*(w),w)\underbrace{\frac{d}{du}f(u,w^*(u))}_{=0} - \partial_2 f(u^*(w),w)\frac{d}{dw}g(u^*(w),w)\frac{dw^*(u)}{du},\\
&= -\partial_2 f(u^*(w),w)\frac{d}{dw}g(u^*(w),w)\frac{dw^*(u)}{du}.
\end{aligned}$$

□

Lemma 3.20. *Let $2\sqrt{k} < m_1 < m_2$ and denote the Jacobian matrix of the kinetic system of (3.92)-(3.95), evaluated at $(u(x), w(x))$ by*

$$\mathcal{B}(x) := \mathcal{B}(u(x),w(x)) = \begin{pmatrix} \partial_u f_r(u(x),w(x)) & \partial_w f_r(u(x),w(x)) \\ \partial_u g_r(u(x),w(x)) & \partial_w g_r(u(x),w(x)) \end{pmatrix} =: \begin{pmatrix} b_{11}(x) & b_{12}(x) \\ b_{21}(x) & b_{22}(x) \end{pmatrix}.$$

Then, for $0 \le w(x) < m_1/(2\sqrt{k}) - 1 =: w_r$ it holds that

$$b_{11}(x)\begin{cases} > 0, & u(x) = u_-(w(x)),\\ < 0, & u(x) = u_+(w(x)),\\ < 0, & u(x) = u_0, \end{cases} \qquad b_{12}(x)\begin{cases} < 0, & u(x) = u_-(w(x)),\\ < 0, & u(x) = u_+(w(x)),\\ = 0, & u(x) = u_0, \end{cases} \tag{3.157}$$

$$b_{21}(x)\begin{cases} > 0, & u(x) = u_-(w(x)),\\ < 0, & u(x) = u_0, \end{cases} \qquad b_{22}(x)\begin{cases} < 0, & u(x) = u_-(w(x)),\\ < 0, & u(x) = u_+(w(x)),\\ < 0, & u(x) = u_0, \end{cases} \tag{3.158}$$

where u_-, u_+, u_0 are defined in Definition 3.15. Moreover, it holds that

$$\det(\mathcal{B}(u_+(w(x)), w(x)) > 0. \tag{3.159}$$

Proof. First, we calculate the Jacobian matrix of the kinetic system for given arbitrary (u, w):

$$\mathcal{B}(x) := \mathcal{B}(u,w)(x) := \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix} := \begin{pmatrix} -(1+w) + m_1 \frac{2u}{(1+ku^2)^2} & -u \\ -w + m_2 \frac{2u}{(1+ku^2)^2} & -(\mu + u) \end{pmatrix}. \tag{3.160}$$

The signs for $u = u_0 = 0$ follow immediately from inserting $u = 0$. The signs of b_{12} and b_{22} for arbitrary u can be derived directly, too.
For $f_r(u, w) = -(1 + w)u + m_1 u^2/(1 + ku^2) = 0$,

$$\begin{aligned} b_{11} &= -(1+w) + \frac{2}{1+ku^2} m_1 \frac{u}{1+ku^2}, \\ &= -(1+w) + \frac{2}{1+ku^2}(1+w), \\ &= \left(-1 + \frac{2}{1+ku^2}\right)(1+w), \end{aligned} \tag{3.161}$$

holds. Combining (3.161) with Lemma 3.16, i.e. $u_-(w) \leq 1/\sqrt{k} \leq u_+(w)$, yields the result for b_{11}.
We investigate b_{21}: Now, $f_r(u, w) = 0$ implies

$$\begin{aligned} b_{21} &= -w + m_2 \frac{2u}{(1+ku^2)^2}, \\ &= -w + \frac{m_2}{m_1}(1+w) + \frac{m_2}{m_1}\left(-1 - w + m_1 \frac{2u}{(1+ku^2)^2}\right), \\ &= \frac{m_2}{m_1} + \left(\frac{m_2}{m_1} - 1\right) w + \frac{m_2}{m_1} b_{11}. \end{aligned} \tag{3.162}$$

The continuity of b_{21} and $b_{11}(w_r) = 0$ implies the result for b_{21}. Recall (3.149), i.e.

$$\frac{d}{dv} g_r(u_+(w), w) < 0, \tag{3.163}$$

and Lemma 3.16, i.e.

$$\frac{d}{dv} u_+(w) < 0. \tag{3.164}$$

Now, application of Lemma 3.19 yields the sign of the determinant. □
Combining the results, we obtain the following Theorem for model (3.92)-(3.94):

Theorem 3.21 (Coexistence of DDI and hysteresis for model (3.92)-(3.94))**.**
Under conditions

$$
\begin{aligned}
&m_1, m_2, k, \mu > 0, \\
&m_1 < \min(m_2, \sqrt{m_2}), \\
&\mu > \frac{1}{m_1}\left(\frac{2m_2 - m_1}{m_1} + 2\sqrt{\left(\frac{m_2}{m_1}\right)^2 - \frac{m_2}{m_1}}\right),
\end{aligned}
$$

there exists

$$0 < k^* \leq \min\left(\left(\frac{m_2 - m_1}{m_1\mu}\right)^2, \frac{m_1^2}{4}\right), \tag{3.165}$$

such that for all $0 < k < k^*$*, the following hold:*

1. *system* (3.92)-(3.95) *has exactly two strictly positive spatially homogeneous steady states,* $(u_-(w_1), w_1)$ *and* $(u_-(w_2), w_2)$ *with* $w_1 < w_2$*,*
2. $(u_-(w_1), w_1)$ *is an unstable steady state of system* (3.92)-(3.95) *and its kinetic system,*
3. $(u_-(w_2), w_2)$ *is a stable steady state of the kinetic system of* (3.92)-(3.95) *and an unstable steady state of* (3.92)-(3.95)*,*
4. $(0, 0)$ *is a stable steady state of system of* (3.92)-(3.95) *and its kinetic system,*
5. *system* (3.92)-(3.95) *has infinitely many* (ε_0, A)*-stable, weak jump-type steady states which are at all* $x \in \overline{I}$ *of class* u_+ *or* u_0*.*

3.6.2 Lengyel-Epstein model

In [LE91], Lengyel and Epstein consider the model

$$\frac{\partial}{\partial t}u = D_1\Delta u + a - \left(1 + 4\frac{v}{1+u^2}\right)u, \qquad (x,t) \in I \times (0,T), \tag{3.166}$$

$$\frac{\partial}{\partial t}v = D\Delta v + b\left(1 - \frac{v}{1+u^2}\right)u, \qquad (x,t) \in I \times (0,T), \tag{3.167}$$

$$\partial_n u = \partial_n v = 0, \qquad (x,t) \in \partial I \times (0,T), \tag{3.168}$$

$$u(x,0), v(x,0) \in C^2(\overline{I}), \tag{3.169}$$

where $a, b \in \mathbb{R}_{\geq 0}$, to describe pattern formation in the CIMA reaction, which was described chemically in [KCDB90]. The authors of [KCDB90] conducted an experiment involving two

reactive species. One of the species acts as inhibitor (v), the other one as activator (u). Since both chemicals diffuse at similar rates, the experiment was performed in a gel reactor, binding the activator and therefore reducing its 'average' diffusion rate. We investigate the behaviour for trivial activator's diffusion rate, i.e. it is 'pinned'. We suggest performing an experiment of this type to give further implication for validation or falsification of the model suggested in [LE91].
By setting $D_1 = 0$ in the system proposed in [LE91], we obtain system

$$\frac{\partial}{\partial t}u = a - \left(1 + 4\frac{v}{1+u^2}\right)u, \qquad (x,t) \in I \times (0,T), \tag{3.170}$$

$$\frac{\partial}{\partial t}v = D\Delta v + b\left(1 - \frac{v}{1+u^2}\right)u, \qquad (x,t) \in I \times (0,T), \tag{3.171}$$

$$\partial_n v = 0, \qquad (x,t) \in \partial I \times (0,T). \tag{3.172}$$

$$(u(x,0), v(x,0) \in (C(\overline{I}) \times C^2(\overline{I})) \tag{3.173}$$

Uniform boundedness

Lemma 3.22. *(Variant of [NT05], Proposition 2.2, for $D_1 = 0$)*
Let $\varepsilon > 0$ be arbitrary. For a solution (u, v) of system (3.170)-(3.173) *with non-negative initial conditions, there exists a $t^* \geq 0$, such that for all $t \geq t^*$ it holds that*

$$0 \leq u(x,t) \leq a + \varepsilon, \tag{3.174}$$

$$0 \leq v(x,t) \leq 1 + a^2 + \varepsilon. \tag{3.175}$$

Proof. First, note that

$$\frac{\partial}{\partial t}v \geq D\Delta v - b\frac{u}{1+u^2}v, \tag{3.176}$$

implies $v \geq 0$. Hence,

$$\frac{\partial}{\partial t}u \leq a - u, \tag{3.177}$$

holds and implies $u \leq a + \varepsilon$. Finally, due to $u \leq a + \varepsilon$,

$$\frac{\partial}{\partial t}v \leq \Delta v + bu - \frac{u}{1+u^2}v, \tag{3.178}$$

implies $v \leq 1 + a^2 + \varepsilon$. □

Existence and (In)stability of steady states

In [NT05], diffusion-driven instability in model (3.166)-(3.169) for $D_1 > 0$ and sufficiently large $D > 0$. Moreover, existence of Turing patterns for $D_1 > 0$ is investigated. We recall the result for DDI, extend it to $D_1 = 0$ and prove existence and stability of jump-type steady states for $D_1 = 0$ and arbitrary $D > 0$.

Lemma 3.23. *Consider system* (3.170)-(3.173).

1. *For sufficiently large $a > 0$, there exist three branches*

$$u_-(v) \leq u_0(v) \leq u_+(v), \tag{3.179}$$

of $f(u,v) := a - \left(1 + 4v/(1+u^2)\right) u = 0$.

2. *For sufficiently large $a \geq 125/3$, there exist infinitely many weak, (ε_0, A)-stable steady states of type*

$$\begin{aligned} u(x) =& \chi(x) u_+(v(x)) + (1-\chi(x)) u_-(v(x)), \\ v \in& C^1(\overline{I}), \end{aligned} \tag{3.180}$$

where χ is the characteristic function of a fat subset of $\overline{I}$.

3. *For sufficiently large $a \geq 125/3$ and $a < b/2 + \sqrt{(b/2)^2 + 25}$, model* (3.170)-(3.173) *exhibits diffusion-driven instability at the unique spatially homogeneous steady state*

$$(\overline{u}, \overline{v}) = \left(\frac{a}{5}, 1 + \left(\frac{a}{5}\right)^2 \right). \tag{3.181}$$

Proof. First, note that $(a/5, 1 + (a/5))$ is the unique non-negative spatially homogeneous steady state. We investigate stability of discontinuous steady states, i.e. steady states of type (3.180). All steady states satisfy

$$a - \left(u + \frac{4vu}{1+u^2}\right) = 0. \tag{3.182}$$

Identity (3.182) is equivalent to

$$-u^3 + au^2 + (4v-1)u + a = 0, \tag{3.183}$$

and, for $u \neq 0$, to

$$v = \frac{(a-u)(1+u^2)}{4u}. \tag{3.184}$$

Identity (3.183) shows that $f(u,v)=0$ has three branches and (3.184) implies that

$$\begin{aligned} \lim_{u\searrow 0} v(u) &= \infty, \\ \lim_{u\nearrow \infty} v(u) &= -\infty, \end{aligned} \tag{3.185}$$

holds. Both sequences are monotone for sufficiently small respectively sufficiently large u. Consequently, we obtain either exactly one branch $u(v)$ of $f(u(v),v)=0$ or exactly three branches $u_-(v) \leq u_0(v) \leq u_+(v)$. If we show $\frac{d}{du}v(u)|_{u=\frac{a}{5}} > 0$, existence of exactly three positive branches follows.
Using the implicit function theorem and $\partial_2 f(u,v) = -4u/(1+u^2)$, we obtain

$$\begin{aligned} \frac{d}{du}f(u,v(u)) =& \frac{dv(u)}{du}\partial_2 f(u,v(u)) + \partial_1 f(u,v(u)), \\ =& 0, \end{aligned} \tag{3.186}$$

and consequently

$$\begin{aligned} \frac{dv(u)}{du} =& \frac{\partial_1 f(u,v(u))}{|\partial_2 f(u,v(u))|}, \\ \operatorname{sgn}\left(\frac{dv(u)}{du}\right) =& \operatorname{sgn}(\partial_1 f(u,v(u))). \end{aligned} \tag{3.187}$$

For $a \geq 125/3$, inequality

$$\partial_u f\left(\frac{a}{5}, v\left(\frac{a}{5}\right)\right) = 2\frac{a\frac{a}{5} - (\frac{a}{5})^2}{1+(\frac{a}{5})^2} - 5 \geq 0, \tag{3.188}$$

holds. Consequently, there exist three branches

$$u_-(v) \leq u_0(v) \leq u_+(v), \tag{3.189}$$

of $f(u,v)=0$ satisfying

$$\partial_1 f(u_-(v),v), \partial_1 f(u_+(v),v) \leq 0 \leq \partial_1 f(u_0(v),v). \tag{3.190}$$

Inequality (3.190) shows that the unique positive spatially homogeneous steady state is unstable for $D>0$, see Lemma 3.2.
Define $g(u,v) := b\left(1 - v/(1+u^2)\right)u$ and denote the Jacobian matrix of the kinetic system at (u,v) as $\mathcal{B}(u,v)$. Since

$$\partial_2 g(u,v) = \frac{1}{4}\partial_2 f(u,v) = -\frac{u}{1+u^2} < 0, \tag{3.191}$$

$$\det(\mathcal{B}(u,v)) = 5\frac{u}{1+u^2} > 0, \tag{3.192}$$

holds, equations (3.190), (3.191), show that steady states of type (3.180) satisfy the conditions of Lemma 3.10. Therefore, they are (ε_0, A)-stable. To prove existence of discontinuous steady states, recall that $(u,v) = (a/5, v(a/5))$ is the unique root of $g(u,v)$ satisfying $f(u,v) = 0$. Moreover, recall that

$$0 < u_-(v) \leq \min_{0 \leq v \leq 1+a^2} u_0(v) \leq \max_{0 \leq v \leq 1+a^2} u_0(v) \leq u_+(v) \leq a, \tag{3.193}$$

holds. Consequently, it holds that

$$\Delta v > 0, \quad u = u_-(v), \tag{3.194}$$

$$\Delta v < 0, \quad u = u_+(v), \tag{3.195}$$

showing that the conditions of Lemma 3.6 are satisfied, hence steady states of type (3.180) exist. It is left to prove stability of $(\overline{u}, \overline{v})=(a/5, 1+(a/5)^2)$ for $D = 0$. We already showed that $\det(\mathcal{B})(u,v) > 0$ holds, see (3.6.2). Therefore, it is left to prove that $\operatorname{tr}(\mathcal{B}(a/5, 1+(a/5)^2)) < 0$ holds: Derivation yields

$$\operatorname{tr}(\mathcal{B}(u,v)) = 4\frac{u^2-1}{v} - 1 - b\frac{u}{v}, \tag{3.196}$$

hence

$$\operatorname{tr}\left(\mathcal{B}\left(\frac{a}{5}, 1+\left(\frac{a}{5}\right)^2\right)\right) = \frac{a^2}{5} - 5 - b\frac{a}{5} < 0, \tag{3.197}$$

is satisfied if and only if

$$a < \frac{b}{2} + \sqrt{\left(\frac{b}{2}\right)^2 + 25}. \tag{3.198}$$

holds. This concludes the proof. □

3.6.3 Numerical results

In this section, we present numerical results. All simulations in this work are performed using the finite element library *deal.ii*, [BHK07]. If not specified differently, cell-wise constant finite elements are used to discretise the ODE and cell-wise linear, globally continuous finite elements are used to discretise the PDE. Crank-Nicholson time-stepping scheme is used for discretisation in time. If used, adaptivity in space is based on a dual estimator proposed in [ELW00], where also an a priori error estimate is given. The scheme is also described in [Här11]

and the order of convergence has been studied in [Här11, HMC14] for a reaction-diffusion-ODE model in the case of emergence of spikes. Since sharp gradient patterns are, in the sence of the H^1 semi norm, similar, we refer to [HMC14] instead of repeating the results. However, for completeness, we show the order of error reduction under mesh refinement for Figure 3.8 in the Appendix. During pattern selection, the solutions are more regular. Hence, stability factors in the sense of [ELW00], which are linked to the constants of the dual error estimate, remain relatively small during pattern selection (due to regularity). However, they increase for large time. But in that case, the analytical results imply stability.
The numerical results motivate the following hypotheses:

1. For D large, the arising pattern depends highly on initial conditions,
2. For D small, the arising pattern depends on the size of the diffusion coefficient,
3. The 'more irregular' the initial conditions, i.e. 'high-frequency', the larger the threshold on D in items 1. and 2.

The first hypothesis in particular is a natural consequence of the fact that, as D tends to infinity, the solution of system (3.1) converges towards the solution of the so called 'shadow system' on a finite-in-time interval, see e.g. [Bob15].

De-novo **pattern formation**

In the first part of the numerical investigations, we choose very smooth initial conditions and decrease the diffusion coefficient. We observe that the number of 'plateaus' (respectively number of jump-discontinuities) of the pattern rises as the diffusion coefficient tends towards zero. As parameter set, we choose, for model (3.92)-(3.95),

Parameter set 3.24.

$$m_1 = 1.44,\ m_2 = 2,\ \mu = 4.1,\ k = 0.01, \tag{3.199}$$

$$\begin{aligned} u(0,x) &= 6.36 + 0.1x^6\cos(4\pi x^2), \\ w(0,x) &= 5.54. \end{aligned} \tag{3.200}$$

Component u of (3.200) *is shown in Figure 3.5.*

In Figure 3.5, we observe, for large D, that the shape of the arising pattern resembles the shape of the initial conditions. However, note that the 'plateaus' in Figure 3.5(right) do neither intersect nor touch any steady state of the kinetics system. The largest steady state of the kinetic system assumes value $u \approx 6.412$. This implies that stability of the pattern does not solely yield from a sufficiently strong stabilising effect of the kinetic system. Moreover, for small $D > 0$, the arising pattern depends on both, initial conditions and diffusion coefficient,

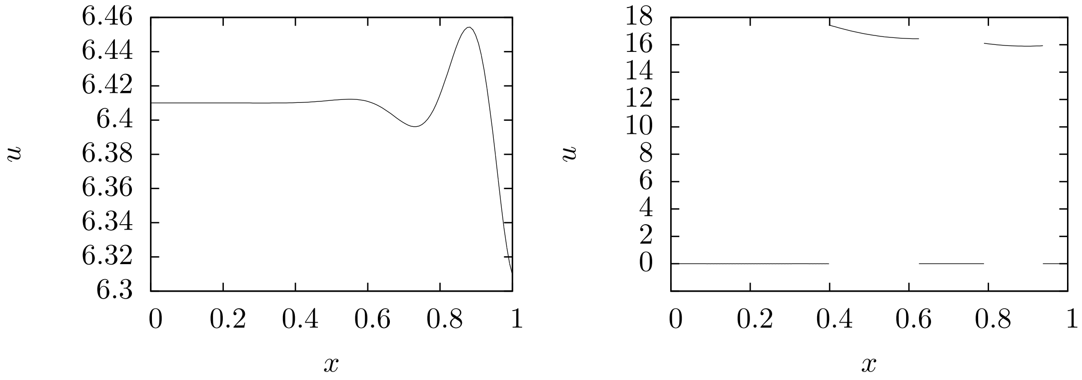

Figure 3.5: Left: Component u of (3.200). Right: Solution's component u for Parameter set 3.24, $D = 10$, $t = 20$. The shape of the pattern resembles the shape of the initial conditions. Note, however that $u = 6.41$ is the largest spatially homogeneous steady state. The phenomenon is therefore not bi-stability as in [Köt13].

as we can observe in Figures 3.6-3.7, where solutions for parameter set 3.24 are shown for different D. The following trend can be observed: As the diffusion coefficient becomes smaller, the number of jump-type discontinuities of the pattern rises. In [HMC14], we already observe a similar phenomenon in another reaction-diffusion-ODE model exhibiting dynamical spike patterns, i.e. grow-up (blow-up in infinity). For models of type (3.1) exhibiting DDI, the first n_D modes are stable and the other modes are unstable. As D tends towards zero, n_D tends towards infinity. We suspect the following distinction of cases:

- In case of in Fourier-sense low-frequency initial conditions, the first unstable mode,
- In case of in Fourier-sense high-frequency initial conditions, the dominating unstable mode of initial conditions,

induces a pre-pattern due to DDI. Once the solution is sufficiently far away from the steady state with DDI, the hysteretic effect shown in this work stabilises the pattern. Note that this effect is *de-novo* formation of irregular patterns. Moreover, note that the DDI observed is different from classical models with finitely many unstable modes.
Another hypothesis is that there exists a maximal measure of the support of a 'plateau' which is determined by D. This corresponds to the rescaling argument in the proof of Lemma 3.6. The second hypothesis is strengthened by the following observation: In the left part of Figure 3.7, we observe breakdown of a too 'large' plateau. Moreover, we observe emergence of patterns 'piece by piece' instead of amplification of modes.

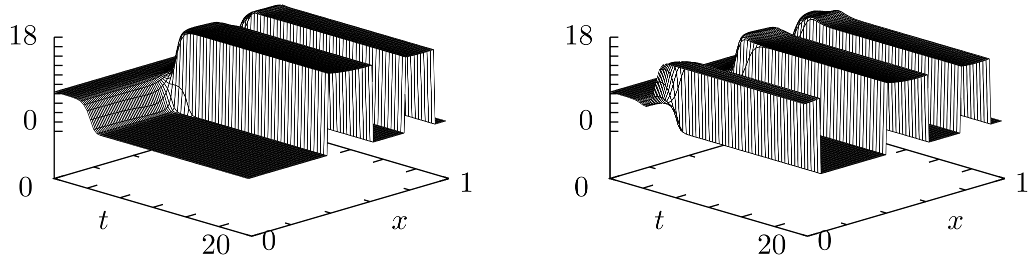

Figure 3.6: Component u of the solution of (3.92)-(3.95) for parameter set (3.24). Left: $D = 10$. Right: $D = 5$

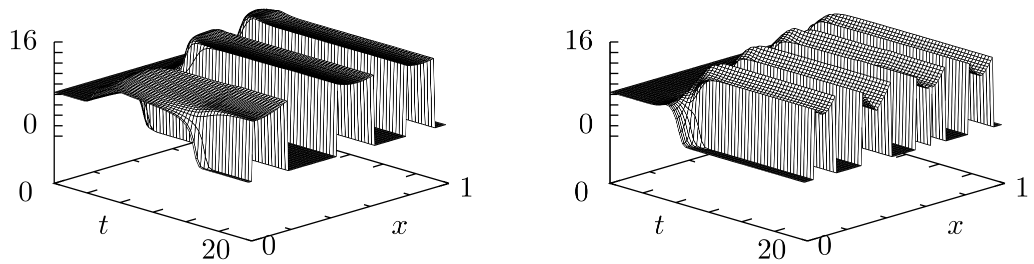

Figure 3.7: Component u of the solution of (3.92)-(3.95) for parameter set (3.24). Left: $D = 2$. Right: $D = 0.2$

Hysteresis: Grafting experiment

As described within the introduction, it is well known that after transplanting head cells of a hydra, an axially shaped fresh-water polyp, it grows an additional head at the position where head cells were transplanted to. While classical systems of reaction-diffusion equations have been shown to be suited for modelling of de-novo formation of regular patterns, see [Tur52, GM72, HPT99, VE09], no results showing their capability for modelling the grafting experiment is known to us. Some proposed reaction-diffusion-ODE models have been shown to reflect the behaviour of the grafting experiment, but lack *de-novo* pattern formation, [MCK06, Köt13]. In the previous section, we showed that construction of irregular patterns is possible for models of type (3.1). In the previous subsection, we presented numerical results indicating that de-novo formation of patterns can be observed. Based on the analytical result given in this work, we conclude that irregular patterns are stable. Here, we will show numerical results implying that model (3.92)-(3.95) might reflect the behaviour of the grafting experiment.
We choose the following

Parameter set 3.25.

$$m_1 = 1.44,\ m_2 = 2,\ \mu = 4.1,\ k = 0.01,\ D = 15, \tag{3.201}$$

$$\begin{aligned} u(0,x) &= 6.36 - 0.1\cos(\pi x), \\ w(0,x) &= 5.54, \end{aligned} \tag{3.202}$$

and approximate the solution until $t = 20$. Component u of (3.200) is shown in Figure 3.5. Since the diffusion coefficient is large, the appearing pattern resembles the shape of the initial conditions. Therefore, there exists a subdomain in which u assumes high values and a subdomain in which u assumes low values. u is assumed to represent the concentration of head cells. At $t = 20$, we 'transplant' head cells onto another position of hydra's body. This is modelled by approximating the solution to the boundary value problem taking $u(20, x) + f(x)$ as initial conditions, where

$$f(x) = \begin{cases} 10\sin(5(x-0.1)\pi) & 0.1 \le x \le 0.3, \\ 0 & \text{else.} \end{cases} \tag{3.203}$$

In Figure 3.8(right), we observe that the concentration of head cell stabilises at the position onto which cells were transplanted. However, the steady state becomes unstable in a neighbourhood of $x = 1$ and u becomes locally trivial. A possible explanation is that the initial values of problem (3.24) are changed at the point of discontinuity defined on the right-hand side of the left arising 'plateau' and therefore reducing the maximal feasible size of the second 'plateau' in order to satisfy the homogeneous Neumann boundary conditions. The solution's component w is shown in Figure 3.9.

Remark 3.26. *We will address the problem of strong dependence on initial conditions in chapter 5 when investigating the shadow system.*

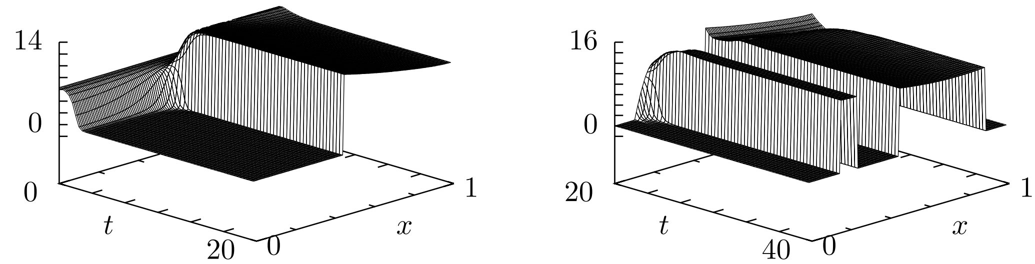

Figure 3.8: Component u of the solution of (3.92)- (3.95) for parameter set 3.25. Grafting (with perturbation (3.203) to u) is performed at $t = 20$. Left: $0 \leq t < 20$. Right: $20 \leq t \leq 40$.

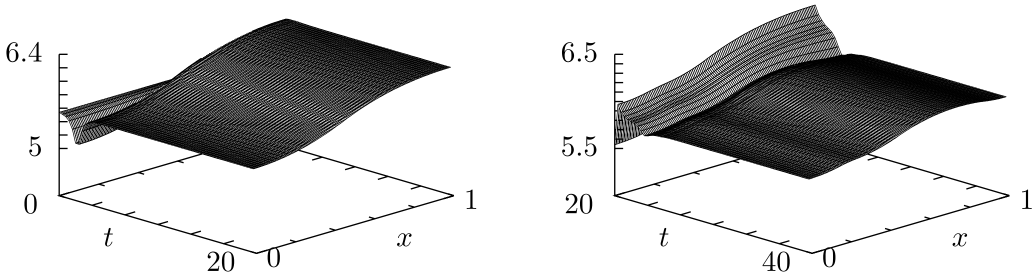

Figure 3.9: Component w of the solution of (3.92)- (3.95) for parameter set 3.25. Grafting (with perturbation (3.203) to u) is performed at $t = 20$. Left: $0 \leq t < 20$. Right: $20 \leq t \leq 40$.

Introduction of weak diffusion of u: Breakdown

In this subsection, we perform the same simulation as above, but instead of performing the grafting experiment, i.e. adding $f(x)$ to $u(15,x)$, we introduce diffusion of u at $t = 15$, i.e. we approximate the solution to

$$\begin{aligned}
\frac{\partial}{\partial t}u =& \begin{cases} -u - uw + m_1 \frac{u^2}{1+ku^2}, & (x,t) \in \overline{I} \times (0,15], \\ \tilde{D}\Delta u - u - uw + m_1 \frac{u^2}{1+ku^2}, & (x,t) \in I \times (15,T), \end{cases} \\
\frac{\partial}{\partial t}w =& D\Delta w - \mu w - uw + m_2 \frac{u^2}{1+ku^2}, \quad (x,t) \in I \times (0,T), \\
\partial_n w =& 0, \\
\partial_n u =& 0, \quad t > 15,
\end{aligned} \tag{3.204}$$

(note that compartment u satisfies homogeneous Neumann boundary conditions at $t = 15$ in Figure 3.10) with

Parameter set 3.27.

$$m_1 = 1.44,\ m_2 = 2,\ \mu = 4.1,\ k = 0.01,\ D = 1,\ \tilde{D} = 0.01, \tag{3.205}$$

$$\begin{aligned} u(0,x) &= 6.36 + 0.1\cos(3\pi x)x^2, \\ w(0,x) &= 5.54. \end{aligned} \tag{3.206}$$

The numerical scheme changes here. For $t < 15$, we use cell-wise constant elements for the ordinary differential equation and cell-wise linear, globally continuous elements for the reaction-diffusion equation. At $t = 15$, the solution for u is interpolated by cell-wise linear, globally continuous elements. As values on the discontinuities of the cell-wise elements, the mean value between neighbording elements is used. This interpolation is then used as initial conditions for $t > 15$, where for both components cell-wise linear, globally continuous finite elements are used for discretisation in space. As before, the Crank-Nicholson time-stepping scheme is used. In Figures 3.10 and 3.11 the numerically approximated solution is shown. We observe a breakdown, even if very small diffusion is introduced, and convergence towards a regular pattern of class C^2. This illustrates the fundamentally different character of arising patterns as $\tilde{D}$ tends towards zero, i.e. the singular nature of the limit regarding stability.

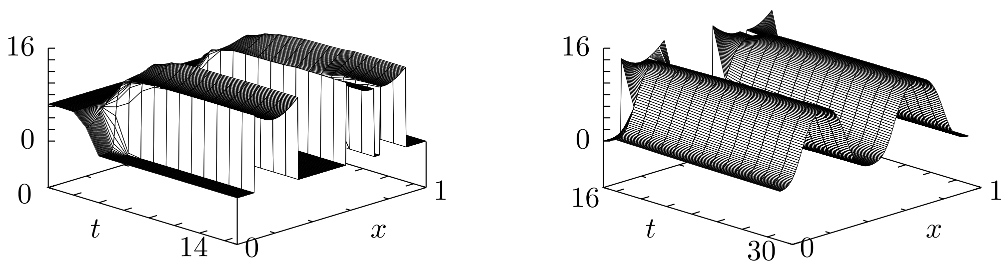

Figure 3.10: Component u of the solution of (3.204) for parameter set (3.27). Diffusion of u is introduced at $t = 15$. Left: $0 \leq t < 15$. Right: $15 \leq t \leq 30$. We observe a breakdown and emergence of a classical regular Turing type pattern.

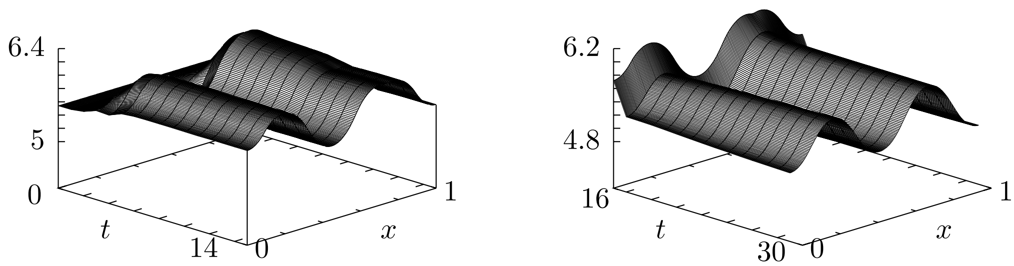

Figure 3.11: Component w of the solution of (3.204) for parameter set (3.27). Diffusion of u is introduced at $t = 15$. Left: $0 \leq t < 15$. Right: $15 \leq t \leq 30$. We observe a breakdown and emergence of a classical regular Turing type pattern.

4 Quasi steady state approximation for reaction-diffusion-ODE systems

In this chapter, we investigate the behaviour of solutions of a certain class of reaction-diffusion-ODE systems under so called 'quasi-steady state reduction'. We are interested in the question whether

- diffusion-driven instability,
- stability of steady states,
- dynamical behaviour on finite time intervals,

are invariant (respectively the dynamical behaviour is similar) under so called quasi-steady state approximation. For $U^\delta = (u_i^\delta)_i$, $V^\delta = (v_i^\delta)_i$ and $W^\delta = (w_i^\delta)_i$, consider a system of type

$$\frac{\partial U^\delta}{\partial t} = f(U^\delta, V^\delta, W^\delta), \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.1}$$

$$\delta\frac{\partial V^\delta}{\partial t} = g(U^\delta, V^\delta, W^\delta), \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.2}$$

$$\frac{\partial W^\delta}{\partial t} = D\Delta W^\delta + h(U^\delta, V^\delta, W^\delta), \qquad (x,t) \in I \times (0,T), \tag{4.3}$$

$$\partial_n w_i^\delta(x,t) = 0, \qquad x \in \partial I, t > 0, \tag{4.4}$$

supplemented classical initial conditions,

$$(U^\delta(x,0), V^\delta(x,0), W^\delta(x,0)) \in (C(\overline{I})^{\dim(U^\delta)+\dim(V^\delta)} \times C^2(\overline{I})^{\dim(W^\delta)}). \tag{4.5}$$

The variables $U^\delta, V^\delta, W^\delta$ can be vector-valued and D is a diagonal matrix with positive entries, i.e. $D = \text{diag}(d_1, ..., d_{\dim(W^\delta(t,x))})$. *If $U, V, W, U^\delta, V^\delta, W^\delta$ are scalar, we denote them $u, v, w, u^\delta, v^\delta, w^\delta$. If they are vector-valued, we denote their components $u_i^\delta, v_i^\delta, w_i^\delta$.* Under 'quasi steady state' approximation, we understand the differential-algebraic equation resulting from setting $\delta = 0$, i.e.

$$\frac{\partial U^0}{\partial t} = f(U^0, V^0, W^0), \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.6}$$
$$0 = g(U^0, V^0, W^0), \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.7}$$
$$\frac{\partial W^0}{\partial t} = D\Delta W^0 + h(U^0, V^0, W^0), \qquad (x,t) \in I \times (0,T), \tag{4.8}$$

also supplemented with homogeneous Neumann boundary conditions for W^0 and initial conditions $(U^0(x,0), W^0(x,0)) \in (C(\overline{I})^{\dim(U^0)} \times C^2(\overline{I})^{\dim(W^0)})$.
By definition, system (4.1)-(4.5) and system (4.6)-(4.8) have exactly the same steady states if they exist. Under

Assumption 4.1. *Assume that* (4.7) *can be solved uniquely for* $V^0(U^0, W^0)$ *for all* (U^0, W^0) *and that* $V^0(U^0, W^0)$ *is continuous in both variables,*

equations (4.6)-(4.8) can be rewritten as

$$\frac{\partial U^0}{\partial t} = f(U^0, V^0(U^0, W^0), W^0), \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.9}$$
$$\frac{\partial W^0}{\partial t} = D\Delta W^0 + h(U^0, V^0(U^0, W^0), W^0), \qquad (x,t) \in I \times (0,T), \tag{4.10}$$

having exactly the same steady states as (4.6)-(4.8). In [Tik52][1], Tikhonov assumes for $D = 0$ that a solution $V^*(U^\delta, W^\delta)$ of $g(U^\delta, V^\delta, W^\delta) = 0$ is a globally stable stationary solution of $\partial V^\delta/\partial t = g(U^\delta, V^\delta, W^\delta)$ for any fixed (U^δ, W^δ). Then, the solution $(U^\delta, V^\delta, W^\delta)$ converges uniformly on any finite time interval towards the solution (U^0, V^0, W^0) of the corresponding system for $\delta = 0$ as δ tends towards zero. Since Tikhonov's result holds for finite time, it does not imply 'transfer of stability' as $\delta \to 0$, only instability. In Lemma 4.5, we prove an analogous result for $D > 0$, showing that the solution for $\delta \to 0$ converges uniformly on any finite time interval towards the solution for $\delta = 0$. This shows that instability is invariant under quasi-steady state approximation for sufficiently small δ. Tikhonov's result is extended onto the time interval $(0, \infty)$ by Hoppenstaedt in [Hop66], showing that in the neighbourhood of an exponentially stable steady state of the reduced system, stability is preserved. We give an alternative proof for $D = 0$, based on investigation of the spectrum. We do not restrict our analysis to the neighbourhood of asymptotically stable steady state of the reduced system, since it is performed for linearisation around an arbitrary state. Consequently, we give conditions under which diffusion-driven instability of the quasi-steady state approximation (4.9)-(4.10) implies diffusion-driven instability of system (4.1)-(4.5) for δ sufficiently small.

[1] The paper is in Russian and referred to usually within this context. The result can be found in [BL14].

More precisely, we can deduce the following implications under certain conditions:

1. From Lemma 4.2, it follows: Assume $D = 0$ and let $(\overline{U}, \overline{V}, \overline{W})$ be a constant steady state. Assume that no eigenvalue of the linearised operator for $\delta = 0$, evaluated at $(\overline{U}, \overline{W})$, has real part equal to zero.

   a) If $(\overline{U}, \overline{V}, \overline{W})$ is stable for $\delta = 0$, it is stable for all sufficiently small δ,

   b) If $(\overline{U}, \overline{V}, \overline{W})$ is unstable for $\delta = 0$, it is unstable for all sufficiently small δ.

2. Assume $D > 0$ and let $(\tilde{U}, \tilde{V}, \tilde{W})$ be a constant or jump-type steady state. From Lemma 4.5, it follows: instability of $(\tilde{U}, \tilde{V}, \tilde{W})$ for $\delta = 0$ implies instability for all sufficiently small δ.

Item 2 shows that stability of a steady state for $\delta = 0$ is a necessary condition for stability for small $\delta > 0$. Note that up to this point, analysis is not restricted to scalar U, V, W. We can prove the reverse implication of item 2 under stricter conditions only. It is not proved based on the technique used to prove the Tikhonov-type result for $D > 0$: the order of divergence from an unstable steady state may depend on δ. Therefore, it is possible that for any fixed δ, the solution 'waits' until time T_δ to cross the boundary on $\left\|(|U^\delta - U^0|, |V^\delta - V^0|, |W^\delta - W^0|)\right\|$ (given in Theorem 4.5). The investigation of 'invariance' of stability of steady states for $D > 0$ is therefore addressed based on (ε_0, A)-stability, see Definition 3.8. It is performed in Lemma 4.7 and is limited to the reduction of a system of two ODEs coupled to one RDE, i.e. $U = u, V = v, W = w$. Note that if the conditions for the Tikhonov-type result and invariance of (in)stability are satisfied, even pattern selection for sufficiently small $\delta > 0$ can be deduced from the reduced system, i.e. the case $\delta = 0$.
In subsection 4.5, we show that models (4.82)-(4.84) and the Lengyel-Epstein model satisfy these conditions. Consequently, the results in section 3.6 carry over to the unreduced models for sufficiently small $\delta > 0$.

4.1 Existence of solutions and steady states

Existence of local-in-time solutions yields from regularity of the right-hand-side, see chapter 3. System (4.6)-(4.8) has exactly the same steady states as system (4.1)-(4.5) if they exist. Existence of global-in-time solutions yields from Assumption 2.1.

4.2 Invariance of (In)stability of steady states of the kinetic system under Tikhonov reduction

Consider a system of ordinary differential equations of type

$$\frac{\partial}{\partial t}u_i^\delta = f_i(U^\delta, V^\delta), \qquad 1 \le i \le n_u, \tag{4.11}$$

$$\delta\frac{\partial}{\partial t}v_i^\delta = g_i(U^\delta, V^\delta), \qquad 1 \le i \le n_v, \tag{4.12}$$

with initial conditions in $\mathbb{R}^{n_u+n_v}$ and where $U^\delta = (u_1^\delta, .., u_{n_u}^\delta)$ and V^δ is defined analogously. We prove that, under suitable conditions, the limit $\delta \to 0$ is regular regarding stability of steady states. In order to see this, we investigate the spectrum of the linearised operator. We show that any eigenvalue of the linearised operator for $\delta > 0$ at a steady state converges either towards an eigenvalue of the linearised operator for $\delta = 0$ or its real-part converges towards $-\infty$ with at least the same order as the imaginary part can diverge.

Lemma 4.2. *Consider system* (4.11)-(4.12)*. Assume that* $g(U^\delta, V^\delta) = (g_i(U^\delta, V^\delta))_i = 0$ *has an isolated solution* $V^*(U^\delta)$ *and that the subsystem describing* V^δ *is a 'stable subsystem', i.e.*

$$\mathrm{Re}(\sigma(\nabla_{V^\delta} g|_{(U^\delta, V^*(U^\delta))})) \subset (-\infty, -c), \tag{4.13}$$

for some $c > 0$*, where* $\nabla_{V^\delta} g|_{(U^\delta, V^*(U^\delta))} = (\partial_{v_j^\delta} g_i|_{(U^\delta, V^*(U^\delta))})_{ij}$*. For* $\delta > 0$*, denote the Jacobian matrix of* (4.11)-(4.12) *at* $(U^\delta, V^*(U^\delta))$ *by* $\mathcal{A}^\delta(x)$ *and denote the spectrum of* $\mathcal{A}^\delta$ *by* $\sigma(\mathcal{A}^\delta)$*. For* $f = (f_i)_i$*, denote the Jacobian matrix of*

$$\frac{\partial}{\partial t}u_i^0 = f_i(U^0, V^*(U^0)), \quad 1 \le i \le n_u, \tag{4.14}$$

evaluated at U^0*, by* $\mathcal{A}^0$*. Then there exists a function* $i : (0, \varepsilon) \times \sigma(\mathcal{A}^0) \to \sigma(\mathcal{A}^\delta) \subset \mathbb{C}$ *which is continuous in the first and injective in the second variable, such that for all* $\lambda_\delta \in \sigma(\mathcal{A}^\delta)$ *exactly one of the following items holds true:*

- *there exists a* $\lambda \in \sigma(\mathcal{A}^0)$*, such that* $\lambda_\delta = i(\delta, \lambda) \to \lambda$ *as* $\delta \to 0$ *or*
- $\mathrm{Re}(\lambda_\delta) \to -\infty$ *and* $\limsup_{\delta\to 0} |\mathrm{Im}(\lambda_\delta)|/|\mathrm{Re}(\lambda_\delta)| < \infty$.

The statement of the Lemma is illustrated in Figure 4.1.

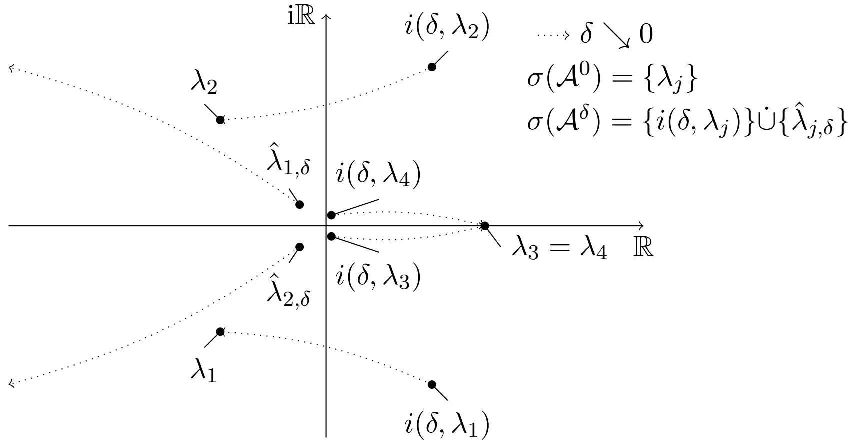

Figure 4.1: Illustration of the statement of Lemma 4.2.

Proof. We denote the Jacobian matrices of systems (4.11)-(4.12) and (4.14), evaluated at $(U^0, V^*(U^0))$ respectively U^0 by

$$\mathcal{A}^\delta := \begin{pmatrix} \nabla_{U^\delta} f & \nabla_{V^\delta} f \\ \nabla_{U^\delta} g/\delta & \nabla_{V^\delta} g/\delta \end{pmatrix} \text{ and } \mathcal{A}^0 := \frac{d}{dU^0} f(U^0, V^*(U^0)), \tag{4.15}$$

and note that $df(U^0, V^*(U^0))/(dU^0) = df(U^\delta, V^*(U^\delta))/(dU^\delta)$.
$\operatorname{Re}\lambda \geq 0$ implies that $\nabla_{V^\delta} g - \delta\lambda$ is regular for all $\delta \geq 0$, hence

$$\det(\mathcal{A}^\delta - \lambda) = \det\left(\frac{\nabla_{V^\delta} g}{\delta} - \lambda\right) \det\left(\nabla_{U^\delta} f - \lambda - \nabla_{V^\delta} f \left(\frac{\nabla_{V^\delta} g}{\delta} - \lambda\right)^{-1} \frac{\nabla_{U^\delta} g}{\delta}\right), \tag{4.16}$$

holds. The second factor can be rewritten as

$$\begin{aligned}
&\det\left(\nabla_{U^\delta} f - \lambda - \nabla_{V^\delta} f \left(\frac{\nabla_{V^\delta} g}{\delta} - \lambda\right)^{-1} \frac{\nabla_{U^\delta} g}{\delta}\right) \\
&\quad = \det\left(\nabla_{U^\delta} f - \lambda + \nabla_{V^\delta} f \frac{d}{dU^\delta} V^*(U^\delta) - \nabla_{V^\delta} f \frac{d}{dU^\delta} V^*(U^\delta) - \nabla_{V^\delta} f \left(\frac{\nabla_{V^\delta} g}{\delta} - \lambda\right)^{-1} \frac{\nabla_{U^\delta} g}{\delta}\right), \\
&\quad = \det\left(\frac{d}{dU^\delta} f - \lambda - \nabla_{V^\delta} f \left(\frac{d}{dU^\delta} V^*(U^\delta) + \left(\frac{\nabla_{V^\delta} g}{\delta} - \lambda\right)^{-1} \frac{\nabla_{U^\delta} g}{\delta}\right)\right), \\
&\quad = \det\left(\frac{d}{dU^\delta} f - \lambda - \nabla_{V^\delta} f \left(\frac{\nabla_{V^\delta} g}{\delta} - \lambda\right)^{-1} \left(\left(\frac{\nabla_{V^\delta} g}{\delta} - \lambda\right) \frac{d}{dU^\delta} V^*(U^\delta) + \frac{\nabla_{U^\delta} g}{\delta}\right)\right), \\
&\quad = \det\left(\frac{d}{dU^0} f - \lambda - \nabla_{V^\delta} f \left(\frac{\nabla_{V^\delta} g}{\delta} - \lambda\right)^{-1} \left(-\lambda \frac{d}{dU^0} V^*(U^0) + \frac{1}{\delta} \frac{d}{dU^0} g(U^0, V^*(U^0))\right)\right),
\end{aligned}$$

where $\frac{d}{dU^\delta} f := \mathcal{A}^0$. Since

$$\frac{d}{dU^0} g(U^0, V^*(U^0)) = \frac{d}{dU^\delta} g(U^\delta, V^*(U^\delta)) = 0, \tag{4.17}$$

holds, this is equal to,

$$\det\left(\frac{d}{dU^0} f - \lambda - \nabla_{V^\delta} f \delta\lambda \left(\nabla_{V^\delta} g - \delta\lambda\right)^{-1} \frac{d}{dU^0} V^*(U^0)\right). \tag{4.18}$$

Consequently, if $\delta\lambda \notin \sigma(\nabla_{V^\delta} g)$, then

$$\det(\mathcal{A}^\delta - \lambda) = \frac{1}{\delta^{\dim(\nabla_{V^\delta} g)}} \det\begin{pmatrix} \frac{d}{dU^0} f - \lambda & \nabla_{V^\delta} f \\ \delta\lambda \frac{d}{dU^0} V^*(U^0) & \nabla_{V^\delta} g - \delta\lambda \end{pmatrix}, \tag{4.19}$$

holds. First, note that $\nabla_{U^\delta} f, \nabla_{V^\delta} f, \nabla_{U^\delta} g, \nabla_{V^\delta} f, df/(dU^0)$ do not even implicitly depend on δ since we fix the point around which we linearise. Note $\sigma(\nabla_{V^\delta} g) \bigcap \{\lambda \in \mathbb{C} |\, \mathrm{Re}(\lambda) \geq 0\} = \emptyset$. Since both sides of (4.19) are polynomials and the equality holds for all $\delta\lambda \notin \sigma(\nabla_{V^\delta} g)$, where $\sigma(\nabla_{V^\delta} g)$ is discrete and finite, it holds on $\mathbb{C}$. Considered as polynomials in λ, the coefficients are polynomials in δ, hence they depend continuously on δ. Roots of polynomials depend continuously on the coefficients. If the m leading coefficients vanish in the limit δ towards zero, m roots converge towards infinity. Consequently, $\dim(V^\delta)$-many eigenvalues of $\mathcal{A}^\delta$ converge towards infinity while the other eigenvalues of $\mathcal{A}^\delta$ converge towards the eigenvalues of $\mathcal{A}^{\delta=0}$. We need to exclude the case that the eigenvalues tending to infinity have positive real part. To see this, consider (4.18). We show that for all sufficiently large $|\lambda|$ with $\mathrm{Re}(\lambda) \geq 0$, this matrix is strictly diagonally dominant. Then, it is regular due to Gerschgorin circles and the determinant is nontrivial.
Indeed,

$$\begin{aligned} |\nabla_{V^\delta} f \delta\lambda (\nabla_{V^\delta} g - \delta\lambda)^{-1} \frac{d}{dU^0} V^*(U^0)|_\infty &\leq c|\nabla_{V^\delta} f|_\infty |\frac{d}{dU^0} V^*(U^0)|_\infty \delta|\lambda||(\nabla_{V^\delta} g - \delta\lambda)^{-1}|_\sigma, \\ &\leq c|\nabla_{V^\delta} f|_\infty |\frac{d}{dU^0} V^*(U^0)|_\infty \frac{\delta|\lambda|}{|\delta\lambda - \tilde{\lambda}|}, \\ &\leq c|\nabla_{V^\delta} f|_\infty |\frac{d}{dU^0} V^*(U^0)|_\infty, \end{aligned} \tag{4.20}$$

where equivalence of the maximum-norm $|.|_\infty$ and the spectral norm $|.|_\sigma$ has been used and

$$\tilde{\lambda} := \{\lambda \in \nabla_{U^\delta} g \,|\, |\tilde{\lambda} - \delta\lambda| < |\lambda' - \delta\lambda| \text{ for all } \lambda' \in \nabla_{U^\delta} g\},$$

denotes the eigenvalue of $\nabla_{V^\delta} g$ which is ‘the closest’ (in Euclidean sense) to $\delta\lambda$. The last estimate holds due to the fact that $\text{Re}(\tilde{\lambda}) < -c$ and $\text{Re}(\delta\lambda) \geq 0$ hold. Consequently, it holds for all large $|\lambda|$ with $\text{Re}(\lambda) \geq 0 > c \geq \max(\text{Re}(\tilde{\lambda})|\tilde{\lambda} \in \sigma(\nabla_{V^\delta} g))$ that, for sufficiently small $\delta > 0$, λ is not an eigenvalue of $\mathcal{A}^\delta$. This proves the statement of the lemma except the ratio of the real and imaginary part of the diverging eigenvalues. To conclude this, apply the findings of [BG09], Theorem 3. □

Corrolary 4.3. *Consider a system of type* (4.1)-(4.5) *satisfying the conditions of Lemma 4.5. If, at a steady state* $(\overline{U}, \overline{V}, \overline{W})$, *the system exhibits DDI for* $\delta = 0$, *then it holds that there exists* $\delta^* > 0$, *such that for all* $0 \leq \delta \leq \delta^*$, *the system exhibits DDI.*

Proof. Stability with respect to spatially homogeneous perturbation is shown in Lemma 4.2. Instability with respect to spatially inhomogeneous perturbation is shown in Lemma 4.5.

□

Remark 4.4. *The following examples show that* δ^* *in Corollary 4.3 is not necessarily greater or equal to* 1.

- *For the system*

$$\frac{\partial}{\partial t} u_1 = 2u_1 + u_2 - 4v, \qquad x \in \overline{I}, t > 0, \tag{4.21}$$
$$\frac{\partial}{\partial t} u_2 = u_1 - 0.5u_2 - 2v, \qquad x \in \overline{I}, t > 0, \tag{4.22}$$
$$\frac{\partial}{\partial t} v = D\Delta v + u_1 + u_2 - v, \qquad x \in I, t > 0, \tag{4.23}$$
$$\partial_n v = 0, \qquad x \in \partial I, t > 0, \tag{4.24}$$

  supplemented with initial conditions in $C(\overline{I})^2 \times C^2(\overline{I})$, *the trivial steady state is unstable, while it is stable as steady state of the quasi-steady state approximation with respect to* u_2.

- *The System*

$$\frac{\partial}{\partial t} u_1 = 1.5u_1 - u_2 - 3v, \qquad x \in \overline{I}, t > 0, \tag{4.25}$$
$$\frac{\partial}{\partial t} u_2 = 2u_1 - u_2 - 1.5v, \qquad x \in \overline{I}, t > 0, \tag{4.26}$$
$$\frac{\partial}{\partial t} v = D\Delta v + u_1 + u_2 - 3v, \qquad x \in I, t > 0, \tag{4.27}$$
$$\partial_n v = 0, \qquad x \in \partial I, t > 0, \tag{4.28}$$

supplemented with initial conditions in $C(\overline{I})^2 \times C^2(\overline{I})$, exhibits diffusion-driven instability. However, the trivial steady state is a stable steady state of the quasi-steady state approximation with respect to u_2 and its kinetic system.

4.3 Tikhonov-type result

In this subsection we prove a Tikhonov-type result for reaction-diffusion-ODE models. The conditions on the component with accelerated reaction are the same as in Tikhonov's theorem. However, additionally to these conditions, we impose a condition on the kinetics of the subsystem of diffusive components. This condition is satisfied if the spectrum of $\nabla_W h$, evaluated at the steady state, is, for all $x \in \overline{I}$, not contained in the right complex half-plane, but actually weaker.

Lemma 4.5. *Consider a system of type*

$$\frac{\partial U^\delta}{\partial t} = f(U^\delta, V^\delta, W^\delta), \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.29}$$

$$\delta \frac{\partial V^\delta}{\partial t} = g(U^\delta, V^\delta, W^\delta), \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.30}$$

$$\frac{\partial W^\delta}{\partial t} = D\Delta W^\delta + h(W^\delta, V^\delta, W^\delta), \qquad (x,t) \in I \times (0,T) \tag{4.31}$$

supplemented with homogeneous Neumann boundary conditions for W^δ and

$$(U^\delta(x,0), V^\delta(x,0), W^\delta(x,0)) \in (C(\overline{I})^{\dim(U^\delta)+\dim(V^\delta)} \times C^2(\overline{I})^{\dim(W^\delta)}). \tag{4.32}$$

For $\delta = 0$, no initial conditions for V^δ are given. Assume that the solutions for $0 \le \delta \le \delta^*$ are uniformly bounded. Denote the spectrum of $\nabla_V g|_{(U,V,W)}$ as $\sigma(\nabla_V g|_{(U,V,W)})$. Assume that there exists some $c < 0$, such that

1. $$\operatorname{Re} \sigma(\nabla_V g|_{(U,V,W)}) \le c < 0, \tag{4.33}$$

   holds for all (U,V,W),

2. *for all vectors $\varphi \in \mathbb{R}_{\ge 0}^{\dim(w(x,t))}$,*

   $$\varphi^T \nabla_W h \varphi \le 0, \tag{4.34}$$

   holds for all (U,V,W).

Then, for any given $T < \infty$,

$$\lim_{\delta\to 0} \left\| U^0 - U^\delta \right\|_{L^\infty((0,T)\times I)} = 0, \tag{4.35}$$

$$\lim_{\delta\to 0} \left\| W^0 - W^\delta \right\|_{L^\infty((0,T)\times I)} = 0, \tag{4.36}$$

$$\lim_{\delta\to 0} \left\| V^0 - V^\delta \right\|_{L^1(0,T;L^\infty(I))} = 0, \tag{4.37}$$

hold.

Proof. First, we rewrite the difference between the solution for $\delta > 0$ and $\delta = 0$, i.e.

$$\alpha := U^\delta - U^0,\ \beta := V^\delta - V^0,\ \gamma := W^\delta - W^0, \tag{4.38}$$

as solution of system

$$\frac{\partial \alpha}{\partial t} = \nabla_U f \alpha + \nabla_V f \beta + \nabla_W f \gamma, \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.39}$$

$$\frac{\partial \beta}{\partial t} = \nabla_U g \alpha + \nabla_V g \beta + \nabla_W g \gamma + \frac{\partial V^0}{\partial t}, \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.40}$$

$$\frac{\partial \gamma}{\partial t} = \nabla_U h \alpha + \nabla_V h \beta + \nabla_W h \gamma + D\Delta\gamma, \qquad (x,t) \in I \times (0,T), \tag{4.41}$$

with homogeneous Neumann boundary conditions for γ and initial conditions $(\alpha_0, \beta_0, \gamma_0) \in (C(\overline{I})^2 \times C^2(\overline{I}))$. The derivatives are evaluated according to the Taylor-Lagrange residual formula. We choose an equidistant partition $\{t_n\}_{n=0,\dots,N}$ of the given interval $(0,T)$ and conclude the result by induction over n. The base case is satisfied by assumption since

$$\begin{aligned} \|\alpha_0\|_{L^\infty(I)}, \|\gamma_0\|_{L^\infty(I)} &= 0 \leq \delta, \\ \int_0^0 \|\beta(\tau)\|_{L^\infty(I)}\, d\tau &= 0 \leq \delta. \end{aligned} \tag{4.42}$$

First, we construct a barrier-functional $C_\gamma : [0,T) \to \mathbb{R}$ for γ, such that $\|\gamma\|_{L^\infty(0,t;L^\infty(I))} \leq C(t)$. Define $(\cdot)_+ := \max(\cdot, 0)$ and $(\cdot)_- = (-\cdot)_+$.
We test equation (4.41) with $\varphi = (C_\gamma + \gamma)_-$. Using the identity $\gamma = -C_\gamma + (C_\gamma+\gamma)_- + (C_\gamma+\gamma)_+$, we obtain that

$$\begin{aligned} -\int_I (\gamma + C_\gamma)_-^T \frac{d}{dt} C_\gamma + \frac{1}{2}\frac{d}{dt}\int_I (\gamma + C_\gamma)_-^2 + \int_I |\nabla(\gamma + C_\gamma)_-^T D \nabla(\gamma + C_\gamma)_-| \\ + \int_I (\gamma + C_\gamma)_-^T \nabla_W h C_\gamma + \int_I (\gamma + C_\gamma)_-^T \nabla_W h (\gamma + C_\gamma)_- = \int_I (\gamma + C_\gamma)_-^T (\nabla_U h \alpha + \nabla_V h \beta). \end{aligned}$$

Due to condition (4.34), it is sufficient to consider the ODE

$$-\frac{\partial}{\partial t}C_\gamma + \nabla_W h C_\gamma = \nabla_U h\alpha + \nabla_V h\beta. \tag{4.43}$$

To conclude $(\gamma + C_\gamma)_- = 0$, i.e. $\gamma \geq -C_\gamma$, we need $\nabla_U h\alpha + \nabla_V h\beta \leq 0$. Define $d = \dim\alpha(x,t) + \dim\beta(x,t) + \dim\gamma(x,t)$.
Indeed, we obtain for

$$\begin{aligned} C_\gamma(t_n) &= C_{\gamma,n}, && (4.44)\\ \frac{\partial C_\gamma}{\partial t} - d\left\|\nabla_W h\right\|_\infty C_\gamma &= d\left\|\nabla_U h\right\|_\infty \left\|\alpha(t)\right\|_{L^\infty(I)} + d\left\|\nabla_V h\right\|_\infty \left\|\beta(t)\right\|_{L^\infty(I)}, && (4.45)\end{aligned}$$

that

$$\begin{aligned} C_\gamma(t) = &\int_{t_n}^{t} e^{d\|\nabla_W h\|_\infty (t-\tau)} d(\left\|\nabla_U h\right\|_\infty \left\|\alpha(\tau)\right\|_{L^\infty(I)} + \left\|\nabla_V h\right\|_\infty \left\|\beta(\tau)\right\|_{L^\infty(I)}) d\tau \\ &+ e^{d\|\nabla_W h\|_\infty (t-t_n)} C_\gamma(t_n), \end{aligned} \tag{4.46}$$

and consequently

$$\begin{aligned} \left\|\gamma\right\|_{L^\infty(t_n,t;L^\infty(\Omega))} \leq & d\left(\left\|\nabla_U h\right\|_\infty \left\|\alpha\right\|_{L^1(t_n,t;L^\infty(\Omega))} + \left\|\nabla_V h\right\|_\infty \left\|\beta\right\|_{L^1(t_n,t;L^\infty(\Omega))}\right) e^{d\|\nabla_W h\|_\infty (t-t_n)} \\ &+ e^{d\|\nabla_W h\|_\infty (t-t_n)} \left\|\gamma(t)\right\|_{L^\infty(I)}, \\ \leq & d e^{2d\|\nabla_W h\|_\infty (t-t_n)} \Big(\left\|\gamma(t_n)\right\|_{L^\infty(I)} + (t-t_n)\left\|\nabla_U h\right\|_\infty \left\|\alpha\right\|_{L^\infty(t_n,t;L^\infty(\Omega))} \\ &+ \left\|\nabla_V h\right\|_\infty \left\|\beta\right\|_{L^1(t_n,t;L^\infty(\Omega))} \Big). \end{aligned} \tag{4.47}$$

Step 2: We estimate α,

$$\begin{aligned} \left\|\alpha(t)\right\|_{L^\infty(I)} \leq & e^{d\|\nabla_U f\|_\infty (t-t_n)} \left\|\alpha(t_n)\right\|_{L^\infty(I)} + \int_{t_n}^{t} e^{d\|\nabla_U f\|_\infty (t-\tau)} \left\|\nabla_V f\beta + \nabla_W f\gamma\right\|_{L^\infty(I)} d\tau, \\ \leq & e^{2d\|\nabla_U f\|_{L^\infty} (t-t_n)} (\left\|\alpha(t_n)\right\|_{L^\infty(I)} + \int_{t_n}^{t} \left\|\nabla_V f\beta(\tau)\right\|_{L^\infty(I)} d\tau + \left\|\nabla_W f\gamma\right\|_{L^1(t_n,t;L^\infty(\Omega))}), \\ \leq & e^{2d\|\nabla_U f\|_{L^\infty} (t-t_n)} (\left\|\alpha(t_n)\right\|_{L^\infty(I)} + d\left\|\nabla_V f\right\|_\infty \left\|\beta\right\|_{L^1(t_n,t;L^\infty(\Omega))} \\ &+ (t-t_n) d\left\|\nabla_W f\right\|_\infty \left\|\gamma\right\|_{L^\infty(t_n,t;L^\infty(\Omega))}). \end{aligned}$$

Using estimate (4.46) and (4.47), it follows that

$$\begin{aligned}\|\alpha(t)\|_{L^\infty(I)} \leq & d\left(\|\alpha(t_n)\|_{L^\infty(I)} + (t-t_n)\|\nabla_W f\|_\infty \|\gamma(t_n)\|_{L^\infty(I)}\right) e^{2d(\|\nabla_W h\|_\infty + \|\nabla_U f\|_\infty)(t-t_n)} \\ & + d\left(\|\nabla_V f\|_\infty + (t-t_n)\|\nabla_W f\|_\infty \|\nabla_V h\|_\infty\right) d e^{2d(\|\nabla_W h\|_\infty + \|\nabla_U f\|_\infty)(t-t_n)} \|\beta\|_{L^1(t_n,t;L^\infty(\Omega))} \\ & + (t-t_n) d \|\nabla_W f\|_\infty \|\nabla_U h\|_\infty \int_{t_n}^{t} \|\alpha(s)\|_{L^\infty(I)} e^{d\|\nabla_W h\|_\infty (s-t_n)} ds.\end{aligned}$$

We can therefore apply Gronwall's lemma to the entity $\|\alpha\|_{L^\infty(t_n,\cdot;L^\infty(I))} : (t_n, t_{n+1}) \to \mathbb{R}$ and obtain,

$$\begin{aligned}\|\alpha(t)\|_{L^\infty(I)} \leq & c\Big(\|\alpha(t_n)\|_{L^\infty(I)} + (t-t_n)\|\nabla_W f\|_\infty \|\gamma(t_n)\|_{L^\infty(I)} \\ & + \left(\|\nabla_V f\|_\infty + (t-t_n)\|\nabla_W f\|_\infty \|h_v\|_\infty\right)\|\beta\|_{L^1(t_n,t;L^\infty(\Omega))}\Big) \\ & \cdot e^{c\|\nabla_W f\|_\infty \|\nabla_U h\|_\infty (t-t_n)^2 e^{c\|\nabla_W h\|_\infty (t-t_n)}} e^{c\max(\|\nabla_W h\|_\infty, \|\nabla_U f\|_\infty)(t-t_n)}.\end{aligned} \tag{4.48}$$

Step 3: Estimate on $\|\beta\|_{L^1(t_n,t;L^\infty(\Omega))}$.
Note that $\left\|e^{-c\tau/\delta}\right\|_{L^q(0,t)} = C\delta^{1/q}$ for $1 \leq q \leq \infty$.
Now, write the solution as

$$\begin{aligned}|\beta(t,x)| \leq & |e^{\int_{t_n}^t \nabla_V g(s,x)ds}\beta(t_n,x) - \int_{t_n}^{t} e^{\int_\tau^t \nabla_V g(x,s)ds}\frac{\partial v^{\delta=0}}{\partial t}(\tau,x)d\tau| \\ & + \frac{1}{\delta}\int_{t_n}^{t} e^{\frac{\lambda(\tau)}{\delta}(t-\tau)}|\nabla_U g\alpha + \nabla_W g\gamma| d\tau,\end{aligned}$$

where $\lambda(\tau)$ denotes the eigenvalue of $\nabla_V g(\tau)$ with largest real part. Recall $\operatorname{Re}\lambda \leq c < 0$. Using Young's inequality yields

$$\|\beta\|_{L^1(t_n,t;L^\infty(\Omega))} \leq \underbrace{\left(\|\beta(t_n)\|_{L^\infty(I)} + \left\|\frac{\partial v^{\delta=0}}{\partial \tau}\right\|_{L^q(t_n,t;L^\infty(I))}\right)}_{=:C^*}\delta \tag{4.49}$$

$$+ C\|\nabla_U g\|_\infty \|\alpha\|_{L^1(t_n,t;L^\infty(\Omega))} + C\|\nabla_W g\|_\infty \|\gamma\|_{L^1(t_n,t;L^\infty(\Omega))}, \tag{4.50}$$

$$\leq C^*\delta + (t-t_n)\|\alpha\|_{L^\infty(t_n,t;L^\infty(\Omega))} + C(t-t_n)\|\gamma\|_{L^\infty(t_n,t;L^\infty(\Omega))}, \tag{4.51}$$

$$\leq C^*\delta + (t-t_n)C(\|\alpha(t_n)\|_{L^\infty(I)} + C(t-t_n)\|\gamma(t_n)\|_{L^\infty(I)} \tag{4.52}$$

$$+ (c + c(t-t_n))\|\beta\|_{L^1(t_n,t;L^\infty(\Omega))}) \tag{4.53}$$

$$+ c(\|\gamma(t_n)\|_{L^\infty(I)} + \|\nabla_U h\|_\infty (t-t_n)\|\alpha\|_{L^\infty(t_n,t;L^\infty(\Omega))}) \tag{4.54}$$

$$
\begin{aligned}
&+ \|\nabla_V h\|_\infty \|\beta\|_{L^1(t_n,t;L^\infty(\Omega))})(t-t_n), && (4.55)\\
&\leq C^*\delta + C(t-t_n)(\|\alpha(t_n)\|_{L^\infty(I)} + (t-t_n)\|\gamma(t_n)\|_{L^\infty(I)} + \|\gamma(t_n)\|_{L^\infty(I)}) && (4.56)\\
&+ C(t-t_n)(c + c(t-t_n) + \|\nabla_V h\|_\infty)\|\beta\|_{L^1(t_n,t;L^\infty(\Omega))} && (4.57)\\
&+ c\|\nabla_U h\|_\infty (t-t_n)(\|\alpha(t_n)\|_{L^\infty(I)} + (t-t_n)\|\gamma(t_n)\|_{L^\infty(I)}) && (4.58)\\
&+ c\|\nabla_W h\|_\infty (t-t_n)(c + c(t-t_n))\|\beta\|_{L^1(t_n,t;L^\infty(\Omega))}, && (4.59)\\
&\leq C^*\delta + C(t-t_n)(\|\alpha(t_n)\|_{L^\infty(I)} + (t-t_n+1)\|\gamma(t_n)\|_{L^\infty(I)} && (4.60)\\
&+ C_!(t-t_n)(1+(t-t_n))\|\beta\|_{L^1(t_n,t;L^\infty(\Omega))}, && (4.61)
\end{aligned}
$$

where $C_!$ does not depend on t. Consequently, we can choose $(t_{n+1}-t_n)$ equal for all n and so small that $C_!(t_{n+1}-t_n)(1+(t_{n+1}-t_n)) < 1/2$. Then,

$$\|\beta\|_{L^1(t_n,t_{n+1};L^\infty(I))} \leq C(\delta + (t_{n+1}-t_n)\|\alpha(t_n)\|_{L^\infty(I)} + (t_{n+1}-t_n+1)\|\gamma(t_n)\|_{L^\infty(I)}) \quad (4.62)$$

Combining (4.47),(4.48) and (4.62) yields the result by the principle of induction over n.

□

4.4 Stability of spatially inhomogeneous steady states

We gave conditions for stability of steady states with jump-type discontinuity in Theorem 3.9 and Corollary 3.10. Lemma 4.5 states that the solution (U^δ, V^δ) remains close to (U^0, V^0) in a suitable topology until a time T_δ. It does not imply $\limsup_{\delta\to 0} T_\delta < \infty$. Therefore, the solution may have a qualitatively different dynamical behaviour for $t > T_\delta$ and consequently different stability properties. However, in Lemma 3.10, we found conditions for stability of steady states. If the quasi-steady state reduction satisfies these conditions and the reduction is of certain type, we derive conditions under which stability of a steady state to the unreduced system can be deduced from the reduced system. In order to prove this, we need the following

Lemma 4.6 (Algebraic dependencies: quasi-steady state reduction)**.** *Consider a system of type* (4.1)-(4.5) *for scalar $u^\delta, v^\delta, w^\delta$. Denote the Jacobian matrix of this system, evaluated at a steady state $(\tilde{u}, \tilde{v}, \tilde{w})$, by*

$$\mathcal{A}^\delta = \begin{pmatrix} \frac{\partial f}{\partial u^\delta} & \frac{\partial f}{\partial v^\delta} & \frac{\partial f}{\partial w^\delta} \\ \frac{\partial g}{\partial u^\delta}/\delta & \frac{\partial g}{\partial v^\delta}/\delta & \frac{\partial g}{\partial w^\delta}/\delta \\ \frac{\partial h}{\partial u^\delta} & \frac{\partial h}{\partial v^\delta} & \frac{\partial h}{\partial w^\delta} \end{pmatrix} := \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21}/\delta & a_{22}/\delta & a_{23}/\delta \\ a_{31} & a_{32} & a_{33} \end{pmatrix}. \quad (4.63)$$

Denote the Jacobian matrix of the quasi-steady-state system (4.6)-(4.8)*, evaluated at* $(\tilde{u}, \tilde{v})$ *by*

$$\mathcal{B} = \begin{pmatrix} \frac{\partial f(u^0, v^*(u^0,w^0), w^0)}{\partial u^0} & \frac{\partial f(u^0, v^*(u^0,w^0), w^0)}{\partial w^0} \\ \frac{\partial h(u^0, v^*(u^0,w^0), w^0)}{\partial u^0} & \frac{\partial h(u^0, v^*(u^0,w^0), w^0)}{\partial w^0} \end{pmatrix} := \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix}. \tag{4.64}$$

Denote the matrix resulting from $\mathcal{A}^\delta$ *by omitting the* $\hat{i} - th$ *row and the* $\hat{j} - th$ *column as* $\mathcal{A}^\delta_{\hat{i}\hat{j}} = (a_{ij})_{i \neq \hat{i}, j \neq \hat{j}}$. *The following algebraic dependencies hold:*

$$b_{11} = a_{22} \det(\mathcal{A}^1_{33}) = a_{22} \det(\mathcal{A}^\delta_{33})\delta, \tag{4.65}$$

$$b_{22} = a_{22} \det(\mathcal{A}^1_{11}) = a_{22} \det(\mathcal{A}^\delta_{11})\delta, \tag{4.66}$$

$$\det(\mathcal{B}) = a_{22} \det(\mathcal{A}^1) = a_{22} \det(\mathcal{A}^\delta)\delta. \tag{4.67}$$

Proof. Recall Assumption 2.1. Since $f(u^0, v^*(u^0, w^0), w^0) = 0$, it holds that

$$a_{21} + a_{22} \frac{\partial v^*(u^0, w^0)}{\partial u^0} = 0 \text{ and } a_{23} + a_{22} \frac{\partial v^*(u^0, w^0)}{\partial w^0} = 0. \tag{4.68}$$

By differentiating $f(u^0, v^*(u^0, w^0), w^0)$ and $h(u^0, v^*(u^0, w^0), w^0)$, we obtain

$$\begin{aligned} b_{11} &= a_{11} + a_{12} \frac{\partial v^*(u^0, w^0)}{\partial u^0}, \; b_{12} = a_{13} + a_{12} \frac{\partial v^*(u^0, w^0)}{\partial w^0}, \\ b_{21} &= a_{31} + a_{31} \frac{\partial v^*(u^0, w^0)}{\partial u^0}, \; b_{22} = a_{33} + a_{32} \frac{\partial v^*(u^0, w^0)}{\partial w^0}. \end{aligned} \tag{4.69}$$

Using these identities, we obtain

$$\det(\mathcal{A}^1_{33}) = a_{11}a_{22} - a_{12}a_{21} = a_{22} \left(a_{11} + a_{12} \frac{\partial v^*(u^0, w^0)}{\partial u^0} \right) = a_{22} b_{11}, \tag{4.70}$$

$$\det(\mathcal{A}^1_{11}) = a_{33}a_{22} - a_{32}a_{23} = a_{22} \left(a_{33} + a_{32} \frac{\partial v^*(u^0, w^0)}{\partial w^0} \right) = a_{22} b_{22}. \tag{4.71}$$

Rewriting $\mathcal{A}^1$ as

$$\det(\mathcal{A}^1) = \det \begin{pmatrix} b_{11} - \frac{\partial v^*(u^0,w^0)}{\partial u^0} a_{12} & a_{12} & b_{12} - \frac{\partial v^*(u^0,w^0)}{\partial w^0} a_{12} \\ a_{21} & a_{22} & a_{33} \\ b_{22} - \frac{\partial v^*(u^0,w^0)}{\partial u^0} a_{32} & a_{32} & b_{22} - \frac{\partial v^*(u^0,w^0)}{\partial w^0} a_{32} \end{pmatrix}, \tag{4.72}$$

yields the result by calculation using identities (4.68) and (4.69). □

Lemma 4.6 allows us to give conditions for stability of steady state of a system of type (4.1)-(4.5) based on investigation of its quasi-steady state approximation.

Lemma 4.7. *Consider system* (4.1)-(4.5) *and its quasi-steady state approximation* (4.9)-(4.10)*. Let* $u^\delta, v^\delta, w^\delta$ *be scalar. Given a weak jump-type steady state* $(\tilde{u}, \tilde{w})$*, assume that the reduced system satisfies the conditions of Corollary 3.10 and Assumption 2.1. Denote the Jacobian matrix analogously to* (4.63)*. If*

1. *the unreduced system* (4.1)-(4.5) *satisfies Assumption 2.1, and*

2. $a_{22}, a_{33} \leq c < 0$*,*

holds, then exists a positive δ^* *such that for all non-negative* $\delta \leq \delta^*$*, it holds that* $(\tilde{u}, v^*(\tilde{u}, \tilde{w}), \tilde{w})$ *is an* (ε_0, A)*-stable steady state of system* (4.1)-(4.5)*.*

Remark 4.8. *It is possible to generalise conditions for a 3-compartment system to general* δ *as we did in joint research, see [HMCT15]. Then, the conditions read: There exists some* $\kappa > 0$*, such that*

$$\operatorname{tr}(\mathcal{A}^\delta(x)) < 0, \quad \operatorname{tr}(\mathcal{A}^\delta(x)) \sum_{j=1}^{3} \det(\mathcal{A}^\delta_{jj}) < \det(\mathcal{A}^\delta(x)) < 0, \tag{4.73}$$

$$\operatorname{tr}(\mathcal{A}^\delta_{33}(x)) \sum_{j=1}^{3} \det(\mathcal{A}^\delta_{jj}(x)) \leq \det(\mathcal{A}^\delta(x)) + \operatorname{tr}(\mathcal{A}^\delta(x)) \det(\mathcal{A}^\delta_{33}(x)), \tag{4.74}$$

$$0 < 3 \det(\mathcal{A}^\delta_{33}(x)) \leq \operatorname{tr}(\mathcal{A}^\delta(x)) \operatorname{tr}(\mathcal{A}^\delta_{33}(x)) + \sum_{j=1}^{3} \det(\mathcal{A}^\delta_{jj}(x)), \tag{4.75}$$

$$a_{33}(x) \leq -3\kappa < 0 \quad \textit{and} \quad \det(\mathcal{A}^\delta_{33}(x)) \geq -3\kappa \operatorname{tr}(\mathcal{A}^\delta_{33}(x)) \geq 18\kappa^2, \tag{4.76}$$

hold at the steady state. The proof is analogous to the proof of Lemma 4.7.

Proof of Lemma 4.7. Denote the matrix resulting from omitting the $\hat{\imath}$-th row and the $\hat{\jmath}$-th column of $\mathcal{A}^\delta$ by $\mathcal{A}^\delta_{\hat{\imath}\hat{\jmath}} = (a_{ij})_{i \neq \hat{\imath}, j \neq \hat{\jmath}}$. The proof follows the same principle as Lemma 3.10. For sufficiently small δ, it holds that $\mathcal{A}^\delta_{33}$ has only eigenvalues with negative real part, see Lemma 4.2. Therefore, $0 < \det(\mathcal{A}^\delta_{33})$ and $\operatorname{tr}(\mathcal{A}^\delta_{33}) < 0$ hold. Hence it holds that $\operatorname{Re}(\sigma(\mathcal{A}^\delta_{33})) \subset (-c_1, -c)$ and $\operatorname{Im}(\sigma(\mathcal{A}^\delta_{33})) \subset (c_{\mathrm{Im},1}, c_{\mathrm{Im},2})$ due to regularity of u, v, f, g and for $c, c_1, c_{\mathrm{Im},1}, c_{\mathrm{Im},2} > 0$. Assume $\lambda \notin (-c_1, -c) \times i(c_{\mathrm{Im},1}, c_{\mathrm{Im},2})$. Then, the equation

$$(\mathcal{A}^\delta - \lambda) \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \psi \end{pmatrix} + D \begin{pmatrix} 0 \\ 0 \\ \frac{\partial^2 \psi}{\partial x^2} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \tag{4.77}$$

can be rewritten as the scalar problem

$$-\begin{pmatrix} a_{31} & a_{32} \end{pmatrix} (\mathcal{A}_{33}^{\delta} - \lambda)^{-1} \begin{pmatrix} a_{13} \\ a_{23}/\delta \end{pmatrix} \psi + (a_{33} - \lambda)\psi + D\frac{\partial^2 \psi}{\partial x^2} = 0, \tag{4.78}$$

which then can be rewritten as

$$\frac{\det(\mathcal{A}^{\delta} - \lambda)}{\det(\mathcal{A}_{33}^{\delta} - \lambda)} + D\frac{\partial^2 \psi}{\partial x^2} = \frac{\det(\mathcal{A}^{\delta} - \lambda)\overline{\det(\mathcal{A}_{33}^{\delta} - \lambda)}}{|\det(\mathcal{A}_{33}^{\delta} - \lambda)|^2} + D\frac{\partial^2 \psi}{\partial x^2} = 0. \tag{4.79}$$

Analogous to the case of one ordinary differential equation coupled to one reaction-diffusion equation, we test formally with ψ and consider the real part of the resulting equation. To do so, we first calculate the real and imaginary parts of $\det(\mathcal{A}^{\delta} - \lambda)$ and $\det(\mathcal{A}_{33}^{\delta} - \lambda)$ and define $\lambda = \lambda_1 + i\lambda_2$ with $\lambda_1, \lambda_2 \in \mathbb{R}$.

$$\begin{aligned} \operatorname{Re}(\det(\mathcal{A}^{\delta} - \lambda)) &= \det(\mathcal{A}^{\delta} - \lambda_1) + \lambda_2^2(3\lambda_1 - \operatorname{tr}(\mathcal{A}^{\delta})), \\ \operatorname{Im}(\det(\mathcal{A}^{\delta} - \lambda)) &= \lambda_2(\lambda_2^2 + (2\operatorname{tr}(\mathcal{A}^{\delta}) - 3\lambda_1)\lambda_1 - \sum_{i=1}^{3}\det(\mathcal{A}_{ii}^{\delta})), \\ \operatorname{Re}(\det(\mathcal{A}_{33}^{\delta} - \lambda)) &= \det(\mathcal{A}_{33}^{\delta} - \lambda_1) - \lambda_2^2, \\ \operatorname{Im}(\det(\mathcal{A}_{33}^{\delta} - \lambda)) &= \lambda_2(2\lambda_1 - \operatorname{tr}(A_{33})). \end{aligned} \tag{4.80}$$

Now, we calculate $\operatorname{Re}(\det(\mathcal{A}^{\delta} - \lambda)\operatorname{Re}(\det(\mathcal{A}_{33}^{\delta} - \lambda) + \operatorname{Im}(\det(\mathcal{A}^{\delta} - \lambda))\operatorname{Im}(\det(\mathcal{A}_{33}^{\delta} - \lambda))$:

$$\begin{aligned} &\Big(-\lambda_1^3 + \operatorname{tr}(\mathcal{A}^{\delta})\lambda_1^2 - \sum_{i=1}^{3}\det(\mathcal{A}_{ii}^{\delta})\lambda_1 + \det(\mathcal{A}^{\delta}) + 3\lambda_1\lambda_2^2 - \operatorname{tr}\mathcal{A}^{\delta}\lambda_2^2\Big) \\ &\qquad\qquad \cdot\Big(\lambda_1^2 - \operatorname{tr}(\mathcal{A}_{33}^{\delta})\lambda_1 + \det(\mathcal{A}_{33}^{\delta}) - \lambda_2^2\Big) \\ &+\lambda_2^2\Big(\lambda_2^2 + 2\operatorname{tr}(\mathcal{A}^{\delta})\lambda_1 - 3\lambda_1^2 - \sum_{i=1}^{3}\det(\mathcal{A}_{ii}^{\delta})\Big)\Big(2\lambda_1 - \operatorname{tr}(\mathcal{A}_{33}^{\delta})\Big). \end{aligned} \tag{4.81}$$

Now, we can interpret this as element of $(\mathbb{R}[\lambda_2])[\lambda_1]$ taking the form

$$\sum_{i=0}^{5} q_i(\lambda_2)\lambda_1^i,$$

where

$$\begin{aligned} q_5(\lambda_2) &= -1, \\ q_4(\lambda_2) &= \operatorname{tr}(\mathcal{A}_{33}^{\delta}) + \operatorname{tr}(\mathcal{A}^{\delta}), \end{aligned}$$

$$
\begin{aligned}
q_3(\lambda_2) =& -(\det(\mathcal{A}^\delta_{33})-\lambda_2^2) - \operatorname{tr}(\mathcal{A}^\delta)\operatorname{tr}(\mathcal{A}^\delta_{33}) - \sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii}) + 3\lambda_2^2 - 6\lambda_2^2,\\
=& -\Big(\det(\mathcal{A}^\delta_{33}) + \operatorname{tr}(\mathcal{A}^\delta)\operatorname{tr}(\mathcal{A}^\delta_{33}) + \sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii}) + 2\lambda_2^2\Big),\\
q_2(\lambda_2) =& \operatorname{tr}(\mathcal{A}^\delta)\det(\mathcal{A}^\delta_{33}) - \operatorname{tr}(\mathcal{A}^\delta)\lambda_2^2 + \sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii})\operatorname{tr}(\mathcal{A}^\delta_{33}) + \det(\mathcal{A}^\delta) - 3\lambda_2^2\operatorname{tr}(\mathcal{A}^\delta_{33})\\
& - \operatorname{tr}(\mathcal{A}^\delta)\lambda_2^2 + 4\operatorname{tr}(\mathcal{A}^\delta)\lambda_2^2 + 3\operatorname{tr}(\mathcal{A}^\delta_{33})\lambda_2^2,\\
=& \operatorname{tr}(\mathcal{A}^\delta)\det(\mathcal{A}^\delta_{33}) + \sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii})\operatorname{tr}(\mathcal{A}^\delta_{33}) + \det(\mathcal{A}^\delta) + 2\operatorname{tr}(\mathcal{A}^\delta)\lambda_2^2,\\
q_1(\lambda_2) =& -\sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii})\det(\mathcal{A}^\delta_{33}) + \sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii})\lambda_2^2 - \det(\mathcal{A}^\delta)\operatorname{tr}(\mathcal{A}^\delta_{33}) + 3\det(\mathcal{A}^\delta_{33})\lambda_2^2 - 3\lambda_2^4\\
& + \operatorname{tr}(\mathcal{A}^\delta)\operatorname{tr}(\mathcal{A}^\delta_{33})\lambda_2^2 + 2\lambda_2^4 - 2\operatorname{tr}(\mathcal{A}^\delta)\operatorname{tr}(\mathcal{A}^\delta_{33})\lambda_2^2 - 2\sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii})\lambda_2^2,\\
=& -\Big(\sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii})\det(\mathcal{A}^\delta_{33}) + \det(\mathcal{A}^\delta)\operatorname{tr}(\mathcal{A}^\delta_{33}) + \sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii})\lambda_2^2 - 3\det(\mathcal{A}^\delta_{33})\lambda_2^2\\
& + \lambda_2^4 + \operatorname{tr}(\mathcal{A}^\delta)\operatorname{tr}(\mathcal{A}^\delta_{33})\lambda_2^2\Big),\\
q_0(\lambda_2) =& \det(\mathcal{A}^\delta)\det(\mathcal{A}^\delta_{33}) - \det(\mathcal{A}^\delta)\lambda_2^2 - \operatorname{tr}(\mathcal{A}^\delta)\det(\mathcal{A}^\delta_{33})\lambda_2^2 + \operatorname{tr}(\mathcal{A}^\delta)\lambda_2^4 - \operatorname{tr}(\mathcal{A}^\delta_{33})\lambda_2^4\\
& + \sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii})\operatorname{tr}(\mathcal{A}^\delta_{33})\lambda_2^2,\\
=& \det(\mathcal{A}^\delta)\det(\mathcal{A}^\delta_{33}) - \Big(\det(\mathcal{A}^\delta) + \operatorname{tr}(\mathcal{A}^\delta)\det(\mathcal{A}^\delta_{33}) - \sum_{i=1}^{3}\det(\mathcal{A}^\delta_{ii})\operatorname{tr}(\mathcal{A}^\delta_{33})\Big)\lambda_2^2\\
& + \Big(\operatorname{tr}(\mathcal{A}^\delta) - \operatorname{tr}(\mathcal{A}^\delta_{33})\Big)\lambda_2^4.
\end{aligned}
$$

Due to Lemma 4.6, it holds for sufficiently small δ that

1. $q_0 < -|c|/\delta^2$, since $a_{22}, \det(\mathcal{A}^1) < 0$ and $\det(\mathcal{A}^1_{33}), \det(\mathcal{A}^1_{11}) > 0$ and $\operatorname{tr}(\mathcal{A}^\delta) - \operatorname{tr}(\mathcal{A}^\delta_{33}) = a_{33} < 0$. The only term which is not necessarily negative for arbitrary $\delta > 0$ is the coefficient of λ_2^2. To see negativity for small $\delta > 0$, note first, that the first term $-\det(\mathcal{A}^\delta) = -\det(\mathcal{A}^1)/\delta$ is of order $\Theta(\delta^{-1})$. The sum of the second and third summand reads (note that it is multiplied by (-1) arising from the negative sign before the bracket):

$$
\begin{aligned}
-\frac{\det(\mathcal{A}^1_{33})}{\delta}(a_{11} + \frac{a_{22}}{\delta} + a_{33}) + \frac{\det(\mathcal{A}^1_{11}) + \det(\mathcal{A}^1_{33})}{\delta}(a_{11} + \frac{a_{22}}{\delta})\\
- \det(\mathcal{A}^1_{22})(a_{11} + \frac{a_{22}}{\delta}).
\end{aligned}
$$

Due to the different orders of δ, this term is, for sufficiently small $\delta > 0$, dominated by

$$\frac{-\det(\mathcal{A}^1_{33}) + \det(\mathcal{A}^1_{11}) + \det(\mathcal{A}^1_{33})}{\delta^2} a_{22} = \frac{\det(\mathcal{A}^1_{11})}{\delta^2} a_{22} < 0.$$

2. $q_1 < -|c|/\delta^2$, since $a_{22}, \det(\mathcal{A}^1) < 0$ and $\det(\mathcal{A}^1_{33}), \det(\mathcal{A}^1_{11}) > 0$.
   The only term which is not necessarily negative for arbitrary $\delta > 0$ is the coefficient of λ_2^2. To see this, note that for sufficiently small $\delta < 0$, the term $\operatorname{tr}(\mathcal{A}^\delta)\operatorname{tr}(\mathcal{A}^\delta_{33})$ is of type $\Theta(\delta^{-2})$, while the other summands are of type $O(\delta^{-1})$. An analogous reasoning as for q_0 shows that $-(a_{22}/\delta)^2 < 0$ dominates for small $\delta > 0$.
3. $q_2 < -|c|/\delta^2$, since $a_{22} < 0$ and $\det(\mathcal{A}^1_{33}), \det(\mathcal{A}^1_{11}) > 0$,
4. $q_3 < -|c|/\delta^2$, since $a_{22} < 0$,
5. $q_4 < -|c|/\delta$, since $a_{22} < 0$,
6. $q_5 = -1 < 0$.

Consequently, for all sufficiently small δ and all $\lambda_2 \in \mathbb{R}$,

$$q_i(\lambda_2) \le c < 0,$$

holds.
Argumentation analogous to the scalar case (beginning from (3.73)) yields the result.

□

4.5 Application to example models

4.5.1 A receptor-based model

Consider system (3.85)-(3.87), i.e.

$$\frac{\partial}{\partial t} u = -\mu_1 u - buw + dv + m_1 \frac{u^2}{1+ku^2}, \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.82}$$

$$\delta \frac{\partial}{\partial t} v = -\mu_2 v + buw - dv, \qquad (x,t) \in \overline{I} \times (0,T), \tag{4.83}$$

$$\frac{\partial}{\partial t} w = D\Delta w - \mu_3 w - buw + dv + m_2 \frac{u^2}{1+ku^2}, \qquad (x,t) \in I \times (0,T), \tag{4.84}$$

$$\partial_n w = 0, \qquad (x,t) \in \partial I \times (0,T), \tag{4.85}$$

with classical initial conditions $(u(0,x), v(0,x), w(0,x)) \in (C(\overline{I})^2 \times C^2(\overline{I}))$.
$D, \mu_1, \mu_2, \mu_3, d, b, m_1, m_2, k, \delta$ are non-negative constants.

In order to prove that the system has stable discontinuous steady states, we have to prove boundedness of solutions first.

Lemma 4.9. *Consider* (4.82)-(4.85) *and let all parameters be positive. For non-negative initial conditions, system* (4.82)-(4.85) *has a global solution in* $C^1(0,\infty; C(\overline{I})^2 \times C^2(\overline{I}))$*. For all* $\varepsilon > 0$ *there exists a* $t^* > 0$*, s.t. for all* $t \geq t^*$ *the solution satisfies*

$$0 \leq \inf_{x\in I} u(t,x) \leq \|u(t)\|_{\sup} \leq \frac{m_1}{k\min(\mu_1,\mu_2)} + \varepsilon, \tag{4.86}$$

$$0 \leq \inf_{x\in I} v(t,x) \leq \|v(t)\|_{\sup} \leq c\frac{m_1 m_2}{k^2\min(\mu_1,\mu_2)\min(\mu_2,\mu_3)(d+\mu_2)} + \varepsilon, \tag{4.87}$$

$$0 \leq \inf_{x\in I} w(t,x) \leq \|w(t)\|_{\sup} \leq c\frac{m_2}{k\min(\mu_2,\mu_3)} + \varepsilon. \tag{4.88}$$

Proof. For $0 \leq u, v, w$ and $0 \leq \delta < 1$, it holds

$$\left(-(\mu_1 + bw) + m_1\frac{u}{1+ku^2}\right) u \leq \frac{\partial}{\partial t}u, \tag{4.89}$$

$$\frac{-(\mu_2+d)v}{\delta} \leq \frac{\partial}{\partial t}v, \tag{4.90}$$

$$D\Delta w - (\mu_3 + bu)w \leq \frac{\partial}{\partial t}w, \tag{4.91}$$

$$\frac{\partial}{\partial t}(u+\delta v) \leq -\min(\mu_1,\mu_2)(u+\delta v) + \frac{m_1}{k}. \tag{4.92}$$

Inequalities (4.89)-(4.91) imply that the solutions stay non-negative. Now, (4.92) implies that

$$\limsup_{t\to\infty} \|u+\delta v\|_{\sup} \leq \frac{m_1}{k\min(\mu_1,\mu_2)} + \varepsilon, \tag{4.93}$$

leading to

$$\limsup_{t\to\infty} \|u\|_{\sup} \leq \frac{m_1}{k\min(\mu_1,\mu_2)} + \varepsilon, \tag{4.94}$$

due to non-negativity of u and v.
Now,

$$\frac{\partial}{\partial t}(w+\delta v) \leq D\Delta w - \mu_3 w - \mu_2 v + \frac{m_2}{k}, \tag{4.95}$$

holds. We estimate only at $x^*(t)$, such that $w(x^*(t)) \geq w(x)$ for all $x \in I$. This allows to construct a subsolution to w (note: not for v). It holds $\Delta w(x^*) \leq 0$.

$$\frac{\partial}{\partial t}(w(x^*) + \delta v(x^*)) \leq -\min(\mu_2,\mu_3)(w(x^*) + \delta v(x^*)) + \frac{m_2}{k}. \tag{4.96}$$

Therefore, we found a boundary on w. Since u and w are uniformly bounded, equation (4.83) yields the result due to existence of a subsolution. This finishes the proof.

□

It holds

$$\frac{\partial(-\mu_2 v + buw - dv)}{\partial v} = -(\mu_2 + d) < 0, \tag{4.97}$$

$$\frac{\partial(-\mu_3 w - buw + dv + m_2 \frac{u^2}{1+ku^2})}{\partial w} = -(\mu_3 + bu) < 0, \tag{4.98}$$

hence all conditions of Lemmas 4.6, 4.7 and 4.5 are satisfied. Consequently, for small δ, system (4.82)-(4.84) exhibits DDI and hysteresis and has a dynamical behaviour similar to that of system (4.9)-(4.10) (resp. (3.81)-(3.83)) on a finite time interval $(0, T_\delta)$, where $T_\delta \to \infty$ as $\delta \to 0$.

4.5.2 Lengyel-Epstein model

In [LE92], the authors derive model (3.166)-(3.169) as quasi-steady state reduction of

$$\frac{\partial}{\partial t} u = D_1 \Delta u + f(u, w) - c_1 u + c_2 v, \tag{4.99}$$

$$\frac{\partial}{\partial t} v = h(u, v) := c_1 u - c_2 v, \tag{4.100}$$

$$\frac{\partial}{\partial t} w = D \Delta w + g(u, w). \tag{4.101}$$

supplemented with homogeneous Neumann boundary conditions for u and w and classical initial conditions $(u(x,0), v(x,0), w(x,0)) \in (C(\bar{I})^2 \times C^2(\bar{I}))$. For $D_1 = 0$, the model is of the type investigated in this work. Moreover,

1. $h(u, v) = 0$ is uniquely solvable for v, and
2. satisfies $\frac{\partial h}{\partial v} = -c_2 < 0$,
3. the kinetic terms for w coincide for the reduced and unreduced system, hence the unreduced system satisfies $\frac{\partial g}{\partial w}(u, v, w) \leq c < 0$ for all (u, v, w).

Consequently,

$$\frac{\partial}{\partial t} u = f(u, w) - c_1 u + c_2 v, \tag{4.102}$$

$$\delta \frac{\partial}{\partial t} v = h(u, v) := c_1 u - c_2 v, \tag{4.103}$$

$$\frac{\partial}{\partial t} w = D \Delta w + g(u, w), \tag{4.104}$$

supplemented with homogeneous Neumann boundary conditions for w and classical initial conditions, exhibits, for sufficiently small positive δ, diffusion-driven instability at the same steady state as model (3.170)-(3.171), see Lemmas 4.2 and 4.5 . If we show uniform boundedness, system (4.102)-(4.104) satisfies all conditions of Lemma 4.7. The uniform boundedness follows from the following observation: $f(u,w) < a-u$ holds, hence f is strictly negative for $u > a+\varepsilon$. Since the kinetics of the system of ordinary differential equations is of type

$$\frac{\partial}{\partial t}u = f(u,w) - h(u,v), \tag{4.105}$$

$$\frac{\partial}{\partial t}v = h(u,v)/\delta, \tag{4.106}$$

$\partial u/\partial t > 0$ implies $\partial v/\partial t < 0$ for $u > a+\varepsilon$. Using the framework of invariant rectangles and stable manifolds, we obtain uniform boundedness for u. Then, an argumentation analogous to the proof of uniform boundedness for $\delta = 0$ yields the result. Note, however, that this argumentation is valid in this generality only for $\delta < 1$.
Summarising, model (4.102)-(4.104) satisfies the conditions for regularity of the limit $\delta \to 0$, i.e. the conditions of Lemmas 4.7, 4.2 and 4.5. Consequently, it exhibits coexistence of DDI and hysteresis. Moreover, the solution converges uniformly on any finite time interval towards the solution of the quasi-steady state approximation.

4.5.3 Numerical results

In the previous sections, we showed analytically that DDI and existence as well as stability of spatially inhomogeneous steady states can be deduced from the reduced model. In this section, we show numerical illustrations of this phenomenon.
However, the analytical results imply that the solution of model (4.1)-(4.5) converges towards the solution of (4.9)-(4.10). Moreover, it implies that stability of certain steady states can be deduced as well. A detailed look at the proofs may yield an upper boundary on δ to ensure 'transfer' of stability, but this boundary is not proved to be necessary. We therefore show numerical approximations for the solution to model (4.1)-(4.5) for

Parameter set 4.10.

$$\mu_1 = \mu_2 = d = 1, \mu_3 = 4.1, b = 2, m_1 = 1.44, m_2 = 2, D = 1. \tag{4.107}$$

Initial conditions for u, w are defined in Parameter set 3.27. $v(x,0) = 2.48$.

for different $\delta > 0$ in Figures 4.2-4.3. We observe that the solution converges towards the solution for $\delta = 0$ as δ tends towards zero. Moreover, the solution tends towards a pattern which is close in L^p-sense. This illustrates the results proved in Lemma 4.5 and 4.7. However, we observe that even for relatively large δ, the solution converges to a similar pattern. This illustrates that if $g(u(x,0), v(x,0), w(x,0)) \approx 0$ and $v(x,0)$ is regular, the transition phase between destabilised steady state and discontinuous pattern may just be extended. Stability appears to 'transfer' onto the unreduced model for larger δ. However, Figure 4.4 shows that the Tikhonov-type result indeed needs small δ. It shows an example with very irregular $v(x,0)$ in Figure 4.4. We observe that the solution converges towards a locally stable steady state which is different from the one the solution converges to for $\delta = 0$. On the other hand, for sufficiently small δ, the Tikhonov type result ensures that the solution stays close to the solution for $\delta = 0$ up to a time T_δ. We see that in case of large δ, T_δ is so small that the pattern selection takes place at a time $t > T_\delta$. For small δ, it appears that the pattern selection takes place at a time $t < T_\delta$.

Remark 4.11. *Note that the above parameters correspond to the parameter set 3.24 for model* (4.9)-(4.10), *as can been seen from the rescaling conducted to obtain system* (3.92)-(3.93).

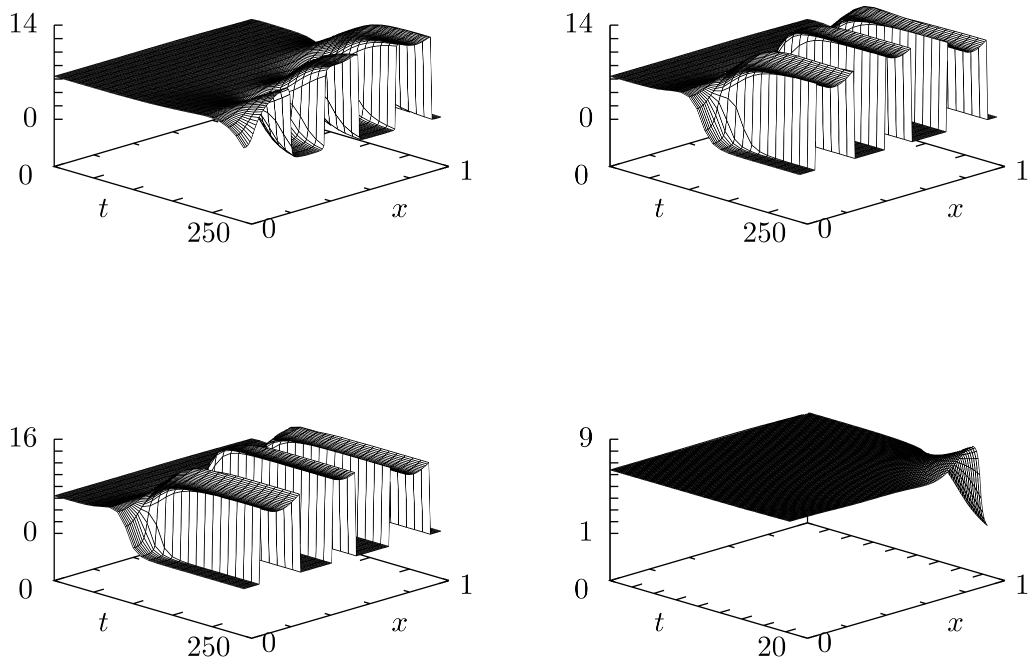

Figure 4.2: Numerically obtained solution to model (4.82)-(4.85) for parameter set 4.10. We observe convergence towards the solution for $\delta = 0$ (see Figure 3.10 (left)) as $\delta \to 0$. Upper left: $\delta = 20$. Upper right: $\delta = 10$. Lower left: $\delta = 8$. Lower right: $\delta = 4$.

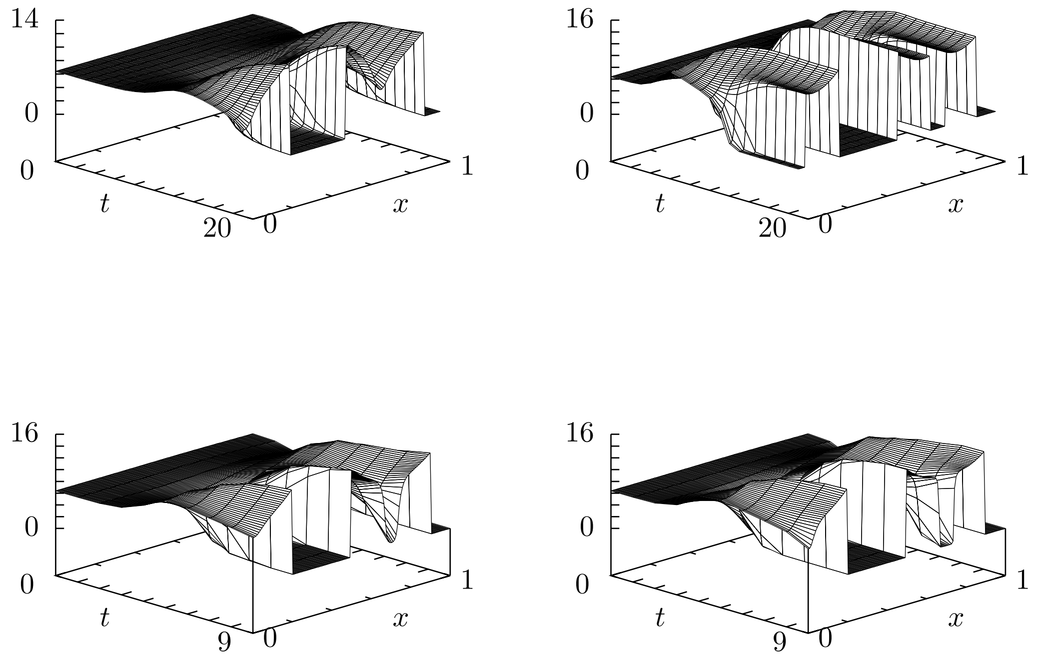

Figure 4.3: Numerically obtained solution to model (4.82)-(4.85) for parameter set 4.10. We observe convergence towards the solution for $\delta = 0$ (see Figure 3.10 (left)) as $\delta \to 0$. Upper left: $\delta = 1$. Upper right: $\delta = 0.25$. Lower left: $\delta = 0.125$. Lower right: $\delta = 0.0625$.

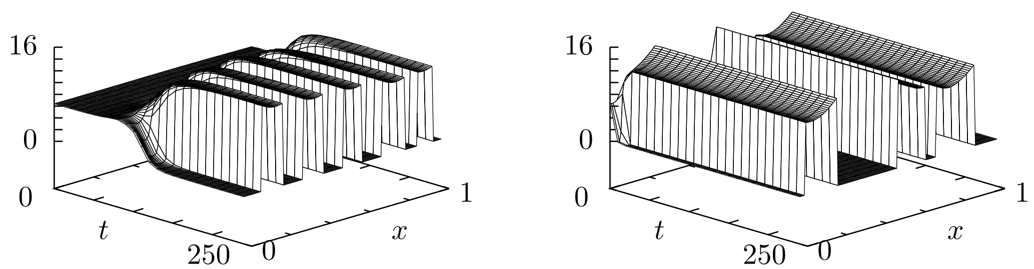

Figure 4.4: Numerically obtained solution to model (4.82)-(4.85) for parameter set 4.10, but $v(x, 0) = 2.48 + 0.1x^2 \sin(10\pi x)$: Left: $\delta = 10$. Right: $\delta = 0.002$. We observe that another pattern is selected for δ large. For δ small, a pattern similar to $\delta = 0$, (see Figure 3.10 (left)), is selected.

5 The shadow system

Let $\Omega \subset \mathbb{R}$ be a bounded domain. For reaction-diffusion equations of type (3.1)-(3.2), we call the limit system for $D \to +\infty$ the shadow system. The idea of this approximation is that existence and stability of steady states may be similar for the shadow system and for D large. We investigate whether the properties of these steady states are reflected by steady states of the shadow system, which reads

$$\frac{\partial}{\partial t}U(t,x) = f(U(t,x),\Xi(t)), \qquad (t,x) \in (0,T) \times \overline{\Omega}, \tag{5.1}$$

$$\frac{\partial}{\partial t}\Xi(t) = \int_{\Omega} g(U(t,x),\Xi(t))dx, \qquad t \in (0,T), \tag{5.2}$$

$$(U(0,x),\Xi(0) \in (C(\overline{\Omega}) \times \mathbb{R}), \tag{5.3}$$

If U respectively Ξ is scalar, we denote it u respectively ξ. Heuristically, as described in [Ni11], this system arises from the assumption that component $V(t,x)$ of system (3.1)-(3.2) tends towards a spatially homogeneous solution as $D \to \infty$. To illustrate this approach, multiply by D^{-1}, and obtain

$$D^{-1}\frac{\partial}{\partial t}V = \Delta V + D^{-1}g(U,V), \tag{5.4}$$

which, heuristically, tends towards

$$0 = \Delta V, \tag{5.5}$$

as D tends towards infinity. Considering homogeneous Neumann boundary conditions, this leads to the assumption that the limit solution's component V is constant. Note that for constant V, it holds that $V(t,x) = \frac{1}{\mu(\Omega)}\int_{\Omega} V(t,x)dx$. If $V(t) \in \mathbb{R}^{\dim(V)}$ for all $t \geq 0$ holds, the second equation of (3.1) is over-determined due to spatial inhomogeneity of the right-hand-side. Keener's idea is to substitute the equation for V by the equation for the mass $\Xi(t) = \int_{\Omega} V(x,t)dx$ for $\mu(\Omega) = 1$, leading to system (5.1)-(5.3). Invariance of Turing-type destabilisation is insofar intuitive as it is the limit $D \to \infty$ and introduction of the diffusion operator changes stability. Following the proof in [MCHKS13], performed for a system of one reaction-diffusion equation coupled to one ordinary differential equations, it is possible to show that solutions behave similar for finite time, if D is sufficiently large. This result has been generalised by Bobrowski in [Bob15], where the author proves, under suitable conditions, that the solution of system (3.1)-(3.2) converges uniformly on any finite time interval towards the solution of system (5.1)-(5.3) as D tends towards infinity. We restate this result of Bobrowski in Theorem 5.1 due to its broader generality. Together with coinciding conditions for stability, it is likely that the solution approaches a steady state which is qualitatively similar. Spatially inhomogeneous steady states of (5.1)-(5.3) are locally constant if the roots $\Xi(U)$ of $f(U, \Xi) = 0$ are isolated, hence the steady states cannot be equal if they are not steady states of the kinetic system. However, for v scalar, Lemma 3.6 and section 5.4 imply that for all $D > 0$ there exist infinitely many steady states of the reaction-diffusion-ODE system in a neighbourhood of a steady state of the integro-differential equation, see Lemma 5.4. For D sufficiently large, numerical simulations suggest that the qualitative difference of the steady states lies, as (ε_0, A)-stability suggests, within a small subdomain surrounding the 'jump points' of the steady states.

Another - from the perspective of modelling ambivalent - finding is high dependence of arising patterns on the choice of initial conditions. For scalar u, this follows immediately if the solution to the equation for $u(x)$ is unique and its right-hand-side does not explicitly depend on $x \in \overline{\Omega}$ since well-posedness implies a maximum principle. The numerical simulations in section 3.6 showed that the pattern does not solely depend on the initial conditions if they are sufficiently regular and D is small. Consequently, considered globally on Ω, the shadow system is truly just an approximation with respect to pattern selection for D large. On the other hand, the shadow system could be interpreted as an approximation of the local behaviour of the solution. However, this interpretation is speculative and is not investigated rigorously. Note that in the previous sections we already pointed out that the set of *stable* steady states for non-diffusive u is not the L^p-closure of the set of *stable* steady states for diffusive u as diffusion's strength tends to zero. In other words, not all stable steady states for non-diffusive u are approximations of stable steady states for weakly diffusing u. This observation is carried over onto shadow-systems. Namely, we show that infinitely many, non-monotone patterns with jump-type discontinuities are stable. However, consider a system of type (1.1) and $d_v \to \infty$ and one-dimensional spatial domain. Stable patterns of its shadow systems satisfy a *non-monotonicity implies instability* principle, as shown in [NPY01]. This implies that introduction of small diffusion with diffusion coefficient $d_u = \varepsilon$ to u is no suitable approximation for non-diffusive u with respect to stability: Even if there exist steady states for weakly diffusing u, which are in L^p-sense close to a stable steady state for non-diffusive u, they must be unstable due to their non-monotonicity. Combined with the result of [Bob15] respectively [MCHKS13], the breakdown of pattern in subsection 3.6.3 appears analytically plausible for large d_v. Let u be diffusive with diffusion coefficient d_u. Denote the solution for diffusion coefficients d_u, d_v by $(u^{d_u,d_v}, u^{d_u,d_v})$ and the solution to the respective shadow-systems by $(u^{d_u,\infty}, \xi^{d_u,\infty})$. For large d_v, the estimate

$$c(t) \leq \left\| u^{d_u,\infty} - u^{d_u,d_v} \right\| + \left\| u^{d_u,d_v} - u^{0,d_v} \right\| + \left\| u^{0,d_v} - u^{0,\infty} \right\|, \tag{5.6}$$

shows breakdown for large d_v since there exists a t^* such that $c(t^*) > \varepsilon$ and d_v can be chosen large such that $\left\| u^{0,d_v} - u^{0,\infty} \right\| + \left\| u^{d_u,\infty} - u^{d_u,d_v} \right\| < \varepsilon/4$ on $(0, 2t^*)$.

5.1 Existence of solutions

Consider model (5.1)-(5.3) with twice continuously differentiable f, g. Then, local Lipschitz continuity yields local existence of a solution $(U, \Xi) \in C^1(0, t; (C^0(\overline{\Omega})^{\dim(U)} \times \mathbb{R}^{\dim(\Xi)}))$ for initial conditions in $(C^0(\overline{\Omega})^{\dim(U)} \times \mathbb{R}^{\dim(\Xi)})$. Since examples such as $f(u, \xi) = u^2$ show that global existence cannot be derived in general for $f, g \in C^1(\mathbb{R}^2)$, global existence of solutions to nonlinear models has to be proved for every model separately, or uniform boundedness of solutions has to be assumed, see Assumption 2.1.

5.2 Shadow limit

Denote the solution of a system of type (3.1)-(3.2) for scalar compartments and diffusion-coefficient D by (u^D, v^D) and the solution of the corresponding shadow system (5.1)-(5.3) by (u, ξ). Then, in [MCHKS13], it was shown that, under suitable conditions, (u^D, v^D) converges almost uniformly on $(0, T)$ towards (u, ξ) as D tends to infinity. This result has been generalised by Bobrowski in [Bob15] onto a broader class of spatial operators and for vector-values U and V:

Theorem 5.1 ([Bob15]). *Let S be a compact metric space, $N_0 \leq N$ natural numbers. Let A_i, $i \in \mathcal{N} := \{1, .., N\}$ be generators of conservative Feller-semigroups in $C(S)$. Assume that there are $\varepsilon > 0, M > 0$ and rank-one projections $P_i, i \in \mathcal{N}_0 := \{1, ...N_0\}$ such that $\left\| e^{tA_i} - P_i \right\| \leq M e^{-\varepsilon t}$ for $t > 0, i \in \mathcal{N}_0$. Let $A_i = 0$ for $i \in \mathcal{N} \setminus \mathcal{N}_0$. Consider the system*

$$\frac{\partial}{\partial t} u_n^D(t) = F(U^D, V^D), \tag{5.7}$$

$$\frac{\partial}{\partial t} v_n^D(t) = D\mathcal{A}V^D + G(U^D, V^D), \tag{5.8}$$

where $U^D = (u_i^D)_i$ and $V^D = (v_i^D)_i$ are vector-valued with dimension N_0 resp. $N - N_0$ and $\mathcal{A}$

generates the product semigroup

$$e^{t\mathcal{A}} \begin{pmatrix} v_1^D(0) \\ .. \\ v_{N_0}^D \end{pmatrix} = \begin{pmatrix} e^{tA_1} v_1^D(0) \\ .. \\ e^{tA_{N_0}} v_{N_0}^D \end{pmatrix}. \tag{5.9}$$

Let F, G be locally Lipschitz continuous maps from $C(S)^N$ to $C(S)^{N_0}$ and $C(S)^{N-N_0}$. Moreover, let (U^D, V^D) be uniformly bounded.
If D tends to infinity, then (U^D, V^D) converge to the solution of

$$\frac{\partial}{\partial t} U = G(U(t), U(t)), \tag{5.10}$$

$$\frac{\partial}{\partial t} V = PF(U(t), V(t), \tag{5.11}$$

with initial conditions $(U(0), V(0)) = (U^D(0), PV^D(0))$ almost uniformly in $t \in (0,T)$ for any finite T, where $P(v_i^D) = P_i(v_i^D)$.

Proof. See [Bob15], Theorem 4.1. □

The Laplace operator with Neumann-boundary conditions generates a Feller-semigroup on $C^2(\overline{\Omega})$ converging towards a rank-one projection for $\Omega \subset \mathbb{R}^n$ convex (otherwise, the limit might not have rank one) and bounded. If Assumption 2.1 is satisfied, F and G are sufficiently regular and solutions are uniformly bounded. However, in order to generalise the result onto a far wider class of operators, the result of Bobrowski lacks order of convergence. The order for systems of type (3.1)-(3.2) for scalar u, v has been investigated in [MCHKS13], yielding, for each $\alpha \in (0, \dim(\Omega)/2)$, that

$$\lim_{D\to\infty} \sup_{0\le t\le T} t^\alpha \left(\left\| u^D - u \right\|_\infty + \left\| v^D - v \right\|_\infty \right) = 0. \tag{5.12}$$

5.3 Integro-driven instability

Similar to the concept of diffusion-driven instability, we introduce the concept of integro-driven instability of the corresponding shadow system. To simplify calculation, we assume without loss of generality that $\int_\Omega 1dx = 1$.

Definition 5.2 (Integro-driven instability)**.** *Assume that a system of ordinary differential equations*

$$\frac{\partial}{\partial t}U(t) = f(U(t), \varXi(t)), \qquad t \in (0,T), \tag{5.13}$$
$$\frac{\partial}{\partial t}\varXi(t) = g(U(t), \varXi(t)), \qquad t \in (0,T), \tag{5.14}$$
$$(U(0), \varXi(0)) \in \mathbb{R}^{\dim(U)+\dim(\varXi)}, \tag{5.15}$$

has a stable stationary solution $(\overline{U}, \overline{\varXi})$.
We say that system (5.13)-(5.15) *exhibits integro-driven instability if* $(\overline{U}(x), \overline{\varXi}) = (\overline{U}, \overline{\varXi})$ *is an unstable stationary solution of system* (5.1)-(5.3).

In [KBHG12], the authors investigate the idea of unstable subsystems for systems of type (3.1)-(3.2) for $D > 0$, in [ASY12] for small diffusion coefficient for U. It turns out that the idea of unstable subsystems can be extended onto systems of type (5.1)-(5.3). The following lemma is a generalisation of Theorem 2.1 in [MCHKS13].

Lemma 5.3. *Consider a system of type* (5.1)-(5.3) *for vector-valued* U *and vector-valued* $\varXi$ *and let* f, g *be twice continuously differentiable. Let* $(\tilde{U}, \tilde{\varXi})$ *denote a stationary solution of* (5.1)-(5.1) *which is constant on a subdomain* $\varOmega_1 \subset \varOmega$ *and denote the value assumed on* $\varOmega_1$ *by* $(\overline{U}, \overline{\varXi})$. *Moreover, assume that the Jacobian matrix of the ODE subsystem,* $\nabla_U f|_{(\overline{U},\overline{\varXi})} = (\partial_{u_j} f_i|_{(\overline{U},\overline{\varXi})})_{ij}$, *has an eigenvalue* λ_0 *with*

$$\operatorname{Re}\lambda_0 \geq c > 0, \tag{5.16}$$

and that all other eigenvalues of $\nabla_U f|_{(\tilde{U},\tilde{\varXi})}(x)$ *satisfy* $|\operatorname{Re}\lambda(x)| \geq c > 0$ *on* $\varOmega$. *Then* $(\tilde{U}, \tilde{\varXi})$ *is unstable.*

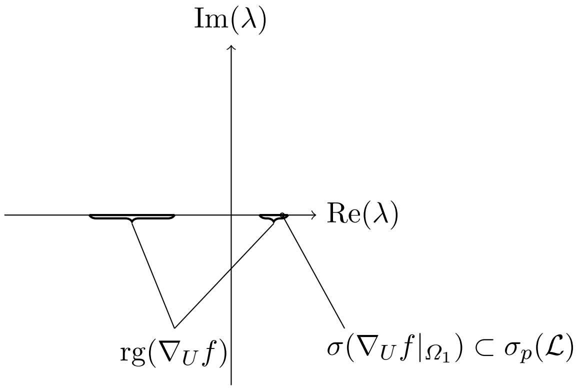

Figure 5.1: Illustration of the spectrum of the operator $\mathcal{L}$ in Lemma 5.3.

Proof. We consider an initial value problem for the perturbation $\varphi(x,t) = U(x,t) - \tilde{U}(x)$ and $\psi(t) = \Xi(t) - \tilde{\Xi}$. The pair $z = (\varphi, \psi)$ is a solution of the following initial value problem,

$$\frac{\partial}{\partial t} z = \mathcal{L}z + \mathcal{N}(z), \tag{5.17}$$

$$z(0) = z_0 = (U_0 - \tilde{U}, \Xi_0 - \tilde{\Xi}), \tag{5.18}$$

where

$$\mathcal{L}z = \mathcal{L}\begin{pmatrix}\varphi(x)\\ \psi\end{pmatrix} = \begin{pmatrix}\nabla_U f|_{(\tilde{U},\tilde{\Xi})}\varphi(x) + \nabla_\Xi f|_{(\tilde{U},\tilde{\Xi})}\psi \\ \int_\Omega \nabla_U g|_{(\tilde{U},\tilde{\Xi})}\varphi(x)dx + \int_\Omega \nabla_\Xi g|_{(\tilde{U},\tilde{\Xi})}\psi dx\end{pmatrix}, \tag{5.19}$$

and $\mathcal{N}$ is a nonlinear term obtained via Taylor expansion, since f and g are twice continuously differentiable. Define $(X, \|.\|_X) := ((L^\infty(\Omega))^n \times \mathbb{R}^m, \|\varphi\|_{L^\infty(\Omega)} + |\psi|)$ and consider $\mathcal{L}$ an operator in X with domain X. $\mathcal{L}$ is a bounded operator and therefore generates a strongly continuous semi-group.

By assumption, $\nabla_U f|_{(\overline{U},\overline{\Xi})}$ has an eigenvalue λ_0 with $\operatorname{Re}\lambda_0 > 0$. We show that λ_0 is an eigenvalue of the operator $\mathcal{L}$. Let $(\lambda_0, e_{\lambda_0})$ be the eigenvalue-eigenvector pair of $\nabla_U f|_{(\overline{U},\overline{\Xi})}$. It is easy to see that $(e_{\lambda_0}\varphi_0, 0)$ is the corresponding eigenvector of $\mathcal{L}$ for every non-trivial $\varphi_0 \in \{\varphi \in C^0(\overline{\Omega}) | \int_{\Omega_1} \varphi = 0 \text{ and } \varphi = 0 \text{ on } \Omega \setminus \Omega_1\}$:

$$\nabla_U f|_{(\overline{U},\overline{\Xi})} e_{\lambda_0}\varphi_0 = \lambda_0 e_{\lambda_0}\varphi_0, \tag{5.20}$$

and

$$\int\limits_\Omega \sum_{i=1}^n (\frac{\partial g_i}{\partial u_j}|_{(\tilde{U},\tilde{\Xi})})_{ij} e_{\lambda_0,i}\varphi_0(x)dx = \sum_{i=1}^n (\frac{\partial g_i}{\partial u_j}|_{(\overline{U},\overline{\Xi})})_{ij} e_{\lambda_0,i} \int\limits_{\Omega_1} \varphi_0(x)dx = 0. \tag{5.21}$$

Consequently, we find $\mathcal{L}(e_{\lambda_0}\varphi_0(x), 0) = \lambda_0(e_{\lambda_0}\varphi_0(x), 0)$. f and g are twice continuously differentiable by assumption. Therefore, since $\mathcal{N}$ results from a Taylor expansion and $\text{meas}(\Omega) < \infty$ holds,

$$\|\mathcal{N}(z)\|_X \leq c\,\|z\|_X^2\,, \tag{5.22}$$

holds. It follows nonlinear instability of the steady state, see e.g. Theorem 1, [SS00]. □

5.4 Existence of spatially inhomogeneous steady states

Consider scalar ξ. By definition, a steady state $(\tilde{U}(x), \tilde{\xi})$ satisfies the following equation for all $x \in \overline{\Omega}$,

$$0 = f(\tilde{U}(x), \tilde{\xi}). \tag{5.23}$$

Assume that this equation has n isolated roots for given $\tilde{\xi}$ and denote these roots $U_i(\tilde{\xi}), 1 \leq i \leq n$. Consider a partition of $\overline{\Omega}$ by disjoint sets $\Omega_i, 1 \leq i \leq n$, where $U(x) = U_i(\xi)$ on Ω_i. Then, we can write $\partial\xi/\partial t = 0$ as

$$\begin{aligned} 0 &= \int_{\Omega} g(\tilde{U}(x), \tilde{\xi}), \\ &= \sum_{i=1}^{n} \int_{\Omega_i} g(U_i(\tilde{\xi}), \tilde{\xi}), \\ &= \sum_{i=1}^{n} \mu(\Omega_i) g(U_i(\tilde{\xi}), \tilde{\xi}), \end{aligned} \tag{5.24}$$

since $U_i(\tilde{\xi})$ is constant on Ω_i. This equation can be solved for coefficients $0 \leq \mu(\Omega_i) \leq \mu(\Omega)$ satisfying $\sum_{i=1}^{n} \mu(\Omega_i) = \mu(\Omega)$ if and only if one of the following conditions are satisfied:

1. there exist at least two roots $U_1(\tilde{\xi}), U_2(\tilde{\xi})$ of $f(U, \tilde{\xi}) = 0$ satisfying

$$g(U_1(\tilde{\xi}), \tilde{\xi}) < 0 < g(U_2(\tilde{\xi}), \tilde{\xi}). \tag{5.25}$$

   This condition allows construction of discontinuous steady states. It is similar to the condition for existence of spatially inhomogeneous steady states for the corresponding reaction-diffusion equation, see Lemma 3.6. For reaction-diffusion equations, this condition is implied by homogeneous Neumann boundary conditions for inhomogeneous steady states.

2. there exists $U_i(\tilde{\xi})$, such that $g(U_i(\tilde{\xi}), \tilde{\xi}) = 0$. This allows construction of steady states assuming the values of steady states of the kinetic system.

Assume that $(\sum_{i=1}^{n} \chi(\Omega_i) U_i(\tilde{\xi}), \tilde{\xi})$ is a steady state of (5.1)-(5.3). It is possible to construct steady states of system (3.1)-(3.2) assuming only values in a neighbourhood of some values $(U_i(\tilde{\xi}), \tilde{\xi})$:

Corrolary 5.4. *Assume that* $(\sum_{i=1}^{n} \chi_{\Omega_i}(x) U_i(\tilde{\xi}), \tilde{\xi})$ *is a steady state of system* (5.1)-(5.3). *Moreover, assume that* $|\det(\nabla_U f)| \geq c > 0$*, evaluated at the steady state, holds point-wise. Then, for all* $\varepsilon > 0$*, there exists a jump-type steady state of system* (5.1)-(5.3) *which assumes only values in* $\bigcup_i B_\varepsilon(U_i(\tilde{\xi})) \times B_\varepsilon(\tilde{\xi})$.

Proof. If $g(U_i(\tilde{\xi}), \tilde{\xi}) = 0$, the steady state is a steady state of the kinetic system, hence the result is clear.
If w.l.o.g. $g(U_i(\tilde{\xi}), \tilde{\xi}) > 0$, then it holds for some $j \neq i$ that $g(U_j(\tilde{\xi}), \tilde{\xi}) < 0$. Since $f, g \in C^1$ and $\det(\nabla_U f) \neq 0$, all conditions of Lemma 3.6 are satisfied. By choosing a sequence $(\varepsilon_n)_{n \in \mathbb{N}}$

with $\varepsilon_n \searrow 0$ in the proof of Lemma 3.6, the proof yields existence of steady states assuming values only in a neighbourhood of $\bigcup_i (U_i(\tilde{\xi}), \tilde{\xi})$. For ε_n sufficiently small, the Jacobian matrix of the kinetic system, evaluated at the steady state is in a neighbourhood of the Jacobian matrix of the kinetic system of the integro-ODE system. Due to continuity of f, g, results on the signs of entries are valid for the steady state of the reaction-diffusion system for sufficiently small ε_n. Due to continuous dependency of the determinant and trace on the entries, results about the signs of them are valid for the steady state of the reaction-diffusion-system for sufficiently small ε_n. □

Note that the constructed steady states do not necessarily have discontinuities a the same spatial positions. More general, for m integro-differential equations and n roots $U_i(\tilde{\xi})$ of $f(\tilde{U}, \tilde{\xi}) = 0$, the equation

$$\begin{pmatrix} g_1(U_1(\tilde{\xi}), \tilde{\xi}) & \cdots & g_1(U_n(\tilde{\xi}), \tilde{\xi}) \\ \vdots & \ddots & \vdots \\ g_m(U_1(\tilde{\xi}), \tilde{\xi}) & \cdots & g_m(U_n(\tilde{\xi}), \tilde{\xi}) \\ 1 & \cdots & 1 \end{pmatrix} \begin{pmatrix} \mu(\Omega_1) \\ \vdots \\ \mu(\Omega_n) \end{pmatrix} = \begin{pmatrix} 0 \\ \vdots \\ 0 \\ \mu(\Omega) \end{pmatrix}, \tag{5.26}$$

must admit a solution satisfying $0 \leq \mu(\Omega_i)$ for all i. Note that the last row of the matrix is dispensable. In case of $\sum_{i=1}^{n} \mu(\Omega_i) \neq \mu(\Omega)$, the constructed solution on $(0, \sum_{i=1}^{n} \mu(\Omega_i))$ can be rescaled by $\hat{x} = x\mu(\Omega)/\sum_{i=1}^{n} \mu(\Omega_i)$. *If not specified differently, we consider scalar* $\Xi = \xi$ *and* $U = u$.

5.5 (ε_0, A)-stability for integro-ODE systems

We define (ε_0, A)-stability for integro-ODE systems analogously to the definition of (ε_0, A)-stability for reaction-diffusion-ODE systems in Definition 3.8. However, for shadow systems of reaction-diffusion-ODE systems, the 'diffusing' component is constant in space. The subspace of constant functions is complete if equipped with Sobolev norms, hence the Sobolev norms are equivalent to the euclidean norm. Therefore, the neighbourhood basis can be defined equivalently by

$$N_\varepsilon(\tilde{u}, \tilde{\xi}) := \{(u, \xi) \in L^p(\Omega) \times \mathbb{R} |\, \exists_{R \subset \Omega} : \|u - \tilde{u}\|_{L^\infty(R)} + |\xi - \tilde{\xi}| \leq \varepsilon \,\text{and}\, \mu(\Omega \setminus R) \leq \varepsilon^2\}. \tag{5.27}$$

We define (ε_0, A)-stability analogously to Definition 3.8:

Definition 5.5. *A stationary solution* $(\tilde{u}, \tilde{\xi})$ *of regularity as in Corollary 5.4 of system* (5.1)-(5.3) *is said to be* (ε_0, A)*-stable for positive constants* ε_0 *and* A *if initial functions* $(u(x, 0), \xi(0))$

satisfy

$$\|u(x,0) - \tilde{u}\|_{L^\infty(R)} + |\xi(x,0) - \tilde{\xi}| < \varepsilon, \tag{5.28}$$

for some $R \subset I$ *with* $\text{meas}(I \setminus R) < \varepsilon^4$*, and* $\varepsilon \in (0, \varepsilon_0)$*, then*

$$\|u(t) - \tilde{u}\|_{L^\infty(R)} + |\xi(t) - \tilde{\xi}| < A\varepsilon, \tag{5.29}$$

for all $t > 0$*.*

5.6 Conditions for stability of spatially inhomogeneous steady states of the 'shadow system'

In section 3.5, we investigated conditions for stability of steady states with jump-type discontinuity of reaction-diffusion-ODE systems. The conditions for (ε_0, A)-stability for shadow systems turn out to be similar. However, the similarity of conditions for stability can be misleading, since in general steady states are only steady states of both systems if they are piece-wise constant.
On the other hand, Corollary 5.4 implies that existence of steady states and the signs of entries of Jacobian matrix evaluated at them can be derived from the shadow-system. Consequently, existence of stable steady states of reaction-diffusion-ODE systems can be derived from existence of certain steady states of the shadow systems. The concept of the proofs of stability is analogous to the proofs in section 3.5.
First, we linearise the right-hand-side of (5.1)-(5.3) around a jump-type steady state $(\tilde{u}, \tilde{\xi})$ and identify the linearised operator $\mathcal{L}$ as bounded operator from $X = L^p \times \mathbb{R}$ to X. Therefore, the spectrum of the operator determines the stability in $L^p \times \mathbb{R}$ since the nonlinearities are sufficiently smooth. Then, we use the (ε_0, A)-topology. *A striking difference between the proof for shadow-systems and reaction-diffusion-ODE systems is that it is not restricted to one-dimension spatial domain for shadow systems.* For reaction-diffusion-ODE systems, the presented proof requires a one-dimensional spatial domain, $I \subset \mathbb{R}$ respectively $\Omega \subset \mathbb{R}$, even though numerical investigations, which are not shown within this thesis, imply existence of stable discontinuous patterns for two- and three-dimensional spatial domain.

Lemma 5.6. *Let* $\Omega \subset \mathbb{R}^n$ *be bounded.*
Consider a spatially inhomogeneous steady state $(\tilde{u}, \tilde{\xi}) \in (L^\infty(\Omega) \times \mathbb{R})$ *of a system of type*

$$\frac{\partial}{\partial t} u(x,t) = f(u(x,t), \xi(t)), \qquad (x,t) \in \overline{\Omega} \times \mathbb{R}_+, \tag{5.30}$$

$$\frac{\partial}{\partial t} \xi(t) = \int_\Omega g(u(x,t), \xi(t))dx, \qquad t \in \mathbb{R}_+. \tag{5.31}$$

$$(u(x,0), \xi(0) \in (C(\overline{\Omega}) \times \mathbb{R}). \tag{5.32}$$

Consider the operator

$$\mathcal{L}\begin{pmatrix}\varphi\\ \psi\end{pmatrix} := \begin{pmatrix}\partial_u f|_{(\tilde{u},\tilde{\xi})}\varphi + \partial_\xi f|_{(\tilde{u},\tilde{\xi})}\psi \\ \int_\Omega \partial_u g|_{(\tilde{u},\tilde{\xi})}\varphi dx + \int_\Omega \partial_\xi g|_{(\tilde{u},\tilde{\xi})}\psi dx\end{pmatrix}, \tag{5.33}$$

an operator in $L^p(\Omega) \times \mathbb{R}$ *with domain* $L^p(\Omega) \times \mathbb{R}$*. If*

1.
$$\partial_u f|_{(\tilde{u},\tilde{\xi})}, \partial_\xi f|_{(\tilde{u},\tilde{\xi})}, \partial_u g|_{(\tilde{u},\tilde{\xi})}, \partial_\xi g|_{(\tilde{u},\tilde{\xi})} \in L^\infty(\Omega), \tag{5.34}$$

2.
$$\partial_u f|_{(\tilde{u},\tilde{\xi})}, \partial_\xi g|_{(\tilde{u},\tilde{\xi})} \leq c < 0 \text{ and } (\partial_u f \partial_\xi g - \partial_\xi f \partial_u g)|_{(\tilde{u},\tilde{\xi})} \geq c > 0, \tag{5.35}$$

then there exist $c_{\mathrm{Re}}, c_{\mathrm{Im}} > 0$*, such that*

$$\{\lambda \in \mathbb{C} | \operatorname{Re}\lambda > -c_{\mathrm{Re}} \vee |\operatorname{Im}\lambda| > c_{\mathrm{Im}}\} \subset \varrho(\mathcal{L}), \tag{5.36}$$

holds for the resolvent set $\varrho(\mathcal{L})$ *of* $\mathcal{L}$*.*

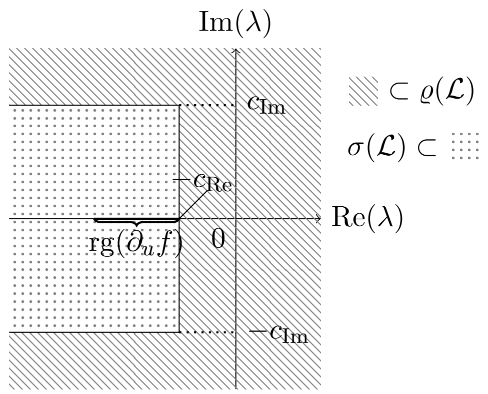

Figure 5.2: Illustration of the spectrum of the operator $\mathcal{L}$ in Lemma 5.6.

Remark 5.7. *Note that for* $f, g \in C^2(\mathbb{R}^2)$ *and steady states* $L^\infty(\Omega) \times \mathbb{R}$ *with finitely many jumps, Assumption* (5.34) *is satisfied. Even more, we can choose* $p = \infty$ *and obtain local exponential stability in* $L^\infty(\Omega) \times \mathbb{R}$ *if* $\sup_{t\geq 0}(\|u(t)\|_{L^\infty} + |\xi(t)|) < \infty$*.*

Proof. Throughout the proof $\partial_u f, \partial_\xi f, \partial_u g, \partial_\xi g$ are always evaluated at $(\tilde{u}, \tilde{\xi})$. By application of Hölder inequality, we see that $\mathcal{L}$ is a bounded operator if considered an operator in

$X = (L^p(\Omega) \times \mathbb{R})$ to X. First, we investigate the resolvent set of $\mathcal{L}$: Let $(\varphi_1, \psi_1) \in L^p(\Omega) \times \mathbb{R}$ be given and consider the following equation for $\lambda \in \mathbb{C}$:

$$(\partial_u f - \lambda)\varphi + \partial_\xi f \psi = \varphi_1, \tag{5.37}$$

$$\int_\Omega \partial_u g \varphi + (\partial_\xi g - \lambda)\psi dx = \psi_1. \tag{5.38}$$

For $\lambda \notin \mathrm{rg}(\partial_u f)$, it is possible to solve (5.37) for φ,

$$\varphi = \frac{\varphi_1 - \partial_\xi f \psi}{\partial_u f - \lambda}. \tag{5.39}$$

Substituting φ in (5.38) yields

$$\int_\Omega \partial_u g \left(\frac{\varphi_1 - \partial_\xi f \psi}{\partial_u f - \lambda} \right) + (\partial_\xi g - \lambda)\psi dx = \psi_1,$$

$$\int_\Omega \underbrace{\left(-\frac{\partial_u g \partial_\xi f}{\partial_u f - \lambda} + \partial_\xi g - \lambda \right)}_{:=A(\lambda)} \psi dx = \psi_1 - \int_\Omega \frac{\partial_u g \varphi_1}{\partial_u f - \lambda}.$$

Analogously to Corollary 3.10, we note that there exist $c_{\mathrm{Re}}, c_{\mathrm{Im}} > 0$, such that

1. for $-c_{\mathrm{Re}} \leq \mathrm{Re}(\lambda)$, it holds $\mathrm{Re}\, A(\lambda) < 0$,
2. for $c_{\mathrm{Im}} \leq \mathrm{Im}(\lambda)$, it holds $\mathrm{Im}\, A(\lambda) > 0$.

Consequently, we can write the formal solution as

$$\psi = \frac{\psi_1 - \int_\Omega \frac{\partial_u g \varphi_1}{\partial_u f - \lambda} dx}{\int_\Omega (-\frac{\partial_u g \partial_\xi f}{\partial_u f - \lambda} + \partial_\xi g - \lambda) dx}. \tag{5.40}$$

It is left to show sufficiently high regularity of the solutions φ and ψ. For $\varphi_1 \in L^p(\Omega)$, we obtain

$$|\psi| \leq c(|\psi_1| + \int_\Omega |\partial_u g||\varphi_1| dx) \leq c(|\psi_1| + \|\partial_u g\|_{L^{p'}} \|\varphi_1\|_{L^p}), \tag{5.41}$$

and, due to (5.39),

$$\|\varphi\|_{L^p} \leq C(\|\varphi_1\|_{L^p} + \|\partial_\xi f\|_{L^p} |(|\psi_1| + \|\partial_u g\|_{L^{p'}} \|\varphi_1\|_{L^p})). \tag{5.42}$$

□

Theorem 5.8. *Consider a system of type* (5.1)-(5.3) *for scalar compartments* (u, ξ)*. Assume that there exists a spatially inhomogeneous steady state* $(\tilde{u}, \tilde{\xi})$ *with finitely many jump-type discontinuities. If the model satisfies the conditions of Lemma 5.6 at the steady state, then there exist* $A, \varepsilon_0 > 0$*, such that* $(\tilde{u}, \tilde{\xi})$ *is* (ε_0, A)*-stable.*

Remark 5.9. *Note that, unlike in Theorem 3.9, no Sobolev type estimate* $\|.\|_{L^\infty} \leq C \|.\|_{H^1}$ *is used. Consequently, stability of steady states of the shadow system can be obtained for arbitrary, finite, finite dimensional spatial dimension.*

Remark 5.10. *Note that the stability result can be extended onto systems with vector-valued* $U = (u_1, u_2)$ *analogous to Theorem 3.9 and 4.7.*

Proof. The proof follows the lines of the proof of stability of steady states for the reaction-diffusion-ODE system.
Again, we write equation (5.1)-(5.3) as

$$\frac{\partial}{\partial t}\begin{pmatrix}\varphi(x,t)\\ \psi(t)\end{pmatrix} = \mathcal{L}\begin{pmatrix}\varphi(x,t)\\ \psi(t)\end{pmatrix} + \begin{pmatrix}\varrho(x,t)\\ \sigma(x,t)\end{pmatrix}, \tag{5.43}$$

where

$$\mathcal{L}\begin{pmatrix}\varphi(x,t)\\ \psi(t)\end{pmatrix} := \begin{pmatrix}\partial_u f|_{(\tilde{u}(x),\tilde{\xi})}\varphi(x,t) + \partial_\xi f|_{(\tilde{u}(x),\tilde{\xi})}\psi(t)\\ \int_\Omega \partial_u f_{(\tilde{u}(x),\tilde{\xi})}\varphi(x,t)dx + \psi(t)\int_\Omega \partial_\xi f|_{(\tilde{u}(x),\tilde{\xi})}dx\end{pmatrix}, \tag{5.44}$$

and

$$\varrho(x,t) := \frac{1}{2}\left(\partial_{uu} f|_{(\alpha,\beta)}\varphi^2 + 2\partial_\xi\partial_u f|_{(\alpha,\beta)}\varphi\psi + \partial_{\xi\xi} f|_{(\alpha,\beta)}\psi^2\right), \tag{5.45}$$

$$\sigma(x,t) := \frac{1}{2}\left(\int_\Omega \partial_u^2 g|_{(\alpha',\beta')}\varphi^2 dx + 2\int_\Omega \partial_\xi\partial_u g|_{(\alpha',\beta')}\varphi dx\psi + \int_\Omega \partial_\xi^2 g|_{(\alpha',\beta')}dx\psi^2\right), \tag{5.46}$$

where $(\alpha(x), \beta), (\alpha'(x), \beta') \in ((u(x), \tilde{u}(x)) \times (\xi, \tilde{\xi}))$ according to the Taylor-Lagrange residual formula. Recall, that Assumption 2.1 holds, hence the solution is uniformly bounded and f, g are twice continuously differentiable. Lemma 5.6 allows us to use the following estimate:

$$\|\varphi(t)\|_1 + |\psi(t)| \leq c\left((\|\varphi_0\|_1 + |\psi_0|)e^{-kt} + \int_0^t (\|\varrho(s)\|_1 + |\sigma(s)|)e^{-k(t-s)}ds\right). \tag{5.47}$$

By integration, we obtain:

$$|\varphi(x,t)| \leq |\varphi_0(x)|e^{-kt} + \int_0^t \left(|\varrho(s,x)| + |\partial_\xi f(x)\psi(s)|\right)e^{-k(t-s)}ds, \tag{5.48}$$

$$|\psi(t)| \leq c \left(|\psi_0| e^{-kt} + \int_0^t \left(|\sigma(s)| + \int_\Omega |\partial_u g(x)\varphi(s)| dx \right) e^{-k(t-s)} ds \right), \tag{5.49}$$

$$\leq c \left(|\psi_0| e^{-kt} + \int_0^t \left(|\sigma(s)| + \|\varphi(s)\|_1 \right) e^{-k(t-s)} ds \right), \tag{5.50}$$

$$\leq c \left((\|\varphi_0\|_1 + |\psi_0|) e^{-kt} + \int_0^t \left(|\sigma(s)| + \|\varrho(s)\|_1 \right) e^{-k(t-s)} ds \right). \tag{5.51}$$

Note that due to the regularity of f and g,

$$|\varrho(x,t)| \leq C(|\varphi(x,t)|^2 + |\psi(t)|^2), \tag{5.52}$$

$$|\sigma(t)| \leq C(\|\varphi(t)\|_2^2 + |\psi(t)|^2), \tag{5.53}$$

hold. Hence,

$$\begin{aligned} |\psi(t)| &\leq c \left((\|\varphi_0\|_1 + |\psi_0|) e^{-kt} + \int_0^t \left(\|\varphi(s)\|_2^2 + |\psi(s)|^2) e^{-k(t-s)} ds \right) \right), \\ &\leq c \left((\|\varphi_0\|_1 + |\psi_0|) e^{-kt} + \int_0^t \left(\|\varphi(s)\|_{L^\infty(R)}^2 + \mu(I \setminus R) + |\psi(s)|^2) e^{-k(t-s)} ds \right) \right), \\ &\leq c \left((\|\varphi_0\|_{L^\infty(R)} + \mu(I \setminus R) + |\psi_0|) e^{-kt} + \left(\sup_{s \in (0,t)} (\|\varphi(s)\|_{L^\infty(R)} + |\psi(s)|) \right)^2 + \mu(I \setminus R) \right), \end{aligned} \tag{5.54}$$

and

$$\begin{aligned} \|\varphi(t)\|_{L^\infty(R)} &\leq \|\varphi_0\|_{L^\infty(R)} e^{-kt} + \int_0^t \left(\left(\|\varphi(s)\|_{L^\infty(R)} + |\psi(s)| \right)^2 + |\psi(s)| \right) e^{-k(t-s)} ds, \\ &\leq c \left(\|\varphi_0\|_{L^\infty(R)} e^{-kt} + \left(\sup_{s \in (0,t)} (\|\varphi(s)\|_{L^\infty(R)} + |\psi(s)|) \right)^2 + \int_0^t |\psi(s)| e^{-k(t-s)} ds \right), \end{aligned} \tag{5.55}$$

follow. Applying (5.54) to (5.55), we obtain

$$|\varphi(t)|_{L^\infty(R)} \leq c \left((\|\varphi_0\|_{L^\infty(R)} + |\psi_0|) + \left(\sup_{s \in (0,t)} (\|\varphi(s)\|_{L^\infty(R)} + |\psi(s)|) \right)^2 + \mu(I \setminus R) \right),$$

and therefore with (5.54)

$$|\varphi(t)|_{L^\infty(R)}+|\psi(t)| \leq C\left((\|\varphi_0\|_{L^\infty(R)}+|\psi_0|)+\left(\sup_{s\in(0,t)}(\|\varphi(s)\|_{L^\infty(R)}+|\psi(s)|)\right)^2+\mu(I\setminus R)\right).$$

Choosing $A > \max(C, 1)$, and ε_0 so small that

$$1 + A\varepsilon_0 + \varepsilon_0 < \frac{A}{C}, \tag{5.56}$$

it follows for all $0 < \delta \leq \varepsilon_0$ that

$$\|\varphi_0\|_{L^\infty(R)} + |\psi_0| < \delta \quad \Rightarrow \quad \forall_{t>0} : \|\varphi(t)\|_{L^\infty(R)} + |\psi(t)| < A\delta. \tag{5.57}$$

□

We showed that under suitable conditions, a steady state of an integro-ODE system is (ε_0, A)-stable.
A natural question arising is whether it is useful to investigate the behaviour of the shadow system if it leads to the same conditions for stability and existence of steady states. A striking difference between reaction-diffusion-ODE systems and their shadow-systems is that we can algebraically reduce a shadow system using a quasi-steady state approximation for a component with integro-right-hand side. If the right-hand side is uniquely solvable for ξ, the resulting reduced system can be investigated easier than a quasi-steady state reduction of a reaction-diffusion-ODE system involving the inverse of Δ or even a shift of type $(\Delta + (\mu + u(x,t))\,\mathrm{id})^{-1}$, where Δ is considered with homogeneous Neumann boundary conditions. This reduction will be addressed in chapter 6.

5.7 Application to example models

5.7.1 A receptor-based model

In this section, we apply the shadow-reduction to system (3.92)-(3.94),

$$\frac{\partial}{\partial t}u = -(1+w)u + m_1\frac{u^2}{1+ku^2}, \qquad x \in \overline{\Omega}, t \in (0,T), \tag{5.58}$$

$$\frac{\partial}{\partial t}w = D\Delta w - (\mu+u)w + m_2\frac{u^2}{1+ku^2}, \qquad x \in \Omega, t \in (0,T), \tag{5.59}$$

$$\partial_n w = 0, \qquad x \in \partial\Omega, t \in (0,T), \tag{5.60}$$

$$(u(0), w(0)) \in (C(\overline{\Omega}) \times C^2(\overline{\Omega})). \tag{5.61}$$

This system satisfies the conditions of Theorem 5.1 respectively of Theorem A.2 in [MCHKS13]. Therefore, for large D and finite T, component u of the solution of system (5.58)-(5.60) exhibits a similar behaviour like the solution of

$$\frac{\partial}{\partial t}u = -(1+\xi)u + m_1\frac{u^2}{1+ku^2}, \qquad (x,t) \in \overline{\Omega} \times (0,T), \tag{5.62}$$

$$\frac{\partial}{\partial t}\xi = -(\mu_3 + \int_\Omega u dx)\xi + m_2\int_\Omega \frac{u^2}{1+ku^2}dx, \qquad t \in (0,T), \tag{5.63}$$

with initial conditions $(u(x,0), \int_\Omega w(x,0)dx)$ defined by the initial conditions of (5.58)-(5.61). However, Theorem 5.1 is limited to finite T, hence it does not imply stability of steady states. We investigate stability based on Theorem 5.8.

Lemma 5.11. *Consider system* (5.58)-(5.61) *and let the parameters satisfy the conditions of Theorem 3.21. Then system* (5.58)-(5.61)

- *has a positive, unique, uniformly bounded solution* $u \in C^1(0,\infty; C(\overline{\Omega}) \times \mathbb{R})$ *for positive initial conditions,*
- *exhibits integro-driven instability at a spatially homogeneous steady state* $(\overline{u}, \overline{\xi})$,
- *has infinitely many spatially inhomogeneous,* (ε_0, A)*-stable steady states.*

Proof. Existence of a local-in-time solution yields from regularity of f, g. Boundedness and positivity of u can be obtained analogously to (3.101). Due to $\int_\Omega m_2u^2/(1+ku^2)dx < \mu(\Omega)m_2/k$ and $\int_\Omega u dx \leq \mu(\Omega)m_1/k$, ξ, positivity and boundedness can be obtained analogously to (3.102).
By setting

$$0 = -(1+\xi) + m_1\frac{u^2}{1+ku^2}, \qquad x \in \overline{\Omega}, \tag{5.64}$$

$$0 = -(\mu + \int_\Omega u dx)\xi + m_2\int_\Omega \frac{u^2}{1+ku^2}dx, \tag{5.65}$$

and solving the first equation for different branches of u, as in Lemma 3.17, we obtain, similar to Lemma 3.20 that there exist three branches, u_0, u_-, u_+ satisfying the following:

For $0 \leq \xi < m_1/(2\sqrt{k}) - 1 =: \xi_r$ it holds that

$$\partial_u f|_{u,\xi}(x) \begin{cases} > 0, & u(x) = u_-(\xi) \\ < 0, & u(x) = u_+(\xi) \\ < 0, & u(x) = u_0 \end{cases} \qquad \partial_\xi f_{u,\xi}(x) \begin{cases} < 0, & u(x) = u_-(\xi) \\ < 0, & u(x) = u_+(\xi) \\ = 0, & u(x) = u_0 \end{cases}$$
$$\partial_u g_{u,\xi}(x) \begin{cases} > 0, & u(x) = u_-(\xi) \\ < 0, & u(x) = u_0 \end{cases} \qquad \partial_\xi g_{u,\xi}(x) \begin{cases} < 0, & u(x) = u_-(\xi) \\ < 0, & u(x) = u_+(\xi) \\ < 0, & u(x) = u_0 \end{cases} \tag{5.66}$$

and,

$$(\partial_u f \partial_\xi g - \partial_u g \partial_\xi f)|_{(u_+(\xi),\xi)}(x) > 0. \tag{5.67}$$

Consequently, for $\overline{\Omega_+}^o = \Omega_+ \subset \Omega$ with $\operatorname{meas}(\Omega_+) \neq 0$, steady states of type

$$\tilde{u} = \chi_{\Omega_+}(x) u_+(\xi), \tag{5.68}$$

satisfy condition (5.35). Condition (5.34) can be verified easily, since the right-hand side is twice continuously differentiable and $\tilde{u}$ is uniformly bounded on $\overline{\Omega}$. Therefore, $\partial_u f, \partial_\xi f, \partial_u g, \partial_\xi g \in L^\infty(\Omega)$ holds at $(\tilde{u}, \tilde{\xi})$.
$\tilde{\xi} \in \mathbb{R}_+$ implies $\nabla_x u = 0$, except on the points of discontinuity. We are particularly interested in steady states connecting one strictly positive branch u_+ with the trivial branch u_0. Consequently, equations (5.64)-(5.65) can be written as

$$0 = -(1+\xi) + m_1 \frac{u^2}{1+ku^2}, \qquad x \in \overline{\Omega}, \tag{5.69}$$

$$0 = -(\mu_3 + \operatorname{meas}(\Omega_+)u)\xi + m_2 \operatorname{meas}(\Omega_+) \frac{u^2}{1+ku^2}. \tag{5.70}$$

Multiplying the second equation by $1/\operatorname{meas}(\Omega_+)$, we obtain the system

$$0 = -(1+\xi) + m_1 \frac{u^2}{1+ku^2}, \qquad x \in \overline{\Omega}, \tag{5.71}$$

$$0 = -\left(\frac{\mu_3}{\operatorname{meas}(\Omega_+)} + u\right)\xi + m_2 \frac{u^2}{1+ku^2}. \tag{5.72}$$

Consequently, existence of spatially inhomogeneous steady states of type (5.68) follows immediately from Lemma 3.17 (2.). □

5.7.2 Lengyel-Epstein model

The shadow system of model (3.170)-(3.171) exhibits integro-driven instability and has infinitely many spatially inhomogeneous, (ε_0, A)-stable steady states. Existence follows analogously to model (5.64)-(5.65) from (3.193). Integro-driven instability and stability of steady states follows from (3.190), (3.191) and (3.198) and Lemmas 5.3 and 5.6.

5.7.3 Numerical result

In this subsection, we illustrate the finding that there exist spatially inhomogeneous, stable steady states. Similar to the reaction-diffusion system, the solution converges towards such steady state. Moreover, the behaviour of solutions is similar on a finite time interval if D is sufficiently large. In Figure 5.3, the solutions to the reaction-diffusion-ODE system (5.58)-(5.61) (for large diffusion coefficient) and its shadow system (5.62)-(5.63) are plotted for the parameter set 3.27. We use cell-wise constant finite elements for u. The spatial integral is interpolated using the rectangle method on the same mesh (since it is exact then and of the same order). Temporal discretisation is performed using the explicit Euler method. Note, that the right-hand side of the differential equation is Lipschitz-continuous. We observe that the dynamical behaviour as well as the pattern is similar. In Figure 5.4, the solution's component u at time $t = 20$ of both systems is plotted. However, in Figure 5.5, we observe that for less regular initial conditions, larger D is necessary for selection of the same pattern. While the solution of the reaction-diffusion-ODE system has a jump-type discontinuity close to $x = 0$, the solution of the shadow system does not. However, the pattern close to the maximum of the initial conditions is similar.

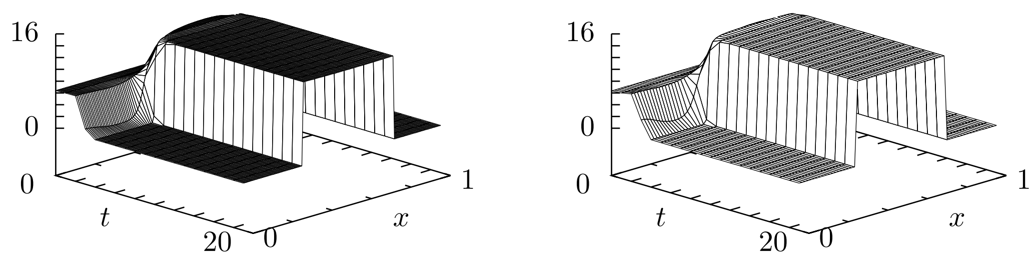

Figure 5.3: Solution u for parameter set 3.27. Left: Reaction-diffusion-ODE system (5.58)-(5.61) for $D = 100$. Right: Shadow system (5.62)-(5.63).

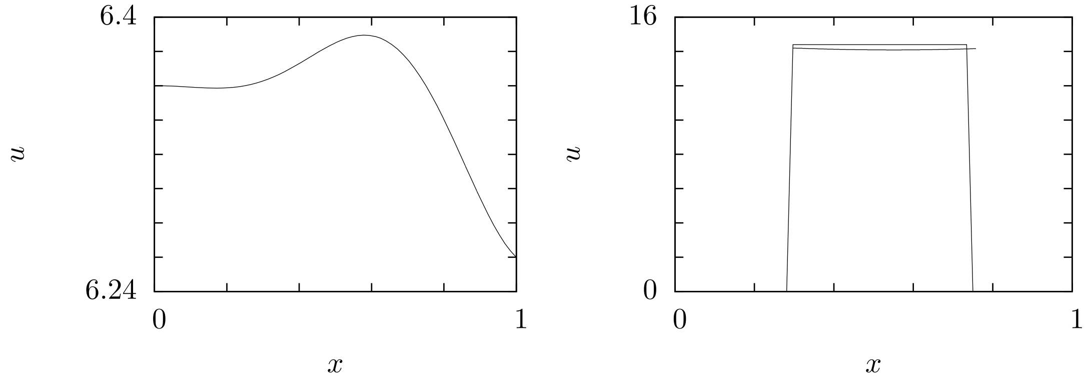

Figure 5.4: Solution u for parameter set 3.27. Left: $t = 0$. Right: $t = 20$. Discontinuous plot: Reaction-diffusion-ODE system (5.58)-(5.60) for $D = 100$. Continuous plot: Shadow system (5.62)-(5.63). Mesh size: $h = 2^{-8}$.

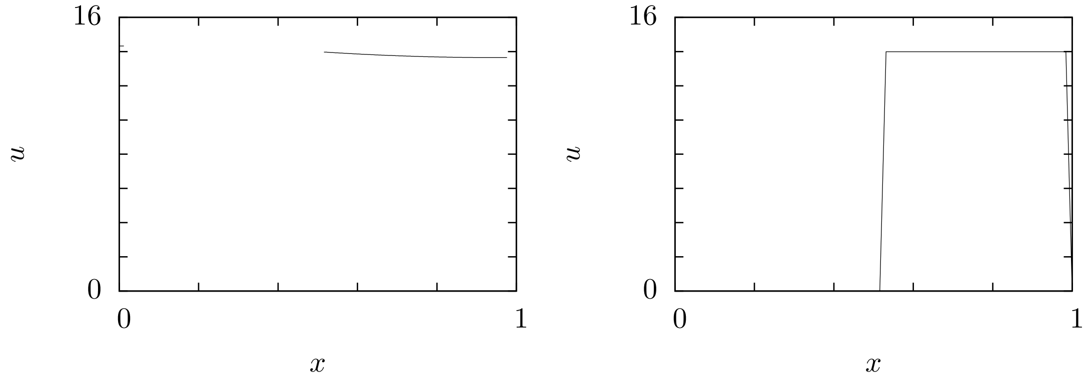

Figure 5.5: Solution u at $t = 20$ for parameter set 3.27, but initial conditions $u(x, 0) = 6.36 - (0.04 + 0.06x^2)\sin(2\pi x^2)$. Left: Reaction-diffusion system-ODE (5.58)-(5.60) for $D = 100$. Right: Shadow system (5.62)-(5.63).

6 A scalar integro-differential equation exhibiting a qualitatively similar pattern

This chapter is devoted to investigation of a steady state approximation of a particular system of type

$$\frac{\partial u^\delta}{\partial t}(t,x) = f(u^\delta(t,x),\xi^\delta(t)), \qquad (t,x) \in (0,T)\times\overline{\Omega}, \tag{6.1}$$

$$\delta\frac{\partial \xi^\delta}{\partial t}(t) = \int_\Omega g(u^\delta(t,x),\xi^\delta(t))dx, \qquad t \in (0,T). \tag{6.2}$$

$$(u^\delta(0,x),\xi^\delta(0)) \in (C(\overline{\Omega})\times\mathbb{R}). \tag{6.3}$$

In case of the kinetic system, stability of steady states is invariant under the limit if $\nabla_\xi g$, evaluated at the steady state, has only eigenvalues with negative real-part. In the first section, we show that under this condition, the solution for $\delta > 0$ converges towards the solution for $\delta = 0$ as $\delta \to 0$ on a finite time interval. The system is an approximation of a system of type (3.1)-(3.2) with $U = (u_1, u_2)$ and scalar v. If the right-hand side of the compartment which is assumed to be in the quasi-steady state has exactly one root, there exists a one-to-one mapping between the set of spatially homogeneous steady states of system (6.1)-(6.2) for $\delta = 0$ and the set of spatially homogeneous steady states of the system of one reaction-diffusion equation and multiple ordinary differential equations. Consequently, we want to know if basic properties like Turing-type destabilisation are preserved. For the kinetic system or equivalently spatially homogeneous perturbations, Lemma 4.2 confirms equivalence. Throughout this chapter, we give conditions under which a Tikhonov-type reduction is regular for systems of type (6.1)-(6.3). The system itself results from a Tikhonov-type reduction of a system of type (3.1) followed by a shadow-reduction, which have been proved to be regular for finite time. Consequently, we conduct that integro-driven instability of (6.1)-(6.3) implies diffusion-driven instability of a system of type

$$\frac{\partial u^\delta}{\partial t}(x,t) = f(u^\delta, v^\delta, w^\delta), \qquad x \in \overline{\Omega}, \tag{6.4}$$

$$\alpha(\delta)\frac{\partial v^\delta}{\partial t}(x,t) = h(u^\delta, v^\delta, w^\delta), \qquad x \in \overline{\Omega}, \tag{6.5}$$

$$\gamma(\delta)\frac{\partial w^\delta}{\partial t}(x,t) = \beta(\delta)^{-1}D\Delta w^\delta + g(u^\delta, v^\delta, w^\delta), \qquad x \in \Omega, \tag{6.6}$$

$$\partial_n w^\delta(t,x) = 0, \qquad x \in \partial\Omega, \tag{6.7}$$

$$(u^\delta(x,0), v^\delta(x,0), w^\delta(x,0)) \in (C(\overline{\Omega})^2 \times C^2(\overline{\Omega})), \tag{6.8}$$

under suitable conditions on the nonlinearities and $\alpha(\delta), \beta(\delta), \gamma(\delta)$ are scalar and converge towards zero as $\delta \to 0$ in suitable orders. Since we are interested in what 'key property' of the system remains after reduction it is natural to investigate the counterpart of diffusion-driven instability in the same sense as for the previously investigated shadow system.
We consider the quasi-steady state approximation of

$$\frac{\partial u^\delta}{\partial t} = -u^\delta - u^\delta \xi^\delta + m_1 \frac{(u^\delta)^2}{1+k(u^\delta)^2}, \qquad (x,t) \in \overline{\Omega} \times (0,\infty), \tag{6.9}$$

$$\delta \frac{\partial \xi^\delta}{\partial t} = -(\mu + \int_\Omega u^\delta dx)\xi^\delta + m_2 \int_\Omega \frac{(u^\delta)^2}{1+k(u^\delta)^2} dx, \qquad t > 0, \tag{6.10}$$

$$(u^\delta(x,0), \xi^\delta(0)) \in (C(\overline{\Omega}) \times \mathbb{R}). \tag{6.11}$$

Setting $\delta = 0$, then solving (6.10) for ξ^0 and inserting this into (6.9), we obtain the following problem

$$\begin{aligned} \frac{\partial u^0}{\partial t} = &-\left(1 + m_2 \left(\mu + \int_\Omega u^0 dx\right)^{-1} \int_\Omega \frac{(u^0)^2}{1+k(u^0)^2} dx\right) u \\ &+ m_1 \frac{(u^0)^2}{1+k(u^0)^2}, \qquad (x,t) \in \overline{\Omega} \times (0,\infty), \\ u^0(x,0) \in &C(\overline{\Omega}). \end{aligned} \tag{6.12}$$

If investigating (6.12), we drop the $\cdot^0$-notation for convenience.

6.1 Existence of solutions

Theorem 6.1. *Problem* (6.12)*, supplemented with positive initial conditions, has a unique, positive, uniformly bounded solution* $u \in C^1(0,\infty; C(\overline{\Omega}))$*.*

Proof. We show existence based on the classical argument of Lipschitz-continuity. Define

$$\mathcal{F}(u) := -\left(1 + m_2 \left(\mu + \int_\Omega u dx\right)^{-1} \int_\Omega \frac{(u)^2}{1+k(u)^2} dx\right) u + m_1 \frac{(u)^2}{1+k(u)^2}. \tag{6.13}$$

First, see that

$$\begin{aligned}
|\mathcal{F}(u)-\mathcal{F}(v)| &\leq |u-v| + m_1 \left| \frac{u^2}{1+ku^2} - \frac{v^2}{1+kv^2} \right| + m_2 \left| \frac{\int_\Omega \frac{u^2}{1+ku^2}dx}{\mu+\int_\Omega u dx} u - \frac{\int_\Omega \frac{v^2}{1+kv^2}dx}{\mu+\int_\Omega v dx} v \right|, \\
&\leq \left(1 + m_1 \frac{3\sqrt{3}}{8\sqrt{k}}\right) |u-v| + m_2 \left| \frac{\int_\Omega \frac{u^2}{1+ku^2}dx}{\mu+\int_\Omega u dx} u - \frac{\int_\Omega \frac{v^2}{1+kv^2}dx}{\mu+\int_\Omega v dx} v \right|.
\end{aligned}$$

We continue by estimating the second term (dropping dx in the first line for convenience):

$$\left| \frac{\int_\Omega \frac{u^2}{1+ku^2}}{\mu+\int_\Omega u} u - \frac{\int_\Omega \frac{v^2}{1+kv^2}dx}{\mu+\int_\Omega v} v \right| = \left| \frac{\int_\Omega \frac{u^2}{1+ku^2}}{\mu+\int_\Omega u} u - \frac{\int_\Omega \frac{v^2}{1+kv^2}}{\mu+\int_\Omega u} u + \frac{\int_\Omega \frac{v^2}{1+kv^2}}{\mu+\int_\Omega u} u - \frac{\int_\Omega \frac{v^2}{1+kv^2}}{\mu+\int_\Omega v} v \right|, \tag{6.14}$$

$$\leq \frac{|u|}{\mu+\int_\Omega u dx} \left| \int_\Omega \frac{u^2}{1+ku^2}dx - \int_\Omega \frac{v^2}{1+kv^2}dx \right| \tag{6.15}$$

$$+ \left| \int_\Omega \frac{v^2}{1+kv^2}dx \right| \left| \frac{u}{\mu+\int_\Omega u dx} - \frac{v}{\mu+\int_\Omega v dx} \right|,$$

$$\leq \frac{|u|}{|\mu+\int_\Omega u dx|} \frac{3\sqrt{3}}{8\sqrt{k}} |u-v| \tag{6.16}$$

$$+ \left| \int_\Omega \frac{v^2}{1+kv^2}dx \right| \left| \frac{u}{\mu+\int_\Omega u dx} - \frac{v}{\mu+\int_\Omega v dx} \right|.$$

Estimating the last term (again dropping dx in the first line for convenience)

$$\begin{aligned}
\left| \int_\Omega \frac{v^2}{1+kv^2}dx \right| \left| \frac{u}{\mu+\int_\Omega u} - \frac{v}{\mu+\int_\Omega v} \right| &\leq \frac{1}{k} \left| \frac{u}{\mu+\int_\Omega u} - \frac{v}{\mu+\int_\Omega u} + \frac{v}{\mu+\int_\Omega u} - \frac{v}{\mu+\int_\Omega v} \right|, \\
&\leq \frac{1}{k\mu}|u-v| + \frac{1}{k\mu^2} \left| \int_\Omega (u-v)dx \right|, \\
&\leq \frac{1}{k\mu}|u-v| + \frac{1}{k\mu^2} \|u-v\|_\infty .
\end{aligned}$$

Consequently,

$$|f(u)-f(v)| \leq \left(1 + \frac{3\sqrt{3}}{8\sqrt{k}}(m_1 + \frac{|u|}{|\mu+\int_\Omega u dx|}) + \frac{1}{k\mu}\right) |u-v| + \frac{1}{k\mu^2} \|u-v\|_\infty , \tag{6.17}$$

holds. Hence, we obtain local existence for $\int_\Omega u dx > 0$. To obtain global existence, it is left to prove that for positive initial conditions, the solution remains positive and uniformly bounded. Then, $\int_\Omega u dx > 0$ follows and the Lipschitz constant remains bounded. We prove positivity of the mass $\int_\Omega u dx$ for positive initial mass. To see this, integrate (6.12) over Ω and

$$\begin{aligned}\frac{\partial}{\partial t}\int_\Omega u dx &= -\int_\Omega u dx - m_2 \int_\Omega \frac{u^2}{1+ku^2}dx \frac{\int_\Omega u dx}{\mu + \int_\Omega u dx} + m_1 \int_\Omega \frac{u^2}{1+ku^2}dx,\\ &\geq -\int_\Omega u - \frac{m_2}{k}\frac{\int_\Omega u dx}{\mu + \int_\Omega u dx},\\ &\geq -(1+\frac{m_2}{k})\int_\Omega u dx,\end{aligned}$$

follows. From positivity of mass, it follows that u stays positive for positive initial conditions since

$$\begin{aligned}\frac{\partial}{\partial t}u &= -u - m_2 \frac{\int_\Omega \frac{u^2}{1+ku^2}dx}{\mu + \int_\Omega u dx}u + m_1 \frac{u^2}{1+ku^2},\\ &\geq -\left(1+\frac{m_2}{k}\right)u + m_1\frac{u^2}{1+ku^2}.\end{aligned}$$

For positive initial conditions, we obtained local existence of a strictly positive solution. To obtain global existence, we show that u is bounded,

$$\begin{aligned}\frac{\partial}{\partial t}u &= -u - m_2 \frac{\int_\Omega \frac{u^2}{1+ku^2}dx}{\mu + \int_\Omega u dx}u + m_1 \frac{u^2}{1+ku^2},\\ &\leq -u + \frac{m_1}{k}.\end{aligned}$$

Therefore, the Lipschitz constant is uniformly bounded and we obtain existence of a unique global, positive, uniformly bounded solution. □

6.2 Tikhonov type result

Throughout this subsection, we assume existence of solutions to problem (6.1)-(6.2) for all sufficiently small $\delta \geq 0$.

Lemma 6.2. *Consider a system of type* (6.1)-(6.2)*, but with vector-valued compartments* U, Ξ*. Assume that system* (6.1)-(6.2) *has for all* $\delta \in [0, \delta^*)$ *a unique classical solution* (U^δ, Ξ^δ) *and the set of solutions* (U^δ, Ξ^δ) *is uniformly bounded in time and* $[0, \delta^*)$*. If the spectrum* σ *of* $\nabla_\Xi g|_{(U,\Xi)}$ *is contained strictly in the left complex half-plane for all* (U, Ξ)*, i.e.*

$$\mathrm{Re}(\sigma(\nabla_\Xi g|_{(U,\Xi)})) \leq c < 0, \tag{6.18}$$

then (U^δ, Ξ^δ) *converges towards* (U^0, Ξ^0) *as* $\delta \to 0$*:*

$$\left\| U^\delta - U^0 \right\|_{L^\infty(0,T;L^\infty(\Omega))} \to 0 \text{ as } \delta \to 0, \tag{6.19}$$

$$\left\| \Xi^\delta - \Xi^0 \right\|_{L^1(0,T)} \to 0 \text{ as } \delta \to 0. \tag{6.20}$$

Proof. Note that $\alpha := U^\delta - U^0$ and $\beta := \Xi^\delta - \Xi^0$ satisfy the following equation

$$\frac{\partial \alpha}{\partial t} = \nabla_U f \alpha + \nabla_\Xi f \beta, \tag{6.21}$$

$$\frac{\partial \beta}{\partial t} = \frac{1}{\delta} \left(\int_\Omega \nabla_U g \alpha dx + \int_\Omega \nabla_\Xi g dx \beta \right) - \frac{\partial \Xi^0}{\partial t}, \tag{6.22}$$

with $\alpha(x,0) = U^\delta(x,0) - U^0(x,0)$ and $\beta(0) = \Xi^\delta(0) - U^0(0)$, and where the derivatives are evaluated according to the Taylor-Lagrange residual formula. Now, the proof essentially follows the lines of the proof of Lemma 4.5. First, we estimate α,

$$\begin{aligned} \|\alpha(t)\|_{L^\infty(\Omega)} &\le e^{\|\nabla_U f\|_\infty (t-t_n)} \|\alpha(t_n)\|_{L^\infty(\Omega)} + \int_{t_n}^t e^{\|\nabla_U f\|_\infty (t-\tau)} \|\nabla_\Xi f\|_\infty |\beta(\tau)| d\tau, \\ &\le e^{\|\nabla_U f\|_\infty (t-t_n)} \left(\|\alpha(t_n)\|_{L^\infty(\Omega)} + \|\nabla_\Xi f\|_\infty \|\beta\|_{L^1(t_n,t)} \right). \end{aligned}$$

The solution β can be written in the form

$$|\beta(t)| = \left| e^{\frac{1}{\delta}\int_{t_n}^t \int_\Omega \nabla_\Xi g dx d\tau} \beta(t_n) - \int_{t_n}^t e^{\frac{1}{\delta}\int_\tau^t \int_\Omega \nabla_\Xi g dx ds} \frac{\partial \Xi^0}{\partial t}(\tau) d\tau + \frac{1}{\delta} \int_0^t e^{\frac{1}{\delta}\int_\tau^t \int_\Omega g_\Xi dx ds} \int_\Omega \nabla_U g \alpha dx d\tau \right|.$$

and consequently, it holds due to Young's inequality and $\nabla_\Xi g$ being stable that

$$\begin{aligned} \|\beta\|_{L^1(t_n,t)} &\le \left(|\beta(t_n)| + \left\| \frac{\partial \Xi^0}{\partial \tau} \right\|_{L^\infty(t_n,t)} (t-t_n) \right) C\delta + \int_{t_n}^t \left\| \int_\Omega \nabla_U g \alpha dx \right\|_{L^\infty(t_n,\tau)} d\tau, \\ &\le \left(|\beta(t_n)| + \left\| \frac{\partial \Xi^0}{\partial \tau} \right\|_{L^\infty(t_n,t)} (t-t_n) \right) C\delta + \|\nabla_U g\|_{L^\infty(t_n,t;L^1(\Omega))} (t-t_n) \|\alpha\|_{L^\infty(t_n,t;L^\infty(\Omega))}, \\ &\le C\delta + (t-t_n)C\delta + C(t-t_n) e^{\|\nabla_U f\|_\infty (t-t_n)} \left(\|\alpha(t_n)\|_{L^\infty(\Omega)} + \|\nabla_U f\|_\infty \|\beta\|_{L^1(t_n,t)} \right), \end{aligned}$$

Choosing $(t_{n+1} - t_n)$ so small that

$$C(t_{n+1} - t_n) < C(t_{n+1} - t_n) e^{\|\nabla_U f\|_\infty (t-t_n)} < \frac{1}{2}, \tag{6.23}$$

yields the result by induction over n analogously to the proof of Lemma 4.5. □

6.3 Integro-driven instability

The approach for investigating integro-driven instability for system (6.12) is similar to the approach used to investigate integro-driven instability for the shadow system. We showed that, under certain conditions, system (5.1)-(5.3) has a spatially homogeneous steady state $(\overline{u}, \overline{\xi})$ which is stable under spatially homogeneous perturbation. If we perturb system (6.1)-(6.2) only with spatially homogeneous perturbations (φ, ψ), then f and g are constant in x. Consequently, the kinetic system reads in all $x \in \overline{\Omega}$,

$$\begin{aligned} \frac{\partial u^\delta}{\partial t}(t) &= f(u^\delta(t), \xi^\delta(t)), \\ \frac{\delta}{\text{meas}(\Omega)} \frac{\partial \xi^\delta}{\partial t} &= g(u^\delta(t), \xi^\delta(t)), \\ (u^\delta(0), \xi^\delta(0)) &= (\overline{u} + \varphi, \overline{\xi} + \psi). \end{aligned} \tag{6.24}$$

Consequently, if $\partial_\xi g|_{(u^\delta, \xi(u^\delta))} \leq c < 0$ holds for all u^δ, where $\xi(u^\delta)$ is defined implicitly by $g(u^\delta, \xi^\delta) = 0$, then regularity Lemma 4.2 can be applied to the limit $\delta \to 0$ and we obtain that a steady state is stable for $\delta = 0$ if and only if it is stable for all sufficiently small $\delta > 0$. To investigate instability under spatially inhomogeneous perturbation for $\delta = 0$, we first consider the linearised operator and investigate linear stability. Then, we conclude nonlinear instability based on Theorem 1 in [SS00]. To investigate (in)stability of steady states with respect to inhomogeneous perturbations, we investigate the linearised operator.

Lemma 6.3. *Consider a system of type*

$$\frac{\partial u}{\partial t}(t,x) = f(u(t,x), \xi(t)), \qquad (x,t) \in (0,T) \times \overline{\Omega}, \tag{6.25}$$

$$0 = \int_\Omega g(u(t,x), \xi(t))dx, \qquad t \in (0,T), \tag{6.26}$$

$$u(0,x) \in C(\overline{\Omega}). \tag{6.27}$$

Assume that there exists a spatially homogeneous steady state $(\overline{u}, \overline{\xi})$ and assume that $\partial_\xi g|_{(\overline{u}, \overline{\xi})}$ is either strictly positive ($\geq c > 0$) or strictly negative ($\leq c < 0$). Moreover, assume that the solution $\overline{\xi} = \xi(\overline{u})$ of (6.26) is isolated.

1. *The spectrum of the linearised operator $\mathcal{L}$ considered as operator in $C(\overline{\Omega})$ consists only*

of the eigenvalues of the linearised kinetic system and $\partial_1 f(\overline{u}, \xi(\overline{u}))$:

$$\sigma(\mathcal{L}) = \left\{ \frac{df(u, \xi(u))}{du}(\overline{u}, \overline{\xi}) \right\} \bigcup \left\{ \frac{\partial f(u, \xi)}{\partial u}|_{(\overline{u}, \xi(\overline{u}))} \right\}. \tag{6.28}$$

2. *If $\partial_u f|_{(\overline{u}, \overline{\xi})} > 0$ and the eigenvalue of the kinetic system linearised at $(\overline{u}, \overline{\xi})$ have nontrivial real part, then $(\overline{u}, \overline{\xi})$ is non-linearly unstable for initial conditions $u(0, x) \in C(\overline{\Omega})$.*

Proof. First, note that g is twice continuously differentiable, hence

$$G : (C(\overline{\Omega}), \|.\|_\infty) \times (\mathbb{R}, |.|) \rightarrow (\mathbb{R}, |.|), \tag{6.29}$$

$$(u, \xi) \rightarrow \int_\Omega g(u(x), \xi) dx, \tag{6.30}$$

is Frechét-differentiable in a neighbourhood of the root $(\overline{u}, \overline{\xi})$ with

$$DG(u, \xi)(\varphi, \psi) = \int_\Omega \partial_1 g(u, \xi)\varphi + \partial_2 g(u, \xi)\psi dx, \tag{6.31}$$

where $\partial_1 g(a, b) := \frac{\partial g(u,\xi)}{\partial u}(a, b)$ and $\partial_2 g(a, b) := \frac{\partial g(u,\xi)}{\partial \xi}(a, b)$. We keep this notation. Note $DG \in C(C(\overline{\Omega}) \times \mathbb{R}; \mathcal{L}(C(\overline{\Omega}) \times \mathbb{R}))$. Moreover, $\int_\Omega \partial_2 g(u, \xi) dx \neq 0$, thus $D(u, \xi)(0, \psi) = \int_\Omega \partial_2 g(u, \xi)\psi dx$ is a Banach space isomorphism from $\mathbb{R}$ to $\mathbb{R}$, thus we can apply the implicit function theorem. Therefore, there exists a continuously differentiable implicit function,

$$\xi : C(\overline{\Omega}) \rightarrow \mathbb{R}, \tag{6.32}$$

$$u \rightarrow \xi(u), \tag{6.33}$$

satisfying $G(u, \xi(u)) = 0$ in $B_C(\overline{u})$ for some positive C.
It holds

$$\begin{aligned} 0 &= \frac{d}{d\tau} \int_\Omega g(u + \tau\varphi, \xi(u + \tau\varphi))|_{\tau=0} dx, \\ &= \int_\Omega \partial_1 g(u, \xi(u))\varphi dx + \int_\Omega \partial_2 g(u, \xi(u)) \frac{d}{d\tau}\xi(u + \tau\varphi)|_{\tau=0} dx. \end{aligned} \tag{6.34}$$

Therefore, the Frechét derivative (due to regularity coinciding with the Gâteaux derivative) reads,

$$D\xi(u)(\varphi) = \frac{d}{d\tau}\xi(u + \tau\varphi)|_{\tau=0} = -\frac{\int_\Omega \partial_1 g(u, \xi(u))\varphi dx}{\int_\Omega \partial_2 g(u, \xi(u)) dx}, \tag{6.35}$$

and consequently

$$\begin{aligned}\frac{d}{d\tau}f(u+\tau\varphi,\xi(u+\tau\varphi)) &= \partial_1 f(u,\xi(u))\varphi + \partial_2 f(u,\xi(u))\frac{d}{d\tau}\xi(u+\tau\varphi)|_{\tau=0},\\ &= \partial_1 f(u,\xi(u))\varphi - \partial_2 f(u,\xi(u))\frac{\int_\Omega \partial_1 g(u,\xi(u))\varphi dx}{\int_\Omega \partial_2 g(u,\xi(u))dx}.\end{aligned} \tag{6.36}$$

Now, consider the operator

$$\begin{aligned}&\mathcal{L} : (C(\overline{\Omega}), \|\cdot\|_{\sup}) \to (C(\overline{\Omega}), \|\cdot\|_{\sup}),\\ &\qquad\varphi \to \partial_1 f(u,\xi(u))\varphi - \partial_2 f(u,\xi(u))\frac{\int_\Omega \partial_1 g(u,\xi(u))\varphi dx}{\int_\Omega \partial_2 g(u,\xi(u))dx}.\end{aligned} \tag{6.37}$$

Since f, g are twice continuously differentiable, this operator is bounded in $(C(\overline{\Omega}), \|\cdot\|_{\sup})$ and consequently generates a uniformly continuous semigroup on $(C(\overline{\Omega}), \|\cdot\|_{\sup})$.
Note that the operator

$$\mathcal{T} : \varphi \to \partial_2 f(u,\xi(u))\frac{\int_\Omega \partial_1 g(u,\xi(u))\varphi dx}{\int_\Omega \partial_2 g(u,\xi(u))dx}, \tag{6.38}$$

is compact and that u and $\partial_2 f(u,\xi(u)), \partial_1 g(u,\xi(u)), \partial_2 g(u,\xi(u))$ are constant. If $\lambda = 0$, then

$$(\lambda - \mathcal{T})\varphi = \lambda\varphi - \partial_2 f(u,\xi(u))\frac{\int_\Omega \partial_1 g(u,\xi(u))\varphi dx}{\int_\Omega \partial_2 g(u,\xi(u))dx} = 0, \tag{6.39}$$

implies $\int_\Omega \varphi dx = 0$, hence

$$\ker(\mathcal{L} - \partial_1 f(u,\xi(u))) = \{\varphi \in C(\overline{\Omega}) | \int_\Omega \varphi dx = 0\}. \tag{6.40}$$

If $\lambda \neq 0$, it implies that φ is constant, thus $\varphi = 0$ or $\partial_1 f(u,\xi(u))$ is element of the spectrum of the linearisation of the kinetic system, i.e.

$$\lambda - \partial_1 f(u,\xi(u)) \in \left\{\frac{df(u,\xi(u))}{du}(\overline{u},\overline{\xi})\right\}. \tag{6.41}$$

Consequently, due to Fredholm's alternative, applied onto $\mathcal{T}$, the spectrum of $\mathcal{L}$ is

$$\sigma(\mathcal{L}) = \left\{\frac{df(u,\xi(u))}{du}(\overline{u},\overline{\xi})\right\} \dot{\bigcup} \{\partial_1 f(\overline{u},\xi(\overline{u}))\}. \tag{6.42}$$

This concludes the statement concerning the spectrum.
For nonlinear instability, apply item 1) to obtain a spectral gap.
It is left to prove that the residual, when approximating using the uniformly continuous

semigroup constructed in the proof of item 1, is at least of order $\|\varphi\|_\infty^{1+\alpha}$. Then, Theorem 1 in [SS00] can be applied.
Due to Taylor expansion, identity

$$\begin{aligned} 0 &= \int_\Omega g(u+\varphi, \xi(u+\varphi))dx, && (6.43)\\ &= \int_\Omega g(u,\xi)dx + \int_\Omega \partial_1 g(\alpha, \xi(u+\varphi))\varphi dx + \int_\Omega \partial_2 g(u,\beta)(\xi(u+\varphi)-\xi(u))dx, && (6.44)\end{aligned}$$

holds for some $\alpha(x) \in (u(x), (u+\varphi)(x))$ and $\beta \in (\xi(u), \xi(u+\varphi))$. Due to continuity of $\xi(u)$ and g being twice continuously differentiable, it holds for sufficiently small φ that

$$|\xi(u+\varphi) - \xi(u)| = \left| - \frac{\int_\Omega \partial_1 g(\alpha, \xi(u+\varphi))\varphi dx}{\int_\Omega \partial_2 g(u,\beta)dx} \right| \leq \frac{C}{c/2} \|\varphi\|_\infty \,, \tag{6.45}$$

where $\partial_2 g(u,\beta) \leq c < 0$ holds by assumption. Inserting this into a Taylor expansion of $f(u+\varphi, \xi(u+\varphi))$ around $(\overline{u}, \xi(\overline{u}))$ yields that

$$\begin{aligned} f(\overline{u}+\varphi, \xi(\overline{u}+\varphi)) =& Df(\overline{u}, \xi(\overline{u})) \begin{pmatrix} \varphi \\ \xi(\overline{u}+\varphi) - \xi(\overline{u}) \end{pmatrix} && (6.46)\\ &+ \quad \begin{pmatrix} \varphi \\ \xi(\overline{u}+\varphi) - \xi(\overline{u}) \end{pmatrix}^T \nabla^2 f|_{\alpha,\beta} \begin{pmatrix} \varphi \\ \xi(\overline{u}+\varphi) - \xi(\overline{u}) \end{pmatrix}, && (6.47)\\ =& \mathcal{L}(\overline{u})\varphi + \mathcal{N}(\varphi), && (6.48)\end{aligned}$$

where α, β are determined by the Taylor-Lagrange residual formula. Moreover,

$$\|\mathcal{N}(\varphi)\|_\infty \leq C\left(\|\varphi\|_\infty^2 + \|\varphi\|_\infty |\xi(\overline{u}+\varphi) - \xi(\overline{u})| + |\xi(\overline{u}+\varphi) - \xi(\overline{u})|^2\right), \tag{6.49}$$

holds. Component ξ is continuous, f is twice continuously differentiable and (6.45) holds, thus C does not depend on φ (if it is sufficiently small), thus

$$\|\mathcal{N}(\varphi)\|_\infty \leq C \|\varphi\|_\infty^2 \,. \tag{6.50}$$

This concludes nonlinear instability due to the spectral properties of $\mathcal{L}(\overline{u})$ as shown in (6.42), see [SS00], Theorem 1. □

Corrolary 6.4. *Under the conditions on parameters in Theorem 3.21, system* (6.12) *exhibits integro-driven instability at $u(x) = u_-(w_2)$, where $u_-(w_2)$ is defined in Theorem 3.21.*

Proof. System (6.12) is a quasi-steady state approximation of system (6.9)-(6.10). Therefore,

$u_-(w_2)$ is a spatially homogeneous steady state since it is a spatially homogeneous steady state of system (6.9)-(6.10).
In Theorem 3.21, it has been shown that system (6.9)-(6.10) exhibits integro-driven instability. Therefore, the determinant of the Jacobian matrix of system (6.9)-(6.10) is positive at this steady state. Since

$$\partial_\xi \left(-(1+u)\xi + m_2 \frac{u^2}{1+ku^2} \right) = -(1+u) < 0,$$

we can apply Lemma 4.6 and obtain

$$\partial_u \left(-\left(1 + m_2 \frac{\frac{u^2}{1+ku^2}}{\mu + u} \right) + m_1 \frac{u^2}{1+ku^2} \right) |_{u_-(w_2)} < 0, \tag{6.51}$$

implying stability with respect to spatially homogeneous perturbation. Moreover, $\partial_u f|_{(u_-(w_2),w_2)} > 0$ holds, see Lemma 3.20. Hence, instability with respect to spatially inhomogeneous perturbations follows from Lemma 6.3. □

6.4 Remarks on dynamical behaviour

Even though numerical investigations imply that the solutions of system (6.12) converge towards spatially inhomogeneous steady states, an analytical proof remains an open question. However, we present some results on the dynamical behaviour

Lemma 6.5. *Consider problem* (6.12)*. Define $u_-(w_2)$ as in Theorem 3.21. Let all parameters satisfy the conditions in Theorem 3.21. Then holds $u_-(w_1) < 1/\sqrt{3k} < w_-(w_2)$. Moreover, if $u_-(w_1) < \int_\Omega u(x,t^*)dx < 1/\sqrt{3k}$ and $\partial/\partial t \int_\Omega u(t^*)dx < 0$ for some t^*, then exists a $k^* > 0$ such that for all $0 < k < k^*$, there exists a non-zero measure subset Ω_+, such that $u(x,t^*) > u_-(w_1)$ for all $x \in \Omega_+$.*

Proof. Write the equation for $\partial \int_\Omega udx/\partial t$ as

$$\frac{\partial}{\partial t}\int\limits_\Omega u = -\left(1 + m_2 \int\limits_\Omega \frac{u^2}{1+ku^2} dx \left(\mu + \int\limits_\Omega udx \right)^{-1} \right) \int\limits_\Omega udx + m_1 \int\limits_\Omega \frac{u^2}{1+ku^2} dx. \tag{6.52}$$

Defining, $f(\mathcal{M}(t)) = \mathcal{M}(t)^2/(1+k\mathcal{M}(t)^2)$ and $\mathcal{M}(t) = \int_\Omega u(x,t)dx$, we obtain,

$$\frac{\partial}{\partial t}\mathcal{M}(t) = -\left(1 + m_2 \frac{\frac{\mathcal{M}(t)^2}{1+k\mathcal{M}(t)^2}}{\mu + \mathcal{M}(t)} \right) \mathcal{M}(t) + m_1 \frac{\mathcal{M}(t)^2}{1+k\mathcal{M}(t)^2}$$

$$
\begin{aligned}
&- \frac{m_2}{2}\frac{\mathcal{M}(t)}{\mu+\mathcal{M}(t)}\int\limits_{\Omega} \frac{2-6k\eta(x)}{(1+k\eta(x)^2)^3}(u(x)-\mathcal{M}(t))dx \\
&+ \frac{m_1}{2}\int\limits_{\Omega} \frac{2-6k\eta(x)}{(1+k\eta(x)^2)^3}(u(x)-\mathcal{M}(t))^2dx, \\
=& -\left(1+m_2\frac{\frac{\mathcal{M}(t)^2}{1+k\mathcal{M}(t)^2}}{\mu+\mathcal{M}(t)}\right)\mathcal{M}(t)+m_1\frac{\mathcal{M}(t)^2}{1+k\mathcal{M}(t)^2} \\
&+ \frac{1}{2}\left(m_1-m_2\frac{\mathcal{M}(t)}{\mu+\mathcal{M}(t)}\right)\int\limits_{\Omega}\frac{2-6k\eta(x)}{(1+k\xi^2)^3}(u(x)-\mathcal{M}(t))^2dx,
\end{aligned}
$$

where

$$
\int\limits_{\Omega} f(u(x)) = f(\mathcal{M}(t)) + f'(\mathcal{M}(t))\underbrace{\int\limits_{\Omega}(u(x)-\mathcal{M}(t))dx}_{=0} + \int\limits_{\Omega}\frac{1}{2}\frac{2-6k\eta(x)}{(1+k\eta(x)^2)^3}(u(x)-\mathcal{M}(t))^2dx,
$$

and $\mu(\Omega)=1$ have been used and $\eta(x)$ is defined by the Taylor-Lagrange residual formula, hence $\eta(x) \in (\int_\Omega udx, u(x))$ respectively $\eta(x) \in (u(x), \int_\Omega udx)$.

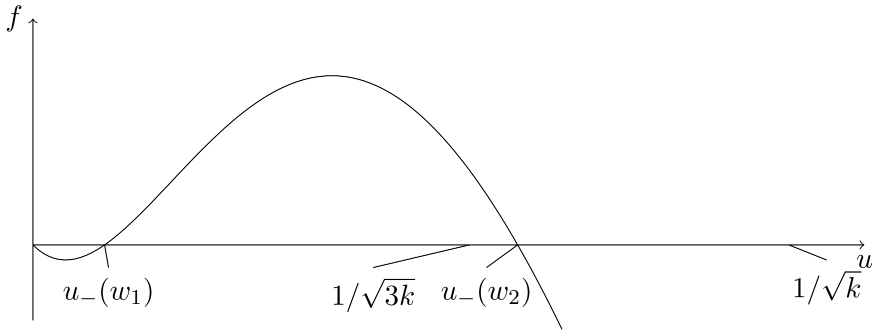

Figure 6.1: Shape of the right-hand side of the kinetic system of (6.12) for parameters satisfying the conditions of Lemma 6.5.

System (6.12) is a Tikhonov type approximation of system (4.9)-(4.10). The steady state equation of (4.10) can be solved uniquely for $\xi(u)$, hence both kinetic systems have the same steady states. Moreover, stability respectively instability of steady states is preserved due to Lemma 4.6 since instability of steady states of (4.9)-(4.10) arises due a strictly negative determinant of the Jacobian matrix, see Lemmas 3.20 and 3.17. Consequently, the right-hand side $r(u) = -(1+m_2u^2/(1+ku^2)(1/(\mu+u)))u + m_1u^2/(1+ku^2)$ of the kinetic system of

(6.12) satisfies

$$r(0) = r(u_-(w_1)) = r(u_-(w_2)) = 0, \tag{6.53}$$

$$r(u) < 0, \quad \text{for } 0 < u < u_-(w_1), \tag{6.54}$$

$$r(u) > 0, \quad \text{for } u_-(w_1) < u < u_-(w_2), \tag{6.55}$$

$$r(u) < 0, \quad \text{for } u_-(w_2), \tag{6.56}$$

as illustrated in Figure 6.1.
Note that

$$f''(\eta) \begin{cases} > 0 & \text{if } 0 \leq \eta < 1/\sqrt{3k}, \\ < 0 & \text{if } 1/\sqrt{3k} < \eta, \end{cases} \tag{6.57}$$

and

$$r\left(\frac{1}{\sqrt{3k}}\right) > 0, \tag{6.58}$$

holds for sufficiently small k. We can rewrite the equation for the kinetic system as

$$r(\mathcal{M}(t)) = \left(-1 + \left(m_1 - m_2\frac{\mathcal{M}(t)}{\mu + \mathcal{M}(t)}\right)\frac{\mathcal{M}(t)}{1 + k\mathcal{M}(t)^2}\right)\mathcal{M}(t), \tag{6.59}$$

hence $r(\mathcal{M}(t)) > 0$ is equivalent to

$$\left(m_1 - m_2\frac{\mathcal{M}(t)}{\mu + \mathcal{M}(t)}\right) > \frac{1 + k\mathcal{M}(t)}{\mathcal{M}(t)}.$$

Therefore, $\mathcal{M}(t) \in (u_-(w_1), u_-(w_2))$ implies

$$\left(m_1 - m_2\frac{\mathcal{M}(t)}{\mu + \mathcal{M}(t)}\right) > 0.$$

$r(1/\sqrt{3k}) > 0$ implies $1/\sqrt{3k} \in (u_-(w_1) + \varepsilon, u_-(w_2) - \varepsilon)$. Consequently,

$$\mathcal{M}(t) \in (u_-(w_1), 1/\sqrt{3k})$$

implies either $\partial/\partial t\mathcal{M}(t) > 0$ or $u(x) > 1/\sqrt{3k}$ on a subset of strictly positive measure. □

Lemma 6.6. *Consider model* (6.12). *Assume that the parameters satisfy the conditions of Theorem 3.21.*
If $0 < u(0,x) < \left(m_1 - \sqrt{m_1^2 - 4k}\right)/(2k)$, *then* $0 < u(x,t) < u(0,x)e^{-ct}$ *for some positive constant* c.

Proof. It holds

$$\frac{\partial}{\partial t}u = -\left(1 + m_2\frac{\int_\Omega \frac{u^2}{1+ku^2}dx}{\mu + \int_\Omega u dx}\right)u + m_1\frac{u^2}{1+ku^2}, \tag{6.60}$$

$$\leq -\left(1 - m_1\frac{u}{1+ku^2}\right)u. \tag{6.61}$$

The roots of (6.61) are

$$u_0 = 0, \tag{6.62}$$

$$u_\pm = \frac{m_1 \pm \sqrt{m_1^2 - 4k}}{2k}. \tag{6.63}$$

Moreover, $\partial u/\partial t < 0$ for $u \in (0, \varepsilon)$ due to the order in u of the summands and their sign. The term in (6.61) is concave on $(0, u_-)$, hence $\partial u/\partial t < -cu$ for $u \in (0, u_- - \varepsilon)$. This concludes the statement.

□

Lemma 6.7. *Consider model* (6.12). *Assume that the parameters satisfy the conditions of Theorem 3.21.*
If additionally $\mu > 4m_2/m_1^2$ *and* $k < (\mu^2 m_1^2 - 4m_2)/(4\mu)$, *then the following implication holds: If* $\|u(t=0)\|_\infty > \hat{u}_-$, *then exists a* $t^* \geq 0$ *such that for all* $t > t^*$, *it holds that*

$$\|u(t)\|_\infty \geq \hat{u}_+, \tag{6.64}$$

where

$$\hat{u}_\pm = \frac{\mu m_1 \pm \sqrt{\mu^2 m_1^2 - 4(k\mu + m_2)}}{2(m_2 + k\mu)}, \tag{6.65}$$

satisfies $\hat{u}_- \leq 1/\sqrt{3k} < u_-(w_1)$ *and* $u_-(w_1)$ *is defined as in Lemma 3.21.*

Proof. The proof uses the principle of super-solutions. It holds

$$\frac{\partial}{\partial t}\|u(t)\|_\infty = -\left(1 + m_2\frac{\int_\Omega \frac{u^2}{1+ku^2}dx}{\mu + \int_\Omega u dx}\right)\|u(t)\|_\infty + m_1\frac{\|u(t)\|_\infty^2}{1+k\|u(t)\|_\infty^2}, \tag{6.66}$$

$$\geq -\left(1 + m_2\frac{\frac{\|u(t)\|_\infty^2}{1+k\|u(t)\|_\infty^2}}{\mu + \int_\Omega u dx}\right)\|u(t)\|_\infty + m_1\frac{\|u(t)\|_\infty^2}{1+k\|u(t)\|_\infty^2}, \tag{6.67}$$

$$\geq -\left(1 + \frac{m_2}{\mu}\frac{\|u(t)\|_\infty^2}{1+k\|u(t)\|_\infty^2}\right)\|u(t)\|_\infty + m_1\frac{\|u(t)\|_\infty^2}{1+k\|u(t)\|_\infty^2}, \tag{6.68}$$

$$=: r_s(\|u(t)\|_\infty), \tag{6.69}$$

where monotonicity of $f(u) = u^2/(1 + ku^2)$ and $\mu(\Omega) = 1$ have been used.
The roots of $r_s(u)$ read

$$\hat{u}_0 = 0, \tag{6.70}$$

$$\hat{u}_\pm = \frac{\mu m_1 \pm \sqrt{\mu^2 m_1^2 - 4(k\mu + m_2)}}{2(m_2 + k\mu)}, \tag{6.71}$$

and $(\partial r_s(u))/(\partial u)(0) < 0$ holds, hence the assertion follows, if the roots are real-valued:

$$\mu^2 m_1^2 - 4(k\mu + m_2) > 0, \tag{6.72}$$

$$\frac{\mu^2 m_1^2 - 4m_2}{4\mu} > k, \tag{6.73}$$

yields the condition on k.

$$\mu^2 m_1^2 - 4m_2 > 0, \tag{6.74}$$

$$\mu > 2\frac{\sqrt{m_2}}{m_1}, \tag{6.75}$$

yields the condition on μ.
Moreover, it holds that

$$\hat{u}_- < \frac{\mu m_1}{2(m_2 + k\mu)} < \frac{\mu m_1}{2m_2}, \tag{6.76}$$

hence, for sufficiently small $k > 0$, it follows

$$\hat{u}_- < \frac{1}{\sqrt{3k}} < u_-(w_1). \tag{6.77}$$

It follows the assertion:

$$\|u(0)\|_\infty > \hat{u}_- \Rightarrow \forall_{\varepsilon>0}\exists_{\infty>t^*\geq 0}\forall_{t>t^*}\ \|u(t)\|_\infty \geq \hat{u}_+ - \varepsilon. \tag{6.78}$$

□

Proposition 6.8. *Consider model* (6.12)*. Assume that the parameters satisfy the conditions of Theorem 3.21 and Lemma 6.7. Moreover, assume that the initial conditions satisfy for some small, but positive* ε_2

$$u(0, x) \leq (m_1 - \sqrt{m_1^2 - 4k})/(2k) - \varepsilon_2 =: \varepsilon, \tag{6.79}$$

on a subset $\Omega_\varepsilon \subset \Omega$, and $\|u(0)\|_\infty > \hat{u}_-$, where $\hat{u}_-$ is defined as in Lemma 6.7. Then

$$\liminf_{t\to\infty} \|u(t)\|_\infty \geq \frac{\mu m_1 + \sqrt{\mu^2 m_1^2 - 4(k\mu + m_2(1-\mu(\Omega_\varepsilon)))}}{2(\frac{m_2(1-\mu(\Omega_\varepsilon))}{\mu}) + k\mu}. \tag{6.80}$$

Proof. It holds

$$\int_\Omega \frac{u^2}{1+ku^2} = \int_{\Omega_1} \frac{u^2}{1+ku^2} + \int_{\Omega\setminus\Omega_a} \frac{u^2}{1+ku^2}. \tag{6.81}$$

where $\Omega_a \subset \Omega_\varepsilon$. Define $\mu(\Omega_\varepsilon) = a_\varepsilon$ and $\mu(\Omega_a) = a$. Then, it holds for all $a \in [0, a_1)$ that

$$\int_\Omega \frac{u^2}{1+ku^2} \leq a_\varepsilon \frac{\varepsilon^2}{1+k\varepsilon^2} + (1-a_\varepsilon)\frac{\|u(t)\|_\infty^2}{1+k\|u(t)\|_\infty^2}, \tag{6.82}$$

$$< a\frac{\varepsilon^2}{1+k\varepsilon^2} + (1-a)\frac{\|u(t)\|_\infty^2}{1+k\|u(t)\|_\infty^2}. \tag{6.83}$$

Therefore, it holds, analogously to (6.68), that

$$\frac{\partial}{\partial t}\|u(t)\|_\infty > -\left(1 + \frac{m_2 a}{\mu}\frac{\varepsilon^2}{1+k\varepsilon^2} + \frac{m_2(1-a)}{\mu}\frac{\|u(t)\|_\infty^2}{1+k\|u(t)\|_\infty^2}\right)\|u(t)\|_\infty + m_1\frac{\|u(t)\|_\infty^2}{1+k\|u(t)\|_\infty^2}.$$

Hence, by rescaling time, we can apply the result of Lemma 6.7 with (abusing notation),

$$m_2 \to \frac{m_2(1-a)}{\mu + \frac{\varepsilon^2}{1+k\varepsilon^2}m_2 a}, \tag{6.84}$$

$$m_1 \to \frac{m_1}{1 + \frac{m_2}{\mu}\frac{\varepsilon^2}{1+k\varepsilon^2}a}. \tag{6.85}$$

Hence, it holds

$$\hat{u}_\pm(a,\varepsilon) = \frac{\mu\frac{m_1}{1+\frac{m_2}{\mu}\frac{\varepsilon^2}{1+k\varepsilon^2}a} \pm \sqrt{\mu^2\left(\frac{m_1}{1+\frac{m_2}{\mu}\frac{\varepsilon^2}{1+k\varepsilon^2}a}\right)^2 - 4\left(k\mu + \frac{m_2(1-a)}{\mu+\frac{\varepsilon^2}{1+k\varepsilon^2}m_2 a}\right)}}{2\left(\frac{m_2(1-a)}{\mu+\frac{\varepsilon^2}{1+k\varepsilon^2}m_2 a} + k\mu\right)}. \tag{6.86}$$

Since $\hat{u}_+(a,\varepsilon)$ is continuous in a on $[0,1]$ and continuous in ε on $[0,c]$ for sufficiently small c and due to Lemma 6.6 ($u(0,x) < \varepsilon \Rightarrow u(x,t) < \varepsilon e^{-ct}$), there exists a function $c(\varepsilon,t)$, such that $\hat{u}_+(a,\varepsilon) \in B_{c(\varepsilon,t)}(\hat{u}_+(a,0))$ with $c(\varepsilon,t) \to 0$ uniformly on any finite $(0,T)$ as $\varepsilon \to \infty$ and

$c(\varepsilon, t) \to 0$ uniformly as $t \to 0$. Therefore, we approximate

$$\tilde{u}_{\pm}(a) := \hat{u}_{\pm}(a, 0) = \frac{\mu m_1 \pm \sqrt{\mu^2 m_1^2 - 4(k\mu + m_2(1-a))}}{2(\frac{m_2(1-a)}{\mu}) + k\mu}, \tag{6.87}$$

and notice $d/da(\tilde{u}_+(a)) > 0$. Hence, for all $t^* \in (0, \infty)$,

$$\hat{u}_+(a_\varepsilon, 0) - c(\varepsilon, t^*) \leq \liminf_{t\to\infty} \|u(t)\|_\infty, \tag{6.88}$$

where $\lim(c(\varepsilon, t)) = 0$ as $t \to \infty$ due to Lemma 6.6, since the super-solution depend continuously on the parameters and

$$\tilde{u}_+ - \tilde{u}_- = \frac{\sqrt{\mu^2 m_1^2 - 4(k\mu + m_2(1-a))}}{\frac{m_2(1-a)}{\mu} + k\mu} \geq c > 0, \tag{6.89}$$

for $a < 1$. □

We summarise our results about the scalar equation (6.12).

Proposition 6.9. *Consider system* (6.12) *and let the parameters satisfy the conditions of Theorem 3.21 and Lemma 6.7.*

1. *There exist three spatially homogeneous steady state $u_1 = 0$ and $u_{-,2} < 1/\sqrt{3k} < u_{-,1}$. $u_{-,1}$ is stable with respect to spatially homogeneous perturbations and unstable with respect to spatially inhomogeneous perturbations.*

2. *If $\|u(t=0)\|_\infty > 1/\sqrt{3k}$, then $\|u(t)\|_\infty > 1/\sqrt{3k}$ for all $t \geq 0$.*

3. *If $u(t=0) < 1/m_1$ on a subset Ω_- and $\|u(t=0)\| > 1/\sqrt{3k}$, then it holds that*

$$u(t) \to 0 \text{ on } \Omega_- \text{ as } t \to \infty,$$
$$\liminf_{t\to\infty} \|u(t)\|_\infty \geq \frac{\mu m_1 + \sqrt{\mu^2 m_1^2 - 4(k\mu + m_2(1-\mu(\Omega_-)))}}{2(\frac{m_2(1-\mu(\Omega_-))}{\mu}) + k\mu}. \tag{6.90}$$

4. *For parameters chosen to comply with the rescaling* (3.92)-(3.95)*, the solution of system*

$$\begin{aligned}
\frac{\partial}{\partial t}u =& -\mu_1 u - buw + dv + m_1\frac{u^2}{1+ku^2}, && (x,t)\in\overline{\Omega}\times(0,T),\\
\alpha(\delta)\frac{\partial}{\partial t}v =& -\mu_2 v + buw - dv, && (x,t)\in\overline{\Omega}\times(0,T),\\
\gamma(\delta)\frac{\partial}{\partial t}w =&\beta(\delta)^{-1}D\Delta w - \mu_3 w - buw + dv + m_2\frac{u^2}{1+ku^2}, && (x,t)\in\Omega\times(0,T),\\
\partial_n w =&0, && (x,t)\in\partial\Omega\times(0,T).
\end{aligned}$$

with initial conditions

$$(u(x,0),v(x,0),w(x,0))\in(C(\overline{\Omega})^2\times(C^2(\overline{\Omega}))), \tag{6.91}$$

converges almost uniformly on any finite time-interval towards the solution of (6.12) *with the same initial conditions for* u *as* δ *tends towards zero under suitable conditions on the convergence rates of* $\alpha(\delta),\beta(\delta),\gamma(\delta)\to 0$ *as* $\delta\to 0$*.*

7 Conclusion and Outlook

In this dissertation, we showed that reaction-diffusion-ODE models exhibit, under rather general conditions, infinitely many weak stationary solutions with irregularly distributed jump-type discontinuities. Moreover, we gave conditions for stability of such stationary solution in a suitable topology, for general twice continuously differentiable zero-order term. We proposed a prototype model exhibiting both properties, DDI and hysteresis. Numerical investigations of the prototype model suggest that the arising pattern resembles the shape of the initial conditions if the diffusion coefficient is large. However, simulations also suggest that the pattern does not resemble the shape of the initial conditions for small diffusion coefficient. We suppose that the pattern selection mechanism is similar to the spike-pattern selection mechanism in [HMC14], where we observed dynamical spike patterns numerically. For large diffusion coefficient, the strong dependence on initial conditions is plausible since the dynamical behaviour is proved to be similar to the dynamical behaviour of the shadow system. The jump-type pattern does not assume values of the non-trivial stationary solutions of the kinetic system, unlike for bi-stable models. The proposed prototype model allows for manipulation of the pattern, similar to hydra's grafting experiment. However, sufficiently regular initial perturbation is necessary in order to avoid *very* irregular patterns. Moreover, we showed that the Lengyel-Epstein model exhibits both properties as well.

Numerical simulations show that stability of steady states changes if diffusion is introduced in the ODE-subsystem. But then representation of hydra's grafting experiment would not be possible for large time. This fact points out clear difference between reaction-diffusion models and reaction-diffusion-ODE models.

On the one hand, natural systems at molecular level exhibit very weak diffusion. On the other hand, reaction-diffusion-ODE models may arise due to application of homogenisation techniques, see e.g [MCP08]. Then, exclusion of diffusion can be reasonable, for example for cells. Certain cells would not spread in space since their movement is limited by neighbouring cells. The measure of this small region may vanish with the same order as the measure of the single cell (relative to the measure of the domain since more cells are considered within the domain). Hence, classical diffusion, with an infinitely fast transport of information to any point of the domain, may not be appropriate. Moreover, even if *very* weak diffusion is considered, the result of Reichelt [Rei14] implies that the dynamical behaviour of the solution of the reaction-diffusion-ODE model is similar for finite time. Hence, stability of steady states of the reaction-diffusion-ODE system implies that the solution for weak diffusion stays close to the steady state on a finite time interval. The finite time interval is determined by the size of the diffusion coefficient, what explains the almost immediate breakdown of patterns in simulations. This observation and the results proved within this work might give rise to a possible field for future research: Reaction-diffusion model in which one diffusion coefficient vanishes in time. Growing domains might be feasible for this type of model: one species diffuses until the size of the spatial domain reaches a certain threshold, while the other continues diffusing. Examples might be cell clusters [vdBBJB$^+$14] which, after achieving a certain number of cells, may form a matrix and the cells become immobile. Another example might be certain types of morphogens: One the one hand, some morphogens, such as Swim [MFC$^+$12], diffuse in cells and in the aquaneous extracellular matrix. On the other hand, certain morphogens, such as Wnt [MFC$^+$12], are hydrophobic. The transport mechanism of Wnt through the extracellular matrix is unknown. Indeed, sharp gradient patterns of morphogen concentrations are observed in [MSHS07] in fruit flies at a *certain* stage in development.

Additional to de-novo formation of irregular patterns with jump-discontinuities, we investigated reductions of ordinary differential equations coupled to reaction-diffusion equations. We gave conditions under which 'stable subsystems' can be reduced. We gave a proof for invariance of stability under reduction for systems with few ordinary differential equations, and for one-dimensional spatial domain. We suppose that the idea can be extended to larger systems and to two- or three-dimensional spatial domain. Numerical investigations for two- and three-dimensional domains suggest stability preservation under reduction of 'stable subsystems'. Such investigations are not included in this work. A proof might be addressed in future research. Within the proof of stability, a Sobolev-type estimate is used, but this estimate does not hold for two-dimensional domains. Hence, any generalisation might need a fundamentally different strategy of proof.

The Tikhonov-type result allows to consider a subsystem as a single species from the viewpoint of modelling. This hypothesis is common in biology, and widely applied for systems of ordinary differential equations. The result shows that this biological hypothesis is reflected in reaction-diffusion-ODE models as well. Even more, it allows to identify such 'reducible' subsystems, leading to an easier analytical investigation of models after reduction. On the one hand, limitation to 'stable subsystem' is a drawback. On the other hand, arbitrarily strong acceleration of an unstable sub-reaction is unlikely to stabilise a steady state. Hence, the drawback is physically plausible.

Regularity of the shadow system approximation has been shown. Moreover, conditions for existence and stability of qualitatively similar patterns were given. We derived conditions under which patterns of reaction-diffusion-ODE models can be investigated based on the shadow system approximation. On finite time intervals, qualitatively similar dynamical behaviour of reaction-diffusion-ODE models and their shadow system has been shown in [Bob15] before. If well-posed, the arising pattern in a shadow system of a system of one ODE and one RDE depends highly on the initial conditions. For biological application, the dependence might be too strong. However, qualitative modelling, such as the question whether the original exhibits certain qualitative properties, can be addressed using this approximation. This investigation of *mechanisms* of pattern formation is the strong aspect of this reduction.

In the last part of the thesis, we reduced the shadow system of our prototype model to a scalar integro-differential equation. We showed that the dynamical behaviour of the shadow system is reflected by the scalar equation on finite time intervals. The main finding of the investigation of the scalar equation is that Turing's' activator-inhibitor pattern formation hypothesis can be extended to non-local operators. It may even be a common pattern forming mechanism of scalar integro-differential equations and reaction-diffusion-ODE models. A question for future research might be the following: Can reaction diffusion models be reduced to scalar integro-differential equations with diffusion? Or systems with a transport term? However, instability of non-monotone stationary solutions of shadow systems of reaction-diffusion systems poses a problem. Unlike for the original model or the shadow system, we were able to prove existence of a lower boundary of the L^∞-norm. Moreover, we showed, for suitable initial conditions, that the solution decays on parts of the spatial domain. The corresponding theorem states that the lower bound increases if the solution decays on a larger part of the spatial domain. The numerical investigation undertaken in this work suggest a similar trend for the original reaction-diffusion-ODE system.

Symbols

We give a non-exclusive list of commonly used symbols.

u, v, w	If lower case letters are used, described compartments are scalar
U, V, W	If upper case letters are used, described compartments vector-valued
u_i, v_i, w_i	Components of vector-valued compartments U,V,W
$\overline{u}, \overline{U}, \overline{v}, ...$	Refers to a spatially homogeneous steady state respectively stationary solution
$\tilde{u}, \tilde{U}, \tilde{v}, ...$	Refers to spatially *in*homogeneous steady state respectively stationary solution
$\nabla_U f$	Defines the Jacobian matrix $(\partial_{u_j} f_i)$ for a vector-valued function $f = (f_i(U))_i$ and a vector $U = (u_j)_j$.
$\mathcal{J} = (b_{ij})_{ij}$	Jacobian matrix
$\mathcal{A}^\delta (a_{ij})_{ij}$	Jacobian matrix
I	Spatial one-dimensional finite, connected domain, i.e. a finite interval
Ω	Spatial multidimensional domain, connected
$BV(I)$	Space of functions with bounded variation
$C^n(\Omega)$	Space of n-times continuously differentiable functions on Ω
$C(\Omega)$	$C^0(\Omega)$, i.e. space of continuous functions
$W^{p,q}(\Omega)$	Sobolev space
$L^p(\Omega)$	Lebesgue space
$W_N^{2,2}$	Space of elements of $W^{2,2}$ satisfying homogeneous Neumann boundary conditions
$\Delta_{w,N}$	Weak Laplace operator with homogeneous Neumann boundary conditions
∇u	$\nabla_x u$
$\nabla_x u$	Jacobian matrix with respect to the spatial variable x, see also $\nabla_U f$
$\Vert u \Vert_i$	$\Vert u \Vert_{L^p(I)}$ or $\Vert u \Vert_{L^p(I)}$, depending on the context.
$\vert A \vert_\infty$	If A is a matrix, it defines the supremum norm for matrices, i.e. $\sup_{n,m} \vert a_{nm} \vert$ If A is a function, it is equal to the L^∞-norm.
$\vert A \vert_\sigma$	Spectral norm of a matrix A
id	Identity-operator; The space depends on the context
$\partial_i f(u, v, w)$	Partial derivative with respect to the i-th increment of f, evaluated at (u, v, w).
$\partial_w f(a, b, c)$	Partial derivative with respect to the increment w, evaluated at (a, b, c). The function is the previously defined as function in w.
f, g, h	If not specified otherwise, f, g, h are twice continuously differentiable functions.
$\mu(\Omega)$	$\int_\Omega 1 dx$
meas(Ω)	$\mu(\Omega)$
$\chi_A(x)$	Characteristic function of a set A.
$\partial_n u, x \in \partial I$	n denotes the outer unit vector, orthogonal to the boundary ∂I of I.

Appendices

We deferred figures illustrating the order of error reduction under mesh refinement for the approximation in Figure 3.8 to the Appendix. As reference solution $(u_{\text{ref}}, w_{\text{ref}})$, we consider an approximation with spatial mesh size $h = 2^{-15}$ and temporal mesh size $k = 10^{-3}$. We refine the spatial mesh. Until $t = 3$, the order of convergence is as expected in [ELW00]. The solution for $t = 3$ is shown in Figure .1. For $t > 3$, the order of convergence differs from the expected order. However, for $t > 3$, the analytically proved (A, ε_0)-stability holds. We assume that the different order of convergence originates from the following: While the solutions u_h are already very close to the projection of the steady state onto the subspace of finite elements associated with their mesh, the reference solution can still approximate a continuous solution on the transition layer. When the transition layer of u_{ref} continues sharpening, values of u_{ref} on cells in the transition layer converge either towards the upper or the lower branch. Then, the error depends on the position of the jump-discontinuity of the solutions u_h.

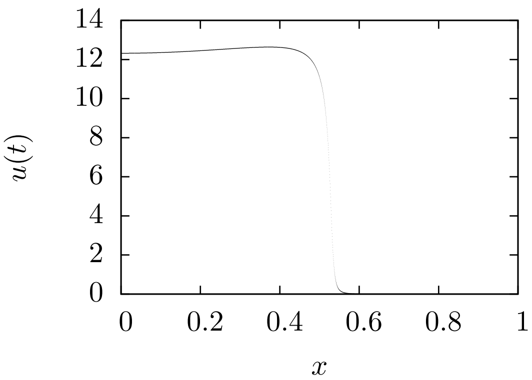

Figure .1: Reference solution at $t = 3$. The approximated solution is mirrored at $x = 0.5$, i.e. initial conditions for u are $u(x, 0) = 6.36 + 0.1\cos(\pi x)$. Due to the point-symmetric mesh and the point symmetric initial conditions, the result is not different.

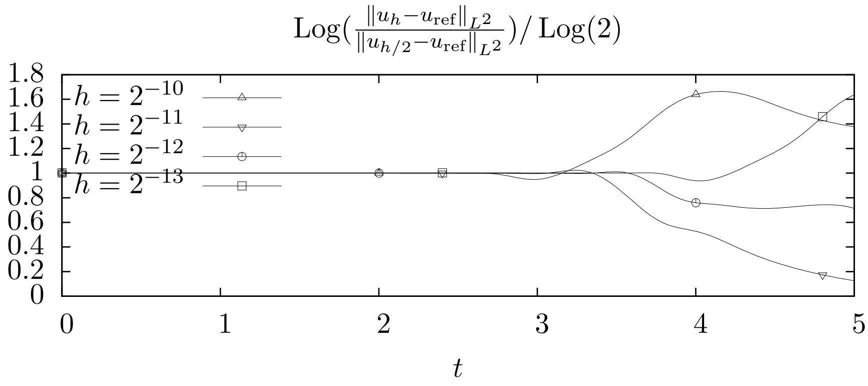

Figure .2: Order of the $L^2(I)$-error reduction for component u. Temporal mesh size = 0.001. Spatial mesh size of the reference solution is $h = 2^{-15}$.

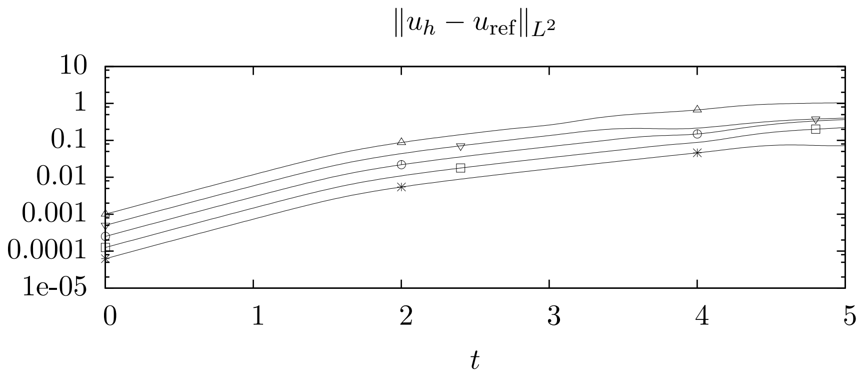

Figure .3: Absolute value of the $L^2(I)$-error for component u. Temporal mesh size = 0.001. Spatial mesh size of the reference solution is $h = 2^{-15}$.

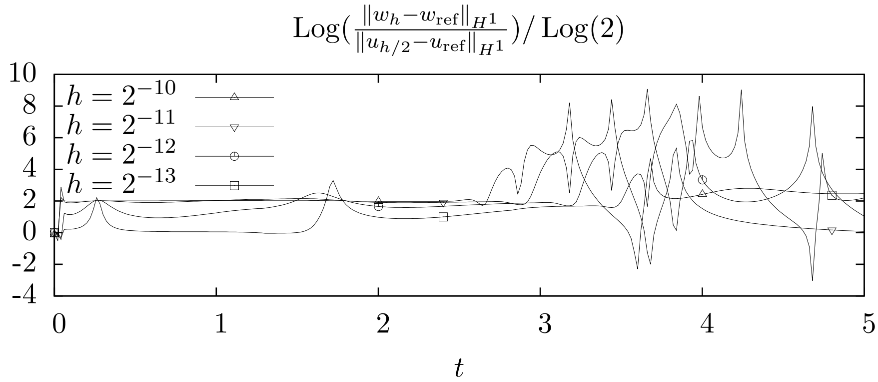

Figure .4: Order of the $H^1(I)$-error reduction for component w. Temporal mesh size = 0.001. Spatial mesh size of the reference solution is $h = 2^{-15}$.

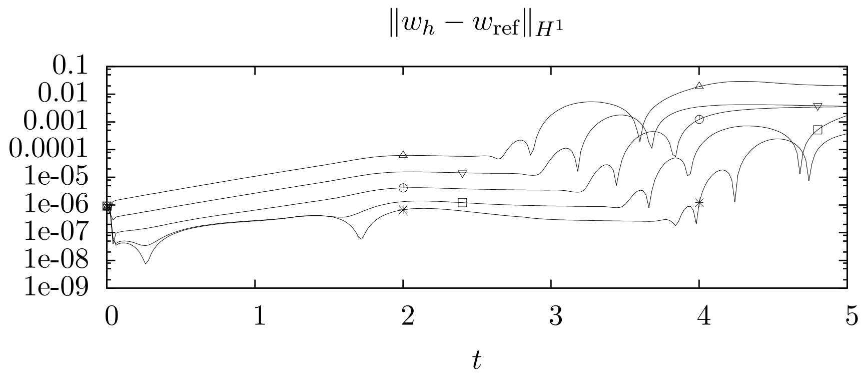

Figure .5: Absolute value of the $H^1(I)$-error for component w. Temporal mesh size = 0.001. Spatial mesh size of the reference solution is $h = 2^{-15}$.

List of Figures

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