Spike patterns in a reaction–diffusion ODE model with Turing instability

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We explore a mechanism of pattern formation arising in processes described by a system of a single reaction–diffusion equation coupled with ordinary differential equations. Such systems of equations arise from the modeling of interactions between cellular processes and diffusing growth factors. We focus on the model of early carcinogenesis proposed by Marciniak-Czochra and Kimmel, which is an example of a wider class of pattern formation models with an autocatalytic non-diffusing component. We present a numerical study showing emergence of periodic and irregular spike patterns because of diffusion-driven instability. To control the accuracy of simulations, we develop a numerical code on the basis of the finite-element method and adaptive mesh grid. Simulations, supplemented by numerical analysis, indicate a novel pattern formation phenomenon on the basis of the emergence of nonstationary structures tending asymptotically to a sum of Dirac deltas. Copyright © 2013 John Wiley & Sons, Ltd.

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1. Introduction

Classical mathematical models of biological or chemical pattern formation have been developed using reaction–diffusion equations, see, for example, [1–5] and references therein. In that framework, there exist essentially two mechanisms of formation of stable spatially heterogeneous structures:

(i) Diffusion-driven instability (DDI) that leads to destabilization of a spatially homogeneous steady state and emergence of Turing patterns.

(ii) A mechanism based on the multistability and hysteresis in the kinetic system, which allows for the formation of transition layer patterns far from equilibrium.

Both mechanisms can also coexist yielding a complex dynamics of the system as, for example, in the Lengyel–Epstein model of chemical reactions [2, 5].

The Turing phenomenon is related to a local behavior of solutions of a reaction–diffusion system in the neighborhood of a constant solution that is destabilized via diffusion. Patterns arising through a bifurcation can be spatially monotone or spatially periodic. The mechanism responsible for such behavior of model solutions is called a DDI (Turing-type instability), which can be formulated in the following way.

Definition 1.1 (Diffusion-driven instability)

A system of reaction–diffusion equations exhibits DDI (Turing instability) if and only if there exists a constant stationary solution that is stable to spatially homogeneous perturbations, but unstable to spatially heterogeneous perturbations.

The original idea was presented by Turing on the example of two linear reaction–diffusion equations [6]. Because of the local character of Turing instability, the notion has been extended in a natural way to the nonlinear equations using linearization around a constant positive steady state. However, nonlinear systems may have multiple constant steady states yielding existence of heterogeneous structures far from the equilibrium. In such cases, global behavior of the solutions cannot be predicted by the properties of the linearized system and a variety of possible dynamics depending on the type of nonlinearities can be observed. On the other hand, Turing instability can be exhibited also in degenerated systems such as reaction–diffusion ODE models or integro-differential equations, for example:
shadow systems obtained through reduction of the reaction–diffusion model, [7, 8]. Following all these observations and the character of Turing’s original system, we define Turing patterns in the following way.

**Definition 1.2**

By Turing patterns we call the solutions of reaction–diffusion equations that are

(i) Stable,
(ii) Stationary,
(iii) Continuous,
(iv) Spatially heterogeneous, and
(v) Arise because of the Turing instability (DDI) of a constant steady state.

Recently, it has been shown that if DDI property is exhibited by a system of a single reaction–diffusion equation coupled to an ordinary differential equation with autocatalysis of non-diffusing component, then it does not lead to Turing patterns. In such models, all continuous patterns are unstable [9]. As a consequence, the question for the long-term behavior of solutions arises. It has been previously shown that a diffusion-driven blow-up in systems of reaction–diffusion equations can occur in finite time, [10]. Even more, blow-up in finite time in $L^\infty$, but global existence of weaker solutions has been shown, leading to so called ‘incomplete blow-up’, see, for example, [11] for uniform boundedness in $L^1$.

In the current paper, we present a phenomenon of diffusion-driven unbounded growth and formation of dynamic spike pattern converging asymptotically to a sum of Dirac deltas. For a reaction–diffusion ODE model arising from applications in biology, we show that introducing diffusion in the ODE systems not only destabilizes the constant steady state but also leads to an unbounded growth of model solutions. Because the solutions of the system with zero diffusion are uniformly bounded, we call the observed phenomenon the diffusion-driven unbounded growth. The total mass ($L^1$ norm) of the solutions is uniformly bounded, but it concentrates in isolated points for time tending to infinity. Using numerical simulations, we investigate how the shape of emerging patterns depends on initial conditions and the scaling coefficient (size of diffusion versus domain size). Interestingly, we find out that the shape of observed patterns are superposition of a near-equilibrium effect of DDI and a far-from-equilibrium effect of multistability exhibited by the model.

## 2. Problem formulation

We study a reaction–diffusion ODE model of the diffusion-regulated growth of cell population, which has the form of two ordinary-partial differential equations

\[
\begin{align*}
  u_t &= \left( a_1 \frac{uw}{1+uw} - d_1 \right) u, & \text{for } x \in [0, 1], t > 0, \\
  w_t &= Dw_{xx} - w - u^2 w + \kappa_1, & \text{for } x \in (0, 1), t > 0, 
\end{align*}
\]

supplemented with homogeneous Neumann (zero flux) boundary conditions for the function $w = w(x, t)$

\[
  w_x(0, t) = w_x(1, t) = 0 \quad \text{for all } t > 0, 
\]

and with nonnegative initial conditions

\[
  u(x, 0) = u_0(x), \quad w(x, 0) = w_0(x). 
\]

$a_1, d_1, Dw, \kappa_1$ denote positive constants.

In this paper, we focus on one-dimensional domain $[0, 1]$ for a clarity of presentation. The results can be obtained also for a model defined on two-dimensional space domain. Obviously, in such case a structure of spatial patterns is richer. Nevertheless, the main aspect of the pattern formation phenomenon exhibited by this model, that is, evolution of spike patterns of mass concentration, is preserved independent on the dimension of the spatial domain. Model (2.1)–(2.4) is a rescaled reduction of the model

\[
\begin{align*}
  u_t &= \left( a \frac{v}{u+v} - d_c \right) u, & \text{for } x \in [0, 1], t > 0, \\
  v_t &= -d_v v + \alpha u^2 w - d_v, & \text{for } x \in [0, 1], t > 0, \\
  w_t &= -w_{xx} - d_w w - \alpha u^2 w + dv + \kappa, & \text{for } x \in (0, 1), t > 0, 
\end{align*}
\]

supplemented with homogeneous Neumann (zero flux) boundary conditions for the function $w = w(x, t)$.

Model (2.5)–(2.7) was proposed in [12] as a receptor-based model of spatially distributed growth of a clonal population of precancerous cells, and its extensions and modifications were studied in [13, 14]. The reduction was proposed in [15], but without further numerical or analytical investigation.

In case of the spatial domain being the unit square, approximation of solutions of model (2.5)–(2.7) have been performed in [15]. Numerical simulations of the model showed qualitatively new patterns of behavior of solutions, including, in some cases, a strong dependence of the emerging pattern on initial conditions and quasistability followed by rapid growth of solutions. However, recently it has been shown using linear stability analysis of nonconstant steady states that all stationary solutions of this model, both continuous and discontinuous, are unstable [16]. A question arises if the model exhibits a formation of any pattern, which persist for long times. Our present research is focused on understanding these phenomena and answering questions on pattern formation in such class of models.
3. Analytical results

In the remainder of this paper, we consider the systems (2.1)–(2.4). It has been obtained using a quasistationary approximation assuming that the dynamics of $v$ variable is faster than the dynamics of other variables. In the present paper, we focus on the reduced model, because it is the simplest reaction–diffusion ODE model exhibiting the spike pattern formation mechanism. A rigorous link between the solutions of the original models (2.5)–(2.7) and its two-equations approximation has been recently shown in [9].

3.1. Existence of solutions

Existence of global, classical solutions can be proven within the framework of ordinary differential equations and the theory of linear semigroups, see, for example, [17, 18]. Moreover, it can be shown using maximum principle that the solutions remain positive for positive initial conditions.

3.2. Existence of steady states

The analytical results concerning existence of regular stationary patterns of (2.1)–(2.2) can be summarized in the following theorem:

**Theorem 3.1**

Under assumptions $a_1 > d_1$ and $\kappa_1 > 2 \frac{d_1}{a_1 - d_1}$, system (2.1)–(2.2) has the following smooth stationary solutions:

(i) Constant steady states $(\mathcal{U}_0, \mathcal{W}_0) = (0, \kappa_1)$, $(\mathcal{U}_+, \mathcal{W}_+) = \left( \frac{d_1}{a_1 - d_1}, \frac{1}{2} \kappa_1 + \sqrt{\left( \frac{\kappa_1}{2} \right)^2 - \left( \frac{d_1}{a_1 - d_1} \right)^2} \right)$ and $(\mathcal{U}_-, \mathcal{W}_-) = \left( \frac{d_1}{a_1 - d_1}, \frac{1}{2} \kappa_1 - \sqrt{\left( \frac{\kappa_1}{2} \right)^2 - \left( \frac{d_1}{a_1 - d_1} \right)^2} \right)$ being stationary solutions of the kinetic system.

(ii) A unique strictly increasing solution $w$ and a unique strictly decreasing solution $w$; $u$ is defined by $U = \frac{d_1}{a_1 - d_1} \frac{1}{w}$.

(iii) A periodic solution $w$ with $n$ modes, increasing on intervals $[0, \frac{1}{n}]$ and its symmetric counterpart $\tilde{W}(x) = W_n(1 - x)$, where $n \in \mathbb{N}$ depends on the diffusion coefficient; and the periodic function $\tilde{W} \in C([0, 1])$ is defined in the following

$$W(x) = \begin{cases} W \left( x - \frac{2j}{n} \right) & \text{dla } x \in \left[ \frac{2j}{n}, \frac{2j+1}{n} \right] \\ W \left( \frac{2j+2}{n} - x \right) & \text{dla } x \in \left[ \frac{2j+1}{n}, \frac{2j+2}{n} \right] \end{cases}$$

for every $j \in \{0, 1, 2, 3, \ldots \}$ such that $2j + 2 \leq n$. $\tilde{U}$ is defined by $U = \frac{d_1}{a_1 - d_1} \frac{1}{\tilde{w}}$.

The proof of this statement is deferred to the Appendix.

3.3. Stability of steady states

We investigate stability of the solutions described in Theorem 3.1, item (i):

The operator resulting from linearization of (2.1)–(2.2) around $(\frac{d_1}{a_1 - d_1}, \mathcal{W}_0)$ reads in the matrix form:

$$J := \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} + D_W \Delta \end{bmatrix} \begin{bmatrix} a_1 - d_1 \\ \frac{d_1}{a_1 - d_1} \end{bmatrix} + \left( \frac{d_1}{a_1 - d_1} \right)^2 + D_W \Delta$$  \hspace{1cm} (3.1)

Assume that a solution of $\frac{d}{dt} \phi = J \phi$ with homogeneous Neumann boundary conditions is of the form $\phi = \phi_k$, where $\phi_k$ denotes the eigenvector of the Laplace operator associated to the $k$th eigenvalue. Then, the dispersion relation, that is, the dependence of eigenvalues of the problem linearized at a constant steady states with the eigenvalues of the Laplace operator, illustrated in Figure 1, is defined by

$$\text{disp}(\lambda, k) = \det \begin{bmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - D_W (\pi k)^2 - \lambda \end{bmatrix},$$  \hspace{1cm} (3.2)

where $(\pi k)^2$ is the $k$th eigenvalue of the Laplace operator considered on $C^2(0, 1)$. Therefore, $\lambda$ is an element of the point spectrum of $J$ if $\text{disp}(\lambda, k) = 0$ for $\lambda \neq a_{11}, 0$.

**Proposition 3.2**

Under assumptions $a_1 > d_1$ and $\kappa_1 > 2 \frac{d_1}{a_1 - d_1}$, the following holds:

(i) $(\mathcal{U}_0, \mathcal{W}_0)$ is a stable stationary solution of (2.1)–(2.2) and its kinetic system.

(ii) $(\mathcal{U}_+, \mathcal{W}_+)$ is an unstable stationary solution of (2.1)–(2.2) and its kinetic system.

(iii) $(\mathcal{U}_-, \mathcal{W}_-)$ is an unstable stationary solution of (2.1)–(2.2).
Theorem 3.3 because of autocatalysis of Lemma 3.4 see Lemma 3.5.

induced by unbounded solutions of the kinetic system, such as shown in [19], we check boundedness properties of the kinetic system,

unbounded growth of the solutions may happen at most in isolated points of the spatial domain. Furthermore, to exclude blow-up

It can be easily shown that the mass of solutions of systems (2.1)–(2.2) is uniformly bounded in time, see Lemma 3.4. Therefore,

underlying phenomenon, we summarize here results on the boundedness of solutions of the model with and without diffusion.

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3.4. Boundedness properties

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It can be easily shown that the mass of solutions of systems (2.1)–(2.2) is uniformly bounded in time, see Lemma 3.4. Therefore, unbounded growth of the solutions may happen at most in isolated points of the spatial domain. Furthermore, to exclude blow-up induced by unbounded solutions of the kinetic system, such as shown in [19], we check boundedness properties of the kinetic system, see Lemma 3.5.

Lemma 3.4

Let \( u(x, t), w(x, t) \) denote a solution of (2.1)–(2.2) for positive initial conditions. Then, it holds

\[
\limsup_{t \to \infty} \left( \frac{1}{a_1} \| u(t) \|_{L^1} + \| w(t) \|_{L^1} \right) \leq \frac{\kappa_1}{\min(d_1, 1)},
\]

\[
\limsup_{t \to \infty} \| u(t) \|_{L^1} \leq \frac{a_1}{\min(d_1, 1)} \kappa_1,
\]

\[
\limsup_{t \to \infty} \| w(t) \|_{L^1} \leq \kappa_1.
\]

Moreover, the solution of the kinetic system of (2.1)–(2.2) is uniformly bounded in time,

Lemma 3.5

Let \( u(x, t), w(x, t) \) denote a solution of the kinetic system of (2.1)–(2.2) for positive initial conditions. Then holds

\[
\limsup_{t \to \infty} u(t) \leq \frac{a_1}{\min(d_1, 1)} \kappa_1,
\]

\[
\limsup_{t \to \infty} w(t) \leq \kappa_1.
\]

Both lemmas can be proven similarly as it was shown in [16] for the three equation model. More details are deferred to the Appendix.

We conclude from Lemma 3.5 that the mass concentration observed in numerical simulations does not result from a blow-up of the solution of the kinetic system.
4. Numerical approach

Numerical approximations of solutions to systems (2.1)–(2.2) presented in this paper are obtained using the program library deal.ii, [20]. Simulations using adaptive grid refinement on the basis of cell-wise evaluation of the proposed error indicators in [21] show a growth of spikes, see Figure 3.

The question of what is seen in numerical simulations motivated us to undertake a numerical study of the pattern formation phenomenon. To allow a rigorous argumentation using classical finite-element analysis, we investigate the asymptotic behavior of the numerical solution for spatially homogeneous meshes.

For space discretization, we use a finite-element scheme with piecewise linear, globally continuous ansatz functions. The time discretization is performed using the implicit Euler scheme or the Crank–Nicholson scheme.

Convergence for such scheme for solutions of systems of type (2.1)–(2.2) is well known, see [21].

The low order of the space discretization is because of the fact that preliminary simulations already showed emergence of spikes, corresponding to a large second derivative in space.

5. Numerical analysis of the pattern formation phenomenon

We choose parameters

\[ a_1 = 2, d_1 = 1, \kappa_1 = 3 \]  
(5.1)

and diffusion coefficient \( D_w = 6 \).

A numerically obtained solution for different parameters, \( a_1 = 2.5, d_1 = 1.5, \kappa_1 = 4 \) is shown in the Appendix in figure A3. It shows qualitatively the same behavior. We recall that system (2.1)–(2.2) exhibits Turing-type diffusion-driven instability, but all positive steady states are linearly unstable.

5.1. Unbounded growth and spike formation

Initial conditions are chosen as a perturbation of the stable stationary solution \((\bar{u}, \bar{w})\) of the kinetics system of (2.1)–(2.2):

\[ u_0(x) = \bar{u}_- + \epsilon_1 p(x), \]
\[ w_0(x) = \bar{w}_-, \]  
(5.2)

where the ‘perturbation function’ \( p(x) \) satisfies the following conditions:

- \( p \) is a polynomial of degree two on \((0, s - \epsilon), (s - \epsilon, s + \epsilon), (s + \epsilon, 1)\),
- \( p \in C^1(0, 1) \),
- \( p(0) = p'(1) = 0 \),
- \( p(0) = p(1) = -1 \),
- \( p(s) = 1 \),

(5.3)–(5.7)

and is thereby uniquely defined by the pair \((s, \epsilon)\). The explicit formula for \( p \) can be found in the Appendix, (A33), an illustration can be found in Figure 2.

In Figure 3, the solution for initial conditions (5.2) for \( s = 0.4, \epsilon_1 = 0.05, \epsilon = 0.1 \) is shown. We observe exponential growth in a single point and decay towards zero otherwise. The maximum value of the numerically obtained solution keeps growing.

**Figure 2.** Illustration of the perturbation function \( p(x) \), defined by (5.3)–(5.7) for \( s = 0.4, \epsilon = 0.1 \). max\(_{x \in \Omega} p(x) \) is always assumed in \((s - \epsilon, s + \epsilon)\).
Figure 3. Numerically obtained solution for initial conditions (5.2) with \( s = 0.4, \epsilon = 0.1, \epsilon_1 = 0.05 \) and diffusion coefficient \( D_w = 6, \overline{v} = 0.25, \overline{w} = 0.1, \overline{D} = 0.05 \) and diffusion coefficient \( D_w = 6 \), \( u \) and \( w \). We observe formation of a spike at \( x = 0.43 \), which keeps growing exponentially in time.

Table I. Position \( x_{\text{max}} \) of the arising spike (\( t = 25 \)) for initial conditions (5.2) with \( D_w = 6 \) and maximum at \( x_{t=0,\text{max}} \). The shape of solutions are as in Figure 3, differing qualitatively only in the position of spike/sink. We observe that a spike grows close to the position of the maximum of the initial conditions.

| \( s \)  | \( x_{t=0,\text{max}} \) | \( x_{t=25,\text{max}} \) |
|---------|----------------|----------------|
| 0.2     | 0.25           | 0.2726         |
| 0.4     | 0.417          | 0.43237        |
| 0.5     | 0.5            | 0.5            |
| 0.7     | 0.66           | 0.645          |
| 0.85    | 0.792          | 0.77           |

5.2. Spike position and initial conditions

Simulations performed using the parameters \( a_1 = 2, d_1 = 1, k_1 = 3, D_w = 6 \) and initial conditions (5.2) show emergence of spikes at the maximum of the initial conditions, see Table I.

For the linearized problem, this is heuristically reasonable because almost all eigenmodes of the Laplace Operator are unstable with almost the same eigenvalue, see Lemma A.2 or Figure 1 for an illustration.

Lemma 5.1

Let \( J \) denote the operator resulting from the linearization of (2.1)–(2.2) around \( \overline{u}, \overline{w} \) and consider the initial value problem

\[
\frac{d}{dt} \begin{bmatrix} \phi \\ \psi \end{bmatrix} = J \begin{bmatrix} \phi \\ \psi \end{bmatrix},
\]

with homogeneous Neumann boundary (zero flux) conditions for \( \psi \).

As initial conditions take \( (\psi_0, \rho_0) = (\phi_k, \lambda_+ a_{21} \overline{x} + D_w \pi^2 \phi_k) \), where \( \phi_k \) denotes the eigenfunction of the Laplace operator (Neumann) associated to the \( k \)th eigenvalue and \( (a_0) \) denotes the Jacobian of the kinetics system at \( (\overline{u}, \overline{w}) \).

Then, \( e^{\lambda_+(k) t} (\psi_0, \rho_0) \) is the solution of (5.8) for homogeneous Neumann boundary conditions.

Heuristically speaking, the initial perturbation of \( u \) is self-amplifying for large \( D_w \) if it is much larger than the perturbation of \( w \), because \( \lambda_+(k) \to a_{11} > 0 \).

This heuristic implication leads to the question what happens for more complex initial conditions. In Figure 4, we plot the numerical solution for initial conditions

\[
\begin{align*}
 u_0(x) &= \overline{u} - \epsilon \cos(4\pi x), \\
 w_0(x) &= \overline{w}.
\end{align*}
\]

And in Figure 5, the numerical solution for initial conditions

\[
\begin{align*}
 u_0(x) &= \overline{u} - \epsilon \cos(4\pi x^2), \\
 w_0(x) &= \overline{w}.
\end{align*}
\]

The convergence of the numerical scheme is illustrated in Figure A8. We note that the initial perturbation seems to be indeed self amplifying. This does not explain the long-time behavior, but numerical simulations indicate that spikes grow close to the maxima of the initial conditions. We also note for initial conditions (5.10) that the spike for larger \( x \) grows faster. Real and imaginary part of the numerically obtained finite Fourier transform \( \hat{f}(\omega) := \int \phi(x) \cos(4\pi x^2) e^{i\omega x} dx \), and the growth rate of the perturbation at the maxima of \( u_0 \) are shown in Figure A1; Figure A2 shows the growth rate of perturbation (5.9).
Figure 4. Numerical solution for initial conditions (5.9) with $\epsilon = 0.05$ and diffusion coefficient $D_w = 2, \Pi = \frac{3 + \sqrt{5}}{2} \approx 2.62, \varpi = \frac{3 - \sqrt{5}}{2} \approx 0.382$. Left: component $u$. Right: component $w$. We observe formation of spikes at the position of local maxima of the initial conditions.

Figure 5. Numerical solution for initial conditions (5.10) with $\epsilon = 0.05$ and diffusion coefficient $D_w = 2, \Pi = \frac{3 + \sqrt{5}}{2} \approx 2.62, \varpi = \frac{3 - \sqrt{5}}{2} \approx 0.382$. Left: component $u$. Right: component $w$. We observe formation of spikes at the position of local maxima of the initial conditions and faster growth at $x = \frac{\sqrt{5}}{2}$ than at $x = \frac{1}{2}$.

5.3. Varying the diffusion coefficient

The roots of the dispersion relation have the form

$$\lambda_{\pm}(k^2) = \frac{\text{tr}(A) - (\pi k)^2 D_w}{2} \pm \sqrt{\left(\frac{\text{tr}(A) - (\pi k)^2 D_w}{2}\right)^2 - |A| + (\pi k)^2 D_w a_{11}}$$

(5.11)

We know that $\lambda_-(k^2) \to -\infty$ and $\lambda_+(k^2) \to a_{11} > 0$ as $k \to \infty$, see Lemma A.1, A.2. Additionally, it holds $\lambda_+(0) < 0$ because $(\bar{\varpi}_-, \bar{\varpi}_-)$ is a stable steady state of the kinetic system of (2.1)–(2.2).

It follows that there exist stable eigenmodes of the Laplace Operator, because $\lambda_-(k^2) < 0$ and

$$\lambda_+(k^2) < 0 \iff k^2 < -\frac{|A|}{a_{11} \pi^2 D_w}$$

(5.12)

This implies dampening of the low frequency part of the initial perturbation $\phi, \psi$.

First, we choose the same initial conditions and parameters as in Figure 3, but vary the diffusion coefficient $D_w$. For smaller diffusion coefficient, $D_w = 1$, we observe growth of multiple spikes for the same initial conditions, see Figure 6. We observe a self-amplification of the high-frequency part of the initial perturbation. The short-time behavior is therefore similar to the idea of a ‘dominant’ eigenvalue.

Figure 6. Numerical solution for initial conditions (5.2) with $s = 0.4, \epsilon = 0.1, \epsilon_2 = 0.05$ and diffusion coefficient $D_w = 1, \Pi = \frac{3 + \sqrt{5}}{2} \approx 2.62, \varpi = \frac{3 - \sqrt{5}}{2} \approx 0.382$. Left: component $u$. Right: component $w$. 

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in classical Turing-type models. However, in this case, we can speak of a ‘self-amplification of the part of the initial perturbation with sufficiently high wavenumber’.

We define,

\[ D_{w,k} := \frac{|A|}{a_{11}(\pi k)^2} = \frac{1}{(\pi k)^2} \cdot \frac{-4d_1^2 + (a_1 - d_1)^2k^2 + \kappa(a_1 - d_1)^2 \sqrt{k_1^2(a_1 - d_1)^2 - 4d_1^2}}{2d_1^2} \].  \hspace{1cm} (5.13)

Figure 7 shows the solution for the corresponding \( D_{w,1} \) for models (2.1)–(2.2). Table II shows the number of spikes for further variation of \( D_w \) for initial conditions (5.2) with \( s = 0.4, \epsilon = 0.1, \epsilon_1 = 0.05 \).

5.4. Evolution of mass

Our simulations indicate a growth of one or multiple spikes, \( u(x) \to \infty \) for some \( x \) as \( t \to \infty \), and decay in all other \( x \). We therefore investigate the evolution of the \( L^1 \)-norm of \( u \). Figure 8 shows the evolution of mass of the solution shown in Figure 3 for homogeneous spatial mesh size \( h = 2^{-16} \) and homogeneous temporal mesh size \( k = 2.5 \cdot 10^{-4} \). The convergence order is shown in the Appendix, see Figure A5–A6. Lemma 3.4 states that the mass of the solution, \( \|u(t)\|_{L^1} \), is uniformly bounded. However, an important question when modeling natural phenomena is positivity of mass if there is no extinction. The numerical simulations of the evolution of the mass suggests that it stays strictly positive. Therefore, on the basis of the numerical simulations, we have a conjecture that the solutions converge asymptotically to the sum of Diracs. This hypothesis supported by numerical simulations needs however a proof.

Figure 7. Numerical solution for initial conditions (5.2) with \( s = 0.4, \epsilon = 0.1, \epsilon_1 = 0.05 \) and diffusion coefficient \( D_w = 5.8541 \approx D_{w,1}, \vartheta = \frac{1 + \sqrt{\kappa^2}}{2} \approx 2.62, \varpi = \frac{1 - \sqrt{\kappa^2}}{2} \approx 0.382 \). Left: component \( u \). Right: component \( w \).

Table II. Number of spikes arising for different diffusion coefficients \( D_1 \), initial conditions (5.2) with \( s = 0.4, \epsilon_1 = 0.05, \epsilon = 0.1 \).

| \( D_1 \) | Spikes |
|---|---|
| \( D_{w,1} = 5.8541 \) | 1 |
| \( \frac{1}{4} D_{w,1} \) | 2 |
| \( \frac{1}{5} D_{w,1} \) | 3 |
| \( \frac{1}{10} D_{w,1} \) | 3 |
| \( \frac{1}{20} D_{w,1} \) | 4 |
| \( \frac{1}{40} D_{w,1} \) | 4 |

Figure 8. Evolution of the \( L^1 \)-norm of the solution shown in Figure 3. Left: component \( u \). Right: component \( w \).
Appendix A

A.1. Derivation of the model

Assume that component $v$ in models (2.5)–(2.7) satisfies the steady state equation

$$0 = \alpha u^2 w + dv - d_b v.$$  

(A1)

Solving for $v$ yields

$$v = \frac{\alpha}{d_b + \alpha} u^2 w.$$  

(A2)

Substituting (A2) into (2.5) and (2.7) yields

$$u_t = \left( \alpha \frac{uw}{\alpha + uw} - d_c \right) u, \quad \text{for } x \in [0, 1], \ t > 0,$$  

(A3)

$$w_t = \frac{1}{\gamma} w_{xx} - d_g w - \sigma^{-1} d_b u^2 w + \kappa, \quad \text{for } x \in (0, 1), \ t > 0.$$  

(A4)

for $\sigma := \frac{d_b + d}{\alpha}$. After rescaling time, $\hat{t} := d_g t$ yields

$$u_t = \left( \alpha \frac{uw}{d_g \alpha + \sigma uw} - d_c \right) u, \quad \text{for } x \in [0, 1], \ \hat{t} > 0,$$  

(A5)

$$w_t = \frac{1}{\gamma d_g} w_{xx} - w - \sigma^{-1} \frac{d_b}{d_g} u^2 w + \frac{\kappa}{d_g}. \quad \text{for } x \in (0, 1), \ \hat{t} > 0.$$  

(A6)

Defining $\hat{u}(x, t) := \sqrt{\frac{d_b}{d_g}} u(x, t)$ and $\hat{w}(x, t) := \sqrt{\frac{d_g}{d_b}} w(x, t)$, we obtain systems (2.1)–(2.2):

$$\hat{u}_t = \left( \alpha \frac{\sigma \hat{u} \hat{w}}{d_g \sigma + \alpha \hat{u} w} - d_c \right) \hat{u}, \quad \text{for } x \in [0, 1], \ \hat{t} > 0,$$  

(A7)

$$\hat{w}_t = \frac{1}{\gamma d_g} \hat{w}_{xx} - \hat{w} - \hat{u}^2 \hat{w} + \frac{\kappa}{\sqrt{d_g d_b \sigma}} \quad \text{for } x \in (0, 1), \ \hat{t} > 0.$$  

(A8)

A.2. Proofs of analytical statements

Proof of Theorem 3.1

Because $v = \frac{\alpha}{d_b + \alpha} u^2 w$ is the unique root of the right-hand side of (2.6), there exists a one-to-one mapping from the set of steady states of (A3)–(A4) into the set of steady states of (2.5)–(2.7) by $(u, w) \rightarrow (\hat{u}, \frac{\alpha}{d_b + \alpha} u^2 w, w)$.

Because model (2.1)–(2.2) is a linear rescaling resp. linear substitution of (A3)–(A4), there exists also a one-to-one mapping between the sets of steady states.

[16], Theorem 2.6 proves Theorem 3.1 for systems (2.5)–(2.7). Because we found a one-to-one mapping between the sets of steady states, statements (ii) and (iii) and existence of the steady states in (i) follow from [16], Theorem 2.6.

It is left to calculate the exact values of the spatially homogeneous steady states.

The right-hand-side of (2.1) has two roots:

$$\begin{align*}
\varpi_0 &= 0, \\
\varpi_1 &= \frac{d_1}{a_1 - d_1} \frac{1}{w}.
\end{align*}$$  

(A9)\hspace{1cm}(A10)

Substituting (A9) into the right-hand side of (2.2) and setting it equal to zero leads to

$$0 = -w + \kappa_1,$$  

(A11)

defining $(\varpi_0, \varpi_0) = (0, \kappa_1)$.

Substituting (A10) into the right-hand side of (2.2) and setting it equal to zero leads to

$$0 = -w - \left( \frac{d_1}{a_1 - d_1} \right)^2 \frac{1}{w} + \kappa_1,$$  

(A12)

with roots $\varpi_-$ and $\varpi_+$.

To prove (3.2), we use the following lemma from linear algebra, proved in [22], Section 2.1.2:
Lemma A.1
Let a real-valued block-matrix
\[ A = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} - Dk^2 \end{bmatrix}, \]
be given with \( D = \text{diag}(d_1, \ldots, d_m), d_i > 0. \)
Let \( \lambda_1, \ldots, \lambda_n \) denote the eigenvalues of \( A_{12} \) and \( \hat{\lambda}_1, \ldots, \hat{\lambda}_{m+n} \) the eigenvalues of \( A. \)
Then, there exists an injective mapping \( j: \{1, \ldots, n\} \to \{1, \ldots, n + m\}, \) s.t. for all \( 1 \leq i \leq n \) holds
\[ \lim_{k \to \infty} \hat{\lambda}_i = \lambda_i, \]
and the real parts of all other eigenvalues of \( A \) converge towards \(-\infty\) as \( k \to \infty. \)

Lemma A.1, applied to stability of spatially homogeneous steady states of ordinary differential equations coupled to reaction–diffusion equations reads:

Lemma A.2
Given a system of ordinary/partial-differential equations:
\[ \begin{align*}
\frac{d}{dt} u_i &= f_i(u), & 1 \leq i \leq n, \\
\frac{d}{dt} u_i &= d_i \Delta u_i + f_i(u), & n < i \leq n + m.
\end{align*} \] \hspace{1cm} (A15)
Let \( \bar{u} \) denote a constant steady state of system (A15) and \( J^0 \) denote the Jacobian of the ODE subsystem at \( \bar{u}: \)
\[ J^0_{ij} = \left( \frac{d}{du_j} f_i(u) \right)_{u=\bar{u}}, \quad 1 \leq i \leq n. \] \hspace{1cm} (A16)
If \( J^0 \) has a positive eigenvalue \( \lambda_+, \) the operator resulting from a linearization of (A15) around \( \bar{u} \) has infinitely many positive eigenvalues.

Proof
The linearization of the right-hand side of (A15) at \( u = \bar{u} \) is of type, written in matrix form:
\[ \begin{bmatrix} J^0 & A_{12} \\ A_{21} & A_{22} - D \Delta \end{bmatrix}, \]
and the corresponding eigenvalue problem in matrix form:
\[ \begin{bmatrix} J^0 - \lambda & A_{12} \\ A_{21} & A_{22} - \lambda - D \Delta \end{bmatrix} \begin{bmatrix} \psi \\ \phi \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}. \] \hspace{1cm} (A18)
Assuming \( \phi_k \) being the eigenfunction of the Laplace operator associated to the \( k \)th eigenvalue, the matrix is of type (A13). It follows that there exists a sequence of solutions \( (\lambda(k), \phi_k) \) of the eigenvalue problem (A18) with \( \lim_{k \to \infty} \lambda(k) = \lambda_+ \), where \( \text{Re}(\lambda_+) > 0. \)

Now, we can prove Lemma 3.2:

Proof of Lemma 3.2
The Jacobian of the kinetic system of (2.1)–(2.2) at \( (\bar{u}_0, \bar{w}_0) = (0, 1) \) reads:
\[ J = \begin{bmatrix} -d_1 & 0 \\ 0 & -1 \end{bmatrix}. \] \hspace{1cm} (A19)
It follows that \( (0, 1) \) is stable solution of (2.1)–(2.2) and its kinetic system.

The Jacobian of the kinetic system of (2.1)–(2.2) at \( \left( \frac{d_1}{a_1 - d_1}, \frac{1}{a_1} \right), \) \( \bar{w} \) reads
\[ J = \begin{bmatrix} (a_1 - d_1)d_1/a_1 - 2d_1/a_1 \delta \Gamma \left( \frac{d_1}{a_1 - d_1} \right)^2 \\ -2d_1/a_1 \delta \Gamma \left( \frac{d_1}{a_1 - d_1} \right)^2 \end{bmatrix} - \left( 1 + \frac{d_1}{(d_1/a_1 - 1)^2} \right)^2 \] \hspace{1cm} (A20)
Because \( J_{11} = (a_1 - d_1)d_1/a_1 \) is positive, both \( (\bar{u}_-, \bar{w}_-), \) and \( (\bar{u}_+, \bar{w}_+) \) are unstable solutions of (2.1)–(2.2), see Lemma A.2. To determine stability as steady state of the kinetic system, we calculate the determinant and trace of \( J \) from (A20):
\[ |J| = \frac{d_1}{a_1(a_1 - d_1)w^2} \left( (a_1 - d_1)^2 w^2 + d_1^2 \right), \] \hspace{1cm} (A21)
\[ \text{tr}(J) = \frac{a_1 - d_1}{a_1} + \left( 1 + \frac{d_1}{(a_1 - d_1)^2} \right)^2. \] \hspace{1cm} (A22)
We note $|J| \to - \frac{d_1(a_1-d_1)}{a_1}$ as $w \to \infty$.

The only roots of the determinant $|J|$ are

$$w_{\pm} = \pm \frac{d_1}{a_1 - d_1},$$ (A23)

Because $w_{\pm} = \frac{k_1}{2} \pm \sqrt{\left(\frac{k_1}{2}\right)^2 - \left(\frac{d_1}{a_1 - d_1}\right)^2}$ and $\frac{k_1}{2} > \frac{d_1}{a_1 - d_1} > 0$, it follows

$$|J(u_+, w_+)| < 0,$$ (A24)

$$|J(u_-, w_-)| > 0,$$ (A25)

what proves instability of $(u_+, w_+)$, because $|J| = \lambda_1 \lambda_2 < 0$.

The stability of $(u_-, w_-)$:

Because $J(u_-, w_-) > 0$, $(u_-, w_-)$ is unstable if and only if $\text{tr}(J(u_-, w_-)) > 0$.

$\text{tr}(J(u_-, w_-)) > 0$ is equivalent to

$$\frac{d_1}{a_1}(a_1 - d_1) - 1 > \left(\frac{d_1}{a_1 - d_1}\right)^2 \frac{1}{w_{\pm}^2},$$

$$\frac{d_1}{a_1}(a_1 - d_1) - 1 > \left(\frac{a_1 - d_1}{d_1}\right)^2 w_{\pm}^2,$$

$$\frac{d_1}{a_1 - d_1}a_1 - \left(\frac{d_1}{a_1 - d_1}\right)^2 > \frac{k_1}{2}^2 + 2\frac{k_1}{2} \sqrt{\left(\frac{k_1}{2}\right)^2 - \left(\frac{d_1}{a_1 - d_1}\right)^2} + \left(\frac{d_1}{a_1 - d_1}\right)^2,$$

$$\frac{d_1}{a_1 - d_1}a_1 - \left(\frac{k_1}{2}\right)^2 > \frac{k_1}{2} \sqrt{\left(\frac{k_1}{2}\right)^2 - \left(\frac{d_1}{a_1 - d_1}\right)^2}.$$

This is not satisfied for $k_1^2 \geq 2\frac{d_1}{a_1(a_1 - d_1)}$. We continue assuming that $\frac{d_1}{a_1 - d_1}a_1 - \left(\frac{k_1}{2}\right)^2 > 0$ and define $x := \frac{k_1}{2}$ and $y := \frac{d_1}{a_1 - d_1}$.

$$y \frac{d^2}{2a_1} - x^2 > x \sqrt{x^2 - y^2},$$

$$\frac{d_1^2}{4a_1^2}y^2 - \frac{d_1^2}{a_1}x^2y > -x^2y^2,$$

$$\left(y - \frac{d_1^2}{a_1}\right)x^2 + \frac{d_1^4}{4a_1^2}y > 0.$$ 

This is satisfied if and only if

$$y > \frac{d_1^2}{a_1},$$ (A26)

$$\left(\Leftrightarrow (d_1 \leq 1) \lor \left(d_1 > 1 \land a_1 > \frac{d_1^2}{d_1 - 1}\right)\right),$$

or

$$x^2 < \frac{d_1^4}{4a_1^2}y \left(\frac{d_1^2}{a_1} - y\right)^{-1},$$ (A27)

$$\left(\Leftrightarrow k_1^2 < \frac{d_1^2}{a_1^2}(a_1 - d_1 - 1)\right).$$

Negation yields the result. 

$\square$
Proof of Lemma 3.4
Adding a multiple of (2.1) and (2.2) and integrating over \( \Omega \) leads to

\[
\frac{d}{dt} \int \frac{1}{\alpha_1} u + w dx = \int \left( \frac{u^2 w}{1 + uw} - \frac{d_1}{\alpha_1} u \right) dx + \left( -w - u^2 w + \kappa_1 \right) dx,
\]

\[
\leq \int \left( -\frac{d_1}{\alpha_1} u - w + \kappa_1 \right) dx,
\]

\[
\leq -\min(d_1, 1) \int \left( \frac{1}{\alpha_1} u + w \right) dx + \kappa_1 \mu(\Omega).
\]

This leads to

\[
\limsup_{t \to \infty} \left( \frac{1}{\alpha_1} \int u dx + \int w dx \right) \leq \frac{\kappa_1}{\min(d_1, 1)} \mu(\Omega).
\]

Additionally, it immediately follows by integrating (2.2) over \( \Omega \):

\[
\frac{d}{dt} \int w dx \leq -\int w dx + \kappa_1 \mu(\Omega).
\]

From (A30) follows

\[
\limsup_{t \to \infty} \int w dx \leq \kappa_1 \mu(\Omega).
\]

Because \( w \geq 0 \), it follows from (A28)

\[
\limsup_{t \to \infty} \int u dx \leq \frac{\alpha_1}{\min(d_1, 1)} \kappa_1 \mu(\Omega).
\]

□

Proof of Lemma 3.5
The proof analogs to the proof of Lemma 3.4, without integrating over \( \Omega \).

□

Proof of Lemma 5.1
The eigenvector associated to the eigenvalue \( \lambda_{+} \) of a 2 \times 2 matrix \( (a_{ij} - \delta_i \delta_j 2D_w k^2) \) is \( v_k := \left[ \begin{array}{c} \frac{1}{a_{12}} \\ \frac{\lambda_{+} - a_{22} + D_w k^2}{\lambda_{+} \delta_2} \end{array} \right] \). It follows that \( v_k \phi_k \) is the eigenvector of \( J \) associated to \( \lambda_{+}(k) \).

□

A.3. Additional figures
In this section, we show numerically obtained solutions, which were referred to in the previous sections. Additionally, we show for convenience the explicit formula for the ‘perturbation’ function \( p \), defined by (5.3)–(5.7):

\[
p(x) = \begin{cases} 
4(-1 + s - \epsilon)(s - \epsilon)(-2s + 2s^2 - \epsilon) x^2 - 1, & x \in [0, s - \epsilon), \\
2(1 + 2 \epsilon) x^2 - 4(s + \epsilon) x + 2s^2 + 2\epsilon - 2s^2 \epsilon - \epsilon^2, & x \in [s - \epsilon, s + \epsilon], \\
(2s + 4s^2 - 2s^2 + 3\epsilon + 3s\epsilon - 2s^2 \epsilon + \epsilon^2 - 8\epsilon(s + \epsilon) + 4x^2(s + \epsilon)) / (-2s + 2s^2 - \epsilon)(-1 + s + \epsilon), & x \in (s + \epsilon, 1].
\end{cases}
\]

(A33)

A.4. Mesh asymptotic
In this section, we investigate the asymptotic behavior of the error because of numerical approximation. Because we do not know the true solution, we investigate the asymptotic behavior of the difference of the solution \( (u, w) \) and a calculated ‘reference solution’ \( (u_{rel}, w_{rel}) \). The reference solution is the numerical solution on a much finer mesh in time and space.

First, we show this error for the approximation of the configuration in the introductory part for large diffusion coefficient. In that case, only a single spike arises close to the position where the initial condition has a maximum. In Figure A5, the error in \( L^2 \) norm and the corresponding order of the error reduction under mesh refinement is plotted for equidistant mesh.

We observe the expected order \( O(h^2) \) of error reduction for piecewise linear approximation, see, for example, [21].

The same observation holds for the same configuration with smaller diffusion coefficient, s.t. growth of more than one spike occurs. The solution is shown in Figure 6, whereas the error is shown in Figure A7.
Figure A1. Left: Finite Fourier transform \( \hat{f}(\omega) = \int_0^1 \cos(4\pi x^2) e^{-i \omega x^2} dx \). Right: Order \( \frac{\log(\frac{\text{Im}(\hat{f}(\omega))}{\text{Re}(\hat{f}(\omega))})}{t} \) of the growth of the perturbation \(-\epsilon \cos(4\pi x^2)\) of \(u_0\) at \(x_0 = 0.250092, x_1 = \frac{1}{3}, x_2 = 0.866028 \approx \frac{\sqrt{3}}{2}\). See Figure 5 for the numerically obtained solution.

Figure A2. Order \( \frac{\log(\frac{\text{Im}(\hat{f}(\omega))}{\text{Re}(\hat{f}(\omega))})}{t} \) of the growth of perturbation \(-\epsilon \cos(4\pi x)\) of \(u_0\) at \(x_1 = 0.250092\) and \(x_2 = \frac{1}{3}\). See Figure 4 for the numerically obtained solution.

Figure A3. Numerically obtained solution for initial conditions (5.2) with \(\epsilon = 0.05, \epsilon_1 = 0.1, s = 0.4, \Sigma = 2.215, \Pi = 0.677123\) and parameters \(a_1 = 2.5, d_1 = 1.5, \kappa_1 = 4\), and \(D_w = 5.8541\). Left: component \(u\). Right: component \(w\).

Figure A4. Numerical solution for initial conditions very close to the stable steady state \((\Pi_u, \Pi_w)\), parameters \(a_1 = 2.5, d_1 = 1.5, \kappa_1 = 4\). Left: component \(u\). Right: component \(w\).
Figure A5. Upper row: Plot of the evolution of the $L^2$-error for a configuration shown in Figure 3 and its $L^1$ norm shown in Figure 8 in the sense of a reference solution. Lower row: Plot of the evolution of the order of error reduction. The reference solution was obtained on a mesh with spatial mesh size $h = 2^{-13}$ and temporal mesh size $k = 0.01$.

Figure A6. Plot of the evolution of the $L^1$-error for a configuration shown in Figure 3 and its $L^1$ norm shown in Figure 8 in the sense of a reference solution. The reference solution was obtained on a mesh with spatial mesh size $h = 2^{-13}$ and temporal mesh size $k = 0.01$.

Figure A7. Plot of the evolution of the $L^2$-error for a configuration shown in Figure 6 in the sense of a reference solution. Figure 6 shows the growth of multiple spikes because of a smaller diffusion coefficient. The reference solution was obtained on a mesh with spatial mesh size $h = 2^{-15}$ and temporal mesh size $k = 0.00025$. 
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Figure A8. Plot of the evolution of the $L^2$-error for a configuration shown in Figure 5 in the sense of a reference solution. Figure 5 shows the growth of multiple spikes due multiple maxima of the initial conditions of shape $u_0 = D + \cos(2\pi x^2)$. The reference solution was obtained on a mesh with spatial mesh size $h = 2^{-16}$ and temporal mesh size $k = 0.00025$. 

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